USE OF HIGH-RESOLUTION ACOUSTIC CAMERAS TO STUDY REEF SHARK BEHAVIORAL ECOLOGY

Douglas J. McCauley^{a□§}, Paul A. DeSalles^{a§}, Hillary S. Young^a, Jonathan P. A.
Gardner^b, and Fiorenza Micheli^c

^aDepartment of Ecology, Evolution, and Marine Biology, University of California, Santa
Barbara, CA 93106 USA. paul.desalles@lifesci.ucsb.edu and
hillary.young@lifesci.ucsb.edu

^bCentre for Marine Environmental and Economic Research, Victoria University of
Wellington, PO Box 600, Wellington 6140 New Zealand. jonathan.gardner@vuw.ac.nz

^cHopkins Marine Station, Stanford University, 120 Ocean View Blvd, Pacific Grove, CA
93950 USA. micheli@stanford.edu

□Corresponding author. E-mail: douglas.mccauley@lifesci.ucsb.edu; Tel: (805) 893-
4972; Fax: (805) 895-5883.

§authors contributed equally

USE OF HIGH-RESOLUTION ACOUSTIC CAMERAS TO STUDY REEF SHARK BEHAVIOR

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 more than 1,000 sightings of shark that traversed through 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.

KEYWORDS: behavior, movement ecology, mobile species, sharks, acoustic camera, sonar

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 necessitate 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 is 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 in even 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 is presented here that was 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.

116 2. MATERIALS AND METHODS

117 2.1 Study Site

118 Palmyra Atoll (5°53'N, 162°05'W) is located in the central Pacific approximately 1,000
 119 miles south of Hawai'i. Palmyra is protected as a U.S. National Wildlife Refuge and its
 120 lagoon and surrounding coastal waters are managed as "no-take" zones. The historic
 121 isolation and modern protection of Palmyra have allowed large reef fishes, particularly
 122 sharks, to persist at high abundances that are rarely observed in inhabited and fished reef
 123 settings (Sandin et al., 2008; McCauley et al., 2012b). At least 7 species of sharks are
 124 common at Palmyra including, blacktip reef sharks (*Carcharhinus melanopterus*),
 125 whitetip reef sharks (*Triaenodon obesus*), grey reef sharks (*Carcharhinus*
 126 *amblyrhynchos*), Galapagos sharks (*Carcharhinus galapagensis*), tiger sharks
 127 (*Galeocerdo cuvier*), scalloped hammerhead sharks (*Sphyrna lewini*), and lemon sharks
 128 (*Negaprion brevirostris*). Other species are likely to be present, but rare.

129 Palmyra's islets and lagoon morphology underwent significant structural
 130 modification during World War II, including extensive expansion of a large natural
 131 channel in the Western Lagoon basin (Collen et al., 2009). This channel in its
 132 contemporary form measures approximately 1.5 km long, 80 m wide, and 8 m deep. It is
 133 characterized by a sandy bottom substratum of relatively uniform depth that is flanked by
 134 near-vertical walls of coral rubble. Turbulent flushing through the channel often creates
 135 visibility conditions which make video or diver observation difficult or impossible. The
 136 channel physically connects Palmyra's forereef and offshore marine habitats to the atoll's
 137 lagoon habitats and has been observed to be an important passageway for marine
 138 megafauna transiting between these two environments (McCauley et al., 2014).

139 *2.2 High-resolution acoustic imaging of shark behavior*

140 The spatially confined nature of Palmyra's main channel presents a tractable arena in
141 which to observe the movement and behavior of sharks transiting between Palmyra's
142 offshore/forereef habitats and lagoon environment. Dual-frequency identification sonar
143 (DIDSON, Sound Metrics Corp., WA, USA) was used to "acoustically gate" a portion of
144 the channel and observe sharks in this corridor (Figure 1). DIDSON is a marine sonar
145 device that permits high-resolution digital imaging of objects within the sonar's field of
146 view (Belcher et al., 2002). The unit was installed mid-way along the channel at 3 m
147 depth on the southern channel side wall. The acoustic camera near-continuously
148 monitored a 41.7 m³ section of channel space (McCauley et al., 2014). The field of view
149 of the acoustic camera is pyramidal in shape with a basal width of 5 m and height of 2.5
150 m. The water volume of the sonar field was calculated as $V = 0.041D^3 - 0.0052 \text{ m}^3$;
151 where D is the range selected (Han and Uye, 2009). The maximum linear distance
152 visualized by the acoustic camera was 10 m, or approximately 13% of the width of the
153 channel. As such, the device does not provide a comprehensive view of shark activity in
154 the channel, but rather an unbiased sub-sample of these behavioral patterns. The acoustic
155 camera was positioned to image a section of space directly perpendicular to the channel
156 and was mounted on a vertical channel wall such that few, if any, sharks would transit
157 above or behind the area viewed. The unit was operated during two daily recording
158 sessions (each averaging 9.5 hours) from 2 July 2009 through 29 July 2009. Recording
159 session length was battery limited and batteries were serviced twice daily at
160 approximately 0700h and 1830h.

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 2,874 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 (1.75m) + 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 hour 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 hour 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 meters depth 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 hour 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

230 Bonferroni post-hoc corrections in instances where multiple comparisons were computed.
 231 All statistics were computed in R (R Development Core Team, 2013).

232

233

234 **3. RESULTS**

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

242 Daily density of sharks observed during the study period was variable, ranging
 243 from 0 to 5.7 sharks $1000 \text{ m}^{-2} \text{ min}^{-1}$ (Figure 2). Daily biomass values ranged from 0 to
 244 105 kg $1000 \text{ m}^{-2} \text{ min}^{-1}$. These daily shark biomass values largely mirrored variations in
 245 daily shark density, except on dates where large sharks were abundant (Figure 2).

246

247 ***3.1 Diel differences in shark behavior***

248 In the two diel classification, the density of sharks moving through the channel at night
 249 was more than three times greater than the density of sharks moving through by day ($W =$
 250 252, $P = 0.02$; Figure 3a). The eight diel classification further revealed that the majority
 251 of this difference in diel usage was driven by sharks swimming through the channel
 252 during the post-dusk period (i.e. 1909-2009 h; $\chi^2 = 37.38$, $df = 7$, $P = 0.0001$; Figure 3b).

The mean density of sharks ($\text{m}^{-3} \text{h}^{-1}$) 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 (Figures 3a and 3b). Density of sharks entering the lagoon at post-dusk was greater than shark densities observed during any other time period and more than 4 times greater than the density of sharks exiting the lagoon during the same time period.

Comparisons of 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. 80% 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 (Figure 4). Differences in shark density between any two different tidal periods, 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 confirms 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 this include: individuals capitalizing on opportunities for

321 higher prey capture rates, thermoregulation, and predator avoidance (Andrews et al.,
322 2009; Garla et al., 2005; McKibben and Nelson, 1986; Sims et al., 2006).

323 Observed peaks in shark densities at the acoustic camera sensing site in Palmyra
324 could represent either a numerical increase in shark abundance (e.g. more sharks arriving
325 during this period to this region to forage) or an increase in the activity of sharks resident
326 in this area (e.g. the same number of sharks looping at higher rates in front of the acoustic
327 camera). Peaks in shark densities specifically recorded during the post-dusk period
328 (1909-2009 h) temporally mirror reported activity peaks (1900-2100 h) in *C.*
329 *melanopterus* individuals tagged with acoustic transmitters at Palmyra that have been
330 hypothesized to be associated with increases in foraging activity during this period
331 (Papastamatiou et al., 2015). Baited observational trials conducted in the region of the
332 acoustic camera (after the instrument had been removed) revealed that the majority of
333 sharks observed during this period were *C. melanopterus* suggesting, at least anecdotally,
334 that this species was disproportionally contributing to the abundances of sharks recorded
335 during this specific peak period.

336 The majority of the sharks recorded during the post-dusk peak in activity were
337 observed entering the lagoons. This may represent a stereotyped movement of sharks
338 from the outer reef regions into the lagoons during this period. While sharks such as *C.*
339 *melanopterus* tracked inside of the lagoons show high site fidelity to particular sections
340 of a lagoon, less is known about the movement of sharks in forereef environments. Stable
341 isotope analysis of reef sharks, particularly blacktips, suggest that sharks captured on the
342 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 *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 profit by preventing 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 are 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 >1,000 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

1
2
3
4 412 better explore the statistical relationships between behavior and core environmental
5
6 413 parameters with increased statistical rigor. New behaviors were also observed. The
7
8
9 414 acoustic camera collected first observations of larger sharks that are too rare to study
10
11 415 rigorously using traditional tagging and underwater observation methods. The data also
12
13
14 416 revealed what appears to be a stereotyped transit of forereef sharks into lagoons that has
15
16 417 not yet been directly observed in this site using other methods. Such observation may be
17
18
19 418 of even greater value in contexts where sharks are more rare and use of alternative data
20
21 419 collection methods is untenable. Acoustic cameras have a great deal of potential for
22
23
24 420 future applications in the study of sharks in a range of contexts. Data collected using this
25
26 421 tool will usefully increase the confidence and completeness of the understanding of shark
27
28
29 422 behavioral ecology and provide a valuable source of new information on habitat
30
31 423 connectivity and shark movement that can be utilized to improve shark management
32
33
34 424 practices.

35 36 425 37 38 426 39 40 427 **ACKNOWLEDGEMENTS**

41
42
43 428 Thanks to The Nature Conservancy and U.S. Fish and Wildlife Service for field support
44
45 429 and research permission. Funding was provided by the National Science Foundation,
46
47
48 430 Stanford University, the Woods Institute for the Environment, and Victoria University of
49
50
51 431 Wellington. Thanks also to Sound Metrics Corp. for providing invaluable technical
52
53 432 assistance. For important contributions in the laboratory and field, thanks to: A. Briggs,
54
55 433 C. Burniske, M. DeGraff, E. Hoffman, T. Jen, A. Miller-ter Kuile, A. McInturff, N.
56
57
58
59
60
61
62
63
64
65

434 Wenner, and E. Wulczyn. This is contribution number 0123 from the Palmyra Atoll
435 Research Consortium (PARC).

436

437

438 REFERENCES

439 Ackerman, J.T., Kondratieff, M.C., Matern, S.A., Cech, J.J., 2000. Tidal influence on
440 spatial dynamics of leopard sharks, *Triakis semifasciata*, in Tomales Bay,
441 California. *Environmental Biology of Fishes* 58, 33–43.

442 doi:10.1023/A:1007657019696

443 Andrews, K.S., Williams, G.D., Farrer, D., Tolimieri, N., Harvey, C.J., Bargmann, G.,
444 Levin, P.S., 2009. Diel activity patterns of sixgill sharks, *Hexanchus griseus*: the
445 ups and downs of an apex predator. *Animal Behaviour* 78, 525–536.

446 doi:10.1016/j.anbehav.2009.05.027

447 Bascompte, J., Melián, C.J., Sala, E., 2005. Interaction strength combinations and the
448 overfishing of a marine food web. *PNAS* 102, 5443–5447.

449 doi:10.1073/pnas.0501562102

450 Becker, A., Whitfield, A.K., Cowley, P.D., Järnegren, J., Naesje, T.F., 2011. An
451 assessment of the size structure, distribution and behaviour of fish populations
452 within a temporarily closed estuary using dual frequency identification sonar
453 (DIDSON). *J. Fish Biol.* 79, 761–775. doi:10.1111/j.1095-8649.2011.03057.x

454 Beets, J., Friedlander, A., 1999. Evaluation of a conservation strategy: a spawning
455 aggregation closure for red hind, *Epinephelus guttatus*, in the U.S. Virgin Islands.
456 *Environmental Biology of Fishes* 55, 91–98. doi:10.1023/A:1007404421518

- 457 Belcher, E., Hanot, W., Burch, J., 2002. Dual-Frequency Identification Sonar (DIDSON),
458 in: Proceedings of the 2002 International Symposium on Underwater Technology,
459 2002. Presented at the Proceedings of the 2002 International Symposium on
460 Underwater Technology, 2002, pp. 187–192. doi:10.1109/UT.2002.1002424
- 461 Block, B.A., Jonsen, I.D., Jorgensen, S.J., Winship, A.J., Shaffer, S.A., Bograd, S.J.,
462 Hazen, E.L., Foley, D.G., Breed, G.A., Harrison, A.-L., Ganong, J.E.,
463 Swithenbank, A., Castleton, M., Dewar, H., Mate, B.R., Shillinger, G.L.,
464 Schaefer, K.M., Benson, S.R., Weise, M.J., Henry, R.W., Costa, D.P., 2011.
465 Tracking apex marine predator movements in a dynamic ocean. *Nature* 475, 86–
466 90. doi:10.1038/nature10082
- 467 Burwen, D.L., Fleischman, S.J., Miller, J.D., 2010. Accuracy and precision of salmon
468 length estimates taken from DIDSON sonar images. *Transactions of the American*
469 *Fisheries Society* 139, 1306–1314. doi:10.1577/T09-173.1
- 470 Campos, B.R., Fish, M.A., Jones, G., Riley, R.W., Allen, P.J., Klimley, P.A., Jr, J.J.C.,
471 Kelly, J.T., 2009. Movements of brown smoothhounds, *Mustelus henlei*, in
472 Tomales Bay, California. *Environ Biol Fish* 85, 3–13. doi:10.1007/s10641-009-
473 9462-y
- 474 Carlisle, A.B., Starr, R.M., 2009. Habitat use, residency, and seasonal distribution of
475 female leopard sharks *Triakis semifasciata* in Elkhorn Slough, California. *Mar*
476 *Ecol Prog Ser* 380, 213–228. doi:10.3354/meps07907
- 477 Cartamil, D.P., Vaudo, J.J., Lowe, C.G., Wetherbee, B.M., Holland, K.N., 2003. Diel
478 movement patterns of the Hawaiian stingray, *Dasyatis lata*: implications for

- 479 ecological interactions between sympatric elasmobranch species. *Marine Biology*
480 142, 841–847. doi:10.1007/s00227-003-1014-y
- 481 Collen, J.D., Garton, D.W., Gardner, J.P.A., 2009. Shoreline changes and sediment
482 redistribution at Palmyra Atoll (Equatorial Pacific Ocean): 1874–Present. *Journal*
483 *of Coastal Research* 711–722. doi:10.2112/08-1007.1
- 484 Compagno, L.J.V., 1984. *Sharks of the world: an annot. and ill. catalogue of shark*
485 *species known to date*. United Nations Development Programme, Food and
486 *Agriculture Organization of the United Nations, Rome.*
- 487 Crossman, J.A., Martel, G., Johnson, P.N., Bray, K., 2011. The use of Dual-frequency
488 IDentification SONar (DIDSON) to document white sturgeon activity in the
489 Columbia River, Canada. *Journal of Applied Ichthyology* 27, 53–57.
490 doi:10.1111/j.1439-0426.2011.01832.x
- 491 Dulvy, N.K., Fowler, S.L., Musick, J.A., Cavanagh, R.D., Kyne, P.M., Harrison, L.R.,
492 Carlson, J.K., Davidson, L.N., Fordham, S.V., Francis, M.P., Pollock, C.M.,
493 Simpfendorfer, C.A., Burgess, G.H., Carpenter, K.E., Compagno, L.J., Ebert,
494 D.A., Gibson, C., Heupel, M.R., Livingstone, S.R., Sanciangco, J.C., Stevens,
495 J.D., Valenti, S., White, W.T., 2014. Extinction risk and conservation of the
496 world’s sharks and rays. *eLife Sciences* 3, e00590. doi:10.7554/eLife.00590
- 497 Ferretti, F., Worm, B., Britten, G.L., Heithaus, M.R., Lotze, H.K., 2010. Patterns and
498 ecosystem consequences of shark declines in the ocean. *Ecology Letters* 13,
499 1055–1071. doi:10.1111/j.1461-0248.2010.01489.x
- 500 Froese, R., Pauly, D., 2015. *FishBase.*

- 501 Garla, R.C., Chapman, D.D., Wetherbee, B.M., Shivji, M., 2005. Movement patterns of
502 young Caribbean reef sharks, *Carcharhinus perezi*, at Fernando de Noronha
503 Archipelago, Brazil: the potential of marine protected areas for conservation of a
504 nursery ground. *Marine Biology* 149, 189–199. doi:10.1007/s00227-005-0201-4
- 505 Han, C.-H., Uye, S.-I., 2009. Quantification of the abundance and distribution of the
506 common jellyfish *Aurelia aurita* s.l. with a Dual-frequency IDentification SONar
507 (DIDSON). *J. Plankton Res.* fbp029. doi:10.1093/plankt/fbp029
- 508 Heithaus, M.R., Marshall, G.J., Buhleier, B.M., Dill, L.M., 2001. Employing Crittercam
509 to study habitat use and behavior of large sharks. *Mar Ecol Prog Ser* 209, 307–
510 310. doi:10.3354/meps209307
- 511 Heupel, M.R., Knip, D.M., Simpfendorfer, C.A., Dulvy, N.K., 2014. REVIEW Sizing up
512 the ecological role of sharks as predators. *Mar Ecol Prog Ser* 495, 291–298.
513 doi:10.3354/meps10597
- 514 Heupel, M.R., Simpfendorfer, C.A., 2015. Long-term movement patterns of a coral reef
515 predator. *Coral Reefs* 34, 679–691. doi:10.1007/s00338-015-1272-4
- 516 Hilty, J.A., Jr, W.Z.L., Merenlender, A., 2012. Corridor Ecology: The Science and
517 Practice of Linking Landscapes for Biodiversity Conservation. Island Press.
- 518 Holmes, J.A., Cronkite, G.M.W., Enzenhofer, H.J., Mulligan, T.J., 2006. Accuracy and
519 precision of fish-count data from a “dual-frequency identification sonar”
520 (DIDSON) imaging system. *ICES J. Mar. Sci.* 63, 543–555.
521 doi:10.1016/j.icesjms.2005.08.015
- 522 Makabe, R., Kurihara, T., Uye, S.-I., 2012. Spatio-temporal distribution and seasonal
523 population dynamics of the jellyfish *Aurelia aurita* s.l. studied with Dual-

- frequency IDentification SONar (DIDSON). *J. Plankton Res.* 34, 936–950.
doi:10.1093/plankt/fbs057
- McCauley, D.J., DeSalles, P.A., Young, H.S., Papastamatiou, Y.P., Caselle, J.E., Deakos, M.H., Gardner, J.P.A., Garton, D.W., Collen, J.D., Micheli, F., 2014. Reliance of mobile species on sensitive habitats: a case study of manta rays (*Manta alfredi*) and lagoons. *Mar Biol* 161, 1987–1998. doi:10.1007/s00227-014-2478-7
- McCauley, D.J., McLean, K.A., Bauer, J., Young, H.S., Micheli, F., 2012a. Evaluating the performance of methods for estimating the abundance of rapidly declining coastal shark populations. *Ecological Applications* 22, 385–392. doi:10.1890/11-1059.1
- McCauley, D.J., Young, H.S., Dunbar, R.B., Estes, J.A., Semmens, B.X., Micheli, F., 2012b. Assessing the effects of large mobile predators on ecosystem connectivity. *Ecological Applications* 22, 1711–1717. doi:10.1890/11-1653.1
- McCook, L.J., Ayling, T., Cappo, M., Choat, J.H., Evans, R.D., Freitas, D.M.D., Heupel, M., Hughes, T.P., Jones, G.P., Mapstone, B., Marsh, H., Mills, M., Molloy, F.J., Pitcher, C.R., Pressey, R.L., Russ, G.R., Sutton, S., Sweatman, H., Tobin, R., Wachenfeld, D.R., Williamson, D.H., 2010. Adaptive management of the Great Barrier Reef: A globally significant demonstration of the benefits of networks of marine reserves. *PNAS* 107, 18278–18285. doi:10.1073/pnas.0909335107
- McKibben, J.N., Nelson, D.R., 1986. Patterns of movement and grouping of gray reef sharks, *Carcharhinus amblyrhynchos*, at Enewetak, Marshall Islands. *Bulletin of Marine Science* 38, 89–110.

- 546 Mumby, P.J., Edwards, A.J., Ernesto Arias-González, J., Lindeman, K.C., Blackwell,
547 P.G., Gall, A., Gorczynska, M.I., Harborne, A.R., Pescod, C.L., Renken, H., C. C.
548 Wabnitz, C., Llewellyn, G., 2004. Mangroves enhance the biomass of coral reef
549 fish communities in the Caribbean. *Nature* 427, 533–536.
550 doi:10.1038/nature02286
- 551 O’Connell, C.P., Hyun, S.-Y., Rillahan, C.B., He, P., 2014. Bull shark (*Carcharhinus*
552 leucas) exclusion properties of the sharksafe barrier and behavioral validation
553 using the ARIS technology. *Global Ecology and Conservation* 2, 300–314.
554 doi:10.1016/j.gecco.2014.10.008
- 555 Papastamatiou, Y.P., Caselle, J.E., Friedlander, A.M., Lowe, C.G., 2009. Distribution,
556 size frequency, and sex ratios of blacktip reef sharks *Carcharhinus melanopterus*
557 at Palmyra Atoll: a predator-dominated ecosystem. *Journal of Fish Biology* 75,
558 647–654. doi:10.1111/j.1095-8649.2009.02329.x
- 559 Papastamatiou, Y.P., Watanabe, Y.Y., Bradley, D., Dee, L.E., Weng, K., Lowe, C.G.,
560 Caselle, J.E., 2015. Drivers of Daily Routines in an Ectothermic Marine Predator:
561 Hunt Warm, Rest Warmer? *PLoS ONE* 10, e0127807.
562 doi:10.1371/journal.pone.0127807
- 563 Papastamatiou, Y.P., Wood, C.L., Bradley, D., McCauley, D.J., Pollock, A.L., Caselle,
564 J.E., 2014. First records of the sicklefin lemon shark, *Negaprion acutidens*, at
565 Palmyra Atoll, central Pacific: a recent colonization event? *Marine Biodiversity*
566 Records 7, e114 (3 pages). doi:10.1017/S175526721400116X

- 567 Pendoley, K.L., Schofield, G., Whittock, P.A., Ierodiconou, D., Hays, G.C., 2014.
568 Protected species use of a coastal marine migratory corridor connecting marine
569 protected areas. *Mar Biol* 161, 1455–1466. doi:10.1007/s00227-014-2433-7
- 570 R Development Core Team, 2013. R: a language and environment for statistical
571 computing. R Foundation for Statistical Computing.
- 572 Sandin, S.A., Smith, J.E., DeMartini, E.E., Dinsdale, E.A., Donner, S.D., Friedlander,
573 A.M., Konotchick, T., Malay, M., Maragos, J.E., Obura, D., Pantos, O., Paulay,
574 G., Richie, M., Rohwer, F., Schroeder, R.E., Walsh, S., Jackson, J.B.C.,
575 Knowlton, N., Sala, E., 2008. Baselines and degradation of coral reefs in the
576 Northern Line Islands. *PLoS ONE* 3, e1548. doi:10.1371/journal.pone.0001548
- 577 Sims, D.W., Wearmouth, V.J., Southall, E.J., Hill, J.M., Moore, P., Rawlinson, K.,
578 Hutchinson, N., Budd, G.C., Righton, D., Metcalfe, J.D., Nash, J.P., Morritt, D.,
579 2006. Hunt warm, rest cool: bioenergetic strategy underlying diel vertical
580 migration of a benthic shark. *J Anim Ecol* 75, 176–190.
- 581 Speed, C.W., Field, I.C., Meekan, M.G., Bradshaw, C.J.A., 2010. REVIEW Complexities
582 of coastal shark movements and their implications for management. *Mar Ecol*
583 *Prog Ser* 408, 275–293. doi:10.3354/meps08581
- 584 Ward-Paige, C., Mills Flemming, J., Lotze, H.K., 2010. Overestimating fish counts by
585 non-instantaneous visual censuses: consequences for population and community
586 descriptions. *PLoS ONE* 5, e11722. doi:10.1371/journal.pone.0011722

FIGURES

Figure 1.

Figure 2.

Figure 3.

Figure 4.

FIGURE LEGENDS (COLOR)

Figure 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.

Figure 2. Daily shark density (*grey bars*) and estimated biomass (*red line*) recorded by acoustic camera during the study period.

Figure 3. Density of sharks (mean $\pm$ SE) recorded across diel periods with directionality (entering, *cross-hatched bars*; exiting, *solid 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.

Figure 4. Density of sharks (mean $\pm$ SE) recorded across four tidal periods with directionality (entering, *cross-hatched bars*; exiting, *solid bars*). No pair of tidal periods were 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.