Non-lethal human-shark interactions and their ecological consequences

by

Aleksandra Maljković

M.Sc., University of East Anglia, 2004
B.Sc. Hons, University of Aberdeen, 1996

Thesis Submitted in Partial Fulfillment of the
Requirements for the Degree of
Doctor of Philosophy

in the
Department of Biological Sciences
Faculty of Science

SIMON FRASER UNIVERSITY
Fall 2018

Approval

Name:	**Aleksandra Maljković**
Degree:	**Doctor of Philosophy (Biological Sciences)**
Title:	**Non-lethal human-shark interactions and their ecological consequences**
Examining Committee:	**Chair:** Margo Moore Professor
	Isabelle M. Côté Senior Supervisor Professor, Dept. of Biological Sciences Simon Fraser University
	Nicholas K. Dulvy Supervisor Professor, Dept. of Biological Sciences Simon Fraser University
	Michael Heithaus Supervisor Professor, Dept. of Biological Sciences Florida International University
	Jonathan Moore Internal Examiner Associate Professor, Dept. of Biological Sciences Simon Fraser University
	Julia Baum External Examiner Associate Professor Biology University of Victoria
Date Defended/Approved:	October 31 2018

Ethics Statement

Abstract

Collapses of predator populations, caused mainly by unsustainable fishing, have been documented in many marine ecosystems. Predators are thought to play critical roles in marine environments where, through direct predation and fear effects, they can shape demographic processes and community structure. My thesis focusses on the effects of two non-lethal anthropogenic impacts on sharks: prey depletion and shark provisioning tourism. Using stable isotopes and a time series of shark vertebrae, I first examine the historical isotope ecology of seven shark species from the southwest Indian Ocean. Two species with generalist diets showed no change over two decades in $\delta^{15}N$ or $\delta^{13}C$ signatures. Large individuals of five primarily piscivorous species exhibited isotope signatures that deviate from historical baselines, suggesting long-term changes in diet and/or foraging strategy. Next, I measure the effects of tourism-related provisioning on the trophic signatures and movement patterns of Caribbean reef sharks (*Carcharhinus perezi*) in the Bahamas. Combining stable isotope analyses, acoustic telemetry and direct observations, I show that individual sharks that are provisioned more frequently have elevated $\delta^{15}N$ signatures, but similar residency and movement patterns to un-provisioned conspecifics, suggesting that their broader ecological roles are not affected by long-term provisioning. Finally, I use the gradient of shark abundance generated by provisioning for ecotourism to reveal the wider coral reef community corollaries of reef shark presence. Benthic community structure varied across this gradient, with less macroalgae and more turf algae at sites with more sharks. Herbivorous parrotfish were abundant but fed less selectively and consumed more macroalgae at sites with more sharks, suggesting that fear effects may drive the patterns observed. Teleost fish biomass was almost twice as high near the provisioning site than further away, a pattern driven by fisher avoidance of areas of more sharks. Effective shark conservation may thus deliver broad cascading benefits to coral reef communities. While most marine predator declines are due to direct fishing mortality, my thesis evokes additional mechanisms by which anthropogenic activities may drive change in predator populations and their communities.

Keywords: shark conservation, stable isotope ecology, predator-prey interactions, prey depletion, trophic cascades, indirect behaviourally mediated interactions

Acknowledgements

I have more people to thank than I could ever possibly have imagined at the start of this work. The first and foremost is my senior supervisor, Isabelle Côté. Isa, where do I even begin? You gave me the opportunity to do the best (and certainly the most fun) science of my life – for that alone I will always be grateful. Despite your initial trepidation, you came to the Bahamas to dive with ‘my’ sharks and my most cherished PhD-related memories are of those times. I’m pretty sure that, for numerous reasons, I must rate as one of your most challenging students ever. Nonetheless, you went above and beyond all reasonable supervisory expectations for me. The fact that I finished this thesis at all is testament only to the respect that I have for you, as both a scientist and a (bloody fine) human being. Your mentorship and friendship have been invaluable to me over the years and ………… this is getting way too gushy. You get the message, right? Thank you for everything, Isa – you’re the best!!!

I am also very grateful to Michael Heithaus and Nicholas Dulvy for their support and encouragement as my supervisory committee. Mike, your enthusiasm for my work was integral in helping me get through those tougher times, and your no-nonsense approach to nonsensical peer reviews was refreshing! Nick, having you as a sounding board for my ideas has been invaluable in helping me focus my work to answer specific questions more clearly. You have both challenged me to be a more thoughtful and rigorous scientist which has improved my work immensely. I would also like to thank Jonathan Moore and Julia Baum for being the internal and external examiners, respectively, for my thesis.

I have been incredibly lucky to be part of the Earth to Ocean research group at SFU. The graduate students, post-docs and faculty provided support, critical feedback and friendship throughout. My thesis and graduate student experience would be poorer without them. In particular, I am very grateful to Morgan Hocking and Jan Verspoor for their help with, and insights into, my initial forays with stable isotope work. Jenny and Joel Harding and Sebastian Pardo deserve special mentions for providing me with several of life’s necessities: humour, ridiculous distraction and fight club (can I mention fight club?).

I would not have succeeded with my data collection efforts without the help of many fantastic field assistants. Jill Brown, Chang Chin and Liz Parkinson literally risked life and limb (more limb than life, really) to help me tag sharks and collect tissue samples. Hui Nee Chin, Travis Van Leeuwen, Tom Parker, James Thompson and Graeme Nicholls were integral in various aspects of fieldwork as well as providing good company.

My work would not have been possible without the very generous logistic support provided by Stuart and Michelle Cove of Stuart Cove's Dive Bahamas. Their contributions to, and enthusiasm for, my research have been unprecedented. I also owe a debt of gratitude to all the boat captains and dive staff at Stuart Cove's for prioritising the dive sites I needed to visit and keeping the tourists away from my fish transects!

For the South African aspect of my thesis I thank the KwaZulu-Natal Sharks Board Operations staff for providing the sharks, and the Laboratory staff for collecting and storing the shark vertebrae. Sabine Wintner and Geremy Cliff provided permissions for using the specimens, as well as data, advice and conviviality.

I am very grateful for the financial support I received from Simon Fraser University in the form of graduate fellowships, scholarships and private awards. In addition, I thank Ms. S. Chang for funding the purchase of telemetry equipment, the American Fisheries Society for awarding me the Steven Berkeley Marine Conservation Fellowship, Project Aware for funding stable isotope work and the American Elasmobranch Society, American Society of Ichthyologists and Herpetologists and the Oceania Chondrichthyan Society for funding travel to conferences.

Finally, thank you Mum for always encouraging me to forge my own path rather than going with the flow. I know that path diverged significantly from what you expected or would have wanted, but you never stood in my way. You spent many hours worrying whether I was still intact while I was 'playing' with sharks in the Bahamas and many more hours tolerating my mercuriality (understatement?) since. Thank you for your patience with me.

Table of Contents

Approval ii
Ethics Statement iii
Abstract iv
Acknowledgements v
Table of Contents vii
List of Tables ix
List of Figures x

Chapter 1. General Introduction 1
Indirect effects of prey depletion on predators 2
Direct and indirect effects of provisioning on predators 3
Structure of the thesis 4
References 5

Chapter 2. Decadal-scale shifts in isotopic signatures of large, predatory sharks in the southwest Indian Ocean 10
Abstract 10
Introduction 10
Methods 13
  Provenance, selection and treatment of shark vertebrae 13
  Statistical analyses 15
Results and Discussion 16
  Ontogenetic patterns 16
  Decadal patterns 24
Conclusions 28
Acknowledgements 29
References 29

Chapter 3. Effects of tourism-related provisioning on the trophic signatures and movement patterns of Caribbean reef sharks[1] 38
Abstract 38
Introduction 39
Methods 40
  Study site and species 41
  Shark identification & behavioural observations 42
  Isotope sample collection and methods 42
  Acoustic telemetry 43
  Data analysis 45
Results 48
  Shark presence and behaviour at shark feeding dives 48
  Isotope signatures 48
  Residency and movement 49
Discussion 51

- Shark presence and behaviour at shark feeding dives 51
- Isotope signatures 52
- Residency and movement 53

Conclusions 55
Acknowledgements 56
References........ 56

Chapter 4. High shark abundance is associated with reserve-like restoration of coral reef communities 61
Abstract........ 61
Introduction 61
Material and methods........ 64
- Study sites and study species........ 64
- Fish surveys and habitat assessment 65
- Shark counts........ 66
- Distribution of fishing boats and fisher success........ 66
- Observations of parrotfish herbivory 67
- Statistical analysis 67

Results........ 69
- Shark and teleost distribution........ 69
- Benthic composition........ 71
- Parrotfish foraging 72
- Fisher distribution and landing success 74

Discussion........ 74
Acknowledgements. 79
References........ 79

Chapter 5. General Conclusions 85
Prey depletion 86
Provisioning reef sharks........ 87
Community consequences of high shark abundance........ 88
References........ 90

Appendix A. 94

Appendix B. 100

List of Tables

Table 2.1 Size and vertebral characteristics of the seven shark species caught off KwaZulu-Natal, South Africa, and sampled in this study for stable isotope analysis. 14

Table 4.1 Documented relationships among the densities of sharks, teleost fishes and benthic communities on coral reefs. P/U: Protected vs unprotected, N/F: Near vs far from human populations, ↑: higher abundance (compared to unprotected or near site), ↓: lower abundance, ↔ : no effect or effect is unclear, NA:notassessed…….. 63

Table 4.2 Results of analyses of variance comparing biomass of reef fish of various trophic groups among the 21 coral reef sites surveyed. Species in each trophic guild are listed in S4.1 Table. Bait-attracted species include the four fish species that came within 5 m of the bait box during shark feeds: *Carangoides ruber*, *Mycteroperca bonaci*, *Ocyurus chrysurus* and *Elagatis bipinnulata*. 72

Table 4.3 Estimates of mean shark biomass on some of the world's most 'pristine' coral reefs. 75

List of Figures

Figure 2.1 $\delta^{15}N$ (top row) and $\delta^{13}C$ (bottom row) enrichment of Blacktip shark (*Carcharhinus limbatus*) vertebrae from individuals caught in the KwaZulu-Natal Sharks Board gill nets, for three size classes over 5-year periods. Size classes were defined in relation to vertebral sub-sample position: second (white bars), third (pale grey bars), and last sub-sample (dark grey bars). Sub-sampling intervals are given in Table 2.1 and estimated mean precaudal lengths of sharks for each sub-sample are shown in Tables S2.1 and S2.2 in Appendix A. Means are presented with bias-corrected accelerated (BCa) bootstrapped standard deviations (bars) and 95% confidence intervals (circles). *n* = 5 individuals 17

Figure 2.2 $\delta^{15}N$ (top row) and $\delta^{13}C$ (bottom row) enrichment of Spinner shark (*Carcharhinus brevipinna*) vertebrae from individuals caught in the KwaZulu-Natal Sharks Board gill nets, for three size classes over 5-year periods. Size classes were defined in relation to vertebral sub-sample position: second (white bars), third (pale grey bars), and last sub-sample (dark grey bars). Sub-sampling intervals are given in Table 2.1 and estimated mean precaudal lengths of sharks for each sub-sample are shown in Tables S2.1 and S2.2 in Appendix A. Means are presented with bias-corrected accelerated (BCa) bootstrapped standard deviations (bars) and 95% confidence intervals (circles). *n* = 5 individuals 18

Figure 2.3 $\delta^{15}N$ (top row) and $\delta^{13}C$ (bottom row) enrichment of bull shark (*Carcharhinus leucas*) vertebrae from individuals caught in the KwaZulu-Natal Sharks Board gill nets, for three size classes over 5-year periods. Size classes were defined in relation to vertebral sub-sample position: second (white bars), third (pale grey bars), and last sub-sample (dark grey bars). Sub-sampling intervals are given in Table 2.1 and estimated mean precaudal lengths of sharks for each sub-sample are shown in Tables S2.1 and S2.2 in Appendix A. Means are presented with bias-corrected accelerated (BCa) bootstrapped standard deviations (bars) and 95% confidence intervals (circles). *n* = 5 individuals. 19

Figure 2.4 $\delta^{15}N$ (top row) and $\delta^{13}C$ (bottom row) enrichment of Ragged-tooth shark, (*Carcharias taurus*) vertebrae from individuals caught in the KwaZulu-Natal Sharks Board gill nets, for three size classes over 5-year periods. Size classes were defined in relation to vertebral sub-sample position: second (white bars), third (pale grey bars), and last sub-sample (dark grey bars). Sub-sampling intervals are given in Table 2.1 and estimated mean precaudal lengths of sharks for each sub-sample are shown in Tables S2.1 and S2.2 in Appendix A. Means are presented with bias-corrected accelerated (BCa) bootstrapped standard deviations (bars) and 95% confidence intervals (circles). *n* = 5 individuals 20

Figure 2.5 $\delta^{15}N$ (top row) and $\delta^{13}C$ (bottom row) enrichment of Tiger shark, (*Galeocerdo cuvier*) vertebrae from individuals caught in the KwaZulu-Natal Sharks Board gill nets, for three size classes over 5-year periods. Size classes were defined in relation to vertebral sub-sample position: second (white bars), third (pale grey bars), and last sub-sample (dark grey bars). Sub-sampling intervals are given in Table 2.1 and estimated mean precaudal lengths of sharks for each sub-sample are shown in

Tables S2.1 and S2.2 in Appendix A. Means are presented with bias-corrected accelerated (BCa) bootstrapped standard deviations (bars) and 95% confidence intervals (circles). *n* = 5 individuals. 21

Figure 2.6 δ15N (top row) and δ13C (bottom row) enrichment of Shortfin mako, (*Isurus oxyrinchus*) vertebrae from individuals caught in the KwaZulu-Natal Sharks Board gill nets, for three size classes over 5-year periods. Size classes were defined in relation to vertebral sub-sample position: second (white bars), third (pale grey bars), and last sub-sample (dark grey bars). Sub-sampling intervals are given in Table 2.1 and estimated mean precaudal lengths of sharks for each sub-sample are shown in Tables S2.1 and S2.2 in Appendix A. Means are presented with bias-corrected accelerated (BCa) bootstrapped standard deviations (bars) and 95% confidence intervals (circles). n = 5 individuals (except for 1970-1975 samples where n = 4)……………………………………………………..22

Figure 2.7 δ15N (top row) and δ13C (bottom row) enrichment of Scalloped hammerhead, (*Sphyrna lewini*). vertebrae from individuals caught in the KwaZulu-Natal Sharks Board gill nets, for three size classes over 5-year periods. Size classes were defined in relation to vertebral sub-sample position: second (white bars), third (pale grey bars), and last sub-sample (dark grey bars). Sub-sampling intervals are given in Table 2.1 and estimated mean precaudal lengths of sharks for each sub-sample are shown in Tables S2.1 and S2.2 in Appendix A. Means are presented with bias-corrected accelerated (BCa) bootstrapped standard deviations (bars) and 95% confidence intervals (circles). n = 5 individuals……………………………………………………………...23

Figure 3.1 Map of study site and receiver positions. The dashed line represents the eastern edge of the Tongue of the Ocean trench………………………………………………………………………..44

Figure 3.2. Bait consumption, sighting frequency and sizes of focal Caribbean reef sharks at New Providence, Bahamas. (a) Proportion of total bait consumed, (b) sighting frequency at shark feeds and (c) shark total length. Filled circles in (a) represent the minimum and maximum proportion of bait consumed by individual sharks in each focal group. Error bars are ± 1 SE. Shark sample sizes: nfed = 9, nunfed = 12, ncontrol = 10…………………………………………………………………..47

Figure 3.3 Stable carbon and nitrogen isotope values of muscle tissue from Caribbean reef sharks under different provisioning regimes off southern New Providence, Bahamas………………………………………………...…………………..49

Figure 3.4 Residency and daily travel distances of focal Caribbean reef sharks at New Providence, Bahamas. (a) Residency (light bars: morning, dark bars: afternoon), measured as the number of detections recorded for an individual shark at a specific home receiver in relation to the total number of detections recorded for that individual across all receivers, and (b) minimum distances travelled, measured as the sum of the straight-line distances travelled by sharks between the receivers over 24 hours. Error bars are ± 1 SE. Shark sample sizes: nfed = 9, nunfed = 12, ncontrol = 10…………………………………………………………………………….…50

Figure 4.1 Variation in fish communities, fishing effort and fishing success. (a) Shark abundance (mean ± SE) and cumulative fishing boat sightings over 60 days, (b) biomass of reef-associated fish guilds (means + SE) (yellow: herbivores; light orange: low-level carnivores; dark orange: piscivores < 50 cm TL; red: piscivores > 50 cm TL; hatched: bait-attracted species, and (c) proportion of hooked fish landed, at varying distances from a shark feeding site…………………………………………………………......70

Figure 4.2 Algal composition in relation to distance from the shark feeding site. Cover of macroalgae, turf algae and crustose coralline algae (CCA) as a percentage of the total algal cover per site (mean ± SE) at varying distances from a shark feeding site. Gaps in the dataset represent sites where the substratum was primarily sand, and therefore not comparable to the other sites. Turf algae cover varied significantly among sites (F20,105 = 4.92, P <0.0001), as did macroalgal cover (F20,105 = 6.23, P <0.0001); the cover of crustose coralline algae was less variable (F20,105 = 1.62, P = 0.06)…………………………………………………….………..….71

Figure 4.3 Parrotfish foraging under variable risk of predation. (A) Bite rate, (B) duration of feeding bouts, (C) diversity of algal targets taken, and (D) proportion of total bites taken on macroalgae, by redband parrotfish *Sparisoma aurofrenatum* at varying distances from a shark provisioning site. The density of predators (sharks and large piscivorous teleost fishes) at these distances is shown in Figure 1. Means are shown ± 1 SD. In all panels, at distance = 0, n = 29; at 500 m, n = 21; at 1000 m, n = 19 parrotfish……………………….……………………………………………..….73

Chapter 1.

General Introduction

Globally, populations of large marine vertebrates such as whales, sharks and tunas have been depleted by both historical and contemporary fisheries (e.g., Jackson et al. 2001; Baum et al. 2003; Myers & Worm 2003). These species often play critical roles in marine ecosystems, and even moderate declines in the abundance of large predatory species can precipitate shifts in marine community structure and alter ecological dynamics (reviewed in Heithaus et al. 2008 & Ferretti et al. 2010). While the direct and indirect impacts of removing predators from marine ecosystems have received increasing research attention over the past two decades, the only broadly agreed outcome is that marine predator populations require more effective conservation strategies than the interventions currently implemented to prevent them from becoming ecologically extinct.

The development and enforcement of strategic conservation initiatives for large, and often wide-ranging, marine species pose many challenges. Notwithstanding, basic ecological data are still lacking for many taxa and, despite their large body size, some species remain cryptic throughout their lives. Technological advancements in, for example, satellite telemetry, DNA analysis and the use of biogeochemical markers have enabled more rapid progress in documenting these species' ecology over the last few decades. However, conservation strategies for large marine predators remain almost entirely limited to fisheries management policies and the establishment of marine protected areas (MPAs); both strategies producing highly equivocal and much debated results to date (Davidson 2012; Chapman et al. 2013; Dulvy 2013; Vianna et al. 2016; Dulvy et al. 2017; Ward-Paige 2017).

Elasmobranch fishes (sharks and rays – herein after 'sharks') are the epitome of this scenario in which divisive policies of species and population management have led to inaction, ineffective action and dilution of species conservation efforts (Dulvy 2013; Davidson et al. 2016; Dulvy et al. 2017). When assessed using the IUCN Red List Criteria (www.redlist.org), approximately one-quarter of all shark species are threatened with an elevated risk of extinction (Dulvy et al. 2014). While it is broadly acknowledged that extractive fisheries are the major cause of population declines in these species (e.g., Baum et al. 2003; Baum & Myers 2004), far less emphasis has been placed on examining alternative mechanisms by which shark populations may be affected by human activities.

In this thesis I start to redress the balance by investigating the effects of two independent, non-lethal, anthropogenic impacts – prey depletion and shark provisioning tourism – on sharks. In addition, I use a novel, semi-experimental approach to determine the community consequences of locally elevated shark abundance.

Indirect effects of prey depletion on predators

Empirically estimating the indirect effects of prey depletion on predators is a current challenge in ecology, particularly in complex food webs where many species interact weakly to produce strong effects (Berlow 1999). However, knowledge of food web structure - and the relative biomasses of its component species - remains central to our understanding of how species' population sizes are regulated (e.g., Elton 1927; Hairston et al. 1960; Trebilco et al. 2013). Understanding the impacts of prey depletion on predators is important in the context of predator recovery from overexploitation (Marshall et al. 2016), but this scenario is further complicated when both the predator and prey species have a history of exploitation (Lee et al. 2016). While the direct effects of prey depletion on predators are usually fairly rapid and hence detectable at an early stage (e.g., reduced breeding success in seabirds (Cury et al. 2011)), the indirect effects of prey depletion on predators that manifest via cascading trophic interactions take longer to develop and may remain undetectable for many years (Babcock et al. 2010).

To my knowledge, there are few examples of diet shifts in predators that have been clearly linked to depletion caused by human exploitation, but natural (e.g., seasonal and annual) variation in prey availability hint at what the trophic effects on predators could be. For example, oystercatchers (*Haematopus ostralegus*) switch to smaller bivalves when their preferred-sized prey become rare (O'Connor & Brown 1977). Similarly, invasive rats (*Rattus rattus*) and cats (*Felix catus*) on tropical islands have been shown to shift from targeting seabirds, their main food source, to alternative prey such as sea turtles (*Chelonia mydas*), insects and rodents when seabirds are not nesting (Caut et al. 2008; Peck et al. 2008). Theory predicts that a generalist habit should facilitate prey switching to track resource availability (Charnov 1976). Therefore, the effects of prey depletion might be expected to manifest more strongly in specialist than generalist species.

Direct and indirect effects of provisioning on predators

Wildlife provisioning is a highly contentious topic, which is currently attracting increased research effort. The explosive rise in wildlife-based tourism over the last three decades (UNEP/CMS 2006; Balmford et al. 2015) has generated a perceived need for predictable wildlife-viewing opportunities for tourists, and this is often achieved using food items to habituate particular species to specific time/place events. This activity is most polarising when provisioning of predators is involved, usually due to human safety concerns, but more recently due to the perceived impacts of provisioning on the target species and their wider community.

The majority of studies examining the effects of provisioning on predators have focussed on the direct impacts of supplemental feeding on the target species. For example, provisioning is associated with increased intraspecific aggression in Formosan macaques (*Macaca cyclopis*: Hsu et al. 2009), abnormally dense aggregations of individuals in Komodo dragons (*Varanus komodoensis*; Newsome & Rodger 2008), increased injury rates in common bottlenose dolphins (*Tursiops truncates*; Christiansen et al. 2016), as well as multiple physiological indicators of reduced fitness in elasmobranchs (e.g., Semeniuk & Rothley 2008, 2009; Barnett et al. 2016).

The indirect, or community impacts, of provisioning predators have received far less attention to date, especially with regard to provisioning in marine environments (reviewed in Brena et al. 2015; Gallagher et al. 2015). However, a handful of studies have started to address the broader ecological impacts of provisioning marine predators, which is critical given the important roles these species play in structuring communities. Meyer et al. (2009), Brunnschweiler & Baench (2011) and Brunnschweiler et al. (2014) found that long-term, site specific provisioning altered the community structure of elasmobranch populations off Hawaii and Fiji, respectively. Specifically, smaller shark species were recorded less commonly as encounter rates with larger species increased over time. These initial findings imply that competitive exclusion of smaller elasmobranchs, and very likely other mesopredator species, could have cascading impacts to lower trophic levels, which warrants further investigation.

Structure of the thesis

In Chapter 2 I examine the historical isotope ecology of seven predatory shark species from the south-west Indian Ocean to assess whether contemporary shark populations feed at, or near to, the same trophic levels as historical populations. Specifically, I use stable isotope analysis of a time series of shark vertebrae to establish isotopic baselines from which current and future changes may be measured. The importance of measuring this baseline is the fact that anthropogenic marine resource exploitation is likely to have altered the structure of predator populations, and their prey communities, prior to the advent of modern scientific monitoring (Pauly 1995, Wing & Wing 2001). Realistic estimation of a species' trophic status, which may have implications for growth and reproduction, under unexploited conditions is therefore not possible using recent data (Holm 2003). Sharks are generally regarded as top predators in marine ecosystems, and assimilation of prey nutrients into their tissues, determined primarily by dietary preferences and prey availability, provides an opportunity to assess the effects of fishery-induced food-web restructuring on their trophic status (Cortés 1999; MacNeil et al. 2005; Estrada et al. 2006).

In Chapter 3 I examine the impacts of shark provisioning tourism on the isotopic signatures and movement patterns of Caribbean reef sharks (*Carcharhinus perezi*) in the Bahamas. Using a combination of direct observations at shark feeding events, remote acoustic telemetry and stable isotope analysis, I compare and contrast the isotope signatures and movement patterns of individuals that are regularly fed as part of a shark-dive tourism venture with their un-provisioned conspecifics. Shark-related tourism is a non-extractive alternative to other forms of commercial exploitation of sharks, and has the potential to contribute to the conservation of many coastal species (Carwardine & Watterson 2002; Topelko & Dearden 2005). It is crucial, however, that these activities are undertaken with due regard for the ecology of both the sharks and their habitat. As such, detecting changes in the feeding ecology and spatial dynamics of these sharks is integral in predicting the potential effects of this activity on their functional role within the community.

In Chapter 4 I reverse the trend of examining the effects of predator losses from marine ecosystems and instead use the inflated shark abundances generated by long-term shark feeding events to elucidate the effect of high shark abundance on coral reef community structure. Across a gradient of Caribbean reef shark abundance, I assessed benthic community structure, fish biomass across trophic guilds, herbivorous fish feeding behaviour, and fisher success at landing catches to determine the mechanisms by which reef shark presence may have cascading effects on coral reef communities. The broader ecological corollaries of high shark abundance have been much debated since the inception of ‘shark sanctuaries’ as a conservation measure, so establishing the wider effects of this guild approach to conservation is of high contemporary relevance.

Finally, I draw together the findings of my thesis and broadly consider their implications for shark populations and their effective conservation. As well as highlighting the novel insights that my thesis provides, I make suggestions for future research that would add to the growing body of literature dedicated to understanding the complex array of variables affecting the restoration and preservation of large, charismatic, marine predator populations.

References

Babcock, R.C., Shears, N.T., Alcala, A.C., Barrett, N.S., Edgar, G.J., Lafferty, K.D., McClanahan, T.R. & Russ, G.R. (2010) Decadal trends in marine reserves reveal differential rates of change in direct and indirect effects. Proceedings of the National Academy of Sciences USA, 107, 18256-18261.

Balmford, A., Green, J.M.H., Anderson, M., Beresford, J., Huang, C., Naidoo, R., Walpole, M. & Manica, A. (2015) Walk on the Wild Side: Estimating the Global Magnitude of Visits to Protected Areas. PLoS Biology, 13, e1002074.

Barnett, A., Payne, N.L., Semmens, J.M. & Fitzpatrick, R. (2016) Ecotourism increases the field metabolic rate of whitetip reef sharks. Biological Conservation, 199, 132-136.

Baum, J.K., Myers, R.A., Kehler, D.G., Worm, B., Harley, S.J. & Doherty, P.A. (2003) Collapse and conservation of shark populations in the northwest Atlantic. Science, 299, 389-392.

Baum, J.K. & Myers, R.A. (2004) Shifting baselines and the decline of sharks in the Gulf of Mexico. Ecology Letters, 7, 135-145.

Berlow, E.L. (1999) Strong effects of weak interactions in ecological communities. Nature, 398, 330-334.

Brena, P.F., Mourier, J., Planes, S. & Clua, E. (2015) Shark and ray provisioning: functional insights into behavioral, ecological and physiological responses across multiple scales. Marine Ecology Progress Series, 538, 273-283.

Brunnschweiler, J.M., Abrantes, K.G. & Barnett, A. (2014) Long-term changes in species composition and relative abundances of sharks at a provisioning site. PLoS ONE, 9, e94118.

Brunnschweiler, J.M. & Baensch, H. (2011) Seasonal and long-term changes in relative abundance of bull sharks from a tourist shark feeding site in Fiji. PLoS ONE, 6, e16597.

Carwardine, M. & Watterson, K. (2002) The Shark Watcher’s Handbook. BBC Worldwide Ltd, London.

Caut, S., Angulo, E. & Courchamp, F. (2008) Dietary shift of an invasive predator: rats, seabirds and sea turtles. Journal of Applied Ecology, 45, 428-437.

Chapman, D.D., Frisk, M.G., Abercrombie, D.L., Safina, C., Gruber, S.H., Babcock, E.A., Feldheim, K.A., Pikitch, E.K., Ward-Paige, C., Davis, B., Kessel, S., Heithaus, M. & Worm, B. (2013) Give Shark Sanctuaries a Chance. Science, 339, 757.

Charnov, E.L. (1976) Optimal foraging, the marginal value theorem. Theoretical Population Biology, 9, 129-136.

Christiansen, F., McHugh, K.A., Bejder, L., Siegal, E.M., Lusseau, D., Berens McCabe, E., Lovewell, G. & Wells, R.S. (2016) Food provisioning increases the risk of injury in a long-lived marine top predator. Royal Society Open Science, 3, 160560.

Cortés, E. (1999) Standardized diet compositions and trophic levels of sharks. ICES Journal of Marine Science, 56, 707-717.

Cury, P.M., Boyd, I.L., Bonhommeau, S., Anker-Nilssen, T., Crawford, R.J.M., Furness, R.W., Mills, J.A., Murphy, E.J., Österblom, H., Paleczny, M., Piatt, J.F., Roux, J.-P., Shannon, L. & Sydeman, W.J. (2011) Global seabird response to forage fish depletion—one-third for the birds. Science, 334, 1703-1706.

Davidson, L.N.K. (2012) Shark Sanctuaries: Substance or Spin? Science, 338, 1538-1539.

Davidson, L.N.K., Krawchuk, M.A. & Dulvy, N.K. (2016) Why have global shark and ray landings declined: Improved management or overfishing? Fish and Fisheries, 17, 438-458.

Dulvy, N.K. (2013) Super-sized MPAs and the marginalization of species conservation. Aquatic Conservation: Marine and Freshwater Ecosystems, 23, 357-362.

Dulvy, N.K., Fowler, S.L., Musick, J.A., Cavanagh, R.D., Kyne, P.M., Harrison, L.R., Carlson, J.K., Davidson, L.N., Fordham, S.V. & Francis, M.P. (2014) Extinction risk and conservation of the world's sharks and rays. eLife, 3, e00590.

Dulvy, N.K., Simpfendorfer, C.A., Davidson, L.N.K., Fordham, S.V., Bräutigam, A., Sant, G. & Welch, D.J. (2017) Challenges and Priorities in Shark and Ray Conservation. Current Biology, 27, 565-572.

Elton, C. (1927) Animal Ecology. Macmillan.

Estrada, J.A., Rice, A.N., Natanson, L.J. & Skomal, G.B. (2006) Use of isotopic analysis of vertebrae in reconstructing ontogenetic feeding ecology in white sharks. Ecology, 87, 829-834.

Ferretti, F., Worm, B., Britten, G.L., Heithaus, M.R. & Lotze, H.K. (2010) Patterns and ecosystem consequences of shark declines in the ocean. Ecology Letters, 13, 1055-1071.

Gallagher, A.J., Vianna, G.M.S., Papastamatiou, Y.P., Macdonald, C., Guttridge, T.L. & Hammerschlag, N. (2015) Biological effects, conservation potential, and research priorities of shark diving tourism. Biological Conservation, 184, 365-379.

Hairston, N.G., Smith, F.E. & Slobodkin, L.B. (1960) Community structure, population control, and competition. American Naturalist, 94, 421-425.

Heithaus, M., Frid, A., Wirsing, A.J. & Worm, B. (2008) Predicting ecological consequences of marine top predator declines. Trends in Ecology & Evolution, 23, 202-10.

Holm, P. (2003) History of marine animal populations: a global research program of the Census of Marine Life. Oceanologica Acta, 25, 207-211.

Hsu, M.J., Kao, C-C. & Agoramoorthy, G. (2009) Interactions between visitors and Formosan macaques (*Macaca cyclopis*) at Shou-Shan Nature Park, Taiwan. American Journal of Primatology, 71, 214-222.

Jackson, J.B.C., Kirby, M.X., Berger, W.H., Bjorndal, K.A., Botsford, L.W., Bourque, B.J., Bradbury, R.H., Cooke, R., Erlandson, J., Estes, J.A., Hughes, T.P., Kidwell, S., Lange, C.B., Lenihan, H.S., Pandolfi, J.M., Peterson, C.H., Steneck, R.S., Tegner, M.J. & Warner, R.R. (2001) Historical overfishing and the recent collapse of coastal ecosystems. Science, 293, 629-638.

Lee, L. C., Watson, J.C., Trebilco, R. & Salomon, A.K. (2016) Indirect effects and prey behavior mediate interactions between an endangered prey and recovering predator. Ecosphere, 7, e01604.

MacNeil, M.A., Skomal, G.B. & Fisk, A.T. (2005) Stable isotopes from multiple tissues reveal diet switching in sharks. Marine Ecology Progress Series, 302, 199-206.

Marshall, K.N., Stier, A.C., Samhouri, J.F., Kelly, R.P. & Ward, E.J. (2016) Conservation challenges of predator recovery. Conservation Letters, 9, 70-78.

Meyer, C.G., Dale, J.J., Papastamatiou, Y.P., Whitney, N.M. & Holland, K.N. (2009) Seasonal cycles and long-term trends in abundance and species composition of sharks associated with cage diving ecotourism activities in Hawaii. Environmental Conservation 36, 104-111.

Myers, R.A. & Worm, B. (2003) Rapid worldwide depletion of predatory fish communities. Nature, 423, 280-283.

Newsome, D. & Rodger, K. (2008) To feed or not to feed: a contentious issue in wildlife tourism. In: Lunney, D., Munn, A. and Meikle, W., (eds.) Too close for comfort: contentious issues in human-wildlife encounters. Royal Zoological Society of New South Wales, Mosman, N.S.W, 255-270.

O'Connor, R.J. & Brown, R.A. (1977) Prey depletion and foraging strategy in the Oystercatcher *Haematopus ostralegus*. Oecologia, 27, 75-92.

Pauly, D. (1995) Anecdotes and the shifting baseline syndrome of fisheries. Trends in Ecology and Evolution, 10, 430.

Peck, D.R., Faulquier, L., Pinet, P., Jaquemet, S. & Le Corre, M. (2008) Feral cat diet and impact on sooty terns at Juan de Nova Island, Mozambique Channel. Animal Conservation, 11, 65-74.

Semeniuk, C.A.D. & Rothley, K.D. (2008) Costs of group-living for a normally solitary forager: effects of provisioning tourism on southern stingrays Dasyatis americana. Marine Ecology Progress Series, 357, 271–282.

Semeniuk, C.A.D. & Rothley, K.D. (2009) Hematological differences between stingrays at tourist and non-visited sites suggest physiological costs of wildlife tourism. Biological Conservation, 142, 1818-1829.

Topelko, K.N. & Dearden, P. (2005) The shark watching industry and its potential contribution to shark conservation. Journal of Ecotourism, 4, 108-128.

Trebilco, R., Baum, J.K., Salomon, A.K. & Dulvy, N.K. (2013) Ecosystem ecology: size-based constraints on the pyramids of life. Trends in Ecology and Evolution, 28, 423-431.

UNEP/CMS. (2006) Wildlife watching and tourism: A study on the benefits and risks of a fast growing tourism activity and its impacts on species. UNEP / CMS Secretariat, Bonn, Germany. 68 pages.

Vianna, G.M.S., Meekan, M.G., Ruppert, J.L.W., Bornovski, T.H. & Meeuwig, J.J. (2016) Indicators of fishing mortality on reef-shark populations in the world's first shark sanctuary: the need for surveillance and enforcement. Coral Reefs, 35, 973-977.

Ward-Paige, C.A. (2017) A global overview of shark sanctuary regulations and their impact on shark fisheries. Marine Policy, 82, 87-97.

Wing, S.R. & Wing, E.S. (2001) Prehistoric fisheries in the Caribbean. Coral Reefs, 20, 1-8.

Chapter 2.

Decadal-scale shifts in isotopic signatures of large, predatory sharks in the southwest Indian Ocean

Abstract

Globally, the abundance, biomass and community structure of marine fish populations have been altered by fishing activities, with deleterious consequences for food web dynamics. To date, the indirect impacts of fishing on the trophic ecology and functional roles of marine apex predators remain unclear. I used stable isotope analysis of a time-series of shark vertebrae to elucidate the trophic responses of seven large, predatory shark species to prey depletion in the southwest Indian Ocean. Two species (*Galeocerdo cuvier* and *Carcharhinus leucas*) with very broad diets showed no change in $\delta^{15}N$ or $\delta^{13}C$ signatures over time, but four primarily piscivorous species (*Carcharhinus limbatus, Carcharhinus brevipinna, Carcharias taurus* and *Isurus oxyrinchus*) showed trends of decreasing $\delta^{15}N$ in larger individuals over time. A single species (*Sphyrna lewini*) exhibited a trend of increasing $\delta^{15}N$ and $\delta^{13}C$ in larger individuals over time, suggesting long-term changes in diet and/or foraging strategy. The differential responses of sharks to changes in prey community structure suggest that while some species appear largely unaffected, others exhibit trophic shifts that may have consequences for growth and recruitment. While most marine predator declines are due to direct fishing mortality, my results evoke an additional, indirect mechanism by which fisheries may drive change in predator populations.

Introduction

Fishing is widely regarded as the most pervasive influence on contemporary marine communities (Pauly et al. 1998, Jackson et al. 2001, Myers and Worm 2005, Swartz et al. 2010). The consequences of human exploitation have most often been estimated for geographically distinct stocks of commercially important species (e.g. Hutchings and

Reynolds 2004, Brander 2007, Dorner et al. 2008, Feltrim 2010, Juan-Jordá et al. 2011), but as management strategies have shifted from a species to an ecosystem focus, there has been increased emphasis on defining the broader ecological corollaries of extractive fishing (Pikitch et al. 2004, Arkema et al. 2006, Crowder et al. 2008, Zhou et al. 2010). Of the many species targeted by industrial fisheries (FAO 2009), large predatory fish (e.g., sharks, tunas and billfish) have undergone some of the most severe population declines in response to exploitation (Baum et al. 2003, Christensen et al. 2003, Myers and Worm 2003, Ward and Myers 2005, Dulvy et al. 2008, Safina and Klinger 2008, Juan-Jordá et al. 2011). As such, most research investigating the broader consequences of fisheries has focused on the cascading impacts of predator depletion on lower trophic levels of marine food webs (Jennings and Polunin 1997, Friedlander and DeMartini 2002, Dulvy et al. 2004, Frank et al. 2005, Myers et al. 2007, Heithaus et al. 2008, Baum and Worm 2009, Ferretti et al. 2010, Palkovacs et al. 2011).

To date, the consequences of fisheries-induced prey depletion for marine apex predators have received little empirical attention (Walker 2007), despite the fact that an ever-increasing number of large predatory species are of conservation concern (Baum et al. 2003, Myers and Worm 2005, Dulvy et al. 2008, Safina and Klinger 2008, Ward-Paige et al. 2010, Juan-Jordá et al. 2011). Yet, such consequences are highly likely. In marine ecosystems, large-bodied sharks are likely to compete with fishers for prey resources given their shared preference for large piscivorous species (Pauly et al. 1998, Christensen et al. 2003, Myers and Worm 2003). Previous studies have documented a large (> 90%) overlap between species in shark diets and fishery landings (Lucifora et al. 2009), as well as prey switching by sharks in areas where there is intense fishing pressure on their usual prey species (Koen Alonso et al. 2002). The serial depletion of large piscivores, as well as other species, from both coastal and pelagic ecosystems by industrial fisheries should therefore have direct impacts on the trophic ecology of large predatory sharks (Stevens et al. 2000, Walker 2007).

There are several impediments to documenting trophic shifts in large sharks. The feeding habits of many species remain poorly documented, due primarily to the difficulties associated with the long-term study of large, wide-ranging marine animals (Heithaus et al. 2001). In species for which data are available, shark diets reflect both seasonal and spatial variation in prey availability (e.g. Stilwell and Kohler 1982, Wetherbee and Cortés 2004, Maia et al. 2006). This trophic plasticity suggests opportunistic feeding strategies (*sensu* Bearzi et al. 2009). Analysis of long-term trends in shark diets should therefore reflect changes in the relative abundance of preferred prey species, but the prerequisite data are lacking in most cases. Further complications include ontogenetic shifts in feeding habits, the large number of empty stomachs encountered during sampling, and the generally poor taxonomic resolution of ingested prey items recovered in stomach contents (Wetherbee and Cortés 2004). An alternative method is clearly needed to elucidate long-term shifts in shark diets in response to exploitation of their prey species.

One such alternative is stable isotope analysis. Because the elemental signatures in the tissues of consumers predictably reflect those of their diets (Vander Zanden and Rasmussen 2001, Post 2002), stable isotope analysis has proven useful in elucidating food web architecture, as well as temporal, spatial, and ontogenetic trends in diets (e.g., Kelly 2000, Vander Zanden et al. 2000, Post 2002, Cherel and Hobson 2005, Estrada et al. 2006). In marine ecosystems, stable isotope ratios of carbon ($\delta^{13}C$) change little (~ 1‰, Peterson and Fry 1987) with each trophic transfer, and are therefore used to determine the basal sources of energy in food webs (Kelly 2000), as well as to infer the relative contributions of benthic and pelagic prey to consumer diets (France 1995). By contrast, the stepwise enrichment of consumer tissues in heavy nitrogen isotopes (^{15}N, enrichment range: 0.6 – 5.1‰, Minagawa and Wada 1984, Vanderklift and Ponsard 2003, Hussey et al. 2014) relative to their diet allows the use of $\delta^{15}N$ as a predictor of an organism's relative trophic position within a defined food web (Post 2002). Given a suitable time-series of shark tissues collected from similar-sized individuals in the same geographical region, it should be possible to use stable isotope analysis to infer the impacts of prey depletion on the trophic status of sharks, based on the known impacts of fisheries on target populations (e.g., Jennings et al. 1999, Jennings and Blanchard 2004, Duplisea and Castonguay 2006). Shark vertebrae provide the ideal tissue to generate time-series of stable isotope information. Vertebral cartilage is laid down incrementally as sharks grow, similar to the growth rings in trees, and once deposited is considered to be metabolically inert (Campana et al. 2002, Estrada et al. 2006). Assimilation of prey nutrients into this tissue, determined primarily by dietary intake, therefore provides an opportunity to assess shark trophic status over the ontogeny of the individual (Estrada et al. 2006).

In this study, I used isotopic analysis of shark vertebrae collected over several decades to investigate how the trophic status of seven large, predatory shark species from the southwest Indian Ocean has changed, both with ontogeny (within species) and over the decades (across species). I predicted that $\delta^{15}N$ values in shark vertebral cartilage would increase with ontogeny, given the positive relationship between trophic position and body size (Elton 1927, Vander Zanden et al. 2000, Cocheret de la Morinière et al. 2003, Woodward et al. 2005, Estrada et al. 2006) and the inherent limitations experienced by small sharks in capturing large-sized prey (Wetherbee and Cortés 2004). I also expected that, relative to the earliest available baseline samples for each species, $\delta^{15}N$ values would be lower in sharks caught more recently due to the general depletion of large, high trophic-level prey species by fisheries. My study represents one of the first efforts to quantify the impacts of prey depletion on marine apex predators, and provides a novel, fisheries-independent method by which the broad-scale ecological impacts of fishing may be measured over time (MacNeil et al. 2005, Estrada et al. 2006).

Methods

Provenance, selection and treatment of shark vertebrae

Shark vertebrae were obtained from collections held at the KwaZulu-Natal Sharks Board, Umhlanga, South Africa. All sharks sampled between 1985 and 2004 were caught in gillnets deployed along a 320-km stretch of KwaZulu-Natal (KZN) coastline to protect bathers (Cliff & Dudley 1992). Vertebrae were obtained from seven species (Table 2.1). An additional four vertebrae from shortfin mako sharks *Isurus oxyrinchus* pre-dating 1985 were obtained from sharks caught on rod and line by sport fishers 1.5 – 2.0 km off Durban, on the KZN coast.

The vertebral centra (i.e., the body of the vertebra ventral to the neural arch) included in this study were obtained from large female sharks (one vertebra per individual) and supplemented, when necessary, with vertebrae from similar-sized males to maintain sample sizes (n = 20 individuals per species). I used equal numbers of sharks captured at the midpoints of four five-year sampling periods (i.e., 1985-1989, 1990-1994, 1995-1999, and 2000-2004). All vertebrae were harvested from the thoracic region above the gill arches and had been either air-dried or frozen for storage. Muscle (or soft tissues) and connective tissues were manually removed from each centrum. After rinsing thoroughly with distilled water, vertebrae were air-dried until constant weight was reached.

Table 2.1 Size and vertebral characteristics of the seven shark species caught off KwaZulu-Natal, South Africa, and sampled in this study for stable isotope analysis.

Species	Common name	Mean vertebral radius ± SD (mm)	Mean precaudal length ± SD (mm)	Vertebral sub-sampling interval (mm)
Carcharhinus limbatus	Blacktip shark	13.3 ± 1.4	1670 ± 153	4.0
Carcharhinus brevipinna	Spinner shark	14.3 ± 1.4	1903 ± 166	4.0
Carcharhinus leucas	Bull shark	13.8 ± 1.7	1824 ± 201	3.0
Carcharias taurus	Ragged-tooth shark	19.9 ± 0.6	2005 ± 124	6.0
Galeocerdo cuvier	Tiger shark	16.2 ± 2.7	2330 ± 365	4.0
Isurus oxyrinchus	Shortfin mako	18.2 ± 2.5	2307.0 ± 272.0	4.5
Sphyrna lewini	Scalloped hammerhead	15.0 ± 1.6	2041.7 ± 208.7	4.0

From each vertebra, sub-samples were collected at regular intervals from the focus (centre = 0 mm) toward the dorsal edge of the corpus calcareum using a hand-held drill fitted with a 1.2 mm bit. After each sub-sample was collected, the drill bit was thoroughly cleaned using KimWipes™ and 95% ethanol, and the vertebra was brushed with a 1.25-cm wide synthetic-fibre paintbrush to prevent contamination of subsequent samples. Distances between sampling points varied among species in relation to vertebral diameter (Table 2.1). Each subsample was freeze-dried for 12 hours prior to being pulverised in a ball-mill grinder to achieve a homogeneous sample. Because vertebral centra are calcified with hydroxyapatite (Koch 2007), an inorganic form of carbon with different $\delta^{13}C$ values to those of proteins, I decalcified samples using EDTA following Kim & Koch (2012). Powdered vertebral tissue (1.0 ± 0.2 mg) was submitted in tin capsules for carbon and nitrogen isotope analysis. Isotopic composition was determined using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ

Europa 20-20 isotope ratio mass spectrometer at the University of California - Davis Stable Isotope Facility.

Statistical analyses

For each vertebral sub-sample, specific isotope abundance was calculated as a parts-per-thousand deviation from the standard using the equation: $\delta X = ((R_{\text{sample}}/R_{\text{standard}}) - 1) \times 1000$, where X is ^{13}C or ^{15}N, R_{sample} is the isotopic ratio ^{13}C:^{12}C or ^{15}N:^{14}N in the sample, and R_{standard} is the isotopic ratio of the relevant international standard (Peterson & Fry 1987). Replicate measurements of internal laboratory standards (ammonium sulphate and sucrose) after every 12 samples, and double-blind sample submissions, produced measurement errors of ± 0.1‰ and ± 0.2‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively. Carbon and nitrogen isotope results are presented in the standard δ notation relative to Pee Dee belemnite and atmospheric nitrogen, respectively.

The use of carbon isotopes to accurately detect changes across time series in samples from marine organisms is compromised by increasing rates of assimilation of isotopically light carbon (^{12}C, Hilton et al. 2006). This phenomenon, termed the Suess Effect, results largely from the burning of fossil fuels, which produces ^{13}C-depleted CO_2. Dissolution of this gas into aqueous systems has led to exponentially accelerating decreases in the $\delta^{13}C$ of dissolved inorganic carbon in sea water (Sonnerup at al. 2000). To account for the Suess Effect, I applied to all raw $\delta^{13}C$ values the mean estimated rate of change in surface water $\delta^{13}C$ (-1.6‰ decade^{-1}) calculated by Sonnerup et al. (2000) for the Indian Ocean.

The isotopic signature at the focus of vertebrae represents pre-birth growth and therefore reflects maternal diet (Olin et al. 2011). To remove the effects of variation in maternal input, I subtracted from all isotopic values obtained for each shark, the corresponding isotopic value at the focus for that individual (*sensu* Estrada et al. 2006), thus: X enrichment = $(X_{x\text{mm}} - X_{0\text{mm}})$, where X is ^{13}C or ^{15}N.

Because the sample sizes were insufficient for parametric statistical testing, I used a bias-corrected accelerated (BCa) bootstrapping method to generate means and standard deviations of both absolute $\delta^{15}N$ and $\delta^{13}C$ values (Tables S2.1 and S2.2 in

Appendix A, respectively) and mean ^{15}N and ^{13}C enrichment values. This resampling method is considered more accurate than a simple bootstrap as it corrects for bias and skewness in the original sample (Efron 1987), an important consideration when using small sample sizes to make population-level inferences. I generated mean ^{15}N and ^{13}C enrichment values for three shark size classes, derived from the second, third, and last sub-sample taken on each vertebra, in each of the four capture periods (five periods for shortfin mako). Two non-parametric BCa bootstrap estimates of dispersion, standard deviation and 95% confidence intervals, were estimated for each group. For each size class by capture period combination, bootstrap distributions were generated by randomly sampling, with replacement, 5000 values from the dataset. Shark size (precaudal length) estimates at each vertebral sub-sampling point were obtained from the linear relationship between vertebral radius and precaudal length for 70 individuals of each species (Figure S2.1 in Appendix A).

Within each species, differences in vertebral ^{15}N and ^{13}C enrichment values among size classes within each time period, and between the first (baseline) and all other time periods within each size class, were established based on comparisons of the 95% confidence intervals bounding mean values (Efron 1987, Johnson 1999, Anderson et al. 2000, MacNeil et al. 2005).

Results and Discussion

Ontogenetic patterns

As predicted, all shark species showed, after controlling for maternal inputs, a step-wise ontogenetic enrichment in δ^{15}N, which was particularly marked between the smallest and subsequent size classes (Figure 2.1A-G). This concurs with previous stable isotope studies of sharks and other piscivorous fish (Cocheret de la Morinière et al. 2003, Estrada et al. 2006, Hussey et al. 2011, Carlisle et al. 2015, Sardenne et al. 2016), and is generally expected in species that ingest increasingly large prey as they grow. However, ontogenetic δ^{15}N enrichment occurred in three clear patterns. In scalloped hammerheads, nitrogen enrichment increased significantly across each size class in each capture period (Figure 2.1 G). Other species (spinner, bull, ragged-tooth and tiger

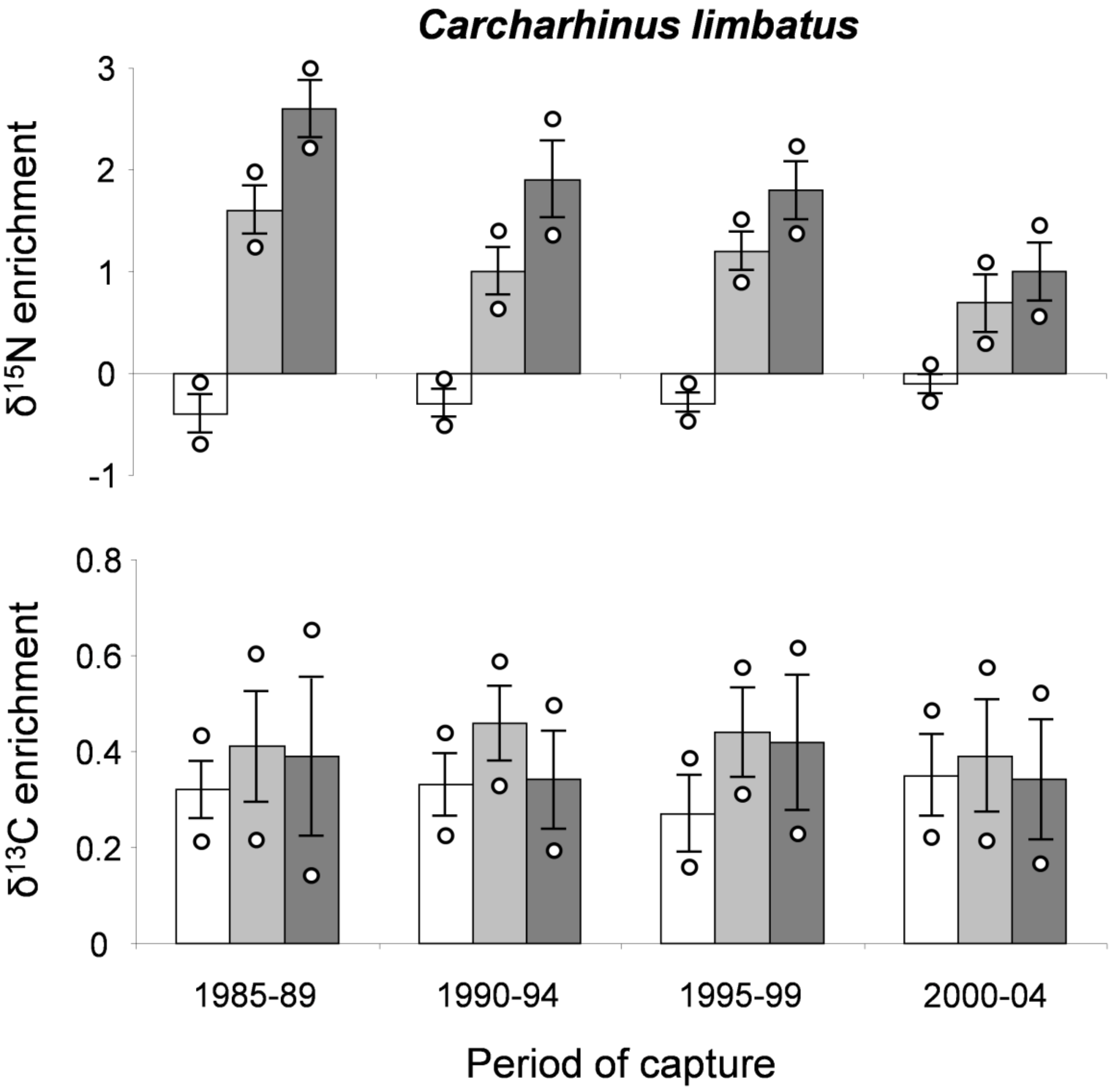


Figure 2.1 δ^{15}N (top row) and δ^{13}C (bottom row) enrichment of Blacktip shark (*Carcharhinus limbatus*) vertebrae from individuals caught in the KwaZulu-Natal Sharks Board gill nets, for three size classes over 5-year periods. Size classes were defined in relation to vertebral sub-sample position: second (white bars), third (pale grey bars), and last sub-sample (dark grey bars). Sub-sampling intervals are given in Table 2.1 and estimated mean precaudal lengths of sharks for each sub-sample are shown in Tables S2.1 and S2.2 in Appendix A. Means are presented with bias-corrected accelerated (BCa) bootstrapped standard deviations (bars) and 95% confidence intervals (circles). *n* = 5 individuals

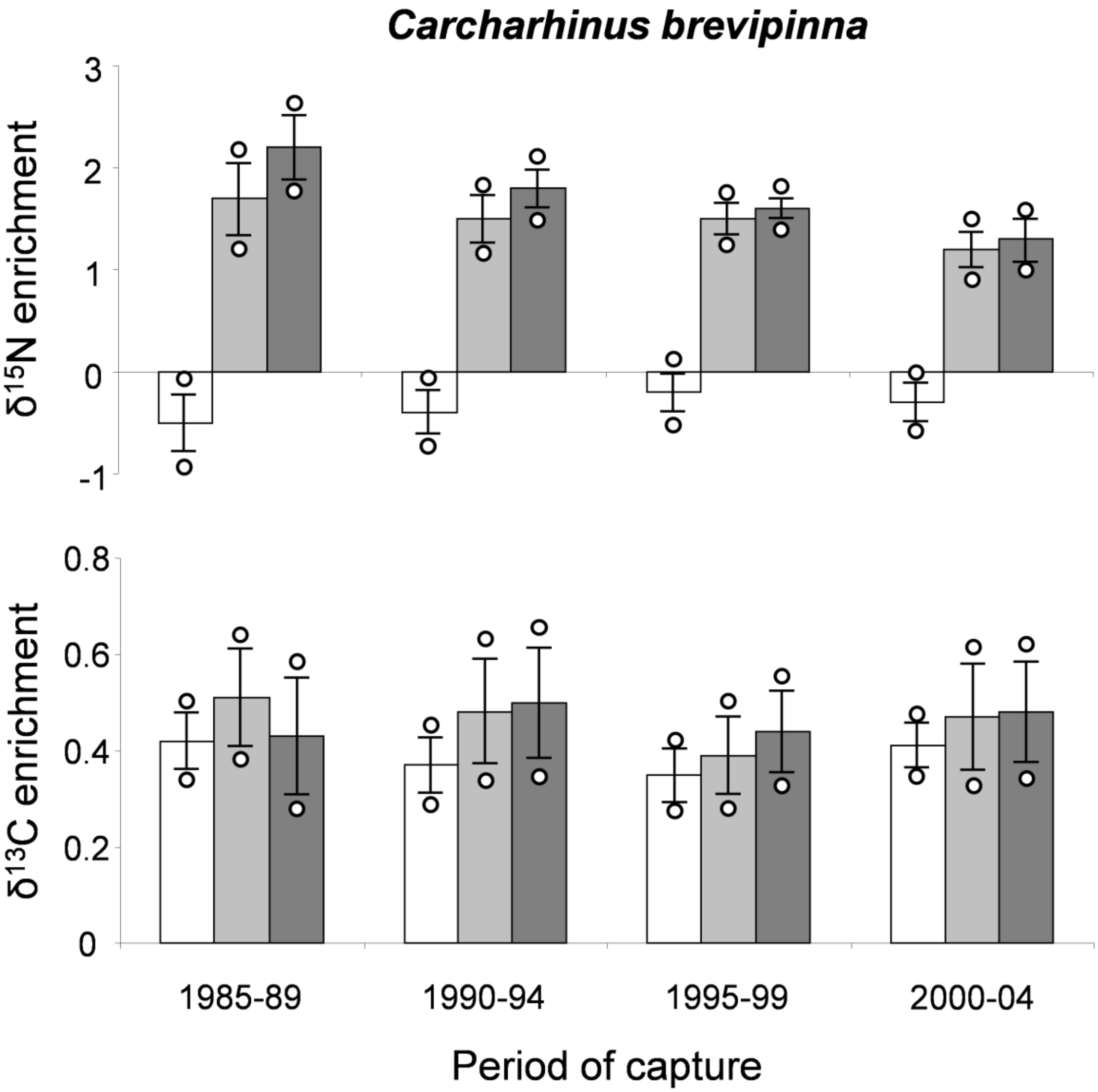


Figure 2.2 $\delta^{15}N$ (top row) and $\delta^{13}C$ (bottom row) enrichment of Spinner shark (*Carcharhinus brevipinna*) vertebrae from individuals caught in the KwaZulu-Natal Sharks Board gill nets, for three size classes over 5-year periods. Size classes were defined in relation to vertebral sub-sample position: second (white bars), third (pale grey bars), and last sub-sample (dark grey bars). Sub-sampling intervals are given in Table 2.1 and estimated mean precaudal lengths of sharks for each sub-sample are shown in Tables S2.1 and S2.2 in Appendix A. Means are presented with bias-corrected accelerated (BCa) bootstrapped standard deviations (bars) and 95% confidence intervals (circles). *n* = 5 individuals

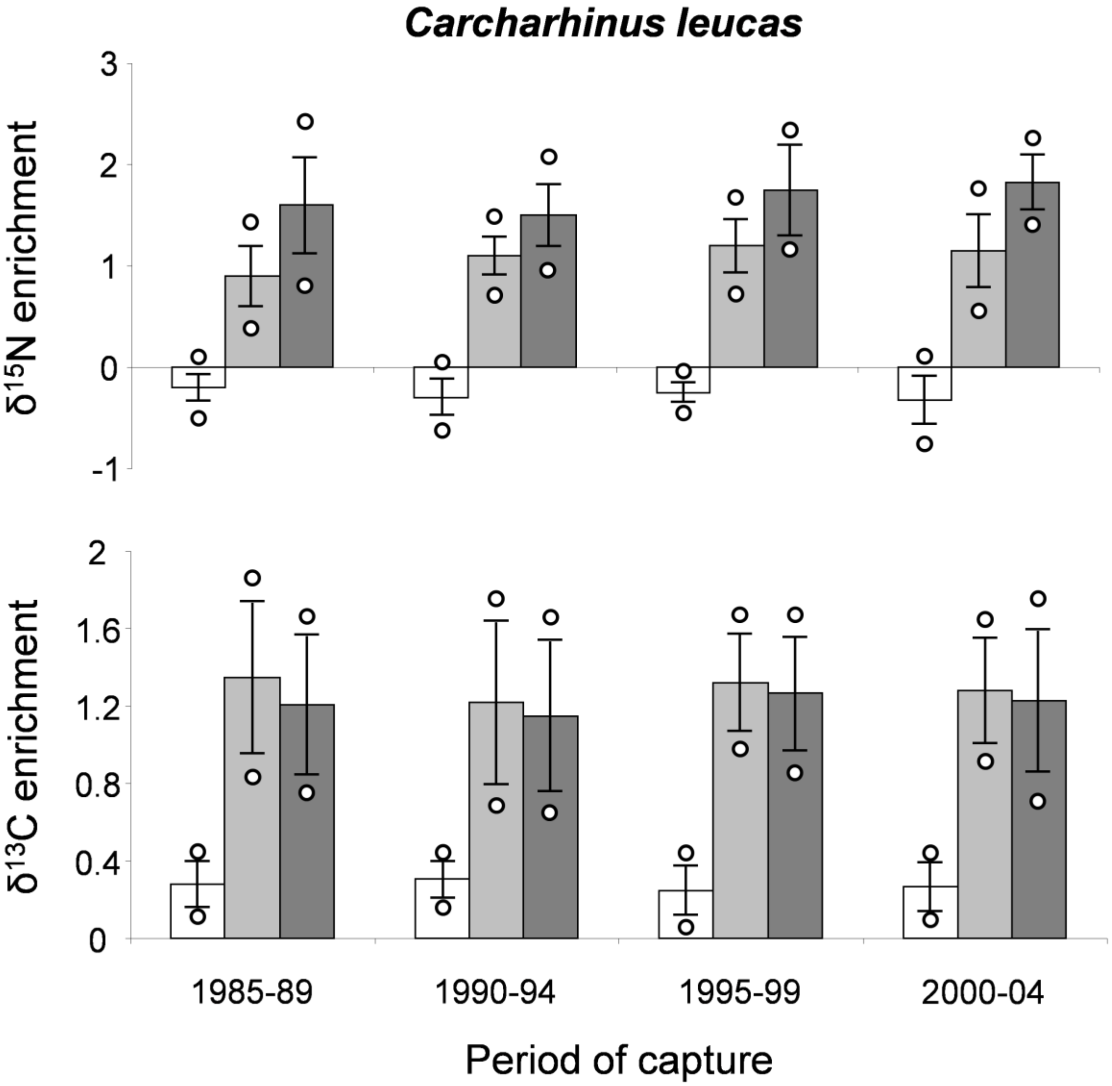


Figure 2.3 $\delta^{15}N$ (top row) and $\delta^{13}C$ (bottom row) enrichment of bull shark (*Carcharhinus leucas*) vertebrae from individuals caught in the KwaZulu-Natal Sharks Board gill nets, for three size classes over 5-year periods. Size classes were defined in relation to vertebral sub-sample position: second (white bars), third (pale grey bars), and last sub-sample (dark grey bars). Sub-sampling intervals are given in Table 2.1 and estimated mean precaudal lengths of sharks for each sub-sample are shown in Tables S2.1 and S2.2 in Appendix A. Means are presented with bias-corrected accelerated (BCa) bootstrapped standard deviations (bars) and 95% confidence intervals (circles). *n* = 5 individuals

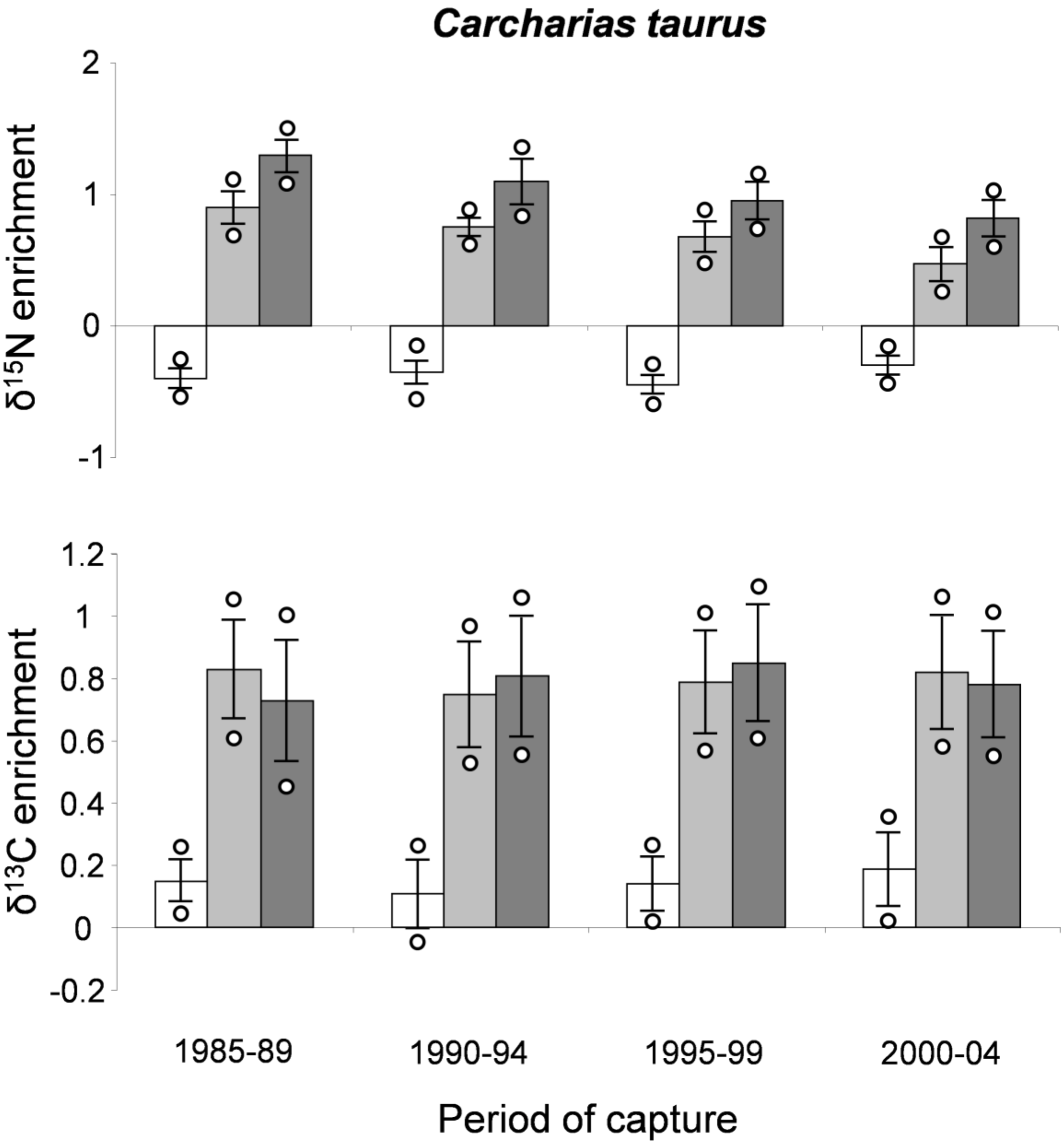


Figure 2.4 $\delta^{15}N$ (top row) and $\delta^{13}C$ (bottom row) enrichment of Ragged-tooth shark, (*Carcharias taurus*) vertebrae from individuals caught in the KwaZulu-Natal Sharks Board gill nets, for three size classes over 5-year periods. Size classes were defined in relation to vertebral sub-sample position: second (white bars), third (pale grey bars), and last sub-sample (dark grey bars). Sub-sampling intervals are given in Table 2.1 and estimated mean precaudal lengths of sharks for each sub-sample are shown in Tables S2.1 and S2.2 in Appendix A. Means are presented with bias-corrected accelerated (BCa) bootstrapped standard deviations (bars) and 95% confidence intervals (circles). *n* = 5 individuals

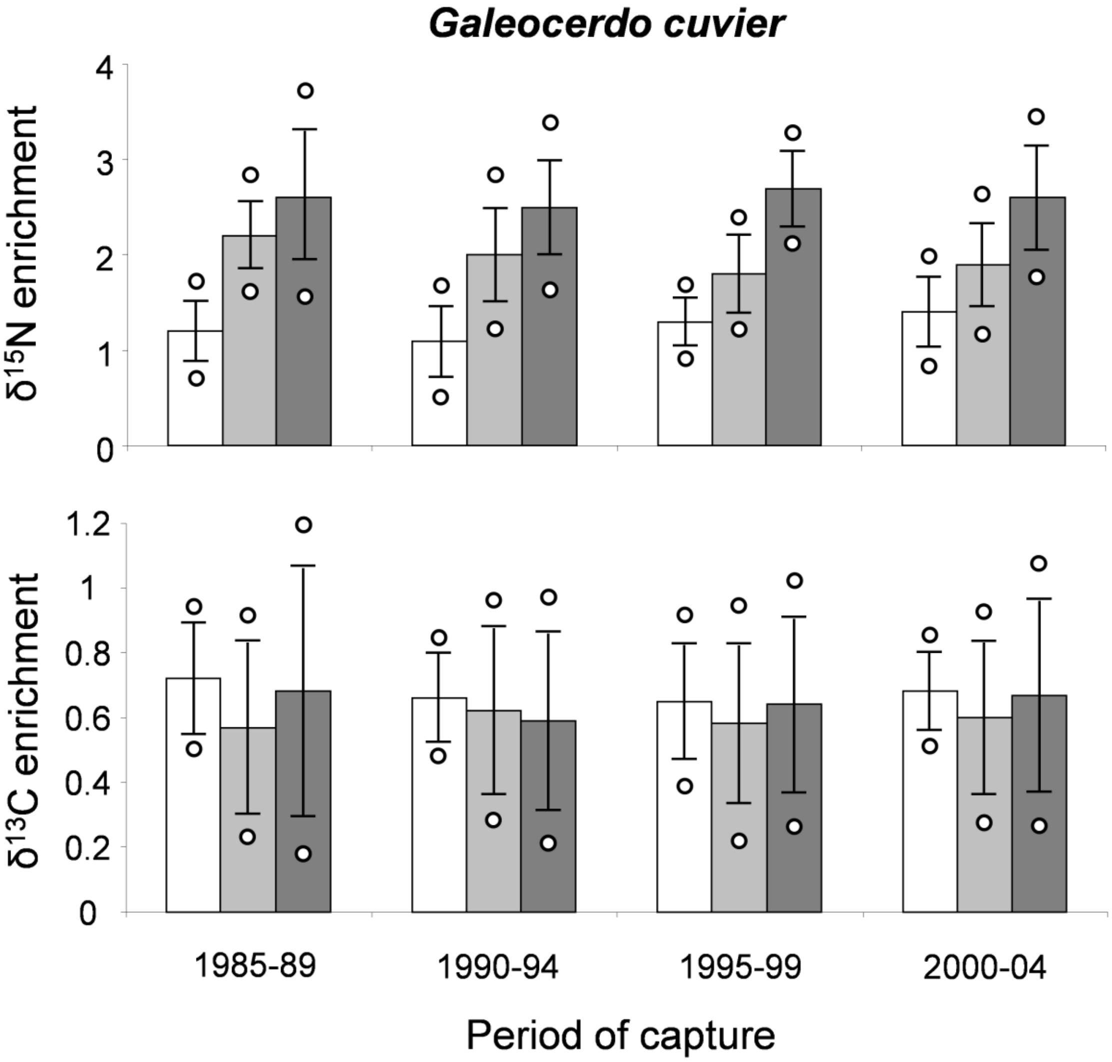


Figure 2.5 $\delta^{15}N$ (top row) and $\delta^{13}C$ (bottom row) enrichment of Tiger shark, (*Galeocerdo cuvier*) vertebrae from individuals caught in the KwaZulu-Natal Sharks Board gill nets, for three size classes over 5-year periods. Size classes were defined in relation to vertebral sub-sample position: second (white bars), third (pale grey bars), and last sub-sample (dark grey bars). Sub-sampling intervals are given in Table 2.1 and estimated mean precaudal lengths of sharks for each sub-sample are shown in Tables S2.1 and S2.2 in Appendix A. Means are presented with bias-corrected accelerated (BCa) bootstrapped standard deviations (bars) and 95% confidence intervals (circles). *n* = 5 individuals

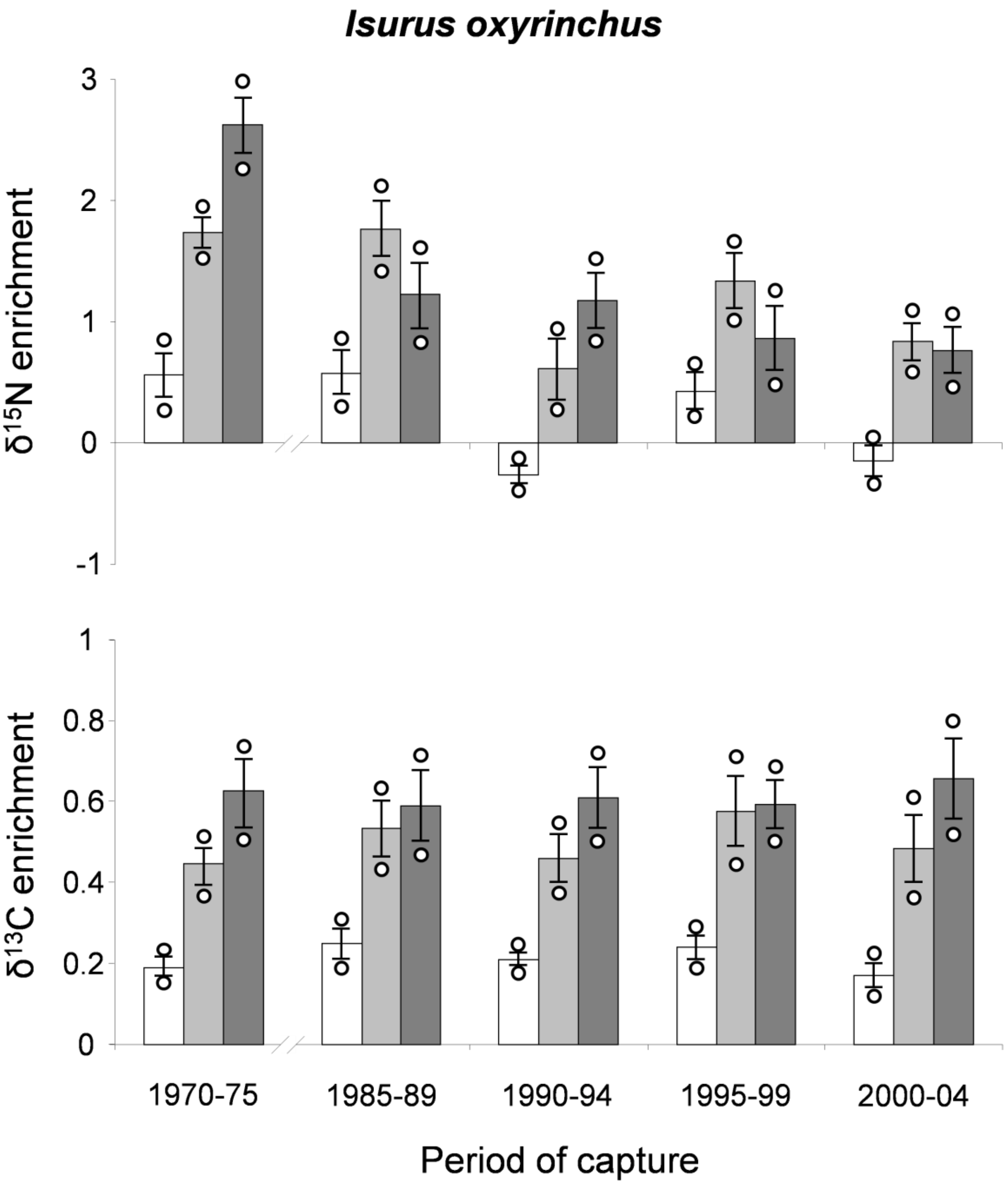


Figure 2.6 $\delta^{15}N$ (top row) and $\delta^{13}C$ (bottom row) enrichment of Shortfin mako, (*Isurus oxyrinchus)* vertebrae from individuals caught in the KwaZulu-Natal Sharks Board gill nets, for three size classes over 5-year periods. Size classes were defined in relation to vertebral sub-sample position: second (white bars), third (pale grey bars), and last sub-sample (dark grey bars). Sub-sampling intervals are given in Table 2.1 and estimated mean precaudal lengths of sharks for each sub-sample are shown in Tables S2.1 and S2.2 in Appendix A. Means are presented with bias-corrected accelerated (BCa) bootstrapped standard deviations (bars) and 95% confidence intervals (circles). *n* = 5 individuals (except for 1970-1975 samples where *n* = 4).

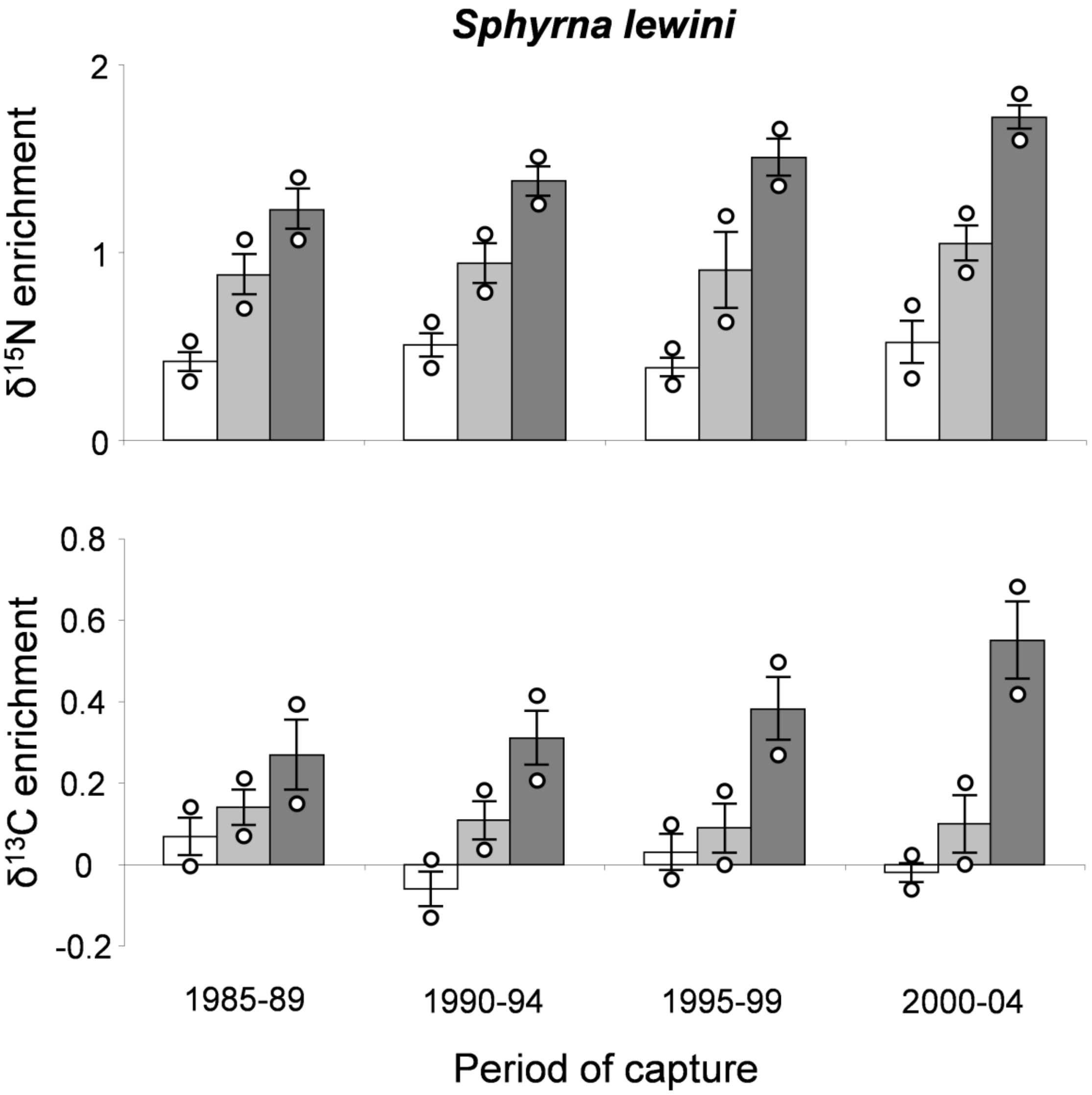


Figure 2.7 $\delta^{15}N$ (top row) and $\delta^{13}C$ (bottom row) enrichment of Scalloped hammerhead, (*Sphyrna lewini)* vertebrae from individuals caught in the KwaZulu-Natal Sharks Board gill nets, for three size classes over 5-year periods. Size classes were defined in relation to vertebral sub-sample position: second (white bars), third (pale grey bars), and last sub-sample (dark grey bars). Sub-sampling intervals are given in Table 2.1 and estimated mean precaudal lengths of sharks for each sub-sample are shown in Tables S2.1 and S2.2 in Appendix A. Means are presented with bias-corrected accelerated (BCa) bootstrapped standard deviations (bars) and 95% confidence intervals (circles). *n* = 5 individuals

sharks) only showed marked nitrogen enrichment between the small and middle size classes, with little enrichment into the large class, a pattern that persisted across capture periods (Figure 2.1 B-E). In contrast, blacktip sharks caught between 1985 and 1989 show clearly defined $\delta^{15}N$ enrichment across all size classes, yet sharks captured in subsequent sampling periods do not maintain significantly different $\delta^{15}N$ signatures between the two largest size classes (Figure 2.1 A). The same pattern is evident in shortfin mako sharks when comparing sharks captured between 1970-1975 and subsequent capture periods (Figure 2.1 F). For both species, there is a clear decline in $\delta^{15}N$ enrichment over time, especially for the largest size class (Figure 2.1 A, F; see below). This compression of $\delta^{15}N$ trophic signatures across size classes might suggest that, over time, there has been increasing overlap in the diets of these shark species across size classes. This could be confirmed with stomach content analyses.

Ontogenetic enrichment in $\delta^{13}C$ was also variable across shark species. In blacktip, spinner, and tiger sharks, there was no evidence of carbon enrichment with increasing size (Figure 2.1 A,B,E). In bull, ragged-tooth and mako sharks, carbon enrichment was significant only between the smallest and larger size classes (Figure 2.1 C,D,F), while in scalloped hammerheads, carbon enrichment was significantly higher but only in the largest size class (Figure 2.1 G). While changes in a predator's carbon signatures are usually associated with shifts in trophic food webs and, often, habitats, known latitudinal gradients in coastal $\delta^{13}C$ exist between the shark capture area in KZN and the Western Cape to the south (Hill et al. 2006). This gradient of increasing coastal $\delta^{13}C$ with increasing distance from KZN is a confounding factor in interpreting our results conclusively. In more recent sampling periods, large female scalloped hammerheads may either be exploiting larger size prey in neritic rather than pelagic habitats or, spending more time foraging for larger prey in more southerly coastal waters.

Decadal patterns

In four species, blacktip, spinner, ragged-tooth and shortfin mako sharks, significant decreases in $\delta^{15}N$ enrichment within size classes were apparent over time (Figure 2.1 A,B,D,F). A single species, the scalloped hammerhead, showed the opposite trend, with an increase in $\delta^{15}N$ signature in the last time period for the largest size class examined

(Figure 2.1 G), and two species, tiger and bull sharks, showed no temporal change in their $\delta^{15}N$ signatures (Figure 2.1 C, E). All but one species exhibited no change in $\delta^{13}C$ enrichment over time (Figure 2.1); the only exception was scalloped hammerhead sharks, with a significantly enriched carbon signature in the last time period (Figure 2.1 G).

Four of the seven shark species examined showed a pattern of declining $\delta^{15}N$ enrichment over time consistent with a shift in diet away from large prey. These four species are primarily piscivorous, with shortfin mako sharks feeding principally on elasmobranchs rather than teleost fishes (Table S2.3 in Appendix A). The lack of matching temporal patterns of $\delta^{13}C$ enrichment suggests that changes in foraging strategies or localities are unlikely to be responsible for the observed shifts in $\delta^{15}N$ signatures. Given the relatively narrow diet of these sharks (Table S2.3 in Appendix A), shifts in $\delta^{15}N$ are more likely to reflect changes in the available prey base. Fisheries have two main direct impacts on target species: a reduction in overall biomass and a reduction in the number of large-sized individuals because fishers prefer large fish. The latter effect is reflected in the falling mean trophic level of global catches (Pauly et al. 1998, but see Essington et al. 2006 for an alternative mechanism), which is likely to also reflect the availability of prey to predators such as sharks (Lucifora et al. 2009). Indeed, it is notable that the shifts in nitrogen signatures I observed have mainly occurred in the large size classes of sharks, i.e. those capable of taking large-sized prey.

There is evidence for large changes in fisheries in the western Indian Ocean (FAO Area 51) that may have driven the shark isotope patterns observed here. This area was one of the last major ocean tracts to be exploited by industrial fisheries, following declines in catches of Atlantic and Pacific pelagic fish stocks (Myers and Worm 2003, Campling 2012). From 1950 until 1985, i.e. prior to the capture of most sharks in my study, the regional mean trophic index (Kleisner et al. 2014) of fisheries in the Agulhas Current Large Marine Ecosystem (i.e., the area where the sharks in this study were caught) was 3.42 (range 3.35 – 3.46), with a mean annual catch of 168131 ± 77346 t, and a mean maximum length of captures of 58 cm (range 52 – 67 cm) (Pauly & Zeller 2015). From 1985 to 2005, i.e. my study period, the regional mean trophic index increased to 3.60 (range 3.41 – 3.75), the mean annual catch increased to 343074 ± 36796 t, and the mean maximum length of captures rose to 82 cm (range 56 – 109 cm) (Pauly & Zeller 2015), providing clear evidence of an increase in the intensity of fishing and a targeting of large fish over that period. Although the region was not pristine (i.e., completely unfished) prior to 1985, the shark vertebrae from the earliest capture periods might provide relatively realistic isotopic baselines against which further change could be measured.

In addition to fishing pressure as a top-down driver of change in prey availability, it is important to accede that bottom-up processes such as shifts in system-wide productivity may also impact prey fish populations (Defriez et al. 2016). Marine ecosystem productivity is highly dynamic and dependent on factors such as sea surface temperature, air-sea fluxes and nutrient inputs to the system (Taylor & Ferrari 2011). A confounding factor in determining the relative impacts of top-down and bottom-up forces on the population dynamics of a given species is the interplay between fisheries and climatic conditions. For example, planktivorous fish play a critical role in linking top-down and bottom-up forces to the extent that even moderate fishery pressure on these taxa may lead to changes in the plankton community, which can cascade to other trophic levels (Lynam et al. 2017).

In this study the importance of recognising the effects of bottom-up processes on fish community structure lies in the fact that the Agulhas Current has been warming since the 1980s (Rouault et al. 2009). This phenomenon, driven by increases in wind stress curl, has led to increases in sea surface temperatures of up to 0.7 °C/decade since 1985 (Rouault et al. 2009). Globally, increasing sea surface temperatures have been linked to changes in the species composition of plankton communities (Alheit & Niquen 2004), increases in planktonic productivity (Wiltshire & Manly 2004), decreases in planktonic productivity (Roemmich & McGowan 1995), range shifts in plankton species distribution (Edinburgh Oceanographic Laboratory 1973) as well as phenological shifts that dictate the appearance of energetically important phytoplankton blooms (Mackas et al. 1998). For my study region, time series of plankton productivity data and planktonic species composition are woefully lacking, and I am therefore unable to speculate as to the effects of increasing sea surface temperature on the basal communities supporting those species, which are prey for large marine predators. There do not appear to be any broad-scale changes in the ^{13}C signatures of sharks in my study, which might reflect shifts at the base of pelagic food webs, but these data should not be used to rule out such shifts occurring. Future isotope studies should seek to include the regular collection of planktivorous fish species, e.g. anchovy (*Engraulis* *capensis*), in association with the collection of shark samples to determine more precisely the relative impacts of fisheries and climatic change on marine top predators.

While I corrected for variations in maternal input to isotopic signatures in the later stages of growth, vertebral sampling points for a single species, the ragged-tooth shark, were consistent with two periods of embryonic growth i.e. where maternal influence is still in effect, across decades. Between 1985-89 and 2000-04, larger embryos showed a stepwise decline in $\delta^{15}N$ enrichment, concomitant with the phases of intrauterine embryophagy and oophagy (Gilmore et al. 2005). These embryonic stepwise declines in $\delta^{15}N$ enrichment mirror almost perfectly the pattern of $\delta^{15}N$ enrichment in larger post-partum sharks (Figure 2.1 D, Table S2.1 in Appendix A). This finding raises interesting questions as to whether depletion of traditional prey species could influence maternal investment in offspring, and whether this phenomenon is common across shark species with differing life history strategies and reproductive modes (Hussey et al. 2010).

Nevertheless, not all shark species appear to be experiencing trophic shifts in recent years. Bull and tiger sharks showed no sign of dietary shifts over time. Stomach content studies reveal that these species prey on a wide range of teleost fishes and elasmobranchs, as well as molluscs, crustaceans, birds, mammals and turtles (Table S2.3 in Appendix A). This generalist diet, which includes a broad range of prey trophic levels and intraguild predation (Table S2.3 in Appendix A), would likely mask the effect of fisheries-driven changes in the abundance of particular prey items. This supposition is upheld by evidence from stomach content analyses for tiger sharks. Dicken et al. (2017) found decadal scale shifts in the diet of tiger sharks in the southwest Indian Ocean, with major changes driven by an increase in cetacean prey and a reduction in elasmobranch prey. It should be noted, therefore, that dietary shifts can occur in the absence of changes in isotope ratios over time, and isotopic studies alone may not be enough to reflect the true nature of these tropho-dynamic shifts. This finding highlights the importance of using, where possible, multiple methods to assess the trophic status of predators.

Finally, the increased enrichment in both $\delta^{13}C$ and $\delta^{15}N$ for large-sized scalloped hammerhead sharks over time is unexpected and puzzling. The matching shifts in both isotope ratios might suggest a change in foraging strategies, e.g. a shift from feeding on pelagic prey to neritic prey, or a long-term change in foraging location, e.g. feeding closer to shore with less reliance on pelagic food webs. Alternatively, scalloped hammerheads may be exploiting a source of higher trophic level prey. The loss of large sharks from coastal ecosystems has been linked to increases in mesopredators (e.g. Myers et al. 2007, Baum & Worm 2009, Ferretti et al. 2010), including smaller shark species and rays (Myers et al. 2007), both of which feature in the diet of scalloped hammerheads (Table S2.3 in Appendix A).

Conclusions

While much recent work has been undertaken to understand the ecological role of large predators in marine environments (reviewed in Heithaus et al. 2008), with few exceptions, these environments have already been altered by the pervasive effects of industrial fisheries. As such, our understanding of the basic feeding ecology of many species is confounded by prey depletion and enforced prey switching. The move from species- to ecosystem-based management strategies relies heavily on knowledge of the component species' ecology and interactions, which is difficult to achieve without effective baselines from which to work (McClenachan et al. 2012).

My study of large, predatory sharks in the southwest Indian Ocean suggests that the feeding ecology of contemporary populations of some species has been affected by extractive fisheries. This finding is consistent with isotopic studies of some teleost species inhabiting heavily fished, prey-depleted habitats (Hinz et al. 2017) and may have consequences for shark growth and recruitment. Of particular concern are the four species exhibiting patterns of declining $\delta^{15}N$ enrichment over time – especially in the largest size class - consistent with the relatively recent depletion of large prey. My results suggest that these large sharks are predominantly encountering and feeding on smaller prey than they would have historically. To meet their daily minimum energy requirements, these sharks might have to spend more time and/or energy hunting and handling prey. While the outcome of increased energetic costs on growth are likely limited to a slowing effect, the implications for reproductive output are probably more complex. My results for ragged-tooth sharks suggest that prey depletion could have an effect on maternal investment in offspring, but how depleted $\delta^{15}N$ signatures translate into altered endogenous resources allocated to pre-term embryos remains to be investigated.

Finally, my use of a time-series of shark vertebrae to discern isotopic drift in shark species over decades may be a useful fisheries-independent tool to gauge the broader-scale ecological impacts of fisheries, as well as the impacts of any conservation or recovery interventions. Ecosystem-based management strategies generally aim to restore as many components of, and linkages within, ecosystems as possible, and the use of historical data and samples to assess pre-disturbance baselines should become more commonplace (e.g. Willis et al. 2007). Future research on this topic should endeavour to combine large-scale isotope studies with stomach content analyses and satellite tagging studies to better interpret the causes and consequences of shifts in marine top predator diets.

Acknowledgements

I thank the KwaZulu-Natal Sharks Board Operations staff for providing the sharks and the Laboratory staff for collecting and storing the shark vertebrae. I acknowledge the work of the Sea Around Us project in compiling and maintaining fisheries catch databases. I also thank the Reynolds Lab, particularly Jan Verspoor and Morgan Hocking, at Simon Fraser University for primers in isotope sample preparation and use of lab equipment. Nigel Hussey provided useful comments on interpretation of the isotope data. AM was funded by a graduate fellowship from Simon Fraser University. IMC was supported by a Discovery grant from the Natural Sciences and Engineering Council of Canada.

References

Alheit, J, Niquen, M (2004) Regime shifts in the Humboldt Current ecosystem. Prog Oceanog. 60: 201–222

Allen B R, Cliff G (2000) Sharks caught in the protective gill nets off Natal, South Africa. 9. The spinner shark *Carcharhinus brevipinna* (Müller and Henle). S Afr J Marine Sci 22: 199-215

Arkema KK, Abramson SC, Dewsbury BM (2006) Marine ecosystem-based management: from characterization to implementation. Front Ecol Environ 4: 525-532

Baum JK, Myers RA, Kehler DG, Worm B, Harley SJ, Doherty PA (2003) Collapse and conservation of shark populations in the northwest Atlantic. Science 299: 389-392

Baum JK, Worm B (2009) Cascading top-down effects of changing oceanic predator abundances. J Anim Ecol 78: 699-714

Bearzi G, Fortuna CM, Reeves RR (2009) Ecology and conservation of common bottlenose dolphins *Tursiops truncatus* in the Mediterranean Sea. Mammal Rev 39: 92-123

Brander K (2007) The role of growth changes in the decline and recovery of North Atlantic cod stocks since 1970. ICES J Mar Sci 64: 211-217

Campana SE, Natanson LJ, Myklevoll S (2002) Bomb dating and age determination of large pelagic sharks. Can J Fish Aquat Sci 59: 450-455

Campling L (2012) The Tuna ‘Commodity Frontier’: Business Strategies and Environment in the Industrial Tuna Fisheries of the Western Indian Ocean. J Agrar Change 12: 252-278

Carlisle AB, Goldman KJ, Litvin SY, Madigan DJ, Bigman JS, Swithenbank AM, Kline TC, Block BA (2015) Stable isotope analysis of vertebrae reveals ontogenetic changes in habitat in an endothermic pelagic shark. Proc R Soc B 282: 20141446

Cherel Y, Hobson KA (2005) Stable isotopes, beaks and predators: a new tool to study the trophic ecology of cephalopods, including giant and colossal squids. Proc R Soc B 272: 1601-1607

Christensen V, Guénette S, Heymans JJ, Walters CJ, Watson R, Zeller D, Pauly D (2003) Hundred-year decline of North Atlantic predatory fishes. Fish Fish 4: 1-24

Cliff G, Dudley SFJ (1991) Sharks caught in the protective gill nets off Natal, South Africa. 4. The bull shark *Carcharhinus leucas* Valenciennes. S Afr J Marine Sci 10: 253-270

Cliff G, Dudley SFJ (1992) Protection against shark attack in South Africa, 1952-90. Mar Freshwater Res 43: 263-272

Cliff, G., S. F. J. Dudley and B. Davis. 1990. Sharks caught in the protective gill nets off Natal, South Africa. 3. The shortfin mako shark *Isurus oxyrinchus* (Rafinesque). S Afr J Marine Sci 9: 115-126

Cocheret de la Morinière E, Pollux BJA, Nagelkerken I, Hemminga MA, Huiskes AHL, van der Velde G (2003) Ontogenetic dietary changes of coral reef fishes in the mangrove-reef continuum: stable isotopes and gut-content analysis. Mar Ecol Prog Ser 246: 279-289

Crowder L, Hazen BEL, Avissar N, Bjorkland R, Latanich C, Ogburn MB (2008) The impacts of fisheries on marine ecosystems and the transition to ecosystem-based management. Annu Rev Ecol Syst 39: 259-278

de Bruyn P, Dudley SFJ, Cliff G, Smale MJ (2005) Sharks caught in the protective gill nets off KwaZulu-Natal, South Africa. 11. The scalloped hammerhead shark *Sphyrna lewini* (Griffith and Smith). Afr J Mar Sci 27: 517-528

Defriez, EJ, Sheppard LW, Reid PC, Reuman DC. (2016) Climate change-related regime shifts have altered spatial synchrony of plankton dynamics in the North Sea. Global Change Biol 22: 2069–2080

Dicken ML, Hussey NE, Christiansen HM, Smale MJ, Nkabi N, Cliff G, Wintner, S (2017) Diet and trophic ecology of the tiger shark (Galeocerdo cuvier) from South African waters. PLoS ONE 12 (6): e0177897

Dorner B, Peterman RM, Haeseker SL (2008) Historical trends in productivity of 120 Pacific pink, chum, and sockeye salmon stocks reconstructed using a Kalman filter. Can J Fish Aquat Sci 65: 1842-1866

Dudley SFJ, Cliff G (1993) Sharks caught in the protective gill nets off Natal, South Africa. 7. The blacktip shark *Carcharhinus limbatus* (Valenciennes). S Afr J Mar Sci 13: 237-254

Dulvy NK, Baum JK, Clarke S, Compagno LJV, Cortés E, Domingo A, Fordham S, Fowler S, Francis MP, Gibson C, Martínez J, Musick JA, Soldo A, Stevens JD, Valenti S (2008) You can swim but you can't hide: the global status of oceanic pelagic sharks and rays. Aquat Conserv18: 459-482

Dulvy NK, Freckleton RP, Polunin NVC (2004) Coral reef cascades and the indirect effects of predator removal by exploitation. Ecol Lett 7: 410-416

Duplisea DE, Castonguay M (2006) Comparison and utility of different size-based metrics of fish communities for detecting fishery impacts. Can J Fish Aquat Sci 63: 810-820

Edinburgh Oceanographic Laboratory (1973) Continuous plankton records: a plankton atlas of the North Atlantic Ocean and North Sea. Bull Mar Ecol 7: 1–174

Efron B (1987) Better Bootstrap Confidence Intervals. J Am Stat Assoc 82: 171-185

Elton C (1927) Animal Ecology. Sidgewick and Jackson, London.

Essington TE, Beaudreau AH, Wiedenmann J (2006) Fishing through marinefood webs. P Natl Acad Sci Biol 103: 3171-3175

Estrada JA, Rice AN, Natanson LJ, and Skomal GB (2006) Use of isotopic analysis of vertebrae in reconstructing ontogenetic feeding ecology in white sharks. Ecology 87: 829-834

FAO (2009) State of the World's Fisheries and Aquaculture 2008. Food and Agriculture Organization of the United Nations, FAO, Rome, Italy.

Feltrim M (2010) Inter-cohort growth variability and its implication for fisherymanagement of the common sardine (*Strangomera bentincki*) stock off the coast of south-entral Chile. Fish Res 106: 368-377

Ferretti F, Worm B, Britten GL, Heithaus MR, Lotze HK (2010) Patterns and ecosystem consequences of shark declines in the ocean. Ecol Lett 13: 1055-1071

Field A (2005) Discovering statistics using SPSS. Sage, London.

France RL (1995) Differentiation between littoral and pelagic food webs in lakes using stable carbon isotopes. Limnol Oceanogr 40: 1310-1313

Frank KT, Petrie B, Choi JS, Leggett WC (2005) Trophic cascades in a formerly cod-dominated ecosystem. Science 308: 1621-1623

Friedlander AM, DeMartini EE (2002) Contrasts in density, size, and biomass of reef fishes between the north-western and the main Hawaiian islands: the effects of fishing down apex predators. Mar Ecol Prog Ser 230: 253-264

Friedman M (1937) The use of ranks to avoid the assumption of normality implicit in the analysis of variance. J Am Stat Assoc 32: 675-701

Gilmore RG, Putz O, Dodrill JW (2005) Oophagy, intrauterine cannibalism and reproductive strategy in lamnoid sharks. In Reproductive biology and phylogeny of Chondrichthyes (Hamlett WM, editor.), pp. 435–463 Science Enfield, NH: Publishers Inc

Heithaus MR, Frid A, Wirsing AJ, Worm B (2008) Predicting ecological consequences of marine top predator declines. Trends Ecol Evol 23: 202-210

Heithaus MR, Marshall GJ, Buhleier BM, Dill LM (2001) Employing Crittercam to study habitat use and behavior of large sharks. Mar Ecol Prog Ser 209: 307-310

Hill JM, McQuaid CD, Kaehle, S (2006) Biogeographic and nearshore–offshore trends in isotope ratios of intertidal mussels and their food sources around the coast of southern Africa. Mar Ecol Prog Ser 318: 63–73

Hilton GM, Thompson DR, Sagar PM, Cuthbert RJ, Cherel Y, Bury S (2006) A stable isotopic investigation into the causes of decline in a sub-Antarctic predator, the rockhopper penguin *Eudyptes chrysocome*. Global Change Biol 12: 611-625

Hinz H, Moranta J, Balestrini S, Sciberras M, Pantin JR, Monnington J, Zalewski A, Kaiser MJ, Sköld M, Jonsson P, Bastardie F, Hiddink JG (2017) Stable isotopes reveal the effect of trawl fisheries on the diet of commercially exploited species. Sci Rep UK 7: 6334

Hussey NE, Wintner SP, Dudley SFJ, Cliff G, Cocks DT, MacNeil MA (2010) Maternal investment and size-specific reproductive output in carcharhinid sharks. J Anim Ecol 79: 184-193

Hussey NE, Dudley SFJ, McCarthy ID, Cliff G, Fisk AT (2011) Stable isotope profiles of large marine predators: viable indicators of trophic position, diet,and movement in sharks? Can J Fish Aquat Sci 68: 2029-2045

Hussey NE, MacNeil MA, McMeans BC, Olin JA, Dudley SFJ, Cliff G, Wintner SP, Fennessy ST, Fisk AT (2014) Rescaling the trophic structure of marine food webs. Ecol Lett 17: 239-250

Hutchings JA, Reynolds JD (2004) Marine fish population collapses: consequences for recovery and extinction risk. Bioscience 54: 297-309

Jackson JBC, Kirby MX, Berger WH, Bjomdal KA, Botsford LW, Bourque BJ, Bradbury RH, Cooke R, Erlandson J, Estes JA, Hughes TP, Kidwell S, Lange CB, Lenihan HS, Pandolfi JM, Peterson CH, Steneck RS, Tegner MJ, Warner RR et al. (2001) Historical overfishing and the recent collapse of coastal ecosystems. Science 293: 629-638

Jennings S, Blanchard JL (2004) Fish abundance with no fishing: predictions based on macroecological theory. J Anim Ecol 73: 632–642

Jennings S, Greenstreet SPR, Reynolds JD (1999) Structural change in an exploited fish community: a consequence of differential fishing effects on species with contrasting life histories. J Anim Ecol 68: 617-627

Jennings S, Polunin NVC (1997) Impacts of predator depletion by fishing on the biomass and diversity of non-target reef fish communities. Coral Reefs 16: 71-82

Kelly JF (2000) Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. Can J Zool 78: 1-27

Kim SL, Koch PL (2012) Methods to collect, preserve, and prepare elasmobranch tissues for stable isotope analysis. Environ Biol Fish 95: 53–63

Kleisner K, Mansour H, Pauly D (2014) Region-based MTI: resolving geographic expansion in the Marine Trophic Index. Mar Ecol Prog Ser 512: 185-199

Koch PL (2007) Isotopic study of the biology of modern and fossil vertebrates. In: Michener RH, Lajtha K (eds.), Stable Isotopes in Ecology and Environmental Science. Blackwell Publishing 99–154

Koen Alonso M, Crespo EA, Garcia NA, Pedraza SN, Mariotti PA, Mora NJ (2002) Fishery and ontogenetic driven changes in the diet of the spiny dogfish, *Squalus acanthias*, in Patagonian waters, Argentina. Environ Biol Fish 63: 193-202

Lucifora LO, Garcia VB, Escalante AH (2009) How can the feeding habits of the sand tiger shark influence the success of conservation programs? Anim Conserv 12: 291-301

Lynam CP, Llope M, Möllmann C, Helaouët P, Bayliss-Brown GA, Stenseth NC (2017) Interaction between top-down and bottom-up control in marine food webs. Proc Nat Acad Sci USA 114: 1952-1957

Mackas DL et al. (1998) Interdecadal variation in developmentaltiming of Neocalanus plumchrus populations at Ocean Station P in the subarctic North Pacific. Can J Fish Aquat Sci 55: 1878–1893

MacNeil MA, Skomal GB, Fisk AT (2005) Stable isotopes from multiple tissues reveal diet switching in sharks. Mar Ecol Prog Ser 302: 199-206

McClenachan L, Ferretti F, Baum JK (2012) From archives to conservation: why historical data are needed to set baselines for marine animals and ecosystems. Conserv Lett 5: 349-359

Maia A, Queiroz N, Correia JP, Cabral H (2006) Food habits of the shortfin mako, *Isurus oxyrinchus*, off the southwest coast of Portugal. Environ Biol Fish 77: 157-167

Minagawa M, Wada E (1984) Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between δ^{15}N and animal age. Geochim Cosmochim Ac 48: 1135-1140

Motta PJ (2004) Prey capture behavior and feeding mechanics of elasmobranchs. Pages 165-202 *in* Biology of Sharks and their Relatives. J. C. Carrier, J. A. Musick and M. R, Heithaus, editors. CRC Press, Florida.

Motta PJ, Wilga CC (2001) Advances in the study of feeding behaviors, mechanisms, and mechanics of sharks. Environ BiolFish 60: 131-156

Myers RA, Worm B (2003) Rapid worldwide depletion of predatory fish communities. Nature 423: 280-283

Myers RA, Worm B (2005) Extinction, survival or recovery of large predatory fishes. Phil Trans R Soc Lon Biol Sci 360: 13-20

Myers RA, Baum JK, Shepherd TD, Powers SP, Peterson CH (2007) Cascading effects of the loss of apex predatory sharks from a coastal ocean. Science 315: 1846-1850

Palkovacs EP, Wasserman BA, Kinnison MT (2011) Eco-evolutionary trophic dynamics: Loss of top predators drives trophic evolution and ecology of prey. PLoS One 6: e18879

Pauly D, Christensen V, Dalsgaard J, Froese R, Torres Jr. F (1998) Fishing down marine food webs. Science 279: 860-863

Pauly D, Zeller D (Editors) (2015) Sea Around Us Concepts, Design and Data (www.seaaroundus.org) Accessed 21 November 2016

Peterson BJ, Fry B (1987) Stable isotopes in ecosystem studies. Annu Rev Ecol Syst 18: 293-320

Pikitch EK, Santora C, Babcock EA, Bakun A, Bonfil R, Conover DO, Dayton P, Doukakis P, Fluharty D, Heneman B, Houde ED, Link J, Livingston PA, Mangel M, McAllister MK, Pope J, Sainsbury KJ (2004) Ecosystem-based fishery management. Science 305: 346-347

Post DM (2002) Using stable isotopes to estimate trophic position: models, methods and assumptions. Ecology 83: 703-718

R Development Core Team (2009) R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.

Roemmich D, McGowan J (1995) Climatic warming and the decline of zooplankton in the California Current. Science 268: 352–353

Rouault M, Penven P, Pohl B (2009) Warming in the Agulhas Current system since the 1980’s. Geophys Res Lett 36: L12602

Safina C, Klinger DH (2008) Collapse of bluefin tuna in the western Atlantic. Conserv Biol 22: 243-246

Sardenne F, Bodin N, Chassot E, Amiel A, Fouché E, Degroote M, Hollanda S, Pethybridge H, Lebreton B, Guillou G, Ménard F (2016) Trophic niches of sympatric tropical tuna in the Western Indian Ocean inferred by stable isotopes and neutral fatty acids. Prog Oceanogr 146: 75-88

Smale MJ (2005) The diet of the ragged-tooth shark *Carcharias taurus* Rafinesque 1810 in the Eastern Cape, South Africa. Afr J Mar Sci 27: 331-335

Sonnerup RE, Quay PD, McNichol AP (2000) The Indian Ocean ^{13}C Suess Effect. Global Biogeochem Cy 14: 903-916

Stevens JD, Bonfil R, Dulvy NK, Walker PA (2000) The effects of fishing on sharks, rays and chimaeras (Chondrichthyans), and the implications for marine ecosystems. ICES J Mar Sci 57: 476-494

Stillwell CE, Kohler NE (1982) Food, feeding habits, and estimates of daily ration of the shortfin mako (*Isurus oxyrinchus*) in the northwest Atlantic. Can J Fish Aquat Sci 39: 407-414

Taylor JR, Ferrari R (2011) Shutdown of turbulent convection as a new criterion for the onset of spring phytoplankton blooms. Limnol Oceanogr 56: 2293-2307

Tricas TC, McCosker JE (1984) Predatory behavior of the white shark (*Carcharodon carcharias*), with notes on its biology. Proc Cal Acad Sci 43: 221-238

Vanderklift A, Ponsard S (2003) Sources of variation in consumer-diet δ^{15}N enrichments: a meta-analysis. Oecologia 136: 169-182

Vander Zanden MJ, Rasmussen JB (2001) Variation in δ15N and δ13C trophic fractionation: implications for aquatic food web studies. Limnol Oceanogr 46: 2061-2066

Vander Zanden MJ, Shuter BJ, Lester NP, Rasmussen JB (2000) Within- and among population variation in the trophic position of a pelagic predator, lake trout *Salvelinus namaycush*. Can J Fish Aquat Sci 57: 725-731

Walker TJ (2007) The state of research on chondrichthyan fishes. Mar Freshwater Res 58: 1-3

Ward P, Myers RA (2005) Shifts in open-ocean fish communities coinciding with the commencement of commercial fishing. Ecology 86: 835-847

Ward-Paige CA, Mora C, Lotze HK, Pattengill-Semmens C, McClenachan L, Arias-Castro E, Myers RA (2010) Large-scale absence of sharks on reefs in the Greater-Caribbean: a footprint of human pressures. PLos ONE 5: e11968

Wetherbee BM, Cortés E (2004) Food consumption and feeding habits. Pages 225-246 *in* Biology of Sharks and their Relatives. J. C. Carrier, J. A. Musick and M. R, Heithaus, editors. CRC Press, Florida.

Willis KJ, Araújo MB, Bennett KD, Figueroa-Rangel B, Froyd CA, Myers N (2007) How can a knowledge of the past help to conserve the future? Biodiversity conservation and the relevance of long-term ecological studies. Phil Trans R Soc Lond B Biol Sci 362: 175-86

Wiltshire KH, Manly BFJ (2004) The warming trend at Helgoland Roads, North Sea: phytoplankton response. Helgoland Marine Research 58: 269-273

Woodward G, Ebenman B, Emmerson M, Montoya JM, Olesen JM, Valido A, Warren PH (2005) Body size in ecological networks. Trends Ecol Evol 20: 402-409

Zeller D, Pauly D (2015) Reconstructing marine fisheries catch data. In: D. Pauly and D. Zeller (eds). Catch reconstruction: concepts, methods and data sources. Online Publication. Sea Around Us (www.seaaroundus.org). University of British Columbia.

Zhou S, Smith ADM, Punt AE, Richardson AJ, Gibbs M, Fulton EA, Pascoe S, Bulman C, Bayliss P, Sainsbury K (2010) Ecosystem-based fisheries management requires a change to the selective fishing philosophy. Proc Nat Acad Sci USA 107: 9485-9489

Chapter 3. [1]

Effects of tourism-related provisioning on the trophic signatures and movement patterns of Caribbean reef sharks[1]

Abstract

Shark feeding, i.e. the provision of bait to generate aggregations of sharks as tourist attractions, occurs around the world. This practice is often promoted as an economic incentive to conserve shark resources, yet has stimulated debate based on the potential for risks to human safety and perceptions of behavioural shifts in provisioned sharks. I studied a population of Caribbean reef sharks (Carcharhinus perezi) in the Bahamas that has been subject to regular provisioning for >20 years. I used a combination of focal observations of sharks during feeding events, remote acoustic telemetry and stable isotope analysis of shark muscle tissue to determine the impacts of shark feeding on the trophic signatures and ranging behaviour of this population. A small number of large sharks monopolised more than 50% of the bait on offer. These 'fed' individuals showed significant 15N enrichment in their tissues compared to conspecifics of the same size that failed to obtain bait at the feeding site, and un-provisioned sharks from a control site. Despite the disparity in trophic signatures, fed, unfed and control sharks exhibited similar degrees of residency at their respective home receiver sites, and travelled similar daily minimum distances. Thus, despite long-term provisioning of this Caribbean reef shark population, there is no evidence for shifts in the behaviours considered which might affect the ecological role of these sharks. However, further research is required to examine potential indirect effects of shark provisioning on sympatric fauna and habitat before this activity can be placed within a sustainable marine conservation framework.

---

[1] A version of this chapter appears as, Maljković, A. & Côté, I.M. (2011) Effects of tourism-related provisioning on the trophic signatures and movement patterns of an apex predator, the Caribbean reef shark. Biological Conservation 144: 859-865.

Introduction

Provisioning wildlife, as a means of enhancing nature-based tourism experiences, is a hotly debated issue (Newsome and Rodger, 2008) which becomes most controversial when involving the feeding of large predatory species (Burns and Howard, 2003; Perrine, 1989). In these cases, human safety issues are usually at the forefront of the debate, with opponents of the practice claiming the potential for predators to learn to associate human presence and food rewards, and proponents citing a lack of empirical documentation of such links (Orams, 2002). Concerns have also been raised about impacts on the provisioned animals themselves, which have only begun to be empirically examined. Regular provisioning of various predators has been shown to lead to increased population densities and interference competition (Semeniuk and Rothley, 2008), increased frequency and duration of aggressive behaviours (Hodgson et al., 2004; Hsu et al., 2009), impoverished body condition and physiological indications of impaired health (Semeniuk and Rothley, 2009).

Shark-viewing tourism is the epitome of this controversy. At over 40% of the 267 globally-distributed shark viewing sites detailed by Carwardine and Watterson (2002), some form of attractant (chum or decoys) or bait is used to increase encounter rates and keep the focal species within viewing distance of paying clients. Yet due to the longstanding difficulties associated with studying large marine predators, the basic ecology of most of these shark species, let alone their responses to provisioning, remains undocumented. Nevertheless, the full spectrum of arguments both for and against the practice of shark feeding has been discussed in several recent papers (Johnson and Kock, 2006; Laroche et al., 2007; Meyer et al., 2009).

The contentious nature of shark provisioning has prompted legislation abolishing the practice in several areas of the world, including Florida, Hawaii, the Cayman Islands and South Africa (Carwardine and Watterson, 2002), with mounting pressure for the activity to be banned in others regions (Topelko and Dearden, 2005). However, the popularity of shark dives, and subsequent success of many shark encounter operations, now makes this activity a valuable source of revenue, particularly in countries that depend on tourism as a major source of foreign earnings (Green and Higgenbottom, 2000; Topelko and Dearden, 2005). For example, an analysis of the economic impact of shark-related tourism in the Bahamas revealed that in 2007, operators facilitated more than 72 500 shark encounters, generating an estimated $ 78 207 338 input to the economy when all local services used by shark dive clients were considered (W. Cline, Cline Marketing Group, unpublished data). The strong economic incentive to maintain, or even promote, shark-related tourism may therefore outweigh the perceived negative effects of this activity on sharks, particularly in light of the absence of strong evidence showing such effects.

Because a substantial part of the debate surrounding shark feeding centres on perceived shifts in the behaviour of sharks in response to provisioning (Guttridge et al., 2009), the aim of my study was to quantify the effects of tourism-related provisioning on the trophic signatures and movement patterns of sharks, i.e. factors for which data may be reliably collected and which might reasonably be expected to reflect direct impacts of supplemental feeding. I focused on Caribbean reef sharks (*Carcharhinus perezi*), which are frequently the focal species at shark dive sites in the Bahamas, and are considered by the Bahamas Dive Association as one of five species which are 'relatively safe' to dive with without the use of an anti-shark cage (W. Cline, unpublished data). More specifically, I compared patterns of site fidelity, daily distances travelled and ^{15}N-based trophic signatures of provisioned sharks with those of un-provisioned conspecifics to elucidate the effects of shark feeding on this species. My study provides data that are currently missing from attempts to weigh the benefits and disadvantages of marine wildlife provisioning. Such information is essential to assess whether provisioning practices can be included in portfolios of management strategies that enhance marine conservation awareness and revenues while not conflicting with other preservation goals

Methods

All methods used in this study were approved by the Canadian Council on Animal Care (permit no. 828B-07) and research was conducted in accordance with a Marine Scientific Research Permit (MAF/FIS/17) issued by the Department of Marine Resources, Government of The Bahamas.

Study site and species

This study was conducted over a period of 13.5 months between May 2007 and February 2009 in New Providence, Bahamas (25° 25'N, 78° 35'W). The focal shark feeding site was located 2.6 km off the south coast of the island where Caribbean reef sharks have been fed almost daily since 1986 as a dive tourism attraction. The shark feeding site is located at a depth of 11 – 12 m on a sand patch adjacent to a coral reef wall which forms the eastern edge of the Tongue of the Ocean trench. Prior to the advent of shark feeding tourism, Caribbean reef sharks were often encountered in this area by divers and fishers, making this site a natural location for shark feeding activities (S.N. Cove, Stuart Cove's Dive Bahamas, personal communication). Shark feeding dives are conducted every afternoon between 14:30 to 16:00, during which 10 – 16 pieces of fish (usually filleted grouper *Mycteroperca* spp and *Epinephelus* spp heads and carcasses obtained from the local fish processing plant) are taken to the feeding site in a metal bait box and fed to the sharks piece by piece using a metal feeding spear. Diving tourists kneel on the sand approximately 5 m from the feeding site to watch the sharks being fed. Shark feeding typically lasted 19 - 24 min.

Caribbean reef sharks are one of the most abundant large-bodied elasmobranchs remaining in the tropical western Atlantic (Compagno, 1984, 2002), and are apex predators in coral reef communities. This species is targeted by commercial and artisanal fisheries throughout most of its broad geographic range (Amorin et al., 1998; Gadig et al., 1989), yet little is known about its ecology, habitat use, or susceptibility to fishing pressure (Chapman et al., 2007). Populations of Caribbean reef sharks in the Bahamas are de facto protected from fishing because permits for long-line fishing, a principal cause of shark declines (Bonfil, 1994), have not been issued since 1986 (http://laws.bahamas.gov.bs/statutes/statute_CHAPTER_244.html). Moreover, since that time, licensing the export of shark products from the country has been contrary to government policy (M.T. Braynen, Bahamas Department of Marine Resources, personal communication).

Shark identification & behavioural observations

I used two methods to identify individual Caribbean reef sharks at the feeding site. Many individuals exhibited obvious distinguishing features such as permanent patches of unusual pigmentation, scars, or deformations of the lower jaw or fins, which allowed reliable long-term identification. To facilitate the identification of sharks without such features, I used individually colour-coded spaghetti dart tags (Floy Tag, Seattle, USA). Sharks were tagged either after being briefly immobilised by hand during the shark feeding dives, or following capture on a baited hook using a rod and line. In the latter case, I used ungalvanised 16/0 circle hooks baited with locally bought snapper *Lutjanus* spp. All sharks were jaw-hooked and brought alongside the boat where the leader wire was bound to a cleat and the tail was secured around the caudal peduncle using a soft rope with a sliding noose. The sharks were thus held in the water, parallel to the boat, for the duration of the procedure (~10-12 min). Once fully secured, sharks became quiescent. An intramuscular dart tag with stainless steel anchor was inserted near the base of the first dorsal fin at a 45° angle relative to the plane of the shark's dorsal surface, using a 5.5 cm tagging needle. Shark total length (TL) was measured to the nearest centimetre, and I also obtained a muscle tissue sample for stable isotope analysis (see section 2.3). Sharks were then released and monitored by two divers until they resumed normal swimming behaviour (~ 2 min). For sharks tagged during provisioning, I visually estimated the TL of individuals to the nearest 10 cm. The sex of all sharks was determined based on the presence or absence of claspers.

During each shark feeding dive I recorded: the total number of sharks present (based on an average of five separate counts undertaken towards the end of the feeding event), which individual sharks were present and which sharks took each piece of bait on offer.

Isotope sample collection and methods

Muscle tissue samples for carbon and nitrogen isotope analysis were collected using a gauge 11 hard tissue biopsy needle from the dorsal musculature adjacent to the trailing edge of the first dorsal fin of each shark caught for tagging. The small (3 mm) diameter and position of the wound made it difficult to assess the rate of healing, but no evidence of infection was seen in any resighted sharks. The white muscle tissue selected for isotopic analysis was isolated from the general biopsy sample by excision. Samples were frozen for storage. In the laboratory, samples were washed in distilled water, lyophilised, and reduced to a fine powder in a ball-mill grinder. The $\delta^{15}N$ and $\delta^{13}C$ values for samples were assessed using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer from 1 ± 0.2 mg of dried material which was submitted for analysis in tin capsules to the University of California - Davis Stable Isotope Facility. Replicate measurements of internal laboratory standards (ammonium sulphate and sucrose) after every 12 samples produced measurement errors of ± 0.1‰ and ± 0.2‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively.

Acoustic telemetry

To establish residency times of sharks at the feeding site, as well as to obtain estimates of daily travel distances, a subset of 21 sharks was fitted with Vemco coded V16 or V16P acoustic tags. Following capture using rod and line (as described above), the tags were surgically implanted into the coelom through a 5 cm incision made just anterior to the origin of a pelvic fin, following the methods described in Chapman et al. (2005). The incision was closed using dissolving braided nylon sutures. All surgical equipment and transmitters were kept in 70% isopropyl alcohol prior to each procedure, which took an average of 11 min to complete. The tags emitted a specific ID code at 69 kHz with a nominal delay of 240 s, allowing us to identify individuals recorded by acoustic receivers. Sharks resighted post-surgery showed no evidence of infection at the wound site, and all sharks were detected by at least two receivers for the duration of the study, indicating a 100% survival rate.

A non-overlapping array of 10 Vemco™ VR2W acoustic receivers was anchored to the substratum over approximately 27 km along the reef wall (Figure 3.1). One receiver was positioned directly adjacent to the shark feeding site, and all receivers were positioned to minimise tag detection interference from underwater structures and areas of high reef relief. To establish the detection range of receivers, an activated coded transmitter was suspended 6 m below the water’s surface from a boat, 450 m (i.e. close

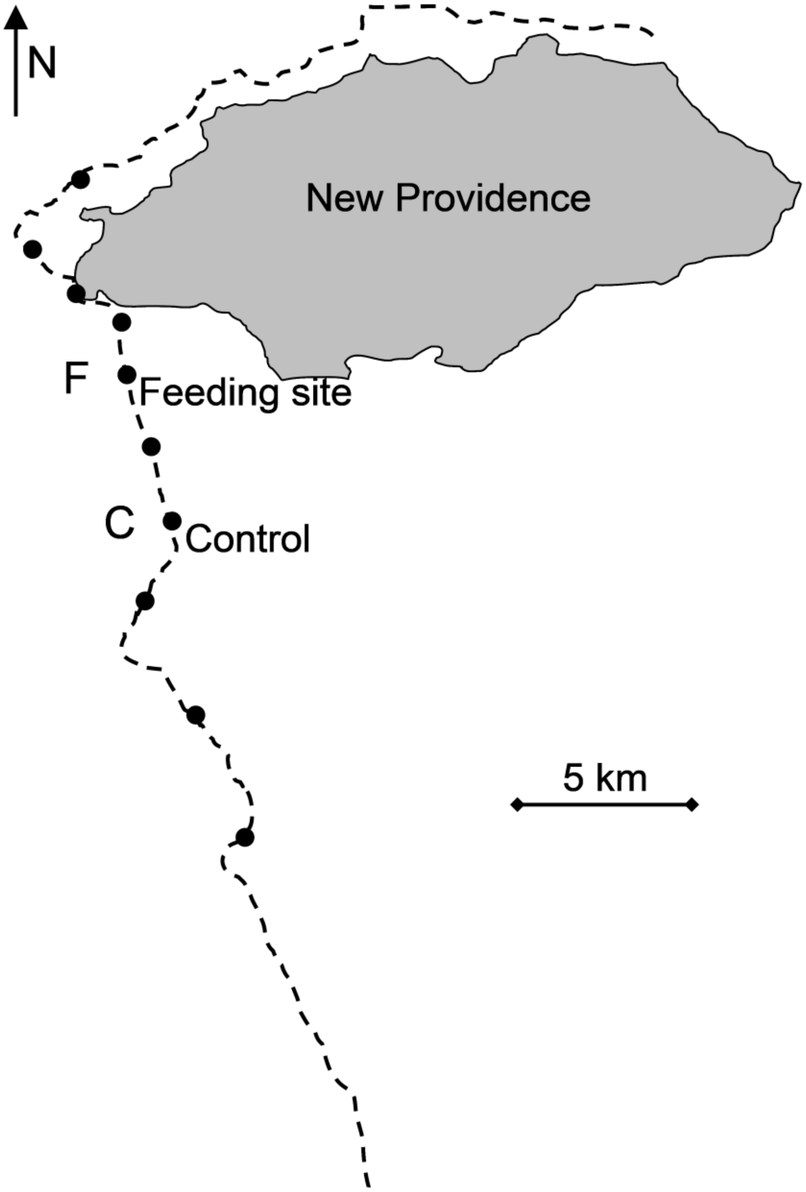


Figure 3.1 Map of study site and receiver positions. The dashed line represents the eastern edge of the Tongue of the Ocean trench.

to the estimated receiver detection limit) from each receiver. I sequentially moved the transmitter away from the receiver, in 10 m increments up to a distance of 550 m, remaining at each new position for 360 s and noting location, obtained with a hand-held GPS, and time. The last time stamp recorded by each receiver in each trial established the detection range. This process was repeated four times for each of the 10 receivers, heading due north, south, east and west. The detection range for V16 transmitters was ~ 500 m (range: 490 – 540 m) for all receivers.

Data analysis

I categorised individual sharks as 'fed' or 'unfed' based on bait consumption (see section 3.1). Fed sharks were those consuming 3% or more of the bait (n = 11 individuals), and unfed sharks were those consuming 1% or less (n = 37 individuals). These cut-off values represented a natural break in the bait acquisition data (see Figure 3.2a). To account for the possible effects of sex- or size-based differences on Caribbean reef shark behaviour, I restricted my analyses of trophic signatures and movement patterns to female sharks (i.e. the most abundant gender) of more than 180 cm TL, with the stipulation that these individuals had to have attended at least 50% of the focal shark feeding events.

In addition, I included a control group of 10 Caribbean reef sharks to test whether the shark feeding activity per se influenced movement patterns and trophic signatures regardless of any bait consumption effect. Sharks in the control group were all females of more than 180 cm TL and, as determined using acoustic telemetry, resided mainly near receiver C (Figure 3.1), approximately 4.6 km from the shark feeding site. Eight of the sharks in the control group were sighted at shark feeds over the course of the study, but they attended very infrequently (n_{total} = 51 sightings; or 0.4 ± 0.03 sightings per shark per month) and none took any of the bait on offer. Muscle tissue samples were collected from these individuals, and they were implanted with Vemco V13 acoustic tags using the methods described above. Receiver detection range for V13 transmitters was established as described in section 2.4, and the detection ranges for V13 and V16 transmitters were not significantly different (V13 tag detection range: 470 – 540 m; paired t-test: $t_{39} = 1.3$, $P = 0.20$).

Specific isotope abundance was calculated as a parts-per-thousand deviation from the standard using the equation: $\delta X = ((R_{sample}/R_{standard}) - 1) \times 1000$, where X is ^{15}N or ^{13}C, R_{sample} is the isotopic ratio $^{15}N{:}^{14}N$ or $^{13}C{:}^{12}C$ in the sample, and $R_{standard}$ is the isotopic ratio for the relevant standard (Peterson and Fry, 1987). The standard reference materials for nitrogen and carbon were atmospheric nitrogen and Pee Dee belemnite, respectively. All isotope results are presented in standard δ notation ± 1 SD. Isotopic signatures of shark muscle tissue were compared across groups using a one-way independent ANOVA and post hoc testing was performed using Gabriel's pairwise tests to account for the slightly different sample sizes in each study group (Field, 2005).

Shark movement was examined in two complementary ways: residency and travel distance. Residency, or site fidelity, was measured as the number of detections recorded for an individual shark at a specific receiver in relation to the total number ofdetections recorded for that individual across all receivers. I focused on two specific receivers: receiver F, i.e. the 'home' receiver of fed and unfed sharks at the feeding site, and receiver C, i.e. the 'home' receiver of sharks in the control group. Expressing residency in terms of proportion of total detections controlled for the shorter nominal delay between transmissions (180 s) of the V13 tags and the V16 tags (240 s). Detections at the respective home receiver sites were calculated for two time categories: morning (06:00 – 12:00) and afternoon (12:00 – 18:00), to examine potential shifts in movements associated with afternoon provisioning. A two-way analysis of variance (ANOVA) was used to determine the effects of feeding status (three categories: fed, unfed and control groups), as a proxy for bait acquisition and attendance at shark feeds, and time of day (two categories: morning and afternoon) on residency at respective home receiver sites.

To generate estimates of daily travel distances for sharks, I sorted acoustic detections by transmitter, followed by time, then by receiver to produce a chronological log detailing the movement patterns of each shark between receivers. Using the known distances between receivers, I then calculated the minimum distances travelled by sharks over the course of each 24 hr period. These daily minimum distances are conservatively defined as the sum of the straight-line distances travelled by sharks between the receivers, assuming that sharks were detected at the periphery of the receiver's detection range (500 m).

All statistical tests were two-tailed and data were checked for normality and heteroscedasticity. Data were analysed using SPSS 16.0.

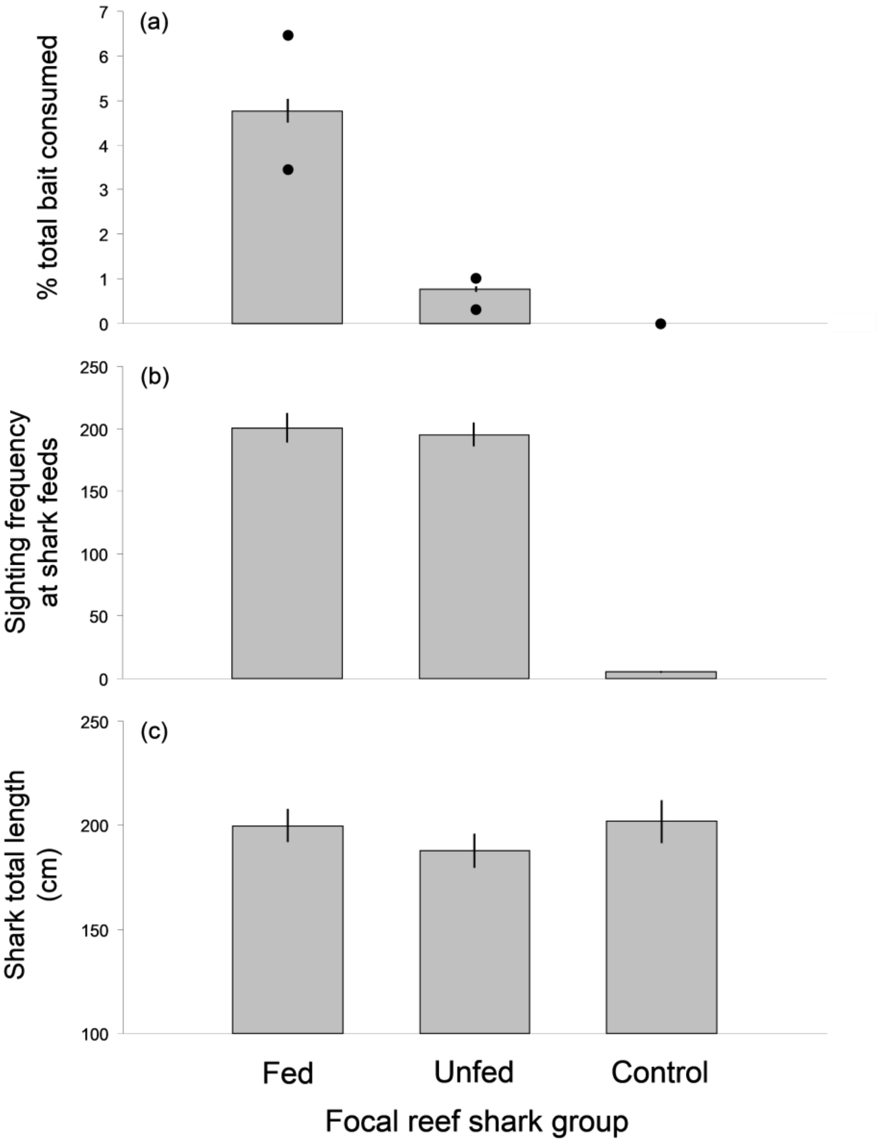


Figure 3.2. Bait consumption, sighting frequency and sizes of focal Caribbean reef sharks at New Providence, Bahamas. (a) Proportion of total bait consumed, (b) sighting frequency at shark feeds and (c) shark total length. Filled circles in (a) represent the minimum and maximum proportion of bait consumed by individual sharks in each focal group. Error bars are ± 1 SE. Shark sample sizes: n_{fed} = 9, n_{unfed} = 12, $n_{control}$ = 10

Results

Shark presence and behaviour at shark feeding dives

Between 24 May 2007 and 13 February 2009, 97 individual Caribbean reef sharks were identified during 293 shark feeding dives, i.e. 48% of all shark dives conducted during this period. Of these sharks, 56 were externally tagged to aid identification. Sharks ranged in size from 90 – 280 cm TL (mean ± SD: 160 ± 35 cm), and the sex ratio was strongly female-biased (1:6.5).

Overall, the number of sharks present at each feeding dive varied between seven and 55 individuals (mean ± SD: 34 ± 9 sharks), and individual sighting frequency varied widely (mean ± SD: 127 ± 84 sightings, range: 1 – 261 sightings, or 0.3 – 89% of feeding events surveyed). Eleven sharks (11% of all individuals recorded; 2 males, 9 females) took over 50% of the bait on offer (n_{total} = 3792 pieces), with no other single shark consuming more than 2% of the remainder. The sharks eating the majority of the bait were significantly larger (mean ± SD: 198.18 ± 26.0 cm) than the remainder of the study population (155.47 ± 33.42 cm; independent t-test: $t_{95} = 4.08$, $P < 0.0001$).

All subsequent analyses consider only the nine females that were highly successful at taking bait (the ‘fed’ group), 12 unsuccessful females that were more than 180 cm TL and attended more than 50% of shark feeding events (the ‘unfed’ group), and 10 females that were more than 180 cm TL, resided near receiver C (Figure 3.1) and attended very few feeding events (the ‘control’ group; Figure 3.2a and 3.2b). There were no size differences among these three groups (ANOVA: $F_{2,28} = 0.76$, $P = 0.48$; Figure 3.2c).

Isotope signatures

Stable nitrogen isotope signatures varied significantly among the three shark groups (ANOVA, $F_{2,28} = 92.57$, $P < 0.0001$; Fig. 3.3). The muscle tissues of fed sharks were significantly enriched in ^{15}N compared to those of both unfed and control sharks

(Gabriel's pairwise tests; fed vs. unfed: $P < 0.0001$, fed vs. control: $P < 0.0001$, unfed vs. control: $P = 0.58$). ^{13}C values did not differ among groups (ANOVA, $F_{2,28} = 1.75$, $P = 0.19$).

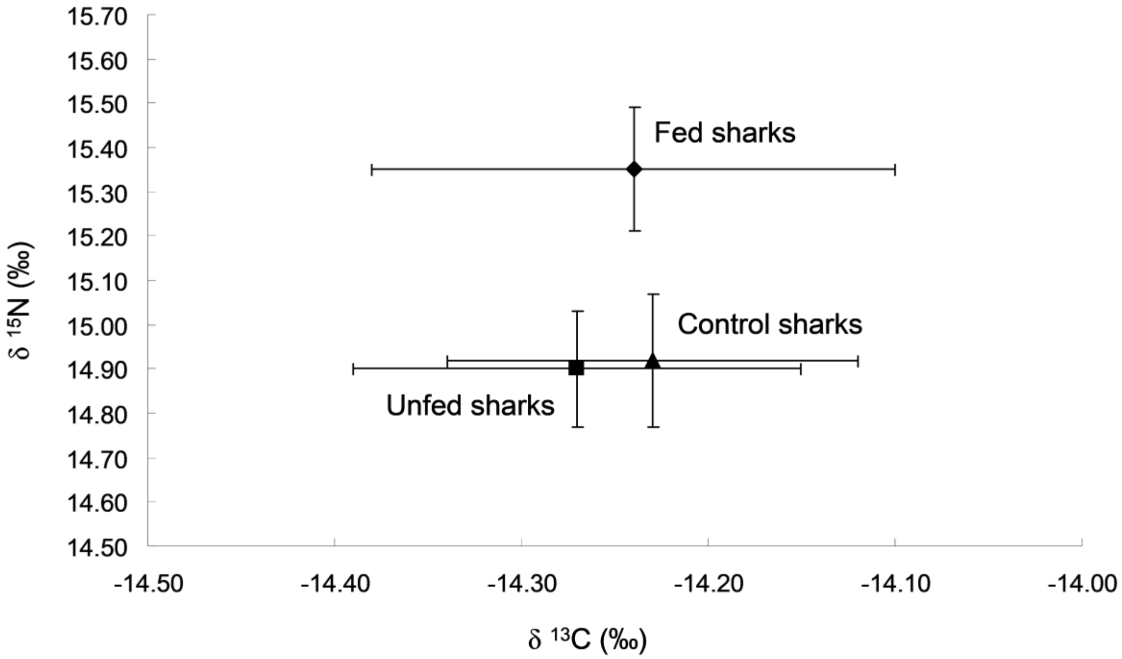


Figure 3.3 Stable carbon and nitrogen isotope values of muscle tissue from Caribbean reef sharks under different provisioning regimes off southern New Providence, Bahamas.

Residency and movement

Over a 195-day period between August 2008 and February 2009, residency, or the proportion of detections at the relevant home receiver site, did not differ between fed (mean ± SE: 51.8 ± 4.3%), unfed (49.8 ± 5.1%), and control group sharks (54.6 ± 6.2%; 2-way ANOVA, $F_{2,26} = 2.26$, $P = 0.12$), and there was no effect of time of day (morning or afternoon) on residency at the home receiver site for any shark group (2-way ANOVA, $F_{1,26} = 2.51$, $P = 0.13$; Figure 3.4a). The interaction between shark group and time of day was not significant (2-way ANOVA, $F_{2,26} = 0.98$, $P = 0.39$).

The minimum distances travelled daily by fed, unfed and control group sharks were not significantly different (ANOVA, $F_{2,28} = 1.09$, $P = 0.35$; Figure 3.4b).

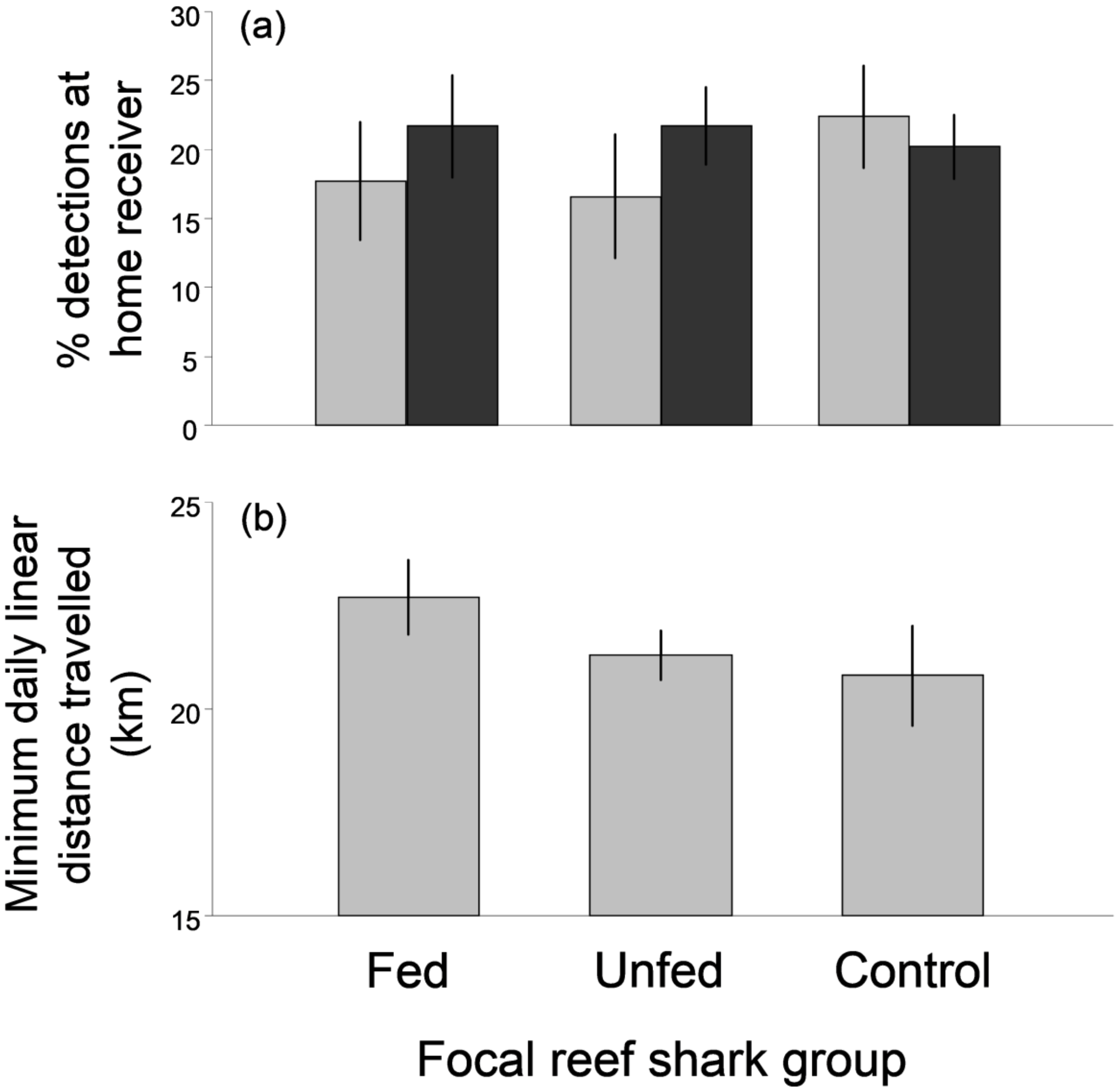


Figure 3.4 Residency and daily travel distances of focal Caribbean reef sharks at New Providence, Bahamas. (a) Residency (light bars: morning, dark bars: afternoon), measured as the number of detections recorded for an individual shark at a specific home receiver in relation to the total number of detections recorded for that individual across all receivers, and (b) minimum distances travelled, measured as the sum of the straight-line distances travelled by sharks between the receivers over 24 hours. Error bars are ± 1 SE. Shark sample sizes: $n_{fed} = 9$, $n_{unfed} = 12$, $n_{control} = 10$

Discussion

The controversy surrounding shark feeding, coupled with a paucity of empirical studies describing its effects on any focal species, has led to much speculation regarding the impacts of provisioning on shark ecology. To my knowledge, this is the first study to investigate the direct effects of provisioning on the behaviour of an inshore population of sharks, other than white sharks *Carcharodon carcharias* (Johnson and Kock, 2006; Laroche et al., 2007), and the first to examine the trophic consequences of provisioning for any shark species. My study yielded two salient results which may help to inform the shark feeding debate. First, the proportion of Caribbean reef sharks acquiring bait at regular feeding events was small compared to the total number of sharks present, and the same few individuals were repeatedly successful at attaining the majority of the bait. Second, despite the elevated ^{15}N signatures of these fed sharks relative to unfed and control sharks, there was no statistically detectable variation in the extent of movement of individuals across groups.

Shark presence and behaviour at shark feeding dives

Attendance at feeding events varied widely among individual sharks. Some of this variation, at a seasonal scale, is attributable to reproductive activity. A mass departure of near-term gravid females, followed quickly by many other females, occurred throughout June. None of the returning sharks, the majority of which reappeared at the feeding site in July, was visibly pregnant and most individuals exhibited extensive scars, usually obtained as a result of mating (Pratt and Carrier, 2001). However, some of the variation in daily individual attendance at feeding events also stems from differences in patterns of residency. Some sharks exhibited a strong degree of fidelity to the feeding area, but many sharks arrived at the site opportunistically, perhaps as a result of attraction to the bait or to the aggregation of conspecifics.

The proportion of Caribbean reef sharks successfully acquiring food rewards at shark feeds was very small. Although this pattern has also been noted in studies of white shark provisioning (Johnson and Kock, 2006; Laroche et al., 2007), it seems surprising here given the larger numbers and tighter spatial aggregation of Caribbean reef sharks at feeding events. Close proximity potentially created the opportunity for multiple individuals to successfully compete for the proffered bait. The fact that only a few large sharks were repeatedly effective at taking the majority of bait suggests that in Caribbean reef sharks, as in many other shark species (Allee and Dickinson, 1954; Bres, 1993), social hierarchies exist in which larger sharks are dominant in competitive situations.

Isotope signatures

Provisioning altered the trophic signatures of the few individuals that repeatedly consumed bait. Whereas all sharks had relatively similar $\delta^{13}C$ values, indicating that all individuals feed on prey items which derive their nutrients from the same primary sources (Peterson and Fry, 1987), their $\delta^{15}N$ signatures were more variable. Sharks that took bait frequently (the 'fed' group) had elevated $\delta^{15}N$ values compared to individuals of similar size and sex that were either often present but unsuccessful at feeds (the 'unfed' group) or rarely present and mostly resident elsewhere (the 'control' group). Caribbean reef sharks are reported to prey on a wide range of reef fish, including other elasmobranchs, and cephalopods (Motta et al., 1999; D. Chapman, personal communication), and groupers (i.e. the predominant species in shark bait) are likely to form at least a part of their natural diet. The abundance of groupers and other high-trophic level coral-associated species has been reduced across the Caribbean as a result of fishing (Bascompte et al., 2005), and such species have been severely depleted on many Bahamian reefs (Mumby et al., 2006). The frequent acquisition of high-trophic level meals (grouper carcasses) at shark feeds is therefore a likely mechanism explaining the ^{15}N enrichment observed in fed sharks.

The broader implications of provisioning-altered trophic signatures are difficult to determine because neither the energetic requirements nor the diet of Caribbean reef sharks have been fully documented. Nevertheless, we can derive a very preliminary, 'ballpark' estimate of the proportion of Caribbean reef shark daily energy requirements contributed by bait consumption. To assess the energy requirements of Caribbean reef sharks, we can use a simple bioenergetic model: $I = M + G + E$ (Brett and Groves, 1979) and apply the estimates of metabolic rate (M), growth (G) and energy lost (E) calculated for captive bull sharks *Carcharhinus leucas*, a morphologically similar congener of Caribbean reef sharks, to approximate daily food intake (I). Based on the values given for bull sharks in Schmid and Murru (1994), I estimate that Caribbean reef sharks would require 7.91 $kcal^{-1}$ kg^{-1} day^{-1}, or ~670 $kcal^{-1}$ day^{-1} for a 180 cm shark weighing 85 kg (with weight estimated from length-weight relationship provided by Pauly and Froese 2009). During my study, approximately 3 kg of bait was fed to the sharks each day, one-quarter of which was considered to consist of indigestible material (ossified parts). Assuming a caloric value of 87 $kcal^{-1}$ $100g^{-1}$ for grouper flesh (Pigott and Tucker, 1990), I estimate that an 85-kg Caribbean reef shark would need to consume ~770 g of grouper (or ~34 % of the bait) per day to meet its minimum energy requirements. In this study, individual sharks were observed to take approximately one-third of the bait during only 13 of the 293 focal shark dives (and on a maximum of four occasions for the same shark), making it highly unlikely that provisioning is the sole source of energy for any of the sharks in this population. In addition, my estimate of daily energetic requirements is likely to be very conservative as it is based on a bioenergetic model of captive sharks which are unlikely to have metabolic demands approaching those of a free-ranging individual.

Residency and movement

Previous studies of animals subject to regular provisioning have shown marked changes in space use and movement of provisioned animals, including increases in the time spent at the site where food is provided and when it is provided (Hodgson et al., 2004; Milazzo et al. 2005; Newsome et al, 2004; Walpole, 2001). Neither shift was evident in my study population. All sharks with transmitters spent a high proportion of their time near a single receiver, regardless of feeding status. Thus, overall, fed sharks did not spend more time at the provisioning site than unsuccessful individuals. In addition, fidelity to a single receiver was evident across the day. Fed, unfed and control group sharks in my study were detected at their respective home receiver sites equally during the morning and afternoon indicating that the regular acquisition of food, or even the potential to acquire food, does not influence the residency patterns of these sharks.

Provisioning also did not appear to affect the extent of movement away from home receivers. All sharks travelled similar daily minimum distances suggesting that successful acquisition of bait did not lead to smaller foraging ranges. Overall, both fed and unfed sharks in my study population exhibited movement patterns that were consistent with previous studies of habitat use in Caribbean reef sharks, which have shown that larger individuals (> 110 cm TL) prefer ocean reef habitats near drop-offs (Pikitch et al., 2005) and exhibit site fidelity, but also make wide-ranging lateral (~ 50 km) and vertical movements (Chapman et al., 2005; Chapman et al., 2007).

In light of the small estimated contribution of bait to the overall energetic budget of the majority of sharks, it is not surprising that shark movement patterns appear to be largely unaffected by provisioning. However, my analyses were restricted to a specific subset of sharks (i.e. females > 180 cm TL) whose behaviour may not be representative of the population as a whole. Future telemetry studies should include a broader range of shark size classes and use active, rather than passive, monitoring to obtain more accurate estimates of daily space use.

The results of my study contrast with the findings of most previous work in which the movement patterns of marine fish in response to provisioning were investigated. In the Mediterranean, Milazzo et al. (2005) found that fish feeding practices influenced the spatio-temporal distribution of saddled bream (*Oblada melanura*) and dusky grouper (*Epinephelus marginatus*), but not ornate wrasse (*Thalassoma pavo*), over large distances (hundreds of metres) and long time scales (months) with increased abundances of these species at fish feeding sites. The behaviour and size structure of snapper (*Pagrus auratus*) populations at a marine reserve in New Zealand were found to be altered at a fish feeding site relative to nearby areas (Cole, 1994), yet the biomass of reef-associated predators in Bonaire was not different between provisioning and marine reserve areas (Hawkins et al., 1999). Despite the fact that these studies use dissimilar metrics (i.e. abundance and biomass data) to those I present here, the most parsimonious interpretation of the results suggest marked changes in space use by some species, but not by others, in response to supplemental feeding. A telemetry study of provisioned and un-provisioned stingrays (*Dasyatis americana*) in the Cayman Islands provides the most comparable dataset to my own, with sharply contrasting findings. Stingrays, which are normally solitary foragers with large home ranges, showed strong site fidelity to the area where provisioning occurred, as well as reduced activity patterns, which resulted in increased aggregation behaviour (Corcoran, 2006). The lack of consensus among the conclusions of fish provisioning studies suggests that species-specific responses to food supplementation are a common feature of marine communities and are perhaps reflective of differences in, for example, home range sizes, habitat associations, habituation thresholds or tolerance levels of the species at provisioning sites to repeated disturbances.

Conclusions

Shark feeding is a contentious practice that has received little empirical attention to date (Meyer et al., 2009; Topelko and Dearden, 2005). My results suggest that regular provisioning of Caribbean reef sharks produced a detectable isotopic signal in the tissues of a small number of sharks, but induced no apparent changes in site fidelity or daily movement patterns, i.e. factors which might affect the ecological role of this reef-associated apex predator.

Although my conclusions may not necessarily be extrapolated to other provisioned shark populations, owing to the potential effects of varying shark species, bait types and modes of bait delivery, my results suggest that provisioning does not necessarily influence animal behaviour in detrimental ways (Orams, 2002). Therefore shark provisioning, when carefully conducted, has the potential to be an effective strategy that can contribute to three key aspects of marine conservation. From an awareness perspective, shark feeding, when accompanied by natural history information, can enhance public realisation of the global plight of shark populations (Carwardine and Watterson, 2002; Topelko and Dearden, 2005). From an ecological perspective, it can augment local shark population densities to mimic pre-exploitation levels which may help to restore fish community structure and ecosystem integrity. Finally, from a financial perspective, shark provisioning is lucrative, thus providing a strong economic incentive for non-consumptive uses of sharks (Clarke et al., 2006; Johnson and Kock, 2006; Meyer et al. 2009; Topelko and Dearden, 2005).

On a cautionary note, there may be indirect effects of shark provisioning which were not considered here. These include increases in diver-sustained damage to habitats at provisioning sites, as well as potential cascading effects of marked local increases in predator abundance. There is a clear need for further ecological research, coupled with studies of the socio-economic benefits of shark-related tourism, before this activity can be safely incorporated within a sustainable-use framework for shark conservation.

Acknowledgements

This study was supported by the Abbott - Fretwell Graduate Fellowship in Fisheries Biology and the Sidney Hogg Memorial Scholarship to A.M.. I.M.C. was supported by the Natural Science and Engineering Research Council of Canada. PADI Project Aware provided financial support for isotopic analysis of shark tissues and S. Chang provided funding for telemetry equipment. We thank S.N. Cove and M.K. Cove of Stuart Cove's Dive Bahamas for allowing access to shark dives and for provision of generous logistic support. We are indebted to A. Duncanson, T. Yamaguchi, H.N. Chin, G. Nicholls, J. Thompson, T. Parker and T.E. Van Leeuwen for logistic and field assistance, as well as to J. Brown, C.S. Chin and E.G. Parkinson for invaluable help with shark tagging activities.

References

Allee, W.C., Dickinson, J.C., 1954. Dominance and subordination in the smooth dogfish, *Mustelus canis* (Mitchell). Physiology and Zoology 27, 356-64.

Amorin, A.F., Arfelli, C.A., Fagundes, L., 1998. Pelagic elasmobranchs caught by longliners off southern Brazil during 1974-97: an overview. Marine and Freshwater Research 49**,** 621-632.

Bascompte, J., Melián, C.J., Sala, E., 2005. Interaction strength combinations and the overfishing of a marine food web. Proceedings of the National Academy of Sciences USA 102, 5443-5447.

Bonfil, R., 1994. Overview of world elasmobranch fisheries. Fisheries Technical Paper 341. FAO, Rome.

Bres, M., 1993. The behaviour of sharks. Reviews in Fish Biology and Fisheries 3, 133-159.

Brett, J.R., Groves, T.D.D., 1979. Physiological energetics, in: Hoar, W.S., Randall, D.J., Brett, J.R. (Eds.), Fish Physiology: bioenergetics and growth. Academic Press, New York, pp. 280-352.

Burns, G.L., Howard, P., 2003. When wildlife tourism goes wrong: a case study of stakeholder and management issues regarding Dingoes on Fraser Island, Australia. Tourism Management 24, 699–712.

Carwardine, M., Watterson, K., 2002. The Shark Watcher's Handbook. BBC Worldwide Ltd., London.

Castro, J.I., Woodley, C.M., Brudek, R.L., 1999. A preliminary evaluation of the status of shark species. FAO Fisheries Technical Paper 380. FAO, Rome.

Chapman, D.D., Pikitch, E.K., Babcock, E.A., Shivji, M.S., 2005. Marine reserve design and evaluation using automated acoustic telemetry: a case-study involving coral-reef associated sharks in the Mesoamerican Caribbean. Marine Technology Society Journal 39**,** 42-53.

Chapman, D.D., Pikitch, E.K., Babcock, E.A., Shivji, M.S., 2007. Deep-diving and diel changes in vertical habitat use by Caribbean reef sharks *Carcharhinus perezi.* Marine Ecology Progress Series 344, 271-275.

Clarke, S.C., McAllister, M.K., Milner-Gullan, E.J., Kirkwood, G.P., Michielssens

C.G.J., Agnew, D.J., Pikitch, E.K., Nakano, H., Shivji, M.S., 2006. Global estimates of shark catches using trade records from commercial markets. Ecology Letters 9, 1115–26.

Cole, R.G., 1994. Abundance, size structure, and diver-oriented behaviour of three large benthic carnivorous fishes in a marine reserve in northeastern New Zealand. Biological Conservation 70, 93-99.

Compagno, L.J.V., 1984. FAO species catalogue vol. 4. Sharks of the world. An annotated and illustrated catalogue of shark species known to date, Part 2. Carcharhiniformes. FAO Fish Synopsis 125.

Compagno, L.J.V., 2002. Carcharhinidae, in: Carpenter, K.E. (Ed.), The living marine resources of the Western Central Atlantic, Vol 1. Introduction, molluscs, crustaceans, hagfishes, sharks, batoid fishes, and chimaeras. FAO species identification guide for fisheries purposes and American Society of Ichthyologists and Herpetologists Special Publication No. 5. FAO, Rome.

Corcoran, M., 2006. The effects of supplemental feeding on the activity space and movement patterns of the southern stingray, Dasyatis americana, at Grand Cayman, Cayman Islands. M.Sc. Thesis, Nova Southeastern University, Fort Lauderdale, FL.

Economakis, A.E., Lobel, P.S., 1998. Aggregation behavior of the grey reef shark, *Carcharhinuc amblyrhynchos*, at Johnston Atoll, Central Pacific Ocean. Environmental Biology of Fishes 51, 129-139.

Field, A., 2005. Discovering statistics using SPSS, second ed. Sage Publications, London.

Froese, R., Pauly, D. (Eds.), 2009. FishBase. World Wide Web electronic publication. <http://www.fishbase.org> (accessed 18.09.09).

Gadig, O.B.F., Bezerra, M.A., Furtado-Neto, M.A.A., 1989. Nota sobre a biologia do tubarão *Carcharhinus perezi* (Poey, 1876) (Chondrichthyes: Carcharhinidae) do norte-nordeste do Brasil. Revista Nordestina de Biologia 11**,** 31-36.

Green, R.J., Higgenbottom, K., 2000. The effects of non-consumptive wildlife tourism on free-ranging wildlife: a review. Pacific Conservation Biology 6**,** 183-197.

Guttridge, T.L., Myrberg, A.A., Porcher, I.F., Sims, D.W., Krause, J., 2009. The role of learning in shark behaviour. Fish and Fisheries 10, 450-469.

Hawkins, J.P., Roberts, C.M., Van't Hof, T., De Meyer, K., Tratalos, J., Aldam, C., 1999. Effects of recreational scuba diving on Caribbean coral and fish communities. Conservation Biology 13, 888-897.

Hodgson, A.J., Marsh, H., Corkeron, P.J., 2004. Provisioning by tourists affects the behaviour but not the body condition of Mareeba rock-wallabies (*Petrogale mareeba*) Wildlife research 31**,** 451-456.

Hsu, M.J., Kaoi, C-C., Agoramoorthy, G., 2009. Interactions between visitors and Formosan macaques (Macaca cyclopis) at Shou-Shan Nature Park, Taiwan. American Journal of Primatology 71, 214–222.

Johnson, R., Kock, A., 2006. White shark cage diving – cause for concern?, in: Nel, D.C, Peshak, T. (Eds.), Finding a Balance: White Shark Conservation and Recreational Safety in the Inshore Waters of Cape Town, South Africa. WWF South African Report Series - 2006/Marine/001. pp. 40–59.

Laroche, R.K., Kock, A.A., Dill, L.M., Oosthuizen, W.H., 2007. Effects of provisioning ecotourism activity on the behaviour of white sharks *Carcharodon carcharias*. Marine Ecology Progress Series 338, 199-209.

Lucifora, L.O., Menni, R.C., Escalante, A.H., 2002. Reproductive ecology and abundance of the sand tiger shark, *Carcharias taurus*, from the southwestern Atlantic. ICES Journal of Marine Science 59, 553–561.

Meyer, C.G., Dale, J.J., Papastamatiou, Y.P., Whitney, N.M., Holland, K.N., 2009. Seasonal cycles and long-term trends in abundance and species composition of sharks associated with cage diving ecotourism activities in Hawaii. Environmental Conservation 36, 104-111.

Milazzo, M., Badalamenti, F., Vega Fernández, T., Chemello, R., 2005. Effects of fish feeding by snorkellers on the density and size distribution of fishes in a Mediterranean marine protected area. Marine Biology 146, 1213-1222.

Motta, F.S., Moura, R.L., Francini-Filho, R.B., Namora, R.C., 1999. Elasmobrânquios dos recifes Manoel Luís – MA. São Carlos, Resumos do XIII Encontro Brasileiro de Ictiologia.

Mumby, P.J., Dahlgren, C.P., Harborne, A.R., Kappel, C.V., Micheli, F., Brumbaugh, D.R., Holmes, K.E., Mendes, J.M., Broad, K., Sanchirico, J.N., Buch, K., Box, S., Stoffle, R.W., Gill, A.B., 2006. Fishing, Trophic Cascades, and the Process of Grazing on Coral Reefs. Science 311, 98-101.

Newsome, D., Lewis, A., Moncrieff, D., 2004. Impacts and Risks Associated with Developing, but Unsupervised, Stingray Tourism at Hamelin Bay, Western Australia. International Journal of Tourism Research 6, 305-323.

Newsome, D., Rodgers, K., 2008. To feed or not to feed: a contentious issue in wildlife tourism, in: Lunney, D., Munn, A., Meikle, W. (Eds.), Too Close for Comfort: Contentious Issues in Human-Wildlife Encounters. Royal Zoological Society of New South Wales, Mosman, pp. 255-270.

Orams, M.B., 2002. Feeding wildlife as a tourism attraction: a review of issues and impacts. Tourism Management 23, 281–293.

Peterson, B.J., Fry, B., 1987. Stable isotopes in ecosystem studies. Annual Review of Ecology and Systematics 18**,** 293-320.

Perrine, D., 1989. Reef fish feeding; amusement or nuisance? Sea Frontiers 35, 272–279.

Pigott, G.M., Tucker, B.W., 1990. Seafood: effects of technology on nutrition. Marcel Dekker Inc., New York.

Pikitch, E.K., Chapman, D.D., Babcock, E.A., Shivji, M.S., 2005. Habitat use and demographic population structure of elasmobranchs at a Caribbean atoll (Glover's Reef, Belieze). Marine Ecology Progress Series 302, 187-197.

Pratt, H.L., Carrier, J.C., 2001. A review of elasmobranch reproductive behavior with a case study on the nurse shark, *Ginglymostoma cirratum*. Environmental Biology of Fishes 60, 157–188.

Rosa, R.S., Mancini, P., Caldas, J.P., Graham, R.T., 2006. *Carcharhinus perezi*. IUCN Red List of Threatened Species. Version 2009.1. <http://www.iucnredlist.org> (accessed 12.09.09).

Schmid, T.H., Murru, F.L., 1994. Bioenergetics of the Bull Shark, *Carcharhinus leucas,* maintained in captivity. Zoo Biology 13, 177-185.

Semeniuk, C.A.D., Rothley, K.D., 2008. Costs of group-living for a normally solitary forager: effects of provisioning tourism on southern stingrays *Dasyatis americana*. Marine Ecology Progress Series 357**,** 271–282.

Semeniuk, C.A.D., Rothley, K.D., 2009. Hematological differences between stingrays at tourist and non-visited sites suggest physiological costs of wildlife tourism. Biological Conservation 142, 1818-1829.

Stevens, J.D., McLoughlin, K.J., 1991. Distribution, size and sex composition, reproductive biology and diet of sharks from Northern Australia. Australian Journal of Marine and Freshwater Research 42, 151-199.

Topelko, K.N., Dearden, P., 2005. The shark watching industry and its potential contribution to shark conservation. Journal of Ecotourism 4, 108-128.

Walpole, M. J., 2001. Feeding dragons in Komodo National Park: a tourism tool with conservation complications. Animal Conservation 4, 67-73.

Chapter 4.

High shark abundance is associated with reserve-like restoration of coral reef communities

Abstract

Apex predators such as sharks are thought to be important in structuring marine communities through direct predation and risk effects. The ecological role of sharks on reefs is still debated, due in part to a paucity of empirical studies. To ask whether high shark abundance can have cascading effects on coral reefs, and elucidate the underpinning mechanisms, I conducted experiments and observational studies across a gradient of shark abundance generated by daily provisioning for ecotourism. Teleost fish biomass was twice as high near the provisioning site than at more distant sites, owing to the higher abundance of piscivores. This pattern was not driven by attraction to bait but by fisher avoidance of shark-rich areas: owing to shark predation, fisher success at landing fish decreased with increasing shark abundance. Benthic community structure varied spatially, with less macroalgae and more turf algae at sites with more sharks. Shark risk effects may drive these patterns since herbivorous parrotfishes fed less selectively, consuming more macroalgae, under higher risk of predation. My study suggests that effective conservation of predators might deliver cascading, ecosystem-wide ecological benefits on coral reefs structure even in the absence of legislated place-based protection.

Introduction

Predators such as sharks are thought to play a critical role in structuring marine ecosystems (Heithaus et al. 2008, Baum & Worm 2009, Ferretti et al. 2010). They can affect prey through direct predation or non-lethal risk effects (e.g., habitat shifts, modified foraging behaviour) (Dill et al. 2003, Frid et al. 2008, Heithaus et al. 2008). Yet, sharks are rapidly disappearing from the world's oceans (Dulvy et al. 2008). Models suggest that the loss of sharks will release mesopredator populations from predation pressure, inducing cascades of destabilising trophic interactions down to the benthos (Okey et al. 2004, Bascompte et al. 2005, Bornatowski et al. 2014), but these theoretical effects appear to be species- and system-dependent (Stevens et al. 2000, Kitchell et al. 2002, Heithaus et al. 2008).

Empirical evidence of full trophic cascades induced by the presence or absence of sharks is limited. The widely cited example involving overfishing of large Atlantic sharks, leading to increased abundance of cownose rays *Rhinoptera bonasus*, and collapse of bay scallop *Agropecten irradians* (Myers et al. 2007), has been called into question (Grubbs et al. 2016). However, in Western Australia, tiger sharks *Galeocerdo cuvier* clearly induce risk-sensitive foraging in their herbivorous prey, sea turtles and dugongs *Dugong dugon*, that results in spatial variation in seagrass communities (Heithaus et al. 2007, Burkholder et al. 2013). On coral reefs, the relationships between the abundances of sharks, mesopredators, herbivores, and benthic communities are highly variable (table 4.1). This may be because top-down effects attenuate quickly in complex marine food webs with many interacting species and/or with high levels of omnivory (Bruno & O'Connor 2005), because many sharks function as mesopredators instead of apex predators (Roff et al. 2016), or because sharks in many locations are no longer abundant enough to trigger the trophic cascades they once initiated.

Previous efforts at understanding the ecological repercussions of shark declines on coral reefs have compared 'near-pristine' (i.e., protected or remote) and exploited sites (i.e., unprotected or near human populations) (e.g., table 4.1). Such comparisons prevent investigation of interactions between humans (fishers) and sharks. Yet, interactions among apex predators should be readily expected because most coral reefs are not protected (Mora et al. 2006), hence sharks and fishers overlap spatially. Humans and sharks also seek the same fish prey (i.e., high trophic-level, large piscivores (e.g., Graham et al. 2005), leading to potential competition. Competitive interactions among predators can modify, and sometimes strengthen, the magnitude of downward trophic cascades (Byrnes et al. 2006), making areas where shark and humans co-occur and interact the most likely locations to observe shark-induced trophic cascades.

Table 4.1 Documented relationships among the densities of sharks, teleost fishes and benthic communities on coral reefs. P/U: Protected vs unprotected, N/F: Near vs far from human populations, ↑: higher abundance (compared to unprotected or near site), ↓: lower abundance, ↔ : no effect or effect is unclear, NA: not assessed.

Site	Comparison	Sharks	Piscivorous fishes	Herbivorous fishes	Algae	Coral
Great Barrier Reef[a]	P/U	↑	↑	↔	NA	NA
Marshall Isl.[b]	N/F	↑	↑	↑ (small) ↓ (large)	↓	↑
Line Islands[c]	N/F	↑	↓	↔	↓	↑
NW Hawaii[d]	N/F	↑	↑	↔	NA	NA
NE Pacific[e]	P/U	↑	↓	↑ (10 m) ↔ (20m)	↔ (10m) ↓ (20 m)	↔
NW Australia[f]	P/U	↑	↓	↑	↔	↔

[a] Rizzari *et al*. 2014, [b] Houk & Musburger 2013, [c] Sandin *et al*. 2008, [d] Friedlander & DeMartini 2002, [e] Friedlander *et al*. 2013, [f] Ruppert *et al*. 2013

Here, I ask whether a high abundance of sharks on coral reefs can have cascading ecological repercussions. I used a natural experiment in which daily provisioning of Caribbean reef sharks (*Carcharhinus perezi*) for diving tourism, occurring at an unprotected coral reef site in the Bahamas, has created a bi-directional gradient of declining shark abundance away from this site. I combined visual surveys of fish abundance and algal community structure to document variation in assemblages in relation to changing shark abundance, with behavioural observations and experiments to elucidate potential underpinning mechanisms. I predicted that if Caribbean reef sharks act as apex predators, patterns of abundance with distance from the provisioning site should alternate in direction from one trophic level to the one below. Thus, with declining shark abundance, I expected an increased abundance of mesopredators and a decrease in herbivorous fish numbers (e.g., Ruppert et al. 2013). Lower herbivory should coincide with increased macroalgal cover (Williams & Polunin 2001, Burkepile et al. 2013), with concomitant declines in turf (Williams & Polunin 2001) and coral cover (Lirman 2001).

Material and methods

This work was conducted under a Marine Scientific Research Permit (MAF/FIS/17) issued by the Department of Marine Resources, Government of The Bahamas. All methods were carried out in accordance with the regulations of the Canadian Council on Animal Care, and all experimental protocols were approved by the Simon Fraser University Animal Care Committee (permit no. 828B-07).

Study sites and study species

This study was conducted between December 2008 and March 2009 in New Providence, Bahamas, (25°25'N, 78°35'W) at 21 study sites distributed along 4 km of coral reef wall forming the eastern edge of the Tongue of the Ocean trench. The central site was located 2.6 km off the south coast of the island where Caribbean reef sharks *Carcharhinus perezi* have been fed almost daily since 1986 as a dive tourism attraction. Shark feeding dives are conducted every afternoon between 14:30 and 16:00, during which 10–16 pieces of fish (usually grouper heads and carcasses) are taken to the feeding site in a metal bait box, without prior chumming, and fed to sharks piece by piece using a metal feeding spear. Shark feeding typically lasts 19–24 min and can attract 7-55 sharks per event, depending on the season (Maljković & Côté 2011).

Few sharks obtain any bait during provisioning events and daily energetic requirements are unlikely be met by bait consumption, even for the most successful sharks (Maljković & Côté 2011). The majority of sharks must therefore hunt wild prey in the surrounding area to meet their daily energy demands. Success at taking bait does not affect residency patterns or foraging ranges (Maljković & Côté 2011). Caribbean reef sharks in this area show some site fidelity but they can also travel up to 20 km per day, easily encompassing the whole of my study area (Maljković & Côté 2011).

Fish surveys and habitat assessment

I surveyed fish communities in the morning at the shark feeding site and at 200 m intervals, up to 2 km, in both directions along the reef wall. At each of these 21 sites, I surveyed two belt transects (30 m x 4 m) at each of three depths (reef crest [11 – 21 m], 17 m and 25 m). Where the depth of the reef crest exceeded the depth of the 17 m transects, replicate transects were conducted on the reef crest to maintain sample sizes. I recorded the number of each fish species and total length (TL) of each fish ≥ 10 cm (visually estimated to the nearest cm). Transects at the same depth within a site were separated by 50 m.

To determine whether attraction to the bait during shark feeding influenced fish community structure at the shark feeding site, I attended 23 afternoon shark feeds over three months and recorded the fish species that came within 5 m of the bait box. Four species were recorded: *Carangoides ruber*, *Mycteroperca bonaci*, *Ocyurus chrysurus* and *Elagatis bipinnulata*.

I recorded benthic composition (% cover of sand, coral rubble, live hard coral, dead coral, soft coral, sponges and algae; assessed visually) in 1 m^2 quadrats placed at 5 m intervals along each fish transect (total: 36 m^2 per site). I also took six rugosity measurements per transect, using a 3-m long fine-link chain laid at 5 m intervals across each transect so as to conform to reef topography. Rugosity was calculated as the ratio of chain length to the linear distance between the ends of the chain conforming to the reef surface. Larger values indicate greater structural complexity.

In addition, I recorded in each quadrat the percent cover of three algal groups, each of which plays an important ecological role. Turf algae, defined as algal growth of ≤ 1 cm in height, are an important food resource for herbivorous reef fish (Randall 1967); macroalgae, i.e. visible fleshy algae > 1 cm in height, are of concern in the context of competition with corals (Lirman 2001), phase shifts and alternative states in coral reef communities (McManus & Polsenberg 2004); and crustose coralline algae (CCA) are structurally important as stabilising agents, which promote accretion of carbonates on reefs and facilitate settlement of coral recruits (Heyward & Negri 1999, Mallela 2013).

Shark counts

I estimated the relative density of Caribbean reef sharks at each site by recording the number of individual sharks present during six 10-min point counts, conducted in the morning to avoid the temporary aggregation effect of afternoon provisioning. Shark counts were conducted only when visibility was at least 20 m. Large point counts have been shown to yield accurate estimates of abundance (McCauley et al. 2012). All counts were performed by a single observer (AM) who remained stationary above the reef, which is less likely to elicit attraction or avoidance by sharks (Cubero-Pardo et al. 2011). I performed no more than one count per day per site, and the six counts at each site were distributed haphazardly over three months. All sharks were either externally tagged with individually colour-coded dart tags (as part of another study), or identifiable owing to unique markings or jaw/fin deformations (Maljković & Côté 2011), which prevented double-counting. Although sharks did exhibit anticipatory behaviour in the afternoon near the start of provisioning events, they showed no sign of attraction to divers in the morning, when counts were performed (AM, personal observations).

Distribution of fishing boats and fisher success

On each of 60 days across the study period, I spent one hour documenting the position of fishing boats (subsistence and recreational) across the study area using a hand-held GPS. Observations were made either mid-morning (10:00 – 11:00) or late afternoon (16:00 – 18:00) from a 3.5 m skiff travelling at slow speed during calm weather (Beaufort sea state ≤ 2). These observations captured the end of morning fishing activity and most evening fishing activity; little fishing occurs mid-day (AM, personal observations).

To estimate fishing success, I employed a local fisher to catch fish using hook and line – the most common fishing method in this area – at the shark feeding site and at 400 m intervals, up to 2 km, in both directions along the edge of the trench. Fishing was conducted using a weighted 30 lb test monofilament hand line with an 8/0 tuna circle hook baited with pieces of snapper (*Lutjanus* sp.). At each site, the fisher attempted to land 10 fish. When a shark took a hooked fish, the fisher stopped fishing that site on that day and moved at least 1 km away (within the study area) to continue fishing. The fate of each hooked fish was recorded as landed or taken by a shark (determined by hook loss or visual confirmation). If the outcome was ambiguous (e.g., when the fish might have escaped the hook), an additional fish was hooked. Using a single fisher to fish at all sites removed potential bias associated with variation in fisher ability.

Observations of parrotfish herbivory

I conducted focal observations of foraging redband parrotfish (*Sparisoma aurofrenatus*) at three sites: the provisioning site, 500 m and 1000 m away. This species was selected because it was abundant, has previously been recorded in the stomach contents of *C. perezi* (A. Maljković, unpublished data), and is a generalist herbivore that consumes turf and fleshy macroalgae (Catano et al. 2014). Observations were undertaken between 09:00 and 16:30, at or near the reef crest (depth range: 12 – 18 m) by an observer on SCUBA. No observations were made during shark provisioning events. Focal fish were all initial-phase individuals and selected on a ‘first seen’ basis. Each individual was observed for 10 min with the diver remaining 2-3 m away.

For each parrotfish I recorded total length (visual estimate), the number of bites taken, the bite target to the lowest possible taxon, and the length of each foraging bout. A foraging bout was considered to be over if the fish ceased biting the substrate for more than 30 sec, took shelter in the reef, or swam ≥ 5 m away from its previous foraging area. No more than two parrotfish were observed on any single dive. Although each fish was not individually recognizable, the high density of this species made repeat observations of the same individuals very unlikely.

Statistical analysis

Fish length estimates were converted to weight using the allometric length-weight conversion: $W = aSL^b$, where W is weight in grams, SL is standard length in mm, and a and b are constants (Bohnsack & Harper 1988, Froese & Pauly 2011). Total length was converted to standard length using published conversion factors (Froese & Pauly 2011).

When length-weight information was not available for a species, the parameters for similar-bodied congeners were used. Weight data were transformed into biomass estimates and pooled by trophic guild (table S4.1 in Appendix B) based on published diet information (Randall 1967). Although reef sharks are often considered to be mesopredators (Roff et al. 2016), at our study site they are the largest common fish species and they have enriched nitrogen isotope signatures compared to teleost piscivores (Maljković & Côté 2011, and unpublished data]. They therefore appear to function as apex predators. The biomass of the four teleost species attracted to shark feed bait was calculated separately.

One-way analyses of variance (ANOVAs) were used to compare overall fish biomass, and biomass per trophic guild, among sites, with Dunnett's post-hoc tests performed using fish biomass at the shark feeding site as the control means.

Coordinates of fishing boat sightings were downloaded to ArcMap 9.1 (ESRI, Redlands, USA) and geo-referenced against the position of the shark feeding site. Boat sightings were grouped into 200 m distance bins relative to the shark feeding site, allowing the total number of boat sightings per distance bin to be calculated.

Habitat variables were averaged across quadrats within each site. Because several habitat variables were correlated (correlation coefficients: 0.52-0.91), a principal components analysis (PCA) was used to produce four uncorrelated factors. All four factors were then included in manual backwards stepwise multiple regressions to explain variation in fish biomass. Prior to analysis, all cover percentages were arcsine-root transformed.

The cover of each algal group was calculated as a percentage of the total algal cover per site to remove the effects of benthic habitat heterogeneity. A one-way ANOVA was used to compare the cover of each algal group among sites, with Dunnett's post-hoc tests using algal cover at the shark feeding site as the control means.

To test for differences among sites in herbivorous fish community structure, which could drive variation in algal community structure, I used an analysis of similarity (ANOSIM) conducted using PRIMER (v 6.0, Clarke & Gorley 2006). Herbivore density was summed by species across the six transects at each site and data were square-root transformed. Each site was considered as a sample, and pairs of sites were compared to produce Bray-Curtis similarity coefficients, which were then used in a non-parametric permutation ANOSIM (n = 999 permutations). The R statistic generated by the ANOSIM usually ranges between 0 (herbivore community structure is as similar within as between sites) and 1 (herbivore communities are more similar within sites than between sites).

The lengths of parrotfish observed, bite rates, length of feeding bouts, total foraging time, total number of algal types targeted and proportion of bites on macroalgae were compared among sites using one-way analyses of variance (ANOVAs). Bite rates were log-transformed and proportions were arcsine-transformed prior to analysis. When there was significant variation among sites, I conducted Tukey-Kramer post-hoc tests to account for the unbalanced samples sizes across groups. All statistical tests were two-tailed and data were checked for normality and heteroscedasticity using residual plots. Data were analysed using SPSS 23.0.

Results

Shark and teleost distribution

Reef shark abundance was highest within 200 m of the provisioning site (figure 4.1a). Shark abundance declined rapidly and dropped to near zero 1 to 1.4 km away from the provisioning site (figure 4.1a).

The overall biomass of reef fish (excluding sharks) mirrored the pattern of shark abundance (n = 21, r = 0.95, $P < 0.0001$; figure 4.1b). Fish biomass at the provisioning site was approximately twice that observed at sites 2 km away (figure 4.1b; table 4.2). Excluding the four piscivorous species that were attracted to the bait during provisioning did not alter the results (figure 4.1b; table 4.2). The abundance of both large and smaller piscivores covaried with shark abundance (n = 21, $r > 0.87$, $P < 0.001$ in both cases; table S4.2), but the abundance of low-level carnivores and herbivorous fish did not (n = 21, $r < 0.30$, $P > 0.19$ in both cases). There was no significant variation across sites in herbivorous fish biomass (table 4.2) or in herbivorous fish community structure (Analysis of Similarity: R = 0.12, P = 0.07).

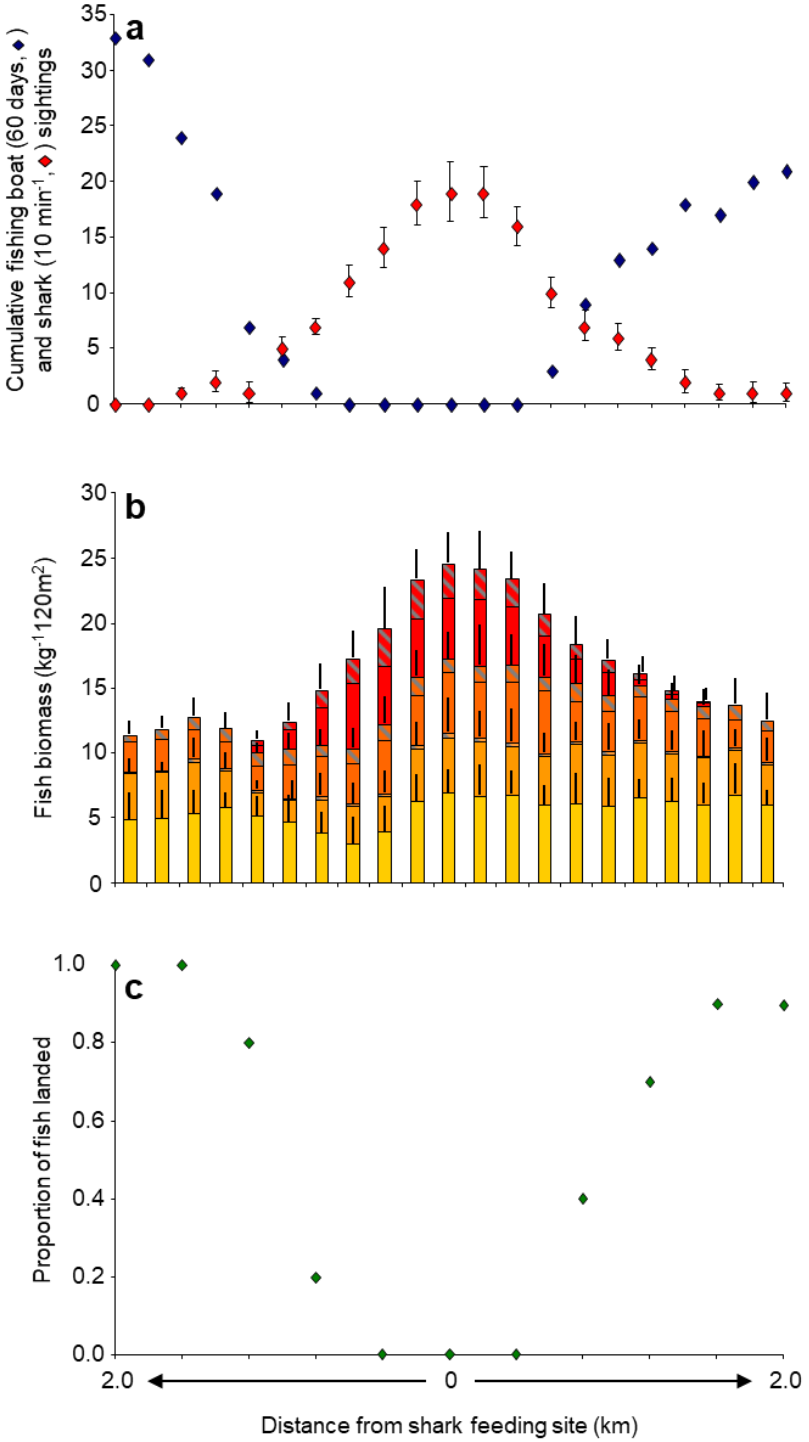


Figure 4.1 Variation in fish communities, fishing effort and fishing success. (a) Shark abundance (◆; mean ± SE) and cumulative fishing boat sightings over 60 days (◆), (b) biomass of reef-associated fish guilds (means + SE) (yellow: herbivores; light orange: low-level carnivores; dark orange: piscivores < 50 cm TL; red: piscivores > 50 cm TL; hatched: bait-attracted species, and (c) proportion of hooked fish landed, at varying distances from a shark feeding site.

Benthic composition

The cover of turf algae (n = 18, r = 0.89, $P < 0.0001$) and crustose coralline algae (CCA) (n = 18, r = 0.92, $P < 0.0001$) increased with increasing shark abundance, while macroalgal cover showed the opposite trend (n = 18, r = -0.92, $P < 0.0001$) (figure 4.2; table S4.3 in Appendix B). Near the provisioning site, algal cover was composed mainly of turf algae (~60%) and CCA (25%) with little macroalgae (10%). In contrast, at sites 2 km away, macroalgae dominated the benthos (~65%), with smaller contributions from turf algae (18%) and CCA (18%) (figure 4.2). Live coral cover ranged from 17.4 % (± 4.1%, SD) to 26.5% (± 5.34%) across sites, but variation among sites was not statistically significant (table S4.3).

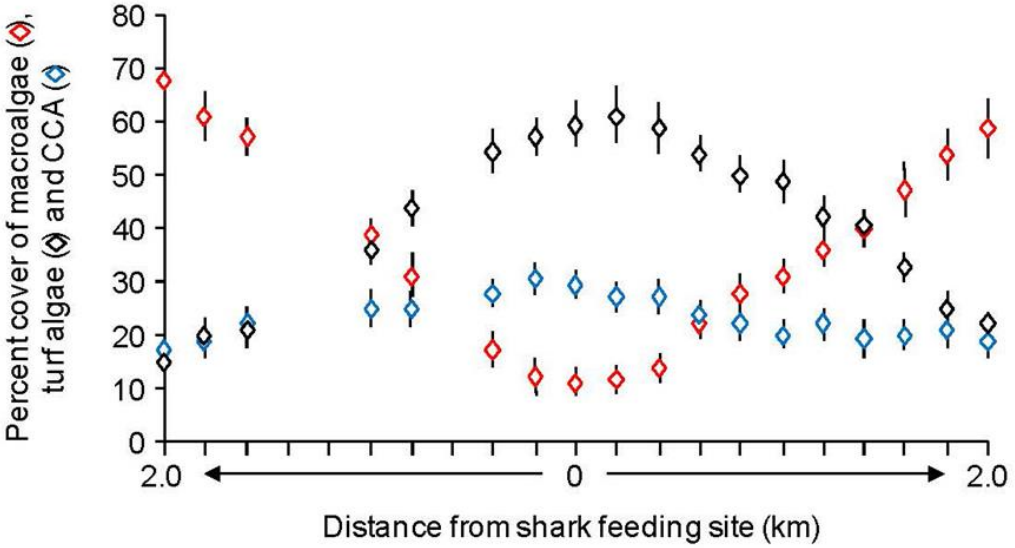


Figure 4.2 Algal composition in relation to distance from the shark feeding site. Cover of macroalgae (◇), turf algae (◇) and crustose coralline algae (CCA; ◇) as a percentage of the total algal cover per site (mean ± SE) at varying distances from a shark feeding site. Gaps in the dataset represent sites where the substratum was primarily sand, and therefore not comparable to the other sites. Turf algae cover varied significantly among sites ($F_{20,105}$ = 4.92, P <0.0001), as did macroalgal cover ($F_{20,105}$ = 6.23, P <0.0001); the cover of crustose coralline algae was less variable ($F_{20,105}$ = 1.62, P = 0.06).

The Principal Components Analysis generated four uncorrelated habitat factors. Factor 1 accounted for 62% of the variation in habitat characteristics and represented a gradient of increasing hard coral cover and rugosity, with decreasing sand cover. Factor 2 accounted for 22% of the variation and represented a gradient of increasing algal cover. The two remaining factors, increasing dead coral/soft coral cover and increasing sponge/decreasing coral rubble cover, accounted for the final 16% of the variability in habitat. None of the multivariate factors describing benthic habitat variability explained a significant amount of variance in fish biomass among sites ($P > 0.05$ in all cases).

Table 4.2 Results of analyses of variance comparing biomass of reef fish of various trophic groups among the 21 coral reef sites surveyed. Species in each trophic guild are listed in S4.1 Table. Bait-attracted species include the four fish species that came within 5 m of the bait box during shark feeds: Carangoides ruber, Mycteroperca bonaci, Ocyurus chrysurus and Elagatis bipinnulata.

Trophic group	***df***	***F***	***P***
Herbivores	20,105	0.98	0.49
Low-level carnivores	20,105	1.21	0.26
Piscivores < 50 cm TL	20,105	1.44	0.12
Piscivores > 50 cm TL	20,105	5.7	< 0.0001
Bait-attracted species	20,105	1.51	0.09
Total	20,105	3.7	< 0.0001
Total excluding bait-attracted species	20,105	3.2	< 0.0001

Parrotfish foraging

Parrotfish bite rates on the substrate varied significantly among sites (one-way ANOVA: $F_{2,65} = 40.27$, $P < 0.0001$, Tukey-Kramer post-hoc tests: $P < 0.05$ in all cases), with foraging rates near the provisioning site ~70% higher than at the most distant site (figure 4.3a). Parrotfish also foraged in significantly shorter bouts near the provisioning site than further away (ANOVA: $F_{2,65} = 91.47$, $P < 0.0001$, Tukey-Kramer post-hoc tests: $P < 0.05$ in all cases; figure 4.3b). Total time spent foraging varied among sites (ANOVA: $F_{2,65} = 32.79$, $P < 0.0001$), with parrotfish near the provisioning site spending half as much time

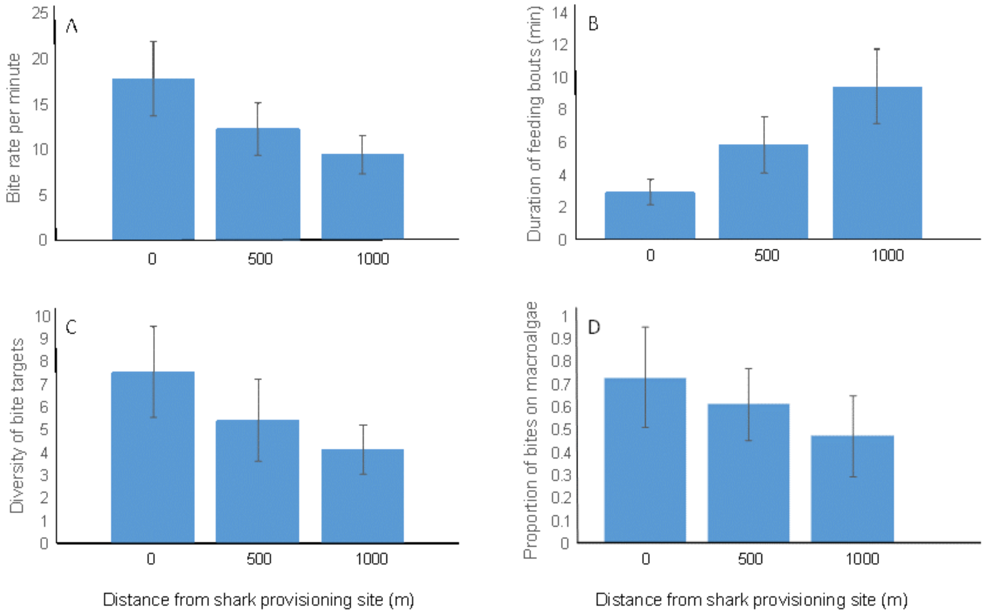


Figure 4.3 Parrotfish foraging under variable risk of predation. (A) Bite rate, (B) duration of feeding bouts, (C) diversity of algal targets taken, and (D) proportion of total bites taken on macroalgae, by redband parrotfish *Sparisoma aurofrenatum* at varying distances from a shark provisioning site. The density of predators (sharks and large piscivorous teleost fishes) at these distances is shown in Figure 1. Means are shown ± 1 SD. In all panels, at distance = 0, *n* = 29; at 500 m, *n* = 21; at 1000 m, *n* = 19 parrotfish.

feeding (mean ± SD: 4.86 ± 1.36 min 10 min^{-1}) than parrotfish at sites further away (500 m: 8.75 ± 2.72 min 10 min^{-1}, 1000 m: 9.67 ± 2.54 min 10 min^{-1}, Tukey-Kramer post-hoc tests, both $P < 0.05$). There was no difference in total parrotfish foraging time between sites 500 m and 1000 m from the provisioning sites (Tukey-Kramer post-hoc test, $P > 0.05$). Parrotfish consumed 15 algal types, including turf algae and the fleshy macroalgae *Lobophora variegata*, *Halimeda opuntia*, *Dictyota pulchellagata*, *Microdictyon marinum* and *Sargassum hystrix*. They targeted significantly more algal types at the provisioning site than at the two sites further away (ANOVA: $F_{2,65} = 23.13$, $P < 0.0001$, Tukey-Kramer post-hoc tests, $P < 0.05$ in both cases; figure 4.3c). The number of algal types consumed did not differ between the two distant sites (Tukey-Kramer post-hoc test, $P > 0.05$). Parrotfish also took a significantly larger proportion of bites on macroalgae at the provisioning site than at the site 1 km away (ANOVA: $F_{2,65}$ =

10.40, $P < 0.0001$; Tukey-Kramer post-hoc test, $P < 0.05$; figure 4.3d). There was no difference in mean length of focal parrotfish across sites (ANOVA: $F_{2,65} = 2.26$, $P = 0.11$).

Fisher distribution and landing success

Over 60 days, I recorded no fishing boats within 400 m of the provisioning site (figure 1a). Boat sightings increased gradually beyond this distance (figure 4.1a). The frequency of boat sightings covaried negatively with shark abundance ($n = 21$, $r = -0.82$, $P < 0.0001$).

During experimental hook-and-lining that simulated the local artisanal fishing method, the proportion of hooked fishes that were successfully landed declined with increasing shark abundance ($n = 11$, $r = -0.94$, $P < 0.0001$; figure 4.1c). Landing success fell to zero within 400 m of the provisioning site (figure 4.1c).

Discussion

Using spatial variation in the abundance of reef sharks generated by tourism-related provisioning, experimental fishing, and behavioural observations, I found that high shark abundance is associated with changes to coral reef communities mediated through behavioural changes by both fishers and herbivorous fishes. My study provides a compelling case study suggesting that behavioural interactions with competitors (fishers) and prey (herbivorous fishes) have the potential to drive the ecological effects of sharks in marine ecosystems.

Densities of Caribbean reef sharks (*Carcharhinus perezi*) were locally elevated off New Providence. Peak shark abundance, which occurred within 200 m of the provisioning site, corresponded to a biomass of ~4.1 t ha^{-1} – an estimate that places my study site at the high end of the global range of estimates of shark biomass on coral reefs (table 4.3). However, this effect was spatially constrained since shark abundance dropped to near zero ~1 km away from the provisioning site. This pattern is similar to that observed for blacktip reef sharks at a provisioning site in French Polynesia (Kiszka

Table 4.3 Estimates of mean shark biomass on some of the world's most 'pristine' coral reefs.

Location	Shark biomass t ha^{-1}	Source
Darwin and Wolf Islands, Galápagos	12.4	Salinas de León *et al*. 2016
Kingman Island (Line Isl)	3.29	Sandin *et al*. 2008
Cuba	3.15	Valdivia *et al*. 2017
Fakarava Atoll, French Polynesia	0.55 – 1.30	Mourier *et al*. 2016
NW Hawaiian Islands	0.33	Friedlander & DeMartini 2002
Great Barrier Reef (no entry zone)	0.15	Robbins *et al.* 2006
Cocos Island	0.09	Robbins *et al*. 2006
Aldabra Atoll, Seychelles	0.014	Stevens 1984
New Providence, The Bahamas	4.1	This study

et al. 2016). Several factors might contribute to high local abundance of sharks. At a national scale, government policy discouraging long-line fishing since 1986, and a prohibition of commercial shark fishing since 2011 (M.T. Braynen, Bahamas Department of Marine Resources, personal communication), might have prevented elasmobranch declines seen globally. Indeed, The Bahamas are now the last stronghold of significant shark numbers in the Caribbean region (Ward-Paige et al. 2010). At a more local scale, it is difficult to disentangle the natural pattern of shark distribution from the effect of long-term, tourism-related shark provisioning. Prior to shark feeding tourism, Caribbean reef sharks were often encountered (~ 8-10 per dive) in this area, making it a natural location for shark feeding activities (S. Cove, personal communication). Since the advent of feeding, however, shark numbers during non-provisioning times (i.e., morning) have increased (~20 per dive), suggesting a permanent aggregating effect of provisioning. Still, shark numbers during provisioning are greater than during non-provisioning times, likely because sharks are drawn from the immediate surrounding area (Gallagher et al. 2015).

Whatever the cause of high shark abundance, the gradient of shark abundance extending in both directions from the provisioning site was associated with marked variation in teleost abundance and composition. Teleost biomass was highest near the provisioning site. This pattern was driven largely by the higher biomass of large piscivores – the primary targets of Bahamian fishers – near the shark feeding site. The abundances of low-level carnivores and herbivores did not vary across sites. These results are not likely to be a consequence of provisioning per se because (1) provisioning provides only a short-lived (once a day for ~20 min) and very limited (up to 16 fish pieces, with no chumming) nutritional input, (2) sharks invariably sequester all of the whole food pieces (AM, personal observations), leaving little for teleosts, and (3) only four teleost species (two piscivores, two low-level carnivores) occasionally scavenged small pieces of detached flesh, and the spatial pattern of teleost biomass remained the same when these four species were omitted. The fact that patterns of abundance with distance from the provisioning site did not alternate in direction from one trophic level to the one below echoes previous studies that found weak or no linkages between populations of high-level predators and of primary consumers (table 4.1). Patterns of fish abundance and community structure are often partly driven by variation in habitat composition and complexity (e.g., Friedlander et al. 2003). However, none of the multivariate factors describing benthic habitat variation explained a significant amount of variance in fish biomass among sites.

At first glance, high shark abundance near the provisioning site appears to have released rather than depressed mesopredators (i.e., piscivorous fishes). Such a counter-intuitive linkage has previously been observed in no-entry areas of the Great Barrier Reef (Rizzari et al. 2014), on an isolated atoll of the Marshall Islands (Houk & Musburger 2013), and on remote reefs of the Northwest Hawaiian Islands (Friedlander & DeMartini 2002) (table 4.1), i.e. areas where fishing pressure is low owing to the protective effects of no-take legislation or isolation.

Although the reefs of New Providence are neither protected nor remote, reduced fishing pressure might still explain the abundance of piscivorous fishes around the provisioning site. Fishing boats were absent within 400 m of the provisioning site, despite the high density of target species, but boat sightings increased gradually beyond this distance, as shark abundance declined. I suggest that this pattern might reflect direct competition between sharks and fishers. Indeed, fisher landing success was highest where sharks were least abundant, and vice-versa. I believe that fishers might be adjusting their distribution in relation to the likelihood of landing hooked fish, trading off a higher abundance of target species (where there are more sharks) for a higher certainty of landing success (where there are fewer sharks). The result is a *de facto*, 1-km-long fisher 'exclusion' zone, centred on the shark provisioning site

I also found significant differences in benthic composition among sites, especially for primary producers. Near the provisioning site, the substrate was covered mainly by turf algae, while further away, fleshy macroalgae dominated. These differences occurred in the absence of significant variation across sites in herbivorous fish biomass, herbivorous fish community structure or density of herbivorous urchins (figure S4.1). I also saw no evidence of a possible matching gradient of nutrient inputs along the 4-km stretch of coast (e.g., in the form of point sources of sewage or agricultural run-off) (personal observations), which could account for the variable growth of macroalgae. Higher coral cover near the provisioning site could concentrate the activity of herbivorous fishes into a smaller foraging area, leading to higher grazing pressure without higher herbivore numbers (Williams et al. 2001, Sandin et al. 2008). However, live coral cover did not vary significantly across sites. Thus, neither grazer numbers nor identity explains observed differences in primary producer communities.

An alternative explanation for the low cover of macroalgae found around the provisioning site is that abundant sharks and large piscivores alter the feeding behaviour of herbivorous fish through intimidation. Predation risk can reduce the opportunity for selective foraging by terrestrial herbivores, resulting in trophic cascades that ultimately influence habitat structure (Ripple et al. 2001). The foraging behaviour of many marine vertebrates is also strongly influenced by risk (Dill et al. 2003, Heithaus et al. 2008, Madin et al. 2016). Similarly, I found that parrotfish near the provisioning site, i.e. with the highest abundance of sharks and large piscivorous fishes, spent less time foraging, had the shortest feeding bouts but the highest biting rates, targeted more algal types, and directed relatively more bites at macroalgae than parrotfish at more distant, presumably safer sites. Such behavioural shifts and trade-offs have been observed in herbivorous fishes foraging under risk of predation (Catano et al. 2014, Rizzari et al.

2014, Catano et al. 2016). At my sites, more indiscriminate feeding and the inclusion of a broader range of less palatable algae, including many macroalgae (Carpenter 1986), in the diet of herbivorous fishes perceiving a high risk of predation coincide with variation in substrate composition.

In New Providence, locally high shark densities appeared to have far-ranging repercussions onto the substrate. The mechanisms underpinning this unconventional cascade of effects seem largely behaviourally mediated. High overall reef fish biomass and a fish community structure biased towards large piscivores appear to result from competitive exclusion of fishers by sharks because fishing success is poor when sharks are abundant. Moreover, the reduction in macroalgae near the provisioning site reflects altered foraging by herbivores under risk of predation by sharks and large piscivores. My results therefore provide evidence that reef sharks can drive trophic cascades that affect benthic communities on coral reefs (Roff et al. 2016). The generality of my current results, however, remains unclear. My study needs to be replicated at other sites where shark densities are naturally high, sharks are protected but their prey are not (e.g., in shark sanctuaries) or where shark provisioning occurs. Such sites offer the potential for humans and sharks to compete for prey, which I surmise is a key trigger for the unconventional ecological cascade we have uncovered. My results are also correlational, but the ideal experimental design, e.g. a Before-After-Control-Impact study starting before shark diving is established, would be virtually impossible to achieve. The advantage of using a well-established site is that the long-term ecological effects of locally high shark densities have become evident.

Because risk effects have been identified in diverse marine settings (Madin et al. 2016) and have been shown experimentally to be capable of cascading to primary producer communities (Burkholder et al. 2013), there is reason to believe that effects similar to those we identified are not uncommon. If my findings are generally applicable, they have implications for coral reef management. For example, local enhancement of sharks following the establishment of provisioning or shark-protection legislation might lead to a redistribution of fishers. Fishers may reap benefits by fishing at the periphery of areas with high shark densities, which they appear to do (figure 4.1a), in a manner similar to ‘fishing the line’ near MPAs to capture spill-over of preferred species (Kellner et al. 2007). This does mean that areas that are more devoid of sharks might experience increased fishing effort, with concomitant ecological consequences (Graham et al. 2005). My results also suggest that the current narrow emphasis on restoring herbivores to reduce macroalgal domination and increase reef resilience in the Caribbean (Hughes et al. 2007, Mumby & Steneck 2008, Jackson et al. 2014) may be too limited. Reductions in macroalgal cover might be achieved without increasing herbivore numbers if healthy predator populations are present to intimidate fish grazers into feeding indiscriminately. Finally, my results suggest that locally high shark abundance might generate a reserve-like restoration of fish communities and benthic habitat structure in the absence of legislated place-based protection. Shark provisioning, or any other method that successfully enhances local abundance of high-trophic-level predators, could be a novel tool to contribute to coral reef conservation.

Acknowledgements.

We thank Stuart and Michelle Cove for logistical support, T. Parker, H.N. Chin and T. van Leeuwen for field assistance, and N. K. Dulvy, J. A. Gill, M. Gore and D. D. Chapman for advice and comments. This study was supported by the Abbott–Fretwell Graduate Fellowship in Fisheries Biology and the Sidney Hogg Memorial Scholarship to A.M., and a Discovery grant of the Natural Science and Engineering Research Council of Canada to I.M.C.

References

Bascompte J, Mellán CJ, Sala E (2005) Interaction strength combinations and the overfishing of a marine food web. Proc Natl Acad Sci U.S.A. 102: 5443–5447

Baum JK, Worm B (2009) Cascading top-down effects of changing oceanic predator abundances. J Anim Ecol 78: 699–714

Bohnsack JA, Harper DE (1988) Length-Weight Relationships of Selected Marine Reef Fishes from the Southeastern United States and the Caribbean. NOAA Technical Report.

Bornatowski H, Navia AF, Braga RR, Abilhoa V, Maia Corrêa MF (2014) Ecological importance of sharks and rays in a structural foodweb analysis in southern Brazil. ICES J Mar Sci 71: 1586–1592

Bruno JF, O'Connor MI (2005) Cascading effects of predator diversity and omnivory in a marine food web. Ecol Lett 8: 1048–1056

Burkepile DE, Allgeier JE, Shantz AA, Pritchard CE, Lemoine NP, Bhatti LH, Layman CA (2013) Nutrient supply from fishes facilitates macroalgae and suppresses corals in a Caribbean coral reef ecosystem. Scient Rep 3: 1493

Burkholder DA, Heithaus MR, Fourqurean JW, Wirsing A, Dill LM (2013) Patterns of top-down control in a seagrass ecosystem: could a roving apex predator induce a behaviour-mediated trophic cascade? J Anim Ecol 82: 1192–1202

Byrnes J, Stachowicz JJ, Hultgren KM, Hughes AR, Olyarnik SV, Thornber CS (2006) Predator diversity strengthens trophic cascades in kelp forests by modifying herbivore behaviour. Ecol Lett 9: 61–71

Carpenter RC (1986) Partitioning herbivory and its effects on coral reef algalcommunities. Ecol Monogr 56: 345–364

Catano LB, Shantz AA, Burkepile DE (2014) Predation risk, competition, and territorial damselfishes as drivers of herbivore foraging on Caribbean coral reefs. Mar EcolProg Ser 511: 193–207

Catano LB, Rojas MC, Malossi RJ, Peters JR, Heithaus MR, Fourqurean JW, Burkepile DE (2016) Reefscapes of fear: predation risk and reef heterogeneity interact to shape herbivore foraging behaviour. J Anim Ecol 85: 146–156

Clarke KR, Gorley RN (2006) PRIMER V6: User manual/tutorial. Plymouth: PRIMER-E.

Cubero-Pardo P, Herrón P, González-Pérez F (2011) Shark reactions to scuba divers in two marine protected areas of the Eastern Tropical Pacific. Aquat Conserv Mar Freshw Ecosyst 21: 239-246

Dill LM, Heithaus MR, Walters CJ (2003) Behaviorally-mediated indirect interactions in marine communities and their conservation implications. Ecology 84: 1151–1157

Dulvy NK, Baum JK, Clarke S, Compagno LJV, Cortés E, Domingo A, Fordham S, Fowler S, Francis MP, Gibson C, Martínez J, Musick JA, Soldo A, Stevens JD, Valenti S (2008) You can swim but you can't hide: the global status of oceanic pelagic sharks and rays. Aquat Conserv Mar Freshw Ecosyst 18: 459–482

Ferretti F, Worm B, Britten GL, Heithaus MR, Lotze HK (2010) Patterns and ecosystem consequences of shark declines in the ocean. Ecol Lett 13: 1055–1071

Frid A, Baker GG, Dill LM (2008) Do shark declines create fear-released systems? Oikos 117: 191–201

Friedlander AM, DeMartini EE (2002) Contrasts in density, size, and biomass of reef fishes between the northwestern and the main Hawaiian Islands: the effects of fishing down apex predators. Mar Ecol Prog Ser 230: 253–264

Friedlander AM, Brown EK, Jokiel PL, Smith WR, Rodgers KS (2003) Effects of habitat, wave exposure, and marine protected area status on coral reef fish assemblages in the Hawaiian archipelago. Coral Reefs 22: 291–305

Friedlander AM, Ballesteros E, Beets J, Berkenpas E, Gaymer CF, Gorny M, Sala E (2013) Effects of isolation and fishing on the marine ecosystems of Easter Island and Salas y Gómez, Chile. Aquatic Conserv Mar Freshw Ecosyst 23: 515–531

Froese R, Pauly D (2011) FishBase. www.fishbase.org (accessed 3-22 January 2011)

Gallagher AJ, Vianna GMS, Papastamatiou YP, Macdonald C, Guttridge TL, Hammerschlag N (2015) Biological effects, conservation potential, and research priorities of shark diving tourism. Biol Conserv 184: 365–379

Graham NAJ, Dulvy NK, Jennings S, Polunin NVC (2005) Size-spectra as indicators of the effects of fishing on coral reef fish assemblages. Coral Reefs 24: 118–124

Grubbs RD, Carlson JK, Romine JG, Curtis TH, McElroy WD, McCandless CT, Cotton CF, Musick JA (2016) Critical assessment and ramifications of a purported marine trophic cascade. Sci Rep 6: 20970

Heithaus MR, Frid A, Wirsing AJ, Dill LM, Fourqurean JW, Burkholder D, Thomson J, Bejder OL (2007) State-dependent risk-taking by green sea turtles mediates top-down effects of tiger shark intimidation in a marine ecosystem. J Anim Ecol 75: 837–844

Heithaus MR, Frid A, Wirsing AJ, Worm B (2008) Predicting ecological consequences of marine top predator declines. Trends Ecol Evol 23: 202–210

Heyward AJ, Negri AP (1999) Natural inducers for coral larval metamorphosis. Coral Reefs 18: 273-279

Houk P, Musburger C (2013) Trophic interactions and ecological stability across coral reefs in the Marshall Islands. Mar Ecol Prog Ser 488: 23–34

Hughes TP, Bellwood DR, Folke CS, McCook LJ, Pandolfi JM (2007) No-take areas, herbivory and coral reef resilience. Trends Ecol Evol 22: 1–3

Jackson JCB, Donovan M, Cramer K, Lam V (2014) Status and Trends of Caribbean Coral Reefs: 1970-2012. Global Coral Reef Monitoring Network.

Kellner JB, Tetreault I, Gaines SD, Nisbet RM (2007) Fishing the line near marine reserves in single and multispecies fisheries. Ecol Appl 17: 1039–1054

Kiszka JJ, Mourier J, Gastrich K, Heithaus MR (2016) Using unmanned aerial vehicles (UAVs) to investigate shark and ray densities in a shallow coral lagoon. Mar Ecol Prog Ser 560: 237-242

Kitchell JF, Essington TE, Boggs CH, Schindler DE, Walters CJ (2002) The role of sharks and longline fisheries in a pelagic ecosystem of the Central Pacific. Ecosystems 5: 202–216

Lirman D (2001) Competition between macroalgae and corals: effects of herbivore exclusion and increased algal biomass on coral survivorship and growth. Coral Reefs 19: 392–399

Madin EMP, Dill LM, Ridlon AD, Heithaus MR, Warner RR (2016) Human activities change marine ecosystems by altering predation risk. Global Change Biol 22: 44–60

Mallela J (2013) Calcification by reef-building sclerobionts. PLOS ONE 8: e60010

Maljković A, Côté IM (2011) Effects of tourism-related provisioning on the trophic signatures and movement patterns of an apex predator, the Caribbean reef shark. Biol Conserv 144: 859–865

McCauley DJ, McLean KA, Bauer J, Young HS, Micheli F (2012) Evaluating the performance of methods for estimating the abundance of rapidly declining coastal shark populations. Ecol Appl 22: 385–392

McManus JW, Polsenberg JF (2004) Coral-algal phase shifts on coral reefs: ecological and environmental aspects. Prog Oceanogr 60: 263–279

Mora C, Andréfouët S, Costello MJ, Kranenburg C, Rollo A, Veron J, Gaston KJ, Myers RA (2006) Coral reefs and the global network of marine protected areas. Science 312: 1750-1751

Mourier J, Maynard J, Parravicini V, Ballesta L, Clua E, Domeier ML, Planes S (2016) Extreme inverted trophic pyramid of reef sharks supported by spawning groupers. Curr Biol 26: 1–6

Mumby PJ, Steneck RS (2008) Coral reef management and conservation in light of rapidly evolving ecological paradigms. Trends Ecol Evol 23: 555–563

Myers RA, Baum JK, Shepherd TD, Powers SP, Peterson CH (2007) Cascading effects of the loss of apex predatory sharks from a coastal ocean. Science 315: 1846–1850

Okey TA, Banks S, Born AF, Bustamante RH, Calvopiña M, Edgar GJ, Espinoza E, Miguel Fariña J, Garske LE, Recke GK, Salazar S, Shepherd S, Toral-Granda V, Wallem P (2004) A trophic model of a Galápagos subtidal rocky reef for evaluating fisheries and conservation strategies. Ecol Model 172: 383–401

Randall JE (1967) Food habits of reef fishes of the West Indies. Stud Trop Oceanogr 5: 665–847

Ripple WJ, Larsen EJ, Renkin RA, Smith DW (2001) Trophic cascades among wolves, elk and aspen on Yellowstone National Park's northern range. Biol Conserv 102: 227–234

Rizzari JR, Bergseth BJ, Frisch AJ (2014) Impact of conservation areas on trophicinteractions between apex predators and herbivores on coral reefs. Conserv Biol 29: 418–429

Rizzari JR, Frisch AJ, Hoey AS, McCormick MI (2014) Not worth the risk: apex predators suppress herbivory on coral reefs. Oikos 123: 829–836

Robbins WD, Hisano M, Connolly SR, Choat JH (2006) Ongoing collapse of coral reef shark populations. Curr Biol 16: 2314–2319

Roff G, Doropoulos C, Rogers A, Bozec YM, Krueck NC, Aurellado E, Priest M, Birrell C, Mumby PJ (2016) The ecological role of sharks on coral reefs. Trends Ecol Evol 31: 395-407

Ruppert LW, Travers MJ, Smith LL, Fortin MJ, Meekan MG (2013) Caught in the middle: combined impacts of shark removal and coral loss on the fish communities of coral reefs. PLOS One 8: e74648

Salinas de León P, Acuna-Marrero D, Rastoin E, Friedlander AM, Donovan MK, Sala E (2016) Largest global shark biomass found in the northern Galápagos Islands of Darwin and Wolf. PeerJ 4, e1911

Sandin SA, Smith JE, DeMartini EE, Dinsdale EA, Donner SD, Friedlander AM, Konotchick T, Malay M, Maragos JE, Obura D, Pantos O, Paulay G, Richie M, Rohwer F, Schroeder RE, Walsh S, Jackson JBC, Knowlton N, Sala E (2008) Baselines and degradation of coral reefs in the Northern Line Islands. PLOS ONE 3: e1548

Stevens JD (1984) Life-history and ecology of sharks at Aldabra Atoll, Indian Ocean. Proc R Soc Lond B 222: 79–106

Stevens JD, Bonfil R, Dulvy NK, Walker PA (2000) The effects of fishing on sharks, rays, and chimeras (chondrichthyans), and the implications for marine ecosystems. ICES J Mar Sci 57: 476–494

Valdivia A, Cox CE, Bruno JB (2017) Predatory fish depletion and recovery potential on Caribbean reefs. Sci Adv 3: e1601303

Ward-Paige CA, Mora C, Lotze HK, Pattengill-Semmens C, McClenachan L, Arias-Castro E, Myers RA (2010) Large-scale absence of sharks on reefs in the Greater-Caribbean: a footprint of human pressures*. PLOS ONE 5:* e11968

Williams ID, Polunin NVC (2001) Large-scale associations between macroalgal cover and grazer biomass on mid-depth reefs in the Caribbean. Coral Reefs 19: 358–366

Williams ID, Polunin NVC, Hendrick VJ (2001) Limits to grazing by herbivorous fishes and the impact of low coral cover on macroalgal abundance on a coral reef in Belize. Mar Ecol Prog Ser 222: 187–196

Chapter 5.

General Conclusions

Conservation efforts aimed at halting declines in, and restoring populations of, large, wide-ranging marine taxa are often impeded by a fundamental lack of knowledge of species' ecological requirements. This is particularly true for elasmobranchs due to their broad functional and ecological diversity (Dulvy et al. 2017). For many commercially valuable, highly migratory species, fishery management policies based on solid scientific evidence, including rigorous stock assessments and detailed species-level biological data, are crucial to protecting extant populations and allow recovery of over-exploited stocks. For elasmobranch species with more restricted ranges, the 'shark sanctuary' approach may be an appropriate conservation strategy. The effectiveness of these management strategies is contingent, however, on general compliance with, and adequate enforcement of, their respective regulations. Globally, broad-scale adoption and enforcement of these conservation actions would likely significantly reduce direct mortality – the primary cause of shark population declines (Stevens et al. 2000; Baum et al. 2003; Dulvy et al. 2008; Worm et al. 2013). However, neither of these management actions addresses the effects of non-lethal anthropogenic activities on sharks, which remain woefully understudied to date.

Fishing affects not only top predators but also lower trophic levels (Pauly et al. 1998), and this top-down disturbance can potentially have substantial indirect effects on predators by altering their prey base (e.g., Bearzi et al. 2006). Indirect impacts of fisheries are becoming increasingly apparent, with perceived shifts in many marine species reflecting the trophic restructuring that occurs following large-scale exploitation (Worm et al. 2006; Myers et al. 2007), yet such effects have seldom been previously quantified in relation to top predator foraging and diets.

A further non-extractive, rapidly expanding commercial use of sharks is in the dive tourism industry where attracting sharks by chumming or provisioning is a widespread practice. Although some headway has now been made in terms of identifying the direct impacts of provisioning activities on the focal taxa (reviewed by Gallagher et al. 2015), the disparity across results of the studies completed to date suggests that either: a) further work across provisioned species is required to generate some form of consensus on the impacts of shark dive tourism, or b) species-specific responses to this activity are diverse and should therefore be investigated and assessed on a species-by-species basis. In either case, shark provisioning research is still in its infancy, especially with regard to the scarcity of studies investigating the broader ecological consequences of aggregating sharks for tourism purposes (Brena et al. 2015; Gallagher et al. 2015; Patroni et al. 2018).

It is in respect of these non-lethal anthropogenic activities and their effects on sharks that I hope my thesis has some impact. While research on this topic has been inadequate so far, my preliminary studies may be sufficient to fuel interest and garner enthusiasm for further work on the subject.

Prey depletion

In Chapter 2, I quantified the isotopic responses to prey depletion of seven shark species from the southwest Indian Ocean. Several conclusions can be drawn from this study, but perhaps the most salient general point is the importance of using historical samples – in my case, shark vertebrae collected decades ago from sharks that were already decades old – to generate realistic baselines against which contemporary change can be measured (McClenachan et al. 2012; Thurstan et al. 2015). Collections of old biological material are too often dismissed simply as products of the Victorian-era attitude towards the study of biology (i.e., kill it, stuff it, display it in a nice cabinet). While attitudes are changing (both with respect to indiscriminate collecting and the use of old samples in contemporary studies), the value of these collections cannot be over-estimated, especially given the technologies now available to extract information from them (e.g., Rowe et al. 2011; Yeates et al. 2016).

My study yielded several novel ecological insights. An important one is that the trajectories of change in isotope signatures over decades were not the same across species, despite the fact that all species studied were large sharks that might justifiably be regarded as apex predators (Roff et al. 2016). This key result supports the idea that shark size (both within and among species) cannot be used as a potential indicator of extent of anthropogenic effects because ecology – in this case dietary breadth (i.e., being a trophic generalist vs specialist) – modulates the effects. Another is that the isotopic shifts observed in Indian Ocean sharks, which I believe are consistent with prey depletion by commercial fisheries, suggest that a pattern already observed on land is also occurring in the ocean. Indeed, prey depletion is a common and wide-ranging threat to large terrestrial carnivores (Wolf & Ripple 2016), which have experienced marked range contractions in regions with high rural human population density, cattle density or cropland, i.e. areas where their prey has become scarce owing to hunting and land conversion (Wolf and Ripple 2017). Like the pattern that is apparent for sharks (Chapter 2), generalist carnivores on land are also less affected by prey depletion than specialists (Wolf and Ripple 2016).

Future work on the effects of prey depletion on marine predators would be facilitated by expanding the methods used to identify impacts, particularly if multiple methods can be used within single studies to identify the source of any effects. For example, an obvious extension of my work in Chapter 2 would be to combine more precise isotopic analysis of individual annuli in vertebrae (e.g., Carlisle et al. 2015) with detailed stomach contents analysis (e.g., Dicken et al. 2017) to more accurately identify the prey species being depleted, and the specific age groups of sharks affected most by prey depletion. In addition, a combination of high-resolution satellite telemetry, fatty acid profiles and environmental DNA (eDNA) sampling could be used to compare contemporary populations in prey-rich and prey-depleted areas, with tracking revealing energy expenditure, fatty acids reflecting body condition and basal sources of prey, and eDNA yielding measures of species abundance (Hansen et al. 2018), which might be easier and cheaper than counting or sampling fish communities.

Provisioning reef sharks

Shark-based tourism is a growing but controversial industry because of concerns for both tourist divers and the species they seek to encounter. Human safety concerns appear to be generally unwarranted (Richards et al. 2015), but the impacts of tourism in general, and provisioning in particular, are variable and understudied (Brena et al. 2015; Gallagher et al. 2015; Patroni et al. 2018). Chapter 3 contributes to closing this knowledge gap at least a little. Caribbean reef sharks at a long-term provisioning site in the Bahamas showed little evidence of altered behaviour in terms of movement and site fidelity. These results echo those found for tiger sharks in the Bahamas (Hammerschlag et al. 2017), bull sharks in Fiji (Brunnschweiler & Barnett 2013) and white sharks in South Africa (Laroche et al. 2007), but are at odds with studies of less mobile chondrichthyans such as stingrays (inverted diel activity and smaller core activity spaces - Corcoran et al. 2013; altered movement patterns and site use - Pini-Fitzsimmons et al. 2018) and highly migratory species such as whale sharks (extended residency at feeding sites - Araujo et al. 2014). It is still too soon to generalise from so few studies.

Future work on the impacts of provisioning on sharks should include more sites, more species, and a multi-faceted approach to detect multiple concomitant effects on behaviour and physiology. Another important area is the extent to which ‘staged’ encounters with sharks alter the public perception of these animals. One argument made in favour of shark tourism is its potential to benefit shark conservation by changing negative attitudes, but the evidence for this benefit is, to my knowledge, inexistent. A handful of studies have examined the correlates of visitor satisfaction with shark and stingray provisioning events (reviewed by Patroni et al. 2018), which can help to guide the development and management of these activities. However, changes in attitudes, including learning and emotional empathy, such as those measured after mediated encounters with dolphins, whales and marine turtles (Zeppel 2010), have yet to be demonstrated for sharks.

Community consequences of high shark abundance

In Chapter 4 I use a novel, semi-experimental method to describe changes in coral reef community structure concomitant with the high reef shark densities generated by long-term shark provisioning. As the first study of its kind to assess the broader ecological impacts of shark provisioning for tourism, this work lays the foundation for future investigations on this topic, and generates some preliminary information which may be useful to marine area managers in three respects. Firstly, the broadly positive community effects of high shark abundance, i.e. restoration of predatory teleost communities and reductions in macroalgal cover on reefs, suggest that regular, site-specific shark provisioning tourism may deliver wider ecosystem benefits than simply ‘bolstering’ local shark populations. Secondly, and in respect of the preceding point, carefully orchestrated shark provisioning (for tourism purposes or otherwise) could be included in portfolios of management options for shark - and possibly coral reef - conservation. Lastly, my results shed some light on the possible cascading effects that are expected to develop as a result of establishing dedicated ‘shark sanctuaries’ to conserve elasmobranchs. Some of the anecdotal controversy surrounding this conservation approach has focussed on how the cascading effects of increased shark abundance will affect other components of the community. My preliminary work on the effects of high shark abundance on coral reef communities suggests positive impacts of increasing shark densities, but much further work is required to assess whether these patterns of community ‘improvement’ hold true across provisioned shark species and habitats.

Of particular interest in Chapter 4 are the mechanisms by which reef shark presence appears to affect wider community structure. In a classic behaviourally mediated indirect interaction (BMII; Dill et al. 2003), reef shark presence appears to alter the structure of algal communities through risk effects, manifested as changes in foraging the behaviour of herbivorous reef fish. The presence of predators has previously been shown to strongly influence primary producer communities in both marine (Steinberg et al. 1995; Madin et al. 2016) and terrestrial (e.g., Ripple et al. 2001) environments. My results therefore add to a growing body of evidence documenting the role of top predators as ecosystem engineers (Coleman & Williams 2002) – species which have a disproportionate influence on the architecture of the habitats in which they occur.

Perhaps the most surprising effect of increased shark density at the provisioning site was the high abundance of teleost mesopredators. It is almost counterintuitive to expect that dense predator aggregations would result in increases of their prey species, yet inclusion of fisher distribution data and fishing success rates in my study seems to adequately explain the patterns of mesopredator abundance observed. If the low-tech (hook and line) fishing strategy used by the vast majority of fishers in this area persists, then so might the ‘marine reserve’ effect created by the presence of sharks. This finding highlights the importance of combining ecological research with local socio-economic conditions to more fully explain the results of studies investigating human-wildlife interactions.

Future work exploring the community effects of high shark abundance generated by provisioning would benefit from using a before-after-control-impact (BACI) approach to allow collection of detailed baseline data (e.g., Francini-Filho & Moura 2008) prior to generating aggregations of sharks. This approach would make it possible to elucidate the timings of any changes, and likely further community effects of, increasing shark abundance. However, the emphasis in the short term should perhaps be on replicating some or all of the methods I describe across a spectrum of shark provisioning dive sites to assess whether any generalities in community responses to provisioned shark populations can be found.

References

Araujo, G., Lucey, A., Labaja, J., So, C.L., Snow, S. & Ponzo, A. (2014) Population structure and residency patterns of whale sharks, Rhincodon typus, at a provisioning site in Cebu, Philippines. PeerJ, 2, e543.

Baum, J.K., Myers, R.A., Kehler, D.G., Worm, B., Harley, S.J. & Doherty, P.A. (2003) Collapse and Conservation of Shark Populations in the Northwest Atlantic. Science, 299, 389-392.

Bearzi, G., Politi, E., Agazzi, S. & Azzellino, A. (2006) Prey depletion caused by overfishing and the decline of marine megafauna in eastern Ionian Sea coastal waters (central Mediterranean). Biological Conservation, 127, 373-382.

Brena, P.F., Mourier, J., Planes, S. & Clua, E. (2015) Shark and ray provisioning: functional insights into behavioral, ecological and physiological responses across multiple scales. Marine Ecology Progress Series, 538, 273-283.

Brunnschweiler, J.M. & Barnett, A. (2013) Opportunistic Visitors: Long-Term Behavioural Response of Bull Sharks to Food Provisioning in Fiji. PLoS ONE, 8, e58522.

Carlisle, A.B., Goldman, K.J., Litvin, S.Y., Madigan, D.J., Bigman, J.S., Swithenbank, A.M., Kline, T.C. & Block, B.A. (2015) Stable isotope analysis of vertebrae reveals ontogenetic changes in habitat in an endothermic pelagic shark. Proceedings of the Royal Society B, 282, 20141446.

Coleman, F.C. & Williams, S.L. (2002) Overexploiting marine ecosystem engineers: potential consequences for biodiversity. Trends in Ecology and Evolution, 17, 40-44.

Corcoran, M.J., Wetherbee, B.M., Shivji, M.S., Potenski, M.D., Chapman, D.D. & Harvey, G.M. (2013) Supplemental Feeding for Ecotourism Reverses Diel Activity and Alters Movement Patterns and Spatial Distribution of the Southern Stingray, Dasyatis americana. PLoS ONE, 8, e59235.

Dicken, M.L., Hussey, N.E., Christiansen, H.M., Smale, M.J., Nkabi, N., Cliff, G. & Wintner, S.P. (2017) Diet and trophic ecology of the tiger shark (*Galeocerdo cuvier*) from South African waters. PLoS ONE, 12, e0177897.

Dill, L.M., Heithaus, M.R & Walters, C.J. (2003) Behaviorally Mediated Indirect Interactions in Marine Communities and Their Conservation Implications. Ecology, 84, 1151–1157.

Dulvy, N.K., Baum, J.K., Clarke, S., Compagno, L.J.V., Cortés, E., Domingo, A., Fordham, S., Fowler, S., Francis, M.P., Gibson, C., Martínez, J., Musick, J.A., Soldo, A., Stevens, J.D. & Valenti, S. (2008) You can swim but you can't hide: the global status and conservation of oceanic pelagic sharks and rays. Aquatic Conservation Marine and Freshwater Ecosystems, 18, 459-482.

Francini-Filho, R.B. & Moura, R.L. (2008) Evidence for spillover of reef fishes from a no-take marine reserve: An evaluation using the before-after control-impact (BACI) approach. Fisheries Research, 93, 346–356.

Gallagher, A.J., Vianna, G.M.S., Papastanatiou, Y.P, Macdonald, C., Guttridge, T.L. & Hammerschlag, N. (2015) Biological effects, conservation potential, and research priorities of shark diving tourism. Biological Conservation, 184, 365-379.

Hammerschlag, N., Gutowsky, L.F.G., Gallagher, A.J., Matich, P. & Cooke, S.J. (2017) Diel habitat use patterns of a marine apex predator (tiger shark, Galeocerdo cuvier) at a high use area exposed to dive tourism. Journal of Experimental Marine Biology and Ecology, 495, 24-34.

Hansen, B.K., Bekkevold, D., Clausen, L.W. & Nielsen, E.E. (2018) The sceptical optimist: challenges and perspectives for the application of environmental DNA in marine fisheries. Fish and Fisheries, 19, 751-768.

Laroche, R.K., Kock, A.A., Dill, L.M. & Oosthuizen, W.H. (2007) Effects of provisioning ecotourism activity on the behaviour of white sharks Carcharodon carcharias. Marine Ecology Progress Series, 338, 199-209.

Madin, E.M.P., Dill, L.M., Ridlon, A.D., Heithaus, M.R. & Warner, R.R. (2016) Human activities change marine ecosystems by altering predation risk. Global Change Biology, 22, 44–60.

McClenachan, L., Ferretti, F. & Baum, J.K. (2012) From archives to conservation: why historical data are needed to set baselines for marine animals and ecosystems. Conservation Letters, 5, 349-359.

Patroni, J., Simpson, G. & Newsome, D. (2018) Feeding wild fish for tourism - A systematic quantitative literature review of impacts and management. International Journal of Tourism Research, 20, 286-298.

Pini-Fitzsimmons, J., Knott, N.A. & Brown, C. (2018) Effects of food provisioning on site use in the short-tail stingray Bathytoshia brevicaudata. Marine Ecology Progress Series, 600, 99-110.

Richards, K., O'Leary, B.C., Roberts, C.M., Ormond, R., Gore, M. & Hawkins, J.P. (2015) Sharks and people: Insight into the global practices of tourism operators and their attitudes to shark behaviour. Marine Pollution Bulletin, 91, 200-210.

Ripple, W.J., Larsen, E.J., Renkin, R.A. & Smith, D.W. (2001) Trophic cascades among wolves, elk and aspen on Yellowstone National Park’s northern range. Biological Conservation, 102, 227–234.

Roff, G., Doropoulos, C., Rogers, A., Bozec, Y.-M., Krueck, N.C., Aurellado, E., Priest, M., Birrell, C. & Mumby, P.J. (2016) The ecological role of sharks on coral reefs. Trends in Ecology and Evolution, 31, 395-407.

Rowe, K.C., Singhal, S., MacManes, M.D., Ayroles, J.F., Morelli, T.L., Ribidge, E.M., Bi, K. & Mortiz, C.C. (2011) Museum genomics: low-cost and high-accuracy genetic data from historical specimens. Molecular Ecology Resources, 11, 1082-1092.

Steinberg, P.D., Estes, J.A. & Winter, F.C. (1995) Evolutionary consequences of food chain length in kelp forest communities. Proceedings of the National Academy of Sciences USA, 92, 8145-8148.

Stevens, J.D., Bonfil, R., Dulvy, N.K. & Walker, P.A. (2000) The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystems. ICES Journal of Marine Science, 57, 476-494.

Thurstan, R.H., McClenachan, L., Crowder, L.B., Drew, J.A., Kittinger, J.N., Levin, P.S., Roberts, C.M., & Pandolfi, J.M. (2015) Filling historical data gaps to foster solutions in marine conservation. Ocean and Coastal Management, 115, 31-40.

Wolf, C. & Ripple, W.J. (2016) Prey depletion as a threat to the world’s large carnivores. Royal Society Open Science, 3, 160252.

Wolf, C. & Ripple, W.J. (2017) Range contractions of the world's large carnivores. Royal Society Open Science, 4, 170052.

Worm, B., Davis, B., Kettemer, L., Ward-Paige, C.A., Chapman, D., Heithaus, M.R., Kessel, S.T. & Gruber, S.H. (2013) Global catches, exploitation rates, and rebuilding options for sharks. Marine Policy, 40, 194-204.

Yeates, D.K., Zwick, A. & Mikheyev, A.S. (2016) Museums are biobanks: unlocking the genetic potential of the three billion specimens in the world's biological collections. Current Opinion in Insect Science, 18, 83-88.

Zeppel, H. (2010) Education and Conservation Benefits of Marine Wildlife Tours: Developing Free-Choice Learning Experiences. Journal of Environmental Education, 39, 3-18.

Appendix A.

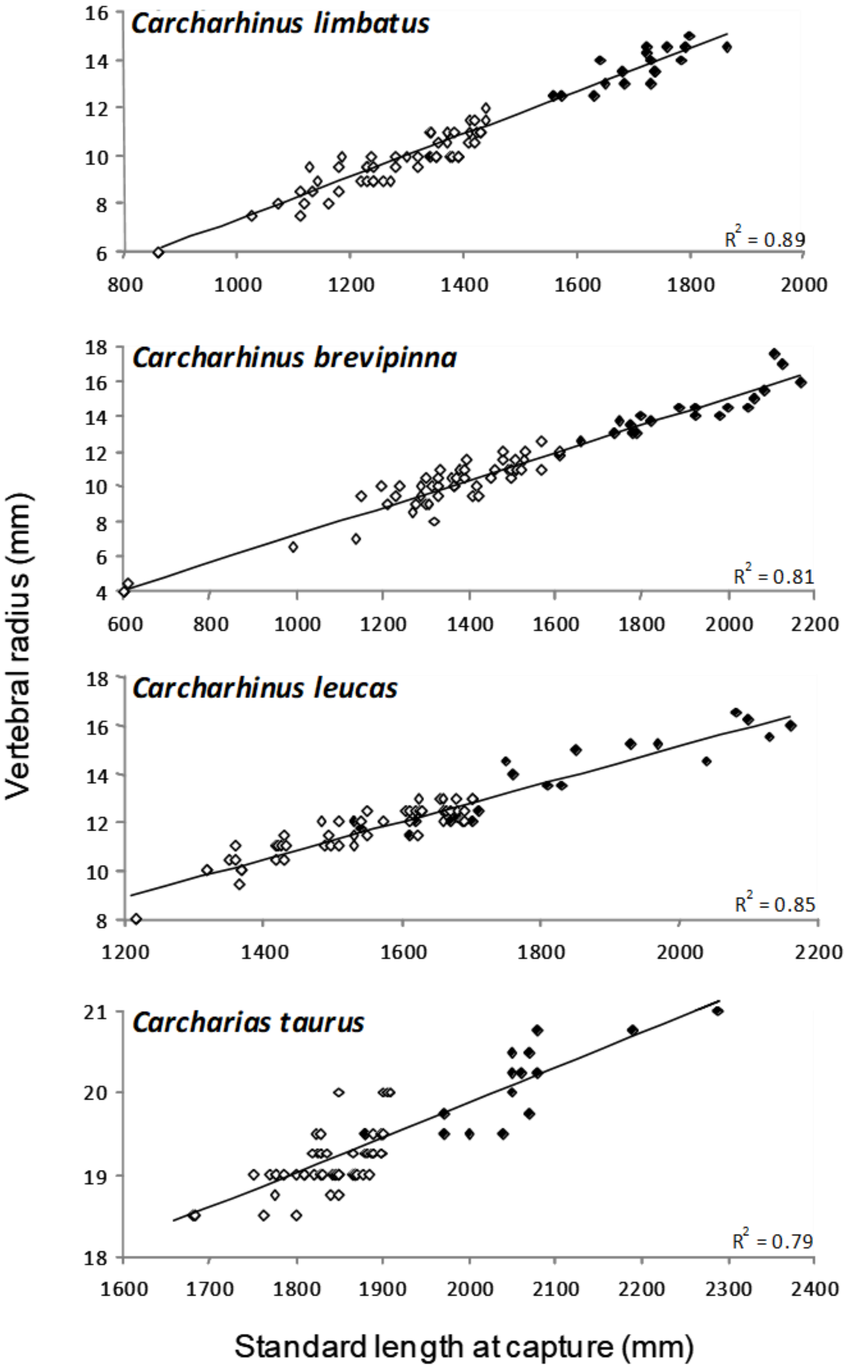
Table S2.1 Mean (± SD) values from bias-corrected accelerated bootstrap estimates of $\delta^{15}N$ for vertebrae of seven shark species caught in the KwaZulu-Natal Sharks Board gill nets over 5-year periods.

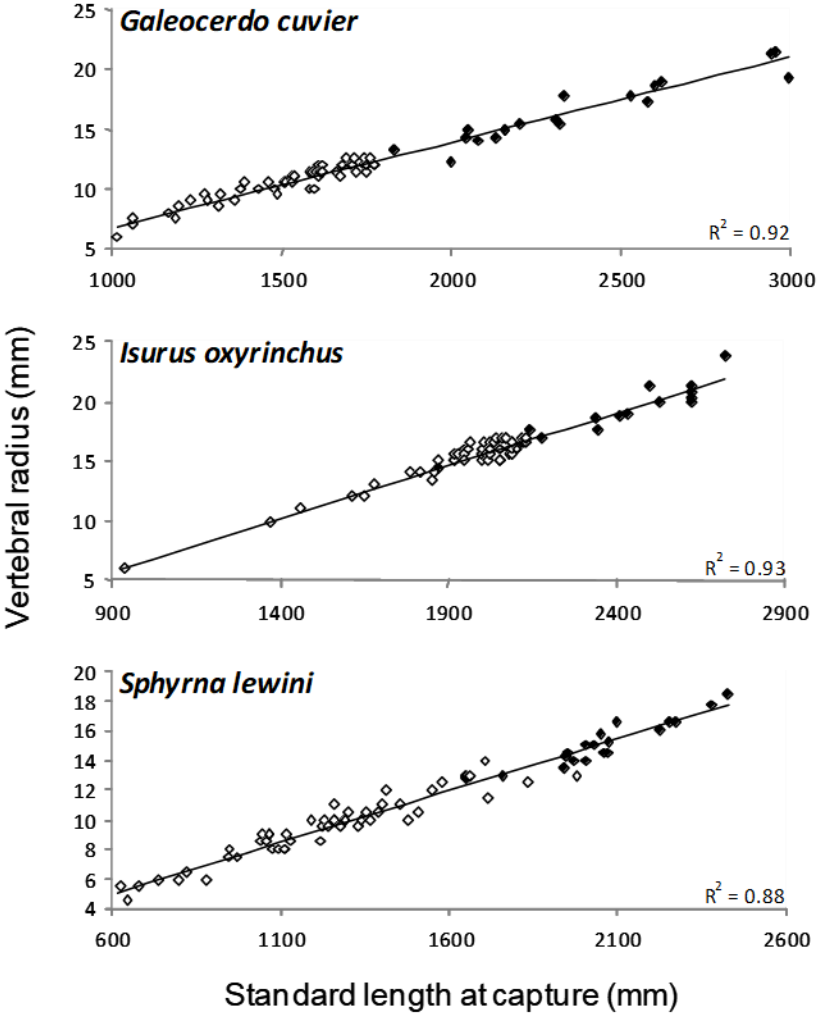
Species	Distance from 0 mm sampling interval (mm)	Estimated precaudal length at sampling interval (cm)	Mean $\delta^{15}N$ (± SD)				
			1970 -1975	1985 -1989	1990 -1994	1995 -1999	2000 -2004
Carcharhinus limbatus	0	-	-	14.2 ± 0.6	14.4 ± 0.5	13.9 ± 0.3	14.1 ± 0.3
	4	61	-	13.8 ± 1.2	14.1 ± 1.1	13.6 ± 0.7	14.0 ± 0.9
	8	108	-	15.8 ± 1.4	15.4 ± 1.2	15.1 ± 0.8	14.8 ± 1.3
	12	152	-	16.8 ± 0.9	16.3 ± 1.3	15.7 ± 0.8	15.1 ± 0.9
Carcharhinus brevipinna	0	-	-	13.1 ± 1.3	13.1 ± 1.1	13.2 ± 0.8	13.4 ± 1.2
	4	59	-	12.4 ± 0.6	12.7 ± 0.6	12.2 ± 0.5	12.0 ± 0.4
	8	110	-	13.8 ± 0.8	13.6 ± 0.5	13.5 ± 0.5	13.2 ± 0.8
	12	161	-	14.2 ± 0.7	13.8 ± 0.4	13.6 ± 0.3	13.3 ± 0.9
Carcharhinus leucas	0	-	-	13.3 ± 1.2	13.5 ± 0.9	13.7 ± 1.4	14.0 ± 1.7
	3	45	-	12.4 ± 0.5	12.2 ± 0.3	12.5 ± 0.4	12.3 ± 0.8
	6	82	-	13.6 ± 0.7	13.7 ± 0.4	13.8 ± 0.8	13.6 ± 0.8
	9	121	-	14.2 ± 1.0	14.1 ± 0.7	14.2 ± 1.3	14.4 ± 0.9
Carcharias taurus	0	-	-	14.8 ± 0.6	14.6 ± 1.1	14.6 ± 0.8	14.9 ± 1.3
	6	embryonic	-	13.7 ± 0.4	13.9 ± 0.5	13.6 ± 0.4	13.8 ± 0.7
	12	embryonic	-	14.9 ± 0.3	14.8 ± 0.4	14.6 ± 0.6	14.3 ± 0.6
	18	155	-	15.4 ± 0.5	15.1 ± 0.7	14.9 ± 0.4	14.7 ± 0.5
Galeocerdo cuvier	0	-	-	12.4 ± 2.1	11.8 ± 1.7	11.4 ± 0.6	11.8 ± 2.0
	4	63	-	11.3 ± 0.6	11.0 ± 0.8	11.1 ± 0.7	11.1 ± 0.9
	8	119	-	12.2 ± 0.7	11.9 ± 1.1	11.6 ± 1.3	11.5 ± 1.4
	12	174	-	12.6 ± 1.5	12.4 ± 1.2	12.7 ± 0.9	12.2 ± 1.5
Isurus oxyrinchus	0	-	15.8 ± 2.2	15.2 ± 1.5	14.6 ± 1.8	14.7 ± 1.1	14.2 ± 0.8
	4.5	75	14.2 ± 0.7	14.3 ± 0.6	13.5 ± 0.3	13.3 ± 0.7	13.7 ± 0.5
	9	129	15.5 ± 0.5	15.6 ± 0.8	14.2 ± 0.7	15.1 ± 0.6	14.7 ± 0.4
	13.5	178	16.4 ± 0.7	15.0 ± 0.7	14.9 ± 0.5	14.6 ± 0.6	14.5 ± 0.6
Sphyrna lewini	0	-	-	15.0 ± 0.9	14.8 ± 2.1	15.2 ± 1.7	14.9 ± 2.0
	4	48	-	14.0 ± 0.3	14.2 ± 0.3	13.9 ± 0.3	14.1 ± 0.8
	8	105	-	14.6 ± 0.7	14.7 ± 0.5	14.5 ± 0.8	14.7 ± 0.5
	12	161	-	14.8 ± 0.6	15.0 ± 0.3	15.1 ± 0.4	15.4 ± 0.3

Table S2.2 Mean (± SD) values of $\delta^{13}C$ from non-parametric bias-corrected accelerated bootstrap estimates for vertebrae of seven shark species caught in the KwaZulu-Natal Sharks Board gill nets over 5-year periods.

Species	Distance from 0 mm sampling interval (mm)	Estimated Precaudal length at sampling interval (cm)	Mean $\delta^{13}C$ (± SD)				
			1970 -1975	1985 -1989	1990 -1994	1995 -1999	2000 -2004
Carcharhinus limbatus	0	-	-	-15.2 ± 0.8	-15.1 ± 1.4	-15.0 ± 1.3	-14.2 ± 1.3
	4	61	-	-14.8 ± 1.2	-14.9 ± 0.7	-14.6 ± 0.8	-14.9 ± 1.5
	8	108	-	-15.4 ± 0.5	-15.3 ± 1.8	-15.4 ± 1.7	-14.7 ± 0.9
	12	152	-	-15.2 ± 1.7	-14.6 ± 1.1	-15.1 ± 1.3	-14.5 ± 1.1
Carcharhinus brevipinna	0	-	-	-13.7 ± 1.4	-13.4 ± 1.6	-12.6 ± 1.3	-13.0 ± 1.8
	4	59	-	-13.2 ± 0.6	-12.8 ± 2.1	-13.0 ± 0.7	-12.8 ± 1.3
	8	110	-	-13.8 ± 1.2	-13.6 ± 1.7	-13.4 ± 1.1	-13.1 ± 0.9
	12	161	-	-13.0 ± 0.7	-13.8 ± 1.9	-13.5 ± 1.4	-13.7 ± 1.2
Carcharhinus leucas	0	-	-	-13.1 ± 1.2	-13.4 ± 1.0	-13.5 ± 0.8	-13.7 ± 1.1
	3	45	-	-14.0 ± 0.5	-14.1 ± 0.7	-14.4 ± 2.0	-14.2 ± 1.5
	6	82	-	-12.9 ± 1.4	-13.1 ± 1.2	-13.9 ± 1.4	-13.5 ± 0.6
	9	121	-	-13.2 ± 2.4	-13.5 ± 0.8	-13.7 ± 1.6	-13.3 ± 1.4
Carcharias taurus	0	-	-	-12.8 ± 1.0	-12.6 ± 0.9	-12.2 ± 0.5	-12.2 ± 0.8
	6	embryonic	-	-13.4 ± 0.4	-13.8 ± 0.5	-13.0 ± 0.7	-12.9 ± 1.1
	12	embryonic	-	-11.9 ± 0.8	-12.6 ± 0.7	-12.9 ± 0.8	-12.4 ± 0.9
	18	155	-	-12.2 ± 0.5	-12.0 ± 0.7	-12.5 ± 1.1	-11.8 ± 1.3
Galeocerdo cuvier	0	-	-	-14.3 ± 2.7	-13.9 ± 1.4	-14.1 ± 2.2	-14.6 ± 2.8
	4	63	-	-14.3 ± 2.4	-13.7 ± 2.3	-13.8 ± 1.6	-13.9 ± 1.6
	8	119	-	-13.8 ± 1.9	-13.2 ± 1.7	-14.0 ± 0.9	-13.4 ± 1.9
	12	174	-	-14.7 ± 2.1	-13.3 ± 1.9	-13.6 ± 1.8	-13.6 ± 1.4
Isurus oxyrinchus	0	-	-13.2 ± 0.9	-13.2 ± 1.3	-13.3 ± 1.7	-13.2 ± 0.8	-13.5 ± 1.1
	4.5	75	-14.1 ± 0.3	-13.9 ± 0.4	-14.2 ± 0.6	-14.4 ± 0.5	-14.6 ± 0.4
	9	129	-13.1 ± 0.6	-13.0 ± 0.8	-13.6 ± 0.8	-13.6 ± 0.9	-13.7 ± 0.9
	13.5	178	-13.9 ± 1.3	-13.3 ± 0.9	-13.0 ± 1.4	-13.9 ± 0.7	-13.1 ± 1.0
Sphyrna lewini	0	-	-	-14.5 ± 0.8	-14.9 ± 0.9	-14.5 ± 1.1	-14.9 ± 0.8
	4	48	-	-15.1 ± 0.6	-15.5 ± 0.7	-15.6 ± 0.8	-15.4 ± 0.9
	8	105	-	-14.8 ± 0.5	-14.9 ± 0.6	-15.1 ± 0.6	-15.0 ± 0.5
	12	161	-	-14.4 ± 0.7	-14.2 ± 0.5	-14.0 ± 1.3	-13.7 ± 0.8

Figure S2.1 Relationships between vertebral radius and precaudal length at capture for seven shark species from the southwest Indian Ocean sampled in this study. Filled symbols indicate vertebrae used in this study.





Galeocerdo cuvier
25
20
15
10
5
1000
1500
2000
2500
3000
$R^2 = 0.92$
Isurus oxyrinchus
25
20
15
10
5
900
1400
1900
2400
2900
$R^2 = 0.93$
Sphyrna lewini
20
18
16
14
12
10
8
6
4
600
1100
1600
2100
2600
$R^2 = 0.88$
Vertebral radius (mm)
Standard length at capture (mm)

Table S2.3 Synopsis of stomach contents for the focal shark species caught in the KwaZulu-Natal Sharks Board gill nets. % occurrence is the number of stomachs containing a particular prey relative to the total number of stomachs containing food; it sums to more than 100% because many stomachs contained more than one prey type.

Shark species (Data source)	No. of stomachs examined (% empty or everted)	Period of data collection	Prey types recorded (% occurrence)	Total prey diversity (mean no. of prey items/stomach)
Carcharhinus limbatus (Dudley & Cliff 1993)	1290 (49.6)	1978 - 1991	Teleosts (82.7) Elasmobranchs (15.7) Molluscs (9.8) Crustaceans (3.7) Cetaceans (< 1)	46 families 50 species (4.2)
Carcharhinus brevipinna (Allen & Cliff 2000)	1230 (71.7)	1983 - 1997	Teleosts (79) Molluscs (17.5) Crustaceans (1.9) Elasmobranchs (1.6)	27 families 34 species (9)
Carcharhinus leucas (Cliff & Dudley 1991)	254 (41.0)	1978 - 1990	Teleosts (54.3) Elasmobranchs (50.7) Mammals (9) Molluscs (4.3) Crustaceans (4) Turtles (2) Birds (0.7)	42 families 75 species (3.1)
Carcharias taurus (Smale 2005)	149 (32.8)	1978 - 2000	Teleosts (NR) Elasmobranchs (NR) Molluscs (NR) Crustaceans (NR)	56 species (NR)
Galeocerdo cuvier (Dicken et al. 2017)	778 (19.3)	1983 - 2014	Elasmobranchs (54.7) Teleosts (51.3) Mammals (40.6) Birds (26.9) Cephalopods (15.5) Crustaceans (12.7) Reptiles (6.2)	192species (NR)
Isurus oxyrinchus (Cliff et al. 1990)	151 (41.7)	1978 - 1989	Elasmobranchs (60.2) Teleosts (40.2) Molluscs (9.8) Cetaceans (< 1)	13 families 18 species (NR)
Sphyrna lewini	1373 (39.4)	1983 - 1998	Teleosts (76.7) Molluscs (24.8)	63 families

(de Bruyn et al. 2005)	Elasmobranchs (11.8) Crustaceans (2.6) Birds (0.2)	80 species (2.5)

NR – not reported

References

de Bruyn P, Dudley SFJ, Cliff G, Smale MJ (2005) Sharks caught in the protective gill nets off KwaZulu-Natal, South Africa. 11. The scalloped hammerhead shark *Sphyrna lewini* (Griffith and Smith). African Journal of Marine Science 27: 517-528

Allen BR, Cliff G (2000) Sharks caught in the protective gill nets off Natal, South Africa. 9. The spinner shark *Carcharhinus brevipinna* (Müller and Henle). South African Journal of Marine Science 22: 199-215

Cliff G, Dudley SFJ (1991) Sharks caught in the protective gill nets off Natal, South Africa. 4. The bull shark *Carcharhinus leucas* Valenciennes. South African Journal of Marine Science 10: 253-270

Cliff G, Dudley SFJ, Davis B (1990) Sharks caught in the protective gill nets off Natal, South Africa. 3. The shortfin mako shark *Isurus oxyrinchus* (Rafinesque). South African Journal of Marine Science 9: 115-126

Dicken ML, Hussey NE, Christiansen HM, Smale MJ, Nkabi N, Cliff G, Wintner S (2017) Diet and trophic ecology of the tiger shark (Galeocerdo cuvier) from South African waters. PLoS ONE 12 (6): e0177897

Dudley SFJ, Cliff G (1993) Sharks caught in the protective gill nets off Natal, South Africa. 7. The blacktip shark *Carcharhinus limbatus* (Valenciennes). South African Journal of Marine Science 13: 237-254

Smale MJ (2005) The diet of the ragged-tooth shark *Carcharias taurus* Rafinesque 1810 in the Eastern Cape, South Africa. African Journal of Marine Science 27: 331-335

Appendix B.

Table S4.1 Trophic guilds of Bahamian reef fish species, based on published diet descriptions[1,2]

Trophic guild	**Family**	**Species**	**Common name**
Herbivores	Scaridae	*Sparisoma viride*	Stoplight parrotfish
		Sparisoma aurofrenatum	Redband parrotfish
		Sparisoma chrysopterum	Redtail parrotfish
		Sparisoma rubripinne	Yellowtail parrotfish
		Scarus iserti	Striped parrotfish
		Scarus vetula	Queen parrotfish
		Scarus taeniopterus	Princess parrotfish
		Scarus coeruleus	Blue parrotfish
		Scarus coelestinus	Midnight parrotfish
		Scarus guacamaia	Rainbow parrotfish

	Acanthuridae	*Acanthurus coeruleus*	Blue tang
		Acanthurus bahianus	Ocean surgeonfish
		Acanthurus chirurgus	Doctorfish
	Pomacentridae	*Stegastes adustus*	Dusky damsel
		Stegastes diencaeus	Longfin damsel
		Stegastes variabilis	Cocoa damsel
		Stegastes partitus	Bicolor damsel
		Microspathodon chrysurus	Yellowtail damsel
		Stegastes planifrons	Threespot damsel
	Monacanthidae	*Aluterus scriptus*	Scrawled filefish
	Kyphosidae	*Kyphosus sectatrix/incisor*	Bermuda/Yellow chub
	Balistidae	*Melichthys niger*	Black durgon
Low-level carnivores	Carangidae	*Elagatis bipinnulata*	Rainbow runner
		Trachinotus goodei	Great pompano

	Trachinotus falcatus	Permit
Pomacentridae	*Chromis cyanea*	Blue chromis
	Chromis multilineata	Brown chromis
Serranidae	*Hypoplectrus unicolor*	Butter hamlet
	Hypoplectrus puella	Barred hamlet
	Hypoplectrus indigo	Indigo hamlet
	Epinephelus guttatus	Red hind
	Epinephelus adscensionis	Rock hind
	Serranus tigrinus	Harlequin bass
	Serranus tortugarum	Chalk bass
	Paranthias furcifer	Creolefish
Haemulidae	*Haemulon album*	Margate
	Haemulon flavolineatum	French grunt
	Haemulon sciurus	Bluestriped grunt
	Haemulon plumierii	White grunt

	Haemulon carbonarium	Caesar grunt
	Haemulon macrostomum	Spanish grunt
	Anisotremus viginicus	Porkfish
	Anisotremus surinamensis	Black margate
Lutjanidae	*Ocyurus chrysurus*	Yellowtail snapper
	Lutjanus synagris	Lane snapper
	Lutjanus griseus	Grey snapper
Labridae	*Clepticus parrae*	Creole wrasse
	Lachnolaimus maximus	Hogfish
	Bodianus rufus	Spanish hogfish
	Halichoeres radiatus	Puddingwife
	Halichoeres cyanocephalus	Yellowcheek wrasse
	Halichoeres poeyi	Blackear wrasse
	Halichoeres bivittatus	Slippery dick

	Halichoeres maculipinna	Clown wrasse
	Halichoeres garnoti	Yellowhead wrasse
Labridae	*Thalassoma bifasciatum*	Bluehead wrasse
Mullidae	*Pseudupeneus maculatus*	Spotted goatfish
	Mulloidichthys martinicus	Yellow goatfish
Holocentridae	*Holocentrus adscensionis*	Squirrelfish
	Holocentrus rufus	Longspine squirrelfish
	Sargocentron coruscum	Reef squirrelfish
	Sargocentron vexillarium	Dusky squirrelfish
	Neoniphon marianus	Longjaw squirrelfish
	Myripristis jacobus	Blackbar soldierfish
Chaetodontidae	*Chaetodon striatus*	Banded butterflyfish
	Chaetodon capistratus	Foureye butterflyfish
	Chaetodon ocellatus	Spotfin butterflyfish
	Chaetodon sedentarius	Reef butterflyfish

Pomacanthidae	*Holacanthus tricolor*	Rock beauty
	Holacanthus ciliaris	Queen angelfish
	Pomacanthus arcuatus	Gray angelfish
	Pomacanthus paru	French angelfish
Monacanthidae	*Cantherhines macrocerus*	Whitespotted filefish
Pempheridae	*Pempheris schomburgki*	Glassy sweeper
Congridae	*Heteroconger longissimus*	Brown garden eel
Grammatidae	*Gramma melacara*	Blackcap basslet
Malacanthidae	*Malacanthus plumieri*	Sand tilefish
Gobiidae	*Microgobius carri*	Seminole goby
Sparidae	*Calamus calamus*	Saucereye porgy
Tetraodontidae	*Canthigaster rostrata*	Sharpnose puffer
Balistidae	*Canthidermis sufflamen*	Ocean triggerfish
Ephippidae	*Chaetodipterus faber*	Atlantic spadefish
Sciaenidae	*Equetus punctatus*	Spotted drum

	Echeneidae	*Echeneis naucrates*	Sharksucker
	Ostraciidae	*Lactophrys triqueter*	Smooth trunkfish
	Gerreidae	*Gerres cinereus*	Yellowfin mojarra
	Inermiidae	*Inermia vittata*	Boga
	Dasyatidae	*Dasyatis americana*	Southern stingray
Piscivores **<50 cm TL**	Carangidae	*Caranx ruber*	Bar jack
		Seriola rivoliana	Almaco jack
		Caranx crysos	Blue runner
	Serranidae	*Epinephelus striatus*	Nassau grouper
		Cephalopholis cruentatus	Graysby
		Cephalopholis fulva	Coney
		Mycteroperca tigris	Tiger grouper
		Mycteroperca interstitialis	Yellowmouth grouper
		Rypticus saponaceus	Greater soapfish

	Lutjanidae	*Lutjanus buccanella*	Blackfin snapper
		Lutjanus mahogoni	Mahogany snapper
		Lutjanus apodus	Schoolmaster
	Aulostomidae	*Aulostomus maculatus*	Trumpetfish
	Scorpaenidae	*Pterois volitans*	Lionfish
	Synodontidae	*Trachinocephalus myops*	Snakefish
Piscivores **>50 cm TL**	Carangidae	*Caranx crysos*	Blue runner
		Caranx latus	Horse-eye jack
		Seriola dumerili	Greater amberjack
		Carangoides bartholomaei	Yellow jack
	Serranidae	*Epinephelus striatus*	Nassau grouper
		Mycteroperca bonaci	Black grouper
		Mycteroperca venenosa	Yellowfin grouper
		Mycteroperca tigris	Tiger grouper

	Mycteroperca interstitialis	Yellowmouth grouper
Lutjanidae	*Lutjanus cyanopterus*	Cubera snapper
	Lutjanus analis	Mutton snapper
	Lutjanus jocu	Dog snapper
Aulostomidae	*Aulostomus maculatus*	Trumpetfish
Rhincodontidae	*Ginglymostoma cirratum*	Nurse shark
Scombridae	*Scomberomorus regalis*	Cero
Muraenidae	*Gymnothorax moringa*	Spotted moray
	Gymnothorax funebris	Green moray
Sphyraenidae	*Sphyraena barracuda*	Great barracuda

1. Randall, J.E. Food habits of reef fishes of the West Indies. Stud. Trop. Oceanogr. 5, 665–847 (1967).

2. Froese, R. & Pauly, D. FishBase (2011). Available: http://www.fishbase.org.

S4.2 Table. Post-hoc comparisons of mean biomass of large piscivores and total fish biomass. Results of Dunnett’s post-hoc tests comparing fish biomass at the shark feeding site (indicated by dark shading) and all other sites. Degrees of freedom = 105 in all cases; t_d values are reported, with their significance: * $P < 0.05$, ** $P < 0.001$.

Distance from feeding site (km)	2.0	1.8	1.6	1.4	1.2	1.0	0.8	0.6	0.4	0.2	0	0.2	0.4	0.6	0.8	1.0	1.2	1.4	1.6	1.8	2.0
Piscivores > 50 cm TL	4.7**	4.7**	4.2**	4.5**	4.0**	3.1*	2.4	0.9	1.0	0.9		0.9	1.2	2.1	2.6	2.5	3.0*	4.1**	4.4**	4.7**	4.9**
Total fish biomass	4.0**	4.1**	3.9**	4.1**	4.2**	3.9**	3.7**	3.0*	2.0	0.5		0.2	0.3	0.8	2.2	3.0*	3.2*	3.7**	3.9**	3.9**	4.1**

Table S4.3 Post-hoc comparisons of mean cover of functional algal groups and coral. Results of Dunnett's post-hoc tests comparing mean algal and live coral cover between the shark feeding site (indicated by dark shading) and all other sites. Degrees of freedom = 105 in all cases; t_d values are reported, with their significance: * P < 0.05, ** P < 0.001.

Distance from feeding site (km)	2.0	1.8	1.6	1.4	1.2	1.0	0.8	0.6	0.4	0.2	0	0.2	0.4	0.6	0.8	1.0	1.2	1.4	1.6	1.8	2.0
Turf algae cover	4.9**	4.8**	4.7**	-	-	3.4**	3.1*	-	2.1	1.5		1.6	1.4	2.1	2.8	2.9	3.2**	3.3**	3.9**	4.5**	4.7**
Macroalgae cover	5.2**	5.0**	4.9**	-	-	3.5**	3.2**	-	2.0	1.5		1.4	1.5	1.8	2.8	3.1*	3.5**	3.8**	4.1**	4.6**	4.9**
Crustose coralline algae cover	3.0*	3.0*	2.9	-	-	2.9	2.9	-	2.7	2.7		2.7	2.7	2.8	2.9	3.0*	2.9	3.0*	3.0*	3.0*	3.0*
Live hard coral cover	0.9	1.2	1.4	-	-	1.0	1.7	-	0.9	1.4		2.1	1.5	1.7	3.1*	1.1	1.9	2.2	1.6	2.0	1.4

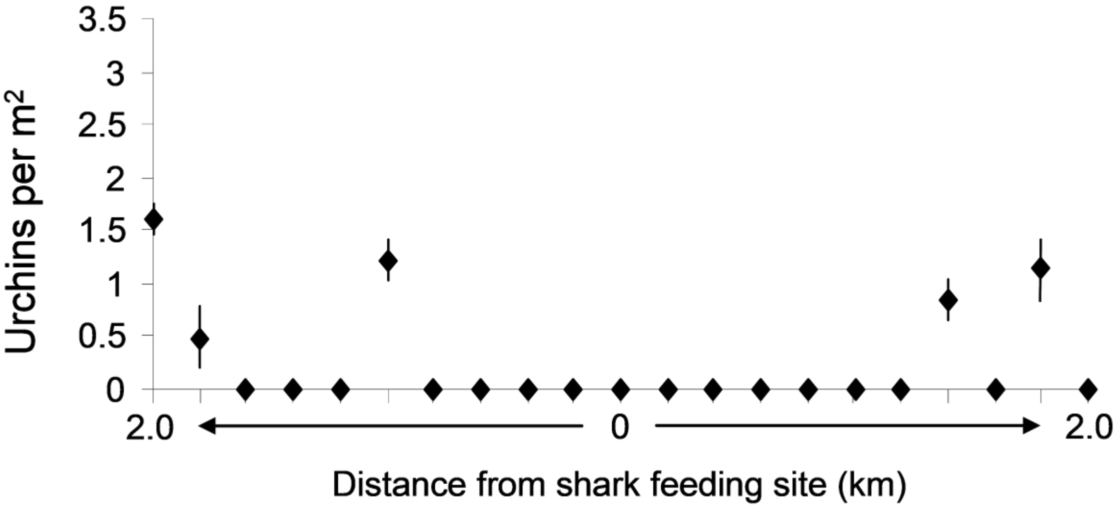


Figure S4.1 Densities of sea urchins *Diadema antillarum* relative to distance from the shark provisioning site (located at Distance = 0). Means ± 1 SE are shown, which are derived from 36 1-m^2 quadrats at each site.