ORIGINAL RESEARCH

Who's the biggest fish in the pond? The story of bull sharks (*Carcharhinus leucas*) in an Australian golf course lake, with deliberations on this species' longevity in low salinity habitats

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ABSTRACT. This article addresses the history of a resident population of bull sharks (*Carcharhinus leucas*) in an isolated stagnant body of water in subtropical Australia. From 1996 to 2013, six bull sharks were landlocked in a golf course lake near Brisbane. The adjacent Logan and Albert rivers trapped sharks due to major floodings. When floodwaters receded, these sharks remained in the lake, which is normally isolated from the river's main channel. While this event was extensively reported in the media and recieved much public attention, it has not been investigated in depth, yet it provides an opportunity for insights into the tolerance of bull sharks to low salinity habitats and euryhalinity in this species. Currently, information on the extent of the bull shark's capability to endure low salinity conditions and its longevity in these environments is scarce. The case reported here provides information on the occurrence of bull sharks for 17 years, which represents the longest uninterrupted duration in a low salinity environment that ever has been recorded in this species. Bull sharks arrived first in the lake as juveniles but through time, they have reached maturity. This occurrence presents not just another ordinary bull shark record from a low salinity environment but instead a record of physiological and scientific importance. Therefore, details of the residency of *C. leucas* in an Australian golf course lake are reported here.

Key words: Australia, Carcharhinidae, elasmobranchs, euryhalinity, floods, low salinity habitats.

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¿Quién es el pez más grande del estanque? La historia de los tiburones toro (*Carcharhinus leucas*) en un lago de un campo de golf australiano, con consideraciones sobre la longevidad de esta especie en hábitats de baja salinidad

RESUMEN. Este artículo aborda la historia de una población residente de tiburones toro (*Carcharhinus leucas*) en un cuerpo de agua aislada en la Australia subtropical. De 1996 a 2013, seis tiburones toro quedaron encerrados en un lago de un campo de golf cerca de Brisbane. Los ríos adyacentes, Logan y Albert, atraparon a los tiburones debido a las grandes inundaciones. Cuando las aguas de la inundación retrocedieron, estos tiburones permanecieron en el lago, el cual normalmente está aislado del canal principal del río. Si bien este evento se informó ampliamente en los medios y recibió mucha atención pública, no se ha investigado en profundidad, pero brinda una oportunidad para comprender la tolerancia de los tiburones toro a los hábitats de baja salinidad y eurihalinidad de la especie. Actualmente, la información sobre la capacidad del tiburón toro para soportar condiciones de baja salinidad y su longevidad en estos ambientes es escasa. El caso reportado aquí proporciona información sobre la ocurrencia de tiburones toro durante 17 años, lo que representa la duración ininterrumpida más larga en un ambiente de baja salinidad que jamás se haya registrado en esta especie. Los tiburones toro llegaron primero al lago como juveniles, pero con el tiempo alcanzaron la madurez. Esta ocurrencia presenta no solo otro registro de tiburón toro de un ambiente de baja salinidad, sino un registro de importancia fisiológica y científica. Por lo tanto, aquí se informan los detalles de la residencia de *C. leucas* en un lago de un campo de golf australiano.

Palabras clave: Australia, Carcharhinidae, elasmobranqios, eurihalinidad, inundaciones, hábitats de baja salinidad.

INTRODUCTION

The bull shark (*Carcharhinus leucas* Valenciennes, 1839) is known for penetrating far, and for prolonged periods, into freshwater bodies in tropical, subtropical, and warm-temperate regions around the globe (Boesemann 1964; Compagno 1984; Gausmann 2021). It is a highly efficient osmoregulator that can travel between freshwater and seawater and respond to sudden changes in salinity with minimal metabolic costs (Pillans et al. 2005, 2008). This euryhaline species has been found circumglobally in freshwater environments, with reported large-scale migrations in major streams, covering thousands of kilometres, such as in the Amazon, Mississippi, and Zambezi rivers (Thorson 1972; Bass et al. 1973; Thomerson et al. 1977).

Carcharhinus leucas rely on low salinity habitats during early life stages (Heupel et al. 2010). These habitats, such as rivers and estuaries, are crucial nursery areas (Heupel and Simpfendorfer 2011). Young bull sharks spend up to five years in these low salinity environments (Pillans 2006; Heupel and Simpfendorfer 2008; Matich and Heithaus 2012), where they are exposed to lower levels of predation by larger sharks (Heupel and Simpfendorfer 2011). In this context, Curtis et al. (2011) found out for Florida's Indian River Lagoon that juvenile bull sharks even remain in this nursery until they have reached an age of nine years before they make the full transition to marine offshore habitats, but this may be exceptional and restricted to this particular locality. Investigations have revealed that *C. leucas* uses low salinity habitats across its range and that its distribution is limited by their availability (Gausmann 2021), emphasizing the importance of these habitats for the life cycle and occurrence of this shark. As a result of the worldwide altering of coastal inshore habitats, as well as estuarine and riverine systems, in combination with fishing pressures throughout its range (O'Connell et al. 2007; Kyne et al. 2012; Seidu et al. 2022), the bull shark is assessed as Vulnerable (VU) on a global scale in the IUCN Red List (Rigby et al. 2021).

Out of all elasmobranchs (sharks, skates, rays, and sawfish), only ~ 5% of the species can live in brackish and freshwater environments (Luciflora et al. 2015; Grant et al. 2019; Kyne and Luciflora 2022), with a minority considered to live permanently in the latter. Within the elasmobranchs, only freshwater stingrays of the Family Potamotrygonidae Garman, 1877 and whiptail stingrays of the Family Dasyatidae D. S. Jordan, 1888 contain obligate freshwater species that are confined to freshwater environments of South America, Africa, and southeast Asia. Because the seawater/freshwater ecocline provides one of the sharpest ecological boundaries in nature (Odum 1971), the residency of euryhaline elasmobranchs in low salinity habitats needs specific anatomical and physiological adaptions to overcome the changing salinities. Only a few elasmobranch species are euryhaline, capable of moving freely from one habitat to the other due to evolved osmoregulation, which is achieved through the control and integration of various organs (rectal gland, kidney, liver, and gills) in response to changes in environmental salinity (Reilly et al. 2011). Rectal glands of bull shark individuals that spend long periods in either freshwater or marine environments show significant differences because these glands are no longer functional in freshwater environments. Oguri (1964) reported that rectal glands from bull sharks found in freshwater environments are smaller and show regressive changes in comparison with individuals from a marine habitat. This is because the rectal gland of *C. leucas* undergoes atrophy during prolonged exposure to freshwater (Oguri 1964).

According to Ballantyne and Fraser (2013), truly euryhaline species, i.e. species living both in seawater and freshwater for prolonged periods, are the rarest within elasmobranchs. Only a few of the extant elasmobranch species are truly euryhaline, such as bull shark, Atlantic stingray (*Hypanus sabinus* Lesueur, 1824), and common sawfish, (*Pristis pristis* Linnaeus, 1758). More recently, Grant et al. (2019) reviewed the use of non-marine habitats by elasmobranchs and developed a classification based on the importance of freshwater habitats for the life history of each species. From the sharks, only 4 species of the Family Carcharhinidae can be considered truly euryhaline: 3 species of river sharks (*Glyphis* Agassiz, 1843) and *C. leucas*, based on their timing and duration of freshwater (≤ 5% salinity) and/or estuarine (> 5 to ≤ 30% salinity) habitat use. Due to its ability to occupy habitats in both freshwater and marine environments and to rapidly switch between them, the bull shark has been the subject of numerous physiological studies (e.g. Thorson and Gerst 1972; Thorson et al. 1973; Pillans and Franklin 2004; Anderson et al. 2005; Pillans 2006; Pillans et al. 2005, 2006, 2008, 2020; Reilly et al. 2011). Although physiology related to freshwater tolerance and euryhalinity of *C. leucas* have been studied extensively, the osmoregulation in this species and its capability to reside in freshwater is not completely understood yet.

In Australia, the bull shark is distributed continuously along Australia's coastline from the Collie River (-33.30° S) ~ 100 km south of Perth in the southwest farther to Wollongong (-34.32° S), ~ 50 km south of Sydney in the southeast (Potter et al. 2000; West 2011). Further, bull sharks have been reported from numerous rivers and freshwater systems in Australia (Thorburn and Rowland 2008; Tillett et al. 2012; Morgan et al. 2014; Gausmann 2021). Natural disasters have led to findings of *C. leucas* in inland waters of Australia. After the tropical Cyclone 'Debbie' in northeastern Australia in March 2017, *C. leucas* individuals were washed out of the Burdekin River onto a nearby street (Clamann 2017; Sandeman 2017). One individual was seen swimming in the flooded streets of Brisbane (Queensland, Australia) during the Queensland floods in 2010-2011 (BBC 2011). Several bull sharks were sighted in one of the main streets of Goodna (Queensland, Australia) shortly after the peak of the Brisbane River flood in January 2011 (Garry 2011). During floodwater events in subtropical Queensland, immature bull sharks were occasionally sighted in overflooded stretches of land, as it has been reported for recent floods in 2022 in Maryborough adjacent to the Mary River, some 300 km north of Brisbane (Pizzirani 2022), and also for the Logan River during the 2017 floods (O'Brien 2017).

Carcharhinus leucas was first reported in the Logan/Albert river system by Thomson (1957) and examined more extensively later by Pillans et al. (2020), revealing that neonate and juvenile *C. leucas* (74-102 cm total length, TL) remained within a narrow band of salinity (6-10%) throughout their tracking period (30 months). These authors found out that sharks have travelled at least 52 km (Logan) and 30 km (Albert) upstream, respectively. Werry et al. (2011) documented the marine-freshwater transition of *C. leucas* in the Moreton Bay Estuary system by acoustically tagging bull sharks and showed that it was also used by large juveniles (125-160 cm TL) but also subadults and adults (175-192 cm TL). Additional information about *C. leucas* records in the Logan River derived from the 'Global Shark Attack File' reported on a fatal attack in 1903 by a shark of estimated 2.7 m TL on a swimmer at Loganholme, ~ 25 km upstream (GSAF 2022). Even though the involved species could not be identified, the habitat suggests that a bull shark was the culprit. This may indicate that, at least occasionally, not only immature but also adult sharks make use of the river.

Evidence of reproductive philopatry in bull sharks has been provided for rivers in northern Australia (Tillett et al. 2012). Currently, it is not known if the Logan and Albert rivers fulfill the criteria of a nursery area according to Heupel et al. (2007). However, Pillans et al. (2020) tagged 36 neonate and juvenile bull sharks during their study in the Logan River between March 2013 and January 2014, indicating that a well-developed immature bull shark population inhabits these rivers (compare Pillans 2006).

In the mid-1990s, several bull sharks were trapped in the lake at Carbrook golf club, Logan City, near Brisbane, because of major floods from the Logan and Albert rivers, resulting in the sharks being trapped in the lake when the floodwaters receded. This situation has been widely reported by the media and received much public attention. The event of the involuntary captivity of several bull sharks provided science with the rare opportunity to measure the time that this species can survive in a low-salinity environment, since until now, information on the longevity of *C. leucas* in these environments is limited and has only been investigated in a few locations (e.g. Lake Nicaragua by Thorson 1971). This unique opportunity now allowed scientists to gain insight into the extent of euryhalinity in *C. leucas*, and this case includes several aspects and findings on the ecology of this species that could not be studied in depth previously due to a lack of occasions.

The case reported herein of an isolated bull shark population that got trapped in a freshwater lake over a timespan of more than one and a half decades leads to the following deliberations and key questions: (i) is the residential time of *C. leucas* in a nearly freshwater environment with approximately < 5% salinity unlimited, and how long are bull sharks able to survive in? (ii) are food resources in this isolated freshwater body sufficient for energetic requirements of resident bull sharks? (iii) do trapped bull sharks have reach maturity in captivity and is there evidence of reproduction?

MATERIALS AND METHODS

Study site

The Carbrook golf club (-27.68° S-153.24° E) is located at Carbrook, a suburb of the City of Logan, southeast of Brisbane, at the junction of the Logan (main estuary) and Albert (tributary) rivers in subtropical southeast Queensland, Australia (Figure 1 A-C). Southeast Queensland experiences a subtropical climate with warm, wet summers and relatively cold, dry winters (Kemp et al. 2016). In summer, intense storms and occasionally prolonged rainfall are generated by tropical depressions or southeast trade winds. Flooding events are frequent in the area and do occur regularly at intervals of several years to decades (Queensland Government 2015).

The concerned Logan/Albert river system (-27.69° S-153.23° E) has a total catchment area of 3,875 km^2 and lies in the southeast corner of Queensland. Major flooding is experienced in both rural and urban areas of the catchment (Middelmann et al. 2000). Therefore, Carbrook's and the city of Logan's subtropical climate combined with their situation in the floodplain lowlands of Albert and Logan rivers cause their vulnerability to natural disasters, such as flooding (Figure 1 D and 1 E). Both Logan and Albert rivers are tidal influenced, which extend about 60 km upstream in both rivers from the mouth of the latter (Matveev and Steven 2014; Pillans et al. 2020). Thus their confluence, which is located about 14 km upstream from the Logan River inlet at Eagleby, is well within the tidally influenced zone, although following events of heavy rainfall in the Logan/Albert river basin, salinity can decrease significantly and the estuary becomes

Figure 1. A) Aerial view of the Carbrook golf course lake located nearby the junction of the Logan and Albert rivers. B) Location of Carbrook on the Australian continent. C) Situation of the Carbrook golf club inside the Brisbane Metropolitan Area (Queensland, Southeast Australia). Data source 1A-1C: © OpenStreetMap and Bing Maps 2022. D) Historical photo of the inundated Carbrook golf club course during the flood event in May 1996. E) Aerial view on the inundated course of Carbrook golf club during the current flood event in February 2022 when the Logan River burst its banks. The view direction is from north to south. (F) Aerial view of the Carbrook golf course lake and the adjacent Logan River (similar location as the left figure) under normal river conditions (average discharge). Data source 1D-1F: © Carbrook golf club.

fresh at the entrance (Table 1). The Logan River is 191 km long and largely unregulated (Loneragan and Bunn 1999), with the Albert River as its largest tributary of 102 km in length.

Water temperature in the Logan River during the austral summer is most of the time 26-28 °C, decreasing to 16 °C in winter (Pillans et al. 2020). No data are available regarding water parameters for the golf course lake mentioned in this study and no investigations on these were conducted, but it can be assumed that the water has a slight salinity (< 5%) and provide oligohaline conditions due to groundwater flow and connectivity that corresponds to the adjacent Logan River. Presumably, the salinity in the lake is much lower than in the adjacent river due to the cut-off from the tidal influence and dilution by precipitation. Both Logan River and golf course lake show remarkable differences in turbidity (Figure 1 F).

The vast lake at Carbrook golf club (Figure 1 A) that was inhabited by several bull sharks is undisturbed and, despite of being artificial, shows characteristics of a natural water body. It is located northeast across from the confluence of the

Table 1. Physiochemical water parameters of the Logan and Albert rivers averaged over the year according to Matveev and Steven (2014). NTU = Nephelometric Turbidity Unit. In Brackets: minimum and maximum values for each parameter in the Logan River according to Pillans et al. (2020).

Parameter	Logan River	Albert River
Salinity (%)	13.63 (1-20)	7.27
Dissolved oxygen (mg l^{-1})	5.66 (3-10)	5.78
Temperature (°C)	23.20 (14-29.5)	23.4
Turbidity (NTU)	46.40 (0-500)	61.4

Albert and Logan rivers at a distance of 0.5 km to the junction (Figure 1 A; -27.69° S-153.24° E). This lake is situated 14 km upstream from the sea (Moreton Bay, southwestern Pacific Ocean). It is ~ 700 m long and ~ 380 m wide at its widest extension and is separated from the Logan River by a ~ 75-100 m land barrier that is impassable for fish during periods without floodwaters. The lake covers an area of ~ 20 ha with a maximum water depth of 15 m. Its origin derives from sand mining activities of a sand mining plant during the late 1970s, at the time the Carbrook golf club was established beyond the end of mining activities (Carbrook Golf Club 2022).

Important flood events

For a complete understanding of the circumstances of how bull sharks found their way into the golf course lake, a short chronological summary of several flood events that have affected the Brisbane metropolitan area and surroundings and which have provided sharks with the opportunity to invade the lake is given (Table 2).

Severe floods in Queensland on December 2010/January 2011 and March 2017 only slightly affected the Logan/Albert river system. They were not leading to the flooding of the land-bridge, which divides the river and the golf course lake, although the latter inundated large parts of Carbrooks golf course (21 October 2022 pers. comm. S Wagstaff).

Data acquisition

As the occurrence of bull sharks in the lake of Carbrook golf club was reported extensively in the media but not in scientific studies, these media reports present an essential part of the references that have been investigated. Media references investigated included video material provided by Carbrook golf club staff (Wagstaff 2011a, 2011b), online newspaper articles, and video footage. An evaluation and assessment regarding the plausibility and reliability of these media contents was conducted following the methodological approach of Schemer et al. (2008) and Kim et al. (2011). Additionally, an interview was conducted with the general manager of Carbrook golf club to obtain firsthand information on the bull shark population at this site firsthand (see Appendix for the catalog of questions). Some additional questions, which arose later in the course of the investigation were clarified via email correspondence between the golf club manager and the author.

Calculation of energetic requirements

For extrapolation of energetic requirements of landlocked bull sharks, a calculation for an estimated bull shark population size of six shark individuals was conducted, whereby the calculation is largely based on similar studies that have already been carried out on this topic by Schmid

Table 2. Chronological overview of flood events during the last three decades affecting the Brisbane metropolitan area including Logan City and Carbrook.

No	Date	Affected area	Rainfall ($l\ m^{-2}$)	Severity	Land-bridge flooding	References
1	7-10th February 1991	Logan/Albert River catchment	200	Severe	Yes	AGBM (1991, 2022a, 2022b)
2	April 1995	Upper reaches of Logan River to Carbrook	?	Moderate	Yes	9 November 2022 pers. comm. S Wagstaff
3	1st-7th May 1996	Brisbane metropolitan area	600	Very severe	Yes	AGBM (2022b, 2022c)
4	26th-28th January 2013	Brisbane River catchment	> 1,000	Very severe	Yes	AGBM (2013, 2022b); Pillans et al. (2020)
5	25th-28th February 2022	Greater	675-1,000	Very severe	Yes	AGBM (2022d)

and Murru (1994) and Brunnschweiler et al. (2018). Information on the energetic content and size calculations of possible prey fish of *C. leucas* was largely obtained from literature and FishBase (Froese and Pauly 2023).

RESULTS AND DISCUSSION

Carcharhinus leucas were observed in a low salinity environment in the vicinity of Brisbane for 17 years (Figure 2 A). Sharks got into the lake after the golf course was inundated three times over a five-year period between 1991 and 1996, due to serious floods of the nearby Logan and Albert rivers. Although the first presence of bull sharks in the lake was reported in 1996, the date of their arrival, the number present, and the exact time of their residency in the lake is unknown. However, it has been reported by the media that they were regularly seen in the lake since the late 1990s and the early 2000s.

Reported sightings are consistent with bull sharks due to their description by Garrick (1982) and Compagno (1984) such as very small eyes, a short blunt snout, coloration, and a first dorsal fin approximately three times as high as the second dorsal fin. Together with an occurrence in a nearly freshwater habitat and occurrences of bull sharks in the nearby Logan and Albert rivers support these observations. Given the date of their first sighting in the golf course lake, it is most likely that these bull sharks were trapped following the flood of the Logan and Albert rivers in 1996 after the major Brisbane floods when these rivers burst their banks (Boswell 2013; Ward 2022) (Table 2). When the floodwaters receded, sharks were trapped in the lake.

Sharks have become, and still are, the golf club's mascot and flagship. This small population of bull sharks in the golf club lake was a good display object for the interested public and most likely contributed to the understanding of sharks in general and of supposedly dangerous species in particular. As there was no immediate risk from sharks to golf course users, the golf club management not only tolerated but welcomed their presence in the lake. However, for preventing shark-human incidents, the managers installed warning

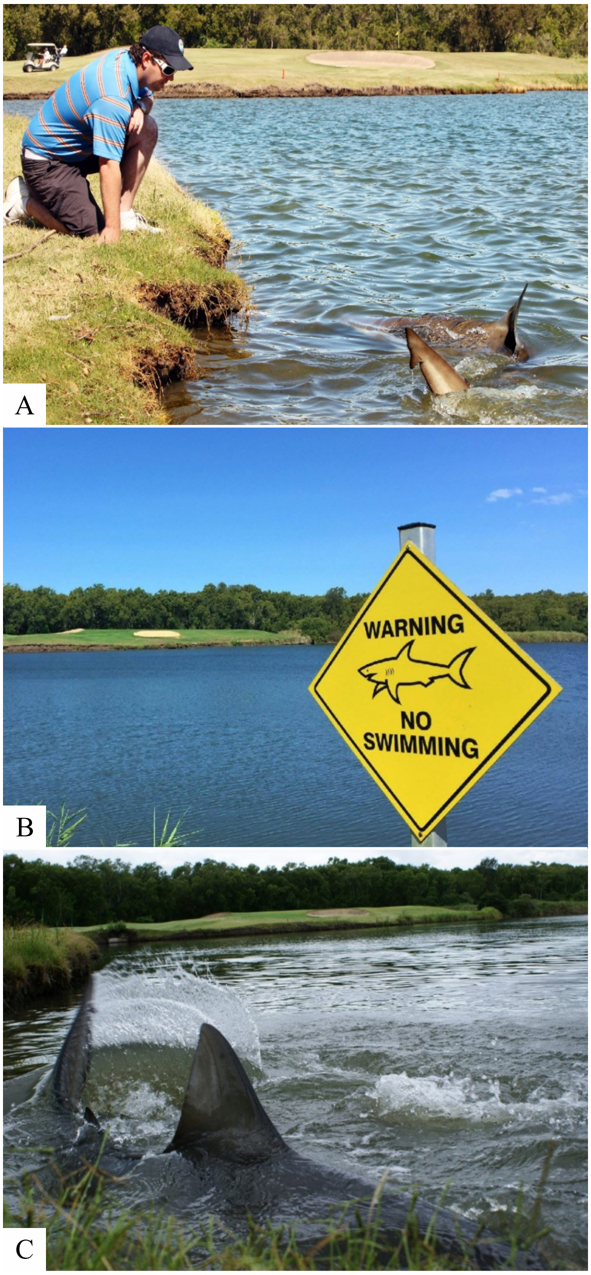

Figure 2. A) Carbrook's golf club staff with a *Carcharhinus leucas* in the lake of the golf course in Carbrook, Queensland, in October 2011. Data source 2A: © Jodie Richter/Newspix. B) A warning sign informed the golf players about the potential risk of bull sharks in the Carbrook golf club lake. C) A *Carcharhinus leucas* close to the shore in 2012. Data source 2B-2C: © Carbrook golf club.

signs around the lake to inform the golf players about the potential risk (Figure 2 B).

History and vitality of the lake's shark population

Five flood events (Table 2) have provided bull sharks the possibility to invade the golf course lake via the adjacent Logan River. Conversely, flood events can also be assumed to have borne the possibility for sharks who reside in the lake to escape from the lake back into the Logan River. However, what is certain is the fact that between 1996 and 2013, no significant floods affected the Carbrook golf club, and in this non-flooding period of 17 years, the fish-impassable landbridge was not inundated. Consequently, during this period, sharks had no opportunity to enter or escape the lake. Therefore, a complete isolation of the bull shark population remaining in the lake can be stated between 1996 and 2013.

It was not possible to investigate precisely how many sharks and in what year they arrived in the lake. Similarly, it also cannot be said with certainty whether sharks subsequently entered the lake during the new millennium flood events in 2013 and 2022, or vice versa, escaping back into the Logan River. Since individuals were not marked, it is not possible to know how many individuals were added during the respective flood events or migrated out of the lake again. Sharks were seen for the last time in the lake in 2015 (21 October 2022 pers. comm. S Wagstaff).

Sharks in the lake were juvenile bull sharks at the time of their arrival, similar in size to those previously reported by Pillians (2006) and Pillans et al. (2020) from the adjacent Logan and Albert rivers. Through time, there was evidence that sharks within the lake increased in size and were reported between 1.8 m and 3 m TL in 2013 (Boswell 2013), which is consistent with previously reported mature Indo-Pacific bull sharks (Cliff and Dudley 1991; Wintner et al. 2002; Figure 2 A and 2 C). Based on the information deriving from the guarantor, six shark individuals simultaneously inhabited the lake (21 October 2022 pers. comm. S Wagstaff), and this information can be valued as trustworthy and reliable. The author found no reliable information and no hints that bull sharks in Carbrook golf club lake have reproduced. Bull sharks rarely breed in rivers and lakes (Thorson 1982), with estuaries and river mouths considered to be nurseries for this species (Heupel and Simpfendorfer 2011; Gausmann 2021).

Boswell (2013) reported sightings of bull sharks in the lake in 2013 and confirmed that they survived major floodings the same year, alleviating the fears of Carbrook golf club officials at that sharks may have escaped through the floodwaters, suffered or died as a result of the storm because they were not seen in there after the flood for some time (Social Golf Australia 2013). However, following this flood event, the number of bull sharks in the lake apparently decreased as it was reported by the guarantor. This observation of decreasing shark numbers is leading to two reasonable explanations: either some individuals must have escaped successfully from the lake into the nearby river during the flood in 2013, or some have died, maybe by suffering from the floodwaters. Assuming that affected sharks were the same individuals that entered the lake in 1996, they could have reached their maturity age in 2013, 17 years after their arrival in the lake. According to the guarantor, only one shark of an estimated 2.7 m TL was ever observed floating dead in the lake over the years, without clearly identifiable reasons for its demise and no visible external influences (21 October 2022 pers. comm. S Wagstaff). Possibly, hunger or diseases are possible causes here, although suffering from a major loss of sodium chloride cannot be excluded completely. The golf club manager recovered the shark carcass, but an autopsy was not conducted. It can be not ruled out that more than one of the landlocked bull shark individuals died in the lake in 2013 shortly after the flood or that dead shark corpses have sunken to the ground of the lake unobserved, or that dead shark bodies were consumed by other sharks that inhabited the lake. Besides environmental changes and in contrast to careful efforts of golf club managers and members on the treatment of sharks, illegal fishing operations in the lake provided a further threat to this small bull shark population. According to the guarantor, illegal recreational fishing activities in the lake have verifiably caused the death of at least one other bull shark over the years (21 October 2022 pers. comm. S Wagstaff).

Food resources and energetic requirements

Bull sharks are opportunistic feeders with a broad diet that undergoes a shift with increasing size (Cliff and Dudley 1991; Daly et al. 2013), including bony fish, elasmobranchs, crustaceans, birds, and large prey items such as sea mammals and sea turtles. However, they are assessed as primarily piscivorous (Compagno 1984; Estupiñán-Montaño et al. 2017; Cottrant et al. 2021). In addition to sharks, access to the golf club lake was provided to other fish that normally inhabit the Logan and Albert rivers, which also entered during floods. According to information from the guarantor, there is a heap of fish species in the lake, and plenty of potential prey species for bull sharks, such as flathead grey mullet (*Mugil cephalus* Linnaeus, 1758), yellowfin bream (*Acanthopagrus australis* Günther, 1859), Indo-Pacific tarpon (*Megalops cyprinoides* Broussonet, 1782), and mangrove red snapper (*Lutjanus argentimaculatus* Forsskål, 1775). All these fish are euryhaline and capable to survive in low salinity habitats (Froese and Pauly 2023). Some of these fish were reported to be between 40-50 cm TL (TAASFA 2011). Although the golf course lake is well-stocked with fish, the golf club staff fed sharks occasionally with meat (chicken, pork) to encourage sharks to come near the surface (Wagstaff 2011b). Sharks within the lake may not meet their energy requirements with this additional feeding.

To estimate the daily energy requirements of bull sharks in the lake for an example calculation, the author adopted routine metabolic rate estimates from previous studies of captive bull sharks by Schmid and Murru (1994) that incorporated measured feeding rates into a bioenergetics model. Schmid and Murru (1994) informed on the energetic requirements of bull sharks held in captivity at a water temperature of 24 °C, meaning a food consumption of 3.4% body mass per week. In this context, Brunnschweiler et al. (2018) informed that requirements for wild living bull sharks studied in Fiji with average water temperatures of 27 °C were lower than in the previous study with 2.7% body mass per week. In detail, Schmid and Murru (1994) reported a routine metabolic rate of 5.7 kcal kg^{-1} d^{-1} for a 78 kg individual *C. leucas* held at a water temperature of 24 °C. Overall, this means a daily energy requirement for a 78 kg individual of 444.6 kcal d^{-1}. Brunnschweiler et al. (2018) calculated the daily energy requirement for 200 kg free-living bull sharks at a water temperature of 27 °C to be 1,087 kcal d^{-1} to maintain growth rates similar to those of captive animals in the previous study from Schmid and Murru (1994). Logically, water temperature has an important influence on energetic demands of fish but, unfortunately, data on water temperature from the Carbrook golf course lake are lacking. Thus, the author calculated with an average water temperature of 24 °C for bull sharks inhabiting the Carbrook golf club lake like the study by Schmid and Murru (1994) because this temperature is close to the mean water temperature of the adjacent Logan River (see Table 1). Therefore, the calculation carried out here is of theoretically character and the result should only be understood as an approximate value.

To calculate daily energy requirements for six bull sharks, which are regarded as the minimum population size that inhabited the golf course lake, the author have used *Mugil cephalus* as a prey item for *C. leucas*. Whitfield (2021) assumed that *C. leucas* feeds heavily on the global distributed flathead grey mullet in South Africa's St. Lucia Estuary. Although general conditions between the present study and the study by Schmid and Murru (1994) are only comparable to a limited extent, since these authors calculated energy requirements for sharks in captivity, it can be assumed that the range of movement of sharks in the golf course lake was also restricted.

The weight-length relationship of fish can differ significantly between sexes and locations due to sexual dimorphism and differences in environmental conditions. Luther (1963) gave information on the weight-length relationship of *M. cephalus* caught at Mandapama along the east coast of India, but this author used the fork length (FL) for its measurement. For the comparability of data, information derived from Luther (1963) was transformed by converting the length from FL to TL using the length-length table for *M. cephalus* provided by FishBase (Froese and Pauly 2023). Therefore, a *M. cephalus* individual of 210 mm FL represents an individual of 231 mm TL after converting. Luther (1963) calculated an average weight of 100 g for individuals of grey mullet of 231 mm TL. This transformation was necessary because Marais and Erasmus (1977) reported a caloric content of 187.4 kcal 100 g^{-1} for undried flesh of *M. cephalus* individuals > 230 mm TL deriving from South Africa's Swartkops River Estuary.

Bull sharks inhabiting the golf course lake were estimated to have the lowest reported length for this locality of 180 cm TL, which represents the smallest reported size at maturity of Indo-Pacific bull sharks (Cliff and Dudley 1991). According to Branstetter and Stiles (1987), this length corresponds to an estimated weight of 50 kg. To correct for the smaller body mass of bull sharks at the Carbrook golf course lake in comparison to the study by Schmid and Murru (1994), the author used the allometric exponent of 0.79 identified in a comparative analysis of shark mass versus swimming metabolic rate (Payne et al. 2015). This correction is leading to an estimated energy requirement of 50 kg bull sharks of 8.22 kcal kg^{-1} d^{-1} and 411 kcal d^{-1}. To meet its daily caloric requirements, a single bull shark thus needs 2.2 *M. cephalus* individuals of 100 g day^{-1}. This corresponds to 0.44% of its body weight per day and 3.08% of its body weight per week.

Considering the energy content of *M. cephalus* as prey for *C. leucas*, and the calculated energetic requirement of a 50 kg and 180 cm TL bull shark derived from Schmid and Murru (1994), a model of the amount of food demands over time for six adults in the lake might looks like: If six bull sharks require 0.44% of their body weight in prey per day and resided in the lake for 1 week/1 month/1 year, then 9.240/40.101/482.143 kg of fish would be needed based on the caloric content of the potential prey (*M. cephalus*), respectively. In concrete terms, this means that six bull sharks of 1.8 m TL require an amount close to half a ton of fish per year to meet their energy needs.

Residential time in the golf club lake

These previously reported finding increase the longest known continuous residence of bull shark individuals in a low salinity environment to 17 years, and are remarkable in that regard because they present the world record for longest residence in an *ex situ* non-marine environment for this species that has ever been recorded. The latest reliable bull shark sighting in the Carbrook golf club lake by golf club officials was in 2015 (21 October 2022 pers. comm. S Wagstaff). Therefore, last bull sharks sighted in 2015 could have reached theoretically an age of 19 years, assuming that they were the same individuals that had already entered the lake in 1996, and not subsequently in 2013. Theoretically, they could even have reached an age of 24 years, assuming that they entered the lake with the first flood event in 1991 (Table 2) and survived until 2015. Today, in 2023, the last verifiable shark sighting in Carbrook golf course lake can be dated back eight years, and their vanishing remains undiscovered. Information is lacking on whether new sharks migrated to the lake during the recent severe flooding in 2022, as it may have provided an opportunity for bull sharks to recolonize the golf course lake. Only increased observation of the lake can provide clarity on this matter. According to the general manager of the golf club, the lake was rapidly recovering from the impact of the last flood and returned to good health in late April 2022, just two months after the flood (21 October 2022 pers. comm. S Wagstaff). However, officials at the Carbrook golf club were disappointed of the vanishing of sharks because they have lost their flagship mascot. The general manager of the golf club visited the sharks in the golf course lake nearly 100 times over many years and has never observed a decreased vitality or symptoms of sickness (e.g. sluggish behavior) in the residential bull sharks (21 October 2022 pers. comm. S Wagstaff). Therefore, the disappearance of sharks from the lake beyond 2015 remains a mystery.

Carcharhinus leucas can inhabit both natural and artificial bodies of water with access to the sea (Werry et al. 2012). Along the east coast of Australia, occurrences of bull sharks in artificial freshwater habitats are neither unusual nor exceptional. Dunn et al. (2014) reported that the highly populated Gold Coast Broadwater, an estuary of the Nerang River including its artificial waterways, provides an additional habitat opportunity for *C. leucas*. However, because of the bull shark's ability to occupy low salinity environments, coupled with the expanding settlement activity in many riverine and coastal areas worldwide, this shark appears near urbanized areas and in unusual inland locations where people do not normally expect it.

From a global perspective, there are further examples of landlocked bull shark populations. Bull sharks have also been cut off from the sea and trapped in South Africas' Lake St. Lucia Estuary system after historic periods of near-continuous mouth closures, in some cases lasting over 10 years. Lake St. Lucia's Estuary system is known to be an important key nursery for bull sharks in the southwestern Indian Ocean (Daly et al. 2021), and it is well-known for the development of increasing salinities (up to 100%) in the system during periods of droughts (Bass et al. 1973). In contrast to Carbrook golf course lake, which is characterized by very low salinity conditions, bull sharks from Lake St. Lucia had to resist long-lasting hypersaline conditions, as drought has led to increasing salinities in most parts of this estuary system during times of mouth closures. Bass et al. (1973) reported that during times when the estuary mouth became blocked, many trapped fish and sharks might die, presumably resulting from high salinity levels in this estuary system. It is confirmed for Lake St. Lucia's Estuary system that an unspecified number of bull sharks remained landlocked in the lake for many years after its mouth was closed and the connection to the sea was interrupted. Herein, they withstood hypersalinity and extreme temperatures and survived in this system for more than 10 years of mouth closure in a period from 2002 to 2013 (29 October 2022 pers. comm. R Daly). Some individuals died during a drought period when the water in some parts of the lake was too shallow, and prey became limited. However, other individuals have survived as long as environmental conditions were tolerable and there were enough preys (29 October 2022 pers. comm. R Daly). As a species withstanding a broad salinity range from 0-53% (Compagno 1984), bull sharks have endured successfully the extreme habitat conditions in Lake St. Lucia for an extended period, in fact for more than 10 years. However, a study that was conducted by Bass et al. (1973) in Lake St. Lucia based on tagging-recapture methods suggests that individuals of *C. leucas* also lived continuously for considerable periods (up to 537 days) in the lake when access to the sea is given.

In addition to the landlocked Australian bull sharks that once inhabited Carbrook golf club lake and South African bull sharks trapped in Lake St. Lucia, until nowadays, to the knowledge of the author, there exists only one other documented case of a local bull shark population that was trapped and survived for years in an isolated body of water, in fact in Panama's Lake Bayano, Central America. This artificial impoundment is characterized by pure freshwater conditions and was disconnected from the sea by damming off the Bayano River. This historical case was accurately documented by Montoya and Thorson (1982) who already hypothesized that due to the ability of *C. leucas* to osmoregulate, it theoretically could survive in landlocked situations for many years. These authors reported that three dead mature female bull sharks of 222-226 cm TL were found in Lake Bayano in 1980, four years beyond the dam closure, indicating that the lifetime of *C. leucas* in freshwater could be limited by physiological constraints, but they presumed that other factors (e.g. herbicides) could have caused the death of these sharks. Further, due to the lack of signs of reduced vitality in the sharks, these authors argued that it does not seem reasonable that either terminal aging or osmoregulatory failure would occur in three sharks simultaneously. However, isolated bull sharks of Lake Bayano survived at least four years trapped in this pure freshwater environment, while Montoya and Thorson (1982) speculated that they almost certainly would be capable of survive longer.

Deliberations on trapped bull sharks lead to two possibilities of being landlocked. Firstly, naturally by natural events such as storms and coupled flooding, which mislocate sharks into stagnant water bodies normally cut off from rivers (e.g. lakes, backwaters, billabongs, dead river branches); and secondly, by human alteration of rivers (e.g. reservoirs, dams) through man-made constructions that could leave sharks behind a dam wall or a barrage after completion. The first scenario also includes mouth closures of rivers and estuaries by sand accumulation or prolonged drought, the latter initiated when the discharge of the river is drastically reduced, both leading to a cut off rivers from the sea and preventing bull sharks from returning to the marine environment. Because many large streams are characterized by pronounced dynamics, natural alteration of river flows occurs in many places, especially in the tropics, which are characterized by high rainfall totals. Considering these scenarios, future captivities of bull sharks can be predicted for several regions within the species' global range. Thus, temporary or permanent landlocked bull sharks should be expected for the numerous freshwater billabongs of Australia's Northern Territory, from which they have been already reported by Stevens et al. (2005) and Pillans et al. (2009), or sections of rivers isolated from the main tidal stream. Due to the recent trend of new hydropower dam construction in the developing world, such as along Brazil's Amazon River system, Iran's Karun River, and southeast Asia's Mekong River, from which *C. leucas* either have been verifiably reported or is suspected to occur (Gausmann 2021), isolated bull shark populations should also be expected in the upper reaches and cut off sections of those rivers. Considering this, to mitigate the risk of shark bites, it is advisable not to swim in stagnant bodies of water adjacent to rivers with access to the sea that are isolated from the main stream of the river in warm temperate, subtropical, and tropical regions. The same applies for reservoir lakes and connected upper river sections after the recent completion of dam constructions because it has now been shown that bull sharks can survive for many years in low salinity environments and in landlocked situations.

Compagno (2002) once stated that *C. leucas* should be expected in any warm-temperate, subtropical, and tropical river and lake with access to the sea that is inside the worldwide range of this species. In addition to this statement, this species should also be expected in unusual shark habitats in regions with risks of natural disasters. Extreme natural events such as floods may provide *C. leucas* individuals the possibility to navigate into water bodies that are normally inaccessible to them. Simultaneously, bull sharks are facing the risk of being trapped in isolated bodies of water when they enter inland waters that are cut off from the main river or stream. Stranding of bull sharks in freshwater bodies containing only sporadic and temporary water, such as Australia's billabongs, carries some additional risks to bull shark life, particularly when these waters dry up, and residence here may result in the death of sharks.

CONCLUSIONS

The finding of bull sharks that have survived over a 17-year period in an *ex-situ* environment with low salinity, coupled with the knowledge that they have also survived for many years in landlocked situations at other locations worldwide, contribute to the knowledge that *C. leucas* has the physiological capability to spend a large proportion of its lifespan in fresh and brackish water habitats. Along with the case reported here, there are now three confirmed records of bull sharks worldwide being entrapped for several years, either in freshwater habitats (Lake Bayano), in low salinity habitats (Carbrook golf club lake), or in extremely high salinity habitats (Lake St. Lucia). Results of this study may contribute to our understanding of the extent of euryhalinity of *C. leucas*, a species of broad halotolerance and virtually no osmoregulatory limits. Moreover, these findings impressively demonstrate the bull sharks' adaptability to environments with salinities lower or higher than seawater.

The period of 17 years that has been proven for the residency of the golf course lake bull sharks represents more than half of the given longevity of 29-32 years that have been reported for free-ranging Indo-Pacific *C. leucas* by Wintner et al. (2002). In similar future cases of landlocked bull sharks, these individuals should be monitored by scientists to gain more insights into the complex biology of this species, as only a small number of elasmobranchs held so much interesting information on adaptation to low salinity environments in this ordinarily marine fish group.

It would be desirable if newcoming sharks in the golf course lake were tagged, monitored long term, and examined in depth to gain more data on physiology and other life parameters. Finally, the status of *C. leucas* in the Carbrook golf course lake remains unclear. The last time the sharks were seen in the lake by the golf club officials was in 2015, eight years ago, and it is currently unclear if new sharks arrived during the latest flood event in 2022. Intensive baiting and fishing activity or the use of further investigation methods such as environmental DNA (eDNA) could bring clarification on this matter. For their detection and future observation, the collaboration between the officials of the Carbrook golf club and shark scientists would be desirable.

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Declaration of interest

The author has nothing to declare.

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APPENDIX

Catalog of questions used for this study:

1) In which year do you have started your profession at Carbrook Golf Club?
2) When were sharks spotted for the first time in the lake of Carbrook Golf Club (date, year)?
3) How many sharks were spotted for the first time at the point of their discovery?
4) How many individuals of sharks were spotted in the lake overall (absolute numbers)?
5) Was the number of sharks in the lake stable over time?
6) Currently, are there still living sharks in the lake, and how much individuals (absolute numbers)? If not, when they disappeared and why (please provide possible explainations)?
7) Were you able to distinguish between different individuals of bull sharks by distinct markings (such as fin shape, damages in the dorsal fin, etc.) or deviating sizes over time?
8) Are there information on food resources for the sharks in the lake? What kind of fish and food items the sharks prey upon?
9) How many times the sharks get additionally feeded by the golf course staff and with what kind of food items (e.g. meat, slaughterhouse waste)?
10) Do you observed hints on sickness or limited vitality of the sharks that inhabit the lake (e.g. sluggish behaviour)?
11) Do you ever have observed dead sharks in the lake? If yes, what do you believe to have caused this deaths (e.g. another flood event, aggression by another shark, sickness)?
12) How many flood events have affected the lake since the first appearance of the sharks?
13) Were the bull sharks of the Carbrook Golf course lake already the subject of a previously conducted scientific investigation?