

**MANAGEMENT OF THE LINEFISH RESOURCE IN SOUTHERN
MOZAMBIQUE: A CASE STUDY FOR MARRECO (*CHRYSOBLEPHUS*
PUNICEUS)**

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Submitted in partial fulfilment of the
requirements for the degree of
Master of Science
in the
Oceanographic Research Institute
Faculty of Science
School of Life and Environmental Sciences
University of Natal - Durban
2001

PREFACE

The work described in this thesis was carried out whilst based at the Instituto Nacional de Investigação Pesqueira (IIP) in Maputo, and at the Oceanographic Research Institute (ORI) in Durban and under the supervision of Mr. Rudy van der Elst (deputy director) and Dr. Anesh Govender.

This study represents original work by the author and has not been submitted in any form to another University. Where use was made of the work or research samples of others it has been duly acknowledged in the text.

ACKNOWLEDGEMENTS

I wish to thank my supervisors Mr. Rudy van der Elst and Dr. Anesh Govender for their assistance, encouragement and advice. To Mr. Sean Fennessy, Ms. Alke Kruger, Mrs. Monica Moodley, Mrs. Maria Malek, Mrs. Vuyiswa Radebe, Mr. Bruce Mann and all staff of the Oceanographic Research Institute, in Durban, for their assistance in preparation of gonads, otoliths and reference material.

I also thank Dr. Adriano Macia, from the Universidade Eduardo Mondlane in Maputo, for supplying me with some formalin. Messers Langa and Tomas, are thanked for lending me a microscope, without which I could not carried out this research successfully.

I would also like to thank Dr. Manuel Mazibe, Director of the Institute for Fisheries Research in Mozambique for having given me the opportunity to undertake this study. To staff of IIP for helping me in data collection. I owe my thanks to Dr. Loforte and Mrs. Ascensão Pinto from IIP for their criticisms on an early draft of this manuscript. To Mrs. Rabia Abdula for helping me in searching references to improve my work.

I am grateful to NORAD for helping me with funds that allowed me to carry out this study.

Finally I thank my husband Francisco Lichucha for his patience and understanding during my study period. I would also like to thank my mother and my father for their patience in looking after my children. To my brothers and sister I thank you for your encouragement. My father and mother - in - law, my brothers and sisters - in - law for understanding my wish to study.

To you all I express my thanks.

ABSTRACT

This study provides information on the biology, stock status and the management of *C. puniceus*, a key linefish resource in southern Mozambique. This is regionally endemic to Mozambique and KwaZulu-Natal. Fairly resident species, is found on the continental shelf ranging north to Závora and south to KwaZulu-Natal and Transkei, and inhabits rocky seabeds, ranging between 20 and 100m. In Mozambique is mainly exploited by semi-industrial fleet, and exported to South Africa.

The reproductive biology, assessed through gonad somatic index as well as microscopic and macroscopic assessment, indicates that spawning extends over the spring months from August to November, peaking in September. It is a protogynous hermaphrodite, relatively slow growing and long lived species.

The length-weight relationships for male and female *C. puniceus* show to be different, and the overall length frequency distribution shows clear difference in size between male and female *C. puniceus*, with male length frequency distribution restricted to the larger size classes. The monthly length frequency distribution of female *C. puniceus* is unimodal and peak at 300 mm FL, male shows unclear year classes.

Age determination was carried out using otoliths and growth was estimated using the model developed by Punt *et al* (1993) for protogynous hermaphrodites reproductive styles. Validation of annuli was done by examining the outer margin of otolith, and also through mark and recapture information. Validation following the first method indicated that the opaque band is laid down twice a year, but the mark recapture results were inconsistent. This contradicts previously published information on *C. puniceus*, and thus, both single and double scenarios were modelled. The Von Bertalanffy growth parameters found for *C. puniceus* suggest relatively slow-growth, with the number of rings found from reading the sectioned otolith ranging from 2 to 18. Reproducibility of age estimates was evaluated using the average percentage error (APE) technique, and was equal to 22%. The age at full recruitment was found to be 2.5 and 5 years for bi-annual and annual

banding, respectively. The analysis of the age-at-50% maturity, based on double band scenario, suggests that *C. puniceus* mature at 1.5 year-old, which corresponds to a mean FL of 240 mm.

A preliminary yield per recruit assessment revealed that at the current fishing mortality, *C. puniceus* fishery is moderately overfished, with the spawning biomass-per-recruit at 35.43% and 36.57%, for one and two bands, respectively, of its unexploited level. Fishing mortality was equal to 0.2 year⁻¹ and 0.41 year⁻¹, for single and double band, respectively. YPR analysis shows that the single band scenario is less conservative than the double band assessment, which has a bearing on the management approach.

It is suggested as the preliminary management strategy a reduction of the number of boats. Indeed the average number of crew per boat, needs to be evaluated in terms of overall effort. To complement this management measures, there is a strong and urgent need to establish marine reserves in order to protect spawning stock, and also, to develop an overall linefish management plan, which will help in the management of the whole linefish resource in Mozambique. Furthermore, an age and growth study for *C. puniceus* over a larger geographical area needs to be done as a mean to overcome the differences between previous study and this study, once *C. puniceus* is being shared between the two countries (Mozambique and KwaZulu-Natal).

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CHAPTER ONE

1. STUDY AREA, GENERAL SAMPLING METHODS AND THE MOZAMBIQUE LINEFISHERY

1.1. Introduction

Mozambique is located in the southern part of East Africa, between latitudes 10° 27' S and 26° 52' S and longitudes 30° 12' E and 40° 51' E (Figure 1.1). The coastline, some 2770 km of it, is the third longest in Africa and is characterised by a large variety of habitats (mangroves, seagrass beds and coral reefs), ecosystems (estuaries and bays) and geomorphology (sandy beaches and rocky shores) (Massinga and Hatton, 1996). The country is divided into ten provinces of which seven are situated along the coast (Figure 1.1). The population is estimated at 15.8 million people, while the GDP per capita is US\$ 185.9 and the population growth currently stands at 2.3% per annum (<http://www.co.mz>, 1999).

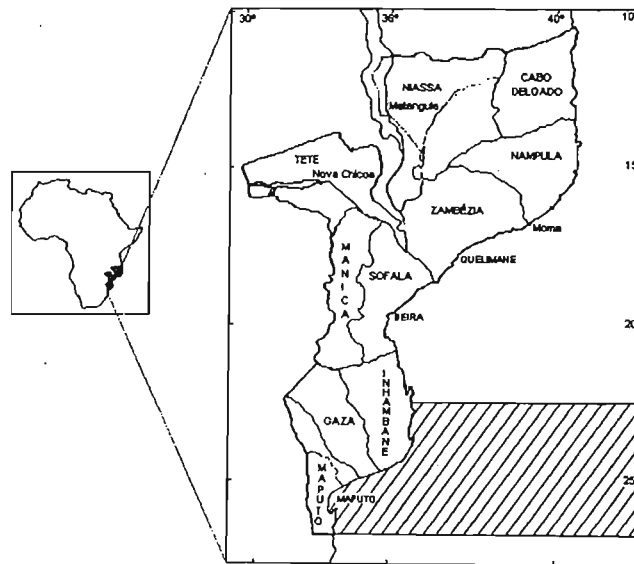


Figure 1.1 - Map of Mozambique and its provinces as well as the southern part of the country where linefishing is practised (hatched area).

Export products include mainly shrimp, finfish, lobster, cotton and wood (<http://www.co.mz>, 1999). Within the marine resources, shrimp has been the most important export for foreign earnings and national income. Linefish, though financially not as valuable to the nation, nevertheless provides essential protein to the diet and contributes to the employment and economy of local communities.

Traditionally, fishery research in Mozambique has been directed at the shrimp fishery due to its economic importance. However, since 1979 the Instituto Nacional de Investigação Pesqueira (IIP) in Mozambique has also been concerned with the lack of research of linefish stocks, and in 1994 started to face the challenge more seriously due to the increase in fishing effort in the semi-industrial linefishery. This increase has been observed since 1985 when Mozambican and South African semi-industrial boats began operations in southern Mozambique (van der Elst *et al*, 1995). Simultaneously, there was an increase in linefish activity related to tourism, originating mostly from South Africa (van der Elst *et al*, 1996). From 1985 to 1998 the number of vessels authorised to develop semi-industrial linefishing increased from 2 to 29 (Lichucha *et al*, 1998).

The species caught by the semi-industrial linefishing varies with *Chrysoblephus puniceus* being one of the most important commercially. This species dominates the catches and formed 47% of the total linefish catch in 1980 (Piotrovski, 1990). In 1997, *C. puniceus* formed only 12% of the total linefish catch offloaded in Maputo harbour. This decline in catch is cause for concern. Other causes for concern are change in mean size. Over 1987 – 1988 and the first half of 1989 the mean size was 407 mm FL for both sexes (Piotrovski, 1990). In 1996 it fell to 311 mm FL (van der Elst *et al*, 1997), and in 1997 the mean size of *C. puniceus* landed in Maputo harbour dropped to 299 mm FL (Lichucha *et al*, 1998). Garratt (1984) and Punt *et al* (1993) showed that in pristine stock the sex ratio of sparids, including *C. puniceus* is between 1:2.3 and 1:5 (m : f). Despite all changes referring to *C. puniceus* cited above, its sex ratio shows only a marginal change. In 1996 it was 1:5.6 (m : f) and in 1997 it was 1:10 (m : f). In 1998 and 1999 was 1 : 6 and 1 : 3 (m : f), respectively.

As there are no management measures to regulate this important resource in Mozambique, this study was undertaken to investigate the dynamics of *C. puniceus* and its fishery, and to develop management regulations for the linefishery. Knowledge of the biology of *C. puniceus*, age and growth, spawning season and mortality rates are all parameters that will contribute to the assessment of *C. puniceus* stocks exploited in Mozambique.

1.2. Study area and general sampling method

This study was confined to the southern part of the Mozambique coast where linefishing is most commonly practised. The main fishing area is from Závora to Ponta de Ouro, that is, between latitudes 24° 52'S and 26° 30'S (Figure 1.2).

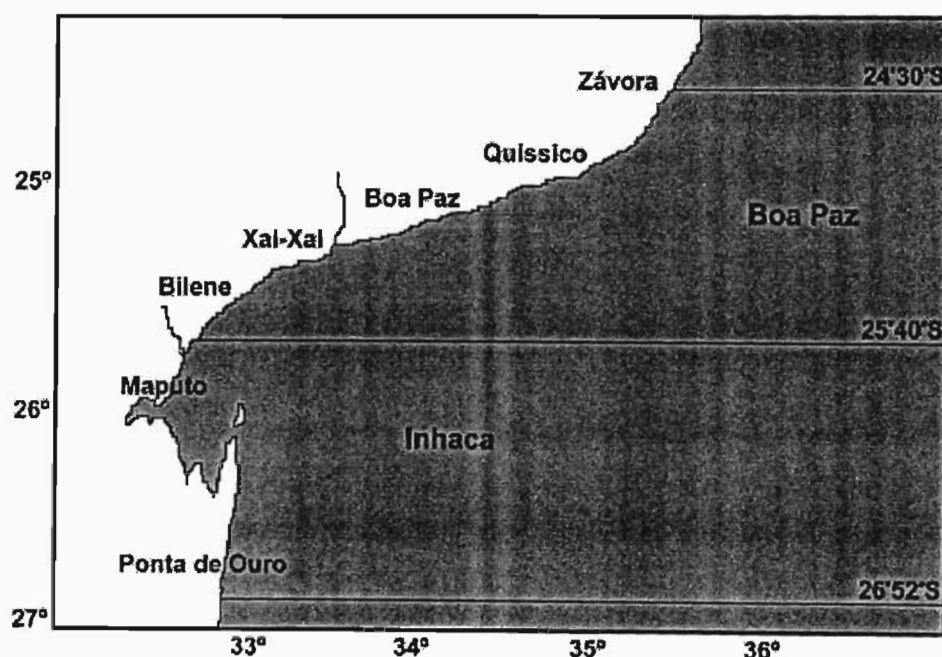


Figure 1.2 – Map of the southern traditional linefishing zone and sampling area, between Závora and Ponta de Ouro.

Biological data were collected during a period of about two years, from February 1997 to April 1999. During this period most samples were obtained from semi-industrial catches offloaded in Maputo fishing port. Samples of *C. puniceus* were taken randomly from

these vessels to the laboratory. From these samples the following information was recorded:

- Date of sampling (which was within an average of ten days of capture).
- Fork length of each fish measured to the nearest millimetre from the tip of the snout to the fork of the tail, lying naturally.
- Total length of each fish measured to the nearest millimetre, from the tip of the snout to the extreme end of the tail.
- Each fish was weighed to the nearest gramme.
- Each fish was sexed and its gonad maturity stage macroscopically assessed.
- Gonads were removed, weighed in grammes and stored in 10 % formalin for histological purposes. Histology was carried out to verify the macroscopic analysis. The tissues were embedded in paraffin wax, sectioned at 7 μm and stained with Erlich's haematoxylin (Drury, and Wallington, 1967) and eosin (Mahoney, 1966).
- Otoliths (sagittae) were also removed, washed in tap water to remove the saccular membranes, dried and stored in envelopes, for the age determination study.

This information was collected mainly by the author, with the help of sampling technicians at the IIP. Because fishers refused for their fish to be gutted, only twenty fish were sexed monthly. However, by the middle of the sampling programme to the end, i.e., from May 1998 up to March 1999, due to market pressure, fish were landed and sold in a gutted state. This change in the market system brought more difficulties to the sampling programme, particularly for sex identification, as the IIP could now only obtain some ungutted fish on request. Catches were also not separated by species, so it was difficult to estimate the total monthly catch of *C. puniceus*. Notwithstanding these limitations, the samples obtained, and the analyses conducted are considered robust and adequate for interpretation.

The information collected was initially recorded on data sheets and then captured on a simple database developed by the informatics technicians based at IIP to store the

information on computer. All information was checked, processed and analysed in Microsoft Excel 97 (Windows 95).

1.3. The Mozambique linefishery

Linefishing is defined as a form of fishing activity in which the basic fishing components consist of rod, reel, line trace and hook (Garratt, 1984).

At least five categories of linefish exploitation are identified by law in Mozambique (Regulamento da pesca marítima, 1996): industrial, semi-industrial, artisanal, subsistence and recreational. The following descriptions apply:

1. Industrial linefishing is conducted from port-based vessels, greater than 20m in length with a hold capacity of 20-30 tons. Catches are preserved frozen or on crushed ice. The horsepower is between 360 to 450 HP. These vessels are constructed of steel or timber with an average crew of 33-36. Equipment used includes handlines, as well as longline (Lichucha *et al*, 1998).
2. Semi-industrial linefishing is conducted from port-based vessels, which are usually of wood or steel construction and range in length from 10 to 20 m. The hold capacity range from 1 to 17 tons. All carry crushed ice to preserve the catch and to extend their range of operation, which is usually between 5 to 10 days fishing. The crew, ranging from 8 to 35 fishers, conduct the fishing. Equipment used includes handlines as well as stout fishing rods with large, non-gearred reels. These vessels are equipped with GPS positioning systems (van der Elst *et al*, 1997).
3. Artisanal linefishing is practised using boats not longer than 10 m in length with traditional propulsion such as paddles, wind or engines with very low power (Baloi and Premegi, 1998). The average number of crew range from 2 to 5, and each fisher typically uses one handline. The lines are between 80 to 100 m in length and the hooks are of variable size (Baloi and Premegi, 1998).

4. Subsistence fishing is practised by rural people. Fishers normally use a single hook and line to catch fish, which is not sold, but is for personal food security. They usually use canoes up to a maximum of 10 m in length.
5. Recreational fishing is conducted by local fishing clubs and by tourist anglers. Most use skiboats (van der Elst *et al*, 1995), which are typically South African built craft, often designed specifically to be launched through heavy surf (Garratt, 1984). They range from 3.8 to 8.1 m in length, with an angling crew ranging from 2 to 8 people.

Within the linefishery, two major groups of fish are caught: pelagic gamefish and demersal reef fish. Demersal reef fish form a higher proportion of the catch in which the family Sparidae is dominant. The species *C. puniceus* is commonly referred to as marreco in Mozambique and as slinger around the world. Is named slinger due to its slinging form when they are caught in great numbers (van der Elst, 1993). This species is endemic to the south-eastern coast of Africa being abundant in KwaZulu-Natal and southern Mozambique (Garratt, 1984). It inhabits rocky seabeds, ranging between 20 and 100m, and often forms large shoals (van der Elst, 1993). It is found on the continental shelf ranging north to Závora and south to KwaZulu–Natal and Transkei (Garratt, 1984). There have also been reports of this species in waters of Madagascar, occasional migrants have been seen as far south as East London; juvenile fish have been found further south near Knysna (Smith and Heemstra, 1986).

This species has been confused for several years with *Chrysoblephus cristiceps*, but there are clear differences between them. While *C. cristiceps* has a dark spot at the base of the last dorsal ray and a faint bar below eye, *C. puniceus* has no dark spot in dorsal ray and the blue bar below eye is heavy (Smith, 1938).

The biology of this species was first investigated by Garratt (1984) who discovered that it is hermaphrodite and change sex from females to male at 5 years and the spawning occurs off KwaZulu-Natal during summer.

CHAPTER TWO

REPRODUCTIVE BIOLOGY OF *CHRYSOBLEPHUS PUNICEUS*

2.1. Introduction

Reproduction is one of the principal events in the life history of living organisms. In some cases the event involves movement of fish from one area to another to spawn (King, 1996). The time of the year in which the spawning occurs, the mean length or age of fish at which it happens, and the nature of the reproductive style, are important criteria for fisheries management (King, 1996), because this information can help to determine closed seasons and the length at which the fish can first be caught (which is usually set above the age-at-50% maturity (Butterworth *et al*, 1989)). Further, if the reproductive style involves sex change the fishing activity (which is usually directed towards large fish) can lead to a reduction of one sex, altering the sex ratio. The awareness of the need to incorporate fish reproductive strategies into fisheries modelling is growing and this aspect becomes more relevant in the case of sex changing fish (Shapiro, 1987; Garratt *et al*, 1993).

In *C. puniceus*, the reproductive strategy was first studied by Garratt (1985), who found it to be protogynous hermaphrodite, which means that males develop from adult female through sex change. His theory was supported by evidence from histological analysis, where he found the presence of a large percentage of degenerating pre-vitellogenic oocytes at certain sizes of fish within hermaphroditic gonads (Garratt, 1985).

The reproductive cycle of fish can be determined by (i) estimation of the monthly gonad somatic index, which assumes that an ovary increases its weight in relation to body size with increasing gonad development (De Vlaming *et al*, 1981; King, 1996), (ii) the histological examination of sectioned gonads (De Vlaming, 1972) and (iii) through macroscopic analysis of the gonads (Coetzee, 1983 and Garratt, 1984).

Although Garratt (1984) studied the reproduction of *C. puniceus* in KwaZulu-Natal, his studies did not extend to southern Mozambique, hence there is no knowledge about the spawning season in Mozambique. This chapter, therefore, will deal with the reproduction of *C. puniceus* to determine the spawning season and the age-at-50% maturity (which is presented in the chapter 4) by using the three methods mentioned above.

2.2. Materials and methods

Sex and maturity stages were identified macroscopically and microscopically, and defined as described by Garratt (1985) and modified for this study following van der Walt (1995) (Table 2.1).

Table 2.1 - Description of the macroscopic maturity stages (Garratt, 1985) used for classification of gonads of *C. puniceus* (modified from van der Walt, 1995).

Stage	Female	Male
1 - Inactive	Ovary occupies less than half of the body cavity and slightly rounded, translucent in colour.	Testicular portion thin and flattened, usually off-white, sometimes not visible.
2 - Active	Ovaries swollen and yellow/orange in colour and occupy half of body cavity, eggs are visible to the naked eye.	Testes swollen and white in colour, sperm is extruded from the main duct if cut and pressure is applied.
3 - Ripe	Ovaries very large and yellow/orange in colour, opaque eggs visible, ovaries may be bloodshot and flaccid if some spawning has occurred.	Testes large and swollen with sperm present in the main duct, white in colour.
4 - Spawning	Ovaries very large and yellow/orange in colour, translucent eggs in the lumen are visible, ovaries may be bloodshot and flaccid.	Testes extremely large, with sperm free flowing from the vent, pinkish in colour.
5 - Spent	Ovaries flaccid, bloodshot and reduced in size.	Testes reduced in size, greyish - white in colour.

In this study the spawning stage was considered as a part of the ripe stage because the spawning condition itself was not observed. So, the total number of stages considered in this study was four, the ripe being the third stage and spent the fourth.

The period of reproductive activity was determined by evaluating the state of gonads on a monthly basis. This assessment included three different techniques, viz:

1. gonad somatic index (GSI) calculated for each month.
2. histological examination of sectioned gonads, and
3. the macroscopic analysis of the state of maturity of gonads.

For the GSI and histological examination only the gonad from ungutted fish were used.

The GSI (De Vlammig *et al*, 1981) was calculated for each fish using the equation, in which the body mass of the fish includes the gonad:

$$GSI = \frac{Gonad\ mass\ (g)}{Body\ mass\ (g)} \times 100 \quad (1)$$

2.3. Results

During the sampling period (February 1997 to April 1999) female gonads were only weighed for the last nine months, i.e., from August 1998 to April 1999. Although data were thus limited for the estimation of GSI (100 female gonads), results indicated that the period of maximum reproductive activity, which is represented by the large number of female fish in ripe condition (stage 3) as being from August up to October, with a peak in September, following this period there was a decline in GSI (Figure 2.1). A slight increase of the gonad index was noted from March and April.

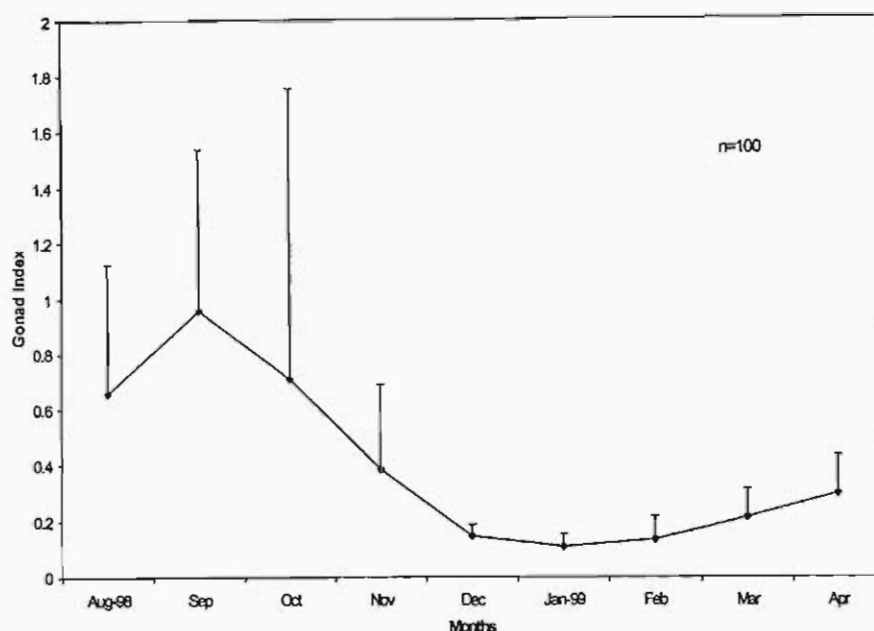
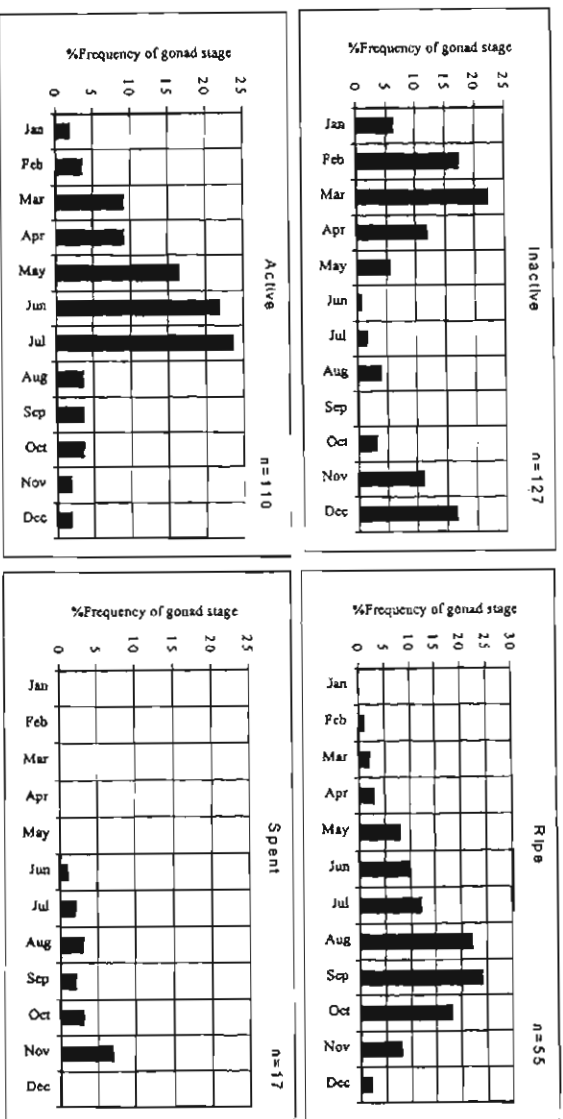


Figure 2.1 - Average annual gonad indices of female *C. puniceus*. Vertical bars represents one standard deviation from the mean.

Monthly distribution of the various gonad maturation stages in female and male *C. puniceus* observed microscopically shows that the development of gonads began in February through July (Figures 2.2A and B). During these months there was a gradual increase in the number of fish in the active phase (stage 2). Fish in a ripe condition occurred in most months, especially between April-May up to November, peaking over August to October, and a decrease of the ripe individuals in November. November also showed an increase in fish in the spent condition (stage 4) (Figures 2.2A, and B). The majority of fish in an inactive phase (stage 1) were observed from October to April (Figures 2.2A, and B). All the above features described for the microscopic observation were also observed in the macroscopic analysis. In the macroscopic analysis it was also observed that fish in an inactive and active stages are found throughout the year. The ripe condition in the macroscopic analysis occurred at a low level throughout the year with a peak observed from August up to November over the year (Figures 2.3A and B).

(A)



(B)

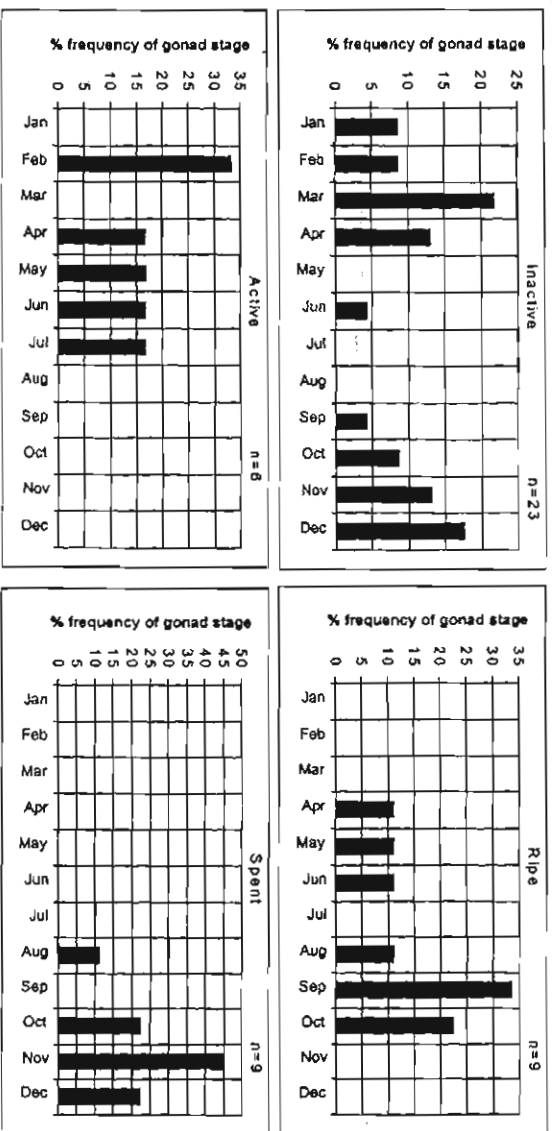
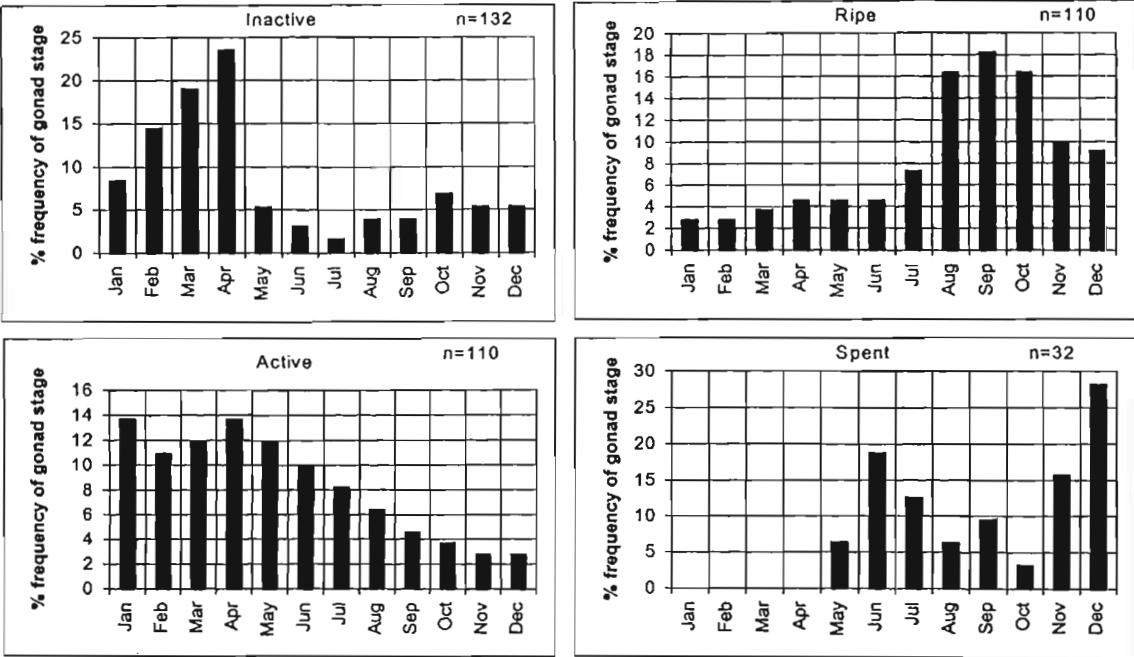


Figure 2.2 - Monthly distribution of various reproductive stages observed microscopically in (A) female and (B) male *C. puniceus*.

(A)



(B)

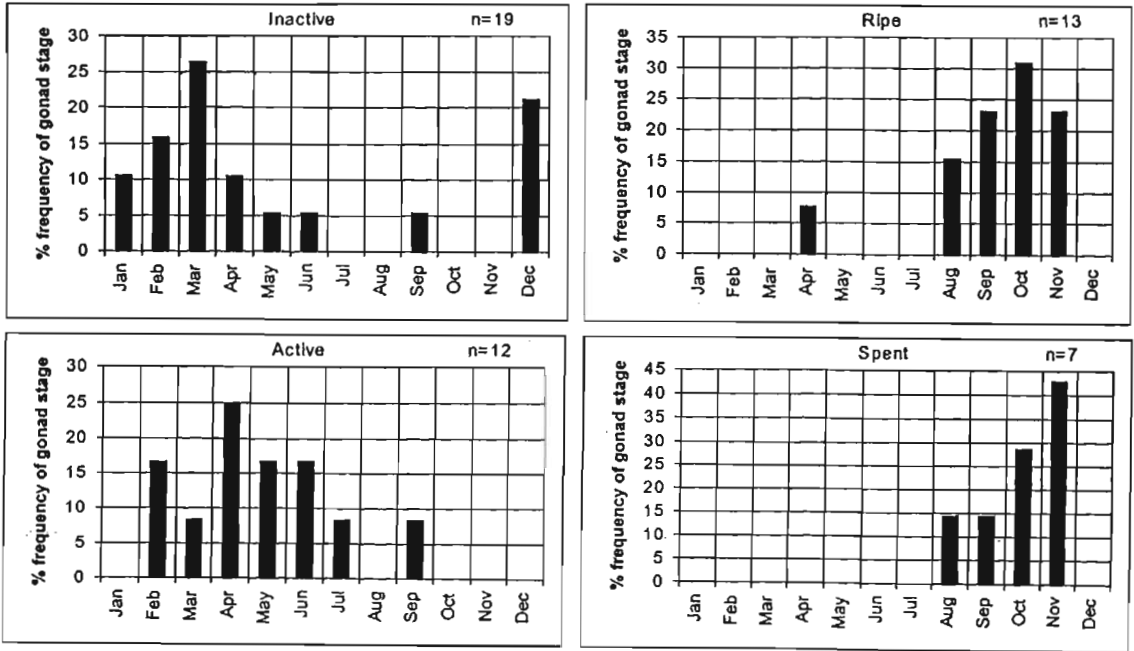


Figure 2.3 - Monthly distribution of various reproductive stages observed macroscopically in (A) female and (B) male *C. puniceus*.

2.4. Discussion

The reproductive seasonality of fishes is influenced, among other factors, by the increase of water temperature, which influences the gonad maturation (De Vlaming, 1972). For instance, the sparids of tropical and sub-tropical waters have a long breeding seasons and usually starts to spawn in winter peaking in spring, while those of temperate water spawn in spring and summer and have shorter breeding season (Garratt, 1984; Buxton and Clarke, 1991). It probably occurs because in tropical and subtropical waters the temperature is warmer during most of the months and it favour the gonad maturation, while in temperate water there is a shorter period of warmer temperature (Fennessy, Oceanographic Research Institute, Durban, personal communication).

According to the type of spawning, fish has been classified into three categories: (i) total synchronous spawners, when all the oocytes within the ovary reach maturity simultaneously; (ii) group synchronous spawners, when two distinct groups of oocytes are present in the sexually mature gonad; (iii) and asynchronous spawners, which are characterised by having oocytes in all stages of development, and the spawning season of these fish is usually protracted (De Vlaming, 1972; Wallace and Selman, 1981). *C. puniceus* fall into this third category (Garratt, 1985).

The reproductive activity of *C. puniceus*, confirmed through analysis of the gonad somatic index (GSI), indicates that it is likely to start during winter in April/May and extends over the spring months from August to November, peaking in September. The seasonality is showed by the decline of GSI after peak reproductive activity. This period was confirmed by the microscopic and macroscopic assessment of the gonads, which shows that the reproductive activity starts soon after April with the peak months in August to November. This occurrence happens synchronously between male and female fishes. Garratt (1984) examined gonads of *C. puniceus* macroscopically off KwaZulu-Natal, and found that there was an extended spawning season, starting in winter and peaking in spring between August and October. He also confirmed this through GSI. Clearly, the *C. puniceus* in both regions have similar spawning, not unexpected considering that both area are tropical. Punt *et al* (1993) in the preliminary results of a

tagging exercise suggests that younger fish of this species migrate between KwaZulu-Natal and Mozambique waters, and they hypothesised that this migration supplements the stock¹ of KwaZulu-Natal.

¹ Stock was defined by Punt *et al* (1993), for the aim of their study, as the management unit, i.e., does not need to be genetically isolated.

CHAPTER THREE

3. SOMATIC RELATIONSHIP AND LENGTH COMPOSITION OF THE CATCH

3.1. Introduction

Fishermen, as opposed to fisheries managers, have different objectives in their fishery. While some fishermen simply maximise the weight of fish to be caught, others specifically target certain lengths or weight of fish, depending on the market demand. As the parameters obtained from these transformations are important input for yield-per-recruitment analysis, scientist must thus take this issue into account before advice managers in drawing up strategies to control the fishery. The equation expressing these conversions could be found in the relationship between length and weight, and between lengths of the fish. In the relationship between length (L_i) and weight (W_i), the weight varies as some power of the length and is expressed by the equation: $W_i = aL_i^b$. The parameters a and b are constants and are specific to each species (Ricker, 1975). The value of b describes the kind of fish growth and varies between 2.5 and 3.5. If it is equal to 3 it indicates isometric growth, which means that a fish has an unchanging body form. If the value of b is greater or lesser than 3, it indicates allometric growth, which means that the body form changes with the fish growth (Ricker, 1975; Pauly, 1984).

Length frequency data and the biological characteristics of the fish are also important input for preliminary assessment of the fish stocks. Length frequency data can be used to estimate growth using the Petersen method (Sparre and Venema, 1997), which follows modal progressions corresponding to the growth of cohorts within the population. However, for this study it was not possible to use the Petersen method or other methods that are based on length frequency analyses because, although some modes were identified, no modal progressions could be determined.

In this chapter computation of equations expressing length-weight and fork length - total length relationship were carried out to provide the means to convert between the measurements. Furthermore, this chapter summarises the length composition of the catches of *C. puniceus*.

3.2. Materials and methods

3.2.1. Somatic relationship

The fork length - weight relationship was described by the following equation (Ricker, 1975):

$$W_{i(g)} = a FL_{i(mm)}^b \quad (1)$$

The parameters a and b were estimated by plotting the logarithm of weight (W_i) against the logarithm of the fork length (FL_i) for fish i of various sizes, b being the slope of the fitted line, and a the exponential of x intercept from the regression of the log-transformation (Ricker, 1975) i.e.:

$$\text{Log} W_{i(g)} = b \text{log} FL_{i(mm)} + \text{log} a \quad (2)$$

Parameters a and b were estimated for males and females separately. A student T-test was applied to establish if the parameters of males and females differ significantly (Zar, 1974).

Total length – fork length relationships were also estimated, and the equations expressing this relationship were derived by the method of least square from the general equation $Y = a + bx$, where Y is the dependent variable, a is the Y intercept, b is the coefficient of the regression and x is the independent variable (Papageorgiou, 1979).

3.2.2. Length composition

During the study period 14915 specimens were measured from commercial catches. From these only 460 could be sexed, as the buyer preferred gutted fish. From this total only 59 were male and the remaining 401 were female fish. The overall sex ratio and sex ratio per length class of *C. puniceus* was estimated. A student T-test was used to determine if there is any significant difference between the mean size of male and female *C. puniceus* (Zar, 1974).

3.3. Results

3.3.1. Somatic relationship

The length – weight relationship of *C. puniceus* for males and females are illustrated in Figures 3.1. The estimates of the parameters of the length-weight relationships are summarised in Table 3.1. The value of r^2 of both sexes is approximately equal to 1, which indicates the adequacy of the formulae to describe the relationships. The test between the two slopes indicates that the difference is significant ($P < 0.001$), the test statistic and the degree of freedom are shown in Table 3.2.

Table 3.1 - Estimates of the parameters of the length-weight relationship of *C. puniceus* by sex.

	n	r^2	Parameter
Males	53	0.96	a = 5.99E-05; b = 2.86
Females	310	0.96	a = 1.16E-04; b = 2.74

Table 3.2 – The result of student T-test comparing the slopes of male and female *C. puniceus*.

(degree of freedom)	t (T-test)	t _{0.05(2), 359} (critical value at 5% significant level)
359	3394.53	1.967

Figure 3.2 shows the fork and total lengths relationship of *C. puniceus* for males and females. The equations expressing this relationship are as follow:

Males: $TL(mm) = 26.9 + 1.16FL(mm)$ $(n = 59, r^2 = 0.88)$

Females: $TL(mm) = -21.36 + 1.3FL(mm)$ $(n = 389, r^2 = 0.97)$

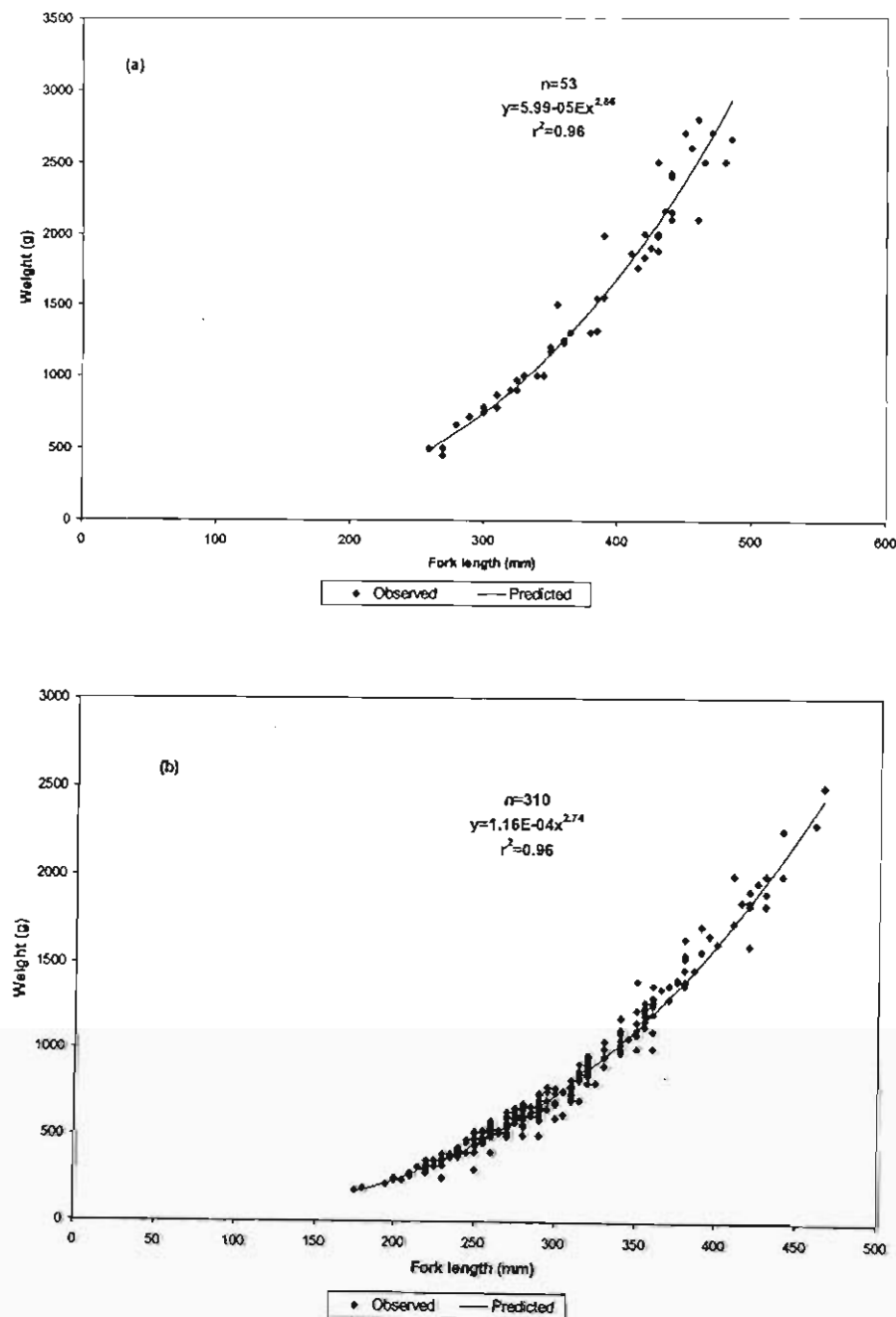


Figure 3.1 – Length-weight relationship for (a) male and (b) female *C. puniceus*.

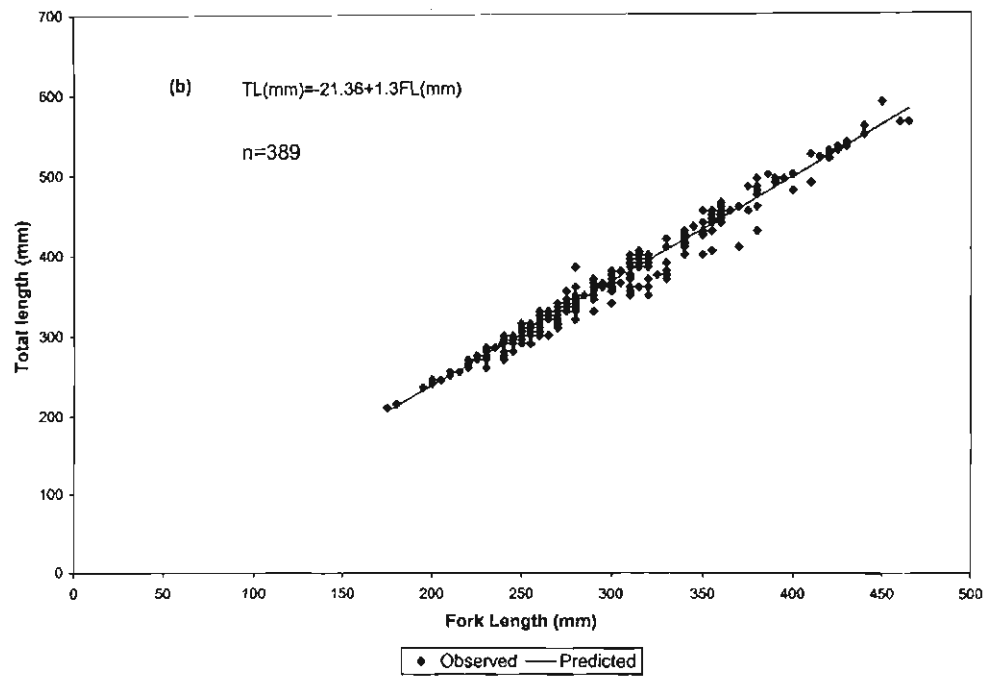
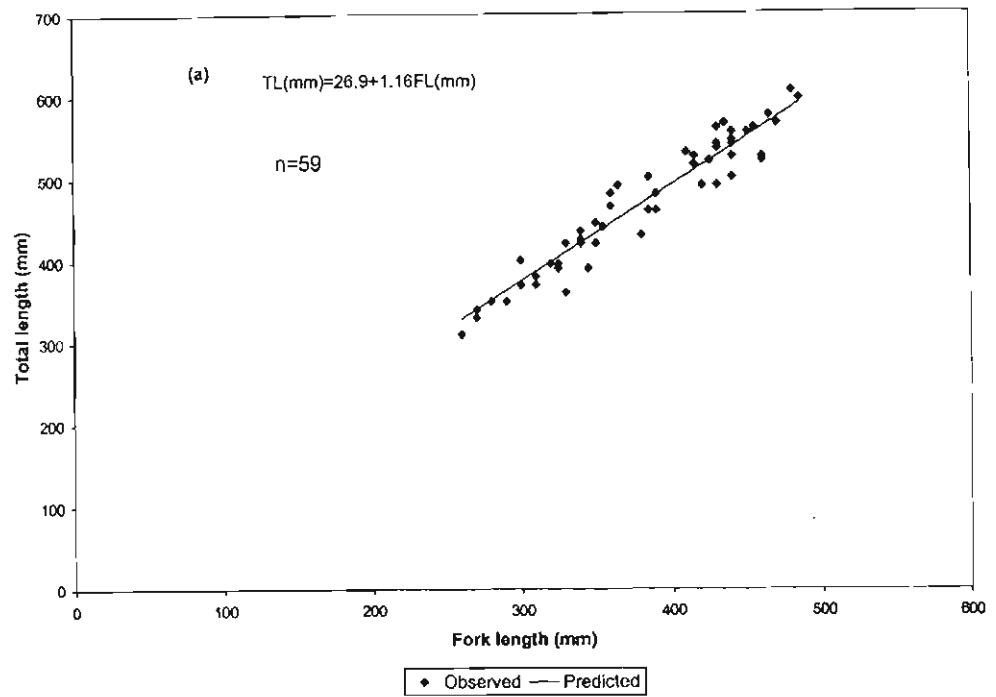


Figure 3.2 – The relationship between fork length and total length for (a) male and (b) female *C. puniceus*.

3.3.2. Length composition of the catch

The overall length frequency distributions of male and female *C. puniceus* are given in Figure 3.3 and Table 3.3. It is evident that there is a marked difference in size of male and female, and males dominated the larger size classes, and females dominate in number per size class. The peak mode in the length distribution occurred at 260 mm FL for females, and for males it was not clear (Figure 3.3). The mean size of male and female was 376.3 mm and 292.6 mm FL, respectively. Figure 3.3 indicates that this species becomes vulnerable to the fishery at approximately 160 mm FL. In the monthly distribution (Figure 3.4) the peak mode is observed at 280 mm FL in the months of February, May, June and July. In January, March, April and August up to December there is a shift to 300 mm fork length (Figure 3.4).

3.3.2. Sex ratio

The overall sex ratio (female:male) estimated for *C. puniceus* from macroscopic observation is 6.8 : 1 (Table 3.3). Looking at the sex ratio by size class a decrease of females in relation to males occurs with increasing length (Table 3.4).

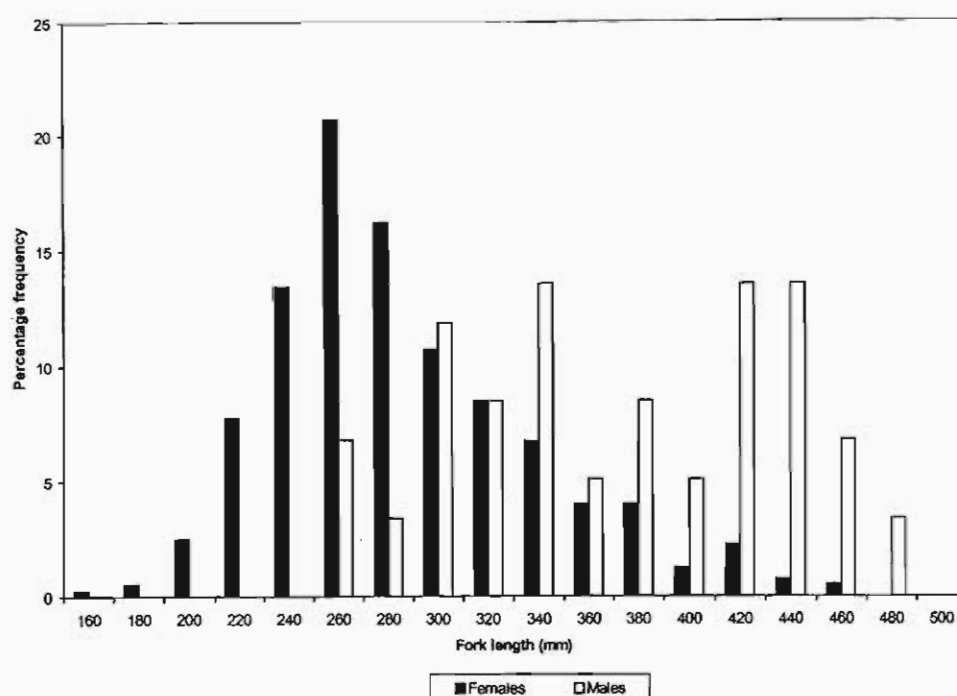


Figure 3.3 – Percentage length frequency distribution of male (n=59) and female (n=401) of *C. puniceus*.

3.4. Discussion

The results obtained for the length-weight relationships are different for male and female *C. puniceus*. The same is observed for *C. puniceus* off KwaZulu-Natal (Garratt, 1984). There is also differences in the lengths relationships for *C. puniceus* in Mozambique and KwaZulu-Natal. Unfortunately, there is no means to compare the results of the length relationship of males and females with that off KwaZulu-Natal, as the length relationships were not done for each sex separately.

The overall length frequency distribution shows clear difference in size between male and female *C. puniceus*. The male length frequency distribution is essentially restricted to the larger size classes, with the modes of male and female clearly different, although the peak mode of the male was not clear. Garratt (1984) observed this difference from the sample of Mozambique and off KwaZulu-Natal, in which the difference between male and

female *C. puniceus* was marked. He also suggests that this difference in the size between male and female is expected in the species that undergoes sex change. Although it is already known that this species change sex we can not always conclude that the difference in the size between male and female of a given species implies sex change. There are many reasons that can cause such difference. For instance, Sadovy and Shapiro (1987) postulate that the difference in the size between male and female fish could be caused, between other factors, by the differences in growth rates and seasonal recruitment of males and females. Furthermore, the different mortality rates, the difference of the fishing areas with small fish, generally composed by females, occupying shallow water and big fish (generally composed by males) abounding deep areas, and if the sampling is not done from sample of intermediate area, it can originate differences in size frequency distribution (Sadovy and Shapiro, 1987).

The monthly length frequency distribution of *C. puniceus*, whose peak mode occurs mostly at 300 mm FL, is unimodal with unclear year classes. In other studies on *C. puniceus* (Garratt, 1984) the length frequency distribution was also shown to be unimodal. This could be related to the extended spawning season, which lasts for seven months (in the case of Mozambique), thus, the modes grow into each other. Furthermore, this could be an indicator that only a certain part of the *C. puniceus* population is accessible to the fishery (Garratt, 1984).

The length-weight relationship of male and female is significantly different. It is explained by the student T-test between the two slopes, which give a $P < 0.001$, which mean that there are marked differences in growth between male and female *C. puniceus* (Ricker, 1975).

The overall sex ratio 1:7 (m : f) found in this study is different from the expected 1:1. Garratt (1984) also observed this from *C. puniceus* when he found a sex ratio (m : f) of 1:2.3 and 1:18 from Mozambique and KwaZulu-Natal samples, respectively. Such a sex ratio could be the result of sex change, growth and longevity (Wenner, 1972). Great fishing pressure on the resource, as that applied on the *C. puniceus* fishery off KwaZulu-Natal (Garratt, 1984), could also cause shift in the sex ratio in favour of females, as

fishers target big fish, which is mainly composed of male fish. It could be justified by the sex ratio per size class showed in Table 3.4, which shows clearly that as the size class approximate to 520 mm FL there is a predominance of male fish, and the sex ratio is almost equal to 1 : 1 (m : f) so that, if there is a search of big fish obviously that will be composed by male, and the sex ratio will become skewed.

Table 3.3 – Fork length frequency distribution of *C. puniceus* (male, female and sexes combined) sampled from 1997 to 1999 in southern Mozambique.

Class (mm)	Males		Females		Both sexes	
	Number	Percent	Number	Percent	Number	Percent
180	0	0	2	0	22	0
200	0	0	5	1	103	1
220	0	0	16	4	429	3
240	0	0	42	10	876	6
260	2	3	67	17	1652	11
280	4	7	81	20	2545	17
300	5	8	48	12	3037	20
320	6	10	54	13	2265	15
340	7	12	21	5	1645	11
360	6	10	23	6	995	7
380	4	7	19	5	518	3
400	3	5	7	2	286	2
420	5	8	7	2	202	1
440	11	19	7	2	193	1
460	3	5	2	0	99	1
480	3	5	0	0	48	0
500	0	0	0	0	12	0
520	0	0	0	0	6	0
540	0	0	0	0	3	0
560	0	0	0	0	1	0
	59		401		14915	

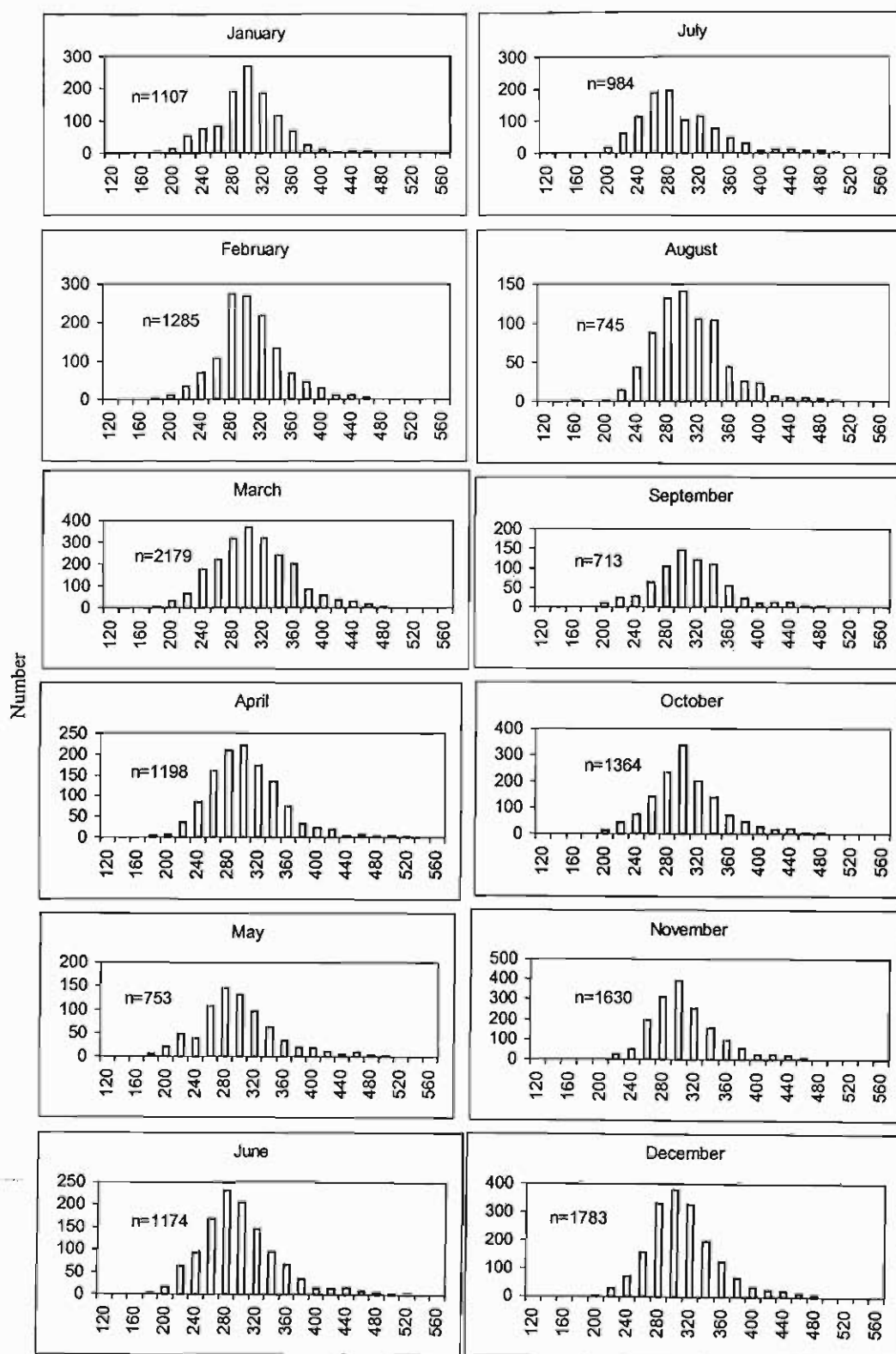


Figure 3.4 – Monthly length frequency distribution of *C. puniceus* sampled in southern Mozambique from 1997 to 1999.

Table 3.4 - The sex ratio per length class and overall sex ratio (male:female) of *C. puniceus* sampled in southern Mozambique.

Class (mm)	Males	Females	Sex ratio (m : f)
180	0	2	-
200	0	5	-
220	0	16	-
240	0	42	-
260	1	67	1:67
280	4	81	1:20.25
300	5	48	1:9.6
320	6	54	1:9
340	7	21	1:3
360	6	23	1:3.83
380	4	19	1:4.75
400	3	7	1:2.3
420	5	7	1:1.4
440	11	7	1:0.63
460	3	2	1:0.66
480	3	0	-
500	1	0	-
520	0	0	-
Overall	59	401	1:6.79

CHAPTER FOUR

4. AGE AND GROWTH

4.1. Introduction

Stock assessment, and rational management of fisheries, require knowledge of the growth of fish harvested. Growth rate data are essential for estimating the yield and determining the rate at which fish can replace themselves under a regime of fishing pressure. For instance, for slow growing species yield per unit stock is low because of a low production of biomass (Brother, 1979; Buxton and Clarke, 1989). So that, having information of the growth rate of a slow growing species will help to understand that due to this characteristic, the species is susceptible to growth overfishing, and after heavy exploitation its recovery will be slower. Knowledge of the age and growth of fish is also needed to estimate important parameters, such as mortality used as inputs in the stock assessment models such as yield-per-recruit, which is a basis for fishery analysis (Brothers, 1979; Pauly, 1987). This is also required for construction of age/length keys, which provide the distribution of lengths for each age-class (Butterworth *et al*, 1989, Campana and Jones, 1992). Age plays an important role in the examination of the past and in the prediction of the future changes in relation to the exploitation of a given resource (Brother, 1979).

Fish are generally cold-blooded animals (Rozin, 1968; Smith and Heemstra, 1986), which means that their body temperature remains close to that of its environment (Pennak, 1964; Smith and Heemstra, 1986), varying by less than one degree from the temperature of water at which they are living (Smith and Heemstra, 1986). Temperature influences the metabolism of fish, and consequently controls the processes of growth and reproduction (van der Elst, 1993). The availability of food also plays an important role in growth of fish (Brothers, 1979; Smith and Heemstra, 1986; Beamish and McFarlane, 1987). Generally, fish tend to grow faster when the food is plentiful, and slower when there is scarce food (Weatherley, 1972).

The presence of bands in hard tissues, such as scales and otoliths, are a response to the seasonal variation in temperature and productivity, resulting from variations in growth rate (Brothers, 1979). The bands on the hard tissues are generally related to the changes in the temperature; in summer the temperature is higher and growth of fish is faster, while in winter the reverse is true. In temperate waters fish have a distinct seasonal growth variation, in summer and in winter, representing periods of faster and slow growing phases, respectively (Smith and Heemstra, 1986), and are thus relatively easy to age. Conversely, in tropical water, fish live in an environment that shows less seasonal variation in temperature all over the year. This makes it more difficult to age these fishes (Brothers 1979; Smith and Heemstra, 1986; Beamish and McFarlane, 1987) as the bands on the otoliths are less developed or even absent (Brothers, 1979). Ageing fish is still more difficult for long-lived species, as the growth becomes slower or stops when the fish get older, the bands in the hard tissue are more crowded together (Brothers, 1979; Beamish, 1979; Smith and Heemstra, 1986). Furthermore, marginal bands generally stack in long-lived species (Smale and Punt, 1991; Buxton and Clarke, 1991; Beckman *et al*, 1991).

There are different techniques used to determine the age of fish. These methods include length-frequency analyses, interpretation of seasonal bands in hard tissue, marking of individual fish and through Walford plots (Weatherley, 1972; Ricker, 1975; Casselman, 1987). All these methods depend on whether the species has a well-defined spawning season, so those cohorts can be more distinctly discriminated.

The length frequency method is based on the length frequency distribution of fish where several modes correspond to distinct age groups (cohorts) (Weatherley, 1972; Casselman, 1987). This is also called the Petersen method. One advantage of this method is that, it is relatively simple to obtain information on length from the fishermen and does not require higher technical skills to interpret the modes and analyse the age and growth of the fish. It is suitable for the fish in which the spawning season is not long and the influx of new recruits occurs over a short period (Casselman, 1987). However, this method has its limitation for tropical fish, where the environment is nonseasonal and constant, which is one of the factor that lead fish to spawn all year round (Fowler, 1995). In this case it

becomes difficult to separate age classes, even for younger fish, due to the overlapping of older age classes (Brothers, 1979; Casselman, 1987). For the interpretation of hard tissue, growth bands in them have been used to estimate the age of fish. These tissues, such as opercular bones, scales, fin rays, vertebrae or otoliths lay down seasonal bands (Casselman, 1987), which can be used for age determination by counting these bands (Casselman, 1987). The age of the fish can also be studied through marking individual fish, which can be tagged with a numbered tag made from metal or plastic or the fish is injected with tetracycline, which produces a chemical mark in the otolith. When recaptured the number of years the fish has been at liberty should coincide with the number of bands laid down after the chemical mark.

From the methods for age determination cited above, the interpretation of hard tissue, in this case otoliths, was chosen for age determination of *C. puniceus* in this study. It is generally acknowledged to be the most reliable method, yields information on age and growth rate of individuals rather than the average fish, thus establishing population parameters (Brothers, 1979). Unlike examination of other hard tissues like scales, otoliths continue to grow as fish grow (Beamish and McFarlane, 1987; Rice, 1987). Although lengths were collected, these were considered less useful for the estimation of age, as the spawning season is shown to be protracted (Chapter three) and the different year classes can overlap, biasing the age estimate (Casselman, 1987).

Otoliths are calcareous structures found in the membrane labyrinth of the ear in vertebrates, including that of fishes (Henderson and Henderson, 1963; Pennak 1964). There are three types of otolith in fish, sagitta, lapillus and asteriscus (Secor *et al*, 1992). In all ageing studies, the sagitta otolith is used for age determination because it is the largest, easiest to remove and handle, and is assumed to contain the widest increments for clearest resolution of microstructural features (Secor *et al*, 1992).

The study of fish growth is also important in the context of its maturation. Age-at-sexual maturity is important in understanding the productivity of a population. One of the most important factors of the future abundance of a fish is the proportion of reproductively active fish in a population. This needs to be determined and managed so as to ensure the

availability of young fish for future generations. An adequate reference point is to consider 50% of fish attaining maturity (Butterworth *et al*, 1989). This parameter is important because in a regulated fishery, the age at which fish are first caught is usually set at level to ensure that fish can first spawn before been caught (Gulland, 1983).

4.2. Materials and methods

4.2.1. Age and growth

As *C. puniceus* otoliths are dense, sectioning was required so that light could be transmitted in order to more clearly identify the bands. Sectioning was carried out by the method described by Hecht and Smale (1986). Sagittae otoliths were mounted in resin in a single row in a plastic mould and sectioned through the nucleus to obtain a thin section of 25 μm . They were then mounted on labelled plain glass slides using DPX, which is a mixture of a synthetic resin mounting media, composed by distyrene (a polystyrene), dibutylphthalate (a plasticizer) and xylene, and viewed under a binocular microscope. Growth bands were counted by reading the otoliths against a black background under reflected light using a low power-dissecting microscope. Opaque bands are optically dense zones, which inhibit the passage of light. These appear dark when viewed under transmitted light, and bright when viewed under reflected light (Summerfelt, *et al*, 1987; Secor *et al*, 1995;). Dark bands were counted from the nucleus to the outer margin of the otolith. In order to ensure the accuracy of the number of bands counted, each otolith was read three times by the same reader with a minimum of one week between readings. If two or more readings per otolith corresponded, or if the difference was of just one band, this was taken as the correct estimate, and the average of the band counts was taken as the age estimate. If the difference between any two of the readings was of more than one band then the otolith was rejected.

Because age determination is so important to stock assessment, and because there is often considerable variability with individual estimates of age, it is important to establish some measure of reliability of readings. Reproducibility of the age estimates was evaluated using the average percentage error (APE) (Beamish and Fournier, 1981), which is used to

compare determinations of different readings or between readers. If for the set of determinations the index is small it means that the readings are precise. APE is described by the expression below:

$$\text{APE} = 100 \left[\frac{1}{N} \sum_{j=1}^N \left[\frac{1}{R} \sum_{i=1}^R \frac{|X_{ij} - \bar{X}_j|}{\bar{X}_j} \right] \right] \quad (1)$$

Where: N is the number of fish aged,
 R is the number of times each fish is aged,
 X_{ij} is i th age determination of the j th fish,
 \bar{X}_j is the average age for the j th fish

The number of growth bands do not necessarily always coincide with the number of annuli, i.e. year bands, as some fish may deposit two bands per year for example. Thus, validation of ring deposition rate is imperative to determine how often the opaque band is actively laid down, i.e., how often it occurs each year (Geffen, 1992). Validation of the opaque band was thus determined by examining visually the outer margin of the otolith for each month of the year. If the outer margin of the otolith were bright, then the opaque zone was laid down in that particular month. The assessment was carried out pooling together all samples and determining the monthly frequency of the occurrence of the opaque zone. Validation of the periodicity of the opaque band was also done by using the time-at-liberty of recaptured fish that had been tagged. In this case, the periodicity of opaque band is confirmed if the growth equations derived from age-length data predict reasonably the increment during the time-at-liberty of tagged individuals. The information on tag-recapture were obtained from Sedgwick's/ORI/WWF tagging programme where 122 *C. puniceus* had been recaptured. The following equation was used to predict the time-at-liberty of tagged fish (Kirkwood, 1983):

$$\text{When } \delta l = -\frac{1}{K} \ln \left(1 - \frac{\delta l}{L_{\infty} - R} \right) \quad (2)$$

re:

δ is the predicted time-at-liberty,
 δl is the length increment between release and recapture,
 R is the release length,

L_{∞} are the asymptotic lengths of males and females,
respectively,
 K are the growth rate parameters for males and females,
respectively.

Because growth rates of male and female *C. puniceus* are different they should be treated differently.

Because there is usually considerable variability in the growth of individual specimens it is useful to express growth on an average basis by fitting an appropriate model to the data. There are several growth models that can describe age-length data, such as the logistic, von Bertalanffy, Richards, Gompertz and Putter growth models. The scientist has to choose which model best describes the data (Schnute, 1981). *C. puniceus* is a sex changing species and growth may be different between the sexes. So, the selection of a growth model must take into account this characteristic. The growth model of von Bertalanffy, modified by Garratt *et al* (1993) to accommodate sex-change, was used to describe the growth of *C. puniceus* in this study. The equations are as follow:

$$\text{Female} \quad L_t^f = L_{\infty}^f \left(1 - e^{-K^f(t-t_0^f)} \right) \quad (3)$$

$$\text{Male} \quad L_t^m = \sum_{\alpha} \beta_{\alpha}^t L_{\infty}^m \left(1 - e^{-K^m(t-t_0^{m,\alpha})} \right) \quad (4)$$

Where: $L_{\infty}^m, L_{\infty}^f$ are the asymptotic lengths of males and females
respectively,
 K^m, K^f are the growth rate parameters for males and females
respectively,
 t_0^f is the age at which females have zero length,
 α^a is the fraction of males of age t which changed sex at age
 α ,
 $t_0^{m,\alpha}$ is selected so that the growth equation for the male

age- α -cohort is continuous at age α .

The growth model of *C. puniceus* was that developed by Garratt *et al*, (1993) taking into consideration the following aspects:

- *C. puniceus* are initially female (protogynous) and follow the same growth equation until the age at sex-change (a_c) after which they adhere to a new growth equation,
- Males are derived from females through the sex change process,
- Males adhere to different growth parameters, following sex change.

Growth parameters were then estimated using the age-length data, considering the above as well as the following four possible scenarios of growth:

- 1) $L_\infty^f \neq L_\infty^m$; $K^f \neq K^m$ females and males have different asymptotic sizes and different growth rates (the most general model).
- 2) $L_\infty^f = L_\infty^m$; $K^f \neq K^m$ females and males have the same asymptotic size, but different growth rates.
- 3) $L_\infty^f = L_\infty^m$; $K^f = K^m$ females and males have the same asymptotic size and the same growth rate.
- 4) $L_\infty^f \neq L_\infty^m$; $K^f = K^m$ females and males have different asymptotic sizes, but the same growth rate.

As different models obviously give different L_∞ , K and t_0 parameters for male and females, the best parameters had to be chosen through a minimisation of the following function:

$$SSQ = \sum_{i=1}^n \left(L_i^m - \hat{L}_i^m \right)^2 + \sum_{i=1}^n \left(L_i^f - \hat{L}_i^f \right)^2 \quad (5)$$

Where: L_i^m ; L_i^f , = the observed lengths of male and female respectively,
 \hat{L}_i^m ; \hat{L}_i^f , = the predicted lengths of male and female respectively,

n = the number of fish.

An F test (Butterworth *et al*, 1989) was carried out to determine which of the sub-models best describes the growth of *C. puniceus*.

Obviously males will have a different t_0 from females as they are derived from females through a sex change process. Hence, t_0 was estimated for males according to Garratt *et al* (1993), following the equation:

$$t_0^{\alpha,m} = \alpha + \ln \left[1 - L_{\infty}^f \left(1 - e^{-k^f(\alpha - t_0^f)} \right) / L_{\infty}^m \right] / K^m \quad (6)$$

Where: L_{∞}^m and L_{∞}^f are the asymptotic length of males and females, respectively; K^m and K^f are the growth rate of males; α is the age-at-sex change, which was estimated graphically.

4.2.2. Age-at-50% maturity

Age-at-50% maturity is defined as the age at which 50% of individuals recruited to a fishery are sexually mature (Butterworth *et al*, 1989; King, 1996). It was decided to confine this study to females only because all males (100%) are automatically mature and the limiting factor in spawning potential is primarily vested in females. Age-at-50% maturity was estimated using data obtained from March 1998 to March 1999, as determined from microscopic gonad staging, and based upon female fish with gonads ranging from active, ripe and spent (stages 2, 3 and 4, respectively). The proportion of mature female sample was estimated by calculating percentage frequencies of mature fish per age class. The following logistic equation (Butterworth *et al*, 1989) was used to estimate the age-at-50% maturity:

$$Y = \frac{1}{1 + \exp(-(X_{mid} - X_{0.5}) / \delta)} \quad (7)$$

where:

- Y = the proportion of mature fish in age class X ,
- X_{mid} = the midpoint of the age interval X ,
- $X_{0.5}$ = the age at-50%-maturity, and
- δ = the constant that determines the width of the maturity ogive.

The parameters $X_{0.5}$ and δ were estimated using a non-linear least squares technique that minimised the residual sum of squares.

4.3. Results

In this study, the estimation of age of *C. puniceus* using otoliths was achieved successfully. The otoliths need to be sectioned because they were dense. Several times they were difficult to interpret the edge of otoliths due to the closeness of the rings at the margins. However for a total of 230 otoliths examined ages were possible to estimated from 199 of them.

4.3.1. Validation

In order to determine the periodicity of rings formation, the analysis of the edge of *C. puniceus* otoliths of the all years combined (1997 to 1999) showed evidence of forming two opaque and two hyaline bands per year. In the case of the opaque zone it forms a major opaque band during May and a minor one during November, while the hyaline zone forms a minor one in February and major one in September (Figure 4.1). The formation of opaque bands starts in February, peaking in May and then a decline is observed. In September a new increase in opaque band is observed, which peaks in November. The opposite is observed for the hyaline formation, which decreases, after a peak in February, through to May and increases from May and peaks in September.

In the annual analysis of growth zone periodicity (1997 to 1999) (Figure 4.2), the occurrence is similar to that of the combined years with formation of the opaque zones, which peak in May and in November, and the hyaline zones that peak in February and

September in both years. Unfortunately, the sample in May 1997 was very low, and none of them were included, as they were unreadable. In 1997 there was a cholera outbreak in Mozambique, and, consequently, the fishing activity was low. The disease extended until 1998 and in January the fishing activity was stopped due to the difficulty in selling and exporting fish. As a result, there was no sample in January 1998.

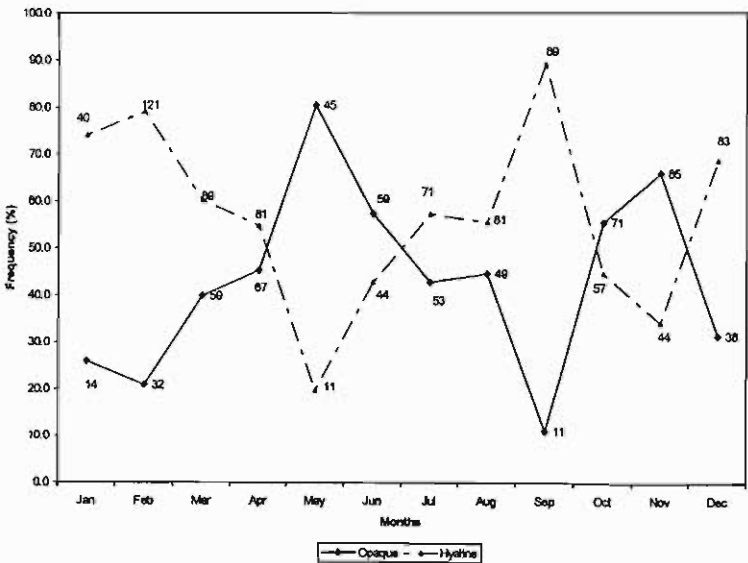


Figure 4.1 – Averaged frequency of the occurrence of opaque and hyaline edges on the otoliths of *C. puniceus* (numbers represents monthly number of bands).

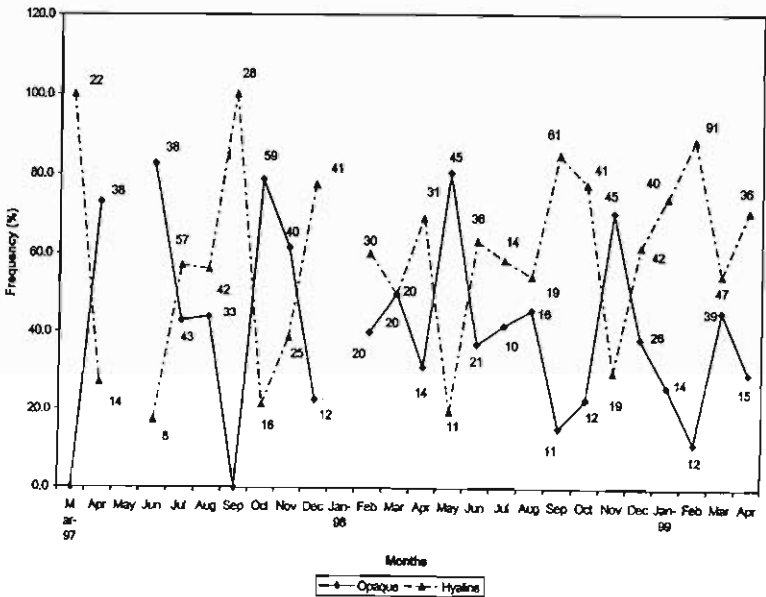


Figure 4.2 – Monthly frequency of the occurrence of edge type on the otoliths of *C. puniceus* (numbers represents monthly number of bands).

4.3.2. Precision

From the 230 otoliths examined, 31 were rejected as unreadable. These otoliths were completely opaque, translucent, or differed by more than one band during successive readings. Of the remaining otoliths (87%), 42% coincided in all readings occasions, while 45% differed by one band. The maximum number of rings observed was 18. The percentage of males and females of the total number of fish sampled is shown in Table 4.1. The average percentage error (APE) value for the three set of age estimates is 22%.

Table 4.1 - Percentage of males and females *C. puniceus* sampled by age during the study period.

Age(years)	Percentage of males	Percentage of females
1-2	0	100
3	37.5	62.50
4	17.24	82.50
5	26.67	73.33
6	9.09	90.91
7	21.74	78.26
8	14.29	85.71
9	14.29	85.71
10	12.5	87.50
11	33.33	66.67
12	80	20.00
13	62.5	37.50
14	0	100
15	33.33	66.67
16	100	0
17	100	0
18	100	0

4.3.3. Growth model

Despite the findings that growth rings appear to be annual (Garratt *et al*, 1993), estimates of the growth parameters were based on the assumption that the opaque band laid down was either annual or bi-annual. The reason for this is the recognition of the discrepancy

between the findings of this study and that of Garratt *et al* (1993) who assumed annual banding. Hence, both scenarios were modelled, although the growth parameters in this study indicate that the L_{∞} value is the same whether one or two rings are deposited each year, while the K value is halved when bi-annual bands are assumed.

The four fits of the growth model to the age length data is shown in Table 4.2A and B. Analysing the SSQ for the different models (in both tables A and B) it is found that the most general model (1) achieves the lowest value of SSQ , followed by model 2. Model 4 has the best value of SSQ after model 1 and 2. When the F test is applied to the data, the results suggest that model (2) is more appropriate, since the difference between models 1 and 2 is not statistically significant, but provides better representation of the growth of *C. puniceus* (Figure 4.3).

The modified von Bertalanffy growth parameters from the chosen model (model 2) suggests that male and female *C. puniceus* have the same asymptotic length ($L_{\infty} = 506$ mm, which is closer to the maximum observed length ($L_t = 480$ mm), but differ in their growth rates ($K = 0.23 \text{ year}^{-1}$ for females and $K = 0.45 \text{ year}^{-1}$ for males), and t_0 obtained for females is equal to -1.33 , if a double band is considered (Table 4.2B). If one opaque band is laid down annually, then the L_{∞} is equal to that of the bi-annual deposition assumption, but $K = 0.11 \text{ year}^{-1}$ for females and $K = 0.33 \text{ year}^{-1}$ for males *C. puniceus*, while t_0 of females is equal to -2.66 (Table 4.2A). For both assumptions t_0 for males are various, this is because it is assumed that a fraction of females changes sex at each age, so that males from different cohorts have different t_0 .

The tagging data is shown in appendix I. From a total of 4071 *C. puniceus* marked by Sedgwick's/ORI/WWF tagging project, 112 (2.7%) were recaptured. From these (122) 43.1% displayed negative growth, 20.7% did not show any growth, 3.4% were not measured, and the remainder (33.9%) showed positive growth. However, the positive growth is very small, with an average increment of 7.24 mm fork length (Appendix I).

Table 4.2 - Four fits of the growth model to the age data for estimation of the growth parameters from a modified Von Bertalanffy growth equation. (A) assuming that one opaque band is laid down annually, and (B) assuming that opaque bands are laid down bi-annually.

(A)

PARAMETER	MODEL			
	1	2	3	4
L_{∞}^f	490	506	534	464
L_{∞}^m	520	506	534	618
K^f	0.12	0.11	0.096	0.13
K^m	0.30	0.33	0.096	0.13
t_o	-2.46	-2.66	-3.6	-2.32
SSQ^f	25826	26033	38350	27194
SSQ^m	5408	5507	44467	7703
SSQ^{tot}	31233	31540	828167	34897
F^{test}		1.884	158.548	22.520
$F^{critical}$		3.89	3.04	3.89

(B)

PARAMETER	MODEL			
	1	2	3	4
L_{∞}^f	490	506	534	464
L_{∞}^m	520	506	534	618
K^f	0.24	0.23	0.19	0.28
K^m	0.42	0.45	0.19	0.28
t_o	-1.23	-1.33	-1.84	-1.16
SSQ^f	25826	26033	38350	27194
SSQ^m	5408	55067	44467	7702
SSQ^{tot}	31233	31540	82817	34897
F^{test}		1.884	158.548	22.520
$F^{critical}$		3.89	3.04	3.89

In the relationship between length and age of male and female *C. puniceus*, it was seen that there is no male in the lowest age class; that they are derived from females. Sex change first start at 3 years if an annual band is assumed, and at 1.5 years if bi-annual periodicity is assumed (Figure 4.3, 4.4 and 4.5). After sex change males exhibit

accelerated growth (Figure 4.3, 4.4 and 4.5). It was also assumed that at each age there is a certain fraction of females changing sex (Figure 4.3).

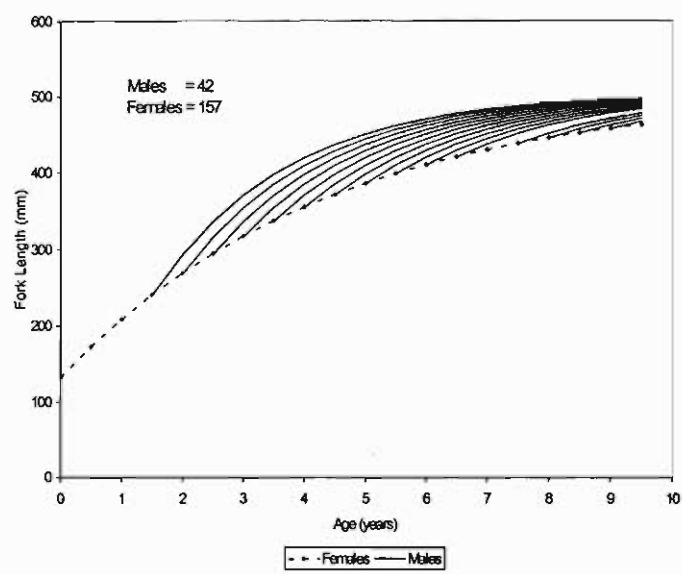


Figure 4.3 – growth curve of female *C. puniceus* with various curves reflecting male growth spurts at different ages of sex change (assuming bi-annual periodicity of opaque band).

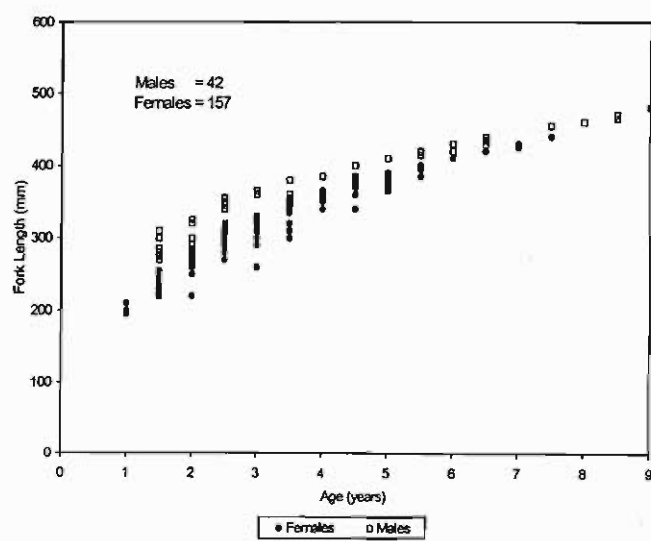


Figure 4.4 – The relationship between fork length and age for *C. puniceus*. Squares represent males, while dots represent females (assuming bi-annual periodicity of opaque band).

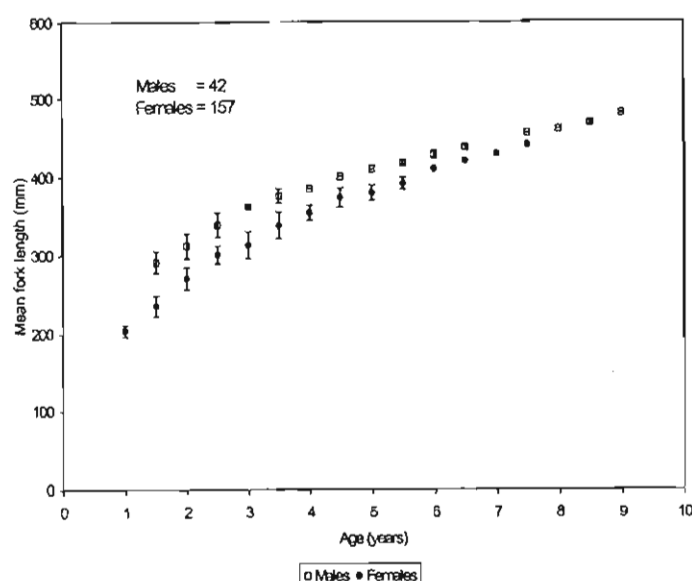


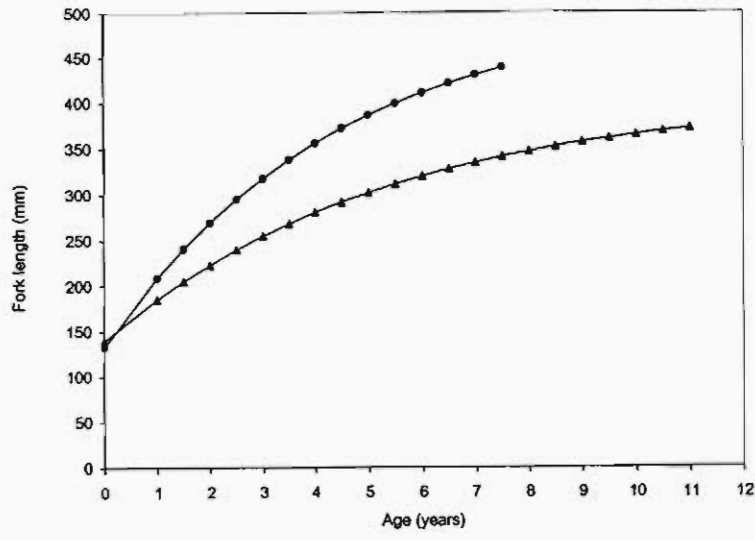
Figure 4.5 - The relationship between mean length and age of male and female *C. puniceus* (assuming bi-annual periodicity of opaque band). Bars represent one standard deviation of the mean length

Comparing growth of *C. puniceus* from Mozambique and KwaZulu-Natal it can be seen that the results show faster growth of females in Mozambique. Females also have a larger asymptotic length in Mozambique than in KwaZulu Natal (Table 4.3; Figure 4.6A), conversely, males after sex change grow slower in Mozambique than in KwaZulu-Natal, if bi-annual periodicity of bands is assumed (Table 4.3; Figure 4.6B). Assuming annual bands, female growth and t_0 are almost the same in both areas, but males exhibit faster growth in KwaZulu-Natal (Table 4.3). The age at which the males have zero age are various in both areas, as for each cohort there are a fraction of females changing sex to male.

Table 4.3 - Values of growth parameters of *C. puniceus* estimated for both areas: Mozambique and KwaZulu-Natal.

Area	L_{∞} (mm)	L_{∞}^m (mm)	K^f (yr ⁻¹)	K^m (yr ⁻¹)	t_0^f (yrs)	t_0^m (yrs)	Source
Mozambique (one band)	506	506	0.11	0.34	-2.67	various	This study
Mozambique (two bands)	506	506	0.22	0.45	-1.33	various	This study
KwaZulu- Natal	406	406	0.187	2.048	-2.253	various	Garratt <i>et al.</i> , 1993

(A)



(B)

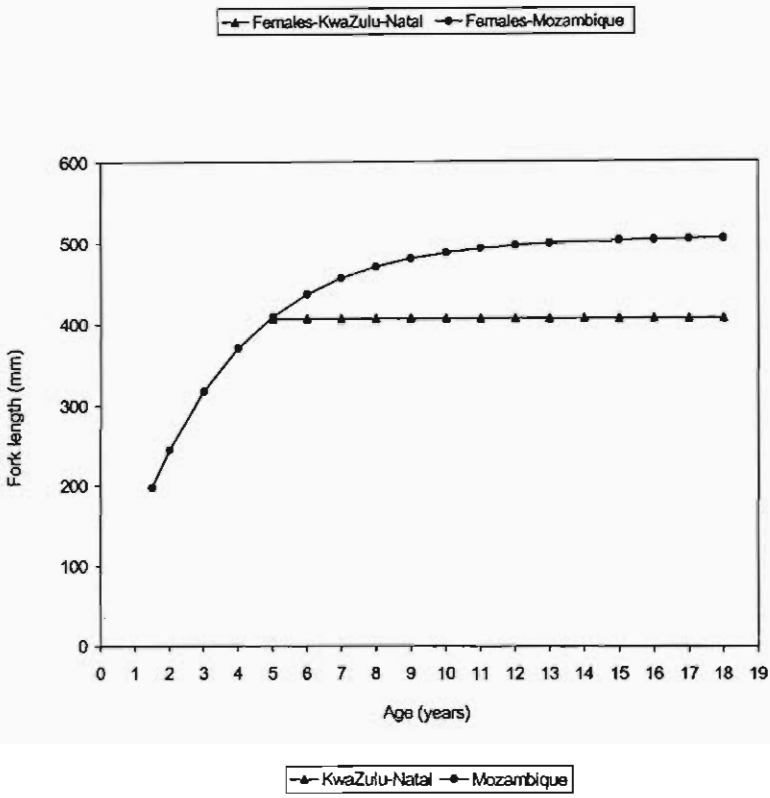


Figure 4.6 – Growth curves comparing the growth of (A) females and (B) males *C. puniceus* between KwaZulu-Natal (annual banding) and Mozambique (bi-annual banding).

4.3.2. Age-at-50% maturity

Age at-50%-maturity is attained at 1.5 years, which corresponds to 240 mm FL (for bi-annual banding), or at 3 years that corresponds to 317 mm FL (for the annual opaque band assumption). The logistic equation, assuming bi-annual periodicity, provides a curve that reasonably fits the maturity data for female *C. puniceus* (Figure 4.7, Table 4.4). The lower *SSQ* and higher coefficient of determination (r^2) value also indicates the best fit of the logistic equation for females *C. puniceus*. Table 4.4 summarises the *SSQ* and coefficient of determination (r^2) values for female *C. puniceus* (for both annual and bi-annual opaque bands).

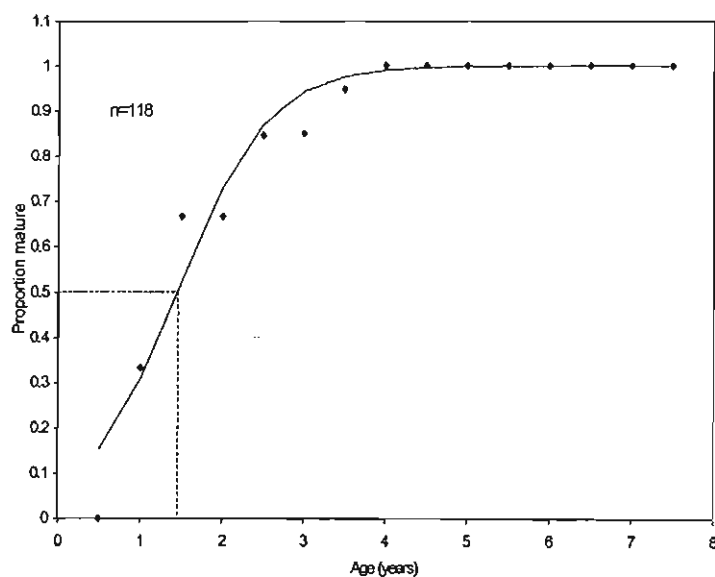


Figure 4.7 – Fit of the logistic equation to maturity data of female *C. puniceus*, assuming bi-annual periodicity of opaque band.

Table 4.4 – Parameters obtained from equation 5 for maturity data of female *C. puniceus*.

Parameter	$X_{0.5}$	δ	<i>SSQ</i>	r^2
Value (1 band)	3 years	1.1	0.06	0.9
Value (2 bands)	1.5 years	0.55	0.06	0.9

4.4 Discussion

The estimation of age of tropical fish is generally difficult due to the lack of distinct environmental seasonality, which influences biological characteristics such as, among others, the spawning period (which tends to be prolonged over several months), recruitment (generally extended over a long period, becoming difficult to separate age classes from one another) and population structure (length classes tend to crowd and overlap) (Weatherley, 1972; Brothers, 1979). Fishes of the Sparidae family are no exception to this rule (Smale and Punt, 1991, Buxton and Clarke, 1991) and *C. puniceus* is one such example.

C. puniceus otoliths are difficult to read because they are dense. For age determination, sectioning was required because it was difficult to read whole otolith. The thickness of otoliths increases with increasing age of fish resulting in stacking of growth zones at the edge.

The formation of bands at the edge of *C. puniceus*, although not easy to interpret were found in this study to occur bi-annually. This observation contrasts that from Garratt *et al* (1993) in which annual ring was reported. This is of concern and may be due to possible difficulties in the interpretation of the edge of *C. puniceus* otoliths by Garratt *et al* (1993). Although the occurrence of one opaque band per year in otoliths of South African sparids have been reported by other researchers e.g., Buxton and Clarke, 1986; Buxton, 1992; Smale and Punt, 1991; Chale-Matsau (1996), the case of bi-annual occurrence is not the first in the history of sparidae age determination. Mann (1992) observed two bands to be formed at the edge of *Diplodus sargus capensis* otoliths, though he concluded that this was a result of smaller sample used in his study, and he, therefore, assumed that the opaque band was formed annually. Difficulties in defining growth zones of sparids were also reported by other workers (Smale and Punt, 1991; Buxton and Clarke 1991; Garratt *et al*, 1993). Clearly this discrepancy requires further study.

Attempts to combine mark-recapture and age-length data to validate the periodicity of bands were undertaken, but proved inconclusive. While validation through examination

the outer margin of otolith showed bi-annual pattern of opaque band, results from mark-recapture were not consistent, some of the fish recaptured showed either negative growth, or zero growth. Furthermore, those fish that indicated positive growth showed slow growth. This could be due to measurement error (Bullen and Mann, 2000), or the negative effect of tagging on growth of *C. puniceus*. Other researchers have shown that tags can affect the growth of fish. McFarlane and Beamish (1980) observed that the placement of tags in a sablefish (*Anoplopoma fimbria*) affected its biology, resulting in slower growth, increased age at-50%-maturity and mortality compared with untagged fish. Attwood and Swart (2000) concluded that tags are not suitable for studying growth rates of *Dichistius capensis* and white *Lithognathus lithognathus* as there were several negative growth records. However it does not mean that validation through mark-recapture is a technique to be forgotten. Other researchers found good agreements between tagging results and other validation technique (MacPherson, 1992; Quartararo and Kearney, 1996; Govender, 1999). As could be seen in the results, the periodicity of opaque bands influence growth parameters of this species, so that, mortality and per recruit analyses will be influenced accordingly. This in turn has significant management implications.

The fact that the formation of the growth zone at the edge of otolith is associated with the spawning season (Casselman, 1987) could be clearly noted in *C. puniceus* otoliths, where the peak of formation of the hyaline zone in September coincides with the peak of the spawning period. In calcified structures, the opaque zones characterise fast growth of fish, while the hyaline identifies the slow growing phase (Brothers, 1979). As the formation of hyaline marks is interpreted as a slow growing phase (Brothers, 1979) it is possible that, while *C. puniceus* enters into the reproductive phase, energy is redistributed from somatic needs to reproductive needs (Weatherley, 1972), thus slowing growth.

During the examination of *C. puniceus* otoliths, there were some that were rejected as unreadable. Several other age studies describe the same difficulty. The precision in reading could also differ from one study to another, even where studies refer to the same species or family. An example includes the study on *Sarpa salpa* (van der Walt and Beckley, 1997) where from 808 otoliths examined, 167 otoliths were rejected as

unreadable, and the APE they obtained was 3.95%. Garratt *et al* (1993) in the study on *C. puniceus* off KwaZulu-Natal, could only obtain the age from 242 of a total of 397 otoliths and recorded an APE of 20% (Govender, Oceanographic Research Institute, Durban. Personal communication), which is smaller than that found in this study. In the study of *Polysteganus undulosus*, Chale-Matsau (1996) recorded an APE of 18.23 %. Although the results of APE are different from one study to another, it does not mean that the estimates are either inaccurate or accurate, it simply reflects the consistency between the different readings. The high value of APE in this study (22%) means that the percent error between readings was high (Beamish and McFarlane, 1983).

The Von Bertalanffy growth parameters found for *C. puniceus*, considering bi-annual periodicity of opaque band, reveal that it is relatively slow-growing, with a maximum recorded age of 9 years, especially if compared with other fish species, such as *Scomberomorus commerson* (Govender, 1992) and *Hilsa kelee* (Gjøsæter and Sousa, 1983). The slow growing of *C. puniceus* was also reported by Garratt *et al* (1993). The sparidae family all seem to be quite slow growing such as *Polysteganus undulosus*, (Chale-Matsau, 1996), *Petrus rupestris* (Smale and Punt, 1991) and *Sparodon durbanensis* (Buxton *et al*, 1991), whose studies reveal that they are very slow-growing and they can reach at least 20, 33 and 30 years respectively.

The analysis of the growth of male and females revealed that after sex change male *C. puniceus* exhibit a growth spurt (shown by its large *K* value in comparison with that of females), which means that they grow faster than the females from which they are derived. The first sex change was observed at 1.5 years, although this continued though to age 8. The age-at-sex change is different from that observed by Garratt *et al* (1993). This difference could possibly be caused due to the fact that in this study two bands were observed annually, so that the age at sex change is less than that observed by Garratt *et al* (1993), which was 5 years. Indeed, part of the samples were obtained off KwaZulu-Natal, also from marine a reserve, in which the fishing activity was non-existent. According to Warner (1988) the age-at-sex change can vary within the same species. Males in protogynous hermaphrodites species monopolise the mating system, if a male is removed from the population, the largest female quickly changes sex to take the place of the

removed male. This adaptive strategy is undertaken in order to increase the reproductive success (Hoffman *et al*, 1985). This removal of a large female influences the mean size of sex change (Warner, 1988). As was discussed in chapter one, there is a decrease in the size of *C. puniceus* landed in Maputo harbour, and it could probably be another reason for early sex change found in this study.

Comparison of growth parameters between *C. puniceus* caught in Mozambique (this study) and KwaZulu-Natal (Garratt *et al*, 1993) show different growth rates in both areas, with females growing faster in Mozambique than in KwaZulu-Natal and the opposite for males. These differences could possibly be due to the fact that Garratt *et al* (1993) applied “mean length-at-age” to the model to estimate the Von Bertalanffy growth parameters, which would, surely, influence the results obtained. Unlike Garratt *et al*’s (1993) study, in this study individual fork length-at-age was used in the estimation of growth parameters.

The analysis of the age-at-maturity suggests that *C. puniceus* in Mozambique becomes 50% mature at 1.5 year-old, which corresponds to 240 mm FL. This species matures at the same size in KwaZulu-Natal, 240 mm FL (Garratt, 1984). Unfortunately, it is not possible to compare the age-at-50% maturity with that of KwaZulu-Natal because no estimation was done in that study. This age-at-50% maturity was estimated considering bi-annual banding. If annual banding were assumed, the age-at-50% maturity would be two times higher (equal to 3 years) than the age estimated from bi-annual opaque band. So this possibility (of one banding) was discarded because this disagrees not only with the result of the current study, but also with Garratt’s (1984) study in which the size they obtained coincides with that of this study assuming two banding. Other long-lived sparids are found to attain maturity at higher ages than *C. puniceus*. This is the case of *Polysteganus undulosus*, which matures at 7.7 years (Chale-Matsau, 1996), but also this species lives three times longer and grows much slower than *C. puniceus*.

CHAPTER FIVE

5. MORTALITY

5.1. Introduction

In the marine environment there is not only fishing mortality that reduces the survival of fish. Indeed, adverse environmental conditions, competition, disease, predation, and old age amongst others act in this reduction, and these factors act together as natural mortality. Thus, the mortality of fish can be divided into natural mortality, and fishing mortality (Ricker, 1975; Gulland, 1985). Both mortalities, when combined are referred to as total mortality. Knowledge of fishing mortality is important for fisheries management, as it helps to define the relationship between catch and stock, and it is used to measure the degree of exploitation of a given resource (Butterworth *et al*, 1989; Jones, 1966). Thus, if fishing mortality increases it can reduce the proportion of the recruited stock which survives (Shepherd, 1988), by reducing the spawning stock to a level that affects recruitment and hence the age at which fish are first caught, thus leading to recruitment overfishing (Laevastu and Favorite, 1988).

All mortalities referred above, can be reported either as annual or instantaneous mortality rates. Annual or the actual mortality rate is that fraction of the fish which die during the year, while instantaneous mortality rate is the number of fish that progressively die in minute time intervals (Ricker, 1958; 1975). Because mortality occurs at small fractions during small intervals of time over a year, the instantaneous mortality rates are normally used in calculations. Another reason for their use is that instantaneous rates can be added together while annual rates cannot.

The rates of mortalities can be calculated from direct or indirect approaches. The direct methods include mark and recapture of fish, and indirect methods include analysis of catch curve data, and the correlation of natural mortality to life history parameters (Campana and Jones, 1992).

Natural mortality is best calculated from an unexploited stock and since there is no fishing mortality natural mortality is equal to total mortality. However, several other techniques have been developed, for instance, by relating natural mortality to the growth parameters and the environmental temperature at which a stock lives (Pauly, 1980). Beverton and Holt (1957) investigated the relationship between natural mortality, longevity, and the age at which 50% of fish stock are sexually mature.

Other methods of estimating natural mortality include the analysis of catch-at-age versus fishing effort data (Shepherd, 1988) and tagging experiments (Shepherd, 1988; Campana and Jones, 1992). The first method compares the trend in total mortality with changing fishing effort, so that the intercept occurs at a time when fishing effort is equal to zero (i.e. effort at zero being an estimate of the natural mortality). This method was not applied in this study because it was not possible to obtain estimates of fishing effort for, and catch-at-age information each year for *C. puniceus*.

The tagging method involves repeated regular releases of marked fish (Shepherd, 1988), and mortality is dependent on the total number of fish tagged and recaptured, the decline in the number of recaptures is the result of mortality excluding the effects of tag shedding or tag-induced mortalities (Campana and Jones, 1992). However, this method usually only provides mortality information for the older age groups (Shepherd, 1988) due to the method of fishing which may target only older/larger individuals or the area where the catch is taken which may exclude younger individuals (Geraldine, 1986). Indeed, several assumptions must be taken into consideration before using the tagging method to estimate mortality. These assumptions are: tagged fish represents the population, there is no emigration, tagging does not effect the survival rate of the fish population from which the mortality information is sought (Gulland, 1983; Campana and Jones, 1992). In the case of *C. puniceus*, tagging experiments indicate that this species does not retain tags very well, and suffer high tagging mortality (Bullen and Mann, 2000).

As the knowledge about mortality of an exploited species is important for management, this chapter will deal with the estimation of natural and fishing mortality for *C. puniceus*.

5.2. Materials and methods

Mortalities were estimated from two sets of data, considering that the opaque band is laid down either annually or bi-annually. The instantaneous natural mortality rate (M) was estimated using the following two methods:

1. Pauly's (1980) empirical equation which is described by the equation below:

$$\text{Log}M(\text{yr}^{-1}) = -0.0066 - 0.279\log L_{\infty}(\text{mm}) + 0.6543\log K(\text{yr}^{-1}) + 0.463\log T(^{\circ}\text{C}) \quad (1)$$

2. Rikhter and Efanov (1977) equation:

$$M = \frac{1.521}{t_m^{0.72}(\text{yr})} - 0.155 \quad (2)$$

Pauly's method requires estimates of the growth parameters (L_{∞} , K) and the mean environmental temperature (T) in which the stock lives (Pauly, 1980), it was taken to be 25°C. To simplify estimates, M was assumed to be independent of time and sex, and as a means of comparing the results of both methods the growth parameters chosen were those estimated in chapter four for females because the age-at-50% maturity was estimated only for females. M was then tested for sensitivity to changes in the temperature values. The Rikhter and Efanov (1977) equation requires an estimate of the age-50%-maturity (t_m), which was estimated in chapter four.

The instantaneous total mortality rate (Z) was estimated using two methods:

1. From the slope of the descending limb of the catch curve. In this method the age frequency is transformed to a natural logarithm and only that section of the graph after full recruitment is considered. The top of the catch curve is considered to be the age-at-full recruitment (Butterworth *et al*, 1989; Ricker, 1975; Campana Jones, 1992). Z is then obtained by regressing the natural logarithm of age frequency against age to all fully recruited ages, the absolute value of the slope

thus obtained is equal to Z , which, by convention, is a positive number. (Butterworth *et al*, 1989; Ricker, 1975; Campana and Jones, 1992; King, 1996).

2. From the following equation (Butterworth *et al*, 1989), which is considered to be statistically superior to the above analysis, in particular, when the numbers caught at any age in the regression equation is low.:

$$Z = \ln \left[1 + 1 / (a_m - a_f) \right] \quad (3)$$

with approximate 95% confidence limits:

$$Z \pm 2 \frac{Z}{\sqrt{N}} \quad (4)$$

where: a_f - is the age at full recruitment;
 a_m - is the mean age of all fully recruited fish sampled, with age $a \geq a_f$;
 N - is the number of fully recruited fish sampled, excluding any fish with ages $a < a_f$.

When estimating the instantaneous total mortality rate (Z) using the first method, a normalised age-length key for both sexes combined was used to transform the length frequency distributions to age frequency distributions (Butterworth *et al*, 1989).

The sensitivity of Z to the age-at-full recruitment (a_f) and to the age-at-50% capture (t_c), was tested for each techniques.

Given the value of the instantaneous natural mortality rate (M), (which was assumed to be equal for male and female), and the instantaneous total mortality rate (Z), the instantaneous fishing mortality rate (F) was then obtained by subtraction:

$$F = Z - M \quad (5)$$

As M was assumed to be the same for male and female *C. puniceus*, then the F value obtained by the equation 5 is equal for both sexes.

5.3. Results

Estimates of the instantaneous natural mortality rate (M) from Pauly's equation, for both patterns of banding (one and two opaque bands in the otolith), are shown in table 5.1. The M value obtained assuming annual band deposition is equal to 0.13 year^{-1} , and for bi-annually deposited opaque bands is about double at 0.27 year^{-1} . Both values are much smaller than those obtained through the Rikhter and Efanov equation, which yielded $M=0.53 \text{ year}^{-1}$, and $M=0.98 \text{ year}^{-1}$, for annual and bi-annual periodicity, respectively. The M values were found to be moderately sensitive to changes in temperature (Table 5.1). As the M values estimated for different temperatures vary, the mean environmental temperature of 25°C , was thus taken as an estimate of M , as being representative.

Table 5.1 - Instantaneous natural mortality rate (M) estimated from two different methods (Pauly's equation and Rikhter and Efanov), assuming annual and bi-annual periodicity of opaque bands. The female growth parameters used for the annual pattern was $L_{\infty} = 505.57 \text{ mm FL}$, $K = 0.11 \text{ year}^{-1}$, $t_m = 3 \text{ years}$, and for the bi-annual pattern was $L_{\infty} = 505.57 \text{ mm FL}$, $K = 0.22 \text{ year}^{-1}$, $t_m = 1.5 \text{ years}$. $T = 20, 25 \text{ and } 30^{\circ} \text{ C}$.

EQUATION	$T (^{\circ} \text{C})$	$M (\text{year}^{-1})^{(1)}$	$M (\text{year}^{-1})^{(2)}$
Pauly	20	0.1	0.24
Pauly	25	0.13	0.27
Pauly	30	0.15	0.31
Average		0.13	0.27
Rikhter and Efanov		0.53	0.98

⁽¹⁾ Annual periodicity of opaque band

⁽²⁾ Bi-annual periodicity of opaque band

Table 5.2 gives the data used in the estimation of Z from the catch curve, assuming bi-annual periodicity. Figure 5.1 shows the regression from the first method (linear regression fitted to the descending limb of the catch curve), considering bi-annual periodicity of opaque bands. The results suggest that, if an annual pattern of opaque band is considered, *C. puniceus* is recruited to the fishery at 5 years of age. If a bi-annual periodicity of opaque bands is assumed, then *C. puniceus* is fully recruited to the fishery at 2.5 years (Figure 5.1).

Table 5.3 shows the result obtained for Z estimated from the two different techniques. The mean value obtained from the estimation of a_m is equal to 8.18 year. The values of the lower and upper 95% confidence interval of the Z estimate are also shown in Table 5.3. The sensitivity to the change of the age-at-50% capture (t_c) and age-at-full recruitment (a_c) suggests that if annual periodicity is assumed, the Z value will be half of that obtained, considering double banding, which means that Z increases with a decrease in banding. The values of Z estimated by the two techniques are markedly different, with the value of Z estimated from the catch curve method, the highest. So, the average values (0.33 year^{-1} and 0.68 year^{-1} for annual and bi-annual periodicity of the opaque band, respectively) was assumed to be Z .

If the value of Z for the annual pattern of opaque band is equal to 0.3 year^{-1} , then by subtraction of M from Z an estimate of the instantaneous fishing mortality (F) is 0.2 year^{-1} (Table 5.3). However, for bi-annual banding, the F value obtained by subtraction of M from Z is equal to 0.41 year^{-1} , which is double of that estimated for the annual banding, as expected. However, it should be noted that both values of F are higher than the M values estimated.

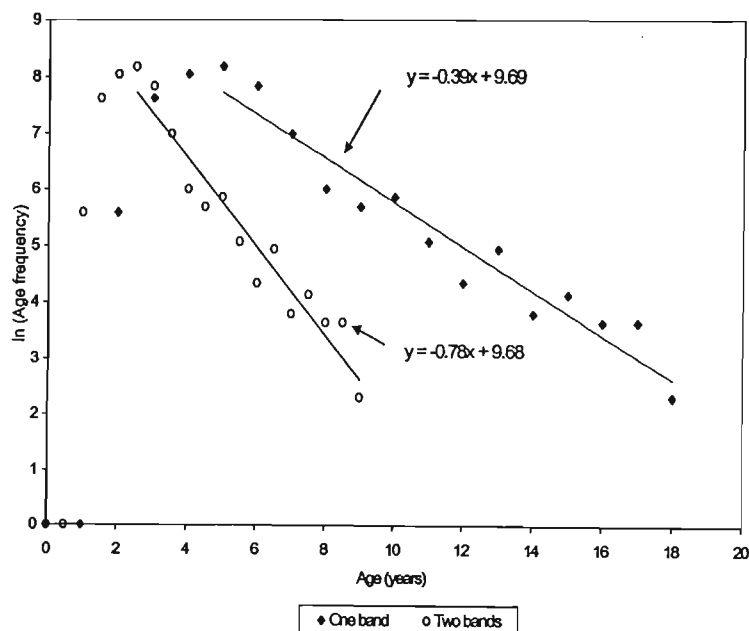


Figure 5.1 – Catch curve of *C. puniceus* showing the regression line fitted to the descending limb for annual and bi-annual banding.

Table 5.2 – Frequencies of the number of rings of *C. puniceus* obtained from transforming the length frequencies, using the age-length key of this species. This information was used in the estimation of total instantaneous mortality (*Z*).

Age (year)	frequency of number of rings (n)
0	0
1	0
2	266
3	2050
4	3125
5	3568
6	2525
7	1086
8	404
9	294
10	350
11	159
12	77
13	140
14	44
15	62
16	38
17	38
18	10

Table 5.3 – Instantaneous total mortality rate (*Z*) for *C. puniceus* estimated using two different methods, with sensitivity tests to the choice of age-at-full recruitment (*a_f*) and age-at-50% capture (*t_c*). The choice was based on the assumption that the occurrence of opaque bands could be either annual or bi-annual.

METHOD	<i>Z</i> (year ⁻¹)	Lower 95% CI	Upper 95% CI	<i>F</i> (year ⁻¹)
ln (age freq) vs age				
<i>t_c</i> = 2.5 ⁽¹⁾	0.78	0.65	0.91	0.51
<i>t_c</i> = 5 ⁽²⁾	0.39	0.46	0.33	0.26
<i>Z</i> = ln[1 + 1/(<i>a_m</i> - <i>a_f</i>)]				
<i>a_f</i> = 2.5; <i>a_m</i> = 4.1 ⁽¹⁾	0.59	0.5	0.68	0.3
<i>a_f</i> = 5; <i>a_m</i> = 8.2 ⁽²⁾	0.27	0.23	0.23	0.14
Average ⁽¹⁾	0.68			0.41
Average ⁽²⁾	0.33			0.20

⁽¹⁾ Bi-annual periodicity of opaque band

⁽²⁾ Annual periodicity of opaque band

5.4. Discussion

The instantaneous natural mortality rate (M) is normally closely related to the growth parameters of a given species, that is, to their maximum size and their K values. Other research have shown that K , derived from the von Bertalanffy growth equation, is related to longevity, and thus to mortality (Beverton and Holt, 1957; Gulland, 1983). For the von Bertalanffy growth equation, the K value describes the rate at which the fish approach the maximum size, thus it is expected that M and K should be closely related (Gulland, 1983). So high values of M are generally related to small asymptotic sizes due to the fact that low values of L_{∞} are linked to high values of K (Pauly, 1980). Cushing (1968) also pointed out that a fish with a high growth rate dies young. Species with slow growth can not have high M s, because that would result in extinction of the stock (Sparre and Venema, 1997). Rikhter and Efanov (1977) demonstrated that fishes that mature earlier have a higher M , hence they reproduce and die earlier. Moreover, they start to mature early and produce larger amount of eggs to compensate for the higher mortality (Rikhter and Efanov, 1977).

Natural mortality is also affected by the mean environmental temperature. Fishes from tropical waters have higher M values than that from temperate waters because they have to eat more to satisfy their higher metabolic needs than those of temperate species. This forces tropical predatory fishes to eat more, resulting in higher natural mortality of the prey fish (Pauly, 1980). And according to Beverton and Holt, (1957), Rothschild (1986) and Laevastu and Favorite (1988), within the several factors that causes natural mortality; predation is considered the greatest cause of high mortality.

The instantaneous natural mortality rate estimate from Pauly's (1980) empirical equation shows it to be lower over the range of the temperature examined, than that obtained from the Rikhter and Efanov (1977) equation. Analysing the M values obtained in this study, it is demonstrated that if one band is assumed, the M value is very low compared with that obtained from the two band assumption. However, M was first estimated by Punt *et al* (1993) from Mozambique samples, in which the fishing activity was not intensive for more than ten years, and the value they obtained is very close to that estimated in this

study assuming bi-annual banding ($M=0.27 \text{ year}^{-1}$). Indeed, the M value obtained assuming two bands confirms the “rule of thumb” of Cushing (1975), Ricker (1975), Shepherd (1988) and Laevastu and Favorite (1988) that because M do not vary systematically is assumed to be constant for a given species.

The higher value of M provided through the Rikhter and Efanov (1977) equation (for both one or two bands) reflects a resource characterised by early maturation and hence a higher M . As *C. puniceus* is a long-lived species the result obtained from the Rikhter and Efanov (1977) equation is not believed to reflect reality for the *C. puniceus* fishery. Though the estimation of M was done using the age-at-50% maturity of females, it is assumed that males have the same M , because *C. puniceus* is a protogynous hermaphrodite with males being derived from females.

The instantaneous total mortality rate (Z) estimate based on the catch curve, yielded a higher value than that estimated from equation 3 for both periodicities of banding assumed. Butterworth *et al* (1989) state that the catch curve technique provides a high value of Z if the numbers caught at any age are low since it provides a steeper regression slope. In this study there were very low numbers of fish caught with 12 to 18 rings. Equation 3 also provides Z values very much different from each other, depending on the banding periodicity. Furthermore, the 95% confidence limits for the Z estimates of the two different ages-at-full recruitment (a_f) values are widely different. Due to this uncertainty in what is the most reasonable estimate of Z for the *C. puniceus* fishery, the average between both methods at the current age-at-full recruitment ($Z= 0.33 \text{ year}^{-1}$ and $Z=0.68 \text{ year}^{-1}$) could tentatively be taken as an estimate of Z .

The estimation of the instantaneous fishing mortality rate (F) from the difference between Z estimated from the catch curve at the current ages at first capture (5 years for annual banding, and 2.5 years for bi-annual banding) and M is high. F value range between $0.51 \text{ year}^{-1} - 0.32 \text{ year}^{-1}$, and $0.26 \text{ year}^{-1} - 0.14 \text{ year}^{-1}$, for bi-annual and annual periodicity of the opaque band, respectively. However, it is difficult to deduce which value actually describes the *C. puniceus* fishery. It was shown by Garratt *et al* (1993), and confirmed in this study, that *C. puniceus* is a protogynous hermaphrodite with males restricted to the

larger sizes. However, as fishers target larger fish they remove males from the population, with females dominating the catches at very higher fishing mortality rates, thus skewing the sex ratio. Punt *et al* (1993) showed that at the current sex ratio 1:19 (m : f) off KwaZulu-Natal indicates that the catch is dominated by females only at fishing mortality rates is as high as 0.8 yr^{-1} . Govender *et al* (1998) also demonstrated that as F increases, females would dominate the catch. Thus, the higher the fishing mortality, the more skewed the sex ratio is in favour of females. Given this hypothesis of estimating F from sex ratios, in the following chapter, F will also be estimated from sex ratios, and the assumption of the periodicity of the opaque banding will be resolved.

CHAPTER SIX

6. YIELD-PER-RECRUIT AND SPAWNING BIOMASS-PER-RECRUIT ANALYSES

6.1. Introduction

The study of growth and mortality in fish populations are generally done with the final objective of estimating the yield of the stock at different levels of exploitation (Ricker, 1975). From the fish stock assessment one can determine the status of a particular resource and evaluate its response to fishing pressure. Attention should especially be addressed to two parameters, that is, the amount of fishing (fishing mortality (F)) and the pattern of its distribution over the range of different sizes or ages of the fish, including the age-at-first capture (t_c) (Gulland, 1983). This can assist in preventing overexploitation by setting optimum levels of fishing effort, estimation of the potential and sustainable yield of the stock at different levels of fishing and the optimum age or size at which fish should first be caught (Jones, 1977; Butterworth *et al*, 1989). If the fishing effort applied to a given resource increases beyond a certain limit, the greater is the probability of the species becoming overexploited and the probability of the average fish size being reduced (Butterworth *et al*, 1989).

There are several techniques that can be used to assess the status of a resource. One method is surplus production modelling (Schaefer-type models) (Schaefer, 1957), another method is dynamic pool models, such as the Beverton and Holt's yield-per-recruit model. The first method estimates the catch and effort in a given year, and gives the dynamic of the stock size (assumed proportional to catch-per-unit effort (CPUE)), considering that the stock can increase or decrease depending on new recruits and natural mortality (Schaefer, 1957). This method requires a time series of catches and relative abundance indices. However, because information regarding catch and effort of *C. puniceus* was not available it was not possible to apply the Schaefer model.

The dynamic pool model uses the ages of fish and relates the biomass of all year classes of fish with time and constant recruitment. It is also known as the yield-per-recruit (*YPR*) model (Beverton and Holt, 1957). This model predicts the ratio of the number or weight of fish caught during the life span of each cohort to the initial abundance of that cohort when it entered the fishing area (Huntsman and Manooch III, 1978). Furthermore, this model assumes that year-on-year fluctuation in growth, mortality and recruitment remain constant, so that all cohorts in one year are used to represent each cohort over its full life. This model has been used in several studies of reef fish (Huntsman and Manooch III, 1978) because linking the age-at-first capture to fishing mortality calculates maximum yield (Pitcher *et al*, 1982; Laevastu and Favorite, 1988). Although this method can be criticised in that annual recruitment is almost always variable (Cushing, 1983) it is considered appropriate for reef fish as the carrying capacity and growth are often the main limiting factors (Huntsman *et al*, 1983). A further refinement of the *YPR* is the spawning biomass-per-recruit (*SBR*) models (Butterworth *et al*, 1989), which, in addition to *YPR*, consider the proportion of spawning stock that survives.

A number of biological reference points can be calculated in terms of fishing mortality (F), including F_{SBR} , F_{max} and $F_{0.1}$ (Sissenwine and Shepherd, 1987). The fishery is considered to be healthy when the spawning biomass-per-recruit is maintained at levels of 35% or above of its average unexploited level (F_{SB35}) (Sissenwine and Shepherd, 1987; Butterworth, *et al*, 1989). F_{max} is related to the maximisation of sustainable yield for recruits already vulnerable to the fishery. However, $F_{0.1}$ is used as alternative to F_{max} because it produces almost as much yield without reducing spawning biomass as much as F_{max} (Sissenwine and Shepherd, 1987) and is defined as the fishing mortality rate which corresponds to a point on the yield-per-recruit curve with a slope of 10% of that at the origin (Gulland and Boerema, 1973; Sissenwine and Shepherd, 1987).

The Beverton and Holt (1957) yield-per-recruit model can be modified to accommodate protogynous and other sex-changing fish (Punt *et al*, 1993). The Punt *et al* (1993) model was based on the knowledge that males are derived from females through sex change and that they grow at different rates. Hence, the model is applied to each sex separately. The

method also accommodates variable growth rates at the time of sex change and predicts male and female sex ratios at different fishing mortality rates.

To determine the optimum level of fishing mortality and the age-at-first capture of *C. puniceus* and, by simultaneously, maintaining an adequate spawning biomass-per-recruit and maximising yield-per-recruit, the modified yield-per-recruit model was applied taking into account the unique biology of this species (sex change and a possible growth spurt after sex change) (Punt *et al*, 1993).

6.2. Materials and methods

The yield-per-recruit and spawning biomass-per-recruit analysis were done for *C. puniceus*, and were performed on the assumptions that the opaque band could be deposited either annually or bi-annually. The following equations (Punt *et al*, 1993) apply:

Yield-per-recruit equations:

$$YPR = YPR^f + YPR^m \quad (1)$$

Females :
$$YPR^f = \sum_t w_t^f + S_t^f F N_t^f (1 - e^{-Z}) / Z \quad (2)$$

Males :
$$YPR^f = \sum_a \sum_t w_t^{m,a} S_t^{m,a} F N_t^{m,a} (1 - e^{-Z}) / Z \quad (3)$$

Where:

YPR_w^f and YPR_w^m	are the yield-per-recruit in weight for females and males;
w_t^m and w_t^f	are the weight of males and females at age t years.
S_t^m	is the selectivity of males at the age- t cohort;
S_t^f	is the selectivity of females at age t years;
F	is the instantaneous fishing mortality rate on fully recruited year classes;
N_t^f	is the number of females at t age years;
N_t^m	is the number of males at age- t cohort;
Z	is the instantaneous total mortality rate;

In this study the selectivity has been assumed to be knife-edged, which means that, theoretically, no fish were caught below the age at first capture (t_c), i.e.:

$$S_t = \begin{cases} 0 & \text{if } t < t_c \\ 1 & \text{if } t \geq t_c \end{cases} \quad (4)$$

where t_c is the age-at-50% capture of the population.

b) Spawning biomass-per-recruit equation:

$$SBR^f = \sum w_t^f P_t^f N_t^f \quad (5)$$

where: w_t^f is the weight of females at age t years;
 P_t^f is the proportion of females at age t years;
 N_t^f is the number of females at t age years;

Spawning biomass-per-recruit was calculated for females because the spawner biomass is assumed to be primarily limited by females. The sensitivity of the model to changes of the frequency of opaque bands deposition was examined. SBR was also tested for different ages-at-first capture (t_c) and for different levels of natural mortality rates (M), and the effect of changing the t_c to the *C. puniceus* fishery, basing on the bi-annual banding. Fishing mortality rates, at which spawning biomass is reduced to 35% and 50% of its unfished level, and F_{msy} were determined graphically (Sissenwine and Shepherd, 1987).

The proportion of males and females in the catch at age t were estimated for this study from the following equations:

$$P_t^m = \frac{m_t}{\sum_{t=0}^{t_{max}} m_t + \sum_{t=0}^{t_{max}} f_t} \quad (6)$$

$$P_t^f = 1 - P_t^m \quad (7)$$

where P^m_t and P^f_t are the proportion of males and females at age t class, respectively. m_t is the catch of males at age t class. m and f are the catch of males and females, respectively.

The predicted sex ratio ($f : m$) of the catch from the remaining total number of male and female *C. puniceus* obtained from the age and growth (see chapter four) was estimated using the equation:

$$f : m = \frac{\sum_{t=0}^{\text{max}} f_t}{\sum_{t=0}^{\text{max}} m_t} \quad (8)$$

max is the maximum age observed.

Given the contrasts of the occurrence of opaque band on the edge of *C. puniceus* otolith between this and Garratt *et al* (1993) study, the YPR and SBR model will be applied for both scenarios (annual and bi-annual) banding. The status of *C. puniceus* fishery will be assessed for both ages-at-first captures (t_c) and instantaneous natural mortality rates (M) and biological reference points will be estimated from annual and bi-annual periodicities of opaque band.

6.3. Results

The input parameters used for the per-recruit analyses are shown in Table 6.1. Figures 6.1A and B illustrate the spawning biomass-per-recruit (*SBR*) for female *C. puniceus*, using both band frequencies, considering the age-at-first capture (t_c) and instantaneous natural mortality (M). Results suggest that at the time of this study the *SBR* had been reduced to 35% of an unexploited level for the assumption of annual opaque banding, and to 36.57% for bi-annually banding at the current t_c (Figure 6.1A; Table 6.2). The same declines are observed in the analyses of instantaneous natural mortality rates for annual and bi-annually periodicity ($M=0.13 \text{ year}^{-1}$ and $M=0.27 \text{ year}^{-1}$) in which the *SBR* drops to 33% and 35.45% from its pristine level, respectively (Figure 6.1B; Table 6.3).

Table 6.1 - Values of the biological parameters of males and females *C. puniceus* used for per-recruit analysis, assuming that the periodicity of opaque band can either be annual or bi-annual.

PARAMETER	VALUE ⁽¹⁾	VALUE ⁽²⁾	SOURCE
L^∞	506 mm	506 mm	Age and growth (Chapter four)
L^m	506 mm	506 mm	Age and growth (Chapter four)
K^f	0.11 yr^{-1}	0.22 yr^{-1}	Age and growth (Chapter four)
K^m	0.33 yr^{-1}	0.45 yr^{-1}	Age and growth (Chapter four)
t_o^f	-2.66 yr	-1.33 yr	Age and growth (Chapter four)
a^f	1.16E-04	1.16E-04	Somatic relationship (Chapter three)
a^m	5.99E-05	5.99E-05	Somatic relationship (Chapter three)
b^f	2.74	2.74	Somatic relationship (Chapter three)
b^m	2.86	2.86	Somatic relationship (Chapter three)
t_c	5 yr	2.5 yr	Mortality (Chapter five)
t_m	3 yr	1.5 yr	Age and growth (Chapter four)
M	0.13 yr^{-1}	0.27 yr^{-1}	Mortality (Chapter five)
F_{current}	0.2 yr^{-1}	0.41 yr^{-1}	Mortality (Chapter five)

⁽¹⁾ Annual periodicity of opaque band

⁽²⁾ Bi-annual periodicity of opaque band

Where:

- L^m, L^f Are the asymptotic lengths of males and females, respectively,
- K^m, K^f Are the growth rate parameters for males and females, respectively,
- t_o^f Is the age at which females have zero length,
- a^m, a^f Are the Y intercept from fork somatic relationship for male and female, respectively,
- b^m, b^f Are the coefficient of the regression from somatic relationship for male and female, respectively,
- t_c Is the age-at-50% capture of the population,
- t_m Is the age-at-50% maturity,
- M Is the instantaneous natural mortality,
- F_{current} Is the current fishing mortality

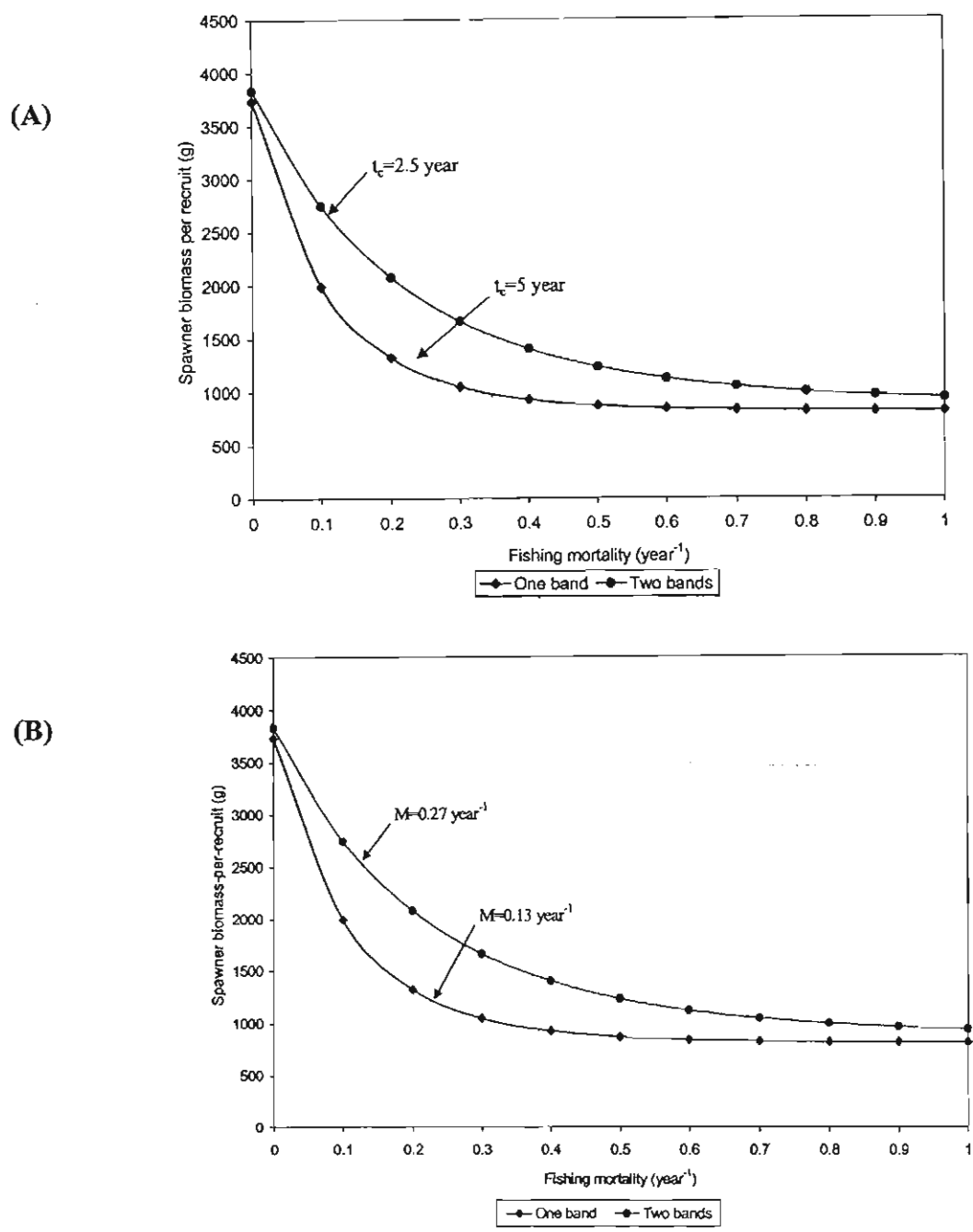


Figure 6.1 – Spawning biomass-per-recruit (A) for age-at-first capture (t_c) and (B) for instantaneous natural mortality rates (M) for *C. puniceus*, assuming different periodicities of the opaque band.

Table 6.2 – Biological reference points estimated in weight for male and female *C. puniceus* for ages at-first-capture and instantaneous natural mortality rates (M), assuming that the periodicity of opaque band can either be annual or bi-annual. F_{curr}^m and F_{curr}^f are the current fishing mortality. F_{max}^m and F_{max}^f are the maximum fishing mortality levels to the maximisation of sustainable yield for male and female *C. puniceus*, respectively.

Parameter (year ⁻¹)	$t_c=5$ years ⁽¹⁾	$t_c=2.5$ years ⁽²⁾	$M=0.13$ years ⁻¹ ⁽¹⁾	$M=0.27$ years ⁻¹ ⁽²⁾
	weight	weight		
F_{curr}^f	0.2	0.41		
F_{max}^f	0.12	0.22		
F_{max}			0.12	0.2
F_{curr}^m	0.2	0.41		
F_{max}^m	0.12	0.16		
F_{SB35}	0.21	0.43	0.2	0.43
F_{SB50}	0.11	0.23	0.11	0.23
SBR	35.43%	36.57%	33%	35.45%

⁽¹⁾ Annual periodicity of opaque band

⁽²⁾ Bi-annual periodicity of opaque band

YPR was also estimated assuming the frequency of opaque bands for both male and female *C. puniceus*. Results suggest that for bi-annual banding, YPR would increase, for male and female *C. puniceus* (Figures 6.2 and 6.3). That is, if two bands were considered F_{max} would be maximised at $F=0.22$ year⁻¹, but if annual banding were considered F_{max} would be attained at $F=0.12$ year⁻¹ (Table 6.2).

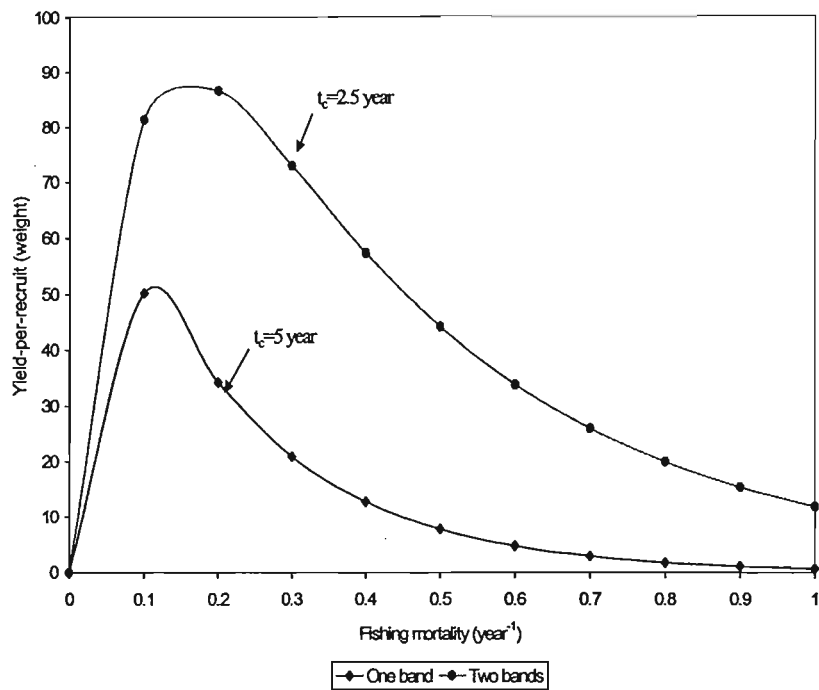


Figure 6.2 – Yield-per-recruit for male *C. puniceus* at age-at-first capture, assuming that the periodicity of opaque band can either be annual or bi-annual.

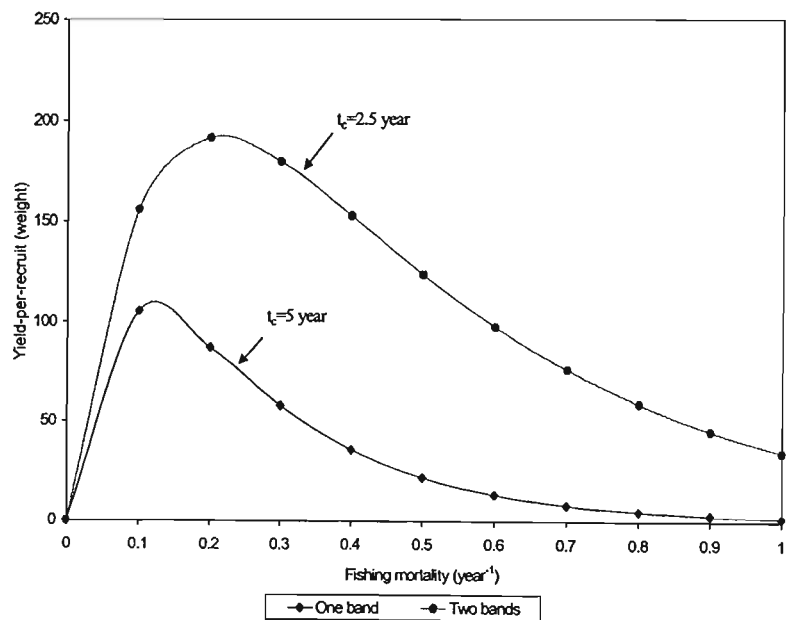


Figure 6.3 – Yield-per-recruit for female *C. puniceus* at age-at-first capture, assuming that the periodicity of opaque band can either be annual or bi-annual.

Figures 6.4 and 6.5 shows curves of YPR against F at different M , depending whether annual or bi-annual bands are deposited. Results suggest that high yields are produced at $M=0.27 \text{ year}^{-1}$ when compared to $M=0.13 \text{ year}^{-1}$, suggesting an increase of yield for bi-annual periodicity of opaque band, for both male and female *C. puniceus*.

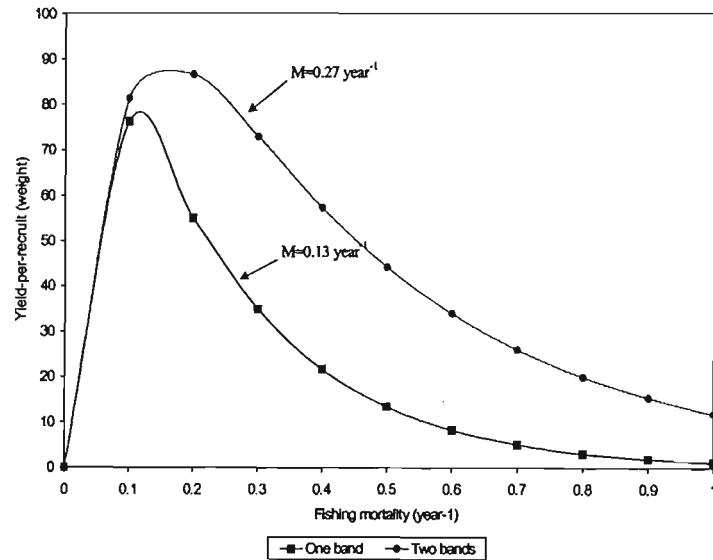


Figure 6.4 – Yield-per-recruit for male *C. puniceus* at instantaneous natural mortality rates (M), assuming that the periodicity of opaque band can either be annual or bi-annual.

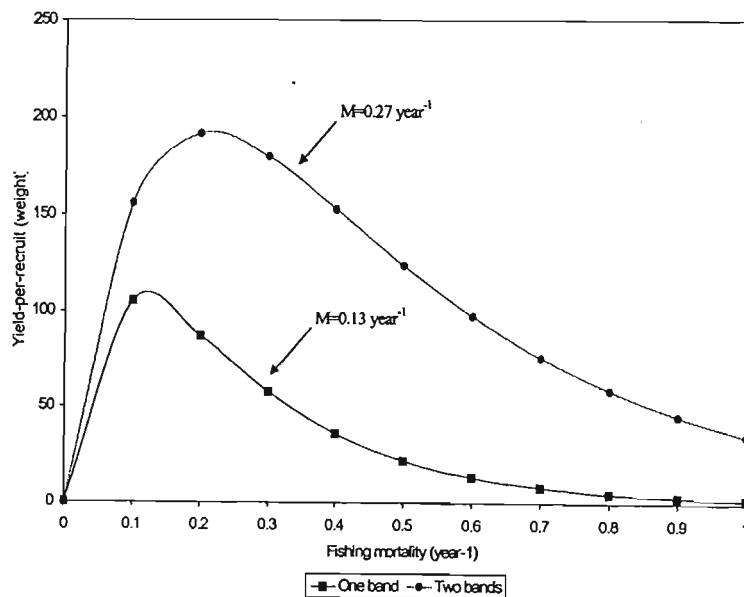


Figure 6.5 – Yield-per-recruit for female *C. puniceus* at instantaneous natural mortality rates (M), assuming that the periodicity of opaque band can either be annual or bi-annual.

Comparing MSY of male and female *C. puniceus*, estimated based on bi-annual banding, it could be seen that the current fishing mortality (F_{curr}) is higher than F_{max} , for both sexes, suggesting an overfishing of *C. puniceus* population. In the case of males (Figure 6.6) it was maximised at a fishing mortality much lower than that of female (Figure 6.6) *C. puniceus*. The biological reference points are shown in Table 6.2.

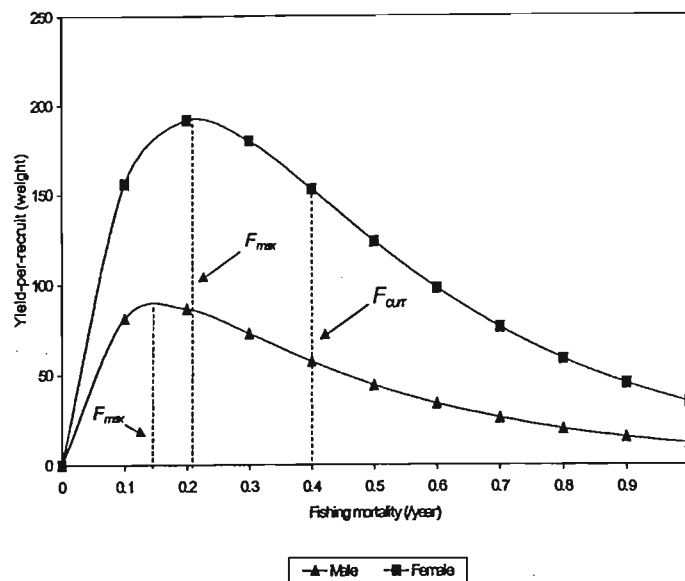


Figure 6.6– Yield-per-recruit curves for male and female *C. puniceus*, assuming bi-annual periodicity of opaque band.

SBR was tested for different ages-at-first capture and different M values. Results suggest that an increase in t_c would result in conservation of the spawner biomass (Figure 6.7A). That is, if the t_c is increased from 2.5 years, (which yielded a SBR of 36.57% (Table 6.2)), to 3 years the SBR would increase to 40.9%, but a reduction to $t_c=1.5$ years (which is the age at-50%-maturity) the SBR would decrease to 31.7%. A higher M would result in the SBR being reduced. It means that, if the M changes from the current 0.27 yr^{-1} to 0.37 yr^{-1} the SBR would be reduced from 35.45% to 24.5% of its pristine level. However, if M drops to 0.17 yr^{-1} it would “benefit” the SBR , increasing to 42.65% (Figure 6.7B).

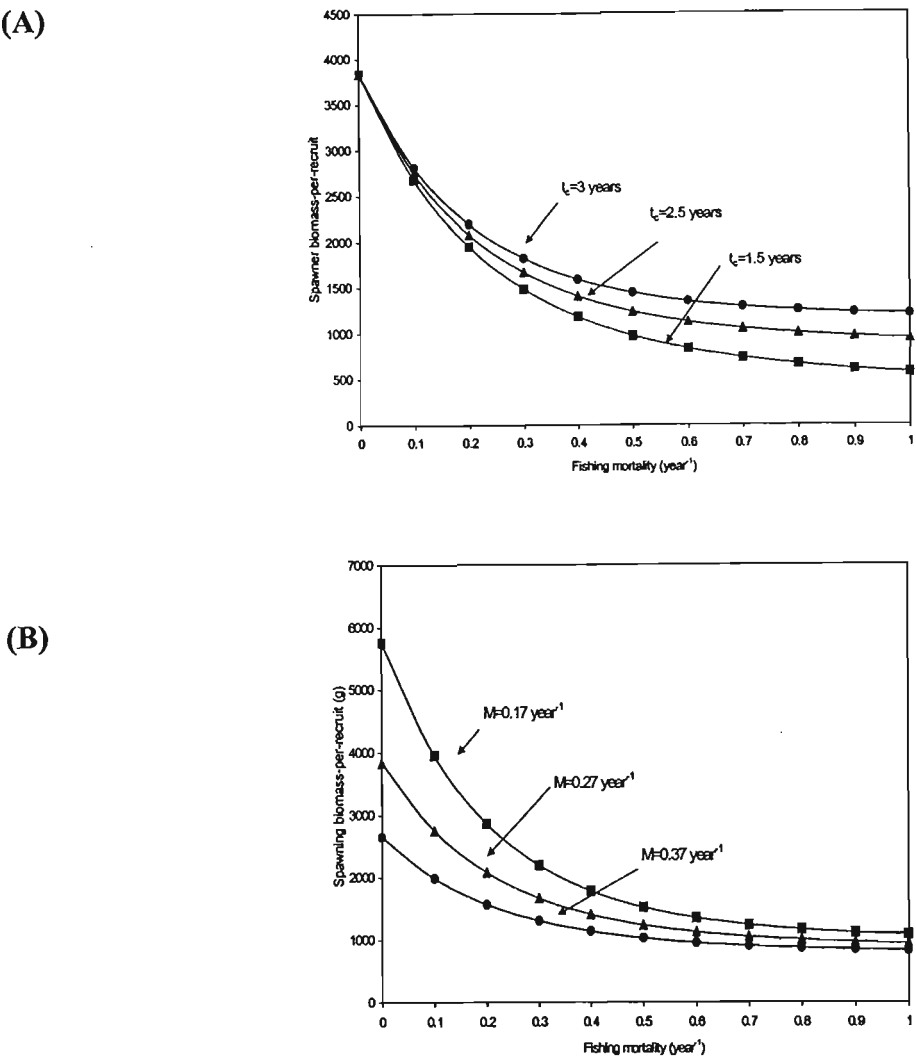


Figure 6.7 – Spawning biomass-per-recruit (A) for three different age-at-first capture (t_c) and (B) at different instantaneous natural mortality rates (M) for *C. puniceus*, assuming bi-annual periodicity of opaque band.

YPR was also tested for three different ages-at-first capture (t_c) and for three different instantaneous natural mortality rates (M), for both sexes combined. An increase in t_c would reduce the *YPR*, which means that if the t_c were changed from 2.5 years to 3 years it would result in a loss of yield (Figures 6.8). However, if the t_c were reduced from 2.5 to 1.5 years it would result in a greater yield. (Figures 6.8).

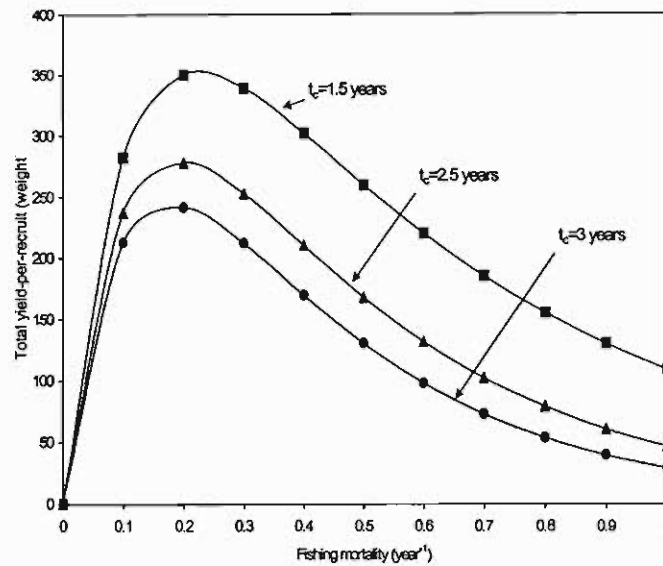


Figure 6.8 – Yield-per-recruit for *C. puniceus* at different age-at-first capture (t_c), assuming bi-annual periodicity of opaque band.

The per recruit model was sensitive towards changes in instantaneous natural mortality rate (M). Figures 6.9 shows curves of YPR against F at different choices of M (0.17, 0.27 and 0.37). High yields were observed at lower M , that is, at $M=0.17 \text{ year}^{-1}$ when compared to $M=0.37 \text{ year}^{-1}$ in number and weight for both sexes combined, so, the higher the M the lower the MSY .

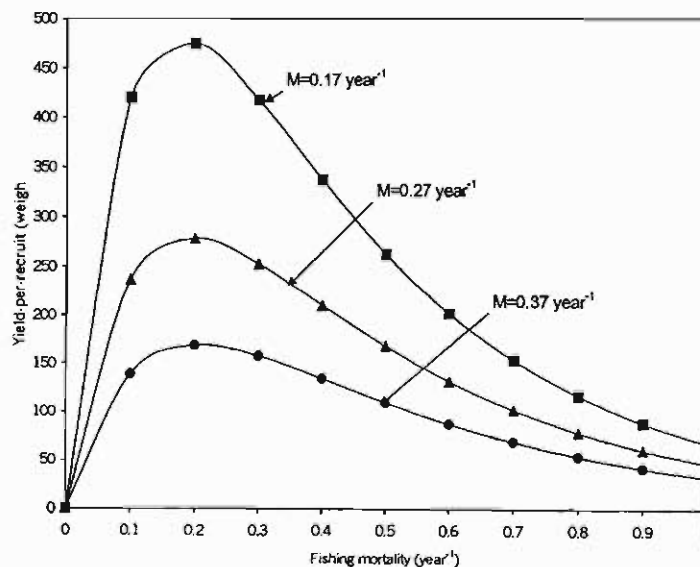


Figure 6.9 – Yield-per-recruit for *C. puniceus* at different instantaneous natural mortality rates (M), assuming bi-annual periodicity of opaque band.

An analysis of changes in the minimum size of male and female *C. puniceus* (Table 6.3) indicates an increase of *YPR* by 43% for males is observed if the age-at-first capture were reduced to 1.5 years, while if there is an increase of t_c to 3 years the *YPR* would drop by 16% (Table 6.4). Moreover, the analyses of females show the same feature as that of male *C. puniceus*. An increase in 45% of *YPR* in weight, for female *C. puniceus* is observed when t_c is reduced to 1.5 years, while if t_c were increased to 3 years *YPR* would drop by 20%. However, *SBR* would increase by 14% if t_c were 3 years and decrease by 16% if t_c were 1.5 years.

Table 6.3 – Effects of changes in minimum size for *C. puniceus* fishery. A plus sign (+) signifies an increase, while a negative sign (-) signifies a decrease.

	Males		Females	
Management variable (%)	$t_c=1.5$ years	$t_c=3$ years	$t_c=1.5$ years	$t_c=3$ years
<i>YPR</i> (w)	+43%	-16%	+45%	-20%
<i>SBR</i>	—	—	-16%	+14%

The sex ratio predicted is equal to 6.78 : 1 (f : m). The predicted sex ratios at various fishing mortality for annual and bi-annual periodicity of opaque band are shown in figure 10. The model predicted that for annual periodicity of opaque band the predicted sex ratio is 4 : 1 (f : m), while for bi-annual banding is 6.8 : 1.

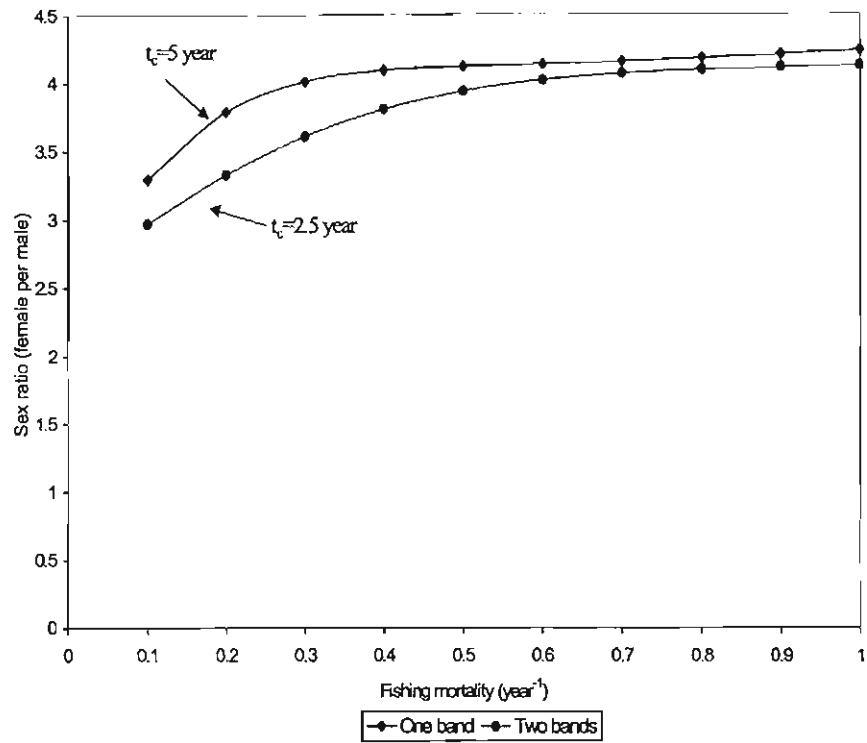


Figure 6.10 – Sex ratio (f : m) for *C. puniceus*, assuming that the periodicity of opaque band can either be annual or bi-annual.

The observed proportion at age t of males and females *C. puniceus* in the catch, used in the per-recruit analysis is shown in Table 6.4.

Table 6.4 – Observed proportion of male and female *C. puniceus* various age classes, assuming bi-annual periodicity of opaque band.

Age (years)	Female	Male
0	0	0
1	0	0
2	1	0
3	0.63	0.38
4	0.83	0.17
5	0.73	0.27
6	0.91	0.09
7	0.78	0.22
8	0.86	0.14
9	0.86	0.14
10	0.88	0.13
11	0.67	0.33
12	0.20	0.80
13	0.33	0.67
14	1	0
15	0.67	0.33
16	0	1
17	0	1
18	0	1

6.4. Discussion

The analysis of yield-per-recruit and spawning biomass-per-recruit suggests that the exploitation of *C. puniceus* in Mozambique is of concern. At the current fishing mortality, considering that for annual banding $F=0.2\text{year}^{-1}$ and for bi-annual banding $F=0.41\text{year}^{-1}$, the spawning biomass-per-recruit is at 35.4% and 36.5% of an unexploited level, respectively, which is only 0.4% and 1.5% above $F_{35\%}$, respectively. However, using the more conservative biological reference point ($F_{50\%}$) the *SBR* is well below its pristine level and it could result in recruitment overfishing. One rule-of-thumb (Butterworth *et al*, 1989) refers that stock biomass should not fall to less than half of its

average unexploited level. This analyses indicate that whatever is the band pattern considered the level of fishing effort is not appropriate for the utilisation of *C. puniceus* resource, and an increase of the level of fishing mortality will deplete even more the spawning stock to a biologically critical level.

With the estimation of *SBR* to determine how far the periodicity of opaque band influences it, what has actually happened is doubling the bands the fishing mortality doubled as well, comparing with that of one band, with the *SBR* remaining almost same. However, changing the pattern of opaque banding seems to influence *M*, in which doubling the bands yielded an increase of *SBR* by 2.45%. Following the citation of some scientists such as Gulland (1974), Laevastu and Favorite (1988) that the higher the fishing mortality, the younger the fish caught and the lesser the surviving biomass, it would be expected that as one band give larger age-at-first capture than that given by two bands, one band would be more conservative. It would also be expected that as for double band the fishing mortality is high, comparing to that of one band, the surviving biomass would consist of younger fish than an unfished population in two bands than in one band as a result of the effect of fishing. Nevertheless, in this analyses the biomass shows to be more influenced by the periodicity of opaque band rather than by the age-at-first capture given by the periodicity of opaque band, or by the fishing mortality. Thus, the bi-annual periodicity of opaque bands shows to be more conservative than the annual banding.

Yield-per-recruit analysis of both male and female *C. puniceus* indicate the vulnerability of male to overexploitation at very low fishing mortality rates. Punt *et al* (1993) point out that the *C. puniceus* resource could collapse at the $F=0.4\text{year}^{-1}$ if the recruitment is dependent on mature male biomass (i.e. sperm limitation) consequently, increasing fishing mortality, males will contribute less and less to the overall fish population (Punt *et al*, 1993). Bannerot *et al* (1987) also investigated the equilibrium of *YPR* over a range of *F* for groupers, which are also protogynous hermaphrodites, and they concluded that at high fishing mortality of 0.5 year^{-1} could result in recruitment overfishing for hermaphrodite populations. The *C. puniceus* resource is shared by Mozambique and KwaZulu-Natal, and in KwaZulu-Natal the *C. puniceus* fishery is already showing signs of depletion (Punt *et al*, 1993; Garratt *et al*, 1993) The non protection of the resource in

Mozambique could collapse the whole resource both in KwaZulu-Natal and in Mozambique. If the recruitment in KwaZulu-Natal is dependent on the Mozambique stock as proposed by Punt *et al* (1993) and Buxton (1992). Comparing the fishing mortality rate in KwaZulu-Natal during the study of 1993 (Punt *et al*, 1993) and the current fishing mortality in Mozambique obtained in this study, if bi-annual periodicity of opaque band were assumed, are both equal ($F=0.41 \text{ year}^{-1}$). In that period in KwaZulu-Natal, at this level of fishing mortality the resource was considered to be depleted (Punt *et al*, 1993). In Mozambique the same level of F was attained and suggests that there is a depletion of the *C. puniceus* resource here too. Furthermore, both male and female reached their maximum sustainable yield (MSY) at fishing mortalities less than the $F=0.41 \text{ year}^{-1}$. It reveals that if this is the current fishing mortality, it should be decreased to further protect this fishery. If the fishing mortality estimated under the assumption of annual periodicity is correct, then the fishing activity should be restricted, because it would not support any more level of fishing, as the resource would collapse at a very low fishing mortality. Thus, F obtained from bi-annual banding reveal to be more realistic comparing to that of annual banding as the *C. puniceus* resource did not reach such a decline reported in annual banding.

The response of YPR model to different periodicity of opaque band predicts that the maximum yield was already attained in both situations. However, comparing the model for both situations itself, the annual periodicity of opaque band produces a decrease of the YPR . The loss of yield by instantaneous natural mortality rate is also observed when the annual periodicity banding is assumed. Here the lower fishing mortality and the higher age-at-first capture encountered in annual banding could justify the decrease of YPR . Although, for both patterns of opaque banding the fishing mortality is high, and an increase in fishing mortality will decline the stock (Cushing, 1968; Laevastu and Favorite, 1988), bi-annual banding shows to be more conservative than annual banding, and more close to the reality of *C. puniceus* species.

The yield-per-recruit model is sensitive to changes of t_c and M , in both number and weight of male and female *C. puniceus*. A decrease in t_c results in higher yield because females would become vulnerable to the fishery at a very low t_c . However, they will now

be captured at ages smaller than the age at maturity (Punt *et al*, 1993), which would lead to a reduction of the spawner biomass. Likewise, lower M values will lead to higher yield. Punt *et al* (1993) observed that in the *C. puniceus* fishery of KwaZulu-Natal increases M leads to a lower yield as the catches would consisted by the small fish.

The sex ratio reveals that at the instantaneous fishing mortality rates of 0.2 year^{-1} and 0.41 year^{-1} female dominant the catch. The decrease of t_c would increase the number of female in the catches and the sex ratio would be skewed towards females. Increasing fishing effort may lead to the situation of a lack of males in the catches and this lack may mean lower rates of fertilisation of eggs as a result of insufficient sperm (Bannerot, *et al*, 1987; Buxton, 1992; Punt *et al*, 1993). Furthermore, results in this study showed *C. puniceus* to have a lower age-at-first maturity and sex change, compared to other sparids, such as *Polysteganus undulosus* (Chale-Matsau, 1996), *Cheimerus nufar* (Coetzee, 1978), *Chrysoblephus cristiceps* (Buxton, 1987), implying that even if fishing mortality were moderate, because t_c is small it would still result in skewed sex ratios.

Comparing this situation with that of KwaZulu-Natal, where the current ratio is 1 : 19 (m :f) (Garratt, 1984) the high fishing mortality rates indicated that the *C. puniceus* fishery became unsustainable because it was speculated that males made progressively smaller contributions to the overall population (Punt *et al*, 1993). However, if the t_c were increased it could protect mature fish and allow sex change to occur, benefiting the sex ratio. A higher M would benefits the sex ratio while fishing mortality is lower. However, at larger fishing mortality rates the sex ratio is higher.

From the sex ratio obtained the from age and growth study F is actually equal to 0.41 year^{-1}

CHAPTER SEVEN

7. IMPLICATIONS FOR FUTURE MANAGEMENT OF THE LINEFISHERY

7.1. Overall conclusions

The most important biological points emerging from this study of *C. puniceus* which, should be related to the development of a management plan for this fishery in Mozambique is summarised below:

- ✦ It has a protracted spawning season, which extends over winter months, from August to October, with a peak in September;
- ✦ It is a relatively slow growing and long-lived species;
- ✦ Two growth scenarios assuming different otolith band deposition periods were evaluated, although it was shown here that *C. puniceus* deposits two opaque bands each year;
- ✦ The age-at-50% maturity is attained at 1.5 years old;
- ✦ M is equal to 0.27 year^{-1} ;
- ✦ F is high at 0.41 year^{-1} ;
- ✦ The current SBR is at 37% of its unfished level.

C. puniceus is an important commercial linefishing species in Mozambique. It is a reef-associated species (Smith and Heemstra, 1986; Garratt, 1984; van der Elst, 1993), which is regionally endemic to southern Mozambique and KwaZulu-Natal (Smith and Heemstra, 1986; Garratt, 1984). In Mozambique, the semi-industrial fleet generally exploits *C. puniceus* and most of the catch is exported to South Africa in fresh or frozen form, while some are also sold locally on Mozambique markets. In KwaZulu-Natal it is exploited by both the commercial and recreational sector (Garratt, 1984; Penney *et al*, 1989). In Mozambique the *C. puniceus* fishery is an open access one and its exploitation has increased over the years. However, in KwaZulu-Natal this species is in the restricted list category and is managed through bag limits of five fish per person per day for recreational sector only, and through a minimum size of 25 cm TL, and marine protected areas (Garratt, 1984; Mann, 2000). Commercial entry in this fishery is also restricted

(Mann, 2000). The importance of this species justifies a strategy that must take into consideration not only its biology, but also the fact that Mozambique and KwaZulu-Natal share this resource, so management should not be undertaken in isolation.

For management decisions to be successful, one must take into consideration the life history characteristics of the species. These characteristics include its distribution, slow growth, sex change, maturity and longevity.

Tagging results (Bullen and Mann, 2000) suggests that *C. puniceus* is fairly resident. Although the tagging results were not as conclusive as in several other sparidae studies, this species did show sedentary behaviour and being endemic makes it very susceptible to local overfishing (Buxton, 1987). The management of this fishery is even more difficult because once the fish is brought to the surface, due to the expansion of the swim bladder, the stomach is everted and forced out of the mouth causing death of many fish. This effect is referred to as barotrauma (Buxton, 1987; Garratt, 1984), and makes the return of unwanted or protected fish (e.g. undersized) very difficult.

Age determination suggests that *C. puniceus* is a relatively slow growing and long lived species. Slow growth is an important fishery management factor to consider because there is a lower yield-per-recruit per stock caused by a lower production per biomass ratio. And according to Adams (1980) and Buxton (1987), species with such characteristics are susceptible to overfishing and stock depletion. Further, once overfished, they require a long period to rebuild to stock levels that can then support economically sustainable fishing.

Another important characteristic of *C. puniceus*, relevant to management, is sex reversal. It was shown that *C. puniceus* is a protogynous hermaphrodite (Garratt, 1984). Thus, as this fishery is basically directed towards the removal of larger fish, one sex is subject to greater fishing mortality. This leads to an unbalanced sex ratio and the removal of males by fishing may affect the reproductive potential of the population (Garratt, 1984). If a viable population is considered as being that which has enough males to fertilise all eggs produced, then the excessive removal of one sex of that population may have serious

problems for the species survival, and hence, the fishery. However, sex change was considered by Liem (1968) as a means by some species to overcome the absence of a particular sex by its removal. Other theories suggest that sex reversal is a means to provide improvement of reproductive success (Shapiro, 1984), because, in the case of protogynous hermaphrodites, females constitute the majority of the population, so the egg production is substantial (Garratt, 1986). Clearly this is of relevance to the management of *C. puniceus* (see below).

The analysis of the periodicity of otolith bands suggests that a bi-annual pattern is likely to occur in *C. puniceus* in Mozambique. However, this assumption needs to be carefully re-examined by doing more studies on age and growth, such as chemical study of the otoliths, as it has implications for management. Until then, the management of this fishery must be undertaken cautiously, associating *YPR* analysis to other stock status indicators. Such indicators could include the analyses of the species composition of the catches, the mean length of the main species caught, the sex ratio and trends in total catch and effort of the fishery.

The yield-per-recruit and spawning biomass-per-recruit analysis, based on two growth scenarios (annual and bi-annual banding), suggests that the *C. puniceus* fishery is at concern exploitation state. The current instantaneous fishing mortality rate is high, it is therefore necessary to reduce F in order to protect the resource, and thus the fishery. Various options exist, such as increasing the spawning biomass (although the overall yield may then be reduced) by reducing fishing effort, and by increasing the age-at-first-capture, delaying exploitation until the majority of fish get mature and spawn at least once.

7.2. Management strategies

Any unregulated and open access fishery, such as the linefishery of Mozambique, is at a risk of collapse as a result of biological or economic overexploitation. A biological overexploitation occurs when biomass drops below the level at which the *MSY* can be achieved (Clarke, 1985; Butterworth *et al*, 1989). While economic overexploitation

occurs when catch rates dropped to the point that the costs of fishing is at the equalised to the same level of the income derived from the sale of the catches, so the fishery is no longer profitable (Clarke, 1985; Butterworth *et al*, 1989).

There are many management approaches that can be applied to a fishery to achieve sustainable fishing, in general. For example minimum size limits allow fish to reach sexual maturity and spawn at least once (Sadovy, 1996), as they ensure that maximum growth is attained before capture. Closed seasons may protect fish against fishing mortality at vulnerable stages of their life history such as the time of spawning, especially if there are aggregations. Closed areas or Marine protected areas provide refuges for exploited species and improve yields in adjacent areas, preventing overexploitation for sedentary species, maintain spawner biomass and supply recruits to fishing grounds (Hockey and Branch, 1997). Catch quotas limit the harvest of fish and license restrictions limit the number of fishers (Penney *et al*, 1989), thus reducing the fishing mortality.

The Mozambique linefishery is a multispecies fishery, which means that it is not selective only for sparid fish or just for *C. puniceus*, but for various other species as well, such as serranidae. This characteristic of the fishery makes it difficult to manage only *C. puniceus*, ignoring other species (Buxton, 1987; Garratt, 1985). For instance, if the introduction of a hook minimum size were proposed for *C. puniceus* it could reduce the fishing mortality of all small fish. However, in practice this is difficult to implement due to the fact that this fishery caught not only *C. puniceus*, but also fish of other species and families, as stated above, and it could cause overexploitation of the catchable species. Firstly because different species of fish, which are caught together in this fishery, have different age-at-50% maturity (and therefore different size-at-50% maturity) and, consequently different opportunity of spawn, thus will be impossible to avoid catching some immature fish of other species. Causing its depleting while others continue supporting higher catch rates. Secondly, hook minimum size is difficult to enforce; hence it is a useless management strategy

Sex change is an advantage physiological adaptative strategy in protogynous hermaphrodites species. Change sex is undertaken in order to increase the reproductive

success, as discussed above (Chapter 5). *C. puniceus* is a sex changing species the minimum size should be set at, or above, the “size-at-first-sex change” to protect males. So, protecting young fish as the only management approach is not sufficient to maintain a healthy resource. Also, the minimum size alone may not be enough to provide protection of the breeding stock (Attwood and Bennett 1990) because fecundity usually increases with an increase in individual fish size. Another problem in *C. puniceus* is barotrauma. The smaller fish, once caught are likely to die if returned to the sea, increasing the mortality.

Closed seasons could be investigated as a management strategy that can help to protect this species. It could be set during the months of peak spawning, when catches are high due to the susceptibility of fish to exploitation, as many sparidae aggregate for spawning (Buxton, 1987; Lau and Sadovy, 2001), and it would also reduce effort during this period. However, as the linefishery is multisectorial and is exploited by subsistence and industrial fishers, this measure would negatively impact on fishers that depend on regular income from *C. puniceus*. However, the closed season strategy may still be attractive because the months confirmed to be the peak spawning season are generally stormy with high windy conditions (Saetre and Silva, 1982), thus lowering fishing activities anyway. Furthermore, due to the multispecies nature of this fishery, neither all sparidae, nor other fish species caught in the linefishery share the same spawning season. All these make the closed season an unsuitable management option for *C. puniceus* and the linefishery in general.

Total allowable catch (TAC) is another management strategy often used. This measure helps to retain the fishery in a healthy state because it maintains the catch at a level that offers protection to the parent stock, ensuring sufficient recruitment (Buxton, 1987; Shepherd, 1992). Catches are also distributed evenly between fishers. However this measure is precluded because of the nature of the linefishery in Mozambique, being an open access and multispecies fishery where targeting is not directed only at *C. puniceus*. Hence, a TAC although it may provide protection for *C. puniceus*, it may compromise the catch of other species because once the TAC of *C. puniceus* is reached fishing would have to stop.

Closed areas or marine reserves may well be a good management option in Mozambique because, as part of protecting the resource, it preserves the biological interaction without which an individual species cannot exist. In the context of fishery management, marine reserves are important because they can maintain a breeding stock, and help re-populate the adjacent areas. Besides, fishers can continue developing their fishing activity throughout the year. However, it is not yet possible to implement this strategy in Mozambique because no study was done so far to identify possible areas that protect breeding stocks. Thus, there is no detailed knowledge of the spawning areas and movement of *C. puniceus* in Mozambique, and hence it is difficult to know where to site the appropriate marine reserves that can benefit the stock of *C. puniceus*. Nevertheless, this management strategy may be one of the most useful in protection, not only of *C. puniceus*, but also the linefishery as a whole.

However, the biggest issue thus far is the open access nature of the Mozambique linefishery, which is threatening the sustainability of the entire linefish resource in southern Mozambique. It is, therefore, suggested that the management of this fishery should include a reduction of the number of boats by applying a scaling down process, as indeed is underway in South Africa. Likewise, the average number of crew per boat needs to be evaluated in terms of overall effort. However, as the semi-industrial and industrial fishers invest in improved technology and fishing efficiency which may lead to overcapitalisation (van der Elst *et al*, 1997), technology must be checked periodically, otherwise limiting effort will be unsustainable.

Summary of management options:

The ○ symbol signifies that the management option is unlikely to rebuild the stock that easily, that the fishers will be negatively impacted, that it will have negative implications for other species and the enforcement will not be easy, while the ✓ symbol means the opposite (Table 7.1).

Table 7.1 – management options that rebuild the stock, the implications for people and other species, and the compliance.

Management option	Stock rebuild	Input		Compliance
		People	Other species	
Minimum size	✓	✓	○	○
Closed season	✓	○	○	✓
TAC	✓	✓	○	○
Closed area	✓	✓	✓	✓
Access control	✓	✓	✓	○

7.3. Future research

C. puniceus is an important species in the Mozambique linefishery. Detailed, and as accurate as possible, biological information on this species is necessary for appropriate management. Hence, it is recommended that future research focus on:

- A larger age and growth study involving samples from Mozambique and KwaZulu-Natal in a joint project to clarify the differences between the two age studies, and help for proper management of the linefish resource in both regions.;
- Investigation of appropriate areas for marine reserves to provide protection of spawning stock;
- Development of an overall management plan for linefish to protect the whole fishery.

Priority must be given to the first study in order to allow that the information obtained be important in conduction of the following studies.

REFERENCES

- ADAMS, P. B., 1980. Life history patterns in marine fishes and their consequences for fisheries management. *Fishery Bulletin*. 78(1): 1 – 12.
- ATTWOOD, C.G. and B. A. BENNETT, 1990. A simulation model of the sport-fishery for galjoen *Coaracinus capensis*: an evaluation of minimum size limit and closed season. *South African Journal of Marine Science*. 9: 359 – 369.
- ATTWOOD C. G. and L. SWART, 2000. Discrepancy between otolith and tag-recovery estimates of growth for two South African surf-zone teleost species. *South African Journal of Marine Science*. 22: 9 – 15.
- BALOI, A. and N. PREMEGI, 1998. Towards sustainable development. The artisanal fisheries of Nampula province, Angoche and Moma districts. Annual report 1997. Instituto Nacional de Investigação Pesqueira, Maputo. 45 pp.
- BANNEROT, S. P., W. W. FOX JR. and J. E. POWERS, 1987. Reproductive strategies and the management of snappers and groupers in the Gulf of Mexico and Caribbean. Tropical snappers and groupers. Biology and fisheries management. J.J. Polovina and S. Ralston, (Eds) Westview Press, Inc., Colorado. 561 – 603.
- BEAMISH, R. J., 1979. Differences in the age of Pacific hake (*Merluccius productus*) using whole otoliths and sections of otoliths. *Journal of Fish Research*. 36: 141 – 151.
- BEAMISH, R. J. and D. A. FORNIER, 1981. A method for comparing the precision of a set of age determination. *Canadian Journal of Fisheries and Aquatic Science*. 38: 982-983.
- BEAMISH, R. J. and G. A. McFARLANE, 1983. The forgotten requirement for age validation in fisheries biology. *Transactions of the American Fisheries Society*, 112: 735-743.

BEAMISH, R. J. and G. A. McFARLANE, 1987. Current trends in age determination methodology. In: Age and growth of fish. Summerfelt, R. C. and G. E. Hall (Eds.). Iowa State University Press, 735 – 743.

BECKMAN, D. W., A. L. STANLEY, J. H. RENDER and C. A. WILSON, 1991. Age and growth rate estimation of sheephead *Arcjosargus probatocephalus* in Louisiana waters using otoliths. Fisheries Bulletin. U. S. 89: 1 – 8.

BEVERTON, R. J. H. and S. J. HOLT, 1957. On the dynamics of exploited fish population. Fisheries Investigation. London, H.M.S.O. 19 (2): 533 pp.

BROTHERS, E. B., 1979. Age and growth studies on tropical fishes. In: Stock assessment for tropical small-scale fisheries. 119-136.

BULLEN, E. and B. Q. MANN, 2000. Sedgwick's/ORI/WWF Tagging Programme: Slinger (*Chrysoblephus puniceus*) data report. Oceanographic Research Institute, Durban. 2000/15: 7pp.

BUXTON, C. D. and J. R. CLARKE, 1986. Age, growth and feeding of the blue hottentot *pachymetopon aenum* (Pisces: Sparidae) with notes on reproductive biology. South African Journal of Zoology. 21: 33 – 38.

BUXTON, C. D., 1987. Life history changes of two reef fish species in exploited and unexploited marine environments in South Africa. Ph. D. thesis, Rhodes University. 220 pp.

BUXTON, C. D. and J. R. CLARKE, 1989. The growth of *Cymatoceps nasutus* (Teleostei: Sparidae), with comments on diet and reproduction. South African Journal of Marine Science. 8: 57 – 65.

BUXTON C. D., and J. R. CLARKE, 1991. The biology of the white musselcracker *Spardon durbanensis* (Pisces: Sparidae) on the eastern Cape coast, South Africa. South African Journal of Marine Science. 10: 285 – 296.

BUXTON, C. D., 1992. The application of yield-per-recruit models to two South African sparid reef species, with special consideration to sex change. Fisheries Research. 15: 1-16.

BUTTERWORTH, D. S., A. E. PUNT, D. L. BORCHERS, J. G. PUGH and G. S. HUGHES, 1989. A manual of mathematical techniques for linefish assessment (incorporating a report of the SANCOR marine linefish programme's workshop on population dynamics, 4 – 6 February, Cape Town). South African National Scientific Programmes. 160: 89 pp.

CAMPANA, S. E. and C. M. JONES, 1992. Analysis of otolith microstructure data. In: Otolith microstructure examination and analysis. Canadian Special Publication of Fisheries and Aquatic Sciences. 117: 73 – 100.

CASSELMAN, J. M., 1987. Determination of age and growth. In Weatherley and H.S. Gill. The Biology of Fish Growth. Academic Press, London, 7: 209 – 242.

CHALE-MATSAU, J. R., 1996. Age and growth of the queen mackerel (*Scomberomorus plurilineatus*) and seventy-four (*Polysteganus undulosus*) off KwaZulu Natal. MSc thesis, Durban, University of Natal: 110 pp.

CLARKE, J. R., 1985. Coastal resources management: Development case studies. Renewable resources Information Services. 3: 1 –179.

COETZEE, P. S., 1978. Aspects of the angling fishes of St Croix Island, with special reference to the biology of *Chameirus nufar* Ehrenberg, 1820 (Teleostei: Sparidae). MSc thesis, University of Port Elisabeth. 221 pp.

COETZEE, P. S., 1983. Seasonal histological and macroscopic changes in the gonads of *Chemirus nufar* (Ehrenberg, 1980) (Sparidae: Pisces). South African Journal of Zoology. 15 (3): 198 – 199.

CUSHING, D. H., 1968. Fisheries biology, a study in population dynamics. University of Wisconsin Press, Madison, 200 pp.

CUSHING, D. H., 1975. The natural mortality of the plaice. Journal du Conseil International pour Exploration de la Mer. 36 (2): 150 – 157.

CUSHING, D. H., 1983. Key papers on fish populations. IRL press, Oxford. 405 pp.

DE VLAMING, V.L., 1972. Reproductive cycling in the estuarine gobiid fish. *Gillichthys mirabilis*. Copeia. (2): 278 – 291.

DE VLAMING, V. L., G. GROSSMAN, and F. CHAPMAN, 1981. On the use of the gonosomatic index. Comp Biochemical Physiology. 73A (1): 104-127.

DE VLAMING, V., 1983. Oocyte development patterns and Hormonal involvements among teleosts. Control process in fish physiology. UK Crook Helm Ltd, London. 176 – 199.

DRURY, R. A. B, and E. A. WALLINGTON, 1967. Carleton's histological technique. New York. 4: 431 pp.

FOWLER, A. J., 1995. Annulus formation in the otoliths of coral reef fish – A review. In: Recent developments in fish otolith research. 19: 45 – 63.

GARRATT, P., 1984. The biology and fishery of *Chrysoblephus puniceus* (Gilchrist & Thomson, 1917) and *Cheimerius nufar* (Ehirenberg, 1830), two offshore sparids in Natal waters. MSc thesis. Durban, University of Natal: 139 pp.

- GARRATT, P., 1985. The offshore linefishery of Natal: II: Reproductive biology of the sparids *Chrysoblephus puniceus* and *Cheimerius nufar*. Investigational Report. 63: 21 pp.
- GARRATT, P., 1986. Sex can complicate management. South African Association for Marine Biological Research. 15:17-19.
- GARRATT, P., A. GOVENDER AND A. E. PUNT, 1993. Growth acceleration at sex change in the protogynous hermaphrodite *Chrysoblephus puniceus* (Pisces: Sparidae). South African Journal of Marine Science. 13: 187 – 193.
- GEFFEN, A. J., 1992. Validation of otolith increment deposition rate. Summerfelt, R. C. and G. E. Hall (Eds.), Age and growth of fish. Iowa State University Press, 101 – 110.
- GERALDINE, H., 1986. Examining methods of fitting age/length data to the von Bertalanffy growth curve with a view to applying a simplified version of the Beverton and Holt yield-per-recruit model. 70 pp.
- GOVENDER, A., 1992. Biology and population dynamics of the king mackerel (*Scomberomorus commerson*, Lacépède, 1800) off the coast of Natal. MSc thesis. Durban, University of Natal. 117 pp.
- GOVENDER, A., E. J. KRIGE, I. D. L. T. LICHUCHA, V. SINGH, P. D. VORWERK and L. J. WALLER, 1998. Estimating fishing mortality rates from sex ratios in a sex-changing sparidae, *Crhysoblephus puniceus*. Unpublished report. 151. 7 pp.
- GOVENDER, A., 1999. A statistical procedure for validating age estimates from otolith bands using mark-recapture data with an illustration for *Pomatomus saltatrix*. South African Journal of Marine Science. 21: 1 – 8.
- GJØSAETER, J. and M. I. SOUSA, 1983. Reproduction, age and growth of the kelee shad, *Hilsa kelee*, (Cuvier, 1822) (Pisces: Fam. Clupeidae) with information on its fishery in Maputo Bay, Mozambique. Revista de Ivestigação Pesqueira. 8: 53 – 80.

GULLAND, J. A., 1969. Fisheries management and the limitation of fishing. FAO. Fisheries Technical Paper. 92. 13pp.

GULLAND, J. and L. A. BOEREMA, 1973. Scientific advice on catch levels. Fishery Bulletin. U.S 71: 325 – 335.

GULLAND, J. A., 1974. Fishery science, and the problems of management. Sea Fisheries Research. 413 – 430.

GULLAND, J. A., 1974. Fishery science, and the problems of management. Sea Fisheries Research. 413 – 430.

GULLAND, J.A., 1983. Fish stock assessment: A manual of basic method. John Wiley & Sons. 223pp.

GULLAND, J. A., 1985. Fish stock assessment: A manual of basic methods. 223pp.

HENDERSON, I. F. and W. D. HENDERSON, 1963. A dictionary of biological terms. (8 ed.). 640pp.

HETCH, T and M. J. (EDS) SMALE, 1986. Proceedings of a workshop on age determination and growth modelling of South Africa marine linefish. Investigational Report, JLB Smith Institute of Ichthyology. 21: 40 pp.

HOCKEY, P. A. R. and G. M. BRANCH, 1997. Criteria, objectives and methodology for evaluating marine protected areas in South Africa. In: Towards a new policy on marine protected areas for South Africa. South African network for coastal and oceanic research. Occasional report. (2): 98 – 118.

HOFFMAN, S. G., M. P. SCHILDHAUER and R. R. WARNER, 1985. The cost of changing sex and the ontogeny of males under contest competition for mates. *Evolution* 39 94) 915 – 927.

HUNTSMAN, G. R. and C. S. MANOOCH III, 1978. Minimum size limits for reef fishes. *Proceedings of Annual Conference of Southeast Association of Fish Wildlife Agencies*. 32: 509 – 513.

HUNTSMAN, G. R., C. S. MANOOCH II and C. B. GRIMES, 1983. Yield per recruit models of some reef fishes of the US South Atlantic Bight. *Fishery Bulletin*. U.S. 81: 679 – 695.

<http://www.co.mz>, 1999 – Dados basicos de Moçambique.

JONES, R., 1966. Manual of methods for fish stock assessment. Part 4. The use of marking data in fish population analysis, Rome. FAO, Fisheries Technical Paper. 51: 100pp.

JONES, R., 1977. A current view of fish population dynamics theory. Meeting on population dynamics in fisheries. Spain, 24 October 1977. *Invest. Pesq (Barc.)*. 43 (1), 1-20.

KING, M., 1996. Fisheries biology, assessment and management. Fishing news books. 331 pp.

KIRKWOOD, G. P., 1983 – Estimation of von Bertalanffy growth curve parameters using both length increment and age-length data. *Canadian Journal of Fish Aquatic Sciences*. 40: 1405 – 1411.

LAEVASTU, T. and F. FAVORITE, 1988. Fishing and stock fluctuations. Fishing news books, Farnham, Surrey, England. 239 pp.

- LAU, P. P. F. and Y. SADOVY, 2001. Gonad structure and sexual pattern in two threadfin breams and possible function of the dorsal accessory duct. *Journal of Fish Biology*. 58: 1438 – 1453.
- LICHUCHA, I. D. L. T., R. P. VAN DER ELST, A. GOVENDER, R. G. ABDULA and C. A. CUCO, 1998. The linefishery of Mozambique report for the year 1997. Unpublished report. Instituto de Nacional de Investigacao Pesqueira, Maputo. 38 pp.
- LIEM, K. F., 1968. Geographical and taxonomic variation in the pattern of normal sex reversal in the teleost fish order Synbranchiformes. *The Zoological Society of London*. 156: 225 – 238.
- MacFARLANE, G. A. and R. J. BEAMISH, 1980. Effect of an external tag on growth of sablefish (*Anoplopoma fimbria*), consequences to mortality and age at maturity. *Canadian Journal of Fish Aquatic and Science*. 47: 1551 – 1557.
- MacPHERSON, G. R., 1992. Age and growth of the narrowbared Spanish mackerel (*Scomberomorus commerson*, Lacépède, 1800) in north-east Queensland waters. *Australian Journal of Marine and Freshwater Research*. 43: 1269 – 1282.
- MAHONEY, R., 1966. *Laboratory techniques in Zoology*, London. 404 pp.
- MANN, B. Q., 1992. Aspects of the biology of two inshore sparidae (*Diplodus sargus capensis* and *Diplodus cervinus hottentotus*) off the south-east coast of South Africa. MSc thesis. Grahamstown, Rhodes University. 125 pp.
- MANN, B. Q., 2000. South African marine linefish status reports. *Oceanographic Research Institute. Special publication*. 7: 257 pp.

MASSINGA, A. and J. HATTON, 1996. Status of the coastal zone of Mozambique. In: Proceedings of the national workshop on Integrated coastal zone management in Mozambique. University Eduardo Mondlane, Maputo. 7 – 68.

PAPAGEORGIOU, N. K., 1979. The length weight relationship, age, growth and reproduction of the roach *Rutilus rutilus* (L.) in Lake Volvi. Journal of Fishery Biology. 14: 529-538.

PAULY, D., 1980. On the interrelationship between natural mortality, growth parameters and mean environmental temperature in 175 fish stocks. Journal du Conseil International pour l'exploration de la Mer. 39 (2): 175 – 192.

PAULY, D., 1984. Fish population dynamic in tropical waters: a manual for use with programmable calculators. ICLARM. 8: 325 pp.

PAULY, D., 1987. Application of information on age and growth of fish to fishery management. In: Summerfelt, R. C. and G. E. Hall (Eds.), Age and growth of fish. Iowa State University Press. 495 – 506.

PENNAK, R. W., 1964. Collegiate dictionary of zoology. University of Colorado, New York. 583pp.

PENNEY, A. J., C., C. D. BUXTON, P. A. GARRATT and M. J. SMALE, 1989. The commercial marine linefishery. In: Oceans of Life off Southern Africa. A. I. L. Payne and R. J. M. Crawford (Eds). South Africa, Vlaeberg. 214 – 229.

PIOTROVSKI, A., 1990. Relatório preliminar da informação existente sobre as pescarias e os recursos capturados pela pesca à linha no sul do país. Relatório nº 17. Instituto de Investigação Pesqueira, Maputo. 64 pp.

PITCHER, T. J., and P. J. B. HART, 1982. Fisheries ecology. Croom Helm, London. 414 pp.

PUNT, A. E., P. A. GARRATT and A. GOVENDER, 1993. On an approach for applying per-recruit methods to a protogynous hermaphrodite, with an illustration for the slinger *Chrysoblephus puniceus* (Pisces: Sparidae). South African Journal of Marine Science. 13: 109 – 119.

QUARTARARO, N. and R. E. KEARNEY, 1996. Effect of dart tags on the growth and survival of captive sapper, *Pagrus auratus* (Sparidae). Fisheries Research. 25: 231 – 238.

RICE, A. J., 1987. Reliability of age and growth-rate estimates derived from otolith analysis. Summerfelt, R. C. and G. E. Hall (Eds.), Age and growth of fish. Iowa State University Press. 167 – 176.

RICKER, W. E., 1958. Handbook of computation for biological statistics of fish populations. Fisheries Research Board of Canada. 119: 300 pp.

RICKER, W. E., 1975. Computation and interpretation of biological statistics of fish populations. Bulletin of the Fisheries Research Board of Canada. 191: 382 pp.

RIKHTER, W. E. and V. A. EFANOV, 1977. On one of the approaches of estimating natural mortality of fish populations. Trudy Atlantiki, NIRO. 73: 77 – 85.

ROZIN, P., 1968. The use of poikilothermy in the analysis of behavior. In: The central nervous system and fish behavior. The University of Chicago Press. Chicago. 181 – 192.

ROTHSCHILD, B. J., 1986. Dynamics of marine fish population. Harvard University press. Cambridge, London. 277 pp.

SADOVY, Y. and D. Y. SHAPIRO, 1987. Criteria for the diagnosis of hermaphroditism in fishes. Copeia. 1: 136-156.

SADOVY, Y. 1996. Reproduction of reef fishery species. In: Reef Fisheries. Polunin, N.V.C. and Roberts, C.M. Eds. Chapman and Hall, London. 15 – 60.

SADOVY, Y., 2000. Groupers and Wrasses specialist group species: Newsletter for the Species Survival Commission. 34: 55pp.

SAETRE, R. and A. J. SILVA, 1982. Water masses and circulation of the Mozambique channel. *Revista de Investigação Pesqueira*. Instituto de Investigação Pesqueira, Maputo. 3: 83 pp.

SCHNUTE, J., 1981. A versatile growth model with statistically stable parameters. *Canadian Journal of Fisheries Aquatic Science*, 38: 1128 – 1140.

SECOR, H. D., J. M. DEAN and E. H. LABAN, 1992. Otolith removal and preparation for microstructural examination. In: *Otolith microstructure examination and analysis*. Canadian Special Publication of Fisheries and Aquatic Sciences. 117: 19 – 57.

SECOR, D. H., M. D. JOHN and S. E. CAMPANA, 1995. Recent developments in fish otolith research. University of South Carolina Press. 735pp.

SHAPIRO, D. Y., 1984. Sex reversal and sociodemographic process in coral reef fishes. In: *Fish Reproduction*. G. N. Potts and R. J. Wootton (Eds). 103 – 118.

SHAPIRO, D. Y., 1987. Differentiation and evolution of sex change in fishes. *Bioscience*. 37 (7): 490 – 497.

SHAEFER, M. B., 1957. Some consideration of population dynamics and economics to the management of the commercial marine fisheries. *Journal of Fisheries Research Board of Canada*. 14 (5): 669 – 681.

SHEPHERD, J. G., 1988. Fish stock assessment and their data requirements. In *Fish population dynamics*, 2: 35 – 62.

SHEPHERD, J. C., 1992. Aide memories on scientific advice on fisheries management. *Laboratory Leaflet*. 70: 18pp.

SISSSENWINE, M. P., and J. G. SHEPHERD, 1987. An alternative perspective on recruitment overfishing and biological reference points. *Canadian Journal of Fisheries and Aquatic Science*. 44: 913-918.

SMALE, M. J. and A. E. PUNT, 1991. Age and growth of the red steenbras *Petrus rupestris* (Pisces: Sparidae) on the south-east coast of South Africa. *South African Journal of Marine Science*. 10: 131 – 139.

SMITH, J. L. B., 1938. The South African fishes of the families Sparidae and Denticidae. *Transactions of the Royal Society of South Africa*. 26 (3): 225 – 306.

SMITH M. M. and P. C. HEEMSTRA (Eds), 1986. *Smith's sea fishes*. Johannesburg, Macmillan, South Africa. 1047 pp.

SPARRE, P. and S.C. VENEMA 1997. *Introdução à avaliação de mananciais de peixes tropicais*, FAO, 2: 404 pp.

SUMMERFELT, R. C. and G. E. HALL, 1987. *Age and growth of fish*. Iowa state university press / Ames. 544 pp.

VAN DER ELST, R., 1993. *A guide to the common sea fishes of southern Africa*. Updated catch restrictions and regulations. 398 pp.

VAN DER ELST, R. P., B. DAVID and A. GOVENDER, 1995. The marine linefish resources of Mozambique: status, development and future research. *Revista de Investigação Pesqueira*, Nº 22. Instituto Nacional de Investigação Pesqueira, Maputo. 3-36.

VAN DER ELST, R. P., L. E. BECKLEY, A. GOVENDER, S. T. FENESSY, I. D. L. T. LICHUCHA, B. DAVID and H. PACULE, 1996. Interim proposals for optimal development and management of tourist angling in southern Mozambique. Unpublished report. Oceanographic Research Institute. 129: 1-21 p.

VAN DER ELST, R. P., A. GOVENDER, I. D. L. T. LICHUCHA, C. A. CUCO, 1997. Annual report for the year 1996: linefish section. Unpublished report nº 125. Instituto Nacional de Investigação Pesqueira. Maputo. 27 pp.

VAN DER ELST, R. P., G. BRANCH, D. BUTTERWORTH, P. WICKENS, and K. COCHRANE, 1997. How can fisheries resources be allocated...Who owns the fish? In: Developing and sustaining world fisheries resources. The state of science and management. 2nd World fisheries congress. CSIRO, Australia. D.A. HANCOCK, D. C. SMITH, A. GRANT, J. P. BEUMER (Eds). 1: 307 – 314 p.

VAN DER WALT, B. A., 1995. Biology and stock assessment of the coastal fish *Sarpa salpa* (Sparidae) off the KwaZulu-Natal coast, South Africa. MSc thesis. Durban, University of Natal. 106 pp.

VAN DER WALT, B. A., and L. BECKLEY, 1997. Age and growth of *Sarpa salpa* (Pisces: Sparidae) off the East Coast of South Africa. Fisheries Research. 31: 241 – 248.

WALLACE, R. A. and K. SELMAN, 1981. Cellular and dynamic aspects of oocyte growth in teleosts. Am Zoology. 21: 325 – 343.

WARNER, R. R., 1988. Sex change and the size-advantage model. Ecology and evolution. 3 (6): 133 – 136.

WEATHERLEY. A. H., 1972. Growth and ecology of fish population. Academic Press. 293 pp.

WENNER, A., 1972. Sex ratio as a function of size in marine crustacea. American Naturalist. 106: 321 – 350.

ZAR, J. H., 1974. Biostatistical analysis. New Jersey; Prentice-Hall. 2: 620 pp.

APPENDIX I

Marking-recapture, observed time-at-liberty and growth increments of *C. puniceus* tagged obtained from the Sedgwick's/ORI/WWF tagging project.

Fish no	Length at		Length increment	Length at Mark	Observed time-at-liberty		Estimated time-at-liberty			
	Mark	Recapture			days	years	Females		Males	
							one band	two bands	one band	two bands
1	350	248	-102	350	180	0.49	-4.58	-2.29	-1.53	-1.12
2	410	409	-1	410	4	0.01	-0.09	-0.05	-0.03	-0.02
3	367	367	0	367	1	0.00	0.00	0.00	0.00	0.00
4	422	420	-2	422	4	0.01	-0.22	-0.11	-0.07	-0.05
5	310	307	-3	310	75	0.21	-0.14	-0.07	-0.05	-0.03
6	280	273	-7	280	176	0.48	-0.28	-0.14	-0.09	-0.07
7	252	252	0	252	1	0.00	0.00	0.00	0.00	0.00
8	292	292	0	292	1	0.00	0.00	0.00	0.00	0.00
9	257	257	0	257	11	0.03	0.00	0.00	0.00	0.00
10	248	236	-12	248	15	0.04	-0.41	-0.21	-0.14	-0.10
11	286	278	-8	286	5	0.01	-0.33	-0.16	-0.11	-0.08
12	256	255	-1	256	6	0.02	-0.04	-0.02	-0.01	-0.01
13	266	264	-2	266	6	0.02	-0.08	-0.04	-0.03	-0.02
14	245	238	-7	245	5	0.01	-0.24	-0.12	-0.08	-0.06
15	255	251	-4	255	6	0.02	-0.14	-0.07	-0.05	-0.04
16	209	208	-1	209	4	0.01	-0.03	-0.02	-0.01	-0.01
17	261	262	1	261	82	0.22	0.04	0.02	0.01	0.01
18	296	298	2	296	82	0.22	0.09	0.04	0.03	0.02
19	275	275	0	275	5	0.01	0.00	0.00	0.00	0.00
20	226	219	-7	226	2	0.01	-0.22	-0.11	-0.07	-0.05
21	266	269	3	266	77	0.21	0.11	0.06	0.04	0.03
22	265	266	1	265	15	0.04	0.04	0.02	0.01	0.01
23	186	258	72	186	92	0.25	2.32	1.16	0.77	0.57
24	256	252	-4	256	91	0.25	-0.14	-0.07	-0.05	-0.04
25	245	0	-245	245	8	0.02	-6.03	-3.01	-2.01	-1.47
26	250	249	-1	250	82	0.22	-0.04	-0.02	-0.01	-0.01
27	287	310	23	287	181	0.50	1.01	0.51	0.34	0.25
28	276	276	0	276	10	0.03	0.00	0.00	0.00	0.00
29	240	240	0	240	1	0.00	0.00	0.00	0.00	0.00
30	356	360	4	356	83	0.23	0.25	0.12	0.08	0.06
31	248	245	-3	248	6	0.02	-0.11	-0.05	-0.04	-0.03
32	320	320	0	320	2	0.01	0.00	0.00	0.00	0.00
33	295	301	6	295	76	0.21	0.26	0.13	0.09	0.06
34	300	295	-5	300	7	0.02	-0.22	-0.11	-0.07	-0.05
35	293	289	-4	293	7	0.02	-0.17	-0.08	-0.06	-0.04
36	256	253	-3	256	82	0.22	-0.11	-0.05	-0.04	-0.03
37	225	227	2	225	81	0.22	0.07	0.03	0.02	0.02
38	264	264	0	264	3	0.01	0.00	0.00	0.00	0.00
39	256	256	0	256	3	0.01	0.00	0.00	0.00	0.00
40	215	219	4	215	4	0.01	0.13	0.06	0.04	0.03
41	232	229	-3	232	4	0.01	-0.10	-0.05	-0.03	-0.02
42	365	360	-5	365	81	0.22	-0.32	-0.16	-0.11	-0.08
43	253	250	-3	253	5	0.01	-0.11	-0.05	-0.04	-0.03
44	363	370	7	363	81	0.22	0.46	0.23	0.15	0.11
45	250	247	-3	250	5	0.01	-0.11	-0.05	-0.04	-0.03
46	260	256	-4	260	5	0.01	-0.15	-0.07	-0.05	-0.04
47	210	210	0	210	5	0.01	0.00	0.00	0.00	0.00
48	263	271	8	263	81	0.22	0.30	0.15	0.10	0.07
49	240	242	2	240	81	0.22	0.07	0.03	0.02	0.02
50	252	249	-3	252	4	0.01	-0.11	-0.05	-0.04	-0.03
51	342	349	7	342	81	0.22	0.40	0.20	0.13	0.10
52	248	250	2	248	5	0.01	0.07	0.04	0.02	0.02
53	231	0	-231	231	4	0.01	-5.55	-2.77	-1.85	-1.36
54	240	241	1	240	81	0.22	0.03	0.02	0.01	0.01
55	243	245	2	243	5	0.01	0.07	0.03	0.02	0.02
56	254	258	4	254	78	0.21	0.15	0.07	0.05	0.04
57	245	240	-5	245	5	0.01	-0.17	-0.09	-0.06	-0.04

Fish no	Length at		Length Increment	Length at Mark	Observed time-at-liberty		Estimated time-at-liberty			
	Mark	Recapture			days	years	Females		Males	
							one band	two bands	one band	two bands
58	233	233	0	233	5	0.01	0.00	0.00	0.00	0.00
59	215	219	4	215	78	0.21	0.13	0.06	0.04	0.03
60	195	195	0	195	1	0.00	0.00	0.00	0.00	0.00
61	241	242	1	241	77	0.21	0.03	0.02	0.01	0.01
62	307	307	0	307	1	0.00	0.00	0.00	0.00	0.00
63	263	270	7	263	76	0.21	0.27	0.13	0.09	0.07
64	251	250	-1	251	76	0.21	-0.04	-0.02	-0.01	-0.01
65	388	392	4	388	85	0.23	0.31	0.16	0.10	0.08
66	407	422	15	407	166	0.45	1.50	0.75	0.50	0.37
67	332	249	-83	332	99	0.27	-3.55	-1.78	-1.18	-0.87
68	365	365	0	365	1	0.00	0.00	0.00	0.00	0.00
69	263	263	0	263	134	0.37	0.00	0.00	0.00	0.00
70	338	333	-5	338	138	0.38	-0.27	-0.13	-0.09	-0.07
71	254	256	2	254	127	0.35	0.07	0.04	0.02	0.02
72	258	254	-4	258	7	0.02	-0.15	-0.07	-0.05	-0.04
73	261	255	-6	261	134	0.37	-0.22	-0.11	-0.07	-0.05
74	256	255	-1	256	127	0.35	-0.04	-0.02	-0.01	-0.01
75	257	256	-1	257	7	0.02	-0.04	-0.02	-0.01	-0.01
76	357	250	-107	357	4	0.01	-4.93	-2.47	-1.64	-1.21
77	383	294	-89	383	4	0.01	-4.96	-2.48	-1.65	-1.21
78	290	294	4	290	8	0.02	0.17	0.09	0.06	0.04
79	250	250	0	250	4	0.01	0.00	0.00	0.00	0.00
80	296	305	9	296	7	0.02	0.40	0.20	0.13	0.10
81	258	260	2	258	5	0.01	0.07	0.04	0.02	0.02
82	253	252	-1	253	5	0.01	-0.04	-0.02	-0.01	-0.01
83	258	238	-20	258	4	0.01	-0.71	-0.35	-0.24	-0.17
84	280	280	0	280	8	0.02	0.00	0.00	0.00	0.00
85	267	268	1	267	8	0.02	0.04	0.02	0.01	0.01
86	235	232	-3	235	5	0.01	-0.10	-0.05	-0.03	-0.02
87	241	244	3	241	8	0.02	0.10	0.05	0.03	0.03
88	262	262	0	262	5	0.01	0.00	0.00	0.00	0.00
89	261	272	11	261	8	0.02	0.42	0.21	0.14	0.10
90	225	200	-25	225	4	0.01	-0.78	-0.39	-0.26	-0.19
91	264	266	2	264	7	0.02	0.08	0.04	0.03	0.02
92	244	244	0	244	1	0.00	0.00	0.00	0.00	0.00
93	256	256	0	256	1	0.00	0.00	0.00	0.00	0.00
94	242	240	-2	242	4	0.01	-0.07	-0.03	-0.02	-0.02
95	236	234	-2	236	133	0.36	-0.07	-0.03	-0.02	-0.02
96	246	246	0	246	133	0.36	0.00	0.00	0.00	0.00
97	212	213	1	212	133	0.36	0.03	0.02	0.01	0.01
98	239	247	8	239	126	0.35	0.28	0.14	0.09	0.07
99	244	239	-5	244	7	0.02	-0.17	-0.09	-0.06	-0.04
100	218	251	33	218	2	0.01	1.11	0.55	0.37	0.27
101	241	243	2	241	127	0.35	0.07	0.03	0.02	0.02
102	262	265	3	262	127	0.35	0.11	0.06	0.04	0.03
103	231	237	6	231	127	0.35	0.20	0.10	0.07	0.05
104	274	0	-274	274	14	0.04	-7.10	-3.55	-2.37	-1.74
105	232	230	-2	232	126	0.35	-0.07	-0.03	-0.02	-0.02
106	352	0	-352	352	37	0.10	-10.83	-5.42	-3.61	-2.65
107	251	240	-11	251	2	0.01	-0.38	-0.19	-0.13	-0.09
108	225	231	6	225	1	0.00	0.20	0.10	0.07	0.05
109	275	270	-5	275	126	0.35	-0.20	-0.10	-0.07	-0.05
110	308	308	0	308	127	0.35	0.00	0.00	0.00	0.00
111	323	317	-6	323	138	0.38	-0.29	-0.15	-0.10	-0.07
112	247	247	0	247	1	0.00	0.00	0.00	0.00	0.00

APPENDIX II

Age-length key for *C. puniceus* , assuming annual periodicity of opaque band.

FL (mm)	Age (Years)																			Total
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	
195			1																	1
200			1																	1
210			2																	2
220				4																4
225				1																1
230				2																2
235				1																1
240				3																3
250				3																3
255				3																3
260					4															4
265					2															2
270					3	2														5
275					5	1														6
280					7	2														9
285					2	1														3
290					1	3	1													5
295						1	1													2
300						6	5													11
305						3	2													5
310						8	2													10
320						3	9													12
325							5	1												6
330							2	3												5
335								1												1
340								5												5
345								4	4											8
350								3	1											4
355								6	1											7
360								2	6	1										9
365									2	1	1									4
370										1	1									2
375										3	1									4
380										5	5									10
385										3	1	2								6
390											2	1								3
395												1								1
400												3								3
410												1	1							2
415												1								1
420												1	1	2						4
425													1	1						2
430													2	1	1					4
435														1	2					3
440														3		2				5
455																1				1
460																	1			1
465																		1		1
470																		1		1
480																			1	1
	0	0	4	17	24	30	27	25	14	14	11	10	5	8	3	3	1	2	1	199

APPENDIX III

Age-length key for *C. puniceus* , assuming bi-annual periodicity of opaque band.

FL (mm)	Age (Years)																			Total
	0	0.5	1	1.5	2	2.5	3	3.5	4	4.5	5	5.5	6	6.5	7	7.5	8	8.5	9	
195			1																	1
200			1																	1
210			2																	2
220				4																4
225				1																1
230				2																2
235				1																1
240				3																3
250				3																3
255				3																3
260					4															4
265					2															2
270					3	2														5
275					5	1														6
280					7	2														9
285					2	1														3
290					1	3	1													5
295						1	1													2
300						6	5													11
305						3	2													5
310						8	2													10
320						3	9													12
325							5	1												6
330							2	3												5
335								1												1
340								5												5
345								4	4											8
350								3	1											4
355								6	1											7
360								2	6	1										9
365									2	1	1									4
370										1	1									2
375										3	1									4
380										5	5									10
385										3	1	2								6
390											2	1								3
395												1								1
400												3								3
410												1	1							2
415												1								1
420												1	1	2						4
425													1	1						2
430													2		1	1				4
435															1	2				3
440															3		2			5
455																	1			1
460																		1		1
465																		1		1
470																		1		1
480																			1	1
	0	0	4	17	24	30	27	25	14	14	11	10	5	8	3	3	1	2	1	199