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Author: Gausmann, Peter

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REVIEW ARTICLE

Synopsis of global fresh and brackish water occurrences of the bull shark *Carcharhinus leucas* Valenciennes, 1839 (Pisces: Carcharhinidae), with comments on distribution and habitat use

Peter Gausmann

Abstract

The bull shark (*Carcharhinus leucas* Valenciennes, 1839) is a large, primarily coastally distributed shark famous for its ability to penetrate far into freshwater bodies in tropical, subtropical, and warm-temperate climates. It is a cosmopolitan species with a geographical range that includes the coastlines of all major ocean basins (Atlantic Ocean, Indian Ocean, Pacific Ocean). As a consequence, freshwater occurrences of *C. leucas* are possible everywhere inside its geographic range. *Carcharhinus leucas* is a fully euryhaline, amphidromous species and possibly the widest-ranging of all freshwater tolerating elasmobranchs. This species is found not only in river systems with sea access that are not interrupted by human impediments but in hypersaline lakes as well. Rivers and estuaries are believed to be important nursery grounds for *C. leucas*, as suggested by observations of pregnant females in estuaries and neonates with umbilical scars in rivers and river mouths. Due to the physical capability of this species to enter riverine systems, the documentation of its occurrence in fresh and brackish water is essential for future conservation plans, fishery inspections, and scientific studies that focus on the link between low salinity habitats, shark nurseries, and feeding areas. The author's review of the available literature on *C. leucas* revealed the absence of a comprehensive overview of fresh and brackish water localities (rivers and associated lakes, estuaries) with *C. leucas* records. The purpose of this literature review is to provide a global list of rivers, river systems, lakes, estuaries, and lagoons with records and reports of this species, including a link to the used references as a base for regional, national, and international conservation strategies. Therefore, the objective of this work is to present lists of fresh and brackish water habitats with records of *C. leucas* as the result of an extensive literature review and analysis of databases. This survey also took into account estuaries and lagoons, regarding their function as important nursery grounds for *C. leucas*. The analysis of references included is not only from the scientific literature, but also includes semi-scientific references and the common press if reliable. The result of 415 global fresh and brackish water localities with evidence of *C. leucas* highlights the importance of these habitats for the reproduction of this species. Moreover, gaps in available distribution maps are critically discussed as well as interpretations and conclusions made regarding possible reasons for the distribution range of *C. leucas*, which can be interpreted as the result of geographic circumstances, but also as a result of the current state of knowledge about the distribution of this species. The results of the examination of available references were used to build a reliable and updated distribution map for *C. leucas*, which is also presented here.

Keywords: Chondrichthyes, conservation, cosmopolitan species, distribution, elasmobranchs, euryhalinity, low salinity environments, review.

Zusammenfassung

Der euryhaline Stierhai (*Carcharhinus leucas* Valenciennes, 1839) ist bekannt dafür, dank seiner osmoregulatorischen Fähigkeiten weltweit über längere Zeiträume hinweg tief in die Süßwassersysteme tropischer, subtropischer und warm-temperierter Klimate vorzudringen. Es ist eine kosmopolitische Art, deren Verbreitungsgebiet die Küstenlinien der drei großen Ozeane (Atlantik, Indik, Pazifik) in beiden Hemisphären umfasst. Als logische Schlussfolgerung sind Vorkommen in Süßwassersystemen überall innerhalb des Verbreitungsgebietes möglich, bei denen die betreffenden Flüsse oder Seen Anschluss ans Meer haben. Möglicherweise ist der Stierhai der am weitesten verbreitete, auch Süßwasserlebensräume bewohnende Knorpelfisch, der darüber hinaus auch in Brackwasserbereiche und hypersaline Seen vorzudringen vermag. Eine Sichtung der vorhandenen Literatur durch den Verfasser offenbarte, dass es bislang augenscheinlich keine umfassende globale Übersicht über die Süßwasser- und Brackwasser-Lokalitäten gab, von denen diese Art nachgewiesen wurde. So ist es ein Ziel dieser Arbeit, eine vollständige Zusammenfassung der relevanten Quellen mit Hinweisen zu bekannten Süßwasservorkommen der Art zu liefern, die es ermöglichen soll, den Kenntnisstand hinsichtlich der Nutzung von nichtmarinen Lebensräumen zu komplettieren. Darüber hinaus werden das Areal, die arealbildenden Faktoren sowie die vorhandenen Verbreitungskarten kritisch diskutiert. Ebenso diskutiert werden Faktoren, welche die Verbreitung von *C. leucas* einschränken, sowie die Bedeutung der Süß- und Brackwasserlebensräume für die Reproduktionsbiologie dieser Art. Ferner wird eine aktualisierte Verbreitungskarte geliefert.

Contents

1 Introduction

Chondrichthyes (sharks, rays, skates, and chimaeras) belong to the vertebrate species groups that are the most data deficient (Johri et al. 2019a). Simultaneously, chondrichthyan fishes include some of the most threatened vertebrates on Earth, due largely to overfishing (Shiffman et al. 2021). Lack of data is a challenge for science, for improving conservation efforts, and for the identification and protection of critical habitats of members of these groups. Several shark species utilize specific inshore locations (coastal embayments, estuaries) as nursery areas as defined by Heupel et al. (2007). Large shark species are often characterized by low reproductive output (Holland et al. 2019), which makes them vulnerable to intensive exploitation, and the protection of the offspring can be evaluated as one aim of conservation efforts and sustainable fisheries management.

The knowledge of elasmobranchs (sharks, rays, and skates) in non-marine environments has lagged behind that in marine environments (Grant et al. 2019). Estuaries and shallow lagoons are supposed to be important nursery areas for a threatened elasmobranch, the bull shark *Carcharhinus leucas* Valenciennes, 1839 (Sadowsky 1971; Thorson 1976a; Bangley et al. 2018a). This species is assessed as "Vulnerable" on a global scale (Rigby et al. 2021). Although plenty of investigations on the use of low salinity habitats by this species were recently made (e.g., Simpfendorfer et al. 2005; Heupel et al. 2010; Heupel & Simpfendorfer 2011; Matich & Heithaus 2015; Pillans et al. 2020), many essential habitats for the reproductive cycle of *C. leucas* and their exact locations remain unknown. Due to the ability of *C. leucas* to invade river systems, documentation of its occurrence in low salinity habitats is essential for future species inventories and ichthyological studies (Feitosa et al. 2016). Today, *C. leucas* is known as

a shark species that relies on estuaries as nursery habitats, as well as for the penetration of river systems for long periods, especially during the early stages of its life history (Pillans 2006; Tillett et al. 2012). Numerous surveys and studies have dealt with estuaries as important nurseries for marine fishes. Many fish species—including several shark species—are estuarine-dependent. These transient fishes make evidence of the connectivity between estuarine and ocean habitats (Able 2005) in the freshwater/seawater ecocline. However, there are no data about the real number of low salinity habitats that are utilized by female adult *C. leucas* and their offspring as nursery grounds on a global scale. This paper deals with a listing of the currently known global occurrences of *C. leucas* in fresh and brackish waters and highlights the importance of low salinity environments for the reproduction of this species. Furthermore, it provides comprehensive lists of the circumglobal fresh and brackish water localities that are utilized by *C. leucas*. This may be of help to scientists for investigations about the ecology and distribution of this species, and illustrate how our understanding has changed through time.

The occurrence of *Carcharhinus leucas* in river systems has attracted research for decades across the globe (Moore 2018). Already Bigelow & Schroeder (1948: 341) stated on bull sharks: "They often run up rivers for considerable distances, and it seems that they do not hesitate to enter fresh water." The ability of the marine transient *C. leucas* to endure 0% salinity in freshwater habitats for extended periods has fascinated ichthyologists over centuries as well as the most astonished public. Although the occurrence of *C. leucas* in rivers and lakes today is well known to ichthyologists and scientists, only some of these records find their way into the scientific literature (Thorson 1972a) and they are more reported in local newspapers. Today, *C. leucas* belongs to one of the 20 best-investigated shark species of the world (Pollerspöck & Straube 2019a) but many aspects of its biology, ecology, and distribution remain unexplored.

Carcharhinus leucas is a fully euryhaline species (Gunter 1956; Thorson et al. 1973; Thorson 1976a; Imaseki et al. 2019) that moves easily between freshwater and marine habitats due to its ability to osmoregulate. The euryhalinity of *C. leucas* is unusual for most elasmobranchs and may be of evolutionary importance (Cowan 1971). Euryhalinity of organisms refers to broad halotolerance and broad halohabitat distribution. Halotolerance breadth varies with the species' evolutionary history, so euryhalinity is regarded as a key innovation trait enabling the exploitation of new habitats and ecological niches (Schultz & McCormick 2013). Thus, besides *Dasyatis sabina* Lesueur, 1824 (Atlantic stingray), *C. leucas* is currently viewed as a model for elasmobranch euryhalinity (Wosnick & Freire 2013). *Carcharhinus leucas* can be considered as one of the classical examples of freshwater adaptation by elasmobranchs (Thorson 1982), with only a few members of this primarily marine organism group adapted to freshwater environments. In this context, Hazon et al. (2003) pointed out that gradual acclimation of marine dwelling elasmobranchs to varying environmental salinities under laboratory conditions has demonstrated that these fish do have the capacity to acclimate to changes in salinity through independent regulation of sodium/chloride and urea levels. The contributions of Thomas B. Thorson in the 1970s on a *C. leucas* population from the Lake Nicaragua/San Juan river system demonstrated the osmoregulatory strategy of *C. leucas* as a fully euryhaline elasmobranch with urea-based osmoregulation.

From an evolutionary point of view, the link between the fossil record of *C. leucas* and its current distribution in global rivers and estuaries seems to be apparent. Data from analysis of fossil records of *C. leucas* from ancient low salinity environments indicate that its behavior of entering rivers, lakes, and estuaries has a long history that can be backdated at least to the Miocene Epoch (Shell & Gardner 2021). The results of palaeoenvironmental investigation make proof of the periods since which low salinity habitats were utilized by *C. leucas*: fossil tooth records of *C. leucas* from the subtropical Mirim Lake (= Lagoa Mirim) of Southern Brazil/Uruguay, a large estuarine lagoon, revealed the ancient utilization of this estuary system by *C. leucas* (Lopes et al. 2020) during the Late Pleistocene-Holocene. Palaeontological studies of the Solimões Formation in southwestern Amazonia by Latrubesse et al. (1997) revealed an occurrence of *C. leucas* in the Amazon basin at least since the Late Miocene/Pliocene. The investigations of Aguilera et al. (2017) in northern Brazil documented the presence of *C. leucas* in the Amazon basin since the Lower (Early) Miocene. Marine incursions by euryhaline sharks of the genus *Carcharhinus* Blainville, 1816 into South America's Amazon river system as far as current Peru were reported by Bloom & Lovejoy (2011) and have been interpreted as evidence of the marine influence of this river system during the Miocene. Monsch (1998) also reported marine incursions in the Amazon basin during the Miocene, with the participation of carcharhinid sharks.

Furthermore, the investigation by Carrillo-Briceño et al. (2019) revealed the presence of fossil *C. leucas* teeth in the Ware Formation of the Neogene (~3.4–2.78 mya) from the Cocinetas Basin of Caribbean Colombia and the utilization of estuaries and rivers during that period by this species. Jumnongthai & Meesook (2001) investigated fossil Holocene teeth of *C. leucas* from the Chian Yai district of peninsular Thailand, located in the adjacent floodplain of the Cha-Uat River, and speculated that this species perhaps occurred also recently in the Mekong River. The wide geographic range of the phenomenon of *C. leucas* entering

rivers, lakes, and estuaries, the physiological adaptations of this species to allow migrations into low salinity environments, and the numerous fossil records since the Miocene, all imply that this behavior has a long history.

Carcharhinus leucas is an amphidromous migratory species (Riede 2004), which means that it travels between saltwater and freshwater; however, its intention isn't to breed in purely freshwater, as breeding presumably occurs in estuarine habitats. Many data support this assumption, even though a live birth event of *C. leucas* in an estuary system has never been observed in the wild. *Carcharhinus leucas* can breed in freshwater, although breeding likely occurs in the high reaches of warm-water estuaries (Montoya & Thorson 1982; Cliff & Dudley 1991; Compagno et al. 2005; Pillans 2006). For the southwest Atlantic Ocean, Sadowsky (1971) observed high numbers of juvenile specimens of *C. leucas*, and occasionally also gravid females or females showing signs of recent parturition, in the inshore waters of Brazil's Cananéia lagoon system during the procreation period. Bass (1976) reported that gravid females of *C. leucas* frequently gave birth in South Africa's St. Lucia estuary system; later on, Bass (1978) reported that the only adult *C. leucas* caught in the St. Lucia system were four large females taken close to the mouth of the estuary. Only two were examined internally by Bass: one proved to be pregnant, with full-term embryos, while the other had recently given birth. Also, the investigations that were conducted by Thorson (1976a, 1982) revealed that adult female *C. leucas* are heavily concentrated around the river mouth of Nicaragua's San Juan River and reproduce along the nearby coast. Thorson's tagging program on *C. leucas* revealed that the sparser population in Lake Nicaragua is recruited almost entirely through upstream movements from the lower river. The results of all these cited studies indicate that estuary systems of the tropics, subtropics, and warm-temperate regions of the world can function as nursery areas and crucial habitats for the reproduction of *C. leucas*.

Thus, low salinity habitats can be considered as important for juvenile specimens of *C. leucas*. Due to the circumstance that many other marine predators (including other sharks) are stenohalyne, the time period spent in rivers and lakes by juvenile *C. leucas* is valued as an effective strategy to reduce mortality and guarantee a higher percentage of surviving immature individuals (Bres 1993; Heupel et al. 2007, 2018). Therefore, the residence of immature *C. leucas* in low salinity habitats is likely part of its natural life cycle (Simpfendorfer et al. 2005; Werry et al. 2012). In this context, Elliott et al. (2007) pointed out that in viviparous fish species it is a classical survival strategy to retain the brood in a location with the highest level of protection. Moreover, evidence of reproductive philopatry in *C. leucas* has been provided (Batcha & Reddy 2007; Tillett et al. 2012; Laurrabaquio-Alvarado et al. 2019; Rider et al. 2021), whereby adult female individuals show fidelity to a particular nursery and/or breeding site. This emphasises the importance of rivers, river mouths, lakes, estuaries and lagoons as critical nursery and breeding areas for *C. leucas*, and the importance of a sustainable management of shark fisheries in these coastal inshore ecosystems.

Only about 5% of living elasmobranch species occur regularly in low salinity environments and beyond the tidal reaches of the sea (Lucifora et al. 2015). Within the family Carcharhinidae (requiem sharks, whaler sharks), seven species are known to enter freshwater, but extended freshwater movements are restricted to *C. leucas* and river sharks of the genus *Glyphis* Agassiz, 1843 (Nelson 2006). Furthermore, *C. leucas* can tolerate a wide range of salinities, from 0–53‰ of pure freshwater to hypersaline conditions (Bass et al. 1973; Compagno 1984), even though Bass (1978) reported that *C. leucas* avoids salinities greater than 50‰. Oligo- and hypersaline environments represent a sharp limit for the distribution of marine biota (Gunter 1961), and the exceptionality of the euryhaline *C. leucas* is to endure not only low salinities but also high ones, i.e., salinities lower and higher than the mean salinity of ocean water bodies (~35‰). The tolerance of a salinity range of more than 50‰ makes *C. leucas* unique within the elasmobranchs.

Numerous recent surveys on *C. leucas* were completed, mostly dealing with the complex ecology and biology of this species, especially at one concrete location or in a particular region. The information about freshwater rivers and lakes with a function as habitats for *C. leucas* is widespread and mentioned in many single publications focusing not only on this species but also on the fish fauna of specific regions. Although there has been significant research on elasmobranchs in freshwater, no study has been published that compiles the previous work about the occurrences of *C. leucas* in freshwater into a single comprehensive report. However, earlier worldwide overviews with the aim to outline the well known freshwater occurrences of *C. leucas* were prepared by Boeseman (1964), who reported 32 freshwater localities, Burke (1979) with 28 inland water systems of putative *C. leucas* occurrences, Compagno (1984) with 22 freshwater localities, and Ballantyne & Fraser (2013) with 19 freshwater localities. Boeseman (1964) was the first scientist to provide an account of freshwater records of *C. leucas* with a global approach, though he noted that it was incomplete. Later on, the list of Boeseman was fully resumed by Thorson (1970b), with a few additions (36 localities).

Besides scientific examinations, early reports of sharks in freshwater from different parts of the world were provided also by travelers with an interest in nature (De La Gironière 1855; Meyer 1875). The first scientific reports of sharks from freshwater environments following a taxo-

Fig. 1. Holotype of *Carcharias* (*Prionodon*) *zambezensis* Peters, 1852 (♂, 760 mm TL; catalog no.: ZMB 4468, Museum für Naturkunde Berlin). – **A**. Dorsal view. **B**. Ventral view. The holotype was collected by Peters (1852: 276) in the Zambezi River: "Zambeze prop Tette et Sena, 17° Lat. austr." [Mozambique]. The exact description of the type locality was made later by Peters (1868), with the report of *Carcharias* (*Prionodon*) *zambezensis* from Tete and Sena along the Zambezi River (Paepke & Schmidt 1988). More than a century later, this specimen was investigated by Garrick (1982) and revised as *Carcharhinus leucas*. This specimen from Mozambique was the first scientific record of the euryhaline *C. leucas* from a pure freshwater environment and represented the first verified report of *C. leucas* from inland waters worldwide, just 13 years after the species was described by Valenciennes in Müller & Henle, 1841. Photos © Museum für Naturkunde Berlin

nomic approach and with classifications of the involved species were made during the second half of the 19th Century and the first half of the 20th Century. This was the time of increasing European colonization of tropical South America, Africa, and Asia, with expeditions producing biological inventories and species catalogs of countries, natural regions, and rivers, with the aim of finding available resources for future exploitations. Many publications from this period dealing with *C. leucas* were produced in this context (Peters 1852, 1868; Günther 1870, 1874; Gill & Bransford 1877; Day 1878; Lutken 1880; Starks 1906, 1913; Rendahl 1922; Svensson 1933; Boeseman 1956a). The first verified record of *C. leucas* from a purely freshwater habitat that was reported to the scientific world derived from the African continent, by Peters (1852), who collected and reported a single juvenile specimen (♂ 760mm TL) from the Zambezi River at Tete (Mozambique) (Fig. 1). He described the specimen as *Carcharias* (*Prionodon*) *zambezensis* Peters, 1852; the type specimen was later deeply investigated by Garrick (1982: 83), who commented: "This specimen, still in the Berlin Museum (ISZZ 4468), agrees with *leucas* in all respects." From this time on, both the public and the scientific world got more and more aware of the fact that the distribution of sharks in freshwater was not a curiosity but a cosmopolitan phenomenon. However, Wood (1875) was astonished by the presence of sharks and sawfish in Laguna de Bay, a freshwater body of the Philippines. Meyer (1875: 167), who was referring to Wood (1875), stated hereupon: "Mr. Wood, of Manila, writes on "Saw-fish inhabiting fresh water", in the Laguna de Baij, Luzon, as on something curious and new. But this fact was known long ago; not only do sharks live in fresh water there, but also elsewhere on the globe." In this context, already Gill (1893: 165) stated: "It is well known to ichthyologists that sharks do live in fresh water.", and more than half a century later, Herre (1955: 417) reported about New Guinea's Lake Sentani (Tab. 10): "Far from being astonished at the presence of sharks and sawfish in Lake Sentani, I would be surprised if they did not occur there."

After this century of expeditions and explorations, more detailed and intensive studies of local freshwater shark populations, including *C. leucas*, were carried out in the tropics, especially by Marinus Boeseman in Indonesia's Lake Jamoer (Boeseman 1963, 1964) and Thomas B. Thorson in Central America's Lake Nicaragua (Nicaragua) and Lake Izabal (Guatemala) (Thorson et al. 1966a, 1966b; Thorson 1976a). The greatest scientific and public attention of all shark occurrences in freshwater has attained by the population of *C. leucas* in the Lake Nicaragua/San Juan River system, where it was deeply investigated by Thorson and his collaborators. From the middle of the 1960s to the beginning of the 1980s, *C. leucas* was under intensive investigation in the freshwaters of Nicaragua, especially in the above-mentioned system, under the auspices of Thorson. Previously, the freshwater shark of Lake Nicaragua had been described by Theodore N. Gill as a distinct species, *Eulamia nicaraguensis* Gill, 1877 (Gill & Bransford 1877), and the belief that this shark species was an isolated species, separate from *C. leucas*, known only from this lake was long-lasting (Bigelow & Schroeder 1961; Thorson 1970b, 1976a). After a century of taxonomic confusion on the freshwater shark of Lake Nicaragua and following on the extensive investigations by Thorson, the knowledge increased that the freshwater sharks of Lake Nicaragua were in fact all specimens of *C. leucas*. Simultaneously to his investigations on the Lake Nicaragua population of *C. leucas*, Thorson also investigated further occurrences of the bull shark in Latin America, delivering additional and impressive data regarding the degree of freshwater penetration by this species. Thorson (1972a) reported an occurrence of *C. leucas* in the Ucayali River, the upper reaches of the Amazon River, at Pucallpa (Peru), nearly 5080 km from the ocean, which still represents the farthest documented freshwater intrusion of a primarily marine and euryhaline elasmobranch fish species.

This paper presents a global overview of verified occurrences of *C. leucas* in low salinity environments, based on a detailed bibliographic review. It further provides a synopsis of ichthyological investigations with the bull shark as a topic, a revised distribution map for *C. leucas*, and a critical discussion of existing older distribution maps.

2 Methods

This survey is based on an intensive analysis of the scientific literature as well as semi-scientific references and popular sources such as local presses and online newspapers. The analysis of the literature included primary references and subsequent reports, and unpublished "gray literature" (theses, technical reports). It represents a global review of the available distribution data and ecological parameters for *Carcharhinus leucas*. Media references were selected based on the authenticity and reliability of the report of *C. leucas* from a single locality, particularly on a clear identification of the species through a high-quality picture with a good view of diagnostic features. The diagnostic features of *C. leucas* (small eyes, round and blunt snout, relation of the first dorsal to the second dorsal fin, absence of an interdorsal ridge) allow a clear distinction of *C. leucas* from similar-looking species like *Carcharhinus amboinensis* Müller & Henle, 1839 (pigeye shark) and river sharks of the genus *Glyphis*. Presumably, *C. amboinensis* was more often confused with *C. leucas* and it is very probable that these species have been confused in some reports. To assure the accuracy of the used literature and internet sources during the review process, references were checked against the criteria of authenticity, reliability, degree of truthfulness, and type of data source. Scientific literature was used when the authors are skilled or experts in fish biology and/or fish ecology. Technical reports were used when they were official papers from reputable institutes or organizations.

Anecdotal reports on sharks in freshwater were not valued as a verified record of *C. leucas*, but they are mentioned in the comments to Tables 1–10, to inform about possible occurrences for future investigations. Internet references were checked especially for objectivity and correctness of the content. In every single case, an informed evaluation was made as to whether the reference was reliable or not. Only authoritative references were included in this work, a checklist of global fresh and brackish water records of *C. leucas*. The results are sorted by continent, and for each locality the primary reference and further important or relevant references are listed. In the column with listed references, these are sorted chronologically. Since some of the included sources represent subsequent citations of the initial record, the lists of references should not be interpreted as confirmation of a continuous presence of *C. leucas* since the initial record from the respective locality.

The exhaustive literature review included journal articles and monographs written in English but even in Arabic, Chinese, Dutch, French, German, Indonesian, Italian, Japanese, Portuguese, Russian, and Spanish, considering historical (> 100 years), old (> 50 years) to recent (> 10 years) and very recent (< 10 years) publications. For completeness, the analysis of the historical literature included reports of *C. leucas* under its numerous synonyms used in different regions (see Garrick 1982; Pollerspöck 2011; Fricke et al. 2020):

Southeast Africa: *Carcharias* (*Prionodon*) *zambezensis* Peters, 1852
Caribbean Sea: *Prionodon platyodon* Poey, 1860
Caribbean Sea: *Squalus obtusus* Poey, 1861
Central America: *Eulamia nicaraguensis* Gill *in* Gill & Bransford, 1877
North and Central America: *Carcharhinus* (*Squalus*) *platyodon* Jordan & Evermann, 1896
Tropical Eastern Pacific: *Carcharias* (*Eulamia*) *azureus* Gilbert & Starks, 1904
East Australia: *Carcharias spenceri* Ogilby, 1910
East Australia: *Galeolamna* (*Bogimba*) *bogimba* Whitley, 1943
West Australia: *Galeolamna greyi mckaili* Whitley, 1945
West Australia: *Galeolamna mckaili* Whitley, 1951
Southeast Africa: *Carcharhinus vanrooyeni* Smith, 1958
North America: *Carcharhinus leucas leucas* Urist, 1962
Central America: *Carcharhinus leucas nicaraguensis* Urist, 1962

Among these synonyms, some (e.g., *C. zambezensis*, *E. nicaraguensis*) reflect the occurrence of *C. leucas* in freshwater. About the confusing and unsatisfying historical nomenclature situation of different genus names for species of the recent genus *Carcharhinus*, which was described by Blainville (1816), see also the early report by Boeseman (1960).

The following synopsis of fresh and brackish water occurrences of *C. leucas* presents a unification of historical and recent records based on a literature review, investigation of media reports, and examination of available online databases. Interestingly, the ability of *C. leucas* to live in freshwater for long periods has led to the mention of this primarily marine shark in plenty of essays about the freshwater fish faunas of certain regions or countries worldwide (see References). The examination of these references delivered additional data. Fishery reports were analyzed as well as academic theses and conference papers with *C. leucas* as a topic. In this context, the investigation of checklists of the FAO (Food and Agriculture Organization of the United Nations), of species identification field guides for certain rivers of the world, and of fish species checklists for certain countries was productive and efficient. The ability to enter freshwater ecosystems has led to the mentioning of *C. leucas* in numerous freshwater fish fauna surveys and fish lists (e.g., Berra 1981, 2007), which were also evaluated. Numerous checklists of marine and freshwater fish were also analyzed to collect information as a basis for building a complete distribution map. In regional studies and historic references using synonyms, only pieces of information that allowed a direct assignment to *C. leucas* were used.

Moreover, an examination of voucher specimens collected from two doubtful locations (Bermuda Island, Easter Island) was carried out by the author. In a few regions with poorly documented *C. leucas* occurrences in rivers and estuaries and insufficient data, local shark experts who were able to identify this species were involved and interviewed. An examination of some important bibliography with references about *C. leucas* was made, especially those from "Eschmeyer's Catalog of Fishes" (Fricke et al. 2020) and "Shark References" (Pollerspöck & Straube 2018), with the intention of reviewing relevant works concerning this species.

In addition, pieces of information were derived from worldwide databases as well as from some museum collection databases. Information was also retrieved from serious fish databases, especially "FishBase" (Froese & Pauly 2018a), and further information was gathered from datasets provided by the "Global Biodiversity Information Facility" (GBIF 2018a, 2018b, 2018c). On a national (continental) scale, the database of the "Atlas of Living Australia" (ALA 2018) offered reliable data regarding freshwater occurrences of *C. leucas* in Australia, so these data were also a highly qualified source for records of this shark in rivers. Furthermore, data were collected from the "Global Shark Attack File" (Shark Research Institute 2018a, 2018b, 2018c, 2018d). Additionally, some scientific web pages were also analyzed. Today, with the ease of collecting and saving data on smartphones, cameras, video recordings, etc., there are numerous internet sources from which sightings of *C. leucas* in rivers can be retrieved, like angling and fishing videos with captures of *C. leucas*. Sometimes, spectacular battles of massive *Crocodylus porosus* Schneider, 1801 (the saltwater crocodile) with young *C. leucas* find their way into the sensation-oriented press (mainly in northern Australia). Of course, the analysis of these data is semi-scientific but offers an important source of additional data, and identification of the involved species is possible in the case of high-quality videos prioviding close views of specimens.

The co-occurrence of the sympatric *C. leucas* and *Glyphis gangeticus* Müller & Henle, 1839 (Ganges shark) in fresh and brackish waters on the Indian subcontinent has resulted in confusion about the taxonomy, presence, and distribution of both species, at least until the middle of the 20th Century (Smith 1952; Boeseman 1960; Ellis 1989). This led to a very confusing situation in the literature, and the assignment to either species of numerous Indian records of *C. leucas* and *G. gangeticus* is nearly impossible based only on the literature and without appropriate voucher specimens, as the scientific names *Carcharias gangeticus*, *Carcharhinus gangeticus*, *Eulamia gangetica*, and *Prionodon gangeticus* (which today are all accepted synonyms of *G. gangeticus* according to Pollerspöck & Straube 2019b), were used for both taxa. Because of this, *G. gangeticus* was blamed for many shark attacks in Indian waters that can be presumably attributed to *C. leucas* (Day 1878; Waite 1921; Halstead 1959). Already Compagno (1984) outlined that most of the Indo-Pacific records of the Ganges shark in which specimens

or adequate descriptive information are available have proved to be based on *C. leucas*.

Günther (1870), who examined material of *Carcharias gangeticus* in the British Museum (Natural History) that was collected from Calcutta (India) and Viti Levu (Fiji), remarked on the difficulties in distinguishing the material of *C. gangeticus* from that of *C. leucas*, and found out that the specimen from Calcutta was *C. gangeticus* (= *G. gangeticus*) and that the specimen from Viti Levu was identical to *C. leucas*. Finally, in the historical literature, the numerous scientific names cited above were used by different authors in a different way, both for *C. leucas* and even for the similar *G. gangeticus*. The confusion with *G. gangeticus* seems to mask records of *C. leucas*, and the opposite is probably also true. By way of this confusion, in the historical literature from the Indo-Pacific region there are distribution points for "*Carcharias gangeticus*" that include a mixture of information relating to both *C. leucas* and *G. gangeticus*, often within the same species report (cf. Day 1878; Misra & Menon 1955). Notably, many of the publications that deal with the elasmobranch fauna of India and were published in the second half of the 20th Century (e.g., Misra 1951, 1969; Venkateswarlu 1984) included "*Carcharhinus gangeticus*" but not *C. leucas*, which is in contrast with the abundances of both species in Indian waters, *G. gangeticus* being rare and *C. leucas* common. The conclusion is that records of *C. leucas* were reported in the literature on the elasmobranch fauna of Southeast Asia under the omnipresent name "*Carcharhinus gangeticus*". Talwar & Kacker (1984) outlined that "*C. gangeticus*" (used by the authors for *Glyphis gangeticus*) is a very rare species in Indian waters and that most information for "*C. gangeticus*" presumably refers to the more abundant *C. leucas*. It is noticeable that the name *C. gangeticus* appears in many ichthyological reports from India even though the true Ganges shark, *G. gangeticus*, is a very rare, seldomly captured species.

Thus, the presumption exists that most of "*C. gangeticus*" from India and adjacent areas truly refer to *C. leucas*. An indication of this comes from Chaudhuri (1916) and Misra (1969), who reported "*C. gangeticus*" from the Tigris River at Baghdad, whereas only *C. leucas* has since been confirmed from this river system (Coad 1991, 2010; Moore 2012; Almojil et al. 2015). Unfortunately, these older names were used in reports about India and adjacent areas until the 1970s and 1980s (James 1973; Talwar & Kacker 1984), resulting in deficient knowledge about the real presence and distribution of sharks in fresh and brackish waters of India and neighboring countries. Following the logical concept of geographical exclusion as it was used by Boeseman (1964: 13: "…most of the recorded *C. gangeticus* from outside the Indo-Pakistan peninsula are identical with *C. leucas* Müller & Henle."), records and reports of "*Carcharhinus* (*Eulamia*) *gangeticus*" outside the confirmed distribution of *Glyphis gangeticus* in Pakistani, Indian and Bangladeshi waters are herein referred to *C. leucas*.

Abbreviations

BMNH	Natural History Museum, London, United Kingdom
CMNFI	Canadian Museum of Nature, Fish Collection, Ottawa, Ontario, Canada
ISZZ	Institut fur Spezielle Zoologie und Zoologisches Museum, Berlin, Germany
MNHN	Museum National d'Histoire Naturelle, Paris, France
MOVI	Museu Oceanográfico do Vale do Itajaí, Itajaí, Brazil
MRAC	Musée Royal de l'Afrique Centrale (= Royal Museum for Central Africa), Tervuren, Belgium
NHM	Natural History Museum, London, United Kingdom
NMW	Naturhistorisches Museum, Wien, Austria
NYZS	New York Zoological Society, New York, USA
RMNH	Rijksmuseum van Natuurlijke Histoire, Leiden, Netherlands
USNM	United States National Museum, Washington, D.C., USA
ZMB	Zoologisches Museum Berlin, Germany
ZSI	Zoological Survey of India, Kolkata

3 Results: A listing of rivers, lakes, estuaries, bays, and lagoons with records of *Carcharhinus leucas*

Due to the lack of data for many regions of the world, the listings provided in this review should not be considered as complete, as they only display the most recent state of knowledge. The listing also includes records of *C. leucas* in brackish water (hyposaline environments with low salinity of 0.5–30‰). The lists are sorted systematically and geographically by continent, including associated islands, and according to the major ocean basins from which the penetration of freshwater bodies and low salinity habitats by *C. leucas* occurs. Occurrences and records in purely fresh water are marked with "F" in the WC (= water conditions) column of each table, whereas localities with brackish water are marked with "B". Localities with a seasonal change of salinity, e.g. influenced by the tide, and estuary systems with a salinity gradient from fresh to brackish are marked with "F/B" and were counted as "brackish" in the account of fresh/brackish water localities. Latitude and longitude (with reference to the geodetic system WGS84) of localities are also given for exact localization of occurrences. The known life history stage of *C. leucas* in each location is included in an additional column (LHS = life history stage) to assess whether or not low salinity habitats are used exclusively as nurseries. Although size at birth of *C. leucas* can show large variability and differ considerably on a regional and global scale (Neer et al. 2005), this study attempts to classify the population structure at particular locations for an evaluation of their importance as nurseries.

Abbreviations of life history stage categories of *C. leucas* (modified from Branstatter & Stiles 1987 and Wintner et al. 2002; TL = total length):

N	neonate (fish with visible umbilical scars, scar open)
Y-O-Y	young-of-the-year (fish with umbilical scars visible but healed)
Juv	juvenile (fish with no umbilical scar present, size between 70–130 cm TL)
Sub	subadult (fish with size between 131–225 cm TL)
Ad	adult (fish with size > 225 cm TL)
U	unknown (size could not be determined)

Where necessary and helpful, important details on the occurrence and/or the locality are provided in the comments. Additionally, Table 11 provides a global overview of the occurrences of *C. leucas* in inland waters, with distances from the coast that reveal the extended movements of this species into continental waters in different parts of the world.

Table 1. Occurrences of *Carcharhinus leucas* in North American rivers, lakes, estuaries, and lagoons: Atlantic Ocean coast including Gulf of Mexico. Abbreviations: WC = water conditions, F = freshwater, B = brackish water up to hypersaline conditions, F/B = salinity gradient from fresh to brackish, LHS = life history stage, Ad = adult, Sub = subadult, Juv = juvenile, Y-O-Y = young-of-the-year, N = neonate, U = unknown. Abbreviations of U.S. States: AL = Alabama; AR = Arkansas; FL = Florida; GA = Georgia; IL = Illinois; LA = Louisiana; MD = Maryland; MO = Missouri; MS = Mississippi; NC = North Carolina; OK = Oklahoma; SC = South Carolina; TN = Tennessee; TX = Texas; VA = Virginia.

No.	WC	Toponym	Country (State)	References	LHS	Comments
1	**B**	**Chesapeake Bay** [39.53°N, -76.10°E]	USA (MD, VA)	Schwartz (1958a, 1959, 1960a, 1960c); Springer (1960); Hoese (1962); Boeseman (1964); Budker (1971); Musick (1972); Metzgar (1973); Lawler (1976); Colvocoresses & Musick (1980); Lippson & Lippson (1984); Smith & Merriner (1986, 1987); White (1989); Branstetter & Musick (1993); Vims (2006); Murdy & Musick (2013); Maryland Biodiversity Project (2018)	Ad	Largest estuary system on the U.S. east coast with brackish water conditions. Verified as far as 200 km inland. Chesapeake fishers regarded large *C. leucas* as rarities. Important nursery area of *Carcharhinus plumbeus* Nardo, 1827 (Springer 1960; Grubbs & Musick 2007; Grubbs et al. 2007)
2	**B**	**Choptank River** [38.63°N, -76.32°E]	USA (MD)	Schwartz (1973)	Ad	Brackish water at the point of the catch
3	**B**	**Patuxent River** [38.40°N, -76.42°E]	USA (MD)	Mansueti (1957); Schwartz (1958a, 1960b); Murdy & Musick (2013)	Ad	Brackish water at the point of the catch at Broomes Island
4	**B**	**Potomac River** [38.09°N, -76.34°E]	USA (MD)	Murdy et al. (1997); Murdy & Musick (2013); Zauzmer (2013)	Ad	Captures of two 2.5 m TL *C. leucas* (Murdy & Musick 2013)
5	**B**	**Big Annemessex River (Tangier Sound)** [38.06°N, -75.86°E]	USA (MD)	Schwartz (1958b)	Ad	Estuary of the Chesapeake Bay (No. 1)
6	**B**	**Yeocomico River** [38.02°N, -76.54°E]	USA (VA)	Garrick (1982)	Ad	Reported from Mundy Point (Garick 1982)
7	**B**	**York River System** [37.24°N, -76.50°E]	USA (VA)	Hewitt et al. (2009)	U	Tributary of the Chesapeake Bay (No. 1)
8	**B**	**Albamarle Sound Complex** [36.08°N, -75.94°E]	USA (NC)	Schwartz (1997)	U	Estuary with brackish water
9	**F**	**Long Shoal River** [35,57°N, -75,87°E]	USA (NC)	Bangley et al. (2018a, 2018b)	N Y-O-Y Juv Ad	Tributary of the Pamlico Sound (No. 10)
10	**B**	**Pamlico Sound** (incl. Currituck Sound) [35.38°N, -75.85°E]	USA (NC)	Schwartz (1995, 1997, 2000, 2012); Limburg et al. (2016); Bangley et al. (2018a, 2018b)	N Y-O-Y Juv Ad	Estuary. Anecdotal reports of catches of *C. leucas* were provided by Aguilar (2003)

No.	WC	Toponym	Country (State)	References	LHS	Comments
11	**F**	**Neuse River** [35.10°N, -76.50°E]	USA (NC)	Schwartz (1995, 1997, 2012); Southern Fried Science (2011); Bangley et al. (2018a, 2018b)	Juv Ad	Tributary of the Pamlico Sound (No. 9). Schwartz (1995) reported *C. leucas* at New Bern in summer
12	**F**	**Cape Fear River** [33.88°N, -77.96°E]	USA (NC)	Schwartz (2000, 2012)	Juv	-
13	**B**	**Winyah Bay** [33.25°N, -79.24°E]	USA (SC)	Fryman (2013); Collatos (2018)	Sub	Estuary with brackish water
14	**B**	**Bulls Bay** [33.00°N, -79.54°E]	USA (SC)	Castro (1993)	Ad	Estuary with brackish water. Castro (1993) reported the capture of one pregnant female in this bay, indicating that it is a potential nursery
15	**B**	**St. Helena Sound** [32.45°N, -80.44°E]	USA (SC)	Farmer (2004)	Sub Ad	Estuary with brackish water
16	**B**	**Calibogue Sound** [32.10°N, -80.83°E]	USA (SC)	Farmer (2004)	Sub Ad	Estuary with brackish water
17	**B**	**Altamaha River Estuary** [31.32°N, -81.36°E]	USA (GA)	Streich & Peterson (2011)	N Y-O-Y Juv Sub Ad	River estuary with a salinity gradient. Nursery area of *C. leucas* (Streich & Peterson 2011)
18	**B**	**Shell Creek** [30.95°N, -81.24°E]	USA (GA)	Worldpress.com (2012)	Ad	Small outlet near the coast on Little Cumberland Island with brackish water
19	**F**	**St. Johns River** [30,41°N, -81,59°E]	USA (FL)	Carrier (2017)	Juv	-
20	**F/B**	**Indian River (Lagoon) System** (incl. St. Lucie River, Banana River, Mosquito Lagoon and Cane Creek) [28.70°N, -80.73°E]	USA (FL)	Dodrill (1977); Gilmore Jr. (1977); Gilmore Jr. et al. (1978, 1981); Snelson & Bradley (1978); Snelson (1979, 1983); Snelson & Williams (1981); Snelson et al. (1984); Castro (1993); Schmid & Murru (1994); Adams (1995); Tremain & Adams (1995); Adams & McMichael (1999); Johnson et al. (1999); Adams et al. (2003); Tremain et al. (2004); Johnson-Restrepo et al. (2005); Adams & Paperno (2007); Curtis et al. (2007, 2011, 2013); Hueter et al. (2007); Curtis (2008); Imhoff et al. (2010); Curtis & Macesic (2011); Adams & Curtis (2012); Barbarite & Kajiura (2012); Weijs et al. (2015); Zokan et al. (2015); Xue et al. (2017); Laurra-baquio-Alvarado et al. (2019, 2021); Roskar (2019); Roskar et al. (2020, 2021)	N Y-O-Y Juv Sub Ad	Estuary system with a gradient of salinities and dominating brackish water conditions. Zokan et al. (2015) collected *C. leucas* from purely freshwater habitats in this system. This ecosystem presents an important nursery ground for *C. leucas* in the southeast USA on the Atlantic Ocean coast (Snelson 1979). Furthermore, Snelson (1979) and Roskar (2021) reported that *C. leucas* is the most abundant shark species in the Indian River System. *Carcharhinus leucas* was known to congregrate near the warm water discharge of the power plants on the Indian River in the winter months (Snelson 1979)

No.	WC	Toponym	Country (State)	References	LHS	Comments
21	**B**	**Lake Worth Lagoon** [26.77°N, -80.04°E]	USA (FL)	Vorenberg (1962)	U	Estuary with brackish to salt water
22	**B**	**Biscayne Bay** [25.85°N, -80.23°E]	USA (FL)	Smith (1896); Evermann & Kendall (1900); Phenix et al. (2019); Shiffman et al. (2019); Gutowsky et al. (2021); Rider et al. (2021)	Sub Ad	Largely human-modified estuary. Evermann & Kendall (1900: 48) reported *C. leucas* under the name "*Carcharinus platyodon*"
23	**B**	**Florida Bay** [24.95°N, -80.67°E]	USA (FL)	Nakamura et al. (1980); Williams et al. (1990); Nelson (1992); Branstetter (1997); Gallagher et al. (2017); Matulik et al. (2017); Shiffman et al. (2019)	Juv Sub Ad	Estuary/lagoon system. Providing different salinities (mostly brackish water); largely human-modified
24	**B**	**Whitewater Bay** [25.29°N, -81.02°E]	USA (FL)	Wiley & Simpfendorfer (2007)	Juv Sub	Estuary with brackish water
25	**F**	**North River** [25.30°N, -80.94°E]	USA (FL)	Odum (1970, 1971); Odum & Heald (1975); Loftus & Kushlan (1987); Nordlie (2003)	Juv Sub	"River channel and ponds" (Odum 1970: 11). Tributary of the White-water Bay (No. 24)
26	**F**	**Watson River** [25.34°N, -80.95°E]	USA (FL)	Tabb et al. (1974); Loftus & Kushlan (1987)	Y-O-Y Juv	Tributary of the White-water Bay (No. 24)
27	**B**	**Shark River System** (Everglades NP incl. Tarpon Bay and Shark River Estuary) [25.35°N, -81.11°E]	USA (FL)	Delius & Heithaus (2007); Heithaus et al. (2009); Wirsing (2009); Matich et al. (2010, 2011, 2015, 2017a, 2019, 2020a); Belicka et al. (2012); Matich & Heithaus (2012, 2014, 2015); Rosenblatt et al. (2013); Matich (2014); Pirog et al. (2019b), Strickland et al. (2020); Van Zinnicq Bergmann et al. (2021)	N Y-O-Y Juv Sub	River/estuary system that provides a gradient of varying salinities
28	**F**	**Squawk Creek** [25.42°N, -80.90°E]	USA (FL)	Loftus & Kushlan (1987)	Y-O-Y Juv	Tributary of the Shark River System (No. 27)
29	**F**	**Southern Everglades** (Part of Everglades NP incl. Southern Glades, excl. Big Cypress Swamp) [25.55°N, -80.88°E]	USA (FL)	Zokan et al. (2015)	U	*C. leucas* was collected from purely fresh water (Zokan et al. 2015)
30	**F**	**Broad River** [25.47°N, -81.15°E]	USA (FL)	Loftus & Kushlan (1987)	Y-O-Y Juv	-
31	**B**	**Big Cypress Swamp** [25.85°N, -81.41°E]	USA (FL)	Zokan et al. (2015)	U	-
32	**B**	**Ten Thousand Islands Estuary** (incl. Fakahatchee, Faka Union and Pumpkin Bay) [25.88°N, -81.57°E]	USA (FL)	Williams et al. (1990); Nelson (1992); Branstetter (1997); Hueter & Tyminski (2002, 2007); Michel (2002); Michel & Steiner (2002); Steiner (2002); Steiner et al. (2007); Hyatt et al. (2018); O´Donnell (2018)	N Y-O-Y Juv Ad	A complex of estuaries with brackish water

No.	WC	Toponym	Country (State)	References	LHS	Comments
33	**B**	**San Carlos Bay** [26.47°N, -81.98°E]	USA (FL)	Simpfendorfer et al. (2005)	Y-O-Y Juv Sub	Estuary of the Caloosahatchee River (No. 34)
34	**B**	**Caloosahatchee River** [26.53°N, -81.97°E]	USA (FL)	Williams et al. (1990); Nelson (1992); Branstetter (1997); Heupel (2004); Simpfendorfer et al. (2005); Hueter et al. (2007); Heupel & Simpfendorfer (2008); Ortega (2008); Ortega et al. (2009); Heupel et al. (2010); Gelsleichter & Szabo (2013); Olin et al. (2011, 2013, 2014); Zokan et al. (2015)	N Y-O-Y Juv Sub Ad	Brackish water with changing salinity degrees in the different parts of the river
35	**B**	**Pine Island Sound** [26,58°N, -82,15°E]	USA (FL)	Simpfendorfer et al. (2005); Heupel et al. (2006); Yeiser et al. (2008)	Juv Sub	Estuary of the Caloosahatchee River (No. 33)
36	**B**	**Charlotte Harbor** (incl. Myakka River Estuary) [26.78°N, -82.09°E]	USA (FL)	Williams et al. (1990); Nelson (1992); Hueter & Manire (1994); Branstetter (1997); Hueter & Tyminski (2002, 2007); Adams et al. (2003); Heupel (2003); Olin et al. (2013); Poulakis et al. (2015); Zokan et al. (2015); Laurra-baquio-Alvarado et al. (2019, 2021)	N Y-O-Y Juv Ad	Estuary of the Myakka River (No. 37) with brackish water
37	**F**	**Myakka River** [26.95°N, -82.22°E]	USA (FL)	Gelsleichter & Szabo (2013); Olin et al. (2011, 2014)	N Y-O-Y	Tributary of Charlotte Harbor (No. 36)
38	**B**	**Tampa Bay** (incl. Hillsborough Bay, Boca Ciega Bay and Terra Ceia Bay) [27.77°N, -82.54°E]	USA (FL)	Springer & Woodburn (1960); Clark & von Schmidt (1965); Williams et al. (1990); Nelson (1992); Hueter & Manire (1994); Branstetter (1997); Heupel & Simpfendorfer (2002); Hueter & Tyminski (2002, 2007); Adams et al. (2003); Gardiner & Wiley (2021)	N Y-O-Y Juv Ad	Estuary with brackish water
39	**F**	**Hillsborough River** [27.95°N, -82.41°E]	USA (FL)	Rozyla (2017)	Y-O-Y	Tributary of the Tampa Bay (No. 38)
40	**F**	**Chassahowitzka River** [28.70°N, -82.60]	USA (FL)	Internet Reference 1	Juv	-
41	**B**	**Yankeetown Estuary System** [29.03°N, -82.75°E]	USA (FL)	Hueter & Tyminski (2007)	N Y-O-Y Juv	Estuary system with numerous inlets
42	**B**	**Waccasassa River Mouth** [29.16°N, -82.80°E]	USA (FL)	Hueter et al. (2007); Imhoff (2018)	N Juv	Estuary
43	**B**	**Suwannee River Mouth** [29.30°N, -83.15]	USA (FL)	Williams et al. (1990); Nelson (1992); Branstetter (1997)	Juv Ad	Estuary
44	**B**	**Apalachee Bay** [30.05°N, -84.08°E]	USA (FL)	Williams et al. (1990); Nelson (1992); Branstetter (1997)	Juv Ad	Estuary

No.	WC	Toponym	Country (State)	References	LHS	Comments
45	**F**	**Aucilla River** [30.08°N, -83.99°E]	USA (FL)	Swift et al. (1977); Burgess & Ross (1980)	Sub	Tributary of No. 44. Swift et al. (1977) reported a 45.4kg *C. leucas* that present a subadult (> 130 cm TL)
46	**B**	**Apalachicola Bay** [29.68°N, -85.00°E]	USA (FL)	Williams et al. (1990); Nelson (1992); Branstetter (1997); Bethea et al. (2009)	Juv Ad	Estuary
47	**F**	**Apalachicola River** [29.73°N, -84.97°E]	USA (FL)	Burgess & Ross (1980); Patrick (1994)	U	Tributary of the Apalachicola Bay (No. 46)
48	**B**	**St. Andrews Bay** [30.12°N, -85.69°E]	USA (FL)	Williams et al. (1990); Nelson (1992); Branstetter (1997)	Juv Ad	Estuary
49	**B**	**Choctawhatchee River** [30.40°N, -86.09°E]	USA (FL)	U.S. Army Corps of Engineers (1971)	U	Tributary of No. 50
50	**B**	**Choctawhatchee Bay** [30.44°N, -86.32°E]	USA (FL)	Williams et al. (1990); Nelson (1992); Branstetter (1997)	Juv Ad	Estuary
51	**B**	**Pensacola Bay** (incl. Santa Rosa Sound) [30.40°N, -87.13°E]	USA (FL)	Cooley (1978); Williams et al. (1990); Nelson (1992); Branstetter (1997)	Juv Ad	Estuary
52	**B**	**Perdido Bay** [30.33°N, -87.44°E]	USA (FL, AL)	Nakamura et al. (1980); Williams et al. (1990); Nelson (1992); Branstetter (1997)	Juv Ad	Estuary
53	**F**	**Alabama/Tensaw River System** [30.85°N, -87.92°E]	USA (AL)	Drymon et al. (2011, 2014, 2020a)	Juv	Tributary of the Mobile Bay (No. 59)
54	**F**	**Blakely River** [30.65°N, -87.92°E]	USA (AL)	Drymon et al. (2011)	U	Part of the Mobile-Tensaw River Delta
55	**F**	**Apalachee River** [30.67°N, -87.95°E]	USA (AL)	Drymon et al. (2011)	U	Part of the Mobile-Tensaw River Delta
56	**F**	**Tombigbee River** [31.26°N, -87.98°E]	USA (AL)	McMurray (2016)	Juv	Tributary of the Mobile River (No. 57). Reported as far as 70 km from the sea at McIntosh
57	**F**	**Mobile River** [30.67°N, -88.03°E]	USA (AL)	Drymon et al. (2011, 2014)	Juv	Tributary of the Mobile Bay (No. 59)
58	**B**	**Dog River** [30.57°N, -88.09°E]	USA (AL)	Drymon et al. (2011)	U	Tributary of the Mobile Bay (No. 59)
59	**B**	**Mobile Bay** [30.50°N, -87.99°E]	USA (AL)	Branstetter (1981, 1997); Parsons & Hoffmayer (2007); Bethea et al. (2015); Drymon et al. (2014); Schweiss et al. (2020)	N Y-O-Y Juv Ad	Branstetter (1981) reported *C. leucas* at the mouth of the Deer River (tributary of the Mobile Bay)
60	**B**	**Fowl River** [30.36°N, -88.18°E]	USA (AL)	Drymon et al. (2011)	U	Tidal influenced river
61	**F**	**Pascagoula River** [30.35°N, -88.60°E]	USA (MS)	Boeseman (1964); Thorson (1970b); Johnson (1978); Havrylkoff (2010)	Juv	Havrylkoff (2010) capured juvenile specimens in spring
62	**B**	**Davis Bayou** [30.39°N, -88.80°E]	USA (MS)	Caira et al. (2005); Hoffmayer et al. (2006); Bethea et al. (2009)	Y-O-Y	Estuary with brackish water

No.	WC	Toponym	Country (State)	References	LHS	Comments
63	**F**	**Pearl River-System** [30.18°N, -89.57°E]	USA (MS, LA)	Blackburn et al. (2007)	N Juv Sub	River system with many river branches
64	**F**	**Tchefuncte River** [30.37°N, -90.15°E]	USA (LA)	Mixson (2017)	Ad	Tributary of No.65
65	**B**	**Lake Pontchartrain** [30.20°N, -90.13°E]	USA (LA)	Darnell (1958, 1961); Levine (1980); Thompson & Verret (1980); Czapla et al. (1991); Nelson (1992); Blackburn (2003); Internet Reference 2; Blackburn et al. (2007); O´Connel et al. (2007); Davis (2009); Hastings (2009); LPBF (2011); Laurrabaquio-Alvarado et al. (2019)	N Juv Sub Ad	Estuary with brackish water; outlet of the Mississippi River System
66	**B**	**Lake Borgne** (incl. adjacent Biloxi Marsh Complex) [30.00°N, -89.64°E]	USA (LA)	Fontenot & Rogillio (1970); Moravec & Little (1988); Czapla et al. (1991); Nelson (1992); Branstetter (1997)	Juv Ad	Estuary with brackish water; outlet of the Mississippi River System
67	**B**	**Breton / Chandeleur Sound** [29.91°N, -89.25°E]	USA (LA)	Christmas et al. (1960); Czapla et al. (1991); Nelson (1992); Branstetter (1997)	Juv Ad	Estuary; outlet of the Mississippi River System
68	**F**	**Mississippi River** [29.15°N, -89.25°E]	USA (LA, MS, AR, TN, MO, IL)	Thomerson et al. (1977); Rasmussen (1979); Burgess & Ross (1980); Compagno (1984); Steel (1985); Hocutt & Wiley (1986); Keller (1987); Hoese & Moore (1998); McEachran & Fechhelm (1998); Ross (2001); Burr et al. (2004); Simpfendorfer & Burgess (2005, 2009); Parsons (2006); Berra (2007); Steuck et al. (2010); Voigt & Weber (2011); Ebert & Stehmann (2013); Klimley (2013); Helfman & Burgess (2014); Schramm et al. (2016); ReefQuest Centre for Shark Research (2018); Doosey et al. (2021); Shell & Gardner (2021)	Juv Sub Ad	One verified record of *C. leucas* was made as far as 2,800 km from the ocean at Alton, Illinois, at 38.88°N, -90.18°E (Thomerson et al. 1977). This record was made by local fishers in 1937 (specimen illustrated in Helfman & Burgess 2014; photo material of the captured specimen was also provided in Thomerson et al. 1977)
69	**B**	**Mississippi Sound (Delta/Mouth)** [29.13°N, -89.18°E]	USA (AL, MS, LA)	Springer (1950, 1960); Christmas et al. (1960); Gilbert et al. (1967); Branstetter (1981, 1997); Ellis (1989); Boschung (1992); Parsons & Hoffmayer (2007); Love et al. (2013); Livernois et al. (2021)	N Juv Ad	Large delta of the Mississippi River (No. 68)
70	**F**	**Lac des Allemands** (= Lake des Allemands) [29.92°N, -90.57°E]	USA (LA)	Thibodeaux (2018)	Sub	Outflow of the Mississippi River System into Lake Salvador (No. 72)

No.	WC	Toponym	Country (State)	References	LHS	Comments
71	**F**	**Bayou des Allemands** [29.78°N, -90.45°E]	USA (LA)	No reference but it is logical under geographic circumstances	Sub	Connection between Lac des Allemands (No. 70) and Lake Salvador (No. 72)
72	**B**	**Lake Salvador** [29.73°N, -90.25°E]	USA (LA)	Arena (2015)	Juv	Estuary with brackish water; outlet of the Mississippi River System
73	**B**	**Barataria Bay / Little Lake System** [29.42°N, -89.94°E]	USA (LA)	Guillory (1982); Czapla et al. (1991); Nelson (1992); Branstetter (1997); Blackburn et al. (2007); Boswell et al. (2010)	N Juv Sub Ad	Estuary with brackish water; outlet of the Mississippi River System
74	**B**	**Terrebonne / Timbarlier Bay System** (incl. Devil´s Bay) [29.10°N, -90.54°E]	USA (LA)	Czapla et al. (1991); Nelson (1992); Branstetter (1997); De Silva et al. (2000); Blackburn (2003); Blackburn et al. (2007, 2010); Del Rio (2009)	N Juv Sub Ad	Estuary with brackish water; outlet of the Mississippi River System
75	**B**	**Bayou DuLarge** (incl. Lake Mechant and Caillou Lake) [29.26°N, -90.93°E]	USA (LA)	DiBenedetto (2009)	U	Estuary with brackish water; outlet of the Mississippi River System
76	**B**	**Saline Lake** [31.33°N, -92.05°E]	USA (LA)	Hoese & Moore (1977, 1998)	U	An inland salt lake connected by some river channels with the Red River (No. 77)
77	**F**	**Red River** (= Red River of the South) [30.98°N, 91.80°E]	USA (LA, AR, OK, TX)	Gunter (1938); Burgess & Ross (1980); Hoese & Moore (1998); Matich et al. (2020b)	Juv Sub Ad	Extension of No. 78. Reported as far as Texas from Harris Ferry (Red River County, TX, 33.72°N, -94.77°E) in 950 km distance from the ocean (Matich et al. 2020b)
78	**F**	**Atchafalaya River** [29.48°N, -91.27°E]	USA (LA)	Gunter (1938); Boeseman (1964); Thorson (1970b); Johnson (1978); Burgess & Ross (1980); Compagno (1984); Ellis (1989); Fremling et al. (1989); Hoese & Moore (1998); McEachran & Fechhelm (1998); Bussing (2002); Blackburn et al. (2007); Voigt & Weber (2011); Ebert & Stehmann (2013); Louisiana Department of Wildlife & Fisheries (2020)	Juv Sub	Part of the Mississippi River System. First reported by Gunter (1938) from the vacation of Simmesport, 160 miles (= 258 km) from the ocean, as "*Carcharias platyodon*"
79	**B**	**Vermillion Bay** [29.70°N, -91.94°E]	USA (LA)	Norden (1966); Caillouet et al. (1969); Hoese (1981); Czapla et al. (1991); Nelson (1992); Branstetter (1997); Blackburn et al. (2007)	N Juv Sub	Estuary of the Mississippi River System
80	**B**	**Calcasieu Lake** [29.92°N, -93.27°E]	USA (LA)	Czapla et al. (1991); Nelson (1992); Branstetter (1997)	Juv Ad	Estuary with brackish water

No.	WC	Toponym	Country (State)	References	LHS	Comments
81	**F**	**Sabine River** [30,00°N, -93,76°E]	USA (LA, TX)	Matich et al. (2020b)	Juv	Tributary of Sabine Lake (No. 83)
82	**F**	**Neches River** [29.97°N, -93.85°E]	USA (TX)	Matich et al. (2020b)	Juv	Tributary of Sabine Lake (No. 83)
83	**B**	**Sabine Lake** (incl. Sabine Pass Inlet) [29.89°N, -93.82°E]	USA (LA, TX)	Nakamura et al. (1980); Monaco et al. (1989); Nelson (1992); Branstetter (1997); Shipley (2005); Froeschke et al. (2010a, 2010b); Yates et al. (2012); Coy et al. (2014); Daugherty et al. (2018); Green et al. (2018); Plumlee et al. (2018); Laurra-baquio-Alvarado et al. (2019); Hernout et al. (2020); Matich et al. (2020b); TinHan et al. (2020); TinHan & Wells (2021)	N Y-O-Y Juv Sub	Estuary of the Neches and Sabine rivers (No. 81 & No. 82) with brackish water. Shipley (2005) identified the Sabine Pass Inlet as an important nursery area for the early life stages of *C. leucas* in the northern Gulf of Mexico
84	**F**	**Trinity River System** [29.74°N, -94.70°E]	USA (TX)	Brashier (2017)	Sub	Reported as far as Liberty, 30 km from the ocean. Additionally, fishers reported anecdotally that they caught a 1.5 m TL *C. leucas* in 2006 below the Lake Livingston Dam, some 65 km farther upriver (Brashier 2017)
85	**B**	**Galveston Bay** [29.47°N, -94.77°E]	USA (TX)	Baughman & Springer (1950); Renfro (1959); Parker (1965); Monaco et al. (1989); U.S. Department of Commerce (1989); Nelson (1992); Branstetter (1997); Froeschke et al. (2010a, 2010b); Yates et al. (2012); Matich et al. (2017b, 2020b); Daugherty et al. (2018); Green et al. (2018); Plumlee et al. (2018); TinHan et al. (2020); Livernois et al. (2021); TinHan & Wells (2021)	Y-O-Y Juv Sub Ad	Estuary with brackish water. Drainage of the Trinity River System (No. 84) and the San Jacinto River. Additionally, there exists a not precisely localized historical record under one of the synonyms of *C. leucas* by Evermann & Kendall (1894: 95) for "*Carcharhinus platyodon*": "Galveston."
86	**F**	**Brazos River** [28.88°N, -95.29°E]	USA (TX)	Matich et al. (2020b)	Juv	-
87	**F**	**San Bernard River** [28.87°N, -95.44°E]	USA (TX)	Matich et al. (2020b)	U	Tributary of the Cedar Lakes (No. 88)
88	**B**	**Cedar Lakes** [28.82°N, -95.52°E]	USA (TX)	Daugherty et al. (2018)	U	Minor estuary system
89	**F**	**Colorado River** [28.68°N, -95.97°E]	USA (TX)	Matich et al. (2020b)	Juv	Tributary of the Matagorda Bay (No. 90)
90	**B**	**Matagorda Bay** [28.55°N, -96.30°E]	USA (TX)	Monaco et al. (1989); Nelson (1992); Branstetter (1997); Froeschke et al. (2010a, 2010b); Yates et al. (2012); Matich et al. (2017b, 2020b); Daugherty et al. (2018); Plumlee et al. (2018); TinHan et al. (2020); TinHan & Wells (2021)	Y-O-Y Juv Sub Ad	Estuary that serves as the drainage of numerous rivers, most notably the Lavaca and Colorado rivers (No. 89)

No.	WC	Toponym	Country (State)	References	LHS	Comments
91	**F**	**Guadalupe River** [28.46°N, -96.82°E]	USA (TX)	Matich et al. (2020b)	Ad	Tributary of the San Antonio Bay (No. 92)
92	**B**	**San Antonio Bay** [28.35°N, -96.75°E]	USA (TX)	Monaco et al. (1989); Nelson (1992); Branstetter (1997); Froeschke et al. (2010a, 2010b); Yates et al. (2012); Matich et al. (2017b, 2020b, 2021); Daugherty et al. (2018); Green et al. (2018); Plumlee et al. (2018); TinHan et al. (2020); Cottrant et al. (2021)	Y-O-Y Juv Sub Ad	Estuary of the Guadalupe River (No. 91)
93	**B**	**Mesquite Bay** [28.13°N, -96.84°E]	USA (TX)	Hoese & Moore (1958)	U	Minor bay system
94	**B**	**Aransas Bay** [28.03°N, -96.98°E]	USA (TX)	Baughman & Springer (1950); Monaco et al. (1989); Nelson (1992); Branstetter (1997); Froeschke et al. (2010a, 2010b); Yates et al. (2012); Matich et al. (2017b, 2020b); Daugherty et al. (2018); Plumlee et al. (2018); TinHan et al. (2020); Swift & Portnoy (2021); TinHan & Wells (2021)	Y-O-Y Juv Sub	Estuary of the Mission River, the Aransas River, and smaller streams such as Copano Creek
95	**B**	**Redfish Bay** [27.91°N, -97.10°E]	USA (TX)	Swift & Portnoy (2021)	Juv	Estuary
96	**B**	**Corpus Christi Bay** [27.78°N, -97.30°E]	USA (TX)	Nakamura et al. (1980); Monaco et al. (1989); Nelson (1992); Branstetter (1997); Froeschke et al. (2010a, 2010b); Yates et al. (2012); Matich et al. (2017b, 2020b); Daugherty et al. (2018); Plumlee et al. (2018); TinHan et al. (2020); Swift & Portnoy (2021); TinHan & Wells (2021)	Y-O-Y Juv Sub	Estuary of the Nueces River and some smaller creeks
97	**B**	**Baffin Bay** [27.26°N, -97.44°E]	USA (TX)	Branstetter (1997)	Juv	Estuary
98	**B**	**Laguna Madre** [26.55°N, -97.42°E]	USA (TX)	Baughman & Springer (1950); Nakamura et al. (1980); Nelson (1992); U.S. Department of State Lead Agency (1996); Froeschke et al. (2010a, 2010b); Yates et al. (2012); Daugherty et al. (2018); Plumlee et al. (2018); TinHan & Wells (2021)	Y-O-Y Juv	Estuary / hypersaline lagoon that receives freshwater inflow from San Fernando Creek through Baffin Bay and the Arroyo Colorado, as well as from surrounding coastal watersheds; brackish, but in parts also hypersaline (> 35‰ salinity) due to high evaporation
99	**F**	**Rio Grande River** (= Rio Bravo del Norte) [25.95°N, -97.14°E]	USA (TX) / Mexico	(conditionally even Thorson 1976a); Miller et al. (2006, 2009); Matich et al. (2020b)	Ad	Thorson (1976a) reported the occurrence of sharks (species not identified but presumably *C. leucas*)
100	**F**	**Soto la Marina River** [23.77°N, -97.75°E]	Mexico	Thorson (1976a); Miller et al. (2006, 2009)	U	-

No.	WC	Toponym	Country (State)	References	LHS	Comments
101	**F**	**Pánuco River** [22.20°N, -97.84°E]	Mexico	Jones (1985); Castro-Aguirre et al. (1999); Miller et al. (2009)	U	Verified as far as Tampico near the river mouth
102	**B**	**Pánuco River Estuary** [22.26°N, -97.79°E]	Mexico	Jordan & Dickerson (1908)	Juv	Jordan & Dickerson (1908) captured a juvenile specimen (2.3 feet) and reported it as "*Carcharias platyodon*"
103	**B**	**Laguna de Tamiahua** [21.60°N, -97.54°E]	Mexico	Bonfil (1997a, 1997b); Laurrabaquio-Alvarado et al. (2021)	Juv	Identified as a nursery area for *C. leucas* (Bonfil 1997a)
104	**F**	**Tuxpan River** (= Pantepec River) [20.95°N, -97.31°E]	Mexico	Castro-Aguirre et al. (1999); Miller et al. (2006, 2009)	U	Verified as far as Tuxpan
105	**B**	**Tuxpan-Tampamachoco Estuarine System** (incl. Tampa-machoco Lagoon) [21.00°N, -97.34°E]	Mexico	Pérez-Hernández & Torres-Orozco B. (2000); González Gándara et al. (2012)	U	-
106	**F**	**Tecolutla River** [20.47°N, -97.00°E]	Mexico	Thorson (1976a); Miller et al. (2006, 2009)	U	-
107	**F**	**Papaloapan River** [18.74°N, -95.74°E]	Mexico	Miller (1966); Thorson (1976a); Jones (1985); Espinosa-Pérez et al. (2004); Miller et al. (2006); Conabio (2018)	U	-
108	**F**	**Coatzacoalcos River** [18.15°N, -94.40°E]	Mexico	Thorson (1976a); Bonfil (1997a); Miller et al. (2006); Kováč (2013)	U	-
109	**B**	**Machona Lagoon** (= Laguna de la Machona) [18.35°N, -93.62°E]	Mexico	Espinosa-Pérez & Huidobro-Campos (2005)	U	-
110	**B**	**Chiltepec (Lagoon) Estuary** [18.40°N, -93.12°E]	Mexico	Castro-Aguirre (1978); Castro-Aguirre et al. (1999); Espinosa-Pérez et al. (2004)	U	Lagoon / estuary system with brackish water and different salinities
111	**F**	**Grijalva River** [18.59°N, -92.68°E]	Mexico	Thorson (1976a); Castro-Aguirre et al. (1999)	U	Forming a river system together with No. 113
112	**F**	**Laguna de las Ilusiones** [18.00°N, -92.93°E]	Mexico	Castro-Aguirre (1978); Castro-Aguirre et al. (1999); Espinosa-Pérez et al. (2004); Miller et al. (2006, 2009)	U	An inland freshwater lake 30 km from the ocean, connected to the ocean by the Grijalva River (No. 111)
113	**F**	**Usumacinta River** [18.60°N, -92.63°E]	Mexico	Miller (1966); Thorson (1976a); Taniuchi (1993, 2002); Kitamura et al. (1996); Sosa-Nishizaki et al. (1998); Castro-Aguirre et al. (1999); Espinosa-Pérez et al. (2004); Miller et al. (2006, 2009); Kováč (2013); Soria-Barreto et al. (2018)	N Juv Ad	Verified as far as Emiliano Zapata, 80 km from the ocean according to Castro-Aguirre et al. (1999), and as far as Piedras Negras and Yaxchilan according to Kováč (2013)
114	**B**	**Laguna de Terminos** (= Terminos Lagoon, incl. Laguna de Pom and Laguna de Atasta) [18.60°N, -91.55°E]	Mexico	Castro-Aguirre (1978); Yáñez-Arancibia et al. (1980); Bonfil et al. (1990); Uribe (1993); Bonfil (1997b); Castro-Aguirre et al. (1999); Espinosa-Pérez et al. (2004); Miller et al. (2009); D. Lon (2019), pers. comm.	U	River basin that is fed by several freshwater rivers, including No. 111 and No. 113. It also includes several smaller lagoons such as Pom and Atasta

No.	WC	Toponym	Country (State)	References	LHS	Comments
115	**B**	**Chetumal Bay** [18.40°N, -88.08°E]	Mexico / Belize	Bonfil et al. (1990); Applegate et al. (1992, 1993); Bonfil (1997a, 1997b); Espinosa-Pérez et al. (2004); Medina-Quej et al. (2009); Schmitter-Soto et al. (2009); Laurrabaquio-Alvarado et al. (2021)	Juv	Estuary of the Hondo River (No. 1, Tab. 3) with brackish water, identified as a *C. leucas* nursery area (Applegate et al. 1993; Medina-Quej et al. 2009)

Additions to Table 1

This list in Table 1 should probably also include the famous tidal influenced Matawan Creek of New Jersey, a tributary of Raritan Bay where in July 1916 a couple of shark attacks on bathers with fatalities occurred at 25 km distance from the ocean, even though the identity of the involved species was never satisfactorily resolved (Klimley 2013). At that time, Fowler (1920) (and later on many further authors) presumed that *Carcharodon carcharias* Linnaeus, 1758 (great white shark) was the involved species. The attacks took place in proximity to the town of Matawan (40.45°N). Considering that this part of the inland waters of New Jersey is a low salinity environment, and because *C. leucas* undertakes expansive seasonal movements along the east coast of the United States to Massachusetts during the summer (see chapter 4.1), it is very likely that the culprit of these attacks was *C. leucas* (Klimley 2013). *Carcharodon carcharias* has never been reported from low salinity habitats or inland waters. However, not focusing on the attacks, this locality could represent the most northern fresh/brackish water occurrence of *C. leucas* in the world. *Carcharhinus leucas* may also occur in the more northern Hudson River (New York, USA) (Smith 1985; Berra 2007; ReefQuest Centre for Shark Research 2018), but this needs verification. Mearns (1898) reported that sharks were frequently captured in the lower course of the Hudson River, and also in the East River. Moreover, Mearns (1898) reported that several specimens of *Carcharhinus obscurus* Lesueur, 1818 (dusky shark) were taken in the lower part of the Hudson River during the summer of 1881, one as far up the river as Peekskill, which is 65 km north of New York City. This record is probably based on a misidentification with another species of shark, and even Smith & Lake (1990) stated that the identification of *C. obscurus* by Mearns is in doubt. However, the tidal influence in the Hudson River reaches as far as 225 km upriver, which gives the lower reaches of this river the character of an estuary, so the occurrence of *C. leucas*, beside other carcharhinids, in the Hudson River seems possible.

Schwartz (1984, 1989) and Musick et al. (1999) reported the occurrence of *C. leucas* in estuaries and lagoons of Virginia, North Carolina, and South Carolina, but without naming any certain localities. Kushlan & Lodge (1974: 116) commented for *C. leucas* in the inland waters of Florida: "Large rivers such as the Caloosahatchee, St. Lucie and the numerous smaller rivers of the southwest coast such as the Shark, Broad and North Rivers of Everglades National Park provide suitable habitat." Brame et al. (2019) provided evidence for *C. leucas* from the Everglades National Park. Hocutt & Wiley (1986) pointed out that in the southeast of North America, mostly on the Florida peninsula, *C. leucas* can be encountered in freshwater with some regularity. Loftus & Kushlan (1987) provided a small distribution map of freshwater occurrences of *C. leucas* in southern Florida. In Florida, *C. leucas* utilizes even the artificial freshwaters of the Miami Canals, where there have been numerous recent sightings of *C. leucas*, the sharks entering these waters via Biscayne Bay (Austin 2015), which brings sharks close to human beings and leads to increasing human-shark interactions. Swift et al. (1977) predicted *C. leucas* for the Ochlockonee River (FL, USA) due to its occurrence in the nearby Aucilla River (Table 1, No. 45) and its ability to enter freshwater. Rogillio (1975) mentioned *C. leucas* as an estuarine sportfish in southeastern Louisiana, and Wharton et al. (1981) mentioned this species as an occasional visitor of the inland open waters and the wetlands of bottomland hardwood forests of the Mississippi/Atchafalaya-Basin in the southeastern United States. In the Mississippi/Atchafalaya system, Gunter (1938) reported sightings by local fishers of sharks caught in the Black River at Jonesville (Louisiana), which is a tributary of the Red River (Table 1, No. 77). Parsons (2006) reported that *C. leucas* is common in and around the marshes of Louisiana. Hubbs (1958) listed *C. leucas* in the checklist of Texas freshwater fishes with the information that this euryhaline species enters coastal streams. For the rivers of Texas, Hubbs et al. (2008) noted that *C. leucas* may travel short distances upstream. Christensen et al. (1997) listed *C. leucas* as a species of the Gulf of Mexico estuaries that are located along the southern U.S. coast. Daugherty et al. (2018) stated that *C. leucas* is the most abundant shark species in Texas bays, especially specimens less than 2 m TL. Already Evermann & Kendall (1894) reported that *Carcharhinus platyodon* (= *C. leucas*) is said to be the most common large shark on the coast of Texas in summer.

García de León et al. (2005) listed *C. leucas* as a euryhaline marine species for the continental inland waters of Tamaulipas in northeastern Mexico, but without providing a certain locality. Additionally, Thorson (1976a) reported the occurrence of sharks (species not identified, but probably *C. leucas*) in the San Pedro River (a tributary of the Usumacinta River; Table 1, No. 112) as reported by fishers, local residents, and ichthyologists. Furthermore, for the inland waters of Mexico, Castro-Aguirre (1978) reported *C. leucas* from the district of Emiliano Zapata, which is drained by the Grijalva River (Tab. 1, No. 110) and the Usumacinta River (Table 1, No. 112). Jones (1985) reported the occurrence of unidentified sharks, in all probability *C. leucas*, observed by local fishers in the Champoton River in Campeche (Mexico). MacBeath (2014) included *C. leucas* in a list of fish species found in Mexican freshwaters, but without providing a certain locality.

No. 1: Schwartz (1957) published a "wanted call" for some shark species, including *C. leucas*, that he suspected to occur at Chesapeake Bay and the Atlantic Ocean off Maryland, to fill gaps in the knowledge about these species. Lawler (1976) reported two examined adult males of *C. leucas* from the Chesapeake Bay, one specimen (2.23 m TL) captured in July 1976 at Fishermen's Island and one specimen (2.39 m TL) captured in 1973 at the mouth of the Coan River, which is tributary of Chesapeake Bay. Lee et al. (1976), presumably referring to the reports of Schwartz from Chesapeake Bay, added *C. leucas* to

a list of freshwater fishes of Maryland and Delaware with the information that *C. leucas* locally occurs in freshwater, but without naming a precise locality. However, Lee et al. (1976) and subsequently Flynn & Mason (1978) reported *C. leucas* from freshwaters of Maryland's coastal plain. Lippson & Lippson (1984) reported that *C. leucas* has been captured by fishers well up the Chesapeake Bay in Maryland waters, near Annapolis and the mouth of the Chester River. Additionally, Musick et al. (1993) reported catches of *C. leucas* from waters adjacent to Chesapeake Bay (Chesapeake Bight).

No. 5: Smith & Bean (1899: 180) reported *Carcharhinus obscurus* in the Potomac River from locations in Maryland and Washington, D.C.: "Occasionally observed in the Potomac between Fort Washington and Alexandria during dry weather when the water becomes brackish. An example 5 feet long, taken at Glymout in August, 1894, was examined by us in Center Market, where a cast of the specimen is now exhibited. Other sharks have also been taken in sturgeon nets at Glymont during dry weather, and many years ago one was captured at Port Washington." This record by Smith & Bean seems doubtful, as *C. obscurus* is not known to enter low salinity habitats and normally does not penetrate brackish waters. In this context, Compagno (1984: 490) wrote about the habitat preferences of *C. obscurus*: "It does not prefer areas with reduced salinities and tends to avoid estuaries." Moreover, the stretch of the Potomac River between Fort Washington and Alexandria is characterized by nearly pure freshwater conditions during the summer months (0–0.5‰ salinity) (Chesapeake Bay Program 2019). At the very least, the report by Smith & Bean has to be assessed as critical and questionable. Although Smith (1893) reported earlier about sharks in the freshwaters of Lake Nicaragua (see Table 3), these authors were not familiar with similar-looking carcharhinids, and presumably this record of *C. obscurus* is based on a misidentification with another member of the genus *Carcharhinus*, probably *C. leucas*. Thus, this historical account could maybe represent an early record of *C. leucas* in the Potomac River.

Nos. 13–16: Castro (1993) reported that sightings of juvenile *C. leucas* in South Carolina estuaries only occur occasionally, as well as reported a catch of a very large female with embryos in Bulls Bay. Ulrich et al. (2007) captured juvenile specimens of *C. leucas* in South Carolina estuaries, but without giving a precise localization of the catches.

Nos. 17–18: Additionally, and for completeness, Belcher (2008) and Belcher & Jennings (2009a, 2009b, 2010) reported only a few subadult individuals (1–2) of *C. leucas* in catches from some of the examined estuaries in Georgia, but without naming the precise locality of the catches. This may indicate that *C. leucas* only occasional utilizes the estuaries of Georgia as nursery areas, although these results are in contrast with those of Streich & Peterson (2011), who provided evidence of a *C. leucas* nursery in Georgia's Altamaha River Estuary (Table 1, No. 18).

No. 68: The occurrence of *C. leucas* in the Upper Mississippi River seems to be such a curiosity that Rasmussen (1979: 36) stated: "Only one straggler species is so unusual that it is worthy of note. This is the bull shark (*Carcharhinus leucas*)." As a result of the rare records from the Mississippi River, *C. leucas* was mentioned in the summary on the inland fishes of Mississippi by Ross (2001). However, recent records and reports of *C. leucas* for the Mississippi River are lacking.

Shell & Gardner (2021) reported that only two specimens of *C. leucas* were captured in the upper portion of the Mississippi River during the entire 20th century. These authors reported that two *C. leucas* swam up the Mississippi River and made it at least as far as St. Louis (Missouri) on two separate occasions. One specimen was reported from Alton (Illinois) and was captured in 1937 (record at first reported by Thomerson et al. 1977; see Table 1, No. 68). The second record was made just south of Festus in the vicinity of St. Louis (Missouri) near Rush Island Power Station in 1995 (Burr et al. 2004; Shell & Gardner 2021). This last record is not well documented except for a newspaper report. Thus, although Shell & Gardner (2021) reported a repeating large-scale migration of *C. leucas* in the Upper Mississippi River, this species seems to be rarely encountered in the upper reaches of this river. The limited number of *C. leucas* records from the Mississippi River Basin during such a wide span of time may lead to the conclusion that *C. leucas* is a cryptic species in the upper portions of this river system, or records are only poorly documented or events of river penetrations by *C. leucas* farther inland than the river's estuary are simply rare.

No. 69: Springer (1950: 6) reported for the mouth of the Mississippi River (Mississippi Sound): "The adults appear in great concentration near the mouth of the Mississippi from May through July and produce their young there." Springer (1960: 33) later commented: "Bull sharks are extremely common around the mouths of the Mississippi and Orinoco Rivers." Even Branstetter (1981) reported *C. leucas* as a common species near the mouth of the Mississippi River. Nakamura et al. (1980: 40) gave the information of occurrences of *C. leucas* in estuarine waters: "West of Mississippi River" and further "East of Mississippi River", but the information provided was quite imprecise.

The large delta of the Mississippi River represents not only an important nursery ground for numerous shark species like *Rhizoprionodon terraenovae* Richardson, 1836 (Atlantic sharpnose shark) and *C. leucas* (Parsons & Hoffmayer 2005, 2007) but also an important feeding habitat for further shark species like *Carcharhinus limbatus* Müller & Henle, 1839 (blacktip shark) and *Carcharhinus isodon* Müller & Henle, 1839 (finetooth shark) (Hoffmayer & Parsons 2003). Moreover, the estuary of the Mississippi River delta system is highly productive and performs a function as an important nursery ground for juvenile marine and estuarine fishes (Madden et al. 1988). The availability of young and small sharks in this estuary may also attract adult *C. leucas* to move in, as this species is known as an intense elasmobranch consumer.

Nos. 70–73: Lac des Allemands, Bayou des Allemands, Lake Salvador, Little Lake, and Barataria Bay are part of the Barataria Basin, a vast Louisiana estuary characterized by a broad amplitude of salinities ranging from fresh to nearly seawater, bordered on the north and east by the Mississippi River and on the south by the Gulf of Mexico. Thompson & Forman (1987) reported *C. leucas* from the Barataria Basin and Alford (2012) from the Barataria estuary system.

Nos. 77–78: The Red River is the extension of the Atchafalaya River in the Mississippi River System of Louisiana State and is connected with the Mississippi River by some river branches. Hoese & Moore (1998) speculated that *C. leucas* may have reached the Red River and Saline Lake also via the Mississippi River. a historical record of an adult *C. leucas* (270 cm TL) from Red River County (Texas) in 1903 was published by Matich et al. (2020b), who investigated historical reports from newspapers. This record expands the distance of freshwater penetration of *C. leucas* in this river up to 950 km from the estuary and the Gulf of Mexico.

Nos. 81, 82, 86, 87, 89, 91: The *C. leucas* records from these rivers were originally taken from newspaper references and summarized by Matich et al. (2020b) (see therein for details on the primary references).

No. 105: Darnell (1962) expected *C. leucas* to occur in the lagoons in the Tampico area, including Laguna de Chairel.

Table 2. Occurrences of *Carcharhinus leucas* in North American rivers, lakes, estuaries, and lagoons: Pacific Ocean coast. Abbreviations: WC = water conditions, F = freshwater, B = brackish water up to hypersaline conditions, F/B = salinity gradient from fresh to brackish, LHS = life history stage, Ad = adult, Sub = subadult, Juv = juvenile, Y-O-Y = young-of-the-year, N = neonate, U = unknown.

No.	WC	Toponym	Country	References	LHS	Comments
1	B	**Altata-Ensenada Lagoon System** [24.52°N, -107.81°E]	Mexico	Ruelas-Inzunza & Páez-Osuna (2005); Ruelas-Inzunza et al. (2014)	U	Estuary of the Culiacán River
2	B	**Urias (Lagoon) Estuary** [23.18°N, -106.36°E]	Mexico	Espinosa-Pérez et al. (2004); Conabio (2018)	U	A lagoon and river outlet with brackish water
3	F	**Presidio River** [23.09°N, -106.28°E]	Mexico	Castro-Aguirre (1978); Castro-Aguirre et al. (1999); Espinosa-Pérez et al. (2004); Miller et al. (2006, 2009)	U	-
4	B	**Teacapán-Agua Brava Lagoon-Estuarine System** [22.54°N, -105.75°E]	Mexico	Saucedo et al. (1982); Manjarrez et al. (1983); Applegate et al. (1992, 1993); Salomón-Aguilar et al. (2009); Rubio-Cisneros et al. (2020)	Juv	Estuary system of the Cañas River and the Acaponeta River (No. 5). Identified as a *C. leucas* nursery (Applegate et al. 1993; Salomón-Aguilar et al. 2009)
5	F	**Acaponeta River** [22.21°N, -105.56°E]	Mexico	Applegate et al. (1992, 1993); CONABIO (2018)	Juv	As far as Acaponeta, 25 km from the ocean (Applegate et al. 1993). Identified as a *C. leucas* nursery area (Applegate et al. 1993)
6	B	**Balsas River Estuary** [17.94°N, -102.13°E]	Mexico	Espinosa-Pérez et al. (2004); Conabio (2018)	U	-
7	B	**Mar Muerto Lagoon** [15.98°N, -93.97°E]	Mexico	Castro-Aguirre (1978); Castro-Aguirre et al. (1999); Miller et al. (2006, 2009)	U	Lagoon with numerous river outlets

Additions to Table 2

Additionally, Anislado-Tolentino et al. (2016) reported a *C. leucas* attack at the mouth of the Pantia River (Guerrero, Mexico), so probably even this river and/or its estuary are utilized by *C. leucas*. The archaeoichthyological analysis of sediments from an archaeological site on the western Mexican coastal plain at Huatabampo, which is located along the Mayo River, by Guzmán (2008) revealed also remains of *C. leucas*. Possibly, this river was utilized by *C. leucas* in ancient times, but it could still be in use. Velázquez-Veláquez et al. (2016) and González-Acosta et al. (2018) reported *C. leucas* from continental waters and estuaries of the state of Chiapas (Mexico), but without providing any certain localities.

Additions to Table 3

Additionally, for the Atlantic Ocean side of Central America, Boesemann (1964: 10) reported on the occurrence of *C. leucas*: "Rivers of South America between the La Plata River and the Rio Magdalena." Subsequently, even Thorson (1970b: 83) reported: "In South America sharks are found in Lake Maracaibo in Venezuela and in a plentitude of east coast rivers from the Magdalena in Colombia to the Rio de la Plata in southern Uruguay." Furthermore, Thorson (1976a) later reported on the occurrence of sharks (species not identified, but probably *C. leucas*) from numerous additional rivers in Central America not listed in Table 3, based on reports of fishers, local residents, and ichthyologists. These include: A) Belize: Belize River; B) Guatemala: Motagua River; C) Honduras/Nicaragua: Coco River; D) Nicaragua: Grande de Matagalpa River, Huahuasan River, Escondido River, Indio River; E) Costa Rica: Pacuare River, Matina River. Also Burke (1979), who was referring to Smith (1893), reported the occurrence of sharks in the Escondido River and one of its tributaries, the Rama River. Gunter (1942) listed *Carcharias platyodon* (= *C. leucas*) in a list of euryhaline fishes that occur both in fresh and seawater from the east coast of Mexico to the southern limit at Panama. Jones (1985) reported the occurrence of unidentified sharks, in all probability *C. leucas*, based on reports by local fishers in the Sabun River (Belize). Possibly, occurrences of *C. leucas* even exist in Guatemala's Polochic and Cahabón rivers, which are tributaries of Lake Izabal (Table 3, No. 3).

Neal et al. (2009) reported *C. leucas* in a list of primarily marine and estuarine fish species collected in freshwater rivers of Puerto Rico, but without naming a precise locality or

Table 3. Occurrences of *Carcharhinus leucas* in South and Central American rivers, lakes, estuaries, and lagoons: Atlantic Ocean coast, including the Caribbean Sea. Abbreviations: WC = water conditions, F = freshwater, B = brackish water up to hypersaline conditions, F/B = salinity gradient from fresh to brackish, LHS = life history stage, Ad = adult, Sub = subadult, Juv = juvenile, Y-O-Y = young-of-the-year, N = neonate, U = unknown.

No.	WC	Toponym	Country	References	LHS	Comments
1	**F**	**Hondo River** [18.48°N, -88.31°E]	Mexico / Belize	Jones (1985); De Carvalho & McEachran (2003); Froese & Pauly (2018a)	Ad	Jones (1985) reported a 3.5 m TL specimen at ~100 km distance from the ocean
2	**F**	**Temash River** [15.97°N, -88.93°E]	Belize	Greenfield & Thomerson (1997); Froese & Pauly (2018a)	U	-
3	**F**	**Lake Izabal** (= Lake Yzabal) [15.48°N, -89.18°E]	Guatemala	Bigelow & Schroeder (1948); Saunders et al. (1950); Cole (1963); Boeseman (1964); Miller (1966); Thorson et al. (1966b); Thorson (1970b, 1976a); Budker (1971); Brinson (1973); Brinson et al. (1974); Dickinson (1974), Brinson & Nordlie (1975); Mathews (1975); Johnson (1978); Garrick (1982); Compagno (1984); Steel (1985); Ellis (1989); McEachran & Fechhelm (1998); Bussing (2002); Michot et al. (2002); Ellison (2004); Alvarado et al. (2005); Orrelana Amador (2010); Voigt & Weber (2011); Ebert & Stehmann (2013)	N Y-O-Y Juv	Bigelow & Schroeder (1948: 341) stated: "…a body of water that is said to vary between fresh and brackish". Recently with dominating freshwater conditions. Holloway (1950: 100, 114, 128) reported an imprecise "*Carcharhinus*" in the species inventory for Lake Izabal, but it is highly probable that the author was referring to *C. leucas*
4	**F/B**	**Dulce River** (incl. Lake El Golfete) [15.73°N, -88.88°E]	Guatemala	Boeseman (1964); Thorson et al. (1966b); Thorson (1970b, 1976a); Budker (1971); Watson & Thorson (1976); Compagno (1984); Steel (1985); Ellis (1989); Ellison (2004)	N Y-O-Y Juv	Drainage of Lake Izabal (No. 3). The water of the Dulce River / Lake El Golfete may vary from fresh to brackish (Saunders et al. 1950)
5	**F**	**Patuca River** [15.80°N, -84.29°E]	Honduras	Strong (1934); Bigelow & Schroeder (1948); Boeseman (1964); Thorson (1970b); Martin (1972); Compagno (1984); Greenfield & Thomerson (1997); McEachran & Fechhelm (1998); Bussing (2002); Matamoros et al. (2009); Matamoros (2010); Esselman & Opperman (2010); Voigt & Weber (2011); Ebert & Stehmann (2013)	Juv	First reported by Strong (1934) at the confluence with the Yapowas Creek. Reported 180 miles (= 290 km) from the ocean (Strong 1934). Greenfield & Thomerson (1997) referred to a *C. leucas* in the "Patula River", which Matamoros et al. (2009) assumed to be an error and the authors in fact referred to the Patuca River (error made also by McEachran & Fechhelm 1998 and Voigt & Weber 2011: "Palula River")
6	**B**	**Pearl Lagoon** (= Laguna de Perlas) [12.51°N, -83.69°E]	Nicaragua	Moreno Pérez & Van Eijs (2002)	U	Estuary system. Tributary of the Kurinwás River and connected with the Rio Grande de Matagalpa

No.	WC	Toponym	Country	References	LHS	Comments
7	**F**	**Maiz River** [11.29°N, -83.87°E]	Nicaragua	Thorson (1973, 1976a)	Juv	Evidence by a recapture of a tagged specimen of the San Juan River population that was investigated by Thorson (1976a)
8	**F**	**San Juan River** [10.93°N, -83.69°E]	Nicaragua	Gill & Bransford (1877); Eigenmann (1893, 1909); Smith (1893); Jordan & Evermann (1896); Gilbert & Starks (1904); Meek (1907, 1967); Regan (1908); Cole (1963); Boeseman (1964); Oguri (1964); Miller (1966); Myers (1966); Thorson et al. (1966a, 1973); Thorson (1965, 1967, 1970a, 1970b, 1971, 1972b, 1973, 1976a, 1976b, 1987); Budker (1971); Williams (1971); Jensen (1972, 1976); Bussing (1976, 2002); Tuma (1976); Watson & Thorson (1976); Johnson (1978); Burke (1979); Berra (1981, 2007); Thorson & Lacy (1982); Villa (1982); Compagno (1984); Steel (1985); Orellana (1986); Keller (1987); Ellis (1989); Kitamura et al. (1996); McEachran & Fechhelm (1998); Ellison (2004); Simpfendorfer & Burgess (2005, 2009); Brizuela (2006); De La Rosa (2006); Kohn et al. (2006); Voigt & Weber (2011); Angulo et al. (2013); Ebert & Stehmann (2013); Kleisner et al. (2013); Portocarrero (2013); Calero & Pérez (2015); Huete-Peréz et al. (2016); McClearn et al. (2016)	N Y-O-Y Juv Sub Ad	Connection between Lake Nicaragua (No. 9) and the Caribbean Sea with a total length of 185 km; outlet of Lake Nicaragua
9	**F**	**Lake Nicaragua** (= Gran Lago de Nicaragua, Lago Cocibolca, Lago Cocobolca) [11.64°N, -85.36°E]	Nicaragua	(conditionally also Belt 1874); Gill & Bransford (1877); Lutken (1880); Gill (1884, 1893); Smith (1893); Jordan & Evermann (1896); Hayes (1899); Gilbert & Starks (1904); Meek (1907, 1967); Regan (1908); Eigenmann (1909); Jordan et al. (1930); Norman & Fraser (1937); Marden (1944); Bigelow & Schroeder (1945, 1948, 1961); Schultz (1949); Carr (1953); Severin (1953); Halstead (1959); Thorson (1962a, 1962b, 1964, 1965, 1967, 1970a, 1970b, 1971, 1972b, 1973, 1976a, 1976b, 1978, 1982, 1987); Urist (1962); Cole (1963, 1976); McCormick et al. (1963); Astorqui (1964, 1967, 1971, 1974);	N Y-O-Y Juv Sub Ad	Already Belt (1874) reported sharks in Lake Nicaragua, but without a species determination. The first scientific report of *C. leucas* from this locality derived from Gill & Bransford (1877) under the name "*Eulamia nicaraguensis*". It was once believed that the local population of *C. leucas* in Lake Nicaragua represented a landlocked, separated and endemic species, *Carcharhinus nicaraguensis* (Bigelow & Schroeder 1948).

No.	WC	Toponym	Country	References	LHS	Comments
				Boeseman (1964); Oguri (1964); Miller (1966); Myers (1966); Swain (1966); Thorson et al. (1966a, 1973); Hagberg (1968); Gerzeli et al. (1969, 1976); Budker (1971); Williams (1971); Jensen (1972, 1976); Burke (1974, 1979); Mathews (1975); Davies (1976); Migdalski & Fichter (1976); Tuma (1976); Villa (1976a, 1976b, 1982); Watson & Thorson (1976); Bussing & López (1977); Johnson (1978); Berra (1981, 2007); Garrick (1982); Thorson & Lacy (1982); Compagno (1984); Stachowitsch (1984); Steel (1985); Orellana (1986); Robins & Ray (1986); Keller (1987); Ellis (1989); Taniuchi (1992); Winemiller & Leslie (1992); Tanaka (1994); McKaye et al. (1995); Ryan (1995); McCrary et al. (1998, 2007); McEachran & Fechhelm (1998); Rojas M. et al. (2000); Gadig (2001); Bussing (2002); McDavitt (2002); Ellison (2004); Camacho & Gadea E. (2005); Simpfendorfer & Burgess (2005, 2009); Brizuela (2006); De La Rosa (2006); Hernández-Portocarrero & Saborido-Rey (2008); Sánchez Crispín et al. (2008); Zárate & Hearn (2008); Orrelana Amador (2010); Voigt & Weber (2011); Chapman et al. (2012); Angulo et al. (2013); Ebert & Stehmann (2013); Kleisner et al. (2013); Portocarrero (2013); Martínez-Serrano et al. (2014); Meyer & Huete-Peréz (2014); Calero & Pérez (2015); Huete-Peréz et al. (2015, 2016); McClearn et al. (2016)		This mistake resulted in the fact that *C. leucas* was for a long time a matter of taxonomic and distributional controversy and confusion at this locality (Bigelow & Schroeder 1961; Thorson 1970b; Ellis 1989)
10	**F**	**Sapoá River** [11.25°N, -85.60°E]	Nicaragua/ Costa Rica	Bussing (2002)	U	Tributary of Lake Nicaragua (No. 9)
11	**F**	**Frío River** [11,11°N, -84,77°E]	Nicaragua/ Costa Rica	Smith (1893); Boeseman (1964); Bussing (2002); Vazquéz (2006); Angulo et al. (2013)	Sub	Tributary of the San Juan River (No. 89), not Lake Nicaragua (Smith 1893)
12	**F**	**Caño Negro Lagoon** [10.94°N, -84.73°E]	Costa Rica	Córdoba Muñoz et al. (1998)	U	An inland freshwater lagoon that feeds the Frío River (No. 11)
13	**F**	**San Carlos River** [10.78°N, -84.19°E]	Nicaragua/ Costa Rica	Thorson (1973, 1976a); Bussing (2002); Angulo et al. (2013)	Juv	Tributary of the San Juan River (No. 8)

No.	WC	Toponym	Country	References	LHS	Comments
14	**F**	**Puerto Viejo River** [10.44°N, -84.01°E]	Costa Rica	Bussing (1993, 2002); McClearn et al. (2016)	U	Tributary of No. 15. Bussing (1993) reported occasional sightings of sharks each year. McClearn et al. (2016) reported rare events of *C. leucas* reaching La Selva
15	**F**	**Sarapiqui River** [10.52°N, -84.02°E]	Costa Rica	Thorson (1973, 1976a); Bussing (2002); Angulo et al. (2013); Farah-Pérez (2016); McClearn et al. (2016)	Juv	Tributary of the Sucio River (No. 16)
16	**F**	**Sucio River** [10.51°N, -84.02°E]	Costa Rica	No reference, but it is logical under geographical circumstances	Juv	Connection between the Sarapiqui River (No. 15) and the San Juan River (No. 8).
17	**F**	**Poco Sol River** [10.98°N, -84.42°N]	Nicaragua	Thorson (1976a)	Juv	Tributary of the San Juan River (No. 8)
18	**F**	**Sábalos River** (= Boca de Sabalos) [11.04°N, -84.47°E]	Nicaragua	Thorson (1976a)	Juv	Tributary of the San Juan River (No. 8)
19	**F**	**Bartola River** [10.97°N, -84.33°E]	Nicaragua	Thorson (1973)	Juv	Tributary of the San Juan River (No. 8)
20	**F**	**Isla Chica River** (= Caño Isla Chica) [11.06°N, -84.54°E]	Nicaragua	Thorson (1973)	Juv	Tributary of the San Juan River (No. 8)
21	**F**	**Colorado River** [10.77°N, -83.59°E]	Costa Rica	Meek (1907, 1967); Cowan (1971); Thorson (1971, 1973, 1976a, 1987); Thorson & Gerst (1972); Thorson et al. (1973); Gerzeli et al. (1976); Jensen (1976); Watson & Thorson (1976); Thorson & Lacy (1982); Villa (1982); Bussing (2002); Taniuchi (2002); Rodriguez-Ortiz et al. (2004); Kohn et al. (2006)	N Y-O-Y Juv Sub	Outlet of the San Juan River (No. 8), connected with the San Juan River to a delta branch at the river mouth. Bussing (2002) reported that newborn young of *C. leucas* were especially common in the numerous lagoons of the Colorado River delta at the locality of Barra del Colorado
22	**F**	**Caño Bravo** [10.73°N, -83.68°E]	Costa Rica	Thorson (1973)	Juv	Branch of the Colorado River (No. 21). Outlet of the San Juan/Colorado River System
23	**F**	**Caño Madre** [11.67°N, -83.67°E]	Costa Rica	Thorson (1973)	Juv	Branch of the Colorado River (No. 21). Outlet of the San Juan/Colorado River System
24	**F**	**Caño Negro** [10.71°N, -83.73°E]	Costa Rica	Thorson (1973)	Juv	Branch of the Colorado River (No. 21). Outlet of the San Juan/Colorado River System
25	**F**	**Laguna Agua Dulce** [10.80°N, -83.60°E]	Costa Rica	Jensen (1976); Thorson (1976a)	Juv	Side channel of the Colorado River (No. 21). A body of freshwater
26	**F**	**Samay Lagoon** (= Laguna Samay) [10.72°N, -83.57°E]	Costa Rica	Thorson & Gerst (1972); Thorson (1973, 1976a); Jensen (1976)	Juv	Outlet of the San Juan/ Colorado River System

No.	WC	Toponym	Country	References	LHS	Comments
27	**F**	**Tortuguero River** [10.52°N, -83.50°E]	Costa Rica	Thorson (1973, 1976a); Angulo et al. (2013)	Juv	-
28	**B**	**Tortuguero River Estuary** [10.57°N, -83.52°E]	Costa Rica	Blaber (1997)	U	-
29	**F**	**Atrato River** [8.19°N, -76.92°E]	Colombia	Dahl (1964); Lasso et al. (2011a, 2011b)	U	Dahl (1964) reported *C. leucas* far inland from the vicinity of Riosucio at ~115 km from the ocean
30	**F**	**Sinú River** [9.34°N, -75.93°E]	Colombia	Dahl & Medem (1964)	U	-
31	**B**	**Sinú River Estuary / Delta** [9.42°N, -75.92°E]	Colombia	Dahl (1964); Mantilla A. (1998)	U	-
32	**F**	**Magdalena River** [11.01°N, -74.78°E]	Colombia	Thorson (1970b); Dahl (1971); Puentes et al. (2009); Lasso et al. (2011a)	U	Recorded as far as Zambrano and Magangué (Dahl 1971; Puentes et al. 2009), at 230 km from the ocean
33	**B**	**Ciénaga Grande de Santa Marta** [10.84°N, -74.40°E]	Colombia	Dahl (1964); Rey & Acero P. (2002); Puentes et al. (2009)	U	Part of the delta system of the Madgalena River (No. 32)
34	**B**	**Lake Maracaibo** (= Lago de Maracaibo) [9.78°N, -71.54°E9	Venezuela	Boeseman (1964); Thorson (1970b); Sánchez & Tavares (2009); Tavares & Sánchez (2012); MPPA & TISPA (2013)	Juv Sub	Actually brackish water in the northern part and freshwater in the southern part of the Lake; transitioning to a freshwater lake
35	**F**	**Catatumbo River Mouth** [9.34°N, -71.73°E]	Venezuela	MPPA & TISPA (2013)	U	Tributary of Lake Maracaibo (No. 34)
36	**F**	**Orinoco River** [8.60°N, -62.22°E]	Venezuela	Lasso et al. (2004a); MPPA & TISPA (2013); Dagosta & Pinna (2017, 2019)	U	Dagosta & Pinna (2019: 64): "*Lower Orinoco*."
37	**B**	**Orinoco River Delta** [8.89°N, -60.82°E]	Venezuela	Springer (1950, 1960); Ponte et al. (1999); Lasso et al. (2004b, 2009); Lasso & Sánchez-Duarte (2011)	Ad	A large river delta with numerous outlets
38	**F**	**Maroni River** [5.64°N, -54.01°E]	Suriname	Keith & Le Bail (2018)	U	-
39	**F**	**Iracoubo River** [5.51°N, -53.24°E]	French Guiana	Keith & Le Bail (2018)	U	-
40	**B**	**Sinnamary River Estuary** [5.45°N, -53.01°E]	French Guiana	Blaber & Barletta (2016)	U	-

No.	WC	Toponym	Country	References	LHS	Comments
41	**F**	**Amazon River** (main channel incl. Ucayali River and Solimões River, the upper reaches of the Amazon River) [-1.89°S, -53.74°E]	Brazil / Columbia / Peru	Starks (1913); Myers (1952); Boeseman (1964); Marlier (1967); Roberts (1972); Thorson (1972a, 1978); Figueiredo (1977); Vizotto & Taddei (1978); Berra (1981, 2007); Werder & Alhanati (1981); Compagno (1984); Keller (1987); Ellis (1989); Bres (1993); Ferrreira (1993); Val & Almeida-Val (1995); Ferreira et al. (1996, 1998); Barthem & Goulding (1997a, 1997b); McEachran & Fechhelm (1998); Soto & Nisa-Castro-Neto (1998); Lessa et al. (1999); Gadig (2001); Soto (2001); Bussing (2002); De Carvalho & McEachran (2003); Soto & Mincarone (2004); Charvet-Almeida et al. (2005); Simpfendorfer & Burgess (2005, 2009); Campbell et al. (2006); Nóbrega et al. (2009); Santos et al. (2010); Voigt & Weber (2011); Bornatowski & Abilhoa (2012); Ortega et al. (2012); Ebert & Stehmann (2013); Klimley (2013); No Amazonas é Assim (2013); Ramírez & Davenport (2013); Carneiro (2016); Portal do Zacarias (2017); Van der Sleen & Albert (2018); Dagosta & Pinna (2017, 2019); Goulding et al. (2019)	Y-O-Y Juv Sub Ad	First reported by Starks (1913) from the Amazon River under the synonym *Carcharhinus platyodon* (one specimen of 73.66 cm TL) from Pará State at Belém. Myers (1952) reported *C. leucas* from Iquitos (Peru), nearly 4,000 km from the Atlantic Ocean. Thorson (1972a) and Ramírez & Davenport (2013) reported *C. leucas* from Leticia (Colombia), nearly 3,480 km upriver. Verified records in the Amazon River System as far as Pucallpa (Peru) in the Ucayali River, 5,080 km from the ocean (Werder & Alhanati 1981). There is not only evidence of neonates, juveniles and immature specimens of *C. leucas* in the Amazon River, but also of adults (both males and females), by Thorson (1972a), Soto (2001) and Soto & Mincarone (2004). No Amazonas é Assim (2013) displayed pictures of a catch of *C. leucas* from the 1970s at Paraná da Eva (~40 km east of Manaus on the Amazon River)
42	**F**	**Madeira River** [-3.59°S, -58.96°E]	Brazil	Ferreira (1993)	U	Large Amazon tributary river
43	**F**	**Tapajós River** [-2.66°S, -55.08°E]	Brazil	Maia (2016)	Sub	Large Amazon tributary river
44	**F**	**Xingú River** [-1.92°S, -52.24°E]	Brazil	Bergleiter (1999); Camargo et al. (2004); Dagosta & Pinna (2017, 2019)	U	Large Amazon tributary stream. Camargo et al. (2004: 131) and Dagosta & Pinna (2019: 64) reported the species from "Lower Xingú."
45	**F**	**Tocantins River** [-1.84°S, -49.24°E]	Brazil	Feitosa & Nunes (2020)	Juv	Reported from Cametá (Feitosa & Nunes 2020)
46	**B**	**Amazon River Estuary** (incl. Tocantins River Estuary) [-0.04S, -49.27°E]	Brazil	Vanni (1992); Barthem (1995); Alencar et al. (2001); Camargo & Isaac (2001); Castro (2009); Karl et al. (2011); Goulding et al. (2019); Cruz et al. (2021); Souza-Araujo et al. (2021)	Y-O-Y Juv Sub Ad	Large estuary/delta with numerous branches and delta islands. Castro (2009) suggested that the Amazon estuary plays an important role in the biology of the southwestern Atlantic *C. leucas* population

No.	WC	Toponym	Country	References	LHS	Comments
47	**F/B**	**Mearim River** (= Rio Mearim) [-3.06°S, -44.61°E]	Brazil	Feitosa et al. (2016); Bezerra et al. (2021)	Juv	As far as Arari City (Feitosa et al. 2016). Periodically tidal-influenced
48	**F**	**Anil River** [-2.51°S, -44.29°E]	Brazil	O Imparcial (2017)	Sub	Reported from São Loís
49	**B**	**Parnaíba River Delta** [-2.74°S, -41.81°E]	Brazil	Aragão et al. (2020)	U	Outlet of the Parnaíba River
50	**F**	**Una River** [-8.82°S, -35.13°E]	Brazil	Portal Nova (2018)	Ad	Reported from Várzea do Una
51	**B**	**Mundaú Lagoon** [-9.63°S, -35.77°N]	Brazil	Anonymous (2020)	Ad	Anonymous (2020) reported catches of adult female *C. leucas*, which may indicate that this lagoon represents a nursery for *C. leucas*
52	**B**	**Jaraguá-Maceió Estuary** [-9.71°S, -35.80°E]	Brazil	Rangely et al. (2010)	U	Outlet of the Mundaú Lagoon
53	**F**	**Parapuca Canal** [-10.49°S, -36.44°E]	Brazil	Alves (2017)	Ad	Tributary of the São Francisco River (No. 54)
54	**F**	**São Francisco River** [-10.48°S, -36.40°E]	Brazil	No reference but it is logical under geographic circumstances	Ad	Connection between the Parapuca Canal (No. 53) and the ocean
55	**B**	**Maraú Estuary** [-13.68°S, -38.97°E]	Brazil	Niella (2016); Niella et al. (2017)	Sub Ad	Estuary of many rivers (e.g., the Santarém and Orojo rivers)
56	**F**	**Sâo Mateus River** [-18.59°S, -39.73°E]	Brazil	Redação Folha Vitória (2015)	Sub	Reported from the river mouth at Conceição da Barra
57	**B**	**Doce River Estuary** [-19.55°S, -39.84°E]	Brazil	ICMBIO (2016); Oliveira et al. (2020)	U	Massively influenced in 2015 by an ecological disaster after the bursting of dams holding off mining wastewater
58	**B**	**Cananêia Lagoon Estuary** [-25.04°S, -47.93°E]	Brazil	Sadowsky (1971); Schaeffer-Novelli et al. (1990)	N Y-O-Y Juv Ad	Sadowsky (1971) reported this locality as a verified nursery area of *C. leucas*, by evidence of pregnant females
59	**B**	**Canal do Superagui** [-25.37°S, -48.24°E]	Brazil	Santos & Gadig (2009)	Juv	Part of the Lagamar estuary system
60	**B**	**Patos Lagoon Estuary** [-31.06°S, -51.41°E]	Brazil	Soto & Nisa-Castro-Neto (1993, 1998); Biazon (2014)	Ad	Largest lagoon system in South America, with varying salinities
61	**B**	**River Plate** (= Río de la Plata) [-35.00°S, -57.36°E]	Uruguay / Argentina	Chiaramonte (1998); Menni & Lucifora (2007)	U	Large estuary/confluence of the Uruguay and the Paraná rivers

a particular river. Van den Berghe (2015) supposed the presence of sharks in the Punta Gorda River (Nicaragua) in the Caribbean Lowlands of Nicaragua, but was not able to make a verified record. Bussing (1966) listed *C. leucas* as a component of the freshwater fishes of Costa Rica based on information by reliable observers, but without providing a certain locality. Alpirez (1984) and Angulo (2013) listed *C. leucas* as a component of the freshwater fish fauna of Costa Rica, also without naming a certain locality. Angulo & Farah-Pérez (2018) named members of the family Carcharhinidae (in all likelihood *C. leucas*) as migratory fishes in freshwater ecosystems in Costa Rica. Cala (1990), presumably referring to *C. leucas*, reported the taxon Carcharhinidae for Colombian freshwaters of the Magdalena and Amazon River basins. For the inland waters of the Orinoco River (Venezuela) there are only a few reports in the literature for *C. leucas*, but, interestingly, there are some cartographic records

of *C. leucas* for this river in some distribution maps like the one provided by Van der Sleen & Albert (2018). Thus, documented occurrences in the inland waters of this river system are rare. However, Anonymous (2013) reported sporadic captures of *C. leucas* by fishers from the Orinoco River, Lake Maracaibo, and from purely fresh waters at the mouth of the Catatumbo River, which is tributary to Lake Maracaibo, but these are unconfirmed records. Springer (1950: 6) commented, for *C. leucas*: "At the mouth of the Orinoco River adults are found in considerable numbers". Le Bail et al. (2012), Mol (2012), and Mol et al. (2012) did not provide any riverine or estuarine records of *C. leucas* for Suriname and French Guiana. Mol (2012) did not report occurrences of *C. leucas* in inland waters of Suriname, but with the common knowledge of intrusions of *C. leucas* in tropical rivers he emphasized that there were no recorded incidents between sharks and swimmers in the Suriname River.

No. 5: At the present state of knowledge, the only river in Honduras with a verified freshwater record of *C. leucas* (Matamoros et al. 2009). The only reliable scientific record for this river was based on a photograph displayed by Strong (1934: 46) of a "fresh-water shark". Moreover, Strong (1934: 47) reported: "While fishing here, some 180 miles from salt water, we caught a 4-foot fresh-water shark, the first to be recorded from these rivers." Strong and his expedition team caught this specimen at the confluence of the Patuca River with the Yapowas Creek. Despite the circumstance that only this single record exists for this Central American river, the presence of sharks in the Patuca River seems to be well-known to local fishers, as a study based on interviews by Esselman & Opperman (2010) revealed; fishers also reported rarely captures of *C. leucas* from the Patuca River.

No. 9: The first observation of freshwater sharks in Lake Nicaragua by Europeans was made in 1535 by Gonzalo Fernández de Oviedo, a Spanish historiographer of the American Indies (Burke 1974, 1979). Interestingly, earlier, in 1526, Oviedo reported sharks from rivers of Central America, unfortunately without naming precise localities, but it appears from the context that he was referring to the mainland around Panama (Jones 1985). The sharks and the sawfishes of Lake Nicaragua were mentioned after the report of Oviedo by several early travelers and writers, but the first scientific treatment of both in a scientific journal appears to be that of Gill & Bransford (1877). Belt (1874: 4, 38) observed large sharks swimming at the outflow of Lake Nicaragua, i.e., the entrance of the San Juan River, and stated: "Beside the alligators, large freshwater sharks appear to be common in the lake." Herre & Boeseman (1956) critically discussed the ability of sharks to pass the rapids in the upper San Juan River and reasoned that these impediments do not prevent sharks from entering Lake Nicaragua.

Geological studies of the area of Nicaragua by Riedel (1976) amplified the results of Thorson's tagging program, suggesting that the freshwater sharks of Lake Nicaragua must have an Atlantic origin. In the inland waters of Nicaragua, a natural physical barrier prevents the migration of sharks from Lake Nicaragua into Lake Managua due to a 3.7 m high waterfall on the Tipitapa River, a non-stable, periodical outlet only under flooding conditions, which prevents elasmobranchs to move into the lake (Thorson 1976a; Villa 1976). In former times, the entire stretch of the lake was occupied by *C. leucas*. Specimens of *C. leucas*, which were tagged by Thorson (1973) in the San Juan/Colorado river system, were recovered at the far end of Lake Nicaragua at the mouth of the Tipitapa River. Further historical records were made from the northwest end of Lake Nicaragua at Los Cocos and Zapatera Island (Thorson 1973; Watson & Thorson 1976), at the greatest known distance to the ocean (~220 miles = 345 km). Camacho & Gadea (2005) reported catches of *C. leucas* from San Carlos and the Solentiname Archipelago at the southern end of Lake Nicaragua.

No. 32: There were earlier indications of the presence of *C. leucas* in the Magdalena River (Colombia) before Dahl (1971) verified *C. leucas* in this river, namely by Miles (1945, 1947). Miles (1945: 453) stated: "*Carcharinus* [sic] sp. (?). – Information obtained from fishermen at Calamar would seem to indicate that a species of shark ascends the Magdalena River at least as far as the junction with the Dique Canal, 112 kilometers from the ocean." Later on, Miles (1947) also mentioned a shark in the fish fauna of the Magdalena River ("*Carcharhinus* spec."), but did not provide any distributional or biological data. De Carvalho & McEachran (2003: 14) also mentioned a shark occurrence for the Magdalena River, but they referred to the old information provided by Miles (1945, 1947: "*Carcharhinus* spec.") and delivered no further information. Ramírez & Davenport (2013) reported that sharks, particularly of the genus *Carcharhinus* and mainly *C. leucas*, venture into Colombian rivers and that they have been reported to venture into some northern rivers of Colombia (presumably the Atrato, Sinú, and Magdalena Rivers).

No. 34: Remarkably, for Lake Maracaibo, Schultz (1949: 9) commented: "In Lago de Maracaibo, sharks, sawfishes, and large stingrays were reported, but I did not have an opportunity to fish for these. Sharks are caught by fishermen as far south as off the mouth of the Río Santa Ana. The occurrence of sharks in fresh-water lakes with access to the sea is not confined to Lago de Maracaibo. In Lake Nicaragua, *Eulamia nicaraguensis* occurs in abundance and reaches a large size." a regional fisheries survey revealed that *C. leucas* was the only registered shark species in Lake Maracaibo (Tavares & Sánchez 2012).

No. 41: For the Peruvian, Brazilian, and Colombian Amazon, Thorson (1972a) delivered a detailed overview of locations and collectors of *C. leucas* along the river, and Soto & Nisa-Castro-Neto (1998) gave a detailed review of *C. leucas* records in Brazil, mainly from the Amazon river system. Thorson (1972a) summarized all records of *C. leucas* in the Amazon river system until 1972. a detailed map with records of *C. leucas* in the Amazon Basin and an extensive bibliography of this species in Brazil was delivered by Soto (2001). Reports estimate that eight to 10 sharks per year are caught near Leticia (Colombia) and sold in local markets (Thorson 1972a). Specimens of *C. leucas* do not appear to occur in large numbers at any point in the Amazon Basin, but they can be looked for occasionally in the Amazon River proper as well as its major tributaries at any place in the lowlands where the water temperature is suitable and the elevation gradient is moderate (Ramírez & Davenport 2013). Even Rosa & Lima (2005) reported that *C. leucas* occasionally enter freshwaters in the Amazon Basin. Verified occurrences of *C. leucas* exist as far as Iquitos (Peru) according to Myers (1952), who identified a single specimen by a photograph, and farther upstream from Pucallpa (Peru), at the confluence of the Ucayali and Marañon rivers in the foothills of the Peruvian Andes, according to Thorson (1972a). Further records of *C. leucas* downstream the Amazon River were made at Leticia (Colombia), Manaus, Juruti, Santarém, and Belém (Brazil) (Soto & Nisa-Castro-Neto 1998; Soto 2001; Carneiro 2016; Fig. 2A). The specimen of the Colombian record from Leticia (catalog no.: CMNFI 1974-0095.1) was collected by C. G. Gruchy in 1973 and later determined by the collector in 1974 as *C. leucas*. There exists photo material of a voucher specimen (adult female, 2.3 m TL, 118 kg) collected from the Solimões River (the upper stretch of the Amazon River above the confluence of this river with

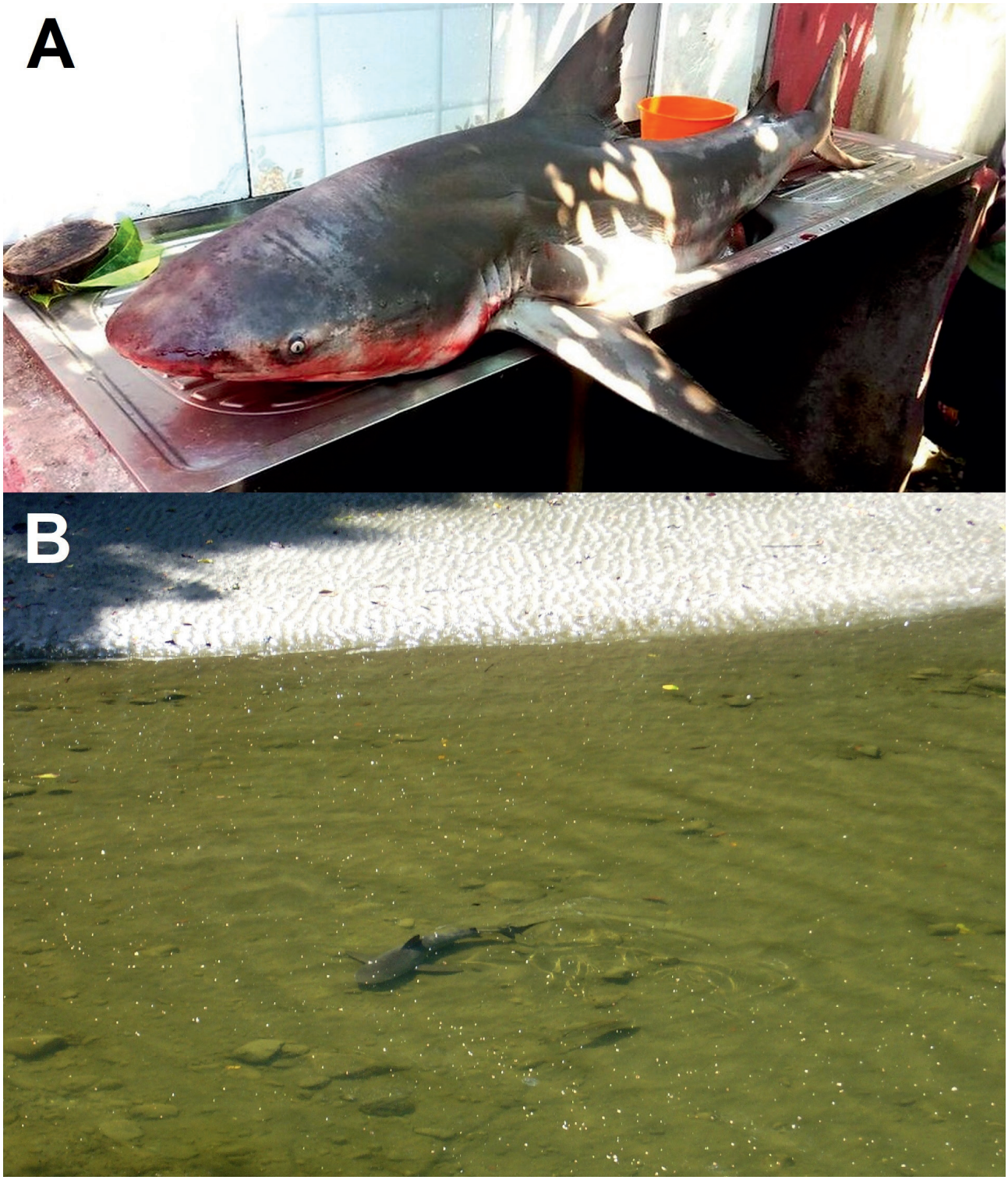

Fig. 2. *Carcharhinus leucas* Valenciennes. – **A.** Subadult male specimen (~1.5 m TL) captured on 29 November 2016 by local fishers along the Amazon River (Table 3, No. 41) at Pinduri (Santarém, Pará, Brazil) (photo © Jeso Carneiro). The record of the farthest freshwater penetration by *C. leucas* (5,080 km) was made in the Amazon River. Although *C. leucas* records in this major river system are a rarity, these occurrences document its repeated use by this species. **B**. Juvenile specimen (~70 cm TL) swimming in shallow water on the banks of the Sirena River Estuary, Costa Rica. This estuary functions as a nursery ground for this species (Table 4, No. 7). © Pedro Francisco Navarro Jimenez

the Rio Negro) at Irinduba, nearly 30 km from Manaus, in the collection of the Itajaí Valley Museum of Oceanography, Itajaí, Brazil (catalog no.: MOVI 10179(1), collected by W. Damasceno, det. Soto; Soto & Mincarone 2004). Although specimens of *C. leucas* are sometimes found at the fish markets of Santarém, they are not utilized as food, but possibly kept there as tourist attractions (Ferreira et al. 1996). Moreover, from a deeper scientific viewpoint, Roberts (1972: 143) summarized: "Specimens of sharks and sawfishes from the Amazon River have yet to be examined by persons competent to identify them." However, although the presence of *C. leucas* in the Amazon river systems is well-known today (Thorson 1972a; Campbell et al. 2006), there is a lack of data about the utilization and function of the tropical Brazilian river systems as nursery grounds for *C. leucas*, and records from the Amazon Basin are scarce (Feitosa & Nunes 2020).

For the Amazon Basin, Cavalcanti et al. (2019) listed *C. leucas* as a member of a group of marine-derived aquatic biota. Perrin et al. (2002) listed *C. leucas* as a potential predator on the Amazon dolphin (*Sotalia fluviatilis* Gervais & Deville, 1853). Probably, *C. leucas* occurs in further large tributaries of the Amazon River in the lowlands of the Amazon Basin that are not interrupted by human impediments and have a connection with the ocean. Rivers with suitable water parameters and a connection to the ocean, situated within the Amazon Basin, with a possible utilization by *C. leucas*, are the following: Araguaia, Iriri, Curuá, Juruena, Purús, Juruá, Javary, Marañon, Cuminá, Maicuri, Paru, Jari, Caquetá, Putumajo, Japurá, Trombetas, Napo, and Araguari. In future ichthyological investigation on these rivers, *C. leucas* should be expected or at least considered.

Ferreira (1993) reported that *C. leucas* is present in the Amazon and Madeira rivers, but without a confirmed presence in the Trombetas River, the study river of that author. Santos & Val (1998) reported *C. leucas* from Amazonia, but without naming a certain river. For the Rio Negro, one of the largest confluences of the Amazon, Thorson (1972a, 1976a) considered that probably neither sharks nor sawfishes occur there as a result of the dominating water parameters like acidity and hardness, but also as a result of the low productivity of the ionic-rich "black water" of this river, which may exclude the presence of *C. leucas* there. Maybe the distribution of *C. leucas* is restricted to the "white water" rivers of the Amazon river system. However, until today, no records of *C. leucas* for the Rio Negro are known (Beltrão et al. 2019). In contrast to the speculations of Thorson for the absence of *C. leucas* from black water rivers in Amazonia, Goulding et al. (1988) reported the rich fish life in the Rio Negro and pointed out numerous piscivorous groups from the Amazon Basin that are present within it, so probably there is enough food available to attract sharks and sawfishes.

Nowadays, intensive hydropower dam-building activities in the Andean Amazon Basin, including the Ucayali River, are endangering its unique freshwater fish fauna and are limiting the migrations of fishes and therefore the connectivity of populations (Anderson et al. 2018), so *C. leucas* is probably affected by the negative ecological influence of this strong human impact.

No. 46: In the Amazon/Tocantins estuaries, juveniles of *C. leucas* are of commercial importance for artisanal fisheries. Juvenile *C. leucas* have been commercially targeted and tons of sharks are landed every year (Castro 2009; Karl et al. 2011). Results of the investigations by Souza-Araujo et al. (2021) suggest that the Amazon River mouth plays an important ecological role as a nursery area for this species in a region that is highly exploited by fisheries.

No. 47: Wosnick et al. (2021) reported *C. leucas* from São Luís (Maranhão) at the mouth of the Mearim River, which is part of the Brazilian Amazon coast.

Table 4. Occurrences of *Carcharhinus leucas* in South and Central American rivers, lakes, estuaries, and lagoons: Pacific Ocean coast. Abbreviations: WC = water conditions, F = freshwater, B = brackish water up to hypersaline conditions, F/B = salinity gradient from fresh to brackish, LHS = life history stage, Ad = adult, Sub = subadult, Juv = juvenile, Y-O-Y = young-of-the-year, N = neonate, U = unknown.

No.	WC	Toponym	Country	References	LHS	Comments
1	F	**Lempa River** [13.25°N, -88.82°E]	El Salvador	Thorson (1976a)	U	-
2	B	**Tamarindo Estuary** (= Estero de Playa Grande) [10.30°N, -85.83°E]	Costa Rica	Ortiz-Araya (2011); Ortiz-Araya et al. (2018)	U	An outlet of the Tamarindo River with brackish water
3	B	**Coyote River Estuary** [9.77°N, -85.26°E]	Costa Rica	Chávez-Calderón (2017)	Juv	An outlet of the Jabillo River with brackish water
4	F	**Térraba River** (= Rio Grande de Térraba) [8.97°N, -83.59°E]	Costa Rica	Angulo et al. (2013)	U	-
5	F	**Sierpe River** [8.77°N, -83.62]	Costa Rica	Bussing (2002); Valerio-Vargas (2018)	U	Recorded as far as Sierpe, 10 km from the ocean (Bussing 2002)
6	F	**Sirena River** (= Rio Corcovado) [8.48°N, -83.59°E]	Costa Rica	Bustamante & Lamilla (2006); Lopez (2016)	Juv	-

No.	WC	Toponym	Country	References	LHS	Comments
7	**B**	**Sirena River Mouth / Estuary** [8.47°N, -83.59°E]	Costa Rica	Winemiller (1983); Fonseca (2010); Gilbert et al. (2016)	Juv Ad	Nursery ground of *C. leucas* (Gilbert et al. 2016)
8	**B**	**Ensenada Santa Cruz** [7.62°N, -81.76°E]	Panama	Vega & Villarreal (2003)	U	Estuary of the Santa Cruz River (Coiba Island)
9	**F**	**Santa Maria River** [8.09°N, -80.48°E]	Panama	Cooke & Ranere (1999)	U	Evidence of *C. leucas* derived by fish remains of Precolumbian fishing activities in this river; verified inland record from Sitio Sierra in freshwater stretches of the river
10	**F**	**Panama Canal** [8.96°N, -79.57°E]	Panama	Bigelow & Schroeder (1948); Schwartz (1958a); Boeseman (1964); Garrick (1982); Compagno (1984); Keller (1987); McEachran & Fechhelm (1998); Bussing (2002); Voigt & Weber (2011); Ebert & Stehmann (2013); Lamar University (2018)	Juv	A verified record of a ~110 cm TL female from Miraflores Locks (Bigelow & Schroeder 1948; Boeseman 1964; Garrick 1982)
11	**F**	**Lake Bayano** [9.15°N, -78.78°E]	Panama	Montoya & Thorson (1982); Candanedo & D'Croz (1983); Flores De Gracia et al. (2009)	Ad	A man-made freshwater impoundment. Bull sharks are extinct at this location due to a river closure by the dam building
12	**F**	**Chepo River** [9.06°N, -79.08°E]	Panama	Montoya & Thorson (1982)	Ad	Drainage of Lake Bayano (No. 11)
13	**F**	**Guayas River** [-2.26°S, -79.84°E]	Ecuador	Starks (1906); Garrick (1982)	Juv Sub	Reported from Guayaquil (Starks 1906; Garrick 1982)

Additions to Table 4

Thorson (1976a) reported, for the Pacific side of Central America, the occurrence of sharks (species not identified, but probably *C. leucas*) from further rivers not mentioned in Table 4, based on reports of fishers, local residents, and ichthyologists. These include Goascoran River (El Salvador/Honduras), Choluteca River (Honduras), and Grande de Térraba River (Costa Rica).

Bussing (1966) listed *C. leucas* as a component of the freshwater fishes of Costa Rica based on information by reliable observers, but without providing a certain locality. Gilbert et al. (2016) reported, for Costa Rica's Osa region, which includes the Sirena River and its estuary (Table 4, Nos. 6, 7), that estuaries are limited in extent there and under the strong tidal influence, and that although small, these estuaries are highly productive habitats, important as nursery areas and foraging habitats for *C. leucas*. Cooke & Jiménez (2008) reported that *C. leucas* travels considerable distances inland in the Tropical Eastern Pacific, including the biogeographical province of Santa Maria, Panama. Lasso et al. (2011b) reported *C. leucas* from continental waters of the Pacific coast of Colombia, but without naming any precise locality.

Nos. 11, 12: Nowadays, dam buildings prevent the migration of sharks into Lake Bayano, an artificial impoundment founded in the 1970s (Montoya & Thorson 1982). Specimens of *C. leucas* were trapped in the lake after the dam was built (Montoya & Thorson 1982), with the long-term perspective of extinction of this local population. However, Montoya & Thorson (1982) showed that *C. leucas* can live in freshwater for extended periods, as they found dead specimens (mature females) four and five years after the closure of the dam wall. Currently, however, it is supposed that there are no longer sharks in Lake Bayano as the entry to this lake is presently closed by a dam wall. The former presence of mature female *C. leucas* in this lake may indicate that it once was a nursery (Montoya & Thorson 1982). The upper stretch of the Chepo River, the drainage of Lake Bayano, is named Bayano River, and drains into the lake. Thorson (1976a) listed the Bayano River as a locality with sharks, but it is unclear if he was referring to the Chepo River or to the upper reaches of the Bayano River, farther inland.

No. 13: Additionally, Orcés (1959) reported *C. azureus* (= *C. leucas*) from Puná Island, at the mouth of the Guayas River.

Additions to Table 5

There is contradictory information regarding the occurrence of *C. leucas* in some freshwater localities in Benin. In the dataset provided by the GBIF (2018a), there is an entry with a record for the Pendjari River at Porga (Benin, Burkina Faso), which

Table 5. Occurrences of *Carcharhinus leucas* in African rivers, lakes, estuaries, and lagoons: Atlantic Ocean coast. Abbreviations: WC = water conditions, F = freshwater, B = brackish water up to hypersaline conditions, F/B = salinity gradient from fresh to brackish, LHS = life history stage, Ad = adult, Sub = subadult, Juv = juvenile, Y-O-Y = young-of-the-year, N = neonate, U = unknown.

No.	WC	Toponym	Country	References	LHS	Comments
1	**B**	**Khnifiss Lagoon** (=Baie de Khnifiss) [28.05°N, -12.23°E]	Morocco	Beaubrun (1976); Schouten et al. (1988); Falcón et al. (2002)	Ad	Falcón et al. (2002) published a picture of a captured adult female. This lagoon may function as a nursery for *C. leucas* in the northeastern Atlantic (Schouten et al. 1988)
2	**F**	**Senegal River** [16.06°N, -16.48°E]	Mauritania / Senegal	Steindachner (1870); Boeseman (1964); Thorson (1970b); Daget (1984)	Juv	Reported as far up the river as Dagana, ~175 km from the ocean, under the name *Carcharias lamia* (Steindachner 1870)
3	**F**	**Saloum River** [14.00°N, -16.70°E]	Senegal	Rochebrune (1883)	U	-
4	**B**	**Sine-Saloum Estuary** [13.77°N, -16.65°E]	Senegal	Diouf (1996); Trape (2008); Simier (2013); Ecoutin et al. (2013, 2014); Simier et al. (2017)	Juv	Estuary system with brackish to hypersaline water conditions (> 40‰) due to drought and intense evaporation
5	**F**	**Gambia River** [13.45°N, -16.13°E]	Gambia	Svensson (1933); Daget (1960, 1961, 1984); Boeseman (1964); Thorson (1970b); Budker (1971); Compagno (1984, 2016); Séret (1990, 2003); Simpfendorfer & Burgess (2005, 2009); De Carvalho et al. (2007); Diallo & Thiam (2010); Voigt & Weber (2011); Ebert & Stehmann (2013); ReefQuest Centre for Shark Research (2018)	Juv	Reported from McCarthy Island at 290 km from the ocean by Svensson (1933), as *Carcharhinus zambezensis*. Svensson (1933) caught three specimens nearly 2.5 feet in length. Sharks were well-known to the natives of Basse and Fattatenda, localities that lie upstream from McCarthy Island (Budker 1971)
6	**B**	**Gambia River Mouth** [13.47°N, -16.56°E]	Gambia	Trape (2008)	U	-
7	**B**	**Casamance River Mouth** [12.56°N, -16.72°E]	Senegal	Trape (2008)	U	-
8	**B**	**Toho Lagoon** (= Lac Toho) [6.61°N, 1.77°E]	Benin	Kingbo & Kiki (2016)	U	Brackish water
9	**B**	**Lake Nokoué** [6.43°N, 2.44°E]	Benin	Kingbo & Kiki (2016)	U	Recently, a man-made salinization turned the freshwater into brackish
10	**F**	**Aho Channel** [10.93°N, 1.11°E]	Benin	Kingbo & Kiki (2016)	U	Tributary of No. 11
11	**F**	**Ouémé River** [6.51°N, 2.54°E]	Benin	No reference but it is logical under geographic circumstances	U	Connection between the Aho Channel and the ocean

No.	WC	Toponym	Country	References	LHS	Comments
12	**F**	**Niger River** [5.14°N, 5.41°E]	Benin / Nigeria	Kingbo & Kiki (2016)	U	No verified records by voucher specimens or photographs are available from this river; this report derives only from an online reference; therefore the record is not confirmed
13	**F**	**Sota River** [10.69°N, 3.23°E]	Benin	Kingbo & Kiki (2016)	U	Tributary of the Niger River (No. 12)
14	**F**	**Mékrou River** [12.40°N, 2.82°E]	Benin / Burkina Faso / Nigeria	Kingbo & Kiki (2016)	U	Tributary of the Niger River (No. 12)
15	**F**	**Ogooué River** [-01.01°S, 8.91°E]	Gabon	(conditionally even Loubens 1964); Boeseman (1964); Thorson (1970b); Budker (1971); Garrick (1982); Compagno (1984, 2016); Gilbert et al. (1989); Séret (1990, 2003); Mbega & Teugels (2003); De Carvalho et al. (2007); Voigt & Weber (2011); Ebert & Stehmann (2013); Cutler et al. (2020)	Juv	-
16	**F**	**Lake Onangue** [-0.95°S, 10.09°E]	Gabon	De Carvalho et al. (2007)	U	Associated with the Ogooué River (No. 15)
17	**F**	**Lake Ezanga** [-1.02°S, 10.19°E]	Gabon	De Carvalho et al. (2007)	U	Associated with the Ogooué River (No. 15)
18	**B**	**Nkomi Lagoon** [-1.51°S, 9.24°E]	Gabon	Mbega & Teugels (2003); De Carvalho et al. (2007)	U	A lagoon with numerous freshwater inflows
19	**F**	**Congo River** (= Zaire River) [-6.07°S, 12.46°E]	Congo / Dem. Republic of the Congo	Keller (1987); Barreiros & Gadig (2011); Lamar University (2018)	U	No verified records and no collected voucher specimens or photographs of *C. leucas* are available from this river; this report derives only from literature and online references and requires confirmation
20	**F**	**Cuanza River** (= Kwanza River) [-9.34°N, 13.15°E]	Angola	Skelton (2019)	U	Skelton (2019: 214) reported: "Some species such as the Bull Shark (*Carcharhinusleucas*) and the Atlantic Tarpon (*Megalops atlanticus*) are well known as gamefish from this river."

is a tributary to the upper reaches of the Volta River (Ghana). The Volta river system includes Lake Volta (Ghana), which has a dam at the outlet of the lake into the lower Volta River. This impediment offers a barrier, which excludes the migration of anadromous fish species into the upper reaches of the Volta system. Therefore, a migration of *C. leucas* into the Pendjari River would appear to be impossible and a plausible explanation would be required for this entry, otherwise it should be considered an erroneous database entry.

For *C. leucas* in Gabon, Ogandagas (2003: 77) noted: "This species has been captured in the Lambaréné lakes." This information is vague as the Lambaréné lakes in the Ogooué river system include Lake Zilé, Lake Azingo, and further small lakes like Lake Nkonié and Lake Ouambé, so the exact location of

the report by Ogandagas (2003) cannot be localized. However, it is almost certain that *C. leucas* occurs also in additional lakes associated with the Ogooué river system, which is rich in tributary waters. Additionally, Whitfield (2005a) reported *C. leucas* in the species inventory of western and central African tropical estuaries.

Nos. 3, 4: At the river mouth of the Saloum River in the Sine-Saloum Estuary, the estuary is divided into numerous small sea arms, so-called "Bolongs", with ranging and strongly varying water conditions from hypersaline to salty and brackish as an effect of high evaporation and the mix of tidal and fresh water that flows toward the ocean from the river. In this suitable habitat for *C. leucas*, there is evidence of its presence from a locality named Bolong Bamboung, by Simier (2013), Ecoutin et al. (2014), and Simier et al. (2017).

No. 12: There are reports of a shark attack in the Forcados River at Burutu (Information Nigeria 2012), even though the involved species of shark remains unclear. Furthermore, a photo-documented catch at Port Harcourt in the Niger Delta exists (Nairaland Forum 2017), which very likely illustrates a *C. leucas* (diagnostic features: small eyes, blunt and rounded snout). It is unclear if these incidents took place in pure freshwater or brackish water, because the Niger Delta is an ecocline between riverine and marine ecosystems.

No. 15: Loubens (1964: 11) reported occasional catches by fisher nets of unspecified sharks (*Carcharhinus* sp.) from the Ogooué river basin, at the town of Lambaréné, and the adjacent southern lakes, which he suspected "to be *Carcharhinus leucas* Müller Henle". Cutler et al. (2020) considered *C. leucas* as a species that will be negative affected by habitat loss and limited in its distribution due to future dam development in rivers of the Ogooué basin.

No. 19: Although there exist a few reports of *C. leucas* for this major African river (Keller 1987; Lamar University 2018), there are neither voucher specimens collected from this river nor photo material that could verifiably confirm the presence of *C. leucas* in this river. Information on extent of freshwater incursions is missing too. However, a verified record of a juvenile *C. leucas* collected by I. Marée at the mouth of the Congo River at Banana Point in 1953 (catalog no.: MRAC 37417) was investigated and verified as *C. leucas* by Garrick (1982). Due to the environmental conditions of the Congo River and to the ecological behavior and distribution of *C. leucas* along the West African coast, the occurrence of *C. leucas* in this river system can be considered very likely.

Table 6. Occurrences of *Carcharhinus leucas* in African rivers, lakes, estuaries, and lagoons: Indian Ocean coast, including Madagascar and Réunion Island. Abbreviations: WC = water conditions, F = freshwater, B = brackish water up to hypersaline conditions, F/B = salinity gradient from fresh to brackish, LHS = life history stage, Ad = adult, Sub = subadult, Juv = juvenile, Y-O-Y = young-of-the-year, N = neonate, U = unknown.

No.	WC	Toponym	Country	References	LHS	Comments
1	**F**	**Ravine des Poux (Saint-Leu)** [-21.15°S, 55.28°E]	Reunion Island (France)	S. Jaquemet (2018), pers. comm.	Juv	A small ravine with only a temporary freshwater flow. Juveniles of *C. leucas* were observed in this small creek (S. Jaquemet 2018, pers. comm.)
2	**B**	**Saint-Etienne River Mouth** (= Riviere Saint-Etienne Estuaire) [-21.30°S, 55.40°E]	Reunion Island (France)	Guyomard (2016)	Juv	Juveniles were captured at this location (Guyomard 2016)
3	**F**	**Lake Kinkony** [-16.14°S, 45.83°E]	Madagascar	Kiener (1963); Kiener & Thérézien (1963); Thérézien (1963); Moreau (1987)	Juv	-
4	**F**	**Mahavavy River** [-15.84°S, 45.81°E]	Madagascar	Kiener (1963)	Juv	Drainage of Lake Kinkony (No. 3)
5	**F**	**Betsiboka River** [-16.06°S, 46.58°E]	Madagascar	Taniuchi et al. (2003)	Juv	-
6	**F**	**Manakara River** [-22.15°S, 48.01°E]	Madagascar	Kiener (1963)	Juv	-
7	**F**	**Canal des Pangalanes** [-22.13°S, 48.01°E]	Madagascar	Kiener (1963)	Juv	A canal that consists of a series of natural rivers, waterways and human-made lakes. The canal begins at the mouth of the Manakara River (No. 6)

No.	WC	Toponym	Country	References	LHS	Comments
8	**B**	**Bay of Saint-Augustin** [-23.56°S, 43.74°E]	Madagascar	McVean et al. (2006)	Juv	Drainage of the Onilahy River
9	**F**	**Jubba River** (= Juba River) [-0.24°S, 42.63°E]	Somalia	Garrick (1982)	Juv	Verified as far as Dolo (= Doolow) (Garrick 1982), 875 km from the ocean
10	**F**	**Galana-Sabaki River System** [-3.16°S, 40.14°E]	Kenya	Okeyo (1998)	U	In the lower reaches (Okeyo 1998)
11	**F**	**Pangani River** [-5.43°S, 38.98°E]	Tanzania	Tanesco (1994); IUCN Eastern Africa Programme (2009)	U	Reported as far as Jambe (Tanesco 1994)
12	**F**	**Ruenya River / Luenha River System** [-17.24°S, 33.08°E]	Mozambique / Zimbabwe	(conditionally even Selous 1893); Jubb (1967); Pienaar (1968); Garrick (1982); Compagno (1984); Fischer & Bianchi (1984); Bell-Cross & Minshull (1988); Marshall (2000); Voigt & Weber (2011)	Juv	Reported 580 km from the ocean (Pienaar 1968). At the confluence with the Cauresi River, the name Ruenya River changes into Luenha River, which drains into the Mazowe River (No. 13), which in turn drains into the Zambezi River (No. 15)
13	**F**	**Mazowe River** (= Mazoe River) [-16.53°S, 33.43°E]	Mozambique	Pienaar (1968)	U	One specimen was caught at the junction of this river with No. 12 (Pienaar 1968)
14	**F**	**Shire River** [-16.55°S, 35.14°E]	Malawi / Mozambique	Pienaar (1968); Tweddle & Willoughby (1979); Fischer & Bianchi (1984); Mepham (1987a); Skelton (2001)	Juv	Tributary to the Zambezi River (No. 15). Tweddle & Willoughby (1979: 20) reported: "…up to Chiromo and beyond."
15	**F**	**Zambezi River** [-18.59°S, 36.25°E]	Mozambique / Zimbabwe / Zambia	Peters (1852, 1868); Von Martens (1869); Boulenger (1905, 1909); Barnard (1925); Smith (1949, 1952); Jackson (1961); Jubb (1961, 1967); Davies (1962, 1964); Boeseman (1964); D´Aubrey (1964); Thorson (1970b); Budker (1971); Bass et al. (1973); Bell-Cross (1972a, 1976); Bass (1978); Johnson (1978); Berra (1981, 2007); Daget (1984); Fischer & Bianchi (1984); Keller (1987); Bell-Cross & Minshull (1988); Paepke & Schmidt (1988); Ellis (1989); Hughes & Hughes (1992); Whitfield (1998); Bills (1999); Marshall (2000); Timberlake (2000); Skelton (2001); Martin (2005); Simpfendorfer & Burgess (2005, 2009); The World Bank (2010); Voigt & Weber (2011); Whitfield et al. (2012); Madiquida (2015); Coetzer (2017)	Y-O-Y Juv Sub Ad	(catalog no.: ZMB 4468, Berlin Museum, Paepke & Schmidt 1988; cited in Garrick 1982 under the catalog no.: ISZZ 4468), which was collected and reported by Peters (1852) from this river, was taken at Tete, 418 km from the ocean (Fig. 1). Smith (1949: 42) reported *C. leucas* for this river under the name "*Eulamia lamia*"

No.	WC	Toponym	Country	References	LHS	Comments
16	**F**	**Buzi River** [-19.88°S, 34.74°E]	Mozambique	Bell-Cross (1972b, 1973)	U	Also reported by local fishers from this river (Froese & Pauly 2018a)
17	**F**	**Save River** (incl. Runde = Lundi River) [-20.92°S, 35.06°E]	Mozambique / Zimbabwe	Bell-Cross & Minshull (1988); Murray (2016)	U	Reported from near the Save/Runde confluence (Bell-Cross & Minshull 1988)
18	**F**	**Limpopo River** [-25.20°S, 33.51°E]	Mozambique / Zimbabwe	Davies (1964); Boeseman (1964); Pienaar (1968); Bass et al. (1973); Compagno (1984); Fischer & Bianchi (1984); Hughes & Hughes (1992); Whitfield (1998); Skelton (2001); Berra (2007); Voigt & Weber (2011); Whitfield et al. (2012)	Sub Ad	Hughes & Hughes (1992) reported that *C. leucas* penetrates the Limpopo River as far as Zimbabwe State
19	**F**	**Luvuvhu River** (= Levubu River) [-22.42°S, 31.30°E]	South Africa	Pienaar (1968); Roux et al. (2008); Siyabona Africa (2017)	Juv	Tributary of the Limpopo River (No. 18). One specimen (~124 cm TL) was caught at the junction with the Limpopo River (No. 18) at Pafuri, 480 km from the ocean (Pienaar 1968)
20	**F**	**Sabie River** [-25.32°S, 32.29°E]	Mozambique / South Africa	Bass et al. (1973); Fischer & Bianchi (1984)	U	Tributary of the Komati River (No. 21)
21	**F**	**Komati River** (= Incomati River) [-25.81°S, 32.72°E]	Mozambique	Weeks et al. (1990)	U	Drainage of the Sabie River (No. 20)
22	**F**	**Pongola River** (= Pongolo River, Phongolo River) [-26.85°S, 32.34°E]	Mozambique / South Africa	Crass (1964); Pienaar (1968); Bass et al. (1973); Whitfield (1998); Skelton (2001); Kyle (2002); Froese & Pauly (2018a); Daly et al. (2021)	Sub	Recorded at the confluence with the Usutu River (No. 23), at 80 km from the ocean (Pienaar 1968)
23	**F**	**Maputo River** (= Usutu River) [-26.19°S, 32.68°E]	South Africa	Crass (1960)	U	Reported as *C. zambezensis* in Crass (1960)
24	**B**	**Kosi River System** (= Kosi Bay) [-26.89°S, 32.88°E]	South Africa	Bass et al. (1973); Blaber (1978); Bruton & Kok (1980); Daly et al. (2021)	U	An estuary system of four interlinked lakes with low salinities, ranging from fresh to brackish; Blaber (1978) reported *C. leucas* only from the estuary, not from the lakes

No.	WC	Toponym	Country	References	LHS	Comments
25	**B**	**Lake St. Lucia** (incl. Wetland Narrows) [-28.00°S, 32.45°E]	South Africa	Smith (1958); D'Aubrey (1964); Davies (1964); Thorson (1970b); Bass et al. (1973); Bass (1976, 1977, 1978); Whitfield & Blaber (1978, 1979); Bruton & Kok (1980); Day et al. (1981); Whitfield et al. (1981); Compagno (1984); Cliff & Wilson (1986); Mepham (1987b); Khalil (1995); Mann (1995, 2003, 2013); Van Niekerk & Olivier (1995); Whitfield (1996, 1998, 1999, 2005b, 2021); Crook & Mann (2002); Mann et al. (2002); Van Oordt (2006); Cyrus & Vivier (2010); Vivier et al. (2010); Cyrus et al. (2011); Van Niekerk & Turpie (2012); Perissinotto et al. (2013); Daly et al. (2021); Jordan (2021)	Y-O-Y Juv Sub Ad	Estuary/lake system. First reported from this location by Smith (1958) under the name *Carcharhinus vanrooyeni*. Bass (1978) reported that adults in the lake were exclusively females. An important nursery ground for *C. leucas* in southern Africa according to Mann (2013). Mepham (1987b: 562) stated for this location: "*Carcharhinus leucas*…penetrate the whole system."
26	**F**	**White Umfolozi River** (= White Mfolozi River) [-28.35°S, 31.97°E]	South Africa	Bourquin et al. (1971); Ezemvelo KZN Wildlife (2012); Froese & Pauly (2018a)	Juv	Upper reach of the Umfolozi River (No. 27). Reported from Siyembeni ~75 km from the ocean (Ezemvelo KZN Wildlife 2012)
27	**F**	**Umfolozi River** (= Mfolozi River) [-28.38°S, 32.42°E]	SouthAfrica	Bass et al. (1973); Daly et al. (2021)	U	The delta of this river is adjacent to the Lake St. Lucia estuary (No. 25)
28	**B**	**Mhlatuze River Estuary / Richards Bay** [-28.80°S, 32.04°E]	South Africa	Cliff & Wilson (1986); Van der Elst (1993); Cliff (1994); Weerts & Cyrus (1998); Palm (1999); Van Oordt (2006); Everett & Fennessy (2007); Beckley et al. (2008); Mann (2013); Daly et al. (2021)	Juv	Estuary with brackish water. According to Van Oordt (2006), this bay forms a nursery ground for *C. leucas*
29	**F**	**Umlalazi River** (= Mlalazi River) [-28.94°S, 31.82°E]	SouthAfrica	Bass et al. (1973); Daly et al. (2021)	U	-
30	**F**	**Matigulu (= aMatigulu) / Nyoni River System** [-29.11°S, 31.61°E]	South Africa	Daly et al. (2021)	U	-
31	**F**	**Tugela River** (=uThukela River) [-29.22°S, 31.49°E]	South Africa	Bass et al. (1973); Daly et al. (2021)	U	-
32	**F**	**Mngeni River** (= uMngeni River) [-29.81°S, 31.04°E]	South Africa	Daly et al. (2021)	U	-
33	**B**	**Durban Bay** [-29.87°S, 31.02°E]	South Africa	Bass et al. (1973); Daly et al. (2021)	U	Estuary with brackish water
34	**F**	**Umkhomazi River** (= uMkhomazi River) [-30.19°S; 30.80°E]	South Africa	Daly et al. (2021)	U	-

No.	WC	Toponym	Country	References	LHS	Comments
35	**F**	**uMzimkhulu River** (= Mzimkhulu River) [-30.73°S, 30.45°E]	South Africa	Lange (2014); Daly et al. (2021)	Y-O-Y Juv	-
36	**F**	**Mtamvuna River** (= uMthamvuna River) [-31.08°S; 30.19°E]	South Africa	Daly et al. (2021)	U	-
37	**F**	**Mtentu River** [-31.24°S; 30.04°E]	South Africa	Daly et al. (2021)	U	-
38	**F**	**Msikaba River** [-31.31°S; 29.96°E]	South Africa	Daly et al. (2021)	U	-
39	**F**	**Umzimvubu River** (= Mzimvubu River) [-31.62°S, 29.54°E]	South Africa	McCord & Lamberth (2009); McCord (2012); Van Niekerk & Turpie (2012); Mann (2013); Daly (2014); Jackson (2017); Daly et al. (2021)	N Y-O-Y Juv	Nursery area of *C. leucas* (McCord & Lamberth 2009; Mann 2013; Jackson 2017)
40	**B**	**Mtakatyi River Estuary** [-31.85°S; 29.27°E]	South Africa	Daly et al. (2021)	U	-
41	**B**	**Umtata River Estuary** (= Mtata River E., Mthatha River E.) [-31.95°S, 29.18°E]	SouthAfrica	Plumstead et al. (1989a); Harrison (2005); Daly et al. (2021)	Juv	-
42	**B**	**Xhora Estuary** [-32.15°S; 28.99°E]	South Africa	Daly et al. (2021)	U	-
43	**F**	**Mbashe River** [-32.22°S, 28.87°E]	South Africa	Plumstead (1990); Daly et al. (2021)	U	-
44	**B**	**Mbashe River Estuary** [-32.24°S, 28.90°E]	South Africa	Plumstead et al. (1989b); Schramm (1991); Whitfield (1996); Skelton & Lutjeharms (1997)	U	-
45	**F**	**Nqabara River** [-32.33°S; 28.78°E]	South Africa	Daly et al. (2021)	U	-
46	**F**	**(Great) Kei River** [-32.67°S; 28.38°E]	South Africa	Daly et al. (2021)	U	-
47	**F**	**Nahoon River** [-32.98°S; 27.95°E]	South Africa	Daly et al. (2021)	U	-
48	**B**	**(Great) Fish River Estuary** [-33.49°S, 27.13°E]	South Africa	Bass et al. (1986); Compagno & Smale (1986); Daly et al. (2021)	Ad	A river outlet with brackish water. Compagno & Smale (1986) reported an adult female *C. leucas* of 292 cm TL
49	**F**	**Swartkops River** (= Zwartkops River) [-33.86°S, 25.63°E]	South Africa	Smith (1952); Boeseman (1964); Daly et al. (2021)	U	-
50	**B**	**Knysna River Estuary** [-34.07°S; 23.05°E]	South Africa	Daly et al. (2021)	U	-
51	**F**	**Breede River** [-34.40°S, 20.84°E]	South Africa	McCord & Lamberth (2009); Van Niekerk & Turpie (2012); Mann (2013); McCord et al. (2013, 2014); Daly et al. (2021); Ebert et al. (2021)	Ad	The world record of the largest *C. leucas* (a 4 m pregnant female) is reported from this river. Simultaneously, it represents the currently southernmost record of *C. leuca*s on the African continent

Additions to Table 6

On Réunion Island, there are stories of local fishers catching juvenile *C. leucas* on the east coast at Rivière du Mât (a perennial river), and the presence of individuals in Ravine Blanche (a temporal creek) at St. Pierre on the south coast of the island. Juveniles, subadults, and adults were regularly observed together in marine habitats at Reunion Island off Etang du Gol and off Etang de St. Paul (S. Jaquemet 2018, pers. comm.). On Réunion Island, even small creeks and temporary water-filled ravines are utilized by juvenile *C. leucas* as breeding areas. Froese & Pauly (2019b) published a picture of a neonate *C. leucas* that was captured at Baie du Cap, Mauritius, near a small freshwater outlet (Rivière du Cap). Possibly, the small creeks and ravines of Mauritius also function as nursery areas for juvenile *C. leucas* in the Mascarene Islands.

Kiilu et al. (2019) reported the capture of a 1.5 m TL *C. leucas* in the vicinity of the Tana River Estuary in Kenya, so possibly this estuary/river system is also utilized by *C. leucas* as a nursery ground. *Carcharhinus leucas* is also mentioned by Eccles (1992: 26) for Tanzania, from "large coastal rivers", but without naming the particular river system; possibly, the Pangani, the Rovuma, and also the Rufiji rivers are meant. There are more reports for the Rovuma River (Tanzania) from local fishers, who have reported that Zambezi sharks (= bull sharks) come way up the river (Holgate 2006). Hughes & Hughes (1992) reported that *C. leucas* is present in most of the large rivers of Mozambique. There are unconfirmed reports by Murray (2016) of Zambezi sharks from Mozambique's and southeastern Zimbabwe's Save River and Runde River (the latter is a tributary of the first at the Mozambique/Zimbabwe border), approximately 300 km from the ocean but only prevented from migrating farther upriver by the Chivirira and Chitove Falls. Murray (2016) further reported that these sharks are bound to river pools on which the sharks rely and that the process of silting has reduced their depth, with the consequence that sharks are not seen there for years.

Bass (1978) reported that *C. leucas* has been recorded from most of the river and lake systems of the East African coast from the Zambezi River to Durban Bay. Later on, for South African *C. leucas*, Bass et al. (1986: 73) stated: "The young often going into rivers, sometimes many kilometers from the sea." Whitfield (2005a) reported *C. leucas* in the species inventories of both tropical East African and subtropical South-East African estuaries. Even Skelton (1994) listed *C. leucas* in a list of fishes associated with southern African estuaries in tropical to warm-temperate climates. Additionally, Perera et al. (2011) and Perera (2013) mentioned *C. leucas* as a breeding resident that inhabits freshwaters of the Maputaland-Pondoland-Albany region of South Africa. Pienaar (1971) reported *C. leucas* from freshwater systems of Kruger National Park in northeastern South Africa. Even Compagno et al. (1989) mentioned *C. leucas* for rivers of the Kruger National Park. Furthermore, Russell (2011) reported *C. leucas* as a primary marine and estuarine species that occasionally penetrates the freshwater systems of the Kruger National Park as a transient. Van Niekerk & Turpie (2012) presumed that additional river systems in South Africa, not listed in Table 6, may offer suitable habitats for *C. leucas*, i.e., Gouritz River, Gamtoos River, Sundays River, and Mngazana River. For some rivers of the east South African coast, there are anecdotal reports and observational evidence of shark occurences, presumably of *C. leucas*, such as Great Kei River, Mtentu River, and other rivers (R. Daly, pers. comm. 2021).

No. 10: The occurrence of *C. leucas* in the Galana-Sabaki river system probably needs verification, as Seegers et al. (2003: 20) noted, about the evidence of *C. leucas* in this river system, that "...records of *Carcharhinus leucas* (Müller & Henle, 1839)… by Okeyo (1998) are unsubstantiated and need confirmation."

No. 12: Selous (1893) reported the catch of a small-sized freshwater shark of three and a half feet (= 1.07 m TL) near the junction of the Ruenya and the Mazowe rivers, with a detailed description of the specimen but without a species determination or diagnostic features. However, the circumstances of a shark at this location in inland waters far away from the ocean, together with the size, are good arguments that this catch was a juvenile *C. leucas*. Furthermore, Selous (1893) discussed this catch with a native who told him that he knew this fish well from the Zambezi River at Tete. Selous added that there are no barriers from the ocean to the Lower Ruenya River that could prevent this shark from swimming upriver. Moreover, Selous didn't believe that *C. leucas* occurs in the Zambezi River above the Victoria Falls, a natural impediment that prevents fishes from swimming upriver (today, the Victoria Falls lie behind two man-made impediments such as the Cabora Bassa Dam wall and the Kariba Dam wall, which prevent migratory fishes from moving up the river).

No. 14: Mepham (1987a) reported *C. leucas* as common in the Shire Swamps, in the floodplain of the Shire River. There exist anecdotal reports suggesting that *C. leucas* may have once been present as a marine vagrant in the Elephant Marsh in the floodplain of the Shire River (Tweddle & Willoughby 1979), although there is no evidence that this species has been observed in the lifetime of the current generation of fishers (Turpie et al. 2016). The absence of *C. leucas* from the Elephant Marsh is most likely due to overfishing or other factors downstream (e.g., barriers), rather than to unsustainable harvesting in the Elephant Marsh itself (Turpie et al. 2016).

No. 15: Peters (1852) described (in Latin) *Carcharias* (*Prionodon*) *zambezensis* from this river. Later, Peters (1868) produced a more detailed description of the species based on a juvenile male specimen caught in 1845 in the Zambezi River at Tete. Peters (1868) underlined that the presence of this species in freshwater was remarkable. Moreover, Peters (1852, 1868) recognized that the collected specimen from this river was closely related to *Carcharhinus leucas*, which was first described by Valenciennes in Müller & Henle (1841) based on specimens collected in the Antilles. Garrick (1982) examined the 760 mm TL specimen collected by Peters from the Zambezi River and determined that it fully agrees with *C. leucas* (Fig. 1). Barnard (1925), presumably referring to Peters (1852), reported *C. leucas* under the name *C. zambesensis* in a monograph of the marine fishes of South Africa, also from Tete on the Zambezi River. Interestingly, Barnard (1925: 25) named it "River Shark" and gave further information of the size of this species as up to 760 mm TL, which indicates that Barnard was in all likelihood referring to the previous record by Peters. Current scientific investigations and records of *C. leucas* in the Zambezi River are scarce, and most reports refer to old records.

There is contrasting information regarding the reach of freshwater incursions by *C. leucas* in the Zambezi River, especially in historical times before regulation of the river. There are reports of *C. leucas* traveling distances of 1,000 km and more up the Zambezi by Bass (1978) and Daget (1984), and 1,120 km by Bass et al. (1973). These authors were presumably referring to reports of the species at Chirundu (Zambia). D'Aubrey (1964: 39) reported, for *C. leucas* in southern Africa, that "Small specimens have been caught over 300 miles [= 482 km] from the sea in the Zambezi River." Bell-Cross & Minshull (1988) reported that prior to the building of the Cabora (Cahora) Bassa Dam

(= Cabora Bassa Gorge), *C. leucas* occurred up the Zambezi River at least as far as the Kariba Gorge. The authors mentioned that *C. leucas* had been caught at Chirundu (Bell-Cross & Minshull 1988), beyond the Cabora Bassa Gorge before it was finished, more than 1,000 km from the ocean, but this record was not listed in earlier publications about the freshwater fish fauna of southern Africa (Jackson 1961; Jubb 1961, 1967). Nowadays, in the Zambezi River, the Cabora Bassa Dam wall and the Kariba Dam wall prevent *C. leucas* from migrating in the upper reaches of the river. The closure of the Kariba Dam in 1959 on the middle Zambezi and of the Cabora Bassa Dam in 1974 allows migratory fishes to travel only approximately 640 km upriver in the Lower Zambezi only. This was confirmed by Hughes & Hughes (1992), who reported that *C. leucas* penetrates the Zambezi River as far as Cabora Bassa. However, *C. leucas* may never have penetrated the Zambezi River beyond the Cabora Bassa Gorge sinces its completion (Marshall 2000).

The Cabora Bassa Gorge is conventionally regarded as a boundary for migrating fish species, particularly primary marine species like *C. leucas*, which may occur inland as far as the gorge but not beyond it (Marshall 2000; The World Bank 2010). Probably, migrations of *C. leucas* up the Zambezi River extended farther in historical times than today. Marshall (2000: 471) further noted, for *C. leucas* in the Zambezi River, that "Several recent sightings ranging from the mouth of the Micelo River to up stream of Morromeu were reported to me during the expedition. Although not positively identified as *C. leucas* (Zambezi or bull shark) this is the most likely species to enter estuarine and riverine environments." About occurrences of *C. leucas* in the Zambezi River in the recent past, Timberlake (2000: 14) noted: "The lungfish, eels and Zambezi shark are all found only in the Lower and Middle Zambezi." Furthermore, Coetzer (2017) provided photo material of a juvenile *C. leucas* captured at Tete in 2010, which is evidence that *C. leucas* still reaches as far up as the Lower Zambezi River. Jackson (1986) listed the family Carcharhinidae in his work dealing with the fish fauna of the Zambezi River; although he did not explicitly mention *C. leucas*, he was presumably referring to this species.

No. 18: For the Limpopo River, a number of shark attacks on swimmers and canoes have been reported at locations far inland and at considerable distances from the ocean, which can be attributed to *C. leucas*. Even when a species determination was not mentioned, it is very likely that specimens of *C. leucas* were involved. The Shark Research Institute (2018d) reported three incidents in 1970 (all on the same day!) at Gijana, 150 km inland, and one incident in 1961 at an undefined location at approximately 190–240 km from the ocean. In 1963 a shark, presumably *C. leucas*, bit a canoe and several other sharks bumped two other canoes at a location approximately 200 km from the ocean (Davies 1964).

No. 25: This estuarine lake system includes hypersaline (salinities of > 50‰, induced by drought) and brackish water conditions near the mouth/drainage into the Indian Ocean and freshwater conditions in regions far away from the ocean (Bass et al. 1973). *Carcharhinus leucas* has been regularly netted in this lake system at salinities up to 47‰ (Bass et al. 1973). Even Whitfield (1996) reported for the St. Lucia lake system of South Africa that specimens of *C. leucas* were regularly netted at salinities up to 47‰. Bass (1978) reported that sharks captured in the lake during times with salinities above 50‰ were in noticeably poor condition, even though food was not scarce. In African rivers and lakes, as opportunistic feeders, the food spectrum of large *C. leucas* may include young hippopotamuses. There are only a few reports of encounters of bull sharks with hippopotamuses. Green (2018) reported a rare encounter of a *C. leucas* with hippopotamuses in the iSimangaliso Wetland Park (KwaZulu-Natal; former Greater St. Lucia Wetland Park), which is a big complex of wetlands, swamps, and lakes that are connected to Lake St. Lucia in South Africa. Filming material from an encounter between a single *C. leucas* and a group of hippopotamuses exists on the internet (Internet Reference 3). Otherwise, there is little information on shark/hippopotamus interactions. In contrast, in Lake St. Lucia, pups of *C. leucas* are prey of another apex predator, the large Nile crocodile (*Crocodylus niloticus* Laurenti, 1768), which also occurs in the lake (Whitfield & Blaber 1979; Perissinotto et al. 2013; Daly et al. 2021).

The "Global Shark Attack File" (Shark Research Institute 2018a) included a couple of shark attacks that occurred in South African freshwater rivers not mentioned in Table 6. Some of the attacks happened not only in the estuaries but also inland, so specimens of *C. leucas* were probably involved in these incidents. For completeness, the rivers are named here: Bilanhlolo, Little Brak, Groot, MaKakatana, Umgeni, Kowie, Riet, and the Umlaas Canal.

Additions to Table 7

Possibly, *C. leucas* also occurs in the Indus River (Pakistan) and the Brahmaputra River (Bangladesh), two major rivers in Asia located within the coastal range of *C. leucas*, but this needs verification. Belcher (2003, 2018) discovered teeth of *C. leucas* in an ancient settlement in Pakistan's Indus River Valley at Bakalot dated ~3000–1700BC, which could be an archaeological indication of the utilization of *C. leucas* specimens from the Indus River as a nursery area and/or as a foraging habitat. Barreiros & Gadig (2011) and Moazzam & Osmany (2021) mentioned *C. leucas* for the Indus River and its estuary, but the source of these records remains unclear. Sajid (1962), and subsequently Mirza (1975), reported *Pristis microdon* Latham, 1794 (the largetooth sawfish) as the only freshwater elasmobranch species from the Indus River near Hyderabad, at about 293 km from the ocean. Considering this record of a further euryhaline elasmobranch in this river and the fact that the Indus Delta is located inside the marine and coastal range of *C. leucas*, its past or present occurrence in this river is quite imaginable.

Day (1878) reported that he caught a specimen of "*Carcharias gangeticus*" at Cuttack along India's Mahanadi River, but it remains unclear if this catch was *Glyphis gangeticus* or *C. leucas*. Mohapatra et al. (1954) reported *Carcharhinus gangeticus* from the Mahanadi River 60 miles (= 97 km) upstream, at the Zobra Barrage. This is here considered unusable information, as both *C. leucas* and *G. gangeticus* probably occur in this river and *Carcharhinus gangeticus* is an early name that was used for both taxa (see Methods). Mohapatra et al. (1954) gave no further information allowing a clear identification, nor did they deposit a voucher specimen in a scientific collection. Thus, the true identity of the sharks reported from the Mahanadi River by Mohapatra et al. (1954) needs clarifying. Until today, there are no confirmed reports of *C. leucas* from the Mahanadi River, but a presence cannot be excluded due to its location inside the coastal range of *C. leucas* and the preference of this species for low salinity habitats.

The Shark Research Institute (2018b) also reported shark incidents at the mouth of the Devi River (an outlet of the Mahanadi River) and in the "Cochin River" (which is quite imprecise because the town of Cochin includes numerous river outlets, canals, and small river systems); although these reports do not include remarks on the involved species, they may be an indication of the use of these freshwater habitats by *C. leucas*.

Table 7. Occurrences of *Carcharhinus leucas* in Asian rivers, lakes, estuaries, and lagoons: Indian Ocean coast incl. Persian Gulf and Pacific Ocean coast. Abbreviations: WC = water conditions, F = freshwater, B = brackish water up to hypersaline conditions, F/B = salinity gradient from fresh to brackish, LHS = life history stage, Ad = adult, Sub = subadult, Juv = juvenile, Y-O-Y = young-of-the-year, N = neonate, U = unknown.

No.	WC	Toponym	Country	References	LHS	Comments
1	**F**	**Tigris River** [31.00°N, 47.44°E]	Iraq / Iran	Günther (1874, 1910); Day (1878); Engelhardt (1913); Chaudhuri (1916); Kennedy (1937); Khalaf (1961); Mahdi (1962); Boeseman (1964); Misra (1969); Thorson (1970b); Budker (1971); Al-Daham (1976); Basson et al. (1977); Young (1977); Garrick (1982); Compagno (1984); Fischer & Bianchi (1984); Randall (1986); Ellis (1989); Coad (1991, 1998, 2010, 2015, 2018); Simpfendorfer & Burgess (2005, 2009); Esmaeili et al. (2010a, 2017, 2018); Voigt & Weber (2011); Hussain et al. (2012); Moore et al. (2012a); Moore (2013, 2018); Rapoza (2014); Almojil et al. (2015); Jouladeh-Roudbar et al. (2015); Moradi (2017); Ali et al. (2018); Jouladeh-Roudbar et al. (2020); Freyhof et al. (2021)	Juv	Two specimens of *C. leucas* were collected in the vicinity of Baghdad [33.43°N, 44.34°E] in historical times, one in 1874 and one fifty years later, in 1924. Günther (1874) reported on a specimen (~760 mm TL) collected in Baghdad by W. H. Colvill and provided to the British Museum by F. R. S. Sharpey. Later on, L. J. V Compagno verified this specimen (catalog no.: NHM 1874.4.28.9) as *C. leucas*. Garrick (1982) examined the head of a specimen (1,244 mm TL) that was collected in 1924 at Karrada near Baghdad (catalog no.: BMNH 1924.10.1.1) and provided to the British Museum by the Bombay Natural History Society. The latter was also verified as *C. leucas* (Garrick 1982)
2	**F**	**Euphrat River** [31.00°N, 47.44°E]	Iraq	Thorson (1970b); Budker (1971); Ellis (1989); Coad (1991, 2010); Suhks (2007); Hussain et al. (2012); Moore (2013, 2018); Rapoza (2014); Almojil et al. (2015); Jawad (2017)	Sub	Verified as far as Nasiriyah (31.03°N, 46.30°E), 260 km from the ocean according to Coad (2010), Hussain et al. (2012), Jawad (2017), and Moore (2018)
3	**F/B**	**Shatt Al-Arab River** (= Arvand River, Arvandrud River, Tigris-Euphrat-Karun Delta) [30.45°N, 48.08°E]	Iraq / Iran / Kuweit	Blegvad & Løppenthin (1944); Hunt (1951); Khalaf (1961); Young (1977); Al-Daham (1982); Garrick (1982); Compagno (1984); Fischer & Bianchi (1984); Randall (1986); Coad & Papahn (1988); Al-Hassan et al. (1989); Coad & Al-Hassan (1989); Mohamed et al. (2001, 2013, 2015); Firouz (2005); Coad (2010); Voigt & Weber (2011); Hussain et al. (2012); Adday (2013); FAO (2014); Lazem (2014); Rapoza (2014); Keivany et al. (2016);	Juv Sub	Confluence of the Tigris (No. 1) and the Euphrat (No. 2) rivers; also an outlet of the Karun River (No. 9). Large freshwater outlet and delta of these three rivers. Hunt (1951) reported sharks not only from Shatt Al-Arab River, but also from adjacent creeks. Moore (2018) reported *C. leucas* from Basrah

No.	WC	Toponym	Country	References	LHS	Comments
				Yaseen et al. (2017); Ali et al. (2018); Moore (2018); Jouladeh-Roudbar et al. (2020); Freyhof et al. (2021)		
4	**F**	**Ashar Canal** [30.52°N, 47.84°E]	Iraq	Coad & Al-Hassan (1989); Coad (2010)	U	A backwater of the Shatt Al-Arab River (No. 3)
5	**B**	**Shatt Al-Arab Estuary / Delta** (incl. Al-Fao-Estuary) [29.93°N, 48.60°E]	Iraq	Coad & Al-Hassan (1989); Moore (2013, 2018); Bishop et al. (2016)	Juv	This delta may represent the only *C. leucas* nursery for thousands of kilometers in the Persian Gulf (Moore 2013, 2018)
6	**F/B**	**Shatt Al-Basrah Canal** (= Basrah Canal; incl. Khawr az-Zubayr Waterway) [30.51°N, 47.72°E]	Iraq	Hussain et al. (2012); Freyhof et al. (2014); Ali et al. (2018)	U	Extended drainage canal for the main outlet of the Tigris (No. 1) and Euphrat (No. 2) rivers
7	**B**	**Khor Al-Zubair Lagoon** [30.00°N, 48.00°E]	Iraq	Hussain et al. (1988); Hussain & Naama (1989); Nasir (2000); Moore (2018); Younis & Al-Shamary (2015); Younis et al. (2019)	U	Extension/outlet of the Shatt Al-Basrah Canal (No. 6)
8	**F**	**Bahmanshir River** (= Bahmanshir Canal, Khowr-e Bahmanshir) [30.41°N, 48.23°E]	Iran	Hunt (1951); Coad & Papahn (1988); Coad (2010, 2015); Keivany et al. (2016); Freyhof et al. (2021)	U	A secondary estuary/ branch of the Karun River (No. 9) that parallels the Shatt Al-Arab River (No. 3)
9	**F**	**Karun River** (= Karoon River, Pasitigris River) [30.42°N, 48.16°E]	Iran	Sykes (1902); Wilson (1942); Hunt (1951); Boeseman (1964); Thorson (1970b); Budker (1971); Johnson (1978); Coad & Papahn (1988); Firouz (2000, 2005); Aberoumand (2010, 2011); Rapoza (2014); Coad (2010, 2015); Almojil et al. (2015); Owfi (2015); Keivany et al. (2016); Jouladeh-Roudbar et al. (2020); Freyhof et al. (2021)	Juv Sub	Tributary of the Shatt Al-Arab River (No. 3). Verified as far as Ahwaz (Firouz 2000) and Shushtar, 420 km from the sea according to Sykes (1902) and Coad & Papahn (1988). Johnson (1978) refered to a "Karum River", which was presumably just a mistake
10	**F**	**"Bombay River"** [~19.32°N, 72.80°E]	India	Keller (1987); Lamar University (2018)	U	The exact location cannot be determined
11	**F**	**Naringre River** [16.27°N, 73.41°E]	India	Gupta et al. (2020)	N	-
12	**F**	**Gad River** [16.08°N, 73.46°E]	India	Gupta et al. (2020)	N	-
13	**F**	**Menik (Ganga) River** [6.36°N, 81.53°E]	Sri Lanka	Jabado et al. (2017); Kyne et al. (2021)	Juv	Juvenile sharks spotted at Yala were misidentified and reported as *C. hemiodon* by De Silva (2014), but later confirmed as *C. leucas* (Jabado et al. 2017; Kyne et al. 2021)
14	**B**	**Pulicut Lagoon** (= Pulicat Lake) [13.57°N, 80.21°E]	India	Ganapathy & Kaliyamurthy (1978); Batcha & Reddi (2007); Mohanray et al. (2009)	Ad	Batcha & Reddi (2007) and Mohanray et al. (2009) reported a pregnant female *C. leucas* in the lagoon; probably a nursery of *C. leucas*

No.	WC	Toponym	Country	References	LHS	Comments
15	**B**	**Chilika Lagoon** (= Chilika Lake) [19.77°N, 85.39°E]	India	Khan et al. (2011); Kumar & Pattnaik (2012); Chilika Development Authority (2014); Mohanty et al. (2015); Mohapatra et al. (2015); Suresh et al. (2018); Mohanty & Panda (2020)	Juv Ad	Largest lagoon in India. Khan et al. (2011) reported only adult female *C. leucas*, most of them pregnant, indicating that this location functions as a nursery for *C. leucas*
16	**F**	**Devi River** [19.97°N, 86.34°E]	India	Thorson (1970b); Budker (1971); Johnson (1978)	U	One of the principal distributaries of the Mahanadi river and estuary
17	**B**	**Champa Canal Mouth** [21.63°N, 87.55°E]	India	Manna & Goswami (1985)	U	Reported as "*Carcharhinus gangeticus*" (Manna & Goswami 1985: 490)
18	**F/B**	**Hooghly River** (= Hugli River) [21.98°N, 88.14°E]	India	Günther (1870); Day (1878, 1889); Budker (1971); Compagno (1984, 1988); Talwar (1991); Kapoor et al. (2002); Venkataraman et al. (2003); Voigt & Weber (2011)	N	Tidally influenced branch/outlet of the Ganges River (No. 19) with low salinities
19	**F**	**Ganges River** (incl. Padma River) [24.80°N, 87.93°E]	India / Bangladesh	Günther (1910); Bigelow & Schroeder (1948); Budker (1971); Johnson (1978); Berra (1981); Ellis (1989); Talwar (1991); Talwar & Jhingran (1991); Martin (2005); Simpfendorfer & Burgess (2005, 2009); López Fernández (2012)	U	-
20	**F**	**Perak River** (= Sungai Perak) [3.99°N, 100.76°E]	Malaysia (Perak)	Boeseman (1964); Thorson (1970b); Compagno & Cook (1995); Kottelat (2013)	U	-
21	**F**	**Mawai Lama River** (= Sungai Mawai Lama) [1.93°N; 104.11°E]	Malaysia (Johor)	Hasan et al. (2021)	Juv	Reported as far as 25 km inland (Hasan et al. 2021)
22	**F**	**Indragiri River** [-0.29°S, 103.23°E]	Indonesia (Sumatra)	Hasan & Widodo (2020)	Juv	As far as 150 km inland (Hasan & Widodo 2020)
23	**F**	**Batang Hari River Basin** [-1.07°S, 104.20°E]	Indonesia (Sumatra)	Tan & Lim (1998); Hui (1999); Hui & Kottelat (2009); Kottellat (2013)	Juv	Verified as far as Jambi (Tan & Lim 1998)
24	**F**	**Musi River** (= Sungai Musi) [-2.71°N, 104.95°E]	Indonesia (Sumatra)	Iqbal et al. (2019a)	Juv	Juveniles (~70 cm TL) were reported from Air Itam Timur and Teluk Kijing, at 75 km from the ocean (Iqbal et al. 2019a)
25	**F**	**Pangkajene River** [-4.84°S, 119.51°E]	Indonesia (Celebes)	Hasan & Islam (2020)	Juv	A ~86 cm TL specimen was reported from 16 km inland (Hasan & Islam 2020)
26	**F**	**Barito River** (= Sungai Barito) [-3.49°N, 114.50°E]	Indonesia (Kali-mantan, Borneo)	Iqbal et al. (2019b)	Juv	Reported as far as 70 km from the sea (Iqbal et al. 2019b)
27	**F**	**Sarawak River** (= Sungai Sarawak) [1.62°N, 110.46°E]	Malaysia (Sarawak, Borneo)	Bartlett (1896); Compagno & Cook (1995); Kottelat (2013)	U	Captured in a branch of the Moratabas River (Bartlett 1896)

No.	WC	Toponym	Country	References	LHS	Comments
28	**B**	**Lupar River Estuary** (= Batang Lupar) [1.52°N, 110.98°N]	Malaysia (Sarawak, Borneo)	Blaber (2000)	U	-
29	**F**	**Kinabatangan River** (= Sungai Kinabatangan) [5.78°N, 118.34°E]	Malaysia (Sabah, Borneo)	Manjaji (2002); Last et al. (2010); Min (2013)	Juv	Verified as far as Sukau (Manjaji 2002)
30	**F**	**Saigon River** (= Sông Sài Gòn) [10.77°N, 106.74°E]	Viet Nam	Tirant (1929); Boeseman (1964); Thorson (1970b),	U	-
31	**F**	**Dongnai River** (= Sông Dông Nai) [10.91°N, 106.83°E]	Viet Nam	Boeseman (1964); Compagno & Cook (1995); Kottelat (2013)	U	-
32	**F**	**Laguna de Bay** (= Lac de Bay) [14.40°N, 121.19°E]	Philippines	(conditionally even De La Gironière 1855; Meyer 1875; Wood 1875 and Harting 1876); Boeseman (1964); Thorson (1970b); Compagno & Cook (1995); Kottelat (2013)	Juv	A freshwater lake, heavily polluted today
33	**F**	**Pasig River** [14.59°N, 120.95°E]	Philippines	No reference but it is logical under geographic circumstances	Juv	Drainage of No. 32 into the Manila Bay (No. 35)
34	**F**	**Saug River** [9.74°N, 123.84°E]	Philippines	Herre (1953); Boeseman (1964); Thorson (1970b); Budker (1971); Compagno & Cook (1995); Compagno et al. (2005); Kottelat (2013)	U	-
35	**B**	**Manila Bay** [14.55°N, 120.76°E]	Philippines	Herre (1953); Compagno et al. (2005)	U	Estuary of the Pampanga and Angat rivers
36	**F**	**Agusan River** [9.01°N, 125.52°E]	Philippines	Herre (1953, 1958); Boeseman (1964); Thorson (1970b); Budker (1971); Compagno & Cook (1995); Compagno et al. (2005); Kottelat (2013)	U	Reported from Monkayo at 252 km from the ocean (Herre 1953, 1958)
37	**F**	**Lake Naujan** [13.18°N, 121.35°E]	Philippines	Herre (1927, 1953, 1958); Roxas & Martin (1937); Boeseman (1964); Thorson (1970b); Budker (1971); Taniuchi (1979); Compagno & Cook (1995); Compagno et al. (2005); Kottelat (2013)	Ad	Herre (1958) reported the sighting of an adult shark of 3 m TL in the lake
38	**F**	**Butas River** [13.28°N, 121.35°E]	Philippines	No reference but it is logical under geographic circumstances	Ad	Drainage of Lake Naujan (No. 37)
39	**F**	**Lake Taal** (= Lake Bombón, Laguna Bombón, Lawa ng Taal) [13.98°N, 121.02°E]	Philippines	(conditionally even Herre 1927 and Villadolid 1937); Herre (1958)	U	Herre (1927: 296) and Villadolid (1937: 198) were unsure of a determination in their surveys and reported only "*Carcharhinus* sp." from this lake
40	**F**	**Pansipit River** [13,87°N, 120,91°E]	Philippines	Mercene & Alzona (1990)	U	Drainage of Lake Taal (No. 39) into Balayan Bay
41	**F**	**Urauchi River** [24,41°N, 123,77°E]	Japan	Tachihara et al. (2003); Matsumoto et al. (2006)	Juv	River with a mangrove estuary (Nanjo et al. 2008)

In the Asian region and especially in India, the name *Carcharhinus gangeticus* was presumably used for records of *C. leucas* at least until the mid 1980s (see Methods). For the inland waters of the Philippines, Herre (1958: 88) reported, for *Carcharias gangeticus*: "It enters all the rivers of Mindanao except those too small or too steep, and ascends the Agusan to Monkayo and beyond." Presumably, Herre was also referring to *C. leucas*.

There is only semi-reliable information from the Mekong River (= Mae Khong River) (Cambodia, Viet Nam, Thailand), by Fernicola (2016); the presence of this species in this river needs clarifying and investigating further. *Carcharhinus leucas* is also mentioned for this river in the checklist by Rainboth (1996: 51): "Expected, but not yet recorded from the Mekong." Later, Rainboth et al. (2012) presented a photograph of a juvenile *C. leucas* (940 mm TL) from a fish market of Kien Giang Province in the Mekong Delta, with the statement that the photo is cited as evidence that this species occurs in the Mekong. Rainboth et al. (2012) mentioned that this species had been sighted by the main author in Mekong Delta markets, but it remains unclear whether the specimens were taken from marine, estuarine, or riverine habitats. Poulsen et al. (2004) listed *C. leucas* in a list of Mekong River fishes, but they didn't provide data allowing validation of this record. The bull shark was also listed in the checklist of freshwater fishes of Viet Nam by Froese & Pauly (2018a). The occurrence of *C. leucas* in the Mekong river system seems very likely, as this major river system provides suitable habitat conditions for the species; however, there are no precise records or locations for *C. leucas* from within the Mekong system. Vidthayanon (2002) reported that *C. leucas* has never been seen in Thai rivers, but that either *Glyphis* cf. *gangeticus* or *C. leucas* were anecdotally reported by the Karen people along the Salween River of the Tak-Mae Hongson Province, northern Thailand. Vidthayanon & Premcharoen (2002) reported nine species of elasmobranchs from the middle reaches of Thailand rivers, but without information on these species.

Carcharhinus leucas was mentioned by Kottelat (1989) for the inland waters of Indochina, Southeast Asia (Laos, Cambodia, Viet Nam, Thailand, Myanmar), but without naming any precise locality or river system. Later, Kottelat (2013) summarized eight records of *C. leucas* from inland waters in Southeast Asia in a literature review. White et al. (2006) reported that *C. leucas* occurs in Indonesian freshwaters, but without naming a particular river. Parenti & Lim (2005) expected sharks of the family Carcharhinidae for the rivers of the Rajang Basin, Sarawak, Borneo (Malaysia). The Department of Fisheries Malaysia (2006) gave the information that *C. leucas* is found in the rivers of Sabah, Borneo. Possibly, *C. leucas* also inhabits the Yangtze River (China), as Garrick (1982) examined a single juvenile specimen (♂, 729 mm TL; catalog no.: BMNH 74.1.16.63) collected from Shanghai, China, which is situated on the estuary of this major Chinese river.

Nos. 1, 2, 3, 9: Verified occurrences of *C. leucas* exist, at least in historical times, from north of Baghdad, 850 km from the sea. For the waters of Iraq, Kennedy (1937: 746) reported: "Sharks are not frequent visitors so high up the Tigris as Baghdad, but isolated ones are heard of every year. In the river at Basrah they are more common." Coad (2010) and Moore (2018) delivered detailed synopses of freshwater occurrences of *C. leucas* and localities of shark attacks for Iraq in the Tigris/Euphrat and Shatt Al-Arab systems. Furthermore, Moore (2018) reported unconfirmed, anecdotal records of juvenile *C. leucas* from the Iraqi Marshes, from north of Ahwaz on the Karun River, and from Abadan on the Shatt Al-Arab River. In the Middle East, the occurrence of sharks in the Tigris/Euphrat system is well-known since antiquity (Moore & McDavitt 2009). Already in the early historical work "The Wonders of Creation" by Qazvini (1263), the author reported sharks as powerful and dangerous fishes that were known from Basrah. The work of Qazvini may represent one of the earliest distributional records of *C. leucas* in the Euphrat-Tigris-Shatt Al-Arab system (Moradi 2017).

More modern reports of sharks in the Mesopotamian rivers are mainly focused on attacks that occurred inland, far from the coast (e.g., Hunt 1951; Thesiger 1964). *Carcharhinus leucas* frequently enters numerous rivers, canals, and creeks in the Tigris/Euphrat Basin of Iran/Iraq, where attacks have also been continuously reported (Armantrout 1980; Coad & Papahn 1988; Coad & Al-Hassan 1989; Coad 2015). In the Tigris/Shatt Al-Arab system and the Karun River (Iran), there are freshwater reports of sharks under different names, such as *Carcharias gangeticus*, *C. lamia*, and *C. menisorrah* (Günther 1874; Kennedy 1937; Khalaf 1961; Mahdi 1962). Even when the specific identity of these large sharks is disputed (Coad 1979), their occurrence in inland waters, far from the coast at Ahwaz (Iran) and farther inland than Baghdad (Iraq) exclude other carcharhinids and leave the euryhaline *C. leucas* as the most plausible species. Jawad (2012) critically discussed the validity of shark reports by numerous authors from the inland waters of Iraq and assigned Günther's (1874) *Carcharias gangeticus* and Kennedy's (1937) *Carcharias lamia* to *Carcharhinus leucas*. Coad (2010) pointed out that studies on carcharhinid sharks and museum specimens indicate that only *C. leucas* occurs in freshwaters of the Tigris/Euphrat Basin. Moreover, Coad (2010) stated that *C. leucas* was the only shark species commonly encountered in inland Iraqi freshwaters in the past. However, the influence of the tide in the Shatt Al-Arab River (200 km in total length) is felt about 140 km inland, with penetration of marine organisms upstream (Rzoska 1980). Besides *C. leucas*, further carcharhinids were reported from the Shatt Al-Arab River. Mohamed & Abood (2017) also reported *Rhizoprionodon acutus* Rüppel, 1837 (milk shark) from the Shatt Al-Arab River. This is a representative of a genus whose members utilize low salinity habitats and that has been reported multiple times from estuaries, river mouths, and the lower parts of certain rivers worldwide (Compagno 1984). Nevertheless, these small members of the family Carcharhinidae are not known for attacks on humans or for penetrating rivers for great distances (Compagno 1984). Since human impediments in the Tigris River prevent sharks from migrating upriver, reports of sharks from or north of above Baghdad have declined. Young (1977) reported that local people spotted sharks at Baghdad frequently but only on rare occasions. According to Coad (2010), *C. leucas* occurred regularly as far upriver as Baghdad before river regulation and building of barrages and dams took place. Jouladeh-Roudbar et al. (2020) reported that since the construction of various dams on the Tigris and Karun rivers, *C. leucas* is found primarily in the Shatt Al-Arab River estuary (= Arvand River estuary). Freyhof et al. (2021) reported, also for the Euphrat and Tigris rivers, that nowadays dam construction terminates the migrations of fishes that started their migrations upriver from the ocean, such as long-distance migrating species like *C. leucas*. For freshwaters of Iraq and particularly the Tigris River, Freyhof et al. (2021) mentioned that bull sharks once traveled up to Baghdad, but that they nowadays only reach as far as Basrah on the Shatt Al-Arab due to dams.

Moore (2018) outlines the Tigris/Euphrat river system as an important nursery area for *C. leucas* due to its rank as one of the few and largest freshwater inflows in the Persian Gulf.

In this context, Jawad (2021) underlined the important role of Iraq's southern marshes for threatened species such as *C. leucas*. Young (1977) recorded reports by the native people of Iraq that small sharks use the Iraqi marshes during flooding. Al-Daham (1982) postulated that sharks regularly ascend the Shatt Al-Arab River, also reaching the southern marshes. Garstecki & Amr (2011) reported *C. leucas* from the freshwaters of the Hammar marsh (Iraq). The Mesopotamian marshlands (Hammar marsh, Chybayisch marsh, Hawizeh marsh), part of the Tigris-Euphrates Basin, and the numerous irrigation canals included there offer suitable habitats for *C. leucas*. Coad (2010) reported the occurrence of *C. leucas* from Hammar marsh in the Mesopotamian marshlands. The Al-Ahwar marshland (East Hammar marsh, West Hammar marsh, Huweizah marsh) in southern Iraq, which is irrigated by discharges of branches of the Tigris/Euphrat river system, was mentioned as a critical habitat for *C. leucas* by Al-Lami et al. (2014), and the authors highlighted *C. leucas* as a key locally migrating species for this region. With regard to the high importance of the Tigris/Euphrat river system as a nursery area for Persian Gulf *C. leucas*, Esmaeili et al. (2010b) reported that dam construction, pollution, drought, overfishing, and habitat destruction are the main threats to the ichthyofauna of the Tigris River Basin. Therefore, conservation efforts in this region are highly demanded.

For Iranian waters, Armantrout (1980) reported "*Carcharias lamia*" for the Tigris River and "*Carcharias gangeticus*" for the Tigris and the Karun rivers, but he was referring to older literature (Gunther 1874; Kennedy 1937) and these are undoubtedly records of *C. leucas*. Armantrout (1980) reported shark attacks in the Karun River near Dezful, which is puzzling as this locality is on the Dez River, a confluent of the Karun. Esmaeili et al. (2010a) gave the information that *C. leucas* occurs in the Tigris River Basin, which include, besides the Tigris River, also the Karun River. *Carcharhinus leucas* probably also occurs in the Dez and Gargar rivers, two side branches of the Karun River. Aberoumand (2010, 2011) reported that he obtained fresh skin of *C. leucas* for pharmaceutical investigations from a local fish market in Ahwaz, Iran, which is located on the Karun River at 275 km from the Persian Gulf. Owfi (2015) reported *C. leucas* for Chuzestan (Iran) and the Karun River Basin. Coad (1999) mentioned that *C. leucas* occurs in rivers of the Iranian province of Chuzestan, up to 420 km from the coast, which presumably refers to records of *C. leucas* in the Karun River, from Shushtar.

No. 10: This toponym is quite imprecise because there are numerous rivers in Mumbai (the former Bombay), like for example the Dahisar, Mithi, Chorna, Oshiwara, Poisar, Tansa, and Tasso rivers. Day (1878) reported the collecting of a juvenile (18 inches = 45.72 cm TL) of *Carcharhinus gangeticus* in Bombay, which may indicate an occurrence of *C. leucas* in this region, although the size of this juvenile specimen seems to be very small for a newborn *C. leucas*, thus his record possibly belongs to *Glyphis gangeticus*.

No. 15: Chaudhuri (1916) reported a catch of a juvenile (747 mm TL) of "*Carcharinus gangeticus*" [sic] in the Chilika Lagoon. *Carcharhinus gangeticus* was mentioned for this lagoon also by Jones & Sujansingani (1954) and Misra (1962), and more recently by Rao & Shibananda Rath (2014). It is unknown whether both *C. leucas* and *G. gangeticus* occur together in this lagoon or if these literature records represent misidentifications of *C. leucas* (see Methods). The description by Menon (1961: 68) of *Carcharhinus gangeticus* from the Chilika Lagoon seem to agree with the diagnostic features of *Glyphis gangeticus*, and therefore a co-occurrence of both *C. leucas* and *G. gangeticus* in the Chilika Lagoon cannot be excluded.

No. 18: Hamilton (1822: 3) commented: "In the mouths of the Ganges sharks are exceedingly numerous, and occasionally, but rarely, come up as far as Calcutta." Blyth (1860) reported an examined specimen of "*Squalus* (*Carcharinus*) *gangeticus*" [sic] from the fish market of Calcutta, but this specimen was probably *Glyphis gangeticus* and the precise location of this catch remains unclear. The verified record of *C. leucas* from the Hooghly River is based on a ♂ 650 mm TL fetus or newborn (catalog no.: ZSI 10250) collected in April 1867 by J. Anderson and misidentified by the collector as "*Squalus gangeticus*" (Compagno 1984; Talwar 1991). Day (1878: 710), reporting on sharks in Indian rivers, wrote: "The most savage species appear to be the ground sharks of the rivers, as *Carcharias Gangeticus*, which seldom loses an opportunity of attacking the bather." Day (1878: 715) further remarked: "This is one of the most ferocious of Indian sharks, and frequently attacks bathers even in the Hooghly at Calcutta, where it is so dreaded that a reward is offered for each that is captured. I have taken it at Cuttack." This description of a ferocious character does not agree with *Glyphis gangeticus*, which feeds primarily on fish (Compagno 1984) and doesn't normally attack humans; therefore, Day (1878) was likely referring to *C. leucas*. Even the description by Day (1878: 711): "Snout obtuse. Teeth in both jaws serrated. Seas of India to Japan; it ascends rivers." seems to be more suitable for *C. leucas* than *G. gangeticus*. McCulloch (1922: 5) reported *Carcharias gangeticus* from the Australian waters of New South Wales with the comment: "A ferocious species in Indian estuaries.", which probably also refers to *C. leucas*.

No. 19: Hamilton (1822: 4) reported sharks in the Ganges River and distinguished different species of shark ("merely sharks" and "ground sharks") occurring in the river; however, it is not possible to make a clear identification of the recorded species, even though it is almost certain that the information refers to *C. leucas* and/or *G. gangeticus*. To bring clarification into the distribution of Australian sharks, Whitley (1940: 105) reported, for "*Platyodon gangeticus*": "This shark, which is much feared in the River Ganges, India, has been recorded doubtfully from North-western Australia, New South Wales and South Australia.", a description that likely refers to *C. leucas*. Venkateswarlu & Menon (1979) reported *Carcharhinus gangeticus* in a taxonomic checklist of the fish fauna of the Ganges River and its branches, but the authors were just referring to the old reports of Hamilton (1822) and Day (1878). The publication by Roberts (2007), which had the aim of clarifying the distribution of *Glyphis gangeticus* as the "Gangetic freshwater shark" of India and Bangladesh was not very helpful at all, as the author was not able to distinguish *Carcharhinus leucas* from *Glyphis gangeticus*. The photographs that were presented by Roberts (2007: 269) of "*Glyphis gangeticus*" specimens, which were obtained from Sittway markets and were caught in the marine waters of the Bay of Bengal, are undoubtedly *C. leucas* (the height of the second dorsal fin in sharks of the genus *Glyphis* Agassiz, 1843 is about three quarters of the height of the first dorsal fin, whereas it is less than three quarters of the height of the first dorsal fin in *C. leucas*). Already Compagno et al. (2010) pointed out that images of juvenile specimens of *G. gangeticus* in Roberts (2007) were misidentifications of *C. leucas*.

Nevertheless, the recent status of *C. leucas* in the Ganges river system remains uncertain, as since the early records by Günther (1870) and Day (1878), no specimens of *C. leucas* were collected and no further reports regarding the occurrence of *C. leucas* in this river system were noted. Compagno (1984) reported in the middle of the 1980s that although sharks are currently caught in the Ganges system, it is not known how

common the true Ganges shark (*Glyphus gangeticus*) is relative to *C. leucas*. It can be estimated that both taxa are nowadays rare in Indian rivers due to high fishing pressure and to the intensive pollution of India's inland waters. However, Mitra (2014: 20) reported about the distribution of *C. leucas* from the mouth of the Ganges, the Sunderbans, and the adjacent Bay of Bengal, as follows: "Entire stretch of Indian Sundarbans and aquatic phase of Bay of Bengal. Throughout the year."

There are some reports from pearl fisheries in the Gulf of Mannar on the east coast of the Indian subcontinent about the risk of a shark attack while harvesting, from species such as *Galeocerdo cuvier* Péron & Lesueur, 1822 (tiger shark) and presumably *C. leucas*. James (1973: 493) reported: "….danger from ferocious sharks like *C. gangeticus* and the tiger shark during pearl fisheries operations in the Gulf of Mannar." Furthermore, James (1973: 488) stated: "Ascends rivers even beyond tidal influence. Known to be one of the most ferocious sharks." There are numerous reports listed in the "Global Shark Attack File" (Shark Research Institute 2018b) of shark attacks on bathers and pilgrims along the Hooghly River at Calcutta, Dakshineshwar, Barrackpore, and Chitpur and along the Ganges River, especially from the end of the 19th century. Even if the involved species cannot be clearly identified and considering the sympatric occurrence with *G. gangeticus* in Indian rivers, these historical attacks can likely be attributed to the opportunistic and more powerful *C. leucas* (Habegger et al. 2012).

No. 20: *Carcharhinus leucas* and other elasmobranchs were not included in the fish checklist of the Perak River by Hashim et al. (2012). Evidence of further carcharhinids besides *C. leucas* was provided for this river. Smith (1931) made investigations on four freshwater elasmobranchs in the Perak River, which also included *Carcharhinus melanopterus* Quoy & Gaimard, 1824 (blacktip reef shark). Besides *C. leucas* and *C. melanopterus*, one further freshwater tolerating elasmobranch *Scoliodon laticaudus* Müller & Henle, 1838 (spadenose shark), was recorded for this river, from the pure freshwaters at Telok Anson, 70 km upstream from the coast (Teshima et al. 1978).

No. 29: A single juvenile specimen of *C. leucas* was taken by a villager in the Kinabatangan River close to the Malbumi Estate in 2010, which is approximately 40 km from the river mouth (Min 2013). This river location is also illustrated in a distribution map of *C. leucas* for Borneo provided by Last et al. (2010).

No. 32: There are existing early reports about the occurrence of sharks in Laguna de Bay, but without identification of the involved species. De La Gironière (1855: 102) narrated: "Deux poissons de mer se sont acclimatés dans le eaux douces du lac: le requin et la scie. Le premier est heureusement assez rare, mais le second est très-abondant ["Two sea fishes have acclimated to the freshwater of the lake: the shark and the sawfish. Fortunately, the first is quite rare, but the second is very common."]. Later, Wood (1875) reported on the occurrence of sawfishes (genus *Pristis* Latham [J. F.], 1794) and small sharks from Laguna de Bay, located near the city of Manila. Harting (1876: 62), who was referring to Wood (1875), reported in a short account the occurrence of sharks in the freshwater of Laguna de Bay: "…zaagvisschen (*Pristis*) en nog een andere soort van kleine haaien." ["…sawfish (*Pristis*) and a further sort of small shark."]. These small sharks, which were observed by Wood (1875) and subsequently by Harting (1876), were in all likelihood juvenile specimens of *C. leucas*, even though the authors made no species determination.

Nos. 39, 40: Papa & Mamaril (2011) reported that sharks were already observed in Lake Taal (Philippines) by Spanish and American explorers in the late 16th Century. Hargrove & Medina (1988) reported that in 1754 the waters of Lake Taal threw up dead alligators and fish, including sharks. Maybe this event was the result of volcanic activity in and around the lake. Today, it is unclear if *C. leucas* still occurs in Lake Taal and its drainage, the Pansipit River. Fishery management of the lake was unsustainable and combined with overexploitation since the 1930s, which has led to the extirpation of sharks in the lake (Hargrove & Medina 1988); it remains unclear if there is still a local population of *C. leucas* there.

Table 8. Occurrences of *Carcharhinus leucas* in Australian rivers, lakes, estuaries, and lagoons: Indian Ocean coast. Abbreviations: WC = water conditions, F = freshwater, B = brackish water up to hypersaline conditions, F/B = salinity gradient from fresh to brackish, LHS = life history stage, Ad = adult, Sub = subadult, Juv = juvenile, Y-O-Y = young-of-the-year, N = neonate, U = unknown. Abbrevations of Australian Territories: N.T. = Northern Territory; QLD = Queensland; W.A. = Western Australia.

No.	WC	Toponym	Country	References	LHS	Comments
1	F	**Collie River** [-33.30°S, 115.69°E]	Australia (W.A.)	Potter et al. (2000); Azevedo (2014); Negus (2014)	Juv Sub	Tributary of No. 2
2	B	**Leschenault Estuary Basin** [-33.26°S, 115.70°E]	Australia (W.A.)	Potter et al. (2000); Platell & Hall (2006)	Juv Sub	Estuary with brackish water
3	F	**Swan River** [-31.96°S, 115.87°E]	Australia (W.A.)	(conditionally even Whitley 1940); Whitley (1945); Boeseman (1964); Thorson (1970b); Chubb et al. (1979); Garrick (1982); Compagno (1984); McAuley et al. (2002); Prokop (2006); Berra (2007); Last & Stevens (2009); Holyoake et al. (2010); Ridley (2011); Voigt & Weber (2011); Macintyre & Dobson (2017)	Juv	Whitley (1940) reported the presence of small sharks of unknown identity in this river (see comments to No. 3 below)

No.	WC	Toponym	Country	References	LHS	Comments
4	**B**	**Swan / Canning River Estuary Basin** [-31.99°S, 115.82°E]	Australia (W.A.)	Loneragan et al. (1987); Malseed & Summer (2001); Holyoake et al. (2010); Hallett et al. (2012); McPhee (2012); Hallett (2016)	Juv	Estuary of the Swan River (No. 3) and the Canning River, with brackish water
5	**F**	**Fitzroy River** (King Sound, Kimberley Region) [-17.58°S, 123.58°]	Australia (W.A.)	(conditionally even Hardman 1884); Whitley (1943); Budker (1971); Chubb et al. (1979); Thorburn et al. (2004a, 2004b, 2004c, 2004d, 2007, 2014); Thorburn (2006); Morgan et al. (2004, 2005, 2017); Whitty et al. (2008, 2009); Last & Stevens (2009); Tillett (2011); Jackson et al. (2012); Tillet et al. (2012); Gleiss et al. (2015, 2017); Pusey & Kath (2015); Lear et al. (2019, 2020); Burrows et al. (2020); Glaus et al. (2020)	Juv Sub	Recorded as far as 320 km from the ocean according to Chubb et al. (1979). Pusey & Kath (2015: 53) reported: "*C. leucas* penetrates well upstream in the river." Thorburn et al. (2014) reported *C. leucas* from Geikie Gorge, ~300 km from the mouth of the main channel of the Fitzroy River, but only in low numbers
6	**F**	**Margaret River** [-18.17°S, 125.62°E]	Australia (W.A.)	(conditionally also Hardman 1884); Budker (1971); ReefQuest Centre for Shark Research (2018)	Sub	Tributary to No. 5. Hardman (1884) reported a shark (species not identified) of 5 ft (= 152 cm TL) from 300 miles (= 483 km) upriver
7	**F**	**Robinson River** [-16.81°S, 123.95°E]	Australia (W.A.)	Thorburn et al. (2004a); Tillet et al. (2012)	Juv	This river is located in the Kimberley Region
8	**B**	**Prince Regent River** [-15.81°S, 124.74°E]	Australia (W.A.)	Allen (1975); Thorburn et al. (2004a); ALA (2018)	U	In parts far inland with brackish water
9	**F**	**Pentecost River** [-15.64°S, 127.87°E]	Australia (W.A.)	Thorburn (2006)	U	Tributary of the Cambridge Gulf and the Timor Sea
10	**F**	**Ord River** [-15.47°S, 128.30°E]	Australia (W.A.)	Storey (2003); Thorburn et al. (2004a); Gill et al. (2006); Thorburn (2006); Trayler et al. (2006); Storey & Trayler (2007); Gehrke (2009); Last & Stevens (2009); Berra (2010); Buckle et al. (2010); Hale & Morgan (2010); Tillet et al. (2012); Storey & Creagh (2014)	Juv	Storey & Creagh (2014) reported catches of juvenile *C. leucas* specimens ranging from 55.4 to 120.0 cm fork length
11	**B**	**Ord River Estuary** (incl. East Arm) [-15.06°S, 128.17°E]	Australia (W.A.)	Robson et al. (2013)	Juv	Estuary influenced by tidal flow, fluctuating salinities, and high turbidity
12	**F**	**Victoria River** [-15.17°S, 129.75°E]	Australia (N.T.)	Rendahl (1922); Boeseman (1964); Thorson (1970b); Johnson (1978); Thorburn et al. (2004a)	U	-

No.	WC	Toponym	Country	References	LHS	Comments
13	**F**	**Daly River** (incl. Elizabeth Creek) [-13.36°S, 130.31°E]	Australia (N.T.)	Merrick & Schmida (1984); Mizue & Hara (1991); Taniuchi & Shimizu (1991); Last & Stevens (1994, 2009); Kitamura et al. (1996); Taniuchi (2002); Thorburn et al. (2004a); Blanch et al. (2005); Thorburn (2006); Underwater-times.com News Service (2007); Larson (2008); Doody (2009); Wynen et al. (2009); Berra (2007, 2010); Tillett (2011); Tillett et al. (2011a, 2011b, 2012, 2014); Warfe et al. (2011); Jackson et al. (2012, 2014); Field et al. (2013); ALA (2018)	Juv	Larson (2008) reported *C. leucas* from Elizabeth Creek in the floodplain of the Daly River. Warfe et al. (2011: 2178) stated: "…bull sharks (*Carcharhinus leucas* Müller & Henle) [sic]…can be found hundreds of kilometres upstream."
14	**F**	**Adelaide River** [-12.23°S, 131.26°E]	Australia (N.T.)	Taniuchi & Shimizu (1991); Last & Stevens (1994, 2009); Taniuchi (2002); Pillans et al. (2005b); Berra (2007, 2010); Winchester (2014); Kyne & Feutry (2017); Buckley et al. (2020)	Juv	-
15	**F**	**Wildman River** [-12.30°S, 132.07°E]	Australia (N.T.)	Larson (2000); Tillett et al. (2011a)	Juv	-
16	**F**	**West Alligator River** [-12.23°S, 132.28°E]	Australia (N.T.)	Thorburn et al. (2004a); Tillett et al. (2011a)	Juv	-
17	**F**	**South Alligator River** [-12.24°S, 132.40°E]	Australia (N.T.)	Larson (2000); Thorburn et al. (2004a); Wynen et al. (2009); Tillett et al. (2011a); Kyne (2014); Every et al. (2014, 2016, 2017, 2019)	Juv	-
18	**F**	**East Alligator River** [-12.10°S, 132.61°E]	Australia (N.T.)	Taylor (1964); Pollard (1974); Garrick (1982); Compagno (1984); Last & Stevens (1994, 2009); Larson (2000); Bishop et al. (2001); Thorburn et al. (2004a); Wynen et al. (2009); Berra (2007, 2010); Tillett (2011); Tillett et al. (2011a, 2011b, 2012); Voigt & Weber (2011); Kyne (2014); ALA (2018)	Juv	Reported from Cahill's Crossing (Taylor 1964) and Cahill's Landing (Garrick 1982)
19	**F**	**Liverpool River / Mann River** [-12.14°S, 134.18°E]	Australia (N.T.)	Boeseman (1964); Thorson (1970b); Johnson (1978); Tillett (2011); Tillett et al. (2011b)	Juv	-
20	**F**	**Roper River** [-14.71°S, 135.35°E]	Australia (N.T.)	Thorburn et al. (2004a); Thorburn (2006); Dally & Larson (2008); Tillett (2011); Tillet et al. (2011b, 2012)	Juv	Dally & Larson (2008) reported a sight record (of a ~1 m TL specimen) from the Elsey and Moroak stations, nearly 200 km from the ocean
21	**F**	**Towns River** [-14.91°S, 135.42°E]	Australia (N.T.)	Thorburn et al. (2004a); Tillett (2011); Tillet et al. (2011b, 2012)	Juv	-

No.	WC	Toponym	Country	References	LHS	Comments
22	**F**	**Limmen River / Cox River** [-15.15°S, 135.64°E]	Australia (N.T.)	Thorburn et al. (2004a); Tillet et al. (2012)	Juv	-
23	**F**	**McArthur River** [-15.91°S, 136.52°E]	Australia (N.T.)	Thorburn et al. (2004a); Thorburn & Morgan (2006)	U	-
24	**F**	**Robinson River** [-16.06°S, 137.24°E]	Australia (N.T.)	Thorburn et al. (2004a); Tillet et al. (2012)	Juv	Should not be confused with No. 7 in this table
25	**F**	**Flinders River** [-17.59°S, 140.59°E]	Australia (QLD)	No reference but it is logical under geographic circumstances	U	Tribute of the Saxby River (No. 26)
26	**F**	**Saxby River** [-18.41°S, 140.86°E]	Australia (QLD)	ALA (2018)	U	Tributary of the Flinders River (No. 25)
27	**F**	**Mitchell River** [-15.23°S, 141.70°E]	Australia (QLD)	Thorburn et al. (2004a); Last & Stevens (2009); Jardine et al. (2011); Tillet et al. (2012)	Juv	-
28	**B**	**Archer River Mouth** [-13.46°S, 141.69°E]	Australia (QLD)	Herbert et al. (1995); ALA (2018)	U	-
29	**B**	**Embley River Estuary** [-12.68°S, 141.87°E]	Australia (QLD)	Blaber et al. (1989, 1990, 2010); Blaber (2000); Barletta & Blaber (2007)	Juv Ad	-
30	**F**	**Mission River** [-12.58°S, 141.96°E]	Australia (QLD)	Thorburn et al. (2004a); Reilly et al. (2011); Tillet et al. (2012)	Juv	-
31	**F**	**Wenlock River** [-12.08°S, 141.92°E]	Australia (QLD)	Herbert et al. (1995); Thorburn et al. (2004a); Peverell et al. (2006); Lyon et al. (2010, 2017); Reilly et al. (2011); Tillet et al. (2012); Dwyer et al. (2020)	N Juv Sub	Herbert et al. (1995) reported *C. leucas* from a site on the river called Stone's Crossing; Dwyer et al. (2020) reported *C. leucas* from 110 km upstream
32	**F**	**Ducie River** [-12.03°S, 142.03°E]	Australia (QLD)	Dwyer et al. (2020)	N Juv	-

Additions to Table 8

Munro (1961: 20) mentioned *C. leucas* under the common name "Swan River whaler shark" for fresh and brackish water habitats of Western Australia: "Bays and rivers, W.A.". Bishop et al. (1990) reported *C. leucas* for freshwaters of the Alligator Rivers Region (Northern Territory). Herbert et al. (1995) sampled the freshwater ichthyofauna of the Cape York Peninsula during the period 1992–1993 and mentioned that local residents reported occurrences of sharks in the Edward River (Queensland), Coleman River (Queensland) at Blazeaway Hole, and from King Junction Hole on the Palmer River, which is a tributary of the Mitchell River (Table 8, No. 27), nearly 300 km from the ocean.

There were unconfirmed reports of *C. leucas* from the Jim Jim Creek drainage, which is a tributary of the South Alligator River, and the Yellow Water Billabong, a side-water of the South Alligator River in Kakadu National Park (Bishop et al. 2001). For the Northern Territory of Australia, and especially for the Kakadu National Park, Thorburn et al. (2004a) and Larson et al. (2013) gave a detailed overview and extended listing of freshwater records of *C. leucas*, based on a literature review. *Carcharhinus leucas* is an inhabitant of the wetlands of the Kakadu Region, northern Australia, where it occurs in estuaries and enters nontidal waters (Larson 1999; Finlayson et al. 2006). Walden & Pidgeon (1998) also mentioned *C. leucas* as a marine species in freshwaters of the Kakadu National Park. Kyne (2014) reported, for Kakadu National Park, that juvenile *C. leucas* were abundant in both the South and East Alligator rivers (and probably elsewhere in Kakadu National Park). Morgan et al. (2014) listed *C. leucas* in an overview of freshwater fishes of Western Australia, with occurrences in the Southwestern and Pilbara Province and the Kimberley Region. Furthermore, Morgan et al. (2014) mentioned several reports of *C. leucas* from the estuaries of the Swan, Canning, Blackwood, and Collie rivers, but none appear to make the transition into freshwaters, possibly due to the seasonality of parturition in this species, which doesn't agree with the defined high flow regimes of the rivers resulting from the Mediterranean climate of the Southwestern Province.

No. 3: Whitley (1940: 101) reported, for the Swan River: "There has been some discussion concerning the identity of the small shark common in the Swan River near Perth. Stead calls it the whaler." Presumably, he was referring to juvenile *C. leucas*, and the Swan River is probably an important nursery area for the species.

No. 8: Although the survey of Allen (1975) dealt with the freshwater fish fauna of the Prince Regent River Reserve, Allen's report of *C. leucas* from the location of his catches at King Cascade indicate tidal influence causes brackish water conditions in this part of the lower reaches of the Prince Regent River.

No. 10 & 11: In the regulated Ord river system, dams now prevent marine vagrant fishes from moving farther upstream. Traveling of sharks is now limited by the dams to about one-

quarter of the former range (Storey & Trayler 2007), and the distribution of *C. leucas* in this river system is restricted to the Lower Ord River. The dam wall of Lake Kununurra (Kununurra Diversion Dam) provides an insurmountable barrier to the movements of *C. leucas* in the Ord system (Gill et al. 2006), as does the second dam wall of Lake Argyle (Ord River Dam). Buckle et al. (2010) speculated that amphidromous fish species like *C. leucas* would have traveled farther upstream, but that they are now limited by the dams. Although there are no data to demonstrate that the fauna of Lake Kununurra and Lake Argyle has changed since the building of the dams in 1990, *C. leucas* is now likely to have disappeared from these systems as a result of the river regulations (Hale & Morgan 2010).

No. 13: Based on indigenous sources, there have been reports of bull sharks from the Daly river system (Northern Territory) far upstream from the King River, which is a tributary of the Katherine River and secondary to the Daly River, which in turn drains into the Timor Sea (Jackson et al. 2014).

Table 9. Occurrences of *Carcharhinus leucas* in Australian rivers, lakes, estuaries, and lagoons: Pacific Ocean coast. Abbreviations: WC = water conditions, F = freshwater, B = brackish water up to hypersaline conditions, F/B = salinity gradient from fresh to brackish, LHS = life history stage, Ad = adult, Sub = subadult, Juv = juvenile, Y-O-Y = young-of-the-year, N = neonate, U = unknown. Abbrevations of Australian Territories: NSW = New South Wales; QLD = Queensland.

No.	WC	Toponym	Country	References	LHS	Comments
1	**F**	**Normanby River** [-14.41°S, 144.14°E]	Australia (QLD)	Thorburn et al. (2004a); Last & Stevens (2009)	Juv	-
2	**F**	**Daintree River** [-16.28°S, 145.45°E]	Australia (QLD)	ALA (2018)	U	-
3	**F**	**Herbert River** [-18.51°S, 146.27°E]	Australia (QLD)	Garrick (1982); Compagno (1984); Berra (2007); Last &Stevens (2009)	Juv	-
4	**F**	**Ross River** [-19.27°S, 146.83°E]	Australia (QLD)	Boeseman (1964); Thorson (1970b)	U	-
5	**F**	**Burdekin River** [-19.65°S, 147.50°E]	Australia (QLD)	Pusey et al. (2003, 2006); Clamann (2017); Sandeman (2017)	Juv Sub	-
6	**F**	**Proserpine River** [-20.45°S, 148.69°E]	Australia (QLD)	Internet Reference 4	Ad	-
7	**F**	**Pioneer River** [-21.13°S, 149.20°E]	Australia (QLD)	Tickle (2021)	U	-
8	**F**	**Fitzroy River** [-23.50°S, 150.76°E]	Australia (QLD)	Hooker (2017)	U	Should not be confused with No. 5 of Table 8
9	**F**	**Calliope River** [-23.82°S, 151.21°E]	Australia (QLD)	Battersby (2015)	Juv	-
10	**F**	**Burnett River** [-24.75°S, 152.38°E]	Australia (QLD)	Thorson (1970b); Greinke (2012), ALA (2018)	Sub	Greinke (2012) reported sigthings of sharks of almost 2 m TL
11	**F**	**Bogimbah Creek** [-25.29°S, 153.04°E]	Australia (QLD)	Whitley (1943); Garrick (1982)	Ad	Locality on Fraser Island from where Whitley (1943) made his description of *Galeolamna* (*Bogimba*) *bogimba* (a synonym of *Carcharhinus leucas*) based on a 254 cm TL specimen
12	**F**	**Mary River** [-25.45°S, 152.87°E]	Australia (QLD)	Tappin (2005); Internet Reference 5	Juv	-
13	**F**	**Noosa River** (= Noosa Creek) [-26.36°S, 153.02°E]	Australia (QLD)	Hammond (2010)	Ad	-
14	**F**	**Maroochy River** (incl. Twin Waters Canals) [-26.64°S, 153.10°]	Australia (QLD)	Motherwell (2015); Barnham (2018)	Juv Ad	-
15	**F**	**Caboolture River** [-27.15°S, 153.03°E]	Australia (QLD)	Tickle (2021)	U	-

No.	WC	Toponym	Country	References	LHS	Comments
16	**F**	**(North) Pine River** [-27.28°S, 153.03°E]	Australia (QLD)	Reilly et al. (2011); The Newsroom (2016)	Juv	-
17	**F**	**Brisbane River** [-27.40°S, 153.14°E]	Australia (QLD)	Ogilby (1910, 1916); McCulloch & Whitley (1925); McCulloch (1929); Fowler (1930b); Boeseman (1964); Whitley (1966); Thorson (1970b); Thomson (1978); Compagno (1984); Keller (1987); Last & Stevens (1994, 2009); Johnson (1999); Whitehead (2002); Collin & Whitehead (2004); Peverell & Pillans (2004); Pillans & Franklin (2004); Anderson et al. (2005a, 2005b); Pillans et al. (2005a, 2005b, 2008); Pillans (2006); Berra (2007), Taylor (2007); Reilly et al. (2011); Whitehead et al. (2015); Werry et al. (2018); Glaus et al. (2020)	N Y-O-Y Juv Sub	First reported from this river by Ogilby (1910) under the name *Carcharias spenceri* and subsequently under further names (*Carcharhinus spenceri*; Ogilby 1916; MacCulloch & Whitley 1925; McCulloch 1929; *Eulamia spenceri*; Fowler 1930b; *Galeolamna spenceri*; Whitley 1966). In this river, verified inland records reported at least up to 50 km from the ocean (Anderson et al. 2005a)
18	**F**	**Bremer River** [-27.58°S, 152.58°E]	Australia (QLD)	Garry (2011)	U	Tributary of the Brisbane River (No. 17)
19	**F**	**Tingalpa Creek** [-27.48°S, 153.19°E]	Australia (QLD)	Jeffery (2014)	Juv	-
20	**F**	**Albert River** [-27.69°S, 153.23°E]	Australia (QLD)	Thomson (1957); Boswell (2013); Pillans et al. (2020)	N Juv Sub	Tributary of the Logan River (No. 21)
21	**F**	**Logan River** [-27.70°S, 153.30°E]	Australia (QLD)	Werry (2010); Boswell (2013); Pillans et al. (2020); Tickle (2021)	N Juv Sub	-
22	**B**	**Coomera River** (= Coomera Creek) [-27.84°S, 153.35°E]	Australia (QLD)	Werry (2010); Werry et al. (2011, 2018); Meynecke et al. (2015); ALA (2018);	Juv Sub	Brackish water with varying salinities
23	**B**	**Gold Coast Broadwater** [-27.95°S, 153.41°E]	Australia (QLD)	Dunn et al. (2014)	U	Estuary of the Nerang River (No. 24)
24	**F**	**Nerang River** (incl. Gold Coast Canals) [-27.97°S, 153.42°E]	Australia (QLD)	Werry (2010); Werry et al. (2011, 2012, 2018); McElroy & Honnery (2017)	Juv Sub	This river is the main drainage of the Gold Coast canal system
25	**F**	**Lake Heron** (Burleigh Waters) [-28.07°S, 153.42°E]	Australia (QLD)	Shark Research Institute (2018c)	U	-
26	**F**	**Tallebudgera Creek** [-28.09°S, 153.45°E]	Australia (QLD)	Werry (2010)	Juv	-
27	**F**	**Currumbin Creek** [-28.12°S, 153.48°E]	Australia (QLD)	Werry (2010)	Juv	-
28	**F**	**Richmond River** [-28.87°S, 153.58°E]	Australia (NSW)	West & Gordon (1994); Moore (2011); White (2015); Paterson (2017); The Daily Telegraph (2017)	Juv Sub	A 2 m TL specimen was reported as far as 115 km from the ocean at Wyrallah (White 2015); juveniles were reported from Coraki at 55 km from the ocean (The Daily Telegraph 2017) and a 1.52 m TL specimen was reported from Pimlico, at 15 km from the ocean (Paterson 2017)

No.	WC	Toponym	Country	References	LHS	Comments
29	**F**	**Evans River** [-29.11°S, 153.43°E]	Australia (NSW)	Hooper (2016)	U	-
30	**F**	**Clarence River** [-29.42°S, 153.35°E]	Australia (NSW)	West & Gordon (1994); Berra (2007); Last & Stevens (2009); Lollback (2010); Bancroft (2011); Heupel et al. (2015); Carey (2018); Lee et al. (2019); Pirog et al. (2019b); Niella et al. (2021a)	N Y-O-Y Juv Sub	Reported from nearby the Grafton Bridge in Grafton (Bancroft 2011)
31	**F**	**Bellinger River** [-30.49°S, 153.02°E]	Australia (NSW)	Carey (2018)	Juv	Reported as far as 20 km from the ocean (Carey 2018)
32	**F**	**Kalang River** [-30.50°S, 152.98°E]	Australia (NSW)	Carey (2018)	Juv	-
33	**F**	**Nambucca River** [-30.64°S, 153.00°E]	Australia (NSW)	Ramsey (2016)	Ad	Ramsey (2016) reported the catch of a 3.02 m TL pregnant female in this river
34	**F**	**Macleay River** [-30.89°S, 153.01°E]	Australia (NSW)	Boeseman (1964); Thorson (1970b); White (2016)	Juv	-
35	**F**	**Belmore River** [-31.02°S, 152.94°E]	Australia (NSW)	Bishop et al. (2001)	U	Tributary of the Macleay River (No. 34)
36	**F**	**Hastings River** [-31.42°S, 152.90°E]	Australia (NSW)	Fairhurst (2015)	Sub Ad	Fairhurst (2015) reported catches of a ~3 m TL pregnant female and subadults
37	**F**	**Gloucester River** [-31.86°S, 152.11°E]	Australia (NSW)	ALA (2018)	U	Tributary of the Manning River (No. 38)
38	**F**	**Manning River** [-31.88°S, 152.67°E]	Australia (NSW)	Eagar (2017)	Ad	Eager (2017) reported a pregnant adult female from this river
39	**F**	**Hunter River** [-32.92°S, 151.77°E]	Australia (NSW)	Bielby (2014)	Y-O-Y	As far as Hinton, 40 km from the ocean (Bielby 2014)
40	**F**	**Nepean River** [-33.61°S, 150.69°E]	Australia (NSW)	NSW DPI (2006)	U	Upper stretch of the Hawkesbury River (No. 41)
41	**F**	**Hawkesbury River** [-33.56°S, 151.24°E]	Australia (NSW)	NSW DPI (2006); Boon (2017)	Ad	Boon (2017) provided a historical photograph of an adult *C. leucas* caught in this river in 1914
42	**F**	**Parramatta River** [-33.84°S, 151.17°E]	Australia (NSW)	Boeseman (1964); Thorson (1970b); Smoothey et al. (2019)	Sub Ad	The report of Boeseman (1964) presumably referred to Whitley (1940) (see comment below—additions to Table 9)
43	**B**	**Sydney Harbour** (incl. Port Jackson Bay) [-33.85°S, 151.24°E]	Australia (NSW)	Bennett (1859); Green et al. (2009); Johnston et al. (2015); West (2015); Heupel et al. (2015); Smoothey et al. (2016, 2019); Lee et al. (2019); Pirog et al. (2019b); Niella et al. (2020b) Espinoza et al. (2021)	Sub Ad	Estuary with numerous tributaries, including the Parramatta River (No. 42) and the Lane Cove River; largely modified by human activities
44	**F**	**Georges River** (incl. Chipping Norton Lake) [-34.00°S, 151.12°E]	Australia (NSW)	Boeseman (1964); Thorson (1970b); Thomas (2016)	U	The report of Boeseman (1964) presumably referred to Whitley (1940) (see comment below—additions to Table 9)

Additions to Table 9

The analysis of shark catches in northeastern Australia by Harry et al. (2011) impressively showed the preference of the euryhaline *C. leucas* for riverine environments, as *C. leucas* was the only species of shark regularly captured in river zones. Herbert & Peeters (1995) stated that *C. leucas* is distributed throughout all coastal rivers of the Cape York Peninsula and is known to penetrate great distances into freshwater. Last (2002) gave information that small specimens of *C. leucas* less than 1 m TL have reportedly nipped at the ankles of swimmers more than 100 km up rivers of Cape York, northern Queensland. Gehrke (1997) reported records of *C. leucas* from unregulated lowland river sites on the north coast of New South Wales, but without naming any precise locations.

The "Global Shark Attack File" (Shark Research Institute 2018c) included a couple of attacks having occurred in Australian rivers and lakes that are not mentioned in Tables 8 and 9. Unfortunately, the involved species could not be identified in these cases. Some of the attacks happened far inland and far up rivers and an associated lake distant from the sea, so the incidents were probably caused by specimens of *C. leucas*. For completeness, these rivers and lake are named here: Tweed River, Cataract River, Maria River (Port Macquarie), and Watson Taylors Lake. Even Whitley (1940) reported shark attacks and shark incidents in Australian rivers from the Sydney area of New South Wales, which presumably can be attributed to *C. leucas*; these occurred in the Lane Cove River, a side river of the Parramatta River (Tab. 9, No. 42), and in Cabramatta Creek, which is a tributary of the Georges River (Table 9, No. 44).

No. 5: The distribution of *C. leucas* in the Burdekin River is nowadays limited to a maximum distance of freshwater penetration of approximately 150 km by the impediment of the Burdekin Falls Dam, which prevents marine vagrants from moving up the river (Pusey et al. 2003).

No. 17: Whitley (1940) reported, from the Brisbane River, a shark attack on the Queensland State Champion outrigger. The Brisbane River is a documented nursery area for *C. leucas* (Last & Stevens 1994), and Pillans (2006) reported juvenile *C. leucas* in high numbers in this river.

Table 10. Occurrences of *Carcharhinus leucas* in Melanesian Island rivers, lakes, estuaries, and lagoons: Indian Ocean coast, including the Timor Sea and Arafura Sea coasts and the South Pacific Ocean coast. Abbreviations: WC = water conditions, F = freshwater, B = brackish water up to hypersaline conditions, F/B = salinity gradient from fresh to brackish, LHS = life history stage, Ad = adult, Sub = subadult, Juv = juvenile, Y-O-Y = young-of-the-year, N = neonate, U = unknown.

No.	WC	Toponym	Country	References	LHS	Comments
1	**F**	**Lake Sentani** (= Danau Sentani) [-2.60°S, 140.51°E]	Indonesia (West Papua)	Van Pel (1955); Herre (1955); Pacific Islands Monthly (1955); Boeseman (1956b)	U	Sharks were first reported from this location by Van Pel (1955). Iqbal et al. (2019c) reported juveniles of *Carcharhinus melanopterus* in freshwater habitats at Sentani, ~20 km from the ocean
2	**F**	**Jafuri River** (= Sungai Jafuri) [-2.72°S, 140.80°E]	Indonesia (West Papua)	Boeseman (1956b)	U	Outlet of Lake Sentani (No. 1) that drains into the Tami River (No. 3)
3	**F**	**Tami River** (= Sungai Tami) [-2.62°S, 140.91°E]	Indonesia (West Papua)	No reference, but it is logical under geographic circumstances	U	Outlet of Lake Sentani (No. 1) and its tributary, Jafuri River (No. 2)
4	**F**	**Mamberamo River** [-1.47°S, 137.88°E]	Indonesia (West Papua)	Boeseman (1964)	U	-
5	**F**	**Lake Jamoer** (= Lake Jamur, Lake Yamur, Danau Yamur, Danau Jamur) [-3.65°S, 134.93°E]	Indonesia (West Papua)	(conditionally even Boeseman 1956a); Boeseman (1964); Thorson (1970b); Berra (1981, 2007); Allen & Boeseman (1982); Garrick (1982); Compagno (1984); Keller (1987); Ellis (1989); Allen (1991, 1992); Polhemus et al. (2004); Tappin (2007); Voigt & Weber (2011); Froese & Pauly (2018a)	Juv, Sub	Already Boeseman (1956a: 24) reported unidentified sharks in Lake Jamoer and stated: "The most spectacular fish collected here was, beyond doubt, a kind of shark probably confined to fresh water." This lake is situated approximately 130 km inland from the Arafura Sea
6	**F**	**Omba River** [-4.20°S, 134.73°E]	Indonesia (West Papua)	No reference, but it is logical under geographic circumstances	U	Indications of an occurrence here are found in Boeseman (1956a). Drainage of Lake Jamoer (No. 5)

No.	WC	Toponym	Country	References	LHS	Comments
7	**F**	**Timika River** [-4.85°S, 136.99°E]	Indonesia (West Papua)	Tappin (2007)	U	-
8	**F**	**Sepik River** [-3.86°S, 144.52°E]	Papua New Guinea	Allen (1991); Kan & Tianuchi (1991); Mizue & Hara (1991); Taniuchi & Shimizu (1991); Taniuchi (2002); Berra (2007); Tappin (2007); Western Australian Museum (2014); White & Ko'ou (2018); Glaus et al. (2020)	Juv	Verified as far up river as Angoram (Kan & Taniuchi 1991) and Magendo (White & Ko'ou 2018)
9	**F**	**Ramu River** [-4.02°S, 144.66°E]	Papua New Guinea	(conditionally even Allen & Coates 1990); Allen (1991); Allen et al. (1992); Berra (2007); Tappin (2007)	U	Allen & Coates (1990) examined fins of a shark from the lower Ramu River, in all likelihood belonging to *C. leucas*
10	**F**	**Purari River** [-7.77°S, 145.16°E]	Papua New Guinea	Haines (1979a, 1983)	U	-
11	**B**	**Purari River Delta** [-7.84°S, 145.18°E]	Papua New Guinea	Haines (1979b)	U	-
12	**F**	**Fly River** [-8.34°S, 142.85°E]	Papua New Guinea	Kailola (1987); Coates (1993); Tappin (2007); Allen et al. (2008); Storey et al. (2009)	U	-
13	**F**	**Bensbach River** [-9.12°S, 141.01°E]	Papua New Guinea	Hitchcock (2002)	U	-
14	**F**	**Ouegoua River** [-20.31°S, 164.31°E]	New Caledonia	Werry & Clua (2013)	Juv	-
15	**F**	**Nera River** [-21.60°S, 165.47°E]	New Caledonia	Werry & Clua (2013)	Juv	-
16	**F**	**Carenage River** [-22.30°S, 166.86°E]	New Caledonia	Werry & Clua (2013)	Ad	Werry & Clua (2013) reported a 3 m TL adult female from this river
17	**B**	**Ouenghi River Mouth / St. Vincent Bay** [-21.95°S, 166.12°E]	New Caledonia	Thollot (1996a)	U	Estuary inside the greater South-West Lagoon
18	**B**	**South-West Lagoon** (= Lagon Sud-Ouest) [-22.00°S, 166.07°E]	New Caledonia	Thollot (1996b)	U	Large estuary system
19	**F**	**Pankumo River** (= Big River) [-16.26°S, 167.64°E]	Vanuatu (Malekula Island)	Amos (2007)	U	Largest river of Malekula Island. Reported from the upper reaches of the river (Amos 2007)
20	**F**	**Jordan River** [-15.17°S, 166.89°E]	Vanuatu (Espiritu Santo)	Kalfatak & Jaensch (2014)	U	-
21	**B**	**Jordan River Estuary** [-15.15°S, 166.89°E]	Vanuatu (Espiritu Santo)	Ceccarelli et al. (2018)	U	-
22	**F**	**Navua River** [-18.25°S, 178.15E]	Fiji (Viti Levu)	Save Our Seas Foundation (2010); Cardeñosa et al. (2016); Baoa (2017); Lee et al. (2018); Glaus (2019); Glaus et al. (2019b); Mangubhai et al. (2019)	N Y-O-Y Juv	-
23	**F**	**Deuba River** (= Ndeumba River) [-18.26°S, 178.11°E]	Fiji (Viti Levu)	Glaus et al. (2019b)	N Y-O-Y Juv	Outlet of the Navua River (No. 22)

No.	WC	Toponym	Country	References	LHS	Comments
24	**F**	**Wainibuka River** [-17.81°S, 178.34°E]	Fiji (Viti Levu)	Baoa (2017)	Y-O-Y	Upper stretch of the Rewa River (No. 25)
25	**F**	**Rewa River** [-18.11°S, 178.53°E]	Fiji (Viti Levu)	Fowler (1959); Thorson (1970b); Ryan (1980); Baoa (2017); DSM (2017, 2019); Marie et al. (2017); Glaus (2019); Glaus et al. (2019a, 2019b)	N Y-O-Y Juv	As far as 40 miles (= 64 km) up the river (Fowler 1959). This river system functions as a nursery ground for numerous shark species (Tuiwawa et al. 2013)
26	**B**	**Rewa River Delta / Estuary** [-18.14°S, 178.53°E]	Fiji (Viti Levu)	Tuiwawa et al. (2013); Brown (2014)	Juv	-
27	**F**	**Sigatoka River** [-18.17°S, 177.51°E]	Fiji (Viti Levu)	Ryan (1980); Baoa (2017); D SM (2017); Flükiger (2018); Glaus (2019); Glaus et al. (2019a, 2019b)	N Y-O-Y Juv	Downgraded river system (Glaus et al. 2019a). Ryan (1980) reported records from Keyasi
28	**F**	**Ba River** [-17.47°S, 177.65°E]	Fiji (Viti Levu)	Lee et al. (2018); Vierus et al. (2018), Paris et al. (2019)	Juv	-
29	**B**	**Ba Estuary** [-17.45°S, 177.64°E]	Fiji (Viti Levu)	Paris et al. (2019)	N Y-O-Y Juv	Mouth of the Ba River (No. 28)
30	**F**	**Dreketi River** [-16.54°S, 178.86°E]	Fiji (Vanua Levu)	Glaus et al. (2019a); Paris (2021)	N Y-O-Y Juv	-
31	**F**	**Nasavu River** [-16.22°S, 179.76°E]	Fiji (Vanua Levu)	Lewis & Pring (1986); Jenkins & Boseto (2003)	U	Jenkins & Boseto (2003) reported *C. leucas* in the lower Nasavu River, near Vitina Village

Additions to Table 10

For completeness, Allen (1996), presumably referring to Lake Jamoer (Table 10, No. 5), included *C. leucas* in a list of freshwater fishes that occur in coastal streams of Irian Jaya (= West Papua, Indonesian New Guinea). Gehrke et al. (2011) reported the harvesting of *C. leucas* in lowland rivers and estuaries in Papua New Guinea, but without naming a precise locality.

For New Caledonia, there are further notes of *C. leucas* in inland waters (freshwater) by Marquet et al. (1997), but without a precise locality. Acoustic tagging of *C. leucas* in the southern province of New Caledonia by Werry et al. (2010) revealed migrations of *C. leucas* into Prony Bay, in which some small creeks (Rivière Bleue, Ruisseau de la Bergerie) drain. Possibly, this is a further breeding place for *C. leucas* in New Caledonia.

The first mention of occurrences of *C. leucas* in freshwaters of Fiji was by Günther (1870: 368), who described a 30 inch (= 76.2 cm TL) juvenile, but with imprecise locality data: "In fresh waters of the island of Viti-Levu." Günther (1870: 368) examined one collected specimen in the Britsh Museum that was identified as *Carcharias gangeticus* and taken at Viti Levu, and which he re-identified as *C. leucas*: "Our examples agree perfectly with Müller and Henle's description of *C. leucas*." However, he later (Günther 1874) made the interesting statement that *Carcharias gangeticus* inhabits the freshwaters of Viti Levu, in a lake separated from the sea by a cataract. Unfortunately, it is not possible to identify the locality referred to by Günther. Nevertheless, several authors reported *C. leucas* from Fiji under the name *Carcharias gangeticus*. Engelhardt (1913: 43) reported *Carcharias gangeticus* "… in süßen Gewässern der Fidschiinseln" [= "in fresh waters of the Fiji Islands"]. *Carcharhinus leucas* was later generically reported from Fiji by Fowler (1928, 1959) under the names "*Eulamia gangeticus*" and "*Eulamia gangetica*" and by Whitley (1927) under the name *Carcharinus gangeticus* [sic]. Ryan (1980: 59) listed *Carcharhinus gangeticus* in the checklist of the brackish and freshwater fishes of Fiji, but he commented: "….it is likely that this shark is *C. leucas*." He (Ryan 1980: 59) further remarked: "Reported from a long way up a number of Fiji rivers." Boseto & Jenkins (2006) compiled the results of earlier works about the fish fauna of Fiji and mentioned *C. leucas* for fresh and brackish water habitats too, but without naming a precise locality. Also Boseto (2006) and Jenkins et al. (2009) mentioned *C. leucas* in listings of freshwater fishes of Fiji, but they didn't provide any localities. Possibly, *C. leucas* occurs in further major rivers in Fiji (see Table 10), as indicated by the anecdotal reports mentioned by Rasalato et al. (2010). Jenkins & Jupiter (2011) listed *C. leucas* as a marine migrant in the freshwaters of Vanua Levu (Kubulau district), again without naming a precise locality. Glaus et al. (2015) reported catches of sharks in Fijian rivers by artisanal fisheries—probably all juvenile *C. leucas*.

No. 1: There is a further indication of the presence of sharks (and sawfishes) in Lake Sentani in Van Pel (1958: 29): "While populated mainly with fresh-water species, it is remarkable that some sea fish are also found in its waters."

No. 5: The first, and so far only, scientific report of sharks in Lake Jamoer, and an early indication of *C. leucas*'s occurrence there, was by Boeseman (1956a: 24): "The most spectacular fish collected here was, beyond doubt, a kind of shark probably

confined to fresh water." Boeseman and his team collected three voucher specimens of *C. leucas* from Lake Jamoer, which are nowadays part of the fish collection of the Naturalis Biodiversity Centerin Leiden (catalog nos.: RMNH 24699, ♂ 146 cm TL; RMNH 24611, ♀ 73 cm TL; RMNH 24697, ♀ 125 cm TL; see Allen & Boeseman 1982). Polhemus et al. (2004) concluded that the population of *C. leucas* in Lake Jamoer, which may or may not still be present, was representative of a remarkably isolated inland population. However, there is no reason to believe that these sharks were isolated, as this lake is connected with the Arafura Sea by the Omba River (Table 10, No. 6). On the other hand, Polhemus et al. (2004) were almost certainly correct in their statement that modern fishing methods (gillnetting) may have played a major role in the presumed demise of *C. leucas* in Lake Jamoer. Allen (1991) reported that *C. leucas* was very common in Lake Jamoer in the 1950s, but its current population size is unknown.

No. 12: On the occurrence of *C. leucas* in the Fly River, Roberts (1978: 10) wrote: "…this species is to be expected in the Lower Fly and might occur in the Middle and Upper Fly, although there is no evidence that it does."

No. 24: Copeland (2013) also reported that the villagers of Viria, located on the Rewa River approximately 50 km upstream from the coast, in the province of Naitasiri, tell anecdotes about the presence of sharks in the river.

Conclusive remarks

The present account of low salinity habitats with occurrences of *C. leucas* shows that the Atlantic Ocean side of the North American continent has the highest number of habitats, followed by the Atlantic side of Central/South America and the Indian Ocean side of the African continent (Fig. 3). The number of identified habitats was lowest for the Atlantic part of Africa and the Pacific part of the American continent.

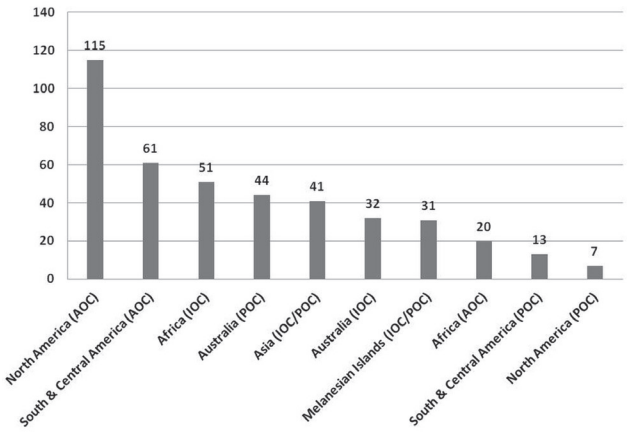

Fig. 3. Absolute numbers of fresh and brackish water localities with verified records of *Carcharhinus leucas* (n = 415) per continent/region, ordered from highest to lowest. Abbreviations: AOC = Atlantic Ocean coast; IOC = Indian Ocean coast; POC = Pacific Ocean coast.

4 Distribution and available distribution maps of *Carcharhinus leucas*

Carcharhinus leucas is a circumglobal warm-water species with populations in tropical to subtropical and warm-temperate parts of both hemispheres (Bass et al. 1986; Compagno 1984, 2001). The greatest latitudinal (north to south) amplitude is in the western Atlantic Ocean, from 41.53°N (Woods Hole, Massachusetts, USA) to -35.00°S (Buenos Aires Province, Argentina). So far, there are no records of this species from the Mediterranean and the Red Sea (Cadenat & Blache 1981; Compagno 1984, 2001; Randall 1986; Golani & Fricke 2018).

The occurrences of highly migratory sharks, including *C. leucas*, depend on and vary with seasonal climatic changes (Calich et al. 2018). Seasonality is a highly influencing factor for the regional distribution of some carcharhinid sharks, including *C. leucas*. Springer (1938) reported that *C. leucas* (as *C. platyodon*) was absent in the Florida waters of Englewood from December to February, when it was replaced by other carcharhinids like *C. plumbeus* and *C. obscurus*. In Fijian waters, the abundance of *C. leucas* is inversely related to that of *C. amblyrhynchos* Bleeker, 1856 (gray reef shark) due to seasonal changes in shark species composition, presumably induced by reproductive behavior. Also in Fiji, the peak of the highest numbers of *C. amblyrhynchos* was recorded from October to December (with the highest abundance from July to December), simultaneously with the lowest numbers of *C. leucas* (Brunnschweiler & Earle 2006; Brunnschweiler & Baensch 2011; Brunnschweiler et al. 2014). The authors suggested that the absence of *C. leucas* during this period was a result of reproductive behavior, so a seasonal competitive exclusion induced by reproduction may affect the dispersal of *C. leucas* at a local or regional scale.

Although knowledge of *C. leucas* and its distribution has increased during the last decades, the full extent of its range in some regions remains unclear. During approximately the last two decades, for example, *C. leucas* was recoreded from the following twenty-five remote oceanic islands, archipelagos, sea banks, and seamounts:

- Abrolhos Archipelago, 65 km off Brazil, western Atlantic Ocean (Bornatowski et al. 2012)
- Vitória-Trindade Seamount Chain, Montague Seamount, ~400 km off Brazil and Trindade Island, ~1,160 km off Brazil, western Atlantic Ocean (Pinheiro et al. 2015)
- Fernando de Noronha Archipelago, ~365 km off Brazil, southwestern Atlantic Ocean (Lessa et al. 1999; Bezerra et al. 2021)
- Rocas Atoll, ~250 km off Brazil, western Atlantic Ocean (Bezerra et al. 2021)
- Los Roques Archipelago, ~125 km off Venezuela, Caribbean Sea (Tavares 2001)

- San Andrés Archipelago, reported from Quita Sueño Bank, ~220 km off Nicaragua, Caribbean Sea (Ballesteros 2007; Puentes et al. 2009; Caldas et al. 2010; Caldas & López-García 2011; Mejía-Falla & Navia 2011; Bolaños-Cubillos et al. 2015; Mejía-Falla et al. 2020)
- Azores Archipelago, ~3,600 km off Massachusetts, USA and ~1,800 km off Morocco, northeastern Atlantic Ocean (first reported by Santos et al. 1997, later confirmed by Gadig et al. 2006; subsequently considered by Arruda 1997; George & Zidowitz 2006; Porteiro et al. 2010; Barreiros & Gadig 2011; Afonso et al. 2013; Ebert & Stehmann 2013; Carneiro et al. 2014, 2019; SRMCT 2014; Barcelos & Barreiros 2020; Santos et al. 2020; Barcelos et al. 2021)
- Cape Verde Islands, ~570 km off the African continent, eastern Atlantic Ocean (Wirtz et al. 2013)
- Principe Island, ~ 225 km off the African continent, eastern Atlantic Ocean (Nuno et al. 2015)
- Comoros Archipelago. Reported from Mayotte, ~300 km off Madagascar and ~495 km off the African continent, western Indian Ocean (Pinault & Wickel 2014; Wickel et al. 2014)
- Glorieuses Archipelago ("Scattered Islands"), ~180 km off Madagascar and ~740 km off the African continent, western Indian Ocean (Le Manach & Pauly 2015)
- Mascarene Islands, reported from Reunion Island, ~700 km off Madagascar and Mauritius, ~900 km off Madagascar, (Fricke 1999; Fricke et al. 2009; Trystram et al. 2016) and recently from Rodrigues, ~1,500 km off Madagascar, western Indian Ocean (Pirog et al. 2019b)
- Seychelles, ~1,500 km off the African continent, western Indian Ocean (Nevill et al. 2007, 2013; Clua et al. 2014; Lea et al. 2015, 2018)
- Chagos-Laccadive Ridge, ~270 km off the Indian subcontinent, northern Indian Ocean (Bineesh et al. 2014)
- Andaman Archipelago. Reported from Interview Island, ~320 km off Myanmar and Nicobar Archipelago, ~400 km off Sumatra, Andaman Sea, eastern Indian Ocean (Tyabji et al. 2018, 2020; Kumar et al. 2018)
- Xisha Islands (= Paracel Islands), ~400 km off the Asian continent and Nansha Islands (= Spratly Islands), ~720 km off the Asian continent, South China Sea, western Pacific Ocean (Deng et al. 2019)
- Okinawa Island (Ryukyu Islands, Japanese Island Chain), ~700 km off the coast of China, Asian continent, western Pacific Ocean (Matsumoto et al. 2006; conditionally even Japanese Group for Elasmobranch Studies 1984, see paragraph 4.3.1)
- Iriomote Island and Ishigaki-jima Island (Yaeyama Islands, Japanese Island Chain), ~450 km off the coast of China, Asian continent, western Pacific Ocean (Tachihara et al. 2003; Matsumoto et al. 2006; Masunaga et al. 2008; Shimose & Taira 2014)
- Tuvalu (Polynesia). Reported from a reef pass near Ava i te Lape, the main passage into Funafuti Lagoon, ~3,300 km off the Australian continent, southern Pacific Ocean (Thaman 2015)
- Tonga (Polynesia), ~3,270 km off the Australian continent, southern Pacific Ocean (Brunnschweiler & Compagno 2008)
- Rurutu (French Polynesia), ~5,600 km off the Australian continent and ~8,000 km off the South American continent, south-central Pacific Ocean (Mourier & Planes 2015)
- Guadalupe Island, ~260 km off Baja California, Mexico, eastern Pacific Ocean (Gallo-Reynoso et al. 2005; Reyes-Bonilla et al. 2010)
- Revillagigedo Islands, ~400 km off Baja California, Mexico, eastern Pacific Ocean (Castro-Aguirre & Balart 2002; Robertson & Allen 2015; Del Moral-Flores et al. 2016; Fourriére et al. 2016)
- Islas Marias Archipelago, ~100 km off from continental Mexico (Nayarit), central-east Pacific Ocean (Pérez-Jiménez et al. 2005; Erisman et al. 2011)
- Malpelo Island, ~400 km off the South American continent, eastern Pacific Ocean (McCosker & Rosenblatt 1975; Prahl 1990; Caldas & López-García 2011; Mejía-Falla et al. 2011, Álvares-León et al. 2013)

Apart from Malpelo Island, *C. leucas* was not known from these oceanic islands until the recent past. These occurrences disprove the long-time belief that *C. leucas* is only a littoral shark species, even though it exhibits a strong link to continental shelves and coasts. Randall (1977) and Johnson (1978) reported *C. leucas* from Rangiroa Atoll, an oceanic island of the remote archipelago of Tuamotu (French Polynesia; ~6,300 km off the Australian continent), as subsequently also reported by Randall (1985) and Siu et al. (2017).

In contrast to these recent records, Bigelow & Schroeder (1948: 341) had presumed that *C. leucas* occurred "…perhaps never very far from land except by accident." Moreover, only thirty years ago, Fischer & Bianchi (1984) mentioned *C. leucas* as "…not occurring off oceanic islands far from continental landmasses." As the numerous records of *C. leucas* from oceanic islands reveal, these statements underline the increase in knowledge in ongoing ichthyological and elasmobranch research.

Chiaramonte (1998) and Menni & Lucifora (2007) outlined a new southern range limit for *C. leucas* in the western South Atlantic, from Argentine waters. Moreover, transoceanic migration between oceanic islands of this primarily coastal species has been proved (Lea et al. 2015). Improved marine research and investigation methods (e.g., determination from teeth, angling and net

Table 11. Verified global records of *Carcharhinus leucas* in inland rivers and lakes, with recorded distances from the ocean ranked from greatest to smallest. Only the primary reference is provided.

No.	Toponym	Country	Distance from ocean (in km)	Reference
1	**Amazon River / Ucayali River**	Peru	5,080	Thorson (1972a)
2	**Mississippi River**	USA	2,800	Thomerson et al. (1977)
3	**Zambezi River**	Mozambique / Zimbabwe / Zambia	1,120	Bass et al. (1973)
4	**Red River**	USA	950	Matich et al. (2020b)
5	**Jubba River**	Somalia	875	Garrick (1982)
6	**Tigris River**	Iraq	850	Günther (1874)
7	**Ruenya River**	Zimbabwe	580	Pienaar (1968)
8	**Limpopo River / Luvuvhu River**	Mozambique / South Africa	480	Pienaar (1968)
9	**Karun River**	Iran	420	Sykes (1902)
10	**Lake Nicaragua**	Nicaragua	345	Watson & Thorson (1976)
11	**Fitzroy River (Kimberley Region)**	Australia	320	Chubb et al. (1979)
12	**Shire River**	Mozambique / Malawi	312	Tweddle & Willoughby (1979)
13	**Gambia River**	Gambia	290	Svensson (1933)
	Patuca River	Honduras	290	Bigelow & Schroeder (1948)
14	**Euphrat River**	Iraq	260	Coad (2010)
15	**Atchafalaya River**	USA	258	Gunter (1938)
16	**Agusan River**	Philippines	252	Herre (1953)
17	**Hooghly River**	India	230	Day (1878)
	Magdalena River	Colombia	230	Dahl (1971)
18	**Roper River**	Australia	200	Dally & Larson (2008)
19	**Senegal River**	Senegal	175	Steindachner (1870)
20	**Indragiri River**	Indonesia	150	Hasan & Widodo (2020)
21	**Lake Jamoer**	Indonesia	130	Boeseman (1964)
22	**Atrato River**	Colombia	115	Dahl (1964)
	Richmond River	Australia	115	White (2015)
23	**Wenlock River**	Australia	110	Dwyer et al. (2020)
24	**Hondo River**	Mexico / Belize	100	Jones (1985)
25	**Pongola River**	Mozambique / South Africa	80	Pienaar (1968)
	Usumacinta River	Mexico	80	Castro-Aguirre et al. (1999)

captures, commercial fishing, diving observations, direct visual observations, baiting) may detect *C. leucas* at localities from where this species was previously not known. Thus, gaps in our knowledge of the distribution of *C. leucas* are being progressively smaller. Although new data about life history traits of *C. leucas* are becoming available (Heupel & Simpfendorfer 2008, 2011; Lea et al. 2015; Brunnschweiler 2018a), the migration patterns of this shark are still poorly understood, so a precise overview of the species' distribution may help understand the migration pathways of *C. leucas*.

Biogeography can help close existing distribution gaps of species. The available distribution maps for *C. leucas* (Compagno 1984, 2001; IUCN 2018) represent the current state of knowledge, but show numerous gaps in its range worldwide. For many regions and countries within its range, there are only a few known recordsof *C. leucas*. In the distribution maps by Compagno and the IUCN, gaps can be found, for example, from the Western Sahara and Mauritania on the West African coast in the eastern Atlantic, along the coast of Pakistan in the northern Indian Ocean, and along the coasts of northern Viet Nam and China in the South China Sea/western Pacific Ocean. The occurrence of this shark along the United States' Pacific coast in southern California has not yet been clarified (Swift et al. 1993). Further investigations in data-poor

regions may close these gaps, increasing the known distribution of *C. leucas* (Cardeñosa et al. 2016). In any case, an informative and reliable distribution map is necessary to better understand the migration paths, population networks, and gene flow of this species.

Migrations of adult female *C. leucas* may be motivated by reproduction (Lea et al. 2015). Young *C. leucas* in particular, and to a lesser extent also adults, are known to undertake large-scale migrations in freshwater environments, particularly in large rivers (Table 11). Due to its primarily tropical stronghold, *C. leucas* especially enters the rivers and lakes of the tropics; this also occurs in the subtropics and the warm-temperate regions of the world (see Tables 1–10), and subtropical riverine and estuarine systems can play a crucial role as nursery grounds for the species (Moore 2013, 2018). In this context, Budker (1971: 136) made an early attempt of localization of the intrusions of sharks into freshwaters: "It should be made clear at the outset that, while marine sharks may stray far from their normal habitat in the tropics, there are no sharks known in the rivers of the temperate zone. Freshwater sharks mainly occur within latitudes 30°N and 30°S. The extreme limit is probably about 35° on either side of the equator." Some recent surveys (e.g., Bangley et al. 2018a, 2018b) have shown that the penetration of freshwater by *C. leucas* even occurs at the margins of its distribution, in temperate regions a little farther than 35°N. Albeit that the statement by Budker (1971) is no longer completely accurate, the majority of freshwater incursions by *C. leucas* occur in the tropics due to its tropical center of distribution.

Budker (1971), with reference to Schwartz (1959), mentioned that *C. leucas* also occurs in the brackish waters of Chesapeake Bay at 37°N. However, McAuley et al. (2007) reported that *C. leucas* is extremely rare in the subtropical and temperate inshore waters of Western Australia at the species' range limit. It seems likely that *C. leucas* is rarer at the limit of its distribution, where it is only a visitor during the summer months due to its seasonally influenced migrations. Jawad (2017), with reference

Fig. 4. Distribution map of *Carcharhinus leucas* based on the present literature review, showing major rivers and uncertain areas ("?").

to Hussain et al. (2012), reported an inland occurrence of *C. leucas* from Nasiriyah City on the Euphrat River of Iraq at 31.03°N, and stated that this record represents the northernmost extension for this species. This is incorrect both for inland and marine waters, because *C. leucas* was reported from north of Bagdhad, in the Tigris River at 33.43°N, from Chesapeake Bay at 39.53°N, and from Woods Hole (Massachusetts) at 41.53°N (see above).

At the west coast of the South American continent (eastern Pacific Ocean), the northerly directed cold Humboldt Current may limit the distribution of *C. leucas*, which prefers the warmer parts of the Pacific Ocean. Furthermore, on the west coast of Africa (eastern Atlantic Ocean), the northerly directed cold Benguela Current (Benguela Upwelling System) likely pushes the distribution limit of *C. leucas* southwards to Angola, so this species is absent in Namibian waters (see distribution maps of Compagno 1984, 2001; IUCN 2018) (Fig. 4). Seasonally affected warming of ocean parts also influences the distribution of *C. leucas*, for example along the east coast of North America (western Atlantic Ocean), where studies have revealed a strong migration behavior of *C. leucas*. It is a rare summer visitor to Virginia's and Maryland's Chesapeake Bay (Smith & Merriner 1986) and farther north along the coasts of New Jersey, New York, and Massachusetts; it also occurs farther south in Georgia and North Carolina, mainly during the summer months (Castro 2011). Compagno (1984, 2001) and Simpfendorfer & Burgess (2009) delivered detailed overviews of the global distribution of *C. leucas*. According to these authors, and considering some further results about the distribution of *C. leucas* (e.g., Sommer et al. 1996; Chiaramonte 1998; Gadig et al. 2006; Brunnschweiler & Compagno 2008; Menni & Lucifora 2007; Satapoomin 2011; Van Overzee et al. 2012; Ebert et al. 2013a, 2013b; Fernando 2014; iNaturalist.org 2018), *C. leucas* inhabits the continental waters, coastlines, and islands of the following major oceans and adjacent states:

- Atlantic Ocean coast (western part): Massachusetts (USA) to Argentina (Buenos Aires Province), Gulf of Mexico and Caribbean Sea including Bahamas, Cuba, Haiti, Jamaica, Dominican Republic, Puerto Rico, Virgin Islands, U.S. Virgin Islands, Greater Antilles, Lesser Antilles (incl. Netherlands Antilles), Mexico, Belize, Guatemala, Honduras, Nicaragua, Costa Rica, Panama, Colombia, Venezuela; Guyana, Suriname, French Guyana, Brazil, Uruguay.
- Atlantic Ocean coast (eastern part): Morocco, Mauritania, Senegal to Angola including Gambia, Guinea-Bissau, Guinea, Sierra Leone, Liberia, Ivory Coast, Ghana, Togo, Benin, Nigeria, Cameroon, Equatorial Guinea, Gabon, Congo, Democratic Republic of the Congo, Cape Verde Islands.
- Central Atlantic Ocean islands: Azores.
- Indian Ocean (western part): South Africa to Somalia and Djibouti, incl. Mozambique, Tanzania, Kenya, Madagascar, Réunion Island, Mauritius, Seychelles, also in inland waters of Malawi, Zambia and Zimbabwe.
- Indian Ocean (northern part): Yemen, Oman, Persian Gulf including Iraq, Iran, Kuwait, Saudi Arabia, Qatar, United Arab Emirates, Pakistan, India, Sri Lanka, Bangladesh.
- Indian Ocean (eastern part): Andaman and Nicobar Archipelagos, Myanmar, Thailand (Bay of Bengal and the Andaman Sea), Malaysia, Indonesia (Sumatra, Borneo, Java, Lombok, West Papua), Western Australia.
- Pacific Ocean (western/southern part): Thailand (Gulf of Thailand), Malaysia, Singapore, Cambodia, Viet Nam, southern and eastern China, Taiwan, southern Japan (Okinawa Prefecture), Philippines, Brunei Darussalam, Indonesia (Sumatra, Borneo, Java, Lombok, West Papua), Republic of Palau, Papua New Guinea, eastern Australia, Solomon Islands, New Caledonia, Vanuatu, Fiji, Tuvalu, Tonga, Samoan Islands (including American Samoa).
- Central Pacific Ocean islands: French Polynesia (Rangiroa Atoll, Tuamotu Archipelago, Rurutu).
- Pacific Ocean (eastern part): Possibly southern USA (California), Guadalupe Island, Revillagigedo Islands, southern Baja California, Gulf of California to Peru (verified as far south as Paita) including Mexico, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, Colombia, Ecuador.

The available distribution maps for *C. leucas* reveal numerous gaps and discontinuous range sections, for different reasons (for example map up-to-dateness or paucity of data). Martin (2004) provided a global map outlining the "hotspots" of worldwide freshwater occurrences of the species. The ReefQuest Centre for Shark Research (2018) provided a very interesting and serious map of a selection of global freshwater recordings of *C. leucas*, with remarkable information about the traveling distance (in km) in particular freshwater systems. The distribution map provided by Compagno (2001) shows gaps in the distribution, probably resulting from lack of data about *C. leucas* from particular regions, although some absences may be real. For example, Compagno's map shows a bigger gap between locality records of this species in the Persian Gulf and locality records in western India and on the east coast of the African continent.

Many maps, especially those available from different internet sources, display erroneous range information for *C. leucas*, and the most reliable maps remain those of Compagno (2001) and the IUCN (2018). Wikipedia (Internet Reference 6) also provides a very detailed

and reliable map based on the IUCN's map, which also includes recent records of this species such as those from the Azores. Fernando (2014) stated that he was extending the range of *C. leucas* by including Sri Lanka, but he did not consider the earlier report by Morón et al. (1998) and historical reports indicating a much more earlier presence of the bull shark in waters of this country. Southwell (1912). Southwell (1912) gave a much earlier indication of an occurrence of *C. leucas* in the waters of Sri Lanka in reporting cestode parasites from "*Carcharias gangeticus*" from examined shark material from that country, which in fact was probably *C. leucas*. Sivasubramaniam (1969: 67) reported "*Carcharhinus gengiticus*" from waters off Ceylon, but it is unclear if the author was referring to *C. leucas* or *G. gangeticus*. Dalpathadu (2012) also reported *C. leucas* in a provisional checklist of marine and brackish water fishes in Sri Lankan waters, and *C. leucas* has been commonly identified from fishery landings and fish markets of different locations along the Sri Lankan coast by DNA barcoding (Peiris et al. 2021). Compagno (1984, 2001) marked areas of possible occurrence of *C. leucas*, such as Peru, the Indian Ocean coast of Yemen and Oman on the Arabian Peninsula, and Pakistan, with question marks and notes, showing how restricted knowledge of the distribution of some shark species was until recently.

4.1 Distribution in the Atlantic Ocean

4.1.1 Distribution in the western Atlantic Ocean

This section is based on Tables 1 and 3 and summarizes the state of knowledge of the distribution of *Carcharhinus leucas* in marine habitats of this ocean basin.

According to Compagno (2002b), the distributional boundaries of *C. leucas* in the western Atlantic range from Massachusetts and New York, where the species is rare, to Uruguay and Argentina. On the east coast of the United States, the distribution of *C. leucas* depends on seasonal fluctuations of seawater temperature, with a northwards movement along the West Atlantic coast during summer from its tropical stronghold, and a southwards retreat when the water cools (IUCN Shark Specialist Group 2007). *Carcharhinus leucas* undertakes expansive seasonal migrations along the east coast of the United States, which lead to temporary range shifts. There is conflicting information in the literature on how far north in the United States *C. leucas* migrates during the summer months. In the tropical waters of Florida, *C. leucas* is a resident throughout the year (Bigelow & Schroeder 1948); however, it is important to note that *C. leucas* is migratory even at the lower latitudes of Florida and Texas, and that the only estuary system in the United States where *C. leucas* is known to reside year-round, based on scientific studies (Matich & Heithaus 2012), is the Shark River Estuary (Table 1, No. 27).

Regarding the northernmost distributional limit of *C. leucas* in the United States, there is an old and uncertain record from Woods Hole near Cape Cod (Massachusetts), based on photographs investigated by Nichols & Breder (1927: 16): "Woods Hole, status uncertain due to confusion with related species." Nichols (1918) and Nichols & Breder (1927) reported large males of *C. leucas* from the south shore of Long Island (New York), and further notes on a sex-separated distribution of *C. leucas* on the east coast of the United States were given by Schwartz (1958a) and Springer (1960). Springer (1960) reported *C. leucas* from Chesapeake Bay to New York, mentioning that *C. leucas* in this area was usually represented by adult males, whereas females and young were only present sporadically. This information is of importance, because the appearance of adult male carcharhinid sharks at the periphery or in the cooler parts of their ranges has been frequently observed (Springer 1960), and gene dispersal in *C. leucas* is assumed to be primarily driven by adult males (Pirog et al. 2019b).

Earlier, Springer (1938) gave the northern range limit of *C. leucas* as farther south, in waters off South and North Carolina, but he later (Springer 1950) revised it to the vicinity of New York Harbor. Bigelow & Schroeder (1945) mentioned that the distribution of *C. leucas* in the Western Atlantic ranges from southern Brazil to North Carolina, and that specimens occasionally stray as far north as New York. For the east coast of the United States, Bigelow & Schroeder (1948: 343) further reported: "Evidently it occurs only as a stray along the sector thence northward as far as New York, where the only report ostensibly referring to it is of one New Jersey specimen." Verifiably, *C. leucas* reaches Chesapeake Bay (Maryland) during the summer months (Schwartz 1958a, 1958b, 1959, 1960a; see Table 1). Tucker (1954) mentioned that the range of *C. leucas* stretches, in the western Atlantic, from New York to southern Brazil. Later, Springer (1960: 33) noted: "Bull sharks occur from Long Island southward and are migratory but their centers of abundance are in the Gulf of Mexico and southward, particularly near the mouths of large rivers." Perlmutter (1961) wrote that *C. leucas* ranges in the western Atlantic from North Carolina to southern Brazil, and north to New York as a stray.

Also D'Aubrey (1964) reported that the distribution of *C. leucas* ranges in the western Atlantic from Brazil to the vicinity of New York. Musick (1972) and White (1989) noted *C. leucas* as an occasional to common summer visitor in the lower and upper Chesapeake Bay (Virginia, Maryland). Schwartz & Burgess (1975) gave more detailed information for North Carolina, i.e., the presence of *C. leucas* in inshore waters from July to September, with a distribution in the western Atlantic that ranges from New York to Brazil. Burgess & Ross (1980: 36) commented, with reference to Bigelow & Schroeder (1948):

"In Atlantic, ranges from Chesapeake Bay (and possibly occasionally as far north as Woods Hole, MA) to Brazil." Robins & Ray (1986) stated that *C. leucas* occurs from southern New England to Brazil. Grace (2001: 19) reported, about the northern range limit of *C. leucas* and its distribution in the western North Atlantic: "From New York south including the Bahamas, Gulf of Mexico, and Caribbean."

Garrick (1982) examined a specimen of *C. leucas* (catalog no.: NMW 61-427, ♂ 820 mm TL; note that the catalog entry was incorrectly written as "NMV" by Garrick) captured in 1874 in waters off Massachusetts, which proves that *C. leucas* has at least occasionally reached as far north as Massachusetts, possibly only in years with an intense warming of ocean water masses and a strong influence of the Gulf Stream. Garrick (1982: 90) further commented: "Western Atlantic from Massachusetts in the north, where leucas is an infrequent visitor." On the other hand, Castro (2011a: 430) stated: "It is likely that bull sharks occasionally reach New Jersey and New York, but I have been unable to verify any record. It is a rare summer visitor to Chesapeake Bay." Murdy & Musick (2013) reported that *C. leucas* is a rare to occasional summer visitor to the Chesapeake Bay, but that it may be expected to occur here more frequently in the future due to climate change and global warming. However, already Schwartz (1984, 1989) reported *C. leucas* from coastal waters off South Carolina, North Carolina, and Virginia. Musick et al. (1999) reported that *C. leucas* is rare in Virginia's lagoons. One large specimen (287 cm TL, sex not determined) of *C. leucas* was reported by Musick (2001) from Virginia Beach, Virginia in September 2001, with the additional information that *C. leucas* is seldomly captured in Virginian waters and is rare in Virginia. In conclusion, *C. leucas* is a summer visitor in states north of Florida along the United States' east coast, and undertakes large-scale seasonal migrations as far as its extreme northern range limit in Massachusetts waters.

There is doubtful information regarding the occurrence of *C. leucas* in Bermuda. The report of *C. leucas* (as *Carcharinus platyodon* [sic]) from Bermuda by Barbour (1905), based on an identification by Garman, seems doubtful, as Garman later misidentified a *Carcharhinus plumbeus* specimen from Guadeloupe as *C leucas* as (Garman 1913) and was clearly unfamiliar with this species and its diagnostic features. Bean (1906) reported *C. leucas* (as *Carcharhinus platyodon*) from Bermuda. In GBIF (2018b), there is an entry for *C. leucas* based on parts of a preserved specimen. Parts of a single voucher specimen from Bermuda (catalog no.: NYZS 25055) were collected in 1929–1930 during the Bermuda Oceanographic Expedition of the New York Zoological Society. Only the caudal fin and a half gill arch of an approximately 2 m TL male shark were preserved (D. Catania 2018, pers. comm.). In all probability, this record is based on a misidentification of *Carcharhinus galapagensis* Snodgrass & Heller, 1905 (Galapagos shark), which is a common carcharhinid around the Bermuda Islands (Compagno 1984), or of another carcharhinid. Without teeth or other diagnostic parts, a morphological determination of the voucher specimen would seem difficult, in which case only DNA barcoding may confirm or exclude the presence of *C. leucas* in Bermuda (see Chan et al. 2003). Briggs (1958) also mentioned *C. leucas* from Bermuda, possibly referring the same, doubtful specimen.

The investigation by Carlson et al. (2010) revealed various movement patterns of *C. leucas* along the southern coast of the United States (Gulf of Mexico), with indications that specimens are found primarily in shallow waters and reside at the same location for long periods, whereas some individuals travel long distances and over open ocean areas. Navia et al. (2016) reported *C. leucas* from offshore waters of the Caribbean Sea and Pacific Ocean. Also Drymon et al. (2010) reported *C. leucas* in offshore waters of the northern Gulf of Mexico. Brunnschweiler & Van Buskirk (2006) reported the open ocean migration of a female *C. leucas* from the Bahamas to a known nursery ground along the Florida coast, which was the first evidence of a movement by *C. leucas* between the Bahamas and Florida. As a large shark species, adults of *C. leucas* are presumably capable of covering large distances easily. Although the activity of *C. leucas* seems mainly limited to small-scale movements, this large shark can be highly migratory under certain circumstances (Bres 1993; Calich 2016), under different driving forces such as seasonal warming/cooling of water bodies and reproduction. Interestingly, like in some other requiem sharks of the genus *Carcharhinus*, *C. leucas* exhibits an ontogenetic increase in the span of its pectoral fins (Iosilevskii & Papastamatiou 2016). This makes adults of *C. leucas* well-adapted to more open waters and pelagic activities, even though juvenile specimens have proportionately larger caudal fins compared to adults (Irschick & Hammerschlag 2015).

The original description of *Carcharhinus leucas* by Valenciennes in Müller & Henle (1841) was based on specimens collected from the Antilles (Garrick 1982). Of the four syntypes, two stuffed specimens (catalog nos.: MNHN A-9650: ♂ 1600 mm TL; MNHN A-9652: ♀ 1869 mm TL) are still preserved in the MNHN, whereas the remaining two are apparently lost (Compagno 1984). Not knowing that Valenciennes had already made a valid species description, Poey (1858, 1875) reported *C. leucas* under the names *Squalus obtusus* and *Eulamia obtuse*, based on specimens that were collected from Cuba. Bigelow & Schroeder (1948), and recently Aguilar et al. (2014), also reported *C. leucas* for the marine waters of Cuba. Additionally, *C. leucas* was reported for the Carib-

bean coast of Lower Central America by Bussing & López (2010). Grace et al. (2000) reported the capture of a 1.7m TL specimen of *C. leucas* from the small uninhabited Navassa Island in the Caribbean Sea. Also for the Caribbean Sea, *C. leucas* was recorded from the U.S. Virgin Islands, where it is reported as an occasional visitor (Smith-Vaniz & Jelks 2014). Van Overzee et al. (2010) reported *C. leucas* from islands of the Netherlands Antilles (Aruba, Bonaire, Saba, St. Eustatius, St. Maarten). Additionally, also for the Caribbean Sea, Hacohen-Domené et al. (2020) reported that *C. leucas* is one of the main components of artisanal fisheries along the coastlines of Mexico's Quintana Roo, Belize, and Honduras in the Mesoamerican Reef region. The same authors reported, in a comparative study of all shark species in the landings of Guatemala's fisheries, that the greatest reduction in size and abundance was observed in the two apex predators *C. leucas* and *G. cuvier*. Quinlan et al. (2021) outlined that *C. leucas* is most important species for the shark fisheries of Belize. Álvares-León et al. (2013) reported *C. leucas* from the Caribbean coast of Colombia, and Mejía-Falla et al. (2020) reported it Colombia's San Andres and Providencia and from Santa Catalina Archipelago in the Caribbean Sea. Cervigón (1992) reported that *C. leucas* is a common shark species along the northern coast of continental South American (Colombia, Venezuela, Guyana, Suriname, French Guiana) and in the southern Caribbean Sea. Cervigón et al. (1993) reported that *C. leucas* occurs not only in coastal waters but also in brackish water bays, estuaries, the lower reaches of rivers, and hypersaline lagoons in the southern Caribbean Sea.

Inland records of *C. leucas* have so far been very scarce for islands of the Caribbean Sea (see Table 3). Neal et al. (2009) reported *C. leucas* in a list of primarily marine and estuarine fish species collected in freshwater rivers of Puerto Rico, which is presumably the only available published information on the occurrence of *C. leucas* in a riverine habitat of the Caribbean Islands.

Due to a possible future range expansion caused by global warming, it may become difficult to distinguish between natural seasonal movements of sharks from movements influenced by human impact. Only two decades ago, the southernmost limit of *C. leucas* in the Atlantic Ocean was estimated to be in Brazilian waters. Sadowski (1971) reported *C. leucas* from the Cananêia Lagoon Estuary, Gadig (1998) reported the species from the Sao Paulo coast, Anderson et al. (2015) reported *C. leucas* as rare along the Santa Catarina coast, Chelotti & Santos (2020) provided information on the presence of *C. leucas* in Rio Grande do Sul, and Soto & Nisa-Castro-Neto (1993, 1998) reported *C. leucas* from the Patos Lagoon Estuary (see Table 3), all locations in southern Brazil. *Carcharhinus leucas* undertakes seasonal migrations along the southwestern Atlantic Ocean coast of South America during the spring and summer months, as observed in the Northern Hemisphere. Anderson et al. (2015) reported Santa Catarina's rocky reef as a southern limit for the Brazilian tropical fish fauna, as well as the limiting effect of cool waters from the South Atlantic Central Water, which can lower the water temperature to 16 °C, also in spring and summer. Additionally, in the southernmost part of the Brazilian coast, the cold La Plata Plume Water that comes from the discharge of the Plate River (at ~ -35°S) reaches coastal areas of Brazil during the winter. The low temperatures generated by these water masses affect the distribution of tropical marine organisms in the region (Anderson et al. 2015), and presumably even the occurrence of the mainly tropical to subtropical *C. leucas*. Nevertheless, there have been records of the species from Argentina and Uruguay.

The first record of *C. leucas* from Argentina was by Chiaramonte (1998), who examined two preserved jaws collected in 1976 and identified them as *C. leucas*. Chiaramonte (1998) mentioned the sporadic nature of *C. leucas* in the Buenos Aires region, which is indicative of seasonal changes in water temperature influenced by changes in current. *Carcharhinus leucas* normally inhabits subtropical and tropical waters, entering temperate waters during warm-water periods, and appears only occasionally in Argentine waters (Chiaramonte 1998). The new southern limits for *C. leucas* in the western South Atlantic, in Uruguayan and Argentine waters, reported by Chiaramonte (1998) and Menni & Lucifora (2007), are therefore not automatic indicators of a response to climate change-induced environmental change in this part of the Southern Hemisphere, but rather evidence that *C. leucas* can stray to these waters during its natural seasonal migrations. The temperatures of Buenos Aires' waters can reach above 20 °C during the summer months (November to March). These temperatures only slightly overlap the minimal preference of *C. leucas* (see section 5), and it is therefore no surprise that this species is rare south of Uruguay (Nicholls 2017). Still, at the beginning of the 1970s, Sadowsky (1971: 71) wrote, about the distribution of *C. leucas* in southern Brazil: "The occurrence of this species has not been recorded in the southernmost Brazilian waters […], nor in Uruguay…". As a conclusion, evidence of a progressive range expansion in the western South Atlantic should be used with caution and should be looked at as progress in knowledge about this species' distribution rather than as a putative effect of climate change.

Carcharhinus leucas strays occasionally to Argentine waters, most likely only during summer, and today this species is well-known from south Brazilian waters (Anderson et al. 2015) as well as from Uruguayan and Argentine waters (Chiaramonte 1998; Menni & Lucifora 2007; Ruarte et al. 2009), probably as a rare summer visitor. The circumstances under which *C. leucas* was reported from Uruguayan and Argentine waters, which

represents an extension of the southern limits of its range in the western South Atlantic, should only be interpreted with caution as a putative result of global warming, as this species was collected already in 1976 from these latitudes. This species is seldomly found in waters south of Brazil, and only in rare cases strays farther south. On the contrary, records of *C. leucas* from the coastal waters of southern Brazil, Uruguay, and Argentina may get rarer in the future, as this species is reported to be overexploited in the waters of the southeastern Brazilian coast (Fogliarini et al. 2021).

4.1.2 Distribution in the northern and central Atlantic Ocean

In the northern and central Atlantic Ocean, evidence of transoceanic migrations by *Carcharhinus leucas* was provided by Santos et al. (1997), Gadig et al. (2006), and Barreiros & Gadig (2011), who reported the capture of a single specimen (estimated 250–270 cm TL) by fishers from the oceanic Azores Islands. This occurrence can possibly be interpreted as a result of transport of tropical fish species by the Gulf Stream, although Barreiros & Gadig (2011: 125) stated, about *C. leucas* for the Azores: "The Azores are not suitable habitat for this species whose presence is certainly sporadic and practically unknown." Afonso et al. (2013) discussed the occurrence of fish species with a tropical to subtropical origin, including *C. leucas*, in the Azores as occasional events or as a process of tropicalization of the waters around this oceanic island group. However, Compagno (2016) critically commented on this record and remarked that it may be based on a misidentification of *Carcharhinus obscurus* or *C. galapagensis*. Nevertheless, the link of adult specimens of *C. leucas* to continental coasts seems not to be as strong as previously believed, as suggested by new records from additional oceanic islands and insular (see section 4). The record of *C. leucas* from the Azores in the Northeast Atlantic has led to mention of this species in the following works: checklist of European marine fishes (Bailly et al. 2001), European chondrichthyans (George & Zidowitz 2006), checklist of European fishes (Hanel et al. 2009), checklists of marine fishes of Portugal (Carneiro et al. 2014, 2019). The record of *C. leucas* from the Azores is the only verified record of this species for a European country. Surprisingly, *C. leucas* was not mentioned in the recent review of elasmobranchs of the Azores Region by Das & Afonso (2017).

4.1.3 Distribution in the eastern Atlantic Ocean

This section is based on Table 5 and summarizes the state of knowledge of the distribution of *Carcharhinus leucas* in marine habitats of this ocean basin.

Information about the elasmobranch fauna of this region is scarce, especially for the Atlantic coast of the African continent. Only a few surveys and reports with carcharhinid sharks as a topic are available for this region. Along the west coast of Africa, the known distribution of *C. leucas* stretches from Mauritania to Angola, with a northern exclave on the coast of Morocco (Fig. 4). This putative gap in its distribution along the West Saharan coast is presumably only due to a lack of data for this region. Pequeño et al.'s (1990) report of *C. leucas* from Namibian/South African waters, which would be the southernmost limit for this species on the west coast of Africa according to the literature (Compagno 1984, 2001; IUCN 2018); however, this should be confirmed by experts and by continuative studies, and *C. leucas* was not reported for Namibian waters by Bianchi et al. (1999). In all probability, the cold Benguela Current limits the southern distribution of *C. leucas* along the West African coast to Angola. Reports of *C. leucas* from the Atlantic coast of Morocco were provided by Lloris & Rucabado (1998) and Menioui (1998), whereas those from Mauritania were given by ter Hofstede (2003). Gushchin (2019) mentioned that *C. leucas* occurs in the eastern Atlantic from Mauritania to Angola, with unconfirmed reports from Morocco, which is incorrect, as its occurrence in the marine waters of Morocco and Moroccan inland waters is confirmed (see Table 5).

Cadenat (1957) reported *C. leucas* from marine waters off Senegal and Cadenat & Blache (1981) reported occurrences of *C. leucas* from Senegal, Guinea, Sierra Leone, Ivory Coast, Benin, and Congo. Grandfils Acino & Muñoz-Chapuli (1982) observed nine adult specimens of *C. leucas* of 240–260 cm TL, which appeared on the fish trading market of Algeciras (Cádiz, Spain) between February and April of 1981. Eight of these specimens originated from fisheries off the coast of Monrovia (Liberia), eastern Atlantic Ocean, wheras one specimen was of uncertain origin but presumably also from tropical waters off East Africa. Séret (1990, 2003) mentioned that *C. leucas* is known from West Africa from the coast of Morocco and from Senegal to Angola. Moreover, Séret (1990, 2003) reported *C. leucas* from the inland waters of Gambia and Gabon (see Tab. 5). Schneider (1990) provided information on the occurrence of *C. leucas* in the marine waters of the Gulf of Guinea, which include the coastal waters from the Ivory Coast to Gabon. Trape (2008) reported *C. leucas* from estuaries of Senegal and Gambia. Verifiable reports of *C. leucas* for the coast of Gambia were given by Moore et al. (2019). Agyeman et al. (2021) identified *C. leucas* in waters off Ghana. Seidu et al. (2021a) reported a depletion of *C. leucas* populations in the waters off Western Ghana due to strong fishing pressure since the beginning of the 2010s. Seidu et al. (2021b) also reported catches in the juvenile to subadult age classes (106.7–143.9 cm TL) of *C. leucas* from three fishing ports of Western Ghana.

These results suggest that its nurseries are in the vicinity of these ports. *Carcharhinus leucas* was also reported by Bianchi (1986) and Mehl et al. (2011) for the marine waters of Angola, and by Skelton (2019) from Angola's inland freshwaters.

Dioup & Dossa (2011) reported high numbers of *C. leucas* in fishery catches from Guinea and Guinea-Bissau, and that it used to be frequent in the waters from Mauritania to Sierra Leone but is now only caught regularly in the waters of the two Guineas. Interestingly, Dioup & Dossa (2011) also mentioned that the Bijagos Archipelago of Guinea-Bissau may be a refuge for residual populations of *C. leucas*, because young specimens, close to the size of newborn pups, have been observed there since the 1990s, and catches there have remained relatively stable despite having plummeted elsewhere. Possibly, the Bijagos Archipelago could serve as a base for this species to recolonize the West African waters, where it is now rare, if given the opportunity. Cross (2015) also reported the presence of both adult and neonate elasmobranchs in catches in the Bajagos Archipelago, suggesting that its numerous islets may function as a nursery area, even though Tous et al. (1998) reported a high fishing pressure for sharks and illegal shark finning for the archipelago. Dioup & Dossa (2011) also provided an unexpected result: the occurrence of juvenile *C. leucas* in putative marine waters of the Bijagos Archipelago. Numerous studies about the life history of *C. leucas* (Heupel & Simpfendorfer 2008, 2011; Matich & Heithaus 2014, 2015) support the assumption that juvenile *C. leucas* depend on low salinity habitats in the early stages of their life. The Bijago Archipelago, off the coast of Guinea-Bissau, provides a marine environment, although it is located in proximity to the delta of the Geba River and its numerous outlets, with a distance of nearly 20 kilometers from the river mouth, the water conditions at this archipelago are fully marine.

There have been no verifiable records of *C. leucas* from the Mediterranean Sea until today. Nevertheless, occurrences of the species in the Mediterranean Sea have been published in the historical literature, presumably based on misidentifications with other carcharhinids. Guichenot (1850: 124) reported "*Carcharias leucos*" from Algeria. This historical record was later reported by Duméril (1865) and in the historical work of Döderlein (1879), where *C. leucas* was also from the Algerian coast of the Mediterranean. At this point, it should be noted that the work of Döderlein includes doubtful and unconfirmed information. Furthermore, *C. leucas* was reported by Jordan & Evermann (1896) for the Mediterranean Sea, but without presentation of verifiable data by the authors, who were possibly referring to the literature cited above. Doubtful information for the Mediterranean Sea was also given by Soldo (2003), but the author did not refer to any voucher specimen and did not provide an illustration (photograph) or other information allowing to verify the record. Serena (2005: 14) noted, for the Mediterranean Sea: "*Carcharhinus leucas* […] is a doubtful species", Maddalena et al. (2016: 33) commented: "…the bull shark is not present in the Mediterranean", and Serena et al. (2020: 508) reported, about *C. leucas*: "There are no confirmed reports of living individuals in the Mediterranean Sea".

Despite the above, it should be noted that in the last four decades some surprising records and unexpected findings of primarily tropical to subtropical, putative warm-water carcharhinids were made in the Mediterranean Sea, probably only of stray individuals. Maddalena et al. (2016) reported one specimen of *Carcharhinus longimanus* Poey, 1861 (oceanic whitetip shark) from the Adriatic Sea in Venice, Italy, captured in 1978. Maddalena & Della Rovere (2005) reported *Carcharhinus amboinensis* from Italian waters off Crotone in the north-west Ionian Sea, and Tobuni et al. (2016) reported neonates of *Galeocerdo cuvier* from Libyan waters (during a seasonally influenced water temperature of 13 °C). Presumably, these records represent casual occurrences in the Mediterranean, or as rare occasional visitors from the Atlantic. From a biogeographical standpoint, the question of their origin is of importance, as all these species occur both in the Atlantic Ocean and in the Red Sea (Compagno 2001; Spaet et al. 2011; Spaet 2019), and it remains unclear how they may have reached the Mediterranean. In order to determine the degree of human impact on the distribution of these species, it would be interesting to know if they are invasives and Lessepsian migrants by migration through the Suez Canal (see section 5) from the Red Sea. Possibly, these species reached the Mediterranean via a natural range expansion from the Atlantic Ocean through the Strait of Gibraltar at the very edge of their normal range. Even if these records are due to rare incursions of these sharks in the Mediterranean and their origin is uncertain (Maddalena et al. 2016), they likely reach the Mediterranean only occasionally as strays. Therefore, it is imaginable that also *C. leucas* could be a rare visitor in the Mediterranean from waters the northwestern Atlantic Ocean coast of Morocco, especially in periods with strong warming of the Mediterranean. However, considering recent climate conditions and prevalent water temperatures in the Mediterranean, the establishment of large stocks of *C. leucas* in this region seems very unlikely.

A sighting of *C. leucas* was reported by a scuba diver in 2000 in El Hierro, the westernmost island of the warm-temperate Canary Islands (Casassovici & Brosens 2017). The identification of sharks of the genus *Carcharhinus*, characterized by a high degree of similar features and several closely related species, by remote visual diagnosis only is difficult and may lead to misidentifications (Brunnschweiler 2009). Although it is unclear if the above record

is reliable or based on a misidentification, the distribution of *C. leucas* may include the Canary Islands pending deeper investigation and verification. Dooley et al. (1985) reported a surface temperature of Canary Island waters varying from 18 °C during winter to 22 °C during summer, which is below average for the latitude due to the cool Canary Current and the cold northwest African upwelling regions. Considering these abiotic conditions, a periodical occurrence of the warm-water *C. leucas* around the Canary Islands seems possible during the summer months as a result of seasonal induced migratory behavior. On the other hand, the occurrence of a residential population seems unlikely, although Brito et al. (2005) recognized a putative tropicalization process of the littoral teleost ichthyofauna in the Canary Islands in the period from 1991 to 2005.

4.2 Distribution in the Indian Ocean

From a biogeographical point of view, one important question concerning the range of *Carcharhinus leucas* in the Indian Ocean is whether its distribution is continuous from the South African coast to the Indian coast and farther to the Southeast Asian coast. Already Fowler (1941) delivered a detailed listing of reports of *C. leucas* (and its numerous synonyms) from the Indo-Pacific region and an intensive study of the available references and literature available at that time. The listing of Fowler (1941) includes numerous doubtful records and errors regarding the distribution of *C. leucas* due to the confusion with *Carcharhinus gangeticus*, a name repeatedly used in studies from this region (see Methods).

4.2.1 Distribution in the western Indian Ocean

This section is based on Table 6 and summarizes the state of knowledge of the distribution of *Carcharhinus leucas* in marine habitats of this ocean basin.

Compagno (1984) and Fischer & Bianchi (1984) reported a continuous distribution of *C. leucas* in the western Indian Ocean from the coast of South Africa in the south to Somalia in the north, including the coasts of Mozambique, Kenya, and Tanzania and the inland states of Malawi and Zimbabwe as a result of freshwater occurrences (see Table 6). Furthermore, Schneider et al. (2005) included *C. leucas* in a checklist of Mozambique marine fishes, Anam & Mostarda (2012) and Pirog et al. (2019b) mentioned *C. leucas* from Zanzibar, Oddenyo et al. (2018) and Kiilu et al. (2019) mentioned an occurrence of *C. leucas* in the marine waters of Kenya, and Sommer et al. (1996) reported *C. leucas* for the Indian Ocean coast of Somalia.

For the Indian Ocean coast of South Africa, at the southern limit of the species' distribution in the southwestern Indian Ocean, a possible range extension of *C. leucas* can be recognized. Bass (1978) mentioned that *C. leucas* is distributed in southern Africa in marine waters from Mombasa to the central Natal. In the mid 1980s, Compagno (1986) and Compagno & Smale (1986) provided the southernmost occurrence of *C. leucas* from the mouth of the Great Fish River (-33.49°S, 27.13°E) on the Eastern Cape coast as well as a range limit for this species in the Eastern Cape Province, while also mentioning that this shark is common in Natal. Previously, D'Aubrey (1964) reported the limit of its distribution in South African waters as a little further south of Knysna (-34.08°S, 23.06°E). Later, Compagno et al. (1989) reported that *C. leucas* ranges as far as Cape St. Francis (-34.21°S, 24.83°E) in southeastern Africa. Heemstra & Heemstra (2004) also mentioned that *C. leucas* ranges as far south as Cape St. Francis in the Indian Ocean along the coast of southern Africa, and that it is rare south of KwaZulu-Natal. Lamberth & Turpie (2003a) mentioned that *C. leucas* utilizes the estuaries of the subtropical KwaZulu-Natal Province but was not known to occur in estuaries of warm-temperate South Africa. However, the more recent investigation by McCord & Lamberth (2009) revealed the presence of *C. leucas* in the Breede River and its associated estuary (-34.40°S, 20.84°E), also in warm-temperate South Africa. This record, backdated in 2003 by the catch of a pregnant female of 400 cm TL, was made at a coastline distance of approximately ~700 km southwest of the Great Fish River Estuary and ~230 km from Knysna. Mann (2013) mentioned that this record of *C. leucas* represents a 366 km southward range extension along the east coast of South Africa. Albano et al. (2021) mentioned that *C. leucas* occurs in and adjacent to the De Hoop Marine Protected Area in South Africa, which is located farther west of the Breede River Estuary and reaches as far as Cape Agulhas (-34.82°S, 20.01°E). This is in fact the southernmost record of *C. leucas* for the African continent and probably the entire Indian Ocean. However, the record of McCord & Lamberth (2009) demonstrates the utilization of the warm-temperate estuaries of South Africa by *C. leucas* as nursery grounds, updating the state of knowledge of the ecology of *C. leucas* in southern Africa. Previously, Whitfield (1994) had reported that *C. leucas* extends into warm-temperate marine waters but has not been recorded entering estuaries there, as has been documented in the subtropical Natal river systems.

The first report of *C. leucas* from the Mascarene Islands in the southwestern Indian Ocean was by Fricke (1999), from Mauritius. Interestingly, in the earlier checklist of marine fishes of Mauritius (De Baissac 1990), *C. leucas* was not yet mentioned, but *Carcharhinus amboinensis* was, which is possibly a misidentification of *C. leucas*. Subsequently, Fricke et al. (2009) mentioned *C. leucas* from Réunion Island as a new record from 2005;

in a previous survey about the marine fish fauna of the island (Letourneur et al. 2004), *C. leucas* was not yet mentioned. Based on the state of knowledge of that time, Compagno (1984) did not report *C. leucas* from islands in the southwestern Indian Ocean such as Madagascar and the Mascarene Islands. The record of Fricke et al. (2009) of *C. leucas* for Réunion Island was based on underwater observations in Saint-Paul Bay in 2005. *Carcharhinus leucas* was recently reported from Rodrigues by Pirog et al. (2019b), but was not listed from there in earlier surveys (Fricke 1999; Heemstra et al. 2004).

Despite its large size, *C. leucas* has long remained surprisingly hidden to scientists in the southwestern Indian Ocean, although ichthyological investigations in this remote area likely not intensive at all. From a biogeographical point of view, the question is whether this recent evidence represents a recent range expansion of *C. leucas* to the Mascarene Islands or whether the species was overlooked there until the beginning of the 21st century. Considering the numerous records of *C. leucas* from oceanic islands worldwide (see section 4) and old records from adjacent areas (e.g., Madagascar) from the beginning of the 20th Century, the second explanation seems more plausible.

Available distribution maps are also fragmentary regarding the presence of *C. leucas* in the southwestern Indian Ocean, and they do not display the recent state of knowledge. For example, nowadays, the presence of *C. leucas* at Réunion Island is a well-known fact (Trystram et al. 2016; Martin & Jaquemet 2019; Pirog et al. 2019a, 2019b; Soria et al. 2019, 2021; Guyomard et al. 2020; Le Croizier et al. 2020; Chynel et al. 2021; Hoarau et al. 2021; Mariani et al. 2021; Mourier et al. 2021; Niella et al. 2021b), but the island was not included in any of the past distribution maps for the species. The same applies to the presence of *C. leucas* in the Seychelles. Until the early 2000s, there was a general lack of information and data regarding the distribution of *C. leucas* in the southwestern Indian Ocean (Compagno 1984, 2001). The maps of Compagno did not reproduce occurrences of *C. leucas* in Madagascar and surrounding islands of this part of the southwestern Indian Ocean. In the past, it was believed that interspecific competition with the close relative *C. amboinensis* was a driving factor influencing the geographical range of *C. leucas* in this part of the world. Some authors have hypothesized a competition-based mutual exclusion of these two species in Madagascar, even though it is well known that both species occur sympatrically along the southeast coast of Africa (Compagno 1984, 2001; Tillett et al. 2011a; Tillett et al. 2014). However, the suggestion that *C. amboinensis* is rare when *C. leucas* is common due to competitive exclusion still exists (White et al. 2018).

The presence of *C. leucas* in Madagascar has been known for a long time. The first published record from the west coast of Madagascar was by Fourmanoir (1961), followed by Kiener (1963), D'Aubrey (1964), Cressey (1967), and Maugé (1967). Bass et al. (1973) reported that *C. leucas* is far more abundant than *C. amboinensis* off the west coast of Madagascar, and that the reverse is true off the east coast; these authors also considered that this may be the result of competitive exclusion. Moreover, both species were often confused in the past (see Compagno 1984). In conclusion, the exact distribution of *C. leucas* in the southwestern Indian Ocean remainsed unclear for a long period. Additionally, the presence of *C. leucas* in Madagascar was documented by a historical picture of a captured *C. leucas* from the 1920s published by Fey & Maliet (2017). Boisier et al. (1995) reported a mass poisoning of local people after they fed on the meat of a *C. leucas* specimen found stranded on the southeast coast of Madagascar, at Manakara. Diogène et al. (2017) reported a specimen of *C. leucas* caught on the east coast of Madagascar, as well as another mass poisoning after consumption of *C. leucas* flesh. Hopkins (2011) reported that *C. leucas* is exploited in Madagascar's coastal fisheries. Finally, an overview of references with *C. leucas* records for Madagascar was given by Fricke et al. (2018), and specimens of *C. leucas* from Madagascar were included in the investigation by Pirog et al. (2019b).

A long-distance, transoceanic movement between islands of the western Indian Ocean was documented by Lea et al. (2015) for a pregnant female *C. leucas*, between the Seychelles and Madagascar, which is one of the rare examples of transoceanic movement by this species. At the same time, this example shows the philopatric behavior combined with site fidelity to a certain low salinity location. In Madagascar, functional breeding habitats of *C. leucas* are known from Lake Kinkony (Kiener 1963; Kiener & Theresien 1963; Moreau 1987) and the Betsiboka River (Taniuchi et al. 2003) (see Table 6). Nevill et al. (2013) reported the catch of a highly pregnant female *C. leucas* from the Seychelles, near the mouth of a river system (Grand River North West), which leads to the question of whether there are suitable breeding habitats for this species in the Seychelles and some females remain in the Seychelles for reproduction. Observations by Seychelles inhabitants of neonate *C. leucas* in a small tidally influenced creek with entry at Beau Vallon Beach at Beau Vallon Bay, Mahé (Internet Reference 7), confirm that reproduction of *C. leucas* takes place in the Seychelles. However, some females migrate from the Seychelles to suitable nursery areas that located in other parts of the southwestern Indian Ocean. These long-distance migrations to breeding places can be explained by philopatric behavior, which has been documented also in other parts of the Indian Ocean (Batcha & Reddy 2007). Apart from this small creek on Mahé, no other nursery grounds of *C. leucas* have been found in the Seychelles, but there

are further reports of juveniles found in coastal habitats of this island group, so evidence of reproduction on the islands has been verified. Occurrences of *C. leucas* in the Seychelles were mentioned by Séret (2002), Nevill et al. (2007, 2013), Lea et al. (2015, 2018), and Pirog et al. (2019b). Unfortunately, several (fatal) attacks by *C. leucas* were recorded during the last decade from the Réunion and from the Seychelles, followed by media reports and scientific investigations concerning these attacks (Daily Mail Reporter 2011; Charc 2015; Blaison et al. 2015; Blaison 2017; Lagabrielle et al. 2018), which have helped confirm the presence of *C. leucas* in these islands. Considering how recent most of these records are, it seems astonishing that such a large shark could have remained undetected in these regions for such a long time, and an alternative explanation could be that *C. leucas* has only relatively recently settled in these Indian Ocean islands. Reproduction of *C. leucas* has currently also been documented in Réunion Island (see Table 6).

There is contrasting information about the occurrence of *C. leucas* in the remote island group of the Maldives. *Carcharhinus leucas* is mentioned in the shark species list of the Maldives by Ali & Sinan (2015), but without verifiable records. Voigt & Weber (2011) also reported *C. leucas* from the Maldives, but the species is not mentioned in other relatively recent ichthyological essays about the marine fish fauna of this region (Anderson & Hafiz 1996; MRS 1997). Therefore, the occurrence of *C. leucas* in the Maldives is unclear and as yet unverified. It should be mentioned that sharks were overexploited in the Maldives over a long period by artisanal and recreational fisheries, with dramatic results. For example, during a field survey by Chabanet et al. (2012) at the Baa Atoll of the Maldives, these authors did not observe any shark species, despite an extensive amount of time spent searching for them.

4.2.2 Distribution in the northern Indian Ocean

This section is based on Table 7 and summarizes the state of knowledge of the distribution of *Carcharhinus leucas* in marine habitats of this ocean basin.

Although the Red Sea is home to an unusually high proportion (41%) of sharks belonging to the family Carcharhinidae (Spaet 2019), *C. leucas* is absent from this sea (Compagno 1984, 2001; Randall 1986; Golani & Bogorodsky 2010; Golani & Fricke 2018; Spaet 2019), and the reasons for its absence have not yet been clarified. Already Compagno (1982) recognized that the shark fauna of the Red Sea is remarkably depauperate in comparison to other marine basins, and that their species composition is the result of dispersal from other areas rather than of their vicariant isolation in that sea. Considering this hypothesis, the absence of *C. leucas* from the Red Sea can be explained by unsuitable environmental conditions and a lack of critical habitats, or by competitive exclusion cause by other shark species; however, data deficiency cannot be excluded altogether. One theory for the absence of *C. leucas* in the Red Sea is the absence of suitable nursery grounds, which are essential to the reproduction of this species. States adjacent to the Red Sea are very arid and poor in inland waters and estuaries. There are no perennial rivers and no consistently freshwater outflows into this sea, but just intermittent rivers and creeks (so-called "wadys"). There are also no estuaries, river mouths, or lagoons with brackish water conditions, on which *C. leucas* depends for reproduction. This was confirmed by Randall (1986: 104), who wrote: "That it [*C. leucas*] is not yet reported from the Red Sea may be related to the limited freshwater drainage to this body of water."

Voigt & Weber (2011) mentioned an occurrence of *C. leucas* in the southern Red Sea, in the waters of Djibouti. However, this is certainly imprecise, as these authors located Djibouti on the Red Sea and not on the coast of the Gulf of Aden, where it actually belongs. At the southern end of the Red Sea is the Bab al-Mandab Strait, a passage only 29 km wide and with a maximum depth of 130 m. This strait has profound effects on water exchange between the Red Sea and the Gulf of Aden and in the past, during periods of lower sea level, has effectively separated these two water bodies (Bonfil & Abdallah 2003). Another aspect to consider is the rise of cold (16 °C), deep-water masses from the bedrock threshold at Bab al-Mandab Strait, which is an impediment for some tropical marine species (Vermeij 1978). However, water temperature alone should not explain the absence of *C. leucas* from the Red Sea. Occurrences of other shark species with similar warm-water preferences, like *Galeocerdo cuvier*, *Carcharhinus longimanus* (Compagno 1984, 2001), and—as a result of recent investigations—the close relative *Carcharhinus amboinensis* (Spaet et al. 2011), which is sympatric with *C. leucas* in certain regions of the world (Tillett et al. 2011a, 2014), seem to eliminate water temperature as factor limiting the occurrence of *C. leucas* in this region. Possibly, *C. leucas* is just a rare migrant or a stray in the Red Sea, but this needs verifying through further studies, as up until now there have been no confirmed records of *C. leucas* for the Red Sea.

The *C. leucas* distribution maps by Compagno (1984, 2001) and the IUCN (2018) show an isolated distribution of this species in the Persian Gulf, a marginal sea of the northern Indian Ocean, without a connection to the adjacent African or Asian continents. This suggests an isolated Persian Gulf population without close affiliation to populations southeastern Africa and India. Marine records of *C. leucas* from neighboring countries around the Persian Gulf were provided by Firouz (2000) for the coast of Iran, by Hussain et al. (1988), Nasir (2000), Abd et al. (2009), Ali (2013), and Al-Faisal & Mutlak (2018)

for the Gulf coast of Iraq, by Kuronuma & Abe (1986), Moore et al. (2012b), Bishop et al. (2016), Henderson (2020), and Edmonds et al. (2021) for Kuweit, by Basson et al. (1977), Krupp & Müller (1994), and Krupp & Almarri (1996) for Saudi Arabia, by Moore et al. (2012a, 2012b) and Henderson (2020) for the marine waters of Qatar, and by Beech (2004), Hellyer & Aspinall (2005), Tourenq et al. (2008), Jabado (2014), Jabado et al. (2015a, 2015b, 2016), and Henderson (2020) for the United Arab Emirates, including Abu Dhabi. Carpenter et al. (1997) and Eagderi et al. (2019) listed *C. leucas* for the waters of the Persian Gulf in general, and Grandcourt (2012) included *C. leucas* in a list of reef fishes from this gulf. Henderson (2020) presumed that *C. leucas* occurs throughout the Persian Gulf, whereas Di Sciara & Jabado (2021) mentioned *C. leucas* for the Persian Gulf, the Gulf of Oman, the Gulf of Aden, and the northern Arabian Sea (from the border with the Gulf of Aden to the border between Pakistan and India).

Interestingly, from the Persian Gulf region, there are more records of *C. leucas* from freshwater habitats than from marine waters (see Table 7). Jawad (2017) considered *C. leucas* as one of the dangerous fishes occurring in the Persian Gulf. Moore (2013, 2018), Almojil et al. (2015), and Bishop et al. (2016) highlighted the regional importance of the Tigris/Euphrat/Shatt Al-Arab system as a nursery area for *C. leucas* in the Persian Gulf region, due to its major ecological importance as perhapsthe only permanent, significant estuary throughout the approximately 10,000 km of arid NW Indian Ocean coastline. Estuaries also appear to either be absent or present only as intermittent or minor features along the coasts of the entire Arabian Peninsula and Iran. On the other hand, Jabado (2014) and Jabado et al. (2016, 2017) reported the catch of one adult pregnant female (219 cm TL) with late-term embryos in December and catches from marine waters at the Persian Gulf coast of the United Arab Emirates of neonate *C. leucas* (68.8–69.2 cm TL) with visible umbilical scars between January and August, even though there are no rivers or estuaries in this region that are suitable as nursery grounds for this species. Jabado (2014) concluded that the reproduction of *C. leucas* occurs at various times of the year in the United Arab Emirates. Additionally, Jabado et al. (2016) found that most male *C. leucas* captured in waters of the United Arabian Emirates were immature, which would indicate that in the United Arab Emirates they are being exploited in crucial habitats, including nursery grounds. The locations of these *C. leucas* catches were far (at least 830 km) from the Tigris/Euphrat/Shatt Al-Arab system. Jabado et al. (2017: 75) remarked, about the reproduction behavior of *C. leucas* and its reliance on low salinity habitats in the Persian Gulf: "This highlights that, at least in the Gulf, this species is potentially not as dependent on these habitats as in other parts of the world."

The above information suggests that the subtropical Tigris/Euphrat/Shatt Al-Arab system is presumably only seasonally used by *C. leucas* during periods with suitable water temperatures, from the summer months to October (see comments under Table 7). Outside of this period, parturition of *C. leucas* probably takes place in the warmer marine waters of the southern Persian Gulf. Thus, further research is needed to identify the nursery areas of *C. leucas* along the Persian Gulf coast of the United Arab Emirates and assess whether females give birth in marine waters in the southern part of the gulf despite the temporally and spatially limited availability of estuaries in this region. Moore (2018) reported the capture of a neonate (81 cm TL) *C. leucas* during a fish survey in marine waters off Fao, Iraq, at the mouth of the Shatt Al-Arab River, which is in the size range (from 56 to 81cm TL) reported by Compagno (1984) for *C. leucas* at birth. This young shark was probably caught shortly after birth before it entered the upper reaches of the Tigris/Euphrat/Shatt Al-Arab system. The water is very shallow near the delta of Shatt Al-Arab at the northwestern end of the gulf. Shatt Al-Arab is considered the main source of freshwater for the Persian Gulf, with a 5 km^3 freshwater output each year) (Al-Shamary et al. 2020). Therefore, the Shatt Al-Arab Estuary can be considered as an important nursery ground for fishes in the Persian Gulf, especially for *C. leucas*, which relies on low salinity habitats during crucial periods of its life.

Steindachner (1907) reported *Carcharias gangeticus* (possibly referring to *C. leucas*) from the east coast of the southern Arabian Peninsula, which includes both Yemen and Oman. Newer investigations and reports (Jabado & Ebert 2015) have confirmed the presence of *C. leucas* from the coasts of Somalia and, farther north, Yemen and Oman on the Arabian Peninsula. Bonfil (2003) provided information about catches of *C. leucas* in local fisheries along the coasts of Djibouti and Yemen and in the Gulf of Aden; subsequently, Abubakr (2004) listed *C. leucas* from Yemeni seas. There are further reports of *C. leucas* from the Indian Ocean coast of the Arabian Peninsula on the internet (Image Du Monde 2018; from Dibba, Gulf of Oman, documented by a photograph) and in the scientific literature, by Randall (1995), Henderson et al. (2007), Al-Jufaili et al. (2010), Henderson & Reeve (2011), and Jabado & Ebert (2015). Manilo & Bogorodksy (2003), and subsequently Jawad (2017), provided evidence of the occurrence of *C. leucas* in the southern part of the Arabian Peninsula (Arabian Sea) on the coast of Oman, in the Gulf of Aden and in the eastern coast of Somalia. This evidence allows closure of the putative distribution gap between the African continent and the Arabian Peninsula, and proves a continuous distribution of *C. leucas* from the South African coast to the Persian Gulf (and farther to India and Sri Lanka—see further on). Additional evidence from the literature for an occurrence of *C. leucas* in the Gulf of Aden

was provided by Bonfil & Abdallah (2003). Interestingly, archaeological studies by Charpentier et al. (2009) about the utilization of shark teeth in the Neolithic and Early Bronze Age in southeastern Arabia have revealed the historical presence of *C. leucas* along the coast of Oman (the Gulf of Oman and Indian Ocean coast). Finally, Jabado et al. (2017) provided an updated distribution map for *C. leucas* in the Arabian Sea, the Persian Gulf, and the northern Indian Ocean, which shows a continuous range from Somalia to western India and Sri Lanka.

Carcharhinus leucas has not yet been reported from the Socotra Island (Yemen) in the northwestern Indian Ocean (Zajonz et al. 2000, 2016). For the coast of Pakistan, some fishery investigations provided records of *C. leucas*, which is mentioned in a field guide by Psomadakis et al. (2015) and in fishery reports from this region by Osmany et al. (2015) and Gore et al. (2019). It was also listed in the reports by Bianchi (1985) and by Psomadakis et al. (2014) as an important coastal fish species for Pakistan fisheries and in a report about the bycatch from tuna gillnet operations in Pakistani seas (Moazzam 2012). The regional-scale distribution maps of Jabado & Ebert (2015) and Jabado et al. (2017) illustrate the occurrence of *C. leucas* along the coast of Pakistan, and thus the information about the presence of *C. leucas* in Pakistani waters can be considered as verified. It will be interesting to see if further ichthyological investigations reveal the presence of *C. leucas* in Pakistan's inland waters, especially the Indus River (see Conclusions).

Day (1889: 14) reported information about *C. leucas* from India and adjacent areas under the name *Carcharias gangeticus*: "Seas of India to Japan, ascending rivers to above tidal influence. It is the commonest form along the Burmese coasts." For the west coast of the Indian subcontinent, records of *C. leucas* were provided by Raje et al. (2002) for the states of Gujarat and Kerala, by Johri et al. (2019b, 2021) also for the state of Gujarat, by Barman et al. (2013) for the state of Karnataka, by Purushottama et al. (2013) for the locality of Mumbai and by Gupta et al. (2020) for the district of Sindhudurg (Maharashtra), the latter including freshwater records in rivers and creeks (see Table 7). Akhilesh et al. (2021) reported landings of *C. leucas* by gillnet fisheries at Sassoon Dock, state of Maharashtra, on the west coast of India. James (1973) presumably reported *C. leucas* from the east coast of India, under the name "*Carcharhinus gangeticus*". The distribution maps of Compagno (1984, 2001) show an absence of the species from the east coast of the Indian subcontinent. However, later records of *C. leucas* from the east coast of India were provided by Raje et al. (2002) and Venkataraman et al. (2003) from the state of Tamil Nadu, by Cmfri (2005), Rajapackiam et al. (2007), and Mohanray et al. (2009) from the city of Chennai, by Cmfri (2008) from the city of Tuticorin (= Thoothukudi), by Batcha & Reddy (2007) and Mohanray et al. (2009) for the Pulicut Lagoon (see Table 7) and by Joshi et al. (2016) for the Gulf of Mannar. Joshi et al. (2018) reported *C. leucas* from India's southwest coast.

The distribution map by Raje et al. (2007), a fisheries survey for elasmobranchs in India, shows a continous distribution of *C. leucas* along the entire stretch of the Indian subcontinent coast, including records derived by commercial fish landings taken from Kanyakumari, at the southern tip of India, to the Indian Sunderbans. For the Indian Sunderbans, *C. leucas* was reported by Pal et al. (2014) and Sen & Mandal (2019). Akhilesh et al. (2014) listed *C. leucas* in a checklist of chondrichthyans occurring in Indian waters. For the state of India, Kizhakudan et al. (2015) reported an occurrence of *C. leucas* from both the west and east coasts. Haque et al. (2018) reported *C. leucas* (together with *Glyphis gangeticus*) from the Sunderbans Reserve Forest of Bangladesh. This record is not surprising, because the occurrence of *C. leucas* in the Hooghly and Ganges Rivers, in India and Bangladesh in the eastern part of the Indian subcontinent, is well known (Compagno 1984) and part of the uninterrupted distribution around the Indian subcontinent (Fig. 4). Rahman (2013), Bfri (2014), and Haroon & Kibria (2021) also reported *C. leucas* from the coastal and marine waters of Bangladesh. Haque et al. (2019) reported that *C. leucas* was commonly landed at ports of Bangladesh's east coast, in the Bay of Bengal.

4.2.3 Distribution in the eastern Indian Ocean

This section is based on Tables 7, 8, and 10 and summarizes the state of knowledge of the distribution of *Carcharhinus leucas* in marine habitats of this ocean basin.

Data for closing the distribution gap for the northeastern Indian Ocean in the maps of Compagno (1984, 2001) and the IUCN (2018), particularly for the regions of the Bay of Bengal and especially Myanmar, were delivered by Moe & Thein (2006), Vankara et al. (2007), Hoq et al. (2011), Roy et al. (2013, 2015a, 2015b), and Howard et al. (2015). Khine (2010) reported *C. leucas* from the Nga Yoke Kaung coastal area of Myanmar and Ahmad et al. (2012) reported it from multiple countries of Southeast Asia (Myanmar, Indonesia, Malaysia, Brunei Darussalam, Cambodia, Thailand, Philippines). Possibly, *C. leucas* also occurs in the oceanic islands Coco Kyun and Preparis in the Ayeyarwady region of Myanmar (Howard et al. 2015). Satapoomin (2011) and Marine Fisheries Research and Development Bureau (2015) reported *C. leucas* from southwestern Thailand and the Andaman Sea. Arshad et al. (2006) mentioned that *C. leucas* was landed at the Hutan Melintang landing site, West Malaysia (Peninsular Malaysia), at the Strait of Malacca. Evidence of *C. leucas* from western Sumatra (Indonesia) was provided by Dharmadi et al. (2016). Furthermore, *C. leucas* was reported from the

south coast of Java in Indian Ocean waters by Dharmadi et al. (2007). Dharmadi et al. (2009) reported *C. leucas* for the Lesser Sunda Island Chain of southeastern Indonesia (southern coasts of Java, Bali, Lombok, and Timor). Winter et al. (2020) reported landings of *C. leucas* by local fisheries from the Bali Strait. Moreover, *C. leucas* has been reported from the east coast of Lombok Island, West Nusa Tenggara, by Sentosa & Hedianto (2016), and from East Nusa Tenggara by Jaiteh (2017). Yulianto et al. (2018) reported landings of *C. leucas* in the port of Tanjung Luar (Lombok, Indonesia), from fishery grounds in marine waters off the southern coasts of the Sumbawa and Sumba Islands, also part of the island chain of southeastern Indonesia. White (2007) reported *C. leucas* from eastern Indonesia, but he gave no information on freshwater records from this region.

West (2011) reported a lack of *C. leucas* attacks along the Indian Ocean coast of Western Australia south of the Swan River (-31.58°S), which presumably represents edge of its range in Western Australia, even though reports of *C. leucas* exist from locations south of this limit (see Table 8). These records of *C. leucas* along the coast of Myanmar and the results of the above-cited studies on elasmobranch fauna occurrences in the northeastern and eastern Indian Ocean suggest a continuous distribution of *C. leucas* in the Indian Ocean from the coast of South Africa to the coast of Indonesia (western Sumatra to Timor), with an interruption from the oceanic waters of the Timor Sea to western and southwestern Australia (Fig. 4).

4.3. Distribution in the Pacific Ocean

Carcharhinus leucas is wide-ranging on both sides of the Pacific Ocean (Compagno 1984), including in its marginal seas. This large ocean basin represents a major geographical barrier that has an enormous impact on the migration of non-pelagic fishes, including coastal sharks. The vast size of this ocean, which is poor in oceanic islands and "stepping stones", successfully prevents transoceanic migrations and gene flow of coastal sharks, including *C. leucas*.

4.3.1 Distribution in the western Pacific Ocean

This section is based on Tables 7, 9, and 10 and summarizes the state of knowledge of the distribution of *Carcharhinus leucas* in marine habitats of this ocean basin.

The exact distribution of *C. leucas* along the coast of China in the western Pacific Ocean remains unclear. The distribution maps of Compagno (1984, 2001) and the IUCN (2018) show an isolated distribution exclave of *C. leucas* along the coast of the East China Sea in the western Pacific Ocean. The information that was used for these maps derives from collected material (catalogue no.: BMNH 74.1.16.63) from Shanghai, China, which was investigated and verified by Garrick (1982) as *C. leucas*. Fowler (1930a) reported *Carcharias gangeticus* for China in general, and was presumably referring to *C. leucas*. Further information about the occurrence of *C. leucas* in the South China Sea was probably given by Orsi (1974: 156), as "*Carcharhinus gangeticus*", for the waters of Viet Nam, with reference to the historical report by Tirant (1929) from Cochinchina and Cambodia. Moreover, evidence from the Indonesian island of Bintan in the South China Sea was provided by Emiliya et al. (2017), who mentioned that *C. leucas* is the most common shark in catches around this island. Ng et al. (2015) reported *C. leucas* from the Strait of Johor in Malaysian and Singaporean waters, and Liu et al. (2021) further reported that *C. leucas* is traded in the fish markets of Singapore. The Marine Fisheries Research and Development Bureau (2015) reported *C. leucas* from the Gulf of Thailand waters.

Evidence of the occurrence of *C. leucas* in the southern South China Sea was also provided by Arshad et al. (2006) and Arai & Azri (2019), for the state of West Malaysia (Peninsula Malaysia). Furthermore, Arshad et al. (2006) and the Department of Fisheries Malaysia (2006) reported *C. leucas* also from Malaysia's federal states of Sarawak and Sabah, Borneo. Fahmi & Adrim (2007) reported *C. leucas* from Kalimantan, Indonesian Borneo. Kottelat (2013) did not report freshwater records of *C. leucas* from Kalimantan, but recently Iqbal et al. (2019b) reported *C. leucas* from a freshwater environment in the Barito River, Kalimantan (see Table 7). Furthermore, a record of a freshwater shark of the genus *Glyphys* (river sharks) from Kalimantan's Sampit Bay was reported by Fahmi & Adrim (2007, 2009). D'Alberto et al. (2019) reported landings of *C. leucas* at Muara Angke landing port, Jakarta, Indonesia between 2001 and 2005.

Randall & Lim (2000) and Compagno (2002c) reported *C. leucas* for the South China Sea in general and Ruiyu (2008: 894) for China and adjacent areas, with its mention from "Taiwan", the "Pan warm-temperate Region", and the "China Sea". Aside from these reports, it should be mentioned that *C. leucas* has so far not been reported from the waters of Hong Kong, located on the coast of the northern part of the South China Sea (see Ni & Kwok 1999). Catches of *C. leucas* are traded in Hong Kong fish markets (Fields et al. 2018), but the origin of these catches remains completely unknown. Zhang et al. (2016) chose *C. leucas* as a keystone species for theoretical modeling of the food web structure in the Pearl River Estuary (= Modaomen Estuary) on the southern coast of China near to the municipal area of Hong Kong. However, this account should not be considered a confirmed record, even though the presence of *C. leucas* along the southern coast of China is very likely. The reconstruction of the

exact distribution of *C. leucas* along the southern Chinese coast is hampered by a lack of data from Chinese waters, although verified records exist from the South China Sea and Taiwan. Reports of the presence of *C. leucas* in Taiwanese waters were given by Chen & Joung (1993), Huang (2001), De Carvalho et al. (2013), and Ebert et al. (2013a, 2013b). De Carvalho et al. (2013) mentioned that *C. leucas* appears to be only rarely encountered in Taiwanese waters, possibly due to the location of Taiwan at its northern subtropical range limit, but maybe also as a result of overfishing. Furthermore, it is unclear how far north *C. leucas* reaches in Chinese waters. At a minimum, there is a gap in its distribution between the South China Sea and the East China Sea (Fig. 4), and information about the real extent of its distribution along the China coast would be highly desirable. Although not a main target species of fisheries in Southeast Asia, *C. leucas* is part of the species composition of the two largest shark fin markets of China, in Guangzhou and Hong Kong (Cardeñosa et al. 2020).

The exact distribution of *C. leucas* in Japan is also still quite unclear. One putative report of *C. leucas* from Japanese waters off the Okinawa Islands was provided by the Japanese Group for Elasmobranch Studies (1984), but the authors were unable to distinguish between *C. leucas* and *C. amboinensis*, so this record could be a misidentification. Nakaya (1993) included *C. leucas* in a list of large dangerous sharks in Japanese waters. According to Nakabo (2002), *C. leucas* is a component of the elasmobranch fauna of Japan. Additional records for Japan were provided by Tachihara et al. (2003), Matsumoto et al. (2006), Masunaga et al. (2008), and Shimose & Taira (2014) for the southern geographical limit of subtropical Japan, from the Okinawa and Iriomote Islands of the Ryukyu and Yaeyama Island groups (Okinawa Prefecture, Japanese Island Chain) west of Taiwan. Yoshigou (2014) provided an extensive bibliography of *C. leucas* records from Japanese waters of the East China Sea (Ryukyu Archipelago). Knowledge of the exact distribution of *C. leucas* in Japanese waters is low, and most of the information from Japan is quite old and unconfirmed (see Fowler 1941). However, there is an old report of "*C. gangeticus*" for Japan (Ryukyu Islands) by Taku & Kobayashi (1962), which could be an early indication of the occurrence of *C. leucas* in Japanese waters due to the long-lasting confusion between *Glyphis gangeticus* and *C. leucas* (see section 2). It is very likely that the warm-water species *C. leucas* is restricted in its distribution to the southern waters of tropical to subtropical Japan (Ryukyu Islands). Nevertheless, the presence of *C. leucas* in Japanese waters is confirmed and this species belongs to the natural Japanese ichthyofauna (Motomura 2020).

Just recently, Hari et al. (2021) reported the first record of *C. leucas* for the Palau Islands in the Western Pacific, which comprise more than 500 remote islands in Micronesia. Furthermore, *C. leucas* occurs primarily across tropical Australia and in southern Queensland and northern New South Wales, and as far south as southern New South Wales during the summer months (Baker 2013). Results of a long-term investigation by Smoothey et al. (2019) on the residence behavior of *C. leucas* in Sydney Harbour have shown it uses estuarine habitats of temperate Australia, particularly during the austral summer, with peak abundances in January and February. In the eastern Australian waters of the southwestern Pacific Ocean, *C. leucas* verifiably occurs as far south as Sydney (Prokop 2006; Smoothey et al. 2019) and a little bit farther south as a summer visitor (see Table 9). West (2011) reported a lack of *C. leucas* attacks along the Pacific Ocean coast of Eastern Australia south of Wollongong, New South Wales (-34.32°S), which presumably represents the edge of its distribution in Eastern Australia. *Carcharhinus leucas* also occur on the east coast of Australia in hypersaline Lake Macquarie, Australia´s largest saltwater lagoon (Compagno 1984). However, on the east coast of Australia, *C. leucas* undertakes seasonal long-range migrations. Espinoza et al. (2015) found out by using acoustic telemetry that 52% of the population of *C. leucas* undertakes long-range migrations along Australia's east coast. Espinoza et al. (2021) reported that specimens of *C. leucas* tagged in Sydney Harbour were mainly present within this temperate estuary in summer and autumn, whereas during the rest of the year individuals were detected in tropical and subtropical habitats in southern and central Queensland. These results agree with the investigation of Smoothey et al. (2019), who showed that seasonal changes in water temperature are a driving force in large-scale movements of this species.

It may not be surprising that *C. leucas* is missing from New Zealand waters due to the strong isolation of this remote island group, but the reasons for its absence should be discussed here at least to provide an overview. The North Island of New Zealand is located nearly 2,000 km east of the Australian continent and exhibits a subtropical climate (16 °C mean annual temperature) in its northern part. In this region, the sea surface temperature reaches 20–21 °C (Garner 1969) and exceptionally 22°C (Paul 1968) during the summer months, providing suitable conditions for *C. leucas* (see section 5), but drops to 16 °C during the winter, which is unfavorable for the species. In conclusion, the abiotic parameters are disadvantageous for the establishment of a persistent population of *C. leucas* in New Zealand waters, although records of some large semipelagic, pelagic and migratory carcharhinids with a preference for warm-water regions like *Galeocerdo cuvier* and *Carcharhinus longimanus* exist from the country's North Island (Compagno 1984; Roberts et al. 2020). It cannot be completely excluded that a few specimens of *C. leucas* possibly occasionally enter New Zealand waters as strays,

or by drifting through warm-water currents of the South Pacific Circulation (= South Pacific Gyre). However, until today, there are no known records of *C. leucas* for New Zealand waters (Roberts et al. 2020).

4.3.2 Distribution in Melanesia and Polynesia

This section is based on Table 10 and summarizes the state of knowledge of the distribution of *Carcharhinus leucas* in marine habitats of Melanesia and Polynesia.

Carcharhinus leucas is widespread in the Melanesian part of the Pacific Ocean (Fig. 4), but gets rarer and rarer in the Polynesian part. Allen & Erdmann (2009) reported *C. leucas* from the Bird's Head Peninsula (= Vogelskop P.) of West New Guinea (Irian Jaya, Indonesia), at Cenderawasih Bay. Boeseman (1956b, 1964) reported freshwater occurrences of *C. leucas* in Lake Jamoer and Lake Sentani, also West New Guinea (see Table 10). Also Allen (1996) and Diah et al. (2018) reported *C. leucas* from West New Guinea. *Carcharhinus leucas* also occurs in Papua New Guinea (Fricke et al. 2014; White et al. 2018, 2019). Furthermore, *C. leucas* is distributed around the oceanic islands of Melanesia's New Caledonia (Fourmanoir & Laboute 1976; Fricke & Kulbicki 2006, 2007; Langlois et al. 2006; Maillaud et al. 2009; Fricke et al. 2011; Gauthier et al. 2020), Vanuatu (Brunnschweiler 2018a, 2018b), the Solomon Islands (Hylton et al. 2017), Fiji (e.g. Brunnschweiler 2005, 2010; Brunnschweiler et al. 2014, 2017, 2018; Brunnschweiler & Marosi 2019; Glaus 2019; Glaus et al. 2015, 2019a, 2019b, 2020; Drew & McKeon 2019; Ward-Paige et al. 2020; Bouveroux et al. 2021), Samoa and American Samoa (Wass 1984).

In Polynesia, *C. leucas* is known from Tuvalu (Thaman 2015), Tonga (Brunnschweiler & Compagno 2008), and French Polynesia (Rangiroa Atoll, Tuamotu Archipelago), and is considered a stray at these locations. Until today, no nursery areas for *C. leucas* have been reported from Polynesia, and there is no recent knowledge about the utilization of freshwater bodies or estuaries by *C. leucas* for reproduction in this region (see Table 10). Furthermore, it remains uncertain whether specimens of *C. leucas* from Polynesia move to nursery grounds in distant locations in Melanesia.

4.3.3 Distribution in the eastern Pacific Ocean

This section is based on Tables 2 and 4 and summarizes the state of knowledge of the distribution of *Carcharhinus leucas* in marine habitats of this ocean basin.

In the eastern Pacific, the confirmed distribution of *C. leucas* along the continental coasts of North, Central, and South America ranges from southern Baja California to Peru, including the Gulf of California. Possibly, *C. leucas* temporarily and occasionally reaches as far north as the Californian waters of the United States. The distribution of *C. leucas* in the eastern Pacific includes the coastal waters of Mexico, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, Colombia, Ecuador, and Peru (Chirichigno 1974; López & Bussing 1982; Díaz 1984; Bussing & López 1993; Martinez 1999; Mejía-Falla et al. 2007; Jacquet et al. 2008; Erisman et al. 2011; Mejía-Falla & Navia 2019; Eisele et al. 2021; González-Acosta et al. 2021). This distribution corresponds exactly to the eastern Pacific Tropical (Panamanian) Faunal Region as defined by Briggs (1961). Due to the strong isolation effects of the Pacific Plate Barrier and the Central American Land Bridge, the Tropical Eastern Pacific is considered as a very autonomous biogeographic region for fish (Hastings & Robertson 2001), with a richness of shore fishes that is higher than in other tropical coastal regions due to a high rate of endemism (Hastings & Robertson 2001; Zapata & Robertson 2007).

Zapata & Robertson (2007) and Robertson & Kramer (2009) described the stretches of the Tropical Eastern Pacific from the Gulf of California to northern Peru. The northern and southern boundaries of the Tropical Eastern Pacific are located near Magdalena Bay in Baja California (~25.00°N) and the southern shore of the Gulf of Guayaquil (~4.00°S) according to Robertson & Kramer (2009). Two cold currents that flow from high to low latitudes were considered by Zapata & Robertson (2007) as limitations for the distribution of tropical warm-water depending fishes: the California Current in the north and the Peru Coastal Current in the south. However, Ashby (1987) documented the presence and the utilization of the Tropical Eastern Pacific waters around Baja California Sur by *C. leucas* since the Late Pliocene (~3.6–2.6 Mya), with fossil tooth findings from the Arroyo Salada site dated to during and beyond the closure of the Isthmus of Panama. a current report of *C. leucas* from the waters of the central and southern Gulf of California was provided by González-Acosta et al. (2021). Erisman et al. (2011) reported a single observation of one specimen of *C. leucas* at one site near Isla María Madre (Islas Marías Archipelago, Mexico) and concluded that this species is rare throughout this island group.

Carcharias azureus Gilbert & Starks, 1904 is an old synonym of *C. leucas* that was commonly used in the historical literature about the tropical East Pacific region (see section 2). The species was described by Gilbert & Starks (1904: 12) from the Pacific coast of Panama (Panama Bay), with the following note: "This species is well known though not abundant at Panama." Even though these authors did not recognize that their new species was identical to *C. leucas*, they realized that "*C. azureus* is extremely near *C. nicaraguensis*, from Lake Nicaragua and its outlet, the San Juan River." Beebee & Tee-Van (1941) reported "*Eulamia azureus*" from the Tropical

Eastern Pacific off Mexico, Costa Rica, Panama, and Ecuador, as far south as Guayaquil. Hildebrand (1946: 39) also reported "*Eulamia azureus*" from the Pacific coasts of Costa Rica, Panama, and Ecuador in the Tropical Eastern Pacific and expected this species for Peru: "Although this species has not been reported from Peru, it may be expected there, as it has been taken at Guayaquil, Ecuador." Rosenblatt & Baldwin (1958) reported a distribution of *C. azureus* in the eastern Pacific that ranges from southern California (USA) and Bahia Magdalena (southern Baja California) to Guayaquil (Ecuador). Evidence of *C. leucas* for the Tropical Pacific Ocean coast of continental Ecuador was provided by Orcés (1959: 75; as "*Eulamia azureus*"), Bearez (1996), and more recently by Coello (2005), Martínez-Ortíz et al. (2007), and Calle-Morán & Béarez (2020). Furthermore, Bostock & Herdson (1985) stated that *C. leucas* is not rare in the continental waters of tropical Ecuador. Coello et al. (2010) listed *C. leucas* in a list of sharks captured in continental Ecuadorian waters in Santa Elena Province, adjacent to Guayaquil. Díaz (1984) reported *C. leucas* from Gorgona Island (Colombia). For the Colombian and Panamanian coasts of the Tropical Eastern Pacific, *C. leucas* was reported by López-Angarita et al. (2021). Eisele et al. (2021) reported that *C. leucas* is common around Costa Rica's Bat Island (= Islas Murciélago).

In the northeastern Pacific Ocean, the presence of *C. leucas* in southern Californian waters of the United States has often been a matter of discussion (Castro 2011), and the mentions of *C. leucas* by Fry Jr. & Roedel (1945) for Anacapa Island, California and by Miller & Lea (1972) seem doubtful and need verification. Nevertheless, Roedel & Ripley (1950: 58) stated, for *C. leucas* in United States Californian waters: "There is definite record of four specimens caught off Southern California." Later, Roedel (1953: 255) added: "This species is very rare in California". Bailey et al. (1960) mentioned that *C. leucas* only occurs on the Atlantic side of the United States and not on the Pacific side. However, Kato et al. (1967) noted that *C. leucas* occasionally wanders as far north as southern California. Furthermore, *C. leucas* is also mentioned in Pequeño et al.'s (1990) list of sharks with distribution along the Pacific coast of the United States from California to Oregon, with a record from California. Swift et al. (1993) critically discussed the presence of *C. leucas* in Californian waters in a literature review, with the conclusion that *C. leucas* is rare or extirpated in California due to the degradation of estuaries in this region. However, Swift et al. (1993) strongly suspected the presence of *C. leucas* in more southern waters of the Magdalena Bay of Baja California Sur, Mexico, at the putative northern limit of this species' range in the eastern Pacific. Eschmeyer & Herald (1983) stated that *C. leucas* possibly reaches southern California, but with the additional comment that its occurrence in United States Pacific waters of North America is uncertain. López & Bussing (1982: 6) reported: "California to Peru." Compagno (1984) did not record *C. leucas* north of southern Baja California. Robins et al. (1991) accepted the species as recorded from the Pacific coast of the United States. There are no records of *C. leucas* for Californian waters in the historical literature (Starks & Morris 1907; Starks 1917).

Further to the above considerations, Hastings et al. (2014) reported a 1963 record of *Carcharhinus obscurus* for southern California and the waters of the United States, from the area of La Jolla near San Diego. Castro (2011) commented that there are no verifiable records of *C. leucas* in California and that previous records were based on misidentifications of *C. obscurus*. Horn et al. (2006) reported a distribution of *C. leucas* in the East Pacific that ranges from 33.00°N to -5.00°S, which would mean that *C. leucas* reaches southern Californian waters just north of San Diego. However, Kyne et al. (2012) mentioned that, in the Californian waters of the Northeast Pacific Ocean, the fauna shifts from a boreal cold-temperate regime to a warm-temperate regime in southern California and that the major change from the cold to the warm-temperate regimes occurs at Point Conception on the Californian coast. Furthermore, Kyne et al. (2012) stated that *C. leucas* may occur in southern Californian waters, adding that its presence had not been confirmed and that its distribution in this region was uncertain. Ebert et al. (2017) also reported that *C. leucas* may occur along the US coast of the northeastern Pacific, but that its distribution is uncertain in this region. In conclusion, *C. leucas* may occur off the southern Californian coast on occasion, but has not yet been confirmed (Ebert 2003; Ebert et al. 2017); Kells et al. (2018: 70) stated, about *C. leucas* in Californian waters: "Rare to uncommon in the area. Reports from CA may be erroneous."

Despite the lack of confirmed records, occasional, brief occurrences of the thermophilic *C. leucas* along the Californian Pacific coast is imaginable as a result of northerly intrusions of warm-water masses. The occurrence in southern Californian waters at Catalina Island (and possibly even in northern Californian waters) of the warm-water *C. longimanus* in 1983, as a result of a warm-water incursion along the California coast (Compagno 1984), suggests that similar movements of *C. leucas* into Californian waters may also occur in this region. Ebert (2003) reasoned that in years with extreme El Niño-related phenomena, the influx of unusually warm water could attract many warm-water species of carcharhinid sharks from southern Baja California to Californian waters, with a short-time range shift towards the north. Species with a normally temperature-restricted range limit in Mexican waters and that possibly temporarily occur in Californian waters include *C. albimarginatus* Rüppell, 1837 (silvertip

shark), *C. altimus* Springer, 1950 (bignose shark), *C. falciformis* Müller & Henle, 1839 (silky shark), and even *C. galapagensis* (Ebert 2003), but maybe even *C. cerdale* Gilbert, 1898 (Pacific smalltail shark), *C. longimanus*, and *C. leucas*. Also Hastings & Robertson (2001) stated that fishes of the Tropical Eastern Pacific periodically (e.g., during El Niño events) cross the thermal barrier to the north and are found in California. Finally, the presence of *C. leucas* in the waters of California remains uncertain and unconfirmed.

Regarding the presence of *C. leucas* in the Gulf of California, Nicholls (2017: 289) stated: "The geographical extent of which is not fully understood, as the species´ American Pacific range has yet to be elucidated". In the more southern waters of the northeastern Pacific, *C. leucas* definitely occurs along the Mexican coast of southern Baja California on the Pacific Ocean and in the Gulf of California. Galván-Magaña et al. (1989, 1996) and numerous further authors reported *C. leucas* from Mexico's southern Baja California and the waters of the Gulf of California. Recently, *C. leucas* was reported from the west coast of Baja California and the Gulf of California by Galván-Magaña et al. (2019). Verifiable records of *C. leucas* in shallow lagoons and bays of Baja California Sur were given by Gonzáles-Acosta et al. (2015) from the locations of Bahía Concepción and Bahía Magdalena, for which historical information was also provided by Rosenblatt & Baldwin (1958).

In the eastern Pacific, not only the northern range limit of *C. leucas* has been a matter of discussion, but also its southern limit, albeit to a lesser extent. Chirichigno (1974) reported the distribution of *C. leucas* in the eastern Pacific as ranging from southern Baja California to Peru. Compagno (1984: 479) only assumed *C. leucas* for the coastal waters of Peru and commented: "…possibly Peru". An earlier report on the distribution of *C. leucas* in the eastern Pacific was provided by Bini & Tortonese (1955), who reported *C. leucas* under the synonym "*C. azureus*" from marine waters off Peru. Later, *C. leucas* was reported from the marine waters off Peru also by Chirichigno (1969). According to Chirichigno (1974) and Love et al. (2005), *C. leucas* occurs as far south as Paita along the Peruvian coast. Also Chirichigno & Cornejo (2001) and Cornejo et al. (2015) reported *C. leucas* from the southeast Pacific off Peru. AFIB (2015) gave a distribution map for *C. leucas* which included an occurrence in northern Peruvian marine waters south to Paita. Additionally, Gonzalez-Pestana et al. (2016) reported that *C. leucas* is part of the Peruvian coastal fisheries.

Notably, the country of Peru hosts two genetically distinct populations of *C. leucas* (Tables 3, Fig. 4): the marine Pacific and the freshwater Atlantic population, albeit without having an Atlantic coastline. *Carcharhinus leucas* was first reported for Peru from freshwaters of the Amazon River at Iquitos by Myers (1952), and subsequently from marine waters by Bini & Tortonese (1955). In this context, Ortega et al. (2012) listed *C. leucas* as a native fish species for the Amazonian and the continental waters of Peru. Finally, the presence of *C. leucas* in the Southeast Pacific Ocean as far south as Paita (-5.08°S), in tropical northern Peru, is confirmed.

There is a doubtful record of *C. leucas* for the Galapagos Archipelago by Tirado-Sanchez et al. (2016), based on database information provided by Appeltans et al. (2010) and on a popular diving guide book (Constant 2007). Considering the seawater temperature of ~20 °C around this archipelago and the habitat preferences of *C. leucas*, it seems very unlikely that *C. leucas* occurs around the Galapagos Islands. The influences of the cold Humboldt Current and the Equatorial Undercurrent, with an upwelling of very cold waters (Bearman 1991), provide unsuitable water conditions for *C. leucas*. Indeed, the list of Galapagos elasmobranchs by Hearn et al. (2014) and of sharks of the Galapagos Islands by Zárate (2002) do not include *C. leucas*, and this species is also not listed in further works regarding the fish fauna of the archipelago (Grove & Lavenberg 1997; McCosker & Rosenblatt 2010).

There is also doubtful information regarding the occurrence of *C. leucas* from around Chile's Easter Island (= Isla de Pascua, Rapa Nui) in the South Pacific Ocean (-27°S), mentioned by GBIF (2018c). Two specimens of a carcharhinid shark were collected in 1965 from this remote island during the Canadian Medical Expedition by marine ecologists Jack A. Mathias and Ian E. Efford (Randall 1970; GBIF 2018c), later deposited in the Fish Collection of the Canadian Museum of Nature (Khidas & Shorthouse 2018). My examination of photo material of these voucher specimens revealed that the information provided by GBIF (2018) is based on a mistake or possibly a wrong entry in the database. One of the voucher specimens (catalog no.: CMNFI 1968-1863.1) is labeled "*Carcharhinus menisorrah*", which is an older name used for several species, i.e., *C. falciformis*, *C. amblyrhynchos*, *C. dussumieri* Müller & Henle, 1839 (whitecheek shark), and *C. sealei* Pietschmann, 1913 (blackspot shark) (Froese & Pauly 2018b). Randall (1970), who wrote a popular account of the Canadian Medical Expedition, first believed that these voucher specimens represented *C. amblyrhynchos*, but he later changed his mind, suggesting that they belonged to *Carcharhinus galapagensis* (Randall et al. 2005). My own examination of photographs of one of the voucher specimens from the Canadian Museum revealed that it has too large eyes for *C. leucas* and has an interdorsal ridge that is missing in *C. leucas*. This examination leads to the conclusion that it presumably belongs to *C. galapagensis*, and not to *C. leucas*. The Galapagos shark is common around Easter Island (Randall & Egaña

1984; Randall et al. 2005) and many other remote oceanic islands in the tropics and subtropics (Compagno 1984, 2001). Moreover, *C. leucas* was so far never reported from Easter Island in literature (Randall & Egaña 1984; Randall et al. 2005). From an ecological point of view, it is questionable whether the water temperature around this remote Pacific Island is suitable for *C. leucas*, as the surface summer temperature is 22–24 °C and the winter minimum is 15.7 °C (Randall et al. 2005). As investigations by Froeschke et al. (2010a) pointed out, *C. leucas* is rare in waters below 20 °C, with the rare exception of the 15 °C Louisiana waters reported by Blackburn et al. (2007). More in general, *C. leucas* presumably does not occur frequently around remote islands in the southern Pacific (see Compagno 1984).

5 Aspects of habitat use and distribution of *Carcharhinus leucas*, with comments on limiting factors, the impact of natural events, and human influences

Habitat selection by elasmobranchs is influenced by a multitude of interacting parameters, such as water temperature, salinity, dissolved oxygen, water depth, turbidity, substrate type, benthic vegetation type, prey distribution and variability, predator distribution, social organization, and reproductive activity (Simpfendorfer & Heupel 2004; Heithaus et al. 2009). Environmental factors are highly influential in determining the short- and long-term movements, the behavior, and even the habitat use of sharks (Schlaff et al. 2014). Knip et al. (2010) stated that there may be different physical factors that affect shark species' distribution and movement within different regions, including nearshore environments. Speed et al. (2010) delivered a good overview of the different parameters that influence the complex movements of coastal sharks in inshore waters. Water parameters like depth, temperature, salinity, and dissolved oxygen are regulating factors that influence the occurrences of sharks. Today, for some shark species and some regions, the relationships between distribution and environmental factors are well studied (Calich et al. 2018; Drymon et al. 2020b; Roskar et al. 2021). However, both physical and biological variables may influence habitat selection, and the interaction between these variables is complex.

Regarding the habitat use of low salinity environments by *Carcharhinus leucas* and parameters that influence the distribution of this circumglobal species in these environments, the affecting parameters differ in many parts of its range and are highly regional and geographically specific. This makes it difficult to make comprehensive statements on the habitat use of *C. leucas*. Although *C. leucas* is a very common species in some regions, especially in the tropics, for many regions very little is known about its habitats (Castro et al. 1999). The habitat use of *C. leucas* has only been intensively investigated in a few regions, for example in the coastal regions of the northern Gulf of Mexico (Blackburn et al. 2007; Simpfendorfer et al. 2005; Heupel & Simpfendorfer 2008; Froeschke et al. 2010a; Heupel et al. 2010; Bethea et al. 2015; Matich & Heithaus 2015; Matich et al. 2017b; Plumlee et al. 2018; Matich et al. 2020b; Rider et al. 2021). Investigations by Froeschke et al. (2010a) have shown that *C. leucas* (immatures up to 170 cm TL) distributions in estuaries along the Texas coast were most strongly influenced by water parameters such as salinity and temperature, which may be the most determining factors shaping the distribution and abundance of *C. leucas* in low salinity environments.

Habitat use of *C. leucas* is highly age- and sex-dependent, with pregnant females thought to give birth in estuaries and river mouths (McCord & Lamberth 2009; Baker 2013), followed by an upriver migration by the offspring. Individuals of *C. leucas* move from lacustrine, riverine, and estuarine environments to coastal habitats during their ontogeny (Simpfendorfer et al. 2005; Heupel & Simpfendorfer 2008). According to Simpfendorfer et al. (2005), the smallest size classes of *C. leucas* live within freshwater bodies of rivers and lakes and move to estuarine habitats after having reached more than 0.95 m TL. *Carcharhinus leucas* exhibits ontogenetic changes in habitat use, as has been observed in many other large carcharhinid species, but it is unique in using low salinity habitats intensively during the early stages of its lifetime. Moreover, it shows seasonal patterns in habitat use in many parts of its subtropical and warm-temperate range, at least partially driven by the cooling and warming of water bodies. a study by Rider et al. (2021) using acoustic tagging found that mature female *C. leucas* displays high residency in Florida's Biscayne Bay during the colder, dry season (November to February) and lower residencies during the warmer, wet season (June to October), with seasonal migrations to adjacent areas (Florida Gulf coast). Likely, these seasonal patterns are partially driven by seasonal changes in environmental variables as well as by the individual's life stage and reproductive behavior.

Carcharhinus leucas can utilize a wide range of habitats due to its adaptation to salinity changes and to its osmoregulatory competencies (Meynecke et al. 2015), and is known for its tolerance of various salinity conditions, which has enormous consequences on distribution, migrations, and habitat use. This shark is commonly found in estuaries, harbors, and creeks (Castro 1983). Its affinity to low salinity habitats has resulted in the colloquial names "estuary shark" (Ogilby 1916), "Swan River whaler" (Whitley 1940, 1951), and "river whaler" (Pusey et al. 2003), names that refer to the preference of *C. leucas* for estuaries and rivers during different life stages. How-

ever, Pillans et al. (2020) concluded that there is a large degree of variation in habitat preference of *C. leucas* (concerning salinity and distance upstream) between studies at national and international scales. Furthermore, these authors noted that the length of time that juveniles reside in rivers and estuaries varies greatly both at small (differences between river systems < 100 km apart) and large (between continents) scales. The time of residence of juvenile *C. leucas* in river and estuary systems was estimated to be as great as five years in the Brisbane River, Australia (Pillans 2006), between three and five years in the Shark River Estuary, Florida (Matich & Heithaus 2012), and as short as one year in the Caloosahatchee River, Florida (Heupel & Simpfendorfer 2008). In this context, it would be of special scientific interest to know how long *C. leucas* resides in large river systems such as the Amazon and Mississippi, for which there are recorded migrations up to thousands of kilometers upriver.

Habitat selection by sharks is complex and variable over space and time. For example, *C. leucas* may occur in turbid or clear water depending on prey availability, and this may change seasonally as further factors such as reproduction become more important drivers. Furthermore, habitat selection by sharks is driven by physical factors as well as biological factors. However, for a better understanding of the parameters and key drivers that influence the occurrence of *C. leucas* in low salinity and coastal nearshore environments, the most important influencing factors are presented and discussed in the following sections. The following explanations can neither reproduce the complete results of many recent studies on habitat use by *C. leucas* nor can they work out the subtle nuances that control and influence the distribution of *C. leucas* in freshwater as well as marine habitats. They are only intended to give an impression of how complex the relationship between environmental conditions and shark distribution is, using some of the most important known parameters.

5.1 Influence of salinity

Elasmobranchs are essentially marine, but ~15% of species occur in brackish or freshwater (Wosnick & Freire 2013). *Carcharhinus leucas* is considered the best known of the 43 species of elasmobranch, in ten genera and four families, to have been reported in freshwater (Compagno & Cook 1995). *Carcharhinus leucas* has a life cycle closely linked to the freshwater-estuarine-marine continuum (Werry et al. 2018), which provides a salinity gradient from 0 up to ~35‰. Although *C. leucas* is not the only euryhaline carcharhinid shark, and river sharks of the genus *Glyphis* also occupy habitats with low salinities in southeast Asia and northern Australia, *C. leucas* is unique in enduring water conditions with nearly no salinity and pure freshwater. This enables this species to enter low salinity environments where no other primarily marine sharks can follow it. Numerous authors have reported the frequency of *C. leucas* in low salinity habitats, and some of them outlined the dependency of this species on these habitats during certain stages of its life history. Moreover, *C. leucas* exhibits salinity preferences (Blackburn et al. 2007; Froeschke et al. 2010a; Drymon et al. 2014) that may regulate its abundance in certain habitats.

Simpfendorfer et al. (2005) reported, from the inland waters of Florida, that juvenile *C. leucas* displayed spatial segregation by body size, thus partitioning available food resources and reducing competition between size classes. This partitioning by juvenile *C. leucas* appears to be driven by temperature and salinity gradients, along with varying preferences for these parameters between size classes (Simpfendorfer et al. 2005; Heupel & Simpfendorfer 2008). In the hot tropical and subtropical river systems of northern and eastern Australia, neonate *C. leucas* travel upstream from estuaries after birth and undertake extensive movements into the upper reaches of rivers, where they can remain in purely fresh water for up to four or five years (Pillans 2006; Thorburn 2006; Thorburn & Rowland 2008; Last & Stevens 2009). Here, they are safe from predation from other sharks. However, in river systems of temperate latitudes, the low water temperatures of the upper reaches of rivers in winter causes the sharks to migrate into environments with higher salinities closer to the river mouth, and their residence in freshwater environments is thus time-restricted. Moreover, tidal influences in estuaries play an essential role in the distribution of juvenile *C. leucas* in estuarine environments, where movements and travel directions of immature *C. leucas* have been positively correlated with different tidal stages due to changes in salinity (Ortega et al. 2009). Pillans et al. (2020) observed movements of juvenile *C. leucas* in two Australian rivers that were correlated to both flow and salinity, with sharks moving downstream in response to increasing flow/declining salinity and upstream during low flow/increasing salinity.

Already Springer (1950: 6) noted, for North America and regarding the distribution and habitat use of *C. leucas*, especially during times of breeding: "*Carcharhinus leucas*...reaches peak abundance near the mouth of large rivers during its summer breeding season. The young frequent bays and are more common where the water is slightly brackish." In this context, McCord & Lamberth (2009) reported that a single pregnant female *C. leucas* that was tracked in South Africa's Breede River Estuary remained within the 15–35‰ salinity ranges and in the lower 20 km of the estuary. This may indicate that adult females of *C. leucas* are partially estuarine-dependent and utilize estuaries as pupping and nursery grounds.

On the other hand, immature *C. leucas* favor lower salinities, which suggests that a change in physiological

tolerances with age contributes to niche separation (Simpfendorfer et al. 2005; Wiley & Simpfendorfer 2007; Heupel & Simpfendorfer 2008). Heupel & Simpfendorfer (2008) found out that juvenile *C. leucas* leave estuaries when salinity declines, which is astonishing for a fully euryhaline shark that is tolerant of a broad salinity amplitude, able to adapt rapidly to salinity changes, and that actively seeks low salinity habitats during the early stages of its lifetime. a study conducted by Pillans et al. (2020) in Australia's Logan and Albert Rivers revealed that despite fluctuations in environmental salinity (0–32‰) in these rivers and a strong declining gradient in salinity with increasing distance upstream, neonate and juvenile *C. leucas* (74–102 cm TL) remained within a narrow band of salinity (6–10‰) throughout the tracking period (30 months). a study by Drymon et al. (2014) showed that juvenile *C. leucas* had the highest affinity for moderate salinities (10–11‰) in Alabama's Mobile Bay. These results support the idea that juvenile *C. leucas* could have a preferred salinity range, or perhaps an ecological optimum salinity range, despite the fact that this shark species can survive in a wide range of salinity values (Ballantyne & Fraser 2013), and this since its earliest life stages (Pillans et al. 2005a) and for extended periods. Considering the energetic costs of osmoregulation in *C. leucas*, the observation made by Heupel & Simpfendorfer (2008) is comprehensible.

Alford (2012) reported the highest abundance of *C. leucas* in Louisiana's Barataria Estuary at salinity ranges between 12 and 23‰, and postulated a significant positive relationship between abundance and salinity (the size of the sharks was not reported). Investigations conducted by Ortega et al. (2009) in Florida's Caloosahatchee River Estuary revealed that juveniles of *C. leucas* (77–104 cm TL) occupied a salinity range between 2.4 and 12.8‰. Streich & Peterson (2011) reported salinities in Georgia's Altamaha River Estuary, at sites 14–18 km upstream, varying from 10.4 to 12.4‰, in which neonates and young-of-the-year *C. leucas* occurred. Tinari & Hammerschlag (2021) listed occurrences of the 142–300 cm TL size-class *C. leucas* in a salinity range of 24–45‰ in waters off South Florida (including the Miami and Keys regions), in a spectrum below and above the mean salinity of seawater (~35‰). Before, Loftus & Kushlan (1987) reported two newborn specimens of *C. leucas* from Florida's Shark River at 0.8‰ salinity, just downstream from the freshwater section of this creek. Also Pillans (2006) revealed, in Australia's Brisbane River, that juvenile *C. leucas* showed a strong preference for the upper freshwater reaches of this river in environments with extremely low salinities. Hueter & Tyminski (2007) recognized for Florida estuaries that although older juvenile *C. leucas* utilize estuarine nursery areas (1.7–41.1‰ salinity), they do not appear to venture as far into freshwater as the neonates and young-of-the-year do.

A study conducted by Dwyer et al. (2020) in a north Australian river found that *Glyphis glyphis* Müller & Henle, 1839 (speartooth shark) used higher salinity environments (mean salinity = 19.22‰) located between 30 and 70 km from the mouth of the river, whereas *C. leucas* occupied freshwater reaches (mean salinity = 1.98‰) between 60 and 110 km upstream. Moreover, this study revealed that climate change plays a role in the behavior of freshwater tolerating sharks. At the onset of the wet season, both *C. leucas* and *G. glyphis* undertook a coordinated downstream migration towards the lower estuary before returning upstream (Dwyer et al. 2020). This spatial segregation could be interpreted as a niche partitioning behavior between river shark species, driven by seasonal fluctuations in environmental salinity. However, juveniles of *C. leucas* were reported from purely freshwater (estimated 0‰ salinity) from numerous locations worldwide (Tables 1–11).

As a euryhaline shark species with a wide amplitude of salinity tolerance, *C. leucas* not only occurs in low salinity habitats but also in hypersaline environments, like some lakes and saltwater lagoons in southern Africa (Lake St. Lucia) and eastern Australia (Lake Macquarie) (Compagno 1984; Last & Stevens 2009). Additionally, occurrences were reported from hypersaline bays like Mexico's La Paz Bay (Abitia-Cárdenas et al. 1994) and hypersaline estuaries like the Sine-Saloum Estuary in Senegal (Diouf 1996). However, sharks in these environments are sometimes found in poor conditions, and these habitats can be considered as suboptimal (Compagno 1984). Therefore, even for a euryhaline species like *C. leucas*, salinity is an environmental limiting its distribution.

Based on a comprehensive assessment of the published literature regarding the osmoregulation competencies of *C. leucas* (e.g., Thorson & Gerst 1972; Thorson et al. 1973; Pillans & Franklin 2004; Anderson et al. 2005a; Pillans et al. 2005a, 2006, 2008), there is no support for a shift in salinity preference based on its physiology; as specimens of *C. leucas* grow, their surface area/volume decreases, which reduces osmotic stress induced by long-time use of low salinity waters. As such, the use of low salinity environments by *C. leucas* is most likely due to biotic factors, particularly predation risk in marine environments, rather than physiological preferences (see also section 5.9). In this context, the results of Pillans et al. (2020) on juvenile *C. leucas* in two Australian River systems indicate that habitat choice by juvenile *C. leucas* is a complex tradeoff between hydrographic factors, physiology, food availability, and predator avoidance, resulting in large differences between adjacent systems and more broadly across the species' range. Notwithstanding this, the utilization of low salinity habitats by immature *C. leucas* throughout its whole geographic range reinforces the thesis that this behavior is mainly driven by instinct and/or inherited behavior.

5.2 Influence of water temperature

The distribution of aquatic animals such as fish is highly affected by parameters of the surrounding element. Water parameters like temperature, salinity, and dissolved oxygen are regulating factors that influence the occurrences of sharks in general and especially of *Carcharhinus leucas* in lacustrine, riverine, estuarine, and also marine environments, during all stages of the species' life history. This greatly influences the distribution of *C. leucas*. In the literature, *C. leucas* is mostly considered a warm-water species with a tropical stronghold. Bass (1978) reported that the distribution of *C. leucas* is basically tropical, and Schwartz & Burgess (1975) stated that *C. leucas* is primarily tropical. As is the case for all biota, also the distribution of *C. leucas* is temperature-restricted, especially in the marginal areas of its range. Water temperature can be estimated as the main factor limiting the range of *C. leucas*, not only in coastal marine habitats but even in freshwater habitats. *Carcharhinus leucas* usually inhabits the continental coast of all tropical to subtropical seas, but it undertakes seasonal migrations into warm-temperate regions with a favorable increase in water temperatures. Adult *C. leucas* can undertake long migrations in marine environments, depending on seasonal warming/cooling of the waters.

The study by Blackburn et al. (2007) revealed occurrences of *C. leucas* in Louisiana's coastal waters between March and September, with a temperature range from 15 to 37 °C, even when occurrences in waters below 20 °C may be an exception (Froeschke et al. 2010a). Results of a study by Drymon et al. (2014) from Alabama's Mobile Bay demonstrated that juvenile *C. leucas* showed the highest affinities for warm water (29–32 °C). Curtis et al. (2007) reported catches of *C. leucas* in Florida's Indian River Lagoon system in a temperature range between 18.5 °C and 37 °C. Hueter & Tyminski (2007) mentioned that young-of-the-year *C. leucas* have been documented in Florida estuaries at temperatures as low as 16.4 °C, but most individuals only remain in these nurseries until as late as November or until water temperatures fall to about 21 °C, at which point they leave the estuaries. Tinari & Hammerschlag (2021) reported occurrences of *C. leucas* in the coastal region of southern Florida in a temperature range between 19 and 33 °C, with a mean temperature of 26.18 °C. Lear et al. (2021) observed movements of subadult and adult *C. leucas* (1.81–2.69m TL) in waters off the west coast of Florida, northern Gulf of Mexico, during the winter months (November to April) in a water temperature range between 19.8 and 26 °C. Carlson et al. (2010) found, for U.S. waters of the northern Gulf of Mexico, that tagged subadult *C. leucas* (1.5–2.0 m FL [fork length]) occupied temperatures primarily between 30.5 and 32 °C, with individuals occupying most temperature between 26 and 32 °C. Specimens of *C. leucas* in Carlson et al.'s (2010) study area were rarely found at temperatures < 20 °C, which agrees with the results of Froeschke et al. (2010a). Ortega et al. (2009) recorded, in Florida's Caloosahatchee River Estuary, movements of juvenile *C. leucas* (77–104 cm TL) in a surface water temperature that ranged between 27 °C and 37.3 °C. Streich & Peterson (2011) reported temperatures during June and July in Georgia's Altamaha River Estuary at sites 14–18 km upstream, varying from 28.8 to 31.4 °C, in which neonates and young-of-the-year *C. leucas* occurred.

Lee et al. (2019) found that on the east coast of Australia, *C. leucas* was present in the study area when the sea surface temperature was between 20 °C and 26 °C, with a peak abundance of sharks at 24 °C. The results of Niella et al. (2020a) also revealed that *C. leucas*'s abundance in southeast Australia was highest at a sea surface temperature above 22 °C. Investigations by Brunnschweiler (2007) on *C. leucas* in the Fiji Islands showed that most time was spent by the sharks in water with temperatures between 26 and 27 °C. Interestingly, the analysis of acoustic tracking data of *C. leucas* tagged in Florida's Biscayne Bay revealed that temperatures above 27 °C had a negative impact on the presence of *C. leucas* in this area (Rider et al. 2021).

Carey et al. (1971) measured the body temperatures of carcharhinid sharks in comparison to the surrounding medium and found that the body temperature of *C. leucas* was just beneath the water temperature. In contrast to some of the thermoregulated mackerel sharks (Lamnidae), in carcharhinid sharks the body temperature depends on the temperature of the aquatic environment in which they stay. However, Hueter & Tyminski (2002) reported, from the inshore waters of Florida, that young-of-the-year and juvenile *C. leucas* have been found in the warm water effluents of the Tampa Bay and Yankeetown power plants during the winter months. It is believed that these sharks become trapped within these warm water plumes when the temperature of the surrounding water falls below the sharks' tolerance level (Hueter & Tyminski 2002). As a result of the ecological behavior of *C. leucas* and its preference for warm water, the water temperature of rivers and lakes may also have a selecting effect for occurrences in freshwater. Thomerson et al. (1977) reported the catch of a single specimen of *C. leucas* in the Mississippi River at Alton (Illinois) in September 1937, with water temperatures of the river of ~27 °C at the location of the catch and ~24 °C at the river mouth, where the freshwater starts penetrating. The authors suggested that the most effective limiting factor for the movement of sharks in this river was water temperature, withtemperatures below 24 °C (i.e., the temperature at the river mouth) limiting the movement of sharks in the Mississippi River. In a spatio-temporal context, Springer (1950) reported that adults

of *C. leucas* appear in great numbers near the mouth of the Mississippi River from May through July and produce their young there. Further, Springer (1950) mentioned that this species disappears from inshore waters of the northern Gulf of Mexico with the onset of cold weather and becomes relatively more abundant than along the Florida coast in the vicinity of the Florida Keys, which indicates a seasonally induced migratory behavior of *C. leucas* in the Gulf.

In all likelihood, also the distribution and occurrence of *C. leucas* in freshwaters of the subtropical Persian Gulf region (Iraq, Iran) are influenced by seasonality, and penetration into freshwater systems here may depend on changes in water temperature. Hussain et al. (1995) reported, for the Shatt Al-Arab River, a water temperature range between a minimum of 11.5 °C in February and a maximum of 30 °C in July, and that water temperatures higher than 20 °C encourage the migration of marine species from the Persian Gulf into this river. In this context, Mohamed et al. (2015) reported an increasing number of marine species in the Shatt Al-Arab River during summer and autumn and a sharp decrease in winter. Possibly, the Tigris-Euphrat-Karun system is only utilized by *C. leucas* during the summer months in the northern hemisphere, as the sharks leave the system in October when water temperatures drop below 14 °C (Bishop et al. 2016). As an example of a record of *C. leucas* in a warm-temperate estuary, McCord & Lamberth (2009) measured a temperature range of 20–24 °C in South Africa's Breede River Estuary in January 2009.

Investigations on the thermal behavior of sharks (Wheeler et al. 2020) revealed that young elasmobranchs are forced to endure suboptimal, local conditions as they arise, and that they experience a broader thermal environment compared to adults. Lear et al. (2019) found that free-ranging juvenile *C. leucas* experienced a 16 °C temperature range (19–35 °C) in a freshwater environment, nearly double that of adults (23–31 °C) in a marine environment. Despite the circumstance that most of the habitats that are utilized by *C. leucas* exhibit variability in water temperature, residential behavior was observed in *C. leucas* in some regions. Seasonal cooling and warming of water bodies affect the distribution of *C. leucas* in both hemispheres and can be understood as one of the drivers of large-scale migrations. For example, in the tropical waters of Florida in the northern West Atlantic, *C. leucas* is a year-round resident (see section 4.1.1), with northward-directed movements during the summer months. North of Florida, at nearly 30.00°N, *C. leucas* changes from being a year-round resident to a summer vagrant that also occurs in other states of the east coast of the United States, including Georgia, South Carolina, North Carolina, Virginia, Maryland, Delaware, New Jersey, New York, Connecticut, Rhode Island, and Massachusetts, at least up to 41.53°N.

5.3 Influence of water depth

Carcharhinus leucas is considered as a coastal, estuarine, riverine, and lacustrine species with a primarily neritic distribution, usually found in water less than 30 m deep; however, on the shelf, it can descend to the shelf edge to a depth of 152 m (Compagno 1984, 2016; White et al. 2006). This shark species shows a preference for shallow waters of the continental shelf with a main accumulation in waters of less than 30 m (Compagno 1984) and was commonly recorded in coastal Florida in shallow waters of 1–2 m depth (Heupel et al. 2006; Wiley & Simpfendorfer 2007). Investigations that were conducted by Carlson et al. (2010) in the northern Gulf of Mexico using pop-up satellite archive tags revealed that subadult *C. leucas* (1.5–2.0m FL) spent the majority of their time in waters less than 20 m deep. Tagged specimens in the study by Carlson et al. (2010) exhibited significant differences with regard to depth behavior, but this was not correlated to time of day. In contrast to these results by Carlson et al., Ortega et al. (2009) found, by using acoustic telemetry, that juvenile *C. leucas* in the estuary of Florida's Caloosahatchee River swam significantly closer to the surface during the night (mean = 0.6 m depth) and remained deeper in the water column during the day (mean = 1.5 m depth).

Brunnschweiler (2007) equipped specimens of *C. leucas* around the Fiji Islands with pop-up satellite archival tags and reported a maximum depth of 204 m for this species during occasional deep-diving vertical movements, which is the greatest depth ever directly measured for *C. leucas*; however, most of the time was spent by the sharks in waters less than 50 m deep, and they remained deeper during the day than at night. Curtis et al. (2007) reported catches of *C. leucas* in Florida's Indian River Lagoon system at depths between 0.2 and 4 m. Tinari & Hammerschlag (2021) reported, for waters off South Florida (including the Miami and Keys regions), occurrences of the 142–300 cm TL size-class of *C. leucas* in a depth spectrum between 2.16 and 44.77m and at a mean depth of 12.79 m.

Depending on the age of individuals, the habitat used by adult *C. leucas* may include also offshore environments during open-ocean migrations (Drymon et al. 2010; Love et al. 2013; Lea et al. 2015); however, sightings of adult *C. leucas* in open-ocean waters are not commonly recorded (Kohler et al. 1998).

5.4 Influence of dissolved oxygen

Besides salinity, additional water parameters such as dissolved oxygen may influence the distribution of *Carcharhinus leucas* in low salinity environments. Heithaus et al. (2009) reported that dissolved oxygen had a greater influence on the distribution of juvenile *C. leucas* in a Florida estuary than salinity, and that the number of

individuals was high when dissolved oxygen levels were high. Pillans et al. (2020) observed, in two Australian rivers, that during periods of negligible flow and stable salinity, juvenile *C. leucas* moved upstream and downstream in response to increasing/decreasing dissolved oxygen. However, it should be considered that the upper stretches of river systems can exhibit limited tidal exchange together with high levels of microbial degradation of organic material, which lead to low oxygen conditions in these river portions. This may decrease the suitability of upper river portions for *C. leucas*.

Individuals of *C. leucas* were observed in a fish kill that occurred in March 1978 in the Belmore River (Macleay river system, northern New South Wales) during rapid deoxygenation of floodwaters (Bishop et al. 2001). Although the exact number and percentage of dead individuals of *C. leucas* were not reported, numerous specimens died during this event, when dissolved oxygen levels dropped below 20% saturation at temperatures ranging between 22 °C and 25 °C (Bishop et al. 2001). Thus, the completely euryhaline *C. leucas* probably depends also on suitable dissolved oxygen levels as well as suitable salinity levels. Ortega et al. (2009) reported, for a Florida estuary, that juveniles of *C. leucas* were observed in a dissolved oxygen range at the water surface of 3.6–9.4 mg/L. For the subadult and adult size-classes of *C. leucas* (142–300 cm TL), Tinari & Hammerschlag (2021) reported the species in a dissolved oxygen range between 1.46–12.00 mg/L (mean dissolved oxygen = 7.01mg/L) in waters off South Florida (including the Miami and Keys regions).

5.5 Influence of underwater visibility

Carcharhinus leucas exhibits a preference for turbid waters (Ellis 1989), as these conditions exist especially in estuaries and river mouths. Already Davies (1962) recognized the affinity of *C. leucas* for the freshwaters and estuaries of South Africa, and that these sharks were attracted by floodwater from rivers; according to this author, this preference is due to an increased likelihood of finding prey organisms in waters with turbidity. Also Compagno (1984) pointed out that *C. leucas* is often found in muddy areas and in the inshore waters of estuaries and river mouths, where few other shark competitors occur. Catch rates of *C. leucas* from South African waters revealed that the number of caught specimens was highest in underwater visibility below 1 m and decreased with increased visibility (Cliff & Dudley 1991; Wintner & Kerwath 2018). However, this information should be used with caution, as visibility may influence the catch rate of *C. leucas* but does not really provide any evidence for the habitat preferences of this species. Blackburn et al. (2007) reported occurrences of *C. leucas* in Louisiana waters with turbidity ranging from 0.1 to 2 m underwater visibility.

Compagno (1984) concluded that the very small eyes of *C. leucas* may have evolved as a result of the species' adaptation to estuarine, riverine, and lacustrine life habitats, where locating prey relies on other senses due to local turbidity. However, *C. leucas* also uses marine coastal waters with high underwater visibility, like reef ecosystems, and is therefore also subject to intensive dive tourism operations worldwide, e.g., in Fiji (Brunnschweiler 2010; Ward-Paige et al. 2020; Bouveroux et al. 2021).

5.6 Influence of sea bottom type

Carcharhinus leucas is both a marine and an estuarine/riverine apex (top) predator (O'Connell et al. 2007; Navia et al. 2010) and has adapted to life in a wide variety of environments, from freshwater rivers to offshore habitats (Love et al. 2013). In marine waters and coastal areas, adult and subadult *C. leucas* inhabit a variety of different benthic habitats from soft-bottom, sand-dominated habitats, including seagrass meadows, to rocky bottoms and coral reefs (Gilmore Jr. 1977; Ceccarelli et al. 2014). a study by Hueter & Manire (1994) in coastal waters off the west coast of Florida revealed that specimens of *C. leucas* showed no clear bottom preference, and were found over sand or mud bottoms as well as over seagrass.

In tropical to subtropical estuaries with brackish water conditions, mangrove forests with halophytic tree and shrub species are the dominating vegetation type of shoreline habitats. In estuarine ecosystems, juveniles of *C. leucas* can be found in mangrove estuaries and even in adjacent wetland marshes (Thollot 1996b; Ley et al. 2002; Matich et al. 2011; Kottelat 2013; Tuiwawa et al. 2013; Gaskins et al. 2020). Gonzáles-Acosta et al. (2015) reported *C. leucas* from the flooded mangrove forests of southern Baja California and Vega & Villarreal (2003) reported it from a mangrove estuary of Panama's Coiba Island, both on the eastern Pacific coast. Mangrove forests function as nurseries for a high number of marine and estuarine fish species (Laegdsgaard & Johnson 1995; Faunce & Serafy 2006) as well as for a high number of elasmobranchs (Nagelkerken et al. 2008), as they provide shelter from larger predators and high amounts of accessible prey. In these environments, as an estuarine top predator, juvenile *C. leucas* are niched in these tidally influenced ecosystems and are part of the estuarine food web, feeding on accessible prey like small bony fishes, elasmobranchs, and crustaceans. Estuaries with mangrove forests represent an important habitat type for the early life stages of *C. leucas* (Heithaus et al. 2009). As strong predators on other elasmobranch species, adult *C. leucas* may move inshore for foraging on other juvenile elasmobranchs in mangrove estuaries.

5.7 Influence of extreme climate events

Extreme climate events can affect the presence and abundance of *Carcharhinus leucas* in riverine and estuarine systems. In rare cases, the occurrence of extreme climate events can have impacts on the small-scale distribution and habitat use of *C. leucas*, especially when they affect the temperature of the water. Even in the tropics, and in regions known to be residential areas for *C. leucas* during the winter such as Florida in the western Atlantic, extreme climate events can have a disastrous effect on *C. leucas* populations in inland waters. Snelson & Bradley (1978), Gilmore Jr. et al. (1978), and Snelson (1979) reported several fatalities in *C. leucas* in the Indian River Lagoon system, caused by the extremely cold winter of 1976–1977 and hypothermal water conditions down to 4 °C. These extreme climatic conditions, which are unsuitable for tropical and subtropical fishes, led to a concentration of high numbers of *C. leucas* around the heated effluents of electricity generating stations (Snelson & Bradley 1978; Snelson 1979). Matich & Heithaus (2012) also reported the effects on juvenile *C. leucas* of an extreme winter weather phenomenon in the Shark River Estuary in Florida, a "cold snap" of nearly two weeks in January 2010 with a water temperature minimum of 9.1 °C at the peak of the event. This extreme climatic event resulted either in the death of sharks or in sharks permanently leaving the estuary system (Matich & Heithaus 2012). As results of long-term monitoring of habitat use by juvenile *C. leucas* in the Shark River Estuary have shown, the recovery of shark abundances and population structure in the river after such events can take up to seven years (Matich et al. 2020a).

Sometimes, natural disasters have led to spectacular findings of *C. leucas*, like after the tropical cyclone "Debbie" in northeastern Australia in March 2017, which washed *C. leucas* specimens out of the Burdekin River onto a nearby street (Clamann 2017; Sandeman 2017). One specimen was seen swimming in the flooded streets of Brisbane (Queensland, Australia) during the Queensland floods in 2010–2011 (BBC 2011). Several bull sharks were sighted in one of the main streets of Goodna (Queensland, Australia) shortly after the peak of of the Brisbane River flood in January 2011 (Garry 2011). a spectacular habitat is the golf course lake at Carbook, Logan City (Queensland, Australia), which is home to several *C. leucas* and has been for more than 20 years. These specimens were trapped in the golf course's lake following a flood of the Logan and Albert rivers in 1996 (Boswell 2013). Some of the sharks inhabiting the lake were found dead after a second flood in 2013 (Boswell 2013). According to Stevens et al. (2005) and Pillans et al. (2009), in rivers of the Northern Territory of Australia specimens of *C. leucas* are often captured in freshwater billabongs or sections of rivers isolated from the main tidal stream during the dry period, when the water level of these rivers decreases.

Some research has focused on the response of *C. leucas* to incoming hurricane events. Investigations on the behavior and spatial distribution of *C. leucas* using acoustic telemetry, conducted by Gutowsky et al. (2021) in the subtropical Biscayne Bay, Florida (USA), showed that most of the tagged *C. leucas* were no longer detected after Hurricane "Irma" in 2017, and that the number of sharks in the study area declined after the hurricane. Presumably, the sharks left the area as a response to the storm. In this context, Strickland et al. (2020) also investigated the effects of Hurricane "Irma" on the behavior and survival of juvenile *C. leucas* that inhabit Florida's Shark River Estuary. They found that most of fourteen tagged sharks attempted to leave the shallow waters of the estuary before the hurricane strike: eight specimens left within days or hours before the hurricane, whereas three left more than a week in before; finally, three specimens supposedly died as a result of the hurricane.

On the other hand, an increase in the number of *C. leucas* recognized in Lake Pontchartrain (Louisiana) was documented after Hurricane "Katrina" in August 2005 (Internet Reference 2). This was possibly a response to low oxygen levels in coastal rivers after the hurricane, which may have reduced the access of sharks to the adjacent rivers (Hoffmayer et al. 2006). However, it may also have been the result of higher amounts of food caused by the flushing of flotsam into the lake. In this context, Van Vrancken & O'Connell (2010) found that Hurricane "Katrina" has an influence on dissolved oxygen as well as salinity and water temperatures in Bayou Lacombe, a small tributary of Lake Pontchartrain. Perret et al. (2010) investigated the effects of Hurricanes "Katrina" and "Rita" in August and September 2005 on the sport fish fauna in the Atchafalaya River Basin and suggested that the loss of sport fish in the basin was the result of either a temporary event such as a precipitous drop in dissolved oxygen levels, or release of hydrogen sulfide causing more subtle changes in habitat.

5.8 Influence of rainfall

Besides seasonal warming of riverine and marine environments, which stimulates shark migrations, natural events such as rainfall can also influence the distribution and presence of *Carcharhinus leucas* in estuarine habitats, with a possible increase of abundance after rainfall due to higher amounts of food in these habitats. Moreover, increased and sustained rainfall/flooding will dramatically alter the salinity in estuarine environments and river mouths. Investigations by Werry et al. (2018) along the coastline of Queensland, Australia, suggest that the activity patterns of *C. leucas* are correlated with rainfall

events, with an increased *C. leucas* catch (both juvenile and adult) from one to eight days after the rainfall—a relationship also confirmed by the movements of acoustically tagged sharks between estuarine and beach areas. In this context, Kiilu et al. (2019) reported, for Kenya's marine waters, that catch rates of *C. leucas* peaked during the months with the highest total rainfall. Werry et al. (2018) postulated two interacting mechanisms as drivers for an increased catch of *C. leucas* after rainfall. First, an increased movement of freshwater drains from a catchment into nearshore areas via rivers may physically push juveniles further towards marine waters. Second, the murky freshwater plumes interact with seawater to create localised in-water fronts. Such fronts aid plankton blooms, supporting the baitfish populations upon which juvenile and adult *C. leucas* feed. Storm events and intensive rainfall can change the salinity gradient in the transition zone of estuary systems dramatically, with a disruption of the normal spatial segregation of *C. leucas* and an abnormal and increased mixing of juveniles and adults (Werry et al. 2018). This may have negative impacts on local populations of *C. leucas*, as large specimens cannibalize smaller conspecifics, resulting in depletion of the juveniles.

5.9 Influence of predators

Habitat use by the euryhaline *Carcharhinus leucas*, especially when immature, is also driven by predation risk. Low salinity habitats and estuary nursery grounds seem to provide low-mortality environments for young *C. leucas* such as neonates, young-of-the-year, and juveniles (Heupel & Simpfendorfer 2011). The penetration of freshwater systems by juvenile *C. leucas* can be understood as an evolutionary strategy to decrease the predation risk of immature *C. leucas* by large coastal sharks in marine habitats, especially by apex predators that are known to be intensive elasmobranch consumers, e.g., *Galeocerdo cuvier*, *Sphyrna mokarran* Rüppell, 1837 (great hammerhead shark), and also adult *C. leucas* itself (Compagno 1984; Clua et al. 2014). *Carcharodon carcharias* and predatory marine mammals such as *Orcinus orca* Linnaeus, 1758 (orca or killer whale) may also include *C. leucas* in their diet (Compagno 2001). The strong predation pressure in coastal marine environments may have been an important driving force in the adaptation of *C. leucas* to use of low salinity environments. *Physeter macrocephalus* Linnaeus, 1758 (the sperm whale) has occasionally been observed to feed on sharks up to 3 m TL (Kawakami 1980), but this species may only represent a threat for adult *C. leucas* during their rare open ocean movements, as sperm whales seldomly move in coastal waters.

Considering the wide amplitude of environmental conditions *C. leucas* can endure, predation risk is likely the primary extrinsic factor shaping its habitat use, especially during the early stages of its lifetime. According to Sadowsky (1971) and Branstetter & Stiles (1987), at 1.24–1.30m TL, juveniles of *C. leucas* begin to occupy primarily continental shelf waters. At this length, they are large enough to avoid predation by larger sharks and further predators because of their size and speed. In contrast, *C. leucas* individuals of 1.5m TL and more have been involved in human-shark interactions in numerous freshwater locations around the world, e.g., in Lake Nicaragua and in the Euphrat-Tigris-Karun river system (Thorson 1976a; Coad & Papahn 1988; Moore 2018), which shows that they can remain in freshwater environments for longer than reported by Sadowsky (1971) and Branstetter & Stiles (1987).

Intraspecific predation is also a habitat-selecting factor for juvenile *C. leucas*. Thorson (1973) reported, about Nicaragua's San Juan River system, that juvenile *C. leucas* are concentrated in some of the side channels of the system, where they presumably are safer from predation by adults. In areas where *C. leucas* is sympatric with river sharks of the genus *Glyphis*, the larger river sharks may also prey on juvenile *C. leucas* in riverine habitats. Moreover, especially in freshwater ecosystems but also in brackish and close-to-shore marine ecosystems, *C. leucas* competes with other apex predators like alligators and crocodiles, which can also prey upon juveniles. In Florida's Everglades National Park and the southeastern United States, besides other freshwater elasmobranchs, *C. leucas* is sometimes prey to *Alligator mississippiensis* Daudin, 1802 (American alligator) (Nifong & Lowers 2017). In the riverine and estuarine habitats of tropical Australasia, *C. leucas* is sympatric with *Crocodylus porosus*, a further apex predator in fresh and brackish water environments. Reports of bull shark/crocodile encounters exist, often with sharks as prey of larger crocodiles (Messel et al. 1981; Doody 2009; Winchester 2014). Similar interactions between *C. leucas* and *Crocodylus niloticus* were reported by Whitfield & Blaber (1979) and Perissinotto et al. (2013) from the St. Lucia Lake system in South Africa. Recently, the occasional feeding behavior of a 2.5 m Nile crocodile consuming a juvenile *C. leucas* was observed in South Africa's St. Lucia Estuary (Jordan 2021). However, predation by reptiles as a natural population-limiting factor does not impact the local population sizes of *C. leucas* in river systems as much as fishing activities. In general, predation can be considered the main driving force regarding habitat selection, abundance, and distribution of juvenile *C. leucas* in low salinity environments.

5.10 Influence of human activities

Carcharhinus leucas has been reported from a wide range of riverine and estuarine environments, both natural

and human-influenced to various degrees (West 2011; Werry et al. 2012; Smoothey et al. 2016) (see Tables 1–10). Estuary systems with a strong human impact that are utilized by *C. leucas* include fully artificial freshwater-ecosystems like the canals of Florida's Indian River Lagoon system (Gilmore Jr. 1977), Australia's Gold Coast canals (Werry et al. 2012), and, in historical times, the freshwater impoundment of Panama's Lake Bayano (Montoya & Thorson 1982). *Carcharhinus leucas* can also live in wastewater-influenced rivers, even though the effects and risks on the individuals of environmental pollution require further investigation (Gelsleichter & Szabo 2013).

Although *C. leucas* can adapt to a broad spectrum of highly human-influenced freshwater and brackish water environments, it is considered to suffer from habitat loss caused by modification of low salinity habitats (Simpfendorfer & Burgess 2009), due to its use of these habitats for reproduction. The location of nursery areas in estuarine and riverine systems and their vicinity to human settlements make this species vulnerable to anthropogenic pollution and habitat alteration. Nowadays, in some of the major rivers with at least historical records of *C. leucas*, technical constructions such as dams prevent the movements of *C. leucas* into the upper stretches of rivers, as these constructions represent barriers for migratory species into areas where they have formerly occurred. For example, nowadays, migrations of *C. leucas* to the upper reaches of the Tigris/Euphrat system and the Mississippi River, from where they were reported historically up to 850 kilometers and 2,800 kilometers upriver, respectively, are prevented by dams (Hussain et al. 2012; Coad 2015; Thomerson et al. 1977; Helfman & Burgess 2014). As a species that relies on low salinity habitats, the interruption of river systems and the degradation of estuaries make *C. leucas* vulnerable to a strong degree of habitat modification.

Overexploitation of stocks and local populations can also influence the small-scale distribution of *C. leucas*. Although not a target species of most fisheries, Kyne et al. (2012) reported that the strong fishing pressure in coastal waters of the western Central Atlantic has shifted the distribution of *C. leucas* to the outer barrier reef. Despite being a common species in many tropical to subtropical rivers, especially juvenile *C. leucas* are often subject to recreational fishing—like in many Australian rivers (West & Gordon 1994), where they are caught in high numbers—that can negatively affect the stability of local populations.

5.11 Influence of ontogeny on habitat shifts

Life history traits of *Carcharhinus leucas* in correlation to low salinity environments have been extensively documented (Simpfendorfer et al. 2005; Heupel & Simpfendorfer 2008), revealing a spatio-temporally dependent pattern of habitat use in this species throughout its life span. As the results of Simpfendorfer et al. (2005) have shown, the youngest age classes of *C. leucas* (young-of-the-year, neonates, juveniles) occur in riverine areas with freshwater (Fig. 2B), moving into coastal lagoons and, finally, offshore areas as they grow older. Chemical and isotope analysis of adult *C. leucas* teeth from the Shark Reef Marine Reserve in Fiji by Kocsis et al. (2015) revealed that in Fiji adults presumably do not return to freshwater habitats during their absence from the reef. This result supports the assumption that mature *C. leucas* progressively emancipate from low salinity habitats during their ontogenesis. However, the analysis revealed that at least adult female *C. leucas* periodically return to estuaries according to a one to two year cycle due to pupping related movements (Tillett et al. 2011b; McMillan et al. 2016). Conversely, the profiles of adult males suggested that they are less likely to return to estuaries throughout their lives (McMillan et al. 2016).

In large rivers, *C. leucas* is able to cover distances of many thousands of kilometers upriver, due to urea-based osmoregulation (Pang et al. 1977; Hazon et al. 2003; Anderson et al. 2005a; Hammerschlag 2006; Trischitta et al. 2012). This large-scale freshwater migration leads to extended periods in freshwater during the early stages of the natural life cycle of *C. leucas* (see Table 11). Already Günther (1910: 479) commented, for *C. leucas*: "This species rises far up in rivers." The greatest penetration into freshwater by *C. leucas* was reported from the Ucayali River, the upper reach of the Amazon River at the locality of Pucallpa (Peru), more than 5,000 km from the mouth of the river and its estuary on the Atlantic coast (Thorson 1972a; Werder & Alhanati 1981; Soto 2001).

5.12 Dependence on low salinity habitat

It is well documented that many species of sharks use inshore protected water bodies (coastal lagoons, estuaries, and bays) as pupping and nursery areas (Snelson et al. 1984; Simpfendorfer & Milward 1993). The availability of freshwater locations seems to influence the distribution of *Carcharhinus leucas*, at least of females, and can be considered a motivation for migrations and therefore a driver shaping the geographical range of this species. Swift et al. (1993: 130) presumed, for *C. leucas* in the northeast Pacific: "Elsewhere in the world this species is closely tied to fresh and low salinity water, and the early demise of this habitat in southern California may have led to its disappearance here." Carlson et al. (2010) found that the majority of subadult *C. leucas* observed in the U.S. waters of the northern Gulf of Mexico stayed in areas located near or adjacent to outflows of freshwater from the Apalachicola, Mississippi, and Caloosahatchee

rivers, and the intercoastal waterway system from Lake Okeechobee. Most of the observed *C. leucas* specimens in that study spent most of their time in waters less than 20 m deep. These results by Carlson et al. (2010) emphasize the importance of the shallow coastal zone for this species as a potentially essential habitat, particularly in areas with high freshwater inflow.

An investigation of the shark composition of the Cayman Islands by Ormond et al. (2017) could not provide evidence of *C. leucas* for this remote island group in the Caribbean Sea. Ormond et al. (2017) suggested that this could be due to the absence of suitable breeding grounds for this species northwestern Caribbean Sea, although female *C. leucas* can travel long distances to find suitable pupping grounds (Lea et al. 2015). Probably, the nursery areas of *C. leucas* in the Caribbean region are around the Central American Isthmus and the north coast of South America (see Table 3). Fanovich et al. (2017) reported that *C. leucas* was observed only rarely (two times in a 14-month period) on the Atlantic side of Tobago (West Indies), possibly due to lack of suitable nursery grounds, but maybe also due to overfishing in this area.

Compagno (2016) pointed out that the littoral species *C. leucas* can also undertake long journeys to oceanic islands far from continental landmasses, which led to the conclusion that areas that do not provide any freshwater locations and which are located far from suitable nursery grounds can be settled by adult *C. leucas*. Furthermore, *C. leucas* has been collected (a single ♂, 225 cm TL) off the remote Quita Sueño Bank (San Andrés Archipelago, Colombia) in the Caribbean Sea (Puentes et al. 2009). This leads to the conclusion that at least adult male *C. leucas* can move to small isolated oceanic islands without fresh and brackish water resources, using river-poor or river-less areas at great distances from low salinity ecosystems. These ocean movements are possibly motivated by foraging, although *C. leucas* seems to be rare or absent around most remote oceanic islands (Ballesteros 2007). In this context, Werry & Clua (2013) highlighted the fact that males and females of this species operate independently during certain periods, especially when parturition is not involved. However, it is still unknown whether there are fresh or brackish water habitats in the Greater Antilles and in the Caribbean that serve as nursery grounds for *C. leucas* (compare Lee et al. 1983), or whether breeding only takes place in continental waters of North, South, and Central America.

6 Discussion on the range and distribution of *Carcharhinus leucas*

Carcharhinus leucas is a cosmopolitan species that inhabits parts of all three major ocean basins (Compagno 1984, 2001; Weigmann 2016). The cosmopolitan character and the shape of its distribution area can be understood as the result of environmental conditions, biological and physical characteristics of this species, and phylogeography (Pirog et al. 2019b). This means that the current distribution area of *C. leucas* can be interpreted resulting from ancient geological processes in combination with recent abiotic environmental factors (ocean and riverine/estuarine/lacustrine water parameters), the preference of *C. leucas* for warm-water areas, and biotic factors such as predation risk. Furthermore, it can be estimated that *C. leucas* represents a phylogenetically old species, as tooth fossils from the Miocene/Pliocene (~5 Mya) indicate, with predecessors and early forms close to the recent *C. leucas* dated back to the late Eocene/early Oligocene (~27–33 Mya) (Adnet et al. 2007). Presumably, in ancient history and before the drifting of landmasses, the Western Atlantic and the Eastern Pacific populations of *C. leucas* were not separated and connected within one closed range, until the period when tectonic processes (Isthmus of Panama) started to divide the former homogeneous population. This affected mainly the North American populations of *C. leucas*, which are now divided into an Eastern Pacific and a Western Atlantic population, as well as divided the Atlantic and Indian Ocean populations (Karl et al. 2011; Testerman 2014; Pirog et al. 2019b).

The Atlantic and Indian Ocean populations of *C. leucas* are today divided by a cold current, under the assumption that the Benguela Current presents a insurmountable barrier for a shark species linked to warm-water conditions (> 20 °C). In this context, Pirog et al. (2019b) outlined that the Benguela Current/Benguela Upwelling System is also constraining for the temperature-sensitive *C. leucas*, as has been the closure of the Isthmus of Panama. Already Misra & Menon (1955) outlined that the distribution of Indo-Pacific elasmobranchs is restricted by the 12 °C isotherm, which borders the southwest coast of Africa beyond the west of the Cape of Good Hope and extends up to a -22°S latitude, serving as a physical barrier for the free dispersal of the Indo-Pacific species into the Atlantic. In this context, Smith (1949: 8) reasoned felicitously about the waters off southwest Africa: "The blanket of cold water along our west coast is so much a barrier to most warm water forms, that to a large extent it prevents the intermingling of the fishes of the tropical Atlantic with those of the Indianic shores of South Africa. Further, the Benguella current flowing northwards tends to limit the penetration of Cape waters by fishes from even the colder parts of the Atlantic, and in consequence the Cape represents a well-defined line of division between the Atlantic and the Indo-Pacific fishes."

Moreover, Smith (1949) speculated—certainly correctly—that the Indo-Pacific species that are simultaneously distributed in the Atlantic are relics of an earlier

intermingling not long ago in geological times, with different environmental conditions, and that there was almost certainly a warm-water connection between the Indian and Atlantic oceans that once allowed an exchange of individuals of warm-water elasmobranchs. Considering these biogeographical facts, a historical process has shaped the recent range of *C. leucas* and of other cosmopolitan carcharhinids, and the result is today's separate populations of *C. leucas* in the major ocean basins of the world.

A reconstruction of the historical distribution of *Carcharhinus leucas* could be achieved through fossil tooth findings, which can help model this species' former range. As a relatively old species, *C. leucas*'s fossil range was influenced by environmental transformations that occurred during the Neogene. Intensive climatic, tectonic, and oceanographic events during the Neogene have been suggested as possible causes of chondrichthyan distributional changes (Long 1993), resulting in biogeographical range shifts in numerous species of elasmobranchs (Villafaña & Rivadeneira 2018).

Carcharhinus leucas represents one of many extant species within the genus *Carcharhinus* (Nielson et al. 2020). It is assumed that the recent form of *C. leucas* has an evolutionary age dating to at least the Miocene/Pliocene (Latrubesse et al. 1997; Marsili 2007, 2008; Ávila et al. 2012; Aguilera et al. 2017). The stratigraphic record of at least early forms of *C. leucas* extends back to the Miocene (Ebersole et al. 2017). Fossils of *C.* cf. *leucas* of this age have been reported from different parts of the world, even from locations where this species presumably is not currently distributed (Fig. 4), like for example Egypt (Cook et al. 2014) and continental Portugal (Antunes et al. 1999; Antunes & Balbino 2004). Fossil tooth findings of *C. leucas* in Italy, dating from the Lower to Middle Pliocene, demonstrate the former occurrence of *C. leucas* in the Mediterranean Sea in periods with a warmer and less seasonal climate, as well as its disappearance from the Mediterranean at the end of the Middle Pliocene (Marsili 2007, 2008). Lessa (1986) pointed out the affinities of the present shark fauna along the northwest coast of Brazil (Maranhão State) with the Miocene shark fauna of the Mediterranean, both with a similar species pool including *C. leucas*.

In fact, not every freshwater occurrence of sharks belongs to *C. leucas*. Several other species of elasmobranchs can penetrate, stay and live for a short time or extended periods in freshwater, especially sharks of the genus *Glyphis*, which has sometimes led to mistakes in determining the exact species recorded from a given freshwater environment. Boeseman (1964: 10) emphasized: "… the fresh water Carcharhinid with the widest distribution and by far the most frequently encountered is *Carcharhinus leucas*." The confusing situation regarding the sympatric distribution of river sharks was best described by Compagno (2002a: 174), who wrote: "The ubiquity of *C. leucas* as a riverine shark, and the vast confusion in the past over identification of Indo-Pacific carcharhinids, tends to mask the presence of other sharks in rivers in the area, particularly other species of *Carcharhinus* that are marginal freshwater species and the river sharks of the genus *Glyphis*. Over the last century the bull shark was generally confused with the true Ganges shark *Glyphis gangeticus*, the pigeye shark *Carcharhinus amboinensis*, and a number of other species including possibly *C. melanopterus* and *C. hemiodon*. This makes many riverine records of sharks in the area impossible to sort out taxonomically unless adequate illustrations, descriptions, or specimens are available to confirm the records."

One question is how strong the dependency and link of *C. leucas* to estuary/river systems for reproduction really is (see section 5). In this context, Wallace et al. (1984) ordered *C. leucas* in a group of fish species of the South African Indian Ocean waters whose juveniles are found mainly in estuaries but also at sea. As a conclusion, Wallace et al. (1984) stated that these species are not entirely dependent on estuarine nurseries, and that although they would survive in South African waters if extensive degradation of estuaries were to take place, their numbers would be drastically reduced. Interestingly, Pillans et al. (2005a) found that newborn specimens of *C. leucas* are fully adapted to life in seawater and endure marine conditions, which enables life in coastal waters during their early life stages. On the other hand, Van Niekerk & Turpie (2012) stated that *C. leucas* utilizes numerous estuarine systems and freshwater rivers in South Africa as pupping and nursery grounds, and that these are therefore critical habitats for the species. Due to the life history traits of *C. leucas*, Lamberth & Turpie (2003b) considered estuary management as playing a crucial role for the species in the South African KwaZulu-Natal region. Regarding the importance of estuarine ecosystems to fishes in South Africa, Whitfield (1994) categorized *C. leucas* as a species whose juveniles occur in estuaries but are more abundant at sea, although the author made no distinction between different age classes (young-of-the-year, neonates). However, Whitfield's categorization differs greatly from the results obtained by others from other tropical to subtropical parts of the world and their estuaries, where juveniles of *C. leucas* are very abundant, especially in the large deltas of the Mississippi, Orinoco and Amazon rivers (Springer 1950; Alencar et al. 2001; Souza-Araujo et al. 2021); these results are a good indicator of the high importance of estuaries as nursery areas for *C. leucas*. As mentioned by Blanch et al. (2005: 18) for *C. leucas* in riverine and estuarine systems in northern Australia: "Juveniles seem to be restricted to fresh or low salinity water." Also the results of the present synopsis of riverine and estuarine habitats used by

C. leucas (Tables 1–10) indicate an essential function of low salinity habitats for reproduction in *C. leucas*.

Surprisingly, Burr et al. (2004) mentioned that *C. leucas* is an exotic, non-indigenous species in the Mississippi River, even though they mentioned that it originates in the Gulf of Mexico and reaches the Mississippi River by dispersal. This statement can be considered false, as freshwater habitats with occurrences of *C. leucas* are widespread throughout the range of this species and are completely a part of its natural distribution. *Carcharhinus leucas* is capable of reaching the upper parts of rivers by its own capability in the absence of physical barriers, and has not been introduced into non-native environments by humans.

Investigations on the spatio-temporal behavior of adult *C. leucas* have revealed that foraging and breeding are the main drivers for large-scale movements of this species. An examination of acoustic telemetry studies of different marine taxa, including sharks, by Brodie et al. (2018) revealed that *C. leucas* is also a roaming species. Lea et al. (2015) reported the long-distance migration of a pregnant adult female *C. leucas* from the Seychelles to Madagascar and back, which was presumably induced by breeding. Therefore, *C. leucas* undertakes long-distance seasonal and breeding migrations along coasts, into estuaries, and up rivers, and is occasionally recorded from oceanic islands (Daly 2014; Heupel et al. 2015; IUCN Shark Specialist Group 2007; Roff et al. 2018). Undoubtedly, several different factors influence movements of *C. leucas*, which makes it difficult to understand the complexity of these movements. As records of *C. leucas* from some oceanic islands (e.g., Azores, Seychelles, Rangiroa Atoll) indicate, possibly a few, single, vagrant individuals are capable to travel long distances across open ocean areas and the so-called "oceanic deserts".

Although affiliated to close-to-shore habitats and mostly valued as a coastal resident (see section 5), *C. leucas* is a strong swimmer (Heupel et al. 2015) able to cover great distances and undertaking rapid migrations over thousands of kilometers (Daly et al. 2014), with recorded distances of 100 km in 24 hours (Kohler & Turner 2001), 180 km in 24 hours (Allen et al. 2002), and 3,000 km in 75 days (Niella et al. 2017). a study about the swimming behavior of different species of sharks held in captivity (Hussain 1991) revealed that *C. leucas* is a very active species. In that study, *C. leucas* was able to maintain a uniform speed with no signs of exhaustion over an observation period of three months. Voluntary swimming speeds of two carcharhinid sharks held under controlled conditions in captivity and measured by Weihs (1981) revealed that *C. leucas* was faster and more active compared to the other studied species, *C. plumbeus*.

As a warm-water species, *C. leucas* has its core area of distribution in the tropics. At the edges of its range, *C. leucas* undertakes northerly-directed seasonal migrations in the Northern Hemisphere and southerly-directed migrations in the Southern Hemisphere, into the subtropical and warm-temperate regions. a northwards movement along the West Atlantic coast during summer from its tropical stronghold and a southwards retreat when the water cools was observed in this species (IUCN Shark Specialist Group 2007). Similarly, a southward directed migration takes place during summer along the east coast of Australia, where it is present in southern Queensland and New South Wales waters primarily as a vagrant during the warmer months (Taylor 2007).

A further important question is whether climate change is impacting the range and habitat use of certain shark species, and whether global warming will lead to an expanse in the distribution of some sharks. In this context, Streich & Peterson (2011) and Bangley et al. (2018a, 2018b) showed that Georgia and North Carolina estuaries and rivers are used as nursery grounds by *C. leucas* on the east coast of the United States, which had previously not been documented north of Florida's Indian River Lagoon system (Curtis 2008; Curtis et al. 2011, 2013). Adams & Curtis (2012) suggested that Florida's Indian River Lagoon represents the northern limit of functional nursery habitat for this species in the northwest Atlantic Ocean, due to a decreasing abundance with increasing latitude within and north of this lagoon system. In addition to the results of Streich & Peterson (2011) and Bangley et al. (2018a, 2018b) and much earlier on, Metzgar (1973) reported the use of irregularly flooded salt marshes of Dorchester County (Maryland) as spawning places for *C. leucas* north of the estuaries of Georgia and North Carolina. Furthermore, juvenile *C. leucas* were reported by Schwartz (2000) from a North Carolina river/estuary system, and the use of this location as a nursery seems to be very likely (Schwartz 2012). It is therefore evident that river/estuary systems north of Florida are occasionally utilized as nurseries by *C. leucas* during seasons with suitable water parameters and particular water temperatures.

Increased water temperature as a result of climate change could cause a northerly shift in the breeding behavior of *C. leucas*, with the occupation of new nursery habitats along the east coast of the United States. Therefore, it will be interesting to monitor future shifts in the northern and southern boundaries of the range of *C. leucas*, to assess whether its range will expand as a result of increases in water temperatures in specific parts of the major ocean basins due to global warming. Range expansion of *C. leucas* from the Atlantic Moroccan coast to the Mediterranean is imaginable, but remains predominantly speculative. Recent investigations by Niella et al. (2020a) discussed and predicted a distributional shift of *C. leucas* south of its current boundaries on the east coast of Australia due to climate change; this seems plausible, as sea surface temperature is assumed to be one of the most

important factors explaining the distribution of *C. leucas* (see section 5). The observations by Niella et al. (2020a) indicate that *C. leucas* has currently extended its range southwards in eastern Australia, and is present for longer periods at more southerly latitudes.

7 Conclusions

Carcharhinus leucas moves frequently between fresh and brackish water and can travel great distances inland. This shark is wide-ranging not only in marine waters in tropical, subtropical, and warm-temperate climates, but also in freshwater rivers, lakes, and estuarine habitats. *Carcharhinus leucas* is one of the few elasmobranch species worldwide to spend a significant proportion of its life in estuaries and freshwater. The species' behavior of entering freshwater habitats is induced by breeding and by the developmental requirements of juveniles, and can be interpreted primarily as a successful evolutionary strategy to reduce the mortality of the offspring. The penetration of rivers and lakes by adult males and females may also be motivated by foraging. Although Albert & Reis (2011) stated that the movements of fishes, including *C. leucas*, between marine and fresh waters in the Amazon Basin are primarily for feeding, the main driving factor for the penetration of freshwater bodies by *C. leucas* is certainly its evolutionary strategy of frequenting low salinity habitats as breeding areas. Juvenile *C. leucas* depend upon low salinity habitats due to their life history traits, and the freshwater/seawater transition is probably a matter of exploitation of an ecological opportunity by the species, which is physiologically adapted to life in both seawater and freshwater (Thorson 1976a; Berra 1981; Pillans et al. 2005a).

Although the juvenile age class of *C. leucas* dominates the shark population structure in some tropical and subtropical freshwater rivers and lakes (Thorson 1976a; Thorburn et al. 2004a), Gunter (1938) reported also adult *C. leucas* from freshwater environments. Later, Gunter (1957) further reported that among the marine fish intrusions into freshwater, and especially among sharks, also large specimens are known to enter freshwater (presumably pregnant adult females). Nevertheless, in northern Australian rivers, 75% of the captured specimens of *C. leucas* were less than 1 m long (Thorburn et al. 2004a), which underlines the importance of freshwater habitats as nurseries for juveniles. Already Compagno (1984) remarked that newborn specimens of *C. leucas* are apparently euryhaline and that juveniles of *C. leucas* commonly migrate into freshwater, which was later confirmed by Pillans et al. (2005a, 2006).

As part of the natural life cycle of this species, the penetration of low salinity habitats occurs globally and throughout its whole range. The results of this review strengthen the conclusion of Compagno (2002a) that *C. leucas* occurs in most tropical, subtropical, and warm-temperate rivers and estuaries around the world that are not strongly modified by human impact, due to its feeding and breeding behavior. One additional result of the present study is that many of the reports and information on fresh and brackish water occurrences of *C. leucas* are quite old (> 30 years; see Tables 1–10). It remains unclear whether all of these locations still have a function as breeding and nursery grounds for *C. leucas* despite environmental pollution, habitat modification, degradation of estuaries, or overfishing of local populations. Careful use of this older and possibly outdated information from the literature is in any case advisable.

Estuaries and river mouths with brackish water are considered to be important nursery grounds for *C. leucas* (Compagno 1984), as well as starting points for the migration of especially neonate *C. leucas* into rivers and lakes from lower salinities to purely freshwater conditions. The aims of the present work were several-fold: 1) to identify important nursery grounds for *C. leucas* as a source for sustainable fishery policies, conservation management, 2) to argue for the protection of riverine and estuarine ecosystems, and most importantly 3) to outline the global scale of the utilization of low salinity habitats by *C. leucas*. This review underlined that rivers and lakes represent an important habitat type for immature individuals of *C. leucas* worldwide, and identified *C. leucas* records from 272 different freshwater localities (rivers, lakes) and 143 bays, lagoons, estuaries, river deltas, and salinity-influenced lakes and rivers with dominant brackish (hyposaline) water worldwide.

The spectrum of freshwater habitats that are penetrated by *C. leucas* ranges from pristine, natural, or semi-natural major to small rivers, creeks, and lakes to artificial impoundments, canals, and waterways. The widespread occurrence of *C. leucas* in freshwater already led Thorson (1976a) to the belief that this species may be expected to penetrate any coastal body of freshwater within its range provided it has a connection with the ocean is deep enough for navigation, has a suitable temperature and elevation gradient, and has sufficient food resources to attract them. For Nicaragua's Lake Nicaragua/San Juan River system, Thorson (1976a: 565) stated: "…the sharks apparently make their way, in pursuit of food, into any channel available to them." The results of this survey not only confirm Thorson's belief, but also the statement of Compagno (2002a) that *C. leucas* should be expected in any warm-temperate, subtropical, and tropical river and lake with access to the ocean that is not heavily altered by human activities. However, the use of rivers and shallow estuarine habitats makes juveniles of this species vulnerable to capture in small-scale fisheries on a global scale.

At the time of writing of this review, the use of estuaries by juvenile *C. leucas* is well documented for certain regions (Simpendorfer et al. 2005; Yeiser et al. 2008; Ortega et al. 2009; Froeschke et al. 2010a; Harry et al. 2011; Heupel & Simpfendorfer 2011; Werry et al. 2011; Matich & Heithaus 2012), and estuaries in the tropics and subtropics must be considerd a crucial habitat for *C. leucas*. Like in many other coastal shark species (McCallister et al. 2013), pups of *C. leucas* are usually born near or within estuary systems (Werry et al. 2011). There are certainly rivers and lakes used by *C. leucas* in addition to those listed in the present survey, but the number of 415 global fresh and brackish water localities (235 of them with evidence of immature specimens and/or pregnant females) highlights the great importance of riverine and estuarine ecosystems for this species, and the need of protection of natural rivers, lakes, and estuaries for successful conservation efforts. For numerous of these 415 localities, information on the current status of *C. leucas* is lacking. In this context, Soto (2001: 78) wrote, about the status of *C. leucas* in the Amazon Basin: "Further studies of the biology and reproduction of this species in the Amazon basin are needed." Also Castro (2009: 57) reasoned that "…the Amazon estuary plays an important role in the biology of the southwestern Atlantic bull shark, and I encourage more studies in this region." Finally, Feitosa et al. (2019) pointed out that details about the elasmobranch fauna that continuously, frequently, or sporadically inhabits the freshwater systems of the Amazon Basin are still relatively unknown.

Data on river and estuary systems with occurrences of *C. leucas* shows that only a few lagoons, estuaries, and river/lake systems are utilized by *C. leucas* on the Pacific side of the American continent (see Tables 2, 4). Although there is a high number of small rivers and river outlets along the west coasts of North, Central, and South America that provide suitable habitats for *C. leucas*, only a few fresh and brackish water systems with records were identified in this literature review. Due to the geographical conditions of the Pacific slope, no major rivers flow into the Pacific Ocean, but only numerous smaller rivers. The major rivers of Central and South America primarily drain into the Atlantic slope and most of them are utilized by *C. leucas* (see Table 3). a small number of minor rivers located on the Pacific Ocean coast are utilized by *C. leucas* (Tables 2, 4), but the absence of large rivers and estuaries means that there is a lower availability of suitable nursery grounds in the eastern Pacific. Thus, the locations of the (most important) nursery areas of *C. leucas* on the eastern Pacific coast of Latin America remain undiscovered. Notably, the small number of records of *C. leucas* in these rivers, lakes, estuaries, and lagoons (Fig. 3) should not be interpreted only as a result of the absence of large rivers, but could also be explained as a lack of data for this region regarding freshwater tolerating elasmobranchs and their distribution.

However, Gilbert et al. (2016) highlighted the importance also of the small estuaries located along the Pacific Ocean coast of Costa Rica as nursery grounds and foraging refuge areas for marine fishes such as *C. leucas*. Possibly, *C. leucas* also occurred historically in the Colorado River (United States, Mexico), which is a tributary of the Gulf of California in the Pacific Ocean, but this needs deeper investigation. Hastings & Findley (2006) and Bonfil (2014) mentioned the occurrence of *C. leucas* in the vicinity of the Colorado River Delta in the northern Gulf of California, and it is plausible that this location was a suitable nursery ground for *C. leucas* in ancient times. However, there are no verifiable records of *C. leucas* from the Colorado River, which runs through the southern United States and northern Mexico. Mascareñas-Osorio et al. (2011) reported, for the northern Gulf of California, that species of large-bodied sharks (e.g., *Carcharhinus leucas* and *Sphyrna lewini* Griffith & Smith, 1834) known to occur on the reefs of the gulf were never observed during dives carried out within their field studies. This may be the result of overharvesting of sharks by commercial fisheries.

In the northern Gulf of California, a further factor that may have negatively affected *C. leucas* is the regulation of the Colorado River by dam wall built at the beginning of the last century, which has changed the freshwater inflow into the Gulf. Hastings et al. (2010) reported that estuarine fishes in the northern Gulf of California suffered major habitat alterations due to damming and changes in water salinity. The lack of a consistent freshwater flow into the northern Gulf has changed the system's conditions from typically estuarine (with low salinity) to hypersaline (Hastings et al. 2010). These environmental changes likely had a major impact on nursery and breeding areas for *C. leucas*. Although *C. leucas* can tolerate high salinities and hypersaline conditions (see section 5), the Colorado Delta is the only large estuary in the northern Gulf of California and was therefore probably of major importance for the *C. leucas* population of the entire gulf. The Tigris-Euphrat-Karun river system in the Persian Gulf has a similar function and importance, offering critical habitat for *C. leucas* (Moore 2018).

As a further result of this survey also showed that there are still some river systems, including some major ones, within the range of *C. leucas* for which no confirmed records or verifiable reports exist, but where past or present occurrences are very likely. These are: the Colorado River (United States/Mexico), the Niger River, the Congo River, the Indus River, the Mahanadi River, the Brahmaputra River, the Mekong River, and the Yangtze River. Further field investigations at particular localities or data from catches by local fishers are necessary to assess

whether these rivers are potential habitats for *C. leucas*. The occurrence of *C. leucas* in these rivers seems highly probable considering the fact that *C. leucas* inhabits the marine coastlines of these regions. Until today, no information has been made available about the occurrence of *C. leucas* in Chinese and Taiwanese fresh and brackish water habitats, in both historical (e.g., Nichols 1943) and recent (e.g., Xing et al. 2016) surveys. To this day, nursery habitats of *C. leucas* in Chinese and Taiwanese waters remain completely unknown. Occurrence data for this species in Asian inland waters are highly desirable for its conservation and management in the western Pacific Ocean. The same applies to the large Niger Congo rivers in Africa, which both drain into the tropical eastern Atlantic inside the tropical range of *C. leucas*, and for which no verifiable occurrence data for this species seem available (see Table 5).

Analysis of the available data on worldwide occurrences of *C. leucas* in freshwater habitats and estuaries shows that the most detailed information come from the United States, South Africa, and Australia (Fig. 3; Tables 1, 6, 8, 9), countries where marine research is well funded. For Australia, the high number of *C. leucas* records in rivers and lakes also results from investigations on other rare and potentially endangered freshwater elasmobranchs (*Glyphis* spp., *Pristis* spp.) in the Northern Territory and adjacent regions (Thorburn et al. 2004a, 2004b; Peverell et al. 2006; Pillans et al. 2009; Berra 2010; Field et al. 2013). Additional records of *C. leucas* in Australian and United States' rivers have been provided as part of angling and fishing reports.

A large body of literature on *C. leucas* is available for the Atlantic coastline, especially from the Gulf of Mexico, as a result of numerous surveys and intensive scientific investigation in this region (Table 1), some of which for fishing purposes. In other parts of the world, especially in developing regions with insufficient scientific research, only a limited amount of occurrence records exist for *C. leucas*, and further research would be desirable to identify important nurseries and breeding habitats of the species in these regions. Some especially data-poor regions are the South American Pacific coastline, West Africa, the Arabian Peninsula, and large areas of Asia including Indonesia, Myanmar, Thailand, Viet Nam, Taiwan, and China. Considering its large land size, there are only a few records of freshwater occurrences of *C. leucas* from the Southeast Asia (Table 7). In conclusion, further studies on the distribution of *C. leucas* and other euryhaline elasmobranchs are highly needed to inform future nature conservation plans for these organisms, and future scientific advances will undoubtedly deliver from regions of the world from where *C. leucas* is poorly known or unknown.

As a summary of available data regarding gaps in the known marine distribution of *C. leucas* (Fig. 4), further evidence from the following data-poor regions or countries would be particularly needed: Bermuda, Western Sahara, Canary Islands, Maldives, China (regions south and north of Shanghai), Japan (islands north of the Okinawa Prefecture), and California (United States).

The analysis of environmental DNA may be an appropriate method to reveal the presence of *C. leucas* in areas where this species is suspected to occur or elusive. Successful use of this method for detecting of *C. leucas* was made in marine (Bakker et al. 2017; Boussarie et al. 2018; Ip et al. 2021; Mariani et al. 2021; Van Rooyen et al. 2021), estuarine (Schweiss et al. 2020), and freshwater environments (Simpfendorfer et al. 2016; Drymon et al. 2020a). Visual-based approved methods, such as underwater visual census and baited remote underwater video stations, can be used to reveal the presence of sharks, including *C. leucas*, in certain areas (Langlois et al. 2006). Future investigations about *C. leucas* or the shark fauna of certain areas may lead to an increase in knowledge and will close present distribution gaps. Some distribution gaps in the Indian Ocean were closed in the present review, by researching available data with reports on *C. leucas*.

In order to produce a reliable and consistent distribution map for *C. leucas* (as well as for most shark species), an intensive study of references and data is necessary. Considering the dynamics in the accumulation of knowledge, continuous work on a distribution map is necessary to display the most recent state of knowledge. With the progression of time and science, the number of well-documented freshwater localities with *C. leucas* reports will rise. For example, since the 1980s, the knowledge about freshwater occurrences of *C. leucas* in North America has been rising rapidly. Burgess & Ross (1980) named only five river systems with inland freshwater occurrences from the United States. Over 40 years later, the present study has allowed to compile a list of 35 river systems with freshwater conditions in the United States from which *C. leucas* has been recorded (Table 1), which documents the ongoing progress in ichthyological research and knowledge in this part of the world.

In order to understand the distribution, migration behavior, life cycle, and ecology of *C. leucas*, a number of important aspects are summarized hereafter:

1. *Carcharhinus leucas* is unusual in its tolerance of both low and high salinities. Compagno (1998) pointed out that no sharks are known to be confined to freshwater, unlike several species of stingrays of the families Dasyatidae and Potamotrygonidae, which are complete freshwater residents. *Carcharhinus leucas* is closely tied to fresh and brackish water habitats due to its reproduction behavior, but its residence in freshwater is time restricted. Low salinity habitats such as rivers and estuaries can be considered critical for *C. leucas*. It is well known that

many species of elasmobranchs rely on nearshore habitats as nursery grounds (Simpfendorfer & Milward 1993). Other carcharhinid shark species, like *Negaprion brevirostris* Poey, 1868 (lemon shark) and *Carcharhinus limbatus*, use brackish water habitats and river mouths as breeding areas too. a unique characteristic of *C. leucas* is the strategy of its juveniles to persistently penetrate freshwater bodies, migrate up rivers, and spent extended periods (up to five years) in freshwater habitats during the early stages of their life. The advantage of low salinity environments as nursery grounds is that they are relatively free from adults of other shark species (Springer 1967), which reduces predation of offspring and provides a good availability of food resources (Simpfendorfer & Milward 1993). Juvenile *C. leucas* inhabit low salinity environments (rivers, lakes, estuaries), from where they move upstream, and gradually move towards marine environments as they age, making an ontogenetic habitat shift from the early to the late life stages. This behavior is deemed to be an adaptative strategy to reduce predation risk in marine environments and optimize growth, rather than reflecting a physiological incapacity to survive in higher salinity environments. *Carcharhinus leucas* is able to colonize freshwater habitats, such as large rivers and lakes, up to thousands of kilometers when these habitats are not interrupted by human or natural impediments such as dams or waterfalls. Adults (both males and females) are also known to enter rivers again to utilize the same habitats, albeit in low numbers (Soto & Mincarone 2004; Schwartz 2012).

Except for some remote islands and island groups with a lack of major riverine and estuarine systems, where adults of *C. leucas* are mostly infrequent and sporadic visitors or strays, low salinity habitats are utilized throughout the whole range of *C. leucas*. As adult *C. leucas* grow older, their salinity tolerance rises and at least the males seem to emancipate themselves from the use of freshwater habitats. As strong swimming sharks, adult males of *C. leucas* can be found in regions far removed from breeding grounds. As results from the western Indian Ocean (Lea et al. 2015) indicate, adult females can also migrate over thousands of kilometers, returning to suitable breeding habitats, such as estuaries and river mouths, for reproduction and to give birth to their pups. Finally, adult *C. leucas* make occur even around remote islands lacking large rivers and suitable nursery grounds, as a result of free-ranging migration and their ability to cross open ocean stretches. However, as a primarily coastal shark, these occurrences are rather scarce in *C. leucas*, whose movements usually take place close to the shores of continental shelves.

2. *Carcharhinus leucas* is a philopatric species whose adult females repeatedly return to certain nurseries, but it remains unclear how individuals find these sites over and over again, including over long stretches of open water (see Lea et al. 2015). Orientation is probably aided by the geomagnetic field or along oceanic currents. Collin & Whitehead (2004) concluded that the distribution of the Ampullae of Lorenzini—electroreceptors on the snout that are found found mostly in cartilaginous fish such as sharks, rays, and chimaeras—in *C. leucas* suggests that this species uses electroreception primarily for spatial discrimination of prey and only secondarily for migratory purposes. Finally, philopatry in this species may lead to a homogenization of the gene pool in local and regional populations (Deng et al. 2019).

3. This review highlights the utilization of fresh and brackish water habitats by *C. leucas* on a global scale. Moreover, it confirms the statement of Compagno (1984: 445) that "The bull shark has a wide range in tropical and temperate rivers and lakes of the world." The numerous records of *C. leucas* from low salinity habitats worldwide support the hypothesis that this shark relies on freshwater and estuary systems for use as nurseries (see Moore 2018). According to Carrier et al. (2004), specimens of *C. leucas* may actively seek low salinity areas as nurseries. This suggests that *C. leucas* could be rare in regions where suitable nursery habitats are absent, which would restrict the distribution of this species in estuary and river-poor regions (Wallace et al. 1984). The absence of *C. leucas* from the estuary-poor Red Sea seems to strengthen this hypothesis. Nevertheless, the question that could not be answered by this review is whether birth always takes place in estuaries and river mouths, or if it can also take place in marine ecosystems in the absence of these habitats, as records of newborn *C. leucas* from the Persian Gulf may indicate.

On the one hand, neonate and young juvenile *C. leucas* have been observed in marine waters with no suitable nursery habitats in the vicinity (or nursery grounds could not yet be identified in these regions), like from Tonga (Brunnschweiler & Compagno 2008) or along the Persian Gulf coast of the Unites Arabian Emirates (Jabado et al. 2017). Moore (2018) highlighted the importance of the Tigris-Euphrat system as a nursery area for *C. leucas* and pointed out its potential major significance for the Persian Gulf region given the absence of similar estuarine habitats for thousands of kilometers along the arid northwestern Indian Ocean coast. On the other hand, adult females are motivated to cover great distances and undertake large-scale migrations with the investment of high amounts of energy to reach suitable nursery grounds (Lea et al. 2015), probably due to philopatric. These seem to be good additional arguments indicating a strong dependency of *C. leucas* on riverine and estuarine habitats. However, a very interesting observation was made regarding the reproduction of *C. leucas* in captivity. The bull shark is a hardy species that can be successfully kept in sea aquariums (Compagno 1984; Hussain 1991; Schmid & Murru 1994). The Okinawa Churaumi Aquarium of Japan (the former Okinawa Commemorative National Government Park

Aquarium), which displays several specimens of *C. leucas* to the public in a 700 m^3 seawater tank, reported the survival of a male *C. leucas* specimen for about 40 years in captivity (Okinawa Churaumi Aquarium 2019). This is presumably a world record for the longest period during which a bull shark has been cared for in captivity, and probably also the greatest life span recorded for this species. The male in question successfully reproduced with females three times, resulting in the birth of many pups, which in turn also produced offspring (Okinawa Churaumi Aquarium 2019). Parturition took place in a sea tank and therefore in a more or less marine environment with seawater conditions and characteristic marine salinities. These observations show that parturition of *C. leucas* is also possible in a marine-like environment. In this context, Pillans et al. (2005a) showed that juvenile *C. leucas* have the osmoregulatory plasticity to acclimatize to seawater, and Pillans et al. (2006) showed that juvenile *C. leucas* tolerate rapid and significant increases in salinity. Based on these results, these authors suggested that the preference of juvenile *C. leucas* for the upper reaches of rivers, where salinity is low, is therefore likely due to predator avoidance and/or increased food abundance rather than to a physiological constraint.

4. Data from the east coast of the United States revealed numerous fresh and brackish water habitats with occurrences of *C. leucas*, located along the entire stretch of the Atlantic and Gulf of Mexico coasts, from Maryland to Texas (Table 1). These riverine and estuarine habitats are potential primary and secondary nursery areas for *C. leucas*. a study conducted along the Texas coastline—which was considered to be, in its entirety, a nursery area for *C. leucas*—found that of the nine estuary bays sampled only two met the criteria for nursery areas as defined by Heupel et al. (2007). This shows that bays where juveniles occur are not necessarily primary nurseries of *C. leucas* (Froeschke et al. 2010). Nevertheless, the numerous estuaries in the northern Gulf of Mexico are likely important for the reproduction of *C. leucas* due to their quantity and availability (Nelson & Monaco 2000; Blackburn et al. 2007). Presumably, most of the estuaries within the range of *C. leucas* are used occasionally as nurseries.

5. The best investigated freshwater localities regarding the ecology, physiology, and (at least historical) distribution of *C. leucas* are the Lake Nicaragua/San Juan River system (Nicaragua, Costa Rica) and the Brisbane River (Australia). Nevertheless, even from these localities there is a lack of data regarding the spatio-temporal utilization of these riverine and lacustrine ecosystems by these sharks. Due to *C. leucas*'s circumglobal distribution, most regions where this species occurs are still data-poor regarding the location of nursery grounds and the utilization of freshwater habitats, especially in the developing world. Moore (2012) emphasized that there have been no published studies of euryhaline elasmobranchs in the Persian Gulf to date, which is perhaps not surprising given the three major conflicts around the Euphrat-Tigris-Karun system and its delta, the Shatt Al-Arab, since the 1980s.

6. The results of this review suggest that especially major estuaries and river deltas (e.g., Mississippi, Orinoco, Amazon, Euphrat/Tigris, Ganges/Sundarbans) are of great importance for the reproduction of *C. leucas* (Springer 1950; Mitra 2014; Moore 2018; Souza-Araujo et al. 2021). The occurrence of juveniles in great numbers in these habitats strengthens this hypothesis, and estuaries were considered a critical habitat for *C. leucas* by Van Niekerk & Turpie (2012). Adult females use the brackish and turbid waters of these habitats primarily for breeding, but adult males also use these waters, presumably for foraging, as these large rivers provide food in large quantities. Alencar et al. (2001) reported the observation of greater abundances of *C. leucas* in catches at the mouth of the Amazon River in the third and fourth quarters of the year, when the flooding period occurs in the Amazon Basin; this suggests a seasonal migration of *C. leucas* into this region motivated by foraging, as food resources are quite abundant during this period.

7. *Carcharhinus leucas* primarily utilizes the rivers and estuaries of tropical and subtropical regions as nursery grounds. Nursery areas in warm-temperate regions—mostly at the limit of its range—are only rarely used. For South African waters, Whitfield (1994) stated that *C. leucas* extends into warm-temperate marine waters but has not been recorded in adjacent estuaries, as has been documented in the subtropical Natal river systems, even though McCord & Lamberth (2009) provided evidence of a nursery in the warm-temperate Breede River and its estuary, also in South Africa.

8. There is a spatio-temporal differentiation in habitat use during the lifetime of *C. leucas*. Depending on the sex and age of individuals, many different habitats are used. Once specimens of *C. leucas* grow to a length between 130 and 150 cm TL, they move from riverine and estuarine environments into the fully saline water of close-to-shore habitats for further growth and breeding (Sadowsky 1971). As adults, their mobility increases and some adult males and females occasionally move back into freshwater or even to offshore locations and oceanic islands.

Throughout the life cycle of *C. leucas* marine, estuarine, and freshwater habitats are essential habitat types. Throughout individual growth, an ontogenetic niche shift in neonates, juveniles, subadults, and adults take place, which corresponds with the use of different habitat types (Matich & Heithaus 2015). For the effective protection of *C. leucas*, the importance of the different habitats used by the species, especially pristine rivers, estuaries, and river mouths, as places for reproduction and growth must be considered. Not only natural low salinity habitats

but also artificially modified freshwater bodies can provide suitable (breeding) habitats (see Tables 1–10) (West 2011; Werry et al. 2011; Curtis et al. 2013). However, the assumed philopatric behavior of pregnant females makes *C. leucas* more vulnerable to habitat modifications compared to other carcharhinids, and habitat degradation can have a massive impact on its reproductive success. Baker (2013) pointed out that the habit of pregnant female *C. leucas* of migrating to estuarine areas to give birth, and the residency of juveniles in these shallow waters for a period before seaward migration, increases the vulnerability of this species to coastal impacts.

9. Despite being primarily marine organisms, juvenile *C. leucas* move between fresh, brackish, and seawater ecosystems and undertake intensive incursions into continental inland waters, river sections, and purely freshwater lakes. This behavior presents the advantage of reducing the mortality in juveniles (Heupel et al. 2007, 2018), guaranteeing high survival rates, and female *C. leucas* invest high amounts of energy to reach suitable nursery areas (Lea et al. 2015). On the flip side, this strong link to low salinity environments could also be a disadvantage in tropical and subtropical regions without permanent and accessible freshwater, or even brackish, habitats, and may limit the distribution of *C. leucas*. This aspect could explain the absence of this species in the Red Sea, a with only a few estuaries and river deltas in inshore waters. In conclusion, the lack of suitable nursery grounds for *C. leucas* may be a further factor limiting the distribution of this truly euryhaline shark, besides water parameters such as depth, temperature, salinity, and dissolved oxygen.

10. *Carcharhinus leucas* moves easily, but not without any efforts due to the osmoregulatory costs, through ecological barriers and between high and low salinity habitats. As an apex predator, it occupies an ecological niche in ecosystems with different salinities, from oligosaline to hypersaline. As a free-moving species that moves between fresh and saltwater environments, *C. leucas* represents a trophic connection between marine and freshwater ecosystems (Every et al. 2017). Like most carcharhinid sharks, also *C. leucas* is an opportunistic feeder (Bell & Nichols 1921; Brunnschweiler & Barnett 2013; Espinoza et al. 2016), and its migration as a primarily marine species into low salinity environments provides access to additional and productive food resources. Ecological transitions from marine to freshwater habitats by euryhaline fishes, which can overcome the physiological stress of the new osmotic environment, can be viewed as the occupation of an open niche space and a form of evolution and adaptive radiation (Betancur-R. et al. 2012).

11. It has been assumed that the penetration of freshwater habitats allows adult *C. leucas* get rid of numerous marine parasites for which it is a host (Southwell 1912; Cressey 1967, 1970; Watson & Thorson 1976; Moravec & Little 1988; Palm 1999; Vankara et al. 2007; Méndez & González 2013). Watson & Thorson (1976) suggested that individual *C. leucas* cleared themselves of infections by moving upriver and lingering in freshwater. Although there are no verified data and evidence for this clearing behavior, maybe this could be another factor motivating adult *C. leucas* to enter freshwater environments. On the hand, there also is a risk for sharks to be infected by freshwater parasites (Bustamante-Avendaño et al. 2015). Stenohaline sharksuckers (*Echeneis* spp., Carangiformes), which can cause stress behavior in sharks (Brunnschweiler 2006), cannot follow *C. leucas* into low salinity environments. Severin (1953) reported catching a specimen of *C. leucas*, near EI Castillo at the San Juan River (Nicaragua), to which were attached two 8-inch remoras—*Echeneis naucrates* Linnaeus, 1759 (Echeneidae); these were practically dead, but were still clinging stubbornly to their host. For a detailed and comprehensive overview of parasites affecting *C. leucas*, see Love & Moser 1976, 1983 and Schaeffner & Smit 2019).

12. From an evolutionary point of view, the statement by Robertson et al. (2004) that *C. leucas* is an Isthmian relict in the Tropical Eastern Pacific leads to some further interesting deliberations. *Carcharhinus leucas* utilizes river systems on both sides of the Central American Land Bridge (Tables 3, 4). This leads to the assumption that osmoregulation in *C. leucas* either evolved before the Atlantic and Pacific oceans divided (~3.1–3.5 Mya) or independently in Atlantic and Pacific populations after the dividing of these two oceans. Because individuals of *C. leucas* worldwide are euryhaline and because these populations were not divided in ancient geological times by a land bridge, the first assumption seems more likely. This means that osmoregulation in *C. leucas* evolved at least ~3.1–3.5 Mya ago, during the Pliocene. This is also supported by paleontological findings suggesting the use of freshwater systems by *C. leucas* in the late Neogene.

13. Regarding the degree of euryhalinity of *C. leucas* and its physiological capability to stay in oligohaline environments, very rare events, such as natural floods or the artificial closure of dams, have trapped small populations of bull sharks in pure freshwater bodies for extended periods. These few cases have provided the opportunity to evaluate the effects on *C. leucas* of years spent in purely freshwater environments. Montoya & Thorson (1982) reported dead specimens of landlocked *C. leucas* on the shore of Panama's Lake Bayano, four and five years after the closure of this barrier lake. This report and observations in an Australian golf course lake next to the Logan and Albert rivers (Boswell 2013) show that permanent residence of *C. leucas* in pure freshwater habitats presumably ends with the death of the individuals after several years to two decades, and therefore a large part of the species' lifespan (a longevity of 27 years was reported

free-ranging Atlantic Ocean specimen by Natanson et al. 2014). These rare events confirm the ability of *C. leucas* to survive in freshwater for long periods, but that the time of residence in pure freshwater seems limited by physiological constraints. As remarked also by Compagno (1984). Nevertheless, the ability of *C. leucas* to survive for extended periods in freshwater environments makes it unique within the Carcharhiniformes together with the river sharks (*Glyphis* spp.).

14. *Carcharhinus leucas*'s rangeoverlaps with those of other freshwater elasmobranchs, especially river sharks (*Glyphis* spp.) and sawfishes (*Pristis* spp.). Besides river sharks and sawfishes, *C. leucas* is the most notorious species of elasmobranch for invading riverine and estuarine ecosystems primarily in the tropics and subtropics, but occasionally also in warm-temperate regions. As regards global fish zoogeography, the worldwide occurrences of *C. leucas* in numerous rivers and lakes lead to faunal similarities between tropical rivers and lakes, as this species is accompanied by other freshwater-tolerant elasmobranchs. The present global review of localities of occurrence of *C. leucas* has revealed a strong faunistic similarity of tropical freshwater lakes and rivers with sea access, especially with regard to fish predators. There is a strong homogeneity of sympatric elasmobranchs in the species inventories of numerous tropical lakes and rivers, although most of the freshwater elasmobranchs are highly endangered and stocks will likely be depleted soon.

Freshwater sawfish have often been found in the same waters as *C. leucas*, pointing to similar habitat preferences of these species. At least in historical times, but possibly also today, Central America's Lake Izabal and Lake Nicaragua, Madagascar's Lake Kinkony, New Guinea's Lake Jamoer and Lake Sentani, and Philippine's Lake Taal probably shared a fish assemblage including *C. leucas* and various vicarious taxa of sawfishes (*Pristis* spp.). Another co-occurrence is that between *C. leucas* and various river sharks (*Glyphis* spp.) in Asian and northern Australian rivers (Thorson et al. 1966b, 1976b; Montoya & Thorson 1982; Lovejoy et al. 2006; Thorburn 2006; Pillans et al. 2009; Kyne 2014; Tillet et al. 2014; Poulakis et al. 2015; Morgan et al. 2017). These species are presumably competitors in freshwater environments, but they are also linked in the tropical riverine, lacustrine, and estuarine food chains (Morgan et al. 2017). *Carcharhinus leucas* and sawfishes are connected by a predator/prey relationship (Thorson 1976a), which determines a trophic connection in tropical to subtropical rivers and lakes. In tropical rivers, *C. leucas* also feeds on other elasmobranchs, especially sawfishes (Morgan et al. 2017, Bonfil et al. 2018, Brame et al. 2019), and often displays aggressive feeding habits (Thorburn 2006). Interestingly, Field et al. (2013) observed no *Glyphis* species in northern Australian rivers at the same time as they were collecting *C. leucas*. As an apex predator, the ecological value of *C. leucas* for riverine ecosystems can be assumed as high, by top-down control of lower trophic cascades, especially in rivers with large numbers of sharks.

15. *Carcharhinus leucas* is mentioned in numerous freshwater fish checklists, mostly as an invader (or vagrant, transient, marine straggler) of marine origin. Skelton (1988) classified *C. leucas* as a sporadic marine component of African rivers and lakes, and already Myers (1966) categorized the species as a sporadic freshwater component of Central America, which means that it occasionally spends long periods away from the ocean Warren Jr. et al. (2000) classified *C. leucas* as an infrequent marine invader of freshwaters in the southern United States. However, fishing methods used in numerous investigations on freshwater fish faunas are inappropriate for finding evidence of large elasmobranchs, and therefore the results of these surveys are probably incomplete. Investigations based on electrofishing only will presumably not reveal the presence of sharks in any body of water. Without the use of appropriate methods, such as gillnet or longline fishing, large, strong-swimming fishes like *C. leucas* may elude surveys dealing with the inland fish fauna of continental freshwaters. Already Swift et al. (1977) stated that the paucity of freshwater records of this species for the continental United States was probably due to inadequate collecting effortswhereas more appropriate techniques would have yielded these sharks at least in the lower portions of rivers. Finally, it can be estimated that *C. leucas* is often underrepresented in checklists dealing with tropical or subtropical freshwater fishes and is an elusive species in many freshwater bodies, and that the absence of records by scientists should not be interpreted as a true absence in cases where inappropriate methods were used. De Silva (1975) reported on the lack of realistic evaluations, in ichthyological surveys, of the larger, swift-swimming fishes that can easily evade capture by most of the methods normally used in estuarine studies, and Thompson & Verret (1980) added that this category of species also includes *C. leucas*. Without the use of adequate methods (gillnet, longline, hook, and line) able to detect it during ichthyological studies of certain fresh or brackish water bodies, *C. leucas* will remain unconfirmed in many river/estuarine systems. Perhaps for this reason, and despite being only a sporadic component of the fauna of in some of these ecosystems due to its life history and seasonal shifts in its utilization of habitats with different salinities, *C. leucas* is not mentioned in the fish checklists of certain rivers, lakes, and estuaries. Roskar (2019) and Roskar et al. (2020) remarked, for Florida's Indian River Lagoon system, that specimens of *C. leucas* are more often caught in gillnets than by longline.

Because of its primarily marine origin, *C. leucas* is not mentioned in the fish checklists of certain rivers,

even those from which records of *C. leucas* are known. The decision of including *C. leucas* in freshwater fish listings may depend on the opinion of the authors of those lists. *Carcharhinus leucas* does not feature in all studies and surveys on the fresh or brackish water ichthyofaunas of the tropics, subtropics, and warm-temperate regions of the world, and its inclusion in literature is heterogeneous due to its periodic, sporadic, and temporary occurrences in freshwater bodies and use of inappropriate methods. This aspect should be considered by scientists in literature reviews, as this species is often not taken into consideration in national, regional, or local checklists of freshwater and inland water fishes. a uniform treatment of this species—as of other marine migrant fish species with freshwater occurrences—for completeness of existing checklists would be desirable. However, *C. leucas* was mentioned in the world checklist of freshwater fish species by Tedesco et al. (2010), due to its affinity for riverine and lacustrine habitats.

16. Although *C. leucas* was not mentioned in some checklists or surveys about the fresh and brackish water fish fauna of certain localities or regions, as a cosmopolitan species it connects the riverine and estuarine ichthyofauna of tropical, subtropical, and warm-temperate regions of the world. In this context, Potter et al. (1990) compared the estuarine fish faunas in temperate Western Australia and southern Africa, with *C. leucas* occurring in both regions. Therefore, this shark contributes to faunistic similarities in the global riverine and estuarine ichthyofaunas.

17. In parts of the Southern Hemisphere influenced by cold currents, the the range limit of the warm-water *C. leucas* is pushed farther to the north, like along the west coasts of South American and Africa (Fig. 4). Conversely, in regions influenced by warm currents, like the east coast of North America, *C. leucas* undertakes seasonal migrations to its seasonally-determined range limits. In these areas, water temperature can be considered as the strongest factor influencing the species' distribution. Due to seasonal warming and cooling of water masses in the subtropical to temperate regions, *C. leucas* undertakes long-distance, temperature-regulated migrations, for example along the coasts of southeastern Africa (Daly et al. 2014) and southeastern Australia (Heupel et al. 2015; Niella et al. 2020a).

18. *Carcharhinus leucas* has occasionally been recorded from very remote oceanic islands (IUCN Shark Specialist Group 2007). Single adults of *C. leucas* can occur offshore, often as strays, in distributional exclaves (e.g., the Azores and the Tuamotu Archipelago), but they do not form large populations at these isolated locations. Small and remote oceanic islands are often poor in riverine and estuarine habitats. An important question is whether sustainable colonization of oceanic islands by *C. leucas* and the foundation of residential populations only take place when suitable riverine habitats are available on these islands, like in Fiji, Réunion Island, and the Okinawa Islands. In cases where rivers and river mouths are absent, it would be highly interesting to know if *C. leucas* is able to breed in coastal saltwater environments or whether this species fully depends on suitable nursery areas far away from these islands and displays philopatric behavior. In this regard, it would be very interesting to know the percentage of pregnant females who migrate back from oceanic islands to their nursery areas, thus showing site fidelity. The results of Lea et al. (2015) indicate that vast distances can be traveled by adult females from their foraging habits to nursery grounds.

19. Large rivers and streams are nowadays under threat worldwide. Due to their great catchment areas, they receive large amounts of contamination due to spillages of domestic and industrial wastewater, nutrient and pesticide losses from agricultural fields, and the intake of pharmaceuticals. Moreover, in many regions, they are more and more degraded by river modifications, impediments, and loss of water for irrigation purposes. This may influence not just the abundance, occurrence, and distribution of *C. leucas* in inland waters, but will affect many additional freshwater biotas. Thus, habitat protection is a further important goal, besides prevention from overfishing, for successful conservation of *C. leucas*, not only in certain regions but also on a regional and global scale.

A proper understanding of the utilization and functionality of each of *C. leucas*'s critical habitats is foundational to the protection and conservation of this species. As a large, slow-growing shark species with late maturity and low recovery potential (Bass 1977; Thorson & Lacy 1982; Branstetter & Stiles 1987; Stevens et al. 2000; Wintner et al. 2002; Cruz-Martínez et al. 2005; Neer et al. 2005; Karl et al. 2011; Tillett et al. 2011a; Natanson et al. 2014), *C. leucas* is potentially vulnerable to overfishing and decline (like most large shark species). Pardo et al. (2018) outlined the low reproduction rate of *C. leucas* due to its small litter size, late maturity, and consequent vulnerability to overfishing. The institution of coastal conservation and protection areas and the preservation of low-influenced, pristine estuarine and lacustrine habitats are necessary for a successful protection of *C. leucas*, and the identification of important nursery grounds and breeding areas is key for realizing this aim. Due to its migrations induced by seasonal temperature changes and to the breeding behavior of females, the conservation and protection of this species can only be effective if multinational policies are adopted (Brunnschweiler & Van Buskirk 2006; Heupel et al. 2015). Unfortunately, very few countries within its range have established any conservation measures for this species, despite its importance to commercial and recreational fisheries, and occasionally dive

tourism, in some regions (IUCN Shark Specialist Group 2007). The bull shark is considered a flagship species for Australian freshwaters (Ebner et al. 2016), to increase awareness of conservation issues in these ecosystems due to human impact.

8 Future aims

This review presents an interim account of the results of scientific ichthyological research, fisheries surveys, and media reports on freshwater occurrences of *Carcharhinus leucas* spanning almost two centuries. Although the freshwater migrations of *C. leucas* have been well studied at particular locations in the past, such as the Lake Nicaragua/San Juan River system (Thorson 1971), little is known about the periodicity of these movements or which proportion of local populations makes these forays from the sea into freshwater bodies (Chapman et al. 2012). Quantifying the marine/freshwater proportion of populations of *C. leucas* would bring new insights into the population biology of this species and would be of value to conservation strategies. As some studies have revealed, females of *C. leucas* are philopatric and show site fidelity, although the degree and nature of this philopatry remain unknown (Van Niekerk & Turpie 2012). Monitoring the putative return of *C. leucas* to breeding areas where this species was nearly extirpated, like Lake Nicaragua and Lake Taal, should be one important aim of fisheries research and elasmobranch studies. a further aim for elasmobranch conservation efforts should be the identification of riverine and estuarine systems important for the reproduction of *C. leucas*. Some of these locations certainly remain undiscovered and were therefore not included in this review, and they are presumably mainly concentrated in developing regions of the world. Due to its important role as a riverine, estuarine, and marine apex predator, marine and limnological scientists working at locations within its range should mention *C. leucas* in ichthyological studies, to ensure its successful conservation and the protection of healthy aquatic ecosystems. The identification of important nursery areas and critical habitats of *C. leucas* in many parts of the tropics (e.g., Southeast Asia, West Africa, Tropical Eastern Pacific) is a further aim for sustainable fishing and the development of successful conservation plans. It will be a challenge for scientists to find a plausible explanation for the contradictory reproductive behavior of *C. leucas* in the southeastern Persian Gulf and to uncover possible nursery grounds in this area—knowledge that would improve our understanding of the complex biology of *C. leucas* in this region.

The present study stresses the need for more in-depth research on the utilization of low salinity environments by *C. leucas*, especially in the underexplored developing world and in localities with old and not recently confirmed records. Furthermore, investigations at localities of biogeographical importance (e.g., the Panama Canal, the Lake Nicaragua/San Juan River system, the Euphrat/Tigris/Shatt Al-Arab system, and the Amazon River Basin) should be intensified due to their function as nurseries and migration pathways for *C. leucas*. One aim of this study is to encourage intensified future research on sharks and elasmobranchs in freshwater ecosystems, using the present account as a starting point.

This survey further highlighted that the available data for numerous locations are quite old and that recent information regarding occurrences of *C. leucas* at these locations is lacking. Since these historical reports, this shark species has not been confirmed from these localities. For example, there have been no records of *C. leucas* from Lake Jamoer (Irian Jaya, West Papua) since Boeseman (1964) first recorded it there. Thus, the status of *C. leucas* at many locations reported in Tables 1–10 is nowadays uncertain. Besides finding new localities at which *C. leucas* occurs, the confirmation of old records for many locations can provide key information for conservation policies and further scientific studies. Distributional data, verified records, and reliable reports of *C. leucas* should be collected and combined by a few main institutions and provided for scientific purposes. The identification of migratory pathways and critical habitats would be fundamental for future conservation efforts regarding *C. leucas*. Unfortunately, numerous shark-human interactions do not find their way to the public and scientific literature. that the fact that *C. leucas* is often targeted by recreational fisheries, both in freshwater and marine environments, is a potential source of data for research on this species and should not remain unused. For example, juvenile *C. leucas* have been taken in large amounts by recreational fisheries throughout the Atchafalaya Basin and in inland bayous and wetlands of Louisiana's inland waters. It would be useful to educate local fishers and sports fishers to release and tag their catches, at best unharmed.

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Author's address:

Holper Heide 5c, 44629 Herne, Germany;
e-mail: peter.gausmann.2@googlemail.com
https://orcid.org/0000-0003-3577-7349

ZooBank registration: http://zoobank.org/References/5AF2FE43-9E77-4A51-B7B1-3AE1895ACF5C

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