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Spatial and temporal trends in yellow stingray abundance: evidence from diver surveys

Christine A. Ward-Paige · Christy Pattengill-Semmens · Ransom A. Myers · Heike K. Lotze

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Abstract Recent concerns about changing elasmobranch populations have prompted the need to understand their patterns of distribution and abundance through non-destructive sampling methods. Since scientific divers represent a small portion of the total number of divers worldwide, the use of non-scientific divers could drastically increase the number of observations needed to monitor broad-scale, long-term trends. Here, we use 83,940 surveys collected by trained volunteer divers to examine spatial and temporal trends of the most frequently sighted elasmobranch species in the greater-Caribbean, the yellow stingray (*Urobatis jamaicensis*). Despite being relatively common and listed as Least Concern on the IUCN Red List, little is known about the status of this species. In total, yellow stingrays were observed on 5,658 surveys (6.7% sighting frequency) with the highest occurrence in the regions surrounding Cuba. Overall, sighting frequency declined from 20.5% in 1994 to 4.7% in 2007—a standardized decline rate of −0.11. However, these trends were not consistent in all regions. The strongest decline occurred in the Florida Keys, the most sampled region, where trends were similar among all areas, habitats and depths. In contrast, sighting frequency significantly increased in Jamaica where large fishes are severely depleted. We discuss possible explanations for these changes including habitat degradation, exploitation and changes in trophic interactions. Our results suggest large-scale changes in yellow stingray abundance that have been unnoticed by the scientific community. Thus, our study highlights the value of non-scientific divers for collecting data that can be used to understand population trends of otherwise poorly studied species.

Keywords Citizen science · Elasmobranch monitoring · Yellow stingray · Diver survey · Population trend · Trophic interactions

Ransom A. Myers: deceased.

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C. A. Ward-Paige (✉) · R. A. Myers · H. K. Lotze
Department of Biology, Dalhousie University,
1355 Oxford St.,
Halifax, NS B3H 4J1, Canada
e-mail: globalshark@gmail.com

C. Pattengill-Semmens
Reef Environmental Education Foundation,
98300 Overseas Hwy., P.O Box 246,
Key Largo, FL 33037, USA

Introduction

Strong changes in elasmobranch populations have been described in marine ecosystems, with precipitous declines in many large sharks that are caught as target or bycatch species in commercial fisheries (Baum et al. 2003; Baum and Myers 2004; Ferretti et al. 2008) and resulting increases in smaller sharks and rays from predation and competition release (Shepherd and Myers 2005; Myers et al. 2007; Ferretti et al. 2010). Despite improvements to our understanding of population trends in some species and regions, a large number of elasmobranchs and systems remain unexplored. In the greater-Caribbean, for example, the yellow stingray (*Urobatis jamaicensis*) is among the most commonly sighted elasmobranch species observed by scuba divers, yet, with the exception of a study in south Florida (Fahy 2004), there is little scientific information on the status of this species. According to the World Conservation Union Red List (IUCN: www.iucnredlist.org), the yellow stingray is listed as Least Concern; however, the same source also states that this species is likely affected by inshore fisheries, habitat degradation and exploitation for the aquarium industry and that temporal trends are unknown. Because they are considered to be abundant and tolerate captivity well yellow stingrays are recommended for scientific experiments (Fahy and Sherman 2000) and their occurrence in the scientific literature is mostly limited to biochemical, neurological, and physiological experiments (Sulikowski and Maginniss 2001; Barnes et al. 2003; Dwivedi and Trombetta 2006). The paucity of ecological information may be explained by the fact that yellow stingrays are not economically important—there is no directed tourism or fishery for this species (www.iucnredlist.org). Since yellow stingrays are relatively small (~76 cm) and often seen singly and infrequently it is unlikely that changes in abundance would be noticed even from anecdotal evidence like that reported for other more valuable species (e.g. groupers: Saenz-Arroyo et al. 2005). Here, we investigate spatial and temporal trends in sighting frequency of the yellow stingray in the greater-Caribbean.

Over the past decade, most studies concerned with trends in elasmobranchs have used catch or bycatch data from fisheries dependent or independent sources to analyze population changes (Baum et al. 2003; Shepherd and Myers 2005; Myers et al. 2007; Ferretti et al. 2008). However, these are not informative for species that are rarely caught and not reported. Also, extractive sampling methods are undesirable for censusing rare or declining species and are not normally permitted in marine reserves, where vulnerable species, like many elasmobranchs, may find refuge. Here, non-extractive methods are essential to provide information on population trends. Underwater visual censuses (UVC) conducted by scientific divers is an established method that has been used widely since the 1950's (Brock 1954) as an alternative to extractive methods for describing and monitoring fish populations. UVC have been used in a range of areas and habitats and sometimes include elasmobranchs where they are relatively abundant (Friedlander and DeMartini 2002; Robbins et al. 2006; Stevenson et al. 2007; Sandin et al. 2008). Often, however, elasmobranchs are excluded from UVC because they occur at low abundance and rarely enter survey boundaries (Kimmel 1985).

Because elasmobranchs have relatively large home ranges, are mobile, and are observed infrequently, they are difficult to study by scientific diver observations alone. Even a well designed scientific survey would have difficulty describing the broad-scale distribution and long-term temporal changes to a population of any elasmobranch species because of logistical reasons and high costs. Similarly, to understand general population trends, a wide variety of areas, habitats and environmental conditions need to be covered, requiring large amounts of data to reduce the variance and distinguish regional trends. Therefore, it would be ideal to have all divers, with their wide range of diving interests, reporting elasmobranch sightings (and non-sightings) from their daily dive activities.

A number of volunteer based projects have specifically censused sharks at local, regional, and global scales. For example, the Thresher Shark Monitoring Project (www.malapascua.net) uses recreational diver reports of the number of thresher sharks seen at Monad Shoal in the Philippines to monitor local changes in abundance. Examples of more regional organized shark counts include the Great Australian Shark Count (www.auf-spearfishing.com.au) where divers report the sharks they see during their daily activities to get estimates of abundance. Also, the Shark Trust asks divers to upload images of opportunistic sightings of any elasmobranch species (www.sharktrust.org) to examine distribution patterns. At the global scale, ECOCEAN Whale Shark Photo-identification Library (www.whaleshark.org) uses photos submitted by all divers to identify individual whale sharks to make estimates of absolute abundance. And the Diver Survey portion of the Global Shark

Assessment is a citizen science based project that has been designed to monitor broad-scale changes in elasmobranch populations (www.globalsharksurvey.com). Despite the prevalence of this type of data, only a few peer-reviewed publications have been produced (Arzoumanian et al. 2005; Theberge and Dearden 2006; Stallings 2009; Ward-Paige et al. 2010b); however, volunteer collected data may provide valuable insight into trends that would otherwise go undetected.

In this paper, we examine spatial and temporal trends of the yellow stingray in the greater-Caribbean and demonstrate the power of large amounts of observational data obtained from trained volunteer scuba divers. We used data collected for the Reef Environmental Education Foundation (REEF: www.reef.org), a dataset that is comprised of more than 100,000 surveys conducted by divers on their daily dive activities. Since divers record environmental and sampling conditions, such as habitat type, depth, and bottom time, REEF data are well-suited to evaluating species distributions (Pattengill-Semmens and Semmens 1998; Stallings 2009; Ward-Paige et al. 2010b) and temporal trends. Because these dive surveys have not remained unchanged through time, this analysis required that we account for variation in survey effort (bottom time and number of surveys), date, location and diver skill level (experience). Therefore, we applied generalized linear models to examine standardized rates of change in sighting frequency as an index of abundance for the greater-Caribbean as a whole, and for 11 regions where the yellow stingray was observed. Then, focusing on the most heavily sampled region, the Florida Keys, we analyzed changes in abundance at a finer resolution by area, habitat, and depth. In the discussion we explore possible drivers of these observed changes, focusing on two regions with opposing temporal trends in yellow stingray sighting frequency, the Florida Keys and Jamaica.

Methods

Data collection

Data were obtained from the REEF database, which comprises >100,000 surveys collected by volunteer divers with a wide-variety of dive objectives and preferences. We used surveys conducted between January 1994 and December 2007 within the greater-Caribbean, which consists of sites within the western central Atlantic from northern Florida to northern Brazil, the Gulf of Mexico and the Caribbean Sea (Fig. 1)—the described distribution for the yellow stingray (Bigelow and Schroeder 1953). REEF surveyors use the Roving Diver Technique (RDT, Schmitt et al. 1993)—a method that enlists divers on their daily dive activities to report the fishes they observe while surveying a variety of habitats within a particular site (Schmitt and Sullivan 1996; Schmitt et al. 2002). The primary goal of the surveyor is to find and report as many species as possible. Fish may be seen at any point during the dive, be any size, located anywhere in the water column and within any microhabitat, and therefore training primarily focuses on identification. Surveyor skill levels are based on fish identification abilities, with novice surveyors achieving up to 80% on Common Fish Quizzes, and expert surveyors achieving at least 90% on the Advanced Fish Quizzes and having conducted >34 surveys. For each survey, divers record environmental variables for the site (current, visibility, habitat type, water temperature, and survey depth), start time, bottom time (time spent surveying) and a checklist of all fish species sighted with binned estimates of abundance, where 1 = 1, 2 = 2–10, 3 = 11–100, and 4 = >100 fish. More detailed information is available on the REEF website (www.reef.org).

Data treatment

Independent datasets were created for the greater-Caribbean as a whole and for the Florida Keys alone. Because the REEF database contains variables that are unlikely to be essential for describing population patterns of yellow stingrays, their inclusion would unnecessarily reduce the amount of available data (records with unknown values are removed) and complicate analyses and interpretations. Therefore, based on our understanding of yellow stingray and diver behaviour, a few variables were excluded. Start time (time of day) was excluded because yellow stingrays utilize relatively small areas and have strong site fixity (Fahy 2004) and are unlikely to vary in abundance throughout the day. Although nocturnal activity levels are relatively high (Fahy 2004), ~96% of the surveys were conducted during the day (07:00

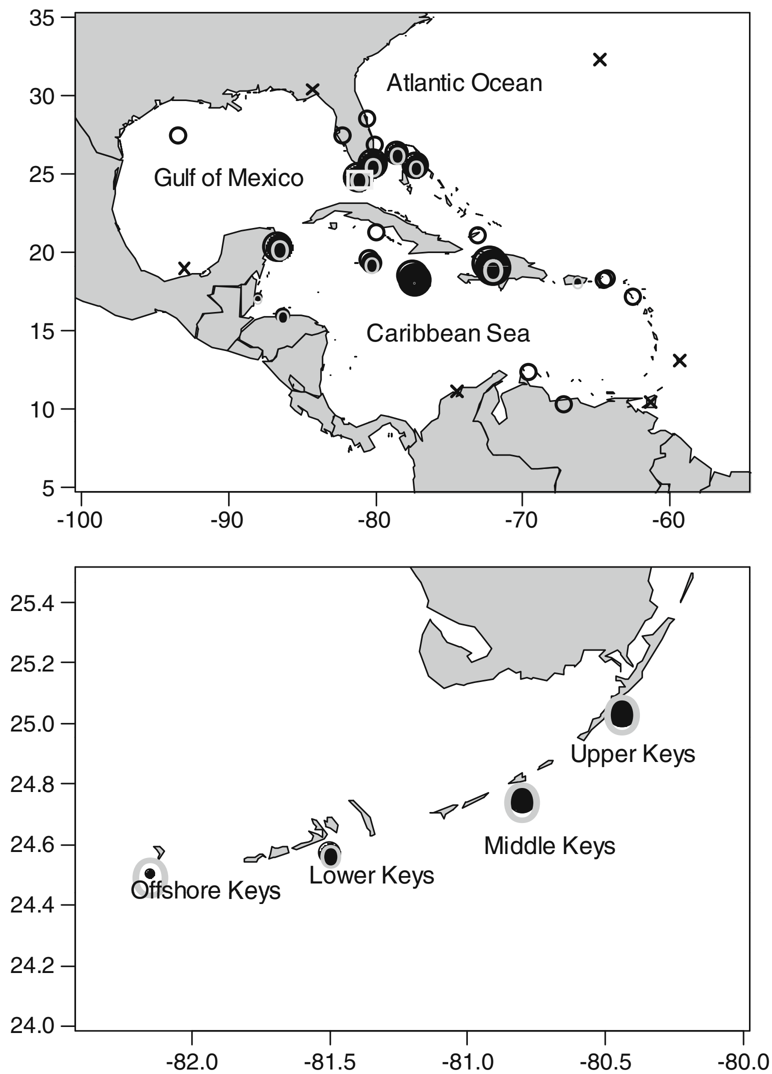

Fig. 1 Distribution and sighting frequency of the yellow stingray in the greater-Caribbean (**a**) and the Florida Keys (**b**, and insert in **a**), US. *Black crosses* = regions with >100 surveys and no yellow stingray sightings. *Open black circles* = regions with <1% sighting frequency. *Black solid circles* = regions with >1% sighting frequency, the size of the circle is the log of the sighting frequency. *Open grey circles* = relative sighting frequency (based on GLM results) for regions with >1% sighting frequency, the size of the circle is the log of the sighting frequency. See Table 1 for greater-Caribbean data and Table 2 for Florida Keys data

to 18:00) and start time is confounded with depth (deeper dives are normally done earlier in the day). Therefore, depth was retained rather than start time because it is known to influence the occurrence of yellow stingrays (Fahy 2004). Water current was also excluded because yellow stingrays are largely stationary and benthic, and current is often strongly associated with site, habitat and depth, which are included in the analyses. Visibility was excluded because yellow stingrays are benthic and relatively inconspicuous and are not likely to be detected at great distances from the observer even under conditions of excellent visibility. In fact, sighting frequency was 7.4% under the lowest visibility conditions and 6.0% under the best visibility conditions. It is likely that habitat (e.g. rugosity) and depth would be more important than visibility for successful detections of yellow stingrays and were thus included in the analyses.

The REEF database also contains variable levels and records that may not be suitable for the analyses of yellow stingrays. Because yellow stingrays are benthic, surveys conducted in open water habitats were not included. Particularly long bottom times (>150 min) were removed to reduce the chance of the diver moving into different sites and because most dives (98.8%) were <2.5 h. Variables with more than 4% missing values were not considered; which excluded only two variables, surface and bottom water temperature (missing 33,280 and 23,544, respectively). The remaining variables were diver experience (expert/novice), bottom time (time spent in the water), depth, habitat, month, year and region or area (for the Florida Keys). Surveys with missing values for any of the remaining variables were not included in the analysis. Also, regions with <100 surveys were excluded. In total, 83,940 surveys conducted by 6,999 surveyors were retained from the original 93,578 submitted for the greater-Caribbean. Surveys were combined into different regions of the greater-Caribbean by geozones as described by REEF (see www.reef.org). Habitats with similar complexity were combined into slope (ledge, wall, and drop-off), reef (high and low profile), and flat (sand, grass, rubble) habitats. Artificial and mixed habitats remained separate.

A separate dataset for the Florida Keys was created from the greater-Caribbean dataset. The Florida Keys are the most heavily sampled region and thus allowed for more detailed analysis. Surveys were combined into areas by latitude, comprising the Upper (Key Largo to Islamorada), Middle (Marathon to Long Key), Lower (Key West to Looe Key) and Offshore Keys (Marquesas to Dry Tortugas). Surveys that did not fit into these areas were removed (i.e., 36 surveys and 1 yellow stingray sighting from the Florida Bay side of the Keys). For more details on habitat type and area delineations see www.reef.org.

Data analysis

Sighting frequency was obtained by dividing the number of dives with yellow stingray sightings by the total number of surveys multiplied by 100. Sighting frequency was analyzed, rather than abundance score because presence and absence data is a sensitive measure of change when only a few individuals are normally seen (Pattengill-Semmens 2002)—71.3% of the records reported yellow stingray abundance to be one.

Then, for all regions with >15 yellow stingray sightings (the number of years in the study plus one) over the study period, standardized estimates of yellow stingray sightings were analyzed using generalized linear models (GLM: Venables and Ripley 1999) with a binomial error structure (Bernoulli trials), logit link and various independent explanatory variables (diver experience, bottom time, depth, habitat, year, month, region/area). Thus, the index of abundance was yellow stingray sightings per region/area or year and the observation on a given dive was assumed to follow a binomial distribution. Models for determining the rates of change in mean sighting frequency (μ_i) of the yellow stingray followed the general model structure,

$$\mathrm{logit}(\mu_\mathrm{i}) = \alpha + \beta year_i + \mathrm{XB}$$

where $\mathrm{logit}(\mu_i) = \mu_i/(1-\mu_i)$, μ_i is the expected value of the index of abundance of yellow stingrays observed in the ith year ($year_i$), α is the intercept, β is a year-effect parameter or the instantaneous rate of change of μ_i over time, X is the matrix of additional covariates affecting the variability of μ_i, B is the vector of their relative parameters. The model therefore accounts for variation in the explanatory variables (e.g. bottom time) and predicts the chance of detection on a dive at a standard location and time. Annual trend rates are given by the slope on the logit scale—where positive values are increases and negative values are decreases in the probability of yellow stingray sightings.

Data analyses were performed at different scales: over the greater-Caribbean, within each region of the greater-Caribbean, and within the Florida Keys by area, habitat, and depth, with different models selected at each scale. All two-way interactions between the response variable (sighting) and explanatory variables (see above) were investigated to build the complete model for the greater-Caribbean and the Florida Keys database. S1 and S2 (Supplementary Material) provide details on how the variables were added to the model; however, we provide a brief description of the reasoning here. Diver experience was added as a categorical term that interacted with year to account for changes in diver skill level. Depth was added as a continuous quadratic term to account for a peak in sighting frequency at an optimal depth. Month was added as a categorical term since sighting frequency varied greatly—peaks in February and August (lows in April and November). Sighting frequency generally increased with bottom time and bottom time depends on dive depth and habitat, which change through time, and therefore interaction terms were included.

The complete model was then compared to alternative models using the 'stepAIC' function in R (www.r-project.org). The models with the lowest Akaike Information Criterion (AIC), which penalizes the deviance by twice the number of parameters, were considered to be the best (final) models (model selections are shown in S1 and S2). Parameter estimates and standard errors (for binomial distributions) were obtained through maximum-likelihood fitting in R. The relative differences in sighting frequency were obtained from the region estimates in the final model for the greater-Caribbean and overall trends (for the greater-Caribbean and the Florida Keys) were obtained by removing year: covariate interactions (i.e. region, area, habitat, depth). Note that insignificant terms were included in the Florida Keys models to demonstrate that trends did not differ between variable levels (e.g. trends were not significantly different between habitats or areas in the Florida Keys—Fig. 3). Therefore, overall year trend estimates vary slightly between models.

Results

Spatial trends

In the greater-Caribbean yellow stingrays were observed on 5,658 out of 83,940 surveys (6.7%). From 1994–2007, reports of yellow stingrays were widely distributed throughout the greater-Caribbean (Fig. 1a) covering the area between central Florida to northern South America, and from the northwestern Gulf of Mexico to the Antilles. However, sighting frequency varied greatly throughout the study area (Table 1; black crosses, open and solid circles in Fig. 1). Although rarely observed in Cuba (<1%), sighting frequency was highest in the areas surrounding Cuba (e.g. Dominican Republic, Jamaica). Standardized sighting frequencies (from GLM results: open grey circles in Fig. 1a) show similar trends with the exception of the Cayman Islands which was smaller than expected. Outside these regions, sighting frequency dropped to <1%. The six surveyed regions with no yellow stingray observations occurred in the regions that were furthest from Cuba.

Within the Florida Keys, yellow stingrays were seen on 2,454 out of 16,692 dives, 43% of the total greater-Caribbean sightings. Yellow stingrays were reported in similar abundances in all areas of the Florida Keys, from the Upper Keys to the Dry Tortugas (Fig. 1b, Table 2). Although yellow stingrays were observed in all habitat types they were rarely found in artificial habitats (Table 2). Yellow stingrays were found in depths ranging from <10 m to >70 m and peaked at about 6 m (20 ft; Table 2).

Greater-Caribbean temporal trends

Throughout the greater-Caribbean yellow stingray sighting frequency declined from 20.5% of dives in 1994 to 4.7% of dives in 2007 (Table 3)—corresponding to an overall standardized decline rate of −0.11 (± 0.01 S.E.) per year (on the logit scale) (S3 demonstrates the effect of each parameter on our model estimates). Note, that for the overall trend the region*year interaction was excluded from the model. However, this trend was not consistent amongst all surveyed regions (Fig. 2). Of the 28 regions sufficiently sampled (>100 surveys) in the greater-Caribbean, we could only assess 11 (Table 1). All other regions only reported the presence of yellow stingrays sporadically, if at all, and were insufficient for trend analysis. Of the 11 regions assessed six showed significant decline rates of up to −0.17 per year (± 0.009 S.E.), two regions had non-significant decreases, while two were unchanged (Fig. 2). Only one region, Jamaica, showed a significant increase (0.37±0.06).

Florida Keys temporal trends

Within the Florida Keys, yellow stingray standardized decline rates ranged from −0.18 (± 0.01 S.E.) to −0.22 per year (± 0.06 S.E.) depending on the model; dropping from 31.8% sighting frequency in 1994 to 4.7% sighting frequency in 2007 (Table 3). Note that the models used in the Florida Keys analyses are different and contain slightly fewer data (36 records were removed from the Florida Bay side of the Florida Keys) than those used for the greater-Caribbean trends. Significant declines occurred in all areas (S4 demonstrates the effect of each parameter on our model estimates); however, the rate of change did not differ significantly between areas, ranging from −0.29 per year (± 0.06 S.E.) in the Lower Keys to −0.18 per year (± 0.06 S.E.) in the Middle Keys (Fig. 3a). Over the 5 habitat types evaluated, all exhibited significant decline rates from −0.37 (±0.11 S.E.) in artificial habitats to −0.12 per year (± 0.07 S.E.) in sloping habitats, but the rates of change were not significantly different among

Table 1 Summary of sample sizes, yellow stingrays, average bottom time and depth (and SE) for regions in the greater-Caribbean where >100 surveys were conducted

Region	Number of surveys	Number of sightings	Sighting frequency (%)	Bottom Time (min)	Mean Depth (ft)
Dominican Republic	503	110	21.9	55.9 (0.4)	3.4 (0.0)
Jamaica	336	62	18.5	37.9 (1.0)	7.1 (0.1)
Mexican Caribbean	4,773	794	16.6	44.7 (0.7)	5.8 (0.1)
Southeast Florida	6,513	998	15.3	43.0 (0.2)	8.4 (0.0)
Florida Keys	16,728	2,456	14.7	48.4 (0.6)	5.4 (0.1)
Central Bahamas	6,428	599	9.3	38.1 (1.7)	8.6 (0.1)
North Bahamas	2,422	184	7.6	71.0 (0.9)	2.7 (0.1)
Cayman Islands	4,041	259	6.4	50.2 (0.3)	5.1 (0.0)
Honduras	2,929	91	3.1	55.0 (0.1)	4.2 (0.0)
Puerto Rico	1,028	21	2.0	51.9 (0.3)	5.1 (0,0)
Belize	2,177	34	1.6	52.5 (0.3)	4.3 (0.0)
Northeast Florida	147	1	0.7	55.4 (0.3)	6.3 (0.0)
North Antilles	1,704	11	0.6	49.5 (0.5)	6.1 (0.1)
Central east Florida	1,021	5	0.5	55.0 (0.2)	6.0 (0.0)
Venezuela	832	4	0.5	42.2 (0.7)	5.8 (0.1)
Northwest Gulf of Mexico	3,211	8	0.2	56.5 (0.2)	6.1 (0.0)
US Virgin Islands	2,219	5	0.2	56.6 (0.3)	5.6 (0.0)
Turks and Caicos	2,705	6	0.2	59.2 (0.3)	5.6 (0.0)
Southeast Gulf of Mexico	932	2	0.2	51.4 (0.5)	5.4 (0.1)
Cuba	562	1	0.2	53.8 (0.4)	5.5 (0.1)
British Virgin Islands	1,940	3	0.2	60.4 (0.4)	4.8 (0.0)
Antilles	14,566	4	0.0	53.8 (0.3)	5.0 (0.0)
Trinidad	583	0	0.0	53.9 (0.3)	5.8 (0.1)
South Gulf of Mexico	445	0	0.0	69.4 (0.4)	5.3 (0.0)
North Gulf of Mexico	214	0	0.0	76.6 (1.3)	5.0 (0.1)
Colombia	401	0	0.0	57.9 (0.4)	5.2 (0.1)
Bermuda	2,169	0	0.0	66.5 (0.1)	5.1 (0.0)
Barbados	2,411	0	0.0	58.1 (0.9)	5.5 (0.1)
Total	83,940	5,658		56.7 (0.1)	5.1 (0.0)

habitats (Fig. 3b). Significant decline rates occurred at all depths (Fig. 3c); however, there was little significant difference in the trends between depths.

Discussion

Using >80,000 diver surveys in the greater-Caribbean, we were able to assess spatial and temporal trends in the sighting frequency of a commonly sighted but little studied elasmobranch, the yellow stingray, for which other data are scarce. Yellow stingrays were observed on 6.7% of the surveys, mainly in the area around Cuba, with the greatest sighting frequency occurring in the Dominican Republic (23.4%) and limited sightings at the boundaries of the study area (e.g. Bermuda, Barbados, north Florida). Between 1994 and 2007 the frequency of occurrence significantly declined (−0.11 per year ± 0.01 S.E.), although this negative trend was not consistent across all regions. Of the 11 regions that had enough yellow stingray sightings for trend analysis, eight showed declines, two were unchanged, and one showed a significant increase (Jamaica). The greatest declines occurred in the Florida Keys, where trends were consistent across all areas, habitats and depths. Our study highlights the value of non-scientific divers for

Table 2 Summary of sample sizes and yellow stingray sightings for areas, habitats and depths in the Florida Keys, US. Note: 36 surveys and 1 yellow stingray sighting were excluded

	Number of surveys	Number of sightings	Sighting frequency (%)
Area			
Upper Keys	9,983	1,896	19.0
Middle Keys	1,679	247	14.7
Lower Keys	2,966	265	8.9
Offshore Keys	2,064	46	2.2
Habitat			
Slopes	864	168	19.4
Mixed	4,732	861	18.2
Reef	9,543	1,348	14.1
Flat	257	32	12.5
Artificial	1,296	45	3.5
Depth (ft)			
snorkel	1,477	179	12.1
<10	521	112	21.5
10–19	3,147	655	20.8
20–29	6,664	1,132	17.0
30–39	2,029	235	11.6
40–49	812	65	8.0
50–59	797	44	5.5
60–69	577	19	3.3
>70	668	13	1.9

collecting species occurrence data that can be used to understand population trends of otherwise poorly sampled and little known species.

Two possible caveats to our analysis regard the quality of the diver data. First, diver collected data on elasmobranch populations, even by standardized surveys conducted by experts, have been subject to criticism. The primary concerns for this type of data focus on correct animal identification and counts that accurately document abundance (Meyer et al. 2009; Ward-Paige et al. 2010a). However, yellow stingrays should be reasonably easy to identify since they are mostly stationary, easily approached by divers and morphologically distinct within their home range. As well, REEF divers are trained to identify as many species as possible, including those much smaller and more cryptic than the yellow stingray, and would likely notice and improve their image recognition of the relatively common yellow stingray. Lastly, because yellow stingrays are mostly stationary it is unlikely that their mobility or behavioural response to the presence of a diver would affect their detection rates and thus counts (Watson and Quinn 1997; Ward-Paige et al. 2010a).

The second caveat concerns the use of non-standardized surveys conducted by volunteer divers on their daily dive activities. Although the goal of a REEF fish surveyor is to locate as many species as possible, it is viable that changes in sighting frequency may be explained by variations in the divers' ability to detect the species in the field—a factor that is not accounted for in our models. For example, high abundance of conspicuous fishes could impede surveyors from detecting more cryptic fishes like the yellow stingray by distracting or obstructing their view. If this were the case, then we would expect very high densities of conspicuous fishes and similar patterns of decline in all other cryptic fishes. However, this does not appear to be the case. In the Florida Keys, targeted fishes (relatively large and arguably conspicuous such as grouper, snapper, grunts, jacks, porgies and hogfish) increased in abundance between 1999 and 2004, but their combined recovered density was only ~0.13 individuals·m^2 (Ault et al. 2006)—not likely high enough to obscure or distract surveyors from sighting yellow stingrays. Additional support may come from increasing trends in other cryptic species within the same area. For example, records from the REEF database show that sightings of three relatively well camouflaged, small (<8.2 cm) goby fishes (bridled, colon, goldspot) increased in sighting frequency between 1994 and 2001 (REEF 2001). Given that these species are smaller than yellow stingrays and occupy similar microhabitats, it is not likely that an increase in goby sightings would result in decreased yellow stingray sightings.

Additional evidence to support the use of REEF diver surveys comes from the similarities between this dataset and what is known about the yellow stingray. First, our maps of their occurrence and sighting frequency show strong similarities to those shown in FishBase (www.fishbase.org), which is based on 521 scientifically verified observations provided to the Ocean Biogeographic Information System (OBIS) and Global Biodiversity Information Facility (GBIF). Both data sources show highest likelihood of occur-

Table 3 Summary of sample size and yellow stingray sightings for each year in the greater-Caribbean and the Florida Keys, US. Note: 36 surveys and 1 yellow stingray sighting were excluded

Year	Greater-Caribbean			Florida Keys		
	Number of surveys	Number of sightings	Sighting frequency (%)	Number of surveys	Number of sightings	Sighting frequency (%)
1994	2,345	481	20.5	1,284	408	31.8
1995	2,355	304	12.9	746	257	34.5
1996	2,876	234	8.1	606	149	24.6
1997	3,068	332	10.8	876	227	25.9
1998	3,098	203	6.6	697	128	18.4
1999	4,057	297	7.3	811	165	20.3
2000	6,054	402	6.6	923	143	15.5
2001	9,155	539	5.9	2,278	252	11.1
2002	10,372	757	7.3	2,568	318	12.4
2003	9,231	475	5.1	1,721	119	6.9
2004	8,706	474	5.4	1,123	103	9.2
2005	7,085	367	5.2	1,083	95	8.8
2006	7,809	432	5.5	1,062	47	4.4
2007	7,729	361	4.7	914	43	4.7
Total	83,940	5,658		16,692	2,454	

rence in the areas surrounding Cuba and low likelihood of occurrence at the boundaries of the survey area (e.g., Bermuda, Barbados, north Florida). Second, to our knowledge, the only reported sighting frequency of yellow stingrays by scientific divers on reefs was 13% for Broward County (Fahy 2004), which is just north of the Florida Keys—encompassing Southeast and Central east Florida by our region groupings in Table 1. The combination of these two areas using the REEF data produces a remarkably similar sighting frequency of 13.3% (1,003 sightings in 7,534 surveys), which suggests that non-scientific underwater survey data may produce results comparable to scientific observers. Third, bi-annual peaks and troughs in yellow stingray sighting frequency observed in the REEF database may correspond with an ontogenetic shift due to the biannual reproductive cycle of the yellow stingray (Fahy et al. 2007). Therefore, it is reasonable to presume that the changes in yellow stingray sighting frequency may represent true changes in the population.

Possible explanations for the decline in yellow stingray sightings are that they have moved to occupy different areas or niches, away from the areas where they would be observed by divers, or that they have declined in abundance as a result of deteriorating habitat quality, direct exploitation, or changes in trophic interactions. Since yellow stingrays are shallow-water benthic species with relatively small home ranges (Fahy 2004) we would not expect that they have moved between regions (e.g., from the Florida Keys to Jamaica). As well, our results and the consistency of our model trends for the Florida Keys indicate that declines occurred across all areas, habitats, and depths, which suggest that movement was not the principal cause of decreased sightings.

The second possibility is that yellow stingrays have declined in response to deteriorating habitat quality. Yellow stingrays are benthic species and likely rely on healthy benthic habitats, including seagrass beds, which are used for parturition (Piercy et al. 2006). Therefore, a decline in yellow stingrays is likely to coincide with the degradation of seagrass and coral reef health across the greater-Caribbean in recent decades. This ecosystem degradation is signaled by the loss of seagrass cover (Robblee et al. 1991; Rogers and Beets 2001; Duarte 2002; Green and Webber 2003), coral diversity and cover (Gardner et al. 2003; Somerfield et al. 2008) and a decline in reef fish density (Paddack et al. 2009), with

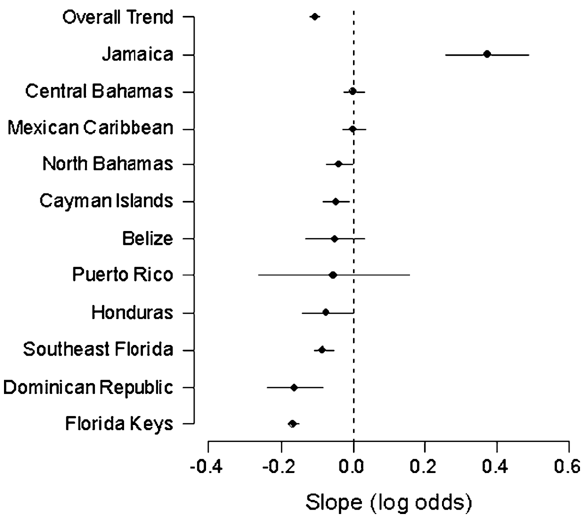

Fig. 2 The estimated rate of change in abundance (±95% CI) of yellow stingrays for regions in the greater-Caribbean. Values are reported on the logit scale. A value of 0 indicates no change in abundance

corresponding increases in coral disease and bleaching (Porter et al. 2001; Rogers 2009) and shifts to more nutrient tolerant species (Lapointe et al. 2005; Ward-Paige et al. 2005). These changes have mainly been attributed to habitat and water quality degradation (Porter et al. 1999; Green and Webber 2003; Mora 2008), seawater warming (Aronson and Precht 2006; Carpenter et al. 2008) and overfishing (Jackson et al. 2001; Pandolfi et al. 2003). However, if the decline in yellow stingray abundance was the result of wide-ranging ecosystem degradation, then we would expect a declining trend across all areas as we do for coral reefs (Gardner et al. 2003). Yet, significant increases in yellow stingray sightings in Jamaica suggest that some regional issues may also be responsible.

A third possibility is that yellow stingrays have declined as a result of direct exploitation. Elasmobranchs have life history characteristics that leave them vulnerable to exploitation, and even mild levels of exploitation may cause their decline (Smith et al. 1998; Myers and Worm 2005; Garcia et al. 2008; Ferretti et al. 2010; Ward-Paige et al. 2010b). Yellow stingrays are targeted for the aquarium industry and are likely caught incidentally by inshore fisheries (www.iucnredlist.org), which may be enough to cause a decline. If this were the case, we would not expect increases in areas with minimal marine protection (Jamaica) and declines in areas with stronger fishing regulations such as no-take marine reserves (Offshore Florida Keys). However, comparison of our trend estimates with the global network of coral reef marine protected areas (MPAs: Mora et al. 2006) indicate that where yellow stingrays are increasing or unchanged, MPAs have extraction restrictions that are predominantly 'take', poaching is 'low', overall risk levels

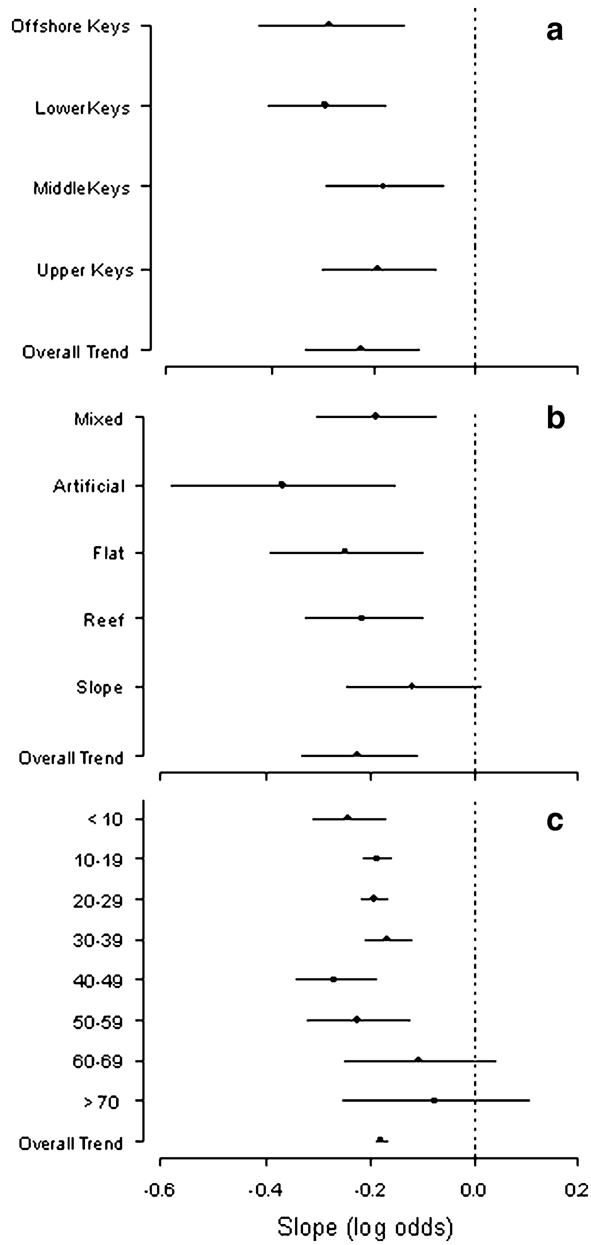

Fig. 3 The estimated rate of change in abundance (±95% CI) of yellow stingrays for (**a**) different areas, (**b**) habitat types and (**c**) depths in the Florida Keys. Values are reported on the logit scale. A value of 0 indicates no change in abundance

that are 'high', and protection summaries (i.e. average of analyzed attributes including extraction, poaching, external risks, MPA size and MPA isolation) that are 'very limited' (Table 4). The exception was the central Bahamas, where human populations are relatively low and strong fishing regulations have been in place for a long period of time. On the other hand, regions where yellow stingrays have declined have mostly 'multi-purpose' MPAs and overall risk levels that are predominantly 'medium' (Table 4). Within the Florida Keys declines occurred in all areas, including the Dry Tortugas which is an enforced no-take zone (http://floridakeys.noaa.gov). Additionally, it is not likely that poachers would travel as far as the Dry Tortugas to obtain yellow stingrays for the aquarium trade when they are relatively common in much easier to reach areas (e.g., south Florida). Thus, exploitation may not be the main driver of the observed yellow stingray declines.

A final explanation for changes in yellow stingray abundance relates to changes in trophic interactions. Yellow stingrays are relatively small predators and their abundance may be strongly influenced by competition and predation from larger predatory fishes (Shepherd and Myers 2005; Myers et al. 2007). Stingrays in general are considered prey for sharks (Strong 1990; Cortes 1999) and other large predatory fishes such as groupers (Silva Lee 1974; www.fishbase.org). There is ample evidence that fishing and marine protected areas alter the abundance and size of species (Ault et al. 2006; Lester et al. 2009; Stobart et al. 2009; Watson et al. 2009), including large fish and sharks (Friedlander and DeMartini 2002; Robbins et al. 2006; Heithaus et al. 2007; Sandin et al. 2008). In the Florida Keys, the region with the strongest decline in yellow stingrays, increasing abundances of targeted fishes (Ault et al. 2006) have been documented, trends which are corroborated by the REEF database (REEF 2002). Also, a moratorium on the capture of the large Goliath grouper (*E. itajara*) has been in place since 1990 after it reached critically low levels of abundance (Sadovy and Eckland 1999; Frias-Torres 2006) and is currently undergoing recovery (Porch et al. 2006). These increases in groupers have been observed in the Florida Keys National Marine Sanctuary, one of the largest and best protected marine sanctuaries in the greater-Caribbean. Although extraction for recreational fishing,

Table 4 Summary of marine protection status for each region assessed for changes in yellow stingray abundance in the greater-Caribbean. Extraction, poaching, risk and summary of protection status are the predominant values for MPAs shown for each area in the supplementary figures (Extraction, Poaching, and Risk) and Fig. 2 (Summary) in Mora et al. (2006)

Names	Trend[a]	Extraction[b]	Poaching[c]	Risk[d]	Summary[e]
Jamaica	increasing	take	low	high	very limited
Central Bahamas	no change	take	low	high	adequate
Mexican Caribbean	no change	take	low	high/medium	very limited
North Bahamas	decreasing	multi-B	low	medium	partial
Cayman Islands	decreasing	multi-B	low	medium	limited
Belize	decreasing	multi-B	medium	medium	partial
Puerto Rico	decreasing	take	medium	high	very limited
Honduras	decreasing	multi-B	medium/low	medium	limited
Southeast Florida	decreasing	multi-B	low	medium	partial
Dominican Republic	decreasing	multi-A	high/none	low	limited
Florida Keys	decreasing	multi-B	low	medium	partial

[a] Trend refers to the change in yellow stingray abundance

[b] Extraction refers to MPA regulations; take, no-take and multipurpose which includes both take and no-take grounds—multipurpose A prohibits commercial harvesting and multipurpose B do not

[c] Poaching is the level of illegal extraction

[d] Risk is a combined reef threat indicator that refers to coastal development, overexploitation, erosion and marine- and inland-based pollution

[e] Summary is an average of extraction, poaching and risk

aquarium trade, scientific purposes and personal use is permitted outside no-take areas, there are controls via fishing regulations, aquarium trade catch limits, and research permits (http://floridakeys.noaa.gov), which allow for increased abundance of predators (Ault et al. 2006) including sharks (Heithaus et al. 2007; Ward-Paige et al. 2010b). Thus, the observed decline in yellow stingrays may be in part the result of increased predation or competition with large predators such as groupers, which live within the same depth range and consume similar prey items (e.g., small fishes and invertebrates, see review in Brule et al. 2005).

In contrast, Jamaica, which is known to be one of the most depauperate regions of the greater-Caribbean (Hawkins and Roberts 2004; Hardt 2009), showed the greatest increase in yellow stingrays sightings. In Jamaica, fishing pressure is very high and large fishes, including sharks and groupers, are well recognized to be rare (Hardt 2009). As a possible consequence smaller elasmobranchs, like the yellow stingray, may have been released from predation and competition. Such releases of smaller elasmobranchs, including rays, has been documented in other ecosystems (Shepherd and Myers 2005; Myers et al. 2007; Ferretti et al. 2010). These examples indicate that observed changes in yellow stingray abundance may be related to altered competition and predation pressure from other species. However, these causes of change are speculative and require further investigation. More generally, differences in management and conservation regimes cause shifts in community structures and trophic interactions that in turn affect the abundance of prey species such as the yellow stingray.

Conclusions

Our study emphasizes the importance of large, volunteer collected datasets, like those collected by the trained divers for REEF, for examining spatial and temporal patterns in species that are wide-ranging, not commercially exploited and not well studied. Volunteer divers can sample large areas and cover a range of habitats, depths and times of the year. These data can be highly valuable for population monitoring as well as for management decisions and conservation planning. Based on volunteer diver data, we were able to assess the spatial distribution and temporal changes in yellow stingrays in the greater-Caribbean. Interestingly, yellow stingrays have decreased in the Florida Keys where some large predators have increased due to strong marine protection measures. In contrast, yellow stingrays have increased in Jamaica where large predators are severely depleted. Several factors may have contributed to the general decline of yellow stingrays including habitat degradation, exploitation, and changes in predation and competition pressure. The abundance of yellow stingrays and other small elasmobranchs may be negatively correlated with the abundance of their predators, and possibly serve as an indicator for the exploitation status of an ecosystem.

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