TAXONOMY, BIOLOGY AND MANAGEMENT OF SOUTH AFRICAN SCIAENID FISH OF THE GENUS *UMBRINA*

by

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DECLARATION

The seven core chapters of this thesis have been written in the format of scientific papers in order to facilitate publication. Thus a degree of repetition, particularly in the introductions and the material and methods was unavoidable. The findings of Chapter 1 have recently been published (*Afr. J. mar. Sci.* **27**(1): 1-21) and Chapter 2 has been accepted for publication (*Fish. Res.* in press.), both in somewhat shortened versions. Co-authorship on these papers is held by my supervisors who provided guidance during the research and made valuable comments on the draft manuscripts. With the exception of where assistance is acknowledged, the candidate was responsible for all hypotheses, data collection, analyses, interpretation and conclusions. Staff of the Department of Genetics at the University of Pretoria were contracted to undertake sequencing of tissue samples collected for population genetic analyses covered in Chapter 6. The candidate spent some time visiting the laboratory, assisted with initial analyses and gained practical experience in the methods of DNA extraction, PCR amplification, sequencing and statistical analyses; but the majority of the laboratory work and statistical analyses of the sequence data was conducted by Mr Arrie Klopper of the above mentioned Department. Although the candidate was solely responsible for the hypotheses, interpretation of the results and conclusions presented in Chapter 6, this section of the thesis must be considered a collaborative effort.

This work has not been submitted for a degree at any other university and any assistance the candidate received is fully acknowledged.

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ABSTRACT

Taxonomy, biology and management of South African sciaenid fish of the genus *Umbrina*.

Kenneth Hutchings, August 2005

Key words: age and growth, distribution, life history, movement patterns, per-recruit stock assessment, population genetics, reproduction, taxonomy, *Umbrina*

This research was initiated in 2001 with the overall objective of providing scientific information relevant to the sustainable management of South African *Umbrina* species. Previously there was confusion over the identity and distribution of *Umbrina* species in South African waters and very little was known of their life histories, population dynamics and stock status. Morphological comparison of a large number of South African *Umbrina* (n = 369) with specimens from the type locality (Canary Islands) confirmed the identity of South African *U. canariensis* Valenciennes, 1843, and allowed for an expanded description of the species. However, differences between specimens of *U. ronchus* Valenciennes, 1843 and those of the second South African species, lead to the resurrection of *U. robinsoni* Gilchrist and Thompson 1908, as a valid name for this species. Spatial analysis of South African specimens collected with a variety of gear revealed *U. robinsoni* to be a shallow water species found from the surf-zone to 40 m depth that is targeted by recreational shore anglers and spear fishers, whilst *U. canariensis* occurs predominantly from 40-100m depth and is predominately landed as a by-catch in the inshore trawl fishery. Although both species occur throughout the South African eastern seaboard, *U. canariensis* is most common west of the Kei River, where the continental shelf is wider.

The life history of *U. canariensis* was investigated by sampling two separate regions of abundance off the South African east coast -the central Agulhas Bank (n = 227) and Algoa Bay (n = 550). Maximum ages recorded, using thin otolith sections were 25 and 27 years for males and females respectively. Statistical comparisons of growth between sexes were equivocal and are not thought to be biologically significant. Growth rates (sexes pooled) did, however, differ between regions with central Agulhas Bank *U. canariensis* attaining a greater asymptotic length (L_∞ = 40 cm TL), but at a slower rate than those in Algoa Bay (L_∞ = 35 cm TL). Trends in monthly proportions of histologically validated macroscopic maturity stages in mature females and average monthly gonadosomatic indices suggested an extended spring-summer spawning season from August to December in both regions. Estimated size at 50 % maturity (L_{50}) did not differ significantly (likelihood ratio tests) between regions or between sexes and was 22 cm for males and 23 cm for females (regions combined). Although female L_{50} did not differ between regions, differences in growth rate resulted in an older age at L_{50} for Algoa Bay (3.2 years) than on the central Agulhas Bank (2.2 years). Per-recruit analyses reveal that stocks in both regions are currently underexploited. The similarity between median age-at-maturity and selectivity by commercial trawl gear, and the presence of spatial refuges in the form of rocky substrata which can not be trawled, probably provide a measure of protection for spawner biomass. However, the life-history characteristics of *U. canariensis* (relatively slow growth, longevity and low natural mortality rate) do make the species vulnerable to exploitation and target reference point estimates will be reached at low levels of fishing mortality.

Spatial variation in the life-history strategies of *U. robinsoni* was investigated by sampling populations in the warm temperate De Hoop Marine Protected Area (MPA) (n = 312) and the Kosi Bay region of the subtropical Maputaland MPA (n = 354). Kosi Bay fish grew faster and attained a significantly larger asymptotic length (L_∞ = 88 cm TL) than De Hoop fish (L_∞ = 60 cm TL) but experienced a higher natural mortality rate (M = 0.35 vs. M = 0.26) and attained a younger maximum age ($t_{\max}$ = 12 vs. 16 years). A clearly defined summer spawning season (October- February) was found for De Hoop fish, whilst spawning within the Kosi Bay population is not synchronized and occurs throughout the year. Kosi Bay females attained 50 % sexual maturity at a significantly larger size (48 vs. 39 cm) but at younger age (2.8 vs. 3.4 years) than those in De Hoop. Long-term mark-recapture data and diver counts during depletion sampling at selected sites indicated that *U. robinsoni* are strongly philopatric with small home-ranges. Analysis of *U. robinsoni* mitochondrial control region sequences (n = 123) from three sites along South Africa's east coast, (False Bay, Stil Bay and Kosi Bay), suggested population level genetic structure, although statistical tests of genetic differentiation between sites were not conclusive. A strong positive correlation between genetic differentiation (pairwise F_{ST}) and geographic distance suggested an isolation-by-distance pattern, indicative of higher levels of gene flow amongst geographically proximal populations than between geographically distant populations. The significant life-history differences, evidence of reduced gene flow between spatially separate populations and high degree of residency of *U. robinsoni* requires that regional populations are considered as separate stocks or management units. Current spawner biomass per-recruit ratios (*SB/R*) for *U. robinsoni* stocks at three sites - False Bay, Stil Bay and the KZN coast, were estimated to be either at or below the 25 % threshold, indicating overexploitation. Reductions in fishing mortality (*F*) necessary to achieve target fishing mortality levels ($F_{SB\,40}$) at the current minimum size limit (l_c 40 cm TL) ranged from 51-57 %. Increasing the l_c to 50 cm is predicted to increase *SB/R* ratios to 36 % $SB/R_{F=0}$ in False Bay, 43 % $SB/R_{F=0}$ in KZN and 52% $SB/R_{F=0}$ in Stil Bay, at current levels of *F*. Biological reference points ($F_{SB\,40}$ and $F_{SB\,25}$) calculated using length-at-age data collected 10 years apart in False Bay showed little variation. This suggests that for moderately long-lived species the frequency of age and growth studies for per-recruit stock assessment purposes can be at least the lifespan of a cohort.

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GENERAL INTRODUCTION

The Sciaenidae are represented by approximately 70 genera and more than 270 species (Chao 1986a) making them one of the largest perciform families. Sciaenids are found in temperate and tropical coastal and shelf edge waters throughout the world, whilst extensive morphological variation allows members of the family to inhabit diverse environments including benthic and pelagic habitats (Sasaki 1989). Sciaenids are commonly referred to as croakers and drums in reference to the sounds made by the males of many species using sonific muscles attached to the swim bladder (Trewavas 1977, Mohan 1984). Considerable variation in life histories also exists within the family; the smallest species e.g. *Larimus fasciatus*, *Cynoscion nothus* and *Johnius dussumieri* only attain total lengths (TL) of approximately 20cm and maximum ages of 1.5-2.5 years, whilst the larger species e.g. *Argyrosomus japonicus*, *Sciaenops ocellatus* and *Pogonias cromis* grow to well over 100 cm TL and live in excess of 40-50 years (De Vries and Chittenden 1982, Standard and Chittenden 1984, Beckman *et al.* 1990, Griffiths and Hecht 1995a, Ross *et al.* 1995, Fennessy 2000). They are widely exploited as food fishes in artisanal and commercial fisheries around the world and constitute as much as 30 % of bottom trawl catches in certain fishing grounds in the north-eastern Atlantic (Chao 1986b) and 6 % of total marine fish landings in India (Mohan 1984). Larger sciaenid species are also highly valued as sport fishes in many countries (Mohan 1984, Chao 1986b, Nieland and Wilson 1993, Griffiths and Heemstra 1995, Ross *et al.* 1995, Nieland *et al.* 2002). In South African waters, three species of kob, *Argyrosomus inodorus*, *A. japonicus*, and *A. thorpei* and the geelbek *Atractoscion aequidens* are important components of recreational and commercial line fisher catches (van der Elst 1993a). The biology and management of these sciaenids in South Africa has been the focus of several scientific studies; the stocks of all four species are currently considered overexploited and severe catch restrictions are enforced (van der Elst *et al.* 1990, Griffiths and Hecht 1995a, b, Griffiths 1996a, b, Griffiths 1997a, b, c).

Amongst the Sciaenidae, only the genus *Umbrina,* comprising 17 species, has a worldwide distribution (Chao 1986a). Walker and Radford (1992) described the eight species found in the eastern Pacific and noted that most of the species in this region are found in shallow coastal waters (collected with beach-seines). Five of the eastern Pacific species, *U. analis*, *U. bussingi*, *U. dorsalis*, *U. wintersteeni* and *U. xanti* attain small-medium maximum size (< 35 cm TL) and are of limited importance to commercial and recreational fisheries but several are valued as good food fish (Walker and Radford 1992, Chao 1995). The three larger species *U. galapogorum*, *U. reedi* and *U. roncador* (maximum size ranges from 45-65cm TL) are more highly valued as food fish and the yellowfin croaker *U. roncador* is an important shore angling species off southern California (Walker and Radford 1992). Four species, all of small to medium size (< 40 cm TL), are known from the western Atlantic (Gilbert 1966, Chao 2002). Two of these species, *U. brussonneti* and *U. coroides* inhabit inshore waters and are occasionally harvested for food or bait (Robins and Ray 1986, Robbins *et al.* 1991). Little information exists on *U. milliae* which is recorded from deep water off Columbia (Chao 2002), whilst *U. canosai* is caught in demersal trawls off southern Brazil (Haimovici and Reis 1984). In the old world, four *Umbrina* species were described (Chao 1986b, Chao and Trewavas 1990). Inhabiting the eastern Atlantic coasts of Europe and north Africa, including the Mediterranean, Black Sea and Sea of Azov, *U. cirrosa* is a large (70 cm TL) inshore species (shoreline to about 100m depth) that is considered a high value commercial and sport fish species (Chao 1986b, Fabi and Fiorentini 1993). *U. steindachneri* is a medium sized (max. 47 cm TL), species that occurs along the West African coast from Guinea to Angola in water depths of 15-100m (Chao and Trewavas 1990). This species appears to be rare and due to a lack of a detailed morphometric description, there had been some doubt about the species validity (Chao 1986b). The other two old world species, *U. canariensis* and *U. ronchus*, were originally described from the Canary Islands and appeared to have particularly wide distributions. The former was thought to occur from the western Mediterranean and West African coast to Cape Point (South Africa) and into the western Indo-Pacific as far as Pakistan and the latter along the west African coast from Gibraltar to Angola, also in the western Indo Pacific off the coasts of South Africa and Mozambique to Oman (Heemstra 1986, Randall 1995, Sasaki 1996).

Along the eastern seaboard of South Africa, *Umbrina* species are an important component of recreational shore angling and spearfishing catches (Bennett *et al.* 1994, Mann *et al.* 1997) as well as constituting a noteworthy by-catch of beach-seines (Lamberth *et al.* 1994), inshore trawlers (Japp *et al.* 1994) and boat-based line-fishers (Brouwer and Buxton 2002). There has been some confusion about the identification and distribution of the species off the South African coast; "*U. ronchus*" was believed to be limited to Natal waters, whilst *U. canariensis* was thought to be the species caught in the eastern and southwestern Cape (Heemstra 1986). However, fishers and researchers maintained that there were at least two species in Cape waters.

Published work on *Umbrina* species in South African waters was mostly limited to mention of their occurrence in catches (Bennett *et al.* 1994, Japp *et al.* 1994, Mann *et al.* 1997, Brouwer and Buxton 2002). Size composition and seasonality for "*U. canariensis*" caught in False Bay beach-seines was provided by Lamberth *et al.* (1994) and Lasiak (1986) provided descriptions of size composition and feeding for "*U. capensis*" that were seine netted in the surf-zone in Algoa Bay. "*U. canariensis*" were recorded (number and length frequency) in experimental trawling along the south and east Cape coast in papers by Beckley (1984) and Wallace *et al.* (1984). Elsewhere, aspects of the biology of *U. canariensis* in the southeast Atlantic, including growth, reproduction and mortality rates, were described by Venidictova (1982, 1983a, 1983b) and embryonic development under laboratory conditions by Podosinnikov (1979). The studies of Venidictova (1982, 1983a, 1983b) were, however, fairly superficial and aimed at assessing the exploitation potential of the stock for the soviet trawler fleet. *U. canariensis* does not occur along the South African west coast or the southern Namibian coast and it is therefore very likely that the southeast Atlantic stocks are separate from those along the South African east coast.

Despite the importance of *Umbrina* species to the recreational fisheries and its occurrence as by-catch in several commercial sectors of South Africa, the biology of the species had never been studied. Many inshore South African fish species have been overexploited and there is an urgent need to develop species-specific, scientifically-based management plans (Griffiths *et al.* 1999). If this was to be achieved for South African *Umbrina* species, clarity on the identification and distribution of stocks or species and information on their life histories was urgently needed. This project was initiated in 2001 with the primary objective of providing scientific information required for the sustainable management of South African *Umbrina* species. In order to achieve this overall objective, the following key questions were asked:

i. What species of *Umbrina* occur in South African waters?

ii. How are these species distributed spatially?

iii. What are the life-history characteristics (growth rate, spawning seasonality, size at maturity, migration and mortality) of *Umbrina* species or stocks?

iv. What is the stock status of exploited *Umbrina* populations?

v. Is there temporal variation in growth rates within a population, and if there is, what are the effects on estimates of mortality and biological reference points?

vi. What recommendations can be made for the sustainable management of the resource?

Thesis outline

An investigation into the taxonomy and distribution of South African *Umbrina* species is presented in Chapter 1. A large collection of preserved South African specimens are compared with museum specimens of *U. canariensis*, *U. ronchus* and *U. steindachneri* from the type localities (Canary Islands and Senegal). The presence of *U. canariensis* within South African waters was confirmed. Differences between the second South African species and *U. ronchus* led to the reinstatement of *U. robinsoni* (previously thought to be a synonym) as a valid name for the species. Expanded morphometric descriptions of all four sub-Saharan African *Umbrina* species are given. The distribution of *U. canariensis* and *U. robinsoni* within South African waters is elucidated through spatial analysis of catches made with a variety of gear types.

Chapter 2 reports on the life history of *U. canariensis* populations sampled from two discrete centres of abundance off the South African south and east coasts. Information on age and growth, reproductive biology and evidence of stock separation is presented and discussed.

Chapter 3 assesses the stock status of these two *U. canariensis* populations using per-recruit methods. The results of per-recruit analysis are discussed in terms of the management of species and suggestions to improve future monitoring and stock assessment are given.

Spatial variation in the life history of *U. robinsoni* is investigated in Chapter 4. Information is provided on age and growth, reproduction and mortality for warm temperate and subtropical populations inhabiting marine reserves. The life-history strategies of the two populations are compared and discussed in terms of environmental differences and in the context of life history theory.

The movement patterns of *U. robinsoni* are investigated in Chapter 5, based on the analysis of long-term mark-recapture data and diver counts during depletion sampling within a marine reserve. The implications of the findings are discussed in relation to stock separation and the impacts of exploitation.

Chapter 6 further examines stock separation of *U. robinsoni* by investigation of genetic structure at the population level. Mitochondrial DNA control region sequences from three spatially separated populations are analysed. Patterns of gene flow amongst populations are inferred from observed differences in haplotype frequencies and the geographic distances between sites. The long-term management implications (relevant to conservation) of the findings are discussed.

The results of per-recruit analysis of three exploited *U. robinsoni* stocks are presented in Chapter 7. The effects of alternative minimum size limits on spawner biomass per-recruit ratios are evaluated, as is the impact of temporal variation in growth rate on biological reference point and mortality estimates. Potential sources of error in the estimation of natural and fishing mortality are discussed and suggestions made for future management measures.

Chapter 8 draws the results together and discusses the advances made in our understanding of *Umbrina* stocks in southern African waters. The life history of the two South African *Umbrina* species are compared to other sciaenids and topics for further research are identified.

CHAPTER 1

IDENTITY AND DISTRIBUTION OF SOUTHERN AFRICAN SCIAENID FISH SPECIES OF THE GENUS *UMBRINA*

ABSTRACT

Two *Umbrina* species - *U. canariensis* Valenciennes, 1843 and *U. robinsoni* Gilchrist and Thompson, 1908 – are recognized from southern Africa. The latter species was hitherto believed to be a synonym of *Umbrina ronchus* Valenciennes, 1843 (type locality Canary Islands). *U. canariensis* is distributed along the South Africa eastern seaboard from Cape Point to Sodwana Bay and *U. robinsoni* is known from False Bay to Madagascar and Oman. African *Umbrina* taxonomy has, however, been hindered by geographic samples that were either too few or consisted of specimens of disparate length; and as a result the identification and distribution of South African *Umbrina* species was confused. Morphological comparison of a large number of South African *Umbrina* with specimens from the type locality (Canary Islands) confirmed the identity of South African *U. canariensis* and allowed for an expanded description of the species. However, differences between specimens of *U. ronchus* and those of the second South African species (n = 251), lead to the resurrection of *U. robinsoni* (Gilchrist and Thompson 1908) as a valid name for this species. *U. robinsoni* differs from *U. ronchus* in having a smaller supraoccipital crest and thus a less steep pre-dorsal profile; a shallower preorbital bone (13 – 21 % HL vs. 21 % HL); and a shorter nostril-orbit distance (2.4-6.9 % head length [HL] vs. 7.8-8.5 % HL). Colour patterns also differ between the two species, with *U. ronchus* lacking the oblique, wavy white stripes evident on the flanks of *U. robinsoni*. *U. ronchus* does not occur in South African waters, and is an Eastern Atlantic species occurring from Gibraltar to Angola. Specimens from the east coast of Africa (Mozambique to Gulf of Oman) that were previously identified as *U. ronchus* are *U. robinsoni*. Differences between *U. robinsoni* and *U. canariensis* include: a lower modal number of soft dorsal fin rays, (22-27 vs. 24-30); less deep body depth, (26-36 % standard length [SL] vs. 33-39 % SL); shorter pectoral fin length, (15-21 % SL vs. 20-25 %SL); longer caudal peduncle length (26-34 % SL vs. 21-28 % SL) and snout length, (27-38 % HL vs. 23-32 % HL); and smaller orbit diameter, (14-33 % HL vs. 23-34 % HL). Otoliths of *U. robinsoni* differ from those of *U. canariensis* in being smaller, less elongate, lacking a massive postcentral umbo and having a post-dorsal spine remnant. The body colour and nature of the striping pattern on the flanks differs markedly between the species: in *U. robinsoni* the oblique stripes are thin, wavy, white lines; in *U. canariensis* the oblique stripes are thicker, nearly straight and brown; *U. robinsoni* also lacks the triangle shaped mark on the outer operculum and the dark pigmentation of the inner operculum that is found on *U. canariensis*. Spatial analysis of South African specimens collected with a variety of gear revealed *U. robinsoni* to be a shallow water species found from the surf-zone to 40m whilst *U. canariensis* occurs predominantly from 40-100m depth. Although both species occur throughout the South African eastern seaboard, *U. canariensis* is most common west of the Kei River, where the shelf is wider. Examination of three specimens of *Umbrina steindachneri* Cadenat, 1950 confirmed the presence of a fourth sub-Saharan *Umbrina* species that is limited to tropical West African waters from Senegal to Angola. *Umbrina steindachneri* differs from

the other African *Umbrina* in having a high number of soft dorsal rays (28-29), a greater 3rd dorsal spine length (25-27 % SL) and a very pronounced and convoluted striping pattern on the flanks.

INTRODUCTION

The genus *Umbrina* is unique amongst the Sciaenidae in having a worldwide distribution; occurring in tropical and temperate continental shelf and upper slope waters (Sasaki 1989, Walker & Radford 1992). It is distinguished from other genera in the family by the presence of a simple (without appendages), wholly abdominal swim bladder and a chin barbel with a median pore at its tip (Trewavas 1964, 1977; Chao 1986b; Walker & Radford 1992).

The taxonomy of the New World *Umbrina* species has been well researched; Gilbert (1966) provides a review of the four species recorded in the western Atlantic and Walker and Radford (1992) reviews the eight Pacific species. In the Old World, four species are described from the eastern Atlantic (Chao 1986b, Chao & Trewavas 1990). Dardignac (1961) analyzed distinguishing characteristics between *Umbrina cirrosa* (Linnaeus 1758), *Umbrina canariensis* Valenciennes 1843 and *Umbrina ronchus* Valenciennes 1843 (using the synonym *Umbrina fusca)* from specimens collected off the coast of Morocco. Two of these, *U. canariensis* and *U. ronchus* appear to have particularly wide distributions. The former was thought to occur from the western Mediterranean and West African coast to Cape Point (South Africa) and into the western Indo-Pacific as far as Pakistan and the latter along the west African coast from Gibraltar to Angola, also in the western Indo Pacific off the coasts of South Africa and Mozambique to Oman (Heemstra 1986, Randall 1995, Sasaki 1996).

The fourth African species, *Umbrina steindachneri* (Cadenat 1950) was described from the coast of Senegal; the type is believed to be lost (Chao & Trewavas 1990) and no detailed description of this species morphometrics exists. Chao (1986b) suspected that *U. steindachneri* might be synonymous with *U. canariensis* but later (Chao & Trewavas 1990) stated that the species was valid.

The holotype of *U. ronchus* was believed to be lost (Trewavas 1964) and Palmer (1966) described a neotype from one of two specimens collected from the type locality, the Canary Islands. The dry and dissected holotype was later found (Bauchot & Desoutter 1987) but owing to its means of preservation is of limited value for morphometric measurements. Palmer (1966) compared the Canary Islands specimens to a single large *Umbrina capensis* Pappe, 1853 specimen from False Bay, South Africa and suggested that the two species may be synonymous (Table 1.1).

In a review of the Indo-Pacific Sciaenidae, Trewavas (1977) examined 12 specimens of *U. canariensis* and *U. sinuata* (Day 1876) including seven South African specimens (Table 1.1) but did not compare these with specimens from the type locality (Canary Islands). Three specimens of *U. ronchus* were examined by Trewavas (1977): the neotype plus another specimen from the Canary Islands and one specimen from False Bay, South Africa (Table 1.1). The morphometrics of these three specimens were compared with those for *Umbrina robinsoni* based on the original descriptions for *U. robinsoni* and *U. angustilineata* by Gilchrist and Thompson (1908, 1911). Trewavas (1977) highlighted the need for further taxonomic research on the South African *Umbrina*, specifically to investigate the possible synonymy of *U. ronchus* and *U. robinsoni* and also the possible presence of both *U. canariensis* and *U. sinuata* in the region.

Later authors accepted the synonymy of *U. ronchus* and *U. robinsoni* as well as that of *U. sinuata* and *U. canariensis*, (Heemstra 1986, Chao & Trewavas 1990) but no researchers had actually compared a large sample of South African specimens of a similar size range with the type specimens. In the most recent review of the Indian Ocean Sciaenidae, Sasaki (1996) did examine a fair sample of South African *U. canariensis* and compared these with specimens from other regions, including a similar size syntype of *U. canariensis* (Table 1.1). Sasaki (1996), however, examined only two small South African *U. ronchus* specimens and the much larger dry holotype. In this review, Sasaki (1996) stressed that most of the diagnostic characters between *U. ronchus* and *U. canariensis* are either overlapping or involve allometric changes, making species separation difficult.

Table 1.1: Old World *Umbrina* specimens examined by earlier researchers.

Author	Specimens examined	Museum and registration number	Locality	Size range SL (mm)
PALMER (1966)	*U. ronchus* (2)	BMNH 1964.12.30. 1-2, neotype + one other	Canary Islands (Las Palmas fish market)	444, 484
	U. capensis (1),= *U. ronchus?*	BMNH – no number provided	South Africa, False Bay	705 TL
	U. canariensis	BMNH – no number provided	Canary Islands	340 TL
TREWAVAS (1977)	*U. ronchus* (2)	BMNH 1964.12.30.1-2	Canary Islands (Las Palmas fish market)	444, 484 (same specimens as Palmer 1966?)
	U. ronchus (1)	BMNH 1808.5.25.1	South Africa, False Bay	595
	U. canariensis (3)	BMNH 1935.5.11.121-123	Angola	229-290
	U. canariensis (7)	BMNH 1935.5.2.171 1897.12.17.15, 1891.10.21.5, 1905.6.8.31, 1919.9.12.17-18, 1903.12.31.1	South Africa, Cape of Good Hope, Mossel Bay, Algoa Bay, Durban, Amatikulu	59.5-361
	U. canariensis (2)	BMNH 1887.11.11.164, (stuffed holotype of *U. striata*) 1891.2.9.16	India, Muscat	334, 258
SASAKI (1996)	*U. ronchus* (2)	ANSP 55096, BMNH 19.3.12.31	South Africa, Durban, Natal	157.7, 82.7
	U. ronchus (1)	MNHN 5764 (dry, dissected holotype of *U. ronchus*)	Canary Islands	434
	U. canariensis (13)	ANSP 63896, BMNH 1891.10.21.5, 1919.2.12.17-18, USNM 324683, (10)	South Africa, Durban, Algoa Bay, Natal (60-70m)	56.9-188 (3 same as Trewavas 1977)
	U. canariensis (4)	USNM 324682	Pakistan (90-101m)	194-280.5
	U. canariensis (2)	BMNH 1887.11.11.164 (holotype of *U. striata*), 1891.2.9.16	India, Muscat	337, 254.1
	U. canariensis (2)	BPBM 35903, 35940	Southern Oman (4-6m)	?, 124
	U. canariensis (2)	CAS (SU) 10584 (holotype of *U. valida*) MNHN A5669 (syntype of *U. canariensis*)	Canary Islands	299.4, 299.5
	U. canariensis (1)	BMNH 1985.7.9.247	Mozambique, Beira	159.4
	U. canariensis (1)	MNHN 7307 (syntype of *U. lafonti*)	Gulf of Gascony	272.5
	U. canariensis (1)	USNM 306321	Gulf of Aden (30-36m)	558 ?

Along the eastern seaboard of South Africa, *Umbrina* species are an important component of recreational shore angling and spearfishing catches (Bennett *et al.* 1994, Mann *et al.* 1997) as well as constituting a noteworthy by-catch of beach-seines (Lamberth *et al.* 1994), inshore trawlers (Japp *et al.* 1994) and boat-based line-fishers (Brouwer and Buxton 2002). There has been some confusion about the identification and distribution of the species; *U. ronchus* was believed to be limited to Natal waters, whilst *U. canariensis* was thought to be the species caught in the eastern and southwestern Cape (Heemstra 1986). Fishers and researchers however maintained that there were at least two species in Cape waters. Many inshore South African fish species have been overexploited and there is an urgent need to develop species specific, scientifically based management plans (Griffiths *et al.* 1999). If this is to be achieved for South African *Umbrina* species, clarity on the identification and distribution of stocks or species is urgently needed.

In this chapter, expanded descriptions of *U. canariensis* and *U. robinsoni* based on large samples (n = 118 & 251) collected along the entire South African eastern seaboard (Cape Point to Mozambique border) are provided. These are statistically compared using 25 morphological measurements to each other and to specimens of *U. ronchus, U. canariensis* and *U. steindachneri* from the type localities (Canary Islands and Senegal). The distribution patterns of South African *Umbrina* are investigated by spatial analyses of specimens collected throughout the shelf region.

MATERIAL AND METHODS

A total of 322 South African specimens were collected and preserved. Catch methods included beach-seining, trawling, spear and line fishing. Gonads and otoliths were removed from specimens prior to preservation, but this was done in a manner to limit damage to the fish (the pectoral girdle was not cut and gills were not removed). Preservation involved injection with 40 % formalin solution and immersion in a 10 % formalin solution for 30 days; thereafter specimens were rinsed in freshwater for three days and stored in 70 % isopropanol. Measurements were only taken after a minimum of thirty days in the isopropanol, i.e. once the specimens had stabilised. Museum specimens examined include an additional 38 South African specimens, two *U. ronchus* from the Canary Islands (type locality), seven *U. canariensis* from the northeast Atlantic (Canary Islands, Morocco and France), and two *U. canariensis* from Angola. Institutional abbreviations follow Leviton *et al.* (1985). Material examined is listed after each description. The letters F (female), M (male) and J (juvenile – specimens too small to be sexed) are used to indicate sex. Standard length (SL) measured using a flat steel ruler to the nearest mm is used throughout, unless otherwise stated. Notes on the colour and pigmentation of species were made from fresh specimens unless indicated otherwise.

Counts and measurements generally follow the methods of Hubbs and Lagler (1964) with modifications listed below. Gill-rakers were counted on the first arch and do not include rudiments (structure wider than longer). The raker at the epibranchial and ceratobranchial joint is included in the "lower gill-raker" count. Counts of rostral pores include marginal pores that are typically lobed whilst the mental pore count does not include the one at the tip of the barbel. Measurements were taken using precision calipers to the nearest 0.1 mm. Body depth was measured between the origins of the dorsal and pelvic fins. The head length (HL) measurement includes the membranous, most posterior edge of the operculum. Nostril-orbit distance was measured from the posterior "long nostril" to the anterior edge of the orbit. The least fleshy interorbital width was measured. The "inter-round nostril" distance was measured between the anterior "round nostrils". The depth of the preorbital (lachrymal) bone was measured as the shortest distance between the margin of the orbit and the ventral margin of the bone close to the origin of the upper jaw. Dorsal caudal peduncle length was measured obliquely from the posterior end of the dorsal fin to the intersection of the lateral line and the caudal fin base. Ventral caudal peduncle length was measured in a similar fashion from the posterior end of the anal fin base. Pelvic and anal fin lengths were measured from the fin origin to the tip of the longest ray. Pectoral fin length was taken from the origin of the most dorsal ray to the tip of the longest ray; if pectoral fin lengths differed, the longest was used. Obviously broken fins or spines (present on many specimens that were obtained by trawling) were not measured. Anal spine width was measured at the base of the spine. Scale measurements were taken from a scale removed where the tip of the appressed pectoral fin touched the body.

Measurements were expressed as percentages of HL and/or SL. For the South African species, *U. canariensis* and *U. robinsoni*, morphometric ratios were arcsine transformed and compared using ANOVAs. Frequency distributions of meristic counts were compared using a Kolmogorov-Smirnov test. The sagittal otoliths of 30 *U. canariensis* and 30 *U. robinsoni* were examined and measurements of otolith length, height and post dorsal edge to cauda distance were taken. These measurements were expressed as proportions; arcsine transformed and compared using t-tests. Linear regressions of fish total length vs. otolith length and height were calculated and the slopes compared using t-tests (Zar 1996). Specimens of *U. ronchus, U. canariensis* and *U. steindachneri* from the type locality were compared to similar sized South African specimens using multivariate methods. Differences in morphometric ratios were displayed in dendrograms and multi-dimensional scaling (MDS) plots based on normalized Euclidean distance using the PRIMER 5.2.2 software package (Plymouth Marine Laboratory, Plymouth, UK). Radiographs of the skulls of two *U. ronchus* from the type locality and 12 *U. robinsoni* from South Africa were examined and the distance from the joint of the first vertebra to the most dorsal point of the supraoccipital crest was measured.

The distributions and habitats of *U. canariensis* and *U. robinsoni* in South African waters were determined by analysis of research and recreational catch data. During sampling it became apparent that in the Cape, *U. canariensis* occurs further offshore, in deeper water (40-150 m depth) than *U. robinsoni*, which typically inhabits the surfzone and shallow sub tidal reefs (Table 1.2). Consequently demersally trawled *Umbrina* from the Cape consist entirely of *U. canariensis* (a few are landed by line-fishing boats operating in deep water) whilst rock and surf anglers, spear fishers and beach-seine operations land *U. robinsoni.*

The South African fisheries authority (Marine and Coastal Management) conducts annual demersal biomass surveys (DBS) based on the swept-area method that are used to provide biomass estimates for species exploited by the South African hake-directed trawl fishery. West coast (Namibian border to Cape Agulhas) and south coast (Cape Agulhas to Port Alfred) cruises are undertaken. On each cruise, stratified (by depth zone: 0-50 m, 51-100 m, 101-200 m, and 200-500 m) semi randomly selected 5 x 5 nautical mile blocks were trawled (according to the ratio of blocks per stratum).

Trawls were conducted over soft substratum using a 180-foot German trawl fitted with a 25-mm mesh liner. Trawl duration was limited to 30 minutes; results of shorter trawls have been standardized to that time. For a more complete description of DBS methods see Badenhorst and Smale (1991).

Catch per unit effort data for *U. canariensis* from DBS's conducted by the South African research vessel "Africana" during the period 1986-1999 was plotted graphically using SURFER 7 software (Golden Software, Golden, USA). Occurrences of *U. robinsoni* were determined from the records of shore-angling and spear-fishing club competitions and research catches made over a two-year period (2001-2002).

Table 1.2: Distribution of *U. canariensis* (U. c.) and *U. robinsoni* (U. r.) specimens showing percentage of total number sampled in different depth zones and regions during 2001 and 2002.

Region	Surf-zone		Surf-zone – 30 m		31 – 150 m		n (all depths)	
	% U .r.	% U. c.	% U .r	% U. c.	% U .r	% U. c.	U. r.	U. c.
SWC	99.9	0.1	*	-	-	-	116	2
SC	100	-	*	-	-	100	330	180
EC	100	-	6	94	-	100	8	469
KZN	100	-	100	-	-	100	365	2
n (all regions)	454	1	365	31		618	819	651

SWC = False Bay – Cape Agulhas
SC = Cape Agulhas - Mossel Bay
EC = Mossel Bay – East London
KZN = East London – Mozambique Border
* *U. robinsoni* is known to occur in this depth zone in the SWC & SC

SYSTEMATIC ACCOUNT

Umbrina Cuvier

Umbrina Cuvier 1816: 297. Type species *Sciaena cirrosa* Linnaeus 1758, by monotypy.

Attilus Gistel 1848: 109. Type species *Sciaena cirrosa* Linnaeus 1758, by monotypy.

Asperina Ostroumoff 1896: 30. Type species *Asperina improviso* (= *U. cirrosa*) Ostroumoff 1896, by monotypy.

Description

Genus description generally follows Trewavas (1977), Chao (1986b) and Walker & Radford (1992). Moderately elongate, deep bodied sciaenid fishes with an arched dorsal profile and relatively straight ventral margin. Wholly abdominal, carrot shaped swim bladder without appendages. Snout protuberant with 10 pores, mouth ventral with a single, pored barbel on chin flanked by two pairs of mental pores. Teeth small and villiform, outer row on upper jaw may be slightly enlarged. Margin of preopercle evenly and finely serrated, opercle ending in two small, flattened spines partly covered by skin. Sagittal otoliths thick, with suculus cauda sharply bent, not reaching ventral margin and ostium nearly reaching anterior edge of otolith. Scales ctenoid, lateral line scales extending to rear edge of caudal fin. Body colour ranges from silver-grey to yellow-brown and many species exhibit oblique stripes most prominent in the mid-dorsal area, usually absent or faint ventrally and on the head. Body colour darkens and stripes become obscure or absent in larger specimens of some species. Caudal fin S-shaped, pointed, truncate or slightly emarginated. Dorsal fin with VIII-XI + I spines (usually X + I) and 21-33 rays. Anal fin with II spines, the second usually long and robust and 5-10 rays.

KEY TO THE SUB-SAHARAN AFRICAN SPECIES OF *UMBRINA*

1a. Body depth 33-39 % SL, orbit diameter 75-111 % of snout length (for fish > 15cm), dorsal fin rays usually 27-29 (24-30)...2

1b. Body depth 26-36 % SL, orbit diameter 39-81 % of snout length (for fish > 15 cm), dorsal fin rays usually 25 (22-27)..3

2a. Pectoral fin length 78-109 % of ventral caudal peduncle length, 3rd dorsal spine length 14-22 % SL, preorbital bone depth 13-17 % HL, inside gill cover darkly pigmented...*U. canariensis*

2b. Pectoral fin length 69-79 % of ventral caudal peduncle length, 3rd dorsal spine length 25-27 % SL, preorbital bone depth 17-18 % HL, inside gill cover white or very lightly pigmented...*U. steindachneri*

3a. Nostril-orbit distance 7.8-8.5 % HL, preorbital bone depth 18-24 % HL, scale length 2.3-2.4 % SL, dorsal head profile (between snout and first dorsal fin) steeply curved with clear inflection point above preopercle.........*U. ronchus*

3b. Nostril-orbit distance 2.4-6.9 % HL, preorbital bone depth 13-21 % HL, scale length 2.4-3.8 % SL, dorsal head profile smoothly convex with no clear inflection point above preopercle.....................................*U. robinsoni*

Umbrina canariensis **Valenciennes 1843**

Fig. 1.1

Umbrina canariensis Valenciennes 1843, *in* Webb and Berthelot, Hist. Nat. Canaries: 24 (Canary Islands)

For details of synonymy see Chao & Trewavas (1990).

Syntypes: MNHN nos. 7608, A 5669 (335 mm, 300 mm SL from Canary Islands)

Diagnosis

Values for the specimens examined are range and mode for meristic counts or mean (in parenthesis) for measurements. In order to distinguish components of the expanded description, counts and measurements by Trewavas (1977) are given in square brackets.

A medium size *Umbrina* species (max. 42 cm TL in 3 893 SA fish measured) with the following combination of characters: dorsal fin rays 24-30 (27) [26-29] *; gill-rakers 4-7 (6) + 8-11 (9); body depth 33-39 (36) [35-42] % SL; pre-dorsal length 35-41 (38) % SL; pectoral fin length 20-25 (23) [19-24] % SL; ventral caudal peduncle length 21-28 (24) % SL; 3rd dorsal spine length 14-22 (16) % SL; anal fin length 16-27 (19) % [13-21]; scale length 3.4-4.7 (4) % SL; upper jaw length 10-13 (11) % SL; head length 29-35 (32) [32-34] % SL; snout length 23-32 (29) [27-31] % HL; horizontal orbit diameter 23-34 (26) [23-33] % HL; nostril-orbit distance 2-5.4 (4) % HL; preorbital bone depth 13-17 (15.5) [15-19] % HL.

*Dardignac (1961) reports a range of 26-31 for specimens from Morocco

Fig. 1.1: *Umbrina canariensis*, F 276 mm SL, RUSI 69876, Angola.

Description

Counts and measurements are presented in Table 1.3. A compressed, deep bodied *Umbrina* species with a relatively large head, orbit and upper jaw and short pointed snout (orbit diameter subequal to snout length). The orbit diameter measurement typically exhibits negative allometry with increasing size, whilst snout length is nearly isometric. The pectoral fin is long, usually the same length or longer than the pelvic fin; caudal fin truncate and body scales large. Drumming muscles are well developed in males, loosely attached to the ribs but firmly joined to the dorsal surface of the swim bladder; absent in females.

Body colour silver-grey, dark dorsally and lighter ventrally; fins generally light brown near bases, becoming dark to black near tips (Fig. 1.1). Dark grey-black, broad stripes run obliquely on the flanks and may extend onto the dorsal part of head; stripes are most prominent dorsally and faint or absent below the level of the pectoral fin. Dark stripes were present on all South African and the two Angolan specimens examined (157-345 mm SL) but are faint if the scales have been lost. On the seven MNHN specimens from the NE Atlantic and Mediterranean that were examined, no stripes were visible, probably a result of the bleaching effect of long storage in alcohol (specimens were yellow or silver in colour). Inner side of operculum dark to black; a clear triangular shaped mark that is blue in fresh specimens, becoming dark or clear in

Table 1.3: Morphological measurements and meristic data of *Umbrina* species examined. The symbols in column 'P' indicate a significant difference (ANOVA) between arc-sine transformed ratios of similar size (157-350 mm) South African *U. canariensis* and *U. robinsoni* for morphometric measurements (df = 127-194) and Kolmogorov-Smirnov test for meristic counts.

		Umbrina canariensis					*Umbrina robinsoni*					*Umbrina ronchus* BMNH 1964.12		*Umbrina steindachneri* MNHN 1913, 1982		
Parameters	P	n	Mean	SD	Min	Max	N	Mean	SD	Min	Max	30.1	30.2	093	1298	1299
Standard Length (mm)		118			60	345	251			78	654	436	465	177	108	116
MEASUREMENTS % SL																
Head length	**	118	32	1.1	29	35	251	29	1.3	26	32	31	31	31	32	32
Body depth	**	118	36	1.4	33	39	251	31	1.7	26	36	31	31	36	36	36
Pre-dorsal length	**	118	38	1.2	35	41	251	35	1.7	31	40	38	39	37	38	37
Snout-Pelvic length	**	118	36	1.1	34	39	251	33	1.4	30	37	32	33	32	34	32
3rd dorsal spine length	**	51	16	1.6	14	22	234	18	2.0	12	22	19		27	25	25
Pectoral fin length	**	113	23	1.0	20	25	250	18	1.0	15	21	18	18	19	21	22
Pelvic fin length	*	118	22	1.4	19	26	251	20	1.5	17	25	20	19	23	24	26
Anal fin length	**	118	19	1.8	16	27	250	20	1.5	16	24	19	19	23	29	27
Dorsal CPD length	**	118	12	0.7	10	14	251	13	0.7	11	14	12	11	12	12	12
Ventral CPD length	**	94	24	1.1	21	28	239	29	1.6	26	34	28	27	28	28	28
CPD depth	**	118	10	0.4	9.0	12	251	10	0.7	8.6	12	8.7	9.5	10	12	10
Scale height	**	75	4.8	0.3	4.1	5.4	244	3.7	0.3	2.9	5.6	3.4	3.7	4	4	4
Scale length	**	75	4.0	0.3	3.4	4.7	244	3.1	0.2	2.4	3.8	2.4	2.3	4	3	3
2'cd anal spine length	ns	116	12	1.3	9.6	18	246	10	1.5	6.3	15	8.9		14	17	14
2'cd anal spine width	*	116	1.3	0.2	0.2	2.1	249	1.1	0.1	0.5	1.5	0.8	0.7	1	2	1
MEASUREMENTS % HL																
Snout length	**	118	29	1.5	23	33	251	34	1.5	27	38	35	38	30	30	30
Horizontal orbit	**	118	26	2.2	23	34	251	19	2.9	14	33	16	16	27	28	28
Vertical orbit	**	118	24	1.9	20	31	251	18	2.6	13	30	15	15	23	24	26
Inter orbital width	**	118	24	1.3	21	28	251	27	1.6	23	31	29	29	26	25	25
Nostril-orbit distance	ns	118	4.0	0.7	2.0	5.4	251	4.6	0.9	2.4	6.9	7.8	8.5	4	4	5
Long nostril	**	114	6.3	0.6	4.1	8.2	247	7.1	0.5	5.8	8.8	7.9	6.4	6	8	5
Inter round nostril	ns	116	20	0.8	18	23	251	20	0.8	18	22	21	21	22	20	19
Barbel length	**	116	6.2	0.9	4.4	8.6	250	5.3	0.6	3.6	8.1	5.7	4.8	6	6	6
Preorbital depth	**	94	16	0.9	13	17	237	18	1.0	13	21	21	21	18	16	18
Upper jaw length	**	118	34	1.4	31	40	251	32	1.0	29	37	32	32	34	33	31
USEFUL RATIOS																
† Orbit % Snout length	**	111	88	7.5	75	111	246	57	8.4	39	81	46	41	89	91	92
Pec. fin % Ventral CPD	**	92	93	5.0	78	109	239	61	5.4	49	73	65	66	68	75	79
MERISTIC DATA		n	Mode		Min	Max	N	Mode		Min	Max					
1st dorsal fin spines	ns	118	10		9	11	249	10		8	10	10	10	10	10	10
2cd dorsal fin spines	-	118	1		1	1	249	1		1	1	1	1	1	1	1
2cd dorsal fin rays	**	117	27		24	30	249	25		22	27	25	25	28	29	29
Pectoral fin rays	ns	117	17		15	17	246	17		15	18	16	16	16	16	16
Anal fin spines	-	118	2		2	2	248	2		2	2	2	2	2	2	2
Anal fin rays	-	118	7		7	7	247	7		7	7	7	7	7	7	7
Upper gill-rakers	**	113	6		4	7	246	5		4	6	3	3	4	4	5
Lower gill-rakers	*	116	9		8	11	248	9		6	10	8	9	9	9	9
Lateral line scales	**	88	49		47	52	229	50		48	54	51	50	49		
Rostral pores	-	118	10		10	10	248	10		10	10	10	10	10	10	10
Mental pores	-	118	4		4	4	248	4		4	4	4	4	4	4	4

ns = P > 0.05, * = P < 0.05, ** = P < 0.01.

† = This ratio does not include fish < 157 mm SL.

CPD = caudal peduncle.

preserved specimens is present on the outer surface of the operculum level with the lower flattened spine.

Sagittal otoliths rectangular, tapering to a blunt point anteriorly, broader and rounded posteriorly, moderately elongate, and becoming very thick with growth (Fig. 1.2). A large, usually smooth and pointed postcentral umbo is present on the lateral face although this may be obscured by extensive ornamentation in some individuals. The dorsal margin is slightly convex with a high-point above the ostium-cauda join; the ventral edge is rounded, tapering upwards anteriorly. The most posterior point of the otolith is near the mid-point of the descending curve of the cauda; i.e. there is no evidence of a post-dorsal spine remnant. Otolith measurements are presented in Table 1.4 and otolith length and height to fish length relationships are shown in Figs. 1.3 and 1.4.

Table 1.4: Measurements of *U. canariensis* and *U. robinsoni* otolith morphology (t-test was conducted on arc-sine transformed ratios).

Parameters	OH:OL	OT:OH	OT:OL	PD-C:OL
U. canariensis				
Mean	0.73	0.65	0.47	0.16
Min	0.59	0.48	0.37	0.13
Max	0.85	0.86	0.57	0.19
U. robinsoni				
Mean	0.77	0.52	0.39	0.22
Min	0.70	0.44	0.32	0.18
Max	0.82	0.62	0.47	0.25
n	30	30	30	30
t-value	2.63380	-6.68647	-7.28894	14.24155
p	< 0.05	< 0.001	< 0.001	< 0.001

OH = otolith height
OL = otolith length
OT = otolith thickness
PD-C = post-dorsal spine – cauda distance.

Remarks

In their studies of old world *Umbrina*, Trewavas (1964), Palmer (1966) and Trewavas (1977) discuss the synonymy of *U. canariensis* with *U. sinuata* Day, 1876 and *U. striata* Boulenger, 1888. The latter two species names were ascribed to deep-bodied South African specimens with a large orbit and high dorsal ray count by Gilchrist and Thompson (1908, 1911, 1917), Barnard (1927) and Smith (1949) (as *Sciaena* *sinuata*). Later authors described specimens from South Africa as *U. canariensis*, *inter alia* Heemstra (1986) and Chao and Trewavas (1990) (based on Trewavas 1977 description of specimens from the region) and Sasaki (1996) who examined 26 specimens, 13 of which came from South Africa (Table 1.1).

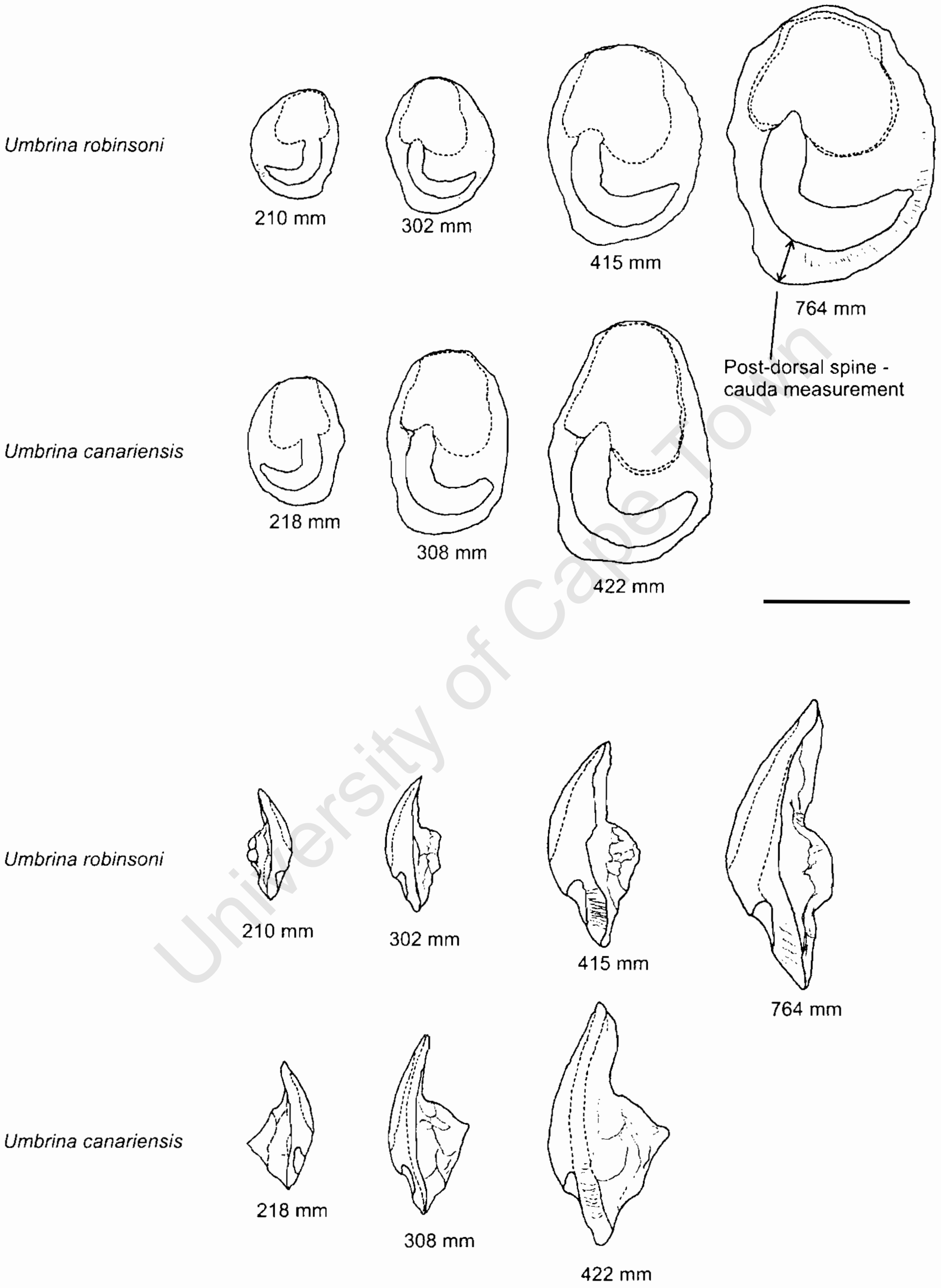


Fig. 1.2: Medial and lateral views of *Umbrina canariensis* and *U. robinsoni* otoliths showing inter-specific differences. Scale bar = 10 mm. Fish lengths (TL) are given.

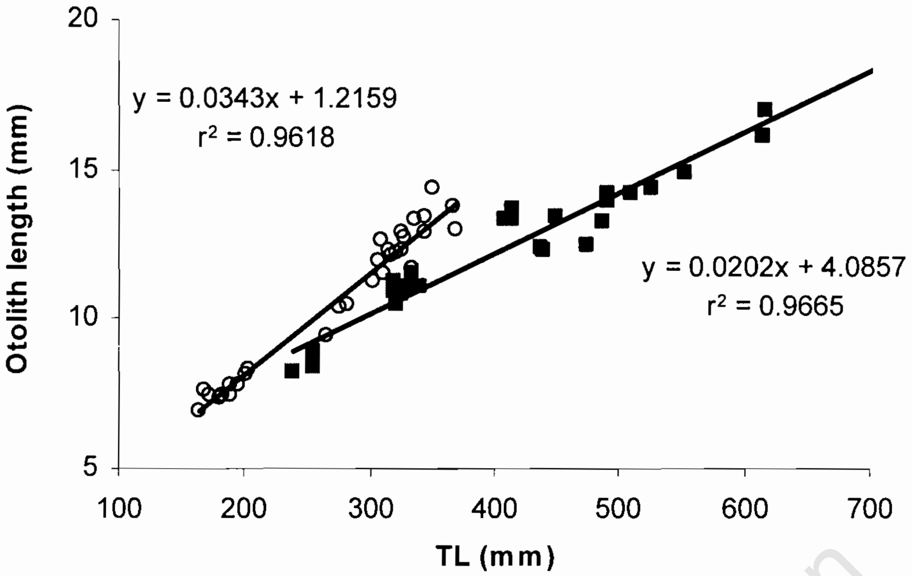


Fig. 1.3: Relationship between otolith length and fish length (TL) for South African *Umbrina canariensis* (circles) and *U. robinsoni* (squares); slopes of regression lines are significantly different, (t = 8.8, P < 0.001).

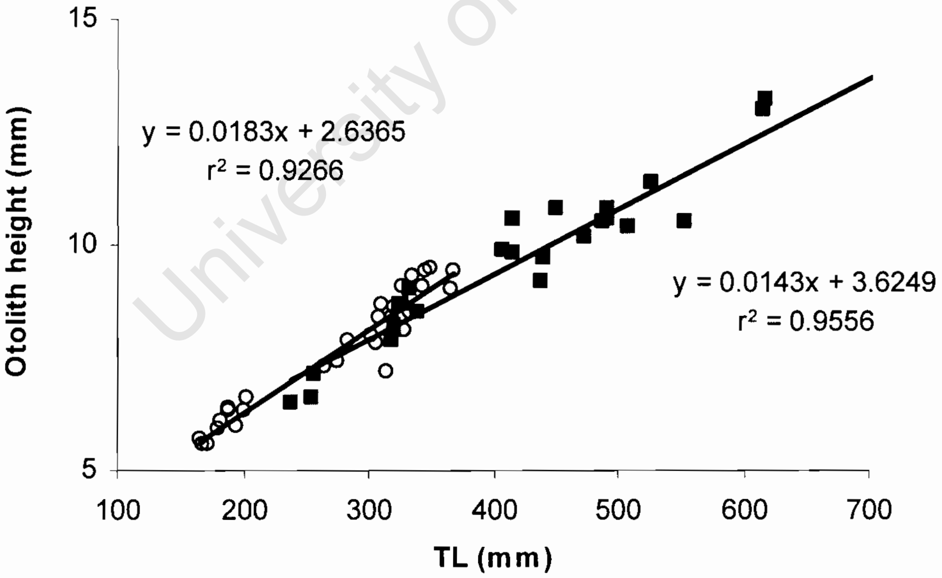


Fig. 1.4: Relationship between otolith height and fish length (TL) for South African *Umbrina canariensis* (circles) and *U robinsoni* (squares); slopes of regression lines are significantly different, (t = 3.09, P < 0.005).

In this study I provide further confirmation of the presence of *U. canariensis* off the coast of Southern Africa by comparison of 109 South African and two Angolan specimens with 7 specimens from the NE Atlantic. Five specimens from the coast of Morocco were much smaller (MNHN 1912-208-212, 60-77 mm SL) than the South African specimens (157-345 mm SL) but two (MNHN 2983, 176 mm SL, Canary Islands – type locality and MNHN 1898-0568, 163 mm SL, Gulf of Gascony, syntype of *U. lafonti* Moreau, 1874) were near the lower end of the range. Meristic data and measurements for these nine specimens fall within the range for the South African specimens or extend the range as expected for features that show allometric growth (Figs. 1.5-1.10). The two larger fish were compared to 61 South African specimens (157-250 mm SL) using multivariate methods. The dendrogram and MDS ordination plots show these two specimens grouping together with the South African fish although slightly separated as would be expected by the smaller size of the specimens (Fig. 1.11).

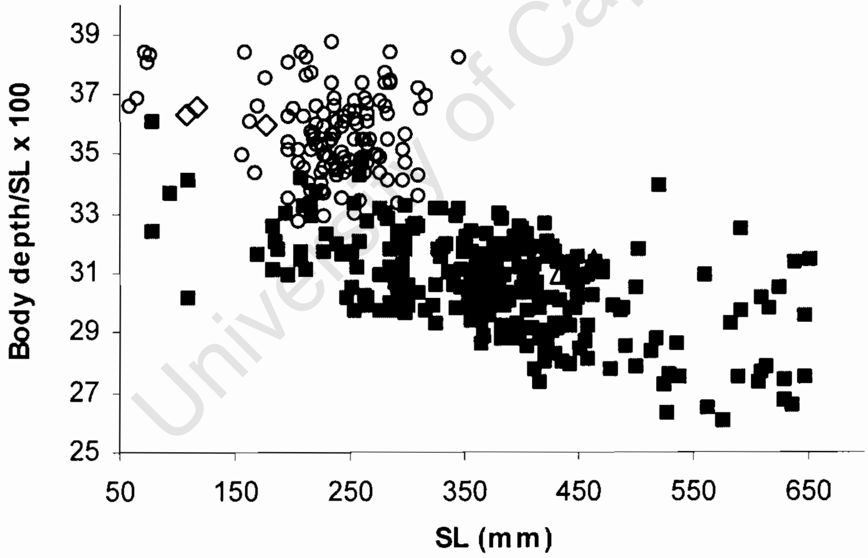


Fig. 1.5: Relationship between body depth as a % SL and SL for *U. canariensis* (circles), *U. robinsoni* (squares), *U. steindachneri* (diamonds) and *U. ronchus* (triangles).

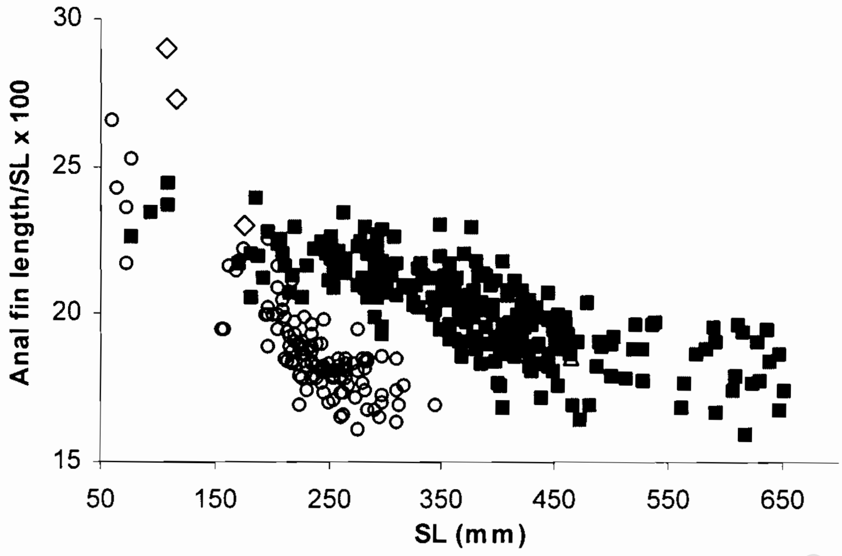


Fig. 1.6: Relationship between anal fin length as % SL and SL for *U. canariensis* (circles), *U. robinsoni* (squares), *U. steindachneri* (diamonds) and *U. ronchus* (triangles).

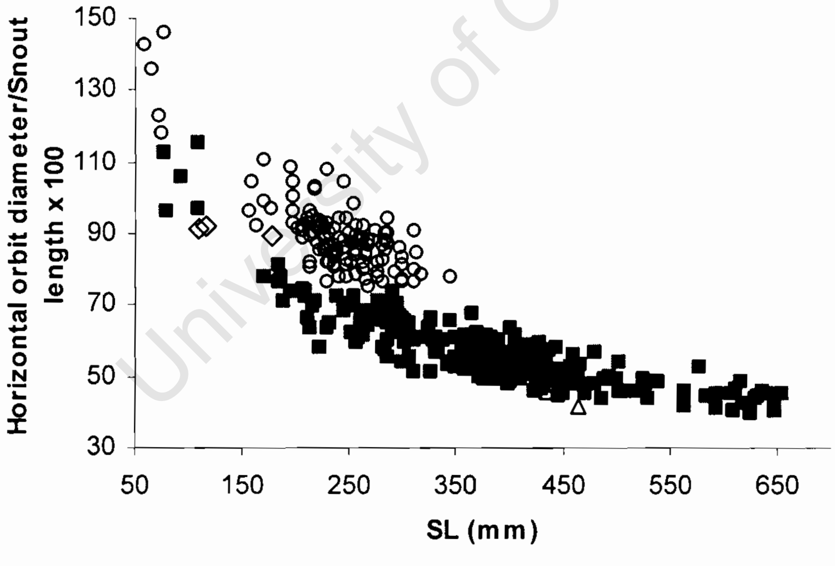


Fig. 1.7: Relationship between orbit diameter as % snout length and SL for *U. canariensis* (circles), *U. robinsoni* (squares), *U. steindachneri* (diamonds) and *U. ronchus* (triangles).

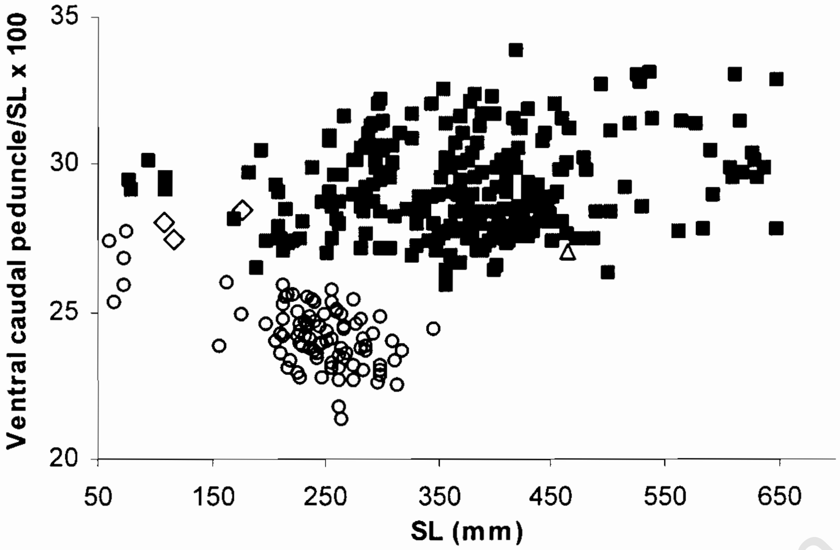


Fig. 1.8: Relationship between ventral caudal peduncle length as % SL and SL for *U. canariensis* (circles), *U. robinsoni* (squares), *U. steindachneri* (diamonds) and *U. ronchus* (triangles).

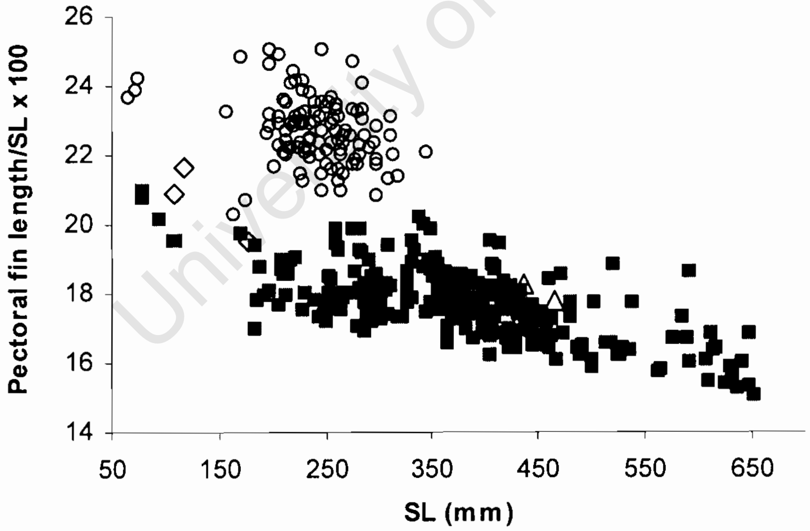


Fig. 1.9: Relationship between pectoral fin length as % SL and SL for *U. canariensis* (circles), *U. robinsoni* (squares), *U. steindachneri* (diamonds) and *U. ronchus* (triangles).

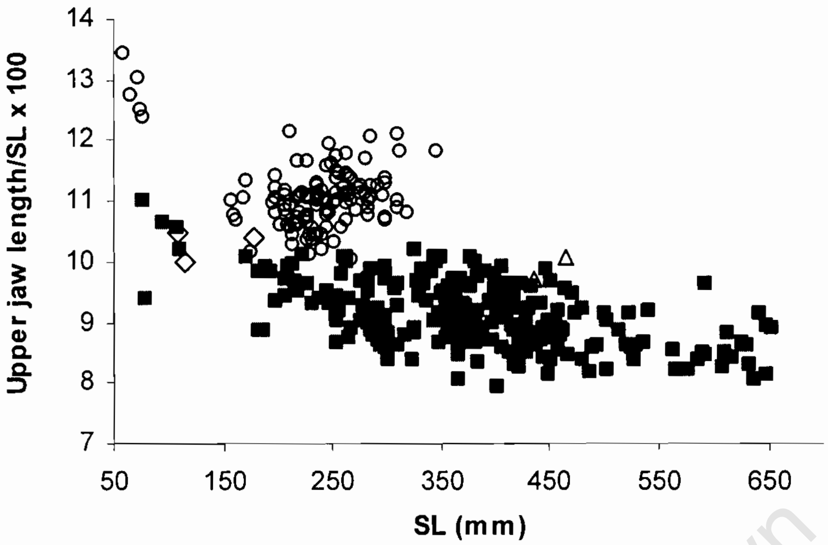


Fig. 1.10: Relationship between upper jaw length as % SL and SL for *U. canariensis* (circles), *U. robinsoni* (squares), *U. steindachneri* (diamonds) and *U. ronchus* (triangles).

Distribution and Habitat

Eastern Atlantic Ocean and western Mediterranean from the Bay of Biscay to Southern Angola (Chao and Trewavas 1990) and possibly off the central-northern Namibian coast (one specimen from Swakopmund, J. H. Holtzhausen, Ministry of Fisheries and Marine Resources, Namibia, pers. comm.). *U. canariensis* appears to be absent from the southern Namibian and South African west coast; possibly due to environmental barriers (e.g. low dissolved oxygen and water temperatures) created by the Benguela upwelling system. Also known from the Western Indian Ocean, from South Africa to Pakistan (Heemstra 1986, Sasaki 1996).

Off the South African coast, *U. canariensis* is most common along the south and east coasts between Cape Agulhas and East London with centers of abundance on the eastern Agulhas Bank and Algoa Bay (Figs. 1.12 & 1.13). Preferred depth range is between 26-75 m (Fig. 1.14) with smaller size classes more abundant in the shallower depth strata (Fig. 1.15). During this study, two small *U. canariensis* (157 and 172 mm SL) were collected from shallow water (5 m) in a False Bay beach-seine (34° 5'S; 18° 35'E) and these specimens probably represents the western extreme of the species

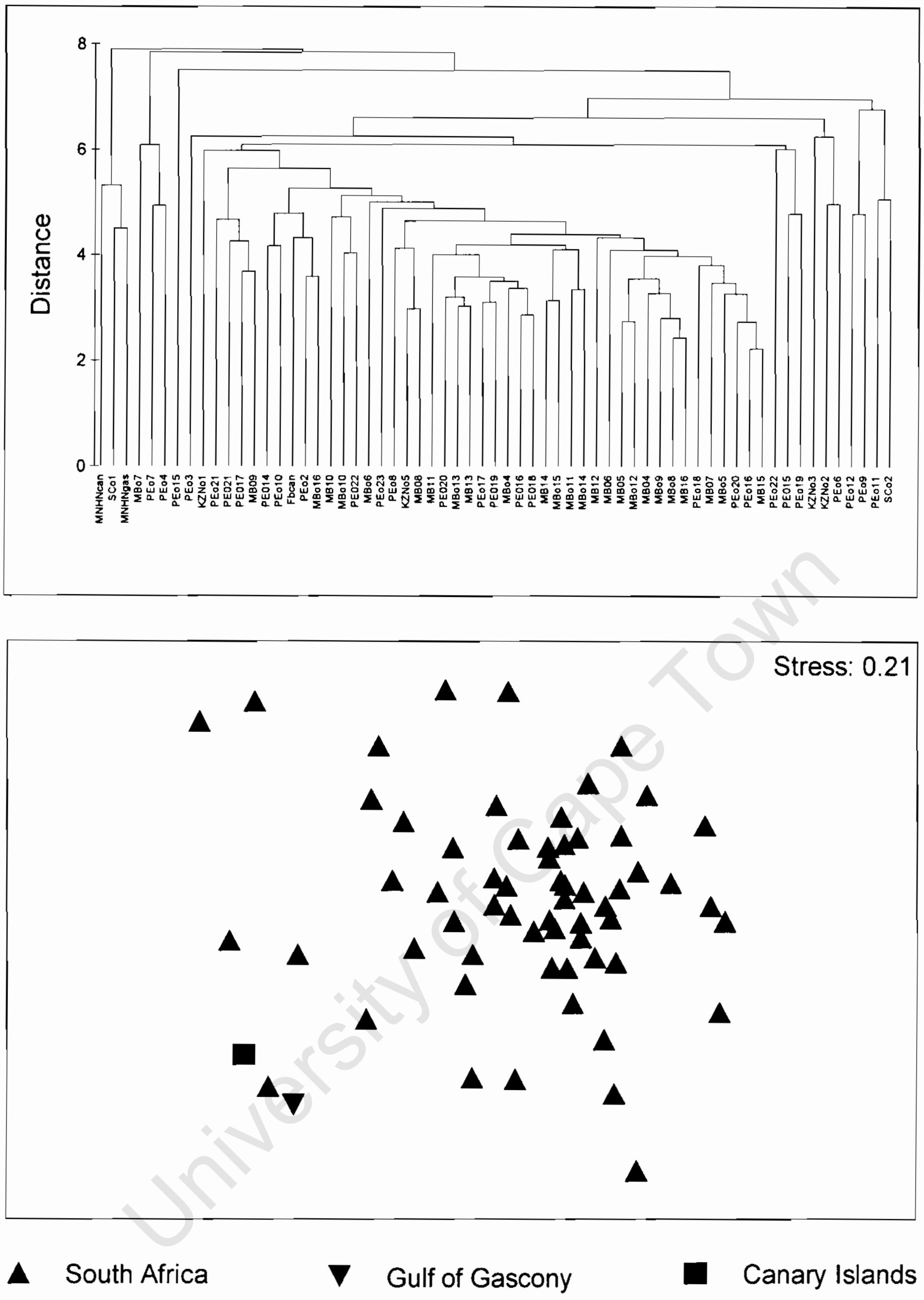


Fig. 1.11: Dendrogram and MDS ordination plot showing relationship between 61 South African *Umbrina canariensis* (collected between False Bay and Durban; 157-250 mm SL) and specimens from the Canary Islands (MNHN 2983) and Mediterranean (MNHN 1898 0568). Dissimilarity matrix derived from the normalized Euclidean distance between specimens based on 19 measurements. MNHNcan = Canary Islands; MNHNgas = Gulf of Gascony; SC = Southern Cape; MB = Mossel Bay; PE = Port Elizabeth; KZN = Kwa-Zulu Natal.

range in South African waters. Another two specimens (227 and 158 mm SL) were collected in deep water (approximately 80 m and 414 m) off the central Kwa-Zulu Natal coast (by line-fishing and crustacean trawl respectively). There are five specimens (169-259 mm SL) in the RUSI collection from Natal waters ("deep water off Pondoland" and "Durban area", 29° 51'S, 31° 00'E). Video footage taken in deepwater (130 m) off Sodwana Bay (Northern KwaZulu-Natal, 32° 41'S, 27° 32'E) during coelacanth surveys confirms the presence of *U. canariensis* in this region (K. Sink, Southern African Institute of Aquatic Biodiversity, pers. comm.) Demersal biomass surveys by the FRS *Africana* are not routinely conducted east of Port Alfred (Fig 1.12), but commercial prawn trawlers do operate off northern KwaZulu-Natal within the depth range 20-450 m and only four *U. canariensis* has been recorded as a by-catch in these fisheries (Fennessy 1994, S. T. Fennessy pers. comm.); suggesting that this species is scarce north of Durban.

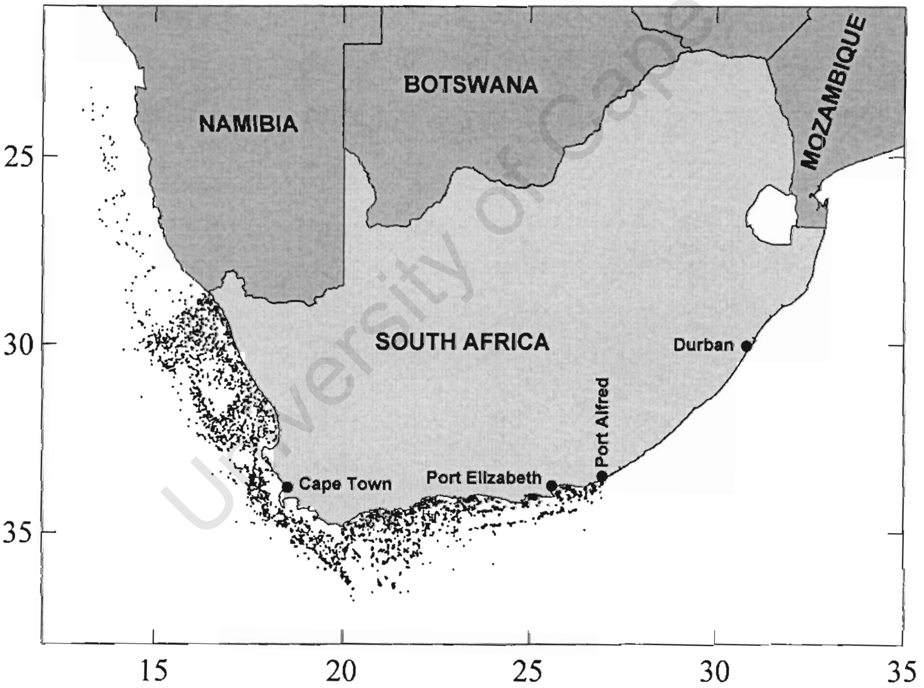


Fig. 1.12: Distribution of DBS trawls conducted by the FRS *Africana* between September 1986 and April 1999.

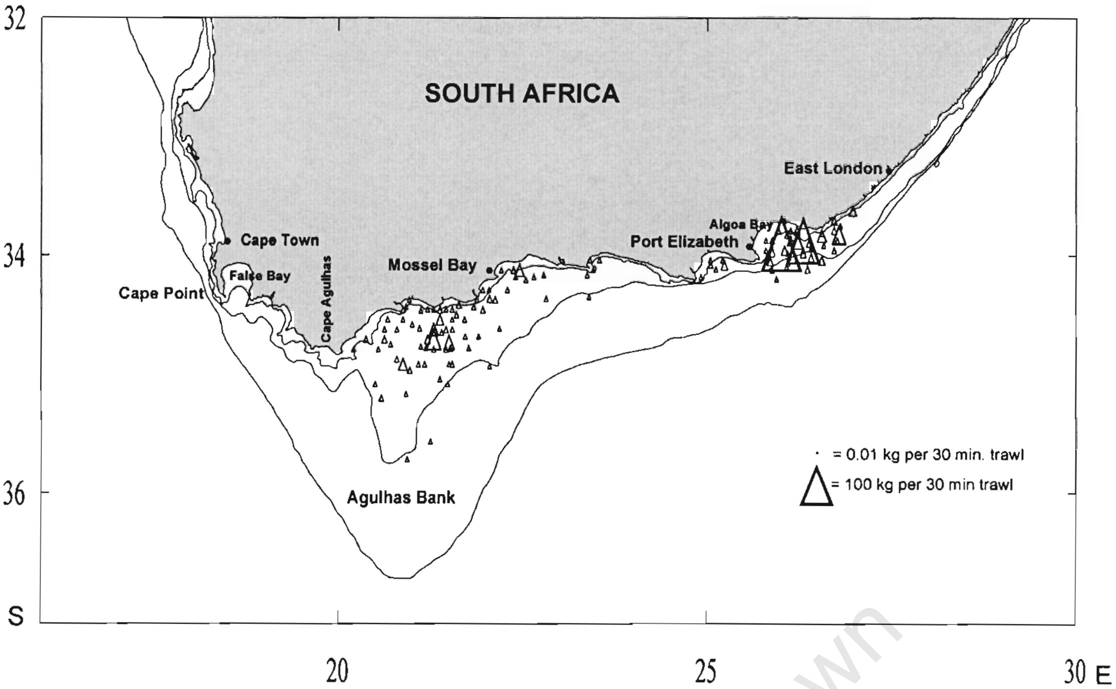


Fig. 1.13: Distribution of *Umbrina canariensis* CPUE (kg. per 30 min. trawl) in 238 DBS trawls conducted between September 1986 and April 1999; 50 m, 100 m and 200 m isobaths are shown.

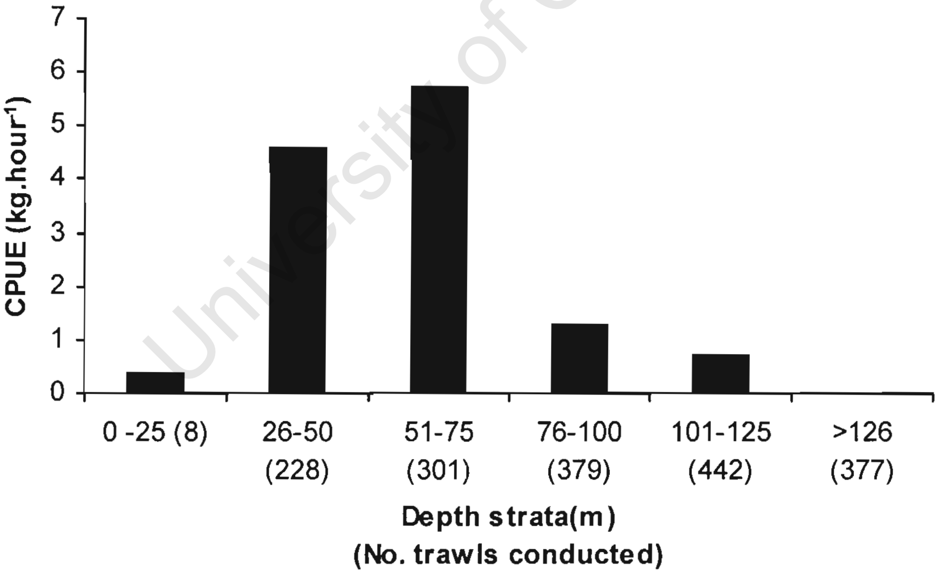


Fig. 1.14: Catch per unit effort (CPUE) of *Umbrina canariensis* caught in DBS trawls by the FRS *Africana* for different depth strata. The number of trawls conducted in each depth strata are provided.

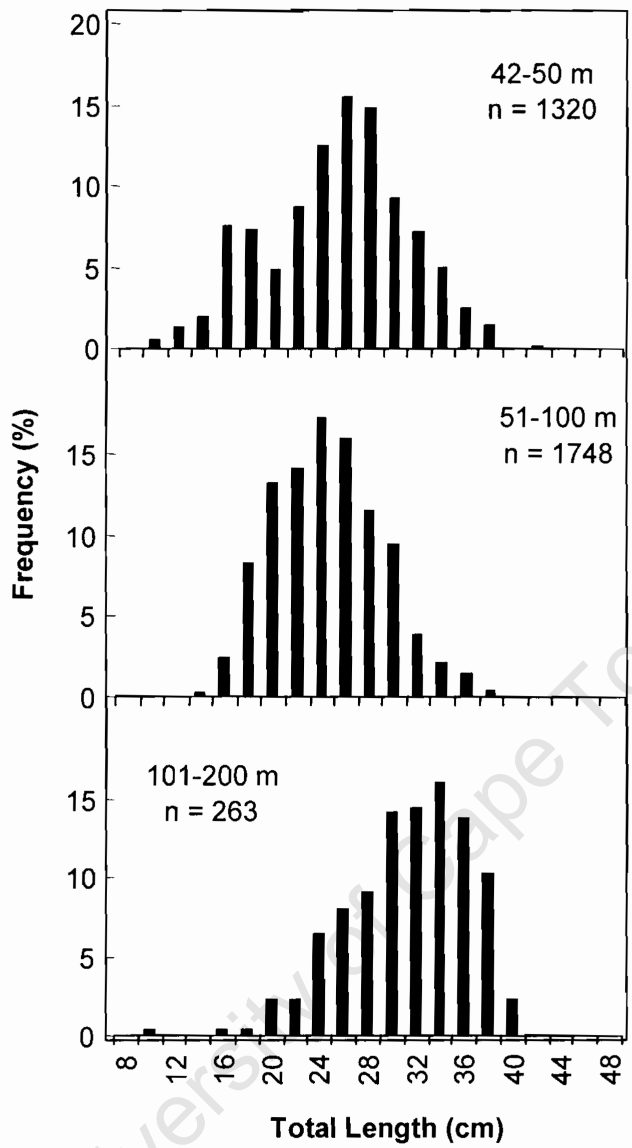


Fig. 1.15: Size frequency distributions of *Umbrina canariensis* caught in DBS trawls by the FRS *Africana* for different depth strata.

Material examined:

CANARY ISLANDS: MNHN 2983 (176 mm). FRANCE (Gulf of Gascony): MNHN 1898-0568 (163 mm, Syntype of *U. lafonti*, Moreau, 1874). MORROCO: MNHN 1912-208 (73 mm); MNHN 1912-209 (74.3 mm); MNHN 1912-210 (76.8 mm); MNHN 1912-211 (66 mm); MNHN 1912-212 (59.6 mm). ANGOLA: RUSI 69876 (F 276mm); RUSI 69875 (M 298 MM). SOUTH AFRICA: Western Cape: RUSI 67515 (J 157 mm). Southern Cape: RUSI 41988 (M 234 mm); RUSI 35546 (M 286 mm); RUSI 35545 (M 281 mm); RUSI 67499 (F 210 mm); RUSI 67500 (F 214 mm); RUSI 67501 (F 228 mm); RUSI 67502 (F 230 mm); RUSI 67504 (F 240 mm); RUSI 67506 (F 251 mm); RUSI 67508 (F

261mm); RUSI 67509 (F 265 mm); RUSI 67512 (F 292 mm); RUSI 67517 (M 216 mm); RUSI 67518 (M 226 mm); RUSI 67519 (M 229 mm); RUSI 67520 (M 236 mm); RUSI 67521 (M 240 mm); RUSI 67522 (M 246 mm); RUSI 67627 (M 267 mm); RUSI 67630 (M 298 mm); RUSI 67631 (M 313 mm); SAM 36068 (7 M 206 mm; 232 mm; 240 mm; 244 mm; 262 mm; 268 mm; 284 mm; 4 F 211 mm; 225 mm; 232 mm; 251 mm). Eastern Cape: RUSI 12333 c (M 254 mm); RUSI 12333a (M 228mm); RUSI 12333b (F 246 mm); RUSI (J 198 mm); RUSI 12767a (F 219 mm); RUSI 12767b (M 221 mm) RUSI 12767c (M 196 mm); RUSI 4918 (F 202 mm); RUSI 41989 (M 218 mm, M 221 mm); RUSI 49104 (F 273 mm); RUSI 12788 (F 159 mm); RUSI 12768 (M 207 mm); RUSI 14918 (F 171 mm); RUSI 13324 (M 198 mm); RUSI 5760 (F 311 mm); RUSI 67503 (F 235 mm); RUSI 67505 (F 247 mm); RUSI 67507 (M 318 mm); RUSI 67510 (F 277 mm); RUSI 67511 (F 282 mm); RUSI 67513 (F 310 mm); RUSI 67514 (F 345 mm); RUSI 67516 (M 198 mm); RUSI 67523 (M 250 mm); RUSI 67626 (M 260 mm); RUSI 67628 (M 274 mm); RUSI 67629 (M 283 mm); SAM 36069 (3 M 226 mm; 255 mm; 299 mm, 6 F 244 mm; 262 mm; 276 mm; 281 mm; 299 mm; 311 mm). KwaZulu Natal: RUSI 5607a (206 mm); RUSI 5607b (169 mm); RUSI 5607c (F 206 mm); RUSI 10697 (259 mm); RUSI 26206; (F 197 mm).

ADDITIONAL MATERIAL EXAMINED: SOUTH AFRICA: Southern Cape: 2001.8.1 (F 244 mm); 2001.8.6 (F 285 mm); 2001.8.10 (M 214 mm); 2001.8.15 (F 218 mm); 2001.8.19 (F 229 mm); 2001.8.22 (M 217 mm); 2001.8.23 (F 264 mm); 2001.8.24 (F 235 mm); 2001.8.28 (F 239 mm); 2001.8.32 (F 228 mm); 2001.8.39 (M 263 mm). Eastern Cape: 2001.16.1 (F 219 mm); 2001.16.4 (F 236 mm); 2001.16.7 (F 265 mm); 2001.16.9 (M 284 mm); 2001.16.10 (F 247 mm); 2001.16.12 (M 212 mm); 2001.16.13 (M 263 mm); 2001.16.15 (M 226 mm); 2001.16.16 (F 257 mm); 2001.16.17 (F 266 mm); 2001.16.19 (F 267 mm); 2001.16.21 (F 255 mm); 2001.16.23 (F 212 mm); 2001.16.24 (F 285 mm); 2001.16.25 (M 255 mm); 2001.16.26 (M 246 mm); 2001.16.29 (F 235 mm); 2001.16.33 (M 236 mm); 2001.16.36 (F 235 mm); 2001.16.38 (F 222 mm); 2001.16.39 (F 227 mm); 2001.16.40 (M 255 mm); 2001.16.42 (M 296 mm).

***Umbrina steindachneri* Cadenat 1950**

(Fig 1.16)

Umbrina steindachneri Cadenat 1950, Poissons mer Sénégal: 221, Fig. 156 (Senegal)

Umbrina cirrhosa var. *canariensis:* Steindachner 1882: 7, pl. 2 (Fig. 1) (Gorée).

Sciaena steindachneri: Collignon 1959: 9; Blache 1962: 59.

Umbrina steindachneri: Dardignac 1961: 274; Trewavas 1964: 113, 115; Sanches 1966: 109, Fig.; Williams, 1968 (distribution); Blache *et al.* 1970: 300, Fig. 790; Chao & Trewavas 1981 (FAO sheets); Seret and Opic 1981:256, 257 Fig.; Chao & Trewavas 1990: 826.

Type lost

Diagnosis

A medium size *Umbrina* species (max. 47 cm TL, Chao & Trewavas 1990) with the following combination of characters: dorsal fin rays 28-31; gill-rakers 4-5 + 9; body depth 36-37 % SL; pre-dorsal length 36-38 % SL; pectoral fin length 20-22 % SL; ventral caudal peduncle length 28-29 % SL; 3'rd dorsal spine length 25-27 % SL; anal fin length 23-29 % SL; scale length 3.4-3.8 % SL; upper jaw length 10-11 % SL; head length 31-32 % SL; snout length 30 % HL; horizontal orbit diameter 27-28 % HL; nostril-orbit distance 4-5 % HL; preorbital bone depth 17-18 % HL.

Fig. 1.16: *Umbrina steindachneri*, F, 177 mm SL, MNHN 1913-0093, Gabon.

Description

Counts and measurements for the three specimens examined are presented in Table 1.3. A deep bodied *Umbrina* species with a relatively large orbit and short rounded snout (orbit diameter subequal to snout length). The 1'st dorsal and anal fins are very long; the pectoral short, shorter than the pelvic fin; caudal fin truncate or S-shaped and body scales large. Body colour of preserved specimens is uniform yellow-brown, with no dorsal-ventral trend; anal, pelvic and 1'st dorsal fins are dark brown-black (Fig. 1.16). Oblique white stripes with dark brown borders were very visible on all three specimens examined. Oblique stripes are very convoluted, particularly in the region of the pectoral fin and extend onto the head above and below the orbit.

Comparisons

Umbrina steindachneri differs from *U. canariensis* in having a shorter pectoral fin (Fig. 1.9); longer 3rd dorsal spine (Fig. 1.17); anal fin (Fig. 1.6.); ventral caudal peduncle (Fig. 1.8); and a deeper preorbital bone depth (Fig. 1.18). External colouration also differs with the oblique striping pattern being much more visible over the whole body, on the head and more convoluted in *U. steindachneri* (Fig. 1.16). The dark pigmentation on the inner side of the operculum and triangular shaped mark on the outer side of the operculum found on *U. canariensis* is absent on *U. steindachneri.*

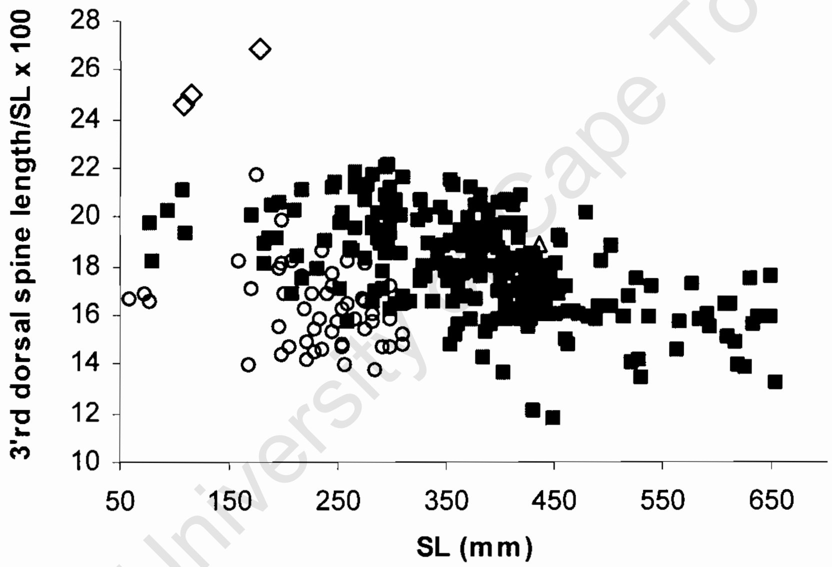


Fig. 1.17: Relationship between 3rd dorsal spine length as % SL and SL for *U. canariensis* (circles), *U. robinsoni* (squares), *U. steindachneri* (diamonds) and *U. ronchus* (triangles).

Remarks

Umbrina steindachneri was named by Cadenat (1950) and based on *Umbrina cirrhosa* var. *canariensis* of Steindachner (1882). No detailed description of this species morphometrics appears to have been published and previous authors have only mentioned one or two distinguishing characteristics. For example: the depth of the preorbital bone and anal fin (Trewavas 1964) or the number of soft dorsal rays (Chao & Trewavas 1990). Consequently there has been some doubt about the species validity e.g. Chao (1986b) suggesting synonymy with *U. canariensis*. In this paper I provide a description and identify distinguishing characters that separate *U. steindachneri* from the other sub-Saharan *Umbrina* species. Multivariate analyses also separated the three *U. steindachneri* specimens from similar size *U. canariensis* and *U. robinsoni* (Fig 1.19). This description is limited in that I only examined three small specimens (10-17 cm SL) and should be expanded with the examination of larger specimens. The drawing in Seret & Opic (1981) of a larger specimen (approximately 30 cm SL), however, suggests that the key characteristics (mainly relative fin size) are not unduly affected by allometry.

Distribution

West African coast from Guinée to Angola; 15-100m depths, rare (Chao & Trewavas 1990).

Material examined: GABON: MNHN 1913 0093 (F 177 mm). SENEGAL: MNHN 1982-1298 (I 108 mm), MNHN 1982-1299 (M 116 mm).

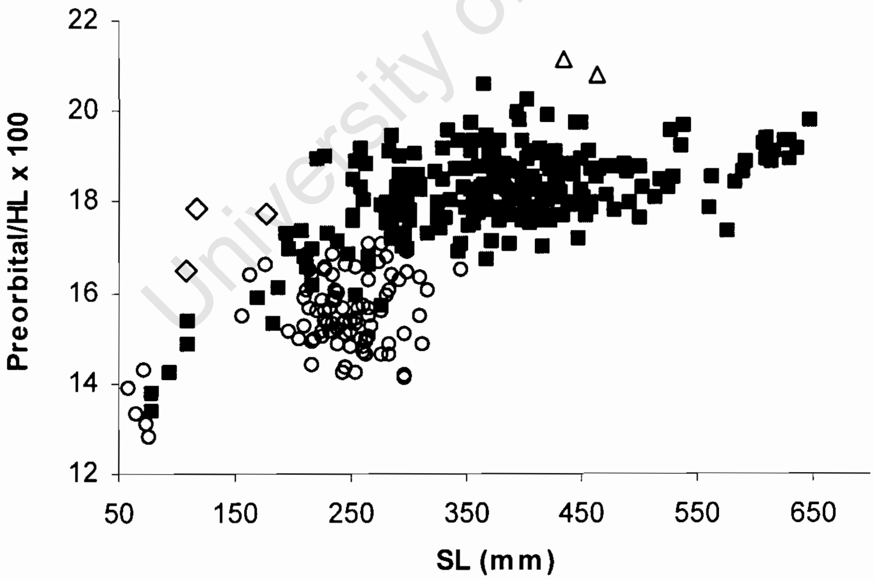


Fig. 1.18: Relationship between preorbital bone depth as % HL and SL for *U. canariensis* (circles), *U. robinsoni* (squares), *U. steindachneri* (diamonds) and *U. ronchus* (triangles).

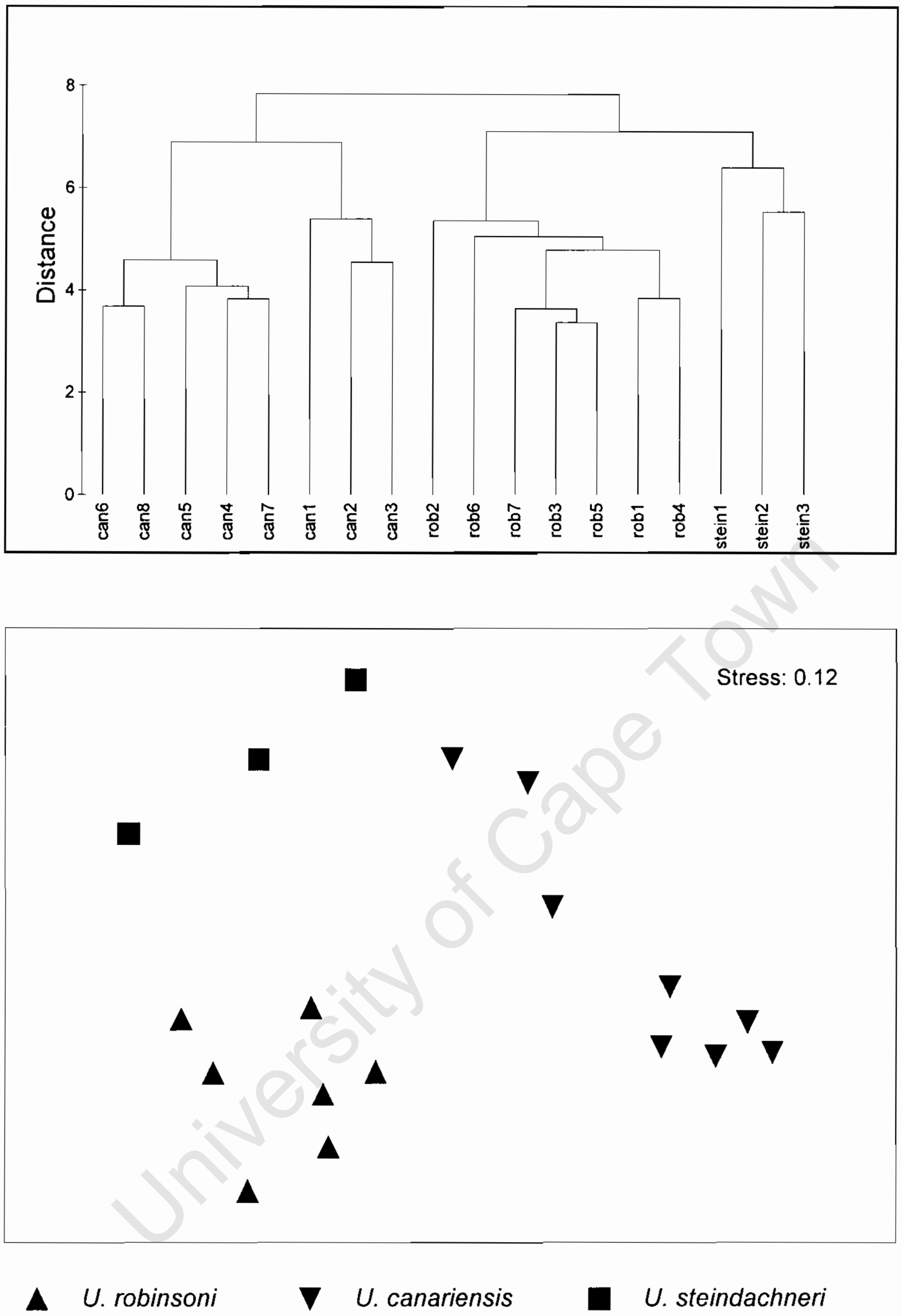


Fig. 1.19: Dendrogram and MDS ordination plot showing relationship between seven South African *U .robinsoni*, 94-183 mm SL (rob 1-7), eight *U. canariensis* from the Canary Islands, Mediterranean, Morocco and South Africa, 60-176 mm SL (can 1-8) and three *U. steindachneri* from Senegal and Gabon, 108-177 mm SL (stein 1-3). Dissimilarity matrix derived from the normalized Euclidean distance between specimens based on 22 measurements and three counts.

Umbrina ronchus Valenciennes 1843

(Fig. 1.20)

Umbrina ronchus Valenciennes 1843, *in* Webb and Berthelot, Hist. Nat. Canaries: 24 (Canary Islands)

Umbrina ronchus: Giglioli 1882: 535; Metzelaar 1919: 237; Chaine 1938: 65, pl. 6 (sagitta); Cadenat 1951: 221, Fig. 158; Trewavas 1964: 113; Palmer 1966: 423, Pl. 6, (excluding False Bay specimen, pl. 7a); Trewavas 1973: 400; Druzhinin 1974: 25; Trewavas 1977: 281, Table. 1; Chao & Trewavas 1981, (FAO sheets); Chao 1986b: 873-874; Chao & Trewavas 1990: 825-826; Sasaki 1996: 84 (excluding Indian Ocean specimens)

Umbrina fusca: Dardignac 1958, *in* Furnestin *et al.* (1958), *Rev. Trav. Inst. Pêches marit.* 22: 441, Fig. 46 (Morocco, type lost)

Sciaena ronchus: Collignon 1959: 8

Umbrina fusca: Dardignac 1961: 264, 266-7, Figs. 4, 5c, 6-13; Williams 1968: 433; Blache *et al.* 1970:301, Fig. 791

Holotype: MNHN, A 5764 (432 mm SL from Canary Islands, found in 1987, Bauchot & Desoutter 1987)

Neotype: BMNH1964.12.30.1 (436 mm SL from Canary Islands, designated by Palmer, 1966)

Diagnosis

Note: Because there was only access to two alcohol preserved specimens from the Canary Islands, the diagnosis and description below are supplemented by Dardignac's (1961) analysis of specimens from the coast of Morocco. Here the values given are those recorded from the two Canary Islands specimens with Dadignac's (1961) ranges in parentheses.

A medium to large *Umbrina* species (attains 77 cm TL) with the following combination of characters: dorsal fin rays 25 (23-27); gill-rakers 3 + 8-9 *; body depth 31 % SL; pre-dorsal length 38-39 % SL; pectoral fin length 18 % SL; ventral caudal peduncle length 27-28 % SL; 3rd dorsal spine length 19 % SL; anal fin length 19 % SL; scale length 2.3-2.4 % SL; upper jaw length 10 % SL; head length 31 % SL; snout length 36.4 (34-40) % HL; horizontal orbit diameter 16 (14-25) % HL; nostril-orbit distance 8-9 % HL; preorbital bone depth 21 (18-24) % HL.

* Palmer (1966) records 5 + 7 gill-rakers plus three tooth patches in the neotype, one tooth patch in the male; we counted 3 + 8-9 when examining the same specimens. Dardignac (1961) does not supply gill-raker counts.

Fig. 1.20: *Umbrina ronchus,* neotype, F, 436 mm SL, BMNH 1964.12.30.1; Canary Islands.

Description

Counts and measurements for the two specimens examined are presented in Table 1.3 An elongate, moderately deep bodied *Umbrina* species with a relatively large, head and steeply inclined pre-dorsal surface. A clear inflection point on the dorsal head profile, near the end of the supraoccipital crest is visible (Fig. 1.20). Orbit small, less than half snout length; posterior nostril far from edge of the orbit (Table 3); snout thick, protrubent, preorbital bone deep; pectoral fin shorter than pelvic fin; caudal fin slightly emarginated, body scales short. Drumming muscles present in male specimen, absent in female.

Body colour of preserved specimens brown to yellow, dark dorsally and lighter ventrally; fins generally dark brown; a dusky, broad band apparent on head of one specimen running laterally across the eye but it is not known if this is a true feature or an artifact of preservation (Fig. 1.20); no oblique brown stripes or markings evident on body. Dardignac (1961) reported that live specimens from Morocco are remarkably dull, mottled brown dorsally and white ventrally. Fish less than 40 cm TL exhibit white blotches with irregular black borders ventrally and two longitudinal white stripes on second dorsal fin. This pigmentation is particularly visible in juveniles (10-30 cm TL) but is not discernable in fish larger than 40 cm TL (Dardignac 1961).

No sagittal otoliths of *U. ronchus*, were examined but Schwarzhans (1993) reports on otoliths of three specimens from east of the Canary Islands. He describes them as very similar to those of *U. canariensis*, rather elongate and thickset with a distinct postcentral umbo on the outer face (particularly in the larger otoliths) and the rims of the smaller otoliths being clearly crenulated. His detailed illustrations show no evidence of a post-dorsal spine remnant.

Comparisons

See Table 1.3. *U. ronchus* differs from *U. canariensis* in having a less deep body (Fig. 1.5); shorter pectoral fins (Fig. 1.9); longer ventral caudal peduncle (Fig. 1.8); smaller scales (Fig. 1.21); longer snout; smaller orbit; greater nostril-orbit distance (Fig. 1.22); a deeper preorbital bone (Fig. 1.18); and a lower modal number of dorsal fin rays and upper gill-rakers.

U. ronchus differs from *U. steindachneri* in having a less deep body (Fig. 1.5); shorter anal fin (Fig.1.6) and 3rd dorsal spine (Fig. 1.17); a deeper preorbital bone (Fig. 1.18); smaller scales (Fig. 1.21); smaller orbit; greater nostril-orbit distance (Fig. 1.22); and a lower modal number of dorsal fin rays.

Remarks

Many authors, e.g. Palmer (1966); Van der Elst (1993a); Heemstra (1986); Chao & Trewavas (1990); Branch *et al.* (1994); Sasaki (1996) have referred to specimens from South African waters and the western Indian Ocean as *U. ronchus*. I believe that the species name *U. robinsoni* (Gilchrist & Thompson 1908) is valid (see description and comparisons below) and that *U. ronchus* is limited in distribution to the eastern Atlantic.

Distribution and habitat

West African coastal waters from Gibraltar to Angola and reported from the western Mediterranean. Found on rocky and sandy substrata from shore to 200 m depth, juveniles occurring in littoral areas, not known to enter estuaries (Chao & Trewavas 1990).

Material examined:

CANARY ISLANDS: BMNH 1964.12.30.1 (F 436 mm); BMNH 1964.12.30.2 (M 465 mm).

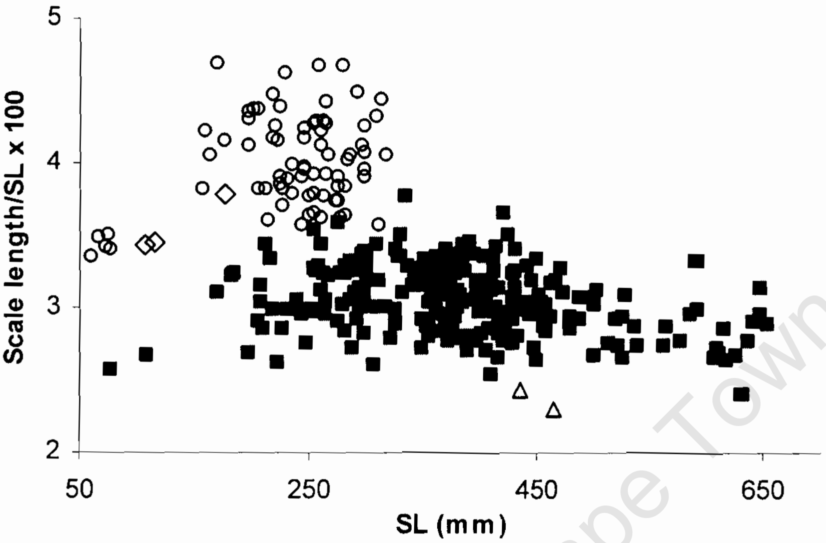


Fig. 1.21: Relationship between scale length as % SL and SL for *U. canariensis* (circles), *U. robinsoni* (squares), *U. steindachneri* (diamonds) and *U. ronchus* (triangles).

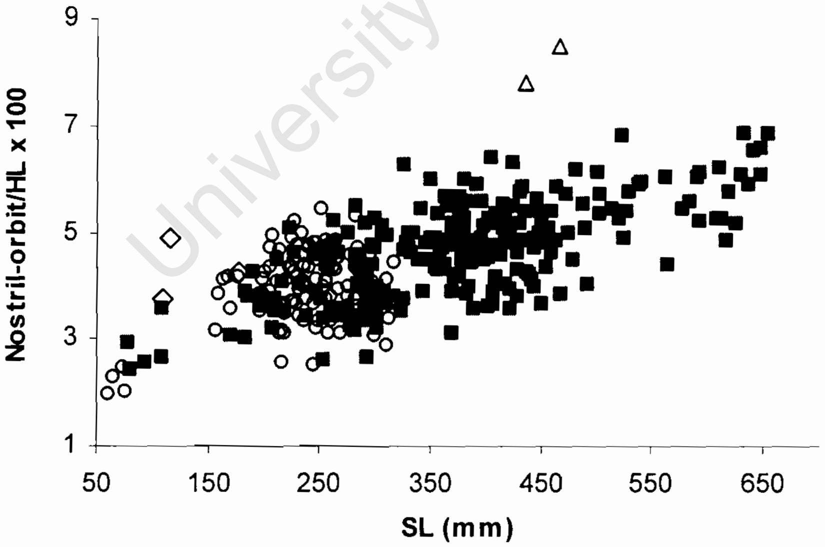


Fig. 1.22: Relationship between nostril-orbit distance as % Head Length (HL) and SL for *U. canariensis* (circles), *U. robinsoni* (squares), *U. steindachneri* (diamonds) and *U. ronchus* (triangles).

Umbrina robinsoni Gilchrist & Thompson 1908

(Fig. 1.23)

Umbrina robinsoni Gilchrist & Thompson 1908, *Ann. S. Afr. Mus.* **6**: 182-183 (Natal).

? *Umbrina capensis* Pappe 1853, Syn. Edible fish. Cape Good Hope, ed. 1:16.
(Original description inadequate, type lost, Palmer (1966); Barnard 1927: 578, pl. 23, fig. 4.

Umbrina angustilineata: Gilchrist & Thompson 1911, *Ann. S. Afr. Mus.* **11**: 38-39.

Sciaena capensis: Smith 1949:227, pl. 26, Fig. 556 (in part).

Sciaena robinsoni: Smith 1949:227, pl. 26, Fig. 557 (in part).

Umbrina robinsoni: Trewavas 1964:114; Trewavas 1977: 281, Table 1.

Umbrina ronchus: Palmer 1966: 425, pl. VII; Van der Elst 1981: 266; Mohan 1984: SCIAEN Umbr 5; Heemstra 1986: 619; Chao & Trewavas 1990: 825; Branch *et al.* 1994: 250, pl. 118.5, Randall 1995: 232, Fig. 604 (not juvenile Fig. 605 which is probably *U. canariensis*); Sasaki 1996: 84.

Holotype of *U. robinsoni*: SAM 9966 (256 mm SL, Natal)

Holotype of *U. angustilineata:* SAM10559 (207 mm SL, Natal)

Diagnosis

A large *Umbrina* species (SA spear-fishing record: 12.6 kg, = 985 mm TL) with the following combination of characters: dorsal fin rays 22-27 (25); gill-rakers 4-6 (5) + 6-10 (9); body depth 26-36 (31) % SL; pre-dorsal length 31-40 (35) % SL; pectoral fin length 15-21 (18) % SL; ventral caudal peduncle length 26-34 (29) % SL; 3rd dorsal spine length 12-22 (18) % SL; anal fin length 16-24 (20) % SL; scale length 2.4-3.8 (3) % SL; upper jaw length 8-11 (9) % SL; head length 26-32 (29) % SL; snout length 27-38 (34) % HL; horizontal orbit diameter 14-33 (19) % HL; nostril-orbit distance 2-5.4 (4) % HL; preorbital bone depth 13-21 (18) % HL.

Description

Counts and measurements are presented in Table 1.3. Body relatively elongate and slender, becoming progressively more robust and deep with growth; upper jaw relatively short (end reaching to vertical of anterior half of orbit); snout moderately long (orbit 1.3-2.5 times in snout for fish > 15 cm), blunt and protrudes beyond mouth, which is ventral. Posterior nostril close to margin of orbit; pectoral fin usually slightly shorter than pelvic fin; caudal fin truncate in smaller specimens (< 12 cm), S-shaped or emarginate in larger fish. Drumming muscles present in males, absent in females.

The body colour ranges from slate-grey to dark brown dorsally and silver to white ventrally; fins dark brown to black (Fig. 1.23). Oblique, narrow, wavy, stripes, that appear electric blue underwater and white after death are most visible on dorsal half of body of nearly all fish less than 40 cm; but are faint or absent on larger fish that become very dark overall. Juveniles (< 10 mm) display a distinctive broad, dark, cross on the flanks and may also exhibit wavy white stripes (Fig. 1.23). Inner side of operculum white or very lightly punctuate near the attachment of the gill arches.

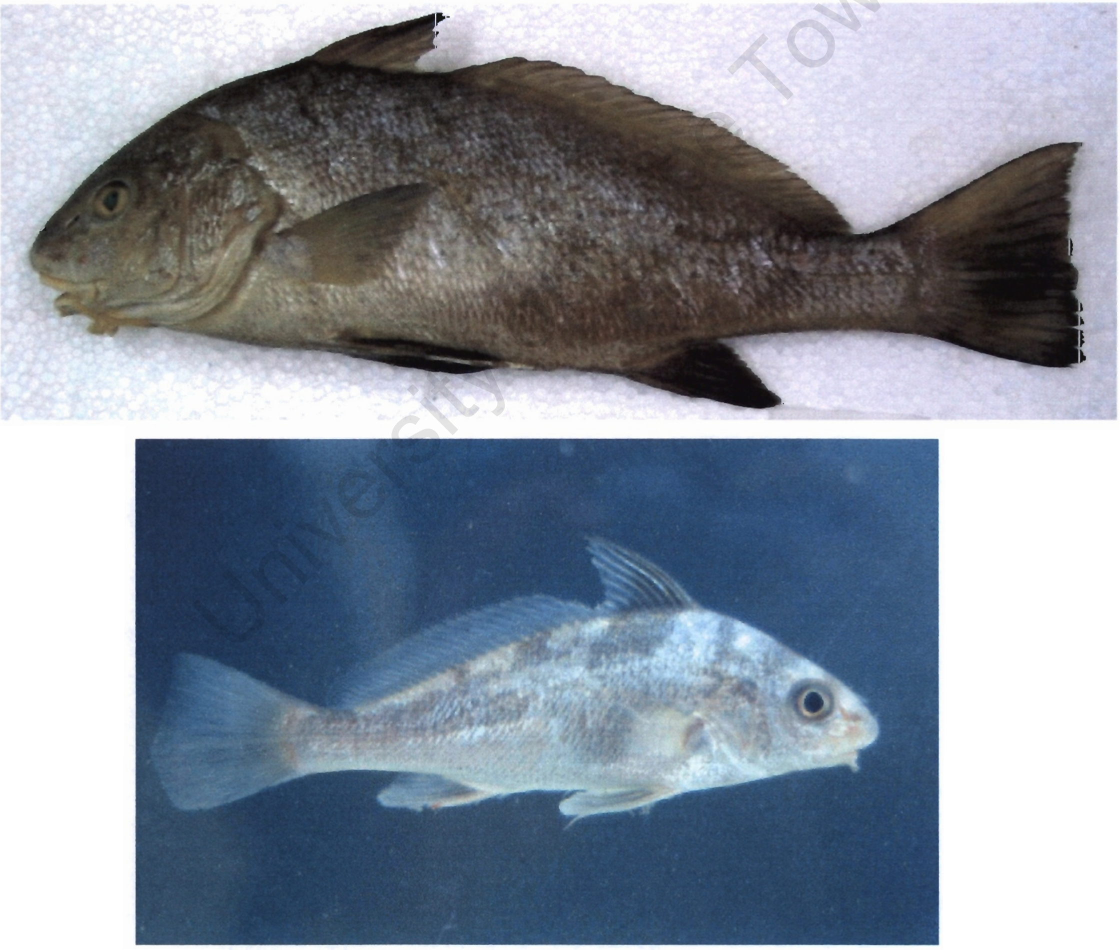


Fig. 1.23: *Umbrina robinsoni* F, 425mm SL, SAM 3602, Cape Agulhas, South Africa (top); juvenile approximately 100 mm SL, False Bay (bottom).

Otoliths oblong, rounded, and thin in smaller fish (< 400 mm) becoming somewhat thicker in larger specimens (Fig. 1.2). A postcentral umbo is present on the lateral face but this is not nearly as massive or pointed as in *U. canariensis*. Dorsal margin fairly straight and ventral margin rounded. A post-dorsal spine vestige is clearly visible on all *U. robinsoni* otoliths examined; i.e. the most posterior point of the otolith is at the dorsal corner. Otolith measurements are presented in Table 1.4 and otolith length and height to fish length relationships are shown in Figs. 1.3 and 1.4.

Comparisons

Umbrina robinsoni differs from *U. canariensis* in having a less deep body (Fig. 1.5); shorter pre-dorsal; head; pectoral fins (Fig 1.9); and upper jaw (Fig. 1.10); longer ventral caudal peduncle (Fig. 1.8); smaller scales (Fig. 1.21); longer snout; smaller orbit (Fig. 1.7); a deeper preorbital bone (Fig. 1.18); and a lower modal number of dorsal fin rays and upper gill-rakers (Table 1.3). The Sagittal otoliths of *U. robinsoni* are less elongate and much less thickset than in *U. canariensis* (Figs. 1.2-1.4). A post-dorsal spine vestige is present on *U. robinsoni* otoliths, absent on the otoliths of *U. canariensis* (see post-dorsal spine – cauda measurement, Table 1.4). The body colour and nature of the striping pattern on the flanks differs markedly between the species: in *U. robinsoni* the oblique stripes are thin, wavy, white lines; in *U. canariensis* the oblique stripes are thicker, nearly straight and brown (Figs. 1.1 & 1.23). *U. robinsoni* lacks the triangle shaped mark on the outer operculum and the dark pigmentation of the inner operculum that is found on *U. canariensis*.

U. robinsoni differs from *U. steindachneri* by having a less deep body (Fig. 1.5); shorter 3rd dorsal spine (Fig. 1.17); shorter scales (Fig. 1.21) and a lower modal number of dorsal fin rays (Table 1.3).

U. robinsoni differs from *U. ronchus* by having a shorter pre-dorsal length (Table 1.3); longer scales (Fig. 1.21); shorter head (Table 1.3); bigger orbit (Table 1.3); shorter nostril-orbit distance (Fig. 1.22) and a less deep preorbital bone (Fig. 1.18). Multivariate analysis of similar sized *U. robinsoni* and *U. ronchus* morphological data shows clear separation of the two species (Fig. 1.24). The pre-dorsal profile of two species is also notably different; in *U. robinsoni* the curve from the snout to the dorsal fin is smoothly convex, in *U. ronchus* it is steeply convex at first, less so after the terminus of the supraoccipital crest (Figs. 1.20 & 1.23). Measurements taken from radiographs of the skulls of 12 *U.* robinsoni and two similar size *U. ronchus* show that the distance between the attachment point of the first vertebra and the top of the supraoccipital crest is slightly greater in *U. ronchus* (Table 1.5). Part of the reason for the striking differences in the external appearance of the pre-dorsal surface may also be due to the steeper angle of the parasphenoid bone in *U. ronchus*. Although I did not have the opportunity to examine otoliths of *U. ronchus*, the drawings by Schwarzhans (1993) show differences from *U. robinsoni* otoliths in having a large postcentral umbo on the outer surface and no evidence of a post-dorsal spine vestige. External pigmentation also appears to be different between the two species with *U. ronchus* lacking the oblique, wavy striping pattern evident on the flanks of *U. robinsoni* and the unique cross-shaped pigmentation of juvenile *U. robinsoni* not recorded on juvenile *U. ronchus* by Dardignac (1961).

Table 1.5: Measurements of *U. ronchus* and *U. robinsoni* skull morphology made from radiographs.

	Area	SL	VT-SOC % SL
U. ronchus			
BMNH 1964.12.30.1	Canary Islands	436	14.15
BMNH 1964.12.30.2	Canary Islands	465	13.93
U. robinsoni			
N = 6	SWC	429 - 490	12.17 - 13.40 (x = 12.78)
n = 4	SC	408 - 464	12.5 - 13.7 (x = 13.3)
n = 2	KZN	457, 460	11.87, 12.54 (x = 12.2)
n = 12	All regions	408 - 490	Average (x) = 12.86

SWC = False Bay – Cape Agulhas
SC = Cape Agulhas - Mossel Bay
KZN = East London – Mozambique Border
VT-SOC = distance from ventral edge of 1st vertebrae to dorsal terminus of supraoccipital crest.

Remarks

U. robinsoni and *U. ronchus* are clearly very similar and many authors have considered them to be synonymous although no researchers had compared a sufficiently large sample of South African specimens with similar sized *U. ronchus* specimens from the type locality. I however believe *U. robinsoni* to be valid; as the main differences between the two species; namely the nostril–orbit distance, preorbital bone depth, scale length and supraoccipital crest height are "hard tissue"

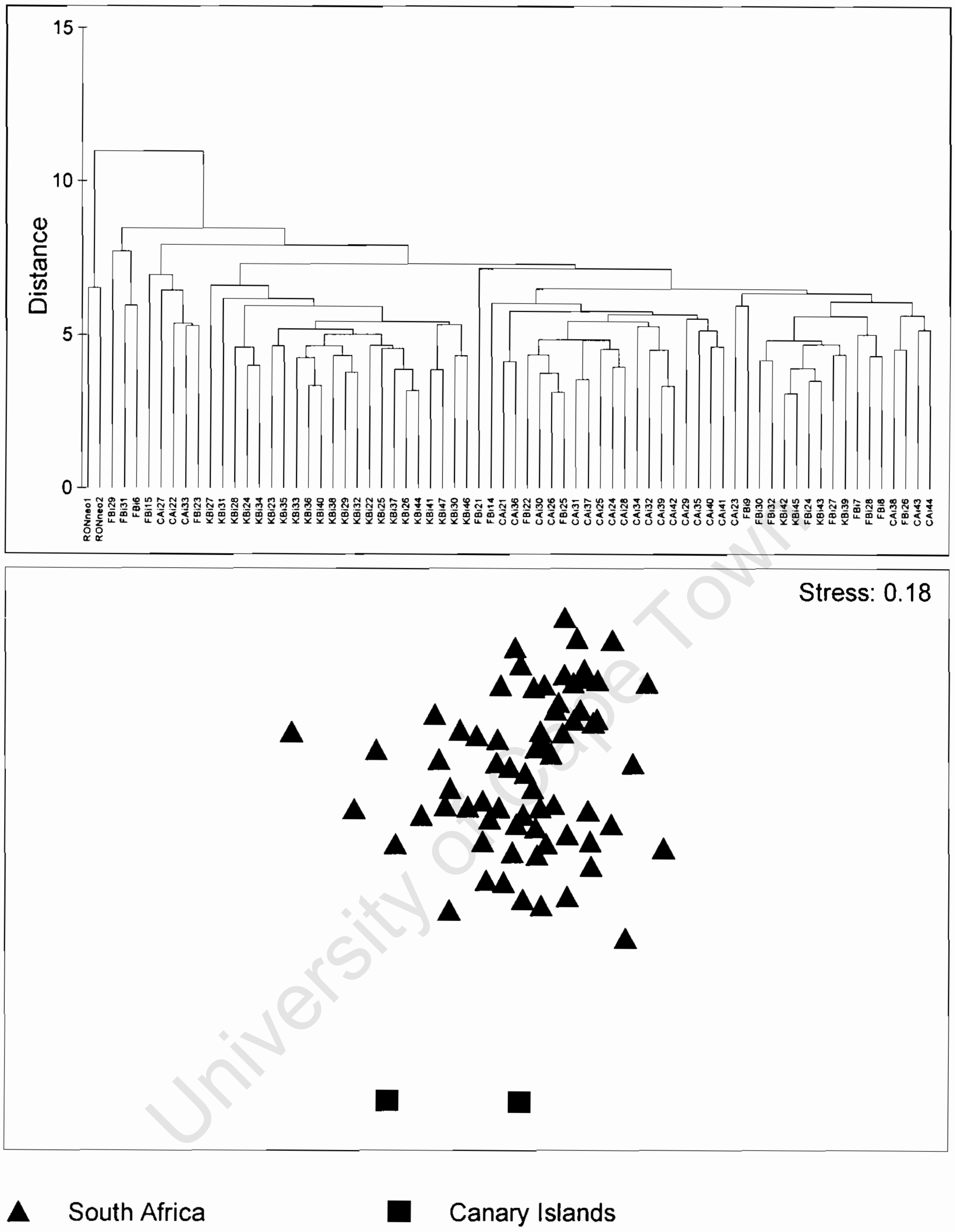


Fig. 1.24: Dendrogram and MDS ordination plot showing relationship between 68 South African *Umbrina robinsoni* (collected between False Bay and Kosi Bay; 401-493 mm SL) and two specimens of *Umbrina ronchus* (BMNH 1964.12.30.1-2) from the Canary Islands. Dissimilarity matrix derived from the normalized Euclidean distance between specimens based on 23 measurements and four meristic counts. RONneo1, 2 = Canary Islands; FBi = False Bay; CAi = Cape Agulhas; KBi = Kosi Bay.

features that are unlikely to be affected by differing preservation techniques. The measurements of these features fall outside the range for our large sample of *U. robinsoni*. The two species populations are also distinctly allopatric with over 2 000 km between the Cape Point, the western limit of *U. robinsoni* range and southern Angola, the likely southern extent of *U. ronchus* distribution. A significant environmental barrier separates the two species in the form of the Benguela upwelling system, which is very likely to prevent propagule dispersal between the two regions. A comparison of morphometric and genetic data between Angolan *U. ronchus* and South African *U. robinsoni* is however desirable to confirm or disprove our conclusion.

Distribution and habitat

Inshore coastal waters of the western Indian Ocean from Cape Point to at least Madagascar (recorded as *U. ronchus* by Mohan 1984) and possibly the Gulf of Oman (Mohan 1984, Heemstra 1986). Off the South African east coast juveniles (< 200 mm TL) frequent mixed rock and sand surf-zone habitats, whilst adult aggregations occur along sandy beaches, mixed rock and sand surf-zones and subtidal reefs; most commonly high structure limestone or sandstone reef. The distribution of catches of *U. robinsoni* by recreational shore anglers and spear fishers in competitions is shown in Fig. 1.25.

Material examined:

SOUTH AFRICA: Western Cape: RUSI 67470 (M 351 mm); RUSI 67471 (F 626 mm); RUSI 67472 (J 109 mm); RUSI 67473 (M 197 mm); RUSI 67474 (M 307 mm); RUSI 67475 (M 351 mm); RUSI 67476 (M 440 mm); RUSI 67477 (M 515 mm); RUSI 67478 (M 648 mm); SAM 36050 (J 78 mm); SAM 36051 (F 366 mm); SAM 36052 (M 610 mm); SAM 36053 (F 194 mm); SAM 36054 (3 M 309 mm; 369 mm; 410 mm; J 183 mm); SAM 36055 (M 451 mm; 2 F 585 mm; 618 mm); SAM 36056 (2 M 210 mm; 255 mm; F 231 mm); SAM 36057 (3 F 398 mm; 450 mm; 488 mm; M 490 mm). Southern Cape: RUSI 35538 (M 377 mm); RUSI 35534 (M 406 mm); RUSI 35532 (M 522 mm); RUSI 35539 (M 593 mm); RUSI 67479 (F 263 mm); RUSI 67480 (F 342 mm); RUSI 67481 (F 410 mm); RUSI 67482 (M 259 mm); RUSI 67483 (M 299 mm); RUSI 67484 (M 399 mm); RUSI 67485 (M 474 mm); RUSI 67486 (M 530 mm); SAM 36058 (F 369 mm); SAM 36059 (2 F 299 mm; 472 mm; M 396 mm); SAM 36060 (3 M 481; 418; 346 mm; F 262 mm); SAM 36061 (F 349 mm; M 377 mm); SAM 36062 (3 F 425 mm; 399 mm; 449 mm; 3 M 460 mm; 260 mm; 283 mm). Eastern Cape: RUSI 12997 (F 641 mm). KwaZulu Natal: RUSI 11618a (244 mm); RUSI 9148 (J 186 mm); RUSI 61878 (F 654 mm); RUSI 17459a (F 349 mm); RUSI 17459b (365 mm); RUSI 9501 (F 267 mm); RUSI 60196 (J 183 mm); RUSI 67487 (F 239 mm); RUSI 67488 (F 355 mm); RUSI 67489 (F 399 mm); RUSI 67490 (F 430 mm); RUSI 67491 (F 520 mm); RUSI 67492 (F 616 mm); RUSI 67493 (F 648 mm); RUSI 67494 (M 254 mm); RUSI 67495 (M 357 mm); RUSI 67496 (M 454 mm); RUSI 67497 (M 540 mm); RUSI 67498 (M 608 mm); SAM 9966 (M 256 mm, holotype); SAM 10559 (M 207 mm, holotype of *Umbrina angustilineata*); SAM 36063 (2 M 526 mm; 612 mm; F 537 mm); SAM 36064 (M 565 mm; 2 F 591 mm; 637 mm); SAM 36065 (6 F 358 mm; 402 mm; 429 mm; 378 mm; 460 mm; 297 mm; 6 M 297 mm; 423 mm; 356 mm; 406 mm; 281 mm; 459 mm); SAM 36066 (F 248 mm); SAM 36067 (M 266 mm).

ADDITIONAL MATERIAL EXAMINED: SOUTH AFRICA: Western Cape: 2001.3.1 (F 381 mm); 2001.4.1 (M 422 mm); 2001.6.2 (F 208 mm); 2001.9.1 (F 209 mm); 2001.15.2 (M 395 mm); 2001.15.4 (M 380 mm); 2001.15.7 (M 218 mm); 2001.15.8 (F 216 mm); 2001.15.11 (J 189 mm); 2001.45.10 (M 446 mm); 2001.45.11 (M 376 mm); 2001.45.12 (M 371 mm); 2001.45.13 (M 384 mm); 2001.46.2 (M 467 mm); 2001.47.1 (F 171 mm); 2001.47.3 (F 222 mm); 2001.48.1 (F 228 mm); 2001.48.2 (F 252 mm); 2001.48.3 (F 429 mm); 2001.48.5 (F 402 mm); 2001.48.6 (F 402 mm); 2001.48.7 (M 357 mm); 2001.48.8 (M 379 mm); 2001.48.10 (F 424 mm); 2001.48.12 (F 430 mm); 2001.48.14 (F 429 mm); 2001.48.15 (M 372 mm); 2001.48.16 (M 463 mm); 2001.48.18 (M 563 mm); 2001.48.19 (M 593 mm); 2001.48.21 (M 433 mm); 2001.48.23 (F 358 mm); 2001.49.5 (M 311 mm); 2001.50.1 (M 213 mm); 2001.52.1 (F 455 mm); 1993.1.1 (J 80 mm); 1993.3.1 (J 110 mm); 1993.3.2 (J 94 mm). Southern Cape: 2000.1.1 (F 355 mm); 2000.1.2 (M 410 mm); 2000.1.3 (F 431 mm); 2000.1.4 (F 405 mm); 2000.1.5 (F 353 mm); 2000.1.6 (F 291 mm); 2001.1.1 (F 405 mm); 2001.1.2 (F 385 mm); 2001.1.3 (F 388 mm); 2001.1.4 (M 331 mm); 2001.1.5 (F 334 mm); 2001.23.3 (F 282 mm); 2001.25.1 (M 501 mm); 2001.26.1 (F 328 mm); 2001.26.2 (M 368 mm); 2001.26.4 (F 391 mm); 2001.26.5 (F 451 mm); 2001.26.7 (F 386 mm); 2001.26.8 (F 343 mm); 2001.26.10 (M 378 mm); 2001.26.11 (F 401 mm); 2001.26.12 (M 363 mm); 2001.26.13 (M 361 mm); 2001.27.1 (F 326 mm); 2001.27.2 (M 413 mm); 2001.27.5 (F 381 mm); 2001.28.1 (M 380 mm); 2001.28.2 (F 412 mm); 2001.28.3 (M 331 mm); 2001.28.4 (M 362 mm); 2001.29.1 (M 416 mm); 2001.29.3 (F 435 mm); 2001.29.4 (M 338 mm); 2001.29.5 (M 405 mm); 2001.29.7 (M 350 mm); 2001.29.8 (F 357 mm); 2001.29.11 (F 408 mm); 2001.29.14 (F 464 mm); 2001.29.15 (F 276 mm); 2001.29.16 (F 446 mm); 2001.29.17 (M 332 mm); 2001.29.20 (M 353 mm); 2001.29.21 (F 433 mm); 2001.29.22 (M 442 mm); 2001.29.23 (F 285 mm). KwaZulu Natal: 2001.10.1 (F 493 mm); 2001.11.1 (M 418 mm); 2001.11.2 (F 397 mm); 2001.11.3 (F 299 mm); 2001.11.5 (F 282 mm); 2001.11.6 (M 502mm); 2001.11.7 (M 528 mm); 2001.11.11 (F 632 mm); 2001.11.13 (M 577 mm); 2001.11.15 (M 417 mm); 2001.11.18 (F 298 mm); 2001.11.19 (F 418 mm); 2001.11.20 (F 382 mm); 2001.11.22 (F 423 mm); 2001.11.24 (F 630 mm); 2001.11.25 (F 457 mm); 2001.12.1 (M 297 mm); 2001.12.2 (M 288 mm); 2001.12.4 (M 383 mm); 2001.12.5 (M 369 mm); 2001.12.6 (F 326 mm); 2001.12.7 (M 278 mm); 2001.12.8 (M 293 mm); 2001.12.10 (M 317 mm); 2001.12.11 (F 291 mm); 2001.12.13 (M 366 mm); 2001.12.14 (F 370 mm); 2001.12.16 (M 389 mm); 2001.12.17 (M 372 mm); 2001.12.19 (M 385 mm); 2001.12.20 (M 421 mm); 2001.12.21 (F 293 mm); 2001.12.22 (F 369 mm); 2001.12.23 (F 362 mm); 2001.12.27 (M 412 mm); 2001.12.28 (F 407 mm); 2001.12.29 (M 389 mm); 2001.12.33 (F 410 mm); 2001.12.35 (F 418 mm); 2001.12.37 (M 387 mm); 2001.12.39 (F 375 mm); 2001.12.40 (F 438 mm); 2001.12.42 (M 445 mm); 2001.12.43 (M 443 mm); 2001.12.47 (M 445 mm); 2001.12.48 (F 416 mm); 2001.12.49 (M 422 mm); 2001.12.50 (M 480 mm); 2001.13.1 (F 302 mm); 2001.13.2 (F 296 mm); 2001.13.3 (F 265 mm); 2001.13.4 (M 281 mm); 2001.13.5 (F 286 mm); 2001.13.7 (F 326 mm); 2001.13.8 (F 276 mm); 2001.13.9 (M 286 mm); 2001.13.12 (M 292 mm); 2001.13.13 (F 302 mm); 2001.13.14 (M 294 mm); 2001.13.15 (F 344 mm); 2001.13.16 (F 299 mm); 2001.13.17 (F 293 mm); 2001.13.18 (M 302 mm); 2001.13.19 (F 294 mm); 2001.13.20 (M 323 mm); 2001.14.1 (M 307 mm); 2001.14.3 (F 287 mm); 2001.14.4 (F 310 mm); 2001.14.5 (F 253 mm); 2001.14.6 (M 294 mm); 2001.14.9 (F 253 mm).

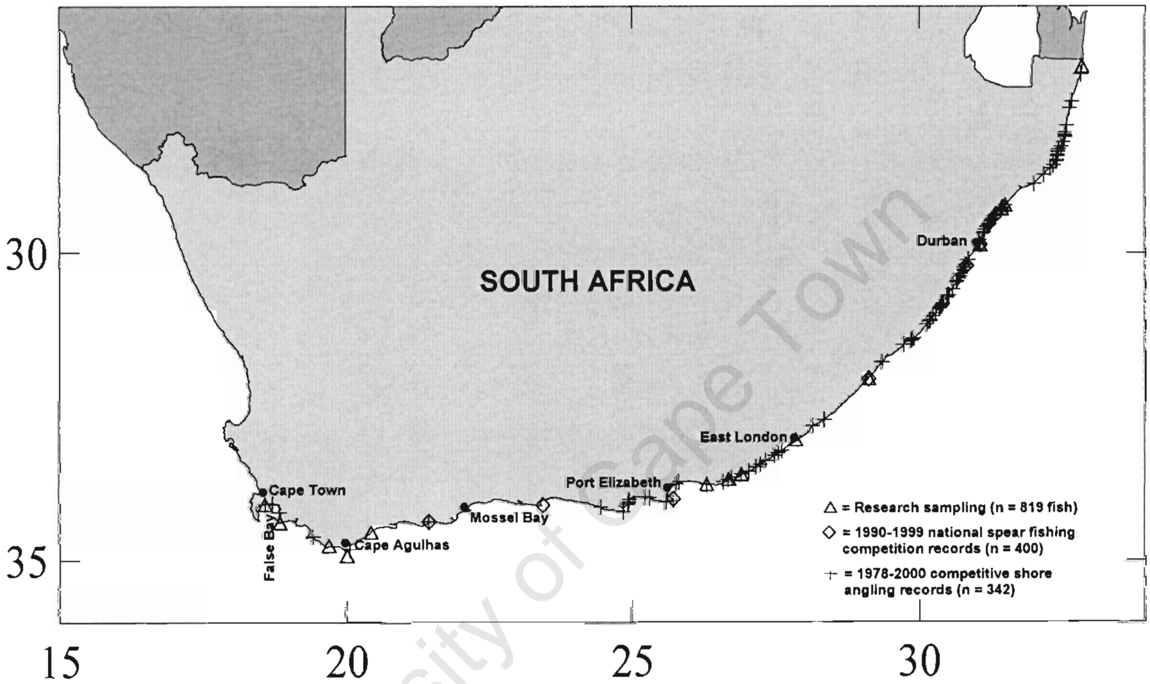


Fig. 1.25: Distribution of *U. robinsoni* angling, spear fishing and research catch off the South African coast.

CHAPTER 2

REGIONAL VARIATION IN THE LIFE HISTORY OF THE CANARY DRUM *UMBRINA CANARIENSIS* (SCIAENIDAE), IN SOUTH AFRICAN WATERS

ABSTRACT

Umbrina canariensis were sampled from two disjunct regions of abundance off the South African east coast - the central Agulhas Bank (n = 227) and Algoa Bay (n = 550) - from March 2001 through February 2003. Marginal increment analyses supported annual deposition of growth zones in sagittal otoliths. Ages recorded using thin otolith sections were 2-23 years and 1-27 years for fish sampled on the central Agulhas Bank and in Algoa Bay respectively. Maximum ages for males and females were 25 and 27 years respectively. Although females were larger than males at most ages, comparisons of growth between sexes - based on t-tests of mean lengths-at-age, likelihood ratio tests of fitted curves and parameters and comparisons of 95 % parameter space - were not unequivocal and are not thought to be biologically significant. Growth rates (sexes pooled) did, however, differ between regions with central Agulhas Bank *U. canariensis* attaining a greater asymptotic length, but at a lower rate than those in Algoa Bay. The fitted von Bertalanffy growth equations for combined sexes are: $L_t = 397\ (1 - e^{-0.16\ (t\ +\ 3.41)})$ for the central Agulhas Bank and $L_t = 352\ (1 - e^{-0.26\ (t\ +\ 1.1)})$ for Algoa Bay. Histological examination of ovary sections confirmed that *U. canariensis* is a serial batch spawner. Trends in monthly proportions of macroscopic maturity stages in mature females and average monthly gonadosomatic indices suggested an extended spring-summer spawning season from August to December in both regions. Females dominated sex ratios over soft strata (i.e. trawl grounds) during the spawning season indicating that they may return to feeding grounds between spawning events. Estimated size at 50 % maturity (L_{50}) did not differ significantly (likelihood ratio tests) between regions or between sexes. L_{50} was 22 cm for males and 23 cm for females (regions combined). Although female L_{50} did not differ between regions, differences in growth rate resulted in a higher corresponding age at L_{50} for Algoa Bay (3.2 years) than on the central Agulhas Bank (2.2 years).

INTRODUCTION

The Canary drum *Umbrina canariensis* has a broad geographical range, occurring around most of the African coast from Gibraltar to central Namibia and from Cape Point (South Africa) to Pakistan (Heemstra 1986, Chapter 1). It is an important by-catch component in demersal trawl fisheries operating off the West African coast (Podosinnikov 1979, Venidictova 1982, 1983a, 1983b) and off the South African south coast (Japp *et al.* 1994, Smale and Badenhorst 1991). Until recently in South African waters *U. canariensis* was frequently confused with a sympatric congeneric

U. robinsoni, an inshore species that occurs from the surf zone to approximately 40 m depth (Chapter 1). Spatial analyses of research trawl data (Chapter 1) revealed that in South African waters; *U. canariensis* occurs predominately between 40-100 m depth, with two centres of abundance: the central Agulhas Bank and Algoa Bay (Fig. 2.1). *U. canariensis* are frequently landed as by-catch in the hake (*Merluccius capensis*) and sole (*Austroglossus pectoralis*) directed inshore trawl fishery (Japp *et al.* 1994) and occasionally by boat-based line-fishers (Brouwer and Buxton 2002). Previous references to the occurrence and size distribution of *U. canariensis* in the catches of beach-seines (e.g. Clark *et al.* 1994, Lamberth *et al.* 1994, 1995) and shore anglers (e.g. Bennett 1991, Bennett and Attwood 1993, Bennett *et al.* 1994) undoubtedly refer to *U. robinsoni* (Chapter 1).

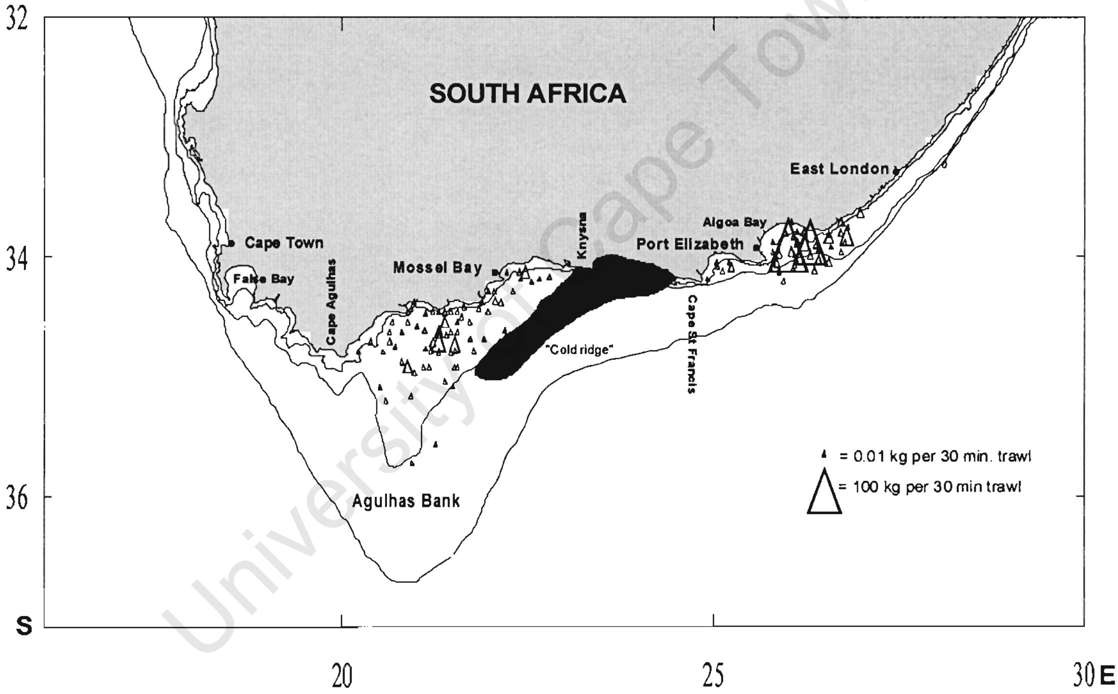


Fig. 2.1: Map of South Africa showing places mentioned in the text and distribution of *Umbrina canariensis* CPUE (kg. per 30 min. trawl) in 238 demersal biomass survey trawls conducted between September 1986 and April 1999; 50 m, 100 m and 200 m isobaths and the approximate position of the "cold water ridge" are shown.

Aspects of the biology of *U. canariensis* in the southeast Atlantic, including growth, reproduction and mortality rates, were described by Venidictova (1982, 1983a, 1983b) and embryonic development under laboratory conditions by Podosinnikov (1979).

The studies of Venidictova (1982, 1983a, 1983b) were, however, fairly superficial and aimed at assessing the exploitation potential of the stock for the soviet trawler fleet. *U. canariensis* do not occur along the South African west coast or the southern Namibian coast (Chapter 1) and it is therefore very likely that the southeast Atlantic stocks are separate from those along the South African east coast. Although the South African inshore trawl fishery does not target *U. canariensis*, the species is retained either for crew consumption or for sale. Current management measures (bag and size limits) for *Umbrina* species are based on limited life history information for the inshore species *U. robinsoni,* targeted by shore anglers and spear-fishers. In this chapter, life-history information for South African *U. canariensis* from each of the two areas of abundance, including spawning seasonality, size at maturity and regional growth rates, is provided.

MATERIAL AND METHODS

Biological sampling

U. canariensis specimens were collected during 2001 and 2002 from the two areas of abundance: the central Agulhas Bank and Algoa Bay (i.e. east and west of 24° E longitude). Samples were bottom trawled by commercial vessels operating from the ports of Mossel Bay and Port Elizabeth (Fig. 2.1) and by research vessels conducting swept area biomass surveys. Attempts were made to collect monthly samples from commercial vessels operating out of both ports, but this was not always possible due to seasonal shifts in effort during the summer months to deeper water (>100m) where *U. canariensis* are less common (no samples were obtained for January). Trawl gear used in the south coast inshore fishery is typically small demersal trawl nets with a cod-end mesh size of 75 mm whilst research trawls are conducted with a 180-foot German trawl and a cod-end liner of 25 mm (stretched mesh) is employed (Badenhorst and Smale 1991). Nearly all fish that were biologically sampled were frozen at sea or shortly after the vessel returned to port, and then defrosted prior to dissection. The total length (TL), standard length (SL) and weight (WT) of all fish collected were recorded to the nearest 1mm and 1g respectively. The relationships between TL – SL and TL – WT (using $\log_{10}$ transformed data) were determined by linear regression. Gonads were removed, weighed (to the nearest 0.1 g) and assigned a macroscopic maturity stage (Table 2.1). Ovarian tissue samples, representative of each maturity stage, were preserved in buffered formalin (10 %) for histological examination. Sagittal otoliths from each fish were extracted from the skull, cleaned in water and stored dry in envelopes.

Reproduction

Preserved ovarian tissue samples were routinely embedded in paraffin wax, sectioned at 5-7 microns and stained using haemotoxylin and eosin. Stained sections were mounted on glass slides, cover-slipped using DPX mountant and examined at 40-400 times magnification under transmitted light. Each histologically prepared ovarian section was then allocated a microscopic maturity stage based on the presence or absence of different stages of oocyte development (Table 2.1, Fig. 2.2).

Male and female size at 50 % maturity was estimated by fitting a logistic ogive to the proportion of mature fish (macroscopic gonad stage 3 +) per 2 cm length class, using an iterative least squares procedure (Microsoft EXCEL SOLVER routine with Newton algorithm option, (Microsoft Corporation 2000)). The logistic function used was:

$$P(\mathrm{L}) = 1/(1 + \exp^{-(L-L_{50})/\delta}) \ldots\ldots (2.1)$$

Where $P(\mathrm{L})$ is the proportion of mature fish in size class L, L_{50} is the length at 50 % maturity and δ the width of the ogive. Only fish sampled during the spawning season (August to February) were used to determine size at maturity. Age at 50 % maturity in each region was calculated using the L_{50} estimates and the fitted von Bertalanffy growth functions. Likelihood ratio tests (Draper and Smith 1966) were used to test for differences between L_{50} estimates for male and female fish as well as between females trawled west (central Agulhas Bank) and east (Algoa Bay) of 24°E longitude. The likelihood ratio test statistic is:

$$X^2 = -2\ ({}^{*}L_{\mathrm{full}} - {}^{*}L_{\mathrm{reduced}}) \ldots\ldots (2.2)$$

where $*L$ is the negative log-likelihood estimate and X^2 is Chi-squared distributed with the difference in the number of parameters between the full and the reduced model equal to the degrees of freedom. Assuming binomial error distribution, $*L$ was calculated as follows:

$$-\ln L = -\sum_{n}\left[y_i \ln\left(\frac{\hat{p}_i}{1-\hat{p}_i}\right) + m_i \ln\left(1-\hat{p}_i\right) + \ln\binom{m_i}{y_i}\right] \quad (2.3)$$

where y_i is the observed number of mature fish in each length class, $\hat{p}_i$ is the predicted proportion of mature fish in each length class and m_i is the number of fish sampled in each length class.

The extent of the spawning season was determined by calculating gonadosomatic indices (*GSIs*) and the monthly percentage frequency of each macroscopic maturity stage (validated by histology) for female fish larger than L_{50}.

$$GSI\,(\%) = W_1/W_2 \times 100 \quad (2.4)$$

Where W_1 is the wet weight of the gonad and W_2 is the wet weight of the fish minus the gonad weight. Sex ratios were tested for deviations from unity using Chi-squared tests. As degrees of freedom when comparing sex ratios are equal to one, the Yates correction for continuity was employed when calculating X^2 values (Zar 1996).

Age and growth

In an attempt to avoid possible bias caused by seasonal variation in growth, otoliths used for age determination and growth curve fitting were randomly selected from fish sampled during the spawning season (August to March). Fish trawled west (central Agulhas Bank) and east (Algoa Bay) of 24° E longitude were analysed separately for regional comparisons. Right side otoliths (unless damaged, then the left side otolith was used) were embedded in clear casting resin and two or three longitudinal sections (approximately 0.5 mm thick) were cut through the central region using a single diamond blade saw to ensure that the nucleus was included. Sections were mounted on glass slides using DPX mountant and examined under reflected light on a black background at 6-12 times magnification.

Table 2.1: Macroscopic and microscopic (ovaries only) descriptions of gonad maturity stages for *Umbrina canariensis*.

Stage		Macroscopic description	Microscopic description
1	Juvenile	Testes thin and threadlike, translucent pink or grey in colour. Ovaries transparent pinkish sacs.	No histological sections of stage 1 ovaries were examined.
2	Immature or inactive	Testes flattened pinkish white. Ovaries translucent orange tubes, longer than in stage 1.	In addition to oogonia and early perinucleolus stage oocytes, late perinucleolus oocytes predominate in ovaries.
3	Active	Testes wider and beige in colour, triangular in cross-section, some sperm is visible in the central duct if the gonad is cut and squeezed. Tiny, yellow, pinprick eggs in a gelatinous orange matrix are just visible to the naked eye.	Ovaries contain primary growth oocytes and numerous yolk vesicle oocytes.
4	Developing	Testes are wider and deeper in cross-section, beige or cream in colour, obvious sperm in the main duct and some present in the tissue. Easily visible eggs occupy the entire ovary which becomes opaque yellow in colour and larger in diameter.	All oocyte stages up to tertiary yolk oocytes present in ovaries.
5	Ripe	Testes become larger and creamier in colour, considerable quantities of sperm are present. Ovaries are opaque yellow in colour and increase in diameter due to an increase in egg size.	All oocyte stages up to tertiary yolk oocytes that occupy most of the space in the ovary.
6	Ripe and running	Testes larger still and uniform cream in colour, they are soft in texture and rupture easily when handled. Sperm are extruded if pressure is applied to the abdomen of the whole fish. Ovaries are amber in colour, very large in diameter and have a substantial portion of hydrated eggs.	Ovaries contain all stages of vitellogenesis including numerous ripe (exhibiting coalescence of yolk granules and the formation of yolk plates) and hydrated oocytes.
7	Spent or recovering	Testes are smaller than in stages 5 and 6, harder in texture and beige or cream in colour, a little viscous semen is present in the main duct. Ovaries are smaller than in stages 5 and 6 and similar in appearance to stage 2. A few yolked oocytes remain.	No histological sections of stage 7 ovaries were examined.

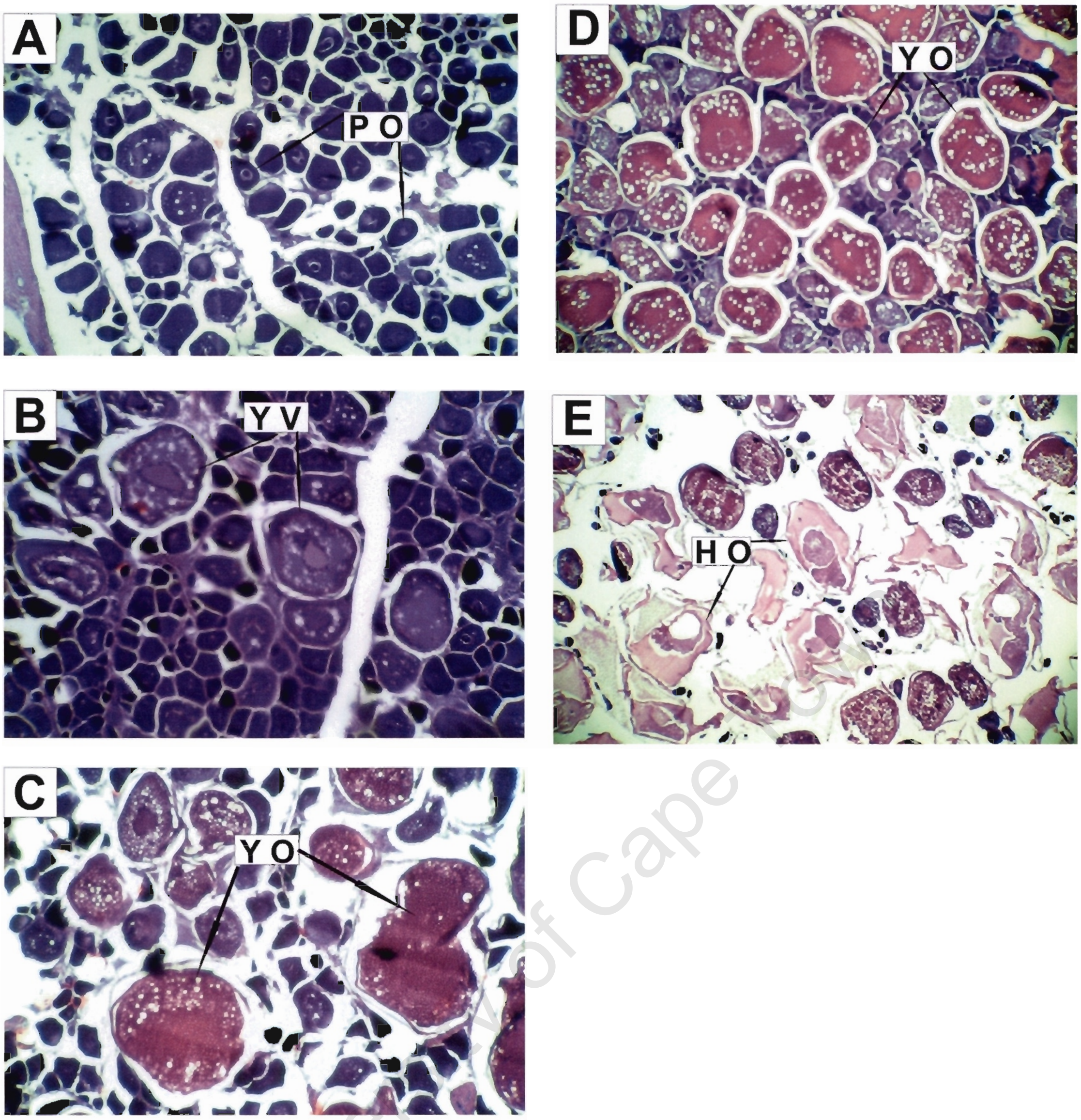


Fig. 2.2: Photomicrographs of *Umbrina canariensis* ovary sections showing oocyte development stages. A: Stage 2, immature or resting, (PO, perinucleolus oocytes), X 100. B: Stage 3, active, (YV, yolk vesicle oocytes), X 100. C: Stage 4, developing, (YO, yolk oocytes), X 100. D: Stage 5, ripe, X 40.E: Stage 6, ripe and running, (HO, hydrated oocytes), X 40.

Each otolith section was read three times, at least one week apart, without reference to fish size, and only if two out of the three readings agreed was the otolith accepted. A fourth reading was taken of otoliths that appeared to be outliers (observed length more than 2 *SD* from mean length-at-age) and if the fourth reading was different from the original designated age but the same as one of the previous three readings, the new age was accepted as correct. Ageing precision was quantified using both the index of average percentage error (*IAPE* Beamish & Fourier 1981) and mean coefficient of variation (*CV* Chang 1982).

Marginal zone analyses and marginal increment analyses (Campana 2001) of fish that were sampled monthly from Algoa Bay were used to validate the formation of annuli. As otoliths used for ageing were limited to fish collected during the spring-summer months, an additional 139 otoliths collected during the rest of the year were sectioned for this purpose. The marginal zone of each section was determined at 25 times magnification and the monthly proportions of opaque (white) and translucent (dark) margins were plotted. Marginal increments were measured from the end of the last complete opaque zone to the proximal otolith margin adjacent to the sulcal groove using an ocular micrometer at 50 times magnification. Given that marginal increments become narrower with age and there were insufficient monthly samples to treat each age class separately, marginal increments were plotted as a proportion of the width of the last completed annulus (opaque and translucent zones combined) (Griffiths 1996a). As the first annulus is disproportionately larger, otoliths from fish in their second growth year (i.e. 1+) were excluded from this analysis.

Three different growth models (the three parameter von Bertalanffy, generalized four parameter von Bertalanffy and the Schnute) were fitted to the observed length at age data for each data set. Models were fitted to each data set using the Microsoft EXCEL SOLVER routine (Microsoft Corporation 2000) by minimizing the negative log-likelihood estimates (equivalent to finding the maximum likelihood estimates) of the model parameters. An additional, normal error structure was assumed and hence the negative log-likelihood estimate of model parameters is equivalent to the non-linear least-squares estimate and takes the form:

$$-\ln L = \frac{n}{2}\ln\sigma^2 + \frac{n}{2} \qquad (2.5)$$

where n is the sample size and σ^2 is the variance.

The goodness of fit of the different growth models were compared by using Akaike's (1973) information criterion (*AIC*):

$$AIC = -2 \ln L + 2p \qquad (2.6)$$

Where $\ln L$ is the negative log-likelihood estimate and p is the number of parameters.

Parametric bootstrapping (1 500 bootstraps) and the percentile method were used to calculate 95 % confidence intervals and standard errors for parameters of the best-fit models. Approximate joint 95 % confidence regions around L_∞ and k were calculated by conditioning on t_0, conducting 1 000 bootstraps and using the percentile method to determine the 95 % confidence interval for each parameter. Growth model parameters and fitted curves for each sex and region were compared using likelihood ratio tests (Draper and Smith 1966). Differences in average observed length-at-age between sexes and regions were tested using t-tests.

RESULTS

Morphometric relationships

The relationships between total length (TL) and standard length (SL) and TL and weight (WT) for the combined regions are described by the functions:

$TL = 1.199\ SL + 7.699$; $n = 466$, $r^2 = 0.995$, range = 156-427 mm TL

$WT = 10^{-5.2969}\ TL^{3.1792}$; $n = 777$, $r^2 = 0.975$, range = 156-427 mm TL, 53-1376 g WT

Reproduction

The majority of samples I used were frozen, or in poor condition due to the extended trips undertaken by trawlers and consequently many of the gonads were not suitable for histological analysis. As a result no examine histological sections of any immature (stage 1) or spent ovaries (stage 7) were examined and only one ripe and running (stage 6) ovary was successfully sectioned. Hydrated oocytes typically burst during freezing and tissue from ripe and running ovaries tended to crumble when sectioned. Examination of histological sections of the ovaries of reproductively active females (stages 3-5) showed multiple stages of oocyte development with simultaneous occurrence of primary, secondary and tertiary yolk stages, indicating that *U. canariensis* are serial batch spawners (Fig. 2.2). This analysis also confirmed that the macroscopic staging criteria accurately reflected oocyte development (Table 2.1).

The monthly proportion of macroscopic gonad stages in mature females from both regions was dominated by developing and ripe ovaries (stages 4 and 5) during the months of August-February, whilst early ovarian development stages (stages 2 and 3) were most common during Autumn and early Winter (Fig. 2.3), suggesting extended spawning during spring-summer. Mean monthly *GSI*s of mature males and females increased rapidly from July; peaked during November and December and decreased thereafter, providing further evidence that spring-summer spawning occurs in both regions (Fig. 2.3).

Size at 50 % maturity (L_{50}) was estimated at 22 cm TL for males from both regions and 23 cm TL (Algoa Bay) and 24 cm TL (Agulhas Bank) for females. Nearly all males and females greater than 27 cm TL (4.1 years) were mature. Likelihood ratio tests indicated no significant differences ($P > 0.05$) in L_{50} between sexes (Algoa Bay) or between regions for female fish and maturity ogives for the regions combined are presented in Fig. 2.4. Age at 50 % maturity (A_m) determined from regional von Bertalanffy growth curves was, however, slightly greater for Algoa Bay females (3.2 years) than males (2.98 years). Algoa Bay females matured a year later than Agulhas Bank females (2.2 years) all be this at similar size.

Sex ratios of *U. canariensis* trawled on the central Agulhas Bank did not deviate significantly from unity but there were significantly more females than males in samples collected from Algoa Bay (Table 2.2). Although there are exceptions, monthly sex ratios were generally skewed towards females just prior to and during the early spawning season (July – November) in both regions (Table 2.2).

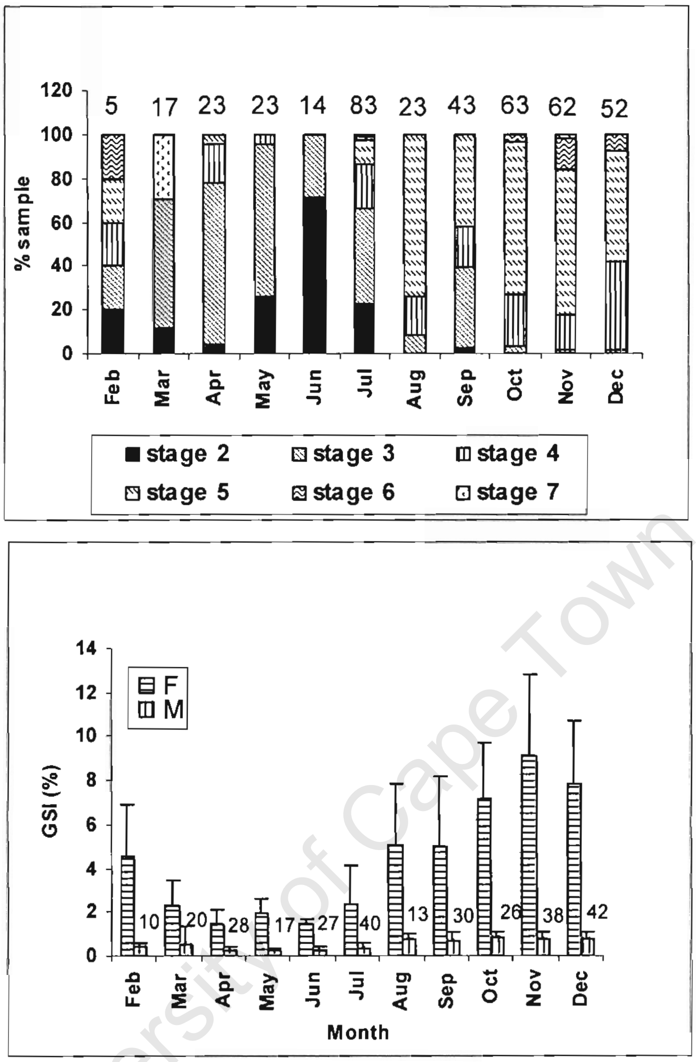


Fig. 2.3: Monthly percentage of macroscopic gonad stages for mature ($>L_{50}$) female *Umbrina canariensis* (regions combined) and average monthly gonadosomatic indices (GSI) for the adults of each sex (+1 *SD*). Monthly sample sizes are shown for mature females (top graph) and mature males (bottom).

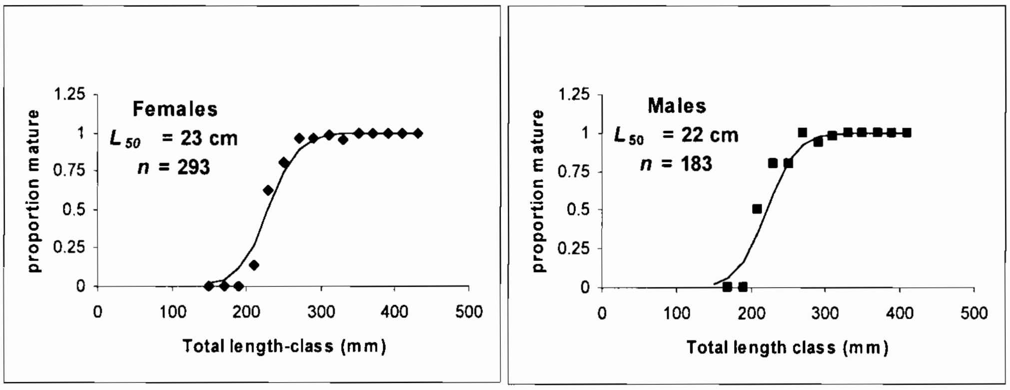


Fig. 2.4: The relationship between size and maturity for female and male *Umbrina canariensis* sampled off the South African southeast coast. Solid line describes the fitted logistic function.

Table 2.2: Monthly male (M) to female (F) sex ratios of *Umbrina canariensis* trawled west (central Agulhas Bank) and east (Algoa Bay) of 24°E longitude.

Month	Central Agulhas Bank			Algoa Bay		
	M:F	*n*	X_c^2	M:F	*n*	X_c^2
February				1:0.5	15	1.07
March	1:2	12	0.75	1:0.6	25	1.44
April	1:0.9	54	0.02			
May				1:1.4	40	0.63
June				1:0.5	41	3.51
July				1:2.1	124	14.91**
August				1:1.8	36	2.25
September	1:0.7	41	0.43	1:1.9	40	3.03
October	1:1.3	37	0.43	1:3.5	63	18.35**
November	1:1.6	26	0.96	1:1.7	112	6.51*
December	1:1.5	57	1.75	1:1.1	46	0.02
TOTAL	1:1.2	227	1.13	1:1.5	542	22.73**

X_c^2 values have been corrected for continuity using the Yates correction
* $P < 0.05$
** $P < 0.01$

Age and growth

Ageing precision

Umbrina canariensis otoliths exhibited alternating, translucent and opaque bands that could be used for ageing purposes (Fig. 2.5). Otolith growth zones were not as clear as in the sympatric congeneric *U. robinsoni*, which inhabits shallower water (Chapter 4). *U. canariensis* otoliths have higher overall opacity, and narrow, poorly defined translucent zones. Average percent error and coefficient of variation were 5.57 and 7.44 for Algoa Bay samples and 6.4 and 8.3 for Agulhas Bank samples (Table 2.3).

Validation of annuli

Marginal zone analyses of otoliths from fish age 2 –27 years sampled in both regions show opaque zone formation during the months of February to August and translucent zone formation during the period September to December (Fig. 2.6); suggesting annual formation of one opaque and one translucent zone. Marginal increment analyses confirmed this pattern with a minimum in mean marginal increment evident in October and November when the translucent zone of the new annulus was deposited (Fig. 2.6).

Table 2.3: Number of *Umbrina canariensis* otoliths read, accepted, index of average percentage error (*IAPE*) and mean coefficient of variation (*CV*).

Parameter	Algoa Bay	Agulhas Bank	Combined
Number read	310	172	482
Number accepted	295*	165	460**
IAPE (3 reads) %	5.57	6.4	5.86
CV (3 reads) %	7.44	8.30	7.78

*: Upon examination of outliers, an apparent transcription error (otolith size and assigned age did not match with fish size) was identified and a batch of 18 otoliths from the Algoa Bay sample was excluded from the analyses, resulting in a total sample size of 277 otoliths for the region.

**: A fourth reading of 13 otoliths from the Agulhas Bank data set resulted in four aged two fish being allocated a new age of three years.

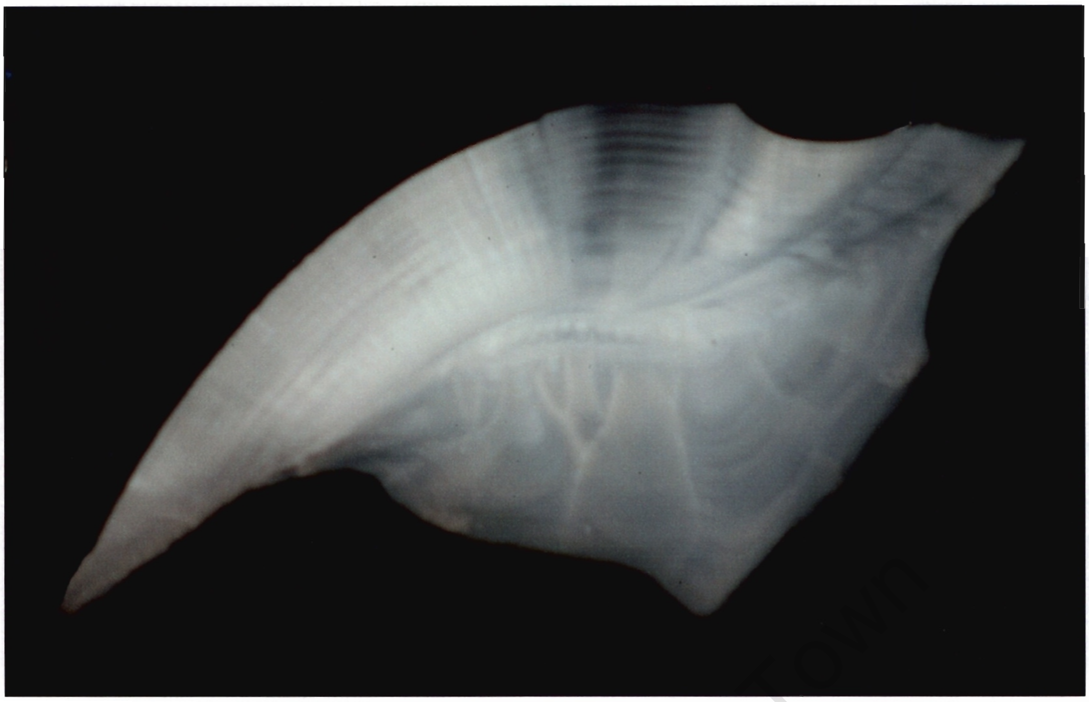


Fig. 2.5: Photomicrograph of *Umbrina canariensis* otolith taken from a fish (32 cm TL) aged at 10 years.

The observed pattern does suggest that growth zones deposit annually in *U. canariensis* otoliths but is not conclusive. The high standard deviations associated with mean marginal increment widths and lack of months with complete dominance of a single marginal band nature is indicative of high variability in the timing of growth zone deposition and also of the difficulty in distinguishing and measuring opaque and translucent zones in *U. canariensis* otoliths. It was not possible to conduct any direct validation (e.g. chemical marking) of annulus formation in *U. canariensis,* but given that growth zones do deposit annually in the other *Umbrina* species found in South African waters (Chapter 4) as well as in all the other sciaenids found in the region, annual deposition of one opaque and one translucent growth zone in *U. canariensis* was assumed.

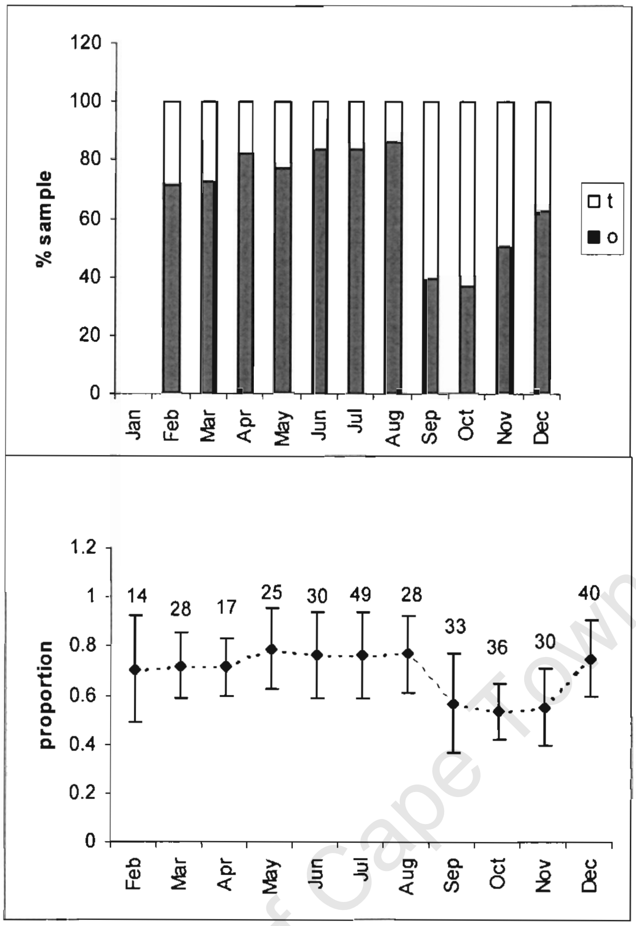


Fig. 2.6: Monthly marginal zone nature and mean marginal increment width expressed as a proportion of previous completed annuli width for *Umbrina canariensis* otoliths from fish aged 2-27 years. Error bars show ± 1 *SD* of the mean, numbers above error bars indicate sample sizes. t = translucent, o = opaque.

Fitting growth models to the data

The three different growth models were fitted to a combined data set, (males and females, both regions); separate male and female data sets (Algoa Bay only) and to separate central Agulhas Bank and Algoa Bay data sets (combined sexes). Akaike's information criterion for all growth models fitted was very similar, being slightly greater for the Schnute model and lowest for the generalized (4 parameter) von Bertalanffy model (Table 2.4). The generalized von Bertalanffy model, however, despite having a lower *AIC*, produced positive t_0 values and in the case of the Algoa Bay data set, the SOLVER routine produced unstable parameter estimates. Given the exceptionally small differences in *AIC* values between the three and four parameter von Bertalanffy models and the more realistic parameter estimates of the former, the special (3 parameter) von Bertalanffy model was chosen for growth comparisons between sexes and regions.

Table 2.4: Akaike's information criterion (*AIC*) for different growth models fitted to the observed length at age data for *Umbrina canariensis* data sets. Lower *AIC* values indicate statistically better fits.

Model and data set	Number of parameters	Negative log-likelihood	AIC
Combined sexes & regions			
Schnute	6	1468	2948
General von Bertalanffy	4	1468	2943
Special von Bertalanffy	3	1471	2948
Agulhas Bank (combined sexes)			
Schnute	6	516	1043
General von Bertalanffy	4	516	1039
Special von Bertalanffy	3	517	1040
Algoa Bay (combined sexes)			
Schnute	6	915	1843
General von Bertalanffy	4	-	-
Special von Bertalanffy	3	918	1841
Males (Algoa Bay)			
Schnute	6	358	728
General von Bertalanffy	4	358	724
Special von Bertalanffy	3	361	728
Females (Algoa Bay)			
Schnute	6	545	1102
General von Bertalanffy	4	545	1098
Special von Bertalanffy	3	546	1098

An unrealistic pattern of very similar observed lengths-at-age for consecutive early year classes (1 - 2 year olds, 4 - 5 year olds) was detected after the initial fitting of the growth curves. This suggests selection of the faster growing individuals of these early year classes. The most likely explanations are either gear selectivity (caused by the cod-end mesh size in commercial trawls) or size dependent movement of juveniles into the sampled areas from the nursery grounds. In order to prevent this pattern from causing bias in the fitted curves, age classes 1 and 4 were not included in the curve fitting procedure in the different regions. The excluded samples are indicated by open symbols in the figures of fitted growth curves. The special von Bertalanffy growth curve fitted to the Algoa Bay, Agulhas Bank (combined sexes), and combined (regions and sexes) data sets are shown in Figure 2.7. The model parameters, standard errors and 95 % confidence intervals for the male and female (Algoa Bay), Algoa Bay and central Agulhas Bank (combined sexes), and combined (regions and sexes) data sets are shown in Table 2.5.

Table 2.5: Fitted von Bertalanffy growth model parameter estimates, standard errors (SE), coefficients of variation (*CV*) and upper (UCI) and lower (LCI) 95 % confidence limits for *Umbrina canariensis* trawled off the South African southeast coast.

Parameter	Combined (Sexes & regions)	Females (Algoa Bay)	Males (Algoa Bay)	Agulhas Bank (Combined sexes)	Algoa Bay (Combined sexes)
L_∞					
Best fit	356.2	355.3	350	397.2	352
SE	2.9	4.3	4.9	10.84	3.2
CV (%)	0.84	1.21	1.4	2.72	0.92
LCI	350.9	347.5	340.7	379.2	346.1
UCI	362.4	364.2	360.9	421.6	358.6
k					
Best fit	0.26	0.27	0.22	0.16	0.26
SE	0.017	0.026	0.024	0.022	0.019
CV (%)	6.65	9.46	10.97	13.54	7.25
LCI	0.23	0.23	0.18	0.12	0.22
UCI	0.29	0.33	0.28	0.20	0.29
t_0					
Best fit	-1.32	-0.93	-1.52	-3.41	-1.1
SE	0.26	0.32	0.475	0.681	0.27
CV (%)	19.1	33.4	30.8	19.7	24.3
LCI	-1.88	-1.59	-2.52	-4.89	-1.67
UCI	-0.87	-0.38	-0.68	-2.27	-0.63

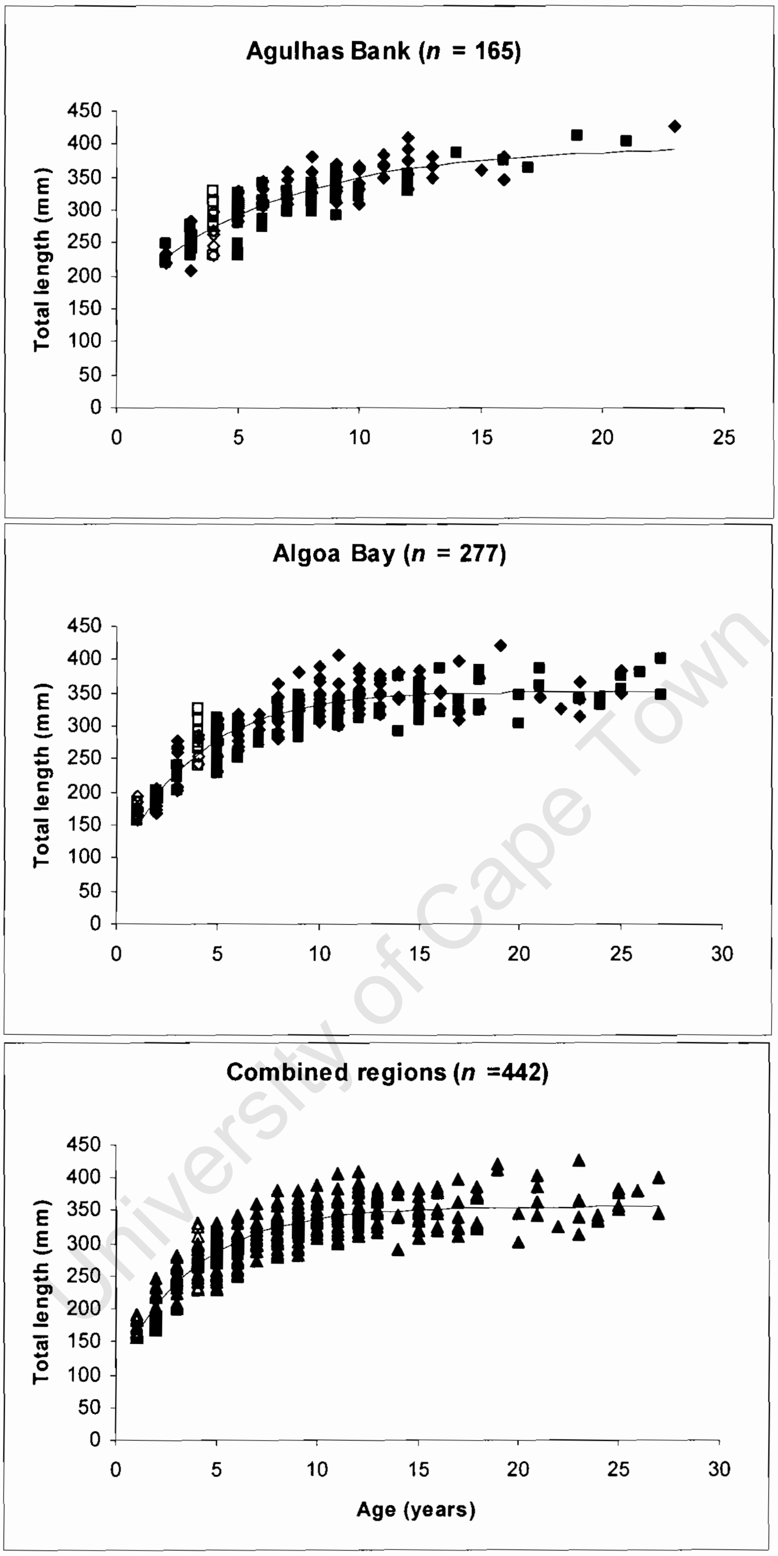


Fig. 2.7: Three parameter von Bertalanffy growth model fitted to the observed length at age data for *Umbrina canariensis* trawled off the South African southeast coast (combined sexes). In the regional plots, males are represented by squares and females by diamonds; open symbols represent excluded year classes.

Growth comparisons between sexes

Maximum ages recorded were 27 and 25 years and 21 and 23 years for males and females from Algoa Bay and the central Agulhas Bank respectively, indicating similar longevity for both sexes. The mean length-at-age of females from both regions was slightly larger than that of males for ages 2-12 years (central Agulhas Bank) and 2-15 years (Algoa Bay) (Tables 2.6 and 2.7). However lengths-at-age were highly variable, with the mean lengths for most ages of either sex falling within one standard deviation of the other sex (Tables 2.6 and 2.7). Due to this high variability, the small differences in mean length-at-age between the sexes, and small sample size for some ages, the mean length at age of females was significantly greater than males only for ages 9, 11 and 13 (Algoa Bay) and ages 5 and 8 (central Agulhas Bank).

The sample size was considered inadequate to allow comparison of sex-specific fitted growth curves for the central Agulhas Bank data set and I limited statistical comparison of growth curves to the Algoa Bay data set. A likelihood ratio test indicated statistically significant differences between sexes (Algoa Bay) in the fitted growth models ($P < 0.01$), but not for any of the model parameters ($P > 0.05$). Comparison of the fitted curves shows that although Algoa Bay female and male *U. canariensis* attain similar asymptotic lengths, females reach this limit at a slightly (but not significantly) faster rate (Fig. 2.8). Comparison of approximate, joint 95 % confidence regions for L_∞ and k suggests that although growth differences between the sexes are statistically significant (with little overlap between the regions), they are not substantial (confidence regions being close together in parameter space) (Fig. 2.9). Given the small differences in growth estimates for males and females, and the inconclusive statistical comparisons, the sexes were combined for regional comparisons.

Table 2.6: Comparisons of mean length (TL mm) at age of male (M) and female (F) *Umbrina canariensis* sampled from Algoa Bay.

Age years	F	M	F (*n*, *SD*.)	M (*n*, *SD*.)	t - test	Conclusion
1	166	177	6, 10	6, 10	$t = -1.81$ $P > 0.05$	
2	191	185	16, 10	8, 9	$t = 1.46$ $P > 0.05$	
3	251	221	9, 28	3, 19	$t = 1.69$ $P > 0.05$	
4	282	265	10, 24	4, 21	$t = 1.28$ $P > 0.05$	
5	289	276	22, 20	14, 25	$t = 1.67$ $P > 0.05$	
6	292	283	14, 17	9, 23	$t = 1.06$ $P > 0.05$	
7	306	280	3, 11	2, 8	$t = 2.72$ $P > 0.05$	
8	307	315	8, 31	6, 18	$t = 0.56$ $P > 0.05$	
9	341	316	7, 19	10, 21	$t = 2.5$ $P < 0.05$	F > M*
10	339	316	14, 23	2, 11	$t = 1.39$ $P > 0.05$	
11	342	314	10, 28	8, 11	$t = 2.65$ $P < 0.05$	F > M*
12	351	334	10, 22	6, 12	$t = 1.75$ $P > 0.05$	
13	356	320	10, 21	2, 6	$t = 2.34$ $P < 0.05$	F > M*
14	351	332	4, 23	2, 60	$t = 0.62$ $P > 0.05$	
15	358	335	5, 19	6, 20	$t = 1.94$ $P > 0.05$	
16	343	342	3, 14	3, 39	Not tested	
17	338	332	4, 40	2, 11		
18	342	357	3, 25	5, 28		
19	420		1			
20		324		2, 31		
21	344	374	1	2, 18		
22	326		1			
23	340	340	3, 25	1		
24		338		3, 5		
25	366	366	2, 23	2, 14		
26		381		1		
27		373		2, 40		

Table 2.7: Comparisons of mean length (TL mm) at age of male (M) and female (F) *Umbrina canariensis* sampled from the central Agulhas Bank.

Age (Years)	F	M	F (*n*, *SD*.)	M (*n*, *SD*.)	t - test	Conclusion
2	230	227	4, 7	5, 12	Not tested	
3	251	248	17, 17	9, 14	$t = 0.47$ $P > 0.05$	
4	286	264	11, 25	7, 21	$t = 1.79$ $P > 0.05$	
5	308	291	15, 12	17, 27	$t = 2.16$ $P < 0.05$	F > M*
6	320	298	5, 17	8, 23	$t = 1.85$ $P > 0.05$	
7	333	317	4, 23	5, 12	$t = 1.34$ $P > 0.05$	
8	350	319	4, 24	7, 18	$t = 2.5$ $P < 0.05$	F > M*
9	342	330	6, 22	7, 22	$t = 1.01$ $P > 0.05$	
10	347	327	7, 21	2, 12	$t = 1.19$ $P > 0.05$	
11	367		4, 14		Not tested	
12	373	342	5, 31	3, 13		
13	365		3, 17			
14		387		1		
15	360		1			
16	362	376	2, 25	1		
17		364		1		
19		412		1		
21		404		1		
23	427		1			

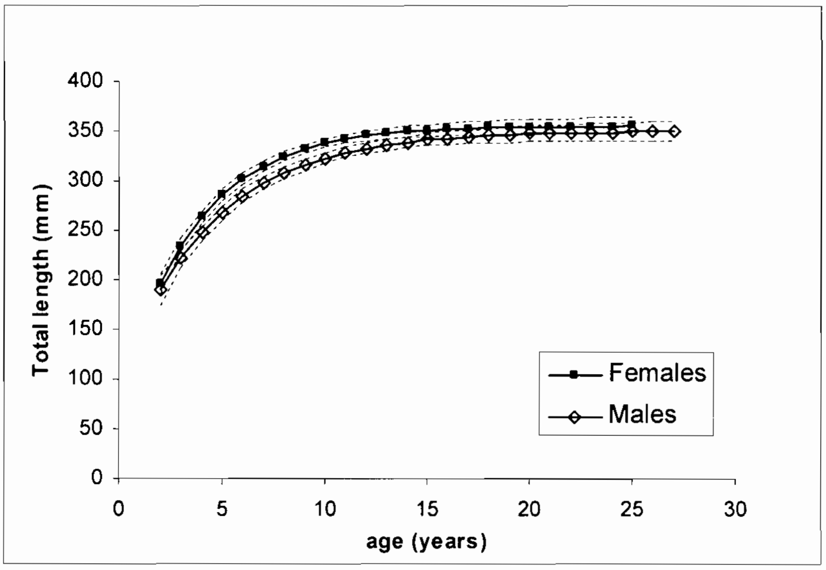


Fig. 2.8: Comparison of three parameter von Bertalanffy growth models fitted to observed length-at-age data of *Umbrina canariensis* males and females sampled from Algoa Bay. 95 % confidence intervals for each curve are indicated with dotted lines.

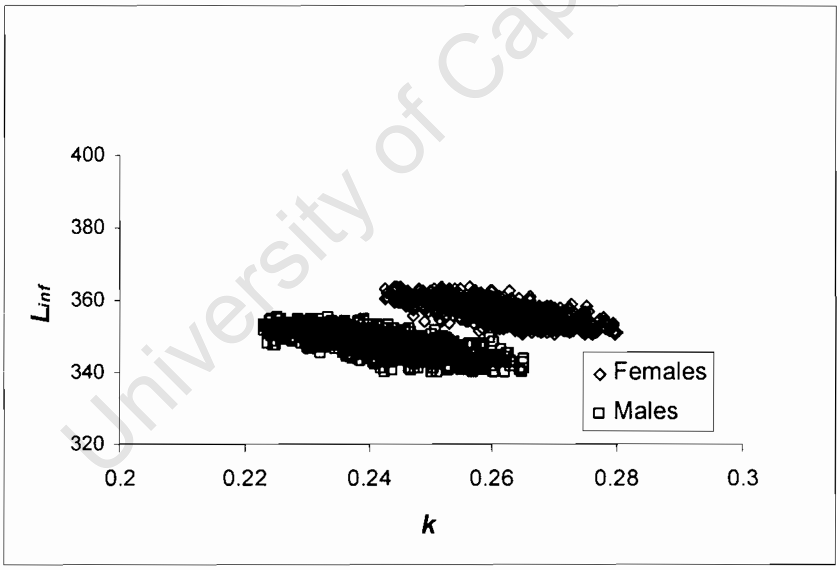


Fig. 2.9: Comparison of the joint. 95 % confidence regions around L_∞ and k calculated by conditioning on t_0 and conducting 1 000 bootstraps for male and female *Umbrina canariensis* (Algoa Bay).

Growth comparisons between regions

Maximum ages recorded were similar in both regions, 23 and 27 years for the central Agulhas Bank and Algoa Bay respectively. A likelihood ratio test indicated statistically significant differences between *U. canariensis* trawled off Algoa Bay and the central Agulhas Bank (combined sexes) in the fitted growth models ($P < 0.01$), the estimated L_∞ value ($P < 0.01$), t_0 ($P < 0.01$) and the estimated growth rate parameter k ($P < 0.01$). Comparison of the fitted curves suggests that central Agulhas Bank *U. canariensis* attain a larger asymptotic length than Algoa Bay *U. canariensis* and take longer to reach this limit (Fig. 2.10). The joint 95 % confidence regions around L_∞ and k are clearly separated in parameter space, suggesting that the growth differences between these two regions are real (Fig 2.11). Comparison and statistical testing of the mean length-at-age of Algoa Bay and central Agulhas Bank *U. canariensis* (Table 2.8) shows the mean length of central Agulhas Bank fish being larger than Algoa Bay fish for all ages up to 17 years, significantly so for ages 2, 5-7, and 11.

DISCUSSION

Several authors have stressed that percentage agreement is not an appropriate measure for comparing ageing precision amongst different stocks or species as it does not take into account the age composition of the sample, and instead recommend the use of *APE* or *CV* (Beamish and Fourier 1981, Chang 1982, Campana 2001). Unfortunately nearly all published studies on sciaenid age and growth have reported percentage agreement as a measure of ageing precision. Published values of percentage agreement for temperate and subtropical sciaenids are: 88-99.8% for *Cynoscion nebulosus* (Murphy and Taylor 1994, Nieland *et al.* 2002), 99-100% for *Cynoscion regalis* (Lowerre-Barbieri *et al.* 1994), 99% for *Micropogonias undulatus* (Barbieri *et al.* 1994a), 90-92% for *Micropogonias furnieri* (Manickchand-Heileman and Kenny 1990), 92% for *Pogonias cromis* (Beckman *et al.* 1990), and 96-100 % for *Sciaenops ocellatus* (Beckman *et al.* 1989, Murphy and Taylor 1990, Ross *et al.* 1995, Murphy and Crabtree 2001). Percentage agreement for the sectioned otoliths of *U. canariensis* used in this study was substantially less than these reported values, only, 43 % agreement between the 1st and 2nd reading rising to 80 % agreement between the 2nd and 3rd reading.

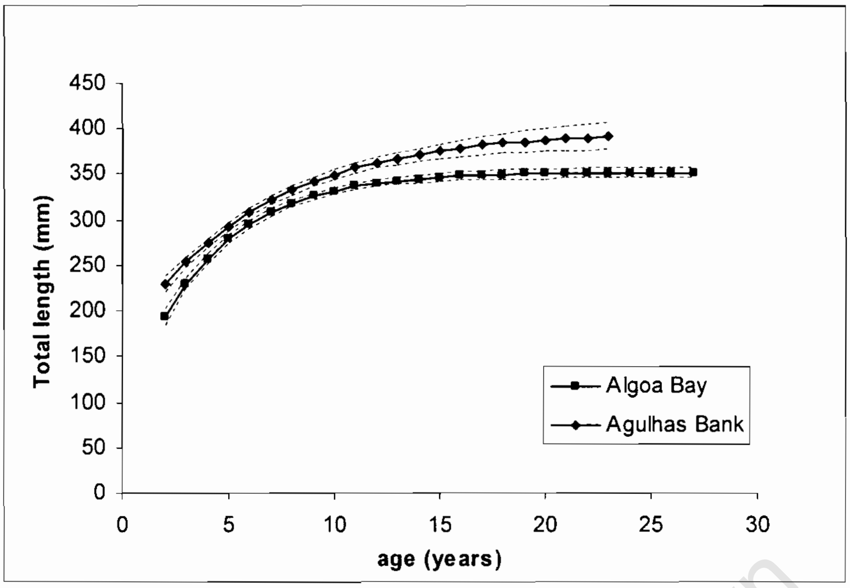


Fig. 2.10: Comparison of three parameter von Bertalanffy growth models fitted to observed length at age data of *Umbrina canariensis* trawled off Algoa Bay and the central Agulhas Bank (combined sexes). 95 % confidence intervals for each curve are indicated with dotted lines.

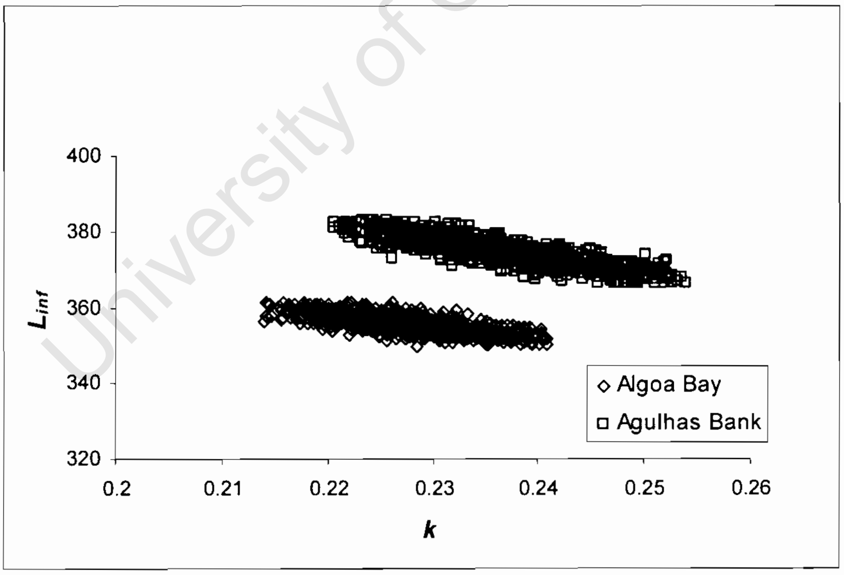


Fig. 2.11: Comparison of the joint. 95 % confidence regions around L_∞ and k calculated by conditioning on t_0 and conducting 1000 bootstraps for *Umbrina canariensis* sampled from Algoa Bay and the central Agulhas Bank (combined sexes)

Table 2.8: Comparison of mean length at age (TL mm) of the central Agulhas Bank (CAB) and Algoa Bay (AB) *Umbrina canariensis* (sexes combined).

Age (Years)	Algoa Bay	Agulhas Bank	Algoa Bay (*n, SD*)	Agulhas Bank (*n, SD*)	t - test	Conclusion
1	172		12, 10			
2	189	228	24, 10	9, 10	$t = 10.0$ $P < 0.001$	CAB > AB**
3	243	250	12, 28	26, 16	$t = 1.48$ $P > 0.05$	
4	277	277	14, 25	18, 26	$t = 0.005$ $P > 0.05$	
5	284	299	36, 23	32, 23	$t = 2.87$ $P < 0.01$	CAB > AB**
6	288	307	23, 20	13, 23	$t = -2.58$ $P < 0.05$	CAB > AB*
7	296	324	5, 19	9, 17	$t = 2.77$ $P < 0.05$	CAB > AB*
8	311	330	14, 26	11, 25	$t = 1.31$ $P > 0.05$	
9	326	336	17, 21	14, 23	$t = 1.15$ $P > 0.05$	
10	336	342	16, 24	9, 21	$t = -0.55$ $P > 0.05$	
11	330	367	18, 26	4, 14	$t = 2.75$ $P < 0.05$	CAB > AB*
12	344	361	16, 21	8, 29	$t = -1.63$ $P > 0.05$	
13	350	365	12, 23	3, 17	$t = -1.01$ $P > 0.05$	
14	345	387	6, 31	1	Not tested	
15	346	360	11, 22	1		
16	342	367	6, 27	3, 19		
17	336	364	6, 31	1		
18	351		8, 26			
19	420	412	1	1		
20	324		2, 31			
21	364	404	3, 21	1		
22	326		1			
23	340	427	4, 20	1		
24	338		3, 5			
25	366		4, 38			
26	381		1			
27	373		2, 40			

The overall *CV* (7.78), however, was close to the median (7.6) of 117 age and growth studies on a variety of fish species reviewed by Campana (2001) which indicates that although ageing precision for sectioned *U. canariensis* otoliths is not as high as typically reported for other sciaenids it is certainly within the range of published values for age and growth studies on other fish species. Griffiths (1996a) also encountered difficulties when ageing the sciaenid, *Argyrosomus inodorus* from the southeastern Cape, a species which inhabits a similar depth range to *U. canariensis*. The growth zones in the otoliths of *A. inodorus* became progressively more distinct in samples obtained further west, where the species inhabits shallower water (Griffiths 1996a). This observation, and the finding that the annuli in the otoliths of the inshore congeneric *U. robinsoni* (*APE* = 0.26 %, average *CV* = 0.36 %), (Chapter 4), and *Argyrosomus japonicus* (*APE* = 0.34 %, average *CV* = 0.46 %) (Griffiths and Attwood in press.) are very clear, suggests that the environmental factors influencing growth zone deposition in sciaenids are weaker in deeper waters. It must, however, be noted that the processes governing growth zone deposition in fish otoliths are not well understood, and are probably a combination of endogenous and environmental factors (Beckman and Wilson 1995).

The mean observed and calculated lengths-at-age for our sample of South African *U. canariensis* were slightly greater than those observed or calculated from a fitted von-Bertalanffy model by Venidictova (1982) for 1-4 year old fish in the southeast Atlantic. For age classes 5-8 years (the maximum age observed by Venidictova 1982), however, the observed or calculated lengths became progressively greater than those observed in the South African stock. Indeed, southeast Atlantic *U. canariensis* with an estimated age of eight years had a mean observed length of 415 mm, a length only obtained by a few South African fish, all in excess of 19 years of age. Although it is possible that South African and southeast Atlantic *U. canariensis* stocks have very different growth rates, the most likely explanation for this discrepancy is the fact that Venidictova (1982) used scales for age estimation rather than sectioned otoliths. Whilst scales may give accurate estimates of age for younger fish, they often underestimate ages of older fish (Carlander 1987, cited in Murphy and Taylor 1994). Amongst sciaenids, the mean number of annuli in sectioned otoliths of *C. nebulosus* older than age two was significantly greater than the mean number counted from scale impressions from the same fish (Wenner *et al.* 1990, cited in Murphy and Taylor 1994). In a comparative study using scales and otoliths to age *U. canosai* from Southern Brazil, Haimovici and Reis (1984) found that otolith reading was the most adequate ageing method, with scales only suitable for ageing fish up to five years. It appears likely that the scale ageing method used by Venidictova (1982) grossly underestimated the age of older *U. canariensis* in the southeast Atlantic and as a result the estimated von Bertalanffy parameters (L_∞ = 1004 mm - more than double the maximum observed length in catches, k = 0.055) are inaccurate and are not comparable with our estimates (L_∞ = 356 mm, k = 0.26). These findings provide further support that sectioned otoliths rather than scales should be used for age and growth studies on sciaenids species that attain ages of greater than 4-5 years.

Umbrina canariensis of similar maximum size were recorded from the central Agulhas Bank and Algoa Bay (427 and 402 mm TL respectively), but significant differences between fitted growth curves indicate that on average, fish trawled on the central Agulhas Bank attain a larger asymptotic length (Fig. 2.10). This appears to be a result of a combination of slower juvenile growth and a shorter period of post-maturity growth in fish occurring in Algoa Bay, which approach asymptotic length more rapidly (k = 0.26) than those occurring on the central Agulhas Bank (k = 0.16). Many studies on age and growth in marine organisms have noted a geographical variation in growth rate with the larger or faster growing animals occurring in cooler latitudes. Amongst sciaenids, Shepherd and Grimes (1983) recorded this trend in *C. regalis* off the North American Atlantic coast, whilst Griffiths (1996a) reports that *A. inodorus* in the South Western Cape initially grew faster than those on the east coast, although growth slowed earlier in the former region. A southern Cape population of the sympatric *U. robinsoni* grows more slowly and attains a significantly smaller asymptotic length than a population from cooler waters further west (Chapter 7). The pattern was also observed in *Rhabdosargus globiceps* (Sparidae), with growth rate and asymptotic size increasing clinally from the South-Eastern Cape through to the South Western Cape (Griffiths *et al.* 2002). These spatial variations in growth rate have been ascribed to physical and biotic environmental factors as well as to fishery effects. I am uncertain of the causes for the regional growth differences observed in South African *U. canariensis*, which is likely a result of a combination of these factors. It is unlikely that increasing water temperatures in areas further east is the sole cause of the regional growth differences as *U. canariensis* occurs in deeper (cooler) water with eastwards movement along the South African coast (Chapter 1). The more rapid juvenile growth of central Agulhas Bank fish does result in a substantially younger age at maturity (A_m) than Algoa Bay fish. Leaman (1991) notes that younger A_m in conjunction with increased growth rates (often as a result of increased fishing mortality) are common, whilst changes in L_{50} are less frequently documented which suggests physiological or environmental constraints on L_{50}. Intuitively, the trade-off due to increased reproductive effort at a younger age should cause an earlier reduction in post-maturity growth rate and result in a smaller asymptotic length, which is contrary to our findings. Optimal age or size at maturity in fishes that evolve strategies that maximise fitness (or lifetime reproductive output) is determined by trade-offs between fecundity, growth rate and mortality (Roff 1992) and at present I have insufficient information on these parameters to interpret regional growth variations within the context of life history theory.

Spring-summer spawning is common amongst South African east coast sciaenids and apart from *U. canariensis* (this study) has been recorded for *A. inodorus, A. japonicus, Atractoscion aequidens, Otolithes ruber, Atrobucca nibe, Johnius dussumieri, Johnius amblycephalus* and *U. robinsoni* (Griffiths and Hecht 1995b, Griffiths 1996b, Griffiths 1997a, Fennessy 2000, Chapter 4). Venidictova (1983b) also reports spring-summer spawning with a November-December peak, most intense at water depths between 50-100 m for *U. canariensis* in the southeast Atlantic, whilst off the northwest coast of Africa, reproductively active fish were noted at 100-200 m depth during April-August (northern hemisphere summer) (Podosinnikov 1979). The timing and duration of spawning in fishes is generally accepted to coincide with periods when environmental conditions are favourable for egg, larval and juvenile survival and growth, as well as the survival and condition of spawning adults (Sadovy 1996). Nutrient and production levels in South African temperate regions typically increase and reach maxima during the spring-summer period in response to increasing daylight, water temperatures and frequency of upwelling events (Shannon 1989) and spawning in many fish species is timed to coincide with this season.

Length frequency analysis of *U. canariensis* (n = 3331) taken by fishery independent swept area trawl surveys off the South African east coast revealed that modal size increased from 27 cm TL to 36 cm TL over the depth range of 37 –50 m and 100-111 m (Chapter 1); suggesting that nursery grounds are found inshore in shallower water. Predominately onshore winds during spring-summer (spawning season for *U. canariensis*) off South Africa's southeast coast would carry the pelagic eggs inshore, whilst relatively weak and retentive currents (10-50 $cm.s^{-1}$) on the inshore Agulhas Bank and Algoa Bay region also tend to move water shoreward (Boyd *et al.* 1992). Tank experiments revealed that *U. canariensis* eggs rose to the surface upon fertilization, they hatched 24 hours later and the prolarvae immediately descended to the substratum where they began to react to visual stimuli after two days (Podosinnikov 1979). The relatively rapid development time and short pelagic phase of *U. canariensis* eggs and larvae, in conjunction with the prevailing oceanographic conditions, would facilitate juvenile recruitment and retention to inner shelf habitats.

Owing to the limitations of the survey and commercial fishing gear, most of the samples for the present study were collected over soft (sand/mud) substrata. Video footage from 120 m depth in KwaZulu-Natal has nevertheless confirmed that *U. canariensis* also associates with reefs of moderate profile (Dr Kerry Sink, Southern African Institute of Aquatic Biodiversity, pers. comm.). The present study revealed that the sex ratio of fish on the trawl grounds was skewed towards females, particularly during the spawning season. Given the lack of ripe and running females (17 of 278 adult females sampled during the spawning season) and dominance of soft bottom prey in their stomachs, the trawl grounds appear to be feeding rather than spawning areas. Although spawning frequency was not investigated for *U. canariensis*, female sciaenids typically spawn once every three to seven days during the spawning season (Comyns *et al.* 1991, Nieland and Wilson 1993, Brown-Peterson *et al.* 2002). It is therefore possible that the skewed spawning season sex ratio for *U. canariensis* is the result of females moving back to the feeding grounds between spawning events. As sperm generation is continuous and less energetic the males are expected to spend more time spawning.

Significant differences in both the growth rate and age at maturity of *U. canariensis* from Algoa Bay and the central Agulhas Bank indicates that each of these areas of abundance comprises a separate population/stock. Although at present there is no information on migration or residency for *U. canariensis*, for example tagging data or temporal shifts in regional catch per unit effort (the species being a non-targeted by-catch component and spatial/temporal shifts in commercial fishing effort are related to movements of target species) extensive movement between the two areas of abundance is unlikely. Tag-recapture studies on two other South African fish species, *A. inodorus* and *Argyrozona argyrozona* (Sparidae) that have similar distribution patterns to *U. canariensis* (separate centres of abundance on the central Agulhas Bank and Algoa Bay), indicate little or no movement between these two areas (Griffiths 1997a, Brouwer *et al.* 2003). Griffiths (1997a) suggested that movement between southern and southeastern Cape stocks of *A. inodorus* was restricted by the presence of cold, bottom mixed layer water (< 12°C) that extends far up the narrowing shelf (close to the coast) in the region between Knysna and Cape St Francis (Swart and Largier 1987, Boyd and Shillington 1994). Several studies have subsequently found evidence that suggests this cold water ridge is a barrier to the movement of many warm-temperate demersal fish species (Griffiths and Wilke 2002, Griffiths *et al.*2002, Brouwer *et al.* 2003). It is reasonable to propose that the distribution of *U. canariensis* is also constrained by the bottom mixed layer water. The area separating the two centres of abundance also has a very narrow 50-100 m depth zone which is preferred by the species (Chapter 1).

Although the moderate longevity of *U. canariensis* indicates that the species may be vulnerable to overexploitation (Buxton 1996, Griffiths 2000), the median age-at-maturity in both regions is similar to the age-at-recruitment into the commercial trawl fishery (Chapter 3), which should provide some protection from recruitment overfishing. However, the South African government is attempting to create more equitable access (amongst population groups) to marine resources (Kleinschmidt *et al.* 2003) and one way of doing so is to increase access to previously under-exploited species. Traditional trawl fish such as hake are becoming increasingly unaffordable for local South Africans (mostly due to high export prices) and previously undesirable by-catch species such as *U. canariensis* are likely to become more acceptable and marketable in the future. It is therefore prudent that stock assessment of South African *U. canariensis* based on the life-history information presented in this chapter and re-evaluation of current management measures, which are clearly inappropriate for the species, be conducted in the near future. Although it may not be practical to implement regionally specific management measures for South African *U.*

canariensis, as the species is not directly targeted, the different growth rates and ages at maturity would have to be taken into account when calculating mortality and biological reference points and separate stock assessments are needed for the two regions.

CHAPTER 3

PER-RECRUIT STOCK ASSESSMENT AND MANAGEMENT OF SOUTH AFRICAN *UMBRINA CANARIENSIS* (SCIAENIDAE)

ABSTRACT

Baardman, *Umbrina canariensis*, are a common by-catch species in inshore demersal trawl catches along South Africa's south and east Cape coast. Yield and spawner biomass per-recruit analyses of *U. canariensis* populations from the central Agulhas Bank and Algoa Bay indicated that stocks from both regions are underexploited. Estimates of instantaneous fishing mortality on the central Agulhas Bank were 0.17 y^{-1} for the period 1995-1998 and 0.06 y^{-1} for 2001-2003; and were predicted to reduce the spawner biomass on the central Agulhas Bank to 41% and 69% of pristine levels, respectively. Although reduction in F between the two periods may be an artifact of sampling error, it is more likely to have resulted from a spatial shift in trawl effort and a change in targeting practises in the inshore fishery. The Algoa Bay stock appears to be very lightly exploited and even using the upper 95% confidence limit estimate of fishing mortality (F) produces a current (2001-2003) SB/R estimate at 91 % of pristine levels. Due to the slow growth, relative longevity and low natural mortality rate (M = 0.15-0.18 y^{-1}) of the species, however, target ($F_{SB\ 40}$) or threshold ($F_{SB\ 25}$) reference points will be reached at relatively low rates of F ($F_{SB\ 40} = 0.18\ y^{-1}$, $F_{SB\ 25} = 0.34\ y^{-1}$). An increase in targeting of the species is not recommended and it should be managed as a trawl by-catch rather than a targeted line fish species. The current bag and size limits for baardman should be reviewed and made species specific to take into account the fact that the current restrictions for the genus are not practically applicable to *U. canariensis* as a trawl by-catch species.

INTRODUCTION

The canary drum *Umbrina canariensis,* locally known as baardman, is a medium-size (maximum size approximately 42 cm TL) sciaenid with a broad geographical rage, occurring in upper shelf habitats around most of the African coast (Chapter 1). In South African waters the species has two discrete centres of abundance: one on the central Agulhas Bank and the other in Algoa Bay (Fig 3.1) (Chapter 1). Aspects of the biology and exploitation potential of the species taken by Soviet fishing trawlers off the west African coast were reported on by Podosinnikov (1979) and Venidictova (1982, 1983a, 1983b).

In the South African demersal trawl fishery, the biology of the principal target species, namely Cape Hakes *Merluccius* species (Botha 1971, 1985, Payne 1986, 1989, and Agulhas Sole *Austroglossus pectoralis* (Le Clus *et al.* 1994,1996, Zoutendyk 1973) has been well researched. Catches of these target species are quota controlled with annual total allowable catches (TAC) set based on demersal biomass surveys (Payne *et al.* 1985, 1986, 1987) monitored landings and the results of complex stock assessment models (e.g. stochastic age-structured production models) (Punt 1988, 1994). Economically important by-catch species such as kingklip *Genypterus capensis* (Japp 1990, Punt and Japp 1994), monk *Lophius vomerinus* (Griffiths and Hecht 1986, Walmsley *et al.* 2005), horse mackerel *Trachurus trachurus capensis* (Badenhorst and Smale 1991, Kerstan and Leslie 1994) and panga *Pterogymnus laniarius* (Sato 1978, Booth and Buxton 1997, Booth and Punt 1998) have also been the focus of biological studies and/or stock assessments.

In contrast, the biology of numerous other low value by-catch species in the South African demersal trawl fisheries have not been investigated or have only recently received research attention e.g. lesser gurnard *Chelidonichthys queketti* (Booth 1997), Cape gurnard *C. capensis* (McPhail *et al.* 2001), redspotted tonguefish *Cynoglossus zanzibarensis* (Booth and Walmsley-Hart 2000), Izak catshark *Holohalaelurus regani* (Richardson *et al.* 1999) and spiny dogfish *Squalus megalops* (Watson and Smale 1998, 1999). Despite this availability of biological data, the stock status of most low value by-catch species in the demersal trawl fisheries is unknown. This is largely a result of a lack of information on catch rates or length composition of catches as these are typically not reported in commercial catch returns. In terms of South Africa's Marine Living Resources Act (MLRA 1998), management measures to ensure the sustainable exploitation of all marine resources (including by-catch species) are required. In order to address this issue, an on-board observer program was implemented initially in 1994 to identify and quantify linefish by-catch and discards in the south coast inshore demersal fisheries (Pheeha 2002) and later (1995) expanded to include all South African demersal fisheries with a view to developing a national observer programme and a by-catch management plan (Walmsley 2004).

Umbrina canariensis occur as regular by-catch in the inshore trawl fishery when targeting Agulhas sole and to a lesser extent when targeting shallow water hake *M. capensis* along the Cape south coast. All catches are landed at Mossel Bay and Port Elizabeth harbours (Fig. 3.1). Although *U. canariensis* has a low market value and is not directly targeted, catches are often retained either for crew consumption or for sale. Smale and Badenhorst (1991) reported on the distribution and calculated a relative abundance index for *U. canariensis* based on annual research trawls (demersal biomass surveys), but noted it was likely that the distributional range of the species was inadequately sampled. Japp *et al.* (1994) recorded *U. canariensis* as the fourth most frequently landed (in terms of percentage contribution by mass to the total catch) "linefish" species in inshore commercial trawl and research survey catches made on the Agulhas Bank. Referring to *U. canariensis* as a "linefish" species was erroneous and reflects the past uncertainty about the taxonomy and distribution of *Umbrina* species in South African waters. The taxonomic issues were recently resolved (Chapter 1) and *U. canariensis*, which inhabits deeper shelf waters (40-120 m depth), is occasionally landed by commercial and recreational boat-based line fishermen (Brouwer and Buxton 2002) but is beyond the reach of shore anglers or spear fishers. Previously published reports on the occurrence or size composition of *U. canariensis* in catches made by beach-seines or shore anglers (e.g. Bennett 1991, Bennett and Attwood 1993, Bennett *et al.* 1994, Clark *et al.* 1994, Lamberth *et al.* 1994, 1995), undoubtedly refer to *U. robinsoni*.

Umbrina canariensis is considered to be of low importance in the sole and hake directed trawl fishery (due to its low monetary value) and as a result landings are seldom reported in catch returns. This lack of accurate catch and effort data prohibits the use of complex stock assessment models (e.g. age-structured production models). In these situations, the use of spawner-biomass per-recruit (*SB/R*) and yield per-recruit (*Y/R*) models are considered the most appropriate methods available (Butterworth *et al.* 1989, Punt 1993, Griffiths 1997b, Griffiths *et al.* 1999). Per-recruit models use estimated growth and mortality rates to predict the relative lifetime yield and spawner biomass of a cohort under different combinations of fishing mortality (*F*) and age at first capture (t_c). Although the assumptions implicit in these models, namely, that the stock is in an equilibrium state and that recruitment is constant, are often not realistic and as a result the estimated ratios may be inaccurate, they do allow for a relative quantitative assessment of the desired level of exploitation and for the comparison of different management options (Griffiths 1997b). In this study, recently researched life-history information (Chapter 2) and per-recruit models are used to assess current exploitation rates of *U. canariensis* stocks on the central Agulhas Bank and in Algoa Bay.

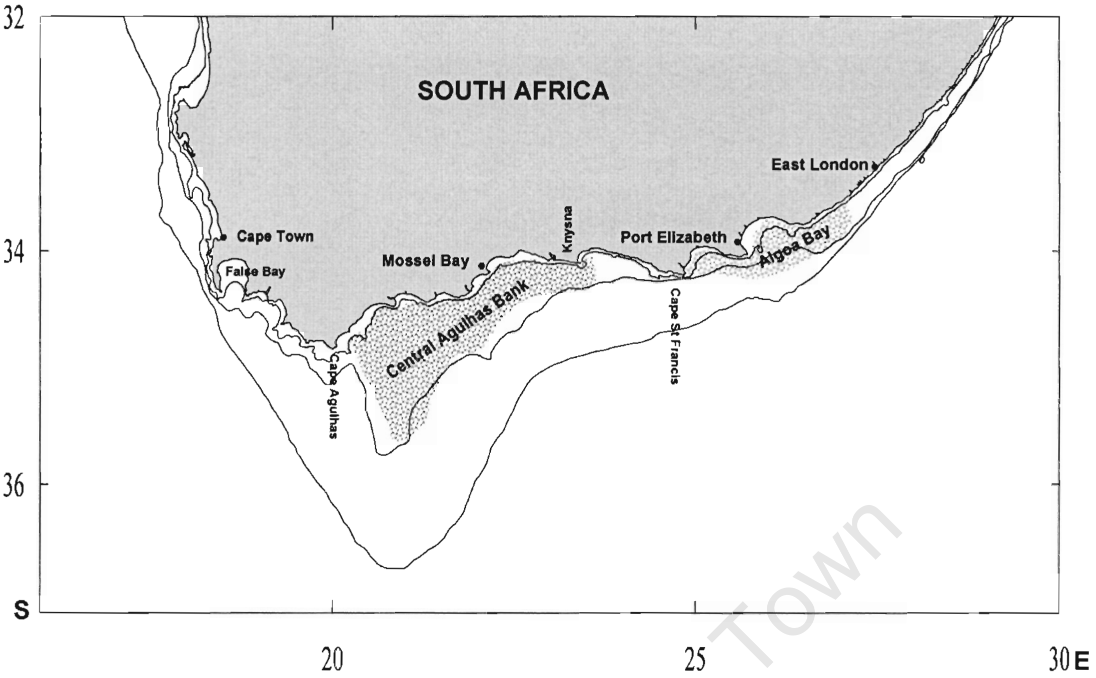


Fig. 3.1: Map of South Africa showing places mentioned in the text and the approximate distribution of the Central Agulhas Bank and Algoa Bay *U. canariensis* stocks. The 50m, 100m and 200m isobaths are shown.

MATERIAL AND METHODS

Biological data

Umbrina canariensis were sampled from commercial and research trawl catches over the period April 2001 - March 2003. Details of the methods used and resulting estimates of the length/mass relationship, size at maturity and the von Bertalanffy growth model parameters are given in Chapter 2. *U. canariensis* from the Central Agulhas Bank (CAB) and Algoa Bay (AB) appear to be spatially separated populations that differ significantly in growth rates and age-at-maturity schedules (Chapter 2). Populations from these two areas were therefore treated as separate stocks, and regionally specific growth data were used in per-recruit models for the two areas. Length-at-age data (from sectioned otoliths) were used to construct age-length keys for both regions (Tables 3.1 and 3.2).

Natural mortality

Natural mortality rate (M) estimates for CAB and AB *U. canariensis* populations were obtained using the following equations:

$\log_{10}M = -0.0066 - 0.2790 \log_{10}L_\infty + 0.6543 \log_{10}k + 0.4634 \log_{10}T$ (Pauly 1980),.(3.1)

where L_∞ and k are parameters from the von Bertalanffy growth model and T is the mean sea surface temperature in degrees Celsius (a value of 17°C was used);

$M = 1.521/t_m^{0.72} - 0.155$ (Rikhter and Efanov 1977),.................................. (3.2)

where t_m is the age-at-50% maturity;

$lnZ = -1.01 \times ln(t_{max}) + 1.46$ (Hoenig 1983),...(3.3)

where t_{max} is the maximum age sampled.

Selectivity and maturity

Minimum size limits are not effective (or appropriate) for controlling the size of trawl caught fish (which is largely dependent on the mesh size and behaviour of the gear during operations) and the use of the current legal size limit to determine selectivity values was not possible. Selectivity of trawl nets is typically a sigmoid function that is best determined through cover net trawl experiments. Financial constraints prevented conducting of cover net experiments during this study. Attempts were made to estimate selectivity by comparison of length frequency distributions of research trawl catches (made with 25 mm cod end mesh liner) with those from commercial (75 mm cod end mesh) trawl catches. Spatial and temporal variation in commercial and research trawl effort, however, complicated this analysis and the results were erroneous. Selectivity of commercial trawl gear for each area was therefore estimated by extension of the linearlized catch curves (Sparre *et al.* 1989). The number of fish at each age present in the trawl area was calculated by solving the regression equation of the descending limb of the catch curve for ages younger than the age at full recruitment (taken as the peak of the catch-at-age distribution) and the number retained by the gear being the actual catch. Although this method makes the unrealistic assumption that total mortality (*Z*) remains constant for all ages (*F* is obviously less for younger ages not fully recruited to the fishery), natural mortality *M* is likely to be higher for smaller fish than for adults and to some degree probably compensates for the decreasing *F*.

A logistic ogive of the form:

$$P(t) = 1/(1 + \exp^{-(t - t_{50})/\delta}), \ldots\ldots (3.4)$$

where $P(t)$ is the proportion of each age retained by the trawl gear, t_{50} is the age at 50% selectivity and δ is the width of the ogive;

was then fitted to the estimated proportion retained using an iterative least squares procedure (Microsoft EXCEL SOLVER routine with Newton algorithm option, Microsoft Corporation 2000) and the predicted values used as selectivity at age (Tables 3.1 and 3.2).

The proportion-at-age of mature fish was estimated by multiplying by the predicted proportion of mature females in each length class (from logistic ogive fitted to observed maturity data, see Chapter 2) through the age-length key, summing the resultant proportions for each age and dividing by the total number of each age in the age-length key (Tables 3.1 and 3.2).

Total and fishing mortality

Catch-at-length data of *U. canariensis* caught in the commercial trawl fishery on the CAB (for two time periods, 1995-98 and 2001-04) and AB (2001-2004) were obtained from length frequency data collected by onboard observers (mainly discarded catch) and shore based fishery compliance officers (landed catch). These data were converted into catch-at-age data using the age-length keys and *Z* was estimated by three different methods: catch curve analysis (Ricker 1975), catch curve analyses incorporating a non-parametric bootstrapping technique (500 bootstraps) and a dynamic age-length key (simultaneous random selection of length-at-age data and length frequency data) and using the following equation:

$Z = ln[1+1/(a_m - a_f)]$, Chapman and Robson (1960) ....(3.5)

where a_m is the mean age of all fully recruited fish sampled and a_f is the age at full recruitment.

Ninety-five percent confidence intervals (CIs) of Z estimates were obtained by non-parametric bootstrapping (as described above) and the percentile method. Fishing mortality (F) was then estimated by subtracting the relevant M estimate ($F = Z–M$).

Per-recruit analysis

Yield-per-recruit (Y/R) and spawner biomass-per-recruit (SB/R) was calculated using the following equations:

$$Y/R = \sum_{t=0}^{t\max} \frac{(FS_t)}{(FS_t + M)} \left(e^{-\sum_{t=0}^{t-1}(FS_t + M)} \right) \left(1 - e^{-FS_t - M}\right) W_t \quad \text{.......................................} (3.6)$$

$$SB/R = \sum_{t=0}^{t\max} \left(B_t \left(e^{-\sum_{t=0}^{t-1}(FS_t + M)} \right) W_t \right) \quad \text{...} (3.7)$$

where F is the instantaneous rate of fishing mortality, S_t is the proportion of fish at age t selected by the trawl gear, W_t is the individual mass of fish of age t and B_t is the proportion of mature females at age t. (see Tables 3.1 & 3.2). SB/R and Y/R curves were constructed by estimating these ratios at varying levels of F (F = 0-1). Target (F_{SB40}, the level of F where SB is reduced to 40 % of the unfished level) and threshold (F_{SB25}) biological reference points (Griffiths *et al.* 1999) were read from the SB/R curves. Current SB/R and Y/R for each of the M estimates tested was determined by calculating these ratios using the estimated F values for each region.

Table 3.1: Age-length key for Algoa Bay *U. canariensis*. MF is the proportion-at-age (1 = 100%) of mature females and selectivity shows the proportion-at-age selected by the commercial trawl gear as used in per-recruit models.

Length class midpoint (mm)	Number of fish at age (years)																										
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
150	1																										
170	8	4																									
190	3	15																									
210		5	3																								
230			2		2																						
250			1	3	4	3																					
270			6	4	8	4	1																				
290				5	9	8	2	5	2					1													
310				1	13	8	2	5	4	3	7	2	2		2	1	1			1			1				
330				1				2	7	7	6	4	2	1	2	2	3	4				1		2			
350								1	3	3	3	7	2	2	4	2	1			1	1		2	1	2		1
370								1		2	1	1	6	1	2			3			1		1		1		
390									1	1		2		1	1	1	1	1			1				1	1	
410											1																1
430																			1								
Total	12	24	12	14	36	23	5	14	17	16	18	16	12	6	11	6	6	8	1	2	3	1	4	3	4	1	2
MF	0.03	0.07	0.57	0.85	0.86	0.90	0.93	0.97	0.98	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Selectivity	0.09	0.22	0.45	0.71	0.88	0.96	0.98	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

Table 3.2: Age-length key for central Agulhas Bank *U. canariensis*. MF is the proportion-at-age (1 = 100%) of mature females and selectivity shows the proportion-at-age selected by the commercial trawl gear as used in per-recruit models.

Length class midpoint (mm)	Number of fish at age (years)																		
	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	19	21	23
210	1	1																	
230	7	3	2	1															
250	1	15	2	2															
270		6	5		2														
290		1	7	10	2	1	1	1											
310			1	15	6	4	2	2	2										
330			1	4	2	2	4	5	2		2								
350					1	2	3	5	1	1	3	1			1				
370								1	4	2	1	1		1	1	1			
390							1			1	1	1	1		1				
410											1						1	1	
430																			1
Total	9	26	18	32	13	9	11	14	9	4	8	3	1	1	3	1	1	1	1
MF	0.53	0.86	0.94	0.98	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Selectivity	0.55	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

RESULTS

Natural mortality rate

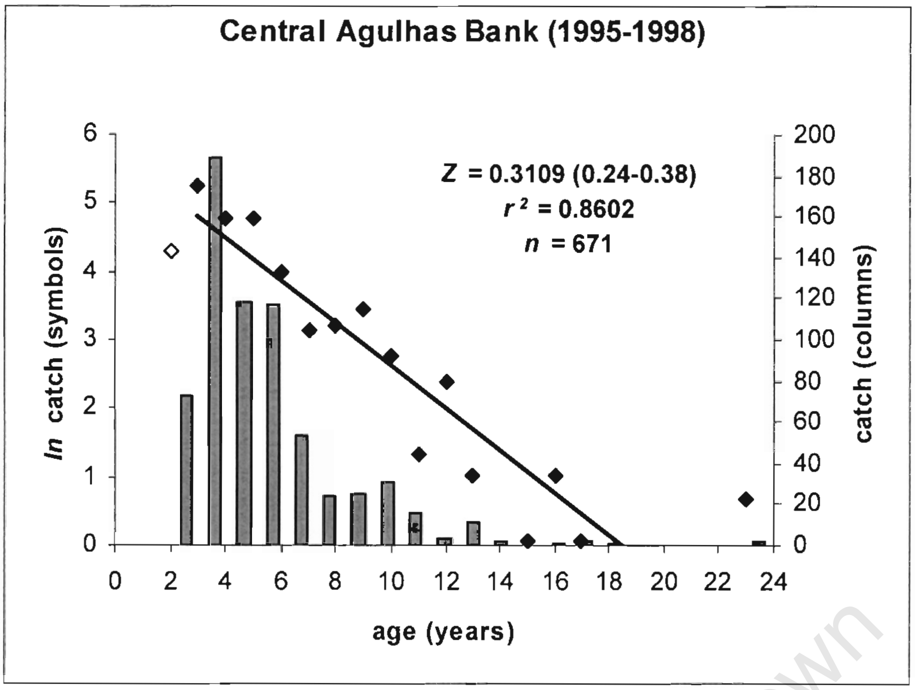
Equations 3.1 and 3.2 produced *M* estimates that were 1.5 to 3.5 times total mortality rate (*Z*) estimates derived from catch curve analyses (see below). This is possibly a result of the typical sciaenid growth pattern of rapid pre-maturity growth that declines quickly thereafter and an early age-at-maturity schedule (relative to longevity). Although equation 3.3 estimates total mortality *Z*, the empirical data from which it was derived pertained to unexploited or lightly fished stocks (Hoenig 1983). Furthermore, even in sciaenid stocks where the numbers of older fish are reduced by fishing mortality, some fish appear to survive to near maximum age even under intensive exploitation (Griffiths 1997b, Griffiths and Hecht 1995a, Ross *et al.* 1995). Good agreement was also obtained for *M* estimates calculated for stocks of the inshore South African co-generic *U. robinsoni* from marine protected areas using catch curve analysis and the Hoenig (1983) equation (Chapter 4). Therefore the value determined using equation 3.3 for *U. canariensis* was taken as a more accurate approximation of *M* than the values obtained using equations 3.1 and 3.2. The sensitivity of per-recruit models to this assumption was tested by varying the *M* estimate plus and minus 50 %.

Central Agulhas Bank

The natural mortality rate (*M*) estimated using equation 3.3 for the CAB *U. canariensis* stock was 0.18 y^{-1} (maximum age sampled = 23 years). Catch-at-age distributions and catch curves for the two time periods for which length frequency data were available are shown in Fig 3.2. The total instantaneous mortality rates (*Z*) and associated 95 % confidence intervals (CIs) estimated using the different methods are given in Table 3.3. For both time periods, estimates derived using equation 3.5 were slightly higher than those estimated by the two catch curve analyses, but the CIs were narrower. For the purposes of estimating current stock status, the average *Z* estimate from the three different methods was used and current *F* estimated by subtracting the *M* estimate. The estimated *Z* for the CAB stock was substantially greater during the earlier period (1995-1998) than during the more recent 2001-2004 period (Fig 3.2, Table 3.3).

Table 3.3: Estimates of total instantaneous mortality rate (*Z*) for *U. canariensis* populations sampled from the central Agulhas Bank (two time periods) and Algoa Bay. Lower (LCI) and upper (UCI) 95 % confidence intervals are given.

Method and sampling site	$Z\ (y^{-1})$	LCI	UCI
Central Agulhas Bank 1995-98			
Catch curve	0.31	0.24	0.42
Bootstrapped catch curve	0.31	0.24	0.42
Chapman & Robson (1960)	0.38	0.33	0.43
Central Agulhas Bank 2001-04			
Catch curve	0.23	0.18	0.27
Bootstrapped catch curve	0.22	0.17	0.27
Chapman & Robson (1960)	0.25	0.22	0.28
Algoa Bay 2001-04			
Catch curve	0.13	0.09	0.17
Bootstrapped catch curve	0.12	0.09	0.15
Chapman & Robson (1960)	0.15	0.14	0.17



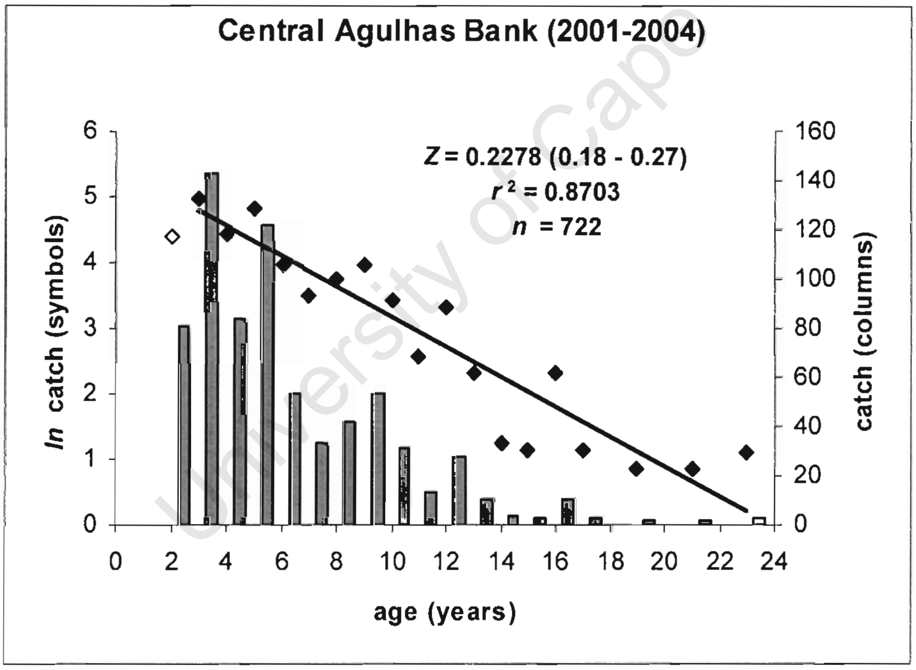


Fig. 3.2: Catch-at-age distributions and catch curves for *U. canariensis* sampled from the central Agulhas Bank over two different time periods. Total mortality (*Z*) was estimated from the slope of the descending limb of the catch curve. Figures in brackets indicate the 95 % confidence intervals of the slopes.

Yield and spawner biomass per-recruit curves for CAB *U. canariensis*, the estimated *SB/R* and *Y/R* at the two different time periods assessed (M = 0.18 y^{-1}) and three alternative M estimates (M = 0.1, 0.18 and 0.26 y^{-1}) are shown in Fig. 3.3. Current estimated *SB/R* at both time periods was greater than 40 % of pristine *SB/R*. Varying fishing mortality with the upper and lower 95 % CI estimates of Z (bootstrapped equation 3.5 estimates) only results in F exceeding the target level (F_{SB40}) for the 1995-1998 period when the upper 95 % CI of Z is used (SB/R = 32%$SB_{F=0}$) (Table 3.4). Under the lowest tested M estimate (M = 0.1 y^{-1}), current *SB/R* (2001-04) is also estimated to be below the target reference point (SB/R = 34% $SB/R_{F=0}$). It is, however, unlikely that the species experiences such a low natural mortality rate, as if M is estimated using equation 3.3, this corresponds to a maximum age of nearly double (40 years) the maximum recorded age in our sample (23 years).

Algoa Bay

The age composition and catch curve for Algoa Bay (AB) *U. canariensis* is shown in Fig. 3.4 and Z estimates in Table 3.3. The natural mortality estimate (M) for this stock was 0.154 y^{-1} (maximum age sampled = 27 years). Yield and spawner biomass per-recruit curves for AB *U. canariensis* showing the estimated *SB/R* and *Y/R* during 2001-2004 and at three alternative M estimates (M = 0.08 y^{-1}, 0.15 y^{-1} and 0.23 y^{-1}) are shown in Fig. 3.5. Current estimated *SB/R* was equivalent to pristine (Z estimate less than M estimate – Table 3.4) and the stock is assessed as being underexploited. Even when the upper 95 % CI estimate of Z is modelled, the *SB/R* is estimated at 91% of pristine ($SB/R_{F=0}$), (Fig. 3.5a). Under the lowest tested natural mortality estimate (M = 0.077 y^{-1}) *SB/R* remains greater than 40 % of pristine biomass (Fig. 3.5b).

Table 3.4: Total annual mortality rates (y^{-1}), lower (LCI) and upper (UCI) 95 % confidence intervals and corresponding estimates of spawner biomass per-recruit (*SB/R*) as a percentage of pristine ($SB/R_{F=0}$) for *U. canariensis* stocks from the central Agulhas Bank (CAB) and Algoa Bay (AB).

Stock	Z	$SBR\%SBR_{F=0}$	Z(LCI)	$SBR\%SBR_{F=0}$	Z(UCI)	$SBR\%SBR_{F=0}$
CAB 95-98	0.35	42	0.33	45	0.43	32
CAB 01-04	0.24	69	0.22	75	0.28	55
AB 01-04	0.15	100	0.14	100	0.17	91

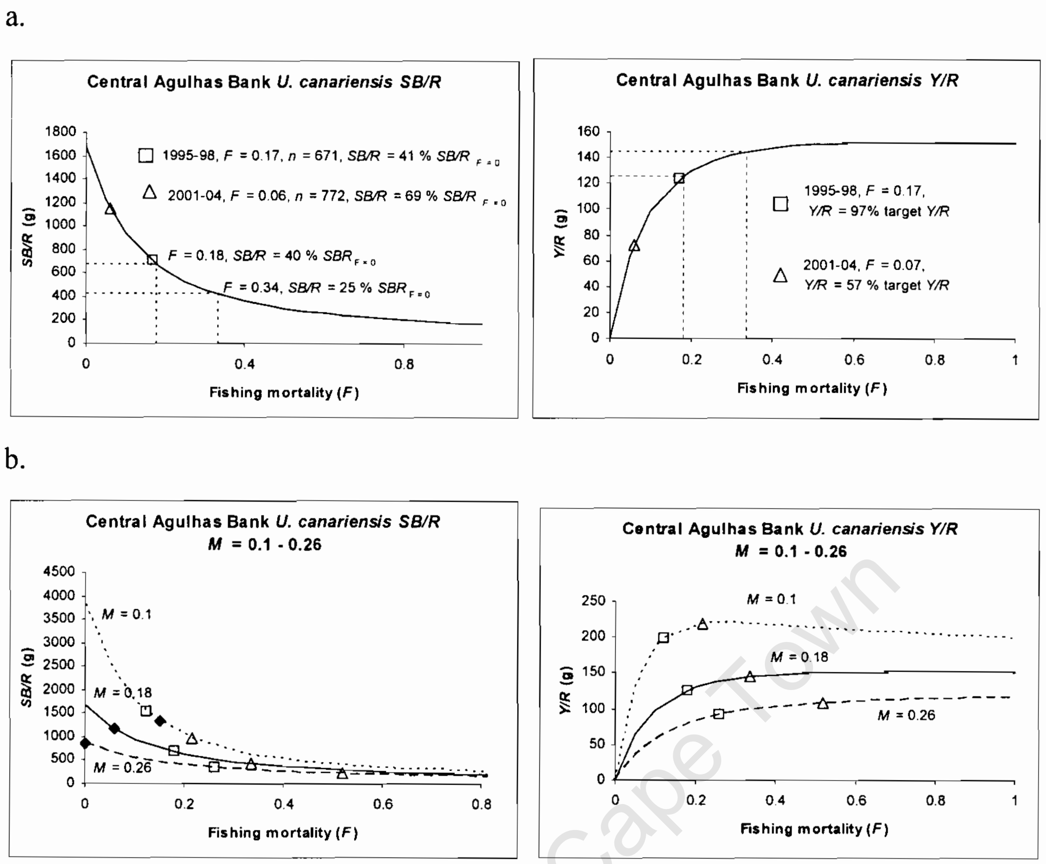


Fig. 3.3: (a) Relationship between spawner biomass (*SB/R*) and yield per-recruit (*Y/R*) and fishing mortality (*F*) for central Agulhas Bank *U. canariensis* showing estimated *SB/R* and *Y/R* at two different time periods. Target (F_{SB40}) and threshold (F_{SB25}) levels of *F* are indicated by dotted lines. (b) *SB/R* and *Y/R* curves at different *M* estimates showing *SB/R* at estimated current *F* (2001-2004) (closed diamonds). Target (F_{SB40}) and threshold (F_{SB25}) levels of *F* are indicated by squares and triangles respectively.

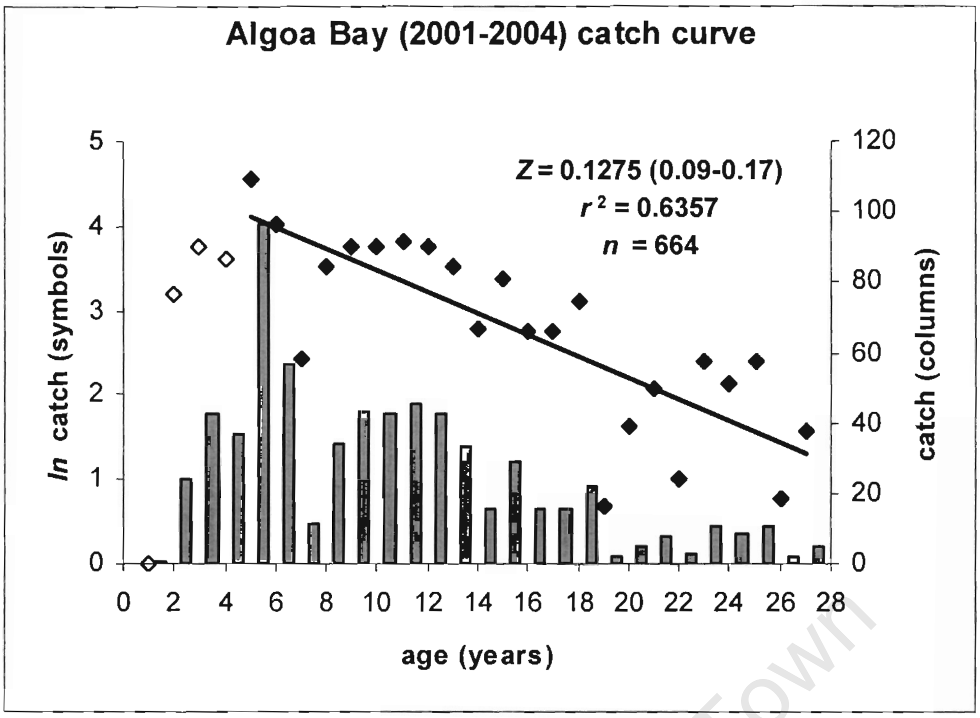


Fig. 3.4: Catch-at-age distribution and catch curve for *U. canariensis* sampled from Algoa Bay Total mortality (*Z*) was estimated from the slope of the descending limb of the catch curve. Figures in brackets indicate the 95 % confidence intervals of the slope.

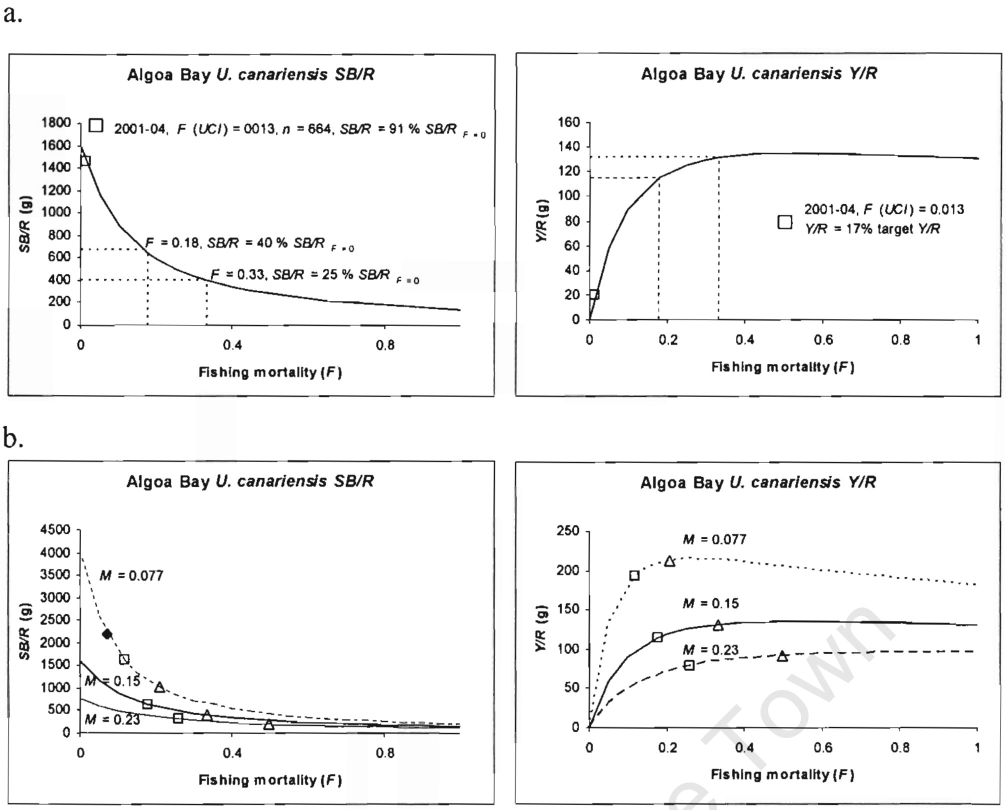


Fig. 3.5: (a) Relationship between spawner biomass (*SB/R*) and yield per-recruit (*Y/R*) and fishing mortality (*F*) for Algoa Bay *U. canariensis* showing estimated current *SB/R* and *Y/R* (squares) (Based on the upper 95 % confidence interval estimate of *Z*). Target (F_{SB40}) and threshold (F_{SB25}) levels of *F* are indicated by dotted lines. (b) *SB/R* and *Y/R* curves at different *M* estimates showing *SB/R* at estimated current *F* (2001-2004) (closed diamonds). Target (F_{SB40}) and threshold (F_{SB25}) levels of *F* are indicated by squares and triangles respectively.

DISCUSSION

In this study stock status is inferred from estimates of Z. Although 95% confidence intervals were reasonable, particularly for estimates of Z obtained using equation 5 (CVs of 5-7%), the sample sizes of length frequency data were small (664-722 measurements) and obtained from relatively few fishing trips (28 and 31 trips for CAB during 1995-1998 and 2001-2004 respectively and 16 trips for Algoa Bay 2001-2004). The number of drags from which length frequency data for the CAB region was obtained represents only about 0.35 % of the total reported effort in this region over the periods assessed. If the size frequency of the sample did not accurately represent that of the total catch for each period and area then Z is unlikely to be reliable. However, low bootstrapped CVs would suggest that between trip variation was low and that estimates of Z are probably reasonable.

The fact that the Z estimates for the CAB stock varied so greatly for the two time periods assessed requires some explanation. It is possible that temporal changes in growth rate (possibly due to exploitation) (Ricker 1981; Rijnsdorp and van Leeuwen 1996; Law 2000), or changes in the natural mortality rate experienced by individuals in the population, caused the differences in Z estimates for the two time periods. These explanations are, however, unlikely and difficult to test, as older fish sampled during the latter period would have experienced the same environmental conditions affecting growth and natural mortality regimes for much of their life spans. Furthermore, growth rate of the inshore congeneric *U. robinsoni* was found to show negligible change over a 10 year period (Chapter 7). The inshore sole-directed fishery has been in existence since 1897 (Japp *et al.* 1994) and if exploitation driven changes in life-history characteristics ("artificial/fishing selection") have occurred, they would almost certainly been manifest prior to 1995. Two of the more plausible explanations for the observed decrease in Z over the two time periods assessed are:

1. The total mortality rate experienced by the CAB stock has not changed, and the observed estimates are inaccurate or biased during one or both periods due to spatial and temporal variation in length frequency sample effort.
2. The total mortality rate for the stock has decreased, most likely due to a decrease in fishing mortality caused by either reduced effort in the inshore

fishery or changes in the spatial distribution of the trawl effort or targeting practises that have resulted in decreased catches of *U. canariensis*.

1. Potential bias in *Z* estimates

Length frequency data from commercial trawl catches used in estimating *Z* were obtained from both onboard observers and shore based monitoring. In an attempt to ensure that the size composition of the entire catch was used when estimating *Z*, catch-at-length data from these two different sources were combined for this analysis. In both cases, however, length measurements are taken subsequent to sorting of the catch and as such contain inherent biases that may result in errors when estimating *Z*. During the pilot onboard observer program, discarded catch composition and length frequency data from monitored inshore trawls were collected after this portion had been separated from the retained catch (Walmsley 2004). Length frequency data from shore based monitoring on the other hand, only represents information on retained catch, as unwanted by-catch is discarded at sea. Larger (older) fish are more likely to be retained whilst less valuable, smaller (younger) fish are more likely to be discarded.

For *U. canariensis* catches this was clearly the case, as the average total length of fish in observer collected samples from the CAB was 6 cm less than that in shore based samples (23cm TL and 29 cm TL respectively), representing approximately 3 years of growth. Use of observer collected length composition data alone would result in a positive bias of the younger age classes in the catch-at-age composition, increasing the negative slope of the catch curve and consequent overestimates of *Z*, whilst use of length frequency data from landed catch only would have the opposite effect. If the proportion of the *U. canariensis* catch retained and discarded in reality is similar to that in our length frequency samples, or remained consistent over the two time periods assessed for the CAB stock, these biases would not influence our *Z* estimates based on combined data. Furthermore, given that the slopes of the catch curves based on combined data are approximately linear and a fair number of age classes are incorporated in the analysis, it is unlikely that the inclusion or exclusion of younger age classes would have a large effect on *Z* estimates.

In an analysis of observer records for 1994-2000, Pheeha (2002) states that only a small proportion of the *U. canariensis* catch is discarded (3.5 %), which is substantially less than the proportion of length frequency data obtained from onboard observers (25-34 %) that was used in this analysis. Catch rates of *U. canariensis* by inshore trawlers provided by Walmsley (2004), who conducted a more detailed analysis of observer records for the period 1996-2000, indicated a total annual catch of approximately 16 tons (assuming a total annual effort of ~ 80 000 inshore trawl hours) of which an estimated 2.75 tons (17 %) was discarded. Although this estimate of discarded proportion is considerably larger than that of Pheeha (2002), it is still apparent that data from discarded catch is overrepresented in the length frequency sample used to estimate Z in this study. The relative proportion of shore based and onboard observer collected measurements in our length data also varied between the two time periods assessed (measures from shore based monitoring comprised 67 % and 75 % of the 1995-1998 and 2001-2004 length data sets respectively). Although it is unlikely, (due to the linear nature of the catch curve), the greater proportion of length measurements from shore based monitoring could have contributed to the decreased Z estimate for the latter period and vice versa for the earlier period (as discussed above). The magnitude of this effect was investigated by estimating Z using catch-at-length data from shore based monitoring only. Exclusion of observer collected length data, however, resulted in no change to the Z estimate for the latter period and only a slight decrease (as expected) in the Z estimate for the earlier 1995-1998 period ($Z = 0.35$ y^{-1} for combined data set, $Z = 0.31$ y^{-1} for landed catch data). This is equivalent to a seven percent increase in estimated SB/R as a percentage of $SB/R_{F=0}$ for the 1995-1998 period. Despite this slight decrease in the Z estimate for the earlier period, it is still substantially greater than the estimate for the latter period, suggesting that the mortality rate for the CAB stock has indeed decreased.

The concern that the length composition of our samples does not match the true length composition of the total catch however remains. Currently a disproportionate amount of catch-at-length sampling effort is allocated to the discarded catch. Although the bias this factor introduces into Z estimates was observed to be minor (0-10%) it is nevertheless preferable to collect length data representative of the total catch. This has implications for the design of South Africa's onboard observer program if the data collected are to be used for catch-at-length/age based stock assessment purposes.

Either shore based monitoring must be synchronised with onboard observer coverage or observers must collect length frequency data from the entire catch (or a random sub-sample thereof) and not focus on discarded catch only. Logistical constraints (time, space, manpower) aboard fishing vessels suggest that the former approach may be more practically applicable.

2. Inshore trawl effort and targeting

Inshore trawling along the Cape south coast is conducted in waters generally shallower than 120m depth, using small (<25 m) side trawlers. The fishery can be further subdivided into sole-directed or hake-directed components, the key differences being that sole trawling is conducted on specific (sand/mud substratum), usually shallower grounds (<100 m depth), and the gear is towed slower (3-4 knots), for longer (mean drag duration = 3.8 hrs.) than in hake directed trawls (4-5 knots, mean drag duration =2.8 hrs.) (P. Simms, Marine and Coastal Management pers. comm.). The catch of both hake-directed and sole-directed trawl operations is dominated by hake (53% and 61 % by mass respectively) but observer data indicate substantial differences in other components of the catch. Most notably the by-catch in hake-directed trawls is dominated by horse mackerel *Trachurus trachurus capensis* (17 %) and panga, *Pterogymnus laniarius* (14 %), whilst sole-directed catches are characterised by larger proportion of sole (17.4 %), silver kob *Argyrosomus inodorus* (2 %) and skates of the genus *Raja* (~10 %) (Walmsley 2004).

Spatial analysis of *U. canariensis* catch-per-unit-effort data from research trawl surveys revealed that the species is most abundant between 30-75 m depth (Chapter 1). This is also the depth zone of highest estimated sole biomass, (Badenhorst and Smale 1991, Le Clus *et al.* 1994, 1996) and as a consequence, *U. canariensis* occurs predominately as a by-catch of the sole-directed trawl fishery. Inshore trawl vessels targeting shallow water hake typically fish in deeper water further east and observer recorded catch rates of *U. canariensis* in hake directed trawls (0.077 kg.hour^{-1}) were substantially less than in sole directed trawls (0.28 kg.hour^{-1}) (Walmsley 2004). There are indications of changes in inshore trawl fishing effort that may explain the observed decline in estimated F for the CAB *U. canariensis* stock over the two time periods assessed. Pheeha (2002) noted a dramatic increase in the observer documented catches of panga by inshore trawlers subsequent to 1997, suggesting a shift in trawl fishing effort from sole-directed to hake-directed. Pheeha (2002), however, did not separate out the effects of targeting (i.e. hake-directed or sole-directed) in his analysis, and inferring a shift in effort in the inshore fishery as a whole, based on changes in catch composition in observed hauls (the observer coverage fell off dramatically during 1999-2000, years when the increase in panga catch was most notable) is undesirable. Particularly since Walmsley (2004) estimated that observer coverage peaked at only 0.62% of total annual effort for the south coast fishery and observers were not placed on vessels in proportion to the actual split in the fishery between hake-directed and sole directed effort.

There are, however, indications of reduced sole-directed effort over the last decade evident in reported sole landings per vessel. Whilst the total number of sea days reported by the inshore fleet as a whole has not shown much variation over time, the number of traditional sole vessels (classified as those reporting > 20 tons of sole per year) active in the inshore fleet on the CAB decreased since 1996 and the number of vessels targeting hake (classified as those reporting < 20 tons sole per year) has increased (Fig. 3.6). The average annual sole catch over the most recent four years (721 tons) has decreased by approximately 14 % from the long term (1984-2000) annual average (830 tons), with the allocated total allowable catch (TAC) not been landed during the last three years of the latter period (P. Simms, Marine and Coastal Management pers. comm.). Sole remains the most valuable target species in the inshore fishery, and increased export prices for hake due to the development of new European markets (2000-2004) are not thought to have had much influence on the targeting practises of traditional sole boats (P. Simms, Marine and Coastal Management pers. comm.). Other vessels in the inshore trawl fleet, however, that are not wholly reliant on the sole resource may well have changed their targeting practises to maximise hake catches. Natural fluctuations in the availability of sole to the inshore fishery (influenced by environmental conditions and recruitment variability) or logistical constraints on new and current rights holders due to recent changes in allocation procedures are also likely to have influenced the observed trend in catch and effort. Specifically, the recent allocations have split the sole TAC into smaller quotas shared amongst more rights holders (11 during 1995-1998 and 18 during 2002-2004), (P. Simms, Marine and Coastal Management pers. comm.), meaning that efficient rights holders now have access to a smaller sole quota volume and this may have led to increased targeting of hake and other valuable by-catch species such as panga. Whatever the true causes for the observed shift in targeting, it does appear that sole-directed effort in the CAB inshore fishery has decreased and this is the most likely explanation for the observed decline in estimated *Z* for the *U. canariensis* stock over the two time periods assessed.

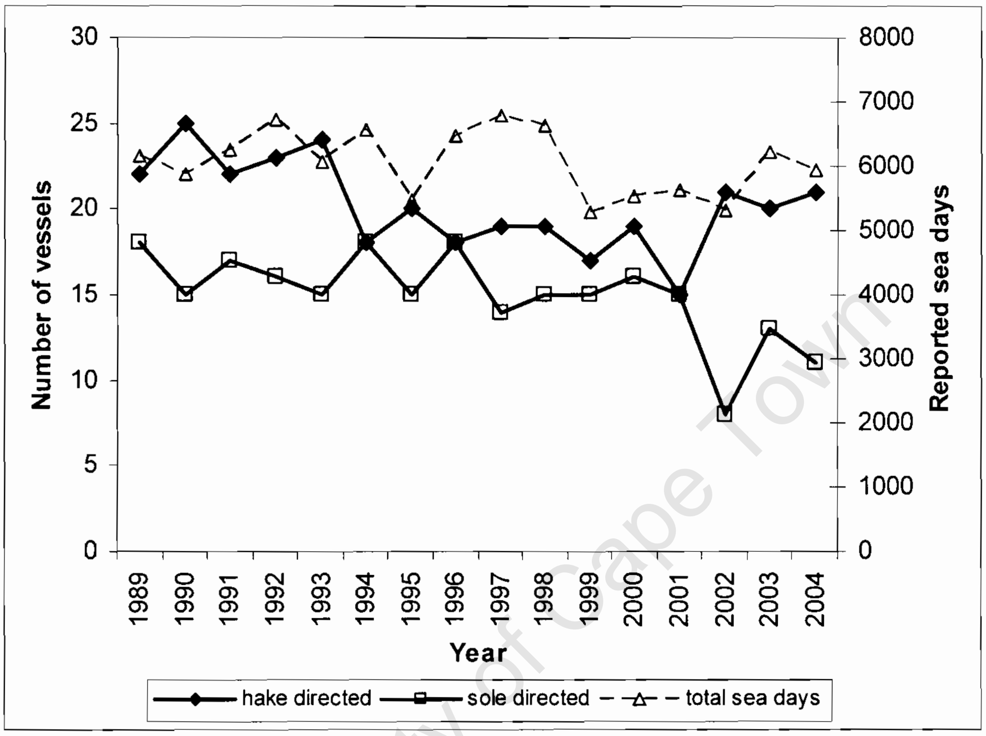


Fig. 3.6: Number of active vessels targeting hake and sole and total annual reported effort (sea days) in the Agulhas Bank inshore fishery. Note that the solid lines depict the number of active vessels and do not correspond to the sea days on the secondary y axis. (Data courtesy of P. Simms, MCM).

Management

The per-recruit analyses do indicate that *U. canariensis* stocks in both regions are not being overexploited by current trawl fishing effort. This is unexpected, given the species life-history characteristics (relatively slow growth and longevity, Chapter 2) and the fact that it has been exposed to intensive, industrial fishing activity (albeit as a by-catch) for more than 100 years. The fact that female age-at-50 % maturity (2.2 and

3.2 years for AB and CAB respectively) approximately coincides with estimated 50 % selectivity into the trawl fishery in both regions means that females are likely able to spawn at least once before being exposed to fishing mortality (resulting in a measure of protection of spawner biomass). Furthermore, it is likely that the primary habitat of *U. canariensis* is rocky reef, and the soft sediment trawl grounds are feeding areas (Chapter 2). The Agulhas Banks has extensive areas of rocky substratum that cannot be trawled (Japp *et al.* 1994, Hutchings *et al.* 2002) and these areas probably constitute a substantial spatial refuge for the species.

Spawner biomass per-recruit models do however indicate that target (F_{SB40}) levels of F will be reached with relatively small increases in fishing effort, and indeed estimated F on the CAB stock during the 1995-98 period was close to the target level (Table 3.4, Fig. 3.3). Although current estimated fishing mortality levels for both stocks are substantially below the target level (F_{SB40}) and as a consequence the current yield from the resource is much less than the estimated sustainable harvest (Figs.3.3a and 3.5 a), there is little need to increase fishing effort on a low volume by-catch species that has low market value (~R 5.kg^{-1}). Furthermore, maximum Y/R for both stocks will only be achieved at levels of F that are predicted to reduce the SB/R ratio to below the threshold level (<25 % $S/B_{F=0}$) (Figs.3.3a and 3.5 a), and thus result in an unacceptable risk of stock collapse.

In conclusion, it appears that *U. canariensis* stocks are not under threat of overexploitation at current levels of fishing effort, however the species should be considered vulnerable due to the sensitivity of the stocks to small changes in F that may result from subtle changes in the spatial distribution of trawl effort and targeting practises. The status of *U. canariensis* stocks should therefore to be monitored on an ongoing basis through collection of catch-at-length data and estimation of current levels of F. Efforts should be made to improve both the quantity and quality (to ensure it is representative of the actual catch) of length frequency data. Additional information on the spatial and temporal distribution of fishing effort must be collected concurrently to facilitate interpretation of any changes in estimated mortality rates.

CHAPTER 4

LIFE-HISTORY STRATEGIES OF *UMBRINA ROBINSONI,* (SCIAENIDAE) IN WARM-TEMPERATE AND SUB-TROPICAL SOUTH AFRICAN MARINE PROTECTED AREAS

ABSTRACT

Biological data for *Umbrina robinsoni* were obtained from fish sampled monthly during 2001-2002 by shore angling in the warm temperate De Hoop marine protected area (MPA) (n = 312), and by means of spear fishing during three trips (May, September and January 2001-2002) to the Kosi Bay region of the subtropical Maputaland MPA (n = 354). Annuli in otolith sections were validated by means of marginal increment analyses and fluorochrome marking (oxytetracycline). Maximum ages recorded were 12 and 16 years at Kosi Bay and De Hoop respectively. Kosi Bay fish obtained a significantly greater asymptotic length than De Hoop fish and mean length-at-age (for ages 2-10 years) was significantly greater. The fitted von Bertalanffy growth equations for combined sexes are: $L_t = 594\ (1 - e^{-0.183\ (t\ +\ 2.42)})$ for De Hoop and $L_t = 875\ (1 - e^{-0.151\ (t\ +\ 2.49)})$ for Kosi Bay. Trends in mean monthly gonadosomatic indices and proportions of histologically validated macroscopic gonad stages indicated a summer spawning season (October- February) at De Hoop, and year-round spawning at Kosi Bay. Relative condition peaked in both spring and autumn in De Hoop but showed little seasonal variation off Kosi Bay. Kosi Bay females attained 50 % sexual maturity at a significantly larger size (48 vs. 39 cm) but at younger age (2.8 vs. 3.5 years) than those in De Hoop. Analysis of maturity schedules indicate that current sizes at maturity are plastic responses that maximize life-time fecundity within local regimes of somatic growth and natural mortality. The instantaneous rate of natural mortality was substantially higher at Kosi Bay than at De Hoop ($M = 0.35\ y^{-1}$ vs. $M = 0.26\ y^{-1}$).

INTRODUCTION

Umbrina robinsoni is a moderately large (maximum size = 12 kg) West Indian Ocean sciaenid fish that is found in east African coastal waters from Cape Point (South Africa) to Oman (Chapter 1). It is an inshore species, occurring from the surf zone to 45 m depth, most commonly associated with high profile limestone reefs or mixed rock and sand habitats (Chapter 1). The taxonomy of Southern African *Umbrina* species was until recently poorly researched, *U. robinsoni* was misidentified as *U. ronchus* throughout the region and also confused with the sympatric *U. canariensis* in the Cape provinces off South Africa (Chapter 1).

Published work on *Umbrina* species in South African waters is mostly limited to catch composition. *U. robinsoni* is targeted by shore-anglers in the South West Cape; it was the fifth most often caught species (misidentified as *U. canariensis*) over the period 1938–1992 (Bennett *et al.* 1994) and contributed significantly to research shore-angling catches in the De Hoop marine reserve (Bennett & Attwood 1993). *Umbrina robinsoni* is among the top ten species targeted by spear fishers along the South African eastern seaboard and accounts for between 3 and 10 % of the total catch (Mann *et al.* 1997). They are also caught as a by-catch by beach-seines in the SW. Cape (Lamberth *et al.* 1994, 1995), and occasionally by boat-based anglers (Brouwer and Buxton 2002; SA Angling Union records). Lasiak (1986) provided descriptions of size composition and feeding for *U. robinsoni* (using the synonym *U. capensis*) that were seine netted in the surf-zone of Algoa Bay.

Despite the importance of *U. robinsoni* to the recreational fisheries and its occurrence as by-catch in several commercial sectors of South Africa, the biology of the species had never been studied. In South African waters, *U. robinsoni* is found along the entire eastern seaboard (Cape Point to Mozambique border, approximately 2 000 km) along which environmental conditions change from temperate to subtropical (Chapter 1). Given this large geographic range, and trends in environmental conditions, spatial variation in *U. robinsoni* life-history strategy is anticipated (Brown-Peterson and Thomas 1988, Berg and Albert 2003, Ye *et al.* 2003).

Reduced abundance due to exploitation has also been shown to alter key life-history processes such as growth rate, size and age at maturity and longevity (Shepherd and Grimes 1983, Buxton 1993, 1996, Jennings and Lock 1996). By limiting the study to populations inhabiting well-established marine reserves it was possible to eliminate the confounding effects of fishing. Baseline information on the life history of unexploited fish populations is essential when attempting to assess the impacts of exploitation (Emmanuel *et al.* 1992; Brouwer and Griffiths 2004). In this chapter the life-history strategies of *U. robinsoni* populations from the warm temperate De Hoop and sub-tropical Maputaland marine protected areas are compared.

MATERIAL AND METHODS

Study areas and sampling methods

Monthly sampling trips (3-5 days duration) were conducted to the Skipskop area (34°32.17' S, 20°25.22'E) of the De Hoop marine protected area (MPA) during the period July 2001- August 2002 (Fig. 4.1). The De Hoop MPA, which protects 51 km of coastline from all exploitation (IUCN category 1 MPA) to three nautical miles offshore, has been in existence since 1985. It is situated centrally within the marine biogeographical zone classified as warm-temperate (Turpie *et al.* 2000) and surf-zone water temperatures measured during sampling trips ranged between 14-24° C (average = 18° C). The four-kilometre stretch of shoreline where fish were sampled was dominated by extensive, shallow, broken limestone reef with sheltered sandy pocket beaches in the west (approximately 1 km-length) and a high-energy exposed sandy beach with a few temporally exposed rocky reefs that extend 9 km eastwards. At this site *U. robinsoni* were captured predominately by rod and line angling in the surf zone (hook sizes Mustad 92570, #1 – 2/O). Bait used was exclusively polychaete worms (*Arenicoli loveni* and *Marphysa* sp.) and fresh white mussel (*Donax serra*). During the summer months when rod and line catch rates were low, fish were also captured using a small beach-seine net (50 m length, 2 m depth, 44 mm stretch mesh) and cast nets (2 m diameter, 10 mm stretch mesh) deployed in the shallow surf-zone. All fish caught were kept in crushed ice for the duration of the field trip and dissected upon return to the laboratory (up to 72 hours after death).

Three sampling trips (10 days duration each) were conducted to the Kosi Bay region of the St Lucia-Maputaland MPA during May and September of 2001 and January 2002 (Fig. 4.1). This 156 km long MPA (established in 1979) lies within the warm subtropical region of South Africa's northeast coast. Water temperature recorded during sampling trips ranged from 22-28°C. Although this MPA consists of multiple zones with limited exploitation allowed in some zones (IUCN category 2 MPA), *U. robinsoni* is effectively protected as spear-fishers and boat-based anglers are limited to pelagic "game-fish" species and shore anglers (shore angling for "reef fish" species is permitted in limited areas) almost never catch the species in this region (B. Q. Mann, Oceanographic Research Institute, Durban, pers. comm.). The area sampled extended from Kosi Bay estuary mouth (26° 54.01'S, 32°53.08'E) southwards to Dog Point (27°05.15'S, 32°51.05'E), a distance of 24 km. The shoreline is predominately sandy beach intercepted by rocky headlands; offshore extensive patches of high profile limestone reef contain some of the southernmost hard coral communities in the Southwest Indian Ocean. Extensive areas of reef in the 2-20 m depth range were searched and *U. robinsoni* collected by spear fishing from a semi-rigid inflatable boat. All fish were dissected upon returning to the shore (2-8 hours after death).

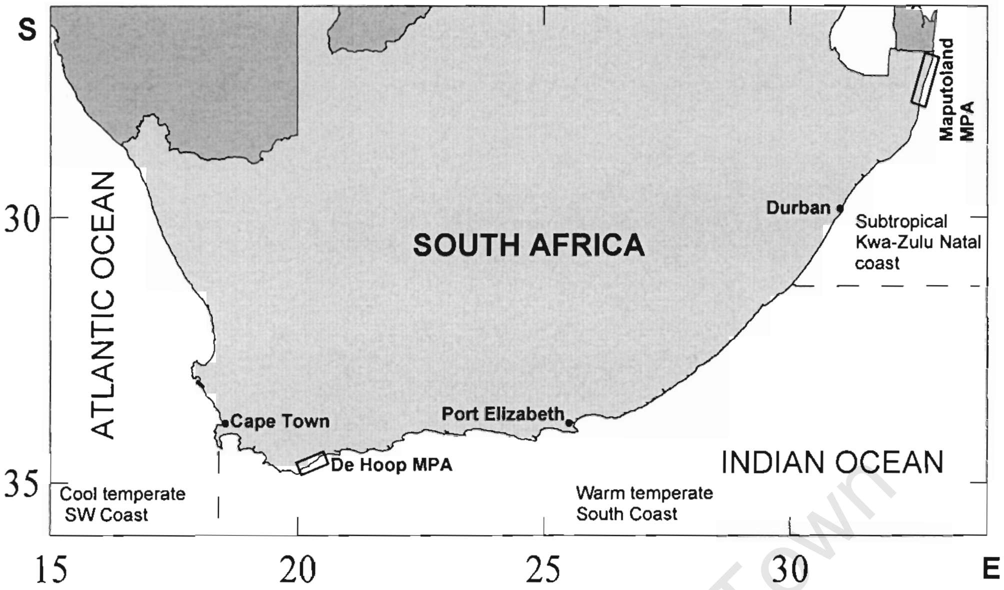


Fig. 4.1: Map of South Africa showing marine biogeographical zones (after Turpie *et al.* 2000) and the two marine protected areas (MPAs) where sampling was conducted.

The total length (TL), standard length (SL) and mass of all fish collected were recorded to the nearest 1mm and 1g respectively. The sex of each fish was determined and allocated a development stage based on macroscopic examination of the gonads (Table 4.1). Gonads were removed, weighed (to the nearest 0.1 g) and samples of each stage were preserved in 10 % buffered formalin for histological examination (for validation of macroscopic staging and fecundity estimates). Sagittal otoliths from each fish were extracted from the skull, cleaned in water and stored dry in envelopes.

Morphometrics

The relationship between TL and standard length (SL) was determined by linear regression, as was the relationship between TL and weight (using the $\log_{10}$ transformed data). The slopes of the TL-weight regressions for each site were compared using t-tests (Zar 1996). Monthly relative condition (*Kn*) was calculated for adult *U. robinsoni* ($\geq L_{50}$) from each population as follows:

$$Kn_j = \frac{\sum_{i}^{n} \frac{W_i}{aTL_i^b}}{n_j} \quad \text{.......................................} (4.1)$$

where W_i is the gonad free weight (g) of the *i*-th individual in the *j*-th month. TL_i is the total length (mm) of the *i*-th individual, and *a* and *b* are constants from the length-weight (gonad free) relationships derived for each population (all months combined). n_j is the number of fish sampled in the *j*-th month.

Age and growth

Otoliths used for age determination were from fish sampled throughout the year at De Hoop (approximately 30 per month) and during September and January at Kosi Bay. Otoliths were embedded in clear casting resin and two-three longitudinal sections (approximately 0.5 mm thick) were cut through the central region using a single diamond blade saw to ensure that the nucleus was included. In an initial trial both transverse and longitudinal sections were made from otolith pairs (n =10), and the longitudinal sections proved more easily readable. Sections were mounted on glass slides using DPX and examined under reflected light on a black background at 6-12 times magnification. Three counts of the number of opaque zones were made at least one week apart without any knowledge of the fish size. The purpose of the first count was primarily to familiarize the reader with the otolith structure and only if the last two counts coincided was the otolith accepted. A clearly visible opaque margin was included as a complete zone.

In order to quantify ageing precision, an index of average percentage error (*IAPE* Beamish & Fourier 1981) and mean coefficient of variation (*CV* Chang 1982) were calculated as:

$$IAPE = 100 \times \frac{1}{N} \sum_{j=1}^{N} \left[\frac{1}{R} \sum_{i=1}^{R} \frac{|X_{ij} - X_j|}{X_j} \right], \quad \text{.......................................} (4.2)$$

and

$$\text{mean}\,CV = 100 \times \frac{1}{N}\sum_{j=1}^{N}\left[\frac{\sqrt{\sum_{i=1}^{R}\left(X_{ij} - X_{j}\right)}}{X_{j}}\right] \qquad (4.3)$$

Where X_{ij} is the ith count of the jth otolith, X_j is the mean count of the jth otolith, R is the number of times each otolith is read and N is the number of otoliths read.

Growth zones were validated using marginal zone and marginal increment analyses (Campana 2001) of fish sampled monthly at De Hoop and fluorochrome marked otoliths (oxytetracycline –OTC) of captive) fish (n = 3). The marginal zone of each section was determined at 25 times magnification and the monthly proportions of opaque (white) and translucent (dark) margins were plotted. Marginal increments were measured from the end of the last complete opaque zone to the proximal otolith margin adjacent to the sulcal groove using an ocular micrometer at 50 times magnification. As marginal increments become narrower with age and there were insufficient monthly samples of each age, marginal increments were plotted as a proportion of the width of the last completed annulus (opaque and translucent zones combined), (Griffiths 1996a).

During August 2001, 19 *U. robinsoni* held in the Two Oceans public aquarium were anaesthetised, measured, weighed and given intramuscular injections (± 2 cm below the origin of the second dorsal fin) with an aqueous solution of the antibiotic oxytetracycline (Engemycin 10%) at a dosage of 100mg.kg fish^{-1} (Lang and Buxton 1993). Wound powder was placed on the site of injection to minimise any leakage of the OTC solution from the puncture wound. The fish were placed in a quarantine tank (PVC portapool ± 3 m diameter, 1.5 m depth) with circulating 19°C aerated seawater under natural light conditions and were fed sardines, *Sardinops sagax*. Post injection mortality was high (due to technical malfunctions with the water circulation system and capture-induced eye infections) and only three fish survived the three weeks in quarantine. These fish were placed in a large display tank (10m X 10m X 6 m deep, filtered seawater, 14° C) with natural lighting on the 22 August 2001 and sacrificed on the 4 October 2002. The otoliths from these fish were prepared as above and viewed using a Leitz Laborlux K epifluorescent photomicroscope equipped with a PL fluotar objective lens and Leitz filterblocks at 100 times magnification under a combination of ultraviolet and oblique white light.

Three different growth models - the special three parameter von Bertalanffy, generalized four parameter von Bertalanffy and the Schnute- were fitted to the observed length-at-age data for each data set. The models were fitted using an iterative non-linear minimization procedure (Microsoft EXCEL SOLVER routine with Newton algorithm option, (Microsoft Corporation 2000)) by minimizing the negative log-likelihood estimates (equivalent to finding the maximum likelihood estimates) of the model parameters. An additive, normal error structure was assumed and hence the maximum likelihood estimate of model parameters is equivalent to the non-linear least-squares estimate. The log-likelihood (ln L) took the form:

$$-\ln L = \frac{n}{2}\ln\sigma^2 + \frac{n}{2} \quad \ldots\ldots (4.4)$$

where n is the sample size and σ^2 is the variance.

The goodness of fit of the different growth models were compared by using the Akaike (1973) information criterion (AIC):

$$AIC = -2 \ln L + 2p \quad \ldots\ldots (4.5)$$

Where ln L is the likelihood function and p is the number of parameters.

Competing growth models were also assessed in terms of the L_∞ values, (the calculated asymptotic length being compared to observed lengths) and residual distributions.

Parametric bootstrapping (1 500 bootstraps) and the percentile method were used to calculate 95 % confidence intervals and standard errors for parameters of the best-fit models. Approximate joint 95 % confidence regions around L_∞ and k were calculated by conditioning on t_0, conducting 1 000 bootstraps and using the percentile method to determine the 95% confidence interval for each parameter. Growth model parameters and fitted curves for each sex and region were compared using likelihood ratio tests (Draper and Smith 1966). The likelihood ratio test statistic:

$$X^2 = -2\ (*L_{\text{full}} - *L_{\text{reduced}}) \quad \text{(4.6)}$$

where $*L$ is the negative log-likelihood estimate and X^2 is chi-squared distributedwith the difference in the number of parameters between the full and the reduced model equal to the degrees of freedom. Differences in average observed length-at-age between sexes and regions were tested using t-tests.

Reproduction

Sex ratios were tested for deviations from unity using Chi-squared tests. As degrees of freedom when comparing sex ratios with Chi-squared tests is equal to one, X^2 values were corrected for continuity using the Yates correction (Zar 1996). Macroscopic maturity stages were validated by preparation of histological slides as follows: cross-sections (approximately 5 mm) of preserved gonad tissue were rinsed in tap water and put through a dehydration sequence of increasing concentrations of ethanol (50-100 %). Samples were then placed in two changes of clearing solution (xylene or toluene), embedded in paraffin wax, sectioned at 5-7 microns and stained using haemotoxylin and eosin. Stained sections were mounted on glass slides, cover-slipped using DPX and examined at 40-400 times magnification under transmitted light. Each histologically prepared gonad section was then allocated a maturity stage based on the presence or absence of different stages of oocyte or spermatocyte development (Table 4.1, Fig. 4.2).

Male and female size at 50 % maturity in each region was estimated by fitting a logistic ogive to the proportion of mature fish (macroscopic gonad stage 3 +) per 5 cm length class. The logistic function used was:

$$P(\mathrm{L}) = 1/(1 + \exp^{-(L - L_{50})/\delta}) \quad \text{(4.7)}$$

Where $P(\mathrm{L})$ is the proportion of mature fish in size class L, L_{50} is the length at 50 % maturity and δ the width of the ogive. The logistic ogive was fitted by minimizing the negative log-likelihood estimates of the ogive parameters using the SOLVER routine (with Newton Algorithm option (Microsoft Corporation 2000)). An additive error structure was used and as the underlying distribution for maturity data are binomial, the likelihood term used was:

$$-\ln L = -\sum_{n}\left[y_i \ln\left(\frac{\hat{p}_i}{1-\hat{p}_i}\right) + m_i \ln(1-\hat{p}_i) + \ln\binom{m_i}{y_i}\right] \qquad (4.8)$$

where -ln$L$ is the negative log likelihood, y_i is the observed number of mature fish in each length class, $\hat{p}_i$ is the predicted proportion of mature fish in each length class and m_i is the number of fish sampled in each length class. Only fish sampled during months when mature ovaries were detected (stage 4 and above) in each region were used to determine size at maturity. Likelihood ratio tests were used to test for differences between L_{50} estimates for male and female fish in each region as well as between De Hoop and Kosi Bay females. Age and weight at 50 % maturity in each region was calculated using the L_{50} estimates, the fitted von Bertalanffy growth functions and calculated length-weight relationships.

The extent of the spawning season in the different regions was determined by calculating gonadosomatic indices (*GSIs*) and the monthly percentage frequency of each macroscopic maturity stage (validated by histology) for female fish larger than L_{50}.

$$GSI\,(\%) = W_1/W_2 \times 100 \qquad (4.9)$$

Where W_1 is the wet weight of the gonad and W_2 is the wet weight of the fish minus the gonad weight. Spawning seasonality for Kosi Bay fish was also inferred from the long-term (1987-1999) average monthly number of *U. robinsoni* eggs collected by inshore plankton-net tows (837 samples) conducted by Dr Allan Connell (Council for Scientific and Industrial Research) along the Kwa-Zulu Natal south coast.

Batch fecundity was estimated gravimetrically using the hydrated oocyte method of Hunter *et al.* (1985). Three sub-samples (approximately 0.5 g) of preserved tissue were removed from one lobe of undamaged, ripe and running (stage 6) ovaries from positions about one-third of the way along the ovary. Sub-samples were weighed to the nearest 0.1 mg and rinsed in flowing tap water through a 100-micron sieve to free the oocytes from connective tissue and to remove smaller non-vitellogenic oocytes.

Table 4.1: Macroscopic and microscopic descriptions of gonad maturity stages for *Umbrina robinsoni*.

Stage		Macroscopic description	Microscopic description
1	Juvenile	Testes thin and threadlike, translucent pink or grey in colour. Ovaries transparent pinkish sacs.	Predominately spermatogonia in testes. Ovaries contain oogonia and early perinucleolus stage oocytes.
2	Immature or inactive	Testes flattened pinkish white. Ovaries translucent orange tubes, longer than in stage 1.	Presence of spermatocytes and spematids in testes. Late perinucleolus oocytes predominate in ovaries.
3	Active	Testes wider and beige in colour, triangular in cross-section, some sperm is visible in the central duct if the gonad is cut and squeezed. Tiny, yellow, pinprick eggs in a gelatinous orange matrix are just visible to the naked eye.	Early stages of spermatogenesis and presence of spermatozoa in testes. Ovaries contain primary growth oocytes and numerous yolk vesicle oocytes.
4	Developing	Testes are wider and deeper in cross-section, beige or cream in colour, obvious sperm in the main duct and some present in the tissue. Easily visible eggs occupy the entire ovary which becomes opaque yellow in colour and larger in diameter.	Testes show all stages of spermatogenesis, most lobules contain spermatozoa. All oocyte stages up to tertiary yolk oocytes present in ovaries.
5	Ripe	Testes become larger and creamier in colour, considerable quantities of sperm are present. Ovaries are opaque yellow in colour and increase in diameter due to an increase in egg size.	All stages of sperm development in testes, well-developed lobes are full of spermatozoa. All oocyte stages up to tertiary yolk oocytes that occupy most of the space in the ovary.
6	Ripe and running	Testes larger still and uniform cream in colour, they are soft in texture and rupture easily when handled. Sperm are extruded if pressure is applied to the abdomen of the whole fish. Ovaries are amber in colour, very large in diameter and have a substantial portion of hydrated eggs.	No histological sections of stage 6 testes were examined. Ovaries contain all stages of vitellogenesis including numerous ripe (exhibiting coalescence of yolk granules and the formation of yolk plates) and hydrated oocytes.
7	Spent or recovering	Testes are smaller than in stages 5 and 6, harder in texture and beige or cream in colour, a little viscous semen is present in the main duct. Ovaries are smaller than in stages 5 and 6 and similar in appearance to stage 2. A few yolked oocytes remain.	Testes similar to stage 2 contain mostly spermatogonia, few spermatozoa present in lobules and sperm duct. Ovary wall considerably thicker than in other stages, large amounts of connective tissue present, perinucleolus stage oocytes most common and may contain atretic yolked oocytes.

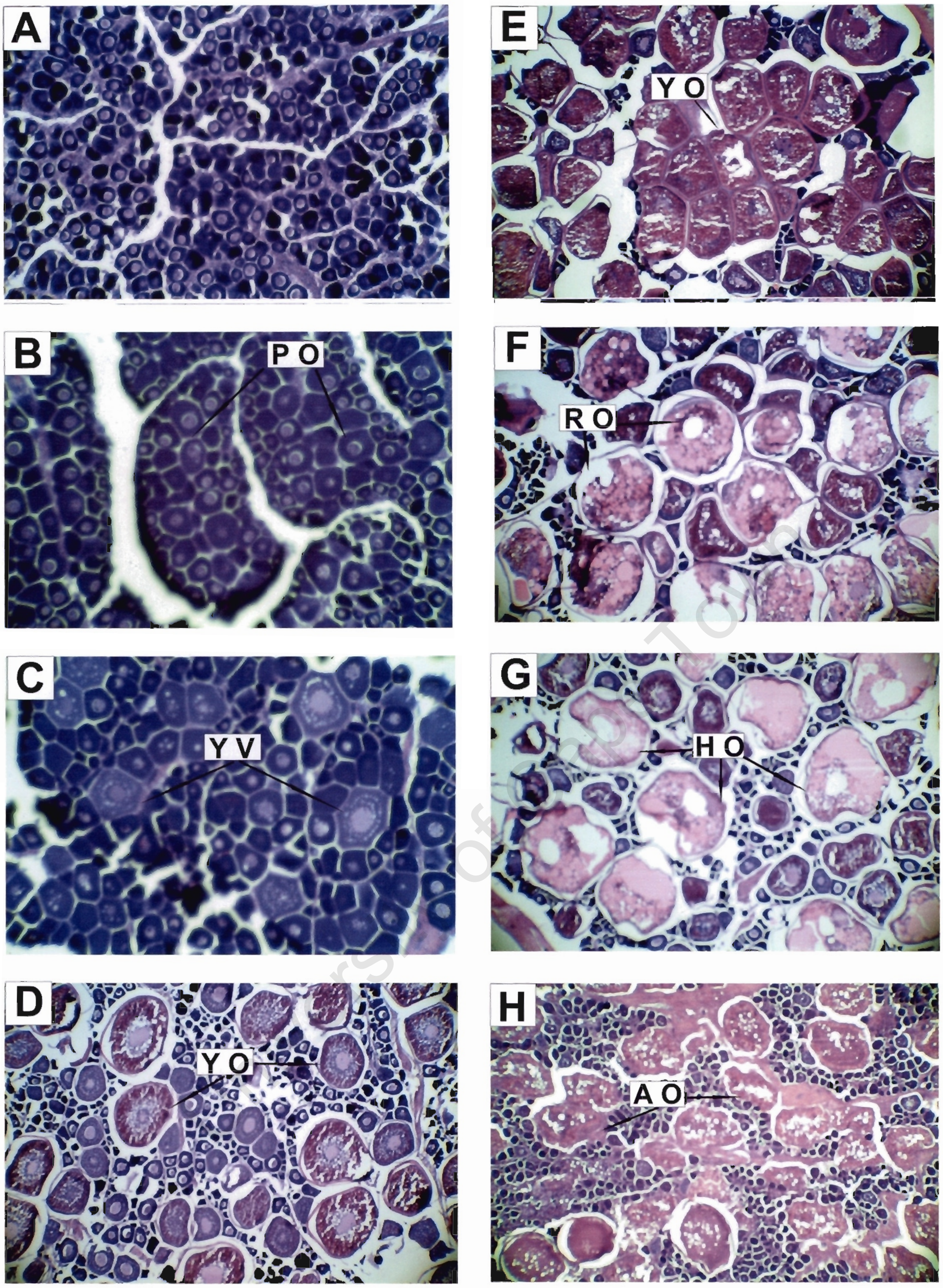


Fig. 4.2: Photomicrographs of *Umbrina robinsoni* ovary sections showing oocyte development. A: Stage 1, immature, showing pre-vitellogenic oocytes, X 100. B: Stage 2, immature or resting, (PO, perinucleolus oocytes), X 100. C: Stage 3, active, (YV, yolk vesicle oocytes), X 100. D: Stage 4, developing, (YO, yolk oocytes), X 40. E: Stage 5, ripe, X 40. F: Stage 6, ripe and running, (R O, ripe oocytes showing coalescence of yolk granules into yolk plates), X 40. G: Stage 6, ripe and running, (HO, hydrated oocytes), X40. H: stage 7, spent or recovering (AO, atretic oocytes) X 40.

Sub-samples were then transferred to a Bogorov tray and the number of hydrated oocytes counted under a dissecting microscope using a hand counter. Batch fecundity was calculated as the average product of the number of hydrated eggs per unit weight in the sub-sample and the ovary weight. Estimates of average relative batch fecundity (batch fecundity divided by stomach and gonad free body weight) for each site were compared using a Mann-Whitney *U* test.

Mortality

The two areas sampled were well established MPAs with fishing mortality (F) equal to zero, and hence estimates of total annual mortality (Z) are equivalent to estimates of natural mortality (M). Length frequency distributions were converted into age frequency distributions using an age-length key (3 cm length-classes) and Z estimated by catch-curve analyses (Ricker 1975). Additional length frequency data for De Hoop was obtained from measurements of fish tagged and released (during the same period as biological sampling) by members of an ongoing fish monitoring project conducted within the MPA. For a more detailed description of the De Hoop tagging programme see Attwood and Swart (2000) and Attwood (2003). Standard procedures for linear regression were used for calculating the 95 % confidence intervals of Z. Given the relatively small sample sizes (n = 460 and n = 352 for De Hoop and Kosi Bay respectively) used in estimating Z, catch curve analyses was also conducted using a non-parametric bootstrapping technique: a dynamic age-length key was used in conjunction with a dynamic length frequency distribution (random selection with replacement of age-length and length data) to generate 500 estimates of Z (calculated as the slope of the descending limb of the resultant catch curves) for each region. The average estimate of Z and 95 % confidence intervals (using the percentile method) were determined. The following equations were also used to obtain estimates for Z:

$$Z = ln\,[1 + 1/(a_m - a_f)] \text{ (Chapman and Robson 1960)} \ldots\ldots\ldots\ldots \text{(4.10)}$$

where a_m is the mean age of all fully recruited fish sampled and a_f is the age at full recruitment. 95 % confidence intervals were calculated using the bootstrapping technique described above;

$ln\ (Z) = -1.01\ ln\ (t_{max}) + 1.46$ (Hoenig 1983).. (4.11)

where t_{max} is the maximum age sampled.

RESULTS

Morphometrics

The size frequency distributions (TL) of fish collected during biological sampling (Fig. 4.3) show a larger size range was sampled at Kosi Bay (236-809 mm) than at De Hoop (268-707 mm). Most notably more large fish (30% > 600 mm TL) were sampled at Kosi Bay compared with De Hoop (2 % > 600 mm TL). The relationships between total length (TL) and standard length (SL) are described by the functions:

De Hoop: TL = 1.1147 SL + 37.192 mm; $n = 312$, $r^2 = 0.995$

Kosi Bay: TL = 1.1611 SL + 22.766 mm; $n = 354$, $r^2 = 0.998$

The relationships between TL and weight for the two populations are shown in Fig. 4.4. The regression coefficients for the two populations are significantly different ($t = 212.6$, $P < 0.001$) with De Hoop *U. robinsoni* being slightly heavier than Kosi Bay fish of equivalent length.

Average monthly condition of mature De Hoop fish was lowest during late summer and winter and peaked during spring and autumn (pre- and post-spawning, see below) (Fig. 4.5). Kosi Bay *U. robinsoni* showed no clear differences in average monthly condition during the three sampling periods, although the lowest value was during the peak of the extended spawning season (Fig. 4.5).

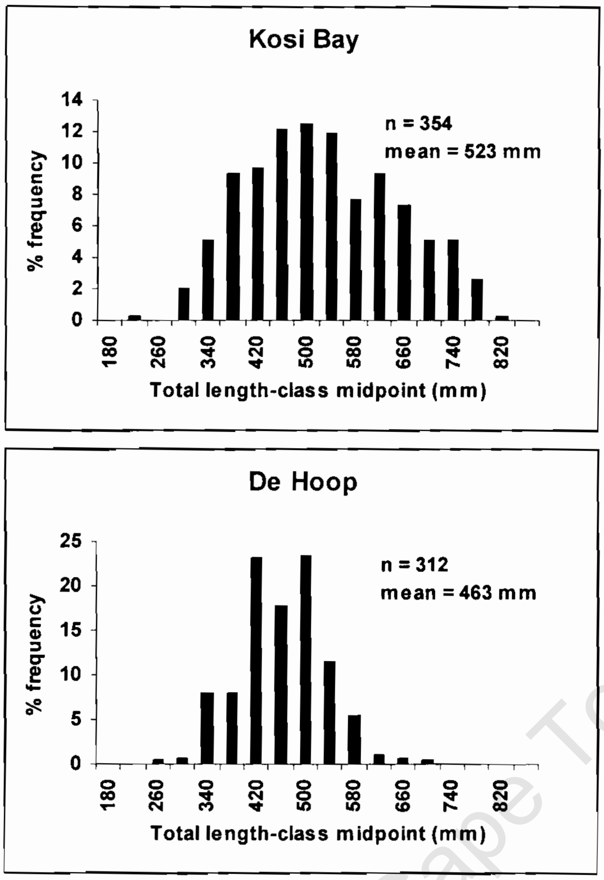


Fig. 4.3: Length frequency distributions of *Umbrina robinsoni* sampled at De Hoop and Kosi Bay based on 4cm size classes.

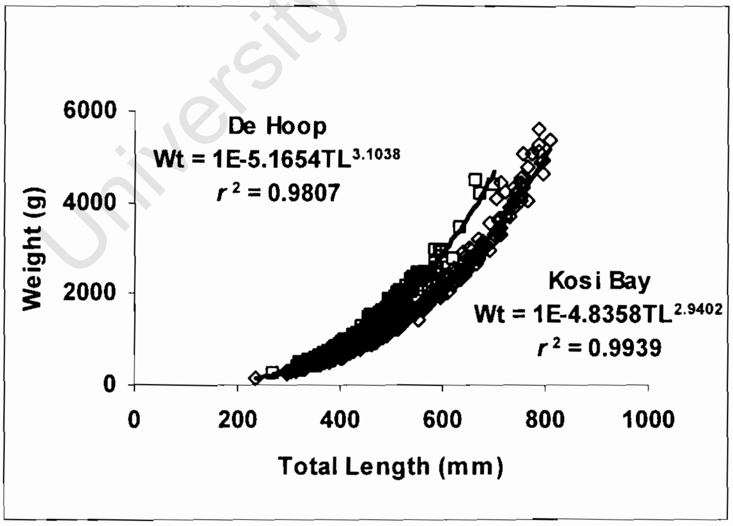


Fig. 4.4: The relationship between total length and weight for *Umbrina robinsoni* sampled at De Hoop (squares) and Kosi Bay (diamonds).

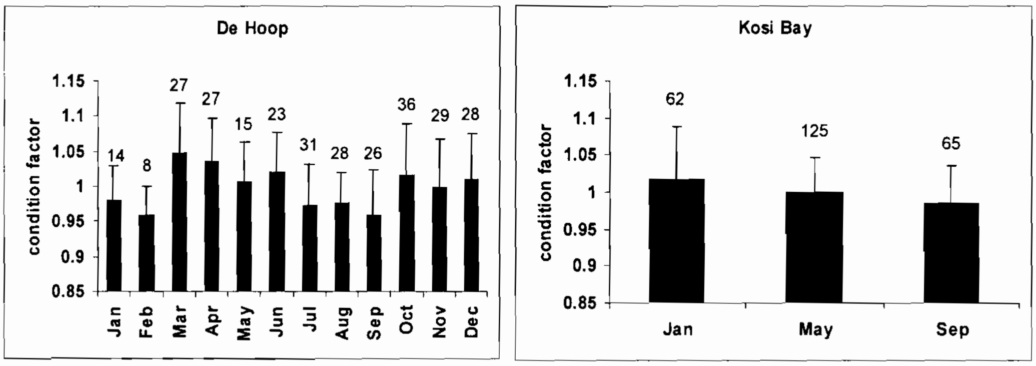


Fig. 4.5: Mean monthly condition factor (+ 1 *SD*) for mature *Umbrina robinsoni* sampled at De Hoop and Kosi Bay. The regional size at 50 % maturity was used to select mature fish at each site. Numbers above columns show monthly sample sizes.

Age and growth

Ageing precision

Umbrina robinsoni otoliths from both regions exhibited clear, alternating, translucent and opaque bands that could easily be counted (Fig. 4.6) Ageing precision was high (CV = 0.36 – 2.5 %, Table 4.2) relative to the modal CV (5 %) reported for 117 studies reviewed by Campana (2001). Although still clear, growth zones in otolith sections of fish collected at Kosi Bay were less distinct than those collected in the De Hoop MPA with opaque bands been more diffuse, hence the higher *IAPE* and mean *CV* for this region (Table 4.2). It is also noteworthy that the opaque zones of Kosi Bay otoliths were relatively wider (particularly the first three annuli) than those of De Hoop otoliths (Fig. 4.6).

Table 4.2: Number of *Umbrina robinsoni* otoliths read, accepted, index of average percentage error (*IAPE*) and mean coefficient of variation (*CV*)

Measure	De Hoop	Kosi Bay
Number read	314	177
Number accepted	308	167
IAPE (2 reads) %	0.26	1.75
CV (2 reads) %	0.36	2.48

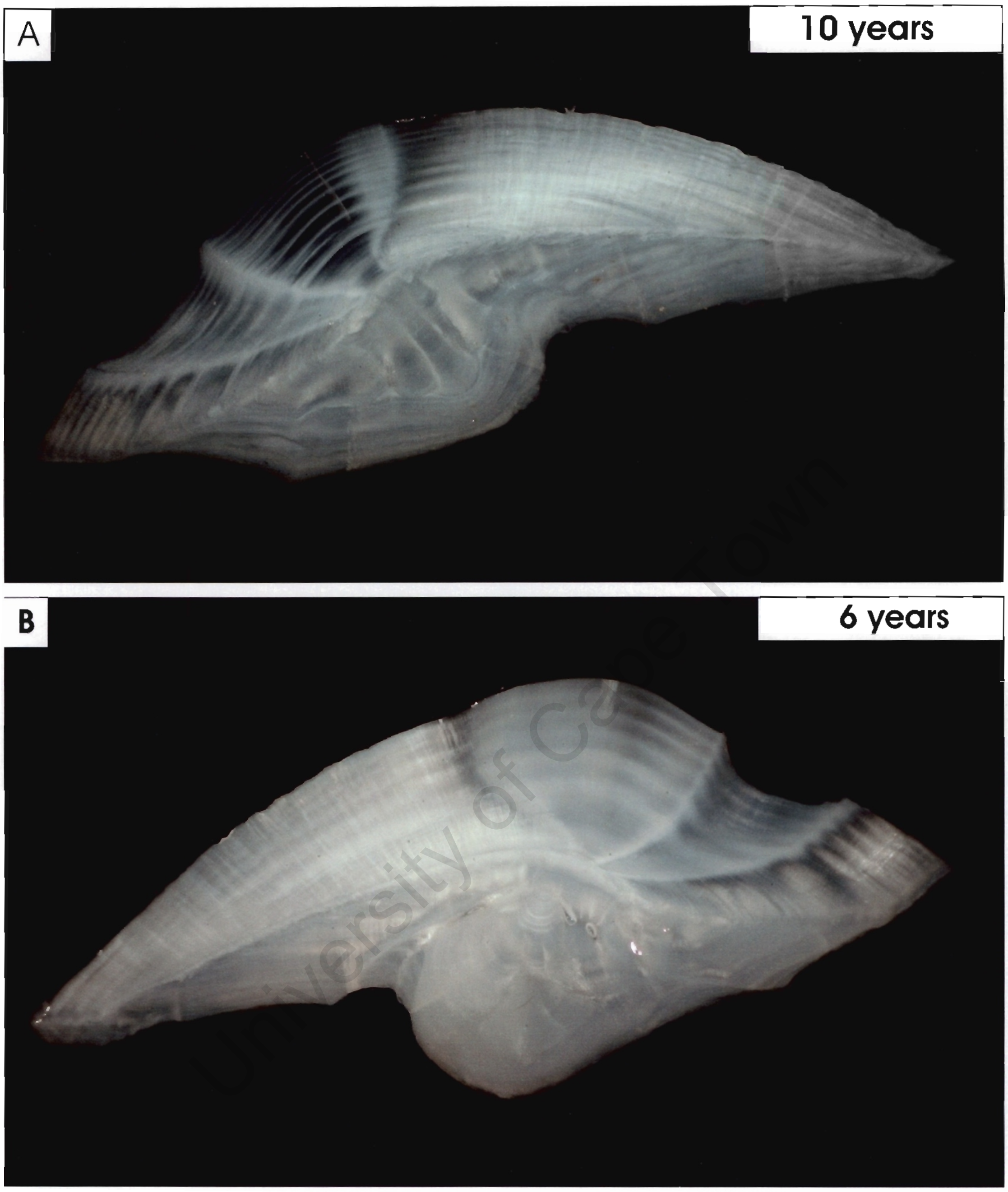


Fig. 4.6: Photomicrographs of sectioned *Umbrina robinsoni* otoliths taken from fish sampled De Hoop (A) and Kosi Bay (B) showing more diffuse nature and greater width of Kosi Bay annuli.

Marginal zone analyses of otoliths from fish sampled in the De Hoop region show opaque zone formation during the months of August to January and translucent zone formation during the period February to July (Fig. 4.7); suggesting annual formation of one translucent and one opaque zone. Marginal increment analyses confirmed this pattern with a single minimum in mean marginal increment evident in February and March (period of new annuli formation = translucent zone) and a gradual increase throughout the rest of the year (Fig. 4.7). Little increase in marginal increment width during the period October to January suggests little growth during this period, which coincides with the spawning season (see below).

The otoliths of 14 of the original 19 fish that were injected with OTC were examined under an epifluorescent microscope. All 14 exhibited a clear fluorescent check, corresponding to the time of injection, when viewed under ultraviolet light indicating successful uptake of the chemical into the otolith tissue (OTC chelates with calcium in bone forming tissue). In the otoliths of the three fish that had survived 14 months after injection, two opaque (one marginal) and one translucent zone were evident adjacent and exterior to the fluorescent check (Fig. 4.8). Given that the fish were injected in August 2001 and sacrificed in October 2002, and that opaque zones are deposited during August-January, this banding is consistent with the deposition of one opaque and one translucent zone each year. The ages of the injected fish ranged from 9 to 17 years.

Fitting of growth models to the data

All three of the growth models tested appeared to fit the observed length at age data (combined sexes) fairly well with realistic L_∞ estimates and no clear trends in residual plots. Akaike's information criteria for all data sets were however lowest for the special (3 parameter) von Bertalanffy model indicating a statistically better fit. This was largely a result of the lower number of estimated parameters as the negative log-likelihood value was very similar for all three models (Table 4.3). The special von Bertalanffy model was therefore chosen for growth comparisons between sexes and regions.

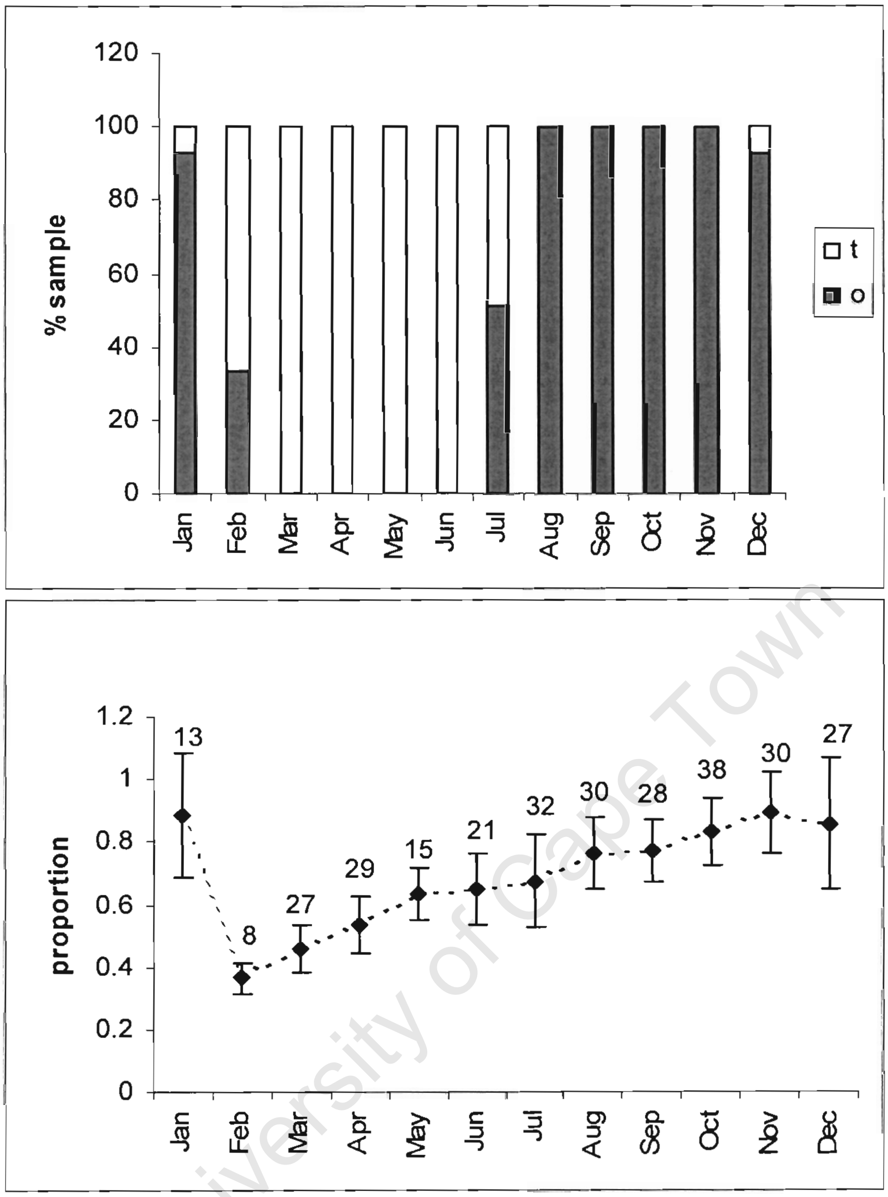
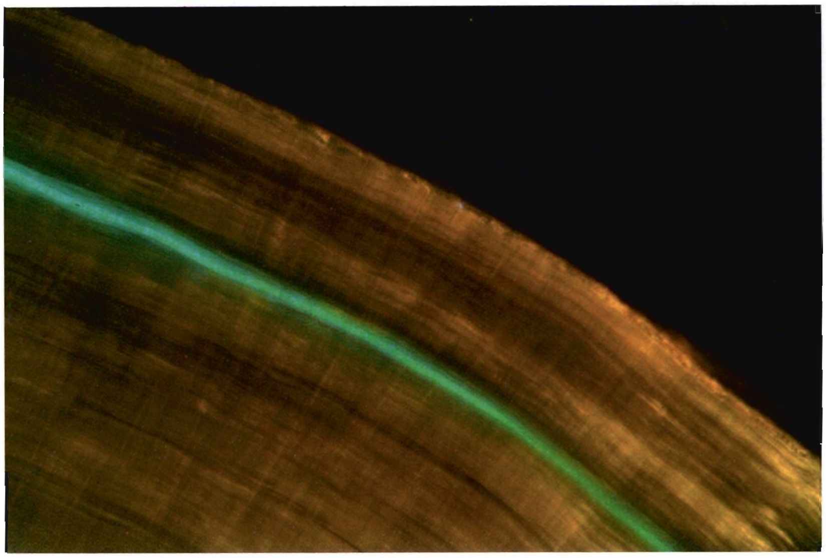


Fig. 4.7: Marginal zone nature and mean marginal increment width expressed as a proportion of the width of the previous completed annulus for *Umbrina robinsoni* otoliths (aged 2-16 years) sampled at De Hoop. Error bars show ± 1 *SD*, numbers above error bars indicate sample sizes. t = translucent, o = opaque



4. 8: Photomicrograph of a sectioned otolith taken from an *Umbrina robinsoni* injected with an OTC dosage of 100mg. kg fish^{-1} during August 2001 and sacrificed during October 2002 viewed at 100 times magnification under a combination of ultraviolet and oblique white light. Note that the fluorescent check is found within a hyaline zone and that one opaque, one translucent (i.e. one annulus) and approximately three quarters of a second opaque zone were deposited during the 14 month period after injection.

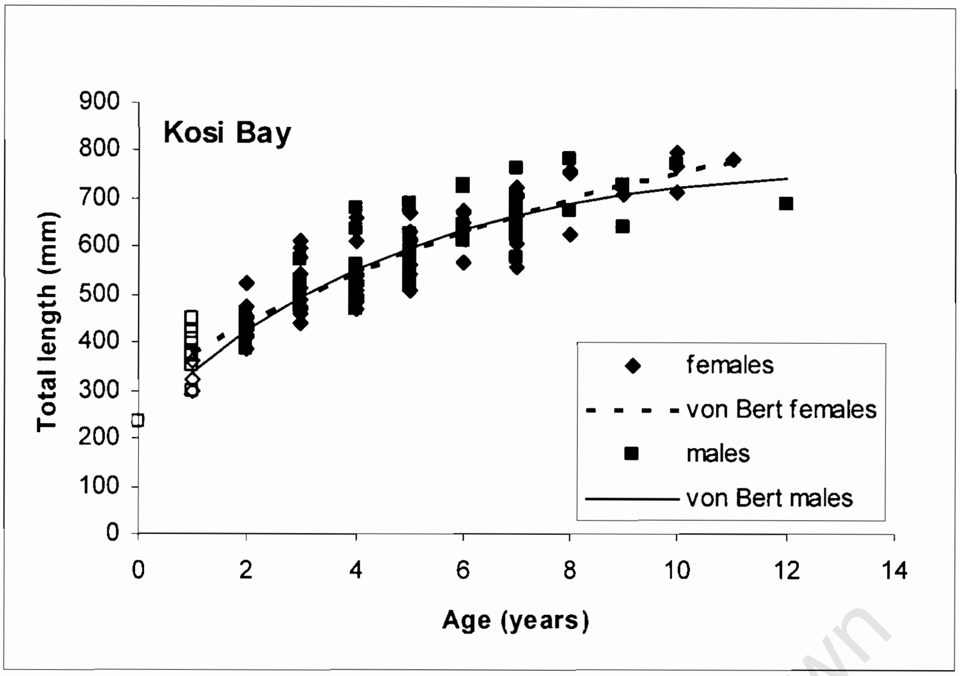
Table 4.3: Akaike's information criteria (AIC) for different growth models fitted to the observed length at age data for *Umbrina robinsoni* sampled at De Hoop and Kosi Bay. Lower AIC values indicate statistically better fits.

Model and sampling site	Number of parameters	Negative log-likelihood	AIC
De Hoop			
Schnute	6	1206.3	2424.6
General Von Bertalanffy	4	1206.5	2421
Special Von Bertalanffy	3	1206.7	2419.5
Kosi Bay			
Schnute	6	661.8	1335.6
General Von Bertalanffy	4	661.8	1331.6
Special Von Bertalanffy	3	661.8	1329.7

An unrealistic pattern of very similar observed lengths at age for consecutive early year classes was detected after the initial fitting of the growth curves. This suggests selection of the faster growing individuals of these early year classes. The most likely explanations for this being either gear selectivity or size dependent movement of juveniles into the sampled areas from nursery grounds. In order to prevent this pattern from causing bias in the fitted curves, year classes 0-2 years were excluded from the curve fitting procedure (Fig. 4.9).

Growth comparisons between sexes

Likelihood ratio tests indicated statistically significant differences between sexes in the fitted growth models ($P < 0.01$), estimated L_∞ value ($P < 0.01$) and the growth rate parameter k ($P < 0.05$) for fish sampled at De Hoop. Fitted growth models for fish sampled at Kosi Bay showed no statistically significant differences ($P > 0.05$) between the sexes. Comparison of the fitted curves for De Hoop fish show very similar growth up to approximately eight years of age after which the curves suggest that males continue to grow at a faster rate and attain a larger maximum size than females (Fig. 4.9). This is however not well supported by the observed lengths-at-age, given the small number of fish sampled at older ages. Comparison and statistical testing of the mean length-at-age of male and female fish sampled in each of the two regions does not support the differences in growth between the sexes for De Hoop fish. The mean lengths are only significantly different for nine-year-old fish ($t_{54,\,0.05} = -3.03$, $P < 0.01$). A plot of the approximate 95 % confidence regions around L_∞ and k (Fig. 4.10) for male and female De Hoop fish are close together in parameter space. This suggests that the statistically significant differences between the fitted growth curves is more likely to be a result of differences in the data spread and curve fitting than any real biologically significant differences in growth between the sexes. Sexes were therefore pooled within each region.



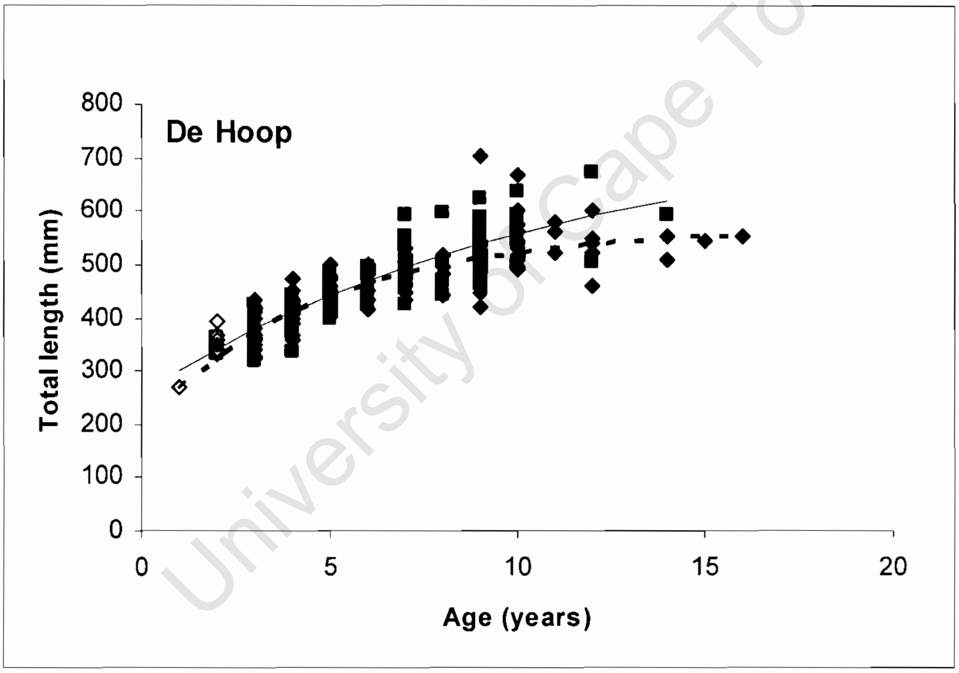


Fig. 4.9: Von Bertalanffy growth curve fitted to the observed length-at-age data for male and female *Umbrina robinsoni* sampled at De Hoop and Kosi Bay. Open symbols indicate year classes that were excluded from the curve fitting procedure.

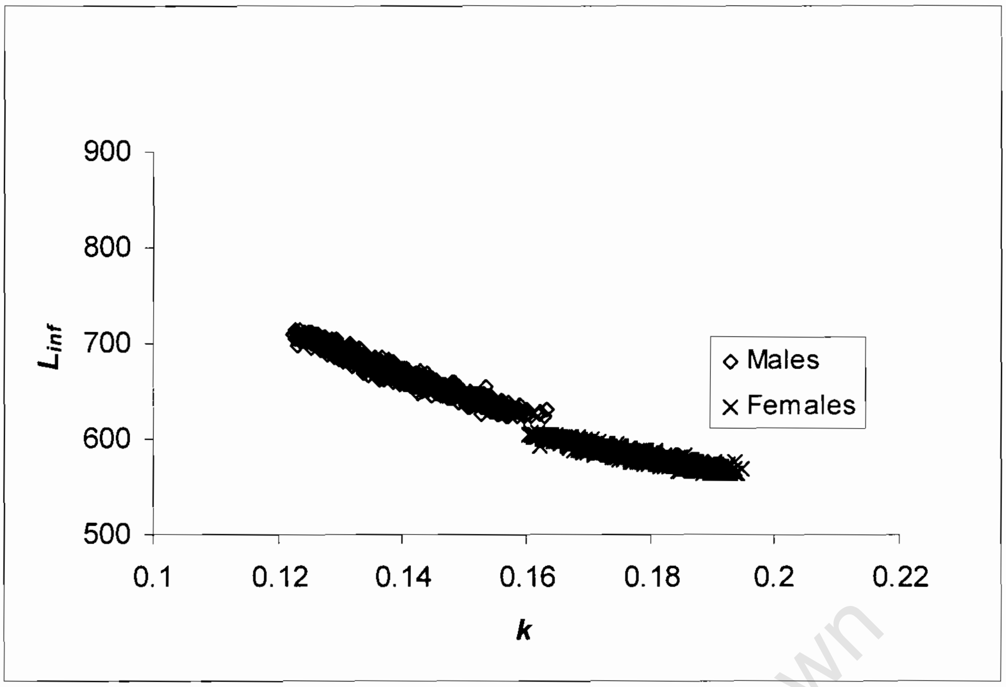


Fig. 4.10: Approximate 95 % confidence regions around L_∞ and k calculated by conditioning on t_0 for male and female *Umbrina robinsoni* sampled at De Hoop.

Spatial comparisons of growth

The special von Bertalanffy growth model fitted to the combined sexes data sets for each region are shown in Fig. 4.11. The model parameters, standard errors and 95 % confidence intervals are given in Table 4.4. The oldest fish aged from the De Hoop sample was a female of 16 years (oldest male was 14 years) whilst the oldest Kosi Bay fish aged was a male of 12 years (oldest female was 11 years). Nearly 15 % of the De Hoop fish aged were 10 years and older whilst less than 5 % of the Kosi Bay sample exceeded 10 years, suggesting greater longevity for De Hoop fish. Likelihood ratio tests indicate significant differences between the two regions for the fitted growth models and estimated L_∞ values ($P < 0.01$). The mean length-at-age, for ages 2-10 years of Kosi Bay fish was significantly greater than for De Hoop fish (Table 4.5). The wide separation of the approximate 95 % confidence regions around L_∞ and k suggest that these differences in growth are statistically as well as biologically significant (Fig. 4.12). Fish sampled at De Hoop grow slower than Kosi Bay fish for all ages and attain a significantly smaller asymptotic length (Table 4.5, Fig. 4.13). The lack of significant difference of the estimated growth rate parameter k between the two regions indicates that although De Hoop fish attain a smaller maximum size than Kosi Bay fish, they attain asymptotic length at similar overall rates in both regions.

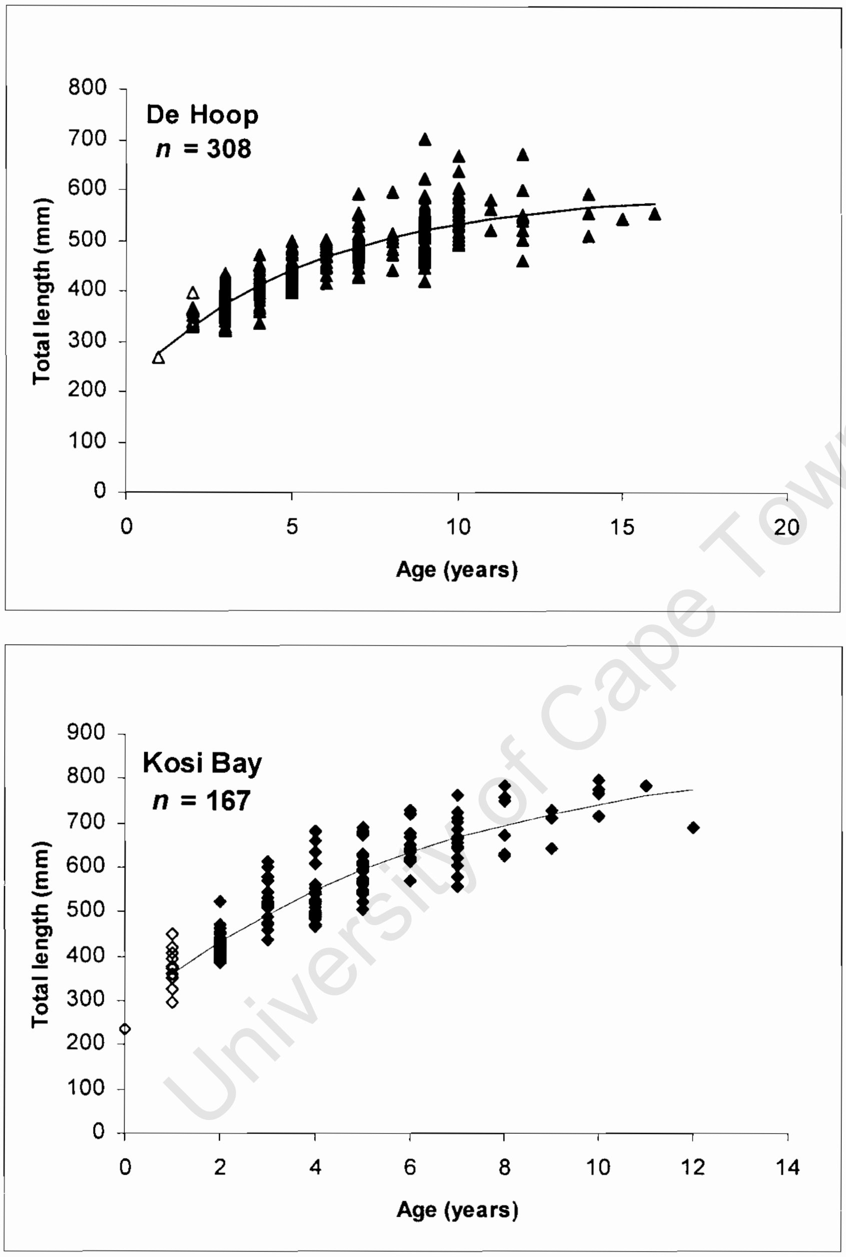


Fig. 4.11: Three parameter von Bertalanffy growth model fitted to observed length-at-age data of *Umbrina robinsoni* sampled at De Hoop and Kosi Bay during 2001-2002 (combined sexes). Open symbols indicate year classes that were excluded from the curve fitting procedure

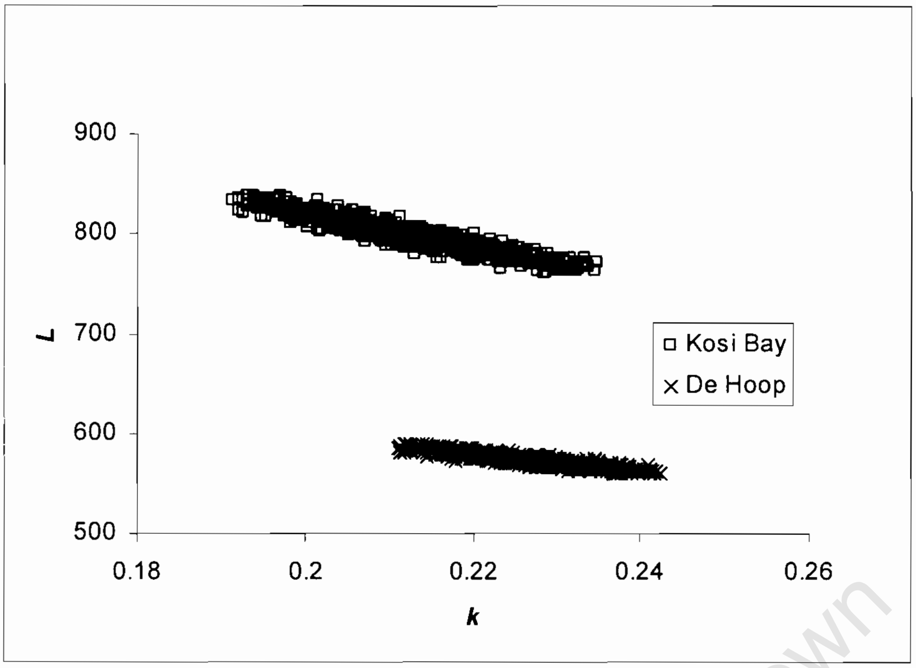


Fig. 4.12: Approximate 95 % confidence regions around L_∞ and k calculated by conditioning on t_0 for *Umbrina robinsoni* sampled at De Hoop and Kosi Bay.

Fig. 4.13: Comparison of von Bertalanffy growth curves fitted to observed length-at-age data of *Umbrina robinsoni* sampled at De Hoop and Kosi Bay. Confidence intervals (95%) for each curve are indicated with dotted lines.

Table 4.4: Von Bertalanffy growth model parameter estimates, standard errors (SE), coefficients of variation (CV) and upper (UCI) and lower (LCI) 95 % confidence limits for *Umbrina robinsoni* sampled at De Hoop and Kosi Bay

Parameter	De Hoop	Kosi Bay
L_∞		
Best fit	594	875
SE	22.7	74.0
CV (%)	3.8	8.3
LCI	563	779
UCI	653	1064
k		
Best fit	0.183	0.151
SE	0.032	0.034
CV (%)	17.4	22.7
LCI	0.120	0.092
UCI	0.247	0.225
t_0		
Best fit	-2.419	-2.498
SE	0.762	0.641
CV (%)	30	25
LCI	-4.29	-3.93
UCI	-1.28	-1.46

Table 4.5: Comparisons of mean length (TL mm) at age of *Umbrina robinsoni* sampled at De Hoop and Kosi Bay.

Age (years)	De Hoop (*n, SD*)	Kosi Bay (*n, SD*)	*t*-test	P value	Conclusion
0		236 (1)			
1	268 (1)	370 (14, 45)			
2	350 (13, 18)	429 (35, 28)	$t_{46, 0.05} = -9.56$	$P < 0.001$	Kosi > De Hoop
3	376 (39, 33)	513 (20, 48)	$t_{57, 0.05} = - 12.99$	$P < 0.001$	Kosi > De Hoop
4	412 (35, 29)	536 (25, 55)	$t_{58, 0.05} = -11.37$	$P < 0.001$	Kosi > De Hoop
5	437 (50, 24)	587 (25, 52)	$t_{73, 0.05} = -17.26$	$P < 0.0001$	Kosi > De Hoop
6	467 (19, 27)	648 (13, 44)	$t_{30, 0.05} = -14.50$	$P < 0.0001$	Kosi > De Hoop
7	494 (45, 30)	664 (18, 52)	$t_{61, 0.05} = - 16.18$	$P < 0.0001$	Kosi > De Hoop
8	493 (8, 49)	704 (6, 70)	$t_{12, 0.05} = - 6.64$	$P < 0.0001$	Kosi > De Hoop
9	514 (56, 47)	694 (3, 46)	$t_{54, 0.05} = - 3.03$	$P < 0.0001$	Kosi > De Hoop
10	548 (27, 43)	770 (5, 33)	$t_{57, 0.05} = -6.4$	$P < 0.0001$	Kosi > De Hoop
11	554 (3, 30)	785 (1)	-		
12	549 (8, 64)	692 (1)			
13					
14	552 (3, 42)				
15	542 (1)				
16	553 (1)				

Reproduction

Sex ratios of the De Hoop sample were skewed, with significantly more females, of both juvenile and adult fish, than males (Table 4.6). The sex ratio of the Kosi Bay sample did not deviate significantly from unity (Table 4.6).

Reproductive style

The extent of the spawning season and length at maturity for *U. robinsoni* sampled in the two regions was based on macroscopic gonad staging (Table 4.1). Macroscopic stages were validated by examination of histological sections (n = 242, Fig. 4.2). Examination of histological sections of the ovaries showed multiple stages of oocyte development in reproductively active females, indicating that *U. robinsoni* are serial batch spawners. The presence of widespread atresia of mature yolked oocytes, a predominance of perinucleolus oocytes, extensive connective tissue and a thickened ovary wall was taken as evidence of cessation of spawning activity (stage 7 - spent). Hydrated oocytes were found in the ovaries of ripe and running (stage 6) females from both regions (n = 4; n = 6 for De Hoop and Kosi Bay respectively), which were used to estimate batch fecundity. Post-ovulatory follicles were not located in any of the ovaries examined and it was therefore not possible to estimate spawning frequency and hence total annual fecundity.

Table 4.6: Male (M) to female (F) ratios of *Umbrina robinsoni* sampled at De Hoop and Kosi Bay showing the results of Chi-squared tests for deviations from unity (X_c^{2} values have been corrected for continuity using the Yates correction)

	De Hoop			Kosi Bay		
	M:F	n	X_c^2	M:F	n	X_c^2
Immature[1]	1:5.3	19	7.58**	1:0.9	101	0.06
Mature						
Oct-Feb[2]	1:2.1	116	14.49**			
Mar-Sept[3]	1:1.3	181	2.21			
All seasons	1:1.5	293	11.48**	1:0.9	253	0.28
Total	1:1.6	312	16.16**	1:0.9	354	0.44

1: The regional size at 50 % maturity was used to select mature fish at each site
2: Months when reproductively active females (stages 4-6) were sampled at De Hoop
3: Months when inactive or resting females were sampled at De Hoop
**: $P < 0.01$

Spawning seasonality

A defined spawning season was evident for fish sampled in the De Hoop area, with a high proportion of developing and ripe female fish (stages 4 and 5) present in samples obtained during November to February and a large percentage of spent females in the March sample indicating the end of the spawning season (Fig. 4.14). A clear peak in the *GSI* was evident in December (Figure 4.14). Some spawning activity was observed in fish collected during all three trips to the Kosi Bay region of the Maputaland MPA. Spent (post spawning – stage 7) females were found during all three sampling trips and ripe and running females during the May and September trips (Fig. 4.14). Although no ripe and running females were sampled during the January trip, there was a high proportion of developing and ripe (stage 4 and 5) females and no resting (stage 2) mature females sampled (Fig. 4.14). Average *GSI* of mature fish was similar during all three trips, showing a weak peak during September, with high variation *(SD)*, suggesting asynchronous spawning (Fig. 4.14). *U. robinsoni* eggs were collected throughout the year but were slightly more abundant from July to November (Fig. 4.15), thereby supporting year-round spawning off subtropical KZN-Natal with a peak in spring (A. Connell, Centre for Scientific and Industrial Research, unpublished data).

Size at maturity

Estimated size at 50 % maturity (L_{50}) for *U. robinsoni* sampled in De Hoop was 37 cm TL (656g whole weight.) for males and 39 cm TL (765g) for females (Fig. 4.16). Using the fitted von-Bertalanffy growth model, these lengths translate into ages of 3.5 years for females and 3 years for males. Likelihood ratio tests indicated no significant difference ($P > 0.05$) between male and female L_{50} for De Hoop fish. As there is no clearly defined spawning season for the Kosi Bay population, L_{50} was estimated using fish collected during all three sampling trips. Estimated L_{50} for female and male *U. robinsoni* from Kosi Bay were 48 cm TL (1109g, 2.8 years) and 43 cm TL (802g, 2 years), respectively (Fig.4.16). Maximum likelihood ratio tests indicated that L_{50} is significantly different for males and females at Kosi Bay ($P < 0.01$); and that female L_{50} at Kosi Bay is significantly greater than for De Hoop females ($P < 0.01$).

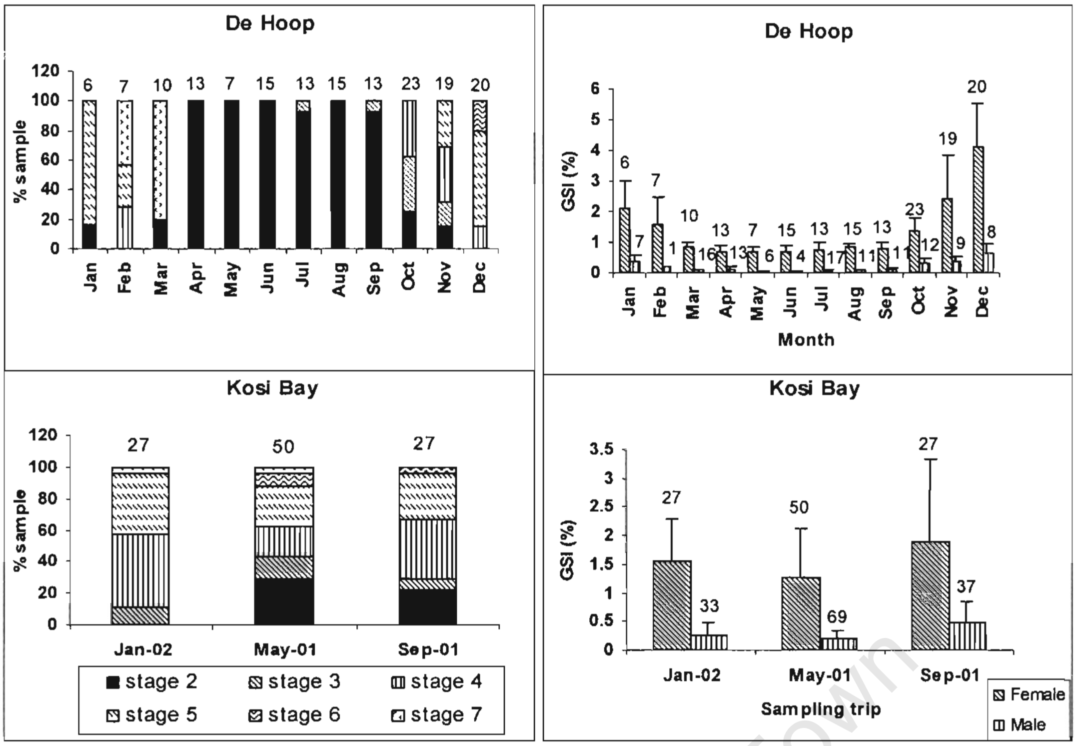


Fig 4.14: Monthly percentage of macroscopic gonad stages for mature female *Umbrina robinsoni* and average monthly gonadosomatic indices for both sexes (GSI) (+1 *SD*). The regional size at 50 % maturity was used to select fish in each region. Sample sizes are shown.

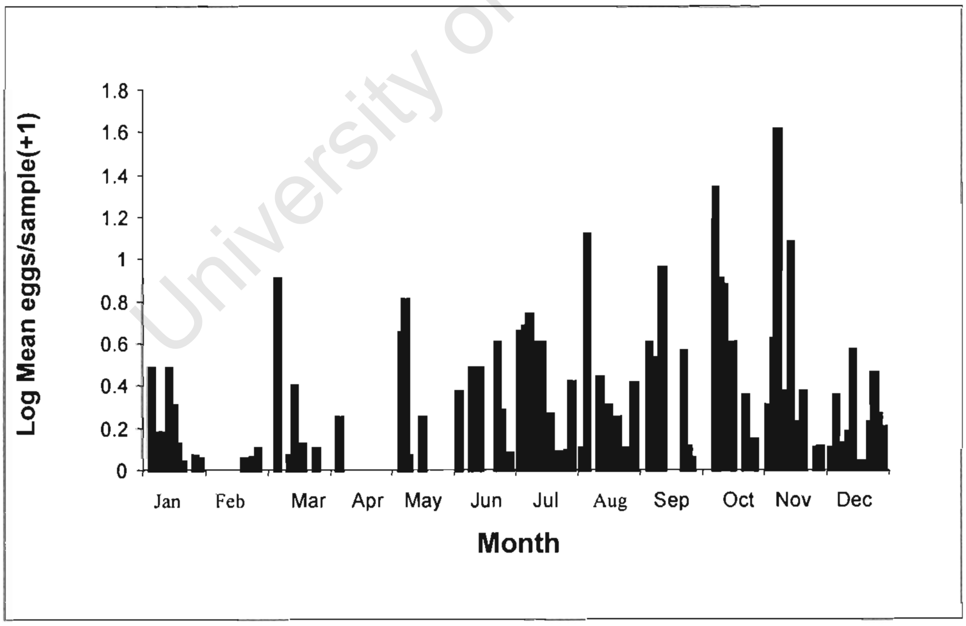


Fig. 4.15: Monthly average collection rates of *Umbrina robinsoni* eggs in plankton-net tows (n = 837) off the KwaZulu-Natal coast during the period 1987-1999. Data courtesy of Allan Connell (Council for Scientific and Industrial Research)

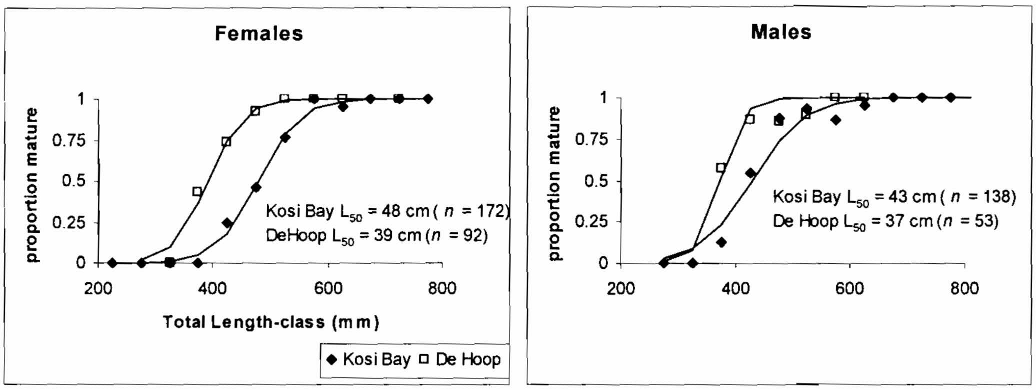


Fig. 4.16: Maturity ogives for male and female *Umbrina robinsoni* sampled at De Hoop and Kosi Bay.

Fecundity

Counts of hydrated oocytes from the ovaries of ripe and running females revealed that large *U. robinsoni* could produce close to four hundred thousand eggs per batch. Notwithstanding the small sample sizes, indications are that De Hoop females have higher batch fecundity than similar sized Kosi Bay females (Fig. 4.17). A Mann-Whitney *U* test indicated that the mean relative batch fecundity (batch fecundity divided by gut and ovary-free body weight, *GOFBW*) of De Hoop females (106 eggs.g^{-1} ± 27 *SD*) is significantly greater than that of Kosi Bay females (58 eggs.g^{-1} ± 31 *SD*), ($U_{(1)\ 4,\ 6} = 22$; $P < 0.05$). It must however be noted that spawning frequency was not established. Given the defined spawning season for De Hoop fish and the evidence of extended spawning throughout the year at Kosi Bay, it is possible that total annual number of spawning events is greater for the Kosi Bay population with potentially similar or even greater total annual fecundity in this region.

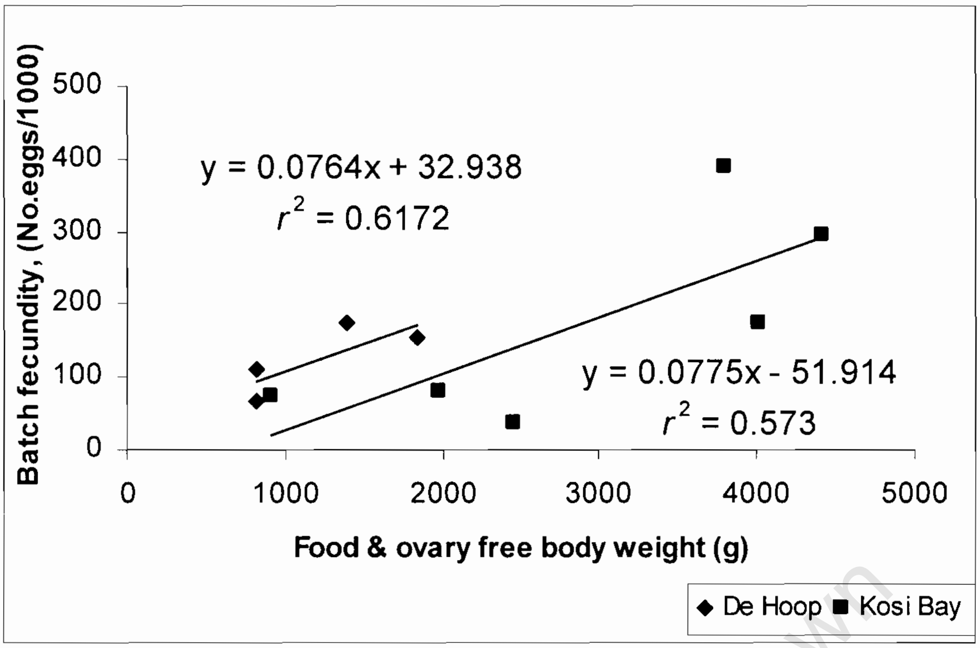


Fig. 4.17: The relationship between body weight and batch fecundity for *Umbrina robinsoni* sampled at De Hoop and Kosi Bay.

Natural mortality

Catch curve analyses indicated a lower total instantaneous mortality rate (*Z*) for the De Hoop population (0.29 y^{-1}) than for the Kosi Bay population (0.39 y^{-1}) (Fig. 4.18). Year-class strength was highly variable, particularly for the De Hoop data set, but the reasonable number of year classes should have balanced out the "strong" and "weak" year classes. A result of the high year-class strength variability, however, was that the 95 % confidence intervals (CIs) of the regression slopes were broad and included the *Z* estimates of both regions (Table 4.7). Estimates of *Z* from the bootstrap routine incorporating the dynamic age-length key were slightly lower than the point estimates obtained from conventional catch curve analyses (0.27 y^{-1} and 0.33 y^{-1} for De Hoop and Kosi Bay respectively) and 95 % CIs were narrower, but still included the *Z* estimates of both regions (Table 4.7). The Chapman & Robson (1960) equation produced very similar *Z* estimates to the above two methods (0.24 y^{-1} and 0.33 y^{-1} for De Hoop and Kosi Bay respectively) and the 95 % CIs determined by bootstrapping showed no overlap between the two regions (Table 4.7). Estimates of *Z* from the Hoenig (1983) equation were similar to the results from the various catch curve estimates for both regions (Table 4.7). The average estimates of Z based on catch curve analyses, bootstrapping, the equation of Chapman and Robson (1960) and the equation of Hoenig (1983) are 0.26 y^{-1} for De Hoop and 0.35 y^{-1} for Kosi Bay indicating a higher mortality rate in the latter region.

Table 4.7: Estimates of total instantaneous mortality rate (Z) for *Umbrina robinsoni* populations sampled at De Hoop and Kosi Bay. Lower (LCI) and upper (UCI) 95 % confidence intervals are given. Estimates of Z are equivalent to natural mortality (M) as the sampled populations are from established marine protected areas.

Method and sampling site	$Z\ y^{-1}$	LCI	UCI
De Hoop			
Catch curve	0.29	0.16	0.41
Bootstrapped catch curve	0.27	0.19	0.34
Chapman & Robson (1960)	0.24	0.22	0.26
Hoenig. (1983)	0.26		
Average	0.26		
Kosi Bay			
Catch curve	0.39	0.27	0.51
Bootstrapped catch curve	0.33	0.24	0.43
Chapman & Robson (1960)	0.33	0.30	0.36
Hoenig (1983)	0.35		
Average	0.35		

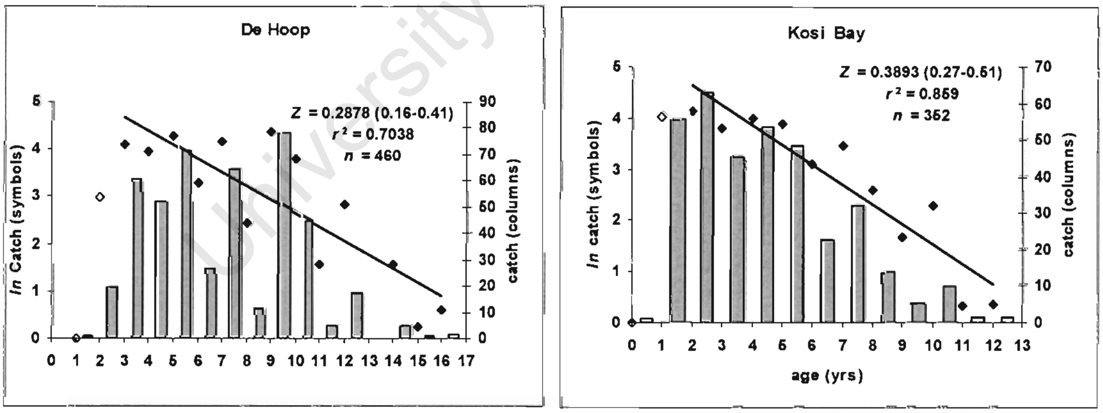


Fig. 4.18: Age distributions and catch curves for *Umbrina robinsoni* sampled at Kosi Bay and De Hoop within marine protected areas. Total mortality ($Z\ y^{-1}$) was estimated from the slope of the descending limb of the catch curve. Figures in brackets indicate the 95 % confidence intervals of the slopes.

DISCUSSION

Methodology

On examining the length frequency distributions of *U. robinsoni* from the two regions (Fig. 4.3), it may be tempting to suggest that the sampling technique (predominately shore angling) at the De Hoop site failed to adequately sample the larger, older size classes. Sampling with seine nets and spearguns at two exploited sites within the warm-temperate zone i.e. False Bay and Stil Bay, approximately 275 km west and 110 km east of De Hoop, respectively - produced numerous fish >60 cm TL (Chapter 7). Examination of the age composition and growth rates (Fig. 4.11, Table 4.5), however, revealed a greater proportion of fish older than 9 years in the De Hoop than in the Kosi samples and that the differences in size composition are simply a function of dissimilar growth. Sampling at both De Hoop and Kosi Bay failed to capture very small, young-of-the-year fish suggesting that these size-classes occupy nursery habitats different from the areas sampled. Lasiak (1982) and Clark *et al.* (1994) report catches of small (< 20cm TL) *U. robinsoni* (recorded using the synonyms *U. capensis* and *U. canariensis* – but verified as *U. robinsoni* from voucher specimens) using seine nets in the surf in Algoa and False Bays. Wallace *et al* (1984) and Beckley (1984) recorded juvenile (3-30 cm TL) "*U. canariensis*" during inshore small-mesh trawling surveys along the Cape south and east coast. Many of these trawl stations were in shallow water (< 20 m depth) and the catches were most likely juvenile *U. robinsoni* with *U. canariensis* caught at the deeper stations. Hook-size selectivity would have precluded capture of these small fish at De Hoop and although seine nets were used on occasion, netting was not attempted over mixed rock and sand substratum – habitats where Clark *et al.* (1994) captured the majority of small *U. robinsoni* during their study (S. J. Lamberth, Marine and Coastal Management, pers.comm.). The shallow surf-zone was not sampled at Kosi Bay. The most likely reasons of nursery habitats being separate from adult reef habitats are to allow young juveniles to undergo early development in environments where predation is less than in the adult habitats, avoidance of intraspecific competition and differing niche requirements (e.g. food and shelter) between adults and juveniles (Roberts 1996).

The sex ratio of *U. robinsoni* sampled in the De Hoop surf zone was biased towards females, particularly during the spawning season (Table 4.6). Based on the spatial distribution of eggs and larvae (A. Connell, Council for Scientific and Industrial Research, pers. comm.), *U. robinsoni* appear to spawn well beyond the breakers. The South African surf-zone is nevertheless a highly productive environment (McLachlan 1983, Wooldridge 1983) and is consequently an important foraging area for predatory teleosts (Griffiths 1997d), including *U. robinsoni* (unpublished data). The most likely explanation for the skewed sex ratio in De Hoop is that females return to the surf-zone between spawning events to feed, whilst males, experiencing lower energy demands and capable of spawning more frequently, spend more time farther offshore on the spawning grounds.

The scarcity of stage 6 (ripe and running) females in our samples can be attributed at least partially to the relatively small sample sizes and short periods of time over which they were collected. The timing of spawning in many fish exhibits lunar (linked to tides) or diurnal patterns that are thought to enhance survival and/or dispersal of eggs or adults (Sadovy 1996). Fish species with pelagic eggs often spawn at dusk or during the night, a strategy postulated to avoid predation of eggs and adults (which may be more vulnerable to predation during spawning activity) by diurnal predators (Robertson 1991). Hydrated oocytes are transitory structures that immediately precede ovulation. Although no published data on the timing of hydration in sciaenids was found, the general consensus is that the process of hydration, ovulation and spawning occurs within a matter of hours (Barbieri *et al.* 1994b, Nieland e*t al.* 2002). Sampling at both sites was conducted during relatively short trips (3-10 days) and was limited to daylight hours (predominantly mornings at Kosi Bay and seldom into dusk at De Hoop). If *U. robinsoni* do spawn after dark or spawning is linked to specific tidal/lunar phases, spawning events could easily have being missed. This is explanation is particularly pertinent to Kosi Bay where a low proportion of mature females appear to be spawning in any given season. Although the De Hoop fish have a distinct spawning season, sampling the feeding rather than the spawning area would also have been a factor.

Absence of POFs precluded estimation of spawning frequency in *U. robinsoni.* According to Nieland and Wilson (1993) spawning frequency in sciaenid species, is typically once every 3 to 10 days. Given that POFs in sciaenid ovaries generally persist for about 24 hours (Nieland *et al.* 2002, Wilson and Nieland 1994) some POFs should have been detected during sampling trips. The lack of POFs is probably the result of poor tissue treatment prior to fixation. De Hoop samples, although kept on ice, were fixed up to 72 hours after death. Kosi Bay specimens were exposed to air temperatures of 20-27 degrees for periods of up to 8 hours before sampling (ice was not available). These delays in preservation could have caused degradation of POFs and probably accounts for the failure to detect these features in histological sections.

Estimates of batch fecundity for *Umbrina robinsoni* ranged from 40 000-400 000 ova per batch. Mean relative batch fecundity estimates were 106 eggs.g^{-1} and 58 eggs.g^{-1} (GOFBW) at De Hoop and Kosi Bay respectively. Despite the small sample sizes, these are within the range reported for sciaenid species. Batch fecundities amongst sciaenid species are related to the size of mature females within the species (Nieland and Wilson 1993). Estimates range from 800-37 000 ova per batch for relatively small species such as white croaker *Geyonemus lineautus* (Love *et al.*1984) to 0.7-1.7 million ova per batch for large species such as *S. ocellatus* (Fitzhugh *et al.* 1988) and 0.5-2.42 million ova per batch for black drum *Pogonius cromis* (Nieland and Wilson 1993). In the case of spotted seatrout (*Cynoscion nebulosus*), an intermediate size (L_∞ = ±600 mm TL), North American east coast species with a warm temperate – subtropical distribution, batch fecundity estimates ranged from 100 00-500 000 (mean = 250 483) ova per batch (Nieland *et al.* 2002) which is similar to our estimates for *U. robinsoni*. Mean relative batch fecundities for *C. nebulosus* (103-390 eggs.g^{-1} ovary free body weight) from estuaries in the Gulf of Mexico (Brown-Peterson *et al.* 2002), however, were greater than the estimates for *U. robinsoni*

High ageing precision when using sectioned otoliths for temperate and sub-tropical sciaenid species is not unusual and has been reported for amongst others, geelbek *Atractoscion aequidens* (Griffiths and Hecht 1995b), *A. japonicus*, (Griffiths and Hecht 1995a), *A. inodorus* (Griffiths 1996a), Atlantic croaker *Micropogonius undulatus* (Barbieri *et al.* 1994a), *C. nebulosus* (Murphy & Taylor 1994, Nieland *et al.* 2002), *P. cromis* (Beckman *et al.* 1990) and *S. ocellatus* (Ross *et al.* 1995). In all of the above-mentioned studies, various forms of independent validation (marginal zone or increment analyses, chemical marking, and counts of daily growth rings) confirmed the annual deposition of growth zones in otoliths. In this study marginal zone and increment analyses and OTC chemical marking was used to validate annulus formation in *U. robinsoni* otoliths. High variation in observed lengths within age groups is also common for sciaenids and was noted in most of the studies cited above. The variation in observed length within age groups for most age classes was greater for the Kosi Bay sample than for the De Hoop sample and did not show progressively increasing variation with age as observed for the De Hoop sample (Table 4.5). High variance for earlier age classes suggests that the protracted spawning season at Kosi Bay is at least partially responsible for the observed variance in observed lengths at age, whilst variation in individual growth rate is the most likely explanation for the observed pattern at De Hoop (Griffiths 1996a).

Reproductive patterns and constraints of the physical environment

During this study, *U. robinsoni* were sampled from two widely separated (> 1500 km) MPAs with distinctive physical and biological environmental characteristics. Mean annual water temperatures were 24.4°C at Kosi Bay and 18.6 °C at De Hoop. Fishes inhabiting temperate waters tend to have more clearly defined reproductive seasonality and more restricted spawning periods than those inhabiting tropical waters (Sadovy 1996, Brown-Peterson and Thomas 1988). Spawning is usually timed to coincide with periods when environmental conditions are favourable for egg, larval and juvenile survival and growth, whilst adult condition and survival will also be important in determining spawning seasonality (Sadovy 1996). The timing and duration of spawning in many fish species, including sciaenids, has been linked to water temperature; with spawning starting during increasing water temperatures and stopping when water temperatures decrease (Brown-Peterson and Thomas 1988, Brown-Peterson *et al.* 2002, Griffiths 1996b, Nieland and Wilson 1993, Nieland *et al.* 2002).

The low winter water temperatures at De Hoop (14-15°C) may adversely affect larval and juvenile survival and is a likely reason for the restriction of spawning to the summer months in this region, whilst higher and less variable year round water temperatures (22-28°C) may permit spawning throughout the year at Kosi Bay. Low average monthly condition of adult fish at De Hoop during the late winter months (August-September) also suggests that food resources are less available or that feeding success is lower during winter. The majority of *U. robinsoni* prey in the region are filter feeding bivalves and polychaetes (unpublished data) and the biomass and productivity of these prey species are likely to be reduced during winter when nutrient rich upwelling events are rare (Hutchings *et al.* 1983). Seasonally reduced food availability could therefore also play a role in restricting spawning to the summer months; adults may simply not be able to obtain surplus energy for reproduction and there may be insufficient food resources for juvenile survival and growth. The low average condition of De Hoop fish during late summer (January and February) is probably related to the energetic costs of reproduction over the duration of the spawning season. The annual bi-modal trend in mean monthly condition therefore appears to reflect both reproductive and environmental seasonality.

The fact that spawning takes place throughout the year at Kosi Bay suggests that environmental conditions do not restrict the timing of spawning in the region. Alternatively year round spawning by Kosi Bay fish could also be a bet-hedging strategy for an oligotrophic environment to ensure that some larvae find themselves in patches of zooplankton before the yolk is completely absorbed. The moderate proportions of mature female fish with inactive or resting gonads and the lower average *GSI* values of Kosi Bay fish indicate that a small proportion of adults are reproductively active at any one time. The complete absence of mesenteric fat deposits (common in De Hoop fish during autumn and spring months of relatively good condition) suggests that energetic constraints may restrict the duration of spawning of individual fish, although a portion of the adult population may be in spawning condition at any given time throughout the year. Kosi Bay fish also appear to allocate a greater proportion of surplus energy into growth (as evidenced by the higher growth rates in the region) and this would also limit fat build up. The relatively constant average condition of Kosi Bay fish reflects the lack of reproductive seasonality in the region. This is in contrast to the pattern at De Hoop, where during the spawning season (November-February) the majority of adult females have developing, ripe or recently spent ovaries and spawning within the population is synchronized. The lower relative batch fecundities of Kosi Bay fish probably reflect the extended duration of spawning in the area, (i.e. Kosi Bay fish spawn smaller batches of oocytes over a longer period than De Hoop fish) and the relative allocation of surplus energy into growth and reproduction.

Life history comparisons

Although estimated lengths-at-age were smaller for the De Hoop population (Fig. 4.13), the derived growth rate parameter for the von Bertalanffy growth function was greater (although not significantly) than for the Kosi Bay population (k = 0.18 vs. 0.15). The reason for this apparent contradiction is that that k and L_∞ are statistical descriptors of the growth curve and do not have independent biological interpretations; both are functions of the age at maturity and the allocation of surplus energy to reproduction versus growth (Roff 1992). If growth rate is correctly defined as the annual increment in length, then it is clearly slower for the De Hoop population than for the Kosi Bay population. Roff (1992) shows both theoretically and empirically, for a wide range of fish species, that k and L_∞ are negatively correlated whilst growth rate and mortality rate are positively correlated. When growth rate and asymptotic length are considered as statistical descriptors of the growth curve then the values obtained from the two *U. robinsoni* populations conforms to the first general pattern but only if growth rate is defined as annual increment is there a positive correlation between growth rate and mortality rate.

Spatial variation in the growth has been documented for numerous sciaenid species, including *A. inodorus* (Griffiths 1996a), *C. nebulosus* (Murphy and Taylor 1994, Nieland *et al.* 2002), *S. ocellatus* (Ross *et al.* 1995), weakfish *Cynoscion regalis* (Shepherd and Grimes 1983) and *M. undulatus* (White and Chittenden 1977). Maximum size and age in the last three mentioned studies was observed in the higher latitudes of the species range. Ross *et al.* (1995) suggest that the evolutionary basis for this counter gradient variation in growth rate may be size-selective winter mortality of juveniles in temperate regions (Conover 1990) or from increased metabolic costs in warmer waters (Edwards 1984). The largest and oldest *U. robinsoni* sampled during this study (up to 8.5 kg and 18 years) came from the temperate waters of False Bay suggesting that this general trend is true for the species. These fish were, however, from an exploited population and fishery/density dependent effects on growth rate cannot be excluded. The largest fish sampled at De Hoop was substantially smaller than the maximum size captured at sub tropical Kosi Bay (702 mm TL, 4.5 kg vs. 809 mm TL, 5.6 kg) and mean length-at-age was significantly smaller for most ages, despite many older fish in the De Hoop sample. This finding is in agreement with the general latitudinal trend in longevity but counter to the trend in body size, providing further evidence that growth rate is somehow constrained at De Hoop. Low water temperature during winter months is the most obvious physical environmental variable that may restrict growth at De Hoop, with the population being at the southern extreme of the species distribution which extends northwards up the tropical east African coast (Chapter 1). Growth in North Atlantic cod *Gadus morhua* is positively related to water temperatures (Berg and Albert 2003). Physiological processes (such as growth) in ectotherms are directly related to environmental temperatures, with the speed of anabolic and catabolic reactions increasing in direct proportion to temperature (within the suitable temperature range for enzyme activity) (Begon *et al.* 1990). However, the decline in condition during winter suggests that energy/food is limited during this period and that energy reserves are used for basic catabolism.

There is a widely held view that predation pressure is higher in the tropics than in temperate regions (Jones 1991). Supporters of this view argue that predation pressure has an important influence on community structure and acts as a major selective agent moulding life-history strategies (Jones 1991). Hixon (1991), however, notes that most of the evidence in support of the predation hypothesis is circumstantial with correlative or experimental evidence less common. The abundance of piscivores on coral reefs, (up to 54 % of the fish community), and morphological, chemical and behavioural prey defences are often cited as circumstantial evidence for the strong selective force of predation (Hixon 1991). The higher estimated natural mortality rate for the subtropical Kosi Bay population (average $M = 0.35$) than for the warm temperate De Hoop population (average $M = 0.26$) provides quantitative support that predation pressure on *U. robinsoni* in South African waters is greater in subtropical habitats.

The two principal factors determining natural mortality rates on reefs are the abundance of predators and the ability of the prey to escape (Roberts 1996). Swimming speed is a function of body size and larger (faster growing) fish would be better able to escape predatory attacks. The faster growth rates demonstrated by Kosi Bay fish would therefore have lowered the rate of natural mortality. Although selection against slower growing individuals may have resulted in a genetic shift, faster growth could also be a plastic response (Leaman 1991) or simply a function of warmer temperatures.

Despite the differences in life-history characteristics between the two *U. robinsoni* populations, a comparison of age and length at maturity as ratios of the regional maximum ages and lengths indicates that the two populations actually have similar life-history strategies. Fifty percent maturity for females in the Kosi Bay population (48 cm) occurs at 54 % of the estimated asymptotic length (88 cm) and for De Hoop females (L_{50} = 39 cm) at 65 % of L_∞ (60 cm). Ages at 50 % maturity (A_m) expressed as a percentage of the maximum ages recorded in each region are almost identical, occurring at 23 % of maximum age at Kosi Bay and 22 % of maximum age at De Hoop. It appears that the age and size schedules of maturity of *U. robinsoni* populations alter in response to growth and mortality rates in two different regions in very similar ways.

According to life-history theory iteroparous marine teleosts will schedule maturity to maximize life-time fecundity within genetic and environmental constraints by optimising the three-way trade off between individual fecundity, survival and growth (Roff 1984, 1992). By way of example delayed maturity would, owing to energetic costs of reproduction, result in larger size, and therefore greater fecundity and low natural mortality at age. Delayed maturity would, however, only be advantageous if there was a good chance of surviving for sufficient time after maturing to offset reproductive losses associated with the delay. Roff (1986) developed a mechanistic model incorporating the trade-off to predict the optimal size at maturity for populations of marine fishes:

$$L(\alpha) = L_\infty\left(\frac{3k}{3k+M}\right)$$

where $L(\alpha)$ is the optimal length at maturity, k and L_∞ are the von Bertalanffy growth model parameters and M is the natural mortality rate.

Based on this model the optimal sizes at maturity for *U. robinsoni* off De Hoop and Kosi Bay were predicted to be 40 cm and 49 cm, respectively. Given that the predicted values were very close to the empirical L_{50} estimates of 39 cm and 48 cm, it appears that the age/size at maturity schedules of the two *U. robinsoni* populations are either evolutionary or plastic responses to maximise individual life-time fecundity.

U. canariensis, a smaller congeneric species that occurs in deeper water (50-150 m) off the South African east coast, also attains L_{50} (23 cm) at a relatively large size, i.e. 58-69 % of L_∞ (35-40cm), but at a relatively younger age (10-12 % of maximum age = 27 years) (Chapter 2.). Amongst other sciaenids of similar size to *U. robinsoni*, e.g. *A. inodorus* (Griffiths 1997a), *C. regalis* (Shepherd and Grimes 1983), *C. nebulosus* (Nieland *et al.* 2002) maturity generally occurs at relatively earlier ages (8-10 % of maximum age) and smaller sizes (26-40 % of L_∞). This suggests that the life-history strategy of *U. robinsoni* involves delayed maturity with losses in early reproductive output offset by relative large size at maturity and moderate longevity. This life-history strategy in combination with the high degree of residency makes *U. robinsoni* vulnerable to exploitation; particularly recruitment overfishing. This study has shown that under natural conditions (in MPAs), the life-history characteristics of the species shows considerable spatial variation and management measures will have to take this into account in order to be effective.

CHAPTER 5

MOVEMENT PATTERNS OF *UMBRINA ROBINSONI,* (SCIAENIDAE) BASED ON MARK-RECAPTURE AND DEPLETION EXPERIMENTS

ABSTRACT

Movement patterns of *Umbrina robinsoni* off the South African east coast were determined from long-term mark–recapture studies and diver counts during depletion sampling at selected sites. A total of 972 fish were tagged and released at three 3.4 km-long sites within the warm-temperate De Hoop Marine Protected Area (MPA) as part of an ongoing study assessing the effectiveness of this reserve. All twenty of the recaptures were made within the respective sites of release, and for eight of these, where mark and recapture locations were recorded to a spatial resolution of 100m, mean coastwise displacement was 550 m (0-1400m). Two hundred and thirteen *U. robinsoni* were also tagged by recreational anglers between 1984 and 2004 as part of a nationwide, public participation tag and release programme. Of the eight *U. robinsoni* recaptured, six showed no displacement (within 1 km) from the site of release, and two showed coastwise movement of approximately 5 km and 14 km. Diver counts within the sub-tropical Maputaland MPA suggested little movement between seven sites over a 20 month period and little recovery of shoals depleted by spearfishing. *U. robinsoni* therefore appear to be strongly philopatric with small home-ranges.

INTRODUCTION

Slender baardman (*Umbrina robinsoni*) are found in inshore waters (surf zone - 45m) along the entire South African eastern seaboard (Cape Point to Mozambique border) and further up the African east coast at least as far as Oman (Chapter 1). Historically in South African waters it was a popular shore angling species (Bennett *et al.* 1994) and a notable by-catch component of beach-seine fisheries (Lamberth *et al.* 1994, 1995) off the Cape coast. It remains an important target species of spearfishers in KwaZulu Natal and the Cape provinces (Mann *et al.* 1997). Until recently very little scientific information on the life history of *U. robinsoni* was available, with published accounts restricted to mentions of occurrence and size composition in catches, where the species was often misidentified as *U. canariensis*.

Based on seasonal trends in angler catch rates from False Bay and the De Hoop marine protected area (MPA), Bennett and Attwood (1991) suspected that *U. robinsoni* was migratory. Recent research, however, has detected significant regional differences in life-history characteristics, including growth rate, longevity, spawning seasonality and size at maturity (Chapter 4). This suggests that the studied populations (De Hoop and Kosi Bay) constitute separate stocks with limited interchange. From a management and conservation perspective, knowledge of movement patterns is desirable for an understanding of stock separation and the impacts of exploitation (Griffiths 1997a) as well as for assessing the size and placement of MPAs, (Bennett and Attwood 1991, Cowley 1999, Griffiths and Wilke 2002, Brouwer *et al.* 2003). This chapter provides information on the movement patterns of *U. robinsoni* in 1) warm-temperate habitats based on two long-term mark-recapture studies and 2) sub-tropical conditions based diving observations and depletion experiments conducted over a 20 month period.

MATERIAL AND METHODS

An ongoing tag and release programme was initiated at two 3.4 km-long sites, Koppie Alleen (34°28.65'S, 20°30.70'E) and Lekkerwater (34°26.92'S, 20°39.15'E) (approximately 11 km apart) within the 51 km long De Hoop MPA in 1987 (Fig. 5.1). A small number of volunteer anglers under the supervision of 1-3 fishery scientists, affiliated either to the University of Cape Town or the state department of Marine and Coastal Management, caught and tagged fish (more than 20 different species) using shore-angling techniques. Fish were captured by rod and line angling in the surf-zone (hook sizes: 1/O – 4/O). Bait used included polychaete worms (*Arenicoli loveni* and *Marphysa* sp.), white mussel (*Donax serra*) and red bait (*Pyura stolonifera*). All fish caught were measured to the nearest mm total length (TL) and tagged (if > 250 mm TL) in the musculature below the second dorsal fin using external plastic dart tags (89 mm long, 1.4 mm diameter) inscribed with a unique code and address. Prior to 1998, recaptures made within the De Hoop MPA were recorded with a spatial resolution equivalent to the study site length (i.e. 3.4 km). From 1998 onwards, the position of tagging or recapture of each fish was recorded to within 100 m by reference to numbered boards that were placed at fixed positions throughout the study sites at the start of each trip. Prior to 1994 twelve field trips (5 days duration) per year were conducted and six trips per year thereafter. All recaptures made at the two sites within the MPA were recorded by the research team whilst recreational anglers are relied upon to report recaptures made outside of the reserve boundaries. For a more detailed description of the De Hoop tagging programme see Attwood and Swart (2000) and Attwood (2003).

During 2001-2002, monthly sampling trips (3-5 days duration) to obtain biological information on *U. robinsoni* were undertaken to Skipskop (34°31.70' S, 20°25.57'E) a third site within the De Hoop MPA, which is approximately 9 km west of Koppie Alleen (Fig. 5.1). As the Koppie Alleen and the Skipskop sites both incorporated approximately 3.5 km of coastline, the minimum distance separating the two sites was only about 3 km. Fish were captured using shore angling techniques similar to those described above and any *U. robinsoni* not required for biological material were tagged and released using the same methods. This chapter uses the data for all *U. robinsoni* marked and recaptured within the De Hoop MPA over the period 1987-2004. The data for recaptured *U. robinsoni* were analysed according to tagging location, days at liberty and minimum distance moved.

A nationwide tagging program (The Sedgwick's/ORI/WWF Tagging Project) was initiated in 1984 and is managed by the Oceanographic Research Institute (ORI). Tagging and recapture of fish were undertaken by members of the public using similar techniques as described above, although larger (114mm, 1.4 mm diameter) plastic dart tags are also used. Data on *U. robinsoni* marked and recaptured over the period 1984-2004 were extracted from a data report by Bullen and Mann (2004). The main difference between this tagging program and the research tagging conducted within De Hoop is the participation of unsupervised volunteer anglers. As a consequence the recording and submission of tagging and recapture information is often inaccurate or incomplete (Attwood 1998, Attwood and Bennett 1994). For this reason, recapture information for *U. robinsoni* from the Sedgwick's/ORI/WWF Tagging Project was analysed separately from the De Hoop data.

Three sampling trips (10 days duration each) were conducted to the Kosi Bay region of the 156 km long St Lucia-Maputaland MPA on the subtropical northern KwaZulu Natal coast (May and September of 2001, January 2002). The area sampled extended from Kosi Bay estuary mouth (26° 54.01'S, 32°53.08'E) to Dog Point (27°05.15'S, 32°51.05'E), a distance of 24 km (Fig. 5.1). Five shoals of *U. robinsoni* were located during the first (May 2001) trip and two further shoals during the September 2001 and January 2002 sampling trips. The positions of all shoals were recorded using a Global Positioning System (GPS) and were visited on subsequent trips (Fig. 5.1, Appendix

1). Shoals were depleted to various degrees using spear guns as part of a biological sampling programme (Chapter 2). Counts of the number of *U. robinsoni* present at each GPS marked site and the number removed during each sampling trip were analysed to investigate net movement of fish to or from sites. A follow up trip to monitor recovery of shoals sampled in this area was undertaken in January 2003; *U. robinsoni* remaining at all of the original seven reefs were counted.

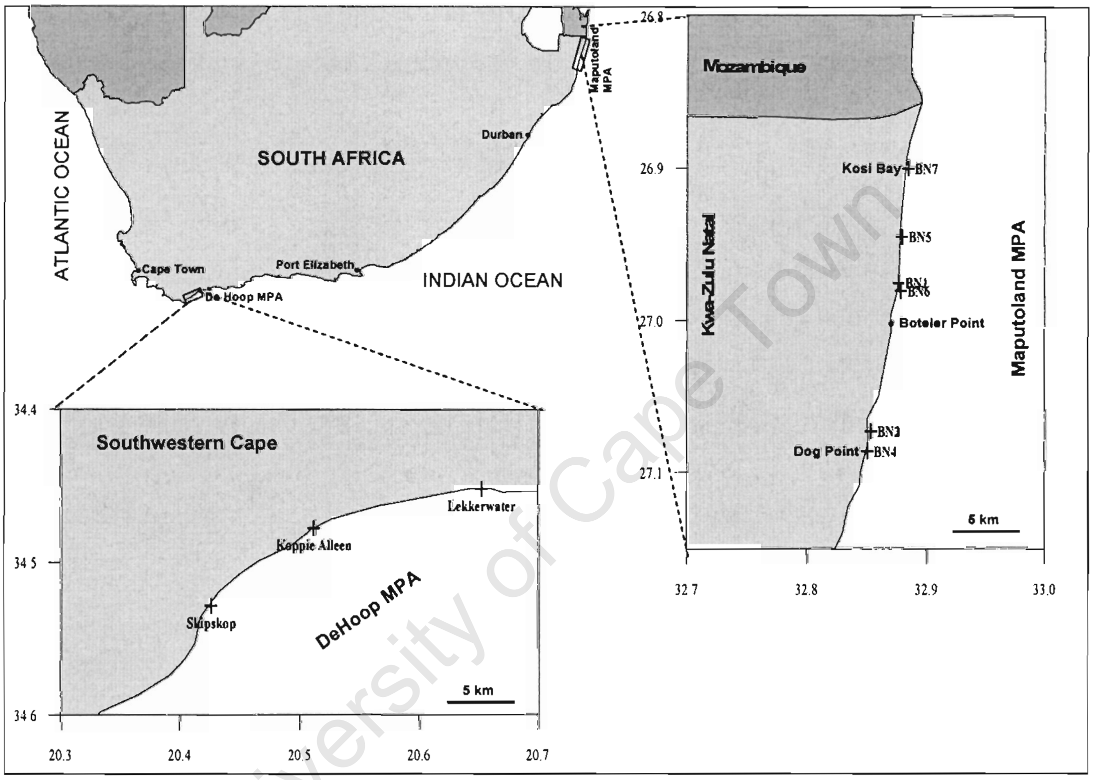


Fig. 5.1: Map of Southern Africa, showing location of study sites within the De Hoop and Maputaland MPAs. (BN 1-7 = reef sites sampled within the Maputaland MPA; BN 2 & 3 overlap).

RESULTS

A total of 972 *U. robinsoni* were tagged and 20 (2.1 %) recaptured within the De Hoop MPA during the period October 1987-August 2004. Time at liberty for recaptured fish ranged from 57-1 531 days and no movement between the three tagging sites (> 10 km) was recorded (Fig. 5.2). No recaptures were reported from outside of the MPA boundaries. Eight fish tagged subsequent to 1998 were recaptured, with a mean displacement of 550m (0-1400m) (Fig. 5.2). These data revealed no trend between time at liberty and distance moved (Fig. 5.2), or between fish size (TL) and displacement (Fig. 5.3)

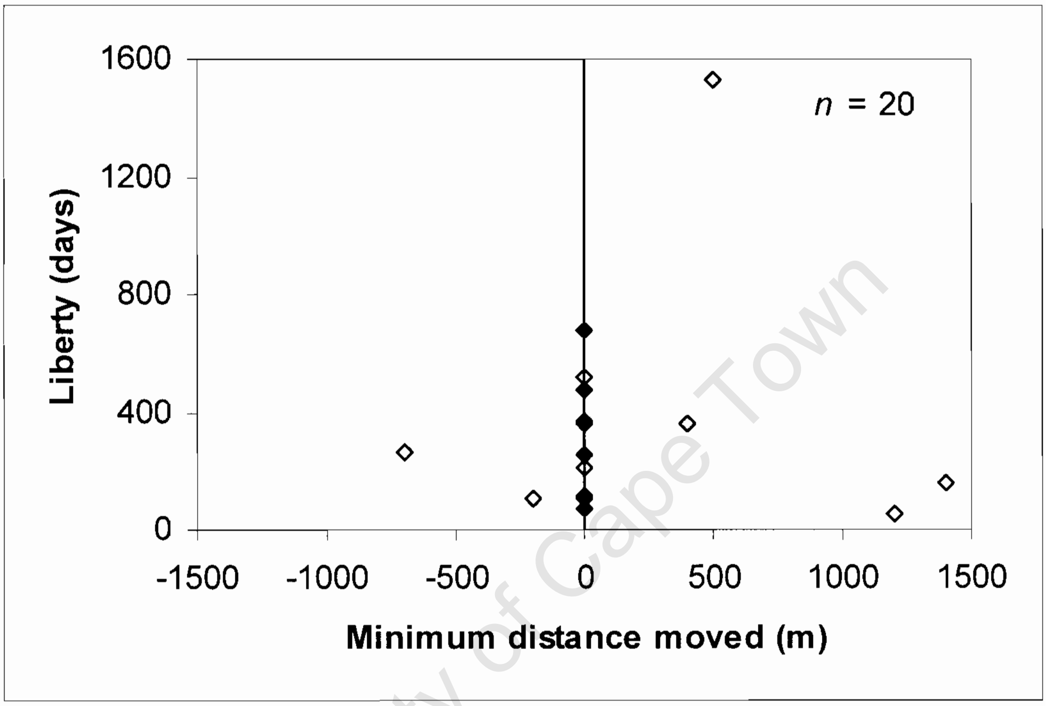


Fig. 5.2: Minimum distance moved vs. days at liberty for *Umbrina robinsoni* tagged and recaptured within the De Hoop MPA. Negative values show coastwise movement to the east and positive values movement to the west. Open symbols represent recaptures where the site of release and recaptured was recorded to within 100 m.

A total of 213 *U. robinsoni* were tagged by recreational anglers between 1984 and 2003 from which eight recaptures (3.75 %) were reported. Although *U. robinsoni* were tagged along the entire South African east coast, the majority were tagged along the warm-temperate south coast with only 10 fish (5 %) tagged in KwaZulu-Natal waters. Just two anglers who operated in False Bay and at Cape St Francis were responsible for nearly half (93 fish) of all the *U. robinsoni* tagged, and six of the eight reported recaptured fish were tagged by these anglers. Time at liberty ranged from 5-

550 days and six of the eight recaptured fish showed no displacement (within 1 km) from the release site. Two of the recaptured fish were reported as having moved a minimum of 8 km and 17 km eastward (time at liberty: 320 and 217 days respectively). Given the absence of this scale of movement for the De Hoop data set, there was a possibility that inaccurate reporting by members of the public of either the release or the recapture locality occurred. In an attempt to validate these data, the anglers who originally tagged the fish were contacted. Fortuitously both anglers had kept detailed records of their tagging activities and in both instances the site of release was found to be approximately 2.5-3 km closer to the reported recapture location. It was only possible to verify the recapture location of the one fish, with the resultant confirmed movement of approximately 5.5 km whilst the reported movement of 17 km (14 km) remains unverified.

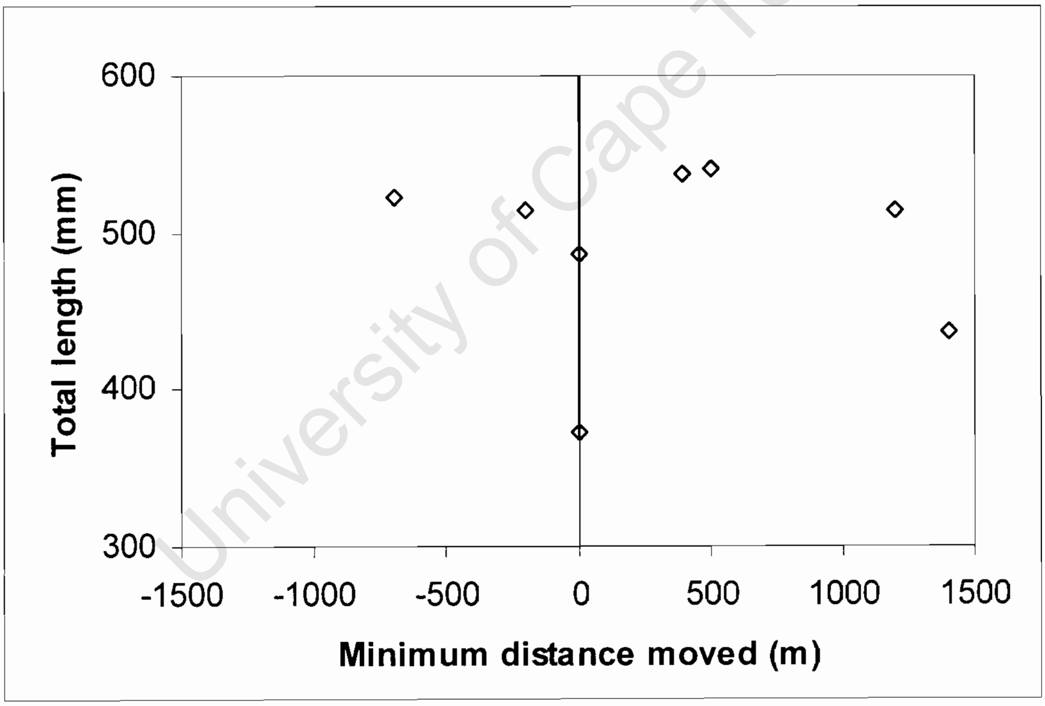


Fig. 5.3: Minimum distance moved vs. total length for eight *Umbrina robinsoni* tagged and recaptured within the De Hoop MPA where the site of release and recaptured was recorded to within 100 m.

The number of *U. robinsoni* at each GPS marked site and the number removed during each sampling trip to the Maputaland MPA are shown in Fig. 5.4. At all the sites where *U. robinsoni* were found, shoals occupied a cave or overhang, usually with a sand bottom, in moderate profile reef. Observations during the eight-month sampling period showed serial depletion of the number of fish at each site (Fig. 5.4). At sites where all observed fish were removed during the first (May 2001) sampling trip (BN 2 & 3), no or very few fish were found on subsequent sampling trips. At sites where a proportion of the shoal was not removed by sampling, (BN 1, 4, 5 & 6) the number of fish found on subsequent trips was approximately equal to this proportion.

A plot of the difference in the number of fish remaining at each site after a sampling event, and found during the subsequent trip to the site, versus time indicate no or very little net movement of fish between sites or from other areas (Fig 5.5). The coefficient of determination value (r^2) is not significant (t-test, $P > 0.05$); indicating no statistical relationship between numbers and time and hence low rates of immigration and emigration (Fig. 5.5). The presence of spear scars on fish at several of the sites confirmed that at least some of the remaining fish were survivors of previous sampling events. Removal of these fish resulted in the absence of the species at these sites during subsequent trips. A follow up trip to monitor recovery of shoals sampled in this area was undertaken during January 2003 (20 months after the first sampling trip and 12 months after the last sampling trip). Very little recovery of sampled shoals was apparent; at four of the reef sites where all fish had been removed (BN 1-3, 6), no recovery had occurred. At the two sites (BN 4 & 5) where a few fish had remained (4 and 1 fish) recovery was limited (6 and 13 fish counted) and was by smaller individuals (< 30 cm TL). Site BN 7 was anomalous in that the reef had sanded over by the January 2003 trip and no *U. robinsoni* were found. It appears that *U. robinsoni* will not readily reoccupy vacant reefs and even when some individuals remain, and recovery (via recruitment of young fish or immigration of older fish) is slow.

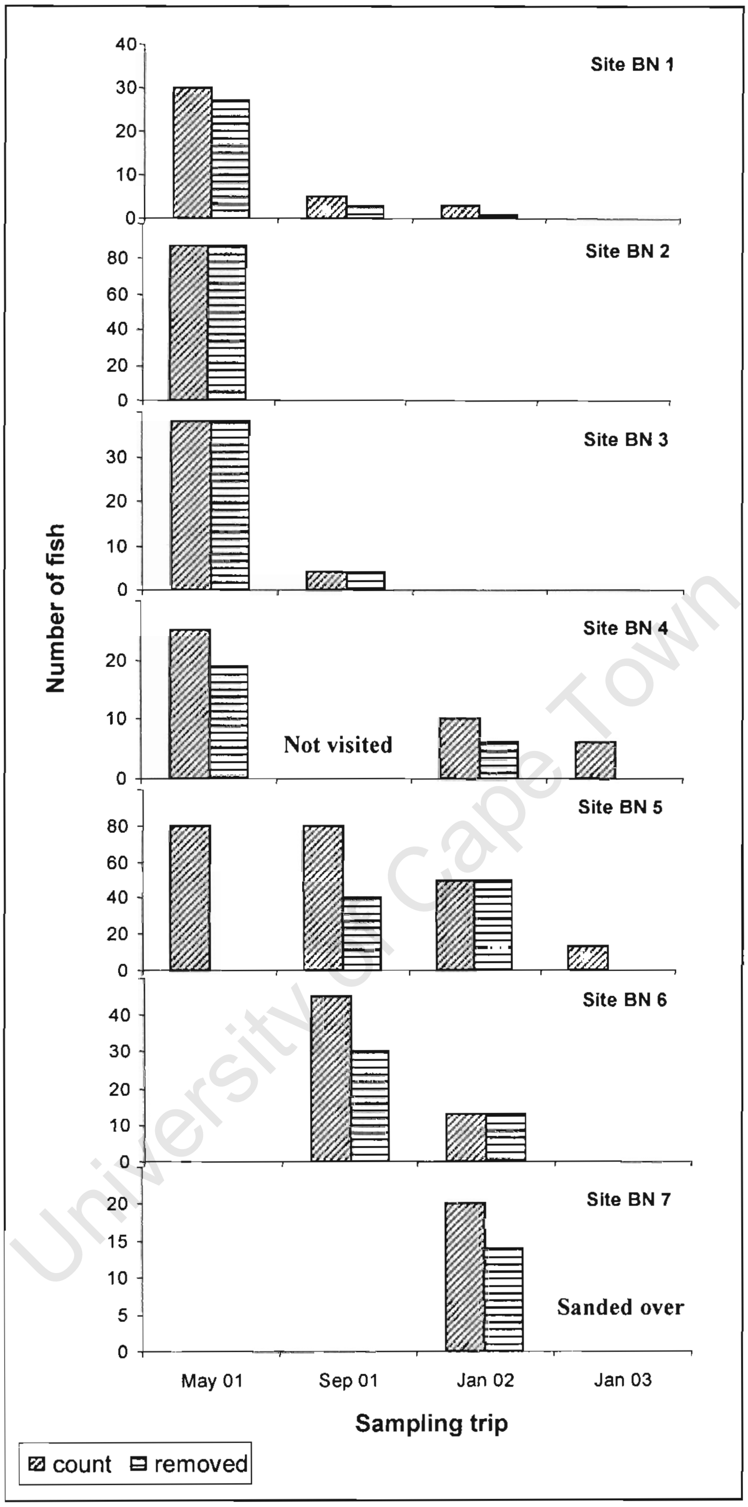


Fig. 5.4: Number of *Umbrina robinsoni* counted and removed by sampling at seven reef sites (BN 1-7) within the St Lucia-Maputaland MPA.

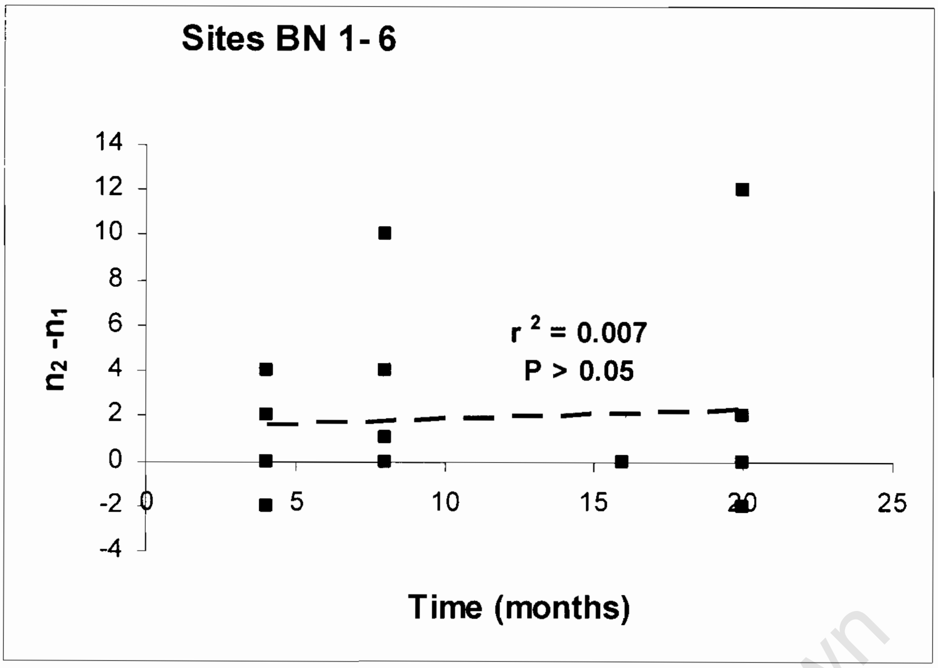


Fig. 5.5: Relationship between the difference in the number of *Umbrina robinsoni* counted at specific reef sites within the Maputaland MPA minus the number counted at the end of the previous sampling trip (n_2-n_1) and time (months).

DISCUSSION

Data from the De Hoop tagging study showed no evidence of *U. robinsoni* movement between the three tagging sites (> 10 km) and no recaptures were reported from outside the reserve. The maximum within site displacement observed was just 1400 m; a scale of movement considerably less than that recorded for other South African surf-zone teleosts that are considered resident. For example, juvenile white steenbras (*Lithognathus lithognathus*), and dusky kob (*Argyrosomus japonicus*) are considered resident within surf-zone habitats, whilst the adults undertake extensive eastwards spawning migrations (Bennett 1993, Griffiths 1996b). Although the majority of tagged juveniles of these species have been recaptured close to the site of release, movements of the order of tens to hundreds of kilometres have been recorded (Griffiths 1996b, Cowley 1999, Griffiths and Attwood in press.). Numerous individuals of other teleost species, e.g. white steenbras, dusky kob, galjoen (*Dichistius capensis*) tagged within the De Hoop MPA have been recaptured at the alternative site from which they were released and outside the MPA boundaries (C. G.

Attwood, Marine and Coastal management, pers. comm.). This suggests that *U. robinsoni* is one of the more philopatric species inhabiting the De Hoop surf-zone.

The unverified evidence of larger scale movement from the Sedgwick's/ORI/WWF Tagging Project, however, indicates that there may be a nomadic/ranging component to *U. robinsoni* populations, but even in this instance the scale of coastal movement is limited (5-17 km). Attwood and Bennett (1994) analysed the spatial and temporal distribution of galjoen recaptures from fish tagged within the De Hoop MPA. The majority (82 %) of recaptures were made within 5 km of the release sites, whilst the remainder were made outside of the reserve boundary (25-1450 km displacement). Based on the results of modelling exercises, Attwood and Bennett (1994) concluded that the De Hoop galjoen population was polymorphic with respect to dispersal behaviour (although Attwood and Cowley (2005) recently proposed an alternative "tourist" model which could also explain galjoen recapture distributions). This pattern of recapture distributions (i.e. a large resident component and smaller dispersing proportion) is not uncommon and has been noted in numerous resident South African reef-fish species, particularly amongst Sparids (Brouwer *et al.* 2003, Griffiths and Wilke 2002, Cowley 1999) and also for the sciaenid, silver kob (*Argyrosomus inodorus*) (Griffiths 1997a). Polymorphism with respect to dispersal behaviour is generally believed to be either adaptive (genetic), allowing for colonization of vacant or new habitats and serving to increase gene flow amongst resident populations (Shields 1984), or conditional as a natural feed–back mechanism of population density control (Stenseth 1984). The two *U. robinsoni* recaptures that had moved some distance from the release site represent only 7 % of all recaptures. This suggests that if there is a ranging morph amongst *U. robinsoni* populations, it is a small proportion that in any case does not move extensively.

A home range is defined as a specific area repeatedly used by individuals during their daily activities (Burt1943, Jewell 1966). The availability and distribution of resources (principally food) is thought to be the primary determinant of home range size (Mace *et al.* 1984). Based on the data from the tag-recapture studies it appears that *U. robinsoni* have small (< 1 500 m) home ranges. Multiple recaptures or telemetry tracking over short time periods are, however, necessary to confirm this (Griffiths and Wilke 2002). Single recaptures only give information on the location of a tagged fish at two discrete points in time and not on the fish's movements during the interim period. On the other hand, diving observations in the St Lucia-Maputaland MPA during sampling trips do provide considerable support for the hypothesis of small home ranges for *U. robinsoni* populations. The presence of apparently the same fish at specific sites associated with an identifiable physical feature (cave or overhang) over periods of days (within trip observations) to up to 20 months indicates that adult *U. robinsoni* are highly philopatric (home loving). Physical shelter appears to be a habitat prerequisite (most likely necessary for reducing predation) for *U. robinsoni*. Diving observations elsewhere on the South African coast confirm that this habitat requirement is not limited to subtropical *U. robinsoni* populations in MPAs (personal observation, M. H. Griffiths pers. comm.). Counts of the number of fish removed at sites and the number remaining on subsequent trips showed no movement between sites, or from other areas, despite the fact that distances between sites were small (in many instances < 5 km). In the light of the philopatric behaviour observed at the Kosi Bay sites, it is proposed that the limited displacements (0-1400m) observed for tag-recaptured De Hoop fish represent movements within a small home-range during foraging activities.

Environmental differences between the two sites are also expected to influence movement behaviour. The physical nature of rocky reefs differs noticeably between the two MPAs, with most of the patch reefs from which *U. robinsoni* were sampled at the Maputaland MPA being at depths of 8-20m and temporally persistent features; whilst rock patches at the De Hoop site occur almost exclusively at depths less than 6 m (within the surf-zone) and extensive sand movement causes them to be covered and uncovered on temporal scales of hours to years (Bennett and Attwood 1991). Water temperature and diurnal periodicity at the warm temperate De Hoop sites also vary more seasonally than those at the sub-tropical Maputaland MPA sites and significant life-history differences have been detected between the two populations (Chapter 4). Given the more dynamic environment at De Hoop, movement of *U. robinsoni* individuals is expected to be greater than at the Maputaland sites. However, evidence from the De Hoop tagging study suggests that adult *U. robinsoni* in this region, despite the more dynamic environment are also highly resident within a small area (over periods of liberty of up to four years).

The St Lucia-Maputaland MPA is a long established reserve and fish populations in the area sampled are believed to be at, or near to, carrying capacity. Given the large aggregations at the sites that were sampled these were clearly ideal habitats for *U. robinsoni*. Sites vacated by depletion sampling were not reoccupied, even over a relatively long time interval (20 months) and despite the fact that there are undoubtedly other *U. robinsoni* shoals within the 156 km long reserve and offshore of the 20 m depth contour (*U. robinsoni* is known to occur down to 45 m depth), (Chapter 1). Horn (1984), notes that individuals who disperse to openings formed by the extermination of local populations will have a selective advantage over individuals that do not disperse. Dispersal in a patchy habitat complex (such as the distribution of suitable reef shelter inhabited by *U. robinsoni*) is however a risky strategy, with individuals that leave a familiar home range to disperse through unknown territory subject to an increased risk of predation (Stenseth 1984). For *U. robinsoni*, the costs of adult ranging (*inter alia* the increased risk of predation) apparently outweigh the potential gains (increased access to resources through reduced intraspecific competition). The passive movement of planktonic eggs and larvae appear to be the principal means of dispersal in the species. The presence of small fish (< 30 cm TL) at the two sites that showed limited recovery (BN 4 & 5) suggests that vacant habitat is colonized via recruitment of young fish from nursery areas (natal dispersal) rather than by movement of adults.

The resident nature, philopatric behaviour and apparently small home-range length of *U. robinsoni* has clear implications for the management of the species. Movement of adults between spatially separate populations is highly unlikely, and interchange between stocks appears to be limited to egg and larval dispersal. The spatial scale of interchange will be largely dependent on regional oceanographic features and the duration and behaviour of the planktonic phase of *U. robinsoni* eggs and larvae. Brouwer *et al.* (2003) measured current strength and direction off the Tsitsikamma MPA on the South African east coast and determined that the eggs and pre-flexion larvae of carpenter (*Argyrozona argyrozona*) could potentially be dispersed several hundred kilometres (42-583 km) during a 30 day planktonic phase. *U. robinsoni* eggs collected in surface plankton net hauls along the KZN south coast hatched in tanks within 24 hours of collection, flexion of the planktonic larvae occurred at 19-20 days post collection and settlement of the larvae (i.e. movement out of the water column to the bottom of the tank) occurred at 25-30 days (A. Connell, Council for Scientific and Industrial Research, pers. comm.). A 1200 MHz Acoustic Doppler Current Profiler (ADCP) moored in 17 m water depth off Black Rocks (27°07' S, 32°51 E, 4 km south of our sampling area) within the Maputaland MPA for the period December 2003-March 2004 revealed a net average (over 3 month period) southward flowing current with an average velocity of 2.45 $cm.s^{-1}$ in the top 5 m of the water column (Reaugh in prep.). This translates into an average potential displacement of planktonic *U. robinsoni* propagules (eggs and larvae) of 53-63 km over 25-30 days during the summer months. Post-flexion larvae of some teleosts undertake vertical migrations or actively swim towards reef habitat and recent research suggests that local retention of larvae and self-recruitment is considerably more widespread than was previously thought (Richards and Lindeman 1987, Leis 1991, Swearer *et al.* 2002, Sponaugle *et al.* 2002, Warner and Cowen 2002, Brouwer *et al.* 2003, Cowen *et al.* 2003, Codling *et al.* 2004). The Black Rock ADCP data revealed a northward flowing counter current in the bottom 10 m of the water column (mean velocity = 1.09 $cm.s^{-1}$). If post-flexion *U. robinsoni* larvae undertake vertical migrations, dispersal within the MPA could be limited to as little as 33-38 km. Studies on the genetic structure of spatially separate *U. robinsoni* populations could potentially provide further information on the dispersal of eggs and larvae in other region.

U. robinsoni populations are extremely vulnerable to localized depletion, being predictable in their distribution and resident at specific reef features (Buxton 1996, Griffiths 2000). Recovery of exploited populations was observed to be slow and reliant on recruitment of juveniles rather than movement of adults from unexploited areas. *U. robinsoni* take 2-3 years to attain the current minimum legal size limit (40 cm TL) (Chapter 4.) and assuming sufficient spawner stock remains in up-current areas to ensure a supply of eggs and larvae, this sets the minimum time period for recovery of a completely denuded population. This may partly explain why Bennett and Attwood (1991) failed to detect a significant increase in the catch-rate of *U. robinsoni* four years after proclamation of the De Hoop MPA. Recent *U. robinsoni* catch rates recorded during 2001-2002 sampling within the De Hoop MPA (0.4 $fish.angler\text{-}hour^{-1}$), however, are considerably greater than in adjacent exploited areas (0.004 $fish.angler\text{-}hour^{-1}$) (Lamberth 1997). Given the highly resident nature and apparent small home-range length of *U. robinsoni*, the species can be expected to derive protection from even small MPAs and natural refuges. Although fisheries adjacent to MPAs or natural refuges will not benefit from emigration of adult *U. robinsoni*, the protected spawner-stock in these areas will function as a source of recruits and may maintain catches in exploited areas.

CHAPTER 6

POPULATION GENETIC STRUCTURE OF SOUTH AFRICAN *UMBRINA ROBINSONI* (SCIAENIDAE) BASED ON SEQUENCE ANALYSIS OF THE MITOCHONDRIAL DNA CONTROL REGION

ABSTRACT

Umbrina robinsoni is a large sciaenid with a broad distribution along the east African coast from Cape Point, South Africa to the coast of Oman. Off the South African coast, *U. robinsoni* inhabits inshore waters (0-40m), exhibits philopatric behaviour to specific reef sites and significant morphological and life-history differences between spatially separated populations have been found, suggesting that the South African population comprises several allopatric stocks. The genetic integrity of putative *U. robinsoni* stocks along the South African coast was investigated by analysis of mitochondrial DNA (mt DNA) control region sequences (350 base pairs) from samples collected at three sites, False Bay (n = 40), Stil Bay (n = 41) and Kosi Bay (n = 42). Thirty-five haplotypes were identified in the 123 individuals sampled and levels of mtDNA diversity were high (haplotype diversity = 0.89, nucleotide diversity = 1.4 %). Haplotypes were not randomly distributed amongst the sampled sites ($X^2 = 113$, $P < 0.001$), and there was an indication of a relationship between haplotype geneology and geographic location evident in a minimum spanning network. Analysis of Molecular Variance, however, allocated only 2 % of the variation between sampling sites and the overall fixation index was not significant ($F_{ST} = 0.021$, P = 0.089). Population pairwise F_{ST} values, although also not significant at the 5 % level, did indicate substantially higher levels of gene flow between the False Bay and Stil Bay ($F_{ST} = 0.0001$) populations than between either of these two populations and the geographically more distant Kosi Bay population ($F_{ST} = 0.0326$ and $F_{st} = 0.0274$ respectively). Removal of eight identified homoplasic sites elevated the population pairwise F_{ST} values for comparisons between Kosi Bay and the other two sites and the value for the False Bay-Kosi Bay comparison was then significant ($F_{ST} = 0.0486$, P = 0.035). The findings strongly suggest an isolation by distance pattern of genetic structure amongst South African *U. robinsoni* populations. Analyses of additional samples from other locations along the South African coast and interpretation of data from independent loci are, however, required to confirm this and further elucidate patterns of gene flow amongst South African *U. robinsoni* populations.

INTRODUCTION

The apparent absence of barriers to gene flow in the marine environment, coupled with the broad distribution, planktonic dispersal of eggs and larvae and the high adult mobility of most marine fishes suggest that low levels of intraspecific population genetic structure would be the norm (Palumbi 1992, Graves 1998, Waples 1998). Indeed, levels of genetic divergence amongst intraspecific marine fish populations (often separated over large spatial scales) are generally substantially lower than those found between anadromous and freshwater fish populations and often orders of magnitude less than those between populations of terrestrial organisms (Ward *et al.* 1994, Graves 1998). Despite the large dispersal potential of marine organisms, this does not necessarily translate into high levels of gene flow between geographically separated populations (Avise 1998) and genetic structure at the population level have been detected in numerous species. Recent examples amongst marine teleosts include milkfish *Chanos chanos* (Ravago-Gotanco and Junio-Menez 2004), damselfish *Dascyllus trimaculatus* (Bernadi *et al.* 2003), sea bass *Dicentrarchus labrax* (Lemaire *et al.* 2005), grouper *Epinephelus polyphekadion* (Rhodes *et al.* 2003), Indo-Pacific tasselfish *Polynemus sheridani* (Chenoweth and Hughes 2003) and red drum *Sciaenops ocellatus* (Gold *et al.* 1999, Gold and Turner 2002). Physical oceanographic processes (currents, fronts and eddies) and life history or behavioural characteristics (e.g. philopatry, duration of the planktonic phase and survival of eggs and larvae, site specific spawning aggregations) are potential mechanisms that may impede gene flow and result in genetic heterogeneity over various temporal and spatial scales (Palumbi 1997, Rhodes *et al.* 2003).

Identification of fish stocks, estimates of the level of gene flow (or reproductive connectivity) between stocks and the conservation of genetic diversity are pertinent management questions for which genetic techniques are most frequently employed (Graves 1998, Waples 1998). In essence, evidence of population level genetic structure, which is indicative of reduced levels of gene flow, is used to infer demographic independence of spatially separated stocks (management units) (Avise 1995). Employing the simple island model of migration (Wright 1943), measures of gene diversity allocated amongst populations (e.g. F_{ST}) are frequently used to estimate the number of genetically effective migrants received by each population per generation (e.g. Gold *et al.* 1999, Naciri *et al.* 1999). Although this approach has numerous limitations in the case of marine species with large populations and high gene flow (Waples 1998); stocks that exhibit genetic heterogeneity (and are thus largely self-recruiting) are unlikely to recover from over-fishing via recruitment from other areas, at least over ecological timescales pertinent to management (Avise 1995, Rhodes *et al.* 2003, Waples 1998). In marine fishes with continuous linear distributions, a pattern of isolation by distance, or one-dimensional stepping-stone model of population structure is frequently observed (Kimura and Weis 1964), whereby gene flow occurs mainly between neighbouring populations, (Gold *et al.* 1999, Gold and Turner 2002, Ravago-Gotanco and Junio-Menez 2004).

The haploid nature, absence of recombination and rapid rate of evolution of the mitochondrial DNA (mtDNA) control region make it a particularly useful marker for population level genetic studies (Beckenbach 1991). Analyses of the mtDNA control region have been shown to be effective in detecting population level genetic structure in numerous marine fish species (e.g. Seyoum *et al.* 1999, Bernardi *et al.*2003, Bernardi and Vagelli 2004, Chenoweth and Hughes 2003, Ravago-Gotanco and Junio-Menez 2004). Studies on the population genetics of South African line-fish species are a relatively recent undertaking. Analysis of the mtDNA control region of dusky kob *Argyrosomus japonicus*, spotted grunter *Pomadasys commersonnii*, (Klopper 2005) and Cape stumpnose *Rhabdosargus holubi* (Oosthuizen, Department of Genetics, University of Pretoria pers. comm.) have revealed little or no spatial heterogeneity in concordance with known life histories.

Temperate and subtropical South African *Umbrina robinsoni* populations, however, have been shown to have significant differences in morphology, otolith structure and life-history strategies (Chapter 4). Although these differences strongly indicate that spatially separate populations need to be treated as separate management units (or stocks), they may simply reflect phenotypic plasticity in response to the differing physical and biological environmental conditions. The inshore distribution of the species, patchy habitat complex (Chapter 1), resident/phylopatric nature of adults and apparent limited dispersal of planktonic eggs and larvae (Chapter 5), however, suggests that there may be a degree of reproductive isolation (and hence population level genetic structure) amongst spatially separate populations. If this is indeed the case, the management implications are clear, in that locally/regionally overexploited populations are unlikely to recover through recruitment from geographically distant populations. In this study, levels of genetic diversity and spatial differentiation among *U. robinsoni* samples collected at three sites (False Bay, Stil Bay and Kosi Bay) along South Africa's eastern seaboard (Fig. 6.1) were investigated through analysis of mtDNA control region sequences.

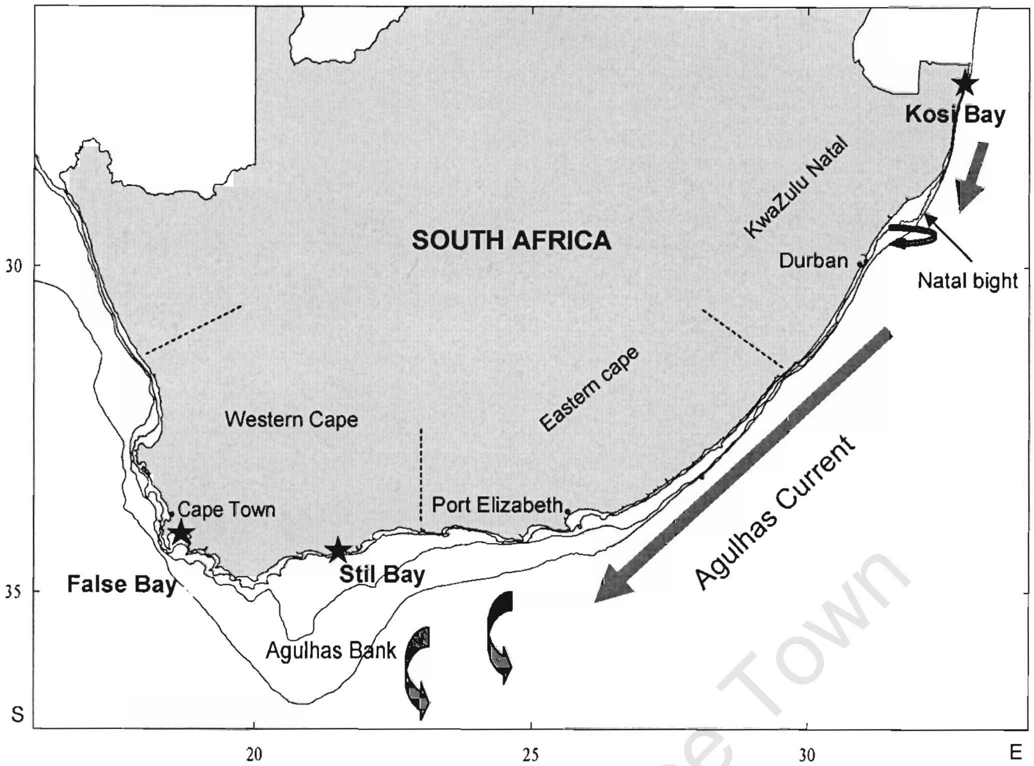


Fig. 6.1: Map of South Africa showing the three sampling localities (stars), oceanographic features and places mentioned in the text

MATERIAL AND METHODS

Sampling

Tissue samples (gill filament, fin clip or skeletal muscle) were taken and preserved in 97 % ethanol from *U. robinsoni* captured for a biological sampling survey during 2001-2003 at three sites, False Bay, Stil Bay and Kosi Bay (Fig. 6.1) along the east coast of South Africa. Fish from False Bay (the most south-westerly extent of the species distribution) were obtained from commercial and research beach-seine and shore angler catches made predominately within the surf-zone, whilst Stil Bay and Kosi Bay samples were obtained by means of spear fishing on near-shore sub-tidal reefs. The total coastline distance between the temperate False Bay and Stil Bay sites is 402 km and the subtropical Kosi Bay site is 2024 km from False Bay.

DNA extraction and amplification

Total genomic DNA was extracted from preserved tissue samples using the protocol described by Estoup *et al.* (1996). Polymerase chain reaction (PCR) (Saiki *et al.* 1988) was used to amplify, initially the full length of the mtDNA control region. Oligonucleotide primers were initially used (PerDLL$_2$ - 5' AGC GCC GGT CTT GTA AAC CG 3' and DLH$_2$ - 5' CAT CTT AAC AGC TTC AGT G 3') that have previously proved successful for amplification of the mtDNA control region for two other South African sciaenid species (A. Klopper, Department of Genetics, University of Pretoria, pers. comm.). Amplification using these primers was often unsuccessful and inconsistent and species specific primers (based on the sequences obtained using the above mentioned primers for 43 individuals) were designed and used for further PCR reactions. The new forward primer, MDLL (5' CCC CCA CCA CTA ATT CCC 3') binds adjacent to the control region within the flanking proline tRNA. The reverse primer, UIntH (5' GGA ACC AAA TGC CAG GAA TAG 3') binds to the central conserved block within the control region. The PCR mixture consisted of 2-5 µl DNA extract (50-150 ng), 2 mM $MgCl_2$, 0.2 mM of each dNTP (Nucleotides, Promega), 10 pmols of each primer, 1.5 U Supertherm DNA polymerase (Taq polymerase, Southern Cross Biotechnology) and 5 µl 10 x reaction buffer made up to a final volume of 50 µl with ultra-high quality purified water. Amplifications were performed on a thermal cycler (Applied Biosystems, model 2720) with the following program: initial 5 min. denaturing step (94°C), followed by 35 cycles consisting of 20s at 94°C, 20s at 57°C (primer annealing), and 20s at 72°C (extension), and a final extension step of 5 min at 72°C. In order to verify successful amplification, PCR products were visualized under UV light on 1 % agar gels (buffered with Tris-borate EDTA (TBE) and stained with ethidium bromide). Successfully amplified PCR products were purified using a sodium acetate precipitation method and the DNA pellet resuspended in15-30 µl water. Following precipitation, DNA was once again visualized on agar gels under UV light.

Sequencing

Sequencing reactions were performed with both the forward and reverse primers (1.6 pmol) using the Big Dye® Terminator Cycle Sequencing Kit (Applied Biosystems) on a thermal cycler (Applied Biosystems, model 2720) using the Big Dye® program. Cycle sequenced products were purified using the same sodium acetate precipitation protocol as for PCR products with the exception that the DNA pellet was resuspended in Hi-Di^{TM} formanide before loading in the ABI 3100 automated sequencer (Applied Biosystems). Sequence Navigator^{TM} ver. 1.01 software (Applied Biosystems 1994) was used to align electropherograms of both sequencing reactions in order to check ambiguous bases. The resulting consensus sequence for each individual was then used to perform a multiple sequence alignment of all individuals in Clustal X version 1.8 (Thompson *et al.* 1997). All mutations identified were again checked against the original electropherograms to ensure accuracy.

Analysis

Aligned sequences of all individuals were imported into the software program ARLEQUIN 2.000 (Schneider *et al.* 2000) for population level analyses. Within sampling locality genetic diversity was estimated by haplotype diversity, h (Nei 1987), a measure of the probability that any two individuals drawn at random from a population have different nucleotide sequences, and nucleotide diversity Π (Tajima 1983, Tajima 1993), a measure of the probability of a mutation at a specific nucleotide position, calculated as the mean number of pairwise differences between specimens. Between sampling locality diversity was estimated as net nucleotide sequence divergence d (Reynolds *et al.* 1983, Slatkin 1995). In order to visually examine genealogical relationships among haplotypes, their frequencies at localities and pairwise differences (number of observed nucleotide substitutions among haplotypes) obtained from ARLEQUIN were used to construct a minimum spanning network.

A genetic marker affected by selection cannot be used to infer reproductive isolation from population genetic structure. Tajima's D (Tajima 1989) and Fu's F_s (Fu 1997) tests were used to determine whether the mtDNA control region sequences were evolving according to neutral expectations. Significantly negative or positive D or F statistics indicate either the presence of selection, a population expansion after a bottleneck or small founder effect, or secondary contact amongst previously isolated populations (Chenoweth and Hughes 2003).

To test the null hypothesis of spatial homogeneity of observed haplotype frequencies amongst samples, a X^2 randomization procedure (Roff and Bentzen 1989) was used.

The proportion of total gene diversity allocated among sampling sites was estimated by calculating the fixation index F_{ST} (Wright 1951) and calculating the statistical significance of this value (by random permutation) at the 5 % level. An analysis of molecular variance (AMOVA, Excoffier *et al.* 1992) was performed to partition variance into intra and inter-population components. In order to examine the relationship between genetic differentiation and geographic distance, population pairwise F_{ST} values were plotted against coastline distance between localities. Examination of the minimum spanning network revealed the presence of a number of alternative links indicating homoplasy within the control region. As homoplasic sites introduce ambiguities into the relationship between haplotypes that may obscure any signal of population structure (Avise and Lansman 1983), AMOVA testing and pairwise F_{ST} values were calculated both before and after the removal of eight identified homoplasic sites.

RESULTS

DNA was extracted and the mtDNA control region successfully amplified from 123 *U. robinsoni* specimens from three sampling sites along the South African east coast (Table 6.1). The oligonucleotide primers amplified a 418 bp (base pair) fragment of the mtDNA control region; consistent high quality sequence data was obtained for a 350 bp fragment for all 123 samples and this was used for further analysis. The relative frequencies of nucleotide bases in the fragment were: adenine 37 %, thymine 28 %, cytosine 21 % and guanine 14 %. Amongst all the 123 samples from the three localities the 350 bp fragment had a total of 33 polymorphic sites, consisting of 30 transitions and 3 transversions. One indel occurred within the fragment that consisted of a deletion of a purine (A) in 21 individuals. An alignment of the variable positions is shown in Table 6.2. Tests of the neutrality of the mt DNA control region sequences were not significant (Tajima D = -0.08664, P = 0.55; Fu's F_s = 0.23849, P = 0.461), indicating that the marker is not under selection and the sampled populations do not appear to have undergone historical population growth.

A total of 35 haplotypes were identified amongst the combined South African samples with an overall haplotype diversity (h) of 0.886 ± 0.02 (SD) and a mean nucleotide diversity (Π) of 1.4 % (Table 6.1). Haplotype diversity (h) within sampling localities was lowest for the False Bay sample (0.804) where only 12 haplotypes occurred amongst the 40 individuals sampled and similar for the Stil Bay (0.902) and Kosi Bay (0.897) samples where 18 and 16 haplotypes were found respectively (Table 6.1). Nucleotide diversity (*Π*) within localities was similar among the three sites and ranged from 1.3-1.5 % (Table 6.1).

Table 6.1: Sampling details and intra-regional genetic diversity estimates for *Umbrina robinsoni.*

Locality	Number of sequences	Number of haplotypes	Endemism index (%)	Haplotype diversity (*h*) ± SD	Nucleotide diversity *Π* (%)
False Bay	40	12	33	0.804 ± 0.06	1.3
Stil Bay	41	18	55	0.902 ± 0.03	1.5
Kosi Bay	42	16	81	0.897 ± 0.03	1.5
South Africa	123	35		0.886 ± 0.02	1.4

The three most common haplotypes were found in 54 individuals from all three sampling localities (haplotype numbers 1, 26 and 30), whilst False Bay and Stil Bay samples shared a further five haplotypes (Fig. 6.2). With the exception of the three common haplotypes, False Bay and Stil Bay shared no other haplotypes with Kosi Bay. It follows that the number of private haplotypes was lowest within the False Bay samples and highest within the Kosi Bay samples where 13 out of the 16 haplotypes not found at the other two sites (endemism index Table 6.1).

Table 6.2: Variable sites defining the 35 haplotypes occurring in the 123 *Umbrina robinsoni* individuals that were sampled. The haplotype number (Nr.) and the frequency (F) of individuals that shared a specific haplotype are given. Shaded columns represent identified homoplasic sites

Nr.	F	Variable sites																																
1	38	C	A	G	A	A	T	C	T	A	C	A	A	A	A	T	G	A	T	T	C	A	T	C	A	A	A	A	C	T	A	T	C	C
2	1	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
3	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
4	1	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
5	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.
6	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.
7	2	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
8	4	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
9	1	.	.	.	.	.	.	.	.	.	.	.	.	G	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
10	1	.	.	.	.	.	C	.	.	.	.	.	G	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
11	3	.	.	.	G	.	.	.	.	G	.	.	G	.	.	G	.	.	.	A	T	.	.	.	.	.	.	.	.	.	.	.	.	.
12	6	.	.	.	G	.	.	.	.	G	.	.	G	.	.	G	.	.	.	C	T	.	.	.	.	.	.	.	.	.	.	.	.	.
13	4	.	.	.	G	.	.	.	.	G	.	.	G	.	.	G	.	.	.	C	T	.	.	.	G	G	.	.	.	.	.	.	.	.
14	4	.	.	.	G	.	.	.	.	G	.	.	G	.	.	G	.	.	.	C	T	.	.	.	.	.	G	.	.	.	.	.	.	.
15	1	.	.	.	.	.	.	.	.	G	.	.	G	.	.	G	.	.	.	C	T	.	.	.	.	.	.	.	.	.	.	.	.	.
16	1	.	.	.	G	.	.	.	C	G	.	.	G	.	.	G	.	.	.	C	T	.	.	.	.	.	.	.	.	.	.	.	.	.
17	2	.	.	A	G	.	.	.	.	G	.	.	G	.	G	G	.	.	.	C	T	.	.	.	.	.	.	.	.	.	.	.	.	.
18	7	.	.	.	G	.	.	.	.	G	T	.	G	.	.	G	.	.	.	C	T	.	.	.	.	.	.	.	.	.	.	.	.	.
19	1	.	.	.	.	.	.	.	.	G	T	.	G	.	.	G	.	.	.	C	T	.	.	.	.	.	.	.	.	.	.	.	.	.
20	7	.	.	.	G	.	.	.	.	.	.	.	G	.	.	G	.	.	.	C	T	.	.	.	.	.	.	.	.	.	-	.	.	.
21	1	.	.	.	.	.	.	.	.	.	.	.	G	.	.	G	.	.	.	C	T	.	.	.	.	.	.	.	.	.	-	.	.	.
22	1	.	.	.	G	.	.	.	.	.	T	.	G	.	.	G	.	G	.	C	T	.	.	.	.	.	.	G	.	.	-	.	.	.
23	1	.	G	.	G	.	.	.	.	.	.	.	G	.	.	G	.	.	.	C	T	.	.	.	.	.	.	.	.	.	-	.	.	.
24	1	.	G	.	G	.	.	.	.	.	.	.	G	.	.	G	.	G	.	C	T	.	.	.	.	.	.	.	A	.	-	.	.	.
25	1	.	.	.	G	.	.	.	.	.	.	.	G	.	.	G	.	G	.	C	T	.	.	.	.	.	.	.	A	.	-	.	.	.
26	7	.	.	.	G	.	.	.	.	.	.	.	G	.	.	G	.	.	.	C	T	.	.	.	.	.	.	.	.	C	-	.	.	.
27	1	.	.	.	G	.	.	.	.	.	.	.	G	.	.	G	.	.	.	C	T	.	.	.	.	.	.	.	.	C	-	.	.	T
28	1	.	.	.	G	.	.	.	.	.	.	.	G	.	.	G	.	.	.	C	T	G	.	.	.	.	.	.	.	C	-	.	.	.
29	2	.	.	.	G	.	.	.	.	G	.	.	G	.	.	G	.	.	.	C	T	.	.	T	.	.	.	.	.	.	.	.	.	.
30	10	.	.	.	G	.	.	.	.	G	.	.	G	.	.	G	.	.	.	C	T	.	.	T	.	G	.	.	.	.	.	C	.	.
31	1	.	.	.	G	G	.	.	.	G	.	.	G	.	.	G	.	.	.	C	T	.	.	T	.	G	.	.	.	.	.	C	.	.
32	2	.	.	.	G	.	.	.	.	G	.	.	G	.	.	G	.	.	C	C	T	.	.	T	.	G	.	.	.	.	.	C	.	.
33	1	.	.	.	.	.	.	.	.	G	.	.	G	.	.	G	.	.	.	C	T	.	.	T	.	G	.	.	.	.	.	C	.	.
34	1	.	.	.	G	.	.	.	.	G	.	G	G	.	.	G	.	.	.	C	T	.	.	T	.	G	.	.	.	.	.	C	.	.
35	1	.	.	.	G	.	.	.	.	G	.	G	G	.	G	G	.	.	.	C	T	.	.	.	.	G	.	.	.	.	.	.	.	.

The most common haplotype (number one) had a number of rare, mostly private haplotypes (numbers 2-10) radiating from it that were separated by one or two mutational steps (Fig. 6.2). The largest break (five mutational steps) in the haplotype genealogy occurred between the most common haplotype (number one) and a cluster of closely related haplotypes (numbers 11-19 and 29) that were almost exclusively found within the south-western Cape samples (False Bay and Stil Bay). Two other clusters of haplotypes were weakly separated (one and two mutational steps respectively) from the SW Cape group. The first cluster contained haplotypes that were overrepresented in samples from Kosi Bay (haplotypes 20-23 and 26-27); whilst the other cluster contained the second most common haplotype that was found in all three localities (number 30). Although there is some indication of a relationship between haplotype genealogy and geographic location, the pattern is not clear with clusters of closely related haplotypes found predominately at specific sites only separated by one or two mutational steps from haplotypes found at other or all sites (Fig. 6.2). The null hypothesis of spatial homogeneity in mtDNA haplotype frequencies amongst the three sampling localities was however rejected ($X^2 = 113$, $P < 0.001$); indicating that haplotypes are not randomly distributed amongst the sampled sites.

Net nucleotide sequence divergence (*d*) values (amongst sampling localities) were similar to intra-regional Π values (Tables 6.1 and 6.3), suggesting that any two randomly selected individuals within a locality differ as much as any two randomly selected individuals drawn from different localities. The very low corrected pairwise difference between the False Bay and Stil Bay samples indicates that these two sites are the most similar, whilst both are divergent from the Kosi Bay site (Table 6.3).

Table 6.3: Inter-regional genetic diversity of *Umbrina robinsoni*. Above diagonal: Average percentage pair wise difference between sampling localities (*d*). Below diagonal: corrected average pair wise difference.

Locality	False Bay	Stil Bay	Kosi Bay
False Bay		1.39	1.42
Stil Bay	0.0007		1.51
Kosi Bay	0.1635	0.1451	

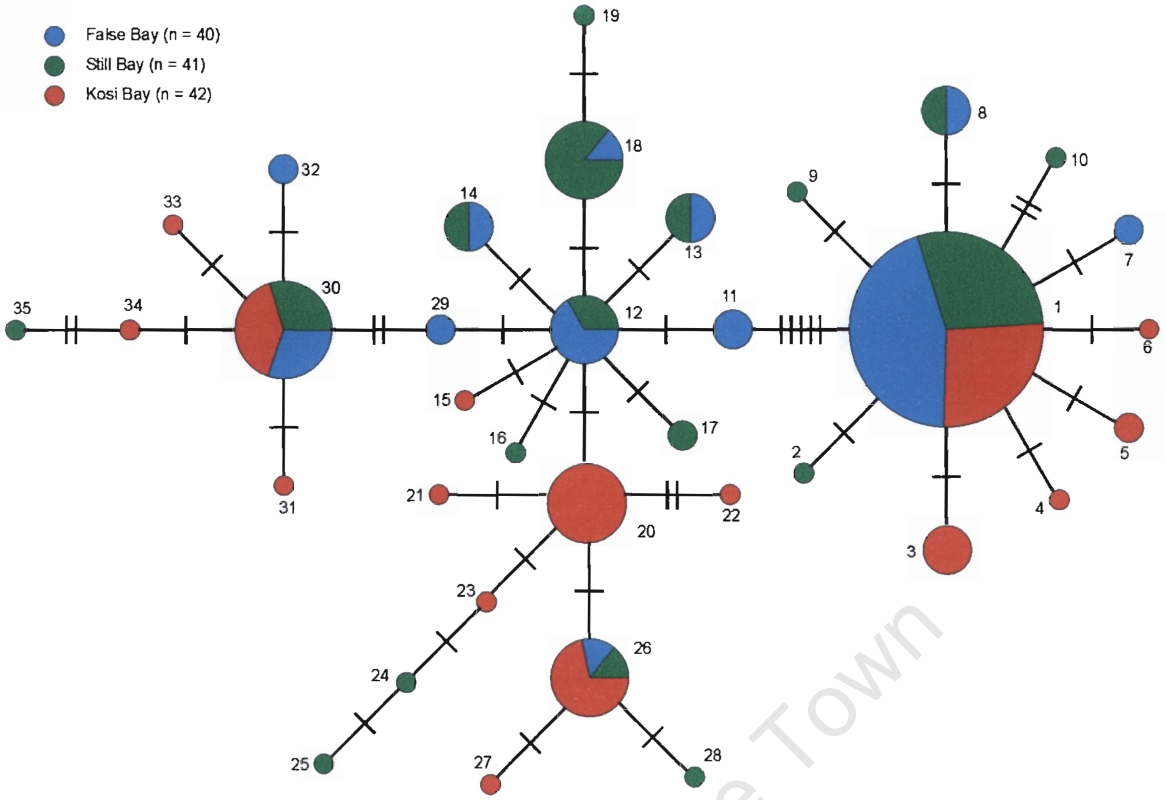


Fig. 6.2: Minimum spanning network of the 35 mt DNA haplotypes detected in *Umbrina robinsoni*. Shading corresponds to the sampling localities in which haplotypes were found and is proportional to the frequency of the haplotype at each locality. The circle diameter is proportional to the haplotypes frequency in the entire sample. Hatch marks on connecting lines indicate the number of mutational steps between haplotypes. Haplotype numbers correspond to those in Table 6.1. Figure adapted from an original byA. Klopper, Department of Genetics, University of Pretoria.

AMOVA revealed that most variation was found among samples within localities (98 %), with only 2 % of the variation allocated between localities. The overall F_{ST} value (0.021) was not significant (P = 0.089), suggesting genetic homogeneity among sampling localities. Removal of the eight identified homoplasic sites (Table 6.2) resulted in 3 % of the variation being allocated amongst localities and increased the overall F_{ST} value to 0.027 which was nearly significant (P = 0.065). Pairwise F_{ST} values prior to the removal of homoplasic sites were also not significant at the 5 % level (Table 6.4), but the low (zero) value obtained for the False Bay-Stil Bay comparison does suggest higher levels of gene flow between these to sampling localities than between the SW Cape and the geographically distant Kosi Bay site. Pairwise F_{ST} values for the False Bay-Kosi Bay and Stil Bay-Kosi Bay comparisons were elevated somewhat by the removal of homoplasic sites and the value for the former became significantly different from zero indicating some population level genetic structure (Table 6.5). Geographic distance between sites and inter-population genetic differentiation (pairwise F_{ST}) were strongly and positively correlated (Fig. 6.3) suggesting an isolation by distance effect. With only three sites sampled, however, the significance of the regression could not be tested (e.g. Mantels test).

Table 6.4: Pairwise F_{ST} and probability (p) values for *Umbrina robinsoni* sampled at three localities prior to the removal of eight identified homoplasic sites. Above diagonal: F_{ST} values. Below diagonal: P values

Locality	False Bay	Stil Bay	Kosi Bay
False Bay		0.0001	0.0326
Stil Bay	0.329		0.0274
Kosi Bay	0.076	0.082	

Table 6.5: Pair wise F_{ST} and probability (p) values for *Umbrina robinsoni* sampled at three localities subsequent to the removal of eight homoplasic sites. Above diagonal: F_{ST} values. Below diagonal: P values, * indicates a significant value at $p < 0.05$

Locality	False Bay	Stil Bay	Kosi Bay
False Bay		-0.0035	0.0486
Stil Bay	0.384		0.0321
Kosi Bay	0.035*	0.078	

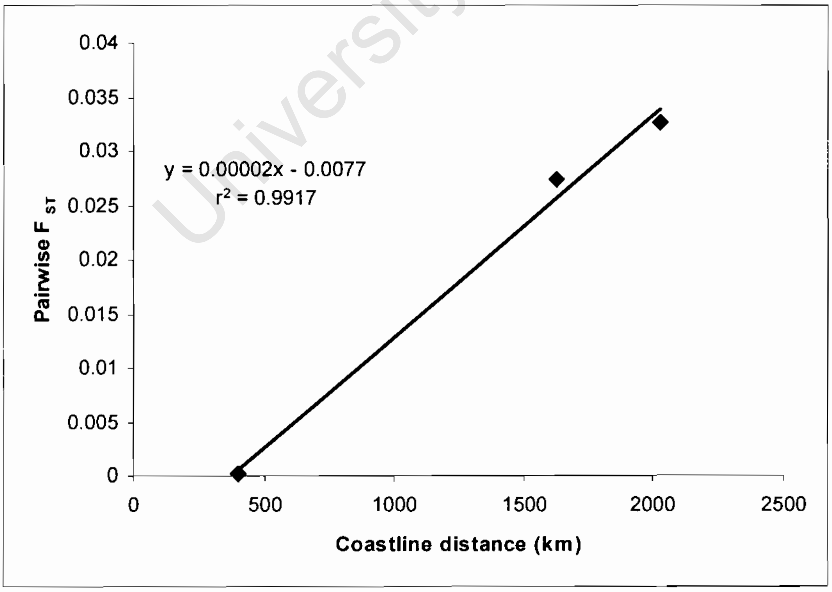


Fig. 6.3: Relationship between genetic differentiation (Pairwise F_{ST}) and geographic distance for *Umbrina* robinsoni sampled at three sites off the South African coast

DISCUSSION

The high levels of mtDNA genetic diversity found for South African *U. robinsoni* are similar to those observed in other marine teleosts. High levels of genetic diversity are expected in species that have large, stable population sizes, but may also be due to secondary contact of previously differentiated allopatric lineages (Grant and Bowen 1998). The haplotype diversity (*h*) values reported here for *U. robinsoni* populations are somewhat lower than those observed for the migratory sciaenids *Argyrosomus japonicus* (range = 0.93-0.98, Klopper 2005) and *Sciaenops ocellatus* (0.95-1, Seyoum *et al.* 2000, Gold *et al.* 1994), but greater than that reported for *Pogonius cromis* (0.78 Gold *et al.* 1994). The nucleotide diversity (Π) values, however, are higher than those found for *A. japonicus* (0.81-0.97 %), *P. cromis* (0.25-0.35 %) and *S. ocellatus* (0.45-0.71 %) (Gold *et al.* 1994, 1999). This inter-specific variation in mtDNA diversity probably reflects inter-specific differences in the evolutionary history and the genetically effective number of female parents of the individuals sampled in the different studies.

There was some variation in intra-population mtDNA diversity among *U. robinsoni* samples, with the False Bay sample having lower levels of haplotype and nucleotide diversity than the Stil Bay and Kosi Bay samples (Table 6.2). If mtDNA sequence evolution and generation times are assumed to be constant amongst localities, differences in mtDNA diversity most probably reflect historical differences in effective female population size (Avise *et al.* 1988, Gold *et al.* 1994). Large populations are expected to have higher levels of genetic diversity than small populations, as the loss of diversity due to drift is slower and mutations accumulate over time (Hauser and Ward 1998). The False Bay population is at the south-western extreme of the species western Indian Ocean distribution (Chapter 1); therefore environmental conditions are expected to be marginal and effective (historical and current) populations sizes may well be smaller than at the other two sampled localities. It is also likely that the number of migrants received by the False Bay population from other populations would be very small and unidirectional and would therefore receive fewer "new" mtDNA haplotypes compared with the Stil Bay and Kosi Bay populations that are more central within the species distribution. There is also the possibility that the reduced level of mtDNA diversity in the False Bay population is due to a large decrease in effective population size caused by fishing mortality, as this site has been exposed to the longest and most intensive history of exploitation.

The primary objective of this study was to ascertain whether the phenotypic and life-history differences between spatially separated *U. robinsoni* populations were reflected in the inter-population genetic structure. For species such as *U. robinsoni* with linear distributions and single generation dispersal distances that are substantially less than the distributional range of the species (Chapter 5), population level genetic heterogeneity consistent with an "isolation by distance" pattern is anticipated (Slatkin 1993, Avise 1995). Heterogeneity of *U. robinsoni* haplotype frequencies across the three sampling localities and an indication of a relationship between haplotype genealogy and geographic location evident in the minimum spanning network did indicate the presence of population genetic structure. The results of other statistical tests of genetic differentiation amongst localities were, however, inconclusive. The overall F_{ST} value was low (0.021) and not significantly different from zero (P = 0.089), whilst AMOVA allocated 98 % of the variation amongst samples within localities. Marine fish populations in general tend to have very low F_{ST} values, the median value from 57 species reviewed by Ward *et al.* (1994) is just 0.02, a result of large effective population sizes and generally high levels of gene flow among populations or stocks (Waples 1998). The overall F_{ST} value estimated for *U. robinsoni* is equivalent to the reported median value, but more than 10 times the value estimated for a migratory South African sciaenid *A. japonicus* (Klopper 2005) indicating a greater level of genetic structure amongst resident *U. robinsoni* populations.

Several factors could lead to a failure to detect statistically significant genetic differences amongst putative stocks. Carvalho and Hauser (1995) provide the following:

1. sufficient (current or historical) gene flow that maintains panmixia (but may be insufficient to affect the demographic independence of populations);
2. sporadic recruitment events from distant populations that could lead to the appearance of genetic homogeneity;
3. stabilizing selection due to similar environmental conditions experienced by populations

4. recent divergence of populations, (which is especially pertinent to analysis such as this one based on a neutral locus in species with large population sizes that are likely to experience slow rates of genetic drift and take a substantial time to reflect differentiation);
5. the molecular technique employed or insufficient sample size.

Little can be done to enhance a signal of population level structure that may be diminished by the first four of the above mentioned factors, but noise in the signal of population structure obtained from genetic data can be substantially reduced by increasing sampling size and considering data from several independent loci (Waples 1998). Waples (1998) showed theoretically that the relative contribution of sampling error to an estimated F_{ST} value declines asymptotically with increases in sample size. With the sample size in this study ($n \sim 40$ individuals per site) and observed level of genetic differentiation, sampling error could constitute as much as 50 % of the F_{ST} estimates. Moderate increases in sample size and the use of data from other independent loci (e.g. microsatellite markers) would substantially increase the power of the statistical tests used to detect potential genetic heterogeneity amongst *U. robinsoni* populations.

Despite the limitations of relatively small sample sizes and the use of only one locus, this study did provide useful information on the spatial extent of gene flow between *U. robinsoni* populations. Pairwise F_{ST} estimates indicated genetic homogeneity between False Bay and Stil Bay populations, that are separated by a coastal distance of approximately 400 km, and substantially reduced levels of gene flow between these two populations and the more distant Kosi Bay population (1 600-2 000 km away). Planktonic eggs and larva spawned by Kosi Bay *U. robinsoni* females appear to have limited dispersal (Chapter 5) despite the proximity of the strong, south-ward flowing Agulhas Current to the shelf edge in this region. The Agulhas Current does not act as a vector for the transport of planktonic propagules of most inshore fish inhabiting South Africa's east coast, with eggs and larvae absent in the current core (Beckley 1993). Planktonic spawning products that do become entrained in the current core itself (flowing at 1-2 m.s^{-1}) would likely be transported rapidly southwards and too far offshore, when the current diverges from the coast as the continental shelf widens in the vicinity of the Agulhas Bank, for successful recruitment to inshore nursery areas

(Hutchings *et al.* 2003). *U. robinsoni* spawns in near-shore coastal waters inshore of the current, and planktonic propagule dispersal distances from the Kosi Bay region, mostly by wind driven currents, appear to be in the region of only 30-60 km (Chapter 5). A persistent clockwise eddy in the vicinity of the Natal bight (a widening of the shelf to the north of Durban) (Lutjeharms *et al.* 2000) may facilitate the retention of eggs and larvae and act as a barrier to gene flow along this stretch of the South African east coast (Fig. 6.1). The positive relationship between genetic differentiation and geographic distance does suggest an "isolation by distance" pattern of gene flow amongst *U. robinsoni* populations along the South African coast. However, additional samples from localities spatially intermediate to those sampled in this study are required to confirm this initial observation and further elucidate levels of population genetic structure amongst South African *U. robinsoni.*

The finding of genetic homogeneity between False Bay and Stil Bay *U. robinsoni* populations does not preclude the possibility that these populations will respond independently to exploitation. Very low levels of gene flow are sufficient to obscure most genetic evidence of stock structure, but are likely to have little effect in rebuilding populations depleted by over-exploitation (Carvalho and Hauser 1995, Waples 1998). In these regions, *U. robinsoni* live to approximately 20 years of age and populations consist of numerous overlapping generations (Chapter 4, Chapter 7). It is conceivable that some planktonic eggs and larvae spawned by females during their relatively long life-spans may disperse the 400 km between the sites (sporadic recruitment), or more probably stepwise gene flow via spatially intermediate populations is sufficient to maintain genetic homogeneity. A widely accepted working definition of a fish stock is: "an intraspecific group of randomly mating individuals with spatial and temporal integrity" (Ihssen *et al.* 1981). Although the False Bay and Stil Bay populations do not have separate genetic integrity, long-term tagging data shows that coastwise movement of adults between the two sites is highly unlikely, indeed adults appear to be strongly phylopatric (Chapter 5), and the two populations can not be considered a single group of randomly mating individuals. Furthermore, significant variation in growth rate between the two populations (Chapter 7) indicates that they would react differently to exploitation and can be considered as separate stocks for the purposes of short-term management (i.e. ensuring sustainable harvesting). The finding of broader scale genetic structure amongst widely distributed

U. robinsoni populations (e.g. Kosi Bay- False Bay) indicates that longer term management objectives should incorporate the conservation of genetic variation.

CHAPTER 7

MANAGEMENT OF SOUTH AFRICAN *UMBRINA ROBINSONI* BASED ON PER-RECRUIT MODELS, WITH NOTES ON THE EFFECT OF TEMPORAL VARIATION IN GROWTH RATE ON BIOLOGICAL REFERENCE POINT ESTIMATES

ABSTRACT

Slender baardman, *Umbrina robinsoni* are an important component of recreational shore angler and spear fisher catches along the eastern seaboard of South Africa. *U. robinsoni* stocks at three sites - False Bay, Stil Bay and the KwaZulu Natal (KZN) coast - were modeled using a per-recruit approach. Total (Z) and fishing (F) mortality rates were estimated by catch curve analyses using measures of individual size (length or weight) recorded by researchers, divers (log books) or during fishing competitions. Current spawner biomass per-recruit ratios were estimated to be either at or below the 25 % threshold: False Bay SB/R = 21 % $SB/R_{F=0}$, Stil Bay SB/R = 25 % $SB/R_{F=0}$, and KZN SB/R = 21 % $SB/R_{F=0}$, suggesting that current rates of fishing mortality (F) are too high. Reductions in F necessary to achieve target fishing mortality levels ($F_{\mathrm{SB}\ 40}$) at the current minimum size limit (l_c 40 cm TL) were 51 % for Stil Bay and the KZN coast and 57 % for False Bay. Based on the bag frequencies from 927 diver outings in KZN (1989-2003), a reduction in bag limit from the current 5 to 2 fish would reduce F in this region by approximately 25 %. Increasing the l_c to 50 cm is predicted to increase SB/R ratios to 36 % $SB/R_{F=0}$ in False Bay, 43 % $SB/R_{F=0}$ in KZN and 52% $SB/R_{F=0}$ in Stil Bay, at current levels of F. Owing to the philopatric nature of *U. robinsoni* and the consequent existence of temporary refugia, catch curves are likely to underestimate fishing mortality. The reductions in F estimated to attain the target reference points are therefore probably conservative. The effect of temporal variation in growth rate on per-recruit model outputs was investigated by comparison of biological reference points obtained using growth curves derived for False Bay *U. robinsoni* populations sampled 10 years apart (1991-1993 and 2001-2003) and applying the two different age-length keys to the 1991-93 length frequency data (n = 1 389) for the estimation of Z, F and current SB/R. The use of the more recent length-at-age data resulted in lower estimates of F (0.61 y^{-1} vs. 1.05 y^{-1}) and a higher spawner biomass per recruit ratio (19.5 % vs. 14.5 %) for the earlier period.

INTRODUCTION

The slender baardman, *Umbrina robinsoni* is a moderately large (maximum mass 12 kg, total length approximately 100 cm) sciaenid that occurs in inshore waters (< 45 m depth) along the east coast of Africa, from Cape Point to Oman (Chapter 1). The species was previously misidentified as *U. ronchus* throughout its range, and in the Western and Eastern Cape provinces of South Africa frequently confused with the sympatric *U. canariensis* which inhabits deeper shelf waters (Chapter 1).

The first reference to the fishery for *U. robinsoni* is found in Biden (1930) where he records that the older Kalk Bay (a fishing harbor in False Bay, Western Cape) fishers were complaining about the almost total disappearance of pufaro (*Polyprion americanus*) and baardman (*Sciaena capensis* – a synomyn for *U. robinsoni*) from catches. This anecdotal evidence suggests that *U. robinsoni* were historically a component of the boat based linefishery in the region whilst they undoubtedly were also landed by beach-seines (South Africa's oldest commercial fishery which dates back to the 1600's) operating along South Africa's eastern seaboard. *U. robinsoni* still occur as an occasional by-catch in beach-seines operating along the northern shore of False Bay (Lamberth *et al.* 1994) and elsewhere along the Cape coast (Marine and Coastal Management, unpublished data).

Although recreational shore angling has been a popular pastime for at least the past century, *U. robinsoni* only became important in catches relatively recently (1960s) when private ownership of four-wheel drive vehicles and technological improvements in angling gear (such as the introduction of the prawn pump, geared reels, monofilament nylon and fiberglass rods) allowed effective targeting of species that feed in the surf zones of sandy beaches (Bennett 1991, Bennett *et al.* 1994). Analyses of the records of three angling clubs active in the False Bay region revealed that *U. robinsoni* were the fifth most often caught species over the period 1938-1992 (Bennett *et al.* 1994). Over the past decade, however, the species has become increasingly scarce in shore angler catches (personal observation). Recreational spear fishers also target *U. robinsoni* throughout the species range in South African waters and the most recent survey revealed that the species accounts for between 3 and 10 % of the total catch (Mann *et al.* 1997). Despite a relatively long history of exploitation there have been no previous attempts to assess the stock status of *U. robinsoni*; primarily due to a lack of scientific information on the taxonomy and biology of the species. Current management measures, largely based on perceived vulnerability to exploitation, comprise a minimum size limit of 40 cm total length (TL) and a bag limit of five fish per angler per day (Marine Living Resources Act, No. 18. of 1998).

The South African living marine resources management authority (Marine and Coastal Management – MCM) approved a Linefish Management Protocol (LMP) during 1998-99 (Griffiths *et al.* 1999). The LMP was derived from the concept of an Operational Management Procedure (OMP) as applied to large, high value fisheries internationally e.g. whale stocks (Kirkwood 1997), South African hake (Punt 1992) and pelagic fisheries (Cochrane *et al.* 1998). South Africa's LMP, however, recognizes the general data deficiency for South Africa's multi-species linefish resource and accounts for risk (associated with management decisions) through the use of biological reference points rather than simulation testing (Griffiths *et al.* 1999).

As with most South African linefish species, catch and effort data for the *U. robinsoni* fishery is scarce, with the little available data specific to certain time periods and/or user groups. For fisheries without accurate long-term catch and effort data or information on the stock-recruitment relationship, spawner-biomass per-recruit (*SB/R*) and yield per-recruit (*Y/R*) models are considered the most appropriate stock assessment methods (Butterworth *et al.* 1989, Punt 1993, Griffiths 1997b, Griffiths *et al.* 1999). Several studies have indicated that the risk of recruitment overfishing (and stock collapse) is high when the relative *SB/R* is reduced to< 20-30% of the pristine level ($SB/R_{F=0}$) (Clark 1991, Mace and Sissenwine 1993, Thompson 1993, Mace 1994); whilst a fishing mortality rate (*F*) that reduces the *SB/R* ratio to 40 % $SB/R_{F=0}$ (F_{SB40}) has been shown to provide high yields with a low risk of stock collapse for species with a wide range of life-history characteristics, regardless of the spawner-recruit relationship (Clark 1993, Punt 1993). The South African LMP adopts the F_{SB40} level as a target reference point (stocks assessed to have a *SB/R* ratio = 40-50 % $SB/R_{F=0}$ are considered to be optimally exploited) and the F_{SB25} point as a threshold reference point (stocks assessed to have a *SB/R* ratio < 25 % $SB/R_{F=0}$ are considered heavily overexploited and there is a high risk of recruitment failure and stock collapse). Any stock assessed as having a *SB/R* ratio of less than 40% $SB/R_{F=0}$ is considered overexploited and management action is required to reduce fishing mortality in order to facilitate stock recovery towards the target level. Management action obviously needs to be progressively more urgent in situations where the threshold reference point is approached or exceeded.

Recent studies have demonstrated limited coastwise movement (Chapter 5) and substantial life-history differences (growth rate, size-at-maturity and longevity) between spatially separate populations of *U. robinsoni* (Chapter 4). In this chapter, the minimum size limit for *U. robinsoni* and current rates of fishing mortality in three regions, - False Bay, Stil Bay and the KwaZulu Natal coast (Fig. 7.1) – are evaluated using per-recruit models.

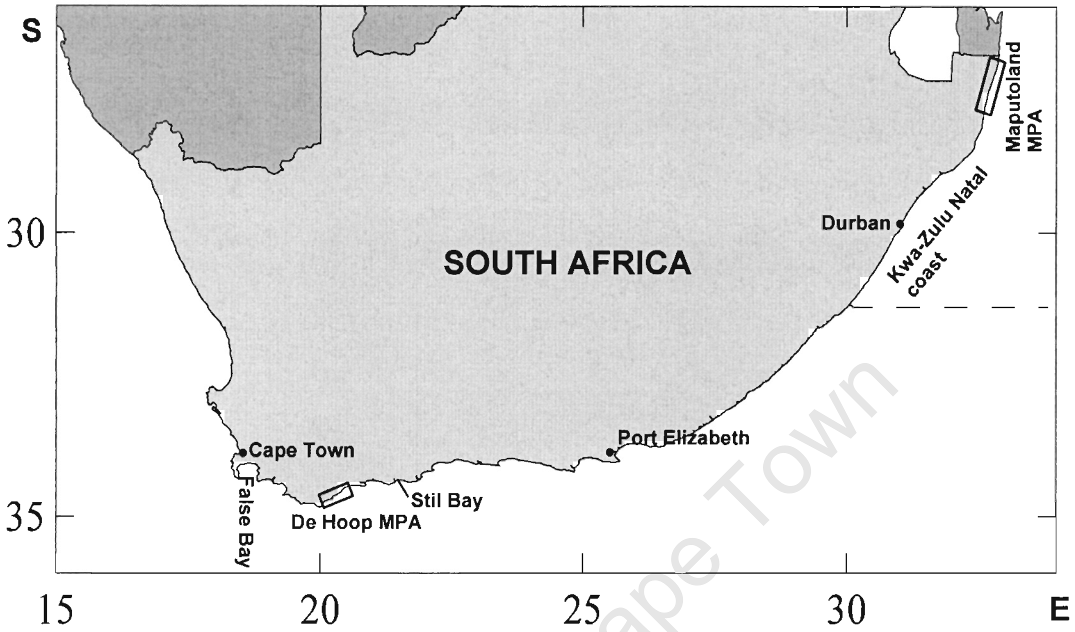


Fig. 7.1: Map of South Africa showing sampling sites and places mentioned in the text

Data requirements for per-recruit stock assessment models are considerably less rigorous than those required for more intensive models such as virtual population analyses or dynamic age-structured production models, but do require accurate data on the length-weight relationship, age/size at maturity (t_m), natural mortality (M), fishing mortality (F) and growth parameters. The collection, sectioning and ageing of large numbers of otoliths is nevertheless expensive; and often difficult to justify for stocks, such as *U. robinsoni*, that generate small economic returns. The cost of age and growth studies is also influenced by the frequency with which age-length keys are updated. Owing to possible temporal variation in growth it is generally accepted that catch should be aged each time that length measurements are collected for mortality estimation. In this chapter the growth of False Bay *U. robinsoni* in 1991-1993 and 2000-2003 is compared and the impacts of failing to update growth rates and length-at-age are evaluated with per-recruit analysis.

MATERIAL AND METHODS

Biological data

Basic data used in the per-recruit analyses were obtained by biological sampling *U. robinsoni* from four sites off South Africa's eastern seaboard during 2001-2004. Two of the sites, De Hoop and Kosi Bay are established marine protected areas, whilst *U. robinsoni* at the other two sites, False Bay and Stil Bay, are exposed to intensive recreational angler and/or spear fishing exploitation (Fig. 7.1). A collection of otoliths and total length (TL) measurements of False Bay *U. robinsoni* collected by S. J. Lamberth (formerly Department of Zoology, University of Cape Town, now MCM) during 1991-1993 were also used to determine growth during this period. The length-mass relationship was determined by linear regression; age was determined using sectioned otoliths and size-at-maturity by fitting a logistic ogive to the observed proportion of mature females (macroscopic gonad stages, validated by histology) per 5 cm length class. For further details on biological sampling, determination of size-at-maturity, age determination and growth curve fitting, see Chapter 4. Sample size, length-mass relationship, female size-at-maturity, and maximum recorded age for each site are shown in Table 7.1. The estimated von Bertalanffy growth model parameters are given in Table 7.2. Observed length-at-age data were used to construct age-length keys for *U. robinsoni* sampled from each of the different regions or time periods.

Table 7.1: Details of biological data for sampled *U. robinsoni* populations used in per-recruit analysis. Sample size (n) is the total number of fish that were biologically sampled in each region; l_m is the estimated female size at 50% sexual maturity (cm TL); t_{max} is the maximum recorded age (years) in the sample; a and b are the parameters in the total length (TL mm) – mass (g) relationship.

Region	n	l_m	t_{max}	a	b
False Bay	175	40	18	$10\wedge^{-4.94}$	3.02
De Hoop	312	39	16	$10\wedge^{-5.16}$	3.10
Stil Bay	74	39	21	$10\wedge^{-5.22}$	3.10
KZN	354	48	12	$10\wedge^{-4.84}$	2.94

Table 7.2: Von Bertalanffy growth model parameter estimates for *Umbrina robinsoni* used in per-recruit models. Standard errors (SE), coefficients of variation (CV), upper (UCI) and lower (LCI) 95 % confidence limits are given Sample size (*n*) indicates the number of fish used in growth curve fitting.

Parameter	False Bay 1991-93	False Bay 2001-03	De Hoop 2001-03	Stil Bay 2004	Kosi Bay 2001-02
n	247	139	295	73	152
L_∞					
Best fit	770	881	594	741	875
SE	30.8	29.4	22.7	88.9	74.0
CV (%)	4.0	3.3	3.8	11.7	8.3
LCI	719	831	563	663	779
UCI	842	949	653	946	1064
k					
Best fit	0.214	0.164	0.183	0.132	0.151
SE	0.023	0.016	0.032	0.039	0.034
CV (%)	10.6	9.9	17.4	29.1	22.7
LCI	0.169	0.133	0.120	0.064	0.092
UCI	0.259	0.197	0.247	0.21	0.225
t_0					
Best fit	-0.271	-0.864	-2.419	-3.22	-2.498
SE	0.202	0.248	0.762	1.067	0.641
CV (%)	70	28	30	31.6	25
LCI	-0.705	-1.39	-4.29	-5.89	-3.93
UCI	-0.068	-0.435	-1.28	-1.7	-1.46

Mortality

Natural mortality estimates

In Chapter 4, natural mortality (*M*) for *U. robinsoni* was estimated from the age structure of unexploited populations in large longstanding Marine Protected Areas. Values of 0.26 y^{-1} (CV = 3.6 %) and 0.35 y^{-1} (CV = 4.8 %) were obtained for warm temperate (De Hoop) and sub-tropical (Kosi Bay) regions, respectively. The sub-tropical estimate was assumed for KZN and the warm-temperate estimate for Stil Bay. False Bay temperatures are substantially cooler than at De Hoop and the *U. robinsoni* from this region appear to live longer and grow faster than those in the latter region. False Bay *M* was therefore taken as the average of the De Hoop estimate and the value (0.24 y^{-1}) calculated using Hoenig's (1983) formula and the maximum age recorded from False Bay (18 yrs). The sensitivity of the per-recruit models to *M* was tested by varying the above estimates by plus or minus 15-20% (i.e. M = 0.2-0.3 y^{-1} for False Bay and Stil Bay, M = 0.3-0.4 y^{-1} for KZN).

Total and fishing mortality

Total mortality (Z) was estimated using the Chapman and Robson (1960) method. Confidence intervals were obtained using a non-parametric bootstrapping procedure (see Chapter 4). Length measurements were obtained from the following sources:

1. Commercial beach-seine catches from False Bay monitored by Mr. S. J. Lamberth over the period 1991-93 (measured to the nearest cm TL).
2. TL measurements (nearest mm) collected from recreational anglers, commercial beach-seine operators and research catches in False Bay during 2001-2003.
3. Recreational, research and competitive spear fisher competition records from Stil Bay for three different time periods (1990-94, 1998, 2000-04). These were converted from mass (nearest 10 g) to TL (mm) using length-mass relationships where necessary.
4. Spear fishing competition records and personal dive records from spear fishers active in KZN covering the period 1989-2003. These were converted from mass (nearest 10 g) to TL (mm) using length-mass relationships and subdivided into four time periods (1989-91, 1992-94, 1995-97 and 2000-2003).

Selectivity and maturity

The proportion-at-age of fish larger than three different minimum size limits (l_c = 30cm, 40 cm and 50 cm TL) that were modeled for each region was calculated by dividing the number of fish in each age class greater than l_c by the total number sampled in each age class (Table 7.3). The proportion-at-age of mature females was estimated by multiplying the number-at-age for each length class (from age-length keys) by the predicted proportion of mature females in each length class (from logistic ogive fitted to observed maturity data), summing the resultant proportions for each age and dividing by the total number of each age in the age-length key (Table 7.3).

Table 7.3: Proportion-at-age of mature female (M F) *Umbrina robinsoni* and of fish larger than each of the three minimum size limits (l_c, = 300, 400 or 500 mm TL) that were modelled.

Age	False Bay 1991-93				False Bay 2001-03				Stil Bay 2004				KZN 2001-02			
	M F	300	400	500	M F	300	400	500	M F	300	400	500	M F	300	400	500
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1	0	0	0	0	0.01	0	0	0	0.05	0.17	0.64	0.02	0.06	0.86	0.29	0
2	0.10	0.93	0	0	0.16	0.71	0	0	0.61	1	1	0.04	0.23	1	0.91	0.03
3	0.41	1	0.31	0	0.66	1	0.69	0	0.78	1	1	0.09	0.68	1	1	0.55
4	0.86	1	0.97	0.22	0.92	1	1	0.27	0.86	1	1	0.19	0.78	1	1	0.76
5	0.97	1	1	0.64	0.98	1	1	0.88	0.87	1	1	0.34	0.93	1	1	1
6	1	1	1	0.96	1	1	1	1	0.99	1	1	0.54	1.00	1	1	1
7	1	1	1	1	1	1	1	1	1	1	1	0.72	1	1	1	1
8	1	1	1	1	1	1	1	1	1	1	1	0.85	1	1	1	1
9	1	1	1	1	1	1	1	1	1	1	1	0.93	1	1	1	1
10	1	1	1	1	1	1	1	1	1	1	1	0.97	1	1	1	1
11	1	1	1	1	1	1	1	1	1	1	1	0.99	1	1	1	1
12	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
t max	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

Per-recruit analysis

Yield-per-recruit (*Y/R*) and spawner biomass-per-recruit (*SB/R*) was calculated using the following equations:

$$Y/R=\sum_{t=0}^{t\max}\frac{(FS_t)}{(FS_t+M)}\left(e^{-\sum_{i=0}^{t-1}(FS_i+M)}\right)\left(1-e^{-FS_t-M}\right)W_t \quad\text{..................................}\ (7.1)$$

$$SB/R=\sum_{t=0}^{t\max}\left(B_t\left(e^{-\sum_{i=0}^{t-1}(FS_i+M)}\right)W_t\right) \quad\text{..}\ (7.2)$$

where F is the instantaneous rate of fishing mortality, S_t is the proportion of fish at age t larger than l_c, W_t is the predicted individual mass of fish of age t and B_t is the proportion of mature females at age t. (see table 7.3). Per-recruit models for the KZN coast were constructed using biological information collected at Kosi Bay, and for Stil Bay using biological data collected at De Hoop and growth information collected at Stil Bay. For False Bay, growth data used in per-recruit models were from samples collected at the two different time periods and biological data (size-at-maturity, length-mass relationship) collected during the latter period. *SB/R* and *Y/R* curves were also calculated for three alternative minimum size limits (l_c = 30 cm, 40 cm and 50 cm).

Effect of temporal variation in growth rate

Three parameter von Bertalanffy growth models for False Bay *U. robinsoni* were fitted to length-at-age data collected 10 years apart (1991-1993 and 2001-2003). The resultant growth models and model parameters were compared using likelihood ratio tests (Draper and Smith 1966). Approximate joint 95% confidence regions around L_∞ and k were determined by conditioning on t_0, conducting 1 000 parametric bootstraps and using the percentile method to determine the 95% confidence interval for each parameter. Observed mean length-at-age for the two time periods was compared using t-tests and Mann-Whitney *U* tests (Zar 1996). For further details on growth curve fitting, likelihood ratio tests and the determination of joint 95% confidence regions see Chapter 4.

SB/R and *Y/R* curves were constructed using the two different growth models. Target (F_{SB40}) and threshold (F_{SB25}) reference points were calculated for the two time periods. In order to investigate the effect of temporal variation in growth rate on estimates of total (*Z*) and fishing (*F*) mortality, these values were calculated using the age-length keys constructed from data collected during the two time periods and applied to random length frequency data collected during 1991-1993 (n = 1389). The length frequency data collected during the earlier period was used for this comparison due to the superior sample size. Current (1990-1993) *SB/R* and *Y/R* values were calculated using each of the age-length keys.

RESULTS

Total and fishing mortality

Estimated total (*Z*) and fishing (*F*) mortality rates for exploited *U. robinsoni* populations at False Bay, Stil Bay and the KZN coast at various periods during the last decade are given in Table 7.4. Variation around *Z* estimates increased with decreasing sample size. Estimated *F* over the period 1990-2004 appeared to decrease at False Bay, remained relatively constant at Stil Bay and increased along the KZN coast (Table 7.4).

Table 7.4: Total (Z) and fishing (F) mortality estimates (y^{-1}) for exploited *Umbrina robinsoni* populations. Number of random lengths (n), upper (UCI) and lower (LCI) 95% confidence intervals and coefficient of variation (CV) for Z are given.

Region and period	n	Z (y^{-1})	LCI	UCI	CV (%)	F (y^{-1})
False Bay						
1991-1993	1389	1.3	1.12	1.48	7	1.05
2001-2003	175	0.8	0.66	0.99	11	0.55
Stil Bay						
1990-1993	140	0.76	0.54	1.07	17	0.51
1998	70	0.80	0.57	1.13	18	0.54
2003-2004	118	0.73	0.52	1.10	20	0.47
KZN						
1989-1991	177	0.57	0.45	0.73	12	0.22
1992-1994	452	0.57	0.46	0.64	9	0.22
1995-1997	106	0.68	0.53	0.87	13	0.33
2000-2003	63	0.88	0.60	1.18	17.4	0.53

Per-recruit analyses

False Bay 1991-93

Yield and spawner biomass per-recruit curves for *U. robinsoni* sampled from False Bay during the period 1991-93 at the current minimum size limit (40 cm TL) and three alternative M estimates (0.2 y^{-1}, 0.25 y^{-1} and 0.3 y^{-1}) are shown in Figs. 7.2a & 7.2b. Estimated F during the period exceeded both the target (F_{SB40}) and threshold reference (F_{SB25}) points indicating that the risk of recruitment over fishing (and stock collapse) at the time was high. A 75 % reduction in F was required at the time to elevate SB/R to the target reference point (F_{SB40}). Decreasing F to the target reference point would have resulted in a predicted 20 % reduction in Y/R ratio, but given that recruitment overfishing was probably occurring at the time, reduced F and consequently larger spawner biomass would potentially have resulted in increased annual yield over the longer term. Although maximum SB/R increased greatly with decreases in the M (Fig. 7.2b), biological reference points only showed moderate change (F_{SB40} = 0.22-0.32 y^{-1}, F_{SB25} = 0.4-0.64 y^{-1} and SB/R = 11-18 % $SB/R_{F=0}$). Under all three M estimates modelled (i.e. 0.2-0.3 y^{-1}); the stock would have been considered collapsed in terms of South Africa's LMP. The effect of altering the minimum size limit (l_c = 30 cm, 40 cm and 50 cm) on *SB/R* and *Y/R* (using the most realistic *M* estimate of 0.25 y^{-1}) is shown in Fig. 7.2c. Decreasing l_c to 30 cm reduced *SB/R* to 3.6% of pristine levels, whilst a 10 cm increase in l_c elevated *SB/R* to above the threshold level (SB/R = 29 % $SB/R_{F=0}$) with little reduction in yield. A further 53 % reduction in *F* was however required to attain the target (SB/R = 40%$SB/R_{F=0}$), indicating that additional regulations (e.g. a reduction in bag limit, closed season or area) would have been necessary at the time in order to protect spawner biomass.

False Bay 2001-03

Yield and spawner biomass per-recruit curves for *U. robinsoni* sampled from False Bay during the period 2001-03 at the current minimum size limit (40cm TL), three alternative natural mortality estimates (M = 0.2 y^{-1}, 0.25 y^{-1} and 0.3 y^{-1}) and three alternative minimum size limits (l_c = 30 cm, 40 cm and 50 cm) are shown in Fig. 7.3. Although estimates of *Z*, and hence *F* were substantially lower (48 %) in 2001-03 than 1991-93 (Table 7.4), the estimates of *SB/R* were only moderately greater in 2001-03 (21 % of $SB/R_{F=0}$ in 2001-03, 14.5 % of $SB/R_{F=0}$ in 1991-93). Under the current l_c, and using the most realistic *M* estimate, the stock is still classified as collapsed ($F > F_{SB25}$), with a 57 % reduction in *F* required to elevate *SB/R* to above the target level (Fig 7.3a). A reduction in *F* of this magnitude would result in a predicted decrease in *Y/R* ratio of only 16 % in the short term. Changing the estimate of *M* (0.2-0.3 y^{-1}) resulted in modest changes in target and threshold reference points (F_{SB40} = 0.2-0.29 y^{-1}; F_{SB25} = 0.36-0.56 y^{-1}), (Fig 7.3b). Using the highest tested natural mortality estimate (M = 0.3 y^{-1}), *SB/R* is estimated at 27 % of pristine; although this is above the threshold reference level the stock is still classified as overexploited. It is also unlikely that *M* for the False Bay stock would be this high, considering that the maximum age sampled in this region (18 years) was greater than that recorded at De Hoop (16 years) where *M* was estimated at 0.26 y^{-1}. A 10 cm increase in the minimum size limit (l_c = 50 cm TL) is predicted to increase *SB/R* to 36 % of $SB/R_{F=0}$ (i.e. above the threshold reference point) at current levels of *F* with negligible change in the *Y/R* ratio. However, a further 20 % reduction in *F* would still be required to elevate the *SB/R* ratio to above the target reference point (Fig 7.3c).

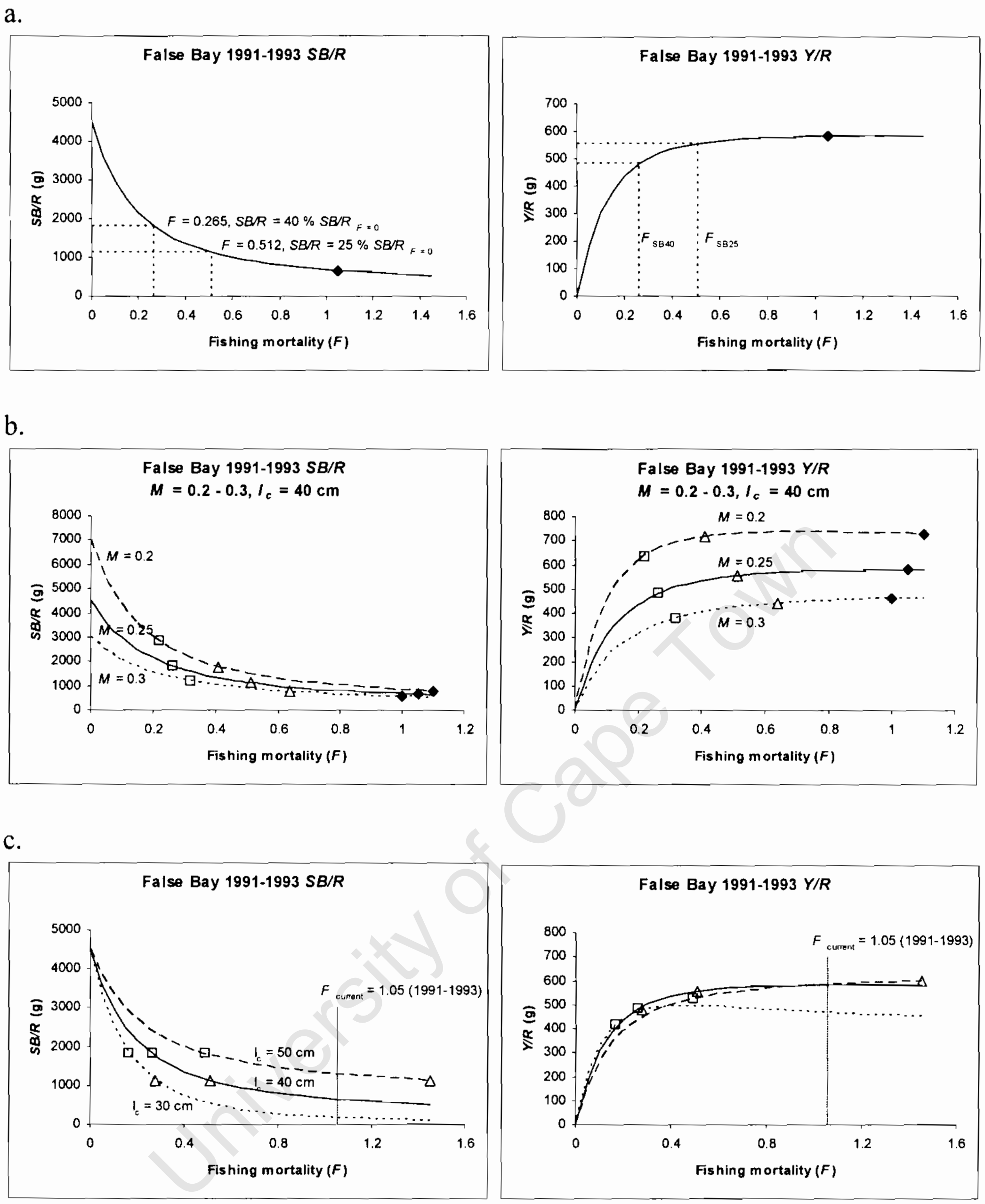


Fig.7.2: (a) Relationship between fishing mortality and spawner biomass (*SB/R*) and yield per-recruit (*Y/R*) for False Bay *Umbrina robinsoni* sampled during 1991-1993. (b) *SB/R* and *Y/R* curves at different *M* estimates. (c) *SB/R* and *Y/R* curves for alternative minimum size limits (l_c). Squares represent the target reference point (F_{SB40}), triangles the threshold reference point (F_{SB25}) and closed diamonds the estimated current (1991-93) fishing mortality.

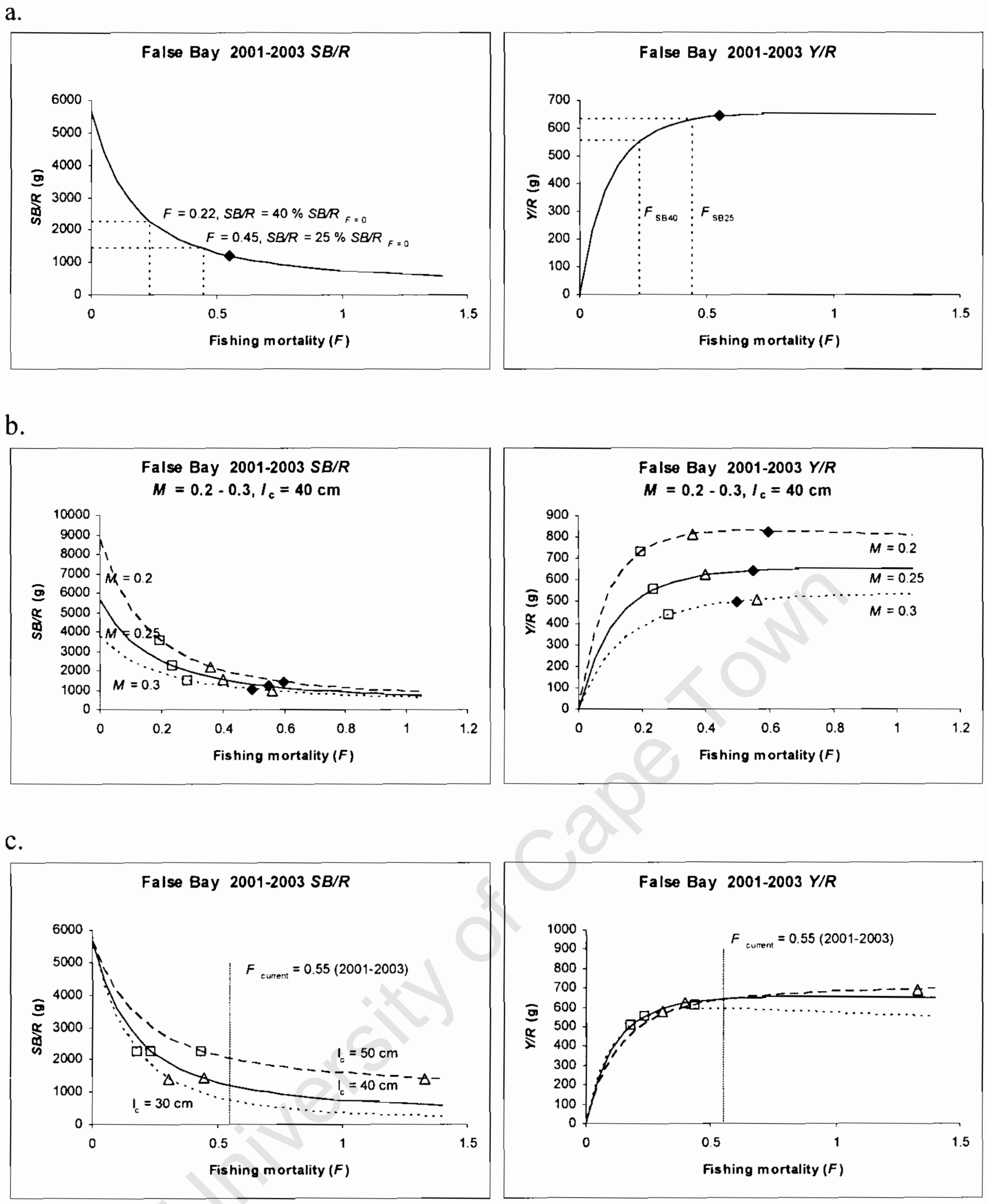


Fig. 7.3: (a) Relationship between fishing mortality (*F*) and spawner biomass (*SB/R*) and yield per-recruit (*Y/R*) for False Bay *Umbrina robinsoni* sampled during 2001-2003. (b) *SB/R* and *Y/R* curves at different *M* estimates. (c) *SB/R* and *Y/R* curves for alternative minimum size limits (l_c). Squares represent the target reference point (F_{SB40}), triangles the threshold reference point (F_{SB25}) and closed diamonds the estimated current (2001-2003) fishing mortality

Stil Bay

Yield and spawner biomass per-recruit curves for *U. robinsoni* sampled from Stil Bay during 2004 at the current minimum size limit (40cm TL) and three alternative M estimates (0.2 y^{-1}, 0.26 y^{-1} and 0.3 y^{-1}) are shown in Fig. 7.4a & 7.4b. Estimates of F for the three periods produced SB/R ratios of 22-24 % of $SB/R_{F=0,}$ i.e. just below the threshold reference point. The required reduction in F to elevate SB/R to the 40 % of pristine level ranges from 51-57 % with a corresponding short term decrease in Y/R of approximately 20 %. The effect of altering the minimum size limit on biological reference points and estimated stock status is shown in Fig. 7.4c. A 10 cm decrease in l_c to 30 cm TL would have little effect on target (F_{SB40}) or threshold (F_{SB25}) reference points, but would decrease current (2001-2004) SB/R to 21 % $SB/R_{F=0,}$ whilst an increase in l_c to 50 cm TL would allow SB/R to recover to above the 40 % of pristine level (Fig. 7.4c). Yield per-recruit with an l_c = 50 cm TL would be reduced by approximately 25 % at current levels of F, but would be slightly increased if the stock was exploited at $F_{SB40.}$

KZN coast

Yield and spawner biomass per-recruit curves for KZN *U. robinsoni* at the current minimum size limit (M = 0.35 y^{-1}, l_c = 40cm TL), three alternative M estimates (M = 0.3 y^{-1}, 0.35 y^{-1} and 0.4 y^{-1}, l_c = 40 cm TL) and three alternative minimum size limits (l_c = 30 cm, 40 cm and 50 cm TL; M = 0.35 y^{-1}) are shown in Fig. 7.5. Estimates of F at four different time periods, show SB/R declining from above the target reference point during the period 1989-1994 to below the target reference point over the period 1995-1998 (SB/R = 33 % $SB/R_{F=0}$) and below the threshold reference point during the latest 4 year period (2000-04, SB/R = 21 % $SB/R_{F=0}$) (Fig. 7.5a). Once again, biological reference points did not alter much with changes in M and under all three of the different M estimates the current estimated F exceeds or is close to the threshold level (F_{SB25}) (Fig. 7.5b). Under the current l_c = 40 cm TL, a 51 % reduction in F is required to elevate SB/R to the target level (40 % of pristine). Analysis of observed bag frequencies of KZN spear fishers (from diver's personal records) indicate that a decrease in bag limit from the current five to one fish per person per day would reduce F by an average of 46 % (over 4 time periods), whilst a bag limit of two would reduce F by an average of just 18 % (Table 7.5). The current bag limit of five fish per person per day is totally ineffective in controlling fishing mortality

(Table 7.5). An alternative management strategy of increasing l_c to 50 cm TL would, however, elevate *SB/R* to above the target reference point with only a small (16 %) decrease in *Y/R* at current (200-04) levels of *F* (Fig. 7.5c). However if recruitment overfishing is occurring at present, a larger spawner biomass should produce larger year classes and ultimately a greater annual yield.

Table 7.5: Observed bag frequencies (Freq.) and the potential percentage reduction in fishing mortality (%*F*) resulting from the enforcement of various daily bag limits (DBLs) for *Umbrina robinsoni* landed by spearfishers along the KZN coast during four different time periods.

DBL	1989-2004		1989-1991		1992-1994		1995-1997		2000-2003	
	Freq	% F	Freq	% F	Freq	% F	Freq	% F	Freq	% F
0	596	100	120	100	373	100	58	100	45	100
1	170	49.7	36	55.8	114	48.6	9	37.0	11	42.6
2	92	25.2	26	31.5	42	26.1	7	7.4	17	5.6
3	29	14.6	6	21.5	20	14.2		3.7	3	0
4	14	8.5	2	14.9	11	7.3	1	0		
5	15	4.6	4	9.4	11	3.3				
6	4	2.9	2	6.1	2	2.0				
7	4	1.8	3	3.9	1	1.3				
8	1	1.4		3.3	1	0.8				
9		1.1		2.8		0.5				
10		0.6		2.2		0.3				
11	1	0.5		1.7	1	0				
12		0.3		1.1						
13		0.2		0.6						
14	1	0	1	0.0						
Total catch (No.)	657		181		395		27		54	
Mean weight (kg)	2.4		2.6		2.5		2.2		1.7	
Diver outings	927		200		576		75		76	
Diver hours	4863		1034.5		3018		407		403	
CPUE (No.fish.100 dive hrs.$^{-1}$)	13.5		17.5		13.1		6.6		13.4	

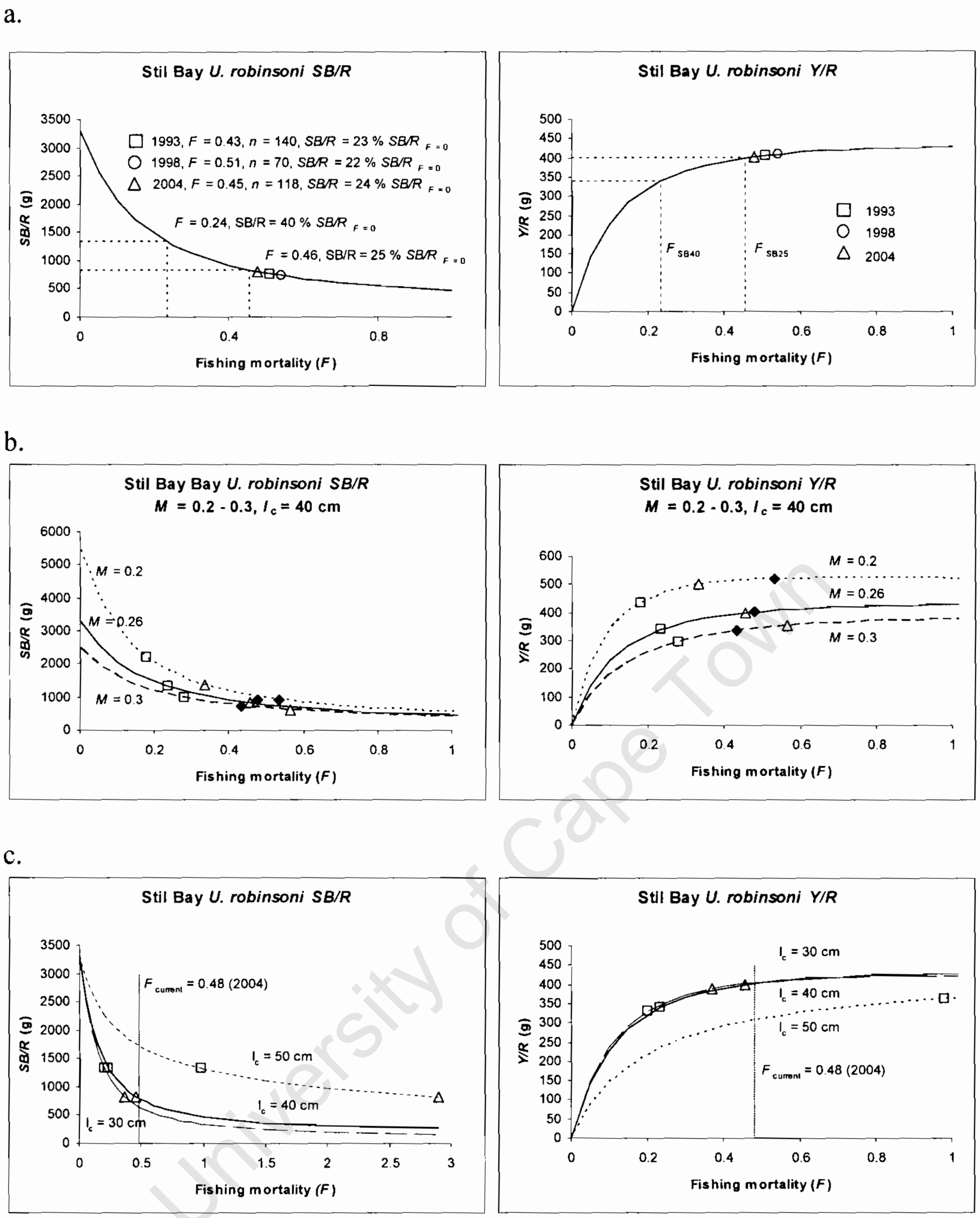


Fig. 7.4: (a) Relationship between fishing mortality (*F*) and spawner biomass (*SB/R*) and yield per-recruit (*Y/R*) for Stil Bay *Umbrina robinsoni* sampled during 2004 showing estimated *SB/R* and *Y/R* at three different time periods. (b) *SB/R* and *Y/R* curves at different *M* estimates showing estimated current *F* (2004). (c) *SB/R* and *Y/R* curves for alternative minimum size limits (l_c). In b and c, squares represent the target reference point (F_{SB40}), triangles the threshold reference point (F_{SB25}) and closed diamonds the estimated current fishing mortality.

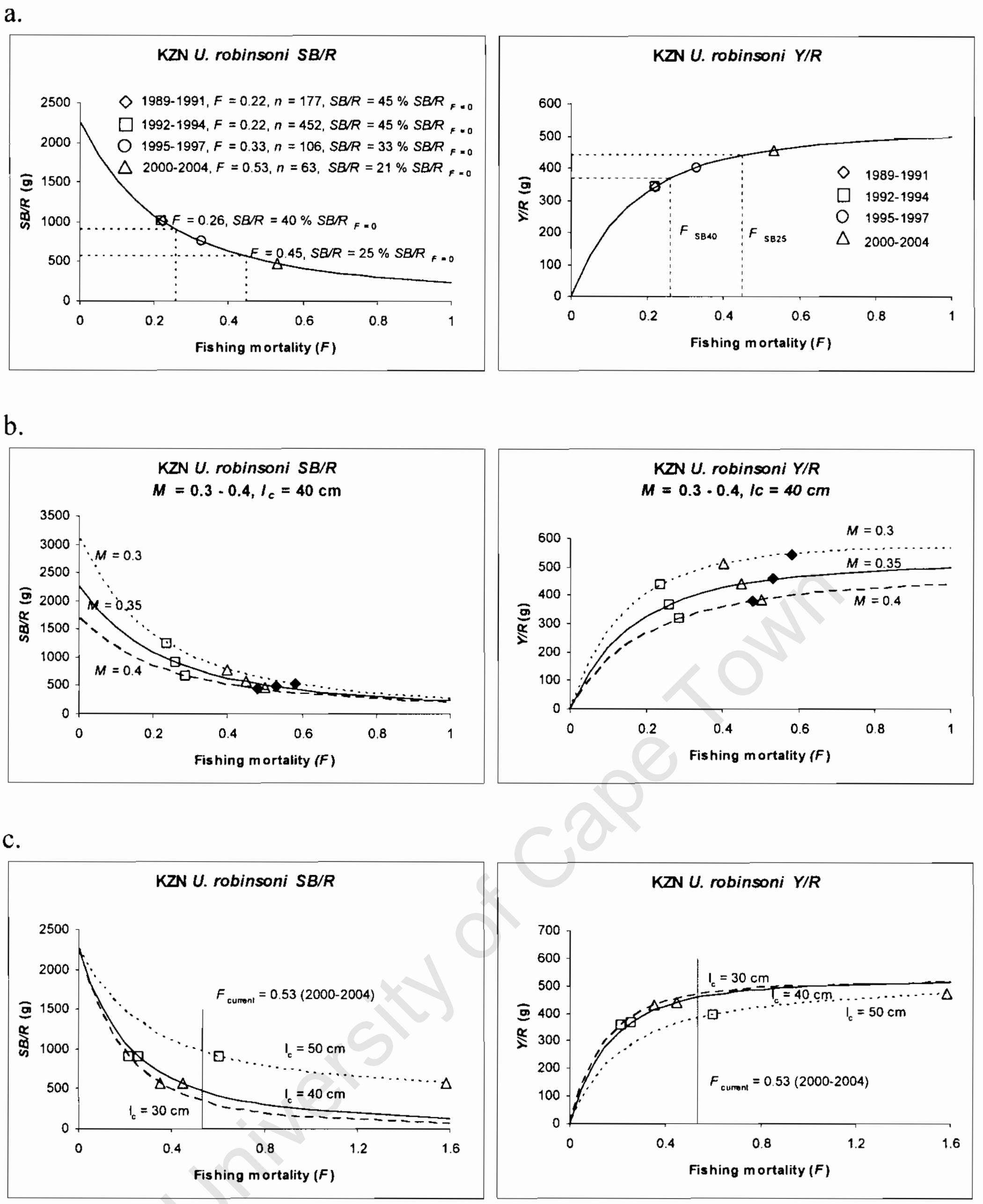


Fig. 7.5: (a) Relationship between fishing mortality (*F*) and spawner biomass (*SB/R*) and yield per-recruit (*Y/R*) for KZN *Umbrina robinsoni* showing estimated *SB/R* and *Y/R* at four different time periods. (b) *SB/R* and *Y/R* curves at different *M* estimates showing estimated current *F* (2000-2004) (c) *SB/R* and *Y/R* curves for alternative minimum size limits (l_c). In b and c, squares represent the target reference point (F_{SB40}), triangles the threshold reference point (F_{SB25}) and closed diamonds the estimated current fishing mortality.

Effects of temporal variation in growth rate

Three parameter von Bertalanffy growth curves fitted to the observed length-at-age data for the two time periods sampled at False Bay are shown in Fig. 7.6. Although likelihood ratio tests show significant differences ($P < 0.05$) for the fitted curve and the estimated L_∞ parameter, comparison of fitted curves 95 % confidence intervals (Fig. 7.6) indicates very similar growth in False Bay during these two time periods (curves are parallel with overlapping confidence limits up to 13 years age). There is an indication that fish sampled during 2001-2003 were slightly larger at age and attained a larger maximum size than fish sampled during 1991-1993. Statistical tests of the mean length-at-age only show this difference to be significant for 3-6 year olds (Table 7.6). The approximate joint 95 % confidence regions around L_∞ and k are also close together in parameter space (Fig. 7.7), which suggests that the statistically significant differences in fitted growth curves may not represent real differences in growth between the two periods.

The effect of these slight differences in fitted growth curves on mortality estimation and per-recruit outputs is shown in Fig. 7.8. The *SB/R* and *Y/R* curves constructed using biological data collected during the two different time periods were very similar, with target ($F_{\mathrm{SB}\,40} = 0.27$ y^{-1} in 1991-1993; $F_{\mathrm{SB}\,40} = 0.24$ y^{-1} in 2001-2003) and threshold ($F_{\mathrm{SB}\,25} = 0.51$ y^{-1} and $F_{\mathrm{SB}\,25} = 0.45$ y^{-1} respectively) reference points differing only slightly (11 %). Current Z and F estimated from the 1991-93 length frequency data (this data set was chosen for the comparison due to the superior sample size) using the two different age-length keys was, however, substantially different (42 % reduction in F when using the 2001-2003 age-length key). Despite the substantially lowered estimate of Z and F when using the more recent age-length key, estimated stock status was only slightly improved (SB/R = 14.5 % $SB/R_{F=0}$, SB/R = 19.5 % $SB/R_{F=0}$ using 1991-93 and 2001-03 length age keys respectively).

Table 7.6: Statistical comparison of mean length (TL mm) at age (years) of False Bay *Umbrina robinsoni* sampled 10 years apart. Students t-test or Mann-Whitney U statistics are given.

Age	1991-1993 (*n, stdev.*)	2001-2003 (*n, stdev.*)	Statistic	p
1	160 (1)	243 (3, 28)	-	
2	321 (15, 25)	328 (14, 44)	$U = 101.5$	$P > 0.05$
3	382 (55, 28)	420 (29,36)	$t = 5.22$	$P < 0.001$
4	463 (116, 40)	481 (34, 35)	$t = 2.39$	$P < 0.05$
5	510 (22, 37)	538 (25, 29)	$t = 2.84$	$P < 0.01$
6	581 (24, 43)	601 (12, 48)	$t = 1.23$	$P < 0.05$
7	622 (7, 57)	597 (3, 16)	$U = 5.5$	$P > 0.05$
8	665 (2, 14)	656 (3, 96)	$U = 2$	$P > 0.05$
9	629 (4, 34)	712 (8, 36)	$U = 1$	$P > 0.05$
10		743 (10, 77)	-	
11	658 (2, 32)	704 (1)	-	
12		783 (2, 29)	-	
13	780 (1)		-	
15		793 (1)	-	
16		805 (1)	-	
18		774 (1)	-	

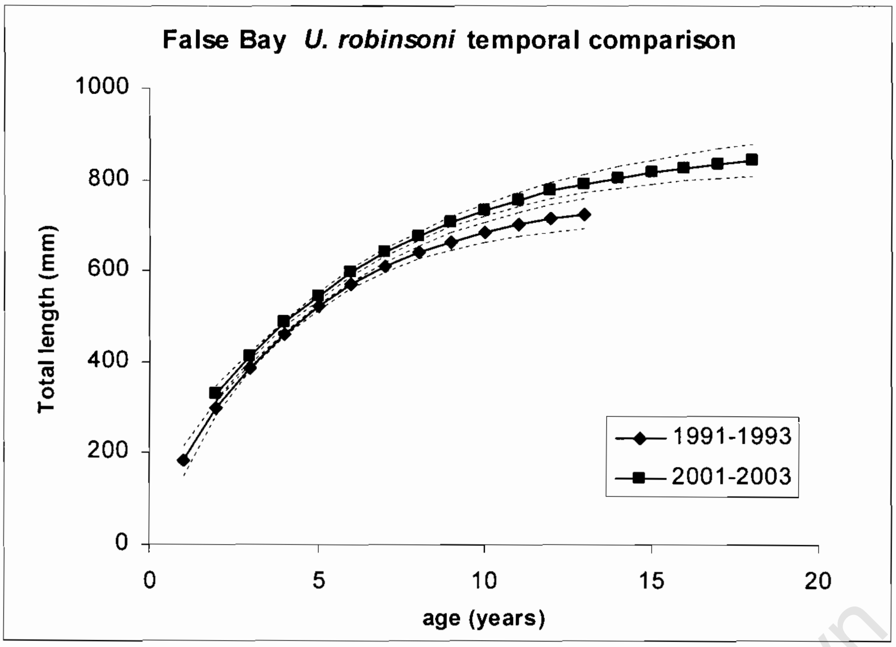


Fig. 7.6: Three parameter von Bertalanffy growth curves fitted to length-at-age data for *Umbrina robinsoni* sampled at False Bay ten years apart. Dotted lines indicate 95 % confidence limits of the fitted curves.

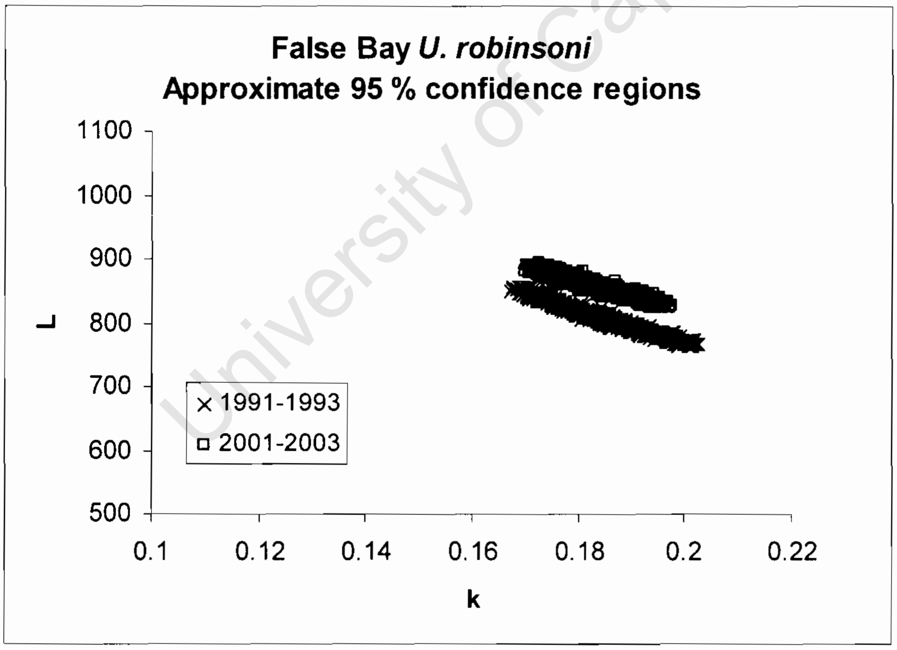


Fig. 7.7: Approximate joint 95 % confidence regions around L_∞ and k calculated by conditioning on t_0 and conducting 1 000 bootstraps for *Umbrina robinsoni* sampled at False Bay during 1991-1993 and 2001-2003.

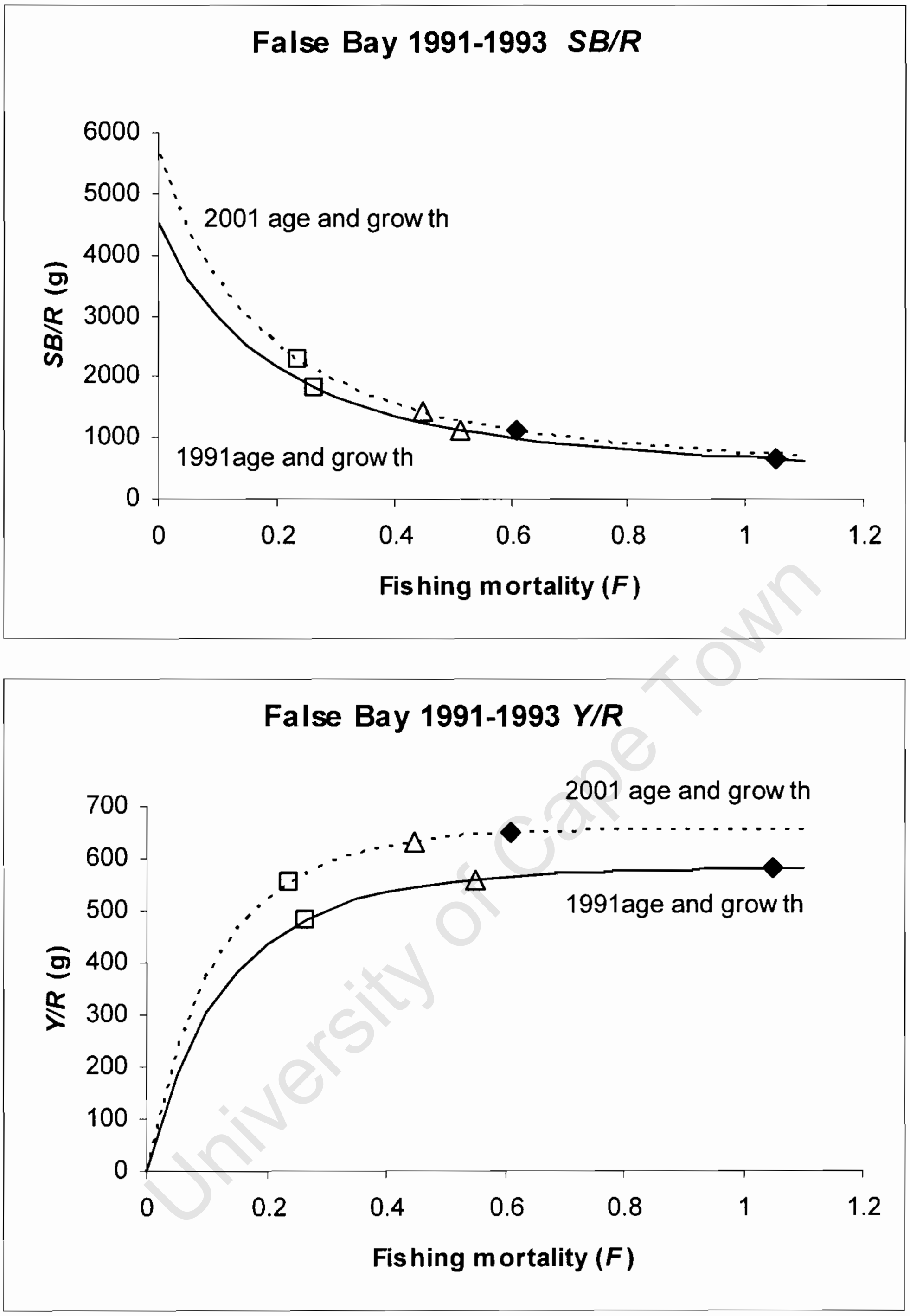


Fig. 7.8: Relationship between fishing mortality (*F*) and spawner biomass (*SB/R*) and yield per-recruit (*Y/R*) for False Bay *Umbrina robinsoni* using age and growth data collected at two different time periods. Squares represent the target reference point (F_{SB40}), triangles the threshold reference point (F_{SB25}) and closed diamonds the current(1991-93) fishing mortality estimated using 1991-93 length data and age-length keys for both periods.

DISCUSSION

Natural mortality

Reliable estimates of natural mortality are essential for per-recruit assessments but are often difficult to obtain in established fisheries. In this study I was fortunate to obtain direct measures of *M* through sampling *U. robinsoni* in established MPAs. Both the De Hoop and Maputaland MPAs have been in existence for a sufficiently long time to allow at least one cohort to attain maximum age in the absence of fishing mortality. As *U. robinsoni* are known to have small home ranges (approximately 1.5 km) and coastwise movement of adults is limited (Chapter 5), the populations within the sampled MPAs are unlikely to have been significantly impacted on by fishing through immigration in to or emigration out of the protected areas. This highlights the value of MPAs as research sites for fisheries assessment of resident species. The sampling of fish within MPAs for determination of length-at-age and *M* is, however, by necessity destructive, and the sites can no longer be considered undisturbed. The biomass of *U. robinsoni* within the sampled areas (in both cases less than 15 % of the MPA coastline was sampled) was certainly substantially reduced and recovery within the Maputaland MPA (monitored by diver counts) was observed to be slow (Chapter 5). The magnitude of the broader ecological impacts of removal sampling is also not known (e.g. effects on prey, predator and competitor species).

As the effects of removal sampling within MPAs are not benign, it is important to consider whether *M* estimates obtained in this manner are transferable to other exploited populations (Attwood 2003). The *U. robinsoni* population in the subtropical Maputaland MPA was found to have a markedly different natural mortality rate (in addition to other life-history parameters such as growth rate, age/size at maturity) than that in the warm temperate De Hoop MPA (Chapter 4). It is likely that the exploited populations elsewhere along the subtropical KZN coast that were assessed experience a similar natural mortality rate to the Maputaland MPA population; there are no major oceanographic discontinuities between the areas and *U. robinsoni* occur in very similar habitat (sub-tidal, moderate profile patch reef) throughout the region. The *M* estimate obtained for the De Hoop MPA population is also conceivably very similar to that experienced by nearby warm temperate southern Cape *U. robinsoni* populations (such as the one assessed at Stil Bay).

The spatial scale over which such extrapolation of *M* estimates can be made is, however, unknown. *U. robinsoni* sampled from False Bay (approximately 280 km west of De Hoop) were found to have a faster growth rate and obtain a significantly larger asymptotic length than those sampled within the De Hoop MPA. This could be due to a number of factors including physical and biotic environmental differences and/or the effects of exploitation. With such a marked difference in growth rate, which is positively correlated with mortality rate (Roff 1992), it is questionable whether the De Hoop MPA *M* estimate is transferable to this region. However, good agreement was obtained between Hoenig's (1983) equation, which is based on maximum age, and catch curve estimates for both the De Hoop and Maputaland MPA populations. As the maximum age recorded in False Bay was similar to that recorded at De Hoop (18 and 16 years respectively), the natural mortality rate experienced by the False Bay population is likely to be close to the De Hoop estimate. Sensitivity analyses (varying the *M* estimates) in any case did not have very large effect on biological reference point or stock status estimates. The question of transferability of *M* estimates obtained from sampling in MPAs to other regions in no way reduces the value of having such estimates (it is certainly preferable to using *M* estimates obtained by extrapolation from studies on other species). As one wouldn't expect substantial changes in natural mortality (particular the "average" value obtained from catch curve analysis – regressed over good and bad recruitment and growth years), destructive sampling in MPAs would not need to be repeated. Indeed this study as a whole could not have been conducted without the valuable life history information obtained by sampling within MPAs, as procuring sufficient samples from exploited areas (for accurate estimates of growth, size-at-maturity etc.) would not have been possible due to the current scarcity of the species in exploited areas.

Fishing mortality

The use of spear fishing records (competitive or personal) when estimating the total mortality rate is not ideal, as spear fishers inherently select the larger fish encountered which leads to positive bias of older year classes in the age composition. This decreases the slope of the catch curve resulting in possible under estimates of *Z*. The magnitude of this effect was somewhat reduced by the fact that the age at full recruitment (peak mode of age composition) from spear fishing data was one (KZN coast) to five years older (Stil Bay) than that for angler or beach-seine data (False Bay = 4 yrs) and the slope of the descending limb of the catch curve was still significantly negative. The use of these data was however unavoidable, as accurate size composition data for *U. robinsoni* from other sources (e.g. catch cards, roving creel or access point surveys) is extremely scarce as well as being spatially and temporally discontinuous (Brouwer *et al.* 1997, Mann *et al.* 1997, Pradervand 2002) The use of spear fisher catch data for the KZN coast was in any case appropriate, as it is by far the dominant fishing method used for *U. robinsoni* in the region (Mann *et al.* 1997).

The Stil Bay *U. robinsoni* population is assessed as overexploited, at three different time periods spanning the last decade, despite the fact that the length frequency data used to estimate Z and F was obtained from spear fishing competition records which could have led to under estimates of these parameters and a consequently optimistic stock status estimate (as discussed above). The failure to detect a negative trend in current SB/R as % $SB/R_{F=0}$ over time may be partly explained by the selective nature of competitive spear fishers. Per-recruit analyses are, however, best used for establishing biological reference points, evaluating current levels of F and minimum size limits and predicting relative movements of SB/R and Y/R in response to changes in l_c and F. Only if a population is in equilibrium, and all cohorts are subject to the same fishing mortality and selectivity conditions, will the estimated current SB/R as % $SB/R_{F=0}$ be equivalent to the actual spawner biomass as a percentage of pristine biomass.

The possibility that a fish population is not in equilibrium, however, can cause errors when estimating current mortality rates using catch-curve methods. In populations that are growing (e.g. within recently closed areas or due to catch restrictions) increasing recruitment will skew the population age distribution towards young fish, resulting in overestimates of mortality rate based on catch-at-age data, whilst a shrinking population (collapsing recruitment) will have the opposite effect (Attwood 2003). The total catch of *U. robinsoni* during three national spear fishing competitions held at Stil Bay during the last decade decreased dramatically (136 fish in 1994, 69 in 1998 and 40 in 2004, SA spear fishing competition records) despite similar skill levels and diver effort, suggesting regional overexploitation. This observed decline in catch-per-unit effort (*cpue*) suggests that the Stil Bay population may indeed be shrinking;

and the failure to detect an increase in the fishing mortality rate over time may be a result of collapsing recruitment. Differences in sea conditions and designated competition areas may, however, have also played roles in causing the observed decline in total catch.

There is no clear trend in *cpue* (in terms of number of fish per diver hour) evident in the dive records of KZN spear fishers, which suggests that the finding of declining stock size over time may not be correct (Table 7.5). This is particularly concerning as the length frequency sample size used in estimating F is considerably smaller during the latter period and hence is less accurate (Table 7.4). The alternative explanation is that KZN spear fishers are still finding *U. robinsoni* but these are smaller and younger fish and the overall stock size has indeed decreased. This does appear to be the case as the average size fish landed by spearfishers in KZN declines over time (Table 7.4). Another factor that may mask a decline in stock size when using *cpue* data (or an increase in mortality rate estimated from catch-at-age/length data) is the resident, philopatric nature of many inshore fish species, such as *U. robinsoni*. An implicit assumption in the catch-curve approach to mortality estimation is that the age structure of the catch is representative of the recruited portion of the population (i.e. fish within the assessment area are homogenous). For resident species with small home ranges, this will only occur if all sites are fished in proportion to the original biomass. Serial depletion of "new" sites by fishing will result in the age structure of the catch and *cpue* remaining similar to that of an unexploited population, whilst the biomass of the population as a whole is substantially reduced. It is likely that this effect caused underestimates of the true mortality rates (experienced by the populations as a whole) of all three *U. robinsoni* stocks assessed.

Temporal variation

Although SB/R of False Bay *U. robinsoni* was estimated as a greater percentage of pristine during the more recent sampling period (21 % of $SB/R_{F=0}$ in 2001-03, 14.5 % of $SB/R_{F=0}$ in 1991-93) it is highly unlikely that the False Bay stock had recovered at all over the 10 year period between sampling events as fishing effort has probably increased. Van der Elst (1993b) estimated that there were 365 000 participants in South Africa's open access recreational shore fishery (the main user group catching *U. robinsoni* in False Bay) in 1991 and that this number would increase at approximately 6 % per year. McGrath *et al.* (1997) used a lower rate of increase (2%) due to a finding of a very low income elasticity of demand and a predominance of white participants. False Bay's proximity to the greater Cape Town metropolis, which has shown considerable population growth in the last 10 years (approximately 4 % per annum, Statistics South Africa 2001), suggests that the growth in recreational shore anglers fishing the area has increased at a similar rate.

Possible explanations for the large discrepancy in estimated Z for the 1991-93 period when using the two different age-length keys include: 1) potential negative bias in the estimate when using the 2001-03 age-length key caused by inadequate sample size of age-length data; 2) the data not being representative of the exploited population as a whole (due to the influence of philopatry and spatial refugia) and 3) the possibility of collapsing recruitment.

1) The lower 2001-2003 estimate of Z could be a result of the much smaller length-at-age data set (142 vs. 249) which included a substantial number of large (old) fish that were captured by research seine-netting in areas not open to commercial seine operators (although shore anglers do target the species extensively in the area). The resulting bias towards older fish in the population age distribution would have led to underestimation of Z. The finding that 1991-1993 SB/R was also estimated at 19.5 % $SB/R_{F=0}$ when using the large 1991-1993 length frequency data set in conjunction with the 2001-2003 age-length key, suggests that this is likely.

2) This is related to the effects of philopatric behaviour (i.e. limited mixing of fish in a population) on the estimation of Z using catch-at-age methods, as discussed above. The Macassar area in False Bay, from which most of the 2001-03 samples were obtained, has extensive areas of offshore mixed reef and sand habitat (ideal for *U. robinsoni*) that cannot be exploited by shore anglers (limited by casting distance) or spear fishers (due to persistent low visibility and the known abundance of large sharks). It is likely that these areas act as spatial refuges for *U. robinsoni* in False Bay. As the False Bay population is at the southern extreme of the species range (Chapter 1), movements in response to changes in water temperature are expected. Populations from these refuge areas appear to become temporarily available to shore anglers (and samplers) when upwelling induced decreases in water temperature cause an inshore

movement of fish. In an analysis of False Bay shore angling club records over the period 1938-1992, Bennett *et al.* (1994) noted a bimodal seasonal trend in catch rates of *U. robinsoni*, with relatively high catch rates recorded during the autumn and spring months (periods when upwelling inducing south-easterly winds are strongest). Griffiths (1997a) also noted a seasonal onshore (summer)-offshore (winter) movement of the sciaenid *Argyrosomus inodorus* in False Bay. By sampling *U. robinsoni* predominately from the Macassar area during periods of temporary availability during 2001-03, it is possible that my estimate of *Z* reflects that of the refuge population rather than that of the exploited population as a whole.

3) Murphy and Crabtree (2001) detected an increase in abundance of adult red drum *Sciaenops ocellatus* (a North American sciaenid species) in observed age distributions and attributed this to increased juvenile survival due to catch restrictions imposed a decade earlier. As there have been no such changes in the catch restrictions for South African *U. robinsoni* over the past decade and fishing effort has probably increased, an alternative and more concerning explanation (given that the risk of stock collapse was already high in 1991-1993) is that recruitment in the False Bay area could be collapsing. This would lead to the loss of the younger year classes in the catch-at-age data and consequently lower, inaccurate *Z* estimate when in reality *F* has increased. The fact that during the period 1991-93 commercial beach-seines landed well over 1000 *U. robinsoni,* whilst during the period 2001-03 less than 100 were caught by the same operators (with approximately the same effort) suggests that this may have occurred. The influence of variable year class strength on the estimation of *Z* cannot be discounted, (e.g. a large cohort of young fish during 1991-93, resulting in overestimation of *Z*) but even in the absence of strong, young year classes and a more than likely underestimate of *Z* and *F* obtained during 2001-03, the False Bay *U. robinsoni* stock is still classified as collapsed.

Given the similarity in the fitted growth curves (Figs. 7.6 and 7.7) and the per-recruit curves (Fig 7.8) it is clear that the major cause of the discrepancy in 1991-1993 *SB/R* ratios is due to the differing estimates of *F* when using the two different age-length keys rather than due to changes in growth rate. As different researchers collected the data during the two time periods, there is a strong possibility that differences in measurement techniques and sampling times influenced the observed length-at-age results. The uncertainty as to the causes of the small temporal variation in growth rate (whether it is real or simply an artifact of sample size and methodology) and the fact that it did not influence per-recruit curves or biological reference point estimates greatly, suggests that for moderately long lived species the frequency of age and growth studies can be at least the lifespan of a cohort if they are to be assessed with a per-recruit approach. The substantial difference in estimated *Z*, however, does highlight the importance of having a large, representative sample of length-at-age data for construction of age-length keys.

Management

Given the overexploited status of the three exploited *U. robinsoni* stocks assessed, management is obligated to implement measures aimed at rebuilding stocks to the target reference level (SB/R = 40 % $SB/R_{F=0}$). Per-recruit model outputs indicate that this would be achieved for stocks occurring off Stil Bay and along the KZN coast through a 10 cm increase in the minimum size limit from 40 cm TL to 50 cm TL. Even with a 10 cm increase in the minimum size limit, however, further reductions in fishing mortality (20-50 %) for heavily fished areas such as False Bay would still be required. There also exists a strong possibility that current fishing mortality for all of the stocks was underestimated and hence the current stock status estimates are optimistic. Analysis of observed bag frequencies of KZN spear fishers indicate that the current daily bag limit of 5 fish.person^{-1}.day $^{-1}$ not limiting fishing mortality in the region (see Table 7.5). A decrease in bag limit from the current five to one fish.person. $^{-1}$.day $^{-1}$ would reduce *F* by an average of 46 %, whilst a daily bag limit of two would reduce *F* by an average of just 18 % (Table 7.5). Data on the bag frequencies of recreational anglers or spear fishers in other regions are unfortunately not available and the effect of alternative daily bag limits on reducing *F* cannot be determined. A bag limit of one fish.person^{-1}.day^{-1} would probably be viewed as draconian by most recreational anglers and spear fishers whilst an increase in the minimum size limit by 10 cm to 50 cm TL should be acceptable by these sectors (given that anglers and divers fishing for sport or food consider the size of the fish caught as important). An increase in the minimum size limit and a reduction in fishing mortality (through bag limit restriction) appears necessary, although the actual combination of these two management measures should be decided on in consultation with the relevant user groups. Co-management with user groups will hopefully ensure support for the restrictions and facilitate compliance (Bohnsack and Ault 1996, Griffiths 1997b).

Although these management measures alone will probably not be sufficient to rebuild stocks to target levels in heavily exploited areas such as False Bay, several other recent management actions will facilitate stock rebuilding, namely: beach-seines have recently been prohibited from retaining and selling *U. robinsoni* and several new marine protected areas have been proclaimed which will be effective in protecting spawning stock (due to the resident nature of adult fish). Although a nationally consistent suite of regulations is preferable, it must be remembered that the species shows considerable spatial variation in life history and stocks should be assessed at relatively small spatial scales. Of particular concern is a complete lack of information on the biology or stock status of the species from the Eastern Cape as insufficient samples were obtained from this region. Attwood (2003) makes several valid criticisms on the use of per-recruit stock assessment techniques (or more specifically the use of catch-at-age data for estimating mortality rates) for South African linefish and recommends the use of *cpue* as a stock status indicator instead. Although in this study attempts were made to address some of the shortcomings of "typical" per-recruit assessments (sampling MPAs in different regions for estimates of *M*, separate regional assessments based on measured life-history parameters, investigation of temporal variation in growth rate) some of Attwoods (2003) concerns are still valid. Specifically the failure to derive estimates of fishing mortality uniformly across all areas (indeed I suspect that the continued occurrence of baardman in False Bay catches, despite the fact that the stock was already classified as collapsed a decade ago, is due to the presence of natural refuges) and the fact that assessments based on catch-at length/age data are retrospective and do not allow for proactive management. Furthermore, although this study took a considerable amount of time, the findings still do not represent a comprehensive assessment of *U. robinsoni* stock status throughout South African waters and realistically, given the financial and manpower constraints is not likely to be repeated or expanded (for a species of limited commercial importance) in the near future.

This study has shown that *U. robinsoni* stocks are over exploited at three different sites along South Africa's coast and that changes in management regulations are required. Once such changes are implemented, future management should focus on monitoring of stock status as part of a nationwide, multi-species linefish monitoring program and make adjustments to restrictions accordingly. Both *cpue* and size/age catch composition data should be collected. The limited effect of temporal variation in growth rate on biological reference point estimates suggests that the per-recruit models presented in this study can be used to assess the relative future changes in biomass in response to changes in F and l_c. In order for *cpue* data to provide an accurate measure of relative biomass, information on factors affecting catchability (e.g. targeting, gear type and environmental conditions) should also be collected.

CHAPTER 8

CONCLUSIONS

Taxonomy

The taxonomic analysis presented in Chapter 1 resolves the previous confusion over the identity and distributions of *Umbrina* species in South African waters and provides comprehensive morphometric descriptions for *U. canariensis* and *U. robinsoni*. Expanded descriptions for the other two sub-Saharan West African species, *U. ronchus* and *U. steindachneri,* are also provided and distinguishing characteristics between all four species are highlighted. The previous misidentification of *U. robinsoni* as *U. ronchus* off the East African coast (e.g. Heemstra 1986, Chao and Trewavas 1990, Sasaki 1996) and its apparent restriction to KwaZulu Natal in South African waters is corrected. *U. robinsoni* is found to have an inshore distribution along the entire South African east coast, from Cape Point to the Mozambique border and further up the east African coast as far as Oman. The other South African species is confirmed as *U. canariensis* which has an unusually broad geographic distribution, occurring around most of the African continent. Although the distributions of the two species overlap completely along the South African coast, *U. canariensis* inhabits deeper shelf waters (predominately 30-120 m, but has been recorded as deep as 400 m) and is seldom found in the inshore zone (0-40 m) inhabited by *U. robinsoni*. Although both species are currently not found along the South African west coast or the southern Namibian coast, the offshore habitat of *U. canariensis* in deeper cooler waters appears to have allowed this species to cross the environmental barrier formed by the Benguela upwelling system (Whitfield 2005) and allowed it to colonize both the west and east African coasts.

Life histories

This study provides the first comprehensive information on the life history of *U. robinsoni* and substantially increases the available scientific information on the life history of *U. canariensis* in South African waters. Given the environmental differences between the habitats and morphological differences between the two species it is not surprising that they differ substantially in life-history characteristics. The key differences in the life histories of *U. canariensis* and *U. robinsoni* are summarized and compared to those of 19 other sciaenids in the form of dimensionless ratios (Beverton 1992) in Table 8.1 (expanded from Griffiths 1995).

Comparison of the life-history parameters of *U. canariensis* with other sciaenids (Table 8.1), reveals that the species is a small to intermediate sized member of the family, but attains a relatively old age compared to other similar sized species. Size and age-at-maturity in *U. canariensis* occurs at a relatively large proportion of asymptotic length (58-69 %); and small proportion of maximum recorded age (10-12 %), a size and age-at-maturity schedule that is fairly consistent for similar sized sciaenid species (Table 8.1). Rapid juvenile growth, which slows dramatically after maturity is typical of most sciaenids (Barbieri *et al.* 1994a, Griffiths and Hecht 1995a, Griffiths 1996a, Ross *et al.* 1995) and seems to be particularly pronounced in *U. canariensis* with 60-70 % of asymptotic length attained by the median age-at-maturity which is only 10-12 % of maximum age (Table 8.1). The relatively great longevity (for a small sciaenid) and particularly slow post-maturity growth rate in *U. canariensis* may be partly due to the movement of adults into deeper, cooler waters (Chapter 1). In the adult habitat, growth rates may be constrained (due to the influence of cooler water on metabolic reactions) and natural mortality rates may be lower than further inshore. The life-history strategy of *U. canariensis* therefore involves early maturity and an energy allocation protocol that favours reproductive output over growth in mature fish. Rapid pre-maturity growth in *U. canariensis* would allow a relatively rapid passage through the vulnerable juvenile size classes, whilst losses in lifetime reproductive output due to early maturity and subsequently small adult body size (fecundity being positively related to female body size), are offset by relative longevity allowing for numerous future spawning events (Roff 1992).

U. robinsoni can be considered a moderately large sciaenid with intermediate longevity (Table 8.1). *U. robinsoni* grow to a much larger size and has a slightly shorter lifespan than *U. canariensis* and although L_{50} is attained at a smaller proportion of asymptotic length, t_{50} occurs at a greater proportion of maximum age (Table 8.1). Comparing *U. robinsoni* to similar sized sciaenids, e.g. *A. inodorus*, *C. regalis* and *C. nebulosus*, which mature at relatively early ages and smaller sizes (Table 8.1); it appears that the life-history strategy of *U. robinsoni* involves delayed maturity with losses in early reproductive output offset by relative large size-at-maturity and hence greater individual fecundity. This is in contrast to the life-history strategy of *U. canariensis* where the number of spawning adults and spawning events are maximised rather than individual adult size.

Table 8.1: Life-history parameters and dimensionless ratios for female sciaenids L_{50} = median length (cm) at maturity, L_∞ = theoretical maximum length (cm), or maximum size sampled if L_∞ was unrealistically high or unavailable, t_{50} = age (years) at L_{50}, and t_{max} = maximum age (years) recorded. TL = Total length and FL = Fork length. Table expanded from Griffiths (1995).

Species	L_{50} (TL)	L_∞ (TL)	t_{50}	t_{max}	L_{50}/L_∞ (%)	t_{50}/t_{max} (%)	Source
Umbrina canariensis							
Central Agulhas Bank	23	40	2.2	23	58	10	This study
Algoa Bay	24	35	3.2	27	69	12	This study
Umbrina robinsoni							
False Bay (SW Cape)	40	88	3.1	18	45	17	This study
De Hoop (S Cape)	39	60	3.5	16	65	22	This study
Stil Bay (SE Cape)	39	74	3.5	21	53	17	This study
Kosi Bay (KZN)	48	89	2.8	12	54	23	This study
Johnius dussumieri	12.5	19.5	-	-	64	-	Fennessy (2000)
Johnius amblycephalus	17	24	-	-	71	-	Fennessy (2000)
Otolithes ruber	24	44	1.7	7	54	24	Fennessy & Radebe (2000)
Atrobucca nibe	29	49	-	-	59		Fennessy (2000)
Argyrosomus thorpei	33	52	2.1	13	63	16	Van der Elst *et al.* (1990)
Argyrosomus inodorus							
S. Cape	38	117	2.4	25	33	10	
SE. Cape	31	117	1.3	25	26	5	Griffiths (1996a, 1997a)
Argyrosomus japonicus	107	147	6	42	73	14	Griffiths(1996b) Griffiths & Hecht 1995a)
Atractoscion aequidens	97	119	5	9	81	55	Griffiths & Hecht (1995b)
Atractoscion nobilis	68	146	4	25	47	16	Clark (1930), Thomas (1968), Fitch & Lavenberg (1971)
Cynoscion nothus	19	23	1	1.5	83	67	De Fries & Chittenden (1982)
Cynoscion arenarius	16	57	0.8	3	28	27	Shlossman & Chittenden (1981)
Cynoscion regalis	26	83	1	11	31	9	Shepherd & Grimes (1983), (1984)
Cynoscion nebulosus	28	69	1	12	40	8	Brown-Peterson *et al.* (2002); Nieland *et al.* (2002)
Larimus fasciatus	15	18	1	2.5	81	40	Standard & Chittenden (1981)
Genyonemus lineatus	15	41	1	12	36	8	Love *et al.* (1984)
Micropogonias furnieri	31	83	2	7	37	29	Manickchand–Heileman & Kenny (1991)
Micropogonias undulatus	18	31	1	8	58	12	Barbieri *et al.* (1994a), (1994b)
Pogonias cromis	65 FL	110 FL	5	43	59	12	Nieland & Wilson (1993); Beckman *et al.* (1990)
Sciaenops ocellatus							
North Carolina	81	116	3	56	70	5	Ross *et al.* (1995)
Florida (Gulf Coast)	82	93	5	24	89	21	Murphy & Taylor (1990)

Spatially separated populations of both species were found to exhibit variation in life-history characteristics. *U. canariensis* populations sampled from two separate centres of abundance (central Agulhas Bank and Algoa Bay) showed significant differences in growth rate and consequently age-at-maturity schedules and it was proposed that movement between these two populations was limited by a persistent cold water ridge (Chapter 2).

During this study, life history information is analysed from four spatially separated *U. robinsoni* populations; two of the sampled populations were from warm temperate and subtropical marine protected areas (De Hoop and Kosi Bay) and the other two (False Bay and Stil Bay) were from exploited populations within the warm temperate biogeographical zone. Significant morphological and life-history differences are found between the warm temperate De Hoop and subtropical Kosi Bay populations, including otolith structure, length-weight relationships, seasonal patterns of relative condition, growth rate, natural mortality rate, size and age-at-maturity, spawning seasonality and batch fecundity (Chapter 4). These differences are interpreted in the context of life history theory and taking cognisance of the environmental differences between the two sites. It is concluded that the size-at-maturity schedules of the two populations are plastic or evolutionary responses that maximise individual fitness (or lifetime fecundity). The benefits of being able to sample in MPAs and interpret life-history differences in the absence of the confounding effects of exploitation are highlighted. *U. robinsoni* populations sampled from False Bay and Stil Bay attained sexual maturity at approximately the same size as De Hoop fish and appear to have the same summer spawning season. An analysis of mitochondrial DNA control region sequences suggests higher rates of gene flow between False Bay and Stil Bay populations than between either of these two populations and the geographically distant Kosi Bay population (Chapter 6). Significant variations in growth rate are, however, detected amongst all four populations sampled (Fig 8.1, Chapter 7) and information on movement patterns indicates that *U. robinsoni* adults are phylopatric with small home ranges (Chapter 5). This suggests that although there is sufficient gene flow between the three Cape populations sampled (False Bay, De Hoop and Stil Bay) to maintain genetic homogeneity, these populations are likely to react independently to exploitation, and for management purposes should be treated as separate stocks.

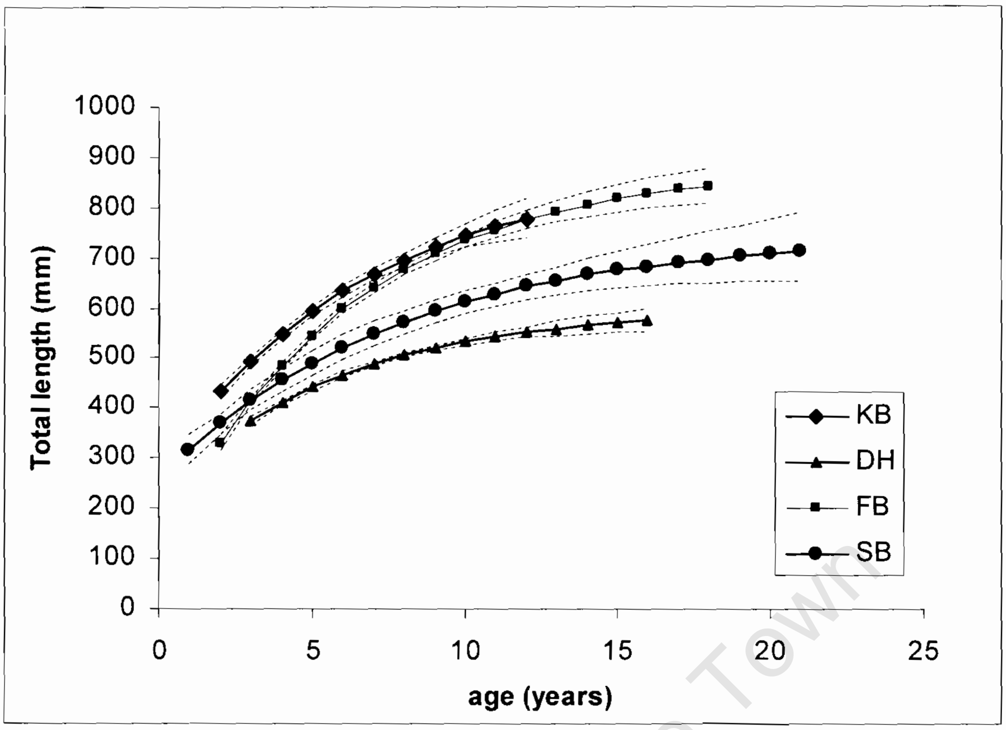


Fig 8.1: Comparison of von Bertalanffy growth curves fitted to observed length-at-age data for *Umbrina robinsoni* sampled from False Bay (FB), Kosi Bay (KB), Stil Bay (SB) and De Hoop (DH). Dotted lines indicate 95 % confidence intervals of the fitted curves.

Management

Per-recruit models are used to assess current levels of fishing mortality and to estimate biological reference points for two *U. canariensis* stocks and three *U. robinsoni* stocks (Chapters 3 and 7). The finding that both *U. canariensis* stocks are underexploited whilst current levels of fishing mortality on the three *U. robinsoni* stocks are estimated to be close to or in excess of the threshold level (F_{SB25}) is surprising. Intuitively, it may be expected that *U. canariensis* stocks, that experience lower natural mortality rates, greater longevity and have been exposed to intensive industrial commercial trawling for over a century would be heavily impacted, whilst it is a common misconception (particularly amongst user groups) that stocks of fish species such as *U. robinsoni* that are primarily targeted by inshore recreational fisheries are unlikely to be overexploited. It appears that the life-history traits of *U. canariensis*, most notably early maturity and an energy allocation protocol favouring reproduction over growth in adult fish in combination with the spatial refugia provided by the primary rocky reef habitat, have created a degree of resilience to trawl exploitation. Per-recruit analyses indicate that *U. canariensis* stocks, although not currently at risk should be considered vulnerable, as target levels of fishing mortality would be (and appear to have been in the past) reached with relatively small increases in *F*, as may occur with changes in trawl effort or targeting practises. There are legal requirements (e.g. South Africa's Marine Living Resources Act of 1998, FAO Code of Conduct for Responsible Fisheries, 1996, of which South Africa is a signatory) that fisheries must be sustainable, both in terms of target and by-catch species. Efforts should therefore be made to improve the quantity and quality of catch-at-length data collected by onboard observers and shore based monitors and the status of South African *U. canariensis* stocks monitored on an ongoing basis. The current South African management measures (minimum size limit of 40 cm TL, daily bag limit of 5 fish.person^{-1}.day^{-1}), which were initially promulgated based on the perceived vulnerability of the inshore species *U. robinsoni* to exploitation, are inappropriate for *U. canariensis* as a trawl by-catch species and will need to be revised.

The inshore distribution, high degree of residency at predictable reef habitat, relatively slow growth, delayed maturity and moderate longevity of *U. robinsoni* make the species particularly vulnerable to exploitation. This study showed that *U. robinsoni* is yet another popular South African angling and spear-fishing species that has been overexploited by predominately recreational fishing effort; other examples include: *A. japonicus*, (Griffiths 1997b), *Dichistius capensis* (Bennett 1988) and *Lithognathus lithognathus* (Bennett 1993). Current management measures have clearly failed to protect spawner biomass and need revision. Per-recruit models indicate that an increase in minimum size limit from 40 cm TL to 50 cm TL is predicted to increase spawner biomass per-recruit ratios towards the target 40 % of pristine level, however, for heavily fished stocks a further reduction in fishing mortality would still be required and a bag limit t reduction was also recommended (Chapter 7). Growth rates estimated for False Bay *U. robinsoni* sampled 10 years apart indicate a small increase and this had little effect on per-recruit outputs and biological reference point estimates. The limitation of the use of catch-at-age approaches to mortality estimation for resident philopatric species where populations are unlikely to be homogenous and under conditions of likely continuously declining recruitment, is an important consideration for future assessment of linefish species.

Future research

The research presented in this thesis has provided information on the taxonomy, life history and stock status on the two *Umbrina* species found in South African waters pertinent to the conservation and sustainable utilization of the resources. Topics for further research include:

1. Clarity on the identification and distribution of *Umbrina* spp. found along the West African coast, specifically morphological and genetic comparisons between South African *U. robinsoni* and the inshore species found off Angola (thought to be *U. ronchus*).
2. Information on the biology and stock status of *U. robinsoni* populations off the Eastern Cape, as inadequate samples were obtained from this region.
3. Improved estimates of batch fecundity and establishment of spawning frequency for *U. robinsoni* and estimates of both for *U. canariensis*
4. Improved understanding of spatial stock structure through a multidisciplinary approach, possibly including additional population genetic analyses, mark–recapture or underwater telemetry tracking techniques.
5. Continued monitoring of sampled populations within the St Lucia-Maputoland MPA in order to ascertain the time period for recovery and long term effects of depletion sampling within MPAs

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Appendix I: Global positioning system coordinates for sampled sites within the Maputaland MPA. These will be necessary if follow-up studies to monitor recovery are conducted in the future.

Site	Latitude	Longitude	*n* 1	*n* January 2003
BN 1	26°58.507’ S	32°52.616’ E	30	0
BN 2	27°04.35’ S	32°51.22’ E	88	0
BN 3	27°4.389’ S	32°51.17’ E	38	0
BN 4	27°5.147’ S	32°51.046’ E	25	6
BN 5	26°56.686’ S	32°52.773’ E	80	13
BN 6	26°58.816’ S	32°51.046’ E	45	0
BN 7	26°54.011’ S	32°53.084’ E	20	0

Positions are WGS84 projection; degrees, decimal minutes. *n* 1 = number of fish counted when site initially found, *n* 2003 = number of fish counted at each site during January 2003.