



# Top predators induce habitat shifts in prey within marine protected areas

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## Abstract

Emerging conservation efforts for the world's large predators may, if successful, restore natural predator–prey interactions. Marine reserves, where large predators tend to be relatively common, offer an experimental manipulation to investigate interactions between large-bodied marine predators and their prey. We hypothesized that southern stingrays—large, long-lived and highly interactive mesopredators—would invest in anti-predator behavior in marine reserves where predatory large sharks, the primary predator of stingrays, are more abundant. Specifically, we predicted southern stingrays in marine reserves would reduce the use of deep forereef habitats in the favor of shallow flats where the risk of shark encounters is lower. Baited remote underwater video was used to survey stingrays and reef sharks in flats and forereef habitats of two reserves and two fished sites in Belize. The interaction between “protection status” and “habitat” was the most important factor determining stingray presence. As predicted, southern stingrays spent more time interacting with baited remote underwater videos in the safer flats habitats, were more likely to have predator-inflicted damage inside reserves, and were less abundant in marine reserves but only in the forereef habitat. These results are consistent with a predation-sensitive habitat shift rather than southern stingray populations being reduced by direct predation from reef sharks. Our study provides evidence that roving predators can induce pronounced habitat shifts in prey that rely on crypsis and refuging, rather than active escape, in high-visibility, heterogeneous marine habitats. Given documented impacts of stingrays on benthic communities it is possible restoration of reef shark populations with reserves could induce reef ecosystem changes through behavior-mediated trophic cascades.

**Keywords** Marine reserves · Behaviorally mediated interactions · Reef sharks · Risk effects · Stingrays

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## Introduction

Human-induced declines in the abundances of top predators on land and in oceans are a nearly ubiquitous disturbance to ecosystems (Ferretti et al. 2010; Estes et al. 2011; Ripple et al. 2014). There remain, however, important questions about how the strength and nature of the impacts of predator removals will cascade through ecosystems. Answering such questions is particularly important as conservation and management practices begin to shift from protecting remnant populations to rebuilding populations of both predators and their prey. Rebuilding populations of mesopredators or primary consumers that can have large impacts on ecosystem structure and function (e.g. sea turtles, stingrays) in the absence of top predators may have negative unintended consequences for terrestrial and marine ecosystems (Soulé et al. 2005; Heithaus et al. 2014; Atwood et al. 2015).

While most of our understanding of the ecological importance of large predators has come from changes induced in ecosystems following declines or even extirpation of these species, the effects of restoring predator populations can also be informative. For example, the reintroduction of wolves to Yellowstone National Park has provided an intriguing opportunity to examine what effect restoring apex predators has directly on prey species and indirectly the whole ecosystem across a large-scale (Beschta and Ripple 2006; Ripple and Beschta 2006). Initial studies suggested that the presence of wolves had relatively rapid and widespread positive impacts on ecosystem function through predator-induced changes in elk behavior (“risk effects”, Laundré et al. 2001; Creel and Christianson 2008; Ripple and Beschta 2012). Recent studies, however, suggest that these non-consumptive mechanisms may provide weaker indirect links between wolves and primary producers (i.e. a weak behavior-mediated trophic cascade, BMTC; Kauffman et al. 2013; Winnie Jr 2014), than initially thought (e.g. Kauffman et al. 2010; Winnie Jr 2012). The lack of strong behaviorally mediated trophic cascades (BMTC) has been linked to the fact that wolves, as roving predators, are expected to have lesser impacts on the behavior of their prey (elk) because the spatial pattern of risk is less predictable, rendering anti-predator behavior less effective (Preisser et al. 2007; Schmitz 2008; Kauffman et al. 2010). This view of weak non-consumptive impacts of roving top predators is supported by experimental studies in relatively homogenous habitats (e.g. Preisser et al. 2007). Field studies in large-scale and heterogeneous marine systems, however, suggest that roving predators can induce strong risk effects in prey (e.g. Heithaus et al. 2009, 2012) that can cascade to primary producer communities (Burkholder et al. 2013). Determining whether risk effects are generally widespread in ecological communities, and the conditions under which they might be expected is particularly important for predicting ecosystem responses to the loss or restoration of top-predator populations and those of their prey (e.g. Cowlshaw 1997; Ripple and Beschta 2012; Heithaus et al. 2008a, b, 2009).

Marine reserves, defined here as marine management zones where all extractive and depositional activities are prohibited (Sobel and Dahlgren 2004), frequently have a positive effect on large exploited predators within their boundaries (Edgar et al. 2014). Marine reserves thus provide an experimental framework for elucidating risk effects. Studies that address the potential for roving marine top predators (e.g. large sharks and marine mammals) to induce risk effects on mobile mesoconsumers (e.g. smaller elasmobranchs, large-bodied herbivores) are important for building a predictive framework of community dynamics (Heithaus et al. 2008b). Such studies are rare (Mumby et al. 2006; Wirsing et al. 2008; Rizzari et al. 2014), especially from heterogeneous coral reef habitats that are ecologically and

economically important (Moberg and Folke 1999; Bellwood et al. 2004). Additionally, coral reefs feature clear waters that might reduce the strength of risk effects because prey can visually detect predators from long distances (Burkholder et al. 2013; Wirsing et al. 2014). Furthermore, studies of top predators on reef habitats are important because of ongoing threats to their populations and uncertainty about their ecological importance in these habitats (Roff et al. 2016a).

Batoids (rays and skates) are common coastal mesopredators, which can structure benthic communities and ecosystems through the removal of invertebrate prey and bioturbation (Peterson et al. 2001; Heithaus et al. 2010; Ajemian et al. 2012). Since stingrays are generally long-lived with low fecundity (Musick 1999; McEachran 2002; Dulvy et al. 2014), they are predicted to invest heavily in anti-predator behavior (see Werner 1998; Frid et al. 2012). Southern stingrays (*Hypanus americanus*), for example, can avoid predators, which are primarily large sharks, through crypsis (e.g. burying themselves in sediment), a tactic that likely is less effective in clear water on coral reefs when compared to turbid coastal areas. They can also flee but have limited maneuverability and swimming speed compared to some predatory sharks (e.g. great hammerheads, *Sphyrna mokarran*, Strong et al. 1990). Southern stingray foraging also likely limits their ability to visually detect predators due to the occurrence of sediment plumes, which could also attract predators in clear water (Semeniuk and Dill 2005; Wirsing et al. 2007). Southern stingrays also refuge from predators in shallow or structurally complex microhabitats such as patch reefs or shipwrecks (Strong et al. 1990; Tilley et al. 2013b). These traits all suggest that southern stingrays living in clear water should invest in reducing encounter rates with sharks rather than relying entirely on flight behavior in response to the immediate presence of a shark (see Wirsing et al. 2010). As a result, we would expect southern stingrays to exhibit shifts into safer habitats if there is predictable spatial variation in reef shark encounter rates (e.g. Heithaus et al. 2009).

Belize, Central America, has developed a network of marine reserves that encompass parts of its coast, offshore atolls and the Mesoamerican Barrier Reef (MBR) (Gibson 2003). Southern stingrays (hereafter referred to as “stingrays”) are the most common large ray species observed in both flats and reef habitats in Belize (Bigelow and Schroeder 1948). Other benthic batoid species encountered in Belize include yellow stingrays (*Urobatis jamaicensis*) and Caribbean whiptail (*Styracura schmardae*). In addition to new fisheries legislation prohibiting the landing of rays, stingrays have never been targeted by any fishery (commercial, artisanal, or recreational), and would, therefore, not be expected to directly respond to reserve establishment. In contrast, Caribbean reef sharks (*Carcharhinus perezi*, hereafter referred to as “reef sharks”), a potential stingray predator, are part of the landings of an active fishery (Castro 1983; Michael

2005; Pikitch et al. 2005). Reef sharks are the numerically dominant large-bodied shark species in these ecosystems (Bond et al. 2017) and are more abundant inside certain well established and enforced marine reserves than similar fished reefs in Belize (Bond et al. 2012). Reef sharks have a wide depth range and use both lagoon, back reef and forereef habitats but they are rare in shallow reef flat habitats (Pikitch et al. 2005; Bond et al. 2012). Therefore, the network of protected and unprotected waters of Belize provides an experiment to examine effects of reef sharks on stingrays because there are deep forereef habitats with relatively high or low shark densities (reserves and fished sites, respectively) that are adjacent to shallow reef flat habitat where encounter rates with reef sharks are always low. The goal of our study was to determine whether fished areas create “fear-released systems” (sensu Frid et al. 2007) that allow mesopredators (southern stingrays) to expand their use of deep reef habitats that would normally be avoided because of higher predation risk from potential predators (Caribbean reef sharks). We assessed Caribbean reef shark and southern stingray abundance across reef flats and deep forereefs of multiple fished and unfished habitats to test a priori hypothesis about the potential drivers, including predation risk, of southern stingray habitat use (Figure S1).

## Methods

Detailed descriptions of study species and sites can be found in ESM 1.

### Baited remote underwater video (BRUV) deployments

Reef shark and southern stingray abundance were surveyed on the fore-reef and the flats at all four sites Glover’s Reef Marine Reserve (GRMR), Caye Caulker Marine Reserve (CCMR), Turneffe Atoll (TU), and Southwater Caye (SC) using baited remote underwater video (BRUV). We focused our analysis on southern stingrays because they were the most commonly observed stingray species and they were recorded in flats and reef habitat at all sites. For more detail on BRUV design, deployment, and analysis methodology refer to Bond et al. (2012) and the ESM.

### Environmental and benthic habitat surveys

Spatial variation in the environmental factors measured during each BRUV deployment (temperature, flow velocity, dissolved oxygen, salinity, and conductivity) across like habitats between all four sites was tested with ANOVAs. Benthic habitat surveys were conducted on the forereef at each site to determine if there was variation in the mean

amount and distribution of soft sediment available for stingrays to bury and forage in. All flats were almost exclusively soft sediment interspersed with seagrass, so they were not surveyed. Within each forereef site, 100 randomly generated GPS points were sampled by photographing a weighted PVC square (1.5 m<sup>2</sup>) that was dropped on the substrate. Each photograph was scored by its percentage of soft substrate. Soft substrate values were arcsine square-root transformed prior to analysis (Jordan et al. 2010). Survey areas were plotted in ArcGIS™ and mean amount of soft sediment per site quantified from the photos was used to estimate the percentage of soft substrate within each sample site. Additionally, each sample value was binned into one of three categories in accordance with the percentage soft substrate it contained: 0–33%; 33–66% and 66–100%. The number of samples within each category was tested between sites using a Pearson’s Chi-squared ( $\chi^2$ ) test in the R software (R Core Team 2016).

### BRUV analysis

Since BRUV observation data were zero-inflated, a conditional approach (Serafy et al. 2007) was taken to analyze the abundance and distribution of stingrays with respect to protection status (reserve or fished) and habitat (forereef or flat). To examine which predictor variables had a significant influence on southern stingray presence (i.e. occurrence) we used a binomial generalized linear model (GLM) with a logit-link (i.e. a logistic regression), and the factors year, reef shark presence, habitat, protection status, location, with location nested within protection status, and the interaction between protection status and habitat. A backwards elimination approach was applied and factors with *p* values > 0.05 were sequentially removed. A log-link GLM was then constructed to test how these factors and associated interactions influenced southern stingray abundance when present (i.e. concentration). Finally, an index of relative abundance was generated from the product of the GLM predicted southern stingray occurrence and concentration values for each site and habitat sampled (Lo et al. 1992). In addition, the influence of protection status, habitat, and location, with location nested within protection status, on reef shark presence was also analyzed by fitting a logistic regression. All models were fitted with the R software using the MASS4 library (Venables and Ripley 2002; R Core Team 2016).

### Stingray appearance and behavior

In addition to testing predictions of the hypothesis that southern stingrays are inhibited from using deep forereef habitat where reef sharks are common we also tested the hypotheses that (1) predation risk is higher in reserves and (2) predation risk is lower on flats. For the former, all

southern stingrays observed on BRUVs that were close enough to observe their whole body were assigned to one of two appearance classes: “undamaged” or “damaged.” The latter class included individuals missing tails (likely to be caused by a predation attempt) or with shark bite scars (crescent-shaped wounds or tooth marks). Appearance class was analyzed using logistic regression that examined the influence of protection status, location nested within protection status, habitat, and the interaction between habitat and protection status on “stingray damage”. Backwards elimination was used to remove non-significant interactions and factors. We predicted that the factor “reserve” would positively influence the incidence of “stingray damage” given the higher abundance of reef sharks in these zones previously documented (Bond et al. 2012). Because foragers are expected to reduce foraging time or cease foraging at higher remaining food densities as the risk of predation increases (see Brown and Kotler 2004), we predicted that southern stingrays would cease interacting with the bait cage sooner as the probability of encountering sharks increased. We defined “bait interaction time” as the time from first contact with the bait cage to the time the southern stingray moved > 3 body lengths from the bait cage. Duration data were log-transformed prior to analysis. We predicted that bait interaction time would be longer in duration in safer flats habitat than more dangerous forereefs.

A potential alternative mechanism to explain higher relative abundances of stingrays on the flats compared with forereef habitat could be that the shallow water flats serve as a nursery area for juveniles. To determine if differences in southern stingray relative abundance between habitats could be driven by one habitat serving as a nursery we estimated individuals disc width using the bait cage as a scale bar. An analysis of variance was performed on these estimated disc-width data to determine if there was a significant difference in southern stingray mean disc width between habitats at each site.

### Boat-based transects

BRUVs do not directly measure density so we also used 500 × 20 m belt transects positioned over flats of two sites (one fished, “SC”; one reserve, “GRMR”). Observers ( $n = 6–10$ ) were positioned facing out from an 8.5 m skiff, traveling at 6 km h<sup>-1</sup>, and were assigned a fixed field of view to survey within 10 m of the boat. The start location and survey direction were randomly generated within the same flats survey area where BRUVs were deployed. Each observer independently recorded the number of stingrays they observed throughout the survey and the mean number across all observers for each side of the vessel was calculated. On the rare occasion, a stingray fled under the boat one was deducted from the mean of the opposite side to ensure

it was not counted twice. Surveys were conducted between 12:00 and 13:00 to minimize surface glare, at wind speeds < 18 km h<sup>-1</sup> and cloud cover < 30%. Negative relationships between reef shark and ray densities could be driven by direct predation of sharks on rays, or by anti-predatory behavior (e.g. avoidance) of rays in high shark areas (i.e. forereef habitats in reserve sites). Both mechanisms could lead to a shift in proportionally fewer stingrays in forereef habitats in reserves. However, if direct predation alone was driving this pattern, then we would expect to observe an overall reduction in stingray densities between reserve and fished sites, driven by predators reducing prey densities on reserve sites. An independent *t* test was used to determine if there were any significant differences in stingray densities between the flats of one reserve and one fished site (GRMR and SC, respectively).

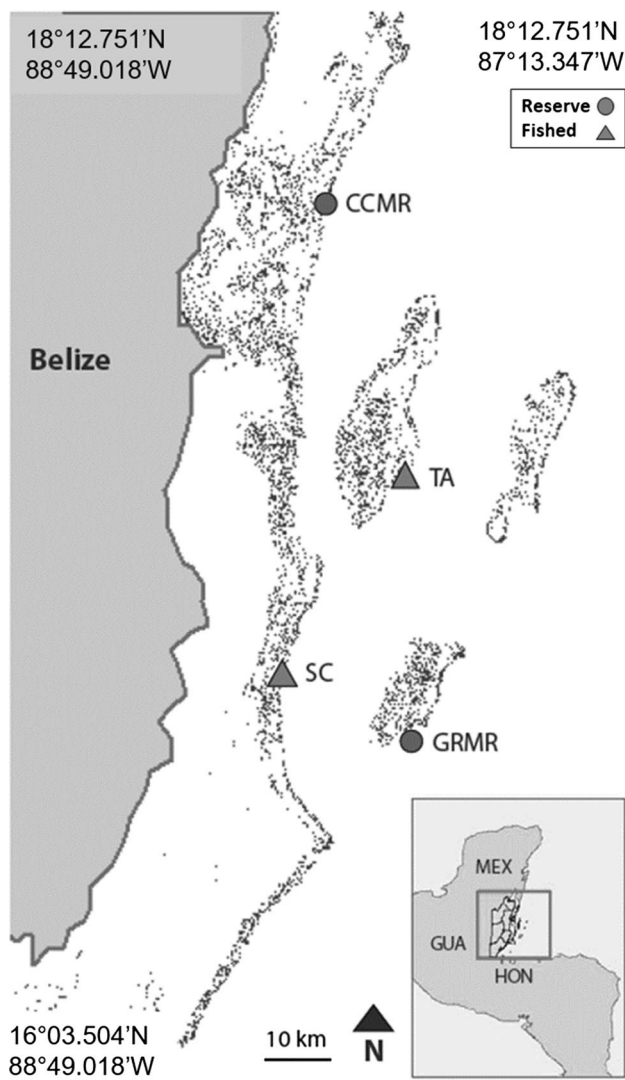
## Results

There were no significant differences in temperature, flow velocity, dissolved oxygen, salinity, and conductivity, between locations across like habitats (see Tables S1 and S2). Because tidal ranges are generally 0.1–0.2 m throughout Belize (Kjerfve et al. 1982), tide state was not specifically measured; however, because BRUVs and boats could only operate in waters greater than 1.75 m depth, all sampling occurred in waters accessible to sharks capable of preying upon rays. There was no significant difference between sites in the mean percentages of soft substrate (a proxy for resting/refuge area and prey abundance) on the fore-reef ~ 2.13, 2.46, 2.5, 2.41 km<sup>2</sup> for GRMR, CCMR, TA, and SC, respectively. The proportion of sites in each category of sand cover (0–33%, 33–66% and 66–100%) was similar across fore reef sites (see Figure S2). Abiotic factors are, therefore, unlikely to be responsible for observed patterns and were excluded from further analysis.

A total of 826 BRUV deployments (totaling 70,210 min) were made between May and July 2009–2013 (Table S3). Sampling year had a significant influence on southern stingray presence, however, when examined in detail this was due to an anomalous year in 2012, in which we had uncharacteristically low sampling effort due to adverse weather conditions, therefore, 2012 was excluded from further analysis (Table S4).

Inside reserves on the fore-reef, reef sharks ( $n = 94$ ) and southern stingrays ( $n = 30$ ) were observed on 33.8% and 15.2% of BRUV deployments, respectively, with 5 out of 30 BRUVs (16.7%) observing multiple stingrays. On fished reefs on the fore-reef, reef sharks ( $n = 18$ ) and southern stingrays ( $n = 110$ ) were observed on 9% and 56% of BRUV deployments, respectively, with 28 out of 110 BRUVs (25.5%) observing multiple stingrays (Table S5).





**Fig. 1** Location of study sites along the Mesoamerican Barrier Reef of Belize, Central America. Glover’s Reef (GRMR, atoll) and Caye Caulker (CCMR, barrier) are marine reserves (circles) and Turneffe Atoll (TA, atoll) and South water Caye (SC, barrier) are fished (triangles)

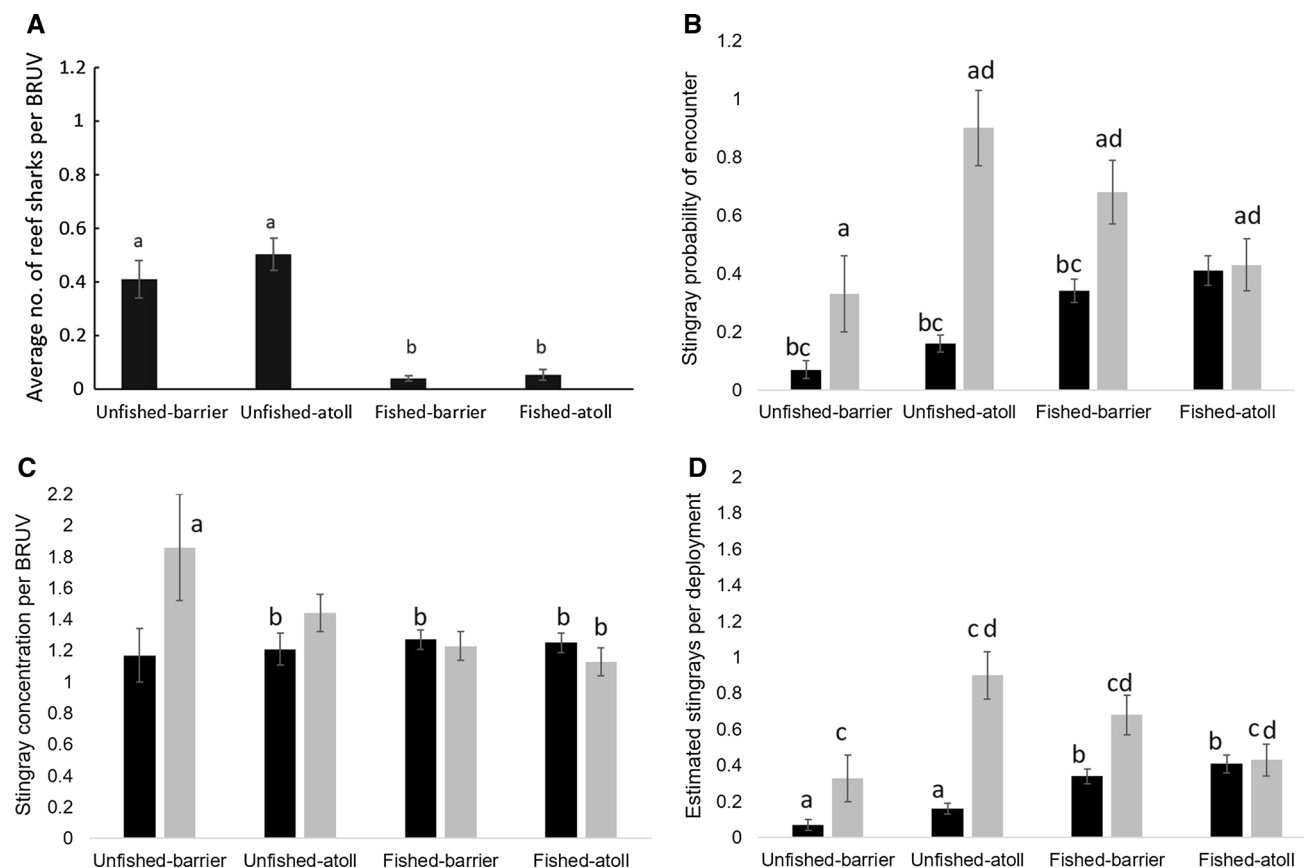
No BRUV deployed at a fished site ever observed multiple sharks, whereas 31 of the 94 BRUVs inside reserves that recorded sharks contained 2–4 individuals (32.9%). During the study we observed other large-bodied shark species at forereef sites including *Galeocerdo cuvier* ( $n = 1$ ; SC), *Negaprion brevirostris* ( $n = 1$ ; TA), and *S. mokarran* ( $n = 1$ ; CCMR). Additional batoid species observed on the BRUVs were yellow stingray, Caribbean whiptail ray, and spotted eagle ray (*Aetobatus narinari*), however, the inconsistency of observations across all sites and habitats resulted in these species being excluded from any analyses (Fig. 1).

The probability of sighting at least one reef shark was influenced by protection status, habitat and the interaction of habitat and protection status (Table 1, Fig. 2a). Reef sharks were absent from all flats BRUVs ( $n = 160$ ) and were more than four times more likely to be present along protected fore-reefs than those that are fished. The probability of observing at least one southern stingray on a BRUV varied with all the main effects: protection status, location nested within protection status, habitat, reef shark presence on a particular BRUV, and the interaction between habitat and protection status (Table 1, Fig. 2). However, the backwards elimination final model included the factors of habitat, protection status and their interaction only. Flats had higher probabilities of occurrence than forereefs across all sites, and the probability of detecting a southern stingray was significantly higher on fore-reefs of fished sites than forereefs of unfished sites (Table S6). The mean number of stingrays seen on BRUVs that detected at least one stingray (concentration) were higher on the fore-reef of the fished reefs (1.23 and 1.25 for SC and TA, respectively) compared with unfished forereefs (1.17 and 1.21 for GRMR and CCMR, respectively, Table S6). Southern stingray concentration values followed a similar pattern to the occurrence metrics. The CC flats recorded the highest mean concentration of stingrays across all sites and habitats. The predicted index of abundance values reflected similar patterns of abundance and distribution to those of occurrence and concentration

**Table 1** Results of GLM analysis on the influence of the factors protection status (MPA), location nested within protection status, habitat, and associated interactions on (1) reef shark occurrence and (2) stingray occurrence and concentration with the additional factor of reef shark presence

Factor	Reef sharks			Stingrays			Concentration		
	Occurrence			Occurrence					
	F	df	p	F	df	p	F	df	p
MPA	105.7	1	<b>&lt;0.001</b>	21.9	1	<b>&lt;0.001</b>	0.14	1	0.24
Shark pres.	–	–	–	4.3	1	<b>0.04</b>	0.1	1	0.32
Habitat	46.8	1	<b>&lt;0.001</b>	32.1	1	<b>&lt;0.001</b>	0.02	1	0.6
MPA/location	2.91	2	0.06	14.7	2	<b>&lt;0.001</b>	0.05	2	0.78
MPA:habitat	28.3	1	<b>&lt;0.001</b>	8.5	1	<b>&lt;0.001</b>	0.44	1	<b>0.03</b>
n	826			826			209		
Adj. R <sup>2</sup>	0.19			0.1			0.04		

Results in bold indicate significant factors that were selected with a backwards elimination approach of factors ( $p$  values >0.05)



**Fig. 2** Reef shark abundance data (a), and southern stingray model results (b–d) from BRUVs for all years combined ( $N=826$ ) presented by habitat, for the fore reef (black,  $N=666$ ) and lagoon (grey,  $N=160$ ): **a** Average number of reef sharks observed across all

BRUVs ( $\pm$ SE), **b** stingray probability of encounter ( $\pm$ SE), **c** stingray mean ( $\pm$ SE) abundance when present, **d** stingray abundance index ( $\pm$ SE). Letters above bars indicate significant differences between sites and/or habitats

(Fig. 2). Mean index of abundance values were consistently highest on the fore-reef of fished reefs and the flats of all sites. Predicted index of abundance values for the flats inside marine reserves were greater than those of fished reef flats. The mean density ( $\pm$ SD) of stingrays observed on the boat-based transects was also significantly higher for the reserve flat (GRMR,  $n=45$  transects,  $3.88 \pm 0.46$  stingrays per  $0.005 \text{ km}^2$ ) than the fished flat (SC,  $n=40$  transects,  $1.52 \pm 0.26$  stingrays per  $0.005 \text{ km}^2$ ;  $t(41)=8.4$ ,  $p<0.001$ ). It should be noted that eagle-rays were observed during boat transect surveys and were easily excluded from analyses, however, it is possible that a Caribbean whiptail ray may have been mis-identified as a southern stingray and included in the counts.

Based on estimated disc-width, all southern stingrays were generally large. Stingrays observed on the flats were on average,  $\sim 20\%$  larger disc-widths, than forereef rays (Table S7). When examining southern stingray disc widths between habitats at each site only GRMR showed any significant difference ( $p<0.001$ ), with stingrays significantly larger on the flats.

Of 271 individual stingrays observed adequately to determine the presence or absence of damage, (20%) had lost a tail ( $n=65$ ) or exhibited a shark bite scar ( $n=2$ , Figure S3). The probability of a southern stingray having damage was significantly influenced by protection status, and habitat ( $F_{1,1}=26.9$ ,  $p<0.01$ ;  $F_{1,1}=5.5$ ,  $p<0.01$ ) but the interaction between protection status and habitat was not significant. Damage was three times more likely to occur in marine reserves (36% of individuals) than fished areas (11.6%). Stingrays observed on the flats were significantly more likely to show signs of damage.

The amount of time stingrays spent interacting with bait varied spatially between sites ( $F_{3,1}=3.9$ ,  $p<0.01$ ), and between habitats within sites ( $F_{1,3}=127.4$ ,  $p<0.001$ ). Stingrays spent significantly longer interacting with the bait on the flats ( $968.3 \pm 99.3$  s) compared to the forereef ( $266.7 \pm 41.4$  s) across all four sites.

## Discussion

We provide evidence that roving predators in high visibility habitats may induce strong risk effects in mesopredators that rely on crypsis and active defense rather than active escape. Encounter rates between predators and prey and conditional probabilities of prey capture can vary with variation in landscape features [see (Wirsing et al. 2010) for a review] and the interaction among prey escape behavior, environmental features, and predator hunting mode are predicted to shape the nature and strength of risk effects (Heithaus et al. 2009). The nature of this three-way interaction, however, remains poorly explored. Based on terrestrial studies (Preisser et al. 2007; Schmitz 2008; Thaker et al. 2011), we might expect relatively weak risk effects in the study system due to good water visibility and roving, less predictable predators. The relatively limited escape capabilities of rays, however, coupled with a tendency to rely on crypsis for avoiding predators in the immediate vicinity, likely leads to the relatively strong risk effects we observed. This extends our understanding of the context dependence of top-down processes in ecosystems, especially risk effects. While previous studies have shown that risk effects on coral reefs may occur at the scale of tens of meters (e.g. Madin et al. 2010), we extend this to scales of kilometers and provide evidence that marine reserves may restore or preserve risk effects in coral reef systems.

Reef sharks, the most common upper trophic level shark on coral reefs in Belize, are more commonly observed on BRUVs inside marine reserves than fished reefs (Bond et al. 2012, 2018). Here, we extended past findings, which were based on several days of sampling, to multiple sampling events across two habitats made over 5 years. Both BRUVs (this study) and longline sampling (Pikitch et al. 2005; Bond et al. 2017) never detected reef sharks on shallow flats even though they occur in adjacent deep lagoon and fore-reef habitats. The unfished atoll and barrier reef sites both had more than four times the reef shark abundance of ecologically similar fished reefs. Notably, there were extremely few observations on BRUVs of any other large species of sharks that would be capable of eating a stingray. This paucity of large-bodied sharks is further supported by a 13-year standardized longline study at GRMR where only a total of 15 individuals from species *G. cuvier*, *S. mokarran*, and *N. brevirostris* were caught compared to 293 *C. perezii* (Bond et al. 2017), suggesting that reef sharks are the most common potential predator of stingrays in our study sites.

Very little is known about the effects of marine reserves on batoids, even though many are threatened (IUCN, Dulvy et al. 2014) and others that are not threatened may exhibit population increases when released from predation

and predation risk [e.g. Myers et al. 2007, but see caveats in Heithaus et al. (2010) and Grubbs et al. (2016)]. We found that reserves had a significant negative effect on the presence of stingrays on forereef habitats, but positive effects on stingray densities on the flats. Taken together, these patterns are consistent with the hypothesis that stingrays respond behaviorally to variation in reef shark densities, but impacts on overall population sizes across flat and forereef habitats in an area may be small (i.e. risk effects are greater than those of direct predation). We detected variation in the numbers of reef sharks and stingrays between our two reserve sites, one atoll and one barrier reef, suggesting that the strength of this effect may be impacted by reef structure and should be further explored. This could possibly explain the significant difference in stingray relative abundance observed between our two reserve sites.

Patterns of stingray abundance were consistent with the a priori predictions of predation-sensitive habitat use and inconsistent with predictions based on other drivers of abundance (see Figure S1). Though it was not possible to isolate the factors that influenced southern stingray occurrence because many factors were significant, when using these data to predict the concentration of stingrays, flats habitat inside reserves was the most significant factor (Table 1, Fig. 2). While direct predation of southern stingrays may partially explain the differences in abundance between fished and unfished forereefs, risk effects likely are a large component of the overall predator effect given that actual predation rates by reef sharks might be relatively low (Frid et al. 2007; Tavares 2009). Predation need not be common, however, to induce strong risk effects and potentially even trophic cascades (e.g. Schmitz et al. 1997; Heithaus et al. 2008a). Our hypothesis was that because the spatial distribution of risk is drastically different between flats and reefs in reserve sites (low/high, respectively) but not so in fished sites (low/low) due to the absence of sharks, there would be large differences in relative abundance of rays across flats and reefs (high/low, respectively) in reserves but less so or none in fished sites. Our results are consistent with this prediction. If direct predation were the primary driver of observed patterns, we would have expected reduced sightings of southern stingrays on BRUVs in marine reserves compared to fished sites across both habitats. Our results were inconsistent with this prediction. Boat based transects detected densities twice as high on flats of reserves despite no fishing for rays in fished sites, and abundances of rays found on forereefs during BRUV sampling were also higher in reserves than fished areas, with variation between reserves also observed. If stingrays increase their use of deeper forereef habitats at fished sites where reef shark density is reduced (as opposed to increases in population size within fished forereef habitats through demographic effects alone) we predicted this

observed pattern of lower stingray densities on the flats of the fished site compared to the reserve.

Stingray behavior and patterns of predator-inflicted injuries further support our hypothesis of predator effects on stingrays. First, southern stingrays spent significantly longer periods at BRUVs on the flats compared to the forereef at all of the study sites. This is consistent with individuals spending more time attempting to feed and less time investing in anti-predator behavior, such as vigilance or refuging, in safer habitats. This indicates that southern stingrays perceive this habitat to have less intrinsic risk. Second, stingrays observed in marine reserves were three times more likely to have predator-inflicted injuries than those in fished areas. Stingrays have few natural predators in a coral reef environment, especially as they approach adult sizes, other than large sharks. Although it is not possible to conclusively attribute all observed stingray damage to interactions with reef sharks or sharks in general, given the limited number of species that could inflict such damage, it is likely that most wounds were inflicted by sharks. Fishers have been known to cut the tails to safely release incidentally caught stingrays, however, this would produce the opposite pattern to that observed with more damaged tails in fished areas. Additional drivers of this pattern could be (i) if the risk of death given an attack is higher in one area, or, (ii) if injured individuals (no matter where they were bitten) then move to a lower-risk area, which both support our conclusion.

Alternative explanations for the observed pattern of stingray abundance appear unlikely. None of the measured environmental factors (salinity, temperature, dissolved oxygen, visibility and current velocity) varied with protection status across a particular habitat type and none correlated with southern stingray sightings on BRUVs. All southern stingrays that were observed were large and those on the flats were generally either similar in size or larger than those on the fore reef within locations. The only significant difference in size between habitats was observed at GRMR where stingrays on the flats were significantly larger, which makes it unlikely that these areas serve as southern stingray nurseries. It is possible that stingrays could be less likely to visit BRUVs in reserves where predation risk was higher, as an artefact of the food versus safety trade-off. This seems unlikely given that UVC surveys (that are not reliant on rays moving or feeding) conducted at GRMR, where predation risk was highest, documented lower abundances of rays on the forereef than on flats (Tilley and Strindberg 2013; Tilley et al. 2013b). We were unable to quantify spatial variation in prey available to stingrays but in Belize they primarily feed on non-commercially exploited infaunal invertebrates (annelids and bivalves; Tilley et al. 2013a). It is, therefore, likely that prey availability correlates to some degree with the amount of soft bottom habitat, which was similar across all forereef sites irrespective of protection status. Because

there were no significant differences in the relative proportion of soft bottom habitat among forereefs of fished and unfished areas, it is likely that neither prey availability nor the availability of resting/refuging habitat are responsible for the differences in stingray abundance between fished and unfished forereefs. Furthermore, populations of large piscivores and commercially exploited macroinvertebrates such as queen conch (*Lobatus gigas*) and spiny lobsters (*Panulirus* spp.) respond positively to marine reserves, including site-specific studies at GRMR (Sobel and Dahlgren 2004; Dahlgren 2014; Tewfik et al. 2017). None of these species compete with stingrays for their infaunal prey (Gilliam and Sullivan 1993; Tilley et al. 2013a), so it is unlikely that differences in the abundance of these species between sites would affect stingrays.

Our results add to the growing evidence that risk effects of large marine predators may be important aspects of marine communities (Heithaus et al. 2008a, b; Burkholder et al. 2013; Wirsing et al. 2014). We provide evidence that roving predators can induce risk effects in heterogeneous marine habitats, even in clear waters. Other large vertebrates, such as dugongs, dolphins, sea turtles, and small sharks at risk of predation by large sharks make trade-offs similar to those we observed for stingrays (Guttridge et al. 2012; Heithaus et al. 2012). The habitat shift we observed may be especially pronounced in stingrays because of their limited flight ability and maneuverability compared to their predators and their reliance on crypsis, refuging and their sting for predator avoidance and defense. This highlights that the nature of predator risk effects is likely driven by an interaction between predator hunting mode, habitat structure and the tactics used by prey for predator avoidance (see Heithaus et al. 2009; Wirsing and Heithaus 2014).

There is considerable interest in the ecological effects of sharks and shark removals on coral reefs (Roff et al. 2016a, b). The overarching focus has been on the effects of direct predation by sharks reducing population sizes of large piscivores that could be transmitted to herbivorous fish and then to coral and fleshy algae (Mumby et al. 2006; Rizzari et al. 2014). Our results highlight that we should also consider risk effects of sharks on large-bodied prey in coral reef ecosystems and the possibility for these to trigger behavior-mediated trophic cascades mediated by stingrays, which can play an important structuring role in soft-bottom habitats, through bioturbation, destruction of seagrasses, and consumption of prey (see Heithaus et al. 2012; O'shea et al. 2012). Stingrays are powerful bioturbators, capable of excavating sediment at large scales while searching for infaunal benthos (O'Shea et al. 2012). Foraging over benthic vegetation (e.g. seagrass) can impact seagrass structure thereby reducing its effectiveness as a nursery (Valentine et al. 1994; Heck Jr et al. 2003; DeWitt and Nelson 2009). Valuable commercial species (e.g. *Panulirus argus*, *L. gigas*)



that depend on seagrass nurseries for survival could be negatively impacted by large scale disturbances because of stingray foraging (Heck Jr et al. 2003; Stoner 2003). Furthermore, the disturbance and resuspension of nutrients and particulate matter that can alter water and sediment chemistry (Gilbert et al. 1995), and provide feeding opportunities for nearby demersal fishes (O’Shea et al. 2012).

Just as national parks are critical tools for conservation of terrestrial biodiversity, marine reserves are increasingly being used to conserve biodiversity in the world’s oceans. There is evidence that they can enhance the biomass, density and body size of exploited species within their boundaries, which sometimes negatively affects these parameters in other species and can have strong cascading effects through the food web. Our study highlights that marine reserves can also restore fear-based systems, by encouraging direct and indirect interactions between predators and prey. There is a need for more studies of these non-consumptive risk effects inside marine reserves and their potential to restore previous ecosystem function.

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