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Coastal Dolphins and Porpoises

Edited by

THOMAS A. JEFFERSON

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COASTAL DOLPHINS AND PORPOISES

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CHAPTER

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Atlantic and Indian Ocean humpback dolphins *Sousa teuszii* (Kükenthal, 1892) and *S. plumbea* (Cuvier, 1829)

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Taxonomy and systematics

Scientific names

The holotype of *S. teuszii* was collected in the "Bucht des Kameruner Kriegsschiffhafens," ("Bay of Warships" or "Man O'War Bay"), in Cameroon, by the Polish (then Prussian) agronomist Eduard Tëusz in the early 1890s. The specimen was sent to the German taxonomist Willy Kükenthal at Jena (Germany), who named it after Tëusz and placed it in the genus *Sotalia* (Kükenthal, 1892; Teusz, 2018; Van Waerebeek et al., 2004), in keeping with established taxonomy (Gray, 1866). The specimen was later transferred to the Natural History Museum, London (catalog number 1893.8.1.1). Subsequent specimens were also assigned to *Sotalia* (e.g., Cadenat, 1956; Fraser, 1949), but were reassigned to *Sousa* once the name came into general use (Fraser, 1966). No subspecies or regional variants are recognized (Jefferson & Rosenbaum, 2014).

The Indian Ocean humpback dolphin became recognized as a distinct species in 2014 following the completion of an extensive global study on humpback dolphin morphology, biology, and genetics (Jefferson & Rosenbaum, 2014). Prior to 2014, humpback dolphins found in the western and northern Indian Ocean, including those in the Red Sea and Persian

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Gulf, were called Indo-Pacific humpback dolphins (*Sousa chinensis*). The holotype originates from the Malabar region on the west coast[1] of India and is stored at the Musée National d'Histoire Naturelle (catalog number A-14378/3503; Robineau, 1990; Jefferson & Rosenbaum, 2014). Humpback dolphins that occur on the east coast of India, from Palk Bay to the waters of Bangladesh and Myanmar may be neither *S. plumbea* or *S. chinensis*, nor hybrids of the two, and could be a separate taxonomic entity entirely (Amaral et al., 2017, 2020). Further study is required to define the eastern limit of *S. plumbea*, but at present it is believed to be limited to the Gulf of Mannar, between Sri Lanka and the southern tip of India.

Common names

The Atlantic humpback dolphin (sometimes Atlantic humpbacked dolphin) was originally referred to as the Cameroon dolphin, based on the collection location of the holotype (Van Waerebeek et al., 2017). Names in other languages include *Dauphin à bosse de l'Atlantique* (French), *Dauphin du Cameroun* (French), *Delfín Blanco Africano* (Spanish), *Delfín Jorobado Del Atlántico* (Spanish), *Bufeo Africano* (Spanish), *Golfinho-corcundo-do-Atlantico* (Portuguese), *West-Afrikaanse kustdolfijn* (Dutch), *Kamerun Delphin*, *Kamerun-Flußdelphin* (German), *Kposso* (Ewe), *Soumbou Nili* (Vili), *Owdenne* (Imraguen), *Furian* (Susu), *Pueyegue* (Susu), *Popos* (Susu).

The Indian Ocean humpback dolphin has also been called the plumbeous dolphin due to its lead gray coloration (Zbinden et al., 1977). The species has many different names in local languages from range states which include: *Boggelrugdolfyn* (Afrikaans), *Dauphin à bosse* (French), *Dukhs* (Arabic), *Suki* (Makua/Koti), *Fesobory* (Malagasy), *Fesodoby* (Malagasy), *Fesoke Manjavany* (Malagasy), *Fukariyo* (Gujarati), *Gada reda* (Marathi), *Gad/Gaadha reda* (Kannada), *Goonu* (Telugu), *Kadal ongi/Kadal panni* (Malayalam), *Sori vedan/Paru vedan/Vella ongi* (Tamil), *Thella thoralu/Goonu* (Telugu), *Malhar* (Sindhi) and *Pomboo nundu mgongo/mgongoni* (Swahili), *Pomboo mweupe* (Swahili-Zanzibar).

Evolutionary history

There is no fossil record for the genus *Sousa* (see Parra & Jefferson, this volume, for more details). Genetic studies suggest that *S. plumbea* and *S. chinensis* types diverged very early in delphinid evolution, about 5.3–10.5 MYA (Cockcroft & Smith-Goodwin, 2002; Perrin et al., 2013). Among extant *Sousa* species, *S. teuszii* is most closely related to *S. plumbea* (Jefferson & Rosenbaum, 2014; Mendez et al., 2013), but recent work has shown that there are no shared mtDNA haplotypes between *S. teuszii* and other *Sousa* species and significant differences in some aspects of skeletal morphology. The ~2000 km distribution gap between *S. teuszii* and *S. plumbea* is dominated by the cold waters of the Benguela upwelling system and provides a plausible mechanism for their separation (Collins, 2015; Jefferson & Van Waerebeek, 2004; Mendez et al., 2013).

Within the range of *S. plumbea*, there is considerable genetic and morphological variation. Several genetic studies involving both mitochondrial and nuclear markers have shown division between animals that occur along the African coast and those from the Arabian Sea

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[1] Jefferson and Rosenbaum (2014) erroneously describe this location as being on the east coast of India.

(Amaral et al., 2017, 2020; Mendez et al., 2013). The roles that oceanography plays in the differentiation of Indo-Pacific *Sousa* species is further described by Amaral et al. (2020), who suggested that sea surface temperature and primary productivity are likely determining factors influencing distribution, leading to species differentiation.

Distribution

Range

The Atlantic humpback dolphin is endemic to a narrow coastal strip of the tropical and subtropical waters of the Atlantic African coast (Fig. 4.1). The species distribution is discontinuous across a range that spans 19 countries, from Western Sahara to Angola (Collins et al., 2017; Van Waerebeek et al., 2004, 2017; Weir & Collins, 2015). Areas of reported occurrence include Dakhla Bay in the non-self-governing territory of Western Sahara (Beaubrun, 1990; Moores, 2018; Notarbartolo di Sciara et al., 1998), the Banc D'Arguin, Mauritania (Robineau & Vely, 1998), the Saloum Delta, Senegal (Minton et al., 2022; Van Waerebeek et al., 2004; Weir, 2016), The Gambia (Dupuy & Maigret, 1980; Murphy et al., 1997; Van Waerebeek

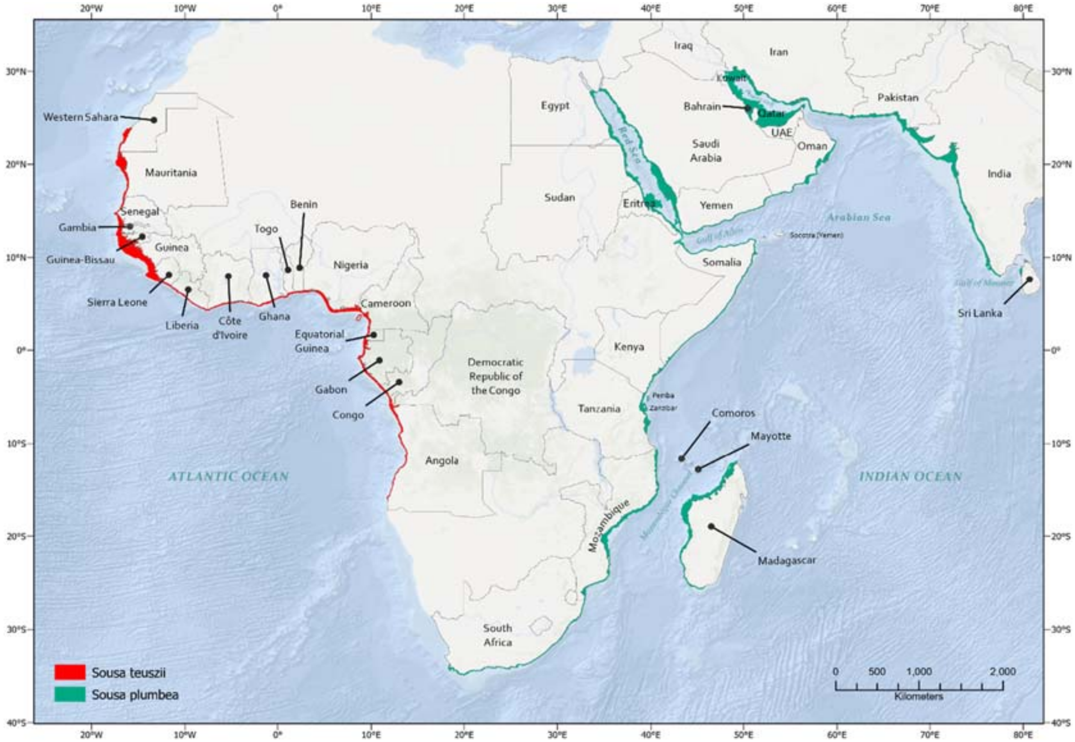

FIG. 4.1 Range map showing the distribution of the Atlantic (*Sousa teuszii*) and Indian Ocean (*Sousa plumbea*) humpback dolphins.

et al., 2004), the islands and rivers of Guinea-Bissau (Fulling et al., 2008; Leeney, Weir, et al., 2015; Spaans et al., 1990), northern Guinea (Bamy et al., 2010, 2021; Minton et al., 2022; Weir, 2015), the Sherbro River Estuary of Sierra Leone (M. Mayer, pers comm.), Togo (Van Waerebeek et al., 2017), Benin (Zwart & Weir, 2014), Nigeria (Van Waerebeek et al., 2017), Cameroon (Ayissi et al., 2014; Kükenthal, 1892; Van Waerebeek et al., 2017), Gabon (Collins, 2015; Minton et al., 2017) the Republic of Congo (Collins, 2015), and at Flamingos in Angola (Weir, 2009). Apparent gaps in distribution may be real, a consequence of very low density and/or limited survey effort (see reviews in Collins et al., 2017; Van Waerebeek et al., 2004; Weir & Collins, 2015). There are no verified records from Liberia, Ghana or Cote D'Ivoire (e.g., Debrah et al., 2010; Van Waerebeek et al., 2004, 2009) and none from Equatorial Guinea or the Democratic Republic of Congo (Mbungu Ndamba et al., 2023). Future work in poorly surveyed areas may well yield new records, but the evidence of current work suggests that densities will be low (Van Waerebeek et al., 2017).

Indian Ocean humpback dolphins are found in a narrow coastal strip of 23 Indian Ocean countries (Fig. 4.1). Their distribution extends from False Bay, South Africa, through the shallow, coastal waters of Eastern Africa, the Horn of Africa, and the Middle East to approximately the southern tip of India and Sri Lanka. This includes the coasts and islands of the Red Sea, Gulf of Aden, the Arabian Sea coasts of Yemen and Oman, the Persian/Arabian Gulf, and several offshore islands including western Madagascar, Mayotte, Pemba, Zanzibar, and Socotra (Braulik et al., 2015, 2023). Information on the distribution and occurrence of *S. plumbea* is much greater than for *S. teuszii*, but significant portions of the species range have not been surveyed, and in many areas their occurrence is known only from a handful of sighting or stranding records. This includes the extensive coastlines of northeast Africa and the Middle East, including Somalia, Djibouti, Eritrea, Sudan, Egypt, Saudi Arabia, and Egypt (Baldwin et al., 2004; Braulik et al., 2015; Notarbartolo di Sciara et al., 2021).

Indian Ocean humpback dolphins occur throughout the Red Sea, including within the Gulf of Suez, among the Farasan Islands of Saudi Arabia, the coastal waters of Egypt near Hurghada, Hamata and Shalateen, and the Dahlak Archipelago in Eritrea (Baldwin et al., 2004; Notarbartolo di Sciara et al., 2017, 2021). They are considered rare in the Gulf of Aqaba (Goffman et al., 2022; Notarbartolo di Sciara et al., 2017, 2021). Humpback dolphins have been observed rarely in the Mediterranean waters of Israel, Turkey, and Greece and are believed to be vagrant animals that have passed from the Red Sea through the Suez Canal (Frantzis, 2018; Özbilgin et al., 2018). The species likely has a broadly continuous distribution along the coasts of the Persian/Arabian Gulf (Baldwin et al., 2004; Notarbartolo di Sciara et al., 2021). Records include the UAE (López et al., 2018; Natoli et al., 2022; Preen, 2004), Qatar (Preen, 2004), Bahrain (Preen, 2004), Saudi Arabia (Preen, 2004; Rabaoui et al., 2021), Kuwait (Bishop & Alsaffar, 2008; Carpenter et al., 1997; Nithyanandan, 2010), Iraq (Al-Robaae, 1974) and along the extensive coastline of Iran (Braulik et al., 2010; Hemami et al., 2018; Mohsenian et al., 2022; Owfi et al., 2016). Sightings and stranding records from 2005 to 2009 along the Pakistan coastline confirm the presence of humpback dolphins at Jiwani, Gwadar, Pasni, Kalmat Khor, Ormara, Miani Hor, Sonmiani Bay, and the Karachi coast, including the Indus River Delta (Kiani et al., 2015; Pilleri & Pilleri, 1979). In India, *S. plumbea* ranges along the west coast, from the Gulf of Kutch to the southern tip of Kerala, encompassing the states of Gujarat, Maharashtra, Goa, Karnataka, and Kerala (Sutaria et al., 2015).

There are no sighting records from oceanic archipelagos, such as the Lakshadweep and Maldive islands or Aldabra (Panicker et al., 2020; Sutaria & Jefferson, 2004), nor from eastern Madagascar (Cerchio et al., 2015) or the Union of Comoros (Kiszka et al., 2010). There are possible gaps in distribution, or very low-density areas along the Wild Coast of South Africa (Plön et al., 2016; Vermeulen et al., 2018) and along parts of the southern coastline of Tanzania (Braulik et al., 2017b). These are all areas with a narrow continental shelf, where deep waters come very close to the coast, and where potential humpback dolphin habitat is very limited. The species also appears to be absent along several hundred kilometers of the Gulf of Oman coast of Oman (Baldwin et al., 2004; Minton et al., 2010), although sightings in the Muscat area were filmed in December 2023 (R. Baldwin, pers. comm.).

Movements

The movements and migrations of Atlantic humpback dolphins are very poorly understood. There is no evidence of dolphins moving between recognized populations despite increased survey effort in recent years. Localized movements (within identified areas of occurrence) have been described and have been linked to feeding opportunities and tidal movements (e.g., Cadenat, 1949; Dupuy, 1983; Maigret, 1980a; Van Waerebeek et al., 2003; Weir, 2009). Transits between Senegal and the Gambia River estuary (<20 km) have been reported (Maigret, 1980a; Murphy et al., 1997; Van Waerebeek et al., 2004). Evidence of movement over greater distances is limited, although it has been inferred or suggested. This includes north and south of the Banc d'Arguin (Maigret, 1980b; Robineau & Vely, 1998). Maigret (1980a) hypothesized that animals from the Saloum Delta could swim to favored areas in Mauritania, an idea later rejected by Van Waerebeek et al. (2003), who had access to more data. Maigret (1980a) also suggested that Senegalese animals from the Saloum Delta might swim to Yene Kao (~100 km north), an idea prompted by records of by-caught dolphins on the Petit Côte (Cadenat, 1956; Cadenat & Paraiso, 1957). Migrations across hundreds of kilometers will likely be atypical although perhaps not completely out of the question (Robineau & Vely, 1998). However, the distances between Dakhla Bay and the Banc d'Arguin (~450 km), and the Banc d'Arguin and Saloum-Niumi (~750 km) could limit exchange (Van Waerebeek et al., 2004). There are no records between Dakar and St. Louis, and very few between St Louis and Nouakchott (Maigret, 1980b; Van Waerebeek et al., 2004). Exchanges may occur between Saloum-Niumi and the Bijagós Archipelago (~280 km; Van Waerebeek et al., 2004) and more recent records suggest opportunities for transboundary movement between Guinea and Guinea Bissau (Bamy et al., 2017; Leeney, Weir, et al., 2015; Van Waerebeek et al., 2017; Weir, 2015). Similar movement can be envisaged between Togo, Benin, and Nigeria (e.g., Van Waerebeek et al., 2017; Zwart & Weir, 2014) and between Gabon and Congo (Collins, 2015). The small population at Flamingos (Angola) appears to be highly localized in its occurrence (Weir, 2009), though very little research has been conducted elsewhere on the Angolan coast.

There is limited information available regarding how Indian Ocean humpback dolphins use their habitat, their degree of residency or migration patterns, but the evidence suggests that while some animals can be locally resident in discrete near-shore areas, others can make considerable along-shore movements of hundreds of kilometers. For example, Richards

Bay in KwaZulu-Natal, South Africa, has a population composed of a small core of residents (5%) along with many transients (81%) that probably range widely along the surrounding coastal areas (Atkins et al., 2016). Comparison of 13 photo-ID catalogs from sites across the coast of South Africa found that resightings of known animals in the same area over several years occurred frequently, indicating a general pattern of site fidelity. However, some matched individuals moved considerable distances, with a median value of 120 km and varying between 30 and 500 km. The maximum distance covered by known females with calves was 275 km (Vermeulen et al., 2018). Data from South Africa did not identify any consistent directional seasonal patterns in movement (Vermeulen et al., 2018). Four photo-identified humpback dolphins were sighted at two different locations 170 km apart in Kenya (Mwango'mbe et al., 2021). Cross border movement has been recorded between Kenya and Tanzania and likely occurs between many other neighboring territories. This propensity for occasional long-distance movement may have led to the Lessepsian migration of several individuals through the Suez Canal into the Mediterranean (Frantzis, 2018).

Habitat

The Atlantic humpback dolphin occurs exclusively within the neritic zone of tropical and warm-temperate waters of the Eastern Atlantic. An extensive review of available records found that Atlantic humpback dolphins inhabit water depths of less than 20 m, and most sightings occur within 1 km of the shore, but they do range up to 13 km from shore when suitable habitat is present (Weir & Collins, 2015). No sightings have been reported from deeper waters despite considerable survey effort (Van Waerebeek et al., 2017; Weir & Collins, 2015). Preferred habitats include large estuarine and mangrove systems (e.g., Saloum Delta, Rio Nuñez, Tristão Island complex), coastal islands (e.g., Arquipélago dos Bijagós), shallow waters with extensive mudflats and seagrasses (e.g., Banc d'Arguin), shallow bays (e.g., Dakhla Bay, Baie de Cap Lopez) and open coasts exposed to swell (e.g., Angola, Congo Republic, southern Gabon and Benin). These areas tend to be tidally dynamic, are frequently turbid and may feature tidally emergent sandbars. The relative importance of each habitat type for species occurrence and density remains unknown (Collins et al., 2017; Weir & Collins, 2015). There is no evidence that they occur in rivers beyond the zone of saline intrusion (Van Waerebeek et al., 2004). Weir (2009) reported that dolphins occasionally foraged over rocky reefs in southern Angola.

Sightings of Atlantic humpback dolphins at greater distances from shore have mostly been recorded in the northern part of the range where the coastal shelf is widest. These include the Banc d'Arguin (3.5–4.5 km), the Canal de Geba-Caió and outer Rio Grande de Buba in Guinea Bissau (3.3–8.9 km), off the Rio Nunez Estuary and Tristão Island in Guinea (5.1–13.1 km). However, they have also been sighted relatively far from shore within the Baie de Cap Lopez, Gabon (to 4.5 km from shore; Weir & Collins, 2015).

Indian Ocean humpback dolphins occur in coastal habitats that include mangroves, rocky reefs, coral reefs, lagoons, estuaries, and shallow protected bays (Braulik et al., 2015). The broad habitat preference appears to be for water less than 25 m deep; however, the species frequently occurs in water only 2–3 m deep and within a few hundred meters of the shore. The mean depth at encounters reported during several different studies from different parts of the range has been around 8 m. In Nosy Be, Madagascar, the mean depth of humpback dolphin sightings was 8.2 m, with 95% of sightings in water less than 20 m deep (Cerchio et al., 2015). Similarly, in Oman the average depth at sightings was 8.3 m (Minton et al., 2010) and in the waters of Abu Dhabi, where one of the largest humpback dolphin populations occurs, they were found within the 1 and 18 m isobaths and at a mean depth of 8.4 m (López et al., 2018). In South Africa, in Algoa Bay, over 80% of sightings were within 400 m of shore and the average depth at sightings was 6.6 m (Karczmarski et al., 2000; Koper et al., 2016; Melly et al., 2018), while in Richards Bay, all humpback dolphin encounters were in water shallower than 20 m and dolphins used the area within 2 km from shore (Atkins et al., 2004). In Gujarat (India), most sightings recorded during surveys were between the coast and 10 m depth, and in Goa sightings were most frequent near river mouths and 60% of sightings were recorded in depths of 6−10 m (Sutaria & Jefferson, 2004). In Maharashtra, humpback dolphins were sighted at a maximum depth of 15.6 m, and approximately half of all groups were in water less than 10 m deep, with the remainder in water between 10−20 m in depth (Jog et al., 2018; Sutaria et al., 2015). Studies in Kerala also reveal that humpback dolphin distribution is notably influenced by salinity and depth; dolphins prefer higher salinity during the monsoon and post-monsoon seasons, but their presence is lower in areas with high salinity during the dry season. Additionally, they favor deeper waters in the monsoon and dry seasons, and shallower waters post-monsoon (Panicker et al., 2018).

Ecological niche modeling based on citizen science data collected between 2012−2019 in the United Arab Emirates identified the Indian Ocean humpback dolphin as the species of small cetacean with the most restricted suitable habitat compared to the Indo-Pacific bottlenose dolphin *Tursiops aduncus* and Indo-Pacific finless porpoise *Neophocaena phocaenoides* (Natoli et al., 2022).

External characteristics

Coloration

Atlantic humpback dolphins are generally dark gray, with a lighter ventral surface that extends from the mandibles to the area of the anal slit (Fig. 4.2). Between the mandible and flippers, the difference between light and dark areas can be well demarcated. There is a faint delphinid bridle evident in some animals (Perrin, 1997), though this is not as evident in calves. Calves and juveniles are noticeably more lightly colored than adults, and the color separation between the ventral surfaces and the darker back is more diffuse than in adults. Some animals (particularly adults) have white margins on the dorsal hump, dorsal fin and flukes, which may be caused by scarring, and some individuals have white and/or dark flecking/mottling on the tail stock, particularly the ventral side (Jefferson & Rosenbaum, 2014; Weir, 2011). Conspecific tooth rakes are clearly seen on many animals (particularly on pectoral flippers, the dorsal fin, around the beak and the dorsal surface of the caudal peduncle), though these may not persist.

Indian Ocean humpback dolphins are a relatively uniform light gray with ventral surfaces an even lighter gray (Fig. 4.2). Calves are pale gray on the flanks, with a ventral side that is

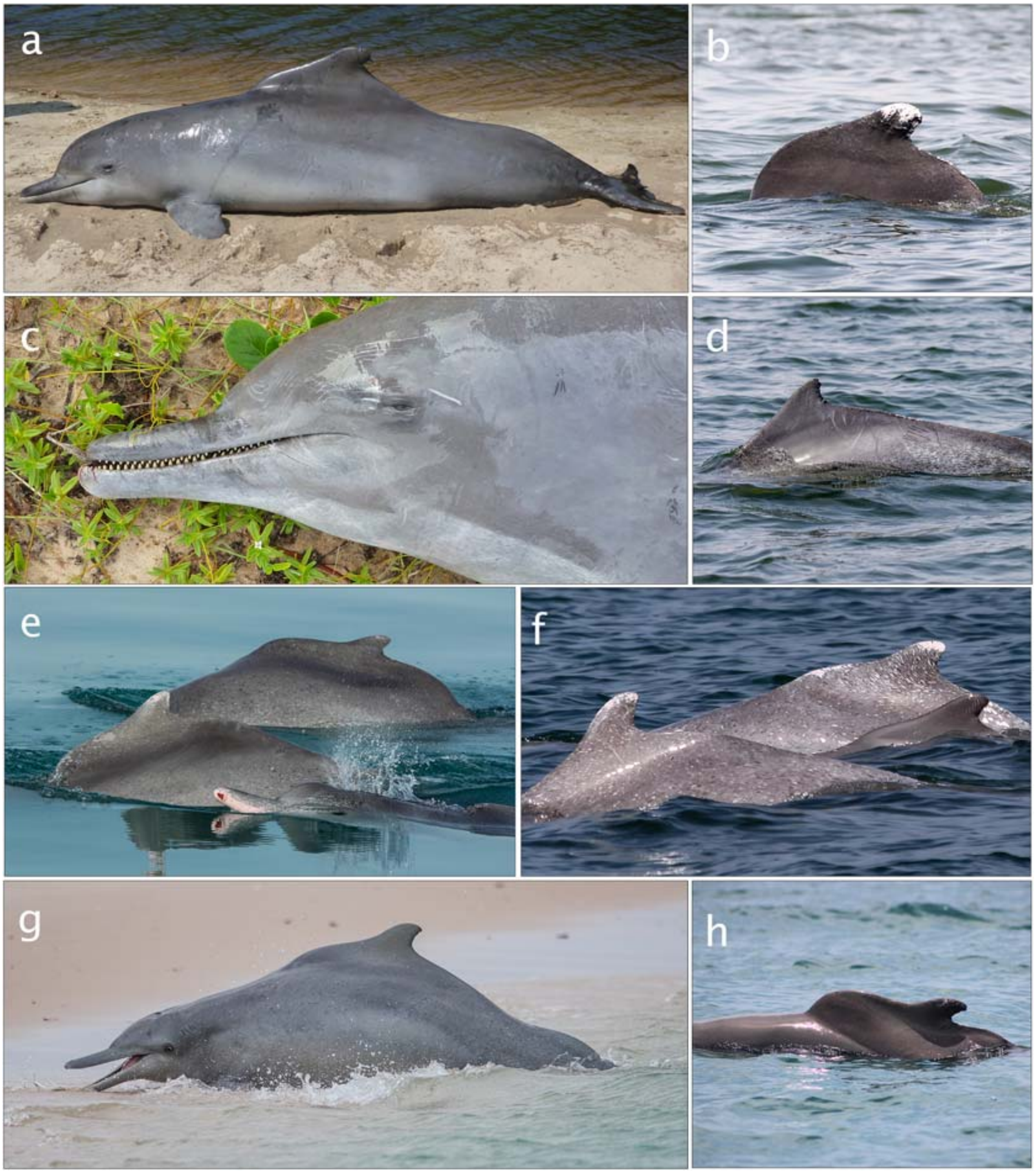

FIG. 4.2 External appearance of Atlantic (*Sousa teuszii*) and Indian Ocean (*Sousa plumbea*) humpback dolphins. (A): a juvenile *S. teuszii* recently recovered from a net in Congo. Colors are paler and the humpback is less evident (T. Collins). (B): Massive hump of a male *S. teuszii* in the Saloum delta (G. Minton). (C): Head and rostrum of an adult *S. teuszii* recovered from a net in Congo, note the faint bridle and net lesions on rostrum (T. Collins). (D): Adult *S. teuszii* swimming in the Saloum delta showing flecking on the flank and tooth rakes (G. Minton). (E): A group of *S. plumbea* surfacing in Bushehr Province, Iran. Note the pinkish rostrum (and recent wound) as well as paler tips to dorsal fins (N. Mohsenian). (F): a group of *S. plumbea* surfacing in Maharashtra, India (M. Sule). (G): A strand-feeding *S. plumbea* in Bazaruto, Mozambique. Animals in southern Africa are less speckled than those further north, but all share the robust body form and prominent keel (N. Perrins). (H): A distinctively humped male *S. plumbea* from Kenya (M. Mwango'mbe).

whiter than in adults (Ross et al., 1994). A diffuse gray stripe (delphinid bridle) runs from the eye toward the flipper, and there can be a distinctive dorsal and ventral keel in mature adults (Best, 2007; Perrin, 1997). Dolphins from southern Africa seem to be lighter ventrally than those from East Africa or the Arabian region. Some animals, particularly in the northern part of the range, occasionally exhibit extensive speckling, and the demarcation between the dark dorsal surfaces and lighter belly can be quite distinct. Larger adults typically have a white margin to the dorsal hump and fin, apparently caused by scarring (Jefferson & Karczmarski, 2001). Along the west coast of India these dolphins exhibit a consistent dark gray coloration with interspersed white mottling on the dorsum, occasionally accompanied by subtle pink hues in some individuals (Jog, unpubl.).

Size and shape

Both Atlantic and Indian Ocean humpback dolphins share a body shape that is generally consistent among *Sousa* species. They have a long and moderately slender rostrum (also called the beak) that is clearly separated from the melon by a shallow crease that is more evident when viewed from the front. The mouth line curves upwards slightly. The body of adults is generally robust with a compressed caudal peduncle that exhibits a distinct keel on both upper and lower surfaces (Best, 2007). The dorsal fin in each species is small and sits on a larger hump of connective tissue near the center of the back (Plön et al., 2018). This arrangement of dorsal fin and hump are unique among odontocetes; the only structure similar in appearance among the Cetacea is found in humpback whales (*Megaptera novaeangliae*). The shape and size of the dorsal hump varies within the genus (Ross et al., 1994), and both *S. teuszii* and *S. plumbea* exhibit pronounced humps, although both also show considerable ontogenetic and sexual variation in hump shape and size. In some mature males the hump can appear massive and almost brick-like. Photographs of the hump have been used extensively in mark-recapture studies of individual humpback dolphins (Karczmarski & Cockcroft, 1998), and it was found to change color in older individuals off South Africa by turning progressively white/gray (Ross et al., 1994). The flippers and flukes in both species are relatively broad with rounded tips, and flukes exhibit a deep notch.

The Atlantic humpback dolphin is the shortest of all the *Sousa* species, reaching a maximum length of 266 cm (Jefferson & Rosenbaum, 2014), although few animals have been measured and even fewer measurements published. The hump ranges between 26%–32% of body length (Ross et al., 1994) and the dorsal fin appears to be more rounded than that of the Indian Ocean humpback dolphin. The rostrum of *S. teuszii* is shorter than in other *Sousa* species (Jefferson & Van Waerebeek, 2004), but is still relatively long (5.9%–6.9% of body length; Best, 2007).

Indian Ocean humpback dolphins are the largest of all the *Sousa* species and animals longer than 3.0 m have been reported from the Arabian and Indian regions, although these have been questioned (Jefferson & Rosenbaum, 2014; Parra & Ross, 2009). In *S. plumbea*, the hump ranges in length from 23%–38% of body length (Best, 2007; Ross, 1984). The dorsal fin is small and noticeably more falcate than those in Atlantic humpback dolphins (Jefferson & Rosenbaum, 2014). The rostrum is long (6.3%–10.1% of body length; Ross et al., 1994).

Cockcroft (1990) reported clear sexual dimorphism for *S. plumbea* from South African waters. Some morphometric measurements are provided by Best (2007), including a difference in maximum total body length between males (2.79 m) and females (2.49 m) and a length/weight relationship for 42 animals of: $W = 0.00000457\,L^{3.183}$ where W = weight (kg), L = length (cm) (Best, 2007; Ross et al., 1994). Neonatal lengths in South African waters range from 97 to 108 cm and maximum body lengths for adults of up to 2.8 m have been recorded for South African waters (Ross et al., 1994).

Weight

Very few Atlantic humpback dolphins have been properly measured and weighed and data are correspondingly very sparse. The highest recorded body mass for *S. teuszii* was 166 kg for an adult male that measured 248 cm (Van Waerebeek et al., 2004).

Morphometric data for Indian Ocean humpback dolphins is skewed toward animals in South Africa, many of which become entangled in bather protection (shark) nets (BPNs). Out of 92 male and 50 female Indian Ocean humpback dolphins examined, the shortest animals measured 145 and 150 cm and weighed 43 and 46 kg, respectively. The longest specimens were a 276 cm long male weighing 280 kg and a 251 cm long female weighing 188 kg (Plön et al., 2012). Maximum weights of 289 kg for males and 176 kg for females have been reported elsewhere (Plön et al., 2015).

Internal anatomy

Skull

As with other species in the genus, the skulls of *S. teuszii* and *S. plumbea* are heavy and robust with long rostra (Fig. 4.3). Skulls of the two species represent both the shortest (*S. teuszii*) and longest (*S. plumbea*) in the genus. In comparison to other species in the genus, *S. teuszii* has a relatively wide skull and short rostrum, with the rostrum representing about 59% of condylobasal length, which can reach at least 511 mm. In *S. plumbea* the rostrum is much longer than in all other species in the genus and represents almost 62% of condylobasal length, which can reach 595 mm (Jefferson & Rosenbaum, 2014; Jefferson & Van Waerebeek, 2004). As with other species in the genus, identifying features of the skull in both *S. teuszii* and *S. plumbea* are large and round temporal fossae, and separation of the pterygoids along the base of the rostrum (Ross et al., 1994). The mandibles have concave margins, and the mandibular symphysis is long, though is notably shorter in *S. teuszii* (~25%) than *S. plumbea* (~32%), or indeed other *Sousa* species (29%–32%; Jefferson & Rosenbaum, 2014). Skulls of *S. plumbea* from the Persian Gulf are smaller than those from India, which may reflect local adaptation (Jefferson & Rosenbaum, 2014; Ross et al., 1994).

Average tooth counts are reported by Jefferson and Rosenbaum (2014) of 27–32 upper and 27–31 lower for *S. teuszii* and 33–39 upper, 31–37 lower for *S. plumbea*. Tooth counts are significantly lower on average in *S. teuszii* than other *Sousa* species (Jefferson & Van Waerebeek, 2004).

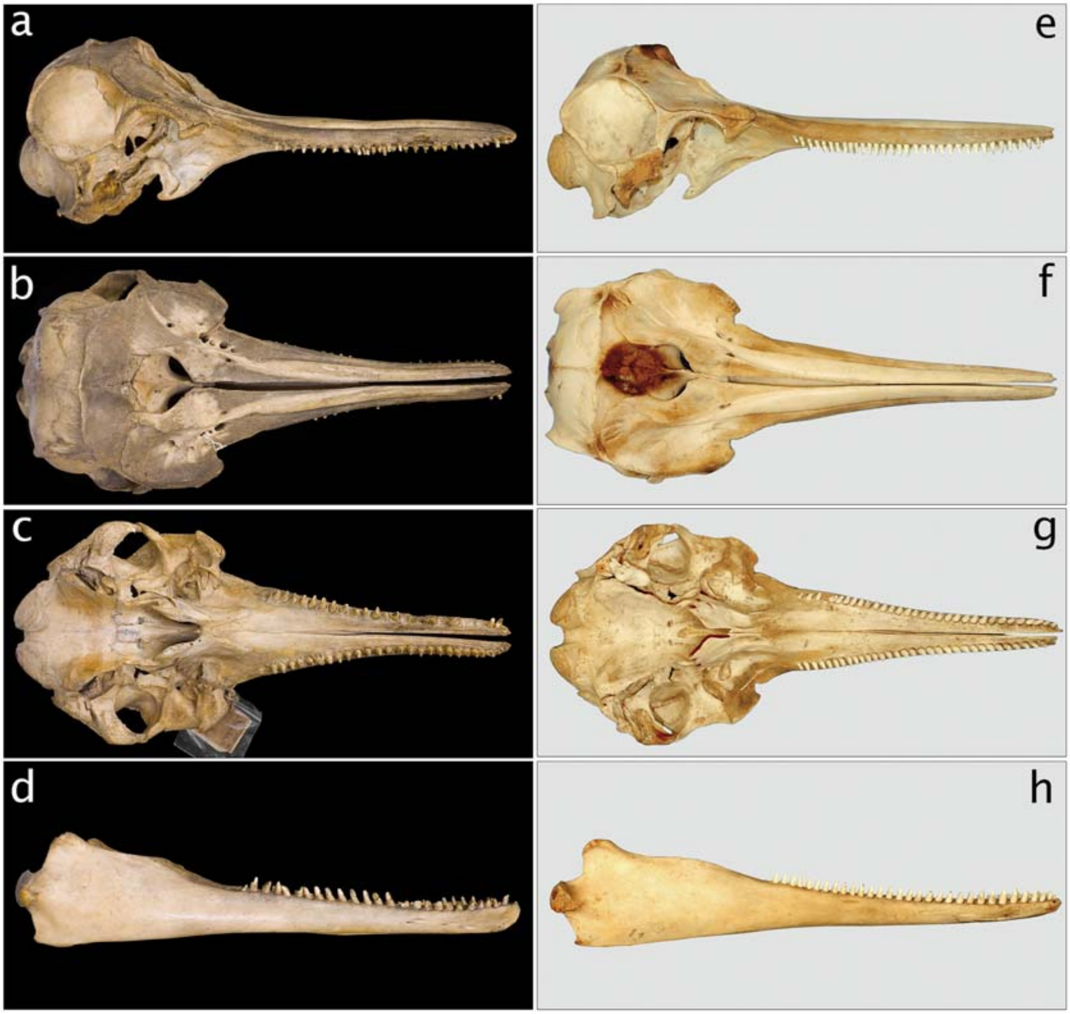

FIG. 4.3 The skulls of the Atlantic (*Sousa teuszii*; images A–D) and Indian Ocean humpback dolphins (*Sousa plumbea*; images E–G): lateral (top), dorsal (upper middle), and ventral (lower middle) views of the cranium, and views of the mandible (bottom). *Images from the library of Peter Best, courtesy of the MRI Whale Unit, University of Pretoria.*

Postcranial skeleton

There is very little information available on the skeletal structure of *S. teuszii* or *S. plumbea*. Based on a very small sample ($n = 2$), *S. teuszii* appears to have more vertebrae on average (52–53) than in *S. plumbea* (50–53) or other species of *Sousa* (49–50; Jefferson & Rosenbaum, 2014). The range of vertebral formulae in 22 South African *S. plumbea* was C_7, $T_{11\text{-}12}$, $L_{9\text{-}12}$, $Ca_{20\text{-}21} = 49–52$, with a mean of C_7, T_{12}, $L_{10.8}$, $Ca_{21.2} = 50.9$ (Ross, 1984; *in* Ross et al., 1994).

Soft anatomy

The details of the soft anatomy of humpback dolphins have not been well studied. Tissue and organ masses have not been reported for *S. teuszii* and the information provided here is limited to *S. plumbea*.

Analysis of *S. plumbea* organ weights (Table 4.1) as a percentage of total body weight from 142 animals incidentally caught in BPNs between 1970 and 2010 indicated that relative heart, liver and kidney weights were significantly smaller in coastal species (*Sousa* and *Tursiops*) than the more oceanic common dolphins (*Delphinus delphis*), likely reflecting differences in activity patterns; relative lung and trachea weights did not differ between the three species (Table 4.1; Plön et al., 2012). Generally smaller organ weights in *S. plumbea* indicate that it is a shallow diving, relatively slow moving, coastal delphinid compared to Indo-Pacific bottlenose dolphins and common dolphins (Plön et al., 2012).

TABLE 4.1 Organ weights for *S. plumbea* from South African waters.

Organ	Metric	n
Heart		131
Minimum weight (g/%)	240/0.36	
Maximum weight (g/%)	1250/0.88	
Mean weight (g) (+/− SD)	591.11 (±219.91)/	
Mean % of body weight (+/−SD)	0.52 (±0.08)	
Lungs and trachea		131
Minimum weight (g/%)	1550/2.39	
Maximum weight (g/%)	8675/6.11	
Mean weight (g) (+/− SD)/	4420.59 (±1808.52)/	
Mean % of body weight (+/−SD)	3.88 (±0.57)	
Lungs		9
Minimum weight (g/%)	1900/2.97	
Maximum weight (g/%)	4700/3.96	
Mean weight (g) (+/− SD)/	3396.11 (±1047.86)/	
Mean % of body weight (+/−SD)	3.25 (±0.33)	
Liver		92
Minimum weight (g/%)	718/0.77	
Maximum weight (g/%)	6100/3.2	
Mean weight (g) (+/− SD)/	2290.23 (±1049.47)/	
Mean % of body weight (+/−SD)	1.93 (±0.39)	

TABLE 4.1 Organ weights for *S. plumbea* from South African waters.—cont'd

Organ	Metric	n
Kidneys		92
Minimum weight (g/%)	263/0.45	
Maximum weight (g/%)	2080/0.96	
Mean weight (g) (+/− SD)/	790.64 (±363.93)/	
Mean % of body weight (+/−SD)	0.67 (±0.12)	
Spleen		61
Minimum weight (g/%)	43/0.02	
Maximum weight (g/%)	211/0.2	
Mean weight (g) (+/− SD)/	94.04 (±38.52)/	
Mean % of body weight (+/−SD)	0.09 (±0.04)	
Testes		26
Relative minimum weight (%)	0.16	
Relative maximum weight (%)	0.7	
Mean % weight (+/− SD)	0.43 (±0.12)	

From Plön et al. (2012).

Genetics

Relatively little work has been conducted on the genetics of *S. teuszii* and neither the chromosome structure nor the karyotype have been described. This is due largely to the limited availability of suitable samples, and a general lack of sample collection effort. Existing data indicate that there are no shared mtDNA haplotypes with other species in the genus, but phylogenetic work indicates that they are most closely related to extant populations of *S. plumbea* from Southeast Africa (Jefferson & Rosenbaum, 2014; Mendez et al., 2013). McGowan et al. (2020) describe the first complete mitochondrial genome of *S. teuszii* (Genbank: MN365274), which is 16,384 base pairs long and includes 13 protein-coding genes, 2 rRNA genes, and 22 tRNA genes.

The chromosome structure and karyotype of *S. plumbea* have not been described. In the process of clarifying the taxonomy of the genus, extensive genetic research was completed by several investigators (e.g., Amaral et al., 2020; Frere et al., 2008; Lin et al., 2012; Mendez et al., 2011; Mendez et al., 2013). However, there has been limited genetic work to demonstrate population structure within the *S. plumbea* species to identify distinct taxonomic units or subspecies. Previous work by Mendez et al. (2011) compared mtDNA from 94 samples from South Africa, Mozambique, Zanzibar, and Oman and found 17 haplotypes. The Oman population displayed the highest genetic diversity indices overall, whereas the

Zanzibar samples showed the lowest indices, and Mozambique and South Africa had intermediate genetic diversity values. The genetic data show highly significant differences between the populations in Oman, Tanzania, and South Africa/Mozambique. Most other genetic studies using both mtDNA and nuclear markers have shown division within the *S. plumbea* species with animals in south and east Africa distinct from those in the Arabian Sea and northern part of the range (Amaral et al., 2017, 2020; Mendez et al., 2013).

In South African waters, the species population structure remains poorly understood (Lampert et al., 2021). A first analysis of the mitochondrial d-loop of 157 museum skin and tooth samples collected between 1963 and 2017 from across the species geographical range in South Africa indicated extremely low mitochondrial diversity (haplotype diversity $= 0.47$; nucleotide diversity, $\pi = 0.2\%$); only three haplotypes were identified (Lampert et al., 2021). However, temporal comparisons over the sample collection period revealed that the mitochondrial genetic diversity had not changed significantly over the past 50 years despite the high levels of by-catch in BPNs during this period. Additionally, there was no evidence of population differentiation within South African waters (Lampert et al., 2021).

Physiology

Thermoregulation and energetics

Investigations into the internal morphology of the uniquely shaped hump and dorsal fin of *S. plumbea* using magnetic resonance imaging (MRI) allowed a characterization of the general arrangement of the dorsal fin vascularization (Plön et al., 2018). Comparison with the Indo-Pacific bottlenose dolphin revealed that although both species presented similar branching patterns, there were distinct differences in the morphology of the center arteries and *S. plumbea* exhibited a higher degree of branching of the blood vessels in the dorsal fin and hump (Plön et al., 2018). In essence, *S. plumbea* has more, but smaller, vessels in its hump and dorsal fin than *T. aduncus*. In both species the main blood vessels were located within the dorsal fin, but the hump in *Sousa* also exhibits extensive vascularization (Plön et al., 2018). The small dorsal fin and hump of *Sousa* combined present a slightly greater surface area, and thus may suggest a slightly larger thermal window, but counter intuitively significantly less blood vessel volume was shown for *Sousa* compared to *Tursiops* (Plön et al., 2018).

The examination of the histomorphology of the blubber of four *S. plumbea* from the subtropical KwaZulu-Natal coast, South Africa, using cell parameters like adipocyte cell size, number, and density, indicated that no stratification was present, which could be ascribed to the species' warmer inshore habitat, large body size, and apparent lower mobility (Roussouw et al., 2022a).

Senses

Plön and Roussouw (2022) reviewed the available literature on the hearing mechanisms (physiology), specialties and sensitivities of *S. plumbea*. While audiograms only exist for a small number of species held in captivity, information on vocalizations can aid in the inference of hearing capabilities, but potential population-level differences may exist. It is generally assumed that a species' frequency of best hearing sensitivity overlaps to a large degree with the frequency of their vocalizations, and the best hearing frequencies for odontocetes are between 20 and 150 kHz (Plön & Roussouw, 2022).

The functional anatomy of sound production in *S. plumbea* has been assessed using computed tomography (CT) imaging and standard gross dissection techniques and revealed that the general arrangement of sound generating structures, that is, air sacs and muscles, was similar to *T. aduncus* (Frainer et al., 2019). The main difference between the two species was a small left posterior branch of the melon in *S. plumbea*, which was absent in *T. aduncus* and, together with the longer rostrum in *S. plumbea*, might reflect an adaptation of directionality for high frequency communication sounds (Frainer et al., 2019).

Life history and population dynamics

Abundance and trends

There are no global estimates of species abundance for either *S. teuszii* or *S. plumbea*, but recent assessments of the available data, as well as expert knowledge, have been used to suggest range-wide abundances for both species.

Abundance data for *S. teuszii* are not available for most areas where they have been reported. Minimum estimates generated using reliable data are available for four areas; Rio Nuñez, Guinea (Weir, 2015), Saloum Delta, Senegal (Weir, 2016), Conkouati-Douli, Congo (Collins 2013) and Flamingos, Angola (Weir, 2009). However, each of these surveys was generally limited in duration or geographic extent, constraining their use for robust abundance estimation at a population level. Approximate estimates have been provided in various forms for many other areas, but these are based on surveys that were either too few, too sporadic, too localized or lacking specific (verifiable) metrics to be useful for conclusive estimates (Collins, 2015; Collins et al., 2017; Van Waerebeek et al., 2004). The few associated "guesstimates" are based on the work and experience of a limited number of researchers and provide a crude index of abundance (Collins et al., 2017). Tiny populations at the northern (Dakhla Bay, Western Sahara) and southern (Namibe, Angola) extremities of the range may indicate the limits of habitat suitability (Weir, 2009).

Available data and information on population size for Atlantic humpback dolphins are provided in Table 4.2. The Dakhla Bay population has been considered very small since it was first described (Beaubrun, 1990; Notarbartolo di Sciara et al., 1998; Van Waerebeek et al., 2004), but recent sightings suggest a few animals persist (Moores, 2018; Weir & Collins, 2015). The Banc d'Arguin (Mauritania) and Saloum-Niumi (Senegal/The Gambia) populations have been estimated repeatedly at ~100 animals since the mid-1970s (Maigret, 1980a; Van Waerebeek et al., 2003, 2004; Weir, 2016). Records for Guinea Bissau suggest the continued occurrence of a significant population of *S. teuszii*, although there is anecdotal evidence of decline (Collins et al., 2017; Leeney, Weir, et al., 2015; Van Waerebeek et al., 2004). Van Waerebeek et al. (2004) guessed "at least several hundred, if not more". Recent sightings suggest that distribution across the Guinea Bissau/Guinea border may be continuous (Van Waerebeek et al., 2017; Weir, 2015). Boat-based surveys in Cameroon in 2011 yielded a single humpback dolphin sighting, and an encounter rate

TABLE 4.2 A summary of available information on abundance reported for *S. teuszii*.

Population	Reported estimates	Estimation method(s)	Source(s)
Western Sahara (Dakhla Bay)	"miniscule"	Ad hoc sightings	Beaubrun (1990)
	"low tens"	Expert opinion	Van Waerebeek et al. (2004)
	4 sightings in 1996 with a mean group size of 6.9 individuals	Boat based survey	Notarbartolo di Sciara et al. (1998)
	Single animal reported in 2022	Ad hoc sightings	Hamid Bouceta & Mrieh Abdel Wadud (pers comm)
Mauritania (Banc D'Arguin)	"probably does not exceed 100 animals"	Ad hoc sightings	Maigret (1980b)
	"stock is apparently fairly small"	Expert opinion	Van Waerebeek et al. (2004)
Senegal—Gambia (Saloum-Niumi)	"low hundreds, maybe less"	Boat based survey	Van Waerebeek et al. (2004)
	"Minimum population size of 103 animals, the highest recorded for *S. teuszii* anywhere in its range"	Photo-ID	Weir (2016)
Guinea Bissau	56 sightings recorded during a 2 month period (1986/1987)	Ad hoc sightings	Spaans (1990)
	"several hundred, maybe more … until at least 1998"	Expert opinion	Van Waerebeek et al. (2004)
	"widespread"	Ad hoc sightings	Leeney, Weir, et al. (2015)
	"still regular in the area but in lower numbers"	Expert opinion	P. Campredon pers. comm.
Guinea	Eight sightings in Rio Nunez—minimum photo-ID estimate of 47	Photo-ID	Weir (2015)
	Single sighting south of Conakry	Ad hoc sighting	Bamy et al. (2010)
	Sighting of ~25 reported near the Tristao Islands	Boat based survey	Bamy et al. (2010)
	Sighting of a ~40 near Katfoura Island (Tristao Islands)	Boat based survey	Van Waerebeek et al. (2017)
Togo	Four individuals	Ad hoc sighting	Zwart and Weir (2014)
	Five sightings of 6,7,7,27,5 animals (2008—15). "sporadic … sightings ….and small group sizes point to low abundance"	Ad hoc sightings	Van Waerebeek et al. (2017)
Benin	Single sighting of 27 reported.	Ad hoc sighting	Van Waerebeek et al. (2017)
Nigeria	Three sightings reported west of Lagos Harbor (2015—21), including one of ~20 individuals	Ad hoc sighting	Andrew Lynch, CCAHD website
Cameroon	Single sighting of 10 reported, "abundance may be very low"	Boat based survey	Ayissi et al. (2014)
Gabon	"low hundreds"	Boat based survey	Collins et al. (2013)
Congo	"low hundreds"	Shore based survey	Collins et al. (2013)
Angola	Ten individuals repeatedly sighted	Photo-ID & shore based survey	Weir (2009)

Table modified and updated from Collins (2015).

of 0.39 sightings per 100 km suggests low abundances (Ayissi et al., 2014). In Gabon, boat-based encounter rates of 0.15 sightings per 100 km were recorded in the Iguela region (2003–06), and 0.13 sightings per 100 km in the Gamba/Sette Cama region (2013–15) (Collins et al., 2010; Minton et al., 2017). Shore-based surveys in Congo were more productive (though are not comparable) and suggest that southern Gabon/Congo coasts harbor a total population in the high tens or low hundreds (Collins et al., 2017). The Angolan coast is largely unsurveyed, but work in Flamingos identified a small resident group of 10 individuals (Weir, 2009). Surveys on the Angolan side of the Congo River mouth (2007–09) failed to yield any sightings (Collins, unpubl.).

There are abundance estimates available for *S. plumbea* from at least seven countries (see Table 4.3) and they clearly demonstrate that humpback dolphins are not highly abundant anywhere in their range and often occur in low numbers and density in locations with suitable habitat. Jefferson and Rosenbaum (2014) stated that the available estimates for specific populations suggest that range-wide abundance is probably no higher than the low tens of thousands. The largest dataset, comprised of 13 different individual photo-ID catalogs, is from South Africa, where abundance in most individual areas was in the region of

TABLE 4.3 Summary of population abundance estimates produced for the Indian Ocean humpback dolphin.

Country	Location	Abundance estimate	Year of study	References
Iran	Mousa Bay	92 (95% CI 64–131)	2014–16	Hemami et al. (2018)
Iran	Dayer-Nakhiloo National Park	30 (95% CI 22–38)	2014–18	Mohsenian et al. (2022)
UAE	Abu Dhabi	701 (95% CI 473–845)	2014–15	López et al. (2018)
Kenya	Wasini/Shimoni	104 (95% CI 67–160)	2006	Meyler et al. (2011)
Tanzania	Menai Bay, Unguja	63 (95% CI 57–95)	1999–2002	Stensland et al. (2006)
Tanzania	Menai Bay, Unguja	19 (95% CI 14–25)	2015	Sharpe and Berggren (2019)
Mozambique	Maputo Bay	105 (95% CI 30–151)	1995–97	Guissamulo and Cockroft (2004)
South Africa	Richard's Bay	170 (95% CI 112–230)	1998–2000	Atkins and Atkins (2002)
South Africa	Richard's Bay	203 (95% CI 185–221)	1998–2005	Johnson (2012)
South Africa	Kwa-Zulu Natal	165 (95% CI 134–229)	1991–92	Durham (1994)
South Africa	Algoa Bay	466 (95% CI 447–485)	1991–94	Karczmarski (1999)
South Africa	Plettenberg Bay	112 (95% CI 75–133)	2002–04	Jobson (2006)
South Africa	Plettenberg Bay	42 (95% CI 42–55)	2012–13	Greenwood (2013)
South Africa	Mossel Bay	125 (95% CI 112–140)	2011–13	James et al. (2015)
India	Sindhudurg coast	721 (95% CI: 693–750)	2014–16	Jog et al. (unpublished)
India	Goa	565 (95% CI: 424–755)	December 2023	I. Samad, pers. comm.

100–200 individuals, and a meta-analysis suggested national abundance was likely to be well below 1000 individuals and possibly closer to 500 (Vermeulen et al., 2018).

In the early 2000s this species was among the most commonly recorded cetaceans in Oman and much of the Arabian Gulf, with reportedly large group sizes of frequently more than 40 individuals and occasionally up to 100 or more (Baldwin et al., 2004). The largest estimate of abundance is from the waters of Abu Dhabi, where open population models were used and 701 (95% CI: 473–845) individuals were estimated. It was concluded that while humpback dolphins occur frequently within Abu Dhabi near-shore waters, the animals appear to have a much larger home range (López et al., 2018). In Maharashtra State, India, surveys on the Sindhudurg coast between 2014 and 2016 provide a preliminary estimate of 721 individuals (95% CI: 693–750) using open population models (Jog et al., unpubl.). The study focused on a 120 km segment of the ∼1400 km west coast of India and had low resighting rates, but many new individuals. Estimated population size in Goa from line transect surveys conducted in December 2023 is approximately 565 individuals (95% CI: 424–755) (I. Samad, unpubl.). This underscores the need for long-term studies to ensure accurate abundance estimates and understand trends.

In places where suitable trend data are available there are indications of significant declines in abundance, relative sighting rate and/or group size (Braulik et al., 2023). In South Africa, in Algoa Bay over a 16-year period, the mean humpback dolphin group size halved (Bouveroux et al., 2018; Karczmarski et al., 1999; Koper et al., 2016), and in Plettenberg Bay, abundance was estimated to have declined from 93 (95% CI 72–114) to 41 (95% CI 28–54) between 2002 and 2013 (Greenwood, 2013; Jobson, 2006). Between the early 1990s and 2012, the number of identified individuals in Algoa Bay, South Africa, decreased from 70 to 50. The number of sightings per kilometer surveyed also decreased substantially from 0.018 sightings/km in 2008 to 0.004 in 2011; the number of animals per kilometer also decreased from 0.042 to 0.009 (Bouveroux et al., 2018; Melly et al., 2018).

Sighting rates of humpback dolphins off Anakao, in the southwest region of Madagascar declined between 2004 and 2013, along with a decrease in mean group size, observations linked to hunting, by-catch, and habitat degradation (Cerchio et al., 2015). Similarly, in the waters of Menai Bay off the coast of Zanzibar, humpback dolphins were encountered 56 times between 1999 and 2001 and abundance was estimated as 63 (log-normal 95% CI 57–95; Stensland et al., 2006). Data collected 13 years later (2015) showed that the population had declined to 19 (95% CI 14–25), a 63% reduction in abundance in less than one generation (Sharpe & Berggren, 2019).

Growth and reproduction

Life history data for *S. teuszii* are almost entirely absent due to the rarity with which carcasses can be studied by trained personnel, and a general lack of capacity for their study within range states. Their life history is probably like that of the *S. plumbea*, their closest congener. Scattered information on reproduction is provided by a few authors. Births in the Saloum Delta were thought to occur in March and April, given observations of juveniles

(Maigret, 1980a), a pattern also suggested for Guinea Bissau (Van Waerebeek et al., 2004, citing Krömer et al., 1994). Weir (2009) notes that an *S. teuszii* calf was born off Flamingos, Angola, in late April/or May, corresponding with the calving period suggested by Maigret (1980a). Lengths at birth may be similar to those reported for *S. plumbea* (e.g., Van Waerebeek et al., 2004; Plön et al., 2015). In Congo, a lactating female caught in a gillnet during May (2013) measured 2.50 m (Collins, 2015). Taylor et al. (2007) estimated a generation length of 18.4 years for *S. teuszii*, although Moore (2015) provided a figure closer to 25 years for *S. chinensis* and *S. plumbea*. The data required to estimate generation length and other *S. teuszii* vital rates remain unavailable.

Life history data for *S. plumbea* are more available, due in large part to an abundance of carcasses of animals caught in BPNs in KwaZulu-Natal (KZN), South Africa, between 1970 and 2017. Studies of the age, growth, and reproduction of 118 *S. plumbea* from South African waters between 1980 and 1998 indicated a longevity of at least 46 years for both males and females, distinct sexual dimorphism (males larger), and an asymptotic length and weight of 269 cm and 262 kg for males, 242 cm and 164 kg for females, respectively (Cockcroft, 2002). Assuming one growth-layer-group (GLG) to be equal to 1 year, females became sexually mature at 10 years, males 2–3 years later. The ovulation rate was calculated as 0.3 per year, indicating a 3-year calving interval. Gestation was indicated to last 1 year (as estimated from the relative mass of neonates and females), with size at birth being 115 cm and 14 kg (calculated from a von Bertalanffy growth curve and from two calves with unhealed umbilici); nursing occurred up to 2 GLGs, deduced from the presence of milk in the stomachs of calves for which the age was estimated, and by comparison with *T. aduncus* data (Cockcroft, 2002). However, a more recent study of 71 male and 38 female *S. plumbea* from the same population using samples collected between 1972 and 2012 yielded a lower maximum age estimate of 24 GLGs for males and 17.7 for females and sexual maturity at 7.5 and 8 GLGs in males and females, respectively (Plön et al., 2015). Size at birth was estimated at 111.6 cm for males and 104.3 cm for females and an ovulation rate of 0.2/year lower than the previous one that was obtained, resulting in a calving interval of 5 years (Plön et al., 2015). These differences may be due to a difference in the interpretation of GLGs between observers or a predominance of young males being caught in the BPNs, resulting in an absence of older individuals in the sample (Plön et al., 2015).

Natural mortality

There is no information available on natural mortality in Atlantic humpback dolphins. Indian Ocean humpback dolphins occasionally show prominent scars on the dorsal fin and dorsal ridge, some of which may be linked to shark attacks (Cockcroft, 1991). Strandings in Eastern Cape waters were routinely recorded in the 1970s and 1980s but are absent since the 1990s; possible population declines and/or scavenging of carcasses by sharks may explain this pattern (Plön et al., 2016). We could identify no records of killer whale (*Orcinus orca*) predation on *S. teuszii* or *S. plumbea*, but occasional attacks are probable given evidence of predation on other coastal dolphins (Jefferson et al., 1991).

Parasites and pathology

Parasites and commensals

Examinations of 77 *S. plumbea* caught in BPNs off KwaZulu-Natal (KZN) from 1970–2017, and skulls of 6 animals stranded along the southern Cape coast in South Africa from 1963–2002 showed that *Crassicauda* spp. (Nematoda) variably affected one or more cranial bones (frontal, pterygoid, maxillary and sphenoid). Prevalence of infection was 13% with no significant difference found between the sexes. However, there was a significant difference in lesion prevalence by age, with immature animals 6.5 times more likely to be affected than adults. As severe osteolytic lesions are unlikely to heal without trace, infection is more likely to have a fatal outcome for immature dolphins, possibly because of incomplete bone development, lower immune competence in clearing parasites or an over-exuberant inflammatory response in concert with parasitic enzymatic erosion (van Bressem et al., 2020).

Disease

Information on disease in *S. teuszii* is nearly absent. However, various types of vertebral column anomalies (lordosis, kyphosis, and vertebral indents) were reported in several individual *S. teuszii* off the coast of Angola and Senegal, with lordosis and kyphosis occurring simultaneously in several individuals (Weir & Wang, 2016).

Necropsy and histopathology examinations of five *S. plumbea* incidentally caught in BPNs off the KwaZulu-Natal coast, South Africa, between 2010 and 2012 yielded first insights into the health of the species (Lane et al., 2014). Pneumonia was found in all specimens and serositis was found in 4 out of the 5 specimens examined; in addition, gastritis and enteritis were present in approximately half the specimens examined. However, no statistical association between thinner blubber and pathology could be demonstrated and all animals were at least in "fair nutritional condition". The first confirmed case of lobomycosis in South African dolphins was reported for one of the *S. plumbea* specimens (Lane et al., 2014).

Unusual rostrum conditions in *S. plumbea* off South Africa were examined using photographs collated from systematic boat surveys and opportunistic sightings between April 1998 and March 2021 in various regions along the coast (Frainer, Elwen, et al., 2023). Overall, 31 unique individuals were found with abnormal rostrum conditions, varying from slight misalignments to severe wounds and/or aberrant morphologies. In most cases, injuries were likely caused by natural events during the animal's life history, such as interactions with sharks and/or reef-associated hunting strategies. Mark–recapture data indicated that individuals had survived with these injuries for up to 10 years (Frainer, Elwen, et al., 2023).

Behavior

Social organization

Atlantic humpback dolphins typically occur in groups of 1–10 animals, although groups at the extremities of the species range in Western Sahara and Angola are typically smaller.

Groups can consist of individuals, pairs, or larger groups, with the largest recorded of over 40 in Senegal (Van Waerebeek et al., 2004) and Gabon (Collins et al., 2004). Larger groups may form as an aggregation of smaller groups during feeding opportunities (Van Waerebeek et al., 2004). Average group sizes vary across the range; those in West Africa and the western Gulf of Guinea range between 6.3–7.4 and those in the central and southern Gulf of Guinea range between 10.2–13.1 (Weir & Collins, 2015). In Angola, observed group sizes ranged from 1–8 animals, with a median of 2 (n = 71). Most sightings comprised single animals or pods of 6–8 animals. Median group sizes were significantly higher in winter (7) than summer (2) and were also significantly higher in groups containing calves (6.5) than in adult-only groups, which may be linked to optimizing care and defense against predators (Weir, 2009). It remains to be seen whether *S. teuszii* live in a fission/fusion society comparable to other species in the genus (e.g., Parra et al., 2011).

Indian Ocean humpback dolphins generally occur in small groups of less than 15 individuals. However, very large group sizes of more than 50 have been recorded off the coast of Pakistan and Oman (Baldwin et al., 2004; Kiani & Van Waerebeek, 2015; Pilleri & Pilleri, 1979) and groups of up to 120 individuals off the west coast of India (Sule et al., 2016). During surveys in Sonmiani Bay (Balochistan, Pakistan) between 2011 and 12, an exceptionally large group of 68 individuals was encountered (Kiani & Van Waerebeek, 2015). In Abu Dhabi, group size ranged from 1 to 24 individuals (mean 6.8 + 1.7) and the most frequently observed were aggregations of two dolphins (23% of the encounters), followed by solitary individuals (15%). Group composition showed that 73% of the observed humpback dolphins were adults; thus, the remaining 27% were categorized as immature and calves (López et al., 2018). In Dayer-Nakhiloo National Park in Iran, humpback dolphin group size ranged from 1 to 14 individuals (mean 5.8 ± SE 0.3; Mohsenian et al., 2022), and in Zanzibar group size ranged from 1 to 7 animals (median = 3; Sharpe & Berggren, 2019), showing a decline when compared with surveys conducted 13 years earlier (Stensland et al., 2006). In both Iran and Abu Dhabi in the Arabian/Persian Gulf, group size was positively correlated with the presence of dependent calves in the group (López et al., 2018; Mohsenian et al., 2022). Group sizes off the west coast of India vary widely (Sutaria et al., 2015). In Gujarat, the observed group sizes ranged from 1 to 11 individuals (mean 3.9) (Sutaria & Jefferson, 2004). In Maharashtra, particularly in the Mumbai Metropolitan region, 48 groups were sighted during line-transect surveys conducted (December 2023–March 2024) with group sizes ranging between 1 and 65 individuals (mean 6.3 ± 9.4). Juveniles and subadults were encountered in 29.5% and 41% of the sightings respectively; and in the morning hours (7:00 a.m.-12 p.m.), foraging was recorded as the predominant activity with 46% (n = 22) of the groups seen engaged in foraging behavior (Modi et al., 2024). In the Sindhudurg region, relatively higher group sizes were sighted (range 1–120 individuals, mean 15.5) (Jog et al., 2024; Sutaria et al., 2015). Of the 175 groups sighted in Sindhudurg, foraging behavior was observed in 29% of groups (n = 50), followed by traveling (21%, n = 37 groups), and socializing (18%, n = 32 groups) (Jog et al., 2024). Foraging (range 1–56, median 5), and socializing (range 2–45, median 8) had relatively higher group sizes (Jog et al., 2024). In Goa, the group sizes ranged from 1 to 35 individuals (mean 6.3) (Sutaria & Jefferson, 2004); with group sizes between 2 and 5 individuals being common (I. Samad, pers comm.). In the Ashtamudi, Kochi, and Munambam estuaries (all Kerala), group sizes were small, ranging from 1 to 8 individuals (mean 2;

Panicker et al., 2018). While, in the waters off Kochi, group sizes of up to 15 individuals were encountered (mean 2.78) (Sutaria et al., 2015).

In Algoa Bay, South Africa, the mean group size of *S. plumbea* decreased from six to three individuals over a 16-year period, linked to an increase in the occurrence of solitary individuals (from 15.4% to 36.3%); an associated change in the predominant behavior from foraging (previously 64%) to traveling (49%) was also observed (Koper et al., 2016). An exceptionally large group for the region was observed in June 2010 in Algoa Bay, where 23 individuals were recorded (Melly et al., 2018).

Interspecies associations

Given their coastal and shallow water habitat preference, the opportunities for Atlantic humpback dolphins to form mixed species groups with other cetaceans are generally limited. The common bottlenose dolphin *Tursiops truncatus* is often sympatric with Atlantic humpback dolphins (e.g., Collins, 2015; Leeney, Weir, et al., 2015; Minton et al., 2017; Van Waerebeek et al., 2016; Weir, 2009) but mixed groups of these two species appear to be relatively uncommon if not rare. Perhaps the most remarkable of these was reported from Mauritania (Busnel, 1973), where single humpback dolphins were twice observed among pods of bottlenose dolphins that were fishing cooperatively with Imraguen fishermen for mullet. Elsewhere, Beaubrun (1990) reports on a sighting of a group of 3 humpback and 2 bottlenose dolphins in Dakhla Bay. An apparently lone Atlantic humpback dolphin persists in Dakhla Bay, where it is often seen in close association with bottlenose dolphins (Moores, 2018). A mixed group of 10 humpback dolphins and 5 bottlenose dolphins was recorded in the Rio Geba in Guinea Bissau by Wolff (1998). Collins et al. (2013) report that among 419 shore-based cetacean sightings recorded in Conkouati-Douli National Park, 230 sightings were of humpback dolphins; 16 (6.9%) of these comprised mixed humpback dolphin and bottlenose groups. Weir (2009) noted that among 71 sightings of humpback dolphins off Flamingos, Angola, only one mixed group was recorded, comprising a single humpback dolphin accompanied by three bottlenose dolphins.

Indian Ocean humpback dolphins are frequently observed in mixed species groups with Indo-Pacific bottlenose dolphins (Fig. 4.4d). Koper and Plön (2016) report on 7 interspecific associations involving *S. plumbea* in Algoa Bay, South Africa. The majority (6 events) were composed of *S. plumbea*-*T. aduncus* associations, with the animals mainly foraging and traveling together. The group sizes of these associations ranged from a total of five to 182 animals during the interactions and *S. plumbea* was primarily observed on the outskirts of bottlenose dolphin groups. One interaction was observed between a southern right whale (*Eubalaena australis*) mother-calf pair and two adult *S. plumbea*, where the animals were seen traveling around the bay together for a protracted period of time (Koper & Plön, 2016).

Locomotion and diving

Humpback dolphins surface in a very characteristic way, pushing the rostrum or occasionally the whole head clear of the water before rolling over tightly, exposing the hump and sometimes the flukes before diving (Best, 2007; Ross et al., 1994). There is very little published

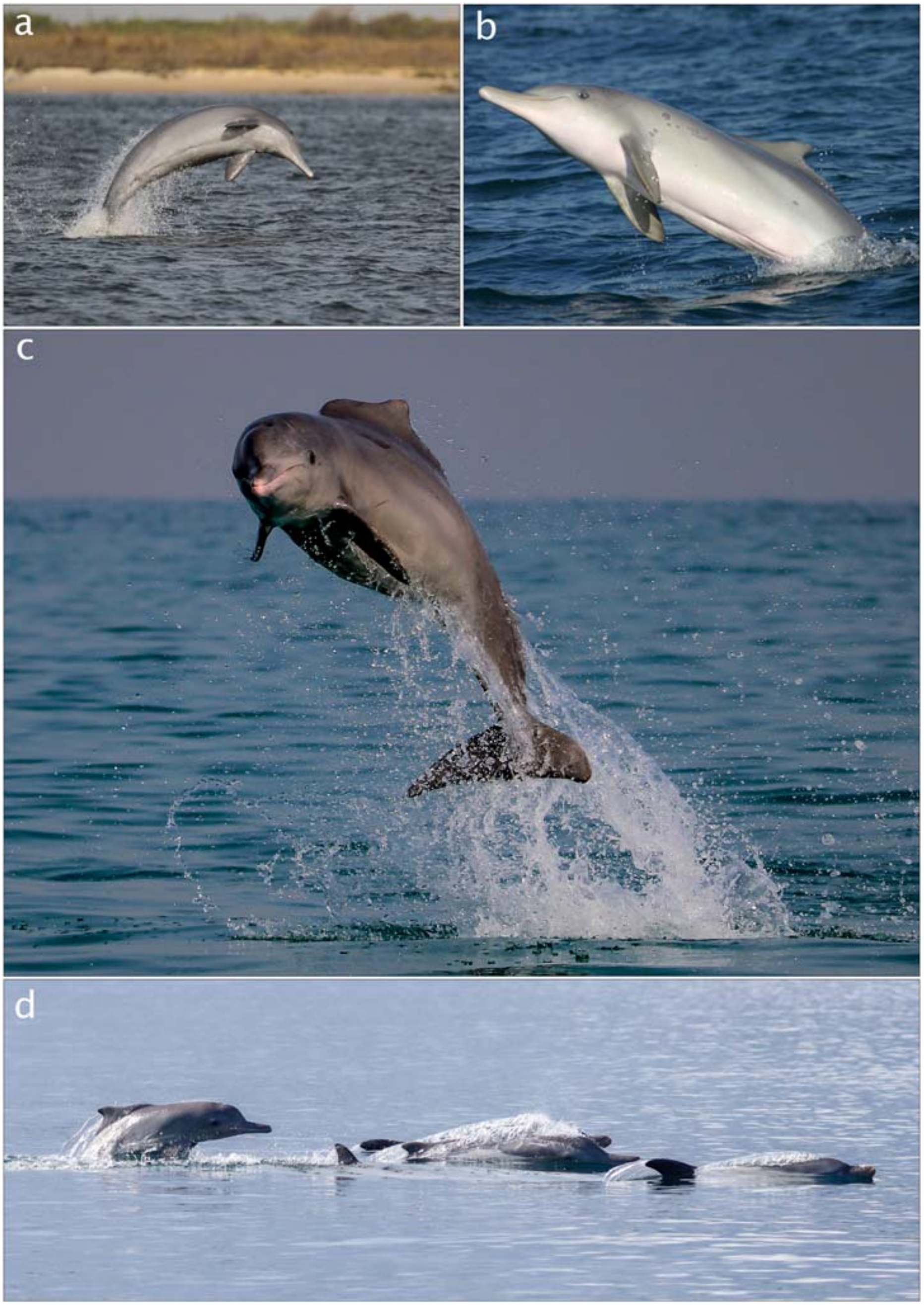

FIG. 4.4 Aerial behavior of Atlantic (*Sousa teuszii*) and Indian Ocean (*Sousa plumbea*) humpback dolphins. (A): An Atlantic humpback dolphin breaching in the Saloum delta (image G. Minton). (B): a curious *S. plumbea* breaching in South Africa (image S. Atkins). (C): A full body breach by an adult *S. plumbea* in the waters of Abu Dhabi, UAE (image R. Pentti). (D): Porpoising is generally rare, and humpback dolphins rarely bowride, but is seen when animals are swimming at speed. Here a young *S. plumbea* porpoises while swimming in a mixed species group with Indo-Pacific bottlenose dolphins (*Tursiops aduncus;* image M. Mwango'mbe).

information on swimming and diving in *S. teuszii*. Foraging on demersal species has been reported several times to commence with the tail up before sounding followed by dives of longer duration by Weir (2009, 2015, 2016). In Guinea tail-up dives were observed more frequently in the relatively deeper waters of the outer Rio Nuñez (Kakandé) estuary than at Taïdi, as was breaching (Weir, 2015). In the Saloum Delta tail-up dives associated with foraging were observed during 16 (53.3%) of 30 encounters.

There is relatively little information on swimming and diving in *S. plumbea*. Saayman and Tayler (1979) recorded four categories of activities-moving, feeding, social activities and resting-accounting for 49%, 27%, 15% and 8% of total observation time, respectively, in Plettenberg Bay, South Africa. Indian Ocean humpback dolphins typically swim slowly (ca. 4.8 km/h), surfacing briefly at intervals of 40–60 s (Saayman & Tayler, 1979; Zbinden et al., 1977). Pilleri and Gihr (1972) recorded longer dives averaging 5 min, apparently in response to their boat (from Ross et al., 1994).

Food and feeding

Kükenthal initially suggested that *S. teuszii* might be riparian, and vegetarian, given a mix-up of the holotype specimen with the remnants of a manatee that were also collected by Tëusz (Kükenthal, 1891, 1892; Van Waerebeek et al., 2004). This idea was reinforced by the Belgian zoologist Pierre Joseph Van Beneden (1892) and persisted until necropsies in the 1950s showed they were piscivorous and marine (Cadenat, 1956; Cadenat & Paraiso, 1957).

Published accounts of the feeding and food habits of Atlantic humpback dolphins collectively provide a picture of a distinct preference for inshore coastal, estuarine, and reef-associated fish (some of which are characteristically vocal). They have been reported to feed on mullet (*Mugil cephalus, Liza aurata*) in several locations, including among common bottlenose dolphins that were fishing cooperatively with Imraguen fishermen (Busnel, 1973). They were reported to chase mullet in the channels between the Tidra and Nair islets, Banc D'Arguin (Duguy, 1976), (with occasional breaching) in the Saloum Delta (Weir, 2016) and in Angola were seen to feed primarily on South African mullet (*Liza richardsonii*), as well as Atlantic bonito (*Sarda sarda*) and sardines (*Sardinella* spp.; Weir, 2009). A compiled list of identified food species is provided in Table 4.4.

Foraging by Atlantic humpback dolphins has been associated with tides by several authors, with daily movements into channels of the Banc D'Arguin and Saloum Delta linked to higher tides (Duguy, 1976; Maigret, 1980a). Conversely, in the Bijagós Archipelago, observations of humpback dolphins mostly occurred during low tides, foraging when fish were concentrated in "gullies and creeks" (Spaans, 1990; Weir, 2009). Foraging at river confluences has been observed within the Rio Grande de Buba (Van Waerebeek et al., 2000). In the Saloum Delta, preferential feeding areas include Djinack Creek, Bandiala, and Sangomar Point (Van Waerebeek et al., 2004). Humpback dolphins observed in the shallow waters west of the Île de Taïdi (Guinea) spent relatively more time foraging than those in the deeper waters of the outer Río Nuñez estuary (Weir, 2015). In Angola, humpback dolphins spent approximately half of their daylight time engaged in travel and foraging; dolphins were observed performing long dives (>1 min) over extended periods (hours) in presumed pursuit of demersal fishes and benthic prey, foraging preferentially around rocks and reefs, as well as at the mouths of rivers (Weir, 2009). Tail-up behaviors consistent with dives on demersal prey were also observed in deeper waters of the Rio Nuñez estuary (Weir, 2015).

Some foraging groups appear to be widely dispersed, including groups observed foraging in the Saloum Delta in Senegal (Maigret, 1980a; Van Waerebeek et al., 2004) and Petit Loango in Gabon (Collins et al., 2004). The formation of larger groups (which may be temporary aggregations of smaller groups) has also been linked to feeding opportunities in the same areas (Collins et al., 2004; Maigret, 1980a; Van Waerebeek et al., 2004).

Indian Ocean humpback dolphins appear to feed predominantly on reef-associated, estuarine, and demersal fish (Barros & Cockcroft, 1991; Ross et al., 1994; Saayman & Tayler, 1973). Studies by Saayman et al. (1972) showed that South African *S. plumbea* foraged over reefs in turbid waters along rocky coastlines within 250 m of shore. Records of demersal inshore fish species in the stomach contents of South African *S. plumbea* are consistent with their use of inshore estuaries, river mouths and enclosed bays (Barros & Cockcroft, 1991; Karczmarski, 1997). However, there is very little information on diet from anywhere other than South Africa for this species. Glass-nosed anchovies (*Thryssa vitrirostris*) appear to make up the largest percentage of the total prey species consumed by South African *S. plumbea*, followed by ribbon fish (*Trichiurus lepturus*), olive grunter (*Pomadasys olivaceum*) and longtooth kob (*Otolithes ruber*; Cockcroft & Ross, 1983; Venter, 2009).

In India, humpback dolphins appear to feed mainly on fish of the mullet family (*Liza macrolepis, L. parsia, Mugil cephalus, Valamugil* spp.) in estuaries (Bijukumar & Smrithy, 2012; Sutaria et al., 2015). Off the west coast of India, particularly in Sindhudurg, Local Ecological Knowledge indicates that these dolphins primarily feed on *Sardinella* spp., mackerel, and mullet (Jog et al., 2018). Humpback dolphins in estuaries, particularly Ashtamudi, predominantly feed on mullet species (*Liza macrolepis*, *L. parsia*, *Mugil cephalus*, *Valamugil* spp.), emphasizing the estuaries' significance as feeding grounds (Bijukumar & Smrithy, 2012; Panicker et al., 2018). Notably, in Ashtamudi, dolphins engage in milling activities to a greater extent than in Munambam and Kochi, indicating the estuary serves purposes beyond feeding. Furthermore, a notable presence of calves/juveniles in Ashtamudi and Sakthikulangara Bay suggests a potential role as a nursing ground (Panicker et al., 2018). In Vengurla, along the Sindhudurg coast of Maharashtra, humpback dolphins are also observed to associate with trawl vessels in harbors, possibly feeding on discards brought in at the end of the day (Jog, unpubl.).

Both *S. teuszii* and *S. plumbea* have been reported to use a variety of barriers, including sandbanks, the shore and fishing nets, against which fish can be herded and captured. *S. teuszii* at Flamingos (Angola) were observed to cooperatively herd/drive South African mullet (*Liza richardsonii*) into the surf using the coast to trap prey (Weir, 2009). *S. plumbea* at Ilha Magaruque (Bazaruto, Mozambique) have been reported to hunt bonefish (*Albula vulpes*) at low tide by either trapping individual fish against sandbanks or by charging at fish schools in order to strand them using the wave of water generated by the dolphin beaching itself; the dolphins reach for stranded fish before sliding back into the water (Peddemors & Thompson, 1994; N. Perrins, pers. comm.; Fig. 4.2g). This behavior appears similar to that reported for *S. sahulensis* (Whiting, 2011). In the Ashtamudi estuary in Kerala, along the southwest coast of India, humpback dolphins have been documented to herd prey, mainly mullet (*Mugil* spp.) against or toward cast-nets (Bijukumar & Smrithy, 2012).

There is some evidence of differences in the use of space and resource partitioning in both *S. teuszii* and *S. plumbea* that is likely linked to foraging and prey preferences. In a comprehensive review of records of humpback dolphins and common bottlenose dolphins in Guinea Bissau, Leeney, Weir, et al. (2015) found that whilst *S. teuszii* and *T. truncatus* were generally sympatric in their distributions, there were statistically significant differences in the distance from shore of sightings of *S. teuszii* (n = 91; mean = 1.75 km) and those of *T. truncatus* (n = 119; mean = 4.74 km), indicating subtle differences in their use of space, although it remains unclear if this is reflected in their respective diets. In South Africa, there is evidence for resource partitioning among coastal delphinids, including *S. plumbea*; an assessment of stable isotope values in skin samples collected from humpback and bottlenose dolphins indicated that the two species selected different prey, or different proportions of the same prey, despite feeding in the same areas (Browning et al., 2014).

TABLE 4.4 Atlantic humpback dolphin prey species compiled from written sources and unpublished strandings data.

Family	Genus	Species	Common name	Locality	Source	Source(s)
Haemulidae	*Pomadasys*	*jubelini*	Sompat Grunt	Joal, M'bour (Senegal)	Bycatch	Cadenat and Paraiso (1957)
Clupeidae	*Ethmalosa*	*fimbriata*	Bongo Shad	Joal, M'bour (Senegal)	Bycatch	Cadenat (1959)
Mugilidae	*Mugil*	sp.	Mullet	Joal, M'bour (Senegal)	Bycatch, Observations	Cadenat (1959) and Weir, 2016
Lutjanidae	*Lutjanus*	*goreensis*	Gorean Snapper	Ilha Canhabaque (Guinea Bissau)	Bycatch	Sequeira and Reiner (1992)
Lethrinidae	*Lethrinus*	*atlanticus*	Atlantic Emperor	Ilha Canhabaque (Guinea Bissau)	Bycatch	Sequeira and Reiner (1992)
Ephippidae	*Chaetodipterus*	*lippei*	West African Spadefish	Ilha Canhabaque (Guinea Bissau)	Bycatch	Sequeira and Reiner (1992)
Sciaenidae	*Pseudotolithus*	*typus*	Longneck croaker	Conkouati (Congo)	Bycatch	Collins, unpubl.
Sciaenidae	*Pseudotolithus*	*senegalensis*	Cassava croaker	Conkouati (Congo)	Bycatch	Collins, unpubl.
Paralichthyidae	Bothidae	sp.	Flounder	Conkouati (Congo)	Bycatch	Collins, unpubl.
Paralichthyidae	*Pseudorhombus*	sp.	Flounder	Conkouati (Congo)	Bycatch	Collins, unpubl.
Haemulidae	*Pomadasys*	sp.	Unidentified grunt	Conkouati (Congo)	Bycatch	Collins, unpubl.

TABLE 4.4 Atlantic humpback dolphin prey species compiled from written sources and unpublished strandings data.—cont'd

Family	Genus	Species	Common name	Locality	Source	Source(s)
Polynemidae	*Pentanemus*	*quinquarius*	Royal Threadfin	Conkouati (Congo)	Bycatch	Collins, unpubl.
Squillidae	*Squilla*	*mantis*	Mantis shrimp	Conkouati (Congo)	Bycatch	Collins, unpubl.
Mugilidae	*Mugil*	*cephalas*	Flathead gray mullet	Nouamghar (Mauritania)	Observation	Busnel (1973)
Mugilidae	*Liza*	*aurata*	Golden gray mullet	Nouamghar (Mauritania)	Observation	Busnel (1973)
Mugilidae	*Liza*	*richardsonii*	South African mullet	Flamingos (Angola)	Observation	Weir (2009)
Scombridae	*Sarda*	*sarda*	Atlantic bonito	Flamingos (Angola)	Observation	Weir (2009)
Clupeidae	*Sardinella*	sp.	Sardine	Flamingos (Angola)	Observation	Weir (2009)

Adapted from Collins (2015).

Reproductive behavior

The socio-sexual behavior (including mating) of *S. teuszii* is essentially unknown, but is presumably not dissimilar to the behavior of other species in the genus. Larger wintertime group sizes observed in Angola may have been related to increased mating opportunities (Weir, 2009).

The examination of indicators of reproductive seasonality in female (follicle formation, corpus index and births) and male (seminiferous tubule diameter, presence/absence of sperm and testis mass) *S. plumbea* yielded no clear indication of a seasonal cycle in South African waters (Plön et al., 2015). A low combined relative testis weight, in combination with a small group size and clear sexual dimorphism, suggested a monogamous or extreme polygamous (harem) mating system (Plön & Bernard, 2007; Plön et al., 2012).

Acoustic behavior

The whistles produced by *S. teuszii* were described by Weir (2010a, 2010b) based on recordings made during dedicated surveys in the Flamingos region of Namibe Province, Angola. The majority of whistles recorded were made when groups were actively foraging, with fewer recorded when groups were traveling. The whistles were generally simple in structure, with 85% having a single inflection point. The fundamental frequency was generally low (MinF = 4.8 kHz, MaxF = 8.2 kHz), the frequency range of individual whistles was low (mean of 3.4 kHz) and at least one harmonic was present in 92% of whistles. The maximum harmonic frequency extended beyond the 44 kHz analysis bandwidth in 14% of recorded whistles.

Two static acoustic monitoring devices (CPOD, Chelonia Ltd., UK) were deployed in Sindhudurg (mean depth 11 m) for a period of 21 days (February 2015) to record dolphin echolocation activity. *S. plumbea* utilizes a broadband frequency range for echolocation (20−160 kHz) and during the 21-day deployment period, a preliminary diel pattern in echolocation activity was observed. This pattern indicated high *S. plumbea* activity (maximum echolocation clicks logged) between 23:00−06:00 h, with a decline until 11:00 h followed by increasing activity (Sule et al., 2016).

The vocalizations of *S. plumbea* were recorded in Puttalam Lagoon (Sri Lanka), and the spectra of broad band click pulses ranged from 8 to >48 kHz, with the highest intensity around 38 kHz. Narrow band, frequency modulated whistles ranged between 5.5 and 17 kHz. Low frequency, narrow band grunt vocalizations were identified between 0.4−2.5 kHz, with their highest intensity around 1 kHz (Jayathilaka & Arulananthan, 2019). In Sindhudurg, Maharashtra, India, *S. plumbea* whistles spanned a wide frequency range between 2.3 and 33.0 kHz, with durations ranging from 0.01 to 1.60 s (Bopardikar et al., 2018).

The use of passive acoustic monitoring for both *S. plumbea* and *S. teuszii* has been challenging, because of the difficulty of correctly identifying the acoustic signals to species with confidence (Yang et al., 2020). In analysis of recordings from Zanzibar, *S. plumbea* clicks had significantly higher peak, centroid, lower −3 and lower −10 dB frequencies compared to sympatric *T. aduncus*, whereas duration and bandwidth parameters were similar for the two species. Random Forest classifiers were applied to determine parameters that could be used to classify the two species from echolocation clicks and achieved 28.6% and 90.2% correct species classification rates for *S. plumbea* and *T. aduncus*, respectively (Yang et al., 2020). Recent developments include the use of Convolutional Neural Networks (CNNs) to differentiate humpback signals in acoustic data, which resulted in the best identification model that correctly identified *S. plumbea* (96.9%), *T. aduncus* (100%), and *D. delphis* (78%) encounters in the testing dataset (Frainer, Dufourq, et al., 2023).

Live maintenance

Very few humpback dolphins have been kept in captivity. Three *S. plumbea* were captured on the January 18, 1963 in Algoa Bay, South Africa, and were kept at the Port Elizabeth Museum/Oceanarium complex (Rowe, 1968); they were named Apple, Sammy and Naidoo. The latter had a jaw deformity, which was thought to be a result of a previous break and seemed to have healed; they nicknamed it "Crossjaw". Sammy died after about a month in captivity, and shortly afterward, within a day or two of one another, the health of Apple and Naidoo also declined and they died. The staff were unable to determine the cause of death of the animals, but it may have been due to their diet of frozen fish (Rowe, 1968). Three *S. plumbea* were kept for a year at a captive facility called "The Dolphin Resort" in Bahrain before being released back into the Gulf in 2023 following a police investigation into the circumstances of their capture (B. Sharp, pers. comm.).

Human impacts

Direct hunting

The use of wild animals by people as a protein source is common within the range of *S. teuszii*. Commonly referred to as "marine bushmeat" or "marine wildmeat", the practice of consuming cetaceans is likely traditional in many areas and provides an important source of nutrition, income, and cultural identity, though it is now a concern for some threatened species, including *S. teuszii* (Ingram et al., 2022; Leeney, Dia, & Dia, 2015; Robards & Reeves, 2011; Weir & Pierce, 2013). There are a few accounts of the deliberate capture of *S. teuszii* (e.g., Cadenat, 1949, 1956, 1959; Duguy, 1976; Maigret, 1980a; Van Waerebeek et al., 2004), but they likely occur more often than reported (Collins et al., 2017; Van Waerebeek et al., 2000, 2017; Van Waerebeek & Perrin, 2007). Given legal prohibitions, captures, both incidental and directed, may be concealed in many areas, hindering the collection of reliable data from interview surveys (Leeney, Dia, & Dia, 2015; Moore et al., 2010; Reeves et al., 2003; Van Waerebeek et al., 2004). The opportunistic use of by-catch, often driven by poverty, may also develop into "directed entanglement" (Clapham & Van Waerebeek, 2007; Weir & Pierce, 2013) or "non-target-deliberate acquisition" (Robards & Reeves, 2011). The scale of this practice is unknown but appears to be part of a developing global trend in the utilization of marine wildmeat and reflective of general fisheries declines (e.g., Alfaro-Shigueto & Van Waerebeek, 2001; Brashares et al., 2004; Clapham & Van Waerebeek, 2007; Ingram et al., 2022; Leeney, Dia, & Dia, 2015; Robards & Reeves, 2011; Uwagbae & Van Waerebeek, 2010; Van Waerebeek et al., 2004; Weir & Pierce, 2013). Dolphin meat is sold for use as shark bait in some fisheries, although it remains unknown if *S. teuszii* is utilized (Debrah et al., 2010; Van Waerebeek et al., 2004; Weir & Pierce, 2013).

Perhaps due to their small group size and cryptic nature, *S. plumbea* are not known to be the target of ongoing direct hunts anywhere other than Madagascar. In southwest Madagascar, dolphins were historically taken with harpoons, but are now targeted with gillnets or in a drive hunt. A minimum of 61 *S. plumbea* catches was estimated between 1985 and 1999 in Anakao, including drive hunts (Andrianarivelo, 2001). Given the relatively small population sizes reported throughout the region, the reported mortality rate due to hunting is likely unsustainable and contributing to local population declines (Cerchio et al., 2015). In other countries, *S. plumbea* by-catch may be eaten or used as bait, but they do not appear to be commonly targeted. Dolphin hunting occurred historically in Menai Bay (Zanzibar), with the last hunt reported in 1996, with the take of *S. plumbea* presumed (Braulik et al., 2015). They were also formerly hunted in the Persian Gulf (Baldwin et al., 2004) and in Maputo Bay, Mozambique (Guissamulo, 2008).

Indirect killing/by-catch

Range-wide, incidental mortality in fishing gear is perhaps the greatest conservation threat to both Atlantic humpback dolphins and Indian Ocean humpback dolphins. These catches, which include incidental captures in BPNs in South Africa, are considered primarily responsible for range-wide declines in abundance for both species. The available data likely represent a fraction of the true scale and there are few, if any, places that offer refuge from this pervasive and seemingly "intractable threat" (e.g., Ayissi et al., 2014; Braulik et al., 2015; Brownell et al., 2019; Clapham & Van Waerebeek, 2007; Collins, 2015; Collins et al., 2013; Debrah et al., 2010; Van Waerebeek et al., 2004; Van Waerebeek & Perrin, 2007; Weir et al., 2011; Weir & Pierce, 2013).

The by-catch of *S. teuszii* in artisanal gillnets has been a tragic backstory to the study of the species, with 4 of the 5 first records being associated with fisheries catches, and these often represent the first verified record for some range states (Senegal, Guinea, Nigeria, Congo). By-catch has been reported across the range, including Western Sahara (Notarbartolo di Sciara et al., 1998), Mauritania (Van Waerebeek et al., 2004), Senegal (Cadenat, 1947, 1949, 1956, 1959; Cadenat & Paraiso, 1957; Fraser, 1949; Maigret, 1980a; van Bree & Duguy, 1965; Van Waerebeek et al., 2004), Gambia (Murphy et al., 1997; Van Waerebeek et al., 2004), Guinea (Bamy et al., 2010; Van Waerebeek et al., 2017; Weir, 2015), Guinea-Bissau (Leeney, Dia, & Dia, 2015; Sequeira & Reiner, 1992), Togo (Van Waerebeek et al., 2017), Nigeria (Van Waerebeek et al., 2017), Cameroon (Ayissi et al., 2014), and the Republic of Congo (Collins, 2015). By-catch risk is likely substantial in some areas, but monitoring is generally very limited (e.g., Debrah et al., 2010; Moore et al., 2010). Work in Congo identified 19 dolphins by-caught across 14 landing sites on a 60 km stretch of beach during 5 years of work (Fig. 4.5). Of these, 10 were *S. teuszii*, and all were caught in gillnets less than 1 km from shore. These by-catches were often lamented by fishers given the associated damage to nets; sales of dolphin meat only partially offset repair costs (Collins et al., 2013). Carcasses are often utilised for food, a practice that has increased in many areas (Ayissi et al., 2014; Bamy et al., 2010; Clapham & Van Waerebeek, 2007; Collins, 2015; Leeney, Dia, & Dia, 2015; Lewison & Moore, 2012; Van Waerebeek et al., 2004, 2017; Weir & Pierce, 2013).

By-catch in gillnets is also a well described concern for *S. plumbea* and significant mortality in gillnets has been reported from most range countries (Atkins et al., 2016; Braulik et al., 2023; IWC, 2002). The best studied by-catch is from South Africa, where 203 *S. plumbea* were captured in BPNs between 1980–2009, amounting to 6.8/per year and 5%–10% of the population per annum (Atkins et al., 2013; Durham, 1994; Keith et al., 2002; Fig. 4.5). In Mozambique, intense coastal fishing effort using gillnets and trawls was considered the main threat to this species across the country (Guissamulo, 2008). By-catch has been documented in Zanzibar (Amir et al., 2002) and although there are no estimates of how many animals were caught, they likely exceed sustainable rates (Stensland et al., 2006). There is some evidence of interaction with fishing gear for humpback dolphins in neighboring Pemba, with 11 of 27 photo-identified humpback dolphins showing clear injuries from previous entanglements in nets (Braulik et al., 2015). In Oman, high incidences of stranded *S. plumbea* were presumed linked to fisheries interactions (Collins et al., 2002). Fisheries takes (both incidental and deliberate) are considered unsustainable in Madagascar (Cerchio et al., 2015).

Necropsy reports and photographs of 18 by-caught *S. plumbea* examined between 2010 and 2017 indicated that only 22% (4 of 18), 2 of which were males (1 adult, 1 juvenile) and 2 were females (both adults) of the by-caught dolphins showed net marks on the skin (Roussouw et al., 2022b). Only a small percentage of by-caught animals presented external signs of entanglement and thus additional evidence, such as histopathological examinations, is required to reliably identify entanglement in stranded animals (Roussouw et al., 2022b).

FIG. 4.5 Some of the major threats to Atlantic (*Sousa teuszii*) and Indian Ocean (*Sousa plumbea*) humpback dolphins. (A): Bycatch is among the greatest threats for *S. teuszii*. Here a dolphin is landed by a fisher in Congo (T. Collins). In some areas of the range of *S. teuszii*, bycatches are butchered for food, a practice that may be increasing as fisheries decline (T. Collins). (C): A lone *S. teuszii* swims near to Kamsar port in the Rio Nunez estuary, Guinea. Ports are often constructed in favored habitats (T. Genov, MBZ/Mubadala). (D): Coastal habitats are increasingly modified in many areas, including the Persian/Arabian Gulf (UAE dolphin project). (E): Bather protection nets in South Africa have inadvertently killed many *S. plumbea* (D. Savides).

Off the west coast of India, in Maharashtra and Kerala, *S. plumbea* frequently feed in proximity to fishing gear, notably gillnets. While fishers note that accidental entanglement is infrequent, it can occur, causing economic losses due to gear damage and associated loss of catch (Jog et al., 2018; Sutaria et al., 2015). In Mumbai, of the total number of dolphin sightings (n = 48), 36% (n = 16) were in the presence of active fisheries. In Sindhudurg (Maharashtra), *S. plumbea* groups forage more frequently in the presence of fishing vessels than not, particularly when gillnet vessels are actively fishing. Overlaps are significant, with the presence of vessels being a stronger predictor of dolphin foraging activity than environmental parameters such as depth and distance from shore (Jog et al., 2024). The study identified eight high-risk areas within ~500 m of the coastline, of which three coincided with high-density dolphin habitat near estuaries. Gillnet fisheries are of particular concern as they overlap more frequently with humpback dolphin habitats than other fisheries (Jog et al., 2024). In Goa, dolphin presence also overlaps with fisheries, with dolphin individuals observed to forage close to fishing vessels (I. Samad, pers. comm.). Between 2014 and 2022, approximately 94 humpback dolphin carcasses were recorded in Maharashtra and Goa (Marine Mammal Research and Conservation Network of India [MMRCNI], www.marinemammals.in, accessed October 9, 2022). Of these, 19 showed signs of fishing gear interactions, such as garrote wounds or dorsal fin lacerations. Estimated *S. plumbea* mortality in Goa is ~19 animals per year, but might be at least 35% higher (I. Samad, pers. comm.). Necropsies in Goa from 2020 to 2021 documented the remnants of fishing gear or possibly ghost nets in the alimentary canal (MMRCNI; Jog et al., 2024).

Contaminants

Environmental pollution is likely a major threat to *S. teuszii* and *S. plumbea*. Their coastal niche is exposed to many anthropogenic contaminants, many originating from land, some of which can bioaccumulate through trophic transfer to high levels in top predators, likely causing a range of health issues in cetaceans, including immune and reproductive dysfunction, birth defects, and cancers (Gui et al., 2016; Aznar-Alemany et al., 2019).

There is no information on contaminants in *S. teuszii*. The preferred habitats of *S. teuszii* are, however, very likely to be exposed to terrestrial sources of pathogens and pollution (Scheren et al., 2002; Weir et al., 2011) and these are likely to increase as development within the range accelerates. Phosphorite mining in coastal Togo is known to contaminate inshore sediments with trace elements, including cadmium (Segniagbeto et al., 2014; Segniagbeto & Van Waerebeek, 2010). Marine and coastal oil and gas activities occur in many range states and may well present risks to the species, particularly from spills and chronic pollution (Collins et al., 2017; Weir & Pierce, 2013). For instance, the Niger Delta region has experienced severe oil pollution since 1958, with spillages estimated in millions of barrels (Amakama et al., 2021; Ukhurebor et al., 2021), and significant consequences for human health (e.g., UNEP, 2011), fisheries (e.g., Osuagwu & Olaifa, 2018) and the environment in general (see review in Ukhurebor et al., 2021). Another major concern that likely affects marine species is the practice of exporting industrial and contaminated wastes to West Africa by developed nations. This has included both contaminated wastes and so-called ‘e-wastes’. Very few ports have the facility to process these chemicals, and environmental and social concerns are many (e.g., Barry & Margai, 2011; Doyon, 2015; Lambrechts & Hector, 2016).

The exposure of *S. plumbea* to environmental contaminants is likely high (Jefferson & Karczmarski, 2001). Coastal urban centers and ports are likely associated with releases of agricultural runoff, as well as human and industrial waste and may be severe (Braulik et al., 2015; Gore et al., 2012). Very high levels of chemical pollution in creeks of the Indus delta cause fish kills, which likely affect inshore cetaceans (Kiani & Van Waerebeek, 2015). Ship scrapping yards in Pakistan release heavy metals, asbestos, dioxins, and other persistent organic pollutants into coastal waters (Braulik et al., 2015). Investigation of blubber samples from three *S. plumbea* by-caught off KwaZulu-Natal, South Africa, showed that the species was the most contaminated by total persistent organic pollutants (21100 ng/glw) among South African dolphins examined and among the highest levels reported in delphinids globally (Table 4.2; Gui et al., 2016). Dominant pollutants were dichlorodiphenyltrichloroethanes (DDTs) followed by polychlorinated biphenyls (PCBs; Gui et al., 2016). A later study revealed that PBDE (polybrominated diphenyl ethers, a type of flame-retardant) levels in five *S. plumbea* sampled from the same region (2012−15) were as high as in more industrialized areas (Table 4.3; Aznar-Alemany et al., 2019). In addition, organophosphorus flame-retardant levels were one or two orders of magnitude higher than PBDE levels (Aznar-Alemany et al., 2019).

Thirty-six major, minor and trace elements were analyzed in *S. plumbea* ($n = 36$; male: 24, female: 12) collected between 2007 and 2017 from KwaZulu-Natal, South Africa (Table 4.4; Plön et al., 2023). Sodium, Antimony, Strontium, and Zinc concentrations were significantly higher in *S. plumbea* compared to *T. aduncus*, and *S. plumbea* had the lowest concentrations for Cadmium, Iron, Selenium, Uranium and Vanadium. Mercury concentrations (maximum 29 mg/kg dry mass) were generally higher than those reported for coastal dolphin species found elsewhere (Plön et al., 2023).

Habitat loss and climate change

Both *S. teuszii* and *S. plumbea* have restricted nearshore distributions that render them particularly vulnerable to habitat loss and climate change (e.g., Davidson et al., 2012). In West Africa, habitats are often shared with some of the densest populations of humans on earth, many of whom rely on the exploitation of marine and coastal resources for their livelihoods (Weir & Pierce, 2013). Populations in coastal areas are set to double within 20−25 years, likely exacerbating current concerns (Ukwe & Ibe, 2010). The coastal zone is also where many industrial and agricultural activities occur (Weir & Pierce, 2013). Industrial projects, including port developments and mines, rarely consider either the direct effects on dolphins associated with their development, or the indirect effects associated with the expansion of communities and infrastructure that projects can entrain. This can be extended to the stepwise expansion of threats along shore; projects tend to consider their impacts in isolation, and frequently only consider the immediate footprint of a particular project, and not the net or cumulative effects of several projects within a particular area (Collins, 2015).

The destruction of inshore habitats is also likely to be one of the greatest threats to *S. plumbea*, including in the southern African region (Atkins et al., 2016; Plön et al., 2016), the Arabian/Persian Gulf and many other rapidly developing urban coastal areas (Baldwin et al., 2004; Karczmarski, 2000). Dredging, land reclamation, construction blasting, port and harbor construction, pollution, boat traffic, oil and gas exploration and development (including inshore seismic surveys), and other coastal development activities occur, or are concentrated within, humpback dolphin habitat and threaten their survival in ways that are challenging to quantify, but likely to be significant (IWC, 2002). Development of both large and small ports and the associated manufacturing and processing is expanding incredibly rapidly around the Indian Ocean rim, and the areas often selected for ports are estuaries and protected bays that are the preferred habitat of humpback dolphins (Sutaria et al., 2015). The continued presence of humpback dolphins in degraded habitats does not rule out that habitat degradation has had adverse behavioral or health effects (IWC, 2002; Piwetz et al., 2015). There are pervasive threats that are increasing throughout the range of this genus and which are unlikely to change in the foreseeable future. Collectively they will have devastating consequences.

Behavioral disturbance

The coastal distributions of both *S. teuszii* and *S. plumbea* leave them vulnerable to anthropogenic disturbance, especially when they occur in heavily populated and industrialized areas, many of which are rapidly expanding (Piwetz et al., 2015; Van Waerebeek et al., 2004; Weir & Pierce, 2013).

There is little direct evidence of behavioral disturbances to *S. teuszii.* The species has frequently been described as boat-shy or timid, including avoidance by dolphins of research boats, suggesting they are innately susceptible to disturbance (e.g., Notarbartolo di Sciara et al., 1998; Van Waerebeek et al., 2004; Weir, 2015). Anthropogenic noise is considered a threat to *S. chinensis* (e.g., Jefferson et al., 2009; Li et al., 2018) and it would be reasonable to presume similar concerns for other *Sousa* species. A particular concern within the range of *S. teuszii* (and *Sousa* species generally) is the relatively rapid development of ports and associated infrastructure within or close to preferred habitats. These may act as barriers to longshore movement and push animals into less favorable habitats (Ayissi et al., 2014; Collins et al., 2017; Weir & Pierce, 2013). The rapid expansion of kitesurfing in Dakhla Bay is considered a potential year-round threat, with many people surfing in optimal habitats for *S. teuszii,* leading to potential displacement (Moores, 2018). We could identify no tourism activities targeting *S. teuszii*, but whale and dolphin watching activities in many range-countries are expanding, and without appropriate guidance will likely cause disturbance.

In Algoa Bay, South Africa, *S. plumbea* appear to be highly susceptible to disturbance caused by vessel traffic, with evidence that dolphins avoid areas of highest vessel use (e.g., Karczmarski, 1997). Later work in Algoa Bay showed that groups of *S. plumbea* reacted negatively (changing direction, increased dive duration and group splits) toward a range of vessels, including high speed vessels, personal watercraft, surf skis, but also (surprisingly) to swimmers and surfers (Koper et al., 2016). Humpback dolphins in the waters of Mousa Bay (Iran) are considered at high risk of disturbance from industrial vessels using Mahshahr Port and Imam Khomeini Port, the busiest among Iranian ports. Humpback dolphins in the shallow waters of Puttalam Lagoon (Sri Lanka) are considered at risk from high-powered fishing and navy vessels (Bröker et al., 2008; Nanayakkara et al., 2014). In Tanzania and Sri Lanka, humpback dolphins are exposed to blast fishing, an activity that frequently occurs nearshore and often within humpback dolphin habitats (Braulik et al., 2017b; Bröker et al., 2008; Cagua et al., 2014; Nanayakkara et al., 2014).

Indian Ocean humpback dolphins are the focus of boat-based dolphin watching activities in several countries. The species is targeted by dolphin watchers across South Africa, with some evidence that the species' Endangered status makes seeing it more desirable. Although national whale watching regulations are inconsistently observed by operators, of greater concern are the activities of recreational boat operators who tend not to observe time, distance, or speed limits. The species preference for navigationally hazardous nearshore waters does provide some protection (M. Witteveen, pers. comm.). A poorly regulated swim-with-dolphins activity occurs year-round in both southwest Zanzibar and in Shimoni, Kenya. The target species in both instances are Indo-Pacific bottlenose dolphins, but Indian Ocean humpback dolphins also occur in the area and although rarer and shier, they are sometimes targeted (Mwango'mbe et al., 2021; Stensland et al., 2006). Dolphin watching that occasionally focuses on humpback dolphins occurs in the Musandam and Dhofar regions of Oman (see https://wwhandbook.iwc.int/en/).

The dolphin-watching industry in India has experienced significant growth since 2010, offering fishers an alternative source of income (Sutaria et al., 2015). Dolphin watching is widespread along the west coast of India, including, Goa, Karnataka, Maharashtra, and Kerala. In Sindhudurg, Maharashtra, dolphin tourism, parasailing, SCUBA diving and snorkeling operations have expanded drastically since 2014 (Sule et al., 2016). Most of these vessels and activities occur within dolphin habitat and have become important sources of alternative income, particularly among younger fishers (Jog et al., 2018). In Goa, dolphins were observed to often change their behavior and direction of movement in response to approaching tour boats, typically diving deeply, and traveling away from these vessels (Sanjeev et al., 2016). The influx of high-speed vessels poses numerous threats, including potential boat strikes, increased engine noise, and disturbances to critical habitat, although at present the consequences remain unclear (Sanjeev et al., 2016; Sule et al., 2016). The enthusiasm of young fishers for dolphin-watching tourism presents an opportunity to involve them in community-led conservation endeavors, such as collaborative responsible tourism initiatives, but the industry will need to be monitored for inclusivity, fair practices, and to ensure that potential threats to dolphin habitats are addressed (Sutaria et al., 2015).

Cumulative impacts

Atlantic and Indian humpback dolphins are threatened by a wide range of anthropogenic stressors, ranging from the broad and as-yet poorly understood consequences of climate change (e.g., Learmonth et al., 2006), competition for fisheries, by-catch, hunts, coastal development, underwater noise, and pollution in a variety of forms (Braulik et al., 2023; Collins et al., 2017; Weir et al., 2011). However, the cumulative effects of multiple threats remain unquantified and poorly recognized (Plön et al., 2021; Van Waerebeek et al., 2004; Weir et al., 2011).

The available evidence indicates that most populations of *S. teuszii* are small and that all have experienced significant declines in recent decades linked to a variety of known and possible threats (Collins et al., 2017; IWC, 2011). Gaps in the distribution of *S. teuszii* may be linked to a range of increasing anthropogenic pressures, raising the extinction risk for individual populations (Collins et al., 2017; Van Waerebeek & Perrin, 2007; Weir et al., 2011).

Declines in abundance of *S. plumbea* over recent decades in South Africa are likely linked to the cumulative impacts of widespread environmental degradation, but understanding the range, relative strength and interplay of threats that affect *S. plumbea* remains poorly understood, making it problematic to set clear priority actions (Plön et al., 2021). These species likely have a limited capacity for rapid population recovery, given long generation times and an apparently high susceptibility to disturbance. Conservation measures will need to be sustained over substantial time frames.

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Dr. Thomas A. Jefferson is the Founder of Clymene Enterprises, a scientific research, conservation, and environmental consulting firm providing services related to the field of marine mammal biology, conservation, and management. He is also an Independent Researcher at NOAA's Southwest Fisheries Science Center. Dr. Jefferson's main interests are the development of marine mammal identification aids, and the systematics and population ecology of the more poorly known species of dolphins and porpoises. His primary research focuses on the conservation biology of Indo-Pacific humpback dolphin (*Sousa chinensis*) and finless porpoise (*Neophocaena phocaenoides*) populations in Hong Kong and surrounding waters. In addition, he is involved in projects focused on the conservation of the critically endangered vaquita (*Phocoena sinus*) and on the taxonomy and population ecology of common dolphins (*Delphinus* spp.).

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