MONITORING ELASMOBRANCH POPULATIONS USING SCUBA DIVERS: PATTERNS, TRENDS AND POTENTIAL BIASES

by

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For RAM,
who took a chance.

And for Nigel,
who led by example.

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ABSTRACT

Around the world, elasmobranch populations have undergone dramatic shifts – many large sharks have reached such low numbers that they may be at risk of extinction, while many smaller sharks and rays have increased in abundance. Over the past decades, the majority of data used to assess population trends in elasmobranchs has come from commercial fisheries and research surveys in major fishing zones, while there is a paucity of information for other areas like coral reefs. Because elasmobranchs are highly vulnerable to exploitation and many species are of increasing conservation concern, it is desirable to use non-extractive monitoring methods. The goal of this thesis is to examine the accuracy, precision and value of data collected by scientific and recreational scuba divers for analyzing trends in abundance and distribution of elasmobranch populations.

Underwater visual censuses (UVC) have been deployed to monitor marine fishes for decades; however, they have only recently been used to study communities that include sharks. Using a simulation model I show that non-instantaneous UVC can produce large overestimates in the counts of mobile fish, and that density estimates need to account for animal mobility and survey methods. This has important implications for descriptions of abundance, biomass and community structure as well as conservation and management targets. Because it is not feasible for scientists to conduct UVC over broad spatial or temporal scales, recreational divers may be a valuable source of data. I used simulations and field studies to demonstrate that methods deployed by non-scientific divers detect fish at lower densities than scientific methods, and that inexperienced divers detect and count elasmobranchs as precisely as experienced divers. Finally, using a volunteer collected database in the greater-Caribbean, I demonstrate the value of non-specialist data for revealing (i) previously undocumented spatial and temporal trends in the commonly sighted yellow stingray, and (ii) contemporary shark distribution and sighting frequency in relation to human population density and exploitation. Overall, this thesis contributes to our knowledge of temporal and spatial trends of elasmobranch populations and provides insight into the precision and limitations of UVC methods conducted by scientific and non-scientific divers for monitoring fish around the world.

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This thesis would not have been completed without the support of many people. I have no idea where I would be today if it had not been for Ransom A. Myers (RAM) who trusted me to accomplish his brilliant idea of using divers' observations – a project that I feel proud to be part of today. RAM taught me about research, biology, math, computers, statistics – but also priorities, balance and enjoying life. In RAM's absence, I was lucky to have the support of Tamara Romanuk, who encouraged me to stay on course and gave me the opportunity to be here today. Heike Lotze has been instrumental for me completing this thesis. Her unwavering support through all of my tribulations has meant so much to me. Boris Worm has been influential in sparking my confidence and passion to continue this work. Joanna Mills Flemming provided statistical support and much more. Hal Whitehead provided valuable comments and suggestions to the thesis.

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CHAPTER 1

INTRODUCTION

Rapid decline in global biodiversity is a critical concern for the functioning of marine and terrestrial ecosystems and the services they provide to a growing human population (Mace et al. 2005). Declines in wild populations have heightened the need to acquire accurate estimates of the abundance and distribution of rare, highly mobile species. Many low-mortality methods have been developed to census different populations with diverse life histories in a variety of habitats. With larger populations spatial surveys are predominantly used. Aerial surveys have been used extensively to conduct direct counts of relatively large highly mobile species such as birds (Dugger et al. 2005), deer (Saugstad 1942), kangaroos (Cairns et al. 2008) and marine mega-fauna (Preen et al. 1997, Small et al. 2008). Track and pellet counts have likewise been used for species such as wolf (Marucco et al. 2009) and rabbits (Ferreira & Alves 2009). As well, visual surveys have been used for birds (Kirk & Hyslop 1998, Gorman & Haig 2002) and sharks (Friedlander & DeMartini 2002, Robbins et al. 2006, Stevenson et al. 2007). However, when populations are relatively small, individuals are often missed in spatial surveys. In these cases, mark-and-recapture methods have been used, for example for bats (Rivers et al. 2006), sharks (Heupel & Bennett 2007, Dicken et al. 2008, Rowat et al. 2009) and whales (Stevick et al. 2003, Larsen & Hammond 2004, Skaug et al. 2004).

Censusing marine animal populations can be challenging. The nature of aquatic ecosystems, with the sheer size and depth of the ocean, makes it difficult to get a representative sample size. The ability of mobile marine animals to move out of their preferred habitat, depth, and home range while conducting a census complicates matters further. In the case of elasmobranchs, their rarity, mobility, high diversity, and subsurface habitat use coupled with the physical characteristics of the marine ecosystem, makes them extraordinarily difficult to census. Many elasmobranchs are quick moving, elusive creatures that often avoid people (Bres 1993). Since elasmobranchs are not directly associated with the surface-water interface like marine mammals and because they do not nest onshore like sea turtles, they spend most of their lives away from human observation. The difficulties of developing accurate estimates of global elasmobranch populations are so overwhelming that almost no attempts have been made to quantify their abundance.

Prior to this century, elasmobranch research focused on documenting patterns in spatial distribution (Gudger 1934, 1939a, Stevens 1984, Simpfendorfer & Milward 1993) and human-shark interactions such as the development of methods of shark repellents (Buffenbarger 1963, Gilbert & Springer 1963, Limbaugh 1963, Springer & Gilbert 1963, Tuve 1963) and shark bite statistics (Hutton 1959). Popular and gray literature during this era also focused on methods of shark removal, and the economic and folkloric importance of shark fisheries (Field 1907, Anglo-American Caribbean Commission 1945, Tuve 1963, Beaumariage 1968, Cooper et al. 2007). Recent widespread evidence documenting large-scale changes in elasmobranch populations (Dulvy et al. 2000, Baum & Myers 2004, Shepherd & Myers 2005, Theberge & Dearden 2006) has spurred more conservation-focused research (Pikitch et al. 2005, Duncan & Holland 2006, Garla et al. 2006, Yokota & Lessa 2006, Wiley & Simpfendorfer 2007). This change in perspective has been accompanied by a shift in research methodology from one based largely on observational studies attempting to document patterns in population distribution (Gudger 1934, Gudger 1939b, Gilbert & Springer 1963), and community descriptions (Coles 1919, Springer 1938, Hutton 1959), to a more predictive framework based on meta-analysis of fisheries data and population modeling (Pitcher 2001, Baum & Myers 2004, Myers & Worm 2005, Shepherd & Myers 2005, Myers et al. 2007, Ferretti et al. 2008). These studies have been based on fisheries dependent data such as catch statistics and fisheries independent data such as observer records and research surveys, all of which are destructive censusing methods. This poses a fundamental problem to censusing rare and vulnerable species, such as elasmobranchs, that continue to be decimated, in some cases for the sole purposes of censusing (Simpfendorfer & Milward 1993, Carlson & Cortes 2003, Lombardi-Carlson et al. 2003). Given that many shark species have declined to dangerously low levels of abundance at alarming rates (Baum & Myers 2004, Shepherd & Myers 2005, Theberge & Dearden 2006, Myers et al. 2007, Ferretti et al. 2008), there is an immediate need to implement non-destructive methods of censusing these highly vulnerable species.

Sharks have long suffered from an undeserved reputation as indiscriminate man-eaters. This unfortunate reputation has been used to justify their extermination (Schultz 1966). Recently, however, growing appreciation of these animals as magnificent and ecologically important apex predators has generated considerable increase in the number of benign encounters between humans and sharks, namely through shark diving expeditions. Regrettably, as the popularity of shark-diving ecotourism increased, so has the demand for shark fins for soup on Asian markets, which puts these two resource users in serious conflict (Clarke et al. 2005). Given that many elasmobranch species have undergone drastic declines in abundance (Baum & Myers 2004, Robbins et al. 2006, Theberge & Dearden 2006) and that their life history traits are such that they reproduce late and slowly, which inhibits recovery, it would be desirable to implement non-extractive methods of censusing elasmobranchs wherever possible. The purpose of this thesis is to evaluate the use of scientific and non-scientific scuba divers' observations for monitoring spatial and temporal trends in elasmobranch populations.

Ever since the development of commercially available underwater breathing apparatuses (by Emile Gagnan and Jacques Cousteau in the early 1940's) scuba divers with a range of interests have been exploring different parts of the world's ocean. The first diver's membership associations were initiated in the 1950's and since then the number of certifications worldwide has risen dramatically. According to PADI (www.padi.org), the world's largest recreational diving organization, 3,226 certifications were awarded in 1967, and in 2008 the number of certifications was 932,486, for a total of 17,532,116 certifications across this time period. In 2008, 393,704 continuing education certifications (i.e. beyond entry level) were granted around the world and in 2008 there were 134,598 worldwide professional members (Divemaster or higher). Therefore, based on the shear number of scuba divers, their observations may be a viable source of data; however, such data need to be appropriately analyzed to ensure that population and community descriptions are accurate.

Today, underwater visual censuses (UVC) are standard techniques used to estimate the abundance of fish in the field (e.g. Dulvy et al. 2004, Eggleston et al. 2004, Hawkins & Roberts 2004, Robbins et al. 2006). Commonly, density is calculated as the number of individuals observed standardized by the area sampled. This method is suitable for stationary organisms such as corals, plants, and slow-moving invertebrates which are unlikely to leave or enter the sample area during the survey. In these cases, surveys produce reliable density estimates because they are essentially instantaneous counts, and the same result would be obtained if the survey was conducted instantaneously or over longer periods of time. For mobile animals like fish, however, counts are highly dependent on the technique used. Ideally, researchers use instantaneous censuses and do not count animals that enter the survey area after the survey has started. In these cases, only animal behaviour (i.e. fish being drawn towards or pushed away from the diver) and detectability need to be considered for potential bias in density estimates. In practice, however, animals entering the survey area within the diver's view are often counted (personal communication with >30 researchers that commonly use UVC), and this may be of advantage to detect rare animals that are otherwise missed. In these cases, however, simple number-per-area calculations may not be appropriate.

In chapter 2, I examine overestimates in counts obtained by non-instantaneous censuses of mobile fish. To quantify the resulting bias between observed and expected counts, I developed a model to simulate counts obtained by scuba divers using belt-transect and stationary point count techniques, two commonly deployed UVC techniques, under a range of fish speeds. I further explored the bias in counts obtained by different patterns of fish mobility (fish speed and turning angle) and different survey methods including survey time, survey dimensions, visibility, and diver speed. Using examples from the scientific literature, I explore the impact these biases have on abundance and biomass estimates as well as on descriptions of community structure. I focus on sharks, which are among the most mobile fishes detected in underwater surveys and likely suffer the greatest bias.

Because elasmobranchs are highly mobile, widely distributed, relatively rare fishes with large home ranges it is not logistically or economically feasible for scientists to conduct visual censuses for long-term or broad-scale trend analysis. However, since elasmobranchs are also widespread, charismatic species that inhabit a wide range of depths, temperatures, and habitats, it may be possible to enlist professional and recreational scuba divers, with their wide variety of interests, to collect data. In chapter 3, I explore the precision of non-scientific divers for providing occurrence and relative abundance data. First, I expand the simulation used in chapter 2, to compare the level of fish detection between the two scientific underwater survey techniques, the belt-transect and stationary point count, and a roving diver technique used by recreational divers. Then, using a field survey, I compare inexperienced with experienced divers in their ability to detect and count elasmobranchs. Finally, I compare results to the documented precision of non-scientific observers engaged in surveys of terrestrial fauna and flora surveys.

In chapter 4, I use volunteer diver observation data from the Reef Environmental Education Foundation (REEF) to examine the distribution and temporal trends of the most frequently sighted elasmobranch species in the greater-Caribbean, the yellow stingray (*Urobatis jamaicensis*). Despite being common, very little is known about the ecology and population status of the yellow stingray. Using 5,606 yellow stingray sightings from 85,062 diver surveys I explore spatial trends in sighting frequency in the greater-Caribbean. Then, using generalized linear models I examine temporal trends in the greater-Caribbean and the Florida Keys. This study highlights the value of non-scientific divers for collecting large amounts of data, and outlines methods that can be used to understand population trends of other species in the REEF database.

In chapter 5, I further explore the REEF database to investigate the contemporary distribution of all sharks on reefs in the greater-Caribbean and to asses the potential role of human population in shaping that pattern. First, I analyzed the current distribution and sighting frequency of all sharks on reefs. Then, I compared the spatial patterns in contemporary shark sighting frequency with records of human population density as a proxy for exploitation and other human impacts. Next, using a population viability analysis I tested the viability of the assessed sharks under a range of fishing mortalities within a 50 year time-frame. Finally, I compare contemporary distribution patterns with habitat suitability and geographical ranges of these sharks and use historical narratives to demonstrate that they were once abundant in the study area.

The overall goal of my thesis is to describe patterns in elasmobranch populations using scuba divers' observations and to investigate the limitations and biases produced by these data. Although getting estimates of the true abundance of mobile animals can be problematic, divers may provide useful information on the occurrence, distribution, and relative abundance of many elasmobranch populations. Gathering data from the thousands of non-scientific divers that visit a range of sites, habitats, and levels of anthropogenic influences, has great potential for divulging broad-scale patterns in population abundance and may provide a significant early warning system for establishing protection measures.

With rare exception, the conceptualization, data analysis, and writing of this thesis were done entirely by Christine Ward-Paige. H.K. Lotze supervised this thesis and edited chapter 1-6. J. Mills Flemming assisted in data analysis and editing chapter 2. R.A. Myers collaborated in conceptualizing chapter 4. C. Mora and R.A. Myers collaborated in conceptualizing chapter 5 and C. Mora contributed human population information. C. Pattengill-Semmens maintains the REEF database used in chapters 5 and 6.

CHAPTER 2

ASSESSING THE ACCURACY OF UNDERWATER VISUAL CENSUSES FOR MOBILE FISH: IMPLICATIONS FOR DENSITY, BIOMASS AND COMMUNITY DESCRIPTIONS

2.1 INTRODUCTION

Underwater visual censuses (UVC) have been used to enumerate fish *in-situ* in a wide range of areas and habitats since the 1950's. Today, UVC made by scuba divers are standard techniques used to estimate the abundance of animals in the field. Fish counts derived from UVC censuses have been used to describe and monitor spatial and temporal trends in populations and communities that include mobile fishes (e.g. Mumby et al. 2006, McClanahan et al. 2007, Forrester et al. 2008, Harborne et al. 2008, Paddack et al. 2009). Recently, these techniques have been deployed in remote oceanic atolls to describe the community structure of relatively pristine reefs (Friedlander & DeMartini 2002, Stevenson et al. 2007, DeMartini et al. 2008, Sandin et al. 2008). These studies have provided invaluable insight into the effect of exploitation on fish communities; however, the absolute values appear high – even for pristine reefs. For example, densities of 200,000-500,000 top predators·km^{-2} (including sharks, jacks and snappers) were reported for the Line Islands (Sandin et al. 2008). In contrast, the density of lions in Tanzania is only about ~0.08-0.13 individuals·km^{-2} (Creel & Creel 1997) and what is considered a high density of cattle on grasslands is 83 individuals·km^{-2} (Gutman et al. 1990).

Today, the belt-transect and stationary-point-count techniques are used regularly to estimate the true density and biomass of underwater organisms (e.g. Dulvy et al. 2004, Eggleston et al. 2004, Hawkins & Roberts 2004, Robbins et al. 2006). In the belt-transect technique, one or two divers swim along a straight line and record the animals they observe within a fixed distance of the line (Brock 1954). In the stationary-point-count technique, the diver remains still and records the fish observed within a fixed distance of the diver for a certain amount of time. Unfortunately, the details of whether or not counts include fish that entered the survey area after the census began are not usually made explicit in the published scientific literature.

Commonly, fish counts are converted to density by standardizing by the area sampled. This calculation is suitable for stationary organisms such as corals, plants, and slow-moving invertebrates which are unlikely to leave or enter the sample area during the survey. In these cases, surveys produce reliable density estimates because they are essentially instantaneous counts, and the same result would be obtained if the survey was conducted instantaneously or over longer periods of time. For mobile animals like fish, however, counts are highly dependent on the technique used. Ideally, researchers use instantaneous censuses and do not count animals that enter the survey area after the survey has started. In practice, however, animals entering the survey area within the surveyors view are often counted (personal communication with >30 researchers using UVC). In these cases, simple number-per-area calculations may result in inaccurate density estimates and related population and community descriptions.

Through our discussions with researchers it was occasionally acknowledged that fish mobility could generate bias in the counts; however, this bias was considered to be insignificant and acceptable as long as the methods were constant between surveys. Studies using UVC usually deploy the same techniques within each study (e.g. belt-transect with constant width and length) to generate data that are directly comparable. Numerous studies have investigated bias, imprecision and variability in counts from visual censuses (Sale & Sharp 1983, Thresher & Gunn 1986, Watson et al. 1995, Cheal & Thompson 1997, Samoilys & Carlos 2000) and have focused on fish behaviour (e.g. reaction to diver), detection, misidentification, and recounting. However, none have addressed the accuracy of counting mobile fish in non-instantaneous UVC.

The importance of fish mobility (e.g. direction) on UVC was previously investigated by Watson and Quinn (1997). Using a simulation program the authors concluded that the speed at which the fish approached the belt-transect diver (not the stationary-point-count diver) caused the most appreciable bias between the observed and true density. However, there were a few differences between the assumptions of their simulation and the practice of the sampling protocols investigated in the current study. Most importantly, for the belt-transect technique the simulated divers did not count fish that entered the survey area within the diver's view. In practice, however, targeted fish that enter the transect area in front of the diver are commonly recorded (personal communications with >30 researchers commonly using UVC). Additionally, for the stationary-point-count technique simulated by Watson and Quinn (1997), the diver surveyed the area from above (i.e. looking down) and did not record fish that entered the survey area after the survey started. In practice, however, stationary-point-count divers often remain in the middle of the circle and turn in one direction while conducting a survey (Bohnsack & Bannerot 1986). Because the diver deploying the stationary-point-count technique remains still it is thought to be a superior sampling method for censusing mobile fishes because it allows the fish to acclimate to the diver's presence and move back into their original positions – within the survey boundaries (Bohnsack & Bannerot 1986).

In this study, our aim was to evaluate the bias caused by fish speed in non-instantaneous UVC. Without accounting for this factor, the bias caused by animal detectability and behaviour (e.g. drawn towards the diver) that exists in instantaneous surveys may be compounded by methodological bias and could lead to unrealistic density, biomass, and community descriptions. Here, we developed a model in R (www.r-project.org) to simulate fish and divers deploying the belt-transect and stationary-point-count UVC techniques. Because sharks are likely the most conspicuous and mobile fishes detected during UVC, we tailored the model to simulate fish speeds to those reported for sharks. We investigate the bias between the observed and expected counts across a range of fish speeds. Then, we investigate the bias that is produced by different survey procedures (visibility, survey time, transect width, transect diver speed, stationary radius) and fish mobility (speed and turning angles) in non-instantaneous UVC. Finally, using examples from the scientific literature, we demonstrate the effect these biases may have on abundance, biomass and community descriptions.

2.2 METHODS AND MATERIALS

2.2.1 MODEL DESCRIPTION

Our model *AnimDens* was written in R (www.r-project.org) to simulate divers counting fish while deploying the belt-transect and stationary-point-count UVC techniques (Appendix A). Simulations were run across a range of fish speeds and survey procedures to determine the effect of these parameters on observed counts. Figure 2.1 shows sample runs for fish that remained still, that moved at $0.5\ \mathrm{m \cdot s^{-1}}$, and at $1.0\ \mathrm{m \cdot s^{-1}}$. For simplicity, the model assumed a sample area that was featureless, flat and 1 m deep. For each simulation, a diver from each of the two census methods was placed in the centre of the sample area and each had an orientation of 90° (each facing in the same direction) at initial time, t_0. The sample area was populated with fish with a random distribution and random initial orientation. At t_0 the number of fish observed and recorded by each diver was a function of the distance and the angle between the diver and each fish (those located within view of the diver). For the stationary-point-count diver, all fish within ±80° of the diver's main orientation were counted (Fig 2.2). For the belt-transect diver, the distance was set to maximum visibility v and an angle of ±90° but only to a distance of transect width (tw) to the right and left of the diver's location (Fig 2.2). Because the belt-transect diver sampled an area directly in front of them the angle was set to 180°. Fish that reached the area boundaries were allowed to leave and return (i.e. not reflected back into the sample area). Note that the simulated divers did not recount fish they already recorded (as if they were all numbered), as divers strive to do in the field (Brock 1954, Thresher & Gunn 1986).

After each time step, the fish moved with a given speed in a restricted randomly selected direction (turning angle) of their last orientation. Although fish often travel at variable speeds, the concern here is the chance of the fish entering the sample area during the census (e.g. 5 minutes) within the diver's field of view. Once the fish enters the sample area it is recorded and its speed is no longer relevant and therefore the fish speed remained constant through each simulation. In reality, divers continuously view the survey area; however, to speed up the simulation process we set the time step to two seconds (i.e. fish were counted every two seconds). For the stationary-point-count we followed the sampling protocol outlined in Bohnsack and Bannerot (1986) and set the divers to remain still and to turn slowly in one direction (here set to +4°) in each time step. Although the belt-transect technique usually does not specify the survey time or swim speed of the diver in published methodology (Sale & Sharp 1983, Samoilys & Carlos 2000, Sandin et al. 2008) we set the belt-transect diver to move forward at a range of speeds, which are reasonable for counting and recording conspicuous fish.

To examine the effect of fish speed alone, we fixed all other parameters to commonly reported values and only varied fish speed. Here, fish density was fixed at 0.2 fish$\cdot$m^{-2}, approximately the maximum apex predator density reported by UVC (Sandin et al. 2008). Fish speeds included 0, 0.001, 0.01, 0.1, 0.2, 0.4, 0.6, 0.8, 1.0, 2.0, 4.0 m$\cdot$s^{-1}, and were based on those attained by sharks. For example, *Ginglymostoma cirratum* Müller and Henle (nurse shark) often rest on the bottom and therefore have swimming speeds of 0 m$\cdot$s^{-1}. Other sharks, including *Negaprion brevirostris* Poey (lemon), *Sphyrna tiburo* Linnaeus (bonnethead) and *Carcharhinus melanopterus* Quoy and Gaimard (blacktip reef) sustain swimming speeds of 0.77-1.29 m$\cdot$s^{-1} (Webb & Keyes 1982). *Carcharhinus leucas* Müller and Henle (bull) has a burst swimming speed of up to 5.3 m$\cdot$s^{-1} (Gray 1971). Fish turning angles (restriction of the amount that fish were able to turn between time steps) were set to 45°, based on C. Ward-Paige's personal observations of reef sharks (*Carcharhinus perezii* Poey, *Carcharhinus limbatus* Müller and Henle, *C. melanopterus*). Few studies report visibility distance in their published survey methods, although it is expected that surveys would not be conducted under conditions of limited visibility (less than the width of the belt-transect or the radius of the stationary-point-count). Here, we set visibility distance to 13 m, which is the average visibility reported by divers to Reef Environmental Education Foundation (REEF: www.reef.org). Transect width was set to 4 m, which is a commonly used transect width for mobile fishes (Friedlander & DeMartini 2002, Stevenson et al. 2007, Sandin et al. 2008) and the stationary-point-count distance was set to 7.5 m, a commonly used radius (Bohnsack & Bannerot 1986). Although, most published methods do not specify the survey time or swim speed of the belt-transect diver (Sale & Sharp 1983, Samoilys & Carlos 2000, Stevenson et al. 2007, Sandin et al. 2008), we set survey time to 300 s which is a commonly reported deployment time used for the stationary-point-count and belt-transect methods (Thresher & Gunn 1986, Cheal & Thompson 1997, Friedlander & DeMartini

2002) and diver speed to 4 $\mathrm{m \cdot min^{-1}}$, which is a reasonable speed for counting conspicuous fishes. This was run as individual models 30 times each (i.e. 30 replications).

To examine the overall patterns of bias produced by fish mobility (speed and turning angle) and survey procedure (i.e. visibility distance, survey dimensions, diver speed, and survey time) on observed counts *AnimDens* was also run across a range of all variables (Table 2.1). Because of the extent of computing time, we ran 1 simulation for each variable combination. Here, fish speeds were set to the same values as before. Fish density was fixed at 0.1 $\mathrm{fish \cdot m^{-2}}$. Fish turning angles ranged from 1° (turning very little) to 45° (turning a lot). Survey times and transect widths covered a wide range of values. Visibility distances covered a range of values reported in the REEF database.

2.2.2 ANALYSES

The results (i.e. counts made by each diver) of each model simulation was used to compare observed count ($c_{s,t}$) and expected count, which were then used to examine trends in bias through the range of survey procedures and fish speeds.

Expected count ($x_{s,t}$) was calculated as:

$$x_{s,t} = d_a * a_{s,t} \quad (1)$$

where (d_a) is the true density (number of fish divided by the total area entered in the simulation) and $a_{s,t}$ is the area surveyed by the stationary-point-count (a_s) or belt-transect (a_t) divers. The area surveyed was calculated for each UVC method as:

$$a_s = \pi r^2 \qquad (2)$$

$$a_t = tw \cdot s_t \cdot t + tw \cdot v \quad (3)$$

where r is the sampling distance (radius) used in the stationary-point-count technique, tw is the transect width, s_t is the swimming speed of the belt-transect diver, t is the survey time and v is the visibility distance (see Fig 2.2 for a visual description of the survey variables). The length of the swim path for the belt-transect diver was a function of swimming speed (s_t) and survey time (t).

The relative bias ($b_{s,t}$) for each UVC method was computed as:

$$b_{s,t} = (c_{s,t} - x_{s,t}) / x_{s,t} \quad (4)$$

The mean relative bias for each model was used to examine how fish speed and survey procedures bias observed densities. Factorial bias was calculated as the bias ($b_{s,t}$) plus one.

2.3 RESULTS

Relative bias for both the belt-transect and stationary-point-count divers increased with fish speed and followed the same pattern and range for both survey techniques under the specified sampling conditions (Fig 2.3). Even counts of very slow moving fish (e.g. 0.01 $m \cdot s^{-1}$) were overestimated. For the belt-transect survey the relative bias increased from -0.04 to 11.84 for fish moving at 0.001 and 1.0 $m \cdot s^{-1}$, respectively. For the stationary-point-count diver, bias increased from -0.0004 to 11.89 for fish moving at 0.001 and 1.0 $m \cdot s^{-1}$, respectively. Thus, over a 300 s survey time, fish moving at 1.0 $m \cdot s^{-1}$, a typical speed for reef sharks, were overestimated by more than an order of magnitude (Fig 2.3) by both UVC techniques. For faster moving fish (4 $m \cdot s^{-1}$), the bias increased up to 60 (Fig 2.3). The standard errors (Fig 2.3) show that there is little variation between simulations.

Across all model combinations, fish speed, fish turning angle and survey procedures had varying effects on bias (Fig 2.4). Overall, fish speed had the greatest effect on bias that increased with fish speed up to 61 for the belt-transect and 31 for the stationary-point-count diver for fish moving at 4 $m \cdot s^{-1}$. Survey time and visibility affected the two survey techniques differently. With longer survey times, the belt-transect diver covers more area while the stationary-point-count diver does not. Bias generally increased with survey time; however the bias for the belt-transect diver reached saturation at 1200 s with a maximum bias of 24 while the bias for the stationary-point-count diver continued to increase up to 1800 s with a bias of 15. Under scenarios of increased visibility, the belt-transect diver surveys more of the transect at a given moment but does not increase the area covered (except at the end of the survey). For the stationary-point-count technique, visibility distance represents the radius that is being sampled and therefore increases the area covered. Therefore, bias increased with visibility distance for the belt-transect diver up to a bias of 23 for 40 m visibility and decreased for the stationary-point-count diver from 17 at a visibility of 10 m down to 4 for a visibility of 40 m. For fish turning angle the maximum bias occurred at intermediate turning angles (22.5°) with a bias of 23 and 11 for the belt-transect and stationary-point-count divers, respectively. The area covered by the belt-transect diver increases with transect width and diver speed. Therefore, as both factors increased the overall bias was reduced from 47 to 6 for transect widths of 1 and 20 m, respectively, and from 32 to 11 for diver speeds of 1 to 7 $m \cdot min^{-1}$, respectively. The biases for each combination of the survey parameters (Table 2.1), 16,632 models in total, are listed in Table X (Appendix B).

2.4 DISCUSSION

Our results indicate that mobile fish are over-counted in non-instantaneous UVC. In general, relative bias increased with fish speed but the extent depended on the UVC technique and survey procedure used. Therefore, setting aside all issues of detection, misidentification, recounting and behaviour of the animal in response to the diver, counts obtained by non-instantaneous UVC only provide approximate estimates of true values (e.g. density) for stationary and very slow moving (<0.001 $m \cdot s^{-1}$) animals. For mobile animals, however, caution needs to be applied when using non-instantaneous UVC and the implication of the bias depends on the goal of the study.

When the goal of a scientific study is to examine relative spatial and temporal differences in the density of a single species surveyed under homogenous sampling conditions, non-instantaneous UVC count data may produce satisfactory information. For example, Robbins et al. (2006) utilized constant belt-transect surveys to compare relative abundance of *Triaenodon obesus* Rüppell (whitetip reef) and *Carcharhinus amblyrhynchos* Bleeker (gray reef) sharks along a gradient of fishing pressure. Their conclusions should be valid regardless of the surveys being conducted instantaneously or not, as long as the fish had similar levels of mobility between sites (e.g. not resting and feeding grounds) and surveys were conducted by consistent methods. However, the technique used (i.e. instantaneous or non-instantaneous) would affect the values of absolute density and all descriptions that are based on these values (e.g. biomass and community structure).

Patterns in absolute density are often extrapolated from observed fish counts obtained by UVC, yet whether or not UVC were done instantaneously is rarely reported. We illustrate this point using the data and photos shown of Kingman and Palmyra atolls – the two locations where sharks dominated the top predator biomass and where the highest top predator biomass has been reported for reefs (Fig 2 & 3 in Sandin et al. 2008). Photos are essentially 'instantaneous snapshots' of the reef and represent counts made by instantaneous UVC techniques (Fig 2.5). In both photos, one top predator (i.e. shark) occurred within ~50 m^2 – a density of 0.02 individuals$\cdot m^{-2}$. However, Sandin et al. (2008) reported densities of ~0.2 individuals$\cdot m^{-2}$ for both Kingman and Palmyra, which corresponds to 10 individuals per 50 m^2 belt-transect. If we assume that the most top-predator-rich photos were used to demonstrate their abundance on reefs at Kingman and Palmyra, then the density would have been overestimated by one order of magnitude. Therefore, it is likely that Sandin et al. (2008) used non-instantaneous surveys to count fish.

In most cases where non-instantaneous UVC have been conducted, the true instantaneous density is unknown. In these cases, the factorial biases given in Table X (Appendix B) may be used to explore the effect that fish speed could have on observed densities under different survey procedures. For example, Sandin et al. (2008) used a belt-transect width of 4 m and covered 100 m^2. Table 2.2 shows the section of Table X (Appendix B) that corresponds to these values for a range of fish speeds, with assumptions of visibility = 20 m (presumably a conservative value for the Line Islands), survey time = 300 s, fish turning angle = 45°, diver swim speed = 1 $m\cdot min^{-1}$. Based on the photographs shown in Sandin et al. (2008, Fig 2a) the sharks appear to be grey reef sharks (*C. amblyrhynchos*). Although the average swimming speed of *C. amblyrhynchos* is not known, we presume that based on the swimming speed of other mobile reef sharks like *Carcharhinus leucas* Müller and Henle (bull), *Carcharhinus melanopterus* Quoy and Gaimard (blacktip reef) and *Negaprion brevirostris* Poey (lemon) which have sustained swimming speeds of 1.3, 0.8, and 1.0 $m \cdot s^{-1}$, respectively (Sambilay 1990), that grey reef sharks swim at ~1 $m \cdot s^{-1}$. Therefore, if top predators at Kingman included *C. amblyrhynchos*, the factorial bias would be 21.5 (Table 2.2). Thus, a better estimate of true density may be obtained by standardizing the observed value by the factorial bias, which gives a density of 0.009 $individuals \cdot m^{-2}$ – 9,000 $individuals \cdot km^{-2}$ which is 191,000 fewer $individuals \cdot km^{-2}$ than the density reported. This density estimate is still high compared to densities reported for no-entry zones on the Great Barrier Reef, which puts grey reef sharks at a density of 250 $individuals \cdot km^{-2}$ (Robbins et al. 2006), however, it may be reasonable since the top predator group in Kingman also includes snapper and jack.

Because bias increases with fish speed additional problems occur when animals of different mobility are compared to each other. For example, on Kingman atoll, densities of top predators (sharks, jacks and snappers) and all other fishes combined (Carnivores, Planktivores, Herbivores) were reported as ~0.2 and ~3.7 $fish \cdot m^{-2}$, respectively (Sandin et al. 2008). Because various species have different swim speeds, their densities may be overestimated to different degrees. Thus, their relative contribution to the overall community structure becomes skewed. Moreover, densities have been converted into standing stock biomass to compare the biomass of trophic levels and sites that have different fish assemblages (e.g. DeMartini et al. 2008, Harborne et al. 2008). Since the most mobile fishes tend to be the largest, the effect of bias caused by fish speed would be magnified when comparing biomasses of different trophic levels. For example, UVC data revealed the presence of inverted trophic biomass pyramids (higher top predator biomass compared to other trophic levels) in a few relatively unexploited reefs (Friedlander & DeMartini 2002, Stevenson et al. 2007, Halpern et al. 2008, Sandin et al. 2008) – a phenomenon that has been rarely demonstrated in other ecosystems (Piontkovski et al. 1995, Buck et al. 1996, Gasol et al. 1997). At Kingman atoll, 85% of the total fish biomass was reported to be top predators – ~4 $t \cdot ha^{-1}$ for top predators compared to ~0.8 $t \cdot ha^{-1}$ for other fish (Sandin et al. 2008). Using the same sampling conditions as described above and biases from Table 2.2 the biomass of top predators moving at ~1 $m \cdot s^{-1}$ may have been closer to 0.187 $t \cdot ha^{-1}$. On the other hand, the 'other' fish category comprises many different fish groups (Carnivores, Planktivores, Herbivores) that travel at variable speeds. Unfortunately, there is very limited information on the swimming speed of most reef fishes. A few reef fish species (e.g. damselfish, anemonefish) have reported field swimming speeds of up to 0.2 $m \cdot s^{-2}$ (Johansen et al. 2007); however, these species have such small home ranges that their effective swimming speed is approximately zero for the purposes of this study (unlikely to enter or leave the survey). Although many of the 'other' sampled fish may have swimming speeds faster than 0.2 $m \cdot s^{-2}$, it is possible that the average swimming speed of the 'other' fish combined would have been ~0.2 $m \cdot s^{-2}$ or slower. If this was the case then the 'other' fish biomass may have been ≥0.204 $t \cdot ha^{-1}$, more than that reported for the top predator fish category – a bottom-heavy trophic biomass pyramid.

Although the effect of overestimating biomass would be greatest for the largest and most mobile fishes, like sharks, it would also occur for smaller and less mobile fishes such as parrotfish and grouper. For example, Mumby et al. (2006) compared predator (mostly groupers) and parrotfish biomass within and outside of the Exuma Cayes Land and Sea Park, Bahamas. Their results showed that *Epinephelus striatus* (Nassau grouper) and parrotfish biomass were higher within the park than outside the park. This statement is likely accurate, assuming the sampling conditions were constant between sites (including visibility and diver speed) and that these fishes maintained the same level of mobility between the sites. However, because grouper and parrotfish have different levels of mobility, if non-instantaneous surveys were used then comparison of their biomass may not be made without accounting for mobility and survey effort.

Our results may also extend to studies that have surveyed communities to obtain species richness – where comparisons are made of animals with different levels of mobility. For example, UVC have been used to compare species richness among sites (Ault et al. 2006, Arena et al. 2007, Tittensor et al. 2007). If non-instantaneous surveys were used to compare sites that had different proportions of sedentary and mobile animals (e.g. groupers versus snappers or damselfish versus surgeonfish) then, compounded with the differences in behaviour and detection, bias attributed to mobility would be disproportionate and would lead to inaccurate comparisons due to the methods alone. The same effect would apply to studies that compared densities of fish in different life stages that have different levels of mobility.

Although not stated explicitly in the scientific literature, based on our inquiries, we believe that non-instantaneous visual surveys are used widely. Our results show that these data do not produce reliable estimates of true density and therefore they should only be used to compare relative differences within species. Since these surveys provide valuable baseline and monitoring data that have been collected for years, if not decades, it may be advantageous to continue to collect data in the same manner to ensure they remain comparable. As well, non-instantaneous surveys are beneficial for rare mobile species, like sharks, because they increase their chance of detection. However, for absolute values (i.e. density or biomass) given the huge bias that is produced for mobile fish, other survey techniques such as mark-recapture (i.e. photo ID or artificial marks), which are currently used for whale (Arzoumanian et al. 2005, Bradshaw et al. 2007, Rowat et al. 2009), white (Domeier & Nasby-Lucas 2007, Gubili et al. 2009), sicklefin lemon (Buray et al. 2009), and grey nurse sharks (Van Tienhoven et al. 2007, Bansemer & Bennett 2008) may produce more accurate estimates of absolute density.

2.5 CONCLUSIONS

Our simulation study indicates that the difference between instantaneous and non-instantaneous counts of mobile fish can be significant. Therefore, we urge that the treatment of mobile fish during a census must be reported in the scientific literature. Moreover, if non-instantaneous UVC have been used, survey procedures need to be accounted for when estimating density or biomass of mobile species. Studies that have reported results based on non-instantaneous surveys may need to reanalyze their data to determine if the general conclusions remain. Our simulation model *AnimDens* may be used to evaluate possible biases for species of different mobility under different survey procedures. Overall, our results have significant consequences for management and conservation decisions because they demonstrate that densities of highly mobile species, such as sharks, may be much less than reported. However, accurate estimates of fish density and biomass are essential to set reasonable management and conservation targets. Overestimates can lead to enlarged quotas for exploitation as well as inadequate protection status.

Table 2.1 Levels of each predictor variable used to examine the bias in fish counts produced by fish speeds and survey procedures. Each combination of the values was run for 1 simulation.

Fish speed ($m{\cdot}s^{-1}$)	Survey time (s)	Visibility (m)	Transect width (m)	Diver speed ($m{\cdot}min^{-1}$)	Fish turning angle (°)
0	60	10	1	1	1
0.001	300	20	2	4	22.5
0.01	600	30	4	7	45
0.1	900	40	5		
0.2	1200		8		
0.4	1800		10		
0.6			20		
0.8					
1					
2					
4					

Table 2.2 Relative and factorial (= relative +1) bias for different fish speeds for belt-transect surveys where survey time = 300 s, transect width = 4 m, visibility distance = 20 m, diver speed = 1 $m \cdot min^{-1}$, fish turning angle = 45°. The diver visually surveyed an area of 100 m^2.

Fish speed ($m \cdot s^{-1}$)	Relative bias	Factorial bias
0	0.01	1.01
0.001	0.03	1.03
0.01	0.13	1.13
0.1	1.28	2.28
0.2	2.92	3.92
0.4	6.72	7.72
0.6	10.99	11.99
0.8	15.47	16.47
1	20.51	21.51
2	47.99	48.99
4	107.97	108.97

Figure 2.1 Example simulations showing the movement of fish at speeds of 0, 0.5 and 1.0 $m \cdot s^{-1}$ (top to bottom). Two divers were simulated, the stationary-point-count diver remained in the centre of the sampling area (circle) and the belt-transect diver followed a straight path (bold solid line).

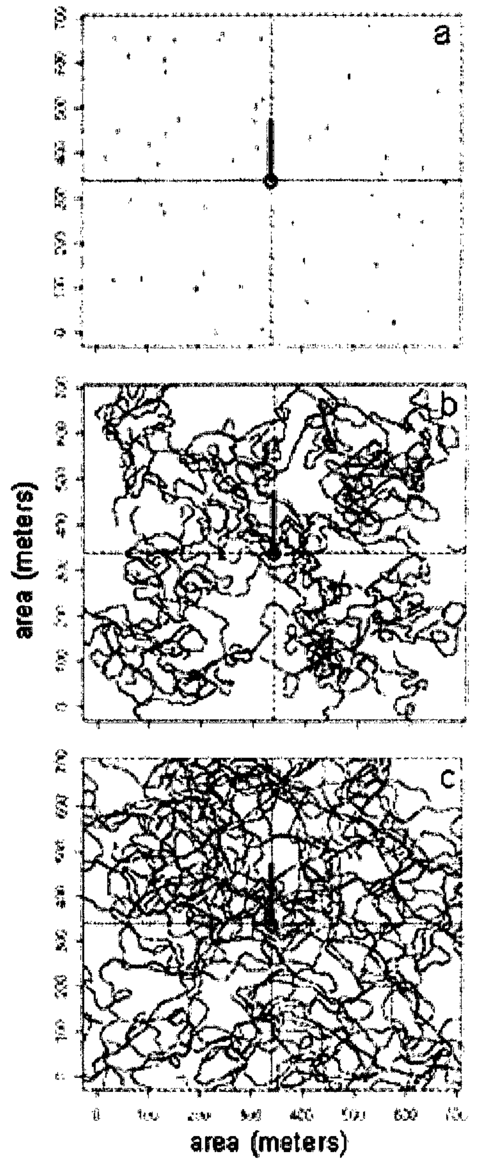


Figure 2.2 Diagram of the visual sampling field for the belt-transect diver (left) and the stationary-point-count diver (right). Symbols: a_t is the total area surveyed by the belt-transect diver; va_t is the area visually surveyed by the belt-transect diver in one time step; tw is the width of the belt-transect; v is the visibility distance; a_s is the total area surveyed by the point count diver; va_s is the area visually surveyed by the point count diver in one time step.

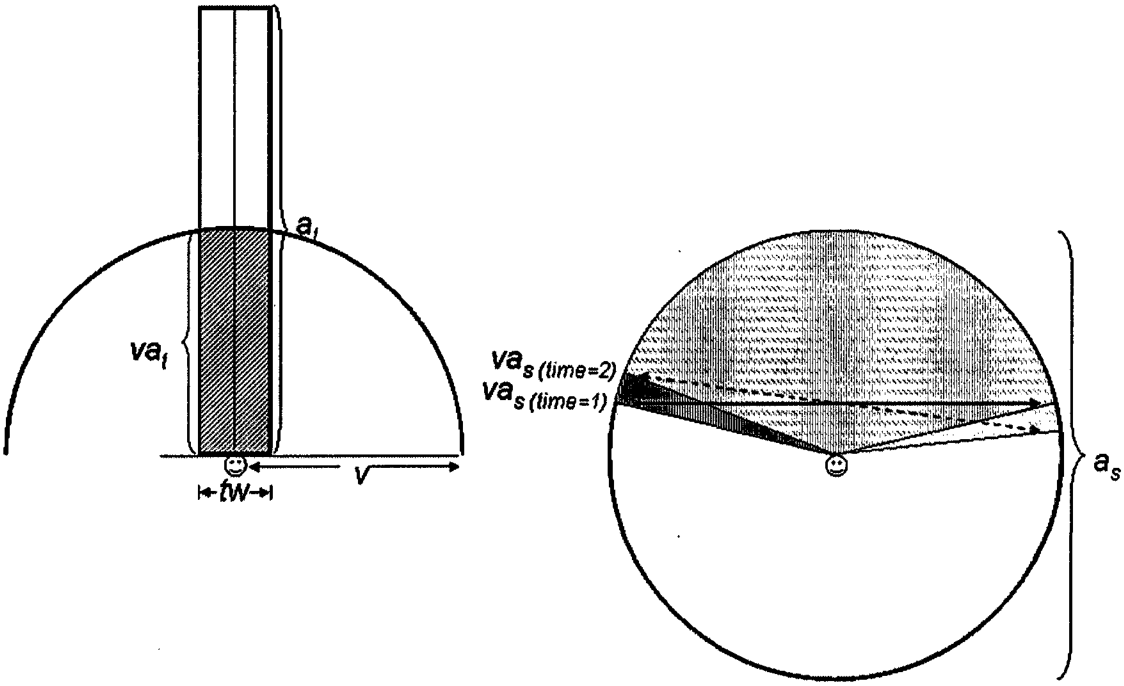


Figure 2.3 Comparison of fish speed with relative bias [(observed count – expected count) / expected count] for belt-transect (a) and stationary-point-count (b) divers for survey time = 300 s, visibility = 13 m, transect width = 4 m, stationary-point-count radius = 7.5 m, diver speed = 4 m·min^{-1}, and fish turning angle = 45°. Shown are the mean values across 30 simulations (x and o) with standard errors (dashed lines).

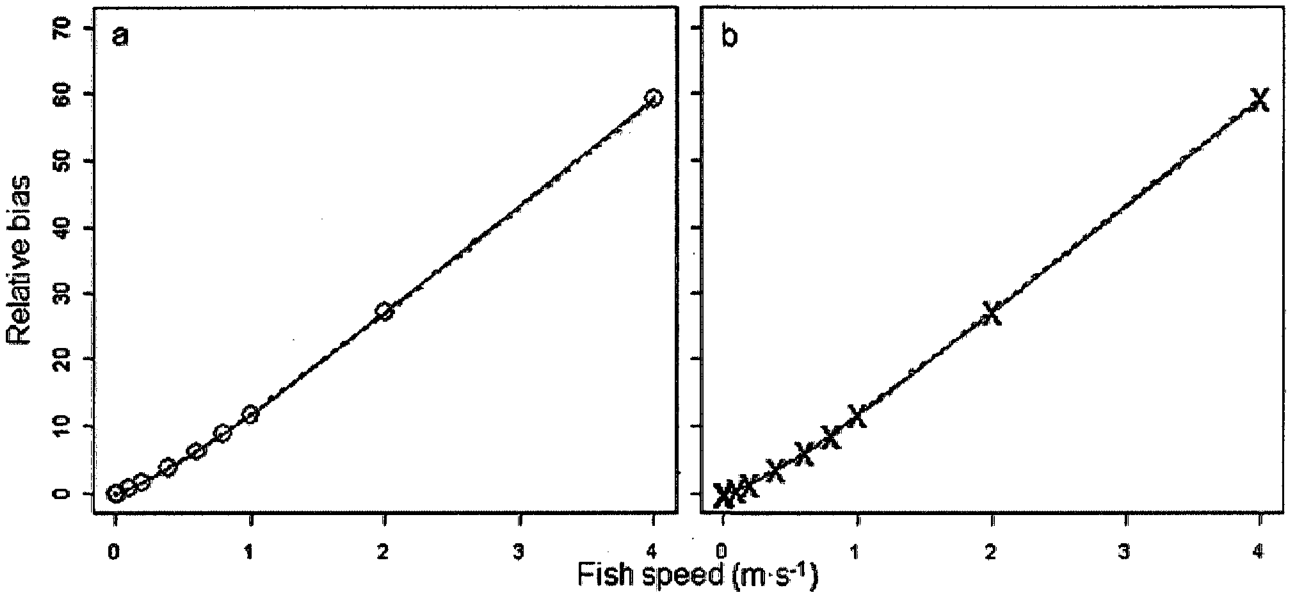


Figure 2.4 The effect of each predictor variable on the average relative bias (solid lines), dashed lines represent ± S.E, across all model combinations. See Table 2.1 for details on predictor variables. x = Belt-transect diver, ◇ = Stationary-point-count diver. Panels e and f are only applicable to the belt-transect.

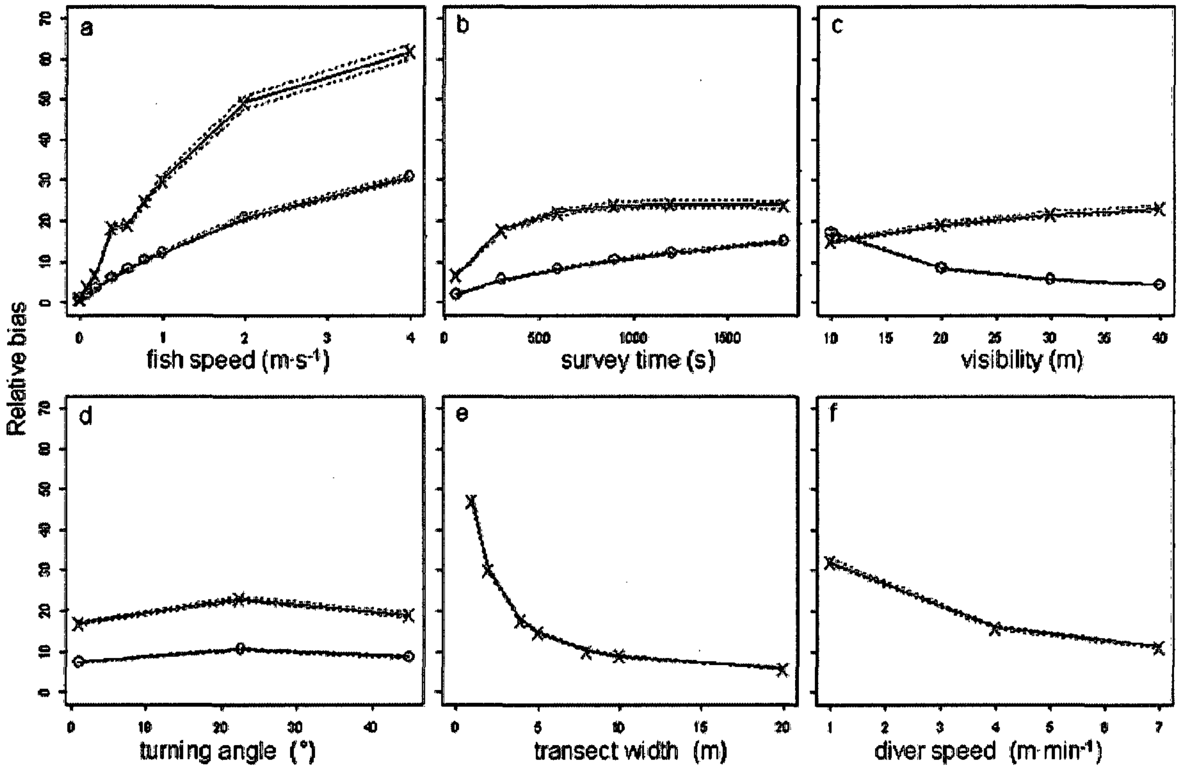
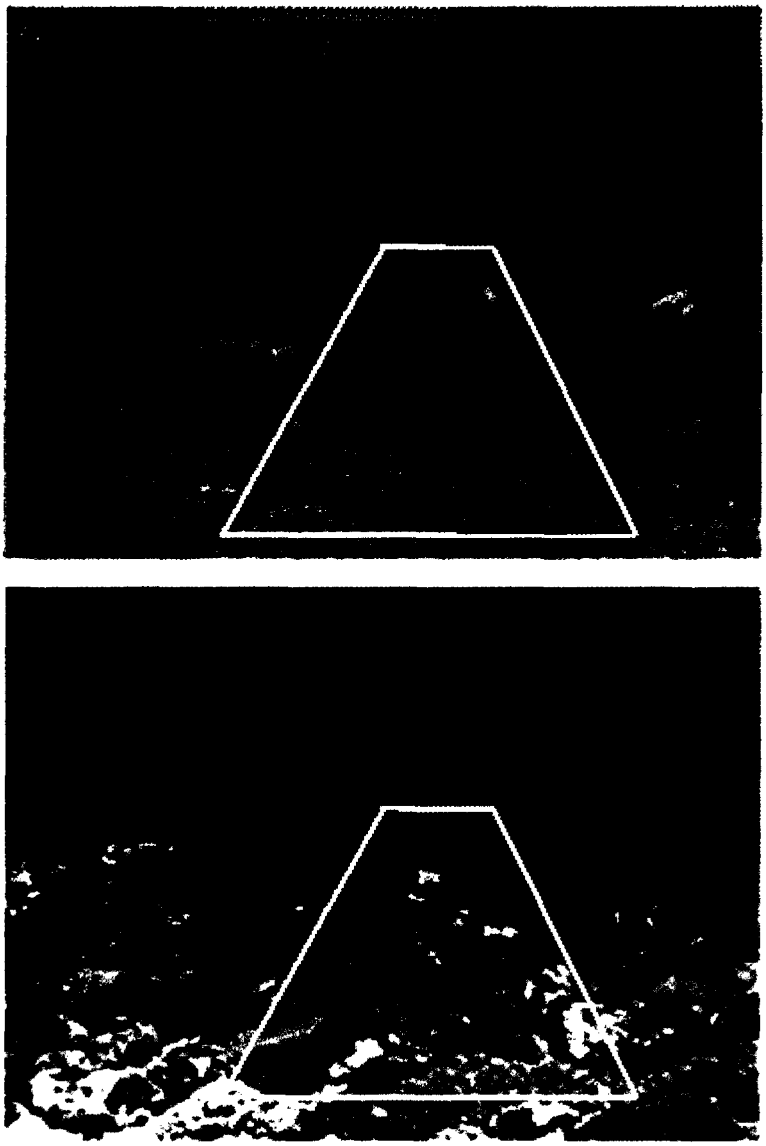


Figure 2.5 Illustration of an instantaneous count (snapshot) of sharks in a belt-transect UVC (photos from Fig 2a and 2c in Sandin et al. 2008). To visualize the area that would be covered by a belt-transect, we have drawn in the approximate survey boundaries of a 50 m^2 transect (~4 m wide x 12.5 m long which is represented by visibility distance). Sandin et al (2008) covered 100 m^2 (4 m wide x 25 m long) per transect – approximately double the area outlined.



CHAPTER 3

ASSESSING THE PRECISION OF NON-SCIENTIFIC DIVERS FOR CENSUSING VULNERABLE FISH

3.1 INTRODUCTION

Recent widespread evidence documenting large-scale shifts in many elasmobranch populations (Dulvy et al. 2000, Baum & Myers 2004, Shepherd & Myers 2005, Theberge & Dearden 2006) has spurred conservation concerns and more conservation-focused research (Pikitch et al. 2005, Duncan & Holland 2006, Yokota & Lessa 2006, Wiley & Simpfendorfer 2007). This change in perspective has been accompanied by a shift in research methodology from one documenting patterns in population distribution (Gudger 1934, 1939a, Gilbert & Springer 1963) and community composition (Coles 1919, Springer 1938, Hutton 1959), to a more predictive framework of population trends based on meta-analysis of fisheries data and population modeling (Pitcher 2001, Baum & Myers 2004, Myers & Worm 2005, Shepherd & Myers 2005, Ferretti et al. 2008). However, this shift has not addressed the fundamental problem with censusing elasmobranch populations, which is that long-lived and potentially rare and declining species continue to be decimated, and in some cases they are removed for the sole purpose of censusing (Simpfendorfer & Milward 1993, Carlson & Cortes 2003, Lombardi-Carlson et al. 2003, Myers et al. 2007). Given that many shark species have declined to dangerously low levels of abundance (Baum & Myers 2004, Shepherd & Myers 2005, Theberge & Dearden 2006, Ferretti et al. 2008), there is an immediate need to implement non-extractive methods of censusing these highly vulnerable species.

Growing appreciation of sharks has generated considerable increase in the number of benign encounters between humans and sharks, namely through diving expeditions. Because elasmobranchs are highly mobile, widely distributed, relatively rare fishes with large home ranges it is not logistically or economically feasible for scientists to conduct enough visual censuses for broad-scale trend analysis. However, since elasmobranchs are also conspicuous species that inhabit a wide range of depths, temperatures, and habitats, it may be possible to enlist professional and recreational scuba divers, with their wide variety of interests, to collect valuable data on their occurrence and abundance.

Three commonly used underwater visual census (UVC) techniques that have been deployed to enumerate fish in-situ are the belt-transect, stationary point count and roving diver techniques. The belt-transect (Brock 1954) and stationary point count techniques (Bohnsack & Bannerot 1986) are the most common census methods used by scientists (Friedlander & DeMartini 2002, DeMartini & Friedlander 2004, Hawkins & Roberts 2004, Frias-Torres 2006, Arena et al. 2007, Sandin et al. 2008, Williams et al. 2008). Although the stationary point count technique has not been used as widely it is thought to be superior for censusing highly mobile fishes because no transect is laid and there is a period of acclimation where the diver remains still prior to commencing the census (Thresher & Gunn 1986), thereby increasing the detection of mobile fishes. Although the precision of the belt-transect and stationary point count techniques has been repeatedly assessed (Thresher & Gunn 1986, Cheal & Thompson 1997, Samoilys & Carlos 2000, Willis 2001), their accuracy for estimating elasmobranch abundance has only recently been analyzed (Ward-Paige et al. Chapter 2).

The third UVC method, the roving diver technique, is rarely the method of choice for scientific studies, however, it has likely been deployed more times than all other census techniques combined and is commonly used by recreational divers. The roving diver technique was designed by the Reef Environmental Education Foundation (REEF: www.reef.org) and deployed in the greater-Caribbean since 1993 to involve the general diving community in data collection and to increase the overall monitoring effort, and has >100,000 surveys submitted to date. This method is quick, easy and requires minimal set-up and instruction, with most of the training directed towards species identification. So far, the REEF data has been used to examine hot-spots in non-native marine fishes (Semmens et al. 2004), to estimate species richness and evenness in no-take and open areas (REEF 2001), and to explore general spatial and temporal trends in fish populations (REEF 2002, Stallings 2009). Yet no study has compared the detection rates of the roving diver to the more established belt-transect and stationary point count techniques.

Here, we examine the precision of non-scientific observer collected data for monitoring elasmobranch populations. Using the simulation program *AnimDens* (Ward-

Paige et al. Chapter 2) we examine the level of detection for the roving, belt-transect, and stationary point count UVC techniques over a range of fish speeds, densities and survey-times. Then, we use field studies to explore the level of experience required for divers to detect and precisely count the number of elasmobranchs present at a site, and examine the variance that is produced by elasmobranch density. In the discussion, we investigate the precision of other non-scientific observers in monitoring birds and suggest that non-scientific observer data collected opportunistically (i.e. without rigorously controlled site selection and data collection) can produce relatively reliable data for assessing trends in animal populations.

3.2 METHODS

3.2.1 COMPARING UVC TECHNIQUES

Scientists commonly utilize the belt-transect or stationary point count UVC techniques to count reef fishes. However, it is likely that the roving diver technique, deployed by volunteer divers, has been used more often than all other scientific UVC combined. To compare the results gained by these different UVC techniques, we used a simulation approach. The simulation program *AnimDens* (Ward-Paige et al. Chapter 2) was developed to simulate divers deploying the belt-transect and stationary point count UVC techniques. Here, we expand the model to compare detection rates of the commonly used scientific UVC methods with the roving diver technique used by recreational divers. The *AnimDens* simulation model provides a two-dimensional simulation of the visual census procedure representing both the movement of the divers and the fish at different densities and speeds (Fig. 1).

For simplicity, the model assumed a sample area that was featureless, flat and 1 m deep. For each simulation, a diver from each of the three census methods was placed in the centre of the sample area with the same original orientation. The sample area was populated with fish that had a random distribution and random initial orientation.

In the stationary point count technique, surveyors remain still and record fish observed within a fixed distance (Bohnsack & Bannerot 1986). In the belt-transect, divers swim along a straight line and record the animals they observe directly in front of them within a fixed distance of the line (Brock 1954). In the roving-diver technique, the surveyor records the fish they observe, regardless of direction or distance as long as a reliable identification can be made, as they follow their regular dive activities (Schmitt et al. 1993). Once the simulation started, the stationary diver remained still, the transect diver moved straight forward at 4 $m \cdot min^{-1}$ (Jones & Chase 1975). The roving diver moved at 4 $m \cdot min^{-1}$ in a direction that changed within a random range of $\pm 4° \cdot 2\ s^{-1}$, which was based on observations of recreational divers in the field. At each time step the divers count the fish they observe within the sample area. Although divers continuously count fish during field surveys, for time sake, we set the time step to 2 s.

Each run contained fish densities that ranged from 2×10^{-6} to 2×10^{-1} $fish \cdot m^{-2}$, which is approximately the maximum density reported for apex predators (Sandin et al. 2008). The fish were set to move at speeds of 0, 0.4, and 1.0 $m \cdot s^{-1}$, covering reasonable values attained by reef sharks (Webb & Keyes 1982). The direction of the fish was allowed to change within a random range of 45° left or right from the previous direction at each time step, which was based on personal observations of reef sharks (e.g., Caribbean reef shark *Carcharhinus perezii*, blacktip shark *C. limbatus*, blacktip reef shark *C. melanopterus*).

In each run, sharks and divers moved for 300 or 3600 seconds. The distance and angle between the three divers and each fish was calculated every two seconds to determine if the fish were within the field of view of the diver. For the stationary point count diver, all fish within 7.5 m and a field of view of 160° of the diver's orientation were detected. For the belt-transect diver, all fish directly in front of their position, within ±2 m of the transect line, to a distance equal to maximum visibility were recorded. For the roving diver, all fish within a distance of maximum visibility and a field of view of 160° of the diver's orientation were recorded. Note that fish that entered the survey area after the survey started were counted (i.e. non-instantaneous) and that the divers did not recount the fish they already recorded as they strive to do in the field (Brock 1954, Thresher & Gunn 1986). This simulation experiment was designed to compare the detection rates among the three different UVC methods for differing fish densities and speeds. Each model combination (Table 1) was run for 30 simulations. The means and standard errors are presented.

3.2.2 EVALUATING THE PRECISION OF COUNTS BY FIELD DIVERS

Field studies were conducted to examine the influence of diver experience on the precision of detection and number of sharks or rays reported and the variance that is produced by shark density. Opportunistic surveys were carried out on tourist dive boats off the island of Koh Phi Phi, Thailand, in May 2008. Boats containing recreational and professional scuba divers were invited to participate. Dive teams consisted of at least one dive instructor and their clients who had a range of diving experience. On most occasions, several dive teams operated from the same boat and traveled in different directions. All divers were made aware of the project prior to the dive and asked to keep track of the number and species of sharks or rays they saw on each dive. Participants were instructed not to talk about their observations until the data was collected.

A total of 145 divers, 48 professional (e.g. dive instructors with >500 dives) and 97 recreational, with diving experience ranging from 2 to 5000 dives participated in the field survey. These were grouped into inexperienced divers (<20 dives: the number of dives required to begin a PADI Divemaster course; n = 28 divers) and experienced divers (>20 dives; n = 117 divers), with some divers being present on multiple dives. In teams of 2-9 (mean = 3.5), divers entered the water with an unknown number of sharks and rays, and were asked to conduct their normal dive activities, but to count the number of different sharks and rays they saw for each species. There were 1-12 different teams diving at the same time on a given dive (total number of dives = 7). Following the dive, participants were asked to report: 1) team number, 2) the number of dives they have done in their life, and 3) the number of sharks and rays they saw of each species on each dive.

Based on the collected data, we first evaluated whether inexperienced divers could detect the presence of sharks as well as experienced divers. To do this, we compared the presence or absence response of each shark or ray species for each diver to the response (e.g. presence) of their dive team (teams consisting of >2 divers: n = 37) for dives where at least one shark or ray was reported (number of dives: n = 5). We assumed no false detections, where the report of the presence of a shark or ray was a correct response (e.g. they did not mistake another fish type for a shark or ray). Therefore, if a diver did not detect the presence of sharks or rays on a dive, but their dive team did, then the difference from the team for that diver would be one. However, if the diver and the team reported the same presence or absence, then the difference from the team would be zero. Diver experience (total number of dives in their life) was then compared to the difference between the diver and their team response. We also evaluated the variability of responses among inexperienced (<20 dives) and experienced (>20 dives) divers.

Again, using teams with > 2 divers and dives where at least one shark or ray was reported, we determined how much experience was required to precisely count the numbers of sharks or rays on a dive (number of divers = 116). Therefore, diver experience was compared to the difference between the number of sharks reported by each diver and the mean number of sharks reported by the dive team. We also examined the variability of counts between inexperienced and experienced divers.

Finally, using the entire database (including teams of one and dives where zero sharks or rays were seen) we examined the variability in counts that was produced by the number of elasmobranchs present on a site. To do this, we compared the mean number of elasmobranchs observed on a dive across all dive teams to the mean reported by each team. Here, we assume that the team mean is the most precise count of elasmobranchs present on the site.

3.3 RESULTS

3.3.1 COMPARING UVC TECHNIQUES

Over 30 simulations, the roving diver technique detected fish at lower densities than the belt-transect or the stationary point count techniques for all fish speeds and survey-times of 300 and 3600 seconds (Fig. 2); however, the difference was diminished with faster fish speeds. As well, the roving diver technique detected fish more often at all fish speeds and densities, with the exception of the highest fish densities where all three methods detected fish 100% of the time. For example, for 300 second survey-times, the roving diver technique started to detect stationary fish at densities one order of magnitude lower (i.e. 13% sighting frequency at a true density of $2\text{x}10^{-4}$ fish$\cdot m^{-2}$) than both the transect and stationary point count techniques over 30 simulations (Fig. 2a). At fish speeds of 1.0 $m\cdot s^{-1}$, all three methods detected fish at a true density of $2\text{x}10^{-5}$ fish$\cdot m^{-2}$, the roving diver detected fish on 7% of the simulations while the stationary or belt-transect divers detected fish 3% of the time (Fig. 2e). However, at higher densities, the effect of fish speed and survey-time was negligible and all three methods reliably detected the presence of fish in the survey area. Survey-time also affected the detectability of fish, with the effect being diminished with increased fish speed and density. For example, fish traveling at 0 $m\cdot s^{-1}$ were detected by all three methods at a true density of $2.0 \text{ x } 10^{-3}$ fish$\cdot m^{-2}$, while they were detected by all three methods at $2.0 \text{ x } 10^{-4}$ fish$\cdot m^{-2}$ for survey-times of 3600 s, one order of magnitude lower.

3.3.2 PRECISION OF DETECTION AND COUNT BY FIELD DIVERS

Participant diving experience did not affect the detection of sharks and rays (Fig. 3). Over 116 individual dives, seven differed from their team in terms of detection. The mean dive experience of these 7 participants was 517 (± 215 S.E.) dives. Only one of these participants had <20 dives, two had 20-30 dives, and the other four had ≥500 dives - arguably experienced divers. The overall variability between inexperienced and experienced divers was not significantly different (Chi-squared $p = 0.86$).

Inexperienced divers also reported similar counts of sharks and rays compared to experienced divers (Figure 4a). The variability amongst the most experienced divers

(≥1000 dives) was ≤1.3 elasmobranchs (Fig. 4a). All outliers (n = 4) that were more than two times this value (>2.6 sharks) occurred for divers with ≤20 dives. Although the overall variability was greater for the inexperienced divers (differing by up to 5 elasmobranchs; Bartlett's K-squared, $p<0.0001$), the means were not significantly different (t-test, $p = 0.89$) (Fig 4b).

Overall variability in the number of elasmobranchs reported by each team increased when there were more elasmobranchs present on a site (Fig 5). When the overall dive mean (across all teams combined) was <1 elasmobranch, the overall variance reached two, or two times the mean. When the overall dive mean was three elasmobranchs, then the variance reached 12, or 4 times the mean.

3.4 DISCUSSION

As expected, given the amount of area covered per unit time, the roving diver technique detected the presence of fish at lower densities than both the belt-transect and stationary point count techniques. However, the difference between these three methods was reduced with faster moving fish. In the field, diver experience did not appear to influence the detection of elasmobranchs. Although elasmobranch counts were similar amongst inexperienced and experienced divers, the overall variability in the number of elasmobranchs reported was greater for inexperienced divers. However, the abundance of elasmobranchs on a site seemed to produce more variability than the experience of the divers.

Under the conditions of our simulation, the roving diver technique was not inferior to the other UVC techniques. Our simulation results show that the roving diver technique, which is most commonly applied by recreational divers, is the most adept for providing presence data on low density, conspicuous fishes like elasmobranchs. Although this difference was largely a result of the roving diver covering more area during a survey, the difference in detection rates between the three UVC techniques was reduced with increased fish density, fish speed and survey-time – assuming that all methods counted fish they detected after the survey started. As well, because the roving diver technique censuses all fish from the beginning to the end of a dive, it would have the added benefit of capturing highly mobile species that may be wary or curious of divers (Bres 1993, Kulbicki 1998, Martin 2007, Quiros 2007), and seen at the beginning or end of a dive and would be missed by the other two UVC techniques that require an initial set-up period. Additionally, the two scientific techniques do not commence until the diver is in place, usually near the bottom, therefore limiting searches to a fixed vertical distance from the bottom substrate, whereas the roving diver technique includes all species observed, regardless of their location in the water column. Therefore, the roving diver technique should be better suited for detecting species that occupy pelagic (e.g. blacktip shark *Carcharhinus limbatus*) and surface (e.g. whale shark *Rhincodon typus*) waters.

A drawback of the roving diver technique is that the method does not report the area covered during a survey, which is essential for estimating density. However, if effort (visibility and bottom time) and environmental characteristics (habitat type, depth, date) are recorded for each dive, the data can be standardized and relative changes through space and time can be determined using generalized linear models (Ward-Paige et al. Chapter 4). In this way, data can be analyzed as presence and absence data, which is a sensitive measure of population change when few individuals are usually seen (Pattengill-Semmens 2002). Because elasmobranchs are often observed as individuals (solitary) or in relatively small groups (Bres 1993), trends observed in presence and absence data should provide useful monitoring information.

As well, the roving diver technique does not require fish length to be reported, which excludes analyses of biomass. Addition of this measurement to the roving diver technique would be problematic since making accurate measurements requires additional training (Darwall & Dulvy 1996) and is time consuming, which would decrease the time spent enumerating fish and would likely lower volunteer participation.

In addition to comparing these three censusing techniques, our simulation results give insight into the true density of a population based on the detection rate (i.e. presence and absence rate) of a species for a given survey type. For example, if a study utilizing 4 m wide belt-transects for 5 min traveling at 4 $m \cdot min^{-1}$, detected the presence of a stationary animal on 40% of its surveys, then the true density of that animal would be approximately 1.0×10^{-3} $individuals \cdot m^{-2}$. However, for animals moving at 1.0 $m \cdot s^{-1}$, under the same sampling scenario as above, the true density would be closer to 1.0×10^{-4} $individuals \cdot m^{-2}$, or one order of magnitude smaller. Obtaining approximate density estimates this way could be very useful for rare species, like sharks, that are often disregarded because individuals rarely enter survey boundaries.

Under the conditions of our field experiments in Thailand, we found that inexperienced divers (those with <20 dives in their life) detected the presence of elasmobranchs as well as experienced divers. This is important because presence and absence data alone can provide valuable information that can be utilized to monitor trends in abundance, distribution and diversity (Wilson & Shmida 1984, Strayer 1999, Royle & Nichols 2003, Ward-Paige et al. Chapter 4, Ward-Paige et al. Chapter 5). And, since many elasmobranchs are often seen singly or in small groups (Bres 1993), we chose to model the data simply as presence and absence rather than the binned abundances. Our results also indicate that counts of elasmobranchs obtained from inexperienced divers are precise compared to experienced divers. Although the absolute value of the outliers was greater for inexperienced divers, the inexperienced divers were just as likely to underestimate abundance as they were to overestimate abundance. Interestingly, the abundance of elasmobranchs on a dive seemed to be more important in the variation of the number reported than the experience of the divers, where higher variability occurred when there were more elasmobranchs present. This suggests that even inexperienced divers can provide valuable data on the presence and abundance of sharks and rays that would be within the variation of those reported by experienced divers. This would be especially true for rarely encountered, conspicuous species such as sharks and rays which are hard to overlook. Although there are only a few large-scale marine monitoring programs that use volunteer data (e.g. REEF, ECOCEAN) to assess populations, our results indicate that a wider use may be valuable for conspicuous fishes like sharks and rays.

Although our results suggest that observations made by non-scientific observers show promise for divulging important trend information for conspicuous species, like elasmobranchs, the limitations of this type of data need to be considered. As we did not perform trials of identification between inexperienced and experienced divers, although all participants in the field study reported the same species as their respective team, we argue that the mistakes in identification would be comparatively minimal for elasmobranchs. A number of elasmobranchs occupy the same niche and have similar morphologies (e.g. blacktip, *Carcharhinus limbatus* and spinner, *C. brevipinna*); however, relative to other groups of animals (e.g. birds and teleost fishes) that are regularly censused by visual observers, there are few elasmobranchs that can be misidentified. For example, analysis of the known minimum depth of all elasmobranchs, puts only 187 sharks and 216 rays and skates in the world within a reasonable maximum depth range obtained by recreational divers (set to 35 m) – many of which are unmistakable (e.g. whale shark, *Rhincodon typus*) or are too rare to be seen by a diver (e.g. Irrawaddy river shark, *Glyphis siamensis*). By comparison, >549 birds are surveyed by non-scientific observers in North America alone (Butcher & Niven 2007). And, because elasmobranchs are diverse and occupy specific habitats, few species with similar morphologies overlap, which should make identification relatively easy. As well, it has been shown that divers drastically improve their fish identification within just one census (Darwall & Dulvy 1996), indicating that little experience is required to sufficiently identify individuals.

In the past, there may have been some reluctance to use opportunistic observations made by scuba divers because they have a range of experience, survey locations are not randomly selected and effort is not standardized. However, in the terrestrial realm, volunteer data have been collected for decades to survey birds in the Christmas Bird Count (CBC; www.audubon.org/bird/cbc/) and the Breeding Bird Survey (BBS; www.pwrc.usgs.gov/BBS/). Although both surveys are collected by volunteers, the BBS is thought to provide much more reliable data than the CBC (Dunn et al. 2005) because surveys are conducted on fixed sites by highly skilled observers at a predetermined period of time. The CBC, on the other hand, is conducted by observers with a range of birding experience at sites selected by the observers sometime over a three-week period. However, comparing 40-year trends of 309 bird species monitored in the CBC and the BBS (data from Butcher & Niven 2007), found that 82% of the species had the same overall trend within a 4% difference, 59% within a 2% difference and 30% had <1% difference (see Table 2 for a breakdown by Order). Inspection of bird types showed that most species within each Order (50% or higher) had trend estimates with <4% difference. Cuculiformes, Gaviiformes, Strigiformes, Coraciiformes, and Piciformes had ≥90% of their species with comparable estimates – most of these are mainly solitary, easily identified, relatively large or conspicuous birds that occupy habitats that leave them relatively exposed (e.g. on a lake or exposed perch) and are likely comparable to many large elasmobranchs in the marine realm. On the other hand, in the Passeriformes (perching birds), which are highly diverse (consisting of more than one half of all bird species) and range widely in size, plumage brightness, and habitat occupancy, 88% of the species were still within 4% agreement in their trend estimates (36% within 1% difference) and may be comparable to the smaller sharks or rays. These findings indicate that broad-scale and long-term temporal trend estimates obtained from observers with a range of observation experience on flexible survey routes are likely comparable to those collected by highly skilled observers on standardized survey routes.

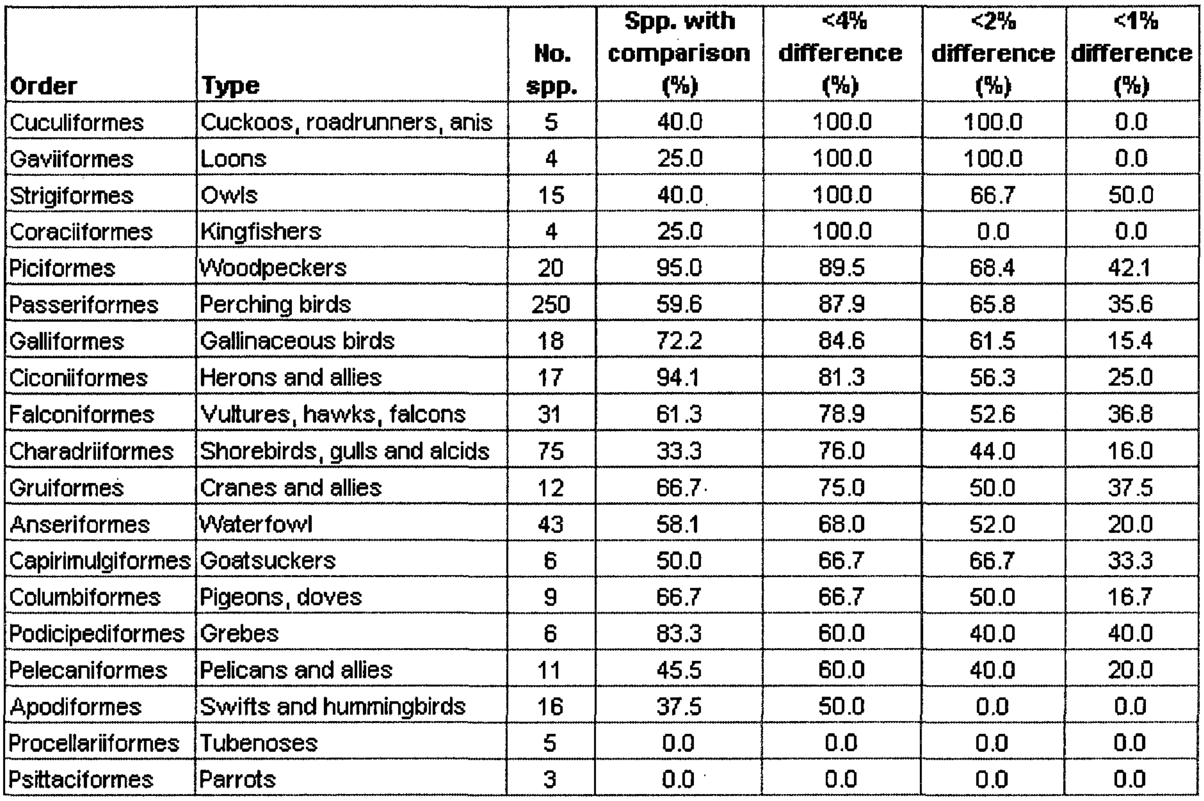
Similarly, other studies have investigated the precision of volunteer data and the value they provide for different monitoring efforts. It has been demonstrated that volunteers reliably identify and detect the presence of frog and toad (Genet & Sargent 2003) and reef fish species with very little training. In a comprehensive study of the monitoring practices of many different species groups (e.g. amphibians, birds, reptiles, insects, plants), it was discovered that with state-of-the-art survey design and data analysis, volunteer-based schemes provide relatively reliable data that can yield unbiased results (Schmeller et al. 2009). The case for using volunteer observations for elasmobranchs is further strengthened by the fact that it is essential to have frequent, regularly monitored sites (Brashares & Sam 2005, Schmeller et al. 2009), and because the number of sites is maximized by volunteer involvement (Schmeller et al. 2009).

Although there is no replacement for the data provided by expert scientific observers, we suggest that non-scientific divers, reporting their observations from daily dive activities, could provide invaluable broad-scale and long-term information that would allow for early identification of changes in elasmobranch and other fish populations. Promoting non-scientific divers to commence recording their observations should be implemented immediately around the globe. In the greater-Caribbean, trained volunteer divers have been collecting fish data from their daily dive activities for REEF since 1993. These data have been used to study diversity patterns and population trends in marine fish in the Caribbean (Brittingham & Temple 1983, REEF 2002, Stallings 2009) and long-term broad-scale trends in elasmobranchs (Ward-Paige et al. Chapter 4, Ward-Paige et al. Chapter 5). However, if collected, similar data recorded by divers could be used to analyze trends in elasmobranch and other fish populations in many other regions worldwide. These data can not only be used to compare current observations with historical anecdotes from the scientific and grey literature, they can also provide baseline data for changes that occur in the future. For example, if we gather observation records from areas today that have no elasmobranch sightings, we can monitor changes to their abundance as marine protection measures are implemented.

Table 3.1 Variable values used in the simulation *AnimDens*.

True density (fish·m^{-2})	Fish speed (m·s^{-1})	Survey-time (s)	Visibility (m)	Transect-width (m)	Stationary radius (m)	Diver speed (m·min^{-1})
2.0×10^{-6}	0	300	13	4	7.5	4
2.0×10^{-5}	0.4	3600				
2.0×10^{-4}	1.0					
2.0×10^{-3}						
2.0×10^{-2}						
2.0×10^{-1}						

Table 3.2 Comparison of 40-year trend estimates produced by the CBC and BBS (data published in Butcher 2007). Bird species are summarized by Order. Listed are the total number of species investigated (No. spp.), the percent of species that had 40-year trend estimates from both the CBC and BBS (Spp. with comparison), the percent of the comparable species that had similar trend estimates within <4, <2 or <1% difference reported in Butcher (2007).



Order	Type	No. spp.	Spp. with comparison (%)	<4% difference (%)	<2% difference (%)	<1% difference (%)
Cuculiformes	Cuckoos, roadrunners, anis	5	40.0	100.0	100.0	0.0
Gaviiformes	Loons	4	25.0	100.0	100.0	0.0
Strigiformes	Owls	15	40.0	100.0	66.7	50.0
Coraciiformes	Kingfishers	4	25.0	100.0	0.0	0.0
Piciformes	Woodpeckers	20	95.0	89.5	68.4	42.1
Passeriformes	Perching birds	250	59.6	87.9	65.8	35.6
Galliformes	Gallinaceous birds	18	72.2	84.6	61.5	15.4
Ciconiiformes	Herons and allies	17	94.1	81.3	56.3	25.0
Falconiformes	Vultures, hawks, falcons	31	61.3	78.9	52.6	36.8
Charadriiformes	Shorebirds, gulls and alcids	75	33.3	76.0	44.0	16.0
Gruiformes	Cranes and allies	12	66.7	75.0	50.0	37.5
Anseriformes	Waterfowl	43	58.1	68.0	52.0	20.0
Capirimulgiformes	Goatsuckers	6	50.0	66.7	66.7	33.3
Columbiformes	Pigeons, doves	9	66.7	66.7	50.0	16.7
Podicipediformes	Grebes	6	83.3	60.0	40.0	40.0
Pelecaniformes	Pelicans and allies	11	45.5	60.0	40.0	20.0
Apodiformes	Swifts and hummingbirds	16	37.5	50.0	0.0	0.0
Procellariiformes	Tubenoses	5	0.0	0.0	0.0	0.0
Psittaciformes	Parrots	3	0.0	0.0	0.0	0.0

Figure 3.1 Example simulations showing the movement of fish with densities of 2 x 10^{-5} and 2 x 10^{-4} fish·m^{-2} (columns, from left to right) that moved at speeds of 0, 0.4 and 1.0 m·s^{-1} (rows, from top to bottom). Three divers were simulated, the stationary point count diver remained in the centre of the sampling area (circle), the belt-transect diver followed a straight path (bold straight line), and the roving diver followed a directed random path (bold curved line) over a 60 minute survey time. Belt-transect and roving divers travelled at 4 m·min^{-1}. The area recorded by each diver is approximated by the length and width of the line that represents them.

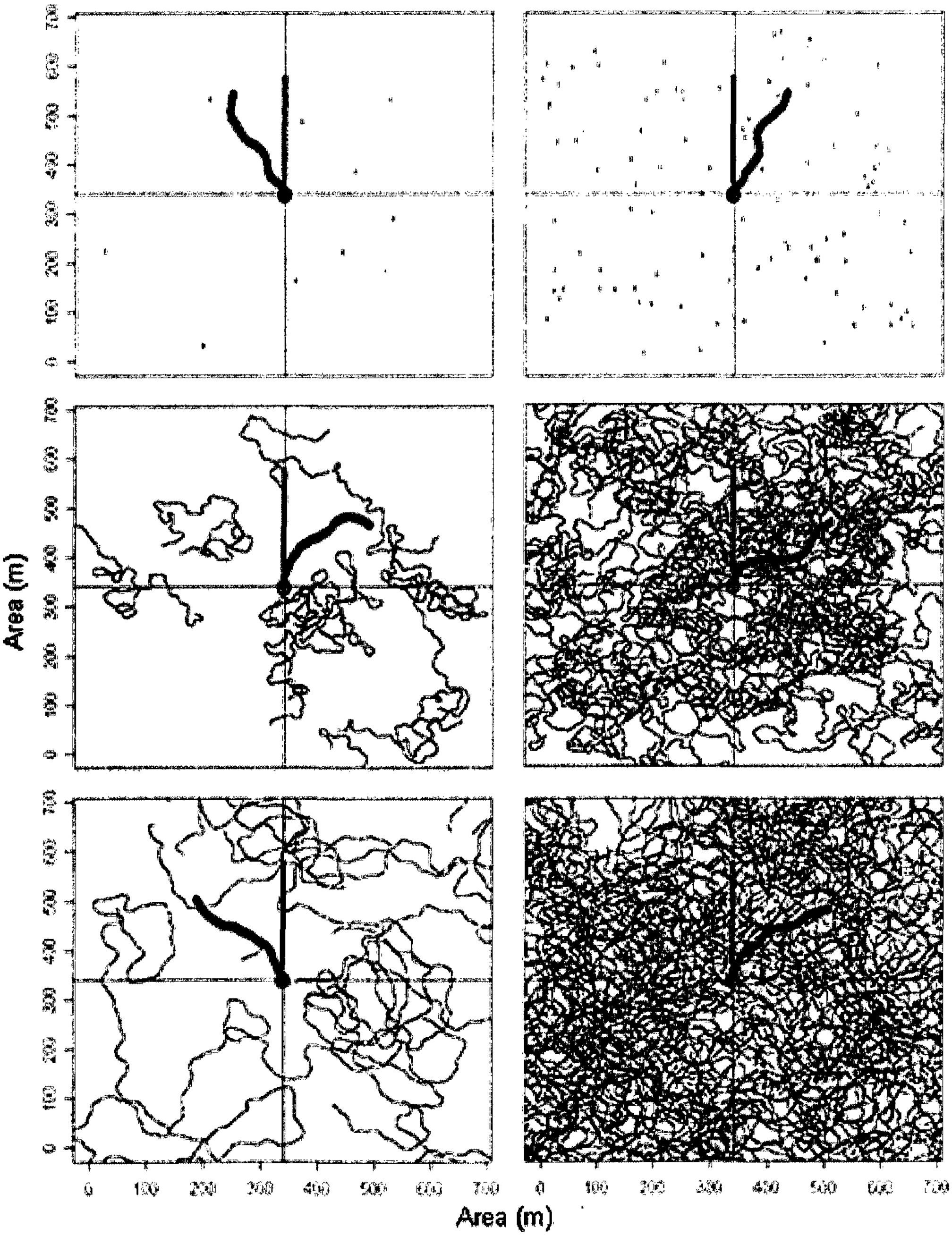


Figure 3.2 Percent of surveys (n = 30 simulations) where fish were detected across a range of fish densities (x-axis) for the roving diver (diamond, solid line), belt-transect (triangle, dotted line), and stationary point count (cross, dashed line). Columns (left to right) show 300 and 3600 second survey-times. Rows (top to bottom) show fish speeds of 0, 0.4, 1.0 $m \cdot s^{-2}$.

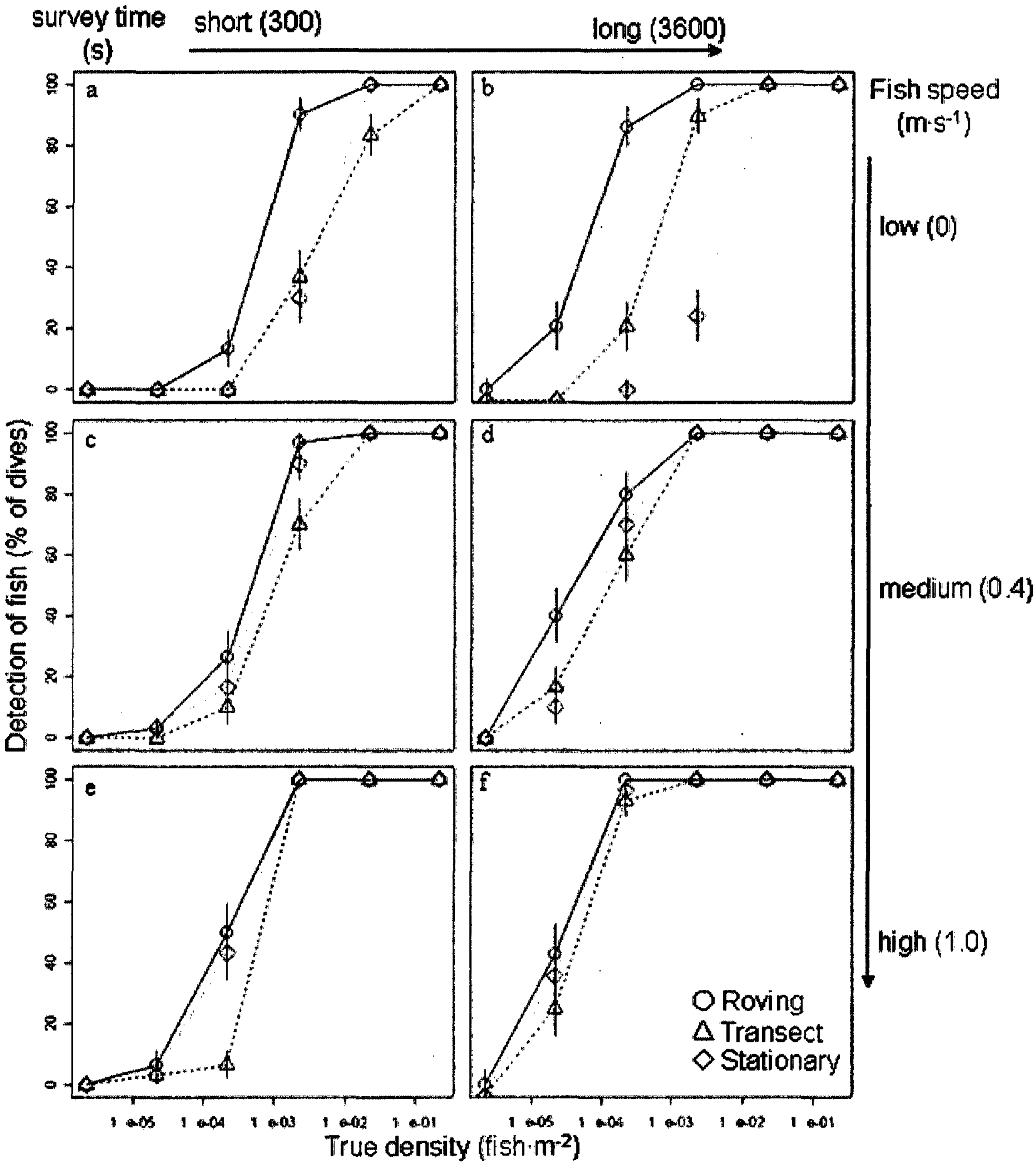


Figure 3.3 Comparison of participant diving experience and elasmobranch detection (presence or absence) with their respective team's detection, where sharks or rays were assumed to be present when at least one team member reported their occurrence (i.e. no false detections).

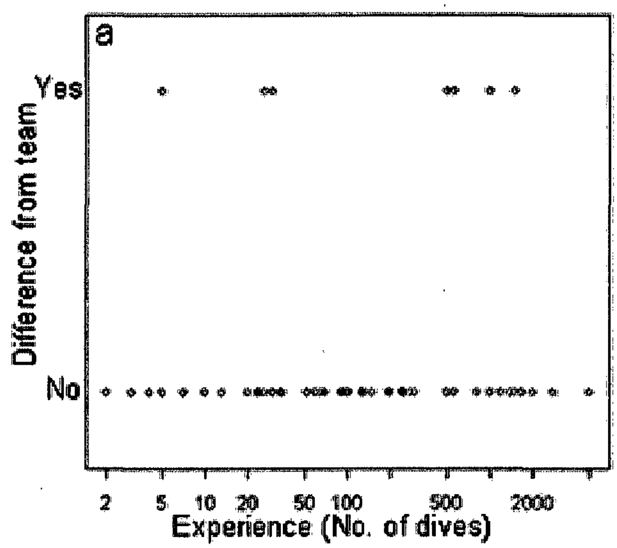


Figure 3.4 a) Comparison of participant diving experience and the difference between the number of elasmobranchs reported by the individual and their team mean. b) Comparison of the variability of counts for inexperienced (≤20 dives) and experienced (>20 dives) divers.

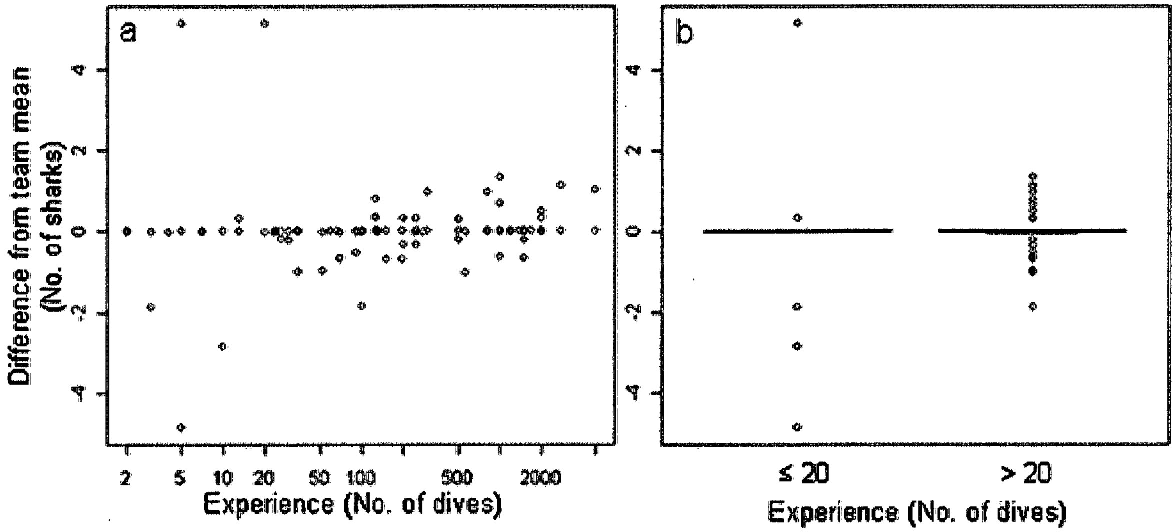
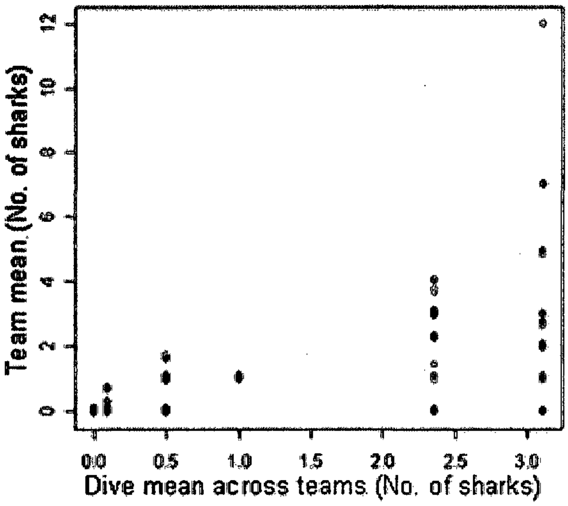


Figure 3.5 Comparison of the variability in team means (mean number of elasmobranchs reported for each team) compared to the mean reported for a dive (mean number of elasmobranchs reported across teams for a dive).



CHAPTER 4

SPATIAL AND TEMPORAL TRENDS IN YELLOW STINGRAY ABUNDANCE: EVIDENCE FROM DIVER SURVEYS

4.1 INTRODUCTION

Dramatic 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 & Myers 2004, Ferretti et al. 2008) and resulting increases in smaller sharks and rays from predation and competition release (Shepherd & Myers 2005, Myers et al. 2007). 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 the most commonly sighted elasmobranch species observed by scuba divers, yet 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. In the Web of Science database only 13 publications (16 including meeting abstracts) are listed for *Urobatis* (or *Urolophus*) *jamaicensis* (access 8 November 2009) – none of which address the population ecology of this species. Because they are considered to be abundant and tolerate captivity well they are recommended for scientific experiments (Fahy & Sherman 2000) and their occurrence in the scientific literature is mostly limited to biochemical, neurological, and physiological experiments (Sulikowski & Maginniss 2001, Barnes et al. 2003, Dwivedi & Trombetta 2006). This 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 (< 10% of all dives: REEF summary report) 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 temporal and spatial trends in the distribution and 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 & 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. Scientific divers have been collecting data via underwater visual censuses (UVC) since 1954 (Brock) as an alternative to extractive methods for describing and monitoring fish populations. UVC have been used in a range of areas sometimes including elasmobranchs where they are relatively abundant (Friedlander & 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 to monitor changes in abundance in the Philippines. 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 absolute 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 & Dearden 2006, Stallings 2009); however, volunteer collected data may provide valuable insight into trends that would otherwise go undetected.

In this paper, we examine the distribution 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 comprises 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, visibility, and bottom time, REEF data are well-suited to evaluating species distributions (Pattengill-Semmens & Semmens 1998) and temporal trends while standardizing for covariates. Therefore, we applied generalized linear models to examine rates of change in sighting frequency as an index of abundance for the greater-Caribbean as a whole, and for eleven 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 observed changes, focusing on two regions with opposing temporal trends in yellow stingray sighting frequency, the Florida Keys and Jamaica.

4.2 METHODS

4.2.1 DATA COLLECTION

Data were obtained from the REEF database from January 1994 to December 2007 in the greater-Caribbean (Fig 4.1). The REEF dataset comprises >100,000 surveys conducted by trained volunteer divers with a wide-variety of dive objectives and preferences. Surveys were collected using the Roving Diver Technique (RDT; Schmitt et al. 1993; Schmitt et al. 1998) – a method that surveys a wide variety of habitats within a particular site (Schmitt et al. 2002, Schmitt and Sullivan 1996). For each survey, divers recorded environmental variables for the site (current, visibility, start time, habitat type, water temperature, and survey depth), 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. Depths ranged from snorkeling at the surface to 89 ft (27.13 m). Time of day ranged from 01:00 to 24:00 with 96% of the surveys taking place between 08:00 and 18:00.

4.2.2 DATA TREATMENT

Because the yellow stingray is considered a benthic species, surveys conducted in open water habitats were not included. Particularly long bottom times (>150 minutes) were removed to reduce the chance of the diver moving into different sites and because most dives (98.8%) were <2.5 hours. Two independent datasets were created for the greater-Caribbean as a whole and for the Florida Keys. Variables with more than 4,000 and 600 missing values (>4% of each dataset) were not considered in the analysis of the greater-Caribbean and the Florida Keys, respectively. Therefore, surface and bottom water temperatures were excluded from the analysis because of too many missing values. The remaining variables in both datasets were diver experience (expert / novice), bottom time, depth, habitat, date, region, current, and start time. Surveys with missing values for any of the remaining variables were not included in the analysis. In total, 5,477 surveys were excluded from the original 90,539 submitted for the greater-Caribbean and 844 surveys excluded from the original 17,336 for the Florida Keys.

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 (for more details on habitat types see www.reef.org). Florida Keys 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).

4.2.3 DATA ANALYSIS

Distribution and sighting frequency analyses were limited to regions with >100 surveys. For each of these regions, as well as for areas in the Florida Keys, sighting frequency was obtained by standardizing yellow stingray sightings by the number of surveys conducted per year. 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.

For all regions with >15 yellow stingray sightings over the study period, estimates of change in yellow stingray sighting frequency were analyzed using generalized linear models (GLM) with a binomial error structure (Bernoulli trials) and a logit link to remove the effect of diving effort, spatial and temporal variation among surveys (Venables & Ripley 1999). Thus, the index of abundance was yellow stingray sightings per 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,

$$\text{logit}(\mu_i) = \alpha + \beta y_i + XB$$

where $\text{logit}(\mu_i) = \log(\mu_i / (1 - \mu_i))$, μ_i is the expected value of the index of abundance of yellow stingrays observed in the ith year (y_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 covariates affecting the variability of μ_i, B is the vector of their relative parameters. The model predicts the chance of detection 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 variables (sightings, diver experience, visibility, bottom time, depth, habitat, year, month, region/area, start time, current) were investigated to build the complex model for the greater-Caribbean and the Florida Keys database. Model selection was conducted using a stepwise procedure minimizing Akiake Information Criterion (Akaike 1974). The 'stepAIC' function from the MASS package (Venables & Ripley 1999) in R (www.r-project.org) was used (model selections are shown in Appendix C). The overall trends for the greater-Caribbean (i.e. region) and the Florida Keys (i.e. area, habitat, depth) were obtained by removing year and corresponding covariate interactions.

4.3 RESULTS

4.3.1 SPATIAL DISTRIBUTION AND SIGHTING FREQUENCY

From 1994–2007, reports of yellow stingrays were widely distributed throughout the greater-Caribbean (Fig 4.1a) 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 4.1; Fig 4.1). In the greater-Caribbean yellow stingrays were observed on 5,606 out of 85,062 dives (6.6%). Although rarely observed in Cuba (<1%), sighting frequency was highest in the areas surrounding Cuba (e.g. Dominican Republic, Jamaica). Outside these regions, sighting frequency dropped to <1%. The eight 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 2,428 out of 16,522 dives, 43% of the total greater-Caribbean sightings. Yellow stingrays have been reported in all areas of the Florida Keys, from the Upper Keys to the Dry Tortugas (Fig 4.1b); however, only one was reported for the Backcountry area on the Florida Bay side (Table 4.2). Although yellow stingrays were observed in all habitat types they were rarely found in artificial habitats (Table 4.2). Yellow stingrays were found in depths ranging from <10 m to >70 m, and were most frequently observed at depths <6 m (20 ft; Table 4.2).

4.3.2 GREATER-CARIBBEAN TEMPORAL TRENDS

Throughout the greater-Caribbean yellow stingray sightings declined from 20.4% of dives in 1994 to 4.6% of dives in 2007 (Table 4.3) – corresponding to an overall standardized decline rate of -0.11 (± 0.01 S.E.) per year on the logit scale (Table 4.4 shows the parameters included in the model with effect sizes). However, this trend was not consistent amongst all surveyed regions (Fig 4.2). Of the 30 regions sufficiently sampled (>100 surveys) in the greater-Caribbean, we could only assess 11 (Table 4.1). 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 instantaneous decline rates of up to -0.17 per year (± 0.009 S.E.), two regions had non-significant decreases, while two were unchanged (Fig. 4.2). Only one region, Jamaica, showed a significant increase (0.37 ±0.06).

4.3.3 FLORIDA KEYS TEMPORAL TRENDS

Within the Florida Keys, the yellow stingray sighting frequency decline rate was -0.22 per year (± 0.06 S.E.); from 31.6% sighting frequency in 1994 to 4.7% sighting frequency in 2007 (Table 4.3). The yellow stingray exhibited a significant decline in all 4 areas (Table 4.5 shows the parameters included in the model with effect sizes); however, the rate of change did not differ significantly between areas, ranging from -0.28 per year (± 0.02 S.E.) in the Lower Keys to -0.29 per year (± 0.06 S.E.) in the Middle Keys (Fig. 4.3a). 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 habitats (Fig. 4.3b). Significant decline rates occurred at all depths (Fig 4.3c); however, there was little significant difference in the trends between depths.

4.4 DISCUSSION

Using >85,000 diver surveys in the greater-Caribbean, we were able to assess spatial and temporal trends in the abundance of a commonly sighted but little studied elasmobranch, the yellow stingray, for which other data are scarce. Yellow stingrays were observed on 6.6% of the dives, mainly in the area around Cuba, with the greatest abundance occurring in the Dominican Republic (22%) and limited observations being made at the boundaries of the study area (e.g. Bermuda, Barbados, north Florida). Between 1994 and 2007 the frequency of occurrence significantly declined (standardized rate = -0.11 per year ± 0.01 S.E.), although this negative trend was not consistent across all regions. Of the eleven 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 were found in the Florida Keys, where sighting frequency dropped from 31.6% in 1994 to 4.7% in 2007 (standardized rate = -0.22 per year ± 0.06 S.E.). These declines were consistent across all areas, habitats and depths. Our study highlights the value of non-scientific divers for collecting species occurrence data that can be used to understand population trends of otherwise poorly sampled and little known species.

Despite being one of the most commonly sighted elasmobranch species in diver surveys in the greater-Caribbean there is little scientific information on the distribution and status of yellow stingrays. However, our maps of the 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 GBIF and OBIS. Both data sources show highest likelihood of occurrence in the areas surrounding Cuba and low likelihood of occurrence at the boundaries of the survey area (e.g. Bermuda, Barbados, north Florida). 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 central and south east Florida by our region groupings in Table 4.1. The combination of these two areas using the REEF data produces a remarkably similar sighting frequency of 13.2%, which suggests that non-scientific underwater survey data produces results that are comparable to scientific observers.

Possible explanations of the decline in yellow stingray observations are that they have moved to occupy different areas or niches or that they have declined in abundance as a result of deterioration in habitat quality, direct exploitation, or as a result of trophic interactions. Since yellow stingrays are shallow-water benthic species with relatively small home ranges (Fahy et al. 2007), we would not expect that they have moved between regions (e.g. from the Florida Keys to Jamaica). As well, our results indicate, at least for the Florida Keys, that declines occurred across all areas, habitats, and depths, which suggest that movement was not the principal cause of declining observations.

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 may 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 & Beets 2001, Duarte 2002, Green & 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 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 & Webber 2003, Mora 2008), seawater warming (Aronson & 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 occurrence 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 & Worm 2005, Garcia et al. 2008). 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 and declines in areas with stronger fishing regulations such as no-take marine reserves. However, comparison of our trend estimates with the global network of coral reef marine protected areas (MPAs: Mora et al. 2006: supplementary figures) indicate that, in general, where yellow stingrays are increasing or unchanged, MPAs have extraction restrictions that are predominantly 'take', poaching is 'low', overall risk levels that are 'high' and summaries (i.e. average of analyzed attributes including extraction, poaching, external risks, MPA size and MPA isolation) that are 'very limited' (Table 4.6). 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 4.6). As well, 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 & Myers 2005, Myers et al. 2007). Stingrays in general are considered prey for sharks (Strong 1990) and other large predatory fishes such as groupers (Silva Lee 1974, www.fishbase.org). There is ample evidence that fishing and marine protected areas (MPA) alter the abundance and size of species (Lester et al. 2009, Stobart et al. 2009, Watson et al. 2009), including large fish and sharks (Friedlander & DeMartini 2002, Robbins et al. 2006). In the Florida Keys, the region with the strongest decline in yellow stingrays, increasing abundances have been reported for the black (*E. mystacinus*), red (*E. morio*) and Nassau (*E. striatus*) groupers (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 & Eckland 1999, Frias-Torres 2006) and is currently undergoing recovery (Porch et al. 2006). These increases in groupers have been observed in one of the largest and best protected marine sanctuaries in the greater-Caribbean, the Florida Keys National Marine Sanctuary (FKNMS). Although extraction for recreational fishing, 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). 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 showed the greatest increase in sighting frequency of yellow stingrays. Jamaica is known to be one of the most depauperated regions of the greater-Caribbean (Hawkins & Roberts 2004, Hardt 2009). In Jamaica, fishing pressure is very high and large fishes, including sharks and groupers, are well recognized to be rare (Hardt 2009, Ward-Paige et al. Chapter 5). 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 & Myers 2005, Myers et al. 2007). These examples indicate that observed changes in yellow stingray abundance may be related to altered predation and competition pressure from other species. 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.

4.5 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. Several factors may have contributed to the general decline of yellow stingrays including habitat degradation, exploitation, and changes in predation and competition pressure. Interestingly, yellow stingrays have decreased in the Florida Keys where large predators have increased due to strong marine protection measures. In contrast, yellow stingrays have increased in Jamaica where large predators are severely depleted. 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.

Table 4.1 Summary of sample sizes and yellow stingray sightings for regions in the greater-Caribbean where >100 surveys were conducted.

Region	**Number of surveys**	**Number of sightings**	**Sighting frequency (%)**
Dominican Republic	470	110	23.4
Jamaica	335	62	18.5
Mexican Caribbean	4737	788	16.6
Southeast Florida	6473	985	15.2
Florida Keys	16592	2437	14.7
Central Bahamas	6302	594	9.4
North Bahamas	2394	179	7.5
Cayman Islands	4001	254	6.3
Honduras	2896	90	3.1
Puerto Rico	1019	21	2.1
Belize	2166	34	1.6
North east Florida	143	1	0.7
North Antilles	1678	11	0.7
Central east Florida	1015	5	0.5
Venezuela	828	4	0.5
Northwest Gulf of Mexico	3184	8	0.3
US Virgin Islands	2187	5	0.2
Turks and Caicos	2672	6	0.2
Southeast Gulf of Mexico	927	2	0.2
Cuba	544	1	0.2
British Virgin Islands	1924	3	0.2
Antilles	14439	4	0.0
Barbados	2398	0	0.0
Bermuda	2152	0	0.0
Maryland	1147	0	0.0
Trinidad	578	0	0.0
South Carolina	562	0	0.0
South Gulf of Mexico	443	0	0.0
Colombia	397	0	0.0
North Gulf of Mexico	212	0	0.0
Total	84815	5604	

Table 4.2 Summary of sample sizes and yellow stingray sightings for areas, habitats and depths in the Florida Keys, US.

	Number of surveys	Number of sightings	Sighting frequency (%)
Area			
Upper Keys	9859	1871	19.0
Middle Keys	1651	246	14.9
Lower Keys	2937	264	9.0
Offshore Keys	2044	46	2.3
Backcountry	31	1	3.2
Habitat			
Slopes	857	167	19.5
Mixed	4704	855	18.2
Reef	9417	1330	14.1
Flat	263	32	12.2
Artificial	1281	44	3.4
Depth (ft)			
snorkel	1469	179	12.2
< 10	519	111	21.4
10-19	3116	650	20.9
20-29	6588	1117	17.0
30-39	2004	232	11.6
40-49	802	64	8.0
50-59	793	43	5.4
60-69	569	19	3.3
> 70	662	13	2.0

Table 4.3 Summary of sample size and yellow stingray sightings for each year in the greater-Caribbean and the Florida Keys, US.

	Greater-Caribbean			Florida Keys		
Year	**Number of surveys**	**Number of sightings**	**Sighting frequency (%)**	**Number of surveys**	**Number of sightings**	**Sighting frequency (%)**
1994	2350	479	20.4	1279	404	31.6
1995	2351	304	12.9	745	257	34.5
1996	2832	232	8.2	596	148	24.8
1997	3040	329	10.8	872	225	25.8
1998	3055	200	6.5	680	126	18.5
1999	4035	292	7.2	795	164	20.6
2000	6012	399	6.6	906	137	15.1
2001	9153	533	5.8	2245	249	11.1
2002	10715	748	7.0	2542	314	12.4
2003	9500	471	5.0	1711	120	7.0
2004	8860	465	5.2	1118	101	9.0
2005	7311	363	5.0	1074	94	8.8
2006	7953	431	5.4	1053	46	4.4
2007	7895	360	4.6	906	43	4.7
Total	85062	5606		16522	2428	

Table 4.4 Parameters in the greater-Caribbean.

Model parameters	Effect size	S.E.	P-value
Intercept	-0.91	0.29	0.00
year	-0.08	0.01	0.00
experience (N)	-0.31	0.08	0.00
bottom time	0.01	0.00	0.00
depth	0.24	0.06	0.00
depth^2	-0.06	0.00	0.00
habitat 2	-0.35	0.18	0.05
habitat 3	-0.81	0.25	0.00
habitat 4	-0.45	0.25	0.07
habitat 5	-0.55	0.18	0.00
month 2	0.45	0.11	0.00
month 3	-0.22	0.11	0.04
month 4	-0.61	0.11	0.00
month 5	-0.34	0.10	0.00
month 6	-0.13	0.10	0.19
month 7	0.01	0.09	0.92
month 8	0.13	0.09	0.16
month 9	-0.11	0.10	0.25
month 10	-0.25	0.10	0.02
month 11	-0.56	0.11	0.00
month 12	-0.12	0.11	0.24
area 34	-0.01	0.16	0.92
area 35	-1.31	0.22	0.00
area 36	-1.38	0.21	0.00
area 37	-1.46	0.22	0.00
area 38	-3.84	0.61	0.00
area 39	-0.62	0.22	0.01
area 40	-2.92	0.36	0.00
area 41	-2.06	0.39	0.00
area 42	0.32	0.23	0.18
area 43	-2.43	1.02	0.02
bottom time * depth	0.00	0.00	0.00
depth * habitat 2	0.02	0.03	0.50
depth * habitat 3	0.16	0.06	0.01
depth * habitat 4	-0.10	0.05	0.06
depth * habitat 5	0.07	0.03	0.04
year * experience (N)	0.02	0.01	0.01
year * region (34)	-0.08	0.02	0.00
year * region (41)	0.04	0.02	0.07
year * region (42)	0.08	0.02	0.00
year * region (52)	0.03	0.02	0.21
year * region (53)	0.45	0.06	0.00
year * region (54)	0.08	0.02	0.00
year * region (55)	0.03	0.04	0.50
year * region (57)	0.00	0.04	0.98
year * region (62)	-0.07	0.04	0.06
year * region (63)	0.03	0.11	0.79

Table 4.5 Parameters in the Florida Keys model.

Model parameters	Effect size	S.E.	P-value
Intercept	0.71	0.68	0.30
year	-0.22	0.06	0.00
experience (N)	-0.48	0.10	0.00
bottom time	0.00	0.01	0.86
depth	0.10	0.18	0.58
depth^2	-0.04	0.01	0.00
habitat 2	-1.11	0.34	0.00
habitat 3	-0.37	0.62	0.55
habitat 4	-0.56	0.65	0.38
habitat 5	-0.81	0.36	0.02
month 2	0.06	0.23	0.78
month 3	-0.30	0.22	0.17
month 4	-1.22	0.24	0.00
month 5	-1.06	0.21	0.00
month 6	-0.47	0.19	0.01
month 7	-0.22	0.19	0.24
month 8	-0.25	0.19	0.19
month 9	-0.62	0.19	0.00
month 10	-0.86	0.20	0.00
month 11	-0.65	0.23	0.00
month 12	-0.45	0.23	0.05
area 2	-0.62	0.40	0.12
area 3	-15.42	527.10	0.98
area 4	-1.41	1.08	0.19
year*depth	0.02	0.01	0.16
bottom time * depth	0.00	0.00	0.11
depth * habitat 2	0.11	0.07	0.10
depth * habitat 3	-0.17	0.17	0.33
depth * habitat 4	-0.17	0.14	0.20
depth * habitat 5	0.06	0.07	0.40
year * experience (N)	0.03	0.01	0.01
year* bottom time	0.00	0.00	0.21
habitat 2 * area 2	0.49	0.29	0.10
habitat 3 * area 2	1.05	0.68	0.12
habitat 4 * area 2	-13.88	456.30	0.98
habitat 5 * area 2	0.11	0.31	0.72
habitat 2 * area 3	15.23	527.10	0.98
habitat 3 * area 3	15.24	527.10	0.98
habitat 4 * area 3	2.24	560.80	1.00
habitat 5 * area 3	15.35	527.10	0.98
habitat 2 * area 4	1.98	1.05	0.06
habitat 3 * area 4	-13.75	603.80	0.98
habitat 4 * area 4	0.40	1.50	0.79
habitat 5 * area 4	0.70	1.07	0.52
depth * area 2	-0.08	0.08	0.30
depth * area 3	-0.23	0.07	0.00
depth * area 4	-0.52	0.09	0.00
year * bottom time * depth	0.00	0.00	0.05

Table 4.6 Summary of marine protection status for each region assessed for changes in yellow stingray abundance in the greater-Caribbean. Extraction, poaching, risk and summary values are the predominant values (largest) for MPAs shown for each area in the supplementary figures (Extraction, Poaching, and Risk) and figure 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 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 coastal development, overexploitation, erosion and marine- and inland-based pollution.

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

Figure 4.1 Distribution and sighting frequency of the yellow stingray in the greater-Caribbean (a) and the Florida Keys (b, and insert in Fig. 4.1a), US. Black crosses = regions with >100 surveys and no yellow stingray sightings (2 regions from the US east coast are not shown). 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 standardized 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 4.1 for greater-Caribbean data and Table 4.2 for Florida Keys data.

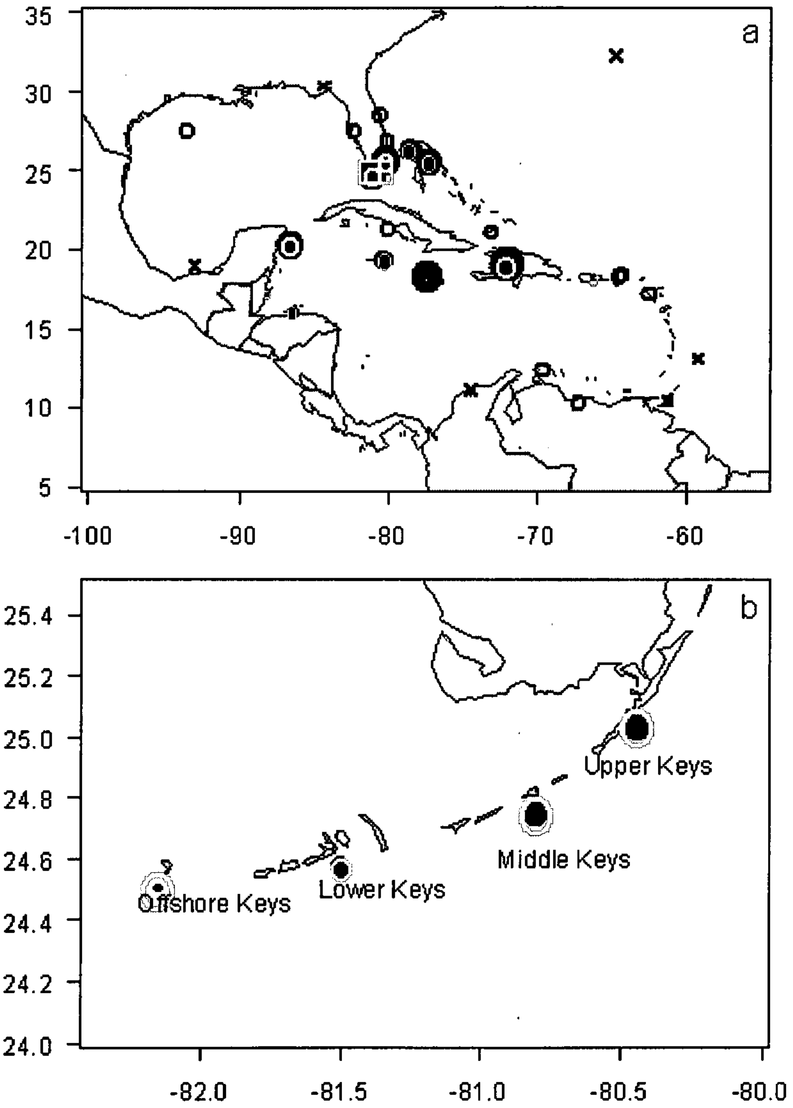


Figure 4.2 The estimated rate of change in abundance (±95% CI) of yellow stingrays for regions in the greater-Caribbean. Values are reported on the logit scale (effect size is the log of the odds ratio). A value of 0 indicates no change in abundance.

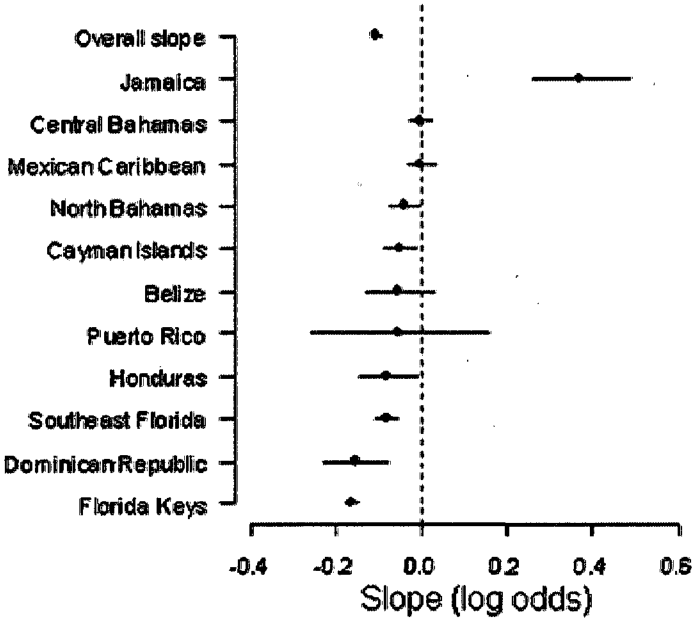
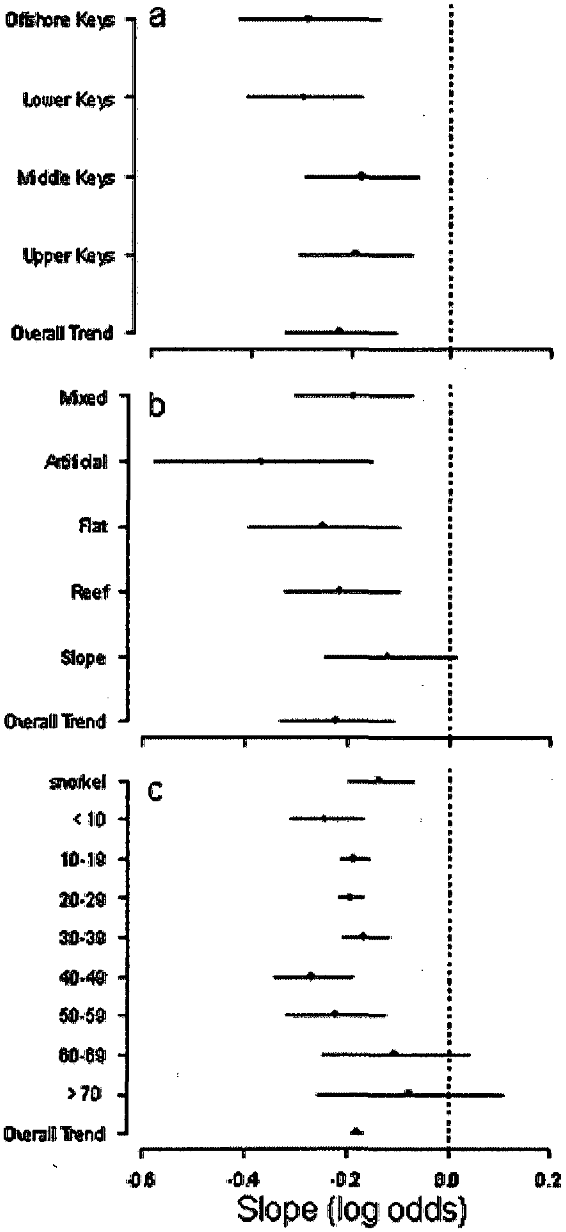


Figure 4.3 The estimated rate of change in abundance (±95% CI) of yellow stingrays for (a) different areas, (b) habitat types and (c) depths in the Florida Keys. Values are reported on the logit scale (effect size is the log of the odds ratio). A value of 0 indicates no change in abundance.



CHAPTER 5

LARGE-SCALE ABSENCE OF SHARKS ON REEFS IN THE GREATER-CARIBBEAN: A FOOTPRINT OF HUMAN POPULATION DENSITY

5.1 INTRODUCTION

Strong declines in the abundance of many large pelagic sharks have been described worldwide and repeatedly linked to industrial fishing (Baum et al. 2003, Baum & Myers 2004, Myers & Worm 2005, Ferretti et al. 2008). The extent of these declines and some ecosystem consequences have been described from a limited number of long-term fisheries datasets, mostly in the pelagic ecosystem (Heithaus et al. 2008). Unfortunately, the status of shark populations in other ecosystems, such as coral reefs, remains poorly known because both modern and historical data are very limited (Dulvy et al. 2008). This lack of data, in combination with the high vulnerability of sharks to fishing (Myers & Worm 2005, Garcia et al. 2008) has prompted the use of a variety of data to shed light on temporal and spatial trends in shark populations. These include the analysis of historical fisheries and market records of sharks in the Mediterranean (Ferretti et al. 2008), trophy photographs of fishing tournaments in Florida (McClenachan 2009), archaeological and historical records on coral reef ecosystem changes worldwide (Pandolfi et al. 2003), and ecological surveys of fish communities across spatial gradients of exploitation (Friedlander & DeMartini 2002, Robbins et al. 2006, Sandin et al. 2008), among others. Although these data sources have been valuable in describing changes in shark populations, these analyses have been opportunistic and restricted to few regions. Here, we explore another source of data based on observations made by trained scuba divers to examine patterns of distribution and sighting frequency of sharks on reefs in the greater-Caribbean.

Trained scuba divers provide a valuable source of information for describing patterns in distribution and sighting frequency. Divers travel to many reefs providing a broad-spatial overview of trends while the robustness of the emerging patterns can be supported by the sheer number of observations (i.e. number of divers and dives). Because they survey a wide range of habitats, depths, and times of the year they also maximize the sighting probability of less common species such as sharks. This non-extractive technique allows data to be obtained for species at risk and from areas where fishing is prohibited.

Although the identification of shark species may be poor, data can be still reliable when looking at patterns of all species of sharks.

In the greater-Caribbean, poor knowledge of the status of sharks on reefs is worrisome given the long history of reef exploitation. More than 2500 years ago overexploitation was already apparent in Caribbean marine ecosystems when the primary foods were fish, turtles and invertebrates from reef and nearshore habitats and local extirpation of marine animals, such as manatees, had already occurred (see review in Fitzpatrick & Keegan 2007). In the course of European colonization, the depletion of large carnivores (including sharks) on reefs and other regions in the greater-Caribbean increased and accelerated during the 20th century (Pandolfi et al. 2003). With the expansion of human population in coastal areas, concurrent recreational and artisanal exploitation of coastal resources has likely increased as much as industrial fishing (Cooke & Cowx 2004). Moreover, habitat degradation or loss, pollution and disturbance from human activities are generally more pronounced in coastal and reef areas compared to offshore regions (Pandolfi et al. 2003, Fitzpatrick & Keegan 2007, Halpern et al. 2008). As a result, it is likely that sharks on reefs, although less likely to be targeted by industrial fishing operations, may be as depleted as their pelagic counterparts. However, this has not been adequately quantified and trends in abundance and distribution of sharks on reefs are urgently needed to substantiate the establishment of conservation strategies.

Here, we used a broad and comprehensive collection of underwater surveys conducted by trained divers in the greater-Caribbean to explore contemporary patterns in shark distribution and sighting frequency. We then compared the sighting frequency of contemporary sharks with data of human population and use population viability analysis to determine the effect that fishing pressure alone could have on shaping the pattern of distribution and sighting frequency of sharks on reefs in the greater-Caribbean.

5.2 METHODS

5.2.1 DISTRIBUTION AND SIGHTING FREQUENCY

Underwater visual censuses were used to describe the contemporary distribution and sighting frequency of sharks on reefs in the greater-Caribbean (Fig 5.1). These surveys were conducted by trained volunteer divers between 1993 and 2008 for the Reef Environmental Education Foundation (REEF, www.reef.org). Using the Roving Diver Technique (RDT: Schmitt et al. 2002), divers survey a wide variety of habitats within a particular site and record all fish that are observed throughout the water column during their regular dive activities. This database contains ~100,000 surveys broadly distributed throughout the greater-Caribbean.

For our purposes, habitats were limited to reef (high and low profile), slopes (dropoff, wall, ledge) and flats (grass, sand, rubble) – termed 'reef' from here on (for more habitat information see www.reef.org). Open water and artificial habitats were excluded. Sites with geo-referenced locations (latitude and longitude) were allocated into 1 km^2 cells. For each cell with more than 5 dives, we quantified the sighting frequency as the number of dives where sharks were reported divided by the total number of dives within that cell.

We limited our analyses to species that are described as reef-dwelling or reef-associated in Compagno et al. (2005) and FishBase (www.fishbase.org) and included bonnethead (*Sphyrna tiburo*), blacknose (*Carcharhinus. acronotus*), Atlantic sharpnose (*Rhizoprionodon terraenovae*), sandtiger (*Carcharias taurus*), blacktip (*Carcharhinus limbatus*), tiger (*Galeocerdo cuvier*), spinner (*Carcharhinus brevipinna*), silky (*Carcharhinus falciformis*), lemon (*Negaprion brevirostris*), bull (*Carcharhinus leucas*), sandbar (*Carcharhinus plumbeus*), nurse (*Ginglymostoma cirratum*), whale (*Rhincodon typus*), Caribbean reef (*Carcharhinus perezii*), scalloped hammerhead (*S. lewini*), great hammerhead (*Sphyrna mokarran*), and smooth hammerhead (*Sphyrna zygaena*). Many shark species overlap in distribution, habitat use, and have similar morphologies, which can make identification difficult during field observations. We therefore combined the records for all these species. We performed an additional analysis excluding nurse sharks (*Ginglymostoma cirratum*), which are stationary, common and reasonably easy to identify, and the main species in our analyses with relatively little commercial value today (Castro 2000). The differences introduced by this single species may provide insights into the reasons why commercially valuable species may be disappearing.

5.2.2 HUMAN POPULATION COMPARISON

We explored the potential effect of humans on sharks by comparing the sighting frequency of all sharks and those excluding nurse sharks to the number of humans nearby. We obtained data on human population from http://sedac.ciesin.columbia.edu/gpw/global.jsp, for the year 2000 at a resolution of 2.5' (~ 5 km^2 cells). For each of the one km^2 cells where the dive surveys were grouped, we added a 10 km buffer and obtained the maximum number of people within this 10 km distance to the reef.

5.2.3 POPULATION VIABILITY ANALYSIS

Human population density surrogates many anthropogenic stressors that may affect shark abundance. Here we use population viability analysis to explore if any relationship between humans and sharks can be explained by fishing mortality. These demographic analyses quantify the resilience of species to different levels of fishing mortality given their life history attributes and were carried out for each shark species that was included in the spatial analysis. Life history attributes were obtained from different sources for each species analyzed in the sightings database and included age at maturity (α), longevity (w), fecundity (b, i.e. female pups per female per year, which was calculated from data on number of pups, gestation period and reproductive frequency), and natural mortality (M) (see Table 5.1 for values). Natural mortality (M) was estimated from longevity using Hoenig's (1983) formula:

$$\ln M = 1.44 - 0.982 \ln w$$

Survival to age at maturity (l_α) was calculated from a variant of the Euler-Lotka equation, in which total mortality (Z) is set at twice the natural mortality (i.e. this condition is applied to minimize the effects of density dependence) and population growth is stable (r=0) (Smith et al. 1998):

$$e^{-Z} + l_{\alpha,Z} b[1 - e^{-Z(w-\alpha+1)}] = 1$$

where $l_{\alpha,Z}$ is survival to age at maturity when total mortality is equal to Z. The intrinsic rate of population increase (r) was calculated as the rebound potential (Smith et al. 1998) or the growth rate of a population in the near absence of density-dependent controls. r was calculated as the value that satisfies the following variant of the Euler-Lotka equation:

$$e^{-(M+r)} + l_{\alpha} b e^{-r\alpha} [1 - e^{-(M+r)(w-\alpha+1)}] = 1$$

Changes in population size (N) at different levels of fishing mortality (F) were calculated in relative terms for each species using density-dependent and density-independent models of population growth:

$$N_{(t+1)} = N_0 + rN_0(1 - \frac{N_0}{k}) - FN_0, \text{ (density-dependent model)}$$

$$N_{(t+1)} = N_0 + rN_0 - FN_0, \text{ (density-independent model)}$$

Given that models were run in relative terms, N_0 and carrying capacity (k) were set to 1. Fishing mortality (F) was set from 0 to 0.5, to assess population viability of the different species under a range of fishing pressures. Fishing mortality for one of our studied species (Atlantic sharpnose shark) has been estimated at 0.46 (Marquez-Farias & Castillo-Geniz 1998).

5.3 RESULTS

5.3.1 SIGHTING FREQUENCY AND DISTRIBUTION

In total we analyzed 76,340 dives across 1,382 one km^2 cells, with an average of 55 (S.E. ±3.3) dives per cell. The average sighting frequency of sharks (i.e. number of dives with sharks present) throughout the greater-Caribbean was 10% (S.E. ±0.004) for all sharks and 3% (S.E. ±0.003) for all sharks excluding nurse sharks. Variation in sampling effort (dives per cell) did not account for variation in sighting frequency (Fig 5.2), suggesting that the variations in sampling effort in this study did not affect our results. In other words, sighting frequencies were similarly low (i.e. 10% or 3%) using 10 or 500 dives in a cell (Fig 5.2).

Throughout the greater-Caribbean sharks were observed in 762 cells (55%; Fig 5.1a). Of these, 441 (32%) contained only nurse sharks, 94 (7%) contained sharks other than nurse sharks and 227 (16%) contained a mixture of nurse and other sharks. Of the cells with sharks, 58% contained only nurse sharks, 12% contained sharks other than nurse sharks and 30% contained a mixture of nurse and other sharks.

The pattern of shark distribution in the greater-Caribbean was clearly affected by the inclusion of nurse sharks. When nurse sharks are considered, sharks were observed on reefs throughout most of the greater-Caribbean (Fig 5.1a). The greatest concentration of cells with high sighting frequency occurred in the Bahamas, southeastern US and Belize. With the exclusion of nurse sharks, however, the number and range of cells where sharks occurred was much smaller (Fig 5.1b). Notably, sharks other than nurse sharks were largely absent in cells around Cuba, Jamaica, Dominican Republic, Puerto Rico, throughout most of the Antilles and central and South America. The greatest concentration of cells with sharks, other than nurse sharks, occurred in the Bahamas.

5.3.2 COMPARISON TO HUMAN POPULATION

Comparison of the sighting frequency of sharks and human population showed that, with the exception of nurse sharks and two cells in southeast Florida, contemporary sharks only occur where human population density is low (Fig 5.3). Additionally, sighting frequency was highest where the local human population approached zero such as in the northern and central Bahamas and north Key Largo.

5.3.3 POPULATION VIABILITY ANALYSIS

As expected, under scenarios of zero fishing mortality ($F = 0$) populations under density dependence remain stable at carrying capacity (Fig 5.4a) and increase under density independence (Fig 5.4b). Under fishing mortalities of $F = 0.1$ all species declined to between 1 and 14% of their initial population size within 50 years under density dependent conditions (Fig 5.4c). With the exception of bonnethead and blacknose sharks, all species declined with fishing mortalities as low as $F = 0.1$ under density independent conditions (Fig 5.4 d). For the remaining scenarios of fishing mortality and density dependence all species declined by 99% within 28 years, with this time frame declining as fishing mortality increased (Fig 5.4 e-l). At fishing mortalities of $F = 0.2$ and $F = 0.5$ all species declined to less than 1% of their original population sizes in less than 28 and 10 years, respectively.

5.4 DISCUSSION

We used an extensive database of fish sightings from trained volunteer divers to extract spatial patterns of sharks on reefs in the greater-Caribbean. Based on data from 1993-2008, contemporary dive surveys indicate that sharks are absent on many reefs, and this pattern of absence is more pronounced when nurse sharks are removed from the analyses. Assessing the drivers of this pattern, we found that contemporary sharks, other than nurse sharks, only occur in areas where human population is low or where fishing is strongly regulated such as in southeast Florida. Assuming that actual fishing mortality is above 0.1, our population viability analysis suggests that fishing pressure alone can explain the observed pattern. In reality, several studies suggest that typical fishing mortality can be on the order of 0.4 for many shark species (Marquez-Farias & Castillo-Geniz 1998, Myers & Worm 2005). Our results indicate that under current fishing mortalities even the most productive sharks (e.g. bonnethead) would be depleted and trend towards extinction.

Two possible caveats to our analyses regard the quality of the data and the fact that sharks may have never existed in the study area. In regards to the quality of the data it is possible that divers miss sharks or avoid sites with sharks. However, scientific diver surveys have been previously used to characterize shark populations in other reef areas of the world where sharks are abundant (e.g. central Pacific Ocean (Friedlander & DeMartini 2002, Stevenson et al. 2007, Sandin et al. 2008); Andaman (Theberge & Dearden 2006); Great Barrier Reef (Robbins et al. 2006)) supporting the reliability of diver data for assessing spatial trends in shark sightings. Moreover, all of these studies found a strong decline of sharks across a gradient of human population or exploitation (Friedlander & DeMartini 2002, Robbins et al. 2006, Sandin et al. 2008), corroborating our results. Sharks are also very conspicuous, which make it unlikely to miss them on a typical dive, even by relatively inexperienced divers (Ward-Paige & Lotze Chapter 3). Finally, if there is a spatial sampling bias it should be towards sites with sharks because of their appeal to recreational divers (Davis et al. 1997, Castro 2000).

The second possible caveat of the interpretation of our results is that sharks never existed in these areas or that they occurred at such low densities that they were missed by divers. However, geographical ranges, based on expert opinions and fisheries data (Compagno et al. 2005), indicate that the analyzed shark species should have occured throughout the study area (Fig 5.5a). Furthermore, the entire study area encompasses habitats of suitable environmental conditions for the presence of the analyzed shark species (see further details in Fig 5.5b). We also found numerous records pointing out the generally high abundance of sharks in the greater-Caribbean in previous times. Although these narratives cannot be directly linked to our study sites, those records that we presume occurred within the depth range of divers and that did not use an attractant (i.e. bait) indicate that sharks, including several of our studied species, were markedly more abundant than what they appear to be today. The earliest written observations of sharks appeared during Columbus' voyages, when a large group of sharks surrounded the explorers' ships off the east-coast of Panama. The sailors were frightened by the number and ferocity of the sharks and "made carnage among them with a chain hook until [sailors] could kill no more" (Colón 1959). The naturalist Hans Sloane wrote of similar encounters with sharks off the coast of Jamaica in the 1680's, and noted that it was "ordinary to have sharks come about the ships" (Sloane 1707); this statement certainly could not be made today, since Jamaica has one of the most depauperate fish populations in the Caribbean (Hawkins & Roberts 2004). In the 1880s, it was common for sharks to "swarm about the wharves, feeding on refuse fishes" in the Florida Keys (Jordan 1884). Sharks were described as "plentiful" (Burdon 1920) and "one of the most common types of fish" throughout the Leeward Antilles (Watkins 1924). In the Florida Keys, in the 1920's, daily catches of 50-100 sharks, consisting mostly of leopard (tiger), dusky, hammerhead, sand (sandtiger), and nurse sharks, were made with nets in just 15 ft (4.57 m) of water (Key West Citizen 1931, Viele 1996) – well within the depth range of divers. Baughman and Springer (1950) stated that sharks were "**expected anywhere at anytime**" in the west-Indian Caribbean; in contrast, our analysis of contemporary dive surveys indicate that with the exception of nurse sharks, sharks are **expected anytime almost nowhere**. This is also corroborated by historical trophy fish photographs that clearly show the loss of sharks and the decline in overall fish size in the Florida Keys (McClenachan 2009).

Although there are many anthropogenic factors that could reduce shark populations on reefs including habitat destruction and pollution (Heupel et al. 2007), our population viability analyses indicate that fishing mortality alone may explain the loss of sharks in the greater-Caribbean. Our results indicate that fishing mortalities as low as 0.1 could cause the decline of shark species. At least one empirical analysis for Caribbean sharks places fishing mortality at $F = 0.46$ (i.e. Atlantic sharpnose shark, Marquez-Farias & Castillo-Geniz 1998). Our simulations of fishing mortality indicate that F of 0.4 over the entire population would be sufficient to extinguish all shark species analyzed, which is corroborated by the results of Myers and Worm (2005) and Garcia et al. (2008), and may explain the striking pattern between the presence of humans and the absence of sharks. The rapid population declines yielded by our simulations have been documented by sharks in other systems. For instance, declines of up to 99% within 30 to 50 years have been documented for bonnethead, scalloped hammerhead populations in the northern Gulf of Mexico (Shepherd & Myers 2005), large pelagic sharks in the Mediterranean Sea (Ferretti et al. 2008) and Gulf of Mexico (Baum & Myers 2004). Overall, these results indicate that reef shark populations are not viable under current levels of fishing pressure. High vulnerability of sharks to fishing pressure is likely exacerbated by the long history of exploitation. 2200 years ago, virtually all islands in the Caribbean were already colonized and recreational and artisanal fishing activities on reefs and nearshore habitats have increased and expanded dramatically since then (Fitzpatrick & Keegan 2007), including a demand for different shark products (e.g. meat, oil, skin, fins) that extends to present times (e.g. Martinez 1947, Viele 1996, Bonfil 1997). Additional evidence of the role of fishing is our results on nurse sharks. This species has a low rebound potential (Table 5.1), suggesting that it would be very vulnerable to even mild levels of fishing. However, it is the most frequently sighted shark on reefs today and compared to the rest of our analyzed species it is the only one not currently targeted for its meat or fins (Castro 2000), highlighting the likely role of fishing on the absence of targeted sharks on reefs. An additional example is the presence of sharks near populated areas, such as in southeast Florida, where strong fishing regulations and large and long-established marine protected areas exist.

5.5 CONCLUSIONS

Our results indicate that human population expansion and exploitation in coastal areas has likely led to the absence of shark populations on many reefs in the greater-Caribbean. Contemporary sharks other than nurse sharks only occur in areas with low human populations or regions with strong fishing regulations or enforced marine reserves such as in southeast Florida. Yet historical records, range maps and habitat suitability models suggest that sharks used to, and still could, occur throughout the greater-Caribbean. The broad-scale loss of sharks on reefs is thus comparable to documented strong declines in many large pelagic sharks worldwide that have been linked to industrial fishing. Because of their life-history characteristics most sharks are extremely vulnerable to even low levels of fishing pressure. Therefore, preventing the extirpation of sharks on reefs in the greater-Caribbean requires urgent management measures to limit fishing pressure and protect sites where sharks still exist. The fact that sharks still occur in densely populated areas where strong fishing regulations are in place indicates the possibility of success and may encourage the implementation of conservation measures that would restore sharks together with their ecological and functional roles on reefs.

Table 5.1 Life history attributes of analyzed shark species and calculated values for natural mortality, survival to age at maturity and intrinsic rebound potential. Data from FishBase (fishbase.org) and complemented with data from Frisk et al. (2004).

		Litter Size									
Common Name	Latin Name	Min	Max	Fecundity period (Years)	Average female pups per female per year	Age at maturity (Years)	Longevity (Years)	Survival until maturity age	Natural mortality	Body Size (cm)	Intrinsic rebound potential
Bonnethead	*Sphyrna tiburo*	3.5	15.5	1	4.8	2.5	9.5	0.13	0.46	150	0.120
Blacknose	*Carcharhinus acronotus*	3	6	1.5	1.5	2.5	5.25	0.54	0.83	200	0.104
Atlantic sharpnose	*Rhizoprionodon terraenovae*	1	9.5	1	2.6	3.35	10	0.22	0.44	110	0.097
Sandtiger	*Carcharias taurus*	2	2	2	0.5	6	13.75	0.95	0.32	320	0.061
Blacktip	*Carcharhinus limbatus*	1	10.5	2	1.4	7	15	0.31	0.30	275	0.054
Tiger	*Galeocerdo cuvier*	10	82	2	11.5	7	39	0.02	0.12	750	0.046
Spinner	*Carcharhinus brevipinna*	4.5	15	2	2.4	7.5	12	0.22	0.37	300	0.045
Silky	*Carcharhinus falciformis*	6	13	1.5	3.2	8.5	25	0.10	0.18	350	0.045
Lemon	*Negaprion brevirostris*	4	17	2	2.6	9.6	26	0.11	0.17	340	0.041
Bull	*Carcharhinus leucas*	3.5	12.5	2	2.0	13.75	29.5	0.13	0.15	350	0.030
Scalloped Hammerhead	*Sphyrna lewini*	21.5	35.5	1	14.3	15	26	0.02	0.17	430	0.027
Sandbar	*Carcharhinus plumbeus*	3	13	2	2.0	16	31	0.13	0.14	250	0.026
Nurse	*Ginglymostoma cirratum*	21	28	2	6.1	15.5	25	0.05	0.18	430	0.025
Whale	*Rhincodon typus*	16	300	2.5	32.0	27.4	70	0.00	0.07	2000	0.016

Note: We did not include Caribbean reef (*C. perezii*), great hammerhead (*S. mokarran*) or smooth hammerhead (*S. zygaena*) because of missing life history data.

Figure 5.1 Distribution and sighting frequency of sharks on reefs within sampled 1 km^2 cells in the greater-Caribbean for a) all species combined, and b) excluding nurse sharks (*Ginglymostoma cirratum*). Note that cells were enlarged for the patterns of distribution to be seen at this scale.

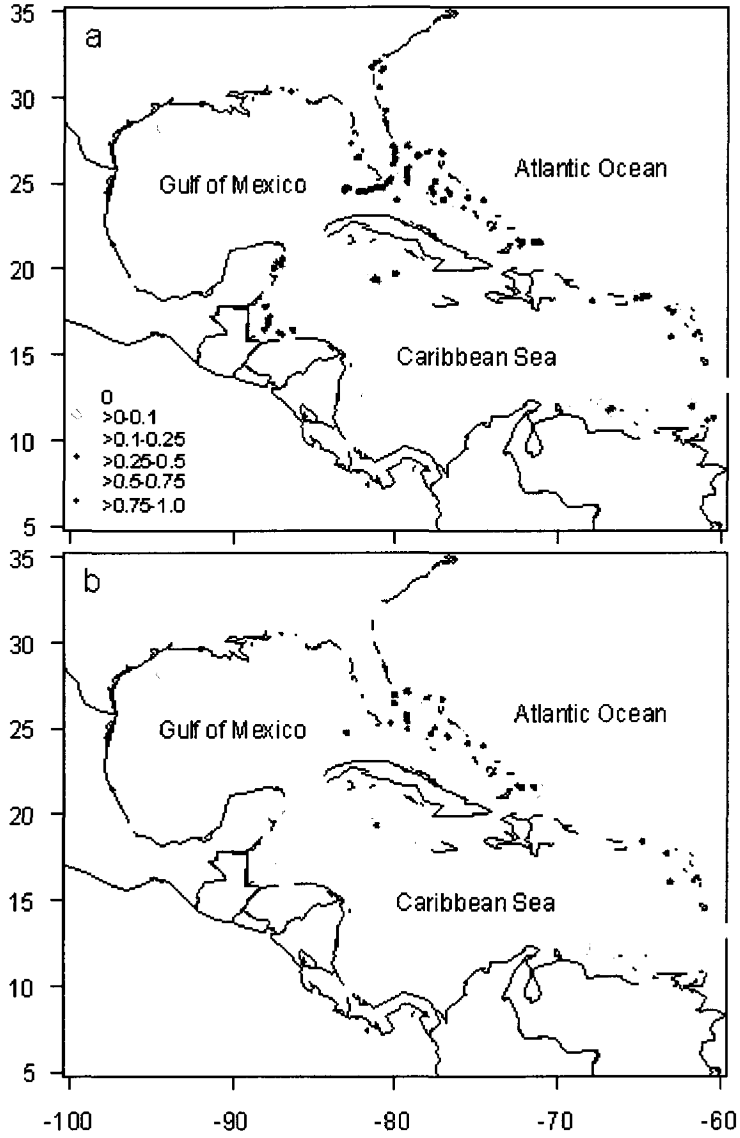


Figure 5.2 Effect of sampling effort on sighting frequency. Relationship between the number of dives per 1 km^2 cell and the sighting frequency of a) all sharks ($r^2 = 0.003$, $p = 0.4$), and b) all sharks excluding nurse sharks ($r^2 = 0.0005$, $p = 0.4$). Solid lines are averages of 10% and 3%, respectively.

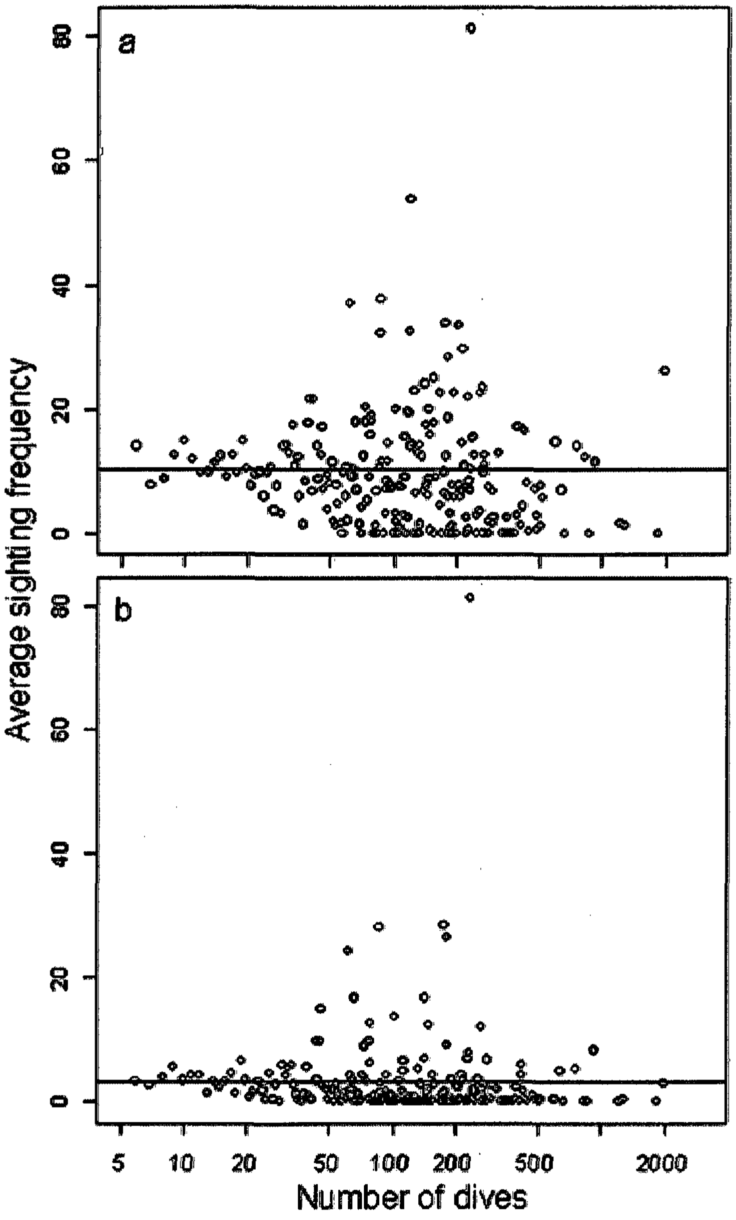


Figure 5.3 Relationship between sighting frequency at surveyed 1 km^2 cells and the number of people within a 10 km radius of each cell for a) all species combined and b) excluding nurse sharks (*Ginglymostoma cirratum*). Data on the number of people was obtained from the Socioeconomic Data and Applications Center at http://sedac.ciesin.columbia.edu/gpw/global.jsp. Trends (solid lines) were fitted using generalized linear models (binomial error structure and logit link) [a) Estimate: -0.33, S.E: 0.009, $p<0.0001$; b) Estimate: -0.39, S.E: 0.017, $p<0.0001$].

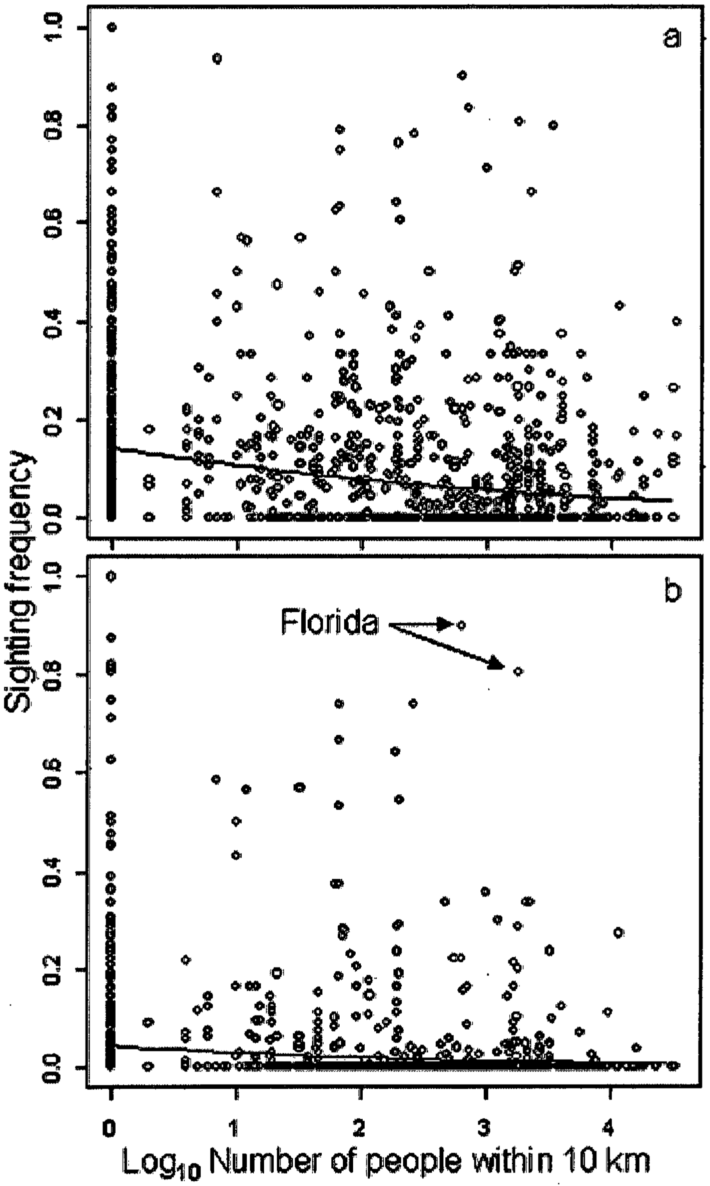


Figure 5.4 Absolute changes in population abundance of 14 shark species (see color code) for density dependent (left column) and density independent (right column) scenarios across a range of fishing mortalities (F): $F = 0$ (a, b), $F = 0.1$ (c, d), $F = 0.2$ (e, f), $F = 0.3$ (g, h), $F = 0.4$ (I, j), $F = 0.5$ (k, l).

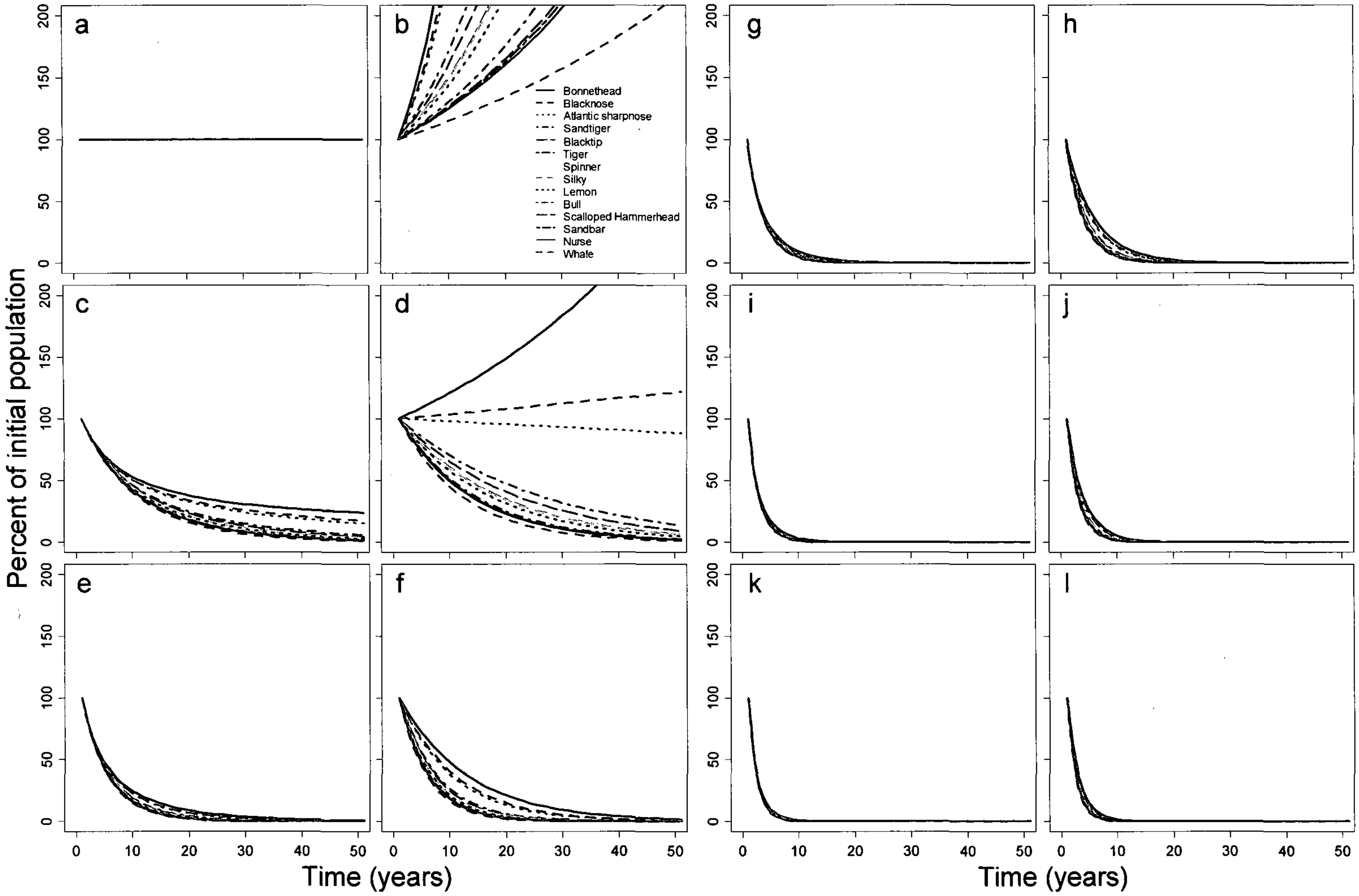
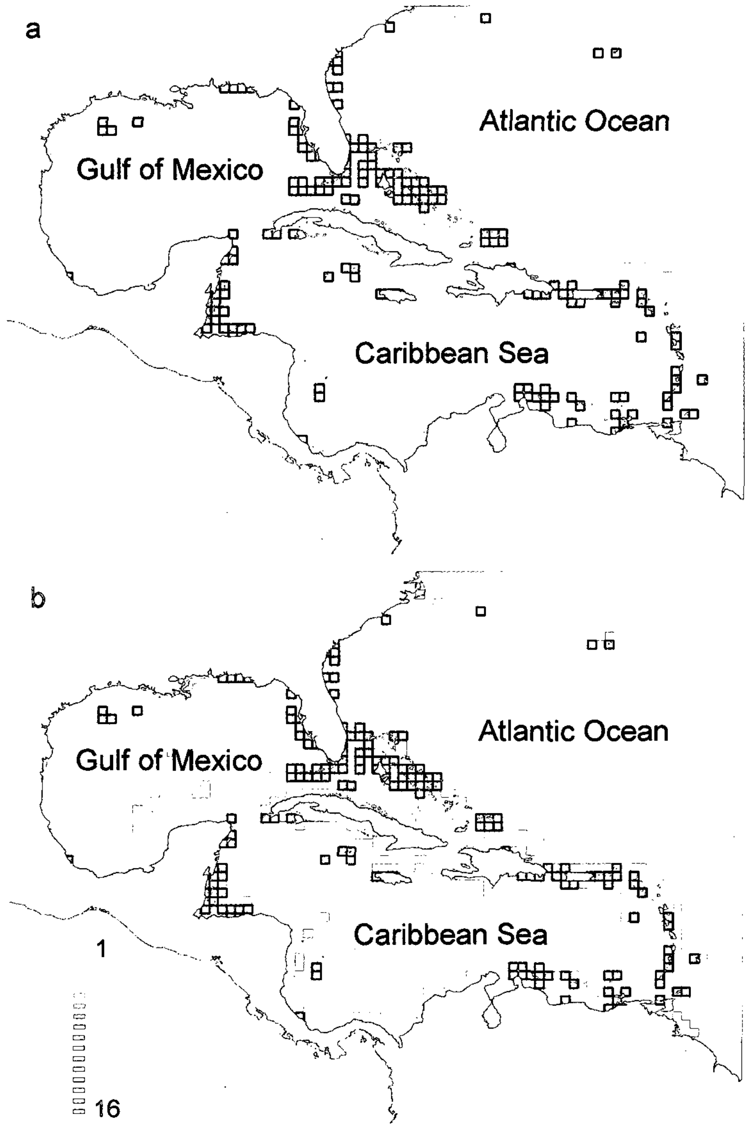


Figure 5.5 Patterns of species richness for the analyzed shark species. Here we show the number of shark species (see color code from 1 to 16) whose (a) geographical ranges and (b) suitable habitats overlap in half-degree cells across the greater-Caribbean. Geographical ranges were extracted from Compagno et al. (2005) and suitable habitats for each species were obtained from AquaMaps (Kaschner et al. 2008). Suitable habitats are based on the envelope of the environmental conditions where each species has been reported. The variables considered include depth, temperature, salinity, primary productivity, and distance to coastal areas. Cells containing diver survey data are outlined with black borders.



CHAPTER 6

CONCLUSION

6.1 THESIS CONCLUSIONS

The goal of this thesis was to investigate the accuracy, precision and value of data collected by scuba divers for analyzing spatial and temporal trends of elasmobranch populations. Due to their life history characteristics, elasmobranchs are vulnerable to exploitation and many populations have undergone strong shifts in abundance over the past decades due to the direct and indirect effects of fishing (Baum et al. 2003, Shepherd & Myers 2005, Robbins et al. 2006, Ferretti et al. 2008). Worldwide, many elasmobranch species are currently listed as near threatened (13%), vulnerable (11%), endangered (4%) or critically endangered (2%) by the World Conservation Union (IUCN), while 47% are data deficient (Camhi et al. 2009). In order to monitor these vulnerable species, it is important to move towards non-destructive sampling techniques where possible. Scuba divers using underwater visual surveys may provide such data, if their observation can be correctly interpreted and integrated. This thesis contributes to our knowledge of temporal and spatial trends of elasmobranch populations in the greater-Caribbean and provides insight into the precision and limitations of underwater visual census (UVC) methods conducted by scientific and non-scientific divers for monitoring fish around the world. The results suggest the need for caution when counting, analyzing and interpreting UVC data. Biases can be large and vary with survey methods and species characteristics. However, the results also show that diver surveys provide valuable, non-destructive and much needed data to monitor broad-scale distribution and temporal trends of elasmobranch populations.

In chapter 1, I provided a general introduction on the current critical state of elasmobranchs throughout the world and the necessity of non-extractive censusing methods to monitor the distribution and trends of vulnerable populations. I also introduced the often destructive methods that have been used to study elasmobranch populations in the past and reviewed the history and use of non-extractive UVC techniques to estimate the abundance of fish in the field.

In chapter 2, I developed a simulation model to evaluate fish counts obtained by divers deploying two standard scientific UVC techniques, the belt-transect and stationary-point-count census. In particular, I was interested in assessing non-instantaneous UVC, which are commonly used by researchers in the field, and the influence of fish mobility on estimated fish densities. Using this simulation I assessed the effect of fish speed and survey procedure (visibility, diver speed, survey time and dimensions) on the bias of fish counts obtained by divers. I found that the bias caused by fish speed alone can be huge, and that survey procedures have a varying effect on bias. These results are important for three reasons. First, it is critically important to take survey procedures and animal mobility into account when analyzing density or biomass based on counts gained from non-instantaneous UVC. Second, the bias in counts of mobile fishes can be so high and depend on factors which are not known with great precision (e.g. fish speed) that alternative census methods such as mark-recapture may be a better choice to derive absolute density estimates for rare, conspicuous animals such as sharks. Finally, studies that have used non-instantaneous UVC may need to be reexamined to adjust reported density and biomass levels and derive more realistic descriptions of community structure.

In chapter 3, I assessed the value and precision of data collected by recreational divers for monitoring elasmobranch populations. First, using an extension of the simulation model from chapter 2, I compared the level of fish detection between two standard scientific underwater survey techniques, the belt-transect and stationary-point-count, and a roving diver technique commonly used by recreational divers. I found that the roving diver detected fish at lower density with greater frequency and that the difference between the three survey methods decreased with increased fish speed. Then, using a field survey I showed that inexperienced divers report the presence and number of elasmobranchs as well as experienced divers and that fish density may affect the variability of results more than observer experience. These findings suggest that the different survey techniques may yield comparable results, and that the roving diver has a higher chance of detecting rare species. Thus, this study supports the idea that recreational scuba divers could be deployed to collect data for broad-scale monitoring of conspicuous species that are easy to recognize such as many sharks and rays; however, it is not suitable for assessing absolute abundance or density.

In chapter 4, I used over 85,000 individual underwater surveys collected by volunteer divers of the Reef Environmental Education Foundation (REEF) to examine trends in the most frequently sighted elasmobranch species in the greater-Caribbean, the yellow stingray (*Urobatis jamaicensis*). I reported previously undocumented spatial and temporal trends in yellow stingray abundance, thereby improving the basic understanding of this species for which ecological information is largely lacking. In general, the spatial distribution of this species may be more restricted than previously thought. Also, I found significant declines in most of the analyzed regions that may be linked to exploitation in unprotected or predation in protected areas. Only in one region had yellow stingray abundance increased which may be caused by the depletion of their predators. This chapter highlights the value of non-scientific divers for collecting data that may be used to understand population trends of otherwise poorly studied species. As well, it demonstrates the way in which volunteer-collected data can be analyzed and may be applicable for other rare, vulnerable or invasive species that require broad-scale monitoring, which is otherwise logistically difficult and expensive.

In chapter 5, I expanded the use of the REEF diver survey database to include records of all sharks on reefs in the greater-Caribbean. I then analyzed the possible role of human population density on the contemporary distribution and sighting frequency of these sharks. Overall, I found that human population density and inferred exploitation pressure in coastal zones have lead to the broad-scale absence of sharks on reefs. In general, the distribution ranges of sharks and suitable habitat encompass all of the greater-Caribbean where they were historically abundant. Yet, I found that sharks were largely absent on reefs today, a pattern that was more pronounced with the exclusion of the most abundant and least exploited species, the nurse shark. A comparison with human population density showed that sharks, other than nurse sharks, only occurred in areas with low human population density or strong fishing regulations and marine conservation. Population viability analysis suggested that sharks are vulnerable to even light levels of fishing pressure, and that under current levels of fishing mortality all shark species on reefs are at risk of extirpation. Overall, these findings suggest that exploitation and other human pressures have likely caused the disappearance of most sharks on reefs in the greater-Caribbean, and that strong fishing regulations and conservation efforts can be effective to prevent further losses and possible extinctions.

6.2 MANAGEMENT IMPLICATIONS

Firstly, the results of my investigation of the effect of fish speed on counts obtained by non-instantaneous UVC (chapter 2) have significant management implications. Overestimating the occurrence of the most mobile fishes, which are often the largest animals on a reef, would not only skew absolute estimates of abundance and biomass of those species, it would also lead to misconceptions about species richness and community structure. If management decisions (e.g. shark fishing quotas) were based on overestimated values then the set quotas may be too high. Similarly, conservation measures would be too weak if based on overestimated abundance levels of a vulnerable species. Finally, marine protected areas may have unrealistic goals if they were expected to restore standing biomass and community structure to target levels that are based on overestimated animal densities in unexploited or remote areas.

Chapter 3 demonstrates that recreational divers can be used for broad-scale monitoring of elasmobranch populations, which could help in the scientific assessment, management and conservation of these populations. As well, the results show that non-destructive sampling is possible for vulnerable, wide-ranging, relatively rare, conspicuous species and provides an important contribution to the overall knowledge and increasing use of citizen science (Silvertown 2009).

Chapter 4 provides important information on the spatial and temporal trends in the sighting frequency of the yellow stingray, a common but little known species (Fahy et al. 2007). Whereas some small elasmobranch species are reported to increase due to a depletion of their predators (Shepherd & Myers 2005, Myers et al. 2007), the yellow stingray appears to be declining in many regions of the greater-Caribbean. Although the decline in some regions may be a result of exploitation or declining habitat, it may also be a signal of ecosystem recovery in protected areas where increased predation or competition may lead to prey declines. This implies that management targets and strategies need to be placed in the context of ecosystem interactions, and that some population declines may be a natural consequence of the recovery of predators (Micheli et al. 2004).

Chapter 5 further supports the use of volunteer observers and provides a large-scale assessment of the distribution and sighting frequency of sharks in the greater-Caribbean relative to human population density and associated pressures. This chapter offers insight into some of the reef areas where protection efforts may be most valuable for preventing the extirpation of sharks on reefs in the greater-Caribbean. As well, this chapter shows that it is possible for sharks to live in proximity to humans if strong, enforced fishing regulations and conservation measures are in place. However, although sharks are still present in some regions, this does not mean that they are not vulnerable or declining, and may require further protection. The population viability analysis indicates that when shark anthropogenic mortality is greater than 10% per year, for all species analyzed, the populations trend toward extinction, indicating that only small levels of fishing mortality are sustainable for these populations. These results provide important information for management decisions and conservation targets.

6.3 THE WAY FORWARD: THE FUTURE OF DIVER COLLECTED DATA

This thesis has provided necessary groundwork for assessing and using scuba diver observations to monitor elasmobranch populations at the local and regional scale. Although the data analysis was restricted to the greater-Caribbean (chapters 4 & 5), my results indicate that there is potential to use scuba diver observations more widely to assess spatial and temporal trends in elasmobranchs on a global scale. In the following, I highlight a few directions for future research that stem directly from this thesis.

Firstly, my results suggest that previous research that has utilized UVC to census mobile marine animal populations should be reexamined and studies that used non-instantaneous UVC identified. Those studies that deployed non-instantaneous UVC should take into account animal mobility and survey procedures, to determine if the original conclusions remain. As well, researchers that have used non-instantaneous UVC in a long-term monitoring program need to weigh the pros and cons of switching to instantaneous UVC to derive more realistic density estimates. In general, instantaneous surveys are useful for obtaining accurate counts of populations to estimate absolute density, biomass and community composition. Non-instantaneous UVC, on the other hand, have a higher chance of detecting the presence of rare and highly mobile species such as many sharks. These surveys provide useful data for documenting relative differences within a species, but they do not provide accurate counts of mobile animals and tend to skew estimates of abundance, biomass, and community structure. Future UVC work should be explicit in the protocols of how surveys were performed and how they accounted for animal mobility. In the case of non-instantaneous UVC the analysis and interpretation of results must consider the bias that is introduced by animal mobility and survey procedures. In the future, if the goal of a study is to get estimates of absolute abundance for rare, wide-ranging and highly mobile animals such as sharks then other sampling procedures, such as mark-recapture, may be more appropriate.

Secondly, my results suggest the need for further investigation of the community structure and presence of 'inverted' (top-heavy) trophic biomass pyramids on pristine coral reefs. If non-instantaneous UVC were used in studies that derived extremely high abundance and biomass estimates of large predators such as sharks and jacks on remote and unexploited reefs (Friedlander & DeMartini 2002, Stevenson et al. 2007, Sandin et al. 2008), then the results and conclusions need to be re-investigated. Based on my study, non-instantaneous UVC would have produced high overestimates in the count of highly mobile reef predators. These overestimated counts would have skewed density estimates and even more biomass estimates, because the most mobile animals are also often the largest. This would have further lead to a distortion of the described community structure and the distribution of biomass across different trophic levels and between areas.

Exploring the possibility that non-instantaneous UVC have been used, I show that accounting for animal mobility alone would transform 'inverse' back to 'regular' trophic biomass pyramids, where most biomass is at lower levels.

Thirdly, the use of non-scientific diver's observations presents many opportunities for establishing baselines and monitoring future elasmobranch populations over large spatial scales. Data provided by recreational divers on their daily dive activities could supply enough data to monitor many shark and ray populations if the data is collected and analyzed appropriately. Diver collected data can be used to analyze spatial and temporal trends (as in chapters 4 and 5) for other species. As well divers could be an important source of data for monitoring the effectiveness of marine protected areas, where extractive census methods are prohibited.

Fourthly, despite being common and listed as Least Concern on the IUCN Red List, results from a large number of diver surveys suggest that the yellow stingray may be declining and should be investigated further. As well, the methods and analyses described in chapter 4 may be used to investigate temporal and spatial trends of other species where REEF data exists (currently the greater-Caribbean, tropical eastern Pacific, Hawaii, western and northeastern North America), including targeted reef species, like groupers, or invasive species, like the Pacific lion fish in the Atlantic.

Finally, non-scientific diver collected data could be used as an early warning system to detect large-scale changes in coastal regions that are poorly monitored by scientific assessment methods. Since recent research indicates that many elasmobranch species are undergoing rapid changes in abundance (Myers et al. 2007, Ferretti et al. 2008) it is essential that efforts to utilize diver-collected data occur in a timely fashion. Today, many thousands of dives are conducted on a daily basis by non-scientific divers on sites distributed around the world. To make use of this untapped source of information I have developed two online surveys (www.globalsharksurvey.com) that quantifies both historical and contemporary divers' observations. These surveys provide information that may be used to understand broad-scale changes, current hot-spots of shark abundance and diversity, the presence of aggregation sites, nurseries or mating grounds, and to monitor the effect of exploitation and protection measures. This thesis has provided necessary information needed for moving forward in the assessment of global shark populations using scuba divers' observations.

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