10

BIOLOGY AND ECOLOGY OF FOUR CATSHARK SPECIES IN THE SOUTHWESTERN CAPE, SOUTH AFRICA

Alison M. Dainty

This thesis is submitted for the degree of
Master of Science

Zoology Department and Marine Biology Research Institute,
University of Cape Town

November 2002

For my parents, James and Dee Marie, and sister, Megan – with all my heart, thank you for your unconditional love, support and encouragement

DECLARATION

I hereby declare that all the work presented in this thesis is my own, except where otherwise stated in the text. This thesis has not been submitted for a degree at any other university.

…………………………………	…………………………………
Alison M. Dainty	Date

TABLE OF CONTENTS

ABSTRACT

This is the first biological study of four endemic catshark species, *Haploblepharus edwardsii, H. pictus, Poroderma africanum* and *P. pantherinum*, from the southwestern Cape. Diets of two hundred and forty-one specimens were examined via stomach contents. Prey were sorted and identified to the lowest possible taxon. An Index of Relative Importance (IRI = %F(%N + %V)) was used to determine the importance of prey items in the catsharks' diets. The most important prey groups for *H. edwardsii* (*n* = 39) were crustaceans (IRI = 6125), annelids (IRI = 4177) and teleosts (IRI = 1859); crustaceans (IRI = 7656), teleosts (IRI = 4154) and molluscs (IRI = 152) for *H. pictus* (*n* = 22); teleosts (IRI = 9694), molluscs (IRI = 784) and crustaceans (IRI = 612) for *P. africanum* (*n* = 121); and molluscs (IRI = 3367) and teleosts (IRI = 2574) for *P. pantherinum* (*n* = 44). Males and females of each species ate similar prey, although the importance of some prey varied. The most important prey taxa were annelids (IRI = 5740) for female and crustaceans (IRI = 7568) for male *H. edwardsii*; crustaceans for both male (IRI = 9300) and female (IRI = 5963) *H. pictus*; teleosts for both sexes of *P. africanum* (male, IRI = 5394; female, IRI = 4760); and molluscs for both male (IRI = 3180) and female (IRI = 2250) *P. pantherinum*. The importance of teleosts decreased with increasing shark size for all four catshark species. An increase of importance of crustaceans with increasing size was apparent for *H. pictus* and *P. africanum*. The importance of molluscs was independent of size for *H. pictus*, although their importance increased with increasing size for both *Poroderma* species. *H. edwardsii*, *H. pictus* and *P. africanum* all seem to be generalist feeders, preying upon a variety of food sources, while *P. pantherinum* has a more specific diet, feeding almost exclusively on teleosts and molluscs.

To estimate gastric evacuation rates of the three catshark species, *Poroderma africanum*, *P. pantherinum* and *Haploblepharus pictus* were maintained in laboratory conditions and fed meals equaling 1% of their body weight (BW). Food items included clipfish, *Clinus spp.*, octopus, *Octopus vulgaris*, and sandprawn, *Callianassa kraussi*. Catsharks were sacrificed at intervals after feeding to measure rates of gastric emptying. Data were fitted to various models to describe the decrease of stomach contents with time. The generalized additive linear model provided the best fit for all food types. Evacuation rates varied between prey types for the three shark species, with octopus (19.5-24.5 hours) taking the least time for 95% of the meal to be evacuated, followed by fish (36-48 hours) and prawn (70 hours – *H. pictus* only). For most data, the model revealed an initial period of maximum evacuation, followed by a decreased rate until complete evacuation. Some data indicated a 'plateau' phase, where the emptying rate decreased after the initial maximum period of evacuation and then continued again in an increased rate until complete evacuation. There were no significant differences ($p<0.001$) of gastric evacuation rates among species fed the same prey item. Passage of food from the stomachs of these three shark species is slow relative to teleost fishes, but comparable to that recorded in other elasmobranch species.

Life history information was collected on 86 *Poroderma africanum*, 71 *P. pantherinum*, 68 *Haploblepharus edwardsii* and 116 *H. pictus* from various sites in the southwestern Cape, South Africa, between February 2000 and May 2002. Gonad characteristics and embryo development suggest a year-round breeding season for all four species in this area. The slopes of the length-weight curves were significantly different ($p<0.001$) between sexes for both *Poroderma* species and for *H. edwardsii,* but there was no significant difference ($p>0.05$) between sexes for *H. pictus*. Total length at 50% maturity was 857 mm for male *P. africanum* and 866 mm for females (91% asymptotic length for both sexes), 590 mm (85% asymptotic length) for male *P. pantherinum* and 595 mm for females (85% asymptotic length). For *H. edwardsii*, sex-combined data reveal a 351 mm TL at 50% maturity (71% asymptotic length). Male *H. pictus* reach 50% maturity at 503 mm TL (78% asymptotic length) in contrast to 491 mm (77% asymptotic length) for females. Resin embedding techniques revealed transluscent and opaque growth band formation on sectioned vertebrae for the four catshark species. Based on the length/weight data of three tagged/recaptured *P. africanum* individuals and the good fits of the Schnute growth model to the length/age data for all specimens, growth band formation was considered annual for the four shark species. Ages calculated for length at 50% maturity were 24 years for *P. africanum*, 17 years for *P. pantherinum*, 7 years for *H. edwardsii* and 15 years for *H. pictus*.

ACKNOWLEDGMENTS

I would first like to thank my entire family for your emotional support throughout my adventure here. Special thanks go to my parents and sister - I could not have asked, wished or dreamed for a more loving and caring family whom I cherish greatly.

To my close friends in Cape Town who have made my time here such an incredible experience, you are the best: Lucille Gibbons, Lyndsay Webster-Rozon, Bruce Becker, Izak Joubert, Paul O'Riordan, François Rozon, and Jodi and Jeroen DeLijster. To my best friends back home: Erin Edwards, Leann Calvi, John Muehrcke, Blake Kuehn, Jeff Watts, Matt Damiano and Bill Altimari. You and your friendships are so important to me; I have missed you terribly these past two and a half years! Thank you, Guy and Emma Elliott, for giving me a home away from home. You and your children are so special; I can never thank you enough for everything you have done for me, especially through the extremely difficult times.

Thank you, Charles Griffiths, for giving me the opportunity to attend this university. My life has changed from this experience – thanks for believing in me enough to give me a chance! Thanks to Leonard Compagno for giving me your time when I needed it, and for helping me through some difficult times when I was especially homesick. Thanks to Anesh Govender, for your insight, support and expertise, and you utter kindness in helping me find my way when I was lost. Thank you Jaqui Sommerville and June Juritz for all the stats help. To the "Arrive and Dive" team: Andrea Plos, Karl Reinecke and Debbie Robertson-Andersson. I could not have done any of my fieldwork without you!

Financial support was provided through a grant provided to CLG and GMB via the Sea and Coast II Project - a joint venture between the National Research Foundation and Department of Environmental Affairs and Tourism.

And finally, thank you Duncan Elliott, for the incredible impact you made on my mind and spirit. I will forever carry with me your energy and passion for life.

GENERAL INTRODUCTION AND METHODS

The order Carcharhiniformes, or groundsharks, is the world's dominant group of sharks comprising eight families and at least 207 known species (Compagno 1999). The group is highly varied, including smaller, more primitive catsharks and some of the larger and most dangerous sharks, such as *Carcharinus leucas* and *Galeocerdo cuvieri.* Scyliorhinidae (catsharks) is the largest of the eight families, comprising at least 15 genera and 100 species (Compagno *et al.*1989). Catsharks are small (rarely exceeding 100 cm total length – TL) demersal sharks, found in temperate and tropical waters, from the intertidal zone to depths of over 2000 m (Compagno 1987).

At least 15 species of catsharks (ten endemics) occur in Southern Africa (Table 1.1) (Compagno *et al.* 1989). *Poroderma africanum, P. pantherinum, Haploblepharus edwardsii* and *H. pictus* are endemic scyliorhinids that occur on inshore reefs along the southwestern Cape coast (Fig. 1.1). *H. pictus* is found from Cape Agulhas to the lower west coast of Namibia, whereas the other three species occur from the southwestern Cape to KwaZulu-Natal (Branch *et al.* 1994).

Although all four species are considered common in the southwestern Cape (Smith and Heemstra 1986; Compagno *et al.* 1989; Branch *et al.* 1994), only two studies have documented estimated density values for these catshark species in this area (Prochazka 1994; Lechanteur in press). Prochazka (1994), using rotenone to collect cryptic fish, estimated scyliorhinid densities at 5 fish.100 m^{-2} in 0-10 m of water, whereas Lechanteur (in press) obtained a much lower density estimate of not more than 0.60 fish.100 m^{-2}, using the instantaneous stationary point count census method. True densities probably lie between these extremes, as catsharks are difficult to see in visual transects, but tend to be attracted to distressed fish in areas distributed with rotenone.

While *Haplobleparus* species favour sand inundated reef, *Poroderma* species are generally found on rocky reefs (Compagno *et al.* 1989). However, all four species can be found among inshore kelp beds. *H. pictus* are most commonly found in shallow waters, while *H.*

Table 1.1. Catshark species recorded from Southern Africa (from Compagno *et al.* 1989). The four species in this study are shown in bold.

Scientific Name	Common Name	Distribution	Depth Range
Family Scyliorhinidae			
Apristurus microps	Smalleye Catshark	Gariep River to Cape Agulhus	700-1016 m
_Apristurus saldanha_*	Saldanha Catshark	Cape Columbine to False Bay	453-717 m
_Cephaloscyllium sufflans_*	Balloon Shark	Natal to Mozambique	40-600 m
Galeus polli	African Sawtail Catshark	South coast of Namibia to southern Morocco	200-720 m
_Halaelurus lineatus_*	Lined Catshark	East London to Mozambique	inshore to 290 m
Halaelurus lutarius	Mud Catshark	Mozambique, Somalia	338-766 m
_Halaelurus natalensis_*	Tiger Catshark	Cape Agulhas to East London	inshore to 172 m
___Haploblepharus edwardsii___*	**Puffadder Shyshark**	**Cape Agulhas to KwaZulu-Natal**	**inshore to 130 m**
_Haploblepharus fuscus_*	Brown Shyshark	West of Cape Agulhas to southern KwaZulu-Natal	shallow water
___Haploblepharus pictus___*	**Dark Shyshark**	**Swakopmund to west of Cape Agulhas**	**inshore**
Holohalaelurus punctatus	African Spotted Catshark	Natal and southern Mozambique, possibly Madagascar, Kenya and Tanzania	220-420 m
Holohalaelurus regani	Izak Catshark	Southern Namibia to southern Mozambique, possibly Kenya and Somalia	160-740 m
___Poroderma africanum___*	**Pyjama Shark**	**Saldanha Bay to north of East London**	**inshore to 100 m**
___Poroderma pantherinum___*	**Leopard Catshark**	**Saldanha Bay to central KwaZulu-Natal**	**inshore to 256 m**
_Scyliorhinus capensis_*	Yellowspotted Catshark	Luderitz to KwaZulu-Natal	26-495 m
Family Proscylliidae			
Eridacnis sinuans	African Ribbontail Catshark	KwaZulu-Natal to southern Mozambique, Tanzania	180-480 m
* endemic to Southern Africa			

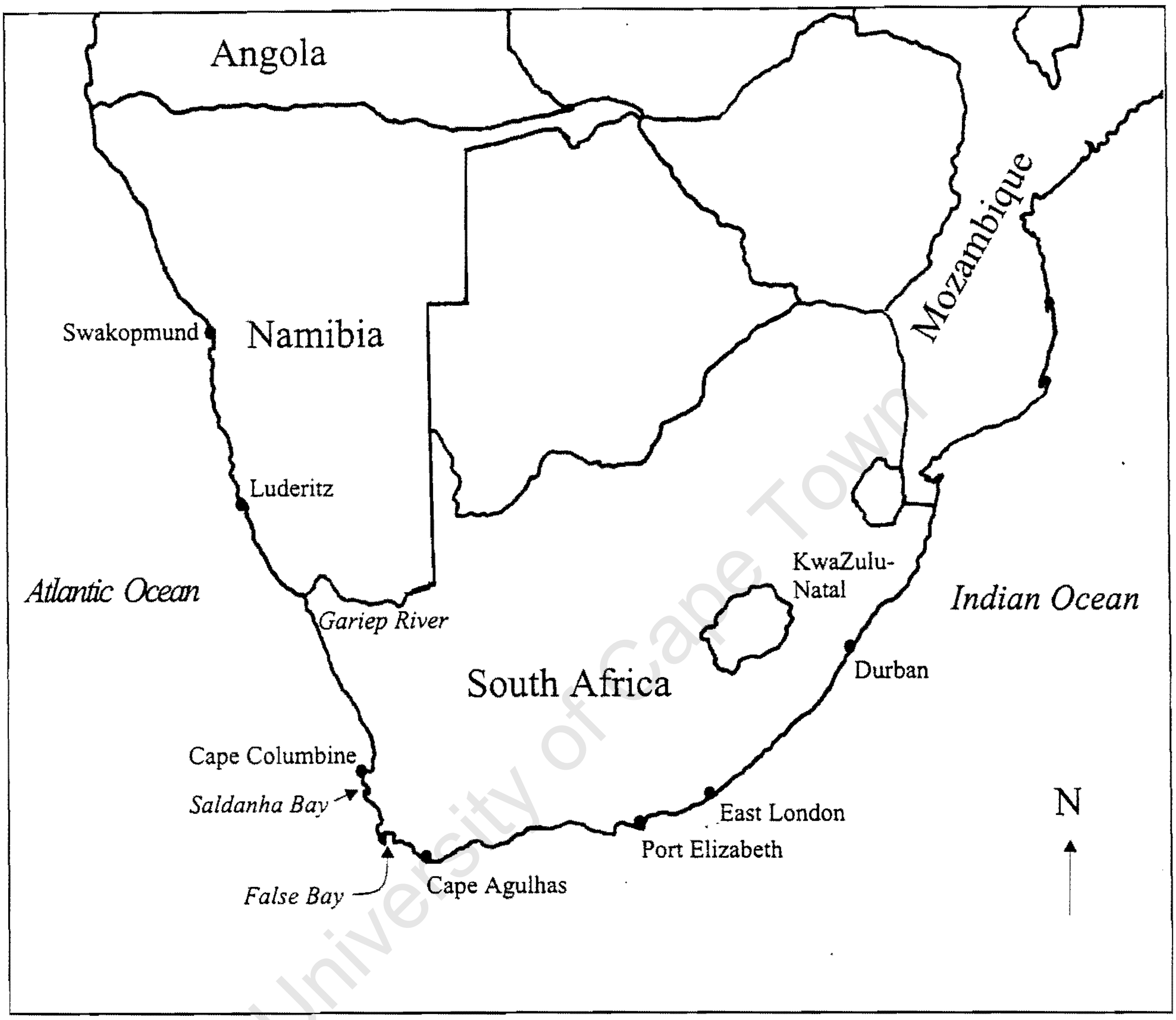


Fig. 1.1. Map of southern Africa showing localities referred to in the text and in Table 1.

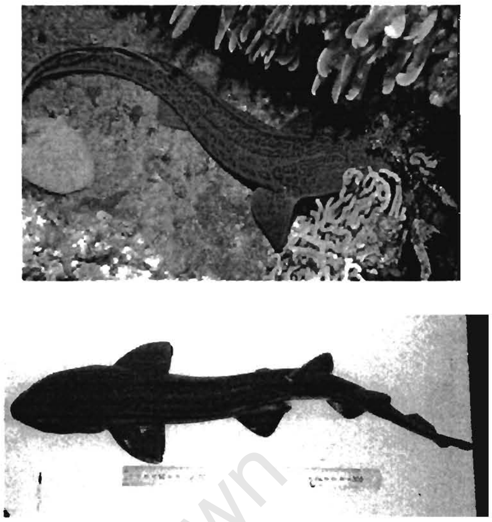
edwardsii can also occur to a depth of 130 m, *P. africanum* to 100 m and *P. pantherinum* to 256 m (Compagno *et al.* 1989).

A common name for the *Haploblepharus* species is 'shyshark', because when aggravated the sharks curl into a ring with their caudal fin covering their snouts (Branch *et al.* 1994). However, the same behaviour has also been observed for both *Poroderma* species (pers. obs.). These sharks were initially called lazy sharks (von Bonde 1945), due to their tendency to huddle in groups within crevices, or to lay immobile on the ocean floor. However, these sharks are mostly nocturnal and are quite active predators at that time. Among the four species, *P. africanum* and *P. pantherinum* are the largest, attaining 1000 and 740 mm, respectively, while *H. pictus* and *H. edwardsii* each reach about 600 mm (Compagno *et al.* 1989).

Although the easiest means of identification of these catsharks is colour markings, there can be significant variations among specimens. There has been only one type of *P. africanum* observed and recorded in the literature (Compagno *et al.* 1989; Smith and Heemstra 1986), with a grayish background and black stripes along the length of the body (Fig. 1.2). There are two forms listed for *H. edwardsii*, a Cape form, with a cream background with tan saddles and white spots, and a KwaZulu-Natal form, with dark, irregular splotches and white spots on a cream background. However, for the remaining two species, there are numerous variations. There are three common color skin color or pattern variations recorded in the literature for *P. pantherinum* (Compagno *et al.* 1989). Of these, only the 'typical' variation with a gray background and black rosettes of spots has been observed during this study. In addition, specimens that are entirely black (except for a white and grayish ventral surface), or specimens that are black but with a visible combination of lines running the length of the shark and spots (as noted in the 'typical' form) were collected (Fig. 1.2). There are also multiple colour differences among *H. pictus*, although only one form, with dark markings and lighter splotches over a yellowish background, has been recorded in the literature (Smith and Heemstra 1986; Compagno *et al.* 1989; Branch *et al.* 1994). However, specimens that have dark brown saddles over a

Poroderma africanum

Poroderma pantherinum



Haploblepharus edwardsii

Haploblepharus pictus

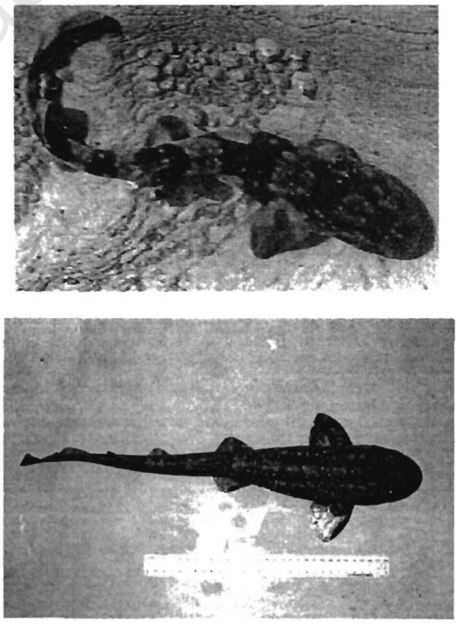


Fig. 1.2. *Poroderma africanum*, *Haploblepharus edwardsii*, and examples of the various color patterns of *P. pantherinum* and *H. pictus*.

dark brown background, or this color pattern with multiple white spots, were collected in this study (Fig. 1.2).

As the four species co-occur between False Bay and Cape Agulhas, this coastline provides a useful area to study various aspects of their ecology and biology. Little research has been done on Southern African catsharks, most likely due to their small size and lack of commercial value. Garman (1913) was the first to describe the species under the genera *Haploblepharus* and *Poroderma*. Von Bonde (1945) published work regarding the external development of *H. pictus* (originally listed as *H. edwardsii*, however was probably *H. pictus*, Bass 1975) and *P. africanum*. Published works since that time consist of only general dietary, morphometric and taxonomic information (Bass *et al.* 1975; Compagno 1984; Michael 1993; Branch *et al.* 1994; Hamlett 1999), but with no direct estimates of diet or growth. Bertolini (1993) conducted preliminary analyses of dietary composition, digestion, age, growth and reproduction of these four species in an MSc thesis project, however this project was never completed or submitted either for degree purposes or for publication.

Catsharks are abundant in kelpbeds (Prochazka 1994; Lechanteur in press) and are likely to be very important predators in that environment. Diet, consumption rates, and age and growth analyses are just a few components of catshark biology, which will lead to a better understanding of their life histories. In turn, this understanding may give insight into not only the impact catsharks have in their environment, but the food webs in South Africa's coastal marine ecosystems. Due to the lack of detailed biological and ecological information regarding these four catshark species, the aims of this thesis are to examine these issues in the following chapters:

> Chapter 2 examines the diet composition of the four catshark species at several sites in the southwestern Cape. Percentages for volume, frequency of occurrence and number are determined to calculate an Index of Relative Importance (IRI) for each prey group consumed.

Chapter 3 measures the gastric evacuation rates of captive sharks, using the major prey components measured from the diet study (Chapter 2). Due to various evacuation rates of different foods, prey analyzed in the diet study may be over- or underestimated as important food sources.

Chapter 4 focuses on age, growth, and sexual maturity of the four catsharks. To calculate age, the number of 'bands' present along a longitudinally sectioned vertebra for each species was examined, based on the assumption that one band pair (hyaline and opaque) represents one year of growth. Tag/recapture methods were used in an attempt to verify annual band deposition. To measure growth, length-weight relationships of captured sharks and neonates hatched in captivity were also examined. To assess maturity and aspects of sexual reproduction, measurements of sexual characteristics for both sexes (i.e. gonad weight, clasper length, basal clasper width, largest egg diameter and shell gland diameter) were measured.

Methods

The following general methodology applies to Chapters 2-4. Additional methods specific to individual sections are given in the relevant chapter. Sharks were collected from a number of sites in the southwestern Cape between June 2000 and February 2002. Maps of these sites are given within each chapter. SCUBA diving or snorkeling in shallow, inshore waters (0-10 m) was required to collect specimens. Bait bags made of shade cloth were filled with pilchards (*Sardinops sagax*) and attached to holdfasts of kelp. Up to six bait bags were placed in the diving area at least 5 m apart. Generally within a few minutes, catsharks were attracted to the area and either circled the bag or fiercely bit it. The sharks were grabbed at mid body and placed in large collection bags. If no sharks approached the area after 5 minutes of attaching the bait bag, the bag was moved to a new location in the dive site. No other sharks besides the four catshark species were ever observed near the bait bags.

Collected specimens were placed in plastic bins filled with seawater and fitted with a portable aerator (when available). Sites were generally limited to an area close to the university in order to reduce stress and prevent casualties. Only a few sharks during the 20-month sampling period died due to stress from the trip between the capture site and the aquarium tanks.

Sharks were held in closed system, portable swimming pools in the Zoology Department at the University of Cape Town. Specimens were fed *ad libitum* freshly frozen and defrosted pilchards (*Sardinops sagax*), generally twice a week, until they were used for the digestion rate experiment. Vertebrae from sharks used in this experiment were subsequently used for age and growth analyses.

DIETS OF FOUR CATSHARK SPECIES FROM THE SOUTHWESTERN CAPE, SOUTH AFRICA

INTRODUCTION

Haploblepharus edwardsii (puffadder shyshark), *H. pictus* (dark shyshark), *Poroderma africanum* (pyjama shark) and *P. pantherinum* (leopard catshark) are species of catshark commonly found inshore off the coast of South Africa. Despite the abundance of these sharks (Prochazka 1994; Lechanteur in press), there is little known regarding their dietary habits, or their roles as predators. Current diet information for these species is based on generalized, descriptive accounts, indicating that crustaceans, teleosts and cephalopods are primary dietary components (Bass *et al.* 1975; Compagno 1984; Smith and Heemstra 1986; Compagno *et al.* 1989). However, as these catsharks may be very important predators in their environment, there is a need for a quantitative diet study directed solely to these species.

These four catsharks are all endemic to southern Africa, with only *H. pictus* occurring from the southwestern Cape, north to Namibia, while the other three species occur from the Cape, eastwards and northwards to Mozambique. Because the habitats of all four species overlap in the southwestern Cape, the dynamics of interspecific competition for food are unique to this area. According to Lechanteur (in press), both *Haploblepharus* and *Poroderma* species are amongst the most abundant macropredatory reef fish species in False Bay, along with red roman (*Chrysoblephus laticeps*). Predatory interactions may also extend to intraspecific competition, since seemingly all class sizes and both sexes can be found in the same areas (pers. obs). Therefore, the predatory role of catsharks is most likely very important and must be evaluated in order to understand the trophic relationships of the inshore marine community in the region.

Several studies have described the dietary components of sharks in South Africa, however, most of these studies deal with large, pelagic sharks - such as *Carcharodon carcharias* (Cliff *et al.* 1989), *Carcharinus leucas* (Cliff and Dudley 1991) and *Carcharhinus brachyurus* (Smale 1991), or large, inshore species like *Notorynchus cepedianus* (Ebert 1991). Of the 15 catshark species found in southern Africa, the only extensive dietary analyses have been of the Izak catshark, *Holoalaelurus regani* (Richardson *et al.* 2000), and a preliminary study on *Apristurus microps, A. saldanha, A. spp., Galeus polli, H. regani* and *Scyliorhinus capensis* (Ebert *et al.* 1996). Both studies showed all these species prey largely upon crustaceans, cephalopods and teleosts. Similarly, international studies on the prey composition of catsharks are few, including those on the false catshark, *Pseudotriakis microdon*, in Japan and New Zealand (Yano and Musick 1992), the redspotted catshark, *Schroederichthys chilensis*, in Chile (Fariña and Ojéda 1993), and the narrow mouthed catshark, *Schroederichthys bivius*, in Argentina (Matallanas *et al.* 1993). These studies also concluded that the catsharks were important predators in their environment. This paper aims to compare the diets of the four most common species, and to determine whether there are size or sex related dietary differences within individual species.

METHODS

Specimens were collected by hand while SCUBA or free diving, or on hook and line, between February 1997 and May 1998 at various sites in the southwestern Cape, South Africa (Fig. 2.1). M.A. Marks (a previous postgraduate student, who began but did not complete this study) collected all sharks and made a preliminary analysis of stomach contents. All species were collected at two sites at Danger Point (34°38'S; 19°19'E and 34°38'S; 19°17'E) and Pearly Beach (34°38'S; 19°26'E). Only *H. edwardsii* were collected at Black Sophie (34°37'S; 19°22'E). All study species except *H. pictus* were collected at Gruis (34°37'S; 19°23'E), and all but *H. edwardsii* at Hout Bay (34°03'S; 18°21'E). For each site, details regarding depth, time of day, environmental conditions and date of capture were recorded. All sharks were sexed, measured to the nearest millimeter (mm) and weighed. Morphometric data collected included; total length (TL), precaudal length (PRC), distance from the second dorsal fin to the tip of the upper lobe of the caudal fin (D2C) and total weight (WT).

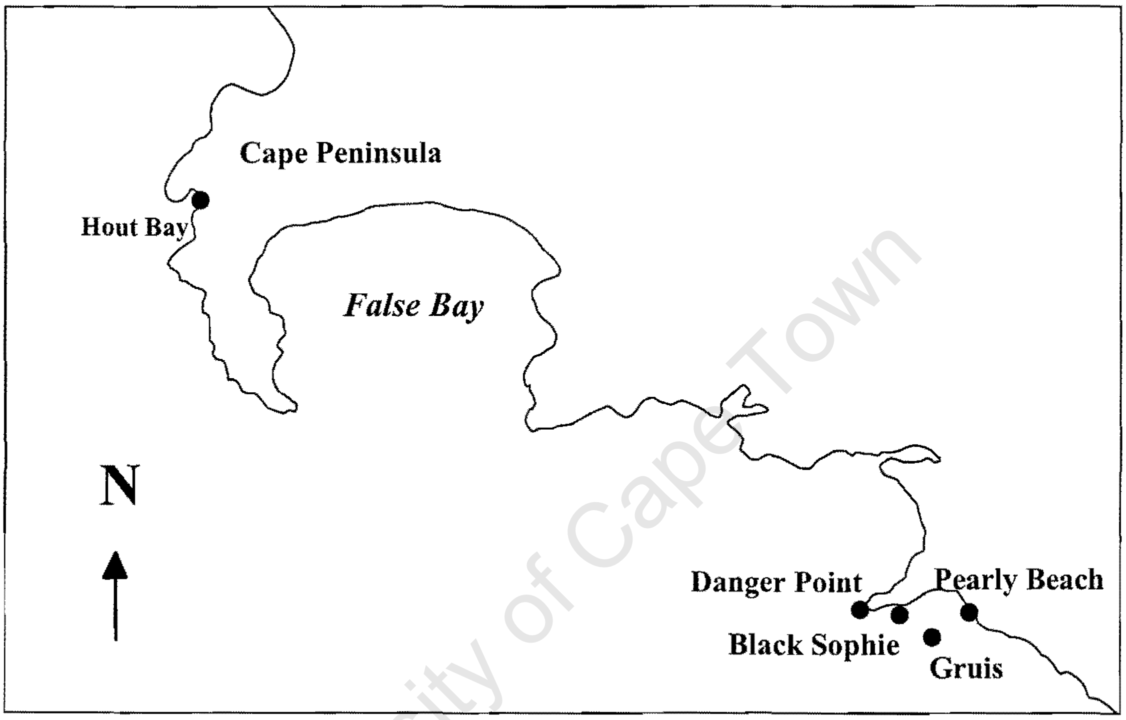


Fig. 2.1. Map of study sites in the southwestern Cape.

Shark stomachs were removed and contents were either sorted immediately or preserved in 10% formalin. Gut contents were run through several sieves, ending with a 280 μm sieve. Prey matter was sorted, counted and identified to the lowest possible taxonomic level.

A direct estimation of food volume was determined through the fluid displacement method previously described by Hyslop (1980), where each food item was sorted from stomach contents and measured in a graduated cylinder by displacement volume. The volume of individual prey items (e.g. *Octopus vulgaris*) and prey categories (e.g. Mollusca), were calculated as a percentage of the total prey items found in all stomach contents (Pinkas *et al.* 1971). Prey groups that made up 5% or more of the total prey volume were considered major dietary sources.

The frequency of occurrence and number of prey items were also calculated as percentages. Frequency was measured as the number of sharks that consumed a particular prey item, rather than how often it occurred in a single individual. The percent number was calculated from the total number of prey identified from all sharks analyzed.

Independently, these measures only give a partial picture as to which prey groups are more important in the diet. For example, very small items, such as copepods, may occur in most sharks, but are insignificant in terms of food volume; whereas large items may represent a large percentage in the volumetric analysis, although are eaten by very few individuals. Therefore, the index of relative importance (IRI) (Pinkas *et al.* 1971) was used to assess which dietary components were the most significant. This index combines percentages for volume (%V), number (%N) and frequency of occurrence (%F) in the following equation:

$$\text{IRI} = \%\text{F}(\%\text{N} + \%\text{V}) .$$

Percentage compositions of major identifiable prey groups among the four catshark species were compared, as well as differences among sexes and class sizes. To compare size - related changes in the diet, sharks were divided into approximately 100 mm size classes. Data (as inherited by M.A. Marks) were only available in pooled form, therefore statistical analyses could not be used to find significant dietary differences between and within catshark species.

RESULTS

Stomach content analyses were performed on 226 sharks – 39 *Haploblepharus edwardsii*, 22 *H. pictus*, 121 *Poroderma africanum,* and 44 *P. pantherinum*. The number of empty stomachs was not recorded, but was minimal. For *H. edwardsii*, 11 females and 28 males were examined and two size classes were assigned: 300 – 399 mm TL (*n* = 28) and 400 – 499 mm TL (*n* = 11). Nine female and 13 male *H. pictus* were analyzed and the three size classes recognized were: 300 – 499 mm (*n* = 7), 500 – 599 mm (*n* = 8) and 600 – 699 mm TL (*n* = 7). Due to the small numbers of specimens in the 300-399 mm (*n* = 3) and 400-499 mm (*n* = 4) TL size classes, these groups were subsequently pooled. For *P. africanum*, there were 40 females and 81 males examined. These were divided into five size classes: 500 – 699 mm (*n* = 9), 700 – 799 mm (*n* = 29), 800 – 899 mm (*n* = 44), 900 – 999 mm (*n* = 13) and 1000 – 1099 mm TL (*n* = 26). There were only two specimens between 500-599 mm TL, so they were pooled with the next class size. Twenty-four female and 20 male *P. pantherinum* were analyzed and three size classes were recognized: 300 – 399 mm (n = 9), 500 – 599 mm (n = 14) and 600-799 mm TL (n = 21). No sharks between 400 and 499 mm TL were collected. Only two specimens were 700 – 799 mm TL, so these were pooled with the lower class size.

Dietary differences between species

A high percentage volume of teleosts was found in the diet of all four species - *Haploblepharus edwardsii* (50%), *H. pictus* (40%), *Poroderma pantherinum* (44%) and *P. africanum* (68%) (Fig. 2.2). The majority of the remaining diet was comprised of annelids (%V = 21) and crustaceans (%V = 29) for *H. edwardsii*, crustaceans (%V = 34) and molluscs (%V = 13) for *H. pictus*, and molluscs for *Poroderma africanum* and *P. pantherinum* (%V =

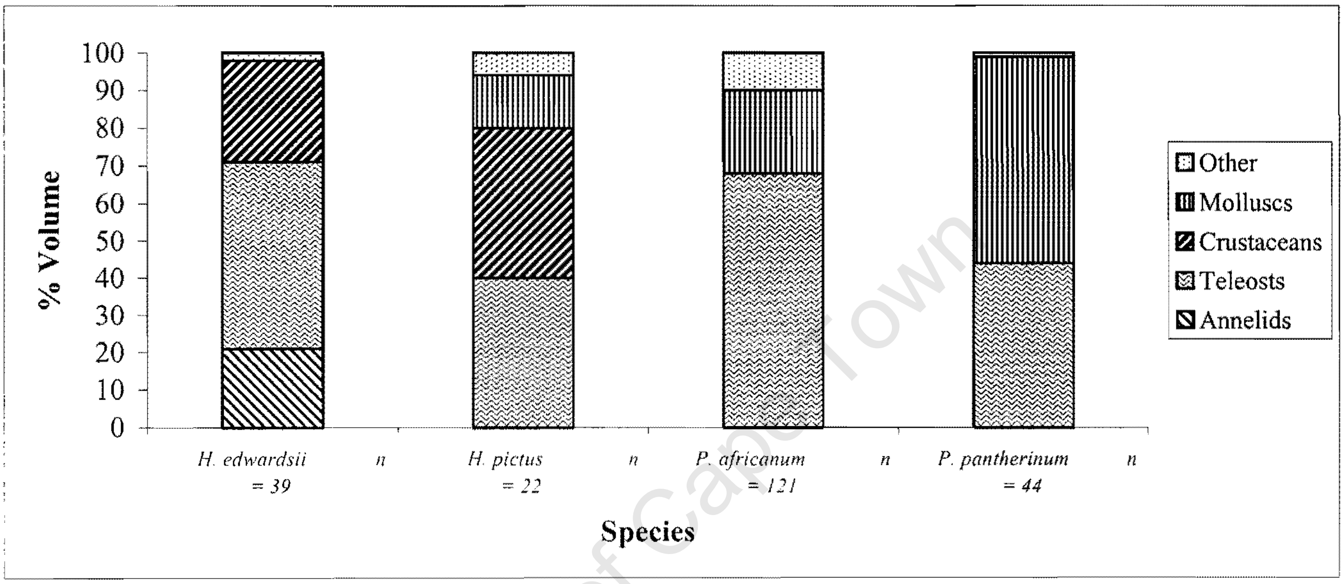


Fig. 2.2. Comparison of major prey items from stomach contents in terms of percent volume for: *Haploblepharus edwardsii, H. pictus, Poroderma africanum* and *P. pantherinum*.

22 and %V = 44, respectively). A more detailed breakdown of the diets of the individual catshark species yielded the following results.

Haploblepharus edwardsii

Crustaceans were the most important phylum consumed (IRI = 6125) by *H. edwardsii* (Table 2.1). Within crustaceans, unidentified crustaceans, ostracods and reptantians were the most abundant prey. Annelids were the second most important prey phylum with an IRI of 4177, followed by chordates (IRI = 1859). Although approximately 28% of *H. edwardsii* consumed cephalopods and the group was important with an IRI of 235, their number (6%) and volume (2%) were quite low. Nereids were identified in the largest numbers (24%), occurred most frequently (44%), and were the most important (IRI = 1589) of any individual group of prey. However, *Sardinops sagax*, the only teleost species to be identified to species, ranked highest in terms of volume (28%) of any individual prey.

Haploblepharus pictus

Teleosts were the most important prey group (IRI = 4807) and were highest in prey volume (49%) for *H. pictus* (Table 2.2). Crustaceans were second in terms of importance (IRI = 2600) and volume (34%), followed by molluscs (IRI = 1305, %V = 13). The majority of the molluscs found were unidentified cephalopods, but the gastropod, *Haliotis midae*, was also recognizable in the diet. Most of the teleosts found in stomach contents could not be identified to species, yet a high proportion in terms of volume (26%) and frequency (23%) were *Sardinops sagax*. Crustaceans numbered the most (47%) of all major groups. Of these, ostracods were the most frequently found prey items with a (11%), but the crab, *Plagusia chabrus*, overwhelmingly had the highest volume (15%). There were only two records of nereids and one record each of echinoids and an unidentified annelid.

Poroderma africanum

For *P. africanum*, the most important prey group was teleosts (IRI = 3648) (Table 2.3). Crustaceans were secondary in dietary importance (IRI = 1400), but made up an extremely low proportion of total volume (< 1%), yet were found in the highest numbers (88%).

Table 2.1. Stomach contents of *Haploblepharus edwardsii* ($n = 39$) expressed as percentage numbers (%N), volume (%V) and frequency of occurrence (%F) as well as Index of Relative Importance (IRI). Percentage and IRI totals for each phylum are in bold print. All other totals represent material identified to the lowest possible taxonomic level (eg. Decapoda = unidentified decapods).

Prey item	%N	%V	%F	IRI
CNIDARIA				
Virgularia schultzei	**0.43**	**0.02**	**2.56**	**1**
ANNELIDA	**39.49**	**20.84**	**69.23**	**4177**
Polychaeta	14.59	7.11	23.08	501
Sabellastarte longa	0.87	1.30	5.13	11
Nereididae	24.03	12.43	43.59	1589
BRACHIOPODA	**0.43**	**0.03**	**2.56**	**1**
CRUSTACEA	**45.91**	**28.74**	**82.05**	**6125**
Malacostraca	1.28	0.15	7.69	11
Amphipoda	5.58	1.10	12.82	86
Decapoda	0.43	0.03	2.56	1
Natantia	1.29	0.33	5.13	8
Reptantia	1.72	9.65	10.26	117
Anomura	1.72	2.39	10.26	42
Brachyura	4.72	1.47	17.95	111
Plagusia chabrus	1.28	5.05	7.69	49
Macrura	1.72	2.39	10.26	42
Euphausiacea	0.43	0.11	2.56	1
Isopoda	1.28	0.29	5.13	8
Glyptiodotea lichtensteini	0.87	0.12	5.13	5
Tylos capensis	0.43	0.01	2.56	1
Mysidacea	0.43	0.02	2.56	1
Stomatopoda	1.28	0.49	5.13	9
Ostracoda	14.16	0.42	15.38	224
Unidentified crustaceans	7.29	4.72	28.21	339
MOLLUSCA				
Cephalopoda	**6.01**	**2.31**	**28.21**	**235**
CHORDATA	**7.73**	**48.06**	**33.33**	**1859**
Teleostei	5.58	20.41	23.08	600
Sardinops sagax	2.15	27.65	10.26	306

Table 2.2. Stomach contents of *Haploblepharus pictus* (*n* = 22) expressed as percentage numbers (%N), volume (%V), frequency of occurrence (%F) and Index of Relative Importance (IRI). Percentage and IRI totals for each phylum are in bold print. All other totals represent material identified to the lowest possible taxonomic level (eg. Brachyura = unidentified brachyurans).

Prey item	%N	%V	%F	IRI
ANNELIDA	**6.16**	**3.14**	**13.64**	**127**
Nereididae	4.62	2.97	9.09	69
Unidentified annelid	1.54	0.17	4.55	8
CRUSTACEA	**47.71**	**34.01**	**31.82**	**2600**
Decapoda				
Reptantia	3.08	0.52	9.09	33
Anomura	1.54	0.10	4.55	7
Brachyura	3.08	2.11	9.09	47
Plagusia chabrus	9.23	14.51	27.27	647
Macrura				
Jasus lalandii	3.08	7.93	9.09	100
Scyllarides elizabethae	4.62	5.92	13.64	144
Isopoda	1.54	0.26	4.55	8
Exosphaeroma kraussii	1.54	0.01	4.55	7
E. laeviusculum	3.08	0.01	4.55	14
Ostracoda	10.77	0.02	13.64	147
Unidentified crustaceans	6.15	2.62	18.18	159
MOLLUSCA	**18.45**	**13.44**	**40.91**	**1305**
Gastropoda				
Haliotis midae	3.08	12.48	9.09	145
Cephalopoda	15.37	0.96	31.82	520
ECHINODERMATA				
Echinoidea	**1.54**	**0.01**	**4.55**	**7**
CHORDATA	**26.14**	**49.40**	**63.64**	**4807**
Teleostei	16.91	23.89	50.00	2040
Sardinops sagax	9.23	25.51	22.73	790

Molluscs were third in importance, with an IRI of 986. Agnathans (IRI = 4), echinoderms (IRI = 1), annelids (IRI = 3) and cnidarians (IRI = 2) also played a role in the diet, but were not considered major food sources. *P. africanum* was the only shark species that had elasmobranch remains in the stomach. This group, however, made a small contribution to the total diet (IRI = 36). Ostracods made up the bulk of all prey identified (76%), but were an extremely small proportion of the total volume (< 1%). Teleosts dominated the total volume of prey identified (68%). Six species of teleosts were identified and *Sardinops sagax* had the highest volume (56%) of any individual prey item.

Poroderma pantherinum

For *P. pantherinum*, the most important food source was teleosts (IRI = 2577), with molluscs almost equally important (IRI = 2463) (Table 2.4). Unidentified cephalopods ranked the most important (IRI = 685) of any individual prey type. The octopus, *Octopus vulgaris*, and the cuttlefish, *Sepia vermiculata*, ranked highly in volume (29% and 22%, respectively), but were of low importance (IRI of 147 and 116, respectively) due to low numbers and frequency. Although crustaceans had a relatively low IRI (178), ostracods were found in the highest numbers (37%) of all prey items, yet contributed very little to the total prey volume (< 1%). Of single prey items, the teleost, *Sardinops sagax*, had the highest percentage of total volume (33%). Teleosts were found in 34% of all stomachs analyzed, but many could not be identified to species. Echinoderms, brachyurans and tunicates were also found in the diet, though combined made less than 1% of the total prey volume.

Dietary differences between sexes

Haploblepharus edwardsii

There were some sexual differences in the diets between male and female *H. edwardsii* (Fig. 2.3). For females (*n* = 11), polychaetes were the most important (IRI = 5740) and the most frequently occurring (82%) prey item, compared to crustaceans (IRI = 7568, %F = 86) for males (*n* = 28). Teleosts comprised the highest volume for both males (39%) and females (66%). A low volume of cephalopods was also found in the stomach contents for males

Table 2.3. Stomach contents of *Poroderma africanum* (*n* = 121) expressed as percentage numbers (%N), volume (%V), frequency of occurrence (%F) and Index of Relative Importance (IRI). Percentage and IRI totals for each phylum are in bold print. All other totals represent material idenitified to the lowest possible taxonomic level (eg. Isopoda = unidentified isopods).

Prey Items	%N	%V	%F	IRI
CNIDARIA				
Anthozoa	**0.05**	**0.01**	**0.83**	**< 1**
ANNELIDA	**0.20**	**0.07**	**3.30**	**< 1**
Nereididae	0.15	0.05	1.65	< 1
Sedentaria	0.05	0.02	0.83	< 1
CRUSTACEA	**88.36**	**0.39**	**15.70**	**1393**
Amphipoda	0.05	0.01	0.83	< 1
Brachyura	0.19	0.01	0.83	< 1
Isopoda	4.36	0.03	7.44	33
Exosphaeroma kraussii	0.48	0.01	2.48	1
E. laeviusculum	6.88	0.03	2.48	17
Macrura				
Jasus lalandii	0.10	0.13	1.65	< 1
Ostracoda	76.30	0.17	15.70	1199
MOLLUSCA	**2.94**	**22.45**	**38.84**	**986**
Cephalopoda	1.78	2.33	25.62	105
Loligo vulgaris reynaudii	0.05	0.04	0.83	< 1
Octopus vulgaris	0.72	19.29	10.74	215
Sepia vermiculata	0.10	0.71	1.65	1
Gastropoda	0.05	0.01	0.83	< 1
Crepidula porcellana	0.05	0.01	0.83	< 1
Fasciolaria lugubris lugubris	0.05	0.05	0.83	< 1
Polyplacophora	0.05	0.01	0.83	< 1
ECHINODERMATA				
Ophiuroidea	**0.05**	**0.01**	**0.83**	**< 1**
CHORDATA	**8.40**	**77.07**	**72.72**	**6215**
Agnatha	0.10	1.00	1.65	2
Eptatretus hexatrema	0.10	1.00	1.65	2
Elasmobranchii	0.05	0.05	0.83	< 1
Haploblepharus edwardsii	0.10	1.33	1.65	2
Haploblepharus pictus	0.05	1.21	0.83	1
Poroderma pantherinum	0.05	2.57	0.83	2
Unidentified egg case	0.05	0.06	0.83	< 1
Teleostei	1.55	7.30	22.31	197
Argyrozona argyrozona	0.05	0.72	0.83	< 1
Liza rechardsonii	0.05	0.55	0.83	< 1
Pachymetopan blochii	0.10	4.28	1.65	7
Pomatomus saltatrix	0.05	0.81	0.83	< 1
Sardinops sagax	6.00	55.60	47.93	2952
Trachurus trachurus	0.10	0.59	1.65	1

Table 2.4. Stomach contents of *Poroderma pantherinum* ($n = 44$) expressed as percentage numbers (%N), volume (%V), frequency of occurrence (%F) and Index of Relative Importance (IRI). Percentage and IRI totals for each phylum are in bold print. All other totals represent material identified to the lowest possible taxonomic level (eg. Cephalopoda = unidentified cephalopods).

Prey item	%N	%V	%F	IRI
CRUSTACEA	**38.88**	**0.29**	**4.55**	**178**
Brachyura	1.85	0.28	2.27	5
Ostracoda	37.03	0.01	2.27	84
MOLLUSCA	**27.80**	**55.56**	**29.55**	**2463**
Cephalopoda	20.80	4.70	27.27	685
Octopus vulgaris	3.50	28.90	4.55	147
Sepia vermiculata	3.50	21.96	4.55	116
ECHINODERMATA				
Echinoidea	**1.85**	**0.02**	**2.27**	**4**
CHORDATA	**31.47**	**44.13**	**34.09**	**2577**
Teleostei	14.81	10.87	22.73	584
Sardinops sagax	14.81	33.25	11.36	546
Tunicata	1.85	0.01	2.27	4

(3%) and females (1%), as well as brachiopods and cnidarians (both < 1%) for males, but these were not considered significant food sources.

Haploblepharus pictus

Crustaceans had the highest dietary importance for male (n = 13) (IRI = 9300) and female (n = 9) (IRI = 5963) *H. pictus* (Fig. 2.3). The most frequently occurring prey was crustaceans (100%) for males, and teleosts (78%) for females. Although teleosts had the highest occurrence of any prey group for female *H. pictus*, they were secondary in importance (IRI = 4212). Crustaceans comprised 60% of the total food volume for females, followed by teleosts (21%) and polychaetes (16%). In contrast, teleosts were first in total volume (45%) for males, with crustaceans (35%) and molluscs (19%) following. Polychaetes were also consumed by male *H. pictus*, but with an IRI of 16, this group was not considered a major food source.

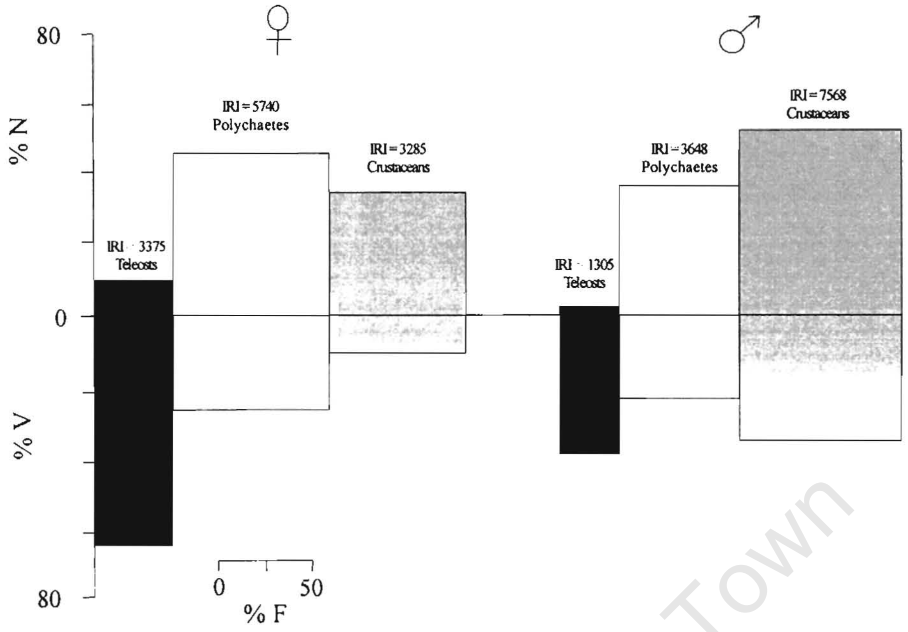
Poroderma africanum

Teleosts were the most important prey, and were highest in frequency and volume for both male (n = 40, IRI = 5394, %F = 62, %V = 80) and female (n = 81, IRI = 4760, %F = 70, %V = 51) *P. africanum* (Fig. 2.4). Molluscs were found in almost half of the females examined, and combined with a substantial volume (34%), were the second most important prey group (IRI = 1968). Crustaceans occurred in very high numbers for males (90%) and females (71%), but made up less than 1% of total volume for both sexes. Annelids and cnidarians were found in both males and females, while agnathans and echinoderms were only in males. However, these prey groups each contributed less than 1% to total volume.

Poroderma pantherinum

Female *P. pantherinum* (n=20) consumed, in order of importance, molluscs (IRI = 2250), teleosts (IRI = 2178) and crustaceans (IRI = 416) as their primary food sources (Fig. 2.4). Molluscs and teleosts were the only two prey found in males (n=24), with molluscs the most important prey group (IRI = 3180). For females, over half the prey items identified were crustaceans, but they made less than 1% of the total food volume and were only found in two specimens (8%). Molluscs made up 58% of total volume and were found in 30% of females

Haploblepharus edwardsii



Haploblepharus pictus

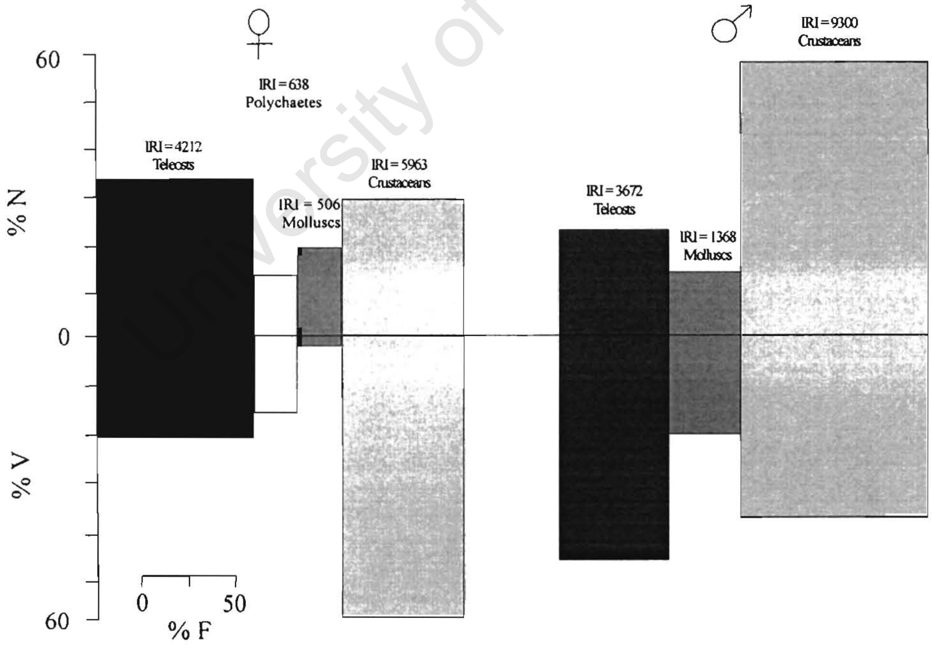


Fig. 2.3. Comparison of numerical importance (%N), volumetric importance (%V) and frequency of occurrence (%F) of major prey components in the diets of male and female: *Haploblepharus edwardsii* (females: *n* = 11; males: *n* = 28) and *H. pictus* (females: *n* = 9 ; males *n* = 13). The index of relative importance, IRI = %F(%N + %V), for each dietary group is represented by the area of the square. *Note*: y-axes differ between species.

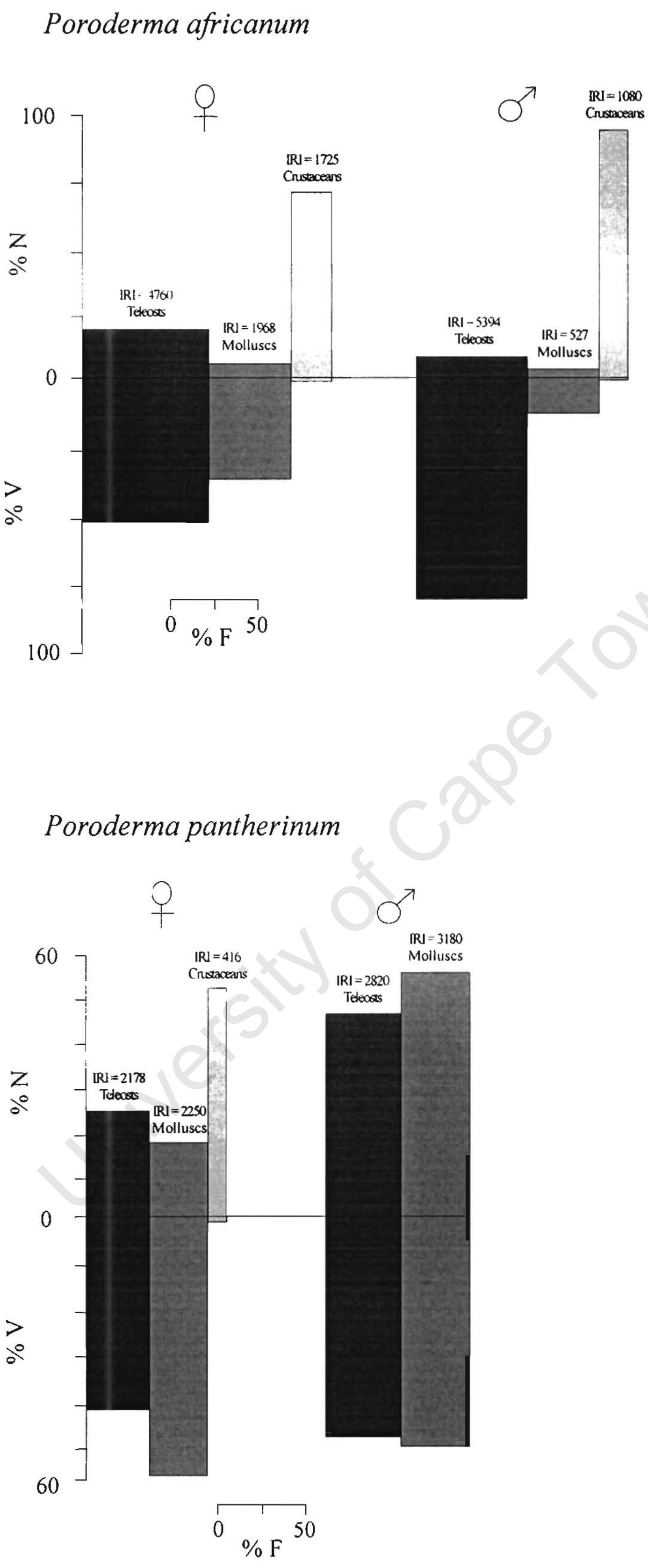


Fig. 2.4. Comparison of numerical importance (%N), volumetric importance (%V) and frequency of occurrence (%F) of major prey components in the diets of male and female:*Poroderma africanum* (females: *n* = 40; males: *n* = 81) and *P. pantherinum* (females: *n* = 24 ; males *n* = 20). The index of relative importance, IRI = %F(%N + %V), for each dietary group is represented by the area of the square. *Note*: y-axes differ between species.

analyzed. Echinoderms and tunicates were also found, but together, comprised less than 1% of the total volume and 6% of prey identified.

Changes in diet with body size

Haploblepharus edwardsii

Teleosts, annelids and crustaceans were the most important prey groups for both (300-399 mm TL and 400-499 mm TL) class sizes (Table 2.5). The IRI for crustaceans was the highest for both classes, but fell from 6052 in smaller sharks to 4400 in larger sharks. The importance of annelids and teleosts also decreased with increasing size, however the volume of crustaceans was the only factor that increased with size, from 20% to 43%.

Haploblepharus pictus

Teleosts, molluscs and crustaceans were the most important prey groups for all classes (Table 2.5). There was a general decrease of importance of teleosts with increasing class size, from an IRI of 5871 to 4970. Molluscs had relatively the same importance for all sizes. The importance of crustaceans increased with increasing size, from an IRI of 5676 in the lowest class (300-499 mm TL) to 9300 in the largest class (600-699 mm TL).

Poroderma africanum

For all classes, teleosts were the most important prey component (Table 2.5). There was a general decrease in importance of teleosts, from an IRI of 14418 in the lower class size (500-699 mm TL), to 6045 in the largest class (1000-1099 mm TL), with size increase. There was an increase of importance for both molluscs (IRI from 429 to 2714) and crustaceans (IRI from 792 to 1026) with increasing size.

Poroderma pantherinum

Teleosts and crustaceans became less important with increasing shark size (from an IRI of 6325 to 1711) (Table 2.5). In contrast, molluscs became much more important in the largest size class (600-699 mm TL, IRI = 4224), though were the least important food source in the

Table 2.5. Percent composition of major prey components for different class sizes of *Haploblepharus edwardsii*, *H. pictus*, *Poroderma africanum* and *P. pantherinum*.

H. edwardsii (*n* =39)	Teleosts				Annelids				Crustaceans			
Size class (mm TL)	%V	%N	%F	IRI	%V	%N	%F	IRI	%V	%N	%F	IRI
300-399 (*n* =28)	53	7	39	2340	26	41	89	5963	20	48	89	6052
400-499 (*n* =11)	41	7	18	864	9	33	18	756	43	37	55	4400

H. pictus (*n* =22)	Teleosts				Molluscs				Crustaceans			
Size class (mm TL)	%V	%N	%F	IRI	%V	%N	%F	IRI	%V	%N	%F	IRI
300-499 (*n* =7)	62	41	57	5871	6	18	43	1032	31	35	86	5676
500-599 (*n* =8)	26	26	63	3276	36	13	38	1862	34	48	75	6150
600-699 (*n* =7)	51	19	71	4970	3	23	43	1118	39	54	100	9300

P. africanum (*n* =121)	Teleosts				Molluscs				Crustaceans			
Size class (mm TL)	%V	%N	%F	IRI	%V	%N	%F	IRI	%V	%N	%F	IRI
500-699 (*n* =9)	99	63	89	14418	< 1	13	33	429	< 1	24	33	792
700-799 (*n* =29)	86	12	69	6831	< 1	84	10	840	3	7	34	340
800-899 (*n* =44)	73	10	52	4316	20	4	41	984	< 1	85	18	1530
900-999 (*n* =13)	34	26	85	5100	58	4	15	930	1	67	15	1020
1000-1099 (*n* =26)	48	45	65	6045	36	23	46	2714	< 1	27	38	1026

P. pantherinum (*n* = 44)	Teleosts				Molluscs				Crustaceans			
Size class (mm TL)	%V	%N	%F	IRI	%V	%N	%F	IRI	%V	%N	%F	IRI
300-399 (*n* = 9)	99	16	55	6325	< 1	4	22	88	< 1	80	22	1760
500-599 (*n* = 14)	88	50	21	2898	11	42	43	2279	1	8	8	72
600-799 (*n* = 21)	24	35	29	1711	75	53	33	4224	0	0	0	0

lowest size class (300 – 399 mm TL, IRI = 88). No crustaceans were found in the largest class.

Dietary comparisons of similar size classes among species

Feeding habits appeared to differ among the four catshark species of similar size classes. However, to some extent, this could be the result of the differences in mean size between species. This section attempts to evaluate whether or not there were significant differences between individuals of different species of the same size class. *Haploblepharus edwardsii*, *H. pictus* and *Poroderma pantherinum* were all represented with sizes between 300 and 499 mm TL (Table 2.5). For *P. africanum*, no specimens were < 500 mm TL and therefore this species could not be included in this comparison. Crustaceans were the most important prey group (IRI = 6125) for *H. edwardsii*, in contrast to teleosts being the most important (IRI = 6325) for *P. pantherinum*. There was little difference in importance of teleosts and crustaceans (IRI = 5871 and IRI = 5676, respectively) for *H. pictus*.

H. pictus, *Poroderma africanum* and *P. pantherinum* were all represented in the class size 500 – 799 mm TL. Although *H. edwardsii* is known to reach 600 mm TL (Compagno *et al.*, 1989), no specimens > 499 mm TL were collected in this study. Teleosts were the most important prey group (IRI = 9694) for *P. africanum*, in contrast to *H. pictus,* where crustaceans were the most important (IRI = 7656). There was some difference in importance of molluscs and teleosts for *P. pantherinum*, with molluscs being the most important (IRI = 3367). Only *P. africanum* reaches a total length > 799 mm TL (Compagno *et al.* 1989), therefore this species could not be compared to any of the other three catsharks in this larger size class.

DISCUSSION

All four catshark species, including both sexes and multiple class sizes, can be found in the same habitat in the southwestern Cape (Prochazka 1994; Lechanteur in press). Therefore, inter- and intraspecific competition could be significant. All four species consume a wide range of prey items, suggesting a generalist approach to feeding. However, *P. pantherinum* had a more restricted diet than that of the other species, consuming almost exclusively teleosts and molluscs. The dominant prey groups were, in order of importance, crustaceans, annelids and teleosts for *Haploblepharus edwardsii*, teleosts, crustaceans and molluscs for *H. pictus* and *Poroderma africanum*, and teleosts and molluscs for *P. pantherinum*. Bass *et al.* (1975) also found that *H. edwardsii* fed mostly on teleosts and crustaceans. However, Compagno *et al.* (1989) concluded that *H. pictus* fed mostly on crustaceans, while *P. africanum* consumed mostly crustaceans and cephalopods. Teleosts, crustaceans and cephalopods were found in the stomach contents of *P. pantherinum* (Compagno 1984), however in this study, crustaceans contributed little to the diet of this species. All this evidence points to the fact that catsharks are opportunistic predators of larger invertebrates and fish.

Dietary differences between sexes

Overall, the diets between males and females of the four catsharks were similar, although there was some variation in the relative importance of prey groups between the sexes. For *H. edwardsii*, teleosts and annelids were more important to females, compared to crustaceans for males. Crustaceans and molluscs were of greater importance in the diets of male *H. pictus*, while teleosts were more important to females. For *P. africanum*, crustaceans and molluscs were more important to females, compared to teleosts for males. Cephalopods and teleosts were of greater importance for both male and female *P. pantherinum*, however, additional prey, such as crustaceans, echinoderms and tunicates were only found in females. Males and females for all species were found at the same study sites all year round, therefore the differences in diet would indicate a prey preference between sexes. Marks (in prep.)

analyzed dentition differences between *H. edwardsii*, *H. pictus*, *P. africanum* and *P. pantherinum* and found that adult males exhibited a wider primary cusp base than adult females. However, this attribute is most likely a function of reproductive behavior (for males to have a firmer grasp on the pectoral fins of females during mating) rather than feeding behavior.

Matallanas *et al.* (1993) found that for narrow mouthed catshark (*Schroederichthys bivius*), males had a more diverse diet than females, where females consumed fewer species of crustaceans, teleosts and polychaetes. In this study, both sexes of *H. edwardsii* consumed the same prey, except cnidarians and brachiopods were found only in males. For *P. africanum*, only males consumed agnathans and gastropods. However, the opposite was true for *H. pictus* and *P. pantherinum*, where females had a more varied diet than males. Echinoderms were found only in female *H. pictus*, while echinoderms, crustaceans and tunicates were only found in the stomachs of female *P. pantherinum*. It has been suggested (Matallanas *et al.* 1993) that larger male sharks might have a more diverse diet than their female counterparts, however, this was not the case in *Dalatias licha* (Matallanas 1982), where the males examined were smaller than the females and yet had a more varied diet. This study also contradicts those findings, since a larger array of prey were found in the stomach contents of female *H. pictus* and *P. pantherinum*. However, in this study, larger sample sizes for both *Haploblepharus* species and *P. pantherinum* may result in more reliable dietary comparisons between sexes.

Dietary differences among size classes

There is evidence of competition for prey among similar class sizes of the four catsharks. Comparisons of the diets of *H. edwardsii*, *H. pictus* and *P. pantherinum* for the smallest class size, 300 – 499 mm TL, showed that crustaceans were most important for *H. edwarsdii*, while teleost were most important for *P. pantherinum*. The importance for teleost and molluscs were approximately equal for *H. pictus*. For the larger size class (500 – 799 mm TL), only *H. pictus*, *P. africanum* and *P. pantherinum* could be included, due to lack of specimens > 500 mm TL for *H. edwardsii*. Teleosts were most important for *P. africanum*, teleosts and molluscs had relatively the same importance for *P. pantherinum*, while crustaceans were most important to *H. pictus*. This suggests a targeting of different prey sources, due to competition among size classes.

Unfortunately, no information was collected for specimens of *H. edwardsii* that exceeded 499 mm, though this species does reach 600 mm (Comapagno *et al.* 1989). With the information collected, however, there seems to be a general decrease in the amount of teleosts and annelids consumed, with an increase of crustaceans. Similarly, *H. pictus* consumed more crustaceans and fewer teleosts with increasing size. There was an increase of mollusc consumption with increasing size for both *Poroderma* species. *P. africanum* has been known to predate on spawning squids, *Loligo vulgaris reynaudii* (Smale *et al.* 1995; current study). Unfortunately, the size of the sharks capturing the squids were not recorded, however the squid were mentioned to be mating adults, indicating larger, mature individuals (*Loligo* reach 30 cm in length, Branch *et al.* 1994). Larger *P. africanum* were most likely the hunters, which coincides with the increase of molluscs in the diet of the larger size classes in this study.

Teleosts contributed to a high volumetric percentage of the total diet for all four shark species. Pilchards, *Sardinops sagax,* were the only teleosts identified to species in the diets of three of the catsharks (except *P. africanum*). All of the sampling sites are heavily fished commercially and *Sardinops* is often used as bait for Snoek (*Thyrsites atun*) and Skipjack tuna (*Katsuwonus pelamis*). Other teleost species found in *P. africanum* are all quick swimming, commercially harvested fish (eg. *Argyrozona argyrozona, Liza richardsonii, Pachymetopan blochii, Pomatomus saltatrix* and *Trachurus trachurus*). It is most likely that these fish were cast overboard by commercial trawlers. Consequently, teleosts would perhaps not be represented as such an important food source if not for these discards. Therefore, dietary analyses may differ among selected sites, depending on the environmental conditions and/or human impact. However, the general decrease of importance of teleosts with increasing size for all class sizes and species may indicate that the larger sharks relied less on scavenging for teleost bait remains, and more on foraging for live food.

The smalleye catshark, *Apristurus microps*, reaches approximately 610 mm (Compagno *et al.* 1989) and is thus similar in size to adult *Haploblepharus* species and adolescent/adult *Poroderma pantherinum* and immature/adolescent *P. africanum* species. Although *A. microps* is a deep-water species, the diets between the two genera are similar. *A. microps* feeds on, in order of importance, teleosts, crustaceans and cephalopods (Ebert *et al.* 1996), which is the same as *H. pictus*. The Yellowspotted catshark, *Scyliorhinus capensis*, similar in size to *P. africanum* and with a partially overlapping depth and area habitat, was found to feed mainly on teleost and crustaceans, followed by cephalopods and polychaetes (Ebert *et al.* 1996). Teleosts were also the most important prey for *P. africanum*. Many catshark species thus appear to have a similar dietary composition and may indicate general trends regarding feeding behavior of multiple Scyliorhinid species.

Predatory behaviour

It is often difficult to distinguish between prey items that have been scavenged or hunted. However, the high consumption of *S. sagax* for all the sharks can most likely be attributed to scavenging. Crustaceans and cephalopods were most likely hunted, as these prey and catsharks are both mostly nocturnal predators.

Capape (1976) has described all chondrichthyes as opportunistic feeders, preying upon the most available food items. Fariña and Ojéda (1992) have described *Schroederichthys chilensis* as a specialized predator, preying mostly on decapod crustaceans. Richardson *et al.* (2000) found the izak catshark (*Holohalaelurus regani*) to be a generalist feeder, preying on a variety of crustaceans, cephalopods and teleosts. Correspondingly, *H. edwardsii*, *H. pictus* and *P. africanum*, fed on a multitude of prey items, and can be described as generalist predators. However, *P. pantherinum* had a more specific diet. Although there were several different prey types found in the stomach contents, *P. pantherinum* fed almost exclusively on molluscs and teleosts. Similarly, *Apristurus spp., A. saldanha* and *Galeus polli* (Ebert *et al.* 1996) fed almost exclusively on teleosts, and were also described as having more specific diets than *H. regani*, *Scyliorhinus capensis* and *A. microps*. *Pseudotriakis microdon* were also very specific in their prey choice, with telosts as the most predominantly consumed item (Yano and Musick 1992). This evidence suggests that catsharks are very important predators in their environments.

GASTRIC EVACUATION RATES OF THREE CATSHARK SPECIES FROM THE SOUTHWESTERN CAPE

INTRODUCTION

Three common catsharks (*Poroderma africanum*, *P. pantherinum* and *Haploblepharus pictus*) occur in subtidal reefs and kelp bed communities in the southwestern Cape. The diets of these species have been analyzed through gut content analyses in Chapter 2. However, gut content analyses can often result in biased estimates of actual ratios of consumed prey items in both bony fishes (Elliott and Persson 1978; Hyslop 1980; Jobling 1986) and elasmobranchs (Cortés 1997). All these studies indicate the need to combine diet and evacuation rate analyses to fully understand the importance of individual prey items in the diet. The assumption that stomach contents are a measure of the amount of food consumed by fish is incorrect, because gastric evacuation is occurring even as the fish continues to feed, leading to inaccurate estimations of food actually consumed (Elliott and Persson 1978). Relative frequencies of harder materials, such as bone and exoskeleton, may be overestimated if these substances have longer retention times in the gut (Fänge and Grove 1979). In contrast, the importance of softer prey items, which may digest more rapidly, may be underestimated in the diet as inferred from stomach contents.

Numerous mathematical expressions such as linear, exponential and Gompertz equations, or transformations of data such as square root, have been used to describe the relationship of food evacuated from the gut after feeding over time in fishes (Pandian 1967; Swenson and Smith 1973; Medved 1985; Macpherson *et al.* 1989; Cortés and Gruber 1992; Sims *et al.* 1996). Jobling (1986) concluded that different expressions best fitted the emptying of different food items, such as an exponential function for small, easily digestible foods, and a linear function for high-energy foods. However, because rates of evacuations vary among shark species and food items, it is often difficult to assign one appropriate mathematical model for gastric evacuation experiments (Jobling 1981). Generalized linear models (GLM) (Hastie and Tibshirani 1990) broaden the regression framework when data do not follow a normal distribution, as is the case for some gastric evacuation data (present study). Fitted values are weighted averages of surrounding data, giving a non-parametric curve that reveal trends in the data that would not be apparent when applying a more conventional model, such as an exponential or linear regression.

Previous studies describing gastric evacuation in elasmobranch species include those of the spiny dogfish, *Squalus acanthias* (Jones and Geen 1977), sandbar shark, *Carcharhinus plumbeus* (Medved 1985), lemon shark, *Negaprion brevirostris* (Schurdak and Gruber 1989; Cortés and Gruber 1992), lesser-spotted dogfish, *Scyliorhinus canicula* (Macpherson *et al.* 1989), little skate, *Raja erinacea* (Nelson and Ross 1995) and leopard shark, *Triakis semifasciata* (Kao 2000). There is a need to evaluate gastric evacuation rates in shark species, as this information is essential when estimating predator-prey relationships, which in turn gives insight into the role of these species as predators in the environment. The three catshark species used in this study are excellent subjects to conduct a gastric evacuation rate experiment, due to their abundance in subtidal, inshore communities, and their hardiness and survival rate in aquarium tanks. The objective of this study is to determine gut turnover times of major prey items consumed by each of three catshark species found in the southwestern Cape.

METHODS

A total of 152 sharks was used in this study. These comprised: 17 female and 23 male *Poroderma africanum*, 24 female and 21 male *P. pantherinum*, and 36 female and 30 male *Haploblepharus pictus*. *H. edwardsii* was not included as an insufficient number of specimens was captured during the study period. Sharks were collected between February 2000 and February 2002 from three sites: Buffels Bay (34°17'S; 18°30'E) and Millers Point (34°11'S; 18°31'E) in False Bay and Granger Bay (33°54'S; 18°24'E) on the Cape west coast (Fig. 3.1). Throughout the study, sea temperatures encountered at all sites ranged between 9°C and 17°C, depending on the season and depth. All three species were found at all three sites. Animals were transferred to the laboratory at the University of Cape Town in

√

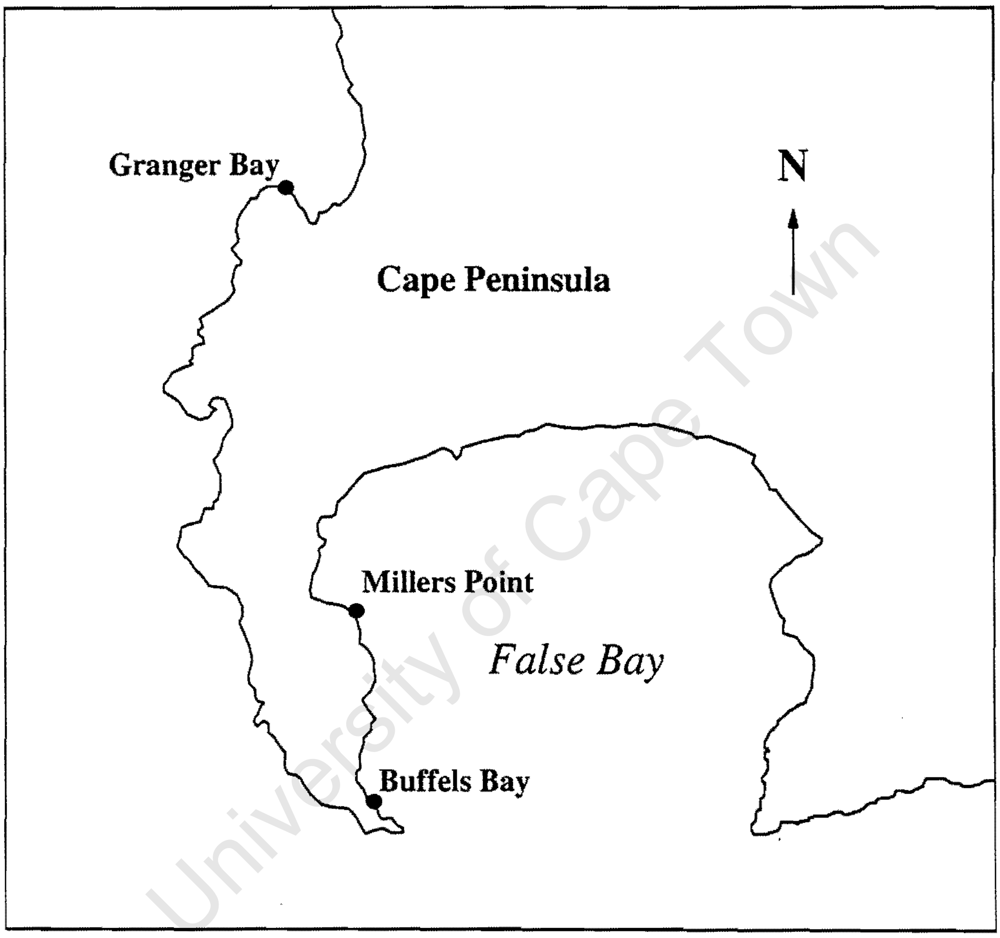


Fig. 3.1. Map showing study sites.

collection bins and maintained in closed system aquaria with circulating seawater. Specimens were kept together in a circular holding tank (305 cm diameter x 76 cm height) at 14°C. Overhead lights were turned off from 5 pm until 6 am to simulate diel rhythms.

Sharks were fed twice a week, ad libitum, with pilchard (*Sardinops sagax*) until used in the digestion rate experiment. Experimental sharks were transferred to a smaller circular tank (198 x 38 cm) and starved for five or six days to ensure that no food remained in the gut. Each experimental shark was then placed in a canvas sling and weighed to the nearest 5 g with a Salter spring scale. Distinctive skin patterns were recorded to differentiate individuals. Both sexes and various size classes > 200 g were used for experimentation. Each shark was fed a preweighed (wet weight to the nearest 0.01 g) meal, equivalent to approximately 1% of its body weight. This percentage was arbitrarily chosen, as a direct estimate of daily ration could not be attained from previous diet data.

Meals were chosen to represent major food components found in the diets of these sharks (Chapter 2), which made up 5% or more of the total volume of identifiable prey. The major prey items were: teleosts, crustaceans and molluscs for *H. pictus*, and teleosts and molluscs for both *Poroderma* species. Prey items used were: freshly frozen and defrosted *Octopus vulgaris* arms for molluscs, whole, intact *Clinus spp.* for teleosts, and sandprawns, *Callianassa kraussi,* for crustaceans. Sharks were only fed one piece of octopus of the desired weight, but either 1-3 prawns or fish were required to make the required weight. Each specimen ate voluntarily, and once fed, sharks were observed for a few minutes to insure that food was not regurgitated. At regular intervals after feeding, sharks were sacrificed by placing them in an ice bath (3°C or below) for approximately 15 minutes to subdue them, and then pithed. The first time period measured was twenty-four hours and the state of digestion of prey at this time was used to decide on the other sampling periods. Generally, four sharks were sampled per time period, and sampling intervals were concluded when at least three of the four sharks dissected had completely digested the prey. Stomach contents were washed with tap water to remove any excess digestive fluid, blotted on paper towels and weighed (wet weight) on a digital balance to the nearest 0.01 g.

The relationship between the percentage of food remaining in the stomach and time elapsed was investigated using a generalized additive model (Hastie and Tibshirani 1990) using Genstat 4.2 for Windows 2000. The fraction of food (π) remaining in the gut after t hours was expressed as a percentage (100π) was fitted to the following equation:

$$100\pi\ (t) = 100(1+\mathrm{Exp}[-\mathrm{Exp}(\mu + \alpha_i + s(t;4)],$$

where α_i is the effect of species i, μ is a constant, and s(t,4) is a non-parametric smooth function. The fitted value at each time point is a weighted average of the four observed, neighboring data points. The initial value of 100 when t=0 was added to the data set, but the model was not forced through this point. Plots of the residuals and comparison of the estimated Y-intercept to the actual initial percentage of food remaining (100%) were used to evaluate the fit of the model. The general additive linear accounted for the change in variability of the data as π (t) decreased, and allowed valid comparisons to be made between species fed the same prey. Statistical comparisons of gastric evacuation times for different prey in a particular shark species by this method could not be done because of the widely different digestion times. Additional models such as least squares regression using various transformations of the data, exponential, or Gompertz curve, did not give a satisfactory fit to the data and are excluded from further discussion.

RESULTS

The average length and weight of the shark species used were: 64.7 cm (± 12.8 SD) total length (TL) and 1.5 kg (±0.918 SD) body weight (BW) for *Poroderma africanum*; 53.9 cm (± 8.6 SD) TL and 0.9 kg (± 0.417 SD) BW for *P. pantherinum*; and 50.5 cm (± 6.9 SD) TL and 0.6 kg (± 0.237 SD) BW for *Haploblepharus pictus*.

The time needed for 95% of octopus to be evacuated was not significantly different ($p>0.05$) for the three species maintained at 14°C and took a mean time of 22 hours (Fig. 3.2). There

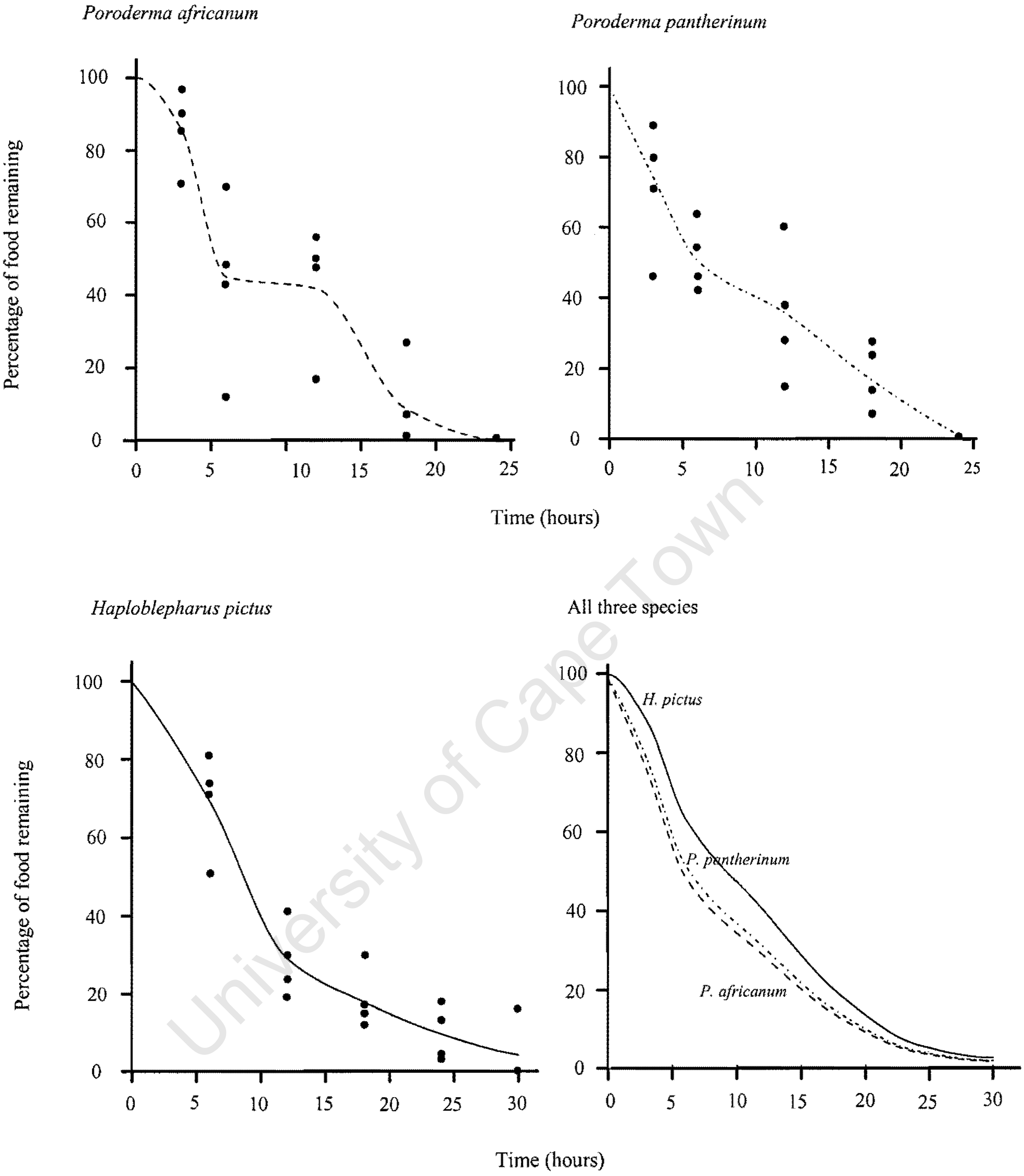


Fig. 3.2. The generalized additive linear model fitted to gastric evacuation data for *Poroderma africanum*, *P. pantherinum*, *Haploblepharus pictus* fed octopus, *Octopus vulgaris*, and all three shark species compared. There was no significant difference ($p<0.001$) between the time for gastric emptying of octopus among the shark species.

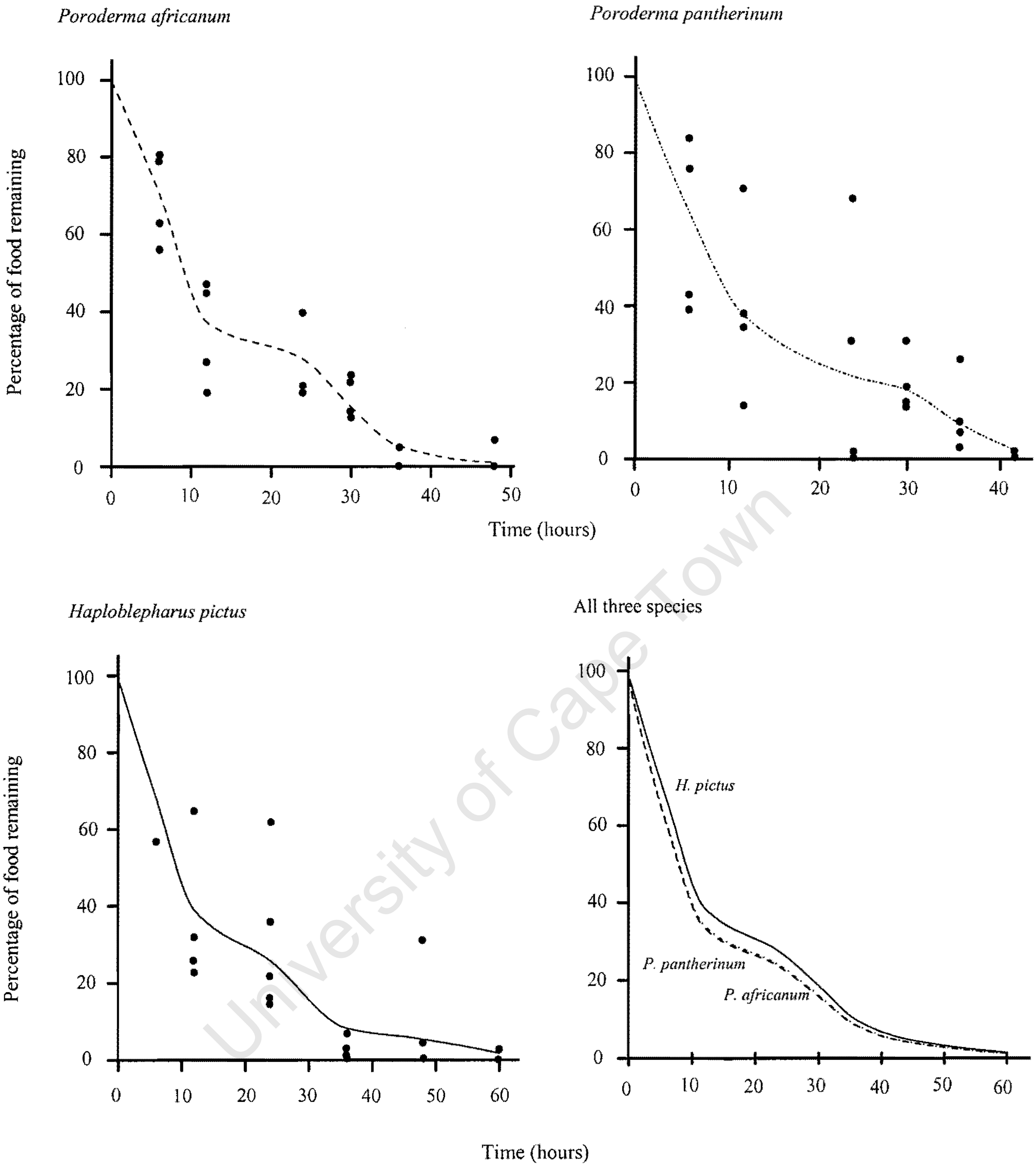


Fig. 3.3. The generalized additive linear model fitted to gastric evacuation data for *Poroderma africanum*, *P. pantherinum*, *Haploblepharus pictus* fed fish, *Clinus spp.*, and all three shark species compared. The regression lines for both *Poroderma* species are approximately the same and therefore are difficult to distinguish from one another. There was no significant difference ($p<0.001$) between the time for gastric emptying among the shark species.

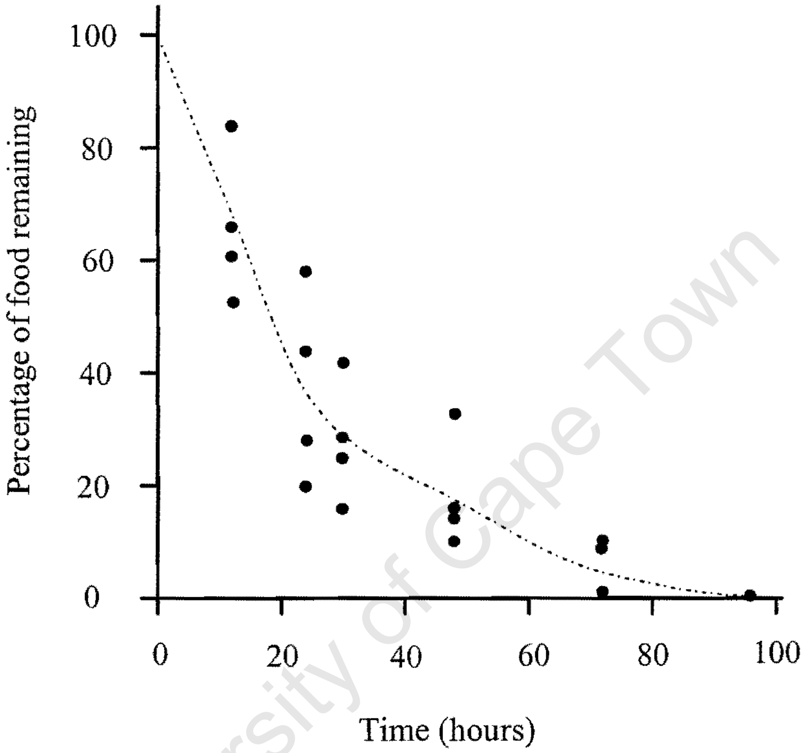


Fig. 3.4. The generalized additive linear model fitted to gastric evacuation data for *Haploblepharus pictus* fed prawn, *Callianassa kraussi*.

is no significant difference (p>0.05) between the times (mean time of 41 hours) for 95% of fish to be evacuation of for the three shark species. The time for 95% of prawn to be evacuated for *H. pictus* is approximately 70 hours (Fig. 3.4). Graphical comparisons of gastric emptying for different prey for each species are shown in Figure 3.5. Overall, octopus required the least time for gastric evacuation, followed by fish, then prawn. Predicted times after feeding required to reach various percentages of food remaining in the stomach are summarized in Table 3.1. The statistical program, GenStat, was unable to estimate the time at the selected percentages remaining, so the time values were approximated from the graphs.

The generalized linear model best described the gastric evacuations of all prey items (octopus, fish, prawn) for the three shark species. Residuals were between 0.05-0.41, and estimated Y-intercepts were only marginally lower than the predicted initial meal size (99.16% – 99.99%), indicating that the model slightly underestimated the amount of food remaining in the gut during the initial stages of gastric evacuation (Table 3.2). F ratios for all data were statistically significant (p<0.001), indicating that the model explains the majority of the variance. Therefore, the residual mean deviances are most likely due to the high variability of gastric emptying among individuals, rather than the model's lack of fit to the data trend.

A common feature of the majority of graphs is a period where gastric emptying begins to slow down, or level off in some cases, after an initial maximal rate of evacuation, then increases again until complete evacuation. For *P. africanum* that were fed octopus, there is an obvious plateau between approximately 5 and 12 hours after ingestion (at 45% of prey remaining in the gut) (Fig. 3.2). This plateau was less apparent in octopus fed *P. pantherinum*, also between approximately 5 and 12 hours, where the food remaining ranged from 50 to 40 % during this time. There was no indication of this leveling period for *H. pictus* that were fed octopus, although the first 10 hours of digestion were maximal, followed by a decreased rate until complete evacuation. The time for 40% of fish to reduce to 35% in

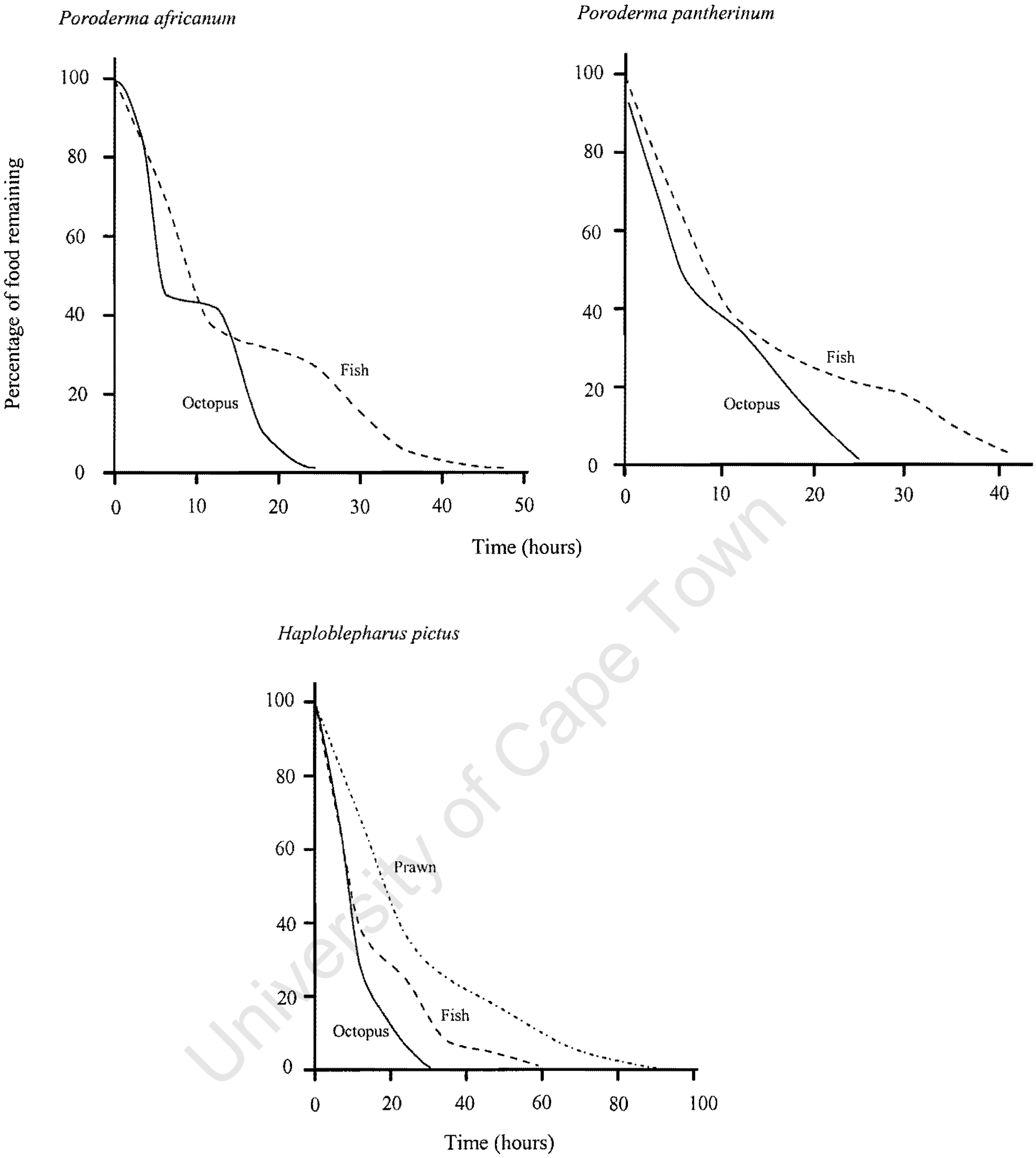


Fig. 3.5. The generalized additive linear model fitted to compare gastric evacuation data for *Poroderma africanum* and *P. pantherinum*, fed octopus, *Octopus vulgaris* and fish, *Clinus spp.* and *H. pictus* fed octopus, fish and prawn.

Table 3.1. Time required to reach various stages of gastric evacuation predicted by the general additive linear model fitted to the data for *Poroderma africanum*, *P. pantherinum* and *Haploblepharus pictus* fed their major prey. Times are approximations, as the estimated points were taken directly from the graphs of % of food remaining in the gut against time.

		Predicted time (h) to given percentage of food remaining in the stomach						
Shark species	prey	90%	75%	50%	25%	10%	5%	1%
P. africanum	octopus	2.5	4.5	6.0	15.0	17.5	19.5	22.0
	fish	2.5	5.0	9.5	25.0	32.5	36.0	48.0
P. pantherinum	octopus	1.5	3.0	6.0	15.0	20.5	22.0	24.0
	fish	2.0	3.0	9.0	20.0	37.0	39.5	N/A
H. pictus	octopus	3.0	6.0	10.0	15.0	21.0	24.5	N/A
	fish	2.0	5.0	9.5	24.5	34.0	48.0	N/A
	prawn	5.0	10.0	20.0	35.0	59.5	70.0	87.5

N/A indicates that the model had a lower asymptote greater than the given percentage of food remaining in the stomach and therefore a predicted time could not be calculated.

P. africanum and *H. pictus* took over 15 hours (between approximately 11 and 26 hours after ingestion) (Fig. 3.3). This slight leveling period occurred between 11 and 30 hours after ingestion for *P. pantherinum* that were fed fish, for the % remaining to reduce from 40 to 20. For prawn fed *H. pictus*, the difference between 30% and 20% remaining occurred between 30 and 48 hours after ingestion (Fig. 3.4).

Table 3.2. Estimated y-intercepts and associated statistics of a generalized additive linear model (Hastie and Tibshirani 1990) fitted to the gastric evacuation data.

	Prey		
	Octopus y-intercept/Residual	**Fish** y-intercept/Residual	**Prawn** y-intercept/Residual
P. africanum	99.99/0.05 $n = 20$	99.65/0.39 $n = 20$	____
P. pantherinum	99.51/0.40 $n = 20$	99.39/0.29 $n = 25$	____
H. pictus	99.95/0.14 $n = 20$	99.16/0.41 $n = 22$	99.64/0.41 $n = 24$

DISCUSSION

Comparing the three shark species fed the same prey; the time for complete gastric evacuation was not significantly different ($p > 0.05$). The mean time needed for octopus to reduce to 5% remaining in the stomach was 22 hours, and 41 hours for fish. *H. pictus* took 70 hours for 95% of prawn to evacuate. This is supported by Windell (1978), who states that species differences do not influence gastric removal rates in fishes. Swenson and Smith (1973) also found no significant difference in the gastric evacuation of fathead minnows fed to walleyes, *Stizostedion vitreum vitreum*, and sauger, *Stizostedion canadense*, or among walleye from three different lakes.

Overall, octopus arms were digested faster (22 hours for 95% evacuated) than fish (41 hours), followed by prawns (70 hours). These differences are most likely due to the presence of bones and scales in fish or chitinous material in prawns that delay complete digestion (Windell 1978; MacPherson *et al.* 1989). Pandian (1967) observed indigestible chitin in the faeces of the Indo-Pacific turpon, *Megalops cyprinoids*, and that protein is most easily digested and absorbed. The sandprawn, *Callianassa kraussi*, used in this study, has a relatively soft-shell, just as the ostrocod prey that constituted the majority of the crustaceans found in the diets of these sharks (Chapter 2). However, ostrocods do not have hard pincers as do prawns, and the pincers were the last parts of the sandprawn to remain in the gut. Small amounts of harder chitinous material, from prey such as West Coast rock lobster, *Jasus lalandii*, were also found in the stomach contents of these shark species, however, these sharks most likely ingest recently molted prey. In laboratory conditions, hard shell Cape rock crabs, *Plagusia chabrus*, and European shore-crabs, *Carcinus maenas*, were offered to the sharks, but were refused. Only after a recently molted European shore-crab was given, did a *H. pictus* readily accept the prey. Therefore, the time for complete gastric evacuation of sandprawns is most likely comparable to that of natural prey.

The times for prey evacuation from the stomachs of *P. africanum*, *P. pantherinum* and *H. pictus* is generally slower than those measured in teleost fish, but comparable to other elasmobranch species. Gastric evacuation rates of different fish species are illustrated in Table 3.3. However, it is difficult to make direct comparisons of evacuation rates between species because of the different prey offered, various models fitted to the data and experimental temperatures used in the different studies. Therefore, only generalities can be drawn from these comparisons. *H. pictus* took approximately three times as long to digest sandprawns at a similar temperature to that of juvenile coho salmon (*Oncoryhnchus kisutch*) fed similar prey. The time for fish to evacuate from the gut was about one and a half times the time for rainbow trout to evacuate brown trout (He and Wursbaugh 1993). Similar times were required for the three shark species in this study to evacuate fish (36-48 hours) compared to the lemon shark (39-55 hours, Cortés and Gruber 1992). However, compared to the sandbar shark that required 80 hours to evacuate 95% of menhaden (Medved *et al.* 1988), the sharks in this study evacuated fish at a slightly faster rate. *H. pictus* emptied prawns (70

Table 3.3. Number of hours for stomachs to empty for various fish species.

Elasmobranch Species	Food	% evacuated	Hours	Temperature (°C)	Model/ transformations	Study
sandbar shark *Carcharhinus plumbeus*	menhaden/ soft blue crab	98	92 /70	22-30	Gompertz	Medved (1985)
lemon shark *Negaprion brevirostris*	snapper or white grunt	99	41	20-25	linear	Cortés and Gruber (1992)
		"	154	"	exponential	
		"	64	"	square root	
little skate *Raja erinacea*	krill/clam feet	100	20/19	10	linear	Nelson and Ross (1995)
			30/31		exponential	
			60/49		square root	
leopard shark *Triakis semifasciata*	staghorn sculpin	100	28	13-18	linear	Kao (2000)
pyjama shark *Poroderma africanum*	octopus/klipfish	95	19.5/36	14	GLM	present study
leopard catshark *Poroderma pantherinum*	octopus/klipfish	"	22/39.5	"	"	"
dark shyshark *Haploblepharus pictus*	octopus/klipfish/ prawn	"	24.5/48/70	"	"	"
Teleost Spcies						
walleye *Stizostedion vitreum vitreum*	minnows	100	16	15	linear	Swenson & Smith (1973)
coho salmon *Oncorhynchus kisutch*	euphausiids	90	28/18	11.4/13.7	exponential	Brodeur & Pearcy (1987)
brown trout *Salmo trutta*	rainbow trout	98	26	14	linear	He & Wurtsbaugh (1993)

hours) at a comparable rate to the sandbar shark fed soft blue crab (80 hours), but the little skate required less time to digest similar prey, even at a lower temperature (10°C). However, times for the little skate to evacuate 100% of krill ranged widely from 20-60 hours, depending on the model. The linear and square root model best described the data in that study, even though the hours to evacuate varied by 40.

Based on the plots of residuals, F ratios and the estimated time of the y-intercept when $t=0$, the generalized additive linear model best described the decrease in stomach contents with time for *Poroderma africanum, P. pantherinum* and *Haploblepharus pictus*. Jobling (1981) predicted that an exponential function would best describe the emptying of small, easily digested, low energy food particles from the stomach, but a linear expression would give a better fit to the data when food consists of high energy, large sized particles. Exponential and linear models and square-root transformations are most often used to describe the relationship between food remaining in the gut and time after feeding (Elliott and Persson 1978; Jobling 1981; Medved 1985; MacPherson *et al.* 1985). However, none of these models adequately described the gastric emptying process for the three shark species in this study. A generalized additive linear model has not been previously used to illustrate gastric evacuation of fishes, and therefore is difficult to compare trends with other studies.

Fitting the generalized linear model to the data revealed a plateau period of evacuation among all but one of the predator/relationships. Probable reasons for this may be do to proteins being digested first and much more quickly than lipids and harder materials (Windell 1978), which would represent the initial, steep slope of gastric evacuation. This is also apparent in the digestion of polychaetes in the little skate, *Raja erinacea* (Nelson and Ross 1995), where the internal tissue digested faster than the cuticle layer. The initial evacuation of easily digestible parts would be followed by the digestion of lipids and other material, represented by the plateau period. Finally, any residual particles would be quickly passed through the gut. Interestingly, the plateau pattern is even apparent for *P. africanum* and *P. pantherinum* fed octopus arms, which do not contain any hard components. The possibility of some proteins being digested more quickly than others (Zarate *et al.* 1999), may account for the leveling off period.

Alternatively, diel periods of increased metabolism my affect the rate of gastric emptying. *P. africanum, P. pantherinum* and *H. pictus* are nocturnal predators, and the time when these sharks were fed for the experiment resulted in the plateau effect occurring at night or in the early hours of the morning. This could be due to the diversion of energy during these peak hunting times for muscle movement, rather than digestion. Once the sharks are less active, more energy may be diverted to gastric emptying. Although each data point represents a different shark and the variability between individuals is high, the pattern is still apparent with almost all species fed different prey. However, more data points per time period, or measuring the rates of gastric evacuation for meals constituting proteins or lipids only, may give insight in to this pattern.

The fact that the sharks used in this experiment varied in size, may have also contributed the high variability of gastric evacuation rates. Although predator body size may effect meal evacuation time (Windell 1978), He and Wurtsbaugh (1993) showed that predator size did not significantly affect rates of evacuation in brown trout (*Salmo trutta*). The use of either single or multiple fish or prawns to make a meal equivalent to 1% of the sharks' body weight was assumed to have a negligible affect on gastric emptying time. It has also been suggested that both surface and volume effects influence the rate of stomach emptying (Swenson and Smith 1973), indicating that a meal of multiple small fish or prawns (as in this experiment) may be digested more rapidly than a one item meal of similar weight. However, even if whole, larger fish, which usually have small surface-to-volume ratios, are fed, digestion probably begins at the surface of a particle, but food volume might influence peristalsis, which facilitates mechanical and chemical breakdown (Windell 1978). This is confirmed by He and Wurtsbaugh (1993), who found seemingly undigested rainbow trout taken from the guts of brown trout had lost 12% of their dry body weight, which suggests digestion of tissue proceeds, even if the skin remains intact.

In conclusion, at 14°C, 95% of a 1% BW meal to be evacuated from the guts of the three catshark species requires 19-24 hours for octopus, 36-48 hours for fish and 70 hours for prawn. The GLM was the best fitting model for the data and highlighted variations in gastric evacuation rates that would not have been apparent with conventional models. There are no significant differences ($p<0.001$) of gastric evacuation rates between shark species fed the same prey item. The different sizes of sharks used and the temperature at which the evacuation rates were measured in the laboratory were chosen to simulate the sizes and approximate mean temperature experienced in the environment.

The purpose of this study was to give insight as to whether the diet study (Chapter 2) accurately represented the importance of major prey items in the catsharks' diet. For the three shark species, teleosts were calculated as being the most important food source in the diet overall, with molluscs as the third most important (second most important for *P. pantherinum*) following crustaceans. The percentage volume of molluscs were also much lower than that of teleosts for the three species. In this chapter, octopus was calculated to take approximately half the time to be evacuated than fish for the three catshark species, indicating that the importance of molluscs are underestimated in the diets, while teleosts are overestimated. In addition, the importance of prawns in the diet of *H. pictus* are also most likely overestimated, yet crustaceans were the second most important prey found in stomach contents (following teleosts). Therefore, the combination of both diet data and gastric evacuation data are necessary to provide a true reflection of the natural diet of sharks.

GROWTH, SEXUAL MATURITY, REPRODUCTION AND AGING OF FOUR CATSHARK SPECIES FROM THE SOUTHWESTERN CAPE

INTRODUCTION

Four catshark species (*Haploblepharus edwardsii, H. pictus, Poroderma africanum* and *P. pantherinum*) are commonly found in kelp bed communities in the southwestern Cape. There is no known commercial value of these sharks, other than for aquarium trade and for lobster bait (L.J.V. Compagno, Shark Research Centre, SAM, *pers. comm.*), but *P. africanum* are commonly caught by shore and ski-boat anglers who discard them as pests (van der Elst 1988). Very little biological and ecological information is available for any of these four cathark species. Age, growth and life history information for *P. africanum* are listed as research priorities in the Southern African Marine Linefish Status Reports (Wright and Compagno 2000), and the other three catshark species are not even listed. Therefore, it is essential to collect information regarding their basic biology.

Elasmobranchs lack true bone, which have often been used for successful age determination in bony fishes (Bennett and Griffiths 1986; Booth and Buxton 1997). Ridewood (1921) described the calcified zones of vertebral centra in sharks and rays, and stated that the vertebral structures are centrifugal in growth, with the outermost layers being the most recently added. Growth information based on age estimates utilizing vertebrae is now common practice when aging sharks (Branstetter 1987; Cailliet *et al.* 1990; Goosen and Smale 1997). Fin spines are also known to have incremental band growth (Holden and Meadows 1962), however this technique is limited to select shark species.

Few studies have attempted to verify and/or validate age and growth rates of sharks by counting the incremental opaque (calcified) and translucent (less calcified) bands that appear in the vertebrae (Casey and Natanson 1992; Ferreira and Vooren 1991; Kusher *et* *al.* 1992). Results from some of these studies differ, i.e. supporting annual growth band formation (one opaque and transluscent band per year) (Branstetter 1987; Walter and Ebert 1991; Parsons 1993; Cowley 1997; Goosen and Smale 1997), or suggesting that band deposition based on somatic growth rather than time (Natanson and Cailliet 1990). Growth band formation may also be family, or even species, specific, depth related or phylogenetic (Cailliet 1990). Aging deep-sea catsharks is also problematic, because of low vertebral calcification (Cailliet *et al.* 1983). Due to these variations, it is necessary to validate the band deposition rates for individual shark species.

Many techniques have been developed to facilitate age analyses. Weber and Ridgway (1962) first described the use of tetracycline, an antibiotic, as a possible tool for chemically marking bones and scales of fish. This has also been successfully used to mark vertebrae in sharks (Branstetter and McEachran 1986; Brown and Gruber 1988; Kusher *et al.* 1992; Parsons 1993). Either consumed or injected, the tetracycline is absorbed into hard tissues of sharks. When viewed under ultraviolet light, the mark can be seen as a fluorescent marker. This technique is particularly useful for sharks retained in captivity for long periods of time. Releasing sharks into the wild after injection can be a more difficult option, as the chances of recapturing the specimens are often low. Back calculation using growth model parameters (Branstetter *et al.* 1987; Carlson *et al.* 1999, Wintner and Dudley 2000), x-radiography (Wintner 2000), electron microbe analysis (Cailliet and Radtke 1987) and X-ray spectrometry (Jones and Geen 1976) have all been used to verify ages of shark species. Using multiple techniques has been encouraged to achieve the best results (Cailliet 1990).

The present study provides growth curves based on vertebral growth ring counts, basic morphological relationships and reproductive data for *Poroderma africanum*, *P. pantherinum, Haploblepharus edwardsii* and *H. pictus* from the southwestern Cape, South Africa.

METHODS

Sharks were collected from a number of sites in the southwestern Cape between June 2000 and February 2002. These sites include: Black Sophie (near Danger Point, 34°35‘S; 19°23 ‘E), Miller’s Point (34°11‘S; 18°31‘E), Buffels Bay (34°17‘S; 18°30‘E), Outer Castle Rock (34°11‘S; 18°31‘E) and Granger Bay (33°54’S; 18°24‘E) (Fig. 4.1).

Growth and sexual maturity

Measurements of all individuals included total length (TL), precaudal length (PRC), girth (G), and body weight (BW). The relationship between BW and TL for both sexes of the four shark species is presented. Power curves were fitted to the data and equations are given for all species. The slopes of the length/weight curves were compared (ANCOVA), and a *t*-test (Zar 1974) was used to see if there was a statistical difference in these slopes between sexes for each species. Primary and secondary sexual characteristics were measured for each specimen collected. These included: inner clasper length (mm), basal clasper width (mm) and gonad weight (g) for males, and shell gland diameter (mm), largest egg diameter (mm) and gonad weight (g) for females. Relationships between TL and gonad weight for both sexes, TL with inner clasper length for males, and TL with shell gland diameter, and shell gland diameter with largest egg diameter for females are graphically shown. Physical maturity of specimens was determined based on modified criteria following Ebert (1996), as listed in Table 4.1. Length at 50% maturity was determined by fitting a logistic curve to the data (Butterworth *et al.* 1989).

Embryo development

Egg cases found in the wild, extracted from dissected females, or found in the aquaria tanks with captive sharks, were measured for length (not including tendrils), width (mm), yolk diameter (mm) and weight (g), and suspended from plastic rods in aerated aquaria

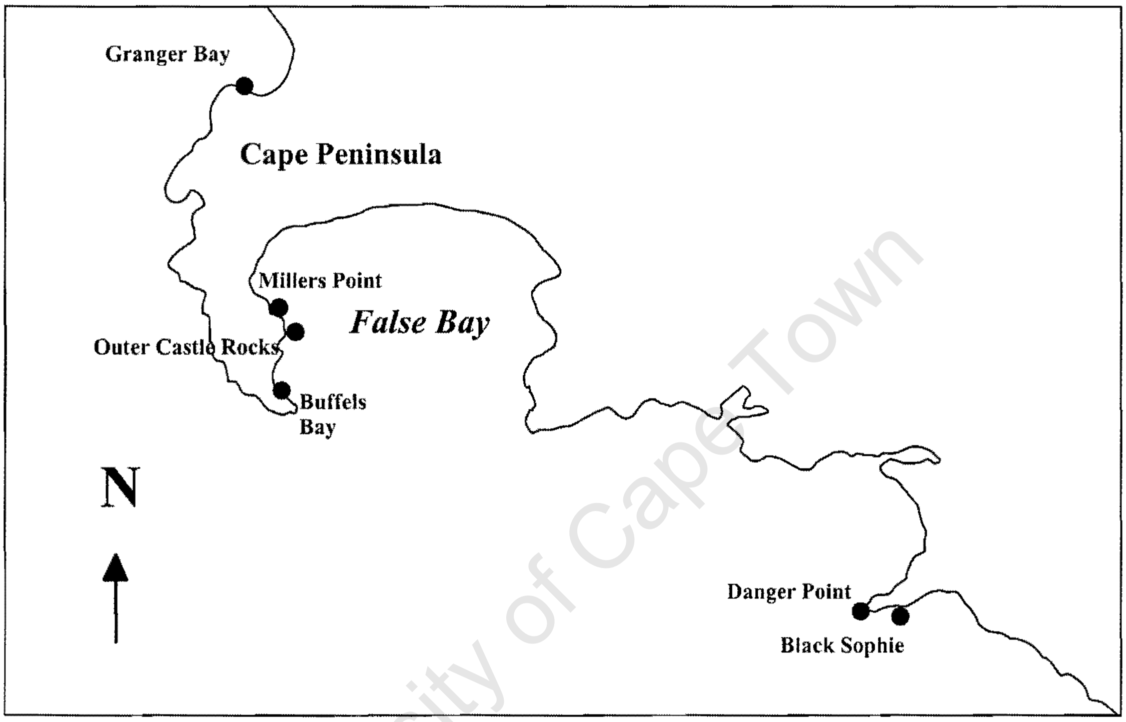


Fig. 4.1. Map of study sites in the southwestern Cape.

Table 4.1. Physical maturity based on modified criteria following Ebert (1996).

	Neonate	**Immature**	**Adolescent**	**Mature**
Males	Newly hatched specimens to captive one year old.	Small, flaccid claspers and gonads. Straight epididymis.	Flaccid or slightly calcified claspers. Some coiling of the epididymis.	Highly calcified claspers. Enlarged testes and heavily coiled epididymis.
Females	Newly hatched specimens to captive one year old.	Small ovary, with pinhead size eggs. No apparent shell glands and straight, constricted oviducts.	Eggs small but vary in size. Small shell glands apparent, but oviducts still constricted.	Eggs large and yellow, or pinhead in size. Shell glands large, oviducts flaccid and/or egg cases found in oviducts.

(TL) of the embryo and diameter of the egg yolk was measured to the nearest millimeter. As the embryo grew (TL measurements were taken monthly), the yolk diameter became tanks at 14°C. Cases were checked weekly for the presence of an embryo by positioning a light behind the egg case. Once an embryo was found, the total length increasingly more difficult to measure, because the yolk was pushed towards the narrow end of the case, where it no longer retained its circular appearance.

Once hatched, neonates were fed pieces of pilchard (*Sardinops sagax*) or octopus (*Octopus vulgaris*) *ad libitum*, three times per week. Once hatched, measurements of total length (TL), precaudal length (PRC), girth (mm) and body weight (BW) (g) were taken. Clasper length (mm) and basal clasper width (mm) were also measured for males. These measurements were taken every month.

Ageing techniques

For each specimen collected, approximately 10 vertebrae were removed from above the origin of the first dorsal fin, as the girths (and vertebrae) of the animals are largest in this area. Most samples were removed from fresh specimens, while some obtained from Marine and Coastal Management, Cape Town, South Africa, were frozen and then processed. Excess tissue was cleared and neural and haemal arches were removed. Vertebrae cleaned of most tissue, neural and heamal arches were placed in commercial bleach (3.5% sodium hypochlorite) for 30 – 60 minutes to dissolve any excess tissue. Care was taken not to soak the samples for too long because intervertebral ligaments dissolved, leaving individual vertebra. Due to the small size of vertebra (< 10 mm), it was easier to prepare the specimens if there were multiple vertebrae attached to one another. Once the samples were sufficiently cleaned, they were soaked in fresh tap water to remove any excess bleach. Up to seven vertebrae were then dried for analysis, while the remaining were either stored dry or in 70% alcohol.

Vertebrae were resin embedded in a mixture (10:1) of EC 103 Araldite and EC 951 hardener and placed in an ice water bath to prevent the contents from boiling. The specimens were set in approximately 24 hours, then cut into transverse sections with an ISOMET 11-1180 low speed diamond saw (Buehler, Ltd.). Once sectioned, cut surfaces were briefly polished on 1600 grit, wet sand paper and glued to frosted, glass slides with a mixture (3:1) of Epotek glue and Epotek 301 hardener. Specimens were left to dry for at least 24 hours before they were again sectioned to approximately 2 mm. Slides were briefly sanded with 1600 grit, wet sandpaper and viewed under a dissecting microscope at x 4/0.1 magnification with transmitted light to see if banding was apparent. Samples were re-sanded if needed until the desired thickness was achieved. The final thickness of slides varied depending on the amount of glue used to set the vertebrae to the slides.

One band pair, consisting of a transluscent (highly calcified) and opaque (poorly calcified) band, was assumed to equal one year of growth. The reason for this assumption is that specimens were not available every month; therefore, a direct comparison of the peripheral band deposition (hyaline or opaque) and time of year of occurrence could not be determined. Whether the most peripheral band or bands near the center were transluscent or opaque was recorded, however the bands were often very fuzzy and difficult to differentiate there. Bands were much more clearly defined near the margin of larger sharks. Two counts were made for each specimen, two days apart. If the two readings matched, that number was recorded as the estimated age. If the two reading differed by no more than three counts, a third reading was taken. If all three counts differed by less than two, then the age was taken as the average of the three readings. However, few readings fell under this initial parameter, therefore vertebral counts that varied by no more four were averaged and included in the calculations. Count reproducibility was determined by calculating the average percentage error (APE) described by Beamish and Fournier (1981). If the APE was larger than 20% after the third count, the vertebrae were rejected. While each count was conducted, there was no knowledge of the size or sex of the specimen. Sexes were combined for all species, as there were too few data points to analyze them individually. The relationships of centrum radius with both shark length and shark weight were analyzed. This was used to verify that centrum growth represents the growth of the shark.

The Schnute growth model (Schnute 1981) is a generalized growth model from which the von Bertalanffy growth (VBG) submodel and other growth models (e.g Gompertz, Richards) are derived. The size and age parameters for the Schnute model are derived from the existing data (i.e. the smallest/youngest and largest/oldest individuals), and hence lead, statistically, to more reliable estimates of the von Bertalanffy parameters (Schnute 1981). The Schnute growth curve (and hence, the von Bertalanffy growth curve) was then fitted to the age-length data using a nonlinear routine (Solver in EXCEL) that finds optimum parameter estimates by the minimizing the sum of squares. Too few data points were available to analyze sexes separately; so all parameters (L , k and t_0) are for combined sexes only. The periodicity of annual growth band formation was corroborated with comparisons to tagged (by M.A. Marks) and recaptured (by author) individuals and sharks hatched and kept in captivity (current study). The number of growth rings present from recaptured sharks was compared to the number of vertebral rings expected for each year the shark was at liberty. Marginal increments were not used to verify growth ring periodicity because of the lack of clarity between bands; therefore, back calculations were not attained. Because vertebrae of the three tagged sharks were not initially injected with a vertebral marker (i.e. OTC), the analysis is considered verification of annual rings rather than validation (Cailliet 1990; Kusher *et al.* 1992).

RESULTS

Growth and sexual maturity

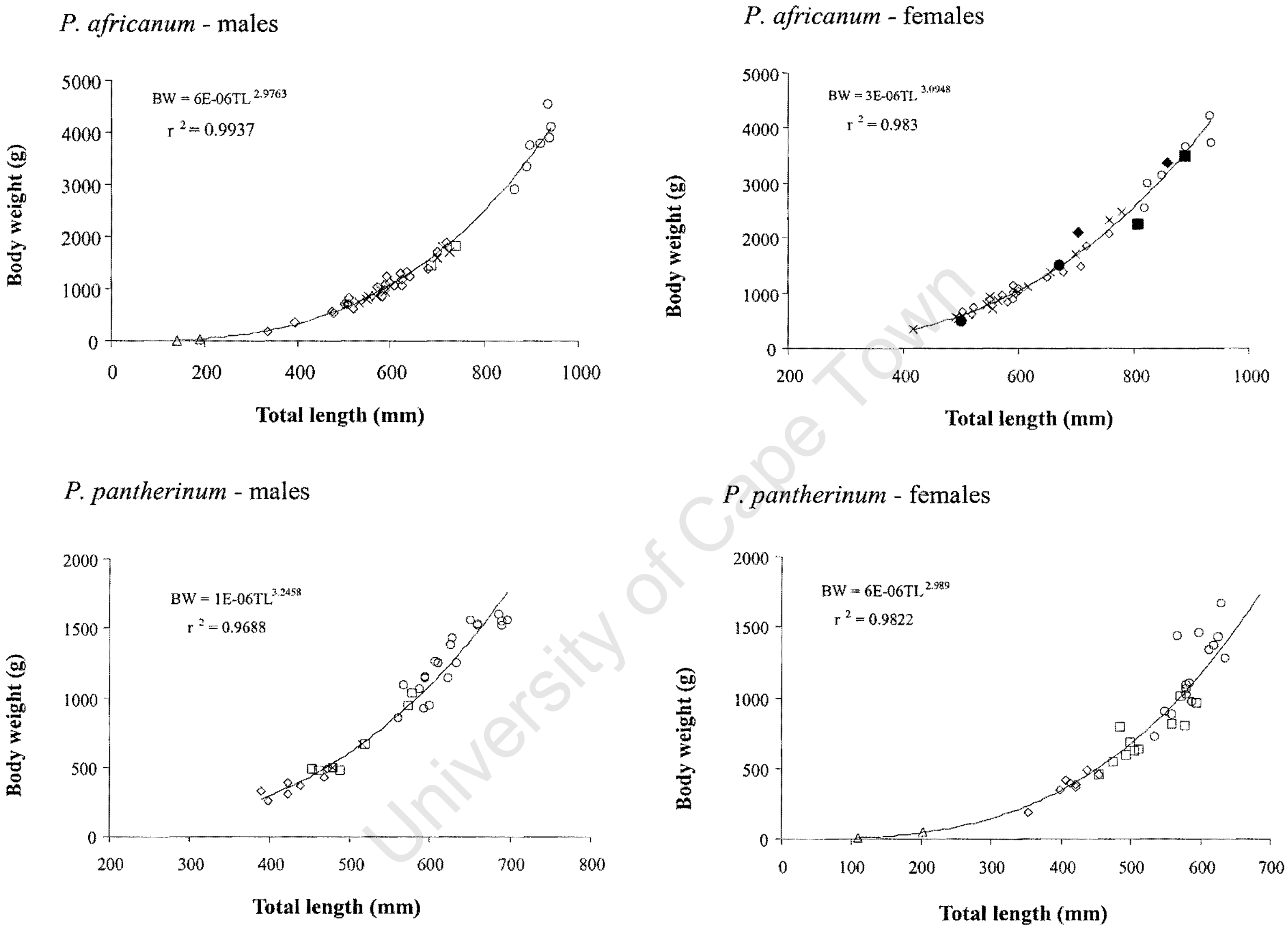
Growth

Poroderma africanum: A total of 44 males and 42 females was examined for length-weight relationships (Fig. 4.2). Average body length and weight for males were 622 mm and 1450 g (range 144 – 935 mm and 13.5 – 4555 g), and 661 mm and 1617 g for females (range 417 – 933 mm and 354 – 4225 g). The slope of the curve was significantly steeper for females than males ($p<0.001$) implying females were bulkier for a given length than males (Table 4.2). Three female specimens tagged by a former student (M.A. Marks) were recaptured during this study. One specimen, at liberty for four years, was initially measured at 500 mm TL/500 g and was later captured measuring 670 mm TL/1500 g (averaging 43 mm and 250 g of growth per year). Another individual was first measured at 808 mm TL/2261 g and was captured four years later and measured 890 mm TL/3500 g (average of 21 mm and 310 g of growth per year). The final individual was at liberty for five years and originally measured 704 mm TL/2100 g, then was recaptured and measured 861 mm/3375 g (average of 21 mm and 310 g of growth per year). The initial body weight of 2100 g for this specimen was calculated using the length-weight equation for females of this species listed in Table 4.2.

Poroderma pantherinum: Length-weight measurements were taken for 35 males and 36 females (Fig. 4.2). Average body length and weight for males were 561 mm and 960 g (range 390 – 696 mm and 255 – 1600 g). It is noteworthy that the smallest and largest males were not the lightest or heaviest specimens, respectively. The average body length and weight for females were 505 mm and 802 g (range 110 – 635 mm and 7.86 – 1675 g). Although the smallest shark also had the lowest body weight, the longest shark was not the heaviest at 1285 g. The slope of the curve for BW versus TL was significantly steeper ($p<0.001$) for males than females, implying that males are bulkier for their size than females (Table 4.2).

Table 4.2. Length-weight equations (males, females and combined) for *P. africanum*, *P. pantherinum*, *H. edwardsii* and *H. pictus*. Slopes of the curves for males and females were significantly different ($p<0.001$) for all species except *H. pictus* ($p>0.05$), therefore only the combined equation is presented for that species.

Species	Males	Females	Combined
P. africanum	$BW = 6E\text{-}6TL^{2.9763}$ $r^2 = 0.99$	$BW = 3E\text{-}6TL^{3.0948}$ $r^2 = 0.98$	$BW = 5E\text{-}6TL^{2.9951}$ $r^2 = 0.99$
P. pantherinum	$BW = 1E\text{-}6TL^{3.2458}$ $r^2 = 0.97$	$BW = 6E\text{-}6TL^{2.989}$ $r^2 = 0.98$	$BW = 5E\text{-}6TL^{3.003}$ $r^2 = 0.98$
H. edwardsii	$BW = 9E\text{-}6TL^{2.8514}$ $r^2 = 0.98$	$BW = 2E\text{-}5TL^{2.7733}$ $r^2 = 0.97$	$BW = 1E\text{-}4TL^{2.4585}$ $r^2 = 0.96$
H. pictus	_______	_______	$BW = 8E\text{-}6TL^{2.8984}$ $r^2 = 0.99$



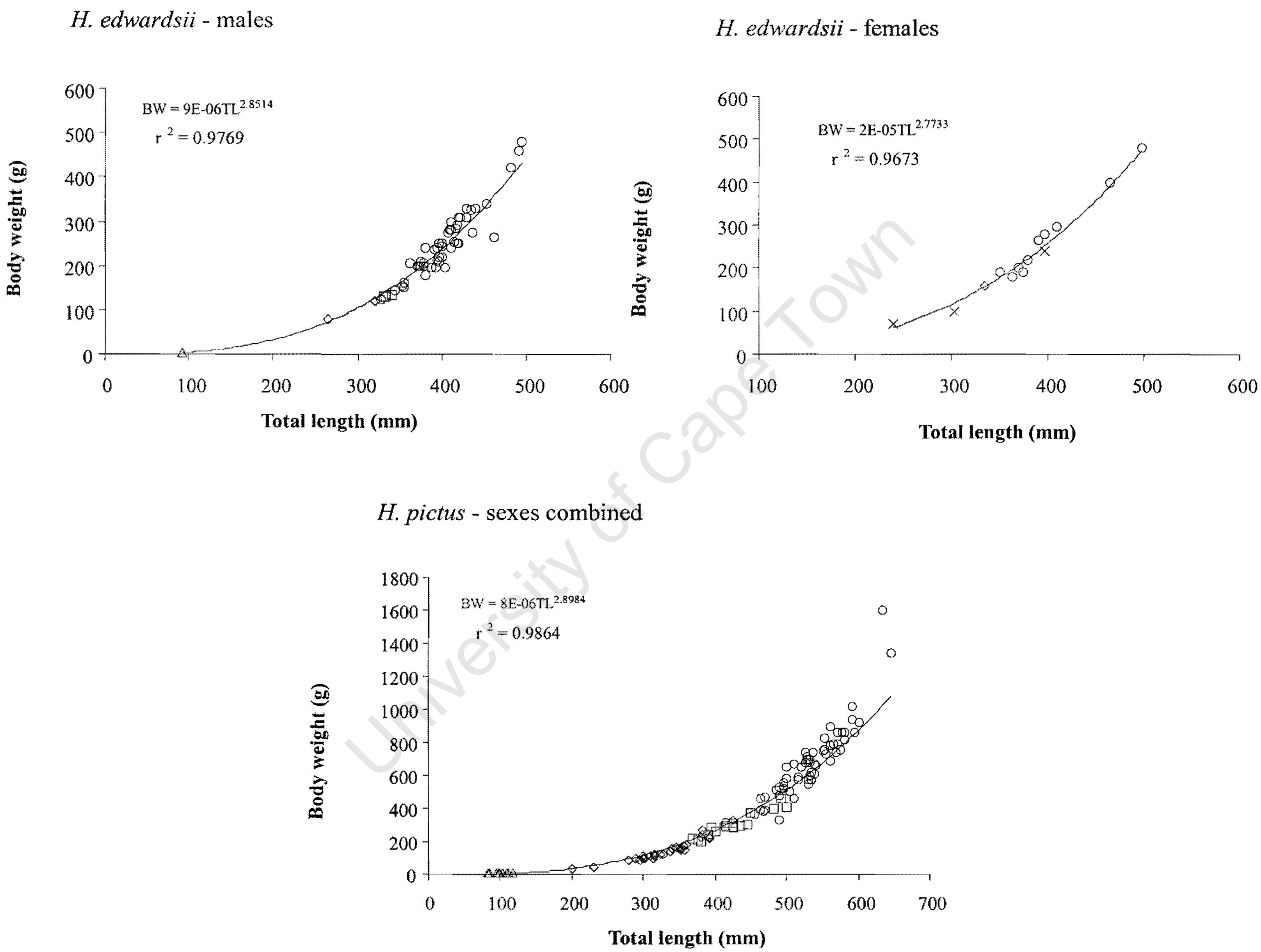
P. africanum - males

P. africanum - females

P. pantherinum - males

P. pantherinum - females

Fig. 4.2. Changes in body weight (BW) with total length (TL) for male and female *Poroderma africanum* and male and female *P. pantherinum*. Symbols represent various stages of maturity: △ neonate, ◇ immature, □ adolescent,○ mature and× maturity not recorded. Additional symbols for female *P. africanum* include recaptured individuals at liberty for: ● , ■ four years and ◆ five years. The neonate symbols for male *P. africanum* represent one specimen from birth to 4 months old and for female *P. pantherinum* represent one specimen from birth to one year old.


H. edwardsii - males

H. edwardsii - females

H. pictus - sexes combined

Fig. 4.3. Changes in body weight (BW) with total length (TL) for male and female *Haploblepharus edwardsii* and *H. pictus*, both sexes. There is no significant difference ($p>0.05$) beteween the length-weight slopes for male and female *H. pictus*, therefore the data are presented on one graph. Symbols represent various stages of maturity: △ neonate, ◇ immature, □ adolescent, ○ mature and × maturity not recorded. The neonate, male *H. edwardsii* data point is from Bertolini (unpubl. data).

Haploblepharus edwardsii: The lengths and weights of 54 males and 14 females were measured (Fig. 4.3). The average length and weight of males were 391 mm and 235 g (range 93 – 494 mm and 3.92 – 480 g). Average length and weight of females were 377 mm and 234 g (range 239 mm – 498 mm and 70 g – 480 g). The slopes of the curves for males and females are significantly different ($p<0.001$), with males being heavier for their size than females (Table 4.2).

Haploblepharus pictus: Length-weight relationships for 59 males and 57 females were examined (Fig. 4.3). Average body length and weight for males were 443 mm and 454 g (range 85 – 645 mm and 4.7 – 1335 g). Average length and weight for females were 424 mm and 434 g (range 82 – 634 mm and 5.26 – 1602 g). There was no significant difference ($p>0.05$) between the slopes of the curves for males and females, therefore only a combined equation is presented (Table 4.2).

Sexual maturity: Males

Poroderma africanum: There was a steady increase in gonad weight, inner clasper length and basal clasper width with TL until approximately 680 mm, after which the curve increased more rapidly (Figs 4.4-4.6). All individuals greater than 865 mm were mature, based on the criteria listed in Table 4.1.

Poroderma pantherinum: The relationship between gonad weight, inner clasper length and basal clasper length with TL was positive for male *P. pantherinum* (Figs 4.4-4.6). The greatest rate of change in gonad weight occurred between 600 and 650 mm TL, for inner clasper length and basal clasper length between 525 and 575 mm TL. The majority of specimens smaller than approximately 480 mm were immature. All individuals greater than *c.* 590 were mature, based on the criteria listed in Table 4.1.

Haploblepharus edwardsii: Only one adolescent specimen was measured for gonad weight, the remaining specimens, greater than *c.* 550 mm TL were all mature (Fig. 4.4). Two immature individuals were measured for basal clasper width with the largest immature specimen measuring *c.* 330 mm TL (Fig. 4.6). There was a rapid increase in

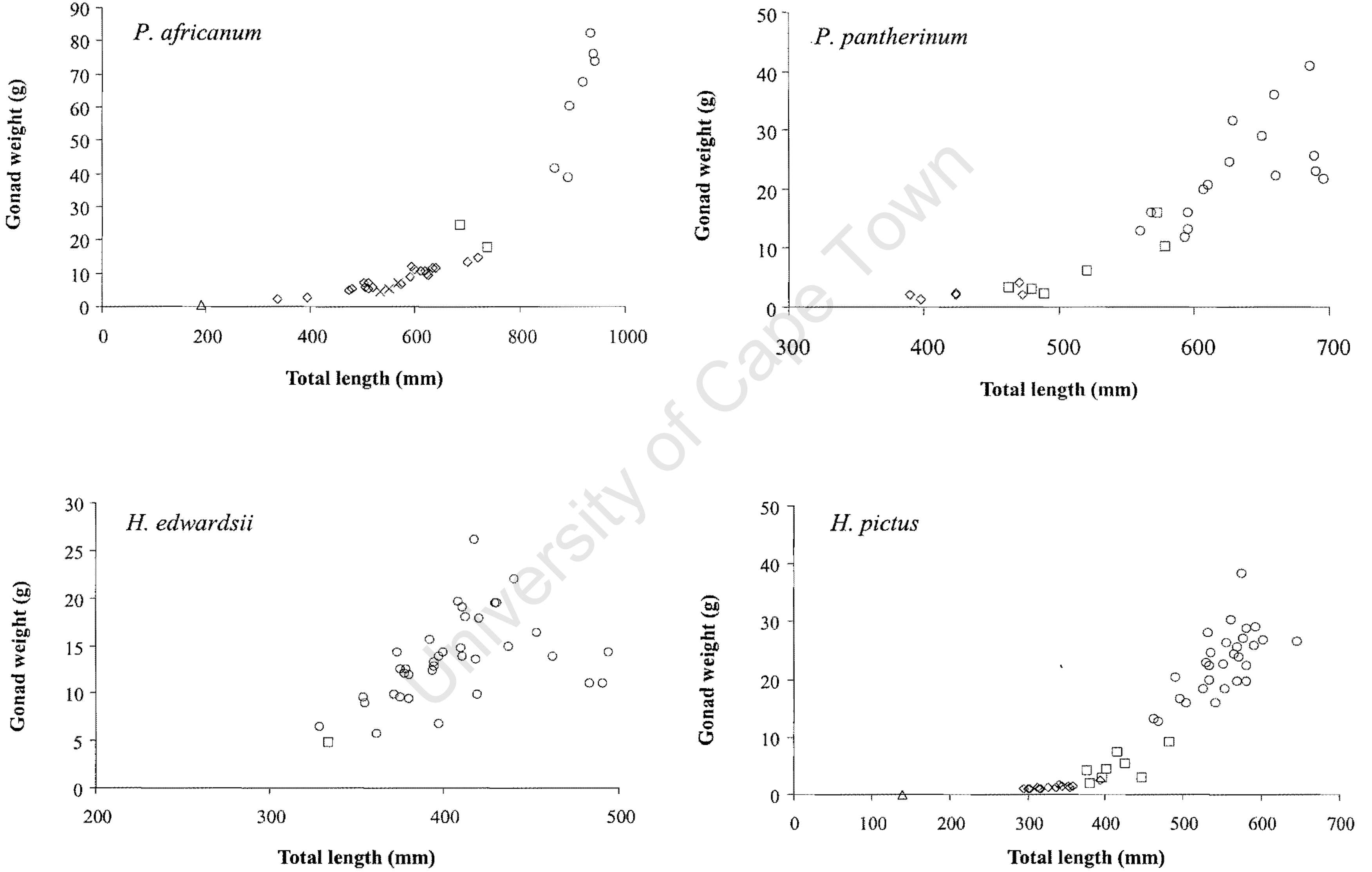


Fig. 4.4. Gonad weight versus total length for male *Poroderma africanum*, *P. pantherinum*, *Haploblephaurs edwardsii* and *H. pictus*. Symbols represent various stages of maturity: △ neonate, ◇ immature, □ adolescent, ○ mature and × maturity not recorded.

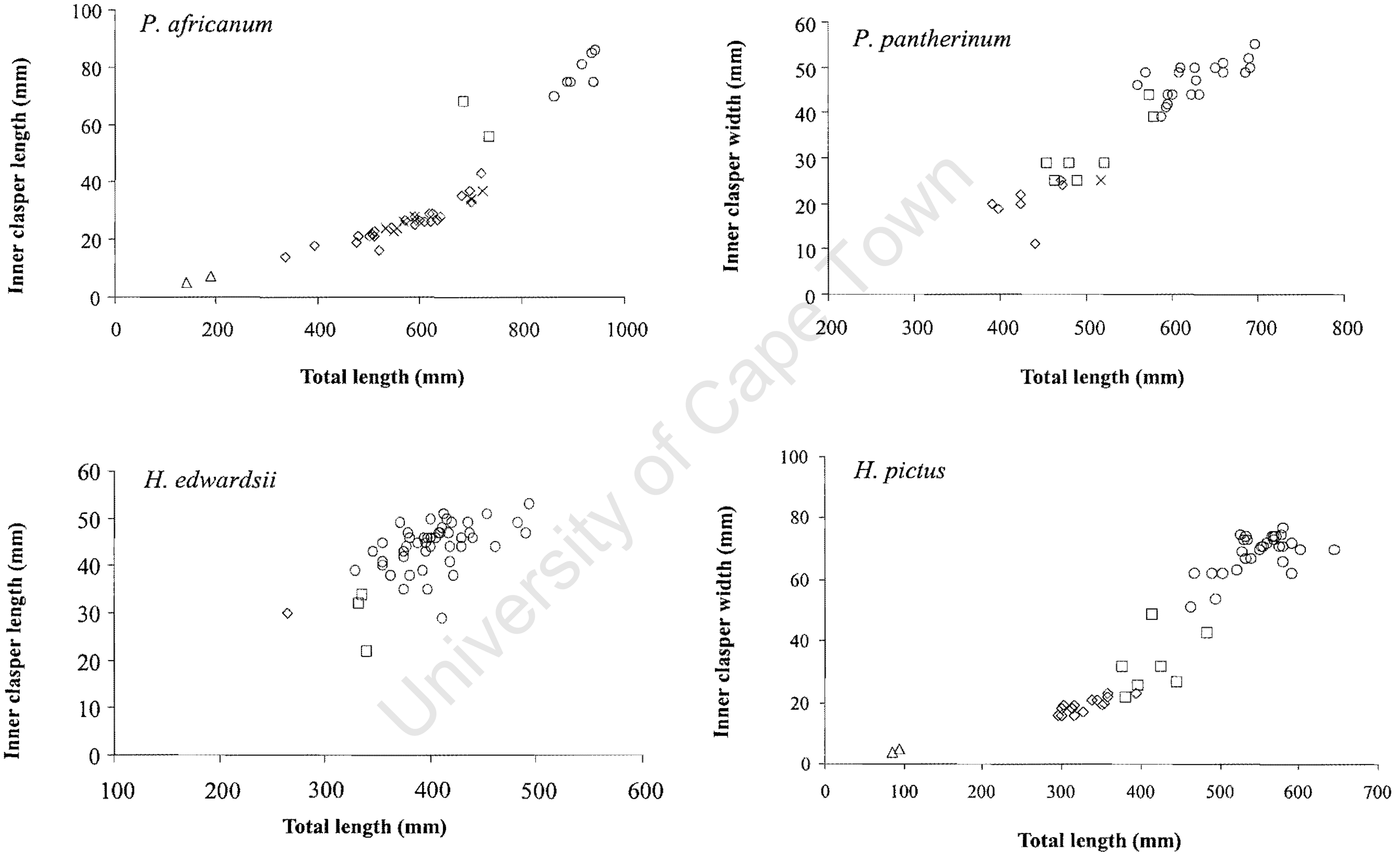


Fig. 4.5. Inner clasper length versus total length for male *Poroderma africanum*, *P. pantherinum*, *Haploblephaurs edwardsii* and *H. pictus*. Symbols represent various stages of maturity: △ neonate, ◇ immature, □ adolescent, ○ mature and × maturity not recorded.

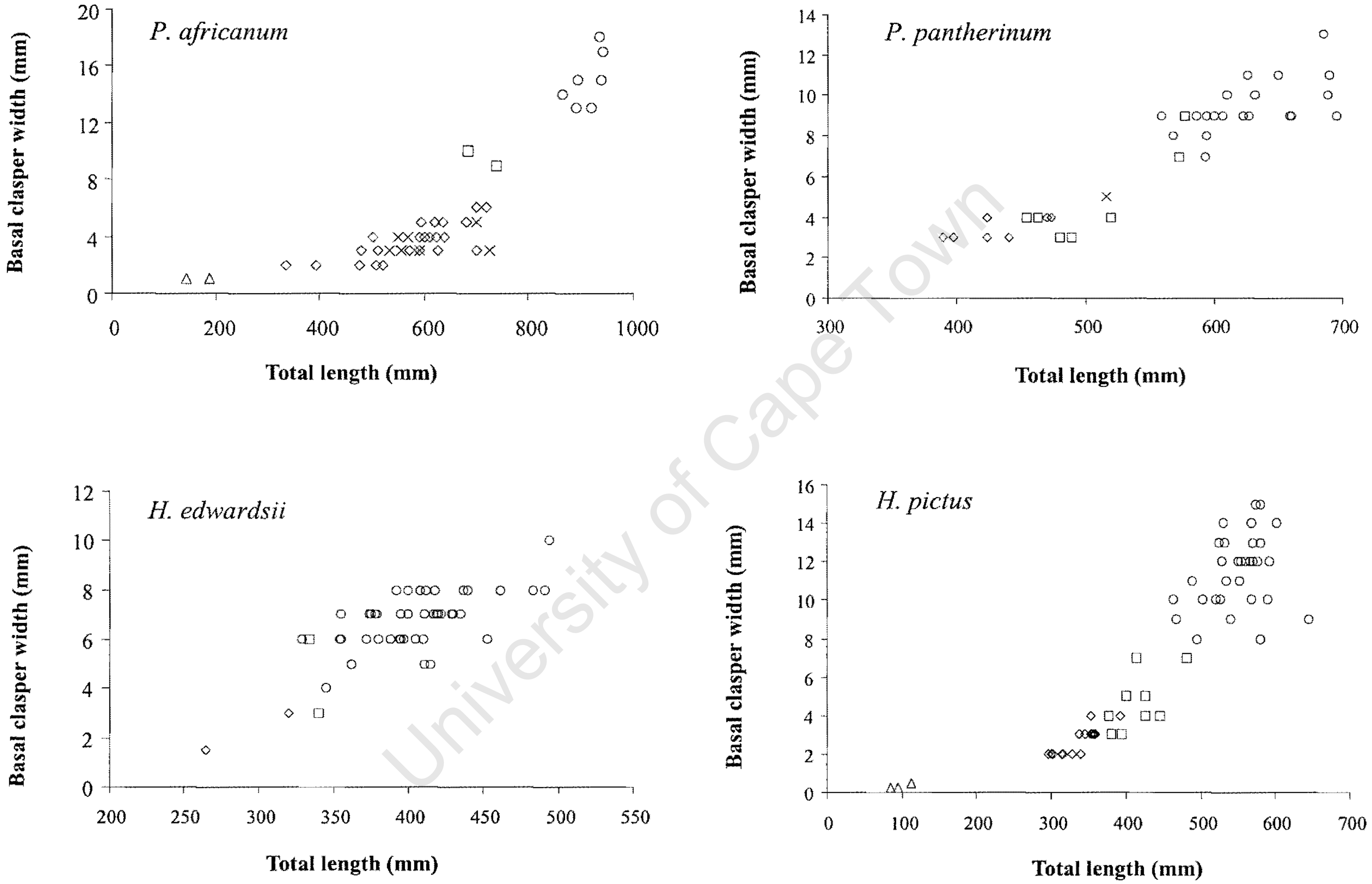


Fig. 4.6. Basal clasper width versus total length for male *Poroderma africanum*, *P. pantherinum*, *Haploblephaurs edwardsii* and *H. pictus*. Symbols represent various stages of maturity: △ neonate, ◇ immature, □ adolescent, ○ mature and × maturity not recorded.

basal clasper width with size after *c.* 350 mm TL. Mature individuals covered a broad spectrum of total lengths, between *c.* 350 and 500 mm TL, yet there was little increase in basal clasper width and inner clasper length (Figs 4.5-4.6) between the smallest and largest mature individuals.

Haploblepharus pictus: At approximately 370 mm TL, individuals entered the adolescent phase of development (Fig. 4.4). A rapid increase in gonad weight, inner clasper weight and basal clasper weight occurred between 450 and 500 mm TL (Figs 4.4-4.6). The smallest mature individual was 463 mm and all sharks greater than c. 490 mm TL were mature.

Sexual maturity: Females

Poroderma africanum: The relationship between gonad weight and TL followed a steady curve, with an abrupt increase at c. 820 mm TL (Fig. 4.7). All individuals greater than this were mature. No adolescent individuals were recorded, however there was little gap between an immature individual and a mature one. Too few data points for shell gland width or largest egg diameter (LED) were recorded for graphical representation. Shell gland diameters were measured for two mature females; 23 mm for an 820 mm TL individual and 39 mm for an 861 mm TL shark. The 820 mm shark had an LED of 5 mm, compared to an LED of 13 mm for the 861 mm shark. The largest immature shark measured 759 mm TL, and no shell glands were apparent for even a shark of this size.

Poroderma pantherinum: Gonad weight and LED increased steadily until a rapid increase occurred at *c.* 550 mm TL (Fig. 4.7-4.8). All specimens greater than 600 mm TL were mature, however the smallest mature individual was 550 mm TL. Shell gland width drastically increased between 425 and 475 mm TL (Fig. 4.9), and this increase was between immature and adolescent individuals. The rate of shell gland width with TL steadily increased between adolescents and mature sharks. All specimens with a shell gland width greater than 19 mm were mature. There was a positive correlation between LED and shell gland width, with LED increasing abruptly between immature and

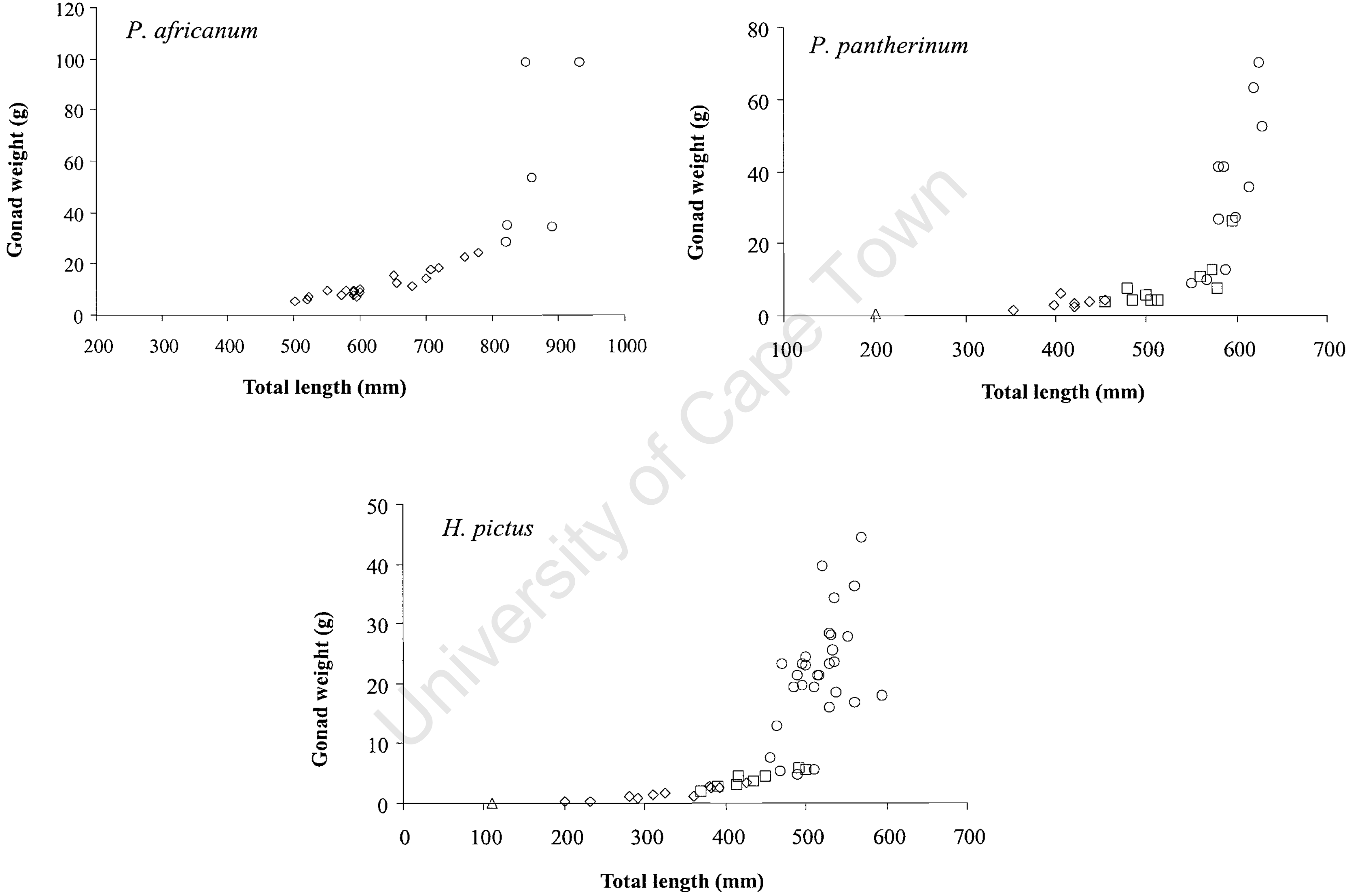


Fig.4.7. Gonad weight versus total length for female *Poroderma africanum*, *P. pantherinum* and *Haploblephaurs pictus*. Symbols represent various stages of maturity: △ neonate, ◇ immature, □ adolescent, ○ mature and maturity not recorded. Too few data points were recorded for *H. edwardsii*.

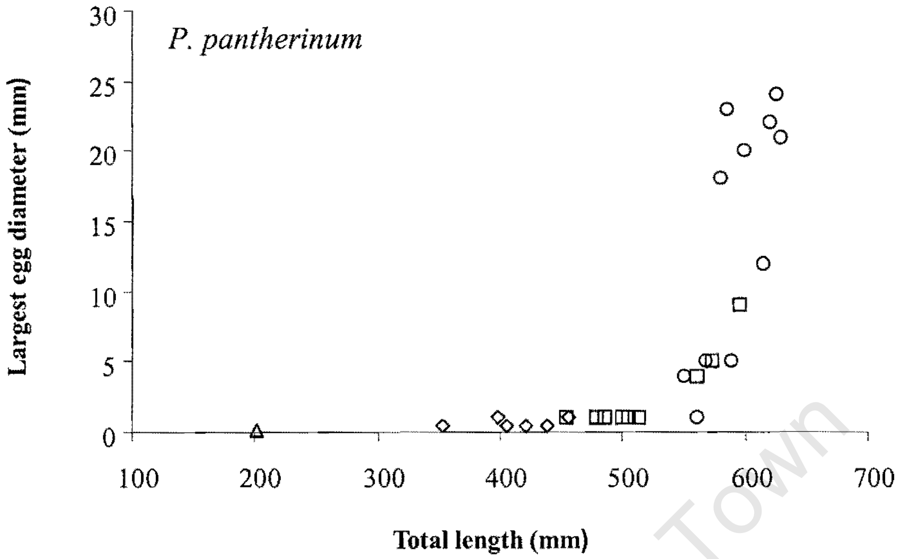
adolescent individuals at a shell gland width of 2 mm (Fig. 4.10). The smallest shell gland width for a mature shark was 4 mm, with a corresponding LED of 19 mm.

Haploblepharus edwardsii: Of the 14 female specimens captured, the maturity of only 11 (10 mature, 1 immature) were described and 4 (mature) were measured for gonad weight, shell gland width and LED. All individuals greater than 350 mm TL were mature. The only immature individual measured was 335 mm TL and 160 g. The lowest and highest gonad weight for a mature female was 7.71 g and 15.91 g, respectively. The average shell gland width and LED of the four mature specimens were 17 mm and 15 mm, respectively.

Haploblepharus pictus: The greatest rate of change in gonad weight with TL was between 425 and 475 mm TL (Fig. 4.7). All individual greater than *c.* 500 mm TL were mature. There was little increase in gonad weight between immature and adolescent individuals. All sharks smaller than 360 mm TL were immature. However, a rapid increase in shell width with TL occurred between *c.* 375 and 425 mm TL and all but one immature specimen in this range were adolescent (Fig. 4.9). A sharp increase between the LED's of adolescent and mature females occurred at approximately 450 mm TL (Fig. 4.8). Except for two individuals, the LED of immature sharks and adolescents were similar. There was also a positive correlation between LED and shell gland width (Fig. 4.10). LED's of mature individuals varied between 5 and 25 mm.

Embryo development

At approximately 2 – 4 weeks after the egg cases were released or dissected from females, embryos became visible. Total lengths (TL) were taken throughout their development, however measurements varied widely, as it was extremely difficult to measure moving individuals. Because so few cases were available, they were not dissected at intermittent times, which would have given more accurate TL measurements over the gestation period.



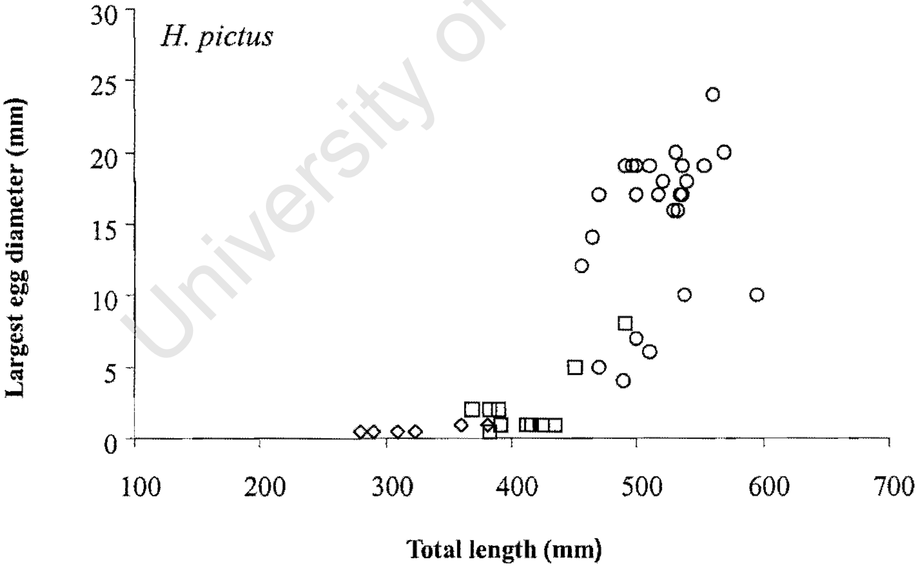


Fig. 4.8. Largest egg diameter versus total length for female *Poroderma pantherinum* and *Haploblephaurs pictus.* Symbols represent various stages of maturity: △ neonate, ◇ immature, □ adolescent and ○ mature. Too few data points were recorded for *P. africanum* and *H. edwardsii* for graphical representation.

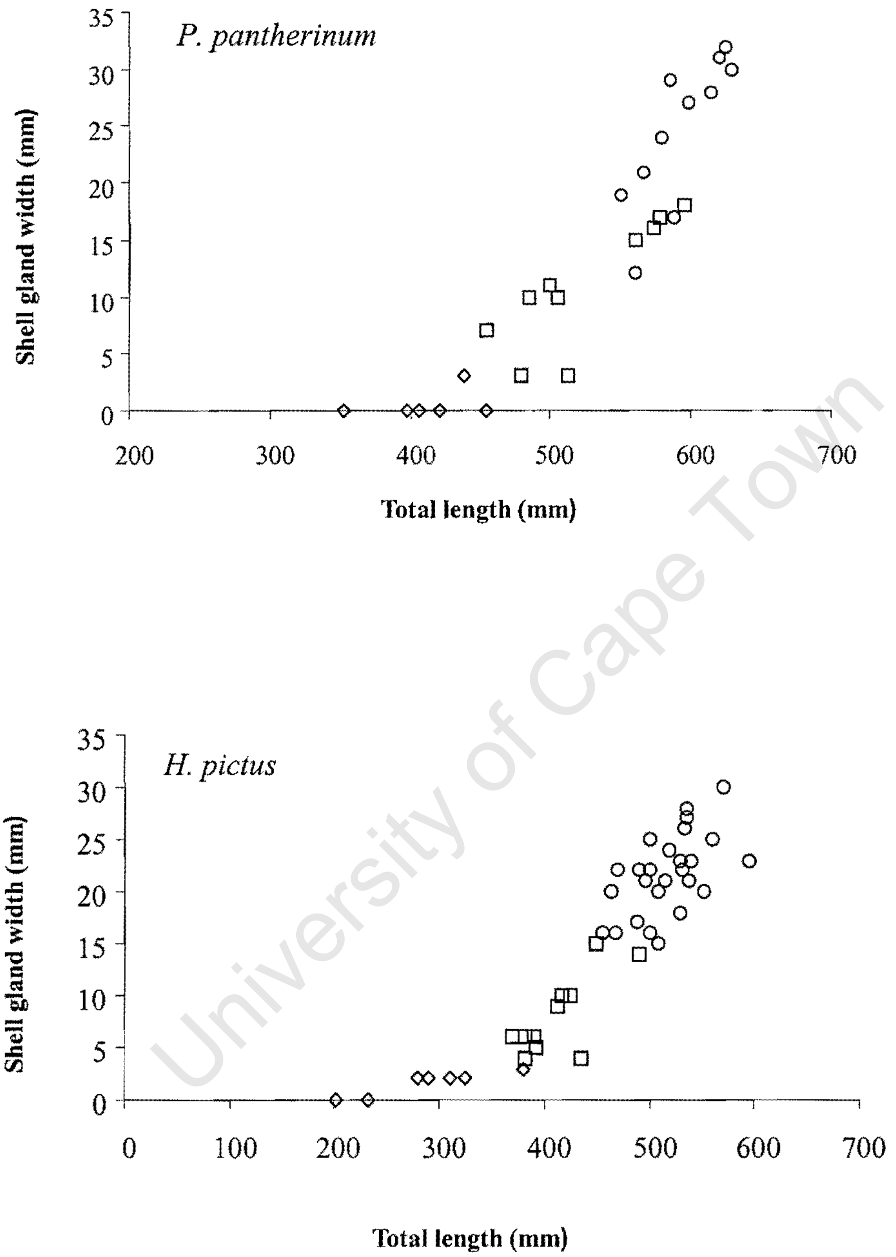


Fig. 4.9. Shell gland width versus total length for female *Poroderma pantherinum* and *Haploblephaurs pictus.* Symbols represent various stages of maturity: ◇ immature, □ adolescent and ○ mature. Too few data points were recorded for *P. africanum* and *H. edwardsii* for graphical representation.

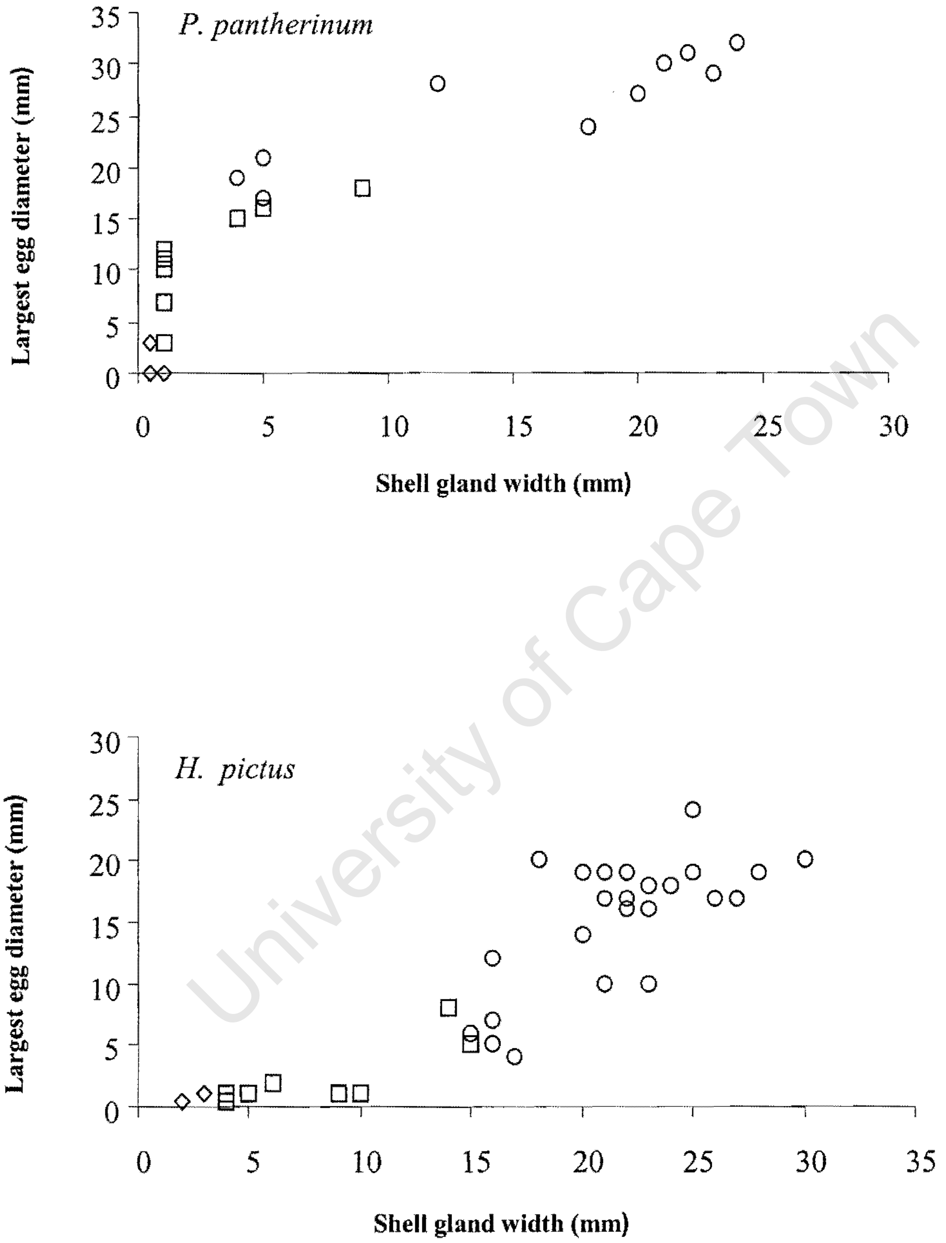


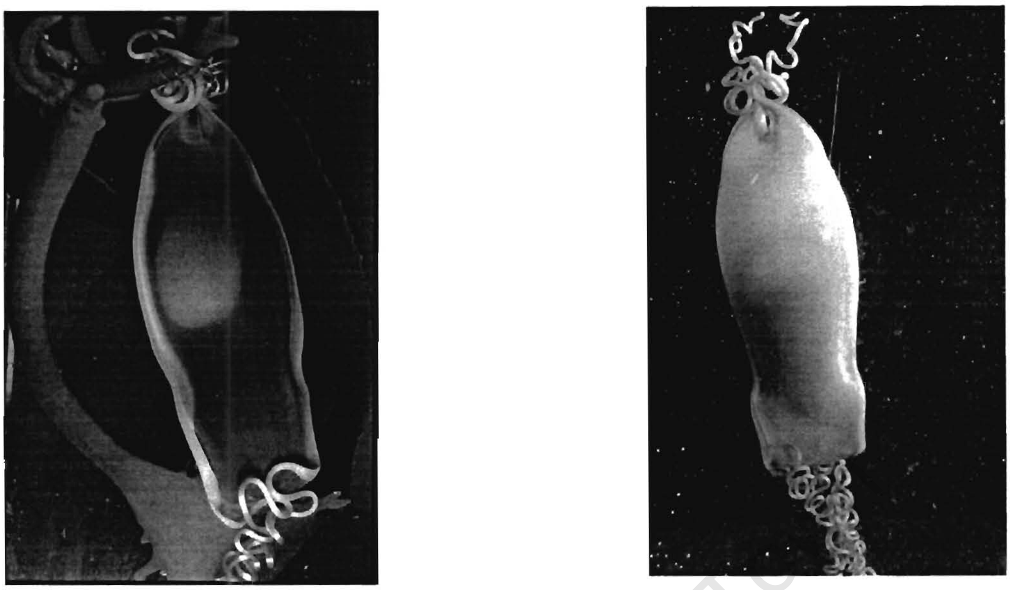
Fig. 4.10. Largest egg diameter versus shell gland width for female *Poroderma pantherinum* and *Haploblephaurs pictus*. Symbols represent various stages of maturity: ◇ immature, □ adolescent and ○ mature. Too few data points were recorded for *P. africanum* and *H. edwardsii* for graphical representation.

Poroderma africanum: Egg cases are light yellow in color (Fig. 4.11). Only one egg case, measuring 100 mm x 39 mm and light yellow in color, of this species was obtained. The case was found in the tank where captive specimens were kept in October 2000. After 12 months, the embryo had still not hatched from its case and was subsequently cut free. The male shark measured 144 mm TL and 13.5 g, but did not seem to be in good health and had difficulty swimming. There was no external yolk sac and the neonate readily ate pieces of recently dissected *H. pictus* meat. After approximately two weeks, the shark began to swim normally. After four months, the neonate had grown to 190 mm TL and weighed 36.7 g. Monthly measurements from birth until dissection after four months are listed in Table 4.3.

Poroderma pantherinum: Cases are light yellow in color (Fig. 4.11). Three egg cases, one found in the wild (June 2000) and the others dissected from a 620 mm TL, 1370 g female (November 2001) were analyzed. The case found in the wild was 71 mm in length and 32 mm wide and the embryo was already present (approximately 25 mm TL) and hatched after 8 months. This female specimen hatched on its own and was 110 mm

Table 4.3. Monthly measurements including total length (TL), precaudal length (PRC), body weight (BW) and inner clasper length/basal width of a male *P. africanum* neonate (maintained in an aquarium at 14°C) from birth until dissection.

Date	TL (mm)	PRC (mm)	BW (g)	Clasper L/W (mm)
9 Oct 01	144	105	13.5	5/1
1 Nov 01	150	114	21.41	6/1
10 Dec 01	174	129	25.38	___
14 Jan 02	181	135	26.39	7/1
11 Feb 02	190	140	32.77	7/1
25 Feb 02	190	140	36.74	7/1



Poroderma africanum

Poroderma pantherinum

Haploblepharus edwardsii

Haploblepharus pictus

Fig. 4.11. Egg cases of *Poroderma africanum, P. pantherinum, Haploblepharus edwardsii* and *H. pictus*. Both P. *pantherinum* and *H. edwardsii* cases contain seven month old embryos.

TL and 7.86 g at birth. Monthly measurements are listed in Table 4. The egg cases dissected from the female were 77 mm in length/30 mm wide and 76 mm in length/31 mm wide. These embryos were not to term as of May 2002, so no additional measurements were taken.

Table 4.4. Monthly measurements including total length (TL), precaudal length (PRC) and body weight (BW) of a female *P. pantherinum* from birth until dissection.

Date	TL (mm)	PRC (mm)	BW (g)
7 Feb 01	110	85	7.86
1 Mar 01	121	95	9.26
26 Mar 01	124	100	11.99
4 Apr 01	132	100	11.28
3 May 01	135	115	14.30
28 May 01	144	115	18.00
28 June 01	150	115	19.04
6 Aug 01	160	122	12.21
3 Sept 01	165	125	22.70
3 Oct 01	166	125	26.44
1 Nov 01	177	136	32.52
10 Dec 01	191	146	40.55
14 Jan 02	199	153	40.17
11 Feb 02	202	155	45.94
25 Feb 02	202	155	36.74

Haploblepharus edwardsii: The cases of this species are small, caramel brown with widely spaced, cream colored bands running the width of the case and long tendrils (Fig. 4.11). Twelve egg cases were obtained either from dissected females or from aquaria tanks holding captive sharks. Egg cases were found in the months of June, July, August, November and December. The average length and width of the cases were 43 x 17 mm (range 41 – 46 mm in length and 15 – 19 mm wide). Six egg cases were extracted from four dissected, mature females that averaged 386 mm TL (range 364 – 410 mm TL) and 240 g (180 – 295 g TL) in November and December 2001. Five of these cases contained embryos, however were not to term in May 2002 and no further measurements were taken. One term *H. edwardsii* was previously recorded (Bertolini, unpub. data) to be 93 mm TL/3.92 g BW at birth. The recorded gestation period was 3 months (temperature unknown), which is much shorter than the observed period of at least 7 months in this study (cases held at 14°C).

Haploblepharus pictus: Egg cases are small, dark brown with long tendrils (Fig. 4.11). Thirty-nine egg cases from this species were either found in the tanks of captive sharks or were found in dissected females. Eight of the cases produced term embryos, 25 died before birth and 6 were unviable. Cases averaged 54 mm long and 22 mm wide (range 44 – 65 mm long and 17 – 29 mm wide). Two of the egg cases that produced term embryos were from dissected females. One term, female embryo from a 52 x 25 mm egg case (dissected from a 529 mm TL/710 g individual) hatched on its own after a 9-month gestation period (from June to March). The neonate was 117 mm TL and 5.93 g. The other male term embryo (egg case 56 mm x 22 mm) dissected from a 464 mm TL/460 g female had a 10-month gestation period and hatched measuring 112 mm TL and 5.88 g.

Table 4.5. Monthly measurements including total length (TL), precaudal length (PRC), body weight (BW) and clapser length and width (L/W) for a male *H. pictus* (maintained in an aquarium at 14°C) from the time it was cut from its case (after a 6-month gestation period) until dissection. The external yolk sac was still apparent when the neonate was cut from the case and disappeared approximately two weeks later.

Date	TL (mm)	PRC (mm)	BW (g)	Clasper L/W (mm)
26 Nov 01	85	65	4.70	____
10 Dec 01	96	70	4.03	4/0.2
14 Jan 02	100	74	3.85	4/0.2
11 Feb 02	111	82	6.03	5/0.3
19 Mar 02	119	89	7.65	5/0.3
9 Apr 02	126	92	10.50	5/0.5
13 May 02	145	110	16.84	6/0.5

Two female embryos from unknown mothers hatched on their own; one after a 6-month gestation period (September to March) and measuring 115 mm TL and 6.14 g at birth, the other after 9 months gestation (May to February) measuring 102 mm TL and 5.12 g. Due to the high mortality of many near-term embryos, four embryos were cut from their cases 6 months after they were laid. All four seemed immature as they weighed much less than the embryos that hatched on their own. The four were 82 mm (female), 85 mm (male), 95 mm (male) and 98 mm (male) mm TL and 5.26 g, 4.7 g, 5.13 g and 5.27 g, respectively. An external yolk sac was still present on the 85 mm TL/4.7 g shark, however after 14 days the sac disappeared. The neonate survived and was not fed until the sac disappeared. Monthly measurements from birth to six months old are listed in Table 4.5. All other specimens that were cut from their cases seemed healthy and ate almost immediately, even though an internal yolk sac would sustain them for the first weeks after hatching (Hamlett and Koob 1999).

Ageing

Of the 227 vertebrae analyzed for the four species, 185 were readable (81%). Any specimen that had an APE of greater than 20% was rejected. The majority of *P. africanum* specimens (95%) had an APE of less than 20%, compared to 75% for *P. pantherinum*, 79% for *H. edwardsii* and 77% for *H. pictus* (Fig. 4.12). The total APE's for all vertebrae read (not rejected and rejected) were: 7% for *P. africanum*, 13% for *P. pantherinum*, 13% for *Haploblepharus edwardsii* and 19% for *H. pictus*.

The relationships between TL and centrum radius (Fig. 4.13) and BW and centrum radius for the four shark species were all significant (Fig. 4.14). The equations of the lines and r^2 values for the graphs, and equations for the inverse relationship of TL/ BW and centrum radius are presented in Table 4.6. Von Bertalanffy growth parameters (L (mm TL), k (year^{-1}), t_0 (years) and n (no. of individuals)) for all four species are listed in Table 4.7.

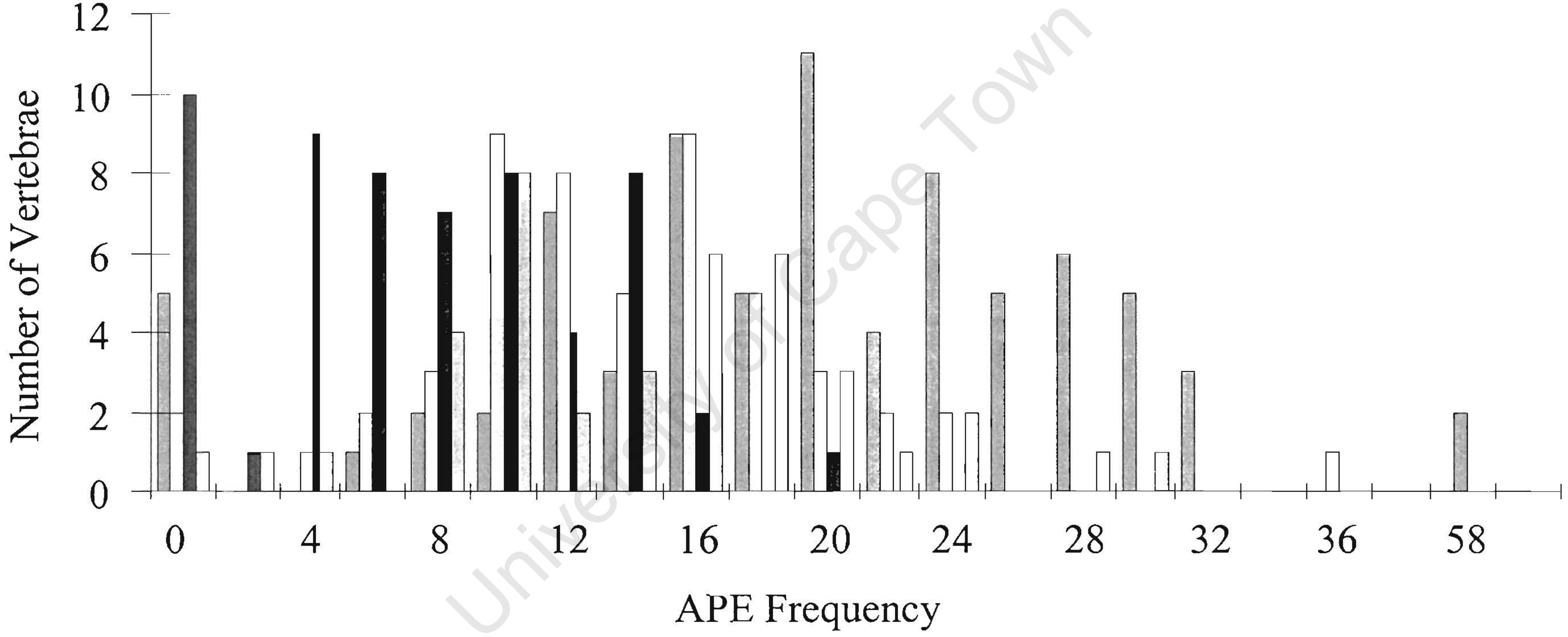


Fig. 4.12. The relationship between frequency of sharks and the average percentage error (APE) between vertebral counts for ■ *Poroderma africanum*, ☐ *P. pantherinum*, ☐ *Haploblepharus edwardsii* and ▨ *H. pictus*. Note that the x-axis is not continuous after 36.

Table 4.6. Fitted equations and coefficient of determination (r^2) values for total length (TL) versus centrum radius (CR), body weight (BW) versus centrum radius and the inverse relationships for both.

Species	**TL vs. centrum radius**	**BW vs. centrum radius**	**Centrum radius vs. TL**	**Centrum radius vs. BW**
P. africanum	$TL = 0.0059CR - 0.0861$ $r^2 = 0.91$	$TL = 1.0829Ln(CR) - 3.9519$ $r^2 = 0.88$	$TL = 149.83CR + 82.083$ $r^2 = 0.91$	$TL = 39.318CR^{2.659}$ $r^2 = 0.9449$
P. pantherinum	$TL = 0.0064CR - 0.1866$ $r^2 = 0.94$	$TL = 0.8845Ln(CR) - 2.6098$ $r^2 = 0.92$	$TL = 147.06CR + 56.842$ $r^2 = 0.94$	$TL = 30.914CR^{2.7505}$ $r^2 = 0.94$
H. edwardsii	$TL = 0.0058CR - 0.1043$ $r^2 = 0.9032$	$TL = 0.7744Ln(CR) - 2.0193$ $r^2 = 0.89$	$TL = 155.95CR + 55.252$ $r^2 = 0.90$	$TL = 29.811CR^{2.6416}$ $r^2 = 0.90$
H. pictus	$TL = 0.0059CR - 0.109$ $r^2 = 0.9557$	$TL = 0.6237Ln(CR) - 1.0655$ $r^2 = 0.93$	$TL = 161.17CR + 37.194$ $r^2 = 0.96$	$TL = 27.443CR^{2.779}$ $r^2 = 0.96$

Table 4.7. Von Bertalanffy growth parameters for combined sexes of *Poroderma africanum*, *P. pantherinum*, *Haploblepharus edwardsii* and *H. pictus*.

Species	**Von Bertalanffy growth parameters**			
	L (mm TL)	**k (year^{-1})**	**t_0 (years)**	**n**
P. africanum	1363	0.036	-3.52	55
P. pantherinum	808	0.069	-2.43	39
H. edwardsii	424	0.217	-1.16	31
H. pictus	694	0.073	-2.13	60

Poroderma africanum: The growth parameters for this species are as follows: L =1365 mm, k=0.036 year^{-1}, t_0=-3.52, n=55. The parameter of L is higher than the largest animal collected (male: 935 mm TL), however this species is known to reach 1 m (Compagno *et al.* 1989). The estimate of t_0 (-3.52) is relatively higher than the observed gestation period of up to 12 months. At 0.036, the k parameter represents a very slow growth rate.

The smallest animal (male, age 0) was born in captivity and was 144 mm in length at birth (Fig. 4.15) and the VBG curve gave a similar estimate of size at birth (160 mm). After 4 months of growth (TL = 190 mm), the animal was sacrificed. The vertebrae were small (< 1 mm) and could not be suitably sectioned to reveal growth bands. The oldest animal aged was 890 mm (female) and estimated to be 26 years old. However, this animal had been tagged, recaptured after four years, and released again, so only an estimate of age could be obtained. The length at the estimated age of tagging and recapture falls squarely on the VBG curve, which supports the accuracy of one band pair per year. Additional evidence comes from two female individuals that were at liberty for 4 and 5 years, and vertebral counts that were conducted on these individuals. The shark at liberty for 4 years was estimated to have 9 growth ring pairs at tagging (500 mm TL) and 13 growth ring pairs at recapture (670 mm TL). The number of growth rings counted for this specimen was 18. The APE between observed and estimated growth ring pairs at recapture was 16%. The shark at liberty for 5 years was estimated to have 17 growth ring pairs at tagging and 22 at recapture, and grew from 704 – 861 mm TL, averaging 31 mm annual growth. Twenty-three growth ring pairs were counted from the vertebrae, which gives only a 2% APE between observed and expected age estimates for the recaptured length.

Total length at 50% maturity is 857 mm for males (91% of asymptotic length), 849 mm for females (91% of asymptotic length) and 866 mm for combined data (92% asymptotic length) (Table 4.8). Comparing the length at 50% maturity of sex-combined data to the growth curve, this species reaches 50% maturity at approximately 24 years.

Poroderma pantherinum: The VBG parameters for this species are: L =808, k=0.069 year^{-1}, t_0=-2.43, n=39. One female *P. pantherinum* individual was kept in captivity for the first year of its life and sacrificed for age analysis. At birth, the neonate was 144 mm TL, which is similar to the estimated age at birth (123 mm) for the VBG curve (Fig. 4.15). After one year, the individual was 202 mm TL and slightly longer than the estimated length (168 mm) for the same age. The estimate for t_0 (-2.43) is higher than that of the observed gestation period of approximately eight months. The largest animal was 696 mm TL and had 19 growth ring pairs. This species is known to reach at least 740 mm TL (Compagno *et al.* 1989), which is closer to the estimated L (808 mm). The smallest mature individual was 500 mm TL and had 13 growth ring pairs, with an estimated age of 12. Total length at 50% maturity is 590 mm (85% asymptotic length) for males, 595 mm for females (94% asymptotic length) and 591 mm for sexes combined (85% asymptotic length) (Table 4.8). Age at 50% maturity for the sexes-combined data is 17 years.

Haploblepharus edwardsii: Data for length at age 0 were available for one male neonate from a former student (Bertolini, unpub. data), however the sample was not available for growth ring analysis. During this study, there were no individuals found < 300 mm TL. Only one of the sharks collected and aged was noted as immature, and the smallest mature individual was 380 mm TL and had 6 growth ring pairs (Fig. 4.15). The oldest animal aged had 22 growth ring pairs and was 494 mm TL, however the largest animal collected was a female at 498 mm TL. This TL measurement is slightly higher than the

Table 4.8. Total length (mm) at 50% maturity, % asymptotic length attained at 50% maturity and age (years) at 50% maturity for *Poroderma africanum*, *P. pantherinum*, *Haploblepharus edwardsii* and *H. pictus*. Too few data points were available for female *H. edwardsii*; therefore, the data were pooled.

Species	**Total length (mm) at 50% maturity**			**% asymptotic length**			**Age (years) at 50% maturity**
	males	**females**	**combined**	**males**	**females**	**combined**	**combined**
P. africanum	857 n=36	849 n=35	866 n=70	91	91	92	24
P. pantherinum	590 n=34	595 n=37	591 n=71	85	94	85	17
H. edwardsii	351 n=53	n/a n=11	351 n=64	70	n/a	71	7
H. pictus	503 n=61	491 n=57	496 n=118	78	77	77	15

L (424 mm TL)(n=31), and this species is known to reach 600 mm TL (Compagno *et al.* 1989). The k parameter is also much higher (0.217 mm year^{-1}) than the other catshark species, indicating a faster growth rate. The gestation period for this species in unknown, however, it is most likely up to 12 months, based on observed embryo development (at 14°C), which is much lower than the estimated t_0 (-1.16). Bertolini (unpub. data) recorded a three-month gestation period for the neonate mentioned above, however, the temperature at which the egg case was maintained was not recorded. Total length at 50% maturity for males and both sexes combined is 351 mm (70 % and 71 % asymptotic length, respectively) (Table 4.8). The maturity state of only 11 females were recorded (from a total of 14 observed and collected) and 10 of these individuals were mature, therefore, the data for both sexes were pooled. *H. edwardsii* reaches 50% maturity at 7 years.

Haploblepharus pictus: Two neonate *H. pictus* specimens were dissected for age analysis, one four days after birth and the other four months after hatching. Vertebral radii were < 1 mm for both individuals, which were too small for the sectioning process to reveal growth bands. The four-month old specimen was 95 mm TL when it was cut from the case and 139 mm TL when it was dissected. The other neonate was 102 mm TL when it hatched on its own. VBG estimate of length at 0 age is 100 mm (Fig. 13). The parameter t_0 is –2.81, which is higher than the observed gestation period of 6 – 10 months. L (694 mm) is similar to the largest specimen recorded from this study (male: 645 mm TL). The oldest individual (male) aged had 25 growth band pairs and measured 550 mm TL, however the largest animal (male) aged was 591 mm and had 18 growth band pairs. Total length at 50% maturity is 503 mm total length (78% asymptotic length) for males, 491 mm total length for females and 496 mm total length for both sexes combined (Table 8). The asymptotic length for both females and combined sexes is 77%. This species reaches 50% maturity at 15 years.

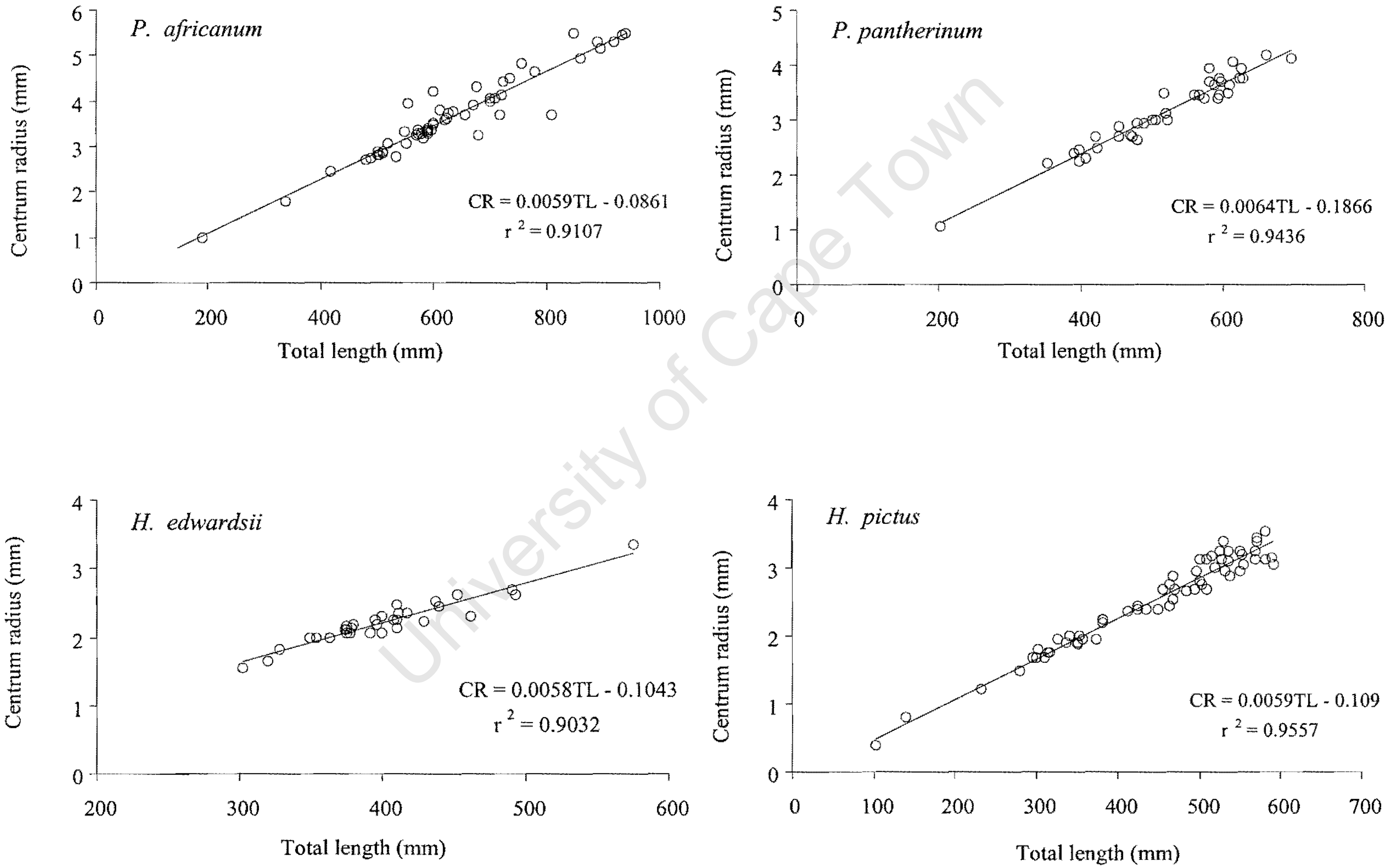


Fig. 4.13. Relationship between centrum radius (CR) and total length (TL) for both sexes of *Poroderma africanum*, *P. pantherinum*, *Haploblepharus edwardsii* and *H. pictus*.

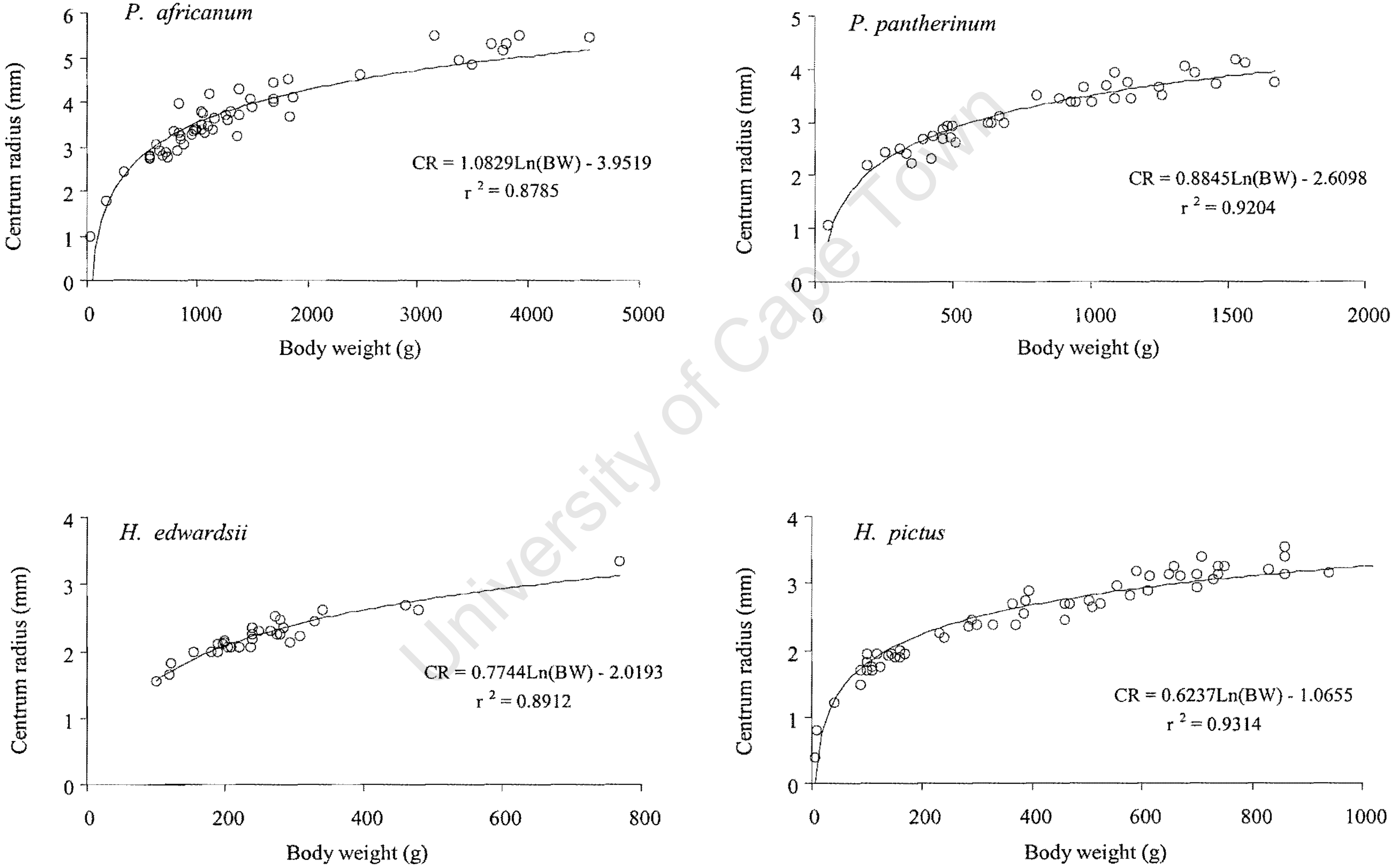


Fig. 4.14. Relationship between centrum radius (CR) and body weight (BW) for both sexes of *Poroderma africanum*, *P. pantherinum*, *Haploblepharus edwardsii* and *H. pictus*.r

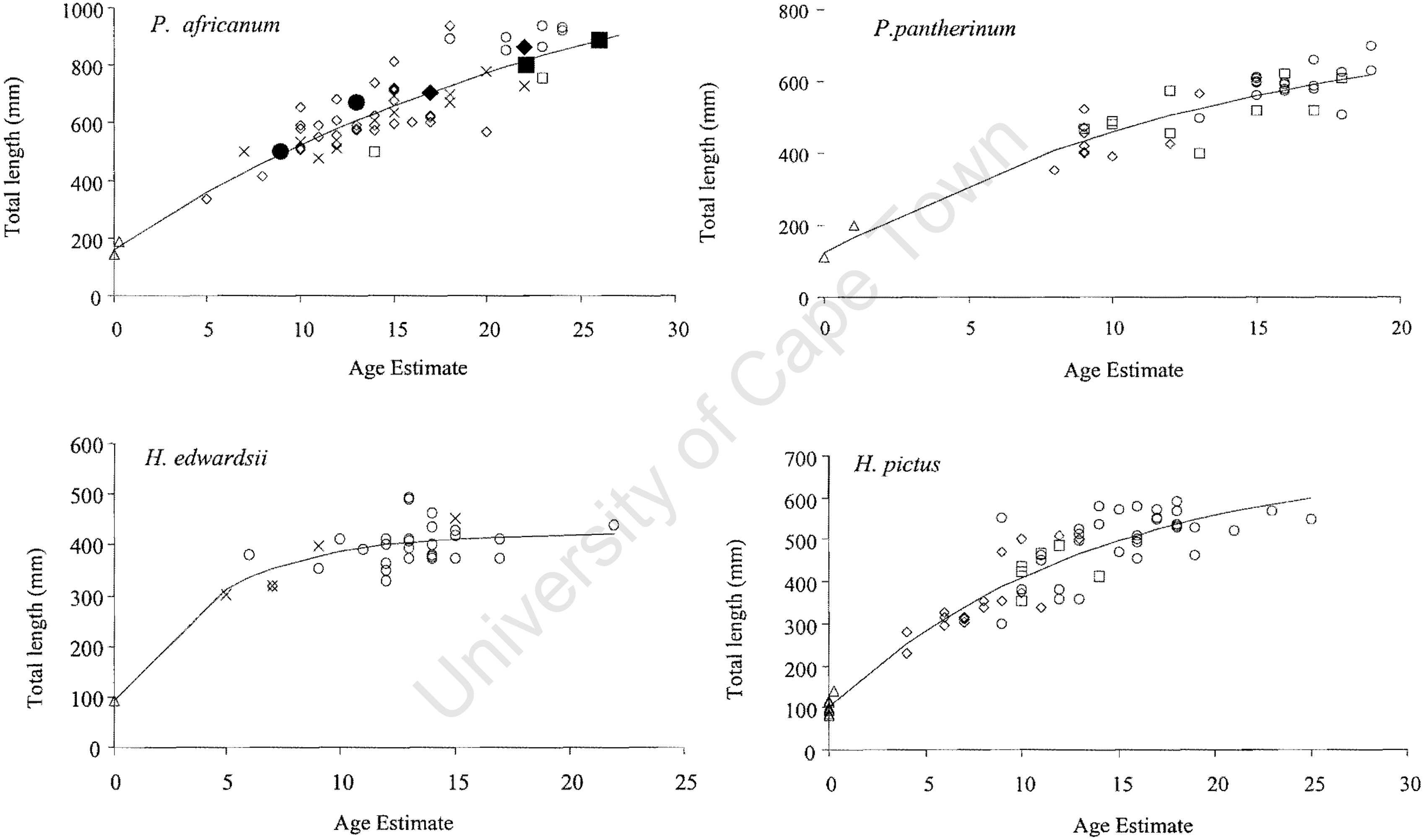


Fig. 4.15. von Bertelanffy growth curves fitted to observed data for both sexes of *Poroderma africanum (n*=55), *P. pantherinum (n*=39). *Haploblepharus edwardsii* (*n*=31) and *H. pictus (n*=60). Symbols represent various stages of maturity: △ neonate, ◇ immature, □ adolescent, ○ mature and × maturity not recorded. For *P. africanum*, additional symbols represent estimated ages for three tagged and recaptured individuals at liberty for ■ , ● four years and ◆ five years. For *P. pantherinum*, the △neonate symmbols represent the same individual from birth to one year old, and for P. africanum the same symbol represents one individual from birth to four months old.

DISCUSSION

Growth and sexual maturity

Poroderma africanum: Both males and females reach approximately the same TL, however the slope of the curve for females was significantly steeper than for males, indicating that females are bulkier for their size (Fig. 4.2). Both males and females reached 50% maturity at a similar size and at 91% of their asymptotic length. There were no female and only two male adolescent individuals noted. There was very little TL growth change between immature and mature individuals, with some obviously immature individuals only slightly smaller in TL than fully mature individuals. This was especially true for females. Although *P. africanum* is known to only reach 1000 mm (Compagno *et al.* 1989), a female shark measuring 759 mm was found to be immature. Similarly, von Bonde (1943) dissected an immature female at 700 mm, indicating late maturity for this species. Based on the tag/recapture information of three specimens, this species also seems highly resident, as recaptured animals were found after up to five years in the exact area where they were tagged. This is supported by the Sedgwick's/ORI/WWF Tagging Programme which resulted in a 5% recapture of tagged specimens traveling a mean distance of 10 km (Wright and Compagno 2000).

Bass *et al.* (1975) found that *P. africanum* reaches 50% maturity at 580-760 mm for males and 650-720 mm for females, which is lower than what was found for males (857 mm) and females (849 mm) in this study. There is much variation in gonad weight between mature female individuals, which can vary by 80 g (Fig. 4.7). This is likely due to the variation in egg development, coinciding with ovulation. Shell gland diameter and LED were measured for only 11 females. Nine of these individuals were immature and the LED were < 1 mm. Two mature females had LED's of 13 mm and 5 mm, respectively and no egg cases were found in any mature females. Eggs were found to vary in size in a given individual, indicating that various groups of eggs develop independently. This suggests that reproduction is continuous throughout the year.

However, data on more individuals is required for further conclusions to be made regarding embryonic development.

Poroderma pantherinum: Male *P. pantherinum* were significantly larger than females, which is common to other scyliorhinids, such as the Izak catshark, *Holohalaelurus regani* (Richardson *et al.* 2000). Males also mature more quickly than females, at 85% of their asymptotic length (590 mm TL), compared to 94% for females (591 mm TL). For males, there was an increase in clasper length, basal clasper width and gonad weight between 550 and 600 mm TL, indicating the onset of maturity. For females, shell gland width and gonad weight increased at 550 mm TL. Once shell gland width reached 2 mm, the LED increased rapidly, ranging from 2 – 12 mm (Fig. 4.10). These specimens were immature or adolescent at this stage, and once the individuals became mature, there was little variation between the LED over increasing shell gland width. Only one dissected female had fully formed egg cases in the uteri, and this individual had a LED of 22 mm, indicating that several groups of eggs develop at one time.

Haploblepharus edwardsii: Males grew to a significantly larger size than females, however there were few data points for female *H. edwardsii*, and a larger set of data would give a more accurate insight as to whether there truly are differences in size at maturity between the sexes. It is interesting to note that over a two-year period, only 14 females were captured. Although this species is considered common in inshore habitats (Branch *et al.* 1994), these individuals were more often encountered in waters > 5 m. The majority of individuals found in the shallower waters (< 5 m) were males, indicating possible habitat preferences between the sexes. The majority of data points were of mature individuals, and therefore a trend increase between immature and mature specimens could not be ascertained. However, males reached 50% maturity at approximately 350 mm, and there was little change in basal clasper width between the largest and smallest mature individuals (Fig. 4.6). Measurements for gonad weight, shell gland diameter and LED were taken for only four mature, female individuals, and therefore were not graphically presented. Gonad weights ranged from 7.71 – 15.91 g. Three of the four females had egg cases that were ready to be released, and the average

LED was large at 15 mm (range 14 – 16 mm). This indicates that several groups of eggs develop at a time and that female reproduction is throughout the year (although not all months were sampled). This continuous reproduction is also apparent in another catshark endemic to southern Africa, *H. regani* (Richardson *et al.* 2000).

Haploblepharus pictus: There was no significant difference between the slopes of the length-weight curves for males and females. Males and females reached 50% maturity at 78% and 77% of their asymptotic length, respectively. This is in contrast to some larger elasmobranch species, where females mature at a considerably larger size than males, such as the sevengill shark, *Notorynchus cepedianus* (Ebert 1986). There was a steady increase in basal clasper length, inner clasper length and gonad weight between approximately 300 – 650 mm TL (Figs 4.4-4.6), with the smallest mature male measuring 463 mm TL. For females, a rapid increase in shell gland diameter and largest egg diameter occurred at 450 mm TL. Mature females had a shell gland width between 15 and 30 mm (Fig. 4.9), and the largest egg diameter varied between 3 and 25 mm (Fig. 4.8), indicating the various ovulation periods between individuals.

Embryo development

Only one egg case of *P. africanum* was found and kept in captivity until the 190 mm TL/36.7 g embryo hatched. The gestation period was approximately one year (the embryo was cut from the case). Although it seemed many of the *H. pictus* embryos in captivity had difficulty freely hatching from the cases, because the internal yolk sac sustains newly hatched embryos for only a few weeks (Hamlett and Koob 1999), a 12-month gestation period at 14°C is most likely a fair estimate. As 14°C is the mean temperature encountered while diving in areas where these species were collected (pers. obs.), this time period most likely also represents the gestation period in these areas. However, water temperatures vary in the habitats of these shark species, and caution should be taken if estimating gestation periods of specimens from warmer or cooler areas.

This gestation period differs to that recorded by von Bonde (1945), who noted a 5-month gestation period for a *P. africanum* embryo. However, the temperature at which the case was kept was not noted. The case measured 103 x 50 mm and was 145 mm TL when it hatched on its own. The 5-month gestation period observed by von Bonde is similar to that of a 5-6 month gestation period of *Scyliorhinus canicula* egg cases kept at 16°C (Ballard *et al.* 1993). Egg cases of the epaulette shark, *Hemiscyllium ocellatum*, required only a few days from laying for embryos to become apparent in the case and approximately three months until hatching at 25°C (West and Carter 1990). This compares to 2 – 4 weeks needed to see a developing embryo in the cases of the four catsharks of this study. Between 11 and 13°C, chain dogfish, *Scyliorhinus retifer*, embryos hatch after approximately 9 months and reach between 106 – 110 mm (Castro *et al.* 1988). After one year, the specimens from the Castro *et al.* study reached 170 mm, growing an average of 5 mm per month, under an unspecified feeding regime and also maintained at 13°C. *P. africanum* in this study grew from 144 – 190 mm in four months, averaging 9 mm per month.

The *P. pantherinum* egg case that produced a term embryo was found in the wild with the embryo already approximately 25 mm in length. The gestation period was 8 months, however an additional month should be added for a total gestation period. After one year, the embryo grew from 110 – 202 mm and 7.86 – 36.74 g, averaging a growth of 8 mm and 2.4 g per month. All embryos in this study were fed pilchard and octopus meat, *ad libitum*, two to three times per week.

For *H. edwardsii*, the only available length at birth is of a male specimen 93 mm/3.92 g after a 3-month gestation period at an unknown temperature (Bertolini unpub. data). In this study, five egg cases kept at 14°C, had still not hatched after 6 months from when they were dissected from pregnant females. Neonates that hatched on their own measured > 100 mm and required a 6-10 month gestation period, and four embryos that were cut after a 6-month gestation were < 100 mm.

Both *Poroderma* and *Haploblepharus* species lay two egg cases at approximately the same time and seemingly throughout the year. The time between the laying of two groups of eggs is unknown. In captivity, the highest embryo mortality rate seemed to occur in specimens that were close to term. A possible reason for this may be that the embryos were unable to release themselves from the cases and therefore starved to death.

Ageing

Resin embedding proved to be the most successful technique to reveal vertebral rings of *Poroderma africanum*, *P. pantherinum*, *Haploblepharus edwardsii* and *H. pictus*. The small size of the vertebrae (the average radii of vertebrae were < 4 mm for all four species), made the samples very difficult to process and analyze. These difficulties are apparent when comparing the average percentage errors (APE's) of the four species (Fig. 4.12). The largest species is *P. africanum*, which reaches up to 1000 mm TL (Compagno *et al.* 1989) and had the largest average centrum radius of 3.72 mm, had the lowest APE of 7 (n=55). The APE's were 13 for both *P. pantherinum* (n=39) and *H. edwardsii* (n=30), and 19 for *H. pictus* (n=60). The APE of *P. africanum* (APE=7) is close to that of the similar size smalltail shark, *Carcharhinus porosus* (APE=6, Lessa and Santana 1998). The APE's for *P. pantherinum*, *H. edwardsii* (APE=13 for both) and *H. pictus* (APE=19) are much higher than recorded values for other sharks such as the leopard shark, *Triakis semifasciata* (APE=4.9; Kusher *et al.* 1992) whiskery shark, *Furgaleus macki* (APE=8.5-10.2, Simpfendorfer *et al.* 2000) and the tiger shark, *Galeocerdo cuvier* (APE=9.2-9.7; Wintner and Dudley 2000). This is most likely due to the much smaller size of the vertebrae compared to the larger sharks that comprise the majority of ageing studies.

Indicators of annual growth band deposition include comparing centrum radii with length and body weight and analyzing band deposition with seasons. There is a linear relationship between centrum radius and length in this study, which was also noted in other shark species, such as the dusky shark, *Carcharhinus obscurus* (Natanson and

Kohler 1996) and the tiger shark, *Galeocerdo cuvier* (Wintner and Dudley 2000). Comparing centrum radius and body weight for the four catshark species revealed a multiplicative relationship. Although these relationships, combined with lengths between band increments and radii of vertebrae, are generally used for back-calculated values for age and growth, back calculations were not done due to the inherent difficulties of measuring marginal increments. Therefore, the relationships of centrum radius with length and body weight were used as indicators that vertebral growth corresponds to the age of the shark (Cailliet *et al.* 1983b). The opaque band (highly calcified) is generally associated with summer growth with the transluscent band (less calcified) representing winter growth (Kusher *et al.* 1992). Too few specimens were collected over an adequate seasonal period, so no clear trend was apparent when comparing the peripheral band with month of capture.

The age and length data for the *Poroderma* and *Haploblepharus* species adequately fit the von Bertalanffy growth equation. Data for both sexes were combined, as there were too few points to analyze sexes separately. The maximum estimated sizes are similar to the observed lengths for both *Poroderma* species (L =1363 and 861; largest observed individual were 935 mm and 696 mm for *P. africanum* and *P. pantherinum*, respectively) and *H. pictus* (L =694, largest observed was 645 mm). However, for *H. edwardsii*, the estimate of L (424 mm) is much lower than the maximum observed length of 498 mm. This species is known to reach up to 600 mm (Compagno *et al.* 1989). The lack of *H. edwardsii* > 300 mm collected and aged accounts for the L_∞ lower than the observed maximum, because the smaller individuals influence the initial rate (k) of the curve, which would increase asymptotic total length as the curve extends through the data points. This is apparent with the other three catshark species, as there are lengths at age 0 and the L is larger than the observed maximum length. Kusher *et al.* (1992) also noted a lower L than the largest observed leopard shark, *Triakis semifasciata*.

Estimated total lengths at age 0 are very similar to those observed for the four catshark species, giving further evidence to the adequacy of the VBG parameters. For *P. africanum*, 160 mm was the estimated length at age 0, compared to the observed length of 144 mm. Von Bonde (1945) followed the development of an embryo of this species and recorded the length at birth for one specimen at 164 mm. The female *P. pantherinum* neonate in this study was born measuring 110 mm TL, compared to the estimated 123 mm. After one year, the individual was 202 mm TL and slightly longer than the estimated length (168 mm) for the same age (Fig. 4.15). This is most likely due to the fact that the growth of captive sharks is generally faster than in the wild, rather than the inaccuracy of the growth curve. The estimated length at age 0 is 94 mm (93 mm observed) and 100 mm (average of 99 mm for 8 individuals) for *H. edwardsii* and *H. pictus*, respectively.

The growth rate parameters (k) for *P. africanum* (0.036 year^{-1}), *P. pantherinum* (0.057 year^{-1}) and *H. pictus* (0.073 year^{-1}) indicate that these sharks grow more slowly than *H. edwardsii* (k=0.171 year^{-1}). Growth rates slow considerably after maturity for *H. edwardsii* (Fig. 4.15). More specimens that are < 300 mm would confirm this assumption, however due to the small size off this species and its susceptibility to predation to larger counterparts, it is not surprising that growth rates are much faster than the other catshark species. Lengths of *H. edwardsii* individuals ranged from approximately 300 – 500 mm, yet the age varied by more than 15 years. This extreme variation is also apparent in the dusky shark, *Carcharhinus obscurus* (Natanson and Kohler 1996), however the k parameter for this species (k=0.040 – 0.047 year^{-1}) is more comparable to both *Poroderma* species and *H. pictus*.

The estimations of age at 50% maturity for both *Poroderma* and *Haploblepharus* species (Table 4.8) indicate a late maturity, like most elasmobranch species. Both sexes of *P. africanum* reached 50% maturity at 91% of their asymptotic length, at 849 mm TL for females and 857 mm TL for males, which corresponds to an age of 24 years for combined sexes. Although both male and female *P. pantherinum* reached 50% sexual maturity at approximately the same TL (590 mm males; 595 mm females), females tend to grow larger than males, therefore, the asymptotic length for females (94%) was higher than that of males (85%). Combined data for *P. pantherinum* indicate an age of 17 years at 50% maturity. The maturity of only eleven female *H. edwardsii* was recorded (ten mature, one immmature), therefore the data for males and females were combined. *H. edwardsii* reaches 50% maturity at 7 years, at 351 mm TL (the same for males alone), which is 71% of their asymptotic length. *H. pictus* reach 50% maturity after 15 years, and both males and females reach maturity at approximately the same TL (males: 503 mm; females: 491 mm) and asymptotic length (males: 78%; females: 77%). Holden (1974) suggests that female elasmobranchs generally reach sexual maturity between 60 and 90 % of their asymptotic length, which accurately describes these four female species. Kusher *et al.* (1992) noted that female leopard sharks, *Triakis semifasciata*, matured at 72 – 93 % of their asymptotic length, which was much higher than that of males of the same species (63-66 %). Of the four catshark species in this study, only *P. pantherinum* demonstrated females attaining 50% maturity at a higher asymptotic length. Both sexes of *P. africanum* and *H. pictus* showed to have similar maturity rates.

Based on close agreement of growth curves estimated from vertebral counts, tagged and recaptured individuals (for *Poroderma africanum* only), and lengths at age 0 from sharks born in captivity, growth ring deposition is considered to be annual for *P. africanum*, *P. pantherinum*, *Haploblepharus edwardsii* and *H. pictus*. Maximum ages from vertebral counts are 24 for *P. africanum*, 19 for *P. pantherinum*, 22 for *H. edwardsii* and 25 for *H. pictus*. However, age estimates from VBG parameters that are based on maximum-recorded sizes are: 34 years for both *Poroderma* species and *H. pictus*. An age estimate based on the maximum-recorded size of 600 mm for *H. edwardsii* is well over a hundred. This is undoubtedly inaccurate and due to the slow growth rate after maturity, which is apparent in the wide range of ages spanning over 15 years for similar size sharks. This study presents much needed information regarding the life histories of these four catshark species. Although these species are considered common (Compagno *et al.*1989), because they are long living and late maturing, like most elasmobranchs these predators would be prone to exploitation if fished.

SYNTHESIS

The objectives of this thesis were to examine the life histories of four catshark species, *Poroderma africanum, P. pantherinum, Haploblepharus edwardsii*, and *H. pictus*, from the southwestern Cape. Chapter 2 dealt with the diet composition of the four shark species, Chapter 3 discussed the gastric evacuation rates of major prey items (found in Chapter 2) for both *Poroderma* species and *H. pictus*, and Chapter 4 examined the age, growth, maturity and reproduction of all four species.

DIET COMPOSITION

This thesis presents the first quantitative, dietary analysis of *Haploblepharus edwardsii, H. pictus, Poroderma africanum* and *P. pantherinum*. The most important prey groups were crustaceans, annelids and teleosts for *H. edwardsii*; crustaceans, teleosts and molluscs for *H. pictus*; teleosts, molluscs and crustaceans for *P. africanum*; and molluscs and teleosts for *P. pantherinum*.

Males and females of each species ate similar prey, although the importance of some prey varied. The most important prey taxa were annelids for female and crustaceans for male *H. edwardsii*; crustaceans for both male and female *H. pictus*; teleosts for both sexes of *P. africanum*, and molluscs for both male and female *P. pantherinum*.

There was a general decrease in the importance of teleosts in the diet with increasing size for all four catshark species. An increase of importance of crustaceans with increasing size was apparent for *H. pictus* and *P. africanum*. Molluscs had relatively the same importance to all sizes of *H. pictus*, although their importance increased with increasing size for both *Poroderma* species. Although specific taxonomic groups dominated the diets of *H. edwardsii*, *H. pictus* and *P. africanum*, these three species seem to be generalist feeders, preying upon a variety of food sources. *P. pantherinum* has a more specific diet, feeding almost exclusively on teleosts and molluscs.

All four catshark species, including both sexes and multiple class sizes (pers. obs.), can be found in the same habitat in the southwestern Cape (Prochazka 1994; Lechanteur in press). Based on the results of Chapter 1, inter- and intraspecific competition between the four catshark species for food seems significant.

GASTRIC EVACUATION RATES

Three catshark species, *Poroderma africanum*, *P. pantherinum* and *Haploblepharus pictus*, maintained in laboratory conditions, were fed meals equaling 1% of their body weight (BW). *H. edwardsii* were not used in this experiment, as too few specimens could be collected in the allotted time. From the findings in Chapter 2, the most important (constituting 5% of total volume or more of the diet) prey items were used for experimentation (i.e. teleosts, molluscs and crustaceans). The foods used to represent these prey groups were clipfish, *Clinus spp*., octopus, *Octopus vulgaris*, and sandprawn, *Callianassa kraussi*. Meals included whole prey, however either single or multiple fish or prawns were used to make weight. The use of either single or multiple food items was assumed to have a negligible affect on gastric emptying time. Various size sharks were used in experimentation, which may have affected times for prey evacuation. However, sharks that were < 200 g were excluded from the experiment and feeding each individual 1% of their body weight was assumed to minimize variation in evacuation times.

The generalized additive linear model best described the decrease of stomach contents over time and highlighted variations in gastric evacuation rates that would not have been apparent with conventional models (i.e. data transformation or linear, exponential and Gompertz equations). At 14°C, the evacuation rates varied between prey types for the three shark species, with octopus (19.5-24.5 hours) taking the least time for 95% of the meal to be evacuated, followed by fish (36-48 hours) and prawn (70 hours – *H. pictus* only). The variation between sharks fed the same prey and dissected after the same time period was most likely due to metabolic differences among individuals.

For all data, the model revealed an initial period of maximal evacuation, followed by a decreased rate until complete evacuation. Curves from the data indicated a 'plateau' phase, where the emptying rate decreased after the initial maximum period of evacuation and then continued again in an increased rate until complete evacuation. There were no significant differences ($p<0.001$) of gastric evacuation rates between species fed the same prey item. Statistical differences between various prey fed to the same shark species could not be analyzed due to the widely different evacuation times. These estimates of gastric emptying for these three shark species are slower relative to teleost fishes, but similar to data recorded for other elasmobranch species.

Based on the gastric evacuation data, molluscs are underestimated as important food sources in the diets of these sharks, while teleosts and crustaceans are overestimated. Therefore, both diet and gastric evacuation data are required to give an accurate representation of the natural diet of these sharks.

GROWTH, SEXUAL MATURITY, REPRODUCTION AND AGING

The slopes of the length-weight curves were significantly different ($p<0.001$) between sexes for both *Poroderma* species and *H. edwardsii*. There was no significant difference ($p>0.05$) between the sexes of *H. pictus*. Resin embedding techniques revealed transluscent and opaque growth band formation for the four catshark species. Based on close agreement of growth curves estimated from vertebral counts, tagged and recaptured individuals (for *Poroderma africanum* only), and lengths at age 0 from sharks born in captivity, growth ring deposition is considered to be annual for *P. africanum*, *P. pantherinum*, *Haploblepharus edwardsii* and *H. pictus*. These four species are long living and late maturing. Gonad characteristics, egg size and embryo development suggest a year round breeding season for all four species.

Both male and female *P. africanum* reach approximately the same TL, however the slope of the curve for females was significantly steeper for females than males. This indicates that females are bulkier for their size than males, which is common among elasmobranch species. Both males and females reached 50% maturity at a similar size and at 91% of their asymptotic length and at approximately 24 years. The maximum age from vertebral counts is 24 years, however, based on records of maximum size recorded (1000 mm) the VBG estimates that this species may reach 34 years. Based on one egg case reared in captivity, the gestation period at 14°C is approximately 12 months. The embryo was cut from its case (due to the high mortality of many sharks that were unable to hatch on their own), and it is unknown whether more or less time was required for an accurate gestation period.

Male *P. pantherinum* were significantly larger than females, which is common for scyliorhinids, including the the Izak catshark, *Holohalaelurus regani* (Richardson *et al.* 2000). Males also mature more quickly than females, at 85% of their asymptotic length (590 mm TL), compared to 94% for females (591 mm TL). The oldest specimen aged was 19 years, however, an age of 34 years was estimated using the VBG curve, based on the maximum-recorded size (740 mm). One embryo was brought to term under laboratory conditions, and the gestation period for this individual kept at 14°C, was 8 months. However, when this case was found in the wild, the embryo was visible. Therefore, the total gestation time for this individual could be approximately 9 months.

Too few data points were available for female *H. edwardsii*, therefore, data were combined for both sexes. This species reaches 50% maturity at 351 mm TL (71% asymptotic length). The maximum age from vertebral counts was 22 years. Using the VBG equation, an age based on the maximum-recorded size of 600 mm for could not be accurately estimated for this species (the estimation was well over a hundred). This is due to the slow growth rate after maturity, which is apparent in the wide range of ages spanning over 15 years for similar size sharks. No embryos came to term during this study, however embryos that were dissected from mature females and kept in captivity, were still not ready to hatch after 6-7 months.

Male *H. pictus* reach 50% maturity at 503 mm TL (78% asymptotic length) in comparison to 491 mm (77% asymptotic length) for females. The age calculated for length at 50% maturity was 15 years for combined sexes. The maximum age from vertebral counts is 25 years. However, an age estimate from VBG parameters that is based on the maximum-recorded size (645 mm, from this study) is 34 years. Eight egg cases produced term embryos, averaging 100 mm TL, 5.4 g and a 6-10 month gestation period.

CONCLUSIONS

This research gives much needed life history information for four catshark species from the southwestern Cape, South Africa. *Poroderma africanum*, *P. pantherinum*, *Haploblepharus edwardsii* and *H. pictus* are active predators and are considered generalist feeders in their environment. They are long living and late maturing, like most elasmobranch species. Although these sharks are regarded as common (van der Elst and Adkin 1991), they are considered pests to fishermen and are often discarded as waste, and large numbers are captured in trawlers (van der Elst 1988). The fact that these sharks are endemic to southern Africa supports the need to ensure these species are not exploited in the future.

LITERATURE CITED

Ballard, W. W., J. Mellinger, and H. LeChenault. 1993. A series of normal stages for development of *Scyliorhinus canicula*, the lesser spotted dogfish (Chondrichthyes: Scyliorhinidae). *The Journal of Experimnetal Zoology* 267: 318-336.

Bass, A. J., J. D. D'Aubrey, and N. Kistnasamy. 1975. Sharks of the east coast of southern Africa, II: The families Scyliorhinidae and Pseudotriakidae. Investigative Report Oceanographic Research Institute, Durban: 1-64.

Beamish, R. J., and D. A. Fournier. 1981. A method for comparing the precision of a set of age determinations. *Canadian Journal of Fisheries and Aquatic Sciences* 38: 982-983.

Bennett, B. A., and C. L. Griffiths. 1986. Aspects of the biology of Galjoen *Coracinus capensis* (Cuvier) off the south-western Cape, South Africa. *South African Journal of Marine Science* 4: 153-162.

Bertolini, A. 1993. Aspects of the biology of four southern African catsharks. Unpublished student report. Zoology Department, University of Cape Town, Cape Town: 96 pp.

Booth, J. B., and C. D. Buxton. 1997. The biology of the panga, *Pterogymnus laniarius* (Teleostei: Sparidae) on the Agulhas Bank, South Africa. *Environmental Biology of Fishes* 49: 207-226.

Branch, G. M., C. L. Griffiths, M. L. Branch, and L. E. Beckley. 1994. *Two Oceans: a Guide to the Marine Life of Southern Africa*. David Philip Publishers, Cape Town: 360 pp.

Branstetter, S., and J. D. McEachran. 1986. Age and growth of four Carcharhinid sharks common to the Gulf of Mexico: A summary paper. In *Indo-Pacific Fish Biology: Proceedings of the Second International Conference on Indo-Pacific Fishes, Ichthyological Society of Japan, Tokyo.* T. Uyeno, R. Arai, T. Taniuchi and K. Matsuura (Eds.): 361-371.

Branstetter, S. 1987. Age and growth validation of newborn sharks held in laboratory aquaria, with comments on the life history of the Atlantic sharpnose shark, *Rhizoprionodon terraenovae*. *Copeia* 2: 291-300.

Branstetter, S., J. A. Musick, and J. A. Colvocoresses. 1987. A comparison of the age and growth of the Tiger Shark, *Galeocerdo cuvieri*, from off Virginia and from the northwestern Gulf of Mexico. *Fishery Bulletin* 85: 269-279.

Brown, C.A., and S.H. Gruber. 1988. Age assessment of the lemon shark, *Negaprion brevirostris*, using tetracycline validated vertebral centra. *Copeia* 3: 747-753.

Butterworth, D.S., A.E. Punt, D.L. Borchers, J.G. Pugh and G.S. Hughes. 1989. A manual of mathematical techniques for linefish assessment (incorporating a report of the SANCOR marine linefish programme's workshop on population dynamics, 4-6 February 1987, Cape Town). *South African National Scientific Programmes Report* 160: 89 pp.

Cailliet, G. M., L. K. Martin, D. Kusher, P. Wolf, and B. Welden. 1983b. Techniques for enhancing vertebral bands in age estimation of California elasmobranchs. In *'Proceedings of the International Workshop on Age Determination of Oceanic Pelagic Fishes: Tunas, Billfishes, and Sharks,* E.D. Prince and L.M. Pulos (Eds.): 157-165.

Cailliet, G.M., and R.L. Radtke. 1987. A progress report on the electron microprobe analysis technique for age determination and verification in elasmobranchs. In *Age and Growth of Fish*, R.C. Summerfelt and G.E. Hall (Eds.), Iowa State University Press, Ames, Iowa: 359-369.

Cailliet, G. M., and S. Tanaka. 1990. Recommendations for research needed to better understand the age and growth of elasmobranchs. *NOAA (Natl. Oceanic Atmos. Admin.) Tech. Rep. NMFS (Natl. Mar. Fish. Serv.)* 90: 505-507.

Cailliet, G. M. 1990. Elasmobranch age determination and verification: an updated review. *NOAA (Natl. Oceanic Atmos. Admin.) Tech. Rep. NMFS (Natl. Mar. Fish. Serv.)* 90: 157-164.

Capape, C. 1975. [Contributions to the Scyliorhinidae biology of Tunisian coasts. 4. *Scyliorhinus stellaris* (Linne 1758). Diet]. [Contribution a la biologie des Scyliorhinidae des cotes tunisiennes. 4. *Scyliorhinus stellaris* (Linne 1758). Regime alimentaire]. Archives de l'Institute Pasteur de Tunis (Tunisia), v. 52(4): 383-394.

Carlson, J. K., E. Cortés, and A. G. Johnson. 1999. Age and growth of the Blacknose Shark, *Carcharhinus acronotus*, in the Eastern Gulf of Mexico. *Copeia* 3: 684-691.

Casey, J. G., and L.J. Natanson 1992. Revised estimates of age and growth of the sandbar shark (*Carcharhinus plumbeus*) from the western North Atlantic. *Canadian Journal of Fisheries and Aquatic Sciences* 49: 1474-1477.

Castro, J. I., P. M. Bubucis, and N. A. Overstrom. 1988. The reproductive biology of the Chain Dogfish, *Scyliorhinus retifer*. *Copeia* 3: 740-746.

Cliff, G., S. F. J. Dudley, and B. Davis. 1989. Sharks caught in the protective gill nets off Natal, South Africa. 2. The great white shark *Carcharodon carcharias* (Linnaeus). *South African Journal of Marine Science* 8: 131-144.

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

Compagno, L. J. V. 1984. Vol. 4. Sharks of the world. An annotated and illustrated catalogue of shark species known to date 2. Carcharhiniformes. *FAO Fisheries Synopsis, No. 125:* 251-655.

Compagno, L. J. V. 1987. Kinds of Sharks. In *Sharks,* J. D. Stevens (Ed.). Facts on File Publications, New York: 18-35.

Compagno, L. J. V., D. A. Ebert, and M. J. Smale. 1989. *Guide to the Sharks and Rays of southern Africa*. Struik Publishers, Cape Town: 160 pp.

Compagno, L. J. V. 1999. Systematics and Body Form, In *Sharks, Skates and Rays The Biology of Elasmobranch Fishes*, W.C. Hamlett (Ed.). The Johns Hopkins University Press, Baltimore: 1-42.

Cortés, E., and S. H. Gruber. 1992. Gastric evacuation in the young lemon shark, *Negaprion brevirostris*, under field conditions. *Environmental Biology of Fishes* 35: 205-212.

Cortés, E. 1997. A critical review of methods of studying fish feeding based on analysis of stomach content: application to elasmobranch fishes. *Canadian Journal of Fisheries and Aquatic Sciences* 54: 726-738.

Cowley, P. D. 1997. Age and growth of the blue stingray *Dasyatis chrysonota chrysonota* from the south-eastern cape coast of South Africa. *South African Journal of Marine Science* 18: 31-38.

Ebert, D. A. 1986. Aspects on the biology of Hexanchid sharks along the California coast. In *Indo-Pacific Fish Biology: Proceedings of the Second International Conference on Indo-Pacific Fishes*, T. Uyeno, R. Arai, T. Taniuchi, and K. Matsuura (Eds.). Ichthyological Society of Japan, Tokyo: 437-449.

Ebert, D.A. 1991. Observations on the predatory behaviour of the sevengill shark *Nototrynchus cepedianus*. *South African Journal of Marine Science* 11: 455-465.

Ebert, D.A. 1996. Biology of the sevengill shark *Notorynchus cepedianus* (Peron, 1807) in the temperate coastal waters of southern Africa. *South African Journal of Marine Science* 17: 93-103.

Ebert, D. A., P. D. Cowley, and L. J. V. Compagno. 1996. A preliminary investigation of the feeding ecology of catsharks (Scyliorhinidae) off the west coast of Southern Africa. *South African Journal of Marine Science* 17: 233-240.

Elliott, J. M., and L. Persson. 1978. The estimation of daily rates of food consumption for fish. *Journal of Animal Ecology* 47: 977-991.

Fänge, R., and D. Grove. 1979. Digestion. In *Fish Physiology*, W. S. Hoar, D. J. Randall, and J. R. Brett (Eds.) Academic Press, New York: 161-260.

Fariña, J. M., and F. P. Ojéda. 1993. Abundance, activity, and trophic patterns of the redspotted catshark, *Schroederichthys chilensis*, on the Pacific temperate coast of Chile. *Copeia* 2: 545-549.

Ferreira, B.P., and C.M. Vooren. 1991. Age, growth, and structure of vertebra in the school shark Galeorhinus galeus (Linnaeus, 1758) from southern Brazil. *Fishery Bulletin, U.S.* 89: 19-31.

Garman, S. 1913. The Plagiostomia. Memoirs of the Museum of Comparative Zoology, Harvard 36, i-xiii: 515 pp.

Goosen, A. J. J., and M. J. Smale. 1997. A preliminary study of age and growth of the smoothhound shark *Mustelus mustelus* (Triakidae). *South African Journal of Marine Science* 18: 85-91.

Hamlett, W.C (Ed.). 1999. *Sharks, Skates and Rays. The Biology of Elasmobranch Fishes*. The Johns Hopkins University Press, Baltimore: 515 pp.

Hamlett, W.C., and T.J. Koob. 1999. Female Reproductive System. In *Sharks, Skates and Rays the Biology of Elasmobranch Fishes*, W. C. Hamlett (Ed.). The Johns Hopkins University Press, Baltimore: 398-443.

Hastie, T. J., and R. J. Tibshirani. 1990. *Generalised additive models*. Chapman and Hall, London: 335 pp.

He, E., and W.A. Wurtsbaugh. 1993. An empirical model of gastric evacuation rates for fish and an analysis of digestion in piscivorous brown trout. *Transactions of the American Fisheries Society* 122: 717-730.

Holden, M. J., and P. S. Meadows. 1962. The structure of the spine of the spur dogfish (*Squalus acanthias* L.) and its use for age determination. *Journal of the Marine Biological Association of the United Kingdom* 42: 179-197.

Hyslop, E. J. 1980. Stomach content analysis-a review of methods and their application. *Journal of Fish Biology* 17: 411-429.

Jobling, M. 1981. Mathematical models of gastric emptying and the estimation of daily rates of food consumption for fish. *Journal of Fish Biology* 19(3): 245-287.

Jobling, M. 1986. Mythical models of gastric emptying and implications for food consumption studies. *Environmental Biology of Fishes* 16(1-3): 35-50.

Jones, B. C., and G. H. Geen. 1977. Age determination of an elasmobranch (*Squalus acanthias*) by X-ray spectrometry. *Journal of the Fisheries Research Board of Canada* 34: 44-48.

Kao, J. S. 2000. Diet, daily ration and gastric evacuation of the leopard shark (*Triakis semifasciata*). Masters Thesis. Department of Marine Science, California State University, Hayward: 90 pp.

Kusher, D. I., S. E. Smith, and G. M. Cailliet. 1992. Validated age and growth of the leopard shark, *Triakis semifasciata*, with comments on reproduction. *Environmental Biology of Fishes* 35: 187-203.

Lechanteur, Y.A.R.G., and C.L. Griffiths. Composition and seasonal variability of suprabenthic fish assemblages in False Bay, South Africa. *African Zoology* (in press).

Lessa, R., and F. M. Santana. 1998. Age determination and growth of the smalltail shark, *Carcharhinus porosus*, from northern Brazil. *Marine and Freshwater Research* 49: 705-711.

Macpherson, E., J. Lleonart, and P. Sanchez. 1989. Gastric emptying in *Scyliorhinus canicula* (L.): a comparison of surface-dependent and non-surface dependent models. *Journal of Fish Biology* 35: 37-48.

Marks, M. A. *in prep*. Comparison of ontogenic heterodonty and gyandric heterodonty of tooth morphology in four species of catshark (*Poroderma africanum, P. pantherinum, Haploblepharus pictus, H. edwardsii*).

Matallanas, J. 1982. Feeding habits of *Scymnorhinus licha* in Catalan waters. *Journal of Fish Biology* 20: 155-163.

Matallanas, J., M. Carrasson and M. Casadevall. 1993. Observations on the feeding habits of the narrow mouthed cat shark *Schroederichthys bivius* (Chondrichthyes, Schyliorhinidae) in the Beagle Channel. *Cybium* 17: 55-61.

Medved, R. J. 1985. Gastric evacuation in the sandbar shark, *Carcharhinus plumbeus. Journal of Fish Biology* 26: 239-253.

Medved, R.J., C.E. Stillwell and J.G. Casey. 1988. The rate of food consumption of young sandbar sharks (*Charcharhinus plumbeus*) in Chincoteague Bay, Virginia. *Copeia* 4: 956-963.

Michael, S. W. 1993. *Reef Sharks and Rays of the World: A guide to their Identification, Behavior and Ecology.* Sea Challengers, Monterey, California.

Natanson, L. J., and G. M. Cailliet. 1990. Vertebral growth zone deposition in pacific angel sharks. *Copeia* 4: 1133-1145.

Natanson, L. J., and N. E. Kohler. 1996. A preliminary estimate of age and growth of the dusky shark *Carcharhinus obscurus* from the south-west Indian oceans, with comparisons to the western north Atlantic population. *South African Journal of Marine Science* 17: 217-224.

Nelson, G.A., and M.R. Ross. 1995. Gastric evacuation in little skate. *Journal of Fish Biology* 46: 977-986.

Pandian, T.J. 1967. Intake, digestion, absorption and conversion of food in the fishes *Megalops cyprinoids* and *Ophiocephalus striatus. Marine Biology* 1: 16-32.

Parsons, G. R. 1993. Age determination and growth of the bonnethead shark *Sphyrna tiburo*: a comparison of two populations. *Marine Biology* 117: 23-31.

Pinkas, L., M. S. Oliphant, and I. L. K. Iverson. 1971. Food habits of albacore, bluefin tuna and bonito in Californian Waters. *California Fish and Game* 152: 1-105.

Prochazka, K. 1994. Habitat partitioning in shallow-water cryptic ichthyoufaunal communities in the western and southwestern Cape, South Africa. Ph.D. thesis. Zoology Department, University of Cape Town, Cape Town: 117 pp.

Richardson, A. J., G. Maharaj, L. J. V. Compagno, R. W. Leslie, D. A. Ebert, and M. J. Gibbons. 2000. Abundance, distribution, morphometrics, reproduction and diet of the Izak catshark. *Journal of Fish Biology* 56: 552-576.

Ridewood, W.G. 1921. On the calcification of the vertebral centra in sharks and rays. *Philosophical Transactions of the Royal Society of London* 210(B): 311-407.

Schnute, J. 1981. A versatile growth model with statistically stable parameters. *Canadian Journal of Fisheries and Aquatic Sciences* 38: 1128-1140.

Schurdak, M. E., and S. H. Gruber. 1989. Gastric evacuation of the lemon shark *Negaprion brevirostris* under controlled conditions. *Experimental Biology* 48: 77-82.

Simpfendorfer, C. A., J. Chidlow, R. McAuley, and P. Unsworth. 2000. Age and growth of the whiskery shark, *Furgaleus macki*, from southwestern Australia. *Environmental Biology of Fishes* 58: 335-343.

Sims, D.W., S.J. Davies and Q. Bone. 1996. Gastric emptying rate and return of appetite in lesser spotted dogfish, *Scyliorhinus canicula* (Chondrichthyes: Elasmobranchii). *Journal of Marine Biology Association of the United Kingdom* 76: 479-491.

Smale, M. J. 1991. Occurrence and feeding of three shark species, *Charcharhinus brachyurus*, *C. obscurus* and *Sphyrna zygaena*, on the Eastern Cape coast of South Africa. *South African Journal of Marine Science* 11: 31-42.

Smale, M. J., W. H. H. Sauer, and R. T. Hanlon. 1995. Attempted ambush predation on spawning squids *Loligo vulgaris reynaudii* by benthic pyjama sharks, *Poroderma africanum*, off South Africa. *Journal of the Marine Biological Association of the United Kingdom* 75: 739-742.

Smith, M. M., and P. C. Heemstra (Eds). 1986. *Smith's Sea Fishes.* Southern Book Publishers, Johannesburg: 1047 pp.

Swenson, W. A., and L. L. Smith. 1973. Gastric digestion, food consumption, feeding periodicity, and food conversion efficiency in Walleye (*Stizostedion vitreum vitreum*). *Journal of the Fisheries Research Board of Cananda.* 30: 1327-1336.

Van der Elst, R. 1988. *A Guide to the Common Sea Fishes of Southern Africa.* C. Struik, Cape Town: 398 pp.

Van der Elst, R. P., and F. Adkin (Eds.). 1991. *Marine Linefish. Priority Species and Research Objectives in Southern Africa.* Oceanographic Research Institute 1: 1-132.

Von Bonde, C. 1945. The external development of the banded dogfish or pofadderhaai *Haploblepharus edwardsii* (M. & H.). *Biological Bulletin* 88(1): 1-11.

Von Bonde, C. 1945. The development of the striped dogfish (Lui-haai), *Poroderma africanum* (Gmelin). *Transactions of the Royal Society of South Africa* 31(5): 465-474.

Walter, J. P., and D. A. Ebert. 1991. Preliminary estimates of age of the bronze whaler *Carcharhinus brachyurus* (Chondrichthyes: Charcharhinidae) from southern Africa, with a review of some life history parameters. *South African Journal of Marine Science.* 10: 37-44.

Weber, D.D., and G.J. Ridgway. 1962. The deposition of tetracycline drugs in bones and scales of fish and its possible use for marking. *The Progressive Fish Culturist* 24(4): 150-155.

West, J. G., and S. Carter. 1990. Observations on the development and growth of the epaulette shark *Hemiscyllium ocellatum* (Bonnaterre) in captivity. *Journal of Aquariculture and Aquatic Sciences.* 5: 111-117.

Windell, J. T. 1978. Digestion and the daily ration of fishes. In *Ecology of Freshwater Fish Production*, S. D. Gerking (Ed.). Blackwell Scientific Publications, Oxford (UK): 159-183.

Wintner, S. P., and S. F. J. Dudley. 2000. Age and growth estimates for the tiger shark, *Galeocerdo cuvier*, from the east coast of South Africa. *Marine and Freshwater Research* 51: 43-53.

Wintner, S.P. 2000. Preliminary study of vertebral growth rings in the whale shark, *Rhincodon typus*, from the east coast of South Africa. *Environmental Biology of Fishes* 59: 441-451.

Wright, R., and L.J.V. Compagno. 2000. *Poroderma africanum*. In *Southern African Marine Linefish Status Reports,* B.Q.E. Mann (Ed.). Oceanograpic Research Institute, Marine Parade: 220-221.

Yano, K., and J.A. Musick. 1992. Comparison of morphometrics of Atlantic and Pacific specimens of the false catshark, *Pseudotriakis microdon*, with notes on stomach contents. *Copeia* 3: 877-886.

Zar, J.H. 1974. *Biostatistical analysis.* New Jersey; Prentice-Hall: 620 pp.

Zarate, D.D., R.T. Lovell and M. Payne. 1999. Effects of feeding frequency and rate of stomach evacuation on utilization of dietary free and protein-bound lysine for growth by channel catfish *Ictalurus punctatus*. *Aquaculture Nutrition* 5(1): 17-22.