Abstract

Oceanic sharks are vulnerable to overexploitation due to their life-history strategies, and efforts to protect them in the wild have been stalled by transjurisdictional conflicts of interest. The pelagic thresher shark (*Alopias pelagicus*) is one such species that visits a seamount in the Philippines where its dependable presence has catalysed a burgeoning dive tourism industry and the designation of a conservation area. Nothing is known of the range and turnover of this population, but the regularity with which these sharks interact with cleaner wrasse on the seamount provides important stability for regional businesses that lack empirical knowledge of their vulnerability. We fitted 14 pelagic thresher sharks with acoustic tags and monitored their fine scale movements for 66 days (June to mid-August 2014). Individuals were present at the seamount for 32% of their days at liberty, and 42% of the tagged sharks were still being detected there at the end of the study. Thresher sharks showed preferences for visiting specific locations on the seamount where they interact with cleaner fish, and estimates of their fidelity to these sites provided scalars for visual census. Pelagic thresher sharks moved away from the seamount after early morning visits to cleaning stations using swim speeds of 3.79 km h^{-1} (± SD 1.43). These movements demonstrated that they have access to the jurisdictional waters of five provincial territories when dispersing from and returning to the seamount on a diurnal basis. While the seamount offers cleaner-associated services and refuge provision for pelagic thresher sharks, their scale of movement leaves them vulnerable to fisheries that operate in the region. Natural history observations provide context and reveal bias for their application in the management and conservation of this rare and vulnerable shark species.

Key Words**:** pelagic thresher shark, acoustic telemetry, cleaning, foraging, marine protection areas, movement patterns, site fidelity.

Introduction

Sharks are under global threat from human interference (Dulvy *et al*., 2014; Ruppert *et al.,* 2017; Strickland, 2017). Oceanic sharks are particularly vulnerable to overexploitation due to their slow growth rates, and the fact that they mature late and produce few offspring (Dulvy *et al*., 2008; Ferretti *et al*., 2010; Heupel *et al*., 2015). While it is clear that pelagic sharks are often subjected to fishing for their meat and valuable fins (Clarke *et al*., 2006), conflicting priorities amongst policy makers and stakeholders have stalled many initiatives to protect them across jurisdictions in the wild (Dulvy *et al*., 2008; Sutherland *et al.*, 2009; Heupel *et al*., 2015). The conservation of mobile shark species that make transboundary movements in the face of such challenges is largely dependent on knowledge of their use of habitats and migration patterns (Chapman *et al*., 2005; Garla *et al*., 2006; Andrews *et al*., 2010; Able, 2016).

Migration strategies employed by sharks are diverse and vary among species and individuals (Heupel *et al*., 2006). Transoceanic migrations between genetically indistinct subpopulations of white sharks (*Carcharodon carcharias*) in South Africa and Australia resulted in mixing between them (Pardini *et al.*, 2001; Bonfil *et al*., 2005), and satellite track data showed that some tiger sharks (*Galeocerdo cuvier*) travel in excess of 7000 km undistracted, presumably to forage on “naïve” juvenile loggerhead turtles in the mid Atlantic (Lea *et al*., 2015). Since access to resources may explain why a shark will travel to and show fidelity for some habitats over others (Jewell *et al*., 2013; Yates *et al*., 2015), understanding how sharks select and use their habitats throughout their growth ontogeny has clear and important implications for developing models to manage and protect species (Heupel *et al*., 2006; Dulvy *et al*., 2017). Exposure to sharks is also a rapidly growing sector of tourism led by guide services (Gallagher *et al*., 2015) and interest in new aspects of their behaviour and ecology attract public attention (Richards *et al*., 2015). Pelagic thresher sharks are one such charismatic species that visit a site in the Central Visayas of Philippines, where their dependable presence has catalysed a burgeoning tourism industry, and the designation of a grass roots conservation area.

The Visayan Sea is a key marine biodiversity area in the Philippines that is known for its abundant coastal and marine resources (Oliver 2012; Oposa *et al.*, 2016). Pelagic thresher sharks (*Alopias pelagicus*) visit cleaning stations at a shallow coastal seamount in the area with such regularity that their associations with cleaner wrasse are thought to be essential to their health and fitness (Oliver *et al*., 2011; Oliver 2012; Cadwallader, *et al*. 2014; Oliver and Bicskos Kazso, 2015). These cleaning stations provide a predictable nexus for interaction between humans and sharks that benefits non-extractive commercial exploitation and research (Oliver *et al.*, 2011; Oliver 2012). Recreational divers visit the seamount to observe pelagic thresher sharks on most days, and dive tourism fuels approximately 80% of the local economy (Oliver 2012; Oposa *et al.*, 2016). The habitat that supports pelagic thresher shark visits on top of the mount is now severely degraded due to decades of dynamite fishing, disturbance from global storms, and SCUBA divers trampling the reef (Oliver *et al*., 2011; Oliver 2012; Oposa *et al*., 2016). Concern over the implications that these impacts may have for the viability of the population and the income that it generates for the region is rising (Oposa *et al*., 2016).

Pelagic thresher sharks are one of three recognised thresher shark species (Alopiidae) that possess a unique scythe-like caudal fin that they use to strike and debilitate their prey when hunting (Oliver *et al*., 2013). Known to frequent warm and temperate offshore waters in the Indo-Pacific (Liu *et al*., 1999; Oliver *et al*., 2011), pelagic thresher sharks mature late, have low fecundity, are listed under Annex II (Co17) of the

Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), and are classed as 'vulnerable' by the International Union for the Conservation of Nature and Natural Resources' (IUCN) Red List (Wahnbaeck *et al*., 2007). Pelagic thresher sharks are important to global fisheries (Liu *et al*. 1999; Baum *et al*. 2003; Tsai *et al*. 2010; White *et al*. 2017), but the extent to which they are exploited in the Philippines is poorly understood.

In this paper we investigate the spatial and temporal patterns associated with pelagic thresher shark movements in the Central Visayas of the Philippines. We quantified thresher shark dispersals to and from a seamount where their occurrence is prized for tourism, to describe the population size and turnover relative to *in situ* observations made by recreational SCUBA divers. More specifically, we used acoustic telemetry to determine: (1) the temporal patterns of individual shark visits to specific cleaning stations on the seamount; and (2) how far thresher sharks that regularly use the seamount disperse. Thresher shark ranging and dispersal behaviour is discussed in the context of their vulnerability, migration, cleaning and foraging ecology, and the resilience of an economy that is bound by the predictability of their sightings.

Method

Research was undertaken with the permission of the Department of Tourism, the Governor of Cebu, and the Municipality of Daanbantayan, and adhered to the Philippine 'Wildlife Resources Conservation and Protection Act'. Tagging was performed under IACUC-compliant protocol No. 04-020 (Rutgers University).

Location

Monad Shoal is a shallow coastal seamount in the Visayan Sea that rises from 250 m to 20 m depths between the provincial islands of Cebu and Leyte (N 11° 19’ 06.7”, E 124° 11’ 31.9”) (Figure 1). The site is the only known location where SCUBA divers can regularly observe thresher sharks. This has catalysed a burgeoning dive tourism industry that generates important income for nearby Malapascua Island and the region (Oliver *et al*., 2011). The seamount has the municipal designation of ‘Shark and Ray Sanctuary’ due to a recent local grass-roots effort to conserve the site for dive tourism that is defined by a rough polygon perimeter marked by buoys along its scalloped margin (Figure 1). This no take preserve is monitored by local maritime police and the Malapascuan community, and is enforced by the region’s municipal governing authorities. Thresher sharks that are observed on the seamount may comprise a single unit stock (Oliver, 2012), but the viability of the population and its habitat range is unknown.

Tagging

Divers tagged thresher sharks with external acoustic tags darted into the interdorsal musculature from 7 to 28 June 2014. The tagging procedure elicited brief threat displays (arched back, lowering of pectoral fins) from some sharks, and no reaction from others. Transmitters (Lotek Wireless Inc. model MM-M-16-25-TP, 16 x 62 mm, 29 g in water) broadcast identification, pressure, and temperature data at 67.8 kHz with sound pressure level of 161 dB re 1 µPa @ 1 m. Unique identifiers broadcast every 3 seconds in a code-division-multiple access (CDMA) signal, without code collision at high signal repeat rates from multiple transmitters (Grothues, 2009). Expected battery life span was 117 days.

Size & Sex

Whenever possible, we estimated the total lengths (TL) of the tagged sharks from still images when both the shark and its tag were in full view, and perpendicular to the axis of observation. Using the known tag length as a standard, we calculated a shark's length using tools in *Photoshop CS4* (Adobe, San Jose, CA). We then expressed shark lengths in coarse juvenile (<2 m TL), transitional (2-3 m TL), and adult (>3 m TL) bins according to Liu *et al.*'s (1999) protocols. The presence or absence of claspers indicated a shark's sex.

Telemetry

Active tracking of thresher shark dispersals

To quantify rates and direction of movement we tracked sharks leaving the seamount from an open skiff (chase boat) equipped with stereo directional hydrophones (LPH_1, Lotek Wireless, Inc.) connected to a logging/processing system (MAP RT-A Lotek Wireless Inc.), which recorded identification number and sound pressure level (SPL, developed below as a proxy for distance) for each data point, as well as alternating depth and temperature data. Global positioning System (GPS) units (Raymarine e125 unit, DG200 mini loggers, and Garmin eTrex) continuously logged the location of the boat. However, two of the units had technical issues that resulted in the loss of time stamps for positional data for some of the shark tracks. In these instances we abandoned shark speed calculations, and used waypoints to estimate shark movements.

Passive monitoring of thresher shark visits to cleaning stations

The frequency, duration, and timing of sharks returning to the seamount were synoptically monitored from an array of four stationary (moored) submersible data loggers (MAP_3050, Lotek Wireles Inc.) that we deployed at four known cleaning stations (A-D) on the edge of the seamount (Oliver *et al*., 2011) (Figure 1). These recorded transmissions from sharks approaching the cleaning stations from within 1.5 km (from the ocean side). Our general range estimates for detecting whether or not tagged sharks were in the study area were based on a collection of previous tests from similar tags in various environments (Grothues et al., 2012; Grothues and Davis, 2013). These demonstrated that the chance of detection (expressed as a percentage of tag transmissions recorded) is strongly correlated with SPL, and with the distance between the tag and the receiver because the number of transmissions that are recorded decay exponentially with distance (Grothues et al., 2012; Grothues and Davis, 2013). Monitoring lasted 66 days (June – mid August 2014). The submersible loggers recorded data in the same way as the RT-A logger that was used for active tracking.

Data Analysis

Active tracking of thresher shark dispersals

Thresher shark movements were classified into two categorical event types: those in which sharks moved away from the seamount, and those in which they remained nearby. The position of the chase boat was used as a proxy for a shark's movements following Holland *et al*. (1996). Lowess smoothing of the GPS tracks with a 25-point moving window (~200 s^{-1}) was sufficient to remove boat loops (used to reacquire signals) from the record and deemphasized boat positioning manoeuvers during tracking. To characterise shark movements we calculated the distance between each successive GPS fix along the smoothed track, the cumulative point-to-point distance, the linear distance (between the first and last track points), and tortuosity (deviation from linearity as the ratio of the cumulative track length to line distance). Where time stamps were available in the GPS record, we calculated instantaneous swim speeds as the distance between points divided by the time between points, and the mean swim speed as the cumulative distance divided by track time. We also calculated total track time using the first and last detection timestamps, and the potential range for sharks that use the seamount on a daily basis as the product of mean hourly swim speed multiplied by 12 hours to allow for the return trip.

Passive monitoring of thresher shark visits to cleaning stations

Since divers carried active tags for attachment, logger records were filtered to remove all detections of a tag prior to the time it was deployed. The remaining logger detections thus indicated a level of acceptance that a tagged shark was within the jurisdiction of the seamount's conservation area. These were plotted against time of day. To provide a scalar for quantifying the turnover of sharks relative to diver observations, the proportion (%) of time that a shark was present at the seamount was calculated using 'day' as the unit of measurement. The average score across all sharks was weighted by the number of weeks that a particular shark was at liberty (from its tagging date until August 11 (2014) when the loggers were recovered). Weighting placed more emphasis on the scores of sharks that were at liberty for longer to acknowledge a higher level of confidence in their visit rates. The 2-week ending rubric was based on observations of visit cycles.

Pelagic thresher sharks may approach and inspect or simply pass a cleaning station, or they may slow, circle, and pose to solicit services from cleaners (i.e. "commit" to cleaning) (Côté 2000; Oliver et al. 2011). We characterised these "commitment" behaviours in the telemetry data on the basis of their concurrent modes in duration and SPL at each cleaning station by filtering the logger data to remove all detections below an SPL of 29 dB (see Grothues and Davis, 2013). This threshold was determined from the SPL frequency distribution for a stationary diver-held control tag at the logger and represented a mean shark-to-cleaning-station distance of ≤15 m. Filtering at this level eliminated 89% of all logged shark detections. The conservative nature of the approach also ensured that differences in detection counts did not result from topographic acoustic shielding because the distance of such features was greater than the cut off point for the filtered detection range. We tested the data for normality with a Shapiro-Wilk goodness-of-fit test, which determined that it was heteroscedastic (sw = 0.5895 $p < 0.01$). We then tested the null hypothesis that the time a shark spent at the loggers was randomly distributed using a nonparametric two-way Kruskal Wallis test (α = 0.0.5) (with sharks as replicates) to assess preferences for specific cleaning stations (Oliver *et al*., 2011).

To standardise for possible differences in the detection frequency among sharks for the total time spent at cleaning stations, the filtered record of each shark was sorted into a histogram of the number of detections in 24 (hourly) time bins for all days combined. The frequency was then standardised to unit variance with a range of 0 to 1 (the maximum detections per hour for an individual shark). The standardised records were then summed across all sharks within each time bin to produce a single cumulative hourly detection frequency distribution, which we used to quantify any diurnal periodicity in the distribution of shark visits to cleaning stations. To provide confidence in our measures of circadian rhythm, we tested the null hypothesis that the population has a uniform circular distribution by converting visit hours to angles $A = ((360 \times h)/24)$ and then applying a Rayleigh test (Berens 2009). All of our statistical analyses applied MATLAB (The MathWorks, Inc., Natick, Massachusetts, USA).

Results

We tagged 14 pelagic thresher sharks overall, and actively tracked ten of these during 21 days of field operations in June 2014 (three on more than one occasion, and one on consecutive days). Seven of the corresponding GPS tracks provided time references that were useful for instantaneous rate of movement (ROM) analyses. Passive logging continued for almost 2.5 months until August 21.

Telemetry

Active tracking of thresher shark dispersals

All of the sharks that we tracked for a linear distance of 2.5 km or more used a specific corridor to disperse north-northeast away from the seamount late in the morning (Figure 2). Although the mean (±SE) linear track distance was 25.02 ± 6.99 km, the geodesic distance that sharks travelled away from the seamount had a mean of 6.82 ± 2.75 km for all tracks combined. The longest track covered a linear distance of 56.35 km and lasted 825 minutes; the shortest covered 9.60 km and lasted 84 minutes (Table 1, Figure 2).

Pelagic thresher sharks swam at an average speed (±SE) of 3.79 ± 0.54 km h^{-1}, with a standard deviation of 1.43 km h^{-1} (0.2 - 0.6 m s^{-1} BL). The fastest track involved a mature female shark (ID 61100) that swam at an average speed of 6.82 km h^{-1}. The slowest track involved a juvenile female shark (ID 60200) that swam at an average speed of 2.51 km h^{-1}. Thresher sharks that returned to the seamount in a 24-hour cycle thus had a potential radial range of 45.41 km with a standard deviation of 17.14 km (Figure 3).

On several occasions we detected and simultaneously tracked two sharks as they moved in close proximity to each other north-northeast away from the seamount for cumulative periods of 38 to 195 minutes. The density (detections per minute) and SPL records for these incidents indicated a separation of 0 to 600 m suggesting that the sharks may have been using a mutually attractive resource.

The tortuosity (T) of shark movements was highly variable (mean 6.88 ± SE 1.79 with standard deviation of 4.74) (Table 1). Female sharks 60300 and 61100 used sharp and erratic twists and turns to stay close to the seamount, which resulted in high tortuosity scores (60300: T = 14.26/1.4 h^{-1}; 61100: T = 12.46/3.3 h^{-1}), whereas male sharks 60000 and 60600 used linear and meandering movements to disperse far away, which resulted in low tortuosity scores (60000: T = 1.95/5.5 h^{-1}; 60600: T = 4.51/13 h^{-1}).

Passive monitoring of thresher shark visits to cleaning stations

The submersible data loggers detected all of the thresher sharks in the vicinity of the seamount on the day that they were tagged, and ten were detected returning to the seamount on subsequent dates (Figure 4). The loggers made 26,176 detections of tagged thresher sharks overall and 5,482 detections of a diver-held control tag. There were no false detections (ghost tags). Individual sharks were present within detection range of the loggers for a mean (±SE) of 8.8 ± 2.35 days (standardised mean fraction 32% ± 3.74% days at liberty, ranging from 3.3% to 87.9%) (Figure 4). Shark 60600 was detected most frequently (30 days). Sharks 60900, 61100 and 61200 were only detected on one day each, while sharks 60000, 60200, 60600 60700, and 60800 made repeated but episodic use of the area within detection range on at least 4 different days extending to the end of the life of the loggers' deployment (Figure 4). The relatively continuous stretches of detection periods for these sharks lasted from hours to days, but they were also absent for periods of more than a week before returning (Figure 4). Visits to the area by the remaining sharks were intermittent (Figure 4). No sharks were continuously present within logger range but there was at least one shark present on 50 of the 66 days that the loggers were deployed. The weighted overturn for the duration of the study was 42%.

Visits during which sharks committed to cleaning stations were strongly bimodal in diurnal periodicity ($z = 109.3119$, $p = <0.0001$), increasing steadily from a near median rate of 1.4 visits between 0000 and 0100 hours to almost 4 at 0900 hours and then falling to few or none between 1100 and 1500 hours before peaking again sharply at 1600 hours and then falling off again.

Ten tagged sharks committed to visits at the cleaning stations overall (Table 2). Three sharks committed to visits at all 4 loggers, and several sharks visited several loggers (Table 2, Figure 5). Station A logged the most detections (n = 1303) followed by B, D and C respectively. Shark 60400 had numerous loud detections (> 29dB) at Station A but none at the other 3 stations (Figure 5). In contrast, shark 60000 had at least 100 detections at Stations A, B and C. Sharks 606000 and 60700 committed to visits at Stations A and C, but were not detected at Stations B and D (Figure 5). Sum SPL and sum detections were highly correlated (rho = 0.9999). The global test for differences in thresher shark visits to specific cleaning stations was not significant at the *a priori* level for significance (p = 0.0963) (Table 3), but the pattern of total detections was reflected in the number of sharks that visited each station, with Station A receiving visits from the most individuals (n = 8). Four sharks (59700, 60800, 61100, and 61200) did not visit any of the logged stations after they were tagged.

Discussion

The use of Marine Protected Areas (MPAs) is widespread, but their efficacy in conserving shark populations is largely dependent on their ability to capture the core habitat that species prioritise during their different life stages (Dulvey *et al*., 2008; White *et al*., 2017). The fine scale movements of individual sharks, their centers of activity, the proportion of time that they spend in potential management areas, their ontogenic shifts in habitat use, and their migration pathways are particularly important considerations for designing MPAs for large mobile species (Werry *et al*., 2014). Our study represents the first attempt to quantify the fine scale spatial movements of pelagic thresher sharks, and supports assertions that cleaner services play an important role in their life history strategies. Understanding the complexities of habitat use, site fidelity, dispersal, and population connectivity in this broad ecological context has clear and important implications for conserving such vulnerable shark species (Dulvy *et al*., 2008; Heupel *et al*., 2015; Able 2016).

While a pattern of discrimination for sharks visiting specific cleaning stations was not significant at the *a priori* level for significance, we caution that Type II error (not finding a difference when there is one) represents a greater risk than Type I error when considering management decisions. In this context, detections from our data loggers showed that sharks returning to the seamount went to specific cleaning stations, and that they spent more time at some stations than others. The sill of the seamount provides habitat for cleaner wrasse that occupy these stations where they remove parasites and dead tissue from thresher shark clients that pose to solicit services from them (Côté, 2000; Oliver *et al*., 2011). In addition to providing parasite removal services, cleaners are known to inspect and take bites from the cloaca of parturient females that go to the area's cleaning stations to give birth (Oliver and Bicskos Kazso, 2015). The frequency with which the tagged sharks returned to the cleaning stations, and the amount of time that they spent at these locations supports previous suggestions that interacting with cleaners is an important strategy for maintaining health and fitness through the various challenges that they face during their different maturity stages (Grutter, 1996; Oliver *et al*., 2011; Cadwallader, *et al*. 2014; Oliver and Bicskos Kazso, 2015).

Our first order account of the frequency and distribution of thresher shark visits among specific sites on Monad Shoal is an important management tool because it demonstrates that thresher sharks may be resilient to the potential loss of some cleaning stations due to natural or anthropogenic disturbance, and provides a starting point for the design of non-invasive, long-term census monitoring of this important population based on *in situ* observations made by SCUBA divers. Visual observations can now be scaled to estimate the size of the local population because we know that the counts among stations are not cumulative, but are redundant with a bias for station A. For example, at stakeholder meetings that were held during the months of our field work, dive guides consistently reported their observations of nine to ten individual sharks per day, and that these occurred most frequently at station A (F. Malagassi 2014, personal communication, 15 June). In this context, our results suggest that dive businesses are being sustained by visits from 28 to 32 thresher sharks, approximately 13 of which are likely to remain in the vicinity of the seamount after two months. Because dive guides' reporting has been consistent since the end of the study, and bolstered by divers occasionally observing tagged thresher sharks, it appears likely that the sharks that leave the area are replaced by others visiting the seamount. Our statistics of dispersion will be of particular interest to conservationists, NGOs, stakeholders, and policy makers working to design management protocols to protect pelagic thresher sharks in the area.

Most of the sharks that we tracked moving away from the seamount used a specific corridor to disperse north-northeast towards Leyte. These movements consistently took place late in the morning. Some oceanic sharks are known to move between habitats within their range to access resources that are essential to their life history strategies (Jewell *et al*., 2013; Yates *et al*., 2015). Habitats may offer food, provide protection from predation, or refuge for mating and social gathering (Bonfil *et al*., 2005, Van Moorter *et al*., 2009; Hoyos-Padilla *et al*., 2016; Pickard *et al*., 2016). When searching for such resources pelagic sharks may undertake rhythmic migrations that are highly structured with defined passages, schedules, and philopatric homing destinations (Jorgesen *et al*., 2009). These routes may incorporate bathymetric features, geomagnetic fields, and hydrodynamic conditions that serve as navigational tools for a shark's broad and/or fine scale movements (Holmes *et al*., 2014; Klimley *et al*, 2017). The spatial and temporal consistency with which pelagic thresher sharks used a specific corridor away from Monad Shoal may be a function of their familiarity with the area's geophysical and environmental characteristics, or a consequence of moving with topographically-steered tidal currents running along western Leyte (O'Shea *et al*., 2010; Gordon *et al*., 2011; Klimley *et al.*, 2017).

It was often unnecessary to run the chase boat's motor to follow a shark because the drift was with it. Drifts were frequently interrupted by a shark's movements becoming highly tortuous, and we would have to turn the motor on and maneuver the boat carefully to track it. The dynamics of these movement patterns are consistent with a Lévy-flight foraging strategy (Viswanathan 2010) in which predators (such as sharks) that are specialised in hunting spatially patchy distributions of prey optimise their search efficiency by making 'random walks' (Cartamil *et al*., 2010; Humphries *et al*., 2010; Sims *et al.* 2012; Méndez *et al*. 2013; Espinoza *et al*., 2015). Since the sharks that we tracked were at depths of 30 to 250 m, it is unlikely that our tortuosity measurements were influenced by the presence of the chase boat (Johnson *et al.* 2009). Rapid cyclical vertical movements (analysed from the tag's pressure and depth sensors and not developed in this paper) support the supposition of these movements being associated with foraging.

The observations suggestive of passive tidal stream transport, time spent near the seamount in deep water, and movements indicative of foraging do not appear to be 'undistracted' or physiologically expensive in the same manner that defines migration (Ramenofsky and Wingfield, 2007), suggesting that the seamount's habitat is contiguous with foraging habitat. We conjecture for further study that thresher sharks' use of the area is part of a strategy that considers both food and cleaner services, or at least trades some food for cleaner services, without being mutually exclusive. The extent of individual fluidity (contingent formation following Secor, 1999) or seasonal turnover also remains to be investigated. The patterns and their causes may be of interest to resource managers in developing models of vulnerability, and site management recommendations for the seamount because the contingent level of organisation better defines the unit at which humans interact with a stock, than does a species or a population. It will also be important for resource managers to know that these patterns are 'discovered' and 'discoverable' beyond conjecture in order to effectively debate policy and secure the support of stakeholders in management decisions (Sobel and Dalgren 2004).

The rate of movement for far-ranging dispersals indicated that thresher sharks that return to the seamount during a 24-hour cycle have access to five jurisdictions on any given day, but a directional bias appears to constrain this nexus. Of concern is the fact that each jurisdiction is governed and policed by autonomous authorities that operate on a regional basis according to the priorities of different local interest groups (Sutherland *et al*., 2009). Leyte, the jurisdiction that was consistently entered by sharks tracked in this study, has an agrarian economy and is an important fishing region for Indian sardines (*Sardinella longiceps*), the pelagic thresher shark's main prey in this area (Oliver *et al*., 2013). Thresher sharks hunting sardines in these waters are frequently caught as by-catch or specifically targeted because they foul fishing gear and are perceived as a nuisance (Oliver, 2012). In contrast, Cebu has a tourist economy that is largely dependent on marine ecotourism, with shark diving forming the economic backbone of many communities in the province. Pelagic thresher sharks are protected in these locations due to the revenue that they generate, but they become vulnerable to fisheries when they venture outside of high tourism traffic areas.

In other provincial jurisdictions thresher sharks are commercially targeted for their meat and valuable fins that are exported to various markets across Asia (Liu *et al*., 2013; Chuang *et al*., 2016). Since fisheries legislation is mandated at the provincial level in the Philippines, it would be necessary to reconcile the differences of at least five territorial governments, and all of the municipalities that have fisheries interests therein (Simpfendorfer *et al*., 2011; Heupel *et al*., 2015; Dulvy *et al*., 2017), to develop and effect conservation policy for the thresher sharks that use Monad Shoal as their philopatric homing destination (Jorgesen *et al*., 2009; Dulvy *et al*., 2017).

As important as the quantification of transjurisdictional movements is the promotion of shallow reef habitat conservation to the population health of such a pelagic species (Roff *et al.*, 2016; Ruppert *et al.*, 2017). A history of poor diving practices and dynamite fishing have devastated most of the reef on Monad Shoal's shallower platform, leaving a fringe of reef and cleaning stations (Oliver *et al.,* 2011; Oliver 2012). The recent grass-roots effort to conserve pelagic thresher sharks for their economic benefit at the seamount may be unique among efforts to protect potentially wide ranging pelagic species in that it recognises the value of very small (meter-scale) shallow water reef microhabitats, and the wider reef that supports them. Local residents understand that these sharks are normally offshore denizens and that their fidelity to this reef is catalysed by their interactions with cleaners (Oliver *et* al., 2011; Oliver 2012; Oposa *et al.,* 2016). Preservation efforts go beyond the community enforcement of shark fishing closures to include education campaigns for sustainable dive practices (no gloves allowed, no touching, proactive buoyancy control and diver trim, specified mooring areas using pre-positioned ground tackle, and delineated shark viewing amphitheaters) to preserve the cleaning stations. A sense of ownership has evolved among competing dive businesses for specific viewing locations (centered around cleaning stations) that promotes space-based conservation (Oliver 2012). Lobster and abalone fisheries provide good examples of the success of territorial use rights (TURFs) in sustaining fisheries even without government involvement (Hilborn *et al*., 2005). Based on the fidelity to cleaning stations shown here, these measures are justified.

Concluding Remarks

While anecdotal reports from the dive community suggest that thresher sharks are present on the seamount throughout the year, future investigations may wish to address questions associated with their long term movements using a combination of telemetry and mark recapture models that involve local citizen scientists. This need is highlighted by the recapture of one of our acoustically tagged sharks by a longline fisherman approximately 180 km south of the study site near Moalboal (southern Cebu Province). Although thresher sharks showed a preference among cleaning stations, their rate of straying was sufficient to allow some resilience given the possibility of future disturbances to the seamount. It also provides a scalar for population size estimate studies of the region’s pelagic thresher sharks that are now in progress. Policy makers will need to reconcile the differences of regional interest groups if thresher sharks are to be protected under new regulatory infrastructure for CITES-listed elasmobranchs in the Philippines, and meet the government’s commitments under the London Declaration on Illegal Wildlife Trade (2014). These actions are particularly important because the archipelago is considered to be situated in the “centre of the centre” of the world’s marine biodiversity (Carpenter, 2005).

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Tables

Table 1. Summary data of tagged and tracked pelagic thresher sharks. Sharks were tagged at one of five cleaning stations on Monad Shoal in June 2014. Total distance travelled ([a]), straight-line distance ([b]), tortuosity ([c]), track time ([d]), and swim speed ([e]) are presented for the GPS tracks of male (M), female (F), juvenile (J), transitional (T), adult (A), and sex/maturity undetermined (ND) sharks that were useful for instantaneous rate of movement analyses (italcis).

TAG ID	Sex	Size	TD (km)[a]	SD (km)[b]	Tort (km)[c]	TT(h^{-1})[d]	SR (km h^{-1})[e]
59900	F	ND	ND	ND	ND	ND	ND
60200	*F*	*T*	*13.52*	*2.47*	*5.47*	*5.38*	*2.51*
60000	*M*	*ND*	*16.35*	*9.94*	*1.95*	*5.52*	*3.51*
60600	*M*	*A*	*45.80*	*10.15*	*4.51*	*12.93*	*3.54*
60700	M	A	ND	ND	ND	ND	ND
59800	*ND*	*A*	*56.35*	*20.67*	*2.73*	*13.76*	*4.09*
59700	ND	A	ND	ND	ND	ND	ND
60400	M	A	ND	ND	ND	ND	ND
60300	*F*	*T*	*20.62, 9.88*	*3.03*	*14.26*	*6.88*	*3.00, 3.04*
60500	ND	A	ND	ND	ND	ND	ND
61200	ND	ND	ND	ND	ND	ND	ND
60900	ND	J	ND	ND	ND	ND	ND
61100	*F*	*A*	*9.60*	*0.77*	*12.46*	*1.40*	*6.82*
60800	F	ND	ND	ND	ND	ND	ND

Table 2. SPL-filtered detections of pelagic thresher sharks at 4 cleaning stations on Monad Shoal as a measure of the time they committed to spending at each station. Time is scaled to a minimum of 3 seconds per detection.

Logger	Tag	Sum SPL	Count	Sum Total SPL	Sum Detections	No. Sharks
A	Control	17536880	1371	33620088	2674	8
	59800	2988608	245			
	59900	1322292	106			
	60000	1668176	137			
	60200	117956	10			
	60300	118856	10			
	60400	6153664	494			
	60600	1126264	93			
	60700	2587392	208			
B	Control	651076	56	5859020	472	5
	60000	1239956	100			
	60200	417076	34			
	60300	112272	9			
	60600	1396092	111			
	60700	2042548	162			
C	Control	0	0	2724236	223	5
	59800	564624	45			
	60000	1468332	121			
	60200	467772	38			
	60600	175224	15			
	60900	48284	4			
D	Control	2031108	167	3556784	295	5
	60000	57784	5			
	60200	941372	78			
	60300	210936	18			
	60500	48268	4			
	60600	267316	23			

Table 3. Results of the Kruskal Wallis test for global difference in the variation of tagged sharks' relative preferences (commitment) for specific cleaning stations.

Source	SS	df	MS	Chi-sq	Prob>Chi-sq
Groups	799.65	3	266.550	6.34	0.0963
Error	4121.35	36	114.482		
Total	4921.00	39			

Figure Legends

Figure 1. Map showing the location of Monad Shoal in the Central Visayas of the Philippines. Submersible data loggers were deployed at known cleaning stations (A-D) spaced approximately 250 m from each other along the southeastern edges of the seamount's drop off (≤25 m depth). The shark and ray sanctuary (highlighted in red) extends 100 to 300 m from the scalloped margin of the seamount as a rough polygon perimeter that is marked by buoys.

Figure 2. Shark tracks that were used to calculate instantaneous rates of movement (ROM). Some tracks reflect the movements of more than one shark for part of the path.

F**igure 3. Potential daily range of thresher shark dispersal.** The mean radial range (middle circle) + (outer circle) – (inner circle) SD are presented for thresher sharks that return to the seamount (*) in a 24 hour cycle.

Figure 4. Time line of detections by moored loggers (all loggers combined) of acoustically tagged thresher sharks.

Figure 5. Logger detections of thresher sharks' respective commitments to different cleaning stations on Monad Shoal. Radius of plot points for logger-specific shark visits scale linearly as the sum SPL of filtered detections/1000.