THE BIOLOGY OF TWO IMPORTANT BY-CATCH SKATE SPECIES ON THE AGULHAS BANK, SOUTH AFRICA.

THESIS

Submitted in fulfilment of the
requirements for the degree of
MASTER OF SCIENCE
of Rhodes University

by

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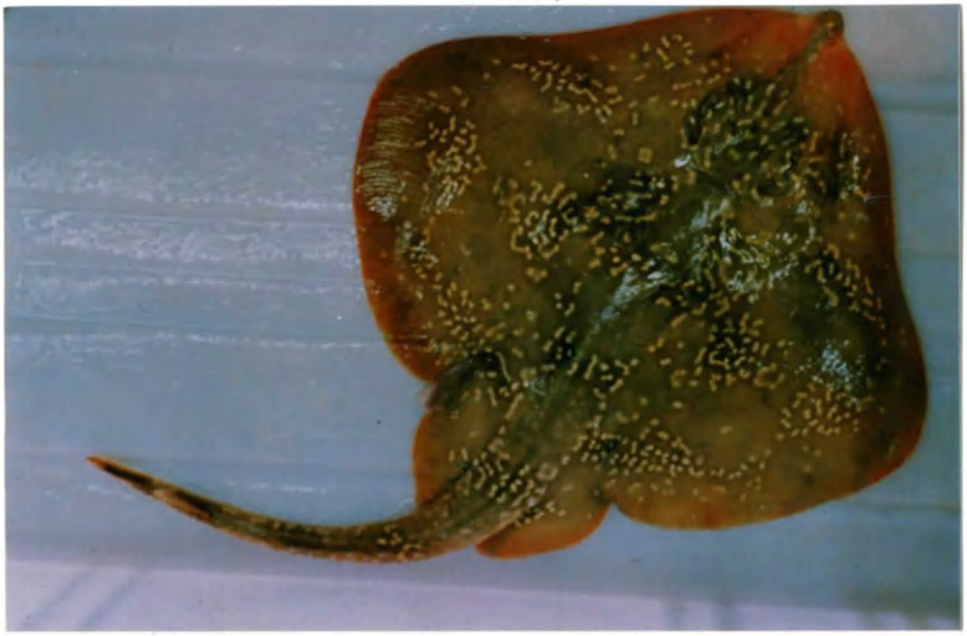
December 1996

To my parents, who were always the wind beneath my wings.



The yellowspot skate, *Raja wallacei*

The slime skate, *Raja pullopunctata*

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ACKNOWLEDGEMENTS

I am deeply indebted to my supervisor Dr. Warwick Sauer for his assistance, guidance, support and enthusiasm over the last two years. I am also grateful to Dr. Colin Buxton who initiated the project and secured the funding. My sincere thanks go to Tony Booth for his unfailing but invaluable computer support, lengthy discussions, his time and unbounded enthusiasm.

I would have got nowhere without the Sea Fisheries Research Institute (SFRI) and my most humble thanks go to the whole of the Demersal team. I would particularly like to thank Sharon Du Plessis, Cliff Hart and John Prinsloo for their help during cruises, for help with the databases, for gathering data, for scribing and for generally being there if I needed anything. I am indebted to the director of the SFRI, Dr. Andy Payne for the opportunity to participate in five research cruises and for access to the research database. My thanks also go to the Master and crew of the *FRS Africana* for many successful voyages. I would finally like to extend my thanks to Mr. Peter Sims in Mossel Bay and Mr. George Kant in Port Elizabeth for collecting fish.

Many of my samples were obtained through the fishing industry and I would like to thank Oosterlig Visserye, in particular the captains and crew of the *F.V.Midhavid* and *F.V.Zuiderzee*.

There are many people to thank within the Department of Ichthyology and Fisheries Science (DIFS). I am deeply grateful to Ms. Abigail Irish who patiently listening to my ravings and tried to hammer some sense into me when I needed it. I would like to thank Mrs. Linda Coetzee for the administrative help; Dr. Tim Andrews for his technical expertise; Mr. Tom Shipton for many healthy arguments and Mr. Paul Cowley for data, advice and interest in my project. To the rest of the department, thanks. I would also like to thank Mrs. Sue Abrahams of the Geography Department for the maps.

I am grateful to the South African Network for Coastal and Oceanic Research (SANCOR) and the Foundation for Research and Development (FRD) for the funding that enabled me to carry out this work.

My thanks and love go to Cliffie for the support and motivation he has given me this year.

Finally, my love and most sincere thanks go to the two people to whom this thesis is dedicated, my parents, who encouraged and supported me no matter how far from home my dreams might take me.

ABSTRACT

Members of the family *Rajidae* are common components of the demersal trawl fishery, contributing around 1% to the total catch. However, apart from a single species all South African rajids are currently discarded. With demands for new protein sources ever-increasing, it is possible that currently underutilised species, such as the skates will be utilized to a greater extent.

Raja wallacei and *R.pullopunctata* are common trawler by-catch species, ranging along most of the South African coast. The current study aimed to further knowledge on the population biology of both species through age and growth, reproductive and feeding studies. The study also aimed to assess whether any of the South African skate species show the potential for utilization as a food source.

Band counts of vertebral centra were used to determine growth parameters and generate growth curves for males and females of both species. Growth was significantly different between the sexes. In both cases, females grew slower than males but reached a greater asymptotic disc width. As with other elasmobranchs, *R.wallacei* and *R.pullopunctata* are long-lived and slow growing.

As with all other skates, the study species are oviparous laying large, yolked eggs in tough, leathery cases on the sea bed. The onset of maturity occurs at a large size (approximately 400mm disc width (10-11 years of age) for *R.wallacei* and 600mm disc width (12-13 years of age) for *R.pullopunctata*) and is very rapid. The oldest *R.wallacei* and *R.pullopunctata* observed were 16 and 18 years of age, respectively. No distinct breeding season was determined and no nursery areas were observed. A large proportion of individuals, especially *R.pullopunctata* was immature.

Both species fed primarily on crustaceans and teleosts with an ontogenetic shift in diet from mysids, amphipods, isopods and bregmatocerids to larger *Gnathophis sp.*, *Mursia cristimanus* and carid shrimps. Large discrepancies were seen in the diet of animals spatially, temporally and between research and commercially-caught animals.

Disc-width frequency data was limited but suggested that both species show preference for depths of 100-300m. Size distribution did not appear to be affected by depth, although the data set was limited. A paucity of large individuals in the catch may indicate that stocks are suffering from growth overfishing by trawling operations.

Historical and observer data showed that although skates are common components of the by-catch, the potential for greater use is limited. The biscuit skate, *R.straeleni*, on the west coast is the only species that could be better utilized. If skates are treated as a single group the potential is increased but this causes problems in assessing stocks.

CHAPTER 1

INTRODUCTION

Twenty years ago, Peter Benchley terrified the world with his tale of a psychotic shark, imprinting the belief that these animals are little more than killing machines on a generation. Although the skates and rays may not inspire the terror that "Jaws" did, they are nevertheless related within the ancient super-order known as Elasmobranchii, and possess many characteristics that make Benchley's villain such a magnificent fish. However, while sharks have received much attention, skates have been largely ignored both scientifically and by the public.

Skates and rays belong to the widely diverse Batoid sub-order that contains some 500 species (Compagno *et al*, 1989). More than 60 new species have been described in the last 30 years. More are expected through exploration and fishing in deeper waters and on the continental slopes (FAO, 1981). The highly diverse Rajiform, or skate, family (Hulley, 1972) contains more than 222 species worldwide, 25 of which are found in southern African waters (Compagno *et al*, 1989). Most occur on soft substrates in all seas except the Antarctic and tropics, from the shallows down the continental slope.

Studies have been scarce due to difficulties distinguishing between species and between adults and juveniles of the same species. Wallace (1967) reviewed the skates of the east coast of South Africa and Hulley (1970), reviewed those of the south and west coasts but both were taxonomic and descriptive. Reviews of skates from the northwest Atlantic and in Japanese waters are found in Bigelow and Schroeder (1953) and Ishiyama (1952, 1958a), respectively.

Considering the wide distribution of the family, relatively little exploitation of skates has occurred. A large multi-species skate fishery has existed in the Irish Sea for several decades (Holden, 1974; Fahy, 1989) and the Japanese catch some 5 000 tons annually for dried skate wings (Ishihara, 1990), but generally skates are considered as trash fish and are discarded.

This is reflected in landing records. During 1987-1993 *Raja sp.* contributed 0.1% or less to the world's marine fish catch (FAO, 1993). In South Africa in 1995, the total landed demersal catch was approximately 301000 tons while the skate catch was only 925 tons (0.3%). At no time between 1979-1995, did skate landings in South Africa contribute more than 1% to the total demersal catch (Sea Fisheries Research Institute (SFRI) data).

Although they may look unappealing skates possess similar nutritional values as sharks and teleost fishes (Ishihara, 1990). They are low in lipid and high in protein and moisture. Their vitamin content is low while the nitrogen content is high. They are also expensive to process. However, with the world's increasing demands for protein it is possible that skates may soon be more fully exploited. For fisheries to be managed effectively, an understanding of the biology and population dynamics of the target species is essential.

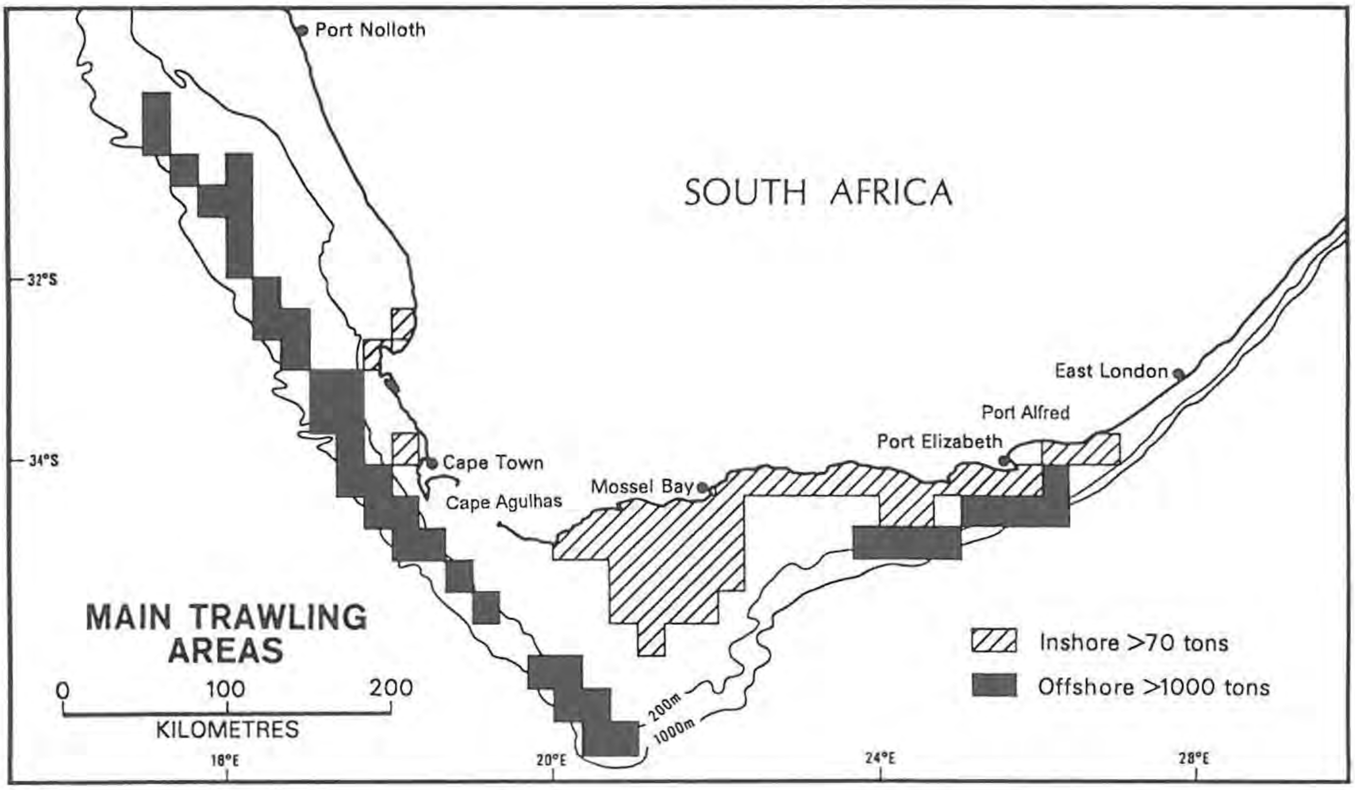


Figure 1.1: The main inshore and offshore fishing areas on the west and south coasts of South Africa in terms of the total catch from each grid square in 1993.

The South African offshore demersal fishery targets four main species - the cape hakes, *Merluccius capensis* and *M.paradoxus*, the sole, *Austroglossus pectoralis*, and the maasbanker, *Trachurus trachurus capensis* (Japp *et al*, 1990). The main inshore and offshore trawling areas on the south and west coasts are found in Figure 1.1. Inshore trawlers are restricted to 30 m in length and 750 h.p. engines while offshore trawlers are required to fish deeper than 110 m.

The yellowspot skate, *Raja (Leucoraja) wallacei* Hulley, 1970, and the slime skate, *Raja (Dipturus) pullopunctata* Smith, 1964, are both endemic to South Africa (Compagno *et al*, 1989). The former, a medium-sized species that attains a size of 59 cm disc width (DW), is a brownish skate with small yellow spots on the dorsal surface and a white belly. Two to four rows of spines are found from the mid-back to the first dorsal fin and adult males possess several rows of alar spines on the lateral edges of the pectoral fins. The yellowspot skate is found along the whole coast from Lüderitz to southern Mozambique at depths of 49-453 m.

The much larger *R.pullopunctata* attains a size of 94 cm DW and is found from Lüderitz to Port Alfred from 49-457 m (Compagno *et al*, 1989). As the name suggests, this skate is covered with copious amounts of slime that becomes tacky upon exposure to air. The brown dorsal surface is covered with many small black spots and a large dark blotch is found in the centre of each wing. The ventral surface is grey with darkly pigmented pores. A large nuchal thorn, situated midway between and posterior to the eyes, is obvious in young animals but may become worn with age. A row of large spines runs along the centre of the tail.

Both species predominate over soft substrates and are commonly caught by the offshore hake trawlers. Although both may form part of the catch in South Africa they are discarded and little is known about either species. The only *Raja* species currently utilized in South Africa is the biscuit skate, *R.straeleni*, which is sold as skate wings (P.Sims, SFRI, pers.com.).

The study on the biology of *R.wallacei* and *R.pullopunctata* centred upon the Agulhas bank, a triangular extension of the continental shelf that protrudes some 200 km from the coast of South Africa at its widest margin. The physical and chemical properties of the bank are determined by two currents - the warm, southward-flowing Agulhas Current in the east and the cold, northward-flowing Benguela Current in the west. The result is a habitat rich in species diversity able to sustain a large biomass of marine organisms (Shannon, 1989). Data were also collected during one research cruise along the west coast.

The differences between by-catch and discards should be noted. By-catch is that retained part of the catch that is incidental to the target catch (Saila, 1983). Some components of this by-catch, such as monk *Lophius vomerinus* and kingklip *Genypterus capensis* are retained due to high market value, while the rest is discarded. Unlike *R.straeleni*, which may be retained, *R.wallacei* and *R.pullopunctata* are both discarded.

This study aimed to investigate the biology, distribution, and potential for exploitation of both species. To this end, age and growth, reproductive biology and feeding preferences were studied. The distribution and possible existence of nursery areas or seasonal migrations were investigated. Finally, an assessment of the potential of both species for greater exploitation was made.

Samples were collected from commercial trawlers and during research cruises. The captains of the *F.V.Midhavid* and *F.V.Zuiderzee* of the Oosterlig Visserye Company, operating out of Port Elizabeth, agreed to collect skates monthly. The initial aim was to collect 50 specimens of each species per month. However, since fishing did not always take place over soft ground, this was not always the case. For some months, no samples could be obtained.

Greater success was had during the participation of research cruises aboard the Sea Fisheries' research vessel the *FRS Africana*. Four cruises along the south coast (from Cape Agulhas to Port Alfred) and one along the west coast (from Cape Agulhas to the Orange River) were undertaken and all skates sampled. However, such data was only collected during January-February (west coast) and April-May or September-October (south coast).

Observer data (defined later) were used to assess the contribution of the study species to the catch and length-frequencies were used to study distribution patterns. Estimates of age and growth parameters for both species are found in Chapter 2. An initial investigation into reproductive behaviour is reported in Chapter 3 and feeding biology in Chapter 4. The importance of all skate species to trawl catches and distribution and migration patterns are examined in Chapter 5. A general discussion and fisheries' considerations are found in Chapter 6.

This study forms part of a larger programme aimed at assessing by-catch within the South African demersal fishing industry, supported by the South African Network for Coastal and Oceanic Research (SANCOR). The programme has several aims: -

1) To quantify the by-catch in the trawl and line fisheries of South Africa and make an assessment of the level of discards.

2) To understand the biology and ecology of important underutilised by-catch species.

3) To investigate the potential development of small-scale fisheries based upon the currently underutilised species to the benefit of small coastal communities.

In order for the by-catch and discards to be quantified and the biological aspects to be investigated, an observer programme was instigated in 1995 to gather quality data on board commercial vessels. Observers were trained to assess the proportion of by-catch species within the total catch, to sub-sample the by-catch and to gather fishing data such as trawl duration and location. Several biological studies are underway into other important by-catch species such as the cape gurnard, *Chelidonichthys capensis*, the spiny dogfish, *Squalus megalops*, and the soupfin shark, *Galeorhinus galeus*. Data will be collated to obtain an overall picture of the levels of by-catch within the fishery. Assessments can be made on further utilization.

CHAPTER 2

AGE AND GROWTH

2.1 - INTRODUCTION

Determinations of age and growth are important tools for fisheries' scientists. Information on the age structure of a population is essential for the calculation of parameters such as growth rates, ages at maturity and mortality. Armed with such parameters, the fisheries' scientist can make a calculated guess about the best way of exploiting a stock in a sustainable manner.

In teleosts otoliths, scales or operculae are usually used to determine age. Elasmobranchs, however, lack these structures (Applegate, 1967) requiring the use of methods (Cailliet *et al*, 1986) such as length-frequency studies (Johnson and Horton, 1972); coupling length-frequency data to tag-recapture data (Grant *et al*, 1979; Casey *et al*, 1983, 1985); tooth replacement rates (Moss, 1972); development of secondary sexual characteristics (Johnson and Horton, 1972); embryonic growth rates (Ketchen, 1972; Francis, 1981). Elasmobranch hard parts may be aged using radiometric geochronologies (Welden *et al*, 1987); x-ray spectrometry (Jones and Geen, 1977) or by using an electron micro probe (Cailliet and Radtke, 1987).

Sectioned dorsal fin spines of elasmobranchs show banding patterns (Holden and Meadows, 1962) and it is assumed that one dark and light band are laid down annually (Sullivan, 1977). Beamish and McFarlane (1985) verified this for *Squalus acanthias* using tetracycline. Assumption of annual ring deposition can only be verified by using such techniques (Beamish and McFarlane, 1983). The use of fin spines is limited by the few living species that possess them.

The most common method of determining age in elasmobranchs is by counting concentric zones in vertebral centra. These zones, first described by Ridewood (1921) are common in elasmobranchs (Applegate, 1967) and are seen as alternating patterns of translucent (less calcified) and opaque (more calcified) bands. Many techniques have been used to enhance these bands

(Cailliet *et al*, 1983; Cailliet, 1986) such as alizarin red S staining (LaMarca, 1966; Gruber and Stout, 1983); silver nitrate staining (Haskell, 1949; Stevens, 1975; Schwartz, 1983; Rossouw, 1984); crystal violet staining (Schwartz, 1983); cobalt nitrate staining (Hoenig and Brown, 1988) and wiping with cedarwood oil (Martin and Cailliet, 1988).

Generally among the batoids, the number of bands increases with size and many authors have assumed that these are annual, with one opaque and one translucent band constituting one year (Smith and Merriner, 1987; Abdel-Aziz, 1992) However, for some species more than one band may be laid down annually (Natanson and Cailliet, 1990). Comparison of ring-count data with disc width-frequency data for *Raja eglanteria* shows an increase in band count with disc width (Daiber 1960) and modal points on the width-frequency plot agree with the width-number of bands.

Validation studies similar to those on dorsal fin spines have been carried out but these are few (Smith, 1984; Branstetter, 1987; Brown and Gruber, 1988).

Once the age of an animal is known growth models can be generated and the parameters L∞, the theoretical maximum length, and K, the growth constant, determined. Comparisons may be made between different species and populations of the same species from different areas or at different times.

Age and growth studies on rajids are few (e.g. Holden, 1972; Abdel-Aziz, 1992) with even fewer validation studies (Holden and Vince, 1973; Natanson, 1993). Ishiyama (1951) working on young *R.fusca* found that ring counts increased with size. Daiber (1960) showed a relationship between ring counts and disc width but did not assume the rings were annual, nor did he test whether this relationship was statistically significant. Waring (1984) calculated growth rates for *R.erinacea* from rings that he termed annuli but did not attempt to verify.

The aim of the study was to describe the growth of *R.wallacei* and *R.pullopunctata* and to compare growth with other rajid species. However, validating these results for either study species was not possible due to time constraints and technical difficulties.

2.2 - MATERIALS AND METHODS

Monthly samples were collected by the commercial trawlers *FV Midhavid* and *FV Zuiderzee* operating out of Port Elizabeth and during hake biomass surveys aboard the *FRS Africana* between February 1995 and August 1996. Trawling from the *Africana* was executed using a German 180-foot bottom trawl with a cod-end lined with pilchard netting during daylight hours. Each trawl lasted approximately 30 minutes. A detailed description of the sampling strategy used in the survey is given in Badenhorst and Smale (1991).

Disc width, total length, mass and sex were recorded for each fish. Approximately 7-8 vertebrae were removed from the region of the abdominal cavity and frozen. The centra were thawed, separated using a scalpel and the neural arches removed. Connective tissue was dissolved using sodium hypochlorite solution. Centra were rinsed in fresh water and stored in 70% propanol (Cowley, 1990). A preliminary study was undertaken to determine the best method of viewing the centra. Whole centra were viewed unstained or stained with cobalt nitrate (Hoenig and Brown, 1988), crystal violet (Johnson, 1979), and alizarin red S (Brown and Gruber, 1988). Unstained centra were embedded in a clear casting resin, sectioned through the nucleus using a double-bladed diamond-edged saw, stained and mounted on a microscope slide using DPX. Sections were approximately 3μm thick (Cowley, 1990). The preparation procedure is shown in Figure 2.1.

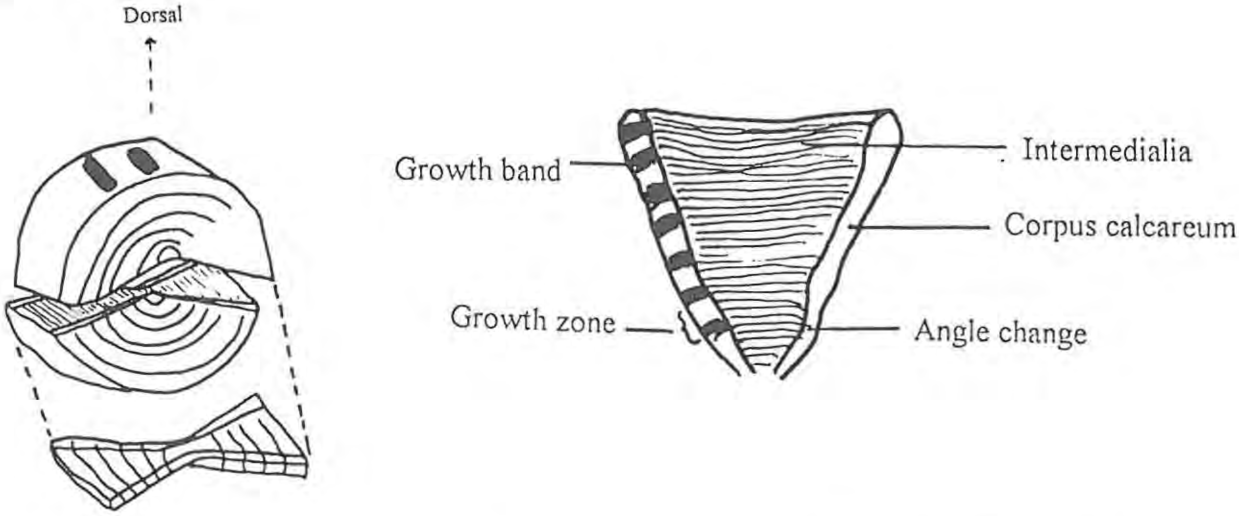


Figure 2.1: Sectioning and embedding procedure resulting in a "bow-tie" shaped vertebral section (after Brown and Gruber, 1988).

Clearest growth bands were obtained with sectioned centra stained with 0.01% crystal violet for 20 minutes and viewed under transmitted light using a dissecting binocular microscope. Band counts were taken twice for each centrum with no reference to fish size or previous counts. If the two disagreed, a third reading was taken. If this reading corresponded to either of the first two, that count was accepted. If all three counts were different but consecutive, for example 2, 3 and 4 rings, the middle reading was taken. If all three readings otherwise disagreed, the centrum was discarded.

In this study, the term "zone" refers to a wide, opaque band (dark purple when stained) followed by a translucent band (much lighter purple when stained). The first dark band was found at an angle change of the centrum and was deemed to be the birth band. Bands were clear in the outer, more calcified corpus calcareum region and were occasionally seen in the inner, less calcified intermedialia (Figure 2.1)

Since one requirement of using hard parts in age and growth studies is that growth of the hard part must follow that of the animal, the centrum diameter was measured using an ocular micrometer. To investigate the periodicity of zone deposition, the characteristics of the centrum edge were examined. To determine the growth of the light and dark bands throughout the year, the distance between the distal edge of the last complete dark band to the centrum edge was measured. Due to time constraints, not all *R.pullopunctata* centra were investigated. Finally, the colour of the ultimate band during the year was noted to investigate whether one light and one dark band are laid down annually (Beamish and McFarlane, 1983).

Disc width-band count data and the PC-Yield 2.2 computer programme (Punt, 1992) were used to determine growth parameters. A non-parametric one-sample runs test was used to test for randomness of the residuals and a Bartlett's test was used to test for homoscedasticity. Variance estimates were calculated by using (conditioned) parametric bootstrap resampling (Efron, 1982) with 500 bootstrap iterations. Standard errors and 95% confidence intervals were constructed from the bootstrap data using the percentile method described by Buckland (1984). The results were fitted to a relative error model, using the von Bertalanffy Equation:

$$l_t = L_\infty \left(1 - e^{-(K(t-t_0))}\right)$$

where l_t = total length at time t; L_∞ = maximum theoretical length; K = growth constant and t_0= theoretical length at age zero (von Bertalanffy, 1938).

2.3 - RESULTS

Disc width-weight and disc width-total length relationships for male and female *R.wallacei* and *R.pullopunctata* were calculated and are found in Table 2.1. The relationship between centrum diameter and disc width was linear for both species (Figure 2.2), satisfying the criterion that the growth of the hard part must be proportional to that of the animal.

Although staining with crystal violet gave the clearest rings, reading the centra was difficult (Plates 2.1 & 2.2) with agreement among the first two counts in only 28% of centra. After the third reading, 86% of the counts agreed.

Band counts were obtained for 139 *R.wallacei* (female n=65; male n=74) and 107 *R.pullopunctata* (female n=54; male n=53). Estimates of K, L_∞ and t_0 were calculated for male, female and combined sexes (Table 2.2). Using a likelihood ratio test, which accounts for non-linearity in the model, rather than in the slopes and intercepts separately, (Draper and Smith, 1966), significant differences were found between male and female *R.wallacei* (F=5.26; df=3,133; $p<0.05$) and *R.pullopunctata* (F=11.92; df= 3,101, $p<0.05$). The growth curve for sexes combined is shown in Figure 2.3 since populations are not likely to be managed separately.

Results from the centrum edge analysis are found in Figure 2.4. The percentage of centra with a light edge was calculated monthly and the results shown in Figure 2.5. Due to a lack of samples in the summer, data for the year were incomplete. Data for *R.wallacei* show a peak in the marginal increment in February and March, falling off in April. Growth through the winter seems slow and may even be halted. Unfortunately due to the paucity of data in the spring and summer months, the resumption or increase in growth could not be determined. Data for

R.pullopunctata are less clear. Again the winter months from April to August show little growth. Due to a lack of data from October to March, spring and summer growth could not be determined. The results would suggest that during one year, one light purple and one dark purple band is laid down.

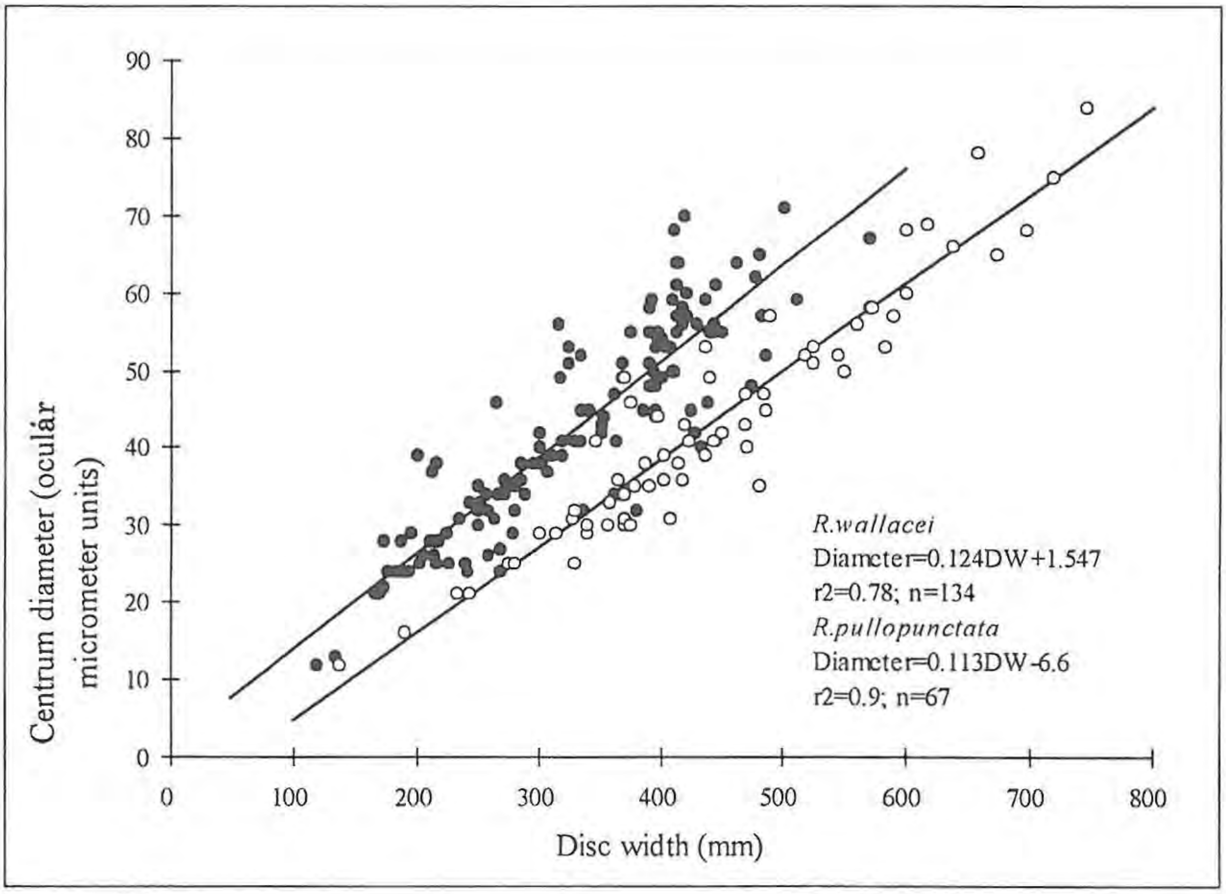


Figure 2.2: Centrum diameter versus disc width for *R.wallacei* (closed circles) and *R.pullopunctata* (open circles).

Species	Regression	R^2	n
R.wallacei			
m	logM=2.990 logDW-4.546	0.94	504
f	logM=2.958 logDW-4.458	0.94	496
R.pullopunctata			
m	logM=2.968 logDW-4.697	0.9	243
f	logM=3.227 logDW-5.384	0.96	199
R.wallacei			
m	TL=1.563DW+33.94	0.92	609
f	TL=1.502DW+53.05	0.93	604
R.pullopunctata			
m	TL=1.295DW+28.79	0.84	261
f	TL=1.433DW+22.15	0.97	217

Table 2.1: Results of disc width-mass and disc width-total length regressions for *R.wallacei* and *R.pullopunctata*.

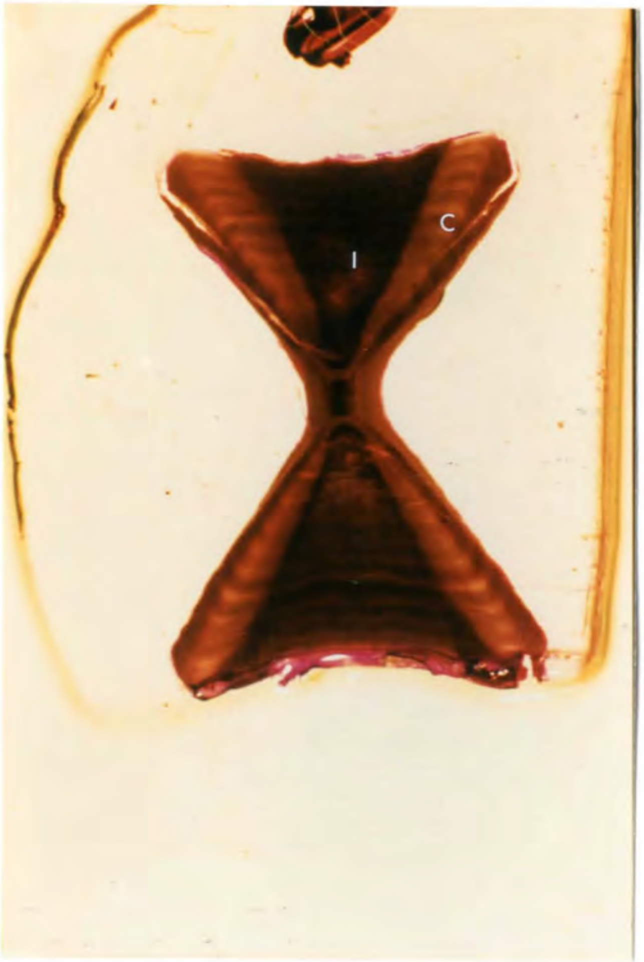


Plate 2.1 The sectioned vertebral centrum of a 10-year-old male *R.pullopunctata,* 598mm DW. I= Intermedialia; C=Corpus calcareum.

Plate 2.2: The sectioned vertebral centrum of a 3-year-old male *R.wallacei*, 230mm DW. B=Birth band

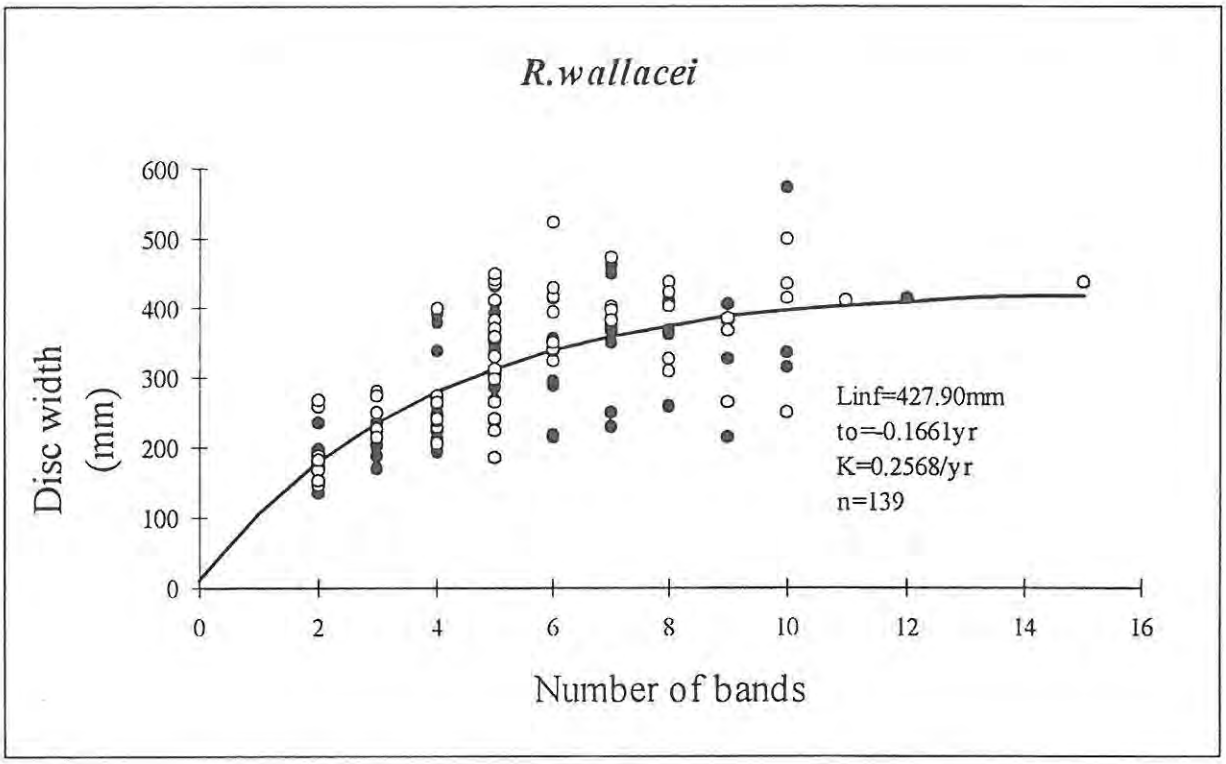
R.wallacei

	Estimate	SE	Left 95% CI	Right 95% CI
males n=65				
t_0	-0.078	0.816	-2.332	0.900
K	0.269	0.119	0.074	0.565
L_∞	405.399	6009.862	339.819	722.410
females n=74				
t_0	-0.206	0.945	-2.790	0.845
K	0.255	0.115	0.077	0.525
L_∞	435.230	13699.842	363.008	738.152
males and females combined n=139				
t_0	-0.166	0.520	-1.458	0.595
K	0.257	0.077	0.129	0.443
L_∞	421.901	42.919	369.367	543.920

R.pullopunctata

	Estimate	SE	Left 95% CI	Right 95% CI
males n=56				
t_0	-2.367	1.560	-6.819	-0.616
K	0.097	0.060	0.002	0.248
L_∞	770.500	43534.330	539.970	1773227.742
females n=51				
t_0	-2.197	0.470	-3.232	-1.470
K	0.047	0.028	0.000	0.106
L_∞	1326.750	89500.390	759.764	443181.7731
males and females combined n=107				
t_0	-1.948	0.612	-3.787	-1.324
K	0.084	0.029	0.000	0.138
L_∞	873.240	59693.120	673.620	212472.260

Table 2.2: Calculated growth parameters for *R.wallacei and R.pullopunctata.*



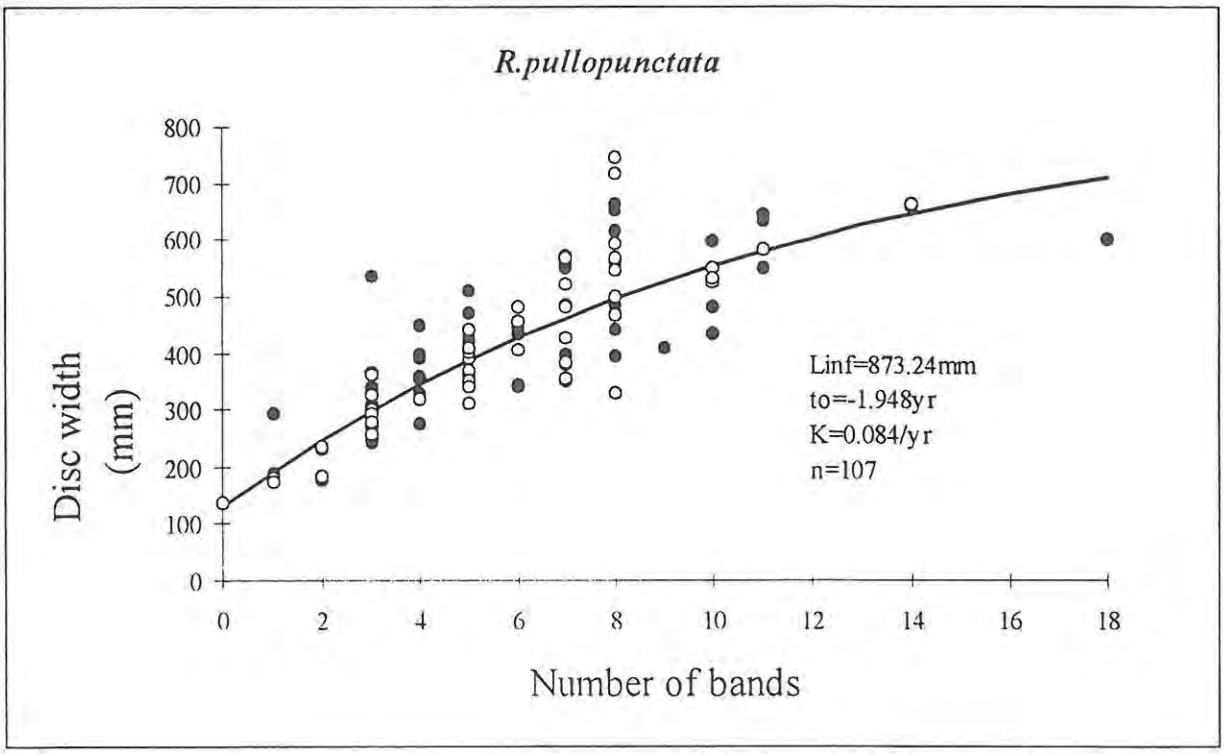


Figure 2.3: Growth curves for male (closed circles) and female (open circles) *R.wallacei* and *R.pullopunctata.*

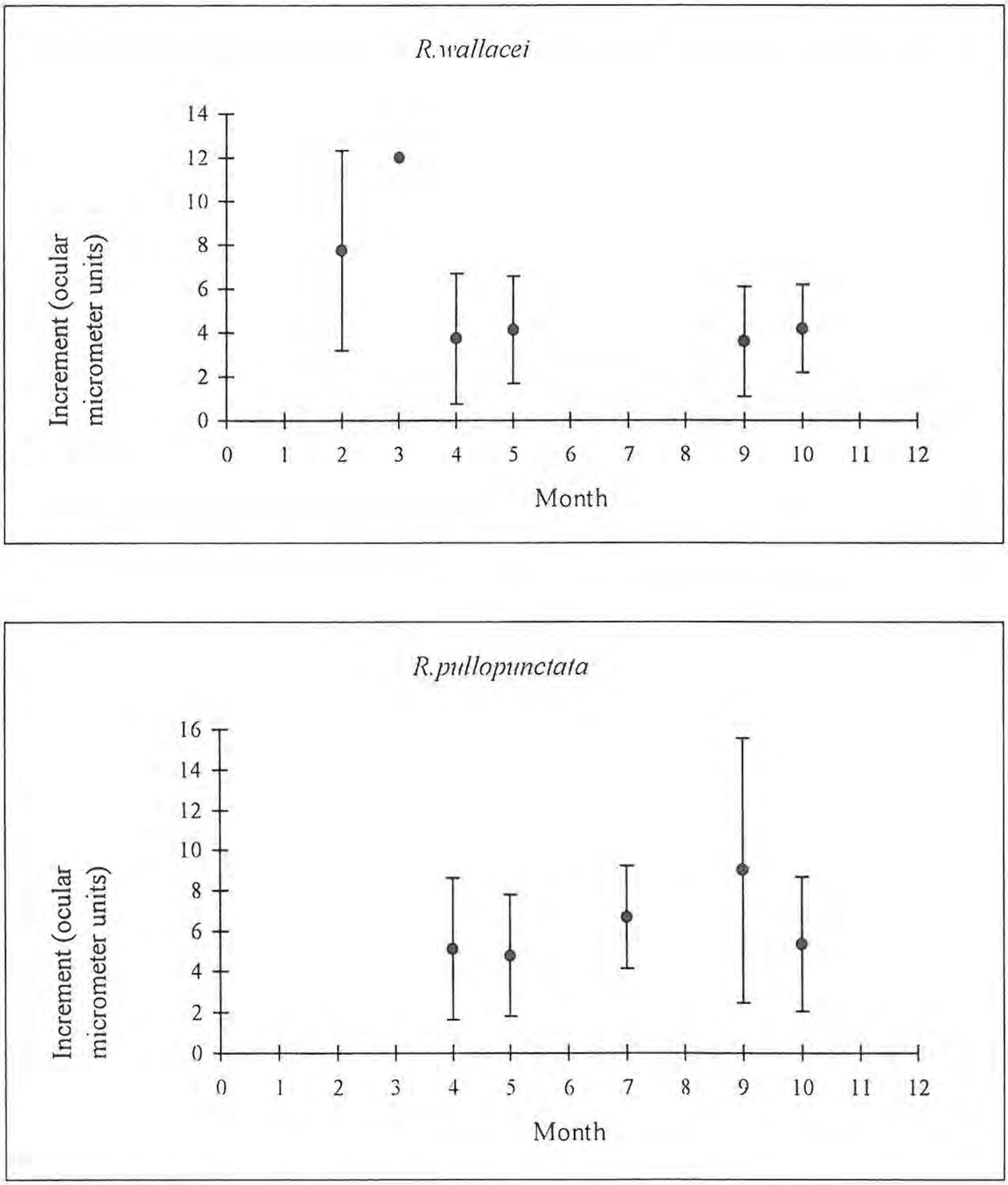
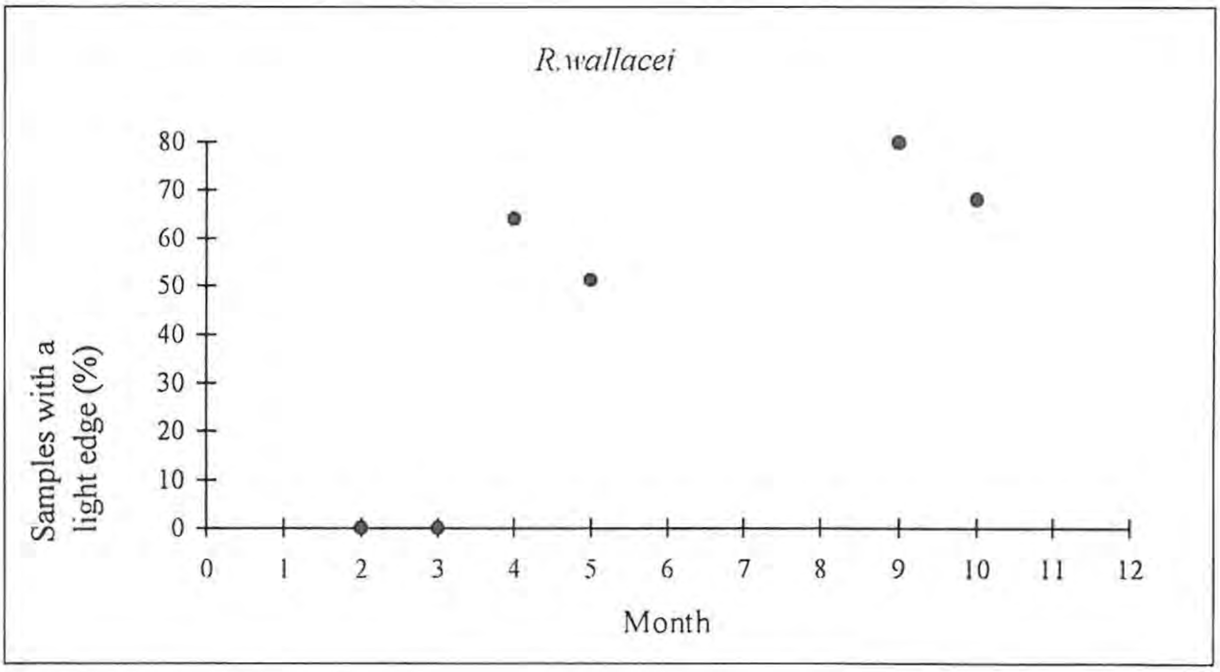


Figure 2.4: Mean distance between the distal edge of the last dark band and the centrum edge for *R.wallacei* and *R.pullopunctata*. Error bars show standard deviations.



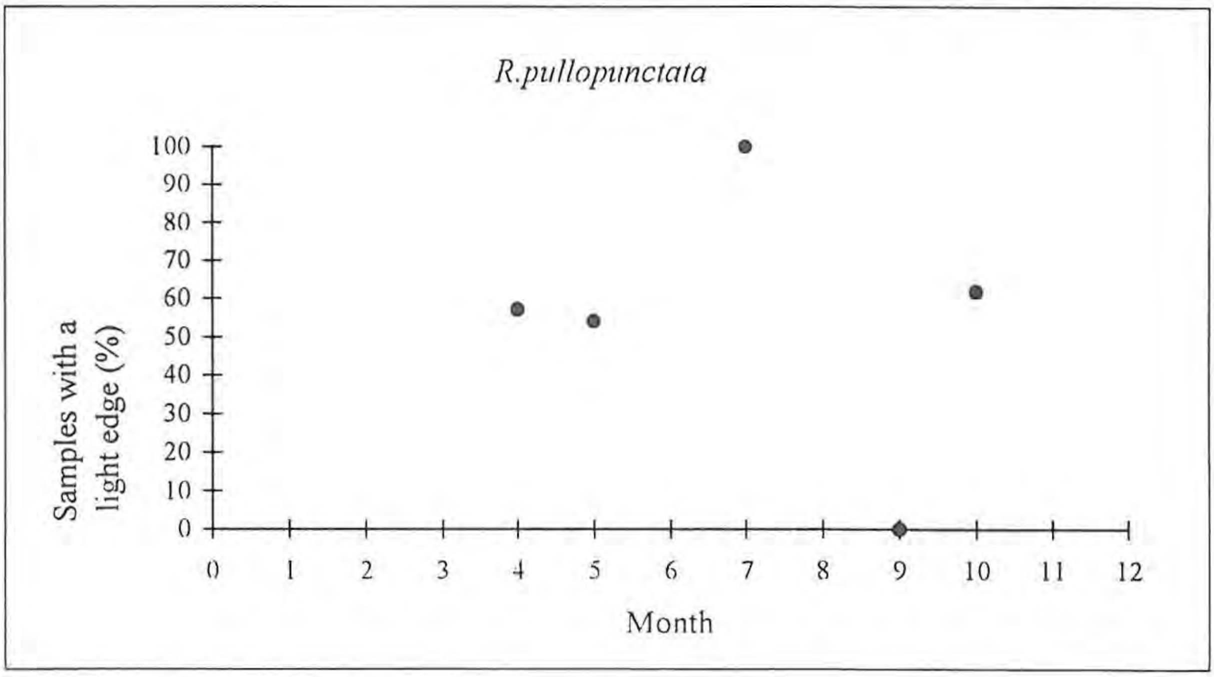


Figure 2.5: Monthly percentage of *R.wallacei* and *R.pullopunctata* centra with a light edge.

2.4 - DISCUSSION

Reading bands within vertebral centra is the only practical method available for ageing skates. However, the ease with which bands can be read and the success of enhancement techniques is highly species-specific. Abdel-Aziz (1992) reported that for *R.miraletus* 1% silver nitrate gave the clearest rings on whole vertebrae, while Holden and Vince (1973) were simply able to use reflected light on whole *R.clavata* centra. Natanson (1993) used haematoxylin to stain sectioned vertebrae in *R.erinacea* while Waring (1984) used paraffin wax, calcium oxide powder and decolouring carbon to enhance bands in sectioned centra of the same species. Even among South African skates, the success of an enhancement technique depends on the species in question. Crystal violet stain gave the clearest rings for both study species but does not enhance the bands in either *R.straeleni* or *R.alba* (Wait, University of Port Elizabeth, pers.com.).

Measurements of the centrum edge suggest that for *R.wallacei*, the developing edge is at its widest during February and March. At this time 100% of the centra examined showed dark edges. The width of the dark band indicates that growth at this time is fast. During the formation of the light bands during the winter months, growth may be reduced and may even halt. The centrum edge is predominantly light during the months from April to October. Although the data set is incomplete, a single dark and light band are probably laid down annually. It is unlikely that two peaks exist in the months during which no data was available. Although less data was obtained for *R.pullopunctata* there might be similar slow growth between April and October, with the centrum edges being predominantly light. Abdel-Aziz (1992), reported a similar trend of an increase in the marginal increment leading to a single peak for the brown ray, *R.miraletus*. In this Mediterranean species, the maximum increment was noted during the winter months (November and December) with the minimum increment during the spring (February and March). Waring (1984) also noted an annual pattern of opaque and translucent banding for *R.erinacea*. A narrow translucent band was observed during the winter months and a narrow, opaque band during the spring and summer months. Investigations of other temperate skate species also indicate that one opaque and translucent band is laid down per year (Holden and Vince, 1973; Natanson, 1993). In both cases, the band counts indicated that one band pair was laid down annually and this assumption was verified using tetracycline. It would appear then that during the summer, when food is plentiful and growth is more rapid, calcification of the vertebrae is more pronounced. During the winter months, when growth is slower, a translucent band forms due to less calcification.

Marginal increment analysis is a common method of determining seasonality in teleost otoliths. These structures are removed whole, unlike vertebrae that are removed in a block and must be physically separated using a knife. It is possible that the centrum edge is damaged during this procedure, and that measurements of centrum diameter are not wholly accurate and spurious results may be obtained. Despite this, the centrum edge analysis data were included since some trends were observed.

Elasmobranchs are characteristically long-lived and exhibit slow growth. The spiny dogfish, *Squalus acanthias*, may live for 70 years but only reaches a metre or so in length (Beamish and McFarlane, 1985). Skates are no exception to this and even a small species such as *R.miraletus* is slow growing (Abdel-Aziz, 1992) with an average K value 0.18. Such characteristics must be taken into account if a species is to be exploited, especially when slow growth is combined with lower reproductive potential than that of most commercial teleost species. Shark fisheries have historically shown patterns of "boom and bust" periods (Holden, 1977) when such factors have been disregarded.

The growth parameters obtained for both study species compare well with those obtained for other skates. A summary of published growth parameters for several skate species is found in Table 3.2. To compare with published data, values of L_∞ generated for *R.wallacei* and *R.pullopunctata* were converted from disc width to total length. Disc width was used through the entire study as the basic skate measurement. This is because research and observer data is recorded using disc width. Values of ϕ prime ($\log K + 2^*\log L_\infty$) were calculated for the published data to compare species more easily. *Phi* prime values calculated for the study species fall well within the spread of values obtained from the published parameters. *R.montagui* is similar in size to *R.wallacei*. The values of ϕ prime obtained by Holden's (1972) data are marginally lower than those of the *R.wallacei*. Values of ϕ prime for *R.pullopunctata* are larger than those of the similar-sized *R.brachyura* Holden (1972) but are also comparable.

SPECIES	SOURCE			L_∞ (cm)	K (/yr)	to (yrs)	ϕ prime
R.brachyura	Clarke (1922)	Plymouth, English Channel	m	138.90	0.12	-1.52	3.36
			f	118.40	0.19	-0.8	3.43
R.clavata			m	85.60	0.21	-0.6	3.19
			f	128.10	0.09	-1.32	3.17
R.montagui			m	68.70	0.19	-0.56	2.95
			f	72.80	0.18	-0.37	2.98
R.brachyura	Holden (1972)	Irish Sea, Bristol Channel	m	115.00	0.19	-0.8	3.40
			f	118.40	0.19	-0.8	3.43
R.clavata			m	85.60	0.21	-0.6	3.19
			f	107.00	0.13	-0.6	3.17
R.montagui			m	68.70	0.19	-0.56	2.95
			f	72.80	0.18	-0.37	2.98
R.batis	Du Buit (1977)	Celtic Sea		253.70	0.057	-1.629	3.56
R.naevus				91.64	0.085	-0.465	2.85
R.clavata	Ryland and Ajayi (1984)	Carmarthen Bay		139.77	0.09	-2.626	3.25
R.microocellata				137.00	0.086	-3.009	3.21
R.montagui				98.70	0.156	-1.719	3.18
R.erinacea	Waring (1984)	US northeast coast		52.73	0.352	-0.449	2.99
R.clavata	Brander and Palmer (1985)	Northeast Irish Sea		105.00	0.215	-0.45	3.37
R.miraletus	Abdel-Aziz (1992)	Mediterranean Sea	m	87.87	0.19	-0.5	3.17
			f	91.92	0.17	-0.25	3.16
*R.wallacei**	This study	Agulhas Bank	m	66.78	0.269	-0.078	3.08
			f	70.68	0.255	-0.206	3.11
*R.pullopunctata**			m	102.66	0.097	-2.367	3.01
			f	190.34	0.047	-2.197	3.23

*Total lengths for *R.wallacei* and *R.pullopunctata* were calculated from the disc width-total length regressions, reported above.

Table 2.3: Published growth parameters for other *Raja* species worldwide

Growth is significantly different between males and females, a common trend in skates (Table 2.3). Females attain a greater size than males but grow at a slower rate (Holden 1972; Abdel-Aziz, 1992). This is a consequence of their different reproductive strategies. Females grow larger to hold the egg-cases within the body cavity while males grow faster to reach sexual maturity.

The value of L_∞ obtained for *R.pullopunctata* females is high, some 40cm greater than the maximum disc width reported by Compagno *et al* (1989) and 60cm greater than the largest female recorded in the present study. It is likely that this is an overestimation caused by the small sample size. The combined L∞ for males and females is much lower and is probably a more realistic estimate. The value of L∞ generated for *R.wallacei* from the PC Yield programme compared better with the disc width of the largest sampled animal. This is probably due to the availability of large individuals resulting in more representative vertebral samples

Although both data sets were incomplete, they do give preliminary estimates of valuable growth parameters. Due to the difficult nature of reading the vertebral rings and the small data sets, the accuracy of the parameters cannot be determined. However, they clearly show that both species are very slow growing and long-lived.

CHAPTER 3

REPRODUCTION

3.1 - INTRODUCTION

The continued success of elasmobranchs over millions of years can largely be attributed to their reproductive strategies (Luer and Gilbert, 1991). Elasmobranch reproduction represents the first appearance of or the establishment of processes such as internal fertilization, viviparity and placental mechanisms for foetal maintenance in the vertebrate line (Wourms, 1977). Despite the obvious importance of elasmobranch reproductive mechanisms, detailed studies are scarce and have generally focused on commercially important species such as *Squalus* sp. (Dodd *et al*, 1983).

All rajids employ oviparity, the most primitive reproductive mode used by elasmobranchs (Luer and Gilbert, 1991). Studies on rajid reproduction have largely centred on copulatory behaviour (Price, 1967; Luer and Gilbert, 1985), egg-laying and gestation (Luer and Gilbert, 1985; Berestovskii, 1994; Ellis and Shackley, 1995) and egg-case structure (McEachran, 1970) and its use in taxonomy (Ishiyama, 1958b). The structure of the rajid testis was described by Pratt (1988) and the ovarian cycle of the cuckoo ray, *R.naevus*, was described by Du Buit (1976).

Data on reproductive biology are not only essential to life history studies but are vital for assessing the ability of stocks to contend with fishing pressure. Gonad development and the size and age of maturity was investigated for *R.wallacei* and *R.pullopunctata*. The existence of a distinct breeding season and the existence of nursery areas was examined. The influence of commercial trawling on the stocks is discussed.

3.2 - MATERIALS AND METHODS

Samples were obtained from the commercial trawlers *Midhavid* and *Zuiderzee* operating out of Port Elizabeth from February 1995 to August 1996. At sea the fish were kept on ice but frozen upon landing before transportation to the lab. Additional samples were obtained during research cruises aboard the *FRS Africana* and were examined on board. Disc width, total length, total mass and gonad mass were recorded. The length of the inner origin of the left clasper to its distal end was recorded for each male. During the first month of the study gonads were assessed visually to determine separate developmental stages and a table of maturity was constructed. Maturity stage was based upon the development of the ovaries, ova, nidamental glands and reproductive tract in the female and development of the testes, seminal vesicles and claspers in the males. If egg-cases were present total length, length, width and height were measured (Figure 3.1).

Marked changes in clasper length and gonad mass with disc width were used as indicators for the onset of maturity. The length-at-maturity was calculated using a two-parameter logistic ogive described by the equation: -

$$P(l)=\frac{1}{1+\exp^{-(l-l50)/\delta}}$$

Where *P(l)* is the percentage of mature fish at length l, l_{50} the length at which 50% of the fish are sexually mature and δ is the width of the ogive (King, 1995).

Testes were collected to assess the validity of the morphological male maturity stages histologically. Due to the large size of mature eggs, ova histology was not investigated. However, mature nidamental glands were sampled to determine whether sperm storage occurs. Histological samples were collected during a hake biomass survey aboard the *FRS Africana* in September and October 1995.

Anterior, median and posterior sections of testis were collected from 5 males at each maturity state for both species. Tissues were fixed in 4% buffered formalin for a maximum of 4 days and transferred to 70% propanol. Tissues were dehydrated through a series of alcohols to xylene and embedded in wax. Sections were made on a rotary microtome at a thickness of 5µm before staining with Gill's haematoxylin and Papanicolaou eosin A (Bernard and Hodgson, 1988).

Length frequency data from research and commercial cruises (observer data) were used to determine whether nursery areas exist and to investigate migration patterns. The morphometric characteristics of the egg-cases were also examined.

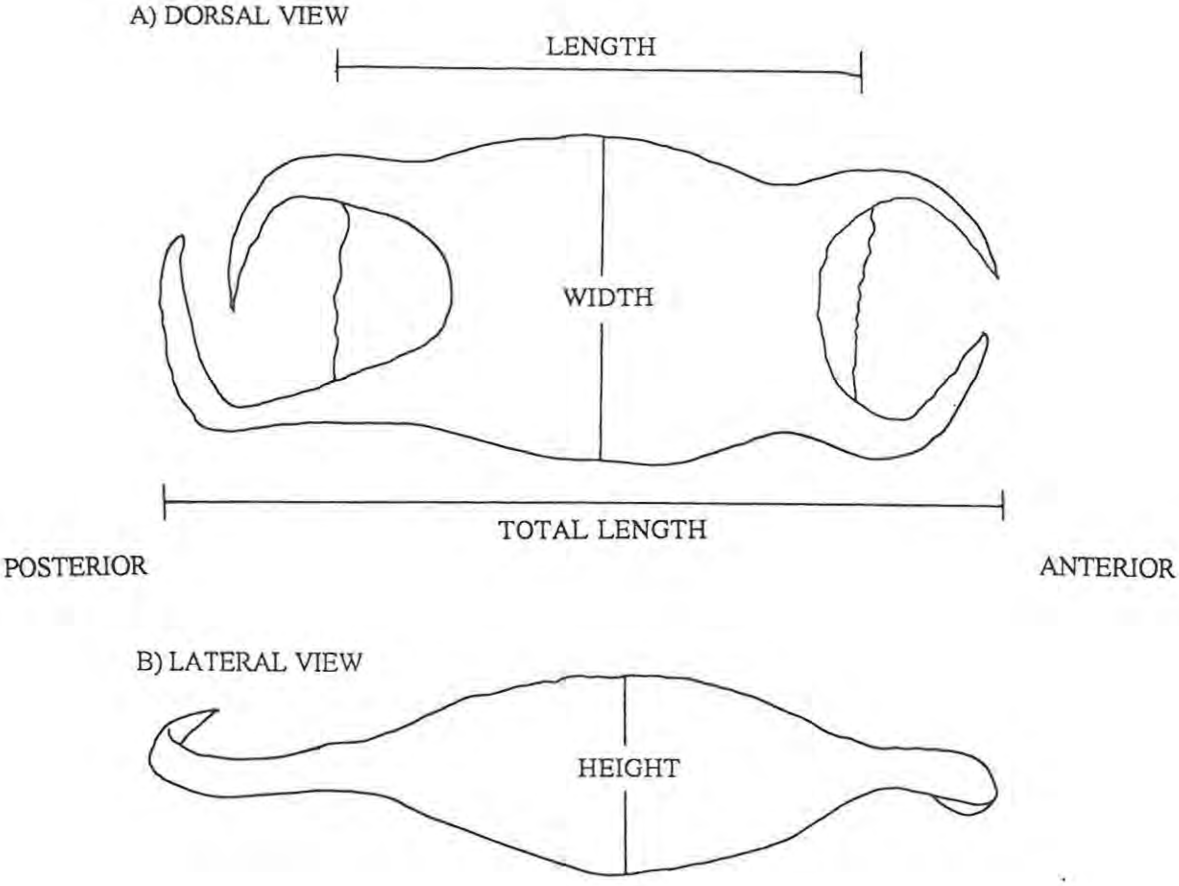


Figure 3.1: Diagrammatic representation of a skate egg-case, showing measurements referred to in the text.

3.3 - RESULTS

A total of 982 *R.wallacei* and 390 *R.pullopunctata* were collected. From the preliminary study, a 5-point scale of maturity for males and a 7-point scale for females was constructed. The criteria used in the study are given in Table 3.1.

	STAGE	OBSERVATIONS
MALES	2	Testes composed of undifferentiated, white tissue. Vas deferens a thin, white line along the dorsal surface of the abdominal cavity. Claspers small and soft.
	2.5	Testes highly vacularised. No development in the seminal vesicles and claspers.
	3	Dorsal surface of testes becomes lobular. Vas deferens begins to thicken. Coiling may be seen within the tissue. Claspers begin to elongate but not calcify.
	3.5	Dorsal surface of testes is fully lobular. Seminal vesicles and vas deferens are highly coiled and developed. Claspers protrude beyond the trailing edge of the pelvic fin and start to become calcified.
	4	Fully mature. Claspers fully calcified and hard. Testes, vas deferens and seminal vesicles are fully developed. Sperm may be present.
FEMALES	2	Ovaries consist of white, undifferentiated tissue. Oviduct is a thin white line on dorsal surface of the abdominal cavity. Nidamental gland is a small swelling on the oviduct.
	2.5	Ovaries become highly vascularised and take on a granular appearance. Slight swelling is seen in the nidamental gland.
	3	Small, immature, opaque eggs can be seen within the ovaries. Nidamental gland is heart-shaped and the oviduct wall begins to thicken.
	3.5	Eggs are white in appearance. Two distinct tissue zones are seen within the nidamental glands. Uterus wall continues to thicken.
	4	Fully mature. Ovaries are full of yellow eggs. Eggs range in size from 40mm in diameter downwards. Nidamental gland is fully developed and uterus wall is thick and muscular.
	4.5	Pregnant. A fully or partially formed egg-case is found within on or both uteri.
	5	Post-parturition. The uterus wall is extremely stretched and flaccid, indicating that eggs have recently been laid.

Table 3.1: Definition of maturity stages for male and female *R.wallacei* and *R.pullopunctata*.

Male gonad development and secondary sexual characters

The male reproductive system of both species is similar to that reported for other oviparous elasmobranchs (Luer and Gilbert, 1991) and consists of paired testes, efferent ducts, vas deferens, seminal vesicles and claspers.

Clasper and gonad growth is linear in the immature animal. During maturity rapid growth in both claspers and gonads is seen (Figure 3.2 and 3.3). Elongation in the claspers begins at approximately 350mm DW for *R.wallacei* and 550mm for *R.pullopunctata*. Faster gonad growth is also seen at this size. However, there is no similar marked change in maturity stage with size (Figure 3.4). The smallest mature male *R.wallacei* measured 338mm DW and the smallest mature male *R.pullopunctata* 584mm DW. The length-at-maturity ogive for *R.wallacei* shows that males mature at 395mm DW (Figure 3.5), which is approximately 9 years of age (Chapter 2). Since only 7 mature male *R.pullopunctata* were obtained during the whole study, a similar ogive could not be calculated.

Validity of histological data

Testes were examined to determine whether the onset of spermatogenesis mirrored the morphological maturity stages. Sperm were found in all stages, even the most immature animals (Plate 3.1). Due to difficulties with the histological sections the presence of a functional efferent duct could not be determined. It appeared that the wax did not fully penetrate the tissues and that xylene, which evaporated upon removal from the wax, was still present even after immersion overnight. Vacuum embedding alleviated the problem but did not entirely solve it. As a result, the tissues became hard and crumbled upon sectioning. The presence of such a duct would suggest that sperm are transported to the seminal vesicles for storage. Random counts of follicles were taken to determine the percentage of follicles with sperm at each maturity stage (Figure 3.6). A noticeable increase in the proportion of follicles with sperm was seen as animals matured. Sperm were present in only 9% of follicles in immature *R.wallacei*, compared with 60% in mature animals. A similar trend was seen for *R.pullopunctata*.

Seasonality

Gonadosomatic indices (GSI) were calculated monthly for males of both species using the formula:

$$GSI = (\text{Total body weight/ Gonad weight}) * 100$$

Changes in GSI are seen in Figure 3.7. Unfortunately, due to problems with obtaining samples from Port Elizabeth, data sets are incomplete. As a result, there are too few months' data from which to observe any trends and draw conclusions about breeding season.

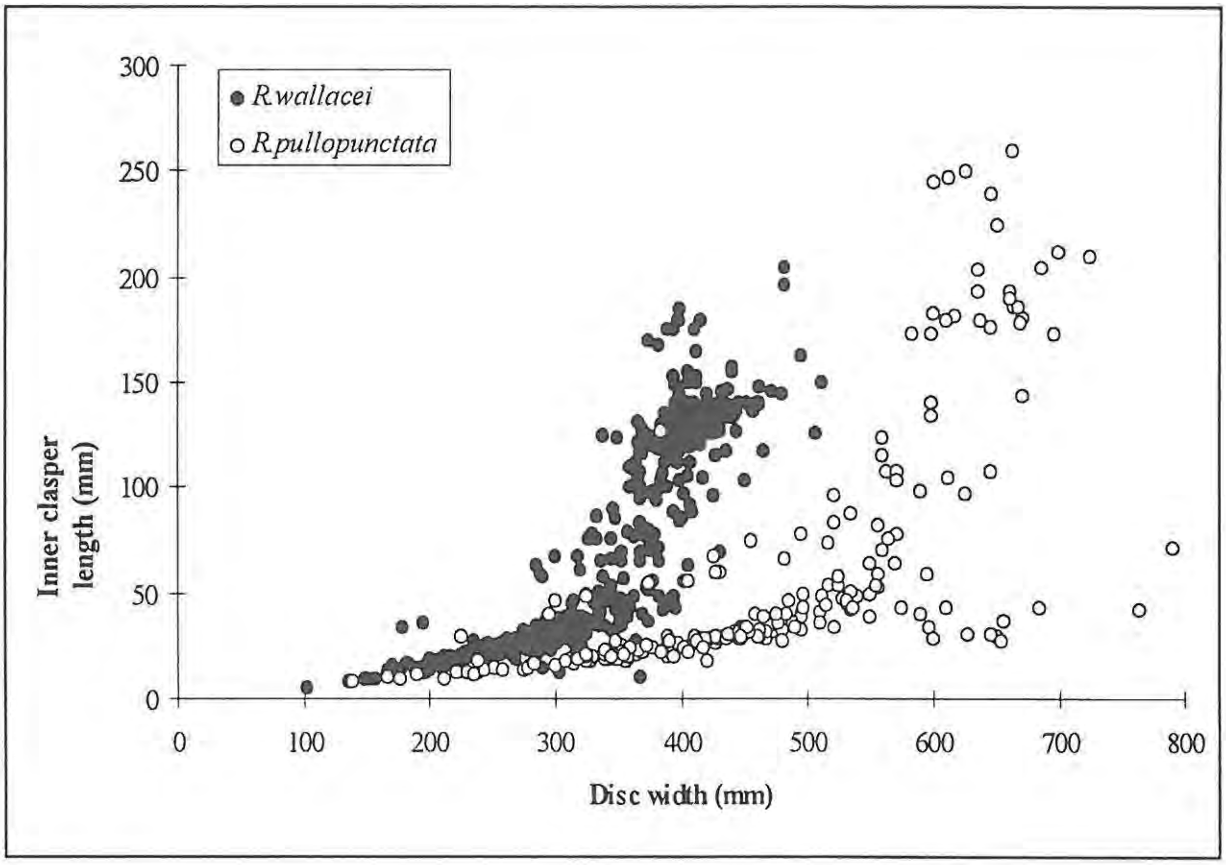


Figure 3.2: Inner clasper length versus disc width for male *R.wallacei* (n=577) and *R.pullopunctata* (n=237).

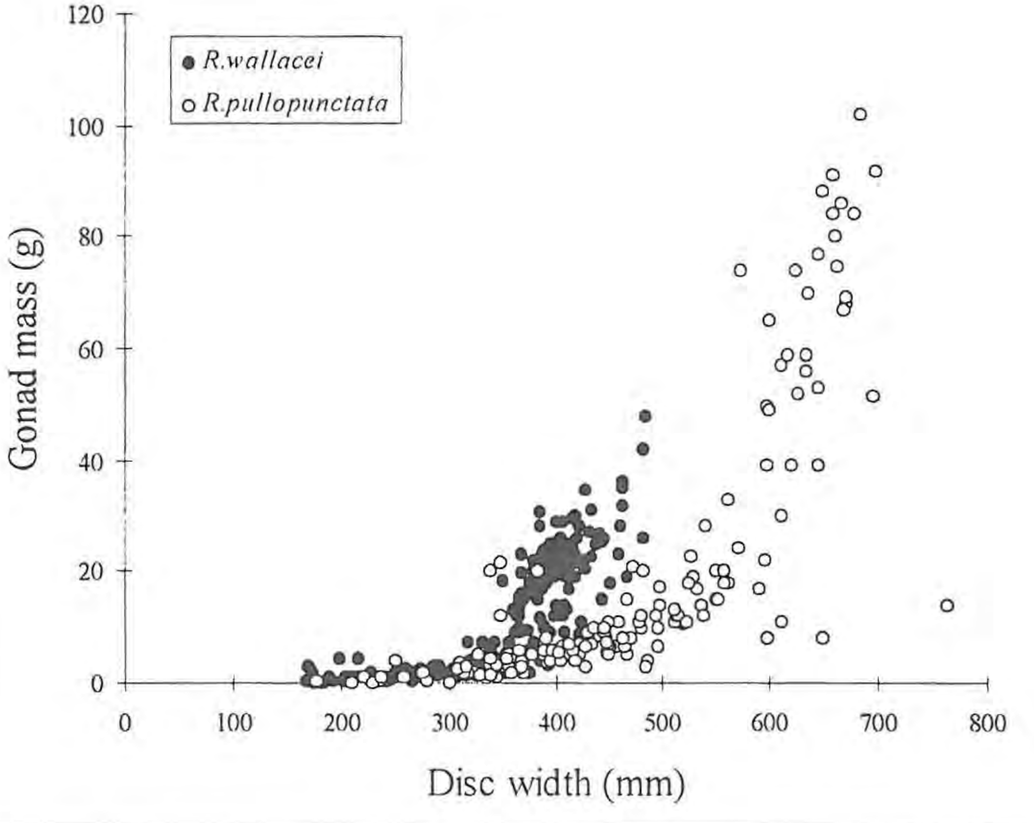
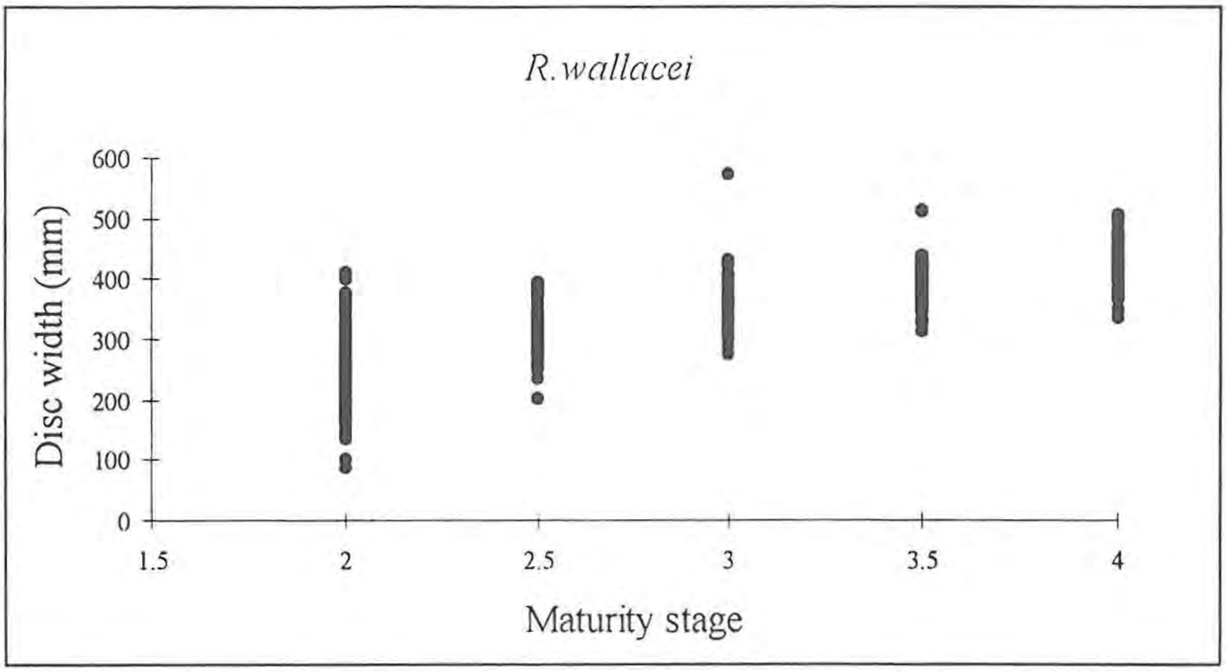


Figure 3.3: Gonad mass versus disc width for male *R.wallacei* (n=238) and *R.pullopunctata* (n=170).



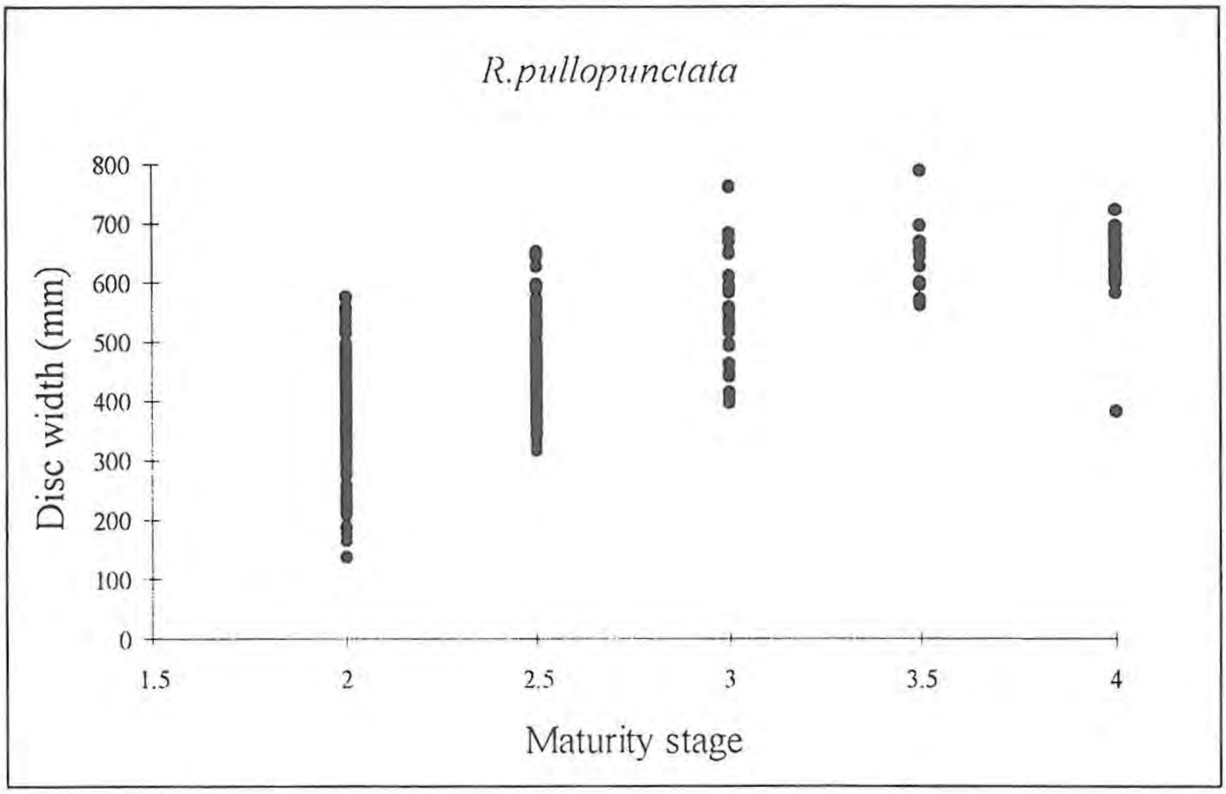


Figure 3.4: Maturity stage versus disc width for male *R.wallacei* (n=607) and *R.pullopunctata* (n=266)

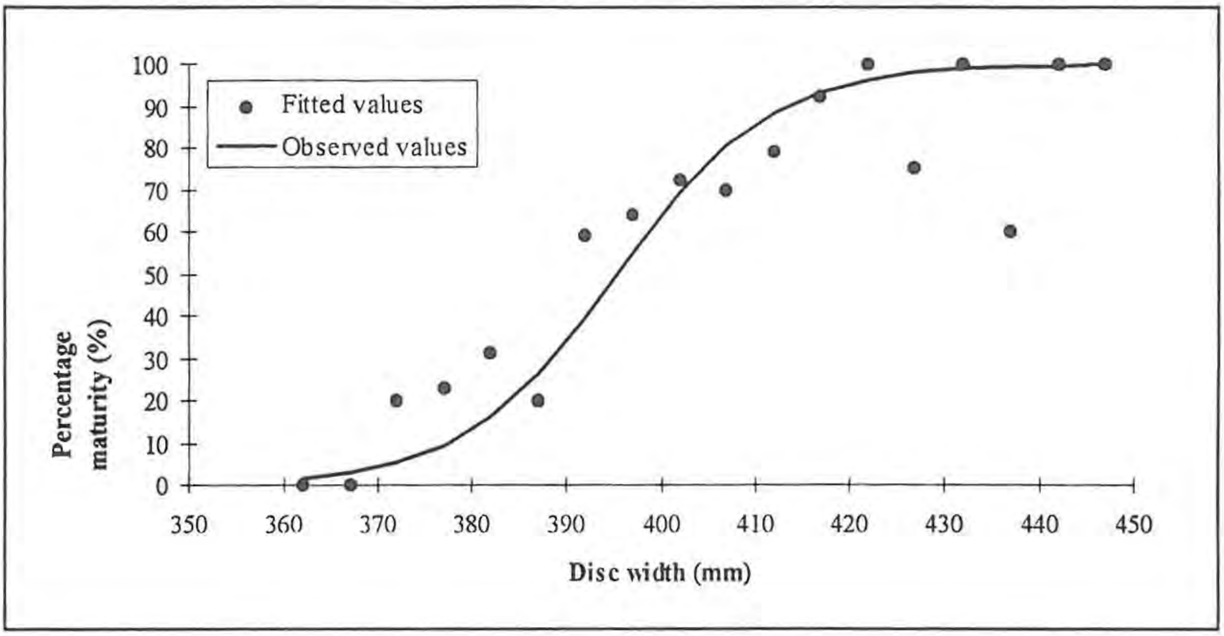


Figure 3.5: Length-at-maturity ogive for male *R.wallacei*.

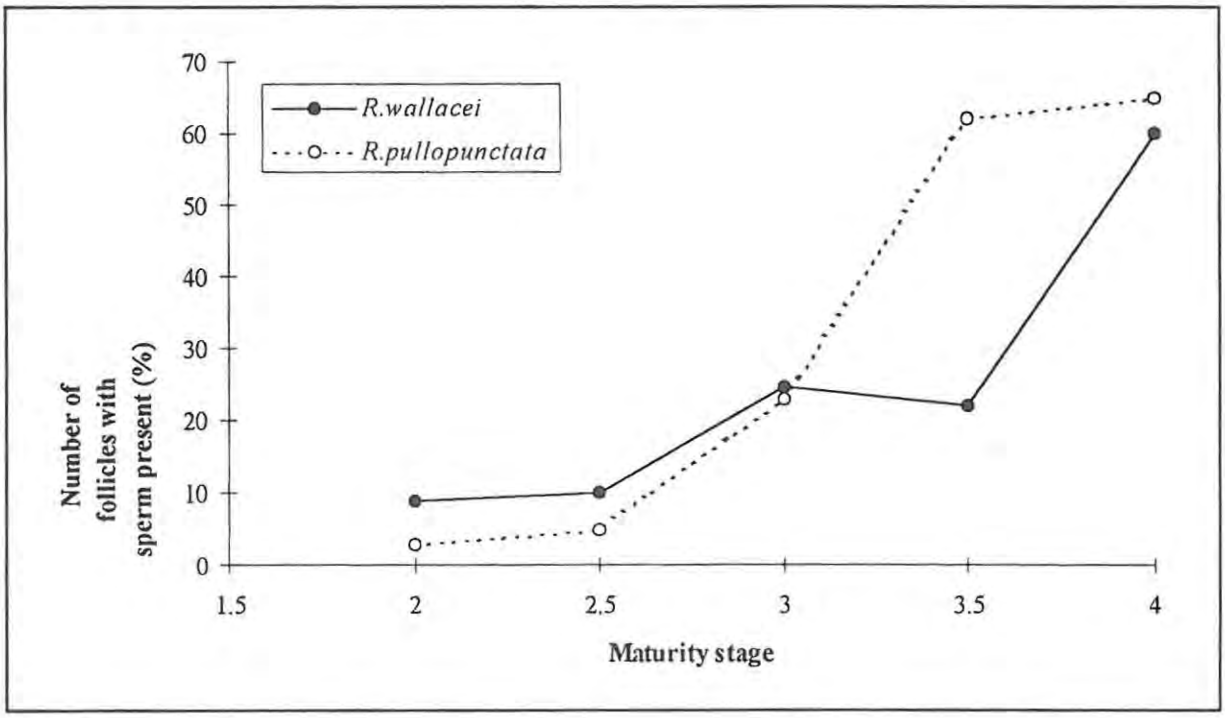
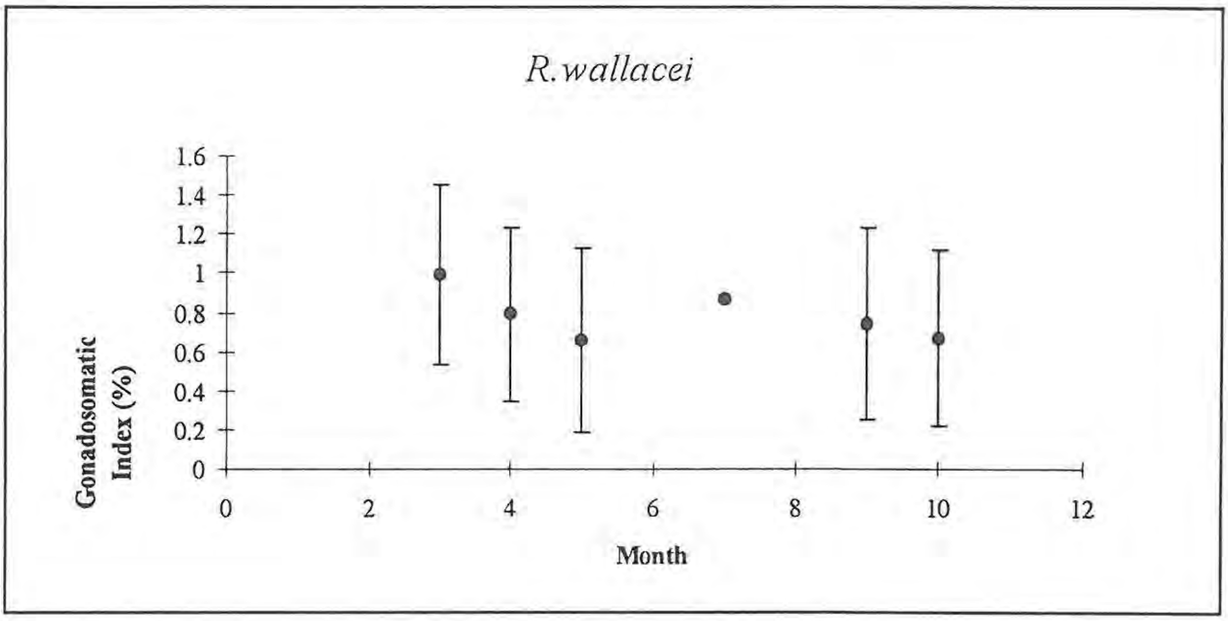


Figure 3.6: Percentage of *R.wallacei* and *R.pullopunctata* seminal follicles containing sperm.



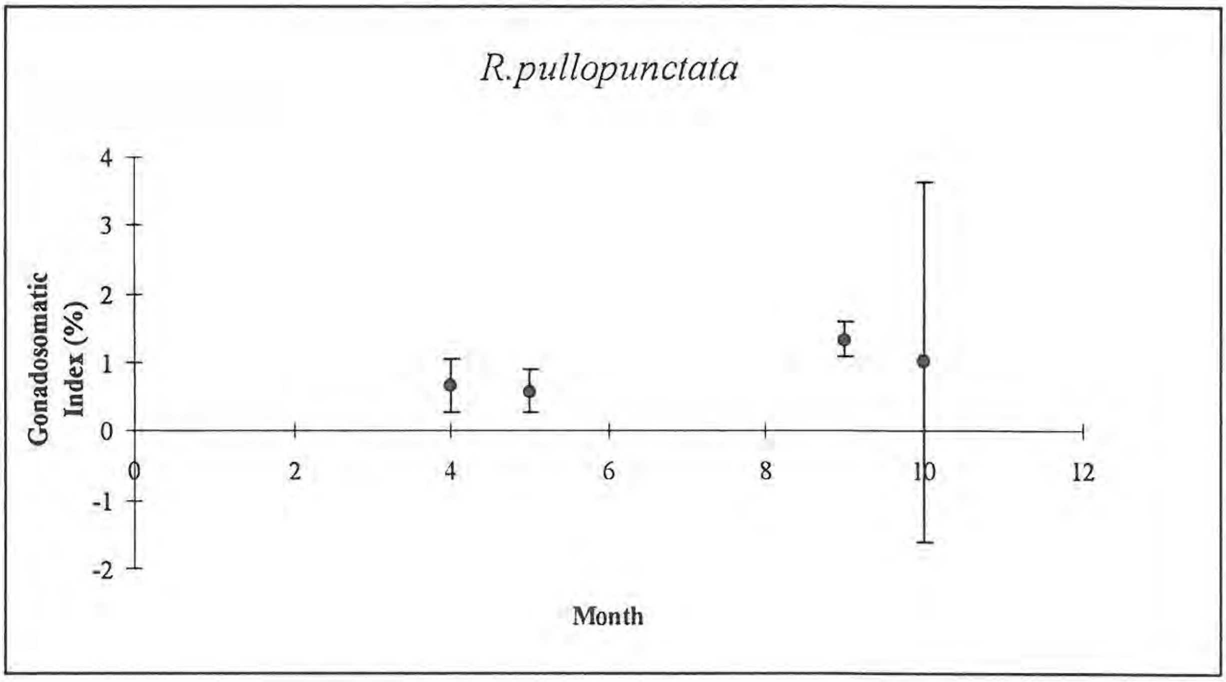


Figure 3.7: Monthly gonadosomatic indices for male *R.wallacei* (n=238) and *R.pullopunctata* (n=170). Vertical bars indicate standard deviations.

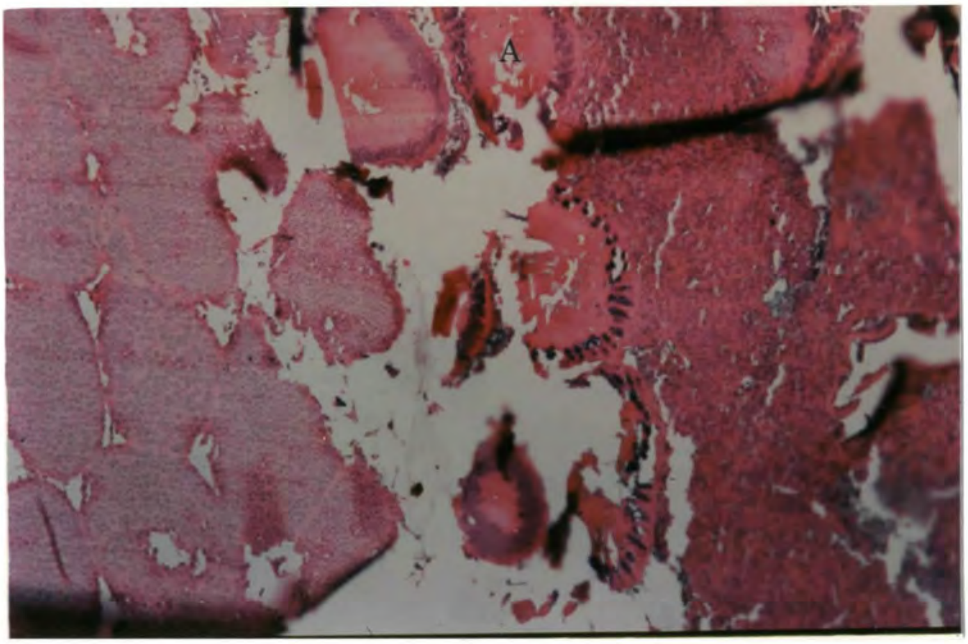


Plate 3.1: Sectioned testis of a stage 2.5 male *R.pullopunctata*, 550mm DW, showing the presence of sperm in the immature testis. A=seminal follicle containing mature spermatozoa.

Female gonad development

The female reproductive tract of *R.wallacei* and *R.pullopunctata* were similar to other species of skates and consists of paired ovaries, oviducts, nidamental gland and a common cloaca (Wourms, 1977). As with males, rapid gonad growth with disc width was seen at the onset of maturity (Figure 3.8). This occurred at around 350mm DW for *R.wallacei* and 650mm for *R.pullopunctata*. However, the smallest fully mature female *R.wallacei* and *R.pullopunctata* were both smaller than the smallest mature males of each species at sizes of 297mm DW and 658mm DW, respectively. A similar rapid increase in maturity stage with disc width was not observed (Figure 3.9). Maturity in female *R.wallacei* begins slightly later and is less rapid than males but these differences were minor. Length-at-maturity data showed that female *R.wallacei* reach maturity at 400mm DW (Figure 3.10), approximately 9 years of age (Chapter 2).

Spawning

Egg-cases were observed in 25 *R.wallacei*. Of these, 5 were found in March, 7 in April and 13 in May suggesting that egg-laying occurs in the autumn only. Studies of incubation period indicate that embryonic development may take 3-9 months (Richards et al, 1963). No pregnant *R.pullopunctata* were sampled.

The total length, height and width of 23 egg-cases were measured and the results given in Table 3.2. Occasionally, the egg-cases were crushed or part of the horn had broken off and all measurements could not be made. The formation of egg-cases within the uterus indicated that capsules begin formation at the anterior end. All full-formed cases were dissected and the number of eggs counted. A single egg was found in all egg-cases examined. In 5 instances, only a single case was present, indicating the other had been deposited before the animal was examined. Of these 5, 2 were found in the left tract and 3 in the right.

Histological sectioning of nidamental glands from mature female *R.wallacei* showed no evidence of sperm storage. However, nidamental glands were sampled in September only and therefore the possibility of sperm storage cannot be rejected.

Nursery areas

Pregnant *R.wallacei* were distributed over the entire bank from depths of 50m in Plettenberg Bay to 200m south of Cape Agulhas (Figure 3.11).

Length frequency data from research cruises was assessed to determine whether nursery areas exist. Distribution data (Chapter 5), although limited, showed no congregations of individuals and any size classes at any depth range. Should the inshore region be used as a spawning area, term and post-partum females and small newborn individuals would be expected to be most abundant.

Parameter	Mean (mm)	Range (mm)	sd (mm)	n
Length	152	136-172	8.7	23
Total length	73	68-80	3.0	21
Height	22	20-23	0.9	13
Width	43	39-49	2.2	23

Table 3.2: Dimensions of measured *R.wallacei* egg-cases.

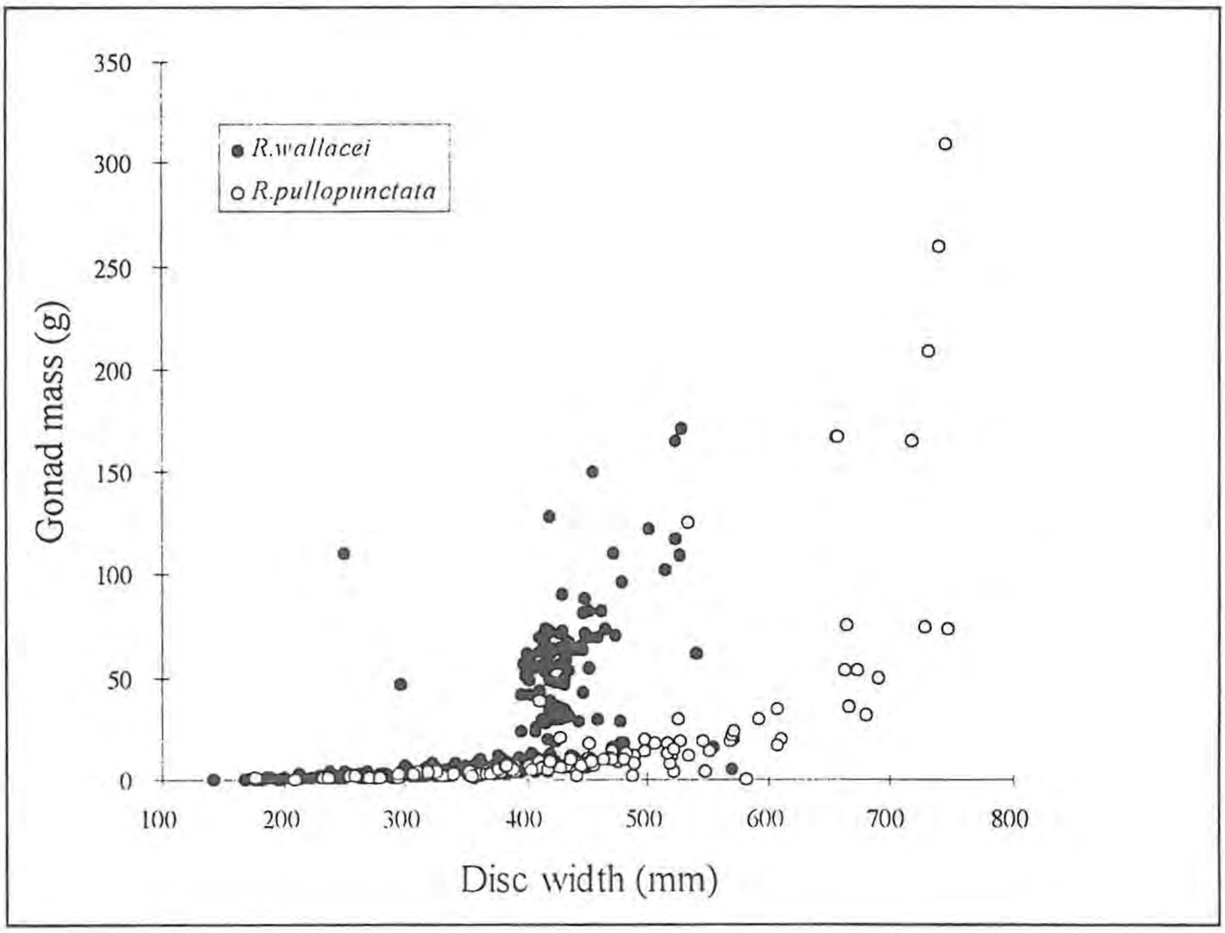
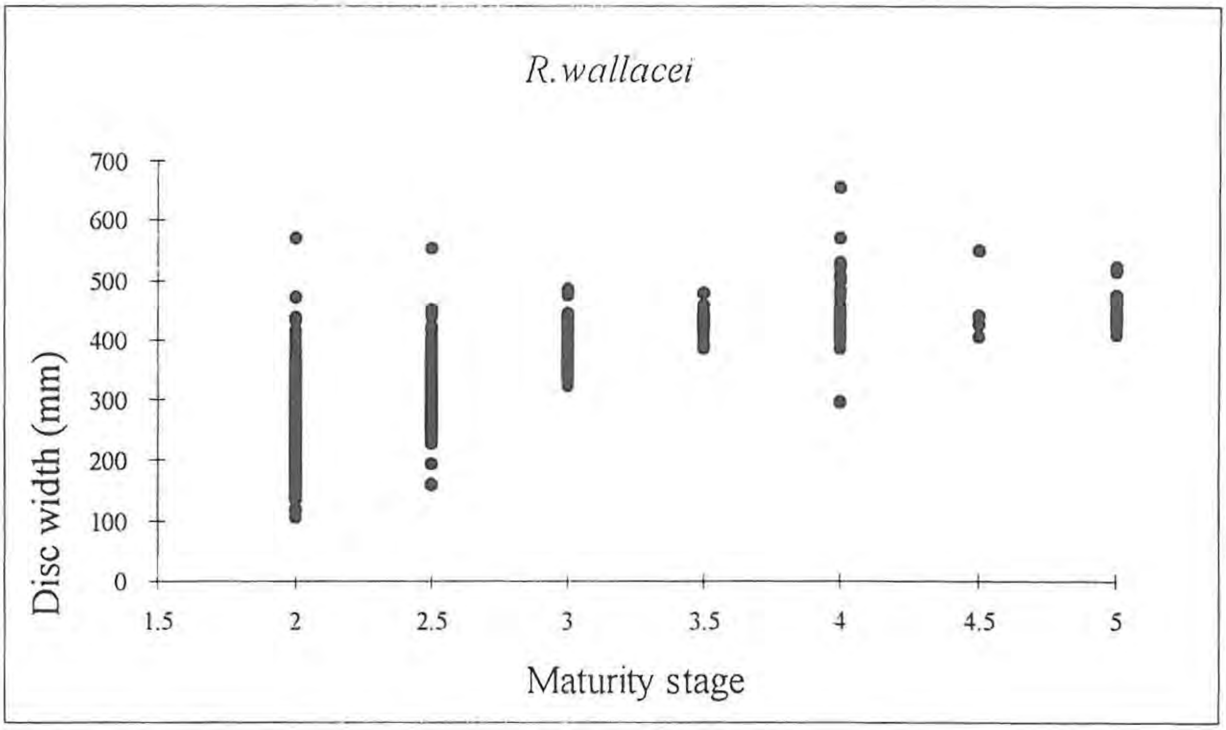


Figure 3.8: Gonad mass versus disc width for female *R.wallacei* (n=232) and *R.pullopunctata* (n=111).



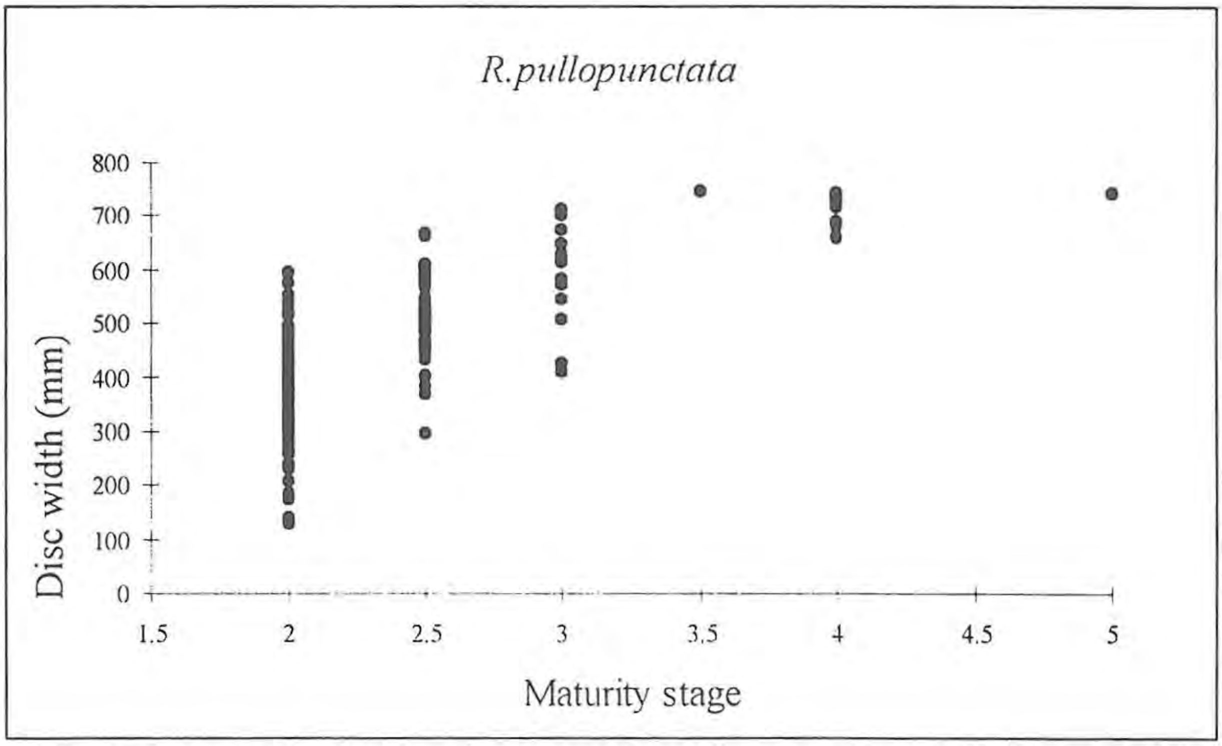


Figure 3.9: Maturity stage versus disc width for female *R.wallacei* (n=600) and *R.pullopunctata* (n=224).

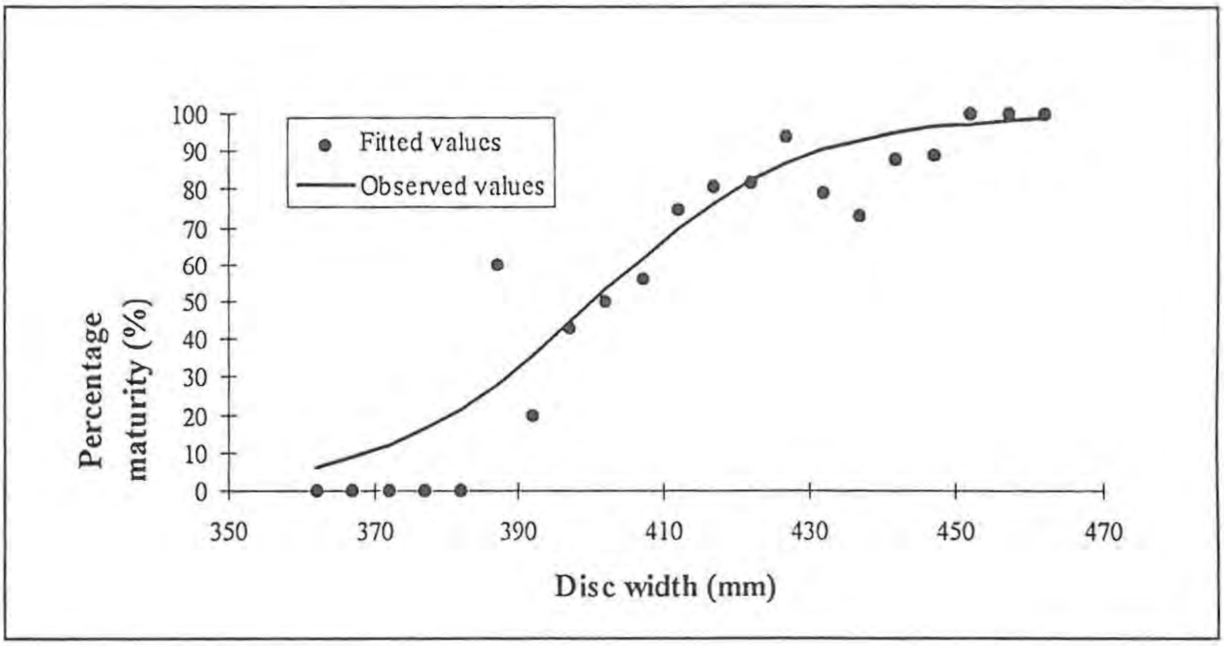


Figure 3.10: Length-at-maturity ogive for female *R.wallacei*.

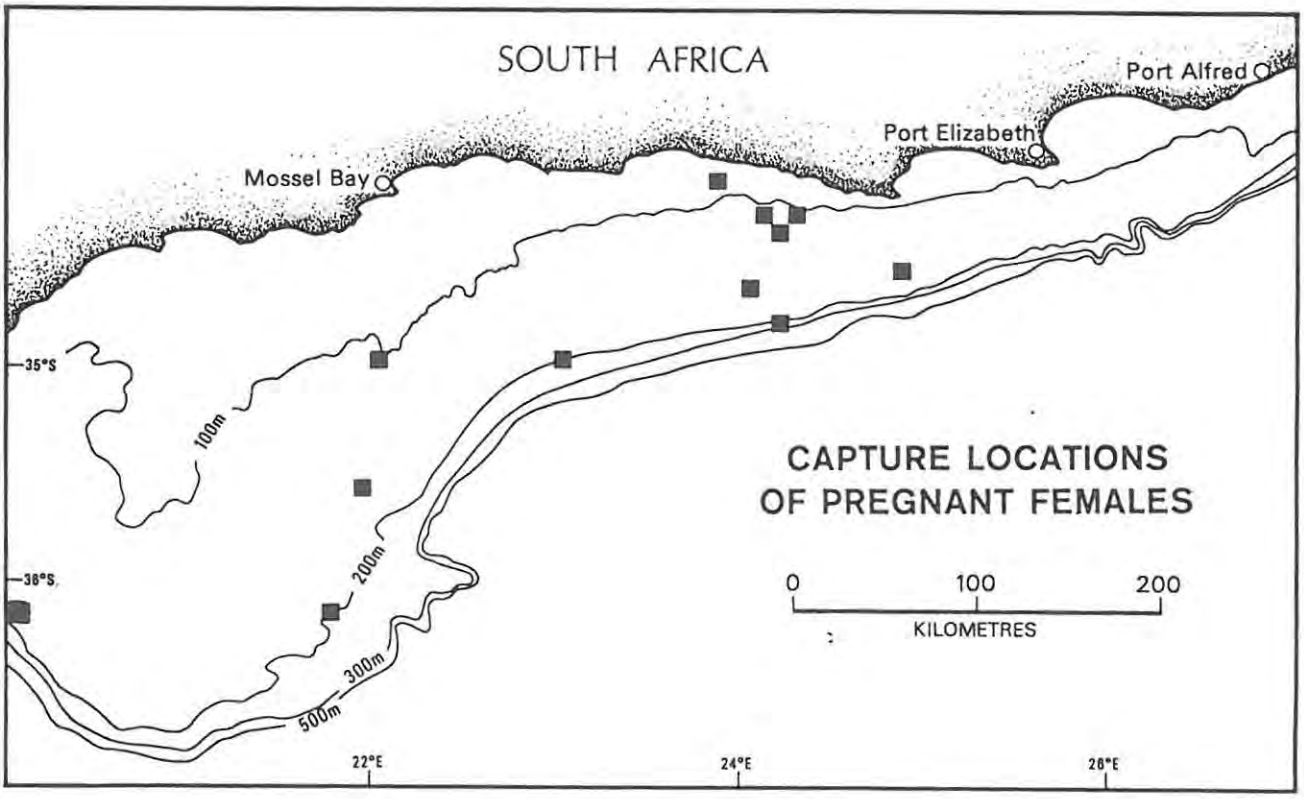


Figure 3.11: Capture locations of pregnant female *R.wallacei*

3.4 - Discussion

All skates are oviparous, showing similar patterns of gonad development, spawning behaviour and embryonic development worldwide (Wourms, 1977).

Spermatogenesis occurs in follicles in the testes suspended from the abdominal cavity by mesorchia (Parsons and Grier, 1992). Development begins on the dorsal surface but as spermatogenesis proceeds, the follicle migrates to the ventral surface where mature spermatozoa are released into the efferent duct (Plate 3.2)(Pratt, 1988). All cells in each follicle are at the same stage of development (Hara and Tanaka, 1990; Parsons and Grier, 1992). The vas deferens carries the sperm to the seminal vesicle where sperm are mixed with seminal fluid (Dodd, 1983). The clasper gland, which produces a viscous white fluid, also empties into the seminal vesicle. This fluid coagulated on contact with seawater and may seal the margins of the clasper groove and aid in sperm suspension and transport (Wourms, 1977). The seminal fluid and sperm are carried via the urogenital sinus and urogenital papilla to the clasper that is then used to transfer them to the female. (Wourms, *op cit.*). The claspers are formed by folding of the pelvic fins and are stiffened by calcified rods in the mature male (Gilbert, 1981). Alar spines are seen on the pectoral fin margin in mature males and are thought to aid in holding the female during copulation (Richards *et al*, 1963).

Steven (1934), studying maturation in live *R.clavata*, reported the same pattern of linear clasper growth followed by a rapid rise as seen here in *R.wallacei* and *R.pullopunctata*. He also reported a similar trend in the cloaca length of females.

Copulatory behaviour has rarely been observed in the wild but has been recorded several times for captive specimens. (Le Danois, 1949 in Richards *et al*, 1963) reported that *R.erinacea* mate ventral sides opposed with both claspers inserted. However, most reports suggest that this is atypical (Libby and Gilbert, 1960; Price, 1967; Luer and Gilbert, 1985). All three studies report that the male bites the trailing edge of the female pelvic fin, swings his tail under hers, flexes his clasper 90° inwards and inserts it into the female cloaca. If the right pelvic fin is being held, the right clasper is inserted. It may take an hour for full clasper insertion. (Luer and Gilbert, 1985).

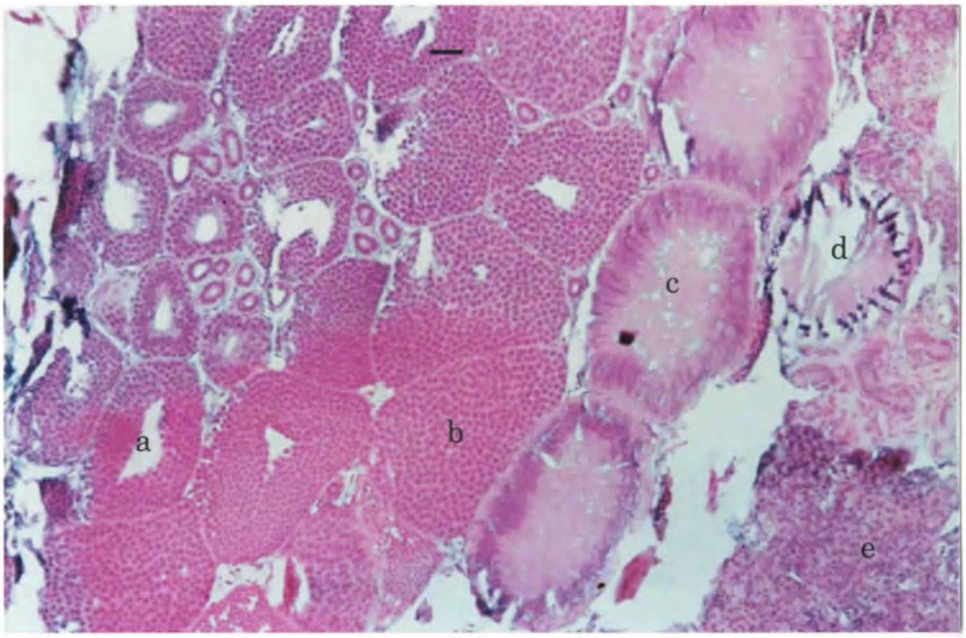


Plate 3.2: Sectioned testis of a stage 3.5 male *R.wallacei*, 410mm DW, showing the formation and migration of the seminal follicle or spermatocyst. (Parsons and Grier, 1992) across the testis. A=Spermatocyst comprising a central clear area surrounded by secondary spermatogonia, B=Spermatocyst containing spermatids, C=sperm, D=Mature spermatocyst, E=degenerating zone.

Sperm transfer is slow and copulation may last hours. This contrasts the sharks in which copulation may take only a few minutes due to the possession of siphon-sacs (Gilbert and Heath, 1972).

Sperm travel up the female genital duct to the nidamental gland, the site of egg fertilization, egg-case formation and sperm storage (Richards *et al*, 1963). Ovulation occurs when the egg is either one-third (Richards *et al, op cit.*) or fully (Templeman, 1982) formed. The egg drops into the case and is surrounded by a viscous gel to protect it. The rest of the egg-case is formed around it.

The egg-cases of *R.wallacei* begin formation at the anterior end, similar to *R.erinacea* and *R.eglanteria* (Fitz and Daiber, 1963). This is in contrast to *Bathyraja aleutica* in which development begins at the posterior end (Teshima and Tomonaga, 1986).

As with many other skate species, all *R.wallacei* egg-cases contain a single egg (Richards *et al*, 1963; Du Buit, 1976; Teshima and Tomonaga, 1986). Only the egg-cases of *R.binoculata* are reported to contain more than one egg (Hitz, 1964 in Teshima and Tomonaga, 1986). Richards *et al* (1963) reported that in the rare instances of an egg-case containing two eggs, its twin was empty, suggesting that multiple oviparity may be a mistake rather than a deliberate strategy.

Typically the right case is deposited first (Fitz and Daiber, 1963; Richards *et al*, 1963; Luer and Gilbert, 1985). Since only 5 *R.wallacei* had a single egg-case in the genital tract, conclusions about which is laid first cannot be made.

Studies have shown skates can produce year-round (Clemens and Wilby, 1949; McEachran, 1970; Du Buit, 1976). Richards *et al* (1963) reported that breeding, as characterised by uterine wounds, took place all year with peaks in pregnancy in November-January and June-July. These peaks corresponded to peaks in gonad mass. Fitz and Daiber (1963) reported similar trends for *R.erinacea* and *R.eglanteria*. They also reported that males carry sperm from maturity to death. Observations from this study on *R.wallacei* males concur with the findings of Fitz and

Daiber (*op cit.*). It is possible that the peak in egg-laying in the autumn ensures hatching in the spring when food is plentiful.

It is interesting that sperm production begins before the animal is physically capable of mating. Gross examination of immature seminal vesicles showed no evidence of sperm storage before the development of secondary sexual characters and no functional efferent duct was found. Although ruptured follicles were found in immature males it is likely that this was caused during the sectioning process. There was no evidence of sperm being released from the follicle in immature animals. This indicates that sperm and follicle development are halted before the latter rupture, storing the sperm within the testis. Why the animals should waste energy on producing sperm before they can use it is unknown. It may be that animals begin producing sperm and store it in the testes so that when they reach physical maturity, sperm are in abundance. This may explain the rapid increase in the percentage of follicles containing sperm with increased maturity.

Seasonal data for females are less clear. All egg-cases were found in March-May and there was no evidence of egg-laying outside these months. However, since the sample size was limited (only 24 females with egg-cases present) this cannot conclusively be termed a spawning season. Ishiyama (1958b) reported that the egg-cases of a given species are of a standard size and shape and may be used for taxonomic purposes. Analysis of the characteristics of *R.wallacei* egg-cases suggests that little variation exists around each parameter and these may also be used fir identification purposes.

Several authors have reported on the deposition of fertile egg-cases some time after isolation from mature males, indicating sperm storage to eliminate the need of finding a mate before ovulation. Clarke (1922) reported that a female *R.clavata* laid a pair of egg-cases one month after isolation. Histological examination of mature *R.wallacei* nidamental glands showed no evidence of sperm storage.

There was no evidence of specific spawning grounds (Chapter 5), although pregnant females were too rare to make definite conclusions. It is possible that females travel to rocky areas unsuitable for trawling to deposit their egg-cases and that such areas have been missed by the sampling procedure. However, Steven (1936) reported that tagging experiments indicate skates are sedentary and do not migrate far from the place of mating to lay their egg-cases.

Incubation may take as little as 3 months (Fitz and Daiber, 1963) or in very cold waters (-3-0.5°C), as long as 5-6 years (Berestovskii, 1994). A fully-formed juvenile that closely resembles the adult eventually hatches.

The samples obtained from commercial trawlers were largely composed of immature or maturing fish. The proportion of very large, mature animals was low. Only 7 mature male *R.pullopunctata* were encountered during the entire study. The largest *R.pullopunctata* sampled measured only 745mm DW. This is some 20cm smaller that the maximum size indicated by Compagno *et al* (1989) and 10cm DW smaller than the L_∞ generated from the growth data. Although the number of large animals in a population would be expected to be low and the sample sizes were limited, disc-width frequency data (Chapter 5) seems to suggest that the large end of the distribution is skewed away from the normal.

It is likely that commercial operators would have retained smaller animals for the study since these take up less space and that commercial samples may not have been entirely representative. Since the commercial observer data did not include length-frequency measurements, the actual length-frequency distributions aboard these vessels could not be investigated. However, a similar lack of large animals was seen in the research samples. This may suggest that both species may be suffering from growth overfishing or that mature animals migrate to areas other than those targeted in the research trawls. The distribution of research-caught animals was investigated to determine whether large animals migrate down the continental slope, beyond the range of research trawls (Chapter 5). No evidence of such a migration was found. It is possible that the larger animals are found elsewhere along the South African coastline such as the east coast. Experimental trawls would be required to test this. It is also possible that large animals are evading the net. However, since large *R.alba* of over 1m SW are caught in both research and commercial trawls (pers. obs.), this appears unlikely.

Due to their body shape, skates are likely to be highly vulnerable to fishing. Although the minimum stretched mesh size for offshore trawlers on the south coast is 85mm, this is likely to afford little chance of escape. Both species are probably vulnerable to fishing shortly after birth. Although they are hardy animals the survival rate will be reduced by the stress of capture, lying in the sun, temperature changes and time spent on deck. Such losses due to fishing are likely to impact on stocks.

Holden (1977) suggested that skates should be able to contend with high levels of fishing pressure. Deriving a formula for Z', the average total mortality rate over the lifespan at which stock replacement will occur, he used data from an unexploited skate population to calculate that skates have a high natural mortality - 0.65 in *R.erinacea*. He compared this with estimates of total mortality of *R.clavata* and concluded that a high average mortality is a feature of rajids. He suggested that mortality in juveniles of less that one year old is extremely high and that for older animals is not higher than 0.3. Using Fitz and Daiber's (1963) data for *R.erinacea* in Block and Long Island Sounds, which were unexploited, he calculated that each female only needed 2 eggs per year to survive to one year for the population to replace itself. Likewise, he calculated that for exploited *R.clavata* populations, 8.5 eggs needed to survive.

The only other estimates of mortality in skates are those of Waring (1984) on *R.erinacea*, a species frequently taken as by-catch and discarded in the mid-Atlantic and New England trawl fisheries. Waring (*op cit.*) calculated values of 0.4-0.5 for natural mortality and 0.72-1.81 for total mortality for *R.erinacea* from the Georges Bank-Delaware region. Although Waring's (1984) estimates of natural mortality are similar to those obtained by Holden (1977), total mortality from fishing pressure is very high. This would indicate that more than 2 egg-cases per female would be required to reach one year old for the population to replace itself.

This high mortality has consequences for the study species. Although they are only exploited as discards, they may be suffering from the same elevated mortalities as *R.erinacea*, requiring the survival of more eggs per female per year for the populations to replace themselves. If the number of mature females is being reduced by trawling operations as the data suggest, the ability of populations to produce these egg-cases may be impaired.

CHAPTER 4

FEEDING BIOLOGY

4.1 - INTRODUCTION

The chondrichthyan group ranks among the apex marine predators, a consequence of diverse feeding strategies and a variety of feeding mechanisms (Moss, 1977). Stomach content analysis is important not only for describing the diet of a species but also for assessing trophic interactions within communities (Hyslop, 1980).

The bottom-dwelling skates have developed short heavy jaws and small close-set, plate-like teeth enabling them to exploit hard-shelled invertebrates and fish by grasping or sucking and crushing (Moss, 1981). There have been relatively few dietary studies on the 25 recognised species of South African skates (Compagno *et al*, 1989). However, results suggest that crustaceans and benthic fish are the main components of the diet (Ebert *et al*, 1991; Smale and Cowley, 1992). Furthermore, there tends to be a shift in the crustacean component from amphipods and mysids to larger prawns and crabs as predator size increases. This trend has also been reported elsewhere (Ajayi, 1982; Gordon and Duncan, 1989; Berestovskiy, 1990; Pedersen, 1995).

Other dietary studies indicate that crustaceans and benthic teleosts are also preyed upon by commercially important members of the South African demersal teleost community such as Cape gurnards, *Chelidonichthys capensis* (Meyer and Smale, 1991a&b). It is likely that there will be competition for resources by animals caught in the same area. It is also possible that regular trawling by the commercial fleet may result in greater availability of prey items and/or cause depletion of food sources by repeated disturbance of the benthos (Kennelly, 1995).

The aim of this study was twofold:

1. To describe and compare the diets of *R.wallacei* and *R.pullopunctata* taken from both research and commercial trawls, determining whether temporal or spatial, sexual, size or seasonal differences affect the diet. Also, since most published South African data are derived from research trawls only, a comparison was made between commercially-caught and research-caught animals to determine whether bias exists between the two sampling strategies.

2. To compare the diets of these skate species with other demersal-feeding species to make an assessment of the position of these two skates within the trophic web.

This work forms part of a wider research programme investigating by-catch and discards from commercial trawlers in South African waters to assess the potential for greater use of currently underutilised species. The observation of commercial trawls will hopefully allow a better understanding of food web interactions on commercial fishing grounds rather than areas historically only during research cruises.

4.2 - MATERIALS AND METHODS

Research samples were obtained during one west and two south coast hake biomass cruises aboard the *FRS Africana* during April-May and Sept-Oct 1995 and Jan-Feb and April-May 1996 (Figures 4.1 and 4.2). A description of sampling strategies used in this twice-yearly survey is given in Badenhorst and Smale (1991). Trawls lasting approximately 30 minutes were executed using a German 180-foot bottom trawl during daylight hours only. The cod-end was lined with pilchard netting to prevent the loss of smaller individuals. Sampling locations from the west coast are shown in Figure 4.1 and from the south coast in Figure 4.2. Further samples were obtained from animals caught by the commercial trawlers operating from Port Elizabeth and along the west coast of South Africa.

Once sorted, weighed and measured, the animals were dissected and the contents of each stomach placed in a labelled jar with 4% buffered formalin to prevent further digestion (Windell and Bowen, 1979). The contents of the spiral valve were liquid and therefore discarded.

Prey items were sorted to the lowest possible taxon. For each stomach the proportion contributed by each prey item, as compared with an arbitrarily chosen item, was recorded in order for percentage volume to be calculated. The contents were dried to constant mass at 60°C and weighed to four decimal places.

No one method of describing contents is wholly unbiased (Hynes, 1950; Windell and Bowen, 1979; Hyslop, 1980), as numerical methods overemphasise the importance of small prey items and gravimetric measurements are biased towards large prey items that take longer to digest. Consequently, the following were calculated for each prey item: -

Percentage frequency of occurrence (%FO) - the proportion of stomachs containing a given prey item.

Percentage volume (%V) - the volume of each prey item, compared with the total volume of all stomach contents.

Percentage mass (%M) - The total weight of each prey item, compared with the total weight of all stomach contents.

An Index of Relative Importance, such as that of Pinkas *et al* (1971) was not calculated. Rather %FO, %V and %M were assessed separately to avoid bias from combining methods. Data were analysed by sex, season, and between the east and west Agulhas Bank as separated by the 22°E line of longitude.

Predators generally aim to derive the highest energy return from hunting. It is therefore possible that body size will affect diet composition. It is also possible that habitat preference will change during the life of an animal and that diet will change accordingly. To investigate this, reproductive data were examined to determine the size ranges of three groups of individuals - immature, maturing and mature. Diet composition was investigated for these three groups. Data were divided in this fashion as real changes in the life history were deemed more useful than splitting data at an arbitrarily chosen disc width. Data were sorted into <300mm DW, 3-400mm DW and >400mm DW (*R.wallacei*) and <400mm DW, 4-500mm DW and >500mm DW (*R.pullopunctata*) groups for immature, maturing and mature animals respectively.

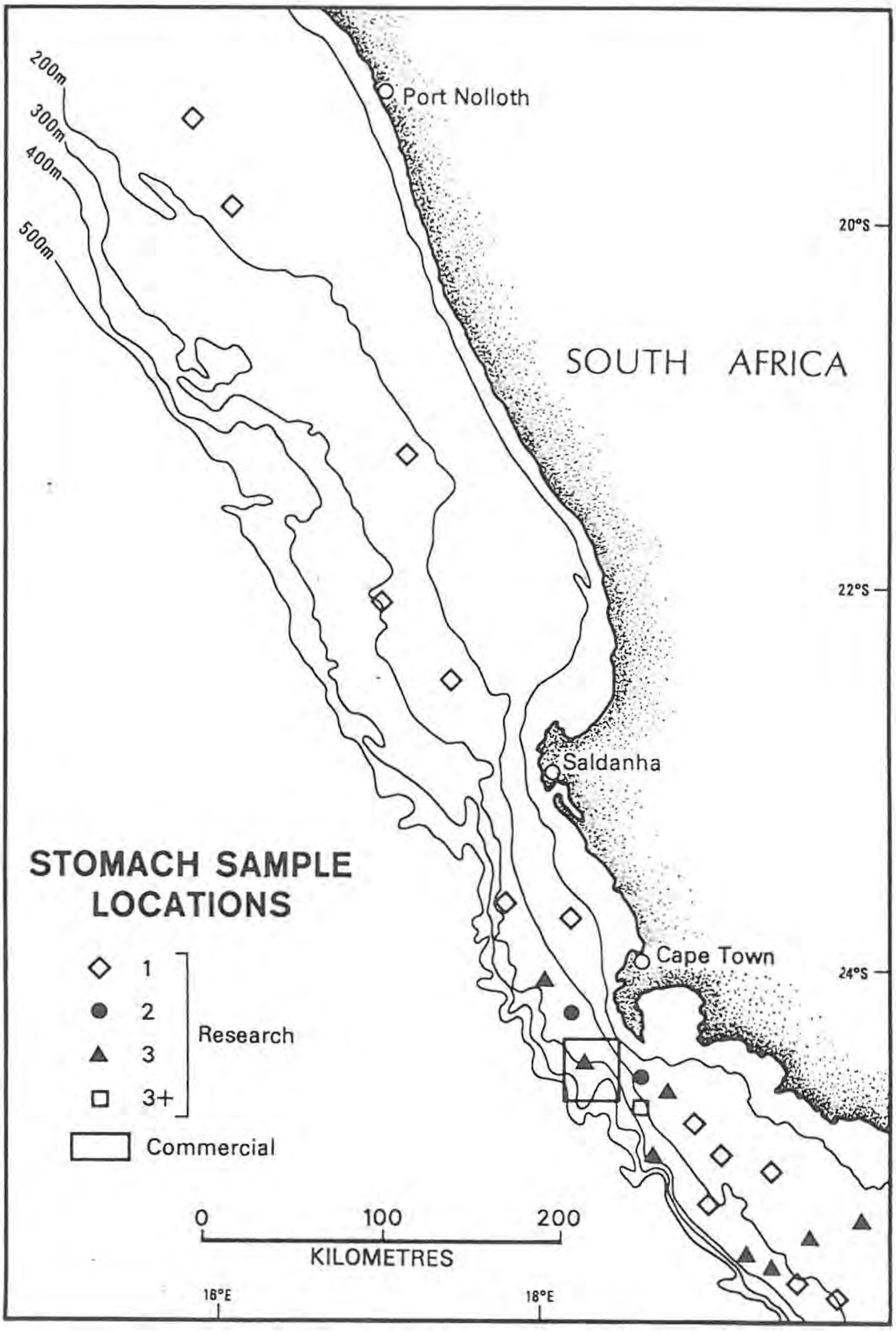


Figure 4.1: Sample sites of research and commercially-caught *R.pullopunctata*, indicating the number of samples from each grid square: ◇ = 1 research sample; ● = 2 research samples; ▲ = 3 research samples; □ = 3+ research samples; large square indicates trawl grid from which all commercial samples were obtained.

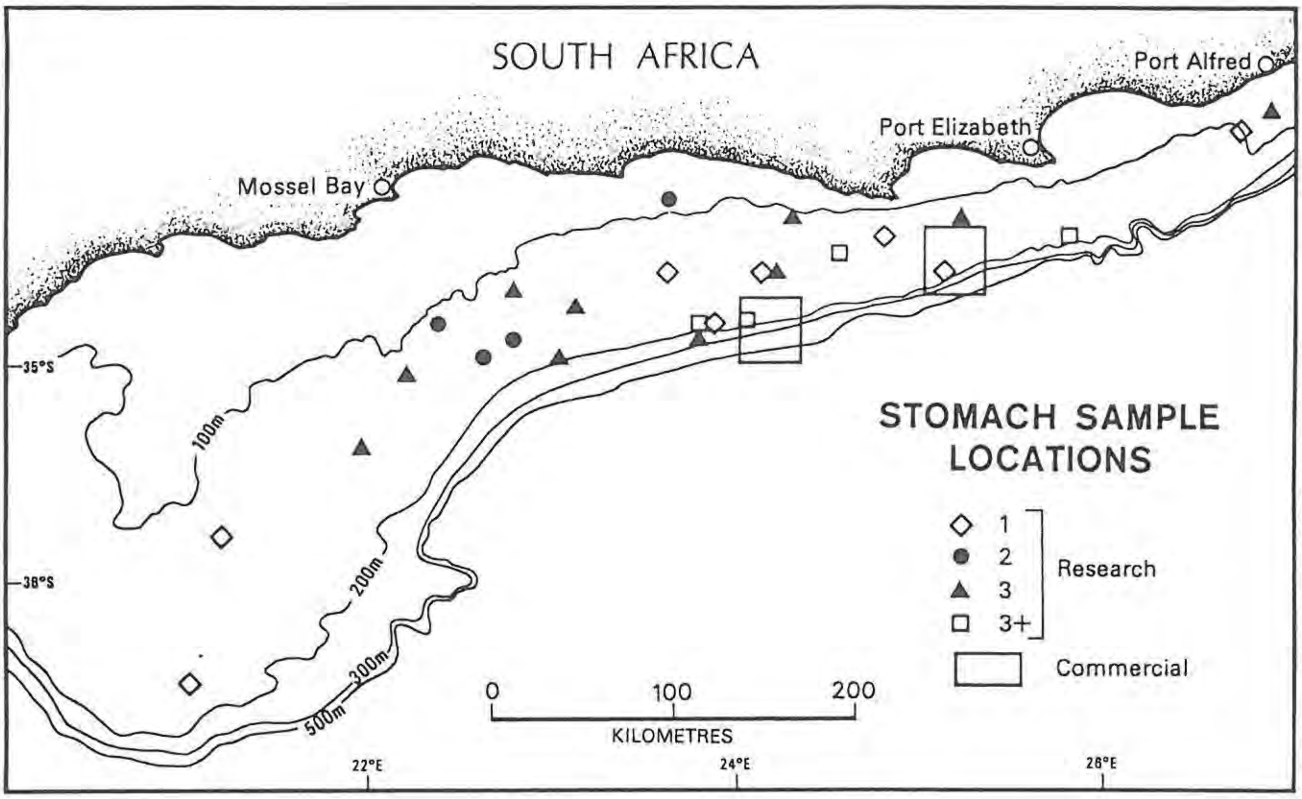


Figure 4.2: Sample sites of research and commercially-caught *R.wallacei*, indicating the number of samples from each grid square: ◇ = 1 research sample; ● = 2 research samples; ▲ = 3 research samples; □ = 3+ research samples; large squares indicates trawl grid from which all commercial samples were obtained.

Total south coast data (research trawls only) was compared with the data published by Smale and Cowley (1992) to determine whether the diet has changed over the last decade. In their study, Smale and Cowley (1992) also collected stomachs from research cruises but often contents were identified only to family and were weighed wet on a triple beam balance. Since differences exist between commercial and research data (see below) only research data collected during this study was used for comparison.

4.3 - RESULTS

Composition of the diet

A total of 217 *R.wallacei* (119mm DW-574mm DW) and 130 *R.pullopunctata* (130mm

DW-732mm DW) were obtained. Total %FO, %V, %M data of prey items found in all stomachs combined for both species are shown in Table 4.1.

Teleosts and crustaceans were the most important prey groups for both species. The conger, *Gnathophis sp.* was the most important identifiable teleost present in the *R.wallacei* diet (FO=25.59%, V=17.24%, M=52.78%). The dragonet, *Paracallionymus costatus* was present almost as frequently (FO=22.37%) but did not make a major contribution in terms of mass (M=5.9%). Overall, teleosts were found in 73.52% of all *R.wallacei* stomachs, constituting 49.53% of the volume and 89.92% of the mass.

In the *R. pullopunctata* diet, *P.costatus* dominated the teleost portion (FO=29.23%, V=13.12%, M=12.09%). Overall, teleosts were taken more frequently in this species (FO=80%) but were not as important in terms of volume or mass (V=41.06%, M=63.14%). *Sardinops ocellata* heads and tails and *Merluccius capensis* heads were taken by both species, suggesting scavenging may take place. A large portion of the teleost component, however, was unidentifiable in both species.

Crustaceans were taken frequently by *R.wallacei* (FO=69.41%) but were unimportant in terms of mass (M=6.4%). Amphipods, mysids, carid shrimps and brachyurans were taken with similar frequency. The orange-eyed mysid was the most frequently taken identifiable species (FO=22.92%) but was insignificant in terms of mass (M=0.64%). The masked crab, *M.cristimanus* (FO=54.62%, V=21.72%, M=17.33%) dominated the brachyuran component of the *R.pullopunctata* diet. Carid shrimps were taken more frequently and in similar volumes to the brachyuran component but contributed less than half the mass (FO=56.92%, V=21.64%, M=7.35%).

The *R.wallacei* diet was more diverse than that of *R.pullopunctata* with 53 and 24 different species identified, respectively.

Nematode parasites were twice as common in the *R.wallacei* stomachs but were insignificant in terms of mass in either species.

	R.WALLACEI			*R.PULLOPUNCTATA*		
	n=217			n=130		
PREY SPECIES	%FO	%V	%M	%FO	%V	%M
NEMATODA	3.2	0.15	0	1.54	0.16	0.01
ANNELIDA						
POLYCHAETA	19.18	3.35	0.5	5.38	1.46	0
ARTHROPODA						
CRUSTACEA						
Crustacean remains	19.63	4.23	0.75	23.85	4.59	1.94
STOMATOPODA						
Mantid remains	0.91	0.57	0.06	1.44	0.6	0.11
P. armata capensis	1.83	0.67	0.37	0.77	0.41	0.3
ANOMURA						
Upogebia capensis	5.48	3.14	1.67	0.77	0.01	0
AMPHIPODA						
Amphipod remains	2.28	0.16	0.01	0.77	0.08	0
Ampelisca palmata	5.02	0.84	0.02			
Unid amphipod 2	0.46	0	0			
White	8.68	0.84	0.1			
Gammarid	0.46	0.04	0.02			
Paramoera capensis	0.91	0.01	0			
Orange-eyed	1.37	0.08	0.01			
Unid amphipod 3	0.46	0.02	0			
Lyianassa ceratina	3.2	0.42	0.04			
Stenopus hispidus				0.77	0.08	0
ISOPODA						
Isopod remains	2.74	0.29	0.07			
Orange-eyed	1.83	0.33	0.04			
Eurydice lonicornis	1.83	0.2	0.03			
Unid isopod 1	0.46	0.21	0			
Black-eyed	0.46	0.01	0			
Mesanthura canenlula	0.46	0.02	0			

Table 4.1: Prey composition of *R.wallacei* and *R.pullopunctata* stomachs (%FO=percentage frequency of occurrence, %V=percentage volume, %M=percentage mass).

MYSIDACEA (unidentified)						
Orange-eyed mysids *	22.92	8.6	0.64	11.54	2.4	0.11
Red-eyed mysids *	5.02	0.84	0.03	2.31	0.25	0.02
Black-eyed mysids *	1.83	0.21	0.01	0.77	0.06	0
CARIDAE						
Carid remains	5.02	0.76	0.06	18.46	4.35	1.26
Leptochela robustus	2.74	1	0.07	14.62	4.26	1.14
Pandalina brevirostris	0.91	0.31	0.27	10	4.08	1.03
Pontophilus sculptus	7.76	1.81	0.43	18.46	4.88	2.13
White shrimp	10.96	3.78	0.33			
Black-eyed shrimp	10.96	2.01	0.13			
Red-eyed shrimp	0.91	0.19	0.01			
Unid shrimp 2				1.54	0.57	0.22
Unid shrimp 3				15.38	3.13	1.5
Pink shrimp				1.54	0.37	0.06
BRACHYURIDAE						
Decapod remains	3.65	1.28	0.22	5.38	0.8	0.16
Mursia cristimanus	10.96	3.38	0.79	54.62	21.72	17.33
Shoveller	0.46	0.15	0.05			
Goneplax angulata	0.91	0.08	0.11	0.77	0.04	0.03
Crab megalopa	6.39	1.01	0.04	0.77	0.06	0.02
MOLLUSCA						
Ostracoda	0.46	0	0			
BIVALVIA	1.37	0.1	0.3			
GASTROPODA	0.91	0.11	0.04			
CEPHALOPODA	2.28	0.45	0.54	7.53	2.16	5.71
CHORDATA						
CHONDRICHTHYES						
Squalus sp.	0.91	0.24	2.37			
Raja pullopunctata	0.46	0.29	0.39			
Chondrichthyan egg-case	0.46	0.12	0.02			

Table 4.1 (Continued)

TELEOSTEI						
Teleost remains	36.53	14.93	8.21	56.15	21.3	28.87
Paracallionymus costatus	22.37	10.78	5.9	29.23	13.12	12.09
Gnathophis sp.	25.59	17.24	52.78	6.15	1.4	4.21
Bregmatoceros sp.	6.39	0.82	0.05	3.08	0.37	0.14
Pleuronectiformes	4.11	1.95	3.69	6.15	1.98	3.61
Anguilliformes	0.46	0.22	2.32			
Cynoglossus zanzibarensis	0.46	0.45	3.06			
Sardinops ocellata head	3.65	2.11	9.36	0.77	0.26	1.98
Sardinops ocellata tail	0.92	0.38	0.76			
Chelidonichthys sp.				0.77	0.67	3.44
Merluccius sp.				0.77	0.77	4.31
Merluccius capensis head				1.54	1.2	4.5
AMORPHOUS MATERIAL	36.07	8.14	2.3	31.06	5.02	3.01

* The taxomony of mysids is currently under review, no scientific names are therefore given.

Table 4.1 (Continued)

Differences between Research and Commercially-Caught Animals

Data were divided between those animals caught during research cruises and by the commercial trawlers. Since differences between spring and autumn samples were minor (see below), data were not further split by season. No commercial *R.wallacei* data were obtained on the west coast or *R.pullopunctata* data on the south coast. Only south coast *R.wallacei* and west coast *R.pullopunctata* data are presented.

R.wallacei

The contribution by teleosts did not greatly differ between the diets of the commercial and research catch (Figure 4.3, Appendix A), although the proportions of the various components did. A contingency table showed that *P.costatus* was significantly more important in the research diet in terms of volume ($p=0.0004$) but not in terms of mass. *Bregmatoceros sp.* and *C.zanzibarensis* did not occur in the commercial samples. The importance of *Gnathophis sp.* was not significantly affected by diet source. The crustacean component greatly differed between commercial and research data. Although the contribution of crustaceans by mass was similar in the two diets, they were less frequent and contributed only two-thirds the volume in the commercial samples. Mysids, prawns, isopods, mantis shrimps and amphipods were all reduced in the commercial trawls. A decrease in species diversity and an increase in scavenged fish heads and tails was noted in the commercial diet.

Contingency table analysis (Cortes *et al*, 1996), aimed at looking at the difference in the proportions of 13 prey groups to the research and commercial diet was performed on the identified prey species. The results are shown in Table 4.2. Prey groups used for the analysis were: - nematodes, polychaetes, amphipods, isopods, mysids, brachyurans, carids, other crustaceans, molluscs, *P.costatus*, *Gnathophis* sp., trawler offal and other fish species. Significant differences were seen in the percentage frequency of occurrence and percentage volume of the proportions of prey groups. The percentage mass of prey groups did not significantly differ between the research and commercial trawls.

	χ^2	df	P-value	Significance
R.wallacei				
%FO	41.67	12	<0.05	*
%V	94.42	12	<0.05	*
%M	20.14	12	>0.05	
R.pullopunctata				
%FO	33.86	5	<0.05	*
%V	27.23	5	<0.05	*
%M	43.01	5	<0.05	*

Table 4.2: Results of contingency table analysis comparing the proportion contribution of 13 (*R.wallacei*) and 6 (*R.pullopunctata*) prey groups in the diets of research and commercially-caught animals. (%FO=percentage frequency of occurrence; %V=percentage volume; %M=percentage mass; * indicates significant difference between diets).

R.pullopunctata

The commercial diet was dominated by teleosts, a large portion of which was unidentifiable (Figure 4.4). This was probably due to the length of time the animals were on ice before the stomachs were removed, allowing digestion of the contents. Differences between the fish components could therefore not be ascertained.

Crustaceans occurred frequently in both research and commercial stomachs but were less important in terms of mass in the latter (research M=42.47%; commercial M=12.60%). As with *R.wallacei* on the south coast, the importance of mysids, prawns and mantis shrimps was reduced in the commercial catches.

Contingency table analysis was performed using 6 groups, reflecting the lower prey diversity in the *R.pullopunctata* diet and the difficulties with identifying commercial stomach samples. Prey groups used for this analysis were: - nematodes, carids, brachyurans, other crustaceans, trawler offal and other fish species. The results showed significant differences between the research and commercial diets in terms of percentage frequency of occurrence, percentage volume and percentage mass (Table 4.2).

A decrease in species diversity was noted. The research diet comprised 16 species compared with only 8 in the commercial diet. However, this difference may be attributable to difficulties in identifying the components of the commercial diet.

Differences between the East and West Bank

The Agulhas Bank was split along the 22° line of longitude to determine whether feeding patterns change with location.

R.wallacei

Teleosts occurred in greater than 75% of the stomachs in the eastern half of the Bank but in only 59% of those in the west. The volume contributed to the diet was also greater but in terms of mass, teleosts were similar across the Bank (Appendix B). The dragonet, *P.costatus*, and *Bregmatoceros sp.* were more important in the eastern half. *Gnathophis sp.* was similar in terms of %FO and %V but contributed more to the western Bank diet in terms of %M. Species diversity was reduced in the west with 21 species identified, compared with 43 in the east. The importance of each crustacean group was similar over the Bank, with any differences being minor ones. As with the teleosts, crustacean diversity was also reduced in the west.

R.pullopunctata

As with *R.wallacei*, teleosts were more important in terms of %FO and %V in the east but were similar in terms of %M. Again, the importance of *P.costatus* was reduced in west Agulhas Bank samples but this difference could not be tested statistically as *P.costatus* occurred in only 6 west Bank stomachs. The importance of *Gnathophis sp.* and *Bregmatoceros sp.* was not notably different across the bank. Crustaceans were equally important in both areas and differences between the various groups were not large. Again, a reduction in species diversity was seen in the west coast samples.

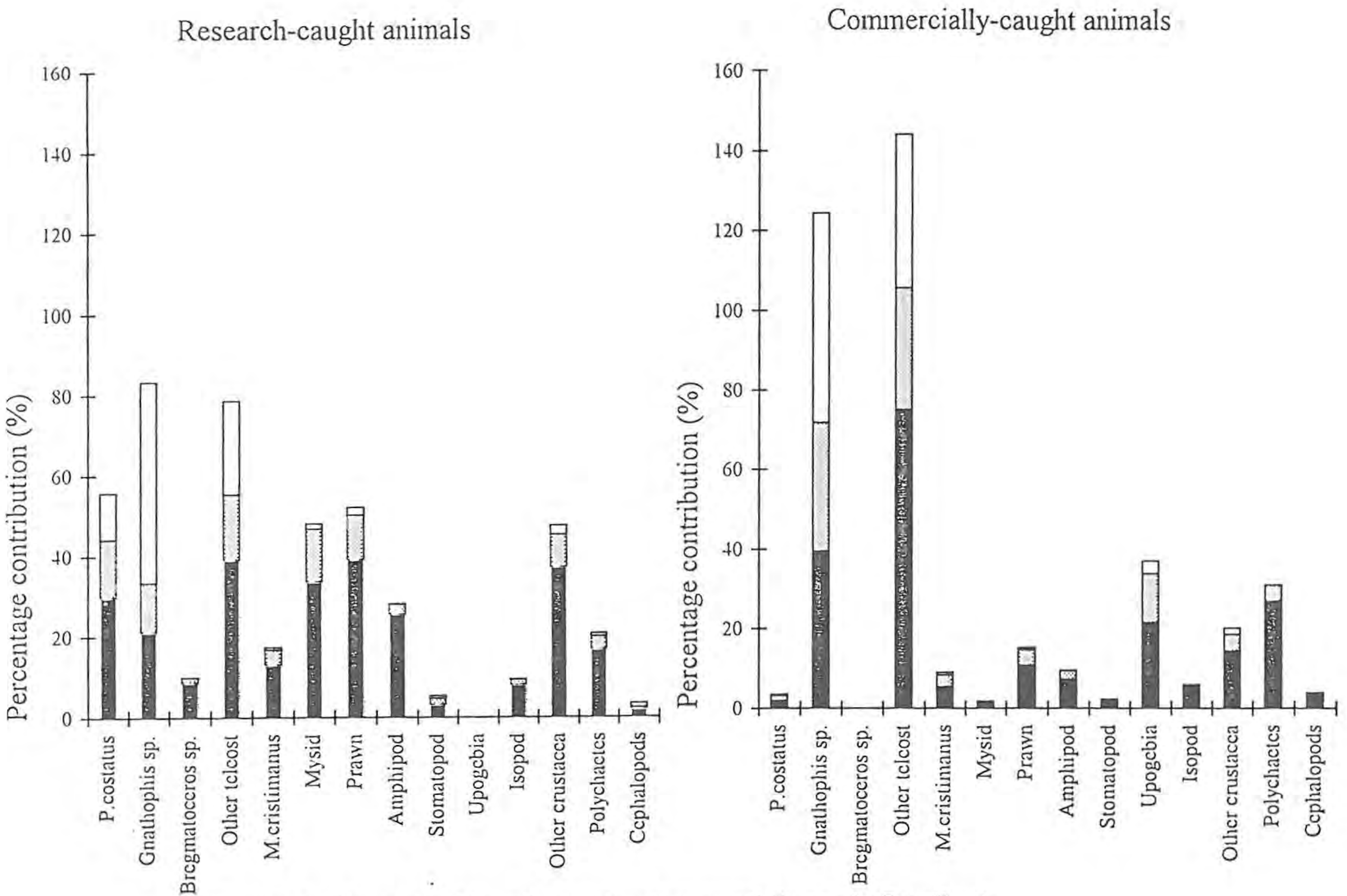


Figure 4.3: Diet composition of research and commercially-caught *R.wallacei*

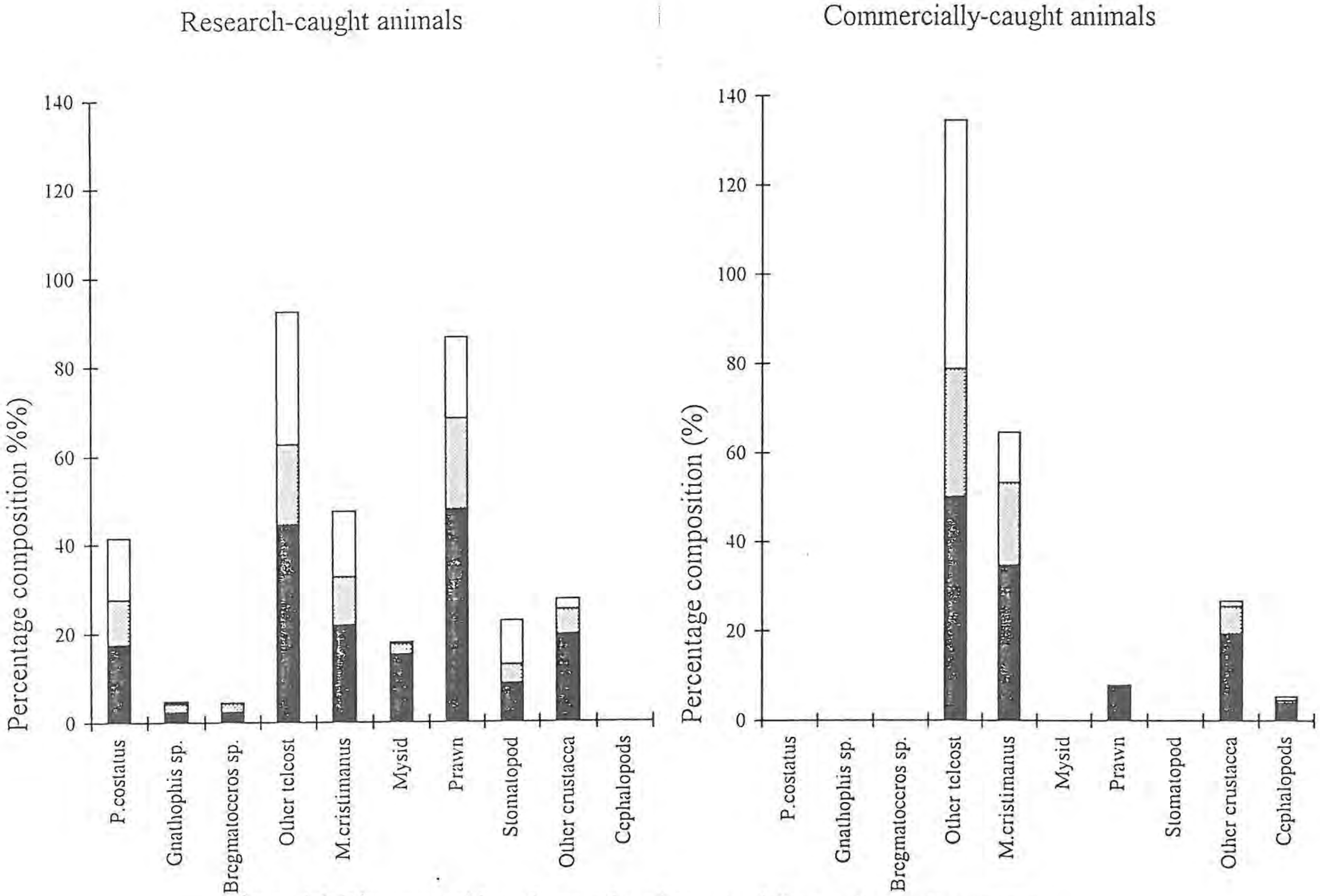


Figure 4.4: Diet composition of research and commercially-caught *R.pullopunctata*

Effect of Body Size on the Diet.

Data were split into immature, maturing and mature categories.

R.wallacei

Diet composition was greatly affected by predator size (Figure 4.5, Appendix C). The %FO, %V and %M of *Bregmatoceros sp.* and *P.costatus* decreased with maturity, while the importance of *Gnathophis sp.* increased. Overall, the importance of teleosts increased with disc width. Immature *R.wallacei* took a range of small crustaceans such as mysids, isopods and amphipods but these were all absent from the diet in mature animals. *M.cristimanus*, prawns and stomatopods were taken by larger animals but were relatively unimportant.

R.pullopunctata

As with *R.wallacei*, a decrease in the importance of *P.costatus* and *Bregmatoceros sp.* and a concomitant increase in *Gnathophis sp.* was seen. A similar increase in the importance of teleosts with disc width was noted (Figure 4.6, Appendix D). Mysids, stomatopods and carids decreased in importance and *M.cristimanus* remained relatively constant with growth.

Effect of Season on the Diet

Since there was a paucity of stomach contents for each month of the study, data were split into autumn (April/ May) and spring (September/ October) samples. Commercial data were omitted from the analysis.

R.wallacei

The diet showed few differences in composition between autumn and spring (Appendix E). Generally any differences observed were marginal. Prawns were significantly more important in terms of mass in the spring ($p=0.0005$) but were not significantly different in terms of volume.

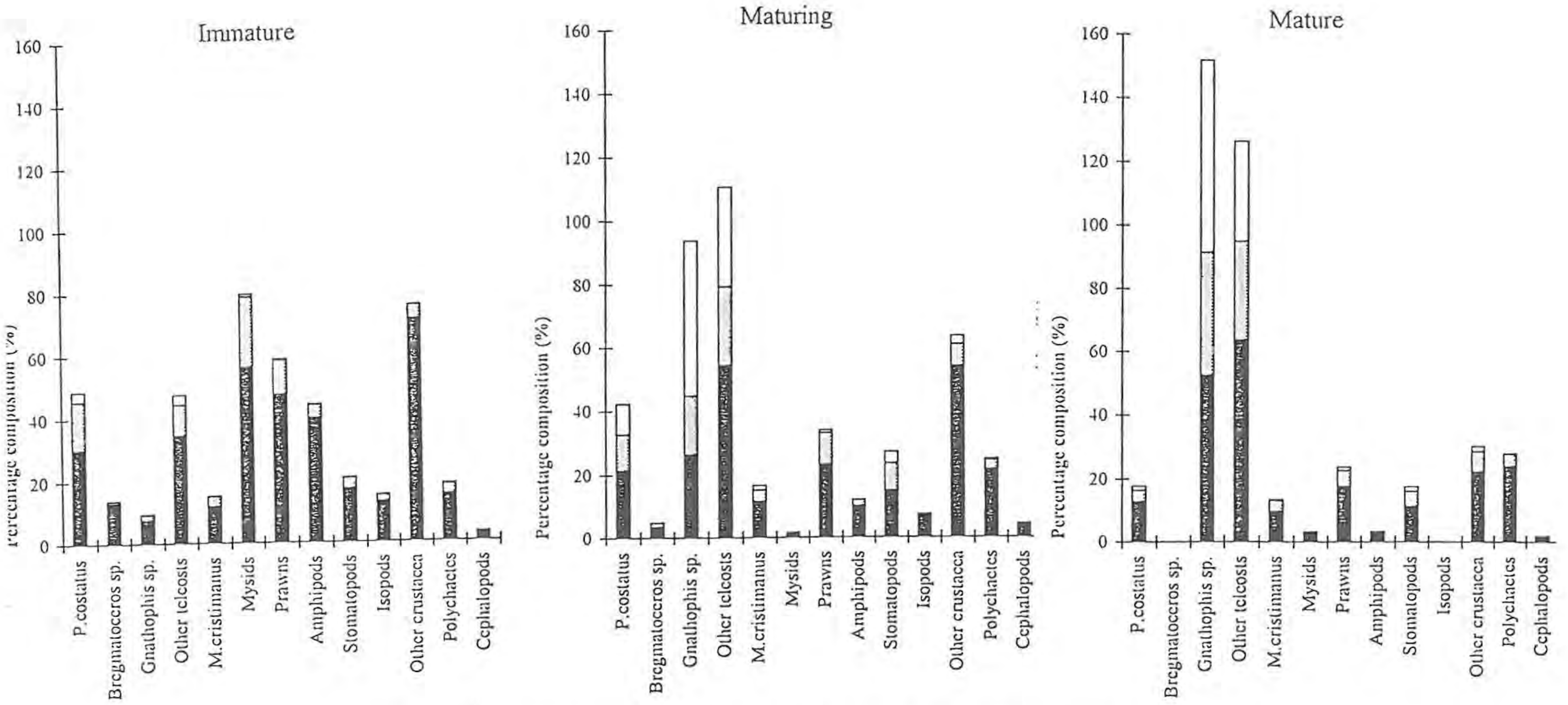


Figure 4.5: Diet composition of immature, maturing and mature *R.wallacei*

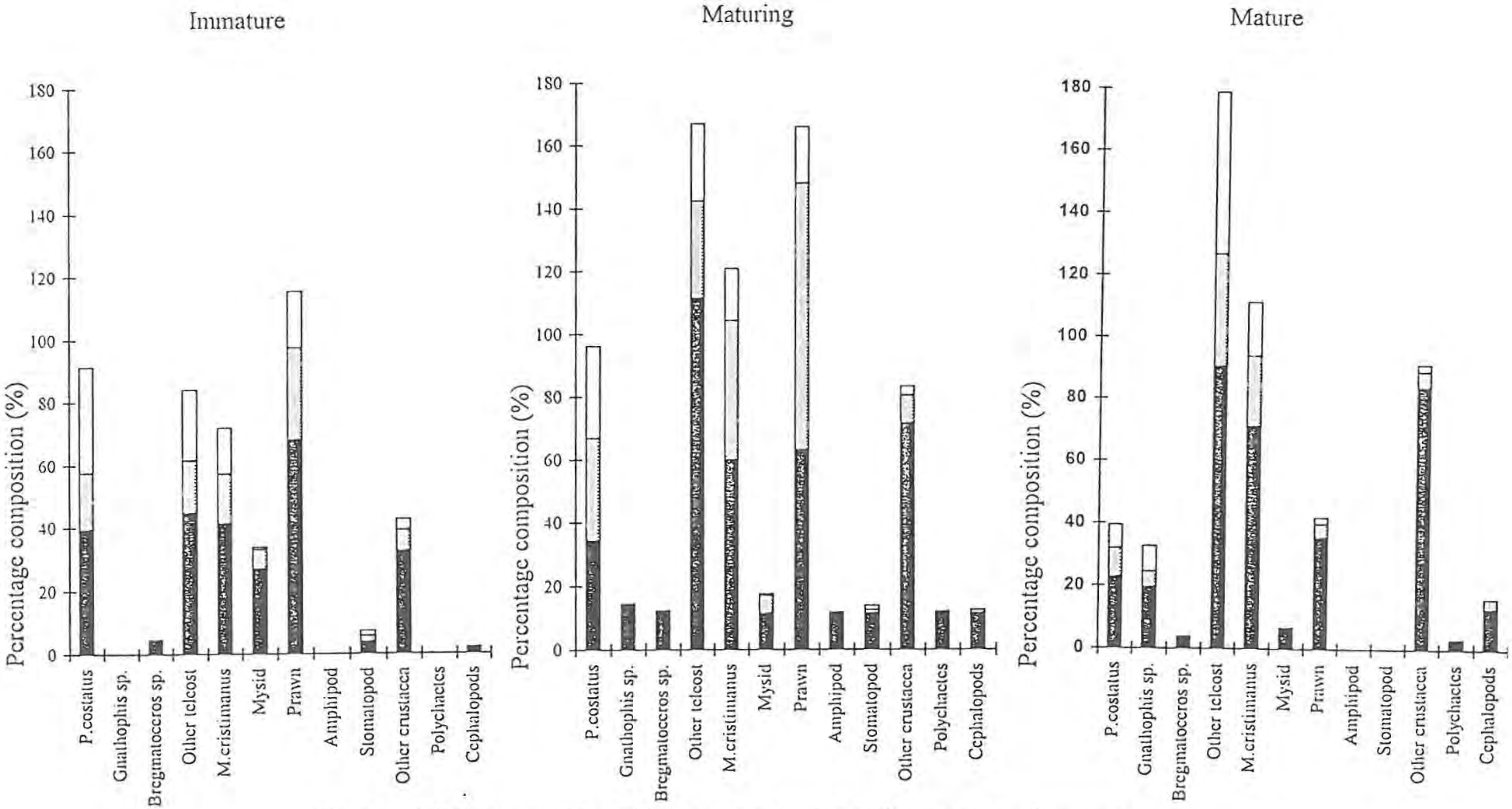


Figure 4.6: Diet composition of immature, maturing and mature *R.pullopunctata*

R.pullopunctata

As with *R.wallacei*, few differences were seen between the spring and autumn diets. Unfortunately, as few samples contained enough of a particular prey item to compare differences statistically, these differences could not be assessed.

The infestation of nematode parasites was unaffected by season in either species.

Differences between the Diet of Males and Females.

R.wallacei

Differences between sexes were slight (Appendix F). However, nematode worms were found seven times more often in females than males and contributed a higher percentage volume.

R.pullopunctata

Few differences were found between *R.pullopunctata* males and females. *P.costatus* were taken as frequently by males and females but constituted a greater mass in the latter, while *Gnathophis sp.* constituted a greater mass to the male diet. However, since only 5 male and 5 female stomachs contained *P.costatus*, this difference could not be assessed statistically. Teleosts were more important to females and crustaceans more important to males.

Temporal Differences in the Diet

R.wallacei

The teleost components of the *R.wallacei* diet in both the Smale and Cowley (1992) study and the current study was dominated by *Gnathophis* and *P.costatus*. However, it would appear that the importance of *P.costatus* to smaller animals has increased while the importance to the diet of larger animals has decreased. In the current study, *P.costatus* contributed FO=29,8%, M=30.9%; FO=21.3%, M=9.6%; FO=12.2%, M=1.4% in immature, maturing and mature animals respectively. However, Smale and Cowley (1992) reported lower values for the small size group (<350mm DW - FO=20%, M=13.05%) and higher figure for the larger group (>350mm DW - FO=11.5%, M=9.19%). The reverse is seen for *Gnathophis sp.* Results reported by Smale and Cowley (1992) of FO=6.67%, M=15.24% for small and FO=40.4%, M=33.72% for large animals. In the current study, FO=7.6%, M=1.8%; FO=26.2%, M=49.1%; FO=51.5%, M=60.3% for immature, maturing and mature animals, respectively.

The occurrence of shrimps has also altered between the two studies. Smale and Cowley (1992) reported that FO=88.89% and M=0.63% for carids in the smaller *R.wallacei* group and FO=1.92% and M=0.08% in the larger group. The present study showed that the frequency of occurrence has decreased since the Smale and Cowley (*op. cit.*) Study but that the percentage mass has increased (immature - FO=6.81%, M=4.54%; maturing - FO=22.95%, M=0.97%; mature - FO=19.2%, M=1.06%) for the same prey group.

R.pullopunctata

The diet of *R.pullopunctata* was also noticeably different between the two studies. Fewer teleost species were identified in the present study, with only 8 species compared with 19 by Smale and Cowley (*op. cit.*). *P.costatus* dominated both diets but *Gonorhynchus gonorhynchus* and *Cynoglossus sp.* which were important to the diet in the first study were absent from the diet in the present study. Differences in the importance of mysids, stomatopods, *M.cristimanus* and prawns seem marginal.

4.4 - DISCUSSION

The dorso-ventrally flattened body and ventrally situated mouth of the skates are indicative of a bottom-dwelling existence and analysis of the diet of *R.wallacei* and *R.pullopunctata* confirms they are opportunistic benthic predators. Benthic teleosts such as *Gnathophis sp.* and *P.costatus* dominate the diet along with the brachyuran *M.cristimanus* and carid shrimps. Such patterns have also been reported locally and worldwide (McEachran *et al*, 1976; Berestovkiy, 1989; Ebert *et al*, 1991; Pedersen, 1995).

The diet of four Namibian skate species was investigated by Macpherson (1986). As with *R.wallacei* and *R.pullopunctata* the diets were diverse, with up to 36 major prey items identified. Three species (*R.clavata, R.straeleni* and *R.doutrei*) fed mainly on fish, crustaceans and polychaetes with the importance of fish and large decapods increasing with predator size.

In his study of skates in the Bristol Channel, Ajayi (1982), found that the diets of *R.clavata* and *R.montagui* were dominated by crustaceans while that of *R.microocellata* was composed of crustaceans and teleosts. In the crustacean component of all three species, the sand prawn *Crangon crangon* dominated in small animals with a shift towards crabs such as *Carcinus maenas* and *Cancer pagurus* in larger animals. Dragonets, *Callionymus lyra* dominated the teleost portion of the diet. Likewise, Gordon and Duncan (1989) and MacPherson and Roel (1987) also found that diets were dominated by crustaceans, fish and polychaetes. A similar shift in the diet of small crustaceans and fish species to larger crabs and more mobile teleosts occurred in the study species. Analysis of the diet did not indicate a change in habitat during the life history of the skate. It is therefore likely that shifts in diet are a result of larger jaws and body size allowing the capture of more mobile and bigger prey items.

Few investigations have assessed the effect of seasons upon diet (McEachran *et al*, 1976; Berestovskiy, 1989; Pedersen, 1995). Pedersen (*op. cit.*) collected data during the summer and autumn of 1990 and 1991. Although the stomach fullness index was generally higher in the autumn-winter period, Pedersen (1995) could determine no clear differences between seasons. Daan *et al* (1993) in Pedersen (1995) also found no clear seasonal effects on the total fullness index of rajids in the North Sea. Differences observed in the present study were marginal and it is unknown whether they are because of seasonal changes in prey availability and/or the effects of prey preference. If shrimps are available in the spring only, the skates may be forced to consume *M.cristimanus* in the autumn although this species may not be the most favoured. Feeding preference studies and data on prey availability would determine this. To determine whether diet mirrors prey availability, sampling should take place over an extended period.

Studies have rarely examined differences in the male and female diet. Ebert *et al* (1991) reported that the teeth of adult male *R.wallacei* and *R.pullopunctata* are sharper than those of the females but they did not investigate whether this affected diet. It has been reported however that during mating, the male grasps the wing of the female in his mouth before swinging round to insert his clasper and that this may account for the dimorphism in dentition. The ability of the male to grasp the more active *Gnathophis sp.* may be an added advantage.

Smale and Cowley (1992) investigated the feeding biology of skates during research cruises between 1986 and 1990. Data from the present study were compared with their published data to determine whether temporal shifts in the diet had occurred.

Comparisons show that notable differences exist between the two studies. These differences may be interpreted in one of two ways. First, these discrepancies may be the result of natural changes within a dynamic system or they may be due to habitat loss through fishing and an indication that the food web is being forced to change. It is also possible that the differences may be due to a combination of the two reasons. A long-term study of species composition changes over a small, untrawled and commercially trawled area would answer some of these questions.

Comparisons between commercially and research caught animals in this study show large discrepancies on the south and west coasts. Possible reasons for this may be a) habitat structure may differ between the commercial and research grounds or b) commercial trawlers may be altering the benthos, reducing prey numbers and diversity over the fishing grounds. Without knowledge of substratum types over the shelf the plausibility of the first theory cannot be assessed. The validity of the second may be inferred from several observations. South coast data suggested that bottom-dwelling organisms such as *P.costatus*, *Bregmatoceros sp.*, carid shrimps and amphipods were the most seriously reduced while the more active *Gnathophis sp.* was not as greatly affected. If the benthos are being disturbed by trawling more active species may re-colonise the area faster than more sedentary ones. Further, although the importance of such small sedentary fish species is being reduced, the overall contribution of teleosts remains the same. This deficit may be largely made up by trawler offal such as heads and tails. However, the consumption of this offal may be a more energy-efficient method of food acquisition than the hunting of live prey and may have no bearing on the altering of the benthos.

Species diversity is considerably reduced in the commercial diet both on the south and west coasts. Since skates are opportunistic feeders, as indicated by the presence of scavenged trawler offal, the diet would be expected to reflect the species composition of the benthos. This would suggest that the species diversity over the commercial grounds is lower than the areas used during research cruises. Commercial vessels and research trawls are both confined to fishing on areas of sand, mud or low profile reef to avoid damaging the nets and species diversity should therefore be expected to be similar. Since this is not so, other explanations for the disparity in the number of prey species must be identified. One explanation is the that lowering of diversity is due to the modification of habitats or the availability of prey items. Modification of the diet of South African fish species from fishing pressure was also reported by Smale (1992).

Dietary studies usually use data obtained through research cruises. However, research is usually conducted in areas uneconomical or hazardous to commercial fishing gear. Since research trawls are usually of a shorter duration than commercial drags, This study has shown that it is likely that species diversity or abundance differs over commercial and research grounds. Care should be taken when interpreting data from one survey method only. The position of species in food webs and the interactions between members of the web cannot be accurately assessed if the diet is not accurately described. The benefits of the SANCOR observer programme are clearly shown by these findings. Sending observers to collect samples from grounds regularly fished by commercial trawlers will allow more detailed knowledge of food-web interactions in these areas to be obtained. Shifts in the diets of commercial and non-target species and increases in the level of competition can then be assessed.

Such a situation not only affects the study species but will affect all members of the food web. The sandrat, *Cynoglossus zanzibarensis*, feeds predominantly on polychaete worms (Meyer and Smale, 1991b). *R.wallacei* shows a shift towards polychaete worms on commercial grounds and is likely to compete with *C.zanzibarensis* for this resource. Although this species is currently discarded, it is caught in considerable numbers and it is likely that it will be retained in the future.

The cape gurnard, *Chelidonichthys capensis* and lesser gurnard, *C.queketti* are both bottom-feeding species. The diet of small cape gurnards is dominated by mysids and carid shrimps with a shift towards brachyurans and penaeids in larger individuals (Meyer and Smale, 1991b). Although not the dominant component, *M.cristimanus* is important in terms of mass for both size classes. *P.costatus*, *M.cristimanus*, mysids and carid shrimps are important components of the *C.queketti* diet. The main components of the gurnard diet are therefore similar to those of the study species. The cape gurnard is occasionally retained for the commercial market and there is potential for greater use. The lesser gurnard is currently discarded but as with the sandrat it may be utilized in the future. The monk, *L.vomerinus*, a commercially important by-catch species also feeds predominantly on *P.costatus* (SFRI unpublished data) and a decrease in prey availability is likely to bring it into competition with *R.wallacei* and *R.pullopunctata*.

The Agulhas Bank is a highly productive and extremely diverse area (Japp *et al*, 1994) in terms of fish and invertebrate species, supporting large demersal and pelagic fisheries. Although few commercial species directly compete with *R.wallacei* and *R.pullopunctata* for food, they are nevertheless part of the same food web. The destruction of prey habitats and reduction of prey abundance through trawling operations may have serious effects on population growth.

CHAPTER 5

DISTRIBUTION AND BY-CATCH

5.1 - INTRODUCTION

The Agulhas Bank and the west coast of South Africa support an abundance of fish species, many of which are endemic to these waters (Van der Elst, 1990). A diversity of substrates offers a profusion of niches to the many species present. On the Agulhas Bank, the inshore, soft sediment areas are dominated by the Agulhas sole, *Austroglossus pectoralis*, while rocky reef areas are home to species such as the red stumpnose, *Chrysoblephus gibbiceps*, (Japp *et al*, 1994). The offshore regions are dominated by the cape hakes, *Merluccius capensis* and *M.paradoxus*, with pelagic species such as the pilchard, *Sardinops ocellatus*, and anchovy, *Engraulis capensis*, also in abundance (Botha 1985).

The distribution and movements of many species are well known. Some species such as the geelbek, *Atractoscion aequidens*, make migrations around the coast growing as they do so and ending their journeys on spawning grounds (Griffiths & Hecht, 1995). Other species such as the panga, *Pterogymnus laniarius* have well-defined nursery areas (Booth *et al*, submitted).

Distribution and migration are important aspects of life history studies and are of special concern if a species is to be utilized. If exploitation occurs on nursery grounds or older individuals are targeted, the population may suffer from growth or recruitment overfishing as seen in the kingklip and pilchard fisheries (Punt and Japp, 1994; Thomas and Boyd, 1985), respectively. Likewise, targeting single-sex aggregations may have repercussions on the spawner stock, especially with females (Punt *et al*, 1993). Ideally, an accurate picture of the seasonal, spatial and depth distribution by size and/or sex through the year should be obtained before exploitation begins.

R.wallacei and *R.pullopunctata* are both common to the south and west coasts and are often recorded in demersal trawls. In contrast to the biscuit skate, *R.straeleni*, which is retained both species are discarded.

Although a species may not be targeted by the fishing industry, it may be indirectly exploited as by-catch or discarded. This may impact upon stocks, especially if survival is low or catches are significantly large (Waring, 1984). If by-catch species are long-lived or slow-growing even low fishing mortality may affect stocks. Analysis of kingklip data showed that trawling had probably depleted the stock to less than 50% of its pristine level before the beginning of long lining (Punt and Japp, 1994). Catches are likely to be influenced by the distribution of the population throughout the year, especially if the species in question is highly migratory and uses different areas for spawning, as nursery areas and as feeding grounds. An assessment of distribution is therefore vital when trying to assess the state of stocks.

Further, if a by-catch species is caught in sufficient quantities or can command a high market value there is the possibility that it could be utilized, as with the kingklip and monkfish.

The aims of this study were twofold: -

A) To investigate the distribution of the study species on the south coast, to determine the existence of any nursery areas and investigate any migrations that may occur.

B) To investigate the contribution that rajids make to the commercial catch and to assess whether any species shows the potential for further utilization.

5.2 - MATERIALS AND METHODS

Data were obtained from 3 sources: - research cruises; observers from the SANCOR by-catch programme on commercial vessels and historical commercial catch records. Demersal research cruises are conducted three times a year, once along the west coast and twice on the south coast of South Africa. Although the main aim is to collect biological data and biomass estimates for the two hake species, *Merluccius capensis* and *M.paradoxus*, all species are weighed and length-frequencies are taken for most of species caught within each trawl.

Observer data were collected as part of the SANCOR by-catch programme (Chapter 1). Briefly, 142 west coast trawls were observed and data on total catch and mass of by-catch species were gathered. Such data are valuable as they give a more accurate picture of the sizes and distributions of by-catch species within the commercial fishery.

Historical commercial data were obtained from the SFRI database. Such data is compiled from log books that skippers are required to fill in by law. Data collected for each trawl include details of the retained catch, grid location and trawling duration.

To investigate the size-based spatial distribution of the study species, disc width-frequency data were collected during 3 research along the south coast. As the survey uses a net lined with pilchard netting it is assumed that most individuals are retained and that trawls accurately reflect the size distributions of animals within each area. The cruises for which disc width-frequency data was obtained were 129 (4th-18th May 1995); 131 (28th September-20th October 1995) and 135 (10th April-2nd May 1996). Unfortunately, data were insufficient to investigate distribution along the west coast.

Using this research data, the size distribution by depth was investigated for both species. It was originally hoped that distribution could be investigated by longitude. Unfortunately, due to the small size of the data sets a high resolution analysis proved to be impossible and data were split by the 22°E line of longitude only. Differences in distribution in the spring and autumn, east and west of this line were investigated.

An indication of abundance by depth, by season and on the eastern and western areas of the Agulhas Bank was determined using the number of *R.wallacei* and *R.pullopunctata* caught per trawl. Since research cruises use the same net and trawl duration, data could be directly compared to obtain a simple catch per unit effort.

By-catch and discard data were collected from the SANCOR observer programme and research cruises. Grid number, time of shooting and hauling the net, starting and finishing latitude and longitude, trawling time and depth were recorded for each trawl. By-catch was sorted to the lowest taxon and each group or a sub-sample, weighed. Data on the total mass of fish landed were obtained to allow determination of the total catch. Data for all skate species were analysed from the commercial data. However, only the importance of *R.wallacei*, *R.pullopunctata* and *R.straeleni* to the research catch was investigated dur to a paucity of data.

To determine the importance of each skate species to the catch, the percentage contribution by mass was calculated by trawl and averaged for all trawls that took place in the same commercial grid square (See below).

Since all the observed commercial trawls took place on the west coast, research data were extracted from west coast cruises only. The percentage contribution by mass of *R.straeleni*, *R.wallacei* and *R.pullopunctata* to the research and commercial catch within the same grid squares was calculated and compared. Data for *R.straeleni* were processed as this is currently the only exploited South African skate species and comparison with data for the study species allowed assessments of their potential to be made.

The positions of commercial trawls are recorded in grids 10km square (Figure 5.1) while research data is captured in grids of only 5km squared. Research data was therefore converted to the commercial scale, using a map with one superimposed on the other. An average contribution for each species per grid was calculated for research and commercial data.

Data on the total landed catch of all demersal fish species from each commercial grid square in 1993 allowed ranking from most to least productive area. The grids were divided into Very Heavily (>10000 tons of fish annually); Heavily (1000-10000 tons); Moderately (100-1000 tons); Lightly (10-100 tons) and Very Lightly Fished (<10 tons) categories, reflecting fishing pressure in each area. The percentage contribution of *R.straeleni* to the research catch was calculated by grid. The effect of fishing pressure on the importance of *R.straeleni* to the catch could then be assessed.

Catch per unit effort data, similar to the size-based distribution data but using mass rather than number of animals was calculated for *R.wallacei*, *R.straeleni* and *R.pullopunctata* for grids of differing fishing pressure. This index of abundance allowed assessments of possible impact of fishing pressure on skate stocks to be made.

Finally, historical data on skate and total demersal fish landings (all species) from 1979 -1995 were extracted from the SFRI database. Skate data were extracted as catches from each area defined by ICSEAF (International Council for South-East Atlantic Fisheries). The division of South African waters into these areas is shown in Figure 5.1. The total landing (all species) data were extracted as the catch from the whole demersal fishery.

Research vessels and commercial trawlers use different gears and trawling practices. Consequently, direct comparison could not be carried out between the sectors and statistical analysis could not be performed. Therefore abundance and distribution data are only described in terms of any trends that could be observed.

5.3 - RESULTS

5.3.1 - Distribution

Disc width-frequency data from the whole south coast was divided into 6 depth ranges; 0-50m, 50-100m, 100-200m, 200-300m, 300-400m and 400-500m. No *R.wallacei* were recorded in waters shallower than 50m and all *R.pullopunctata* were found in the ranges between 50 and 300m. Disc width-frequency histograms for both species are seen in Figure 5.2. Due to the small data sets, no definite conclusions could be drawn. However, the total distribution of both *R.wallacei* and *R.pullopunctata* may be skewed by a scarcity of older individuals.

Larger numbers of *R.pullopunctata* were noted in the shallower waters. A notable number of individuals more than 50 cm DW were found in the 50-100m depth range. This may be an indication of an onshore migration to feed or lay eggs but due to the paucity of data, no conclusions can be drawn. No such pattern was noted for *R.wallacei*.

Data were split seasonally and east and west of the bank (Figure 5.3). Since there seemed to be no segregation by depth, data from all depths were combined. Analysis of the *R.wallacei* data suggests there are more juvenile animals on the west bank in the winter but larger numbers of adults on the same grounds in the spring. During the autumn, there were 92 juvenile (<350mm DW) *R.wallacei* on the west bank but only 84 in the spring. Eighty-nine adults were collected from the west Bank in the autumn compared with only 57 in the spring. The length-frequency distribution appears to suggest a bimodal distribution of individuals with peaks at 27cm and 39cm DW. The location of the missing sub-adults is unknown.

More *R.pullopunctata* were caught on the west bank than the east in the spring (east bank n=40; west bank n=167) with the reverse noted in the autumn (east bank n=103; west bank n=89). However, the data set was small and no further trends could be seen.

The highest catch per unit effort was in the 200-300m depth range for both species (Figure 5.4), with an increase in abundance down to this depth. There was a notable catch of *R.wallacei* in the 400-500m depth range.

The abundance of *R.wallacei* was not affected by season (Table 5.1). On both the east and west banks, the number of animals caught per trawl was between 4.1-5.8. However, *R.pullopunctata*was more abundant on the west bank in the spring months but abundance was unaffected on the east bank. It was interesting to note for both species that in a high proportion of trawls only 1-3 skates were recorded. However, in a small number of cases more than 10 individuals were recorded from a single trawl. Whether this is evidence of aggregations of animals for feeding or mating purposes is unclear. These large numbers did not appear to be composed of one sex or the other and occurred in the spring and autumn and east and west samples.

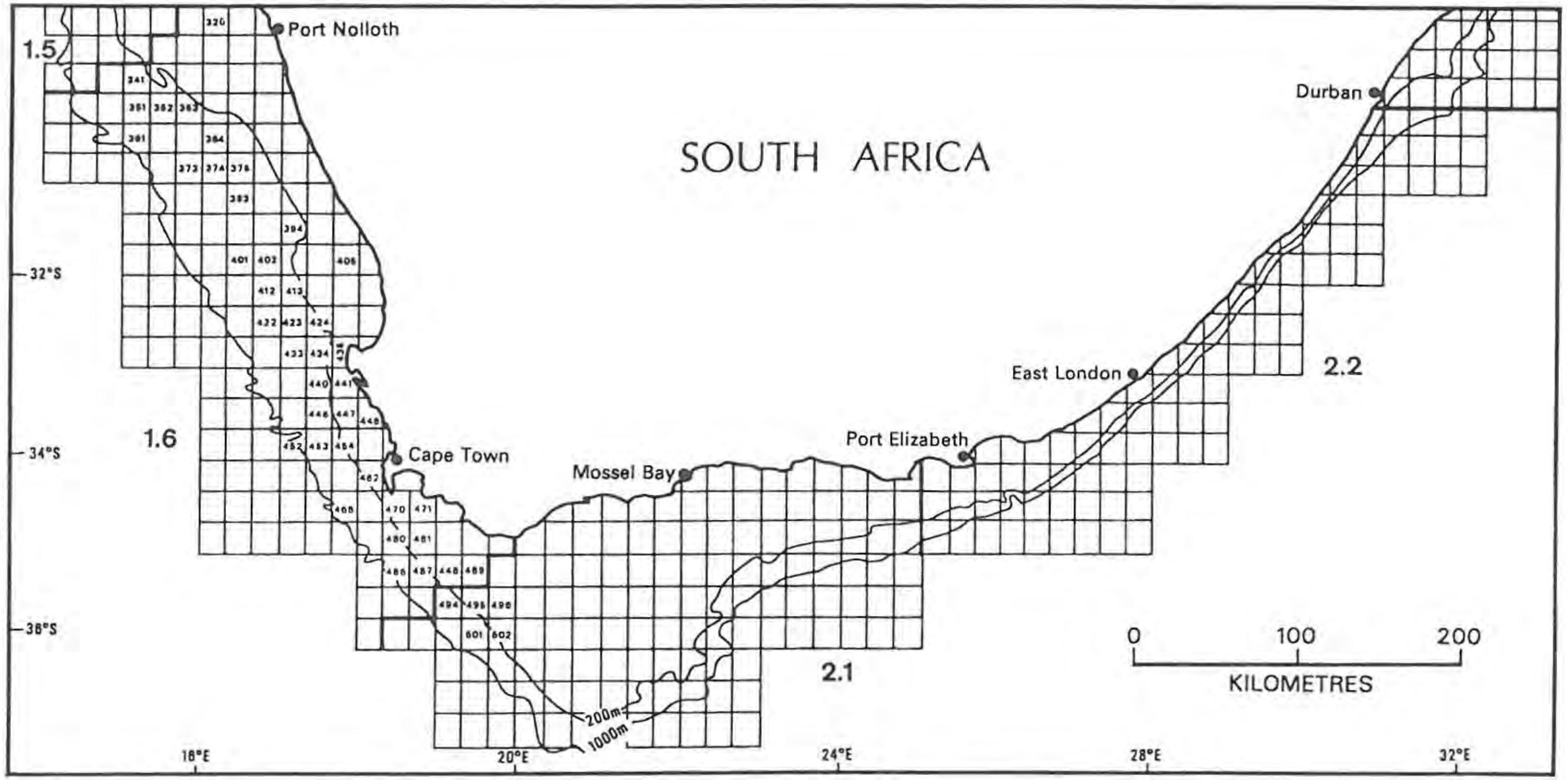
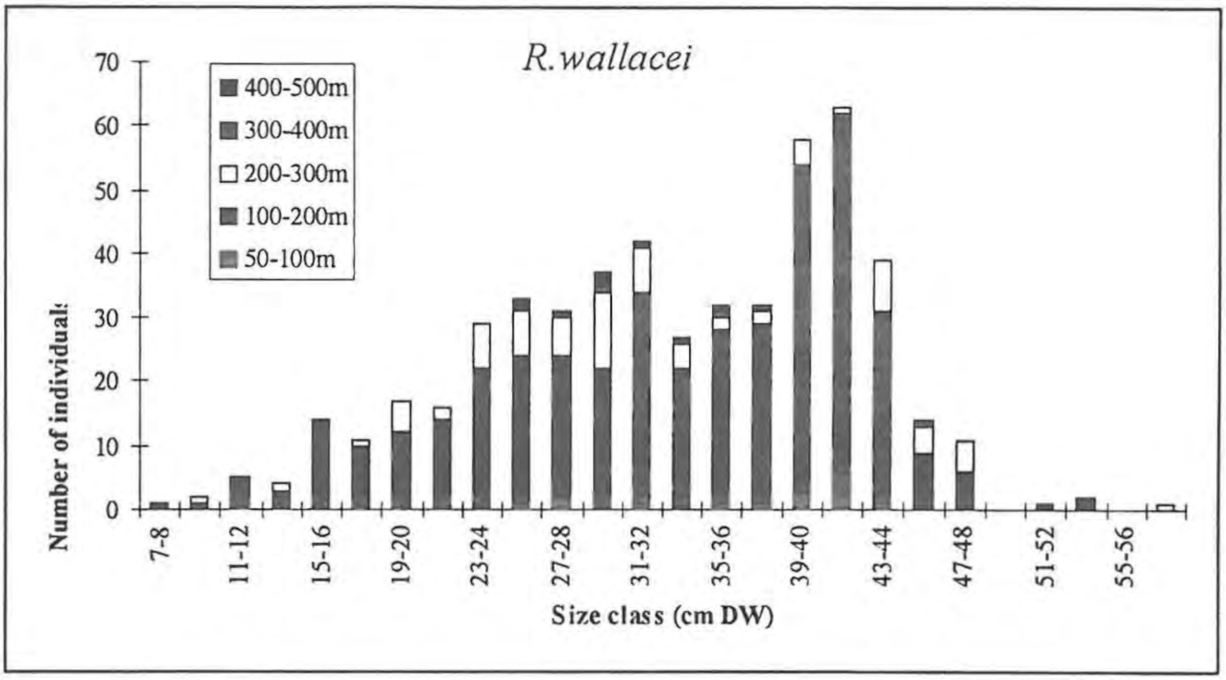


Figure 5.1: Commercial trawling grid squares and ICSEAF fishing divisions around the South African coast, showing grid numbers referred to in the text



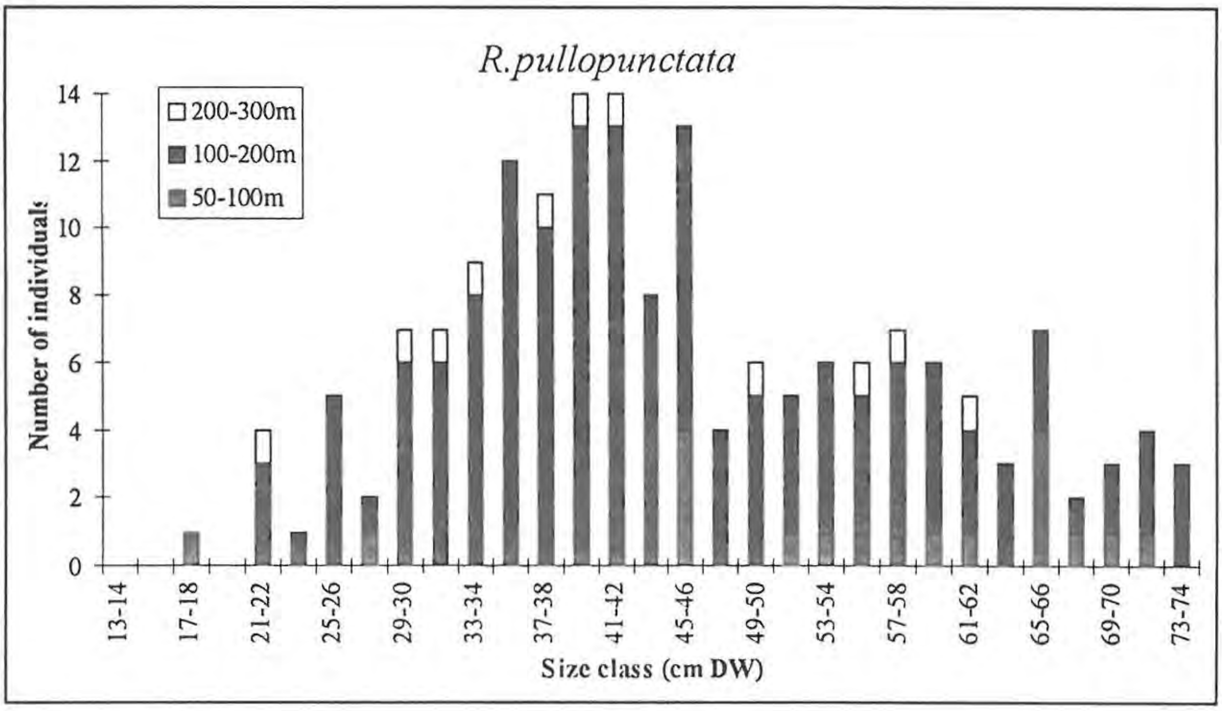
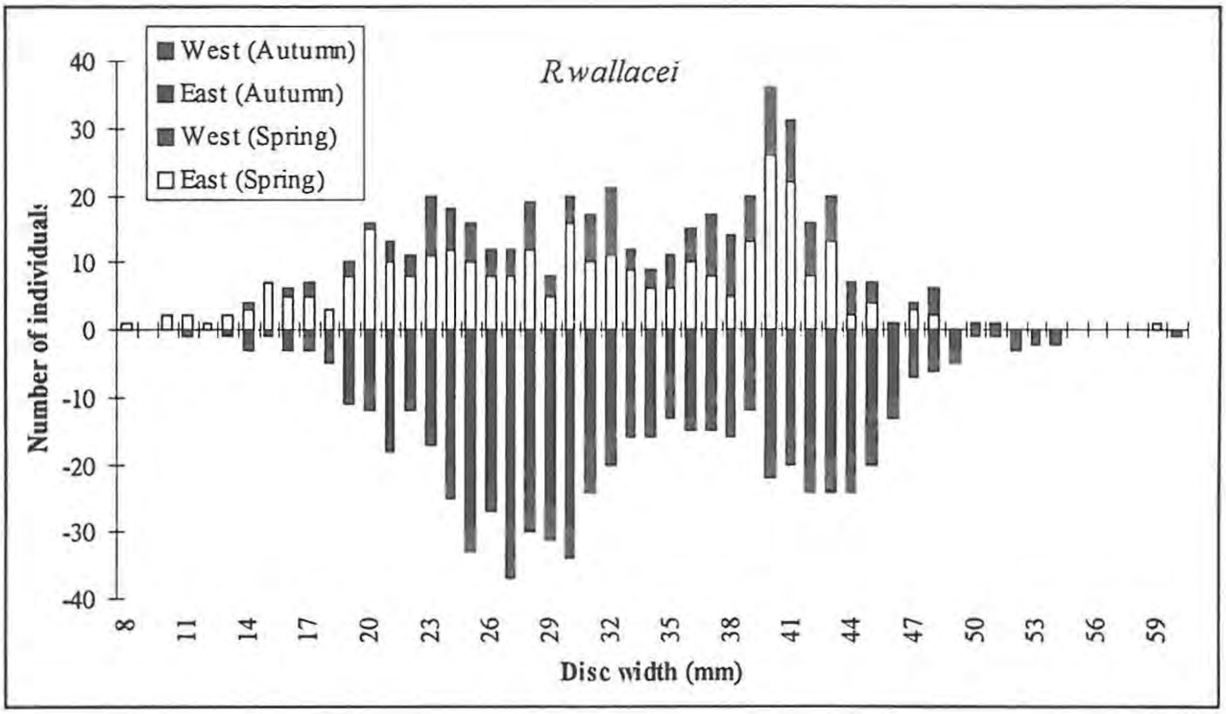


Figure 5.2: Disc width-frequency by depth (m) of *R.wallacei* and *R.pullopunctata*.



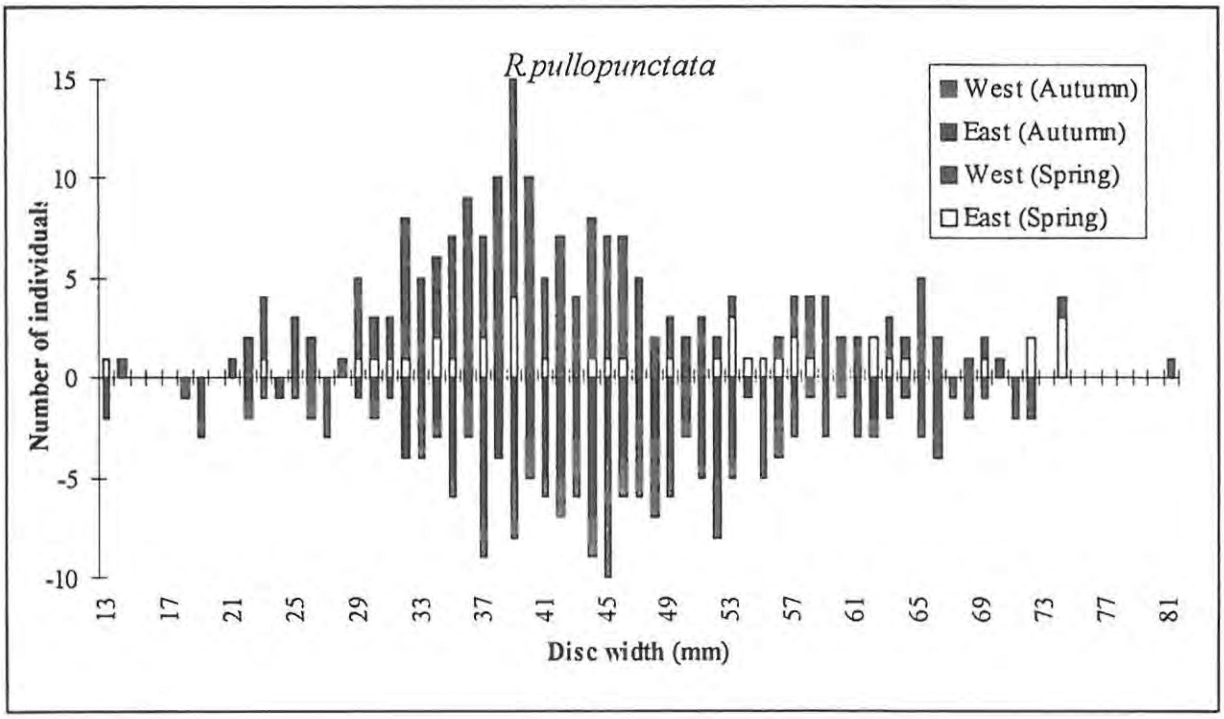


Figure 5.3: Seasonal and temporal differences in disc width-frequency of *R.wallacei* and *R.pullopunctata* on the east and west Agulhas Bank.

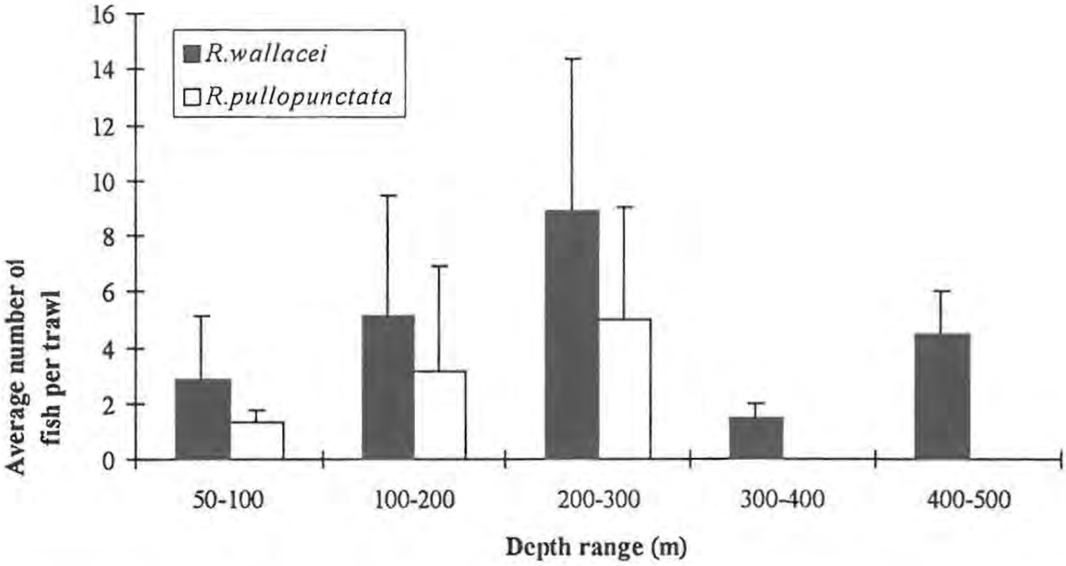


Figure 5.4: Research catch per trawl by depth for *R.wallacei* and *R.pullopunctata*.

	West Bank	East Bank
R.wallacei		
Spring	5.8+/-4.5 (n=19)	5.5+/-5.4 (n=35)
Autumn	4.1+/-4.0 (n=16)	5.8+/-3.6 (n=20)
R.pullopunctata		
Spring	7.0+/-5.4 (n=20)	2.2+/-1.9 (n=13)
Autumn	1.8+/-1.2 (n=22)	2.0+/-1.2 (n=4)

Table 5.1: Average number of *R.wallacei* and *R.pullopunctata* per research trawl seasonally and spatially. Numbers in parentheses indicate the numbers of trawls sampled.

5.3.2 - By-Catch

From the observer data the contribution of each skate species to the catch in each grid was calculated (Table 5.2) Since all trawls observed were offshore a comparison between inshore and offshore skate by-catch could not be made. However, historical data show that the majority of landed skates come from inshore vessels (Figure 5.5). For definitions of inshore and offshore, see page 2.

As can be seen in Table 5.2, the contribution to the total catch is small and highly variable in all species. *R.wallacei* contributed only 0.17-0.37% to the catch when present and *R.pullopunctata* contributed 0.07-0.24%. *R.straeleni* contributed between 0.05% and 7.59% to the catch. On average, when skates were present in a trawl they contributed 1.79% to the total catch.

Catch data averaged over all trawls, even those in which the study species were not present showed that *R.wallacei* contributed only 0.007% and *R.pullopunctata* 0.015% to the 142 trawls.

R.straeleni was the most commonly caught species, occurring in 40 (28.17%) of the trawls. *R.wallacei* and *R.pullopunctata* occurred in only 2.82% and 6.34% of the trawls, respectively. Rajids were present in 81 (57.04%) of the trawls observed.

The percentage contribution made by *R.straeleni* to research and commercial trawls were compared (Table 5.3). *R.straeleni* did not appear to be of more importance to either the research or commercial catch. Percentage contribution of *R.straeleni* to the total catch varied greatly in both the commercial and research samples. Research trawls retain smaller species and individuals than commercial trawls where such animals may escape. This will affect the species composition within the net and the contribution of *R.straeleni* to the research catch may have been expected to differ from the commercial data. This discrepancy may be due to the small data set or sampling period. All research cruises occurred in January/February while commercial data was collected between June and November. However, these were the only available data. It appeared that

R.straeleni may contribute more to the commercial catch in the heavily fished grounds and more to the research catch in lightly fished grounds. Due to a lack of overlap between commercial and research data, a similar comparison could not be made for *R.wallacei* and *R.pullopunctata*.

The commercial grids were ranked according to productivity and fishing pressure. The contribution of *R.straeleni* to the research catches made within the commercial area was assessed to determine whether this contribution was affected by the level of trawling (Table 5.4). This did not appear to be the case and no discernible trend was seen.

Data on total landings (all species) and skate landings around the South African coast between 1979-1995 are given in Table 5.5.

Data on the catch per unit effort in *R.wallacei*, *R.pullopunctata* and *R.straeleni* to research trawls on grounds of differing fishing pressure are shown in Table 5.6. No discernible trend of increasing or decreasing catch per unit effort with increased fishing pressure was seen for any of the three species. However, there was a great deal of variation around the results and the data sets were small.

	Grid square													
Species	401	411	432	439	440	446	447	453	461	468	469	480	487	493
Raja straeleni	0.29	0.12	0.05		0.72	2.36	0.11	1.59	7.59	0.04	2	3.69	3.99	1.31
(40 trawls)	(-; 1)	(0.04; 3)	(-; 1)		(0.66; 2)	(3.47; 5)	(-; 1)	(2.00; 3)	(9.26; 7)	(0.04; 8)	(2.71; 3)	(-; 1)	(-; 1)	(0.28; 4)
Raja pullopunctata				0.33		0.14			0.07				0.34	0.19
(9 trawls)				(-; 1)		(0.07; 2)			(-; 1)				(0.27; 3)	(0.05; 2)
Raja wallacei				0.23	0.37						0.17			
(4 trawls)				(0.17; 2)	(-; 1)						(-; 1)			
"Rough nose"		0.13	0.16	0.26		0.01		0.21	0.09	0.57	0.08	0.02		0.06
(20 trawls)		(-; 1)	(-; 1)	(-; 1)		(-; 1)		(-; 1)	(-; 1)	(1.00; 4)	(0.12; 6)	(-; 1)		(0.04; 3)
Bathyraja smithii		1.27								1.12				
(10 trawls)		(-; 1)								(1.56; 9)				
Raja dissimilis						0.19				0.6				
(4 trawls)						(-; 1)				(.84; 3)				
Cruriraja parcomaculata				0.12		0.32				0.23	2.99			
(22 trawls)				(0.08; 4)		(0.56; 7)				(0.19; 9)	(0.11; 2)			
Raja caudaspinosa				0.32		0.3		0.19		0.18				
(14 trawls)				(-; 1)		(0.02; 2)		(0.18; 2)		(0.31; 9)				
Raja leopardus			0.03	0.05		0.58		0.52		0.66	1.42	0.68		
(15 trawls)			(-; 1)	(-; 1)		(0.15; 2)		(0.15; 2)		(0.72; 7)	(-; 1)	(-; 1)		
Raja alba			0.18					8.31		0.39				
(4 trawls)			(-; 1)					(-; 1)		(0.30; 2)				
Raja confundens										0.02				
(2 trawls)										(0.01; 2)				
Unidentified *Raja*						0.002				0.36				
(6 trawls)						(-; 1)				(0.27; 5)				

Table 5.2: Percentage contribution to the commercial catch by grid of all skate species from 142 observed trawls. Figures in the top line indicate percentage contribution to the catch, figures in parentheses indicate standard deviations and the number of trawls in which the species was present.

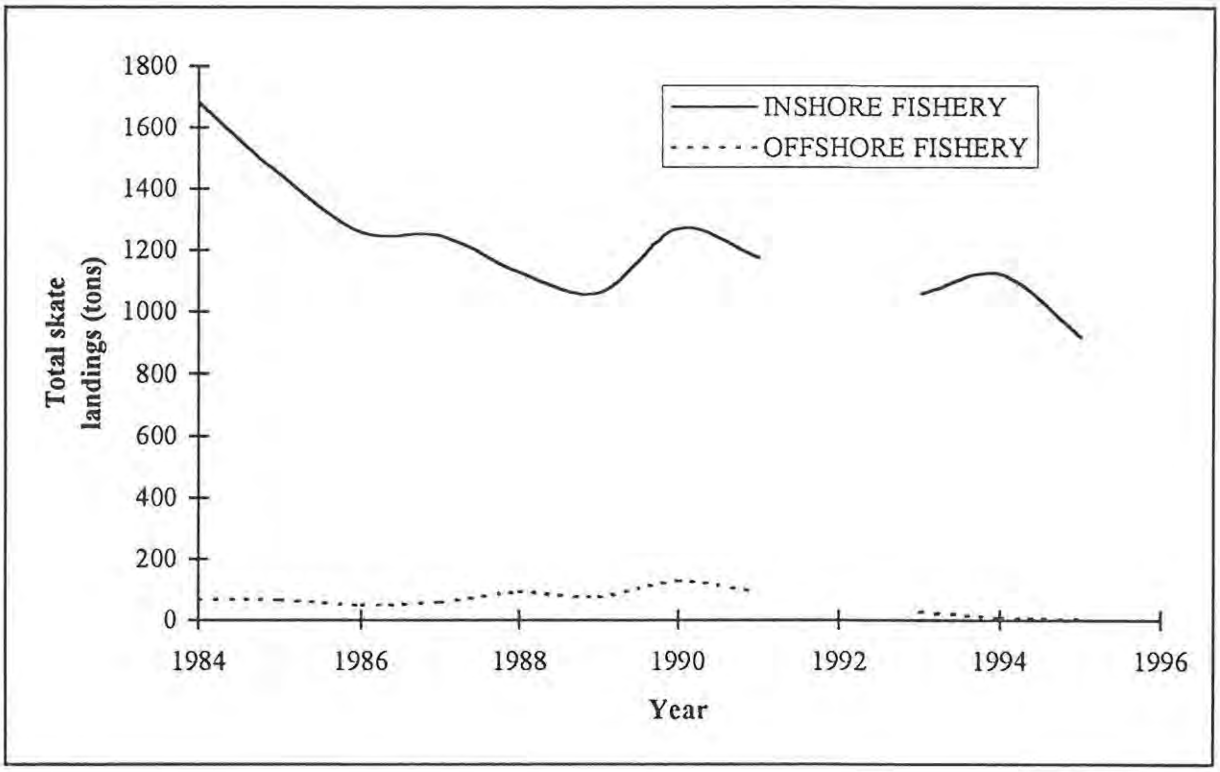


Figure 5.5: Total skate landings from the inshore and offshore fisheries 1984-1995. (SFRI data, no data could be obtained for 1991 and 1992).

Grid	Commercial catch Percentage Contribution (%)	sd	n	Research catch Percentage Contribution (%)	sd	n	Fishing Pressure
453	1.59	1.63	3	6.17	0.79	2	Very heavy
446	2.35	3.1	5	1.23	0.96	4	Very heavy
487	3.99		1	0.13	0.07	3	Heavy
480	3.69		1	0.96	0.52	6	Heavy
468	0.04	0.03	8	1.55		1	Heavy
440	0.72	0.47	2	1.65		1	Heavy
469	2	2.21	3				Heavy
461	7.59	8.58	7				Heavy
432	0.05		1				Heavy
411	0.12	0.03	3				Heavy
401	0.29		3	2.12	0.64	2	Moderate
493	1.31	0.24	4				Moderate
447	0.11		1	1.08	0.93	4	Very light

Table 5.3: Percentage contribution of *R.straeleni* to commercial and research catches.

Fishing Pressure	Grid square	% contribution to catch	sd	Fishing Pressure	Grid square	% contribution to catch	sd
Very heavy	453	6.17	0.79	Light	454	3.18	3.37
	446	1.23	0.96		353	0.65	0.54
	Mean	3.7	2.47		412	0.37	0.29
Heavy	422	0.22			452	1	
	374	1.05	0.62		413	0.22	0.14
	487	0.13	0.07		486	1.42	
	480	0.96	0.52		352	1.04	0.04
	361	0.59			441	2.89	3.95
	468	1.55			462	1.42	0.71
	440	1.65			470	2.28	1.01
	494	1.14	0.85		375	1.38	1.08
	Mean	0.91	0.53		471	9.06	
Moderate	351	0.24	0.11		402	1.16	
	364	1.47	0.86		481	2.63	0.9
	401	2.12	0.64		326	1.33	0.72
	501	0.32	0.32		Mean	2.00	2.07
	502	3.5	0.01	Very light	394	3.21	3.4
	361	1.96	0.66		496	2.8	2.52
	373	1.39			447	1.08	0.93
	433	1.26			424	0.61	0.17
	434	0.57			489	1.7	0.07
	495	1.07	0.76		448	0.99	
	423	1.78	0.18		383	0.48	0.15
	341	0.72	0.39		448	2.21	0.58
	435	1.71	1.37		405	0.96	0.06
	Mean	1.39	0.84		Mean	1.56	0.92

Table 5.4: Percentage contribution of *R.straeleni* to research trawls in areas of differing fishing pressure.

	Skate catches (nominal tons) by ICSEAF division					Total landed	Skate catch as
Year	1.5	1.6	2.1	2.2	Total	catch (tons)	% of total
1979	8.5	421.3	1108.6	196.4	1734.5	219783	0.8
1980		165.8	1048.3	121.8	1186.7	193096	0.6
1981						177893	0
1982						275233	0
1983	7.3	12	1422.1	100.5	1541.9	190299	0.8
1984	0.1	10.6	1622.8	119.6	1753.1	174885	1
1985		3.8	1444.1	102	1510.5	177640	0.9
1986	0.4	4.4	1196.5	103.4	1307.6	186612	0.7
1987	1.3	1.2	1205.1	87.6	1306.8	199565	0.7
1988		29.6	1099.5	94.4	1218.4	200468	0.6
1989		59.8	945.8	131.6	1137.5	217395	0.5
1990		80.7	1200.2	117.4	1398.3	234861	0.6
1991		273	1153.5	83.7	1268.4	184468	0.7
1992						140582	0
1993		31.8	936.4	71.3	1083.4	205533	0.5
1994		4.3	1089.3	36.8	1130.4	181069	0.6
1995		3.5	896.3	25.1	924.9	309832	0.3

Table 5.5: Catches of skates by ICSEAF division and total landed catches of all species within the South African demersal fishery 1979-1995 (SFRI database).

Fishing pressure	*R.straeleni*	*R.wallacei*	*R.pullopunctata*
Very Heavy	54.0+/-69.0 (n=4)		5.5+/-5.7 (n=6)
Heavy	12.7+/-18.11 (n=17)	3.9+/-3.4 (n=13)	5.8+/-3.6 (n=14)
Moderate	12.1+/-13.4 (n=25)	7.0+/-6.9 (n=20	10.5+/-10.3 (n=16)
Light	13.6+/-20.1 (n=30)	4.15+/-2.6 (n=18)	3.74+/-4.18 (n=14)
Very Light	2.7+/-2.3 (n=2)	1.9+/-1.9 (n=6)	8.8+/-8.2 (n=6)

Table 5.6: Catch per unit effort (kilograms per trawl for three species of skates caught in research trawls over commercial grounds of differing fishing pressure.

5.4 - DISCUSSION

If the distribution of a species and its population structure are to be understood, data on size or age-frequency are essential. Ideally, data on distribution should be collected monthly so that spawning migrations may be determined. In practice however this is not an easy task, especially in a species that is infrequently caught. At present only limited research cruises take place, surveying the entire south or west coast in one month. An observer programme may be the most useful method of obtaining quality data, for example in Australia (Kennelly, 1995). The SANCOR by-catch programme has secured limited funding for such investigations and it is hoped that this may answer many of the questions of by-catch composition and dynamics. Placing observers aboard commercial vessels goes a long way to solving this problem if the limitations of the sampling strategy are understood by the observers and users of the data. Examples of these limitations are the lack of observers and funds to cover all aspects of trawling such as the freezer vessels and the possible differences in data collection by different observers.

However, to date observers from the by-catch programme have concentrated on quantifying discards and length-frequency data has not been collected. As a result, the only disc width-frequency data for *R.wallacei* and *R.pullopunctata* are from 3 research cruises and is therefore limited.

Due to the small data set, analysing the results statistically using an ANOVA was not possible. It is clear however, that both species predominate in the 200-300m range. Other common skate species such as *R.straeleni*, *R.alba* and *R.miraletus* predominate in shallower waters (Smale and Cowley, 1992). It is possible that competition for resources will exist between the study species. This has already been shown in Chapter 4 where the diets of both species are dominated by 3 major prey items; *P.costatus*, *Gnathophis sp.* and *M.cristimanus*.

Due to time constraints, disc width-frequency data from the research database could be obtained for the study species only. Both species may show a skewed distribution with a lack of larger individuals and *R.wallacei* may show a bimodal distribution with a paucity of sub-adults. If this is the case, there may be several explanations: - that older individuals are not being caught;

that they exist elsewhere, either the east coast or down the continental slope to depths greater than 500 m out of the range of trawlers, similar to the hakes that move from the shallows deeper to water as they grow (Botha, 1985); or that the population is suffering from trawling. Large *R.alba* of 40kg are often caught within the nets (pers. obs) and it is unlikely that older *R.wallacei* and *R.pullopunctata* are escaping with greater success than this species. The theory of larger individuals moving to the east coast cannot be proved without experimental trawling taking place. Changes in distribution with depth did not suggest that animals move down the continental shelf as they grow.

There was insufficient data to determine whether aggregations of very term or post-parturition females and small animals occur, indicating nursery areas. It is possible that more large *R.pullopunctata* are found in shallower waters. Whether this is evidence of an onshore movement to nursery areas or to mate is unknown. It is possible that females lay their eggs in areas too rocky for trawling and that nursery areas may be missed. Richards *et al* (1963), found gravid *R.erinacea* distributed over several substrate types in Long Island and Block Island Sounds and could not determine whether a single nursery area existed.

Drawing conclusions from the seasonal and spatial distribution is difficult since numbers are limited. The notable increase in the numbers of *R.pullopunctata* on the west bank in the autumn is interesting but no definite conclusions may be drawn as to the reason for this.

Observer data indicate that rajids contribute on average 1.8% to the catch when present and occur in 57% of trawls. The most common species, *R.straeleni* occurs in only 28% of trawls. The remainder are infrequently caught and make only minor contributions to the catch. Smaller species may be caught in high numbers but these possess small wings with little meat. The only currently utilized species is the biscuit skate, *R.straeleni*. This is probably the only species that shows the potential for greater utilization. However, rough catch per unit effort estimates from the research data indicate that around 10kg of skate may be caught per trawl. Whether trawling companies would think it worthwhile to keep such quantities is a consideration that cannot be ignored. A greater catch per unit effort would be obtained if skates were treated as a single group.

If the larger rajids were treated as a group and processed together, they may be utilized. Holden (1977) reported that the skate fishery in the Irish Sea is composed of 5 major species and 6 minor ones. However, problems with assessing separate stocks will occur if landings are recorded as one group.

Together, the skate group contributes 1.8% by mass to trawls in which at least one skate species is present. Overall, a total of 568.1 tons of fish was caught in the 142 observed trawls. Of these, 491.7 tons were retained (86.6%) and 5.6 tons were *Raja sp.* (0.996%). It can be seen that although skates contribute only some 1% to the total catch and not all skates caught can be utilized, since more than 5 tons were landed from only 142 trawls, the further use may be worth considering.

It may be possible to target areas where skates contribute a high proportion of the catch but a more detailed study of distribution and by-catch would be required and extra problems would be encountered by catching quota species as by-catch. However, it would only be worthwhile processing rajids if they could command a high price. Skates do not command such a price in South Africa where they are sold at R3-4/kg but if a market in the east could be found, it is possible that they could be exported. At present only 1000 tons are landed annually, most of which is sent to the Johannesburg fish markets (P.Sims, SFRI, pers. com.).

Historical data show that the contribution of skates to the total landed catch is approximately half of that to observed catches. However, since the majority of skates are landed in Mossel Bay (ICSEAF Division 2.1) on the south coast and the observer data is drawn from trawls on the west coast, it cannot be assumed that the potential for greater utilization may be double the current levels. The topography of the south and west coasts should be considered. The Agulhas Bank protrudes some 200km offshore and most of the shelf is shallower than 100m, the preferred depth of *R.straeleni*. The continental slope on the west coast drops off more sharply with a reduced area shallower than 100m. It is possible that the biscuit skate may possess the potential for greater utilization on the south coast.

Overall, the importance of *R.straeleni* was similar between commercial and research trawls. However, it did appear that this species contributed more to the commercial catch on the heavier-fished grounds and more to the research catch in lighter-fished areas. The reason for this is unknown, since fishing pressure appeared to have no effect upon the contribution of *R.straeleni* to research catches. It is likely that this trend is merely a consequence of the small data set and that a larger data set would allow better comparison.

Unfortunately, comparisons on the contribution of *R.wallacei* and *R.pullopunctata* to research and commercial trawls could not be made.

The data obtained through the distribution and by-catch study is limited and no definite conclusions can be drawn. However, the length-frequency data and catch (in numbers per trawl) do give a preliminary picture of distribution and abundance down the continental slope. The by-catch data clearly indicates that the contribution of skates to trawls is highly variable. Only a long-term data series would show whether this variability can be predicted and maybe utilized.

CHAPTER 6

GENERAL DISCUSSION AND FISHERIES CONSIDERATIONS

The west and south coasts of southern Africa are highly abundant in fish species and biomass (Japp *et al*, 1994). Although the more temperate south coast supports more fish species (Smale, 1992) the west coast, aided by upwelling events and an influx of nutrients, probably supports a greater biomass. The dynamics of pelagic fish stocks such as anchovy and pilchard in the Benguela system have demanded a great deal of scientific attention in the form of the long-running Benguela Ecology Programme. However, studies on the south coast are fewer and have not been coordinated under a single programme.

Studies on chondrichthyan resources on the Agulhas Bank are limited due to the low profile of sharks, skates and rays. Assessment of catches is limited by the trawling industry that discards the greater proportion of its catch (Japp *et al*, 1994). However, chondrichthyans contribute on average 20.5% by mass to research trawls (Japp *et al*, *op. cit.*) And cannot therefore be ignored as a group. Recently, the commercial value of sharks has increased with the introduction of long-lining for larger species such as *Galeorhinus galeus*. Research data suggest that the smaller *Squalus megalops*, another discard species, is a frequent and abundant component of trawls. The biology and fishery potential of both *S.megalops* and *G.galeus* are currently under investigation within the SANCOR programme. Hopefully the SANCOR by-catch programme will aid in a better understanding of the dynamics and interactions between species inhabiting the Agulhas Bank.

Initial biomass index estimates from research cruises suggest that the total rajid biomass on the south and west coasts are approximately 59849 nominal tons and 17978 nominal tons, respectively (SFRI, unpubl. data). Unfortunately, these figures are calculated from only 265 trawls on the south coast and 95 trawls on the west coast and extrapolate over untrawlable areas, and they must be accepted as very rough estimates. However, they indicate that the available biomass far exceeds current exploitation levels.

Demersal trawling is one of the least selective fishing techniques, capturing large quantities of non-target fish. Due to net construction and bottom time, many individuals are damaged in the net and many suffer barotrauma during hauling. Stress, oxygen deficiency and temperature changes will lower survival rates and even if fish survive to be released, the loss of scales may cause infection and finally, death. The dumping of such large quantities of dead fish is a great waste, particularly in view of the huge world demand for protein.

It is highly unlikely, with the worldwide investment in demersal trawling, that fishing practices could and/or would be changed to protect by-catch or currently discarded species. Although nets in prawn fisheries may be modified to allow the escape of unwanted fish (Isaksen *et al*, 1992), it is unlikely that such modifications could be made to nets targeting hakes. Unless demersal trawling is disregarded in favour of a more selective strategy, the impact of fishing on non-target stocks must be accepted as unavoidable. Efforts to utilize fully such animals must be made. Discarding species such as the skates is unlikely to boost stocks of commercial species, since hakes do not scavenge on large skates, nor do they compete for resources (Payne *et al*, 1987).

Some countries, retain some or all of their non-target catch for human consumption or processing into animal feed (Kennelly, 1995). However, apart from "luxury" by-catch species such as monk and kingklip, most of South Africa's non-target catch is discarded. These discards not only comprise unwanted species but also include undersized hakes or soles that are too small for the market. Such losses may affect the accuracy of modelling commercial stocks.

Several problems must be addressed when considering the retention and use of discards. The most important for trawling companies, is that discards have little value and take up space that more profitable species could and/or should be using. Secondly, South Africa is currently trying to enter foreign markets, in particular in Europe. However, European Union regulations state that discard species may not be kept in the same hold space as fish destined for export. This creates huge problems in vessels with limited space. Finally, the main tenet of the SANCOR by-catch programme is that the utilization of discards should be benefiting small, local communities. However, most of South Africa's discards are derived from the large trawling companies. How the better use of discards will eventually benefit small-scale community is unknown at present. This aspect of the programme is under investigation by a team of socio-economists within the SANCOR programme.

At present, no quantitative data exist on the level of by-catch or discards in the South African trawl or line fisheries. However, if markets could be found, discards could be utilized to provide employment and much-needed income. This issue is of concern and has the attention of both the fishing industry and scientists. Provision for determining by-catch and discard composition and mass and for assessing the possibility of greater utilization was made in the Draft National Marine Fisheries Policy Document (Section 4.3.3) submitted to the Minister of Environmental Affairs and Tourism in June 1996.

The first step towards the greater use of discards is to obtain detailed knowledge on species distribution and abundance, as far as this is possible. Kennelly (1995) reports that by-catch composition and abundance are highly variable temporally and spatially. The primary aim of the SANCOR by-catch programme is to understand these variations.

The very fact that by-catch species are removed from the sea means that they are essentially a fishery and stocks suffer mortalities above the natural level. Population parameters will determine the impact fishing may have on stocks and the ability of species to contend with this.

R.wallacei and *R.pullopunctata* are common members of the catch in the offshore hake-directed fisheries. Their biology, distribution and abundance were investigated to determine whether they could be utilized in the same way as *R.straeleni*.

Unfortunately the data sets for both study species, especially *R.pullopunctata*, were limited. Monthly biological data could not be obtained for the whole year due to problems with relying on the commercial trawlers. During most months, the target of 50 animals could not be met and for some months, no samples were obtained at all.

Consequently, the age and growth study was restricted and trends in gonad seasonality could not be drawn with confidence. Also, due to the low priority of both species during research cruises in the past, disc width-frequency and distribution data were scarce. Although research cruises allowed the collection of a larger size range of individuals, they could not be used to make up the shortfall in monthly data. Due to time restraints, the study could not be extended for a further year. Conclusions drawn from such data are therefore tentative.

The study is valuable however, since some preliminary conclusions may be drawn and the question of whether either species shows the potential for greater utilization may be answered. It also allows the first assessments of the importance of both species to the commercial catch to be made.

Age and growth studies revealed that both species are slow growing and long-lived, a common elasmobranch trait. *R.wallacei* takes some 9-10 years to reach its asymptotic size. A lack of large *R.pullopunctata* meant that an accurate asymptotic size for this species could not be calculated. Such parameters are of concern when species suffer from exploitation, even when they are simply removed as by-catch. Many elasmobranchs that have become the target of directed fisheries have suffered from "boom and bust" periods when these life-history characteristics have not been taken into account (Holden, 1977; Anderson, 1990) and Waring (1984) clearly showed the occurrence of elevated mortality in an *R.erinacea* population under similar by-catch conditions as skates in the South African fishery.

If a species cannot replace itself under fishing pressure, it will become overfished. Recruitment must equal natural losses plus fishing mortality or stocks will decline. Most classical fishery models for teleosts do not assume a direct relationship between stock and recruitment although such a relationship must exist (Ricker, 1975). The relationship between stock and recruitment is extremely important in species such as elasmobranchs that produce few, well-developed young (Hoenig and Gruber, 1990). A reduction in the reproductively-active portion of the population will affect recruitment.

Both *R.wallacei* and *R.pullopunctata* mature late in life. *R.wallacei* begins to mature at around 400 mm DW, some 7-9 years of age, while *R.pullopunctata* matures at around 600mm DW or 10-12 years of age. Disc width-frequency data suggests there may be a paucity of large, mature individuals in the research catch. If the mature portion of the population is being reduced, recruitment will decrease and stocks may fail. Taking into account the slow growth-rate, even small-scale removal of adults may have a serious impact on populations. However, without more data, estimates of current levels of biomass cannot be made.

As no observer disc width-frequency data was collected, the proportion of immature animals in commercial trawls could not be determined. However, due to the mesh size used by the offshore trawlers all size classes are likely to be vulnerable to the net. It is therefore likely that the proportion of immature animals caught during commercial operations will be similar to that caught in research trawls. According to Holden (1977), a reduction in numbers of mature females will mean that more eggs laid by each remaining female must survive to the age of one year for the population to replace itself. Whether the population is capable of such a density-depended response is unknown.

If by-catch skates are to be utilized, one of two strategies may be employed: - to treat each species separately or to treat them as a single group. If skates are dealt with on a single species basis, the potential for greater use is likely to be limited since each species is caught infrequently. If they are treated as a group, this potential may be increased, since observer data indicates that skates of some description will be caught in 57% of trawls and will comprise on average 1.8% of the catch on the west coast. However, problems will be encountered in trying to model stocks if landings are recorded as a single group.

The final point when considering the further utilization is: if skate by-catch is retained, will it be used? Obviously, retaining skates would be ridiculous if no market existed. The low market value and current landing figures suggest that at present, there is a very small market for these fish within South Africa. However, the possibility of small-scale companies exporting such by-catch to the east or Europe should not be completely disregarded. At the current exchange rate, export would be more beneficial to the country's economy than trying to find a market within South Africa.

The observer programme has now been running for 12 months, although only 6 months of data have been collected to date. Initial results have been encouraging, despite the limitations of the sampling strategy. Further data collection is required to give a picture of by-catch throughout the year and over a wider range of the Agulhas Bank and west coast. Unfortunately, no data has been collected from the inshore regions of the west coast, the offshore region of the Agulhas Bank or from freezer vessels. Getting observers aboard such vessels is difficult as they take up space required by crew members.

Data collected by observers on the Cape south and west coasts are useful in that they allow comparisons between research data and the commercial situation to be made. The applicability of scientific decisions made based solely on research data can then be assessed. A long-running programme will hopefully lead to an understanding of the spatial and temporal abundances of by-catch and discard species and to changes in these abundances. However, such a programme is expensive to run. Although the importance of the efficient use of discards is highlighted in the draft fisheries policy, it is likely to be of low priority. Such a detailed, long-running programme also requires the prolonged goodwill of the trawling company, skippers and trawler men involved. Having observers aboard trawlers upsets the running of the ship as crew members have to be left behind to make space for the newcomers. Company bosses and skippers in particular are suspicious of observers and may believe that the measuring of discards and by-catch will result in changes to quotas or rules governing the dumping of fish. A better working understanding between the parties involved would help to allay such fears. Dedicated observers are required to ensure that the quality of data obtained are high and that measurements are consistent. It is not always possible to get and keep such observers. However, the benefits from such a programme should outweigh these problems.

The observer programme is planned to continue until the end of 1998. Hopefully this will help to answer some of the vital questions on by-catch composition and abundance.

APPENDIX A

Diet compostion of animals from research and commercial trawls. (%FO=percentage frequency of occurrence; %V=percentage volume; %M=percentage mass).

	R.WALLACEI (SOUTH COAST)						*R.PULLOPUNCTATA* (WEST COAST)					
	RESEARCH			COMMERCIAL			RESEARCH			COMMERCIAL		
	n=81			n=56			n=36			n=17		
PREY SPECIES	%FO	%V	%M	%FO	%V	%M	%FO	%V	%M	%FO	%V	%M
NEMATODA	1.23	0.35	0.01	3.57	0.03	0.00	25.00	1.19	0.95	17.65	0.07	0.28
ANNELIDA												
POLYCHAETA	22.22	3.86	0.80	26.79	4.09	0.21						
ARTHROPODA												
CRUSTACEA												
Crustacean remains	20.99	3.44	0.37	8.93	1.19	0.97	11.11	3.68	0.86	29.41	9.50	1.18
STOMATOPODA												
P.armata capensis	0.62	0.62	0.05	1.79	0.45	0.08	11.11	5.26	11.30			
ANOMURA												
Upogebia capensis				21.40	12.30	3.26						
AMPHIPODA												
Amphipod remains	4.94	0.32	0.03	1.79	0.15	0.00						
Ampelisca palmata	9.88	0.33	0.02	1.80	1.70	0.01						
White	3.70	0.18	0.12									
Gammarid				1.80	0.20	0.04						
Paramoera capensis	2.47	0.02	0.01									
Orange-eyed	2.47	0.12	0.01									
Unid amphipod no. 1				0.33	0.02							
ISOPODA												
Isopod remains	3.70	0.38	0.04	5.36	0.57	0.10						
Orange-eyed	1.23	0.03	0.04									
Eurydice lonicornis	3.70	0.52	0.07									
MYSIDACEA(unid)												
Orange-eyed mysids	25.93	13.65	1.21	1.78	0.04	0.00	13.89	1.74	0.17			
Red-eyed mysids							5.56	0.77	0.06			
Black-eyed mysids	1.23	0.03	0.00									
CARIDAE												
Shrimp remains	3.70	0.10	0.01	5.36	0.31	0.04				5.88	0.06	0.02
Funchalia woodwardi							13.89	7.84	16.48			
White shrimp	9.88	2.55	0.57	3.57	1.87	0.07						
Leptochela robustus	3.70	1.36	0.09							5.88	0.06	0.02
Pandalina brevirostris	1.23	0.81	0.73									
Pontophilus sculptus	9.88	2.85	0.27	1.79	1.79	0.51	2.78	2.78	0.24			
Orange							25.00	9.94	3.22			
Black-eyed	2.47	0.58	0.06				5.56	1.52	0.29			
Unid shrimp 322.2							5.56	1.82	0.05			

APPENDIX A (continued)

BRACHYURIDAE												
Decapod remains	6.17	1.66	0.36	5.36	2.61	0.18						
Mursia cristimanus	16.05	3.39	0.63	5.36	2.92	0.77	16.67	7.14	8.31	52.94	28.34	11.51
Shoveller	1.23	0.40	0.14									
Goneplax angulata	2.47	0.21	0.30				2.78	1.11	1.25			
Megalopa	6.17	0.54	0.03				2.78	1.90	0.25			
MOLLUSCA												
Ostracoda				1.79	0.00	0.00						
BIVALVIA	2.47	0.10	0.02	1.79	0.26	0.57						
GASTROPODA	2.47	0.30	0.11									
CEPHALOPODA	3.70	0.91	1.49	3.57	0.43	0.00				5.88	1.01	0.90
CHORDATA												
CHONDRICHTHYES												
Squalus sp.				3.57	0.94	4.63						
Raja pullopunctata				1.79	1.12	0.75						
Egg-case				1.79	0.49	0.03						
TELEOSTEI												
Teleost remains	25.93	11.01	8.25	50.00	23.26	9.53	27.78	9.25	26.35	76.47	44.05	55.23
P.costatus	25.93	11.02	9.72	1.79	1.43	0.35	22.22	12.92	15.93			
Gnathophis sp.	28.40	17.00	55.16	39.29	32.42	52.57						
Bregmatoceros sp.	14.82	2.09	0.12				2.78	2.78	0.08			
Pleuronectiformes	6.17	3.01	3.67	5.36	2.69	4.40	2.78	0.37	0.60			
Anguilliformes				1.79	0.85	4.54						
C.zanzibarensis	1.23	1.21	8.36									
S.ocellata head	1.23	0.91	2.02	10.71	1.15	14.77						
S.ocellata tail	1.23	0.63	1.67				5.56	2.01	3.98			
Chelidonichthys sp.												
Merluccius sp.												
M. capensis head										11.76	9.21	25.67
AMPORPHOUS MATERIAL	35.81	9.02	2.63	30.58	3.91	1.61	50.00	23.73	9.65	29.41	7.16	4.47

APPENDIX B

Diet composition of animals from the east and west Agulhas Bank. (%FO=percentage frequency of occurrence; %V=percentage volume; %M=percentage mass).

	R.WALLACEI						*R.PULLOPUNCTATA*					
	EAST			WEST			EAST			WEST		
	n=191			n=26			n=70			n=52		
PREY SPECIES	%FO	%V	%M	%FO	%V	%M	%FO	%V	%M	%FO	%V	%M
NEMATODA	3.68	0.18	0				22.73	0.15	0.1	31.25	0.74	0.27
ANNELIDA												
POLYCHAETA	18.42	3.05	0.46	25.93	5.74	0.86	3.03	0.32	0.02			
ARTHROPODA												
CRUSTACEA												
Crustacean remains	20.53	4.14	0.82	14.81	5.21	0.18	16.67	2.36	1.72	29.17	5.1	2.77
STOMATOPODA												
Mantid remains	1.58	0.58	0.41	3.7	1.32	0.04	1.52	0.59	0			
P. armata capensis	1.58	0.58	0.41	3.7	1.32	0.04	1.52	0.13	0.04			
ANOMURA												
Upogebia capensis	6.32	3.61	1.86									
AMPHIPODA												
Amphipod remains	2.63	0.18	0.01				1.52	0.15	0.003			
Ampelisca palmata	4.74	0.63	0.01	7.41	2.34	0.04	1.52	0.04	0.006			
Unid amphipod 2	0.53	0	0									
White	8.95	0.81	0.11	7.41	1.18	0.02						
Gammarid	0.53	0.05	0.02									
Paramoera capensis	1.05	0.01	0									
Orange-eyed	1.58	0.09	0.01									
Unid amphipod 3												
Lyianassa ceratina	3.68	0.48	0.05									
Stenopus hispidus												
ISOPODA												
Isopod remains	3.16	0.33	0.08									
Orange-eyed	2.11	0.38	0.04									
Eurydice lonicornis	1.58	0.22	0.03	3.7	0.09	0.04						
Unid isopod 1				3.7	1.67	0						
Black-eyed	0.53	0.01	0									
Mesanthura canenlula	0.53	0.02	0									
MYSIDACEA (unid)												
Orange-eyed mysids	21.05	8.68	0.6	29.63	8.72	1.01	13.64	3.09	0.08	12.5	2.31	0.24
Red-eyed mysids	5.26	0.93	0.03	3.7	0.26	0.01	1.51	0	0	4.17	0.68	0.08
Black-eyed mysids	2.11	0.24	0.01							2.08	0.18	0.01

APPENDIX B (continued)

CARIDAE												
Shrimp remains	4.21	0.24	0.34	11.1	4.5	0.03	18.18	3.02	1.25	22.92	7.76	2.08
White shrimp	11.05	2.8		11.11	6.93	0.57	3.03	1.12	0.42			
Leptochela robustus	1.58	0.58	0.03	11.11	4.07	0.47	7.58	1.38	0.63	27.08	9.73	2.86
Pandalina brevirostris				7.41	2.54	2.24	1.52	1.08	0.72	22.92	9.5	2.26
Pontophilus sculptus	8.42	2.02	0.48	3.7	0.49	0.01	3.03	1.12	0.42			
Unid shrimp 2							15.15	3.72	2.94	29.17	8.27	2.8
Unid shrimp 3							24.24	4	2.19	8.33	3.04	1.13
Black-eyed	10	2.03	0.11	18.52	2	0.28						
Red-eyed	1.05	0.22	0.01									
Pink prawn							1.52	0.12	0.07	2.08	0.85	0.08
BRACHYURIDAE												
Decapod remains	4.21	1.48	0.25				7.58	1.17	0.19	4.17	0.55	0.2
Mursia cristimanus	11.58	3.6	0.87	7.41	0.04	0.19	50	19.4	19.38	60.42	22.59	17.32
Shoveller	0.53	0.17	0.06									
Goneplax angulata	1.05	0.09	0.12				1.52	0.02	0.001			
Megalopa	6.84	0.64	0.04	3.7	3.7	0.03				2.08	0.12	0.12
MOLLUSCA												
Ostracoda	0.53	0	0									
BIVALVIA	1.58	0.12	0.33									
GASTROPODA	1.05	0.13	0.04									
CEPHALOPODA												
Sepiid remains	2.63	0.51	0.61				1.52	0.3	0.62	6.25	1.01	2.25
Sepia officinalis							7.58	3.04	8.48			
CHORDATA												
CHONDRICHTHYES												
Squalus sp.	1.05	0.28	2.64									
Raja pullopunctata	0.53	0.33	0.43									
Egg-case	0.53	0.14	0.02									
TELEOSTEI												
Teleost remains	38.95	15.58	9.01	27.22	11.5	10.89	57.58	19.6	15.28	45.83	15.46	38.96
P. costatus	24.74	11.94	6.48	7.41	3.4	0.92	45.46	22.07	19	16.17	5.28	6.51
Gnathophis capensis	25.79	16.91	50.1	25.93	20.9	75.38	9.09	5.34	7.17	4.17	0.3	1.2
Bregmatoceros sp.	6.84	0.93	0.05	3.7	0.14	0.05	3.03	0.3	0.07	1.17	0.6	0.38
Pleuronectiformes	4.21	2.43	10.5	4.21	1.72	3.92	10.61	3.79	6.55			
Anguilliformes	0.53	0.25	2.6									
C.zanzibarensis	0.53	0.51	3.42									
Sardinops ocellata head	4.21	2.43	10.5				1.52	0.51	3.66			
Sardinops ocellata tail	1.05	0.45	0.86									
Chelidonichthys sp.							1.52	1.32	6.36			
Merluccius sp.										2.08	2.13	15.36
M. capensis head												
AMORPHOUS MATERIAL	35.26	7.63	2.04	44.4	12.3	4.52	40.91	5.95	3.48	18.75	3.17	1.28

APPENDIX C

Diet composition of immature (<300mmDW), maturing (300-400mmDW) amd mature (>400mmDW) *R.wallacei*. (%FO=percentage frequency of occurrence; %V=percentage volume; %M=percentage mass).

	R.WALLACEI								
	IMMATURE n=94			MATURING n=61			MATURE n=64		
PREY SPECIES	%FO	%V	%M	%FO	%V	%M	%FO	%V	%M
NEMATODA	4.26	0.32	0.04				4.69	0.05	0
ANNELIDA									
POLYCHAETA	14.89	3.03	3.51	21.31	3.09	0.42	23.44	3.98	0.18
ARTHROPODA									
CRUSTACEA									
Crustacean remains	35.11	6.88	3.14	6.56	0.92	0.08	9.38	3.48	0.76
STOMATOPODA									
Mantid remains	2.13			1.64	1.59	0.08	1.59	0.4	0.06
P.armata capensis	2.15	1.08	1.12	3.28	0.7	1.03			
ANOMURA									
Upogebia capensis				9.84	6.37	2.58	9.38	4.46	1.47
AMPHIPODA									
Amphipod remains	5.32	0.36	0.16						
Ampelisca palmata	9.57	0.91	0.14	1.64	1.48	0.02	1.56	0.08	0
Unid amphipod 2	1.06	0.01	0.01						
White	20.21	1.97	1.36						
Gammarid				1.64	0.15	0.08			
Paramoera capensis				3.28	0.03	0.01			
Orange-eyed	2.13	0.14	0.06	1.64	0.06	0			
Unid amphipod 3	1.06	0.06	0.02						
Lyianassa ceratina	5.32	0.73	0.33	1.64	0.29	0.03	1.56	0.06	0.01
ISOPODA									
Isopod remains	3.19	0.33	0.21	4.92	0.51	0.19			
Orange-eyed	3.19	0.75	0.35	1.64	0.04	0.05			
Eurydice lonicornis	4.26	0.48	0.4						
Unid isopod 1	1.06	0.48	0						
Black-eyed	1.06	0.02	0						
Mesanthura canenlula	1.06	0.05	0						
MYSIDACEA(unid)									
Orange-eyed mysids	47.87	20.01	8.47	1.64	0.04	0	3.13	0.02	0.01
Red-eyed mysids	11.7	1.96	0.41						
Black-eyed mysids	4.26	0.48	0.13						

APPENDIX C (continued)

CARIDAE									
Prawn remains	9.56	0.62	0.24	3.28	1.66	0.12	1.55	0.07	0.01
White shrimp	13.83	2.69	1.36	11.48	5.96	0.76	6.25	1.42	0.03
Leptochela robustus	5.32	2.26	0.77				1.56	0.1	0.02
Pandalina brevirostris	1.06	0.03	0.01				1.56	1.03	0.41
Pontophilus sculptus	6.38	1.36	0.4	8.2	1.73	0.07	9.38	2.5	0.59
Black-eyed	23.4	4.24	1.64	3.28	0.65	0.03			
Red-eyed	2.13	0.45	0.15						
BRACHYURIDAE									
Decapod remains	5.32	1.43	0.75	1.64	0.45	0.07	3.13	1.83	0.22
Mursia cristimanus	11.7	3.14	1.48	11.48	3.61	1.54	9.38	3.4	0.39
Shoveller	1.06	0.35	0.69						
Goneplax angulata	2.13	0.18	1.46						
Megalopa	14.89	2.35	0.55						
MOLLUSCA									
Ostracoda				1.64	0	0			
BIVALVIA	1.08	0.07	0.01	1.64	0.03	0	1.59	0.23	0.45
GASTROPODA	1.06	0	0	1.64	0.37	0.15			
CEPHALOPODA	2.13	0.48	3.59	3.28	0.83	0.42	1.56	0.01	0.18
Sepiid remains									
Sepia officinalis									
CHORDATA									
CHONDRICHTHYES									
Squalus sp.							3.13	0.82	3.67
Raja pullopunctata							1.56	0.98	0.6
Egg-case				1.64	0.43	0.06			
TELEOSTEI									
Teleost remains	29.79	7.9	7.94	42.62	19.3	10.53	40.63	20.81	8.79
P.costatus	29.79	15.01	30.85	21.31	11.4	9.57	12.15	3.61	1.39
Gnathophis sp.	7.45	1.7	1.81	26.23	18.43	49.1	51.56	38.35	60.34
Bregmatoceros sp.	12.77	0.85	0.61	3.28	1.59	0.02			
Pleuronectiformes	2.13	0.51	2.87	4.92	3.19	1.33	6.25	2.79	4.82
Anguilliformes							1.56	0.74	3.6
C.zanzibarensis				1.64	1.55	10.95			
Sardinops ocellata head	1.06	0.79	9.8	3.28	1.55	8.45	7.81	4.54	9.7
Sardinops ocellata tail	1.06	0.55	8.07				1.56	0.52	0.24
AMORPHOUS MATERIAL	43.62	11.71	5.11	22.95	5.27	1.7	37.5	5.49	2.23

APPENDIX D

Diet composition of immature (<400mmDW), maturing (400-500mmDW) and mature (>500mmDW) *R.pullopunctata*. (%FO=percentage frequency of occurrence; %V=percentage volume; %M=percentage mass).

	R.PULLOPUNCTATA								
	IMMATURE n=56			MATURING n=36			MATURE n=32		
PREY SPECIES	%FO	%V	%M	%FO	%V	%M	%FO	%V	%M
NEMATODA	12.5	0.13	0.1	8.3	0.73	0.25	28.13	0.37	0.15
ANNELIDA									
POLYCHAETA				2.78	0.59	0.04	3.13	0	0
ARTHROPODA									
CRUSTACEA									
Crustacean remains	25	6.16	3.05	22.22	2.55	0.91	21.88	2.73	2.25
STOMATOPODA									
P.armata capensis	3.57	1.95	1.7	2.78	0.62	0.69			
ANOMURA									
Upogebia capensis							3.13	1.22	0
AMPHIPODA									
Amphipod remains				2.78	0.28	0.01			
ISOPODA	11.43	0.24	0.03						
MYSIDACEA(unid)									
Orange-eyed mysids	21.43	5.37	0.66	2.78	0.03	0.01	6.25	0.33	0.01
Red-eyed mysids	5.36	0.57	0.14						
Black-eyed mysids	1.79	0.15	0.02						
CARIDAE									
Shrimp remains	21.43	6.69	4.48	19.44	4.37	1.94	12.5	1.01	0.29
Leptochela robustus	21.43	7.04	3.44	11.11	3.73	2.12	6.25	0.63	0.31
Pandalina brevirostris	10.71	4.06	1.08	19.44	8.41	4.14			
Pontophilus sculptus	23.21	8.42	5.94	22.22	3.53	4.9	9.38	1.14	0.34
Unid shrimp 2				5.56	2.06	1.08			
Unid shrimp 3	21.43	2.53	2.65	13.89	5.65	2.25	9.38	1.95	1.22
Pink shrimp	3.57	0.86	0.39						
BRACHYURIDAE									
Decapod remains	5.36	0.64	0.52	5.56	0.42	0.16	6.25	1.63	0.09
Mursia cristimanus	41.07	16.15	14.6	66.67	29.87	27.42	68.75	25.16	17.22
Goneplax angulata				2.78	0.16	0.16			
Megalopa	1.79	0.03	0						
CEPHALOPODA									
Sepiid remains	1.79	0.31	0	5.56	1.56	7.71	18.75	6.33	7.55

APPENDIX D (continued)

CHORDATA									
TELEOSTEI									
Teleost remains	35.71	12.64	6.96	63.89	18.83	25.81	71.88	30.78	29.63
P.costatus	39.29	18.23	33.97	25	10.04	13.98	21.88	10.09	7.57
Gnathophis sp.				5.56	0.04	0.71	18.75	5.63	8.15
Bregmatoceros sp.	3.57	0.37	0.66	2.78	0.2	0.1	3.13	0.63	0.03
Pleuronectiformes	7.14	2.99	9.75	5.56	0.67	2.58	6.25	2.06	3.05
Sardinops ocellata head							3.13	1.04	3.97
Chelidonichthys sp.							3.13	2.72	6.89
Merluccius sp.							3.13	3.13	8.64
M. capensis head	1.79	1.25	5.64						
AMORPHOUS MATERIAL	30.36	4.83	3.24	30.56	5.81	2.94	34.38	2.93	2.29

APPENDIX E

Diet composition of animals caught in the spring and winter months. (%FO=percentage frequency of occurrence; %V=percentage volume; %M=percentage mass).

	R.WALLACEI						*R.PULLOPUNCTATA*					
	APRIL/ MAY			SEPT/ OCT			APRIL/ MAY			SEPT/ OCT		
	n=125			n=92			n=72			n=60		
PREY SPECIES	%FO	%V	%M	%FO	%V	%M	%FO	%V	%M	%FO	%V	%M
NEMATODA	2.38	0.24	0	4.3	0.03	0.01	27.78	0.25	0.18	21.67	0.48	0.2
ANNELIDA												
POLYCHAETA	22.22	4.5	0.51	15.05	1.8	0.43	2.78	0.3	0.01			
ARTHROPODA												
CRUSTACEA												
Crustacean remains	17.46	2.34	0.73	22.58	6.8	0.9	23.61	3.35	2.25	23.33	5.98	1.44
STOMATOPODA												
Mantid remains	0.74	0.2	0.04	1.08	1.08	0.17						
P.armata capensis	1.59	0.35	0.33	2.15	1.1	0.59	2.78	0.67	0.31	1.67	1.39	0.58
ANOMURA												
Upogebia capensis	9.52	5.45	1.94				1.39	0.54	0			
AMPHIPODA												
Amphipod remains	3.17	0.16	0.01	1.08	0.15	0.02	1.39	0.14	0			
Ampelisca palmata	8.73	1.45	0.02									
Unid amphipod 2	0.79	0	0									
White	2.38	0.12	0.05	17.2	1.82	0.43						
Gammarid	0.79	0.08	0.02									
Paramoera capensis				2.15	0.02	0.01						
Unid amphipod 3				1.08	0.06	0.01						
Lyianassa ceratina	3.17	0.27	0.01	3.23	0.18	0.04						
Stenopus hispidus							1.39	0.04	0.01			
ISOPODA												
Isopod remains	4.76	0.5	0.08									
Orange-eyed	0.79	0.02	0.02	3.23	0.76	0.19						
Eurydice lonicornis	3.17	0.35	0.03									
Unid isopod 1				1.08	0.48	0						
Black-eyed				1.09	0.02	0						
Mesanthura canenlula				1.08	0.05	0.01						
MYSIDACEA(unid)												
Orange-eyed mysids	17.46	8.94	0.59	27.96	8.15	0.96	9.72	2.69	0.06	13.33	1.98	0.18
Red-eyed mysids				11.83	1.95	0.22	2.78	0.23	0.01	1.67	0.23	0.04
Black-eyed mysids				4.3	0.49	0.07				1.67	0.14	0.01

APPENDIX E (continued)

CARIDAE												
Shrimp remains	7.14	0.38	0.04	2.15	1.28	0.16	27.78	6.93	1.87	6.67	1.11	0.3
White shrimp	3.17	1.74	0.05	21.51	5.38	2.01						
Leptochela robustus	0.79	0.03	0	5.38	2.32	0.49	5.56	1.03	0.55	25	7.99	2.06
Pandalina brevirostris	0.79	0.02	0	1.08	0.71	1.88	4.17	1.25	0.66	16.67	7.34	1.6
Pontophilus sculptus	7.14	2.05	0.44	8.6	1.48	0.39	15.28	4.97	2.25	21.67	4.62	1.96
Unid shrimp 2							2.78	1.03	0.37			
Unid shrimp 3							27.78	5.66	2.45			
Black-eyed	2.38	0.25	0.03	22.58	4.4	0.76						
Red-eyed				2.15	0.45	0.08						
Pink shrimp							2.78	0.67	0.1			
BRACHYURIDAE												
Decapod remains	5.56	1.43	0.16	1.08	1.07	0.61	6.94	0.45	0.2	3.33	1.19	0.1
Mursia cristimanus	13.49	3.36	0.68	7.53	3.41	1.51	51.39	16.42	17.13	56.67	27.36	17.64
Shoveller	0.79	0.26	0.06									
Goneplax angulata	1.59	0.13	0.13				1.39	0.08	0.05			
Megalopa	3.17	0.2	0.01	10.87	2.13	0.22	1.39	0.02	0			
MOLLUSCA												
Ostracoda	0.79	0	0									
BIVALVIA	1.59	0.16	0.35	1.08	0.02	0						
GASTROPODA	1.59	0.19	0.05									
CEPHALOPODA												
Sepiid remains	3.97	0.77	0.63				8.33	2.83	8.07	6.67	1.08	2.02
CHORDATA												
CHONDRICHTHYES												
Squalus sp.	1.59	0.42	2.76									
Raja pullopunctata	0.79	0.5	0.45									
Egg-case	0.79	0.22	0.02									
TELEOSTEI												
Teleost remains	38.1	15.7	8.29	34.41	14.33	14.78	51.39	14.81	18.55	60	28.38	44.94
P.costatus	19.05	8.52	5.62	26.88	13.83	7.64	45.83	20.7	18.55	8.33	3.58	1.99
Gnathophis sp.	30.16	21.65	51.94	19.35	11.26	8.05	9.72	2.18	6.86	1.67	0.41	0.07
Bregmatoceros sp.	9.52	1.34	0.05	2.15	0.13	0.05	2.78	0.27	0.06	3.33	0.47	0.27
Pleuronectiformes	5.56	2.34	3.97	2.15	1.42	2.04	11.11	3.58	5.92			
Anguilliformes	0.79	0.38	2.71									
C.zanzibarensis	0.79	0.78	3.56									
Sardinops ocellata head	6.35	3.61	10.9				1.39	0.46	3.24			
Sardinops ocellata tail	0.79	0.41	0.71	1.08	0.36	1.11						
Chelidonichthys sp.							1.39	1.21	5.64			
Merluccius sp.										1.67	1.67	11.03
M.capensis head										3.33	2.61	11.54
AMORPHOUS MATERIAL	38.1	8.4	2.03	33.33	7.8	3.92	45.48	6.84	3.57	13.33	2.85	2.13

APPENDIX F

Diet composition of males and females. (%FO=percentage frequency of occurrence; %V=percentage volume; %M=percentage mass).

	R.WALLACEI						*R.PULLOPUNCTATA*					
	MALES			FEMALES			MALES			FEMALES		
	n=107			n=112			n=62			n=70		
PREY SPECIES	%FO	%V	%M	%FO	%V	%M	%FO	%V	%M	%FO	%V	%M
NEMATODA	0.93	0.01	0.01	5.36	0.29	0.01	27.42	0.4	0.14	22.86	0.31	0.25
ANNELIDA												
POLYCHAETA	17.76	3.07	0.72	20.54	3.63	0.39	3.23	0.35	0.02			
ARTHROPODA												
CRUSTACEA												
Crustacean remains	25.23	4.33	1.13	14.29	4.15	0.56	27.42	4.32	1.42	20	4.7	2.5
STOMATOPODA												
Mantid remains	0.93	0.93	0.07	0.89	0.22	0.06						
P. armata capensis	1.87	0.95	0.25	1.79	0.4	0.43	1.61	1.34	0.44	2.86	0.69	0.39
ANOMURA												
Upogebia capensis	1.87	0.87	0.65	8.93	5.3	2.19	1.61	0.16	0			
AMPHIPODA												
Amphipod remains	1.87	0.1	0.02	2.68	0.21	0.01	1.64	0.17	0			
Ampelisca palmata	4.67	1.45	0.03	5.36	0.25	0.01				1.43	0.04	0.01
Unid amphipod 2	0.93	0.01	0									
White	12.15	1.21	0.11	5.36	0.94	0.1						
Gammarid	0.93	0.09	0.06									
Paramoera capensis	0.93	0	0.01	0.89	0.01	0						
Orange-eyed	1.87	0.09	0.01	0.89	0.06	0						
Unid amphipod 3	0.79	0.04	0.01									
Lyianassa ceratina	2.8	0.54	0.07	3.57	0.3	0.03						
Stenopus hispidus												
ISOPODA												
Isopod remains	2.8	0.25	0.05	2.68	0.32	0.08						
Orange-eyed	2.8	0.52	0.1	0.89	0.16	0.01						
Eurydice lonicornis	1.87	0.16	0.03	1.79	0.24	0.03						
Unid isopod 1				0.89	0.4	0						
Black-eyed				0.89	0.01	0						
Mesanthura canenlula				0.89	0.04	0						
MYSIDACEA(unid)												
Orange-eyed mysids	29.91	11.24	1.18	14.29	6.09	0.36	11.29	1.47	0.06	11.43	3.16	0.17
Red-eyed mysids	5.61	0.96	0.04	4.46	0.73	0.03	1.61	0.52	0.05	1.43	0	0
Black-eyed mysids	1.87	0.36	0.02	1.79	0.06	0	1.61	0.13	0.01			

APPENDIX F (continued)

CARIDAE												
Shrimp remains	6.54	0.34	0.05	3.57	1.17	0.06	12.9	4.98	0.98	21.43	3.67	1.57
White shrimp	9.35	2.77	0.68	12.5	3.27	0.15						
Leptochela robustus	1.87	1.47	0.11	3.57	0.55	0.05	22.58	6.32	1.77	7.14	2.3	0.51
Pandalina brevirostris	0.93	0.02	0	0.89	0.59	0.4	11.29	4.01	0.75	8.57	4.02	1.33
Pontophilus sculptus	7.48	2.88	0.94	8.04	0.79	0.17	25.81	5.48	3.63	11.42	4.22	0.6
Unid shrimp 2							1.61	0.39	0.38	1.43	0.71	0.07
Unid shrimp 3							12.9	2.31	0.48	17.14	3.77	2.57
Black-eyed	13.08	2.38	0.27	8.93	1.66	0.06						
Red-eyed				1.79	0.37	0.02						
Pink shrimp										2.86	0.69	0.13
BRACHYURIDAE												
Decapod remains	1.87	0.14	0.03	5.36	2.37	0.32	9.68	1.63	0.28	1.43	0.04	0.04
Mursia cristimanus	14.02	4.77	1.06	8.04	2.05	0.66	51.61	20.02	19.15	55.71	22.61	15.63
Shoveller				0.89	0.29	0.08						
Goneplax angulata	0.93	0.04	0.08	0.89	0.11	0.13				1.43	0.08	0.07
Megalopa	9.35	1.6	0.08	3.57	0.45	0.02	1.61	0.02	0			
MOLLUSCA												
Ostracoda	0.79	0.93	0									
BIVALVIA	1.87	0.19	0.88	0.89	0.02	0						
GASTROPODA	1.87	0.22	0.12									
CEPHALOPODA												
Sepiid remains	0.93	005	0.1	3.57	0.83	0.77	9.68	2.75	7.8	2.86	1.3	2.92
CHORDATA												
CHONDRICHTHYES												
Squalus sp.				1.79	0.47	3.59						
Raja pullopunctata				0.89	0.56	0.58						
Egg-case	0.93	0.26	0.05									
TELEOSTEI												
Teleost remains	35.51	13.26	6.9	37.5	16.53	10.4	50	18.13	25.37	60	23.5	32.84
P.costatus	20.56	10.92	9.34	24.11	10.64	4.14	27.42	10.62	6.59	30	14.95	17.94
Gnathophis sp.	22.43	14.34	51.35	28.57	20.01	53.52	6.45	1.65	5.62	5.71	1.13	2.8
Bregmatoceros sp.	7.48	1.31	0.09	5.369	0.36	0.03	1.61	0.13	0.18	4.29	0.57	0.11
Pleuronectiformes	2.8	1.97	3.66	5.36	1.92	3.71	1.61	0.45	0.33	10	3.28	7.06
Anguilliformes				0.89	0.43	3.52						
C.zanzibarensis				0.89	0.87	4.63						
S. ocellata head	4.67	3.01	16.05	2.68	1.26	5.92	1.61	0.54	3.9			
S.ocellata tail	0.93	0.31	0.47	0.89	0.46	0.92						
Chelidonichthys sp.							1.61	1.4	6.78			
Merluccius sp.							1.61	1.13	1.77	1.43	1.24	7.39
M.capensis head							1.61	1.61	8.49			
AMORPHOUS MATERIAL	32.71	7.44	3.15	39.29	8.82	1.86	35.48	7.41	2.94	27.14	4.68	3.11

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