Yates, Peter Matthew (2014) ***Diversity in shark nursery area function in the Great Barrier Reef*****. PhD Thesis, James Cook University.**

https://doi.org/10.25903/zp3z%2D2d35

Yates, Peter Matthew (2014) ***Diversity in shark nursery area function in the Great Barrier Reef*****. PhD thesis, James Cook University.**

Diversity in Shark Nursery Area Function in the Great Barrier Reef

Thesis submitted by
Peter Matthew Yates
BSc Honours (University of Queensland)

For the degree of
Doctor of Philosophy
Centre for Sustainable Tropical Fisheries and Aquaculture
& College of Marine and Environmental Sciences
James Cook University
Townsville, Queensland
December 2014

STATEMEMENT OF ACCESS

I, the undersigned author of this work, understand that James Cook University will make this thesis available within the University Library, and via the Australian Digital Theses network, for use elsewhere. I declare that the electronic copy of this thesis provided to the James Cook University Library is an accurate copy of the print thesis submitted, within the limits of the technology available.

I understand that, as an unpublished work, a thesis has significant protection under the Copyright Act and;

> All users consulting this thesis must agree not to copy or closely paraphrase it in whole or in part without the written consent of the author; and to make proper public written acknowledgement for any assistance which they obtain from it. They must also agree to obtain prior written consent from the author before use or distribution of all or part of this thesis within 12 months of its award by James Cook University.

Beyond this, I do not wish to place any restrictions on access to this thesis.

5th December 2014

Signature Date

STATEMEMENT OF SOURCES

DECLARATION

I declare that this thesis is my own work and has not been submitted in any form for another degree or diploma at any university or other institution of tertiary education. Information derived from the published or unpublished work of others has been acknowledged in the text and a list of references is given.

5th December 2014

Signature Date

STATEMEMENT ON THE CONTRIBUTION OF OTHERS

Financial Support

- Australian Government’s National Environmental Research Program
- Australian Postgraduate Award
- College of Marine and Environmental Sciences, James Cook University
- Oceania Chondrichthyan Society (travel support)
- Passions of Paradise, Cairns (travel support)

In-Kind Support

- Centre for Sustainable Tropical Fisheries and Aquaculture, James Cook University
- College of Marine and Environmental Sciences, James Cook University

Data Collection

- Stephen Moore, James Cook University
- Jonathan Smart, James Cook University
- Field volunteers, including Girringun Aboriginal Rangers

Tag Deployment (Chapter 7)

- Dr. Andrew Tobin, James Cook University
- Jonathan Smart, James Cook University
- Dr. Alastair Harry, James Cook University

- Staff and students at the Centre for Sustainable Tropical Fisheries and Aquaculture, James Cook University
- Staff of the Queensland Government Fisheries Observer Program and Long Term Monitoring Project

Statistical and Analytical Support

- Prof. Colin Simpfendorfer, James Cook University
- Dr. Michelle Heupel, Australian Institute of Marine Science
- Dr. Andrew Tobin, James Cook University
- Prof. Rhondda Jones, James Cook University
- Prof. Marcus Sheaves, James Cook University

Supervision and Editorial Support

- Prof. Colin Simpfendorfer, James Cook University
- Dr. Michelle Heupel, Australian Institute of Marine Science
- Dr. Andrew Tobin, James Cook University

Provision of Spatial Data

- Maps in Chapters 3 and 7 incorporate spatial data that are copyright Commonwealth of Australia (Great Barrier Reef Marine Park Authority; 2012).
- Mangrove data (Chapter 5) was provided by the State of Queensland (Department of Environment and Resource Management; 2012).

PERMITS AND ETHICS

Field sampling for this thesis was conducted under a Queensland Department of Agriculture, Fisheries and Forestry General Fisheries Permit (no. 144482) and Great Barrier Reef Marine Park Authority Permit (no. G11/34618.1).

The research presented and reported in this thesis was conducted in compliance with the National Health and Medical Research Council's Australian Code of Practice for the Care and Use of Animals for Scientific Purposes, 7th Edition, 2004 and the Queensland Animal Care and Protection Act, 2001. All procedures were approved by James Cook University's Animal Ethics Committee (no. A1566, 1933).

PUBLICATIONS ARISING FROM THIS THESIS

Yates PM, Heupel MR, Tobin AJ, Simpfendorfer CA (2012) Diversity in young shark habitats provides the potential for portfolio effects. Mar Ecol Prog Ser 458:269-281

Yates PM, Heupel MR, Tobin AJ, Moore SK, Simpfendorfer CA (2015) Diversity in immature shark communities along a tropical coastline. Mar Freshw Res 66. doi: 10.1071/MF14033

Yates PM, Heupel MR, Tobin AJ, Simpfendorfer CA (2015) Spatio-temporal occurrence patterns of young sharks in tropical coastal waters. Estuar Coasts. doi: 10.1007/s12237-015-9952-4

Yates PM, Heupel MR, Tobin AJ, Simpfendorfer CA (2015) Ecological drivers of shark distributions along a tropical coastline. PLoS ONE 10:e0121346

Yates PM, Tobin AJ, Heupel MR, Simpfendorfer CA (In preparation) Benefits of marine protected areas for tropical coastal sharks

Simpfendorfer CA, Tobin AJ, Heupel MR, Yates PM, Munroe SE (2014) Drivers of juvenile shark biodiversity and abundance in inshore ecosystems of the Great Barrier Reef. Final report for NERP Tropical Ecosystems Hub, Project 6.2

CONFERENCE AND MEETING PRESENTATIONS

Yates PM, Fritsches KA, Hart NS (2011) What do sharks and rays see? Spectral sensitivity and temporal resolution in elasmobranchs. Oceania Chondrichthyan Society, Gold Coast (Best Student Poster Award)

Yates PM, Heupel MR, Tobin AJ, Simpfendorfer CA (2012) Variability in shark assemblage along an environmentally heterogeneous coastal stretch. School of Earth and Environmental Sciences Conference, Townsville (Outstanding Presentation Award)

Yates PM, Simpfendorfer CA, Heupel MR, Tobin AJ (2013) Diversity in shark nursery areas along a tropical coastline. National Environmental Research Program, Cairns

Yates PM, Simpfendorfer CA, Heupel MR, Tobin AJ, Moore SM (2013) Diversity in immature shark communities along a tropical coastline. School of Earth and Environmental Sciences Conference, Townsville

Yates PM, Simpfendorfer CA, Heupel MR, Tobin AJ, Moore SM (2013) Diversity in immature shark communities along a tropical coastline. Oceania Chondrichthyan Society, Brisbane

Yates PM, Simpfendorfer CA, Heupel MR, Tobin AJ, Moore SM (2013) Diversity in immature shark communities along a tropical coastline. Australian Marine Sciences Association, Gold Coast

Yates PM, Simpfendorfer CA, Heupel MR, Tobin AJ, Moore SM (2014) Diversity in shark nursery area function in the Great Barrier Reef. Sharks International, Durban

ACKNOWLEDGMENTS

I have been fortunate to work with some excellent scientists during this project. I am especially grateful to my advisors, Colin Simpfendorfer, Michelle Heupel and Andrew Tobin for supporting my professional development in every way possible. Colin, thank you for the opportunity to undertake a fascinating and well-resourced project, and for always making time to discuss my results and help me to see the forest for the trees. To Michelle, thank you for your meticulous reviews that helped me to improve my writing and develop clear and precise ideas. Andy, your extensive knowledge of coastal systems has been extremely helpful. Thank you for trusting us with the Viking, it made field work much easier. I have had a fantastic PhD experience and I look forward to collaborating with each of you in the future.

I am very grateful to Steve Moore for a significant contribution to data collection. Your experience, hard work and dedication were critical to the success of this project. This project was only possible with the skill and boundless enthusiasm of numerous field volunteers. In particular, I would like to thank Lauren Meyer, Teleah Healy, Madi Green, Samantha Munroe, Chris Mull, Thimo Ruediger, Frank Fingerlos, Nick Hill, Ari Sztypel, Merritt Adkins, Vinay Udyawer, Emilia Chorazyczewska, Fernanda de Faria, Daniela Waltrick, Chris Mirbach and Daniel Kraver. I am grateful to the Girringun Aboriginal Rangers for assisting with data collection in Cardwell. I would also like to thank the commercial and recreational fishers, field volunteers, JCU personnel, the Queensland Government Fisheries Observer Program and Long Term Monitoring Project for contributing to tag-recapture data.

Each member of the Centre for Sustainable Tropical Fisheries and Aquaculture supported me during this project and provided a great team environment. I am especially grateful to Jonathan Smart for generously assisting in the field and with database queries, Al Harry for advice on assigning life-history stages, and Leanne Currey for many motivating conversations. I would also like to thank Elodie Lédée, Vinay Udyawer, Merritt Adkins and Mario Espinoza for teaching me new skills in various computer programs.

Dedicated staff at the College of Marine and Environmental Sciences ensured the smooth running of my candidature. In particular, I would like to thank Andrew Norton, Rebecca Steele, Melissa Crawford, Jo Scheffler, Beth Moore, Angela Ryan, Glen Connolly, Clive Grant and Rob Scott for help with many little things that made a big difference. I am grateful to James Moloney and Adella Edwards for teaching me GIS skills; and Rhondda Jones and Marcus Sheaves for valuable statistical advice. In addition, much of my statistical ability is credited to the fantastic courses and books by Alain Zuur and Elena Ieno. I hope to see you again on your next trip to Australia!

To my friends in Townsville, I have benefited enormously from the comradery we have shared. Thank you for adding so much richness to my PhD experience and for broadening my view of the world. In addition to those mentioned above (and others), I would like to thank Chris Cleguer for lots of advice and for inviting me to catch dugongs; a real highlight of my PhD. I’ve thoroughly enjoyed sharing an office with you. Thanks also to Kim Riskas, Taka Shimada, Jordan Matley and Madi Green for many fun times and for your support. I am also grateful to Susan Theiss for being a mentor for me throughout my honours and PhD research. To Miranda, I could write a second thesis describing how important your support has been over the years. Without you I would have accomplished a lot less.

Finally, I would like to thank my family for helping me reach this point. Jeffa, thanks for supporting me from across the country, your random snapchats provided many happy breaks from study. Andy and Monica, it was great having your friendly faces down the road. Thank you for the awesome chills and dinners. The biggest thanks of all go to my parents. There are no words to express how grateful I am for everything that you have done to help me achieve my dreams. Ever since I declared as a kid my plan to become “one of those people who drives boats and tags sharks”, you helped me get there; and so this thesis is dedicated to you!

TABLE OF CONTENTS

STATEMEMENT OF ACCESS i
STATEMEMENT OF SOURCES ii
STATEMEMENT ON THE CONTRIBUTION OF OTHERS iii
PERMITS AND ETHICS v
PUBLICATIONS ARISING FROM THIS THESIS vi
CONFERENCE AND MEETING PRESENTATIONS vii
ACKNOWLEDGMENTS viii
TABLE OF CONTENTS x
LIST OF FIGURES xii
LIST OF TABLES xvii
LIST OF PLATES xx
LIST OF APPENDICES xxi
ABSTRACT 1
CHAPTER 1
General Introduction 5
CHAPTER 2
Diversity in Young Shark Habitats Provides the Potential for Portfolio Effects 11
    2.1 Introduction 12
    2.2 Diversity in young shark habitats 16
    2.3 Potential drivers of portfolio effects in sharks 23
    2.4 Implications for management and conservation 28
CHAPTER 3
General Methods 35
    3.1 Study sites 36
    3.2 Survey design 37
    3.3 Sampling methods 38
    3.4 Animal processing 39
    3.5 Determining life-history stage 40
    3.5 Environmental and spatio-temporal data 41
CHAPTER 4
Diversity in Immature Shark Communities along a Tropical Coastline 52
    4.1 Introduction 53
    4.2 Methods 55
    4.3 Results 57
        4.3.1 Shark size and life-history stage 57
        4.3.2 Immature shark community structure 58
    4.4 Discussion 61
        4.4.1 Shark size and life-history stage 62
        4.4.2 Variation in immature shark community structure 63
        4.4.3 Diversity in shark nursery function 66

CHAPTER 5

Ecological Drivers of Shark Distributions along a Tropical Coastline 77
5.1 Introduction 78
5.2 Methods 81
5.2.1 Site variability 81
5.2.2 Species associations 82
5.2.3 Variables influencing shark catch 82
5.3 Results 85
5.3.1 Catch composition 85
5.3.2 Site variability 85
5.3.3 Species associations 86
5.3.4 Variables influencing shark catch 87
5.4 Discussion 89

CHAPTER 6

Spatio-temporal Occurrence Patterns of Young Sharks in Tropical Coastal Waters ... 107
6.1 Introduction 108
6.2 Methods 110
6.3 Results 111
6.3.1 Catch composition 111
6.3.2 Occurrence patterns 112
6.4 Discussion 115

CHAPTER 7

Benefits of Marine Protected Areas for Tropical Coastal Sharks 130
7.1 Introduction 131
7.2 Methods 134
7.2.1 Fishery and marine protected area description 134
7.2.2 Data collection 135
7.2.3 Shark abundance 136
7.2.4 Length-frequency distribution 137
7.2.5 Species composition 138
7.2.6 Tag-recaptures 139
7.3 Results 139
7.3.1 Shark abundance 139
7.3.2 Length-frequency distribution 140
7.3.3 Species composition 141
7.3.4 Tag-recaptures 142
7.4 Discussion 144

CHAPTER 8

General Discussion 159
8.1 Conclusions and implications 160
8.2 Future research directions 165
REFERENCES 169
APPENDICES 203

LIST OF FIGURES

Figure 2.1 Approximate areas utilised by neonate or young-of-the-year (YOY) common blacktip *Carcharhinus limbatus* (grey circles) and sandbar *Carcharhinus plumbeus* (black circles) sharks in the Gulf of Mexico and North Atlantic Ocean as indicated by capture locations in McCandless et al. (2002, 2007a). Note that a range of areas and habitats are utilised, however not all of these will be classified as nurseries according to criteria in Heupel et al. (2007). 32

Figure 2.2 Young-of-the-year (YOY) bull shark *Carcharhinus leucas* abundance in eight estuarine embayments along the Texas coast (A = whole region, B–I = locations corresponding to Table 2.1). Inter-annual variation in $\log_{10}$ catch per unit effort (CPUE; sharks h^{-1}) within each site is evident (B–I; circles = annual mean). Abundance in some sites fluctuates above and below the population mean (broken line), and therefore they vary in their suitability to meet the first criterion for a shark nursery (abundance in the area is greater than mean abundance over all areas; Heupel et al. 2007). Portfolio effects may operate across these YOY habitats because variability in mean CPUE for the whole region (A) is less than the variability in individual sites. (From Froeschke et al. 2010b. With permission)............................33

Figure 3.1 Study region. Google Earth^{TM} aerial image of the nine study bays and their location along northern Queensland, Australia. Four of the bays were sampled once (grey text) and five were selected for ongoing seasonal sampling for Chapters 4–7 (white text)...42

Figure 3.2 Rockingham Bay. Longline (black lines) and gill-net (grey lines) shots within 16 transect strips (dashed lines). Diagonal-shading and no-diagonal-shading indicate areas closed and open to commercial gill-net fishing, respectively. Black fill represents inshore reef habitat. Dark-grey shading represents mangroves. Dash-dot lines indicate bathymetry..43

Figure 3.3 Bowling Green Bay. Longline (black lines) and gill-net (grey lines) shots within 16 transect strips (dashed lines). Diagonal-shading and no-diagonal-shading indicate areas closed and open to commercial gill-net fishing, respectively. Black fill represents inshore reef habitat. Dark-grey shading represents mangroves. Dash-dot lines indicate bathymetry..44

Figure 3.4 Upstart Bay. Longline (black lines) and gill-net (grey lines) shots within 16 transect strips (dashed lines). Diagonal-shading and no-diagonal-shading indicate areas closed and open to commercial gill-net fishing, respectively. Black fill represents inshore reef habitat. Dark-grey shading represents mangroves. Dash-dot lines indicate bathymetry..45

Figure 3.5 Edgecumbe Bay. Longline (black lines) and gill-net (grey lines) shots within 16 transect strips (dashed lines). Diagonal-shading and no-diagonal-shading indicate areas closed and open to commercial gill-net fishing, respectively. Black fill represents inshore reef habitat. Dark-grey shading represents mangroves. Dash-dot lines indicate bathymetry..46

Figure 3.6 Repulse Bay. Longline (black lines) and gill-net (grey lines) shots within 16 transect strips (dashed lines). Diagonal-shading and no-diagonal-shading indicate areas closed and open to commercial gill-net fishing, respectively. Black fill represents inshore reef habitat. Dark-grey shading represents mangroves. Dash-dot lines indicate bathymetry. 47

Figure 3.7 Gill-net (top) and longline (bottom) sampling gear. A = float line, B = lead line, C = anchor, D = large inflatable buoy, E = small marker buoy, F = longline mainline, G = gangion. Water column is indicated in blue. Diagrams are not drawn to scale. 48

Figure 4.1 Length-frequency distributions of the most abundant sharks. Lengths at 50% maturity (reviewed in Last & Stevens 2009, Harry 2011) are denoted by dashed lines (larger dashes for *Carcharhinus limbatus*, *B*). n = the number of length measurements recorded for each species. Bar shading denotes the sampling method (white = gill-net, grey = longline). Data are from years 2012 and 2013. 69

Figure 4.2 Comparison of cumulative length profiles between immature (grey) and mature (black) sharks. Data are pooled into 100-mm bins and span years 2012 and 2013. 70

Figure 4.3 Immature shark catch compositions. Mean relative abundance and species composition of immature sharks in five bays. Count data are averaged across sampling rounds. Data are from years 2012 and 2013. 71

Figure 4.4 Ordination of immature shark communities. Non-metric multidimensional scaling (MDS) ordination of the Bray-Curtis similarity matrix derived from the catch of immature sharks from 15 species groupings (*Carcharhinus tilstoni* and *Carcharhinus limbatus* were grouped together). Each symbol appears twice, with narrow outlines for 2012 samples and thick outlines for 2013 samples. Stress value is shown in the top-right corner. 72

Figure 5.1 Length-frequency distributions of blacktip *Carcharhinus tilstoni/Carcharhinus limbatus*, pigeye *Carcharhinus amboinensis* and scalloped hammerhead *Sphyrna lewini* sharks. Bar shading denotes the sampling method (dark grey = longline, light grey = gill-net). Lengths at 50% maturity (reviewed in Last & Stevens 2009, Harry 2011) are denoted by broken lines (larger dashes for the common blacktip shark; A). The lengths at 50% maturity for common blacktip, pigeye and scalloped hammerhead sharks differ between sexes and so the smallest is given (male in all cases). Data are from years 2012–2014. 97

Figure 5.2 Relative importance of ecological variables. Parameters are listed according to mean Relative Variable Importance (RVI) across all species/sampling-method combinations. Parameters that were ubiquitous within the confidence set (i.e. models with ΔAIC < 2) have a RVI value of 1.0. The numbers of models included in model averaging are provided in parentheses. 98

Figure 5.3 Modelled relationships between the abundance of immature blacktip sharks *Carcharhinus tilstoni/Carcharhinus limbatus* in gill-nets and highly influential variables**.** Shading represents 95% confidence intervals and points are partial residuals. Effects were plotted with additional variables held at their medians.

The model containing turbidity, distance to mangroves and depth had dispersion statistic = 1.15 and negative binomial variance parameter *k* = 0.32. Note that low values of secchi depth indicate high turbidity. 99

Figure 5.4 Modelled relationships between the abundance of immature pigeye sharks *Carcharhinus amboinensis* and highly influential variables in longline (A) and gill-net (B, C) samples. Shading represents 95% confidence intervals and points are partial residuals. Effects were plotted with additional variables held at their medians. To visualise interactions, cross-sections were taken at the 10th, 50th and 90th percentiles of the second variable of interest. The plotted longline model had dispersion statistic = 1.00 and negative binomial variance parameter *k* = 0.13. The plotted gill-net model had dispersion statistic = 0.84 and *k* = 0.11. Note that low values of secchi depth indicate high turbidity. 100

Figure 5.5 Modelled relationships between the abundance of immature scalloped hammerhead sharks *Sphyrna lewini* in gill-nets and highly influential variables. Shading represents 95% confidence intervals and points are partial residuals. Effects were plotted with additional variables held at their medians. The influence of turbidity is plotted at the 10th, 50th and 90th percentiles of salinity. The model containing turbidity, salinity and temperature had dispersion statistic = 0.82 and negative binomial variance parameter *k* = 0.16. Note that low values of secchi depth indicate high turbidity...101

Figure 6.1 Length-frequency distributions of blacktip *Carcharhinus tilstoni/Carcharhinus limbatus* (A), pigeye *Carcharhinus amboinensis* (B), scalloped hammerhead *Spynra lewini* (C) and spot-tail *Carcharhinus sorrah* (D) sharks. Bar shading denotes life-history stage (white = neonate, light grey = YOY, medium grey = juvenile > 1 year, dark grey = adult). Data are pooled across bays, seasons, years and sampling methods. Note that neonates are a subset of YOY. Data are from years 2012–2014. 122

Figure 6.2 Temporal distribution of neonate (A) and young-of-the-year (YOY; B) sharks. Black circles represent individual sharks. Grey shading delineates sampling rounds. Upper-case letters above the plot indicate the designated season; DS = dry season, EW = early wet season, LW = late wet season, '–' = data excluded from seasonal analyses. Note that YOY includes neonates. Points are jittered on the y axes to aid visualisation of individual points..123

Figure 6.3 Young-of-the-year (A) and neonate (B) blacktip shark *Carcharhinus tilstoni/Carcharhinus limbatus* occurrence in gill-nets. Black lines indicate the estimated probability of occurrence, grey boxes are 95% confidence intervals, and grey circles are partial residuals. Bays that do not share a lower-case letter were significantly different (Tukey multiple comparisons test, *P* < 0.05; Appendix 8). RO = Rockingham, BG = Bowling Green, UP = Upstart, ED = Edgecumbe, RE = Repulse. DS = dry season (May–June), EW = early wet season (October–December), LW = late wet season (January–April). Confidence intervals were not plotted for groups with zero encounters. Data are from years 2012–2014. 124

Figure 6.4 Seasonal variation in the occurrence of YOY pigeye sharks *Carcharhinus amboinensis* in longlines (A) and gill-nets (B). Black lines indicate the estimated probability of occurrence, grey boxes are 95% confidence intervals, and grey circles are partial residuals. DS = dry season (May–June), EW = early wet season (October–December), LW = late wet season (January–April). Confidence intervals were not plotted for groups with zero encounters. Data are from years 2012–2014. 125

Figure 6.5 Spatial variation in the occurrence of young-of-the-year scalloped hammerhead sharks *Sphyrna lewini* in gill-nets. Black lines indicate the estimated probability of occurrence, grey boxes are 95% confidence intervals, and grey circles are partial residuals. Bays that do not share a lower-case letter were significantly different (Tukey multiple comparisons test, P < 0.05; Appendix 10). RO = Rockingham, BG = Bowling Green, UP = Upstart, ED = Edgecumbe, RE = Repulse. Confidence intervals were not plotted for groups with zero encounters. Data are from years 2012–2014. 126

Figure 6.6 Seasonal variation in the occurrence of YOY spot-tail sharks *Carcharhinus sorrah* in longlines. Black lines indicate the estimated probability of occurrence, grey boxes are 95% confidence intervals, and grey circles are partial residuals. DS = dry season (May–June), EW = early wet season (October–December), LW = late wet season (January–April). Data are from years 2012–2014. ……………………………………………………………………………..127

Figure 7.1 Spatial distribution of fishery-dependent and fishery-independent sampling within coastal waters of the Great Barrier Reef Marine Park (GBRMP). Diagonal shading = closed zones, no shading = open zones. Nine labelled bays were included in investigation of movements between locations (Aim 4): RO = Rockingham Bay, HB = Halifax Bay, CB = Cleveland Bay, BG = Bowling Green Bay, UP = Upstart Bay, AB = Abbot Bay, ED = Edgecumbe Bay, WD = Woodwark/Double Bays, RE = Repulse Bay. The broken line in panel A denotes the outer extent of the GBRMP. Additional detail of sampling within Cleveland and Bowling Green Bays is provided in panel B. In panel B, black circles = longline samples and grey circles = gill-net samples. 150

Figure 7.2 Significant effects of the factor ‘zone’ on shark abundance. Circles are estimated shark abundance (white = open zone, black = closed zone) and vertical lines are 95% confidence intervals. Significant interactions between zone and bay were detected in panels B, C and D. Lower-case letters denote significantly different groups (Tukey multiple comparisons, *P* < 0.05). Note that the y axes vary among panels. ………………………………………………………………………..151

Figure 7.3 Significantly different length-frequency distributions between open (light grey) and closed (dark grey) zones (Kruskal-Wallis rank sum test and Kolmogorov-Smirnov test, *P* < 0.05). Broken lines indicate sample median. Data are pooled across bays. Note that the axes vary among panels. 152

Figure 7.4 Geographic scale of movement (A) and movement among zone types (B) as indicated by tag-recapture locations. Points in panel A indicate the minimum distance travelled between the first and last capture of each individual. Values on the right-hand-side of panel A indicate two large movements beyond 400 km. MC = moved from an open zone to a closed zone, MO = moved from a closed zone to an open zone, SC = stayed in closed zone/s, SO = stayed in open zone/s. Species are listed in decreasing order of mean distance travelled. Only individuals with precise capture and recapture locations are included. 153

Figure 7.5 Proportion of sharks that remained within (dark grey) and left (light grey) their initial capture location (panel A) or zone type (panels B and C). Panel C shows movements of recaptured sharks that were tagged in Cleveland Bay closed zones, and recaptured in Cleveland Bay closed zones (dark grey) or elsewhere (light grey). Numbers above the bars indicate the total number of recaptured sharks that were initially tagged in each category. RO = Rockingham Bay, HB = Halifax Bay, CB = Cleveland Bay, BG = Bowling Green Bay, UP = Upstart Bay, AB = Abbot Bay, ED = Edgecumbe Bay, WD = Woodwark/Double Bays, RE = Repulse Bay, Other = all other locations. Panel A includes 44 additional sharks with approximate capture locations. ……………………………………………………………………………..154

Figure 7.6 Times at liberty verses minimum distances travelled for shark species with > 10 recaptures. Each point represents a recaptured individual. Note that the axes vary among panels. 155

LIST OF TABLES

Table 2.1 Mean $\log_{10}$ catch per unit effort (CPUE; sharks hour^{-1}) and variability in $\log_{10}$ CPUE of young-of-the-year (YOY) bull sharks *Carcharhinus leucas* within eight Texas embayments between years 1976–2006 (John T. Froeschke pers. comm.). Note that variability in abundance across the region (Total) is less than variability in abundance in individual embayments, suggesting that portfolio effects may occur across this region. 34

Table 3.1 Comparison of nine sampled bays listed in order from north to south. Bays marked with an asterisk were selected for repeated sampling. Geographic measurements and assessment of coastline type were conducted using Google Earth Pro^{TM}. Coastline (MM:S:R) = the percentage of coastline that was mudflat or mangrove (MM), sandy beach (S) and rocky (R) shore, respectively. Orientation = direction of the bay towards open water. Values in parentheses are estimated average annual runoff volumes (km^3) from the region’s major catchment basins. 49

Table 3.2 Timing of eight fishery-independent sampling rounds across four years. Nine bays were sampled in the first round (dark grey) and five bays were sampled in all subsequent rounds (light grey). Rounds occuring during January–March were considered late wet-season; May–June, dry season; and October–Decemebr, early wet-season. 50

Table 3.3 Summary of fishing effort in nine study bays. Data are from years 2011–2014 combined. Bays marked with an asterisk were selected for seasonal sampling spanning the period of January 2012 to March 2014. Standardised soak hours = sum of 100-hook-hours and 100 m-net-hours for longlines and gill-nets, respectively. Hook number is mean per shot ± SD. 51

Table 4.1 Summary of fishing effort in five study bays. Standardised soak hours = sum of 100-hook-hours and 100 m-net-hours for longlines and gill-nets, respectively. Data are from years 2012 and 2013. 73

Table 4.2 Life-history stage composition of 22 shark species captured during fishery-independent sampling along the tropical coast of Queensland. Data are pooled across study bays and sampling rounds (years 2012 and 2013 only). The number of sharks in each category is followed by its proportion of the species’ total maturity-assigned catch in parentheses. YOY = young-of-the-year. In the presence of > 1 life-history stage the most prevalent stage is indicated in bold. 74

Table 4.3 Comparison of the proportions of immature sharks among five bays along the tropical coast of Queensland. Data are pooled across years and sampling rounds (2012 and 2013 only). Proportion of immature sharks in the catch is followed by the total number of maturity-assigned sharks in parentheses. Uneven proportions of immature:mature individuals are indicated by asterisk (Chi-square test, $df = 1$, $P < 0.05$). 75

Table 4.4 Species contributions to average Bray-Curtis dissimilarities among bays (SIMPER). Results are for years 2012 and 2013 combined. Only bays that were distinguished on the basis of immature shark communities (ANOSIM) are included. Av. diss. = average of the Bray-Curtis dissimilarities between all pairs of samples. Species that contributed up to 70% of cumulative contribution to Av. diss. are ordered in decreasing contribution. Average relative abundance values are square-root transformed as is relevant to the dissimilarity calculations. 76

Table 5.1 Spatial variation in ecological variables. Data were pooled across sampling rounds and years. Values are mean ± 1 SD. For each variable, bays without a shared letter were significantly different (multiple comparison test following Kruskal-Wallis rank sum test, $df = 4$, $P < 0.05$). 102

Table 5.2 Measures of association involving blacktip, pigeye and scalloped hammerhead sharks using longlines and gill-nets. Included are the species/life-history-stage groups with the highest (High AS) and lowest (Low AS) association values. I = immature, M = mature, n = the total number of sharks in the comparison group. Trips = the number of trips that caught the comparison group, Both = the number of trips that caught the comparison group and the focal group (underlined), AS = Association Statistic, % CO = percent common occurrence. All Genus abbreviations are for *Carcharhinus*, *Rhizoprionodon* or *Sphyna*. The maximum value of the Association Statistic, provided in italics, depended on the proportion of trips that caught the focal group. Comparison groups with ≤ 10 sharks were excluded. 103

Table 5.3 Comparison of best-performing models of immature shark abundance. Each row contains the intercept and coefficients that comprised a single model, along with the number of parameters (*df*), log-likelihood and Akaike metrics. All models contained fishing effort as an offset variable. AIC = Akaike Information Criterion, ΔAIC = increase in AIC relative to the lowest-AIC model, *w* = Akaike weight. 104

Table 5.4 Effects of highly influential variables (identified using Relative Variable Importance values; RVI). Standardised model-averaged coefficients (with shrinkage) ± standard error are followed by the associated *P*-value in parentheses (i.e. Pr(>|Z|)). Coefficients are on the linear (log) scale and so their effect is additive. Variables are listed according to mean RVI across species/sampling-method combinations. Asterisks denote variables that were not significant in model averaging but were significant ($P < 0.05$*; $P < 0.0001$**) in a single model containing only high-RVI variables. Although the coefficients for turbidity for pigeye and scalloped hammerhead sharks were positive, strong interaction with salinity or depth produced an overall negative relationship with decreasing turbidity (Figure 5.4; Figure 5.5).106

Table 6.1 Total numbers of neonate and young-of-the-year (YOY) sharks. Data are from years 2012–2014. 128

Table 6.2 Significance of spatial and temporal factors (likelihood ratio test) in logistic regression models. Data are from years 2012–2014. 129

Table 7.1 Summary of standardised fishery-independent surveys in open and closed zones within three study bays (for Aims 1–3). Zoning (C:O) = the respective percentage of total bay area that was closed (C) and open (O) to commercial gill-net fishing. Standardised soak hours = sum of 100-hook-hours and 100 m-net-hours for longlines and gill-nets, respectively. Number of shots and standardised soak hours in closed zones (C) are followed by those is open zones (O). 156

Table 7.2 Relationships between shark abundance and spatial covariates. Results are from likelihood ratio tests between nested generalised linear mixed models (GLMM). The interaction term was removed if it was not significant. OLRI = observation-level random intercept. Non-significant interactions were removed prior to the calculation of main-effect parameters. 157

Table 7.3 Comparison of length-frequency distributions between bays and zones. KW = Kruskal-Wallis rank sum test, KS = Kolmogorov-Smirnov test. LL = longline, GN = gill-net. Dashes indicate cases where differences in shape precluded comparison of length-frequency distributions using the Kruskal Wallace test. Crosses indicate insufficient sample sizes for analysis (i.e. < 15 observations in ≥ 1 group). Bay comparisons were limited to Rockingham and Bowling Green Bays for pigeye sharks in longline samples, Rockingham and Bowling Green Bays for blacktip sharks in longline samples, and Rockingham and Upstart Bays for spot-tail sharks in longline samples. 158

LIST OF PLATES

Plate 1 Sunrise in Repulse Bay (August 2012). 5

Plate 2 Coastal environments can comprise a mosaic of habitat types (top left = mudflat in Upstart Bay; top right = mangrove forest in Rockingham Bay; bottom left = sandy beach in Edgecumbe Bay; bottom right = rocky reef in Rockingham Bay). 11

Plate 3 Gill-net survey from Research Vessel 'Viking' in Edgecumbe Bay (June 2012). ………………………………………………………………………….35

Plate 4 Coastal environments of northern Queensland are occupied by a variety of shark species (clockwise from top left: zebra shark *Stegostoma fasciatum*, blacktip shark *Carcharhinus tilstoni* or *Carcharhinus limbatus*, tiger shark *Galeocerdo cuvier*, whitecheek shark *Carcharhinus coatesi*, spot-tail shark *Carcharhinus sorrah*, pigeye shark *Carcharhinus amboinensis*). 52

Plate 5 Turbid conditions in Repulse Bay (February 2013). 77

Plate 6 Repulse Bay (February 2013). 107

Plate 7 Tagging a longline-caught nervous shark *Carcharhinus cautus* in a Conservation Park Zone within Upstart Bay (February 2013). 130

Plate 8 Sunset in Upstart Bay (January 2012). 159

LIST OF APPENDICES

Appendix 1 Sequence of sampling during each round. Sampling of Cleveland and Halifax Bays, and Upstart and Edgecumbe Bays was overlapping in the first sampling round. 203

Appendix 2 Catch composition of elasmobranchs caught by fishery-independent sampling in five bays along the tropical coast of Queensland. Data, grouped by order and sorted alphabetically, are from 142 days of sampling across seven sampling rounds (2012–2013 only). LL = longline, GN = gillnet. 204

Appendix 3 Comparison of stretch total lengths between two sampling methods. Where only a single length measurement is available it is given as the maximum length with other fields left blank. Kolmogorov-Smirnov (KS) tests compared length-frequency distributions of sharks between sampling methods. Bold text indicates significant differences (*P* < 0.05). Dashes indicate insufficient sample size for comparison of length-frequency distributions. Data are from years 2012 and 2013 only (Chapter 4). 206

Appendix 4 Species and life-history-stage composition of sharks captured during fishery-independent sampling along the tropical coast of Queensland. Numbers represent the number of sharks caught. The number of young-of-the-year (YOY) sharks that were neonates (as indicated by an un-healed umbilical scar) is presented in parentheses. Data are from years 2012 to 2014 (i.e. the full fishery-independent time series) and are pooled across study bays and sampling methods. 207

Appendix 5 Measures of association involving immature blacktip sharks *Carcharhinus tilstoni/Carcharhinus limbatus* using longlines and gill-nets (Chapter 5). I = immature, M = mature. n = the total number of sharks caught in each comparison group, Trips = the number of trips that caught each comparison group, Both = the number of trips that caught the comparison group and ≥ 1 immature blacktip shark, AS = Association Statistic, % CO = percent common occurrence. The maximum value of the Association Statistic, provided in the column headings, depends on the proportion of trips that caught ≥ 1 immature blacktip shark. Groups are listed according to average % CO. Comparison groups with < 10 sharks were excluded. 208

Appendix 6 Measures of association involving immature pigeye sharks *Carcharhinus amboinensis* using longlines and gill-nets (Chapter 5). I = immature, M = mature. n = the total number of sharks caught in each comparison group, Trips = the number of trips that caught each comparison group, Both = the number of trips that caught the comparison group and ≥ 1 immature pigeye shark, AS = Association Statistic, % CO = percent common occurrence. The maximum value of the Association Statistic, provided in the column headings, depends on the proportion of trips that caught ≥ 1 immature pigeye shark. Groups are listed according to average % CO. Comparison groups with < 10 sharks were excluded. 209

Appendix 7 Measures of association involving immature scalloped hammerhead sharks *Sphyrna lewini* using longlines and gill-nets (Chapter 5). I = immature, M = mature. n = the total number of sharks caught in each comparison group, Trips = the number of trips that caught each comparison group, Both = the number of trips that caught the comparison group and ≥ 1 immature scalloped hammerhead shark, AS = Association Statistic, % CO = percent common occurrence. The maximum value of the Association Statistic, provided in the column headings, depends on the proportion of trips that caught ≥ 1 immature scalloped hammerhead shark. Groups are listed according to average % CO. Comparison groups with < 10 sharks were excluded. 210

Appendix 8 Blacktip shark *Carcharhinus tilstoni/Carcharhinus limbatus* logistic regression model coefficients (gill-net data; Chapter 6). Significant factors and pairwise comparisons are indicated by asterisk (*P* < 0.05). RO = Rockingham, BG = Bowling Green, UP = Upstart, ED = Edgecumbe, RE = Repulse. DS = dry season (May–June), EW = early wet season (October–December), LW = late wet season (January–April). Data are from years 2012–2014. 211

Appendix 9 Pigeye shark *Carcharhinus amboinensis* logistic regression model coefficients (Chapter 6). Significant factors and pairwise comparisons are indicated by asterisk (*P* < 0.05). RO = Rockingham, BG = Bowling Green, UP = Upstart, ED = Edgecumbe, RE = Repulse. DS = dry season (May–June), EW = early wet season (October–December), LW = late wet season (January–April). Data are from years 2012–2014. ………………………………………………………………………..212

Appendix 10 Scalloped hammerhead shark *Sphyrna lewini* logistic regression model coefficients (gill-net data; Chapter 6). Significant factors and pairwise comparisons are indicated by asterisk (*P* < 0.05). RO = Rockingham, BG = Bowling Green, UP = Upstart, ED = Edgecumbe, RE = Repulse. DS = dry season (May–June), EW = early wet season (October–December), LW = late wet season (January–April). Data are from years 2012–2014. 213

Appendix 11 Spot-tail shark *Carcharhinus sorrah* logistic regression model coefficients (longline data; Chapter 6). Significant factors and pairwise comparisons are indicated by asterisk (*P* < 0.05). RO = Rockingham, BG = Bowling Green, UP = Upstart, ED = Edgecumbe, RE = Repulse. DS = dry season (May–June), EW = early wet season (October–December), LW = late wet season (January–April). Data are from years 2012–2014. 214

Appendix 12 Significance of spatial and temporal factors (likelihood ratio test) based on penalised likelihood ratios in Firth logistic regression (Chapter 6). Data are from years 2012–2014. Significant factors are indicated by asterisk (*P* < 0.05). 215

Appendix 13 Significant variations in shark abundance between bays (Chapter 7). Circles are estimated shark abundance and vertical lines are 95% confidence intervals. Lower-case letters denote significantly different groups (Tukey multiple comparisons, *P* < 0.05). Note that the y axes vary among panels. 216

Appendix 14 Comparison of length-frequency distributions of Australian sharpnose sharks *Rhizoprionodon taylori* between Rockingham (A), Bowling Green (B) and Upstart (C) Bays (Chapter 7). Groups that do not share the same lower-case letter were significantly different (Kruskal-Wallis multiple comparison test, *P* < 0.05). Data are pooled across management zones. 217

Appendix 15 Non-metric multidimensional scaling (MDS) ordination of shark community structure among bays and zones (Chapter 7). Triangles = Bowling Green Bay, circles = Rockingham Bay, diamonds = Upstart Bay. White symbols = open zone, black symbols = closed zone. 218

Appendix 16 Species contributions to the average Bray-Curtis dissimilarity between open and closed zones (two-way crossed SIMPER; Chapter 7). Species that contributed up to 70% of cumulative contribution to the average dissimilarity (53.28) are ordered by decreasing contribution. Average relative abundance values are fourth-root transformed as is relevant to the dissimilarity calculations. Back-transformed average relative abundances are provided in parentheses. 219

Appendix 17 Shark tagging effort for the collection of tag-recapture data (Chapter 7), including all fishery-dependent and fishery-independent sources. Dark grey = longline shots, light grey = gill-net shots. Note that the distribution of effort between zones and sampling methods varied in Cleveland Bay compared to outside of Cleveland Bay. Shots with missing or unreliable spatial coordinates were excluded as they could not be assigned to a zone. 220

Appendix 18 Tag-recapture summary (Chapter 7). Species are listed in decreasing order of recapture rate. Sex ratio excludes sharks of unknown sex. Species that were rarely captured inshore or were not recaptured are not listed. 221

ABSTRACT

Understanding spatio-temporal patterns in habitat use is critical for assessing the ecological role of a species, its vulnerability to human impacts and environmental change, and the efficacy of conservation and management strategies. Investigating these patterns for young sharks (neonates, young-of-the-year [YOY], and juveniles) can also improve understanding of the functioning of shark nurseries, and the potential benefits of marine protected areas (MPAs). The overall objectives of this thesis were to (1) characterise spatio-temporal patterns in coastal shark distributions, (2) explore the ecological drivers of these patterns, and (3) evaluate the potential implications of heterogeneous space use for population sustainability and the efficacy of coastal MPAs.

Portfolio theory predicts that contributions from a diverse range of young shark habitats may reduce variability in the overall production of adults, and maintain population resilience. This thesis examined case studies of portfolio effects in teleost fish and evaluated the relevance and potential implications of these processes for shark populations. Environmental heterogeneity in young shark habitats can result in locally adapted habitat-use patterns and life-history traits. Therefore, young shark habitats may be differentially impacted by anthropogenic disturbance or environmental change, with different habitats being productive at different times. In addition, increased stability in productivity may occur when the effects of localised disturbance in one area are buffered by production in others. Understanding intra-population variations in abundance and habitat use, and the extrinsic drivers of these, is fundamental to understanding the potential for portfolio effects in shark populations.

In the context of portfolio effects, multi-year fishery-independent surveys of shark communities were used to investigate diversity in shark nursery area function along a 400 km stretch of coastline in north Queensland, Australia. Multivariate analyses were used to explore spatio-temporal variations in immature shark community structure. Generalised linear models were used to identify spatial, seasonal and inter-annual variations in the occurrence or abundance of young sharks, and the ecological drivers of these variations. Potential benefits of MPAs for tropical coastal sharks were explored on the basis of variations in shark abundance, length-frequency distributions and species composition. In addition, tag-recapture data from fishery-dependent and fishery-independent sources were used to investigate the movements of individuals across MPA boundaries.

A total of 1987 sharks from six families and 22 species were captured in fishery-independent surveys, with 19 species of Carcharhiniformes dominating (99.2%) the total catch. Australian sharpnose *Rhizoprionodon taylori* (52%) and blacktip *Carcharhinus tilstoni/Carcharhinus limbatus* (12%) sharks were numerically dominant. Spot-tail *Carcharhinus sorrah* (8%), pigeye *Carcharhinus amboinensis* (6%), scalloped hammerhead *Sphyrna lewini* (5%), milk *Rhizoprionodon acutus* (5%) and whitecheek *Carcharhinus coatesi* (5%) sharks were moderately abundant. In total, 642 sharks were classified as immature, including 383 YOY individuals. Immature sharks from 18 species were present; however, interspecific variation in life-history-stage composition was apparent. Catch data also indicated community-wide spatial structuring of sharks on the basis of body size rather than life-history stage. Multivariate analyses identified significant spatial heterogeneity in immature shark communities among bays. In addition to building on traditional shark nursery paradigms, these results demonstrated that data on nursery function from restricted areas may not accurately portray patterns occurring over broader geographic scales.

General and species-specific patterns in shark abundance were characterised by a range of biotic and abiotic variables. Relationships with turbidity and salinity were similar across multiple species, highlighting the importance of these variables in the functioning of communal shark nurseries (i.e. those used by multiple species). In particular, turbid environments were important for all species at typical oceanic salinities. Mangrove proximity, depth and water temperature were also important, however their influence varied between species. These extrinsic factors, along with intrinsic life-history-associated factors, were identified as potential drivers of interspecific variations in the occurrence of young sharks. Seasonal variations characterised the occurrence of YOY pigeye, YOY spot-tail and neonate blacktip sharks, whereby relative occurrences peaked during all or part of the summer wet season. In contrast, spatial variations were more pronounced for YOY blacktip and scalloped hammerhead sharks, with higher respective occurrences in Repulse and Rockingham Bays compared to other locations. Such varied utilisation of coastal ecosystems has important implications for the management of coastal habitats and the conservation of shark populations.

Species composition varied significantly between management zones, and overall shark abundance was higher inside MPAs. In addition, length-frequency distributions of blacktip and pigeye sharks inside MPAs comprised a greater proportion of larger-bodied individuals compared to those in open zones. Tag-recapture locations indicated repeated or prolonged occupancy of MPAs by some species. These results suggested that sub-bay-sized coastal MPAs may increase the survival of young sharks to maturity or shelter parts of breeding stocks. Therefore, MPAs do not necessarily need to be large to benefit multiple sympatric species comprising diverse life histories and habitat use patterns.

Spatial heterogeneity in shark occurrence and abundance suggested that proximate bays are likely to vary in terms of the services they provide to young sharks, and thus their level of contribution to adult populations. Further, the occurrence of young sharks appeared to be more complex than would be predicted by the timing of parturition alone. The ecological drivers of habitat use identified in this thesis may promote spatial diversity in habitat use along environmentally heterogeneous coastlines, and may therefore have important implications for population resilience. By being among the first studies to investigate the implications of heterogeneous space use by young sharks, this thesis may serve as a model to facilitate future research on portfolio effects and the associated benefits for shark populations.

CHAPTER 1

General Introduction

Plate 1 Sunrise in Repulse Bay (August 2012).

General Introduction

Understanding the spatial ecology of species (including spatio-temporal distributions, habitat use, and movements) is critical for the identification of important habitats and the factors that influence habitat use (Block et al. 2011). This information can improve understanding of a species' vulnerability to anthropogenic impacts and responses to environmental change. It is particularly important to conserve habitats that make disproportionally large contributions to population productivity (Beck et al. 2001, Heupel et al. 2007, Kinney & Simpfendorfer 2009), or enhance population resilience and stability (Schindler et al. 2010). In recognition of the need to identify important habitats, the location and functioning of nurseries has been the focus of extensive research (reviewed in Beck et al. 2001).

Nurseries presumably provide population-level benefits, however not all areas occupied by young individuals are nurseries. In marine environments, nurseries support greater contributions to adult recruitment; and assessment of nursery value should ideally incorporate data on (1) the density of juveniles, (2) growth rates, (3) survival, and (4) recruitment to adult habitats (Beck et al. 2001). However, the identification of nurseries continues to challenge ecologists; mainly due to uncertainty about how nurseries should be defined (Dahlgren et al. 2006, Sheaves et al. 2006), the scarcity of multi-faceted data with adequate spatio-temporal scope (Layman et al. 2006, Heupel et al. 2007), and ambiguity in the number and type of comparison-units to be considered (Sheaves et al. 2006, Froeschke et al. 2010b). Nonetheless, nursery criteria can provide a consistent approach to guide the focus of management efforts towards areas or habitats that are currently most productive. However, the emphasis on identifying nurseries has left the potential implications of habitat diversity largely unexplored. In particular, there are scarce data on the importance of contributions from areas where young individuals occur but which may not currently fulfil nursery criteria. The variable nature of coastal ecosystems and their vulnerability to anthropogenic impacts (Gillanders et al. 2011) suggest that the distribution of highly-productive areas may change over time, and therefore habitat diversity may be an important factor in the sustainability of marine populations (Schindler et al. 2010).

Shark nurseries have received less research attention compared to teleost and invertebrate nurseries (Heupel et al. 2007). Through integration of the theoretical considerations of Beck *et al.* (2001) and their practical application for sharks, Heupel *et al.* (2007) defined shark nurseries as areas with (1) high relative abundance of neonates and young juveniles, (2) site fidelity, and (3) stable use across multiple years. These criteria have been used to identify nurseries for bull sharks *Carcharhinus leucas* in the Gulf of Mexico (Froeschke et al. 2010b) and north-west Atlantic (Curtis et al. 2011), and dusky sharks *Carcharhinus obscurus* in South Africa (Hussey et al. 2009). An area may provide nursery habitat for multiple species, and sympatric young sharks inhabiting ‘communal shark nurseries’ may benefit from reduced predation risk afforded by limited spatio-temporal overlap with mature sharks of multiple species (Simpfendorfer & Milward 1993). Although single-species and communal shark nurseries have been identified, the majority of research has focused on restricted spatial scales, such as within a single coastal bay or estuary (e.g. DeAngelis et al. 2008, Drymon et al. 2014).

Coastal environments can be important for young sharks comprising a diverse range of species (Compagno 1984, McCandless et al. 2007a), presumably because of their potential to provide young sharks with ample food or protection from predators

(Branstetter 1990). Young sharks can be broadly distributed along coastal stretches, where variable abiotic and biotic conditions can influence spatial variations in their habitat use (Froeschke et al. 2010a, Schlaff et al. 2014). Multiple models have been proposed to characterise the use of coastal habitats by sharks through ontogeny. These have been linked with varied life histories (Cortés 2004), and were based on the theoretical optimisation of trade-offs between rapid growth and avoiding predation (Springer 1967, Branstetter 1990, Heithaus 2007, Knip et al. 2010). One model describes species that use coastal nurseries as juveniles before moving offshore to adult habitats (Springer 1967). An alternative model describes species that complete their entire life cycle within coastal environments (Knip et al. 2010). Species described by the second model may roam widely within coastal environments (Parsons & Hoffmayer 2005, Munroe et al. 2014), use comparably restricted areas (Sims et al. 2001), or change their space-use through ontogeny (Knip et al. 2012c). For some coastal species, co-occurrence of immature and mature sharks suggests that not all shark species utilise nurseries (Beck et al. 2001). These varied habitat use patterns have implications for population sustainability. For example, species that depend on coastal environments during critical (Kinney & Simpfendorfer 2009) or all (Knip et al. 2010) life-history stages may be especially vulnerable to the degradation of coastal environments.

Coastal environments of north-eastern Australia are occupied by a diverse range of shark species; including approximately 25 live-bearing carcharhiniform species, most of which give birth entirely or predominantly during the summer wet season (Harry et al. 2011b). Eight of these species are thought to utilise coastal bays as communal nurseries (Simpfendorfer & Milward 1993). Inter- and intraspecific partitioning of space and resources have been observed (Kinney et al. 2011, Knip et al. 2012b); and environmental conditions including freshwater flows (Knip et al. 2011a), turbidity (Kinney 2011) and benthic habitats (Munroe et al. 2014) appear to influence habitat use over small spatial scales (i.e. within a single bay c. 250 km^2). However, this coastal region is typical of many in that the following questions remain unanswered: (1) how does shark community structure and the habitat use of individual species vary across broader spatial scales, (2) what factors influence heterogeneous space use, (3) what are the population-level implications of heterogeneous space use, and (4) are current spatio-temporal management approaches likely to benefit coastal sharks? In particular, the benefits of marine protected areas (MPAs) for mobile species remain poorly understood (Gruss et al. 2011, Knip et al. 2012a). These questions are important avenues of research because understanding spatio-temporal patterns in shark occurrence, and the drivers of these, is critical for assessing the ecological role of a species, its vulnerability to environmental change, and the efficacy of conservation and management strategies.

The overall objectives of this thesis were to characterise spatio-temporal patterns in coastal shark distributions, explore the ecological drivers of these variations, and evaluate the potential implications of heterogeneous space use for population sustainability and the efficacy of coastal MPAs. Although this thesis focused on the occurrence of immature sharks and nursery areas, the importance of mature sharks in influencing this occurrence was also considered. Chapter 2 examined case studies of the implications of heterogeneous space use in teleost fish and evaluated the relevance of these processes for sharks. Chapter 3 described the study region and the field methods for a large-scale fishery-independent survey of shark fauna. Chapters 4–7 explored the theoretical considerations of Chapter 2 in light of real-world data from fishery-independent surveys. Specifically, Chapter 4 documented the shark species and life-history stages present in the study area, characterised the co-occurrence of immature and mature sharks, and investigated spatial variation in immature shark community structure across a broad spatial scale. Chapter 5 then investigated the ecological drivers of heterogeneous space use of the young of individual species. Chapter 6 focused on the spatio-temporal occurrence patterns of young-of-the-year and neonate sharks. Chapter 7 incorporated data on shark abundance, community structure, length-frequency distributions and tag-recaptures to evaluate the effectiveness of MPAs for tropical coastal sharks. Finally, Chapter 8 synthesised information from the previous chapters to provide new insights into the importance of tropical coastal environments for a diverse range of shark species and life-history stages, the population-level implications of heterogeneous space use, and important considerations for future research and the conservation of tropical coastal sharks.

CHAPTER 2

Diversity in Young Shark Habitats Provides the Potential for Portfolio Effects

Plate 2 Coastal environments can comprise a mosaic of habitat types (top left = mudflat in Upstart Bay; top right = mangrove forest in Rockingham Bay; bottom left = sandy beach in Edgecumbe Bay; bottom right = rocky reef in Rockingham Bay).

Accepted as a review paper, 16th April 2011:

Yates PM, Heupel MR, Tobin AJ, Simpfendorfer CA (2012) Diversity in young shark habitats provides the potential for portfolio effects. Mar Ecol Prog Ser 458:269-281

2.1 Introduction

Sharks are high-order predators and a crucial component of marine ecosystems. However, the harvest of sharks has considerable social and economic significance around the world, and therefore many species are heavily utilised in fisheries. The life history characteristics of some shark species increase their vulnerability to exploitation, and estimated population declines in some species (Graham et al. 2001, Dudley & Simpfendorfer 2006) have fuelled global interest in their conservation and management (Dulvy et al. 2008). Effective management of shark populations requires a detailed understanding of essential habitats and of how these are utilised by sharks. Accordingly, the location and functioning of shark nurseries has been a focus of recent research (Heupel et al. 2007, McCandless et al. 2007a, Heupel & Simpfendorfer 2011). Appropriate management of inshore shark nurseries is particularly important because they can be utilised by numerous shark species (Simpfendorfer & Milward 1993) and are increasingly susceptible to a range of anthropogenic impacts and environmental change (Chin et al. 2010, Knip et al. 2010, Koehn et al. 2011).

The majority of marine nursery research has aimed to identify the most productive juvenile habitats in order to guide the focus of management and conservation efforts (Beck et al. 2001). Similarly, the designation of Essential Fish Habitat, Habitat Areas of Particular Concern, and Critical Habitat by the US National Marine Fisheries Service (NMFS) provides additional focus toward habitats that are of high importance to the long-term productivity of fish populations or that are particularly vulnerable to degradation. The juveniles of many marine species are spatially dispersed and utilise a wide range of habitats. For example, young-of-the-year (YOY) common blacktip *Carcharhinus limbatus* and sandbar *Carcharhinus plumbeus* sharks utilise numerous environmentally heterogeneous inshore waters along the Gulf of Mexico and east coast of the USA (Figure 2.1; McCandless et al. 2002, 2007a). Beck et al. (2001) emphasise that marine nursery areas contribute disproportionately to adult stocks, and comprise only a subset of all habitats and regions where juveniles occur. However, comparison of multiple nursery areas in terms of their contributions to the maintenance of adult stocks is difficult to quantify. In addition, it is now well accepted that not all areas or habitats where young sharks are found necessarily function as shark nurseries, and non-nursery habitats may contribute significantly to the adult population in some situations (Dahlgren et al. 2006). For example, changes in environmental or anthropogenic factors may mean that currently productive young shark habitats fail, and other previously less-productive habitats may form a strong component of future production.

Heupel et al. (2007) provided three criteria for the identification of a shark nursery: (1) relatively high abundance of neonates or young juveniles, (2) site fidelity, and (3) stable use across multiple years. These criteria provide a consistent approach to identifying the most important habitats for young sharks. For example, estuarine waters along the entire Texas coast were traditionally regarded as nursery areas for bull sharks *Carcharhinus leucas* based on the presence of young individuals; however only two estuaries function as nurseries for juvenile bull sharks according to the Heupel et al. (2007) criteria (and only one for YOY sharks; Froeschke et al. 2010b). Few other shark (or ray) nurseries have been classified in this way, primarily due to a lack of data with adequate spatial and temporal scope (but see DeAngelis et al. 2008, Hussey et al. 2009, Curtis et al. 2011, Dale et al. 2011). The identification of shark nurseries using these criteria relies on the assumption that the locations of critical young shark habitats (i.e. those classified as nurseries) are stable through time. Similarly, temporal stability in abundance has been used as an indicator of nursery value in teleost fish (Fodrie & Levin 2008, Colloca et al. 2009). However, the assumption of temporal stability in inshore nurseries is potentially problematic given the highly dynamic nature of inshore ecosystems (Robertson & Duke 1987) and their susceptibility to anthropogenic alteration (Chin et al. 2010, Knip et al. 2010).

Locations utilised by young sharks (neonates, YOY, and juveniles) can be classified as either ‘nurseries’ or ‘other young shark habitats’ (a concept originally proposed for teleost fish and invertebrates; Beck et al. 2001). These other habitats are utilised by young sharks, but are used inconsistently or by fewer individuals (Heupel et al. 2007). Further, reduced growth rates, survival and movement to adult populations can diminish the productivity of habitats and thus their suitability to be classified as nurseries (Beck et al. 2001). The contribution of other young shark habitats to the long-term sustainability of shark populations is poorly understood. For example, young school sharks *Galeorhinus galeus* used to be abundant in sheltered inshore systems of Tasmania and Victoria, Australia (Olsen 1954). More recently, Stevens & West (1997) reported relatively low catches of young school sharks in these inshore systems, and estimated that their contribution to total pup production was small (< 10%); and recruitment may now be maintained by production in other areas, such as exposed beaches, that were not traditionally regarded as pupping sites (Olsen 1954). This suggests that although exposed beaches may not have been significant nurseries prior to anthropogenic disturbance (that has resulted in substantially reduced abundance), they may contribute much of the current pup production of school sharks.

Diversity within teleost fish stocks can reduce variability in production and contribute to long-term sustainability (Tilman 1996, Luck et al. 2003, Moore et al. 2010, Schindler et al. 2010). This reduction of variance is known as the portfolio effect (Figge 2004), and has been quantified within a sockeye salmon *Oncorhynchus nerka* stock in Bristol Bay, Alaska (Schindler et al. 2010). Portfolio effects may also be occurring for sockeye salmon in Bear Lake, Alaska (Boatright et al. 2004). These stock complexes are comprised of several hundred discrete breeding populations structured by morphological and life history traits including asynchronous migrations to different spawning habitats (Hilborn et al. 2003, Doctor et al. 2010, Greene et al. 2010). Differences in water temperature between spawning streams are an important driver of this stock structuring (Boatright et al. 2004). Complementary patterns in productivity between these populations are thought to have allowed sockeye salmon stock complexes to sustain productivity despite large-scale environmental variations (Hilborn et al. 2003, Schindler et al. 2010). Further, the variability in commercial landings of sockeye salmon in Bristol Bay is 2.2 times lower than it would be in the presence of a more homogeneous population (i.e. the dominant age classes in the average stream population; Schindler et al. 2010). This variance dampening resulted in ten times fewer fishery closures than would have occurred in the presence of a more homogeneous population (Schindler et al. 2010). In contrast, extensive fish hatchery production and damming in the Snake River Basin, Washington State, appears to have caused synchronisation of > 90% of spawning populations within the stock, raising serious conservation concerns and increasing the variability in annual sockeye salmon landings (Moore et al. 2010).

The definition of shark nurseries described by Heupel et al. (2007) can be used to identify the most heavily and consistently utilised young shark habitats (i.e. nurseries) and is an important tool for the management and conservation of sharks. The Heupel et al. (2007) definition is used to examine whether a specific area is nursery, whereas portfolio effects operate over broader spatial and temporal scales. Thus portfolio theory considers multiple habitats through time rather than focusing on a specific habitat or location. For example, this framework could be used to compare contributions of multiple nursery areas to the adult stock. In instances when discrete nurseries cannot be identified, the portfolio approach may be a useful means of examining the contributions of other young shark habitats. This approach can also be used to compare the importance of individual nursery areas (or nursery versus non-nursery areas) and examine variability in production over time.

The possibility of portfolio effects operating within shark stocks is unknown. However, the characteristics that allow portfolio effects to operate within sockeye salmon stocks may be shared by some shark species in their use of young shark habitats. This review outlines and discusses what is currently known about intraspecific diversity in habitat use by young sharks. The possibility of variance-dampening portfolio effects within young shark habitats will be explored, as well as the potential implications of these processes for shark populations and how they are managed.

2.2 Diversity in young shark habitats

Inshore environments typically support high biodiversity and productivity (Robertson & Duke 1987, Blaber et al. 1989, Beck et al. 2001), and therefore provide important habitat for many shark species (Branstetter 1990, Simpfendorfer & Milward 1993, White & Potter 2004, Knip et al. 2010). The utilisation of inshore environments varies considerably between shark species; however, most are described by two general models. One model describes species that utilise inshore nurseries as juveniles before moving offshore to adult habitats (Springer 1967). Large coastal sharks such as the common blacktip conform to this model (Springer 1967, Castro 1996). In contrast, the second model describes species that complete their entire life cycle within inshore environments (Knip et al. 2010) such as the Australian sharpnose shark *Rhizoprionodon taylori*. A portion of the species represented by this model exhibit site fidelity within restricted inshore sites (Sims et al. 2001), and others traverse larger areas (Parsons & Hoffmayer 2005, Carlson et al. 2008). Because of this diversity in inshore habitat use through ontogeny, anthropogenic impacts occurring within inshore habitats will affect different species in different ways. Sharks that complete their life cycle within inshore environments may be affected to a greater extent by unfavourable conditions because all age classes may be affected concurrently (Knip et al. 2010).

Not all species utilise discrete nursery areas (Heupel et al. 2007), and those that do may benefit from them in different ways (Heithaus 2007). Small sharks are both predators and prey, and how a species balances the trade-off between predator avoidance and energy uptake can often be related to its life history (Branstetter 1990), as well as competitive interactions between individuals (Brown 1999, Heithaus 2004, Heithaus 2007). It is widely assumed that nursery areas benefit young sharks by providing ample food and protection from predators (Springer 1967, Branstetter 1990, Ryer et al. 2010, Heupel & Simpfendorfer 2011). There are some notable exceptions to this long-standing assumption, including indications that these two factors may be mutually exclusive in at least some cases (Heithaus 2007, Heupel et al. 2007). For example, resource limitation occurs in some protected nurseries (Lowe 2002, Bush 2003, Hoffmayer et al. 2006), and movements of young sharks are driven by predator avoidance and not prey distribution in other nurseries (Heupel & Hueter 2002, Heupel & Simpfendorfer 2005b). Some energetically productive nurseries offer abundant food for small sharks, but may be frequented by large predatory sharks for the same reason (Branstetter 1990), in some cases necessitating fine-scale spatial partitioning (Kinney 2011). In general, large-bodied and slow-growing shark species may receive greater benefit from predator avoidance than small-bodied, fast-growing species (Branstetter 1990). Accordingly, the former typically utilise more protected nurseries. There remains scarce information on how life history factors, as well as abiotic environmental factors, influence the selection and use of nurseries by young sharks (Heithaus 2007).

In addition to interspecific variation in habitat use based on life history patterns, space utilisation within young shark habitats varies between species. Juvenile pigeye sharks *Carcharhinus amboinensis* have been shown to occupy relatively small home ranges in coastal waters (Knip et al. 2011b). In contrast, sandbar sharks have been reported to use larger areas, although usually remaining within the confines of a single estuary or embayment (Grubbs et al. 2007, Conrath & Musick 2010). How young sharks utilise space has important implications for their resilience to localised impacts occurring within their ranges, with some species having a greater ability to move away from unfavourable conditions than others. For example, juvenile lemon sharks *Negaprion brevirostris* are strongly site-attached to mangrove and seagrass habitats within isolated nursery lagoons. In one such lagoon, Jennings et al. (2008) reported a 23.5% reduction in juvenile survival in the year following localised dredging activities and associated declines in seagrass coverage. Negligible migration between lemon shark nurseries appears to be the norm (Gruber et al. 1988, Morrissey & Gruber 1993b, a, Gruber et al. 2001, DiBattista et al. 2007, Jennings et al. 2008), and this strong site attachment may have precluded movement away from the degraded habitat. In contrast, bull sharks move out of their usual young shark habitats and into adjacent embayments in response to low salinity events (Simpfendorfer et al. 2005, Heupel & Simpfendorfer 2008). Portfolio theory suggests that resilience might also be improved when conspecific young sharks are distributed among multiple young shark habitats along environmentally heterogeneous coastal stretches.

Environmental heterogeneity has been shown to influence habitat use within and between young shark habitats, as well as through time. For example, how young sharks optimise predator avoidance and foraging success may be facilitated and influenced by heterogeneity in environmental factors (Kinney 2011). High turbidity is thought to provide protection from predation for juvenile estuarine fish (Blaber & Blaber 1980). Similarly, multiple species of young sharks in Cleveland Bay, Australia, were more abundant in shallow (< 5 m), turbid habitat whereas adults usually inhabited deeper waters further from shore (Kinney 2011, Knip et al. 2011b). In contrast, juvenile spot-tail sharks *Carcharhinus sorrah* showed a preference for deeper, less turbid habitat, which may represent a trade-off against predator avoidance in order to reduce resource competition with other juvenile sharks (Kinney 2011). Similarly, juvenile slit-eye sharks *Loxodon macrorhinus* in Hervey Bay, Australia, showed a preference for shallow areas with lower turbidity, which may represent predator avoidance or resource partitioning in order to optimise foraging success (Gutteridge et al. 2011). In Florida, juvenile bull sharks displayed spatial segregation by body size, thus partitioning available food resources and reducing competition among size classes (Simpfendorfer et al. 2005). This partitioning by bull sharks appears to be driven by temperature and salinity gradients along with varying preferences for these parameters among size classes (Simpfendorfer et al. 2005, Heupel & Simpfendorfer 2008). These findings highlight the importance of environmental variables as determinants of habitat use by young sharks and the imperative for improved understanding of how anthropogenic disturbances, habitat restoration and climatic change will affect shark populations.

Over large spatial scales, intraspecific differences in habitat use may be driven by varying environmental conditions associated with changes in latitude. For example, inshore systems in the northwestern Atlantic are some of the most seasonally dynamic aquatic habitats in the world, where temperature differences range up to 28°C between summer and winter (Coutant 1985, Grubbs et al. 2007). Accordingly, the majority of teleost and shark fauna in these habitats are seasonal migrants (Musick et al. 1985, Grubbs et al. 2007, Heupel 2007). In contrast, young shark habitats in tropical and subtropical regions are utilised year-round, although species composition may change seasonally (Simpfendorfer & Milward 1993). The implications of seasonal and year-round use of young shark habitats for their inhabitants are unclear. Seasonal migrations, and thus large expenditures of energy, are typically not required in tropical young shark habitats (Simpfendorfer & Milward 1993). This may provide more energy for growth in tropical areas, as well as mitigate the presumed increase in predation risk on young sharks during seasonal migrations (Branstetter 1990). However, sharks in tropical regions may be challenged in other ways. For example, inter-annual variations in water temperature are generally smaller in tropical marine environments than those in temperate environments. As a result, tropical fish species may be less resilient to elevated temperatures and climate warming (Munday et al. 2008), a pattern that is also reported in terrestrial ecosystems (Williams et al. 2003, Deutsch et al. 2008). Tropical young shark habitats can also undergo significant seasonal fluctuations in other environmental variables such as rainfall (Knip et al. 2011a) and prey availability (Staples 1979, Simpfendorfer & Milward 1993), and these fluctuations represent potential stressors for tropical shark species. These different challenges suggest that the effects of environmental changes might vary within shark stocks that span climatic transition zones.

Intraspecific differences in habitat use over large spatial scales may also be driven by differences in available habitat types. Differences in biotic and abiotic characteristics may require sharks to adopt different strategies in different areas (see Knip et al. 2010 for review). This suggests that habitat plays a crucial role in driving how sharks use space and that populations will alter their habitat-use patterns as required. For example, juvenile sandbar sharks inhabit discrete areas within inshore systems of the northwest Atlantic (Conrath & Musick 2010). However, in the eastern Indian Ocean, juvenile sandbar sharks utilise larger areas further offshore (McAuley et al. 2007). These two populations of the same species use different habitats which suggests that inshore habitats are more beneficial to juveniles off the coast of North America, while offshore habitat must provide greater benefits to juveniles in the eastern Indian Ocean. Therefore, it is possible that differences in available habitats along environmentally heterogeneous coastal stretches may influence intraspecific differences in nursery use over smaller spatial scales.

Sharks are known to exhibit intraspecific differences in habitat use over smaller spatial scales than those described above (for example see Taylor et al. 2011), and the unique and dynamic nature of inshore areas suggests that proximate inshore systems should not be treated interchangeably in terms of the services they provide young sharks (Knip et al. 2010). For example, habitat utilisation by young sandbar sharks varied between two large adjacent embayments in the northwest Atlantic Ocean. In Delaware Bay, YOY sharks were most abundant in shallow, slow current areas and both YOY and juveniles avoided deep channels with faster currents (McCandless et al. 2007b). In contrast, juvenile sandbar sharks in Chesapeake Bay were more abundant in deeper channels (> 5.5 m), which were protected from strong currents (Grubbs & Musick 2007). One explanation for this variation between the two embayments may be that young sandbar sharks prefer areas with slower currents. Alternatively, predation risk from sand tiger sharks *Carcharias taurus* present in deep channels within Delaware Bay, but absent in Chesapeake Bay, may also explain the observed differences in habitat use between these sites (McCandless et al. 2007b). Further comparison of sandbar shark habitat use between Chesapeake and Delaware Bays may facilitate a greater understanding of the most important environmental factors for young sharks in this region, and may help managers to preserve those attributes, as well as to rehabilitate other areas where anthropogenic impacts have occurred (Heithaus 2007). In addition, variation in habitat use between young shark habitats might allow for portfolio effects. Since sandbar sharks demonstrate different patterns of habitat use between areas, the effects of environmental change may not affect this species in these two areas equally. Therefore, this kind of combined occurrence of multiple heterogeneous young shark habitats potentially contributes to population resilience and sustainability.

2.3 Potential drivers of portfolio effects in sharks

In sockeye salmon, precise natal philopatry for spawning, coupled with the ability to thrive in a wide range of environmental conditions, facilitates reproductive isolation and local adaptation to natal streams and thus portfolio effects (Taylor 1991, Hilborn et al. 2003, Doctor et al. 2010, Schindler et al. 2010). Sharks are also reported to demonstrate reproductive philopatry (Hueter et al. 2004), as well as local adaptations and life history diversity between different regions (Harry et al. 2011a), albeit at a much larger geographic scale than in sockeye salmon. For example, in some regions, male scalloped hammerhead sharks *Sphyrna lewini* disperse to occupy offshore environments as adults (Hazin et al. 2001, De Bruyn et al. 2005), whereas males in other regions remain in inshore areas (Harry et al. 2011a). These habitat-use patterns are also associated with differences in body size and longevity, and may have resulted from the influence of regional habitat differences in a trade-off between reproductive success and reproductive opportunity (Harry et al. 2011a). Taken together, results from genetic, vertebral microchemistry and life history studies indicate stock structuring within a single genetic stock of scalloped hammerhead sharks that extends c. 2000 km along eastern Australia (Welch et al. 2011). This range crosses a transition between tropical inshore lagoons to subtropical rocky shores (Ovenden et al. 2011, Welch et al. 2011). Stock structuring in scalloped hammerhead sharks is facilitated by site fidelity, although limited regional migration provides connectivity between sub-stocks and may allow for replenishment of depleted populations (Welch et al. 2011). These findings suggest that like sockeye salmon, some shark populations cover a range of environmental and habitat conditions, and can be structured according to local adaptations to their environment. Spatially distinct components of the stock may therefore perform differently, allowing for portfolio effects to operate over large spatial scales.

Over smaller spatial scales (e.g. c. 500 km; Froeschke et al. 2010a), the young of some shark species are distributed across environmentally heterogeneous coastal stretches (McCandless et al. 2007a, Ovenden et al. 2011, Welch et al. 2011), and this habitat diversity may also facilitate portfolio effects. Variations in depth (Grubbs & Musick 2007), turbidity (Ortega et al. 2009, Knip et al. 2011b), vegetation and substratum type (Morrissey & Gruber 1993b, White & Potter 2004), salinity (Simpfendorfer et al. 2005, Abel et al. 2007, Ubeda et al. 2009, Knip et al. 2011a), dissolved oxygen (Heithaus et al. 2009, Ortega et al. 2009) and temperature (Froeschke et al. 2010a, Espinoza et al. 2011) have been found to influence habitat use by young sharks. In some teleost fish, environmental heterogeneity appears to drive localised adaptation and thus differences in behaviour (Mariani et al. 2011) and species richness (Sheaves & Johnston 2009) between proximate estuaries. In addition, some seagrass- and mangrove-associated teleosts exhibit varying levels of flexibility in habitat use through time and between nearby locations (Kimirei et al. 2011). High inter-annual environmental variability within inshore waters is known to produce starkly contrasting fishery productivities in some teleosts (Balston 2009). However, the degree to which heterogeneity in environmental factors drives intraspecific diversity in young shark habitat use within a region is largely unknown, as are the effects of environmental changes.

Utilisation of multiple heterogeneous habitats improves the adaptability of a species to anthropogenic disturbance and environmental change where these effects unevenly impact throughout a species distribution (Secor et al. 2009). This act of ‘bet-hedging’ is an example of the portfolio effect. Diversity in juvenile shark habitats may drive portfolio effects whereby the effects of unfavourable conditions in one place or habitat type are buffered by production in others. Low-salinity events (Knip et al. 2011a), toxic algae blooms (Nam et al. 2010), pollution (Gelsleichter et al. 2005), coastal development (Jennings et al. 2008), resource limitation (Lowe 2002) and localised fisheries (Stevens & West 1997) are examples of events that can create unfavourable conditions for young sharks. Over longer temporal scales, different populations can perform well at different times, and young shark habitats that are minor producers during one environmental (e.g. climatic) regime can be major producers in others, as is the case for sockeye salmon (Hilborn et al. 2003).

Long-term fishery-independent catch data along the Texas coast indicate that the productivity of young bull sharks within eight embayments was not static through time (Froeschke et al. 2010b). Rather, abundance fluctuated within these sites, and it is their combined occurrence that might allow for complementary dynamics in productivity between bay systems (Figure 2.2). Of the eight sites sampled, only Matagorda Bay satisfied all three criteria for classification as a nursery (according to Heupel et al. 2007) for YOY bull sharks (Froeschke et al. 2010b). However, it is important to consider the contributions of other YOY habitats, because cumulatively they reduced Texas' total variance in the abundance of YOY bull sharks (Table 2.1; Figure 2.2). This reduced variance has population-level implications, because the abundance of young sharks (e.g. catch per unit effort) can be used as a proxy for young shark habitat productivity (Garofalo et al. 2011). Therefore, this collection of embayments may act to stabilise total recruitment of adult bull sharks in this region and hence annual yield of the fisheries in which they are captured.

Philopatry (the tendency of individuals to return to or stay in their natal [birth] sites, or other adopted localities; Mayr 1963) is an important consideration in the discussion of the potential for portfolio effects in young shark habitats. The combination of precise natal philopatry and the ability to thrive in a range of environmental conditions contributes to portfolio effects in sockeye salmon because it allows for reproductive isolation, localised adaptations to a large number of natal streams, and asynchronous spawning migrations. Portfolio effects operate in sockeye salmon because environmental changes do not affect production across all natal streams equally (Schindler et al. 2010). Sharks demonstrate various forms of philopatry, including juveniles returning to specific summer habitats (Castro 1996, McCandless et al. 2007b, Conrath & Musick 2010), and adult females returning to broad mating and pupping regions (Feldheim et al. 2004, Hueter et al. 2004, Keeney et al. 2005, DiBattista et al. 2008). However, the spatial scale and precision of philopatry in sharks remains poorly understood, as do the implications of philopatry for portfolio effects.

If environmental conditions remain stable, philopatry may increase the likelihood of offspring experiencing suitable environmental conditions, therefore enhancing survival. However, philopatry may reduce adaptability to anthropogenic impacts or environmental change, whereby individuals might return to the same place to reproduce even if conditions become unfavourable (Secor et al. 2009), thus compromising offspring survival and fitness and creating population-level problems. In addition, recovery of philopatric shark species from localised impacts (such as overfishing) will be slow compared to less-philopatric species because they will receive less replenishment from production in other areas (Hueter et al. 2004, DiBattista et al. 2008). Therefore, mating- or pupping-site fidelity in adults might limit portfolio effects, especially if a species is philopatric to a narrow range of habitats or geographic locations. Similarly, many teleost species repeatedly aggregate at specific locations to spawn, which drastically increases their susceptibility to overfishing and localised extirpation (Sala et al. 2001). The risks associated with philopatry may be mitigated if sharks utilise multiple environmentally heterogeneous young shark habitats (Secor et al. 2009).

Straying of young sharks away from where they were born might also overcome some of the potential risks of reproductive philopatry. It has generally been assumed that young shark habitat location is governed by where parturition occurs whereby young sharks remain in the vicinity of where they were born, with the ability to only select microhabitats within these areas (Springer 1967, Heithaus 2007). However, there are numerous examples of young sharks – even in species with philopatric young – moving away from where they were born, suggesting that birth location may be less influential in determining where young shark habitats occur than traditionally thought (Castro 1993, Heupel et al. 2004, Aubrey & Snelson 2007, McCandless et al. 2007b, Farrugia et al. 2011). Movement of young sharks around or away from where they were born might influence the amount of diversity in young shark habitat use within a species (Branstetter 1990), as young sharks may spread themselves across a mosaic of habitats. In addition, movements of young sharks away from where they were born in response to localised impacts might facilitate portfolio effects by boosting production in the habitats to which they move.

Most shark species possess life history traits that are different to those of sockeye salmon and other teleost fish, and it is important to consider whether these differences might limit the potential for, or the magnitude of the benefits obtained from, portfolio effects in young shark habitats. K-selected life history characteristics observed in sharks allow for the production of relatively stable numbers of large-bodied and actively-swimming offspring. In contrast, most teleost fish produce vast numbers of smaller-bodied offspring that are highly dependent on environmental variables (Cole & McGlade 1998, Balston 2009). Although environmental and habitat variables have been shown to influence neonate shark survival and fitness (Lowe 2002, Bush 2003, Hoffmayer et al. 2006, Jennings et al. 2008, Nam et al. 2010), they presumably are less impacted by their environment than are larval fish. Therefore, the benefits obtained from portfolio effects may be limited in young shark habitats because temporal stability in production could be achieved through their life histories rather than portfolio effects among numerous fluctuating habitats.

2.4 Implications for management and conservation

This review has demonstrated the potential for portfolio effects to operate within young shark habitats as well as the factors that may promote or limit the occurrence and magnitude of portfolio effects. However, further research is required to confirm whether portfolio effects occur in these habitats, and if they should be considered in management decisions. Portfolio effects were quantified in Alaskan sockeye salmon by comparing the variability in annual fish landings of the stock complex with the variability in fish landings in individual rivers (Schindler et al. 2010). A similar method could be used to quantify the occurrence and strength of portfolio effects in young shark habitats, whereby the variability (e.g. coefficient of variation [CV]) in young shark abundance across a range of habitats is compared to the variability in abundance within individual habitats of the same region. Abundance surveys across a range of young shark habitats can be used to test the prediction that although abundance in individual habitats is highly variable through time, the overall abundance and thus recruitment across the population or region is relatively stable (e.g. Froeschke et al. 2010b). More recently, Carlson & Satterthwaite (2011) discuss some of the limitations of using CV as a metric of stability in teleost fish, and promote the use of additional metrics such as correlations in productivity among stock components, an idea also explored by Schindler et al. (2010).

Identification of whether portfolio effects operate in young shark habitats is important because these processes are likely to provide population-level benefits for sharks and may be a critical consideration for shark management and conservation. The current method for identifying shark nurseries (Heupel et al. 2007) assumes that the location of the most important habitats (i.e. shark nurseries) is stable through time. However, sharks generally occur in low densities and with high temporal and spatial variability in abundance (Froeschke et al. 2010a). Significant temporal variability in bull shark abundance within the most heavily utilised young shark habitats was recorded in the Gulf of Mexico, including periods when shark abundance in these areas fell below the population mean, and therefore violated one of the criteria for classification as a nursery (Fig. 2.2; Froeschke et al. 2010b). In the presence of portfolio effects, these fluctuations should not be as significant at the population level. Therefore, the importance of young shark habitats may be a function of their individual contributions to adult recruitment, as well as their combined occurrence and relationship with each other; an idea originally proposed for teleost fish (Meynecke et al. 2007). Accordingly, the conservation of a geographically diverse range of juvenile habitats has been identified as an important factor in the recovery of the endangered smalltooth sawfish *Pristis pectinata* in the USA by minimising the risk of stochastic local-scale disasters including hurricanes and fish kills (NMFS 2009). Indeed, toxic dinoflagellate algae blooms (red tides) have caused mass fish mortality within inshore embayments within the range of smalltooth sawfish (Flaherty & Landsberg 2011), and the population-level impacts of these events will be partially mitigated by production of juveniles in other less-affected areas. In the absence of such extreme events, portfolio effects across multiple areas may also stabilise the population-level production of juvenile smalltooth sawfish, and facilitate population recovery.

Portfolio theory provides the ability to consider contributions of a range of young shark habitats, including those that currently appear relatively unproductive or are not classified as shark nurseries according to Heupel et al. (2007). Portfolio theory can be used to explore whether habitats that are not classified as Essential Fish Habitat, Habitat Areas of Particular Concern, or Critical Habitat at one point in time may contribute to the sustainability of shark stocks over the long term. For example, YOY bull shark abundance in Galveston Bay and Sabine Lake, Texas, has increased over the last decade to above the population mean and therefore these sites may now qualify as nurseries (Fig. 2.2; Froeschke et al. 2010b). This demonstrates that nursery use and habitat quality may not be stable through time, and these changes may influence the production of young sharks across a range of areas (Froeschke et al. 2010b). Additional threats such as fishing pressure will continue to alter the productivity of these habitats. Non-uniform harvest of the natal streams of sockeye salmon (e.g. through temporally selective fishing) threatens to reduce their phenotypic and genetic diversity (Doctor et al. 2010). Theory predicts that this homogenisation erodes portfolio performance, thus increasing vulnerability to environmental change and the likelihood of synchronous population crashes (Heino et al. 1997, Engen et al. 2002, Moore et al. 2010). Similarly, spatially selective fishing in young shark habitats could reduce their phenotypic and genetic diversity, and may therefore compromise the long-term sustainability of shark fisheries and the conservation of endangered shark populations. Further, shark populations with weak or no portfolio effects may be more susceptible to depletion and therefore should be managed more conservatively.

Criteria for classifying young shark habitats are essential for identifying the most important habitats for juveniles, and allow fisheries managers and scientists to optimise the effectiveness of management, conservation and research efforts. However, the young of many shark species are spatially dispersed and utilise a wide range of habitats, some of which do not currently meet the criteria for classification as shark nurseries. The contribution of these various habitats to the long-term sustainability of shark populations remains poorly understood. In response to environmental change, areas of high shark density may change over time, and less important habitats under one set of conditions may be more important during others. Portfolio theory predicts that contributions from a wide range of young shark habitats should stabilise the population-level recruitment of adults.

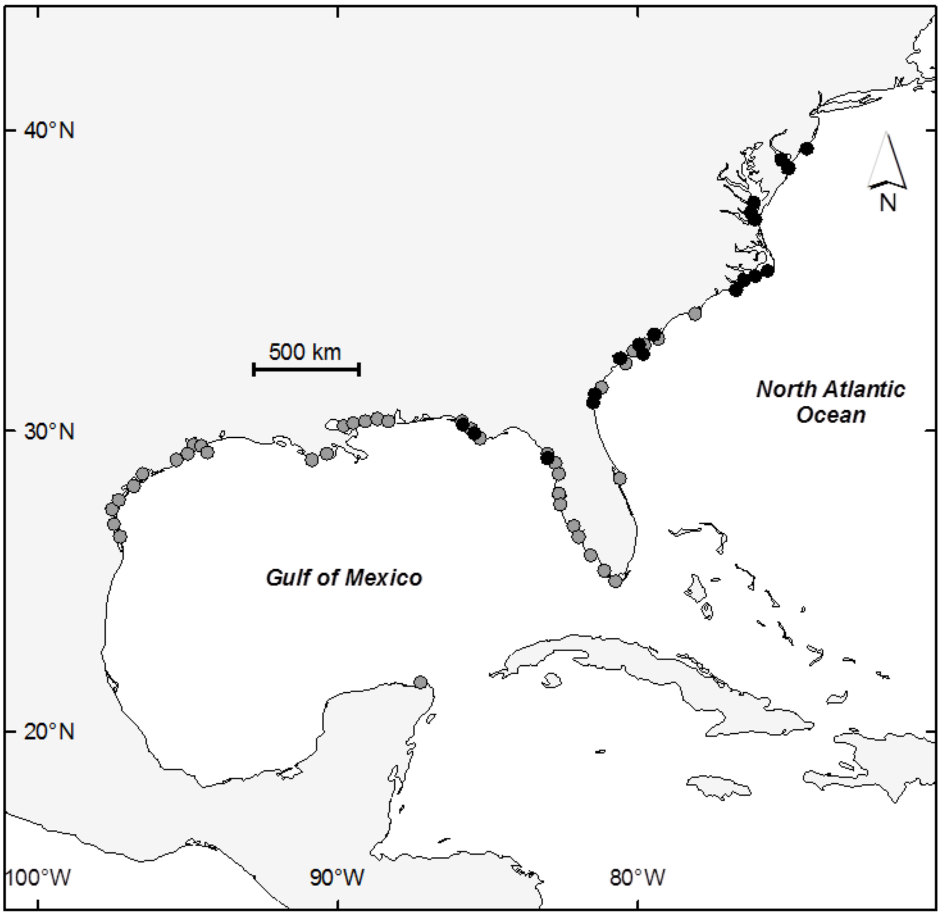


Figure 2.1 Approximate areas utilised by neonate or young-of-the-year (YOY) common blacktip *Carcharhinus limbatus* (grey circles) and sandbar *Carcharhinus plumbeus* (black circles) sharks in the Gulf of Mexico and North Atlantic Ocean as indicated by capture locations in McCandless et al. (2002, 2007a). Note that a range of areas and habitats are utilised, however not all of these will be classified as nurseries according to criteria in Heupel et al. (2007).

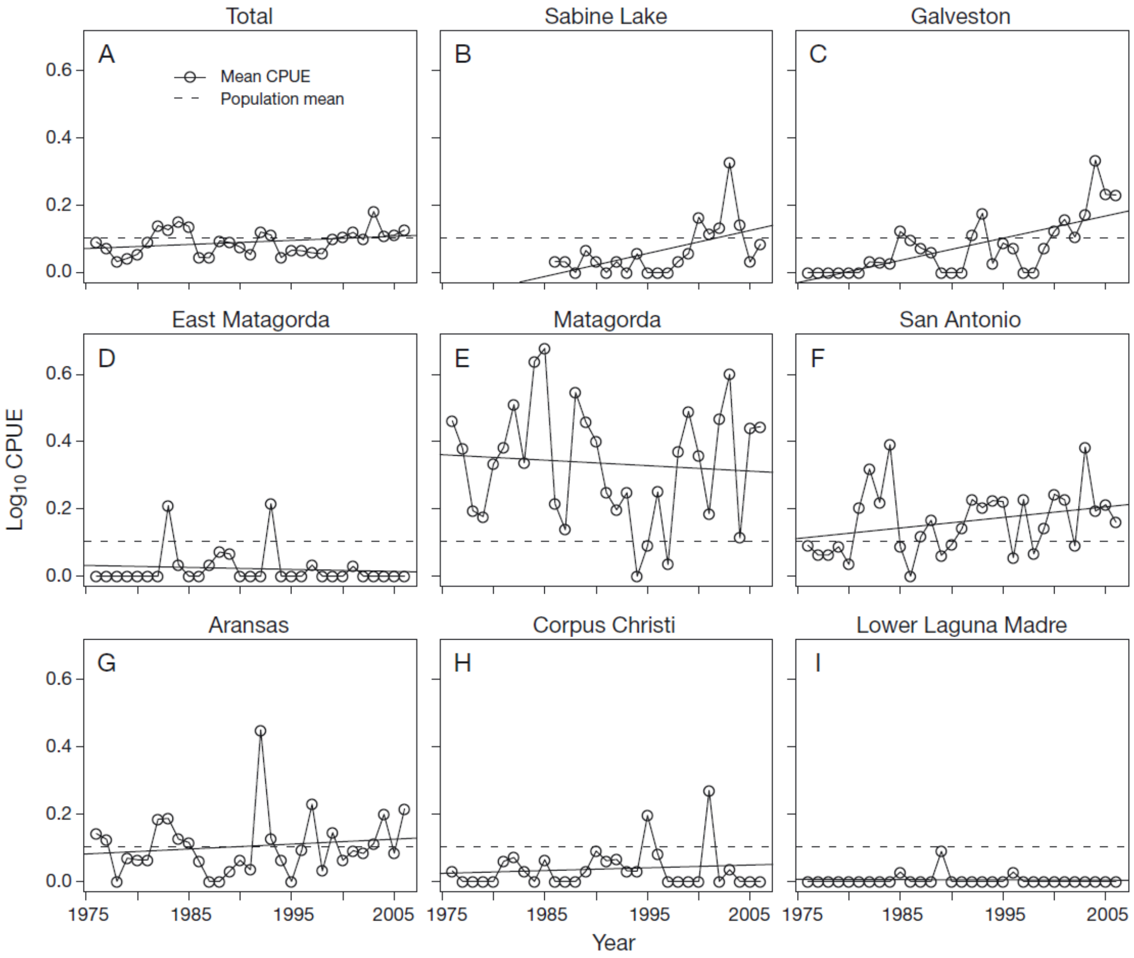


Figure 2.2 Young-of-the-year (YOY) bull shark *Carcharhinus leucas* abundance in eight estuarine embayments along the Texas coast (A = whole region, B–I = locations corresponding to Table 2.1). Inter-annual variation in $\log_{10}$ catch per unit effort (CPUE; sharks h^{-1}) within each site is evident (B–I; circles = annual mean). Abundance in some sites fluctuates above and below the population mean (broken line), and therefore they vary in their suitability to meet the first criterion for a shark nursery (abundance in the area is greater than mean abundance over all areas; Heupel et al. 2007). Portfolio effects may operate across these YOY habitats because variability in mean CPUE for the whole region (A) is less than the variability in individual sites. (From Froeschke et al. 2010b. With permission).

Table 2.1 Mean $\log_{10}$ catch per unit effort (CPUE; sharks hour^{-1}) and variability in $\log_{10}$ CPUE of young-of-the-year (YOY) bull sharks *Carcharhinus leucas* within eight Texas embayments between years 1976–2006 (John T. Froeschke pers. comm.). Note that variability in abundance across the region (Total) is less than variability in abundance in individual embayments, suggesting that portfolio effects may occur across this region.

Location	Mean $\log_{10}$ CPUE	Standard Deviation	Coefficient of Variation
Sabine Lake	0.063	0.078	1.236
Galveston Bay	0.075	0.086	1.136
East Matagorda Bay	0.005	0.017	3.674
Matagorda Bay	0.335	0.176	0.526
San Antonio Bay	0.162	0.097	0.601
Aransas Bay	0.105	0.091	0.864
Corpus Christi Bay	0.037	0.061	1.639
Lower Laguna Madre	0.022	0.054	2.432
Total	0.102	0.042	0.411

CHAPTER 3

General Methods

Plate 3 Gill-net survey from Research Vessel ‘Viking’ in Edgecumbe Bay (June 2012).

3.1 Study sites

Sampling was conducted within coastal bays along approximately 400 km of the tropical north coast of Queensland (146.0–148.8ºE, 18.1–20.6ºS; Figure 3.1). Initially, nine bays were sampled from November 2011–March 2012. Thereafter, a subset of five bays, ranging in size from approximately 200–500 km^2 (Table 3.1), was selected for ongoing seasonal sampling: Rockingham, Bowling Green, Upstart, Edgecumbe and Repulse Bays. This selection included a variety of habitat types and environmental characteristics, and thus permitted investigation of spatial diversity in the distribution patterns of sharks as well as the factors that influenced this diversity.

The bays were shallow (predominantly < 15 m; Figure 3.2–Figure 3.6) and sheltered from ocean swells by the Great Barrier Reef. Consequently, they were dominated by silty substrates and mudflat or mangrove-lined foreshores (Table 3.1). Mangrove extent ranged from c. 29 km^2 in Edgecumbe Bay up to c. 205 km^2 in Rockingham Bay (including Hinchinbrook Channel). Inshore coral reefs were also present predominantly within Edgecumbe and Cleveland Bays (Table 3.1). Seagrass abundance was higher during the dry season, and in areas with low or medium relative wave exposure and a small tidal range (Grech & Coles 2010). Seagrass distribution across the region is highly susceptible to extreme weather events (Furnas 1993) and remains poorly understood following Tropical Cyclone Yasi in 2011.

The coastal environments sampled were spatially and temporally variable. For example, rainfall was seasonal with 60–80% typically occurring during the summer wet season (November–April), which in turn influenced significant seasonal fluctuations in the physical and trophic dynamics of these systems (Furnas 1993). The supply of freshwater from rivers typically varied among the bays depending on catchment size and the spatial distribution of rainfall (Furnas 1993). Average river runoff volumes, presented as a general guide in Table 3.1, should be viewed with consideration of considerable inter-annual fluctuation (Finlayson & McMahon 1988) and transport of river plumes beyond their bay of origin. Typically, the earth's Coriolis force and south-easterly trade winds combine to deflect river plumes towards the north (Furnas 1993). For example, large flood plumes from the Burdekin River can extend for hundreds of kilometres along the coast and influence physio-chemical conditions in Bowling Green, Cleveland, Halifax and Rockingham Bays (Wolanski & Jones 1981). The environmental characteristics of sampling locations are described further in Chapter 5.

All sampling sites were within the Great Barrier Reef Marine Park which includes a variety of management zones defining the activities which can occur in specific locations. North Queensland's East Coast Inshore Finfish Fishery (ECIFF) accounts for the majority of commercial shark landings. Carcharhiniform sharks contribute a large component of the ECIFF (Harry et al. 2011b) as well as a small component of local recreational fisheries (Lynch et al. 2010). Chapter 7 provides additional information on GBRMP zoning and the ECIFF.

3.2 Survey design

Surveys were designed to facilitate comparison of shark catch between multiple bays throughout the year. Between November 2011 and March 2014, eight rounds of fishery-independent surveys were undertaken to collect data on shark fauna across the region (Table 3.2). Each round comprised four days of sampling in each bay, with bays sampled in an order largely guided by weather conditions (Appendix 1). Within each bay, sampling occurred randomly within 16 0.9-km-wide transects (Figure 3.2–Figure 3.6). Two groups of eight transects were placed within each bay to spread the sampling across different habitat types and management zones where both zone types were present (i.e. open and closed to commercial gill-net fishing). During each round, each bay was sampled over four days allowing for two days of sampling in each group of transects. The bays vary in size and so the relative proportion of the area and coastline sampled varied among bays (Table 3.1).

3.3 Sampling methods

Two methods were used to sample across a broad range of shark sizes. A minimum of five longline shots or four gill-net shots were deployed per day between dawn and dusk (shot refers to single deployment of sampling gear). A random-number generator was used to select transects to be sampled on each day. During a total of 183 days of sampling, 504 longline shots and 386 gill-net shots were deployed totaling 413.3 and 349.0 h, respectively (Table 3.3). Sampling in five focal bays spanned 162 days.

Bottom-set gill-nets comprised 18-ply, 11.4-cm-stretched monofilament mesh with a depth of 33 meshes (c. 3.2 m fishing depth). A single gill-net was deployed for c. 1 h (81% between 45 and 75 min) and checked every 15 min to minimise capture mortalities, and facilitate tagging and release (Figure 3.7). In accordance with the Great Barrier Reef Marine Park Authority’s Dugong Protection Areas, a maximum net length of 200 m was used in ‘Dugong Sanctuary A’ zones (Cleveland Bay, Upstart Bay and southern portions of Rockingham and Halifax Bays) and within 2 m water depth in ‘Dugong Sanctuary B’ zones (Bowling Green Bay, Edgecumbe Bay and northeastern Repulse Bay). Gill-nets up to 400 m in length were used elsewhere (Table 3.3). In addition, exclusion of data from 16.5-cm-stretched mesh gill-nets, which were discontinued in March 2012 due to low catches, resulted in effective net lengths of 100 m during the January–February round of 2012.

Bottom-set longlines comprised 800 m of 6-mm nylon mainline, with an anchor and float at both ends (Figure 3.7). Gangions were attached to the mainline c. 8–10 m apart, and comprised 1 m of 4-mm nylon cord, 1 m of 1.5-mm wire leader, and a baited size 14/0 Mustad tuna circle hook. A variety of fresh and frozen baits were used, which consistently comprised a combination of squid *Loligo sp.* and various teleost fish (butterfly bream *Nemipterus sp.,* blue threadfin *Eleutheronema tetradactylum* and mullet *Mugil cephalus*). Up to two longlines were deployed simultaneously for c. 40 min shots (72% between 40 and 60 min). Longline and gill-net shot durations were the length of time in which the entire gear was deployed (i.e. excluding the time taken to deploy and retrieve the gear). Longline and gill-net sampling was conducted in water depths of 0.5–5 m. Longlines were usually deployed parallel to the shore whereas gill-nets were deployed perpendicular to the shore or significant depth contours where possible. Each round comprised a minimum of eight gill-net samples bay^{-1} round^{-1} and 10 longline samples bay^{-1} round^{-1}.

3.4 Animal processing

Captured sharks were identified to species level, tagged on the first dorsal fin (Dalton Rototag or Superflex tag), measured, sexed, assessed for clasper calcification, examined for umbilical scar condition, and released at their capture site. Stretch total length (STL) was measured according to Compagno (1984). Small sharks (≤ 1000 mm) were placed ventral side down on a measuring board and measured to the nearest mm with the upper lobe of the caudal fin depressed in line with the body axis. Larger sharks were secured beside the boat and measured to the nearest cm with a measuring tape. Additional measurements of fork length and pre-caudal length were recorded.

3.5 Determining life-history stage

Life-history stage was determined using length-at-age data (reviewed in Last and Stevens 2009; Harry 2011) and observation of umbilical scars and clasper calcification. Young-of-the-year (YOY) sharks were either ≤ length at one year or had un-healed umbilical scars. Neonate sharks comprised a subset of YOY sharks and were those with an un-healed umbilical scar which indicated recent birth (i.e. within 1-2 weeks; Duncan & Holland 2006). Juvenile sharks were between the length at one year and length at 50% maturity. Mature sharks were ≥ length at 50% maturity or were males with calcified claspers. Some sharks escaped prior to the collection of these data and thus their life-history stage was unknown.

Two morphologically similar species, Australian blacktip *Carcharhinus tilstoni* and common blacktip *Carcharhinus limbatus*, were indistinguishable in the field and therefore grouped together as unidentified blacktip sharks *C. tilstoni/ C. limbatus*. These two species occur in approximately equal frequencies in northern Australia (Ovenden et al. 2010). *Carcharhinus limbatus* matures at a larger size than *C. tilstoni* and therefore the proportions of each life-history stage for unidentified blacktip sharks were considered approximations. The length-at-age estimates for *C. tilstoni* were used to determine life-history stage to ensure that no mature sharks were misclassified as immature (similar to Harry et al. 2011a).

3.5 Environmental and spatio-temporal data

For each fishing shot, water depth was recorded to the nearest 0.1 m using the vessel's depth sounder (Garmin EchoTM 500C) and taken as the mean of measurements from both ends of the shot. Sea-surface water temperature (ºC), salinity (ppt), and DO (mg/L) were recorded using a YSI Model 85 multiprobe (YSI Incorporated). Secchi depth was recorded to the nearest 0.1 m as a proxy for turbidity. The secchi disk was visible on the sea floor during 7% of fishing shots, however these occurrences were spread across the full range of depths sampled. Therefore, the secchi disk being visible on the bottom was not a reliable indicator of low turbidity and so these occurrences were treated as missing values (e.g. in shallow water the secchi disk may be visible on the bottom even in relatively turbid conditions). Geographic coordinates were recorded at both ends of fishing deployments. Mangrove proximity was calculated using ArcMap 10.2.1 (ESRI) as the shortest straight-line distance (km) to any mangrove polygon within the same bay.

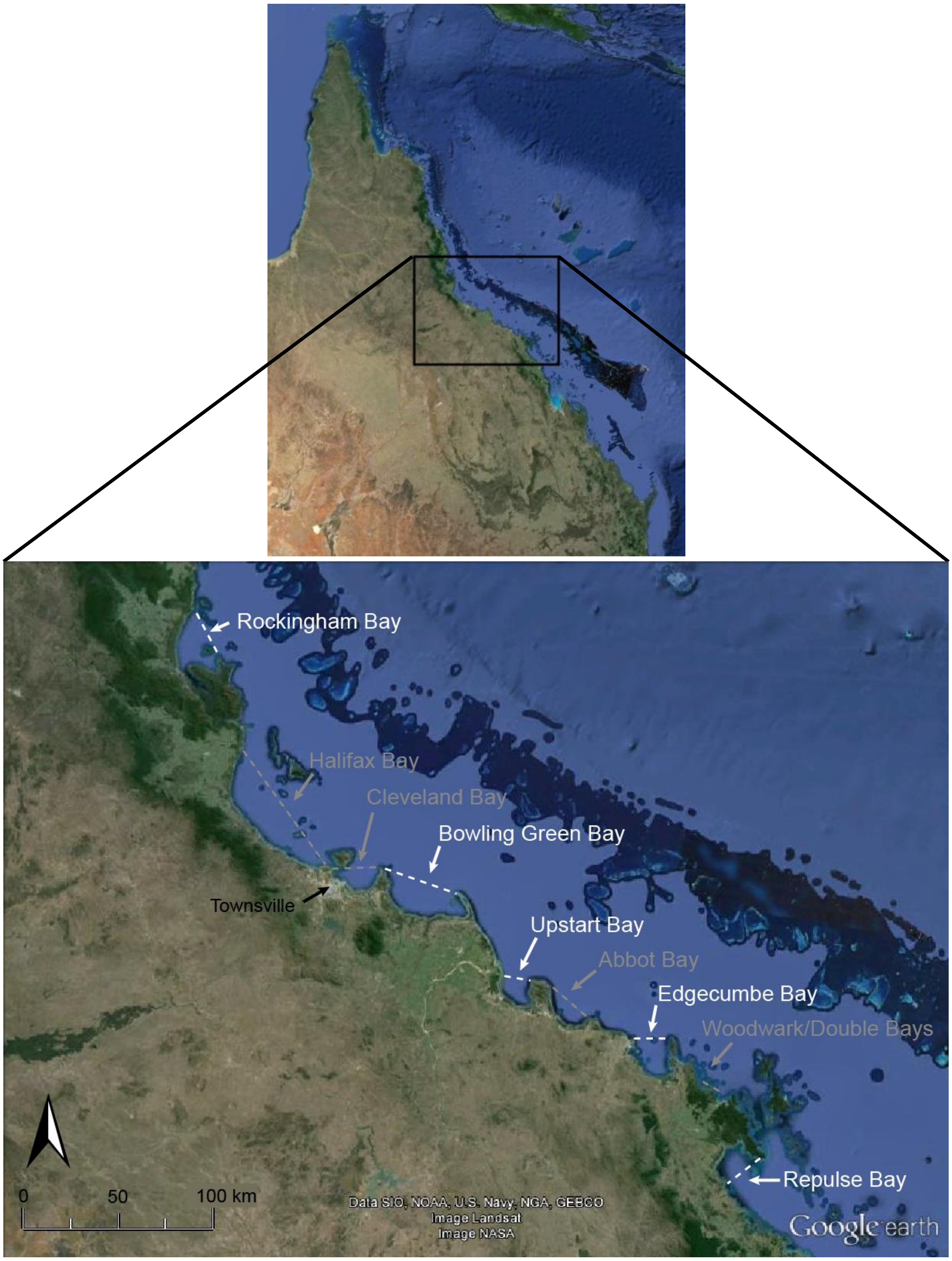


Figure 3.1 Study region. Google Earth^{TM} aerial image of the nine study bays and their location along northern Queensland, Australia. Four of the bays were sampled once (grey text) and five were selected for ongoing seasonal sampling for Chapters 4–7 (white text).

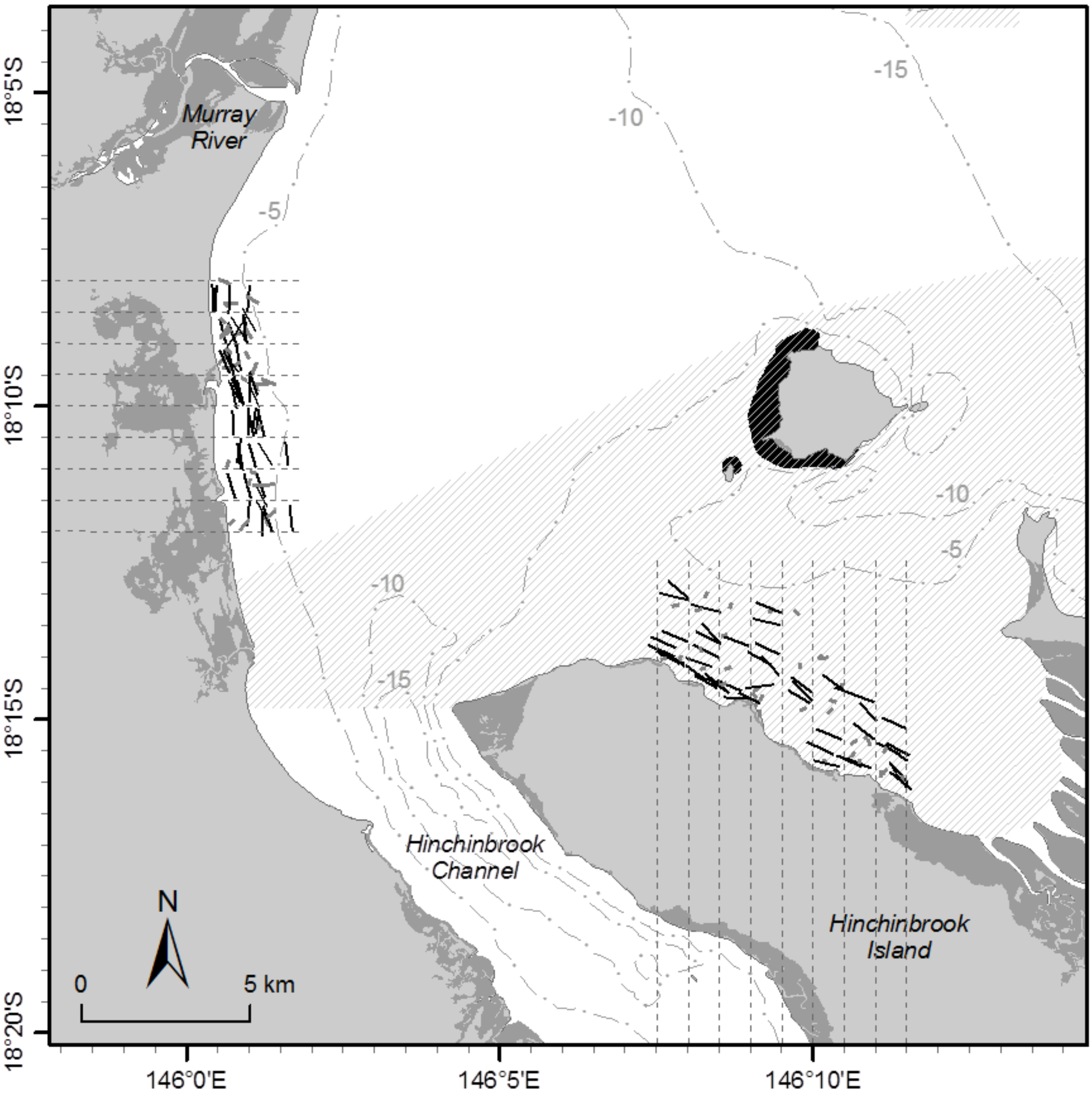


Figure 3.2 Rockingham Bay. Longline (black lines) and gill-net (grey lines) shots within 16 transect strips (dashed lines). Diagonal-shading and no-diagonal-shading indicate areas closed and open to commercial gill-net fishing, respectively. Black fill represents inshore reef habitat. Dark-grey shading represents mangroves. Dash-dot lines indicate bathymetry.

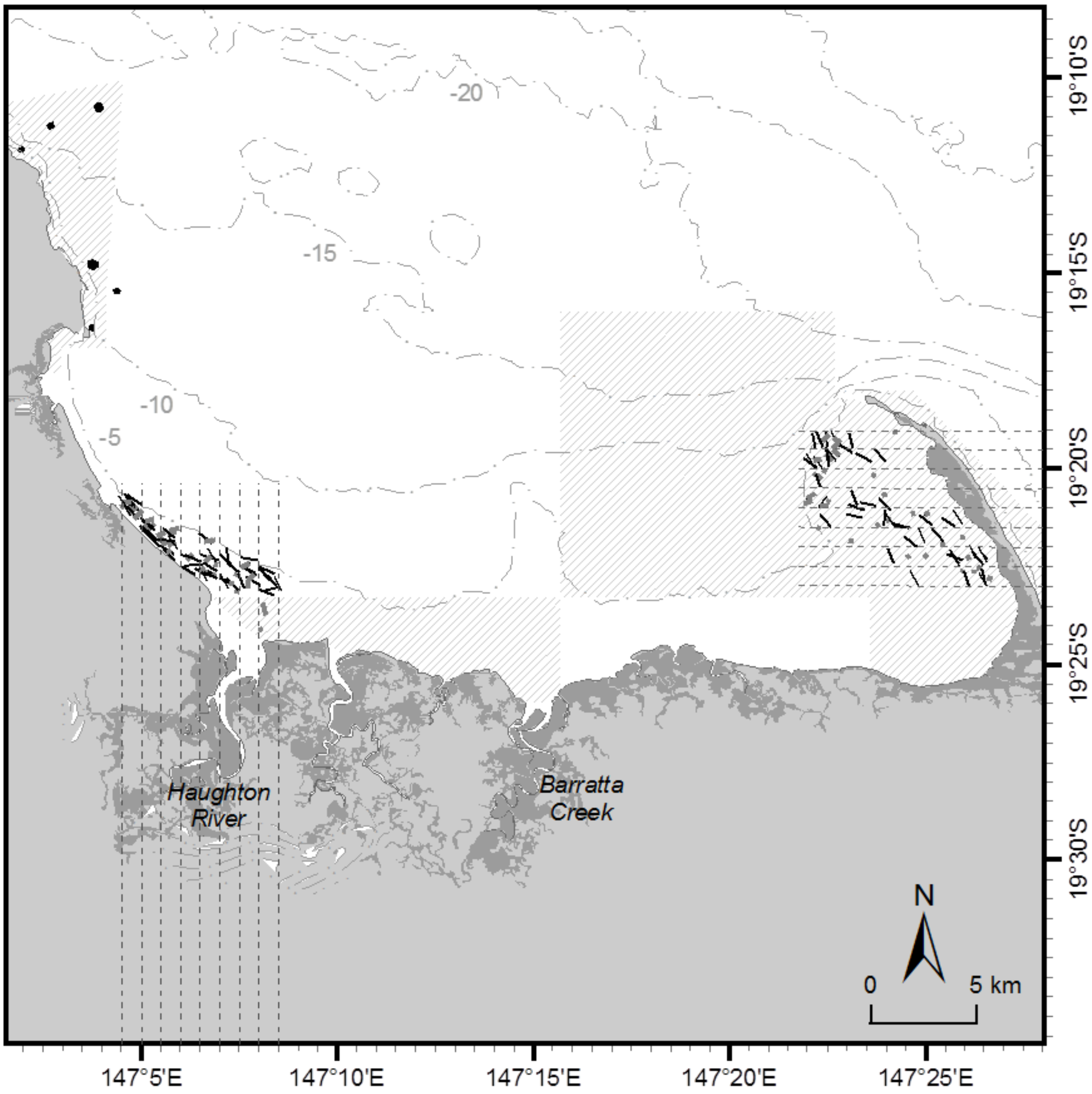


Figure 3.3 Bowling Green Bay. Longline (black lines) and gill-net (grey lines) shots within 16 transect strips (dashed lines). Diagonal-shading and no-diagonal-shading indicate areas closed and open to commercial gill-net fishing, respectively. Black fill represents inshore reef habitat. Dark-grey shading represents mangroves. Dash-dot lines indicate bathymetry.

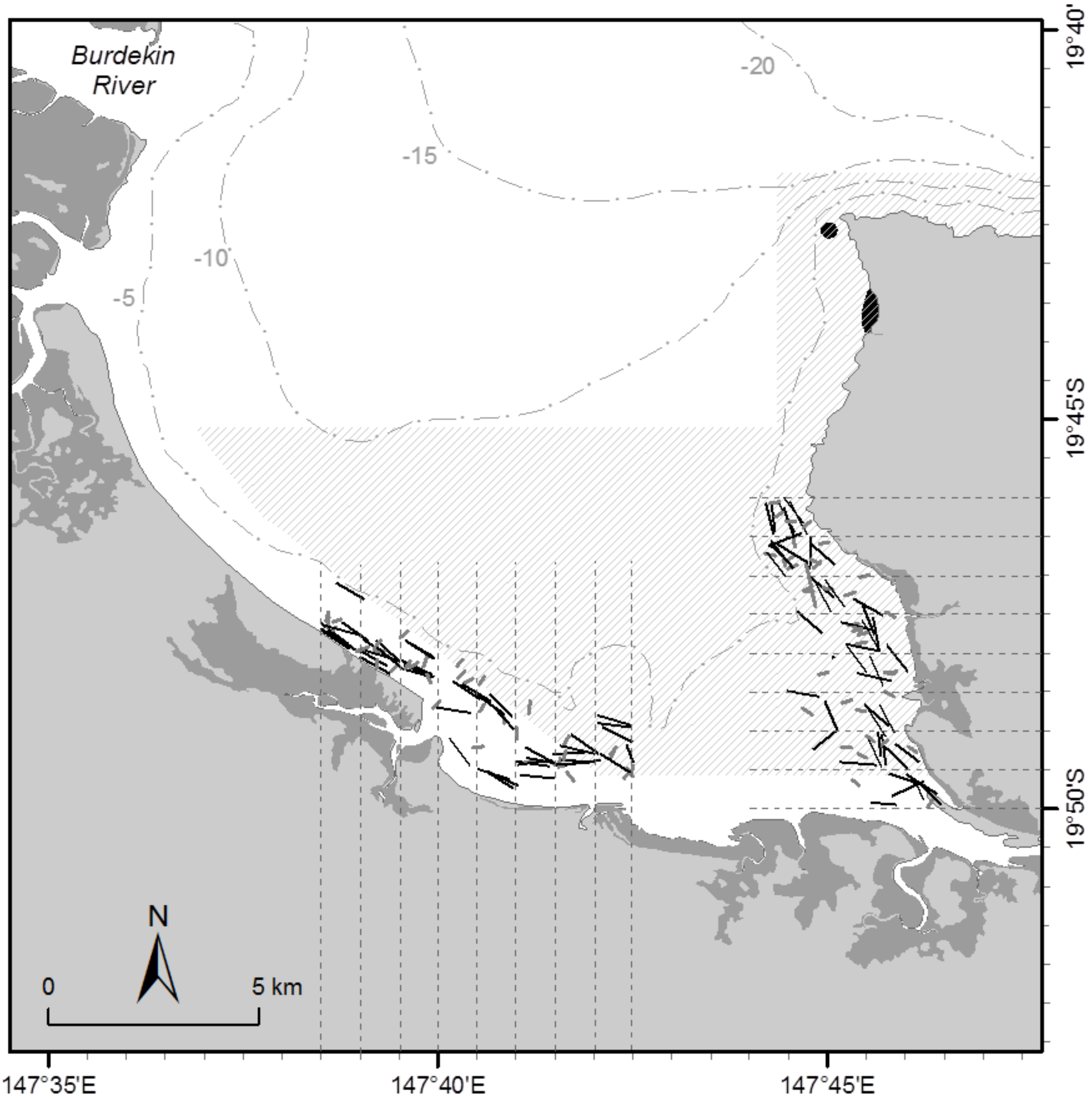


Figure 3.4 Upstart Bay. Longline (black lines) and gill-net (grey lines) shots within 16 transect strips (dashed lines). Diagonal-shading and no-diagonal-shading indicate areas closed and open to commercial gill-net fishing, respectively. Black fill represents inshore reef habitat. Dark-grey shading represents mangroves. Dash-dot lines indicate bathymetry.

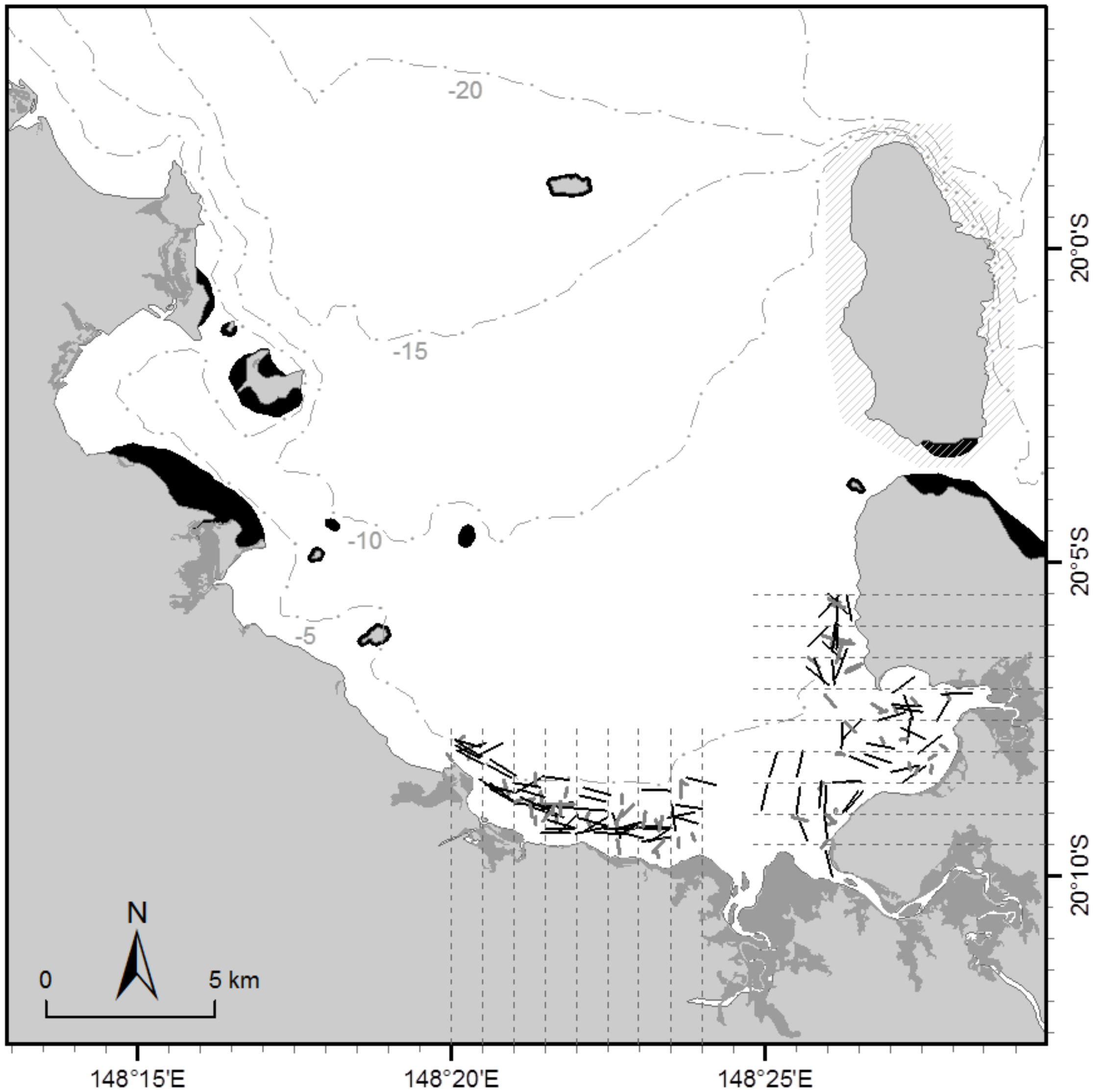


Figure 3.5 Edgecumbe Bay. Longline (black lines) and gill-net (grey lines) shots within 16 transect strips (dashed lines). Diagonal-shading and no-diagonal-shading indicate areas closed and open to commercial gill-net fishing, respectively. Black fill represents inshore reef habitat. Dark-grey shading represents mangroves. Dash-dot lines indicate bathymetry.

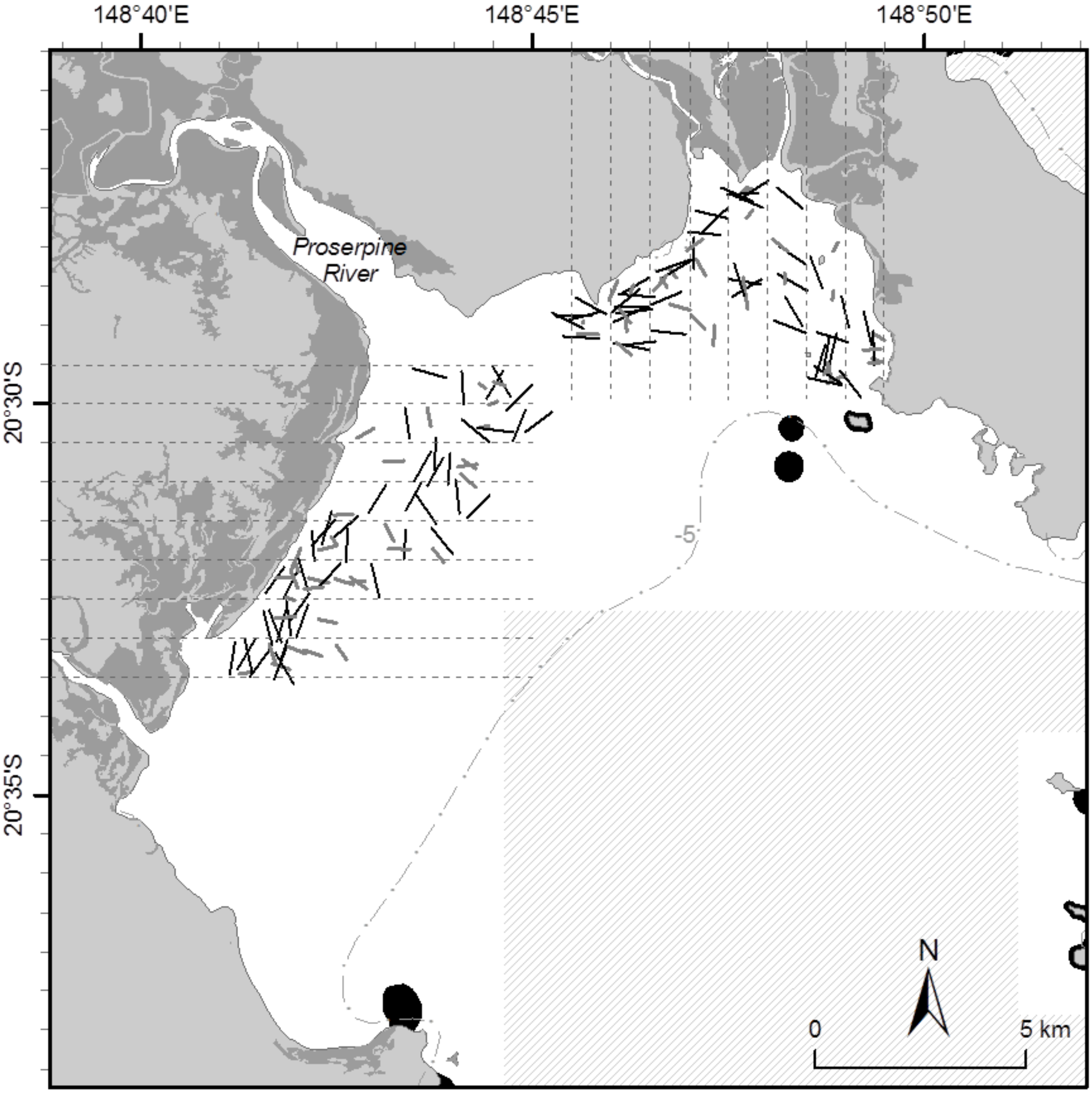


Figure 3.6 Repulse Bay. Longline (black lines) and gill-net (grey lines) shots within 16 transect strips (dashed lines). Diagonal-shading and no-diagonal-shading indicate areas closed and open to commercial gill-net fishing, respectively. Black fill represents inshore reef habitat. Dark-grey shading represents mangroves. Dash-dot lines indicate bathymetry.

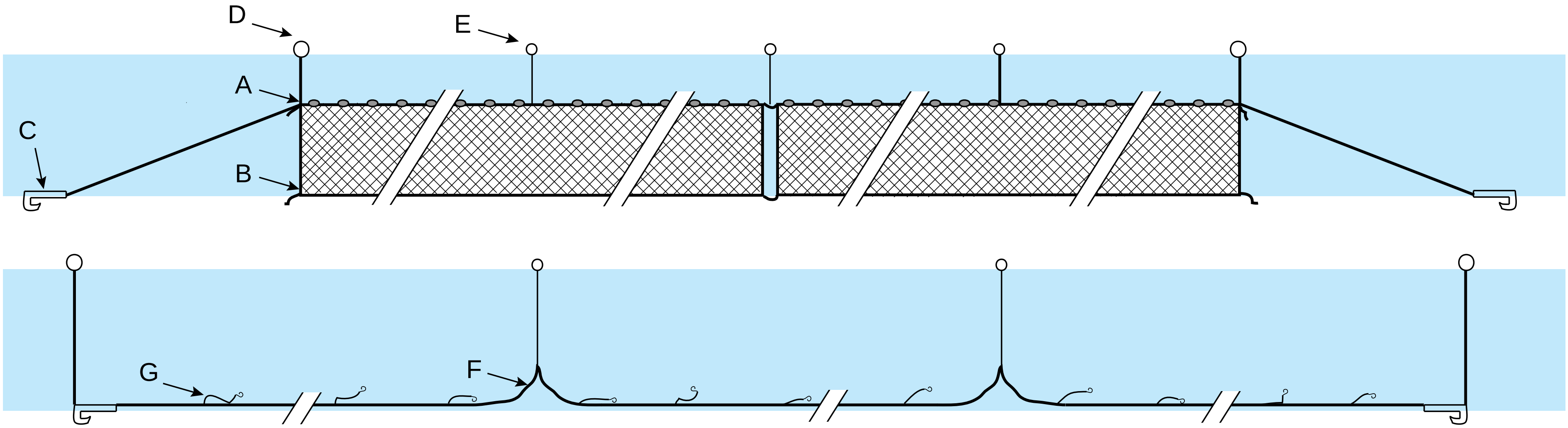


Figure 3.7 Gill-net (top) and longline (bottom) sampling gear. A = float line, B = lead line, C = anchor, D = large inflatable buoy, E = small marker buoy, F = longline mainline, G = gangion. Water column is indicated in blue. Diagrams are not drawn to scale.

Table 3.1 Comparison of nine sampled bays listed in order from north to south. Bays marked with an asterisk were selected for repeated sampling. Geographic measurements and assessment of coastline type were conducted using Google Earth Pro™. Coastline (MM:S:R) = the percentage of coastline that was mudflat or mangrove (MM), sandy beach (S) and rocky (R) shore, respectively. Orientation = direction of the bay towards open water. Values in parentheses are estimated average annual runoff volumes (km^3) from the region's major catchment basins.

Bay	Size (km^2)	Coastline (MM:S:R)	Proportion of bay area sampled	Proportion of coastline sampled	Orientation	GBRMPA zones (largest areas in bold)	Coral reef (km^2)[1]	Mangrove (km^2)[1]	Freshwater input (adjusted runoff volume, km^3)[2]
Rockingham*	481.7	46:52:2	0.08	0.24	E	**General use, conservation park**, habitat protection, marine national park	3.6	205.2	High. Tully River (3.29), Murray River (1.06)
Halifax	1180	35:64:1	0.02	0.16	NE	**General use, marine national park,** conservation park, habitat protection	3.3	79.5	High. Herbert River (4.01), Black River (0.38)
Cleveland	247.4	63:23:14	0.18	0.42	N	**Non marine park (port zone), conservation park**, general use, habitat protection	10.0	28.5	Moderate. Ross River (0.49)
Bowling Green*	518.9	70:29:1	0.13	0.31	N	**General use, marine national park**, conservation park, habitat protection	0.3	111.8	Moderate. Haughton River (0.74)
Upstart*	219.8	53:38:9	0.15	0.38	N	**General use, marine national park**, conservation park, habitat protection	0.3	66.1	Limited. Burdekin River (10.29; usually transported north[2])
Abbot	126.4	13:79:8	0.18	0.58	NE	**General use**, conservation park, habitat protection, marine national park	0.4	16.0	Limited, Don River 17km to the ESE (0.75)
Edgecumbe*	365.5	60:25:15	0.12	0.35	N	**Habitat protection,** general use zone, conservation park	13.2	29.3	Limited
Woodwark/Double	31.3	69:3:28	0.33	0.48	NE	**General use**, conservation park, habitat protection, marine national park	1.4	1.3	Negligible
Repulse*	277.9	82:1:17	0.19	0.41	SE	**Marine national park**, general use, habitat protection	2.6	64.1	Moderate. Proserpine River (1.08), O'Connell River (1.54)

[1] Calculated using data from Commonwealth of Australia (Great Barrier Reef Marine Park Authority) [2012]; Furnas (1993)[2]

Table 3.2 Timing of eight fishery-independent sampling rounds across four years. Nine bays were sampled in the first round (dark grey) and five bays were sampled in all subsequent rounds (light grey). Rounds occuring during January–March were considered late wet-season; May–June, dry season; and October–Decemebr, early wet-season.

	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec
2011											▓	▓
2012	▓	▓	▓		░	░		░	░		░	░
2013		░	░		░	░				░	░	
2014		░	░									

Table 3.3 Summary of fishing effort in nine study bays. Data are from years 2011–2014 combined. Bays marked with an asterisk were selected for seasonal sampling spanning the period of January 2012 to March 2014. Standardised soak hours = sum of 100-hook-hours and 100 m-net-hours for longlines and gill-nets, respectively. Hook number is mean per shot ± SD.

	Longline				Gill-net			
	Number of shots	Total soak hours	Standardised soak hours	Hooks per shot	Number of shots	Total soak hours	Standardised soak hours	Net lengths (m)
Rockingham*	93	74.3	40.3	54 ± 9	67	58	134.2	100, 200, 400
Halifax	11	10.6	6.4	61 ± 12	9	8.5	12.9	100, 200
Cleveland	23	20.1	11.3	56 ± 8	22	19.8	29.6	100, 200
Bowling Green*	91	76.3	39.6	52 ± 11	66	64.6	181.5	100, 200, 400
Upstart*	93	75.4	39.7	52 ± 9	76	63.1	121.4	100, 200
Abbot	11	8.1	5.1	63 ± 8	8	6.8	14.2	100, 200
Edgecumbe*	88	72.9	39.3	54 ± 11	69	64.7	170.9	100, 200, 400
Woodwark/Double	6	4.4	2.7	62 ± 4	4	4.3	6.5	100, 200
Repulse*	88	71.2	38	53 ± 9	65	59.4	174.9	100, 200, 400
Total (all bays)	504	413.3	222.4	54 ± 10	386	349.0	846.1	100, 200, 400
Total (* only)	453	370.1	196.9	53 ± 10	343	309.8	782.9	100, 200, 400

CHAPTER 4

Diversity in Immature Shark Communities along a Tropical Coastline

---

Plate 4 Coastal environments of northern Queensland are occupied by a variety of shark species (clockwise from top left: zebra shark *Stegostoma fasciatum*, blacktip shark *Carcharhinus tilstoni* or *Carcharhinus limbatus*, tiger shark *Galeocerdo cuvier*, whitecheek shark *Carcharhinus coatesi*, spot-tail shark *Carcharhinus sorrah*, pigeye shark *Carcharhinus amboinensis*).

Accepted as an original research paper, 8th September 2014:

Yates PM, Heupel MR, Tobin AJ, Moore SK, Simpfendorfer CA (2015) Diversity in immature shark communities along a tropical coastline. Mar Freshw Res 66. doi: 10.1071/MF14033

4.1 Introduction

There is a growing need to improve our understanding of broad-scale habitat-use patterns of marine species, especially within environments facing increasing anthropogenic disturbance. Coastal environments in tropical and subtropical regions are often utilised by a diverse range of shark species (Compagno 1984, Knip et al. 2010). For example, 10 shark species from five families were captured during gill-net sampling within a subtropical bay in Western Australia (White & Potter 2004). Despite the ecological significance of coastal environments and their importance to commercial and recreational fisheries (e.g. Harry et al. 2011b), in most cases the distribution of sharks in these habitats remains poorly understood.

Coastal environments can provide high prey densities (Robertson & Duke 1987), along with protection from larger-bodied predators (Heupel & Simpfendorfer 2011), and are thereby traditionally regarded as nursery habitats for numerous shark species (Springer 1967, Simpfendorfer & Milward 1993). Some large coastal species such as the common blacktip shark *Carcharhinus limbatus* utilise inshore nurseries as immature individuals before moving offshore to adult habitats (Springer 1967, Castro 1996). In contrast, some smaller-bodied species including the Australian sharpnose shark *Rhizoprionodon taylori* complete their entire life cycle within coastal environments and may not utilise discrete nursery areas (Knip et al. 2010). Thus, coastal habitats are critical to various species and life-history stages of sharks, not just to immature individuals.

Shark nurseries make important contributions to population stability, albeit in conjunction with other habitats that are utilised by older age classes (Kinney & Simpfendorfer 2009). Heupel et al. (2007) provided the following three criteria for the classification of a shark nursery: (1) high relative abundance of neonates and young juveniles, (2) site fidelity and (3) stable use across multiple years. These criteria provide a valuable approach to identifying the most important habitats for immature sharks. However, the highly dynamic nature of coastal ecosystems (Sheaves 2006) and their susceptibility to anthropogenic alteration (Chin et al. 2010) prompted Yates et al. (2012) to consider the importance of spatial diversity in immature shark habitats (Chapter 2).

A large amount of research effort has been dedicated to shark nursery areas (e.g. McCandless et al. 2007a), although the majority has focussed on a single or a few species across restricted spatial scales (e.g. Morrissey & Gruber 1993b, DeAngelis et al. 2008, Knip et al. 2011b). As a result, the scales at which localised findings are applicable more broadly remain largely unknown. In addition, the importance of diversity in immature shark habitats for overall population resilience is poorly understood (Chapter 2). Proximate coastal systems are unique and dynamic and so variability in their functionality as shark nurseries is presumed but rarely examined or quantified. On the basis of a long-term fishery-independent dataset, Froeschke et al. (2010b) reported that only one of nine Texas bays satisfied the nursery area criteria of Heupel et al. (2007) for young-of-the-year (YOY) bull sharks *Carcharhinus leucas*. Similarly, habitat utilisation by immature sandbar sharks *Carcharhinus plumbeus* varied between two large adjacent bays in the north-western Atlantic Ocean (Grubbs et al. 2007, McCandless et al. 2007b). Therefore, environmental changes may not affect sandbar sharks in these two bays equally. The occurrence of multiple heterogeneous immature shark habitats potentially contributes to population resilience and sustainability in the long term (Chapter 2).

To improve the understanding of spatial heterogeneity in shark habitats, the present study used relative catch rates from fishery-independent surveys to examine the distribution and abundance of sharks along a tropical coastline. Because coastal waters are known to provide important habitats for immature sharks, including nursery areas, we were particularly interested in the occurrence of immature sharks, but also in understanding the importance of adults in influencing this occurrence. The specific aims were to (1) document the shark species and life-history stages present and characterise the co-occurrence of immature and mature sharks, (2) compare the community structure of immature sharks among bays within the study area, and (3) determine whether there were seasonal or inter-annual changes in immature shark community structure.

4.2 Methods

Chapter 4 used data from seven rounds of fishery-independent surveys spanning the period of January 2012 to November 2013 (Table 3.2). Data were from Rockingham, Bowling Green, Upstart, Edgecumbe and Repulse Bays (Figure 3.1; Table 4.1). The Kolmogorov–Smirnov (KS) test was used to determine whether the length-frequency distributions of sharks caught with longlines and gill-nets were significantly different. For each species, the Chi-Square statistic was used to identify uneven proportions of immature and mature sharks.

Multivariate analyses to identify spatial and temporal variations in the immature shark community (i.e. YOY and juveniles of all species) were conducted using Primer 6.0 (Clarke & Warwick 2001, Clarke & Gorley 2006). The August–September sampling round of 2012 was omitted from all multivariate analyses to provide equal effort and similar schedules between years. To investigate intra-annual variation, samples from each bay were grouped as either late wet-season (January–March), dry season (May–June) or early wet-season (October–December). Fishing effort was similarly distributed across bays, rounds and seasons, particularly in terms of the number and duration of longline and gill-net shots (Table 4.1). The standardised sampling design provided a rare opportunity to combine the data from two sampling methods for a more-robust representation of shark communities from single analyses. Therefore, shark counts from each four-day sampling event (i.e. two days of longline sampling plus two days of gill-net sampling) were pooled to constitute one sample for each bay per round. Count data for the various species were square-root-transformed and a similarity matrix was constructed containing Bray-Curtis similarity coefficients calculated between every pair of samples (Bray & Curtis 1957). Non-metric multi-dimensional scaling (MDS; Clarke 1993) was employed to create a visual representation of the ‘closeness’ of the species composition between samples. Two-way crossed analysis of similarities (ANOSIM; Clarke & Green 1988, Clarke 1993) was used to test for significant differences in the immature shark community among bays, rounds and years. Two-way crossed ANOSIM removed the effects of one factor while considering significance of the other factor. One-way ANOSIM using data from individual years was used to further investigate the temporal stability of spatial patterns in community structure. Similarity percentages (one-way SIMPER; Clarke 1993) were used to identify the species that typified the catch of immature sharks in each bay, and those that were principally responsible for any significant variation among bays. This was achieved by respectively decomposing average Bray-Curtis similarities and dissimilarities among and between groups into percentage contributions from each species.

4.3 Results

During a total of 142 days of sampling spanning years 2012 and 2013, 397 longline shots and 300 gill-net shots were deployed, totalling 326.9 and 273.2 h respectively (Table 4.1). In total, 1806 sharks were captured from six families, comprising 84% of the total elasmobranch catch by number (i.e. excluding batoids; Appendix 2). Of the 22 shark species encountered, 19 species of carcharhiniform sharks made up 99.2% of the total shark catch. Australian sharpnose (52%) and blacktip *Carcharhinus tilstoni*/ *C. limbatus* sharks (12%) were numerically dominant (Appendix 2). Spot-tail *Carcharhinus sorrah* (7%), pigeye *Carcharhinus amboinensis* (5%), scalloped hammerhead *Sphyrna lewini* (5%), milk *Rhizoprionodon acutus* (5%) and whitecheek *Carcharhinus coatesi* (5%) sharks were moderately abundant. Species selectivity varied between longlines and gill-nets, with some species being captured predominantly by one gear type (Figure 4.1). For example, longlines contributed 96 and 70% of the total catch of spot-tail and milk sharks, respectively. Conversely, gill-nets captured 77% of scalloped hammerhead sharks.

4.3.1 Shark size and life-history stage

Length-frequency distributions for the eight most abundant shark species (or species group in the case of blacktip sharks) indicated interspecific variation in body sizes and the proportion of immature sharks (Figure 4.1). Overall, small sharks (i.e. < 1000 mm STL) comprised 88% of all measured sharks. Further, mature and immature sharks shared similar cumulative length profiles (Figure 4.2), indicating broadly similar body sizes across the sampled community. Although there was overlap in STL between longline- and gill-net-caught individuals, the length-frequency distributions were significantly different (KS-test, D = 0.31, *P* < 0.001; Appendix 3). Longlines sampled a broader range of sizes (325–3700 mm, mean ± SD = 848 ± 335 mm, n = 896) compared with gill-nets (395–2550 mm, mean ± SD = 708 ± 197 mm, n = 860; Appendix 3).

Of the 1806 sharks, 1196 were mature and 567 were immature, including 336 YOY individuals, and 43 did not have maturity stage recorded. Excluding the abundant Australian sharpnose shark, 308 sharks were mature and 519 were immature, including 296 YOY. In all, 18 of 22 shark species occurred as YOY or juveniles; however, there was interspecific variation in the life-history stages present (Table 4.2). Samples of blacktip, scalloped hammerhead, pigeye, bull, great hammerhead *Sphyrna mokarran* and spinner *Carcharhinus brevipinna* sharks were biased towards immature individuals (Table 4.3). In contrast, Australian sharpnose and whitecheek sharks were predominantly mature.

4.3.2 Immature shark community structure

Mean numbers of common species indicated spatial variation in immature shark community structure (Figure 4.3). For example, scalloped hammerhead sharks contributed 14% of the total catch of immature sharks, of which 71% were caught in Rockingham Bay. In contrast, this species was not recorded in Edgecumbe Bay during 2012–2013 and was relatively scarce elsewhere. Further, although pigeye sharks were also scarce in Edgecumbe Bay, spinner sharks were recorded only there. The MDS ordination showed some separation in immature shark community structure among bays (Figure 4.4). For example, samples from Edgecumbe Bay formed a cluster that was largely non-overlapping with samples from Repulse or Rockingham Bays. However, some overlap of samples between bays, such as Rockingham and Upstart Bays, was indicative of broad similarities in shark fauna across the region. Two-way crossed

ANOSIM identified significant variation in immature shark communities across the five bays, while accounting for any variation between rounds (Global *R* = 0.23, *P* = 0.017) or years (Global *R* = 0.29, *P* = 0.001). Conversely, when the effects of bay were removed, no significant variation in immature shark communities were detected between rounds (Global *R* = 0.06, *P* = 0.347) or years (Global *R* = 0.18, *P* = 0.067). Taken together, the MDS ordination and modest ANOSIM Global *R* values indicated that differences among bays were not extreme. However, there were significant differences among bays in species composition and the occurrence of individual species, and thus the null hypothesis of no 'bay' effect was rejected.

In general, the more abundant species were primarily responsible for typifying the catch within individual bays. Blacktip sharks accounted for 39, 25, 49 and 38% of the respective average similarities within Bowling Green, Upstart, Edgecumbe and Repulse Bays where they were the most typifying species group. Pigeye sharks made the second-highest contribution to average similarities within Bowling Green (19%) and Repulse (19%) Bays. Spot-tail sharks made the second-highest contribution to average similarities within Edgecumbe (31%) and Upstart (24%) Bays. Scalloped hammerhead sharks followed by blacktip sharks were the highest contributors to average similarities within Rockingham Bay, contributing 37 and 30% respectively.

Pairwise comparisons (one-way ANOSIM) showed that the overall variation in immature shark communities was primarily driven by differences between Edgecumbe and Rockingham (*R* = 0.64, *P* = 0.002) Bays, and Edgecumbe and Repulse (*R* = 0.46, *P* = 0.009) Bays. Relatively small *R* values of < 0.30 indicated that variations in immature shark communities between other bay pairings contributed little overall.

Seven species (or species groups in the case of blacktip sharks) were principally responsible for the differences in immature shark communities in the aforementioned bay pairings (Table 4.4). The absence of the scalloped hammerhead shark in Edgecumbe Bay made it the most influential species in differentiating the catch in Edgecumbe Bay from that in Rockingham Bay (Table 4.4). In addition, variations in the average relative abundance of pigeye, blacktip, spot-tail, spinner and whitecheek sharks distinguished immature shark communities between Rockingham and Edgecumbe Bays (Table 4.4). Disparity in spot-tail shark relative abundance between Edgecumbe and Repulse Bays (Figure 4.3) made it the most influential species in distinguishing the catch between these sites, along with Australian sharpnose, blacktip, pigeye, scalloped hammerhead and great hammerhead sharks (Table 4.4).

Concerning the analysis of data from individual years, one-way ANOSIM demonstrated significant variation in immature shark communities across the five bays in both 2012 (Global $R = 0.27$, $P = 0.023$) and 2013 (Global $R = 0.31$, $P = 0.009$). One-way ANOSIM between rounds indicated no significant temporal variation within 2012 (Global $R = -0.01$, $P = 0.507$) or 2013 (Global $R = 0.02$, $P = 0.360$), and therefore samples from multiple rounds provided temporal replication within bays. On the basis of the magnitude of the R statistic, three bay pairings were among the top four primary drivers of overall spatial variation in immature shark assemblage in both years; although their influence relative to each other varied between years. Immature shark assemblages in Edgecumbe Bay differed from those in Rockingham (2012: $R = 1.00$, $P = 0.100$; 2013: $R = 0.70$, $P = 0.100$), Repulse (2012: $R = 0.33$, $P = 0.200$; 2013: $R = 0.89$, $P = 0.100$), and Upstart (2012: $R = 0.37$, $P = 0.100$; 2013: $R = 0.53$, $P = 0.100$) Bays. In addition, variation between Bowling Green and Upstart Bays (*R* = 0.44, *P* = 0.100) was influential in 2012, as was variation between Bowling Green and Edgecumbe Bays (*R* = 0.65, *P* = 0.100) in 2013.

4.4 Discussion

Sampling over an expanse of tropical coastline revealed variation in immature shark communities across a broad spatial scale. There are reports of variations in the relative abundance of immature carcharhinid sharks across similar spatial scales (Froeschke et al. 2010b, Curtis et al. 2011); however, spatial changes in the structure of immature shark communities have been largely ignored. In the present study, spatial heterogeneity in community structure and the distribution of individual species suggested variability in nursery function among bays. Nonetheless, shark populations may derive benefits from inhabiting a range of bays through a ‘portfolio effect’, whereby contributions from diverse habitats stabilise the overall production of immature sharks over time (Chapter 2).

The diversity of species encountered highlights the importance of tropical coastal environments as communal habitats for young sharks (Simpfendorfer & Milward 1993). The species diversity was higher than that reported from previous fishery-independent sampling within the study region (12 species; Simpfendorfer & Milward 1993, 9 species; Tobin et al. 2014a), possibly because of the broader spatial scope and multiple gears used in the present study. Notwithstanding the differences in methodologies and scales, species diversity was similar to that in other tropical and subtropical regions including the Everglades National Park, Florida (16 species; Loftus 2000, Wiley & Simpfendorfer 2007), Moreton Bay, Australia (13 Carcharhiniformes; Taylor & Bennett

2013) and the Gulf of Carpentaria, Australia (13 species; Blaber et al. 1995). It is possible that an even greater diversity of sharks utilise the bays studied here. For example, commercial gill-net catch in the region from water depths of up to 25 m included 28 shark species (Harry et al. 2011b), compared with 22 species in the present study. Species that were unrepresented in the present study may utilise these bays infrequently or sporadically, or inhabit depths in excess of those sampled.

4.4.1 Shark size and life-history stage

Despite the co-occurrence of immature and mature sharks reported here, the predominance of small-bodied sharks is in accordance with the shark nursery model of Springer (1967) describing nurseries as a safe haven for YOY and juveniles of larger-bodied species. Tropical coastal environments are inhabited by a diversity of sharks with varying life-history characteristics. For example, in contrast to many larger-bodied species (Simpfendorfer et al. 2002), some smaller-bodied coastal species such as Australian sharpnose and slit-eye *Loxodon macrorhinus* sharks exhibit relatively fast growth and early maturation, and often remain in coastal waters throughout their life cycle (Simpfendorfer 1992, 1993, Knip et al. 2010, Gutteridge et al. 2013). In the present study, immature and mature sharks shared similar cumulative length profiles. This similarity in the proportions of the sizes present between life-history stages suggests that body size may be more influential in the spatial structuring of tropical coastal shark communities than is life-history stage. Indeed, body size has implications for energetic requirements, preferred prey and hunting ability (Cortés & Gruber 1990, Lowe et al. 1996, Simpfendorfer et al. 2001, McElroy et al. 2006). Body size is also considered to be a critical factor in susceptibility to predation (Heithaus 2007) and thus a driver of anti-predator behaviours and habitat use (Guttridge et al. 2012). Therefore, communities of small sharks comprising various life-history stages may receive similar benefits, specifically, optimising energy intake or avoiding predation by co-inhabiting coastal bays.

4.4.2 Variation in immature shark community structure

Variation in immature shark community structure among bays indicated unequal use by immature sharks. Comparisons of shark communities across similar spatial scales are scarce in the literature. However, elasmobranch communities were shown to vary within a large (c. 4800 km^2) subtropical bay in eastern Australia (Gutteridge 2011, Gutteridge et al. 2011). Taylor et al. (2011) also demonstrated spatial changes in elasmobranch communities, comprising mainly large sharks, along approximately 220 km of subtropical eastern Australian coastline. Further studies on spatial variations in shark communities, including interspecific partitioning, are recommended because this information can inform the designation of marine reserves to optimise the protection of multiple species (Speed et al. 2010; see Chapter 7).

Potential drivers of spatial variations in coastal shark communities include spatial variations in resource abundance, competition, predation pressure, environmental conditions (Chapter 5) and anthropogenic impacts (Chapter 7). The influence and relative importance of these factors are likely to vary among species and life-history or body-size cohorts. For example, nursery utilisation by large-bodied, slow-growing species such as scalloped hammerhead (Harry et al. 2011a) and pigeye sharks (Tillett et al. 2011) may be disproportionally driven by the need to avoid predators (Branstetter 1990). In contrast, smaller-bodied species such as the Australian sharpnose shark (Simpfendorfer 1992, 1993) may derive greater benefits from broader movement patterns, so as to optimise foraging success (Branstetter 1990). Accordingly, these life-history traits may partially explain the relatively restricted or variable distributions of scalloped hammerhead and pigeye sharks compared with Australian sharpnose sharks.

Differences in abiotic and biotic characteristics may require sharks to adopt different strategies in different bays or to avoid certain bays altogether. In particular, further investigation is required to identify the factors that influence the distinctive assemblage encountered in Edgecumbe Bay. For example, none of the major drainage basins of the study region discharge into Edgecumbe Bay (Furnas 1993) and this may have implications for sharks occurring there. Indeed, variations in river discharge are known to influence the distributions of coastal sharks (Knip et al. 2011a, Drymon et al. 2014). A wide range of abiotic variables have been shown to influence shark distribution and habitat use (reviewed in Schlaff et al. 2014). For example, distributions of multiple species along the Texas coast were closely linked to heterogeneity in salinity, temperature and proximity to tidal inlets (Froeschke et al. 2010a). In Delaware Bay, United States, immature sandbar sharks were abundant in shallow, slow-current areas and avoided deep channels with fast currents (McCandless et al. 2007b). In contrast, immature sandbar sharks in adjacent Chesapeake Bay were more abundant in deeper channels that were protected from strong currents (Grubbs & Musick 2007). Therefore, different environmental conditions induced different behavioural and distribution patterns in the same species within two adjacent bays. In addition, heterogeneity in biotic factors including larval supply, prey fauna and vegetation cover across multiple spatial scales is common in tropical coastal regions (Staples 1979, Sheaves 2006, Grech & Coles 2010), and these variations can influence the spatial distribution of sharks (White & Potter 2004, Torres et al. 2006). Thus, a combination of abiotic and biotic variables is likely to have influenced the patterns in shark communities observed here (see Chapter 5).

Competitive and predatory interactions among species may also drive spatial variations in coastal shark communities. High productivity and abundant food resources in some coastal environments are thought to alleviate interspecific competition among immature sharks in communal nurseries (Simpfendorfer & Milward 1993). However, how immature sharks share or partition space and resources within these environments remains unclear. For instance, food availability can be a limiting factor in some cases (Bush & Holland 2002, Lowe 2002). The present study revealed interspecific structuring of immature sharks over a broad spatial scale, suggesting that habitat partitioning may occur among bays. Kinney (2011) and Kinney et al. (2011) reported fine-scale spatial partitioning among immature sharks within Cleveland Bay, Australia, as well as interspecific partitioning of food resources. Within Herald Bight, Western Australia, lemon sharks *Negaprion acutidens* were captured entirely in unvegetated sites, whereas milk sharks were captured almost exclusively in seagrass habitats (White & Potter 2004). Similarly, the slit-eye shark was the only species to show affinity for a clear-water site in Hervey Bay, Australia; potentially as a strategy to avoid predators or reduce interspecific competition (Gutteridge et al. 2011). The shark communities sampled here include a diverse array of species and life-history cohorts and, although spatial variation in catch composition was identified, further research is required to better understand inter- and intraspecific partitioning within these environments.

No seasonal variations in shark communities were detected. This was surprising given the predominance of summer pupping in several species including scalloped hammerhead, common blacktip and Australian blacktip sharks (Stevens & Wiley 1986, Stevens & McLoughlin 1991), followed generally by short nursery area residency times (Simpfendorfer & Milward 1993). Inter-annual variability in the number of newborn recruits to coastal environments remains poorly understood. Mean annual abundance of YOY bull sharks in Texas fluctuated above and below the population mean, including within relatively productive bays (Froeschke et al. 2010b). This suggests that nursery areas may experience years of relatively low recruitment, and the modest spikes in YOY abundance during the summers sampled here may have impeded detection of seasonal variations. Gear selectivity may have influenced the catch of YOY sharks of some species. For example, Australian sharpnose sharks are born at 220–260-mm STL (Simpfendorfer 1992), and thus they may be less susceptible to the gears used here. YOY sharks may also utilise habitats in which sampling was not possible, including depths of <0.5 m or among mangroves. In addition, although habitat use changes with age, juvenile pigeye sharks are reported to remain inshore for up to 587 days (Knip et al. 2011b). Further, newborn scalloped hammerhead sharks remained within a protected nursery in Hawaii for up to one year (Duncan & Holland 2006). The combination of the aforementioned factors, along with the abundance of year-round coastal inhabitants (such as Australian sharpnose and spot-tail sharks; Simpfendorfer & Milward 1993), may have precluded the detection of seasonal variation in immature shark communities.

4.4.3 Diversity in shark nursery function

Consistently high catches of numerous shark species highlight the importance of tropical coastal bays for the young of multiple species, especially those of the Order Carcharhiniformes. The present study did not examine site fidelity and therefore it was not possible to classify the various bays as nurseries for individual species using all of the criteria provided by Heupel et al. (2007). Nonetheless, the spatial patterns in immature shark community structure were consistent across the two years of sampling, indicating temporal stability in community-wide habitat use. In addition, the present study revealed that immature sharks were not distributed evenly among bays, suggesting that the bays function differently for individual species and should not be treated interchangeably in terms of the services they provide. For example, patchy distributions of immature scalloped hammerhead sharks suggest that some bays are likely to provide nursery habitat for this species, whereas others may not. Further, for some species such as the whitecheek shark, the shallow coastal waters sampled are important for mature individuals although not as a nursery for juveniles. Accordingly, these findings have important implications for the conservation and management of coastal sharks.

Portfolio theory predicts that contributions from a wide range of immature shark habitats should stabilise the population-level recruitment of adults (Chapter 2). Data reported here suggest that sharks may benefit from portfolio effects through use of multiple bays as potential nursery areas. For example, utilisation of multiple bays may enhance population resilience whereby the effects of localised unfavourable conditions in one bay may be buffered by production in others. In addition, given considerable environmental heterogeneity across the region, more widespread environmental changes may not affect immature sharks in these bays equally. Long-term fishery-independent catch data along the Texas coast indicated that the productivity of immature bull sharks within eight bays was not static through time (Froeschke et al. 2010b). Rather, abundance fluctuated within these sites with their combined occurrence possibly allowing for complementary dynamics in productivity among bay systems. Significant heterogeneity in both environmental conditions and shark communities indicate the potential for these processes to occur in northern Queensland.

In conclusion, this study demonstrated broad-scale diversity in immature shark communities along the tropical coast of Queensland. Diverse communities including multiple life-history stages were encountered, and the results suggest that body size may be more influential in the spatial structuring of coastal shark fauna than is life-history stage. Spatial variations in shark fauna indicated that data on shark community structure and nursery function from restricted areas may not accurately portray patterns occurring over larger geographic scales. Further research is required to identify the drivers of this variability and to better understand how anthropogenic disturbances and climatic change will affect shark populations.

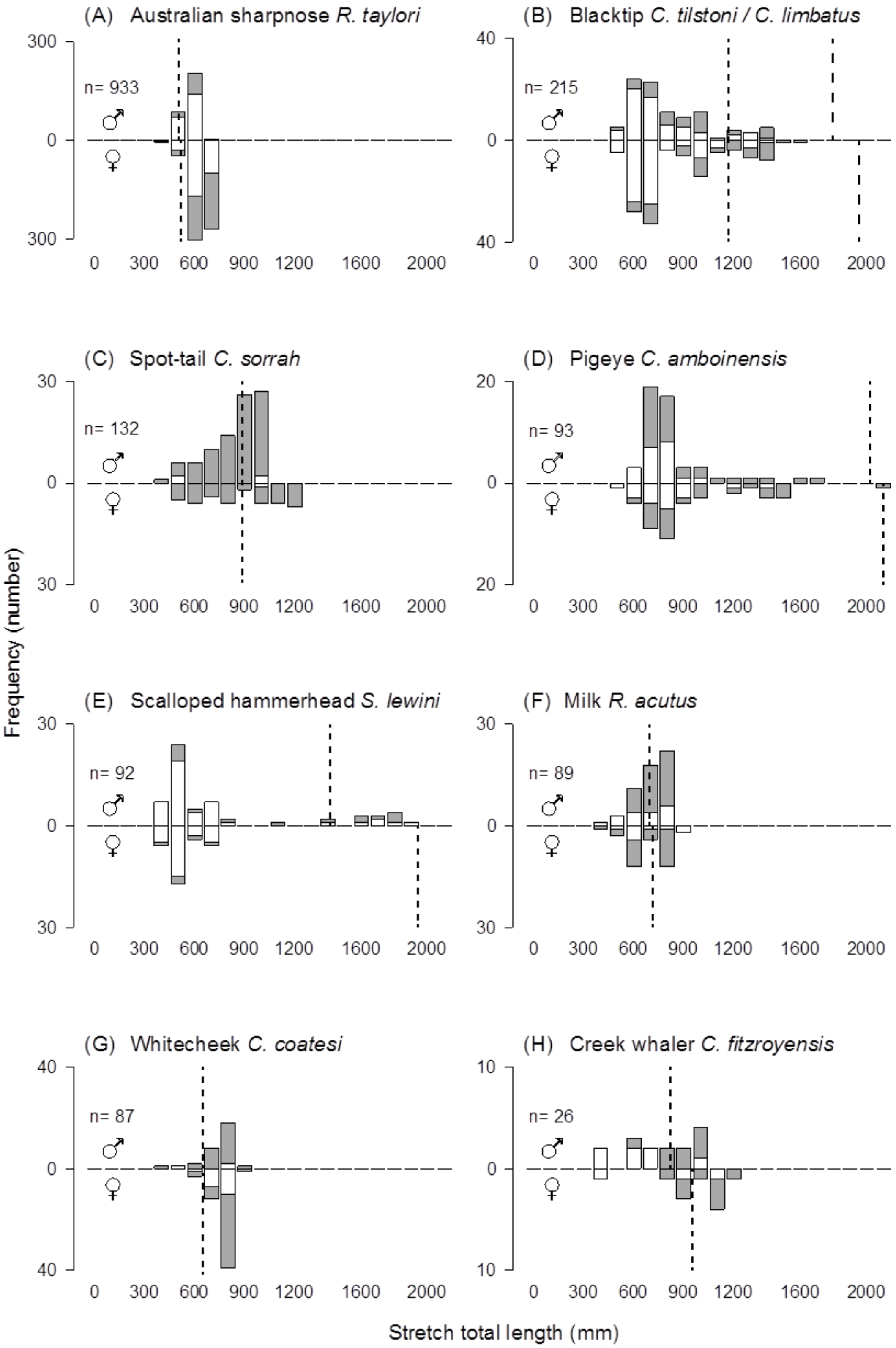


Figure 4.1 Length-frequency distributions of the most abundant sharks. Lengths at 50% maturity (reviewed in Last & Stevens 2009, Harry 2011) are denoted by dashed lines (larger dashes for *Carcharhinus limbatus*, *B*). n = the number of length measurements recorded for each species. Bar shading denotes the sampling method (white = gill-net, grey = longline). Data are from years 2012 and 2013.

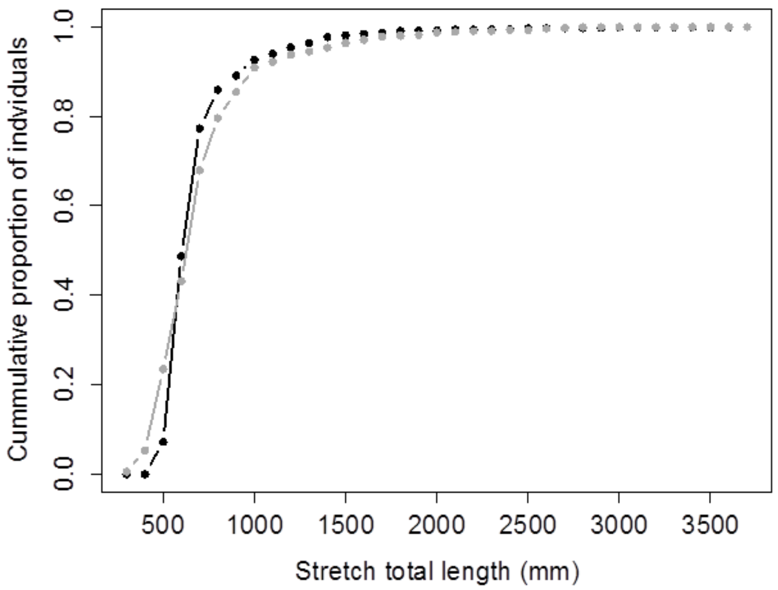


Figure 4.2 Comparison of cumulative length profiles between immature (grey) and mature (black) sharks. Data are pooled into 100-mm bins and span years 2012 and 2013.

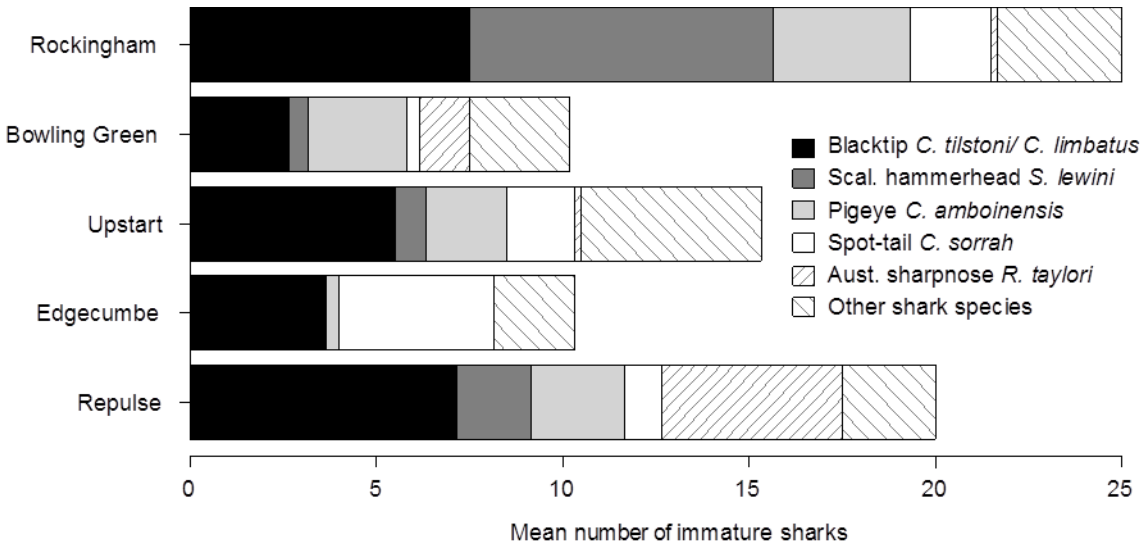


Figure 4.3 Immature shark catch compositions. Mean relative abundance and species composition of immature sharks in five bays. Count data are averaged across sampling rounds. Data are from years 2012 and 2013.

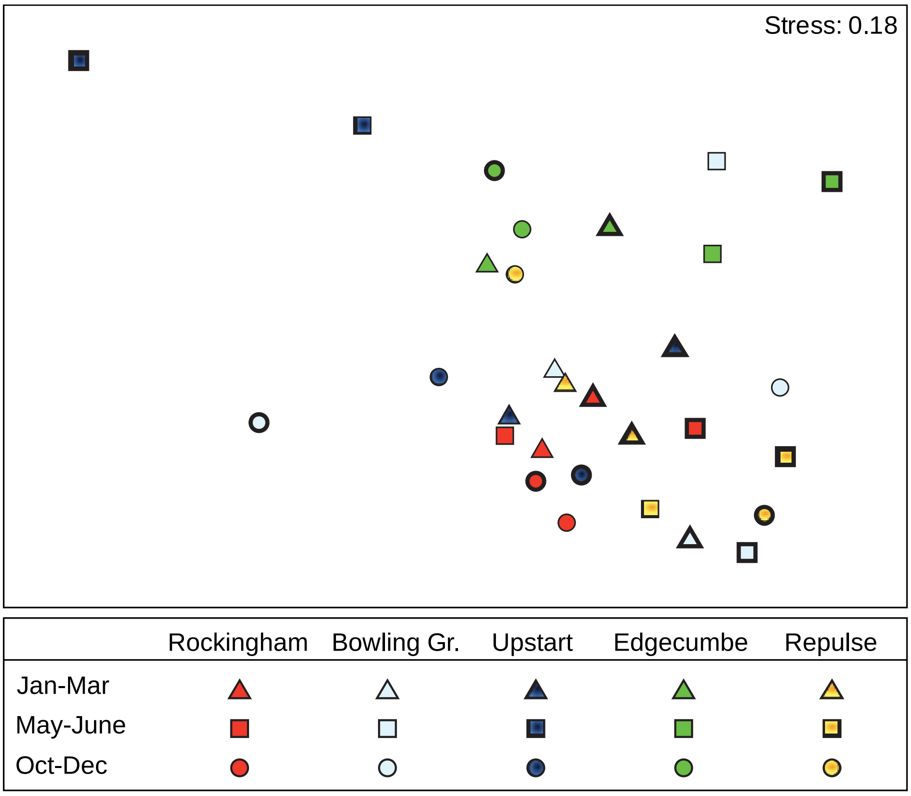


Figure 4.4 Ordination of immature shark communities. Non-metric multidimensional scaling (MDS) ordination of the Bray-Curtis similarity matrix derived from the catch of immature sharks from 15 species groupings (*Carcharhinus tilstoni* and *Carcharhinus limbatus* were grouped together). Each symbol appears twice, with narrow outlines for 2012 samples and thick outlines for 2013 samples. Stress value is shown in the top-right corner.

Table 4.1 Summary of fishing effort in five study bays. Standardised soak hours = sum of 100-hook-hours and 100 m-net-hours for longlines and gill-nets, respectively. Data are from years 2012 and 2013.

	Longline			Gill-net		
	Number of shots	Total soak hours	Standardised soak hours	Number of shots	Total soak hours	Standardised soak hours
Rockingham	82	65.2	36.0	58	51.0	120.2
Bowling Green	79	66.9	35.5	58	57.8	154.8
Upstart	81	66.8	36.1	66	55.2	105.6
Edgecumbe	78	65.3	35.9	61	56.9	143.5
Repulse	77	62.7	34.5	57	52.4	152.6
Whole region	397	326.9	178.0	300	273.2	676.8

Table 4.2 Life-history stage composition of 22 shark species captured during fishery-independent sampling along the tropical coast of Queensland. Data are pooled across study bays and sampling rounds (years 2012 and 2013 only). The number of sharks in each category is followed by its proportion of the species' total maturity-assigned catch in parentheses. YOY = young-of-the-year. In the presence of > 1 life-history stage the most prevalent stage is indicated in bold.

			Life-history stage				
Family	Species	Common name	YOY	Juvenile	Mature	Unknown	Total
Carcharhinidae	*Carcharhinus amboinensis*	Pigeye shark	**47 (0.49)**	**47 (0.49)**	1 (0.02)	4	99
	Carcharhinus brevipinna	Spinner shark	**3 (0.60)**	2 (0.40)		1	6
	Carcharhinus cautus	Nervous shark		5 (0.28)	**13 (0.72)**		18
	Carcharhinus coatesi	Whitecheek shark	4 (0.05)	2 (0.02)	**81 (0.93)**		87
	Carcharhinus fitzroyensis	Creek whaler	4 (0.15)	10 (0.38)	**12 (0.46)**	1	27
	Carcharhinus leucas	Bull shark	5 (0.45)	**6 (0.55)**			11
	Carcharhinus macloti	Hardnose shark			3 (1.00)		3
	Carcharhinus melanopterus	Blacktip reef shark			1 (1.00)		1
	Carcharhinus sorrah	Spot-tail shark	26 (0.20)	33 (0.25)	**73 (0.55)**	1	133
	Carcharhinus tilstoni/ C. limbatus	Unidentified blacktip	**110 (0.51)**	71 (0.33)	35 (0.16)	7	223
	Galeocerdo cuvier	Tiger shark	1 (0.11)	**5 (0.56)**	3 (0.33)	8	17
	Rhizoprionodon acutus	Milk shark	17 (0.19)	19 (0.21)	**54 (0.60)**		90
	Rhizoprionodon taylori	Australian sharpnose	40 (0.04)	8 (0.01)	**888 (0.95)**	10	946
		Unidentified whaler shark				9	9
Hemigaleidae	*Hemigaleus australiensis*	Australian weasel shark		1 (0.17)	**5 (0.83)**		6
	Hemipristis elongata	Fossil shark			2 (1.00)		2
Sphyrnidae	*Eusphyra blochii*	Winghead shark		1 (1.00)			1
	Sphyrna lewini	Scalloped hammerhead	**76 (0.83)**	2 (0.02)	14 (0.15)	1	93
	Sphyrna mokarran	Great hammerhead	4 (0.21)	**12 (0.63)**	3 (0.16)	1	20
Ginglymostomatidae	*Nebrius ferrugineus*	Tawny nurse shark			1 (1.00)		1
Hemiscylliidae	*Chiloscyllium punctatum*	Grey carpetshark		1 (0.25)	**3 (0.75)**		4
Stegostomatidae	*Stegostoma fasciatum*	Zebra shark		**6 (0.67)**	3 (0.33)		9
Total			336 (0.19)	231 (0.13)	**1196 (0.68)**	43	1806

Table 4.3 Comparison of the proportions of immature sharks among five bays along the tropical coast of Queensland. Data are pooled across years and sampling rounds (2012 and 2013 only). Proportion of immature sharks in the catch is followed by the total number of maturity-assigned sharks in parentheses. Uneven proportions of immature:mature individuals are indicated by asterisk (Chi-square test, $df = 1$, $P < 0.05$).

		Bay					
Family	Name	Rockingham	Bowling Gr.	Upstart	Edgecumbe	Repulse	Total
Carcharhinidae	*Carcharhinus amboinensis*	1.00 (23)*	1.00 (24)*	0.93 (14)*	1.00 (2)	1.00 (33)*	0.99 (96)*
	Carcharhinus brevipinna				1.00 (6)*		1.00 (6)*
	Carcharhinus cautus		0 (2)	0.33 (12)	0.25 (4)		0.28 (18)
	Carcharhinus coatesi	0.42 (12)	0.05 (22)*	0 (17)*	0 (32)*	0 (4)	0.07 (87)*
	Carcharhinus fitzroyensis	1.00 (4)	0.33 (18)	1.00 (2)		1.00 (2)	0.54 (26)
	Carcharhinus leucas	1.00 (4)	1.00 (1)		1.00 (1)	1.00 (5)*	1.00 (11)*
	Carcharhinus macloti			0 (1)		0 (2)	0 (3)
	Carcharhinus melanopterus					0 (1)	0 (1)
	Carcharhinus sorrah	0.64 (22)	0.18 (11)*	0.35 (31)	0.42 (59)	0.78 (9)	0.45 (132)
	Carcharhinus tilstoni/ C. limbatus	0.74 (68)*	0.67 (30)	0.83 (40)*	1.00 (34)*	1.00 (45)*	0.84 (217)*
	Galeocerdo cuvier	1.00 (2)	0.5 (4)		0.67 (3)		0.67 (9)
	Rhizoprionodon acutus	0.42 (19)	0.23 (13)	0.79 (29)*	0 (22)*	0.29 (7)	0.40 (90)
	Rhizoprionodon taylori	0.01 (80)*	0.06 (309)*	0.01 (125)*	0 (46)*	0.08 (376)*	0.05 (936)*
Hemigaleidae	*Hemigaleus australiensis*	1.00 (1)	0 (1)	0 (2)	0 (2)		0.17 (6)
	Hemipristis elongata			0 (1)	0 (1)		0 (2)
Sphyrnidae	*Eusphyra blochii*					1.00 (1)	1.00 (1)
	Sphyrna lewini	0.85 (65)*	0.57 (7)	0.83 (6)		1.00 (14)*	0.85 (92)*
	Sphyrna mokarran	1.00 (1)	0.75 (4)	0.33 (3)	1.00 (4)	1.00 (7)*	0.84 (19)*
Ginglymostomatidae	*Nebrius ferrugineus*				0 (1)		0 (1)
Hemiscylliidae	*Chiloscyllium punctatum*		0.5 (2)		0 (1)	0 (1)	0.25 (4)
Stegostomatidae	*Stegostoma fasciatum*	1.00 (2)	0.6 (5)	0 (1)	1.00 (1)		0.67 (9)

Table 4.4 Species contributions to average Bray-Curtis dissimilarities among bays (SIMPER). Results are for years 2012 and 2013 combined. Only bays that were distinguished on the basis of immature shark communities (ANOSIM) are included. Av. diss. = average of the Bray-Curtis dissimilarities between all pairs of samples. Species that contributed up to 70% of cumulative contribution to Av. diss. are ordered in decreasing contribution. Average relative abundance values are square-root transformed as is relevant to the dissimilarity calculations.

Species	Average relative abundance (former bay/ latter bay)	Average dissimilarity	Contribution (%)	Cumulative contribution (%)
Edgecumbe verses Rockingham (Av. diss. = 67.81)				
Sphyrna lewini	0 / 2.79	17.17	25.32	25.32
Carcharhinus amboinensis	0.24 / 1.62	9.33	13.76	39.08
Carcharhinus tilstoni/ C. limbatus	1.69 / 2.56	8.09	11.93	51.01
Carcharhinus sorrah	1.64 / 1.31	7.77	11.46	62.47
Carcharhinus brevipinna	0.69 / 0	4.14	6.1	68.57
Carcharhinus coatesi	0 / 0.62	3.64	5.37	73.94
Edgecumbe verses Repulse (Av. diss. = 67.84)				
Carcharhinus sorrah	1.64 / 0.57	10.6	15.62	15.62
Rhizoprionodon taylori	0 / 1.47	9.82	14.47	30.09
Carcharhinus tilstoni/ C. limbatus	1.69 / 2.37	9.05	13.34	43.43
Carcharhinus amboinensis	0.24 / 1.37	8.67	12.78	56.2
Sphyrna lewini	0 / 1.23	8.53	12.57	68.78
Sphyrna mokarran	0.5 / 0.86	4.95	7.3	76.08

CHAPTER 5

Ecological Drivers of Shark Distributions along a Tropical Coastline

Plate 5 Turbid conditions in Repulse Bay (February 2013).

Accepted as an original research paper, 19th February 2015:

Yates PM, Heupel MR, Tobin AJ, Simpfendorfer CA (2015) Ecological drivers of shark distributions along a tropical coastline. PLoS ONE 10:e0121346

5.1 Introduction

Understanding the relationship between sharks and their environment can facilitate the identification of critical habitats for the sustainable management and conservation of shark populations (Simpfendorfer & Heupel 2012). In particular, the factors that influence use of nursery areas by young sharks have been a focus of recent research (McCandless et al. 2007a, Froeschke et al. 2010a). Shark nurseries are defined as areas with (1) relatively high abundance of young sharks, (2) site fidelity and (3) stability in use across multiple years (Heupel et al. 2007). The use of nursery areas presumably enhances the fitness or survival of young sharks (Branstetter 1990), which in turn can influence population productivity (Cortés 2002). Therefore, data on the location and functioning of shark nurseries may enhance management and conservation of shark populations.

Coastal environments can provide young sharks with abundant prey (Robertson & Duke 1987, Rojas et al. 2014) and refuge from larger-bodied predators (Heupel & Simpfendorfer 2011). In addition, some coastal regions are used by multiple species and may function as communal shark nurseries (Simpfendorfer & Milward 1993). The distribution and habitat use of sharks in coastal environments can often be attributed to spatio-temporal variation in environmental conditions (Schlaff et al. 2014). Coastal environments can be susceptible to a range of human impacts (reviewed in Knip et al. 2010) and environmental change (Chin et al. 2010), and the identification of factors that influence the habitat use of coastal sharks can improve understanding of how they may respond to changes within their environment.

A wide range of abiotic variables are thought to influence the habitat use of coastal sharks (reviewed in Schlaff et al. 2014). For example, water temperature (McCallister et al. 2014), depth (Ward-Paige et al. 2014), salinity (Froeschke et al. 2010a, Drymon et al. 2014), turbidity (Ortega et al. 2009) and dissolved oxygen concentration (DO; Heithaus et al. 2009, Drymon et al. 2013) have been identified as important factors for multiple species. Influences of abiotic variables may be dictated by a species' physiological requirements. For example, ectothermic sharks are hypothesised to use behavioural thermoregulation to optimise energetic uptake and expenditure (reviewed in Bernal et al. 2012), and avoid lethal temperatures (Heupel 2007). Coastal sharks may also occupy particular salinities to reduce the metabolic demands of osmoregulation (Froeschke et al. 2010a), although their salinity preferences can change with age (Compagno 1984, Simpfendorfer et al. 2005, Heupel & Simpfendorfer 2008). Thus a range of factors, including physiology, age, size and other biotic variables are likely to shape how abiotic conditions influence a species.

Biotic variables are widely cited as determinants of habitat selection by sharks (Torres et al. 2006, Heithaus 2007, Barnett & Semmens 2012). For example, predation risk was implicated in the habitat use and aggregation of juvenile lemon sharks *Negaprion brevirostris* within a subtropical mangrove-inlet (Guttridge et al. 2012). Shark abundance has also been linked with the abundance of potential teleost prey, albeit over broad spatial scales (Torres et al. 2006). In addition, biotic ecosystem features such as mangroves and seagrass beds may provide multiple benefits including abundant prey and refuge from predators (Morrissey & Gruber 1993b, White & Potter 2004). Relationships between sympatric young sharks, and other life-history stages, may also influence habitat use. Competition for limited resources may necessitate inter- or intraspecific partitioning of space and food resources (White & Potter 2004, Kinney et al. 2011). Conversely, aggregation behaviour may reduce susceptibility to predation. For example, schooling fish benefit from the dilution of predation risk (Morgan & Godin 1985), and therefore young sharks may derive similar benefits by having similar spatio-temporal occurrences and habitat use patterns (Heithaus 2004, Heupel & Simpfendorfer 2005b, Jacoby et al. 2012). A variety of biotic factors are important for the habitat use of coastal sharks including varied trade-offs between predation risk and energetic requirements.

Although a large portion of research on shark nurseries has occurred across restricted spatial scales (e.g. Ubeda et al. 2009, Heupel & Simpfendorfer 2011), there are examples of intraspecific variation in habitat use between nearby inshore systems. For example, contrasting habitat use patterns of immature sandbar sharks *Carcharhinus plumbeus* between two adjacent bays along the eastern United States may have coincided with spatial variation in hydrodynamics and predation pressure (Grubbs et al. 2007, McCandless et al. 2007b). Salinity was most influential in the habitat use of juvenile bull sharks in the Caloosahatchee River, Florida (Heupel & Simpfendorfer 2008), but exerted a relatively small influence relative to DO in the Florida Everglades (Heithaus et al. 2009). Salinity fluctuations were larger in the Caloosahatchee River, which may have necessitated a more pronounced salinity response by sharks occurring there compared to those in the Florida Everglades (Heithaus et al. 2009). Intraspecific variations in habitat use highlight the importance of sampling within multiple habitats to gain a more comprehensive understanding of shark habitat use across a region.

Coastal habitats along north-eastern Australia support a diverse and abundant shark assemblage (Harry et al. 2011b), within which immature Australian blacktip *Carcharhinus tilstoni*, common blacktip *Carcharhinus limbatus*, pigeye *Carcharhinus amboinensis,* and scalloped hammerhead *Sphyrna lewini* sharks are relatively abundant (Chapter 4). The scarcity of data on the distribution and abundance of these species hinders the identification of critical habitats and understanding of the impacts of environmental change. The aim of this study was to investigate the influence of abiotic and biotic variables on the distribution of immature blacktip, pigeye and scalloped hammerhead sharks across a broad spatial scale and provide information for the sustainable management of important habitats.

5.2 Methods

Chapter 5 used data from eight rounds of fishery-independent surveys spanning the period of January 2012 to March 2014 (Table 3.2; Table 3.3). Data were from Rockingham, Bowling Green, Upstart, Edgecumbe and Repulse Bays (Figure 3.1).

5.2.1 Site variability

To investigate broad-scale environmental heterogeneity, Kruskal-Wallis rank sum tests (R package 'stats'; R Development Core Team 2014) were used to identify significant variations in environmental measurements among bays. Significant variations were investigated with a multiple comparison test which identified where variations existed (R package ‘pgirmess’; Giraudoux 2013).

5.2.2 *Species associations*

To investigate the potential for intra- and interspecific association or segregation, the degree of association in catch between species and life-history stages was examined using the Association Statistic and % Common Occurrence (described in Cass-Calay & Bahnick 2002, Cass-Calay & Schmidt 2003). Data were aggregated by day and association metrics were calculated based on shark presence/absence in longline and gill-net samples separately. The Association Statistic and % Common Occurrence for each pairwise comparison were calculated as:

$$\text{Association Statistic} = \frac{\text{no. samples with groups A \& B}}{\text{no. samples with group A}} \div \frac{\text{no. samples with group B}}{\text{total no. of samples}}$$

$$\text{\% Common Occurrence} = \frac{\text{no. samples with groups A \& B}}{\text{no. samples with group B}} \times 100$$

Measures of association were calculated between each of the focal groups (immature blacktip, pigeye and scalloped hammerhead sharks) and all other species/life-history-stage groups with ≥ 10 individuals (i.e. ‘comparison groups’). An Association Statistic equal to 1 implied that both groups were distributed randomly with respect to each other. Values > 1 indicated that two groups were encountered together more frequently than random chance would predict; and conversely for values < 1 (Cass-Calay & Bahnick 2002). Percent Common Occurrence ranged from 0 (two groups were never captured together) to 100 (two groups were always captured together).

5.2.3 *Variables influencing shark catch*

Generalised linear models (R package ‘MASS’; Venables & Ripley 2002) were used to examine the relationship between environmental variables and the abundance of blacktip, pigeye and scalloped hammerhead sharks across the study region. Longline and gill-net data were analysed separately. The abundance of immature sharks within putative nursery areas was the focus of this study therefore analyses were limited to immature individuals. Low abundance of scalloped hammerhead sharks in longline samples precluded further analysis of this sampling method for this species. Prior to model fitting, data exploration was carried out according to Zuur et al. (2009) and Zuur et al. (2010). Cleveland dotplots were used to check for outliers. Conditional boxplots, pairwise scatterplots, Pearson correlation coefficients and variance inflation factors (VIF; R package ‘car’; Fox & Weisberg 2011) were used to investigate relationships between variables. Spatio-temporal variables (bay and sampling round) were confounded with multiple environmental variables and were therefore excluded from analyses. In addition, high VIF (i.e. ≥ 3; Zuur et al. 2012) indicated collinearity between temperature and DO. Ninety-seven percent of DO measurements were > 4.5 mg/L thus DO was deemed unlikely to be a limiting factor for sharks and was excluded from further analyses. Subsequently, VIF were < 1.3 for remaining variables (Table 5.1). There were only two cases of a shark being captured twice during the same four-day trip, therefore individual fishing samples were assumed to be independent.

To avoid over-fitting of the data with spurious relationships, investigations were limited to an *a priori* selection of ecologically relevant covariates and interactions (Burnham & Anderson 2002, Whittingham et al. 2006). For each species/sampling-method combination, the following ‘starting’ model was created containing the main effects and interactions of interest:

$$\log(Abundance_i) = \beta_1 + \beta_2 \times Depth_i + \beta_3 \times Temperature_i + \beta_4 \times Salinity_i + \beta_5 \times Secchi\ depth_i \\ + \beta_6 \times Mangrove\ distance_i + \beta_7 \times Secchi\ depth_i * Depth_i + \beta_8 \times Secchi\ depth_i * Salinity_i \\ + offset(log[Fishing\ effort_i])$$

Shark abundance was assumed to be negative binomial distributed, and the logarithm link between expected shark abundance ($Abundance_i$) and the selected covariates ensured that all fitted values were non-negative. Standardised fishing effort was calculated as the logarithm of 100-hook hours for longlines or the logarithm of 100m-net hours for gill-nets. Interaction terms were selected based on putative implications of depth and turbidity for vulnerability to predation (Branstetter 1990, Heithaus 2007), and the potential for interaction between turbidity and salinity during the summer wet season (Knip et al. 2011a).

To identify the most influential drivers of shark abundance, a dredge function (R package ‘MuMIn’; Barton 2013) was used to identify more-parsimonious nested models according to the Akaike Information Criterion (AIC). This approach required prior omission of samples containing missing values (31 longline shots and 27 gill-net shots). The rule of marginality was applied whereby interactions were only considered in models that contained both main effects. Additionally, a maximum of eight parameters were specified per model and the offset variable was ‘fixed’ within all models. A ‘confidence set’ of models with ΔAIC < 2 were considered equivalent and included in model averaging; from which the Relative Variable Importance values (RVI; calculated from the sum of AIC weights of models within the confidence set in which the parameter of interest appears) were used to identify important variables. If multiple variables shared the same RVI, the magnitude of the standardised model-averaged coefficient provided an alternative measure of relative influence. A single model containing only highly influential variables, identified as those preceding a sharp decline in RVI, was used for visual representation of variable effects (R package ‘visreg’; Breheny & Burchett 2013), calculation of explained deviance, and assessment of adherence to model assumptions. Cook's distances were used to check for observations with disproportionally high influence. Pearson residuals were plotted against fitted shark abundance as well as included and excluded covariates to check for homogeneity, independence and model fit. Pearson residuals were plotted by geographic position according to their sign and magnitude. Minor spatial structuring of residuals was observed for pigeye and scalloped hammerhead sharks, however this was not improved by the inclusion of bay, transect group or sampling round as random intercepts (R packages 'glmmADMB' and 'lme4'; Skaug et al. 2012, Bates et al. 2014).

5.3 Results

5.3.1 Catch composition

A total of 1987 sharks were captured from six families. In total, 22 shark species were captured, and catch composition was similar to that presented in Chapter 4 (i.e. years 2012–2013 only). Across years 2012–2014, Australian sharpnose *Rhizoprionodon taylori* (52%) and blacktip (12%) sharks were numerically dominant (Appendix 4). Spot-tail (8%), pigeye (6%), scalloped hammerhead (5%), milk *Rhizoprionodon acutus* (5%) and whitecheek *Carcharhinus coatesi* (5%) sharks were moderately abundant. The catch of immature sharks was dominated by blacktip (31%), pigeye (17%) and scalloped hammerhead (14%) sharks. Length-frequency histograms indicated that these species were predominantly immature (Figure 5.1).

5.3.2 Site variability

There was significant variation in water temperature (Kruskal-Wallis rank sum test; χ^2 = 23.7, $df = 4$, $P < 0.001$), salinity (χ^2 = 142.4, $df = 4$, $P < 0.001$), turbidity (χ^2 = 167.4, $df = 4$, $P < 0.001$), and mangrove proximity (χ^2 = 187.7, $df = 4$, $P < 0.001$) among study bays (Table 5.1). For example, mean salinity was ≥ 2.4 ppt lower in Rockingham and Repulse Bays compared to the other three bays (Table 5.1). In addition, turbidity was significantly lower (i.e. secchi depth was higher) in Edgecumbe Bay, followed by Upstart Bay. This spatial heterogeneity created an ideal study region for investigating the drivers of shark abundance. Sampled water depths did not vary significantly among bays (Kruskal-Wallis rank sum test; $\chi^2 = 1.1$, $df = 4$, $P = 0.90$), confirming that a comparable spectrum of depths were sampled across bays.

5.3.3 Species associations

The maximum value of the Association Statistic depended on the proportion of trips that caught the focal species/life-history-stage group. Therefore, comparison groups with the highest and lowest association were compared between the three focal groups (Table 5.2; Appendix 5–Appendix 7). Overall, associations were variable between focal groups and sampling methods. For example, mature whitecheek sharks *Carcharhinus coatesi* were one of the most associated groups with immature blacktip sharks in longline samples, but these two groups had relatively low association in gill-net samples. Nonetheless, there were multiple examples of relatively high associations between immature blacktip, pigeye and scalloped hammerhead sharks in gill-nets (Table 5.2). In addition, across immature blacktip, pigeye and scalloped hammerhead sharks, 83% of relatively high associations were with other immature groups. Conversely, 72% of relatively low associations were with mature groups. Therefore, immature sharks across multiple species were more often encountered together than they were with mature sharks.

5.3.4 Variables influencing shark catch

Variation in shark abundance was associated with complex combinations of main effects and interactions. Overall, turbidity and salinity were the most influential variables on shark abundance (Figure 5.2). Most notably, excluding blacktip sharks on longlines, turbidity was present in all best-performing models (i.e. those with ΔAIC < 2; Table 5.3). Mangrove proximity, depth and water temperature were also important however their influence varied among species.

Blacktip shark

A total of 86 and 161 blacktip sharks were captured using longlines and gill-nets, respectively. Of these, 60 and 141 immature individuals were included in longline and gill-net analyses, respectively. For longlines, a weakly significant effect of mangrove proximity was detected (Table 5.4), however the explained deviance of 4% indicated that the influence of this variable was negligible. Turbidity and depth were highly influential in gill-net samples (Figure 5.3; Table 5.4). In addition, the influence of mangrove proximity in gill-net samples corroborated the otherwise equivocal longline results. Overall, blacktip shark abundance decreased with decreasing turbidity (i.e. increasing secchi depth) and distance from mangroves, and increased with depth (Figure 5.3). These three variables were present in all best-performing models (Table 5.3) and together explained 18% of deviance in blacktip shark abundance in gill-nets.

Pigeye shark

A total of 68 and 44 pigeye sharks were captured using longlines and gill-nets, respectively. Of these, 63 and 41 immature individuals were included in longline and gill-net analyses, respectively. For both sampling methods, turbidity and its interaction with salinity were the most influential drivers of shark abundance (Table 5.3; Table 5.4). Abundance generally decreased with decreasing turbidity, however the opposite occurred at low salinities using both sampling methods (c. 30–31 ppt; Figure 5.4A, B). For gill-nets, interaction between turbidity and depth suggested that relatively low-turbidity and shallow environments provided suitable habitat for young pigeye sharks (Figure 5.4C). All high-order parameters were significant in model averaging (Table 5.4), and together explained 13% and 45% of deviance in pigeye shark abundance in longline and gill-net samples respectively. A negative relationship between pigeye shark abundance and distance from mangroves was also included in two of the three best-performing gill-net models (Table 5.3), however the RVI was relatively low (0.78), the model-averaged coefficient was non-significant ($Z = 1.34$, $P = 0.18$), and the coefficient in a single high-RVI model was weakly significant ($Z = -2.17$, $P = 0.03$). Therefore results on the influence of mangrove proximity on pigeye sharks were inconclusive.

Scalloped hammerhead shark

A total of 81 scalloped hammerhead sharks were captured in gill-nets and 73 immature individuals were included in the analysis. Scalloped hammerhead shark abundance decreased with decreasing turbidity, however this trend deteriorated at low salinities around 31 ppt (Figure 5.5A). In addition, scalloped hammerhead shark abundance increased with temperature (Figure 5.5B). Turbidity, salinity and temperature were present in all best-performing models (Table 5.3) and, together with interaction between turbidity and salinity, explained 29% of deviance in scalloped hammerhead shark abundance in gill-nets.

5.4 Discussion

The relative abundance of immature sharks along an expanse of tropical coastline was related to environmental conditions. Of the 22 species sampled, blacktip, pigeye and scalloped hammerhead sharks were relatively abundant suggesting these species are important components of coastal ecosystems. Despite the overlapping distributions of these species, results indicated general and species-specific patterns in abundance which were characterised by a range of biotic and abiotic variables. In particular, relationships with turbidity were similar across species highlighting the importance of this variable in the functioning of coastal habitats and communal shark nurseries. Further, the influence of turbidity on the abundance of pigeye and scalloped hammerhead sharks varied similarly depending on salinity. Shark abundance and community structure have been found to vary along coastal stretches (Chapter 4, Froeschke et al. 2010b, Bethea et al. 2014). In the present study, species-environment relationships, along with the demonstrated environmental heterogeneity among bays indicate that environmental variables are likely drivers of spatial variation in shark abundance and nursery function among bays.

The use of turbid coastal environments is considered to be an anti-predator strategy employed by young sharks (Clarke 1971, Heithaus 2004), although relatively few studies have investigated this relationship empirically. Turbid environments may also provide abundant prey for small sharks (Blaber & Blaber 1980) or facilitate stealthy hunting strategies (Heithaus 2004). Immature blacktip, pigeye and scalloped hammerhead sharks were generally more abundant in turbid conditions, which aligns with previous findings for these species in northern Australia (Kinney 2011, Knip et al. 2011b) and in other locations (Clarke 1971, Taylor 2007, Gutteridge 2011). In contrast, some small-bodied coastal species including spot-tail sharks *Carcharhinus sorrah* and slit-eye sharks *Loxodon macrorhinus* demonstrate a preference for relatively low turbidity, which may lead to reduced interspecific resource competition (Gutteridge et al. 2011, Kinney 2011). There are also examples of turbidity having a modest (Froeschke et al. 2010a) or negligible (Blaber et al. 1995) effect on shark catch rates, potentially due to relatively uniform turbidity in some coastal waters (e.g. Froeschke et al. 2010a). Therefore, the influence of turbidly appears to be species- and context-specific.

Salinity and temperature have important physiological implications for sharks (Pang et al. 1977, Bernal et al. 2012) and there are numerous examples of their influence on shark habitat use (Ubeda et al. 2009, Froeschke et al. 2010a, McCallister et al. 2014). For example, the occurrence of immature scalloped hammerhead sharks in the north-eastern Gulf of Mexico increased with both salinity and temperature (Ward-Paige et al. 2014). The utilisation of warmer water may represent behavioural thermoregulation (Bernal et al. 2012) or may be related to seasonal fluctuations in the occurrence of this species. The influence of salinity on pigeye and scalloped hammerhead sharks was primarily related to its interaction with turbidity. The relatively high abundance in turbid water diminished at salinities often associated with coastal flood plumes (i.e. < 33 ppt; Furnas 1993). Previous acoustic tracking of immature pigeye sharks in northern Australia revealed that individuals moved away from freshwater sources during times of high freshwater input (Knip et al. 2011a), which likely corresponded with increased turbidity and lower salinity. Similar movements in response to high river flows have been reported for juvenile rig *Mustelus lenticulatus* in a New Zealand estuary (Francis 2013). Stenohaline sharks typically inhabit a narrow range of salinities (Schlaff et al.

2014). Therefore, immature pigeye and scalloped hammerhead sharks may have increased their use of relatively low-turbidity water to avoid low-salinity, albeit suitably turbid, conditions; thereby alleviating the metabolic costs of osmoregulation in salinities outside of their preferred range.

Sharks in shallow-water nurseries have been hypothesised to benefit from reduced predation risk because these depths can limit the access of large-bodied predators (Springer 1967, Morrissey & Gruber 1993b, Heithaus 2004). Contrary to this, the abundance of blacktip sharks in gill-nets increased with water depth suggesting that moderate depths up to 5 m also provide suitable habitat for young sharks in coastal environments. Immature common blacktip sharks were also shown to prefer depths around 5 m in the northern Gulf of Mexico (McCallister et al. 2014, Ward-Paige et al. 2014). In contrast to blacktip sharks, acoustic tracking of pigeye sharks in north-eastern Australia revealed youngest individuals utilised depths around 2 m, although the depths occupied increased with age (Knip et al. 2011b). In the present study, although pigeye sharks were more abundant in turbid water, there was no clear influence of turbidity at depths around 1.5 m suggesting that shallow water alone may provide suitable refuge regardless of turbidity level. Therefore, the habitat use of young sharks is likely shaped by a multitude of direct, indirect and interacting relationships with their environment.

The results of this study showed blacktip sharks were more abundant in close proximity to mangroves. Because mangroves covered a large portion of coastline it was difficult to separate the influence of mangroves from that of distance from shore. However, other examples of positive associations between sharks and mangrove habitats corroborate the ecological relevance of this association. For example, elasmobranch abundance and number of species were higher in sites adjacent to mangroves in the eastern Indian Ocean (White & Potter 2004) and young lemon sharks typically inhabit waters near or within mangroves (Morrissey & Gruber 1993b). The structural complexity of mangrove habitats may provide refuge for sharks within close proximity (Guttridge et al. 2012). In addition, the high productivity of mangrove habitats can support large populations of teleosts and invertebrates on which young sharks feed (Robertson & Duke 1987). However, high prey abundance does not necessarily increase prey availability for sharks. For example, the presence of prop roots or branches may impede successful hunting (Gotceitas & Colgan 1989). Alpheid burrows and seagrass are also thought to decrease the hunting success of young sharks (Morrissey & Gruber 1993b, Bush & Holland 2002). The present study indicated that mangroves may be important for young blacktip sharks, although the nature of this relationship remains poorly understood.

Similar species-environment relationships were observed between sampling methods, especially for pigeye sharks, providing support for the reliability of the results. For example, interaction between turbidity and salinity for pigeye sharks was apparent with both gears. However, some variation between gears emphasises the necessity to consider associated biases. For example, turbidity was less-influential for blacktip sharks on longlines compared to gill-nets. Low turbidity may improve the ability of sharks to detect and avoid gill-nets (Cui et al. 1991) and thereby disproportionately affect gill-net efficacy. In addition, highly sensitive olfaction in sharks (Gardiner et al. 2012) may broaden the effective sampling range of baited longlines. The activity-specific nature of shark habitat use (e.g. feeding verses refuging; Holland et al. 1993, Heithaus 2007) may also dictate spatio-temporal variation in gear susceptibility. Similarly, Ulrich et al. (2007) reported variation in the relative abundance and size composition of multiple species between gill-net and longline samples in coastal waters of South Carolina. Hence a combination of gears may provide a more-robust representation of shark abundance.

Investigations of species-habitat relationships are influenced by the spatio-temporal scales and variables considered, and the sampling and analysis methods used (Burnham & Anderson 2002, Whittingham et al. 2006, Ward-Paige et al. 2014). It was not possible to include all possible drivers of abundance in this study. Tides (Ackerman et al. 2000), river flows (Knip et al. 2011a), DO (Heithaus et al. 2009), pH (Ortega et al. 2009), substrate type (Morrissey & Gruber 1993b), prey distribution (Torres et al. 2006), seagrass (White & Potter 2004), coral reefs (Chin et al. 2012), and photoperiod (Grubbs et al. 2007) have also been related to the habitat use of sharks in coastal environments. Thus some or all of these variables may be important for immature blacktip, pigeye and scalloped hammerhead sharks along north-eastern Australia. Further, the correlative nature of our results leaves the underlying causative mechanisms unconfirmed. Nonetheless, this study provided a useful foundation for future studies by identifying the variables most strongly associated with shark abundances.

Variability in association measures between species and sampling gears may have been influenced by the geographic scale considered. For example, variation in occurrence patterns and community structure between bays (Chapter 4) may have increased the variability in association metrics calculated across the region. Nonetheless, there were indications of relatively low spatio-temporal association between immature and mature sharks. This aligned with the traditional view of shark nurseries as areas inhabited by young sharks and not mature individuals (Springer 1967). It is also likely that interspecific similarities in environmental drivers influenced species association results, or vice-versa. For example, instances of relatively high association between immature blacktip, pigeye and scalloped hammerhead sharks in the gill-net catch may be a reflection of a shared preference for turbid conditions.

Evidence that sharks respond to variations in environmental conditions coupled with significant spatial heterogeneity in these conditions among bays reveals them as probable drivers of spatial variation in habitat use among bays. Indeed, variable habitat use among bays is likely given stark variations in community structure and the relative abundance of individual species among inshore areas in this (Chapter 4) and other locations (Froeschke et al. 2010b, Bethea et al. 2014, McCallister et al. 2014, Ward-Paige et al. 2014). For example, Rockingham Bay had the highest turbidity and highest abundance of immature scalloped hammerhead sharks (Chapters 4 and 6); whereas Edgecumbe Bay had the lowest turbidity and only one recorded scalloped hammerhead shark. Given that turbid water was identified as the strongest driver for this species, spatial variation in turbidity is a probable mechanism behind variations in abundance among bays. Similar patterns involving turbidity and the abundance of pigeye sharks were apparent between Repulse and Edgecumbe Bays. Spatial variation in the abundance of sharks has been demonstrated in other regions. For example, variations in the occurrence of common blacktip, bull and bonnethead *Sphyrna tiburo* sharks among Texas bays were attributed to variations in salinity, water temperature and proximity to tidal inlets (Froeschke et al. 2010a). Therefore, habitat diversity coupled with environmental preferences may drive intraspecific heterogeneity in shark nursery function across a region.

The habitat use of coastal sharks is particularly relevant in light of increasing anthropogenic impacts on coastal ecosystems such as fishing and coastal modification (reviewed in Knip et al. 2010). In addition, climatic events can cause extensive loss of seagrass and mangroves (GBRMPA 2011, McKenzie et al. 2012). The impacts of these disturbances on sharks remain poorly understood; although mangrove loss (Jennings et al. 2008) pollution (Gelsleichter et al. 2005), thermal effluent (Curtis et al. 2011, Curtis et al. 2013), and hydrodynamic changes (Espinoza et al. 2011) have been reported to influence the habitat use or fitness of coastal sharks. Port capacity along north-eastern Australia is predicted to triple by 2020 (BREE 2012), and this may exacerbate numerous pressures including benthos disturbance, hydrodynamic changes, pollutant introduction and remobilization, elevated suspended sediments, and noise pollution (reviewed in Grech et al. 2013). Given that this study identified turbidity, salinity and mangrove proximity as potential drivers of shark abundance, the aforementioned disturbances are likely to have direct effects on the occurrence and habitat use of the study species. Although multiple species were positively associated with turbid conditions, further research is needed to understand the ecosystem-level consequences of any perturbations to shark habitat use.

The use of environmentally heterogeneous landscapes provides the potential for portfolio effects which can mitigate the effects of environmental changes (Chapter 2, Oliver et al. 2010, Schindler et al. 2010). If young sharks in different bays are differentially impacted by environmental change or localised impacts, populations may benefit from enhanced resilience whereby the effects of disturbance in one area are buffered by production in others (Chapter 2). In addition, contributions from a diversity of habitats can reduce variability in the production of individuals across a region

(Froeschke et al. 2010b), which can in turn influence population growth (Cortés 2002). Therefore the variable distributions of sharks observed here (Chapter 4) may be an effective strategy to enhance population viability.

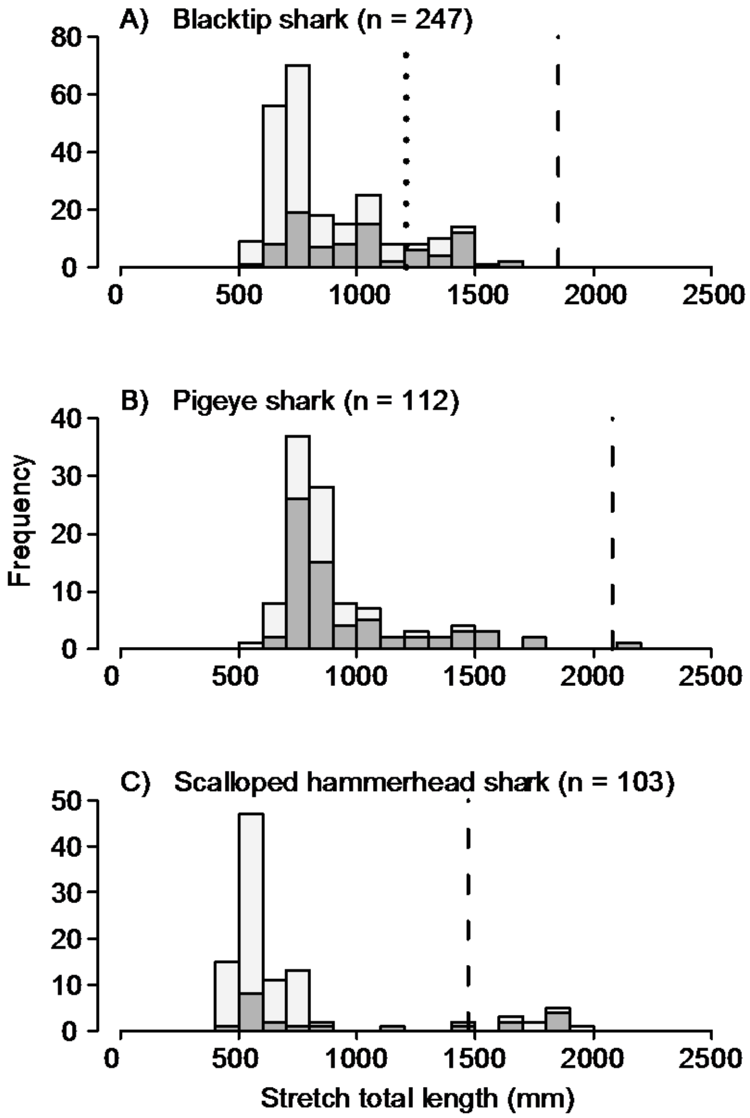


Figure 5.1 Length-frequency distributions of blacktip *Carcharhinus tilstoni/Carcharhinus limbatus*, pigeye *Carcharhinus amboinensis* and scalloped hammerhead *Sphyrna lewini* sharks. Bar shading denotes the sampling method (dark grey = longline, light grey = gill-net). Lengths at 50% maturity (reviewed in Last & Stevens 2009, Harry 2011) are denoted by broken lines (larger dashes for the common blacktip shark; A). The lengths at 50% maturity for common blacktip, pigeye and scalloped hammerhead sharks differ between sexes and so the smallest is given (male in all cases). Data are from years 2012–2014.

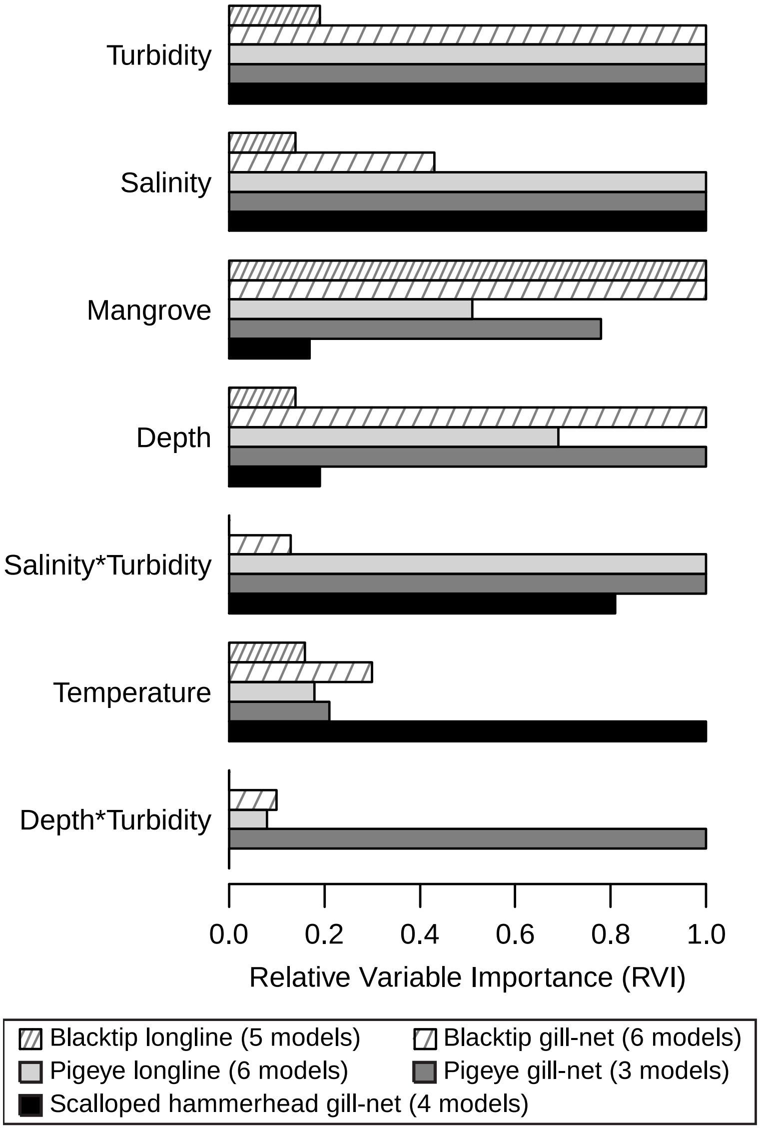


Figure 5.2 Relative importance of ecological variables. Parameters are listed according to mean Relative Variable Importance (RVI) across all species/sampling-method combinations. Parameters that were ubiquitous within the confidence set (i.e. models with ΔAIC < 2) have a RVI value of 1.0. The numbers of models included in model averaging are provided in parentheses.

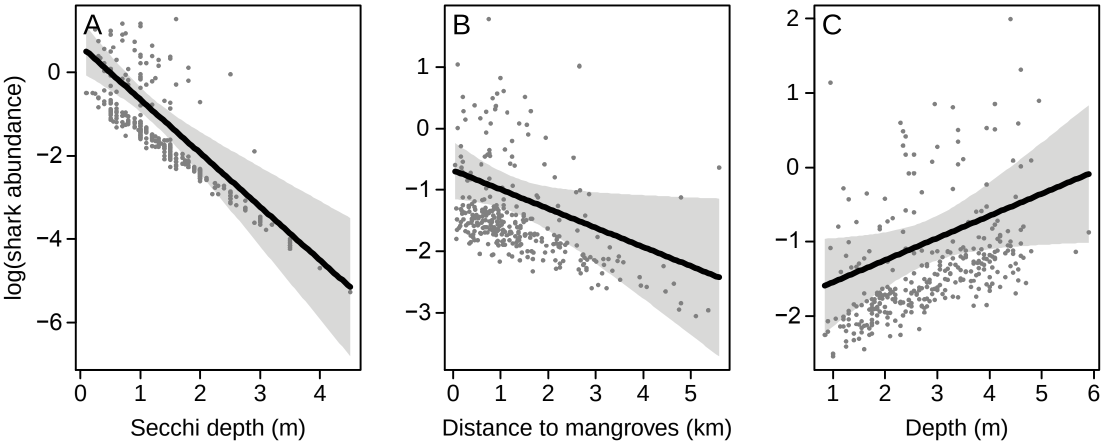


Figure 5.3 Modelled relationships between the abundance of immature blacktip sharks *Carcharhinus tilstoni/Carcharhinus limbatus* in gill-nets and highly influential variables**.** Shading represents 95% confidence intervals and points are partial residuals. Effects were plotted with additional variables held at their medians. The model containing turbidity, distance to mangroves and depth had dispersion statistic = 1.15 and negative binomial variance parameter *k* = 0.32. Note that low values of secchi depth indicate high turbidity.

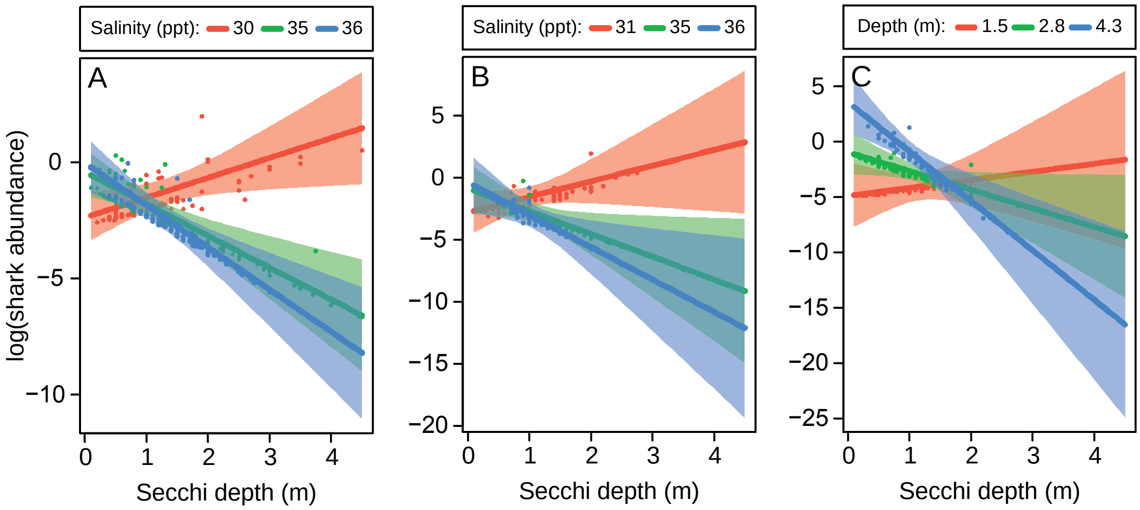


Figure 5.4 Modelled relationships between the abundance of immature pigeye sharks *Carcharhinus amboinensis* and highly influential variables in longline (A) and gill-net (B, C) samples. Shading represents 95% confidence intervals and points are partial residuals. Effects were plotted with additional variables held at their medians. To visualise interactions, cross-sections were taken at the 10th, 50th and 90th percentiles of the second variable of interest. The plotted longline model had dispersion statistic = 1.00 and negative binomial variance parameter $k = 0.13$. The plotted gill-net model had dispersion statistic = 0.84 and $k = 0.11$. Note that low values of secchi depth indicate high turbidity.

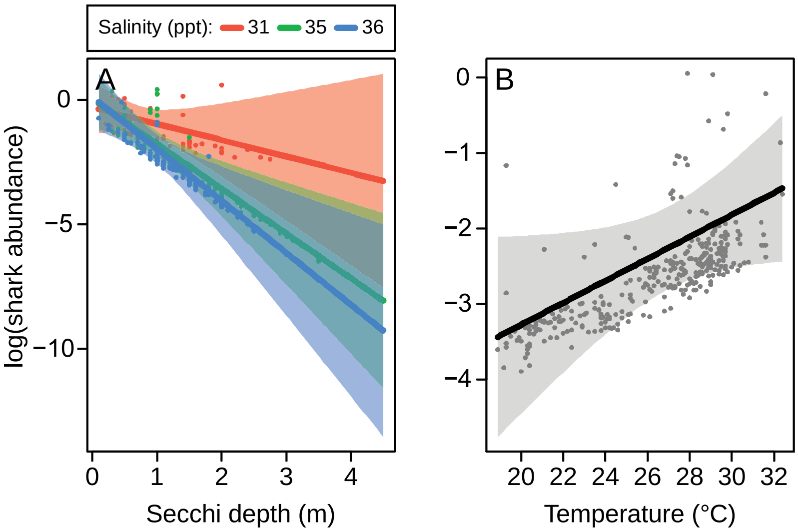


Figure 5.5 Modelled relationships between the abundance of immature scalloped hammerhead sharks *Sphyrna lewini* in gill-nets and highly influential variables. Shading represents 95% confidence intervals and points are partial residuals. Effects were plotted with additional variables held at their medians. The influence of turbidity is plotted at the 10th, 50th and 90th percentiles of salinity. The model containing turbidity, salinity and temperature had dispersion statistic = 0.82 and negative binomial variance parameter k = 0.16. Note that low values of secchi depth indicate high turbidity.

Table 5.1 Spatial variation in ecological variables. Data were pooled across sampling rounds and years. Values are mean ± 1 SD. For each variable, bays without a shared letter were significantly different (multiple comparison test following Kruskal-Wallis rank sum test, *df* = 4, *P* < 0.05).

	Depth (m)	Temperature (ºC)	Salinity (ppt)	Secchi depth/turbidity (m)	Distance to mangroves (km)
Rockingham	2.7 ± 1.0[a]	27.1 ± 2.6[a]	32.3 ± 4.0[b]	1.0 ± 0.5[a]	0.95 ± 0.65[a]
Bowling Green	2.9 ± 1.2[a]	26.2 ± 3.0[ab]	34.9 ± 1.4[a]	1.2 ± 0.7[ab]	2.34 ± 1.24[b]
Upstart	2.8 ± 1.1[a]	25.6 ± 3.6[b]	35.1 ± 1.2[a]	1.7 ± 0.8[c]	0.85 ± 0.46[a]
Edgecumbe	2.8 ± 1.1[a]	25.3 ± 3.5[b]	34.8 ± 1.3[a]	2.0 ± 0.7[d]	0.91 ± 0.54[a]
Repulse	2.8 ± 1.0[a]	25.8 ± 3.8[b]	32.4 ± 3.7[b]	1.4 ± 0.8[b]	1.59 ± 1.01[c]
Overall	2.8 ± 1.1	26.0 ± 3.4	33.9 ± 2.9	1.4 ± 0.8	1.32 ± 1.01

Table 5.2 Measures of association involving blacktip, pigeye and scalloped hammerhead sharks using longlines and gill-nets. Included are the species/life-history-stage groups with the highest (High AS) and lowest (Low AS) association values. I = immature, M = mature, n = the total number of sharks in the comparison group. Trips = the number of trips that caught the comparison group, Both = the number of trips that caught the comparison group and the focal group (underlined), AS = Association Statistic, % CO = percent common occurrence. All Genus abbreviations are for *Carcharhinus*, *Rhizoprionodon* or *Sphyna*. The maximum value of the Association Statistic, provided in italics, depended on the proportion of trips that caught the focal group. Comparison groups with ≤ 10 sharks were excluded.

	Comparison group		Longline					Gill-net						
	Species	Maturity	n	Trips	Both	AS	% CO	Species	Maturity	n	Trips	Both	AS	% CO
Immature blacktip shark *C. tilstoni/ C. limbatus*. *n = 58 (longline) and 142 (gill-net). Max. AS = 2.73 (longline) and 1.72 (gill-net).*														
High AS	*C. leucas*	I	10	5	3	1.6	60	*C. amboinensis*	I	41	14	11	1.4	79
	C. sorrah	M	80	40	19	1.3	48	*S. mokarran*	I	11	9	7	1.3	78
	C. coatesi	M	63	23	10	1.2	43	*S. lewini*	I	75	24	18	1.3	75
Low AS	*C. fitzroyensis*	M	14	7	1	0.4	14	*C. coatesi*	M	21	10	5	0.9	50
	R. acutus	I	22	9	2	0.6	22	*R. acutus*	M	12	8	4	0.9	50
	R. taylori	I	21	8	2	0.7	25	*C. fitzroyensis*	I	14	9	5	1	56
Immature pigeye shark *C. amboinensis*. *n = 67 (longline) and 41(gill-net). Max. AS = 3.42 (longline) and 5.29 (gill-net).*														
High AS	*C. fitzroyensis*	M	14	7	6	2.9	86	*R. taylori*	I	32	11	4	1.9	36
	R. taylori	I	21	8	5	2.1	63	*S. lewini*	I	75	24	7	1.5	29
	C. leucas	I	10	5	3	2.1	60	*C. tilstoni/limbatus*	I	142	43	11	1.4	26
Low AS	*C. sorrah*	I	65	26	2	0.3	8	*C. coatesi*	M	21	10	1	0.5	10
	C. sorrah	M	80	40	6	0.5	15	*R. acutus*	M	12	8	1	0.7	13
	C. coatesi	M	63	23	4	0.6	17	*C. tilstoni/limbatus*	M	12	7	1	0.8	14
Immature scalloped hammerhead *S. lewini*. *n = 14 (longline) and 75 (gill-net). Max. AS = 7.45 (longline) and 3.08 (gill-net).*														
High AS	*R. acutus*	I	22	9	2	1.7	22	*R. taylori*	I	32	11	6	1.7	55
	C. leucas	I	10	5	1	1.5	20	*R. acutus*	I	15	6	3	1.5	50
	C. sorrah	I	65	26	5	1.4	19	*C. amboinensis*	I	41	14	7	1.5	50
Low AS	*R. taylori*	I	21	8	0	0	0	*C. coatesi*	M	21	10	0	0	0
	C. cautus	M	13	10	0	0	0	*C. tilstoni/limbatus*	M	12	7	1	0.4	14
	C. sorrah	M	80	40	2	0.4	5	*R. taylori*	M	533	51	17	1	33

Table 5.3 Comparison of best-performing models of immature shark abundance. Each row contains the intercept and coefficients that comprised a single model, along with the number of parameters (*df*), log-likelihood and Akaike metrics. All models contained fishing effort as an offset variable. AIC = Akaike Information Criterion, ΔAIC = increase in AIC relative to the lowest-AIC model, *w* = Akaike weight.

Intercept	Turbidity	Salinity	Mangrove	Depth	Temp.	Salinity* Turbidity	Depth* Turbidity	*df*	Log-likelihood	AIC	ΔAIC	*w*
Blacktip shark *Carcharhinus tilstoni/ C. limbatus* on longlines												
-0.60	-	-	-0.47	-	-	-	-	3	-168.5	343.0	0.00	0.266
-0.34	-0.19	-	-0.46	-	-	-	-	4	-168.2	344.4	1.34	0.136
0.03	-	-	-0.47	-	-0.02	-	-	4	-168.4	344.8	1.74	0.111
-0.71	-	-	-0.49	0.04	-	-	-	4	-168.5	345.0	1.92	0.102
Blacktip shark *Carcharhinus tilstoni/ C. limbatus* in gill-nets												
-0.59	-1.28	-	-0.31	0.30	-	-	-	5	-237.7	485.5	0.00	0.203
-2.48	-1.35	0.06	-0.32	0.32	-	-	-	6	-237.1	486.3	0.80	0.136
-1.92	-1.21	-	-0.29	0.27	0.05	-	-	6	-237.2	486.3	0.85	0.133
-5.56	2.83	0.15	-0.33	0.32	-	-0.12	-	7	-236.5	487.0	1.50	0.096
-3.59	-1.28	0.05	-0.30	0.29	0.05	-	-	7	-236.6	487.3	1.80	0.083
-0.53	-1.34	-	-0.31	0.28	-	-	0.02	6	-237.7	487.5	1.99	0.075
Pigeye shark *Carcharhinus amboinensis* on longlines												
-15.07	14.36	0.43	-0.31	0.36	-	-0.45	-	7	-157.1	328.1	0.00	0.182
-14.46	13.89	0.40	-	0.29	-	-0.44	-	6	-158.1	328.2	0.07	0.176
-13.22	14.19	0.39	-	-	-	-0.44	-	5	-159.2	328.4	0.25	0.160
-13.46	14.59	0.41	-0.22	-	-	-0.46	-	6	-158.7	329.3	1.17	0.101
-13.73	13.87	0.42	-0.33	0.38	-0.04	-0.44	-	8	-156.9	329.8	1.64	0.080
-13.52	13.54	0.39	-	0.31	-0.02	-0.43	-	7	-158.0	330.0	1.89	0.071
Pigeye shark *Carcharhinus amboinensis* in gill-nets												
-27.88	30.01	0.53	-0.79	3.04	-	-0.77	-1.71	8	-80.7	177.4	0.00	0.432
-27.21	30.52	0.49	-	3.03	-	-0.78	-1.86	7	-82.7	179.3	1.90	0.167
-27.29	29.92	0.52	-0.80	3.05	-0.01	-0.77	-1.71	9	-80.7	179.4	1.98	0.160

Table 5.3 continued

Intercept	Turbidity	Salinity	Mangrove	Depth	Temp.	Salinity* Turbidity	Depth* Turbidity	*df*	Log-likelihood	AIC	ΔAIC	*w*
Scalloped hammerhead shark *Sphyrna lewini* in gill-nets												
-7.64	8.20	0.08	-	-	0.15	-0.29	-	6	-131.8	275.6	0.00	0.287
-8.04	8.43	0.09	-	0.15	0.14	-0.30	-	7	-131.7	277.3	1.66	0.125
-0.99	-1.37	-0.14	-	-	0.17	-	-	5	-133.7	277.3	1.70	0.123
-7.65	8.24	0.09	-0.06	-	0.15	-0.29	-	7	-131.8	277.6	1.92	0.110

Table 5.4 Effects of highly influential variables (identified using Relative Variable Importance values; RVI). Standardised model-averaged coefficients (with shrinkage) ± standard error are followed by the associated *P*-value in parentheses (i.e. $\Pr(>|Z|)$). Coefficients are on the linear (log) scale and so their effect is additive. Variables are listed according to mean RVI across species/sampling-method combinations. Asterisks denote variables that were not significant in model averaging but were significant ($P < 0.05$*; $P < 0.0001$**) in a single model containing only high-RVI variables. Although the coefficients for turbidity for pigeye and scalloped hammerhead sharks were positive, strong interaction with salinity or depth produced an overall negative relationship with decreasing turbidity (Figure 5.4; Figure 5.5).

	Blacktip *C. tilstoni/ C. limbatus*		Pigeye *C. amboinensis*		Scal. hammer. *S. lewini*
	Longline	Gill-net	Longline	Gill-net	Gill-net
Turbidity		-0.48 ± 1.28 (0.71)**	17.42 ± 3.97 (< 0.001)	36.81 ± 11.52 (0.001)	5.53 ± 5.30 (0.30)
Salinity			1.87 ± 0.67 (0.006)	2.35 ± 1.27 (0.07)	0.14 ± 0.47 (0.77)
Mangrove	-0.93 ± 0.41 (0.02)	-0.27 ± 0.13 (0.04)*			
Depth		0.26 ± 0.15 (0.08)*		5.12 ± 1.32 (< 0.001)	
Salinity*Turbidity			-19.14 ± 4.20 (< 0.001)	-33.29 ± 11.44 (0.004)	-7.11 ± 5.61 (0.21)
Temperature					0.55 ± 0.28 (0.05)
Depth*Turbidity				-8.87 ± 3.16 (0.005)	

CHAPTER 6

Spatio-temporal Occurrence Patterns of Young Sharks in Tropical Coastal Waters

Plate 6 Repulse Bay (February 2013).

Accepted as an original research paper, 12th September 2015:

Yates PM, Heupel MR, Tobin AJ, Simpfendorfer CA (2015) Spatio-temporal occurrence patterns of young sharks in tropical coastal waters. Estuar Coasts. doi: 10.1007/s12237-015-9952-4

6.1 Introduction

Coastal environments are often utilised by a variety of shark species (Compagno 1984). In particular, coastal environments can provide young sharks with abundant resources and protection from predators (Branstetter 1990), and many are thought to function as shark nurseries (Heupel et al. 2007). Due to the highly dynamic nature of coastal ecosystems (Furnas 1993, Knip et al. 2010), the occurrence and habitat use of coastal sharks typically varies across multiple spatial and temporal scales (e.g. Froeschke et al. 2010a, Curtis et al. 2011, Taylor et al. 2011). Understanding these variations is critical for assessing the ecological role of a species (Andrews & Harvey 2013), its vulnerability to anthropogenic threats and environmental change, and the efficacy of spatio-temporal management strategies (Carrier & Pratt 1998, Knip et al. 2012a).

Temporal fluctuations in the occurrence of sharks within coastal environments can often be related to reproductive cycles in conjunction with environmental conditions (Conrath & Musick 2012). Elasmobranch reproduction can be categorised as aseasonal, partially seasonal or seasonal (Wourms 1977, Conrath & Musick 2012). Seasonal temperature fluctuations along sub-tropical–temperate coastlines can necessitate marked seasonality in both parturition and nursery utilisation; including large-scale seasonal migrations by young sharks between climatic zones (Grubbs et al. 2007, McCandless et al. 2007b). Sub-tropical–tropical waters experience comparably small temperature changes, however there are seasonal fluctuations in other variables including rainfall (Knip et al. 2011a) and prey availability (Staples 1979, Wai et al. 2012). Accordingly, shark species occurring in sub-tropical–tropical waters exhibit a range of reproductive cycles from aseasonal (Harry et al. 2010) to seasonal (Stevens & Lyle 1989), and species composition often changes throughout the year (Simpfendorfer & Milward 1993, Taylor

& Bennett 2013). However, the degree to which reproductive seasonality explains broad scale occurrence patterns of young sharks remains poorly understood.

Seasonal patterns in the occurrence of young sharks can influence their survival and fitness. For example, sharks born during warmer months may benefit from enhanced energetic uptake (Bernal et al. 2012) or seasonal pulses in ecosystem productivity and food resources (Kneebone et al. 2012, Wai et al. 2012, Matich & Heithaus 2014). Temporal dynamics may also influence vulnerability to natural and anthropogenic impacts. For example, extreme weather events (Matich & Heithaus 2012, Udyawer et al. 2013) or fishing pressure (Sala et al. 2001) that coincide with spatio-temporal concentrations of individuals can have disproportionally large impacts on a population (Sala et al. 2001). Conversely, patterns in shark occurrence and habitat use can provide opportunities for spatio-temporal management approaches (Hunter et al. 2006) and may therefore play an important role in the management of shark populations.

Coastal waters of north-eastern Australia provide nursery habitat for multiple species that give birth inshore entirely or predominantly during the summer wet season (Stevens & Wiley 1986, Stevens & Lyle 1989, Harry et al. 2013). However, regional (Yamaguchi et al. 2000), and inter-annual (Harry et al. 2012) variations in the timing of parturition remain poorly understood. In addition, spatial variability in the occurrence of young sharks (i.e. neonates and YOY) across multiple tropical bays has not been explored. The objective of this study was to characterise the occurrence of young sharks along an expanse of tropical coastline. Specific aims were to: (1) investigate local timing of parturition as indicated by the presence of neonates, (2) investigate spatial, seasonal and inter-annual variations in the occurrence of young sharks, and (3) provide information on the relative importance of tropical coastal environments for these species.

6.2 Methods

Chapter 6 used data from eight rounds of seasonal fishery-independent surveys spanning the period of January 2012 to March 2014 (Table 3.2; Table 3.3). Data were from Rockingham, Bowling Green, Upstart, Edgecumbe and Repulse Bays (Figure 3.1). Young-of-the-year (YOY) sharks were either ≤ length at one year or had un-healed umbilical scars. Neonate sharks comprised a subset of YOY sharks and were those with an un-healed umbilical scar which indicated recent birth (i.e. within 1-2 weeks; Duncan & Holland 2006). Logistic regression was used to examine spatial and temporal variations in the occurrence of commonly caught species (R package 'stats'; R Development Core Team 2014). In addition, sufficient neonate blacktip sharks *Carcharhinus tilstoni/Carcharhinus limbatus* were captured in gill-nets to permit separate analyses. Sampling in May–June was categorised as dry season; October–November as early wet season; and January–April as late wet season. Sampling during August–September in 2012 and February–April in 2014 was omitted from logistic regression analyses to provide similar sampling effort between seasons and years. Fishing effort was similarly distributed across bays, seasons and years, particularly in terms of the number and duration of longline and gill-net shots (Table 3.3). Longline and gill-net data were analysed separately. Low occurrences of scalloped hammerhead sharks *Sphyrna lewini* in longline samples and spot-tail sharks *Carcharhinus sorrah* in gill-net samples precluded further analysis of these sampling methods for these species. Consistency in results between sampling methods was checked to identify sampling bias.

For each species/sampling-method combination, a single logistic regression model was applied with the log odds of shark occurrence (i.e. logit link) as a linear function of the explanatory variables; bay, season and year. Interactions were not included because initial data exploration identified few or zero shark occurrences in multiple two-way factor-level combinations. The significance of factors was assessed using likelihood ratio tests (R package 'stats'; R Development Core Team 2014). Significant effects were further investigated using Tukey multiple comparison tests (controlling for type I error) to identify which factor levels were significantly different (R package 'multcomp'; Hothorn et al. 2008). In addition, each model was compared with the respective null model (i.e. with intercept only) using a likelihood ratio test (R package 'lmtest'; Zeileis & Hothorn 2002). Estimated probabilities of occurrence were plotted using R package ‘visreg’ (Breheny & Burchett 2013). Whether factors were confounded was assessed *a priori* using conditional boxplots and *a posteriori* by comparing estimated parameters, standard errors and *P* values between the full model and the full suite of nested models in order to identify type II errors caused by the inclusion of correlated factors. To investigate potential bias in maximum likelihood estimation caused by low shark occurrences, models were re-fit and compared using Firth’s penalised likelihood procedure (Firth 1993, R package 'logistf'; Heinze et al. 2013).

6.3 Results

6.3.1 Catch composition

The catch of YOY (n = 383) and neonates (n = 91) was dominated by blacktip, scalloped hammerhead, pigeye *Carcharhinus amboinensis*, and spot-tail sharks (Table 6.1; Appendix 4); and therefore the occurrences of these species were further analysed using logistic regression. Interspecific variations in body size and life-history-stage composition were observed for these species (Figure 6.1).

6.3.2 Occurrence patterns

Overall, neonate blacktip, pigeye, scalloped hammerhead and spot-tail sharks were encountered between October–March (Table 6.1; Figure 6.2). Neonate blacktip and scalloped hammerhead sharks shared similar and broad temporal presence between October–February, whereas the presence of neonate pigeye sharks was more temporally constrained to January–March (Table 6.1; Figure 6.2). Neonate spot-tail sharks were present only between January–February. Young-of-the-year sharks from all species generally occurred in all temporal samples, with the notable absence of pigeye sharks in the early wet seasons of both years (November–December 2012 and October–November 2013).

Relationships with spatio-temporal factors varied among species and life-history stages (Table 6.2). When significant variations were detected, low shark occurrence rates often precluded the detection of significant pairwise differences between factor levels (Appendix 8–Appendix 11). In these cases, plotted estimated occurrence probabilities provided insight into the factor levels primarily responsible for significant variations. Comparison of main effects and pairwise comparisons across all full models and their respective nested models did not reveal confounding between factors. Further, refitting models with Firth’s penalised likelihood did not influence model outcomes (Appendix 12).

Blacktip shark

A total of 247 blacktip sharks were captured and 120 were YOY (Table 6.1). Within the six rounds included in the logistic regression model, YOY blacktip sharks were present in 17 and 38 longline and gill-net samples, respectively. The YOY/gill-net model was significantly different to the null model (likelihood ratio test, $\chi^2 = 25.46$, $df = 7$, $P = 0.0006$). There was significant spatial variation in YOY occurrence (Table 6.2; Figure 6.3A), particularly between Edgecumbe and Repulse Bays (Tukey multiple comparisons test, $Z = 2.76$, $P = 0.04$; Appendix 8). The odds of encountering a YOY blacktip shark in Edgecumbe Bay was 95% lower than in Repulse Bay. For longlines, the full model was equivalent to the null model (likelihood ratio test, $\chi^2 = 11.53$, $df = 7$, $P = 0.12$) thus no spatio-temporal variations could be detected with this sampling method.

Neonate blacktip sharks were present in 18 gill-net shots, and their occurrence in gill-nets varied significantly between seasons (Table 6.2). Although no significant pairwise comparisons were detected, the estimated probability of occurrence peaked during the early wet season and no neonates were encountered during the dry season (Figure 6.3B).

Pigeye shark

A total of 112 pigeye sharks were captured and 57 were YOY (Table 6.1). Young-of-the-year pigeye sharks were present in 13 and 8 longline and gillnet shots, respectively. Longline and gill-net models were significantly different to their respective null models (likelihood ratio test: longline, $\chi^2 = 29.15$, $df = 7$, $P < 0.001$; gill-net, $\chi^2 = 14.17$, $df = 7$, $P = 0.048$) and similar seasonal variations were detected between methods (Table 6.2; Figure 6.4). Year and bay were marginally significant for longlines (Table 6.2), but crossed the decision threshold of $P = 0.05$ using Firth’s penalised likelihood estimation

(Appendix 12). For both sampling methods, predicted occurrence probability was highest during the late wet season and no YOY pigeye sharks were encountered during the early wet season (Figure 6.4).

Scalloped hammerhead shark

A total of 103 scalloped hammerhead sharks were captured and 86 were YOY (Table 6.1). Within the six rounds included in the analysis, YOY scalloped hammerhead sharks were present in 24 gillnet shots, and the full model was significantly different to the null model (likelihood ratio test, $\chi^2 = 35.03$, $df = 7$, $P < 0.0001$). Occurrence varied among bays (Table 6.2; Figure 6.5), and was significantly higher in Rockingham Bay compared to Bowling Green (Tukey multiple comparisons test, $Z = -2.90$, $P = 0.02$) and Upstart ($Z = -3.04$, $P = 0.01$) Bays (Appendix 10). Compared to Rockingham Bay, the odds of encountering a YOY scalloped hammerhead shark in gillnets was 86% lower in Bowling Green Bay and 96% lower in Upstart Bay.

Spot-tail shark

A total of 151 spot-tail sharks were captured and 31 were YOY (Table 6.1). Young-of-the-year spot-tail sharks occurred in 17 longline shots, and the full model was significantly different to the null model (likelihood ratio test, $\chi^2 = 17.60$, $df = 7$, $P = 0.01$). Significant seasonal variation was detected (Table 6.2), and although no pairwise comparisons were significant, occurrence was higher during the early and late wet season (Figure 6.6).

6.4 Discussion

Spatio-temporal heterogeneity in the occurrence of young sharks was detected along an expanse of tropical coastline. The relatively high abundances of blacktip, pigeye, scalloped hammerhead and spot-tail sharks within the sampled community suggested that their distributions can be important for the functioning of coastal ecosystems. Temporal variations in occurrence were detected for pigeye and spot-tail sharks whereas spatial variations characterised the occurrences of blacktip and scalloped hammerhead sharks. Although tropical coastal environments are typically occupied by a diverse group of young sharks (Chapter 4, Compagno 1984, Harry et al. 2011b), differences in occurrence patterns may be associated with interspecific resource competition (White & Potter 2004) and variable susceptibilities to anthropogenic impacts (Chin et al. 2010, Knip et al. 2010). Such varied utilisation of coastal ecosystems has important implications for the conservation of shark populations and the management of coastal habitats.

Spatio-temporal occurrence patterns were likely influenced by life-history-associated factors including reproductive seasonality and degree of nursery utilisation. For instance, the lack of strong seasonal variation in the occurrence of YOY scalloped hammerhead sharks was likely reflective of year-round parturition in this species (Clarke 1971, Stevens & Lyle 1989, White et al. 2008). Similarly, no monthly variations were detected in the occurrence of immature scalloped hammerhead sharks in the north-eastern Gulf of Mexico (Ward-Paige et al. 2014). However, given that neonates comprised a small portion of YOY catch, factors additional to the timing of parturition were likely important. The absence of spatial variation in spot-tail shark occurrence aligns with previous reports that immature individuals occupy a broad range of coastal habitats and depths rather than discrete nursery areas (Kinney 2011, Knip 2011). For species that employ this more generalist habitat use pattern, strong spatial variation in YOY occurrence would not be expected, and a variety of habitats across multiple bays may be equally important. For example, YOY sharks of generalist species may benefit from increased foraging success, reduced competition, and faster growth (Heithaus 2007, Knip et al. 2010). This suggests that intrinsic life-history-associated factors are likely to operate in conjunction with a range of extrinsic factors to shape the habitat use of young sharks in coastal environments.

Immature coastal sharks can alter their movements and occupancy through time in response to seasonal fluctuations in environmental conditions and prey availability. For example, juvenile pigeye sharks shifted their core home ranges further away from creek mouths following seasonal freshwater inflow, presumably to alleviate the metabolic costs incurred by low salinities (Knip et al. 2011a). Similar movements in response to high river flows were reported for juvenile rig *Mustelus lenticulatus* (Francis 2013). Seasonal variation in habitat use may also represent behavioural thermoregulation to optimise a range of physiological processes (Bernal et al. 2012, Jirik & Lowe 2012, Knip et al. 2012b). Juvenile bull sharks *Carcharhinus leucas* can increase their use of upstream channels to exploit seasonally available marsh prey (Matich & Heithaus 2014), and may coincide their occupancy of downstream habitats to exploit prey displaced by high freshwater influxes (Ortega et al. 2009). Therefore a multitude of abiotic and biotic fluctuations including salinity, water temperature and prey distributions may have influenced temporal patterns in the occupancy or foraging activity of YOY sharks in the shallow coastal environments sampled here.

Spatial variations detected for blacktip and scalloped hammerhead sharks suggest that the occurrence of young sharks along tropical coastlines is dynamic. In particular, over larger geographic scales, some bays may provide nursery habitat for these species while others may not (Chapter 4). Heupel et al. (2007) provided three criteria for the identification of a shark nursery: (1) relatively high abundance of neonates or young juveniles, (2) site fidelity and (3) stable use across multiple years. Based on the relatively high occurrence of YOY scalloped hammerhead and blacktip sharks in Rockingham and Repulse Bays, respectively, these locations may meet the first nursery area criterion and therefore be particularly important for these species. The relative importance of various bays may be shaped by spatial heterogeneity in resource abundance, competition, predation pressure or environmental conditions. Evidence that sharks respond to variations in turbidity, salinity, depth, temperature, and proximity to mangroves; coupled with significant spatial heterogeneity in these conditions among bays revealed these environmental variables as probable drivers of spatial variation in habitat use among bays. For example, significant spatial variation in turbidity was related to high abundance of immature sharks in Rockingham Bay and low abundance in Edgecumbe Bay (Chapter 5). Similarly, variable depth utilisation by immature sandbar sharks *Carcharhinus plumbeus* within (Rechisky & Wetherbee 2003) and between (Grubbs & Musick 2007, McCandless et al. 2007b) adjacent bays in the north-west Atlantic may have been influenced by spatial heterogeneity in hydrodynamics, prey distributions and predation risk (McCandless et al. 2007b). These results suggest that, in response to biotic and abiotic conditions, young sharks may adopt different strategies in different bays or avoid certain bays altogether (Chapter 5).

The temporal distribution of neonates corroborates the general predominance of summer parturition in the study species across tropical Australia (Last & Stevens 2009). During summer, neonate and YOY sharks may benefit from enhanced energetic uptake in warmer temperatures (Bernal et al. 2012) and seasonal pulses in ecosystem productivity (Kneebone et al. 2012, Wai et al. 2012, Matich & Heithaus 2014). However, neonate pigeye sharks occurred slightly later than expected based on the published months of parturition in Australian waters (around November or December; Last & Stevens 2009). There is evidence of stock structuring in this species between northern Australia and Queensland (Tillett et al. 2012a), which may translate into spatial variation in reproductive traits including the timing of parturition (Yamaguchi et al. 2000, Walker 2007, Gutteridge et al. 2013). Environmental conditions can play a crucial role in shaping reproductive traits (Walker 2007) and habitat use (Schlaff et al. 2014), and further research is needed to investigate the presence and drivers of regional variation in the parturition of pigeye sharks across northern Australia.

The temporal distribution of neonate pigeye sharks (January–March) was contracted and delayed relative to blacktip and scalloped hammerhead sharks. Neonate survival is expected to decrease with increasing population density (Gruber et al. 2001, Gedamke et al. 2007), therefore temporal asynchrony may alleviate interspecific competition (Yokota & Lessa 2006, Harry et al. 2012, Taylor & Bennett 2013). Temporal separation may be particularly beneficial for blacktip and pigeye sharks because their broadly-overlapping diets (Stevens & Wiley 1986, Stevens & McLoughlin 1991, Simpfendorfer & Milward 1993, Taylor 2007) and similar body sizes may intensify resource competition between them (Bethea et al. 2004). Alternatively, asynchronous temporal occurrences may be related to interspecific differences in optimal conditions for parturition or offspring fitness (Speed et al. 2010), inter-annual plasticity in the timing of parturition (Harry et al. 2012), or may be an artefact of when sampling occurred (e.g. there was limited sampling in December). These results suggested that, despite broad overlap in the timing of parturition, spatial and temporal partitioning may occur.

Low occurrence of YOY sharks across factor combinations prohibited investigation of interaction between spatio-temporal factors. However, spatial changes in seasonal occurrence patterns are possible given the variable nature of coastal environments. For instance, over longer temporal scales, inter-annual fluctuations in the relative abundance of immature bull sharks were not consistent across nine Texas Bays (Froeschke et al. 2010b). Within years, fluctuations in water temperature were thought to drive seasonal patterns in the relative abundance of immature bull sharks within the Indian River Lagoon, Florida, however these seasonal patterns were not consistent among the Lagoon's subregions (Curtis et al. 2011). Within this large (c. 225 km long) and environmentally heterogeneous coastal system, some regions may serve as over-wintering grounds for bull sharks while others may not (Curtis et al. 2011). Coastal environments along north-eastern Queensland are similarly environmentally heterogeneous, including variations in bay geomorphology, riverine inputs (Furnas 1993), and turbidity (Chapters 3 and 5). Therefore, sharks in different bays may experience different environmental fluctuations or be differentially affected by wide-spread seasonal changes. Populations that occupy environmentally heterogeneous habitats may benefit from enhanced stability and resilience (Chapter 2). Further research is needed to explore interactive spatio-temporal patterns in the occurrence of tropical coastal sharks.

Sampling bias arising from gear selectivity is an important consideration for the interpretation of these results. The study species were captured at their size of birth (reviewed in Harry 2011) using both longlines and gill-nets, indicating that these gears successfully produced relative occurrence rates for the complete neonate/YOY cohort. Neonates of these species were also susceptible to capture in Queensland's East Coast Inshore Finfish Fishery using 114–216 mm stretched mesh gill-nets (Harry et al. 2011b). In addition, relatively low catch rates of scalloped hammerhead and spot-trail sharks across all sizes in longlines and gill-nets, respectively, highlight the importance of sampling methodologies that incorporate complimentary gears. For pigeye sharks, consistency in results between sampling methods provides additional support for their representation of true shark occurrences.

Managing anthropogenic impacts on coastal ecosystems can be challenging where a diversity of species with contrasting life histories occur. In such circumstances, management strategies may be best directed toward groups of species with similar characteristics and vulnerabilities (Harry et al. 2011b). For example, coastal sharks in north-eastern Australia can be grouped for management purposes according to similarities in life history traits and their susceptibility to capture by fisheries (Harry et al. 2011b). The characterisation of spatio-temporal occurrence in this study provides additional information for grouping species for management. Significant spatial heterogeneity in the occurrence of some species suggests that spatial management approaches may be especially useful, whereas temporal management strategies may benefit other species whose occurrence is most predictable by season. Changes in occurrence patterns between neonates and YOY individuals (i.e. for blacktip sharks) suggested that a combination of strategies may be required for some species. Grouping species or life-history stages may be particularly useful in tropical regions where diverse shark assemblages can provide an imposing a hurdle for species-specific management.

This study demonstrated interspecific differences in the occurrence patterns of neonate and YOY sharks along an expanse of tropical coastline. Spatio-temporal variations in the occurrence of young sharks may have important implications for their survival and fitness, which can in turn influence population productivity (Smith et al. 1998, Cortés 2002). In particular, spatial variations in the occurrence of some species suggested spatial heterogeneity in nursery function and the relative importance of coastal habitats. Variable habitat use among bays by a broader range of species is likely given stark variations in community structure along this tropical coastline (Chapter 4). Varied occurrence patterns may be related to reproductive seasonality, degree of nursery utilisation, predation pressure, prey distributions or environmental conditions. Ongoing research on the spatio-temporal occurrences of coastal sharks is required to improve our understanding of the relative importance of coastal habitats and the efficacy of spatio-temporal management approaches.

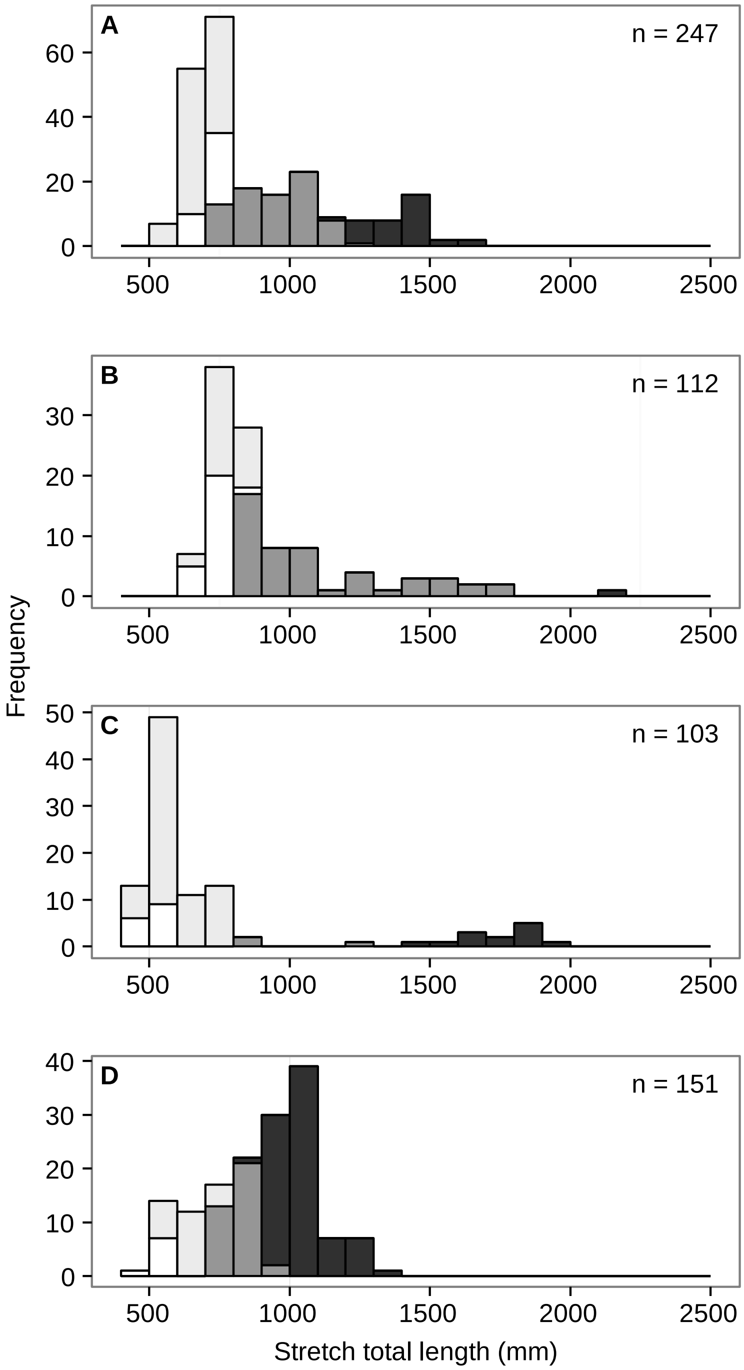


Figure 6.1 Length-frequency distributions of blacktip *Carcharhinus tilstoni/Carcharhinus limbatus* (A), pigeye *Carcharhinus amboinensis* (B), scalloped hammerhead *Spynra lewini* (C) and spot-tail *Carcharhinus sorrah* (D) sharks. Bar shading denotes life-history stage (white = neonate, light grey = YOY, medium grey = juvenile > 1 year, dark grey = adult). Data are pooled across bays, seasons, years and sampling methods. Note that neonates are a subset of YOY. Data are from years 2012–2014.

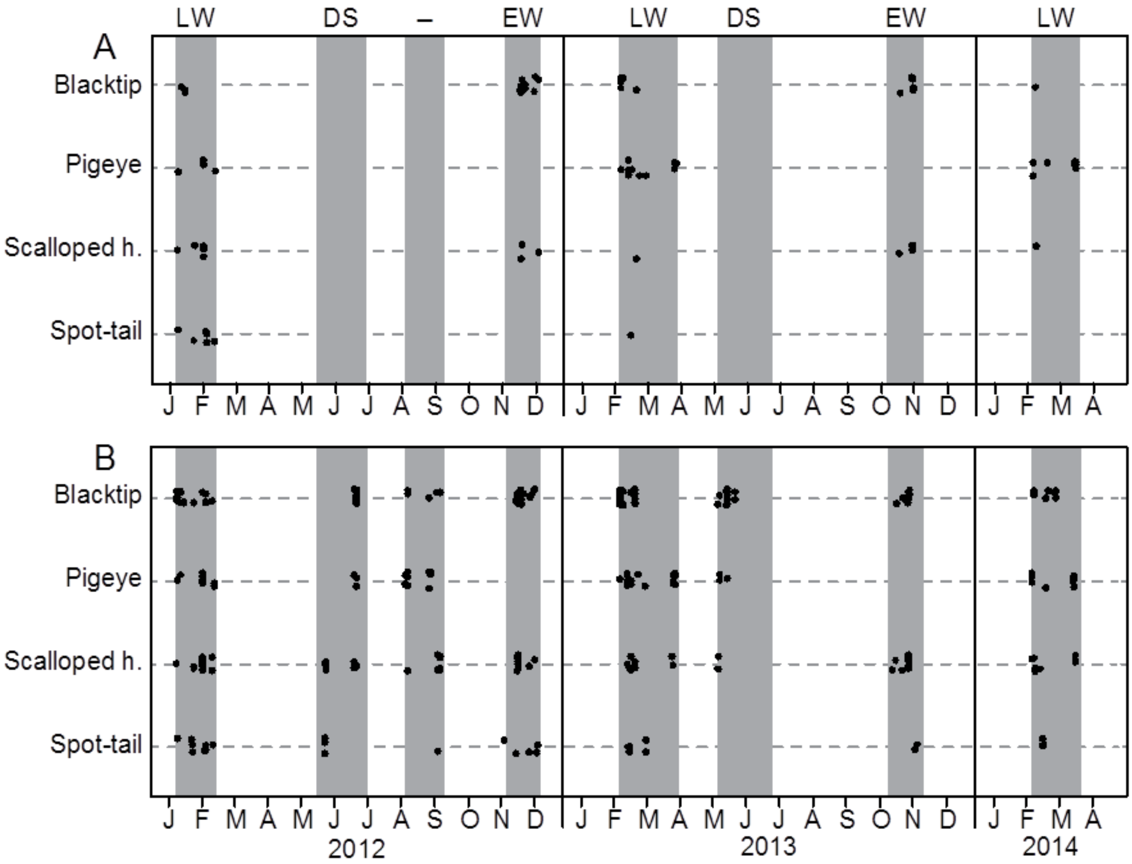


Figure 6.2 Temporal distribution of neonate (A) and young-of-the-year (YOY; B) sharks. Black circles represent individual sharks. Grey shading delineates sampling rounds. Upper-case letters above the plot indicate the designated season; DS = dry season, EW = early wet season, LW = late wet season, '–' = data excluded from seasonal analyses. Note that YOY includes neonates. Points are jittered on the y axes to aid visualisation of individual points.

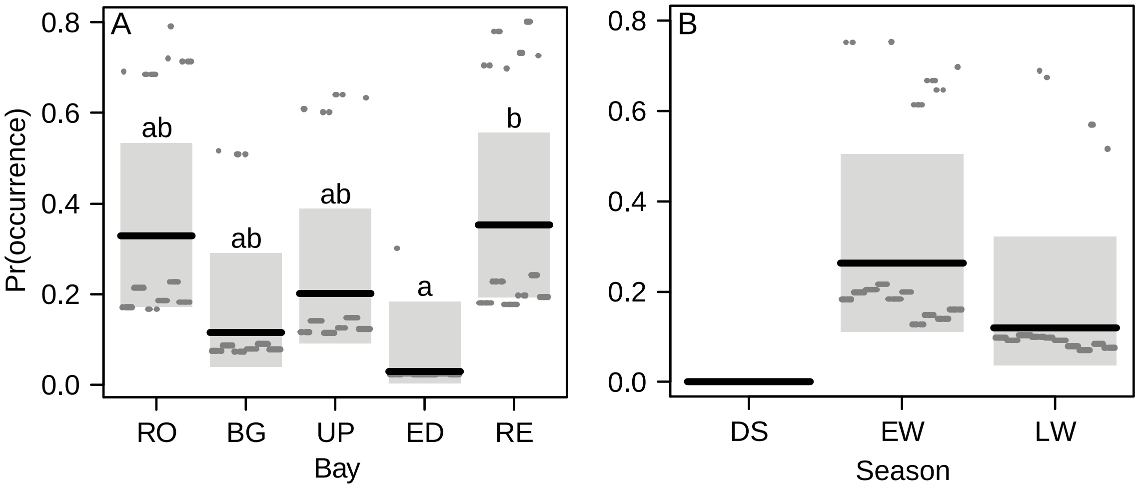


Figure 6.3 Young-of-the-year (A) and neonate (B) blacktip shark *Carcharhinus tilstoni/Carcharhinus limbatus* occurrence in gill-nets. Black lines indicate the estimated probability of occurrence, grey boxes are 95% confidence intervals, and grey circles are partial residuals. Bays that do not share a lower-case letter were significantly different (Tukey multiple comparisons test, $P < 0.05$; Appendix 8). RO = Rockingham, BG = Bowling Green, UP = Upstart, ED = Edgecumbe, RE = Repulse. DS = dry season (May–June), EW = early wet season (October–December), LW = late wet season (January–April). Confidence intervals were not plotted for groups with zero encounters. Data are from years 2012–2014.

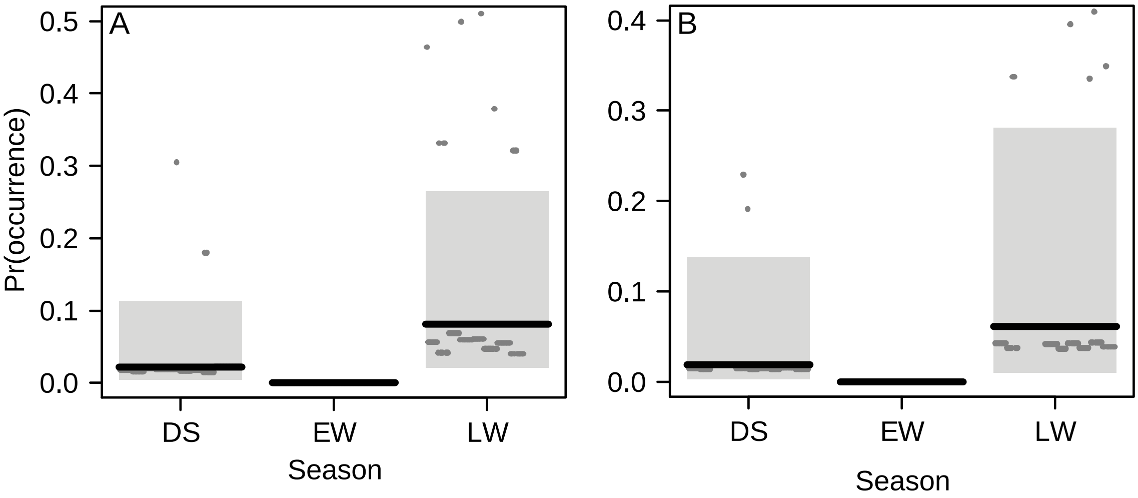


Figure 6.4 Seasonal variation in the occurrence of YOY pigeye sharks *Carcharhinus amboinensis* in longlines (A) and gill-nets (B). Black lines indicate the estimated probability of occurrence, grey boxes are 95% confidence intervals, and grey circles are partial residuals. DS = dry season (May–June), EW = early wet season (October–December), LW = late wet season (January–April). Confidence intervals were not plotted for groups with zero encounters. Data are from years 2012–2014.

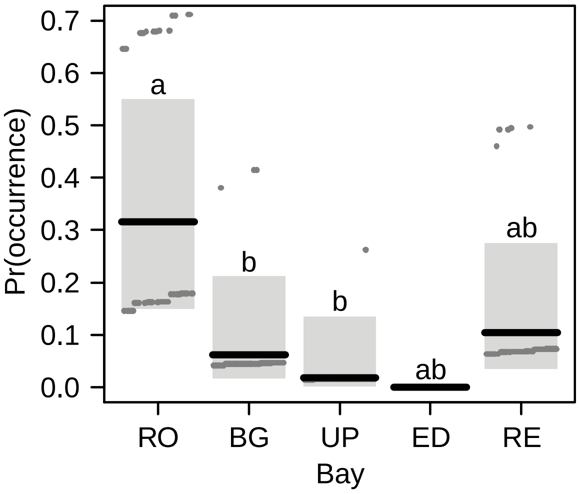


Figure 6.5 Spatial variation in the occurrence of young-of-the-year scalloped hammerhead sharks *Sphyrna lewini* in gill-nets. Black lines indicate the estimated probability of occurrence, grey boxes are 95% confidence intervals, and grey circles are partial residuals. Bays that do not share a lower-case letter were significantly different (Tukey multiple comparisons test, $P < 0.05$; Appendix 10). RO = Rockingham, BG = Bowling Green, UP = Upstart, ED = Edgecumbe, RE = Repulse. Confidence intervals were not plotted for groups with zero encounters. Data are from years 2012–2014.

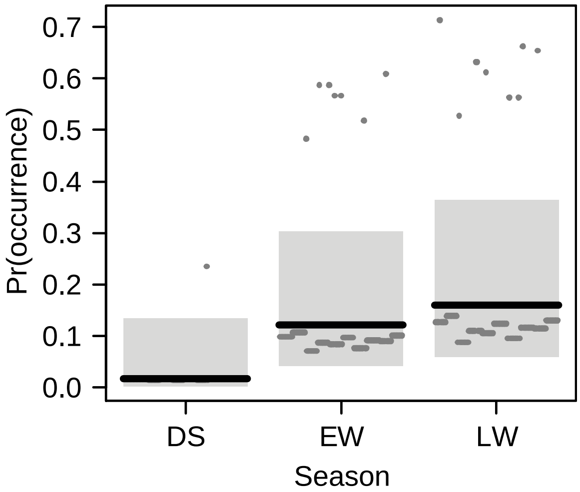


Figure 6.6 Seasonal variation in the occurrence of YOY spot-tail sharks *Carcharhinus sorrah* in longlines. Black lines indicate the estimated probability of occurrence, grey boxes are 95% confidence intervals, and grey circles are partial residuals. DS = dry season (May–June), EW = early wet season (October–December), LW = late wet season (January–April). Data are from years 2012–2014.

Table 6.1 Total numbers of neonate and young-of-the-year (YOY) sharks. Data are from years 2012–2014.

Species	YOY	Neonate	Total	Neonate occurrence
Blacktip *C. tilstoni/C. limbatus*	120	32	247	October–February
Pigeye *C. amboinensis*	57	27	112	January–March
Scalloped hammerhead *S. lewini*	86	15	103	October–February
Spot-tail *C. sorrah*	31	8	151	January–February
Total	294	82	613	October–March

Table 6.2 Significance of spatial and temporal factors (likelihood ratio test) in logistic regression models. Data are from years 2012–2014.

Species	Life-history stage	Sampling method	Explained deviance (%)	Factor	*df*	χ^2	*P*
Blacktip *C. tilstoni/C. limbatus*	YOY	Gill-net	11.8	Bay	4	20.07	0.0005*
				Season	2	4.65	0.10
				Year	1	0.67	0.41
	Neonate	Gill-net	21.3	Bay	4	8.93	0.06
				Season	2	18.45	<0.0001*
				Year	1	0.97	0.32
Pigeye *C. amboinensis*	YOY	Longline	26.4	Bay	4	9.82	0.04*
				Season	2	15.84	0.0004*
				Year	1	4.14	0.04*
	YOY	Gill-net	19.9	Bay	4	4.12	0.39
				Season	2	9.81	0.01*
				Year	1	0.69	0.41
Scalloped h. *S. lewini*	YOY	Gill-net	22.0	Bay	4	34.08	<0.0001*
				Season	2	0.41	0.81
				Year	1	0.55	0.46
Spot-tail *C. sorrah*	YOY	Longline	13.0	Bay	4	5.61	0.23
				Season	2	8.67	0.01*
				Year	1	3.53	0.06

CHAPTER 7

Benefits of Marine Protected Areas for Tropical Coastal Sharks

Plate 7 Tagging a longline-caught nervous shark *Carcharhinus cautus* in a Conservation Park Zone within Upstart Bay (February 2013).

Manuscript in preparation:

Yates PM, Tobin AJ, Heupel MR, Simpfendorfer CA (In preparation) Benefits of marine protected areas for tropical coastal sharks

7.1 Introduction

Marine protected areas (MPAs) are a common management tool for maintaining ecological functions and sheltering vulnerable species or habitats from exploitation (reviewed in Jones 2001). The effectiveness of MPAs likely varies depending on a species' intrinsic vulnerability and susceptibility to fishing mortality, the portion of the population receiving protection and movement of individuals across MPA boundaries (Bonfil 1999, Gruss et al. 2011). Marine protected areas may be especially beneficial for species that exhibit strong site attachment (Garla et al. 2006a, Barnett et al. 2012, Vianna et al. 2013). For example, reports of high abundances of reef sharks in non-fished sites compared to fished sites have highlighted that MPAs can benefit sharks (Garla et al. 2006b, Heupel et al. 2009, Espinoza et al. 2014). However, the benefits of MPAs for species that inhabit coastal environments at various stages of ontogeny remain poorly understood (Knip et al. 2012a).

Coastal environments are inhabited by a variety of shark species with varied habitat use patterns. Some species, including common blacktip *Carcharhinus limbatus* and sandbar *Carcharhinus plumbeus* sharks, utilise coastal waters during early life-history stages before moving offshore to adult habitats (Springer 1967, Castro 1996). In contrast, some smaller-bodied species, such as bonnethead *Sphyrna tiburo* and Australian sharpnose *Rhizoprionodon taylori* sharks, complete their entire life-cycle inshore (Simpfendorfer & Milward 1993, Heupel et al. 2006, Ulrich et al. 2007). Species that depend on coastal environments during critical or all life-history stages are particularly vulnerable to changes occurring within them (Knip et al. 2010), and therefore, the potential benefits obtained from MPAs vary.

In addition to broad patterns of habitat use through ontogeny, the movements and dispersal of individuals can influence MPA function (Gruss et al. 2011, Knip et al. 2012a). Although movements across boundaries can reduce MPA effectiveness (Bonfil 1999), a high degree of mobility does not necessarily prevent MPAs from benefiting marine species (Claudet et al. 2010). For example, the protection of young sharks in nursery areas may increase the number of animals reaching maturity (Heupel & Simpfendorfer 2005a). Conversely, protection of highly-resident adults will increase survival of the breeding stock; thereby increasing the number, size and fecundity of breeding females (Stevens et al. 2000, Knip et al. 2012a). Marine protected areas may also be used to shelter vulnerable mating or pupping aggregations (Carrier & Pratt 1998). Strategically sized and placed MPAs can benefit mobile species if they coincide (spatially and temporally) with biologically important bottlenecks, or the habitat use of critical or vulnerable demographic groups (Roberts 2000, Gruss et al. 2011, Le Port et al. 2012).

Fishing pressure can modify the structure of aquatic communities and drive differences in community structure between areas open and closed to fishing (Allison et al. 1998, Ley et al. 2002, Friedlander et al. 2003). Fishing affects species in different ways depending on the target species, fishing methods and gears used, and species-specific susceptibility and vulnerability to fishing mortality (Jennings & Kaiser 1998, Stevens et al. 2000, Ferretti et al. 2013). Fishing often removes the largest species first and then progresses down the food chain catching progressively smaller species (Pauly et al. 1998). Similar patterns have been observed in sharks, whereby smaller sharks proliferated as larger and more vulnerable species were depleted (van der Elst 1979). Fishing mortality can also drive changes in the body-size structure of aquatic communities and individual populations (Walker et al. 1998, Johnson et al. 1999, Ley et al. 2002), which can influence overall reproductive potential (Cortés 2000). These changes may be a direct result of disproportional mortality of faster-growing immature sharks, or slower-growing mature sharks (Stevens et al. 2000). Fishing can also trigger indirect ecosystem-wide trophic responses via the disruption of biological interactions including predation and competition (Stevens et al. 2000, Edgar et al. 2004). Therefore, community-level responses to exploitation are complex and difficult to predict (Ferretti et al. 2013).

North-eastern Australia's Great Barrier Reef Marine Park (GBRMP) is a multi-use area comprising one of the world's largest networks of MPAs. In 2004, approximately 33% of the GBRMP was designated as 'Marine National Park' and protected from extractive activities like fishing (Fernandes et al. 2005). In lieu of comprehensive data on species distributions, MPAs were distributed across multiple bioregions to conserve biodiversity (Fernandes et al. 2005). Within coastal waters of the Great Barrier Reef lagoon, GBRMP zoning influences the spatial distribution of fishing. There is some evidence that MPAs in coral-reef bioregions of the GBRMP benefit teleosts and sharks (Robbins et al. 2006, Russ et al. 2008, Heupel et al. 2009, McCook et al. 2010). However, the benefits of MPAs for coastal bioregions and their biodiversity remain poorly understood. The objective of this study was to explore the effectiveness of coastal MPAs for the diverse assemblage of tropical coastal sharks occurring in the GBRMP (Chapter 4, Harry et al. 2011b). Specific aims were to: (1) identify whether MPAs coincide with areas of high shark abundance, (2) compare shark length-frequency distributions between management zones, (3) compare shark species composition between management zones, and (4) use recapture information to assess dispersal and assess the degree of exchange between management zones.

7.2 Methods

7.2.1 Fishery and marine protected area description

Queensland's East Coast Inshore Finfish Fishery (ECIFF) accounts for the majority of shark landings within the Great Barrier Reef lagoon, which are mainly comprised of carcharhiniform sharks (Harry et al. 2011b). Fishers generally use gill-nets (typically 115–165 mm mesh size) which are commonly hauled by hand. A generalist shark fishery operates year-round, targeting common blacktip *Carcharhinus limbatus*, Australian blacktip *Carcharhinus tilstoni* and spot-tail *Carcharhinus sorrah* sharks (Harry et al. 2011b). The total allowable catch of sharks within the GBRMP is 420 tons year^{-1}.

In the present study, GBRMP zones were classified as closed (Marine National Park, Conservation Park, Scientific Research, Buffer, Preservation or Commonwealth Island Zones) or open (General Use or Habitat Protection Zones) to commercial gill-net fishing; and are hereafter referred to as 'open' and 'closed', respectively. In total, closed zones comprised approximately 38% of the GBRMP. Coastal closed zones were generally small (c. 100–300 km^2) and encompassed approximately half of the available space within individual bays. Although limited recreational and small-mesh bait netting was permitted inside Conservation Park Zones (c. 1.5% of total GBRMP area), the effects of these activities on sharks were assumed to be minimal. Sharks are generally not targeted by recreational fishers (Lynch et al. 2010, De Faria 2012).

7.2.2 Data collection

Fishery-independent surveys of shark communities

Fishery-independent surveys were undertaken from January 2012 to March 2014 to investigate shark abundance and community structure in open and closed zones of Rockingham, Bowling Green and Upstart Bays (i.e. the same data that were used in Chapters 5 and 6, but for three bays only; Table 3.3). These data were used to address Aims 1–3. The three bays included approximately equal proportions of closed area, and sampling effort was standardised between zones (Table 7.1; Figure 3.2–Figure 3.4). During 98 days of sampling, 277 longline shots and 209 gill-net shots were deployed (Table 7.1) totalling 226.0 and 185.7 hours, respectively. Each sampling round included a minimum of four gill-net samples bay^{-1} round^{-1} zone^{-1} and five longline samples bay^{-1} round^{-1} zone^{-1}.

Tag-recapture data collection

Tag-recapture data, used to address Aim 4, was sourced from multiple fishery-dependent and fishery-independent research projects undertaken at James Cook University's Centre for Sustainable Tropical Fisheries and Aquaculture. Shark tagging occurred between March 2008 and March 2014, and spanned c. 1000 km of coastline between Cairns and Gladstone (Figure 7.1). Fishery-independent data sources included: (1) the aforementioned shark surveys in Rockingham, Bowling Green and Upstart Bays along with similar surveys in six additional bays (i.e. Halifax, Cleveland, Abbot, Edgecumbe, Woodwark/Double and Repulse Bays; Figure 7.1; Table 3.3), and (2) complementary fishery-independent tagging trips undertaken predominantly within Cleveland Bay. Fishery-dependent tagging was part of a large-scale project investigating shark fishing mortality in the ECIFF; and was concentrated near the regional centres of Cairns, Townsville, Bowen, Mackay and Rockhampton (Tobin et al. 2014b). All projects deployed the same tags, and only sharks in healthy condition were tagged. Recaptures occurred during all projects, and were also reported by commercial and recreational fishers via a dedicated phone number printed on each tag.

7.2.3 Shark abundance

Generalised linear models (GLM; R package 'stats', R Development Core Team 2014) and Generalised linear mixed models (GLMM; R package 'lme4', Bates et al. 2014) were used to compare shark abundance between bays (Rockingham, Bowling Green and Upstart Bays) and zones (open and closed), and test for interaction between bay and zone. All models included standardised fishing effort as an offset variable; which was calculated as the logarithm of 100-hook hours for longline samples, or the logarithm of 100m-net hours for gill-net samples. Analyses were carried out for all shark species pooled and for common species individually (i.e. Australian sharpnose, blacktip complex, pigeye, scalloped hammerhead and spot-tail sharks). All life-history stages were pooled together, however longline and gill-net data were analysed separately. Prior to model fitting, Cleveland dotplots and conditional boxplots were used to check for outliers and investigate relationships between variables.

For each species/sampling-method combination, Poisson GLMs (with log link) were over-dispersed. Accordingly, Cook’s distances were used to check for observations with disproportionally high influence, and Pearson residuals were plotted against fitted shark abundance and included and excluded covariates to check for homogeneity, independence and model fit. Residual patterns among sampling rounds indicated that temporal auto-correlation was a likely cause of over-dispersion. Therefore, sampling round was included as an eight-level random intercept in Poisson GLMMs with log link. In the majority of cases, over-dispersion of Poisson GLMM (>1.2) prompted the inclusion of an observation-level random intercept (OLRI, i.e. a latent variable that models any information that cannot be explained with the covariates; Elston et al. 2001). The significance of factors was assessed using likelihood ratio tests (R package 'stats'; R Development Core Team 2014). Limited model selection was applied whereby the interaction between bay and zone was dropped from the model if it was not significant. Significant effects were further investigated using Tukey multiple comparison tests (controlling for type I error) to identify which factor levels were significantly different (R package 'multcomp'; Hothorn et al. 2008). Whether factors were confounded was assessed *a priori* using conditional boxplots and *a posteriori* by comparing estimated parameters, standard errors and *P* values between the full model and the full suite of nested models in order to identify type II errors caused by the inclusion of correlated factors. Significant effects were plotted on the scale of the linear predictor (log[shark abundance]), however the vertical axis was labelled on the response scale to preserve the linear structure of the model while permitting interpretation of actual abundance values (R package 'effects'; Fox 2013).

7.2.4 Length-frequency distribution

Length-frequency distributions of common species were compared between bays (Rockingham, Bowling Green and Upstart Bays) and zones (open and closed). Analyses were carried out for all life-history stages pooled, however longline and gill-net data were analysed separately. For all species/sampling-method combinations, the presence of < 15 sharks in multiple two-way factor-level combinations precluded investigation of interaction between bay and zone. In addition, skewed or multi-modal length-frequency distributions required non-parametric analyses. In all cases, similarly-shaped distributions among bays permitted use of the Kruskal-Wallis rank sum test to compare median STL among bays (both zones pooled; R package 'stats', R Development Core Team 2014). Significant variations were investigated with a multiple comparison test (R package 'pgirmess'; Giraudoux 2013). A combination of Kruskal-Wallis and Kolmogorov-Smirnov tests (R package 'stats'; R Development Core Team 2014) were used to compare length-frequency distributions between open and closed zones (with all bays pooled). The Kolmogorov-Smirnov test can also detect differences in variance and distribution shape, and was used in isolation when visually-detected differences in shape between zones precluded use of the Kruskal-Wallis test.

7.2.5 Species composition

Multivariate analyses to identify spatial variations in species composition were carried out using Primer 6.0 (Clarke & Warwick 2001, Clarke & Gorley 2006). Because fishing effort was similarly distributed across bays and zones, data from two days in each zone per bay (i.e. one day of longline sampling plus one day of gill-net sampling) were pooled to constitute one sample for each zone/bay/round combination. Species count data (all life-history stages pooled) were fourth-root transformed and a similarity matrix was constructed containing Bray-Curtis similarity coefficients calculated between each pair of samples (Bray & Curtis 1957). Non-metric multi-dimensional scaling (MDS; Clarke 1993) was employed to create a visual representation of the ‘closeness’ of the species composition between samples. Two-way crossed analysis of similarities (ANOSIM; Clarke & Green 1988, Clarke 1993) was used to test for significant differences in species composition between bays and rounds. Similarity percentages (two-way SIMPER; Clarke 1993) were used to identify the species that were principally responsible for any significant variation between bays and zones.

7.2.6 Tag-recaptures

Tagging and recapture locations were plotted in ArcMap 10.2.1 to categorise their location and zone. Comparison of each individual's categorisation between tagging and recapture events allowed for the investigation of movements between locations and zones. Examination of movements between locations was limited to nine geographically-distinct bays: Rockingham, Halifax, Cleveland, Bowling Green, Upstart, Abbot, Edgecumbe, Woodwark/Double and Repulse Bays (Figure 7.1). Capture events outside of these bays (i.e. further from shore or along relatively straight coastline) were grouped as 'other location'. Minimum distance travelled was calculated as the shortest straight-line-segmented distance between tagging and most-recent-recapture location, while not crossing land (and via sequential locations for 18 sharks with > 1 recapture). Time at liberty was calculated as the number of days between tagging and most-recent recapture.

7.3 Results

7.3.1 Shark abundance

Total shark abundance in longline samples was significantly higher in closed zones compared to open zones; and in Bowling Green Bay compared to Rockingham (Tukey multiple comparisons test, $P < 0.0001$) and Upstart (Tukey multiple comparisons test, $P < 0.0001$) Bays (Table 7.2). A significant interaction between bay and zone was detected for total shark abundance in gill-net samples. Although no pair-wise factor-level combinations were significantly different using gill-net data (Tukey multiple comparisons, $P \geq 0.05$), estimated shark abundances in open and closed zones of Bowling Green Bay were outside of alternate 95% confidence intervals (Figure 7.2), suggesting higher shark abundance in closed areas compared to open areas.

Significant interaction between bay and zone characterised the abundance of Australian sharpnose sharks using both gears (Table 7.2), indicating variation at a finer spatial scale than that of entire bays. However, this variation did not coincide consistently with zoning, indicating that zoning was an unlikely driver of spatial variation in Australian sharpnose shark abundance. Abundance in longline samples was highest in Bowling Green Bay, and there were variable and insignificant pairwise variations between zones within individual bays using longlines and gill-nets (Tukey multiple comparisons, $P \geq 0.05$; Figure 7.2).

For blacktip, pigeye, scalloped hammerhead *Sphyrna lewini* and spot-tail sharks; open and closed zones did not coincide with measurable heterogeneity in shark abundance (Table 7.2). However, there were variations in the abundances of these species among bays using ≥ 1 sampling method. Rockingham Bay had high relative abundances of blacktip and scalloped hammerhead sharks, Bowling Green Bay had low relative abundances of blacktip and spot-tail sharks, and Upstart Bay had low relative abundance of pigeye sharks (Appendix 13).

7.3.2 Length-frequency distribution

Stretch total length was measured for 1163 of the 1203 sharks captured within Rockingham, Bowling Green and Upstart Bays. Across the three bays, median STL of Australian sharpnose (longline samples), blacktip (longline and gill-net samples), and pigeye (longline samples) sharks were significantly larger inside closed areas (Table 7.3, Figure 7.3). For blacktip and pigeye sharks, these differences were predominantly due to an absence or relative scarcity of larger size classes in open zones. In addition, significant variation in median STL among bays was detected for Australian sharpnose sharks in gill-net samples (Table 7.3), whereby the presence of a relatively larger proportion of medium sized sharks c. 550–650 mm in Bowling Green Bay resulted in a significantly smaller median size there (660 mm) compared to Upstart Bay (690 mm; Kruskal-Wallis multiple comparison test, $P < 0.05$; Appendix 14). For Australian sharpnose sharks, the small and inconsistent effect of zone between sampling gears indicated that spatial variation in STL was not necessarily attributable to zoning. No significant spatial variations in STL were detected for scalloped hammerhead or spot-tail sharks (Table 7.3).

7.3.3 Species composition

A total of 1197 sharks were identified to species level in Rockingham, Bowling Green and Upstart Bays. The MDS ordination did not reveal obvious differentiation in shark community structure between zones (Appendix 15). However, there was a significant effect of zone (ANOSIM; $R = 0.20$, $P = 0.001$) and bay (ANOSIM; $R = 0.29$, $P = 0.001$) on community structure. The small magnitude of the R statistic indicated that these differences were not extreme. Eight species cumulatively contributed up to 70% of the average Bray-Curtis dissimilarity between open and closed zones (53.28; two-way SIMPER; Appendix 16). The average relative abundances of seven of those species were higher in closed zones. High relative abundance of multiple species in closed zones aligned with the results for all species pooled using GLMMs (Aim 1).

All pairwise comparisons between bays were significantly different; and in order of largest to smallest contribution to the Global ANOSIM, they were: Bowling Green verses Rockingham (R = 0.39, P = 0.001), Rockingham verses Upstart (R = 0.30, P = 0.001), and Bowling Green verses Upstart (R = 0.21, P = 0.004). Blacktip, Australian sharpnose, spot-tail and scalloped hammerhead sharks were among the top three most influential species in at least two pairwise comparisons between bays.

7.3.4 Tag-recaptures

Fishery-independent and fishery-dependent fishing was distributed between closed (n = 1202 shots) and open (n = 1818 shots) zones. As a result of concentrated fishery-independent sampling in Cleveland Bay, tagging effort within this bay was predominantly within closed zones using longlines (Appendix 17). In contrast, tagging effort elsewhere was predominantly fishery-dependent gill-net shots within open zones. Therefore, the movements of recaptured sharks were in part a function of the spatial distribution of fishing effort and gears, and movements between zones could not be extrapolated to the population level. A total of 4944 sharks were tagged and released within coastal waters. By September 2014, 299 tagged sharks from ≥ 20 species had been recaptured (Appendix 18). No sharks were recaptured outside the GBRMP (i.e. without considering ports and shipping channels which were enclosed within, but not part of, the GBRMP). The proportion of recaptured sharks predominantly included pigeye (28%), blacktip (23%), spot-tail (11%) and blacktip reef *Carcharhinus melanopterus* (9%) sharks (Appendix 18). Pigeye (0.17) and blacktip reef (0.13) sharks had high recapture rates; while other commonly-tagged species such as Australian sharpnose (0.01), whitecheek *Carcharhinus coatesi* (0.1) and milk *Rhizoprionodon acutus* (0.02) sharks had low recapture rates.

Some species demonstrated large travel distances (e.g. > 300 km). However, the majority of individuals moved short minimum distances (< c. 50 km; Figure 7.4A) and were recaptured in the same bay where they were tagged (Figure 7.5A). Of all recaptured sharks tagged in closed zones, 61% were also recaptured in closed zones (Figure 7.5B). The relationship between minimum distance travelled and time at liberty varied among and within species (Figure 7.6). Most movements of pigeye (76%) and blacktip (58%) sharks were < 25 km. Variation in movements by pigeye and blacktip sharks indicated that most individuals used restricted areas over prolonged periods while others moved more broadly over a range of temporal scales. Spot-tail (78%) and blacktip reef (96%) sharks were typically recaptured within 15 km of their tagging location. For these two species, consistently small travelling distances indicated prolonged site attachment (or repeated use) over multiple years.

A total of 166 recaptured sharks were tagged within Cleveland Bay closed zones. Of these, 60% were also recaptured in Cleveland Bay closed zones, and this percentage was ≥ 33% for any species (Figure 7.5C). Most notably, 100% of recaptured blacktip reef and scalloped hammerhead sharks, and 71% of recaptured spot-tail sharks tagged in Cleveland Bay closed zones were also recaptured in those zones. This pattern was similar for multiple species and over the whole study region. For example, the majority of blacktip reef and scalloped hammerhead sharks were recaptured in closed zones (but not necessarily the same polygon; Figure 7.4B). In contrast, 84.5% of recaptured blacktip sharks remained in open zones or moved from closed to open zones (Fi.g 7.4B).

7.4 Discussion

Previous studies have demonstrated that coastal MPAs have the potential to benefit sharks by sheltering a portion of their spatial distribution from fishing pressure (Heupel & Simpfendorfer 2005a, Knip et al. 2012a, da Silva et al. 2013). The present study was among the first to evaluate whether the inferred benefits of coastal MPAs for sharks had been realised through increases in abundance or body size. Significant variations in shark abundance, size and species composition between areas open and closed to commercial gill-net fishing were congruent with the documented effects of fishing on sharks, including reduced abundance (Heupel et al. 2009) and the disproportionate removal of large-bodied individuals in open areas (Stevens et al. 2000). For some species, tag-recapture data suggested short minimum travelling distances and prolonged or repeated use of MPAs. Results suggested that coastal MPAs do not necessarily need to be large (Heupel & Simpfendorfer 2005a) or designed for a particular species (Roberts 2000) to provide benefits. However, inter-specific variations in the magnitude of MPA benefits are likely influenced by patterns of occupancy through ontogeny and the spatial distribution of individuals (Gruss et al. 2011).

Differences in length-frequency distributions between zones for blacktip and pigeye sharks may have been driven by the disproportionate removal of large-bodied individuals by fishing. Ontogenetic changes in space use within coastal environments have been observed for multiple species, including blacktip and pigeye sharks (Heupel et al. 2004, Knip et al. 2011b), which may also have influenced the spatial mismatch in length-frequency distributions. However, the significant effect of ‘zone’ and the consistency in results across species spanning multiple environmentally heterogeneous bays (Chapter 5) indicated that fishing pressure was a likely driver of spatial variation in length-frequency distributions. The head morphology of scalloped hammerhead sharks makes them susceptible to capture at all sizes (Harry et al. 2011b). This likely limited the potential for length-selective harvest of this species, and thus the potential for differences in length-frequency distributions between zones. In addition, high natural mortality of young scalloped hammerhead sharks (Lowe 2002) may have obscured some of the effects of zoning if fishing mortality within closed zones partially replaced natural mortality (Tobin et al. 2014b). Differences in apparent zoning effects between species suggested that a wide array of intrinsic and extrinsic factors may influence inter-specific variation in MPA function.

Coastal environments can provide important habitat (e.g. nursery areas) for the young of multiple shark species (Heupel et al. 2007). Coastal MPAs may benefit these species by increasing survival (Roberts 2000). Immature sharks that are site-attached to restricted areas are likely to benefit from sub-bay-sized coastal MPAs if they encompass areas of high use. Pigeye sharks were predominantly immature, and 36% of recaptured individuals that were tagged in Cleveland Bay closed zones were also recaptured in those zones. These results were consistent with previous acoustic tracking, which revealed that individuals were strongly-associated with shallow turbid habitats adjacent to creek mouths within MPAs (Knip et al. 2011b, Knip et al. 2012a). By sheltering highly-resident young sharks from fishing pressure, sub-bay-sized coastal MPAs likely improved the survival of young pigeye sharks.

Immature scalloped hammerhead and blacktip sharks also demonstrate site attachment within coastal environments (Heupel & Hueter 2002, Duncan & Holland 2006). In the present study, the majority of blacktip sharks were recaptured within close proximity to their tagging location (e.g. 53% of movements were ≤ 20 km), but some individuals were recaptured several-hundred kilometres away and moved between management zones. Nonetheless, length-frequency analyses suggested that the degree of residency displayed by immature blacktip sharks may have facilitated fishing-induced heterogeneity in body size between zones. The fact that most scalloped hammerhead sharks were tagged and recaptured in closed zones suggests that GBRMP zoning may also benefit this species. Depending on the degree of overlap between juvenile space use and MPAs, shark populations may benefit from varied enhancements to juvenile survival, and the results of this study suggested that these benefits may have been realised for blacktip sharks.

The survival of mature sharks, and those approaching maturity, is critical to population stability and recovery (reviewed in Kinney & Simpfendorfer 2009). Therefore, species that occupy MPAs during these stages are likely to receive the greatest benefit (Knip et al. 2012a). In the present study, the majority of mature spot-tail and blacktip reef sharks were captured and recaptured within MPAs. Minimum distances travelled were generally < 15 km and distances did not increase with time at liberty. This indicated prolonged use of restricted areas within MPAs over multiple years. Telemetry studies have also revealed prolonged residency of these species to restricted areas (Papastamatiou et al. 2009, Knip et al. 2012c, Chin 2013). Given the site fidelity of spot-tail sharks, localised fishing may be expected to drive spatial variations in their abundance or length-frequency distributions. However, variable MPA residency among individuals and frequent excursions across MPA boundaries (Knip et al. 2012a), coupled with the inclusion of more-vagrant immature conspecifics (Kinney 2011, Knip 2011), may have provided sufficient mixing between zones to impede the detection of zone effects. Nonetheless, the prolonged protection of mature individuals within MPAs may have contributed to the low mortality rate of spot-tail sharks observed in Cleveland Bay (Knip et al. 2012d). For blacktip reef sharks, MPA benefits may be even greater via the concurrent protection of multiple life-history stages (Bonfil 1999). These benefits are not limited to tropical species, for example mature and immature common smoothhound sharks *Mustelus mustelus* spent the majority of their time within a small (34 km^2) no-take zone on the Western Cape of South Africa (da Silva et al. 2013). In tropical coastal waters of the GBRMP, varied patterns of occupancy through ontogeny mean that different species are likely to benefit from coastal MPAs in different ways.

Low recapture rates and variable travelling distances for Australian sharpnose, milk and whitecheek sharks suggested broad space use and low residency within MPAs. Therefore, these species may not receive significant MPA benefits. Previous studies have also concluded that Australian sharpnose sharks are likely to move and forage across multiple bays (Munroe 2014, Munroe et al. 2014). This pattern of habitat use is common among small-bodied coastal species. For example, Atlantic sharpnose sharks *Rhizoprionodon terraenovae* and gray smooth-hound sharks *Mustelus californicus* also use a range of coastal habitats and exhibit low residency to individual coastal areas (Carlson et al. 2008, Espinoza et al. 2011). Although this likely limits MPA effectiveness, reports of MPA benefits for teleost species with wide home ranges (Claudet et al. 2010) indicate that further investigation of MPA benefits for small-bodied coastal sharks is warranted.

Observational studies investigating the effects of MPAs on aquatic communities require careful consideration of confounding factors (Barrett et al. 2007). Because the present study provided the first baseline fishery-independent data on shark abundance across coastal MPAs in the GBRMP, it could not be confirmed whether results were driven by fishing or other geographic, habitat or ecological factors. For example, apparent zoning effects can be present prior to the enforcement of fishing restrictions (Edgar et al. 2004), and habitat attributes can influence the magnitude and timing of MPA benefits (Monaco et al. 2007). Marine protected areas in Rockingham, Bowling Green and Upstart Bays were relatively sheltered from the prevailing south-easterly trade winds compared to each corresponding open zone, and this shelter can influence abiotic and biotic conditions in coastal environments (Grech & Coles 2010). Spatial heterogeneity in abiotic and biotic conditions including turbidity, salinity and aquatic vegetation cover has been linked with spatial variation in the abundance and habitat use of coastal sharks in north-eastern Australia (Chapter 5, Chin et al. 2012), and in other locations (Froeschke et al. 2010a, Schlaff et al. 2014). However, the inclusion of three environmentally unique bays (Chapter 5, Furnas 1993) likely alleviated the influence of potentially confounding environmental variables such as turbidity and salinity (Chapter 5). By identifying a link between coastal MPAs and shark communities, the present study provides a foundation for future research.

Further research is critical for improving understanding of how anthropogenic impacts influence shark populations. For example, post-release mortality from commercial and recreational fishing remains largely unexplored (Lynch et al. 2010, De Faria 2012), as do the effects of fishing near MPA boundaries (Walters 2000). In addition, this study was unable to evaluate the cumulative stock-wide benefits of the full network of MPAs within the Great Barrier Reef World Heritage Area. It is also important to understand the benefits of other management measures which are used in conjunction with MPAs;

including the limited allocation of fishing licenses, total allowable catch, restrictions on the processing of shark fins, maximum size limits and the declaration of no-take species (Harry et al. 2011b, DEEDI 2011). Finally, the influence of heterogeneous fishing pressure on intra-population diversity remains poorly understood. Marine protected areas may not necessarily protect the full biological diversity of populations that display spatial intra-population genetic and behavioural diversity (Knip et al. 2012a). Subsequent reductions in biological diversity can influence population-level vulnerability to environmental changes (Chapter 2, Moore et al. 2010).

In conclusion, the present study provided additional support for the conservation potential of MPAs for tropical coastal sharks. In addition, differences in shark abundance, species composition and length-frequency distributions between management zones suggested that the inferred benefits of coastal MPAs have been realised for some species. The broad spatial scale considered and the consistency in results between species provided additional support for zoning effects. Although multiple species often co-inhabit coastal environments, differences in their habitat use and life histories mean that MPA effectiveness is likely to vary among species. Further research is required to improve our understanding of the population-level implications of coastal MPAs for sharks.

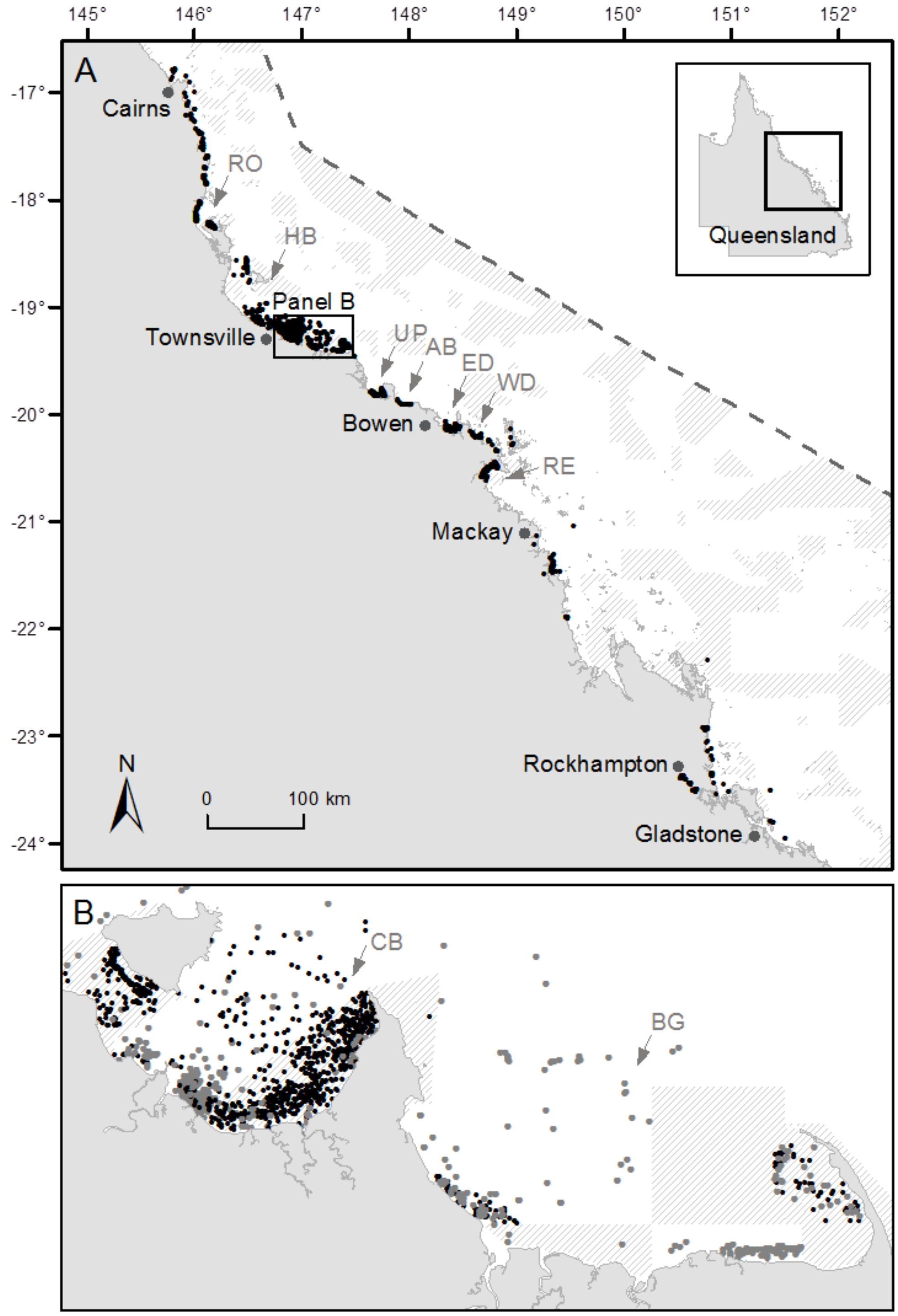


Figure 7.1 Spatial distribution of fishery-dependent and fishery-independent sampling within coastal waters of the Great Barrier Reef Marine Park (GBRMP). Diagonal shading = closed zones, no shading = open zones. Nine labelled bays were included in investigation of movements between locations (Aim 4): RO = Rockingham Bay, HB = Halifax Bay, CB = Cleveland Bay, BG = Bowling Green Bay, UP = Upstart Bay, AB = Abbot Bay, ED = Edgecumbe Bay, WD = Woodwark/Double Bays, RE = Repulse Bay. The broken line in panel A denotes the outer extent of the GBRMP. Additional detail of sampling within Cleveland and Bowling Green Bays is provided in panel B. In panel B, black circles = longline samples and grey circles = gill-net samples.

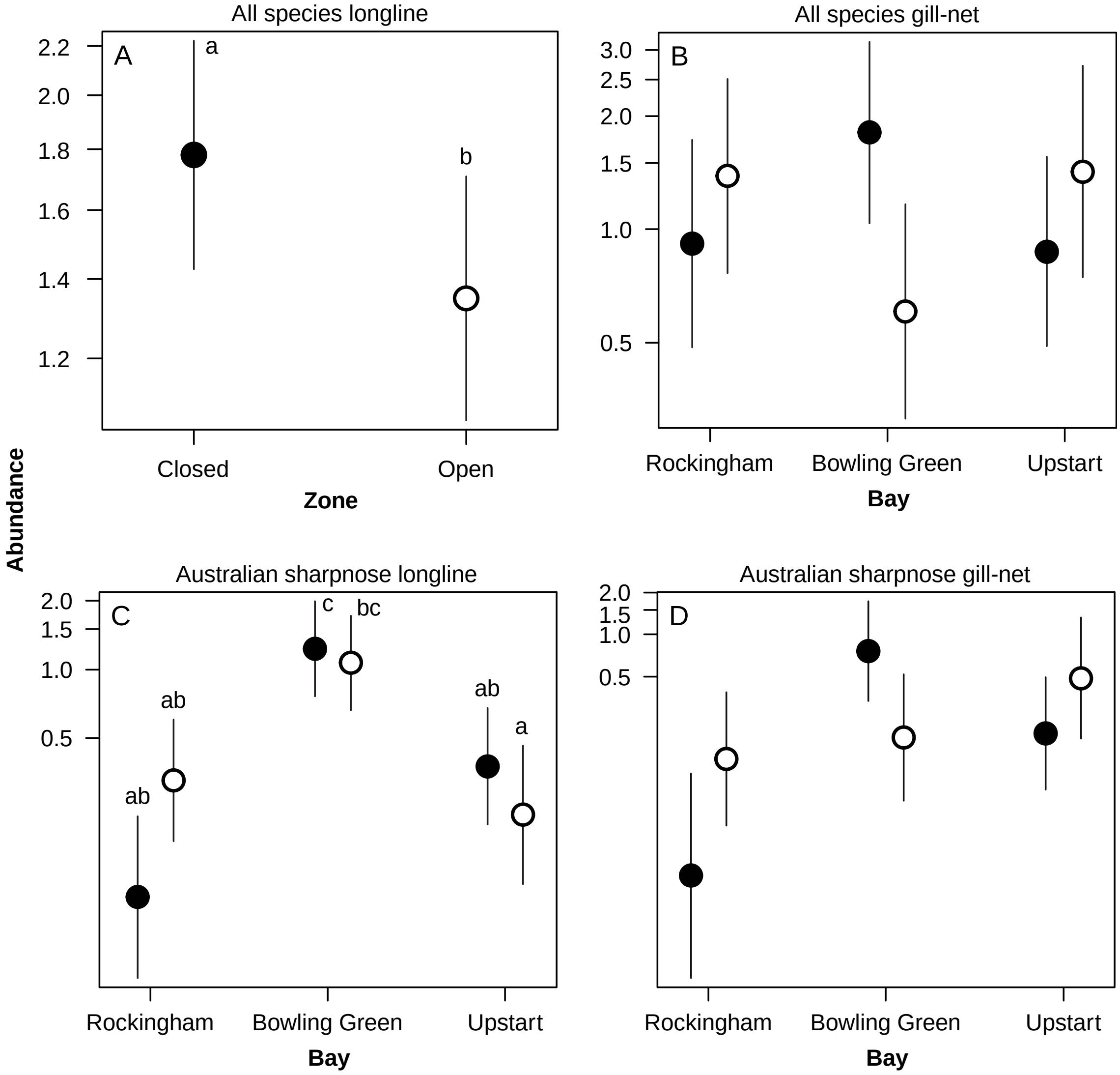


Figure 7.2 Significant effects of the factor 'zone' on shark abundance. Circles are estimated shark abundance (white = open zone, black = closed zone) and vertical lines are 95% confidence intervals. Significant interactions between zone and bay were detected in panels B, C and D. Lower-case letters denote significantly different groups (Tukey multiple comparisons, $P < 0.05$). Note that the y axes vary among panels.

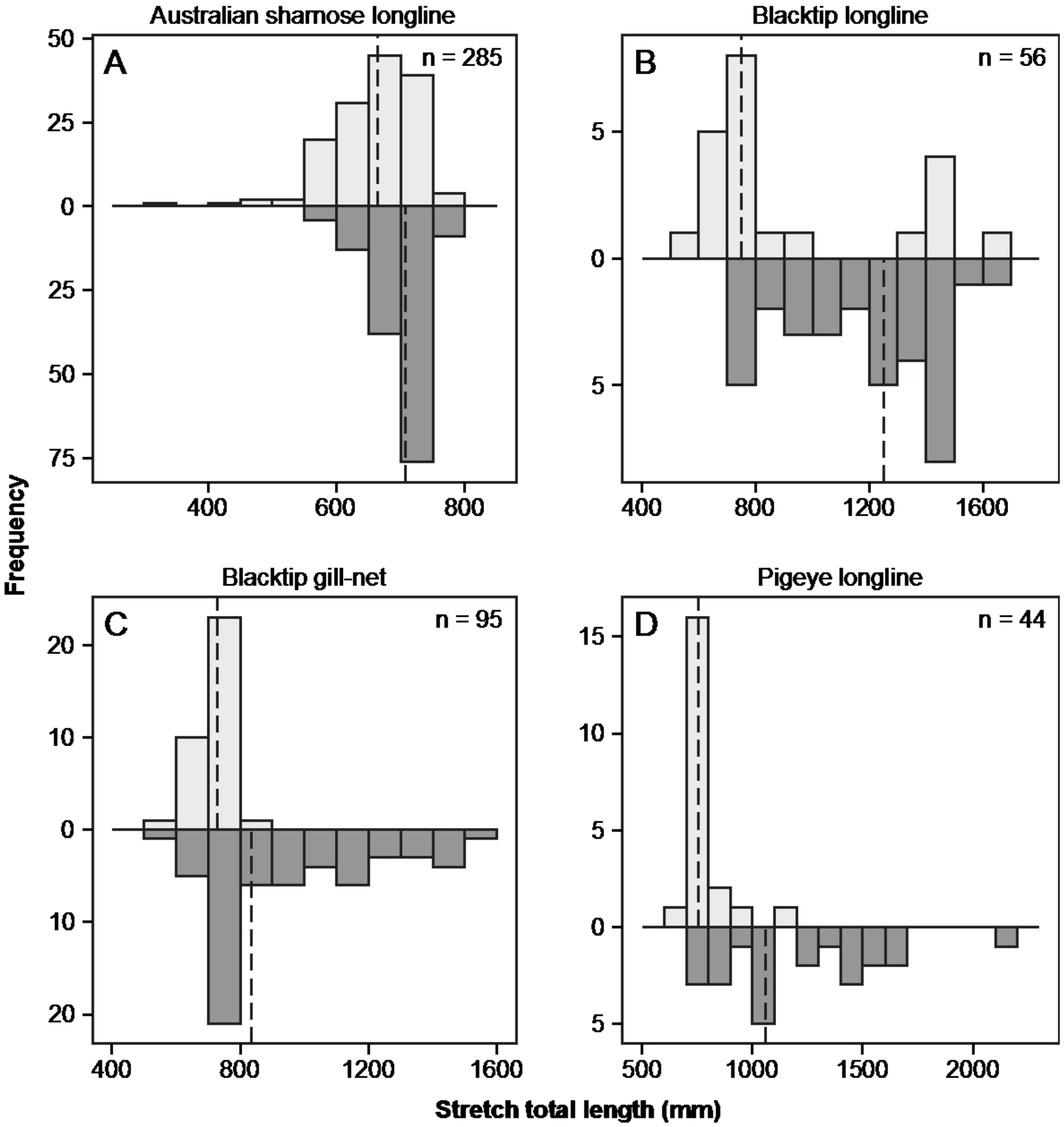


Figure 7.3 Significantly different length-frequency distributions between open (light grey) and closed (dark grey) zones (Kruskal-Wallis rank sum test and Kolmogorov-Smirnov test, $P < 0.05$). Broken lines indicate sample median. Data are pooled across bays. Note that the axes vary among panels.

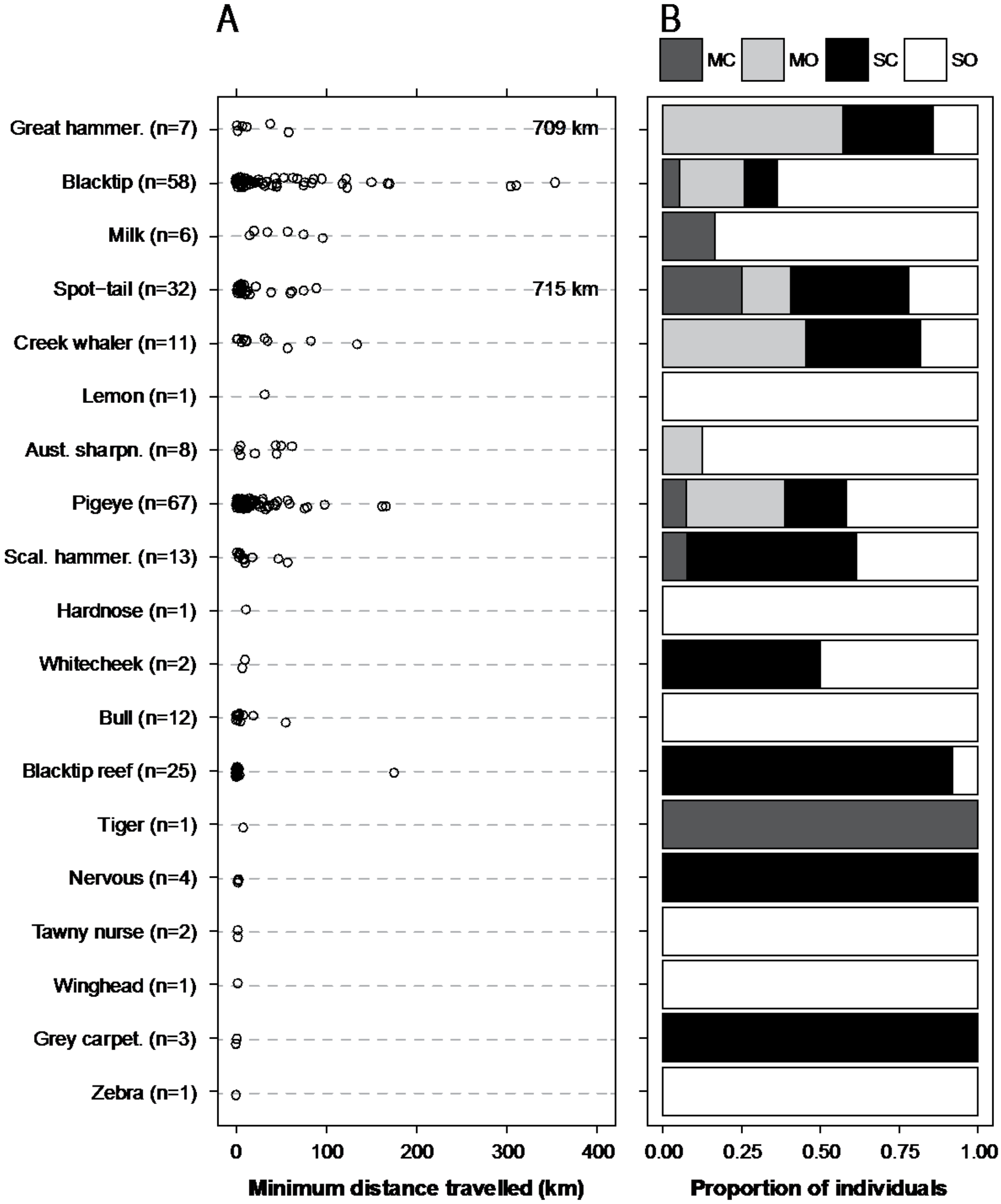


Figure 7.4 Geographic scale of movement (A) and movement among zone types (B) as indicated by tag-recapture locations. Points in panel A indicate the minimum distance travelled between the first and last capture of each individual. Values on the right-hand-side of panel A indicate two large movements beyond 400 km. MC = moved from an open zone to a closed zone, MO = moved from a closed zone to an open zone, SC = stayed in closed zone/s, SO = stayed in open zone/s. Species are listed in decreasing order of mean distance travelled. Only individuals with precise capture and recapture locations are included.

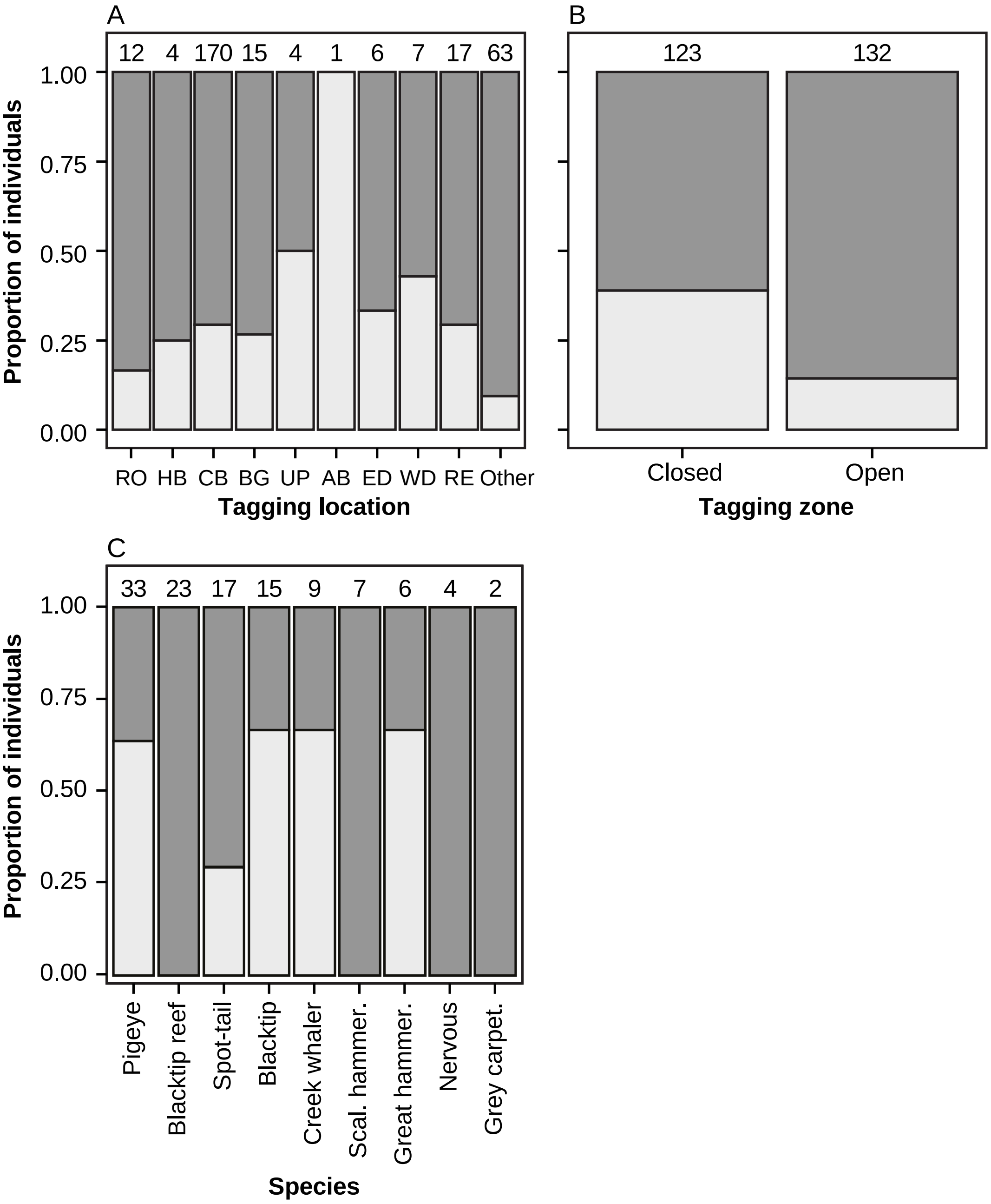


Figure 7.5 Proportion of sharks that remained within (dark grey) and left (light grey) their initial capture location (panel A) or zone type (panels B and C). Panel C shows movements of recaptured sharks that were tagged in Cleveland Bay closed zones, and recaptured in Cleveland Bay closed zones (dark grey) or elsewhere (light grey). Numbers above the bars indicate the total number of recaptured sharks that were initially tagged in each category. RO = Rockingham Bay, HB = Halifax Bay, CB = Cleveland Bay, BG = Bowling Green Bay, UP = Upstart Bay, AB = Abbot Bay, ED = Edgecumbe Bay, WD = Woodwark/Double Bays, RE = Repulse Bay, Other = all other locations. Panel A includes 44 additional sharks with approximate capture locations.

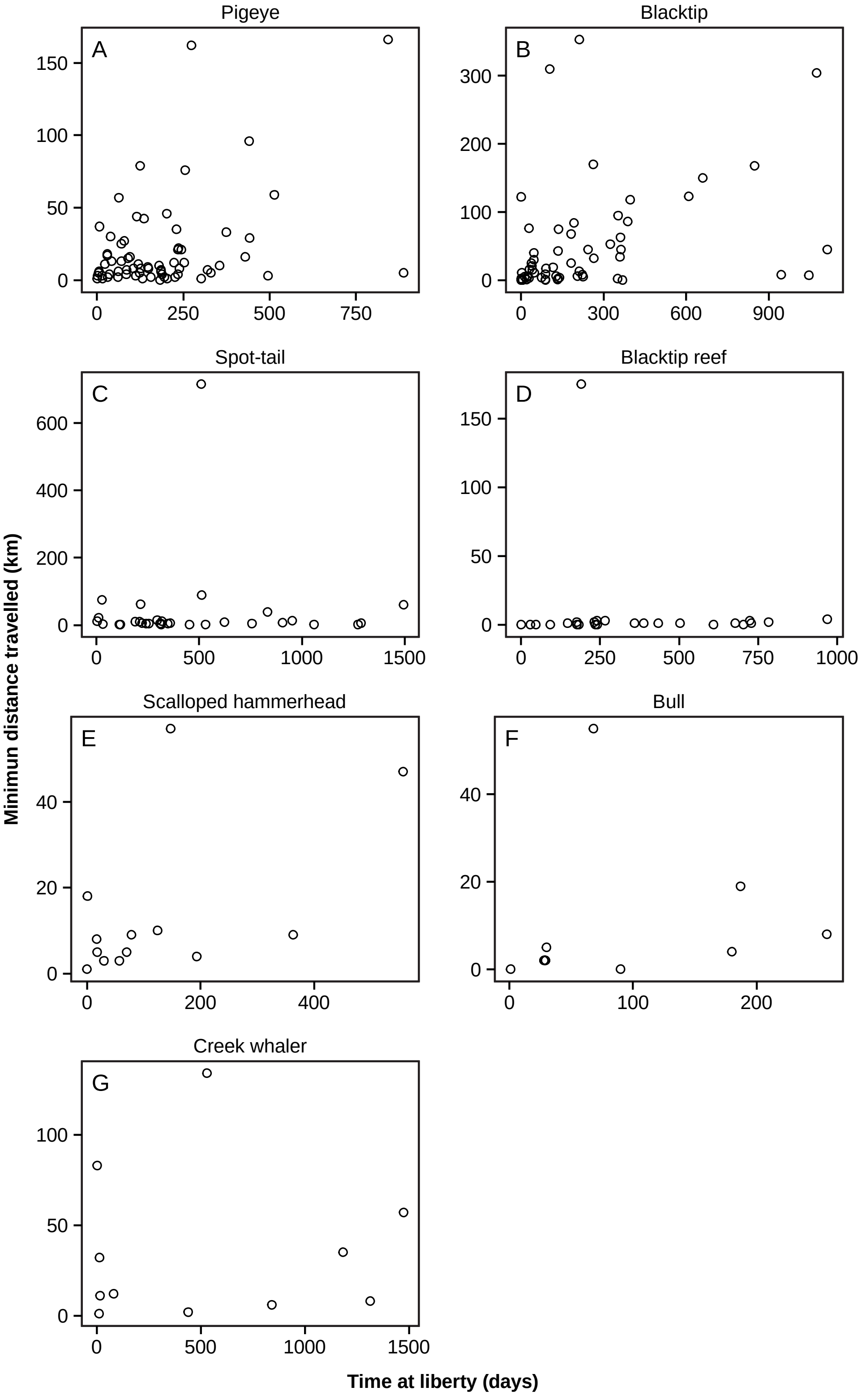


Figure 7.6 Times at liberty verses minimum distances travelled for shark species with > 10 recaptures. Each point represents a recaptured individual. Note that the axes vary among panels.

Table 7.1 Summary of standardised fishery-independent surveys in open and closed zones within three study bays (for Aims 1–3). Zoning (C:O) = the respective percentage of total bay area that was closed (C) and open (O) to commercial gill-net fishing. Standardised soak hours = sum of 100-hook-hours and 100 m-net-hours for longlines and gill-nets, respectively. Number of shots and standardised soak hours in closed zones (C) are followed by those is open zones (O).

Bay	Zoning (C:O)[1]	Longline		Gill-net	
		Number of shots (C:O)	Standardised soak hours (C:O)	Number of shots (C:O)	Standardised soak hours (C:O)
Rockingham	42:58	47:46	21:20	33:34	57:78
Bowling Green	47:53	43:48	20:20	34:32	93:89
Upstart	46:54	47:46	22:18	45:31	73:48

[1] Calculated using data from Commonwealth of Australia (Great Barrier Reef Marine Park Authority) [2012].

Table 7.2 Relationships between shark abundance and spatial covariates. Results are from likelihood ratio tests between nested generalised linear mixed models (GLMM). The interaction term was removed if it was not significant. OLRI = observation-level random intercept. Non-significant interactions were removed prior to the calculation of main-effect parameters.

Species	Sampling method	No. of sharks (% samples with ≥ 1 shark)	Model type	Factor	*df*	χ^2	*P*
All species	Longline	627 (72)	Poisson GLMM + OLRI	Zone	1	4.72	0.03*
				Bay	2	28.82	<0.0001*
				Zone*Bay	2	2.15	0.34
	Gill-net	576 (59)	Poisson GLMM + OLRI	Zone*Bay	2	9.70	0.008*
Aust. sharpnose	Longline	293 (39)	Poisson GLMM + OLRI	Zone*Bay	2	8.03	0.02*
	Gill-net	292 (33)	Poisson GLMM + OLRI	Zone*Bay	2	11.60	0.003*
Blacktip	Longline	57 (16)	Poisson GLMM + OLRI	Zone	1	1.29	0.26
				Bay	2	3.72	0.16
				Zone*Bay	2	5.10	0.08
	Gill-net	104 (23)	Poisson GLMM + OLRI	Zone	1	3.65	0.06
				Bay	2	8.12	0.02*
				Zone*Bay	2	3.64	0.16
Pigeye	Longline	45 (10)	Poisson GLMM	Zone	1	0.04	0.84
				Bay	2	32.06	<0.0001*
				Zone*Bay	2	1.35	0.51
	Gill-net	30 (6)	Poisson GLMM + OLRI	Zone	1	0.46	0.50
				Bay	2	0.54	0.76
				Zone*Bay	2	0.83	0.66
Scalloped h.	Gill-net	69 (13)	Poisson GLMM + OLRI	Zone	1	2.12	0.15
				Bay	2	18.04	0.0001*
				Zone*Bay	2	3.95	0.14
Spot-tail	Longline	68 (17)	Poisson GLMM + OLRI	Zone	1	0.02	0.90
				Bay	2	8.30	0.02*
				Zone*Bay	2	4.15	0.13

Table 7.3 Comparison of length-frequency distributions between bays and zones. KW = Kruskal-Wallis rank sum test, KS = Kolmogorov-Smirnov test. LL = longline, GN = gill-net. Dashes indicate cases where differences in shape precluded comparison of length-frequency distributions using the Kruskal Wallace test. Crosses indicate insufficient sample sizes for analysis (i.e. < 15 observations in ≥ 1 group). Bay comparisons were limited to Rockingham and Bowling Green Bays for pigeye sharks in longline samples, Rockingham and Bowling Green Bays for blacktip sharks in longline samples, and Rockingham and Upstart Bays for spot-tail sharks in longline samples.

	Bay KW			Zone KW			Zone KS	
	df	χ^2	*P*	*df*	χ^2	*P*	*D*	*P*
Aust. sharpnose LL	2	5.84	0.05	1	32.67	<0.0001*	0.39	<0.0001*
Aust. sharpnose GN	2	15.58	0.0004*	-	-	-	0.15	0.09
Blacktip LL	1	0.96	0.33	1	8.53	0.003*	0.53	0.001*
Blacktip GN	2	0.29	0.87	-	-	-	0.60	<0.0001*
Pigeye LL	1	0.01	0.92	1	20.47	<0.0001*	0.73	<0.0001*
Scal. hammerhead GN	x	x	x	1	2.75	0.10	0.32	0.13
Spot-tail LL	1	3.44	0.06	1	3.68	0.05	0.32	0.07

CHAPTER 8

General Discussion

Plate 8 Sunset in Upstart Bay (January 2012).

8.1 Conclusions and implications

Sharks play an important role in marine ecosystems (Ferretti et al. 2013), however many species are facing increasing pressure from anthropogenic impacts and environmental change (Chin et al. 2010). Critical to mitigating these impacts is an understanding of the spatio-temporal distributions of sharks and the factors that influence their habitat use and vulnerability. This thesis highlighted that tropical coastal environments are important for a variety of shark species. Similarly, high species diversity has been observed in other tropical and subtropical locations (Blaber et al. 1995, Taylor & Bennett 2013). Despite the co-occurrence of multiple species, an array of biological, ecological and physical factors combine and interact to shape inter- and intraspecific variations in shark habitat use. The findings of this thesis have implications for our understanding of the broader functioning and structure of tropical coastal systems. In accordance with the thesis objectives outlined in Chapter 1, this study was among the first to investigate heterogeneous space use by mobile marine predators, the factors that influence these variations, and the associated population-level implications.

Tropical coastal environments are used by sharks in a variety of ways. Although nursery areas were the primary focus of this thesis, Chapter 4 revealed that coastal waters are important for multiple life-history stages. Catches of several large-bodied coastal species, including blacktip *Carcharhinus tilstoni/Carcharhinus limbatus,* pigeye *Carcharhinus amboinensis* and scalloped hammerhead *Sphyrna lewini* sharks, were dominated by immature individuals in accordance with the theoretical pattern of nursery use described by Springer (1967). In contrast, some small-bodied species, including Australian sharpnose sharks *Rhizoprionodon taylori*, completed their entire life-cycle inshore (Knip et al. 2010). Body-size analyses in Chapter 4 revealed spatial structuring of shark communities based on size rather than life-history stage. Small-bodied individuals comprising a variety of species and life-history stages may share similar trophic positions (Bethea et al. 2004) and predation pressures (Branstetter 1990), and may therefore receive similar benefits from coastal environments. Accordingly, current paradigms concerning the use of coastal environments by sharks may need to be re-examined, possibly in a size-based context rather than the traditional life-history-stage-based context.

The majority of shark nursery research has aimed to identify the most productive young shark habitats in order to guide the focus of management and conservation efforts (Heupel et al. 2007). This thesis built upon current thinking in this field by widening our view of critical young shark habitats to include those that enhance population resilience and stability, but may not necessarily be among the most productive currently. The highly dynamic nature of coastal ecosystems (Furnas 1993) and their susceptibility to anthropogenic impacts (Chin et al. 2010) mean that the location of the most productive young shark habitats may change over time (e.g. Froeschke et al. 2010b). Portfolio theory predicts that contributions from a diverse range of young shark habitats may reduce variability in the overall production of adults and thus maintain population resilience (Schindler et al. 2010, Chapter 2). Examination of case studies of portfolio effects in teleost fish identified that understanding intra-population variations in abundance and habitat use (Chapters 4 and 6), and the extrinsic drivers of these (Chapter 5 and 7), is fundamental to understanding the potential for portfolio effects in shark populations.

Within the context of portfolio effects, Chapter 4 provided one of the first investigations of broad-spatial-scale heterogeneity in young shark community structure, and revealed that proximate tropical bays can differ markedly in their functioning as communal shark nurseries. Heterogeneous space use by young sharks may be a strategy to achieve population-stabilising portfolio effects. The consequence for management of such a strategy is that the condition of a range of young shark habitats must be protected in order to maintain portfolio performance. At the community level, portfolio effects among the variety of shark species documented in Chapter 2 may influence their collective role within coastal ecosystems. For example, complementary dynamics among species that perform similar ecosystem functions can maintain temporally-stable ecosystem services (Tilman 1996). However, understanding intra-population portfolio effects also requires investigation of the habitat use of individual species.

The collective findings of Chapters 5–7 revealed that underlying the spatial variation in community structure identified in Chapter 4 were complex patterns in spatio-temporal occurrences/abundances of individual species. Similar broad-scale spatial variations in relative immature shark abundances have been observed in other locations (Froeschke et al. 2010b, Curtis et al. 2011, Bethea et al. 2014), and these have been linked with spatial variations in environmental conditions (Froeschke et al. 2010a, McCallister et al. 2014, Ward-Paige et al. 2014). However, Chapter 6 identified that these variations were more apparent for some species than for others. This suggested that not all species use discrete nursery areas. For example, the young of some small-bodied species, such as the spot-tail shark *Carcharhinus sorrah*, may obtain greater benefits from use of a wide range of habitats (Branstetter 1990, Heithaus 2007, Knip et al. 2010). In contrast, significant spatial heterogeneity in the occurrences of young scalloped hammerhead and blacktip sharks indicated habitat specificity. The identification of important habitats is fundamental to effective spatial management for the conservation of endangered species such as the scalloped hammerhead shark (Baum et al. 2007). In response to biotic and abiotic conditions, young sharks may adopt different strategies in different bays, or avoid certain bays altogether (Rechisky & Wetherbee 2003). Nonetheless, a broad range of bays may still be important over the long term in the context of portfolio effects, and investigation of the drivers of heterogeneous space use is critical to understanding how these dynamics may occur.

Chapter 5 linked spatial variations in shark abundance with spatial variations in environmental factors including turbidity, salinity, depth, temperature and proximity to mangroves. For example, the near-absence of scalloped hammerhead sharks in Edgecumbe Bay (Chapter 4) was linked with apparently-unfavourable low-turbidity conditions. Conversely, high turbidity may have influenced the high relative abundances of scalloped hammerhead and pigeye sharks in Rockingham and Repulse Bays, respectively. As a result of environmental heterogeneity among bays, sharks in different bays may experience different seasonal fluctuations or be differentially impacted by localised and widespread environmental changes. In a similar way, environmental heterogeneity within large coastal systems in Florida meant that some areas served as overwintering grounds for immature bull sharks *Carcharhinus leucas* while others did not (Curtis et al. 2011). By identifying relationships between multiple shark species and their environment, Chapter 5 provided useful information for the identification of critical habitats and understanding the impacts of environmental change.

Marine protected areas (MPAs) within offshore coral reef environments of the Great Barrier Reef Marine Park (GBRMP) are reported to promote localised high relative abundances of teleosts and sharks (McCook et al. 2010). Chapter 7 demonstrated that MPAs can provide similar benefits for coastal sharks. However, interspecific differences in MPA effectiveness were likely influenced by a species' intrinsic vulnerability and susceptibility to fishing, the portion of the population receiving protection, and movement of individuals across MPA boundaries (Bonfil 1999, Gruss et al. 2011). For some species, strong environmental preferences coupled with habitat discontinuity may inhibit movement between distant patches of suitable habitat (Heupel & Simpfendorfer 2013, Espinoza et al. 2014); thus the species-environment relationships identified in Chapter 5 also have implications for MPA effectiveness. For example, strong association between immature pigeye sharks and shallow turbid areas adjacent to creek mouths (Knip et al. 2011b, Chapter 5) likely predisposed their prolonged occupancy of sub-bay-sized MPAs (Knip et al. 2012a; Chapter 7), as wells as their susceptibility to localised fishing outside of MPAs (Tobin et al. 2014b). In contrast, the apparent suitability of moderate water depths (c. 5 m) for immature blacktip sharks (also see McCallister et al. 2014, Ward-Paige et al. 2014) may have facilitated movements by some individuals across or between bays and management zones (Chapter 7). Therefore the integration of multiple data sources can facilitate the evaluation of MPA effectiveness for a variety of species.

Links between GBRMP zoning and shark abundance, size-distributions and community structure (Chapter 7) built upon the results of previous chapters, and also contributed to evaluation of the mechanisms behind portfolio effects. In addition to the biotic and abiotic drivers discussed in Chapters 4 and 5, fishing pressure can also have direct effects on coastal shark communities (Ley et al. 2002). Non-uniform harvest through time or space can influence intra-population diversity (Doctor et al. 2010). For example, if spatial variations in habitat use are associated with genetic or behavioural diversity, MPAs may not necessarily protect the full biological ‘portfolio’ of a shark population (Knip et al. 2012a). Subsequent homogenisation of biological diversity can erode portfolio performance and increase vulnerability to environmental change (Moore et al. 2010). Because biological diversity can be slow to restore (Anderson et al. 2013), this thesis highlighted the importance of further investigation into the effects of heterogeneous human impacts across young shark habitats.

The collective results of this thesis suggested that coastal zoning of the GBRMP is likely to increase the likelihood of sustainable populations if adequate measures are taken in areas outside of MPAs to restrict fishing mortality to management targets. Depending on the species, coastal MPAs may enhance survival to maturity or shelter parts of the breeding stock (Chapter 7). Explicit operating principles for the designation of GBRMP MPAs included: (1) protection of all known habitat types, (2) replication of MPAs within each bioregion and (3) representing cross-shelf and latitudinal diversity (Fernandes et al. 2005). These operating principles framed the protection of a diverse range of young shark habitats and in turn may have positive implications for the stability and resilience of shark stocks that are harvested in the East Coast Inshore Finfish Fishery (ECIFF).

8.2 Future research directions

This thesis provided important advances to knowledge in the field of shark spatial ecology, including the identification of topics that require further study. The identification of shark nurseries that currently make a disproportionally large contribution to the production of adults is valuable for management and should continue. In particular, investigation of differences in nursery use between common and Australian blacktip sharks will aid in unravelling the complexity of issues surrounding the management of this species complex. Future shark nursery research will ideally broaden in scope to include shark communities beyond shallow coastal environments and a variety of reproductive modes (e.g. investigation of whether oviparous species utilise nurseries). Demographic models demonstrate the high relative importance of individuals nearing maturity (reviewed in Kinney & Simpfendorfer 2009), thus future investigation of shark nursery value should include investigation of connectivity between juvenile and adult habitats to inform integrated landscape-level management (Beck et al. 2001, Sheaves et al. 2006). The investigation of links between juvenile and adult habitats may also help to resolve uncertainty surrounding current proxies of nursery value. These include the density (Beck et al. 2001) or overall abundance (Dahlgren et al. 2006) of young individuals in a particular area or habitat. For both of these proxies, ongoing investigation of shark habitat use and movements will inform the designation of the most appropriate spatial comparison unit for a given species (e.g. bay/estuary, or part thereof; Sheaves et al. 2006).

Due to the observational nature of this study, the causative mechanisms behind the observed variations in shark occurrence and abundance remain unconfirmed. However, turbidity, salinity (Chapter 5) and GBRMP zoning (Chapter 7) are strong candidates for further investigation. Manipulative experiments are required to unravel the multitude of direct, indirect and interacting relationships between sharks and their environment. Although there are practical constraints to studying sharks under controlled conditions

(Gruber & Myrberg 1977), the small size of most species' juveniles may allow for controlled experiments in laboratories (e.g. Clark 1963, Duncan & Holland 2006) or sea pens (e.g. Guttridge et al. 2013). In particular, separating the interacting relationships involving turbidity and salinity (Chapter 5) will be an important advancement in understanding and mitigating the effects of anthropogenic perturbations of these variables within coastal environments (Chin et al. 2010, Grech et al. 2013).

The most significant extensions of this thesis will be the quantification of portfolio effects in shark populations and further investigation of whether they should be considered in management decisions. Portfolio effects have been quantified in teleost stocks by comparing the variability in annual fish landings from the stock complex with the variability in fish landings from individual rivers (Schindler et al. 2010). Similarly, abundance surveys across a range of young shark habitats can be used to test the hypothesis that, although abundance in individual habitats is highly variable through time, the overall abundance across the population or region is relatively stable (e.g. using the coefficient of variation; Anderson et al. 2013). When environmental time-series data are available, it may be possible to investigate suspected mechanisms through which the environment could drive population dynamics (for example by modelling environmental-response diversity through a mechanistic model; Ives et al. 2003, Anderson et al. 2013, Thibaut & Connolly 2013). Finally, the strength of portfolio effects can be assessed based on the nature and magnitude of correlations in productivity among young shark habitats (Schindler et al. 2010, Carlson & Satterthwaite 2011). Although frameworks for investigating portfolio effects already exist, the scarcity of the required data may limit their application to sharks.

Due to the temporal scales over which portfolio effects can operate, data used to explore these processes will ideally span multiple decades (Moore et al. 2010, Schindler et al. 2010). Although the standardised fishery-independent approach used here provided a more-robust representation of shark communities, a major drawback of this approach is high operating costs (Rago 2005) which often limit temporal scope (but see Taylor et al. 2011, Holmes et al. 2012, Froeschke et al. 2013). Fishery-dependent data represents a cost-effective alternative, however these data can lack the species, spatial and life-history-stage resolution needed to investigate portfolio effects in shark nurseries (Tillett et al. 2012b, Tobin et al. 2014b). The implementation of concurrent fishery-independent and fishery-dependant sampling may provide a suitable compromise between data resolution and scope (Gutteridge 2011). Despite these challenges, by being among the first studies to investigate the implications of heterogeneous space use by young sharks, this thesis may serve as a model to facilitate future research on portfolio effects and the associated benefits for shark populations in a changing world.

REFERENCES

Abel DC, Young RF, Garwood JA, Travaline MJ, Yednock BK (2007) Survey of the shark fauna in two South Carolina estuaries and the impact of salinty structure. Am Fish Soc Symp 50:109-124

Ackerman JT, Kondratieff MC, Matern SA, Cech JJ (2000) Tidal influence on spatial dynamics of leopard sharks, *Triakis semifasciata*, in Tomales Bay, California. Environ Biol Fishes 58:33-43

Allison GW, Lubchenco J, Carr MH (1998) Marine reserves are necessary but not sufficient for marine conservation. Ecol Appl 8:79-92

Anderson SC, Cooper AB, Dulvy NK (2013) Ecological prophets: quantifying metapopulation portfolio effects. Methods Ecol Evol 4:971-981

Andrews KS, Harvey CJ (2013) Ecosystem-level consequences of movement: seasonal variation in the trophic impact of a top predator. Mar Ecol Prog Ser 473:247-260

Aubrey CW, Snelson FF (2007) Early life history of the spinner shark in a Florida nursery. Am Fish Soc Symp 50:175-189

Balston J (2009) Short-term climate variability and the commercial barramundi (*Lates calcarifer*) fishery of north-east Queensland, Australia. Mar Freshw Res 60:912-923

Barnett A, Semmens JM (2012) Sequential movement into coastal habitats and high spatial overlap of predator and prey suggest high predation pressure in protected areas. Oikos 121:882-890

Barnett A, Abrantes KG, Seymour J, Fitzpatrick R (2012) Residency and spatial use by reef sharks of an isolated seamount and its implications for conservation. PLoS ONE 7:e36574

Barrett NS, Edgar GJ, Buxton CD, Haddon M (2007) Changes in fish assemblages following 10 years of protection in Tasmanian marine protected areas. J Exp Mar Biol Ecol 345:141-157

Barton K (2013) *MuMIn*: multi-model inference. R package version 1.9.11. Available: http://CRAN.R-project.org/package=MuMIn. Accessed 27 August 2014

Bates D, Maechler M, Bolker B, Walker S (2014) *lme 4*: Linear mixed-effects models using Eigen and S4. R package version 1.1-7. Available: http://CRAN.R-project.org/package=lme4. Accessed 27 August 2014

Baum J, Clark S, Domingo A, Ducrocq M, Lamónaca AF, Gaibor N, Graham R, Jorgensen SJ, Kotas JE, Medina E, Martinez-Ortiz J, Monzini Taccone di Sitizona J, Morales MR, Navaro SS, Pérez JC, Ruiz C, Smith W, Valenti SV, Vooren CM (2007) *Sphyrna lewini*. In IUCN 2010, IUCN Red List of Threatened Species. Available: http://www.iucnredlist.org/. Accessed 12 November 2014

Beck MW, Heck KL, Able KW, Childers DL (2001) The identification, conservation and management of estuarine and marine nurseries for fish and invertebrates. Bioscience 51:633-641

Bernal D, Carlson JK, Goldman KJ, Lowe CG (2012) Energetics, metabolism, and endothermy in sharks and rays. In: Carrier JC, Musick JA, Heithaus MR (eds) Biology of sharks and their relatives, 2nd edition. CRC Press, Boca Raton, p 211-237

Bethea DM, Buckel JA, Carlson JK (2004) Foraging ecology of the early life stages of four sympatric shark species. Mar Ecol Prog Ser 268:245-264

Bethea DM, Ajemian MJ, Carlson JK, Hoffmayer E, Imhoff JL, Grubbs D, Peterson CT, Burgess GH (2014) Distribution and community structure of coastal sharks in the northeastern Gulf of Mexico. Environ Biol Fish 98:1233-1254

Blaber SJM, Blaber TG (1980) Factors affecting the distribution of juvenile estuarine and inshore fish. J Fish Biol 17:143-162

Blaber SJM, Brewer DT, Salini JP (1989) Species composition and biomasses of fishes in different habitats of a tropical northern Australian estuary: their occurrence in the adjoining sea and estuarine dependence. Estuar Coast Shelf Sci 29:509–531

Blaber SJM, Brewer DT, Salini JP (1995) Fish communities and the nursery role of the shallow inshore waters of a tropical bay in the Gulf of Carpentaria, Australia. Estuar Coast Shelf Sci 40:177-193

Block BA, Jonsen ID, Jorgensen SJ, Winship AJ, Shaffer SA, Bograd SJ, Hazen EL, Foley DG, Breed GA, Harrison AL, Ganong JE, Swithenbank A, Castleton M, Dewar H, Mate BR, Shillinger GL, Schaefer KM, Benson SR, Weise MJ, Henry RW, Costa DP (2011) Tracking apex marine predator movements in a dynamic ocean. Nature 475:86-90

Boatright C, Quinn T, Hilborn R (2004) Timing of adult migration and stock structure for sockeye salmon in Bear Lake, Alaska. Trans Am Fish Soc 133:911-921

Bonfil R (1999) Marine protected areas as a shark fisheries management tool. In: Seret B, Sire JY (eds) Proceedings of the 5th Indo-Pacific fish conference, Noumea 1997. Societe Francaise d’Ichtyologie and Istitut de Recherche pour le Developement, Paris, p 217-230

Branstetter S (1990) Early life-history implications of selected carcharhinoid and lamnoid sharks of the northwest Atlantic. NOAA Tech Rep NMFS 90:17-28

Bray JR, Curtis JT (1957) An ordination of the upland forest communities of Southern Wisconsin. Ecol Monogr 27:325-349

Breheny P, Burchett W (2013) *visreg*: visualization of regression models. R package version 2.0-4. Available: http://CRAN.R-project.org/package=visreg. Accessed 27 August 2014

Brown JS (1999) Vigilance, patch use and habitat selection: foraging under predation risk. Evol Ecol Res 1:49-71

Bureau of Resources and Energy Economics (BREE) (2012) Australian bulk commodity export and infrastructure: outlook to 2025. Australian Department of Resources, Energy and Tourism, Canberra

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information theoretic approach. Springer, New York

Bush A (2003) Diet and diel feeding periodicity of juvenile scalloped hammerhead sharks, *Sphyrna lewini*, in Kāne'ohe Bay, Ō'ahu, Hawai'i. Environ Biol Fishes 67:1-11

Bush A, Holland K (2002) Food limitation in a nursery area: estimates of daily ration in juvenile scalloped hammerheads, *Sphyrna lewini* (Griffith and Smith, 1834) in Kāne'ohe Bay, Ō'ahu, Hawai'i. J Exp Mar Biol Ecol 278:157-178

Carlson JK, Heupel MR, Bethea DM, Hollensead LD (2008) Coastal habitat use and residency of juvenile Atlantic sharpnose sharks (*Rhizoprionodon terraenovae*). Estuar Coasts 31:931-940

Carlson SM, Satterthwaite WH (2011) Weakened portfolio effect in a collapsed salmon population complex. Can J Fish Aquat Sci 68:1579-1589

Carrier JC, Pratt HL (1998) Habitat management and closure of a nurse shark breeding and nursery ground. Fish Res 39:209-213

Cass-Calay SL, Bahnick M (2002) Status of the yellowedge grouper fishery in the Gulf of Mexico: Assessment 1.0. Sustainable Fisheries Division Contribution SFD-02/03-172. Southeast Fisheries Science Center, Miami

Cass-Calay SL, Schmidt TW (2003) Standardized catch rates of juvenile goliath grouper, *Epinephelus itajara*, from the Everglades National Park Creel Survey, 1973–1999. Sustainable Fisheries Division Contribution SFD-2003-0016. Southeast Fisheries Science Center, Miami

Castro JI (1993) The shark nursery of Bulls Bay, South Carolina, with a review of the shark nurseries of the southeastern coast of the United States. Environ Biol Fishes 38:37-48

Castro JI (1996) Biology of the blacktip shark, *Carcharhinus limbatus*, off the southeastern United States. Bull Mar Sci 59:508-522

Chin A (2013) The biology and ecology of the blacktip reef shark *Carcharhinus melanopterus* (Quoy & Gaimard, 1824) and implications for management. PhD thesis, James Cook University, Townsville

Chin A, Kyne PM, Walker TI, McAuley RB (2010) An integrated risk assessment for climate change: analysing the vulnerability of sharks and rays on Australia's Great Barrier Reef. Glob Change Biol 16:1936-1953

Chin A, Tobin A, Simpfendorfer C, Heupel M (2012) Reef sharks and inshore habitats: patterns of occurrence and implications for vulnerability. Mar Ecol Prog Ser 460:115-125

Clark E (1963) The maintenance of sharks in captivity with a report on their instrumental conditioning. In: Gilbert GW (ed) Sharks and survival. D.C. Heath and Company, Boston, p 115-149

Clarke KR (1993) Nonparametric multivariate analyses of changes in community structure. Aust J Ecol 18:117-143

Clarke KR, Green RH (1988) Statistical design and analysis for a biological effects study. Mar Ecol Prog Ser 46:213-226

Clarke KR, Warwick RM (2001) Change in marine communities: an approach to statistical analysis and interpretation. PRIMER-E, Plymouth

Clarke KR, Gorley RN (2006) PRIMER v6: user manual/tutorial. PRIMER-E, Plymouth

Clarke TA (1971) The ecology of the scalloped hammerhead shark, *Sphyrna lewini*, in Hawaii. Pac Sci 25:133-144

Claudet J, Osenberg CW, Domenici O, Badalamenti F, Milazzo M, Falcón JM, Bertocci I, Benedetti-cecchi L, García-Charton J-A, Goṅi R, Borg JA, Forcada A, de Lucia GA, Perez-Ruzafa Á, Afonso R, Brito A, Guala I, Le Diréach L, Sanchez-Jerez. P, Somerfield PJ, Planes S (2010) Marine reserves: fish life history and ecological traits matter. Ecol Appl 20:830-839

Cole J, McGlade J (1998) Clupeoid population variability, the environment and satellite imagery in coastal upwelling systems. Rev Fish Biol Fish 8:445-471

Colloca F, Bartolino V, Lasinio GJ, Maiorano L, Sartor P, Ardizzone G (2009) Identifying fish nurseries using density and persistence measures. Mar Ecol Prog Ser 381:287-296

Compagno LJV (1984) Sharks of the world: an annotated and illustrated catalogue of shark species known to date. Parts 1 and 2. FAO Fish Synop 4:1-655

Conrath CL, Musick JA (2010) Residency, space use and movement patterns of juvenile sandbar sharks (*Carcharhinus plumbeus*) within a Virginia summer nursery area. Mar Freshw Res 61:223-235

Conrath CL, Musick JA (2012) Reproductive biology of elasmobranchs. In: Carrier JC, Musick JA, Heithaus MR (eds) Biology of sharks and their relatives, 2nd edition. CRC Press, Boca Raton, p 291-311

Cortés E (2000) Life history patterns and correlations in sharks. Rev Fish Sci 8:299-344

Cortés E (2002) Incorporating uncertainty into demographic modeling: application to shark populations and their conservation. Conserv Biol 16:1048-1062

Cortés E (2004) Life history patterns, demography, and population dynamics. In: Carrier JC, Musick JA, Heithaus MR (eds) Biology of sharks and their relatives. CRC Press, Florida, p 449-470

Cortés E, Gruber SH (1990) Diet, feeding habits and estimates of daily ration of young lemon sharks, *Negaprion brevirostris* (Poey). Copeia 1990:204-218

Coutant CC (1985) Striped bass, temperature, and dissolved oxygen: a speculative hypothesis for environmental risk. Trans Am Fish Soc 114:31-61

Cui G, Wardle CS, Glass CW, Johnstone ADF, Mojsiewicz WR (1991) Light level thresholds for visual reaction of mackerel, *Scomber scombrus* L., to colored monofilament nylon gillnet materials. Fish Res 10:255-263

Curtis TH, Adams DH, Burgess GH (2011) Seasonal distribution and habitat associations of bull sharks in the Indian River Lagoon, Florida: a 30-year synthesis. Trans Am Fish Soc 140:1213-1226

Curtis TH, Parkyn DC, Burgess GH (2013) Use of human-altered habitats by bull sharks in a Florida nursery area. Mar Coast Fish 5:28-38 da Silva C, Kerwath SE, Attwood CG, Thorstad EB, Cowley PD, Okland F, Wilke CG, Naesje TF (2013) Quantifying the degree of protection afforded by a no-take marine reserve on an exploited shark. Afr J Mar Sci 35:57-66

Dahlgren CP, Kellison GT, Adams AJ, Gillanders BM, Kendall MS, Layman CA, Ley JA, Nagelkerken I, Serafy JE (2006) Marine nurseries and effective juvenile habitats: concepts and applications. Mar Ecol Prog Ser 312:291-295

Dale JJ, Wallsgrove NJ, Popp BN, Holland KN (2011) Nursery habitat use and foraging ecology of the brown stingray *Dasyatis lata* determined from stomach contents, bulk and amino acid stable isotopes. Mar Ecol Prog Ser 433:221-236

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

De Faria F (2012) Recreational fishing of sharks in the Great Barrier Reef World Heritage Area: species composition and incidential capture stress. MSc thesis, James Cook University, Townsville

DeAngelis BM, McCandless CT, Kohler NE, Recksiek CW, Skomal GB (2008) First characterization of shark nursery habitat in the United States Virgin Islands: evidence of habitat partitioning by two shark species. Mar Ecol Prog Ser 358:257-271

Deutsch CA, Tewksbury JJ, Huey RB, Sheldon KS, Ghalambor CK, Haak DC, Martin PR (2008) Impacts of climate warming on terrestrial ectotherms across latitude. Proc Natl Acad Sci USA 105:6668-6672

DiBattista JD, Feldheim KA, Gruber SH, Hendry AP (2007) When bigger is not better: selection against large size, high condition and fast growth in juvenile lemon sharks. J Evol Biol 20:201-212

DiBattista JD, Feldheim KA, Thibert-Plante X, Gruber SH, Hendry AP (2008) A genetic assessment of polyandry and breeding-site fidelity in lemon sharks. Mol Ecol 17:3337-3351

Doctor KK, Hilborn R, Rowse M, Quinn T (2010) Spatial and temporal patterns of upriver migration by sockeye salmon populations in the Wood River system, Bristol Bay, Alaska. Trans Am Fish Soc 139:80-91

Drymon JM, Ajemian MJ, Powers SP (2014) Distribution and dynamic habitat use of young bull sharks *Carcharhinus leucas* in a highly stratified northern Gulf of Mexico estuary. PLoS ONE 9:e97124

Drymon JM, Carassou L, Powers SP, Grace M, Dindo J, Dzwonkowski B (2013) Multiscale analysis of factors that affect the distribution of sharks throughout the northern Gulf of Mexico. Fish Bull 111:370-380

Dudley SFJ, Simpfendorfer CA (2006) Population status of 14 shark species caught in the protective gillnets off KwaZulu-Natal beaches, South Africa, 1978-2003. Mar Freshw Res 57:225-240

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

Duncan KM, Holland KN (2006) Habitat use, growth rates and dispersal patterns of juvenile scalloped hammerhead sharks *Sphyrna lewini* in a nursery habitat. Mar Ecol Prog Ser 312:211-221

Edgar GJ, Bustamante RH, Fariṅa JM, Calvopiṅa M, Martínez C, Toral-Granda MV (2004) Bias in evaluating the effects of marine protected areas: the importance of baseline data for the Galapagos Marine Reserve. Environ Conserv 31:212-218

Elston DA, Moss R, Boulinier T, Arrowsmith C, Lambin X (2001) Analysis of aggregation, a worked example: numbers of ticks on red grouse chicks. Parasitol Int 122:563–569

Engen S, Lande R, Sæther BE (2002) The spatial scale of population fluctuations and quasi-extinction risk. Am Nat 160:439-451

Espinoza M, Farrugia TJ, Lowe CG (2011) Habitat use, movements and site fidelity of the gray smooth-hound shark (*Mustelus californicus* Gill 1863) in a newly restored southern California estuary. J Exp Mar Biol Ecol 401:63-74

Espinoza M, Cappo M, Heupel MR, Tobin AJ, Simpfendorfer CA (2014) Quantifying shark distribution patterns and species-habitat associations: implications of marine park zoning. PLoS ONE 9:e106885

Farrugia TJ, Espinoza M, Lowe CG (2011) Abundance, habitat use and movement patterns of the shovelnose guitarfish (*Rhinobatos productus*) in a restored southern California estuary. Mar Freshw Res 62:648-657

Feldheim KA, Gruber SH, Ashley MV (2004) Reconstruction of parental microsatellite genotypes reveals female polyandry and philopatry in the lemon shark, *Negaprion brevirostris*. Evolution 58:2332-2342

Fernandes L, Day J, Lewis A, Slegers S, Kerrigan B, Breen D, Cameron D, Jago B, Hall J, Lowe D, Innes J, Tanzer J, Chadwick V, Thompson L, Gorman K, Simmons M, Barnett B, Sampson K, De'ath G, Mapstone B, Marsh H, Possingham H, Ball I, Ward T, Dobbs K, Aumend J, Slater D, Stapleton K (2005) Establishing representative no-take areas in the Great Barrier Reef: large-scale implementation of theory on marine protected areas. Conserv Biol 19:1733-1744

Ferretti F, Osio GC, Jenkins CJ, Rosenberg AA, Lotze HK (2013) Long-term change in a meso-predator community in response to prolonged and heterogeneous human impact. Sci Rep 3. doi: 10.1038/srep01057

Figge F (2004) Bio-folio: applying portfolio theory to biodiversity. Biodivers Conserv 13:827-849

Finlayson BL, McMahon TA (1988) Australia *v.* the World: a comparative analysis of streamflow characteristics. Academic Press, Sydney

Firth D (1993) Bias reduction of maximum-likelihood-estimates. Biometrika 80:27-38

Flaherty KE, Landsberg JH (2011) Effects of a persistent red tide (*Karenia brevis*) bloom on community structure and species-specific relative abundance of nekton in a Gulf of Mexico estuary. Estuar Coasts 34:417-439

Fodrie FJ, Levin LA (2008) Linking juvenile habitat utilization to population dynamics of California halibut. Limnol Oceanogr 53:799-812

Fox F, Weisberg S (2011) *car*: an R companion to applied regression, 2nd edition. R package. Available: http://socserv.socsci.mcmaster.ca/jfox/Books/Companion. Accessed 27 August 2014

Fox J (2013) Effect displays in R for generalised linear models. Journal of Statistical Software 8:1-27

Francis MP (2013) Temporal and spatial patterns of habitat use by juveniles of a small coastal shark (*Mustelus lenticulatus*) in an estuarine nursery. PLoS ONE 8:e57021

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

Froeschke J, Stunz GW, Wildhaber ML (2010a) Environmental influences on the occurrence of coastal sharks in estuarine waters. Mar Ecol Prog Ser 407:279-292

Froeschke J, Stunz GW, Sterba-Boatwright B, Wildhaber ML (2010b) An empirical test of the 'shark nursery area concept' in Texas bays using a long-term fisheries-independent data set. Aquat Biol 11:65-76

Froeschke JT, Froeschke BF, Stinson CM (2013) Long-term trends of bull shark (*Carcharhinus leucas*) in estuarine waters of Texas, USA. Can J Fish Aquat Sci 70:13-21

Furnas M (1993) Catchments and corals: terrestrial runoff to the Great Barrier Reef. Australian Institute of Marine Science, Townsville

Gardiner JM, Hueter RE, Maruska KP, Sisneros JA, Casper BM, Mann DA, Demski LS (2012) Sensory physiology and behavior in elasmobranchs. In: Carrier JC, Musick JA, Heithaus MR (eds) Biology of sharks and their relatives, 2nd edition. CRC Press, Boca Raton, p 349-402

Garla RC, Chapman DD, Wetherbee BM, Shivji M (2006a) Movement patterns of young Caribbean reef sharks, *Carcharhinus perezi*, at Fernando de Noronha Archipelago, Brazil: the potential of marine protected areas for conservation of a nursery ground. Mar Biol 149:189-199

Garla RC, Chapman DD, Shivji MS, Wetherbee BM, Amorim AF (2006b) Habitat of juvenile Caribbean reef sharks, *Carcharhinus perezi*, at two oceanic insular marine protected areas in the southwestern Atlantic Ocean: Fernando de Noronha Archipelago and Atol das Rocas, Brazil. Fish Res 81:236-241

Garofalo G, Fortibuoni T, Gristina M, Sinopoli M, Fiorentino F (2011) Persistence and co-occurrence of demersal nurseries in the Strait of Sicily (central Mediterranean): implications for fishery management. J Sea Res 66:29-38

Gedamke T, Hoenig JM, Musick JA, DuPaul WD, Gruber SH (2007) Using demographic models to determine intrinsic rate of increase and sustainable fishing for elasmobranchs: pitfalls, advances, and applications. N Am J Fish Manage 27:605-618

Gelsleichter J, Manire CA, Szabo NJ, Cortés E, Carlson J, Lombardi-Carlson L (2005) Organochlorine concentrations in bonnethead sharks (*Sphyrna tiburo*) from four Florida estuaries. Arch Environ Contam Toxicol 48:474-483

Gillanders BM, Elsdon TS, Halliday IA, Jenkins GP, Robins JB, Valesini FJ (2011) Potential effects of climate change on Australian estuaries and fish utilising estuaries: a review. Mar Freshw Res 62:1115-1131

Giraudoux P (2013) *pgirmess*: data analysis in ecology. R package version 1.5.8. Available: http://CRAN.R-project.org/package=pgirmess. Accessed 27 August 2014

Gotceitas V, Colgan P (1989) Predator foraging success and habitat complexity: quantitative test of the threshold hypothesis. Oecologia 80:158-166

Graham KJ, Andrew NL, Hodgson KE (2001) Changes in relative abundance of sharks and rays on Australian South East Fishery trawl grounds after twenty years of fishing. Mar Freshw Res 52:549-561

Great Barrier Reef Marine Park Authority (GBRMPA) (2011) Extreme weather and the Great Barrier Reef. Great Barrier Reef Marine Park Authority, Townsville

Grech A, Coles RG (2010) An ecosystem-scale predictive model of coastal seagrass distribution. Aquat Conserv-Mar Freshw Ecosyst 20:437-444

Grech A, Bos M, Brodie J, Coles R, Dale A, Gilbert R, Hamann M, Marsh H, Neil K, Pressey RL, Rasheed MA, Sheaves M, Smith A (2013) Guiding principles for the improved governance of port and shipping impacts in the Great Barrier Reef. Mar Pollut Bull 75:8-20

Greene CM, Hall JE, Guilbault KR, Quinn TP (2010) Improved viability of populations with diverse life-history portfolios. Biol Lett 6:382-386

Grubbs RD, Musick JA (2007) Spatial delineation of summer nursery areas for juvenile sandbar sharks in Chesapeake Bay, Virginia. Am Fish Soc Symp 50:63-86

Grubbs RD, Musick JA, Conrath CL, Romine JG (2007) Long-term movements, migration, and temporal delineation of a summer nursery for juvenile sandbar sharks in the Chesapeake Bay region. Am Fish Soc Symp 50:87-108

Gruber SH, Myrberg AA (1977) Approaches to the study of the behavior of sharks. Am Zool 17:471-486

Gruber SH, Nelson DR, Morrissey JF (1988) Patterns of activity and space utilization of lemon sharks, *Negaprion brevirostris*, in a shallow Bahamian lagoon. Bull Mar Sci 43:61-76

Gruber SH, de Marignac JRC, Hoenig JM (2001) Survival of juvenile lemon sharks at Bimini, Bahamas, estimated by mark-depletion experiments. Trans Am Fish Soc 130:376-384

Gruss A, Kaplan DM, Guenette S, Roberts CM, Botsford LW (2011) Consequences of adult and juvenile movement for marine protected areas. Biol Conserv 144:692-702

Gutteridge AN (2011) Community structure and biology of the elasmobranchs of Hervey Bay, southeast Queensland, Australia. PhD thesis, University of Queensland, Brisbane

Gutteridge AN, Bennett MB, Huveneers C, Tibbetts IR (2011) Assessing the overlap between the diet of a coastal shark and the surrounding prey communities in a sub-tropical embayment. J Fish Biol 78:1405-1422

Gutteridge AN, Huveneers C, Marshall LJ, Tibbetts IR, Bennett MB (2013) Life-history traits of a small-bodied coastal shark. Mar Freshw Res 64:54-65

Guttridge TL, van Dijk S, Stamhuis EJ, Krause J, Gruber SH, Brown C (2013) Social learning in juvenile lemon sharks, *Negaprion brevirostris*. Anim Cogn 16:55-64

Guttridge TL, Gruber SH, Franks BR, Kessel ST, Gledhill KS, Uphill J, Krause J, Sims DW (2012) Deep danger: intra-specific predation risk influences habitat use and aggregation formation of juvenile lemon sharks *Negaprion brevirostris*. Mar Ecol Prog Ser 445:279-291

Harry AV (2011) Life histories of commercially important tropical sharks from the Great Barrier Reef World Heritage Area. PhD thesis, James Cook University, Townsville

Harry AV, Simpfendorfer CA, Tobin A (2010) Improving age, growth, and maturity estimates for aseasonally reproducing chondrichthyans. Fish Res 106:393-403

Harry AV, Tobin AJ, Simpfendorfer CA (2013) Age, growth and reproductive biology of the spot-tail shark, *Carcharhinus sorrah*, and the Australian blacktip shark, *C. tilstoni*, from the Great Barrier Reef World Heritage Area, north-eastern Australia. Mar Freshw Res 64:277-293

Harry AV, Macbeth WG, Gutteridge AN, Simpfendorfer CA (2011a) The life histories of endangered hammerhead sharks (Carcharhiniformes, Sphyrnidae) from the east coast of Australia. J Fish Biol 78:2026-2051

Harry AV, Morgan JAT, Ovenden JR, Tobin AJ, Welch DJ, Simpfendorfer CA (2012) Comparison of the reproductive ecology of two sympatric blacktip sharks

(*Carcharhinus limbatus* and *Carcharhinus tilstoni*) off north-eastern Australia with species identification inferred from vertebral counts. J Fish Biol 81:1225-1233

Harry AV, Tobin AJ, Simpfendorfer CA, Welch DJ, Mapleston A, White J, Williams AJ, Stapley J (2011b) Evaluating catch and mitigating risk in a multispecies, tropical, inshore shark fishery within the Great Barrier Reef World Heritage Area. Mar Freshw Res 62:710–721

Hazin F, Fischer A, Broadhurst M (2001) Aspects of reproductive biology of the scalloped hammerhead shark, *Sphyrna lewini*, off northeastern Brazil. Environ Biol Fishes 61:151-159

Heino M, Kaitala V, Ranta E, Lindström J (1997) Synchronous dynamics and rates of extinction in spatially structured populations. P Roy Soc Lond B Bio 264:481-486

Heinze G, Ploner M, Dunkler D, Southworth H (2013) *logistf*: Firth's bias reduced logistic regression. R package version 1.21. Available: http://CRAN.R-project.org/package=logistf. Accessed 27 August 2014

Heithaus MR (2004) Predator-prey interactions. In: Carrier JC, Musick JA, Heithaus MR (eds) Biology of the sharks and their relatives. CRC Press, Boca Raton, p 487-521

Heithaus MR (2007) Nursery areas as essential shark habitats: a theoretical perspective. Am Fish Soc Symp 50:3-13

Heithaus MR, Delius BK, Wirsing AJ, Dunphy-Daly MM (2009) Physical factors influencing the distribution of a top predator in a subtropical oligotrophic estuary. Limnol Oceanogr 54:472-482

Heupel MR (2007) Exiting Terra Ceia Bay: an examination of cues stimulating migration from a summer nursery area. Am Fish Soc Symp 50:265-280

Heupel MR, Hueter RE (2002) Importance of prey density in relation to the movement patterns of juvenile blacktip sharks (*Carcharhinus limbatus*) within a coastal nursery area. Mar Freshw Res 53:543-550

Heupel MR, Simpfendorfer CA (2005a) Using acoustic monitoring to evaluate MPAs for shark nursery areas: The importance of long-term data. Mar Technol Soc J 39:10-18

Heupel MR, Simpfendorfer CA (2005b) Quantitative analysis of aggregation behavior in juvenile blacktip sharks. Mar Biol 147:1239-1249

Heupel MR, Simpfendorfer CA (2008) Movement and distribution of young bull sharks *Carcharhinus leucas* in a variable estuarine environment. Aquat Biol 1:277-289

Heupel MR, Simpfendorfer CA (2011) Estuarine nursery areas provide a low-mortality environment for young bull sharks *Carcharhinus leucas*. Mar Ecol Prog Ser 433:237-244

Heupel MR, Simpfendorfer CA (2013) Importance of environmental and biological drivers in the presence and space use of a reef-associated shark. Mar Ecol Prog Ser 496:47-57

Heupel MR, Simpfendorfer CA, Hueter RE (2004) Estimation of shark home ranges using passive monitoring techniques. Environ Biol Fishes 71:135-142

Heupel MR, Carlson JK, Simpfendorfer CA (2007) Shark nursery areas: concepts, definition, characterization and assumptions. Mar Ecol Prog Ser 337:287-297

Heupel MR, Simpfendorfer CA, Collins AB, Tyminski JP (2006) Residency and movement patterns of bonnethead sharks, *Sphyrna tiburo*, in a large Florida estuary. Environ Biol Fishes 76:47-67

Heupel MR, Williams AJ, Welch DJ, Ballagh A, Mapstone BD, Carlos G, Davies C, Simpfendorfer CA (2009) Effects of fishing on tropical reef associated shark populations on the Great Barrier Reef. Fish Res 95:350-361

Hilborn R, Quinn TP, Schindler DE, Rogers DE (2003) Biocomplexity and fisheries sustainability. Proc Natl Acad Sci USA 100:6564-6568

Hoffmayer ER, Parsons GR, Horton J (2006) Seasonal and interannual variation in the energetic condition of adult male Atlantic sharpnose shark *Rhizoprionodon terraenovae* in the northern Gulf of Mexico. J Fish Biol 68:645-653

Holland KN, Wetherbee BM, Peterson JD, Lowe CG (1993) Movements and distribution of hammerhead shark pups on their natal grounds. Copeia 1993:495-502

Holmes BJ, Sumpton WD, Mayer DG, Tibbetts IR, Neil DT, Bennett MB (2012) Declining trends in annual catch rates of the tiger shark (*Galeocerdo cuvier*) in Queensland, Australia. Fish Res 129:38-45

Hothorn T, Bretz F, Westfall P (2008) Simultaneous inference in general parametric models. Biom J 50:346-363

Hueter RE, Heupel MR, Heist KJ, Kneey DB (2004) Evidence of philopatry in sharks and implications for the management of shark fisheries. J Northwest Atl Fish Sci 35:239-247

Hunter E, Berry F, Buckley AA, Stewart C, Metcalfe JD (2006) Seasonal migration of thornback rays and implications for closure management. J Appl Ecol 43:710-720

Hussey NE, McCarthy ID, Dudley SFJ, Mann BQ (2009) Nursery grounds, movement patterns and growth rates of dusky sharks, *Carcharhinus obscurus*: a long-term tag and release study in South African waters. Mar Freshw Res 60:571-583

Ives AR, Dennis B, Cottingham KL, Carpenter SR (2003) Estimating community stability and ecological interactions from time-series data. Ecol Monogr 73:301-330

Jacoby DMP, Croft DP, Sims DW (2012) Social behaviour in sharks and rays: analysis, patterns and implications for conservation. Fish Fish 13:399-417

Jennings DE, Gruber SH, Franks BR, Kessel ST, Robertson AL (2008) Effects of large-scale anthropogenic development on juvenile lemon shark (*Negaprion brevirostris*) populations of Bimini, Bahamas. Environ Biol Fishes 83:369-377

Jennings S, Kaiser MJ (1998) The effects of fishing on marine ecosystems. Adv Mar Biol 34:201-352

Jirik KE, Lowe CG (2012) An elasmobranch maternity ward: female round stingrays *Urobatis halleri* use warm, restored estuarine habitat during gestation. J Fish Biol 80:1227-1245

Johnson DR, Funicelli NA, Bohnsack JA (1999) Effectiveness of an existing no-take fish sanctuary within the Kennedy Space Center, Florida. N Am J Fish Manag 19:436-453

Jones PJS (2001) Marine protected area strategies: issues, divergences and the search for middle ground. Rev Fish Biol Fish 11:197-216

Keeney DB, Heupel MR, Hueter RE, Heist EJ (2005) Microsatellite and mitochondrial DNA analyses of the genetic structure of blacktip shark (*Carcharhinus limbatus*) nurseries in the northwestern Atlantic, Gulf of Mexico, and Caribbean Sea. Mol Ecol 14:1911-1923

Kimirei IA, Nagelkerken I, Griffioen B, Wagner C, Mgaya YD (2011) Ontogenetic habitat use by mangrove/seagrass-associated coral reef fishes shows flexibility in time and space. Estuar Coast Shelf Sci 92:47-58

Kinney MJ (2011) The communal nursery area paradigm revisited: niche overlap versus niche separation among juvenile shark species of Cleveland Bay. PhD thesis, James Cook Univeristy, Townsville

Kinney MJ, Simpfendorfer CA (2009) Reassessing the value of nursery areas to shark conservation and management. Conserv Lett 2:53-60

Kinney MJ, Hussey NE, Fisk AT, Tobin AJ, Simpfendorfer CA (2011) Communal or competitive? Stable isotope analysis provides evidence of resource partitioning within a communal shark nursery. Mar Ecol Prog Ser 439:263-276

Kneebone J, Chisholm J, Skomal GB (2012) Seasonal residency, habitat use, and site fidelity of juvenile sand tiger sharks *Carcharias taurus* in a Massachusetts estuary. Mar Ecol Prog Ser 471:165-181

Knip DM (2011) Spatial ecology of mobile predators in a nearshore tropical environment and its implications for marine protected areas. PhD thesis, James Cook University, Townsville

Knip DM, Heupel MR, Simpfendorfer CA (2010) Sharks in nearshore environments: models, importance, and consequences. Mar Ecol Prog Ser 402:1-11

Knip DM, Heupel MR, Simpfendorfer CA (2012a) Evaluating marine protected areas for the conservation of tropical coastal sharks. Biol Conserv 148:200-209

Knip DM, Heupel MR, Simpfendorfer CA (2012b) Habitat use and spatial segregation of adult spottail sharks *Carcharhinus sorrah* in tropical nearshore waters. J Fish Biol 2012:1-18

Knip DM, Heupel MR, Simpfendorfer CA (2012c) To roam or to home: site fidelity in a tropical coastal shark. Mar Biol 159:1647-1657

Knip DM, Heupel MR, Simpfendorfer CA (2012d) Mortality rates for two shark species occupying a shared coastal environment. Fish Res 125:184-189

Knip DM, Heupel MR, Simpfendorfer CA, Tobin AJ, Moloney J (2011a) Wet-season effects on the distribution of juvenile pigeye sharks, *Carcharhinus amboinensis*, in tropical nearshore waters. Mar Freshw Res 62:658-667

Knip DM, Heupel MR, Simpfendorfer CA, Tobin A, Moloney J (2011b) Ontogenetic shifts in movement and habitat use of juvenile pigeye sharks *Carcharhinus amboinensis* in a tropical nearshore region. Mar Ecol Prog Ser 425:233-246

Koehn JD, Hobday AJ, Pratchett MS, Gillanders BM (2011) Climate change and Australian marine and freshwater environments, fishes and fisheries: synthesis and options for adaptation. Mar Freshw Res 62:1148-1164

Last PR, Stevens JD (2009) Sharks and rays of Australia. CSIRO Publishing, Melbourne

Layman CA, Dahlgren CP, Kellison T, Adams AJ, Gillanders BM, Kendall MS, Ley JA, Nagelkerken I, Serafy JE (2006) Marine nurseries and effective juvenile habitats. Mar Ecol Prog Ser 318:307-308

Le Port A, Lavery S, Montgomery JC (2012) Conservation of coastal stingrays: seasonal abundance and population structure of the short-tailed stingray *Dasyatis brevicaudata* at a marine protected area. ICES J Mar Sci 69:1427-1435

Ley JA, Halliday IA, Tobin AJ, Garrett RN, Gribble NA (2002) Ecosystem effects of fishing closures in mangrove estuaries of tropical Australia. Mar Ecol Prog Ser 245:223-238

Loftus WF (2000) Inventory of fishes of Everglades National Park. Fla Sci 63:27-47

Lowe CG (2002) Bioenergetics of free-ranging juvenile scalloped hammerhead sharks (*Sphyrna lewini*) in Kāne'ohe Bay, Ō'ahu, HI. J Exp Mar Biol Ecol 278:141-156

Lowe CG, Wetherbee BM, Crow GL, Tester AL (1996) Ontogenetic dietary shifts and feeding behavior of the tiger shark, *Galeocerdo cuvier*, in Hawaiian waters. Environ Biol Fishes 47:203-211

Luck GW, Daily GC, Ehrlich PR (2003) Population diversity and ecosystem services. Trends Ecol Evol 18:331-336

Lynch AMJ, Sutton SG, Simpfendorfer CA (2010) Implications of recreational fishing for elasmobranch conservation in the Great Barrier Reef Marine Park. Aquat Conserv-Mar Freshw Ecosyst 20:312-318

Mariani S, Boggan C, Balata D (2011) Food resource use in sympatric juvenile plaice and flounder in estuarine habitats. Mar Ecol-Evol Persp 32:96-101

Matich P, Heithaus MR (2012) Effects of an extreme temperature event on the behavior and age structure of an estuarine top predator, *Carcharhinus leucas*. Mar Ecol Prog Ser 447:165-178

Matich P, Heithaus MR (2014) Multi-tissue stable isotope analysis and acoustic telemetry reveal seasonal variability in the trophic interactions of juvenile bull sharks in a coastal estuary. J Anim Ecol 83:199-213

Mayr E (1963) Animal species and evolution. Belknap Press, Cambridge

McAuley RB, Simpfendorfer CA, Hyndes GA, Lenanton RCJ (2007) Distribution and reproductive biology of the sandbar shark, *Carcharhinus plumbeus* (Nardo), in Western Australian waters. Mar Freshw Res 58:116-126

McCallister M, Ford R, Gelsleichter J (2014) Abundance and distribution of sharks in northeast Florida waters and identification of potential nursery habitat. Mar Coast Fish 5:200-210

McCandless CT, Pratt HL, Kohler NE (eds) (2002) Shark nursery grounds of the Gulf of Mexico and the east coast waters of the United States: an overview. An internal report to NOAA's Highly Migratory Species Office. NOAA Fisheries, Narragansett

McCandless CT, Kohler NE, Pratt HL, editors (eds) (2007a) Shark nursery grounds of the Gulf of Mexico and the east coast waters of the United States, Symposium 50. American Fisheries Society, Bethesda

McCandless CT, Pratt HL, Kohler NE, Merson RR, Recksiek CW (2007b) Distribution, localized abundance, movements, and migrations of juvenile sandbar sharks tagged in Delaware Bay. Am Fish Soc Symp 50:45-62

McCook LJ, Ayling T, Cappo M, Choat JH, Evans RD, De Freitas DM, Heupel M, Hughes TP, Jones GP, Mapstone B, Marsh H, Mills M, Molloy FJ, Pitcher CR, Pressey RL, Russ GR, Sutton S, Sweatman H, Tobin R, Wachenfeld DR, Williamson DH (2010) Adaptive management of the Great Barrier Reef: a globally significant demonstration of the benefits of networks of marine reserves. Proc Natl Acad Sci USA 107:18278-18285

McElroy WD, Wetherbee BM, Mostello CS, Lowe CG, Crow GL, Wass RC (2006) Food habits and ontogenetic changes in the diet of the sandbar shark, *Carcharhinus plumbeus*, in Hawaii. Environ Biol Fishes 76:81-92

McKenzie L, Collier C, Waycott M (2012) Reef rescue marine monitoring program: inshore seagrass, annual report for the sampling period 1st July 2010–31st May 2011. Fisheries Queensland, Cairns

Meynecke J, Lee SY, Duke N, Warnken J (2007) Relationships between estuarine habitats and coastal fisheries in Queensland, Australia. Bull Mar Sci 2007:773-793

Monaco ME, Friedlander AM, Caldow C, Christensen JD, Rogers C, Beets J, Miller J, Boulon R (2007) Characterising reef fish populations and habitats within and outside the US Virgin Islands Coral Reef National Monument: a lesson in marine protected area design. Fish Manag Ecol 14:33-40

Moore JW, McClure M, Rogers LA, Schindler DE (2010) Synchronization and portfolio performance of threatened salmon. Conserv Lett 3:340-348

Morgan MJ, Godin JGJ (1985) Antipredator benefits of schooling behavior in a Cyprinodontid fish, the banded killifish (*Fundulus diaphanus*). Z Tierpsychol 70:236-246

Morrissey JF, Gruber SH (1993a) Home range of juvenile lemon sharks, *Negaprion brevirostris.* Copeia 1993:425-434

Morrissey JF, Gruber SH (1993b) Habitat selection by juvenile lemon sharks, *Negaprion brevirostris*. Environ Biol Fishes 38:311-319

Munday PL, Jones GP, Pratchett MS, Williams AJ (2008) Climate change and the future for coral reef fishes. Fish Fish 9:261-285

Munroe SEM (2014) Habitat and dietary selectivity of nearshore shark populations. PhD thesis, James Cook University, Townsville

Munroe SEM, Simpfendorfer CA, Heupel MR (2014) Habitat and space use of an abundant nearshore shark, *Rhizoprionodon taylori*. Mar Freshw Res 65:959–968

Musick JA, Colvocoresses JA, Foell EJ (1985) Seaonality and the distribution, availiability and composition of fish assemblages in Chesapeake Bight. In: Yanez-Arancibia A (ed) Fish community ecology in estuaries and coastal lagoons: towards an ecosystem integration. Universidad Nacional Autónoma de México (UNAM) Press, Mexico, p 451-474

Nam DH, Adams DH, Flewelling LJ, Basu N (2010) Neurochemical alterations in lemon shark (*Negaprion brevirostris*) brains in association with brevetoxin exposure. Aquat Toxicol 99:351-359

National Marine Fisheries Service (NMFS) (2009) Recovery plan for smalltooth sawfish (*Pristis pectinata*). Prepared by the Smalltooth Sawfish Recovery Team for the National Marine Fisheries Service, Maryland.

Oliver T, Roy DB, Hill JK, Brereton T, Thomas CD (2010) Heterogeneous landscapes promote population stability. Ecol Lett 13:473-484

Olsen AM (1954) The biology, migration and growth rate of the school shark, *Galeorhinus australia* (Macleay) (Carcharhanidae) in the southeastern Australian waters. Mar Freshw Res 5:353-410

Ortega LA, Heupel MR, Van Beynen P, Motta PJ (2009) Movement patterns and water quality preferences of juvenile bull sharks (*Carcharhinus leucas*) in a Florida estuary. Environ Biol Fishes 84:361-373

Ovenden JR, Morgan JAT, Street R, Tobin A, Simpfendorfer C, Macbeth W, Welch D (2011) Negligible evidence for regional genetic population structure for two shark species *Rhizoprionodon acutus* (Ruppell, 1837) and *Sphyrna lewini* (Griffith & Smith, 1834) with contrasting biology. Mar Biol 158:1497-1509

Pang PKT, Griffith RW, Atz JW (1977) Osmoregulation in elasmobranchs. Am Zool 17:365-377

Papastamatiou YP, Lowe CG, Caselle JE, Friedlander AM (2009) Scale-dependent effects of habitat on movements and path structure of reef sharks at a predator-dominated atoll. Ecology 90:996-1008

Parsons GR, Hoffmayer ER (2005) Seasonal changes in the distribution and relative abundance of the Atlantic sharpnose shark *Rhizoprionodon terraenovae* in the north central Gulf of Mexico. Copeia 4:914-920

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

Queensland Department of Employment, Economic Development and Innovation (DEEDI) (2011) Plan for assessment of Queensland east coast shark resources 2009–14. Available: http://www.environment.gov.au/system/files/pages/0537f425-aec1-49d7-bebb-2b40f6288ef0/files/plan-2009-14.pdf. Accessed 30 October 2014

R Development Core Team (2014) R: a language and environment for statistical computing. Vienna: R Foundation for Statistical Computing. Available: http://www.R-project.org/. Accessed 27 August 2014

Rago PJ (2005) Fishery-independent sampling: survey techniques and data analyses. In: Musick JA, Bonfil R (eds) Management techniques for elasmobranch fisheries, FAO Fisheries Technical Paper Vol 474. FAO, Rome, p 265-286

Rechisky EL, Wetherbee BM (2003) Short-term movements of juvenile and neonate sandbar sharks, *Carcharhinus plumbeus*, on their nursery grounds in Delaware Bay. Environ Biol Fishes 68:113-128

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

Roberts C (2000) Selecting marine reserve locations: optimality versus opportunism. Bull Mar Sci 66:581-592

Robertson AI, Duke NC (1987) Mangroves as nursery sites: comparisons of the abundance and species composition of fish and crustaceans in mangroves and other nearshore habitats in tropical Australia. Mar Biol 96:193-205

Rojas YET, Osuna FP, Herrera AH, Magaña FG, García SA, Ortíz HV, Sampson L (2014) Feeding grounds of juvenile scalloped hammerhead sharks (*Sphyrna lewini*) in the south-eastern Gulf of California. Hydrobiologia 726:81-94

Russ GR, Cheal AJ, Dolman AM, Emslie MJ, Evans RD, Miller I, Sweatman H, Williamson DH (2008) Rapid increase in fish numbers follows creation of World's largest marine reserve network. Curr Biol 18:R514-R515

Ryer CH, Laurel BJ, Stoner AW (2010) Testing the shallow water refuge hypothesis in flatfish nurseries. Mar Ecol Prog Ser 415:275-282

Sala E, Ballesteros E, Starr RM (2001) Rapid decline of Nassau grouper spawning aggregations in Belize: fishery management and conservation needs. Fisheries 26:23-30

Schindler DE, Hilborn R, Chasco B, Boatright CP, Quinn TP, Rogers LA, Webster MS (2010) Population diversity and the portfolio effect in an exploited species. Nature 465:609-612

Schlaff AM, Heupel MR, Simpfendorfer CA (2014) Influence of environmental factors on shark and ray movement, behaviour and habitat use: a review. Rev Fish Biol Fish 24:1089-1103

Secor DH, Kerr LA, Cadrin SX (2009) Connectivity effects on productivity, stability, and persistence in a herring metapopulation model. ICES J Mar Sci 66:1726-1732

Sheaves M (2006) Scale-dependent variation in composition of fish fauna among sandy tropical estuarine embayments. Mar Ecol Prog Ser 310:173-184

Sheaves M, Johnston R (2009) Ecological drivers of spatial variability among fish fauna of 21 tropical Australian estuaries. Mar Ecol Prog Ser 385:245-260

Sheaves M, Baker R, Johnston R (2006) Marine nurseries and effective juvenile habitats: an alternative view. Mar Ecol Prog Ser 318:303-306

Simpfendorfer CA (1992) Reproductive strategy of the Australian sharpnose shark, *Rhizoprionodon taylori* (Elasmobranchii, Carcharhinidae), from Cleveland Bay, northern Queensland. Aust J Mar Freshwater Res 43:67-75

Simpfendorfer CA (1993) Age and growth of the Australian sharpnose shark, *Rhizoprionodon taylori*, from north Queensland, Australia. Environ Biol Fishes 36:233-241

Simpfendorfer CA, Milward NE (1993) Utilisation of a tropical bay as a nursery area by sharks of the families Carcharhinidae and Sphyrnidae. Environ Biol Fishes 37:337-345

Simpfendorfer CA, Heupel MR (2012) Assessing habitat use and movement. In: Carrier JC, Musick JA, Heithaus MR (eds) Biology of sharks and their relatives, 2nd edition. CRC Press, Boca Raton, p 579-601

Simpfendorfer CA, Goodreid AB, McAuley RB (2001) Size, sex and geographic variation in the diet of the tiger shark, *Galeocerdo cuvier*, from Western Australian waters. Environ Biol Fishes 61:37-46

Simpfendorfer CA, McAuley RB, Chidlow J, Unsworth P (2002) Validated age and growth of the dusky shark, *Carcharhinus obscurus*, from Western Australian waters. Mar Freshw Res 53:567-573

Simpfendorfer CA, Freitas GG, Wiley TR, Heupel MR (2005) Distribution and habitat partitioning of immature bull sharks (*Carcharhinus leucas*) in a southwest Florida estuary. Estuaries 28:78-85

Sims DW, Nash JP, Morritt D (2001) Movements and activity of male and female dogfish in a tidal sea lough: alternative behavioural strategies and apparent sexual segregation. Mar Biol 139:1165-1175

Skaug H, Fournier D, Bolker B, Magnusson A, Nielsen A (2012) *glmmADMB*: generalized linear mixed models using AD model builder. R package version 0.8.0. Available: http://glmmadmb.r-forge.r-project.org/. Accessed 27 August 2014

Smith SE, Au DW, Show C (1998) Intrinsic rebound potentials of 26 species of Pacific sharks. Mar Freshw Res 49:663-678

Speed CW, Field IC, Meekan MG, Bradshaw CJA (2010) Complexities of coastal shark movements and their implications for management. Mar Ecol Prog Ser 408:275-293

Springer S (1967) Social organization of shark populations. In: Gilbert PW, Mathewson RW, Rall DP (eds) Sharks, skates and rays. John Hopkins Press, Baltimore, p 149-174

Staples DJ (1979) Seasonal migration patterns of post-larval and juvenile banana prawns, *Penaeus merguiensis* de Man, in the major rivers of the Gulf of Carpentaria, Australia. Aust J Mar Freshwater Res 30:143-157

Stevens JD, Wiley PD (1986) Biology of two commercially important Carcharhinid sharks from northern Australia. Aust J Mar Freshwater Res 37:671-688

Stevens JD, Lyle JM (1989) Biology of three hammerhead sharks (*Eusphyra blochii, Sphyrna mokarran* and *S. lewini*) from northern Australia. Aust J Mar Freshwater Res 40:129-146

Stevens JD, McLoughlin KJ (1991) Distribution, size and sex composition, reproductive biology and diet of sharks from northern Australia. Aust J Mar Freshwater Res 42:151-199

Stevens JD, West GJ (1997) Investigation of school and gummy shark nursery areas in south eastern Australia. FRDC Project No. 93/061. CSIRO Marine Research, Hobart

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

Taylor EB (1991) A review of local adaptation in Salmonidae, with particular reference to Pacific and Atlantic salmon. Aquaculture 98:185-207

Taylor S (2007) Population structure and resource partitioning amoung Carcharhiniform sharks in Moreton Bay, Southeast Queendland, Australia. PhD thesis, University of Queensland, Brisbane

Taylor S, Bennett M (2013) Size, sex and seasonal patterns in the assemblage of Carcharhiniformes in a sub-tropical bay. J Fish Biol 82:228-241

Taylor S, Sumpton W, Ham T (2011) Fine-scale spatial and seasonal partitioning among large sharks and other elasmobranchs in south-eastern Queensland, Australia. Mar Freshw Res 62:638-647

Thibaut LM, Connolly SR (2013) Understanding diversity-stability relationships: towards a unified model of portfolio effects. Ecol Lett 16:140-150

Tillett BJ, Meekan MG, Field IC, Hua Q, Bradshaw CJA (2011) Similar life history traits in bull (*Carcharhinus leucas*) and pig-eye (*C. amboinensis*) sharks. Mar Freshw Res 62:850-860

Tillett BJ, Meekan MG, Broderick D, Field IC, Cliff G, Ovenden JR (2012a) Pleistocene isolation, secondary introgression and restricted contemporary gene flow in the pig-eye shark, *Carcharhinus amboinensis* across northern Australia. Conserv Genet 13:99-115

Tillett BJ, Field IC, Bradshaw CJA, Johnson G, Buckworth RC, Meekan MG, Ovenden JR (2012b) Accuracy of species identification by fisheries observers in a north Australian shark fishery. Fish Res 127:109-115

Tilman D (1996) Biodiversity: population versus ecosystem stability. Ecology 77:350-363

Tobin A, Mapleston A, Harry AV, Espinoza M (2014a) Big fish in shallow water; use of an intertidal surf-zone habitat by large-bodied teleosts and elasmobranchs in tropical northern Australia. Environ Biol Fishes 97:821–838

Tobin A, Harry A, Smart S, Saunders R, Simpfendorfer C (2014b) Estimating fishing mortality of major target species and species of conservation interest in the Queensland east coast shark fishery. FRDC Project No. 2010/006. Centre for Sustainable Tropical Fisheries and Aquaculture, James Cook University, Townsville

Torres LG, Heithaus MR, Delius B (2006) Influence of teleost abundance on the distribution and abundance of sharks in Florida Bay, USA. Hydrobiologia 569:449-455

Ubeda AJ, Simpfendorfer CA, Heupel MR (2009) Movements of bonnetheads, *Sphyrna tiburo*, as a response to salinity change in a Florida estuary. Environ Biol Fishes 84:293-303

Udyawer V, Chin A, Knip DM, Simpfendorfer CA, Heupel MR (2013) Variable response of coastal sharks to severe tropical storms: environmental cues and changes in space use. Mar Ecol Prog Ser 480:171-183

Ulrich GF, Jones CM, Driggers WB, Drymon JM, Oakley D, Riley C (2007) Habitat utilization, relative abundance, and seasonality of sharks in the estuarine and nearshore waters of South Carolina. Am Fish Soc Symp 50:125-139 van der Elst RP (1979) A proliferation of small sharks in the shore-based Natal shark fishery. Environ Biol Fishes 4:349–362

Venables WN, Ripley BD (2002) Modern applied statistics with S. Springer, New York

Vianna GMS, Meekan MG, Meeuwig JJ, Speed CW (2013) Environmental influences on patterns of vertical movement and site fidelity of grey reef sharks (*Carcharhinus amblyrhynchos*) at aggregation sites. PLoS ONE 8:e60331

Wai TC, Yeung JWY, Lam VYY, Leung KMY, Dudgeon D, Williams GA (2012) Monsoons and habitat influence trophic pathways and the importance of terrestrial-marine linkages for estuary sharks. Ecosphere 3:1-31

Walker TI (2007) Spatial and temporal variation in the reproductive biology of gummy shark *Mustelus antarcticus* (Chondrichthyes:Triakidae) harvested off southern Australia. Mar Freshw Res 58:67-97

Walker TI, Taylor BL, Hudson RJ, Cottier JP (1998) The phenomenon of apparent change of growth rate in gummy shark (*Mustelus antarcticus*) harvested off southern Australia. Fish Res 39:139-163

Walters C (2000) Impacts of dispersal, ecological interactions, and fishing effort dynamics on efficacy of marine protected areas: how large should protected areas be? Science 66:745-757

Ward-Paige CA, Britten GL, Bethea DM, Carlson JK (2014) Characterizing and predicting essential habitat features for juvenile coastal sharks. Mar Ecol 2014:1-13

Welch DJ, Ovenden J, Simpfendorfer C, Tobin A, Morgan J, Street R, White J, Harry AV, Schroeder R, Macbeth WG (2011) Stock structure of exploited shark species in north-eastern Australia. FRDC Project No. 2007/035. Fishing &

Fisheries Research Centre Technical Report No 12, James Cook University, Townsville

White WT, Potter IC (2004) Habitat partitioning among four elasmobranch species in nearshore, shallow waters of a subtropical embayment in Western Australia. Mar Biol 145:1023-1032

White WT, Bartron C, Potter IC (2008) Catch composition and reproductive biology of *Sphyrna lewini* (Griffith & Smith) (Carcharhiniformes, Sphyrnidae) in Indonesian waters. J Fish Biol 72:1675-1689

Whittingham MJ, Stephens PA, Bradbury RB, Freckleton RP (2006) Why do we still use stepwise modelling in ecology and behaviour? J Anim Ecol 75:1182-1189

Wiley TR, Simpfendorfer CA (2007) The ecology of elasmobranchs occuring in the Everglades National Park, Florida: implications for conservation and management. Bull Mar Sci 80:171-189

Williams SE, Bolitho EE, Fox S (2003) Climate change in Australian tropical rainforests: an impending environmental catastrophe. Proc R Soc Lond B 270:1887-1892

Wolanski E, Jones M (1981) Physical properties of Great Barrier Reef lagoon waters near townsville. 1. effects of Burdekin River floods. Aust J Mar Freshwater Res 32:305-319

Wourms JP (1977) Reproduction and development in chondrichthyan fishes. Am Zool 17:379-410

Yamaguchi A, Taniuchi T, Shimizu M (2000) Geographic variations in reproductive parameters of the starspotted dogfish, *Mustelus manazo*, from five localities in Japan and in Taiwan. Environ Biol Fishes 57:221-233

Yates PM, Heupel MR, Tobin AJ, Simpfendorfer CA (2012) Diversity in young shark habitats provides the potential for portfolio effects. Mar Ecol Prog Ser 458:269-281

Yokota L, Lessa RP (2006) A nursery area for sharks and rays in northeastern Brazil. Environ Biol Fishes 75:349-360

Zeileis A, Hothorn T (2002) *lmtest*: diagnostic checking in regression relationships. R package. Available: http://CRAN.R-project.org/doc/Rnews/. Accessed 27 August 2014

Zuur AF, Ieno EN, Elphick CS (2010) A protocol for data exploration to avoid common statistical problems. Methods Ecol Evol 1:3-14

Zuur AF, Saveliev AA, Ieno EN (2012) Zero inflated models and generalized linear mixed models with R. Highland Statistics Ltd., Newburgh

Zuur AF, Ieno EN, Walker N, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer, New York

APPENDICES

Appendix 1 Sequence of sampling during each round. Sampling of Cleveland and Halifax Bays, and Upstart and Edgecumbe Bays was overlapping in the first sampling round.

Round	Trip 1	Trip 2	Trip 3	Trip 4	Trip 5	Trip6	Trip 7	Trip 8	Trip 9
Nov 2011–Mar 2012	Cleveland and Halifax Bays (24 Nov–5 Jan)		Bowling (6–9 Jan)	Upstart (11–12 Jan; 22–23 Jan), Edgecumbe (13–14 Jan; 2–21 Jan)		Rockingham (31 Jan–3 Feb)	Repulse (8–11 Feb)	Woodwark/Double (22–23 Feb)	Abbot (5–8 Feb)
May–June 2012	Upstart (14 May), Rockingham (22–25 May)	Edgecumbe (3–6 Jun)	Bowling (12–15 Jun)	Repulse (19–22 Jun)	Upstart (26–29 Jun)				
Aug–Sept 2012	Repulse (6–9 Aug)	Upstart (13–16 Aug)	Edgecumbe (20–23 Aug)	Bowling (27–30 Aug)	Rockingham (4–7 Sept)				
Nov–Dec 2012	Edgecumbe (5–9 Nov)	Rockingham (15–18 Nov)	Bowling (20–23 Nov)	Upstart (28–30 Nov)	Repulse (3–6 Dec)	Cleveland (16–19 Dec)			
Feb–Mar 2013	Upstart (5–8 Feb)	Rockingham (12–15 Feb)	Repulse (19–22 Feb)	Edgecumbe (26 Feb–1 Mar)	Bowling (25–28 Mar)				
May–Jun 2013	Rockingham (6–9 May)	Repulse (13–16 May)	Bowling (20–24 May)	Upstart (3–6 Jun)	Edgecumbe (19–22 Jun)				
Oct–Nov 2013	Bowling (7–12 Oct)	Upstart (14–18 Oct)	Repulse (22–25 Oct)	Rockingham (28–31 Oct)	Edgecumbe (4–8 Nov)				
Feb–Mar 2014	Rockingham (5–8 Feb)	Edgecumbe (13–16 Feb)	Repulse (18–21 Feb)	Upstart (26 Feb–1 Mar)	Bowling (15–18 Mar)	Cleveland (25–29 Mar)			

Appendix 2 Catch composition of elasmobranchs caught by fishery-independent sampling in five bays along the tropical coast of Queensland. Data, grouped by order and sorted alphabetically, are from 142 days of sampling across seven sampling rounds (2012–2013 only). LL = longline, GN = gillnet.

		Rockingham		Bowling Gr.		Upstart		Edgecumbe		Repulse		Total
Family	Species	LL	GN	LL	GN	LL	GN	LL	GN	LL	GN	
Carcharhinidae	*Carcharhinus amboinensis*	15	8	18	7	1	15	2		20	13	99
	Carcharhinus brevipinna							5	1			6
	Carcharhinus cautus			2		10	2	4				18
	Carcharhinus coatesi	6	6	18	4	12	5	27	5	2	2	87
	Carcharhinus fitzroyensis		4	13	6	2				1	1	27
	Carcharhinus leucas	4		1				1		4	1	11
	Carcharhinus macloti					1					2	3
	Carcharhinus melanopterus										1	1
	Carcharhinus sorrah	21	2	11		30	1	57	2	9		133
	Carcharhinus tilstoni/ C. limbatus	27	44	14	17	13	28	21	14	3	42	223
	Galeocerdo cuvier	4		6		2		5				17
	Rhizoprionodon acutus	10	9	8	5	21	8	18	4	6	1	90
	Rhizoprionodon taylori	38	44	172	141	50	76	28	18	133	246	946
	Unidentifed whaler shark		1	1	1		2	1		2	1	9
Hemigaleidae	*Hemigaleus australiensis*		1	1			2		2			6
	Hemipristis elongata					1			1			2
Sphyrnidae	*Eusphyra blochii*										1	1
	Sphyrna lewini	11	54	2	5	4	2			4	11	93
	Sphyrna mokarran		1	3	1	2	2	3	1	2	5	20
Ginglymostomatidae	*Nebrius ferrugineus*							1				1
Hemiscylliidae	*Chiloscyllium punctatum*			1	1			1		1		4
Stegostomatidae	*Stegostoma fasciatum*		2	3	2	1		1				9
Rhinobatidae	*Glaucostegus typus*	15	2	12		23	2	29	2	18	1	104

Appendix 2 continued

		Rockingham		Bowling Gr.		Upstart		Edgecumbe		Repulse		Total
Family	Species	LL	GN	LL	GN	LL	GN	LL	GN	LL	GN	
Rhynchobatidae	*Rhynchobatus australiae*	8	1	12	1	13	2	15	4	35	2	93
Rhinopteridae	*Rhinoptera neglecta*				2		2		1		2	7
Myliobatidae	*Aetobatus narinari*		1		4				2			7
	Aetomylaeus nichofii		3		29		11		12			55
	Aetomylaeus vespertilio										1	1
Dasyatidae	*Himantura uarnak*					1		2		1		4
	Unidentifed stingray	1	3	3	2		3	4	1	5		22
Pristidae	*Anoxypristis cuspidata*		3		8		5				45	61
Total		160	189	301	236	187	168	225	70	246	378	2160

Appendix 3 Comparison of stretch total lengths between two sampling methods. Where only a single length measurement is available it is given as the maximum length with other fields left blank. Kolmogorov-Smirnov (KS) tests compared length-frequency distributions of sharks between sampling methods. Bold text indicates significant differences ($P < 0.05$). Dashes indicate insufficient sample size for comparison of length-frequency distributions. Data are from years 2012 and 2013 only (Chapter 4).

		Stretch total length (mm)						KS-test
		Longline			Gillnet			*P*
Family	Name	Min.	Max.	Mean	Min.	Max.	Mean	
Carcharhinidae	*Carcharhinus amboinensis*	660	2150	1004	600	1500	839	0.08
	Carcharhinus brevipinna	726	1300	967		795		-
	Carcharhinus cautus	710	1310	1034	925	1170	1048	-
	Carcharhinus coatesi	465	970	808	550	887	794	0.47
	Carcharhinus fitzroyensis	665	1290	993	415	1195	732	**0.01**
	Carcharhinus leucas	663	1890	1244		701		-
	Carcharhinus macloti		785		765	818	792	-
	Carcharhinus melanopterus					1370		-
	Carcharhinus sorrah	495	1300	910	529	1050	833.8	0.50
	Carcharhinus tilstoni/ C. limbatus	575	1620	1023	560	1500	805	**< 0.001**
	Galeocerdo cuvier	1200	3700	2676				-
	Rhizoprionodon acutus	490	899	772	450	923	726	0.18
	Rhizoprionodon taylori	325	865	680	395	786	651	**< 0.001**
Hemigaleidae	*Hemigaleus australiensis*		805		550	924	813	-
	Hemipristis elongata		1270			1440		-
Sphyrnidae	*Eusphyra blochii*					905		-
	Sphyrna lewini	495	1880	1019	445	1990	678	**0.03**
	Sphyrna mokarran	953	2650	1899	730	2550	1431	0.23
Ginglymostomatidae	*Nebrius ferrugineus*		2500					-
Hemiscylliidae	*Chiloscyllium punctatum*	880	1050	947		769		-
Stegostomatidae	*Stegostoma fasciatum*	1290	2170	1612	670	1430	896	-
	All shark species pooled	325	3700	848	395	2550	708	**< 0.001**

Appendix 4 Species and life-history-stage composition of sharks captured during fishery-independent sampling along the tropical coast of Queensland. Numbers represent the number of sharks caught. The number of young-of-the-year (YOY) sharks that were neonates (as indicated by an un-healed umbilical scar) is presented in parentheses. Data are from years 2012 to 2014 (i.e. the full fishery-independent time series) and are pooled across study bays and sampling methods.

Family	Species	YOY (Neonate)	Juvenile	Mature	Unknown	Total
Carcharhinidae	*Carcharhinus amboinensis*	57 (27)	49	1	5	112
	Carcharhinus brevipinna	3	2		1	6
	Carcharhinus cautus		7	15		22
	Carcharhinus coatesi	4	3	84		91
	Carcharhinus fitzroyensis	8 (4)	14	18	1	41
	Carcharhinus leucas	5 (4)	6			11
	Carcharhinus macloti			4		4
	Carcharhinus melanopterus			1		1
	Carcharhinus sorrah	31 (8)	36	83	1	151
	Carcharhinus tilstoni/ C. limbatus	120 (32)	80	37	10	247
	Galeocerdo cuvier	1	5	3	8	17
	Rhizoprionodon acutus	18 (1)	19	56		93
	Rhizoprionodon taylori	45	8	961	12	1026
	Unidentified whaler shark				10	10
Hemigaleidae	*Hemigaleus australiensis*		4	5		9
	Hemipristis elongata			2		2
Sphyrnidae	*Eusphyra blochii*		1	1		2
	Sphyrna lewini	86 (15)	3	13	1	103
	Sphyrna mokarran	5	15	3	1	24
Ginglymostomatidae	*Nebrius ferrugineus*			1		1
Hemiscylliidae	*Chiloscyllium punctatum*		1	3	1	5
Stegostomatidae	*Stegostoma fasciatum*		6	3		9
Total		383 (91)	259	1294	51	1987

Appendix 5 Measures of association involving immature blacktip sharks *Carcharhinus tilstoni/Carcharhinus limbatus* using longlines and gill-nets (Chapter 5). I = immature, M = mature. n = the total number of sharks caught in each comparison group, Trips = the number of trips that caught each comparison group, Both = the number of trips that caught the comparison group and ≥ 1 immature blacktip shark, AS = Association Statistic, % CO = percent common occurrence. The maximum value of the Association Statistic, provided in the column headings, depends on the proportion of trips that caught ≥ 1 immature blacktip shark. Groups are listed according to average % CO. Comparison groups with < 10 sharks were excluded.

Comparison group		Longline					Gill-net				
Species	Maturity	n	Trips	Both	AS (max. 2.73)	% CO	n	Trips	Both	AS (max. 1.72)	% CO
Sphyrna mokarran	I						11	9	7	1.34	78
Carcharhinus leucas	I	10	5	3	1.64	60					
Carcharhinus amboinensis	I	67	24	9	1.03	38	41	14	11	1.35	79
Carcharhinus tilstoni/limbatus	M	25	14	6	1.17	43	12	7	5	1.23	71
Carcharhinus fitzroyensis	I						14	9	5	0.96	56
Sphyrna lewini	I	14	11	4	0.99	36	75	24	18	1.29	75
Rhizoprionodon taylori	I	21	8	2	0.68	25	32	11	8	1.25	73
Carcharhinus sorrah	M	80	40	19	1.30	48					
Rhizoprionodon taylori	M	428	58	21	0.99	36	533	51	30	1.01	59
Carcharhinus coatesi	M	63	23	10	1.19	43	21	10	5	0.86	50
Rhizoprionodon acutus	I	22	9	2	0.61	22	15	6	4	1.15	67
Rhizoprionodon acutus	M	44	22	8	0.99	36	12	8	4	0.86	50
Carcharhinus sorrah	I	65	26	9	0.95	35					
Carcharhinus cautus	M	13	10	3	0.82	30					
Carcharhinus fitzroyensis	M	14	7	1	0.39	14					

Appendix 6 Measures of association involving immature pigeye sharks *Carcharhinus amboinensis* using longlines and gill-nets (Chapter 5). I = immature, M = mature. n = the total number of sharks caught in each comparison group, Trips = the number of trips that caught each comparison group, Both = the number of trips that caught the comparison group and ≥ 1 immature pigeye shark, AS = Association Statistic, % CO = percent common occurrence. The maximum value of the Association Statistic, provided in the column headings, depends on the proportion of trips that caught ≥ 1 immature pigeye shark. Groups are listed according to average % CO. Comparison groups with < 10 sharks were excluded.

Comparison group		Longline					Gill-net				
Species	Maturity	n	Trips	Both	AS (max. 3.42)	% CO	n	Trips	Both	AS (max. 5.29)	% CO
Carcharhinus fitzroyensis	M	14	7	6	2.93	86					
Carcharhinus leucas	I	10	5	3	2.05	60					
Rhizoprionodon taylori	I	21	8	5	2.14	63	32	11	4	1.92	36
Carcharhinus tilstoni/limbatus	M	25	14	8	1.95	57	12	7	1	0.76	14
Sphyrna lewini	I	14	11	4	1.24	36	75	24	7	1.54	29
Carcharhinus cautus	M	13	10	3	1.03	30					
Rhizoprionodon taylori	M	428	58	19	1.12	33	533	51	13	1.35	25
Carcharhinus tilstoni/limbatus	I	58	30	9	1.03	30	142	43	11	1.35	26
Rhizoprionodon acutus	I	22	9	3	1.14	33	15	6	1	0.88	17
Carcharhinus fitzroyensis	I						14	9	2	1.17	22
Sphyrna mokarran	I						11	9	2	1.17	22
Rhizoprionodon acutus	M	44	22	4	0.62	18	12	8	1	0.66	13
Carcharhinus sorrah	M	80	40	6	0.51	15					
Carcharhinus coatesi	M	63	23	4	0.59	17	21	10	1	0.53	10
Carcharhinus sorrah	I	65	26	2	0.26	8					

Appendix 7 Measures of association involving immature scalloped hammerhead sharks *Sphyrna lewini* using longlines and gill-nets (Chapter 5). I = immature, M = mature. n = the total number of sharks caught in each comparison group, Trips = the number of trips that caught each comparison group, Both = the number of trips that caught the comparison group and ≥ 1 immature scalloped hammerhead shark, AS = Association Statistic, % CO = percent common occurrence. The maximum value of the Association Statistic, provided in the column headings, depends on the proportion of trips that caught ≥ 1 immature scalloped hammerhead shark. Groups are listed according to average % CO. Comparison groups with < 10 sharks were excluded.

Comparison group		Longline					Gill-net				
Species	Maturity	n	Trips	Both	AS (max. 7.45)	% CO	n	Trips	Both	AS (max. 3.08)	% CO
Carcharhinus fitzroyensis	I						14	9	4	1.37	44
Sphyrna mokarran	I						11	9	4	1.37	44
Rhizoprionodon acutus	I	22	9	2	1.66	22	15	6	3	1.54	50
Carcharhinus amboinensis	I	67	24	4	1.24	17	41	14	7	1.54	50
Carcharhinus tilstoni/limbatus	I	58	30	4	0.99	13	142	43	18	1.29	42
Rhizoprionodon taylori	I	21	8	0	0.00	0	32	11	6	1.68	55
Rhizoprionodon taylori	M	428	58	9	1.16	16	533	51	17	1.03	33
Rhizoprionodon acutus	M	44	22	2	0.68	9	12	8	3	1.16	38
Carcharhinus leucas	I	10	5	1	1.49	20					
Carcharhinus sorrah	I	65	26	5	1.43	19					
Carcharhinus tilstoni/limbatus	M	25	14	2	1.06	14	12	7	1	0.44	14
Carcharhinus fitzroyensis	M	14	7	1	1.06	14					
Carcharhinus sorrah	M	80	40	2	0.37	5					
Carcharhinus coatesi	M	63	23	2	0.65	9	21	10	0	0.00	0
Carcharhinus cautus	M	13	10	0	0	0					

Appendix 8 Blacktip shark *Carcharhinus tilstoni/Carcharhinus limbatus* logistic regression model coefficients (gill-net data; Chapter 6). Significant factors and pairwise comparisons are indicated by asterisk ($P < 0.05$). RO = Rockingham, BG = Bowling Green, UP = Upstart, ED = Edgecumbe, RE = Repulse. DS = dry season (May–June), EW = early wet season (October–December), LW = late wet season (January–April). Data are from years 2012–2014.

Factor	Levels	*β*	*SE*	*Z*	*P*
YOY					
Bay*	BG - RO	-1.33	0.62	-2.13	0.19
	UP - RO	-0.66	0.51	-1.29	0.68
	ED - RO	-2.82	1.07	-2.65	0.06
	RE - RO	0.11	0.47	0.24	1.00
	UP - BG	0.67	0.65	1.03	0.83
	ED - BG	-1.49	1.14	-1.31	0.67
	RE - BG	1.44	0.62	2.33	0.13
	ED - UP	-2.16	1.08	-2.00	0.25
	RE - UP	0.77	0.51	1.53	0.53
	RE - ED	2.93	1.06	2.76	0.04*
Season	EW - DS	0.95	0.49	1.93	0.13
	LW - DS	0.88	0.51	1.74	0.19
	LW - EW	-0.07	0.42	-0.16	0.99
Year	2013 - 2012	-0.30	0.37	-0.82	0.41
Neonate					
Bay	BG - RO	-1.46	0.85	-1.71	0.41
	UP - RO	-0.31	0.63	-0.49	0.99
	ED - RO	-2.20	1.11	-1.98	0.26
	RE - RO	-1.48	0.86	-1.73	0.40
	UP - BG	1.15	0.86	1.34	0.66
	ED - BG	-0.73	1.26	-0.58	0.98
	RE - BG	-0.02	1.04	-0.02	1.00
	ED - UP	-1.89	1.12	-1.69	0.43
	RE - UP	-1.17	0.87	-1.35	0.65
	RE - ED	0.72	1.26	0.57	0.98
Season*	EW - DS	17.76	1123.00	0.02	1.00
	LW - DS	16.80	1123.00	0.02	1.00
	LW - EW	-0.96	0.57	-1.71	0.17
Year	2013 - 2012	-0.52	0.53	-0.97	0.33

Appendix 9 Pigeye shark *Carcharhinus amboinensis* logistic regression model coefficients (Chapter 6). Significant factors and pairwise comparisons are indicated by asterisk ($P < 0.05$). RO = Rockingham, BG = Bowling Green, UP = Upstart, ED = Edgecumbe, RE = Repulse. DS = dry season (May–June), EW = early wet season (October–December), LW = late wet season (January–April). Data are from years 2012–2014.

Factor	Levels	*β*	*SE*	*Z*	*P*
Longline					
Bay*	BG - RO	-0.11	0.73	-0.14	1.00
	UP - RO	-18.90	3178.00	-0.01	1.00
	ED - RO	-1.76	1.13	-1.55	0.47
	RE - RO	-0.57	0.79	-0.73	0.94
	UP - BG	-18.80	3178.00	-0.01	1.00
	ED - BG	-1.65	1.16	-1.42	0.56
	RE - BG	-0.47	0.82	-0.57	0.97
	ED - UP	17.10	3178.00	0.01	1.00
	RE - UP	18.30	3178.00	0.01	1.00
	RE - ED	1.18	1.19	0.99	0.83
Season*	EW - DS	-17.90	2555.00	-0.01	1.00
	LW - DS	1.35	0.69	1.96	0.10
	LW - EW	19.20	2555.00	0.01	1.00
Year*	2013 - 2012	1.30	0.69	1.88	0.06
Gill-net					
Bay	BG - RO	-0.02	1.05	-0.02	1.00
	UP - RO	-0.15	1.04	-0.14	1.00
	ED - RO	-18.40	3727.00	-0.01	1.00
	RE - RO	0.08	1.05	0.07	1.00
	UP - BG	-0.12	1.04	-0.12	1.00
	ED - BG	-18.30	3727.00	-0.01	1.00
	RE - BG	0.10	1.05	0.09	1.00
	ED - UP	-18.20	3727.00	-0.01	1.00
	RE - UP	0.22	1.05	0.21	1.00
	RE - ED	18.40	3727.00	0.01	1.00
Season*	EW - DS	-17.80	2946.00	-0.01	1.00
	LW - DS	1.22	0.84	1.46	0.27
	LW - EW	19.00	2946.00	0.01	1.00
Year	2013 - 2012	0.62	0.76	0.82	0.41

Appendix 10 Scalloped hammerhead shark *Sphyrna lewini* logistic regression model coefficients (gill-net data; Chapter 6). Significant factors and pairwise comparisons are indicated by asterisk ($P < 0.05$). RO = Rockingham, BG = Bowling Green, UP = Upstart, ED = Edgecumbe, RE = Repulse. DS = dry season (May–June), EW = early wet season (October–December), LW = late wet season (January–April). Data are from years 2012–2014.

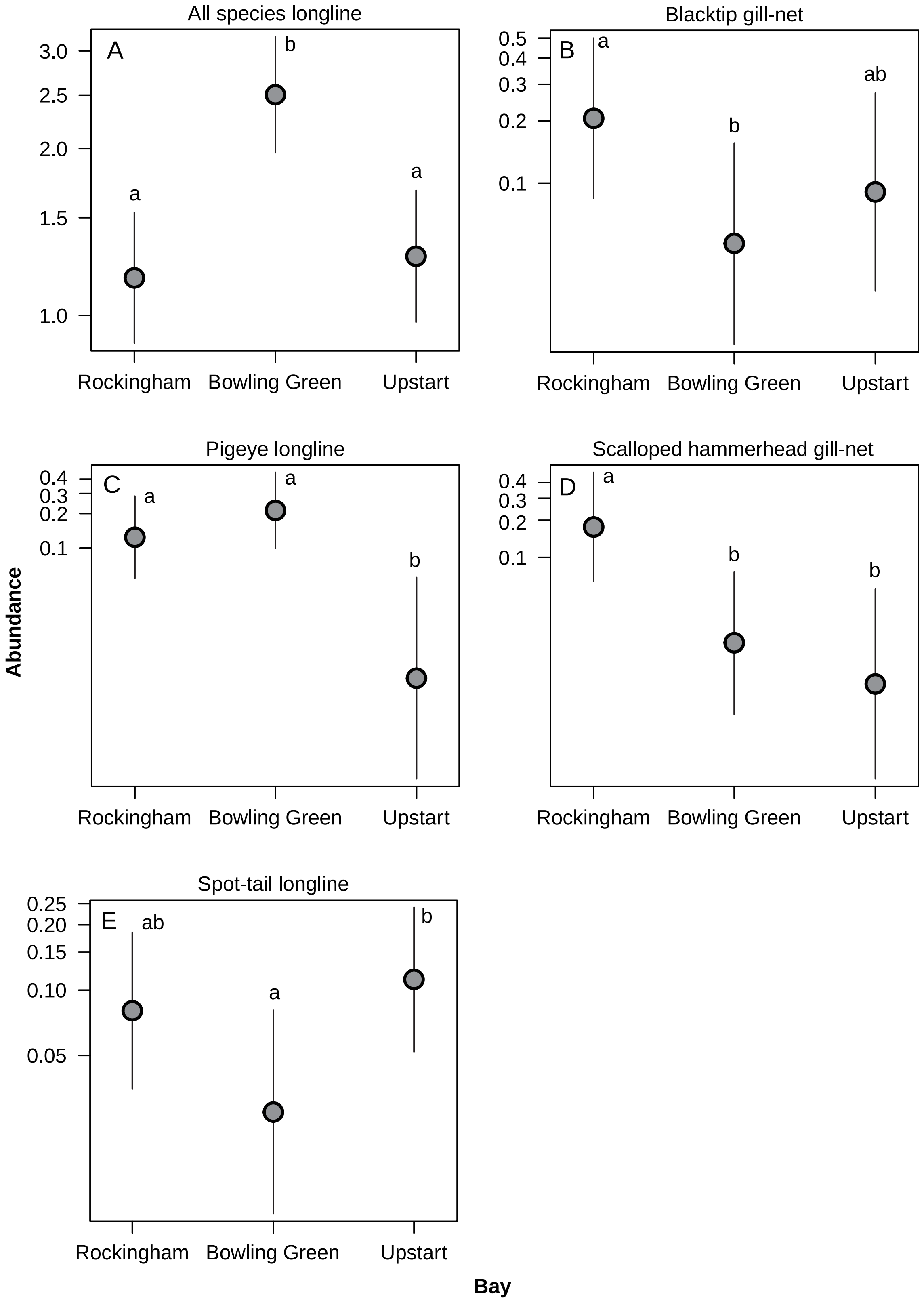
Factor	Levels	*β*	*SE*	*Z*	*P*
Bay*	BG - RO	-1.90	0.67	-2.90	0.02*
	UP - RO	-3.21	1.06	-3.00	0.01*
	ED - RO	-190.00	1486.00	-0.00	1.00
	RE - RO	-1.40	0.57	-2.40	0.08
	UP - BG	-1.30	1.17	-1.10	0.78
	ED - BG	-17.00	1486.00	-0.00	1.00
	RE - BG	0.56	0.76	0.74	0.93
	ED - UP	-16.00	1486.00	-0.00	1.00
	RE - UP	1.83	1.12	1.64	0.41
	RE - ED	17.40	1486.00	0.01	1.00
Season	EW - DS	-0.00	0.58	-0.00	1.00
	LW - DS	0.30	0.57	0.52	0.86
	LW - EW	0.32	0.55	0.58	0.83
Year	2013 - 2012	-0.40	0.47	-0.70	0.46

Appendix 11 Spot-tail shark *Carcharhinus sorrah* logistic regression model coefficients (longline data; Chapter 6). Significant factors and pairwise comparisons are indicated by asterisk ($P < 0.05$). RO = Rockingham, BG = Bowling Green, UP = Upstart, ED = Edgecumbe, RE = Repulse. DS = dry season (May–June), EW = early wet season (October–December), LW = late wet season (January–April). Data are from years 2012–2014.

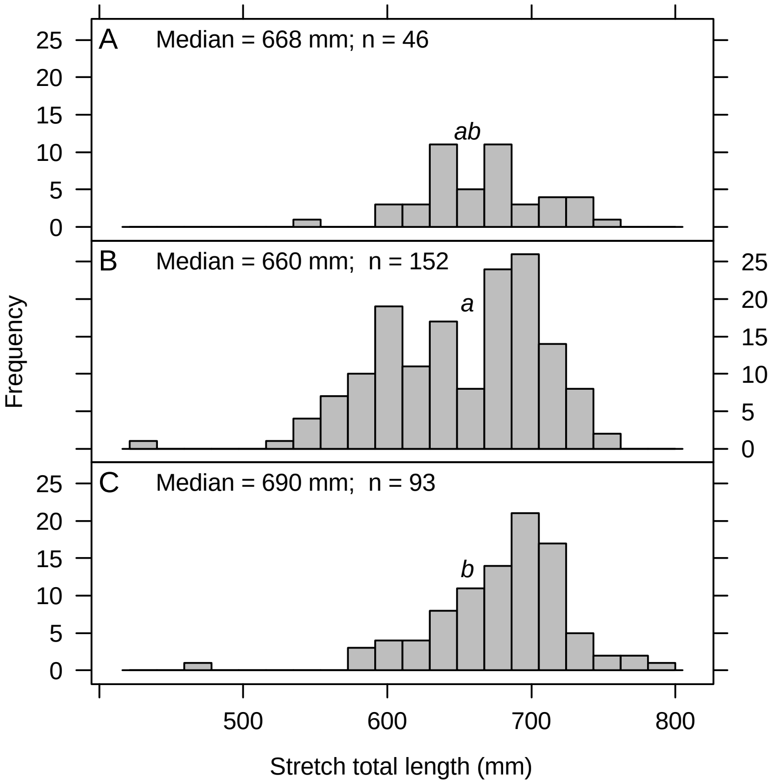
Factor	Levels	*β*	*SE*	*Z*	*P*
Bay	BG - RO	-1.60	1.12	-1.40	0.59
	UP - RO	-0.90	0.87	-1.10	0.83
	ED - RO	0.32	0.65	0.50	0.99
	RE - RO	-0.50	0.77	-0.60	0.97
	UP - BG	0.71	1.25	0.57	0.98
	ED - BG	1.94	1.11	1.75	0.39
	RE - BG	1.15	1.18	0.97	0.86
	ED - UP	1.23	0.85	1.45	0.58
	RE - UP	0.44	0.94	0.47	0.99
	RE - ED	-0.80	0.75	-1.10	0.82
Season*	EW - DS	2.04	1.08	1.89	0.13
	LW - DS	2.36	1.07	2.21	0.06
	LW - EW	0.32	0.53	0.60	0.81
Year	2013 - 2012	-1.00	0.56	-1.80	0.07

Appendix 12 Significance of spatial and temporal factors (likelihood ratio test) based on penalised likelihood ratios in Firth logistic regression (Chapter 6). Data are from years 2012–2014. Significant factors are indicated by asterisk (P < 0.05).

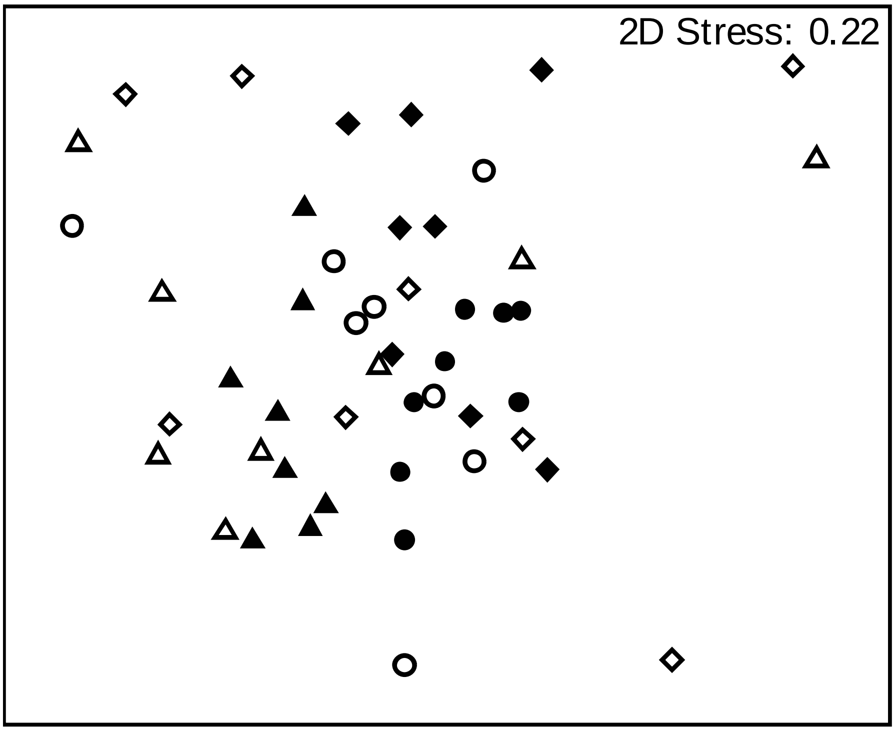
Species	Life-history stage	Sampling method	Factor	*df*	χ^2	*P*
Blacktip	YOY	Gill-net	Bay	4	18.39	0.001*
			Season	2	4.38	0.11
			Year	1	0.64	0.43
	Neonate	Gill-net	Bay	4	7.72	0.10
			Season	2	15.19	0.0005*
			Year	1	0.88	0.35
Pigeye	YOY	Longline	Bay	4	7.29	0.12
			Season	2	12.81	0.002*
			Year	1	3.71	0.05
	YOY	Gill-net	Bay	4	2.56	0.63
			Season	2	7.34	0.03*
			Year	1	0.60	0.44
Scalloped h.	YOY	Gill-net	Bay	4	29.59	< 0.0001*
			Season	2	0.39	0.82
			Year	1	0.51	0.48
Spot-tail	YOY	Longline	Bay	4	4.78	0.31
			Season	2	7.63	0.02*
			Year	1	3.27	0.07



Appendix 13 Significant variations in shark abundance between bays (Chapter 7). Circles are estimated shark abundance and vertical lines are 95% confidence intervals. Lower-case letters denote significantly different groups (Tukey multiple comparisons, *P* < 0.05). Note that the y axes vary among panels.



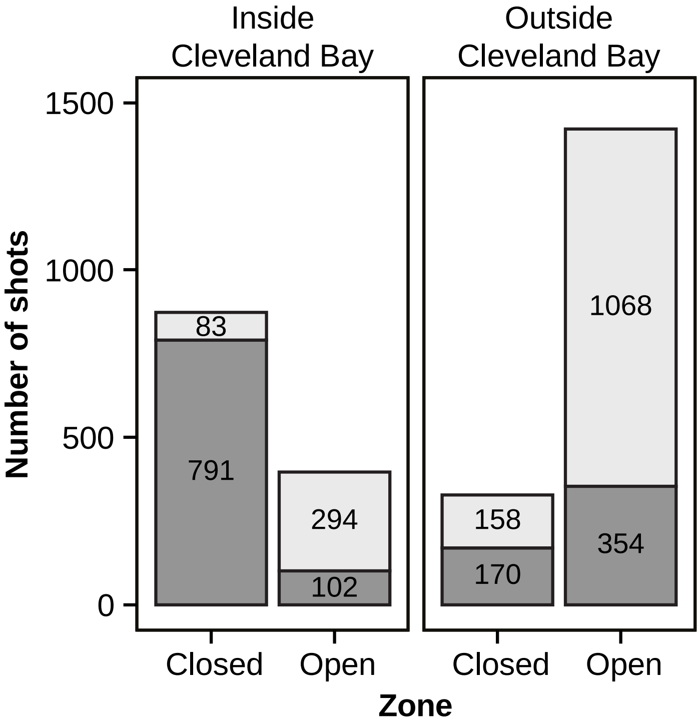
Appendix 14 Comparison of length-frequency distributions of Australian sharpnose sharks *Rhizoprionodon taylori* between Rockingham (A), Bowling Green (B) and Upstart (C) Bays (Chapter 7). Groups that do not share the same lower-case letter were significantly different (Kruskal-Wallis multiple comparison test, $P < 0.05$). Data are pooled across management zones.



Appendix 15 Non-metric multidimensional scaling (MDS) ordination of shark community structure among bays and zones (Chapter 7). Triangles = Bowling Green Bay, circles = Rockingham Bay, diamonds = Upstart Bay. White symbols = open zone, black symbols = closed zone.

Appendix 16 Species contributions to the average Bray-Curtis dissimilarity between open and closed zones (two-way crossed SIMPER; Chapter 7). Species that contributed up to 70% of cumulative contribution to the average dissimilarity (53.28) are ordered by decreasing contribution. Average relative abundance values are fourth-root transformed as is relevant to the dissimilarity calculations. Back-transformed average relative abundances are provided in parentheses.

Species	Average relative abundance		Average dissimilarity	Contribution (%)	Cumulative contribution (%)
	Closed zones	Open zones			
Whitecheek	0.79 (0.39)	0.04 (<0.01)	5.74	10.77	10.77
Australian Sharpnose	1.65 (7.41)	1.51 (5.20)	5.66	10.62	21.40
Blacktip	1.18 (1.94)	0.82 (0.45)	5.66	10.62	32.02
Milk	0.69 (0.23)	0.40 (0.03)	5.29	9.92	41.94
Pigeye	0.70 (0.24)	0.57 (0.11)	5.14	9.64	51.58
Spot-tail	0.74 (0.30)	0.68 (0.21)	5.12	9.61	61.18
Scalloped hammerhead	0.63 (0.16)	0.74 (0.30)	3.74	7.02	68.21
Creek whaler	0.38 (0.02)	0.29 (0.01)	3.29	6.17	74.38



Appendix 17 Shark tagging effort for the collection of tag-recapture data (Chapter 7), including all fishery-dependent and fishery-independent sources. Dark grey = longline shots, light grey = gill-net shots. Note that the distribution of effort between zones and sampling methods varied in Cleveland Bay compared to outside of Cleveland Bay. Shots with missing or unreliable spatial coordinates were excluded as they could not be assigned to a zone.

Appendix 18 Tag-recapture summary (Chapter 7). Species are listed in decreasing order of recapture rate. Sex ratio excludes sharks of unknown sex. Species that were rarely captured inshore or were not recaptured are not listed.

					Stretch total length of recaptured sharks (mm)		Time at liberty (days)		Minimum distance travelled (km)	
Species	Number tagged	Number of recaptures	Recapture rate	Sex ratio of recaptured sharks (F:M)	Range	Mean	Range	Mean	Range	Mean
Carcharhinus leucas	55	14	0.25	7:7	738-880	815	1-257	82	0-55	8.4
Nebrius ferrugineus	9	2	0.22	1:1	930-1030	980	462-462	462	2-2	2.0
Carcharhinus amboinensis	498	84	0.17	39:43	630-1840	872	1-1299	207	0-166	21.3
Negaprion acutidens	7	1	0.14	1:0	2800	-	150	-	32	-
Carcharhinus melanopterus	210	28	0.13	20:8	670-1503	1194	0-1352	396	0-175	8.0
Eusphyra blochii	16	2	0.13	0:1	680	-	33-183	108	2	-
Chiloscyllium punctatum	40	4	0.10	3:1	910-1060	1011	75-453	293	0-1	0.3
Sphyrna mokarran	87	8	0.09	5:3	1284-2190	1778	0-1293	462	1-709	118.1
Carcharhinus cautus	51	4	0.08	2:2	980-1310	1125	176-1201	506	2-3	2.3
Carcharhinus tilstoni/ C. limbatus	1044	69	0.07	37:29	580-1580	849	0-1113	234	0-353	51.6
Carcharhinus sorrah	478	33	0.07	21:12	695-1280	1031	4-1495	459	1-715	37.8
Sphyrna lewini	235	14	0.06	3:11	532-2120	1550	0-557	146	1-57	13.8
Carcharhinus fitzroyensis	205	13	0.06	12:1	519-1285	947	3-1475	505	1-134	34.6
Galeocerdo cuvier	18	1	0.06	1:0	2455	-	173	-	8	-
Carcharhinus macloti	67	2	0.03	2:0	745-905	825	73-356	215	11	-
Carcharhinus brevipinna	32	1	0.03	1:0	1000	-	278	-	-	-
Stegostoma fasciatum	35	1	0.03	1:0	1300	-	135	-	0	-
Rhizoprionodon acutus	404	7	0.02	3:4	804-865	821	19-667	302	15-96	49.7
Rhizoprionodon taylori	1267	9	0.01	7:2	610-810	683	45-356	184	3-62	29.4
Carcharhinus coatesi	153	2	0.01	0:2	833	-	38-107	73	7-10	8.5

Appendix 18 continued.

Species	Number tagged	Number of recaptures	Recapture rate	Sex ratio of recaptured sharks (F:M)	Stretch total length of recaptured sharks (mm)		Time at liberty (days)		Minimum distance travelled (km)	
					Range	Mean	Range	Mean	Range	Mean
Hemigaleus australiensis	19	0	-	-	-	-	-	-	-	-
Fossil	14	0	-	-	-	-	-	-	-	-
Total	4944	299	0.06	166:127	519-2800	988	0-1495	276	0-715	31.1