



Social behaviour in sharks and rays: analysis, patterns and implications for conservation

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Abstract

There are widespread records of grouping behaviour in both adult and juvenile sharks and rays (Class Chondrichthyes, Subclass Elasmobranchii). Yet despite burgeoning descriptions of these events, many of the proximate and ultimate causes of group living in these top predators remain elusive. Given the documented negative anthropogenic effects on many shark populations globally, there is an increasing need to understand how behaviourally mediated grouping influences population distributions and abundance, and the role this plays in exacerbating vulnerability to fishing mortality. Here, we analyse group living in elasmobranchs: we describe our current understanding of the patterns, mechanisms and functions of both aggregation (where grouping is not driven by social mechanisms) and social grouping (where grouping is influenced by social interaction) and discuss some of the current methods used to study social behaviour in this taxa. In particular, social preferences in elasmobranchs have received relatively little attention. We propose that the study of shark aggregations may benefit from a more fine-scale analytical approach offered by detailed exploration of social interactions using social network analysis. Better understanding of the frequency and longevity of social relations, in conjunction with current long-term data on habitat use and site philopatry, will likely serve for a more informed approach to coastal and pelagic elasmobranch conservation initiatives.

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Received 25 Feb 2011
Accepted 15 Jul 2011

Keywords Aggregation, fisheries impact, sharks, social behaviour, social networks, social organization

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Introduction

Group living and social behaviour have been documented in animals from a wide range of terrestrial, freshwater and marine taxa (Krause and Ruxton 2002). The formation of social groups may involve both active and passive processes. For example, individuals may actively prefer to associate with conspecifics and orientate to their direction of locomotion (Couzin *et al.* 2005; Guttal and Couzin 2010). Some fish species, for example, show both polarized *schooling* behaviour, defined by highly synchronous swimming when moving from one place to another or evading a predator, and less organized, uncoordinated *shoaling* behaviour when aggregating for social purposes (Pitcher 1983). Such patterns of grouping can be maintained by each individual obeying a few simple, localized rules of attraction orientation and repulsion (Couzin *et al.* 2002; Sumpter 2006). In contrast, many animal aggregations do not involve social attraction and form as a result of animals being drawn to aggregate because of a limited resource such as food or specific habitat requirements (Johnson *et al.* 2002) or because of synchronized patterns of daily or seasonal activity (Guttal and Couzin 2010). Thus, an important distinction needs to be made between aggregations that do not involve social attraction (referred to hereafter simply as aggregation) and those that do (hereafter, social groups). For the purposes of this review, 'aggregation' will also be referred to when there is no clear indication or sufficient research to support that grouping is socially derived, although future research will surely address these current grey areas.

Animal groups arise from a complex trade-off of costs and benefits associated with both conspecific and heterospecific interaction. Freshwater teleost fishes, for example, gain antipredator benefits such as the dilution of risk or the confusion effect when shoaling with group mates (Krause and Ruxton 2002; Hoare *et al.* 2004). Schooling behaviour in larger fish and, equally, formation flight in some migratory birds also appear to facilitate a reduction in the energetic costs associated with movement

(Cutts and Speakman 1994; Herskin and Steffensen 1998). Conversely, there are costs associated with grouping behaviour, typically a reduction in foraging efficiency or an increased risk of parasite or disease transmission (Johnson *et al.* 2002; Hoare *et al.* 2004) to name a few. As a result, the fitness of an individual in a group is likely to vary as a function of both group size and composition and the context under which grouping has occurred. Unsurprisingly, group living has been the subject of intense research by behavioural ecologists with particular focus on optimum group size and the decision to join or leave a group (Caraco 1979; Côté and Poulin 1995; Krause and Ruxton 2002), the genetic consequences of interacting with kin (Hamilton 1964; Hain and Neff 2007), the mechanisms underlying patterns of social organization (Krause *et al.* 2000; Croft *et al.* 2005) and those required to support repeated individual interaction such as social recognition and familiarity (Barber and Wright 2001; Tibbetts and Dale 2007; Ward *et al.* 2007).

The evolution of both shoaling and schooling behaviour has been highly selected for in extremely variable three-dimensional (3D) aquatic environments. Some small freshwater teleost fish, however, also shoal under laboratory conditions, and therefore, much of what we know today about social behaviour in fish can be attributed to research on model teleost species such as the guppy (*Poecilia reticulata*, Poeciliidae; Magurran *et al.* 1994; Croft *et al.* 2004) or the three-spined stickleback (*Gasterosteus aculeatus*, Gasterosteidae; Ward *et al.* 2002, 2008; Frommen *et al.* 2007).

Sharks and rays (Class Chondrichthyes, Subclass Elasmobranchii; known collectively as elasmobranchs) are also frequently observed grouping in large numbers; however, little is known about the mechanisms driving this behaviour. Indeed, quantifying aggregation or social interactions in marine fishes presents a significant challenge in comparison with smaller, freshwater teleost species. Laboratory experiments have repeatedly demonstrated that predator avoidance behaviour constitutes a common driver of shoaling among many teleost fishes (Lachlan *et al.* 1998; Krause *et al.* 2000; Hoare

et al. 2004). This idea, although never empirically tested, is often alluded to in the studies of juvenile elasmobranch behaviour (Morrissey and Gruber 1993; Heupel and Simpfendorfer 2005), whom themselves are likely to be vulnerable to a range of larger predators. With the exception of human fishing behaviour, however, many highly predatory species of shark occupy apex positions within their respective food webs, suggesting that there are arguably other significant factors dictating elasmobranch grouping behaviour, in adults at least. Shark aggregations and the physical or environment variables that underpin these events are reasonably well documented in the scientific literature (Economakis and Lobel 1998; Heupel and Simpfendorfer 2005; Dewar *et al.* 2008). In contrast, there is considerably less known about the occurrence of social groups in wild sharks, although some species have been hypothesized to engage in diel periods of social refuging behaviour (Sims 2003). It is well known, for instance, that scalloped hammerhead sharks (*Sphyrna lewini*, Sphyrnidae), which are largely solitary foragers, exhibit regular, polarized schooling behaviour associated with specific locations such as underwater seamounts (Klimley and Nelson 1984) and that these social groups may exhibit fission–fusion properties. Refuging behaviour has been observed in a number of other elasmobranchs and includes group resting behaviour in some demersal species, whereby individuals refuge, often in close physical proximity or contact, at regular periods throughout the day or year (Sims *et al.* 2001, 2005; Powter and Gladstone 2009). The proximate causes of such behaviours and the functions underlying aggregation and social grouping in these top predators remain relatively unexplored.

This review aims to synthesize the existing research on aggregation and social grouping in elasmobranch fishes and summarize our current understanding of the mechanisms and functions underpinning group-related behaviours in this taxa. We compare and contrast our current knowledge of group living in elasmobranchs with that of teleost fishes, with particular focus on the patterns, mechanisms and functions of these events. The latter section of the review considers the methodological developments which have promoted current research into elasmobranch grouping behaviour and may aid future development of this field. We consider the use of social network analysis as a theoretical framework with which to study repeated

interactions in gregarious animals whilst discussing the benefits of applying such analyses to a K-selected species of marine predator. With important recent advances in telemetry technology for large marine predators (Sims 2010) taken together with appropriate analytical approaches, the review concludes by proposing a more holistic approach to the understanding of shark social behaviour, and with it the potential to influence how elasmobranch populations are managed under ever more intensive fishing pressure (Baum *et al.* 2003).

Patterns of grouping behaviour in elasmobranch fishes

Elasmobranchs are highly diverse, marine vertebrate taxa that have adapted to fill apex predatory roles within the estuarine, coastal and oceanic environment. In general contrast to bony fish, elasmobranchs are much slower to gain maturity, produce fewer, more well-developed offspring and regularly live for periods of decades, rather than years. These K-selected life-history traits are consistent across all species of elasmobranch despite substantial variation in reproductive mode and behavioural strategy. Some benthic sharks such as catsharks (Scyliorhinidae) or bullhead sharks (Heterodontidae), for example, are typically found within coastal regions (Sims *et al.* 2001; Powter and Gladstone 2009), foraging on invertebrates and undergoing oviparous reproduction. In contrast, large pelagic species, such as Sphyrnid or Carcharhinid sharks, are highly mobile, viviparous and may forage on other elasmobranchs or large migratory teleost fish (Klimley 1987; Carey *et al.* 1990). Across these different life-history strategies, group living behaviour appears relatively common in both the juvenile (Rowat *et al.* 2007; Guttridge *et al.* 2009a) and adult phases (Economakis and Lobel 1998; Hight and Lowe 2007). In addition, elasmobranchs are also characterized by a high brain mass to body mass ratio (Northcutt 1977), and this may be an indication of their potential to develop and maintain complex social behaviours such as dominance hierarchies and stable social bonds (Dunbar and Shultz 2007).

In the last 20 years, there has been an abundance of research devoted to the assessment of conspecific and heterospecific aggregation in many species of shark and ray (Economakis and Lobel 1998; Semeniuk and Dill 2006; Dudgeon *et al.* 2008). The distinction has already been made

between non-social aggregation through synchronized behaviours or for limited resources and social grouping behaviour; it is noteworthy to mention here that the majority of the literature discussed falls into the former category. Some species may show both aggregation and social grouping, and indeed, aggregation may well in some cases be an important prerequisite for the development of social groups (Fig. 1) (Sims *et al.* 2000). A summary of the species documented as demonstrating group behaviours and the context and timings of these events is given in Table 1.

Aggregation

There is widespread evidence of elasmobranchs aggregating in both single- and mixed-sex communities (McKibben and Nelson 1986; Litvinov 2006; Semeniuk and Dill 2006). Such aggregations have been correlated with numerous environmental and biological variables from geographic locations (Klimley and Nelson 1984) and time of year (Heupel and Simpfendorfer 2005; Robbins 2007) to areas of high prey abundance (Hulbert *et al.* 2005; Martin *et al.* 2009). Some of the earliest insights into how

shark aggregations may be structured were gained from analysing the catches from commercial trawlers. Landings of spurdog (*Squalus acanthias*, Squalidae) and small-spotted catshark (*Scyliorhinus canicula*, Scyliorhinidae) in Plymouth in the early 1900s offered the first indication of the average group sizes and sexual segregation of the individuals occurring on the trawling grounds (Ford 1921). Geographic segregation of the sexes is a widespread phenomenon in sharks (see Wearmouth and Sims 2008 for review) and consequently may lead to differential anthropogenic exploitation of the sexes (Mucientes *et al.* 2009) through spatially focused fishing pressure (see Implications and future directions).

Research into elasmobranch aggregation includes both the easily accessible coastal and benthic species and also the highly mobile, oceanic migrants (Klimley 1985; Robbins 2007; Riley *et al.* 2010). An example of the latter is the aggregation of white sharks (*Carcharodon carcharias*, Lamnidae), albeit sparse over a large area, during a seasonal migration from the coast of Baja, California, to a region of the eastern Pacific Ocean (Weng *et al.* 2007; Jorgensen *et al.* 2009). White sharks frequenting



Figure 1 Aggregation for food resources leading to social grouping. (a) Photograph of three basking sharks *Cetorhinus maximus* (arrowed) conducting courtship 'following' behaviour in the western English Channel. Basking sharks are solitary but aggregate in thermal fronts to feed on rich zooplankton patches; it is at this time that they also conduct social behaviour typified by 'following' of females by males, a behaviour that can last for many hours. (b) Close-up of two basking sharks conducting close following behaviour; when one shark turns, the other follows. At such times when courtship behaviour occurs, full body breaching is also observed, which may be part of courtship. See Sims *et al.* (2000). Photographs courtesy of the Marine Biological Association of the UK.

Table 1 Summary of elasmobranch literature documenting aggregation and social behaviours. Species are listed by taxonomic order and by family within order.

Aggregation/ social	Species	Scientific name	Predominant sex	Time of year	Study/function	Data collection technique	Source
	Spurdog	<i>Squalus acanthias</i>	Mixed	Not specified	Population distribution and sexual segregation	Fisheries landings	Ford (1921)
	Port Jackson shark	<i>Heterodontus portusjacksoni</i>	Female	Aggregate year round, more abundant July–October, some dispersal	Reproductive strategies and sexual segregation Site fidelity and refuging	Observational, fisheries landings Observational and active telemetry	McLaughlin and O’Gower (1971) Powter and Gladstone (2009)
	Nurse shark	<i>Ginglymostoma cirratum</i>	Mixed (male bias)	Not specified	Reproductive strategies	Observational	Carrier et al. (1994)
	Zebra shark	<i>Stegostoma fasciatum</i>	Mixed (female bias)	November–April	Reproduction strategies	Mark–recapture, photo-identification	Dudgeon et al. (2008)
	Whale shark	<i>Rhincodon typus</i>	Male	April–June, plankton blooms/coral spawning	Population distribution	Photo-identification	Riley et al. (2010)
	Basking shark	<i>Cetorhinus maximus</i>	Not specified	September–October	Reproductive strategies	Aerial photography	Wilson (2004)
	White shark	<i>Carcharodon carcharias</i>	Not specified	August–February	Philopatry and population distribution	Satellite and acoustic tagging, genetic analyses	Jorgensen et al. (2009)
	Small-spotted catshark	<i>Scyliorhinus canicula</i>	Single-sex groups	Aggregate year round (?)	Environmental conditions and population distribution Movement, philopatry and sexual segregation	Trawl survey	Rodriguez-Cabello et al. (2007)
	Leopard shark	<i>Triakis semifasciata</i>	Single-sex groups	Daytime aggregation (summer months)	Behavioural thermoregulation	Mark–recapture and acoustic telemetry	Sims et al. (2001)
	Grey reef shark	<i>Carcharhinus amblyrhynchos</i>	Female	Daytime aggregation (March–May)	Environmental conditions	Active and passive telemetry	Hight and Lowe (2007)
	Blacktip shark	<i>Carcharhinus limbatus</i>	Mixed	Daytime aggregation (June, October & November)	Site fidelity and movement Environmental conditions and nursery habitat use	Observational and passive telemetry Active telemetry and observational	Economakis and Lobel (1998) McKibben and Nelson (1986)
	Lemon shark	<i>Negaprion brevirostris</i>	Mixed (juveniles)	Not specified	Activity patterns/habitat use	Passive telemetry	Heupel and Simpfendorfer (2005)
			Not specified			Active telemetry and observational	Gruber et al. (1988)

Table 1 (Continued)

Aggregation/ social	Species	Scientific name	Predominant sex	Time of year	Study/function	Data collection technique	Source
	Blue shark	<i>Prionace glauca</i>	Single-sex groups	Not specified	Sexual segregation and habitat use	Fisheries landings	Litvinov (2006)
	Whitetip reef shark	<i>Triaenodon obesus</i>	Mixed	Not specified	Reproductive strategies	Video analysis	Whitney <i>et al.</i> (2004)
	Scalloped hammerhead shark	<i>Sphyrna lewini</i>	Female	Daytime aggregation year round (offshore)	Schooling behaviour	Observational/photographic	Kimley (1985)
	Southern stingrays	<i>Dasyatis americana</i>	Mixed	n/a (anthropogenic influence)	Population distribution	Observational and passive telemetry	Hearn <i>et al.</i> (2010)
	Cowtail stingrays and Whiprays	<i>Pastinachus sephen</i> and <i>Himantura uarnak</i>	Not specified	Not specified	Ecotourism impacts	Photo-identification	Semeniuk and Rothley (2008)
	Spotted eagle ray	<i>Aetobatus narinari</i>	Mixed	Not specified	Mixed-species aggregations and predator avoidance	Observational	Semeniuk and Dill (2006)
	Giant mania ray	<i>Manita birostris</i>	Not specified	Summer (North), Winter (South)	Activity patterns and behavioural ethogram	Active telemetry and observational	Silliman and Gruber (1999)
Social	Severngill shark	<i>Notorynchus cepedianus</i>	Not specified	Not specified	Site fidelity and movement	Passive telemetry	Dewar <i>et al.</i> (2008)
	Basking shark	<i>C. maximus</i>	Mixed	May–July	Group foraging and social facilitation	Observational	Ebert (1991)
	White shark	<i>Carcharodon carcharias</i>	Mixed	n/a (anthropogenic influence)	Environmental conditions and reproductive strategies	Observational	Sims <i>et al.</i> (2000)
	Small-spotted catshark	<i>S. canicula</i>	Female	n/a captive	Social ethogram	Observational	Sperone <i>et al.</i> (2010)
	Nursehound	<i>Scyliorhinus stellaris</i>	Not specified	n/a captive	Social networks	Captive study	Jacoby <i>et al.</i> (2010)
	Smooth dogfish	<i>Mustelus canis</i>	Mixed	n/a captive	Social refuging	Captive study	Scott <i>et al.</i> (1997)
	Lemon shark	<i>N. brevirostris</i>	Mixed (juveniles)	Interactions predominantly May–December	Dominance hierarchies	Captive study	Allee and Dickinson (1954)
	Scalloped Hammerhead shark	<i>Sphyrna lewini</i>	Not specified	Daytime aggregation year round	Social organization	Captive study	Guttridge <i>et al.</i> (2009a, 2009b)
	Bonnethead shark	<i>Sphyrna tiburo</i>	Mixed	n/a captive	Social organization and Social refuging	Wild observational and Active telemetry	Guttridge <i>et al.</i> (2011) Kimley and Nelson (1984)
					Dominance hierarchies	Captive study	Myrberg and Gruber (1974)

this area have also been extensively catalogued using photo-identification methods outlined in Domeier and Nasby-Lucas (2007), which offers the prospect of monitoring individual co-occurrences at different coastal and oceanic locations to test ideas about preferential association (see Social grouping). The function of these aggregation events in such wide-ranging predators remains largely speculative, although social interactions in white sharks have now begun to be quantified (Sperone *et al.* 2010). Alternatively, within a coastal environment, Heupel and Simpfendorfer (2005) studied the movements and interactions of neonate blacktip sharks (*Carcharhinus limbatus*, Carcharhinidae) over a period of 3 years revealing persistent aggregation during daylight hours and dispersal at night. Sharks demonstrated high site fidelity when aggregating and seasonal patterning of interactions (Heupel and Simpfendorfer 2005). Although there are significantly fewer studies considering batoid aggregation behaviour, some species such as the spotted eagle ray (*Aetobatus narinari*, Myliobatidae) exhibit remarkable aggregation and schooling behaviour typically consisting of between 5 and 50 individuals, arranged in a variety of swimming formations (Silliman and Gruber 1999). It is not yet known whether social factors underpin this behaviour.

Aggregation behaviour of sharks documented in studies to date appears largely motivated by a desire to understand species abundance and distribution within a changing environment. Research on wide-ranging planktivorous elasmobranchs such as the giant manta ray (*Manta birostris*, Mobulidae) and the whale shark (*Rhincodon typus*, Rhincodontidae), for example, is generally aimed at describing site fidelity and ranging behaviour of individuals between areas/populations (Dewar *et al.* 2008), with a view to conserving known aggregation sites (Riley *et al.* 2010). Knowledge of the spatial and temporal dynamics of these events is extremely important, not least as it contributes to improved conservation and fisheries management practices for these species. It is unclear whether many of these aggregation events may also serve to facilitate some exchange of social information. It is possible, though, that species often considered solitary might in fact integrate some aspect of social interaction into their behavioural repertoire. Whilst we remain some way from determining the extent to which novel information is transmitted between conspecifics, studies examining social learning in elasmobranchs suggest that sharks have the cognitive

potential required for such information exchange (see Guttridge *et al.* 2009b for review).

Social grouping

In contrast to the burgeoning research on aggregation, there is a distinct paucity of literature on the descriptions and specific patterns of elasmobranch social behaviour (cf. Table 1). Springer (1967) identified this knowledge gap over 40 years ago whilst considering the social organization of the many species of shark in the Gulf of Mexico. Although unclear at the time, because of a lack of supporting evidence, Springer offered the view that '...some shark populations exhibit complex behaviour that constitutes part of their social organization', and based on anecdotal evidence from aerial surveys '...that large sharks (and rays) are often in groups and not randomly distributed'. In this early study, Springer observed synchronized, collective behaviours such as echelon swimming, milling and size assortment that have become indicative of social interaction in some shark species (Myrberg and Gruber 1974; Sims *et al.* 2000). Indeed, assortment by size, coloration, familiarity and kinship are all well documented in teleost fishes (see Krause *et al.* 2000 for review) and have been shown to confer individual benefits such as minimizing predation risk through phenotypic oddity and reducing competition and aggression between size classes (Hoare *et al.* 2000). Size assortment has also recently been demonstrated as important in the structuring of juvenile lemon shark groups (Guttridge *et al.* 2011), a study that represents the first quantification of associative preferences and social organization in a free-ranging shark population. It is worth emphasizing, for future research, the importance of empirical data and hypothesis testing as demonstrated by Guttridge *et al.* (2011) for what currently remains largely anecdotal evidence of social organization in sharks. This is important particularly because it is equally likely that assortment of individuals may occur through passive processes such as variable swimming speeds between different sized individuals or habitat features (e.g. temperature) that are favourable for some but not others (Croft *et al.* 2003; Wearmouth and Sims 2008).

In contrast to teleost fishes, experimental research on the social interactions of sharks has been few and far between (for exceptions see Guttridge *et al.* 2009a; Jacoby *et al.* 2010). The

earliest research into elasmobranch social behaviour began with Allee and Dickinson (1954), who conducted the first quantitative analyses of dominance and subordination in captive smooth dogfish, now known as the dusky smooth hound (*Mustelus canis*, Triakidae). Later, Myrberg and Gruber (1974) identified an extensive dominance hierarchy among mature bonnethead sharks (*Sphyrna tiburo*, Sphyrnidae). These data revealed a size-dependent dominance hierarchy and an apparent predominance of males over females. Direct observations and passive acoustic tracking of another closely related species, the scalloped hammerhead (*S. lewini*), showed highly coordinated schooling behaviour within large groups of individuals, made up almost exclusively of females (Klimley and Nelson 1984; Klimley 1987). The authors proposed a social refuging hypothesis during the resting phase of the sharks' diel behavioural cycle as foraging behaviour was never witnessed during schooling events (Klimley and Nelson 1984).

Mechanisms and functions of grouping

Aggregation

Many elasmobranch species demonstrate high levels of philopatric behaviour to specific habitat locations (Hueter *et al.* 2005). During early life stages particularly, site fidelity is common in sharks with shallow, coastal waters offering ideal nursery areas for juveniles to aggregate (Simpfendorfer and Milward 1993). Immature lemon sharks (*Negaprion brevirostris*, Carcharinidae) at a subtropical lagoon in Bimini, Bahamas, for example, disperse relatively slowly from their natal breeding grounds with locally born individuals being recaptured within the same areas up to 6 years after birth (Chapman *et al.* 2009). The shallow-water, mangrove habitat favoured by groups of juvenile lemon sharks offers suitable conditions for individuals to increase somatic growth in the warm prey-abundant waters whilst at the same time avoiding larger elasmobranch predators (Morrissey and Gruber 1993). This extended opportunity for juvenile lemon sharks to interact has clearly influenced the behavioural strategy of this species with large aggregations observed in both juvenile and adult phases of this species (Gruber *et al.* 1988; Wetherbee *et al.* 2007; Guttridge *et al.* 2009a). Site-attached behaviours periodically bring elasmobranchs together, for a variety of resource requirements. These aggrega-

tions are often associated with specific times of day or months of the year. Preferences for a specific thermal niche, for example, appear to favour adult females of some shark species, resulting in single-sex aggregation in warm, shallow coastal habitat (Economakis and Lobel 1998; Hight and Lowe 2007). Equally, aggregations of adult scalloped hammerhead sharks (*S. lewini*) utilize the inshore waters of Kaneohe Bay, Oahu, Hawaii, between the months of April and October for mating and delivery of pups (Clarke 1971) but, as previously discussed, are also known to form large daily social groups (social refuging) around underwater seamounts in the Gulf of California (Klimley and Nelson 1984). This species serves to illustrate the potential overlap between aggregation and social grouping behaviour in some elasmobranch species.

A widespread characteristic of shark aggregation is sexual segregation that may be influenced by a range of factors including sexual dimorphism in body size or differential activity budgets between the sexes (see Wearmouth and Sims 2008 for review). In many species of elasmobranch, asymmetry in gamete production and thus differential reproductive success from multiple mating events may be sufficient to cause very different behavioural strategies and movement patterns (Sims 2003, 2005). Different life-history traits between the sexes, for example, may select for male sharks to invest more time in pursuit of mates than female sharks that may themselves allocate a higher percentage of time in search of suitable environment conditions to aid gestation or egg incubation (Hight and Lowe 2007). Indeed, a high level of male harassment in some teleost fish has been shown to drive spatial segregation of the sexes (Darden and Croft 2008). Shark mating behaviour, however, is notoriously aggressive, with females often sustaining bite marks and serious abrasions to the body and pectoral fins (Carrier *et al.* 1994). Therefore, it is perhaps unsurprising that sexual segregation is relatively common among elasmobranchs (Ford 1921; Klimley 1987; Sims *et al.* 2001; Litvinov 2006; Mucientes *et al.* 2009). The need for females to avoid energetically expensive and potentially damaging multiple mating events is a commonly hypothesized mechanistic driver of single-sex, female refuging behaviour in sharks (Economakis and Lobel 1998; Sims *et al.* 2001) and sexually segregated schooling behaviour in teleost fish (Croft *et al.* 2006a; Darden and Croft 2008). Furthermore, with no recorded evidence of parental care observed in any species of

elasmobranch, it is possible that segregation might occur from a relatively young age (Litvinov 2006).

Despite such widespread sexual segregation, there comes a point when both males and females must find a mate and consequently mating aggregation behaviour might even occur within species that are typically found at very low densities. Group reproductive behaviours have been observed in several species (Carrier *et al.* 1994; Whitney *et al.* 2004) and have been closely linked to both transient and permanent environmental conditions such as increases in zooplankton abundance (Sims *et al.* 2000) and rocky reef habitat (Powter and Gladstone 2009), the latter indicating the possibility of discrete breeding populations even in some species that disperse widely. It seems apparent that there are numerous temporal as well as spatial influences on aggregation and segregation behaviour in elasmobranch fishes. One example is the dispersal of juvenile sharks of different sexes away from nursery habitat. Blue sharks (*Prionace glauca*, Carcharinidae) are the most widely distributed elasmobranch species in the epipelagic ocean environment, and they also demonstrate sexual segregation at the earliest age. Male blue sharks appear to move offshore very early in life (at <70 cm total length) and occupy dense aggregations around oceanic seamounts, seemingly leaving the females in shallower coastal waters until nearly three times this size (Litvinov 2006). Nearshore environments are commonly utilized by elasmobranch species to aggregate (Knip *et al.* 2010). It is evidently easier to study this type of behaviour in shallow coastal waters, and as such, aggregation at depth is currently best inferred from fisheries data (Girard and Du Buit 1999). However, nearshore habitats are likely to offer high levels of prey diversity and abundance for elasmobranch predators, and consequently, many species periodically return inshore to forage and/or breed, permitting juveniles a greater chance of survival in the shallow, sheltered waters (Heupel *et al.* 2004; Chapman *et al.* 2009). Behaviourally, these aggregation events may serve additional functions as well as protection from larger predators, given that some smaller benthic or demersal species occupy coastal habitat for the duration of their life (Sims *et al.* 2001; Dudgeon *et al.* 2008). Passive acoustic monitoring techniques have been employed to quantify the levels of site fidelity in leopard shark (*Triakis semifasciata*, Triakidae) aggregations. This study suggested that female leopard sharks selectively occupy warmer, inshore refuges as a means of

behavioural thermoregulation (Hight and Lowe 2007). It is hypothesized that thermoregulation behaviour serves to enhance the gestation and periods of embryonic development in this species, a theory not without support from observations of groups in other shark species. Sims *et al.* (2001, 2006) used a combination of active acoustic telemetry, archival tagging and laboratory experiments to explain the differential sexual strategies in another benthic predator, the small-spotted catshark (*S. canicula*). They concluded that the apparent spatial separation in this species was attributable to the females' ability to store sperm and thus avoid male copulation attempts during periods of gestation and egg laying (Sims *et al.* 2001). As a result, female *S. canicula* in the wild are seen in tightly packed groups on top of one another inside shallow-water, rocky crevices (Sims 2003; Fig. 2). This proposed male avoidance appears a significant selection pressure causing disruption among weakly socially associated females (Jacoby *et al.* 2010) and forcing them to occupy areas outside of their preferred thermal/metabolic niche (Sims 2003).

Social grouping

The adaptive significance of elasmobranch social behaviour is poorly understood despite a growing ecological threat to many species globally (Baum *et al.* 2003). During the juvenile phase of development, avoiding predation is a likely driver of aggregation (Morrissey and Gruber 1993; Economakis and Lobel 1998). Indeed in stingrays, the antipredator benefits of aggregation by cowtail



Figure 2 Aggregation of four female small-spotted catshark (*Scyliorhinus canicula*) in a narrow rock gully off Plymouth, UK. Female-only refuging aggregations are common in this species and are thought to arise from the avoidance of males. Photograph courtesy of Paul Naylor.

stingrays (*Pastinachus sephen*, Dasyatidae) are greater in heterospecific groups than in single-species groups, suggesting that a social mechanism is maintaining groups that have formed for protection. Heterospecific grouping is apparently because of the quicker flight responses and thus earlier warning of approaching predators by the reticulate whipray (*Himantura Uarnak*, Dasyatidae; Semeniuk and Dill 2006). Until recently, the mechanisms and functions underpinning social grouping in elasmobranchs have been speculative. Anecdotal evidence and observational data, however, still provide the most reliable assessment of social interactions particularly in wild sharks (Sims *et al.* 2000; Sperone *et al.* 2010) revealing some unusual adaptive mechanisms in some species. Predatory sevengill sharks (*Notorynchus cepedianus*, Hexanchidae) appear to utilize multiple feeding strategies depending upon the prey size and type. Sevengills are thought to use social facilitation and pack hunting strategies in order to tackle larger prey items such as Cape fur seals (*Arctocephalus pusillus pusillus*, Otariidae; Ebert 1991). More recently, the burgeoning popularity of studying animal social networks (Croft *et al.* 2008) accompanied by developments in computational and analytical power has resulted in more hypothesis-led studies of shark social behaviour under semi-wild or captive conditions (Guttridge *et al.* 2009a; Jacoby *et al.* 2010).

Active partner preference has long been inferred in teleost fishes using binary choice experimental manipulation (Lachlan *et al.* 1998; Griffiths and Magurran 1999; Croft *et al.* 2006b). Whether slow-growing, wide-ranging elasmobranchs are also capable of showing active partner preference has remained unexplored until recently. Guttridge *et al.* (2009a) used similar binary choice experiments to demonstrate that juvenile lemon sharks (*N. brevirostris*) show significant associative preferences for both conspecific over heterospecific (nurse sharks, *Ginglymostoma cirratum*, Ginglymostomatidae) groups and size-matched over non-size-matched conspecifics, clearly indicating an overall active preference for social behaviour. Active partner preference demonstrates a social mechanism by which some sharks appear to maintain social groups. These social preferences may in fact be driven by population-level processes such as intersexual conflict whereby the individuals associating are each attempting to maximize their own reproductive success. The impact of male behaviour upon female small-spotted catshark (*S. canicula*) aggregations, for

example, was recently tested in the laboratory and showed that the strength of social bonds between females within aggregations is non-random (i.e. social groups were exhibited), but was also unevenly distributed, and that weakly associated females may be more susceptible to disruption by male behaviours that are costly to females (Jacoby *et al.* 2010). Inferring this level of information in wild populations, though, is clearly more challenging.

In an attempt to summarize the relatively scarce literature surrounding the functions of elasmobranch social groups, it is important to draw again on comparisons with their teleost counterparts. The benefits of schooling behaviour in teleost fish have been shown to include a variety of antipredatory functions (Magurran 1990; Krause and Ruxton 2002), reduced energetic demand and oxygen consumption (Herskin and Steffensen 1998), information transfer and cooperation (Croft *et al.* 2006b) and more efficient collective decision making (Ward *et al.* 2008). It is unknown which of these, if any, apply to apex predatory sharks despite a number of species that have been documented schooling in large numbers (Klimley 1985; Wilson 2004). In a comparative study of teleost and elasmobranch schooling behaviour, Klimley (1985) observed that scalloped hammerhead shark (*S. lewini*) schools comprised predominantly of females with larger individuals aggressively vying for central positions within the school. This study concludes social refuging behaviour and potential exchange of information between resting sharks (Klimley 1985). It has been discussed that sharks are capable of active partner choice (Guttridge *et al.* 2009a, 2011) implying some form of recognition or phenotype matching mechanism. If so, there are probable benefits to associating with unfamiliar conspecifics, as these individuals are arguably more likely to possess information about resources outside an individuals' home range (Goodale *et al.* 2010). Thus, these refuge aggregations, particularly in facultative schoolers like the scalloped hammerhead, may serve to disseminate novel information throughout a population via fission–fusion behaviour and social learning, something which has been qualified in free-ranging French grunts (*Haemulon flavolineatum*, Haemulidae) on coral reef habitat (Helfman and Schultz 1984). Within these social groups, it is also probable that there is some degree of hierarchy and/or assortment between individuals (Allee and Dickinson 1954; Myrberg and Gruber 1974).

Alternatively, social groups may be rather brief and sporadic, functioning merely as a means of finding and mating with the opposite sex (Sims *et al.* 2000). The basking shark (*Cetorhinus maximus*) is the world's second largest fish, and they appear to conduct annual social behaviours associated with tidal and thermal oceanographic fronts. These behaviours include close following behaviour, parallel and echelon swimming in what are thought to be courtship displays that include full body breaching, although mating has never been conclusively observed in this species (Sims *et al.* 2000; Fig. 1).

To conclude this section on the patterns, mechanisms and function of aggregation and social grouping behaviour in elasmobranchs, it is important to reiterate that evidence of social interaction among sharks is, in part, likely to result from common behavioural strategies such as migration and collective movement or aggregation around a specific resource. These may include thermal habitat for gestation or incubation (Hight and Lowe 2007), suitable topographic or environmental features to avoid male harassment (Sims *et al.* 2001, 2005) or oceanographic attributes which provide a familiar 'way-point' on a migratory route (Jorgensen *et al.* 2009). Determining the relative influence of social interaction on the initial formation of shark aggregations is still a relatively new endeavour, but will surely prove an interesting and challenging area for future research.

Methods for studying shark social behaviour

Tracking and telemetry

The spatial and temporal dynamics of gregarious animal interactions are highly complex. Tracking these interactions through time requires extensive records of specific individuals, something which has, perhaps unsurprisingly, proven extremely difficult to obtain for free-ranging elasmobranchs. Acoustic telemetry has developed considerably in the past 25 years, particularly in its application to monitoring the movements and behaviours of marine fish such as sharks (Sims 2010). As a functional, yet rather more labour-intensive predecessor to passive telemetry, active tracking using ultrasonic telemetry relies on following an acoustically tagged shark from a boat using a directional hydrophone. This technique has proved successful in revealing polarized schooling behaviour in several large elasmobranch predators (Klimley and Nelson 1984;

McKibben and Nelson 1986). More recently, passive acoustic and satellite telemetry techniques have shed light on the movements and interactions of elasmobranch species at a variety of spatial scales (Eckert and Stewart 2001; Sims *et al.* 2006). Although expensive to begin with, the continual development of smaller and cheaper acoustic tags has promoted the widespread use of passive acoustic telemetry as a means of tracking large numbers of teleost and elasmobranch species as they interact through space and time (Sims 2010). Heupel and Simpfendorfer (2005), for example, used omnidirectional passive acoustic receivers to study the movement and interactions of juvenile blacktip sharks (*C. limbatus*, Carcharhinidae). Nearest neighbour analysis of the telemetry data revealed that shark aggregations were more common in the late summer during which there were also strong diel patterns to aggregation events (Heupel and Simpfendorfer 2005). This serves to demonstrate that it is now possible to monitor continuously multiple individual sharks and their movements within a designated area, provided the receivers encompass at least a good proportion of the activity space (or home range) of the species in question. Given that arrays of acoustic receivers are often spatially limited, this often means studies are restricted to those on juvenile or neonate sharks that have smaller core activity spaces. However, large-scale deployments for long periods in deep-water areas are now being made to track adult movement patterns (Fig. 3). Regardless of spatial scale, though, this technique provides one of the few means to determine the habitat use and home range dynamics of sharks (Heupel *et al.* 2004) in addition to their tendency to form large daily aggregations (Economakis and Lobel 1998).

Determining the precise occurrence and scale of social interactions from presence/absence data on omnidirectional acoustic receivers is still problematic without high levels of range overlap. Field of view overlap of receiver stations is often traded off against increased area coverage within acoustic arrays, and consequently, new technology that accounts for proximity of individuals is required to facilitate the analyses of social behaviour in wide-ranging animals (Krause *et al.* 2011). Novel studies on both Galapagos sharks (*Carcharhinus galapagensis*, Carcharhinidae; Holland *et al.* 2009) and juvenile lemon sharks (Guttridge *et al.* 2010) employed specialized, prototype transmitter/receiver tagging techniques or proximity loggers to test the reliability



Figure 3 Large-scale acoustic receiver arrays are being used to track movements of adult sharks and rays over large scales and time periods. (a) Acoustic receivers borne on 2-m-high seabed landers enable passive tracking of transmitter-tagged fish in open ocean habitats and over many years, with data upload from receivers by ship every few months. (b) A small-eyed ray *Raja microocellata* fitted with an acoustic transmitter mounted on a regular Petersen disc. Individuals of this species have been tracked for over 1 year using an array of seabed landers. Photographs courtesy of the Marine Biological Association of the UK.

of coded data exchange between sharks within a given range of one another. The devices used in the lemon shark study were capable of detecting individuals within 4 m (~ 4 body lengths) of each other, but rarely when at 10-m distance, emphasizing the

value of this technique for recording close interactions between individual sharks (Guttridge *et al.* 2010). Once developed further, these techniques offer huge scope for advancing our understanding of the ways in which animals interact in the wild. It seems likely that significant rapid progress will be made by combining this new technology with social network analyses (Krause *et al.* 2011).

Social network analysis

There are a variety of interactions between group living animals that have the potential to greatly influence population structure and dynamics. Social animal systems may be highly complex, involving hundreds and sometimes thousands of individuals but can still be successfully interpreted by understanding the influence of individuals or groups at different scales. Social network theory offers a useful tool with which to study social organization on a multitude of levels, from individual behaviours to population-level processes (Krause *et al.* 2009). Central to this theory is the idea that individuals differ in their importance within a network and thus their ability to influence group decisions (information transfer) or indeed pathogen transmission. Network analysis is therefore becoming increasingly popular among behavioural ecologists, and interested readers should be directed to Croft *et al.* (2008) for a more thorough discussion on its application to animal grouping behaviour. Social network analysis provides a means of analysing the global properties of a system based on a variety of dyadic interactions (an interaction or relationship between two individuals) from aggression bouts and dominance hierarchies to cooperation and reciprocal altruism (Krause *et al.* 2000; Croft *et al.* 2005). Networks can be represented through simple graphical format where each individual in a group is represented by a node and a tie or edge between two nodes represents some form of interaction (Fig. 4a). Network diagrams may be enhanced by representing the edges between nodes as *directional* indicating an asymmetry in the observed dyadic interaction (Fig. 4b) or *weighted*, pertaining to the frequency an interaction is observed between individuals (Fig. 4c). Furthermore, accompanying every descriptive network diagram is a corresponding $n \times n$ association matrix upon which statistical analyses of the association data may be performed, such as testing for non-random associative preferences or clustering within the network.

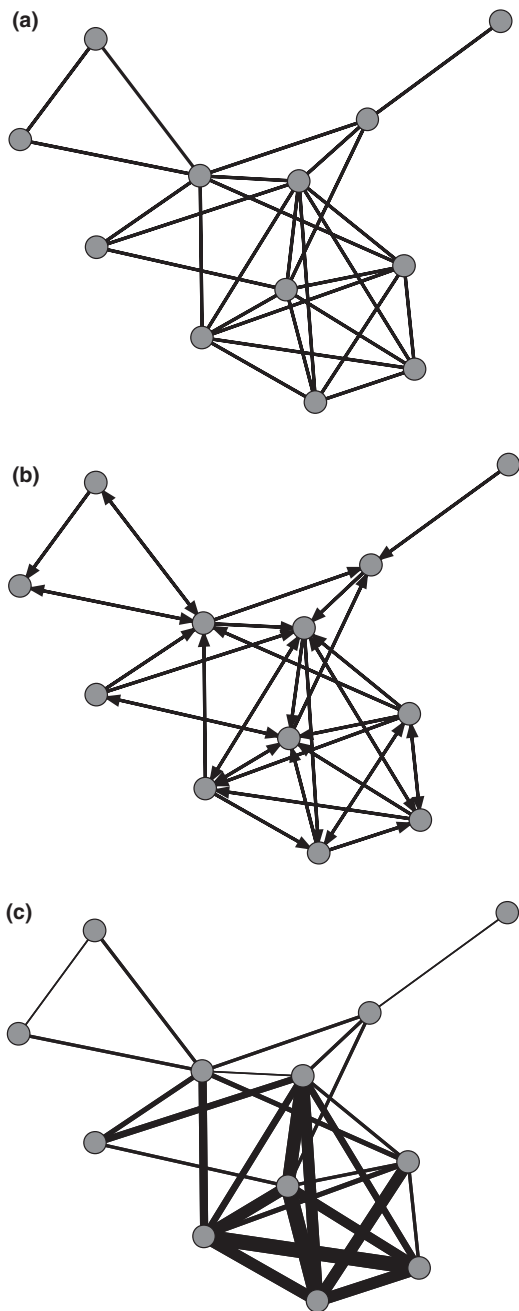


Figure 4 Illustration of a simple (a), a directed (b) and a weighted (c) network where circles represent nodes (i.e. individual organisms) and the ties between them represent interactions (i.e. aggressive displays and social grouping).

Perhaps one of the major benefits to studying interaction behaviour in a network format is the ability to overlay large amounts of biological or 'attribute' data on top of a social network.

Substantial insight can then be gained by highlighting within the network data those individuals of a particular size, sex, coloration or age class. For example, we may ask whether the social connectivity of an individual can be predicted by its attributes or whether there is positive or negative assortment in the network based on phenotypic traits. Furthermore, it might be of particular interest to directly compare the matrices of social interaction with data on the genetic relatedness of individuals within a group, giving potentially important insight into the benefits, or indeed costs, of associating with kin (Hain and Neff 2007; Frère *et al.* 2010). Statistical analyses may then be performed either on the complete network or on data restricted to specific attribute or kin groups allowing considerable flexibility for specific hypothesis-driven research. Care needs to be taken however, when testing hypotheses using social network data as relational data are non-independent and thus often violate the assumptions of common statistical approaches (see Croft *et al.* 2011 for a discussion and a review of approaches to overcome this issue).

The variability in interactions between different species is an important consideration when determining data collection techniques. What constitutes a social interaction, and at what scale we might expect this interaction to occur, largely depends on the species in question. Group resting behaviours, such as those observed in some benthic elasmobranchs (Sims *et al.* 2001; Hight and Lowe 2007), command a different set of associative parameters at a different scale, than those required for studying wide-ranging facultative schoolers, for example (Klimley 1985). A social network, however, is only of interest if it accounts for the suite of natural behaviours exhibited by the target species, and it is therefore crucial to be mindful of incorporating both biological relevance and scale when defining interaction parameters (Lusseau *et al.* 2008). With these considerations in mind, an implicit understanding of these interactions demonstrates how sociality may influence individual- and group-level behaviour (Wey *et al.* 2008). Furthermore, by integrating attribute data such as sex, age or size within the social network, the biological relevance of aggregation behaviour becomes clearer (Wolf *et al.* 2007; Croft *et al.* 2008) with foraging behaviour (Morrell *et al.* 2008), sexual harassment (Darden *et al.* 2009) and size assortment (Croft *et al.* 2005) having all been explored in teleost fish using a social network approach. These studies, among

others, also serve to reiterate the pivotal role teleost fish have thus far played as a model for understanding the ecological and evolutionary processes dictating the development of sociality within fish populations. Similar analyses, however, have also been adopted to help reveal the complex community structuring in a number of wide-ranging marine mammals (Connor *et al.* 2001; Gowans *et al.* 2001; Lusseau 2003) using photo-identification techniques that are now being adopted to study elasmobranch aggregations (Domeier and Nasby-Lucas 2007; Riley *et al.* 2010). The use of such photo-identification in concert with social network analyses might enable more detailed understanding of shark aggregation events that could prove important in the future management and conservation of many vulnerable elasmobranch species.

Implications and future directions

So far, we have discussed the individual benefits that elasmobranchs are likely to gain when aggregating or forming social groups. Anthropogenic influences impose costs at the population level (i.e. fishing pressure and habitat destruction) that are likely to be exacerbated by behavioural mechanisms such as grouping/schooling behaviour, sexual segregation and site philopatry (Wearmouth and Sims 2008; Mucientes *et al.* 2009). Sharks pose a particularly interesting and indeed worrying model for examining these costs, especially given their K-selected life-history traits and the fact that many species occupy an apex position within their ecological niche and, thus, their ability to influence processes at lower trophic levels (Heithaus *et al.* 2008). By repeatedly aggregating *en masse* at specific locations, at specific times, slow-growing elasmobranchs make themselves particularly vulnerable to overfishing (Mucientes *et al.* 2009). Now, with modern and efficient fishing equipment, countries where shark landings represent a major economic advantage can substantially increase their catch per unit effort through simple targeted fishing practices and knowledge of these ecological events. One example of this is the basking shark (*C. maximus*, Cetorhinidae) fishery at Achill Island, Co. Mayo, Republic of Ireland where 12 360 sharks were landed between 1947 and 1975 (Sims 2008). Of these total reported landings, 75% were caught between 1950 and 1956 with mean catch per year being reduced from 1323 individuals to just 60 by 1962–75. Basking sharks have long gestation

periods (between 1 and 2 years) and show particularly low fecundity even among elasmobranchs. It is proposed that one explanation for this dramatic reduction in this north-eastern Atlantic population is that a large majority of the sharks taken were probably mature adult females engaging in seasonal coastal aggregation behaviour (Sims *et al.* 2000; Sims 2008). This putative differential exploitation of the sexes is pertinent when we consider that females of some pelagic shark species seek shallow inshore waters during parturition (Feldheim *et al.* 2002; Hueter *et al.* 2005), potentially enhancing encounter rates with fishing vessels. Furthermore, it highlights the urge for more detailed research on the composition of shark aggregations and for the evaluation of minimum group size thresholds at which reproduction will remain viable within a population, particularly for short-term mating aggregations in more solitary species.

In fisheries where sharks are not the principal target species, such as pelagic longline fisheries (for tunas and billfish), the tendency for pelagic shark species to school can increase elasmobranch by-catch, further inflating mortality rates (Gilman *et al.* 2008). Worldwide declines in shark populations and the ecological consequences of these declines have been reported widely (Myers and Worm 2003; Worm *et al.* 2006; Myers *et al.* 2007; Heithaus *et al.* 2008). One consideration to help stem these trends must be conservation and management strategies that consider these behaviourally mediated increases in fisheries mortality. With philopatric behaviour being such a prevalent characteristic among elasmobranch populations, there are now calls for shark fisheries to incorporate spatially structured management strategies that account for the degree of site philopatry of the respective target species (Hueter *et al.* 2005; Robbins *et al.* 2006; Knip *et al.* 2010). Furthermore, the use of detailed analyses of aggregation events, including their seasonality and dynamics, should also be considered in future management policies (Mucientes *et al.* 2009).

A second implication for elasmobranch grouping behaviour is an increase in popularity among people wishing to dive with sharks and rays with a concomitant surge in ecotourism operations around the world. In parts of the world where elasmobranchs were once prized for their meat and fins, communities are now adjusting their focus to conserve these species and their aggregation sites. Ecotourist ventures seek to utilize local knowledge

and ecological events, such as periodic grouping, in offering experiences interacting with animals that would otherwise be targeted for food or fins. Whether tourism offers a sufficient economic alternative to fishing for some communities is still open to debate (Topelko and Dearden 2005) and is, to a large extent, dictated by culture-driven consumer demand, particularly within the Far Eastern markets where shark products are prized as delicacies and for medicinal purposes. From a conservation perspective, ecotourist ventures appear important in the publicity of threatened elasmobranch species at a global level. Furthermore, under the correct management, ecotourist operators may also provide an invaluable source of temporal data on the nature of shark aggregations that may inform future conservation initiatives (Theberge and Dearden 2006).

Conclusions

The complexities of conserving elasmobranch populations through a combination of scientific research and conservation strategies go well beyond the scope of this review. However, briefly touching on these issues serves to demonstrate the holistic approach required in this endeavour. Furthermore, whilst studying the temporal interactions of large wide-ranging sharks is clearly a challenge, there are a number of intermediate-sized species that still fulfil elevated predatory functions within the food web, but that are also highly tractable sharks to maintain in groups under laboratory conditions (Sims 2003). Benthic sharks, such as the widely distributed small-spotted catshark (*S. canicula*, Scyliorhinidae), are known to demonstrate site philopatry and single-sex refuging behaviour and may prove a useful species in which to tackle some of the questions this review highlights.

Developments in marine tracking technology and visual identification methods continue to enhance our knowledge of site philopatry and refuging behaviour in elasmobranchs. Determining what drives predatory elasmobranchs to group is important, not only for understanding interactions at lower trophic levels but also for the future conservation and management of populations and areas associated with their fundamental life-history traits. This review offers an appraisal of where and when such groups have been documented to occur and considers some of the suggested mechanisms and functions of this behaviour.

Finally, social network theory is appealing in its relevance to our own behaviour, and the idea of animal social networks is both engaging and accessible. Detailed knowledge of how sharks associate in the wild will provide insight into population distribution and assortative behaviour such as sexual segregation, which can substantially influence fishing mortality (Wearmouth and Sims 2008; Mucientes *et al.* 2009). It is therefore hoped that this will encourage a more fine-scale approach to studying grouping behaviour in sharks and rays.

Acknowledgements

This study was supported by a Fisheries Society of the British Isles studentship for postgraduate study to D.M.P. Jacoby. D.P. Croft was supported by the NERC (NE/E001181/1) and D.W. Sims by an MBA Senior Research Fellowship and by the UK NERC *Oceans 2025* Strategic Research Programme (Theme 6: Science for Sustainable Marine Resources). D.M.P. Jacoby is grateful to Tristan L. Guttridge, Serene Hargreaves and two anonymous referees for feedback and improvements on earlier drafts.

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