Behavioural ecology of the critically endangered grey nurse shark (*Carcharias taurus*) and the interaction with scuba diving tourism off eastern Australia

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Abstract

The critically endangered grey nurse shark (*Carcharias taurus*) off eastern Australia is the focus of a non-consumptive, economically important marine wildlife tourism (MWT) industry centred on scuba diving with the sharks. This industry has been identified as a potential threat to the continued survival and recovery of the species. Legislative guidelines and a national code of conduct for scuba diver behaviour were developed to mitigate adverse impacts of MWT on the sharks. This research assessed the putative impacts of scuba diving MWT on grey nurse shark behaviour and the efficacy of management strategies across differing life-history stages and aggregation sites. Underwater stereo-video photogrammetry was used to develop a partial ethogram of the swimming and non-swimming behaviours of grey nurse sharks at locations within aggregation sites during daylight hours without MWT. Predominantly low-energy behaviours were exhibited and no threatening agonistic behaviours were observed. Underwater visual census also documented primarily low-activity swimming behaviours in sharks during interactions with MWT scuba divers of varying demographics and revealed absolute diver compliance with management guidelines. Passive acoustic telemetry showed sharks may have exhibited more active swimming when patrolling between two locations within a site but adopted low-energy swimming behaviours for the majority of the time during daylight hours regardless of scuba diving MWT. Sharks at differing life-history stages probably conserved energy at aggregation sites in association with their migratory movements and reproductive cycles. Differences in the swimming and patrolling behaviours of sharks were attributed to natural variation in environmental conditions (i.e. topography and currents) at the sites as they were not consistent with scuba diving MWT activity. This research strongly suggested that management strategies are effective at protecting the east Australian population of grey nurse sharks from MWT disturbance. Consequently, the grey nurse shark scuba diving MWT industry in its current form is ecologically and economically sustainable.

Student declaration

I, Kirby Rae Smith, declare that the PhD thesis by publication entitled ‘Behavioural ecology of the critically endangered grey nurse shark (*Carcharias taurus*) and the interaction with scuba diving tourism off eastern Australia’ is no more than 100,000 words in length including quotes and exclusive of tables, figures, appendices, bibliography, references and footnotes. This thesis contains no material that has been submitted previously, in whole or in part, for the award of any other academic degree or diploma. Except where otherwise indicated, this thesis is my own work.

Signature: [redacted] **Date:** 1 April 2016

Details of included papers

Chapter	Paper title	Publication status	Publication title and details
Two	Behaviour of aggregated grey nurse sharks (*Carcharias taurus*) off eastern Australia: similarities and differences among life-history stages and sites	Published	Published 2 October 2014, *Endangered Species Research*
Three	Does the grey nurse shark (*Carcharias taurus*) exhibit agonistic pectoral fin depression? A stereo-video photogrammetric assessment off eastern Australia	Published	Published 11 March 2016, *Pacific Conservation Biology*
Four	A re-examination of evidence for agonistic behaviour in sharks	Currently under review	Submitted 16 June 2015, *Marine and Freshwater Behaviour and Physiology*
Five	Potential errors in paired-laser photogrammetric estimates of aggregated grey nurse sharks (*Carcharias taurus*) off eastern Australia: a stereo-video photogrammetric assessment	To be submitted for review	
Six	Scuba diving tourism impacts and environmental influences on the patrolling behaviour of grey nurse sharks (*Carcharias taurus*): a preliminary assessment using acoustic telemetry at Fish Rock, Australia	Accepted for publication	Accepted 5 January 2016, *Tourism in Marine Environments*
Seven	Scuba diving tourism with critically endangered grey nurse sharks (*Carcharias taurus*) off eastern Australia: tourist demographics, shark behaviour and diver compliance	Published	Published 2 May 2014, *Tourism Management*

Declaration by: Kirby Rae Smith **Signature:** [redacted] **Date:** 1 April 2016

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Dedication

This PhD thesis and all of the love, dedication and pride therein is dedicated from a loving daughter to her dearly missed mother, Caron Jones, who died unexpectedly and prematurely on 4 May 2013. Sometimes science reveals more questions than answers, and that is okay.

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Chapter 1

Introduction

1.1 MARINE WILDLIFE TOURISM

Non-consumptive marine wildlife tourism (MWT) provides humans with opportunities to view, photograph, swim with, feed (i.e. provision) and touch marine animals in captive and wild settings (Orams 1999; Zeppel & Muloin 2008b). This worldwide industry has grown substantially in recent decades and increasing demand for opportunities to observe and interact with free-ranging marine wildlife has generated a diverse range of MWT experiences (Orams 1999; Dobson 2006; Higham & Lück 2008; Lück & Higham 2008; Semeniuk et al. 2010). The most popular focal species are large, charismatic megafauna (Gallagher & Hammerschlag 2011) including cetaceans (e.g. Mangott *et al*. 2011; Howes *et al*. 2012), pinnipeds (e.g. Cowling *et al*. 2014), turtles (e.g. Waayers *et al*. 2006) and elasmobranchs (e.g. Newsome *et al*. 2004; Cubero-Pardo *et al*. 2011). Those that are potentially dangerous and/or threatened are especially sought after (Orams 1999; Reynolds & Braithwaite 2001; Miller 2008).

Marine wildlife tourism provides an ecologically-important and economically-viable alternative to consumptive (i.e. lethal) use of wildlife (e.g. Clua *et al*. 2011; Gallagher & Hammerschlag 2011; O’Malley *et al*. 2013). The industry contributes considerably to local, regional and national economies (Sorice *et al*. 2006; Cisneros-Montemayor *et al*. 2010) through direct income to MWT operators and indirect but significant revenue from tourist expenditure on accommodation, food, transport (e.g. airfares, car hire and fuel) and other recreational activities (e.g. Wilson & Tisdell 2003; Jones *et al*. 2009; Mustika *et al*. 2012). Subsequently, MWT can improve employment opportunities and living standards for local and regional communities (e.g. Cisneros-Montemayor *et al*. 2010; Mustika *et al*. 2012; O’Malley *et al*. 2013). Importantly, the socio-economic value of MWT can translate into conservation outcomes as communities and other stakeholders recognise and harness the long-term potential of responsible, non-consumptive use of marine resources (e.g. Brunnschweiler 2010). The experiential and educational benefits of MWT for tourists can foster pro-environmental attitudes (Smith *et al*. 2009) and behaviours which can also realise short- and long-term conservation benefits for target species and the marine environment (Wilson & Tisdell 2003; Christensen *et al*. 2007; Zeppel & Muloin 2008a).

Marine wildlife tourism can also adversely affect target species via pollution (e.g. Newsome *et al*. 2004; Lachmuth *et al*. 2011) and alterations to respiratory (e.g. Lusseau *et al*. 2006), feeding (e.g. Dans *et al*. 2012), resting (e.g. Visser *et al*. 2010), reproductive (Reynolds & Braithwaite 2001) and social (e.g. Scarpaci *et al*. 2000; Steckenreuter *et al*. 2012) behaviours. The spectrum of disturbance ranges from immediate but temporary disruption (e.g. Waayers *et al*. 2006), followed by short-term avoidance of tourists and/or tour vessels (e.g. Stamation *et al*. 2010; Filby *et al*. 2014), then culminates with long-term habitat abandonment/displacement (e.g. Bejder *et al*. 2006b). Modifications to essential behaviours may lead to energetic deficits (e.g. King & Heinen 2004), biochemical changes (e.g. Semeniuk *et al*. 2009), reduced reproductive success (e.g. Lusseau & Bejder 2007), inbreeding (e.g. Clua *et al*. 2010), orphaned young (e.g. Osinga *et al*. 2012), injurious or fatal collisions with vessels (e.g. Ilangakoon 2012; Parsons 2012) and increased predation risk (Christiansen *et al*. 2010) with implications for individual and population fitness. Provisioning introduces another dimension to MWT and deleterious impacts on target species include malnourishment, injury from aggressive competition for resources and from inappropriate human contact, disease, increased exposure to parasites, habituation to provisioning, reduced parental care and attraction to humans and boats (e.g. Newsome *et al*. 2004; Semeniuk *et al*. 2007; Semeniuk & Rothley 2008; Foroughirad & Mann 2013).

The association of people and boats with food increases the susceptibility of provisioned animals to collisions with vessels, their exposure to harvesting and there is also serious concern that it poses risks to human safety (Newsome *et al*. 2004; Dobson 2008).

A range of mandatory (i.e. government legislated) and voluntary (i.e. self-regulated) management strategies have been devised to protect target species from potentially deleterious impacts of MWT. Licensing systems restrict the number of operators allowed in a MWT industry and are typically competitive, involve fees and require adherence to strict regulations (e.g. Scarpaci *et al*. 2003; Mau 2008; Catlin *et al*. 2012). Tourist entry fees can limit the numbers of tourists and prevent overcrowding by dissuading visitation and/or economically excluding some individuals (Orams 1999; Newsome *et al*. 2004). Raising entry fees during peak seasonal periods may also encourage visitation spread (Orams 1999; Newsome *et al*. 2004). The generation of revenue from entry fees should serve a dual function as a user-pays system for management of the MWT industry (Orams 1999; Newsome *et al*. 2004). The user-pays approach charges levies to tourists to directly contribute towards management costs and research (e.g. Mau 2008). Marine protected areas provide target species with varying degrees of refuge from anthropogenic disturbances (e.g. King & Heinen 2004; Howes *et al*. 2012) dependent on the classification of the area. Marine protected areas include the many types of sanctuary zones, reserves and parks ranging widely from strict exclusion to multiple-use zones (Miller 2008). Management guidelines direct the behaviour of MWT operators and/or tourists during interactions with marine wildlife. Legislative regulations (e.g. Scarpaci *et al*. 2004; Allen *et al*. 2007) are legally enforceable with fines, prohibition and/or imprisonment for breaches (Orams 1999) whereas voluntary codes of conduct are managed by the MWT industry (e.g. Parsons & Woods-Ballard 2003; Strong & Morris 2010). Education programs can encourage MWT operators and tourists to adopt environmentally-responsible behaviours through printed material (Scarpaci *et al*. 2004), interpretative signage (e.g. Acevedo-Gutierrez *et al*. 2010), multimedia (e.g. Ballantyne *et al*. 2009), tour guides (e.g. Christensen *et al*. 2007) and scientific presentations (e.g. Foroughirad & Mann 2013). Wildlife management authorities may employ one or several of these approaches (e.g. Mau 2008) and engage with stakeholders and scientists to drive decision-making and the design of management strategies (Miller 2008; Higham *et al*. 2009).

It is important to evaluate the effectiveness of implemented management strategies as success cannot be assumed (e.g. Scarpaci *et al*. 2003; Whitt & Read 2006). Scientific research can inform wildlife managers and stakeholders of the suitability of management regimes and provide recommendations for improving ecological and social outcomes. Monitoring tourist visitation rates and comparing the amount of revenue generated from entry fees and levies with the realised costs of management determines the efficacy of user-pays systems (e.g. Mau 2008). Surveying MWT operators and tourists can gauge the influence of education programs on their behaviour during and after MWT interactions (e.g. Ballantyne *et al*. 2009). Compliance of MWT operators (e.g. Scarpaci *et al*. 2004; Wiley *et al*. 2008) and tourists (e.g. Waayers *et al*. 2006; Acevedo-Gutierrez *et al*. 2010) with licence conditions, marine protect area restrictions, regulations and codes of conduct indicates their ability and willingness to interpret and observe limitations to their behaviour during interactions with marine wildlife. Crucially, the behaviour of target species provides a tangible measure of disturbance and has shown that compliance does not ensure their adequate protection from adverse MWT impacts (e.g. Quiros 2007; Strong & Morris 2010). Assessing compliance and focal species behaviour in tandem is necessary to obtain a holistic assessment of the effectiveness of management strategies (e.g. Curtin *et al*. 2009;

Cowling *et al*. 2014) and to facilitate adaptive management practices (Higham *et al*. 2009).

1.2 SHARKS AND MARINE WILDLIFE TOURISM

Sharks, batoids and chimeroids comprise the cartilaginous fishes of the Class Chondrichthyes (Compagno 2001). The single Order Chimaeriformes in the Subclass Holocephali comprises the chimeroids whereas the Subclass Elasmobranchii is divided into the two Superorders Squalimorphi and Galeomorphi and includes the sharks and batoids (Compagno 2001). Generally, chondrichthyans are characterised by slow growth, late maturation and low fecundity (Dulvy & Forrest 2010). Elasmobranchs mainly occupy marine environments but some species are found in brackish and/or freshwater habitats (Compagno 2001). Sharks represent all of the elasmobranchs with pectoral fins that are not fused to the head and include almost 500 extant species which are contained within four orders from each superorder (Compagno 2001). Importantly, the majority of large shark species (i.e. maximum total lengths exceeding 3.00 metres, Ferretti *et al*. 2010) dominate marine trophic systems and exert considerable influence on ecosystem structure and health (Myers & Worm 2005; Heithaus *et al*. 2008, 2012). Consequently, removal of these apex predators can have disastrous cascading effects as greater mesoconsumer prey populations increase predation on resource species and primary producers with implications for habitat integrity, pollution and oxygen production (Stevens *et al*. 2000; Myers *et al*. 2007; Heithaus *et al*. 2008).

Large sharks have few, if any, natural predators but they are exposed to several serious anthropogenic threats with targeted and incidental (i.e. bycatch) fishing for fins, meat and liver oil most severe, followed by habitat destruction, shark control programs and climate change (Myers & Worm 2005; Topelko & Dearden 2005; Dobson 2008; Dulvy & Forrest 2010; Ferretti *et al*. 2010; Dulvy *et al*. 2014). Industrialised fishing has caused rapid worldwide shark population declines and it was estimated that between the 1950s and 1990s shark populations were reduced to an average 3.3% of their former abundances (Myers & Worm 2003, 2005). The *K*-selected (Pianka 1970), or more recently equilibrium (Winemiller 2005), life-history traits of most sharks make them particularly sensitive to industrialised exploitation and it has been shown that they have twice the extinction risk of bony fishes from fishing mortality (Myers & Worm 2005). Currently, 15.9% of all known shark species (i.e. 465 species) are listed as threatened on the International Union for the Conservation of Nature (IUCN) Red List of Threatened Species with 2.4% considered 'Critically Endangered', 3.2% 'Endangered' and 10.3% 'Vulnerable' (Dulvy *et al*. 2014). Moreover, these are conservative figures as a substantial 45.0% of shark species are 'Data Deficient' (Dulvy *et al*. 2014). It is more likely that 24.7% of all known shark species are threatened as 19.6% of Data Deficient species were also estimated to be threatened (Dulvy *et al*. 2014). A further 14.4% of species are 'Near Threatened' leaving only 24.7% of 'Least Concern' (Dulvy *et al*. 2014).

Shark MWT is a global industry that provides an ecologically important, non-consumptive economic alternative to shark fishing (Brunnschweiler 2010; Techera & Klein 2013) and research has shown that the economic value of a live shark as tourism attraction far outweighs the single-use income retained from fishing (Anderson & Waheed 2001; Topelko & Dearden 2005; Clua *et al*. 2011; Gallagher & Hammerschlag 2011; Vianna *et al*. 2012). Shark MWT has become increasingly popular over the past two decades (Topelko & Dearden 2005; Dobson 2006; Dearden *et al*. 2008; Vianna *et al*. 2012) and tourists can interact with at least 28 species in a wide variety of wild settings (Topelko & Dearden

2005; Gallagher & Hammerschlag 2011). Importantly, 46.4% of these species are listed as Threatened on the IUCN Red List with 39.3% Vulnerable, 7.1% Endangered, 50.0% Near Threatened and 3.6% Data Deficient (IUCN 2015). The filter-feeding basking (*Cetorhinus maximus*) and whale (*Rhincodon typus*) sharks are the two largest fish species in the world and can be observed from aboard boats (Topelko & Dearden 2005; Dobson 2008) and during snorkelling interactions (e.g. Quiros 2007; Mau 2008; Catlin & Jones 2010; Gallagher & Hammerschlag 2011). The Galapagos (*Carcharhinus galapagensis*), scalloped hammerhead (S*phyrna lewini*), silky (*Carcharhinus falciformis*), whale and white-tipped reef (*Triaenodon obesus*) sharks (e.g. Cubero-Pardo *et al*. 2011), grey nurse (*Carcharias taurus*, e.g. Smith *et al*. 2010; Barker *et al*. 2011), grey reef (*Carcharhinus amblyrhynchos*, e.g. Vianna *et al*. 2014) and pelagic thresher (*Alopias pelagicus*, e.g. Oliver *et al*. 2011) sharks form natural aggregations and/or frequent known locations which have facilitated the development of scuba diving MWT operations. In contrast, some MWT operators use chum (i.e. blood and liquefied fish) and/or bait attractants to increase the likelihood of interactions for tourists (Dobson 2008). These more contrived experiences include snorkelling and scuba diving with the bull (*Carcharhinus leucas*, e.g. Brunnschweiler & Barnett 2013), Caribbean reef (*Carcharhinus perezi*, e.g. Maljković & Côté 2011), sicklefin lemon (*Negaprion acutidens*, e.g. Clua *et al*. 2010), silky (e.g. Clarke *et al*. 2011), tiger (*Galeocerdo cuvier*, e.g. Dicken & Hosking 2009; Hammerschlag *et al*. 2012) and whitetip reef (e.g. Fitzpatrick *et al*. 2011) sharks. Provisioning is also used for cage diving interactions with the blue (*Prionace glauca*) shark (e.g. Dobson 2008), Galapagos, sandbar (*Carcharhinus plumbeus*) and tiger (e.g. Meyer *et al*. 2009b) sharks, and white (*Carcharodon carcharias*) shark (e.g. Laroche *et al*. 2007; Huveneers *et al*. 2013; Techera & Klein 2013).

Research on the behaviour of wild sharks is necessary to identify and manage anthropogenic impacts, but can be difficult due to their often elusive nature (Nelson 1977; Pratt & Carrier 2001). Sharks are generally highly mobile (Gruber & Myrberg 1977; Baum & Worm 2009; Chapman *et al*. 2009), wide-ranging (Nelson 1977), often solitary (Guttridge *et al*. 2009) and/or inhabit oceanic environments. An ethogram describes the behaviours of a species and is an important management tool for discerning MWT mediated responses from the natural behaviours of sharks (e.g. Pierce *et al*. 2010). Importantly, sharks have an advanced array of sensory organs (Bres 1993) that preclude the documentation of their finer-scale behaviours under completely natural conditions. A lateral line system sensitive to water displacement and electroreceptors on the snout and head called the ampullae of Lorenzini enable sharks to locate prey (Bres 1993) and other objects in the water including research vessels, cameras and in-water observers. While the potential influence of researcher presence cannot be completely overcome when constructing an ethogram for sharks it can be minimised with careful consideration of sampling technique and design.

The natural migratory behaviour of many shark species have been documented via traditional mark-recapture tagging techniques (e.g. Kohler *et al*. 1998) and more recently with satellite telemetry (e.g. Weng *et al*. 2007; Werry *et al*. 2014). Several migratory movement studies that used satellite telemetry also recorded the vertical movements of the sharks (e.g. Brunnschweiler *et al*. 2010; Stevens *et al*. 2010; Saunders *et al*. 2011; Jorgensen *et al*. 2012). The residencies and localised movements of numerous shark species have been identified using mark-resight tagging techniques (e.g. Heyman *et al*. 2001) and passive (e.g. Heupel *et al*. 2006; Huveneers *et al*. 2006; Hearn *et al*. 2010; Bessudo *et al*. 2011; Dudgeon *et al*. 2013; Werry *et al*. 2014) and active (e.g. Klimley &

Nelson 1984; Gruber *et al*. 1988; Strong *et al*. 1992; Goldman & Anderson 1999; Rechisky & Wetherbee 2003) acoustic telemetry. Similarly, shark foraging behaviour has been documented with passive acoustic telemetry (e.g. Klimley *et al*. 2001; Meyer *et al*. 2009a) and a combination of active acoustic telemetry and animal-borne conventional video cameras (e.g. Heithaus *et al*. 2002). Passive acoustic telemetry has also been used to study the swimming (e.g. Johnson *et al*. 2009), social (e.g. Guttridge *et al*. 2010) and aggregation (e.g. Economakis & Lobel 1998; Heupel & Simpfendorfer 2005) behaviours of sharks. Other techniques used to describe aggregation behaviour include aerial photography (e.g. Wilson 2004), aerial surveys (e.g. de la Parra Venegas *et al*. 2011) and conventional videography (e.g. Rezzolla *et al*. 2014).

The tendency of several species to form aggregations has facilitated research on the finer-scale behaviours of sharks. Schooling behaviour has been quantified using still stereo photogrammetry (e.g. Klimley & Brown 1983; Klimley 1981/82, 1985). Foraging behaviour has been assessed from the surface using videography (e.g. Heyman *et al*. 2001; Martin & Hammerschlag 2012) and visual observations (e.g. Martin *et al*. 2005). Reproductive behaviour has been documented underwater with videography and/or still photography (e.g. Pratt & Carrier 2001; Whitney *et al*. 2004) and using accelerometry (e.g. Whitney *et al*. 2010). Agonistic behaviour has been described using still stereo photogrammetry (e.g. Klimley 1981/82, 1985) and photographs of non-aggregated individuals (e.g. Brunnschweiler & Pratt 2008). In contrast, agonistic behaviour purposefully elicited under non-provisioned and provisioned conditions was documented by scuba divers (e.g. Johnson & Nelson 1973) and from within a submersible (e.g. Nelson *et al*. 1986) using videography and underwater visual census (UVC). The swimming and social behaviours of sharks in semi-natural settings were also quantified from visual surface observations and UVC (e.g. Myrberg & Gruber 1974).

Various behaviours of sharks associated with MWT in non-provisioned and provisioned settings have been documented at several spatial and temporal scales. Research using surface observations and UVC documented avoidance behaviours in whale sharks that were significantly related to the distance of MWT snorkelers (Quiros 2007) and boats, and the arrival of a second group of snorkellers (Pierce *et al*. 2010). Whale sharks also exhibited avoidance behaviours and violent shudders when they were feeding and when snorkelers obstructed their path, touched them or used flash photography (Quiros 2007). Another UVC study reported short-term avoidance behaviours in Galapagos, scalloped hammerhead, silky, whitetip reef and whale sharks when MWT scuba divers approached the sharks directly and/or at distances less than 4 metres, exhibited sudden movements and moved while observing the sharks (Cubero-Pardo *et al*. 2011). Initial observations using remote videography documented some interruption to the grooming behaviour of pelagic thresher sharks with the arrival of MWT scuba divers (Oliver *et al*. 2011).

Studies of provisioning MWT using UVC showed that the abundance of bull sharks (Brunnschweiler & Baensch 2011) and residency of sicklefin lemon sharks (Clua *et al*. 2010) significantly increased over the years at feeding sites and the sicklefin lemon sharks exhibited more aggression towards conspecifics and divers during provisioning. A study that used underwater videography also reported agonistic behaviour in blacktip sharks (*Carcharhinus limbatus*) towards scuba divers as they ascended from a feeding site (Ritter & Godknecht 2000). Research that used a combination of UVC and passive acoustic telemetry found that bull sharks (Brunnschweiler & Barnett 2013) also spent significantly more time at provisioning sites on days when attractants were used as did other passive acoustic telemetry work on silky (Clarke *et al*. 2011) and white (Huveneers *et al*. 2013) sharks. Moreover, studies using time-depth recorders reported significantly more vertical activity in whitetip reef sharks during daylight hours on days with provisioning MWT (Fitzpatrick *et al*. 2011). Conversely, studies that used UVC and passive acoustic telemetry showed that provisioning did not alter the site residency or localised movements of Caribbean reef sharks (Maljković & Côté 2011) and that conditioning of white sharks to a provisioning vessel was unlikely as only brief responses to chum were elicited (Laroche *et al*. 2007). Research with satellite telemetry also found that there were no significant differences in the long-range migrations and habitat usage of tiger sharks between sites with and without provisioning MWT (Hammerschlag *et al*. 2012). Similarly, MWT operator logbook information indicated that cage diving did not permanently attract Galapagos, sandbar and tiger sharks to provisioning sites but sandbar sharks were excluded from the sites over the years by the larger Galapagos and tiger sharks (Meyer *et al*. 2009b).

1.3 GREY NURSE SHARK (*Carcharias taurus*)

The grey nurse shark (*Carcharias taurus* Rafinesque 1810) is a galeomorph in the Order Lamniformes (mackerel sharks), is one of three species in the Family Odontaspididae (odontaspidids) and is known elsewhere as the sandtiger (United States of America) and raggedtooth (South Africa) shark (Compagno 2001). The grey nurse shark is an ideal target species for MWT and ethological research due to its large size, deceivingly formidable appearance, relatively placid temperament and propensity to form natural aggregations at known locations (Pollard *et al*. 1996; Compagno 2001; Otway & Ellis 2011). Aggregation sites are typically inshore rocky reefs and islands where the sharks are often observed by scuba divers swimming slowly or hovering motionless near the seabed in and around sand-, shell grit- and boulder-filled gutters, swim-throughs and underwater caves at depths usually between 15 and 25 metres (Pollard *et al*. 1996; Compagno 2001; Hayward 2003; Otway & Ellis 2011).

The grey nurse shark has a widespread but disjunct global distribution in warm-temperate and tropical coastal waters (Compagno 2001) with the major extant populations now restricted to the east coasts of North and South America, South Africa and Australia where there are two genetically-distinct populations on the east and west coasts (Cavanagh *et al*. 2003; Stow *et al*. 2006; Ahonen *et al*. 2009). The shark primarily feeds on fish (Bass *et al*. 1975), grows to approximately 3.20 metres (Last & Stevens 2009), has longevity of about 35 years (maximum estimates: males = 30 years, females = 40 years, Goldman *et al*. 2006), is slow to mature (50.0% sexual maturity: males = 2.10 metres at 6-7 years, females = 2.59 metres at 10-12 years, Goldman *et al*. 2006; Otway & Ellis 2011) and has low fecundity with a maximum of two pups born biennially (0.95-1.20 metres) after a 9-12 month gestation that includes intrauterine cannibalistic and oophagous phases (Gilmore *et al*. 1983; Compagno 2001). These *K*-selected or equilibrium life-history traits necessitate decades for recovery from worldwide population declines caused by targeted and incidental commercial and recreational fishing and accordingly, the grey nurse shark is listed globally as ‘Vulnerable’ on the IUCN Red List (Cavanagh *et al*. 2003; Otway *et al*. 2004).

The east Australian population of grey nurse sharks has been subjected to intense anthropogenic pressure from commercial (Cavanagh *et al*. 2003) and recreational fishing (Pepperell 1992), spearfishing (Cropp 1964) and shark control programs (Dudley 1997; Reid *et al*. 2011), and is now restricted to coastal waters from Yeppoon in southern

Queensland to Eden in southern New South Wales (NSW, Otway & Ellis 2011). Consequently, this population is currently estimated to comprise between 1146 and 1662 sharks (Lincoln Smith & Roberts 2010) and is listed as ‘Critically Endangered’ by the IUCN (Cavanagh *et al*. 2003) and under Commonwealth (*Environmental Protection and Biodiversity Conservation Act 1999*) and state (Queensland: *Nature Conservation Act 1992*, NSW: *Fisheries Management Act 1994*) legislation.

The migratory and localised movements of grey nurse sharks off eastern Australia have been documented using mark-resight tagging techniques (Otway & Burke 2004), active and passive acoustic telemetry (Bruce *et al*. 2005; Bansemer & Bennett 2009; Otway *et al*. 2009) and satellite telemetry (Otway & Ellis 2011). The six recognised life-history stages of grey nurse sharks comprising pups at 0-1 years, juvenile males, juvenile females, adult males, gestating females and adult, resting-phase females exhibit differing migratory movements that are interspersed with residencies at aggregation sites of less than a day to in excess of six months (Bansemer & Bennett 2009; Otway *et al*. 2009; Otway & Ellis 2011). The sharks spend most of the time (i.e. ≈74.0%) at depths less than 40 metres but have been recorded as deep as 232 metres (Otway & Ellis 2011). Adult male and female sharks undertake respective annual and biennial migrations between Queensland and NSW of up to 4500 kilometres in association with the reproductive cycle (Otway *et al*. 2009; Bansemer & Bennett 2009; Otway & Ellis 2011). Adult males travel north to Queensland during autumn and winter then return south to NSW in late spring and summer for mating in early autumn (Otway & Parker 2000; Otway *et al*. 2009; Otway & Ellis 2011). Adult females also migrate north to Queensland during autumn and winter with mating at aggregation sites from the mid-north coast of NSW to southern Queensland (Otway & Parker 2000; Bansemer & Bennett 2009). Copulation ceases in late spring and early summer when gestating females segregate from the remainder of the population by maintaining residency off southern Queensland (Bansemer & Bennett 2009). Currently, Wolf Rock is the only known east Australian aggregation site where this occurs (Bansemer & Bennett 2009). Gestating females then migrate south over winter and spring for parturition at aggregation sites off central and southern NSW (Otway *et al*. 2003; Otway & Ellis 2011). Postpartum, resting females remain off central and southern NSW for the next year to replenish energy reserves expended during gestation for impending reproduction (Otway & Ellis 2011). It is likely that the pups remain at parturition sites for around eight months before cooler seawater temperatures drive them into warmer offshore waters (Castro 1993; Dicken *et al*. 2006). Juvenile male and female sharks occupy aggregation sites off the mid-northern and higher southern latitudes of NSW for the majority of the year then exhibit smaller southerly migrations of 100-400 kilometres in accordance with seasonal changes to sea surface temperatures during spring and summer (Otway & Parker 2000; Otway *et al*. 2009; Otway & Ellis 2011). The localised movements of grey nurse sharks at east aggregation sites are generally restricted to within 1.5 kilometres of the main structure (Bruce *et al*. 2005; Bansemer & Bennett 2009; Otway *et al*. 2009; Otway & Ellis 2011).

Many of the east Australian grey nurse shark aggregation sites support a long-standing MWT industry centred on scuba diving with the sharks. Preliminary work found that the grey nurse shark scuba diving MWT industry contributes substantially to local, regional and state economies with an annual revenue estimate of approximately $9 million AUD gauged solely from the direct income of selected MWT operators (Hassall & Associates Pty Ltd & Gillespie Economics 2004). Importantly, this MWT industry has also been identified as a potential threat to the continued survival and recovery of this critically endangered species (EA 2002). Consequently, federal (*Environmental Protection and Biodiversity Conservation Act 1999*, DSEWPC 2012) and state (Queensland: *Marine Parks Act 2004*, QG 2010a, 2010b, NSW: *Fisheries Management Act 1994*, NSWG 2010) legislative guidelines for scuba diver behaviour were implemented to mitigate any adverse impacts of MWT on the sharks. The Code of Conduct for Diving with Grey Nurse Sharks was also developed following consultation with MWT operators and recreational scuba divers (Otway *et al*. 2003) and incorporated in the national recovery plan for the species in 2002 (EA 2002).

A preliminary study using UVC reported 88.0-100.0% compliance with legislative and voluntary management guidelines by MWT scuba divers at one grey nurse shark aggregation site in NSW (Smith *et al*. 2010). Despite high compliance, the sharks increased swimming activity during interactions with more than six divers and exhibited some non-swimming behaviours when there were six or more divers present at distances less than two metres (Smith *et al*. 2010). Similarly, a study (Hayward 2003) that used UVC at a different NSW aggregation site documented 66.0-100.0% compliance with the code of conduct by divers and increased shark swimming activity when divers were at distances less than 4 metres. In contrast, videography was used to quantify the swimming and respiratory behaviours of grey nurse sharks at a separate site in NSW and found that activity increased in response to purposeful breaches of management guidelines (Barker *et al*. 2011). Importantly, passive acoustic telemetry research showed that scuba diving MWT did not affect the localised movements of grey nurse sharks as they did not leave aggregation sites when dive vessels and scuba divers were present (Otway *et al*. 2009).

1.4 AIMS OF THE STUDY

The continued survival and recovery of the critically endangered east Australian population of grey nurse sharks is hinged on the mitigation of adverse anthropogenic influence on the species. This research sought to enhance and expand existing assessments of the impacts of scuba diving MWT on the behaviour of grey nurse sharks and the efficacy of management strategies by using differing techniques to sample various life-history stages across multiple aggregation sites. The specific aims of this research were to:

(1) Develop a partial ethogram for east Australian grey nurse sharks by studying their swimming and non-swimming behaviours during daylight hours across differing life-history stages and aggregation sites in the absence of scuba diving tourism and commercial and recreational fishers;

(2) Quantify grey nurse shark pectoral fin angles in relation to the distances of scuba divers across multiple life-history stages (i.e. time) and aggregation sites (i.e. space);

(3) Examine the data and citations used to determine the degree of support for the putative agonistic behaviours reported for 23 shark species in a previous review;

(4) Use stereo-video photogrammetric angular and morphometric measurements to assess the accuracy of paired-laser photogrammetric length estimates of critically endangered east Australian grey nurse sharks;

(5) Document the patrolling behaviour of grey nurse sharks at Fish Rock (off South West Rocks, NSW) and to assess the putative impacts of scuba diving on this behaviour; and

(6) Provide a preliminary understanding of grey nurse shark scuba diving tourist demographics, quantify the behaviours of divers and grey nurse sharks during diver-shark interactions, and assess the compliance of divers with regulatory and voluntary grey nurse shark scuba diving guidelines in the coastal waters off eastern Australia.

Chapter 2

Behaviour of aggregated grey nurse sharks (*Carcharias taurus*) off eastern Australia: similarities and differences among life-history stages and sites

Declaration of co-authorship and co-contribution: papers incorporated in thesis by publication

Declaration by: Kirby Rae Smith **Signature:** [redacted]

Date: 1 April 2016

Paper Title: Behaviour of aggregated grey nurse sharks (*Carcharias taurus*) off eastern Australia: similarities and differences among life-history stages and sites

In the case of the above publication, the following authors contributed to the work as follows:

Name	**Contribution %**	**Nature of contribution**
Kirby R Smith	70	Study concept, experimental design, fieldwork, data collection, statistical analysis and interpretation, manuscript writing, manuscript editing
Nicholas M Otway	15	Study concept, experimental design, fieldwork, data collection, advice on statistical analysis and interpretation, manuscript editing
Carol Scarpaci	10	Study concept, experimental design, data collection, manuscript editing
Brett M Louden	5	Fieldwork, data collection

DECLARATION BY CO-AUTHORS

The undersigned certify that:

1. They meet criteria for authorship in that they have participated in the conception, execution or interpretation of at least that part of the publication in their field of expertise;
2. They take public responsibility for their part of the publication, except for the responsible author who accepts overall responsibility for the publication;
3. There are no other authors of the publication according to these criteria;
4. Potential conflicts of interest have been disclosed to **a)** granting bodies, **b)** the editor or publisher of journals or other publications, and **c)** the head of the responsible academic unit; and
5. The original data is stored at the following location(s):

Location(s): College of Engineering and Science, Victoria University, Melbourne, Victoria, Australia

and will be held for at least five years from the date indicated below:

		Date
Kirby R Smith	[redacted]	12 November 2014
Nicholas M Otway	[redacted]	7 November 2014
Carol Scarpaci	[redacted]	10 November 2014
Brett M Louden	[redacted]	7 November 2014

ABSTRACT

Stereo-video photogrammetry was used to document swimming and non-swimming behaviours of various life-history stages of the grey nurse shark (*Carcharias taurus*) at eight east Australian aggregation sites (during daylight) in the absence of scuba diving tourism and fishers. Swimming behaviours included hovering, milling and active swimming with significantly greater milling. Rates of movement were least during milling and greatest for active swimming. Pectoral fins were held 20-24° below horizontal which was consistent with holding positions reported in shark swimming studies. Significantly lower caudal fin positions during hovering probably minimised forward propulsion. Tail beat frequency decreased significantly with increasing total length and was likely due to greater propulsion from larger caudal fins. Low activity indicated sharks minimised energy expenditure when aggregated which was associated with migratory and reproductive behaviours. Significantly different pectoral fin positions among sites likely resulted from differing navigational requirements. Non-swimming behaviours were infrequent. Chafing, gill puff, head snapping and palatoquadrate protrusion were generally categorised as grooming behaviour. One gill puff sequence and all but one rapid withdrawal event were categorised as ‘flight’ response agonistic behaviour. The remaining rapid withdrawal and stand back were to avoid collision and categorised as swimming behaviour. The absence of ‘fight’ response agonistic behaviour was consistent with previous descriptions of the species as docile. This partial ethogram will enhance ecological understanding, assist assessment and management of diving tourism, and contribute to the recovery and long-term conservation of this critically endangered species.

2.1 INTRODUCTION

An ethogram provides a descriptive account of behaviours exhibited by a species and can be enhanced with quantitative analyses of the durations, frequencies and extent of events. Behavioural events are instantaneous (Altmann 1974), sequences of events comprise repeated similar or differing events in a random or specific order, whereas behavioural states exist for extended periods of time (Altmann 1974; Mann 1999). Preliminary observations are important to discriminate between behavioural events or states so the most appropriate, efficacious sampling methods can be identified. A comprehensive ethogram can be developed for a species by studying behavioural events and states across differing life-history stages and spatial and temporal scales, and may also identify factors influencing behaviour. Ethograms produced in natural conditions provide baseline data that has been used to identify essential habitat (e.g. Lusseau & Higham 2004) and assess human impacts on animal behaviour (e.g. Lundquist *et al*. 2012b). This information has subsequently revealed the need for management intervention (e.g. Pierce *et al*. 2010) and been used to formulate and/or improve management strategies to mitigate disturbances (e.g. Bruce *et al*. 2005; Dans *et al*. 2012). Behavioural studies have largely focused on terrestrial vertebrates, particularly birds and mammals (Bonnet *et al*. 2002; Jennions & Møller 2003; Ord *et al*. 2005), and have extended to the marine environment with cetacean research dominant (e.g. Mann 1999). Studies of reptiles and fish are less prevalent (Bonnet *et al*. 2002; Jennions & Møller 2003) but advances in electronic tags and photography have facilitated increased research.

The behaviours of sharks are among the least understood as they are a diverse taxon with almost 500 extant species (Compagno 2001) and occupy numerous habitats (Bres 1993).

Large-scale migratory behaviours have been documented through cooperative tagging programs (Kohler *et al*. 1998), satellite (e.g. Brunnschweiler *et al*. 2010; Stevens *et al*. 2010) and acoustic tagging (e.g. Werry *et al*. 2014). Conversely, aggregated sharks have facilitated behavioural observations of reproduction (e.g. Pratt & Carrier 2001; Whitney *et al*. 2004) and social interactions (e.g. Klimley & Nelson 1984; Guttridge *et al*. 2009), foraging/feeding (e.g. Heyman *et al*. 2001; Heithaus *et al*. 2002), habitat selection and usage (e.g. Gruber *et al*. 1988; Werry *et al*. 2012), agonistic interactions (e.g. Johnson & Nelson 1973; Martin 2007), interactions with tourist snorkelers or scuba divers (e.g. Quiros 2007; Cubero-Pardo *et al*. 2011) and abnormal/stereotypic displays associated with provisioning tourism (e.g. Laroche *et al*. 2007; Miller *et al*. 2011; Brunnschweiler & Barnett 2013) for various species.

The grey nurse (sandtiger, ragged-tooth) shark, *Carcharias taurus*, (Rafinesque 1810) has a disjunct distribution in warm-temperate and tropical regions (Compagno 2001), primarily feed on fish (Bass *et al*. 1975), are slow to reach reproductive maturity (Goldman *et al*. 2006; Otway & Ellis 2011) and have a maximum of two pups born biennially (Gilmore *et al*. 1983). Fishing has resulted in worldwide population declines requiring decades for recovery (Mollet & Cailliet 2002; Otway *et al*. 2004) and globally, grey nurse sharks are listed as ‘Vulnerable’ by the International Union for the Conservation of Nature (IUCN) (Cavanagh *et al*. 2003). In Australian waters, two genetically-distinct grey nurse shark populations exist on the east and west coasts (Stow *et al*. 2006; Ahonen *et al*. 2009). Historically, the east coast population has been subjected to numerous anthropogenic impacts (Otway *et al*. 2004; Otway & Ellis 2011), is estimated to comprise 1146 to 1662 individuals (Lincoln Smith & Roberts 2010) and is listed as ‘Critically Endangered’ by the IUCN (Cavanagh *et al*. 2003) and under Commonwealth and state legislation. Off eastern

Australia, adult grey nurse sharks undergo annual (male) and biennial (female) migrations between New South Wales (NSW) and Queensland (QLD) waters (≈4500 kilometres) linked to their reproductive cycles (Bansemer & Bennett 2009; Otway & Ellis 2011). Juvenile sharks migrate over smaller spatial scales (≈100-400 kilometres) within NSW waters according to seasonal sea-surface temperatures (Otway *et al*. 2009; Otway & Ellis 2011). The migratory movements are punctuated by the occupation of aggregation sites for varying periods of time (Otway *et al*. 2009; Otway & Ellis 2011). Many of these sites also support a marine wildlife tourism industry focused on passive scuba diver-shark interactions (Smith *et al*. 2010, 2014; Barker *et al*. 2011). This sector has previously been identified as a potential threat to the species' recovery (EA 2002) and consequently, a voluntary code of conduct and regulations for scuba diving were implemented to mitigate possible adverse impacts on the sharks (EA 2002; Talbot *et al*. 2004; Smith *et al*. 2014).

The propensity of grey nurse sharks to aggregate also makes them particularly well-suited to ethological study, yet little is known about their behaviours at these sites. Consequently, the aim of this study was to develop a partial ethogram for east Australian grey nurse sharks by studying their swimming (states) and non-swimming (events) behaviours during daylight hours across differing life-history stages and aggregation sites in the absence of scuba diving tourism and commercial and recreational fishers. Importantly, this sampling strategy enables greater generalisation of observed behaviours to the entire population and an improvement on previous studies focusing on few life-history stages and/or sites. Behavioural information obtained in the absence of scuba diving tourism is also fundamental to assessing the impacts of this marine wildlife tourism sector and directing its future management. The ethogram developed will provide a baseline for behavioural comparison that will enhance existing and future assessments of the sustainability and management of this tourism industry (i.e. Hayward *et al*. 2003; Otway *et al*. 2009; Smith *et al*. 2010, 2014) by enabling modifications to natural behaviour to be identified.

2.2 MATERIALS AND METHODS

2.2.1 Study sites and sampling

Observations of swimming and non-swimming behaviours were obtained by a maximum of three scuba divers using underwater stereo-video photogrammetry in the absence of scuba diving tourism (Smith *et al*. 2014) and commercial/recreational fishing. Sampling was conducted at eight aggregation sites spanning ≈800 kilometres of the Australian east coast (Figure 2.1) from March to May in the austral autumn of 2010 to target five grey nurse shark life-history stages (Table 2.1) comprising juvenile males, juvenile females, adult males, gestating females and resting females known to occupy the sites at various times of year (Bansemer & Bennett 2009; Otway & Ellis 2011).

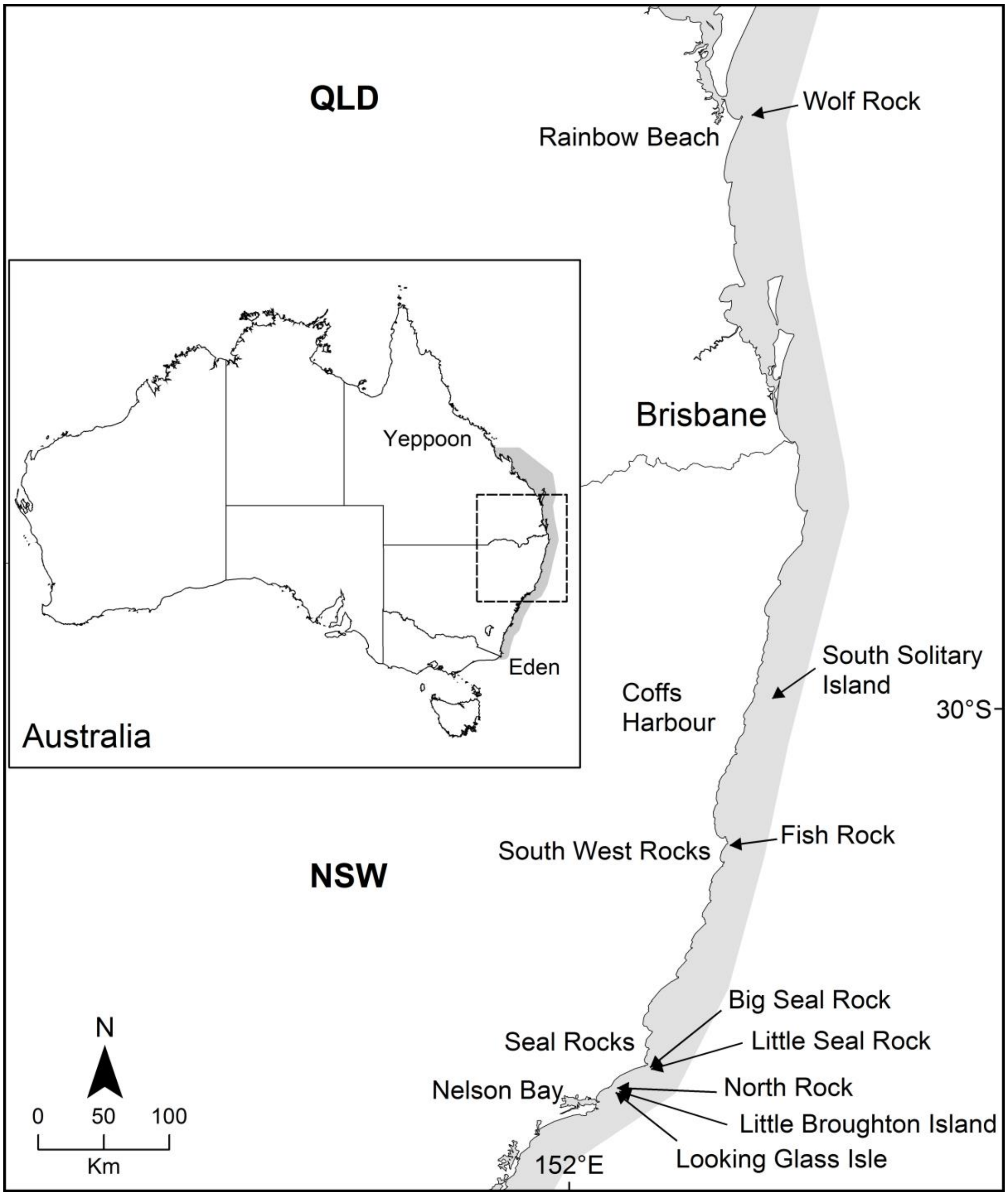

Figure 2.1. Map showing the geographic range (grey shading) of the grey nurse shark (*Carcharias taurus*) and the location of Wolf Rock, South Solitary Island, Fish Rock, Big Seal Rock, Little Seal Rock, North Rock, Little Broughton Island and Looking Glass Isle sampled from March to May 2010 to document the swimming and non-swimming behaviours of sharks along the east coast of Australia.

Habitats at these sites (Table 2.1) vary spatially, exhibit general similarities (e.g. gutters, overhangs) but differ in physical and biological variables (e.g. the kelp *Ecklonia radiata*, Underwood *et al*. 1991) with sea-surface temperatures ranging from 19 to 28°Celsius annually as a result of interacting processes (Otway & Ellis 2011). Frequent adverse weather events occur throughout the year limiting site access and scuba diving.

Table 2.1. Summary of the coastal towns, aggregation sites (physical and biological attributes) and sampling periods in 2010 used to document the swimming and non-swimming behaviours of the grey nurse shark (*Carcharias taurus*) at different life-history stages (LHS, juvenile males = JM; juvenile females = JF; adult males = AM; gestating females = GF; resting females = RF).

Coastal town	Aggregation site	Sampling period	LHS present	Physical and biological attributes of aggregation site		
				Depth (metres)	Topography	Presence of kelp (*Ecklonia radiata*)
Rainbow Beach	Wolf Rock	May	GF	25-35	Sand-filled gutters	None
Coffs Harbour	South Solitary Island	May	JM, JF, AM	10-35	Rock arch, sand-filled gutters and overhangs	None
South West Rocks	Fish Rock	May	JM, JF, AM, RF	10-35	Cave and sand/shell grit-filled gutters	None
Seal Rocks	Big Seal Rocks	April	JM, JF, RF	10-35	Caves and sand-filled gutters with boulders	None
Seal Rocks	Little Seal Rocks	April	JM, JF, RF	20-40	Caves and sand-filled gutters with boulders	None
Nelson Bay	North Rock	March	JM, JF, RF	15-20	Sand-filled gutter with boulders	On gutter wall in shallow water (5 metres)
Nelson Bay	Little Broughton Island	March	JM, JF, RF	5-10	Topographically complex with cave, boulders and small crevices. Surge from breaking waves reaches the seabed	Widely distributed across entire habitat
Nelson Bay	Looking Glass Isle	March	JM, JF, RF	15-35	Sand/boulder-filled gutter	None

2.2.2 Underwater stereo-video photogrammetry system

A purpose-built, underwater stereo-video photogrammetry system (USVPS) comprising two Sony digital video cameras (Model DCR VX2100E) that recorded 24 frames per second was operated by a single scuba diver to capture videos of grey nurse sharks (further details: Otway *et al*. 2008; Shortis & Harvey 1998). The cameras were attached 77 centimetres apart to a precisely-machined aluminium base bar and were angled inwardly by 4° to ensure overlapping left and right images. A synchronisation unit at the distal end of a 125 centimetre-long aluminium rod was mounted at the middle of and perpendicular to the base bar. Prior to field sampling the USVPS was calibrated using a standardised protocol in a public swimming pool with a 140 × 140 × 140 centimetre anodised aluminium calibration cube with 80 predetermined, reflective points and subsequent use of specialised software (Cal Version 1.20, ©SeaGIS Pty Ltd). The USVPS enabled stereo images of sharks with a total length (TL) of 3.00 metres at a minimum range of 3.00 metres, additional morphometric measurements (Compagno 2001) and the documentation of swimming and non-swimming behaviours.

After field sampling, videos were downloaded and saved in AVI format with Adobe Premiere (Version 6.0) and then analysed with EventMeasure (©SeaGIS Pty Ltd) which uses a ‘point and click’ approach with synchronised images from the left and right cameras to measure various lengths. The software computed various lengths and the range to the base bar (in millimetres) with estimates of a known length obtained accurate and precise to ±0.2 and ±0.3-1.2%, respectively (Otway *et al*. 2008).

2.2.3 Grey nurse shark life-history stages

Grey nurse shark life-history stages present at each site were determined using the general methods of Smith *et al*. (2014) and USVPS length measurements. Precaudal length (PCL, Figure 2.2a) was measured from the tip of the snout to the precaudal pit (Compagno 2001; Last & Stevens 2009) and selected because of greater accuracy than TL (Francis 2006). Total length was then calculated (nearest millimetre) using a significant linear regression (i.e. TL = 1.368PCL + 0.069 with TL and PCL in metres, $n = 66$, $R^2 = 0.99$, $P < 0.001$) developed via necropsies (Otway *et al*. 2004, 2008). Sexual maturity was determined from gender (claspers in males), TL and maturity ogives (i.e. 50.0% sexual maturity: males = 2.10 metres at 6-7 years, females = 2.59 metres at 10-12 years, Goldman *et al*. 2006; Otway & Ellis 2011). The numbers (percentages) of juvenile male, juvenile female, adult male, gestating female and resting female sharks occupying each site were then quantified.

2.2.4 Grey nurse shark swimming behaviours

Previously-described swimming behaviours of grey nurse sharks (Table 2.2) were quantified at each site from the stereo-videos using instantaneous scan samples (Altmann 1974) separated by 30-second intervals. Scanning commenced when the entire body of at least one shark was present within the field of view for at least 10.00 seconds. During the scan, the swimming behaviour of each shark within 10.00 metres of the USVPS was recorded and the proportions of sharks exhibiting different swimming behaviours were calculated. Scanning ceased when all sharks left the field of view for ≥5 seconds (i.e. 120 frames). The number of scans of sharks in each behavioural state (hovering, milling and active swimming) at each site and across all sites were then calculated as percentages of the total number of scans per site and sites combined (Smith *et al*. 2014).

Table 2.2. Descriptions of the swimming and non-swimming behaviours of the grey nurse shark (*Carcharias taurus*) previously observed in the wild and in captivity (* denotes reference was used for behavioural description only and was taken from a different shark species).

Behaviour category Behaviour type	General description	Grey nurse sharks	
		Location observed	Reference
Swimming			
Active/accelerated swimming	Persistent movement in a general direction at a greater speed than milling	Wild	Hayward (2003); Smith *et al*. (2010, 2014)
Cruising	Low level of activity without directional change	Wild	Hayward (2003)
Hovering	Sharks appear to be motionless	Wild	Hayward (2003); Smith *et al*. (2014)
Milling	Low level of activity with frequent directional changes within the same area	Wild	Smith *et al*. (2010, 2014)
Non-swimming			
Feeding			
Solitary	Solitary individuals take prey	Captivity	Gilmore *et al*. (1983)
Cooperative	Shark school surrounds and concentrates schooling prey, sometimes with tail slapping to stun prey and subsequent tail popping	Wild	Compagno (2001); Cliff (1988), cited in Martin (2007)
Reproductive			
Clasper flexion	Movement of a clasper forward and outward	Wild Captivity	*Myrberg & Gruber (1974); Smith *et al*. (2010) Gordon (1993)
Cupping	Female forms a cup-like shape with pelvic fins immediately prior to flaring	Captivity	Gordon (1993)
Flaring	Outward flaring of pelvic fins to expose the cloaca	Captivity	Gordon (1993)
Following/tailing	Shark closely follows conspecific, restricting the movement of its caudal fin	Captivity	*Myrberg & Gruber (1974); Gordon (1993)

Table 2.2 continued. Descriptions of the swimming and non-swimming behaviours of the grey nurse shark (*Carcharias taurus*) previously observed in the wild and in captivity (* denotes reference was used for behavioural description only and was taken from a different shark species).

Behaviour category Behaviour type	General description	Grey nurse sharks	
		Location observed	Reference
Non-swimming			
Reproductive			
Nosing	Male approaches female from behind and underneath to place his snout beneath her cloaca	Captivity	Gordon (1993)
Shielding	Female shark swims close to the substrate to avoid male shark approaches to her cloaca	Captivity	Gordon (1993)
Snapping	Male inflicting a swift bite to a perceived threat	Captivity	Gordon (1993)
Splaying	Extension of both claspers upward and/or outward or crossing of claspers	Captivity	Gordon (1993)
Stalking	Circling and closely swimming past other species	Captivity	Gordon (1993)
Stalling	Ceasing forward motion to hover above the substrate	Captivity	Gordon (1993)
Submission behaviour	Female swims very slowly with her head lowered (approximately 15° below the longitudinal axis) to expose her pelvic region	Captivity	Gordon (1993)
Mating bites	Male bites the pectoral fins of a female to hold her in position for mating, causing scarring around her pectoral fins and head	Wild Captivity	Bass *et al*. (1975); Gilmore *et al*. (1983); Bansemer & Bennett (2009) Gordon (1993)
Parturition	Gestating female shark gives birth to a maximum of two pups born headfirst	Captivity	Gilmore *et al*. (1983); Henningsen *et al*. (2004)

Table 2.2 continued. Descriptions of the swimming and non-swimming behaviours of the grey nurse shark (*Carcharias taurus*) previously observed in the wild and in captivity (* denotes reference was used for behavioural description only and was taken from a different shark species).

Behaviour category Behaviour type	General description	Grey nurse sharks	
		Location observed	Reference
Non-swimming			
Respiratory			
Active ventilation/ buccal pumping	Opening and closing of the mouth to facilitate water movement over the gills	Wild Captivity	Smith *et al*. (2010); Barker *et al*. (2011) Hannon & Crook (2004)
Passive/ram ventilation	Slight opening of the mouth to enable water to pass over the gills, typically adopted during milling and active swimming	Wild Captivity	Barker *et al*. (2011) Hannon & Crook (2004)
Grooming			
Chafing	Rolling of the body along the substrate to remove possible parasites	Wild	*Myrberg & Gruber (1974); Hayward (2003)
Gill puff	Sustained or momentary expansion of the gills to remove object(s) and/or readjust muscular control	Wild	*Myrberg & Gruber (1974); Smith *et al*. (2010)
Agonistic			
Charging	Fast approach towards a perceived threat, usually concluded by a quick turn away when close	Wild	Martin (2007)
Flank displaying	Sustained (i.e. >5 seconds) exposure of the underside toward a perceived threat	Wild	Martin (2007)
Give-way	Shark changes course of direction to avoid an approaching conspecific	Captivity	*Myrberg & Gruber (1974); Hannon & Crook (2004)
Jaw gaping	Slow, sustained opening of the mouth and wider than during ram ventilation	Wild	Martin (2007); Smith *et al*. (2010)
Open jawed tooth raking	Upper dentition of shark makes forceful and injurious contact with a perceived threat	Wild	Martin (2007)

Table 2.2 continued. Descriptions of the swimming and non-swimming behaviours of the grey nurse shark (*Carcharias taurus*) previously observed in the wild and in captivity (* denotes reference was used for behavioural description only and was taken from a different shark species).

Behaviour category Behaviour type	General description	Grey nurse sharks	
		Location observed	Reference
Non-swimming			
Agonistic			
Pectoral fin depression	Sustained (i.e. >5 seconds) and severe depression of both pectoral fins	Wild	*Johnson & Nelson (1973); Martin (2007); Barker *et al*. (2011)
Rapid withdrawal	Fast movement away from a perceived threat	Wild	Martin (2007); Smith *et al*. (2010)
Reduced swimming efficiency	Shark appears almost stationary despite exaggerated swimming movements	Wild	Martin (2007)
Stiff or jerky movement	Awkward body movements during swimming	Wild	Martin (2007); Smith *et al*. (2010)
Tail cracking/popping	Loud, abrupt sound sometimes generated by the very fast movement of the caudal fin during rapid withdrawal	Wild	Hayward (2003); Martin (2007); Smith *et al*. (2010); Barker *et al*. (2011)
Tail slapping	Swift movement of the caudal fin at the surface, hitting or splashing a perceived threat	Wild	Martin (2007)

2.2.4.1 Tail beats

Grey nurse shark tail beat frequency (TBF, in beats per minute) when hovering, milling and active swimming was documented for each shark sampled for pectoral fin angle (PFA) and caudal fin angle (CFA). A tail beat was defined as the movement of the tail from the midline to the left or right and back to the midline (Hannon & Crook 2004; Barker *et al*. 2011) and were counted for each shark whilst in the field of view.

2.2.4.2 Rates of movement

Estimates of the rate of movement (ROM, in metres per second) were obtained from grey nurse sharks selected using continuous observation (Altmann 1974) at each site. The ROM was only quantified for milling or active swimming as there is no forward motion when hovering. The PCL, gender and time elapsed from when the shark snout entered the field of view until the anterior edge of the precaudal pit became visible were recorded.

2.2.4.3 Pectoral fin positions

Continuous observation (Altmann 1974) was again used to select grey nurse sharks for sampling the left or right PFA, gender and PCL whilst hovering, milling and active swimming at each site. The PFA (Figure 2.2a, b) was defined as the angle subtended by point *A* (see below), the pectoral fin insertion (point *B*) and the pectoral fin apex (point *C*). The USVPS was used to measure (nearest millimetre) the length from the top (point *D*) to the bottom (point *E*) of the fifth gill slit (line *DE*, Figure 2.2a, c), pectoral fin length (PFL) from the pectoral fin origin at the bottom of fifth gill slit (point *E*) to the pectoral fin free rear tip (point *F*, line *EF*), and the length between the pectoral fin apex and the top of the fifth gill slit (line *CD*). Further regression relationships developed from necropsy data were used to assist with some pectoral fin calculations. Pectoral fin height (PFH, line *BC*, Figure 2.2a, c) was calculated using PFL in a significant linear regression of PFH = 1.212PFL - 22.752 ($n = 53$, $R^2 = 0.96$, $P < 0.001$). Pectoral fin base length (PFBL, line *BE* = *AD*, Figure 2.2a, c) was then calculated using PFL in a significant linear regression of PFBL = 0.671PFL - 25.537 ($n = 53$, $R^2 = 0.94$, $P < 0.001$) as the pectoral fin insertion (point *B*) could not always be observed in the video frames. As point *A* could not be accurately identified on the shark, it was located at the top of an imaginary line of equal length to the fifth gill slit (i.e. line $AB = DE$) and positioned perpendicular to the pectoral fin insertion (point *B*, Figure 2.2c). With lengths *AD* and *CD* known, the length of line *AC* was calculated using the Pythagorean formula. Finally, PFA (angle *ABC*) was calculated using the law of cosines (De Sapio 1976) with $ABC = \arccos [(BC^2 + AB^2 - AC^2)/2(BC \times AB)]$. The PFA of turning sharks together with the turn duration (seconds) were quantified where possible.

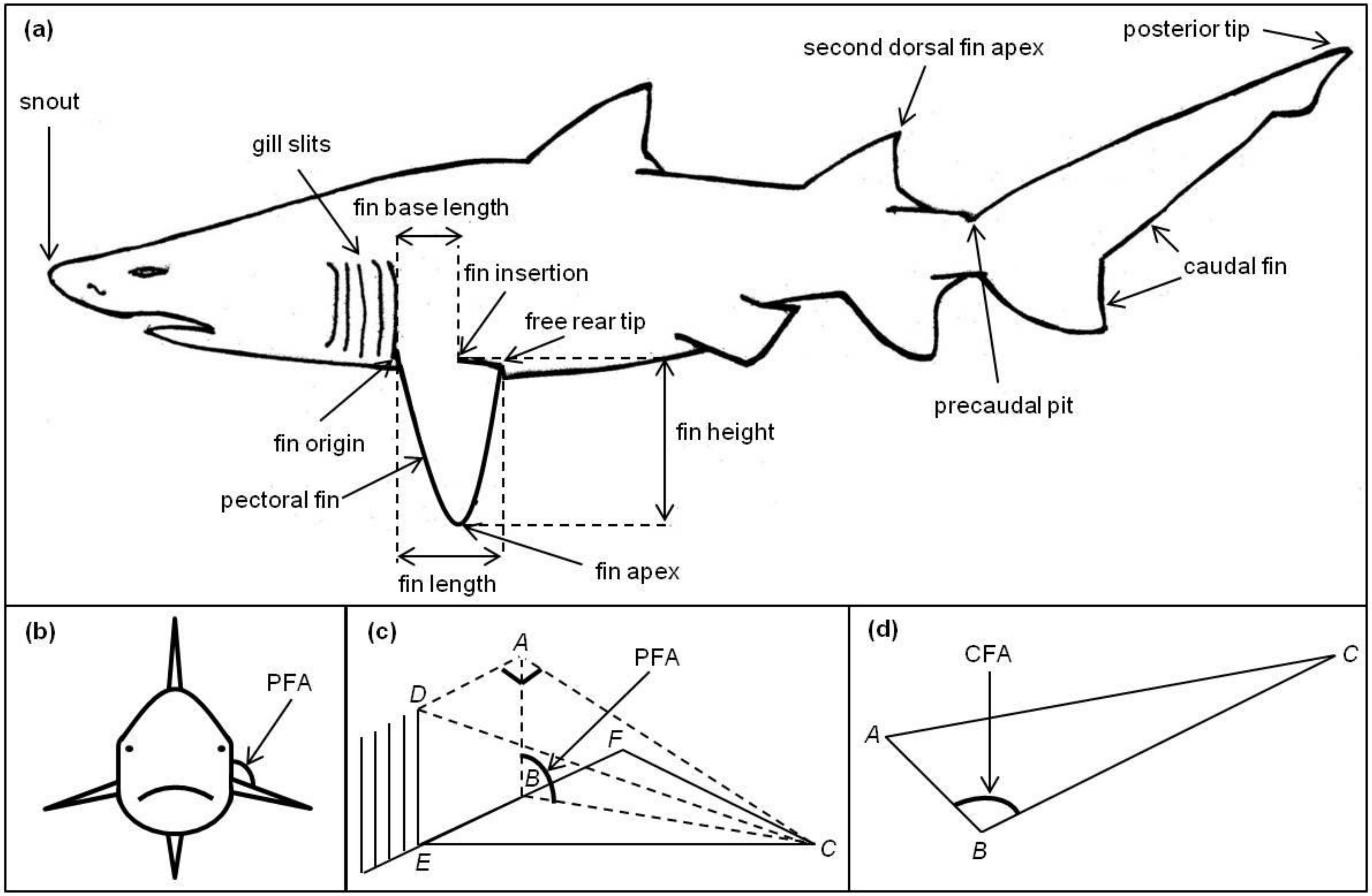

Figure 2.2. Illustration showing the morphometric (a, b) and trigonometric (c, d) distances measured to calculate the pectoral fin angle (PFA) and caudal fin angle (CFA) of the grey nurse shark (*Carcharias taurus*).

2.2.4.4 Caudal fin positions

The CFA (Figure 2.2a, f) was defined as the angle subtended by the second dorsal fin apex (point *A*), the anterior edge of the precaudal pit (point *B*) and the caudal fin posterior tip (point *C*) and was measured after the PFA was quantified. Lengths *AB*, *BC* and *AC* were measured (nearest millimetre) with the USVPS and CFA calculated using the law of cosines.

2.2.5 Grey nurse shark non-swimming behaviours

Non-swimming behaviours of grey nurse sharks (Table 2.2) were quantified from the stereo-videos obtained at each site using continuous observation (Altmann 1974) of all sharks simultaneously and the general methods of Smith *et al*. (2010). Active respiration rates (i.e. buccal pumping) were quantified as the number of buccal pumps per minute for hovering and milling sharks. For other non-swimming behaviours the focal shark's gender, PCL and distance to the nearest conspecific (nearest millimetre), behaviour duration (nearest hundredth of a second), number of conspecifics ≤10.00 metres from the USVPS and likely behavioural trigger(s) were documented. Where possible, PFA and CFA were measured and additional morphometric measurements were obtained for some behaviours. Behavioural events repeated by the same shark within 20.00 seconds of the initial occurrence were considered components of a sequence (Altmann 1974).

2.2.6 Statistical analyses

Statistical analyses were done with an initial Type I (α) error rate of $P = 0.05$. Data for TBF, PFA and CFA were repartitioned into swimming behaviours, life-history stages, sites and gender so each dataset generated four separate analyses. Consequently, the familywise error rate was calculated using the Šidák-Bonferroni adjustment (Šidák 1967) which resulted in a significance level of $P < 0.05$ in these analyses. Grey nurse shark life-history stages were summarised for each site and compared using a contingency table analysis. Sampling effort and swimming behaviour (including TBF and ROM, where possible) were examined using balanced 1- or 2-factor analyses of variance (ANOVA) with arcsine transformation of proportional data and Cochran's test for homogeneity of variances (Underwood 1997). When variances were heterogeneous a power transformation was used for ordinal data. The existence of serial correlation was examined via plots of residuals against time and tested with the Durbin-Watson statistic (Durbin & Watson 1950, 1951; Farebrother 1980). To enhance data independence, approximately 30.0% of the scans recorded per site were randomly selected and used for analyses (Smith *et al*. 2014). Where possible, *post-hoc* pooling of the interaction term and subsequently either main effect in the fully-orthogonal, 2-factor ANOVA was done when the terms were not significant at $P \geq 0.25$ (Underwood 1997) to increase the power of the test. After ANOVA, significant differences among means were identified using Student-Newman-Keuls (SNK) tests (Underwood 1997). The TBF and ROM were plotted against TL for swimming behaviours and examined for significant linear relationships. The PFA and CFA were also plotted against TL and TBF for all swimming behaviours to test for associations.

Analyses of PFA and CFA among swimming behaviours, life-history stages, sites and gender were done using various tests associated with the Von Mises (circular normal) distribution (Batschelet 1981). Rayleigh tests determined whether there were significant mean directions among PFA and CFA according to swimming behaviours, life-history stages, sites and gender (Batschelet 1981). Angular variances were calculated and significant differences among mean angles were examined using Watson-Williams two- and multi-sample *F* tests (Batschelet 1981).

2.3 RESULTS

2.3.1 Sampling effort

Stereo-videos were obtained during 29 research dives across the eight sites and yielded 35, 46, 41, 53, 43, 47, 46 and 16 scans at Wolf Rock, South Solitary Island, Fish Rock, Big Seal Rock, Little Seal Rock, North Rock, Little Broughton Island and Looking Glass Isle, respectively. The mean duration of synchronised video per dive (range = 8.27-11.09 minutes) did not differ significantly among sites (ANOVA: $F_{7,8} = 1.18$, $P = 0.41$). Similarly, the duration of observations assessing shark life-history stages and swimming and non-swimming behaviours did not differ significantly among sites (ANOVA: $F_{7,8} = 2.65$, $P = 0.10$) indicating consistent sampling effort across all sites. Numbers of grey nurse sharks varied markedly across sites (range = 9-79 sharks) and totalled 273 individuals from five life-history stages comprising 14 juvenile males, 138 juvenile females, 53 adult males, 18 gestating females, eight resting females and a further 42 sharks of undetermined gender.

2.3.2 Grey nurse shark life-history stages

Numbers of grey nurse sharks in the five life-history stages varied and proportions of juveniles and adults differed significantly among sites (chi-square test: $\chi^2_7 = 107.92$, $P < 0.001$). The Wolf Rock population (*n* = 18) comprised gestating females (100.0%) whereas at South Solitary Island sharks (*n* = 22) were mainly adult males (72.7%) and some juveniles (27.3%). At Fish Rock, the population (*n* = 15) comprised juveniles and adults of both genders with adult males (40.0%) and juvenile females (33.3%) predominant. Similarly, at Big Seal Rock sharks (*n* = 79) comprised mainly juvenile females (46.8%) and adult males (34.2%). Sharks at Little Seal Rock (*n* = 33) were primarily juvenile females (81.8%), but there were some adults (12.1%). The North Rock population (*n* = 67) comprised juveniles and adults, but was dominated by juvenile females (89.6%). Lastly, sharks at Little Broughton Island (*n* = 30) and Looking Glass Isle (*n* = 9) were all juveniles and included at least four pups.

2.3.3 Grey nurse shark swimming behaviours

Hovering, milling and active swimming were the main swimming behaviours exhibited by grey nurse sharks in this study (Figure 2.3).

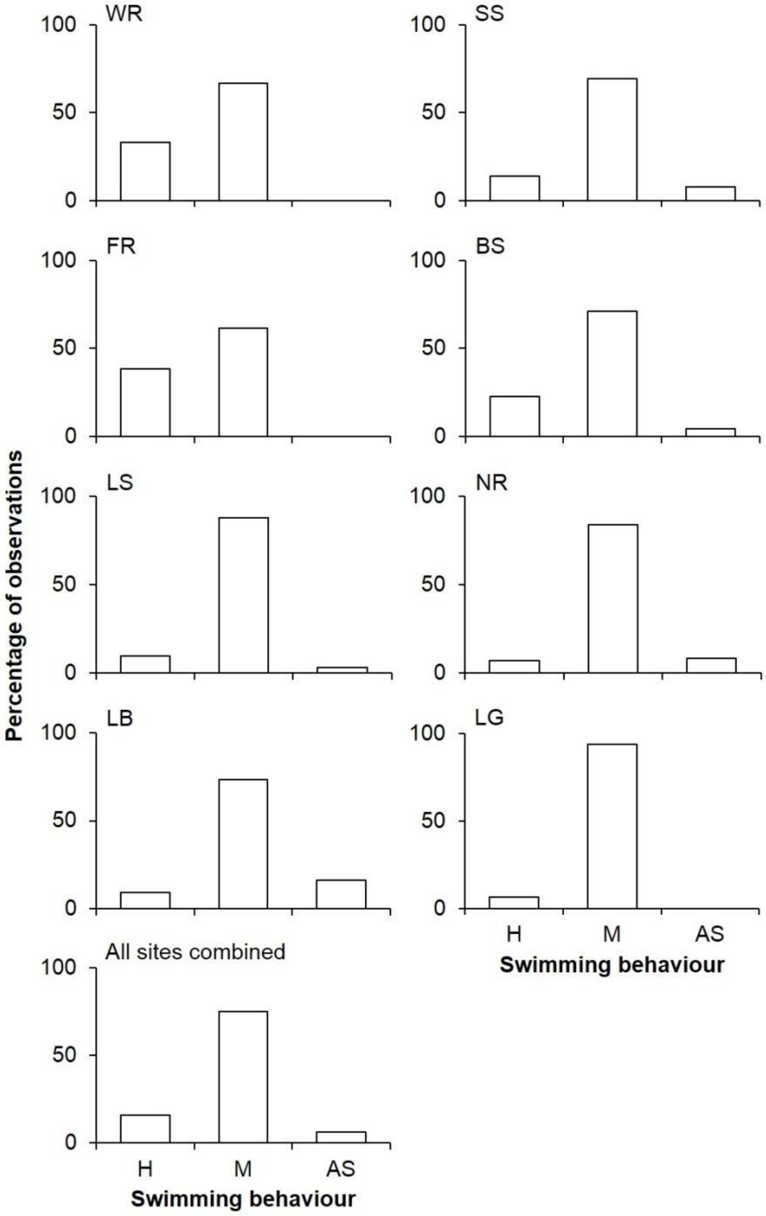

Figure 2.3. Observations of the swimming behaviour of the grey nurse shark (*Carcharias taurus*) with the frequency of occurrence of hovering (H), milling (M) and active swimming (AS) sampled at Wolf Rock (WR), South Solitary Island (SS), Fish Rock (FR), Big Seal Rock (BS), Little Seal Rock (LS), North Rock (NR), Little Broughton Island (LB) and Looking Glass Isle (LG) from March to May 2010.

Hovering sharks faced into a current and did not gain net forward motion as their tail beats maintained a stationary position in the water column (Table 2.3). Milling comprised slow movements and incorporated frequent directional changes either confined to a particular area within a gutter or encompassed the entire gutter with turns at either end (Table 2.3). Turning was achieved by momentary depression of a pectoral fin to initiate a horizontal turn in the direction of the depressed fin. The mean (±SD, range) duration of measured turns was 5.61 (± 3.46, 2.04-10.20) seconds with the relevant measureable pectoral fin depressed to 134° and a mean (angular variance, range) CFA of 78 (6, 59-97)°. Active swimming sharks were generally solitary individuals that showed unidirectional movements at greater speeds than milling and covered the spatial extent of an entire gutter (Table 2.3).

Table 2.3. Mean (±SD, range) tail beat frequencies (TBF, in beats per minute) and rates of movement (ROM, in metres per second) of the grey nurse shark (*Carcharias taurus*) with sample sizes (*n*) and mean (±SD, range) shark total lengths (TL, in metres) according to swimming behaviours, life-history stages, sites and gender sampled at Wolf Rock, South Solitary Island, Fish Rock, Big Seal Rock, Little Seal Rock, North Rock, Little Broughton Island and Looking Glass Isle from March to May 2010.

Category	TBF			ROM		
Variable	*n*	Mean frequency (±SD), range	Mean TL (±SD), range	*n*	Mean rate (±SD), range	Mean TL (±SD), range
Swimming behaviours						
Hovering	46	12.76 (14.11), 0.00-48.83	2.33 (0.30), 1.57-2.98	0	-	-
Milling	139	20.04 (15.08), 0.00-67.42	2.23 (0.37), 1.45-3.13	9	0.55 (0.16), 0.36-0.81	2.10 (0.34), 1.64-2.52
Active swimming	33	58.28 (19.15), 26.43-109.89	2.00 (0.38), 1.44-2.93	3	0.88 (0.08), 0.81-0.97	1.93 (0.32), 1.63-2.27
Life-history stages						
Juvenile males	6	18.71 (18.33), 0.00-53.98	1.96 (0.13), 1.71-2.09	0	-	-
Juvenile females	107	29.73 (24.48), 0.00-109.89	1.95 (0.07), 1.44-2.57	9	0.62 (0.20), 0.36-0.85	1.96 (0.33), 1.63-2.52
Adult males	76	20.92 (17.16), 0.00-63.97	2.38 (0.14), 2.13-2.71	2	0.74 (0.33), 0.51-0.97	2.31 (0.06), 2.27-2.35
Gestating females	18	18.50 (13.43), 0.00-47.35	2.80 (0.15), 2.53-3.01	0	-	-
Resting females	11	7.19 (6.94), 0.00-19.62	2.83 (0.15), 2.63-3.13	0	-	-
Sites						
Wolf Rock	18	18.50 (13.43), 0.00-47.35	2.80 (0.15), 2.53-3.01	0	-	-
South Solitary Island	53	17.81 (15.54), 0.00-63.97	2.33 (0.19), 1.93-2.71	0	-	-
Fish Rock	23	19.85 (16.18), 0.00-55.40	2.33 (0.32), 1.57-2.86	1	0.51	2.35
Big Seal Rock	31	23.72 (20.22), 0.00-64.05	2.25 (0.28), 1.75-2.79	4	0.63 (0.25), 0.39-0.97	2.41 (0.13), 2.27-2.52
Little Seal Rock	29	24.48 (16.25), 0.00-73.71	2.00 (0.26), 1.71-2.65	3	0.64 (0.26), 0.36-0.85	1.80 (0.09), 1.74-1.90
North Rock	38	25.40 (23.75), 0.00-74.07	2.21 (0.36), 1.57-3.13	2	0.69 (0.16), 0.58-0.81	2.03 (0.06), 1.98-2.07
Little Broughton Island	18	50.98 (32.53), 3.49-109.89	1.63 (0.17), 1.44-2.00	1	0.81	1.63
Looking Glass Isle	8	29.25 (19.25), 0.00-67.42	1.82 (0.18), 1.55-2.01	1	0.40	1.64

Table 2.3 continued. Mean (±SD, range) tail beat frequencies (TBF, in beats per minute) and rates of movement (ROM, in metres per second) of the grey nurse shark (*Carcharias taurus*) with sample sizes (*n*) and mean (±SD, range) shark total lengths (TL, in metres) according to swimming behaviours, life-history stages, sites and gender sampled at Wolf Rock, South Solitary Island, Fish Rock, Big Seal Rock, Little Seal Rock, North Rock, Little Broughton Island and Looking Glass Isle from March to May 2010.

Category		TBF			ROM		
	Variable	*n*	Mean frequency (±SD), range	Mean TL (±SD), range	*n*	Mean rate (±SD), range	Mean TL (±SD), range
Gender							
	Male	82	20.76 (17.13), 0.00-63.97	2.35 (0.18), 1.71-2.71	2	0.74 (0.33), 0.51-0.97	1.96 (0.33), 1.63-2.52
	Female	136	26.42 (23.32), 0.00-109.89	2.13 (0.43), 1.44-3.13	9	0.62 (0.20), 0.36-0.85	2.31 (0.06), 2.27-2.35

Swimming behaviour data were not serially correlated as plots of residuals against time showed random patterns and Durbin-Watson tests were not significant ($d = 1.44$-1.83 across all tests, $P > 0.05$). The fully-orthogonal, 2-factor ANOVA with sites (random) and swimming behaviour (fixed) showed the sites × swimming behaviour interaction and sites main effect were non-significant ($P = 0.55$ and $P > 0.99$, respectively). *Post-hoc* pooling of these terms showed milling (74.9%) was exhibited significantly more than hovering (15.9%) which was, in turn, significantly greater than active swimming (6.2%) (ANOVA: $F_{2, 117} = 46.64$, $P < 0.0005$ and SNK test: $P < 0.05$). Mean TBF differed significantly among swimming behaviours and sites (ANOVA: $F_{2, 96} = 76.31$, $P < 0.0005$ and $F_{7, 56} = 2.22$, $P < 0.05$, respectively) but not life-history stages or gender (ANOVA: $F_{4, 25} = 1.22$, $P = 0.33$ and $F_{1, 162} = 0.15$, $P = 0.70$, respectively). Mean TBF was significantly greater during active swimming compared with milling and hovering which did not differ (Table 2.3, SNK test: $P < 0.05$). Although the SNK test was inconclusive, the mean TBF was substantially greater at Little Broughton Island than other sites (Table 2.3). Quantifying the ROM proved more difficult and constrained the number of replicates obtained, hence data were not analysed statistically and merely tabulated (Table 2.3). Nevertheless, there was a trend towards a greater mean ROM for active swimming compared with milling (Table 2.3). The TBF significantly decreased as TL increased for milling and active swimming, but these linear regressions only accounted for 11.6 and 34.8% of the respective variances (Table 2.4). Conversely, there was no significant linear regression relationship with TBF on TL when sharks were hovering or between ROM and TL when milling and active swimming were combined.

Table 2.4. Linear regression equations (test statistic = *F*) of tail beat frequency (TBF, in beats per minute) and rates of movement (ROM, in metres per second) on total length (TL, in metres) for the grey nurse shark (*Carcharias taurus*) when hovering, milling and active swimming with sample sizes (*n*) and goodness of fit (R^2) sampled at Wolf Rock, South Solitary Island, Fish Rock, Big Seal Rock, Little Seal Rock, North Rock, Little Broughton Island and Looking Glass Isle from March to May 2010.

Relationship Swimming behaviour	Equation	*n*	R^2	*F*	*P*
TBF on TL					
Hovering	$y = -0.6987x + 14.388$	46	0.0002	0.01	0.92
Milling	$y = -13.857x + 50.903$	139	0.1164	18.05	0.0004
Active swimming	$y = -29.857x + 117.96$	33	0.3479	16.54	0.0003
ROM on TL					
Milling and active swimming combined	$y = -0.06x + 0.7536$	12	0.0093	0.09	0.77

Mean PFA did not differ significantly among swimming behaviours, life-history stages or gender (Watson-Williams tests: $F_{2, 205} = 0.33$, $P > 0.25$; $F_{4, 203} = -0.54$, $P > 0.25$; $F_{1, 206} = -0.25$, $P > 0.25$, respectively) but exhibited significant differences among sites ($F_{7, 200} = 4.83$, $P < 0.0005$). Mean PFA was greatest at Little Broughton Island, least at Wolf Rock and North Rock, and similar at the remaining sites (Table 2.5).

Mean CFA differed significantly among swimming behaviours (Watson-Williams tests: $F_{2, 215} = 12.39$, $P < 0.0005$), but not life-history stages, sites or gender (Watson-Williams tests: $F_{4, 213} = 1.28$, $P > 0.10$; $F_{7, 210} = 1.36$, $P > 0.25$; $F_{1, 216} = -66.53$, $P > 0.25$, respectively). Mean CFA was least when sharks were active swimming or milling and greatest when hovering (Table 2.5). The PFA and CFA were not correlated with TL or TBF during hovering, milling or active swimming.

Table 2.5. Mean (angular variance, range) pectoral fin angles (PFA, in degrees) and caudal fin angles (CFA, in degrees) of the grey nurse shark (*Carcharias taurus*) with sample sizes (*n*), tests for significance of directionality (Rayleigh test statistic = *z*) and mean (±SD, range) shark total lengths (TL, in metres) according to swimming behaviours, life-history stages, sites and gender sampled at Wolf Rock, South Solitary Island, Fish Rock, Big Seal Rock, Little Seal Rock, North Rock, Little Broughton Island and Looking Glass Isle from March to May 2010 where $P \geq 0.05$ = not significant, denoted by 'ns' and $P < 0.05$ = *; $P \leq 0.01$ = **; and $P \leq 0.001$ = *** with Šidák-Bonferroni adjustment (Šidák 1967).

Category	PFA				CFA			
Variable	*n*	Mean angle (angular variance), range	*z*	Mean TL (±SD), range	*n*	Mean angle (angular variance), range	*z*	Mean TL (±SD), range
Swimming behaviours								
Hovering	44	110 (6), 67-152	39.79***	2.32 (0.30), 1.57-2.98	46	113 (1), 93-132	4.87***	2.33 (0.30), 1.57-2.98
Milling	135	112 (5), 65-178	123.11***	2.24 (0.36), 1.55-3.13	139	106 (2), 84-139	134.80***	2.23 (0.37), 1.45-3.13
Active swimming	29	114 (4), 75-152	26.90***	2.07 (0.35), 1.49-2.93	33	102 (2), 65-127	32.03***	2.00 (0.38), 1.44-2.93
Life-history stages								
Juvenile males	6	117 (1), 100-124	5.87***	1.96 (0.13), 1.71-2.09	6	108 (1), 98-115	5.93***	1.96 (0.13), 1.71-2.09
Juvenile females	99	116 (5), 71-178	90.98***	1.98 (0.25), 1.49-2.57	107	106 (2), 84-139	103.42***	1.95 (0.27), 1.44-2.57
Adult males	75	111 (4), 67-159	69.91***	2.38 (0.14), 2.13-2.71	76	109 (1), 91-129	74.55***	2.38 (0.14), 2.13-2.71
Gestating females	17	100 (7), 65-152	14.98***	2.80 (0.15), 2.53-3.01	18	105 (5), 65-138	16.55***	2.80 (0.15), 2.53-3.01
Resting females	11	98 (7), 67-136	9.65***	2.83 (0.15), 2.63-3.13	11	112 (1), 98-128	10.75***	2.83 (0.15), 2.63-3.13

Table 2.5 continued. Mean (angular variance, range) pectoral fin angles (PFA, in degrees) and caudal fin angles (CFA, in degrees) of the grey nurse shark (*Carcharias taurus*) with sample sizes (*n*), tests for significance of directionality (Rayleigh test statistic = *z*) and mean (±SD, range) shark total lengths (TL, in metres) according to swimming behaviours, life-history stages, sites and gender sampled at Wolf Rock, South Solitary Island, Fish Rock, Big Seal Rock, Little Seal Rock, North Rock, Little Broughton Island and Looking Glass Isle from March to May 2010 where $P \geq 0.05$ = not significant, denoted by 'ns' and $P < 0.05$ = *; $P \leq 0.01$ = **; and $P \leq 0.001$ = *** with Šidák-Bonferroni adjustment (Šidák 1967).

Category	PFA				CFA			
Variable	*n*	Mean angle (angular variance), range	*z*	Mean TL (±SD), range	*n*	Mean angle (angular variance), range	*z*	Mean TL (±SD), range
Sites								
Wolf Rock	17	100 (7), 65-152	14.98***	2.80 (0.15), 2.53-3.01	18	105 (5), 65-138	16.55***	2.80 (0.15), 2.53-3.01
South Solitary Island	53	115 (4), 77-159	49.43***	2.33 (0.19), 1.93-2.71	53	109 (1), 84-129	51.78***	2.33 (0.19), 1.93-2.71
Fish Rock	22	112 (2), 93-135	21.17***	2.33 (0.32), 1.57-2.86	23	109 (1), 93-124	22.56***	2.33 (0.32), 1.57-2.86
Big Seal Rock	30	116 (2), 90-136	28.84***	2.24 (0.28), 1.75-2.79	31	104 (1), 87-126	30.31***	2.25 (0.28), 1.75-2.79
Little Seal Rock	28	118 (5),91-178	25.46***	2.01 (0.26), 1.71-2.65	29	109 (1), 91-127	28.50***	2.00 (0.26), 1.71-2.65
North Rock	38	103 (5), 67-132	34.88***	2.21 (0.36), 1.57-3.13	38	108 (2), 88-130	36.90***	2.21 (0.36), 1.57-3.13
Little Broughton Island	12	123 (3), 110-152	11.42***	1.70 (0.15), 1.49-2.00	18	104 (3), 87-139	17.20***	1.63 (0.17), 1.44-2.00
Looking Glass Isle	8	109 (14), 71-167	6.17***	1.82 (0.18), 1.55-2.01	8	105 (4), 87-138	7.49***	1.82 (0.18), 1.55-2.01
Gender								
Male	81	112 (4), 67-159	75.72***	2.35 (0.18), 1.71-2.71	82	109 (1), 91-129	80.48***	2.35 (0.18), 1.71-2.71
Female	127	112 (6), 65-178	114.03***	2.16 (0.42), 1.49-3.13	136	106 (2), 65-139	130.58***	2.13 (0.43), 1.44-3.13

2.3.4 Grey nurse shark non-swimming behaviours

Feeding and reproductive behaviours were not observed at any site. Most grey nurse sharks exhibited passive (ram) ventilation across all sites but active respiration (buccal pumping) rates were documented for five sharks (2.10-2.60 metres TL) with a mean (±SD, range) rate of 20.4 (0.55, 20-21) buccal pumps per minute. Chafing, gill puff, head snapping, palatoquadrate protrusion, rapid withdrawal and stand back behaviours were exhibited by 18 (6.6%) sharks, with one shark exhibiting gill puff, head snapping and palatoquadrate protrusion in a sequence. Combined, non-swimming behaviours accounted for 0.8% of time spent observing sharks pooled across all sites. Descriptions and other details for these non-swimming behaviours are summarised in Table 2.6.

Table 2.6. Descriptions of the non-swimming behaviours of the grey nurse shark (*Carcharias taurus*) with life-history stages (LHS, juvenile males = JM; juvenile females = JF; adult males = AM; gestating females = GF; and, resting females = RF), shark total lengths (TL, in metres), durations (seconds), numbers of events per sequence and mean (angular variance, range) pectoral fin angles (PFA, in degrees) and caudal fin angles (CFA, in degrees) sampled at South Solitary Island (SS), Fish Rock (FR), Big Seal Rock (BS), Little Seal Rock (LS), North Rock (NR) and Little Broughton Island (LB) from March to May 2010. Bolded text denotes the same shark.

Behaviour (No. sharks)	Description	Site	LHS	TL	Duration	Sequence (No. events)	Mean angle (angular variance), range	
							PFA	CFA
Chafing (1)	Shark rolls and swims laterally so the trunk and tail abrade the substrate	BS	JF	1.62	13.20	Yes (2)	-	96 (4), 81-111
Gill puff (5)	Gill slits widen briefly and usually successively from the first gill slit. Potentially analogous to mammalian coughing	SS	**AM**	2.30	9.60	Yes (5)	110 (3), 91-131	95 (1), 88-104
			AM	2.29	0.60	No	99	106
		FR	AM	2.71	3.00	Yes (2)	117 (2), 107-126	86 (2), 75-96
		BS	JM	1.97	2.40	Yes (2)	100 (2), 91-109	115 (6), 97-134
		NR	JF	2.13	5.40	Yes (3)	85 (1), 78-91	84 (2), 72-95
Head snapping (4)	Rapid, unilateral movement of the head from and returning to the longitudinal axis	SS	**AM**	2.30	4.80	Yes (2)	92 (2), 84-101	-
		FR	JF	1.92	1.20	No	-	79
			AM	2.58	0.60	No	-	-
		BS	AU	2.66	0.60	No	-	103

Table 2.6 continued. Descriptions of the non-swimming behaviours of the grey nurse shark (*Carcharias taurus*) with life-history stages (LHS, juvenile males = JM; juvenile females = JF; adult males = AM; gestating females = GF; and, resting females = RF), shark total lengths (TL, in metres), durations (seconds), numbers of events per sequence and mean (angular variance, range) pectoral fin angles (PFA, in degrees) and caudal fin angles (CFA, in degrees) sampled at South Solitary Island (SS), Fish Rock (FR), Big Seal Rock (BS), Little Seal Rock (LS), North Rock (NR) and Little Broughton Island (LB) from March to May 2010. Bolded text denotes the same shark.

Behaviour (No. sharks)	Description	Site	LHS	TL	Duration	Sequence (No. events)	Mean angle (angular variance), range	
							PFA	CFA
Palatoquadrate protrusion (1)	(1) mandible depression; (2) cranium elevation; (3) maxilla (palatoquadrate) protrusion; (4) further cranium elevation and maxilla retraction; (5) cranium depression and completion of maxilla retraction; and, (6) mandible elevation as cranium depression concludes	SS	**AM**	2.30	15.60	Yes (3)	98 (21), 58-144	-
Rapid withdrawal (7)	Rapid departure of a shark away from a disturbance, often incorporating a severe turn	BS	JF	1.81	1.80	No	-	-
		LS	JF	1.76	0.06	No	-	96
			JF	1.68	0.06	No	-	85
		NR	JF	1.84	3.00	No	-	107
		LB	JF	1.50	0.06	No	-	141
			JF	1.97	4.80	No	117	104
			JF	1.60	0.60	No	-	-
Stand back (2)	Simultaneous rapid withdrawal exhibited by two oncoming sharks to avoid collision	LB	JF	1.77	0.60	No	-	116
			JF	1.56	6.00	No	-	125

Rapid withdrawal was the most frequent non-swimming behaviour, followed by gill puff, head snapping and equal occurrences of chafing, palatoquadrate protrusion and stand back. Non-swimming behaviours were exhibited by 12 juvenile females (8.7% of all juvenile females), four adult males (7.6% of all adult males), one juvenile male (7.1% of all juvenile males) and one adult shark of unknown gender (Table 2.6). Ranges in PFA and CFA were similar to those for swimming behaviours (Tables 2.5 and 2.6). The mean (±SD, range) distance between a shark exhibiting a non-swimming behaviour and the closest conspecific was 2.12 (± 1.61, 0.28-4.53) metres. The onset of non-swimming behaviours did not appear to be related to the number of conspecifics in close proximity as the mean (±SD, range) number of conspecifics ≤10.00 metres from the USVPS present when these behaviours were observed was 1.05 (± 0.97, 0-3). The shark that exhibited gill puff, head snapping and palatoquadrate protrusion had a mean (±SD, range) maximum gape of 300 (± 50, 251-350) millimetres. During stand back one juvenile female exhibited a second burst of speed 5.40 seconds after the initial retreat at a distance of 5.64 metres from the other juvenile female.

A gill puff event exhibited by an adult male and six rapid withdrawal events exhibited by juvenile females were likely attributable to research diver presence (Table 2.6) and only accounted for about 0.1% of observation time pooled across all sites. The gill puff occurred at South Solitary Island in association with three camera flashes. After the third flash, the shark altered its swimming behaviour from milling to active swimming, but resumed milling after 10.28 seconds and did not leave the area. Rapid withdrawals occurred when a shark swam to within 3.00 metres of the USVPS base bar once at Big Seal Rock and Little Seal Rock and twice at Little Broughton Island. Rapid withdrawal was also observed at Little Broughton Island after one diver approached to within 1.00 metre of a shark. In contrast, exhaled air bubbles from a diver made contact with a shark and elicited a rapid withdrawal event at Little Seal Rock. The final rapid withdrawal occurred when surge moved a shark close to a rock wall of the North Rock shark gutter.

2.4 DISCUSSION

Significant sexual and size segregation of grey nurse sharks was evident among aggregation sites off eastern Australia and consistent with previous research (Bansemer & Bennett 2009; Otway *et al*. 2009; Otway & Ellis 2011). There were also overlaps which enabled behavioural analysis of different life-history stages at each site and the development of a partial ethogram. While it is not possible to completely eliminate the potential effects of observers when developing an ethogram for sharks due to their sensory capabilities (Bres 1993), in this study the presence research divers did not overtly alter grey nurse shark behaviour as possible responses accounted for <0.1% of observation time. This is consistent with a recent study documenting interactions between grey nurse sharks and tourist scuba divers at four sites (Smith *et al*. 2014). Nevertheless, the possibility of observer influence on shark behaviour cannot be completely discounted.

2.4.1 Grey nurse shark swimming behaviours

Sharks exhibited hovering, milling and active swimming at most sites, a finding similar to other behavioural (Hayward 2003; Smith *et al*. 2010, 2014) and localised movement (Bansemer & Bennett 2009; Otway *et al*. 2009) studies. Hovering and milling accounted for more than 90.0% of swimming behaviour observations with significantly more milling which accords with other studies (Hayward 2003; Smith *et al*. 2010, 2014). Swimming speed (i.e. ROM) provides an important measurement of energy expenditure in sharks with rates of less than 2.00 metres per second for all continuously swimming wild sharks assessed (Bone 1989; Shadwick & Goldbogen 2012). Grey nurse shark swimming speeds did not exceed this ROM and were least when milling and greatest when active swimming suggesting low levels of activity and energy expenditure when aggregated during daylight hours.

Hovering sharks used slow tail beats to maintain station with the caudal fin placed significantly lower in the water column likely minimising forward propulsion. Laboratory studies of swimming biomechanics in the North American leopard shark (*Triakis semifasciata*) showed pectoral fins were held at negative dihedral angles (i.e. below horizontal) of approximately 5, 23 and 35° when descending, holding and ascending, respectively (Wilga & Lauder 2000; Maia *et al*. 2012). Assuming these observations apply to grey nurse sharks, the PFA documented in this study enables comparisons. Whilst hovering, the mean dihedral angle of grey nurse sharks was consistent with North American leopard sharks. Milling sharks also swam with slow tail beats but held their caudal fins higher and had a greater range in CFA. The mean dihedral angle was similar to that during hovering but had a larger range with the fins used for manoeuvring. In contrast, active swimming sharks used significantly more tail beats, but the caudal fin positions reflected those when milling with the fin held high. However, the range in dihedral angles was similar to hovering and contributed to ascent and descent as few turns were observed. Reduced TBF with increased TL during milling and active swimming suggested the propulsive force generated by tail beats was greater in larger sharks. This may have resulted from increased mass of aerobic red muscle for continuous swimming and anaerobic white muscle for burst swimming (Bone 1989; Shadwick & Goldbogen

2012), and differing drag coefficients linked to denticle patterns (Gilligan & Otway 2011) and/or smaller surface area to volume ratios.

Similarities and differences in swimming behaviour occurred among sites and life-history stages. Wolf Rock was occupied by gestating females that exhibited hovering and milling with a greater frequency of hovering compared to all other sites except Fish Rock. Sharks spent the majority of time hovering in currents and/or milling near the seabed using their pectoral fins to maintain station. This low level of activity was likely adopted as maternal fasting occurs during the pre-parturition phase of gestation facilitating energy conservation for the southerly migration in the late austral winter for parturition in spring in NSW waters (Bansemer & Bennett 2009; Otway & Ellis 2011).

Sharks inhabiting South Solitary Island, Fish Rock and Big Seal Rock comprised various life-history stages (adult males, resting females and juveniles), exhibited low levels of activity as evidenced by hovering and milling, and the mean dihedral angles indicated that sharks were holding their positions in the water column. The associated variances and range were less than when hovering and milling (pooled across all sites) indicating that changes in direction were less pronounced, and provided further evidence of minimal energy expenditure. Previous research (Otway & Ellis 2011) showed that adult male grey nurse sharks punctuate their annual northerly migration with occupation of these and other sites for varying durations. Whilst at these sites, it is likely adult males were optimising energy use as previously documented for scalloped hammerhead sharks (*Sphyrna lewini*) aggregated around a seamount (Klimley & Nelson 1984). Similarly, resting female sharks at Fish Rock and Big Seal Rock would have been replenishing energy stores expended during their previous pregnancy. It is probable the low levels of activity exhibited by resting females were adopted to conserve energy for reproduction and the associated migration to gestation sites off QLD (Bansemer & Bennett 2009).

Little Broughton Island is a highly dynamic site characterised by complex bottom topography with narrow gutters and crevices, variable currents, surge from breaking waves reaching the shallow seabed and expanses of kelp across much of the substratum. This habitat is typical of the shallow, inshore rocky reefs found along the NSW coast (Underwood *et al*. 1991) and is used for substantial periods of time by juvenile grey nurse sharks (Otway & Ellis 2011). The occupation of similar habitats occurs in juvenile grey nurse (ragged-tooth) sharks off the Eastern Cape of South Africa (Bass *et al*. 1975; Smale 2002; Dicken *et al*. 2006). Only juvenile sharks were observed at Little Broughton Island and whilst they mainly exhibited milling, the greater frequency of active swimming and the larger TBF suggested a greater level of activity at this site. The mean dihedral angle was greater than those at other sites with the reduced range and variance likely due to the fins being held in a more consistent position to maintain station (*sensu* Wilga & Lauder 2000; Maia *et al*. 2012) or counteract downward forces exerted by the surge of breaking waves.

Little Seal Rock, North Rock and Looking Glass Isle were predominantly occupied by juvenile sharks that exhibited mainly milling. The range in dihedral angles suggested pectoral fins were used for turning and maintaining position. The low activity swimming behaviours exhibited at these sites further suggested that the sharks expended minimal energy during daylight hours.

2.4.2 Grey nurse shark non-swimming behaviours

Grey nurse sharks use active (buccal pumping) and passive (ram) ventilation depending on their respiratory needs and swimming behaviour (Otway *et al*. 2009). Whilst most sharks in the current study exhibited ram ventilation, those that used buccal pumping had rates of 20-21 buccal pumps per minute which were similar to those documented by Barker *et al*. (2011) at Fish Rock and Magic Point off Sydney, NSW.

Other non-swimming behaviours comprising chafing, palatoquadrate protrusion, head snapping, gill puff, rapid withdrawal and stand back (Myrberg & Gruber 1974; Compagno 2001; Martin 2007) were infrequently observed. Non-swimming behaviours were mainly exhibited by juvenile sharks and occurred across six sites. Chafing was achieved by altering the PFA (Wilga & Lauder 2000; Maia *et al*. 2012) and was probably done to remove external parasites. This grooming behaviour has been recorded for captive bonnethead (*Sphyrna tiburo*) and lemon (*Negaprion brevirostris*) sharks (Myrberg & Gruber 1974) and in grey nurse sharks at Julian Rocks off Byron Bay, NSW (Hayward 2003).

A behavioural sequence incorporating palatoquadrate protrusion, gill puff and head snapping occurred distant from the divers with the USVPS and in the absence of prey (i.e. not feeding behaviour). It was likely used to realign cartilaginous jaw elements and therefore should be categorised as grooming behaviour. Similar palatoquadrate protrusion events and sequences have been observed in non-feeding Caribbean reef sharks (*Carcharhinus perezi*, Ritter 2008). The isolated gill puff events and sequences observed were probably grooming behaviours to clear the orobranchial cavity of debris as previously observed in semi-captive bonnethead sharks (Myrberg & Gruber 1974). A further two head snapping events occurred and were also likely grooming behaviour possibly to reposition cartilaginous elements, remove debris or may have been involuntary muscular contractions as documented in captive grey nurse and sandbar (*Carcharhinus plumbeus*) sharks (Hannon & Crook 2004). Another gill puff immediately followed by a brief switch to active swimming was likely elicited by three camera flashes in quick succession and, in this context, the behaviour was considered a ‘flight’ response and categorised as agonistic behaviour (Martin 2007).

Rapid withdrawal events accounted for 36.8% of the non-swimming behaviours. Four rapid withdrawal events were preceded by investigative approaches to the USVPS and diver, whereas another was probably elicited by a diver approaching the shark. These events should be categorised as agonistic behaviour as they represented ‘flight’ responses to identified stimuli and together with the agonistic gill puff accounted for <0.1% of the total observation time. Similar rapid withdrawals (‘flight’ responses) have been observed in grey reef sharks (*Carcharhinus amblyrhynchos*) by Johnson & Nelson (1973) and were often followed by further agonistic (‘fight’/threat) displays. In contrast, grey nurse sharks did not follow any rapid withdrawal with aggressive/threatening displays. Another rapid withdrawal occurred when exhaled air bubbles from a diver made contact with a shark, a ‘flight’ response also observed in aggregated scalloped hammerhead sharks (Klimley 1981/82). Additionally, the frequency of rapid withdrawal by juvenile sharks was similar to behavioural observations of small bonnethead, lemon, silky (*Carcharhinus falciformis*) and reef (*Carcharhinus springeri*) sharks compared with their larger conspecifics (Myrberg & Gruber 1974).

During stand back, two approaching sharks turned simultaneously and retreated to avoid collision and did not exhibit any other non-swimming behaviours immediately thereafter. Similarly, a shark exhibited rapid withdrawal to avoid collision when surge forced the shark close to the rock wall of a shark gutter. Neither event was associated with threatening displays and merely represented extended swimming behaviour. Rapid withdrawal and stand back have previously been classified as agonistic behaviours (Martin 2007), but both could have been categorised as swimming or agonistic behaviour in this study. To eliminate future ambiguity, rapid withdrawal and stand back behaviours exhibited during navigation should be categorised as a swimming behaviour and referred to as collision avoidance. This would permit the continued use of stand back and rapid withdrawal as types of agonistic behaviour. These results also highlighted the importance of identifying the stimuli that elicit behaviours and the use of appropriate terminology when describing, defining and/or categorising the behaviours of sharks and other animals.

2.4.3 Scuba diving tourism impacts on grey nurse shark behaviour

Underwater visual observations have previously been used to assess the potential impacts of scuba diving tourism on grey nurse shark behaviour at sites off eastern Australia (Smith *et al*., 2010, 2014; Barker *et al*. 2011). The first study at Fish Rock (Smith *et al*. 2010) documented a significant decrease in milling behaviour when more than six divers were present and a high rate of diver compliance with management guidelines (code of conduct and relevant legislation). The second study at Magic Point off Sydney, NSW (Barker *et al*. 2011) reported significantly greater swimming rates when 12 divers simultaneously approached to within three metres of the sharks. By doing so, divers breached the code of conduct as the group exceeded 10 divers, interrupted the sharks' swimming patterns and trapped them within the entrance to a cave. A study at Wolf Rock, Julian Rocks, South Solitary Island and Fish Rock (Smith *et al*. 2014) found no significant changes to grey nurse shark swimming behaviour irrespective of diver numbers or distances to the sharks and complete compliance by divers with management guidelines.

Putative agonistic pectoral fin depression (i.e. a ‘fight’ response) following approaches by scuba divers has been reported using visual observations of grey nurse sharks at Fish Rock (Barker *et al*. 2011) and sandtiger (grey nurse) sharks at two wrecks off North Carolina (Martin 2007). These observations are contrary to numerous reports of this species as docile (e.g. Compagno 2001; EA 2002; Otway & Ellis 2011). Confirming the existence of this threatening, non-swimming behaviour requires accurate quantification of pectoral fin positions (angles) during interactions with tourist divers. The USVPS used in this study enabled the PFA and other components of behaviour (e.g. TBF, ROM, CFA, and non-swimming behaviours) to be accurately quantified in the absence of tourist divers. This partial ethogram can be used as a baseline for cost-effective and efficacious assessments of scuba diving tourism impacts on grey nurse shark behaviour. Future research using stereo photogrammetry at these and other aggregation sites will enable behavioural changes to be documented and determine the need for alterations to current management strategies to facilitate the ongoing sustainability of scuba diving tourism with this species.

2.4 CONCLUSION

A partial ethogram was developed for grey nurse sharks by sampling their behaviours (during daylight hours) across different life-history stages and aggregation sites in the absence of scuba diving tourism and commercial and recreational fishers. The USVPS enabled accurate and precise measurements of lengths, distances and durations of observed behaviours, and maximised the information obtained from each dive. Milling and hovering were the most frequent swimming behaviours exhibited by grey nurse sharks across all sites and were correlated with slow ROM. The range in PFA indicated that the sharks used their pectoral fins to maintain their position in the water column. The low levels of activity of grey nurse sharks suggested that they minimised their energetic output whilst at aggregation sites in contrast to the greater energy expenditure associated with the migratory behaviours linked to their reproductive cycle. Little Broughton Island is a highly dynamic, topographically-complex site and sharks used their pectoral fins more actively to navigate in and around this habitat. Non-swimming behaviours were infrequently observed and comprised grooming and agonistic behaviours. The agonistic behaviours exhibited by grey nurse sharks accounted for less than 0.1% of the entire observation time and represented ‘flight’ rather than ‘fight’ responses. The absence of threatening agonistic behaviour across all life-history stages and aggregation sites was consistent with previous studies that have described the species as docile and placid. While this ethological research did not include observations of feeding, reproductive and/or nocturnal behaviours for logistical reasons, passive acoustic tracking will be used to address some of the gaps. This partial ethogram for grey nurse sharks has enhanced the ecological understanding of the species at aggregation sites, will assist with the ongoing assessment and management of potential impacts of scuba diving tourism, and contribute to recovery efforts and the long-term conservation of this critically endangered species.

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Chapter 3

Does the grey nurse shark (*Carcharias taurus*) exhibit agonistic pectoral fin depression? A stereo-video photogrammetric assessment off eastern Australia

Declaration of co-authorship and co-contribution: papers incorporated in thesis by publication

Declaration by: Kirby Rae Smith **Signature:** [redacted]

Date: 1 April 2016

Paper Title: Does the grey nurse shark (*Carcharias taurus*) exhibit agonistic pectoral fin depression? A stereo-video photogrammetric assessment off eastern Australia

In the case of the above publication, the following authors contributed to the work as follows:

Name	Contribution %	Nature of contribution
Kirby R Smith	70	Study concept, experimental design, fieldwork, data collection, statistical analysis and interpretation, manuscript writing, manuscript editing
Nicholas M Otway	15	Study concept, experimental design, advice on statistical analysis and interpretation, manuscript editing
Carol Scarpaci	10	Study concept, experimental design, manuscript editing
Brett M Louden	5	Fieldwork, data collection

DECLARATION BY CO-AUTHORS

The undersigned certify that:

1. They meet criteria for authorship in that they have participated in the conception, execution or interpretation of at least that part of the publication in their field of expertise;
2. They take public responsibility for their part of the publication, except for the responsible author who accepts overall responsibility for the publication;
3. There are no other authors of the publication according to these criteria;
4. Potential conflicts of interest have been disclosed to **a)** granting bodies, **b)** the editor or publisher of journals or other publications, and **c)** the head of the responsible academic unit; and
5. The original data is stored at the following location(s):

Location(s): College of Engineering and Science, Victoria University, Melbourne, Victoria, Australia

and will be held for at least five years from the date indicated below:

		Date
Kirby R Smith	[redacted]	12 November 2014
Nicholas M Otway	[redacted]	7 November 2014
Carol Scarpaci	[redacted]	10 November 2014
Brett M Louden	[redacted]	7 November 2014

ABSTRACT

Underwater stereo-video photogrammetry was used to document the pectoral fin positions of various life-history stages of the critically endangered east Australian population of the grey nurse shark (*Carcharias taurus*) during normal swimming behaviour at multiple aggregation sites. A wide range in pectoral fin positions was recorded with dihedral pectoral fin angles ranging from -25 to 88°. Pectoral fin angles varied significantly among sites and this was attributed to the differing navigational and energetic requirements of the sharks. There was no significant relationship between pectoral fin angles and distances separating the shark and scuba diver. The wide range in pectoral fin angles, interactive use of the fins during swimming, low-energy behaviours of the sharks at aggregation sites and absence of ‘fight’ response agonistic behaviour indicated that the species does not exhibit agonistic pectoral fin depression. Reports of agonistic pectoral fin depression in the grey nurse shark obtained with visual estimates should be treated as preliminary observations requiring further testing using accurate sampling methods such as stereo photogrammetry. It is important that diver compliance with existing management guidelines that prohibit divers from chasing or harassing grey nurse sharks and blocking cave and gutter entrances is maintained.

3.1 INTRODUCTION

Agonistic behaviour encompasses all fearful, threatening and aggressive actions exhibited by animals (Brown & Hunsperger 1963; Hill *et al*. 2014). Animals present the fight or flight response when exposed to a perceived risk (Suresh *et al*. 2014), with the threat of injury (e.g. exposing the teeth) and actual physical aggression (e.g. biting) considered 'fight' reactions whereas fearful behaviours (e.g. fleeing) represent 'flight' responses (Hill *et al*. 2014). Stimuli that can induce the fight or flight response include predators, other species, conspecifics and unfamiliar objects. The motivation for responding to such stimuli may be self-defence, protection of young, territory or food, maintaining or challenging dominance within a social hierarchy, or competition for mates.

The agonistic behaviour of sharks has been documented for a variety of species with that of the grey reef shark (*Carcharhinus amblyrhynchos*) most known (Johnson & Nelson 1973; Nelson 1981/82; Nelson *et al*. 1986). A conspicuous threat display described for this species and later termed 'hunch' (Myrberg & Gruber 1974) was exhibited in response to rapid approaches by a scuba diver (Johnson & Nelson 1973). The display incorporated a laterally exaggerated swimming motion, rolling, snout elevation, sustained pectoral fin depression, back arching and lateral bending (Johnson & Nelson 1973). More recently, a review described the agonistic behaviours putatively exhibited by 23 shark species including the grey reef shark (Martin 2007). Twenty-nine behaviours were reported with pectoral fin depression evident across all 23 species (Martin 2007). Agonistic pectoral fin depression was defined as the sustained (>5 seconds), bilateral lowering of the pectoral fins more than during normal swimming behaviour (Martin 2007) and the pectoral fin angle (PFA) was measured as the dihedral angle (i.e. the position of the pectoral fin below the horizontal plane) in accordance with laboratory studies of the North American leopard shark (*Triakis semifasciata*) (Wilga & Lauder 2000; Maia *et al*. 2012). Underwater visual estimates were previously used to quantify the PFA of sharks (Johnson & Nelson 1973; Martin 2007), but more recent research (Harvey *et al*. 2004) has shown that there are substantial errors and observer subjectivity inherent in this method. In contrast, stereo photogrammetry is not a new technique and provides much greater accuracy and precision when measuring lengths and angles (Harvey & Shortis 1995; Harvey *et al*. 2004). For example, stereo photogrammetry with still photographs was used to document lengths, orientations and nearest neighbour distances of sharks to describe the three-dimensional schooling behaviour of scalloped hammerhead (*Sphyrna lewini*) sharks (Klimley 1981/82, 1985; Klimley & Brown 1983).

Underwater visual estimates and rapid scuba diver approaches were used by researchers to document agonistic pectoral fin depression in the grey nurse (sandtiger, ragged-tooth) shark (*Carcharias taurus*, Rafinesque 1810) at two shipwrecks off North Carolina, United States of America (USA) (Martin 2007). Underwater visual estimates were also used to report a single instance of agonistic pectoral fin depression in a grey nurse shark during interactions with approaching tourist scuba divers in a cave at Fish Rock off New South Wales (NSW), Australia (Barker *et al*. 2011). In contrast, stereo photogrammetry with video was recently used to quantify the swimming behaviours of various life-history stages of the grey nurse shark at multiple aggregation sites along the Australian east coast and included the measurement of PFA (Smith *et al*. 2015). This research showed that a wide range of PFA was evident across the sites sampled and attributed it to variation in navigational and energetic requirements associated with the depth, topography and water movement (Smith *et al*. 2015). The sharks did not exhibit any other threatening/aggressive (‘fight’ response) agonistic behaviours in the presence of the researchers (Smith *et al*. 2015).

The grey nurse shark, unlike the grey reef shark, has been consistently referred to as a docile species (Pollard *et al*. 1996; Compagno 2001; Otway & Ellis 2011) although it is known to take fish from spearfishers (Compagno 2001). This relatively large shark (males and females grow to approximately 3.00 and 3.20 metres, respectively) has a widespread but fragmented distribution in warm-temperate and tropical coastal waters across the globe (Compagno 2001; Goldman *et al*. 2006; Last & Stevens 2009). It is slow to reach sexual maturity (50.0% sexual maturity: males = 2.10 metres at 6–7 years, females = 2.59 metres at 10–12 years, Goldman *et al*. 2006; Otway & Ellis 2011), has low fecundity (maximum of two pups biennially) and has experienced global population declines from targeted and indirect commercial and recreational fishing (Cavanagh *et al*. 2003; Otway *et al*. 2004). Consequently, the species is listed globally as ‘Vulnerable’ on the International Union for the Conservation of Nature (IUCN) Red List of Threatened Species (IUCN 2015). In Australia, there are two genetically-distinct grey nurse shark populations that occur off the east and west coasts (Stow *et al*. 2006; Ahonen *et al*. 2009). The eastern population occurs along the Queensland and NSW coasts, and following numerous anthropogenic impacts (Otway & Ellis 2011) is currently estimated to comprise 1146 to 1662 individuals (Lincoln Smith & Roberts 2010). Accordingly, the population is listed as ‘Critically Endangered’ by the IUCN (Cavanagh *et al*. 2003; IUCN 2015) and under Commonwealth and state (Queensland and NSW) legislation (Smith *et al*. 2014). The east Australian population exhibits annual (male) and biennial (female) migrations (≤4500 kilometres) which are associated with the reproductive cycle and punctuated with visits to numerous aggregation sites (Bansemer & Bennett 2009; Otway *et al*. 2009; Otway & Ellis 2011).

The tendency of grey nurse sharks to aggregate combined with their docile nature (Pollard *et al*. 1996; Compagno 2001; Otway & Ellis 2011) has enabled the operation of a successful wildlife tourism industry involving passive interactions between scuba divers and the sharks (Smith *et al*. 2014). To mitigate potential adverse impacts on the sharks, the activities of this tourism sector are managed via a voluntary code of conduct and federal and state legislation (Smith *et al*. 2014). Management guidelines prohibit the feeding of grey nurse sharks whereas other marine wildlife tourism industries rely on provisioning target species including the bull (*Carcharhinus leucas*, e.g. Brunnschweiler & Barnett 2013), Caribbean reef (*Carcharhinus perezi*, e.g. Maljković & Côté 2011), Galapagos (*Carcharhinus galapagensis*, e.g. Meyer *et al*. 2009b), sandbar (*Carcharhinus plumbeus*, e.g. Meyer *et al*. 2009b), sicklefin lemon (*Negaprion acutidens*, e.g. Clua *et al*. 2010), silky (*Carcharhinus falciformis*, e.g. Clarke *et al*. 2011), tiger (*Galeocerdo cuvier*, e.g. Meyer *et al*. 2009b; Hammerschlag *et al*. 2012), white (*Carcharodon carcharias*, e.g. Laroche *et al*. 2007) and whitetip reef (*Triaenodon obesus*, e.g. Fitzpatrick *et al*. 2011) sharks. Shark provisioning tourism may induce the sharks to exhibit aggressive agonistic behaviour towards humans because of the association with food (Laroche *et al*. 2007) or towards conspecifics due to increased competition for the food (e.g. Semeniuk & Rothley 2008).

The reports of agonistic pectoral fin depression in grey nurse sharks relative to decreasing diver distances (i.e. Martin 2007; Barker *et al*. 2011) contrast with the wide range of PFA documented for the species during typical swimming behaviour (i.e. hovering, milling and active swimming) (Smith *et al*. 2015). The aim of this study was to quantify grey nurse shark PFA in relation to the distances of scuba divers across multiple life-history stages (i.e. time) and aggregation sites (i.e. space). This research will contribute to the developing ethogram for the species (Smith *et al*. 2015) and to the assessment and management of this tourism industry.

3.2 MATERIALS AND METHODS

3.2.1 Study sites

Sampling of the PFA of grey nurse sharks was done by a maximum of three scuba divers in the absence of commercial and recreational fishing and tourist scuba divers (Smith *et al*. 2014) over eight aggregation sites along ≈800 kilometres of the east Australian coast during the austral autumn of 2010 (Figure 3.1). These sites were selected as they are inhabited differentially by five life-history stages (juvenile males, juvenile females, adult males, gestating females and resting females) of the grey nurse shark (Bansemer & Bennett 2009; Otway & Ellis 2011). The sites are influenced by a 1–2 metre south-easterly swell, onshore winds, the 1–4 knot East Australian Current and sea surface temperatures varying annually between 19.0 and 28.0°Celsius (Otway & Ellis 2011; Smith *et al*. 2014, 2015). The sites vary physically (topography, substratum, water movement) and biologically (presence of kelp, invertebrate and vertebrate fauna) to differing degrees (Smith *et al*. 2015).

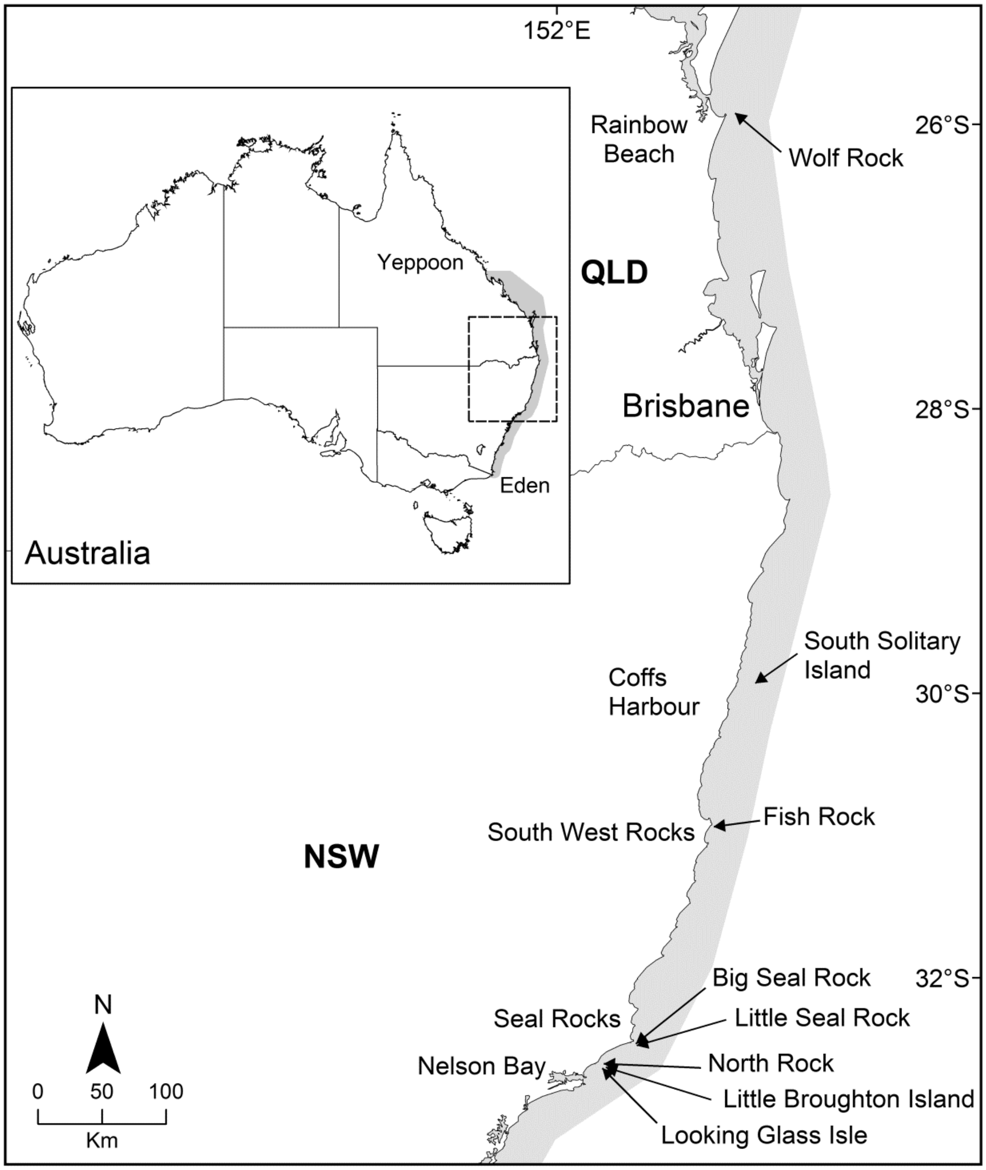

Figure 3.1. Map (QLD = Queensland and NSW = New South Wales) showing the geographic range (grey shading) of the grey nurse shark (*Carcharias taurus*) and the locations of Wolf Rock, South Solitary Island, Fish Rock, Big Seal Rock, Little Seal Rock, North Rock, Little Broughton Island and Looking Glass Isle sampled from March to May 2010 to document the pectoral fin angles of sharks along the east coast of Australia.

3.2.2 Underwater stereo-video photogrammetry system

The underwater stereo-video photogrammetry system (USVPS) used to capture videos of grey nurse sharks comprised two digital video cameras attached with an inward angle of 4° (to produce some overlap of the left and right images) to an aluminium base bar (further details: Otway *et al*. 2008; Smith *et al*. 2015, Figure 3.2). An image synchronisation unit was affixed to the end of an aluminium rod that was mounted at a right angle to the middle of the base bar (further details: Otway *et al*. 2008; Smith *et al*. 2015, Figure 3.2).

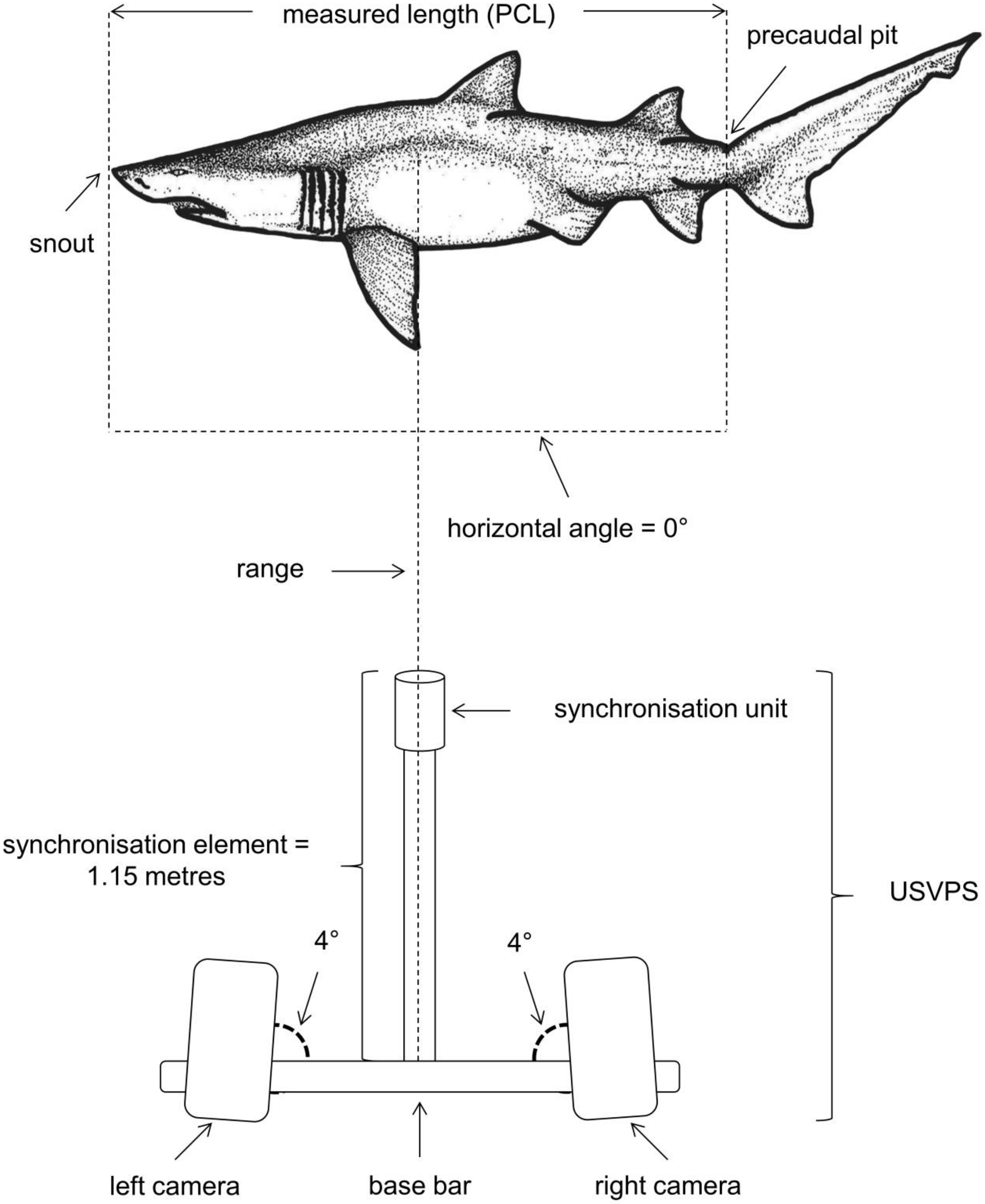

Figure 3.2. Line diagram of the underwater stereo-video photogrammetry system (USVPS) and a precaudal length (PCL) measurement of a grey nurse shark (*Carcharias taurus*) with the range and horizontal angle of the shark to the base bar.

The USVPS was calibrated before sampling, recorded 24 frames per second and allowed stereo images of sharks that were 3.00 metres in total length (TL) at a minimum distance of 3.00 metres from the base bar of the system (further details: Otway *et al*. 2008; Smith *et al*. 2015, Figure 3.2). The videos were then downloaded with Adobe Premiere (Version 6.0) and analysed using EventMeasure (©SeaGIS Pty Ltd, further details: Smith *et al*. 2015). This software enabled length measurements (millimetres) to be quantified with great accuracy (±0.2%) and precision (±0.3–1.2%) irrespective of the shark's three-dimensional position in the water column (Otway *et al*. 2008).

3.2.3 Life-history stages of the grey nurse shark

The precaudal length (PCL) of each shark (i.e. tip of the snout to the precaudal pit, Compagno 2001) was measured (Figure 3.2) rather than TL due to reduced error (Francis 2006) and the varying elevation and oscillations of the caudal fin (Smith *et al*. 2015). A significant linear regression relationship developed from necropsies of 150 grey nurse sharks (Otway *et al*. 2008; Otway 2015) was used to calculate TL from PCL (i.e. TL = 1.368PCL + 0.069 with TL and PCL in metres, $n = 66$, $R^2 = 0.99$, $P < 0.001$). The life-history stage of each shark was then determined from their TL, gender (i.e. presence of claspers identified males) and maturity ogives (Otway & Ellis 2011).

3.2.4 Pectoral fin angles in the grey nurse shark

Individual grey nurse sharks were identified using 20 standard morphometric measurements (Bass *et al*. 1975; Compagno 2001; Otway 2015) obtained with the USVPS (to the nearest millimetre) when quantifying swimming behaviour (Smith *et al*. 2015) and

PFA. Retained fishing gear (i.e. hooks and line), tail ropes and obvious spots and/or scars (Bansemer & Bennett 2009; Barker *et al*. 2011; Otway 2015) were used to augment the morphometric measurements for individual identification.

Additional morphometric length measurements were quantified and used together with significant regression relationships and standard geometric equations to calculate the PFA of grey nurse sharks. Continuous observation (Altmann 1974) was used to select sharks suitable for measuring the left or right PFA during normal swimming behaviour (i.e. hovering, milling and active swimming) (Smith *et al*. 2014, 2015) which was recorded for each shark measured. The PFA represented the position of the pectoral fin in the water column relative to the trunk (Figure 3.3a) and fins that were perpendicular to the trunk, raised or lowered had a PFA of 90°, <90° and >90°, respectively. The PFA was defined as the angle subtended by a point (point *A*) at the top of a straight imaginary line equal in length to the fifth gill slit and perpendicular to the pectoral fin insertion, the pectoral fin insertion itself (point *B*) and the pectoral fin apex (point *C*) (Figure 3.3b, c). The USVPS was used to measure the lengths between: (1) the top (point *D*) and the bottom (point *E*) of the fifth gill slit (line *DE* = *AB*); (2) the pectoral fin apex (point *C*) and the top of the fifth gill slit (point *D*) (line *CD*); and (3) the pectoral fin length (PFL) from the pectoral fin origin at the bottom of the fifth gill slit (point *E*) to the pectoral fin free rear tip (point *F*) (line *EF*) (Figure 3.3b, c). The pectoral fin height (PFH, line *BC*, Figure 3.3b, c) was calculated from PFL using a regression (PFH = 1.212PFL - 22.752, $n = 53$, $R^2 = 0.96$, $P < 0.001$). As the pectoral fin insertion was not always visible, the pectoral fin base length (PFBL, line *BE* = *AD*) was determined from PFL via a regression (PFBL = 0.671PFL - 25.537, $n = 53$, $R^2 = 0.94$, $P < 0.001$). The length between the top of the imaginary line and the pectoral fin apex (line *AC*) was then calculated from lines *AD* and *CD* using Pythagoras' theorem. The

PFA (angle ABC) was calculated with the law of cosines (De Sapio 1976) where ABC = arcos $[(BC^2 + AB^2 - AC^2)/2(BC \times AB)]$. EventMeasure also provided the range (millimetres) of the shark relative to the base bar (Figure 3.2). This enabled the separation distance, defined as the minimum distance between each individually-identified shark and the diver with the USVPS, to be calculated once as the range minus the length of the synchronisation element (1150 millimetres) for each PFA measurement.

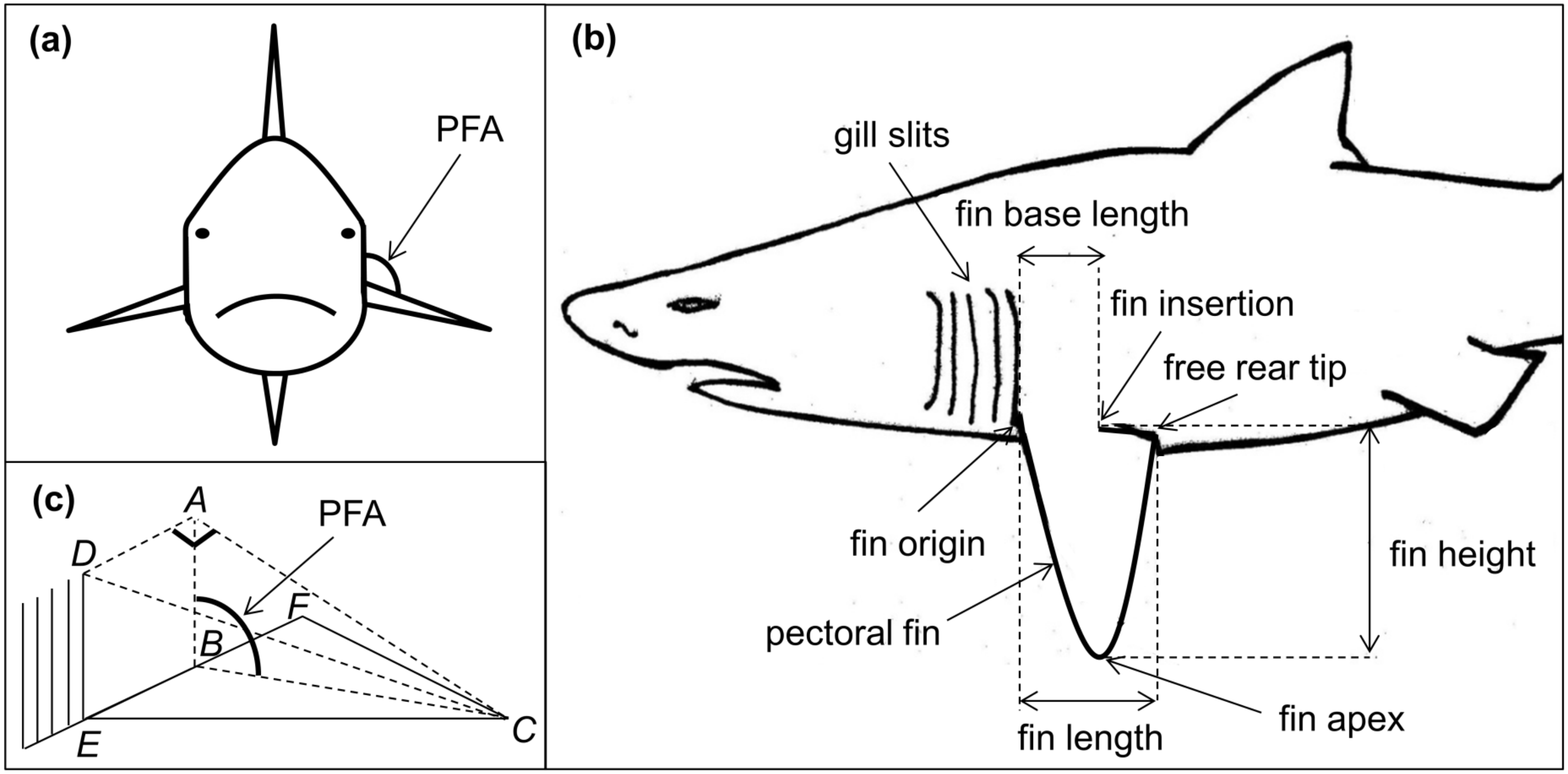

Figure 3.3. Illustration showing the (a) pectoral fin angle (PFA) of the grey nurse shark (*Carcharias taurus*) and (b) morphometric and (c) trigonometric lengths quantified and used to calculate the PFA.

3.2.5 Statistical analyses

The timing and duration of occupation of aggregation sites by grey nurse sharks is dependent on several environmental and biological (e.g. sexual segregation, reproductive cycle and migratory behaviour) factors resulting in unavoidable confounding of sites and life-history stages. Nevertheless, separate statistical analyses among sites and life-history stages were done to determine if more general patterns existed. All statistical analyses were conducted with a Type I (α) error rate of $P = 0.05$. The mean and angular variance of grey nurse shark PFA among and across all aggregation sites and life-history stages were calculated using tests associated with the Von Mises (circular normal) distribution (Batschelet 1981; Zar 2010). Rayleigh tests examined for significant mean PFA directions and Watson-Williams multi-sample F tests for significant differences among mean PFA according to sites, life-history stages and swimming behaviours (Batschelet 1981; Zar 2010). If grey nurse sharks exhibit agonistic pectoral fin depression then previous research (Johnson & Nelson 1973; Nelson *et al*. 1986) predicts that the PFA would increase with decreasing distance between the approaching diver and the shark. To test this hypothesis, the PFA of each grey nurse shark was examined against separation distance at the eight sites, among the five life-history stages and the pooled data were plotted. The respective angular-linear correlation coefficients were then calculated and their significance tested (Batschelet 1981; Zar 2010).

3.3 RESULTS

3.3.1 Life-history stages of the grey nurse shark

Across the eight study sites, 273 grey nurse sharks were individually identified from morphometric measurements and retained fishing gear, tail ropes, spots and/or scars when present. Grey nurse sharks at Wolf Rock only comprised gestating females (n = 18) 2.55-2.80 metres TL. The population at South Solitary Island (n = 22) included mostly adult males (72.7%) with some adult females and juveniles of both genders, and ranged from 1.77-2.63 metres TL. At Fish Rock, the population (n = 15) comprised juvenile and adult males and females 1.88-2.56 metres TL. The sharks at Big Seal Rock (n = 79) were juveniles and adults of both genders that ranged from 1.50-2.70 metres TL. At Little Seal Rock, the shark population (n = 33) comprised primarily juvenile females (81.8%) with some juvenile males and adults, and ranged from 1.44-2.45 metres TL. The sharks at North Rock (n = 67) were mainly juvenile females (89.6%) but also included juvenile males and adults, and ranged from 1.52-2.92 metres TL. The population at Little Broughton Island (n = 30) comprised juvenile males and females including some pups and ranged from 1.27-1.86 metres TL. The sharks at Looking Glass Isle (n = 9) were all juvenile males and females 1.42-1.78 metres TL.

3.3.1 Pectoral fin positions in the grey nurse shark

The mean PFA of grey nurse sharks differed significantly among aggregation sites (Watson-Williams test: $F_{7,\,200}$ = 4.83, P <0.0005) but not life-history stages (Watson-Williams test: $F_{4,\,203}$ = -0.54, P >0.25) or the three swimming behaviours exhibited

(Watson-Williams test: $F_{2, 205} = 0.33$, $P > 0.25$). Generally, pectoral fins were held lowest at Little Broughton Island and highest at Wolf Rock and North Rock (Table 3.1, Figure 3.4). While not significant, there was a trend towards greater mean PFA for juvenile sharks (Table 3.1).

Table 3.1. Mean (angular variance, minimum and maximum) pectoral fin angles (degrees) of the grey nurse shark (*Carcharias taurus*) with sample sizes (*n*), tests for directionality (Rayleigh test statistic = *z*) and mean (±SD, minimum and maximum) distances (metres) separating the shark from the diver with the underwater stereo-video photogrammetry system with sample sizes (*n*) according to aggregation site and life-history stage sampled at Wolf Rock, South Solitary Island, Fish Rock, Big Seal Rock, Little Seal Rock, North Rock, Little Broughton Island and Looking Glass Isle from March to May 2010.

Category	Pectoral fin angle						Separation distance			
Variable	*n*	Mean	Rayleigh's test		Variance	Minimum-maximum	*n*	Mean	SD	Minimum-maximum
			z	*P*						
Aggregation sites										
Wolf Rock	17	100	14.98	0.001	7	65-152	4	2.65	0.76	1.77–3.61
South Solitary Island	53	115	49.43	0.001	4	77-159	40	2.99	0.68	1.42–4.27
Fish Rock	22	112	21.17	0.001	2	93-135	18	2.85	0.70	1.38–3.74
Big Seal Rock	30	116	28.84	0.001	2	90-136	24	1.63	0.72	0.71–3.48
Little Seal Rock	28	118	25.46	0.001	5	91-178	24	2.17	0.70	0.97–3.76
North Rock	38	103	34.88	0.001	5	67-132	38	2.65	0.90	0.43–4.71
Little Broughton Island	12	123	11.42	0.001	3	110-152	9	1.55	0.28	0.96–1.93
Looking Glass Isle	8	109	6.17	0.001	14	71-167	7	2.68	0.85	1.11–3.44
Life-history stages										
Juvenile males	6	117	5.87	0.001	1	100-124	4	2.35	0.55	1.79–3.07
Juvenile females	99	116	90.98	0.001	5	71-178	84	2.25	0.86	0.43–4.05
Adult males	75	111	69.91	0.001	4	67-159	59	2.66	0.85	0.90–4.27
Gestating females	17	100	14.98	0.001	7	65-152	4	2.65	0.76	1.77–3.61
Resting females	11	98	9.65	0.001	7	67-136	13	3.12	0.96	1.36–4.71
Total	208	112	189.72	0.001	5	65-178	164	2.48	0.89	0.43–4.71

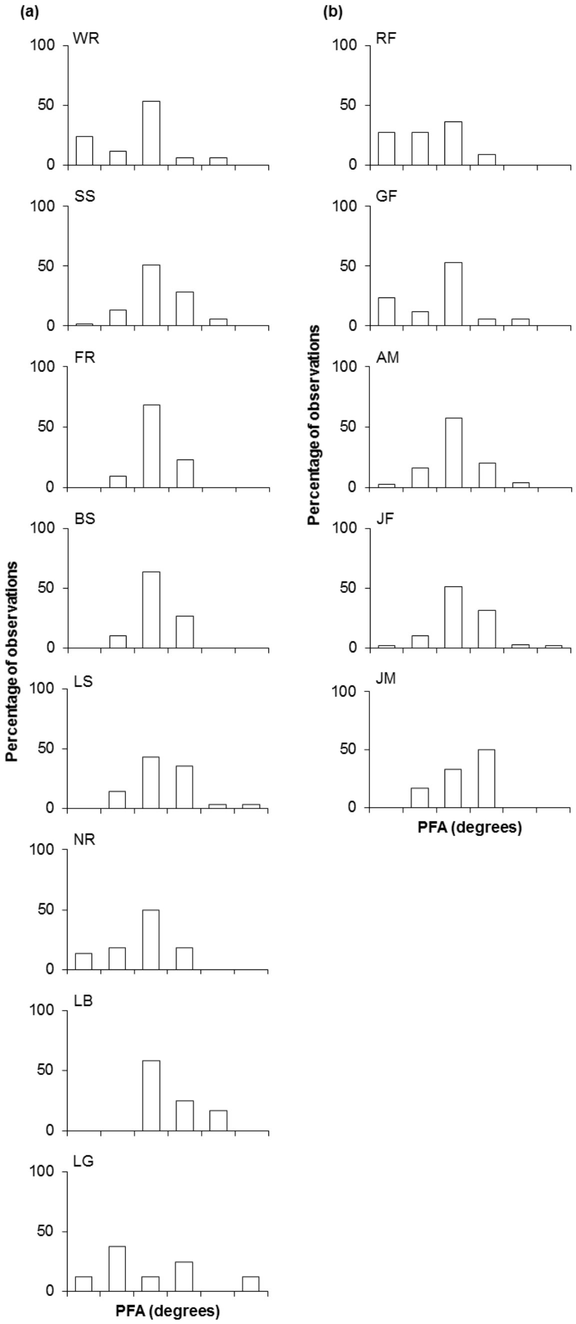

Figure 3.4. Percentages of grey nurse shark (*Carcharias taurus*) pectoral fin angles (PFA) observed according to (a) aggregation site and (b) life-history stage (LHS, juvenile males = JM, *n* = 6; juvenile females = JF, *n* = 99; adult males = AM, *n* = 75; gestating females = GF, *n* = 17; resting females = RF, *n* = 11) sampled at Wolf Rock (WR, *n* = 17), South Solitary Island (SS, *n* = 53), Fish Rock (FR, *n* = 22), Big Seal Rock (BS, *n* = 30), Little Seal Rock (LS, *n* = 28), North Rock (NR, *n* = 38), Little Broughton Island (LB, *n* = 12) and Looking Glass Isle (LG, *n* = 8) from March to May 2010. Note: midpoints of PFA range categories are plotted.

Samples of PFA and separation distances at Wolf Rock, Little Broughton Island and Looking Glass Isle were small (Table 3.2, $n \leq 9$) due to a combination of few individual grey nurse sharks and environmental constraints with a likely lack of power in the respective angular-linear correlation analyses. Sample sizes at the remaining five sites were reasonable (Table 3.2, $n \geq 18$), but there were still no significant correlations between the PFA and separation distances of sharks from the diver with the USVPS among aggregation sites (Table 3.2). Sample sizes for juvenile males, gestating females (only present at Wolf Rock) and resting females were small (Table 3.2, $n \leq 13$) and also likely resulted in low power in the respective angular-linear correlation analyses. Larger sample sizes were obtained for juvenile females and adult males (Table 3.2, $n \geq 59$), but again there were no significant correlations between the PFA and separation distance among life-history stages (Table 3.2, Figure 3.5). Combining the data across all sites and life-history stages ($n = 164$) showed there was no relationship between PFA and separation distance (Figure 3.5).

Table 3.2. Tests for angular-linear correlation (test statistic = *nr*2*al*) between grey nurse shark (*Carcharias taurus*) pectoral fin angles (degrees) and distances (metres) separating the shark from the diver with the underwater stereo-video photogrammetry system with sample sizes (*n*) according to aggregation site and life-history stage sampled at Wolf Rock, South Solitary Island, Fish Rock, Big Seal Rock, Little Seal Rock, North Rock, Little Broughton Island and Looking Glass Isle from March to May 2010.

Category Variable	n	nr^2_{al}	P
Aggregation sites			
Wolf Rock	4	2.98	> 0.10
South Solitary Island	40	5.62	> 0.05
Fish Rock	18	1.14	> 0.50
Big Seal Rock	24	0.02	> 0.99
Little Seal Rock	24	4.39	> 0.10
North Rock	38	0.16	> 0.90
Little Broughton Island	9	5.12	> 0.05
Looking Glass Isle	7	2.35	> 0.25
Life-history stages			
Juvenile males	4	3.61	> 0.10
Juvenile females	84	2.19	> 0.25
Adult males	59	3.74	> 0.10
Gestating females	4	2.98	> 0.10
Resting females	13	3.66	> 0.10
Total	164		

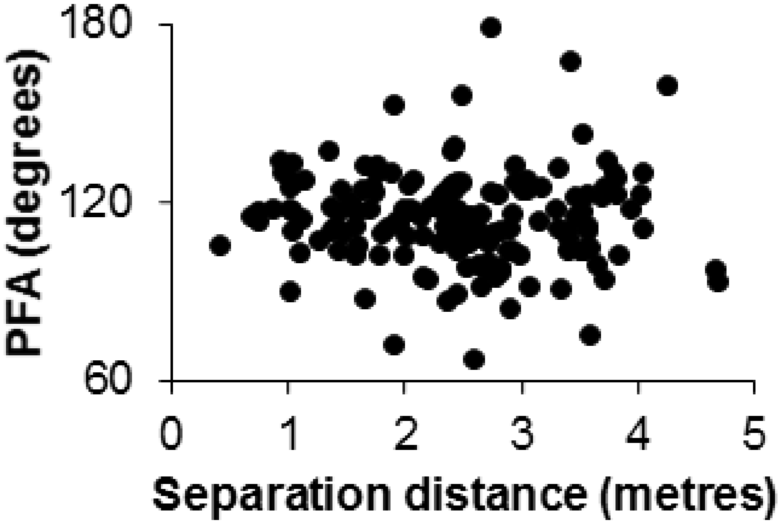

Figure 3.5. Grey nurse shark (*Carcharias taurus*) pectoral fin angles (PFA) with increasing separation distances from the diver with the underwater stereo-video photogrammetry system pooled across aggregation sites and life-history stages (*n* = 164) sampled from March to May 2010.

3.4 DISCUSSION

The occupation of Wolf Rock by gestating female grey nurse sharks (i.e. sexually-segregated from males) during autumn was entirely consistent with previous research (Bansemer & Bennett 2009; Smith *et al*. 2014). South Solitary Island, Fish Rock, Big Seal Rock, Little Seal Rock and North Rock were occupied by varying numbers of grey nurse sharks in the remaining life-history stages and these patterns were also similar to earlier studies (Otway *et al*. 2009; Otway & Ellis 2011; Smith *et al*. 2014). In contrast, Little Broughton Island and Looking Glass Isle were only inhabited by juvenile male and female sharks as previously documented (Otway *et al*. 2009).

Grey nurse sharks at five different life-history stages and at eight aggregation sites off eastern Australia exhibited a wide range of PFA during usual swimming behaviour (hovering, milling and active swimming) with dihedral angles (*sensu* Wilga & Lauder 2000) from 25° above the horizontal to 88° below. There was also significant variation in the mean PFA among aggregation sites but the pectoral fins were held in a depressed position with the mean dihedral angles between 10 and 33° below the horizontal during normal swimming. The mean PFA at Little Broughton Island was significantly greater than those at other sites and this was likely due to the pectoral fins being used by the juvenile sharks to maintain station (*sensu* Wilga & Lauder 2000; Maia *et al*. 2012) in this dynamic site with variable currents and surge from breaking waves that reach the shallow, complex seabed topography (Smith *et al*. 2015).

The ranges in PFA documented in this study encapsulated previous observations of putative agonistic pectoral fin depression (30 to 50°) in grey nurse sharks at two shipwrecks off North Carolina, USA, in 2002 following rapid approaches by scuba divers (Martin 2007). The well-documented agonistic ‘hunch’ display exhibited by grey reef sharks (Johnson & Nelson 1973; Nelson *et al*. 1986) comprising pectoral fin depression with laterally exaggerated swimming, rolling, snout elevation, back arching and lateral bending was elicited by divers charging to within 4.00 metres (on average). However, this display did not occur during passive interactions with divers at an average separation distance of 2.00 metres (Johnson & Nelson 1973). Grey nurse sharks did not exhibit agonistic pectoral fin depression during any approaches by divers to within <0.5 metres of the shark and this was clearly evidenced by the absence of significant relationships between PFA and separation distances across all of the sites and life-history stages sampled. Moreover, none of the other elements of the 'hunch' display were exhibited by grey nurse sharks in this study or previous research along the east coast of Australia (Smith *et al*. 2010, 2015; Barker *et al*. 2011). These findings are also consistent with the absence of changes in normal swimming behaviour (hovering, milling and active swimming) during interactions with up to ten tourist divers participating in two consecutive dives over a period of three hours (Smith *et al*. 2014).

The above results contrasted greatly with the increased intensity of agonistic pectoral fin depression as separation distance decreased reported in a previous study (Martin 2007) and this may have been attributable to differences in diver behaviour. However, the degree of diver influence cannot be assessed as the other study (Martin 2007) did not quantify separation distances nor were any of the observations analysed statistically. Moreover, details of the methods used to quantify the PFA, sample sizes and the life-history stages of the sharks observed were not provided. Recent sampling of grey nurse sharks using underwater stereo photogrammetry has shown that there are substantial inaccuracies in visual estimates of shark angles (unpublished data). It is probable that there were inaccuracies in previous observations (Martin 2007; Barker *et al*. 2011) of agonistic pectoral fin depression in grey nurse sharks as the angle between the pectoral fin and an imaginary, horizontal plane in three-dimensional space was visually estimated. Importantly, accurate measurement of lengths and angles of a three-dimensional object (i.e. a shark) in three-dimensional space requires the use of a calibrated stereo photogrammetry system (Harvey & Shortis 1995; Harvey *et al*. 2004) and fixed reference points that are easily and routinely discerned.

Descriptions of non-agonistic behaviours (e.g. swimming, feeding and reproduction) are also necessary for the appropriate identification of agonistic pectoral fin depression and associated behaviours. The swimming behaviours of the grey reef shark were described which enabled clear recognition of the agonistic ‘hunch’ display (Johnson & Nelson 1973). Whilst earlier work (Martin 2007) that reported agonistic pectoral fin depression in grey nurse sharks acknowledged the similarities between the positions of pectoral fins during signalling (i.e. agonistic display) and swimming, neither descriptions nor reference to previous studies of normal swimming and/or non-swimming behaviours in the species were provided. In contrast, this study and previous work (Smith *et al*. 2015) has shown that grey nurse sharks actively engaged their pectoral fins for navigation (i.e. ascending, descending and turning) and stabilisation (i.e. maintaining position) akin to the North American leopard shark (Wilga & Lauder 2000; Maia *et al*. 2012) and the grey reef shark (Barlow 1974) with PFA varying according to physical and energetic parameters.

The review of shark agonistic behaviours noted that the presence of other agonistic behaviours can also aid identification of agonistic pectoral fin depression (Martin 2007). The absence of ‘fight’ response agonistic behaviours exhibited by grey nurse sharks along the east coast of Australia together with their low-energy swimming behaviours (Smith *et al*. 2015) indicated that this species adopts energy-conservation measures when at aggregation sites. These findings strongly suggested that grey nurse sharks are unlikely to expend energy on agonistic pectoral fin depression display, instead opting to flee from perceived threats (i.e. rapid withdrawal) as previously documented (Smith *et al*. 2015) and are in line with prior descriptions of its placid temperament (Pollard *et al*. 1996; Compagno 2001; Otway & Ellis 2011). Rapid withdrawal in response to the presence of a submersible has also been recorded for blackfin reef, silvertip and whitetip reef sharks (Nelson *et al*. 1986).

The results of this study indicated that the grey nurse shark does not exhibit agonistic pectoral fin depression in contrast to previous work (Martin 2007; Barker *et al*. 2011). Instead, grey nurse sharks exhibit the flight response (Smith *et al*. 2015) rather than the overt, aggressive agonistic behaviour displayed by grey reef sharks (Johnson & Nelson 1973; Nelson 1981/82; Nelson *et al*. 1986) when exposed to perceived threats. Consequently, tourism management guidelines that stipulate scuba divers must not chase or harass grey nurse sharks or block cave and gutter entrances (EA 2002; NSWG 2010) are appropriate for minimising disturbance the sharks. Moreover, it is important that existing satisfactory diver compliance with these management guidelines (Smith *et al*. 2010, 2014) is maintained to effectively protect the sharks from behavioural stressors.

3.5 CONCLUSION

This study using stereo photogrammetry showed that agonistic pectoral fin depression was not exhibited by grey nurse sharks at various life-history stages in the presence of scuba divers off eastern Australia. Instead, pectoral fin depression occurred during normal swimming behaviour and was attributed to the differing navigational and energetic requirements of the sharks in habitats with varying physical conditions. Moreover, at aggregation sites grey nurse sharks adopted energy conservation regimes and exhibited ‘flight’ rather than ‘fight’ responses to perceived threats. The contrasting results in two earlier studies were derived from visual estimates of PFA and anecdotal reports of agonistic pectoral fin depression in grey nurse sharks. When the three studies are considered together, the weight of quantitative evidence suggests the grey nurse shark does not exhibit agonistic pectoral fin depression in the absence of aggressively approaching divers. Reports of agonistic pectoral fin depression in the grey nurse shark obtained with visual estimates should be considered preliminary observations in need of further testing using rigorous scientific methodology such as stereo photogrammetry. It is important that diver compliance with current tourism management guidelines is maintained to protect the sharks from behavioural stressors.

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Chapter 4

A re-examination of evidence for agonistic behaviour in sharks

Declaration of co-authorship and co-contribution: papers incorporated in thesis by publication

Declaration by: Kirby Rae Smith **Signature:** [redacted]

Date: 1 April 2016

Paper Title: A re-examination of evidence for agonistic behaviour in sharks

In the case of the above publication, the following authors contributed to the work as follows:

Name	Contribution %	Nature of contribution
Kirby R Smith	70	Study concept, experimental design, data collection, data analysis and interpretation, manuscript writing, manuscript editing
Nicholas M Otway	20	Study concept, experimental design, advice on data interpretation, manuscript editing
Carol Scarpaci	10	Study concept, experimental design, manuscript editing

DECLARATION BY CO-AUTHORS

The undersigned certify that:

6. They meet criteria for authorship in that they have participated in the conception, execution or interpretation of at least that part of the publication in their field of expertise;
7. They take public responsibility for their part of the publication, except for the responsible author who accepts overall responsibility for the publication;
8. There are no other authors of the publication according to these criteria;
9. Potential conflicts of interest have been disclosed to **a)** granting bodies, **b)** the editor or publisher of journals or other publications, and **c)** the head of the responsible academic unit; and
10. The original data is stored at the following location(s):

Location(s): College of Engineering and Science, Victoria University, Melbourne, Victoria, Australia

and will be held for at least five years from the date indicated below:

		Date
Kirby R Smith	[redacted]	12 November 2014
Nicholas M Otway	[redacted]	7 November 2014
Carol Scarpaci	[redacted]	10 November 2014

ABSTRACT

A previous review of shark agonistic displays (Martin 2007) reported 29 agonistic behaviours in 23 species. Examination of citation accuracy in the review showed limited support for many of the behaviours reported and these should be treated as preliminary observations requiring further testing. Future behavioural research should use appropriate citation practices to ensure that accurate information about sharks is presented to management and/or the public.

4.1 INTRODUCTION

Agonistic behaviour comprises the fearful, threatening and aggressive acts of animals (Brown & Hunsperger 1963; Hill *et al*. 2014). Agonistic behaviour may be elicited by predators, other species, conspecifics or inanimate objects and have the purpose of defending self, offspring, access to resources (e.g. food, mates, territory) and/or social rank. A recent review of the non-human agonistic behaviour literature from the past 20 years (Hill *et al*. 2014) found that the majority of studies were focused on mammals (36.7%), followed by invertebrates and birds (21.5 and 21.0%, respectively), then fish (14.7%), with minimal research on reptiles (4.1%) and amphibians (2.1%). However, comparison of the three main types of social interactions (i.e. affiliative, agonistic and sexual) across these six taxonomic groups showed that fish and reptiles were used significantly more than expected by chance alone to study agonistic interactions (Hill *et al*. 2014).

The agonistic behaviours of several shark species have been reported but are well documented for the grey reef (*Carcharhinus amblyrhynchos*) shark (Johnson & Nelson 1973; Nelson 1981/82; Nelson *et al*. 1986) followed by the bonnethead (*Sphyrna tiburo*) shark (Myrberg & Gruber 1974). A later review defined and summarised the putative agonistic behaviours of a further 21 shark species in addition to the grey reef and bonnethead sharks (Martin 2007). The review reported 29 behaviours among the 23 species (Martin 2007) and was subsequently conveyed to a wider public readership via a popular literature publication (i.e. Nowak 2007). Considering this substantial increase in information and its dissemination, the aim of this study was to examine the data and citations used to determine the degree of support for the putative agonistic behaviours reported for the 23 shark species reviewed.

4.2 MATERIALS AND METHODS

The 33 citations provided for the table summarising shark agonistic displays in the review (i.e. Table 2 in Martin 2007) were examined to identify evidence for the behaviours in each of the 23 shark species listed. Citations (i.e. Church 1961, Fellows & Murchison 1967 and Klimley 1985) that were listed as footnotes to, but were omitted from, the table (i.e. Table 2 in Martin 2007) were included in the assessment for the appropriate species to give the author of the review (Martin 2007) the benefit of the doubt (*sensu* Todd *et al*. 2010). In assessing the citations, they were initially categorised as peer-reviewed publications (journal article, book chapter, conference proceedings, 'present study'- i.e. Martin 2007) or anecdotal reports (popular literature, undergraduate coursework, personal observation, personal communication) and their frequencies tabulated. The authors independently scrutinised all peer-reviewed publications cited for each species for evidence of the agonistic behaviours documented in the table (i.e. Table 2 in Martin 2007) as per Todd *et al*. (2007, 2010) and Todd & Ladle (2008). Each agonistic behaviour was deemed an assertion (*sensu* Todd *et al*. 2007, 2010) and this necessitated the assessment of multiple assertions in each publication. The behavioural descriptions provided in the publication were compared with the respective definitions in the review (Martin 2007) to determine the degree of agreement and were tabulated for each species. Every publication was then classified using the hierarchical citation accuracy categories of: (1) clear support; (2) ambiguous; (3) empty citation; and (4) no support, as defined by Todd *et al*. (2007, 2010) for each behaviour. A citation was classified as 'ambiguous' if the relevant behaviour did not comply with the minimum duration defined in the review (Martin 2007) or another aspect of the definition, was exhibited in a non-agonistic context, was not explicitly mentioned but could be inferred from other behaviours or was only documented in the discussion of the citation. The number of behaviours reported for each species in the summary table (i.e. Table 2 in Martin 2007) were summarised according to citation accuracy category, tabulated and plotted to align with Todd *et al*. (2007, 2010). The existence of an agonistic behaviour for a species was accepted if it was 'clearly supported' by at least one peer-reviewed publication. In contrast, those behaviours that lacked 'clear support' *sensu* Todd *et al*. (2007, 2010) or were only supported by anecdotal reports were treated as preliminary observations. Finally, the remaining agonistic behaviours in the anecdotal reports were tabulated for each species.

4.3 RESULTS

Three of the 33 citations that appeared as footnotes to the table summarising shark agonistic displays in the review (i.e. Table 2 in Martin 2007) were not cited in the table including two journal articles (i.e. Fellows & Murchison 1967 and Klimley 1985) and a popular literature publication (i.e. Church 1961). The 'present study' (Martin 2007) was not cited in the table (i.e. Table 2 in Martin 2007) for the Caribbean reef shark despite the species' inclusion in the study. A conference proceedings publication (i.e. Collier 1993) was cited for the grey reef shark but as the study focused on the white shark this was deemed a miscitation (*sensu* Todd & Ladle 2008). Similarly, a journal article (i.e. Miller & Collier 1980) that described an attack on a spearfisher by an unidentified species of hammerhead shark off San Diego, California, USA, was cited for the smooth hammerhead shark. Two other hammerhead shark species also inhabit the waters where the incident occurred (Compagno 1984) so this was considered another miscitation (Todd & Ladle

2008). No citations were provided for the two agonistic behaviours (i.e. pectoral fin depression and stiff or jerky movement) reported for the great hammerhead shark in the summary table (i.e. Table 2 in Martin 2007).

Less than half of the citations used for the agonistic behaviours reported for the 23 shark species in the summary table (i.e. Table 2 in Martin 2007) were peer-reviewed publications (Table 4.1).

Table 4.1. Frequencies and percentages of citation types provided for the agonistic behaviours reported for 23 shark species in the summary table in the review (i.e. Table 2 of Martin 2007) including citations listed as footnotes (i.e. Church 1961 = [a]; Fellows & Murchison 1967 = [b]; and Klimley *et al*. 1985 = [c]) and a miscitation (i.e. Collier 1993 = [d]).

Citation type	Frequency	Percentage
Peer-reviewed publications	12	36.3
Journal article[b,c,d]	9	27.3
Book chapter	1	3.0
Conference proceedings	1	3.0
Martin (2007)- ‘present study’	1	3.0
Anecdotal reports	21	63.6
Popular literature[a]	9	27.3
Undergraduate report	1	3.0
Personal observation	1	3.0
Personal communication	10	30.3
Total	33	100.0

Similarly, the 12 peer-reviewed publications cited in the table (i.e. Table 2 in Martin 2007) encompassed less than half of the shark species presented in the table (Table 4.2).

Table 4.2. Numbers of citations (undergraduate report = undergrad. report; personal observation = pers. obs.; personal communication = pers. comm.) provided for the agonistic behaviours reported for 23 shark species in the summary table in the review (i.e. Table 2 of Martin 2007), including citations listed as footnotes (i.e. Fellows & Murchison 1967 = [a]; and Klimley et al. 1985 = [b]) and Martin (2007)- 'present study' where it was not cited for a species ([c]).

Scientific name Common name	Total	Peer-reviewed publications				Anecdotal reports			
		Journal article	Book chapter	Conference proceedings	Martin (2007)	Popular literature	Undergrad. report	Pers. obs.	Pers. comm.
Carcharias taurus Sandtiger	4	0	0	0	1	1	0	1	1
Cetorhinus maximus Basking	1	0	0	0	0	0	0	0	1
Carcharodon carcharias White	12	1	1	0	1	3	0	1	5
Isurus oxyrinchus Shortfin mako	2	0	0	0	0	1	0	1	0
Mustelus canis Dusky smoothhound	1	1	0	0	0	0	0	0	0
Galeocerdo cuvier Tiger	2	0	0	0	0	0	0	1	1
Carcharhinus acronotus Blacknose	1	1	0	0	0	0	0	0	0
Carcharhinus albimarginatus Silvertip	1	0	0	0	1	0	0	0	0
Carcharhinus amblyrhynchos Grey reef	6[a]	3[a]	0	1	0	1	0	1	0
Carcharhinus falciformis Silky	1	1	0	0	0	0	0	0	0
Carcharhinus galapagensis Galapagos	2	0	0	0	1	1	0	0	0

Table 4.2 continued. Numbers of citations (undergraduate report = undergrad. report; personal observation = pers. obs.; personal communication = pers. comm.) provided for the agonistic behaviours reported for 23 shark species in the summary table in the review (i.e. Table 2 of Martin 2007), including citations listed as footnotes (i.e. Fellows & Murchison 1967 = [a]; and Klimley et al. 1985 = [b]) and Martin (2007)- 'present study' where it was not cited for a species ([c]).

Scientific name Common name	Total	Peer-reviewed publications				Anecdotal reports			
		Journal article	Book chapter	Conference proceedings	Martin (2007)	Popular literature	Undergrad. report	Pers. obs.	Pers. comm.
Carcharhinus leucas Bull	1	0	0	0	0	0	0	0	1
Carcharhinus limbatus Blacktip	1	1	0	0	0	0	0	0	0
Carcharhinus longimanus Oceanic whitetip	2	0	0	0	0	1	0	0	1
Carcharhinus melanopterus Blackfin reef	2	0	0	0	0	0	0	1	1
Carcharhinus perezi Caribbean reef	5[c]	0	0	0	[c]1	1	1	1	1
Carcharhinus plumbeus Sandbar	3	0	0	0	1	0	0	1	1
Negaprion brevirostris Lemon	2	1	0	0	0	0	0	1	0
Prionace glauca Blue	1	0	0	0	0	1	0	0	0
Sphyrna lewini Scalloped hammerhead	3[b]	1[b]	1	0	0	0	0	1	0
Sphyrna mokarran Great hammerhead	0	0	0	0	0	0	0	0	0
Sphyrna tiburo Bonnethead	1	1	0	0	0	0	0	0	0
Sphyrna zygaena Smooth hammerhead	3	1	0	0	0	1	0	1	0

Of the total number of agonistic behaviours reported for the 23 species, 43.7% were mentioned in the peer-reviewed publications cited (including Martin 2007- ‘present study’) with 47.9% attributed solely to anecdotal reports and the remaining 8.4% with no correct citations (Table 4.3).

Table 4.3. Numbers (percentages) of agonistic behaviours reported for 23 shark species in the summary table in the review (i.e. Table 2 of Martin 2007) and numbers (percentages) of those behaviours actually present in the citations provided, including citations listed as footnotes (i.e. Fellows & Murchison 1967 and Klimley *et al*. 1985) and Martin (2007)- ‘present study’ where it was not cited for a species.

Scientific name Common name	Total	Peer-reviewed publications	Peer-reviewed publications plus Martin (2007)- ‘present study’	Anecdotal reports
Carcharias taurus Sandtiger	8	0 (0.0)	2 (25.0)	6 (75.0)
Cetorhinus maximus Basking	3	0 (0.0)	0 (0.0)	3 (100.0)
Carcharodon carcharias White	15	3 (20.0)	6 (40.0)	9 (60.0)
Isurus oxyrinchus Shortfin mako	8	0 (0.0)	0 (0.0)	8 (100.0)
Mustelus canis Dusky smoothhound	5	3 (60.0)	3 (60.0)	0 (0.0)
Galeocerdo cuvier Tiger	7	0 (0.0)	0 (0.0)	7 (100.0)
Carcharhinus acronotus Blacknose	7	4 (57.1)	4 (57.1)	0 (0.0)
Carcharhinus albimarginatus Silvertip	7	0 (0.0)	7 (100.0)	0 (0.0)
Carcharhinus amblyrhynchos Grey reef	14	12 (85.7)	12 (85.7)	2 (14.3)
Carcharhinus falciformis Silky	8	6 (75.0)	6 (75.0)	0 (0.0)

Table 4.3 continued. Numbers (percentages) of agonistic behaviours reported for 23 shark species in the summary table in the review (i.e. Table 2 of Martin 2007) and numbers (percentages) of those behaviours actually present in the citations provided, including citations listed as footnotes (i.e. Fellows & Murchison 1967 and Klimley *et al*. 1985) and Martin (2007)- 'present study' where it was not cited for a species.

Scientific name Common name	Total	Peer-reviewed publications	Peer-reviewed publications plus Martin (2007)- 'present study'	Anecdotal reports
Carcharhinus galapagensis				
Galapagos	8	0 (0.0)	6 (75.0)	2 (25.0)
Carcharhinus leucas				
Bull	3	0 (0.0)	0 (0.0)	3 (100.0)
Carcharhinus limbatus				
Blacktip	8	3 (37.5)	3 (37.5)	0 (0.0)
Carcharhinus longimanus				
Oceanic whitetip	5	0 (0.0)	0 (0.0)	5 (100.0)
Carcharhinus melanopterus				
Blackfin reef	8	0 (0.0)	0 (0.0)	8 (100.0)
Carcharhinus perezi				
Caribbean reef	8	0 (0.0)	1 (12.5)	7 (87.5)
Carcharhinus plumbeus				
Sandbar	5	0 (0.0)	3 (60.0)	2 (40.0)
Negaprion brevirostris				
Lemon	9	3 (33.3)	3 (33.3)	6 (66.6)
Prionace glauca				
Blue	4	0 (0.0)	0 (0.0)	4 (100.0)
Sphyrna lewini				
Scalloped hammerhead	10	4 (40.0)	4 (40.0)	6 (60.0)
Sphyrna mokarran				
Great hammerhead	2	0 (0.0)	0 (0.0)	0 (0.0)
Sphyrna tiburo				
Bonnethead	11	11 (100.0)	11 (100.0)	0 (0.0)
Sphyrna zygaena				
Smooth hammerhead	4	2 (50.0)	2 (50.0)	2 (50.0)

At least a quarter of the agonistic behaviours reported for the dusky smoothhound (40.0%), blacknose (42.9%), silky (25.0%) and blacktip (62.5%) sharks were not mentioned in the peer-reviewed citations nor were anecdotal reports cited for these species (Tables 4.2 and 4.3). Just over a third of the agonistic behaviours in the peer-reviewed citations (excluding Martin 2007- 'present study') had clear support (38.6%) with the majority classified as ambiguous (48.6%) and the remainder empty citations (12.9%) (Figure 4.1).

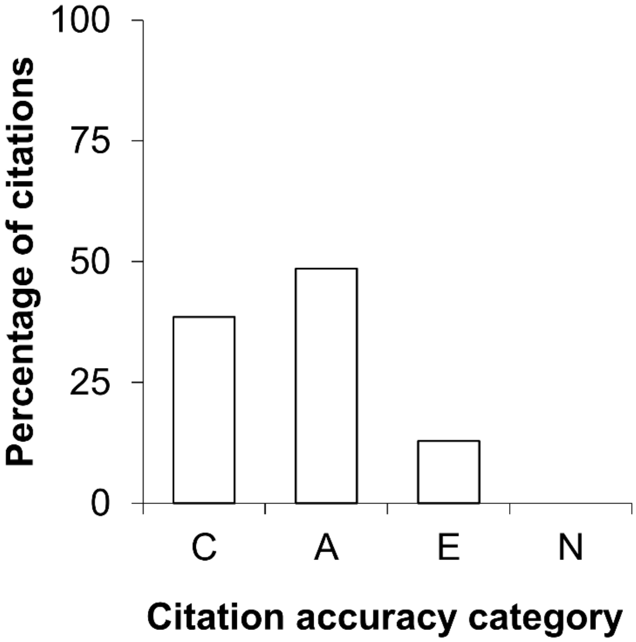

Figure 4.1. Percentages of citation accuracy (clear support = C; ambiguous = A; empty citation = E; and no support = N) for the agonistic behaviours reported for 23 shark species in the summary table in the review (i.e. Table 2 of Martin 2007).

Of the 29 behaviours classified as ambiguous, 37.9% were not presented as results but merely referred to in the discussion of the cited publication (Table 4.4). A further 27.6% were presented in the results of the respective paper but did not meet the durations of the behaviours defined by Martin (2007), with an additional 10.3% differing in other ways from the definitions (Table 4.4). Another 10.3% were not exhibited in an agonistic context, 6.9% were results inferred from other behaviours and the remaining 6.9% were results reported for an unidentified species (Table 4.4).

Table 4.4. Citation accuracies for the agonistic behaviours reported for 23 shark species in the summary table in the review (i.e. Table 2 of Martin 2007) with clear support (C, bolded text), ambiguous support (A, i.e. where defined duration was not met or no duration stated = [a]; other aspect of definition not met = [b]; non-agonistic context = [c]; inferred from other behaviour = [d]; unidentified species = [e]; documented in the discussion only = [f]) and empty citations (E) in the peer-reviewed publications (Allee & Dickenson 1954 = 1; Fellows & Murchison 1967 = 2; Johnson & Nelson 1973 = 3; Myrberg & Gruber 1974 = 4; Miller & Collier 1980 = 5; Klimley *et al*. 1985 = 6; Nelson *et al*. 1986 = 7; Collier 1993 = 8; Klimley *et al*. 1996 = 9; Ritter & Godknecht 2000 = 10; Martin *et al*. 2005 = 11) including citations listed as footnotes ([g]) and miscitations ([h]).

Scientific name Common name		Citation accuracy according to agonistic behaviour																							
	Citation	Stiff or jerky movement	Pectoral fin depression	Back arching	Tail flexure	Tail depression	Snout elevation	Head shaking	Jaw gaping	Ritualistic jaw snapping	Open jawed tooth raking	Gill pouch billowing	Torso thrusting	Clasper flexion	Tail slapping	Body tilting or rolling	Rapid, tight pattern swimming	Laterally exaggerated swimming	Looping	Corkscrewing	Reduced swimming efficiency	Charging	Ramming with snout	Give way	Rapid withdrawal
Carcharodon carcharias	9														**C**										E
White	1		A[a,f]												E										
	1																								
Mustelus canis	1							**C**														**C**			**C**
Dusky smoothhound																									
Carcharhinus acronotus	4	A[f]	A[a]	A[a]																					A[b]
Blacknose																									

Table 4.4 continued. Citation accuracies for the agonistic behaviours reported for 23 shark species in the summary table in the review (i.e. Table 2 of Martin 2007) with clear support (C, bolded text), ambiguous support (A, i.e. where defined duration was not met or no duration stated = [a]; other aspect of definition not met = [b]; non-agonistic context = [c]; inferred from other behaviour = [d]; unidentified species = [e]; documented in the discussion only = [f]) and empty citations (E) in the peer-reviewed publications (Allee & Dickenson 1954 = 1; Fellows & Murchison 1967 = 2; Johnson & Nelson 1973 = 3; Myrberg & Gruber 1974 = 4; Miller & Collier 1980 = 5; Klimley *et al*. 1985 = 6; Nelson *et al*. 1986 = 7; Collier 1993 = 8; Klimley *et al*. 1996 = 9; Ritter & Godknecht 2000 = 10; Martin *et al*. 2005 = 11) including citations listed as footnotes ([g]) and miscitations ([h]).

Scientific name Common name	Citation	Citation accuracy according to agonistic behaviour																							
		Stiff or jerky movement	Pectoral fin depression	Back arching	Tail flexure	Tail depression	Snout elevation	Head shaking	Jaw gaping	Ritualistic jaw snapping	Open jawed tooth raking	Gill pouch billowing	Torso thrusting	Clasper flexion	Tail slapping	Body tilting or rolling	Rapid, tight pattern swimming	Laterally exaggerated swimming	Looping	Corkscrewing	Reduced swimming efficiency	Charging	Ramming with snout	Give way	Rapid withdrawal
Carcharhinus	2[g]																	**C**				**C**			
amblyrhynchos	3	A	**C**	**C**			A		A^{d}		E					**C**		**C**	**C**		A	E			A
Grey reef	7	**C**	**C**	**C**			**C**		A^{d}		**C**					**C**		**C**	E		**C**	**C**			**C**
	8[h]																								
Carcharhinus falciformis Silky	4	A^{f}	A^{f}	A^{f}													$A^{d,f}$					$A^{a,f}$			$A^{a,f}$

Table 4.4 continued. Citation accuracies for the agonistic behaviours reported for 23 shark species in the summary table in the review (i.e. Table 2 of Martin 2007) with clear support (C, bolded text), ambiguous support (A, i.e. where defined duration was not met or no duration stated = [a]; other aspect of definition not met = [b]; non-agonistic context = [c]; inferred from other behaviour = [d]; unidentified species = [e]; documented in the discussion only = [f]) and empty citations (E) in the peer-reviewed publications (Allee & Dickenson 1954 = 1; Fellows & Murchison 1967 = 2; Johnson & Nelson 1973 = 3; Myrberg & Gruber 1974 = 4; Miller & Collier 1980 = 5; Klimley *et al*. 1985 = 6; Nelson *et al*. 1986 = 7; Collier 1993 = 8; Klimley *et al*. 1996 = 9; Ritter & Godknecht 2000 = 10; Martin *et al*. 2005 = 11) including citations listed as footnotes ([g]) and miscitations ([h]).

Scientific name Common name		Citation accuracy according to agonistic behaviour																							
	Citation	Stiff or jerky movement	Pectoral fin depression	Back arching	Tail flexure	Tail depression	Snout elevation	Head shaking	Jaw gaping	Ritualistic jaw snapping	Open jawed tooth raking	Gill pouch billowing	Torso thrusting	Clasper flexion	Tail slapping	Body tilting or rolling	Rapid, tight pattern swimming	Laterally exaggerated swimming	Looping	Corkscrewing	Reduced swimming efficiency	Charging	Ramming with snout	Give way	Rapid withdrawal
Carcharhinus limbatus	1		A[a]		A[a]											A[a]									
Blacktip	0																								
Negaprion brevirostris	4	A[d,f]																				A[f]			A[f]
Lemon																									
Sphyrna lewini	6[g]							**C**					**C**							**C**			**C**		
Scalloped hammerhead	9							E					E							E			E		

Table 4.4 continued. Citation accuracies for the agonistic behaviours reported for 23 shark species in the summary table in the review (i.e. Table 2 of Martin 2007) with clear support (C, bolded text), ambiguous support (A, i.e. where defined duration was not met or no duration stated = [a]; other aspect of definition not met = [b]; non-agonistic context = [c]; inferred from other behaviour = [d]; unidentified species = [e]; documented in the discussion only = [f]) and empty citations (E) in the peer-reviewed publications (Allee & Dickenson 1954 = 1; Fellows & Murchison 1967 = 2; Johnson & Nelson 1973 = 3; Myrberg & Gruber 1974 = 4; Miller & Collier 1980 = 5; Klimley *et al*. 1985 = 6; Nelson *et al*. 1986 = 7; Collier 1993 = 8; Klimley *et al*. 1996 = 9; Ritter & Godknecht 2000 = 10; Martin *et al*. 2005 = 11) including citations listed as footnotes ([g]) and miscitations ([h]).

Scientific name Common name	Citation accuracy according to agonistic behaviour																								
	Citation	Stiff or jerky movement	Pectoral fin depression	Back arching	Tail flexure	Tail depression	Snout elevation	Head shaking	Jaw gaping	Ritualistic jaw snapping	Open jawed tooth raking	Gill pouch billowing	Torso thrusting	Clasper flexion	Tail slapping	Body tilting or rolling	Rapid, tight pattern swimming	Laterally exaggerated swimming	Looping	Corkscrewing	Reduced swimming efficiency	Charging	Ramming with snout	Give way	Rapid withdrawal
Sphyrna tiburo Bonnethead	4	A[d]	A[a]			A[a]	A[a]	**C**		**C**		A[c]		A[c]									A[b]	A[c]	A[b]
Sphyrna zygaena Smooth hammerhead	5																A[e]								A[d,e]

4.2 DISCUSSION

Analysis of the 12 peer-reviewed publications in the review (Martin 2007) using the hierarchical citation accuracy categories of Todd *et al*. (2007, 2010) revealed clear support for only 38.6% of the assertions (i.e. each specified agonistic behaviour) which contrasted with Todd *et al*. (2007, 2010) who showed clear support for approximately 76.0% of the assertions made in ecological (i.e. 76.1%) and marine biological (i.e. 75.8%) literature. The preponderance of ambiguous and empty citations led to a miscitation rate of 61.4% (compared with ≈24.0%, Todd *et al*. 2007, 2010) and had substantial implications (Todd & Ladle 2008; Frazer *et al*. 2012) for nine of the 10 shark species as there was inadequate scientific evidence for the agonistic behaviours reported.

Anecdotal reports dominated the purported evidence of agonistic behaviours for the majority of the shark species considered in the review (Martin 2007). The pioneering research of Nelson (1981/82) highlighted the prevalence of anecdotal reports of shark agonistic behaviour and emphasised the need to scientifically test these observations. Excepting the behaviours documented in the grey reef shark (Johnson & Nelson 1973; Nelson et al. 1986), the synthesis of shark agonistic behaviours in the review (Martin 2007) should, where appropriate, be treated as preliminary observations that require future scientific research to test hypotheses concerning the agonistic behaviour of sharks.

4.2 CONCLUSION

Many of the agonistic behaviours reported for the 23 shark species had limited support and should be considered preliminary observations that require further scientific examination. It is imperative that future behavioural studies use appropriate citation practices to ensure that accurate information about sharks is presented to management and/or the public.

ACKNOWLEDGEMENTS

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Chapter 5

Potential errors in paired-laser photogrammetric estimates of aggregated grey nurse sharks (*Carcharias taurus*) off eastern Australia: a stereo-video photogrammetric assessment

Declaration of co-authorship and co-contribution: papers incorporated in thesis by publication

Declaration by: Kirby Rae Smith **Signature:** [redacted]

Date: 1 April 2016

Paper Title: Potential errors in paired-laser photogrammetric estimates of aggregated grey nurse sharks (*Carcharias taurus*) off eastern Australia: a stereo-video photogrammetric assessment

In the case of the above publication, the following authors contributed to the work as follows:

Name	Contribution %	Nature of contribution
Kirby R Smith	80	Study concept, experimental design, data collection, statistical analysis and interpretation, manuscript writing, manuscript editing
Nicholas M Otway	15	Study concept, experimental design, advice on statistical analysis and interpretation, manuscript editing
Carol Scarpaci	5	Study concept, experimental design, manuscript editing

DECLARATION BY CO-AUTHORS

The undersigned certify that:

1. They meet criteria for authorship in that they have participated in the conception, execution or interpretation of at least that part of the publication in their field of expertise;
2. They take public responsibility for their part of the publication, except for the responsible author who accepts overall responsibility for the publication;
3. There are no other authors of the publication according to these criteria;
4. Potential conflicts of interest have been disclosed to **a)** granting bodies, **b)** the editor or publisher of journals or other publications, and **c)** the head of the responsible academic unit; and
5. The original data is stored at the following location(s):

Location(s): College of Engineering and Science, Victoria University, Melbourne, Victoria, Australia

and will be held for at least five years from the date indicated below:

		Date
Kirby R Smith	[redacted]	13 November 2014
Nicholas M Otway	[redacted]	7 November 2014
Carol Scarpaci	[redacted]	10 November 2014

ABSTRACT

Paired-laser photogrammetry relies on the fundamental assumption that measured objects are perpendicular to the laser projections of the system. In contrast, stereo-video photogrammetry is not constrained by this requirement. Stereo-video photogrammetric angular and morphometric measurements of the critically endangered grey nurse shark (*Carcharias taurus*) aggregated off eastern Australia were used to assess the accuracy of paired-laser photogrammetric length estimates. Of 611 sharks measured, 96.1% did not meet the fundamental assumption underlying paired-laser photogrammetry. The potential errors in paired-laser photogrammetry estimates of the precaudal length were much smaller than those of total length due to the angle of the caudal fin. The substantial errors inherent in paired-laser photogrammetric total length estimates of sharks have serious implications for subsequent population size-structure patterns. Future sampling of free-swimming bony fishes, sharks and other marine megafauna should consider using stereo-video photogrammetry when accurate and precise length estimates need to be obtained in a dynamic underwater setting, particularly when target species continuously change their orientation in three-dimensional space.

5.1 INTRODUCTION

Several non-invasive sampling techniques have estimated lengths, distances and angles associated with the size and behaviour of unrestrained wild marine megafauna. Underwater visual census (UVC, e.g. Heyman *et al*. 2001; Pierce *et al*. 2010) is a time- and cost-effective technique (Pita *et al*. 2014), but photogrammetry systems generally provide more accurate and precise length estimates (Harvey *et al*. 2001, 2004; Rohner *et al*. 2011). However, paired-laser photogrammetry estimates (e.g. Rezzolla *et al*. 2014; Leurs *et al*. 2015) are inaccurate if measured objects are not perpendicular to the laser projections (i.e. parallax error) as this is a fundamental assumption underlying the technique (Deakos 2010; Rohner *et al*. 2011; Jeffreys *et al*. 2013). Moreover, the accuracy of paired-laser photogrammetric length estimates cannot be determined unless the angle of the measured objects to the laser dots is known. In contrast, stereo-photographic (e.g. Klimley 1981/82, 1985; van Rooij & Videler 1996; Bräger & Chong 1999; Chong & Schneider 2001) and stereo-video (e.g. Dunbrack 2006; Otway *et al*. 2008) photogrammetry are not constrained by this requirement and thus present the most accurate and precise sampling techniques for measurement of lengths and angles (Klimley & Brown 1983; Harvey *et al*. 2004).

Paired-laser (Bansemer & Bennett 2009, 2010, 2011; Barker & Williamson 2010; Barker *et al*. 2011) and stereo-video (Otway *et al*. 2008; Smith *et al*. 2015) photogrammetry and UVC (Hayward 2003; Martin 2007; Smith *et al*. 2010, 2014) have been used to document the life-history stages and behaviours of the grey nurse (sand tiger, ragged-tooth) shark (*Carcharias taurus* Rafinesque 1810) in the wild. Globally, grey nurse sharks have a widespread, but disjointed distribution in the coastal waters of warm-temperate and tropical regions (Compagno 2001). Male and female grey nurse sharks grow to about 3.00 and 3.20 metres total length (TL), respectively (Compagno 2001; Goldman *et al*. 2006; Last & Stevens 2009). With slow sexual maturation (50.0% sexual maturity: males = 2.10 metres TL at 6-7 years, females = 2.59 metres TL at 10-12 years, Goldman *et al*. 2006; Otway & Ellis 2011) and low fecundity (maximum of two pups born biennially, Bass *et al*. 1975; Gilmore *et al*. 1983; Compagno 2001), the species takes decades to recover from worldwide population declines caused by targeted and indirect commercial and recreational fishing (Otway *et al*. 2004; Otway & Ellis 2011). Consequently, the grey nurse shark is listed globally as ‘Vulnerable’ on the International Union for the Conservation of Nature (IUCN) Red List of Threatened Species 2000 (Cavanagh *et al*. 2003). Off Australia, there are two genetically-distinct grey nurse shark populations along the east and west coasts (Stow *et al*. 2006; Ahonen *et al*. 2009). The eastern population in southeast Queensland and New South Wales (NSW) waters has experienced substantial decline from multiple anthropogenic impacts (Otway *et al*. 2004; Otway & Ellis 2011), comprises between 1146 and 1662 sharks (Lincoln Smith & Roberts 2010), and is listed as ‘Critically Endangered’ by the IUCN (Cavanagh *et al*. 2003) and under Commonwealth and state legislation. These sharks undertake annual (male) and biennial (female) migrations (up to ≈4500 kilometres) connected with their reproductive cycles and interrupted by visits of varying durations to numerous aggregation sites (Bansemer & Bennett 2009; Otway *et al*. 2009; Otway & Ellis 2011). Many of these sites also support a longstanding marine wildlife tourism (MWT) sector centred on scuba diving with the sharks. This industry was identified as a possible threat to the recovery of this critically endangered population so a voluntary code of conduct and federal and state legislation were implemented to manage the potential adverse impacts of MWT (EA 2002; Smith *et al*. 2014).

Paired-laser photogrammetric estimates of the precaudal length (PCL) (Barker & Williamson 2010; Barker *et al*. 2011) and natural TL (Bansemer & Bennett 2009, 2010, 2011) of grey nurse sharks were used with gender and size at sexual maturity to assign life-history stages at several east Australian critical habitat sites. These studies used paired lasers mounted on a single underwater video camera separated by 200 millimetres (Barker & Williamson 2010; Barker *et al*. 2011; Barker, personal communication) or 500 millimetres (Bansemer & Bennett 2009, 2010, 2011). The researchers subsequently selected suitable video frames of grey nurse sharks with minimal lateral body flexure and then used the known distance between the laser dots on the shark as a scale bar to estimate PCL or natural TL. The stated errors associated with the angle of a shark to the paired-laser photogrammetry system for PCL and natural TL estimates were <3% (Barker & Williamson 2010) and ±5% (Bansemer & Bennett 2009, 2011), respectively. Importantly, the research off Queensland (Bansemer & Bennett 2009, 2010, 2011) did not acknowledge the potential for caudal fin flexure to influence natural TL measurements whereas that off New South Wales (Barker & Williamson 2010; Barker *et al*. 2011) recognised this source of error and consequently estimated PCL instead.

The aim of this research was to use stereo-video photogrammetric angular and morphometric measurements to assess the accuracy of paired-laser photogrammetric length estimates of critically endangered east Australian grey nurse sharks. The information gleaned from this study is important for future sampling design and will thus contribute to the expanding assessment and management of the potential impacts of this MWT sector.

5.2 MATERIALS AND METHODS

5.2.1 Study sites and sampling

Observations of various lengths and the horizontal angles of grey nurse sharks in the absence of MWT scuba divers were made from digital videos recorded with an underwater stereo-video photogrammetry system (USVPS) during the austral autumn of 2010 across eight aggregation sites spanning ≈800 kilometres of the east Australian coast (Figure 5.1). Sampling was designed to target juvenile males, juvenile females, adult males, gestating females and resting females (i.e. five life-history stages) that occupy these sites at particular times of the year (Bansemer & Bennett 2009; Otway & Ellis 2011).

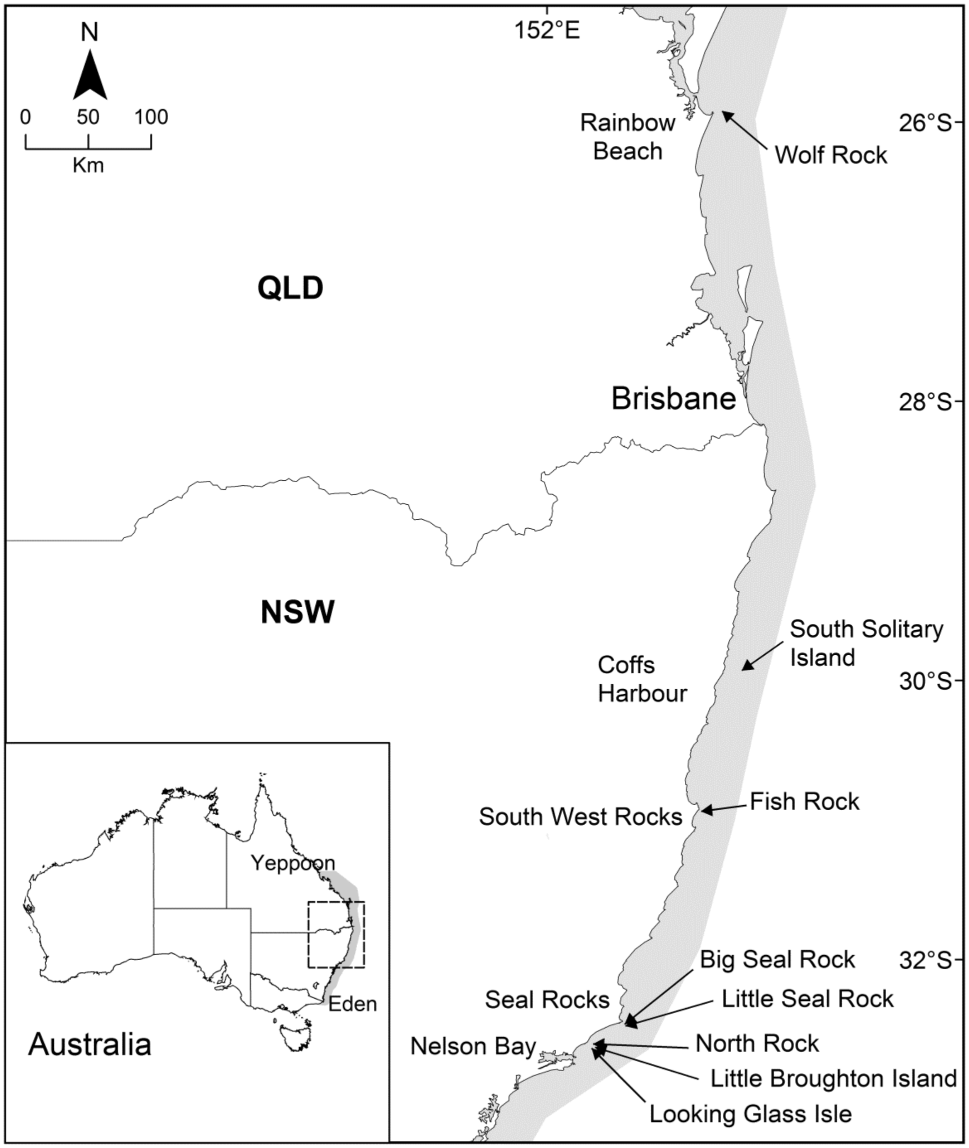

Figure 5.1. Map (QLD = Queensland and NSW = New South Wales) showing the geographic range (grey shading) of the grey nurse shark (*Carcharias taurus*) and the locations of Wolf Rock, South Solitary Island, Fish Rock, Big Seal Rock, Little Seal Rock, North Rock, Little Broughton Island and Looking Glass Isle sampled from March to May 2010 to document the accuracy of angular measurements used in documenting the behaviours of the sharks along the east coast of Australia.

5.2.2 Underwater stereo-video photogrammetry system

The USVPS comprised two digital, high definition video cameras that recorded 24 frames per second (Sony, Model DCR VX2100E), were attached to a precisely-machined aluminium base bar 770 millimetres apart and were angled inwardly by 4° to ensure partial overlap of the left and right images (Figure 5.2a, b). An image synchronisation element was attached to the distal end of a 1150 millimetre-long aluminium rod extending from the middle of and perpendicular to the base bar (Otway *et al*. 2008; Smith *et al*. 2015, Figure 5.2a, b). The USVPS was calibrated before use following a standardised protocol in a public swimming pool using a 1400 × 1400 × 1400 millimetre anodised aluminium calibration cube with 80 reflective points at fixed locations. The USVPS was maintained in a stationary position and recorded the calibration cube as it was rotated into various positions. The videos from both cameras were downloaded with Adobe Premiere (Version 6.0), saved in AVI format and used with specialised software (Cal Version 1.20, ©SeaGIS Pty Ltd) to calibrate the USVPS (Otway *et al*. 2008; Smith *et al*. 2015). The USVPS was operated by a single scuba diver (Figure 5.2b) and enabled stereo images of grey nurse sharks 3000 millimetres TL at a minimum distance of 3000 millimetres from the base bar (Otway *et al*. 2008; Smith *et al*. 2015).

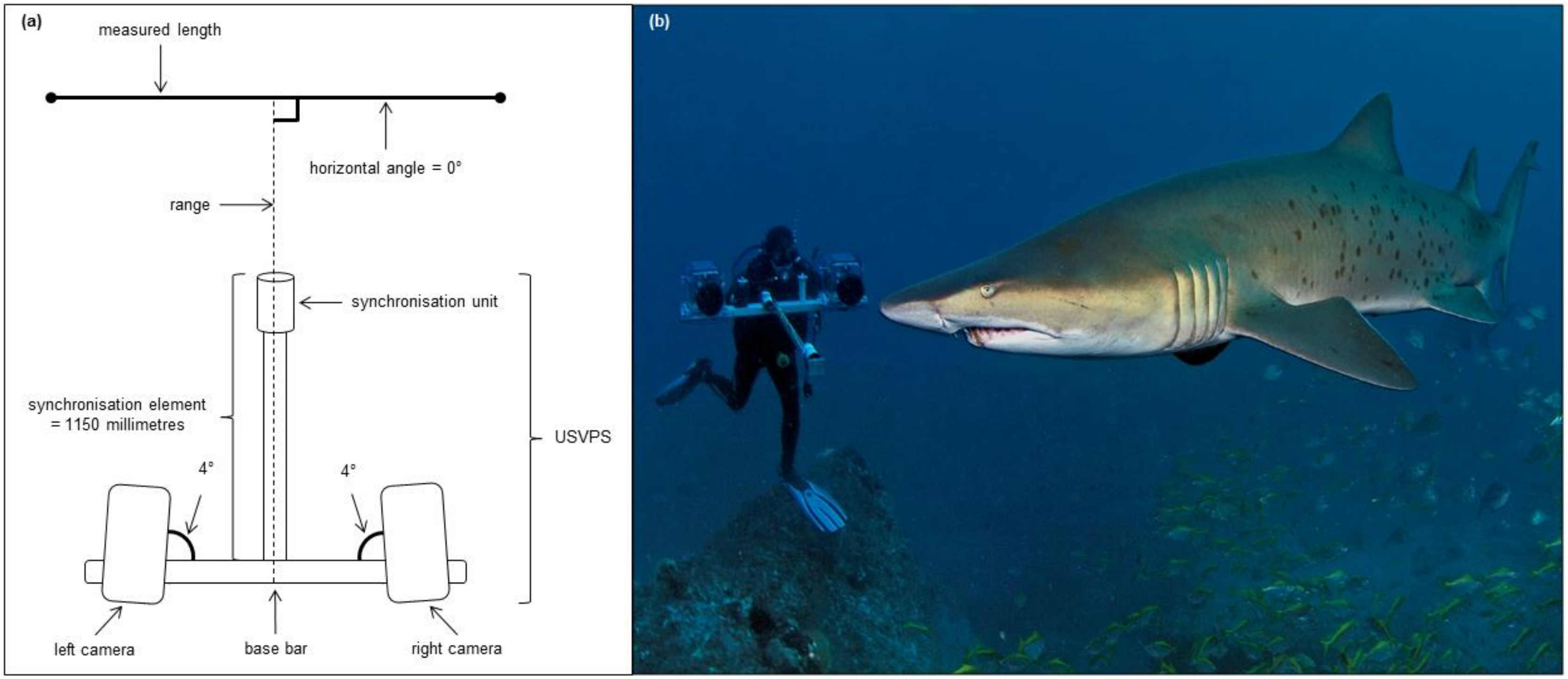

Figure 5.2. (a) Line diagram of the underwater stereo-video photogrammetry system (USVPS) with the length, range and horizontal angle of the measured object to the base bar and (b) photograph of a scuba diver using the USVPS to record digital images of a female grey nurse shark (*Carcharias taurus*) at Fish Rock in April 2007.

Videos of grey nurse sharks were downloaded with Adobe Premiere in AVI format then analysed with EventMeasure software (©SeaGIS Pty Ltd) which uses synchronised images from the left and right cameras and an on-screen ‘point and click’ approach. The software facilitates highly accurate estimates (±0.2%) of a special-purpose bar with reflective targets separated by known lengths (millimetres) and precise estimates (±0.3-1.3%) of PCL of grey nurse sharks irrespective of their three-dimensional position in the water column (Otway *et al*. 2008). It also provides simultaneous estimates of their horizontal and vertical angles (degrees) and distances (millimetres) relative to the USVPS.

5.2.3 Grey nurse shark life-history stages

Precaudal length is typically used to calculate shark TL due to greater accuracy (Francis 2006) and is measured as the straight-line length from the snout to the precaudal pit (Compagno 2001) rather than over the curve of the body (Figure 5.3a). It is also readily observed underwater and measured using the USVPS. In contrast, TL is measured as a straight line from the tip of the snout to the posterior tip of the caudal fin (Compagno 2001) with the tail in the depressed position (Francis 2006).

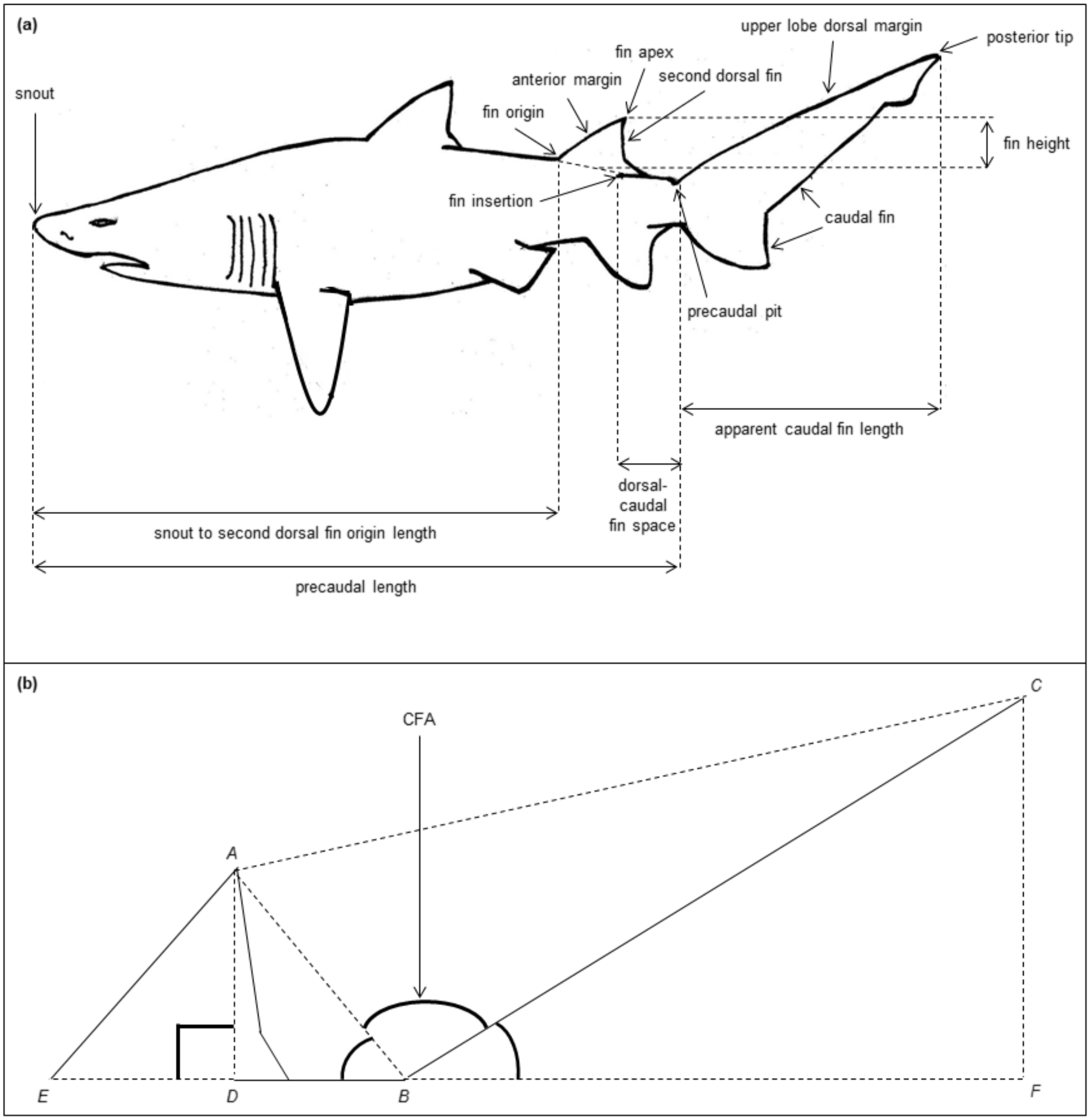

Figure 5.3. Illustration showing the (a) morphometric and (b) trigonometric distances measured to calculate the precaudal length, total length and caudal fin angle (CFA) of the grey nurse shark (*Carcharias taurus*).

Instantaneous 30-second scan samples (Altmann 1974) were used to select video frames for the subsequent measurement of the PCL of each grey nurse shark within 10.00 metres of the USVPS (Smith *et al*. 2015). The TL of the shark with the tail depressed was determined from PCL in a significant linear regression (Regression 1, Table 5.1) developed from necropsies of 150 grey nurse sharks (Otway *et al*. 2008; Otway 2015) caught in the New South Wales shark meshing program and by commercial and recreational fishers (Otway *et al*. 2004). Shark life-history stage was determined from TL, gender (i.e. presence of claspers identified males) and the maturity ogives (Otway & Ellis 2011).

Table 5.1. Linear regression relationships between total length (TL) with the caudal fin in the depressed position and precaudal length (PCL), second dorsal fin height (2DFH), second dorsal fin base length (2DFBL) and snout to second dorsal fin origin length (S2DFOL) for the grey nurse shark (*Carcharias taurus*) obtained via necropsies off eastern Australia with sample sizes (*n*) and goodness of fit (R^2).

Regression	Equation	Unit	*n*	R^2	*P*
1	TL = 1.368PCL + 0.069	Metres	66	0.99	< 0.001
2	2DFH = 0.065TL - 9.210	Millimetres	72	0.95	< 0.001
3	2DFBL = 0.0662TL + 4.0185	Millimetres	72	0.95	< 0.001
4	S2DFOL = 0.59TL - 0.023	Metres	66	0.99	< 0.001

5.2.4 Potential errors in paired-laser photogrammetric estimates of grey nurse shark lengths

5.2.4.1 Accuracy of visual estimates of horizontal angles

The USVPS was used to determine the potential errors that may be associated with PCL and natural TL estimates of grey nurse sharks obtained with paired-laser photogrammetry systems. A shark that was parallel to the base bar of the USVPS had a horizontal angle of 0° and this was equivalent to a shark that would have been perpendicular to the laser projections of a paired-laser photogrammetry system. The videos were viewed and the most appropriate frames were selected where a grey nurse shark appeared to be as close to parallel to the base bar to meet the assumption of paired-laser photogrammetry. The visual estimate of the horizontal angle of each shark was recorded as parallel or not parallel. The USVPS was then used to measure the PCL and horizontal angle of the shark in each frame. The accuracy of each visual estimate was subsequently determined from the corresponding USVPS measurement. The horizontal angle measurements of the sharks were then partitioned into 10° bins with the numbers of sharks and correct visual estimates calculated as percentages.

5.2.4.2 Propagation of errors in precaudal length estimates

Examples of the potential errors associated with paired-laser photogrammetric estimates of PCL were calculated for sharks at horizontal angles of 0° to the base bar of the USVPS and for the upper bound of every 10° bin where incorrect visual estimates occurred. The minimum and maximum PCL of juvenile and adult male and female grey nurse sharks (i.e. from field and necropsy measurements, Otway 2015) were used for all calculations. Percentage errors in paired-laser photogrammetric estimates of PCL were also calculated using the horizontal angle and PCL of each shark measured with the USVPS. The propagation of error for each PCL estimate was calculated using the product rule (Ku 1966; Pentz & Shott 1988; Taylor 1997). The errors within a PCL estimate were divided by the respective true measured values then the quadrature of the fractional errors was taken to give the total error for the estimate (Ku 1966; Pentz & Shott 1988; Taylor 1997). Shark length (W, in millimetres) in an onscreen video image was assumed to have a mensurative error (w) of 1 millimetre. An onscreen scale bar (X) which also had a mensurative error of 1 millimetre (x) was provided by dots from two lasers actually separated by 150 millimetres (Y). A measurement error (y) in actual scale bar length occurs when a shark is not perpendicular to the laser projections of a paired-laser photogrammetry system. The magnitude of this error increases as the horizontal angle of the shark deviates from 0° and was calculated using the horizontal angle quantified independently with the USVPS together with Pythagorean formulae. This error was expressed as a change in scale bar length (millimetres) to ensure consistency in measurement units necessary for generating the combined error using the product rule (Pentz & Shott 1988). Combined errors were calculated to the nearest millimetre using the product rule formula where Error = PCL ($\sqrt{[(w/W)^2 + (x/X)^2 + (y/Y)^2]}$), subsequently converted to percentages of the actual minimum and maximum PCL for each life-history stage and tabulated. The combined error associated with paired-laser photogrammetric estimates was calculated as a percentage of the PCL of each shark measured with the USVPS and plotted against the corresponding quantified horizontal angle.

5.2.4.3 Propagation of errors in total length estimates

In addition to the errors associated with quantifying PCL, photogrammetric estimates of natural TL are subject to another source of error due to the fluctuating elevation of the caudal fin (Figure 5.3a) that produces varying caudal fin angles (CFA, Figure 5.3b) and changes the apparent caudal fin length (CFL). Consequently, the range that the dorsal margin of the upper lobe of the caudal fin (Figure 5.3a) deviated from the depressed position was calculated for the minimum (65°) and maximum (139°) CFA previously documented for grey nurse sharks (Smith *et al*. 2015) using standard trigonometric equations. Various lengths needed in the trigonometric equations were obtained from morphometric relationships derived from necropsies (Otway 2015). Briefly, the CFA was subtended by the second dorsal fin apex (point *A*), the anterior edge of the precaudal pit (point *B*) and the posterior tip of the upper lobe of the caudal fin (point *C*) (Figure 5.3a, b). The CFA (angle ABC) was then calculated from USVPS measurements of lengths *AB*, *BC* and *AC* using the law of cosines (De Sapio 1976) with $ABC = \arccos [(AB^2 + BC^2 - AC^2)/2(AB \times BC)]$ (Smith *et al*. 2015). The second dorsal fin height (line *AD*, Figure 5.3a, b) extended from the fin apex (point A) to the fin insertion (point *D*) and was determined from TL via a linear regression (Regression 2, Table 5.1). The second dorsal fin base length (line *DE*, Figure 5.3a, b) from the fin origin (point *E*) to the fin insertion (point *D*) was also calculated using TL via a linear regression (Regression 3, Table 5.1). The straight line from the snout to the second dorsal fin origin (Figure 5.3a) was then determined from TL using a linear regression (Regression 4, Table 5.1). The snout to the second dorsal fin origin length and the second dorsal fin base length were summed then subtracted from the PCL to give the length of the dorsal-caudal fin space (line *BD*) from the second dorsal fin insertion (point *D*) to the precaudal pit (point *B*) (Figure 5.3a, b). The angle subtended by the second dorsal fin apex (point *A*), the precaudal pit (point *B*) and the second dorsal fin insertion (point *D*) was then calculated from the second dorsal fin height (line *AD*) and dorsal-caudal fin space (line *BD*) using Pythagoras' theorem. Angle *ABD* was summed with the CFA then subtracted from 180° to give the angle subtended by the precaudal pit (point *B*), the caudal fin posterior tip when elevated (point *C*) and the posterior tip when depressed (point *F*) (Figure 5.3a, b). The cos of angle *BCF* was multiplied by the true CFL (i.e. CFL = TL – PCL, in millimetres) to give the estimated apparent CFL. The apparent CFL was then subtracted from the true CFL to calculate the measurement error (z) for the true TL (Z). The fractional error associated with the caudal fin position was included in all TL error propagation calculations using the product rule formula where Error = TL $(\sqrt{[(w/W)^2 + (x/X)^2 + (y/Y)^2 + (z/Z)^2]})$.

5.2.4 Statistical analyses

Statistical analyses were done with a Type I (α) error rate of $P = 0.05$. The mean and angular variance of grey nurse shark horizontal angles to the USVPS were analysed using tests associated with the Von Mises (circular normal) distribution (Batschelet 1981).

Rayleigh tests examined for significant mean angles and a Watson-Williams multi-sample F test was done to determine if there was a significant difference among mean horizontal angles according to life-history stages (Batschelet 1981). Sharks of unknown gender were excluded from analyses among life-history stages.

5.3 RESULTS

5.3.1 Potential errors in paired-laser photogrammetric estimates of grey nurse shark lengths

5.3.1.1 Shark horizontal angles

The overall mean (angular variance, range) horizontal angle of grey nurse sharks to the USVPS (n = 611) was 19 (5, 0-83)° which was significant (Rayleigh test: z = 554.41, P = <0.001). The genders of 175 sharks could not be determined and the remaining 436 sharks were partitioned into five life-history stages. Mean horizontal angles differed significantly among life-history stages (Watson-Williams test: $F_{4,\ 431}$ = 2035.79, P < 0.0005) with the mean angle greatest for juvenile males followed by juvenile females, adult males and resting females, and least for gestating females (Table 5.2).

Table 5.2. Means, angular variances and ranges of horizontal angle (degrees) of grey nurse sharks (*Carcharias taurus*) to the underwater stereo-video photogrammetry system with sample sizes (*n*) and tests for significance of directionality (Rayleigh test statistic = *z*) according to life-history stages sampled at Wolf Rock, South Solitary Island, Fish Rock, Big Seal Rock, Little Seal Rock, North Rock, Little Broughton Island and Looking Glass Isle from March to May 2010 where $P > 0.05$ = not significant, denoted by 'ns'; $P \leq 0.05$ = *; $P \leq 0.01$ = **; $P \leq 0.001$ = ***.

Life-history stage	Mean angle	Angular variance	Range	*n*	*z*
Juvenile males	22	8	0-83	23	19.95***
Juvenile females	15	4	0-78	222	207.06***
Adult males	15	4	0-67	128	119.39***
Gestating females	6	3	0-36	40	37.75***
Resting females	12	2	1-49	23	22.13***

Almost all (96.1%) of the grey nurse sharks across all sites and life-history stages had horizontal angles >0° to the base bar of the USVPS when their PCL was measured with 74.7% between 1 and 30° (Table 5.3).

Table 5.3. Numbers and percentages of grey nurse sharks (*Carcharias taurus*) with measured horizontal angles (degrees) partitioned into 10° bins and the numbers and percentages of sharks where the visual estimates of horizontal angle were correct sampled at Wolf Rock, South Solitary Island, Fish Rock, Big Seal Rock, Little Seal Rock, North Rock, Little Broughton Island and Looking Glass Isle from March to May 2010.

Horizontal angle	Number (percentage) of sharks in 10° bin	Number (percentage) of sharks where visual estimate of horizontal angle was:	
		Correct	Incorrect
Parallel			
0	24 (3.9)	5 (20.8)	19 (79.2)
Not parallel	587 (96.1)	538 (91.7)	49 (8.3)
1-10	238 (39.0)	197 (82.8)	41 (17.2)
11-20	134 (21.9)	128 (95.5)	6 (4.5)
21-30	84 (13.8)	82 (97.6)	2 (2.4)
31-40	49 (8.0)	49 (100.0)	0 (0.0)
41-50	39 (6.4)	39 (100.0)	0 (0.0)
>50	43 (7.0)	43 (100.0)	0 (0.0)
Total	611 (100.0)	543 (88.9)	68 (11.1)

The accuracy of visual estimates of grey nurse sharks at a horizontal angle of 0° to the base bar of the USVPS was low (20.8%, Table 5.3). The accuracy of visual estimates of the horizontal angles of sharks (in 10° bins) progressively improved as the angle increased and all sharks with horizontal angles >30° were correctly classified as not parallel (Table 5.3).

5.3.1.2 Propagation of errors in precaudal and total length estimates

The combined percentage errors in paired-laser photogrammetric estimates of the PCL of each shark measured with the USVPS ranged from 2.2-15.7% for horizontal angles of 1-

30° (Figure 5.4). Percentage errors increased dramatically thereafter with an error of 57.0% evident for a shark with a horizontal angle of 50° (Figure 5.4).

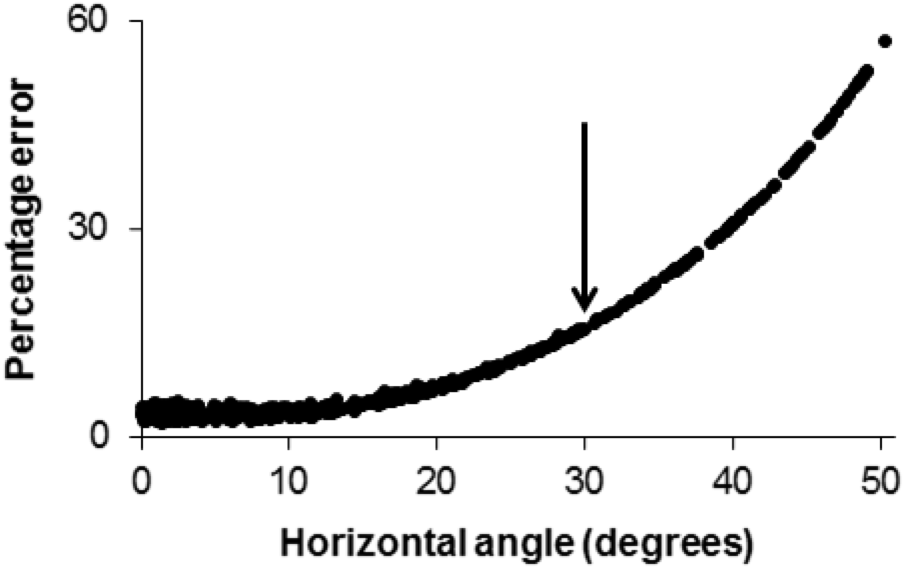

Figure 5.4. Plot of combined percentage errors (*n* = 568) of paired-laser photogrammetric precaudal length (PCL) estimates of the grey nurse shark (*Carcharias taurus*) at horizontal angles between 0-50°. Accurate measurements of PCL and horizontal angle were obtained simultaneously with an underwater stereo-video photogrammetry system (USVPS). Arrow highlights horizontal angle of 30° beyond which all angles were visually identified as not parallel to the USVPS base bar with 100.0% accuracy.

The combined errors in paired-laser photogrammetric estimates of the PCL for each grey nurse shark life-history stage when at a horizontal angle of 0° were 16-116 millimetres (±1.9-5.1%, Table 5.4). The combined errors associated with paired-laser photogrammetric estimates of natural TL for sharks at a horizontal angle of 0° were substantially greater (Table 5.4). When the caudal fin was slightly elevated from the depressed position (i.e. CFA = 139°) natural TL estimates were 32-228 millimetres (2.7-7.1%) smaller than the TL (Table 5.4). Estimates of the natural TL of sharks with caudal fins that were greatly elevated (i.e. CFA = 65°) were 237-649 millimetres (19.8-20.3%) less than the TL (Table 5.4). Combined errors in PCL and TL estimates generally worsened as the horizontal angles and sizes of the sharks increased (Table 5.4). Errors in PCL estimates of sharks at horizontal angles greater than 0° and at varying life-history stages ranged from 20-372 millimetres (±2.4-16.3%). The smallest errors in TL estimates for sharks that were not parallel to a paired-laser photogrammetry system were evident with juvenile male and female sharks at horizontal angles of 10° and with CFA of 139° (Table 5.4). The greatest errors occurred with adult female sharks at horizontal angles of 30° with CFA of 65° (Table 5.4).

Table 5.4. Potential errors (millimetres and percentages) in paired-laser photogrammetric estimates of the minimum and maximum precaudal lengths (PCL, in millimetres) and total lengths (TL, in millimetres) of grey nurse sharks (*Carcharias taurus*) according life-history stages with horizontal angles (degrees) of the sharks to a paired-laser photogrammetry system and the minimum and maximum caudal fin angles (CFA, in degrees) sampled at Wolf Rock, South Solitary Island, Fish Rock, Big Seal Rock, Little Seal Rock, North Rock, Little Broughton Island and Looking Glass Isle from March to May 2010.

Life-history stage	Horizontal angle	PCL ± error (percentage)		CFA = 65		CFA = 139	
				TL ± error (percentage)			
		Minimum	Maximum	Minimum	Maximum	Minimum	Maximum
Juvenile male		835	1414	1200	2000	1200	2000
	0	16 (1.9)	45 (3.2)	237 (19.8)	395 (19.7)	32 (2.7)	89 (4.5)
	10	20 (2.4)	50 (3.5)	238 (19.8)	396 (19.8)	37 (3.1)	94 (4.7)
	20	56 (6.7)	101 (7.2)	249 (20.8)	415 (20.8)	84 (7.0)	156 (7.8)
	30	130 (15.6)	223 (15.8)	301 (25.1)	501 (25.1)	188 (15.7)	322 (16.1)
Juvenile female		835	1775	1200	2500	1200	2500
	0	16 (1.9)	70.0 (4.0)	237 (19.8)	497 (19.9)	32 (2.7)	139 (5.6)
	10	20 (2.4)	75 (4.2)	238 (19.8)	499 (20.0)	37 (3.1)	144 (5.8)
	20	56 (6.7)	134 (7.5)	249 (20.8)	523 (20.9)	84 (7.0)	212 (8.5)
	30	130 (15.6)	283 (16.0)	301 (25.1)	630 (25.2)	188 (15.7)	411 (16.4)
Adult male		1486	2137	2100	3000	2100	3000
	0	49 (3.3)	102 (4.8)	415 (19.8)	605 (20.2)	98 (4.7)	200 (6.7)
	10	54 (3.7)	107 (5.0)	416 (19.8)	607 (20.2)	103 (4.9)	206 (6.9)
	20	107 (7.2)	171 (8.0)	436 (20.8)	635 (21.2)	167 (7.9)	278 (9.3)
	30	235 (15.8)	346 (16.2)	527 (25.1)	762 (25.4)	339 (16.2)	505 (16.8)

Table 5.4 continued. Potential errors (millimetres and percentages) in paired-laser photogrammetric estimates of the minimum and maximum precaudal lengths (PCL, in millimetres) and total lengths (TL, in millimetres) of grey nurse sharks (*Carcharias taurus*) according life-history stages with horizontal angles (degrees) of the sharks to a paired-laser photogrammetry system and the minimum and maximum caudal fin angles (CFA, in degrees) sampled at Wolf Rock, South Solitary Island, Fish Rock, Big Seal Rock, Little Seal Rock, North Rock, Little Broughton Island and Looking Glass Isle from March to May 2010.

Life-history stage	Horizontal angle	PCL ± error (percentage)		CFA = 65 TL ± error (percentage)		CFA = 139	
		Minimum	Maximum	Minimum	Maximum	Minimum	Maximum
Adult female		1848	2282	2600	3200	2600	3200
	0	76 (4.1)	116 (5.1)	519 (19.9)	649 (20.3)	150 (5.8)	228 (7.1)
	10	81 (4.4)	121 (5.3)	520 (20.0)	651 (20.3)	156 (6.0)	233 (7.3)
	20	141 (7.6)	187 (8.2)	545 (21.0)	681 (21.3)	225 (8.6)	307 (9.6)
	30	296 (16.0)	372 (16.3)	656 (25.2)	816 (25.5)	429 (16.5)	545 (17.0)

5.4 DISCUSSION

Only 3.9% of the 611 grey nurse sharks measured were parallel with the base bar of the USVPS when PCL was quantified and of those, 79.2% of the visual estimates of parallelism (i.e. 0°) were inaccurate. This indicated that paired-laser photogrammetric length estimates often do not fulfil the fundamental assumption of the measured object being perpendicular to the lasers. While the ability to visually discern the horizontal angles of sharks between 1 and 30° to the base bar was 89.3% accurate, only angles >30° were identified with 100.0% accuracy. Although the majority (81.8%) of sharks had horizontal angles of ≤30° to the USVPS base bar when PCL was measured, the maximum errors quantified for paired-laser photogrammetric PCL estimates of grey nurse sharks with horizontal angles of 10, 20 and 30° still ranged from 5.3-16.3% across the five life-history stages. The position of the caudal fin also exerted considerable influence on paired-laser photogrammetric natural TL estimates with maximum errors of 20.3-25.5% which supported an earlier recommendation that measurement of natural TL be avoided (Francis 2006) and the previous measurement of PCL (Barker & Williamson 2010; Barker *et al*. 2011) rather than natural TL (Bansemer & Bennett 2009, 2010, 2011). Importantly, these errors were greater than those stated in previous research that used paired-laser photogrammetry to estimate the PCL (i.e. <3.0%, Barker & Williamson 2010) and natural TL (i.e. ±5.0%, Bansemer & Bennett 2009, 2011) of grey nurse sharks off the Australian east coast. Moreover, paired-laser photogrammetry systems are unable to quantify the horizontal angle or CFA of the measured shark so the associated errors in PCL and natural TL estimates cannot be accurately determined using the technique. These findings clearly indicated that paired-laser photogrammetry is not suitable for quantifying lengths of free-swimming sharks without substantial error. This suggests that previous demographic and movement patterns reported for the east Australian grey nurse shark population based on paired-laser photogrammetric estimates of natural TL (Bansemer & Bennett 2009, 2010, 2011) are problematic. Nevertheless, paired-laser photogrammetry may be acceptable for estimating shark lengths if PCL (and not natural TL) is used and parallax errors are quantified using field measurements of a scale bar at known angles (e.g. Deakos 2010; Jeffreys *et al*. 2013).

Previous research that used paired-laser photogrammetry to estimate the natural TL of the scalloped hammerhead (*Sphyrna lewini*) and grey reef (*Carcharhinus amblyrhynchos*) sharks (Rezzolla et al. 2014) did not acknowledge the effects of parallax error, CFA or caudal fin flexure on natural TL estimates. Interestingly, a study on the white shark (*Carcharodon carcharias*) identified the influence of lateral caudal fin flexure but not CFA on paired-laser photogrammetric natural TL estimates (Leurs *et al*. 2015). When there was no curvature of the caudal region the PCL and natural TL were measured, otherwise only PCL estimates were obtained (Leurs *et al*. 2015). Nevertheless, the effect of the vertical position of the caudal fin in the water column on paired-laser photogrammetric natural TL estimates cannot be accounted for or quantified. The study also included an assessment of the parallax error in paired-laser photogrammetric estimates of an object of known length positioned at horizontal angles of 15° incremental deviations from 0° to the system and at distances of 6 and 12 metres (Leurs *et al*. 2015). Mean length estimates of the object at a horizontal angle of 15° were 6.3 and 7.3% smaller than the actual size at distances of 6 and 12 metres, respectively (Leurs *et al*. 2015). Parallax error more than doubled when the horizontal angle was increased to 30° with the length of the object underestimated by 17.9 and 18.1% when at distances of 6 and 12 metres, respectively (Leurs *et al*. 2015). Despite these considerable errors and the inability of paired-laser photogrammetry to measure the horizontal angle and CFA of sharks, the study concluded that future research using the technique may yield accurate length estimates to determine growth rates, life-history characteristics and population structures for white sharks (Leurs *et al*. 2015).

Studies on the whale shark (*Rhincodon typus*) have recognised the sources of error in paired-laser photogrammetric natural TL estimates and the subsequent inaccuracies in growth rates, sizes at maturity and population structures (Rohner *et al*. 2011; Jeffreys *et al*. 2013). These studies predicted TL from paired-laser photogrammetric estimates of PCL using linear regression relationships derived from direct measurements (Rohner *et al*. 2011) and paired-laser photogrammetric estimates (Jeffreys *et al*. 2013). The more recent study (Jeffreys *et al*. 2013) also calculated the parallax error in paired-laser photogrammetric length estimates by measuring the known length of a scale bar at specific horizontal angles and distances from the system. Length estimates decreased as horizontal angles increased and when the scale bar was positioned at 10° from the system and at distances of 2.00, 4.00 and 6.00 metres the margins of error were 2.0, 1.0 and 0.7%, respectively (Jeffreys *et al*. 2013). If the 1.0% margin of error was applied to a measurement of a male whale shark ≈8.00 metres in TL at first maturity (i.e. from the 50.0% maturity ogive off Western Australia, Norman & Stevens 2007) it would result in an underestimation of TL by 0.08 metres. In this case, the TL estimate would need to be rounded to the nearest metre for the shark to be classified as mature and this has important implications for population size-structure surveys.

Another study used paired-laser photogrammetry to measure disc lengths of the manta ray (*Manta alfredi*) and a linear regression relationship to obtain disc widths for comparison with other research reporting sizes and life-history stages (Deakos 2010). Interestingly, the study improved the likelihood that the rays were perpendicular to the paired-laser photogrammetry system by measuring their discs when they were prone on the seabed (Deakos 2010), but this still may not have accounted for the position of the system when held by the diver in the water column. The parallax error associated with measurements of a pipe of known length at horizontal angles of 10, 20 and 30° to the system was also calculated with mean errors of -4.9, -6.1 and -8.8%, respectively (Deakos 2010). While these parallax errors are smaller than the maximum combined errors quantified for grey nurse sharks, they do not include the other sources of error identified in the present study. Moreover, the method employed to reduce parallax error is inapplicable to sharks that inhabit the water column but may be suitable for measuring the lengths of demersal sharks and rays that spend time stationary on the seabed such as the leopard (*Stegostoma fasciatum*), Port Jackson (*Heterodontus portusjacksoni*) and wobbegong (e.g. *Orectolobus halei*) sharks, and the fiddler (e.g. *Trygonorrhina fasciata*), shovelnose (e.g. *Rhinobatos typus*) and smooth (*Dasyatis brevicaudata*) rays.

While stereo photogrammetry does not rely on meeting the underlying assumption of the measured object being perpendicular to the system, the precision of PCL estimates does decrease slightly with increasing horizontal angles and distances between sharks and the USVPS (Otway *et al*. 2008). Despite this, precision remains within 1.2% for grey nurse sharks (i.e. 2.60 metre PCL) that are at horizontal angles of 0-30° and at a maximum distance of 5.00 metres from the base bar of the USVPS (Otway *et al*. 2008) which provides simple selection parameters for measurements. Importantly, stereo-video photogrammetry enables the selection of video frames with grey nurse sharks at reduced horizontal angles and distances from the system which simultaneously maximises the visibility of measurement points and facilitates optimal accuracy and precision of length estimates.

Logistically, greater opportunities to position the base bar of the USVPS approximately parallel to grey nurse sharks occur when they are hovering as this swimming behaviour is characterised by the uniform, horizontal orientation of sharks in the water column (Smith *et al*., 2015). A previous study documented greater frequencies of hovering in gestating and resting female grey nurse sharks compared with other life-history stages and attributed this to energy conservation associated with the reproductive cycle (Smith *et al*. 2014, 2015). Combined, these factors probably accounted for the significantly smaller mean horizontal angles, decreased angular variances and substantially reduced ranges in the horizontal angles of gestating and resting female sharks observed in the current study. Regardless, the majority (64.8%) of PCL measurements were made when the sharks were at horizontal angles of up to 20° from the USVPS base bar. This indicated that stereo-video photogrammetry enables the quantity (i.e. sample sizes), accuracy and precision of length estimates to be maximised, and the development of various regression relationships between numerous morphometric measurements. Consequently, stereo photogrammetry is a superior technique compared with paired-laser photogrammetry for research on bony fishes, sharks and other marine megafauna.

5.5 CONCLUSION

Stereo-photogrammetric angular and morphometric measurements showed that paired-laser photogrammetric length estimates of free-swimming grey nurse sharks were generally very inaccurate. The substantial error inherent in the visual identification of sharks at 0° to the photogrammetry system have serious implications for the validity of existing population size-structure estimates obtained using paired-laser photogrammetry. Moreover, natural TL should not be estimated via UVC or paired-laser and stereo photogrammetry systems due to the influence of caudal fin position. Future sampling of the lengths of free-swimming marine megafauna should consider alternative techniques to paired-laser photogrammetry if accurate estimates are required in a dynamic underwater setting, particularly when target species continuously change their orientation in three-dimensional space.

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Chapter 6

Scuba diving tourism impacts and environmental influences on the patrolling behaviour of grey nurse sharks (*Carcharias taurus*): a preliminary assessment using acoustic telemetry at Fish Rock, Australia

Declaration of co-authorship and co-contribution: papers incorporated in thesis by publication

Declaration by: Kirby Rae Smith **Signature:** [redacted]

Date: 1 April 2016

Paper Title: Scuba diving tourism impacts and environmental influences on the patrolling behaviour of grey nurse sharks (*Carcharias taurus*): a preliminary assessment using acoustic telemetry at Fish Rock, Australia

In the case of the above publication, the following authors contributed to the work as follows:

Name	Contribution %	Nature of contribution
Kirby R Smith	80	Study concept, experimental design, fieldwork, data collection, statistical analysis and interpretation, manuscript writing, manuscript editing
Nicholas M Otway	15	Study concept, experimental design, fieldwork, data collection, advice on statistical analysis and interpretation, manuscript editing
Carol Scarpaci	5	Study concept, manuscript editing

DECLARATION BY CO-AUTHORS

The undersigned certify that:

1. They meet criteria for authorship in that they have participated in the conception, execution or interpretation of at least that part of the publication in their field of expertise;
2. They take public responsibility for their part of the publication, except for the responsible author who accepts overall responsibility for the publication;
3. There are no other authors of the publication according to these criteria;
4. Potential conflicts of interest have been disclosed to **a)** granting bodies, **b)** the editor or publisher of journals or other publications, and **c)** the head of the responsible academic unit; and
5. The original data is stored at the following location(s):

Location(s): College of Engineering and Science, Victoria University, Melbourne, Victoria, Australia

and will be held for at least five years from the date indicated below:

		Date
Kirby R Smith	[redacted]	12 November 2014
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Chapter 7

Scuba diving tourism with critically endangered grey nurse sharks (*Carcharias taurus*) off eastern Australia: tourist demographics, shark behaviour and diver compliance

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DECLARATION BY CO-AUTHORS

The undersigned certify that:

1. They meet criteria for authorship in that they have participated in the conception, execution or interpretation of at least that part of the publication in their field of expertise;
2. They take public responsibility for their part of the publication, except for the responsible author who accepts overall responsibility for the publication;
3. There are no other authors of the publication according to these criteria;
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ABSTRACT

Guidelines and a national code of conduct were implemented to manage scuba diving tourism with the critically endangered grey nurse shark (*Carcharias taurus*) along the Australian east coast. The demographics of diving tourists, swimming behaviour of grey nurse sharks at various life-history stages and compliance of divers to the guidelines/code of conduct were simultaneously assessed during diver-shark interactions at four sites from March 2011 to February 2012. Milling was the most frequent swimming behaviour observed and no significant changes occurred with the number of divers or distance to sharks. Divers exhibited 100.0% compliance with all guidelines investigated. Satisfactory compliance may have been attributable to guideline clarity, the ease of establishing diver-shark interactions, stakeholder involvement in management processes and diver perceptions of sharks. Similar sampling of group and individual shark behaviour should be done to further enhance the understanding of the beneficial and adverse impacts of this marine wildlife tourism sector.

7.1 INTRODUCTION

Marine wildlife tourism (MWT) has experienced dramatic growth in recent times and demand for opportunities in which humans can observe and interact with free-ranging marine megafauna is increasing (Birtles *et al*. 2002a; Dobson 2006; Gallagher & Hammerschlag 2011; Hammerschlag *et al*. 2012). Marine wildlife tourism also benefits local, regional and national economies (Sorice *et al*. 2006), often by providing alternatives to consumptive uses of the natural environment (e.g. whale-watching versus whaling, Bejder *et al*. 2006a) and may encourage participants to adopt pro-environmental attitudes and behaviours which can, in turn, aid environmental conservation (Wilson & Tisdell 2003; Christensen *et al*. 2007; Powell & Ham 2008; Zeppel & Muloin 2008a). Conversely, the industry can affect target species by causing malnourishment (e.g. Semeniuk *et al*. 2007), disease (Semeniuk et al. 2007) and behavioural changes that may be detrimental to individual and population fitness (King & Heinen 2004; Williams *et al*. 2006; Stockin *et al*. 2008; Higham *et al*. 2009). Short-term behavioural alterations in focal species can negatively affect the time and energy available for resting (e.g. Christiansen *et al*. 2010; Steckenreuter *et al*. 2012), feeding (e.g. Stockin et al. 2008; Steckenreuter et al. 2012) and reproduction (Reynolds & Braithwaite 2001) and may lead to displacement (Bejder et al. 2006b; Catlin & Jones 2010) and increased predation risk (Christiansen et al. 2010; Parsons 2012).

A range of management options exist to mitigate potential deleterious impacts of MWT. These include restricting the number of tour operators and/or vessels in the industry via licences (e.g. Davis *et al*. 1997; Scarpaci *et al*. 2003), charging visitor fees (e.g. Newsome *et al*. 2004), the establishment of protected areas (e.g. King & Heinen 2004), self-regulatory codes of conduct (e.g. Davis *et al*. 1997; Allen *et al*. 2007), the enforcement of legislative requirements (Scarpaci *et al*. 2003) and the education of tour operators and tourists (Scarpaci *et al*. 2003; King & Heinen 2004).

Previous studies (e.g. Scarpaci *et al*. 2003; Sorice *et al*. 2007; Duprey *et al*. 2008; Wiley *et al*. 2008) have used compliance as an indicator of the effectiveness of regulations and voluntary codes of conduct. However, one of the limitations of these studies is that only compliance was documented; perhaps due to the notion that compliance equates to the eradication of tourism-related disturbance to target species. Further compliance studies (e.g. Allen *et al*. 2007; Quiros 2007; Smith *et al*. 2010; Strong & Morris 2010; Stafford-Bell & Scarpaci, in review) that incorporated behavioural observations of the target species indicated that satisfactory compliance does not necessarily guarantee adequate protection. Therefore, compliance and the behaviour of focal species and tourists need to be assessed simultaneously during human-wildlife interactions to evaluate accurately the effectiveness of management regimes. Furthermore, when target species segregate based on gender, age and/or the reproductive cycle (i.e. life-history stages), studies should be conducted across a range of sites to ensure that representative samples of the differing life-history stages are included as this will enable the appropriateness and efficacy of various management strategies to be critically evaluated.

The grey nurse shark (*Carcharias taurus*, Rafinesque 1810) has a widespread, albeit disjunct, global distribution and inhabits the coastal waters of warm-temperate and tropical regions (Compagno 2001; Last & Stevens 2009). Grey nurse sharks attain approximately 3.20 metres total length (TL, Last & Stevens 2009), are slow to reach sexual maturity (50.0% sexual maturity: males = 2.10 metres TL at 6-7 years, females = 2.59 metres TL at

10-12 years, Goldman *et al*. 2006; Otway *et al*. 2009; Otway & Ellis 2011) and have low fecundity with two pups born biennially (0.95-1.20 metres TL) after intrauterine cannibalistic and oophagous phases (Gilmore *et al*. 1983). No parental care is invested post parturition. The species requires decades to recover from declines in abundance (Smith *et al*. 1998; Mollet & Cailliet 2002; Otway *et al*. 2004) and with widespread overfishing (Musick *et al*. 2000; Myers & Worm 2003), has been listed globally as 'Vulnerable' on the IUCN Red List of Threatened Species 2000 (Cavanagh *et al*. 2003). The major extant grey nurse shark populations are now restricted to the east coasts of North and South America, South Africa and Australia where two separate, genetically-distinct populations occur on the east and west coasts (Cavanagh *et al*. 2003; Stow *et al*. 2006). The east Australian population occurs off New South Wales (NSW) and Queensland (QLD), has been subjected to numerous anthropogenic disturbances over the past century (Cropp 1964; Pepperell 1992; Otway *et al*. 2004; Reid *et al*. 2011) and the current population estimate lies between 1146 and 1662 sharks (Lincoln Smith & Roberts 2010). As a result, this population is listed as 'Critically Endangered' by the IUCN (Cavanagh *et al*. 2003) and under Commonwealth (*Environmental Protection and Biodiversity Conservation Act 1999*) and state (NSW *Fisheries Management Act 1994*; QLD *Nature Conservation Act 1992*) legislation.

Off eastern Australia, grey nurse sharks aggregate in sand- or boulder-filled gutters, caves and overhangs around inshore rocky reefs and islands from southern QLD to southern NSW (Otway & Ellis 2011; Figure 7.1).

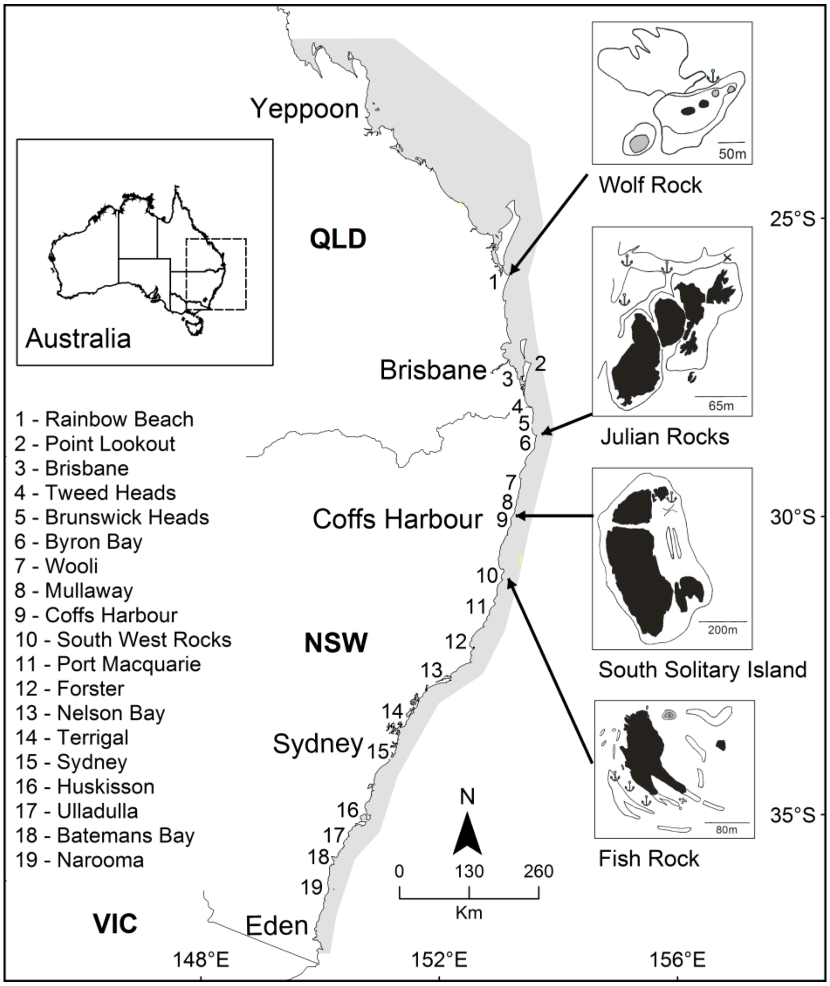

Figure 7.1. Map showing the geographic range (grey shading) of grey nurse sharks (*Carcharias taurus*) in coastal waters off Queensland (QLD) and New South Wales (NSW), the coastal towns/cities (numbered) with grey nurse shark scuba diving marine wildlife tourism operators and the location of Wolf Rock, Julian Rocks, South Solitary Island and Fish Rock sampled from March 2011 to February 2012 to document the behaviour of tourists and sharks during diver-shark interactions along the east coast of Australia. Note: black shading = emergent rock; grey shading = submerged pinnacle; black outline polygons = submerged topographic features; anchors = moorings; cross in Julian Rocks insert = Cod Hole; cross in South Solitary Island insert = Manta Arch; and VIC = Victoria.

They spend the majority of their time (i.e. ≈74.0%) in waters less than 40 metres but have been recorded as deep as 232 metres (Otway & Ellis 2011). The species has six recognisable life-history stages (i.e. pups at 0-1 years, juvenile males, juvenile females, sexually-mature males, gestating females and sexually-mature, resting-phase females) which exhibit differing migratory and localised movements and residencies at east Australian aggregation sites according to the reproductive cycle (Otway *et al*. 2003; Otway *et al*. 2004, 2009; Otway & Ellis 2011). Parturition likely occurs in late winter and early spring at various aggregation sites along the central and southern NSW coast (Otway *et al*. 2003; Otway & Ellis 2011). Grey nurse shark pups off eastern Australia probably display similar patterns of movement to those along the South African coast and remain at parturition sites for about eight months until colder water temperatures prompt them to move into warmer offshore areas (e.g. Castro 1993; Dicken *et al*. 2006). Juvenile male and female grey nurse sharks inhabit aggregation sites in the coastal waters between the mid-northern and higher southern latitudes of NSW for most of the year, before a migration of 100-400 kilometres further into southern NSW across spring and summer with visits to a range of aggregation sites (Otway & Parker 2000; Otway *et al*. 2009; Otway & Ellis 2011). Sexually-mature male grey nurse sharks exhibit an annual migration north to QLD during autumn and winter then return south to NSW in late spring and summer to mate in early autumn (Otway & Ellis 2011; Otway & Parker 2000; Otway *et al*. 2009). Whilst the extent of the southerly migration is somewhat variable, sexually-mature, migrating males may travel up to 4500 kilometres annually with periods of occupancy at numerous aggregation sites throughout (Otway & Ellis 2011). Sexually-mature female grey nurse sharks undertake a biennial migration north to QLD over autumn and winter, interspersed with mating at aggregation sites from the mid-north coast of NSW to southern QLD (Otway & Parker 2000; Bansemer & Bennett 2009). Copulation ceases in late spring and early summer when gestating females segregate from the rest of the population for the majority of their pregnancies by remaining off southern QLD (Bansemer & Bennett 2009). Wolf Rock is the only known aggregation site along the Australian east coast where this behaviour occurs (Bansemer & Bennett 2009). Gestating females then migrate 1000-1500 kilometres south during winter and spring to parturition sites in NSW (Otway & Ellis 2011). Postpartum, resting-phase female grey nurse sharks stay in central and southern NSW waters for the ensuing year to replenish energy reserves that were depleted during gestation prior to the next reproductive event (Otway & Ellis 2011). The durations of occupancy of aggregation sites by grey nurse sharks varies considerably from less than a day to more than six months (Otway *et al*. 2009). The sharks utilise a range of areas at the sites and their localised movements generally occur within a 1500 metre radius of the main structure (Bruce *et al*. 2005; Bansemer & Bennett 2009; Otway *et al*. 2009; Otway & Ellis 2011). Understanding the different localised and migratory movements of grey nurse sharks that underpin their reproductive ecology is required to ascertain the breadth of anthropogenic influence on the species.

The opportunity to observe large, free-ranging sharks up close in a relatively safe manner is much sought after by scuba divers worldwide and shark diving MWT operations can make substantial differences to the economies of local communities (e.g. Dicken & Hosking 2009; Brunnschweiler 2010; Clua *et al*. 2011; Vianna *et al*. 2012). The large size, generally slow movements, propensity to aggregate and relatively placid nature (Otway *et al*. 2003; Bruce et al. 2005; Otway & Ellis 2011) of the grey nurse shark make it an ideal candidate for MWT along eastern Australia as scuba divers can readily interact with the sharks without risk of attack. Consequently, a MWT industry specialising in scuba diving with grey nurse sharks has been established for many years at coastal towns in close proximity to aggregation sites (Figure 7.1) and is summarised in more detail in Table 7.1. Although the sites are accessible by boat, regional weather and oceanographic conditions limit visitation to approximately 40.0% of the year. When sea conditions are reasonable, MWT operators take scuba divers to local grey nurse shark aggregation sites and consequently the vast majority of sites are subjected to contemporaneous scuba diving with tourism pressure dependent on the coastal town, aggregation site, season and overall demand. The MWT operators utilise vessels ranging from a 5 metre rigid-hulled inflatable boat up to an 18 metre purpose-built dive vessel which necessitate different launching or harbouring and boarding requirements, although most use vessels ≤11 metres (90.0%, Table 7.1). Trips generally include two dives separated by an appropriate surface interval (i.e. a 'double dive' at a cost of $120-240 AUD including hire of all equipment) and divers are required to observe strict scuba diving procedures to ensure safe, no-decompression diving which forces a degree of consistency in diver behaviour. Whilst preliminary work (HAGE 2004) suggests that this MWT industry contributes considerably to local, regional and state economies, there is a dearth of data to quantify and distinguish to what extent as well as limited knowledge of the duration of personal touristic visits and the spatial and temporal variation in MWT site visitation rates. Annual revenue (≈$9 million AUD) was gauged solely from the income of MWT operators that dived at 11 NSW critical habitat sites (HAGE 2004) and not across the entire industry. Also, it did not incorporate other economic contributions associated with this MWT sector. These include the initial purchase of dive vessels and equipment and the subsequent fuel and/or maintenance costs, MWT operator expenditure on dive trip refreshments, and tourist travel (e.g. airfares, car hire and fuel), accommodation, food and miscellaneous expenses. However, detailed investigation of the socio-economic aspects of the grey nurse shark MWT industry along the Australian east coast is now underway.

This MWT sector has also been identified as a possible threat to the continuing survival and recovery of this species in the national recovery plan for the grey nurse shark in Australia (EA 2002). As such, federal (*Environmental Protection and Biodiversity Conservation Act 1999*, DSEWPC 2012) and state legislation (QLD *Marine Parks Act 2004* and NSW *Fisheries Management Act 1994*, NSWG 2010; QG 2010a, b) have provided regulations and guidelines pertaining to scuba diver behaviour to mitigate potential adverse impacts on grey nurse sharks. A Code of Conduct for Diving with Grey Nurse Sharks was also developed by Otway *et al*. (2003) following extensive consultation with the NSW diving industry and implemented as part of the national recovery plan in 2002 (EA 2002). Since inception, these legislative and voluntary guidelines have been promoted widely to scuba divers and the general public via government and non-government websites, publications and posters and are still readily accessible through websites, various scuba diving publications and MWT operators who display the guidelines at their dive centres and include them in their dive briefs. However, the efficacy of management regimes has only been assessed in a single study at one aggregation site (Fish Rock) in NSW waters (Smith *et al*. 2010). Currently, there is little information concerning the factors that may be responsible for promoting or hampering compliance. Vectors of compliance can include clarity of guidelines (Cole 2007; Jett *et al*. 2009; Smith *et al*. 2010), the locality of the target species (Smith *et al*. 2010; Stafford-Bell & Scarpaci, in review), tourist perceptions of focal animals (Smith *et al*. 2010), the qualifications and experience of the scuba divers (tourists) and the involvement of stakeholders in management processes (Otway *et al*. 2003).

While the environmental attitudes and knowledge of tourists has been documented (Smith *et al*. 2009), there have been no published studies investigating the demographics of the divers which are likely to be important in the design and implementation of management strategies. Finally, only a few studies have investigated the impacts and sustainability of this industry (Hayward 2003; Otway *et al*. 2009; Smith *et al*. 2010; Barker *et al*. 2011) and with the exception of Otway *et al*. (2009), all of these focused on single sites and particular life-history stages of the shark. This has prevented the generalisation of the results to other sites utilised by the MWT industry for diver-shark interactions.

Consequently, this study enhances those by Smith *et al*. (2009, 2010) and assesses the degree of scuba diver compliance with grey nurse shark scuba diving management guidelines and the impact of diving tourists interacting with various life-history stages of the target species across multiple locations. The aim of the study was to: (1) provide a preliminary understanding of grey nurse shark scuba diving tourist demographics; (2) quantify the behaviours of divers and grey nurse sharks during diver-shark interactions; and, (3) assess the compliance of divers with regulatory and voluntary grey nurse shark scuba diving guidelines in the coastal waters off eastern Australia. Lastly, the environmental sustainability of scuba diving with grey nurse sharks is considered and compared with that of other MWT sectors.

7.2 MATERIALS AND METHODS

7.2.1 Study sites and sampling periods

As the grey nurse shark scuba diving MWT industry extends over much of the species' east Australian range, it was important to ensure that sampling covered multiple aggregation sites and represented the various life-history stages (and associated movement patterns) of the shark. Pups were not targeted due to the unreliability of their presence at inshore sites caused by their relative rarity and large inter-annual variation. Thus, data concerning MWT with grey nurse sharks were collected at four aggregation sites: Wolf Rock, Julian Rocks, South Solitary Island and Fish Rock. These sites span ≈600 kilometres of the east coast of Australia (Figure 7.1) and are influenced by onshore winds, a prevailing 1-2 metre south-easterly swell and the 1-4 knot East Australian Current (EAC, Tranter *et al*. 1986). Mean sea surface temperatures range from ≈28.0°Celsius in the austral summer to ≈19.0°Celsius in winter. Reversals of the EAC, internal waves and upwellings also cause substantial fluctuations in daily seawater temperatures with the variation greatest in summer and least in winter (Otway & Ellis 2011). These underlying oceanographic conditions interact with the movement of cold fronts and east coast low pressure systems bringing gale force winds, dangerous seas and swell (i.e. 2-3 metre seas on a 3-6 metre swell) and torrential rainfall causing flooding river plumes that can reduce visibility to <1 metre at the sites for up to 10 days after the weather event (Trenaman & Short 1987). During summer, the regular north-easterly sea breeze often reaches 20-30 knots by mid-afternoon and produces dangerous sea conditions for small- to medium-sized watercraft. Consequently, accessing the dive sites is extremely weather-dependent and even when sea conditions are reasonable diving can be hazardous due to strong currents, varying visibility and substantial water depths.

Wolf Rock lies 2 kilometres offshore of Double Island Point near Rainbow Beach (QLD) within a marine national park zone of the Great Sandy Marine Park (QG 2006). The rock comprises five pinnacles (four large, one small) that are aligned in a north-easterly direction in ≈35 metres of water. The rocky reef supports an extensive, sub-tropical fish community and aggregations of grey nurse sharks occur at various times of the year (Bennett & Bansemer 2004). Gestating females are particularly abundant from December to June (Bansemer & Bennett 2009) and are often observed swimming very slowly around the rock. With fair sea conditions, the only MWT operator from Rainbow Beach visits Wolf Rock on a weekly basis throughout the year (Table 7.1). The MWT operation involves scuba divers swimming down a mooring line that is fixed to the seabed in close proximity to a series of gutters on the north-western side where grey nurse sharks aggregate.

Table 7.1. Static overview of the grey nurse shark (*Carcharias taurus*) scuba diving marine wildlife tourism (MWT) industry along the east coast of Australia summarising the coastal towns/cities with grey nurse shark MWT operators (and number), the primary grey nurse shark aggregation site dived from the coastal towns/cities, the grey nurse shark scuba diving MWT season (summer = S; autumn = A; winter = W; spring = Sp.), the boat boarding procedure/s, whether a bar crossing is required, the approximate boat travel time to the site, boat lengths and the maximum numbers of boats at the dive site, divers per boat and dives at the site a day per MWT operator. Reference numbers are assigned to the coastal towns/cities and are used to illustrate their locations in Figure 7.1.

Reference number in Figure 7.1	Coastal town/city (and number of MWT operators)	Primary aggregation site dived	MWT season	Boat boarding procedure/s	Bar crossing	Boat travel time to site (minutes)	Boat length/s (metres)	Maximum number of boats at site	Maximum number of divers per boat	Maximum number of dives a day at site per MWT operator
1	Rainbow Beach (1)	Wolf Rock	S, A, W, Sp.	Boat ramp	Yes	60	6	1	6	2
2	Point Lookout (1)	Flat Rock	W, Sp.	Beach launch	No	15	6-7	3	10-12	2
3	Brisbane (2)	Flat Rock	W, Sp.	Jetty	Yes	75	11	3	16	2
		Cook Island	W	Boat ramp	Yes	20	8	6	10	2
4	Tweed Heads (3)	Cook Island	W	Boat ramp, jetty	Yes	15-20	7-15	6	10-24	2
		Windarra Banks	W	Jetty	Yes	20	9-15	3	12-24	2
5	Brunswick Heads (1)	Windarra Banks	W	Jetty	Yes	30	9	3	10	2
		Julian Rocks	W	Jetty	Yes	30	9	6	10	2

Table 7.1 continued. Static overview of the grey nurse shark (*Carcharias taurus*) scuba diving marine wildlife tourism (MWT) industry along the east coast of Australia summarising the coastal towns/cities with grey nurse shark MWT operators (and number), the primary grey nurse shark aggregation site dived from the coastal towns/cities, the grey nurse shark scuba diving MWT season (summer = S; autumn = A; winter = W; spring = Sp.), the boat boarding procedure/s, whether a bar crossing is required, the approximate boat travel time to the site, boat lengths and the maximum numbers of boats at the dive site, divers per boat and dives at the site a day per MWT operator. Reference numbers are assigned to the coastal towns/cities and are used to illustrate their locations in Figure 7.1.

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6	Byron Bay (2)	Julian Rocks	W	Beach launch	No	10	7-7	6	12-14	3
7	Wooli (1)	Pimpernel Rock	A, W, Sp.	Jetty	Yes	45	11	1	14	2
		North Solitary Island	A, W, Sp.	Jetty	Yes	20	11	3	14	2
8	Mullaway (1)	North Solitary Island	A, W, Sp.	Beach launch	No	35-45	7	3	8	4
9	Coffs Harbour (2)	South Solitary Island	S, A, W, Sp.	Boat ramp, jetty	No	30-40	8-12	2	10-22	2-4
10	South West Rocks (2)	Fish Rock	S, A, W, Sp.	Boat ramp	Yes	30	7-8	6	6-13	4

Table 7.1 continued. Static overview of the grey nurse shark (*Carcharias taurus*) scuba diving marine wildlife tourism (MWT) industry along the east coast of Australia summarising the coastal towns/cities with grey nurse shark MWT operators (and number), the primary grey nurse shark aggregation site dived from the coastal towns/cities, the grey nurse shark scuba diving MWT season (summer = S; autumn = A; winter = W; spring = Sp.), the boat boarding procedure/s, whether a bar crossing is required, the approximate boat travel time to the site, boat lengths and the maximum numbers of boats at the dive site, divers per boat and dives at the site a day per MWT operator. Reference numbers are assigned to the coastal towns/cities and are used to illustrate their locations in Figure 7.1.

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11	Port Macquarie (1)	Cod Grounds	S, A, W, Sp.	Boat ramp	Yes	15	8	1	11	2
12	Forster (3)	Forster Barge	S, A, W, Sp.	Jetty	No	15	6-11	4	8-18	2-4
		Latitude Rock	S, A, W, Sp.	Jetty	No	15-30	6-11	4	8-18	2-4
		The Pinnacle	S, A, W, Sp.	Jetty	No	15-30	6-11	4	8-18	2-4
		Big Seal Rock	S, A, W, Sp.	Shore-to-boat 50 metre swim	No	15	6-11	4	8-18	2-4

Table 7.1 continued. Static overview of the grey nurse shark (*Carcharias taurus*) scuba diving marine wildlife tourism (MWT) industry along the east coast of Australia summarising the coastal towns/cities with grey nurse shark MWT operators (and number), the primary grey nurse shark aggregation site dived from the coastal towns/cities, the grey nurse shark scuba diving MWT season (summer = S; autumn = A; winter = W; spring = Sp.), the boat boarding procedure/s, whether a bar crossing is required, the approximate boat travel time to the site, boat lengths and the maximum numbers of boats at the dive site, divers per boat and dives at the site a day per MWT operator. Reference numbers are assigned to the coastal towns/cities and are used to illustrate their locations in Figure 7.1.

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12	Forster (3)	Little Seal Rock	S, A, W, Sp.	Shore-to-boat 50 metre swim	No	20	6-11	4	8-18	2-4
13	Nelson Bay (2)	North Rock	S, A, W, Sp.	Jetty	No	35-60	7-12	3	8-22	2
		Broughton Island	S, A, W, Sp.	Jetty	No	30-60	7-12	3	8-22	2
14	Terrigal (2)	Foggy Cave	A	Boat ramp, jetty	No	25-30	7-9	3	8-13	1-2
15	Sydney (13)	Magic Point	S, A, W, Sp.	Beach launch, boat ramp, jetty	No	2-50	5-13	16	4-25	1-16

Table 7.1 continued. Static overview of the grey nurse shark (*Carcharias taurus*) scuba diving marine wildlife tourism (MWT) industry along the east coast of Australia summarising the coastal towns/cities with grey nurse shark MWT operators (and number), the primary grey nurse shark aggregation site dived from the coastal towns/cities, the grey nurse shark scuba diving MWT season (summer = S; autumn = A; winter = W; spring = Sp.), the boat boarding procedure/s, whether a bar crossing is required, the approximate boat travel time to the site, boat lengths and the maximum numbers of boats at the dive site, divers per boat and dives at the site a day per MWT operator. Reference numbers are assigned to the coastal towns/cities and are used to illustrate their locations in Figure 7.1.

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16	Huskisson (3)	The Docks	S, A	Boat ramp, jetty	No	30	5-18	5	4-25	4
17	Ulladulla (1)	Brush Island	S, A	Boat ramp	Yes	10-15	7	1	12	2
18	Batemans Bay (1)	Tollgate Islands	S, A	Boat ramp	No	10-15	9	1	11	2
19	Narooma (2)	Montague Island	S, A	Jetty	Yes	30-35	10-11	3	12-13	2-4

Julian Rocks is situated 4 kilometres offshore of Byron Bay (NSW) and comprises four aligned rocky outcrops in 20 metres of water surrounded by rocky reefs and sand-filled gutters (Otway & Ellis 2011). The site was declared a grey nurse shark critical habitat in December 2002 and is within a sanctuary zone of the Cape Byron Marine Park (NSWG, n.d.). Julian Rocks supports a diverse tropical and temperate fish community throughout the year (Harriott *et al*. 1997) and grey nurse sharks primarily aggregate in the gutters to the north during the austral winter months (Otway & Parker 2000; Otway *et al*. 2003). Sexually-mature males on their annual northward migration are generally more abundant in June, while putatively pregnant females are present during July prior to migrating further south for parturition (Otway *et al*. 2009; Otway & Ellis 2011). When sea conditions permit, one MWT operator from Brunswick Heads and two from Byron Bay offer weekly and daily visits to Julian Rocks, respectively (Table 7.1). Marine wildlife tourism (i.e. snorkelling and scuba diving) occurs predominantly on the northern side of the site and MWT operators use standard dive paths (described in Hayward 2003) that commence at moorings away from grey nurse sharks followed by a swim to the ‘Cod Hole’ (Figure 7.1) where the sharks frequently aggregate (Otway & Parker 2000; Otway *et al*. 2003, 2009).

South Solitary Island lies 9 kilometres northeast of Coffs Harbour (NSW) in 10-35 metres of water and has the largest spatial topography of the investigated sites. The extensive rocky reef has caves, overhangs, sand-filled gutters and a diverse temperate fish community enhanced by tropical species particularly over the warmer months (Malcolm *et al*. 2010). Grey nurse sharks aggregate over the austral autumn to spring months at three locations (Otway & Parker 2000), but spend substantially more time around the gutters and a swim-through (‘Manta Arch’, Figure 7.1) off the north-eastern corner of the island (Otway *et al*. 2003, 2009; Otway & Ellis 2011), which is now partly within a sanctuary zone of the Solitary Islands Marine Park (NSWMPA 2007). In June/July, the grey nurse shark population at South Solitary Island mainly comprises sexually-mature males on their annual migration north together with some juveniles and a few gravid females migrating south to pup (Otway & Ellis 2011). When sea conditions allow, two MWT operators based in Coffs Harbour run daily trips to South Solitary Island throughout the year (Table 7.1). The MWT operators secure their vessels to NSW Marine Parks Authority (MPA) moorings that are in close proximity to the gutters where grey nurse sharks aggregate and the scuba divers descend the mooring lines and are able to interact with the sharks on reaching the substrate.

Finally, Fish Rock is located 2 kilometres offshore of Smoky Cape (NSW) in 20-40 metres of water and was declared as a grey nurse shark critical habitat in December 2002 (Talbot *et al*. 2004). The surrounding rocky reef provides habitat for aggregations of grey nurse sharks and a diverse temperate fish community with some tropical species present during the warmer months (Otway *et al*. 2003; Breen *et al*. 2004). Immature and mature grey nurse sharks of both genders utilise the waters surrounding Fish Rock and occupy several different gutters for varying periods of time throughout the year (Otway *et al*. 2003). From December to April, the grey nurse shark population comprises juveniles, post-copulatory males and sexually-mature females in their year-long reproductive resting phase (Otway *et al*. 2003). While the sharks circumnavigate Fish Rock, they often spend proportionally more time in the gutters on the western and south-western side (Otway *et al*. 2009; Otway & Ellis 2011) where there is a series of moorings. If sea conditions are acceptable, two MWT operators based in South West Rocks provide scuba divers with daily trips to Fish Rock (Table 7.1). Up to six dive boats are secured to the moorings which scuba divers descend along and interact with grey nurse sharks almost immediately.

Diver-shark interactions were quantified across five of the six grey nurse shark life-history stages (i.e. sexually-immature males and females, sexually-mature migrating males, gestating females and sexually-mature, resting-phase females). Sampling via double dives took place at Wolf Rock over two weeks in February 2012 to target gestating females. Julian Rocks and South Solitary Island were sampled over four weeks in June-July 2011 to specifically target sexually-mature, migrating males. Sampling at Fish Rock was conducted for two weeks in March-April 2011 to target juveniles of both genders, post-copulatory males and sexually-mature, resting-phase females.

As well as adverse and difficult environmental conditions there are physiological, MWT industry-specific and ecological factors that constrain underwater visual research at the sites. Water depths and the requirement for no-decompression scuba diving limit dive durations and hence the quantity of data that can be obtained. The accumulation of residual nitrogen in human tissues from repetitive diving over several days can further reduce dive durations. Given that MWT operators utilise all of the grey nurse shark aggregation sites when sea conditions are favourable, there are no readily accessible sites to use as controls for a Before After Control Impact (BACI) experimental design (Underwood 1997). However, the necessity of control sites was reduced as earlier research (Otway *et al*. 2009) that incorporated acoustically-tagged grey nurse sharks and BACI designs showed that the localised movements of the sharks are not significantly influenced by the presence of scuba divers. Furthermore, grey nurse shark swimming behaviour in the presence and absence of tourist divers has been sampled using underwater stereo-photogrammetric footage (Otway *et al*. 2008) and preliminary observations indicated minimal differences in shark behaviour. Finally, pre-tourist diver-shark interaction data was not obtained due to scuba diving-imposed air restrictions and to avoid hampering the typical operational conduct and safety procedures of the MWT businesses. The selected grey nurse shark aggregation sites are occasionally visited by great white (*Carcharodon carcharias*), tiger (*Galeocerdo cuvier*) and bull (*Carcharhinus leucas*) sharks (Burgess & Callahan 1996; Otway *et al*. 2009; West 2011) and given that these species have caused serious and fatal injuries to humans (West 1996, 2011; Last & Stevens 2009), MWT operators prefer divers to enter the water together.

7.2.2 Scuba diver (tourist) demographics

Demographic data from all scuba divers at each site (excluding dive centre staff) were collected using anonymous verbal interviews at each dive centre. Information on gender, age, nationality, preferred language, highest scuba diving certification, the total number of scuba dives completed, prior experience diving with grey nurse sharks, awareness of relevant legislation and awareness of the code of conduct was recorded once from each scuba diver. Demographic data were then calculated as percentages of the total number of divers at each site and combined across all four sites.

7.2.3 Grey nurse shark life-history stages

The total number of grey nurse sharks and their precaudal lengths (PCL) and genders (presence of claspers distinguished males) were recorded during instantaneous 2-minute scan samples (Altmann 1974). Observations were made alongside or behind the divers (Cubero-Pardo *et al*. 2011), followed the sampling procedure of Smith *et al*. (2010), commenced when grey nurse sharks and scuba divers (including MWT staff) were first visible to the senior author and continued until either all the sharks or divers had left the shark gutter. Precaudal length was estimated within range categories of 0.50 metre increments as the distance from the tip of the snout to the precaudal pit (Compagno 2001; Last & Stevens 2009) and was selected because of greater accuracy than total length (TL, Francis 2006). Total length was then calculated using a linear regression of TL on PCL (i.e. TL = 1.3682PCL + 0.0685, with lengths in metres), developed from necropsies of grey nurse sharks caught in the NSW shark meshing program and/or by commercial and recreational fishers (Otway *et al*. 2004). The sexual maturity of each individual shark was assigned using TL. The percentages of sexually-mature and sexually-immature males and females were then calculated using data from the scans to quantify the life-history stages present at each site.

7.2.4 Grey nurse shark swimming behaviour and diver-shark interactions

The grey nurse shark swimming behaviours most frequently observed and documented in previous research using underwater visual observations were hovering, cruising, milling and active swimming (Hayward 2003; Smith *et al*. 2010, Table 7.2).

Table 7.2. Descriptions of grey nurse shark swimming behaviours.

Swimming behaviour	Description	Reference
Hovering	Sharks appear to be motionless	Hayward 2003
Cruising	Low level of activity without directional changes	Hayward 2003
Milling	Low level of activity with frequent directional changes within the same area	Smith *et al*. 2010
Active swimming	Persistent movement in a general direction at a greater speed than milling	Hayward 2003; Smith *et al*. 2010

In this study, the swimming behaviours of grey nurse shark groups (cruising was considered a form of milling for this research) were quantified using the instantaneous 2-minute scans utilised to document grey nurse shark life-history stages. The swimming behaviour exhibited by the group of grey nurse sharks (i.e. ≥50.0% of the sharks) was recorded at each scan. The periods of time that the different swimming behaviours were displayed by grey nurse sharks were extrapolated from the respective number of 2-minute scans taken during the observed diver-shark interactions. These were then calculated as percentages of the cumulative amount of time during which diver-shark interactions occurred. Finally, the number of scuba divers and the distance between the nearest scuba diver to the sharks was estimated during each scan using distance categories as per Smith et al. (2010) with mean values used in data analyses.

7.2.5 Compliance with guidelines/code of conduct

To avoid influencing diver behaviour, the senior author ensured that the MWT operator and staff treated the researchers as normal customers and the research was not discussed in detail with the other divers prior to diving. Compliance with various guidelines specified under the QLD *Marine Parks Act 2004* (QG 2010a, b), NSW *Fisheries Management Act 1994* (NSWG 2010) and the national Code of Conduct for Diving with Grey Nurse Sharks (EA 2002; Otway *et al*. 2003) by divers (Table 7.3) was continuously assessed (Altmann 1974) using the methods of Smith *et al*. (2010) to ensure any instances of non-compliant behaviour were recorded.

Table 7.3. Studied diver guidelines in the Queensland (QLD) *Marine Parks Act 2004*, New South Wales (NSW) *Fisheries Management Act 1994* and the Code of Conduct for Diving with Grey Nurse Sharks (EA 2002; NSWG 2010; QG 2010a, b).

Guideline (abbreviation)	Presence of guideline in management strategy (yes or no)		
	Marine Parks Act 2004 (QLD)	*Fisheries Management Act 1994* (NSW)	Code of Conduct for Diving with Grey Nurse Sharks
Do not touch grey nurse sharks	Yes	Yes	Yes
Do not feed grey nurse sharks	Yes	Yes	Yes
Do not chase grey nurse sharks	Yes	Yes	Yes
Do not harass grey nurse sharks	Yes	Yes	Yes
Do not interrupt the swimming patterns of grey nurse sharks	Yes	No	Yes
Do not block entrances to caves or gutters	Yes	Yes	Yes
Do not trap, or attempt to trap, grey nurse sharks	Yes	No	Yes
Do not dive in groups totalling more than 10 divers (tourism operators in QLD may have groups of up to 12 divers provided the extra divers are instructors or guides)	Yes	No	Yes
Do not wear or use mechanical apparatus i.e. electronic shark-repelling device, powered scooter, horns	Yes	Yes	Yes

The acceptable level of compliance was set at 80.0% or greater in accordance with previous studies (Allen *et al*. 2007; Quiros 2007; Smith *et al*. 2010; Howes *et al*. 2012). Compliance for each guideline was calculated per dive and then expressed as a percentage of the total number of dives per site. Finally, compliance with the ban on night diving with grey nurse sharks at critical habitat sites was not quantified as the local MWT operators do not offer night diving opportunities at the sites studied. Similarly, ambiguous guidelines (as described in Smith *et al*. 2010) were omitted from the study to avoid equivocal results.

7.2.6 Statistical analyses

All statistical analyses were done with a Type I (α) error rate of $P = 0.05$. Diver demographic and grey nurse shark life-history stage data were summarised for each site and examined using contingency table analysis based on chi-square (χ^2) tests. Grey nurse sharks of unknown gender or sexual maturity were not included in the analysis among sites. Sampling effort, shark swimming behaviours and potential behavioural differences according to the numbers of divers present and the distances between divers and sharks within and among life-history stages were analysed using 1-factor analyses of variance (ANOVA) following examination for homoscedasticity using Cochran's test (Underwood 1997). When heterogeneity was evident, ordinal data were transformed using standard procedures whereas proportional data were arcsine transformed (Underwood 1997).

Balanced designs were used in all ANOVAs and were derived via the random selection of replicates from the available data at each site. This approach was also used to prevent the use of serially-correlated data with approximately 30.0% of all scans selected at random for use in subsequent balanced analyses.

The potential for weather-induced breaks in sampling, variations in size and gender ratios of grey nurse sharks between dives and among days per study site, along with the scale of localised movements of sharks at aggregation sites (Otway *et al*. 2009; Otway & Ellis 2011) which suggests that the same sharks would not be observed continuously during the sampling periods, further lessened the likelihood of serially correlated data. Nevertheless, the existence of serial correlation in the data used in ANOVAs was examined by looking for trends in the plots of the residuals against time and using Durbin-Watson tests (Durbin & Watson 1950; Savin & White 1977; Farebrother 1980).

A priori and *post hoc* power analyses were done to determine the replication required to detect significant, small-magnitude differences (i.e. differences among means of 25.0%) with power of 0.80 (i.e. Type II error rate of $\beta = 0.20$), an acceptable level in ecological studies (Underwood 1997), using G-Power (Version 3.1.6, ©University of Kiel, Germany) and Pop-Tools (Version 3.2.5, Greg Hood, CSIRO). Following ANOVA, significant differences among means were identified using Student-Newman-Keuls (SNK) tests (Underwood 1997). When differences among means could not be unequivocally determined, the ranked means were simply examined for trends.

7.3 RESULTS

7.3.1 Scuba diver (tourist) demographics

Demographic data were collected from 78 individual divers participating in dives with grey nurse sharks at the studied sites. The proportions of scuba divers of differing gender, age groups, nationalities, preferred language and prior experience diving with grey nurse sharks did not differ significantly among sites (Table 7.4, chi-square tests: $P > 0.05$).

Table 7.4. Percentages of divers and chi-square test ($\chi^{2)}$ results for gender, age, nationality, preferred language, scuba certification (highest attained), number of scuba dives completed, prior experience diving with grey nurse sharks (GNS), awareness of the relevant legislation and awareness of the code of conduct at Wolf Rock (WR), Julian Rocks (JR), South Solitary Island (SS) and Fish Rock (FR) from March 2011 to February 2012.

Variable		WR	JR	SS	FR	Sites combined	χ^2	df	*P*
Gender							2.50	3	>0.50
	Male	80.0	73.1	88.5	87.5	82.1			
	Female	20.0	26.9	11.5	12.5	18.0			
Age group							20.18	12	>0.10
	<18	0.0	0.0	11.5	25.0	9.0			
	18-25	0.0	7.7	3.9	12.5	6.4			
	26-35	40.0	50.0	23.1	12.5	32.1			
	36-45	30.0	23.1	19.2	6.3	19.2			
	46-≥51	30.0	19.2	42.3	43.8	33.3			
Nationality							7.01	3	>0.10
	Australian	70.0	65.4	88.5	93.8	79.5			
	Other	30.0	34.6	11.5	6.3	20.5			
Language							5.46	3	>0.25
	English	70.0	88.5	88.5	100.0	88.5			
	Other	30.0	11.5	11.5	0.0	11.5			
Scuba certification							24.47	3	<0.001
	Professional	80.0	38.5	7.7	6.3	26.9			
	Recreational	20.0	61.5	92.3	93.8	73.1			
Dives completed							18.63	15	<0.005
	≤10-50	10.0	46.2	65.4	68.8	52.6			
	51-500	50.0	38.5	34.6	31.3	37.2			
	501->1000	40.0	15.4	0.0	0.0	10.3			
Diving with GNS							0.97	3	>0.90
	Yes	70.0	73.1	80.8	68.8	74.4			
	No	30.0	26.9	19.2	31.3	25.6			
Legislation							0.59	3	>0.90
	Yes	70.0	57.7	65.4	62.5	62.8			
	No	30.0	42.3	34.6	37.5	37.2			
Code of conduct							0.44	3	>0.95
	Yes	60.0	53.9	61.5	62.5	59.0			
	No	40.0	46.2	38.5	37.5	41.0			

The majority of scuba divers at all sites were Australian, English-speaking males (Table 7.4). Ages of divers varied among sites, but 84.6% of participants across all sites were 26 to ≥51 years old. The proportions of divers that were aware of the relevant legislation and/or the Code of Conduct for Diving with Grey Nurse Sharks were not significantly different among sites (Table 7.4, chi-square tests: $P > 0.05$). Approximately 60.9% of the divers surveyed over all sites were aware of the legislation and/or the code of conduct. Of the divers that were not aware of the legislation/code of conduct, 36.0% (on average) were overseas tourists. Furthermore, 24.6% of the divers (on average) that were not aware of the legislation/code of conduct were <25 years old. At Fish Rock, the proportions of divers aware of mandatory and voluntary management strategies were equal, whereas at the other three sites, the proportions of divers aware of the relevant legislation were slightly greater (≤10.0%) than those for the code of conduct. Almost 75.0% of all divers had previously dived with grey nurse sharks. In contrast, the proportions of divers with differing scuba certification levels (i.e. recreational or professional) differed significantly among sites (Table 7.4, chi-square test: $P < 0.001$). At Wolf Rock, 80.0% of the scuba divers had professional qualifications, whereas the majority of divers at the other sites (i.e. 82.5% on average) had recreational qualifications (Table 7.4). The divers possessing professional qualifications were ‘Divemasters’ (18.0%) or ‘Instructors’ (9.0%), whereas those with recreational qualifications comprised ‘Open Water divers’ (38.5%), ‘Advanced Open Water divers’ (28.2%) and a few ‘Rescue divers’ (6.4%). Finally, the proportions of divers with differing numbers of scuba dives completed prior to this study were also significantly different among sites (Table 7.4, chi-square test: $P < 0.005$).

7.3.2 Diving sampling effort

Sampling was done from March 2011 to February 2012, but inclement weather and the need to remain within the limits for no-decompression diving constrained the research to 42 individual dives (Table 7.5) which represented 41.1% of the days allocated for sampling across all sites.

Table 7.5. Sampling summary and means (±SD) and ranges of research dive length, numbers of divers and grey nurse sharks observed per scan, time to the first diver-shark interaction observation and diver-shark interaction time at Wolf Rock (WR), Julian Rocks (JR), South Solitary Island (SS) and Fish Rock (FR) from March 2011 to February 2012 (untransformed data presented).

Study site	Number of dives with diver-shark interactions (and total number of dives conducted)	Mean (±SD), range				
		Research dive length (minutes)	Number of divers per scan	Number of grey nurse sharks per scan	Time to the first diver-shark interaction (minutes)	Diver-shark interaction time (minutes)
WR	9 (9)	47.33 (7.11) 32-54	3.23 (1.13) 1-5	4.67 (3.73) 1-18	7.67 (3.78) 3-14	20.22 (5.43) 12-30
JR	11 (12)	43.75 (4.9) 32-52	4.12 (1.66) 1-11	2.19 (1.37) 1-6	12.09 (3.45) 4-17	10.00 (5.14) 2-20
SS	9 (10)	45.40 (6.31) 35-53	4.67 (1.89) 2-9	3.19 (3.14) 1-14	8.33 (13.72) 1-43	15.11 (9.7) 2-32
FR	9 (11)	46.55 (7.66) 35-61	4.65 (1.85) 1-11	3.12 (2.12) 1-9	5.22 (5.04) 1-17	15.56 (10.09) 2-28
Total	38 (42)	45.64 (6.42) 32-61	4.12 (1.74) 1-11	3.39 (2.96) 1-18	8.53 (7.69) 1-43	14.95 (8.37) 2-32

Adverse sea conditions forced sporadic diving with breaks of 0-14 days between individual sampling events. Interactions between divers and varying numbers of grey nurse sharks at different life-history stages were observed during 38 (90.5%) dives (Table 7.5). The mean duration of research dives (Table 7.5) did not differ significantly among sites (ANOVA: $F_{3,\ 32} = 0.72$, $P = 0.55$). Importantly, the mean proportions of research dives spent observing diver-shark interactions were not significantly different among sites (ANOVA: $F_{3,\ 32} = 1.44$, $P = 0.26$, Table 7.5), ensuring equivalent sampling effort across all four sites.

7.3.3 Grey nurse shark life-history stages

The size and gender ratios of grey nurse sharks varied between dives and among days at each site. At Julian Rocks the sexual maturities and genders of sharks were similar across consecutive dives on most days, yet the numbers of sharks within two of the length categories often differed between dives. For example, on one particular sampling day the numbers of grey nurse sharks observed within two length categories increased from the first to the second dive (i.e. from nine to twelve sharks at 2.26-2.81 metres TL and from eight to fourteen sharks at ≥2.94 metres TL). In contrast, at Fish Rock the numbers of grey nurse sharks at various life-history stages differed between days. For instance, over the first two days of sampling the numbers of immature male and female sharks observed during the first dives of each day increased substantially (e.g. from one male and four females on the first day to fourteen males and eight females on the second day).

The frequencies of grey nurse sharks at particular life-history stages also differed significantly among sites (chi-square test: $\chi^2 = 1486.72$, $P < 0.01$). At Wolf Rock, 100.0%

(mean ±SD, range = 4.67 ± 3.72, 0-18 sharks per scan) of the grey nurse sharks were sexually-mature, gestating females (Figure 7.2). In contrast, at Julian Rocks the grey nurse shark population was dominated by sexually-mature, migrating males (89.0%, mean ±SD, range = 1.96 ± 1.27, 0-6 sharks per scan, Figure 7.2), a few sexually-mature females on their southerly migration for parturition (2.0%, mean ±SD, range = 0.03 ± 0.17, 0-1 sharks per scan) and fewer juvenile males (0.7%, mean ±SD, range = 0.01 ± 0.12, 0-1 sharks per scan). The grey nurse shark population at South Solitary Island was primarily composed of sexually-mature, migrating males (71.3%, mean ±SD, range = 2.38 ± 2.71, 0-12 sharks per scan, Figure 7.2), but also included some sexually-mature, resting-phase females (12.7%, mean ±SD, range = 0.42 ± 0.55, 0-2 sharks per scan) and juvenile males (11.0%, mean ±SD, range = 0.37 ± 0.76, 0-4 sharks per scan), and minimal juvenile females (1.3%, mean ±SD, range = 0.04 ± 0.20, 0-1 sharks per scan). At Fish Rock, the grey nurse shark population comprised several life-history stages dominated by juvenile males (29.9%, mean ±SD, range = 0.99 ± 0.92, 0-4 sharks per scan) and females (41.1%, mean ±SD, range = 1.35 ± 1.19, 0-5 sharks per scan) and much lower frequencies of sexually-mature, resting-phase females (7.9%, mean ±SD, range = 0.26 ± 0.55, 0-2 sharks per scan) and sexually-mature, post-copulatory males (3.3%, mean ±SD, range = 0.10 ± 0.38, 0-2 sharks per scan). Moreover, the gender ratio of immature grey nurse sharks (1:1.38) at Fish Rock was significantly biased toward females (chi-square test: $\chi^2 = 4.26$, $P < 0.05$). Across all sites, the genders of 66 (6.3%) grey nurse sharks could not be identified.

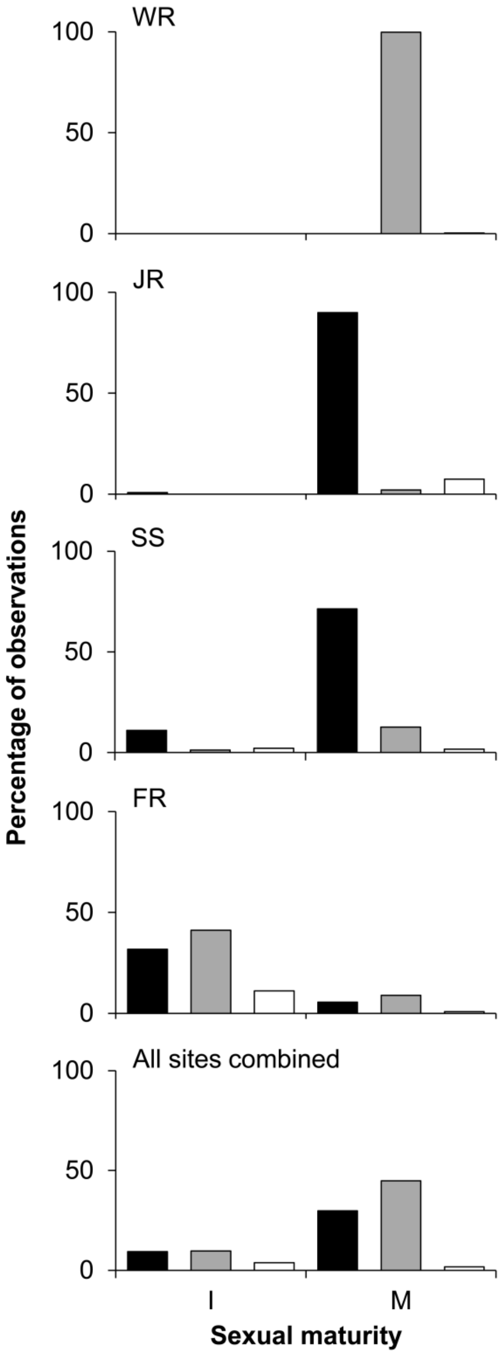

Figure 7.2. Percentages of sexually-immature (I) and sexually-mature (M) male (■) and female (▨) grey nurse sharks (*Carcharias taurus*) and those of undetermined gender (□) observed at Wolf Rock (WR), Julian Rocks (JR), South Solitary Island (SS) and Fish Rock (FR) from March 2011 to February 2012. Note: two sharks of unknown gender are not shown as their maturity could not be determined.

7.3.4 Grey nurse shark swimming behaviour and diver-shark interactions

The three swimming behaviours comprising hovering, milling and active swimming documented in previous studies (Hayward 2003; Smith *et al*. 2010) were also exhibited by the populations of grey nurse sharks observed at the four sites sampled. While the most frequent swimming behaviour exhibited by grey nurse sharks during diver-shark interactions at all sites was milling followed by hovering and active swimming (Figure 7.3a), there were differences among sites that were highlighted by the site specific analyses.

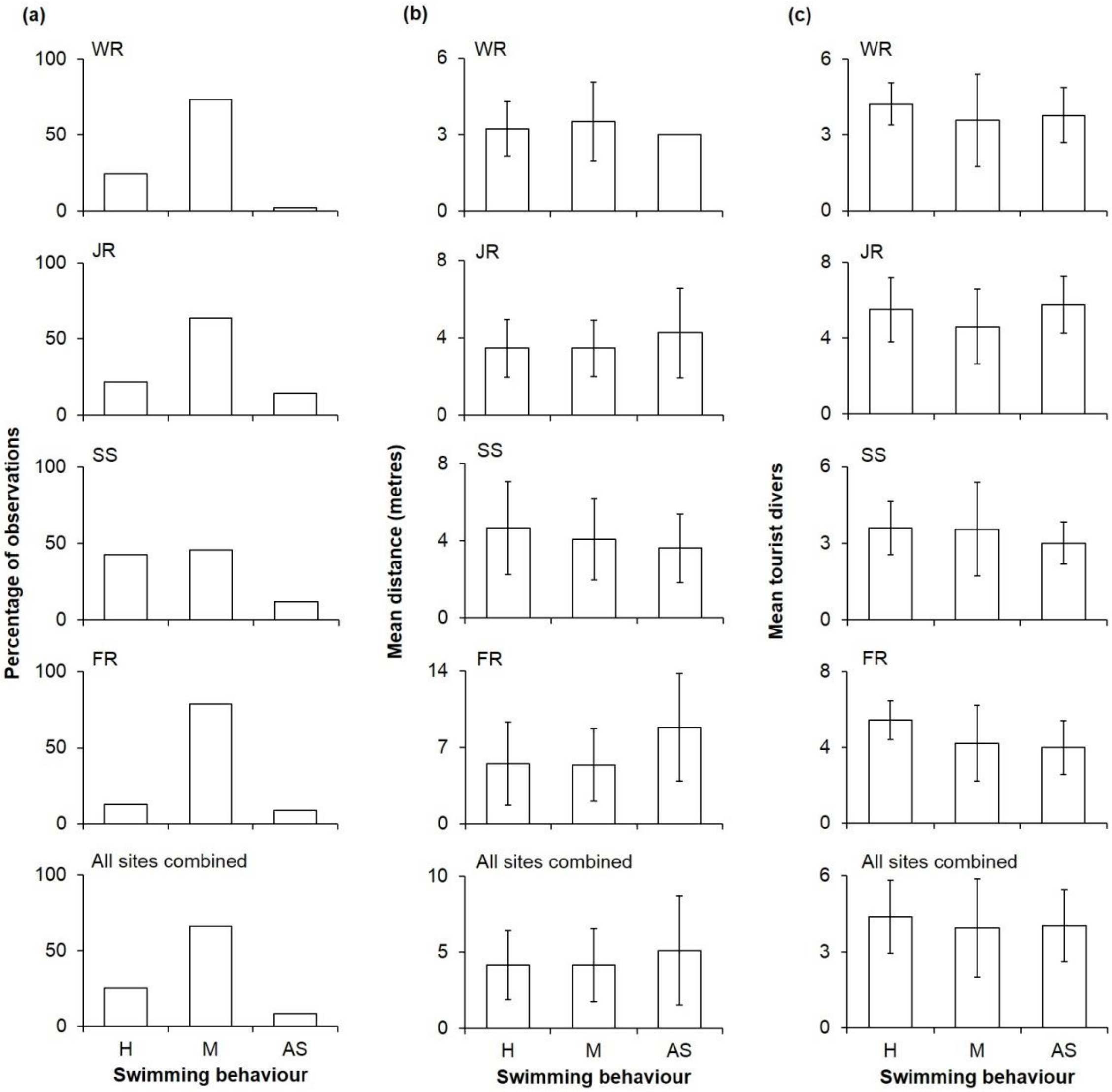

Figure 7.3. Observations of swimming behaviour of grey nurse sharks (*Carcharias taurus*) with (a) the frequency of occurrence of hovering (H), milling (M) and active swimming (AS), (b) the mean (±SD) distance between divers and sharks for each swimming behaviour, and (c) the mean (±SD) number of divers present for each swimming behaviour during diver-shark interactions at Wolf Rock (WR), Julian Rocks (JR), South Solitary Island (SS) and Fish Rock (FR) from March 2011 to February 2012 (*n* = 283 scans across all sites).

The swimming behaviour data used in ANOVAs were not serially correlated as plots of the residuals against time showed random patterns and Durbin-Watson tests were not significant (d = 1.90-2.10 for each test, $P > 0.05$). The *a priori* power analyses indicated that 17 replicate scans of swimming behaviour for each site would enable differences of 25.0% among means to be detected with power of 0.80 (Type I and II error rates of α = 0.05 and β = 0.20, respectively). This result was confirmed by the *post hoc* power analyses. At Wolf Rock, the gestating grey nurse sharks exhibited all three swimming behaviours (Figure 7.3a), but the mean frequency of milling was significantly greater (ANOVA: $F_{2,48} = 20.46$, $P < 0.001$) than those of hovering and active swimming which did not differ significantly (SNK test: $P < 0.05$). At Julian Rocks, all three swimming behaviours were exhibited by the mainly sexually-mature, migrating male sharks (Figure 7.3a), however milling was significantly more frequent than hovering and active swimming which were not significantly different (ANOVA: $F_{2,48} = 6.83$, $P = 0.0025$ and SNK test: $P < 0.05$). At South Solitary Island, the grey nurse shark population comprised mostly of sexually-mature migrating males, also exhibited hovering, milling and active swimming (Figure 7.3a), and whilst the mean frequencies of hovering and milling did not differ significantly from each other they were significantly greater than that of active swimming (ANOVA: $F_{2,48} = 6.07$, $P = 0.0045$ and SNK test: $P < 0.05$). At Fish Rock, the grey nurse shark population (dominated by juveniles) exhibited all three swimming behaviours (Figure 7.3a), but milling occurred significantly more (ANOVA: $F_{2,48} = 17.29$, $P < 0.001$) than hovering and active swimming which did not differ significantly (SNK test: $P < 0.05$). Finally, when pooled across all sites the most frequent swimming behaviour exhibited by grey nurse sharks during diver-shark interactions (Figure 7.3a) was milling (66.1%) and this was significantly greater than the frequencies of hovering (25.4%) and active swimming (8.5%) which did not differ significantly (ANOVA: $F_{2,48} = 15.82$, $P < 0.001$ and

SNK test: $P < 0.05$).

The numbers of divers participating in the shark dives ranged from 1-11 divers across all sites, varied within and among sites, and averaged 4.12 divers per dive per site when pooled across all sites and dives (Table 7.5). Contemporaneously, the numbers of grey nurse sharks observed ranged from 1-18 individuals across all sites, varied within and among sites, and averaged 3.39 sharks per dive per site when pooled across all sites and dives (Table 7.5). On entering the water, the mean period of time that elapsed prior to the first diver-shark interaction (Table 7.5) differed significantly among sites (ANOVA: $F_{3, 32} = 3.90$, $P = 0.02$), but an SNK test could not unequivocally determine the differences. However, examination of the means (Table 7.5) suggested that more time elapsed prior to the first diver-shark interaction at Julian Rocks. The mean duration of diver-shark interactions varied within sites (Table 7.5) and did not differ significantly among sites (ANOVA: $F_{3, 32} = 1.87$, $P = 0.15$). The duration of a diver-shark interaction, pooled across all sites and dives, averaged about 15 minutes and represented one third of the total dive duration (Table 7.5).

There were no apparent patterns in the distances between scuba divers and grey nurse sharks during diver-shark interactions when the animals were hovering, milling or actively swimming at any of the sites sampled (Figure 7.3b). Moreover, when pooled across sites, the mean (±SD, range) distance during diver-shark interactions did not differ significantly (ANOVA: $F_{2, 18} = 0.10$, $P = 0.91$) when the sharks were hovering (4 ± 2, 3-13 metres), milling (4 ± 2, 3-13 metres) or active swimming (5 ± 4, 3-13 metres). Similarly, there were no relationships between the swimming behaviour (i.e. hovering, milling or active swimming) of grey nurse sharks and the mean number of divers present during diver-shark interactions (Figure 7.3c). Furthermore, when pooled across sites, the mean number of divers present during diver-shark interactions did not differ significantly among swimming behaviours (ANOVA: $F_{2, 18} = 1.20$, $P = 0.33$).

7.3.5 Compliance with legislation and/or code of conduct

Divers observed interacting with grey nurse sharks demonstrated 100.0% compliance with the investigated guidelines in the relevant legislation and/or the code of conduct at all sites. The total number of scuba divers in the water exceeded 10 on two occasions, once at Julian Rocks and again at Fish Rock. However, on each occasion the divers present were divided into two separate and distinct groups each with fewer than 10 divers and thus were not considered in breach of the code of conduct.

7.4 DISCUSSION

Although sea conditions constrained diving and reduced sample sizes, the methodological approach ensured that grey nurse sharks at key life-history stages were sampled with sufficient power to detect small changes in the behaviours of the divers (tourists) and sharks. For example, the sampling method enabled the difference between the dive profile followed by divers at Julian Rocks (i.e. swim from mooring line to shark location) compared with the other sites (i.e. divers descended from above the sharks) to be detected statistically. Additionally, the grey nurse shark population structures at the sites were as predicted from previous studies (Otway *et al*. 2003, 2009; Bansemer & Bennett 2009; Otway & Ellis 2011) and differences in shark length frequency distributions and life-history stages were apparent between dives and among days and sites. The ANOVAs examining shark swimming behaviour were also significant and had sufficient statistical power to detect differences of 25.0% among means. The sampling of multiple sites and key life-history stages together with the consistent profile of this MWT sector across the region enables the generalisation (statistically) of the results to other sites that are utilised for diver-shark interactions with grey nurse sharks. Combined, the demography of scuba divers interacting with grey nurse sharks, the five life-history stages of the shark populations at the four aggregation sites, the behaviour of divers and sharks during diver-shark interactions, and compliance of divers to the guidelines/code of conduct have provided an understanding of the impacts of this MWT industry on the swimming behaviour of groups of grey nurse sharks. These results also provide direction for future research on the impacts of the industry on individual shark behaviour.

The behavioural results indicated that aggregating grey nurse sharks exhibited their usual range of swimming behaviours (Hayward 2003; Smith *et al*. 2010) when in the presence of divers complying with the guidelines/code of conduct at the four sites. Milling was significantly more evident during diver-shark interactions (66.1% of time), followed by hovering (25.4% of time) and active swimming (8.5% of time). These results are consistent with those of an earlier study at Fish Rock (Smith *et al*. 2010) where grey nurse sharks were milling (inclusive of hovering) for 85.0% of the time during diver-shark interactions. Milling and hovering behaviours were characterised by low levels of activity with slow to no net movement. None of the investigated swimming behaviours were significantly affected by distances between grey nurse sharks and divers or by the numbers of divers during interactions with the sharks. In contrast are the findings of Barker *et al*. (2011) describing significant increases in swimming rates of female sharks during interactions with groups comprising 12 divers at distances of 3 metres at Magic

Point, NSW. These differing results may be attributed to the approach method utilised in the respective experimental designs. The previous study applied specific pre-determined treatments of coordinated, direct approaches of up to 12 divers at decreasing distances to grey nurse shark schools within a confined space (i.e. cave entrance) and was contrary to the guidelines/code of conduct. The present study utilised methods reflective of the tourism setting with passive diver approaches that did not breach the guideline/code of conduct of a maximum of 10 divers during shark/diver interactions. Although the disparity of the study designs limits direct comparison of results, the outcomes are consistent with previous marine mammal tourism and shark behavioural research that has described alterations to animal behaviour in response to direct rather than passive human or vessel approaches (Johnson & Nelson 1973; Quiros 2005; Filla & Monteiro-Filho 2009). Combining the results of this study with Smith *et al*. (2010) and Barker *et al*. (2011) suggests that the existing management guidelines/code of conduct are appropriate for ensuring minimal impacts on grey nurse sharks. Moreover, maintaining the threshold at 10 divers during diver-shark interactions is an important outcome as this MWT sector makes a considerable contribution to the economies of coastal communities (HAGE 2004).

The study revealed absolute compliance (i.e. 100.0%) to all investigated guidelines irrespective of the demographic profiles of the scuba divers, and no significant short-term changes in the behaviour of grey nurse sharks across multiple sites with various shark life-history stages. While it is possible that the presence of researchers may have influenced diver behaviour, the potential for bias was considered minimal. This MWT industry has a long history (>20 years) of assisting researchers at numerous sites along the Australian east coast (e.g. Harriott *et al*. 1997; Smith *et al*. 2010; Barker *et al*. 2011; Otway & Ellis 2011). Consequently, tourist divers rarely change their diving behaviour as they are familiar with the frequent presence of researchers on dive vessels and during dives. It is also possible that subtle physiological and/or biochemical responses to the presence of scuba divers may occur in grey nurse sharks which could lead to long-term consequences. Such alterations may include the release of stress hormones and could lead to reduced growth, reproduction and fitness (Skomal & Bernal 2010). Determining the existence of these impacts generally requires intrusive sampling techniques (i.e. capture, physical restraint and extraction of blood and/or tissues) which when combined with other anthropogenic activities (e.g. fishing) represent alternative stressors and thus confound interpretation of results. Whilst the potential for additional impacts should not be disregarded and warrants further investigation, the results of this study indicate that the existing guidelines afford the species adequate protection from scuba diving tourism pressure occurring at the present time.

These findings contrast with widespread accounts of MWT operator (e.g.Scarpaci *et al*. 2003, 2004; Wiley *et al*. 2008; Howes *et al*. 2012) and tourist (e.g. King & Heinen 2004) noncompliance, and studies that have identified significant behavioural changes in target species despite satisfactory compliance by MWT operators (e.g. Allen *et al*. 2007; Strong & Morris 2010) and tourists (Quiros 2007; Smith *et al*. 2010). The potential vectors of compliance elucidated from this study include the exclusivity of the activity, diver familiarity with the target species, guideline clarity (Cole 2007; Jett *et al*. 2009; Smith *et al*. 2010), operational logistics and the involvement of stakeholders in management processes. This information may aid managers to improve the sustainability of other less compliant MWT industries.

Diving with grey nurse sharks differs from other MWT sectors in that it is often the prime reason for visiting a holiday destination (Wilson & Tisdell 2003; Vianna *et al*. 2012) rather than an add-on activity (Parsons *et al*. 2003). Moreover, this MWT sector requires the substantial expenditure of time and money to acquire the necessary scuba diving skills as evidenced by the level of scuba qualifications (i.e. Advanced Open Water and above) held by 61.5% of divers sampled across all sites. Also, travel to sites and associated accommodation provide additional costs. Hence, when compared with wildlife watching and snorkelling activities, the costs and experience (i.e. ≥68.8% of all divers had prior grey nurse shark diving experience) suggest that these scuba divers are dedicated (Fredline & Faulkner 2001) or specialist (Catlin & Jones 2010) wildlife tourists rather than general interest (Parsons *et al*. 2003; Curtin *et al*. 2009; Catlin & Jones 2010) visitors participating in MWT. It is likely that dedicated wildlife tourists possess pro-environmental attitudes (Catlin & Jones 2010), a model supported by the findings of Smith *et al*. (2009) who showed that grey nurse shark diving tourists at Fish Rock possessed biocentric attitudes.

The degree of remoteness of studied locales, qualification and experience levels of divers, site-specific diving conditions (in relation to difficulty and dive length), diver to shark ratios and the life-history stages of aggregations did not result in variation of compliance among sites. Wolf Rock was the most remote of the four study sites in terms of its accessibility from an urban centre and travel time from boat launch to site arrival (Table 6.1), and it presented the most difficult diving conditions (personal observation). Probably not by coincidence, the divers sampled at Wolf Rock were more qualified, had more diving experience and participated in longer dives than those sampled at the other sites. Furthermore, Wolf Rock was the only site where the mean number of divers was less than the mean number of sharks, all of which were large and most likely gestating females.

Whilst the combination of these factors suggests that divers at Wolf Rock were likely quite confident during diver-shark interactions, the absolute compliance at all sites demonstrated that tourist confidence can be eliminated as a potential deterrent or motivator of compliance for this activity.

Although diver perceptions of the sizes of grey nurse sharks were not of significance to among-site compliance outcomes, it may be an important facet of the industry that distinguishes it from some other MWT sectors that have displayed poor compliance. Grey nurse sharks are larger in size (Compagno 2001) than some other MWT target species such as juvenile fur seals (e.g. Acevedo-Gutierrez *et al*. 2011) and turtles (e.g. Waayers *et al*. 2006). Diver perceptions of the size of grey nurse sharks and a general awareness of the risks of serious injury (albeit unlikely) associated with many shark species may have resulted in a level of concern for personal safety that dissuaded noncompliant behaviour that has otherwise been revealed in alternate MWT settings that are focused on smaller animals and/or species perceived as sociable or harmless (e.g. Scarpaci *et al*. 2003, 2004; Stafford-Bell & Scarpaci, in review).

Each particular guideline investigated was concise, quantifiable and/or not open to interpretation. Most stipulations had a ‘did’ or ‘did not’ outcome; for example, divers either did or did not touch a grey nurse shark. Moreover, the few dive participants that did not stipulate English as their preferred language (11.5% of divers pooled across sites) still demonstrated total compliance which suggests interpretation of management conditions was not affected by language preference. The importance of clear guidelines has also been described by Scarpaci *et al*. (2004) who documented dolphin swimming tour operator compliance to a single quantifiable condition (i.e. the number of allowable swimmers per interaction) in an otherwise non-compliant industry. Additionally, there are also occasions where it is not possible to comply with management guidelines such as preserving specific minimum distance requirements. For example, this can occur during some marine mammal watching and snorkelling tourism operations when they are subjected to inclement weather or have to approach/are approached by submerged focal animals (Scarpaci *et al*. 2004; Wiley *et al*. 2008; Strong & Morris 2010; Mangott *et al*. 2011). Importantly, these issues are not relevant to tourist and tour operator compliance in the grey nurse shark MWT industry.

Similarities between grey nurse shark diving and other MWT sectors extend further, particularly in relation to operational logistics. Little, if any, searching is required by tour operators and tourists to snorkel with and/or watch pinnipeds (Curtin *et al*. 2009; Stafford-Bell & Scarpaci, in review). The same is true for scuba diving with grey nurse, whitetip and grey reef sharks (Smith *et al*. 2010; Vianna *et al*. 2012) as interactions can occur almost immediately on descent of the divers. Moreover, these MWT operations often display a greater degree of compliance with management guidelines (Curtin *et al*. 2009; Smith *et al*. 2010; Stafford-Bell & Scarpaci, in review). The site fidelity and low levels of activity exhibited by grey nurse sharks at aggregation sites (i.e. 85.5-97.8% of time per site) may have further reduced the motivation for tourists to actively pursue the animals and breach management guidelines. Conversely, cetacean snorkelling (Scarpaci *et al*. 2003, 2004; Allen *et al*. 2007) and watching (Wiley *et al*. 2008), and whale shark snorkelling (e.g. Quiros 2007; Catlin *et al*. 2012) activities are highly search-intensive and industry tour operators and tourists have displayed some, if not total, noncompliance to management guidelines.

The grey nurse shark aggregation sites off eastern Australia also provide habitat for a wide variety of other marine species such as wobbegong sharks (Huveneers *et al*. 2006), leopard sharks (Dudgeon *et al*. 2013), stingrays, turtles, moray eels, pelagic fish, octopus, cuttlefish, nudibranchs and lobsters (Harriott *et al*. 1997; Breen *et al*. 2004; Malcolm *et al*. 2010; personal observation). These animals present diving tourists with secondary wildlife interactions and alternative subjects for those divers with prior grey nurse shark diving experience (≥68.8% of divers at each site), with the latter possibly providing greater interest as indicated by underwater cameras fitted with equipment for macro photography. In contrast, other MWT sectors that focus on solitary, non-aggregating and/or highly mobile species are unable to provide immediate secondary wildlife options and thus the tourists are compelled to pursue the focal species to maximise their interactions. This likely accounts for their unsatisfactory compliance (e.g. Heckel *et al*. 2003; Scarpaci *et al*. 2003, 2004; Wiley *et al*. 2008; Howes *et al*. 2012).

Scuba divers and MWT operators were extensively consulted during the development of the code of conduct (Otway *et al*. 2003) and this also formed the basis for the regulatory guidelines. Satisfactory compliance to both was evident in this and a previous study restricted to Fish Rock (Smith *et al*. 2010). Averaged across all sites, 36.0% of the diving tourists that were not aware of the code of conduct or similar legislation regulating this activity prior to their dive were overseas tourists and a further 24.6% of divers were ≤25 years of age. The lack of awareness within these demographics is understandable given that the promotion of the guidelines were focused on domestic tourists and occurred prior to the younger divers undertaking their scuba diving training (i.e. <18 years of age). Irrespectively, the MWT operators at each site provided informative and enthusiastic pre-dive briefs that included direct and more informal explanations of the scuba diving guidelines. Furthermore, operators and tourists conversed positively about the species throughout the dive trip (personal observation). The management guidelines were also displayed at each tourism operation's dive centre and on their websites (personal observation). This demonstrates tour operator understanding, support and potentially a sense of ownership of the management strategies prescribed by the relevant management agencies. Likewise, dwarf minke whale snorkelling tourism operators at the Great Barrier Reef, Australia, provided tourists with detailed activity briefings and reinforcement of code of practice guidelines that were developed collaboratively by researchers, managers and the operators. Unfortunately, the effectiveness of this approach in promoting tourist compliance was not assessed (Birtles *et al*. 2002a; Valentine *et al*. 2004). The value of consultation with MWT stakeholders during the preparation of management strategies has been repeatedly identified (Birtles *et al*. 2002b; Higham *et al*. 2009; Curtin 2010), and is supported by high levels of tour operator compliance where it occurred (Davis *et al*. 1997; Allen *et al*. 2007) and low compliance where tour operators (Beasley *et al*. 2010) and tourists (Morris *et al*. 2007) were not involved in management planning. Limited resources often impedes enforcement of management guidelines (Kessler & Harcourt 2010; Strong & Morris 2010; Acevedo-Gutierrez *et al*. 2011; Howes *et al*. 2012), particularly those for MWT industries located in regional areas (Orams 1996; Birtles *et al*. 2002b) and/or that occur underwater (Davis *et al*. 1997). Thus, maintaining the involvement of the grey nurse shark MWT industry stakeholders in management processes is important for promoting compliance now and into the future.

7.5 CONCLUSION

Absolute compliance with all of the management guidelines investigated for scuba diving with grey nurse sharks was evident with all scuba divers (tourists) during diver-shark interactions and was independent of the tourist profile, aggregation site or the life-history stage of the sharks. As grey nurse sharks exhibited their usual swimming behaviours during interactions with compliant divers, the existing management strategies (guidelines and/or code of conduct) appear effective at protecting the sharks from adverse, short-term behavioural impacts stemming from this MWT industry at current usage levels. Similar sampling at the same and other aggregation sites in the future should be done to further enhance the understanding of the beneficial and adverse impacts of this MWT sector and enable spatial and temporal trends to be identified. Such results could assist in the recovery and long-term conservation of the species. Future research should also be conducted to investigate the potential impacts of this MWT sector on the behaviour of individual sharks. Compliance was likely promoted through familiarity of divers with grey nurse sharks, guideline clarity, operational logistics, secondary options for wildlife interactions and stakeholder involvement in the management processes. Continued liaison with grey nurse shark MWT operators and tourists and ongoing monitoring of their activities should ensure the persistence of this sector that is economically important to coastal communities along the east coast of Australia. Finally, the contemporaneous sampling methodology adopted here across multiple sites provided valuable information for management of MWT involving a critically endangered species. This approach and the outcomes of the research (i.e. vectors of compliance with effective management guidelines) could be beneficial in the wider MWT realm.

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Chapter 8

Conclusion

Grey nurse shark scuba diving marine wildlife tourism (MWT) operations off eastern Australia vary considerably in operational logistics (e.g. dive vessels and boarding procedures), seasonality, patronage, diving intensity and diver experience. Despite this variation, the findings of this study strongly indicated that scuba diving MWT does not negatively impact the short-term behaviour of aggregated, critically endangered grey nurse sharks off eastern Australia at current usage levels. The use of multiple sampling techniques enabled behavioural data to be quantified and compared across several temporal and spatial scales in the absence and presence of MWT to produce an efficacious and broad assessment of the putative impacts of and current management strategies for this non-consumptive, economically important industry. The sampling approach adopted ensured that the research findings were not restricted to specific life-history stages of the sharks, tourist demographics or MWT operations and could be generalised to the entire grey nurse shark population and MWT sector off eastern Australia.

Stereo-video photogrammetry was used to develop a partial ethogram of the swimming and non-swimming behaviours of aggregated grey nurse sharks during daylight hours in the absence of MWT and revealed that the sharks predominantly exhibit low-energy swimming behaviours when in and around gutters, overhangs, swim-throughs and caves, and use their pectoral fins interactively to navigate these surroundings and localised environmental conditions. Moreover, the absence of threatening agonistic behaviour was consistent with previous reports of the docile nature of this species and provided further evidence of minimal energy expenditure by the sharks when aggregated. Underwater visual census (UVC) confirmed the prevalence of low-activity swimming behaviours in grey nurse sharks when occupying locations within aggregation sites during interactions with

MWT scuba divers. While passive acoustic telemetry showed that grey nurse sharks may have exhibited more active swimming when patrolling between two locations (i.e. at a larger spatial scale) within an aggregation site, the sharks still conserved energy by adopting hovering and/or milling swimming behaviours for the majority of the time during daylight hours.

The predominance of low-activity behaviours by grey nurse sharks at differing life-history stages whilst occupying aggregation sites was most likely a mechanism for conserving energy for migratory movements. It is probable that adult male sharks conserved energy for their annual northerly and southerly migrations in the austral winter and spring, respectively. In contrast, the low activity levels of gestating female sharks were probably due to maternal fasting and their impending large southerly migration in the late austral winter for parturition off central and southern New South Wales in the austral spring. Similarly, adult female sharks in the resting phase of their biennial reproductive cycle most likely adopted low-activity behaviours to aid the replenishment of energy stores expended during the previous gestation and for future reproductive events with their associated northerly migration in the late austral spring for mating and subsequent gestation at aggregation sites off Queensland.

The partial ethogram provided a crucial baseline for establishing changes in shark behaviour during interactions with MWT divers. Importantly, inappropriate diver behaviour was not observed in this study and led to absolute compliance with regulatory and voluntary management guidelines. Stereo-video photogrammetry and UVC showed that milling was significantly the most frequent swimming behaviour regardless of the presence of MWT divers with only minimal overall decreases in hovering and milling across comparable life-history stages and aggregation sites. The minor differences in the frequencies of swimming behaviours were likely due to natural variation in environmental conditions (i.e. currents) at the sites as the overall frequencies the behaviours with and without MWT were almost identical. Similarly, passive acoustic telemetry detected significant differences in the patrolling behaviour of sharks between locations on days with and without scuba diving MWT but this was not consistent with diving activity or changes in seawater temperatures and was instead attributed to the variable current regime at Fish Rock.

The research revealed the similarities, differences, advantages and disadvantages associated with the use of stereo-video photogrammetry, passive acoustic telemetry and UVC to quantify the swimming, non-swimming and patrolling behaviours of aggregated grey nurse sharks during daylight hours. Stereo-video photogrammetry and UVC require at least two scuba divers (i.e. one researcher and one assistant) to be underwater with the sharks whereas passive acoustic telemetry eliminated the potential effects of diver presence on shark behaviour. The use of stereo-video photogrammetric and UVC techniques are subject to environmental conditions (e.g. poor visibility, strong currents) and the constraints imposed on researchers by physiological scuba diving limitations (i.e. air supply, nitrogen absorption and accumulation). Some of these disadvantages are overcome with stereo-video photogrammetry as observations of shark behaviour are made after initial data collection using software that enables the videos to be paused, skipped, slowed down, sped up, magnified and revisited with 24 frames recorded per second. These attributes allow more quantitative and accurate finer-scale data to be extracted from the videos such as tail beat frequencies, rates of movement, pectoral and caudal fin angles, and other morphometric measurements that would be difficult or impossible to obtain using UVC. Nevertheless, the behavioural data in the video footage was restricted to the field of view whereas UVC provided a more holistic view of the sharks in their environment. A disadvantage of this broader perspective was that the overwhelming amount of information available from UVC could not be documented by a single researcher and an assistant. Passive acoustic telemetry further expanded the temporal and spatial scope of this behavioural research and, if possible, would have been expensive and logistically demanding to achieve using stereo-video photogrammetry or UVC. However, passive acoustic telemetry does not permit finer-scale details (e.g. pectoral and caudal fin angles and non-swimming behaviours) to be quantified.

The sampling techniques used in this research were complementary and provided independent validation of the results obtained. Combined, the techniques enabled the swimming, non-swimming and patrolling behaviours of aggregated grey nurse sharks to be quantified, the putative impacts of scuba diving MWT to be examined and the effectiveness of management strategies to be assessed in an efficacious manner. Crucially, the research indicated that scuba diving MWT has negligible short-term impact on the primarily low-energy behaviours exhibited by aggregated grey nurse sharks during daylight hours. Maintaining natural behaviours unaffected by scuba diving MWT and other anthropogenic disturbances is essential for the recovery and long-term conservation of this critically endangered species. These findings coupled with the total compliance exhibited by MWT divers of varying demographics with grey nurse shark scuba diving guidelines strongly suggested that management strategies are effective at protecting the east Australian population of grey nurse sharks from MWT disturbance. Consequently, the grey nurse shark scuba diving MWT industry in its current form is ecologically and economically sustainable.

Regular monitoring of shark behaviour and scuba diver compliance into the future using stereo-video photogrammetry, passive acoustic telemetry, UVC and potentially other new technologies at the various aggregation sites along the east coast of Australia would ensure that disturbances are identified promptly. This would ensure that the long-term sustainability of this MWT industry is maintained at existing levels and/or expanded in an ecologically sustainable manner to meet future demand. This would further enhance the many local economies along the Australian east coast that depend on this MWT sector. Finally, future impact assessments should focus on other more deleterious sources of anthropogenic disturbances (i.e. fishing) to this critically endangered population of grey nurse sharks.

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Appendix A

Chapter 2 publication

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ENDANGERED SPECIES RESEARCH
Endang Species Res

Behaviour of aggregated grey nurse sharks *Carcharias taurus* off eastern Australia: similarities and differences among life-history stages and sites

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ABSTRACT: Stereo-video photogrammetry was used to document swimming and non-swimming behaviours of various life-history stages of the grey nurse shark *Carcharias taurus* at 8 east Australian aggregation sites (during daylight) in the absence of scuba diving tourism and fishers. Swimming behaviours included hovering, milling, and active swimming with significantly greater milling. Rates of movement were least during milling and greatest for active swimming. Pectoral fins were held 20 to 24° below horizontal, which was consistent with holding positions reported in shark swimming studies. Significantly lower caudal fin positions during hovering probably minimised forward propulsion. Tail-beat frequency decreased significantly with increasing total length and was likely due to greater propulsion from larger caudal fins. Low activity indicated that sharks minimised energy expenditure when aggregated, which was associated with migratory and reproductive behaviours. Significantly different pectoral fin positions among sites likely resulted from differing navigational requirements. Non-swimming behaviours were infrequent. Chafing, gill puff, head snapping and palatoquadrate protrusion were generally categorised as grooming behaviour. One gill puff sequence and all but one rapid withdrawal event were categorised as 'flight'-response agonistic behaviour. The remaining rapid withdrawal and stand back were to avoid collision and categorised as swimming behaviour. The absence of 'fight'-response agonistic behaviour was consistent with previous descriptions of the species as docile. This partial ethogram will enhance ecological understanding, assist assessment and management of diving tourism, and contribute to the recovery and long-term conservation of this critically endangered species.

KEY WORDS: Shark · *Carcharias taurus* · Critically endangered · Ethogram · Stereo photogrammetry · Fin angles · Tail beats · Rates of movement

INTRODUCTION

An ethogram provides a descriptive account of behaviours exhibited by a species, and can be enhanced with quantitative analyses of the durations, frequencies and extent of events. Behavioural events are instantaneous (Altmann 1974), sequences of events comprise repeated similar or differing events in a random or specific order, whereas behavioural states exist for extended periods of time (Altmann 1974, Mann 1999). Preliminary observations are important to discriminate between behavioural events or states so the most appropriate, efficacious sampling methods can be identified. A comprehensive ethogram can be developed for a species by studying behavioural events and states across differing life-history stages and spatial and temporal scales, and may also identify factors influencing behaviour.

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Appendix B

Chapter 3 publication

CSIRO PUBLISHING

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Does the grey nurse shark (*Carcharias taurus*) exhibit agonistic pectoral fin depression? A stereo-video photogrammetric assessment off eastern Australia

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Abstract. Underwater stereo-video photogrammetry was used to document the pectoral fin positions of various life-history stages of the critically endangered east Australian population of the grey nurse shark (*Carcharias taurus*) during normal swimming behaviour at multiple aggregation sites. A wide range in pectoral fin positions was recorded with dihedral pectoral fin angles ranging from –25 to 88°. Pectoral fin angles varied significantly among sites and this was attributed to the differing navigational and energetic requirements of the sharks. There was no significant relationship between pectoral fin angles and distances separating the shark and scuba diver. The wide range in pectoral fin angles, interactive use of the fins during swimming, low-energy behaviours of the sharks at aggregation sites and absence of 'fight' response agonistic behaviour indicated that the species does not exhibit agonistic pectoral fin depression. Reports of agonistic pectoral fin depression in the grey nurse shark obtained with visual estimates should be treated as preliminary observations requiring further testing using accurate sampling methods such as stereo photogrammetry. It is important that diver compliance with existing management guidelines that prohibit divers from chasing or harassing grey nurse sharks and blocking cave and gutter entrances is maintained.

Additional keywords: agonistic behaviour, critically endangered, pectoral fin angle, stereo photogrammetry.

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Introduction

Agonistic behaviour encompasses all fearful, threatening and aggressive actions exhibited by animals (Brown and Hunsperger 1963; Hill *et al.* 2014). Animals present the fight or flight response when exposed to a perceived risk (Suresh *et al.* 2014), with the threat of injury (e.g. exposing the teeth) and actual physical aggression (e.g. biting) considered 'fight' reactions whereas fearful behaviours (e.g. fleeing) represent 'flight' responses (Hill *et al.* 2014). Stimuli that can induce the fight or flight response include predators, other species, conspecifics and unfamiliar objects. The motivation for responding to such stimuli may be self-defence, protection of young, territory or food, maintaining or challenging dominance within a social hierarchy, or competition for mates.

The agonistic behaviour of sharks has been documented for a variety of species with that of the grey reef shark (*Carcharhinus amblyrhynchos*) most known (Johnson and Nelson 1973; Nelson 1981–82; Nelson *et al.* 1986). A conspicuous threat display described for this species, and later termed 'hunch' (Myrberg and Gruber 1974), was exhibited in response to rapid approaches by a scuba diver (Johnson and Nelson 1973). The display incorporated a laterally exaggerated swimming motion, rolling, snout elevation, sustained pectoral fin depression, back arching and lateral bending (Johnson and Nelson 1973). More recently, a review described the agonistic behaviours putatively exhibited by 23 shark species including the grey reef shark (Martin 2007). Twenty-nine behaviours were reported with pectoral fin depression evident across all 23 species (Martin 2007). Agonistic pectoral fin depression was defined as the sustained (>5 s), bilateral lowering of the pectoral fins more than during normal swimming behaviour (Martin 2007) and the pectoral fin angle (PFA) was measured as the dihedral angle (i.e. the position of the pectoral fin below the horizontal plane) in accordance with laboratory studies of the North American leopard shark (*Triakis semifasciata*) (Wilga and Lauder 2000; Maia *et al.* 2012). Underwater visual estimates were previously used to quantify the PFA of sharks (Johnson and Nelson 1973; Martin 2007), but more recent research (Harvey *et al.* 2004) has shown that there

Appendix C

Chapter 7 publication

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Scuba diving tourism with critically endangered grey nurse sharks (*Carcharias taurus*) off eastern Australia: Tourist demographics, shark behaviour and diver compliance

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HIGHLIGHTS

- Key grey nurse shark life-history stages were sampled at four tourism sites.
- Most tourists were recreational divers with prior grey nurse shark experience.
- Milling was the most frequent shark swimming behaviour observed.
- No significant changes to shark behaviour occurred during diver–shark interactions.
- Tourists exhibited 100% compliance with all of the scuba diving guidelines.

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ABSTRACT

Guidelines and a national code of conduct were implemented to manage scuba diving tourism with the critically endangered grey nurse shark (*Carcharias taurus*) along the Australian east coast. The demographics of diving tourists, swimming behaviour of grey nurse sharks at various life-history stages and compliance of divers to the guidelines/code of conduct were simultaneously assessed during diver–shark interactions at four sites from March 2011 to February 2012. Milling was the most frequent swimming behaviour observed and no significant changes occurred with the number of divers or distance to sharks. Divers exhibited 100% compliance with all guidelines investigated. Satisfactory compliance may have been attributable to guideline clarity, the ease of establishing diver–shark interactions, stakeholder involvement in management processes and diver perceptions of sharks. Similar sampling of group and individual shark behaviour should be done to further enhance the understanding of the beneficial and adverse impacts of this marine wildlife tourism sector.

1. Introduction

Marine wildlife tourism (MWT) has experienced dramatic growth in recent times and demand for opportunities in which humans can observe and interact with free-ranging marine megafauna is increasing (Birtles, Valentine, Curnock, Arnold, & Dunstan, 2002; Dobson, 2006; Gallagher & Hammerschlag, 2011; Hammerschlag, Gallagher, Wester, Luo, & Ault, 2012). Marine wildlife tourism also benefits local, regional and national economies (Sorice, Shafer, & Ditton, 2006), often by providing alternatives to consumptive uses of the natural environment (e.g. whale-watching versus whaling, Bejder, Samuels, Whitehead, & Gales, 2006) and may encourage participants to adopt pro-environmental attitudes and behaviours which can, in turn, aid environmental conservation (Christensen, Rowe, & Needham, 2007; Powell & Ham, 2008; Wilson & Tisdell, 2003; Zeppel & Muloin, 2008). Conversely, the industry can affect target species by causing malnourishment (e.g. Semeniuk, Speers-Roesch, & Rothley, 2007), disease (Semeniuk et al., 2007) and behavioural changes that may be detrimental to individual and population fitness (Higham, Bejder, & Lusseau, 2009; King & Heinen, 2004; Stockin, Lusseau, Binedell, Wiseman, & Orams, 2008; Williams,

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Appendix D

Conference oral presentation

Abstract

An underwater stereo-video photogrammetry system and underwater visual observation were used to document the swimming and non-swimming behaviours of aggregated, critically endangered grey nurse sharks off eastern Australia in the absence and presence of tourist scuba divers. The similarities, differences, advantages and disadvantages of the two non-invasive sampling techniques were compared. The techniques facilitated behavioural comparison across shark life-history stages and aggregation sites, shared the same personnel requirements and were effective in similar visibilities. Whilst visual observation provided a more holistic outlook, the photogrammetry system allowed more data to be collected and quantitatively so. Stereo-video photogrammetry estimates of shark perpendicularity to the system, precaudal length and pectoral/caudal fin positions were much more precise, accurate and detailed. Milling was significantly the most frequent swimming behaviour observed regardless of tourist diver presence and the frequency of non-swimming behaviours was slightly lower during tourist diver-shark interactions. These results and those of previous studies strongly suggested that any external, short-term effects of this marine wildlife tourism industry on grey nurse shark behaviour are negligible at present usage levels. Continual monitoring of this industry via simultaneous use of both sampling techniques and passive acoustic tracking was recommended to ensure its long-term sustainability into the future. In light of these and earlier findings, future research of anthropogenic impact on this population should focus on other activities such as fishing.

Reference

Smith, KR, Scarpaci, C & Otway, NM 2014, ‘A comparison of sampling techniques documenting the swimming and non-swimming behaviours of aggregated grey nurse sharks (*Carcharias taurus*) in the absence and presence of tourist scuba divers’, *AMSA’s 51st annual conference: investigating our marine nation*, Canberra, ACT, 6-10 July 2014.