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Population density estimation of southern stingrays Dasyatis americana *on a Caribbean atoll using distance sampling*

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ABSTRACT

1. The southern stingray *Dasyatis americana* is a benthic mesopredator found in varying densities throughout Caribbean shallow reef systems, yet despite its increasing inclusion in fisheries, many aspects of its population ecology are still unknown.

2. Belt transects and distance sampling techniques were used to estimate seasonal abundance of an unexploited, isolated population of southern stingrays in lagoon and forereef habitats at Glovers Reef Atoll, Belize.

3. Southern stingrays were the most abundant elasmobranch in both shallow lagoon margin (< 5 m) and shallow forereef (< 15 m) habitats in all sampling seasons. Lagoon density showed no seasonal variation and was estimated at 245 (95% CI 226–265) individuals per km^2.

4. Forereef sampling indicated lower densities compared with the lagoon habitat, as well as seasonality with a significantly lower stingray density in November of 25 (16–37) compared with either of the April surveys of 100 (71–141) and 78 (53–116). Total population size for all lagoon habitat was estimated as ~8400 stingrays (7700–9100, 4%CV).

5. This is the first study known to utilize distance sampling techniques on benthic elasmobranchs. Absolute estimates of population density are crucial in wildlife management and will be an important tool in tracking community and trophic dynamics in affected systems of declining top predators, particularly in species devoid of natural identifying marks.

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KEY WORDS: lagoon; reef; survey; ecological status; fish; fishing

INTRODUCTION

The influential role of benthic elasmobranchs in structuring intertidal and subtidal ecosystems through bioturbation is well documented (Thrush *et al.*, 1991; Lohrer *et al.*, 2004; O'Shea *et al.*, 2011), but very few detailed population estimates have been carried out for elasmobranch species due to the implicit logistical difficulties of rarely seen, non-surfacing marine organisms. The southern stingray *Dasyatis americana* (Hildebrand and Schroeder, 1928) is an opportunistic forager, feeding on a wide range of benthic invertebrates and teleosts (Randall, 1967; Gilliam and Sullivan, 1993) including commercially important Caribbean species such as the spiny lobster *Panulirus argus* (Smith and Herrnkind, 1992) and queen conch *Strombus gigas* (Gilliam and Sullivan, 1993). Stingrays can exert direct pressure on crustacean prey populations, and are likely to be drivers of

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prey population dynamics (Dale, 2011), hence the abundance of *D. americana* seen in Caribbean shallow reef systems implies considerable influence on these communities, and is becoming more poignant in light of declining populations of their shark predators (Myers and Worm, 2003).

Accurate estimates of population size are virtually unknown for batoids other than a limited number of recent studies using genetics (Le Port and Lavery, 2012) and visual markings (Marshall *et al.*, 2011). Population studies of elasmobranchs have traditionally utilized mark–recapture techniques using naturally occurring or artificially applied visual markings to identify individuals (Castro, 2005; Marshall *et al.*, 2011). However, non-invasive studies are restricted to species with unique patterning, and studies capturing marked individuals can be subject to biases when factors contributing to heterogeneity in capture probabilities are not accounted for (Heupel and Bennett, 2007). Distance sampling has been successfully used in analysing many terrestrial populations and cetaceans for some time (Buckland *et al.*, 2001), and a study on reef fish found distance transects to be 4–10 times more efficient than regular belt transects at detecting differences in density (Kulbicki and Sarramégna, 1999).

Our knowledge of species population dynamics is crucial not only to managing them as a resource, but also in terms of managing coral reef systems and the fisheries they support, in light of changing climate. Declining numbers of top predators may cause cascading effects through these systems, where mesopredators released from predation risk alter aspects of their trophic ecology (Steneck and Sala, 2005). Rays have not traditionally made up a large percentage of catches in the largest targeted elasmobranch fisheries (Bizzarro *et al.*, 2007), however, in recent years the percentage catch of rays, and their importance to fisheries, have been increasing (Smith *et al.*, 2008). Stingrays are a common by-catch species in long-line fisheries (Piovano *et al.*, 2010), and are becoming increasingly targeted commercially in some developing regions (Francis, 1998) such as Colombia (Grijalba-Bendeck *et al.*, 2007), Costa Rica (Garro *et al.*, 2009) and Mexico (CONAPESCA-INP, 2004). As with many elasmobranchs, *D. americana* exhibits a K-selected life-history strategy, commonly defined by long gestation periods, slow growth and maturity, and long life span (Hoenig, 1990; Stevens *et al.*, 2000; Frid *et al.*, 2008), and as such have been seen to have low resilience to fishing pressure (Smith *et al.*, 2008).

Moreover *D. americana* is believed to be one of the longest living of the family Dasyatidae, with maximum longevity estimated at 31.5 years (Henningsen and Leaf, 2010). Populations of stingrays are not currently targeted at Glovers Reef and by-catch is low due to a ban on gill nets and bottom long-lines, hence it provides an ideal situation to study a relatively pristine population of mesopredators in an isolated system. The aim of this study was to compare stingray abundance and density in lagoon and forereef habitats of Glovers Reef and estimate total population size for the atoll.

METHODS

Study site

The study was undertaken on Glovers Reef Atoll (16° 44' N, 87° 48' W), the southernmost of four coral atolls in the Mesoamerican Barrier Reef System, situated approximately 70 km east of the Belizean coast, and 30 km east of the main barrier reef. Glovers Reef covers approximately 254 km^2 most of which is made up by the lagoon, surrounded by a reef crest, and insular reef shelf to ~20 m depth. Total area of marine habitat is approximately 253 km^2. Sand flat habitat covers ~34.2 km^2, and forereef slope represents ~26 km^2. The Glovers Reef Marine Reserve managed by the Belize Fisheries Department incorporates the entire atoll, however, a no-take zone in the south prohibits fishing of any kind in an area of ~71 km^2 (Figure 1).

Field surveys

Three marine macrohabitats making up Glovers Reef were sampled for stingrays and other elasmobranchs: lagoon margin ($<$ 5 m), deep lagoon (5–18 m) and forereef ($<$ 15 m). Lagoon margin surveys were conducted monthly between June 2009 and July 2010 (excl. Dec–Jan) making use of shallow clear sand flats for identification of elasmobranchs from a skiff. Twelve sites in the lagoon margin around the interior edge of the atoll were selected using a stratified systematic design with random start points, according to water depth and structure of benthos with as even spatial coverage as possible (Figure 1). Owing to boat sampling methods, transects were required to be between 1 and 5 m in depth. Each 1.6 km transect was covered at a constant speed of 2 $\mathrm{km\,h^{-1}}$,

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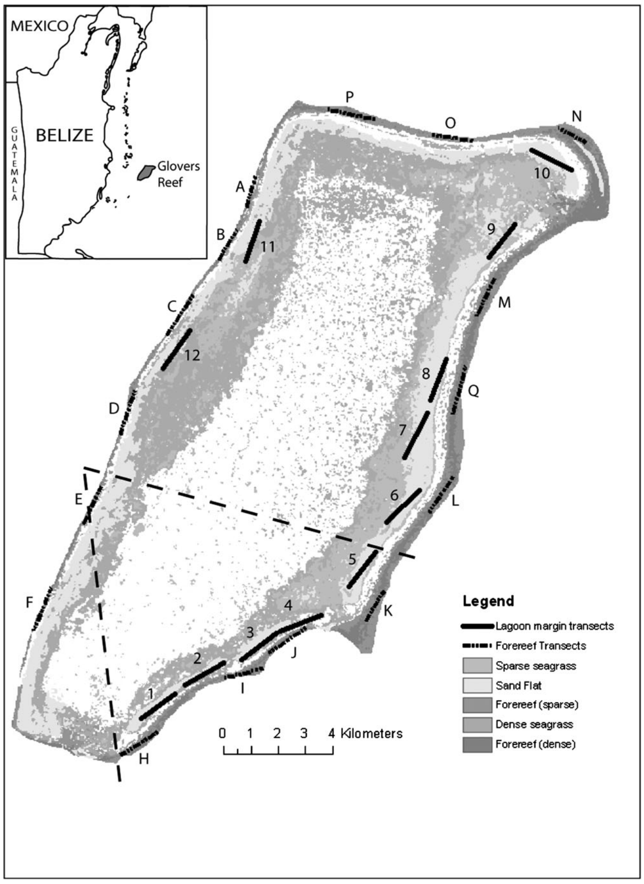

Figure 1. Map depicting location of Glovers Reef Atoll within Belize, and transect locations for lagoon margin (1–12) and forereef habitats (A–Q). The boundaries of the somewhat triangular no-take zone of the marine reserve are marked with a black dashed line.

with two observers standing on the bow of the boat, recording sightings with information on species and perpendicular distance from the transect line. Transects were conducted in conditions of up to Beaufort scale 2 to minimize sampling bias caused by poor visibility. Southern stingrays are largely sedentary and move slowly while foraging so we believe movement does not cause significant bias to detection. Cryptic stingrays buried in the sand are flushed by the boat and are observed while moving away with observers taking distance measurements to the position where the stingray was first sighted.

Forereef slope habitat was surveyed using in-water transects conducted at 16 sites around the atoll bi-annually in April and November between November 2008 and April 2010. Sites were selected by stratified systematic design with random start points to cover the full circumference of the atoll while avoiding sites too deep to sample beyond the forereef habitat. One hour swim transects were run parallel to the forereef habitat, using teams of 6–8 observers spread from ~4 m depth to the reef edge (<15 m), spaced approximately 10 m apart (Figure 2). Variations in width, depth, and visibility of forereef habitat necessitated adaptation to swimmer number and spacing, and hence effort was adjusted to ensure accurate estimates of

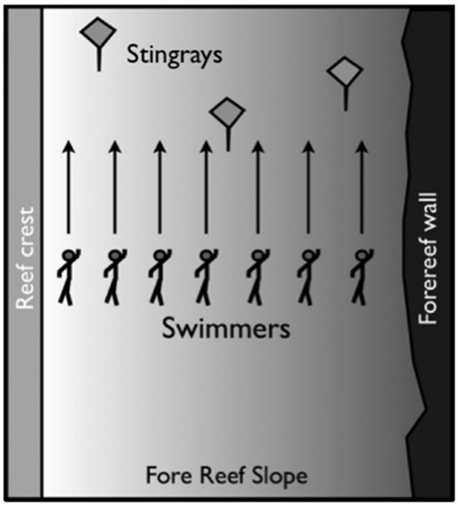

Figure 2. Diagram depicting forereef elasmobranch sampling method involving a team of 6–8 swimmers sweeping along the forereef slope parallel to the reef crest, recording individual elasmobranch encounters.

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encounter rates and density. Each swimmer counted the total number of each elasmobranch species seen during each 1 h swim period that were then totalled and recorded at the end of the 1 h period. To avoid duplicate sightings, swimmers signalled observations to the person on either side of them.

Deep lagoon habitat was surveyed using 30 min straight-line scuba transects, with two observers finning at constant speed (~40 kick cycles min^{-1}) in a west to east direction counting elasmobranch species detected. Deep lagoon transects were initially conducted monthly at two randomly selected sites in the deep lagoon (12–18 m), however, after initial findings of zero encounters of any elasmobranch species, sampling effort was decreased to bi-annual repetition in April and November (these transects are not shown in Figure 1).

Data analysis

The sampling year for the lagoon habitat was divided into three seasons based upon the reproductive cycle and gestation periods reported in the literature (Henningsen, 2000; Chapman *et al.*, 2003; Henningsen and Leaf, 2010) (Season 1 = January–April, Season 2 = May–August, Season 3 = September–December). Perpendicular distance data from lagoon margin surveys were analysed using Distance 6 (Thomas *et al.*, 2010). Encounter rate was stratified by survey season and its variance was estimated empirically using the replicate transect lines as samples. Maximum likelihood methods were used to estimate the variance of the effective strip width. Exploratory analyses were first conducted to examine options for truncation and grouping intervals to improve model fit for the detection function. Analyses where observations were stratified by season and pooled across seasons to fit the detection function were considered. Following Buckland *et al.* (2001), a variety of key functions and adjustment term combinations were considered to model the detection function (e.g. uniform + cosine or simple polynomial, half-normal + cosine or simple polynomial, hazard rate + cosine or hermite polynomial). Goodness of fit tests were used to identify violations of assumptions. Akaike's Information Criterion (AIC) was used in model selection, with particular attention paid to model fit at distances near zero since the fit of the shoulder near zero is most important for robust estimation (Buckland *et al.*, 2001). Seasonal estimates of density and abundance were obtained, as well as overall estimates obtained by taking the mean of the seasonal estimates weighted by seasonal effort with each season treated as a replicate. Seasonal density was tested for statistically significant difference at the 5% significance level using a two-sided z test.

For analysis of the forereef data no perpendicular distances were available for southern stingray observation, as sea turtles were the main target for the forereef surveys. Thus, stingray counts were adjusted to take account of imperfect detection using results from distance sampling analyses for sea turtles collected during the same surveys, where estimated detection probability was 0.50, 0.63, and 0.57 for the April 2009, November 2009 and April 2010 surveys, respectively, with an effective strip half-width of ~4–5 m. The raw encounter rates for the stingrays were adjusted using these survey-specific turtle detection probabilities. However, detection probability of stingrays on the forereef is likely to be significantly higher than values used for turtles because of the less cryptic coloration and habitat use by stingrays.

Dasyatis americana encounter rates from transects were log transformed to achieve normality and then compared using ANOVA by site (transect), time of day (am/pm), month and management type using JMP 9 statistical software (SAS Institute Inc.). Habitat areas for population estimates were calculated using ArcMap 9.3 (ESRI) using a predefined, georeferenced habitat raster map of the atoll, with total number of raster pixels for a habitat type, multiplied by the pixel area.

RESULTS

Nine species of elasmobranchs (five sharks, four batoids) were observed across all habitat surveys, with the southern stingray being the most commonly sighted species in lagoon margin and forereef habitats. During the shallow lagoon transect surveys, 846 southern stingrays, 14 nurse sharks (*Ginglymostoma cirratum)*, 9 eagle rays (*Aetobatus narinari*) and uncounted observations of yellow stingrays (*Urolophus jamaicensis*) and juvenile green and hawksbill marine turtles were recorded.

Encounter rate (rays km^{-1}) of stingray individuals by sampling season are detailed in Table 1. Encounter rates were unaffected by month (ANOVA $F = 0.88$, $df = 94$, $P = 0.54$) or time of day (ANOVA $F = 1.73$, $df = 94$, $P = 0.10$), however, significant

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Table 1. Estimates for the lagoon habitat. Seasonal stingray encounter rates ($n\ L^{-1}$) in number km^{-1} with their 95% confidence intervals (95% CI) and estimates of density ($\hat{D}$) in number km^{-2} and abundance ($\hat{N}$) for each survey season and overall with their 95% confidence intervals (95% CI) and overall percentage coefficient of variation (%CV)

Survey	$n\ L^{-1}$	95% CI	$\hat{D}$	95% CI	$\hat{N}$	95% CI	(%CV)
Season 1	5.3	(4.3–6.7)	249.28	(198.11–313.67)	8525	(6775–10 728)	10.79
Season 2	5.2	(3.4–8.0)	243.55	(157.37–376.93)	8329	(5382–12 891)	20.23
Season 3	5.2	(3.9–6.9)	240.07	(178.64–322.62)	8210	(6110–11 034)	13.62
Total			244.57	(225.56–265.19)	8364	(7714–9069)	4.11

differences were seen between sampling sites (ANOVA F = 2.84, df = 94, $P = 0.003$) with the highest mean frequencies seen at site 10, near to the main NE channel through the reef (Figure 1). Transects outside the no-take zone (sites 6–12) showed significantly higher abundance than those inside (ANOVA F = 22.29, df = 1, $P < 0.0001$).

In total, 302 *D. americana*, 162 *G. cirratum*, 67 *A. narinari*, and 20 *Carcharhinus perezi* (Caribbean reef shark) were recorded in 58 daytime hours by 6–8 swimming observers on the forereef slope (<15 m). *D. americana* was significantly more abundant than all other elasmobranchs, with an overall mean count of 3.3 ± 1.5 across all transects.

D. americana forereef counts were significantly higher in April than November (Wilcoxon signed-ranks test Z = –3.886 $P < 0.0001$), similarly for *G. cirratum* (Wilcoxon Z = –2.160 $P = 0.03$) (Figure 3).

Density estimates

For the final analysis, lagoon data were grouped into seven equal-sized intervals with truncation at 20 m (n = 802). Considering AIC values and model fit close to zero, the hazard rate with no adjustment terms fit to data pooled across seasons was selected (Figure 4). The effective strip half-width was estimated as 10.7 m with 95% confidence interval (9.9–11.6), which corresponds to an estimated detection probability of 0.54 (0.50–0.58). This indicates that the probability of detecting an individual ray within a distance of 20 m from the transect line is 0.54. Seasonal and average density and abundance estimates are shown in Table 1.

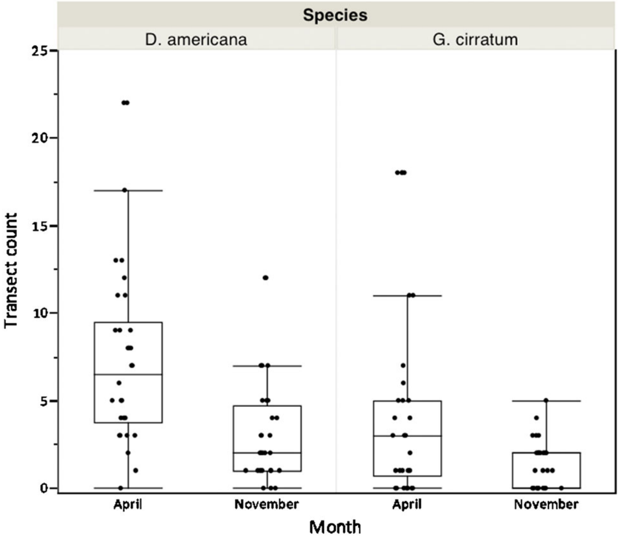

Figure 3. Counts per transect of *Dasyatis americana* and *Ginglymostoma cirratum* (black dots) from Glovers Reef forereef swim surveys conducted in April 2009 and 2010, and November 2008 and 2009. Boxplots represent lower, median and upper quartiles, with bars depicting 95% confidence intervals.

Forereef stingray encounter rates showed significant seasonal variation. Seasonal forereef density and abundance estimates adjusted using survey-specific turtle detection probabilities are shown in Table 2. Mean density across seasons (~68 rays km^{-2}) was more than three times lower than mean lagoon density.

During all scuba sampling of the deep lagoon no stingrays (or other elasmobranchs) were observed, so stingray density in this habitat was treated as zero for total atoll population calculations.

DISCUSSION

Dasyatis americana was most abundant in the shallow lagoon margins of Glovers Reef, and absent from all survey sampling in the deep lagoon. Stingray distribution was not homogenous throughout the lagoon sample sites, with higher densities outside of the no-fishing zone of the marine reserve. This is likely to be an effect of the opportunistic foraging strategy of *Dasyatis americana*, and the location of some sampling sites near to areas used regularly by fishermen to clean their catch.

Stingray density in the lagoon showed no seasonal variation, whereas significant differences in forereef encounter rates between November and April sampling phases suggests seasonality in stingray use of this habitat. Stingray population structure in lagoon margins at Glovers Reef reflects data from Atol das Rocas in Brazil

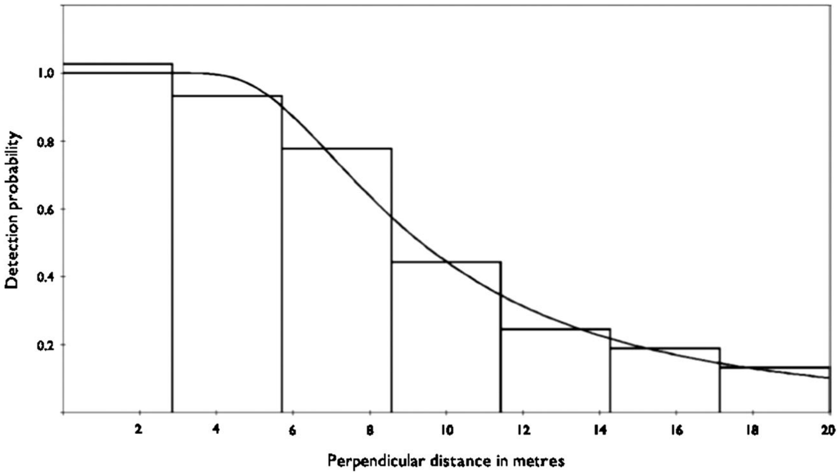

Figure 4. Detection function (hazard rate with no adjustment terms) fitted to the perpendicular distances of observations of all southern stingrays pooled across three survey seasons.

Table 2. Estimates for the forereef habitat. Seasonal stingray encounter rates ($n\ L^{-1}$) in number km^{-1} with their 95% confidence intervals (95% CI) and estimates of density ($\hat{D}$) in number km^{-2} and abundance ($\hat{N}$) for each survey season and overall with their 95% confidence intervals (95% CI) and overall percentage coefficient of variation (%CV). Distance sampling results unavailable for Nov 2008 so only encounter rate listed

Survey	$n\ L^{-1}$	95% CI	$\hat{D}$	95% CI	$\hat{N}$	95% CI	(%CV)
Nov 2008	0.37	-	-	-	-	-	-
Apr 2009	0.82	(0.60–1.13)	100.47	(71.35–141.49)	2612	(1855–3679)	17.59
Nov 2009	0.26	(0.17–0.39)	24.65	(16.23–37.41)	640	(422–973)	21.53
Apr 2010	0.74	(0.49–1.11)	78.48	(52.93–116.36)	2040	(1376–3025)	20.29

(Carvalho *et al.*, 2010), with females dominating the population by 3:1; forereef sex ratios did not differ from 1:1 (Tilley, unpubl. data). This implies reproduction may drive habitat selection of female rays, utilizing shallow areas for mating or parturition, as suggested by Pikitch *et al.* (2005) following sightings of neonates and pregnant sharks in shallow lagoon margins. Parturition in wild southern stingrays has been observed in shallow sand flats in late August and early September in the Cayman Islands (Chapman *et al.*, 2003), yet as lagoon densities showed no seasonal variation, it seems unlikely that there is significant movement between lagoon and forereef areas. Increased water temperatures have been seen to correlate with greater elasmobranch abundance in shallow areas (Heithaus, 2001; Vaudo and Heithaus, 2011), yet acoustic tracking of *D. americana* in a separate study at Glovers Reef suggests they utilize small home ranges and are highly resident to specific areas (Tilley, unpubl. data), indicating immigration into the atoll population is likely to be low.

A detection probability of 0.54 indicates that approximately half of the stingrays present in the sampled areas either side of the transect lines in the shallow lagoon margin were observed during surveys. Stingrays were far more abundant than any other elasmobranch at Glovers Reef, and such a dense population of rays is likely to have significant influence in structuring prey communities, substantially affecting commercially important decapods (Mintz *et al.*, 1994) and driving the population dynamics of other prey species (Dale, 2011). Fluctuations in ray population density may have knock-on effects throughout the trophic system if strong interactions exist with certain prey species (O'Gorman and Emmerson, 2009). Recent research highlights the significant top down control of predatory sharks in their ecosystems through indirect influence over prey movements and habitat selection (Frid *et al.*, 2008; Heithaus *et al.*, 2008), and the connections made to batoid population dynamics remain contentious with suggestions such as 'Eat a ray, save the bay' (Berlin, 2011). Further studies investigating the interaction of rays and apex predators in the Caribbean will bring greater understanding of the importance of these large elasmobranchs in reef systems.

Many recent studies of elasmobranchs have utilized visual tagging (Farrugia *et al.*, 2011) or natural markings (Castro and Rosa, 2005; Marshall *et al.*, 2011) to estimate population size with

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mark–recapture techniques. Distance sampling has the advantage over these methods in eliminating potential biases associated with heterogeneity in capture probabilities and requiring only a single sampling session. Detection probability of rays in lagoon margin habitat at Glovers Reef may vary with substrate type (seagrass and sand), and is also complicated by cryptic behaviour of rays burying in sand, however, distance sampling takes account of imperfect detectability and variations in detectability in different substrates given consistent application of the method in the field, and provides an average detection probability across those habitats. Cryptic burial in sand would be a problem if rays were missed on the transect line – as this violates a key assumption and may cause underestimation of ray density and abundance. In this case, it is unlikely to affect stingray estimates due to the shallow water depth and short stingray flight distances observed during sampling, as rays directly under the boat are 'flushed out' and recorded. The distance recorded was to the initial position of the ray before movement to avoid negatively biased estimates that arise when perpendicular distances are consistently overestimated due to movement away from the boat.

The lack of perpendicular distance estimates for forereef stingray transects decreases the robustness of total atoll population calculations. Nonetheless, based on the detection probability of turtles using data collected simultaneously, total encounter rates and density estimates for stingrays were far lower than lagoon habitats. Incorporating in-water distance sampling techniques in future monitoring will bring greater accuracy to atoll population estimates, and provide a powerful tool for conservation managers in identifying community fluctuations. This study illustrates that distance sampling can be effectively utilized as a non-invasive technique to estimate abundance of shallow water elasmobranchs. As many elasmobranchs utilize shallow water habitats during certain life stages for reproduction or as juvenile nursery grounds (Heupel *et al.*, 2007), where conservation is of prime importance, this technique will provide an effective management tool for low impact monitoring of species that return to natal areas. This study provides important baseline information on population size and density of stingrays on Glovers Reef Atoll, facilitating further studies on their population dynamics and demonstrating a tool for conservation managers to monitor the health of shallow water elasmobranchs in light of their global decline.

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REFERENCES

Berlin J. 2011. Eat a Ray, Save the Bay? [Online]. 5 January 2011. National Geographic Magazine Blog. Available from: http://blogs.ngm.com/blog_central/2011/01/eat-a-ray-save-the-bay.html. [Accessed: 1 December 2011].

Bizzarro JJ, Smith WD, Fernando Marquez-Farías J, Hueter RE. 2007. Artisanal fisheries and reproductive biology of the golden cownose ray, *Rhinoptera steindachneri* Evermann and Jenkins, 1891, in the northern Mexican Pacific. *Fisheries Research* **84**: 137–146.

Buckland S, Anderson DR, Burnham K, Laake J, Borchers D, Thomas L. 2001. *Introduction to Distance Sampling: Estimating Abundance of Biological Populations*. Oxford University Press: Oxford.

Carvalho F, Oliveira P, Hazin F, Piercy A, Burgess G. 2010. Population structure and habitat utilization of the southern stingray *Dasyatis americana* (Hildebrand and Schroeder, 1928) at the Atol das Rocas Biological Reserve, Brazil. *Brazilian Journal of Oceanography* **59**: 104–111.

Castro A, Rosa RS. 2005. Use of natural marks on population estimates of the nurse shark, *Ginglymostoma cirratum*, at Atol das Rocas Biological Reserve, Brazil. *Environmental Biology of Fishes* **72**: 213–221.

Chapman DD, Corcoran M, Harvey G, Malan S, Shivji MS. 2003. Mating behavior of southern stingrays, *Dasyatis americana* (Dasyatidae). *Environmental Biology of Fishes* **68**: 241–245.

CONAPESCA-INP. 2004. Plan de Acción Nacional para el Manejo y Conservación de Tiburones, Rayas y Especies Afines en México. Comisión Nacional de Acuacultura y Pesca e Instituto Nacional de la Pesca, Secretaría de Agricultura, Ganadería, Desarrollo Rural, Pesca y Alimentación, Mazatlán, México.

Dale J. 2011. Life history, foraging ecology, metabolic rates and bioenergetics of the brown stingray, *Dasyatis lata*. PhD thesis. University of Hawaii.

Farrugia TJ, Espinoza M, Lowe C. 2011. Abundance, habitat use and movement patterns of the shovelnose guitarfish (*Rhinobatos productus*) in a restored southern California estuary. *Marine and Freshwater Research* **62**: 648–657.

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Francis M. 1998. New Zealand shark fisheries: development, size and management. *Marine and Freshwater Research* **49**: 579–591.

Frid A, Baker G, Dill LM. 2008. Do shark declines create fear-released systems? *Oikos* **117**: 191–201.

Garro A, Vargas R, Zanella I, Le Foulgo L. 2009. Análisis de las capturas de tiburones y rayas en las pesquerías artesanales de tárcoles, pacífico central de Costa Rica. *Revista Ciencias Marinas y Costeras* **1**: 145–157.

Gilliam D, Sullivan K. 1993. Diet and feeding habits of the southern stingray *Dasyatis americana* in the central Bahamas. *Bulletin of Marine Science* **52**: 1007–1013.

Grijalba-Bendeck M, Polo-Silva C, Acero A. 2007. Una aproximación a la abundancia de los Batoideos capturados artesanalmente en Santa Marta (Colombia). *Boletín de investigaciones Marinas y Costeras* **36**: 251–268.

Heithaus M. 2001. The biology of tiger sharks, Galeocerdo cuvier, in Shark Bay, Western Australia: sex ratio, size distribution, diet, and seasonal changes in catch rates. *Environmental Biology of Fishes* **61**: 23–36.

Heithaus M, Wirsing AJ, Thomson JA, Burkholder DA. 2008. A review of lethal and non-lethal effects of predators on adult marine turtles. *Journal of Experimental Marine Biology and Ecology* **356**: 43–51.

Henningsen A. 2000. Notes on reproduction in the Southern Stingray, *Dasyatis americana* (Chondrichthyes: Dasyatidae), in a captive environment. *Copeia* **3**: 826–828.

Henningsen A, Leaf R. 2010. Observations on the captive biology of the Southern Stingray. *Transactions of the American Fisheries Society* **139**: 783–791.

Heupel M, Bennett MB. 2007. Estimating abundance of Reef-dwelling Sharks: a case study of the Epaulette Shark, *Hemiscyllium ocellatum* (Elasmobranchii: Hemiscyllidae). *Pacific Science* **61**: 383–394.

Heupel M, Carlson J, Simpfendorfer CA. 2007. Shark nursery areas: concepts, definition, characterization and assumptions. *Marine Ecology Progress Series* **337**: 287–297.

Hildebrand S, Schroeder W. 1928. *Fishes of Chesapeake Bay*. United States Fish and Wildlife Service. Fishery Bulletin 43, part 1: Washington DC. 366p.

Hoenig J. 1990. Life-history patterns in the elasmobranchs: implications for fisheries management. NOAA Technical Report NMFS.

Kulbicki M, Sarramégna S. 1999. Comparison of density estimates derived from strip transect and distance sampling for underwater visual censuses: a case study of Chaetodontidae and Pomacanthidae. *Aquatic Living Resources* **12**: 315–325.

Le Port A, Lavery S. 2012. Population structure and phylogeography of the Short-Tailed Stingray, *Dasyatis brevicaudata* (Hutton 1875), in the southern hemisphere. *Journal of Heredity* **103**: 174–185.

Lohrer A, Thrush SF, Gibbs M. 2004. Bioturbators enhance ecosystem function through complex biogeochemical interactions. *Nature* **431**: 1092–1095.

Marshall AD, Dudgeon CL, Bennett MB. 2011. Size and structure of a photographically identified population of manta rays *Manta alfredi* in southern Mozambique. *Marine Biology* **158**: 1111–1124.

Mintz J, Lipcius R, Eggleston D, Seebo M. 1994. Survival of juvenile caribbean Spiny Lobster - effects of shelter size, geographic location and conspecific abundance. *Marine Ecology Progress Series* **112**: 255–266.

Myers RA, Worm B. 2003. Rapid worldwide depletion of predatory fish communities. *Nature* **423**: 280–283.

O'Gorman E, Emmerson M. 2009. Perturbations to trophic interactions and the stability of complex food webs. *Proceedings of the National Academy of Sciences* **106**: 13393–13398.

O'Shea O, Thums M, van Keulen M. 2011. Bioturbation by stingrays at Ningaloo Reef, Western Australia. *Marine and Freshwater Research* **63**: 189–197.

Pikitch E, Chapman DD, Babcock E, Shivji MS. 2005. Habitat use and demographic population structure of elasmobranchs at a Caribbean atoll (Glover's Reef, Belize). *Marine Ecology Progress Series* **302**: 187–197.

Piovano S, Clò S, Giacoma C. 2010. Reducing longline bycatch: the larger the hook, the fewer the stingrays. *Biological Conservation* **143**: 261–264.

Randall J. 1967. *Food Habits of Reef Fishes of the West Indies*. Studies in Tropical Oceanography: Miami **5**: 665–847.

Smith K, Herrnkind W. 1992. Predation on early juvenile spiny lobsters *Panulirus argus* (Latreille): influence of size and shelter. *Journal of Experimental Marine Biology and Ecology* **157**: 3–18.

Smith WD, Cailliet GM, Cortés E. 2008. Demography and elasticity of the diamond stingray, *Dasyatis dipterura*: parameter uncertainty and resilience to fishing pressure. *Marine and Freshwater Research* **59**: 575.

Steneck R, Sala E. 2005. Large marine carnivores: trophic cascades and top-down controls in coastal ecosystems past and present. In *Large Carnivores and the Conservation of Biodiversity*, Ray J, Redford K, Steneck R, Berger J (eds). Island Press: Washington DC. 110–137.

Stevens J, Bonfil R, Dulvy NK, Walker P. 2000. The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystems. *ICES Journal of Marine Science* **57**: 476–494.

Thomas L, Buckland ST, Rexstad EA, Laake JL, Strindberg S, Hedley SL, Bishop JRB, Marques TA, Burnham KP. 2010. Distance software: design and analysis of distance sampling surveys for estimating population size. *Journal of Applied Ecology* **47**: 5–14.

Thrush SF, Pridmore R, Hewitt J, Cummings V. 1991. Impact of ray feeding disturbances on sandflat Macrobenthos - do communities dominated by Polychaetes or shellfish respond differently. *Marine Ecology Progress Series* **69**: 245–252.

Vaudo J, Heithaus M. 2011. Dietary niche overlap in a nearshore elasmobranch mesopredator community. *Marine Ecology Progress Series* **425**: 247–260.

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