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How robust are estimates of coral reef shark depletion?

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ABSTRACT

On coral reefs, diver-surveys of shark abundance indicate that populations are severely depleted, even in no-take zones with low-levels of illegal fishing, but are protected by strictly enforced no-entry zones. These findings have been questioned, on the grounds that diver-surveys overestimate shark abundance. We evaluated whether divers encounter sharks at higher rates when they first enter the water, and whether these effects vary among reefs that are subject to different levels of human interaction due to management zoning. We also examined the consistency of abundance estimates derived from multiple survey methods. For timed-swim, towed-diver, and baited-remote-underwater-video (BRUV) surveys, encounter rates were constant over time. For audible-stationary-count (ASC) surveys, encounter rates were elevated initially, then decreased rapidly, but the extent of upward bias did not differ between management zones. Timed-swim, BRUV, and ASC surveys produced comparable estimates of shark density, however, towed-diver-surveys produced significantly lower estimates of shark density. Our findings provide no evidence for biases in diver-surveys: encounter rates with sharks were not elevated when divers first entered the water; behavioural responses of sharks were consistent across management zones; and diver-surveys yielded abundance estimates comparable to other stationary methods. Previous studies using underwater counts have concluded that sharks are vulnerable to low levels of illegal fishing in no-take management zones, and that additional measures are needed to protect species, which, like sharks, have demographic characteristics that make them vulnerable to low levels of exploitation. Our results support the robustness of the abundance estimates on which those conclusions have been based.

1. Introduction

Apex predators are large carnivores that occupy the top trophic level of food webs. They are typically characterized by conservative life history traits, such as slow growth rates, late sexual maturity, and low fecundity. These traits make them particularly susceptible to over-harvesting, and apex predators often are preferentially targeted by humans for food or game (e.g. Myers and Worm, 2003). Consequently, apex predators are typically the first to become extinct or locally extirpated. This loss of apex predators may have extensive, adverse effects on ecosystem structure and function. In terrestrial, marine and freshwater systems, for example, changes in apex predator abundance have affected herbivore populations, with substantial flow-on effects to plant communities that provide the primary production and habitat structure that support biodiversity in these ecosystems (Estes et al., 2011).

In marine food webs, sharks are common apex predators, and also are socio-economically valuable resources (Heithaus et al., 2008). This is most apparent in tropical ecosystems, such as coral reefs, where reef sharks are believed to play an important role in ecosystem resilience (e.g. Ruppert et al., 2013), and they generate ~$1billion USD annually from ecotourism and fisheries (Cisneros-Montemayor et al., 2013). However, recent surveys of sharks of the Red Sea (Berumen et al., 2013), the Great Barrier Reef (GBR; Hisano et al., 2011; Robbins et al., 2006), the Indian Ocean (Graham et al., 2010), the Pacific Ocean (Nadon et al., 2012) and the Caribbean (Ward-Paige et al., 2010b) indicate substantial declines compared to estimated baseline populations, which have been primarily attributed to increased fishing pressure. Given the putative ecosystem functions provided by sharks, the need for accurate assessments of population status is crucial for effective coral reef management and to sustain the livelihoods of people who depend on their ecosystem goods and services.

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Currently, the severity of shark population declines on coral reefs is disputed (e.g. Heupel et al., 2009). Differences in survey method selection are commonly cited as a potential cause for discrepancies in abundance estimates (e.g. Graham et al., 2010; Ruppert et al., 2013; Ward-Paige et al., 2010a). Sharks may respond variably to different stimuli such as noise, bait, divers, and boats, which are employed in different ways in different types of surveys (Cubero-Pardo et al., 2011; Fitzpatrick et al., 2011; Ward-Paige et al., 2010a). In addition, some methods, particularly diver-based counts, have been criticized for potentially producing biased estimates of differences in shark abundance along gradients of human interaction (Ward-Paige et al., 2010a). If sharks are less accustomed to people at unfished or remote locations, they may be more likely to approach divers, leading to over-estimates of abundance in those locations, relative to areas with more human activity (Graham et al., 2010).

Recent studies have concluded that reef shark populations in fished areas are severely depleted, and that low levels of poaching render no-take marine reserves much less effective than strictly enforced no-entry zones (Ayling and Choat, 2008; Robbins et al., 2006). Because estimates of population status in these studies have relied heavily on relative abundances from diver-based surveys, resolving the controversy about the validity of these approaches is crucial for evaluating the effectiveness of no-take marine protected areas for protecting apex predators with low intrinsic population growth rates, such as reef sharks, and for determining how best to assess the status of such populations. In particular, for estimates of baseline shark densities to be unbiased, sharks should neither actively avoid, nor approach, divers conducting surveys. Consequently, estimates of population depletion based on relative abundances estimated in fished and unfished areas, will be compromised if any such biases differ in magnitude in areas with different levels of fishing pressure. To date, the only study to investigate the performance of survey methods for sharks was undertaken at a single remote location (Palmyra Atoll, Line Islands) where sharks may be naïve towards humans (McCauley et al., 2012). Thus, an assessment of sharks' responses to alternative survey methods across a gradient of human interaction, and the responses' implications for estimates of absolute and relative abundance, is needed to assess the robustness of recent conclusions about the status of reef shark populations and their vulnerability to poaching in no-take marine reserves.

Here, we address this issue by comparatively evaluating four visual survey techniques that are commonly used for estimating shark abundance: (1) timed-swim, (2) towed-diver, (3) stationary-point-count (SPC), and (4) baited-remote-underwater-video (BRUV). In addition, we trialed a novel survey method, (5) audible-stationary-count (ASC), which uses low frequency sound to attract sharks to a stationary point. During each replicate survey, we recorded any observed behavioural response of sharks to divers, as well as the time at which each shark was observed. If sharks are attracted to divers, then we expect encounter rates with new individuals to be high when divers first enter the water to commence counting, and to decrease thereafter. Conversely, if sharks respond neutrally to divers, encounter rates should not increase or decrease over the course of a survey time. Each method was repeated across a gradient of human interaction in order to quantify whether any such biases vary, depending on the prevalence of human activity on the reef. To achieve this, we conducted our study in the Great Barrier Reef Marine Park (GBRMP), a system of spatial zoning that includes: (1) no-entry zones, which are strictly enforced exclusion areas; (2) no-take zones, which are conservation areas where fishing is prohibited, but non-extractive activities (e.g. diving) are allowed and where low levels of illegal fishing have been recorded (Davis et al. 2004); and (3) fished zones, which are general use areas that allow fishing and other extractive activities. Finally, we converted all shark counts to density estimates, and we tested for any differences between survey methods in shark abundance estimates, allowing for potential interactive effects with management zone and habitat type.

2. Methods

2.1. Study sites and species

Surveys were performed at Rib Reef (fished zone), Little Kelso Reef (no-take zone) and Bandjin Reef (no-entry zone) in the central Great Barrier Reef (GBR), and Northwest Reef (fished zone), Tryon Reef (no-take zone) and Wreck Reef (no-entry zone) in the southern GBR (Fig. 1). At each reef, zone boundaries are a minimum of 1–2 km from the reef edge. All six reefs are comparable in morphology and distance from shore, with a well-developed reef slope, reef flat and back reef, and each reef has an intact faunal community that is typical of reefs in the GBR (Done, 1982; Frisch et al., 2014; Newman et al., 1997). More than 4000 recreational vessels, >200 commercial line-fishing vessels and dozens of dive-charter vessels operate in the central and southern GBR (Lunow and Holmes, 2011; Taylor et al., 2012). During the course of this study, up to ten boats were observed fishing at Rib and Northwest Reefs at one time, while up to three boats were observed (anchored) at Little Kelso and Tryon Reefs at one time, and no boats were observed at Bandjin or Wreck Reefs at any time. This steep gradient of human presence is typical for these reefs and occurs year-round (J. Aumend, surveillance unit, Great Barrier Reef Marine Park Authority, pers. comm.). Thus, fished, no-take and no-entry reefs represent a steep gradient in the frequency of shark-human interactions. Estimates of abundance were recorded for whitetip reef sharks, *Triaenodon obesus,* grey reef sharks, *Carcharhinus amblyrhynchos* and blacktip reef sharks, *C. melanopterus*, as they are the dominant shark species on Indo-Pacific coral reefs (Ceccarelli et al., 2014; Robbins et al., 2006; Sandin et al., 2008). Multiple previous studies have demonstrated that the majority of all three reef shark species exhibit a high level of site fidelity, typically remaining on single reefs for long periods of time (Speed et al., 2011, 2012; Whitney et al., 2012; Vianna et al., 2013). Although reef sharks are capable of moving large distances in relatively short periods of time, only a small proportion of individuals move between reefs (Barnett et al., 2012; Field et al., 2011; Heupel et al., 2010; Whitney et al., 2012). This supports our assumption that inter-reef movements are sufficiently infrequent to establish and maintain a strong gradient in the frequency of human interactions experienced by sharks in the different management zones.

2.2. Survey methodology

Survey methods consisted of timed-swims, towed-diver, SPC, ASC, BRUV (described below). Fourteen to 24 surveys were performed per method per reef, except for the towed-diver method, which entailed five to eight surveys per reef due to the large size of each replicate tow ($\sim$1.5 km) relative to the size of each reef and the need for spatial separation between replicate tows. For all survey methods, replication was stratified across three habitat types (reef slope, reef flat, back reef); however, shark counts on the reef flat were too low (<8% of total sharks observed) to allow parameter estimation in our encounter rate and generalized linear model analyses, so we focus our analysis on the slope and back reef data only. When a shark was observed, we recorded the time (to the nearest second), species, and other identifying characteristics such as estimated total length (TL), colour patterns, and scars, to minimize the risk of multiple-counting of the same individuals.

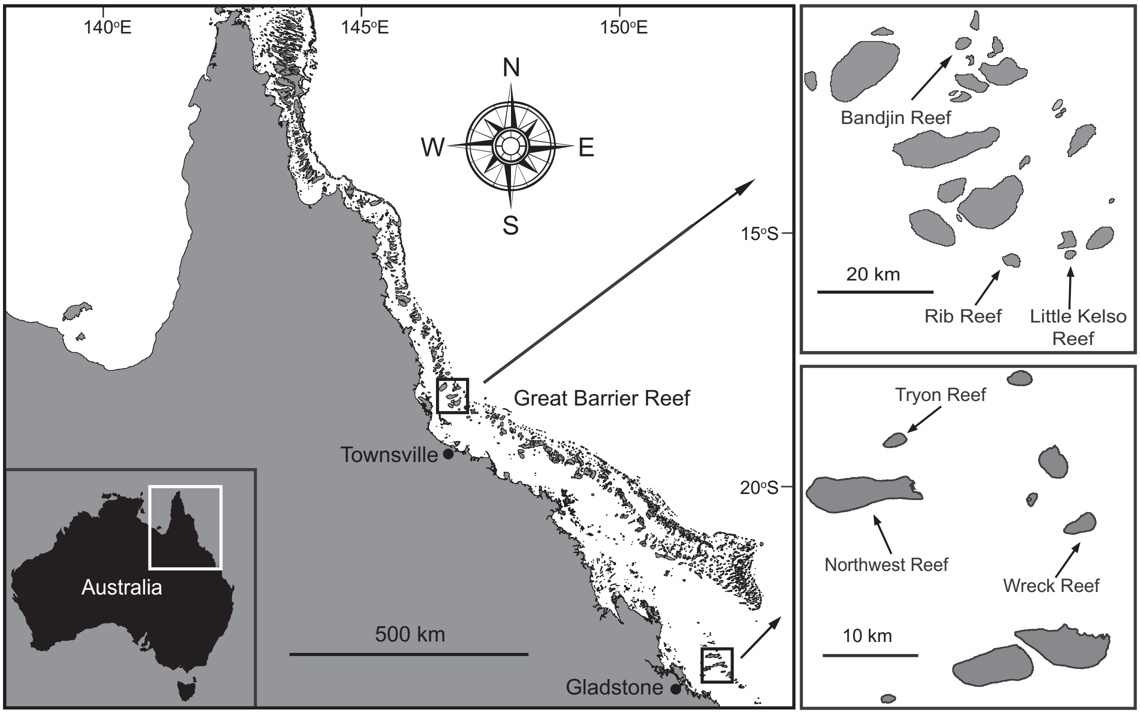

Fig. 1. Map showing the location of study sties. Rib and Northwest Reefs are within fished zones, Little Kelso and Tryon Reefs are within no-take zones, and Bandjin and Wreck Reefs are within no-entry zones.

In a subset of timed-swims (minimum of 10 per reef), the behavioural response of individual sharks was recorded at the moment they were first sighted (one observation per shark). Responses were categorized as 'evasive' (immediate change of direction away from the diver), 'interested' (direct, head-on approach or immediate change of direction toward the diver) or 'neutral' (no change of direction), as per Cubero-Pardo et al. (2011). Replicate surveys were separated by a minimum distance of 500 m, and different survey methods were performed during different weeks to avoid habituation. Each method was implemented in random order through time and space, except that Rib, Little Kelso and Bandjin Reefs were visited during November 2011–June 2012 and Northwest, Tryon and Wreck Reefs were visited during April–May 2013.

Timed-swim surveys involved a diver swimming for 45 min, which closely corresponds to that used in previous shark-specific studies (e.g. Ayling and Choat, 2008; Robbins et al., 2006), but involves longer transects than those used in more taxonomically broad fish count studies (DeMartini et al., 2008; Friedlander and DeMartini, 2002; Sandin et al., 2008). Towed-diver-surveys were designed to be similar to those used in other shark-specific studies (e.g. Nadon et al., 2012; Richards et al., 2011). Specifically, they involved a diver towed 60 m behind a small outboard powered vessel (6.2 m in length) for 24 min at a constant speed of approximately 1.5 knots. A distance of 60 m was chosen in order to maximize the distance between the observer and tow-vessel and limit any potential confounding effects on shark behaviour as a result of vessel noise. The observer used a small tow-board (40 cm $\times$ 60 cm), constructed of marine-grade plywood, with handholds and a secured data sheet, connected to the 60 m trailing line. For both timed-swim and towed-diver-surveys, only sharks in front of, and within 10 m either side of, the observer were counted (20 m transect width). A GPS unit (towed at the surface during timed-swims) was used to calculate survey area and enable standardization of data to units of density (ha^{-1}). The mean length ($\pm$ standard error, SE) of timed-swim and towed-diver-surveys was 779 $\pm$ 22 m and 1618 $\pm$ 49 m, respectively.

Stationary-point-count (SPC) involved a diver scanning 360° from a fixed point and counting all sharks observed within a 10 m radius during a 3 min period. Short survey duration is standard for SPC (Samoilys and Carlos, 2000) and is intended to reduce bias caused by shark behaviour (Ward-Paige et al., 2010a). This protocol differs slightly from other studies (e.g. Bohnsack and Bannerot, 1986; Nadon et al. 2012), where for vagile species, such as sharks, if multiple individuals are observed during the sampling time period, only the first individual is recorded in the quantitative data.

Audible-stationary-count (ASC) surveys were similar to SPC except that the diver rapidly and repeatedly squeezed the sides of an empty plastic drink bottle. Recreational divers know this method as the 'squeaky-bottle' technique because it attracts sharks via emission of low frequency sound. Each survey lasted for 10 min and commenced after a 3 min acclimation (silence) period. To convert counts to an estimate of absolute density (and thus enable comparison of ASC with other methods), it was necessary to estimate the distance over which sharks responded to the auditory stimulus (i.e. to estimate the area of attraction, AoA). Sharks have excellent hearing that enables them to rapidly localize and home-in toward low frequency sounds that are up to 250 m away (Myberg, 2001; Nelson and Gruber, 1963). However, the average response distance is likely to be considerably less than 250 m because of individual variation (Myberg, 2001). By placing an acoustic transmitter at a known distance from a multi-species shark aggregation site in the Bahamas, Myberg et al. (1976) demonstrated that a suite of shark species could be reliably attracted to low frequency sound at a distance of 80 m, with a modal response time of approximately 1 min. During a pilot study on the GBR, we found that reef sharks (*T. obesus* and *C. amblyrhynchos*) responded to 'squeaky-bottle' sounds with temporal characteristics (e.g. mean time to first arrival and modal response time) that were almost identical to those reported by Myberg et al. (1976). Therefore, the response distance for the present study was assumed to be approximately 80 m and the theoretical AoA was estimated as:

$$\mathrm{AoA_{ASC}} \approx \pi r^2/10^4,$$

where r is the radius (80 m) and 10^4 converts m^2 into hectares. Using this simple model, we estimated that the AoA for ASC surveys was 2.01 ha. Note that, for comparisons of ASC counts on different reefs or in different habitats, this conversion of counts to density has no effect, since all counts are converted by the same constant. Any biases in the estimate of density would influence only comparisons of abundance across methods (and are considered in the Discussion).

Baited-remote-underwater-video (BRUV) units consisted of a steel frame and centrally-mounted plastic housing which contained a battery-operated video camera (Cappo et al., 2004, 2007). A bait bag containing approximately 1 kg of crushed pilchards (*Sardinops sagax*) was mounted 1.5 m from the front of the camera, and filming occurred continuously for 60 min after deployment. Previous BRUV studies presented results as time-to-first-arrival (Priede and Merrett, 1996), maximum number of individuals viewed at any one time (MaxN; Willis et al., 2000), or catch-per-unit-effort (CPUE, the number of individuals 'caught' on film; Brooks et al., 2011). In the present study, we used total catch as the preferred index of abundance because (1) soak time was uniform (60 min), (2) sharks were relatively rare, such that MaxN was consistently small and meaningless, and (3) individual sharks could be readily identified from their unique characteristics (see above), which helped to avoid double-counting.

To estimate absolute density (and thus enable comparison of BRUV with other methods), it was necessary to estimate the area over which the bait plume dispersed in 60 min (i.e. estimate the AoA). To do this, a SCUBA diver released 30 ml of red food dye underwater. After 3 min, the distance and angle of dye dispersal was calculated via tape measure and trigonometry. After ten trials at representative locations and tide cycles, mean current velocity and dispersal angle was calculated to be 3.40 m min^{-1} and 23.5° respectively. These results are similar to published hydrodynamic data for the GBR (Cresswell and Greig, 1978; Wolanski and Jones, 1980) and correspond to observed dispersal patterns of pilchard oil under prevailing conditions (authors' pers. obs.). Accordingly, the AoA was approximately:

$$\mathrm{AoA_{BRUV}} \approx \pi (T_{\mathrm{soak}} \times V_{\mathrm{current}})^2 \times A_{\mathrm{d}}/10^4,$$

where T_{soak} is the duration of filming (60 min), V_{current} is the water current velocity (3.40 m min^{-1}), A_{d} is the angle of dispersal (23.5°; expressed as a proportion of 360°), and 10^4 converts m^2 into hectares. Using this simple model, we estimated that the AoA for BRUV surveys was 0.85 ha. As with the AoA for ASC surveys, this conversion does not affect comparisons of abundances between reefs or habitats because all BRUV counts were normalized by the same constant.

2.3. Data analysis

To test for biases due to shark behavioural responses to divers, two types of analyses were performed. Firstly, a 'scaled' χ^2 homogeneity test (Lawal and Upton, 1984) was used to evaluate the distribution of behavioural responses (evasive, interested, neutral) during timed-swim surveys in each management zone. Secondly, we fit several alternative models for shark encounter rates. In the first model, shark encounter rate is high (or low) initially, and then asymptotically approaches a baseline level over time:

$$f_{\mathrm{var}}(t) = \mu(1 - \beta e^{-\alpha t}) \quad (1)$$

where t is time elapsed since the start of the transect, β is the bias (the amount by which the encounter rate is elevated above baseline at the start of the transect), and α is the rate at which that encounter rate asymptotically approaches the baseline ($\beta > 0$, $\alpha > 0$ implies attraction when divers enter the water; $\beta < 0$, $\alpha < 0$ implies avoidance). μ is a normalization constant: because $f_{\mathrm{var}}(t)$ is a probability distribution, it must integrate to 1. μ is normalization constant (since Eq. (1) is a probability distribution, it must integrate to 1):

$$\mu = \frac{\alpha}{\alpha t_{\mathrm{f}} - \beta(1 - e^{-\alpha t_{\max}})} \quad (2)$$

where $t_{\max}$ is the duration of the transect. We used maximum likelihood methods to estimate the values of α and β that provided the best fit of Eq. (1), given the observed encounter times of sharks, and the replicate duration $t_{\max}$. We considered the following models where the parameters α and β: (1) vary between reefs and habitats, (2) are identical for reefs within the same management zone, but vary between management zones and habitats (as might be expected if sharks' attraction to divers depends upon their past experience with human interaction), (3) are the same across management zones but differ by habitat, and (4) are the same across all management zones and habitats. We also fit a model (5) assuming no bias in the counts ($\beta = 0$), implying that sharks were encountered at a constant rate. We used likelihood ratio tests to assess the evidence for bias in encounter rates, and if it was present, whether the degree of bias varied among habitat, management zone, or reef.

To test for differences in abundances between zones, habitats, and survey methods, we used a generalized linear mixed model (GLMM), using the MASS library's function glmmPQL() in *R* (R Development Core Team, 2008), with reef included as a random effect, and a quasi-poisson error structure. We excluded SPC from this analysis, because the uncertainty in estimates with this method was very high, and because the mean–variance scaling of counts suggested its inclusion could bias the rest of the analysis (Appendix A). Because the quasi-poisson error structure is not a true probability distribution, likelihood-based model selection (e.g., likelihood ratio tests, AIC, BIC, etc.) could not be used. Instead, we adopted a sequential testing procedure based on the *P*-values of individual effects: starting with the full model containing all fixed effects and interactions, we removed the non-significant highest-order interaction terms in sequence until all remaining terms were statistically significant. As a check on the robustness of this analysis, we removed the random effect of reef from all models, re-fitted the entire model set, and conducted model selection using a quasi-likelihood procedure based on adjusted model deviances (Zuur et al., 2009).

Different shark species tend to have slightly different behaviours: *C. amblyrhinchos* and *C. melanopterus* swim constantly and are relatively timid, whereas *T. obesus* often rest on the seafloor and are less timid (Cubero-Pardo et al., 2011). To test whether differences in species-specific behaviour affect estimates of abundance, frequency distributions of shark species among survey methods were analysed by a 'scaled' χ^2 homogeneity test (Lawal and Upton, 1984). Detection rates of all survey methods were calculated as the proportion of surveys where one or more reef sharks was observed.

3. Results

We found no direct observational evidence of differences in behavioural responses to divers across management zones. Individual sharks were found to be visibly unique (in terms of species, size, sex, colour patterns, scars, etc.) and no shark was knowingly observed more than once during a single survey. Frequency distributions of behavioural responses among management zones were homogeneous ($\chi^2_4 = 4.21$, $P > 0.25$; Fig. 2). Across all management zones, only a small proportion of sharks were evasive (6–23%) or interested (9–18%), with the majority of sharks behaving neutrally (64–78%) and showing no apparent behavioural response to the

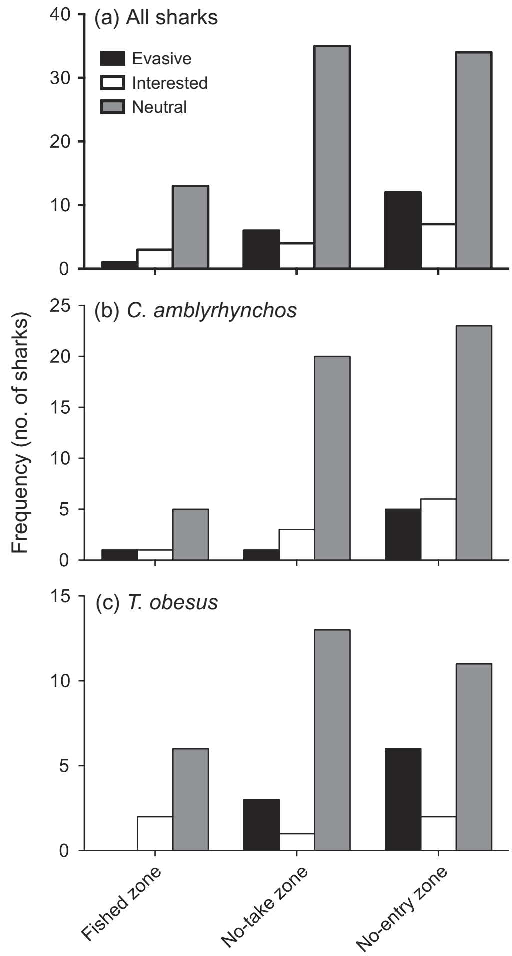

Fig. 2. Behavioural responses of sharks to a SCUBA diver at fished, no-take and no-entry zones. Data are presented for (a) all sharks combined (including *Carcharhinus melanopterus*), (b) *Carcharhinus amblyrhynchos* and (c) *Triaenodon obesus*. Note that *C. melanopterus* was not analysed separately as too few sharks were observed to warrant meaningful comparisons (see Appendix C). Response categories are defined in the Section 2. Note different scales of *y*-axis.

diver, regardless of taxon or management zone. Similar findings were obtained when behavioural responses were considered separately by species (Fig. 2).

Encounter rates of sharks did not exhibit significant differences between reefs within management zone, or between management zones, for any method for either slope or back reef habitats (Table 1). Indeed, consistent with our behavioural observations, we found no evidence of elevated initial rates of encounter with sharks, with the exception of ASC, where the near-instantaneous transmission of sound beyond the diver's field of vision would be expected to attract sharks rapidly. Specifically, the best-fitting probability distributions of times of observation were uniform (i.e., constant over time) for the timed-swim, towed-diver, and BRUV surveys (Fig. 3a–c; Table 2). For ASC, there was statistically significant support for initially high encounter rates that decreased over time (Fig. 3d; Table 2); however, there was no evidence for differences in the strength of this effect among management zones (Table 1). Model selection by AICc (not shown) yielded the same best-fitting model for each method as the likelihood ratio tests.

The analysis of abundances based on GLMMs yielded strong evidence for main effects of survey method, management zone, and habitat on shark density, but not for any two-way or three-way interactions (Fig. 4; Table 3). Specifically, towed-diver density estimates were significantly lower than those of the other three methods, but ASC, timed-swim, and BRUV were highly consistent with one another (Fig. 4; Table 4). Specifically, 95% confidence intervals on effect sizes for survey method indicate that BRUV, ASC and timed-swim surveys differ at most by no more than about ~30–45%, whereas towed-diver surveys were estimated to be approximately two- to ninefold (200–900%) lower than the other methods. Shark densities in no-entry zones were also significantly higher than densities in fished zones. Mean densities also were higher on no-take reefs than fished reefs, but the difference was non-significant (Fig. 4; Table 3). In addition, shark abundances were significantly higher on the reef slope than the back reef (Fig. 4; Table 3). When we excluded the random effect of reef, and conducted model selection based on adjusted deviances, we obtained a slightly different best-fitting model: management zone × habitat interactions were included in the best-fitting model (the magnitude of the increase in abundance on no-entry and no-take reefs relative to fished reefs was different on the slope and the back reef). However, the effects of survey method were unchanged (BRUV, ASC and timed-swim produced comparable estimates; towed-diver estimates were significantly and substantially lower). This alternative procedure is summarized in Appendix B.

The frequency distribution of shark species among survey methods was significantly different ($\chi^2_8 = 51.76$, $P < 0.001$). In general, timed-swim and BRUV surveys recorded more *C. amblyrhynchos* than *T. obesus*, but towed-diver-surveys recorded up to fourfold more *T. obesus* than *C. amblyrhynchos* (Appendix C). Total shark counts, detection rates and patterns of variability are summarized in Appendix C.

4. Discussion

While there is wide agreement that reef sharks are in decline in many regions of the world, the appropriateness of baseline population estimates and the effectiveness of no-take areas for protecting

Table 1
Results from likelihood ratio tests for the variable-rate models of shark encounter. The effects of reef, management zone, and habitat on shark encounter rate are shown for timed-swim, towed-diver, baited-remote-underwater-video (BRUV) and audible-stationary-count (ASC) survey methods. *R* is the likelihood ratio statistic. A statistically significant result indicates rejection of the simpler model (with reef, management zone, or habitat pooled) in favour of the more complex one (with different parameters for different reefs, management zones, or habitats, respectively). For instance, the tests under "Reefs (within management zone)" show that reefs from the same management zone do not differ significantly in their encounter rate parameters (Eq. (1)).

Method[a]	Reefs (within management zone)						Management zone (reefs pooled)						Habitat (management zones pooled)		
	Slope			Back reef			Slope			Back reef					
	R	df	*P*	*R*	df	*P*	*R*	df	*P*	*R*	df	*P*	*R*	df	*P*
Timed-swim	1.76	6	0.94	0.87	2	0.65	1.81	4	0.77	0.66	4	0.96	0.75	2	0.69
Towed-diver	–	–	–	–	–	–	7.31	4	0.12	–	4	–	0.97	2	0.62
BRUV	2.47	6	0.87	2.81	2	0.25	2.16	4	0.71	2.38	4	0.67	2.61	2	0.27
ASC	9.16	6	0.17	0.48	2	0.79	8.23	4	0.08	2.33	4	0.68	1.24	2	0.54

[a] '–' Indicates insufficient data.

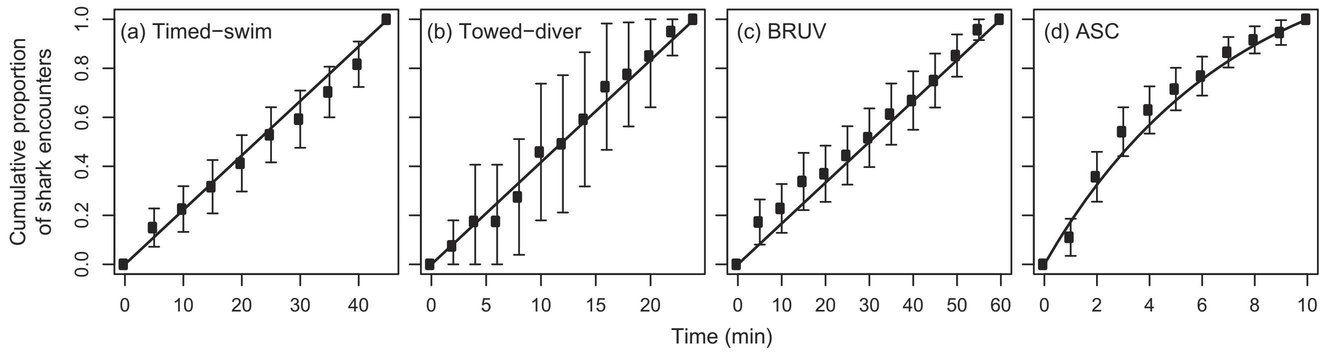

Fig. 3. Observed cumulative proportion of shark encounters (mean ± 95% confidence intervals) through time during (a) timed-swim, (b) towed-diver, (c) baited-remote-underwater-video (BRUV), and (d) audible-stationary-count (ASC) surveys. Best-fit cumulative distributions from the encounter rate models, as indicated by model selection, are the thick solid lines. Note that a straight diagonal line (a–c) indicates a constant encounter rate model, whereas a decelerating line (d) indicates higher encounter rates earlier in the survey. For each survey method, all samples were combined for model fitting. Note different scales of *x*-axis.

Table 2
Results from the likelihood ratio test comparing, for each survey method, the best-fitting variable-rate model of shark encounter from Table 1 (management zones and habitats pooled) with a constant rate model.

Method[a]	*R*	df	*P*
Timed-swim	2.32	4	0.68
Towed-diver	3.02	4	0.55
BRUV	7.66	4	0.11
ASC	31.98	4	<0.001*

[a] Survey methods are ASC, audible-stationary-count; BRUV, baited-remote-underwater-video.
* Statistically significant differences ($P < 0.05$) indicate rejection of the constant-rate model in favour of the variable-rate model.

shark populations have been the subject of increasing debate, especially over the past five years (Heupel et al., 2009; Hisano et al., 2011; Nadon et al., 2012). Much of the controversy has revolved around the reliability of diver-based estimates of absolute and relative abundances of sharks in areas with negligible human interaction versus areas subject to fishing. Although arguments that sharks' vagility and/or behavioural responses towards divers may bias survey outputs are plausible on biological grounds (e.g. Dickens et al., 2011; Watson et al., 1995), we find no evidence that they markedly bias abundance estimates from diver-based timed-swims, despite considering multiple lines of evidence. Firstly, behavioural responses of sharks were consistent across management zones (i.e. degree of human interaction). Secondly, shark encounter rates were not significantly higher or lower when divers first entered the water, regardless of management zone. Thirdly, estimates of shark density from timed-swims (assuming zero AoA; i.e., no attraction to divers) were comparable to densities estimated from BRUV and ASC surveys, once their respective AoA were taken into account. Fourthly, no interaction between survey method and management zone was detected for estimates of shark abundance, implying that any biases in the methods are consistent across management zones (or that biases of timed-swims, towed-diver, ASC, and BRUV all happen to vary with management zone in exactly the same way – a possibility that seems highly implausible given the fundamental logistical differences between the methods). Finally, even the rate of decrease over time in encounter rates for ASC (specifically designed to attract sharks quickly) was not significantly different across management zones. These results suggest that estimates of shark abundance from timed-swims are robust to any attraction to or avoidance of divers by sharks.

In addition to the consistency of timed-swims with BRUV and ASC surveys in this study, timed-swim estimates of relative abundances in no-take versus fished zones are highly consistent with other studies on the GBR that have used timed-swims, and with experimental catch rate data (Fig. 5). Similarly, Hisano et al.

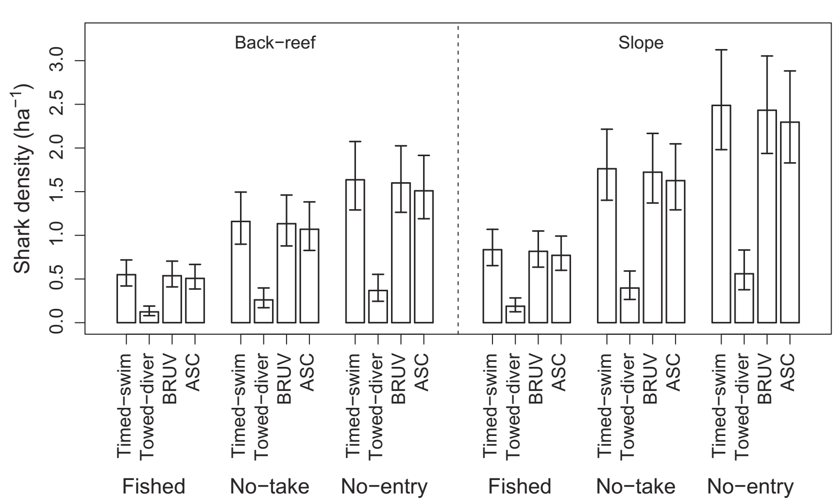

Fig. 4. Estimates of absolute shark density (mean ± standard error) as a function of management zone (degree of human interaction), survey method and habitat, from the fitted GLMM (Table 3). For baited-remote-underwater-video (BRUV) and audible-stationary-count (ASC) surveys, absolute density was estimated using an area of attraction (AoA) model (see Section 2).

Table 3
Parameter estimates for the best-fitting generalized linear mixed-effects (GLMM) model, with a random effect of reef, and a quasi-binomial error distribution. Note that the response variable is log-transformed. The "intercept" parameter corresponds to the predicted natural logarithm of density (ha^{-1}) for the back reef habitat in a fished zone that was surveyed by the towed-diver method. All other terms represent effect sizes. Colons indicate interactions. For example, the predicted natural logarithm of density for a timed-swim on the reef slope in a no-take zone would be intercept + method (timed-swim) + zone (no-take) + habitat (slope), or −2.09 +1.49 + 0.75 + 0.42 = 0.57, implying $e^{0.57} = 1.77$ sharks ha^{-1}. The estimated standard deviation for the random effect of reef was 0.26 (95% CI: 0.12–0.54); the estimated residual standard error was 1.10 (95% CI: 1.00–1.20). $n = 246$.

Effect[a]	Estimate	SE	df	t-statistic	P
(Intercept)	−2.09	0.44	236	−4.80	<0.0001*
Method (ASC)	1.41	0.37	236	3.85	0.0002*
Method (timed-swim)	1.49	0.37	236	4.08	<0.0001*
Method (BRUV)	1.47	0.37	236	4.01	<0.0001*
Zone (no-take)	0.75	0.32	3	2.35	0.10
Zone (no-entry)	1.09	0.31	3	3.49	0.04*
Habitat (slope)	0.42	0.14	236	2.90	0.004*

[a] Survey methods are ASC, audible-stationary-count; BRUV, baited-remote-underwater-video.
* Statistically significant effects ($P < 0.05$).

Table 4
Estimated differences in log-abundance between survey methods. Comparisons with the towed-diver method are identical to the corresponding effects in Table 3. For comparisons among audible-stationary-count (ASC), timed-swim, and baited-remote-underwater-video (BRUV), the values are analogous. For instance, "ASC – timed-swim" gives the ASC effect that would have been obtained if timed-swim (rather than towed-diver) had been the method incorporated in the intercept parameter of Table 3. P-values are calculated based on the corresponding t-statistics (df = 236 in all cases). Because there are six pairwise comparisons, the critical P-value for a conventional Bonferroni correction is 0.008. In the final column, we report 95% confidence intervals on the ratio of abundances (the first divided by second) between the two methods, which are calculated from the effect size estimate and standard error as $e^{\mathrm{Estimate} \pm 1.96\mathrm{SE}}$.

Difference[a]	Estimate	SE	t-statistic	P	Ratio (95% CI)
ASC – towed-diver	1.41	0.37	3.85	0.0002*	1.98–8.46
Timed-swim – towed-diver	1.49	0.37	4.08	<0.0001*	2.14–9.16
BRUV – towed-diver	1.47	0.37	4.01	<0.0001*	2.11–8.98
Timed-swim – ASC	0.07	0.16	0.44	0.66	0.78–1.47
BRUV – ASC	0.05	0.16	0.31	0.76	0.77–1.44
BRUV – timed-swim	−0.02	0.16	−0.13	0.90	0.72–1.34

[a] Survey methods are ASC, audible-stationary-count; BRUV, baited-remote-underwater-video.
* Statistically significant effects (corrected alpha value of 0.008).

(2011) found that estimated differences in abundance between no-entry and fished reefs were highly consistent with differences based on population projections using estimates of per-capita demographic rates. Our findings therefore suggest that previous conclusions drawn from shark-oriented timed-swim data are satisfactorily robust. This is important because reef sharks are vulnerable to even low levels of fishing, as might be expected in no-take areas (e.g. Davis et al., 2004; McCook et al., 2010). Hence, high abundance of sharks in no-entry zones appears to be real and not an artefact of shark behaviour towards divers, suggesting that even small no-entry zones can effectively preserve high shark abundances.

Shark density estimates were influenced by survey method, but these effects were highly consistent across management zones and habitat types. Of the four methods that we tested comprehensively, timed-swim, BRUV and ASC surveys generated consistent estimates of shark density, within ∼30–45% of one another. Based on the typically low densities of sharks, most estimates show relatively high amounts of variability and broad confidence intervals.

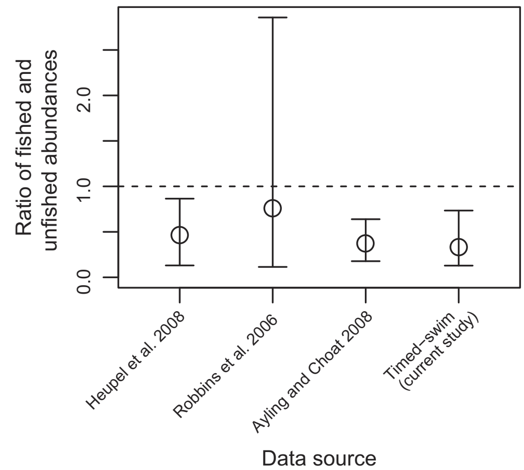

Fig. 5. Ratio of fished to unfished shark abundances from catch-per-unit-effort data (Heupel et al. 2008) and two other studies that used the same protocol for timed-swims as this study (Robbins et al. 2006; Ayling and Choat 2008). Whiskers indicate 95% bootstrap confidence intervals on the abundance ratios, generated by Monte-Carlo simulation (see Hisano et al. 2011). The dotted line represents where the abundance in fished and unfished zones are equal; values below the line indicate lower abundances in fished zones. Note that data are only from fished and no-take zones, as there are no catch rate data from no-entry zones. All data are from the Great Barrier Reef, Australia.

However, differences in shark densities across locations (e.g., across management zones) often span one or more orders of magnitude. As such, differences of <50% are likely to be small relative to the variation expected by chance in estimating densities for low-density, vagile species. In contrast, towed-diver-surveys generated density estimates that were substantially (∼200–900%) lower than those generated by timed-swim surveys. Similarly, elsewhere in the Pacific Ocean (i.e. Hawaiian, Line and Mariana Islands), towed-diver-surveys generated density estimates that were three- to twenty-fold lower than those generated by diver-based transect surveys (which are similar to our timed-swim method: *c.f.* Friedlander and DeMartini, 2002; Richards et al., 2011; Sandin et al., 2008). Nadon et al. (2012) reconciled the differences between methods by suggesting that towed-diver-surveys reduce the positive bias of shark behaviour towards divers by rapidly moving divers into new areas to prevent aggregation effects. In the present study, however, we found no evidence of aggregation effects during timed-swims, and there was strong congruence between timed-swim and (diver-independent) BRUV surveys. Thus, in our view, it is more likely that towed-diver-surveys under-estimate shark density, perhaps due to sharks engaging in avoidance behaviour when being approached by a motorized tow-vessel.

Of the methods that we evaluated, only ASC yielded evidence of declining shark encounter rates over time. This method is designed to quickly attract sharks to a stationary point: the 'squeaky bottle' simulates wounded prey, to which sharks respond vigorously and can hear from approximately 80 m away (Myberg, 2001; Myberg et al., 1976). Audible-stationary-count (ASC) therefore enables very rapid assessment of local shark populations, which is ideal for studies that utilize catch-mark-resight methodology. The only method we trialed that was incapable of generating ecologically meaningful estimates of abundance was SPC, due to its very low survey area and consequent low shark counts (seven sharks in 91 surveys), which yielded confidence intervals spanning around three orders of magnitude of abundance. In areas with much higher shark densities, of course, SPC may produce enough sightings to provide less uncertain estimates of abundance. For instance, in a previous study at remote Palmyra Atoll, Line Islands (where reef shark density is likely much higher than on the GBR), McCauley et al. (2012) considered SPC surveys to produce acceptable abundance estimates.

While BRUV and ASC surveys are alternatives to more conventional methods, quantitative comparisons of survey methods are challenging because it is difficult to estimate the area-of-attraction (AoA) for such surveys. In this study, we developed two models to estimate survey area and thus convert data from relative density to absolute density. However, we recognize that these first-order estimates do not account for all factors that may cause this quantity to vary. For example, results from BRUV and ASC surveys are dependent on the assumption that all species of sharks will have similar responses to attractants, such as the bait plume or sound. However, this may not be the case as there is likely to be variation in the ecology and behaviour among shark species (Bres, 1993; Heuter et al., 2004). For BRUVs, the AoA will depend on a sharks' ability to detect olfactory cues associated with the bait. Further, the associated water currents will influence the dispersion strength of the bait plume. For this reason, dispersion will vary among sites and within the same site over time. For ASCs, the AoA is dependent on sound detection capabilities of different shark species. This can be severely affected by a range of biological and environmental factors (Au and Hastings, 2008), which are also likely to vary over time, and according to reef topography may affect the AoA of ASC surveys. Consequently, local reef conditions may influence bait plume dispersion and sound transmission, which generates additional uncertainty regarding density estimates derived from attractant methods, such as BRUV and ASC surveys. Thus, future studies comparing locations with substantially different sound transmission properties, or small-scale circulation patterns, should assess these quantities on a site-by-site basis. Despite this, our AoA models (for BRUV and ASC surveys) generated estimates that were consistent with one another, and with the timed-swim data. In this context, it is important to note that our finding that estimates of relative abundances are comparable across survey methods (i.e., that there was no interaction between survey method and either management zone or habitat) is robust to the accuracy or otherwise of the AoA that we used, since the AoA modifies all abundance estimates for a given method by a common factor.

The fact that we found no evidence that consistent responses of sharks to divers were biasing abundance estimates, either in the timing of shark encounters or in our qualitative observations of their behaviour, suggests that diver-based underwater counts can provide reliable estimates of abundance in a broad range of management situations. The extent to which our findings apply to extremely remote locations, however, depends upon the assumption that inter-reef movements of reef sharks are sufficiently infrequent that sharks in no-entry zones have little or no experience with divers. We believe that two lines of evidence support this assumption. Firstly, there have been four recent studies on movement in grey reef sharks, which are the most mobile of our study species. Three of these found high site fidelity: 85% (23 out of 27 individuals; Barnett et al., 2012), 79% (31 out of 39 individuals; Vianna et al., 2013) and 100% (26 out of 26 individuals; Field et al., 2011) of individuals remained on a single reef for extended periods of time. The exception, Heupel et al. (2010), found that 4 out of 9 tagged sharks moved between reefs. However, given that this latter study was conducted in the Ribbon Reefs of the Great Barrier Reef, a nearly contiguous reef system with very short inter-reefal distances, we believe that the balance of evidence from these studies supports relatively high site fidelity for reefs such as those we studied (for which inter-reefal distances range from about $\sim$3–15 km). Secondly, we, along with previous studies (Ayling and Choat, 2008; Robbins et al., 2006), have found a large gradient in abundances of reef sharks between reefs in different management zones. This large gradient seems difficult to reconcile with very high movement rates. Nevertheless, we cannot rule out the possibility that some sharks in our no-entry reefs would have had some prior exposure to divers or boats during sojourns on reefs in other management zones.

Although no single survey method will be a panacea under all practical situations and research objectives, our findings indicate that diver-based timed-swims of the kind employed here will produce relatively unbiased estimates of absolute and relative shark abundance, comparable to those produced by diver-independent methods such as BRUV, or even auditory attraction methods used by recreational divers (ASC), once their respective AoA's are accounted for. Importantly, we find no evidence that estimated relative differences in shark abundance across gradients of human interaction vary between methods: the effect of management zone was consistent across all of the methods we considered. However, for areas that do not have very high shark densities, the low shark counts observed using the towed-diver method may reduce statistical power whenever this method is used in isolation. Previous studies using diver-based, underwater surveys have concluded that very high levels of compliance in protected areas are likely to be required to provide effective protection for species such as sharks, whose demography and life history give them very slow rates of potential population replenishment and recovery. Our findings support the robustness of the abundance estimates on which those conclusions have been based.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2014.05.003.

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