



Repeated long-range migrations of adult males in a common Indo-Pacific reef shark

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Abstract The grey reef shark, *Carcharhinus amblyrhynchos*, is one of the most abundant coral reef sharks throughout the Indo-Pacific. However, this species has been critically impacted across its range, with well-documented population declines of > 90% attributed to human activities. A key knowledge gap in the successful implementation of grey reef shark conservation plans is the understanding of large-scale movement patterns, along with the associated biological and ecological drivers. To address this shortfall, we acoustically monitored 147 adult and juvenile grey reef sharks of all sexes for more than 2 yr across the New Caledonian archipelago, West Pacific. Here, we document multiple adult males undertaking return journeys of up to nearly 700 km in consecutive years. This constitutes the first evidence of repeated long-range migrations for this species. Although only a limited number of adult males were definitively tracked undertaking

migrations, similar timing in changes in the detection patterns of a further 13 animals, mostly adult males, suggests this behavior may be more common than previously thought. The paucity of evidence for juvenile migrations and timing of adult movements suggest that mating is the motivation behind these migrations. Our results have important implications for management, given the potential of mature individuals to recurrently travel outside managed or protected areas. Future management of this species clearly needs to consider the importance of large-scale migratory behaviors when developing management plans.

Keywords Reef shark · Migration · Male-biased dispersal · Telemetry · New Caledonia

Introduction

Migration is an iconic and critical movement pattern across the animal kingdom. The terrestrial environment has many examples of animals migrating for food acquisition, including wild geese (Owen and Gullestad 1984) and

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monarch butterflies (Urquhart and Urquhart 1978) traveling between winter and summer grounds, or wildebeest herds following water and suitable grazing grounds in the Serengeti (Thirgood et al. 2004). Despite the inherent difficulty in tracking marine animals over long distances and time periods, some migrations are similarly documented for large marine vertebrates. These include baleen whales (Katona and Beard 1990; Double et al. 2014), sea turtles (Hays et al. 1999; Read et al. 2014), tiger sharks (Werry et al. 2014) and tunas (Block et al. 2005), each of which undergo long seasonal migrations between feeding and reproductive grounds. However, such migratory movements are poorly documented in elasmobranchs, particularly in smaller species. Migrations can put these species at risk, as such movements can bring them to face numerous threats and to travel beyond the scale of traditional management units (Harrison et al. 2018).

Shark migrations are thought to be driven by several biological and environmental factors. Temperature variations are a common cause of seasonal shark movements, through either direct or indirect means. Lemon sharks, *Negaprion brevirostris*, maintain their thermal range by migrating along the Florida coast in response to seasonal changes in water temperature (Reyier et al. 2014). Similarly, Port Jackson sharks, *Heterodontus portusjacksoni*, show comparative summer–winter movement patterns along the south-east coast of Australia (Bass et al. 2017). Dusky sharks, *Carcharhinus obscurus*, seasonally migrate along the coast of South Africa. However, this is more likely an indirect response to temperature, as they follow the winter migrations of the sardine, *Sardinops sagax* (Hussey et al. 2009). The reproductive cycle of species, including mating and parturition, can also be a driver behind sharks migrations. Annual and bi-annual migrations for reproduction have, respectively, been observed in grey nurse sharks, *Carcharias taurus*, along the east coast of Australia (Bansemmer and Bennett 2011) and great white sharks, *Carcharodon carcharias*, across the Eastern and Western Pacific (Domeier and Nasby-Lucas 2013; Bruce and Bradford 2015; Robbins et al. 2015). Similarly, sandbar sharks, *Carcharhinus plumbeus*, also seasonally relocate toward likely mating sites in Hawaii (Papastamatiou et al. 2010).

The grey reef shark, *Carcharhinus amblyrhynchos*, is one of the most abundant sharks on tropical Indo-Pacific coral reefs. However, severe depletions in populations have been documented across its range. Reductions in abundance of over 90% have been reported in New Caledonia (Juhel et al. 2017), the Australian Great Barrier Reef (GBR; Robbins et al. 2006), and across the Hawaiian Islands (Friedlander and DeMartini 2002). This is a serious cause for concern, given that grey reef sharks exert both

direct and indirect effects on prey species abundance and distribution (Rizzari et al. 2014; Rasher et al. 2017), which can extend to a wide variety of coral reef prey species (Robbins and Renaud 2015; Roff et al. 2016). Given the potential role grey reef sharks may play in reef trophodynamics, factors relevant to this species' conservation and vulnerability, such as movement patterns and migratory behavior, are essential to understand.

Dispersal patterns are relatively well documented in grey reef sharks. On the world's largest contiguous coral reef, the Australian GBR, high levels of mitochondrial DNA differentiation have been found in the grey reef shark population, particularly for female sharks (Momigliano et al. 2017). However, relatively low levels of nuclear DNA differentiation also occur (Momigliano et al. 2015), suggesting greater levels of male movement. This hypothesis of female philopatry in this species, with gene dispersal biased toward males, is empirically supported by limited movements of tagged females observed during the parturition season, combined with higher rates of movements for male grey reef sharks in the central GBR (Espinoza et al. 2015). Although grey reef sharks generally show high levels of residency (Vianna et al. 2013; Espinoza et al. 2015) and long-term site-fidelity (Field et al. 2010; Barnett et al. 2012), satellite and acoustic telemetry have revealed occasional long-range movements of up to 900 km from tagging location (Barnett et al. 2012; White et al. 2017).

These large-scale movements of grey reef shark have yet not revealed any cyclical patterns, nor directionality, which could be considered as evidence of migration (Dingle and Drake 2007). Yet, such behavior is certainly possible, and would explain some of the large-scale male-biased genetic and dispersal patterns previously documented (Momigliano et al. 2015, 2017). Understanding the extent of the potential bias toward male dispersal is important for population health assessment, as this introduces further complexity in population dynamics. Moreover, the existence of migrations in grey reef sharks has large implications for the management of this species as current measures are often based on spatial fishing regulation (i.e., GBR), whose benefits would be negated for the components of the population migrating outside protected areas.

This study aims at determining if grey reef sharks, and especially males, are migrating. To achieve this, 147 sharks were fitted with acoustic transmitters and their long-range movement patterns were investigated over consecutive years across the New Caledonian archipelago. Our study provides novel information on the movement behavior of the grey reef shark and discusses its conservation and population dynamics implications.

Materials and methods

Study area

New Caledonia is a vast archipelago located in the Coral Sea, West Pacific. It has a 400 km-long main island surrounded by a continuous barrier reef encompassing one of the largest coral reef lagoons in the world. The main island's barrier reef is characterized by a strong gradient of human impact, ranging from the densely populated southern capital of Noumea to the uninhabited northern lagoon (D'Agata et al. 2016; Juhel et al. 2017, 2019; Fig. 1). The archipelago also includes remote atolls, such as D'Entrecasteaux atolls, separated from the main island northern lagoon by a 35 km-wide deep sea channel, and Chesterfield atoll, located in the center of the Coral Sea, more than 400 km west of the main island.

Acoustic receiver array

Sixty-two VR2W acoustic receivers (VEMCO Ltd., Halifax, Canada) were deployed from July 2015 to November

2017 in four regions of the New Caledonian archipelago (D'Entrecasteaux, Chesterfield, Great Northern Lagoon [GNL], Noumea; Fig. 1). Eight additional receivers were deployed along the west coast of the main land to monitor inter-regional movements. Receivers were anchored on the reef slope at 20 m depth, approximately 1 m from the substrate facing upwards. This configuration has previously been found to be suitable for monitoring grey reef sharks on coral reef habitats (Field et al. 2010; Heupel et al. 2010). Moorings consisted of a 3 m-long nylon rope, maintained vertically by 20 cm-wide pressure-proof buoy, and attached to the reef matrix by a 2 m-long galvanized steel chain and shackle. Receivers were attached to the rope with cable ties, and covered with three layers of antifouling paint to prevent benthic organisms from colonizing the sensor and impairing reception performance (Heupel et al. 2008). Data were downloaded and batteries replaced at least once a year. Range tests were performed over 33 receivers of the array and revealed decreasing detection probability with increasing distance, following a sigmoidal curve with $D_{50} = 153$ m (distance for which 50% of emissions are detected, see ESM A for more details).

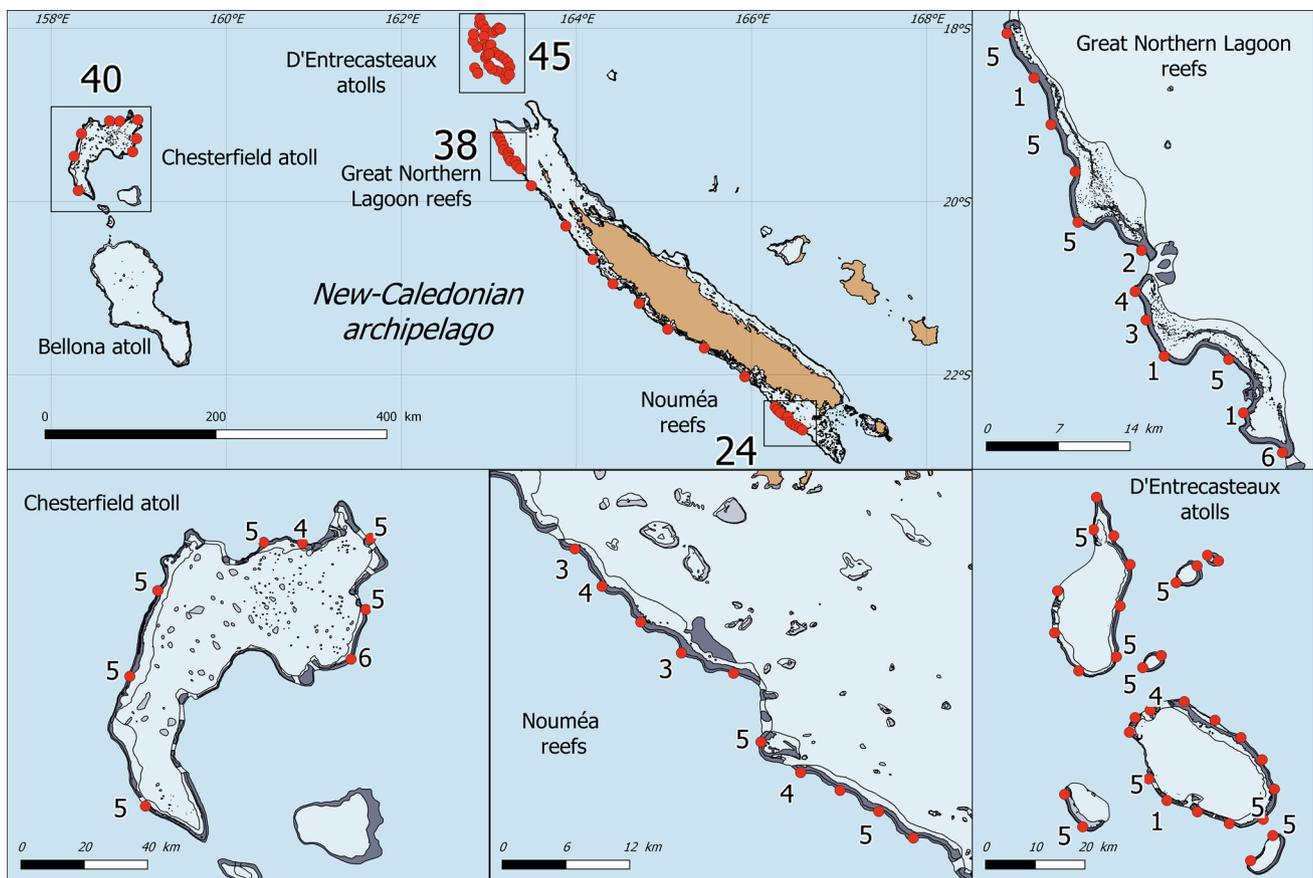


Fig. 1 Acoustic receivers array and sampling effort. Each red dot represents a VR2W acoustic receiver. Numbers of caught and tagged grey reef sharks, *Carcharhinus amblyrhynchos*, for each region and at each receiver location are indicated

Shark tagging

A total of 147 grey reef sharks were tagged along the outer slope of barrier reefs, at some of the locations where receivers were deployed (Fig. 1). Sharks were caught on a 16/0 barbless circle hook attached to a floating drum line. Hooks were removed from sharks before release when possible. Captured animals were processed while supported in dorsal posture in a tonic state, alongside a small run-about, where total length (TL), sex and maturity stage were determined. Maturity stage was determined for males based on the extension and calcification of the claspers; for females it was extrapolated from total length according to Robbins (2006). Sharks were internally tagged with V16 acoustic coded transmitters (68 mm × 16 mm; frequency: 69 kHz; high power output; transmission delay times ranging from 30 to 90 s; VEMCO Ltd., Halifax, Canada).

Individual movement patterns

Each shark's detection pattern was individually examined and categorized as migratory or non-migratory, and resident or not. Sharks were considered migratory if they underwent return trips outside their tagging region identified by detections on acoustic receivers leading away from the tagging region and subsequently returning to it. The timing of recorded migrations were compared and used to identify potential seasonal patterns in sharks' behavior. Where possible, a "migration season" was defined as the months encompassing all migrations events. Sharks were considered resident if they were detected on their tagging region array on all months outside the migration season. Resident migratory sharks referred to animals that were both residents and migratory, as migratory behavior did not exclude individuals from being resident for the remaining non-migration season.

Migratory sharks

For resident migratory individuals, the duration of absences from tagging region that corresponded to migration events could be measured. A minimum migration duration (MMD) was thus defined as the minimal value observed among all these measures. For each migration event, maximal recorded distance was calculated as the most direct sea distance between the furthest receiver reached during this migration and the closest receiver of the tagging region array. To identify any potential link between maximal recorded distance and shark body length, a linear model was built with shark total length and shark identity as predictor variables. Swimming speeds between receivers during a migration event were calculated using the departure and arrival dates and times at each receiver and their

most direct sea distances. The correlation between maximal recorded distance and absence duration for each migration event was also analyzed.

Potential migratory sharks

Some non-resident but migratory sharks may have been tagged during a migration event, thus remaining mostly undetected year-round in their tagging region except during the migration season. In order to attempt identifying such individuals, we considered that migratory behavior was possible for animals that were present in their tagging region at most one month outside the migration season and at least one month during the migration season.

Some resident migratory sharks may also have migrated to regions outside our receiver array. A two-step procedure was used to attempt identifying such migratory animals. First, we identified resident sharks that were undetected for periods longer than the MMD during the migration season, assuming that the MMD could be used as a benchmark to determine whether these periods were long enough to allow migration to occur. Second, Wilcoxon paired tests were used to assess if maximal absence during the migration season was longer than absences outside the migration season, considering that similar absence durations should not raise particular suspicion about a migratory behavior.

Residency and mobility within the tagging region

To test whether residency varied with gender and maturity stage, proportions of resident adult males, adult females and juveniles were compared with a Pearson's χ^2 test. For resident individuals, mobility was calculated as the cumulative straight-line distance travelled between consecutively visited acoustic receivers inside the shark's tagging region. Mobility values were calculated separately for the migration and the non-migration season and standardized to daily values. The ratio of mobility between the two seasons was calculated and then compared to one for adult males, adult females and juveniles with a two-sided Wilcoxon test. Here, a ratio of one indicates similar mobility during and outside the migration season, and a ratio greater than one indicates greater mobility during the migration season.

Results

Among the 147 grey reef sharks fitted with acoustic transmitters, 30 showed no detection after a 2-week post-capture period and were subsequently excluded from all analyses. Three other individuals were excluded from analyses, as the receiver they were tagged at was lost,

preventing identification of their residency status. These three animals were never detected outside their tagging region. Analyses were therefore performed on 114 individuals, comprising 51 adult males, 18 adult females and 45 juveniles (Table 1). Overall, these individuals were monitored over a 29 calendar-month period, equating to 2215 individual tracking months.

Three main movement patterns were identified in relation to migratory behavior, with (i) six individuals showing unequivocal evidence for migration, (ii) thirteen individuals showing potential migratory behavior, and (iii) 46 individuals showing unequivocal absence of migration. Data were insufficient to categorize the remaining 49 individuals.

Evidence of long-range migration for six adult males

Six sharks (IDs 92, 97, 101, 104, 108 and 111) underwent a long-range return migration between July and September, travelling up to 340 km from their tagging region. All were similar-sized adult males (mean TL 160 ± 5 cm SD) caught at Noumea. Migrations consisted of consecutive northward detections along the west coast, followed by a southward return. Migrations were observed on two consecutive years (2016 and 2017) for four individuals (IDs 92, 97, 101 and 104; Fig. 2) and on a single year (2017) for the remaining two animals (IDs 108 and 111; ESM B), totalling ten conclusive migration events. Detections off the west coast receivers corresponding to the migrations were temporally consistent across the 2 yr, occurring between 17 July and 13 September in 2016, and between 2 July and 23 August in 2017. A migration season was thus identified as July–September. The two individuals showing a single year's migration (IDs 108 and 111) were tagged in late September 2016, which thus appears too late to detect migration that year.

All but one migratory shark were resident to the Noumea region (Fig. 3). While IDs 92, 97, 101, 104 and 108 left their region of residency in Noumea between July and September, ID 111 was detected only briefly in this region in both 2016 and 2017. Instead, this individual was repeatedly detected on the *Bourake* receiver, 53 km north of Noumea, suggesting residency in this area (ESM B).

Absence periods corresponding to migration events were measured for the five resident migratory sharks and ranged from 14 to 86 days, with an average of 41 days (SD = 24 days). The minimal migration duration (MMD) was thus defined as 14 days. Maximal recorded distance from Noumea for the ten migration events ranged from 113 to 340 km, with an average of 233 km (SD = 78 km). The duration of absence from Noumea was not correlated to travelled distance (Spearman's $\rho = 0.56$, p value = 0.11), indicating that sharks either swam at different speeds, paused during their journeys or undertook travel outside the acoustic array range. Linear regression of the maximal recorded distance over shark length and identity resulted in a good fit (model p value = 0.003, adjusted- $R^2 = 0.94$) and revealed that maximal recorded distance was better explained by shark identity (80% of total explained variance) than shark length (20% of total explained variance). This implies that sharks travelling far on a given year were also travelling far on the following year. Swimming speeds recorded for movements between the west coast receivers ranged from 1.49 to 80 km/day, with an average of 31 km/day.

Comparison with other individual's detection patterns

Apart from the six migratory individuals, only three other sharks were detected outside their tagging region. Once again, all were adult males. However, their movement

Table 1 Gender, ontogenetic stage and sex ratio of grey reef sharks sampled in the four studied regions

	Chesterfield	Entrecasteaux	Great Northern lagoon	Noumea
Juvenile female	17	5	4	0
Adult female	0	11	5	2
Juvenile male	5	5	4	5
Adult male	10	14	11	16
Sex ratio	Balanced (binomial test p value = 0.86)	Balanced (binomial test p value = 0.74)	Balanced (binomial test p value = 0.31)	Male-biased (binomial test p value < 0.001)
Adult sex ratio	Male-biased (binomial test p value = 0.002)	Balanced (binomial test p value = 0.69)	Balanced (binomial test p value = 0.21)	Male-biased (binomial test p value = 0.001)

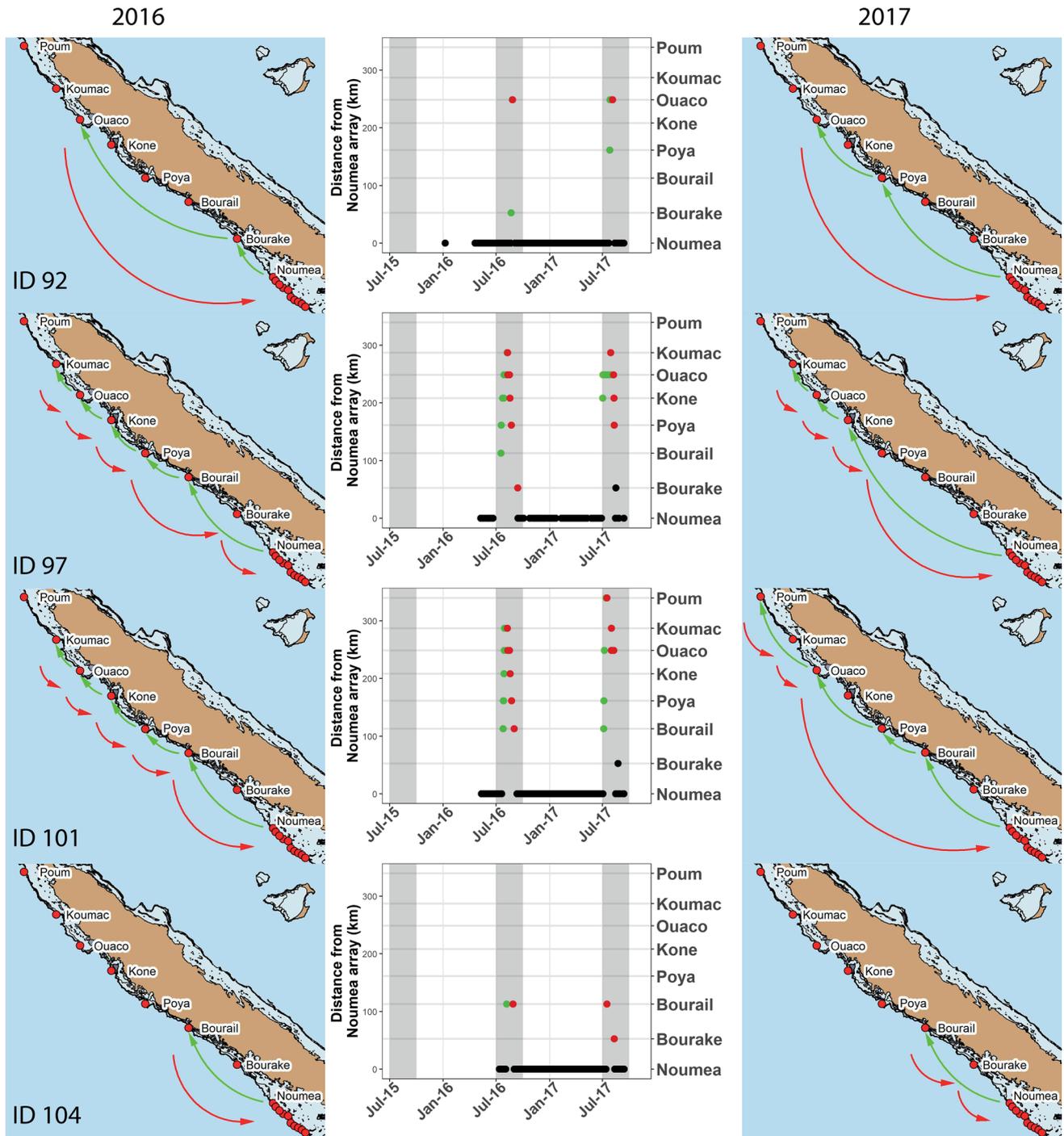


Fig. 2 Consecutive long-range migrations of four adult males caught in Noumea. Arrows represent movements during migration events, colored in green for forward movements and in red for return movements. Central charts show the detections on acoustic arrays

outside (black dots) and during migration events (red and green dots, corresponding to movements presented by arrows). Vertical shading represents the migration season (July–September)

patterns differed from the migratory individuals. One individual was tagged in the GNL (ID 81) and two at Noumea (IDs 107 and 113). ID 81 was resident to the GNL and was detected once in August 2016 on the nearby *Wala* receiver, 25 km south of the GNL on the west coast. This

shark was absent from the GNL less than 7 days during this trip, suggesting this did not correspond to a migration. IDs 107 and 113 were detected off the west coast (*Bourail* and *Bourake* receivers; *ESM C*), located 113 and 53 km north of Noumea, respectively. Both sharks were only detected in

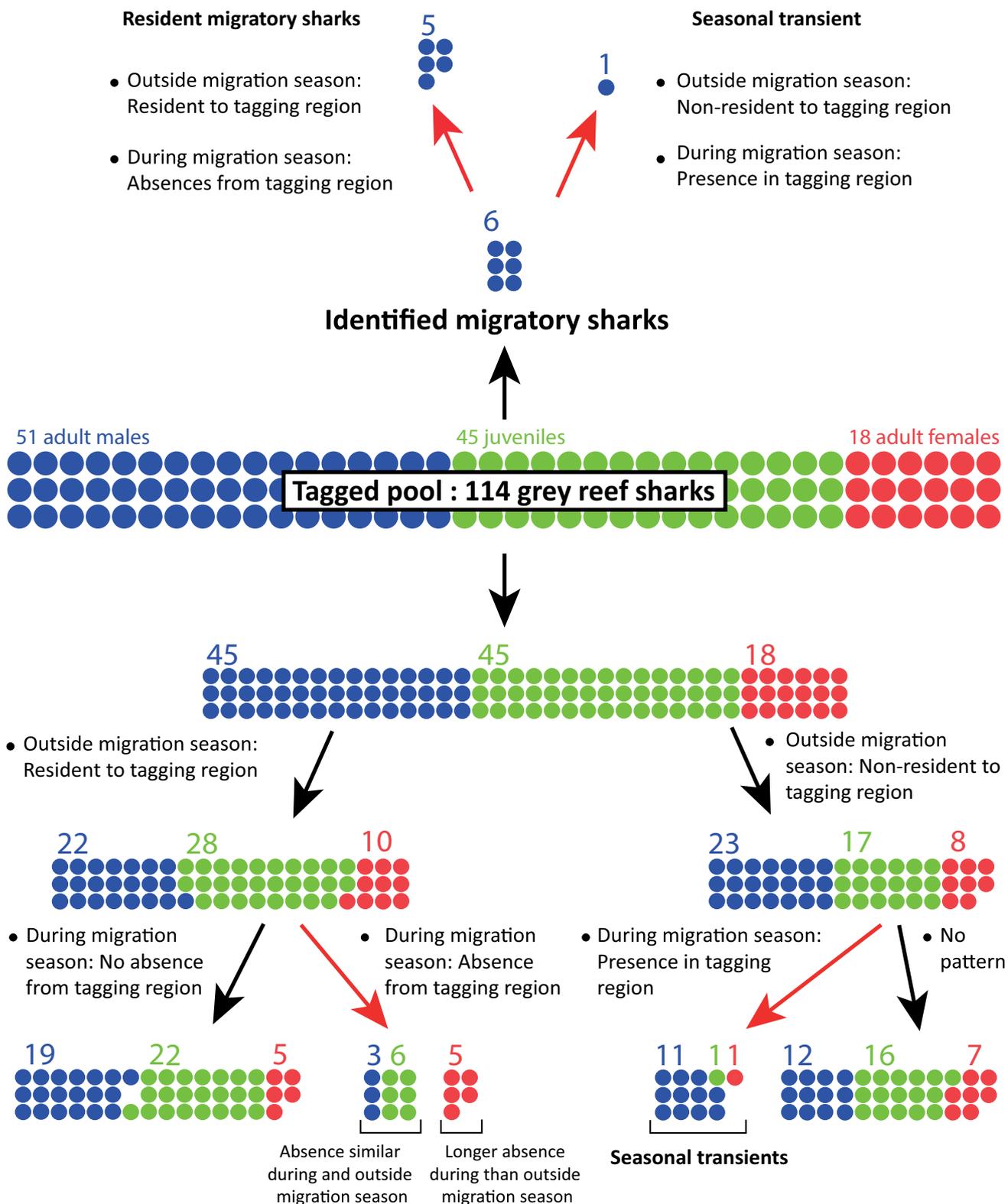


Fig. 3 Classification of detection patterns. The upper part of the diagram represents the individuals—represented as red, blue and green spots for adult female, adult male and juvenile individuals—whose detection pattern evidenced a migratory behavior. The lower

part of the diagram represents the rest of individuals, for which similarities with identified migratory sharks were searched for in their tagging region detection pattern

their tagging region, Noumea, during the migration season, at the time they were tagged and the year after. ID 107 was detected on the *Bourail* receiver on eight out of 9 months between October 2016 and June 2017, suggesting residency around this receiver. ID 113 was not detected in our array outside the migration season.

Overall, IDs 107 and 113 displayed similar patterns to migratory individual ID 111: They were detected in their tagging region on two consecutive years exclusively during the migration season and the time of capture matched with the migration season. This strongly suggests that these animals were tagged during migratory movements. Eleven other sharks displayed a similar detection pattern, being mostly absent from their tagging region outside the migration season and detected during the migration season on two consecutive years. However, none of them were detected on any receiver outside their tagging region. These eleven sharks were nine adult males tagged in D'Entrecasteaux ($n = 1$), Chesterfield ($n = 4$) and GNL ($n = 4$), one juvenile male tagged in Chesterfield and one adult female tagged in D'Entrecasteaux (Fig. 3). These 13 suspected migratory animals (including IDs 107 and 113), together with migratory ID 111, will hereafter be called seasonal transients (ESM C).

On the other hand, and similarly to the five resident migratory individuals, three other adult males that were resident to their tagging region outside the migration season showed an absence period greater than the MMD (14 days) during the migration season (Fig. 3, ESM D). One was tagged in the GNL (ID 34: maximal absence period of 23 days during migration season) and the other two in Noumea (ID 114: 17 days, ID 112: 51 days). These absences were of sufficient duration for migration to have occurred, however, given they were of comparative duration to absences observed throughout the rest of the year (paired Wilcoxon test p value = 0.38), we could not conclude whether it corresponded to migration. Nineteen other resident adult males did not show any absence greater than 14 days during the migration season and were therefore considered as non-migratory (Fig. 3, ESM C).

Most resident juvenile sharks did not show potential for migration to have occurred. Twenty-two out of the 28 resident juveniles did not show any absence greater than 14 days during the migration season and were therefore considered as non-migratory. The remaining six resident juveniles showed absence periods ranging from 14 to 43 days (mean 23 ± 3 days SD; Fig. 3, ESM D), however again, given these absences were comparable to absence periods observed during the rest of the year (paired Wilcoxon test p value = 0.66) we could not determine whether these absences were due to migration.

In contrast, 5 out of 10 resident adult females did show an absence (24–36 days; mean 31 ± 5 days SD) greater

than 14 days during the migration season and significantly greater than the absence outside the migration season (Wilcoxon paired test p value = 0.03; Fig. 3, ESM D). However, none of these females were detected outside their tagging region. The other five resident adult females did not show any absence greater than 14 days during the migration season and were therefore considered as non-migratory.

Among the 48 non-resident sharks, 13 were suspected to be migratory (seasonal transients) and 35 (12 adult males, 16 adult females, 7 juveniles) showed insufficient data to conclude about potential migration.

Increased mobility of adult males during the migration season

Resident sharks represented 65 out of the 114 studied individuals (57%), among which 27 were adult males, 10 were adult females and 28 were juveniles. Non-resident sharks consisted of 24 adult males, 8 adult females and 17 juveniles. The proportion of residents was not significantly different between the three groups (χ^2 test p value = 0.66). Among the residents, mobility of adult males was significantly greater during than outside the migration season (Wilcoxon test p value < 0.001), while no significant difference was observed for adult females or juveniles (Wilcoxon test p value = 0.90 and 0.55, respectively; Fig. 4). This pattern remained when the five resident migratory adult males were excluded from the test (adult males: Wilcoxon test p value = 0.002), and when all sharks from the Noumea region were excluded (adult males: Wilcoxon test p value = 0.007). These results show that adult males are clearly undertaking the greatest movements during the migration season.

Discussion

This study presents four definitive records of return migration on two consecutive years, and two definitive records of single-year return migration in male grey reef sharks, suggesting male-biased migration in this species. All migrations occurred within a specific, narrow time-frame, suggesting seasonality could be an important factor in this behavior. Tracked movements ranged from 226 to 680 km, constituting the first empirical evidence of long-range return migration in this species. Detections on successive acoustic receivers suggest individuals travelled with definite directionality, although this may in part be due to the topography of the western New Caledonian coastline, and the subsequent acoustic array positioning. Yet the overall directionality of these trips, together with the time of year and long-range scope far beyond the usual

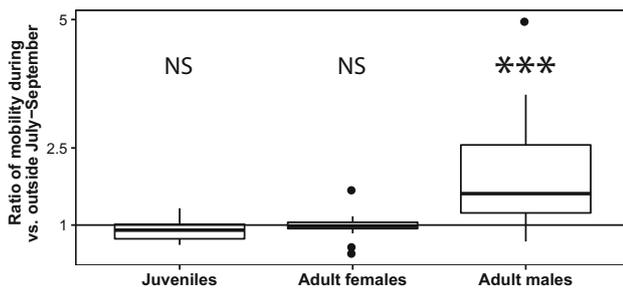


Fig. 4 Relative mobility during versus outside the migration season for juveniles, adult females and adult males. For each shark, mobility between receivers inside tagging region arrays was measured during and outside migration season as daily values. A ratio was computed to test for a significant increase in mobility during migration season (ratio > 1: increased mobility during migration season)

home range reported for this species (Vianna et al. 2013; Espinoza et al. 2015), correspond to the definition of migration (Dingle and Drake 2007).

Altogether, migratory behavior was confirmed for six adult males, and postulated for a further 13 individuals, 12 of which were also male. Although investigating absence periods in resident sharks revealed that five adult females showed absence periods long enough to enable migration, this information alone cannot support the hypothesis of a migratory behavior. Unlike seasonal transients, they were not detected on many different receivers during the migration season (ESM E). Moreover, general movement patterns of adult females, with no increase in mobility and no long-range movement observed during this season, cannot suggest relocation far away from their residency area. While it appears that these females did undertake some form of relocation during migration season, this could instead be consistent with displacement toward close-by but un-monitored parts of the reefs, like lagoons and reef passes.

It is possible that our observations of male-biased migration may be in part due to significantly more adult males ($n = 51$) being investigated than adult females ($n = 18$), particularly given extensive movements were only observed in adult males tagged in Noumea, where few adult females were sampled ($n = 2$). Yet, several other lines of evidence corroborate a male bias in migratory behavior: (i) no adult females were detected outside their tagging region, while nine adult males were; (ii) mobility was found to increase during the migration season for adult males but not for adult females; this pattern remained when excluding sharks from Noumea; and (iii) seasonal transients, for which migratory behavior is strongly suspected, are almost exclusively adult males with only one adult female. This pattern of enhanced male movements is supported by previous tracking work on the GBR (Espinoza et al. 2015).

Several hypotheses arise concerning the drivers of male-biased migrations. Migratory behavior in sharks can be linked to various processes, including mating and parturition (Papastamatiou et al. 2010; Bansemer and Bennett 2011; Domeier and Nasby-Lucas 2013; Feldheim et al. 2014) or, in the context of a temporally variable environment, chasing a window of suitable conditions regarding prey availability (Hussey et al. 2009) or physiological demands such as thermal optimums (Reyier et al. 2014). Environmental variability is unlikely to be driving migrations found, as not all tagged grey reef sharks were observed or suspected to migrate. Moreover, tropical environments are not subject to major thermal fluctuations, and the New Caledonian coral reef habitat remains suitable for reef sharks throughout the year. In addition, migratory sharks left Noumea as temperature was dropping, and returned at a time when water was colder (ESM F). Yet, temperature decline could still be a temporal cue for the timing of migrations, the cool season in New Caledonia being from June to September.

Sex-biased dispersal and the narrow window of these movements suggest that mating was the motivation behind the sharks' migrations. Mating season occurs between August and October on the Australian GBR, based on ovulation stage and mating scars (Robbins 2006). With New Caledonian sharks travelling between July and September, such migrations appear to begin just prior to the mating season, which would allow animals sufficient time to travel to mating locations. This hypothesis is supported by fresh bite marks being found on an adult male believed to have been caught shortly after returning from migration (ID 111, ESM G), potentially indicating competition from other males, or retaliatory bites from females following mating activity (Gilmore et al. 1983; Gordon 1993).

Further evidence that migrations were mating-oriented comes from the paucity of female and juvenile migration. Feeding on localized seasonal food sources such as fish spawning events have been documented for grey reef sharks, where large aggregations of camouflage grouper, *Epinephelus polyphekadion*, drive grey reef shark movements in the Fakarava pass in the Tuamotu archipelago, French Polynesia (Robbins and Renaud 2015; Mourier et al. 2016). However, it is unlikely that adult females and juveniles would not display similar movement patterns if food acquisition was the driving motivation for migrations in New Caledonia.

Habitat continuity has been suggested as a factor enabling large-scale grey reef shark movements (Heupel et al. 2010). As such, the wide deep channels separating the mainland and D'Entrecasteaux and Chesterfield reefs may provide sufficient barrier to hinder annual migrations among these locations. This may explain why we only

identified unequivocal migration from males captured alongside the main island of New Caledonia. Although there were 52 adult males tagged across four areas of the archipelago, with seasonal transients identified in each of the four study regions, a clear pattern of migration was only found in individuals originating from the more human-populated southern Noumea region, and migrating northward along continuous reef. No adult males from the northern uninhabited GNL region were observed undergoing such migration south. While grey reef sharks therefore migrated along continuous reef, the pattern of directionality may be linked to anthropogenic pressure.

Human proximity is already known to affect grey reef shark populations in New Caledonia, by both lowering abundance (Juhel et al. 2017) and inducing cautious behaviors toward bait (Juhel et al. 2019). Our results suggest that human proximity could also affect males' movement behavior, although the underlying mechanisms are not yet clear. One possible hypothesis would be related to the Allee effect, with low southern shark population densities negatively affecting males' mating opportunities. Southern males may therefore move northwards during mating season to take advantage of higher shark densities, and more chances to encounter a potential mate. Another related hypothesis arises from the possibility of sexual segregation occurring in the southern region. Sexual segregation has occasionally been documented for this species (Economakis and Lobel 1998; Field et al. 2010), and given only two adult females were caught in the southern region compared with 16 adult males, the southern region showed a significant male bias in sex ratio in captures. As there is no reason to suspect that the observed sex ratio of captured sharks around Noumea does not reflect the actual proportions of males and females, then males would increase their mating opportunities by northward migrations given no such bias was found in the northern GNL region. Alternatively, a combination of male philopatry and spill-over of individuals from north to south due to differential abundances could also explain why only males caught in Noumea were observed to migrate. These migratory individuals could be northern males that settled in Noumea and came back to their natal ground for reproduction. No matter what the cause, it is unlikely that the predominantly northwards migration pattern is random, given migrating individuals actively moved from a lower-density area to higher-density regions.

These hypotheses can be further informed by the case of the long-range return trip of a grey reef shark from Osprey Reef, Coral Sea, to the GBR, reported by Barnett et al. (2012). This individual was an adult male as well and showed similar timing, leaving its home region in late June and returning to it in October. Yet, it presented opposite patterns than reported here, with an origin presenting a

strong female-biased sex ratio and a destination characterized by higher human impact. This case suggests that other unknown factors could also have a role in driving migrations in this species and could explain that only individuals from Noumea were observed to migrate.

Not all adult males tagged in Noumea showed migration patterns. Seven out of 16 adult males were not observed nor suspected to have migrated, of which five were shown to remain in their region during the migration season. This suggests different modalities in the trade-off between the gain of mating in the northern region compared to the energy expenditure and risks involved with the journey. Given that all individuals undertaking migratory movements in 2016 undertook similar movements the following year, this suggests that the migrations observed here represent an individual strategy rather than an environment-dependent process. Reduction in inbreeding and lower competition with offspring can result in increased fitness irrespectively of the individual origin while reduction in competition with siblings can enhance inclusive fitness if the individual was born in its region of residency. Individual origin is not a known variable here but might thereby constitute a reason for the contrast in individual behavior observed in Noumea. This dichotomy could also come from individual actual ability to undergo such a trip, but our data did not support this hypothesis as body length was not found to be greater in migratory individuals and health status information was not available to inform the question.

While male-biased migratory behaviors in grey reef sharks may have ecological benefits, it can also make effective conservation of grey reef shark populations problematic. Male-biased dispersal introduces complexity into the spatial management of the species, as it suggests differential spatial requirements for males and females. As such, if all sexual and ontogenetic stages of a grey reef shark population are to equally benefit from spatial protection, then management must take migratory behaviors into consideration. However, given the large spatial scale in which males have been observed to move here and elsewhere (Barnett et al. 2012; White et al. 2017), protecting migrating males may be difficult. Large-scale annual movements similarly limit the efficacy of individual reef zonations such as those found on the GBR (Australian Government 2004), when males may travel across reefs of multiple fishing management zones. Instead, the specific timing of mating migrations lend itself to increased benefit from seasonal protection measures, such as fishing gear restrictions (Shiffman and Hammerschlag 2016) or seasonal closures. The identification of mating sites and migratory corridors would be similarly useful for the implementation of local protection measures as our results, besides highlighting their potential existence, bring

tangible information to narrow down their location and the time window when mating would occur.

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Compliance with ethical standards

Conflict of interest On behalf of all authors, L. Bonnin states that there is no conflict of interest.

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