Use of high-resolution acoustic cameras to study reef shark behavioral ecology

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ABSTRACT

Shark species play an important role in shaping marine communities, ecosystems, and community assemblages, yet their high mobility and low abundances in certain locations makes studying the way they interact with these systems difficult. Here high-resolution acoustic cameras are demonstrated as effective tools to study the ecology and behavior of reef and coastal sharks that operate in the vicinity of a near-pristine coral reef atoll. The acoustic camera generated detailed imagery and size measurements from >1000 sightings of sharks that traversed a discrete corridor linking two of the atoll's distinct marine habitats, the forereef and offshore pelagic habitat with the atoll's lagoon. Daily shark density and estimated biomass values varied considerably through time, but generally approximated values calculated using less comprehensive and more labor-intensive techniques at this same atoll. Diel patterns in shark movements revealed elevated shark presence during low-light periods of the day (e.g. peak sighting density just after dusk), but weaker links between shark movement patterns and tides. Data gathered through use of this tool extends and reinforces some of the observations made of smaller numbers of sharks using traditional data collection methods while providing unique additional insights into the ways that larger numbers of sharks operate at fine spatial scales over longer periods of time. Behavioral information of this type is critical to developing effective management plans for these vulnerable species.

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1. Introduction

Sharks play important roles in maintaining the health, diversity, and resilience of many marine ecosystems. Their presence in marine communities can have multiple direct or indirect effects on trophic interactions, community biomass regulation, and potential whole-ecosystem phase shifts (Bascompte et al., 2005; Ferretti et al., 2010; Heupel et al., 2014). Properly managing shark species and consequently marine ecosystems requires a deeper understanding of how sharks operate within the habitats they frequent and how they transit between habitats (Block et al., 2011; Heupel and Simpfendorfer, 2015; Speed et al., 2010). This enterprise is made doubly important given the fact that many shark species are classified as Near-threatened, Vulnerable, or Endangered (Dulvy et al., 2014).

The reduced abundance of certain shark species in a variety of locations coupled with their sometimes transient presence in ecosystems and any potential biases (Ward-Paige et al., 2010) for or against

interacting with humans necessitates the exploration and adaptation of new sensing technologies to passively observe shark ecology and behavior in situ, and across a range of spatial scales. The current suite of tools used to study the spatial biology of elasmobranchs (e.g. visual surveys, acoustic telemetry, satellite telemetry, animal-borne cameras, stable isotope analysis) has expanded and continues to produce new insights into the movement patterns of sharks but many of these methods are time, labor, or cost intensive and may sometimes be less well suited to describe fine-scale patterns of utilization of particular marine habitats (Block et al., 2011; Heithaus et al., 2001; McCauley et al., 2014, 2012b). The details of these small-scale movements and behaviors are vitally important to developing a complete understanding of shark ecology and behavior. For instance, previous studies utilizing stable isotope analyses have indicated high connectivity and frequent movement of reef-associated sharks across different habitat types – reefs, lagoons and pelagic habitat (McCauley et al., 2012b) – but direct observation and quantification of these within-system movements are still scarce.

High-resolution acoustic cameras may play an important role in filling this gap in shark research. Acoustic cameras use sonar technology, or pulsed sound wavelengths to produce fast-frame, detailed imaging even in low-light, turbid environments that surpass the range capture and clarity capabilities of traditional optical cameras (Belcher et al., 2002); these cameras also allow for size measurements of detected

targets. This technology was recently adapted for ecological applications. Acoustic cameras have been widely used for the study of salmonid behavior but they have been also employed to passively record the behavior and movements of other marine and freshwater organisms (Becker et al., 2011; Burwen et al., 2010; Holmes et al., 2006; Makabe et al., 2012). Some of the previous applications have included surveying the size structure of fish populations (e.g. cape silverside) in estuaries (Becker et al., 2011), describing the behavior of sturgeon in river spawning areas (Crossman et al., 2011), and counting salmon as they migrated upriver (Holmes et al., 2006). Acoustic cameras have also been used in trials to test the willingness of sharks to cross over experimental magnetic barriers to obtain offered baits as means of examining the efficacy of this type of experimental shark deterrent (O'Connell et al., 2014).

Data are presented here that were collected using one class of acoustic camera to study the behavior and space use of a large population of reef sharks that inhabit the waters surrounding Palmyra Atoll – a near-pristine coral ecosystem in the central Pacific Ocean. As a U.S. National Wildlife Refuge with an especially high biomass of apex predators (Sandin et al., 2008), Palmyra confers a unique and valuable opportunity to survey the abundance and size structure of an unexploited reef shark population, and study how sharks transit across reef habitats and how these movements may be related to abiotic variability. This study reports what can be ascertained using the acoustic camera about the density and size structure of sharks in this habitat as well as how shark behavior varied with time of day and tidal period – two abiotic factors that have been shown to affect movement behavior in multiple other shark populations.

A major value of using acoustic cameras in marine ecological studies is the potential to gain long-term continuous observations of large numbers of sharks interacting with important parts their environment – insight that may not necessarily be obtained through other methods. This non-invasive tool also obviates the need to capture and tag individuals, captures a greater proportion of the population than may be assessed via fishing methods, and does not influence animal behavior.

The behavioral patterns reported here demonstrate the kinds of insight that can be gained from this tool regarding how sharks operate both within and across marine habitats. Proper management of these often highly sensitive species requires access to high quality information about when sharks use a given habitat, what their ecological needs are from that space, and how these dependencies vary temporally and spatially.

2. Materials and methods

2.1. Study site

Palmyra Atoll (5°53′N, 162°05′W) is located in the central Pacific approximately 1700 km south of Hawaii. Palmyra is protected as a U.S. National Wildlife Refuge and its lagoon and surrounding coastal waters are managed as "no-take" zones. The historic isolation and modern protection of Palmyra have allowed large reef fishes, particularly sharks, to persist at high abundances that are rarely observed in inhabited and fished reef settings (Sandin et al., 2008; McCauley et al., 2012b). At least 7 species of sharks are common at Palmyra, including blacktip reef sharks (*Carcharhinus melanopterus*), whitetip reef sharks (*Triaenodon obesus*), grey reef sharks (*Carcharhinus amblyrhynchos*), Galapagos sharks (*Carcharhinus galapagensis*), tiger sharks (*Galeocerdo cuvier*), scalloped hammerhead sharks (*Sphyrna lewini*), and lemon sharks (*Negaprion brevirostris*). Other species are likely to be present, but rare.

Palmyra's islets and lagoon morphology underwent significant structural modification during World War II, including extensive expansion of a large natural channel in the Western Lagoon basin (Collen et al., 2009). This channel in its contemporary form measures approximately 1.5 km long, 80 m wide, and 8 m deep. It is characterized by a sandy

bottom substratum of relatively uniform depth that is flanked by near-vertical walls of coral rubble. Turbulent flushing through the channel often creates visibility conditions which make video or diver observation difficult or impossible. The channel physically connects Palmyra's forereef and offshore marine habitats to the atoll's lagoon habitats and has been observed to be an important passageway for marine megafauna transiting between these two environments (McCauley et al., 2014).

2.2. High-resolution acoustic imaging of shark behavior

The spatially confined nature of Palmyra's main channel presents a tractable arena in which to observe the movement and behavior of sharks transiting between Palmyra's offshore/forereef habitats and lagoon environment. Dual-frequency identification sonar (DIDSON, Sound Metrics Corp., WA, USA) was used to "acoustically gate" a portion of the channel and observe sharks in this corridor (Fig. 1). DIDSON is a marine sonar device that permits high-resolution digital imaging of objects within the sonar's field of view (Belcher et al., 2002). The unit was installed mid-way along the channel at 3 m depth on the southern channel side wall. The acoustic camera near-continuously monitored a 41.7 m^3 section of channel space (McCauley et al., 2014). The field of view of the acoustic camera is pyramidal in shape with a basal width of 5 m and height of 2.5 m. The water volume of the sonar field was calculated as $V = 0.041 D^3 - 0.0052$ m^3; where D is the range selected (Han and Uye, 2009). The maximum linear distance visualized by the acoustic camera was 10 m, or approximately 13% of the width of the channel. As such, the device does not provide a comprehensive view of shark activity in the channel, but rather an unbiased sub-sample of these behavioral patterns. The acoustic camera was positioned to image a section of space directly perpendicular to the channel and was mounted on a vertical channel wall such that few, if any, sharks would transit above or behind the area viewed. The unit was operated during two daily recording sessions (each averaging 9.5 h) from 2 July
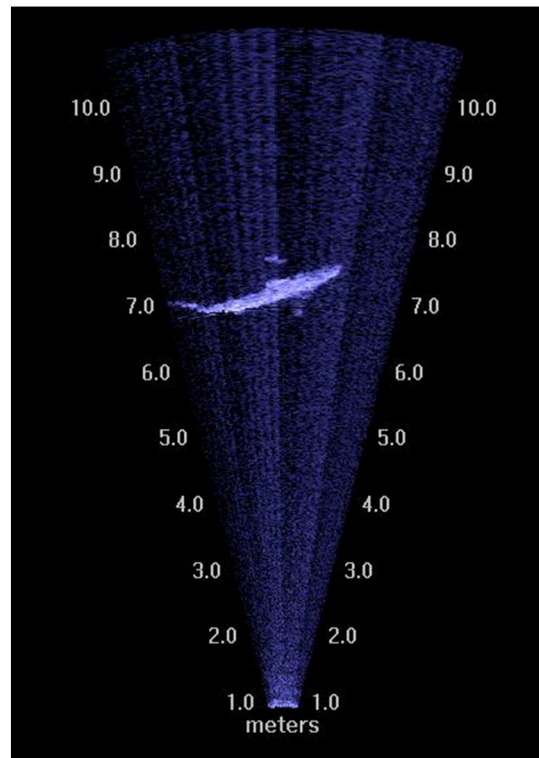

Fig. 1. Acoustic camera recorded image of a shark (2.8 m TL) moving through the sonar unit's field of view. Numbers alongside the field-of-view represent object distance from camera.

2009 through 29 July 2009. Recording session length was battery limited and batteries were serviced twice daily at approximately 0700 h and 1830 h.

Collected data were pre-processed to remove all object-free sections using the DIDSON operating system software. Remaining acoustic footage was manually reviewed and all sharks were enumerated and measured (total length). Field tests of the DIDSON acoustic camera that were conducted using the same range settings as those used in this work report that mean DIDSON measurements of 2874 fish (sockeye salmon) were on average 1.6 cm longer than mean lengths obtained from manual measurements (Holmes et al., 2006). Similarly high levels of measurement correspondence were found in other field tests of length using tethered fish and that this correspondence was not range dependent (Burwen et al., 2010). DIDSON derived measurements of shark length in this study were used without correction. The direction of travel of all sharks was categorically recorded (i.e. "entering" lagoon; "exiting" lagoon). Sharks would occasionally change their direction of travel while in the field of view of the acoustic camera. In such instances the sharks' direction was recorded as the final direction by which they exited the field of view. Acoustic camera sensing does not permit identification of unique individuals and consequently individuals that exited and reentered the field of view were necessarily treated in this analysis as new sighting records. Time standardized shark density estimates were generated using the duration of acoustic camera recordings and the water area or volume monitored (for daily shark densities and diel/tidal shark movement patterns, respectively).

2.3. Shark abundance

Daily shark densities (pooled "entering" and "exiting" sharks) were calculated from acoustic camera recordings, and standardized by water area monitored and recorded minutes. Although the acoustic camera monitors a three-dimensional swath of water, shark density estimates were expressed in two dimensions (m^2; following (McCauley et al., 2012a)) to facilitate comparison with density values estimated using other survey techniques at Palmyra and elsewhere. Estimates of daily biomass were generated from daily shark counts and lengths of recorded individuals using length-weight conversion values reported in Froese and Pauly (2015). Because DIDSON cannot identify individual shark species, two length-weight conversions were used that reflect two general size groupings of sharks (large sharks and all other sharks) species that frequent Palmyra. Lengths of large sharks (i.e., sharks >1.9 m TL; calculated from the largest *C. amblyrhynchos* measured by DJM at Palmyra (1.75 m) +10% to be conservative) were transformed to biomass values using algorithm constants that were averaged for *G. cuvier* and *N. brevirostris*. Based on measurements of >300 sharks captured at Palmyra (McCauley et al., 2012a, 2012b) and reported species-specific size data (Compagno, 1984), these "large shark" observations can with a high degree of certainty be ruled out as grey reef (*C. amblyrhynchos*), blacktip (*C. melanopterus*), and whitetip (*T. obesus*) sharks, the three most common species of sharks recorded on Palmyra's reefs (McCauley et al., 2012a). Lengths of all other sharks were transformed to biomass using algorithm constants that were averaged for *C. melanopterus*, *T. obesus*, and *C. amblyrhynchos*.

2.4. Diel differences in shark behavior

To examine diel variation in shark behavior shark density, directionality of travel, and shark size were compared across a diel partitioning scheme that included two and eight divisions (standardized by water volume monitored and recorded hours). The "two diel" classification divided each 24 h period into "day" and "night"; day = 0620–1930 h (defined as the beginning to end of local civil twilight), night = 1930–0620 h. The "eight diel" classification divided each 24 h period into: pre-dawn (0548–0648 h), dawn (0648–0806 h), post-dawn

(0806–0906 h), day (0906–1658 h), pre-dusk (1658–1758 h), dusk (1758–1909 h), post-dusk (1909–2009 h), and night (2009–0548 h).

This sequential narrowing of diel categories allowed for tiered analysis of daily variation in shark behavior. Boundaries of diel categories were based on measured daily fluctuations in light levels in Palmyra's channel measured directly by light loggers (Onset Computer Corp., MA, USA) placed at 2 and 4 m depths in the channel adjacent to the acoustic camera.

2.5. Influence of tide on shark behavior

Shark density and directionality of travel were similarly compared across four tidal periods (standardized by water volume monitored and recorded hours): ebb, flow, high slack, and low slack. High slack and low slack were defined as 1 h periods either side of peak high or low tide events (Cartamil et al., 2003). Local tidal events for Palmyra were determined directly using a pressure sensor (TruBlue 555 KPSI, Esterline Pressure Systems, WA, USA) installed in the West Lagoon.

2.6. Statistical analyses

Comparisons of shark density (across diel/tidal periods), directionality ("entering" versus "exiting" within each diel/tidal period), and size (across diel periods) were made using nonparametric Wilcoxon and Kruskal-Wallis tests, coupled with Holm's sequential Bonferroni post hoc corrections in instances where multiple comparisons were computed. All statistics were computed in R (R Development Core Team, 2013).

3. Results

A total of 1196 shark observations were made during 443 h of acoustic camera recording in Palmyra's main channel. Measurements of shark sizes ranged from 0.5 to 3.4 m total length (Fig. S1), with a mean size of 1.0 ± 0.01 m. No species-specific diagnostic morphologies (e.g. the hammerhead of *S. lewini* sharks) were observed during recordings. The maximum number of sharks observed in a single frame was 10 individuals. Individual sharks typically spent 2–10 s within the field of view of the acoustic camera. Ten sharks measured >1.9 m TL, ranging from 2.0 to 3.4 m.

Daily density of sharks observed during the study period was variable, ranging from 0 to 5.7 sharks 1000 m^{-2} min^{-1} (Fig. 2). Daily biomass values ranged from 0 to 105 kg 1000 m^{-2} min^{-1}. These daily shark biomass values largely mirrored variations in daily shark density, except on dates where large sharks were abundant (Fig. 2).

3.1. Diel differences in shark behavior

In the two diel classification, the density of sharks moving through the channel at night was more than three times greater than the density of sharks moving through by day ($W = 252, P = 0.02$; Fig. 3a). The eight
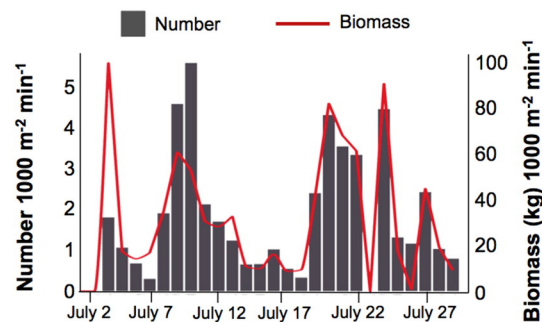

Fig. 2. Daily shark density (*grey bars*) and estimated biomass (*red line*) recorded by acoustic camera during the study period. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
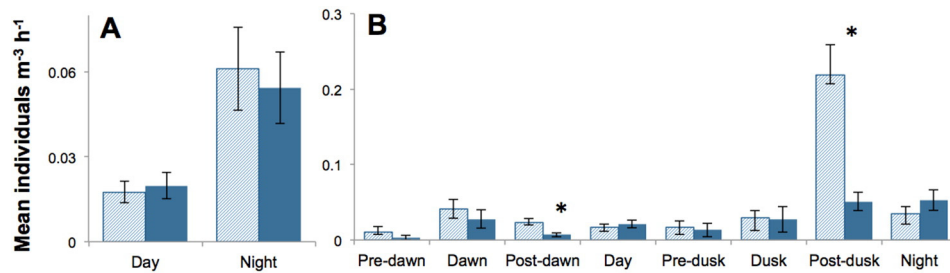
Fig. 3. Density of sharks (mean ± SE) recorded across diel periods with directionality (entering, *light blue bars*; exiting, *dark blue bars*). A. Two diel classification. Diel periods were not significantly different (after post-hoc correction; entrances and exits pooled). There were no statistical differences between entrance and exit rates within each period. B. Eight diel classification. Pre-dawn, post-dawn, day, pre-dusk, and dusk were significantly different from post-dusk, and pre-dusk was significantly different from night (after post hoc correction; entrances and exits pooled). Diel periods marked with an asterisk denote statistical difference between entrance and exit rates within that period.

diel classification further revealed that the majority of this difference in diel usage was driven by sharks swimming through the channel during the post-dusk period (i.e. 1909–2009 h; $\chi^2 = 37.38$, $df = 7$, $P = 0.0001$; Fig. 3b). The mean density of sharks ($m^{-3} h^{-1}$) recorded at post-dusk was approximately 7 times greater than values observed during the full light diel periods (i.e. post-dawn, day, and pre-dusk).

Evaluations of differences in shark directionality within both the two and eight diel classification schemes were only significant for eight diel, with more sharks observed entering the lagoon during post-dawn and post-dusk ($W = 197$, $P = 0.04$ and $W = 407$, $P = 0.0001$, respectively) than exiting the lagoon during the same periods (Fig. 3a and b). Density of sharks entering the lagoon at post-dusk was greater than shark densities observed during any other time period and >4 times greater than the density of sharks exiting the lagoon during the same time period.

Mean shark sizes in the channel during each of the different diel periods were significantly different for both diel classifications (two diel, $W = 78702.05$, $P = 0.0001$; eight diel, $\chi^2 = 213.61$, $df = 7$, $P = 0.0001$), with larger sharks tending to move through the channel at times characterized by lower ambient light (night, post-dusk, pre-dawn). Elucidating specific diel patterns of movement through the channel for the pool of "large sharks", >1.9 m TL, was statistically difficult given the low sample size ($n = 10$), but the majority of these large individuals were observed exiting the lagoon during the day. Eighty percent of these large shark observations were made at a distance of ≥8 m from the acoustic camera, potentially suggesting behavioral avoidance of the channel ledge.

3.2. Influence of tide on shark behavior

Measurements of pooled shark density through the channel were significantly different when compared across tidal periods ($\chi^2 = 8.57$, $df = 3$, $P = 0.035$) with highest shark densities observed during high slack and lowest densities observed during flood tides (Fig. 4). Differences in shark density between any two different tidal periods,
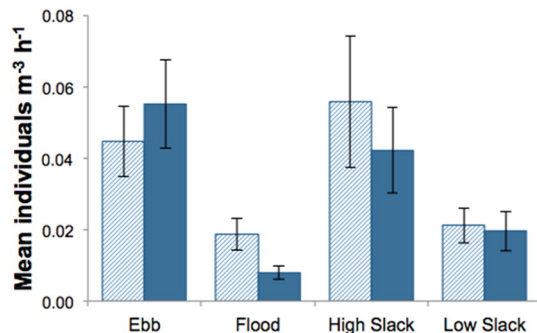

Fig. 4. Density of sharks (mean ± SE) recorded across four tidal periods with directionality (entering, *light blue bars*; exiting, *dark blue bars*). No pair of tidal periods was significantly different from each other (after post hoc correction; entrances and exits pooled). There were no statistical differences between entrance and exit rates within each period.

however, were only weakly pronounced such that post hoc analysis yielded no significant pair-wise differences. Comparisons of directionality within each tidal period did not yield any significant differences.

4. Discussion

This study provides a novel demonstration of how acoustic cameras can be used to describe detailed attributes of the space use and behavior of sharks that provide a valuable complement to data collected using more traditional shark observation methods. The imaging capability of the acoustic camera allowed near-continuous capture of multiple weeks of movement data on shark species that transit across an important habitat boundary at Palmyra Atoll. Insight yielded from acoustic camera observation provides unique bulk insight into the behavioral patterns of populations, rather than just individuals. This tool provides the opportunity for similar kinds of new question asking in research involving other difficult to observe large marine species (e.g. marine mammals, sea turtles) in similar contexts.

The acoustic camera data collected during this study provide valuable insight into the structure and behavior of the shark population using the main channel at Palmyra. Smaller sized sharks (i.e. <1.9 m TL) were most commonly observed, matching observation from visual surveys that such species (e.g. blacktip, whitetip, grey reef) are numerically dominant at Palmyra. Blacktip sharks, *C. melanopterus*, are the most common shark observed in Palmyra's lagoons and previously reported mean sizes for *C. melanopterus* at Palmyra (Papastamatiou et al., 2009) closely match the mean shark sizes recorded here by the acoustic camera. Additionally, recordings of the ten "large sharks" (i.e. >1.9 m TL) quantitatively confirm the reports of intermittently sighted large shark species (e.g. *G. cuvier* or *N. brevirostris*) in Palmyra's lagoons (Papastamatiou et al., 2014). The mean density of sharks observed using the acoustic camera (1.8 sharks 1000 m^{-2} min^{-1}, SE 0.3 sharks 1000 m^{-2} min^{-1}), while highly variable across days, was similar to average shark density values reported by McCauley et al. (2012a) at Palmyra using traditional video surveys (approximately 1.2 sharks 1000 m^{-2} min^{-1}). In addition to corroborating data gathered through more time and labor-intensive methods, the acoustic camera highlighted a large temporal variability in the abundance and estimated biomass of sharks transiting through the main channel – continuous temporal information that warrants further investigation into these shark movement patterns and that may not have been collected through traditional video or diver surveys due to physical or time constraints.

4.1. Diel differences in shark behavior

The higher density of sharks transiting through the main channel during low-light level hours reflects observations made elsewhere of increased crepuscular activity in several different reef and coastal sharks. Explanations offered for heightened levels of activity for non-filter feeding sharks like these include: individuals capitalizing on opportunities for higher prey capture rates, thermoregulation, and predator avoidance

(Andrews et al., 2009; Garla et al., 2005; McKibben and Nelson, 1986; Sims et al., 2006).

Observed peaks in shark densities at the acoustic camera sensing site in Palmyra could represent either a numerical increase in shark abundance (e.g. more sharks arriving during this period to this region to forage) or an increase in the activity of sharks resident in this area (e.g. the same number of sharks looping at higher rates in front of the acoustic camera). Peaks in shark densities specifically recorded during the post-dusk period (1909–2009 h) temporally mirror reported activity peaks (1900–2100 h) in *C. melanopterus* individuals tagged with acoustic transmitters at Palmyra that have been hypothesized to be associated with increases in foraging activity during this period (Papastamatiou et al., 2015). Baited observational trials conducted in the region of the acoustic camera (after the instrument had been removed) revealed that the majority of sharks observed during this period were *C. melanopterus* suggesting, at least anecdotally, that this species was disproportionally contributing to the abundances of sharks recorded during this specific peak period.

The majority of the sharks recorded during the post-dusk peak in activity were observed entering the lagoons. This may represent a stereotyped movement of sharks from the outer reef regions into the lagoons during this period. While sharks such as *C. melanopterus* tracked inside of the lagoons show high site fidelity to particular sections of a lagoon, less is known about the movement of sharks in forereef environments. Stable isotope analysis of reef sharks, particularly blacktips, suggest that sharks captured on the forereef at Palmyra derive some of their energy from lagoonal prey (McCauley et al., 2012b). More work will be required to fully elucidate these forereef/lagoon shark movement patterns.

Seven of the ten "large shark" (>1.9 m TL) observations recorded using the acoustic camera entered the channel during daylight hours; the limited number of large individuals observed, however, makes it difficult to assess whether these larger sharks exhibit diel patterns in their usage of Palmyra's lagoons.

4.2. Influence of tide on shark behavior

Shark densities across tidal periods were also significantly different overall, however, these tidal differences were much more muted than observed diel differences in density. The highest shark densities occurred during ebb tide and high slack. These results align with Papastamatiou et al. (2015) who also reported that *C. melanopterus* activity at Palmyra was secondarily driven by tidal periods (after time of day), with greatest shark activity occurring during ebb tide. Large scale water movement across Palmyra's sand flats during ebb tides is believed to hydraulically force small fishes off sand flat habitats along discrete corridors, potentially increasing shark foraging success (Papastamatiou et al., 2015, 2009). Likewise, transits into previously inaccessible habitats for food resources during high slack has been observed in other shark populations (Ackerman et al., 2000; Campos et al., 2009; Carlisle and Starr, 2009) and could potentially explain high shark densities during this high water tidal period.

4.3. Application to conservation and management

Data derived from acoustic cameras can play an important role in designing more strategic interventions to conserve and manage shark populations. In regions where complete large-scale fishing closures (e.g. island level) are not tenable, management can be made more intelligent and effective by demarcating specific habitats that are more readily used for protection or by preventing harvest during times when species activity in a habitat is particularly elevated. Such information could be relevant, for example, to regions like the Great Barrier Reef that have adaptive multi-tiered zoning plans (McCook et al., 2010) and to the placement of temporal closures that have been considered as tools for protecting coral reef predators (Beets and Friedlander, 1999).

Results from this work at Palmyra, for example, suggest that shark populations would likely benefit from prevention of artisanal reef gillnetting during post-dusk hours in reef channels when shark transit rates peak. Lastly, this data can help in important ways to identify the location and use of marine corridors by sensitive marine species. While the conservation significance and ecological use of corridors by large consumers has been well studied on land (Hilty et al., 2012) – data deficiency abounds in ocean ecosystems, despite recognition that corridors may be important in reef and coastal settings (Mumby et al., 2004; Pendoley et al., 2014).

5. Conclusions

This work helps to demonstrate how high-resolution acoustic cameras can be employed to describe important attributes of shark behavioral ecology in field settings. This tool is not, however, without its weaknesses. Its principle shortcoming is that it cannot identify individuals. This complicates attempts to estimate true densities of sharks, introduces the problem of over-counting survey targets, and makes it more challenging to differentiate between peaks in shark density and peaks in activity level. Some of these deficiencies problematize other survey methods (e.g. video observation), although unique markings that can help differentiate individuals can be more apparent in these other methods.

The utility of the acoustic camera in this study was maximized by the physical setting in which sensing took place, i.e. an ecologically important corridor and a discrete habitat type where visibility makes observation using alternative means challenging. Future studies can likewise capitalize on the value of this tool by using it in environments where fishes are physically constrained through natural or artificial environmental gateways (e.g. mouths or channels in harbors, estuaries, bays or mangroves) or where activity takes place on relatively discrete marine habitats (e.g. patch reefs, wrecks, boulder fields, or seamounts). In such situations the tool should most often be conceived of as a method for sub-sampling behavioral patterns, as the sensing area of the acoustic camera may not cover the entire area of the environmental feature. All such contexts represent environments where additional data on shark behavior would be of value. Alternatively, acoustic camera units could be operated in series to cover more area and extend the reach of question-asking possibilities for mobile targets like sharks.

This case study provides a useful view of how acoustic cameras can efficiently confirm and extend the observations of shark ecology and behavior made using alternate methods. At Palmyra, the >1000 shark sighting records generated using the acoustic camera help us to confirm that the tens of animals tagged in this system are exhibiting behaviors similar to those exhibited by the broader shark population and were able to better explore the statistical relationships between behavior and core environmental parameters with increased statistical rigor. New behaviors were also observed. The acoustic camera collected first observations of larger sharks that are too rare to study rigorously using traditional tagging and underwater observation methods. The data also revealed what appears to be a stereotyped transit of forereef sharks into lagoons that has not yet been directly observed at this site using other methods. Such observation may be of even greater value in contexts where sharks are more rare and use of alternative data collection methods is untenable. Acoustic cameras have a great deal of potential for future applications in the study of sharks in a range of contexts. Data collected using this tool will usefully increase the confidence and completeness of the understanding of shark behavioral ecology and provide a valuable source of new information on habitat connectivity and shark movement that can be utilized to improve shark management practices.

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.jembe.2016.04.012.

Acknowledgements

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