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Evaluating the performance of methods for estimating the abundance of rapidly declining coastal shark populations

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Abstract. Accurately surveying shark populations is critical to monitoring precipitous ongoing declines in shark abundance and interpreting the effects that these reductions are having on ecosystems. To evaluate the effectiveness of existing survey tools, we used field trials and computer simulations to critically examine the operation of four common methods for counting coastal sharks: stationary point counts, belt transects, video surveys, and mark and recapture abundance estimators. Empirical and theoretical results suggest that (1) survey method selection has a strong impact on the estimates of shark density that are produced, (2) standardizations by survey duration are needed to properly interpret and compare survey outputs, (3) increasing survey size does not necessarily increase survey precision, and (4) methods that yield the highest density estimates are not always the most accurate. These findings challenge some of the assumptions traditionally associated with surveying mobile marine animals. Of the methods we trialed, 8 × 50 m belt transects and a 20 m radius point count produced the most accurate estimates of shark density. These findings can help to improve the ways we monitor, manage, and understand the ecology of globally imperiled coastal shark populations.

Key words: belt transect; coastal; computer simulation; conservation; density; ecology; fishing; mark and recapture; point count; shark; survey; video.

INTRODUCTION

Humans, largely as a result of overfishing, appear to have caused >90% declines in the abundance of multiple shark species in a wide variety of marine habitats (Friedlander and DeMartini 2002, Baum and Myers 2004, Shepherd and Myers 2005, Robbins et al. 2006, Myers et al. 2007, Stevenson et al. 2007, Ferretti et al. 2010). Because losses of sharks are known to cause cascading changes in ecosystem structure and function (Shepherd and Myers 2005, Myers et al. 2007, Heithaus et al. 2008, McCauley et al. 2010) we are forced to consider the possibility that sizable portions of the world's oceans, which are now depauperate of sharks, may be undergoing radical, but unnoticed, ecological transformations.

In order to effectively detect such ecological changes, monitor trends in shark populations, and design management actions to respond to shark depletions, we must have at our disposal a set of effective and standardized tools for measuring shark abundance. Monitoring shark numbers has thus far proven difficult. Sharks are naturally rare, highly mobile, and respond variably to underwater surveyors: all features that can compromise survey efficacy (MacNeil et al. 2008). To date there has been minimal effort devoted to investigating the accuracy and potential biases associated with the methods commonly employed for measuring shark abundance. An examination of the performance of shark surveys in the literature suggests that such an undertaking is overdue. Existing studies attempting to measure shark abundance have been plagued by a worrisome lack of comparability (e.g., ∼600% differences between observers at the same site; Sandin et al. 2008; D. J. McCauley, H. S. Young, R. B. Dunbar, J. A.

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Estes, and F. Micheli, *unpublished manuscript*) and reproducibility (e.g., ~300% differences between resurveys of the same site; Sandin et al. 2008, Friedlander et al. 2010). Outputs from shark survey efforts have critically important downstream effects on policy, economics, and higher-order ecological exercises. Thus assessing the accuracy and learning the limitations of different shark survey methods is essential.

In this study, we stringently tested and evaluated four of the most commonly used methods for measuring shark abundance in coastal environments: (1) belt transects, (2) stationary point counts, (3) un-baited remote video surveys, and (4) mark and recapture population estimates. We focused this investigation on surveys suitable for use in coastal contexts because sharks in these environments have been disproportionately impacted by humans and are especially in need of careful monitoring (Knip et al. 2010). We field tested these four survey methods at Palmyra Atoll, a remote wildlife refuge that hosts one of the world's highest densities of reef sharks (Stevenson et al. 2007). By working at a location with especially high shark abundances, we were afforded the rare opportunity to make statistically robust comparisons between the different methods we trialed. To help interpret results from field trials we built a computer simulation that realistically modeled both shark behavior and our shark survey procedures. Conclusions gathered from empirical trials in the data-rich environment of Palmyra and from observations in our controlled simulations provide a unique and useful means to compare the performance and biases of these selected survey methods.

METHODS

Shark abundance was field measured at the Palmyra Atoll U.S. National Wildlife Refuge (5°52′ N, 162°04′ W, USA; see map in Appendix A), located in the central Pacific. The three most common coastal sharks at Palmyra are *Carcharhinus amblyrhynchos*, *C. melanopterus*, and *Triaenodon obesus*. Visibility on the Palmyra's forereefs is generally >25 m. We used four methods to field survey shark abundance on the forereefs (reefs seaward of the reef crest) of Palmyra: belt transects, stationary point counts, un-baited remote video, and mark and recapture surveys. Belt, point, and video are collectively referred to throughout as "underwater surveys."

In belt transect surveys, a diver on scuba inventoried all sharks present in a 50 × 8 m rectangle for 5 minutes. Sharks were counted if they wholly or partially intersected the survey area in front of the observer as the observer swam the length of the rectangle. Point counts were performed by a stationary diver in the center of circle with a radius of 10 m. Point counts also lasted 5 minutes. Video surveys were conducted using cameras attached to the seafloor that recorded two seconds of video every 30 s. Dimensions of the camera viewing area were measured in a pool and modeled as isosceles triangles; two camera models were used, one with a viewing area 11.3 m base × 20.0 m height, the second with an area 13.0 m base × 15.0 m height. Divers running belt and point surveys and recorders taking data from video all endeavored to count unique sharks only once. Belt transects and point counts were conducted during daytime hours along a 10–12 m depth isobath during the same dive at nine forereef sites; each replicated seven times per site. Video surveys were conducted at five of these sites, with two to eight replicates made per site. Video surveys were set during the day but continued to record data until ambient light failed. The same observer recorded sharks in all belt, point, and video surveys.

Mark and recapture surveys were conducted at Palmyra for *C. amblyrhynchos* only. Individuals were captured using baited hand lines, marked with unique dorsal fin tags, and released (Appendix J). Mark and recapture efforts were conducted during 4–5 h sampling events always at the same location on the forereef. Sharks were sampled five times in 2008 (124 individuals marked) and three times in 2009 (88 individuals marked), with 1–3 days spaced between intra-year replicates. To estimate the size of the "super-population" of *C. amblyrhynchos* present at this reef site, we employed the POPAN parameterization of the Jolly-Seber models in program MARK (Schwarz and Arnason 1996; for additional details on implementation see Appendix B).

Shark densities are reported from belt, point, and video surveys as the number of unique individuals per square meter per minute; average detection rates were recorded as the proportion of surveys where > 0 sharks were observed. Arguably, density estimates for mobile subjects like sharks should be represented in terms of volume, not area (Appendix C). However, in order to make our conclusions broadly comparable, we focus mostly upon results produced using the convention of standardizing by area. The prevalence of zeros in underwater survey data necessitated that statistical comparisons between methods be made using nonparametric Kruskal-Wallis tests followed by pairwise Mann-Whitney comparisons adjusted using Holm's sequential Bonferroni corrections. We compared survey outputs for each of the three most common reef shark species at Palmyra and for "all sharks" (three species pooled). To determine if shark abundance estimates changed with the approach of nightfall, we compared density estimates from video surveys run during the daytime (before 1730) and evening (post-1730). Daytime/evening cutoff times were determined using data from light sensors stationed on the forereef (Onset Computers, Bourne, Massachusetts, USA). We also compared shark presence/absence data ("all shark" only) between our three survey methods using Pearson's chi-square tests. Last, we employed a bootstrapping procedure that drew values at random from empirical data (1000 iterations per replicate level) to measure the effects of increasing survey replication on data quality. All statistics were computed in R (R Development Core Team 2011). Significance levels throughout are calculated relative to $\alpha = 0.05$.

In order to investigate the operation and biases of belt, point, and video methods, we designed a computer simulation in which we measured shark density in a two-dimensional space using the same underwater survey methods (point, belt, video) as implemented in the field. Mark and recapture surveys were not accounted for in the simulation. The simulation was populated with a single shark type (thus analogous to "all shark" field density estimates) whose movement was parameterized using empirical data collected from observations of reef sharks at Palmyra. Because the simulation contained a known density of sharks, we were able to evaluate the deviation between the predicted and true values of shark density (percent error) produced by each survey method. Simulations were run in two scenarios: an "unfished" scenario with shark densities set to approximate those at Palmyra; and a "fished" scenario where shark densities were reduced by one order of magnitude (thus more closely matching shark densities observed in fished coastal environments [Robbins et al. 2006]). In addition to testing the three underwater survey methods implemented at Palmyra in the simulation, we also trialed one longer and larger belt transect (20 × 400 m; 40 minutes) and one larger point count (radius = 20 m; 5 minutes). To mechanistically examine the operation of belt, point, and video surveys we derived algorithms that describe the behavior of each survey in the simulation and predict the density estimates that each might yield. See Appendix D and the Supplement for a full description of simulation methods and source code.

RESULTS

All three of the dominant coastal shark species at Palmyra were observed in field trials of point counts and video surveys: *C. amblyrhynchos*, *C. melanopterus*, and *T. obesus*. Belt transects detected the two most common shark species only; *T. obesus* was not observed. Video and point surveys generated the highest shark density estimates (Fig. 1) and the highest shark detection rates (Appendix E). Belt transects always yielded the lowest density estimates (although not significantly lower than point counts for *T. obesus*; Table 1). Comparisons made using presence/absence data (all sharks) instead of density data, showed similar trends (Appendix F). Density estimates generated from video data collected during daytime hours did not differ significantly from estimates generated during evening periods (all sharks; $W = 220$, $P = 0.84$). Bootstrapping analyses used to investigate the effects of increasing sampling effort on data precision showed that rates of change in coefficients of variation for all three survey types began to diminish around 10–15 replicates (Appendix G). Standardizing survey outputs by volume produces generally the same trends as seen in data standardized by area, but between-method patterns of significance were different for two out of the four shark species/species combinations (Appendix C). To interpret our mark and recapture data we used a fully time-dependent model {capture probability ρ_t, survival rate ϕ_t, entry probability b_t} that estimated that the size of the super-population of *C. amblyrhynchos* utilizing our sampling region during the timeframe of this study was 661 individuals; SE = 183; 95% confidence interval: 415–1170 (Appendix B).

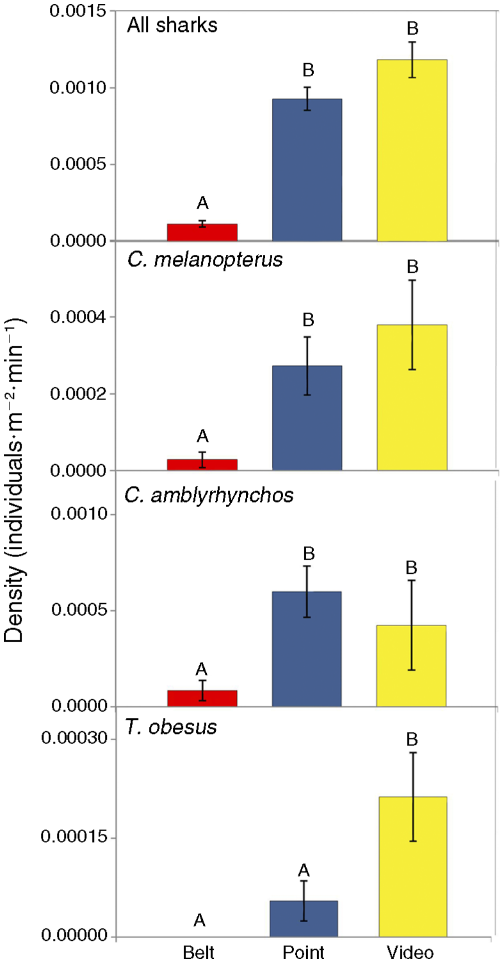

FIG. 1. Comparisons of shark density estimates (mean ± SE) generated using belt, point, and video surveys in the field at Palmyra Atoll. Densities are reported for *Carcharhinus amblyrhynchos*, *C. melanopterus*, *Triaenodon obesus*, and all sharks (three species pooled). Surveys marked with the same letters in a panel are not significantly different.

Outputs from computer simulations run using unfished conditions showed a similar pattern to underwater survey data collected at Palmyra. Video and point surveys again both yielded higher mean estimates than belt transects (Fig. 2A). The significance of these differences in the simulation however varied from our Palmyra field observations: belt transects were not

TABLE 1. Statistical comparisons of density outputs from field and simulation trials of different shark survey methods (*W* or χ^2 [presence/absence data only]; *P*).

	B vs. P		B vs. V		P vs. V		B vs. BL†		P vs. PL†	
Species or scenario	*W* or χ^2	*P*	*W* or χ^2	*P*	*W* or χ^2	*P*	*W* or χ^2	*P*	*W* or χ^2	*P*
Field trial										
All sharks	213.5	<0.0001*	96.5	<0.0001*	318.5	0.11				
Carcharhinus amblyrhynchos	315	<0.0001*	289	<0.01*	535	0.06				
Carcharhinus melanopterus	425.5	<0.01*	232	<0.001*	354	0.25				
Triaenodon obesus	560	0.08	245	<0.001*	290	<0.01*				
Presence/absence (all sharks)	28.2	<0.0001*	36.1	<0.0001*	2.6	0.11				
Simulation trial										
Unfished scenario	119 965	0.10	44 656	<0.0001*	201 376	<0.0001*	58 525	<0.0001*	139 180	<0.0001*
Fished scenario	126 274	0.21	91 179	<0.0001*	92 787	<0.0001*	104 270	<0.0001*	122 616	0.09

Notes: Survey methods are B, belt transect; P, point count; V, video survey; BL, large belt transect; PL, large point count. Survey dimensions are reported in Table 2.

* Statistically significant differences ($P < 0.05$) post-correction.

† Surveys implemented in the simulation only.

significantly different from point counts and point counts were significantly different from video counts (Table 1). Increasing the size of both belt and point counts reduced the density estimates they yielded (Fig. 2A). Overall, the smaller sized belt transect (modeled after belt transects used in the field) and the larger point count produced outputs closest to the true density of sharks in the simulation (Table 2). In the fished scenario simulation, with reduced shark densities, the detection rates of all methods fell dramatically and the variability in density estimates generally increased (Fig. 2B; Table 2). The best detection rates in this fished scenario were made using video surveys. The most accurate predictions of the true shark density in this version of the simulation were again produced by the belt and larger point counts, with the latter predicting the precise density of sharks in the simulation. The algorithms we derived to model the operation of belt, point and video surveys in the simulation predicted the density estimates that each yielded with decent accuracy (mean |percent error| = 17%; SE = 5.5%; Appendix H).

DISCUSSION

Empirical results from surveys of sharks at Palmyra Atoll indicate that survey method selection has a strong impact on the estimates of abundance that are produced. Parallel observations made in computer simulations provide a means for quantitatively interpreting some of this variability. Collectively our results show that the surveys we tested have strengths and limitations, both of which need to be considered when matching a methodology to the needs of a particular study.

Of the three underwater survey methods that we field tested at Palmyra, video and point surveys generated the highest shark density estimates, each often one order of magnitude greater than belt transect estimates. However, performance trials in our unfished computer simulation indicate that belt transects likely produced the most reliable density estimates (Fig. 2A; Table 2). This suggests that the "true" density of sharks (species pooled) at Palmyra is approximately 1×10^{-4} individuals/m^2, a value lower than previously reported estimates from this site (Stevenson et al. 2007; D. J. McCauley, H. S. Young, R. B. Dunbar, J. A. Estes, and F. Micheli, *unpublished manuscript*). Examinations of the performance of underwater survey methods in our fished (shark depleted) simulation scenario indicate that survey method accuracy is not especially sensitive to shark density, with the caveat that video surveys produced more accurate (and lower) estimates in reduced shark environments.

When estimating shark densities from underwater field survey data we standardized density outputs by survey duration. Density is typically reported without regard for survey time presumably because many underwater survey subjects move little and their home ranges are believed to be encapsulated within survey boundaries. This assumption does not hold when working with highly mobile subjects like sharks that have sizable home ranges that can overlap considerably. If standardizations by survey duration are not undertaken, then longer lasting surveys produce unrealistically high density estimates. We chose to standardize our density estimates by the number of minutes in each survey because one minute meaningfully approximates the time required to comprehensively survey a section of coastal habitat for sharks without introducing significant risk of over counting these vagile targets. Using this approach, long surveys are effectively treated more as if they were composites of near-instantaneously replicate measures (Ward-Paige et al. 2010). Differences in significance patterns between some of the cases that were standardized by volume instead of area (Appendix C) demonstrated that choices made about dimensional

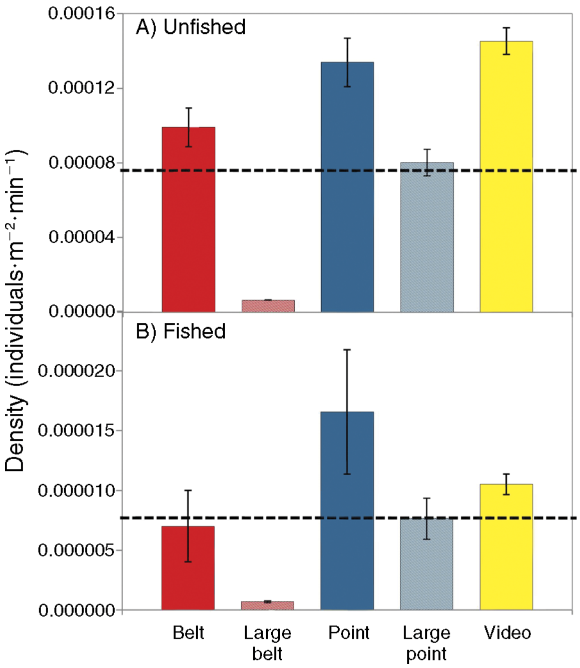

FIG. 2. Shark density estimates predicted by the computer simulation (mean ± SE) run under (A) the unfished scenario with high shark densities and (B) a fished scenario with densities one order of magnitude lower. Solid bars represent survey methods that were field trialed at Palmyra. Stippled bars indicate methods that were implemented in the simulation only. Survey method details and statistics are listed in Tables 1 and 2. Black dashed line indicates the true density of sharks (sharks/m^2) in each simulation scenario.

standardizations also influence the nature of density outputs.

One important issue to consider when interpreting outputs from diver-based underwater surveys (i.e., point and belt counts) is the potential biases created by having human observers in the water with the sharks being surveyed (Watson and Harvey 2007). Some sharks may be attracted to divers, while others may actively avoid them, and these reactions can change by context and over time. Examinations of background patterns in survey data from Palmyra and comparisons to diver independent video surveys suggest that such biases are present at this site, but do not exert a major influence on the inter-method differences we observed (Appendix I). At other research sites where biases of this kind are more intense, sharks may be best surveyed using video surveys that operate largely without these human biases. An added benefit of using video is that it consistently showed some of the highest rates of shark detection (Appendix E). Presumably these detection rates could be increased even further in areas where sharks are especially rare by adding bait lures to these cameras (Colton and Swearer 2010). While the focus of this paper is on measuring shark abundance, researchers primarily interested in estimating shark species richness or detecting uncommon shark species may profit by surveying with video.

There is a natural tendency among researchers to increase the size of a survey when the studied subjects occur at low densities. Outputs from our simulation suggest, however, that in the case of sharks the benefits of doing this are variable. The larger belt counts we trialed severely underestimated shark density but the larger point counts consistently generated more accurate density estimates. Simulation trials conducted using multiple different sized belt and point counts (not reported here) reveal that density estimates generally decline with increasing survey size and duration. Declines of this type are desirable only when working with survey methods that overestimate shark abundance (e.g., point counts). The algorithms that we developed to model the operation of belt, point, and video surveys provide some mechanistic insight into how the geometry and operation of these different surveys determine the density estimates they yield (Appendix H).

Our examination of the effects of increasing survey replication on the variability of our field results (Appendix G) shows that a minimum of 10 replicates should be conducted when measuring shark density using belt, point, or video surveys. This threshold matches conclusions drawn from other trials of similar underwater survey methods (Samoilys and Carlos 2000). However, detection rate data from field and simulation exercises both suggest that much higher sampling is needed when working in environments where sharks are especially rare or when using methods with particularly poor detection capabilities (e.g., belt transects).

TABLE 2. Results of performance tests and parameter values for shark survey methods trialed in the computer simulation.

Method	Dimensions (m)	Time (min)	Percent error Unfished	Percent error Fished	Detection rate Unfished	Detection rate Fished
Belt (B)	8 wide × 50 long	5	0.29	−0.08	0.17	0.01
Belt large (BL)	20 wide × 400 long	40	−0.91	−0.91	0.85	0.18
Point (P)	10 radius	5	0.74	1.17	0.19	0.02
Point large (PL)	20 radius	5	0.04	0	0.37	0.04
Video (V)	11.3 base × 20 height	330	0.88	0.38	0.98	0.29

Notes: Percent error represents the deviation between the density of sharks predicted by each method and the known density of sharks in the simulation. Detection rates are expressed as the proportion of surveys recording >0 sharks. Values are reported for both unfished (high shark density) and fished (low shark density) simulation scenarios.

FIG. 3. (A) With one of the world's highest densities of coastal sharks, Palmyra Atoll provided an ideal environment to compare the performance of shark surveys with statistical rigor. (B, C) Mark and recapture surveys of gray reef sharks *Carcharhinus amblyrhynchos* provide population size estimates that complement density estimates yielded from underwater surveys. (D) Shark harvesting at neighboring Tabuaeran Atoll and elsewhere in the tropical Pacific has severely reduced reef shark populations. Understanding and managing these declines requires having an adequate understanding of the accuracy of shark survey methods. Photos A and C are included courtesy of K. Pollock.

Some species of sharks are thought to become more active with the onset of nightfall raising concern about how well density estimates calculated during the day approximate overall shark densities in a habitat. We, however, found no differences between density estimates made during daytime and evening periods in our video surveys. This finding provides preliminary support for the conclusion that our outputs from diurnal surveys can serve as good overall proxies for shark density at this location.

Mark and recapture field surveys conducted with the shark *C. amblyrhynchos* provided a baseline measure of the population size of this species at our study locality (Fig. 3), a valuable source of information that can be difficult to derive from the density estimates produced using underwater surveys. Comparing population size estimates from mark and recapture outputs to density estimates from underwater methods is however problematic because often neither the size of the area being sampled by mark and recapture nor the overall ecosystem-wide quantity of habitat subsampled using underwater surveys is known. Our population size estimate of *C. amblyrhynchos* would accord with belt transect density estimates of this species if bait fishing activities used during mark and recapture surveys sampled an area ~2700 × 2700 m, a perhaps not unreasonable assumption given the active patterns of water movement at Palmyra and the well-developed olfactory capacity of sharks (Tester 1963). However, because there are myriad factors that determine the area being sampled using mark and recapture techniques such as this, it is best to treat abundance measures generated using this method as information sources that are complimentary, but independent of those gathered using underwater censuses.

CONCLUSIONS

Results from trials of underwater surveys bring to light three important conclusions about their performance and utilization. First, our results highlight the value and importance of standardizing abundance estimates by survey duration. The rather good overall correspondence between predicted and true density values in all simulations suggests that one-minute intervals may be an appropriate unit for temporal standardizations. Second, it appears that shark surveys that produce the highest abundance estimates are not always the most accurate. This conclusion contrasts with commonly held assumptions that marine animals are cryptic and therefore methods that produce the highest abundance estimates are necessarily superior (Sale 1997, Colton and Swearer 2010). Last, we conclude that larger and longer surveys are also not always better. Simulation results demonstrate that increasing survey size/duration systematically reduces density estimates, an effect that is only beneficial when using methods that overestimate shark abundance.

Making precise recommendations for the selection of field methods is difficult given the wide variability of questions and local conditions that confront researchers. However, in light of data generated in the field and simulation we conclude that survey accuracy can be optimized by using small belt transects and large point counts, provided that a sufficient number of replicates are undertaken, one-minute standardizations are made, and shark densities are not below detection thresholds. Video surveys consistently overestimate shark density, but provide excellent shark detection capacity (particular useful when monitoring rare sharks) and can help to investigate the confounding influence of observer bias in shark counts. Where feasible to undertake, mark and recapture surveys provide an insightful alternate way to collect data on shark population size, but the spatially independent qualities of this method permit only qualitative comparisons to be made between mark and recapture outputs and data from underwater surveys.

Continuing to refine our understanding of the performance of these and other shark survey methods will help further improve our ability to manage and understand shark populations. Given the precipitous global declines in shark abundance and the presumed impact that these reductions are having on marine ecosystems, it is imperative that we advance these discussions immediately.

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Supplemental Material

Appendix A

Map showing location of Palmyra Atoll, USA (*Ecological Archives* A022-024-A1).

Appendix B

Methodological details of mark and recapture model (*Ecological Archives* A022-024-A2).

Appendix C

Comparisons of shark density outputs standardized by area and by volume (*Ecological Archives* A022-024-A3).

Appendix D

Methodological details of computer simulation and description of simulation parameters (*Ecological Archives* A022-024-A4).

Appendix E

Detection rates of sharks in field surveys (*Ecological Archives* A022-024-A5).

Appendix F

Statistical comparisons of shark presence/absence data from field surveys (*Ecological Archives* A022-024-A6).

Appendix G

Evaluation of variability of density estimates as a function of survey replication (*Ecological Archives* A022-024-A7).

Appendix H

Algorithms that model the operation of simulation-implemented survey methods (*Ecological Archives* A022-024-A8).

Appendix I

Role of behavioral biases in shark surveys (*Ecological Archives* A022-024-A9).

Appendix J

Video clip of mark and recapture surveys of shark *Carcharhinus amblyrhynchos* (*Ecological Archives* A022-024-A10).

Supplement

Source code for simulation model, simulation readme, and associated parameter files (*Ecological Archives* A022-024-S1).