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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.

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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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Lusseau, & Hammond, 2006). Short-term behavioural alterations in focal species can negatively affect the time and energy available for resting (e.g. Christiansen, Lusseau, Stensland, & Berggren, 2010; Steckenreuter, Möller, & Harcourt, 2012), feeding (e.g. Steckenreuter et al., 2012; Stockin et al., 2008) and reproduction (Reynolds & Braithwaite, 2001) and may lead to displacement (Bejder, Samuels, Whitehead, Gales, Mann, et al., 2006; 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, Banks, Birtles, Valentine, & Cuthill, 1997; Scarpaci, Nugegoda, & Corkeron, 2003), charging visitor fees (e.g. Newsome, Lewis, & Moncrieff, 2004), the establishment of protected areas (e.g. King & Heinen, 2004), self-regulatory codes of conduct (e.g. Allen, Smith, Waples, & Harcourt, 2007; Davis et al., 1997), the enforcement of legislative requirements (Scarpaci et al., 2003) and the education of tour operators and tourists (King & Heinen, 2004; Scarpaci et al., 2003).

Previous studies (e.g. Duprey, Weir, & Würsig, 2008; Scarpaci et al., 2003; Sorice, Flamm, & McDonald, 2007; Wiley, Moller, Pace, & Carlson, 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, Scarr, & Scarpaci, 2010; Stafford-Bell & Scarpaci, 2014; Strong & Morris, 2010) 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 m total length (TL, Last & Stevens, 2009), are slow to reach sexual maturity (50% sexual maturity: males = 2.10 metres TL at 6–7 years, females = 2.59 m TL at 10–12 years, Goldman, Branstetter, & Musick, 2006; Otway & Ellis, 2011; Otway, Storrie, Louden, & Gilligan, 2009) and have low fecundity with two pups born biennially (0.95–1.20 m TL) after intrauterine cannibalistic and oophagous phases (Gilmore, Dodrill, & Linley, 1983). No parental care is invested post parturition. The species requires decades to recover from declines in abundance (Mollet & Cailliet, 2002; Otway, Bradshaw, & Harcourt, 2004; Smith, Au, & Show, 1998) 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, Kyne, Fowler, Musick, & Bennett, 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 Queensland (QLD) and New South Wales (NSW), has been subjected to numerous anthropogenic disturbances over the past century (Cropp, 1964; Otway et al., 2004; Pepperell, 1992; Reid, Robbins, & Peddemors, 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, Fig. 1). They spend the majority of their time (i.e. ≈74%) in waters less than 40 m but have been recorded as deep as 232 m (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, Burke, Morrison, & Parker, 2003; Otway & Ellis, 2011; Otway et al., 2004, 2009). Parturition likely occurs in late winter and early spring at various aggregation sites along the central and southern NSW coast (Otway & Ellis, 2011; Otway et al., 2003). Grey nurse shark pups off eastern Australia probably display similar patterns of

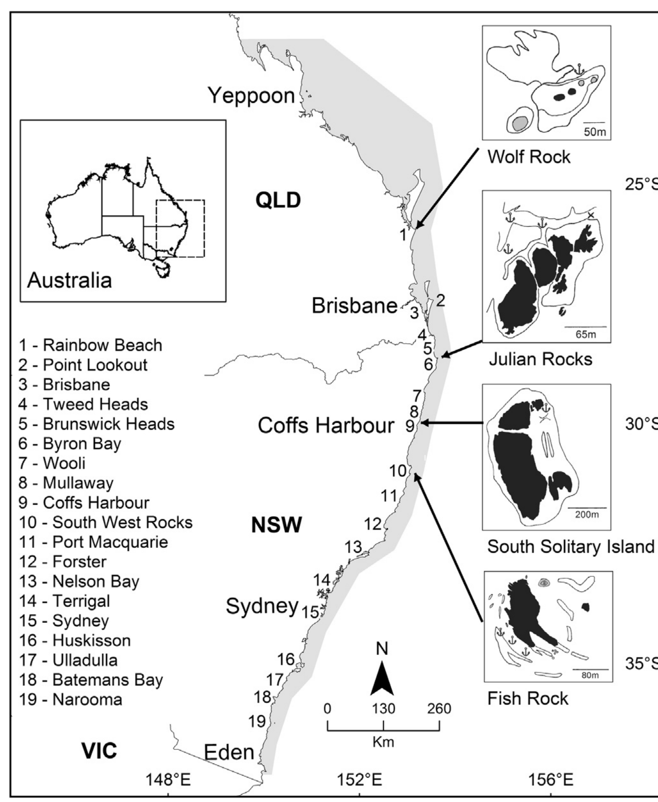

Fig. 1. Map showing the geographic range (grey shading) of grey nurse sharks (*Carcharias taurus*) in coastal waters off Queensland (QLD) and New South Wales (NSW), the coastal towns/cities (numbered) with grey nurse shark scuba diving marine wildlife tourism operators and the location of Wolf Rock, 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.

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, Smale, & Booth, 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 km further into southern NSW across spring and summer with visits to a range of aggregation sites (Otway & Ellis, 2011; Otway & Parker, 2000; Otway et al., 2009). 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 km 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 (Bansemer & Bennett, 2009; Otway & Parker, 2000). 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 km 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 m radius of the main structure (Bansemer & Bennett, 2009; Bruce, Stevens, & Bradford, 2005; Otway & Ellis, 2011; Otway et al., 2009). 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. Brunnschweiler, 2010; Clua, Buray, Legendre, Mourier, & Planes, 2011; Dicken & Hosking, 2009; Vianna, Meekan, Pannell, Marsh, & Meewig, 2012). The large size, generally slow movements, propensity to aggregate and relatively placid nature (Bruce et al., 2005; Otway & Ellis, 2011; Otway et al., 2003) 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 (Fig. 1) and is summarised in more detail in Table 1. Although the sites are accessible by boat, regional weather and oceanographic conditions limit visitation to approximately 40% 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 m rigid-hulled inflatable boat up to an 18 m purpose-built dive vessel which necessitate different launching or harbouring and boarding requirements, although most use vessels $\leq$11 m (90%, Table 1). Trips generally include two dives separated by an appropriate surface interval (i.e. a 'double dive' at a cost of $120–240 AUD including hire of all equipment) and divers are required to observe strict scuba diving procedures to ensure safe, no-decompression diving which forces a degree of consistency in diver behaviour. Whilst preliminary work (Hassall & Associates Pty Ltd & Gillespie Economics, 2004) suggests that this MWT industry contributes considerably to local, regional and state economies, there is a dearth of data to quantify and distinguish to what extent as well as limited knowledge of the duration of personal touristic visits and the spatial and temporal variation in MWT site visitation rates. Annual revenue ($\approx$\$9 million AUD) was gauged solely from the income of MWT operators that dived at 11 NSW critical habitat sites (Hassall & Associates Pty Ltd & Gillespie Economics, 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 (Environment Australia, 2002). As such, federal (*Environmental Protection and Biodiversity Conservation Act 1999*, Department of Sustainability, Environment, Water, Population and Communities, 2012) and state legislation (QLD *Marine Parks Act 2004* and NSW *Fisheries Management Act 1994*, New South Wales Government, 2010; Queensland Government, 2010a, 2010b) 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, Thapa, & Ko, 2009; Smith et al., 2010), the locality of the target species (Smith et al., 2010; Stafford-Bell & Scarpaci, 2014), 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, Scarr, & Scarpaci, 2009), there have been no published studies investigating the demographics of the divers which are likely to be important in the design and

Table 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 Fig. 1.

Reference number in Fig. 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 (min)	Boat length/s (m)	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
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
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 m swim	No	15	6–11	4	8–18	2–4
		Little Seal Rock	S, A, W, Sp.	Shore-to-boat 50 m 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
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

implementation of management strategies. Finally, only a few studies have investigated the impacts and sustainability of this industry (Barker, Peddemors, & Williamson, 2011; Hayward, 2003; Otway et al., 2009; Smith et al., 2010) 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.

2. Materials and methods

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 km of the east coast of Australia (Fig. 1) and are influenced by onshore winds, a prevailing 1–2 m south-easterly swell and the 1–4 knot East Australian Current (EAC, Tranter, Carpenter, & Leech, 1986). Mean sea surface temperatures range from ≈28.0°Celcius in the austral summer to ≈19.0°Celcius 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 m seas on a 3–6 m swell) and torrential rainfall causing flooding river plumes that can reduce visibility to <1 m 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 km offshore of Double Island Point near Rainbow Beach (QLD) within a marine national park zone of the Great Sandy Marine Park (Queensland Government, 2006). The rock comprises five pinnacles (four large, one small) that are aligned in a north-easterly direction in ≈35 m 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 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.

Julian Rocks is situated 4 km offshore of Byron Bay (NSW) and comprises four aligned rocky outcrops in 20 m 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 (New South Wales Government, n.d.). Julian Rocks supports a diverse tropical and temperate fish community throughout the year (Harriott, Davis, & Banks, 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 & Ellis, 2011; Otway et al., 2009). 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 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' (Fig. 1) where the sharks frequently aggregate (Otway & Parker, 2000; Otway et al., 2003, 2009).

South Solitary Island lies 9 km northeast of Coffs Harbour (NSW) in 10–35 m 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, Jordan, & Smith, 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', Fig. 1) off the north-eastern corner of the island (Otway & Ellis, 2011; Otway et al., 2003, 2009), which is now partly within a sanctuary zone of the Solitary Islands Marine Park (New South Wales Marine Parks Authority, 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 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 km offshore of Smoky Cape (NSW) in 20–40 m of water and was declared as a grey nurse shark critical habitat in December 2002 (Talbot, Molloy, Chapman, & Riches, 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 (Breen, Avery, & Otway, 2004; Otway et al., 2003). 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 & Ellis, 2011; Otway et al., 2009) 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 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, Louden, Storrie, & Gilligan, 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 (Last & Stevens, 2009; West, 1996, 2011), MWT operators prefer divers to enter the water together.

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.

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-min scan samples (Altmann, 1974). Observations were made alongside or behind the divers (Cubero-Pardo, Herrón, & González-Pérez, 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 m 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.

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 2). 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-min scans utilised to document grey nurse shark life-history stages. The swimming behaviour exhibited by the group of grey nurse sharks (i.e. ≥50% 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-min 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.

Table 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

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, 2010b), 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 3) was continuously assessed (Altmann, 1974) using the methods of Smith et al. (2010) to ensure any instances of non-compliant behaviour were recorded. The acceptable level of compliance was set at 80% or greater in accordance with previous studies (Allen et al., 2007; Howes, Scarpaci, & Parsons, 2012; Quiros, 2007; Smith et al., 2010). 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.

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% 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

Table 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, 2010b).

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

movements of sharks at aggregation sites (Otway & Ellis, 2011; Otway et al., 2009) 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; Farebrother, 1980; Savin & White, 1977).

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%) 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.

3. Results

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 4, chi-square tests: $P > 0.05$). The majority of scuba divers at all sites were Australian, English-speaking males (Table 4). Ages of divers varied among sites, but 85% 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 4, chi-square tests: $P > 0.05$). Approximately 61% 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% (on average) were overseas tourists. Furthermore, 25% 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%) than those for the code of conduct. Almost 75% 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 4, chi-square test: $P < 0.001$). At Wolf Rock, 80% of the scuba divers had professional qualifications, whereas the majority of divers at the other sites (i.e. 83% on average) had recreational qualifications (Table 4). The divers possessing professional qualifications were 'Divemasters' (18%) or 'Instructors' (9%), whereas those with recreational qualifications comprised 'Open Water divers' (39%), 'Advanced Open Water divers' (28%) and a few 'Rescue divers' (6%). Finally, the proportions

Table 4
Percentages of divers and chi-square test (χ^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	73	89	88	82			
Female	20	27	12	13	18			
Age group						20.18	12	>0.10
<18	0	0	12	25	9			
18–25	0	8	4	13	6			
26–35	40	50	23	13	32			
36–45	30	23	19	6	19			
46–≥51	30	19	42	44	33			
Nationality						7.01	3	>0.10
Australian	70	65	89	94	80			
Other	30	35	12	6	21			
Language						5.46	3	>0.25
English	70	89	89	100	89			
Other	30	12	12	0	12			
Scuba certification						24.47	3	<0.001
Professional	80	39	8	6	27			
Recreational	20	62	92	94	73			
Dives completed						18.63	15	<0.005
≤10–50	10	46	65	69	53			
51–500	50	39	35	31	37			
501–>1000	40	15	0	0	10			
Diving with GNS						0.97	3	>0.90
Yes	70	73	81	69	74			
No	30	27	19	31	26			
Legislation						0.59	3	>0.90
Yes	70	58	65	63	63			
No	30	42	35	38	37			
Code of conduct						0.44	3	>0.95
Yes	60	54	62	63	59			
No	40	46	39	38	41			

of divers with differing numbers of scuba dives completed prior to this study were also significantly different among sites (Table 4, chi-square test: $P < 0.005$).

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 5) which represented 41% of the days allocated for sampling across all sites. 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 (91%) dives (Table 5). The mean duration of research dives (Table 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 5), ensuring equivalent sampling effort across all four sites.

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 m TL and from eight to fourteen sharks at ≥2.94 m 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% (mean ± SD, range = 4.67 ± 3.72, 0-18 sharks per scan) of the grey nurse sharks were sexually-mature, gestating females (Fig. 2). In contrast, at Julian Rocks the grey nurse shark population was dominated by sexually-mature, migrating males (89%, mean ± SD, range = 1.96 ± 1.27, 0–6 sharks per scan, Fig. 2), a few sexually-mature females on their southerly migration for parturition (2%, mean ± SD, range = 0.03 ± 0.17, 0–1 sharks per scan) and fewer juvenile males (1%, 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%, mean ± SD, range = 2.38 ± 2.71, 0–12 sharks per scan, Fig. 2), but also included some sexually-mature, resting-phase females (13%, mean ± SD, range = 0.42 ± 0.55, 0–2 sharks per scan) and juvenile males (11%, mean ± SD, range = 0.37 ± 0.76, 0–4 sharks per scan), and minimal juvenile females (1%, 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 (30%, mean ± SD, range = 0.99 ± 0.92, 0–4 sharks per scan) and females (41%, mean ± SD, range = 1.35 ± 1.19, 0–5 sharks per scan) and much lower frequencies of sexually-mature, resting-phase females (8%, mean ± SD, range = 0.26 ± 0.55, 0–2 sharks per scan) and sexually-mature, post-copulatory males (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%) grey nurse sharks could not be identified.

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 (Fig. 3a), there were differences among sites that were highlighted by the site specific analyses. 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% among means to be detected with power of 0.80 (Type I and II error rates of $\alpha = 0.05$ and $\beta = 0.20$, respectively). This result was confirmed by the *post hoc* power analyses. At Wolf Rock, the gestating grey nurse sharks exhibited all three swimming behaviours (Fig. 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

Table 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 (min)	Number of divers per scan	Number of grey nurse sharks per scan	Time to the first diver–shark interaction (min)	Diver–shark interaction time (min)
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

significantly (SNK test: $P < 0.05$). At Julian Rocks, all three swimming behaviours were exhibited by the mainly sexually-mature, migrating male sharks (Fig. 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 (Fig. 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 (Fig. 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 (Fig. 3a) was milling (66%) and this was significantly greater than the frequencies of hovering (25%) and active swimming (9%) 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 to 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 5). Contemporaneously, the numbers of grey nurse sharks observed ranged from 1 to 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 5). On entering the water, the mean period of time that elapsed prior to the first diver–shark interaction (Table 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 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 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 min and represented one third of the total dive duration (Table 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 (Fig. 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 m), milling (4 ± 2, 3–13 m) or active swimming (5 ± 4, 3–13 m). 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 (Fig. 3c). Furthermore, when pooled across sites, the mean number of divers present during diver–shark interactions did not differ significantly among swimming behaviours (ANOVA: $F_{2,\ 18} = 1.20$, $P = 0.33$).

3.5. Compliance with legislation and/or code of conduct

Divers observed interacting with grey nurse sharks demonstrated 100% 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.

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 (Bansemer & Bennett, 2009; Otway & Ellis, 2011; Otway et al., 2003, 2009) 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% 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

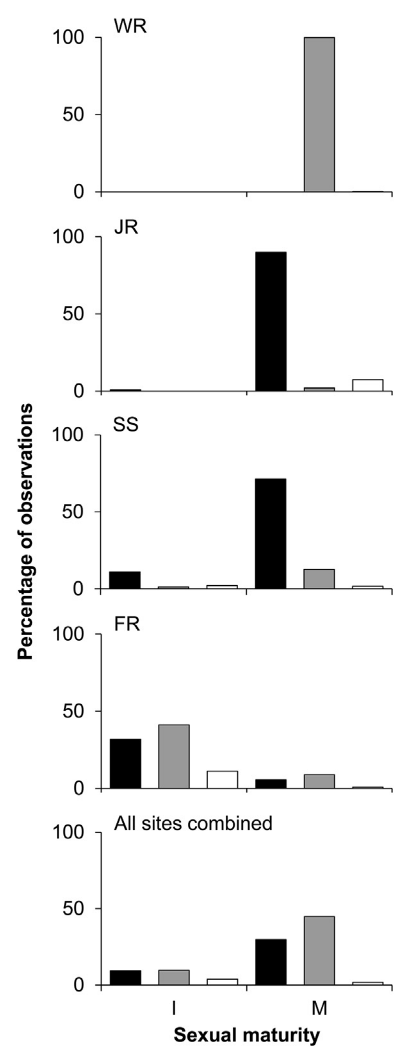

Fig. 2. Percentages of sexually-immature (I) and sexually-mature (M) male (■) and female (■) grey nurse sharks (*Carcharias taurus*) and those of undetermined gender (□) observed at Wolf Rock (WR), Julian Rocks (JR), South Solitary Island (SS) and Fish Rock (FR) from March 2011 to February 2012. Note: two sharks of unknown gender are not shown as their maturity could not be determined.

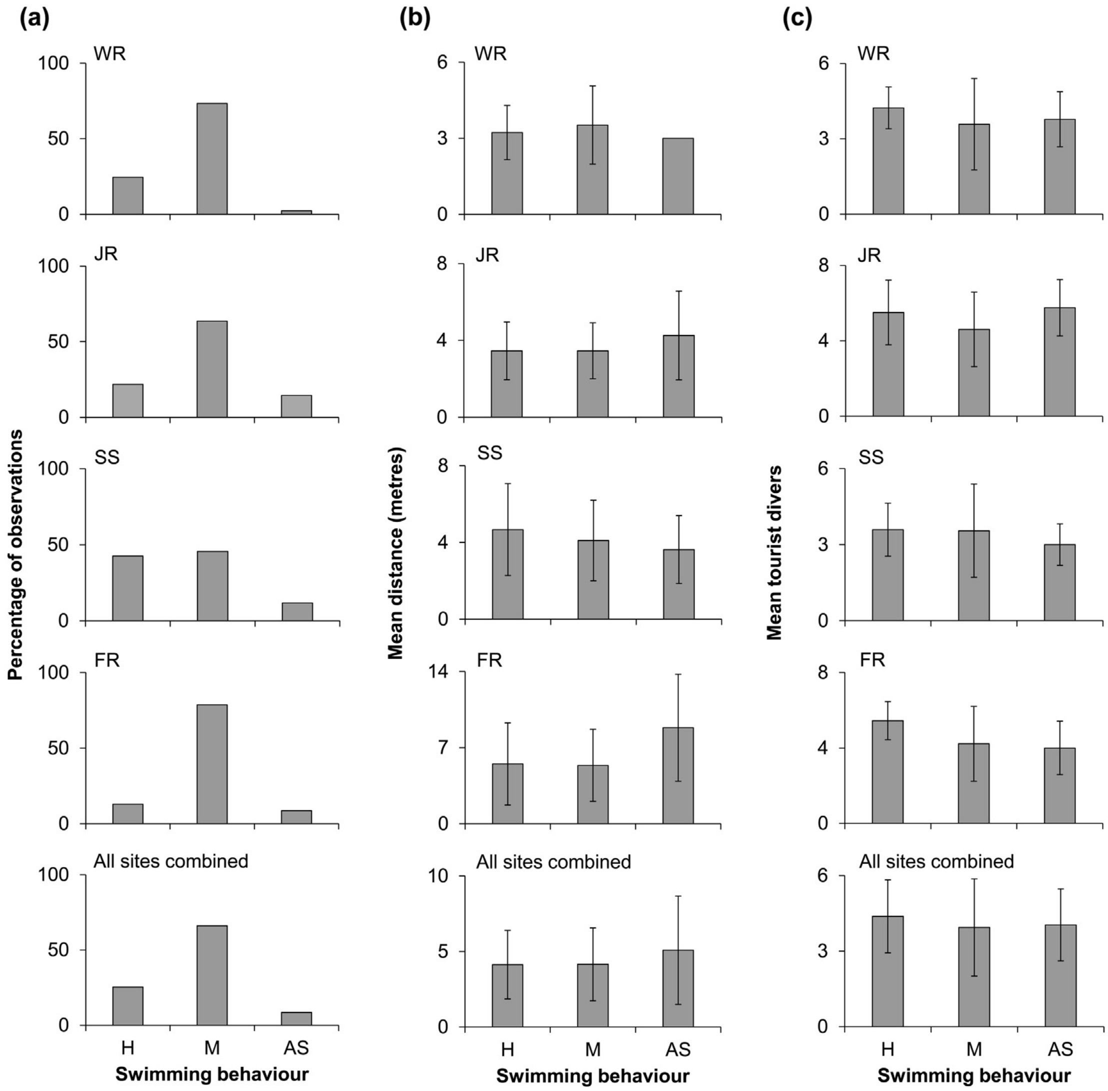

Fig. 3. Observations of swimming behaviour of grey nurse sharks (*Carcharias taurus*) with (a) the frequency of occurrence of hovering (H), milling (M) and active swimming (AS), (b) the mean (±SD) distance between divers and sharks for each swimming behaviour, and (c) the mean (±SD) number of divers 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).

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% of time), followed by hovering (25% of time) and active swimming (9% 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% 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 m 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 (Filla & Monteiro-Filho, 2009; Johnson & Nelson, 1973; Quiros, 2005). 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 (Hassall & Associates Pty Ltd & Gillespie Economics, 2004).

The study revealed absolute compliance (i.e. 100%) 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. Barker et al., 2011; Harriott et al., 1997; Otway & Ellis, 2011; Smith et al., 2010). 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. Howes et al., 2012; Scarpaci et al., 2003; Scarpaci, Nugegoda, & Corkeron, 2004; Wiley et al., 2008) 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 (Vianna et al., 2012; Wilson & Tisdell, 2003) 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% 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. ≥69% 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 (Catlin & Jones, 2010; Curtin, Richards, & Westcott, 2009; Parsons et al., 2003) 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 1), and it presented the most difficult diving conditions (pers. obs.). 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, Acevedo, & Boren, 2011) and turtles (e.g. Waayers, Newsome, & Lee, 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, 2014).

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 (12% 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 (Mangott, Birtles, & Marsh, 2011; Scarpaci et al., 2004; Strong & Morris, 2010; Wiley et al., 2008). 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, 2014). 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, 2014). The site fidelity and low levels of activity exhibited by grey nurse sharks at aggregation sites (i.e. 86–98% of time per site) may have further reduced the motivation for tourists to actively pursue the animals and breach management guidelines. Conversely, cetacean snorkelling (Allen et al., 2007; Scarpaci et al., 2003, 2004) and watching (Wiley et al., 2008), and whale shark snorkelling (e.g. Catlin, Jones, & Jones, 2012; Quiros, 2007) 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, Harcourt, & Otway, 2006), leopard sharks (Dudgeon, Lanyon, & Semmens, 2013), stingrays, turtles, moray eels, pelagic fish, octopus, cuttlefish, nudibranchs and lobsters (Breen et al., 2004; Harriott et al., 1997; Malcolm et al., 2010; pers. obs.). These animals present diving tourists with secondary wildlife interactions and alternative subjects for those divers with prior grey nurse shark diving experience ($\geq$69% 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, Espejel, & Fischer, 2003; Howes et al., 2012; Scarpaci et al., 2003, 2004; Wiley et al., 2008).

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% 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 25% of divers were $\leq$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 (pers. obs.). The management guidelines were also displayed at each tourism operation's dive centre and on their websites (pers. obs.). 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, Valentine, et al., 2002; Valentine, Birtles, Curnock, Arnold, & Dunstan, 2004). The value of consultation with MWT stakeholders during the preparation of management strategies has been repeatedly identified (Birtles, Arnold, & Dunstan, 2002; Curtin, 2010; Higham et al., 2009), and is supported by high levels of tour operator compliance where it occurred (Allen et al., 2007; Davis et al., 1997) and low compliance where tour operators (Beasley, Bejder, & Marsh, 2010) and tourists (Morris, Jacobson, & Flamm, 2007) were not involved in management planning. Limited resources often impedes enforcement of management guidelines (Acevedo-Gutierrez et al., 2011; Howes et al., 2012; Kessler & Harcourt, 2010; Strong & Morris, 2010), particularly those for MWT industries located in regional areas (Birtles,Arnold, et al., 2002; Orams, 1996) 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.

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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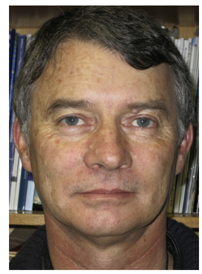

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