Seasonal occurrence and sexual segregation of great white sharks *Carcharodon carcharias* in Mossel Bay, South Africa

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Abstract The seasonal occurrence and temporal sexual segregation of great white sharks *Carcharodon carcharias* have been widely documented in various temperate and sub-tropical waters across the globe. Yet, there is limited understanding of the relationship between the life stages and habitat use of *C. carcharias*, particularly in the Southern Cape. In this study, we investigated the population dynamics of *C. carcharias* in Mossel Bay, South Africa, between 2009 and 2013, using skipper logbooks and citizen research data obtained by a cage-diving vessel. A total of 3064 sharks, ranging in life history stages from young-of-the-year to subadult, were sighted during 573 trips. Juveniles dominated the sightings throughout the study, and there was marked sexual segregation, with females dominating the total sightings of sharks. *C. carcharias* were most abundant during the cooler, winter season, with females differing in abundance seasonally and males maintaining a low abundance throughout the year but peaking in

the winter. In addition, sea surface temperature was the best indicator of *C. carcharias* presence. Abundance was greatest when vertical water visibility exceeded 3 m, with cloud cover influencing overall abundance negatively. Likely reasoning for the aggregation of *C. carcharias* in Mossel Bay includes the favourable conditions and abundance of food. Juvenile sharks may also utilise this area as a training ground to learn from larger conspecifics. This research demonstrates that information on population size and structure of *C. carcharias* can be obtained effectively through a compilation of logbook and citizen science data to assess and identify potential critical habitats in the quest to develop appropriate management strategies. This research also shows value in commercial cage-diving operations deriving international data sets needed to assess global populations of *C. carcharias*.

Keywords Population dynamics · Ecotourism · Logbooks · Juvenile · Nursery ground · Social learning

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Introduction

Identifying critical habitats for wildlife offers the development of appropriate management strategies (Simpfendorfer et al. 2011). However, such research requires information on movement patterns (Speed et al. 2010; Simpfendorfer et al. 2011) and site fidelity of species (Knip et al. 2012). Great white sharks *Carcharodon carcharias* are highly migratory, apex predators, distributed throughout temperate and

subtropical coastal ecosystems (Compagno 1991; Bonfil et al. 2005; Domeier and Nasby-Lucas 2012). The major regions of abundance occur in the coastal waters of California, Mexico, Australia, New Zealand and South Africa (Ferreira and Ferreira 1996; Compagno 2001; Anderson and Pyle 2003; Robbins 2007; Jorgensen et al. 2010). Their extensive distribution within coastal waters makes *C. carcharias* susceptible to disruptive anthropogenic activities, such as fisheries, pollution and shark control programs (Bruce and Bradford 2012; Kock et al. 2013; Dulvy et al. 2014). In addition, the life history of this species, characterised by low fecundity (Uchida et al. 1996), slow growth (Wintner and Cliff 1999) and late maturity (Francis 1996), demonstrates high intrinsic vulnerability to over-exploitation (Smith et al. 1998; Stevens et al. 2000; Dulvy et al. 2008, 2014; Rigby et al. 2019).

Through advances in acoustic and satellite telemetry, it is known that *C. carcharias* take extensive migrations before demonstrating site fidelity at coastal aggregations (Pardini et al. 2001; Boustany et al. 2002; Bonfil et al. 2005; Bruce et al. 2006; Weng et al. 2007; Domeier and Nasby-Lucas 2008; Jorgensen et al. 2010, 2012; Bruce and Bradford 2012). Consequently, the degree of site fidelity is believed to have a strong influence on the species' exposure to disruptive anthropogenic activities (Bruce and Bradford 2012; Dulvy et al. 2014).

Seasonal variations and consequent changes in environmental parameters greatly influence *C. carcharias* abundance, segregation and activity (Pyle et al. 1996; Martin et al. 2005; Hammerschlag et al. 2006; Robbins 2007; Kock et al. 2013; Towner et al. 2013), and individuals of different sizes and life stages are likely to have a varied tolerance to abiotic factors (Hussey et al. 2012; Kock et al. 2013). For example, White et al. (2019) reported that juvenile *C. carcharias* abundance in Southern California Bight was highest when water temperatures were greater than 19 °C. Sexual segregation of sharks can occur due to differences in age, habitat selection and nutritional requirements (Magurran and Garcia 2000; Wearmouth and Sims 2008). Anderson and Pyle (2003) identified that female visitation to aggregation sites in California was linked to their gestation period (12–18 months), displaying biennial residency, whereas males visited annually. However, there is strong evidence to suggest that sexual segregation is not restricted to adult *C. carcharias* (Kock et al.

2013); thus, an understanding of habitat use of young-of-the-year (YOY), juvenile and subadult sharks is required.

Several studies have also demonstrated that *C. carcharias* foraging behaviour and predation is influenced by variations in ocean temperature (Weltz et al. 2013; Skubel et al. 2018), water visibility (Pyle et al. 1996; Hammerschlag et al. 2006), lunar phase (Fallows et al. 2016), tidal height and swell (Anderson et al. 1996; Pyle et al. 1996). There is strong evidence to suggest that low ambient light and poor water visibility increase *C. carcharias* stealth resulting in successful predation upon pinnipeds at the surface (Strong et al. 1992; Pyle et al. 1996; Hammerschlag et al. 2006).

Despite their circum-global distribution (Boustany et al. 2002; Bonfil et al. 2005; Weng et al. 2007; Domeier and Nasby-Lucas 2008; Jorgensen et al. 2010), *C. carcharias* aggregation sites are typically associated with pinniped colonies (Compagno et al. 1997; Goldman and Anderson 1999; Bruce et al. 2005), particularly within South Africa (Ferreira and Ferreira 1996; Johnson 2003; Martin et al. 2005; Fallows et al. 2012; Jewell et al. 2013; Towner et al. 2013; Rykclief et al. 2014). For example, adult and subadult *C. carcharias* often undertake offshore migrations, likely due to seasonal prey availability and possible mating opportunities (Bonfil et al. 2005; Dudley 2012). Consequently, reports have revealed that *C. carcharias* sighted at pinniped colonies appear to be either largely transient or temporarily absent, which is defined as returning after an absence of one or more years (Hewitt et al. 2017), with a few long-term residents occupying the area for consecutive years (Strong et al. 1992; Klimley and Anderson 1996). In contrast, in False Bay, South Africa, *C. carcharias* are resident throughout the year, but their abundance is directly influenced by the seasonal presence of young cape fur seals *Arctocephalus pusillus pusillus*. It has been suggested that in the absence of adolescent seal pups, *C. carcharias* undergo a dietary shift and prey upon summer fish species such as yellowtails *Seriola lalandi* and bronze whale sharks *Carcharhinus brachyurus* which are located closer to the shore (Martin et al. 2005). Ontogenetic dietary changes in sharks are caused by a shift in foraging behaviour and habitat use (Tricas and McCosker 1984; Hussey et al. 2012; Kim et al. 2012). This can be evidenced by social learning and physical maturation (Meyer 1986;

Ciaccio 2008; Guttridge et al. 2009, 2012; Pouca et al. 2020). Therefore, the foraging behaviours and habitat utilisation of juvenile *C. carcharias* may differ to that of older conspecifics (Carlisle et al. 2012; French et al. 2018; Tamburin et al. 2019).

In Australian waters, Malcolm et al. (2001) noted there was a tendency for juveniles to occur in different areas to subadults and adults, with juveniles more commonly encountered in inshore areas, often in the vicinity of open coast beaches. Currently it is not known what stimulates *C. carcharias* to drastically change a life history pattern that keeps them near the continental shelf as juveniles to another that leads them seasonally into a deep pelagic habitat (Domeier and Nasby-Lucas 2012). Nevertheless, Kock (2014) found no difference in residency periods between small or large sharks, or between males and females, or any sex or size-based segregation, at Seal Island in False Bay, South Africa. In fact, sharks of both sexes and a range of sizes were often recorded on a single day, although not always at the same time.

The movement patterns and seasonal abundance of individuals among aggregation sites have largely been identified using a variety of telemetry and visual identification methods. However, an invaluable source of data is derived from logbooks used by permitted marine tourism operators (Malcolm et al. 2001; Bonfil et al. 2005; Johnson and Kock 2006; Jewell et al. 2013; Towner et al. 2013) to monitor shark *C. carcharias* populations. The potential for shark-watching ecotourism as a vehicle for collecting scientific data on the status of shark populations has been recognised by researchers in several countries as an optimum, long-term method of data collection which has minimal delay (Malcolm et al. 2001; Theberge and Dearden 2006; Meyer et al. 2009). Mossel Bay, South Africa, is one such location of shark-watching ecotourism that provides an excellent inshore region for a plethora of *C. carcharias* population investigations.

This study aims to utilise logbook data to investigate the seasonal occurrence and sexual segregation of *C. carcharias* occupying Mossel Bay over a 5-year period, to understand the habitat preferences of different life-stages. This is important because it will help to ascertain whether Mossel Bay is a critical habitat for particular life stages and if this habitat requires conservation management to facilitate the sustainability of the population.

Materials and methods

Study site

Mossel Bay (S' 34° 10, E' 22° 10, Fig. 1) is a semi-closed bay that lies approximately 400 km to the east of Cape Town and is situated centrally within the Agulhas marine bioregion on the southern Cape coast of South Africa (Gubili et al. 2009). The bay encloses three estuaries, Kleinbrak, Grootbrak and Hartenbos, which hosts a diverse ecosystem with many estuarine-dependent marine species (James and Harrison 2008; Johnson et al. 2009a, b). A notable feature within the bay is Seal Island (S' 34° 09, E' 22° 07), which consists of a rocky outcrop located approximately 700 m off the East coast (Gubili et al. 2009) and is host to a cape fur seal *Arctocephalus pusillus pusillus* colony of approximately 4500–5000 individuals (Jewell et al. 2013). The bay is relatively shallow (~20 m) with a flat seabed consisting of exposed reefs and sand (Johnson et al. 2009a, b) and is partially protected from prevailing winds from the south west by the peninsula, resulting in a calm bay ideal for tourism and study (Levy 2016).

Data collection

Data collection was conducted onboard 'Shark Warrior', a shark cage-diving vessel previously owned by White Shark Africa and currently the only commercial dive operator in Mossel Bay. During each outing, the vessel anchored at Seal Island (S' 34° 09, E' 22° 07), and the anchoring position and depth were recorded using the vessel's Furuno NavNet VX2 equipment. Approximately 5 kg of chum consisting of sardine oils and seawater, creating an attractant to *Carcharodon carcharias* (Strong et al. 1992), was deployed during each outing. As *C. carcharias* naturally aggregate in this area, individuals were occasionally observed at the anchor site prior to using any attractant; however, the chum was initiated to attract *C. carcharias* closer to the boat and aid with shark identification. Data collection took place during the full period on the shark observation trip which notably lasted 3 h per time.

The number of individual sharks sighted on each trip was estimated by experienced observers on deck, based on markings on the shark's body, estimated size, sex and presence of any tags recorded on ID sheets. A counted observation was based on the amount of time an individual was in proximity to the boat or interacted with the

Fig. 1 Map of Mossel Bay, showing Seal Island, and the inset map of Mossel Bay on the South African coast. Contour lines indicate depth in metres

bait. If an individual was present for over one minute, it was classed as one observation. The sex of each shark was recorded based on the presence or absence of claspers within the pelvic area, determined by both surface and underwater observations. Individuals that could not be sexed were recorded as unknown. Shark total length (TL) was estimated to the nearest 0.1 m against known dimensions of the shark cage, following Jorgensen et al. (2010), Kock et al. (2013) and Towner et al. (2013). Individuals were categorised into size class, as proposed by Bruce and Bradford (2012): YOY (< 1.75 m), juvenile (1.75–3.0 m), subadult male (3.1–3.6 m), subadult female (3.1–4.8 m), adult male (> 3.6 m) and adult female (> 4.8 m). Individuals were identified based on visible scars, bite wounds, fin notches and coloration, all of which were drawn on physical characterisation data sheets in order to prevent miscounting and an overestimation of shark observations. This information was logged during each trip to provide baseline assessments of species composition and relative abundances, which can yield insights into seasonal cycles and presence in relation to environmental parameters (Theberge and Dearden 2006; Nazimi et al. 2018). A combination of experienced spotters,

both on the boat and in the shark-viewing cage, assisted in eliminating any potential errors associated with poor vertical and horizontal water visibility with *C. carcharias* sightings.

Environmental variables

Sea surface temperature (SST), water temperature at 10 m, cloud cover and vertical water visibility were recorded on anchoring the research vessel, as each variable has been suggested to influence relative abundance of *C. carcharias* (Pyle et al. 1996; Martin et al. 2005; Hammerschlag et al. 2006; Jewell et al. 2013; Kock et al. 2013). SST (measured to the nearest 0.5 °C) was recorded manually using a thermometer placed approximately 2 m into the water column. In instances whereby SST was not recorded, monthly averages were obtained from the NASA Giovanni portal (<http://disc.sci.gsfc.nasa.gov/giovanni>) covering an area of 490 km² in Mossel Bay from the peninsula to Grootbrak river. Water temperature at 10 m was recorded at a depth of 10 m, using the same method for SST. Vertical water visibility (measured to the nearest 0.2 m) was recorded

using a Secchi disk, and cloud cover was recorded to the nearest 5% using human observation.

Data analysis

A Poisson regression analysis was undertaken on the number of *C. carcharias* sighted per trip, with season and sex as categorical predictors, plus interactions between the terms. In addition, a linear regression analysis was undertaken on *C. carcharias* size, with season and sex as categorical predictors, plus interactions between the terms. Individuals of unknown sex were omitted from analyses but have been presented in figures for comparison.

A generalised additive model (GAM) with a negative binomial distribution and a log link function was undertaken on the number of *C. carcharias* sighted per trip, with SST, cloud cover and vertical water visibility as continuous predictors, as the relationship between the response and predictor variables was non-linear. Cubic regression splines were restricted to a maximum of four degrees of freedom. Data were explored following Zuur et al. (2012), and water temperature at 10 m was omitted from the model due to collinearity with SST. Analyses were initially performed using Minitab version 18.2, with further analyses undertaken using RStudio Version 1.2.5001 with the “gam” and “mgcv” packages (Wood 2011).

Results

Over the 5-year study period, 573 cage-diving trips were made to Mossel Bay (Table 1). A total of 3064 *Carcharodon carcharias* were sighted in the Mossel Bay region, ranging in size from 1.1 to 4.0 m. The majority of *C. carcharias* sightings were females (56.9%) and unsexed individuals, with males making up only 6.9% of sightings (Fig. 2). Juveniles dominated the demographic structure (81.1%), and the remaining sightings were primarily subadults, as YOY made up < 1% of *C. carcharias*, and no adult *C. carcharias* were identified in this study.

Abundance and seasonal variation

Significantly more females than males were sighted per trip in Mossel Bay ($\chi^2_{1, 1138} = 245.68$,

$p < 0.001$). In addition, there were significantly more *C. carcharias* sighted per trip during the winter season (June–August) ($\chi^2_{3, 1138} = 46.34$, $p < 0.001$; Fig. 2). There was also a significant interaction between sex and season, whereby the number of females sighted per trip was highest in winter and differed significantly each season, but the number of males sighted per trip was only significantly different (higher) during the winter ($\chi^2_{3, 1138} = 46.11$, $p < 0.001$; Fig. 2). Unsexed *C. carcharias* were sighted more frequently than males throughout the seasons, with highest abundance in the winter months (Fig. 2).

Size and seasonal variation

Female *C. carcharias* were significantly larger than males ($F_{1, 1946} = 24.45$, $p < 0.001$). There was no effect of season on the size (TL) of *C. carcharias* present at the study site ($F_{3, 1946} = 3.31$, $p = 0.069$), although there was a significant interaction between sex and season, whereby smaller males were sighted more frequently during the summer, smaller females were sighted more frequently during the autumn, and larger females were sighted more frequently during the winter ($F_{3, 1946} = 3.67$, $p = 0.012$, Fig. 3). The size of unsexed *C. carcharias* remained relatively constant throughout the year, with smaller individuals sighted during the autumn, and larger *C. carcharias* sighted in the winter months (Fig. 3).

Abundance and environmental variables

Sea surface temperature and vertical water visibility had a significant effect on *C. carcharias* abundance (SST: $z = 17.78$, $p < 0.001$; vertical water visibility: $z = 2.16$, $p < 0.05$), with SST being the most influential variable (adjusted R-squared = 13.3%; Fig. 4). Findings revealed that *C. carcharias* abundance decreased when SST rose, with abundance showing least variation around 16–18 °C and peaked at a vertical water visibility of 5 m (Fig. 4). Although not significant ($z = -1.83$, $p = 0.067$), it was observed that cloud cover had a negative effect on *C. carcharias* abundance with greatest sightings recorded when cloud cover was lower than 70% (Fig. 4).

Table 1 Summary of trips per month and total sightings of *C. carcharias* between November 2009 and February 2013 in Mossel Bay, South Africa

Month	Season	Total number of trips	Total shark sightings
January	Summer	42	260
February	Summer	52	204
March	Autumn	43	151
April	Autumn	36	111
May	Autumn	41	221
June	Winter	64	451
July	Winter	56	429
August	Winter	41	324
September	Spring	35	241
October	Spring	35	130
November	Spring	81	333
December	Summer	47	209
Total		573	3064

Discussion

Abundance and size

Mossel Bay was dominated by sightings of juvenile *Carcharodon carcharias* throughout the study period. This is in agreement with Strong et al. (1996), who suggest that smaller sharks limit their spatial use to

reduce interactions with larger conspecifics. This is further supported by Rykief et al. (2014), who observed a large proportion (78%) of juvenile *C. carcharias* in Mossel Bay, suggesting that these individuals prefer sheltered conditions which may serve to increase their rates of growth and development, and to avoid predation (Branstetter 1990; Heupel et al. 2007). There was also a high predominance of sightings of female

Fig. 2 Average (mean ± SE) number of male, female and unsexed *C. carcharias* per month and season in Mossel Bay, South Africa from 2009 to 2013

Fig. 3 Average (mean $\pm$ SE) length of male, female and unsexed *C. carcharias* per month and season in Mossel Bay, South Africa from 2009 to 2013

Fig. 4 Response plots from generalised additive model (GAM) of environmental variables relative to the presence-absence of *C. carcharias* in Mossel Bay, South Africa. Estimated smooth

functions (solid lines) with 95% confidence interval (shaded area) are shown for each explanatory variable

C. carcharias, whereas male presence was relatively low (Fig. 2), consistent with findings at other seal colonies in South Africa (Cliff et al. 1996; Ferreira and Ferreira 1996; Martin et al. 2005; Fallows et al. 2012; Towner et al. 2013; Rykclief et al. 2014; Hewitt et al. 2017). These findings are similar to Findlay et al. (2016), who identified that 74% of individuals in Mossel Bay were juvenile females. Despite an equal sex ratio at birth (Bruce 2008), high female abundance throughout the year is a common observation in the Southern Cape (Cliff et al. 1996; Towner et al. 2013, 2016; Kock et al. 2013; Hewitt et al. 2017). It is possible that females commonly inhabit the inshore areas, either due to competitive exclusion (Klimley et al. 2001), with larger sharks feeding at sites elsewhere, or to avoid mating harassment (Sims et al. 2001).

The co-occurrence of both sexes throughout the year has been recorded at several locations (Ferreira and Ferreira 1996; Kock and Johnson 2006; Robbins and Booth 2012; Towner et al. 2013, 2016; Kock 2014) and is suggested to be due to shelter, mating opportunities and prey availability. Indeed, Mossel Bay provides sheltered conditions that remain relatively stable throughout the year (Jewell et al. 2013). However, it is unlikely that mating opportunities are an explanation for the occurrence of both sexes in Mossel Bay, as no sharks were large enough to be sexually mature (Fig. 3). This is further supported by Rykclief et al. (2014) and Findlay et al. (2016) who recorded a low number of sexually mature individuals and YOY in the Mossel Bay area. Interestingly, during the winter, there is an abundance of adolescent *Arctocephalus pusillus pusillus* in Mossel Bay (Johnson et al. 2009a). Juvenile *C. carcharias* feed primarily on teleosts and small elasmobranchs before they exhibit an ontogenetic shift in prey preferences (Ainley et al. 1985; Klimley 1985; Hubbell 1996; Jorgensen et al. 2010; Kim et al. 2012). Therefore, despite the fact that juvenile *C. carcharias* predominantly prey on fish, *C. carcharias* are clearly attracted to Mossel Bay during the winter season, likely due to the abundance of vulnerable pinnipeds in the area. Indeed, males and larger (i.e. older) females, as well as unsexed individuals, were sighted more frequently during the winter months (Fig. 3) indicating that they are on the cusp of their ontogenetic shift in prey preferences and likely honing their predatory skills on inexperienced, adolescent seals (Dicken and Booth 2013).

It has been demonstrated that sharks have the potential for social learning within an association which

allows individuals to acquire locally adaptive information (Guttridge et al. 2009, 2012; Pouca et al. 2020). It is possible that the high concentration of juvenile *C. carcharias* in Mossel Bay is observing larger conspecifics and their interactions with prey in which the younger individual learns something (Guttridge et al. 2012). Interestingly, Hammerschlag et al. (2006) observed *C. carcharias* between 2.2 and 4.6 m TL predated upon seals in False Bay, South Africa. This indicates that predation is not entirely limited to sub-adult *C. carcharias* in Mossel Bay, and juveniles may be taking advantage of social learning to facilitate predation before they exhibit changes in their own dietary preferences.

Heupel et al. (2007) defined a nursery area based on the criteria that (1) sharks are more commonly encountered in the area than other areas; (2) sharks have a tendency to remain or return for extended periods; and (3) the area or habitat is repeatedly used across years. Although YOY *C. carcharias* presence was low, they were still observed in the vicinity of Seal Island, and the high concentration of juvenile sharks in Mossel Bay throughout the study duration gives credence to the hypothesis that there is a potential nursery ground in the area. In addition, the co-occurrence of juvenile *C. carcharias* and adolescent seals in the area, particularly during the winter, provides ample opportunity for inexperienced sharks to use this site as a training ground. Juvenile sharks have been witnessed attacking seals in the area on several occasions by the authors during the observation trips. Consequently, Mossel Bay serves as critical habitat for the population of *C. carcharias* in the Cape indicating from the study that *C. carcharias* occupy this area throughout the year. It is therefore essential that this coastal habitat requires a full review of conservation management and it be implemented accordingly to ensure *C. carcharias* are not adversely impacted upon by anthropogenic activities (Heupel et al. 2007; Yates et al. 2012; Kock et al. 2013; Rigby et al. 2019).

Seasonal variation

C. carcharias have an extensive distribution encompassing several sites that they utilise for feeding (Bruce et al. 2005), suggesting seasonal migrations. It is recognised that *C. carcharias* distribution and segregation corresponds with seasonal changes in sea surface temperatures (Ainley et al. 1985; Abascal et al. 2011).

As an endothermic species, *C. carcharias* is capable of tolerating varied temperatures across wide distributions (Graham 1983; Goldman 1997; Boustany et al. 2002). The water temperature in Mossel Bay varied seasonally from 13 to 23.5 °C during the study period and as expected was coolest during the winter season. More sharks, particularly males, were sighted during the cooler winter season, in agreement with previous studies where males were less common in warmer water (Figs. 2 and 4) (Robbins 2007; Robbins and Booth 2012; Dicken and Booth 2013; Kock et al. 2013; Towner et al. 2013). Although likely to vary between species, male sharks occupy waters of cooler temperatures for optimal sperm production (Kime and Hews 1982). However, given the predominance of juveniles present in Mossel Bay, it is unlikely that this is reasoning for males favouring cooler temperatures. The increase in juvenile *C. carcharias* sightings in colder waters in Mossel Bay is contrary to White et al. (2019) but does support other findings that juvenile *C. carcharias* are coastally associated. It is believed that indirect influences of water temperature such as prey availability and differing metabolism may affect *C. carcharias* abundance (Robbins and Booth 2012; Schlaff et al. 2014). As such, our findings suggest that although the abundance of inexperienced *A. pusillus pusillus* pups during the winter months is a controlling factor on *C. carcharias* distribution, the increase in sightings is also indirectly influenced by water temperature.

Vertical water visibility in Mossel Bay varied seasonally from 1 to 12 m. A significant trend between *C. carcharias* abundance and vertical water visibility was observed in this study. Despite an increase in *C. carcharias* sightings with higher visibility, *C. carcharias* were most abundant when vertical water visibility was between 3 and 7 m (Fig. 4). Pyle et al. (1996) demonstrated that lower visibility is favourable for *C. carcharias* stalking ability and is assumed to be a learned tactic in larger sharks (Hammerschlag et al. 2006). The notion that *C. carcharias* are taking advantage of lowered visibility in Mossel Bay for predation cannot be fully supported here. Before undergoing their ontogenetic dietary shift, juvenile *C. carcharias* feed predominantly upon midwater and bottom-dwelling fish, and as a result are less likely to feed at the surface, and therefore will not need to remain cryptic in lower visibility. As aforementioned, high juvenile *C. carcharias* abundance in winter may be factored by

social learning, it is plausible that inexperienced individuals observe the hunting strategies of larger sharks upon adolescent *A. pusillus pusillus* pups in low visibility.

C. carcharias abundance in Mossel Bay was negatively associated with cloud cover (Fig. 4). It has been demonstrated that increased cloud cover and low water visibility are factors which contribute towards *C. carcharias* predation success (Pyle et al. 1996; Martin et al. 2005; Hammerschlag et al. 2006). However, our findings suggest that juvenile *C. carcharias* may not yet fully comprehend the benefits of crypticity for predation on pinnipeds, or simply these techniques are not necessary for predating on mid-water and teleost prey. When interpreting these data, it must be appreciated that increased cloud cover and low vertical water visibility can impede on shark sightings, and not all *C. carcharias* present at Seal Island may be detected by the methods used in this study. Ontogenetic dietary changes in sharks are likely facilitated by adjustments in their hunting abilities (Tricas and McCosker 1984). Further, physical maturation may cause predatory behaviours to change due to improvement in neuromuscular coordination and increased sensory abilities (Meyer 1986; Ciaccio 2008). It is conceivable that maturation improves *C. carcharias* sensory abilities, including visual acuity and electroreception, resulting in larger *C. carcharias* taking advantage of predation in turbid conditions, particularly in areas surrounding pinniped colonies. Therefore, immature, inexperienced *C. carcharias* may be prevalent in conditions which compensate for minimal visual acuity such as low cloud cover which increases ambient light levels.

C. carcharias occupy Mossel Bay throughout all months of the year (Fig. 2 and Table 1); in addition to sheltered conditions and an abundance of prey, it is also likely that juvenile sharks select this coastal environment as an anti-predatory strategy (Heithaus 2007). Findlay et al. (2016) found that *C. carcharias* in Mossel Bay were loosely asocial, meaning that clustering of juveniles was possibly due to protection and hunting efficiency through learned behaviour and scavenging techniques, thus supporting the findings in this study. In the absence of adult *C. carcharias*, juveniles can take advantage of the coastal habitat and learn locally adaptive information such as foraging behaviours and predation. Bruce and Bradford (2012) hypothesised that juvenile sharks may learn to feed on passing prey, rather than actively chasing it down, to maximise predatory

efficiency and minimise energy expenditure. As such, behaviour may have been transmitted culturally, through observing conspecifics in their surroundings, demonstrating how inexperienced sharks can learn from larger sharks in order to develop appropriate hunting strategies.

Nevertheless, the habitat preferences of *C. carcharias* remain uncertain, and aggregations are believed to be loosely structured by sex and size (Findlay et al. 2016; Hewitt et al. 2017). As wildlife tourism can provide industry-based data sources to investigate species abundance and habitat use (Nazimi et al. 2018), the use of mandatory logbook reporting and citizen science data provides a valuable resource in local population studies. Therefore, studies of movements between different sites would greatly benefit our understanding of *C. carcharias* ecology. For example, future research involving tagging individuals or fin identification (Jewell et al. 2011, 2013) could be combined with previous tracking and sighting data gathered at Mossel Bay during cage-diving trips, which would complement the existing data set. This information may aid in future management strategies, identify the critical habitats of *C. carcharias* and emphasise the value in commercial cage diving operations which can produce international data sets needed to assess global populations of *C. carcharias*.

The findings from this study indicate that Mossel Bay has a high concentration of both juvenile and female *C. carcharias*, further strengthening the expectation of female presence in the Southern Cape. It is suggested that, due to the abundance of prey and favourable environmental conditions, Mossel Bay is a nursery ground in the area, providing a crucial habitat for the population of *C. carcharias*. The potential for social learning among juvenile *C. carcharias* in Mossel Bay indicates that this habitat may act as a training ground which minimises the costs and risks of individual exploration and provides distinct behavioural advantages such as predation. Ultimately this could be evidence of a *C. carcharias* training ground, and thus, it should be managed appropriately, with the potential to develop management strategies to help safeguard the future of this vulnerable species.

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Author’s contributions NR, EJ and CF conceptualised the data.

NR, EJ and CK curated the data.

NR, HM and LG analysed the data.

HM, NR and LG led the writing of the manuscript.

All authors contributed critically to the drafts and gave final approval for publication.

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Data availability We agree to archive the data associated with this manuscript should the manuscript be accepted to Nottingham Trent University’s Institutional Repository.

Declarations

Ethics approval Procedures accorded with the standards of Nottingham Trent University’s ethics committee. All research methods were permitted and conducted under the South African Department of Environmental Affairs (D.E.A.) and Forestry and Department of Agriculture, Forestry and Fisheries (D.A.F.F) (Permit reference: V1/8/5/1).

Consent All authors consent to participation and publication of this manuscript.

Conflict of interest The authors declare no conflicts of interest.

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