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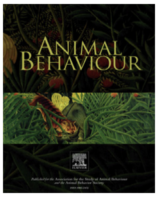

Integrating social network analysis and fine-scale positioning to characterize the associations of a benthic shark

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Many shark species form groups; yet the drivers of this behaviour are not well understood. Aggregations have been presumed to be a function of resource availability or phenology. However, recent studies have suggested that some sharks display preferences in their associations with conspecifics and that complex social networks may underpin their movement patterns, demographic distribution and fitness. This study used a network approach to investigate patterns of sociality of a benthic predator, the spotted wobbegong shark, *Orectolobus maculatus* (Family Orectolobidae), in a small marine reserve. Spatial data obtained from fine-scale passive acoustic telemetry were used to infer association preferences of 15 tagged sharks over a 15-month period. Thirty-five associating dyads emerged, with permutation tests indicating that these were nonrandomly formed. Many dyads were temporally stable, with some persisting even after sharks returned to the reserve from their seasonal migration. A complete but sparse network was observed and although association patterns were evident at the dyadic level, indication of stable communities or network structure was limited. The population was not found to be gregarious and exclusive pairs were not observed, with 14 sharks associating with more than one individual. Assortative mixing (by sex, size and familiarity) was not present and range overlap did not strongly correlate with association indices. This suggests that these relationships are not a random result of nonsocial grouping behaviours but can be explained, at least in part, by genuine social affiliation. As such, anthropogenic influences on the population may have more complex impacts than previously thought.

Sociality exists on a spectrum, from solitary species that meet only to breed to obligate social species exhibiting complex, eusocial behaviours (Alexander, 1974). Group living can improve foraging success (Clark & Dukas, 1994), enhance antipredator defence (Caro, 2005), provide access to information (Conradt & Roper, 2003; Lusseau, 2003) and confer energetic advantages (Giraldeau & Caraco, 2000). Sociality can also induce fitness costs, with increasing group size leading to competition for resources, exposure to pathogens (Côté & Poulin, 1995), and increased conspicuousness to predators and prey (Krause & Ruxton, 2002, but see Ioannou, Bartumeus, Krause, & Ruxton, 2011). The evolution of sociality, therefore, reflects an ongoing sequence of trade-offs that balance the benefits and risks of associating with others, with the optimal group size being mediated by ecological and biological constraints (Krause & Ruxton, 2002).

While grouping behaviour is often observed in elasmobranch fishes, such aggregations were until recently thought to primarily consist of individuals either attracted to a common resource, such as food, microhabitat features or access to mates, or collectively avoiding predation or conspecific aggression (reviewed in Jacoby, Croft, & Sims, 2012). It is now thought that active partner preferences may result in the formation of nonrandom groups, with sharks displaying persistent associations and extensive social networks (reviewed in Wilson, Croft, & Krause, 2014). The capacity of sharks to be social has been suggested by the presence of complex behaviours such as dynamic dominance hierarchies (Allee & Dickinson, 1954; Myrberg Jr & Gruber, 1974), social learning (Guttridge, Myrberg, Porcher, Sims, & Krause, 2009; Guttridge et al., 2013) and personalities (Jacoby, Fear, Sims, & Croft, 2014), and is supported by a brain mass to body mass ratio comparable to that found in mammals (Northcutt, 1977; Yopak et al., 2010). Together,

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these studies suggest that sociality may be an important component of shark behaviour.

Improving our understanding of the social behaviour of ecologically different shark species may help elucidate the drivers underpinning associations between individuals and the trade-offs influencing the establishment of social populations. Recent studies have investigated the sociality of benthopelagic species, such as lemon sharks, *Negaprion brevirostris* (Guttridge et al., 2011; Guttridge, Gruber, et al., 2009; Wilson et al., 2015), reef-associated species, including blacktip reef sharks, *Carcharhinus melanopterus* (Mourier, Vercelloni, & Planes, 2012), as well as that of small benthic mesopredators (e.g. small-spotted catshark, *Scyliorhinus canicula*, Jacoby, Busawon, & Sims, 2010; Jacoby, Sims, & Croft, 2012). However, comparatively little is known about the social behaviour of benthic predators. The spotted wobbegong, *Orectolobus maculatus*, is a medium-size demersal shark endemic to Australian waters. They are benthic ambush predators that can reside within relatively small areas for prolonged periods of time (Huveneers, Harcourt, & Otway, 2006; Lee, Huveneers, Peddemors, Boomer, & Harcourt, 2015). A previous study showed that wobbegongs are frequently observed in close proximity and can form small groups (median distance from each other was 5.1 m; see Appendix 1 based on data from Lee, Huveneers, Gimenez, Peddemors, & Harcourt, 2014). Whether these aggregations involve social preferences or are a byproduct of phenological synchrony, ranging preferences or resource availability is unknown.

The study of sociality is inherently complex, involving relational data and many sources of uncertainty. However, advances in analytical techniques, coupled with developments in the ability to track animal movements remotely (Hussey et al., 2015), have resulted in increasing flexibility and robustness in the exploration of social behaviour. Social network analysis incorporates the concepts that individuals differ in their experience of, and contribution to, the wider population and that indirect connections are important elements of social dynamics (Krause, Croft, & James, 2007). A network approach can capture social complexity at the individual, dyadic, community and population levels by using a powerful composite of tailored quantitative tools (Croft, James, & Krause, 2008; Wey, Blumstein, Shen, & Jordán, 2008). Recently, these have been applied in elasmobranch social studies (reviewed in Jacoby, Croft, et al., 2012; Wilson et al., 2014) and more widely to movement and co-occurrence networks in fish (Finn et al., 2014; Lédée, Heupel, Tobin, Knip, & Simpfendorfer, 2015; Stehfest et al., 2013). Such studies require animals to be uniquely identified, and telemetry is one method in which spatial data can be obtained from specific individuals for this purpose. The combination of remotely sensed telemetry with network analysis presents great potential for investigating the behaviour of species that are difficult to observe directly. Although acoustic telemetry has been used successfully to monitor shark behaviour (Klimley et al., 2001; Sims et al., 2006), such an integrated approach has had limited application in the study of shark sociality (but see Guttridge, Gruber, Krause, & Sims, 2010; Jacoby, Brooks, Croft, & Sims, 2012).

In this study, we aimed to characterize the patterns of association between free-ranging wobbegongs using fine-scale positioning derived from acoustic telemetry. Our approach is based on the conceptual framework developed by Hinde (1976), in which dyadic association patterns can be abstracted to provide a broad picture of social organization. Specifically, we investigated whether assortative mixing and incidental range overlap could explain the association patterns of a spotted wobbegong population within a marine reserve. We aimed to (1) determine whether association patterns can be identified between individuals, (2) assess whether these patterns indicate active social preferences or can be explained by nonsocial behaviours, (3) test whether these associations are temporally persistent, and (4) characterize any emergent social organization.

METHODS

Study Area

This study was conducted in Cabbage Tree Bay Aquatic Reserve (CTBAR, 33°47′57″S, 151°17′44″E), located in Sydney, Australia. CTBAR is a small (about 0.2 km^2) no-take marine reserve that was declared a protected area in 2002 in recognition of its high species diversity. The reserve comprises a heterogeneous mosaic of habitats, typical of subtidal inshore rocky reefs of temperate, southeastern Australia (Underwood, Kingsford, & Andrew, 1991). There are two distinct reefs separated by 120 m of sand. The spotted wobbegong population is estimated at up to 150 sharks during the summer months (Lee et al., 2014).

Tagging and Vemco Positioning System (VPS)

Twenty-three wild ($N = 11$) and captive-bred ($N = 12$) wobbegongs were internally tagged with acoustic transmitters (V13-1L-69 KHz; power output: 147 dB; nominal interval: 150–250 s; estimated tag life: 1623 days, Vemco Ltd, Nova Scotia, Canada; Appendix 2). While scuba diving, we captured wild sharks using a hand-held net (diameter: 1 m; mesh size: 3 cm) and brought them onto the research vessel where they were placed in a 200-litre tub containing an oxygen-enriched solution of 30 ppm eugenol (AQUI-S, AQUI-S New Zealand Ltd, Wellington, New Zealand) for anaesthetic induction. Once the sharks were fully anaesthetized, a coded V13-1L acoustic transmitter was inserted into the coelomic cavity by making a small incision (2–3 cm) anterior to the anus. The incision was then sutured closed. The sharks were also fitted with an external identification tag, containing a unique number, which was placed in the musculature below the first dorsal fin. Wild sharks were released at the capture location. Captive-bred sharks were housed in indoor aquaria (of 1000 to 2.2 million litres capacity depending on their size) at Manly Oceanworld in Sydney, and were tagged using the same techniques prior to release off the CTBAR beach (about 200 m from the wild shark release location; Lee et al., 2015). The sex and total length (TL) were recorded for all sharks and those with a TL of less than 115 cm were classed as juveniles (Huveneers, Walker, Otway, & Harcourt, 2007). Three of the wild sharks were tagged 7 days before the start of this study and the remaining wild sharks were tagged 12–15 months prior to this. The captive-bred sharks were released into the area in September 2008 ($N = 3$), February 2009 ($N = 2$), January 2010 ($N = 5$) and May 2010 ($N = 2$).

Shark locations were recorded from October 2009 to December 2010 using the Vemco Positioning System (VPS), a passive acoustic telemetry system that uses hyperbolic positioning to calculate near-continuous, fine-scale animal locations (Espinoza, Farrugia, Webber, Smith, & Lowe, 2011). It comprised eight fixed acoustic receivers (VR2W-69 KHz; Vemco Ltd, Nova Scotia, Canada) positioned in an overlapping array (Fig. 1). Receivers were deployed at 6–12 m depths, on 1.35 m long steel poles set in concrete-filled tyres in areas with sandy substrate. Local testing was conducted to determine the effective detection range of the receivers and estimated at a minimum of 200 m in all oceanic conditions (Lee et al., 2014). Eight synchronization tags (V16-4L; power output: 152 dB; nominal interval: 300–900 s; Vemco Ltd, Nova Scotia, Canada) were deployed to correct for clock drift between receivers and to assess the efficacy of the positioning algorithm. Downloaded data were postprocessed by Vemco using proprietary software. The data returned included the latitude, longitude and projected