SPECIAL ISSUE

CSIRO PUBLISHING

Marine and Freshwater Research
http://dx.doi.org/10.1071/MF16122

Long-term migration patterns and bisexual philopatry in a benthic shark species

Nathan Charles Bass[A], *Johann Mourier*[A], *Nathan A. Knott*[B], *Joanna Day*[C], *Culum Brown*[A,E] *and Tristan Guttridge*[D]

[A]Macquarie University, Department of Biological Sciences, North Ryde, NSW 2109, Australia.
[B]NSW Department of Primary Industries, Marine Ecosystems Research, 4 Woollamia Road, Huskisson, NSW 2540, Australia.
[C]Taronga Conservation Society Australia, Mosman, NSW 2088, Australia.
[D]Bimini Biological Field Station Foundation, 15 Elizabeth Drive, South Bimini, Bahamas.
[E]Corresponding author. Email: culum.brown@mq.edu.au

Abstract. Knowledge of the broad-scale movement patterns of sharks is essential to developing effective management strategies. Currently there is a large bias in studies focusing on species that are either large apex predators or found in tropical to subtropical regions. There is limited knowledge of the movements and migrations of benthic and temperate shark species. The present study used passive acoustic telemetry to investigate the movement patterns of a benthic shark species, the Port Jackson shark (*Heterodontus portusjacksoni*). Individuals were tagged with acoustic transmitters between 2012 and 2014 and their movements were monitored within Jervis Bay and along the east Australian coastline for up to 4 years. Male and female Port Jackson sharks demonstrated high levels of philopatry to both Jervis Bay and their tagging location across multiple years. Although males and females did not differ in their arrival times, females departed from Jervis Bay later than males. Approximately half the tagged individuals migrated in a southward direction, with individuals being detected at Narooma, Bass Strait and Cape Barron Island. This study provides conclusive evidence of bisexual philopatry in a benthic temperate shark species, confirming previous hypotheses, and presents the most detailed migration route for Port Jackson sharks to date.

Additional keywords: dispersal, ecology, elasmobranch, mark–recapture, site fidelity.

Received 29 January 2016, accepted 23 August 2016, published online 23 September 2016

Introduction

Quantifying the broad-scale movement patterns of sharks is fundamental to understanding their biology, ecology and behaviour. Many species are classified as data deficient by the International Union for Conservation of Nature (IUCN) with regard to their basic biology, ecology and stock assessment (Dulvy *et al.* 2014), and data on philopatry are particularly sparse. Given their roles as apex and mesopredators in marine ecosystems, their biology, ecology and behaviour can also significantly affect ecological communities (Heithaus *et al.* 2008). Further, species that have complex movement patterns or species that repeatedly return to specific areas for reproduction or foraging present unique management challenges, and accurate data are needed to develop effective management strategies (Bonfil 1997; Speed *et al.* 2010).

Studies on the movement patterns of sharks are typically limited to two subgroups: larger, apex predator species or species that occur in tropical and subtropical regions (Chapman *et al.* 2015). Much of what is known about the movement patterns of smaller, temperate shark species is limited to a few studies. These studies found that smoothhound sharks (da Silva *et al.* 2013), leopard sharks (Carlisle and Starr 2009) and banded wobbegongs (Huveneers *et al.* 2006) all demonstrated high levels of site fidelity and residency on a reef or regional scale. Da Silva *et al.* (2013) also found that individuals exhibited consistency in movement patterns across multiple years after returning from migrations. However, none of these studies investigated the migratory behaviour of tagged individuals.

Much of the evidence on the broad-scale movements and migrations of benthic species comes from research conducted on Port Jackson sharks (McLaughlin and O'Gower 1971; O'Gower and Nash 1978; O'Gower 1995; Powter and Gladstone 2009). Previous tagging studies have found that Port Jackson sharks form large seasonal breeding aggregations along the New South Wales (NSW) coast and may return to these locations for many years (McLaughlin and O'Gower 1971; O'Gower and Nash 1978; Powter 2006; Powter and Gladstone 2008, 2009). It has also been suggested that individuals migrate distances of up to 760 km to southern foraging refuges outside the breeding season (O'Gower 1995). O'Gower (1995) theorised that individuals may develop detailed spatial maps that they use to return to the same locations over multiple years. These high levels of philopatry and large migrations make Port Jackson sharks a model species in which to investigate the broad-scale movements of benthic shark species.

Previous studies on Port Jackson shark movement used conventional tagging methodologies and thus relied on data collected from visual surveys or fishery capture records to track individuals. Conventional tagging methods are subject to biases arising from limitations in conducting SCUBA surveys, variation in fishing effort to recapture tagged individuals, non-recovery and non-reporting of tags and tag shedding (Kohler and Turner 2001). Furthermore, recapture rates from conventional tagging studies are often very low because only a small proportion of tagged animals is resighted or recaptured, which can greatly affect the conclusions regarding broad-scale movement patterns. Alternative methods, such as passive acoustic telemetry and genetic techniques, can be used to study the movements of these cryptic and highly mobile species. Acoustic transmitters are used to continuously monitor the position of individuals within an acoustic receiver array. However, passive acoustic telemetry studies are limited to areas covered by receivers and thus only provide information on the presence or absence of individuals within those areas (Heupel *et al.* 2006). Nevertheless, this technique is a powerful tool to monitor the long-term movement patterns of individuals and highlight consistencies and idiosyncrasies of individual behaviour (Heupel *et al.* 2006).

The present study used passive acoustic telemetry to investigate the philopatry and migratory patterns of Port Jackson sharks tagged at two seasonal aggregation sites in Jervis Bay, Australia. We examined whether males and females show differences in their return rates to and arrival and departure from Jervis Bay, and whether these patterns are affected by the size of individuals. Second, we investigated the migration routes of Port Jackson sharks over a 4-year period.

Materials and methods

Study site

The present study was conducted in Jervis Bay, a 102-km^2 bay on the south coast of NSW, Australia. Jervis Bay has a wide variety of marine ecosystems, including shallow and deep rocky reefs, sandy benthos, seagrass communities and mangroves, and has previously been identified as a major breeding aggregation site for Port Jackson sharks (J. Pini-Fitzsimmons, E. Byrnes, N. Bass, and C. Brown, unpubl. data). To investigate the migratory behaviour and philopatry of these individuals, we tagged adult Port Jackson sharks captured from two locations in Jervis Bay: Orion Beach (35°4′8.04″S, 150°41′3.42″E; $n = 35$) and Moona Moona Creek (35°2′58.32″S, 150°40′53.40″E; $n = 19$; see Fig. S1 available as Supplementary material to this paper). Both these sites are subtidal rocky reefs ranging in depth from 1 to 10 m with a matrix of sand, kelp and rocky reef benthos. These sites, and most reefs within Jervis Bay, are monitored by acoustic receivers (Vemco VR2W) deployed by the NSW Department of Primary Industries (DPI; Fig. S1; for more details on the array, see Ferguson *et al.* 2013).

Tagging procedures

Adult Port Jackson sharks were hand-captured by SCUBA divers and snorkelers and slowly brought to the surface. They were then transported to shore in a canoe, where they were immediately transferred to a trough containing fresh seawater. The total length (TL) of individuals was measured to the nearest centimetre. Females ranged from 91 to 129 cm TL, whereas males ranged from 88 to 113 cm TL. Individuals were sexed based on the presence or absence of claspers, fin clipped for genetic and isotopic analysis and tagged with passive integrated transponder (PIT) tags (FDXB transponders; Microchips Australia) for individual identification. Individuals were then sedated in a solution of tricaine methanesulfonate (MS-222; 150 mg mL^{-1}) and an acoustic transmitter (Vemco V16) was implanted in their peritoneal cavity through a 2.5-cm incision, which was then sutured using five interrupted sutures and superglue (Mulcahy 2003). Transmitters were programmed with a nominal delay of 90 s and an expected battery life of 2805 days. All individuals were revived and released at their site of capture.

All capture and tagging procedures were conducted in accordance with an Animal Research Authority permit (2012/009) granted by the Macquarie University Animal Ethics Committee and two NSW Fisheries permits (P08/0010–3.1 and P08/0010–4.2).

Acoustic receiver arrays

Detections of acoustically tagged individuals were uploaded to the Integrated Marine Observing System (IMOS) animal tracking database, a national collaborative research initiative consisting of 112 acoustic receiver installations around the Australian coastline and managed by various universities, government and private research institutions. For the present study, tagged individuals were detected in four installations: the NSW DPI Jervis Bay array, the IMOS Narooma Line, the Bass Strait 2015 Installation and the Cape Barron Island Installation (for a description of installations, see Table 1).

Table 1. Description of acoustic arrays on Integrated Marine Observing System (IMOS) animal tracking database that detected Port Jackson sharks between 2012 and 2015

NSW, New South Wales; DPI, Department of Primary Industries; JBMP, Jervis Bay Marine Park

Installation	Owners	Distance from Jervis Bay (km)	Description
NSW DPI Jervis Bay array	Nathan Knott	n/a	Array monitoring reefs in JBMP ($n = 52$ receivers)
AATAMS Narooma line	Phillip McDowall, Andrew Boomer	200	Curtain between Narooma and Montague islands ($n = 10$ receivers)
Bass Strait	Barry Bruce, Russ Bradford	800	Two sites ~35–40 km off Victoria ($n = 40$ receivers)
Cape Barron Island	Andrew Boomer, Jayson Semmens	1080	Curtain from Cape Barron Island to 30 km offshore ($n = 42$ receivers)

Data analysis

A Chi-Square test for associations was used to determine whether the return rates of males and females to Jervis Bay were different within each year. Binary logistic regression was used to determine the effect of site fidelity on the return of individuals to a particular reef.

A general linear mixed model was used to analyse the effects of the sex and size of individuals on their arrival and departure times from Jervis Bay. Individual identification (ID) was incorporated into the model as a random factor to account for repeated observations of the same individuals (Venables and Dichmont 2004). The arrival dates and densities were excluded for individuals in the year they were tagged because tagging occurred in the middle of the season. Kolmogorov–Smirnov tests were used to compare the density distributions of males and females within each year and to determine whether they showed similarities in their arrival and departure patterns.

The data on migration behaviour are largely descriptive because of low sample sizes of individuals that were detected south of Narooma ($n = 9$). A Chi-Square test was used to determine whether there was a difference between the number of males and females detected outside Jervis Bay. One-way analysis of variance (ANOVA) was used to determine whether there were significant differences between the migration distances of males and females. A general linear model was used to determine whether the sex of individuals or the direction of migration affected the speed of migration.

All statistical analyses were performed in R Studio (ver. 3.3.0, R Foundation for Statistical Computing, Vienna, Austria) using the 'lme4' and 'stats' packages. Data used in the linear models met the assumptions of normality.

Results

Two tagged individuals returned no data, possibly due to tag malfunction, and were excluded from the analyses. Thus, the data analysis is based on 51 sharks. Aside from two females that remained in Jervis Bay for the duration of the study, no individual was detected in Jervis Bay outside the breeding season (Table 2)

Port Jackson sharks showed high return rates to Jervis Bay in the years following tagging, with 78.9% returning in 2013, 82.9% returning in 2014 and 89.1% returning in 2015 (Table 2). Further, 86% of individuals were detected in Jervis Bay over multiple seasons (Table 2). We found no significant difference in the return rates of males and females for 2013 ($\chi^2 = 0.014$; d.f. = 1; $P = 0.906$), 2014 ($\chi^2 = 0.925$; d.f. = 1; $P = 0.336$) or 2015 ($\chi^2 = 0.000$; d.f. = 1; $P = 1.000$). Furthermore, the majority of tagged individuals ($n = 37$; i.e. 73% of tagged sharks) consistently returned to and primarily used the same reef within Jervis Bay over the study period. There was no difference

Table 2. Seasonal philopatry for females and males detected in Jervis Bay

TY, tagging year in Jervis Bay; YR, years in which individuals returned; ND, the individuals who did not depart from Jervis Bay between years

Females						Males					
ID	2012	2013	2014	2015	Annual returns	ID	2012	2013	2014	2015	Annual returns
F34785	TY	ND	ND	ND	–	M34794	TY				0/3
F34793	TY	ND	ND	ND	–	M34789	TY	YR	YR		2/3
F34797	TY				0/3	M34779	TY				0/3
F34788	TY	YR		YR	2/3	M34783	TY	YR	YR		2/3
F34782	TY	YR	YR		2/3	M34787	TY	YR	YR	YR	3/3
F34780	TY				0/3	M34791	TY	YR	YR	YR	3/3
F34778	TY	YR	YR	YR	3/3	M34792	TY	YR	YR	YR	3/3
F34784	TY	YR	YR	YR	3/3	M34795	TY	YR	YR	YR	3/3
F32598		TY	YR		1/2	M34786	TY	YR	YR	YR	3/3
F32590		TY	YR	YR	2/2	M34781	TY	YR	YR	YR	3/3
F32585		TY			0/2	M32596		TY	YR	YR	2/2
F32581		TY	YR	YR	2/2	M32594		TY	YR	YR	2/2
F32582		TY	YR	YR	2/2	M32602		TY	YR	YR	2/2
F32588		TY	YR	YR	2/2	M32578		TY	YR	YR	2/2
F32591		TY	YR	YR	2/2	M32587		TY	YR	YR	2/2
F32601		TY	YR	YR	2/2	M32604		TY	YR	YR	2/2
F32606		TY	YR		1/2	M32608		TY	YR	YR	2/2
F32595		TY	YR	YR	2/2	M32579		TY	YR	YR	2/2
F32584		TY	YR	YR	2/2	M32580			TY	YR	1/1
F32609		TY	YR	YR	2/2	M32599			TY	YR	1/1
F32610		TY	YR	YR	2/2	M32589			TY	YR	1/1
F32605			TY	YR	1/1	M32583			TY	YR	1/1
F32603			TY	YR	1/1	M32592			TY	YR	1/1
F32612			TY	YR	1/1	M32611			TY	YR	1/1
F32577			TY	YR	1/1	M32600			TY	YR	1/1
						M32597			TY	YR	1/1
						M32586			TY	YR	1/1

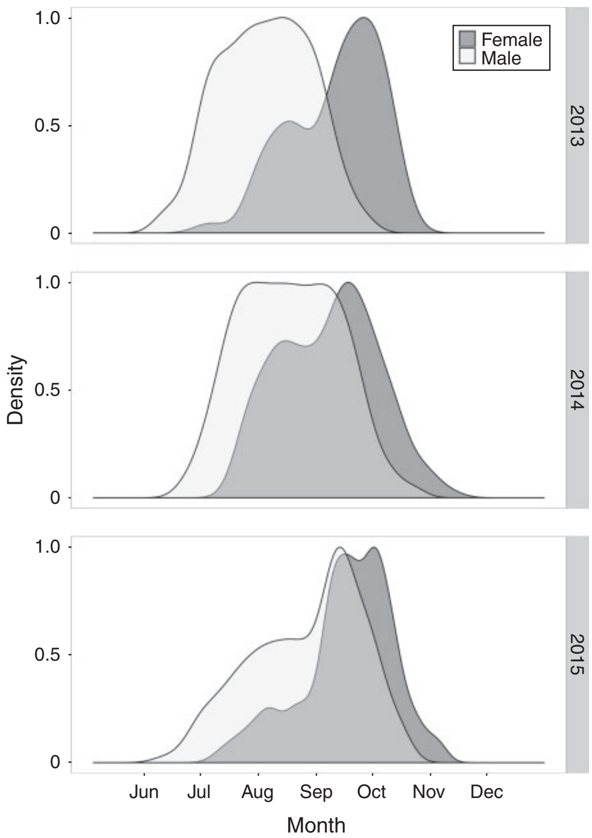

Fig. 1. Density of male and female Port Jackson sharks within Jervis Bay that were tagged in previous years.

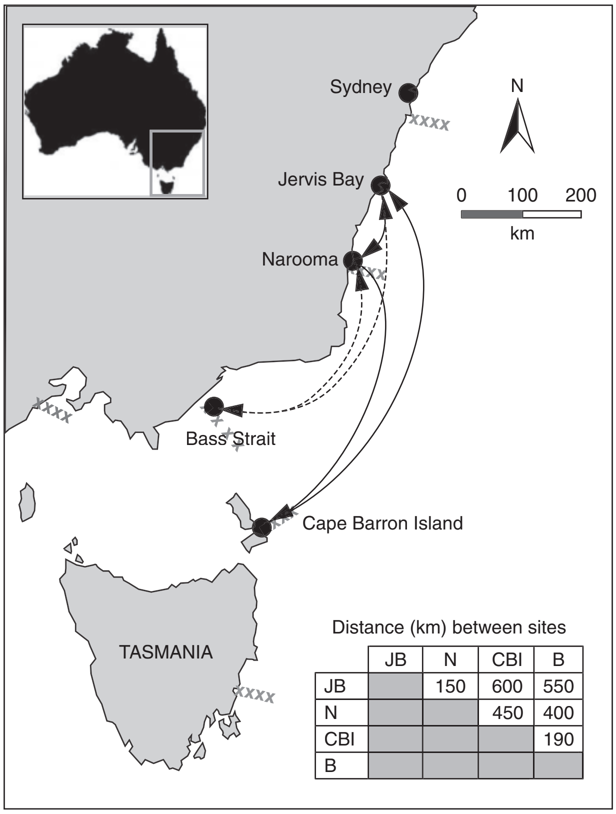

Fig. 2. Detection of tagged Port Jackson sharks at four locations along the east coast of Australia over the 4-year study period. Locations of receiver arrays that detected tagged individuals are indicated by filled circles and available barriers of receivers are indicated by crosses (XXXX). Lines connecting locations represent movements between those sites. The distance matrix represents the minimum distance between locations. JB, Jervis Bay; N, Narooma; CBI, Cape Barron Island; B, Bass Strait.

in the likelihood of males and females returning to the same reef in subsequent years ($\chi^2 = 0.22$; d.f. = 13, 50; $P = 0.637$). Binomial logistic regression found that individuals that demonstrated higher levels of site fidelity within a given year were more likely to return to the same reef in subsequent years ($\chi^2 = 15.22$; d.f. = 13, 50; $P < 0.001$).

Arrival and departure of individuals

Individual Port Jackson sharks that departed Jervis Bay showed consistency in both arrival ($t = -0.004$, d.f. = 38, $P = 0.997$) and departure ($t = 0.219$, d.f. = 91, $P = 0.827$) dates across the years (Fig. 1). There was no significant difference between arrival times of males and females ($t = -1.712$, d.f. = 38, $P = 0.095$) within Jervis Bay. However, males departed Jervis Bay significantly earlier than females ($t = -3.028$, d.f. = 91, $P = 0.003$). On average, males left Jervis Bay on 28 September and females departed Jervis Bay on 11 October. There was no significant relationship between the arrival and departure times of individuals and their size for either males (arrival: $t = 0.814$, d.f. = 21, $P = 0.425$; departure: $t = 0.250$, d.f. = 48, $P = 0.803$) or females (arrival: $t = -0.826$, d.f. = 18, $P = 0.420$; departure: $t = 0.184$, d.f. = 40, $P = 0.855$). The density distributions of male and female Port Jackson sharks were significantly different in 2013 ($D = 0.17383$, $P < 0.001$), 2014 ($D = 0.15039$, $P < 0.001$) and 2015 ($D = 0.18945$, $P < 0.001$). Females showed a bimodal distribution in each year, with the peak of female density coinciding with the departure of males (Fig. 1).

Port Jackson migration

More than half the tagged individuals ($n = 30$) were detected at one or two locations south of Jervis Bay. Individuals were detected at the Narooma line ($n = 25$) between June and November, in Bass Strait ($n = 5$) between April and June and at Cape Barron Island ($n = 4$) between December and April (Figs 2, 3). Interestingly, 21 of the 30 sharks detected outside the Jervis Bay array were not detected at Narooma, Bass Strait or Cape Barron Island in their year of tagging, but were detected in subsequent years. There was no statistically significant difference between the number of males and females detected by receivers outside Jervis Bay ($\chi^2 = 0.670$; d.f. = 1; $P = 0.413$). Thus, males and females seem to be exhibiting the same migratory behaviour. Of the 47 tagged individuals that returned to Jervis Bay in subsequent years, 17 were not detected by receivers outside the Jervis Bay acoustic receiver array.

The minimum distance that tagged individuals moved during migration events ranged from 140 km (between Jervis Bay and Narooma) to 645 km (between Jervis Bay and Cape Barron

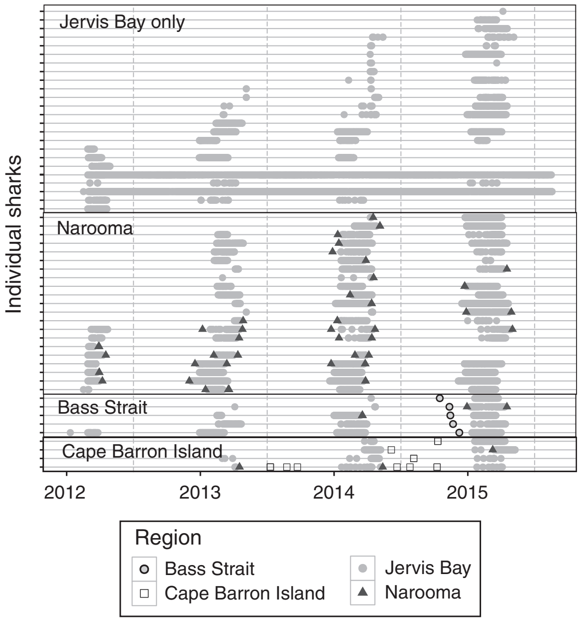

Fig. 3. Daily acoustic detections of each individual at each of the four locations. Panels arrange individuals by maximum distance detected from Jervis Bay. Within each panel, individuals are arranged by the year in which they were tagged.

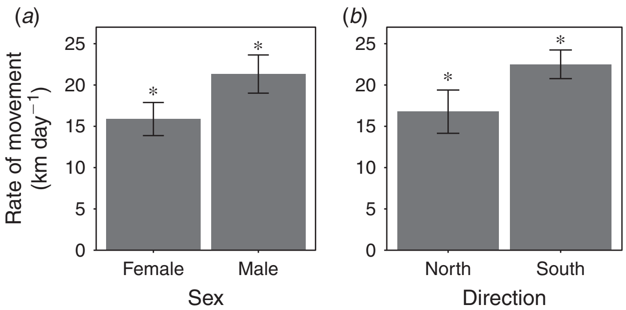

Fig. 4. Rates of movements of migrating Port Jackson sharks split by (*a*) the sex of the individuals and (*b*) the direction of movement. Data are the mean ± s.e.m. *, $P < 0.05$.

Island; Figs 2, 3). There was no difference in the migratory distance between males and females ($t = -0.593$; d.f. = 21; $P = 0.559$). Analysis of the rates of movement of individuals found that males migrated significantly faster than females ($t = 2.247$; d.f. = 43; $P = 0.030$; Fig. 4). In addition, individuals of both sexes migrated significantly faster in a southward direction than in a northern direction ($t = 2.228$; d.f. = 43; $P = 0.031$; Fig. 4), which is consistent with the presence of the East Australian Current.

Discussion

The present study presents the first long-term acoustic monitoring study of the broad-scale movements of Port Jackson sharks, and provides evidence of long-distance migrations and site-specific philopatry for both males and females. Approximately 84% of sharks returned to the Jervis Bay area in subsequent years, and many of these individuals returned to the same reefs at which they were tagged. Although males and females were found to arrive in Jervis Bay at the same time each year, males generally left Jervis Bay earlier than females. Moreover, the bulk of the males tended to arrive before the females. Analysis of migration data suggests that some Port Jackson sharks migrate from the winter breeding site in Jervis Bay in a southward direction along the east coast of Australia to Wilsons Promontory and out to Bass Strait via King and Cape Barron islands for summer. Males migrated significantly faster than females, and migration in a southward direction was typically faster than northward migrations.

High levels of philopatry were found, with individuals of both sexes returning to Jervis Bay multiple years after tagging. Bisexual philopatry is a rare phenomenon in shark species. Previous studies in requiem sharks have found that females exhibit high levels of philopatry, whereas males generally move between regions and mediate gene flow (Feldheim *et al.* 2002; Keeney *et al.* 2005; Clarke *et al.* 2011; Mourier and Planes 2013). Nosal *et al.* (2014) found that both male and female leopard sharks exhibited philopatry but that this philopatry was to different locations for each sex. Nosal *et al.* (2014) suggested that female leopard sharks may choose different sites from males to avoid sexual harassment. Alternatively, Wearmouth and Sims (2008) suggested that sexual segregation may result from sex-specific habitat selection to maximise fecundity. Thus, it is rather rare to find both sexes showing high fidelity to the same location at the same time. It has previously been suggested that female Port Jackson sharks show preference for rocky gutters and crevices on reefs to avoid male harassment, thus allowing them to co-occur at the same sites (Powter and Gladstone 2009). Smaller males may avoid rocky gutters and crevices because of the presence of spotted wobbegongs in these habitats, which have previously been found to predate upon Port Jackson sharks (Huveneers *et al.* 2007).

The high levels of philopatry by both sexes found in the present study may have important implications for population structuring. High levels of site fidelity may lead to population structuring both within and between embayments. The presence of subpopulations has potential to limit the genetic diversity of individuals within the population and may potentially lead to inbreeding within the population (Hueter *et al.* 2005). Using mitochondrial (mt)DNA and microsatellite markers on genetic tissue obtained from adult and juvenile Port Jackson sharks within Jervis Bay and elsewhere, Clark (2015) suggested that females exhibit reproductive philopatry within Jervis Bay and that males facilitate gene flow among populations. Given that both male and female Port Jackson sharks exhibit high levels of site fidelity as adults, males may disperse in the juvenile or subadult stages to decrease the risk of inbreeding within the population (Clark 2015).

Previous studies have found much lower rates of philopatry in Port Jackson sharks, ranging from 1.5% (McLaughlin and O'Gower 1971) to 15% (O'Gower 1995). These studies used conventional visual tagging methods to identify individuals and thus relied on divers resighting and reporting tagged individuals. Furthermore, many of the surveys in these studies were only conducted under suitable diving conditions (fine weather, daytime surveys) and were thus unable to effectively monitor the presence of tagged individuals on the reefs. Acoustic telemetry technologies are far better suited to examine the rates of movements of individuals with more accuracy and in greater detail than conventional mark–recapture studies because they allow constant monitoring of animal's movements limited only by the number of receivers in the array.

Another benefit of using acoustic telemetry was the effective monitoring of the arrival and departure of Port Jackson sharks to and from Jervis Bay. Although we found no significant difference in the arrival times of male and female Port Jackson sharks, we found that males departed from Jervis Bay on their southward migration before females. Preliminary results suggest that it is this late departure of females that accounts for correlations between the abundance of Port Jackson sharks and sea surface temperature (Pini-Fitzsimmons *et al.*, unpubl. data). Moreover, the shapes of the density curves differ significantly between the sexes. Females tagged in the present study exhibited a bimodal density distribution on the reefs within each season. Females appear to occur in lower densities early in the season, possibly to avoid males and minimise energy expenditure on mating. As male density begins to decrease, female density reaches a peak and coincides with oviposition. These findings provide support to the thermal niche fecundity hypothesis, whereby each sex may occupy different thermal niches to maximise reproductive output (Wearmouth and Sims 2008). Given the lower abundance of males on the reefs because of their earlier departure, females likely delay egg laying to decrease the likelihood of egg mortality by predation by males (O'Gower and Nash 1978), thus maximising the survival rates of the eggs laid late in the season.

The present study found that Port Jackson sharks migrated in a southward direction at the end of the breeding season. Tagged individuals were detected at Narooma between June and November, Cape Barron Island from December to April and Bass Strait from April to June; thus, it is likely that both sexes undergo long-distance southerly migrations for summer months. These findings are in line with previous studies on the migrations of Port Jackson sharks (McLaughlin and O'Gower 1971; O'Gower and Nash 1978; O'Gower 1995). However, we found that ~55% of acoustically tagged individuals were detected south of Jervis Bay, which is higher than the 0.8% resightings of conventionally tagged individuals (N. C. Bass, unpubl. data) and 1.5–6% of recaptures of conventionally tagged Port Jackson sharks in other studies (McLaughlin and O'Gower 1971; O'Gower and Nash 1978). Once again, these data highlight the benefits of acoustic tagging technology over conventional tagging techniques.

It is important to note that some of the sharks were not detected outside the breeding season. Apart from the IMOS Narooma Line, there are only two receivers along the southern NSW and Victorian coastlines between Jervis Bay and Bass Strait. The absence of detections of these individuals from the Jervis Bay array and other receiver arrays suggests that they are moving into or through areas that are not monitored by acoustic receiver arrays. Two broad-scale movement patterns may explain where undetected individuals reside outside the breeding season. First, adult Port Jackson sharks may demonstrate partial migration and undetected individuals may move to areas around Jervis Bay that are not monitored by acoustic receivers. Partial migration is the propensity of some individuals to migrate and some individuals to remain resident (Chapman *et al.* 2012) and there is evidence of partial migration in tiger sharks (Papastamatiou *et al.* 2013), bull sharks (Espinoza *et al.* 2016) and in two spiny dogfish populations (McFarlane and King 2003; Campana *et al.* 2009). In the present study, two females remained within Jervis Bay year round and were frequently detected by receivers, providing some possible evidence for partial migration in Port Jackson sharks. Anecdotal evidence from local dive operators suggests some individuals may form aggregations at deep rocky reefs ~5 km south of Jervis Bay that are not monitored by acoustic receivers (P. Daniels, pers. comm.). These aggregations warrant further study to determine whether they contain any individuals tagged with acoustic transmitters or PIT tags within Jervis Bay.

Alternatively, undetected individuals may be following the same southward migration pattern as other individuals using alternative routes. To date, none of the acoustically tagged Port Jackson sharks from Jervis Bay or Sydney (C. Brown, E. Byrnes, C. Villa Pouca, S. Chambers, J. Kadar, and C. Gervais, unpubl. data) have been detected north of their tagging sites. Receivers are deployed along the coast north of Jervis Bay and the nearest receiver line is ~130 km north of Jervis Bay. Therefore, if undetected individuals are migrating, it is likely that they are moving south. Individuals may not be moving as far south as Narooma or may not be detected by the receiver line between Narooma and Montague Island. Four of the five individuals detected in Bass Strait and three of the four individuals detected at Cape Barron Island were not detected at Narooma before being detected at these more southern localities. It is important to note that the receiver line at Narooma only extends ~9 km off the coast between Narooma and Montague Island and that the continental slope is ~20 km east of Narooma; thus, the array only covers approximately half the continental shelf. If these individuals are following the East Australian Current southwards, as proposed by O'Gower and Nash (1978), they are likely to be moving on the eastern side of Montague Island and are thus not detected by the receiver line at Narooma. Anecdotal fishing evidence suggests that Port Jackson sharks may migrate southwards using deeper offshore waters (A. K. O'Gower, pers. comm.). Detection windows of individuals at Narooma are typically less than 2 h in length and do not represent significant residence events at these sites. Thus, detections of tagged individuals at Narooma are likely to represent individuals who deviate from the migration pathway to forage or rest in the waters around Montague Island. The large gaps in receiver coverage south of Jervis Bay make it difficult to determine exactly where individuals are moving when outside of Jervis Bay, particularly if they travel offshore. Tracking these individuals remains a challenge for future work.

We found evidence for differences in the rate of movement between sexes that previous studies had failed to detect because of low recapture rates. In the present study, males migrated between regions significantly faster than females undertaking the same movements. Further, the calculated rate of movement in the present study (19.5 km day^{-1}) was substantially greater than those reported in previous studies of 1.8 km day^{-1} (McLaughlin and O'Gower 1971) and 6.5 km day^{-1} (O'Gower and Nash 1978). However, it is important to note that the rates of movement we found are still likely to underestimate the swimming speeds of individuals; these rates are calculated based on the minimum distance between two receivers and therefore do not take any vertical movements or deviations from this straight line into consideration. Moreover, they assume the animal is constantly swimming, which is unlikely to be the case. Nonetheless, it is surprising to note that the maximum movement rates of 48.9 km day^{-1} herein are similar to the maximum cruising speeds calculated by Ryan *et al.* (2015) of 49.2 km day^{-1} using stereo-baited remote underwater video systems.

The estimated rates of movement in the present study also provide some evidence that individuals may use the East Australian Current to assist with southward migration outside the breeding season (O'Gower and Nash 1978). First, southward movements of individuals were significantly faster than northward movements. Second, it is highly likely that the tagged individuals in the present study are migrating at a rate greater than the maximum cruising speed calculated by Ryan *et al.* (2015). Third, the timing of the southwards and northwards movements of individuals corresponds to the maximum and minimum velocities of the East Australian Current respectively. Previous research on the movements of manta rays on the east coast of Australia suggests that they may be using the fast-flowing waters of the East Australian Current to minimise the energy expenditure of broad-scale migrations along the eastern coastline (Couturier *et al.* 2011). Here, we suggest that Port Jackson sharks may similarly use the East Australian Current to migrate south over the Austral summer.

In summary, we confirm evidence for strong, long-term site-specific bisexual philopatry in a small temperate shark species and present a migratory pathway along the eastern coast of Australia. This strong philopatry of both sexes exacerbates the potential consequences of localised stock depletions through fishing pressures or habitat degradation and may have implications for the management of this species (Hueter *et al.* 2005). Further investigation is needed into the philopatry and migrations of Port Jackson sharks at other aggregation sites and in relation to sympatric shark species.

Supplementary material

Fig. S1 shows the location of study sites and acoustic receivers in Jervis Bay. The Supplementary material is available from the journal online (see http://www.publish.csiro.au/?act=view_file&file_id=MF16122_AC.pdf).

Acknowledgements

The authors thank Sue Newson and various volunteers for assistance with tagging in the field. The authors thank Barry Bruce and Russ Bradford from CSIRO, IMOS and Ocean Tracking Network for access to data from their acoustic receiver arrays. The authors also thank E. E. Byrnes and C.V. Pouca for helpful comments on the manuscript. This research was funded by Sea World Research and Rescue Foundation Inc., Taronga Zoological Society and the Department of Biological Sciences, Macquarie University.

References

Bonfil, R. (1997). Status of shark resources in the Southern Gulf of Mexico and Caribbean: implications for management. *Fisheries Research* **29**, 101–117. doi:10.1016/S0165-7836(96)00536-X

Campana, S. E., Joyce, W., and Kulka, D. W. (2009). Growth and reproduction of spiny dogfish off the eastern coast of Canada, including inferences on stock structure. In 'Biology and Management of Dogfish Sharks'. (Eds V. F. Gallucci, G. A. McFarlane, and G. G. Bargmann.) pp. 195–208. (American Fisheries Society: Bethesda, MD, USA.)

Carlisle, A. B., and Starr, R. M. (2009). Habitat use, residency, and seasonal distribution of female leopard sharks *Triakis semifasciata* in Elkhorn Slough, California. *Marine Ecology Progress Series* **380**, 213–228. doi:10.3354/MEPS07907

Chapman, B. B., Skov, C., Hulthén, K., Brodersen, J., Nilsson, P. A., Hansson, L. A., and Brönmark, C. (2012). Partial migration in fishes: definitions, methodologies and taxonomic distribution. *Journal of Fish Biology* **81**, 479–499. doi:10.1111/J.1095-8649.2012.03349.X

Chapman, D. D., Feldheim, K. A., Papastamatiou, Y. P., and Hueter, R. E. (2015). There and back again: a review of residency and return migrations in sharks, with implications for population structure and management. *Annual Review of Marine Science* **7**, 547–570. doi:10.1146/ANNUREV-MARINE-010814-015730

Clark, J. A. (2015). Female reproductive philopatry and male-mediated gene flow in NSW Port Jackson Sharks. M.Res. Thesis, Macquarie University, Sydney.

Clarke, C., Lea, J. S. E., and Ormond, R. F. G. (2011). Reef-use and residency patterns of a baited population of silky sharks, *Carcharhinus falciformis*, in the Red Sea. *Marine and Freshwater Research* **62**, 668–675. doi:10.1071/MF10171

Couturier, L. I., Jaine, F. R., Townsend, K. A., Weeks, S. J., Richardson, A. J., and Bennett, M. B. (2011). Distribution, site affinity and regional movements of the manta ray, *Manta alfredi* (Krefft, 1868), along the east coast of Australia. *Marine and Freshwater Research* **62**, 628–637. doi:10.1071/MF10148

da Silva, C., Kerwath, S. E., Attwood, C. G., Thorstad, E. B., Cowley, P. D., Økland, F., Wilke, C. G., and Næsje, T. F. (2013). Quantifying the degree of protection afforded by a no-take marine reserve on an exploited shark. *African Journal of Marine Science* **35**, 57–66. doi:10.2989/1814232X.2013.769911

Dulvy, N. K., Fowler, S. L., Musick, J. A., Cavanagh, R. D., Kyne, P. M., Harrison, L. R., Carlson, J. K., Davidson, L. N., Fordham, S. V., Francis, M. P., Pollock, C. M., Simpfendorfer, C., Burgess, G. H., Carpenter, K. E., Compagno, L. J. V., Ebert, D. A., Gibson, C., Heupel, M. R., Livingstone, S. R., Sanciango, J. C., Stevens, J. D., Valenti, S., and White, W. T. (2014). Extinction risk and conservation of the world's sharks and rays. *eLife* **3**, e00590. doi:10.7554/ELIFE.00590

Espinoza, M., Heupel, M. R., Tobin, A. J., and Simpfendorfer, C. A. (2016). Evidence of partial migration in a large coastal predator: opportunistic foraging and reproduction as key drivers? *PLoS One* **11**, e0147608. doi:10.1371/JOURNAL.PONE.0147608

Feldheim, K. A., Gruber, S. H., and Ashley, M. V. (2002). The breeding biology of lemon sharks at a tropical nursery lagoon. *Proceedings of the Royal Society of London. Series B, Biological Sciences* **269**, 1655–1661. doi:10.1098/RSPB.2002.2051

Ferguson, A. M., Harvey, E. S., Taylor, M. D., and Knott, N. A. (2013). A herbivore knows its patch: luderick, *Girella tricuspidata*, exhibit strong site fidelity on shallow subtidal reefs in a temperate marine park. *PLoS One* **8**, e65838. doi:10.1371/JOURNAL.PONE.0065838

Heithaus, M. R., Frid, A., Wirsing, A. J., and Worm, B. (2008). Predicting ecological consequences of marine top predator declines. *Trends in Ecology & Evolution* **23**, 202–210. doi:10.1016/J.TREE.2008.01.003

Heupel, M. R., Semmens, J. M., and Hobday, A. J. (2006). Automated acoustic tracking of aquatic animals: scales, design and deployment of listening station arrays. *Marine and Freshwater Research* **57**, 1–13. doi:10.1071/MF05091

Hueter, R. E., Heupel, M. R., Heist, E. J., and Keeney, D. B. (2005). The implications of philopatry in sharks for the Management of shark fisheries. *Journal of Northwest Atlantic Fishery Science* **35**, 239–247. doi:10.2960/J.V35.M493

Huveneers, C., Harcourt, R. G., and Otway, N. M. (2006). Observation of localised movements and residence times of the wobbegong shark *Orectolobus halei* at Fish Rock, NSW, Australia. *Cybium* **30**, 103–111.

Huveneers, C., Otway, N. M., Gibbs, S. E., and Harcourt, R. G. (2007). Quantitative diet assessment of wobbegong sharks (genus *Orectolobus*) in New South Wales, Australia. *ICES Journal of Marine Science* **64**, 1272–1281.

Keeney, D. B., Heupel, M. R., Hueter, R. E., and Heist, E. J. (2005). Microsatellite and mitochondrial DNA analyses of the genetic structure of blacktip shark (*Carcharhinus limbatus*) nurseries in the northwestern Atlantic, Gulf of Mexico, and Caribbean Sea. *Molecular Ecology* **14**, 1911–1923. doi:10.1111/J.1365-294X.2005.02549.X

Kohler, N. E., and Turner, P. A. (2001). Shark tagging: a review of conventional methods and studies. *Environmental Biology of Fishes* **60**, 191–224. doi:10.1023/A:1007679303082

McFarlane, G. A., and King, J. R. (2003). Migration patterns of spiny dogfish (*Squalus acanthias*) in the North Pacific Ocean. *Fishery Bulletin* **101**, 358–367.

McLaughlin, R. H., and O'Gower, A. K. (1971). Life history and underwater studies of a heterodont shark. *Ecological Monographs* **41**, 271–289. doi:10.2307/1948494

Mourier, J., and Planes, S. (2013). Direct genetic evidence for reproductive philopatry and associated fine-scale migrations in female blacktip reef sharks (*Carcharhinus melanopterus*) in French Polynesia. *Molecular Ecology* **22**, 201–214. doi:10.1111/MEC.12103

Mulcahy, D. M. (2003). Surgical implantation of transmitters into fish. *ILAR Journal* **44**, 295–306. doi:10.1093/ILAR.44.4.295

Nosal, A. P., Caillat, A., Kisfaludy, E. K., Royer, M. A., and Wegner, N. C. (2014). Aggregation behavior and seasonal philopatry in male and female leopard sharks *Triakis semifasciata* along the open coast of southern California, USA. *Marine Ecology Progress Series* **499**, 157–175. doi:10.3354/MEPS10632

O'Gower, A. K. (1995). Speculations on a spatial memory for the Port Jackson shark (*Heterodontus portusjacksoni*) (Meyer) (Heterodontidae). *Marine and Freshwater Research* **46**, 861–871. doi:10.1071/MF9950861

O'Gower, A. K., and Nash, A. R. (1978). Dispersion of the Port Jackson shark in Australian waters. In 'Sensory Biology of Sharks, Skates, and Rays'. (Eds E. S. Hodgson and R. F. Mathewson.) pp. 529–544. (Office of Naval Research, Department of the Navy: Arlington, VA, USA.)

Papastamatiou, Y. P., Meyer, C. G., Carvalho, F., Dale, J. J., Hutchinson, M. R., and Holland, K. N. (2013). Telemetry and random-walk models reveal complex patterns of partial migration in a large marine predator. *Ecology* **94**, 2595–2606. doi:10.1890/12-2014.1

Powter, D. (2006). Conservation biology of the Port Jackson shark, *Heterodontus portusjacksoni*, in New South Wales. Ph.D. Thesis, University of Newcastle.

Powter, D. M., and Gladstone, W. (2008). The reproductive biology and ecology of the Port Jackson shark Heterodontus portusjacksoni in the coastal waters of eastern Australia. *Journal of Fish Biology* **72**, 2615–2633. doi:10.1111/J.1095-8649.2008.01878.X

Powter, D. M., and Gladstone, W. (2009). Habitat-mediated use of space by juvenile and mating adult Port Jackson sharks, *Heterodontus portusjacksoni*, in Eastern Australia. *Pacific Science* **63**, 1–14. doi:10.2984/1534-6188(2009)63[1:HUOSBJ]2.0.CO;2

Ryan, L. A., Meeuwig, J. J., Hemmi, J. M., Collin, S. P., and Hart, N. S. (2015). It is not just size that matters: shark cruising speeds are species-specific. *Marine Biology* **162**, 1307–1318. doi:10.1007/S00227-015-2670-4

Speed, C. W., Field, I. C., Meekan, M. G., and Bradshaw, C. J. (2010). Complexities of coastal shark movements and their implications for management. *Marine Ecology Progress Series* **408**, 275–293. doi:10.3354/MEPS08581

Venables, W. N., and Dichmont, C. M. (2004). GLMs, GAMs and GLMMs: an overview of theory for applications in fisheries research. *Fisheries Research* **70**, 319–337. doi:10.1016/J.FISHRES.2004.08.011

Wearmouth, V. J., and Sims, D. W. (2008). Sexual segregation in marine fish, reptiles, birds and mammals: behaviour patterns, mechanisms and conservation implications. *Advances in Marine Biology* **54**, 107–170. doi:10.1016/S0065-2881(08)00002-3