CHAPTER 18: Network analysis and theory in shark ecology - methods and applications

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18.1   Introduction

In recent decades network analyses have become ubiquitous in ecology, facilitating our understanding of linkages between paired entities, whether it be genes, proteins, individuals, species or habitats (Proulx *et al.* 2005; Krause *et al.* 2007; Blüthgen *et al.* 2008; Croft *et al.* 2008; Wey *et al.* 2008). Network theory (also known as 'graph theory') originates from the mathematical and social sciences but has developed concurrently across many disciplines, including computational science, physics, management, genetics and epidemiology (Newman 2010), to name but a few. Widespread uptake of these developments in behavioral ecology have ensured that network analyses, and in particular social network analyses (SNA) are now one of the go-to tool kits for researchers wishing to measure animal association and aggregation, species interactions or animal-mediated habitat connectivity (James *et al.* 2009; Krause *et al.* 2009a; Fletcher *et al.* 2011; Jacoby *et al.* 2012a; Farine and Whitehead 2015). Given the challenges that face researchers studying sharks (slow growth, low fecundity, wide-ranging and cryptic) and indeed behavior in any subsurface marine organism, it is perhaps not surprising that this exciting branch of ecology has only really found a home in shark biology in the last 10 years (Krause *et al.* 2015); before this, records of shark social behavior were rare and often anecdotal (Jacoby *et al.* 2012b).

Guided by the pioneering work on teleost fishes such as the three-spined stickleback *Gasterosteus aculeatus* and the guppy *Poecilia reticulata*, and also by the work on marine mammal societies (predominantly cetaceans), network methods now offer a robust framework to quantify and analyze components of shark behavior that until recently have proven extremely difficult (Krause and Ruxton 2002; Ward *et al.* 2002; Croft *et al.* 2008; Whitehead 2008). Do individual sharks have preferential social partners? Are shark groups assorted by phenotypic traits and if so, over what spatial and temporal scales? Are sharks capable of learning from social partners? Observational experiments on small groups of

captive or semi-wild individuals have driven our initial understanding of social networks in sharks (Guttridge *et al.* 2009; Jacoby *et al.* 2010), but see Krause *et al.* (2009b) and Mourier *et al.* (2012) for some of the first wild examples. Technological advances are now driving the progress of new analytical techniques that can handle very large data sets, such as those obtained from biotelemetry. Thus technology in combination with network approaches have recently helped to facilitate the scaling of some of these questions to wild sharks at the population level (Krause *et al.* 2013; Jacoby *et al.* 2016; Jacoby and Freeman 2016).

Although widely used and often easily implemented in bespoke programs or R packages, network analyses are highly nuanced, and need to be tailored specifically to a species or study system. In this chapter, we explore the two core principles of network application in shark ecology; 1) shark social networks, that is the how, why and with whom sharks associate and 2) shark spatial networks, understanding how the movements of individuals can link discrete locations as a movement network. These components are far from mutually exclusive, reflecting the fact that social processes are inextricably linked to the distribution of sharks in space. Network analyses offer a unique set of statistical tools that help us to understand how individual behavioral patterns can influence group and population-level processes, how overall network structure can select for behavior at the individual level and also how both direct and indirect connections within a population can matter greatly (Krause *et al.* 2009a; Croft *et al.* 2016).

18.1.1 *What is a network? Basics of network theory*

A network (or graph) consists of a set of nodes and edges. As a visual illustration the simple network depicted in Fig. 18.1 has 6 nodes (i.e. six individual sharks for social networks and six locations for spatial networks) and 10 edges (i.e. 10 associating pairs for social networks and 10 movement paths between locations for spatial networks), with the interactions

between all possible pairs represented with an accompanying adjacency matrix, A [a quantitative version of the network]. These interactions can be represented in various ways depending on which components of the shark's behavior is being measured. For example, in Fig. 18.1A a binary directed network is presented in which an edge represents directed interactions such as '1 is dominant over 2' (social) or a movement from location 1 to location 2 (spatial). Fig. 18.1B shows a binary undirected network with a 1 or a 0 to indicate presence or absence of an interaction within the adjacency matrix. Fig. 18.1C shows the same network but with weighted edges proportional to the frequency or strength of association generally between 0 (no association) and 1 (constant association)]. Note that each edge appears twice in the adjacency matrix of an undirected network (i.e. symmetric) while upper and lower triangles of the matrix are different in directed networks.
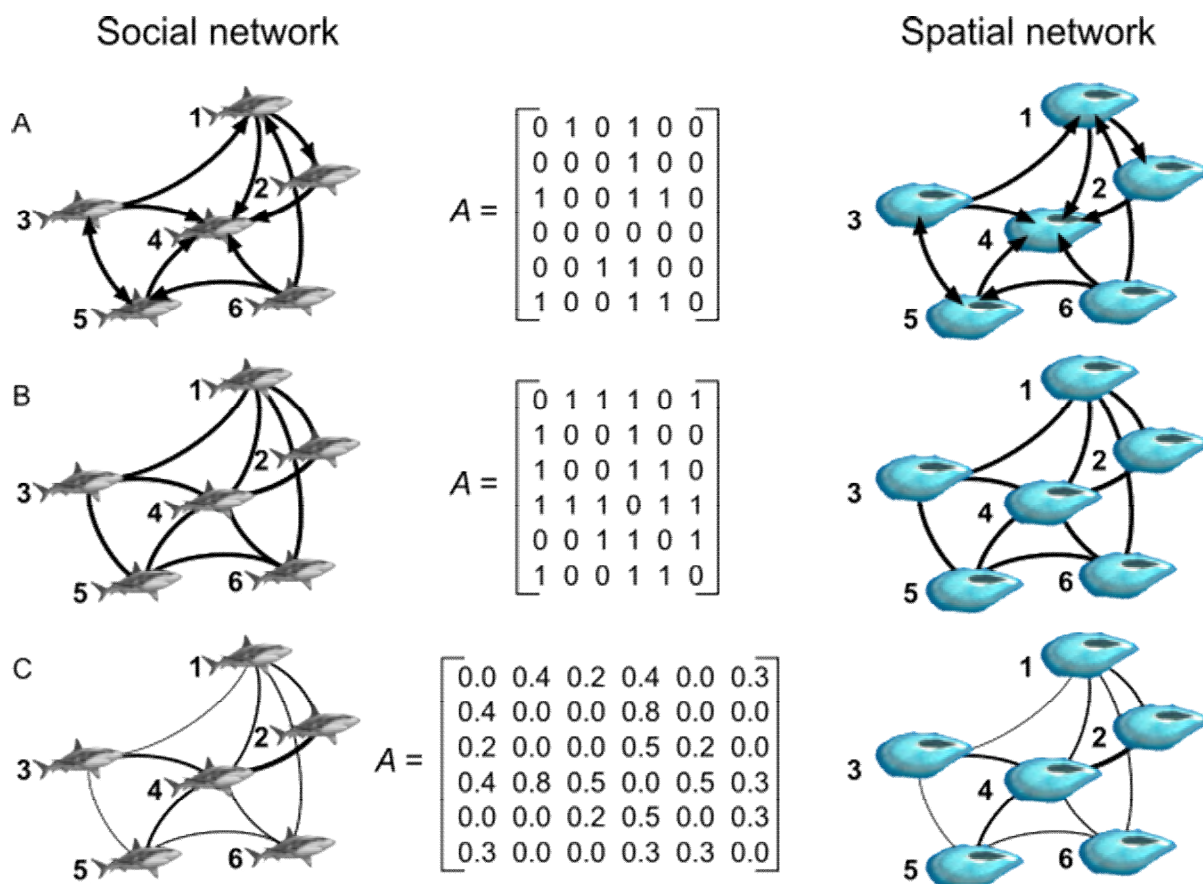
Figure 18.1: Examples of social (left) and spatial (right) networks. Different representations are displayed: (A) directed binary networks with an associated non-symmetrical adjacency matrix, (B) undirected binary networks with symmetrical adjacency matrix, and (C) weighted undirected networks with symmetrical adjacency matrix.

Network analyses offer a set of quantitative metrics or test statistics that allow us to characterize and analyze its structure (Table 18.1). These are used to measure structural properties at the node, group or network level. For example, one can assess the centrality of individual sharks to differentiate the social importance or influence of members of the population. For example, node degree or the strength also known as weighted degree can help identify the most gregarious individuals in the population and the potential influence they have over other members of the population (Croft *et al.* 2008). For binary directed networks (e.g. Fig. 18.1A), out-degree and in-degree, the number of edges leaving and arriving at a node, respectively, can be used to better determine the centrality of nodes (e.g. identify hubs in the network) and identify the directionality of interactions or movements. Such node-based metrics are useful for understanding the position and relative importance of sharks in their network (Jacoby *et al.* 2010; Mourier *et al.* 2017b). Such centrality metrics are also useful for movement networks to better identify the central locations most pertinent to conservation and management (Jacoby *et al.* 2012a; Jacoby and Freeman 2016). Beyond the individual-level metrics, many networks contain groups of nodes which are better connected among themselves than they are to the rest of the network and these clusters of well-connected nodes are usually referred as 'communities'. Community detection analyses, for example, were used to demonstrate that blacktip reef sharks *Carcharhinus melanopterus* in French Polynesia could form well-defined, mixed-sex communities within a small portion of the reef (Mourier *et al.* 2012).

It is important to note that social and spatial networks are often correlated as social networks are usually derived from spatial proximity (co-occurrences) and therefore are dependent on the movement of sharks between locations (Fig. 18.2; Jacoby and Freeman 2016; Jacoby *et al.* 2016). Although social networks are to an extent somewhat dependent on the spatial proximity of their members, non-random, preferential associations can emerge beyond those predicted through overlap of spatial ranges (Mourier *et al.* 2012). This interplay can be captured by bimodal networks that consist of links between two sets of nodes belonging to different classes such as individuals linked to locations (Fig. 19.2). As before, these bimodal networks can also be (1) unweighted or binary, only showing the presence or absence of the interactions, or (2) weighted if cells in a matrix represent, for instance, the number of visits by animal species to a monitoring receiver. Bimodal networks, made of similar set of nodes, are often analyzed after projecting them into unimodal ones. In unimodal social networks, for example, individuals are linked if they share locations.
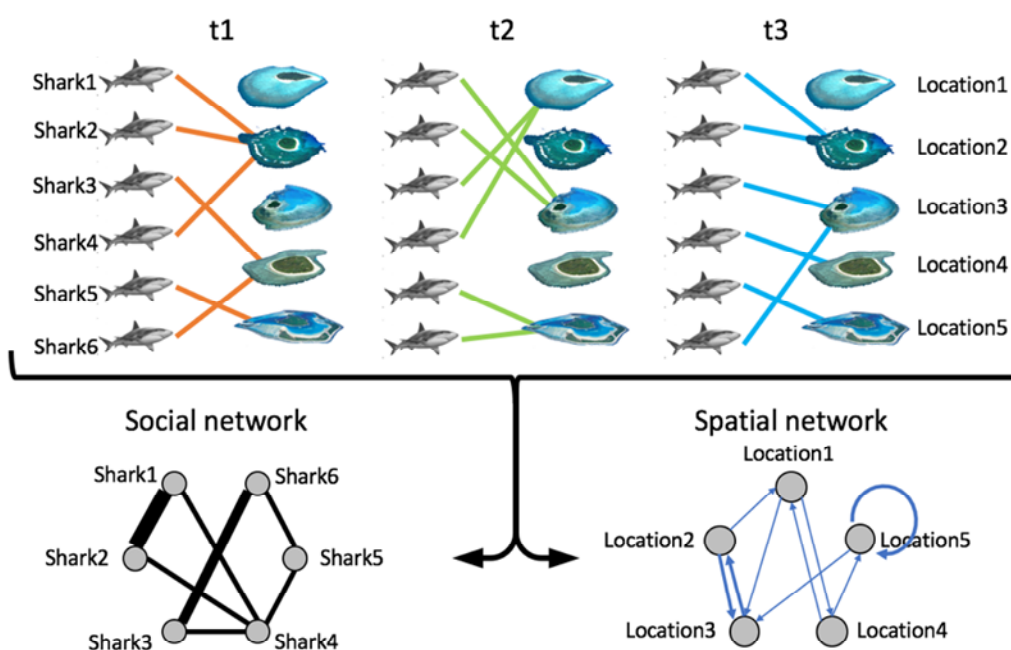

Figure 18.2: The emergence of social and spatial networks from shark movements. Sharks moving between reefs from time *t1* to time *t3* create a directed and aggregated movement

network made up of the frequency of movements of all individuals accumulated between reefs and through time. As sharks move in the seascape, their co-occurrences can be used to create a social network defined by the frequencies of associations between individuals in space and time.

Networks can have very different properties but can sometimes be defined by characteristic structural properties (Fig. 18.3). In regular networks, all nodes have the same degree. For example, a circular network is a type of regular network with all the nodes in the network with a degree of 2. It also displays additional characteristics such as no clustering coefficient and long average path length (Table 18.1) that indicates that most nodes must pass through many other nodes to reach anything other than their immediate network neighbors (Csárdi and Nepusz 2006). Random networks are characterized by a normal node degree distribution (Erdös and Rényi 1959) whereas small-world networks are characterized by a small diameter (longest path between any pair of nodes; Table 18.1) relative to the number of nodes, as well as a higher clustering coefficient and a smaller average path length compared with random network (Watts and Strogatz 1998). Other networks can have scale-free properties characterized by a power law node degree distribution (or right skewed distribution) where just a few nodes have a disproportionately high degree (many connections) but the majority have a low degree (few connections) (Barabási and Albert 1999).
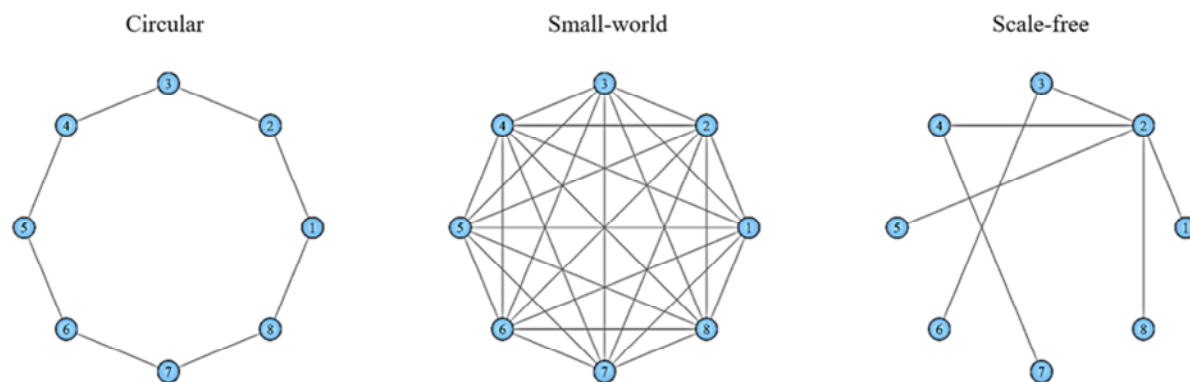
Figure 18.3: Examples of theoretical networks using a circle layout. Modified from (Lédée *et al.* in review).

18.1.2 Sampling a network: data collection methods

Building networks is not an easy process and requires collecting a large amount of relational data (interactions or movements) under a robust sampling design. Many methods and approaches are available to collect data to construct a network, all of which hinge on the ability to individually identify sharks.

Figure 18.4: Example of methods to identify individual sharks and track them in space and time to build networks. (A) Coloration patterns or notches on a blacktip reef shark's body

used for photo identification (see Chapter X); (B) fluorescent elastomer tag inserted under the skin of a catshark to follow individuals in a captive environment; (C) a small spaghetti tag inserted externally on the dorsal fin of a juvenile lemon shark with a unique code; and (D) a proximity logger attached to the dorsal fin of a juvenile lemon shark to construct a social network.
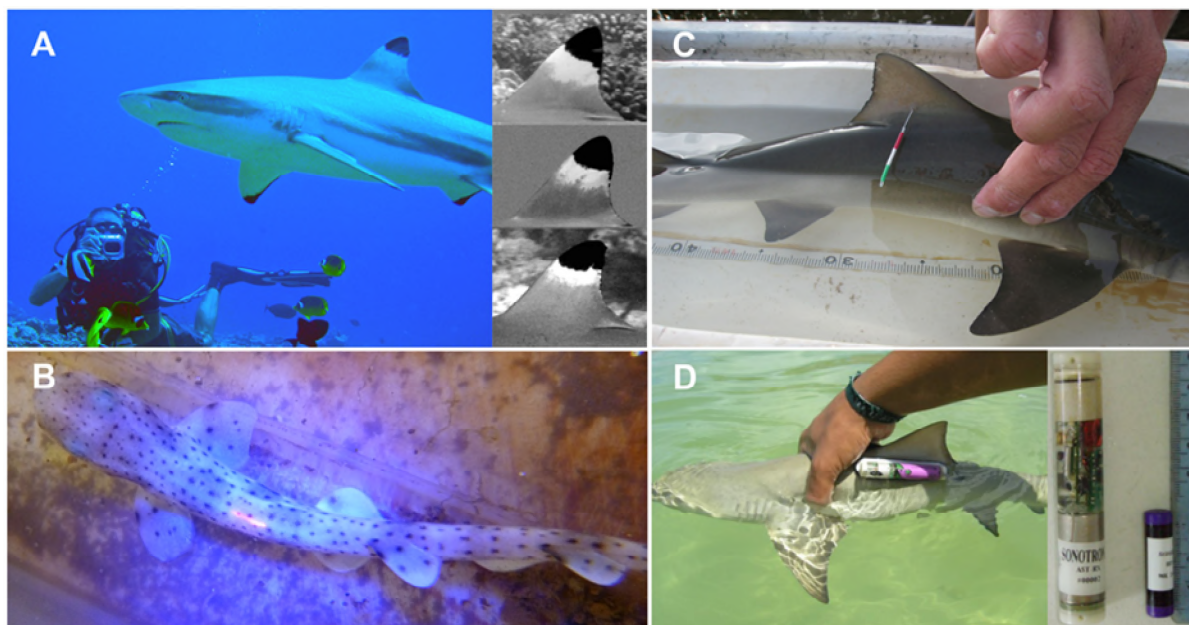
First, SNA requires that individuals are identified to track their associations, group membership and movements. Sharks can be identified using body coloration, patterns or fin notches which are specific to each individual. This technique of photo-identification is non-invasive and has been used for many elasmobranch species (Marshall and Pierce 2012) and to track shark and ray associations and movements, including blacktip reef sharks (Mourier *et al.* 2012), spotted eagle rays *Aetobatus narinari* (Krause *et al.* 2009c) and even the sicklefin lemon shark *Negaprion acutidens* which has a rather homogenous body coloration (Buray *et al.* 2009) (Fig. 18.4A). However, other studies on species in which individuals are hard to identify used externally attached visual color-coded tags (Fig. 18.4C; Jacoby *et al.* 2010; Guttridge *et al.* 2011) or fluorescent visible implant elastomer tags inserted subcutaneously on the dorsal surface (Fig. 18.4B; Jacoby *et al.* 2012c, 2014). Each species comes with its own challenges. Nevertheless, the difficulty in tracking elusive sharks in the wild and the necessity to record repeated interactions has pushed the development of autonomous tracking devices for inferring contact rates between individuals. For instance, the use of proximity loggers has been employed in several studies (Guttridge *et al.* 2010; Haulsee *et al.* 2016; Mourier *et al.* 2017a). Here, a shark-borne logger which records every tagged shark it encounters within a certain proximity (Fig. 18.4D). However, the difficulty is that the shark needs to be recaptured to retrieve the tag and data so this method is often confined to semi-captive or more resident shark species. Acoustic telemetry has been proposed to track

movements of tagged sharks and build a social network from their co-occurrence within an array of acoustic receivers (Jacoby *et al.* 2016; Jacoby and Freeman 2016), but this method requires careful interpretations of the data and robust analyses to tease apart preferred associations from random encounters under quite wide and often variable detection ranges (Mourier et al. 2017a). Acoustic telemetry has mainly been employed to build movement networks in sharks and analyze the properties of the movement patterns in a population (Jacoby *et al.* 2012a; Lédée *et al.* 2015; Papastamatiou *et al.* 2015; Stehfest *et al.* 2015; Espinoza *et al.* 2015; Jacoby and Freeman 2016; Lea *et al.* 2016). In this case, nodes of the networks are represented by receivers and edges are the frequency of movement between pairs of receivers.

There are both direct and indirect methods of sampling and constructing a social network. Observers can identify and follow a focal individual within the population and record its interactions with others forming an *ego-centric* social network. Separate ego-centric networks can also be combined into a global network to explore population structure. This approach was taken by Wilson *et al.* (2015) with juvenile lemon sharks *Negaprion brevirostris* in a mesocosm in the Bahamas. For each network session, an individual shark was randomly chosen as a focal individual and tracked continuously for a predefined amount of time, 100 sec and its associations with the nearest group member (if present) were recorded every 10 sec. Sharks were considered to be associating if they were within one body length of each other during the sampling interval. After an observation period was finished, another shark was chosen as the next focal individual until all individuals had been recorded so that they were all recorded for every session.

Alternatively, a social network can build on repeated samples of associations (co-occurrences) or interactions of dyads and can follow the "gambit of the group" approach where groups are defined as co-occurrences of individuals within a defined distance and

sampling period. Such approaches have been used to construct social networks in blacktip

reef sharks, where individual sharks were considered as part of the same group if observed

together during a dive (Mourier *et al.* 2012) or for constructing a network of white sharks

Carcharodon carcharias aggregating around a chumming boat (Findlay *et al.* 2016). How

associations are defined, the frequency, duration and interval between sampling periods and

the spatial area over which sampling takes place will be highly dependent on the

characteristics of species and systems and requires considerable thought, because all these

factors will directly influence the eventual structure of our network. For visual observations,

there are different association indices designed to account for different sampling

methodologies (i.e. the probability of encountering one individual might differ from another

at specific locations). As an example, the simple ratio index is used when observations are

rarely missed and the half-weight index when individuals are frequently missed in samples.

More details on how to choose an appropriate association index can be found in Farine and

Whitehead (2015).

An intermediate approach can also be adapted using automated recording of individual

movements which offers a means to reconstruct social structure in intractable species from

the frequency of paired spatial associations between tracked individuals. Using Bayesian

inference, specifically Gaussian mixture modelling (GMM) approaches, an automated

approach explores the inherent structure present in the visitation profile of tagged animals.

This machine learning approach is used to detect the most likely 'clustering events' in the

time-series of tag detections (at an acoustic receiver for example) and then uses these clusters

as a basis for constructing a social network. Crucially, these clusters can vary in size

temporally, reflecting the variation expected in dynamic animal societies with code offering

built-in permutation tests to remove random co-occurrences. Jacoby *et al.* (2016) explored

the utility of GMMs for retrieving inference on social network structure from telemetry data

of spatiotemporal co-occurrences of tagged grey reef sharks *Carcharhinus amblyrhynchos*, modifying the available methodologies to extract additional behavioral information on the timing and directionality of dyadic interactions.

Another important factor to consider alongside measures of association is information on the attributes of individuals, such as phenotypic traits (e.g. sex, size or age) or details about individual state (e.g. personality, dominance rank or maturity). These attributes can be used to determine how sociality and network structure is mediated by individual traits. For example, Mourier *et al.* (2012) showed that blacktip reef sharks tended to group with individuals of a similar size and sex (homophily).

Another important parameter to consider is independence of data since the persistence of associations and autocorrelation of interactions usually preclude this. For example, data collected by following a focal individual shark for a certain period will be pseudo-replicated. Therefore, using sampling periods where data is aggregated to generate independent samples can reduce the effects of temporal partitioning.

18.1.3 Assumptions and randomization analysis

Once relational data have been gathered using the most appropriate sampling method for the question and species of interest it is extremely useful to visualize the data to help guide further, more quantitative analyses. Network visualization is particularly compelling and intuitive, and in some instances can generate informative patterns. It is important to remember that these observed networks typically represent a subset of the true underlying relationships between individuals because network sampling rarely captures all the nuances that dictate how individuals are likely to interact (Farine and Whitehead 2015). In highly connected systems, there might be the temptation to *threshold* the data above a specific edge weighting in order to help reveal underlying structural characteristics that might be masked

by a 'birds nest' of connected nodes. It is crucial, however, to *only* use thresholding for visual exploration, in order to avoid misleading and inaccurate metrics or measures of community structuring (Farine and Whitehead 2015).

Because network data are inherently non-independent (i.e. the link between any two nodes is directly influenced by other links in the network) it is important to consider how to approach null hypothesis significance testing (Croft *et al.* 2011). To determine whether the patterns observed in visualizations are significant, it is important to compare the observed result (e.g. one or several metrics calculated from our observed data) to a distribution of that same metric from a large number of network permutations (Farine 2017). Only the realized movements of pig-eye *Carcharhinus amboinensis* and spot-tail sharks *Carcharhinus sorrah* between acoustic receivers in Cleveland Bay, Eastern Australia for example, were randomized to generate a null spatial network against which the coefficient of variation in the observed movement network was compared (Lédée *et al.* 2015). In spatial networks these methods are designed to control for the bias introduced by the physical layout of the receivers from which data are generated. The subtleties of deciphering the most appropriate null model to use and deciding at which stage to permute the data (matrix permutation vs data stream permutation), in addition to how to statistically deal with overlapping spatial and social processes, are beyond the scope of this chapter. For more information on these issues we direct the interested reader to a number of excellent papers that discuss the pros and cons of different statistical approaches (James *et al.* 2009; Croft *et al.* 2011; Farine 2015; Farine and Whitehead 2015; Furmston *et al.* 2015; Spiegel *et al.* 2016a; Farine 2017). Given that network structure can inform the emergence of crucial ecological and evolutionary processes, such as sexual segregation or cooperative hunting, developing rigorous null models and factoring in the violation of statistical assumptions in network data analysis, is of upmost importance; as is the interpretation of the network.

18.1.4 Interpretation and output of network analysis

The interpretation of any network should be approached with caution. First, is the sample size of the network sufficient to make population-level inferences? This is particularly important for SNA because networks with low numbers of individuals can be unreliable (Silk *et al.* 2015). Ideally, social analyses should incorporate as many members of a population as possible to capture the variability within social dynamics; indeed missing individuals can have important consequences for the description of the structure of the population. Given that spatial network analyses are often driven by very different questions, robust results can sometimes be obtained from a smaller representative sample of the population. It is increasingly being found, however, that individuals within populations of sharks can exhibit substantial differences in movements and feeding behavior (REFS) as well as personality traits (REFS), which may necessitate larger sample sizes.

Second, before interpreting the outputs of a network analysis, it is important to return to the original research question of the study and interpret the results in the context of this. For example, a network is simply a graphical representation of links between individuals or locations and it can be built from any kind of random data. Therefore, before drawing conclusions about the social structure of a shark population it is crucial to verify if the network is based on non-random associations between some individuals because random associations would be meaningless in the context of testing the social structure of a population. Every interpretation should therefore be made in the light of initial ecological question/hypothesis tested.

For spatial networks, the resulting structure of aggregated networks, or the average of all individual movement networks, can be highly dependent on the number of individuals included in the study. Indeed, the density of the network (i.e. the number of edges in the

network divided by the total possible edges) is dependent on the diversity of individual movement, as the centrality of a node (i.e. location) can be, because increasing the number of individuals in the analysis will consequently increase the number of different edges constituting the network (Mourier *et al.* in review). This translates into considering mono- or multilayer networks and is an area of future development in the field of networks in ecology.

<mark>**Insert Table 18.1**</mark>

18.2   Network applications in shark biology

18.2.1 Shark social networks

Over the past decade our understanding of the mechanisms and functions that shape shark social lives has progressed rapidly (see Jacoby *et al.* 2012b; Wilson *et al.* 2014). This is in part due to advances in remote monitoring devices, such as biotelemetry (acoustic telemetry) and biologging (archival loggers) (Hussey *et al.* 2015), but also our ability to collect, handle and analyze ever larger datasets. The use of SNA has made important contributions to this improved understanding by providing a framework to quantify associations. To date, 16 studies have used SNA with questions typically focused on whether sharks have non-random associations (Table 18.2). And if so, what attributes (i.e. sex, size) influence group joining decisions? And whether these associations persist temporally and or spatially? Just ten species have been used in these studies, however focal species have varied considerably in body size (12cm small-spotted catsharks *Scyliorhinus canicula* to 400cm great white sharks), life stage (neonates to adults), reproductive mode (oviparous to viviparous), and habitat types (benthic to reef-associated or pelagic). Importantly, the versatility of the SNA approach has prompted the use of diverse data collection methods; from direct observations of social behaviors [e.g. nose to tail following (Guttridge *et al.* 2011) or tactile resting (Jacoby *et al.*

2010)], to co-occurrences at provisioning / dive sites (Mourier *et al.* 2012; Findlay *et al.* 2016) and more recently triangulation of acoustic detections (Armansin *et al.* 2016), use of shark-borne proximity receivers (Mourier *et al.* 2017a) and machine learning algorithms to infer social associations from time-series data (Jacoby *et al.* 2016). Further, the temporal and spatial scales used to examine shark social networks have varied considerably. For example, the focal follows conducted by Wilson *et al.* (2015) on ten juvenile lemon sharks in a mesocosm, recorded their nearest neighbor every 10s for a 100s sampling period – completing their study in 8-days. By contrast, Mourier *et al.* (2012) completed 190 dives over 2-years, recording co-occurrences of 133 blacktip reef sharks across seven locations spanning 10km. To further explore the outcomes and SNA tool kits used by researchers working with sharks, the following section considers lab-based and semi-captive studies separately to those conducted on free-ranging species.

18.2.1.1 Lab and semi-captive studies

To date two shark species, the lemon and small-spotted catshark have been used in lab or semi-captive experiments. Both species form groups, are abundant and can be easily maintained in captivity (Sims 2003; Guttridge *et al.* 2009). Jacoby *et al.* (2010, 2012c, 2014) conducted a series of experiments, using juvenile and adult small-spotted catsharks. In the first study social network structure, temporal stability, and activity profiles were analyzed to examine the impact of introduced males on social structure of four captive groups of mature female catsharks. Social networks were constructed from symmetric tactile association behaviors (i.e. sharks resting in contact with each other) and through examining network measures (eigenvector centrality, weighted degree, and average path length; Table 18.1) before and during male introduction, results showed that shark groups differed in their tendency to aggregate in a unisex environment and in social responses to male presence. In

their next experiments, juvenile catsharks hatched in captivity provided greater numbers (N = 300) and the rare opportunity to manipulate the social environment and habitat of treatment tanks to examine preferred associations, repeatability in social behavior, and the role of familiarity and habitat type in aggregation formation. Randomizations revealed non-random associations, with familiar sharks forming more groups of greater size. Finally, network measures (e.g. clustering coefficient and reach) were employed to characterize individual repeatability of social traits across habitats to explore social personality types. Keller *et al.* (2017) also investigated the potential role of familiarity in group formation and social behavior of juvenile lemon sharks using a remote camera and an automated tracking system which allowed the inference of interactions between individual juvenile sharks moving around a holding pen. These experiments showed that juvenile lemon sharks preferred social interactions with familiar individuals.

Building on this idea of behavioral phenotypes in shark social behavior, Wilson and colleagues used a novel fission-fusion model based on Markov chains to explain juvenile lemon shark social dynamics (see Wilson et al. 2015 for details). Individual-level differences in sociality (leadership and network measures – e.g. node strength, weighted node betweenness and weighted clustering coefficient) were determined for 10 sharks across 8-days of observations (Wilson *et al.* 2015). In addition, sharks were fitted with tri-axial accelerometers to provide locomotor profiles (e.g. duration spent fast / steady swimming) in a rare example of multiple independent approaches to quantifying social behavior. Interestingly, lemon sharks did not show consistency in their social network positions but preferred to associate with other individuals of similar locomotor profiles. Although a small sample size and short study duration likely limited the conclusions that could be drawn from these results, the integration of SNA tools with accelerometers holds considerable promise for exploring the energetic benefits or costs to grouping.

18.2.1.2 Free-ranging studies

Patterns of association for wild sharks are difficult to quantify due to the concealing nature of their environment (Jacoby *et al.* 2012b). Taking advantage of shallow water and sheltered mangrove inlets, Guttridge *et al.* (2011) explored the social structure of a population of juvenile lemon sharks in Bimini, Bahamas. Across 2-years, the social behavior (e.g. nose-to-tail following, circling) of 38 sharks was observed from wooden platforms and recorded at 2-min intervals. Networks were constructed at 10 and 60 min sampling periods (to avoid issues with independence) revealing that juvenile lemon sharks showed repeated social interactions, with group structure mostly explained by body length, and possibly by preference for relatives but not sex. In addition, they also documented differences in leadership tendencies of sharks, with lead individuals usually significantly larger than other group members (Guttridge *et al.* 2011).

Mourier and colleagues (2012, 2017b) conducted an extensive study examining social structure of a population of free-ranging blacktip reef sharks. Unique fin markings were used to identify individuals and dive surveys were completed at provisioned and non-provisioned sites. Their incorporated community analyses (e.g. modularity matrix clustering technique; Whitehead 2008) and further use of lagged association rates and egocentric network measures (e.g. strength, eigenvector centrality, reach, clustering coefficient and affinity). Findings revealed the first evidence for communities in sharks, which were characterized by non-random associations, with size and sex driving preferences in some locations. Interestingly, when spatial overlap was included in the analysis this explained much of the community separation, however this was not exclusive suggesting active social preferences probably influenced associative patterns within communities (Mourier *et al.* 2012). More recent exploration of the data quantified impacts of node removal on the network properties

and robustness to catch and release fishing. These simulations revealed that the global network was resilient and did not fragment, even when 25% of the individuals were removed. Catch and release fishing conducted for 30 min after dives provided an interesting experimental component to this study, showing that sharks learned to avoid capture with decreases in capture probability with increased sighting rates (Mourier *et al.* 2017b).

Direct observations were also used by Findlay *et al.* (2016) to monitor co-occurrences of 323 great white sharks in six locations, across six years (2008-2013). This was the first attempt to examine the social preferences of a highly migratory pelagic species. Despite finding random associations in white shark social networks it highlighted further the applicability of SNA to co-occurrence data and the opportunities for generating this type of data during ecotourism operations (Gallagher *et al.* 2015). A similar approach was also used to define communities of sicklefin lemon sharks visiting a provisioning site in French Polynesia showing that visitation patterns were structured into shark communities based on co-occurrences (Clua *et al.* 2010).

Similar to the semi-captive experiments by Keller *et al.* (2017), remote cameras have been recently employed to track interactions between free ranging individual adult sicklefin lemon sharks under an artificial food stimulus (Brena *et al.* in review). This technique not only allowed recording associations between individuals around a food source but also the construction of a social hierarchy of the members of the network without human interference. In this case, individual sharks were free to come and interact with the food and other individuals.

More recently a handful of studies have explored the use of SNA to provide insights into shark social structure by examining data collected from acoustic tracking. Armansin *et al.* (2016) used spatial data obtained from fine-scale passive acoustic telemetry (VPS) to infer association preferences of 15 tagged wobbegong sharks *Orectolobus maculatus* over a 15-

month period. Despite being presumed to be solitary, this species showed non-random casual and long-term associations. Home-range overlap did not correlate with associations, but changes in social cohesion were documented before and during the breeding season. Similarly, Haulsee *et al.* (2016) found that male sandtiger shark *Carcharias taurus* interactions varied seasonally. Using implanted acoustic transceivers they generated egocentric networks of con and heterospecific interactions across a year. Networks were only visually depicted, however, and neither randomization tests nor exploration of the network properties was conducted.

Another exciting approach used GMMs (Gaussian mixture models); see section 18.1.2 for description (Jacoby *et al.* 2016). Using the number of times individuals co-occurred and the duration of these co-occurrences at different locations, it was possible to make inferences about the leadership patterns within populations of wild grey reef sharks. SNA was used to analyze co-occurrence count and duration data, with leadership scores based on the proportion of an individual's degree that was represented by *in degree* (see Jacoby *et al.* 2016 for details). This novel method for extracting social structure from acoustic tracking data would benefit from validation with direct observations. Given the vast passive acoustic receiver arrays that are maintained globally and the great diversity of species that can be equipped with tracking devices (Hussey *et al.* 2015) this method holds tremendous promise.

Finally, Mourier *et al.* (2017a) explored the efficacy of three types of receivers (Vemco, VR2W; MiniSUR & Proximity receivers; Sonotronics) differing in detection range to generate co-occurrence networks for a benthic shark species. By using SNA, it was possible to compare networks across receivers effectively by examining the correlation between association indices and whether centrality rank was consistent across methods. Results revealed that VR2W receivers were not able to capture co-occurrences at an

appropriate spatial scale to infer social associations for a relatively immobile species, the Port

Jackson shark *Heterodontus portusjacksoni*. Further, the consistency of individuals' ranks

was not significant when comparing the network produced by the receivers with small ranges

(10 – 60m), with those constructed with the larger range (400m). This study highlights the

importance of considering the ecology of the study species and defining the scale of

biologically meaningful interactions between individuals.

18.2.2 Shark movement networks

Recently, the use of network analysis to study animal spatial ecology has gained momentum

(Jacoby and Freeman 2016). In this section, we review research that has examined shark

space use, movement, habitat use and drivers of shark movement using various network

analysis techniques. It is worth noting that, to date, most studies have used network analysis

in combination with passive acoustic telemetry to understanding shark movement networks.

Network analysis enables the exploration of shark movement and space use particularly as

the visualization tools associated with network packages are so intuitive and versatile. For

example, Jacoby *et al.* (2012a) and Lédée *et al.* (2015) used spring embedding algorithms,

which sort randomly placed nodes into a desirable layout that satisfies the aesthetics for

visual presentation (i.e. symmetry, non-overlapping nodes, etc.), to visually compare changes

in Caribbean reef *Carcharhinus perezii* and pig-eye sharks space use, respectively. Ontogeny

was identified as a possible explanation for the observed changes in Caribbean reef shark

space use, while responses to acute changes such as freshwater incursions were a prominent

feature of pig-eye space use. Using centrality metrics, researchers can further capture distinct

aspects of a location's importance in network space and distinct patch use (Jacoby and

Freeman 2016; Nicol *et al.* 2016). Single or multiple metrics might be used to determine the

most important patches and the differential use of patches in the network depending on the

research question. Three studies have used descriptive network statistics to examine space use of sharks (Jacoby *et al.* 2012a; Lédée *et al.* 2015; Stehfest *et al.* 2015). Degree (Jacoby *et al.* 2012a), eigenvector (Stehfest *et al.* 2015) and a combination of centrality metrics (i.e. node strength, closeness and eigenvector; Table 19.1 Lédée *et al.* 2015) are among the tools used to determine the most important patches and examine their use within networks. Using degree, Jacoby *et al.* (2012a) demonstrated segregation in core patches and movements between male and female small-spotted catsharks. Stehfest *et al.* (2015) used the eigenvector to examine the movement network of broadnose sevengill sharks *Notorynchus cepedianus* and found male and female spatial segregation; with each sex using a different core area. Finally, by combining node strength, closeness and eigenvector, Lédée *et al.* (2015) defined the core and general use areas of two nearshore shark species and identified the importance of movement corridors within core areas for both species.

Observed individual spatial networks can also be compared with simulated networks that have known structural properties (e.g. circular, small-world and scale-free networks – Fig. 18.3) to examine individual movement patterns within the landscape. To date, only a small number of studies had used this technique (Heupel *et al.* in prep; Jacoby *et al.* Submitted; Lédée *et al.* in review). Heupel *et al.* (in prep) and Lédée *et al.* (in review) found that the movement of silvertip *Carcharhinus albimarginatus*, grey reef, blacktip reef, whitetip *Triaenodon obesus*, tiger *Galeocerdo cuvier* and Australian weasel *Hemigaleus australiensis* sharks within the Great Barrier Reef exhibited small-world and scale-free properties. These characteristics facilitate dispersal through alternative pathways (small-world) and enhance resilience to random disturbances (scale-free) (Fortuna *et al.* 2006; Minor and Urban 2008).

In the context of habitat use, two types of habitat network can be created; unimodal and bimodal which we have been touched on briefly in previous sections. Unimodal habitat

networks represent the movement of individuals, a population or species between habitat types and may be used to examine habitat use. While bimodal habitat networks represent how frequently habitat types (i.e. first set of nodes) are used during a specified period (i.e. second set of nodes, e.g., monthly, seasonally etc.; Fig 18.2; Borgatti 2012; Opsahl 2013) allowing the examination of habitat use. To date, three studies have used network analysis to examine habitat use of shark species (Heupel *et al.* in prep; Papastamatiou *et al.* 2015; Lea *et al.* 2016). Papastamatiou *et al.* (2015) quantified habitat use of Galapagos sharks *Carcharhinus galapagensis* at an Hawaiian atoll by measuring the degree and betweenness centrality metrics in unimodal habitat networks. Deep habitats within the atoll were found to be more important for Galapagos sharks than the shallow habitat surrounding the atoll. Lea *et al.* (2016) measured node strength and betweenness, and edge density from unimodal habitat networks to examine the habitat use of silvertip, grey reef, blacktip reef, tawny nurse *Nebrius ferrugineus* and sicklefin lemon sharks in the Seychelles. Habitat use varied among species, with blacktip reef and lemon sharks using mostly lagoon areas, and grey reef and silvertip sharks using mainly coastal reefs and drop-offs. Tawny nurse sharks showed habitat segregation by size within the atoll, with small individuals found inside the lagoon and large individuals outside (Lea *et al.* 2016). Finally, Heupel *et al.* (in prep) used a canonical correspondence analysis on monthly bimodal habitat networks (Fig. 18.5) to examine habitat partitioning of six inshore shark species, the pig-eye, creek whaler *Carcharhinus fitzroyensis*, blacktip reef, Australian blacktip *C. tilstoni*, spot-tail and Australian sharpnose *Rhizoprionodon taylori* sharks. Results showed that blacktip reef shark used more complex reef habitat while the other species followed a vertical distribution within the bay, with spot-tail shark using deeper areas, pig-eye and Australian sharpnose sharks using seagrass areas and Australian blacktip and creek whaler using shallower habitat. These examples showed

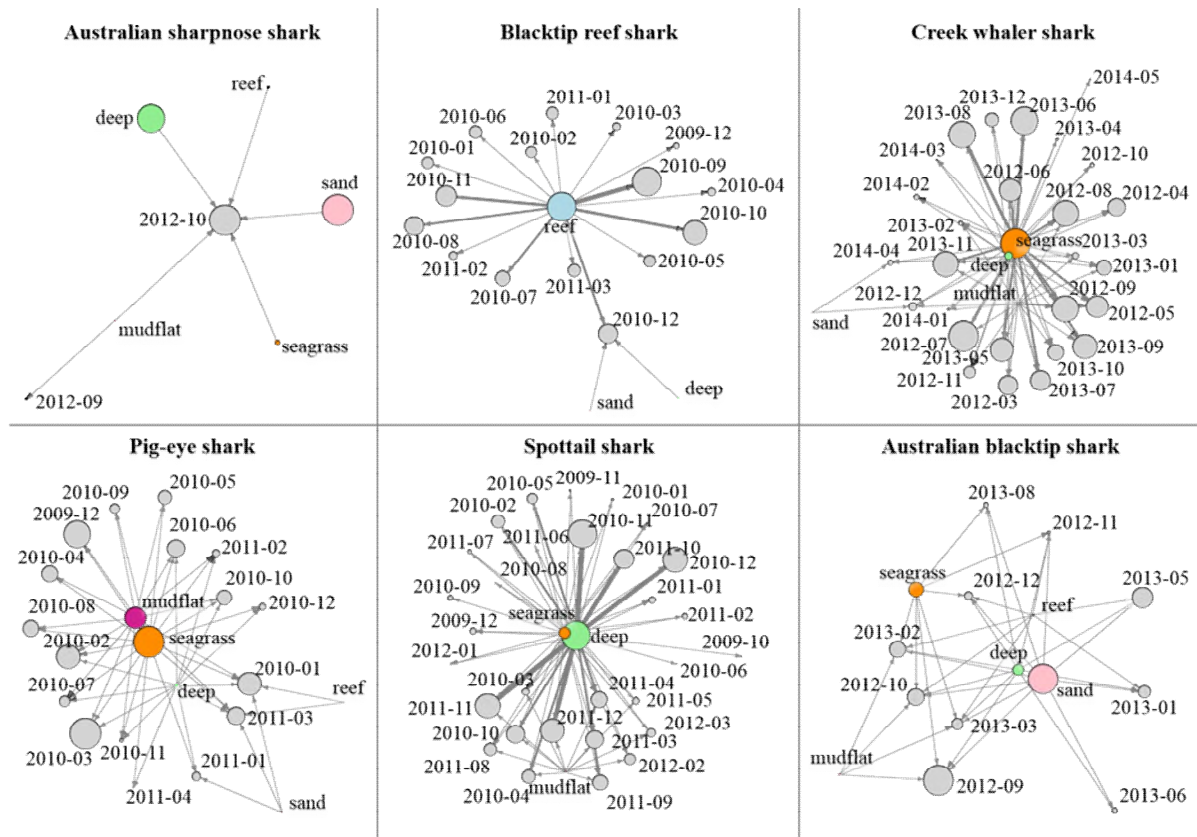that network analysis visualization and analysis techniques can easily be applied to examine habitat use.

Figure 18.5: Examples of monthly bimodal habitat networks for six inshore species of sharks, pig-eye *Carcharhinus amboinensis*, creek whaler *C. fitzroyensis*, blacktip reef *C. melanopterus*, Australian blacktip *C. tilstoni*, spot-tail *C. sorrah* and Australian sharpnose *Rhizoprionodon taylori* sharks within the Great Barrier Reef, Australia. Modified from (Heupel *et al.* in prep).

Approaches such as Multiple Regression Quadratic Assignment Procedures (MRQAP; a variant of the Mantel test with multiple factors) and mixed effect models can help to evaluate the influence of biological and environmental factors on movement and habitat networks structures by incorporating node attributes (Dekker *et al.* 2007; Pinter-Wollman *et*

al. 2014) and network metrics into the models, respectively. One study has used MRQAP (with the double-Dekker semi-partialing method) to examine factors influencing shark movement. Jacoby *et al.* (2012a) used MRQAP to study the influence of inshore versus offshore locations, mean depth and habitat complexity on the movement of female and male small-spotted catsharks. Another study combined network analysis with mixed effects models to determine the biological factors affecting shark movement between habitat types. Heupel *et al.* (in prep) used mixed effect models on pathway/edge number and frequency to reveal that species movements within the same habitat were more prevalent than between habitats and species shared the same pathways with high frequency. Sex and body length had no effect on their movement.

Insert Table 18.2

18.2.3 Limitations of network analyses

Despite the successful contribution of network analysis to understanding shark ecology, it is important to acknowledge the current limitations. For example, as automated and indirect methods are being used increasingly to infer sociality rather than measuring it with direct observations it is critical to understand and test the assumptions underlying indirect measures. Importantly network-based tools are being used in studies of movement ecology (see section 18.2.2) and statistical methods are already emerging (Jacoby *et al.* 2016; Spiegel *et al.* 2016b). Wilson *et al.* (2015) used accelerometers to generate locomotor profiles for juvenile lemon sharks simultaneously to collecting social data. This is a powerful approach as sharks could assort by energetic profiles or energy budgets and it is now possible to use acoustic tracking devices that have inbuilt accelerometers and pressure sensors (Shipley *et al.* 2017).

Thus, in theory it would be possible to add some context to social interactions, e.g. during resting, fast swimming or steady swimming.

As alluded to earlier, care must be taken when interpreting results especially when small numbers of animals are used in studies. For example, Wilson *et al.* (2015) found evidence for sex segregation in juvenile lemon sharks, however the literature for movement ecology, diet and social structure in other locations did not support this finding (e.g. Guttridge *et al.* 2011).

Experimental studies that validate the indirect methods for assessing social interactions and elucidate the mechanisms underpinning associations are particularly important. Species like juvenile lemon, Port-Jackson and blacktip reef sharks are accessible for direct observation as well as acoustic tracking methods allowing dedicated validation studies. As discussed in Mourier *et al.* (2017a) sharks can socialize in different ways and so testing methods on species that exhibit variation in how they socialize (i.e. resting or schooling) will ensure inference methods are applicable to a broader number of species.

Most spatial network studies reviewed here, used passive acoustic monitoring to examine shark movement which is well suited to network analysis due to the use of discrete moored acoustic receivers as nodes, but that limits interpretations to specific/local areas. For large migratory species of sharks, acoustic monitoring studies only provide a local snapshot of their movements, and must be combined with other tracking technologies, such as satellite tags to provide a more accurate interpretation of their movement. For more localized species or those that show considerable site fidelity, careful consideration should be taken when choosing what a node represents to allow comparison between individuals or between species.

Network analysis provides a simple way to display complex processes that instantly reveals information on spatial and temporal changes in animal space use (Jacoby *et al.* 2012,

Lédée *et al.* 2015). However, compared to traditional analyses, network analysis does not estimate activity space or provide an exact match of individual core use areas measured using kernel utilization distribution or Brownian bridge, as shown in Lédée *et al.* (2015). Therefore, while network analysis alone is useful in providing information on animal pattern, combining traditional and network analyses might provide a more realistic picture of animal movement (Bascompte 2007). Furthermore, caution should be used in selecting metrics to answer specific questions and in interpreting results from networks with low numbers of nodes and connections; for example, the precision of betweenness and clustering coefficient declines as the number of nodes decrease (Silk *et al.* 2015). Also, missing data (e.g. low acoustic receiver coverage in acoustic monitoring studies or unknown habitat use in mark-recapture studies) may influence measures of movement between locations or habitat types (Silk et al., 2015). Thus with limited or missing data the use of network analysis may not adequately represent animal movement and traditional analyses may be more suited (Whitehead 2008).

Networks are a static representation of movement or habitat use ignoring the temporal dynamics of movement (Cumming *et al.* 2010; Stehfest *et al.* 2015). Temporal dynamics need to be taken into consideration when examining the movement of animals, and comparison with other methods may be crucial to validating each approach. Two approaches might be used to compensate for this aggregation of samples through time (e.g. data gathered over months/years represented as a single network); intervals more relevant to the biology and ecology of the species studied, or time-ordered networks can be used (see Snijders *et al.* 2010; Blonder *et al.* 2012 for details). For example, networks can be created at different temporal scales to incorporate some temporal dynamic of the movement. However, pathways (i.e. edge) between acoustic receivers (i.e. nodes) are created regardless of the time taken to travel from one receiver to the next, which is misleading if data are missing for long periods (e.g., outside of receiver range). Information on maximum speed of a species could be used to

create the network. Observed speed can be calculated for each edge and added to attributes. Then, using an edge threshold analysis any edge with a value greater than the maximum speed of a species could be removed to obtain a more realistic network.

Approaches such as Multiple Regression Quadratic Assignment Procedures (MRQAP) requires detailed information at the node level. Telemetry data often lack information on environmental factors where and when the individual was detected. Including environmental sensors with tags or receivers could not only record individual ID and time and date of detection but also the environmental conditions at the time of detection. There are a number of commercially available (acoustic) tags that enable this already (e.g. Vemco's V16TP). Furthermore, a habitat and/or video survey or remotely sensed environmental data at node locations could be gathered to obtain more information about an individual's habitat which could then be included in the analyses. Therefore, providing more accurate information about movement and environmental factors at the time the individual was present in the area could be used to refine conservation and management measures (Hastings *et al.* 2011).

Movements in the marine environment are multi-dimensional (i.e. include depth), and constrained by spatial features, therefore rarely follow a straight path. Movement between two locations or habitat types within a network are shown as a straight path (Tremblay *et al.* 2006; Stehfest *et al.* 2015) and so are unrealistic in most situations. Standardizing path length with actual distance between node, constrained by spatial features (e.g. land, coral reefs) or use of multilayer networks to incorporate depth information from tags (Mourier *et al.* in review) might provide a better representation of pathes used by individuals.

18.3   Future developments and research directions

18.3.1 Technological challenges and developments

This field of network analysis is progressing rapidly with improvements in technology and analytical methods. For example, much more detailed inferences about the social networks of sharks and rays would be obtained using a combination of mobile receivers (e.g. Vemco Mobile Transceiver VMT) recording the tagged individuals encountered within a reduced range (Mourier *et al.* 2017a) and efficient data transfer to fixed listening stations (Holland *et al.* 2009). Alternatively, proximity receivers could communicate with other animal-borne device providing the location of the animal as well as remotely transferring the data from the proximity logger. This idea is currently under development with Vemco Mobile Transceiver (VMT) communicating with Service Argos via Bluetooth to remotely transmit data (Lidgard *et al.* 2014) and offers an exciting opportunity for future research on shark sociality. Proximity loggers are likely the most accurate method to infer small scale interactions in marine animals but technological drawbacks still weaken their effectiveness.

The use of multi-sensor tagging will provide complementary information that can be integrated into more detailed network analyses. Promising technological developments such as Encounternet's adaptation to the marine environment (Tentelier *et al.* 2016) will benefit social interaction studies of sharks. This will requires to develop (1) a set of small tags emitting individually coded high frequency signals, receives signals from other tags and its proximity, and logs perceived encounters in an on-board memory, (2) a set of base stations, fixed at known positions and recording encounters with tags, uploading the logs stored in the tags' memory and transmitting information between tags and the third component of the system, and (3) an interface between the user and the system (i.e. a transmitter/receiver node mounted on a laptop) collect the data from the base stations (Fig. 18.6A).

New technology can also help in developing remote monitoring of interactions between sharks. Automated underwater vehicles AUVs such as gliders or drifting robots (Fig.

18.6B,C) can record interactions at sea if they are fitted with acoustic receivers (Blonder *et al.* 2012; Haulsee *et al.* 2015, 2016). The recent development of unmanned aerial vehicle UAVs (Kiszka *et al.* 2016; Chapter 5) can provide a means to track shark movements and interactions (Fig. 18.6D), although battery life issues limit the time scales for sampling. The use of underwater animal-borne cameras (see Chapter 6) can provide data on interactions with other individuals, as well as the environmental context of interactions using on-board sensors. This technology will be especially useful in species where individuals can be distinguished by photo-identification (e.g. blacktip reef sharks, Fig. 18.6E; Chapter 13) providing a novel method for obtaining an egocentric network. Finally, citizen science programs at dive tourism sites can help in collecting data on interactions within shark aggregations especially for species prone to photo-identification.
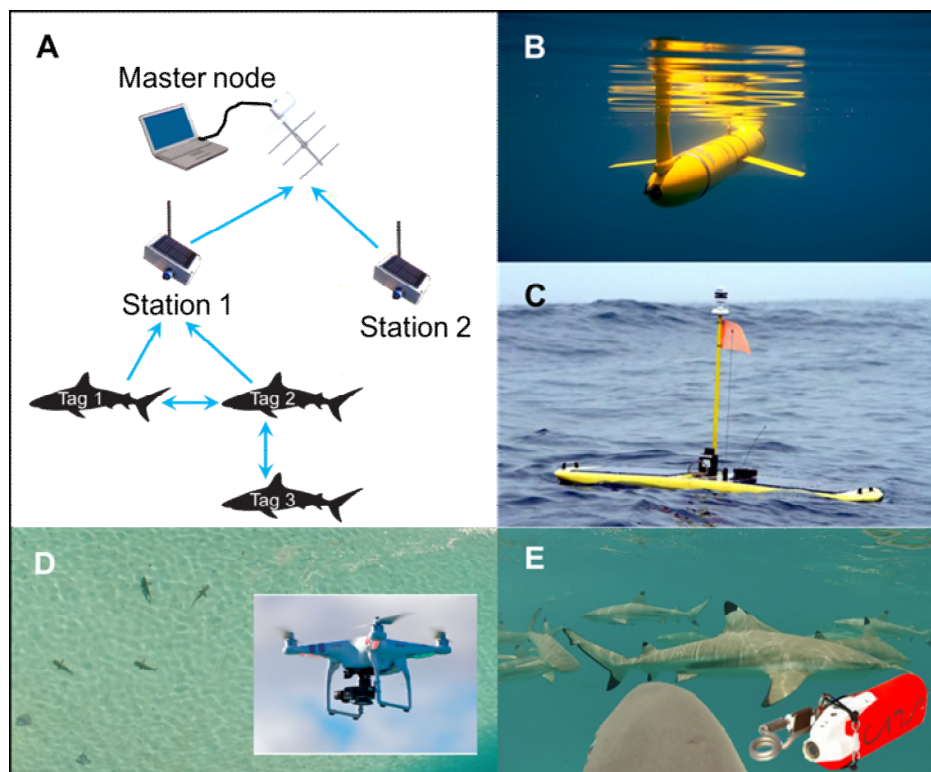

Figure 18.6: Emerging technologies for shark interaction monitoring. (A) Encounternet-like system can be developed to track shark encounters automatically; (B) Glider Automated underwater vehicle AUV able to record tagged sharks at sea and, (C) a surfing robot having similar purposes; (D) unmanned automated vehicle UAV able to track shark interactions

during stationary fly; and (E) animal-borne cameras attached to a dorsal fin potentially able to capture interactions with other known sharks using photo-identification.

18.3.2 Analytical challenges and developments

Network approaches are still relatively new in shark ecology and the field remains predominantly focused on determining appropriate sampling methodologies with a view to describing movement or social patterns. Many challenges remain. Analytical developments will be critical, allowing researchers to make more of the data (and technologies) that are currently available. This is in part because some of the logistic limitations - such as the speed of remote download from animal to receiver of logged environmental or social data – that likely will remain for some time to come.

To our knowledge, there is no research that considers the depths at which we sample or measure the network? Acoustic tags are capable of recording and transmitting pressure (and thus depth) readings to local receivers, and so it seems prudent that we begin to explore inferred social interactions at different depth ranges, enabling us to better piece together the mechanistic drivers of social behaviors in sharks (Jacoby *et al.* 2012b). Multilayer networks will likely play a role in providing new network metrics for networks that operate at multiple levels. For example, shark movements can be highly variable within a population (e.g. REFERENCES) but movements are often aggregated across the full or subsets of the population (e.g. sexes). By considering each shark as a separate layer in a multilayer network we can explore the role of individual movements on habitat connectivity and flow using a more suitable framework (Mourier *et al.* in review). Indeed, these approaches should have considerable impact on the burgeoning research on individual specialization, personality traits and cognitive variation in sharks (Guttridge and Brown 2014; Jacoby *et al.* 2014; Finger *et al.* 2017) in addition to defining new research directions. One promising avenue might

consider the role of social behavior in the development of cooperation and social hunting strategies amongst pelagic sharks relying on diffuse prey fields (Lang and Farine 2017).

18.3.3 New ideas and future research questions

18.3.3.1 Social networks

The use of SNA has revealed complexities in the social lives of sharks. However, we have only just scratched the surface of what is possible given integration of SNA with other tools. For example, in addition to the biotelemetry and biologging techniques discussed above, stable isotope analyses (SIA) could be incorporated to add isotopic niche as a node attribute within a social network, helping unlock the role of foraging on social behavior of sharks. Tissues (e.g. whole blood, plasma, muscle or skin) have different turnover rates and can inform variation in resource or habitat use across short and long-time scales (Hussey *et al.* 2012). Where and what an animal eats can have important implications for social interactions, especially when considered in parallel with body condition or nutrition (Senior *et al.* 2016).

Further, with improved husbandry and careful selection of the study species it is possible to have enough subjects to manipulate and replicate networks. Only through controlled experiments will social networks be able to provide definitive causative evidence for socially mediated mechanisms underpinning evolutionary processes (Farine and Whitehead 2015). There are numerous small-bodied, abundant species that could provide tractable models of behavior [e.g. Port Jackson sharks (Mourier *et al.* 2017a) and gummy shark (Frick *et al.* 2010)]. Juvenile scalloped hammerheads *Sphyrna lewini* were used effectively in a series of electroreception studies in semi-captive arenas (Kajiura and Holland 2002). This species is probably the most recognized for its social tendencies, forming huge schools at seamounts. However, despite ground-breaking studies in the 1980s (Klimley 1987)

documenting size and sex segregation within schools and evidence for intraspecific communication (e.g. head shakes, corkscrew) no further advances have been made. Whale, *Rhincodon typus* and basking sharks, *Cetorhinus maximus* both form aggregations (Sims *et al.* 2000; de la Parra Venegas *et al.* 2011) and can be identified individually via spots or fin notches. These species are threatened (IUCN Redlist), and thus studies enhancing our understanding of the mechanisms that underpin group formation will help to improve how we conserve and manage these species.

18.3.3.2 Spatial networks

Recent advances in telemetry have allowed researchers to monitor long-term social behavior and movement patterns of multiple species over vast areas (Espinoza *et al.* 2015). Animal movement, and space and habitat use are often explained only using biological and environmental factors, rarely including individual variation (Nathan *et al.* 2008). Behavior, fitness and social position within the population can influence individual movement, and generate a more comprehensive picture on how populations may respond to changes to their environment and what this means for their conservation (Spiegel *et al.* 2017; Snijders *et al.* 2017). Therefore, combining social and spatial network analysis using movement multilayer networks (Mourier *et al.* in review) for example, can provide a better understanding of spatial patterns in shark ecology.

Lastly, many studies often focus on a single species of shark and/or areas without considering interactions between species or the threat status of the species. The affordability of the tracking technologies and easier online access to the data greatly facilitate the establishment of collaborative effort over larger area (Hussey *et al.* 2015). The challenge here is how best to standardize the design of the movement networks across the different study areas (i.e. node arrangement might be different between areas) for useful comparisons. One

possible solution is to create a grid that covers all the areas of interest (Dilts *et al.* 2016) with each grid representing a node within the movement network. Another possible solution, would be to create networks for each area of interest separately and compare standardized network properties (e.g. degree correlations…etc.).

18.3.4 *Applications for management and conservation*

Network analysis provides a toolbox of methods that can be used to assess and model risks- such as habitat loss and fragmentation, climate change and fisheries exposure - and help design and evaluate the effectiveness of management, thus guiding conservation practices (Cumming *et al.* 2010; Galpern *et al.* 2011; Borrett *et al.* 2014).

Using centrality metrics, the importance of each patch (node) or corridor (edge) in maintaining or contributing to landscape connectivity can be determined to help prioritize areas for management and conservation (Rayfield *et al.* 2016; Nicol *et al.* 2016). For example, species habitat fragmentation can be identified by looking at communities using metrics such as component and cluster (Table 18.1). Knowing how habitats are connected or fragmented can help inform management plans to protect clusters of habitat, stepping stones and corridors (Bodin *et al.* 2006; Thomas *et al.* 2014). Degree and cut-node removal analyses can be used to examine population source and sink to restore populations by identifying potential corridors (Treml *et al.* 2008). Finally, seascape connectivity can be measured by determining habitat availability and dispersal probabilities between habitat patches to help design or evaluate effectiveness of marine protected area networks (Espinoza *et al.* 2015; Engelhard *et al.* 2017). Using patch and edge removal and/or edge thresholding analyses, the role these patches and corridors have in maintaining connectivity in the landscape can be examined under different patch- and edge-loss scenarios. The advantage of these methods is that researchers can simulate the destruction of patches or corridors and rank them by their

contributions to landscape/seascape connectivity, thereby allowing managers to make decisions based on which patches and corridors are most critical to connectivity (Kurvers *et al.* 2014), not just for one species but multiple species within the same landscape. Alternatively, network analysis techniques can be used to assess management and conservation plans. For example, network analysis can inform managers about fishing activity pattern. Martin *et al.* (2017) used reservoir (i.e. node) removal analysis to examine the differences in participation among anglers within a regional fishery and assess resilience of the regional fishery to disturbance (e.g. disease, invasive species etc.). Network analysis can also evaluate the efficacy of species protection effort across borders. Treml *et al.* (2015) compared species dispersal network with institutional networks across multiple countries within the Coral Triangle to determine if both fit in an effort to assist management efforts in prioritizing and strengthening species protection. Finally, network theory can be applied to social science to better understand the spread of information among fishermen and better manage resources. Using these approaches, Barnes *et al.* (2016) found that enhanced communication channels across segregated fisher groups could have prevented the incidental catch of over 46,000 sharks between 2008 and 2012 in a single commercial fishery.

Therefore, network analysis is advantageous for developing, guiding and assessing management measures; it allows for assessment of species movement and behavior, for prediction about consequences of anthropogenic and natural disturbances by testing and experimenting on a variety of species at different scales and under multiple scenarios; and it allows for assessment of management and conservation plans across borders.

18.4   Conclusion

Network analyses are becoming increasingly used in shark behavioral ecology. Here we present a broad overview of the utility and challenges of applying network analyses and describe the early progress this field has had in informing shark behavior. Developments in

SNA across other taxonomic groups (particularly in terrestrial systems) continue to help guide and inform the tools available for underwater social networks in conjunction with advances in tracking technologies. At present, the number of studies and shark species adopting these approaches remains relatively small, however we hope that this chapter will help stimulate ideas and research directions that continue to push for developments in shark network ecology. Importantly, new social or spatial network studies on different species and/or systems will certainly contribute to improving our understanding of the main drivers affecting the evolution of social behavior in sharks and rays as well as their spatial ecology. This in turn will provide us with much-needed information to take a more informed and location-specific approach to their conservation. We are excited by the burgeoning developments in this area, by how these developments might guide the design of new technologies and ultimately by the impact this holistic approach might eventually have on shark conservation.

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