ResearchOnline@JCU

This file is part of the following reference:

Simpfendorfer, Colin Ashley (1993) The biology of sharks of the family Carcharhinidae from the nearshore waters of Cleveland Bay, with particular reference to Rhizoprionodon taylori. PhD thesis, James Cook University.

Access to this file is available from:

http://eprints.jcu.edu.au/24126/

The author has certified to JCU that they have made a reasonable effort to gain permission and acknowledge the owner of any third party copyright material included in this document. If you believe that this is not the case, please contact <u>ResearchOnline@jcu.edu.au</u> and quote <u>http://eprints.jcu.edu.au/24126/</u>



The biology of sharks of the family Carcharhinidae from the nearshore waters of Cleveland Bay, with particular reference to *Rhizoprionodon taylori*.

Thesis submitted by Colin Ashley SIMPFENDORFER BSc (Hons) (JCUNQ) in April 1993

for the degree of Doctor of Philosophy in the Department of Zoology at James Cook University of North Queensland.



FRONT PIECE: Rhizoprionodon taylori

"This is the most common of all the smaller galeids on our coast"

J. Douglas Ogilby. 1915 Mem. Qld. Mus., 3, p.132

DECLARATION

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 Information derived from the published or unpublished works of others has been acknowledged in the text and a list of references is given.

Colin A. Simpfendorfer

Date

Statement of Access

I, the undersigned, the author of this thesis, understand that James Cook University of North Queensland will make it available for use within the University Library and, by microfilm or other photographic means, allow access to users in other approved libraries. All users consulting this thesis will have to sign the following statement:

"In consulting this thesis I agree not to copy or closely paraphrase it in whole or in part without the written consent of the author; and to make proper written acknowledgement for any assistance which I have obtained from it."

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

29/4/93

(date)

Colin A. Simpfendorfer

ABSTRACT

Sharks of the family Carcharhinidae occurring in the nearshore waters (<5m depth) of Cleveland Bay, northern Queensland, were studied between June 1987 and February 1990. Specimens were collected using gillnets at three sites in Cleveland Bay, as well as demersal otter trawls throughout Cleveland Bay. The aims of the study were to examine the biology of the species of carcharhinid sharks that occur in the nearshore waters of Cleveland Bay and to determine the importance of this area to populations of carcharhinid sharks.

Thirteen species of the family Carcharhinidae were examined. One species - *Rhizoprionodon taylori* - was particularly abundant and most of the research was directed at this species. Of the remaining twelve species all were normally caught as juveniles. At least six species, not including *R. taylori*, utilise Cleveland Bay as a communal nursery area. Two patterns of nursery area utilisation were identified. Juvenile *R. taylori* also occurred, but their distribution overlapped with that of the adults. The importance of nearshore waters to populations of carcharhinid sharks, and the role that the sharks have in these areas, are discussed.

The distribution of R. *taylori* was analysed using catch rates from gillnets. There was no significant difference in the catch rate of R. *taylori* between bottom or surface set nets, or between nets set at each of the three main sampling sites. The catch rate of R. *taylori* was significantly different between seasons and years of this study, and was influenced by temperature, salinity, tidal variation and the amount of teleost by-catch. Mechanisms for the possible action of these factors are discussed.

Age and growth of *R. taylori* were studied using the techniques of vertebral ageing, back calculation and length frequency analysis. Vertebrae contained circuli produced annually in January or February, possibly as a result of stress during mating. The oldest male examined was 5.7 years old, and the oldest female 6.9 years. The age

iii

at maturity was one year. Von Bertalanffy growth parameters estimated from vertebral ageing data for males were $t_0=0.41$ yr, K=1.337, $L_{\infty}=652$ mm TL, and for females $t_0=0.46$ yr, K=1.013, $L_{\infty}=733$ mm TL. Growth parameters estimated by length frequency and back calculation techniques concurred with those from vertebral ageing.

Stomach content analysis was used to investigate the food and feeding habits of R. *taylori*. The most common identifiable prey were members of the demersal teleost families Leiognathidae, Clupeidae and Teraponidae, the prawn family Penaeidae, and the squid family Loliginidae. 59.4% of specimens had no food in their stomachs. The mean weight of prey in the stomachs containing food was 14.1g (1.1% body weight), and the mean weight of original prey items (prior to digestion) was estimated to be 29.5g (2.3% body weight). It was estimated that individual *R. taylori* feed, on average, every two days, normally on a single prey item.

Maturity in *R. taylori* occurs at 560mm TL in males and 575mm TL in females. Mating occurs in late January and early February. Mature females mate every year, producing litters of one to ten offspring. The gestation period of 11.5 months is divided into an initial seven month period of embryonic diapause, followed by a 4.5 month period of development. During the diapause period embryos remain at the blastoderm stage. Nutrition of the embryos is initially lecithotrophic, however, embryos over 30mm TL have structures to absorb secretions from the uterus and a yolk sac placenta forms during the third month of development. The young of *R. taylori* are born in mid-January of each year at sizes ranging from 220 to 260mm TL.

The results indicate that *R. taylori* has an atypical life history when compared to other members of the family Carcharhinidae. Factors that may cause intra- and inter-specific variations in life history traits are discussed. Finally, the results are discussed in relation to the management of shark stocks and nearshore waters.

iv

TABLE OF CONTENTS

Declaration	i
Statement of Access	ii
Abstract	iii
Table of Contents	v
Table of Figures	viii
Table of Plates	XV
Acknowledgments	xix
	_
Section I. Introduction, study area and sampling	1
Chapter 1 Consent Introduction	2
Chapter 1. General Introduction	2
Chapter 2 Study area and compling methods	11
2 1 Study area	11
2.1. Sludy dica	12
2.1.1. Sampling sites	15
2.2. Sampling methodology	15
2.2.1. Gillnetting	15
2.2.2. Demersal otter trawling	10
2.3. Data collected on sampling trips	18
2.3.1. Environmental parameters	18
2.3.2. Identification of catch	19
2.3.3. Measurement of the catch	19
Section II Biology of Phizoprionadan taylari	22
Section II. Biology of Natophonouon layton	
Chapter 3. Catch statistics and distribution of <i>Rhizoprionodon taylori</i>	23
3.1. Introduction	23
3.2 Materials and methods	24
3.3 Results	27
3.3.1 Catch rates of 10cm gillnets	27
3 A Discussion	38
5.4. Discussion	50
Chapter 4. Age and growth of <i>Rhizoprionodon taylori</i>	42
4 1 Introduction	42
4.1.1 A review of shark age and growth with particular reference to	
the family Carcharhinidae	42
4.2 Materials and methods	50
4.2. Matchars and methods	54
A 3 1 Centrum mornhology	54
4.3.2. Longth at ago	54
4.5.2. Length at age	54
4.5.5. Length frequency	50
4.3.4. Size and age at maturity	57
4.4. Discussion	02
Chapter 5 Food and feeding of <i>Rhizoprionodon taylori</i>	65
5.1 Introduction	65
5.1.1 Food and feeding of carcharbinid charbs	65
5.1.1. FOOD and notheds	75
5.2.1 Data collection	75
5.2.2. Analysis	77
J.L.L. AIIAIYSIS	11

5.3. Results	80 80
5.3.2 Variation in liver weight and body condition	83
5.4 Discussion	01
J.4. Discussion	91
Chapter 6 Reproductive biology of Rhizoprionodon taylori	97
6.1 Introduction	97
6.1.1 A review of reproduction in sharks from the family	21
Carcharhinidae	90
6.2 Materials and methods	107
6.3 Desults	109
6.3.1 Maturation	109
6.3.2 Reproductive cycle	109
633 Litter size	111
6 3 4 Size at hirth	111
6.3.5 Sex ratios	112
6 1 Discussion	121
0.4. Discussion	121
Chapter 7 Embryonic development of <i>Rhizoprionodon taylori</i>	126
7.1 Introduction	126
7.1.1. A review of the embryonic development of carcharhinid sharks	127
7 1 1 1 Introduction	127
7.1.1.2. Function of the oviducal gland in relation to embryonic	
development	130
7.1.1.3. Farly embryonic development	131
7.1.1.4. Gestation periods and embryonic growth rates of	
carcharhinid sharks	133
7.1.1.5. Delays during the early stages of embryonic development	135
7.1.1.6. The accommodation of pregnancy	137
7.1.1.7. Embryonic nutrition	139
7.1.1.8. Conclusions	145
7.2. Materials and methods	148
7.3. Results	151
7.3.1. Ovulation and the functions of the oviducal gland	151
7.3.2. Development of embryos	154
7.3.2.1. Description of embryos	155
7.3.3. Accommodation of pregnancy	158
7.3.3.1. Mucosa	159
7.3.3.2. Submucosa	159
7.3.3.3. Muscularis and serosa	160
7.3.4. Structure of tissues possibly associated with embryonic	
nutrition	160
7.3.4.1. Yolk sac and stalk	160
7.3.4.2. Appendiculae	161
7.3.4.3. External branchial filaments	162
7.3.4.4. Placentae	162
7.4. Discussion	186
7.4.1. The oviducal gland and its functions	186
7.4.2. Embryonic diapause	188
7.4.3. Developing embryos	190
7.4.4. Embryonic nutrition	191
-	
Section III. Other species of the family Carcharhinidae	197
Chapter 8 Biology of other carcharhinid species from Cleveland Bay	198

 8.1.1. A review of the literature on the occurrence and utilisation of nursery areas in the family Carcharhinidae 8.2. Materials and methods 8.3. Results 8.3.1. Abundance and distribution 8.3.2. Size distributions 8.3.3. Reproduction 8.3.4. Feeding 8.4. Discussion 8.4.1. Utilisation of Cleveland Bay as a nursery area 8.4.2. Other aspects of carcharhinid biology Section IV. General Discussion 9.1. Life history of <i>Rhizoprionodon taylori</i> 9.2. Nearshore waters and sharks of the family Carcharhinidae 9.3. Application of the results to the management of shark stocks References cited 	8.1. Scope and aims	1
nursery areas in the family Carcharhinidae 8.2. Materials and methods 8.3. Results 8.3.1. Abundance and distribution 8.3.2. Size distributions 8.3.3. Reproduction 8.3.4. Feeding 8.4.1. Utilisation of Cleveland Bay as a nursery area 8.4.2. Other aspects of carcharhinid biology Section IV. General Discussion 9.1. Life history of <i>Rhizoprionodon taylori</i> 9.2. Nearshore waters and sharks of the family Carcharhinidae 9.3. Application of the results to the management of shark stocks References cited	8.1.1. A review of the literature on the occurrence and utilisation of	
 8.2. Materials and methods 8.3. Results 8.3.1. Abundance and distribution 8.3.2. Size distributions 8.3.3. Reproduction 8.3.4. Feeding 8.4. Discussion 8.4.1. Utilisation of Cleveland Bay as a nursery area 8.4.2. Other aspects of carcharhinid biology Section IV. General Discussion 9.1. Life history of <i>Rhizoprionodon taylori</i> 9.2. Nearshore waters and sharks of the family Carcharhinidae 9.3. Application of the results to the management of shark stocks References cited 	nursery areas in the family Carcharhinidae	1
 8.3. Results 8.3.1. Abundance and distribution 8.3.2. Size distributions 8.3.3. Reproduction 8.3.4. Feeding 8.4. Discussion 8.4.1. Utilisation of Cleveland Bay as a nursery area 8.4.2. Other aspects of carcharhinid biology Section IV. General Discussion 9.1. Life history of <i>Rhizoprionodon taylori</i> 9.2. Nearshore waters and sharks of the family Carcharhinidae 9.3. Application of the results to the management of shark stocks References cited 	8.2. Materials and methods	2
 8.3.1. Abundance and distribution 8.3.2. Size distributions 8.3.3. Reproduction 8.3.4. Feeding 8.4. Discussion 8.4.1. Utilisation of Cleveland Bay as a nursery area 8.4.2. Other aspects of carcharhinid biology Section IV. General Discussion 9.1. Life history of <i>Rhizoprionodon taylori</i> 9.2. Nearshore waters and sharks of the family Carcharhinidae 9.3. Application of the results to the management of shark stocks References cited Appendices 	8.3. Results	2
 8.3.2. Size distributions 8.3.3. Reproduction 8.3.4. Feeding 8.4. Discussion 8.4.1. Utilisation of Cleveland Bay as a nursery area 8.4.2. Other aspects of carcharhinid biology Section IV. General Discussion 9.1. Life history of <i>Rhizoprionodon taylori</i> 9.2. Nearshore waters and sharks of the family Carcharhinidae 9.3. Application of the results to the management of shark stocks References cited Appendices 	8.3.1 Abundance and distribution	2
 8.3.3. Reproduction	8 3 2 Size distributions	5
 8.3.4. Feeding 8.4. Discussion 8.4.1. Utilisation of Cleveland Bay as a nursery area 8.4.2. Other aspects of carcharhinid biology Section IV. General Discussion Chapter 9. General Discussion 9.1. Life history of <i>Rhizoprionodon taylori</i> 9.2. Nearshore waters and sharks of the family Carcharhinidae 9.3. Application of the results to the management of shark stocks References cited Appendices 	8 3 3 Deproduction	5
 8.3.4. Freeding 8.4. Discussion	9.2.4 Ecoding	2
 8.4. Discussion	0.5.4. Foculing	2
 8.4.1. Utilisation of Cleveland Bay as a nursery area	8.4. Discussion	4
 8.4.2. Other aspects of carcharhinid biology Section IV. General Discussion Chapter 9. General Discussion	8.4.1. Utilisation of Cleveland Bay as a nursery area	2
Section IV. General Discussion Chapter 9. General Discussion 9.1. Life history of <i>Rhizoprionodon taylori</i> 9.2. Nearshore waters and sharks of the family Carcharhinidae 9.3. Application of the results to the management of shark stocks References cited Appendices	8.4.2. Other aspects of carcharhinid biology	2
Chapter 9. General Discussion 9.1. Life history of <i>Rhizoprionodon taylori</i> 9.2. Nearshore waters and sharks of the family Carcharhinidae 9.3. Application of the results to the management of shark stocks References cited	Section IV. General Discussion	2
 9.1. Life history of <i>Rhizoprionodon taylori</i> 9.2. Nearshore waters and sharks of the family Carcharhinidae 9.3. Application of the results to the management of shark stocks References cited Appendices 	Chapter 9. General Discussion	2
 9.2. Nearshore waters and sharks of the family Carcharhinidae 9.3. Application of the results to the management of shark stocks References cited	9 1 J ife history of Rhizoprionodon taylori	5
9.3. Application of the results to the management of shark stocks References cited	0.7 Nearshare waters and sharks of the family Carcharhinidae	· 5
References cited	9.2. Application of the results to the management of shark stocks	4
References cited	9.5. Application of the results to the management of shark stocks	4
Appendices	References cited	2
	Appendices	2

.

.

TABLE OF FIGURES

Figure 1.1	Region of shark fisheries related research previously	5
	carried out in northern Australia (stippled; from Fig. 1,	
	Stevens and McLoughlin 1991) and location of the study	
	area in Cleveland Bay, North Queensland (arrow).	

Figure 1.2 Catches of sharks reported by Queensland's commercial 8 fishers between 1964/65 and 1989/90. Information from Australian Bureau of Statistics (1964/65 to 1979/80) and the QFMA/QDPI (1988/89 to 1989/90). No data are available for the period from 1980/81 to 1987/88.

- Figure 2.1 Details of the Cleveland Bay study area. The letters A-C 12 signify the three main sampling sites: A, Strand; B, southern Bay; and C, Middle Reef. Dots represent other sampling sites. Isobaths are indicated by dashed lines.
- Figure 2.2 Total seasonal effort, in netting hours, of night set 10cm 17 gillnets at three sites in Cleveland Bay between Winter 1987 and Summer 1990.
- Figure 2.3 Length measurements taken from specimens caught in 21 Cleveland Bay. TL, total length; FL, fork length.
- Figure 3.1 Length frequency distribution of *Rhizoprionodon taylori* 31 specimens caught in 10cm monofilament gillnets set in Cleveland Bay.
- Figure 3.2 The effect of set time on (a) the number, and (b) catch rate, 32 of *Rhizoprionodon taylori* caught in 10cm gillnets set in Cleveland Bay. s.n.h, sharks net⁻¹hr⁻¹.

Figure 3.3 Frequency distribution of catch rates of *Rhizoprionodon* 33 taylori caught in 10cm gillnets set in Cleveland Bay. s.n.h, sharks net⁻¹hr⁻¹.

Figure 3.4 Mean catch rates of *Rhizoprionodon taylori* caught in night 34 set 10cm gillnets at three sampling sites in Cleveland Bay. Error bars plus one standard error; s.n.h, sharks net⁻¹hr⁻¹.

Figure 3.5

Mean annual (a), and seasonal (b), catch rates of 35 *Rhizoprionodon taylori* in night set 10cm gillnets at The Strand, Cleveland Bay, between Winter 1987 and Summer 1990. Error bars plus one standard error; s.n.h, sharks $net^{-1}hr^{-1}$.

Figure 3.6

Mean seasonal catch rates of *Rhizoprionodon taylori* in 36 Cleveland Bay for all years of this study. Error bars plus one standard error; s.n.h, sharks net $^{-1}hr^{-1}$.

Figure 3.7

Mean monthly salinity and temperatures for Cleveland Bay 37 from data collected during the sampling program. Error bars plus and minus one standard error.

49

Figure 4.1

Diagrammatic sections of vertebrae showing features referred to in the text. (a) whole vertebrae showing plane of section, (b) vertebra with opaque (indicated by arrows) and translucent bands, and (c) vertebra with circuli (arrows). CC, corpus calcareum; and I, intermedialia.

Figure 4.2

Relationship between centrum radius and total length for 58 151 *Rhizoprionodon taylori* caught in Cleveland Bay.

Figure 4.3

Marginal increments for *Rhizoprionodon taylori* from 59 Cleveland Bay based on individuals with 4, or less, circuli (including the circulus formed at birth). 1 OMU = 0.027mm.

- Figure 4.4 Von Bertalanffy growth curve fitted to length at age data 60 for (a) 52 male and (b) 85 female *Rhizoprionodon taylori* caught in Cleveland Bay.
- Figure 4.5 Length frequency data for (a) male and (b) female 61 *Rhizoprionodon taylori* caught in Cleveland Bay. The von Bertalanffy growth curves calculated using ELEFAN I for the first four years are shown. Data for juvenile males and females (< 580mm TL) are combined.
- Figure 5.1 Cumulative diversity of stomach contents of 85 *Rhizoprionodon taylori* from Cleveland Bay using the method of Hoffman (1979).
- Figure 5.2 Wet weight of stomach contents from 149 *Rhizoprionodon* 86 *taylori* specimens: (a) raw wet weight data; and (b) estimated original weight of prey based on correction factors for different digestive states (see text for description of method).
- Figure 5.3 Wet weight of (a) stomach contents, and (b) estimated 87 original prey weight, as a proportion of total body weight, of 149 *Rhizoprionodon taylori* specimens from Cleveland Bay. Weights of prey determined from digestive state (see text for description of method).
- Figure 5.4 Frequency distribution of state of digestion index (SDI) for 88 149 *Rhizoprionodon taylori* from Cleveland Bay (see text for details of SDI values).
- Figure 5.5 Monthly variation in the hepatosomatic index (HSI) of (a) 89 male, and (b) female, *Rhizoprionodon taylori* specimens from Cleveland Bay. Circles represent monthly means, bars plus and minus one standard error.

x

Figure 5.6 Monthly variation in the condition factor (K) of (a) male, and (b) female, *Rhizoprionodon taylori* specimens from Cleveland Bay. Circles represent monthly means, bars plus and minus one standard error. 90

94

- Figure 5.7 Simple food chain for Cleveland Bay.
- Figure 6.1 Relationships between, (a) the maximum length and the 104 size at birth (SAB), and (b) the maximum length and the size at birth relative to maximum size, for species of the family Carcharhinidae. Where more than one report exists for a species all points are shown. Data from Appendix C.
- Figure 6.2 Size at maturity (SAM) as a proportion of maximum length 105 in sharks of the family Carcharhinidae, (a) males, and (b) females. Where more than one report exists for a species all points are shown. Data from Appendix C.
- Figure 6.3 Relationships between, (a) the maximum litter size and 106 maximum length, and (b) mean litter size and maximum length, for species of the family Carcharhinidae. Where more than one report exists for a species all points are shown. Data from Appendix C.
- Figure 6.4 Relationship of clasper length (as a percentage of total 113 length) to total length in 165 male specimens of *Rhizoprionodon taylori* from Cleveland Bay.
- Figure 6.5 Percentage occurrence of maturity groups (juvenile, 114 sub-adult and adult) in 10mm size classes of the female *Rhizoprionodon taylori* population from Cleveland Bay. See text for description of maturity groups.

xï

- Figure 6.6 Percentage occurrence of maturity groups (juvenile, 115 sub-adult female and adult) of *Rhizoprionodon taylori* at the three principal sampling sites in Cleveland Bay. Numbers above bars are sample sizes.
- Figure 6.7 Mean monthly values (all years pooled) of gonadosomatic 116 index (GSI) for, (a) male, and (b) female, *Rhizoprionodon taylori* from Cleveland Bay. Error bars, plus one standard error.
- Figure 6.8 Mean monthly values of maximum ova diameter (MOD) 117 for 29 adult female *Rhizoprionodon taylori* from Cleveland Bay. Error bars, plus one standard error.
- Figure 6.9 Relationship between maternal length and litter size in 221 118 female *Rhizoprionodon taylori* from Cleveland Bay.
- Figure 6.10 Proportions of mature male and female *Rhizoprionodon* 119 taylori caught each month in Cleveland Bay during this study. Numbers above bars are sample sizes for each month (all years pooled).
- Figure 7.1 Longitudinal section of the uterus of *Carcharhinus* 146 *plumbeus* containing three embryos (only the one in the left compartment is shown) showing the location of a compartment (C), embryo (E), storage chamber (SC), uterine wall (U), and yolk sac (YS). Redrawn from Figure 12b in Baranes and Wendling (1981).
- Figure 7.2 The three types of placenta that occur in the family 147 Carcharhinidae: (a) entire (mature), (b) discoidal (mature) and (c) stalked (early, redrawn from Setna and Sarangdhar 1948). A, Appendiculae; DP, distal portion of placenta; PP, proximal portion of placenta; TB, trophonematous bulb; TC, trophonematous cord; TS, trophonematous stalk; TU, trophonematous cup; U, umbilical cord; Ut, uterus; YS, yolk sac. Asterisk indicates tissues of maternal origin.

xii

Figure 7.3 General morphology of the oviducal gland of 164 *Rhizoprionodon taylori*, and distribution of tubule types A (stippled), B (hatch rising right) and C (hatch rising left) in the basal portion (section A) and the lateral horns (section B). BP, basal portion; Ca, caudal oviduct; Cr, cranial oviduct; L, lumen; LH, lateral horn.

Figure 7.4 Variation in the size (length and width) of the oviducal 165 glands of *Rhizoprionodon taylori* by month. 1, January;
2, February; 3, March; 8, August; 9, September; D, other.

- Figure 7.5 Growth of *Rhizoprionodon taylori* embryos. Open circles, 166 stage I embryos; closed circles, stage II embryos; open triangles, free embryos; solid squares, mean monthly sea surface temperature for Townsville (from Kenny 1974).
- Figure 7.6 Oblique view (a), and longitudinal section (b), of a 167 diapausing blastoderm of *Rhizoprionodon taylori* based on a reconstruction from serial sections of an embryo from a female caught in May 1988. E, embryo; SC, segmentation cavity; Y, yolk. Anterior of sections is to the right.

Figure 7.7

- Relationship between the mean weight of individuals in 168 litters and the litter size, indicating that females that have smaller litters produce larger young.
- Figure 7.8 Accommodation of (a) diapausing, (b) mid-term, and (c) 169 full-term, embryos within the uteri of *Rhizoprionodon taylori*. E, egg; EC, egg case; Em, embryo; P, placenta; S, septa; U, umbilical cord; Ut, uterus.
- Figure 8.1 Mean catch rates of *Carcharhinus tilstoni* at three sites in 214 Cleveland Bay. Error bars, plus one standard error; s.n.h., sharks net⁻¹hr⁻¹.

xiii

- Figure 8.2 Mean (a) annual, and (b) seasonal, catch rates of 215 Carcharhinus tilstoni, in night set 10cm gillnets at the Strand site. Error bars, plus one standard error; s.n.h., sharks net⁻¹hr⁻¹.
- Figure 8.3 Mean seasonal catch rates of *Carcharhinus tilstoni*, caught 216 in night set 10cm gillnets at the Strand site, for each year of the study between winter 1987 and summer 1990. Error bars, plus one standard error; s.n.h., sharks net⁻¹hr⁻¹.
- Figure 8.4 Mean catch rates of *Rhizoprionodon acutus* at three sites 217 in Cleveland Bay. Error bars, plus one standard error; s.n.h., sharks net⁻¹hr⁻¹.
- Figure 8.5 Mean (a) annual, and (b) seasonal, catch rates of 218 *Rhizoprionodon acutus*, in night set 10cm gillnets at the Strand site. Error bars, plus one standard error; s.n.h., sharks net⁻¹hr⁻¹.
- Figure 8.6 Mean seasonal catch rates of *Rhizoprionodon acutus*, 219 caught in night set 10cm gillnets at the Strand site, for each year of the study between winter 1987 and summer 1990. Error bars, plus one standard error; s.n.h., sharks net⁻¹hr⁻¹.
- Figure 8.7 Length frequency distributions of (a) *Carcharhinus tilstoni* 220 and (b) *Rhizoprionodon acutus* caught in Cleveland Bay using 5 and 10cm gillnets. S.A.B., size at birth; S.A.M., size at maturity. Estimates of the sizes at birth and maturity based on data from Stevens and Wiley (1986), Stevens and McLoughlin (1991), and the present study.
- Figure 8.8 Clasper length as a proportion of total length to demonstrate 221 the size at maturity of male *Rhizoprionodon acutus* from Cleveland Bay. Open circles, uncalcified claspers; solid circles, calcified claspers.

TABLE OF PLATES

Plate 4.1	Section of a centrum from a 738mm TL female caught in January and estimated to be 5+ years. Arrows indicate circuli; B, circulus formed at birth; 1-5, circuli formed after 1-5 years.	53
Plate 6.1	Dissected adult female <i>Rhizoprionodon taylori</i> caught in early February showing the presence of large yolky ova (arrow heads) in the ovary prior to ovulation. Scale bar, 10mm.	120
Plate 6.2	Dissected adult female <i>Rhizoprionodon taylori</i> caught in late February. The yolky ova have been ovulated and eggs are present in the uteri (arrow heads). A large corpora atretica is present in the ovary (asterisk). Scale bar, 10mm.	120
Plate 7.1	Eggs from the uterus of a female <i>Rhizoprionodon taylori</i> showing the egg case (a) uncoiled, and (b) in natural position. E, egg; EC, egg case. Scale bars, 10mm.	170
Plate 7.2	Histological section through type A tubules of an adult female <i>Rhizoprionodon taylori</i> caught in early February, showing the presence of spermatozoa (arrow heads) in the lumen. Scale bar, 0.02mm.	171
Plate 7.3	Histological section of the lumen of the lateral horn from the oviducal gland of <i>Rhizoprionodon taylori</i> , showing the column shaped lamellae at the base of which type B tubules open. CL, columnar lamellae; L, lumen of gland. Scale bar, 0.1mm.	172
Plate 7.4	Histological section of part of the lateral horn of <i>Rhizoprionodon taylori</i> during ovulation showing the tufted	172

xv

lamellae and production of the sheet-like secretion (arrow heads) in type C tubules. L, lumen of gland; TL, tufted lamellae. Scale bar, 0.2mm.

- Plate 7.5 Sagittal histological sections through a diapausing 173 blastoderm of *Rhizoprionodon taylori* from a female caught in April 1988. Section (a) shows the anterior portion of the embryo, and (b) the posterior section. Em, embryo; SC, segmentation cavity; Y, yolk. Scale bars, 0.1mm (a) and 0.25mm (b).
- Plate 7.6 Development of *Rhizoprionodon taylori* embryos. (a) 6mm 174 embryo (arrow shows location of embryo), (b) 16mm embryo, (c) 38mm embryo, (d) 68mm embryo, (e) 133mm embryo, and (f) 235mm embryo. E, egg; F, fin buds; U, umbilical cord (or yolk stalk); X, external branchial filaments.
- Plate 7.7 Histological sections shoing the development of the yolk 175 stalk and umbilical cord in *Rhizoprionodon taylori* embryos. (a) 16mm embryo, (b) 38mm embryo, (c) 133mm embryo, and (d) 235mm embryo. A, appendiculae; D, ductus vitello-intestinalis; VA, vitelline or umbilical artery; VV, vitelline or umbilical vein. Scale bars, 0.2mm (a), 0.5mm (b), 0.3mm (c) and 0.4mm (d).
- Plate 7.8Histological section through a uterine septum of 176Rhizoprionodon taylori.M, mucosa; SG, sheet-like gland;SM, submucosa.Scale bar, 0.25mm.
- Plate 7.9 Histological section through the uterus of a mid-term 176 *Rhizoprionodon taylori* illustrating the four tissue layers.
 EC, egg case; M, mucosa; Mu, muscularis; Se, serosa; and SM, submucosa. Scale bar, 0.08mm.
- Plate 7.10 Histological sectionsd of the uterine mucosa of 177 *Rhizoprionodon taylori* from (a) the diapause, and (b) the

developmental, periods. The epithelial cells of the mucosa produce an apocrine secretion into the lumen of the uterus. B or arrows, blood vessels; EC, egg case; M, mucosa (epithelium); SM, submucosa. Scale bars, 0.05mm.

Plate 7.11 Histological section of the sheet-like gland (see text for 178 description) present in the submucosa of the uterus of *Rhizoprionodon taylori*. Arrows indicate tububles that make up the gland. Scale bar, 0.04mm.

Plate 7.12 Transmission electron micrographs of the epithelial cells 179 of the ductus vitello-intestinalis of *Rhizoprionodon taylori* showing vesicles (asterisk), microvilli (arrows) and cilia (arrow heads). (a) 10000 times, and (b) 5000 times, magnification.

Plate 7.13Histological sections of appendiculae of Rhizoprionodon180taylori, showing the form of the epithelial cells. (a) 36mmembryo, (b) 68mm embryo, and (c) 235mm embryo.36mmArrows, apocrine secretion; Arrow heads, microvilli; B,
blood vessel; CC, connective tissue; Ep, epithelium. Scale
bars, 0.02mm.500

Plate 7.14

Surface view of the epithelial cells of appendiculae of 181 *Rhizoprionodon taylori* showing absorptive cells (AC) with apical microvilli and secretory cells (SC) . (a) 36mm embryo, (b) 90mm embryo, and (c) 235mm embryo. Scales indicated on photographs.

Plate 7.15

External branchial filaments of *Rhizoprionodon taylori*. (a) 182 transverse histological sections, and (b) scanning electron micrograph. B, blood vessel; Ep, epithelial cells. Scale bar for (a) 0.03mm, scale for (b) on photograph.

- 183 Plate 7.16 General morphology of mature placenta of a A, appendiculae; DP, distal Rhizoprionodon taylori. portion of placenta (enveloped in uterine tissue); PP, proximal portion of placenta. Scale bar, 2mm.
- Plate 7.17 Histological section of a proximal portion of the mature 183 placenta of Rhizoprionodon taylori. Arrows, apocrine secretion; CC, connective tissue; Ep, epithelium. Scale bar, 0.06mm.
- Plate 7.18 Histological sections of the early placenta 184 of Rhizoprionodon taylori showing the developing interdigitation (a) and the tissue layers present at the maternal and embryonic interface (b). B, blood vessels; EC, egg case; EE, embryonic endoderm; ES, embryonic squamous epithelium; MS, maternal squamous epithelium; Y, Yolk. Scale bars, 0.3mm (a) and 0.04mm (b).

Plate 7.19

Histological sections of the mature placenta of Rhizoprionodon taylori showing the complex interdigitation of the uterus and yolk sac (a) and the cellular detail at the maternal-embryonic interface (b). Arrow heads, maternal-embryo interface; B, blood vessel; EC, egg case; RS, remnant submucosa; Y, yolk. Scale bars, 0.3mm (a) and 0.015mm (b).

xviii

185

Acknowledgements

There are many people without whom this project would not have been a success. Thanks firstly to Associate Professor Norm Milward who provided me with the opportunity of study such fascinating creatures, and who supervised my project. The assistance of the many people who assisted me in the field is gratefully acknowledged. Most were residents of St. Paul's College, in particular I would like to thank Tim Graham, Mitch Rologas, Bernie Reid and Rob Marano for their assistance through the years. Special thanks must also go to Glen Kleidon for his assistance in the laboratory, especially with the preparation of vertebrae.

The support staff in the School of Biological Sciences were also invaluable; thank you for your patience and support. In particular to Jon Peters and Phil Osmond for their helpfulness with nautical matters. Heather Winsor provided valuable assistance with the preparation of specimens for electron microscope work. The assistance of Zolly Florian with photomicrography is also gratefully acknowledged. A very special thank you must also be extended to Leigh Winsor, a genius in the histology lab, for his advice and assistance on a whole range of technical matters.

The advise of fellow shark researchers is also gratefully acknowledged. In particular John Stevens and Jeremy Lyle provided information and advice from their extensive experience in northern Australia.

To my fellow post-graduatye students, thank you for your help, support and encouragement. Thanks also to all the inhabitants of the Biological Sciences Building who tolerated the smell of dead sharks. Finally I would like to thank my family and friends for their support during this project. And to , thank you for your patience and support.

xix