THE TAXONOMY, LIFE-HISTORY AND POPULATION DYNAMICS OF BLACKTAIL, *DIPLODUS CAPENSIS* (PERCIFORMES: SPARIDAE), IN SOUTHERN ANGOLA

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ABSTRACT

The blacktail, *Diplodus capensis*, is an inshore sparid fish distributed from Mozambique to Angola. This species forms an important component of coastal fisheries within its distribution, one being the subsistence handline fishery in southern Angola. With this fishery being critically important to the livelihoods of local communities, a biological study and stock assessment was conducted to provide information for the management of this species in southern Angola. However, with molecular evidence suggesting that the Benguela current may have separated the southern African populations of many inshore fish species over two million years ago, a morphological, taxonomic analysis was considered necessary to first investigate whether there was evidence for allopatry in this species.

A total of 46 morphometric measurements and 18 counts were carried out on specimens collected from various locations in southern Angola and South Africa. Results were analysed using multi-dimensional scaling (MDS) and the significance of clusters was tested using analysis of similarities (ANOSIM). Biological samples of *D. capensis* were collected monthly from an unexploited area from April 2008 to March 2009. Additional biological samples were collected from the subsistence fishers in an exploited area during May, June and December 2009. Standard biological laboratory techniques were employed for the life-history comparison between the exploited and unexploited area. A per-recruit analysis was conducted using the life-history parameters from both areas in order to assess the current status of the subsistence fishery and to investigate the potential short-falls of the per-recruit assessment approach.

The morphometric comparison showed that there was not sufficient evidence for speciation between the southern Angolan and South African populations of *D. capensis*. There was, however, sufficient morphological evidence to suggest that these populations are separate stocks. This indicated that the existing reference points on which the management of the South African population is based are unsuitable for the Angolan population. *Diplodus capensis* in southern Angola is omnivorous, feeding predominantly on algae, barnacles and mussels. An ontogenetic shift from algae to barnacles and mussels was correlated with allometric growth patterns in their feeding apparatus. This species is a rudimentary hermaphrodite in southern Angola with peak spawning in June and July. The overall sex ratio

(M: F) was 1: 4.7 in the unexploited area and 50% maturity was attained at 149.5mm FL and five years. *Diplodus capensis* in southern Angola exhibits very slow growth with the maximum age observed being 31 years (validated using mark recapture of chemically injected fish). Females [$L_{(t)} = 419.5(1-e^{-0.045(t-3.4)})$] grew significantly faster (LRT, $p < 0.05$) than males [$L_{(t)} = 297.4(1-e^{-0.077(t-2.7)})$], and females dominated the larger size classes and older age classes. In the exploited area, the length and age frequencies were severely truncated, the maximum observed age was greatly reduced (17 years) and the sex ratio was less female biased at 1: 2.2. Although there was no evidence for a physiological response to exploitation through alterations in growth or size/age at sexual maturity between the two areas, there was an increase in the proportion of small females in the exploited area, which may have been a compensatory response for the loss of large females. A combination of an underestimate of longevity, different estimates of the Von Bertalanffy growth parameters and overestimates of the natural mortality rate in the exploited population resulted in a 92% underestimate of the pristine spawner biomass-per-recruit (SBR) value. An assessment based on the actual pristine SBR estimate from the unexploited area revealed that the subsistence fishery had actually reduced *D. capensis* to 20% of its pristine SBR levels and highlighted the value of pre-exploitation life-history information for the application of per-recruit models.

This study has shown that *D. capensis* in southern Angola displays life-history characteristics that render it susceptible to overexploitation, even at low levels of fishing pressure. The current lack of infrastructure and enforcement capacity in the fisheries department of Angola renders traditional linefish regulatory tools, such as size limits, bag limits and closed seasons, inappropriate. Therefore, suitably designed marine protected areas are recommended as the best management option for this species.

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CHAPTER 1

Introduction

There are an estimated 38 million people in the world that are classified as fishers and fish farmers, of which 90% are classified as small-scale (FAO 2005). The majority of these people live in remote rural areas, where there are few alternative sources of income and employment offering significant potential to contribute to livelihood strategies. Fish is an important source of dietary protein, micro-nutrients and essential fatty acids for millions of the world's poor and contributes significantly to their caloric intake (FAO 2005).

Small-scale fisheries play a critical role in food security, employment opportunities and in the development of local economies in many developing countries (Bailey and Jentoft 1990, Kent 1997, Hotta 2000, McGoodwin 2001, Béné and Heck 2005a, 2005b, FAO 2005, Andrew et al. 2007). Middle and high income people consume more fish than low income people, however, even though they consume less, many low income people are completely dependant on fish as their source of animal protein (Kent 1997). For this reason, a decrease in fish supply is likely to be seen as little more than an inconvenience to middle and high income people, while it is likely to have serious consequences to the poor in terms of both economics and nutrition (Kent 1997).

Due to capacity, budgetary and infrastructural constraints in the countries where small-scale fisheries exist, their management is generally restricted and/or neglected (Anon 2002, Andrew et al. 2007). This situation is exacerbated by the perceived need for stock assessment based management (developed by scientists in developed countries for large-scale fisheries) rather than by the need to implement the most effective management regime possible given the available resources (Mahon 1997). Since it is now commonly accepted that even a low level of small-scale fishing can have a big impact on target fish populations (Jennings et al. 1995, Jennings and Polunin 1996, Russ and Alcala 1996, Pinnegar and Engelhard 2008), there is a need for increased management of these fisheries in order to maintain their function as a critical source of food security in developing countries.

Angola, located on the West Coast of Africa, is a large country with a land area of 1 246 700 km^2 and a coastline of 1650km. This country has suffered from an extended period of socio-political instability. Angola was a Portuguese colony from the 15^{th} century until attaining independence in 1975 after 14 years of anti-colonial war. After a subsequent 27 years of civil war, the country's infrastructure, agriculture and human capital were destroyed. During this period the fishing industry collapsed and the inland population underwent large-scale shifts to the coastal towns where a large proportion of the population still has no access to water, basic sanitation, medical care and education (Duarte et al. 2005). The situation is exacerbated in the south of the country, where the coastal region is dominated by the very dry and barren Namib Desert. With little opportunities for agriculture in this region, the coastal fisheries play a critical role in providing a source of food security and income to the local population.

According to Angolan legislation, subsistence fishing involves the fisher capturing fish for family consumption but occasionally sells the surplus catch (Duarte et al. 2005). Preliminary results from a socio-economic study have indicated that there is a significant subsistence fishery close to the town of Namibe in southern Angola (WM Potts, unpublished data). The blacktail (locally known as mariquita), *Diplodus capensis*, forms the bulk of the catch of this fishery (87%). The above study has also revealed that there is evidence that this species is in danger of overexploitation since 91% of the fishermen said that effort had increased in the past five years, 92% said that the fish have gotten smaller and all the fishermen said that *D. capensis* had declined the most out of all the target species. This fishery provides a critical source of food security to the local people in this region.

Diplodus capensis belongs to the Sparidae family, which is comprised of approximately 115 species in 33 genera (Nelson 2006). Sparids, commonly known as seabreams or porgies, inhabit temperate and tropical waters of all oceans and are usually concentrated along the shore in fairly shallow water (Smith and Heemstra 2003). The genus *Diplodus* is comprised of 19 species worldwide (de la Paz 1975), making it the most speciose genus in the family. *Diplodus capensis* is a medium sized (attains 45cm FL, 3kg) sparid distributed from Angola, through Namibia, around the South African coast and into southern Mozambique (Heemstra and Heemstra 2004). This species is abundant on turbulent inshore reefs (Mann 1992) but has also been recorded in the surf zone of sandy beaches (Lasiak 1986, Bennett 1989) and in the lower reaches of estuaries (Whitfield 1985). *Diplodus capensis* is an omnivore, feeding on a variety of plant and animal organisms (Christensen 1978, Joubert and Hanekom 1980, Whitfield 1985, Coetzee 1986, Lasiak 1986, Mann and Buxton 1992). This species is a rudimentary hermaphrodite (Joubert 1981b), with some studies showing evidence of partial protandry (Coetzee 1986, Mann and Buxton 1998). Sparids are generally slow growing, long-lived and late maturing species and this renders them particularly susceptible to overexploitation (Acosta and Appeldoorn 1992, Chale-Matsau et al. 2001, FAO 2001). *Diplodus capensis* displays these typical sparid life-history characteristics, with ages of over 20 years having been recorded for this species in South Africa (Mann and Buxton 1997). Slow growth, high longevity, relatively late maturation, habitat preference and sex change are all considered to be influential traits that govern the decisions on the management of the recreational *D. capensis* fishery in South Africa (Mann 1992).

Due to budgetary and capacity constraints in the research institutions and fishery departments, there is a general lack of knowledge about the local fish biology, fisheries and fish stock status in developing countries (Aas 2002). Understandably, Angola is no exception, and the facilities and infrastructure needed to support a progressive fisheries sector are either completely inadequate or in a severely degraded state (Duarte et al. 2005). Therefore, priority should be given to the development of policy and management strategies using rigorously collected biological, ecological, economic and social information on the fisheries sector (Potts et al. 2009). Duarte et al. (2005) identified, amongst others, two urgent requirements in Angola. Firstly, appropriate fishery controls on the capture of largely resident reef fish and possibly other species of line fish, and secondly, biological research on vulnerable species, so that appropriate models may be developed to ensure sustainable resource use. They further suggested that length frequencies, growth rates, age-length keys, breeding cycles and size at maturity were some of the essential data required (Duarte et al. 2005).

Thesis outline

The overall aim of this study was to assess the biology and population dynamics of *D. capensis* in southern Angola in order to contribute to informed and applicable management recommendations for its sustainable harvest.

To achieve this aim, the body of this thesis has been divided into five data oriented chapters. Each data chapter either addresses a step towards the assessment of the *D. capensis* fishery, or develops further ecological knowledge on this species.

It was initially necessary to conduct a taxonomic study on this species in order to investigate whether there is evidence for speciation or stock separation between the South African and Angolan populations (Chapter two). This portion of the thesis was considered necessary in order to confirm the taxonomic status of *D. capensis* in southern Angola and because defining the distribution of fish stocks is considered crucial for effective fishery management.

Chapter three and four address the lack of ecological knowledge of this species. The diet of *D. capensis* in southern Angola is described in Chapter three with a specific focus on possible ontogenetic dietary shifts and whether there is evidence for a correlation between morphology and diet in this species.

Chapter four gives a detailed description of the reproductive style, gametogenesis and reproductive seasonality of this species. Sparid fishes display complex forms of sexuality, some of which are difficult to diagnose. As a result there has often been disagreement on the reproductive style of single species. In this chapter, a detailed study was undertaken, using a variety of methods, to investigate which reproductive style is displayed by *D. capensis* in southern Angola, which has important management implications.

In Chapter five, the life-history parameters of this species were compared between a proximate unexploited and exploited area with similar physical characteristics. This part of the study was conducted in order to assess to what extent subsistence fishing is affecting the *D. capensis* population and whether there is evidence of a life-history response to exploitation.

The life-history parameters determined from the unexploited and exploited areas were used in a series of spawner biomass-per-recruit (SBR) and biomass-per-recruit (BR) analyses in Chapter six. The aim of this chapter was to assess the stock status of *D. capensis* in the subsistence fishery and investigate to what extent fishery induced alterations in life-history can affect the results of a per-recruit assessment.

This thesis culminates in Chapter seven which is a general discussion with management considerations based on the life-history information collected in the previous chapters. Future research priorities for the region are also suggested.

Study area

Sampling was conducted in the coastal zone between the towns of Namibe (15° 11' S, 12° 09' E) and Tombua (15° 48' S, 11° 50' E) in southern Angola (Figure 1.1). The marine environment in this region is influenced by two major ocean currents, the northward flowing cold Benguela current and the southward flowing warm Angola current. The confluence of

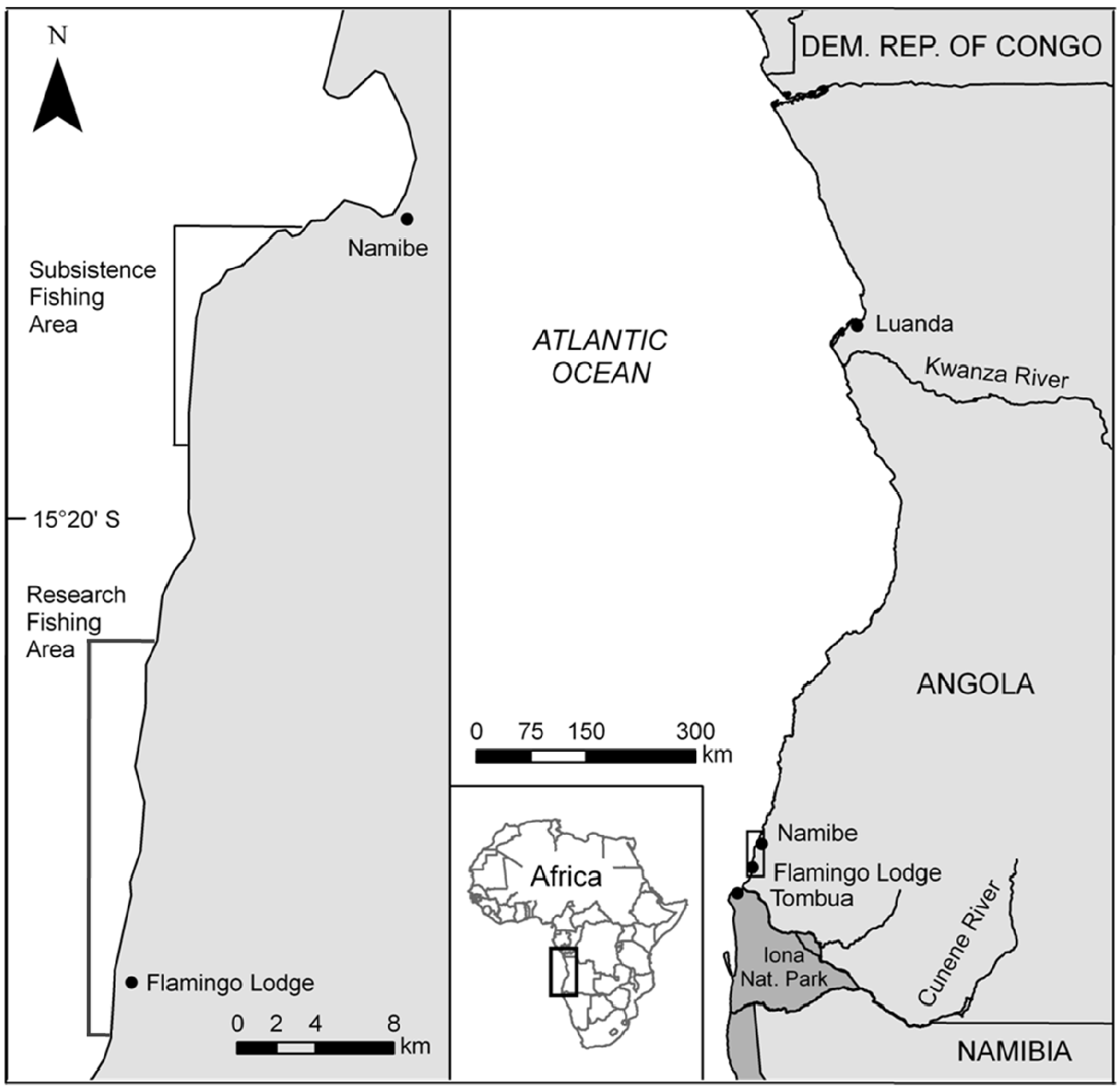

Figure 1.1: Map of the study area indicating the towns mentioned in the text.

these currents gives rise to the Angola-Benguela Frontal Zone (ABFZ) which is a permanent feature but demonstrates seasonal variation in its location (Meeuwis and Lutjeharms 1990, Veitch et al. 2010). The mid-front isotherm has been documented to move up to 750km along the south-west African shore (Meeuwis and Lutjeharms 1990). During the austral autumn and winter, the strength of the Angola current is weakest, allowing the Benguela current to push further north, while the opposite occurs during spring and summer (Shannon et al. 1987, Meeuwis and Lutjeharms 1990, Kostianoy and Lutjeharms 1999, Veitch et al. 2006). The seasonal variability of these currents is reflected in the inshore water temperature (Figure 1.2) and, as a result, Whitfield (2005) characterised the southern Angola region as a subtropical biogeographic zone. During the austral winter, the Benguela current brings cool chlorophyll *a* - rich water into southern Angola thus increasing primary productivity (Hutchings et al. 2009). Conversely, during summer the Angola current dominates and primary productivity and algal abundance decreases in the region (Hutchings et al. 2009). The intertidal zone in southern Angola is dominated by sandy beach interspersed with sandstone rocky outcrops. The continental shelf at these latitudes is approximately 36km wide (Duarte et al. 2005).

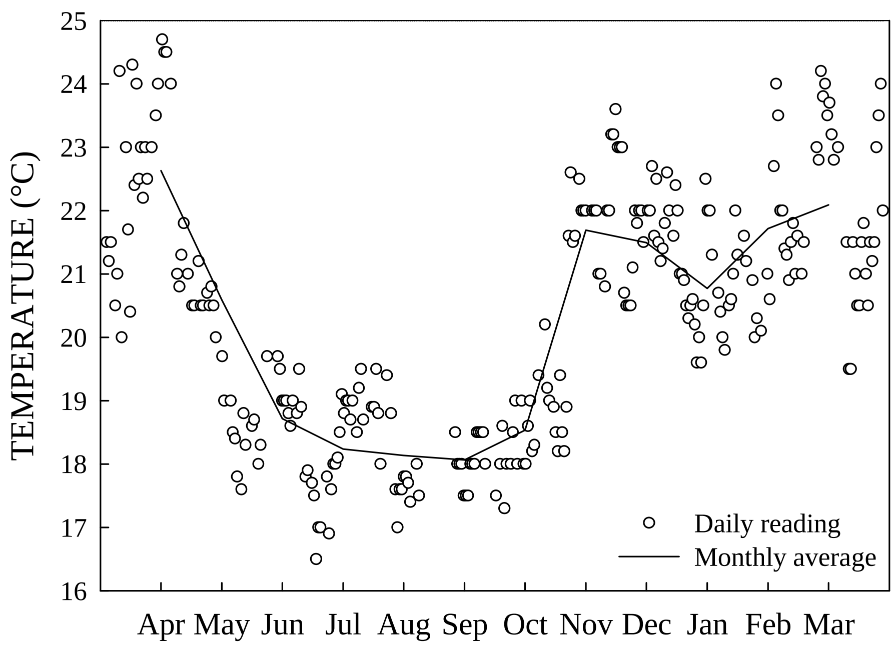

Figure 1.2: Daily (n = 269) and monthly average surf zone water temperature measured at Flamingo Lodge during the study period.

CHAPTER 2

Morphological comparison of *Diplodus capensis* between South Africa and southern Angola

Introduction

As mentioned in the previous chapter, the Sparidae family is comprised of predominantly coastal species and are considered valuable in inshore recreational (Mann 1992, Götz et al. 2008a), subsistence (Richardson et al. submitted, Chapter 5), artisanal (Pajuelo and Lorenzo 2002, Pajuelo et al. 2003, Dominguez-Seoane et al. 2006) and commercial fisheries (Goncalves et al. 2003, Pajuelo et al. 2006). The genus is believed to have originated in the north-eastern Atlantic and Mediterranean Sea and the subsequent diversification and speciation that has occurred is thought to be a result of a series of rapid colonization events, which is supported by both morphological (de la Paz 1973) and molecular (Summerer et al. 2001) phylogenies.

Diplodus capensis is the dominant *Diplodus* species in southern Angola. Other species in the genus recorded in Angola include *D. vulgaris*, *D. puntazzo*, *D. cervinus* and *D. sargus cadenati*, all of which are easily distinguished from *D. capensis* based on gross morphological appearance (de la Paz 1975, Fischer et al. 1981). *Diplodus capensis* was originally described as *Sargus capensis* by Andrew Smith in 1846. Boulenger (1887) re-described this species as *Sargus rondeletii*, which was subsequently changed to *Diplodus rondeletii* by Barnard (1927). J.L.B Smith (1965) re-described the species as *Diplodus sargus capensis*, but this subspecies was assigned its current name by Heemstra and Heemstra (2004). The recorded distribution of *D. capensis* is from Angola, through Namibia, around the South African coast and up to the south of Mozambique (de la Paz 1975, Heemstra and Heemstra 2004). Although this distribution is thought to be continuous, there are limited specimens available from the west coast of southern Africa and there have been no studies to confirm the taxonomic status of these specimens. In addition, the cold Benguela current which formed approximately two million years ago (Shannon 1985, Marlow et al. 2000), is considered to be a potential oceanographic and geographic barrier capable of producing divergence and speciation in sparid fishes (Floeter et al. 2008) and other fishes, including Sciaenids of the genera *Atractoscion* (Henriques 2009) and *Argyrosomus* (Griffiths and Heemstra 1995, Henriques 2009).

The demonstration of morphological variation between fish populations has two important applications. Firstly, morphometric characters have been used as the primary tool in fish taxonomy for centuries and still remain the primary means of describing new species (King 1993, Inoue and Nakabo 2006, Iwatsuki et al. 2006, Kume and Yoshino 2006, Sakai and Nakabo 2006, Tseng et al. 2009). Secondly, morphological variation can be used as a tool to identify discrete fish stocks which is important for fisheries management purposes (Elliot et al. 1995, Begg et al. 1999, Begg and Waldman 1999, Palma and Andrade 2002, 2004). At this point it is important to define exactly what is meant by a "species" and a "stock".

There are a number of different (many of which are conflicting) species concepts, the most common being the morphological (or typological) (MSC), the biological (BSC), the recognition, the cohesion, the evolutionary, the ecological and the phylogenetic species concepts (Mayr 1963, 1974, King 1993, Mayr 1996, Turner 1999). When dealing with morphological variation only two of these concepts need be considered, the MSC and the BSC.

The MSC was developed by Linnaeus, the father of modern taxonomy. The underlying philosophy of this concept is that all species are well-defined and constant in form. With the advent of evolutionary theory, this concept does not hold for two main reasons. The first of these is the presence of conspicuous morphological differences among conspecific individuals and populations (intraspecific variation) and, secondly, the virtual absence of morphological differences among some populations (sibling species) (Mayr 1963). Despite its inadequacy in these respects, the MSC is still a widely used concept and remains the baseline for the taxonomic description of all living things today.

The BSC is a more recently defined concept and has been the most widely used definition of a species in the past 50 years (Turner 1999). The key decision which created the BSC was the recognition by Dobzhansky (1937) that the process responsible for speciation was the development of reproductive isolating mechanisms (King 1993). Based on this idea, the BSC states that species are groups of interbreeding natural populations which are reproductively isolated from other such groups (Mayr 1942, 1974). Unlike the MSC which uses degree of morphological difference as the primary criterion for species status, the BSC can use morphological evidence together with various other kinds of evidence in order to determine whether or not a population deserves species rank (Mayr 1974).

The concept of a stock has also been the topic of much debate with no agreement on one definition. Stock identification is however fundamental to fisheries management. It is important to understand the stock structure of a species and how fishing effort and mortality are distributed in order to design appropriate management regulations (Ricker 1981, Begg and Waldman 1999). A single species may display variation in life-history characteristics in different areas and such populations need to be managed independently in order to achieve management goals. A workable definition of fish stocks are arbitrary groups of fish large enough to be essentially self-reproducing, with members of each group having similar life-history characteristics (Hilborn and Walters 1992). Stocks of fish can be identified in various ways, for example through mark-recapture experiments, catch data, parasites, otolith microchemistry and genetics (Begg and Waldman 1999). Stocks can also be identified through morphological variation (Begg and Waldman 1999). Countable, morphological structures have historically served as an important basis for identifying fish stocks since they are discreet and allow for statistical analysis (Begg and Waldman 1999). Meristic characters are generally set early in ontogeny and remain stable throughout life making them more reliable than morphometric measurements. Morphometrics include the analysis of body shape, or the shape of particular morphological features of various body dimensions or parts (Begg and Waldman 1999).

The definitions involved in species and stock concepts are complicated and there is much discord in their use. However, the underlying basis for using morphological variation in order to address either of these concepts is that there is sufficient genetic differentiation between two fish populations to be manifested as morphological variation.

The aim of this study was to use comparative morphometric data for *D. capensis* in South Africa and Angola to confirm the current taxonomic status of this species in southern Angola, and to provide evidence for or against stock separation of this species in the two regions. Although the methods available to address these questions are diverse, most of them were beyond the scope of this study, and thus morphological variation was the single method used. There is clearly a fine line between differentiating two populations of the same species as different stocks or different species since there are no clear-cut criteria that researchers can follow in order to assign species rank or separate stocks when dealing with morphology. Therefore, it is important to define exactly what was accepted in this study. In order to diagnose species rank, at least one meristic count or morphometric measurement had to differ between the South African and Angolan samples with no overlap in their ranges. In order to diagnose stock separation, any multivariate statistically significant difference in meristic or morphometric data was considered sufficient.

Material and Methods

Sample collection and preservation

Fish were collected using rod and line from 10 sites in South Africa and four sites in southern Angola. In Angola, all samples were preserved in 10% formalin immediately after capture. In South Africa, however, due to the reliance on external help for sample collection, some samples were frozen before they were preserved. After at least three weeks in 10% formalin, samples were transferred into 10% and 50% ethanol for three days each and then stored in 70% ethanol.

Morphometric measurements

A total of 46 measurements were made on each fish. Measurements generally followed the methods of Hubbs and Lagler (1947), with modifications and additions listed in Table 2.1. Measurements were made using digital callipers to the nearest 0.01mm.

Table 2.1: Morphometric measurements made on *Diplodus capensis* that are not described (or were modified) in Hubbs and Lagler (1947), and those that were added for this study.

Measurement	Description
Predorsal length	Distance from the tip of the snout to the structural base of the first dorsal spine
Preanal length	Distance from the tip of the snout to the structural base of the first anal spine
Prepectoral length	Distance from the tip of the snout to the structural base of the first pectoral ray
Prepelvic length	Distance from the tip of the snout to the structural base of the first pelvic spine
Front of dorsal - pelvic distance	Distance from the structural base of the first dorsal spine to the structural base of the first pelvic spine
Front of dorsal - front of anal distance	Distance from the structural base of the first dorsal spine to the structural base of the first anal spine
Front of dorsal - back of anal distance	Distance from the structural base of the first dorsal spine to the structural base of the last anal ray
Back of dorsal - back of anal distance	Distance from the structural base of the last dorsal ray to the structural base of the last anal ray
Back of dorsal - front of anal distance	Distance from the structural base of the last dorsal ray to the structural base of the first anal spine
Pelvic - anal fin distance	Distance from the structural base of the first pelvic spine to the structural base of the first anal spine
Head length	Taken to exclude the membranous edge of the operculum
Postorbital length of head	Taken to exclude the membranous edge of the operculum
Length of eye	Horizontal distance between the free orbital rims
Length of orbit	Horizontal distance between the cartilaginous orbital rims
Pelvic flap length	Length of the flap of skin at the base of the pelvic fin

Meristic counts

A total of 16 counts were made on each fish (Table 2.3). Counts generally followed Hubbs and Lagler (1947), however the lateral line scale count included those scales that were posterior to the structural caudal base, and the top and bottom incisor counts were also included.

Data analysis

The meristic data from fish of all sizes was used in the comparison, however, to prevent size bias caused by allometric growth patterns, the morphometric comparisons were only conducted on fish of a similar size range. All morphometric measurements were expressed as ratios (percentage of SL). Differences between the morphometric ratio and meristic character means were tested using a student's *t*-test.

The entire morphometric and meristic data sets were analysed using multi-dimensional scaling (MDS) based on the Bray Curtis similarity measure. Differences between sites were examined using one-way analysis of similarities (ANOSIM) with the Primer v.6 software package (Plymouth Marine Laboratory, Plymouth, UK). Differences between sites were considered significant at $p < 0.05$. The significance of the ANOSIM result is based on the R statistic. The value of R lies within the range (-1 - 1) and is a useful comparative measure of the degree of separation of sites (Clarke and Warwick 1994). Values of R usually range from zero to one; an R value of one indicates that all replicates within sites are more similar to each other than any replicates from the other sites and an R value of zero indicates that the similarities between and within sites will be the same on average (Clarke and Warwick 1994). An R value substantially less than zero is unlikely as it would imply that the similarities are greater between sites than within sites (Clarke and Warwick 1994).

Some of the South African samples were frozen before preservation, which introduced the potential for bias in the morphometric measurements caused by alterations in body proportions (Engel 1974, Treasurer 1990, Jawad 2003, Florin and Lingman 2008). Therefore, to test whether freezing had an effect on the measurements a preliminary analysis was conducted. This analysis included MDS and *t*-tests as above, to compare samples that had been frozen prior to preservation with those that had been preserved directly after capture from the same area.

Results

A total of 88 fish were collected, of which 53 were from South Africa and 35 from Angola (Table 2.2). Fifteen of the 46 measurements differed significantly (student's *t*-test, $p < 0.05$) between samples that were frozen or fresh before preservation from the Eastern Cape. The MDS ordination plot displayed two significantly different clusters but with a high degree of overlap (ANOSIM, $R = 0.154$, $p < 0.05$) (Figure 2.1). Based on these results, it was concluded that there is sufficient evidence to suggest that freezing the samples before preservation had an effect on their body proportions and therefore, all samples that had been frozen prior to preservation were excluded from the morphometric analyses.

Table 2.2: Summary of the number of *Diplodus capensis* samples collected from various locations in southern Angola and South Africa used in the morphometric and meristic analyses.

Country	Province	Location	*n*	Size Range (mm FL)	*n* used for morphometrics	*n* used for meristics
Angola	Namibe	Flamingo Lodge	15	163.7 - 317.7	15	15
		"My Beach"	6	187.2 - 264.9	5	6
		Namibe	12	80.8 - 184.9	0	12
		Santa Marta	2	108.6 - 217.8	1	2
South Africa	Kwa-Zulu Natal	Cape Vidal	4	170.2 - 216.09	0	4
		Port Shepstone	2	192.4 - 197.9	0	2
	Eastern Cape	Cape St. Francis	12	174.0 - 255.9	4	12
		Dwesa	6	139.4 - 267.0	0	6
		Hluleka	12	134.7 - 271.8	11	12
		Jeffrey's Bay	3	151.4 - 201.4	3	3
		Kasouga	6	222.3 - 280.2	0	6
		Riet River	2	257.1 - 290.7	0	2
	Western Cape	Breede River	6	161.9 - 216.6	0	6

Five of the 16 meristic count means (Table 2.3) and 18 of the 46 morphometric ratio means (Table 2.4) were significantly different (student's *t*-test, $p < 0.05$) between the Angola and South Africa samples. Despite even highly significant differences ($p < 0.01$), there was still a degree of overlap in the ranges of each count and each morphometric ratio. The MDS ordination plots for meristic counts (Figure 2.2) and morphometric ratios (Figure 2.3) separated individuals into two groups corresponding to the Angola and South Africa samples. The ANOSIM results indicate that the groupings are significantly different from one another (R = 0.34, $p < 0.01$ for morphometric data and R = 0.35, $p < 0.01$ for meristic data). The R statistic was similar for both the morphometric and meristic ANOSIM results and the value suggests that there is a relatively low degree of separation between the Angola and South Africa populations.

Table 2.3: Meristic data for *Diplodus capensis* from southern Angola (n = 35) and South Africa (n = 53). *p* - values from students *t*-tests are presented (ns = $p > 0.05$, * = $p < 0.05$, ** = $p < 0.01$)

	Southern Angola					South Africa					
	Mean	Median	SD	Min.	Max.	Mean	Median	SD	Min.	Max.	*p*
Dorsal spines	12.0	12	0.2	12	13	12.0	12	0.3	11	13	ns
Dorsal rays	14.1	14	0.8	12	15	14.3	14	0.8	13	16	ns
Anal spines	3.0	3	0.0	3	3	3.0	3	0.2	2	4	ns
Anal rays	13.5	14	0.5	13	14	13.7	14	0.7	12	15	ns
Pectoral spines	0.0	0	0.0	0	0	0.0	0	0.0	0	0	-
Pectoral rays	16.1	16	0.6	15	18	15.9	16	0.6	15	17	ns
Pelvic spines	1.0	1	0.0	1	1	1.0	1	0.0	1	1	-
Pelvic rays	6.3	6	0.5	6	7	6.4	6	0.5	6	7	ns
Pored lateral line (LL) scales	69.5	69	2.1	66	75	72.4	73	3.1	64	79	**
Scales between LL and 4th dorsal spine	9.1	9	0.6	7	10	9.4	9	0.6	8	10	ns
Scales between LL and anal origin	16.4	17	0.8	14	18	17.2	17	0.9	16	19	**
Cheek scale rows	4.7	5	0.7	4	6	5.2	5	0.6	3	6	**
Number of top incisors	8.1	8	0.4	7	10	8.0	8	0.3	8	10	ns
Number of bottom incisors	8.0	8	0.2	7	8	8.0	8	0.0	8	8	ns
Upper gill rakers	7.5	7	0.7	7	9	7.2	7	0.5	6	8	**
Lower gill rakers	11.2	11	0.5	10	12	9.6	10	0.7	7	11	**

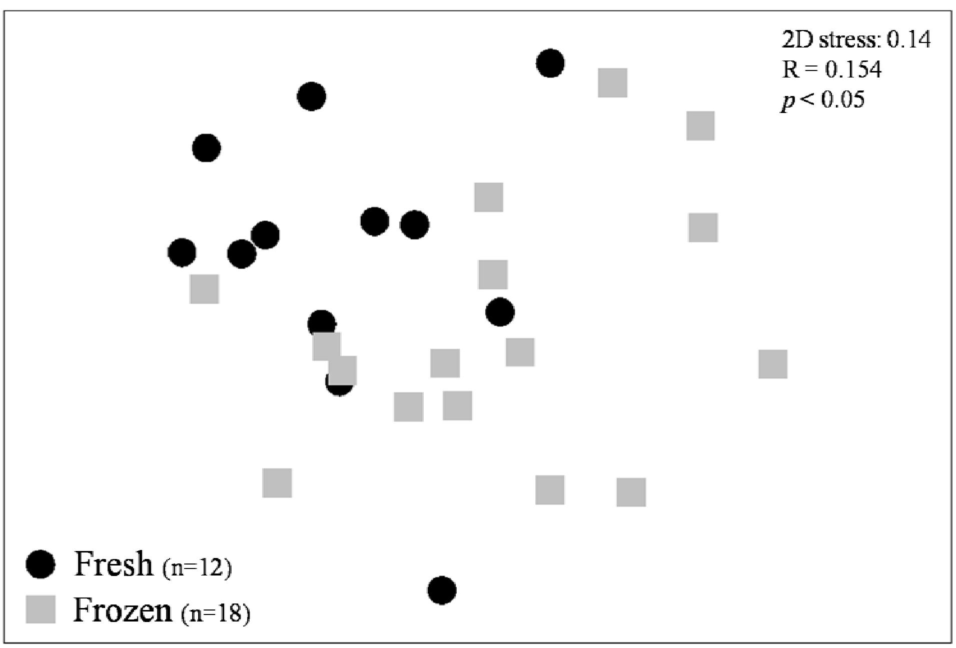

Figure 2.1: Multi-dimensional scaling (MDS) ordination plot of 46 morphometric measurements of frozen or fresh (before preservation) specimens of *Diplodus capensis* from the Eastern Cape.

Table 2.4: Morphometric measurements of *Diplodus capensis* from southern Angola (n = 21) and South Africa (n = 18). p - values from students t-tests are presented (ns = $p > 0.05$, * = $p < 0.05$, ** = $p < 0.01$)

	Southern Angola				South Africa				
	Mean	SD	Min.	Max.	Mean	SD	Min.	Max.	p
Standard length (mm)	193.06	36.57	141.81	277.81	176.58	37.93	117.81	240.96	-
Measurements (% SL)									
Fork length	115.1	0.9	112.3	116.6	113.6	0.6	112.5	114.7	**
Total length	133.5	2.0	128.6	136.1	132.6	1.3	129.6	134.5	ns
Caudal peduncle depth	11.0	0.3	10.3	11.5	11.7	0.4	10.9	12.4	**
Caudal peduncle length	14.9	0.7	13.3	16.3	15.3	0.7	13.9	16.7	ns
Predorsal length	47.6	1.9	44.4	52.0	47.6	1.5	45.9	51.5	ns
Preanal length	69.4	0.7	67.7	70.6	69.6	1.3	66.9	71.8	ns
Prepectoral length	33.5	1.3	31.6	36.5	33.6	1.2	32.1	36.4	ns
Prepelvic length	39.7	1.0	37.9	41.6	40.6	1.0	38.9	42.9	**
Front of dorsal - pelvic distance	47.7	1.3	44.9	49.9	48.4	1.9	45.0	51.2	ns
Front of dorsal - front of anal distance	58.5	1.3	56.2	60.5	59.1	1.9	55.4	62.2	ns
Front of dorsal - back of anal distance	63.1	1.4	61.2	65.7	62.9	1.1	61.5	65.2	ns
Back of dorsal - back of anal distance	14.7	0.7	13.3	15.9	16.0	0.6	14.9	17.2	**
Back of dorsal - front of anal distance	35.4	0.9	33.5	36.9	36.3	1.0	34.9	38.2	**
Pelvic - anal fin distance	31.4	1.1	29.9	33.1	30.7	1.3	28.6	33.5	ns
Dorsal base	56.7	1.7	53.7	59.8	55.5	1.1	53.8	57.7	*
Anal base	24.9	0.8	23.4	26.4	25.2	0.7	23.8	26.2	ns
Length of pectoral fin	38.7	1.5	35.0	41.3	37.6	1.4	35.1	40.3	*
Length of pelvic fin	24.1	1.7	18.0	26.5	22.5	1.0	20.9	24.5	**
Head length	31.7	1.5	29.2	34.7	31.0	0.8	29.7	32.7	ns
Depth of head	27.1	1.3	25.2	30.6	27.6	0.9	26.2	29.1	ns
Interorbital distance	11.0	0.5	10.0	12.3	11.5	0.4	10.6	12.2	**
Snout length	14.0	1.3	12.1	17.2	14.2	0.9	12.6	15.8	ns
Postorbital length of head	12.7	0.7	11.7	14.5	11.9	0.4	11.2	12.5	**
Orbit to angle of preopercle	11.1	0.9	9.8	13.2	10.6	0.6	9.4	11.5	ns
Length of eye	8.1	0.6	6.8	8.9	8.1	0.8	7.0	9.7	ns
Length of orbit	9.6	0.7	8.0	10.7	9.7	0.8	8.5	11.2	ns
Length of upper jaw	11.4	1.3	9.6	14.8	11.1	0.8	10.0	12.8	ns
Length of mandible	9.1	1.2	7.5	12.3	8.8	0.7	7.8	10.5	ns
Width of gape	10.3	1.1	9.0	12.9	10.2	0.5	8.9	10.9	ns
Least distance between orbit and maxilla	6.8	0.7	5.7	8.6	6.9	0.5	5.8	7.7	ns
Top caudal ray length	34.1	2.2	29.7	37.9	33.3	1.4	31.2	36.4	ns
Middle caudal ray length	15.7	0.9	14.2	17.1	14.2	0.7	12.9	15.2	**
Bottom caudal ray length	29.8	1.8	25.6	32.4	29.0	1.3	26.6	32.0	ns
1st dorsal spine length	5.7	1.0	3.6	8.2	5.6	0.9	4.2	8.1	ns
2nd dorsal spine length	9.0	1.0	7.5	10.6	8.6	1.2	5.9	11.7	ns
3rd dorsal spine length	12.1	1.1	10.1	14.5	11.2	1.2	8.3	13.2	*
4th dorsal spine length	13.6	1.5	8.3	15.0	12.4	1.1	9.6	13.9	**
5th dorsal spine length	14.1	0.8	12.1	15.5	12.3	1.2	10.4	14.1	**
6th dorsal spine length	13.6	0.8	11.8	15.1	11.8	0.9	9.9	13.6	**
7th dorsal spine length	12.8	1.2	10.1	14.7	10.8	1.0	9.1	12.8	**
1st anal spine length	6.6	1.8	4.6	14.1	5.9	0.7	4.4	7.1	ns
2nd anal spine length	10.5	1.2	8.1	12.9	9.4	1.0	8.3	11.8	**
3rd anal spine length	8.5	1.5	3.4	10.1	8.6	1.9	6.2	14.9	ns
Pelvic spine length	16.3	1.6	11.5	18.8	14.7	1.8	8.1	16.6	**
Pelvic flap length	9.1	1.3	6.2	10.9	8.4	1.3	5.0	10.6	ns

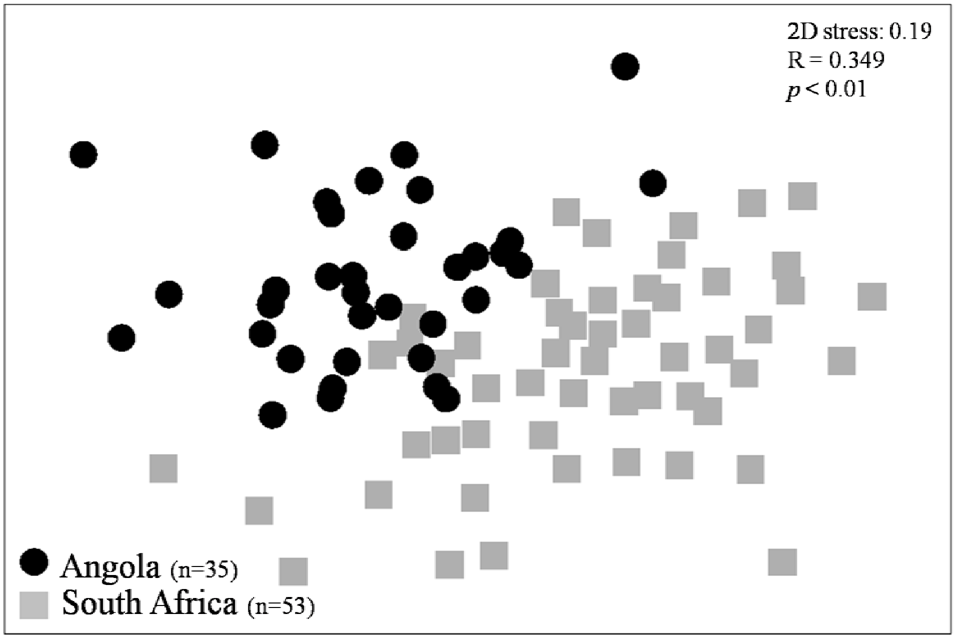

Figure 2.2: Multi-dimensional scaling (MDS) ordination plot based on 18 meristic counts of *Diplodus capensis* from southern Angola and South Africa.

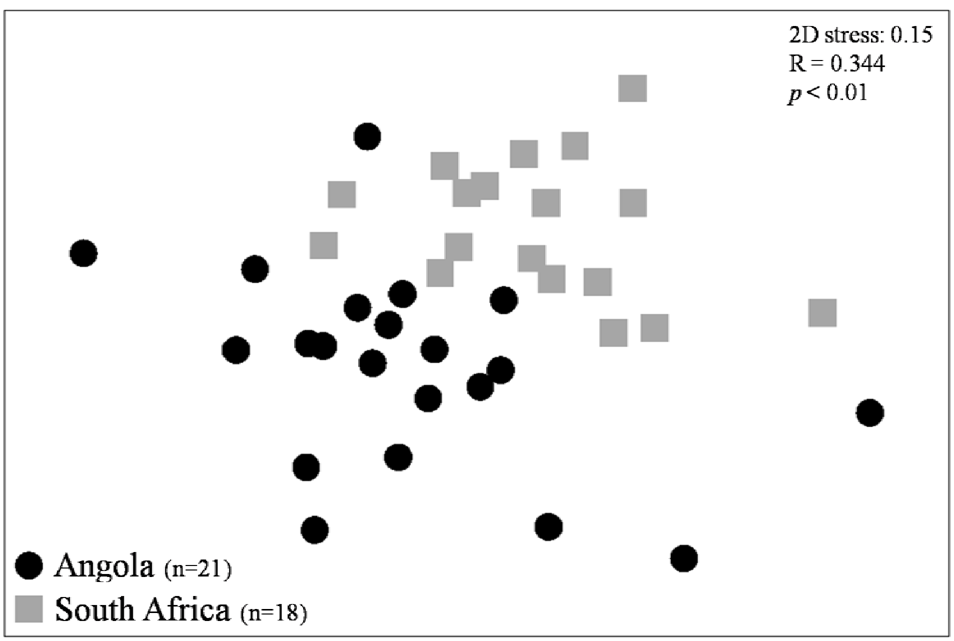

Figure 2.3: Multi-dimensional scaling (MDS) ordination plot based on 46 morphometric measurements of *Diplodus capensis* from southern Angola and South Africa.

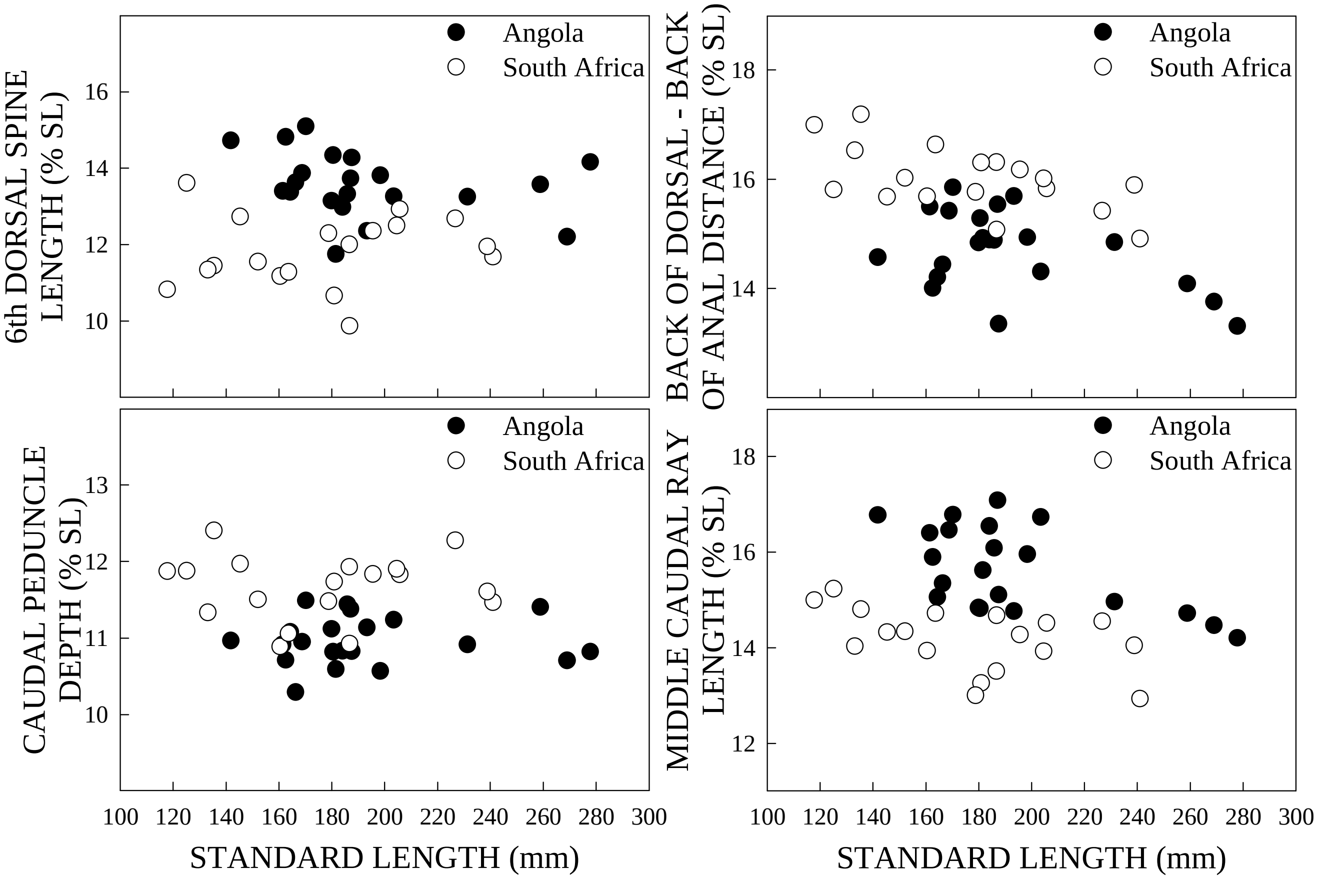

Figure 2.4: Relationship between standard length (SL) and (a) 6th dorsal spine length (%SL), (b) back of dorsal to back of anal distance (%SL), (c) caudal peduncle depth (%SL) and (d) middle caudal ray length in *Diplodus capensis* from southern Angola and South Africa. Differences between these measurements from the two regions were highly significant (student's *t*-test, $p < 0.01$).

Discussion

Despite significant differences in the mean number of some of the meristic characters and a cluster of the fish in each of the two regions in the MDS plot, the R statistic (0.324) in the ANOSIM indicated a degree of similarity between the *D. capensis* from southern Angola and South Africa. This similarity is evidenced by the overlap in the range of all meristic characters investigated in the fish from the two regions. Meristic counts are based on more primitive characters than morphometric measurements, and would therefore provide stronger evidence for speciation.

The results from the morphometric data portrayed a very similar pattern to that of the meristic data. A number of morphometric ratios were found to differ significantly between the South

Africa and Angola samples. Furthermore, when the entire morphological data set was analysed using MDS, the Angola and South Africa groups were found to differ significantly from one another. However, the R statistic of 0.344 indicates a relatively high amount of overlap between sites and the overlap in the morphometric ratios suggests that none of these features could be used as diagnostic characters to separate the two populations. As outlined above, species status would only be accepted if there was no overlap in the range of at least one of the meristic characters or morphometric ratios investigated. This was not the case and the blacktail in South Africa and southern Angola can, based on this morphometric analysis, be considered the same species, *D. capensis*.

Based on the significant differences between the means of some of the meristic counts and morphometric ratios and the clustering of fishes in the two regions by the MDS, there is evidence to suggest that *D. capensis* in southern Angola and South Africa represent separate stocks. Stock separation is a fundamental tool for effective fisheries management (Dizon et al. 1992, Begg et al. 1999, Begg and Waldman 1999, Waldman 1999). The purpose of stock separation is to direct management efforts to a taxon below a species to ensure that populations that are uniquely adapted to given areas are not irreversibly reduced by harvest or habitat destruction (Dizon et al. 1992). Therefore, since the Angolan population represents a separate stock, management strategies should be based on information gathered for this species in southern Angola and not simply transferred from South Africa.

The morphological variation demonstrated by *D. capensis* between South Africa and Angola implies a degree of reproductive isolation between these two populations. This suggests that the Benguela current is acting as a barrier to gene flow in this species. However, *D. capensis* occurs throughout Namibia and the west coast of South Africa. This suggests that the barrier is only partial since the species is found within the barrier itself. A concurrent molecular comparison of the individuals used in this analysis (Henriques 2009) showed however that there were no shared haplotypes between southern Angola and South African specimens, confirming their reproductive isolation. Further, Henriques (2009) concluded that with a genetic divergence of ~1% for the CO1 and ND2 genes, these populations were separate stocks, probably on a path towards speciation.

Based on the results of this study [and that of Henriques (2009)], the Angolan *D. capensis* population needs to be managed independently of that in South Africa. The design of effective management strategies is dependent on reliable biological, ecological and population dynamics information. The following chapter will address the feeding biology of *D. capensis* in southern Angola.

CHAPTER 3

The feeding biology of *Diplodus capensis* in southern Angola: an ecomorphological approach

Introduction

Like all animals, fishes need sufficient nutrition in order to survive and grow (Lagler et al. 1962). Feeding studies have become standard practice in fish ecology (Hyslop 1980). While most feeding studies simply describe the diet of a species and its nutritional standing within the fish community (Talbot 1955, Blaber 1974, Joubert and Hanekom 1980, Coetzee 1986, Buxton and Clarke 1992), some studies address more complicated questions. These include studies that determine the trophic relationship between species (Hobson 1974, Christensen 1978); the dietary overlap between species (Mann and Buxton 1992, Sala and Ballesteros 1997, Pita et al. 2002); the assimilation efficiency and digestibility of food items (Fish 1951, Montgomery and Gerking 1980, Gerking 1984); or the ontogenetic changes in the diet of species (Tonkin et al. 2006, Zimmerman et al. 2009) and their relationship with fish morphology (Stoner and Livingstone 1984, Eggold and Motta 1992, Wainwright and Richard 1995, Adams and Huntingford 2002, Lima-Junior and Goitein 2003, Ward-Campbell and Beamish 2005, Cassemiro et al. 2007).

The relationship between predator and prey abundance has been demonstrated in feeding studies (Hay 1984, Lewis 1986, McClanahan and Shafir 1990). A decrease in the abundance of a predator may alter the natural balance found in an ecosystem and relationships such as these can have irreversible consequences throughout the food chain (Knowlton 1992). Thus, exploitation of fishes at one trophic level can alter the organisation and structure of entire marine communities through cascading trophic chain reactions (Steneck 1998). Gaining an understanding of the trophic functioning of fish communities is therefore valuable when implementing an ecosystem approach to fisheries management (EAF).

In general, resource utilisation is related to body size and, as a result, many fishes will undergo ontogenetic dietary shifts (Werner and Gilliam 1984). As fish grow their ability to handle larger prey increases and as a result different taxa become available to the individual (Werner and Gilliam 1984, Wainwright and Richard 1995). Essentially, this increase in the type of prey available is reflected in the diet and perceived as an ontogenetic dietary shift (Wainwright and Richard 1995). One of the most important ecological implications of ontogenetic dietary shifts is that different life stages of a species are able to exploit entirely different resources (Osenberg et al. 1992), thus reducing intraspecific competition for food. Ontogenetic change in diet is common and well documented in fishes (e.g. Garcia-Berthou and Moreno-Amich 2000, Tonkin et al. 2006, Zimmerman et al. 2009). Many such changes are also associated with a morphological change, other than an increase in body size.

Ecomorphology is the study of morphological variation in an ecological context and ecomorphological studies of fishes generally investigate relationships between morphology and resource use (Wainwright and Richard 1995). A number of studies have addressed ontogenetic dietary change and associated morphological change in fishes (Stoner and Livingstone 1984, Eggold and Motta 1992, Adams and Huntingford 2002, Lima-Junior and Goitein 2003, Ward-Campbell and Beamish 2005, Cassemiro et al. 2007). Assuming isometric growth, an increase in body size would result in an increase in mouth size, which would allow for an increase in the size of food particles available to the predator. However, allometric growth patterns may allow species to radically change the size of prey consumed, creating distinct ontogenetic dietary shifts. In general, feeding efficiency in fishes is governed by morphological characters that directly affect the capture and intake of prey (Ward-Campbell and Beamish 2005). These characters are typically associated with the mouth, head and body shape. Therefore, for fish that demonstrate considerable ontogenetic shifts in their diet, it can be expected that allometric growth patterns in these characters will be observed.

Diets of fishes of the family Sparidae vary greatly from benthic carnivores (Coetzee and Baird 1981, Buxton 1984, Buxton and Clarke 1986, 1989, Bennett 1993), to omnivores (Talbot 1955, Blaber 1974, Christensen 1978, Joubert and Hanekom 1980, Coetzee 1986, Buxton and Clarke 1991, Mann and Buxton 1992, Pita et al. 2002, Figueiredo et al. 2005) and herbivores (Christensen 1978, Joubert and Hanekom 1980, Buxton and Clarke 1992). Fishes of the genus *Diplodus* are largely generalist omnivores. There is agreement between feeding studies on *Diplodus* fishes and results show that the major prey items ingested are a variety of crustaceans, molluscs, echinoderms, polychaetes, poriferans, bryozoans and algae (Christensen 1978, Joubert and Hanekom 1980, Stoner and Livingstone 1984, Whitfield 1985, Coetzee 1986, Lasiak 1986, Mann and Buxton 1992, Sala and Ballesteros 1997, Pita et al. 2002, Figueiredo et al. 2005). The importance of these food items in the diets of *Diplodus* species' varies between studies and appears to be habitat specific. For example, Mariani et al. (2002) showed a lack of consistency between the diets of some *Diplodus* species in adjacent Mediterranean lagoons. Differences in diets can be expected between populations as one of the fundamental factors in shaping patterns of prey use is that the predator can only consume food items that are present in the environment (Wainwright and Richard 1995). Prey availability may also demonstrate seasonal variation within a particular habitat. This highlights the importance of studying the diet of a species in a variety of habitats over a time scale that incorporates seasonal change.

The diet of *Diplodus capensis* has been studied in a variety of habitats (Christensen 1978, Joubert and Hanekom 1980, Whitfield 1985, Coetzee 1986, Lasiak 1986, Mann and Buxton 1992). In accordance with other studies on *Diplodus* species, results show that *D. capensis* is omnivorous, feeding on a wide range of plant and animal food items. A number of studies have investigated the diet of juvenile *D. capensis* in nursery areas (Christensen 1978, Whitfield 1985, Lasiak 1986). In intertidal rock pools, juveniles (<150mm SL) were shown to feed predominantly on copepods, amphipods, algae, isopods, polychaetes and ostracods, while in estuaries Whitfield (1985) showed that chironomid larvae and filamentous algae were of most importance to *D. capensis* fry (<20mm SL). In the surf zone, another nursery area for juvenile sparid fish, Lasiak (1986) found that copepods, algae, decapods and ostracods dominated the diet of small *D. capensis* (<90mm TL).

As with juveniles, sub-adult and adult *D. capensis* feed on a variety of food items. In South Africa, Mann and Buxton (1992) found that echinoids, polychaetes and anthozoans were the dominant prey items of *D. capensis* (>150mm FL) in the Tsitsikamma National Park, while off St Croix Island in Algoa Bay, Coetzee (1986) found that cirripeds, chlorophytes, rhodopytes and bivalves dominated the diet of fish of a similar size range. In KwaZulu-Natal waters, Joubert and Hanekom (1980) also found algae to make up a large proportion of the diet of *D. capensis* (>100mm FL), however the Porifera, Pelecypoda and Ascidiacea groups were also well represented.

From the results of these studies, there appears to be an ontogenetic and seasonal change in the diet of *D. capensis.* Small juveniles generally feed on small invertebrates (benthic or in the water column), while larger juveniles become more reliant on algae and adopt a largely benthic feeding strategy. Larger individuals become less reliant on algae in their diets and feed on a wide variety of benthic invertebrates. Body size appears to have an effect on feeding in *D. capensis*, however, these changes have never been investigated using an ecomorphological approach in this species. Seasonal trends have also been reported in the diet of *D. capensis.* Mann and Buxton (1992) and Joubert and Hanekom (1980) found an increase in the amount of algae consumed during summer months and concluded that this was the result of increased water temperatures and photoperiod resulting in greater productivity and abundance of epiphytic diatoms.

The aim of this study was to investigate whether ontogenetic shifts in the diet of *D. capensis* are reflected by allometric growth patterns in the morphology of their feeding apparatus, and to investigate whether there is seasonal change in the diet of this species and if it is related to a seasonal environmental change that may influence prey availability.

Material and Methods

General methods and description of diet

A total of 114 *Diplodus capensis* (76mm - 336mm FL) were collected between April 2008 and March 2009 for stomach content analysis. Fish were caught primarily using rod and line, however, a cast net was used to augment the number of fish captured in smaller size classes (70 - 140mm FL). Fish were sampled at random times throughout the day. Fish were weighed to the nearest 0.1g and measured to the nearest mm (FL). Fish stomachs were removed by severing the oesophagus at the buccal cavity and the intestine immediately anterior to the pyloric caecae. Stomachs were stored in 10% formalin.

In the laboratory, the stomach content of each fish was weighed. Food items were identified to the lowest taxonomic group deemed necessary (e.g. Division Chlorophyta for green algae; Class Holothuroidea for sea cucumbers; Infraorder Brachyura for crabs), dabbed with absorbent paper and weighed to the nearest 0.0001g. In some instances, stomachs contained a large amount of inseparable food items (e.g. green and red algae). In such cases, food items were separated as far as possible, but the remaining inseparable matter was weighed and food items were assigned a visual percentage volume in order to back calculate their mass.

Food items were quantified using the percent frequency of occurrence (ratio of stomachs containing that item to total number of stomachs containing food - expressed as a percentage) and percentage mass (the weight of a particular food item as a percentage of the total weight of that stomach's contents) methods (Berg 1979). The relative importance of each food item was assessed using a ranking index (RI), which was calculated as the product of the frequency of occurrence and average percent mass of each item (Hobson 1974). The RI for individual food items was presented as a percentage of the sum of the RI's for all food items to facilitate direct comparison between size classes.

Ontogenetic changes in diet

To investigate the possibility of ontogenetic changes in diet, samples were initially divided into two length classes (< 200mm FL and > 200mm FL) and tabulated in order to assess the relative importance of different food items. For a size comparison with higher resolution, the four most important food items in the diet of *D. capensis* (green algae, red algae, barnacles and mussels) were assessed for four different length classes (< 150mm FL; 150-200mm FL; 200-250mm FL and > 250mm FL) in terms of their importance (ranking index) and their contribution to the diet based on average percent mass.

Feeding seasonality

Possible seasonal variation in diet was investigated by comparing the stomach content of fish sampled in autumn (March - May), winter (June - August), spring (September - November) and summer (December - February). To test for differences in average percent mass between seasons a one-way analysis of variance (ANOVA) was performed for each food group. When the ANOVA indicated significant differences ($p < 0.05$), a Tukey HSD post hoc test was performed.

Feeding intensity

To investigate seasonal or size related differences in feeding intensity, a stomach fullness index (SFI) (Man and Hodgkiss 1977) was calculated as:

$$SFI = \frac{Stomach\ content\ mass}{Eviscerated\ \ fish\ mass} \times 100$$

Seasonal and size class differences in SFI were tested using ANOVA.

Allometric growth patterns related to feeding

A total of 35 *D. capensis* (80 - 320mm FL) were captured and preserved in 10% formalin for morphological analysis. Fourteen morphological characters were measured to the nearest 0.01mm using digital callipers (Table 3.1). Two gape indices were calculated. Firstly, the cross-sectional area of the gape (Vincent et al. 2007) was calculated as:

$$CG = (\pi \times UJ \times JW)/4$$

where *CG* is the cross-sectional area of the gape, *UJ* is the upper jaw length and *JW* is the jaw width. Secondly, the gape height (Adams and Huntingford 2002) was calculated as:

$$GH = 2 \times UJ \times \sin(0.5 \times 45°)$$

where *GH* is the gape height and *UJ* is the upper jaw length. As the 35 individuals were the basis of a taxonomic analysis (Chapter 2) for this species and could not be damaged, 26 additional individual *D. capensis* were sampled to measure the total gut length and the intestine length (mm). Total gut length was measured from the oesophagus at the start of the stomach to the anus and intestine length was measured from the start of the intestine immediately anterior to the pyloric caecae to the anus. The intestine was removed and unravelled in a straight line prior to measuring the gut and intestine lengths. The relative gut length (G/S) (Al-Hussaini 1974) was calculated as:

$$G / S = \frac{GL}{SL}$$

where GL is the total gut length (mm) and SL is standard length (mm).

Regression analysis was used to investigate possible allometric growth patterns in this species. Each character was plotted against standard length (SL) in logarithmic scale such that the allometric function:

$$y = ax^{b}$$

was transformed to:

$$\ln(y) = \ln(a) + b\ln(x)$$

where *y* is the independent variable (standard length), *x* is the dependent variable (morphometric character), *a* is the scaling coefficient and *b* is the slope coefficient (Burton 1998). If *x* increases at the same rate as *y*, then $b = 1$ (in the transformed equation) and growth is isometric. Therefore, allometric growth was tested under the null hypothesis that the slope coefficient of a regression line through the observed measurements is equal to 1. The slope t-statistic was calculated as:

$$t = \frac{EST - H_0}{SE}$$

where *EST* is the estimated slope of the regression line, H_0 is the null hypothesised slope value (i.e. 1) and *SE* is the standard error of the regression line. The p-value was obtained from a two tailed t-distribution with n-2 degrees of freedom and the null hypothesis was rejected at $p < 0.05$. Values of $b > 1$ indicate positive allometry, whereas values of $b < 1$ indicate negative allometry.

Table 3.1: Morphometric characters measured and calculated for 35 *Diplodus capensis* (80 - 320mm FL) from southern Angola.

Morphometric character	Description
Standard length (SL)	Linear distance from the base of the front incisors of the top jaw to the structural base of the middle caudal ray
Head length (HL)	Linear distance from the base of the front incisors of the top jaw to the most distant point on the opercular bone
Snout length (SnL)	Linear distance from the base of the front incisors of the top jaw to the centre of the orbit
Postorbital length of head (PoH)	Linear distance from the centre of the orbit to the most distant point on the opercular bone
Orbit to angle of preopercle (OA)	Linear distance from the centre of the orbit to the point at which the subopercular bone meets the interopercular bone under the preopercular bone edge
Upper jaw length (UJ)	Linear distance from the base of the front incisors of the top jaw to the most distant point on the maxillary bone
Lower jaw length (LJ)	Linear distance from the base of the front incisors of the bottom jaw to the point at which the angular bone meets the maxillary bone
Orbit to maxilla (OM)	Least distance from the centre of the orbit to the maxillary bone
Right incisor width	The distal width of the right hand middle incisor of the top jaw
Left incisor width	The distal width of the left hand middle incisor of the top jaw
Average front incisor width (IW)	The average of the two front incisor measurements
Length of orbit (OL)	Horizontal distance between the free orbital rims
External width of mouth (MW)	Greatest distance, measured externally, between the points at which the angular bone meets the maxillary bone on either side of the mouth
Depth of head (HD)	Vertical distance between the last row of scales on the occiput and the bottom of the head
Interorbital distance (ID)	The distance, measured externally, between the top of each orbit
Cross-sectional area of gape (CG) (calculated)[a]	This index is based on the expected contributions of mouth width and upper jaw length to overall gape and represents the cross-sectional area as the area of an ellipse with major and minor axes equal to upper jaw length and mouth width, respectively
Vertical height of gape (GH) (calculated)[b]	This index is the theoretical maximum vertical gape at the arbitrary jaw angle of 45° and is based on the expected contribution of the upper jaw length to overall gape
Intestine Length (IL)	Linear distance between the anterior base of the pyloric caecae to the anus

[a] Vincent et al. 2007; [b] Adams and Huntingford 2002

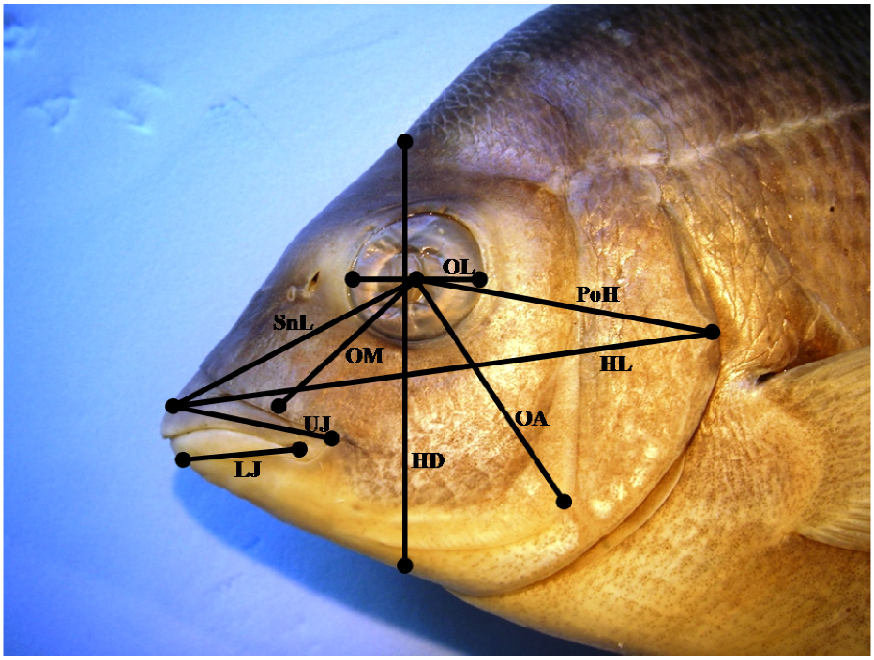

Figure 3.1: Diagram of the head of a *Diplodus capensis* sample showing some of the morphological variables measured. Certain characters are not indicated in the figure as they were calculated, measured on a different plane or measured internally. Variable codes correspond to those described in Table 3.1.

Results

Relative importance of dietary components

Of the 114 *Diplodus capensis* stomachs examined, only two (1.8%) were empty. Chlorophyta (green algae), Rhodophyta (red algae), Cirripedia (barnacles) and Bivalvia (mussels) were the most important food groups and collectively, comprised 72.4% and 74.4% of the RI in the diet of fish less than and greater than 200mm FL, respectively (Tables 3.2 & 3.3). However, Chlorophyta and Rhodophyta were more important in the diet of smaller fish (Table 3.2), while Cirripedia and Bivalvia were dominant in the diet of larger fish (Table 3.3). Although of lesser importance, amphipods and mysids were prevalent in the diet of smaller fish, while gastropods and poriferans were commonly found in the stomachs of larger fish.

A large amount of unidentifiable matter was found in the stomach contents of *D. capensis.* This was originally thought to be digested mussel or barnacle meat; however, it became apparent that both small and large fish had similar amounts of unidentified matter in their stomachs. Since the results show that small *D. capensis* do not feed on large amounts of barnacles and mussels, it was assumed that the unidentified matter is most likely to be bait (usually sardine fillet) used for the capture of these fish. This could also explain the relatively common occurrence of fish scales in the stomachs of *D. capensis.*

Table 3.2: Food items found in the stomachs of 45 *Diplodus capensis* (76 - 199mm FL) sampled in southern Angola between April 2008 and March 2009.

Food item	% freq. of occurrence	Average % mass	Ranking index
Chlorophyta	93.33	35.57	41.45
Rhodophyta	84.44	21.67	22.85
Cirripedia	46.67	8.27	4.82
Bivalvia	48.89	5.43	3.32
Sand	48.89	3.37	2.06
Amphipoda	17.78	0.85	0.19
Mysidacea	8.89	1.10	0.12
Pisces (Scales)	11.11	0.68	0.09
Polychaeta	17.78	0.32	0.07
Porifera	8.89	0.41	0.05
Gastropoda	17.78	0.04	0.01
Brachyura	2.22	0.21	0.01
Insecta	6.67	0.04	<0.01
Polyplacophora	4.44	0.04	<0.01
Caridea	2.22	0.04	<0.01
Pycnogonida	2.22	0.01	<0.01
Isopoda	2.22	<0.01	<0.01
Cephalopoda	2.22	<0.01	<0.01
Unidentified	91.11	21.94	24.96

Ontogenetic changes in diet

Due to of the dominance of chlorophytes, rhodophytes, cirripeds and bivalves in the diet of *D. capensis*, the ontogenetic and seasonal analyses focused on these food items. These four food items were assessed for different length classes in terms of their importance (ranking index) (Figure 3.2) and their contribution to the diet based on average percent mass (Figure 3.3). The importance of barnacles and mussels increased with increasing fish size, while the importance of green algae decreased with size. Red algae were only important to fish between 150 - 200mm FL (Figure 3.2a). When prey items were grouped, the importance and mass of hard items (i.e. barnacles and mussels) increased with fish size while that of soft items (green and red algae) decreased with size (Figures 3.2b & 3.3). Barnacles and mussels were dominant in the diet of larger fish, green algae were dominant in the diet of smaller fish and red algae were only prevalent in medium sized fish.

Table 3.3: Food items found in the stomachs of 67 *Diplodus capensis* (200 - 336mm FL) sampled in southern Angola between April 2008 and March 2009.

Food item	% freq. of occurrence	Average % mass	Ranking index
Cirripedia	79.10	29.33	38.58
Bivalvia	55.22	18.11	16.63
Chlorophyta	65.67	12.31	13.44
Rhodophyta	52.24	6.56	5.70
Sand	37.31	4.51	2.80
Gastropoda	16.42	2.32	0.63
Porifera	14.93	2.11	0.52
Pisces (Scales)	13.43	2.26	0.51
Amphipoda	11.94	0.22	0.04
Holothuroidea	1.49	1.34	0.03
Polychaeta	5.97	0.23	0.02
Polyplacophora	4.48	0.29	0.02
Caridea	5.97	0.21	0.02
Insecta	5.97	0.17	0.02
Isopoda	5.97	0.07	0.01
Mysidacea	11.94	0.04	0.01
Brachyura	1.49	0.22	0.01
Bryozoa	1.49	0.01	<0.01
Unidentified	64.18	19.68	21.01

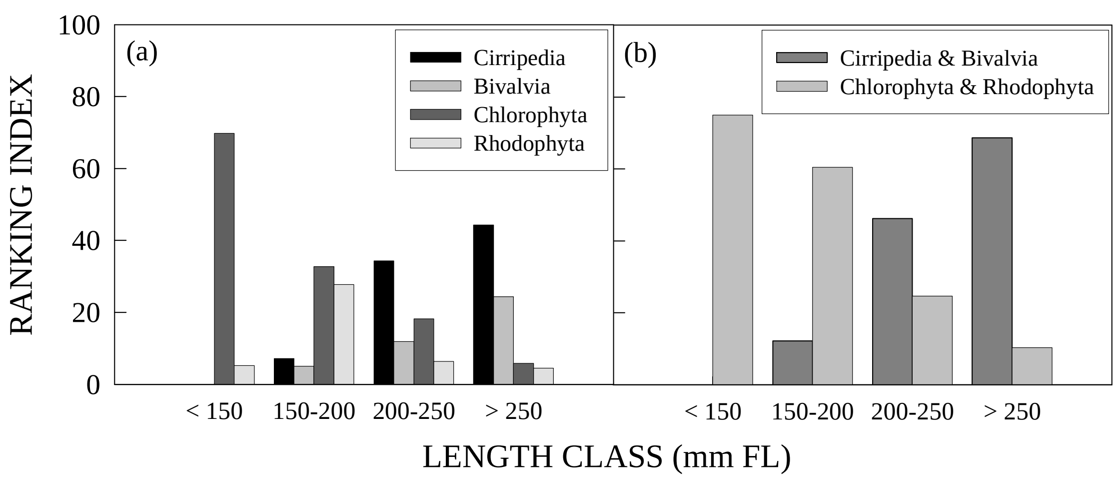

Figure 3.2: The importance (ranking index) of the four dominant food items per length class in the diet of *Diplodus capensis* in southern Angola. Graph (a) shows each prey item separately, while graph (b) shows algae grouped together and barnacles grouped with mussels.

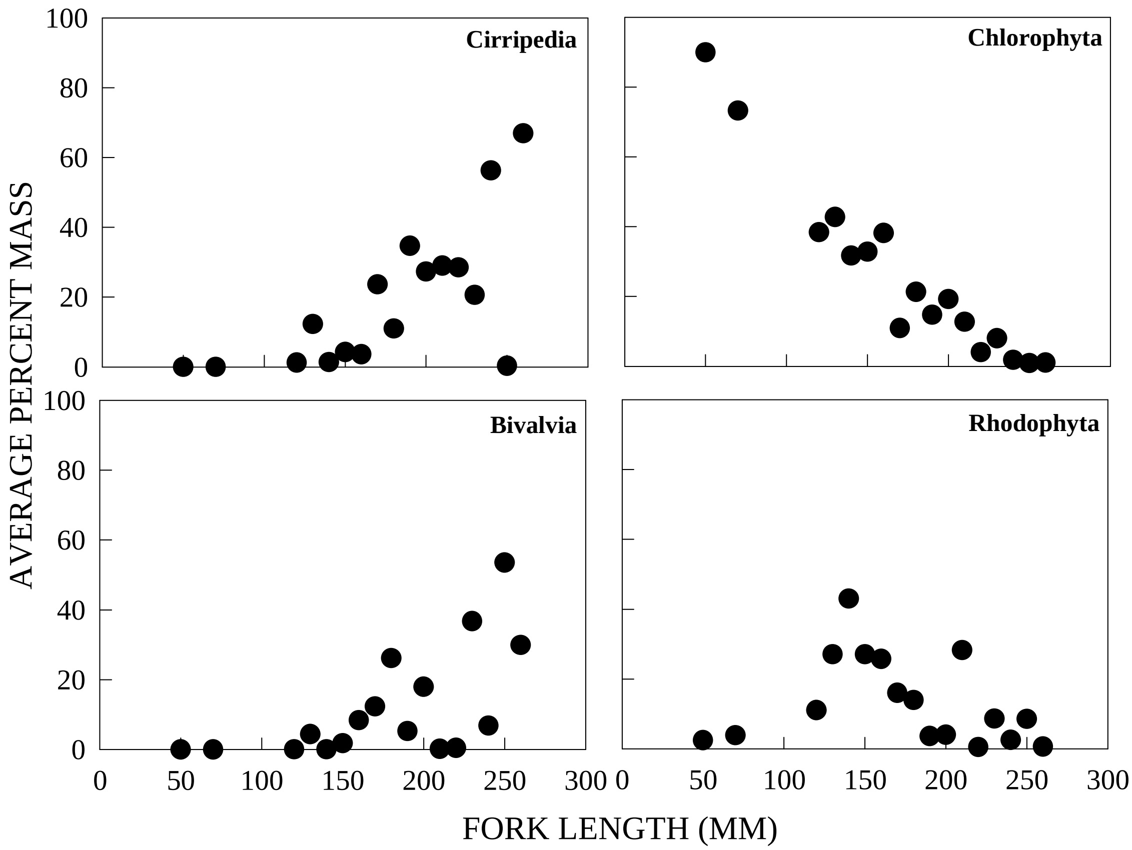

Figure 3.3: The contribution (average % mass) of cirripedia (barnacles), bivalvia (mussels), chlorophyta (green algae) and rhodophyta (red algae) per 10mm length class to the diet of *Diplodus capensis* in southern Angola. Length classes with n = 1 were excluded.

Feeding seasonality

Based on the ontogenetic results from this study, small (< 150mm FL) and large (> 225mm FL) fish were excluded from the seasonal analyses in order to exclude the potential bias of highly selective individuals. There was an increase in the importance of algae (both red and green) in the diet during winter and spring, which coincided with a decrease in surface water temperature (Figure 3.4). The average percent mass contribution of algae to the diet was significantly greater during winter and spring than autumn (ANOVA, $p < 0.001$; Tukey HSD, $p < 0.001$). There was also a significant difference between the proportion of algae consumed by the fish during spring and summer (ANOVA, $p < 0.05$; Tukey HSD, $p < 0.01$). The opposite trend was observed when the seasonal contribution of barnacles and mussels to the diet was considered, with the importance of barnacles decreasing during the colder months of the year. There was a significant reduction in the amount of barnacles and mussels consumed between autumn and spring (ANOVA, $p < 0.01$; Tukey HSD, $p < 0.01$).

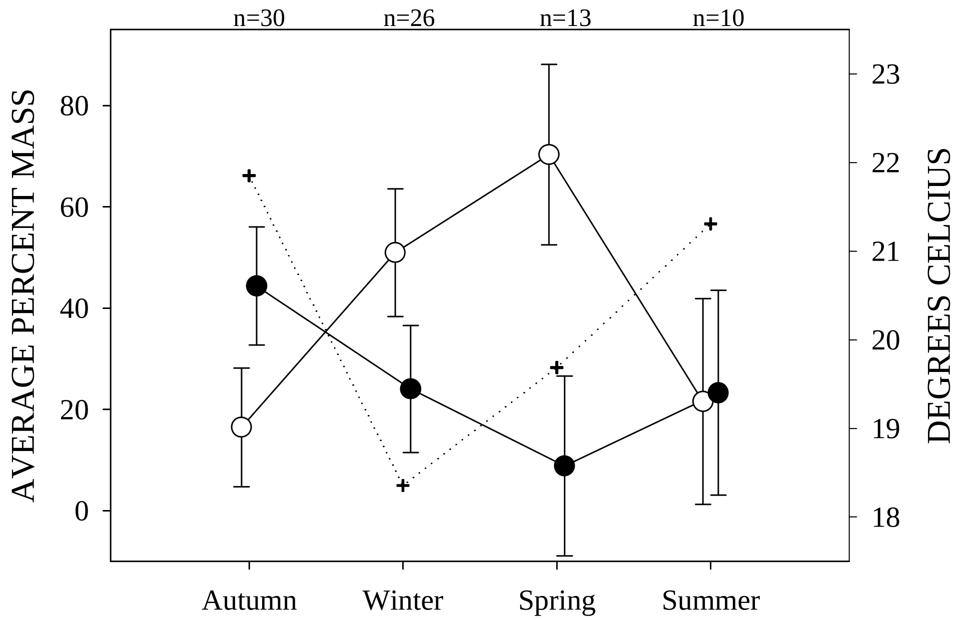

Figure 3.4: Seasonal contribution (average percent mass) to the diet of the major prey items of *Diplodus capensis* (150 - 225mm FL) in southern Angola. Cirripedia is grouped with Bivalvia (filled circles) and Chlorophyta is grouped with Rhodophyta (open circles). Crosses denote mean surface water temperature. Sample sizes are indicated above the graph.

Feeding intensity

Although fish sampled during winter and summer had a higher mean stomach fullness index (SFI = 0.86 & 0.80, respectively) compared to those sampled during autumn and spring (SFI = 0.52 & 0.57, respectively) (Figure 3.5), these differences were not statistically significant (ANOVA, $p > 0.05$). A decrease in SFI was observed with an increase in fish size (Figure 3.6). Fish of less than 150mm FL displayed a significantly higher feeding intensity (ANOVA, $p < 0.05$; Tukey HSD, $p < 0.05$) than fish of larger size classes.

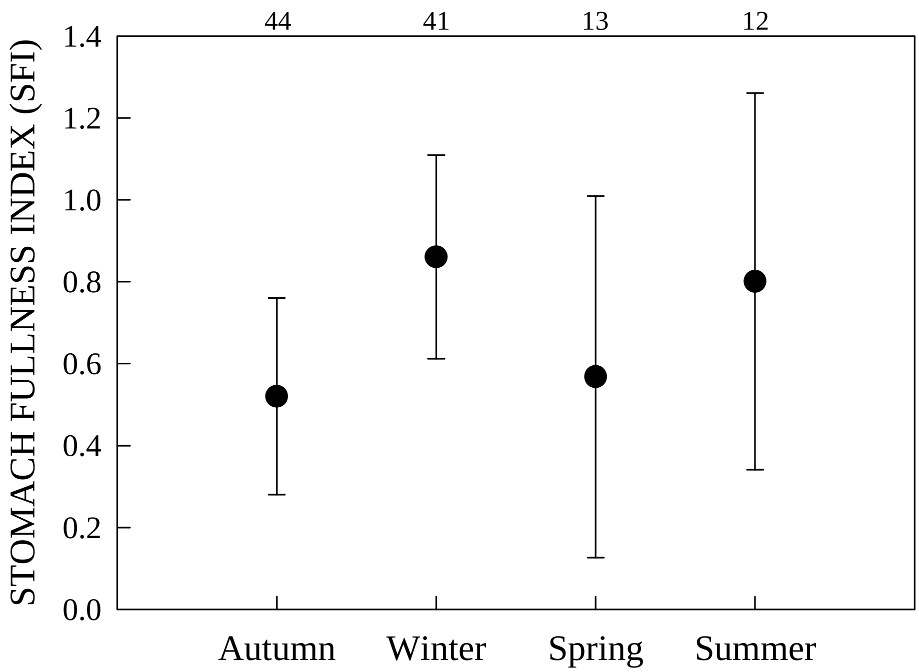

Figure 3.5: Seasonal change in stomach fullness index (SFI) for *D. capensis* sampled from southern Angola. Vertical bars denote 95% confidence intervals. Sample sizes are indicated above the graph.

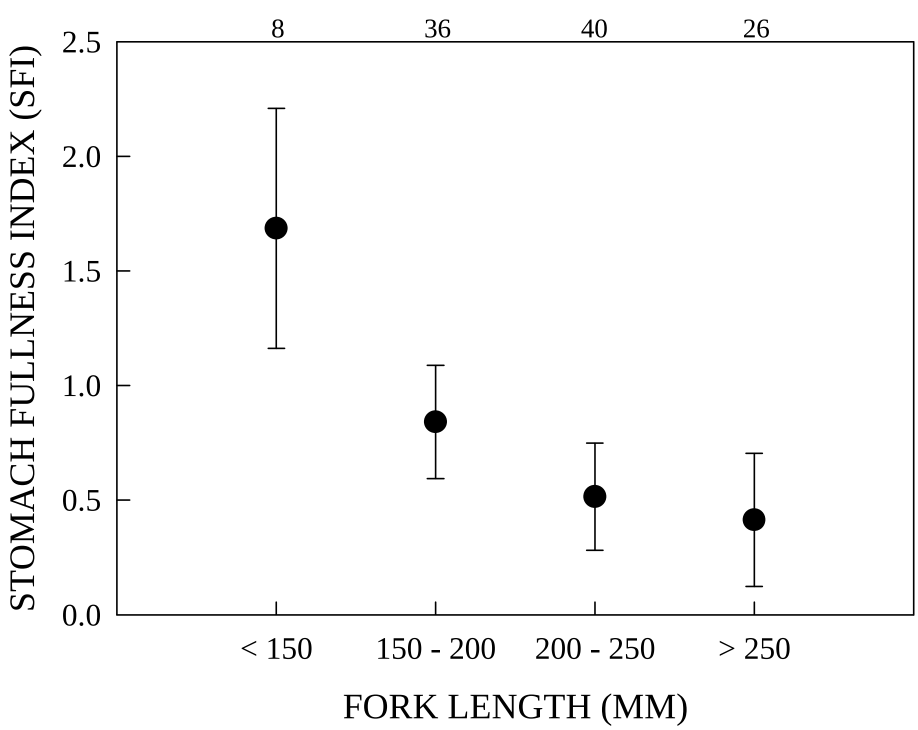

Figure 3.6: Change in stomach fullness index (SFI) with body size in *D. capensis* sampled from southern Angola. Vertical bars denote 95% confidence intervals. Sample sizes are indicated above the graph.

Allometric growth patterns related to feeding

Of the 15 morphological variables investigated, 13 showed allometric growth patterns (i.e. $b \neq 1$) (Figure 3.7). Orbit diameter was the only variable to demonstrate negative allometry ($b < 1$), while all other variables demonstrated positive allometry ($b > 1$). The slope coefficients for the regression lines of these variables that demonstrated the greatest difference from 1 were the cross sectional area of the gape ($b = 2.505$), lower jaw length ($b = 1.348$), average front incisor width ($b = 1.341$), vertical height of gape ($b = 1.284$), length of orbit ($b = 0.724$) and upper jaw length ($b = 1.248$). The average G/S ratio was 1.54.

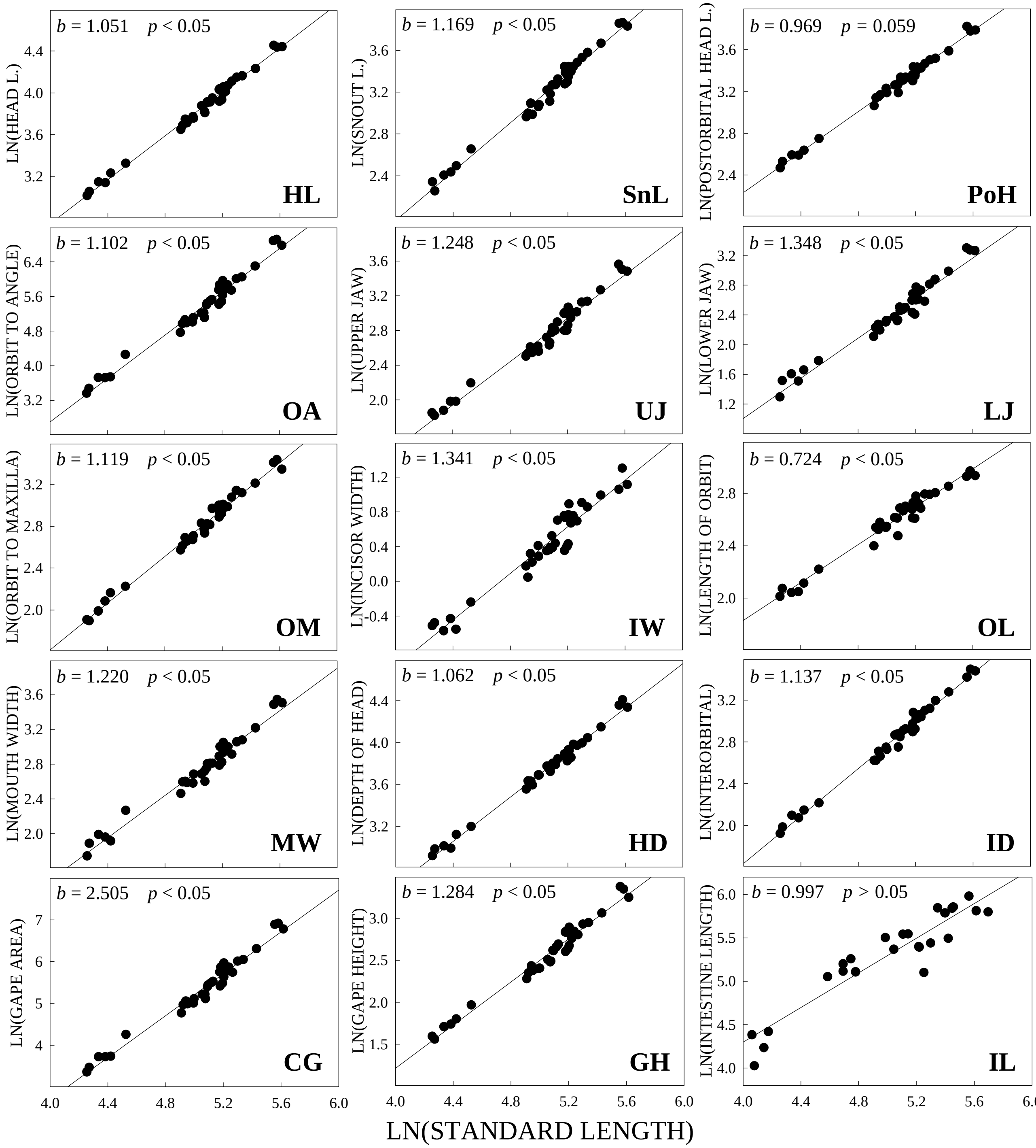

Figure 3.7: Relationship between 15 morphological variables and standard length of *Diplodus capensis* in southern Angola. The value of the slope coefficient of the regression line (b) is presented for each variable. Values of $b \neq 1$ indicate allometric growth and differences were considered significant if $p < 0.05$. Codes in the bottom right corner of each graph represent the variables described in Table 3.1.

Discussion

In agreement with other feeding studies on this species (Christensen 1978, Joubert and Hanekom 1980, Whitfield 1985, Coetzee 1986, Lasiak 1986, Mann and Buxton 1992), results from this study show that *Diplodus capensis* is omnivorous, feeding on a wide variety of food organisms. Across all length classes, the most important food items belonged to the groups Cirripedia (barnacles), Bivalvia (mussels), Chlorophyta (green algae) and Rhodophyta (red algae). However, smaller fish fed predominantly on algae, while barnacles and mussels were more important in the diet of larger fish. The change from an herbivorous to a carnivorous diet appeared to be gradual, and medium sized fish fed on varying amounts of the above food items.

There was seasonal variation in the diet of *D. capensis*. Algae were most prevalent in the diet during winter and spring, while the importance of barnacles and mussels increased during summer and autumn. While food abundance was not measured directly during this study, the oceanographic conditions in the region appear to play an important role in determining food availability. The Angola-Benguela Frontal Zone (ABFZ) is situated off the coast of southern Angola and is the confluence of the cold northward-flowing Benguela current and the warm southward-flowing Angola current (Meeuwis and Lutjeharms 1990). The ABFZ is a permanent feature, but demonstrates seasonal variation in its location. The mid-front isotherm has been documented to move up to 750km along the south-west African shore (Meeuwis and Lutjeharms 1990). During autumn and winter, the strength of the Angola current is weakest, allowing the Benguela current to push further north, while the opposite occurs during spring and summer (Meeuwis and Lutjeharms 1990). Due to its high nutrient content, the Benguela current increases the primary productivity in the southern Angolan region during winter and into spring, leading to higher algal abundance during these periods (Hutchings et al. 2009). Conversely, when the nutrient poor Angola Current dominates, primary productivity and algal abundance decreases (Hutchings et al. 2009). Thus, *D. capensis* appear to vary their diet in response to changing environmental conditions by increasing their algal intake during periods of increased primary productivity.

Algae have been shown to be an important food item for *D. capensis* in a variety of habitats (Christensen 1978, Joubert and Hanekom 1980, Whitfield 1985, Coetzee 1986, Lasiak 1986) and herbivory is common in other inshore sparid fishes (Stoner and Livingstone 1984, Buxton and Clarke 1992, Sala and Ballesteros 1997, Pita et al. 2002, Figueiredo et al. 2005). However, there is no evidence to suggest that teleosts possess cellulase (Lagler et al. 1962, Montgomery and Gerking 1980, Gerking 1984) and therefore, digestibility of algae is likely to be low. Furthermore, aquatic macrophytes are generally a poor source of dietary protein (0.7 - 3.5% protein, fresh basis) to fish (Tacon 1990) and the benefits of consuming algae are unlikely to be directly related to the nutritive value of plant material alone. Although not quantified in this study, it was noted that algae appeared to pass through the entire alimentary canal without being digested. Joubert and Hanekom (1980) reported a similar result and investigated the possibility that *D. capensis* digested the epiphytic diatoms (which are silica, not cellulose based) that are commonly found on seaweed. They found that the density of diatoms in the stomach was higher than in the intestine, and concluded that all seaweeds ingested by *D. capensis* act merely as a substrate for diatoms. Similar results have been found for the sparids *Sarpa salpa* (Christensen 1978) and *Rhabdosargus holubi* (Blaber 1974). It has also been suggested that fish may consume algae in order to ingest the animals that live on their surface (Talbot 1955, Coetzee 1986). This is unlikely to be the case for *D. capensis* in this study, as many stomachs were found to be packed full of algae but contained very little, if any, small animals. Therefore, in accordance with other studies, it can be concluded that *D. capensis* in southern Angola most likely ingest algal matter for the nutritive value of their associated epiphytic diatoms.

The importance of benthic invertebrates in the diet of small *D. capensis* should not be overlooked. Amphipods, polychaetes and gastropods were represented in the stomachs of 18% of the small fish (< 200mm FL) examined. Although these items contribute little in terms of mass to the diet of these fish, their nutritive value and digestibility may be higher than that of diatoms and their importance may be masked by the sheer volume of plant material consumed. However, the cost of searching for these prey items may exceed the nutritional benefits derived from their digestion and, although of lower nutritive value, the consumption of large amounts of abundant plant matter may be favoured. Animal prey is thus likely to be consumed on an opportunistic basis rather than an obligatory one in small *D. capensis*.

The volume of algae consumed decreased with an increase in fish size. In the diet of larger fish (> 200mm FL), algae was replaced by barnacles and mussels (Table 3.3). This coincided with an increase in the absolute size, strength and robustness of the feeding apparatus, which allows for a broader choice of food items. Body size and mouth gape are among the main factors that govern ontogenetic changes in diet (Wainwright and Richard 1995). These variables set an absolute limit on the range of prey types that a predator can capture or consume, and may influence the efficiency with which a predator captures and consumes a particular prey type (Wainwright and Richard 1995). In agreement with these factors, the ontogenetic changes in diet observed in *D. capensis* in this study appear to be governed by body size and gape. Small fish feed predominantly on algae and there is a dietary shift to animal prey as the fish grow larger. Although their hard calcium shells are indigestible, mussels and barnacles contain a large amount of flesh. The protein content of mussels is on average higher than plant matter, ranging from 9-13% (Waterman 2001). While there is little information on the nutritional value of barnacles, their protein content is expected to be similar. Kichuki and Sakaguchi (1997) suggested that a closely related blue mussel (*Mytilus edulis*) could be used to replace over 60% of the fishmeal in the diet of juvenile Japanese flounder (*Paralichthys olivaceus*). This attests the nutritional value and digestibility of mussels to teleost fishes.

Mussels and barnacles are abundant in the inshore reef habitat in southern Angola and thus little energy would have to be expended to locate them. It is therefore unsurprising that they are the primary food source for larger *D. capensis*. However, other food items are likely to be taken on an opportunistic basis. This can be supported by evidence from individual examples; one fish (336mm FL) only had two large sea cucumbers in its stomach, while another individual (228mm FL) only had one large limpet in its stomach.

The SFI is used as a measure of feeding intensity in fish (Man and Hodgkiss 1977). Although there were no seasonal trends in SFI, smaller fish displayed a higher SFI than larger fish. With the high proportion of plant matter in the diet of small fishes, it is likely that small individuals need to consume greater amounts of food (i.e. have a high feeding intensity) than larger individuals, and since marine diatoms are a relatively poor source of dietary protein (2.9% protein, fresh basis) to fish (Tacon 1990), it is unsurprising that small individuals have to eat large amounts of macrophytes (the substrate for epiphytic diatoms) to meet their energy requirements. Once *D. capensis* begins to feed on animal prey (with higher nutritive value) their feeding intensity appears to decrease. The SFI values calculated in this study (0.684 for winter and 0.680 for summer) are considerably greater than those reported by Mann &

Buxton (1992) (0.298 for winter and 0.435 for summer) for *D. capensis* sampled in the Tsitsikamma National Park in South Africa. This may be due to the high proportion of plant matter (and its associated epiphytic diatoms) in the diet of *D. capensis* from southern Angola, which would necessitate a higher feeding intensity.

Since algae, barnacles and mussels are abundant in the inshore zone, and there appears to be no clear habitat shift between small and large *D. capensis* in southern Angola, the results from this study provide evidence for an ontogenetic change in feeding strategy. The proportion of barnacles and mussels in the diet of *D. capensis* increases from approximately 150mm FL, which coincides with the length at 50% maturity for this species in this region (149.5mm). With the onset of sexual maturity, additional energy is needed to develop gonad tissue. The higher nutritional value of animal matter would thus be favoured in the diet of mature fish.

Besides the absolute increase in body size and mouth gape having an effect on diet through ontogeny in this species, there is evidence for allometric growth patterns in various morphological characters that may be directly related to feeding performance. The observed ontogenetic change in diet shows a shift from soft plant matter to larger, hard animal prey (barnacles and mussels). These sedentary animals have hard shells and attach themselves firmly to the reef substrate in the intertidal zone. With the large amount of force required to grab and remove mussels and scrape off barnacles, one would expect that larger, stronger and more robust morphological feeding apparatus would be favoured. While an increase in the absolute size of these feeding apparatus would enhance feeding performance in this species, positive disproportionate growth rate of these features would be favourable. It was found that 13 of the 15 morphological characters measured in this study demonstrate allometric growth. All these characters are associated with the feeding apparatus.

A number of variables pertaining to the size and shape of the head and mouth were measured, and, with the exception of the postorbital length of the head, all of these characters demonstrated positive allometry. Although it is difficult, and perhaps unsound, to make conclusions about causal links between form and function from individual measurements, when considered collectively it is clear that positive allometry in these characters strongly corroborates the link between feeding morphology and ontogenetic dietary shifts in this species. Allometric growth patterns facilitate an increase in the size and strength of bones and muscles associated with the head. Disproportionate growth in head length (HL), head depth (HD) and interorbital distance (ID) imply an increase in the overall size and strength of the head. Positive allometry in the distance between the orbit and angle of the preopercle (OA) provides evidence for an increase in the size of the adductor mandibulae, the muscle process that powers jaw closing in teleost fishes (Westneat 2003), which is likely to be a limiting factor when feeding on hard prey items that are firmly attached to the substrate. An increase in snout length (SnL) and the distance between the orbit and maxilla (OM) imply an increase in the protrusion of the mouth. When one considers the tightly packed organisation of mussels and barnacles in the intertidal zone, increased protrusion of the predators mouth would aid in extraction of these prey items. Positive allometric growth in morphological variables related to the mouth [upper and lower jaw length (UJ & LJ), mouth width (MW), gape height (GH) and cross-sectional area of gape (CG)] provides increased ability to feed on larger and harder prey items. Similarly, an allometric increase in the width of the front incisors provides increased strength in one of the primary feeding apparatus. Thin incisors (characteristic of small *D. capensis*) would be favoured in an herbivorous diet as they would be effective for cutting soft plant matter. Conversely, wider and thus stronger incisors would be more useful when grabbing mussels and scraping barnacles off a reef.

Orbit length was the only character that demonstrated negative allometry. This suggests that vision may be more important to smaller fish. The smallest individuals investigated in this study ranged from 80 - 110mm FL, and algae were the dominant food item in these fishes. However, other studies suggest that small benthic and pelagic invertebrates are important food items in the diet of smaller (<80mm FL) shoaling juvenile *D. capensis* (Christensen 1978, Whitfield 1985, Lasiak 1986, Mann and Buxton 1992). These prey items require the predator to actively search for them, and good vision would increase feeding success. As fish grow they start feeding on larger, mostly sessile, prey items for which sight becomes less important. Although the possible explanations for negative allometric growth of the orbit in this species fits well with its dietary change through ontogeny, it is important to note that a similar result has been observed for many other fish species (Piet 1998, Lima-Junior and Goitein 2003, Ward-Campbell and Beamish 2005, Cassemiro et al. 2007) and it may be that the evolution of this character followed selective pressures other than feeding (e.g. predation) (Lima-Junior and Goitein 2003).

Gut length is an indicator of dietary tendencies in fishes (Weatherly 1972). Herbivores usually have long gut lengths in relation to their body size in order to maximize digestion and nutrient uptake of plant matter. The higher nutritional value and digestibility of animal matter allows carnivorous fishes to have short gut lengths, while omnivores display a wide range of gut lengths in relation to body size. The average G/S ratio for *D. capensis* in southern Angola (1.54) fell comfortably within the range for carnivores (0.5 - 2.4) reported by Al-Hussaini (1974) and was within the lower portion of the range given for omnivores (1.3 - 4.2). Together with the fact that this species possesses well developed pyloric caecae, it can be said that the gross gut morphology of *D. capensis* is more characteristic of a carnivorous fish than an omnivorous one.

It is known that most fish species demonstrate positive allometric growth in gut length, the significance of which is to maintain relative absorptive area with increasing fish size (Kramer and Bryant 1995). However, in the present study, isometric growth was observed in the gut length of *D. capensis* between 48mm and 298mm SL. Although an allometric relationship may have been found if smaller fish (< 50mm FL) were included in this study, most allometric growth patterns in gut length do not reach an isometric asymptote with increasing fish size (Kramer and Bryant 1995). Isometric growth of gut length results in a relative decrease in the absorptive capacity of the gut with an increase in fish size (Kramer and Bryant 1995), and therefore the isometric relationship found in the current study may be an adaptation for *D. capensis* to switch from an herbivorous diet to a carnivorous one.

Conclusion

Diplodus capensis is omnivorous in southern Angola, feeding on a wide variety of plant and animal matter. Small fish fed mainly on aquatic macrophytes but it was concluded that these were of little nutritional importance and that small *D. capensis* eat algae because of their associated epiphytic diatoms. Medium sized fish had a similar diet to small fish, however, the proportion of mussels and barnacles in the diet increased gradually with body size, and large fish fed almost exclusively on these prey items. Seasonal patterns in the diet were associated with the effect of the ABFZ on the marine environment in southern Angola. Increased productivity during winter and spring corresponded with an increase in the proportion of algae in the diet of *D. capensis.* The ontogenetic dietary shift observed in *D. capensis* was supported by the allometric growth patterns for various morphological characters related to feeding. These facilitate an increased ability to feed on hard sessile animal prey with increasing fish size. The isometric growth in gut length and relative decrease in absorptive capacity with increasing size further confirms an ontogenetic dietary shift towards animal prey in this species.

CHAPTER 4

Aspects of the reproductive biology of *Diplodus capensis* in southern Angola

Introduction

The perpetuation of a species is dependent on successful reproduction and recruitment. Through years of evolution, fishes have developed reproductive strategies that confer a degree of "fitness" and adaptations to the unique conditions found in their environment. Included amongst these strategies are the optimisation of the seasonality and timing of reproduction and the development of a specific reproductive style.

The environment plays an important role in the timing of spawning in fishes and many events related to the reproductive life of fishes occur with clear periodicity (Sheaves 2006). Many such patterns of reproductive timing have clear explanations. The timing of spawning can be determined by a number of ecological, physiological and phylogenetic reasons, which can operate either through their effect on adults, gametes, eggs, larvae, juveniles, or a combination of these (Sheaves 2006). For example, the timing of spawning may be geared to minimize egg predation, maximize dispersal, or provide larvae with maximum opportunity to survive in waters with patchy and irregular distribution of food (Shapiro et al. 1988). The timing of spawning in fishes is governed by proximate causal factors (i.e. directly cueing adult fishes) and ultimate causal factors (i.e. developed by natural selection acting on survivorship and recruitment of larvae) (Lobel 1989). Water temperature and/or photoperiod have long been recognised as important proximate cues for spawning in fishes (Lobel 1989, Sheaves 2006). Sheaves (2006) used the existing information on sparid spawning seasons to assess the effect of sea surface temperature on the timing of spawning in this family. It was concluded that the exact timing of spawning is not an unchanging characteristic of a particular species, but varies over the range of the species and that sea surface temperature is at least correlated with, and probably has an influence on, the timing of spawning in sparids (Sheaves 2006). These two conclusions are evident in the timing of spawning in *D. capensis*. In Kwa-Zulu Natal (KZN) peak spawning occurred during late winter (Jul - Sep) (Joubert 1981b), while in the more temperate Eastern Cape reproductive activity was greatest during early spring and summer (Aug - Dec) (Coetzee 1986, Mann and Buxton 1998). Mann and Buxton (1998) reported that spawning along the temperate Cape coast is likely to occur during summer when optimum, stable temperatures prevail after westerly winds. Based on correlation between months of peak spawning and mean monthly temperatures, it appears that optimum spawning temperatures for *D. capensis* in South Africa range from 17 to 20°C (Mann and Buxton 1998).

Reproductive styles in the family Sparidae are diverse and well documented (Atz 1964, Reinboth 1970, Buxton and Garratt 1990). Most sparids display some type of hermaphroditism. In fact, the most diverse expressions of hermaphroditism are found within the family Sparidae (Atz 1964), with representatives displaying rudimentary hermaphroditism (e.g. Mehl 1973, Coetzee 1983, Buxton and Clarke 1991, 1992), protogyny (e.g. Penrith 1972, Robinson 1976, Buxton and Clarke 1986, Garratt 1986, Buxton 1989, Buxton and Clarke 1989), protandry (e.g. Etessami 1983, Pollock 1985) and in a single case, simultaneous hermaphroditism (Williamson 1911).

All *Diplodus* species demonstrate hermaphroditism, the most common form being partial protandry, where a portion of the male population undergoes sex inversion. However, there are conflicting reports of the type of hermaphroditism displayed for certain species in the genus. For example, *Diplodus sargus* has been reported to be a protandrous (Micale et al. 1987, Micale and Perdichizzi 1994) and partially protandrous hermaphrodite (Morato et al. 2003, Mouine et al. 2007). Similarly *Diplodus puntazzo* has been described as a rudimentary (Micale et al. 1996) and a partially protandrous hermaphrodite (Pajuelo et al. 2008).

The reproductive style of *Diplodus capensis* has been studied in South Africa. Again there are contradicting conclusions, with results suggesting that this species displays rudimentary hermaphroditism (Joubert 1981b) and partial protandry (Coetzee 1986, Mann and Buxton 1998). Penrith (1972) suspected that *D. capensis* displays “normal bisexual development”, an

Table 4.1: A summary of reproductive styles reported for *Diplodus* species.

Rudimentary Hermaphrodites	Protandrous Hermaphrodites	Partially Protandrous Hermaphrodites
Diplodus capensis (Penrith 1972) *Diplodus cervinus hottentotus* (Mann and Buxton 1998) *Diplodus puntazzo* (Micale et al. 1996)	*Diplodus sargus* (Micale et al. 1987, Micale and Perdichizzi 1994)	*Diplodus capensis* (Coetzee 1986, Mann and Buxton 1998) *Diplodus puntazzo* (Pajuelo et al. 2008) *Diplodus sargus* (Morato et al. 2003, Mouine et al. 2007) *Diplodus sargus kotschyi* (Abou-Seedo et al. 1990) *Diplodus vulgaris* (Goncalves and Erzini 2000, Pajuelo et al. 2006)

ambiguous statement, which could be interpreted as gonochorism, as in Buxton and Garratt (1990), or rudimentary hermaphroditism. However, with no data to support his conclusions, Penrith's statement is questionable.

In their review of the reproductive styles in the Sparidae, Buxton and Garratt (1990) suggest that some of the diversity of reproductive styles found within the Sparidae may be due to a lack of clarity in terminology and in some instances superficial observation. For these reasons, they suspect that many of the sparids classified as protandrous are not different from those that have been classified as rudimentary hermaphrodites. Hermaphroditism can be inferred from two aspects of population structure: comparative size/age frequency distributions of males and females, and adult sex ratios (Sadovy and Shapiro 1987). However, as variable growth and mortality rates between sexes may influence conclusions, neither of these features represent strong evidence for hermaphroditism. It is now commonly accepted that, besides size frequency and sex ratio information, in order to infer hermaphroditism results need to be accompanied by a comprehensive histological examination (Sadovy and Shapiro 1987). Rudimentary hermaphrodites contain a non-functional ovotestis in the juvenile phase, with both male and female gonad tissue, while the testes of mature protogynous species contain an ovarian lumen (Sadovy and Shapiro 1987). Protandry is more difficult to diagnose; intermediate individuals with degenerating spermatogenic and developing ovarian tissue is considered to be good evidence for protandrous sex change (Sadovy and Shapiro 1987).

The evolution of hermaphroditism has been a topic of much debate (Ghiselin 1969, Chan 1970, Shapiro 1987, Warner 1988, Shapiro 1989, Baroiller et al. 1999, Munday et al. 2006). Hermaphroditism is widespread in fishes, evident in 20 taxonomic families in nine orders, which together with the many different gonad forms observed, suggests that hermaphroditism has evolved many times independently (Smith 1975, Mank et al. 2006). Chan (1970) speculated that, in the family Sparidae, synchronous species are primitive, from which protandrous, protogynous and gonochoristic species evolved. This may have explained the lack of gonochoristic sparids as there is little competitive advantage of losing a hermaphroditic lifestyle. However, with the advent of molecular technology, more recent literature suggests that hermaphroditism in teleost fish is a polyphyletic and derived condition relative to gonochorism (Mank et al. 2006, Avise and Mank 2009).

The functional significance of hermaphroditism has also been the topic of much discussion (Ghiselin 1969, Warner 1975, Charnov 1982, Warner 1988, Munoz and Warner 2004, Warner and Munoz 2008). The central hypothesis for sex change in fishes, known as the size advantage model, was first developed by Ghiselin (1969) and still remains a singularly powerful explanation for sequential hermaphroditism today (Ghiselin 2006). The theory predicts that sequential hermaphroditism will be favoured if an individual reproduces most efficiently as a member of one sex when small or young, but as a member of the other sex when it gets older or larger (Ghiselin 1969). Therefore, for protandry to be a viable alternative, the reproductive success of large females must be greater than that of smaller ones. The ability for an individual to change sex thus increases its lifetime reproductive output. According to Atz (1964), a gonochorist would nearly double its reproductive potential if it were to function as a sequential hermaphrodite. Clearly sequential hermaphroditism has advantages at both the individual and population level, and owing to the remarkably plastic nature of the sexual determination process in fishes (Francis 1992, Shapiro 1992), it is unsurprising that hermaphroditism is a common condition in teleosts.

But why is hermaphroditism not more widespread among teleosts if their sex determination is so plastic and hermaphroditism is so beneficial? The answer lies in the fact that sex change comes with associated costs (Charnov 1982, Munday and Molony 2002). Sex change incurs costs in terms of both the energy expended in reorganising gonadal tissue, and lost mating opportunities during or after transition (Hoffman et al. 1985). It can thus be expected that when the cost of sex change is high, a gonochoristic pattern of sex allocation would be favoured (Iwasa 1991). This may explain the high prevalence of rudimentary hermaphroditism within the family Sparidae. This condition is not one of hermaphroditism by the true definition of the word. According to Sadovy and Shapiro (1987) and Sadovy de Mitcheson and Liu (2008), a species is hermaphroditic if a substantial proportion of individuals in a population function as both sexes, either simultaneously or sequentially, at some time during their life. Rudimentary hermaphrodites merely possess a bipotential ovotestis in the juvenile phase after which normal sexual development occurs along the female or male pathway. Therefore they can be considered gonochorists which delay the process of sex determination until just prior to sexual maturity, hence their alternative name, "late gonochorists" (Buxton and Garratt 1990). This premise has reduced the interest in fishes displaying this reproductive style, which has resulted in a paucity of literature on the processes affecting the evolution and development of rudimentary hermaphroditism in fishes, as these species are neither "true" hermaphrodites nor "true" gonochorists. The bipotentiality of the sparid ovotestis is considered to be a pre-adaptation for the development of sequential hermaphroditism in species in which reproductive success is size related (Buxton and Garratt 1990). The adaptive significance of this condition cannot be explained by the size advantage model as individuals only ever function as one sex. Like the stability found in higher vertebrates, the mechanism for sex determination in teleosts was originally thought to be genetically predetermined (Baroiller et al. 1999), however, it has become increasingly apparent that environmental and demographic factors play an intricate role in this process and that fishes demonstrate plasticity in their sexual development (Francis 1992, Shapiro 1992, Avise and Mank 2009). This plasticity may have initiated the evolution to a rudimentary hermaphroditic lifestyle with the obvious advantage of providing a species with more time before sex determination occurs, with environmental and demographic processes acting as mechanisms that control this process.

The reproductive style of a species may affect its resilience to exploitation and thus has important implications for fisheries management. Sequentially hermaphroditic species are at great risk to the effects of exploitation as the size selective nature of fishing will result in one sex being more readily targeted than the other. This has the potential to dramatically alter the population's sex ratio and change its reproductive dynamic and output. For example, Buxton (1987) found an exceptionally female skewed sex ratio (13:1) for *Chrysoblephus laticeps*, a protogynous hermaphrodite, in a heavily exploited area. However, Götz et al. (2008b) have shown that, at light levels of fishing mortality, the same species is able to maintain a normal sex ratio through reductions in size-at-maturity and sex-change. Protandrous fish species are perhaps even more susceptible to exploitation as the large female individuals will be removed first, greatly reducing the population fecundity.

For digynic (partially protandrous) and diandric (partially protogynous) species, similar effects might apply, however, it can be expected that such species would be more resilient to fishing pressure as their ability to maintain the balance found in an unexploited situation would be increased. Such a reproductive style may be advantageous in an exploited scenario if sex change can operate as a response to the removal of large individuals from the population. However, it is likely that rudimentary hermaphrodites would be most resilient to exploitation and would have the greatest ability to maintain a population structure found in an unexploited situation due to the non-selective removal of larger individuals of both sexes. Furthermore, irrespective of the reproductive style of a species, even low levels of exploitation will reduce population fecundity and recruitment, as fecundity is generally exponentially greater in larger fish (Brouwer and Griffiths 2005, Kamler 2005, 2006).

The aim of this study was to use a combination of macroscopic staging and histological analysis to determine the seasonality of reproduction, and to use a combination of length frequency, age frequency, sex ratio and histological evidence to determine the reproductive style of *D. capensis* in southern Angola. This information was used to gain an understanding of the potential impacts of global climate change on the spawning seasonality of this species and the potential population persistence when exposed to various levels of exploitation.

Material and Methods

Samples of *D. capensis* were collected monthly between April 2008 and March 2009 using rod and line, however the sample was supplemented using a cast net in order to include small individuals (< 120mm FL). Each fish was weighed (0.1g), measured (mm, FL) and sexed according to the macroscopic appearance of the gonads (Tables 4.2 & 4.3). The gonads and viscera were removed and weighed separately (0.1g). If both male and female tissue were clearly present in a single gonad through macroscopic examination, the individual was classed as "intersex". If neither male nor female tissue was distinguishable macroscopically in a gonad, the individual was classed as juvenile. A representative sample of male (29), female (39) and juvenile (6) gonads were stored in 10% formalin for histological analysis. All of the gonads staged as "intersex" (4) were stored for analysis. Histological samples were prepared by embedding gonad tissue in paraffin wax, sectioned at 5 to 6 microns and stained with haematoxylin and eosin (Austin and Austin 1989).

The spawning season was identified by comparing the proportion of ripe and ripe running individuals (see Tables 4.2 & 4.3 for macroscopic staging of gonads) in each monthly sample and was corroborated by examining peaks in the mean monthly gonadosomatic index (GSI), where:

$$GSI = \frac{gonad\ mass}{eviscerated\ \ fish\,mass}$$

Differences in mean GSI values between males and females were tested using a student's *t*-test. Tests were conducted for the entire sample, the months during the spawning season, and the months outside of the spawning season. Differences were considered significant if $p < 0.05$.

The cyclic pattern of reproductive activity was assessed using a periodic regression (Flury and Levri 1999) of the form:

$$Logit(\theta) = \beta_0 + \beta_1 \sin\left(\frac{2\pi}{P} M_i\right) + \beta_2 \cos\left(\frac{2\pi}{P} M_i\right)$$

where M_i is the month of the year (with April being assigned a value of 1 and March 12), P is the periodicity of reproductive activity (in months) and β_0, β_1 and β_2 the regression parameters to be estimated. Model parameters were estimated through sum of squares minimization with a log-normal error structure. The potential effect of temperature on reproductive seasonality was investigated by adding average monthly surf zone temperature as a variable in the periodic regression such that:

$$Logit(\theta) = \beta_0 + \beta_1 \sin\left(\frac{2\pi}{P} M_i\right) + \beta_2 \cos\left(\frac{2\pi}{P} M_i\right) + \beta_3 (TM_i)$$

where β_3 is an additional parameter to be estimated and T is the temperature variable for the month M_i. The model that best described the change in reproductive activity was selected by conducting a likelihood ratio test (LRT) and calculating Akaike's information criterion (AIC). A log likelihood function was calculated as:

$$\ln L = n \ln \sigma$$

where n is the total number of individuals in the sample and σ is the model variance. The LRT p-value was obtained from a chi-square distribution:

$$\chi_k^2 = 2\left(\ln L_{full} - \ln L_{reduced}\right)$$

where $\ln L_{full}$ is the model containing temperature as an environmental variable, $\ln L_{reduced}$ is the model without temperature as a variable and k is the degrees of freedom (difference in the number of parameters to be estimated between the two models). The period (P) was estimated as a parameter in both models, therefore the full model had five parameters and the reduced model had four parameters. The full model was accepted as adequately describing reproductive activity if $p < 0.05$. The AIC was calculated as:

$$AIC = 2 \times \left(\ln L + Z\right)$$

where Z is the number of model parameters. The highest AIC value indicates the best model fit. Once the best model was selected to describe the change in reproductive activity in *D. capensis*, an LRT was conducted in order to test whether the periodic cycle of this activity followed an annual pattern (i.e. $P = 12$). The LRT was conducted as above, but for the full model P was estimated and for the reduced model P was fixed at 12 months. The null hypothesis (i.e. $P \neq 12$) was rejected if $p < 0.05$.

The effect of photoperiod on reproductive activity could not be assessed because, due to its consistent periodicity, it is autocorrelated with time of year (i.e. month).

The size and age structure of the population was investigated using length frequency and age frequency distributions (see Chapter 5). The overall sex ratio was calculated using fish greater than the length at 50% maturity.

Results

Reproductive seasonality

Macroscopic staging and GSI

A total of 647 *D. capensis* were collected during the sampling period. Based on size, colour and general appearance of the gonads, seven macroscopic stages were identified (Tables 4.2 & 4.3). Gonad development, based on macroscopic appearance, followed a clear seasonal trend (Figure 4.1). From June to October, developing and ripe gonads were most prevalent indicating an extended spawning season. Gonads in a resting state were most prevalent between November and March. The GSI substantiated an extended winter spawning season, with high GSI values being recorded during this period (Figure 4.2). For the entire study period, the average GSI for males (2.24) was significantly higher than that of females (1.84) (*t*-test, $p < 0.05$) (Table 4.4). Although the male GSI values were still higher, a statistically significant difference was not observed when the test was conducted separately for the months during the spawning season and the months outside of the spawning season.

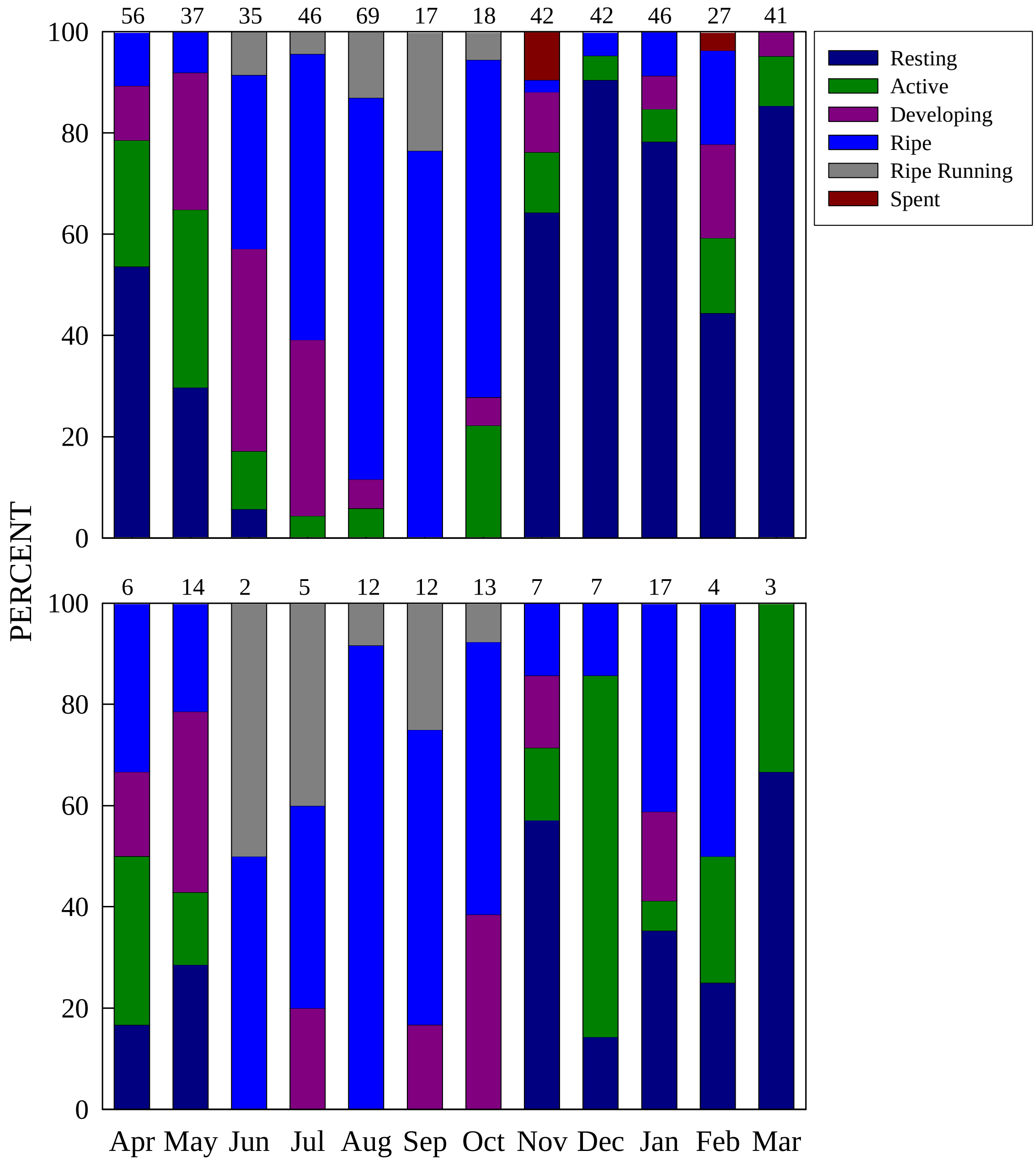

Figure 4.1: Monthly percentage of each macroscopic stage for gonads of mature female (top) and male (bottom) *Diplodus capensis* from southern Angola. Monthly sample sizes are presented above each graph.

Table 4.2: Staging criteria used to macroscopically assess the gonads of female *Diplodus capensis*, and their respective microscopic description, sampled from southern Angola between April 2008 and March 2009. Adapted from Brouwer and Griffiths (2005) and Mann and Buxton (1998)

Stage	Macroscopic description	Microscopic description
1. Juvenile	Ovotestis appears as a thin transparent vessel	Both ovarian and testicular tissue present in similar proportions. Only oogonia and perinuclear oocytes present in ovarian tissue.
2. Resting	Ovaries appear as thin translucent light yellow tubes. No eggs visible to the naked eye.	Ovarian tissue dominates. Oogonia and perinuclear oocytes proliferate. Very few cortical alveoli stage oocytes present.
3. Active	Slight increase in diameter. Ovaries become orange/yellow in colour. Some eggs visible to the naked eye.	First appearance of secondary and tertiary yolk vesicle oocytes. Cortical alveoli oocytes more prevalent.
4. Developing	Ovaries increase in diameter and become yellow in colour. Eggs clearly visible to the naked eye. Veins and arteries become visible on ovaries.	Secondary and tertiary yolk vesicle oocytes proliferate and the first appearance of enlarged cortical alveoli in the nuclear region.
5. Ripe	Ovaries large in diameter and yellow in colour. Eggs large. Veins and arteries large and plentiful.	Tertiary yolk vesicle oocytes dominate. First appearance of hydrated oocytes, which collapsed during tissue preparation. Migratory nuclei prevalent.
6. Ripe running	Ovaries similar in appearance to ripe ovaries, but with reddish patches. Veins and arteries large and plentiful.	Ovary dominated by collapsed hydrated oocytes.
7. Spent	Ovaries reduced in size and flaccid. Deep red in colour.	Undetermined

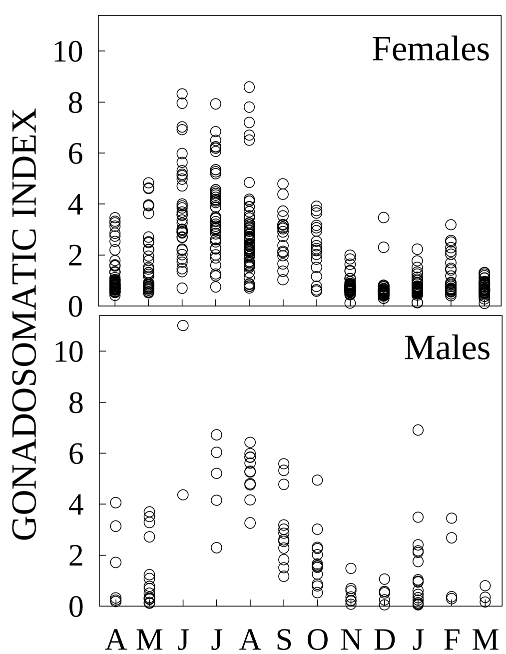

Figure 4.2: Individual gonadosomatic indices (GSI) for male and female *Diplodus capensis* from southern Angola.

Table 4.3: Staging criteria used to macroscopically assess the gonads of male *Diplodus capensis*, and their respective microscopic description, sampled from southern Angola between April 2008 and March 2009. Adapted from Brouwer and Griffiths (2005) and Mann and Buxton (1998)

Stage	Macroscopic description	Microscopic description
1. Juvenile	Ovotestis appears as a thin transparent vessel	Both ovarian and testicular tissue present in similar proportions. Only spermatogonia present in testicular tissue.
2. Resting	Testes thin and white. No sperm in tissue.	Spermatogonia dominate. Some spermatozoa may be present from the previous spawning season.
3. Active	Slight increase in width of testes. Triangular in cross section.	All stages of spermatogenesis present. Spermatozoa begin to fill the main sperm duct.
4. Developing	Testes increase in width and become creamy white in colour. Presence of sperm in main sperm duct if the testes are cut and gently squeezed.	All sages of spermatogenesis present. Spermatozoa dominate the secondary and main sperm ducts.
5. Ripe	Testes large and creamy white in colour. Sperm plentiful if the testes are cut and gently squeezed.	All stages of spermatogenesis present. Spermatozoa proliferate and dominate the section.
6. Ripe running	Testes similar in appearance to ripe testes, but with pinkish patches. Testicular tissue is easily broken when handled.	Similar to stage 5
7. Spent	Testes reduced in size and pinkish in colour. Sperm may still be present in the main sperm duct.	Undetermined

Table 4.4: Average gonadosomatic indices calculated for female and male *Diplodus capensis* sampled from southern Angola and *p*-values from *t*-tests conducted for the average GSI during different periods.

	Average GSI ± S.D.		
	Females	Males	*p* - value
All months	1.84 ± 1.61	2.24 ± 2.14	0.035
During spawning season	3.14 ± 1.70	3.60 ± 2.17	0.132
Outside spawning season	1.0 ± 0.49	1.18 ± 3.20	0.190

Histological appearance

Oogenesis

The process of oocyte growth and development was consistent with that described for other sparids (Coetzee 1983, Buxton 1990, Micale et al. 1996, Booth and Hecht 1997, Mann and Buxton 1998, Pajuelo et al. 2006, Pajuelo et al. 2008) and teleosts in general (Yamamoto 1956, Wallace and Sellman 1981, Tyler and Sumpter 1996).

Primary growth phase: The first recognisable stage of the female gamete was the oogonia. Oogonia were present in "nests" and recognised by their small size, large nucleus to cytoplasm ratio and lightly basophilic cytoplasm (Figure 4.3a). Together with rapid oocyte growth, the appearance of nucleoli marks the start of the perinuclear oocyte stage. Three types of perinuclear oocytes are present (Figure 4.3a). Pre-perinuclear oocytes are polygonal in shape, have a strongly basophilic cytoplasm and the nucleus contains one or two large nucleoli and many small ones. Early-perinuclear oocytes are larger in size, more ovoid in shape, have a slightly less basophilic cytoplasm and the nucleoli are large and numerous. Late perinuclear oocytes are circular in shape, their cytoplasm is weakly basophilic and begins to take on a granular appearance and the nucleoli tend to be flattened on the inner surface of the nuclear membrane. The formation of the zona granulosa and the zona radiata occurred in late-perinuclear oocytes and marked the end of the primary growth phase. Both these zones become more distinct as the oocyte develops.

Cortical alveoli phase: The appearance of cortical alveoli (primary yolk vesicles) in the periphery of the cytoplasm of late-perinuclear oocytes marks the beginning of this phase (Figure 4.3b). Cortical alveoli are white in color and become more numerous as the oocyte progresses, and fill the entire cytoplasm before the onset of vitellogenesis.

Vitellogenesis: The appearance of acidophilic secondary yolk vesicles in the cytoplasm marked the beginning of vitellogenesis (Figure 4.3c). These became more numerous with oocyte growth and, in tertiary yolk vesicle oocytes, filled the entire cytoplasm (Figure 4.3d). During vitellogenesis the zona radiata and zona granulosa were very prominent (Figure 4.3e). Towards the end of vitellogenesis the cortical alveoli become enlarged around the nucleus, yolk begins to coalesce and a lipid droplet forms in the region of the nucleus (Figure 4.3f). This droplet displaces the nucleus, which migrates to the periphery of the oocyte, and marks the completion of vitellogenesis (Figure 4.3g).

Maturation phase: After the completion of vitellogenesis, hydration occurs, which gives rise to mature oocytes. Histological examination of mature eggs was not possible due to oocytes collapsing during tissue preparation (Figure 4.3h).

Spermatogenesis

The male testis consisted of a number of seminiferous tubules leading into secondary sperm ducts and finally into the main sperm duct (Figure 4.4a). Spermatogenesis was initiated in the periphery of the testis within cysts that were present in the seminiferous tubules. Spermatogonia were easily recognised by their relatively large size, small nucleus and lightly basophilic cytoplasm (Figure 4.4b). Spermatogonia undergo a mitotic division to produce spermatocytes, which were smaller in size, had a strongly basophilic nucleus and a high nucleus to cytoplasm ratio (Figures 4.4b & c). Spermatocytes generally formed clumps in between the spermatogonia. Spermatocytes gave rise to spermatids, which were recognised by their small size and visible lack of a cytoplasm (Figure 4.4d). The final stage of spermatogenesis was spermatozoa, which were exceptionally small and had a strongly basophilic nucleus (Figure 4.4d). Spermatozoa congregated in cysts surrounded by spermatids within the seminiferous tubules. The main sperm duct of ripe fish was filled with spermatozoa. The process of spermatogenesis was consistent with that described by Mann and Buxton (1998) for *D. capensis* in South Africa and for other sparids (Micale and Perdichizzi 1994, Booth and Hecht 1997).

Histological validation of macroscopic staging

The microscopic examination of gonads of each stage indicated that the macroscopic staging criteria used in this study were adequate. There were minor qualitative differences observed between the microscopic and macroscopic appearance of gonad stages (Figures 4.5 & 4.6; Tables 4.2 & 4.3).

Juvenile ovotestes contained ovarian tissue with oogonia and perinuclear oocytes and testicular tissue with spermatogonia present (Figures 4.5a & 4.6a).

Resting ovaries were dominated by perinuclear oocytes with very few oocytes in the cortical alveoli phase (Figure 4.5b). Active ovaries contained a prevalence of cortical alveoli oocytes with the first appearance of secondary and tertiary yolk vesicle oocytes giving the ovary a slightly yellowish appearance (Figure 4.5c). In developing ovaries, secondary and tertiary yolk vesicle oocytes proliferated and the first appearance of enlarged cortical alveoli in the nuclear region was noted (Figure 4.5d). Ripe ovaries were dominated by tertiary yolk vesicle oocytes with the first appearance of hydrated oocytes and migratory nuclei (Figure 4.5e). The major macroscopic difference between developing and ripe ovaries was their relative size.

Ripe running ovaries were dominated by collapsed hydrated oocytes (Figure 4.5f). The microscopic appearance of spent ovaries was not determined.

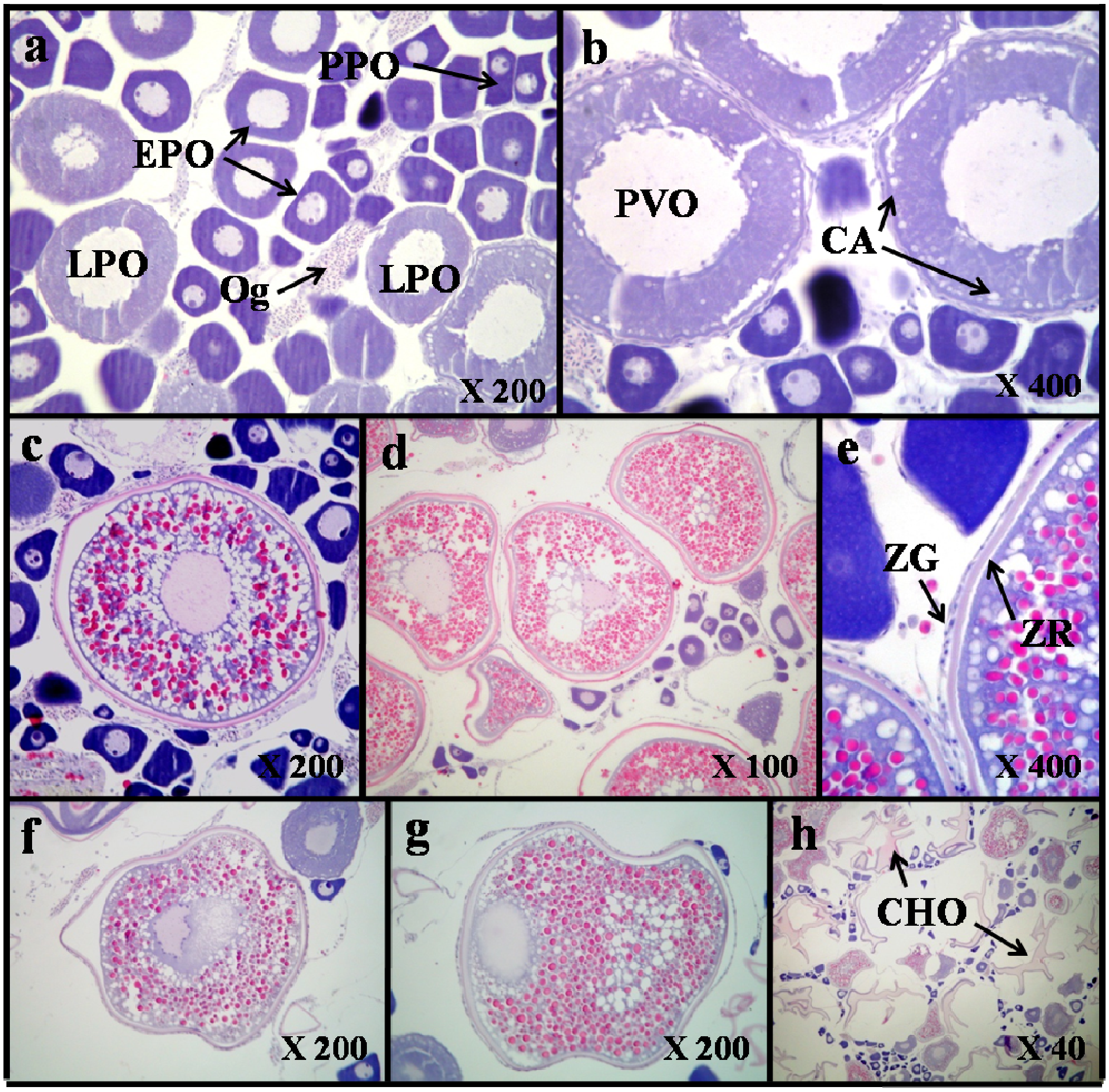

Figure 4.3: Transverse sections through ovaries of *Diplodus capensis* illustrating oogenesis. (a) Resting ovary containing oogonia (Og), pre-perinuclear oocytes (PPO), early-perinuclear oocytes (EPO) and late-perinuclear oocytes (LPO). (b) Primary yolk vesicle oocytes (PVO) with the first signs of cortical alveoli (CA) in the periphery of the cytoplasm. (c) Secondary yolk vesicle oocyte showing the proliferation of cortical alveoli and the first signs of acidophilic secondary yolk vesicles in the cytoplasm. (d) Tertiary yolk vesicle oocytes showing the proliverations of acidophilic tertiary yolk vesicles in the cytoplasm and the enlarged cortical alveoli in the nuclear region, which occurred just prior to lipid droplet formation. (e) During vitellogenesis the zona granulosa (ZG) and zona radiata (ZR) are well developed. (f) Tertiary yolk vesicle oocyte showing lipid droplet formation in the region of the nucleus and the first signs of nucleus migration. (g) The completion of vitellogenesis occurs when the nucleus migrates to the periphery of the oocyte. (h) Hydration and maturation occurred after nucleus migration, however, mature oocytes (CHO) collapsed during tissue preparation.

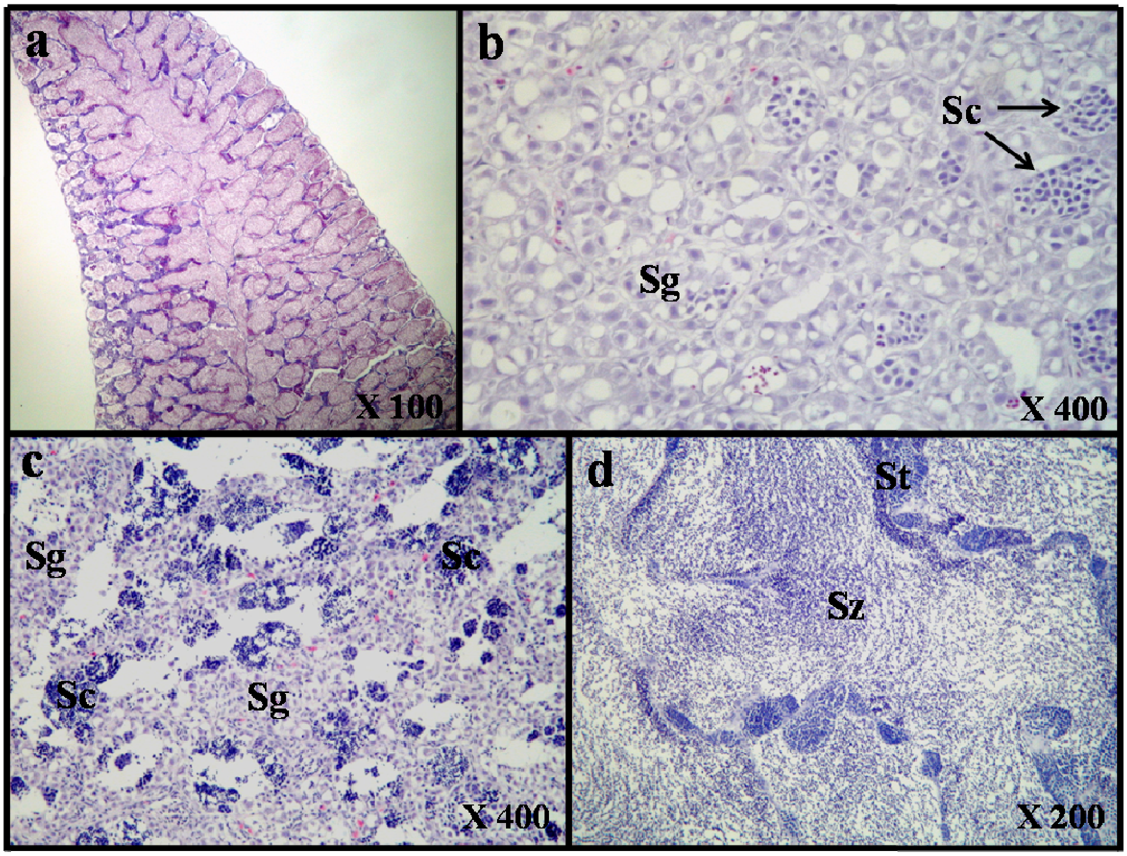

Figure 4.4: Transverse sections through testes of *Diplodus capensis* illustrating spermatogenesis. (a) Functional male testis indicating the organisation of outer seminiferous tubules, intermediate secondary sperms ducts and the central main sperm duct. (b) The proliferation of spermatogonia (Sg) towards the outer regions of the testis, showing the first signs of spermatocytes (Sc). (c) Groups of spermatocytes surrounded by spermatogonia. (d) The proliferation of spermatozoa (Sz) in a ripe individual's main sperm duct with cysts of spermatids (St) present.

Differences between the microscopic appearance of the macroscopic stages of testes were less pronounced. Resting testes were dominated by spermatogonia and groups of spermatocytes (Figure 4.6b). From the active stage, all stages of spermatogenesis were present in the testis. In active testes spermatozoa began to fill the secondary sperm ducts (Figure 4.6c) and the main sperm duct in developing testis (Figure 4.6d). Ripe and ripe running testes were dominated by spermatozoa (Figures 4.6e & f).

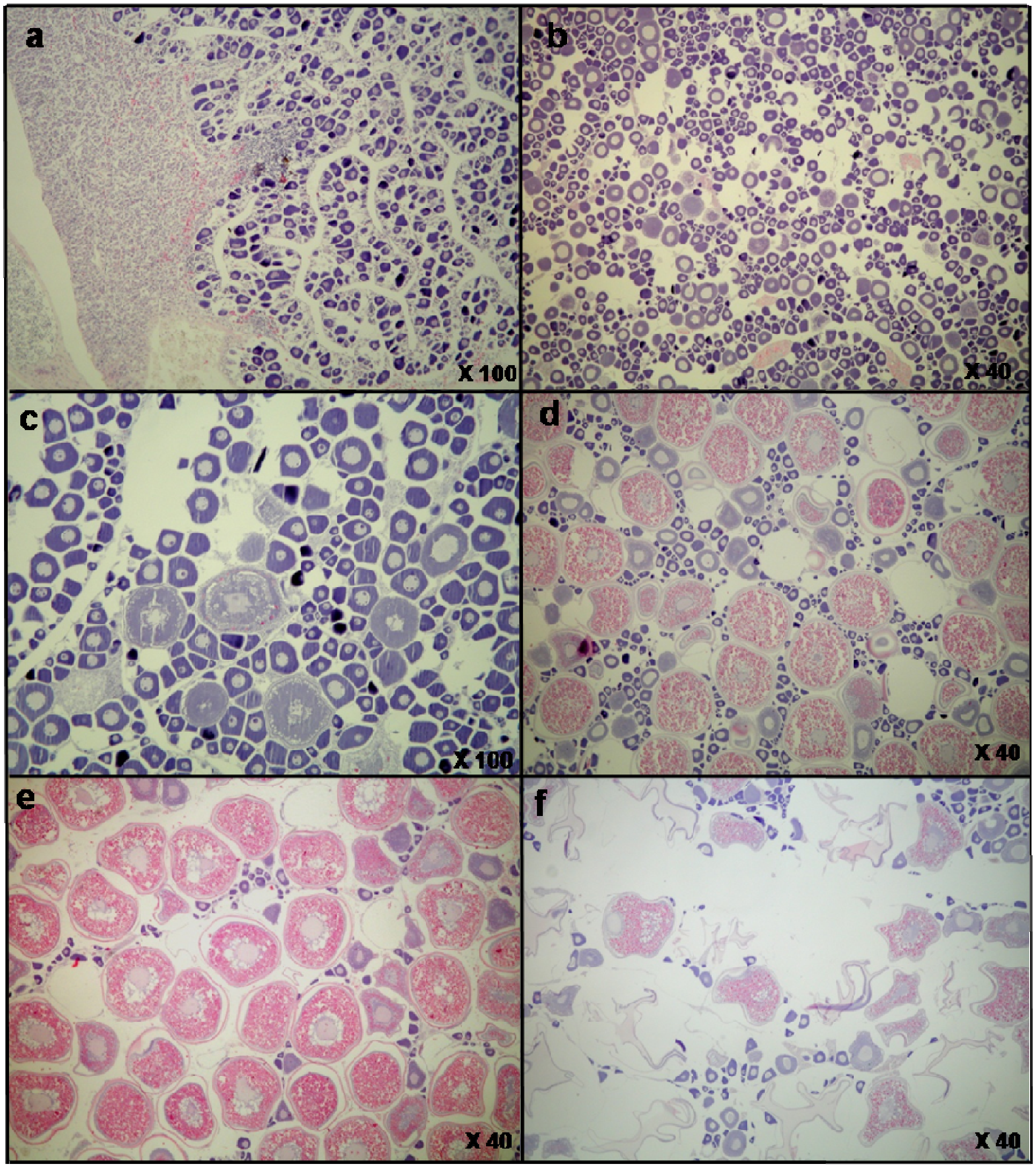

Figure 4.5: Transverse sections through ovaries of *Diplodus capensis* illustrating the microscopic appearance of macroscopic stages one to six. (a) Juvenile ovotestis (stage one) with only oogonia and perinuclear oocytes present in ovarian portion. (b) Stage two ovary resembles ovarian portion of juvenile ovotestis with few cortical alveoli stage oocytes present. (c) Stage three ovary contains more cortical alveoli oocytes and secondary and tertiary yolk vesicle oocytes start to appear. (d) Stage four ovary contains many secondary and tertiary yolk vesicle oocytes and the first enlarged cortical alveoli appear around the nucleus. (e) Stage five ovary is dominated by tertiary vesicle oocytes with the first appearance of hydrated oocytes. (f) Stage six ovary is dominated by collapsed hydrated oocytes.

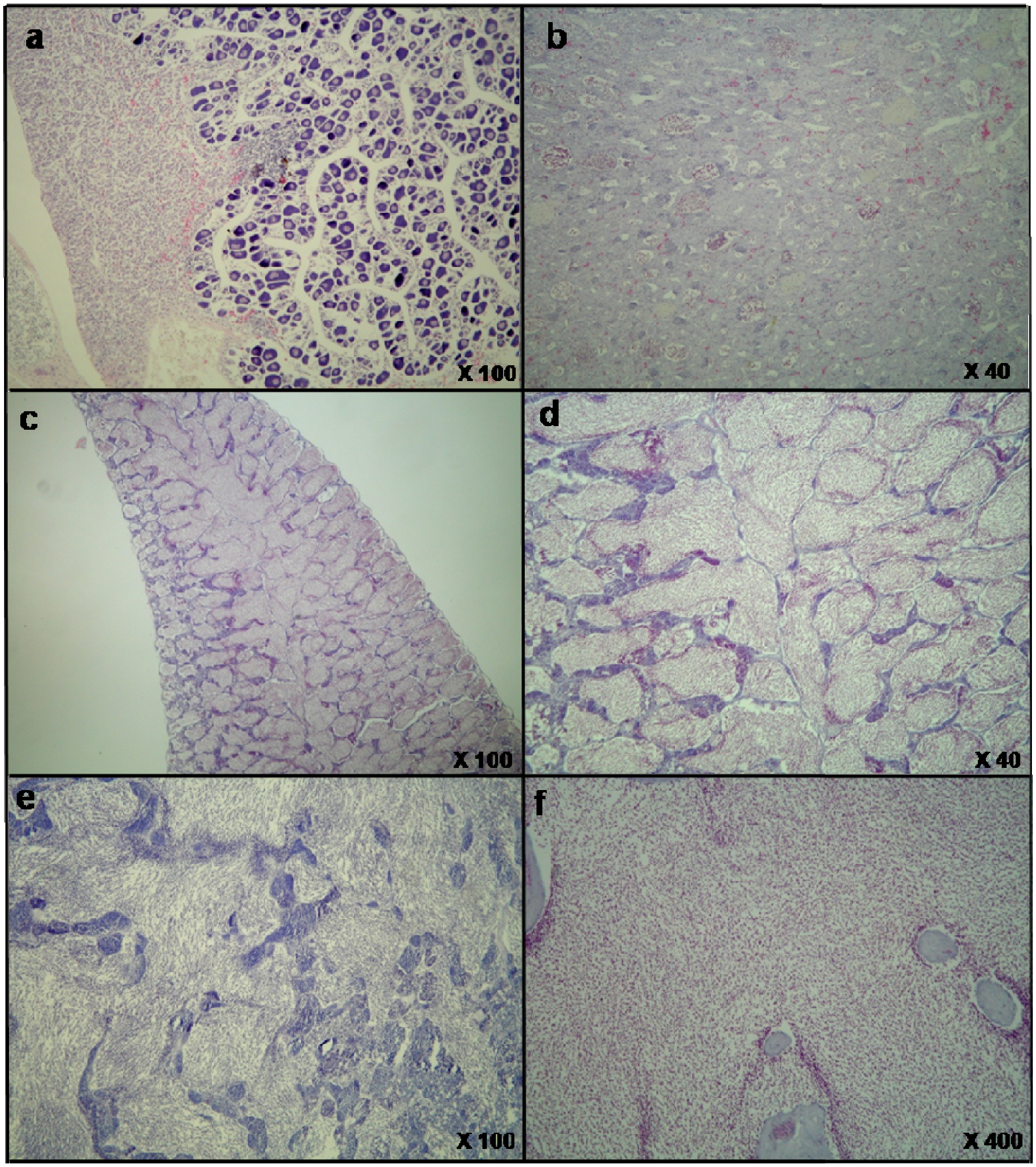

Figure 4.6: Transverse sections through testes of *Diplodus capensis* illustrating the microscopic appearance of macroscopic stages one to six. (a) Juvenile ovotestis (stage one) with only spermatogonia present in the testicular portion. (b) Stage two testis resembles testicular portion of juvenile ovotestis. (c) Stage three testis contains all stages of spermatogenesis with spermatozoa filling the main sperm duct. (d) Stage four testis showing the proliferation of spermatozoa in the main sperm duct. (e) Stage five testis showing the domination of spermatozoa. (f) Stage six testis is similar to stage five, with an almost complete proliferation of spermatozoa.

Association of environmental variables with reproductive activity

Reproductive activity appeared to be strongly linked to surf zone water temperature, with GSI increasing in response to decreasing water temperatures (Figure 4.7). A small increase in GSI was observed during the summer months (January and February) which appeared to be in response to a decrease in average water temperature during this period. Spawning activity also appears to be related to photoperiod, with GSI values increasing with shorter day lengths.

The cyclic pattern of reproductive activity was best described by the periodic regression model with temperature as an added variable (Figure 4.8; Table 4.5). The period of this model was not found to differ from 12 (LRT, $p > 0.05$), therefore it can be concluded that reproductive activity follows an annual pattern and surf zone water temperature has a significant effect on gonad development in *D. capensis* in southern Angola.

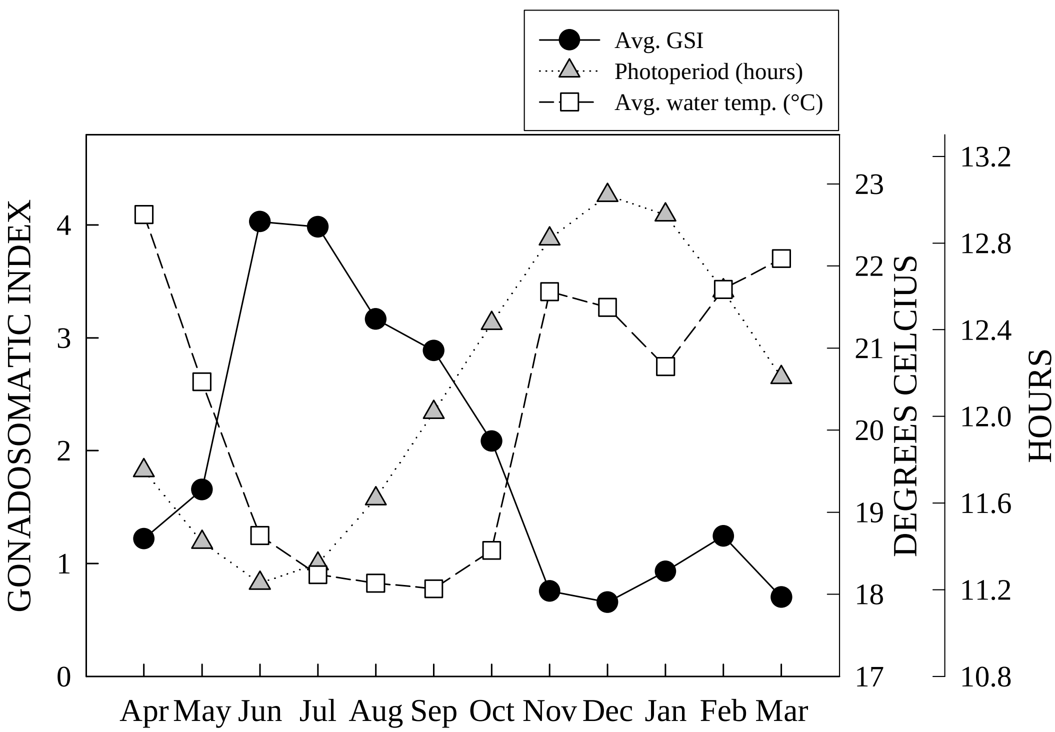

Figure 4.7: Average monthly gonadosomatic indices (GSI) of *Diplodus capensis*, surf zone water temperatures and photoperiod from southern Angola from April 2008 - March 2009.

Table 4.5: Parameter estimates, log likelihood function (ln*L*), Akaike's information criterion (AIC) and likelihood ratio test (LRT) results for periodic regression models fitted to observed monthly gonadosomatic index (GSI) for *Diplodus capensis* in southern Angola. The best model was that which incorporated surf zone water temperature as a variable and the period (*P*) was fixed at 12 months ($PR2_{red}$).

									Likelihood ratio test†	
	β_0	β_1	β_2	β_3	P	# parameters	ln$L$	AIC	γ	p - value
PR1	-4.32	0.84	-0.33	-	11.09	4	216.08	440.17	-	
$PR2_{full}$	0.74	0.43	0.15	0.25	12.11	5	234.41	478.82	36.657	1.41×10^{-09}
$PR2_{red}$	0.65	0.45	0.13	0.25	12*	4	234.40	476.80	0.025	0.876

* period was fixed at 12 and was not estimated as a parameter

† LRT results are displayed for the test conducted with the previous model on the table

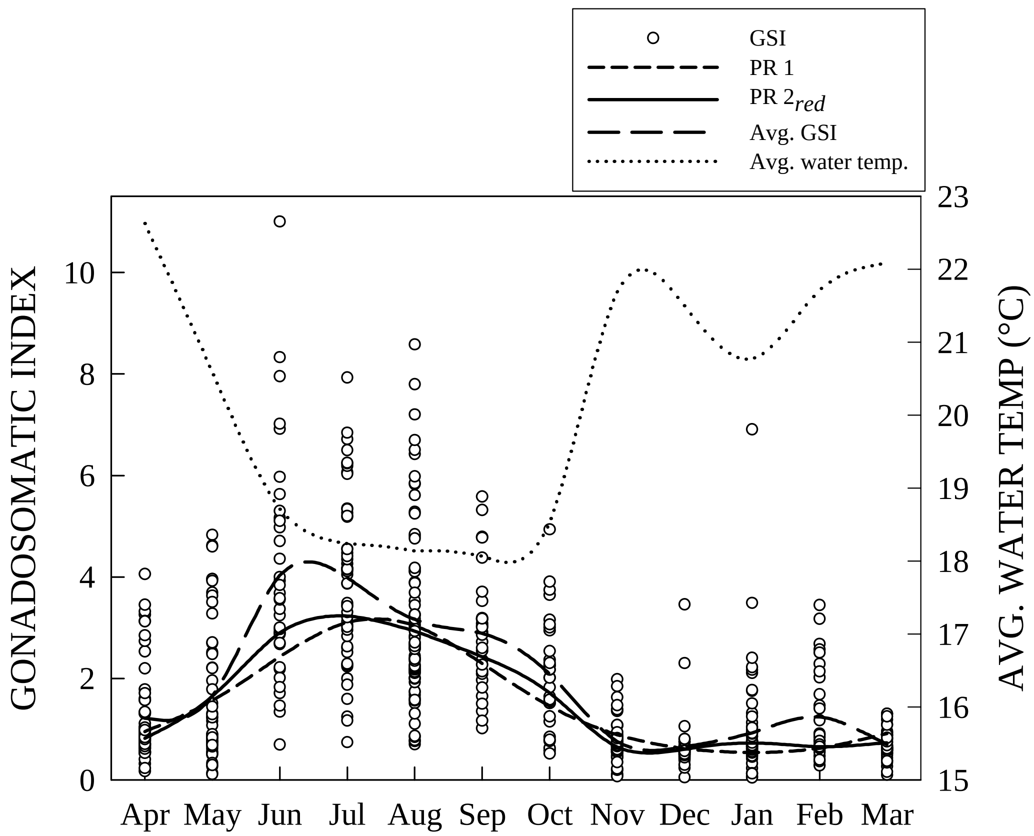

Figure 4.8: Observed average gonadosomatic index (GSI) and surf zone water temperature with fitted periodic regression model curves for *Diplodus capensis* in southern Angola. The model incorporating temperature as a variable (PR 2_{red}) better described the change in GSI than the model without (PR 1) (likelihood ratio test, $p < 0.05$) and the cyclic pattern of reproductive activity for this model was not found to differ from 12 months (likelihood ratio test, $p > 0.05$).

Reproductive style

Population structure

The length frequency distribution displayed slight bimodality with the modal length class for males 2cm less than females (Figure 4.9). The proportion of males was also low in the larger length classes. In contrast, the age frequency distributions for males and females were similar, although the proportion of males was reduced in the older year classes (Figure 4.9). The average length of females and males was 223.9mm and 198.1mm FL, respectively. The overall sex ratio for mature fish was 1 male: 4.7 females. There was considerable variation in the sex ratio with increasing length classes with females becoming increasingly dominant with increasing size (Figure 4.10 & Table 4.6).

Histological analysis

Histological analysis revealed that the gonads of *D. capensis* developed from a nonfunctional intersex phase with an ovo-testis containing both ovarian and testicular tissue separated by connective tissue, a typical sparid pattern (Atz 1964) (Figures 4.11a & b). Testicular and ovarian gametes were only discernable in gonads of fish greater than 115mm FL in which male and female tissue was present in similar proportions. After this period of non-functional bisexuality, either reproductive tissue may develop and become dominant. While the length at which sexual differentiation occurred was variable, all gonads of fish larger than 150mm FL had developed into either a functional male or female. Gonad tissue in intersex fish could not be discerned macroscopically and consequently these fish were classed as juveniles.

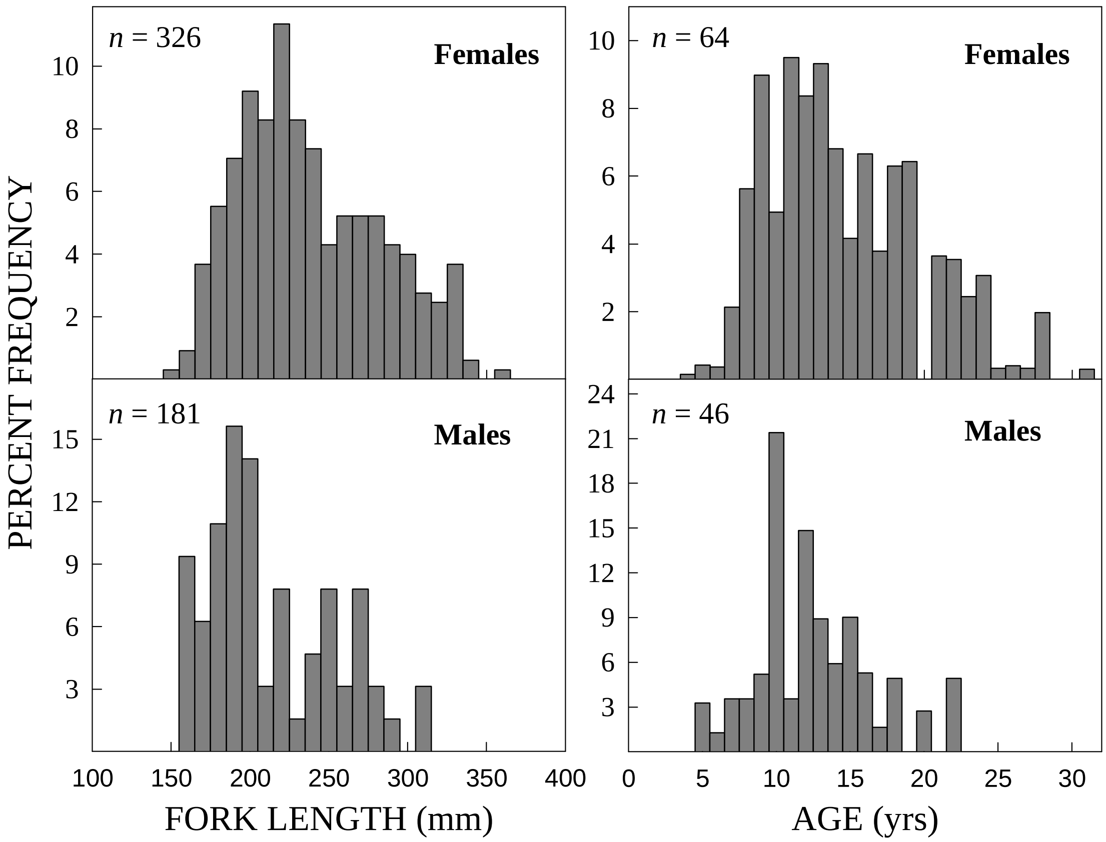

Figure 4.9: Size and age frequency distributions for *Diplodus capensis* sampled in southern Angola between April 2008 and March 2009. Note that histological examination invalidated individuals that were staged as "intersex", which were actually functional males.

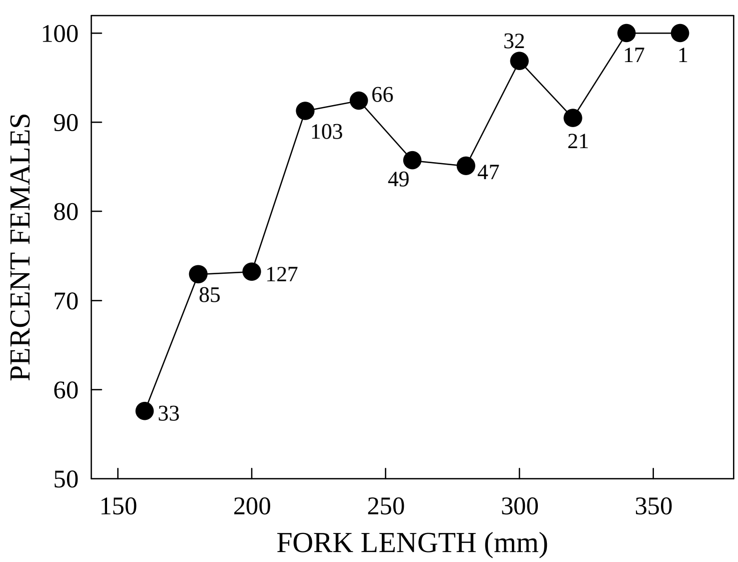

Figure 4.10: Proportion of female *Diplodus capensis* with increasing length in southern Angola sampled between April 2008 and March 2009. Sample sizes for each 20mm length class are indicated on the graph.

Table 4.6: The change in sex ratio with increasing size of *Diplodus capensis* from southern Angola.

Length class (mm FL)	Number of Males	Number of Females	Sex Ratio (M:F)
150 - 200	71	169	1: 2.4
200 - 250	19	176	1: 9.3
250 - 300	10	92	1: 9.2
300 - 350	2	36	1: 18

In functional females, the ovarian portion became dominant and the testicular tissue was greatly reduced (Figures 4.11e & f). This reduction appeared to occur immediately after sexual maturity. In many cases, the vestigial testicular tissue was not visible in the functional female gonad. In functional males, the testicular portion was dominant and the ovarian tissue was generally reduced to a thin band containing very few oocytes in the perinuclear phase (Figures 4.11c & d). As with females, this reduction usually occurred immediately after sexual maturity. However, in some cases, the ovarian tissue persisted in functional males which were macroscopically staged as “intersex individuals” because of the presence of an integral ovarian portion. This ovarian portion did not contain any oocytes past the late-perinuclear phase suggesting that it had merely persisted from the juvenile intersex phase (Figure 4.12). The state of development of the testicular tissue in the gonads of macroscopically staged “intersex individuals” was variable, but in all cases contained all stages of spermatogenesis and no signs of degenerative tissue. This “late” degeneration of the ovarian portion of the nonfunctional ovo-testis was rare (four individuals), only occurred in small individuals (153, 158, 172 and 178mm FL) and these fish were sampled at random times throughout the sampling period (27 Jan, 22 Apr, 13 Aug and 27 Oct).

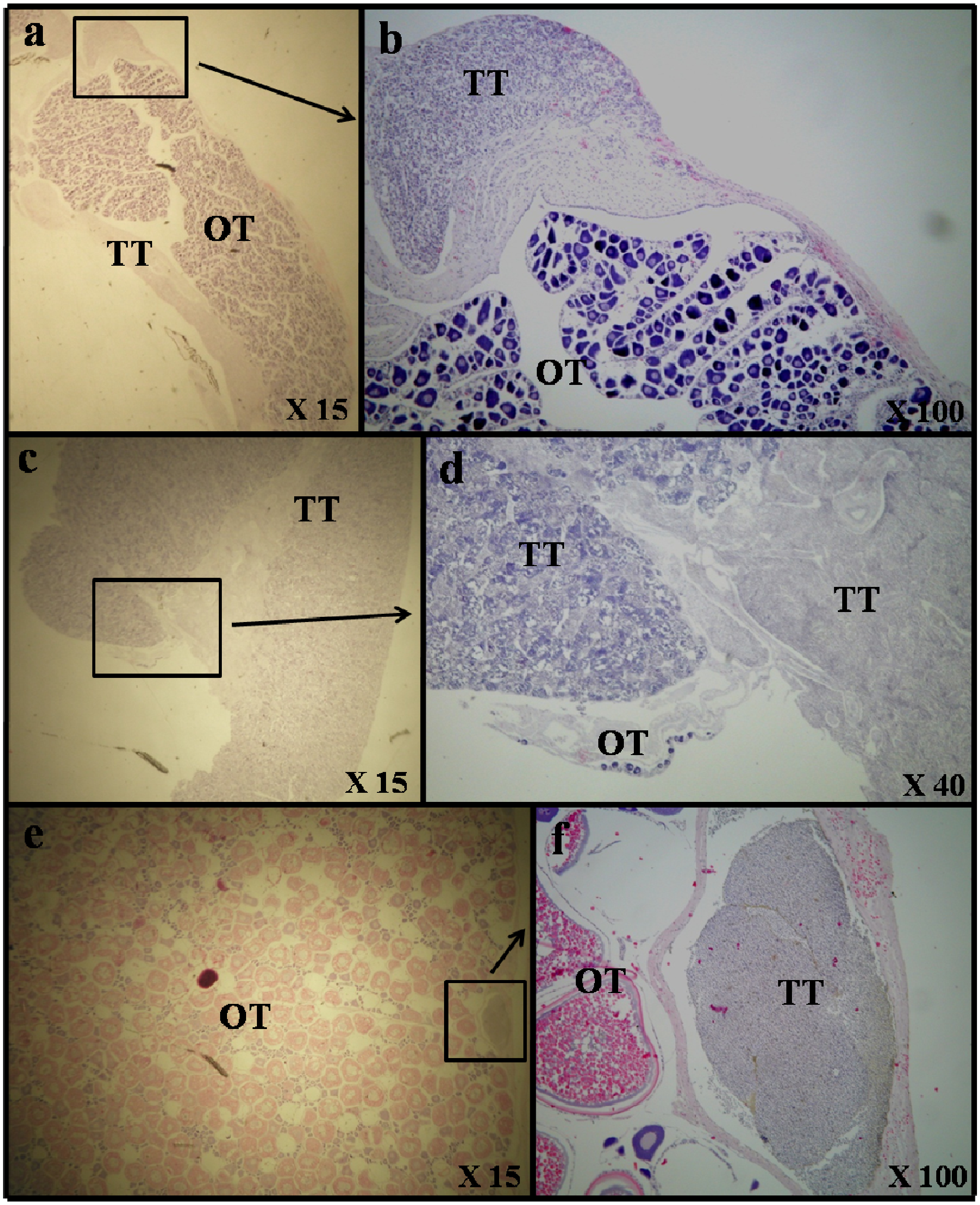

Figure 4.11: Transverse sections of the gonads of *Diplodus capensis* illustrating their development. (a & b) Non-functional intersex juvenile phase (142mm FL) with both ovarian (OT) and testicular tissue (TT). Spermatogonia were present in the testicular portion and oocytes up to the late-perinuclear phase were present in the ovarian portion. (c & d) A functional male testis (171mm FL) with a band of vestigial ovarian tissue containing a small number of perinuclear oocytes. The testicular tissue was well developed and the main sperm duct was filled with spermatozoa. (e & f) A functional female ovary (301mm FL) indicating the small portion of testicular remnants. The ovarian tissue was well developed and contained all stages of oocyte growth up to the tertiary yolk vesicle oocyte stage.

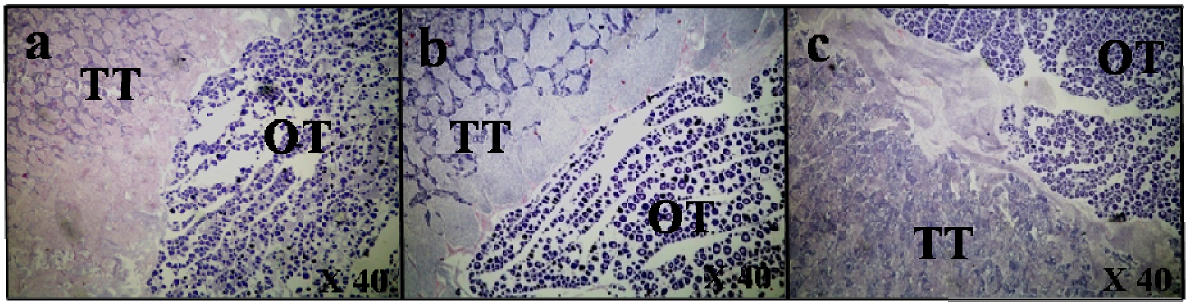

Figure 4.12: Transverse sections of the gonads of *Diplodus capensis* (a = 172mm, b = 178mm, c = 158mm FL) that were macroscopically identified as "intersex" individuals. Histological examination revealed that they were in fact functional males with an ovarian portion that had persisted from the juvenile ovotestis.

Discussion

Both macro- and microscopic examination of the gonads of *D. capensis* indicated that this species has an extended spawning season in southern Angola, with the greatest evidence for reproduction during the winter and spring (June - October). The GSI results corroborated this extended spawning season. Extended spawning seasons are characteristic of asynchronous spawning species (Garratt 1985b), where individuals reproduce multiple times during one spawning season. The presence of oocytes in various stages of development in the ripe ovaries of *D. capensis* further corroborates an asynchronous spawning strategy. Asynchronous spawning over an extended spawning season has the advantage of ensuring a portion of larval and juvenile survival by "not putting all their eggs into one basket". If spawning only occurred once during a season, unfavourable conditions might wipe out an individual's entire progeny. However, with a multiple spawning strategy, survival of gametes is ensured even if some batches are released during unfavourable conditions. A similar spawning strategy has been documented for *Argyrozona argyrozona*, which spawns at least 30 times per year in order to avoid a loss of fecundity due to short-term upwelling on the Tsitsikamma coast, South Africa (Brouwer and Griffiths 2005).

In agreement with the study of Mann and Buxton (1998), reproductive activity appears to be associated with photoperiod and water temperature in *D. capensis*. Indeed, photoperiod and water temperature are the most important environmental variables that control the timing of teleost reproduction (de Vlaming 1972, Bye 1984). The consistent nature of photoperiod as an environmental variable makes it likely to be the proximate cue in triggering reproductive activity in this species. Furthermore, despite observing a large proportion of active and developing gonads in March and April, the first significant drop in water temperature only occurred in May and June. Water temperature appears to follow the periodic pattern of photoperiod to a certain degree, however, due to the inherent unpredictability of water temperature in the marine environment, anomalies are not surprising. This appeared to be the case in mid summer (January) during the sampling period, when there was a considerable drop in average water temperature. Unsurprisingly, the periodic regression showed a significant relationship between GSI and water temperature and the spike in the GSI values in January therefore provides evidence that temperature is an important ultimate cue for triggering reproductive activity in this species. The model also predicted an annual cycle of reproductive activity indicating that *D. capensis* has a periodic spawning season, but has the ability to respond to favourable spawning conditions. This was confirmed by an increase in the percentage of ripe individuals observed during January, and the presence of spent gonads indicated that spawning had occurred.

Water temperature has been shown to be an important environmental factor in the regulation of the timing of spawning in sparid fishes (Sheaves 2006). One of the major findings of the study of Sheaves (2006) was that spawning at lower latitudes was concentrated close to the month of lowest sea surface temperature, while spawning at higher latitudes was more variable with greater deviations from the month of minimum sea surface temperature. The reproductive seasonality of *D. capensis* appears to be consistent with this pattern. Similar to that in southern Angola, the reproductive activity of *D. capensis* in KZN reaches a peak from June to September, during the cold water months (Joubert 1981b), while on the Eastern Cape coast spawning is delayed until westerly winds bring stable, warmer water temperatures during summer, and spawning occurs from August to December (Mann and Buxton 1998). Although there is little difference in latitude between KZN and the Eastern Cape coast, the prevailing environmental conditions are remarkably different and the two areas are considered to be sub-tropical and warm-temperate, respectively. This pattern is further supported by the spawning seasons of other members of the Sparidae family in KZN [e.g. *Cheimerius nufar* (Garratt 1985b), *Chrysoblephus puniceus* (Garratt 1985b), *Sarpa salpa* (Joubert 1981b)] and the Eastern and Southern Cape [e.g. *Argyrozona argyrozona* (Brouwer and Griffiths 2005), *Cheimerius nufar* (Coetzee 1983), *Chrysoblephus cristiceps* (Buxton 1990), *Chrysoblephus laticeps* (Buxton 1990), *Diplodus cervinus hottentotus* (Mann and Buxton 1998), *Pachymetopon aeneum* (Buxton and Clarke 1986), *Sparodon durbanensis* (Buxton and Clarke 1991)].

Sheaves (2006) provided possible explanations for why tropical sparids restrict spawning to the coolest part of the year while their more temperate counterparts do not. The most parsimonious explanation lies within the physiological tolerances of adults, gametes, eggs and larvae. Based on this and other studies on *D. capensis*, it appears that optimal temperatures for spawning range between 17 and 20°C (Mann and Buxton 1998). By utilising winter spawning, tropical sparids can spawn over similar temperature ranges to more temperate species and/or populations (Sheaves 2006). Essentially, tropical sparids may be members of a temperate group, limited in distribution by the temperature tolerances of gametes, eggs or larvae (Sheaves 2006). If adults possess the ability to withstand high temperatures, targeting spawning at times of minimum water temperatures is an obvious tactic to allow a species to maximize penetration into warmer waters (Sheaves 2006). The cold Benguela current penetrates well into Angola during winter and it is therefore likely that this oceanographic phenomenon plays a major role in facilitating the survival and colonising ability of *D. capensis* in this region. A common explanation for the observed spawning seasonality of a particular fish species is to produce larvae during times when their planktonic prey is most abundant (Bye 1984, Shapiro et al. 1988, Sheaves 2006). The Benguela is an extremely productive system and when its nutrient rich waters extend into the southern Angolan region increased productivity and subsequent algal growth can be expected to occur. This increased productivity would bring about an increased abundance of zooplankton for planktonic larvae to feed upon. Therefore, water temperature is likely to act as an ultimate cue for triggering gonad development and spawning in *D. capensis* because it provides a means for natural selection to function on survivorship and recruitment of larvae. Adult fish that spawn during cold water periods are more likely to produce viable progeny due to favourable conditions for gamete, egg and larval survival.

Assuming that spawning in *D. capensis* is limited by the temperature tolerance of gametes, eggs and larvae, the spawning success/potential over a particular season could be predicted from water temperature data, which can have useful management applications. Furthermore, the need for this species to spawn during the cooler months of the year could have far reaching implications when one considers the imminent increase in water temperature over the next few decades due to global warming (Gröger and Plag 1993). If *D. capensis* can only spawn in cold water, which is during the coldest time of the year in southern Angola, an increase in water temperature will reduce the potential time available for spawning in this region. Species such as this would have to shift their geographic ranges in order to remain in waters with favourable conditions for gamete, egg and larval survival. At low latitudes, this would equate to a southerly distributional shift.

Juvenile *D. capensis*, like most sparid fishes, have a non-functional ovotestis. However, after sexual differentiation in this phase, there was no evidence of later sex change and it was concluded that *D. capensis* is a rudimentary hermaphrodite in southern Angola. This is in agreement with the findings of Joubert (1981b), however Coetzee (1986) and Mann and Buxton (1998) concluded that part of the male population retains the ability to change sex after initially functioning as a male (partial protandry) in this species in South Africa. The conclusions of Joubert (1981b) were based on macroscopic analysis of the gonads, while that of Coetzee (1986) and Mann and Buxton (1998) were based on microscopic evidence for degenerative testicular tissue and developing ovarian tissue in the same individual. A small proportion (four individuals, 0.6%) of the fish gonads in this study were categorised macroscopically as "intersex". While these gonads were initially thought to be those of hermaphrodites, changing sex from male to female, the microscopic examination revealed that there was no evidence for tissue degeneration and they were functional males with a persistent ovarian portion from the juvenile ovotestis. According to Sadovy and Shapiro (1987), this cannot be used as evidence of protandry because there was no evidence of degenerating testicular tissue accompanied by a developing ovarian portion. Furthermore, all four individuals containing these gonads were smaller than 180mm FL (marginally larger than the size at 50% maturity), providing further evidence that this was a persistence of the juvenile ovotestis. It is unlikely that males would gain a competitive advantage from protandry at such a small size. Fish typically change sex when they reach approximately 70 - 80% of their maximum body size and are about 2.5 times their initial age at sexual maturity (Allsop and West 2003). This would equate to a size and age of about 250 - 285mm FL and 17 years, respectively. Sex change is, however, not genetically predetermined so the size and age at which it occurs may vary (Francis 1992, Shapiro 1992, Baroiller et al. 1999, Avise and Mank 2009). Mann and Buxton (1998) found a larger proportion of the adult population to consist of intersex individuals (3.3%) and these individuals were found over a large size range (150 - 296mm FL). Other studies that have reported partial protandry in *Diplodus* species also found higher proportions of intersex individuals (1.3 - 7.8%) and these were not confined to fish of a similar size to that of 50% maturity (Goncalves and Erzini 2000, Morato et al. 2003, Pajuelo and Lorenzo 2004, Pajuelo et al. 2006, Mouine et al. 2007, Pajuelo et al. 2008). Mann and Buxton (1998) reported a low number of intersex individuals (1.7%) for *D.*

cervinus hottentotus. Histological examination of these gonads showed that they consisted of developing testicular tissue with a dormant ovarian portion. Similar to the current study, they suspected that this was probably representative of the retention of a non-functional, juvenile ovotestis and it was concluded that *D. cervinus hottentotus* is a rudimentary hermaphrodite.

The modal length frequency distribution for males was slightly smaller than that for females. Protandric hermaphrodites usually demonstrate bimodal size (or age) frequencies; with modal size of males being less than that of females (Sadovy and Shapiro 1987). Bimodal length frequency distributions have been used as supporting evidence for protandry (e.g. Hesp et al. 2004), however, bimodal size (or age) frequencies can be produced by mechanisms other than hermaphroditism and many gonochorists display bimodal size frequencies (Sadovy and Shapiro 1987). Amongst these mechanisms are size dimorphism and differential rates of growth, differential rate of mortality, spatial segregation by sex and selective sampling. In this study, the observed difference in modal size of males and females is very small (one 2cm length class) and it is likely that this is an artifact of one or more of the aforementioned mechanisms. The modal age frequency distribution for males and females was similar suggesting that the difference in length frequencies is due to differential rates of growth between sexes. Indeed, males display significantly slower growth than females and attain a smaller maximum size (likelihood ratio test, $p < 0.05$) (see Chapter 5). Males were, however, lacking from the older age classes indicating that they may undergo higher rates of natural mortality. Spatial segregation may also occur with males occupying deeper reefs than females. Females would thus be selected for with the sampling gear used in this study (shore angling). However this is unlikely as there are no morphological differences between sexes that would make males more suited to deeper reefs. Furthermore, if the difference in length frequency was a consequence of a proportion of the male population which had changed sex to female (growth and mortality rates being equal), then there should be some large and old males in the population. The lack of large and old males, therefore, supports the idea of differential growth and mortality rates between the sexes in this species.

The overall sex ratio was extremely female-biased (1 male: 4.7 females) in this study. Mann and Buxton (1998) found a similar pattern, however the difference was not as pronounced (1 male: 1.9 females). Contrastingly, Joubert (1981b) reported a male-biased sex ratio of 1.3 males: 1 female. Although the sex ratio in the study of Joubert (1981b) was male-biased, females dominated the larger size classes. Sampling took place in a heavily fished area and it could be that the reduced number of females in the population is a direct effect of exploitation (Mann and Buxton 1998). Sex ratios of other *Diplodus* species range from unity (1:1) to roughly one male to every three females (Goncalves and Erzini 2000, Morato et al. 2003, Pajuelo and Lorenzo 2004, Pajuelo et al. 2006, Mouine et al. 2007, Pajuelo et al. 2008). Interestingly, the sex ratio for *D. cervinus hottentotus*, a rudimentary hermaphrodite, was male biased (1 : 0.8) in South African waters (Mann and Buxton 1998). It may be argued that the heavily skewed sex ratio documented in the present study is indicative of partial protandry, however, if this was the case there would surely be a prevalence of intersex individuals in the intermediate size classes. In a group spawning situation, one male could fertilize the eggs of many females. Therefore, it makes evolutionary sense for there to be more females in the population than males, as females are more likely to limit the number of possible offspring that can be produced. Not only were females more abundant but they also dominated the larger size classes. Under an exploited scenario, the larger individuals would be removed first, which would reduce the sex ratio disparity, thus changing the dynamic of the population and possibly reducing its reproductive output. This study therefore presents valuable information for this species in an unexploited environment.

It is apparent that selection pressures have not favoured partial protandry for the unexploited Angolan population of *D. capensis* and therefore the size advantage model is inadequate in explaining the evolution of the demonstrated reproductive style of this species. Various alternative selective pressures appear to have acted in shaping the reproductive characteristics of this species. Some observations on the spawning behaviour of this species were made during the study period, which are very useful in order to understand the significance of certain reproductive characteristics. Spawning behaviour was observed on a few occasions from elevated positions on the coast line. Several individuals (approx. 8-15) were seen to be swimming vigorously amongst one another in a “ball” close to the surface in relatively shallow (< 6 m) water. Such behaviour is indicative of a group spawning strategy where a number of individuals of each sex gather and simultaneously release large amounts of sperm and eggs into the water. Similar spawning behaviour has been observed for other sparids that demonstrate rudimentary hermaphroditism (Garratt 1985b, 1985a, 1988).

For males of a group spawning species it would be beneficial to have a large testis to increase the number of sperm released and thus the number of possible eggs fertilized. Gonad size is a distinctive character with regards to reproductive style in sparids, and rudimentary hermaphrodites have equitable gonad sizes between the sexes (Buxton and Garratt 1990, Sadovy 1996). The average male GSI was very high in this study (2.24) and significantly exceeded that of females (1.84). This further confirms a group spawning strategy, as males of pair spawning species have a much lower GSI than females (Buxton and Garratt 1990). In a group spawning situation there is the possibility of sperm competition, therefore selection would favour males that could release the greatest amount of sperm at a spawning event in order to maximize the number of eggs fertilized. In a pair spawning situation, males could afford to put less energy into gonad development because of the lack of sperm competition. A large testis would result in wasted sperm and it is likely that selection would operate on alternative characteristics such as body size or colour in such species. A large testis may therefore have evolved as an alternative to sex change in *D. capensis* in southern Angola.

Differential growth (see Chapter 5) may have also been an alternative to sex change in this species. For protandrous species, it is assumed that the reproductive value of large females exceeds that of smaller ones (Ghiselin 1969). This may be the case for *D. capensis* in this study, however, selection may have favoured females to become larger and older rather than for part of the male population to undergo the costly process of sex change.

The evolution and control of sex change has been extensively studied since Ghiselin's initial size advantage model proposed in 1969. However, studies have generally focused on reef fish that occupy territories and demonstrate a complicated social organisation. Knowledge concerning the genetic determination of hermaphroditism is limited (Baroiller et al. 1999), and as far as is known, sex change is initiated by behavioural or demographic alterations within a fish's social system (Shapiro 1989). For example, in the bluehead wrasse, *Thalassoma bifasciatum*, individuals can mature as either a female or primary male which look almost identical. Adult females can then change sex if they have an opportunity to take over the territory of a large male, after which the individual takes on a distinct bright colouration (Munday et al. 2006). Similar patterns have been shown experimentally for other sex changing fish with complex social organisations (Cole 1983, Shapiro 1987, Warner 1988, Ross 1990, Munoz and Warner 2004). From diving observations carried out during the study period, *D. capensis* do not appear to hold territories or have a complicated social organisation (T. J. Richardson and W. M. Potts, pers. obs.). This species is by far the most abundant inshore reef fish in southern Angola, further suggesting that there is unlikely to be a complex social organisation. However, a sex determining mechanism is still likely to operate on an external or demographic basis in rudimentary hermaphrodites. The ability to be more labile in their sex determination is an adaptive advantage in this species and favours rudimentary hermaphroditism over gonochorism. Possible demographic processes that may influence sex determination in this species are population density or population sex ratio.

Conclusion

Diplodus capensis demonstrated an extended spawning season (June - October) in southern Angola. The process of oogenesis and spermatogenesis was consistent with that described for other sparids and teleosts in general. Spawning occurred during periods of reduced water temperature and shorter day lengths. Mean monthly surf zone water temperature was significantly correlated to GSI and the periodic regression predicted a 12 month cyclic pattern of reproductive activity. Histological analysis of gonads revealed that this species is a rudimentary hermaphrodite, with individuals possessing a non-functional bipotential ovotestis in the juvenile phase. The sex ratio was heavily female-biased (1 male: 4.7 females) and the average male GSI value was high, exceeding that of females. This, together with anecdotal observations on spawning behaviour, suggests that this species is a group spawner. The female-biased sex ratio, large testis size, and differential growth rates between the sexes in this species are suggested as evolutionary alternatives to sex change in the southern Angolan population of *D. capensis*.

CHAPTER 5

A comparison of the life-history parameters of *Diplodus capensis* in an exploited and unexploited area in southern Angola

Introduction

Life-history theory attempts to explain the evolution of an organisms traits (related to reproduction) as adaptations to its physical and demographic environment (Winemiller and Rose 1992, Winemiller 2005). Many unidimensional life-history models (e.g. Cole 1954, Murphy 1968, Schaffer 1974) have been developed to explain such adaptation and it is the *r*-*K* continuum (Pianka 1970) that is the most widely used idea for comparing life-history strategies. The *r*-*K* continuum is, however, an inadequate model for comparing life-history strategies of fishes (Winemiller 1992), and the Winemiller and Rose (W&R) model has been proposed as an alternative for describing life-history evolution (Winemiller 1989, Winemiller 1992, Winemiller and Rose 1992). The W&R model, based on patterns of life-history variation in tropical freshwater fishes (Winemiller 1989) and North American freshwater and marine fishes (Winemiller and Rose 1992), is a triangular model of life-history evolution which recognises three endpoint strategies: (1) opportunistic (short generation time, high reproductive effort, small body size, low batch fecundity, and low investment per offspring), (2) periodic (long generation time, moderate reproductive effort, large body size, high batch fecundity, and low investment per offspring), and (3) equilibrium (moderate to long generation time, low reproductive effort, variable body size, low batch fecundity, and high investment per offspring) (Winemiller 2005). The opportunistic endpoint is considered to be a colonising strategy favoured in productive habitats that are subject to frequent intense disturbances (e.g. ephemeral pools, intermittent streams and salt marshes) (Winemiller 2005). The periodic endpoint maximizes fitness when environmental variation influencing early life stage survival is periodic (e.g. seasonal) and large scale (Winemiller and Rose 1992, Winemiller 2005). The equilibrium endpoint appears to be favoured in environments having persistent or frequent density dependant influences, or in stressful habitats (Winemiller 2005). While these endpoint strategies have evolved over millions of years to optimise the survival of fishes in their unique environments, the effect of fishing is a “recent” evolutionary pressure, which may induce a life-history change.

The immediate and most obvious effect of fishing is a reduction of fish density and truncation of size and age structure of the population (Haedrich and Barnes 1997, Goñi 1998, Jennings et al. 1999, Hutchings 2005). This is a direct consequence of the selective nature of fishing, with gear designed to capture a particular size range of fish (most often the larger and older individuals) (Law 2000). The selectivity of gear results in differential mortality rates between fishes in different size classes. This causes different selective pressures on a variety of life-history traits and can ultimately cause alterations in the life-history parameters of fishes (Heino and Godo 2002). These changes may also operate on a density-dependent basis, where a reduction in population density will induce a compensatory change in growth, survival, reproduction or movement (Rose et al. 2001). Various life-history traits have been shown to change in response to, or as a result of, exploitation. A decrease in the size and/or age at sexual maturity is a well documented effect of fishing (Rijnsdorp 1993, Coleman et al. 1996, Saborido-Rey and Junquera 1998, Haugen and Vøllestad 2001, Grift et al. 2003, Götz et al. 2008b, Tunley et al. 2009). Exploitation can also cause an increase in growth rate (Bowering and Brodie 1991, Millner and Whiting 1996, Rijnsdorp and van Leeuwen 1996, Helser and Almeida 1997, Heino and Godo 2002), which is likely due to a density dependant response to a reduction in food competition (Sanchez Lizaso et al. 2000, Rose et al. 2001). While many of these changes may be phenotypic and caused by short-term exposure to a fishery induced selective pressure (Lenfant 2003), in the long-term, these changes may manifest themselves as genetic changes (Heino and Godo 2002, Grift et al. 2003, Pérez-Ruzafa et al. 2006), which can ultimately be passed through generations.

It can be expected that the main driver of life-history change is the requirement of a fish to optimise its reproductive capacity. Consequently, most other life-history aspects (i.e. growth, age and size at maturity etc.) are shaped by natural selection that is geared to achieving maximum reproductive success (Thresher 1984). While monitoring changes in the reproductive strategies of fishes in response to fishing provides some information, the documentation of the changes to all life-history characteristics is preferable to gain an understanding of the true impact of fishing.

Growth rate and longevity are important characteristics when investigating the life-history strategy of a species. The earliest reference to age estimation of fishes dates back to the seventeenth century (Jackson 2007). Since then ageing techniques have advanced and, according to Hilborn and Walters (1992), age information is the most valuable of the life history variables in the study of fisheries biology today. Fish are commonly aged by counting growth increments on calcified hard structures (Campana 2001) such as scales (e.g. Regier 1962), vertebrae (e.g. Wintner and Cliff 1999), fin rays (e.g. Beamish 1981), cleithra (e.g. Harrison and Hadley 1979) and opercula (e.g. Donald et al. 1992). However, otoliths have become the dominant and most widely used structures for age determination in fishes (Campana 2001).

The life-history aspects of the southern African sparid fauna have been studied extensively and have revealed that fish in this family are generally slow growing, long-lived and late maturing (Coetzee and Baird 1981, Buxton and Clarke 1986, 1989, 1991, Smale and Punt 1991, Buxton and Clarke 1992, Bennett 1993, Brouwer and Griffiths 2005). Slow growth and high longevity render a species particularly vulnerable to overexploitation, even at low levels of fishing (Acosta and Appeldoorn 1992, Chale-Matsau et al. 2001). Along with late maturity, it is believed that these characters led to the economic extinction of *Polysteganus undulosus*, an endemic South African sparid. *Diplodus capensis* displays the typical sparid life-history characteristics, with ages of over 20 years having been recorded for this species in South African waters (Mann and Buxton 1997). Joubert (1981b) found the length at 50% maturity to be between 150 - 160mm FL in the subtropical waters of KZN, while Mann and Buxton (1998) reported a length of 225mm FL (4 yrs) in the warm temperate Tsitsikamma National Park (TNP).

Research on the effects of exploitation on fish populations involves either looking for changes over time and relating them to fishing pressure, or comparing exploited and unexploited areas (Götz et al. 2008b). The problem with the first approach is that ecological systems change naturally over time and therefore the observed life-history changes may not be solely explained by fishing (Götz et al. 2008b). The problem with the second approach is that replication, control and randomization are very difficult to attain (Hilborn and Ludwig 1993).

Variation in life-history characteristics has been documented in sparids and may occur as adaptations to different environmental conditions or as a result of exploitation (Tunley et al. 2009, Attwood et al. 2010). Most reef associated sparids display highly resident behaviour (Bennett and Attwood 1991, Attwood and Bennett 1995a, Cowley et al. 2002, Griffiths and Wilke 2002), and therefore they provide a good opportunity to study the effect of exploitation by comparing proximate fished and unfished areas. Three such studies have been conducted on South African sparids. Buxton (1993) compared populations of red roman (*Chrysoblephus laticeps*) and dageraad (*C. cristiceps*) from the protected TNP no-take marine reserve with the surrounding exploited areas. *Chrysoblephus cristiceps* displayed a significantly smaller size-at-sex-change outside the TNP. This species also displayed significantly slower growth outside of the reserve. This result was counter-intuitive, as it would be expected that growth rate would increase in exploited areas due to a reduction in competitive interactions (Buxton 1993). The author conceded that the differences in growth rate could have been as a result of intrinsic differences between the populations. No difference in growth or size at sex change was found for *C. laticeps.* Both species displayed a higher proportion of females in the exploited areas. This is unsurprising since both species are protogynous hermaphrodites (female first), therefore the larger males would be selectively removed from the population by fishing. Götz et al. (2008b) investigated the effect of fishing on the life-history of *C. laticeps* by comparing populations from the Goukamma MPA and surrounding exploited areas. The sampling sites chosen for their comparisons were adjacent and physically similar therefore removing the potential confounding factor that Buxton (1993) encountered (populations were possibly intrinsically different). Götz et al. (2008b) found that *C. laticeps* had a higher density and mean size inside the protected area than outside. Age-at-maturity and age-at-sex-change were lower in the exploited area, which maintained a constant sex ratio between exploited and unexploited areas. A similar comparison was conducted in Langebaan Lagoon for the protogynous hermaphrodite, steentjie (*Spondyliosoma emarginatum*), where fish were compared between protected and exploited areas within the lagoon (Tunley et al. 2009). There were few large and old fish and a sex ratio skewed towards relatively more females in the exploited area compared with the reserve. There were no differences in the size- and age-at-sex-change between the reserve and the exploited area, suggesting that steentjies have not shown a physiological response to exploitation and are unable to compensate for a skewed sex ratio (Tunley et al. 2009).

The southern Angola situation presented an ideal opportunity to study the effects of fishing by comparing exploited and unexploited areas. Sampling for the biological portion of this study was conducted in the Flamingo Lodge area (Figure 1.1). The only fishing activity that takes place at the lodge is recreational and the target species are west coast dusky kob (*Argyrosomus coronus*), garrick (*Lichia amia*) and shad (*Pomatomus saltatrix*) (Potts et al. 2009). The lodge has a catch and release policy and fish are only kept for culinary purposes. Most of the fishing is done with artificial lures which are not suitable for targeting *D. capensis*. If bait is used it is usually put on a large hook (5/0 - 8/0) and if any *D. capensis* are caught as bycatch they are generally released. There is no commercial or subsistence fishing that occurs in the sampling area and therefore fishing mortality is almost certainly zero. In contrast to this, the area adjacent to the town of Namibe has a significant subsistence fishery (Figure 1.1). A concurrent socio-economic study revealed that *D. capensis* makes up 87% of the subsistence fishery's catch; 91% of the fishermen said that effort had increased in the past five years; 92% said that the fish have gotten smaller and they all said that *D. capensis* had declined the most out of all the target species (WM Potts, unpublished data). Subsistence fishers use a handline from the shore with small baited hooks. This method is very effective at targeting *D. capensis* and the CPUE is high (mean = 3.03 fish.fisher.hour^{-1}, min = 1.05 fish.fisher.hour^{-1}, max = 10.76 fish.fisher.hour^{-1}). Fishermen typically walk south from Namibe along the beach, although some have access to motorbikes, and when the tide allows, these fishermen can cover larger distances. However, the southernmost observation of subsistence fishing effort during almost weekly observations in 2005, 2006 and 2008 was made approximately 15km north of the Flamingo Lodge area. The inshore marine habitat from Flamingo Lodge to Namibe is physically similar. This provided an opportunity to use standard, comparable methods to compare the life-history of fish in exploited and unexploited areas with similar habitats and, due to their proximate location, where the fish are likely to come from the same source of recruitment. This comparison is also made possible due to the high degree of residency displayed by *D. capensis* (Bennett and Attwood 1991, Attwood and Bennett 1995a, Cowley et al. 2002, Watt-Pringle 2009) resulting in little immigration/emigration between areas.

It was hypothesised that the size and age structure of the exploited population would be truncated, the size- and age-at-50% maturity of these fish would be reduced, and that the fish in the exploited area would grow faster and have a higher condition factor than those in the unexploited area.

Material and Methods

Sampling

Fish were collected from the unexploited area (Figure 1.1) between April 2008 and March 2009 and from the exploited area in May, June and December 2009. While fish were predominantly captured using rod and line (hook gape = 10 - 11mm) in the unexploited area, fish in the exploited area were purchased from the subsistence fishermen while they were fishing on the beach (hook gape 6 - 7.5mm). Each fish sampled was weighed (0.1g), measured (mm, FL), sexed (juvenile, male, female, intersex) and the saggital otoliths removed and stored for age estimation. If the entire catch of each fisherman was not available for purchase, the remainder of the catch was measured in order to maintain a representative size sample. Smaller fish (< 120mm FL) were captured using a cast net in both areas. Additional length data for the subsistence fishers catches were obtained during concurrent quarterly roving creel surveys.

Data analysis

Length-weight relationships and condition factor

The relationship between fork length (FL) and total length (TL) was assessed using a linear regression of the form:

$$FL = mTL + c$$

where m and c are the slope and intercept coefficients, respectively. The relationship between FL and weight (Wt) was estimated using the exponential relationship of the form:

$$Wt = \alpha FL^{\beta}$$

where α and β are the model parameters to be estimated.

The length-weight relationships of fish from the exploited and unexploited areas were converted to log-scale, such that:

$$\ln(Wt) = \ln(\alpha) + \beta \ln(FL)$$

and compared using analysis of covariance (ANCOVA) at a 95% confidence level.

The condition factor (CF) (Weatherly 1972) was calculated using the equation:

$$CF = Wt / FL^3$$

After testing for normality and equality of variance, a suitable *t*-test was used to compare the mean CF between the unexploited and exploited areas.

Otolith preparation and reading

A pilot study was conducted in order to identify the most suitable method of preparing otoliths for growth zone counts. Five methods of preparation were investigated; whole otoliths, longitudinal sections, burned longitudinal sections, transverse sections, and transverse burned sections. The otolith pairs of 30 fish were used for this investigation. Firstly, otoliths were read whole, however, this immediately proved unsatisfactory as growth zones were only identifiable towards the outer edge of the otolith. Subsequently, 15 pairs were used to investigate longitudinal sections and 15 for transverse sections. Of each group of 15, one otolith of each pair was lightly burned over a methylated spirits flame until golden brown. Otoliths were set in clear casting resin and sectioned at 0.4mm using a twin-blade diamond edged saw. Each otolith was assigned a random number and the number of visible opaque zones was counted on two occasions by the author and once by an independent reader using a low powered dissecting microscope under transmitted light. Each otolith was assigned a readability index from zero to five, with zero being unreadable and five being easily readable. The ease of growth zone interpretation was assessed by averaging the readability index across all readings for a particular method. Readability values were only recorded for otoliths of fish from the unexploited area.

The consistency of growth zone counts was assessed by calculating an index of average percent error (IAPE) (Beamish and Fournier 1981) as:

$$IAPE = \frac{1}{n}\sum_{j=1}^{n}\left[\frac{1}{R}\sum_{i=1}^{R}\frac{\left|X_{ij} - \overline{X}_{j}\right|}{\overline{X}_{j}}\right] \times 100$$

where *n* fish are aged, *R* is the number of times each fish *j* is aged, *Xij* is the *i*th age determined for the *j*th fish and *X j* is the average age calculated for the *j*th fish.

The preparation method that yielded the highest average readability index and lowest IAPE was considered the most appropriate for *D. capensis* otoliths and was subsequently used for the entire sample. Otoliths were then read three times by the author, the first of which was rejected, and once by an independent reader. If two of the three counts agreed, that count was accepted as the age of that fish. If three counts of a section resulted in a succession of numbers, e.g. 5, 6 and 7, the middle count was accepted as the age of that fish. A large number of growth zones were evident on the otoliths of larger fish. Such otoliths have a larger chance of having inconclusive counts, therefore, for otoliths that had three counts over 14, the reading was accepted if all three counts differed by two or less (e.g. 15, 16 and 18 was accepted as 16.3). If two of the readings were in excess of 20 and differed by two counts, the average of the two closest readings was accepted (e.g. 21, 23 and 27 was accepted as 22). Otolith readability and the consistency of readings were assessed as above.

Validation of growth zone deposition rate

Intramuscular application of an oxytetracycline (OTC) marker was used for age validation in this study, as this method has been suggested for validating the periodicity of growth zone formation in the otoliths of *D. capensis* and other sparids (Lang and Buxton 1993, Potts and Cowley 2005). Prior to the initiation of the biological sampling period of this study, a total of 255 *D. capensis* were captured and injected with High-Tet 120 oxytetracycline hydrochloride (± 0.1ml. kg^{-1}) and, before release, tagged with Hallprint plastic dart (model PDL) or T-bar anchor (model TBA-2) tags (depending on fish size). Recaptured fish were sacrificed, measured and their saggital otoliths removed and stored in envelopes in the dark to minimize deterioration of OTC fluorescence. Otoliths were prepared for examination as described above. Otoliths were photographed using transmitted white light and ultra violet light in order to view the location of the OTC band in relation to the opaque growth zones. The number of visible growth zones between the OTC band and the otolith margin was counted and related to the time spent at liberty.

Growth model

The growth of *D. capensis* was estimated by fitting the three parameter von Bertalanffy growth function (VBGF) (Ricker 1975) to observed length-at-age data. An age correction value was applied to age estimates using the 1st of July as a theoretical birth date based on the observed maximum in reproductive activity (see Chapter 4). The VBGF is described by the equation:

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

where $L_{(t)}$ is the predicted length-at-age t, L_{∞} is the theoretical asymptotic length, K is the growth co-efficient and t_0 is the age-at-zero length. Model parameters were estimated through a downhill simplex search routine (Nelder and Mead 1965). Variability of the parameter estimates were calculated using a parametric bootstrapping procedure (Efron 1982) with 1000 iterations and 95% confidence intervals were constructed from the bootstrap data using the percentile method (Buckland 1984). A likelihood ratio test (LRT) was used to compare growth between males and females. Because of the lack of mature individuals smaller than the size at 50% maturity, juveniles were included in both the male and female curves in order to maintain biological realism. This presented a problem in the analysis, as the same juvenile individuals were represented in both growth curves, resulting in the pooled model having a lower overall sample size than the sum of the two reduced models. In order to overcome this problem the residuals (difference in predicted and observed length) and the sample size of the juveniles were halved in the reduced models. Observed mean length at age data for five year age classes were compared for males and females using a student's *t*-test. All differences were considered statistically significant at $p < 0.05$. Age and length frequency analysis was used to corroborate any observed differences in growth. An age-length key was constructed for both sexes in order to convert the length frequency into an age frequency. The growth of *D. capensis* in the exploited and unexploited areas was compared using an LRT.

Length and age at sexual maturity

Length-at-50% maturity (L_{50}) was calculated by fitting a logistic ogive to the observed proportion of mature fish per 10mm length class. The two parameter logistic ogive is described by the equation:

$$P(L) = \frac{1}{1 + e^{-(L - L_{50})/\delta}}$$

where *P(L)* is the proportion of mature fish in length class *L*, L_{50} is the length-at-50% maturity and δ is the width of the ogive curve. Age-at-50% maturity was calculated by fitting a logistic ogive to the observed proportion of mature fish per one year age class. Due to the relatedness of the male and female samples (juveniles were represented in both ogives) and the lack of a suitable sample size, no statistical test was conducted to test for differences in length- and age-at-50% maturity between the sexes. An LRT was used to test for differences in length- and age-at-50% maturity between the exploited and unexploited areas.

Hook selectivity

In order to facilitate a size and age frequency comparison between the exploited and unexploited areas, it was necessary to correct for selectivity because the hook size used in the subsistence fishery was smaller than that used by the research anglers in the unexploited area. It was assumed that 100% selection was reached at the peak of the length frequency distribution and selectivity was modelled by fitting a logistic ogive to the cumulative length frequency. This was achieved by initially multiplying the exploited area length frequency by the inverse of its own selection ogive to simulate what would have been caught in this area if the effect of hook selectivity was removed. Then in order to simulate what would have been caught by the researchers in the exploited area, the length frequency was multiplied by the selection ogive of the unexploited area. The resulting "corrected" length frequencies were used to generate age frequencies.

Population structure

The population structure of *D. capensis* was investigated using length and age frequencies and adult sex ratios. To avoid selectivity bias, biological samples were only used for the exploited area length frequency if the total catch of each fisherman was purchased. This information was supplemented with the lengths recorded from the creel surveys. Length-at-age data was converted to an age frequency using an age length key (Butterworth et al. 1989).

Results

Length and weight relationships

The relationship between FL and TL was described linearly by the equation TL = 1.142 FL + 3.452 (R^2 = 0.998). Using observations from their overlapping length ranges (94 - 299mm FL), there was no significant difference in the length-weight relationships between the exploited and unexploited areas (ANCOVA, p > 0.05) (Table 5.1). The exponential relationship for the pooled sample was described by the equation $Wt = 0.0000108\ FL^{3.15}$ (Figure 5.1).

Table 5.1: Parameters of the length-weight relationship for *Diplodus capensis* in southern Angola.

	α	β	R^2
Unexploited area	0.0000131	3.115	0.995
Exploited area	0.0000171	3.046	0.976
Pooled sample	0.0000108	3.153	0.994

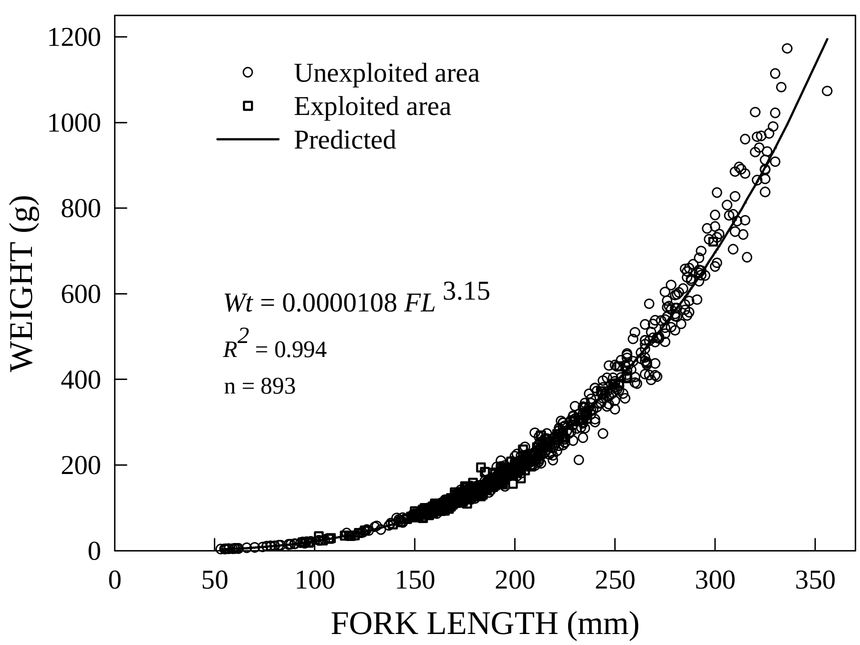

Figure 5.1: Length-weight relationship for *Diplodus capensis* sampled from an exploited and unexploited area(pooled data) in southern Angola.

Condition factor

The mean CF for fish of the same size range (100 - 250mm) was calculated as 0.0240 and 0.0239 for the exploited and unexploited areas, respectively. The CF data were normally distributed (p = 0.072 and p = 0.092 unexploited and exploited, respectively), however their variances were not comparable ($p < 0.05$). Therefore a Welch's t - test was used to compare the mean CF values from the two areas and it was concluded that they are not statistically different (p = 0.186).

Otolith reading

A total of 733 otolith pairs were used for age analysis in this study of which 531 were from the unexploited area and 202 from the exploited area. Although growth zones were apparent on prepared otoliths of all methods investigated, unburned transverse sections were found to be the most suitable method of preparing otoliths for reading in this study (Figure 5.2). This method had the highest readability index and lowest IAPE (Table 5.2).

Table 5.2: Average readability (AR) indices and index of average percent error (IAPE) for four methods of sectioned sagittal otolith preparation of *Diplodus capensis* southern Angola.

Method of preparation	AR ± SD	IAPE
Burned longitudinal sections	1.36 ± 1.19	19.71%
Unburned longitudinal sections	1.36 ± 1.09	13.72%
Burned transverse sections	2.74 ± 1.06	13.68%
Unburned transverse sections	3.18 ± 0.81	11.70%

Age estimates were accepted for 357 (49%) of the 733 fish investigated and the IAPE for the entire sample was 15.1%. Readability values were only recorded for otoliths of fish from the unexploited area. High readability values corresponded to lower IAPE's (Table 5.3). The otoliths of larger and thus older fish were more readable and had lower IAPE's than those of smaller fish (Figure 5.3).

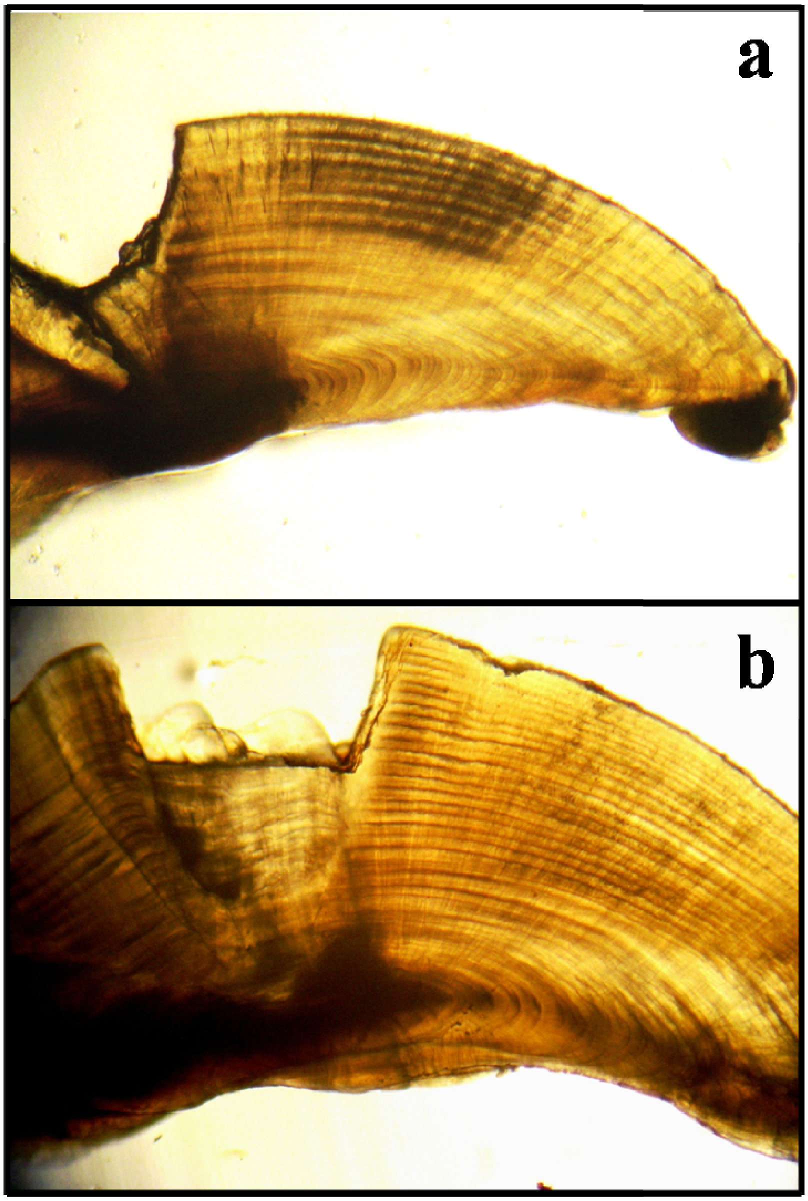

Figure 5.2: Transverse sections of *Diplodus capensis* sagittal otoliths viewed under transmitted light indicating a 12 year old (a) and 27 year old (b) individual.

Table 5.3: Index of average percent error (IAPE) and average fork length (mm) of *Diplodus capensis* sectioned sagittal otoliths assigned certain readability indices. The 0-2 group was pooled because of low sample sizes.

Readability index	Index of avg. % error	Avg. FL (mm)	Sample size
0-2	30.2	155.0	16
2-3	19.7	188.6	91
3-4	14.7	212.3	303
4-5	11.7	239.7	120

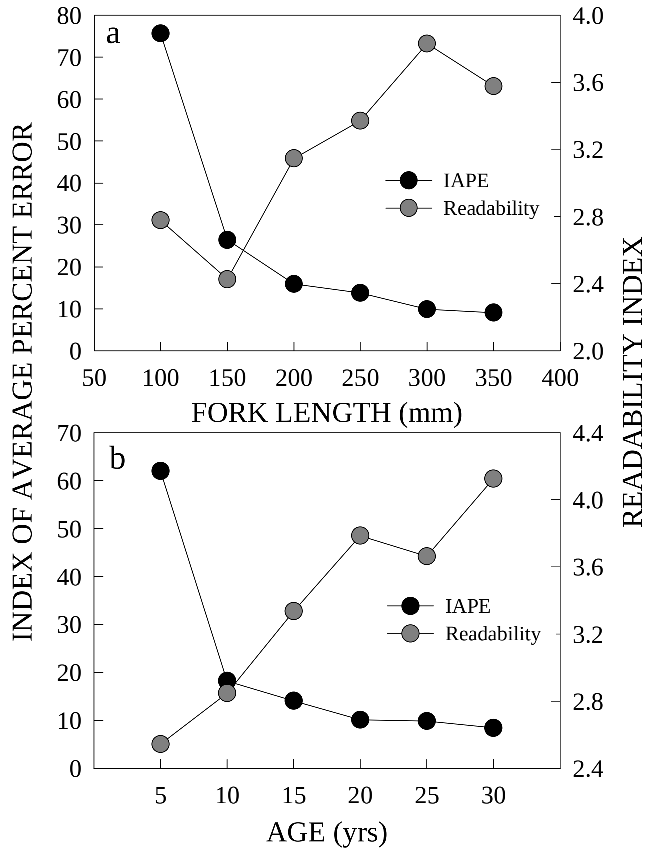

Figure 5.3: Relationship between fork length (a) and age (b) and the index of average percent error (IAPE) and average readability index of sectioned saggital otoliths of *Diplodus capensis* from southern Angola.

Validation of growth zone deposition rate

Of the 255 individuals tagged and injected with OTC, four (1.6%) were recaptured (Table 5.4). The time between first capture and recapture ranged between four and 747 days and only one individual had been at liberty for more than one year. The otoliths of this individual were examined to investigate the number of growth zones that had been deposited on the otolith between the time of tagging and recapture. A dull OTC band was visible in the otolith when viewed under ultra violet light (Figure 5.4). Inspection of the otolith through transmitted white light revealed that two opaque zones were present between the OTC band and the otolith margin, confirming that opaque zones are equivalent to annuli in this species in southern Angola.

Table 5.4: Size at first capture, recapture and days at liberty of fish injected with oxytetracycline (OTC) in southern Angola.

Date of OTC injection	Size at first capture (mm FL)	Date of recapture	Size at recapture (mm FL)	Days at liberty
26 Nov 2007	238	1 Dec 2007	238	4
21 Mar 2008	184	12 April 2008	183	21
1 Dec 2007	193	8 Jun 2008	194	188
30 Nov 2007	310	18 Dec 2009	326	747

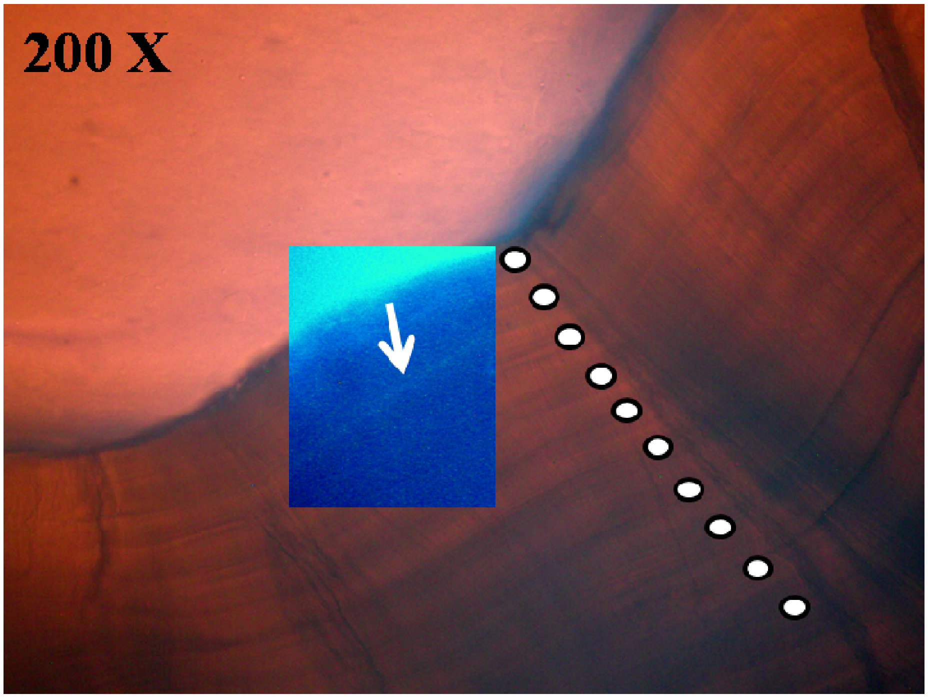

Figure 5.4: Transverse section of the peripheral region of an otolith from a 326mm FL *Diplodus capensis* that was tagged and injected with oxytetracycline (OTC) and recaptured after 747 days (2.05 yrs) at liberty. The main picture is viewed through transmitted white light, while the insert is a portion of the otolith viewed under reflected ultra violet light to enhance the fluorescent OTC band (arrow). Dots indicate opaque zones.

Growth

Females grew significantly faster (LRT, d.f. 3, $p < 0.05$) than males in the unexploited area, but the growth curves were similar (LRT, d.f. 3, $p = 0.346$) for males and females in the exploited area (Figure 5.5). Males had a lower mean length-at-age than females in the unexploited area, although these differences were not statistically significant (student's t-test, $p > 0.05$) (Table 5.6). The oldest female and male in the unexploited area was 31 years (356mm FL) and 24 years (307mm FL), respectively. In contrast, the oldest female and male in the exploited area was 17 years (299mm FL) and 15 years (243mm FL), respectively.

There was no significant difference in the growth of males or females between the two areas (LRT, d.f. 3, p = 0.308 and p = 0.378 females and males, respectively). Point estimates and summary statistics for the Von Bertalanffy growth function parameters derived from a parametric bootstrap procedure with 1000 iterations are presented in Table 5.6.

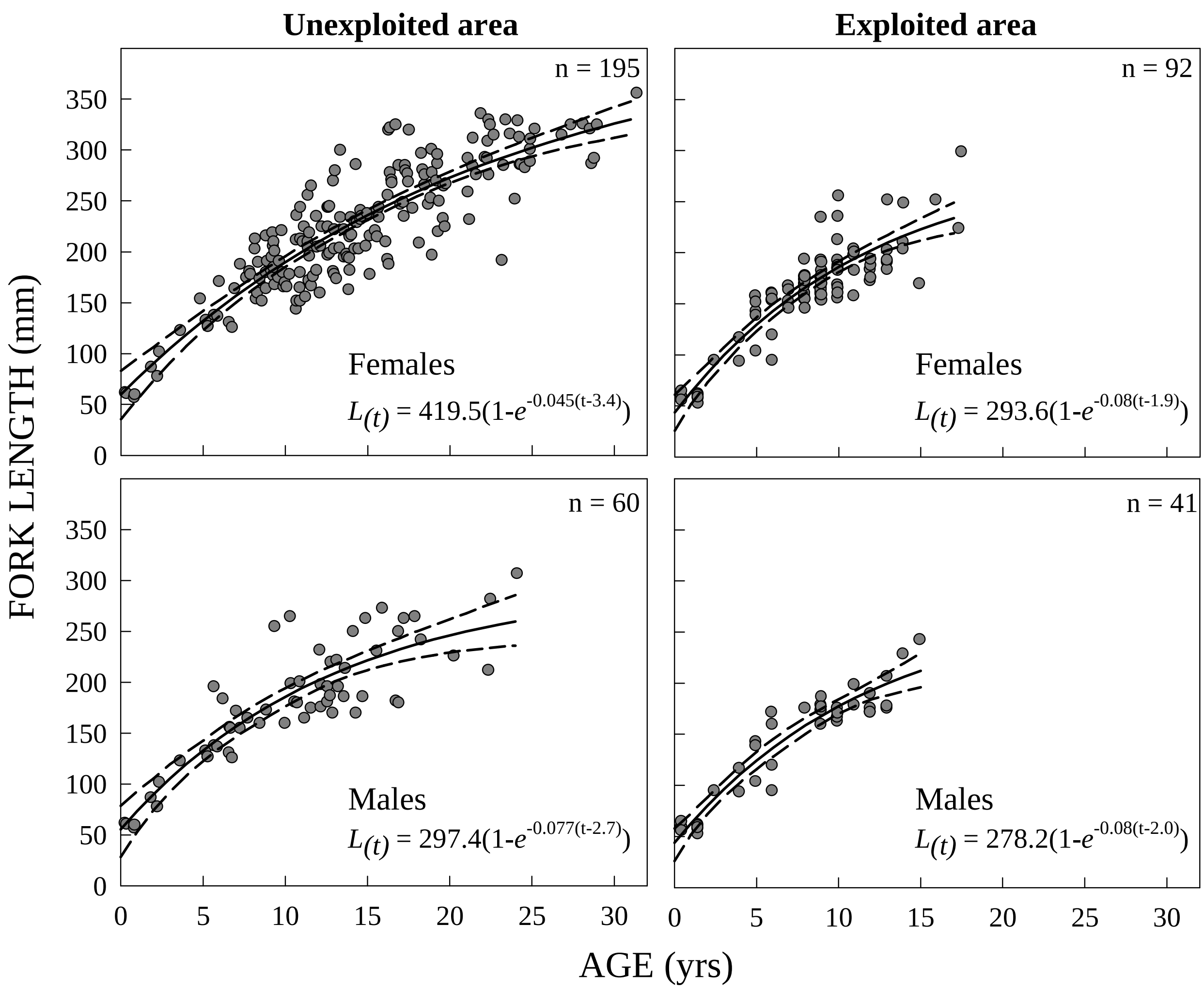

Figure 5.5: Von Bertalanffy growth function fitted to observed length-at-age data for female (top) and male (bottom) *Diplodus capensis* sampled from an unexploited (left) and exploited area (right) in southern Angola. Dotted lines represent 95% confidence intervals.

Table 5.5: Observed mean length (mm FL) at age (± S.D.) for female and male *Diplodus capensis* in five year age classes sampled from an unexploited and exploited area in southern Angola.

	Unexploited area					**Exploited area**				
Age class	Females		Males		*t* - test	Females		Males		*t* - test
(years)	Mean ± S.D.	*n*	Mean ± S.D.	*n*	*p* - value	Mean ± S.D.	*n*	Mean ± S.D.	*n*	*p* - value
0 - 4	154.0	1	-	-	-	155.0 ± 4.24	2	-	-	-
5 - 9	184.4 ± 19.0	32	175.5 ± 29.4	11	0.257	173.6 ± 22.5	51	172.0 ± 7.8	13	0.800
10 - 14	209.8 ± 33.9	66	200.6 ± 29.2	23	0.249	195.6 ± 23.5	19	192.8 ± 24.3	11	0.762
15 - 19	256.3 ± 36.8	46	235.75 ± 36.3	8	0.151	-	-	-	-	-
20 - 24	292.7 ± 32.2	27	256.75 ± 45.1	4	0.056	-	-	-	-	-
25 - 29	314.0 ± 15.6	8	-	-	-	-	-	-	-	-
30 - 34	356.0	1	-	-	-	-	-	-	-	-

Table 5.6: Point estimates and summary statistics for the von Bertalanffy growth function parameters for female and male *Diplodus capensis* sampled from an unexploited and exploited area in southern Angola.

			Summary statistics					
	Parameter	Point estimate	Mean	Coefficient of variation	Standard error	Lower-upper, 95% confidence intervals	Minimum	Maximum
Unexploited area								
Females	L_∞(mm FL)	419.51	429.48	12.22%	52.46	359.59 - 548.74	33\6	895.15
(n = 195)	K (year^{-1})	0.045	0.045	21.08%	0.010	0.027 - 0.063	0.013	0.079
	t_0 (years)	-3.43	-3.48	30.84%	1.07	-5.70 - -1.70	-9.08	-0.73
Males	L_∞(mm FL)	297.38	310.81	21.25%	66.04	244.82 - 463.80	232.46	1209.13
(n = 60)	K (year^{-1})	0.077	0.079	31.88%	0.025	0.031 - 0.129	0.008	0.201
	t_0 (years)	-2.65	-2.82	44.94%	1.27	-5.71 - -0.98	-10.42	0.35
Exploited area								
Females	L_∞(mm FL)	293.55	302.61	15.73%	47.61	241.76 - 420.33	219.92	791.63
(n = 92)	K (year^{-1})	0.084	0.086	26.26%	0.022	0.045 - 0.130	0.018	0.171
	t_0 (years)	-1.92	-1.98	33.70%	0.67	-3.48 - -0.85	-4.78	-0.45
Males	L_∞(mm FL)	278.21	303.43	36.43%	110.53	219.16 - 555.64	205.68	1628.05
(n = 60)	K (year^{-1})	0.084	0.086	35.01%	0.030	0.027 - 0.147	0.008	0.183
	t_0 (years)	-2.03	-2.09	33.85%	0.71	-3.75 - -0.99	-5.21	-0.56

Size and age at sexual maturity

The length and age-at-50% maturity was similar for both sexes in both the unexploited and exploited areas. When the sexes were combined, the length at 50% maturity was calculated as 149.5mm FL in both areas (Figure 5.6). The age at 50% maturity was calculated as 5.4 years and 5.3 years for the unexploited and exploited areas, respectively (Figure 5.6). The length at maturity ogive was narrow with all fish maturing within 20mm. The length and age at maturity was not significantly different between the exploited and unexploited areas (LRT, d.f. 2, $p > 0.05$).

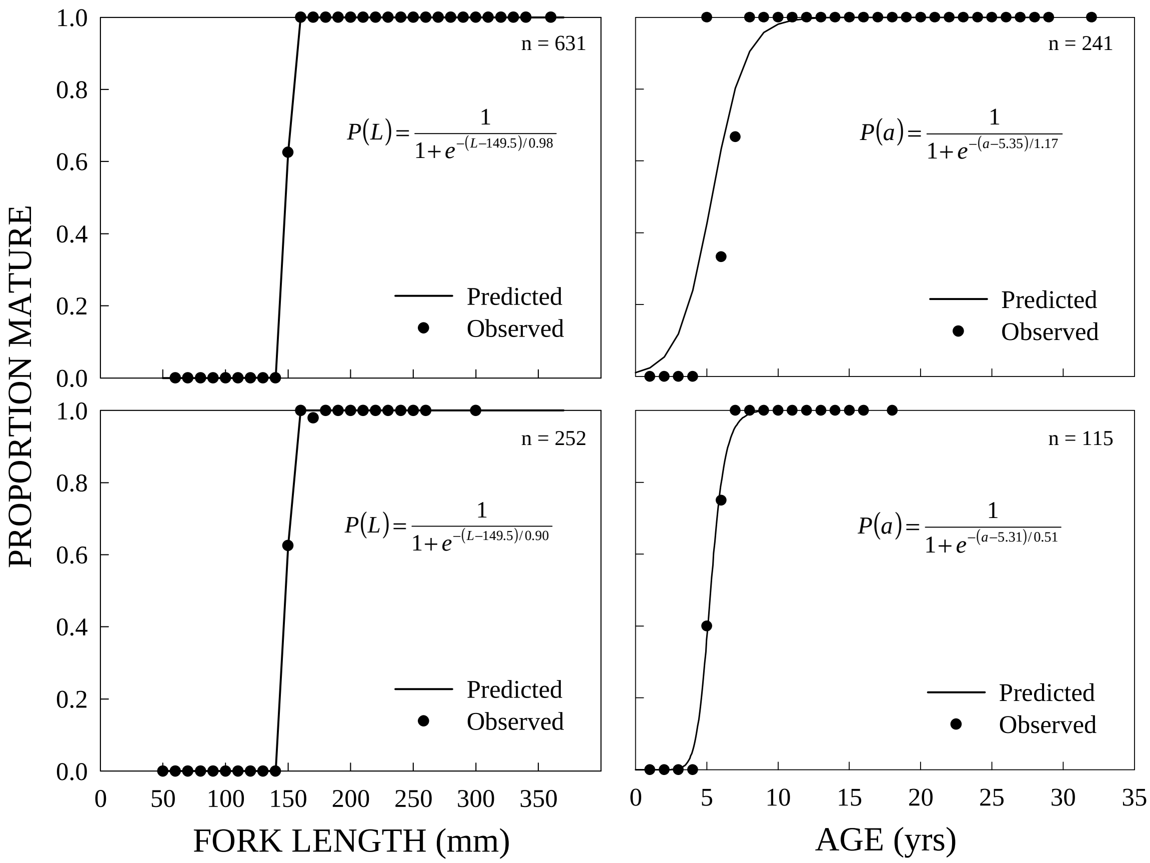

Figure 5.6: Logistic ogives fitted to the observed proportion of mature individual in 10mm length classes (left) and one year age classes (right) for *Diplodus capensis* sampled from an unexploited (top) and exploited (bottom) area in southern Angola.

Table 5.7: A summary of life-history parameters obtained for female and male *Diplodus capensis* sampled from unexploited and exploited areas in southern Angola.

Life-history parameter	Unexploited area	Exploited area
Age and Growth		
L_∞ (female)	419.5 mm FL	293.6 mm FL
L_∞ (male)	297.4 mm FL	278.2 mm FL
K (female)	0.045 y^{-1}	0.084 y^{-1}
K (male)	0.077 y^{-1}	0.084 y^{-1}
t_0 (female)	-3.4 yrs	-1.9 yrs
t_0 (male)	-2.7 yrs	-2.0 yrs
max. age (female)	31 yrs	17 yrs
max. age (male)	24 yrs	15 yrs
Reproduction		
Length at 50% maturity (all)	149.5 mm FL	149.5 mm FL
Age at 50% maturity (all)	5.4 yrs	5.3 yrs

Hook selectivity

The length at 50% selection for the subsistence fishery (hook gape = 6 - 7.5mm) and the research fishing gear (hook gape = 10 - 11mm) was 169mm and 186mm FL, respectively (Figures 5.7a & b). After applying a correction factor to the subsistence fishery catches, the resulting length frequency was directly comparable with the unexploited one (Figure 5.7c).

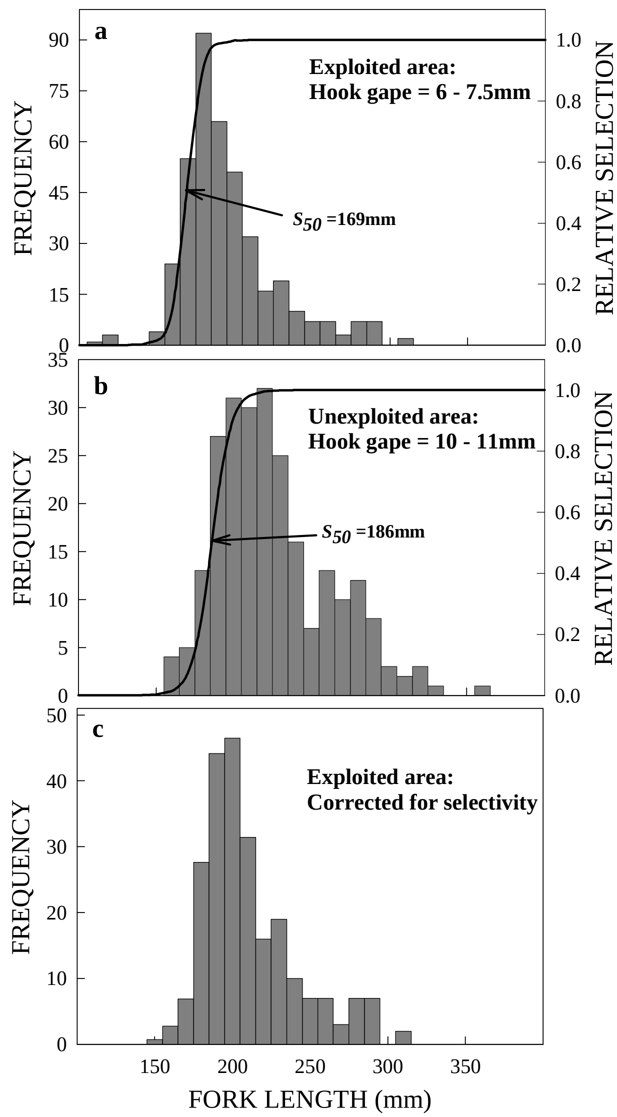

Figure 5.7: Observed length frequencies and selectivity ogives for *Diplodus capensis* from the exploited (a) and unexploited area (b) in southern Angola, and the resulting length frequency for the exploited area after correcting for selectivity bias (c).

Population structure

Females dominated the larger length classes and older age classes in the unexploited area (Figures 5.8 and 5.9). In contrast, the length and age frequency distributions were similar for males and females in the exploited area. The absence of large and old individuals of both sexes in the exploited area resulted in a severely truncated length and age frequency distribution.

The sex ratio (M: F) was calculated as 1: 4.7 and 1: 2.2 in the unexploited and exploited area, respectively. With the exception of the smallest length class in the exploited area, the number of females relative to males increased with increasing fish size (Figure 5.10).

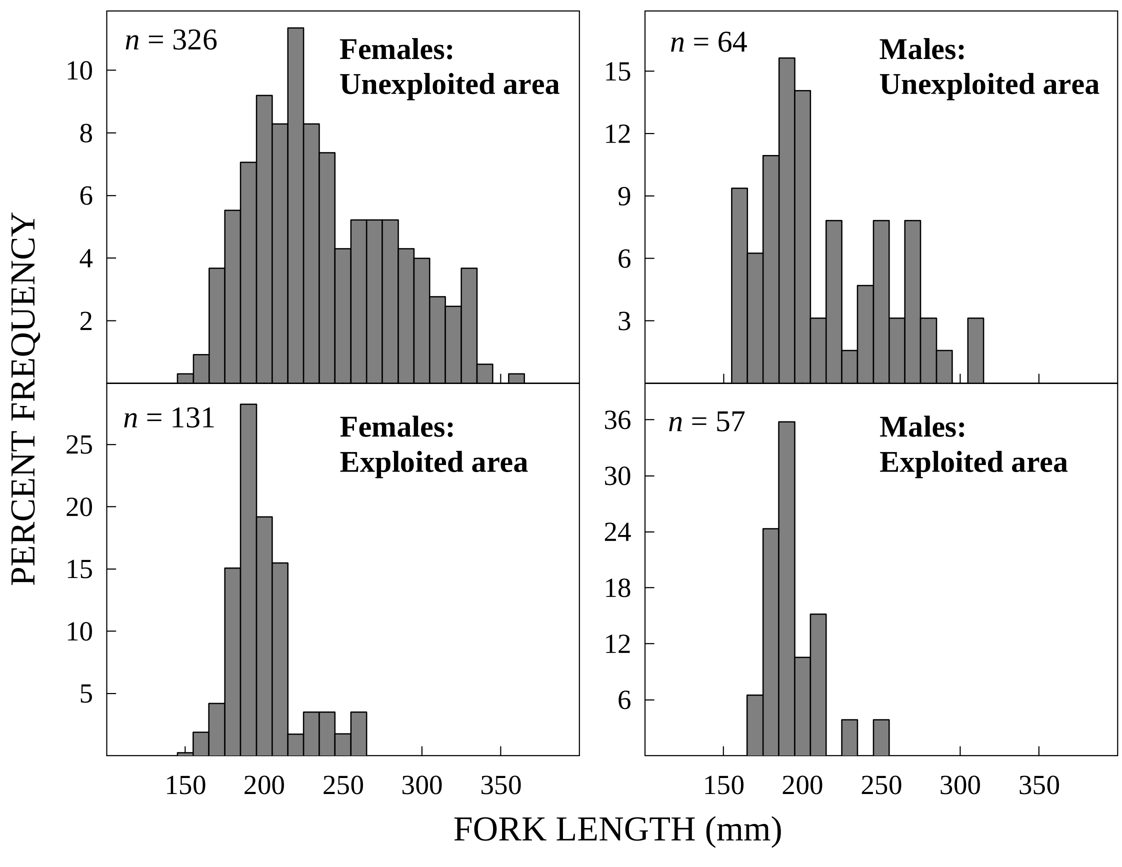

Figure 5.8: Comparative size frequency distributions for female (left) and male (right) *Diplodus capensis* in an unexploited (top) and exploited (bottom) area of southern Angola.

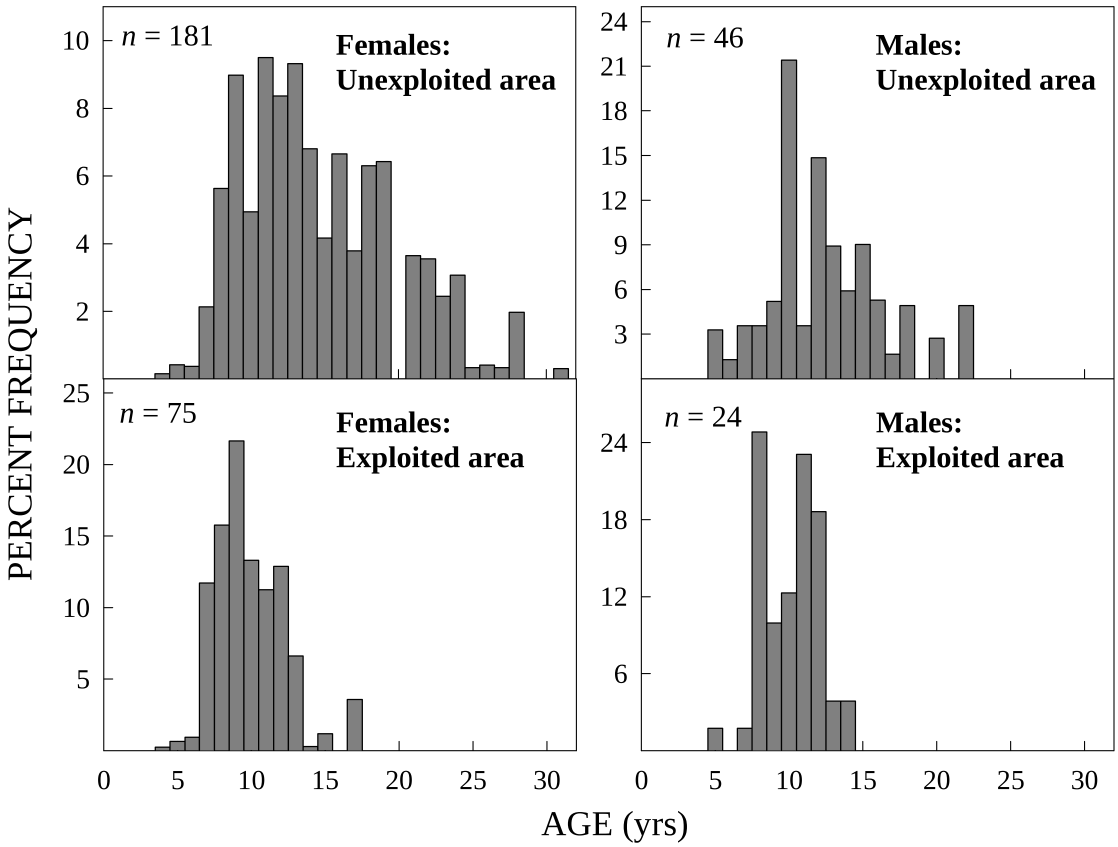

Figure 5.9: Comparative age frequency distributions for female (left) and male (right) *Diplodus capensis* in an unexploited (top) and exploited (bottom) area of southern Angola.

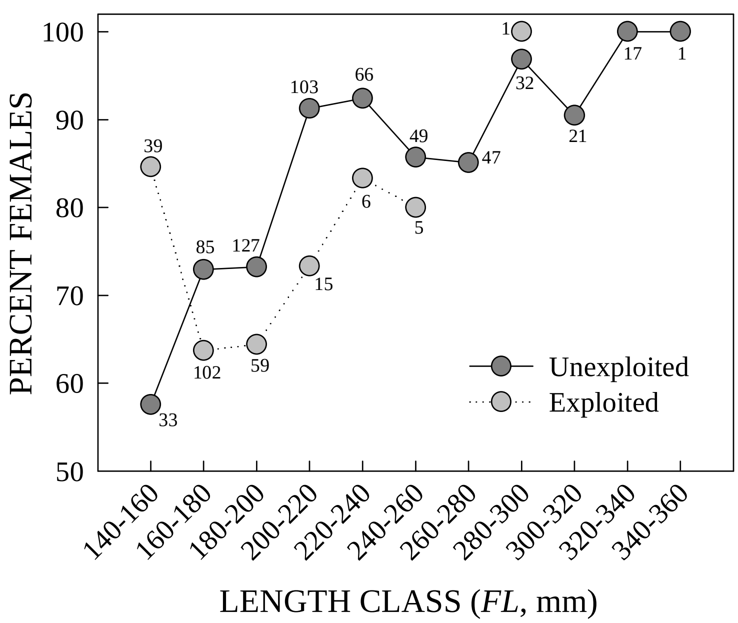

Figure 5.10: Relationship between the percentage of female *Diplodus capensis* and fish length (in 20mm length classes) in an exploited and unexploited area of southern Angola. Sample sizes are indicated next to each data point.

Discussion

The results of this study show that *Diplodus capensis* is a slow-growing, long lived species in southern Angola capable of reaching ages in excess of 30 years. Mann and Buxton (1997) reported a maximum age of 21 years for this species in South Africa and studies on other sparids have shown that slow growth and high longevity is normal in this family (Coetzee and Baird 1981, Buxton and Clarke 1986, 1989, 1991, Smale and Punt 1991, Buxton and Clarke 1992, Bennett 1993, Chale-Matsau et al. 2001, Brouwer and Griffiths 2004).

Unburned sectioned otoliths were easiest to read and produced the most consistent age estimations for *D. capensis*, however, the consistency of otolith readings was relatively poor for this study (IAPE = 15.4%). Higher IAPE's can be expected for long-lived species and it is important to note that the IAPE is a measure of reproducibility and not accuracy (Campana 2001). Nevertheless readings can be consistently wrong, which prompted a strict age acceptance protocol that lead to the rejection of over half (51%) of the otoliths examined in this study. The otoliths of small fish were more difficult to read and had less consistent readings than those of larger fish. The daily growth increments are generally wider and less defined in small fishes because their growth rate is faster (Francis et al. 1992, Mann-Lang and Buxton 1996). This caused the annual growth zones of small fish to be wide and less distinct, resulting in difficulty when determining the start and end of the opaque zones. Differential size-specific growth rates may also lead to growth zone "stacking", which has been observed in the otoliths of old sparid fish (Buxton and Clarke 1992, Mann-Lang and Buxton 1996). However, the outer growth zones of larger fish, in contrast to smaller fish, were thin, closely spaced and easily discernable, suggesting that there was no zone "stacking".

Of critical importance in a life-history study of this nature is the validation of growth zone deposition rate (Beamish and McFarlane 1983, Campana 2001). Mann and Buxton (1997) made use of an indirect validation method, the marginal zone analysis. However, they concluded that this method provided only weak evidence that one opaque and one hyaline zone are formed annually in this species and used information presented in other South African sparid studies to corroborate their findings. The appearance of opaque and translucent looking zones at different regions on the margin of a single otolith in the current study suggested that, as in the study of Mann and Buxton (1997), this is an unsuitable validation method for this species. The crenulated appearance of the otolith margin in some otoliths may also have contributed to the inadequacy of this method (Smale and Punt 1991). Lang and Buxton (1993) subsequently made use of a direct validation technique (OTC injection) to investigate the periodicity of daily and annual growth zone deposition rates in juvenile (< 2 years) *D. capensis*. They concluded that one opaque and one hyaline zone were formed per year. In the present study, age was validated directly (OTC injection) using a large mature individual and, in support of the study of Lang and Buxton (1993), it was concluded that an opaque and hyaline zone represents one year in *D. capensis*.

Female *D. capensis* in southern Angola grew significantly faster and reached older ages than males. Although the VBGF parameters were relatively poorly estimated and the male sample size small, the truncated male length frequency distribution is strong evidence supporting a hypothesis of faster female growth in this species. Sexual growth dimorphism, where females reach larger sizes than males, is not uncommon in teleosts (Lozán 1992, Fontaine et al. 1997, Imsland et al. 1997, Pongthana et al. 1999, Saillant et al. 2001). A higher potential for growth in one sex may be maintained by mechanisms of natural selection (Saillant et al. 2001). For an asynchronous group spawning species such as *D. capensis* (see Chapter 4), it would be advantageous for females to outlive males and attain larger sizes than males, as males do not limit the population's reproductive output. Furthermore, since fecundity usually increases exponentially with increasing fish size (Sadovy 1996, Brouwer and Griffiths 2005, Jakobsen et al. 2009), larger females would have the ability to produce more offspring and increase their reproductive success.

Based on the results from this study, this species can be classified as a periodic strategist, according to the W&R model. The periodic life-history strategy typically evolves in seasonal environments, where selection favours the production of large numbers of small offspring in pulses that coincide with predictable periods of conditions favourable for growth and survival of juveniles (Boyce 1979, Winemiller 1992). Each endpoint strategy of the W&R model evolves as a result of life-history trade-offs which are optimised by specific environmental conditions. Periodic strategists are characterised by long generation times, moderate reproductive effort, relatively large body size, high batch fecundity, and low investment per offspring. Such species maximize age-specific fecundity at the expense of optimising turnover time and juvenile survivorship (Winemiller and Rose 1992). However, fishes with high longevity, slow growth and late reproduction are considered susceptible to fishing pressure. According to the guidelines by the FAO (2001), which use life-history traits to classify finfish species by productivity, the relatively slow growth rate, late sexual maturity and old maximum age of *D. capensis* places it into the low productivity category. Consequently, the effects of exploitation on this species are likely to be pronounced, even at relatively low levels of fishing pressure.

The effects of fishing were clearly illustrated in the exploited area where there was an absence of large and old fish. While females dominated the larger size and older age classes in the unexploited area, the size and age distribution of the sexes was more equitable in the exploited area. This trend was unsurprising as fishing gear is usually selective and typically targets the larger and older individuals in the population (Law 2000). Exploited populations therefore often have truncated size and age structures (Goñi 1998, Hutchings 2005). In the case of *D. capensis* in Angola, the dominance of large females in the unexploited area, when compared with the exploited one, provides strong evidence for the selectivity of the fishing gear. Similar comparisons of *Diplodus spp.* from exploited and unexploited areas have been conducted in the Mediterranean Sea. Bell (1983) found *D. sargus* and *D. vulgaris* to be more abundant and larger in the Banyuls-Cerbère marine reserve than in the surrounding unprotected areas. In the same reserve, Lenfant (2003) found a similar pattern but also concluded that there were a greater number of older fish in the protected area. Genetic analyses revealed that the “reserve effect” was purely a demographic one because there was not sufficient genetic differentiation between the sites to account for them being different populations. The sites investigated by Lenfant (2003) were five kilometres apart and the genetic similarity means that gene flow through adult migration and/or exportation of eggs and larvae is sufficient to maintain the same allele frequencies between the marine reserve and the unprotected site. Similarly, the sampling sites in the present study were relatively close to one another (roughly 15km apart). Therefore, based on the proximity of the sites, the homogeneity of the habitat between them, and the likelihood that fish from the two areas originated from the same recruitment source, it is likely that the difference in size and age structure is purely a demographic effect and not a consequence of genetic variation.

A major consequence of these demographic effects is the different rate of mortality between individuals in the exploited and unexploited areas. This places selection pressures on certain life-history traits (Heino and Godo 2002). Male and female longevity was greatly reduced from 31 and 24 years (females and males, respectively) in the unexploited area to 17 and 15 years in the exploited area. With the reduced proportion of larger individuals, it is also likely that there is an overall reduction in fish density in the exploited area. Density-dependant growth refers to a situation where the feeding rate of an individual is reduced by the presence of other members of the same population (Rose et al. 2001), and since competition is one of the primary factors driving population regulation (Hixon et al. 2002), it is intuitive that a reduction in fish density will cause an increase in growth rate. There is a distinct shift from herbivory to carnivory in *D. capensis* (Chapter 3). Adults predominantly feed on macroinvertebrates such as barnacles and mussels, while smaller fishes feed predominantly on algae. It is likely that food competition increases down the food web. Thus, reduced competition amongst larger individuals is likely to have an effect on their growth rate. However, in the current study there was no significant difference in the growth rate between fish from the exploited and unexploited areas. This is in contrast to a number of authors (Bowering and Brodie 1991, Millner and Whiting 1996, Rijnsdorp and van Leeuwen 1996, Helser and Almeida 1997, Heino and Godo 2002) who have observed increased growth rates in exploited fish populations. A possible reason for the similar growth rate of fish in both areas may be that food availability is exceptionally high in this region and it does not have a large mediating effect on growth rate. Although a reduction in growth rate is common in exploited populations, it is not necessarily the rule of thumb. Harris and McGovern (1997) found a reduction in growth rate for red porgy (*Pagrus pagrus*) as a result of fishing. They suggested that this may have occurred as a response to sustained 20-year overexploitation that has selectively removed individuals predisposed towards rapid growth.

Although there was no statistically significant difference in growth between the two areas, the variation in the values of the von Bertalanffy growth curve cannot be ignored. For females, the theoretical asymptotic length (L_∞) was greatly reduced in the exploited area (293.6mm FL and 419.5mm FL exploited and unexploited, respectively) and the brody growth coefficient (K) was almost doubled (0.084 y^{-1} and 0.045 y^{-1} exploited and unexploited, respectively). Although these model parameters vary greatly, when comparing the growth curves and length-at-age for the overlapping age-classes of both areas (0 - 20 yrs), it is clear that the growth rate is very similar in the exploited and unexploited areas. Therefore, it is likely that the differences in growth parameters are an artefact of the reduced longevity rather than a physiological response to exploitation. This highlights the value of obtaining baseline information from a truly unexploited area because fishing can alter our estimates of life-history parameters, even in the absence of a physiological change in growth. This may have an impact on stock assessments, as many stock assessment models use growth characteristics as input parameters (see Chapter 6).

With the selective removal of large females the population fecundity would be greatly reduced in the exploited area. This is not only due to a reduction in the number of females but also the reduction in the mean length of females as fecundity usually increases exponentially with fish size (Sadovy 1996, Brouwer and Griffiths 2005, Jakobsen et al. 2009). To compensate for this loss of reproductive potential, many fishes have reduced their size and/or age at sexual maturity (Rijnsdorp 1993, Coleman et al. 1996, Saborido-Rey and Junquera 1998, Haugen and Vøllestad 2001, Grift et al. 2003, Götz et al. 2008b, Tunley et al. 2009). However, the size and age at sexual maturity of *D. capensis* was identical between the exploited and unexploited areas (149.5mm FL) and the hypothesis that the exploited population would have a smaller size and age at sexual maturity is therefore rejected. This indicates that either *D. capensis* does not have the ability to reduce its size and/or age at maturity to compensate for a loss in reproductive potential, or that the current level of fishing pressure is not high enough to elicit a response. If this species is unable to adapt its life-history characteristics in response to fishing pressure, it is possible that other environmental factors may play a role in determining the size at sexual maturity. Since *D. capensis* in the sub tropical KZN waters were observed to mature at a smaller size (Joubert 1981b) than those in the temperate TNP region (Mann and Buxton 1998), it is possible that the difference in size at maturity is an adaptation to the selective pressures exerted in the sub tropical environment.

The heavily female skewed sex ratio in the unexploited area (1: 4.7) was due to the dominance of females in the larger and older size classes. In the exploited area, the disparity was greatly reduced (1: 2.2) due to the selective removal of large individuals and higher mortality rate of females. Joubert's (1981b) and Mann and Buxton's (1998) findings show a similar trend with a greater proportion of males in the exploited area of KZN (1.3: 1), when compared to the unexploited TNP (1: 1.9). With the comparatively low proportion of females in these populations, it is likely that the sex ratio in the southern Angolan exploited area is still sufficient for the population to remain productive, suggesting that a response by the species is not yet necessary. However, when comparing the sex ratio per 20mm length class, it was apparent that there were a greater proportion of small females (140 - 160mm FL) in the exploited area. This may indicate a response to exploitation and it is possible that this species may compensate for a reduction in population fecundity by increasing the proportion of small females in the population. The ability to do this is afforded by its reproductive style. As a rudimentary hermaphrodite (Chapter 4), this species is capable of determining its sex at a late stage of its life and presumably environmental (and possibly social) cues are ultimately responsible for the development of one or the other sex.

Ultimately, if *D. capensis* does not compensate for the effects of exploitation by reducing its size and age at maturity, or by increasing its growth rate, a length based analysis of the sex ratio of the population could be a good indicator of the stock status of the species. However, this should be investigated further.

Conclusion

Results of this study show that *D. capensis* is a slow-growing, long-lived and late maturing species. According to the W&R model, these characteristics make this species a periodic strategist, a life-history strategy that evolves in seasonal environments where selection favours the production of large numbers of small offspring in pulses that coincide with predictable periods of conditions favourable for growth and survival of juveniles. Such species are particularly susceptible to exploitation, even at low levels of fishing. This was seen in the heavily truncated size and age structure of the population in the exploited area. Despite this, there was no evidence suggesting a physiological response to fishing pressure through changes in growth or maturity. However, the fish did appear to compensate for the loss of reproductive potential by increasing the proportion of small females in the exploited area. This indicates that *D. capensis*, either does not have the ability to respond to fishing at a physiological level, or that the current level of fishing pressure was not high enough to elicit a physiological response.

CHAPTER 6

An assessment of the subsistence fishery for *Diplodus capensis* in southern Angola with an investigation into the value of unexploited area life-history information for meaningful spawner biomass-per-recruit assessments

Introduction

Stock assessment involves the use of various statistical and mathematical calculations to make quantitative predictions about reactions of fish populations to alternative management choices (Hilborn and Walters 1992). Stock assessment models are diverse and vary with respect to their input and output requirements.

Surplus production models (biomass dynamic models) are the simplest of the commonly used stock assessment models. These models are based on an extremely simple view of population dynamics as all the complexities of age and spatial structure, and so on, are ignored (Hilborn and Walters 1992). Although age-structured models are favoured for fisheries stock assessments due to their superior output measures, their intensive data requirements are prohibitive. For example, virtual population analysis (VPA) requires information on the previous age-structure of the population to make predictions for the future, and an historical abundance index such as catch per unit effort (CPUE) is often required to strengthen the predictions and make meaningful management recommendations. VPA falls under the blanket of dynamic pool models. The concept of the dynamic pool is simple; the population consists of all individuals alive at any time and this population is continuously reduced in size by deaths, due to natural and fishing mortality, and is augmented by recruitment of younger fish (Shepherd and Pope 2002a).

The estimation of a spawner stock-recruitment relationship is difficult, and it is for this reason that the yield-per-recruit (YPR) model was developed. YPR models are an abbreviation of the full dynamic pool model because they cancel out the recruitment factor by making the crude assumption that the parameters for recruitment, growth and natural mortality are constant from one year to the next and, therefore, that the stock is in a steady state. In reality, this assumption is unreasonable because it would be impossible to overfish a stock that had constant recruitment, since in this case YPR never reduces to zero, however high the value is taken for fishing mortality (Shepherd and Pope 2002b). For this reason the target reference points (TRP's) that form the basis of the management recommendations of any YPR analysis only provide an indication of the level of growth overfishing (i.e. harvesting fish before they have reached their optimal growth and therefore yield potential), but completely fail to address the threat of recruitment overfishing (i.e. harvesting too many large adult fish so that future recruitment is depleted to levels that cannot sustain the population), which is thought to be the leading cause of stock collapse and depletion of many species (Myers et al. 1997). Therefore, it is useful to incorporate the results of spawner biomass-per-recruit (SBR) models in TRP recommendations in order to maintain reproductive capacity of stocks within safe biological levels (Butterworth et al. 1989).

The SBR (Beverton and Holt 1957) approach has been widely used for the assessment of many southern African reef fish stocks (Bennett 1988, Pulfrich and Griffiths 1988, Smale and Punt 1991, Buxton 1992, Bennett 1993, Punt et al. 1993, van der Walt and Govender 1996, Booth and Buxton 1997, Chale-Matsau et al. 2001, Mann et al. 2002, Götz 2005). These models have been favoured because they are cost-effective and are not data intensive. Furthermore, directed catch and effort data, length- or age-based catch data, and other historical biological data pertinent to the application of other age-based models is often lacking.

The SBR approach has, however, been criticised as a stock assessment tool as it bears no relation to the absolute size of the stock, being independent of recruitment, and is dependent on a reliable estimate of natural mortality rate (M) (Attwood 2002, Götz 2005). For these reasons, Attwood (2002) suggested that the SBR should only be used as a relative measure of the spawning potential of the average recruit at a given fishing mortality rate (F). However, the difficulty of obtaining reliable estimates of mortality presents one of the greatest challenges in fisheries stock assessment (Hilborn and Walters 1992, Bohnsack 1993, Ludwig et al. 1993, Pascual and Iribarne 1993, Hutchings 2000). Typically, *F* is calculated by subtracting *M* from total mortality rate (*Z*). Up to now, most studies that use SBR analysis have relied on Pauly's (1980) empirical formula to calculate *M*. The reliance on this model to estimate *M* is largely because most fisheries assessments are carried out on already exploited populations. However, in situations where there is no fishing effort, *M* can be directly calculated from the more reliable catch-curve based methods (e.g. Chapman and Robson 1960, Ricker 1975), because $F = 0$.

Most SBR assessments compare the current SBR to that of "pristine" levels. For such comparisons to be valid, it is crucial that the estimate of the "pristine" level is accurate, which is usually simply back-calculated from the exploited stock information by simulating an unfished scenario (i.e. $F = 0$). However it has been shown that fisheries induced selection can alter certain variables such as growth, size/age at maturity and longevity (Jennings et al. 1999). In such cases, estimates of pristine levels are likely to be inaccurate if parameters that resemble an unexploited state of the population are unknown.

In southern Angola, it was shown that the size and age composition of *D. capensis* was heavily truncated and the growth parameters were altered in an exploited area compared to an unexploited one (Chapter 5). The aim of this study was therefore to assess the stock status of *D. capensis* in the exploited area. To do this, the only option was to use the standard SBR and biomass-per-recruit (BR) analyses, since there is no historical catch information for this species in Angola. However, the unexploited area provided an ideal opportunity to investigate the reliability of these types of assessments. Various combinations of exploited and unexploited area input information were used to investigate to which extent the results of this assessment approach can be misleading due to fishery induced changes in life-history parameters. Like most other reef associated sparids, *D. capensis* displays a high degree of residency (Bennett and Attwood 1991, Attwood and Bennett 1995a, Cowley et al. 2002, Watt-Pringle 2009) resulting in little immigration/emigration between areas and making it an ideal subject species for such a study.

Material and Methods

Estimates of growth, maturity, selectivity and the length-weight relationship were obtained from an unexploited and exploited area for *D. capensis* in the previous chapter (Table 6.1). Therefore, only methods pertaining to mortality rate estimation and the per-recruit approach are described here.

Mortality rate estimates

Total mortality rate (Z)

The methods described by Ricker (1975) and Chapman and Robson (1960) were used to estimate *Z*.

For Ricker's (1975) method, the natural logarithm of the age frequency was plotted and the negated slope of a linear regression through the descending arm of these data points was used to provide an estimate of *Z*.

The Chapman and Robson (1960) method is based on obtaining a minimum variance unbiased estimator for the related survival parameter, $S = e^{-z}$ (Dunn et al. 2002), and is defined as:

$$Z = \log_e\left(\frac{1+\bar{a}-1/n}{\bar{a}}\right)$$

where $\bar{a}$ is the mean age (above the recruitment age) and n is the sample size. Age classes that were not well represented in the sample were excluded from the analyses.

Natural mortality rate (M)

The estimate of *Z* was considered to be the best estimate of *M* for the unexploited area because it is based on observed catch-at-age data. However, two empirical equations were also used to estimate natural mortality for the exploited and unexploited areas.

Firstly, Pauly's (1980) empirical equation is expressed as:

$$\ln(M) = -0.0066 - 0.279\ln(L_\infty) + 0.6543\ln(K) + 0.463\ln(T)$$

where L_∞ (cm) and K (y^{-1}) are parameters estimated from the Von Bertalanffy growth function, and T (°C) is the mean annual surface water temperature (20.4°C).

Secondly, Hoenig's (1983) empirical equation is expressed as:

$$\ln(M) = 1.46 - 1.01\ln(t_{\max})$$

where $t_{\max}$ (yrs) is the maximum observed age in each area.

<u>*Fishing mortality rate (F)*</u>

Fishing mortality was assumed to be negligible (i.e. $F = 0$) in the unexploited area and was calculated by subtraction ($F = Z - M$) in the exploited area.

Spawner biomass- and biomass-per-recruit analysis

In Chapter five it was found that growth differed significantly between males and females in the unexploited area. Therefore, as in Bennett (1988), Punt et al. (1993) and Sun et al. (2005), data could not be pooled for the sexes. However, males were excluded from the analysis because the small sample size in the exploited area reduced the reliability of the estimates of natural mortality. Therefore, the SBR and BR analyses below were conducted on female data only.

Based on the input parameters summarized in Table 6.1, SBR and BR were calculated as a function of fishing mortality (F) and age at selectivity (S_t), such that:

$$SBR(F, S_t) = \sum_{t=0}^{\max} W_t \tilde{N}_t \psi_t$$

and

$$BR(F, S_t) = \sum_{t=0}^{\max} W_{t+1/2} \tilde{N}_t$$

where W_t is weight of fish at age t, ψ_t is the maturity at age t and max is the age of the oldest aged fish in the population. The relative number of fish at age t, $\tilde{N}_t$, was calculated as:

$$\tilde{N}_t = 1 \qquad \text{if } t = 0$$

$$\tilde{N}_t = \tilde{N}_{t-1} e^{-M - S_{t-1} F} \qquad \text{if t} > 0$$

In SBR and BR analyses, the impact of the estimated current F can then be quantitatively assessed against the assumed pristine steady state of the population (SBR_0 and BR_0, respectively) which are usually simply estimated by setting $F = 0$.

The life-history information from the unexploited and exploited areas and the range of mortality estimates available for *D. capensis* in this study provided an opportunity to conduct a series of analyses to evaluate the sensitivity of the per-recruit approach to variation in life-history parameters and mortality rate estimates.

1. *Basic model - Analysis of the stock using data from the exploited area only*

This analysis was based purely on the exploited area life-history parameters and mortality estimates and was conducted to simulate what would have been done in a normal situation where only exploited information is available to assess a stock and there is no information available from an unexploited area.

2. *Sensitivity of the SBR model to M*

This analysis was conducted as above, however the unexploited area estimate of M was used to estimate F. The aim of this analysis was to investigate the potential bias when using an empirical equation to estimate M.

3. *Estimation of pristine levels using information from the unexploited area*

This analysis incorporated the life-history information from the unexploited area to obtain an estimate of pristine levels. The aim of this analysis was to assess the current level of SBR and

BR as a percentage of the actual pristine stock calculated from the unexploited area. This analysis was considered to represent the most accurate stock assessment for *D. capensis* in the exploited area.

4. *“Shifting baseline” analysis*

A step-wise analysis was conducted to investigate to what degree the observed differences in longevity, life-history parameters and *M* estimates between exploited and unexploited areas would influence the estimation of the baseline SBR_0 and BR_0.

Firstly, SBR_0 and BR_0 were calculated as a function of the life-history parameters and *M* estimates from the unexploited area. These quantities were then set as a baseline against which different estimates of SBR_0 and BR_0 were evaluated.

Secondly, to investigate the consequence of reduced longevity, the same calculation was conducted but with the maximum observed age from the exploited area.

Thirdly, to investigate the effect of altered life-history parameters, the previous calculation was repeated with the life-history parameters from the exploited area.

Finally, to investigate the consequence of different estimates of *M*, the previous calculation was repeated incorporating the estimate of *M* from the exploited area.

Table 6.1: Biological and fishery parameters used for the application of spawner biomass- (SBR) and biomass-per-recruit (BR) models to female *Diplodus capensis* in southern Angola.

Parameter	Unexploited area	Exploited area
L_∞ (asymptotic length) (mm FL)	419.5	293.55
K (Brody growth coefficient) (y^{-1})	0.045	0.084
t_0 (age at zero length) (y)	-3.4	-1.9
max. age	31	17
a (length-weight parameter) (mm)	0.0000131	0.0000171
b (length-weight parameter) ($g.mm^{-1}$)	3.12	3.05
ψ_t (age-at-50% maturity) (y)	5.35	5.31
$\delta\psi_t$ (inverse rate of maturity curve) ($mm.y^{-1}$)	1.17	0.51
S_t (age-at-50% selection) (y)	6.1	6.1
δS_t (inverse rate of selectivity curve) ($mm.y^{-1}$)	0.35	0.35

Results

Mortality rate estimation

Unexploited area

The linear based catch curve (Ricker 1975) (Figure 6.1a) and the Chapman and Robson (1960) estimate of *Z* were similar for females in the unexploited area (Table 6.2). The average of these estimates was considered to be the best estimate of *M* (0.10 y^{-1}). The Hoenig (1983) (0.13 y^{-1}) and Pauly (1980) (0.18 y^{-1}) methods appeared to overestimate the rate of *M* (Table 6.2) when compared to the linear based catch curve (Ricker 1975) (Figure 6.1b) and the Chapman and Robson (1960) estimates of *Z*. The latter estimates were also higher for males than females in the unexploited area (Table 6.2). Again, the Hoenig (1983) (0.17 y^{-1}) and Pauly (1980) (0.29 y^{-1}) methods appeared to overestimate the rate of *M*.

Exploited area

There was a greater disparity between the *Z* estimates in the exploited area, with the Chapman and Robson (1960) estimate (0.27 y^{-1}) higher than the Ricker (1975) estimate (0.21 y^{-1}) (Figure 6.1c). The Pauly (1980) and Hoenig (1983) estimates of *M* (0.31 y^{-1} and 0.25 y^{-1}, respectively) were considerably higher than the catch curve estimate in the unexploited area. It was not possible to estimate mortality rates for males in the exploited area due to the lack of a suitable sample size.

Table 6.2: Estimates of natural mortality (*M*) and total mortality (*Z*) obtained for *Diplodus capensis* sampled from an unexploited and exploited area in southern Angola.

	Females		Males
	Unexploited	Exploited	Unexploited
M (Pauly 1980)	0.18	0.31	0.29
M (Hoenig 1983)	0.13	0.25	0.17
Z (Ricker 1975)	0.09	0.21	0.14
Z (Chapman and Robson 1960)	0.11	0.27	0.15

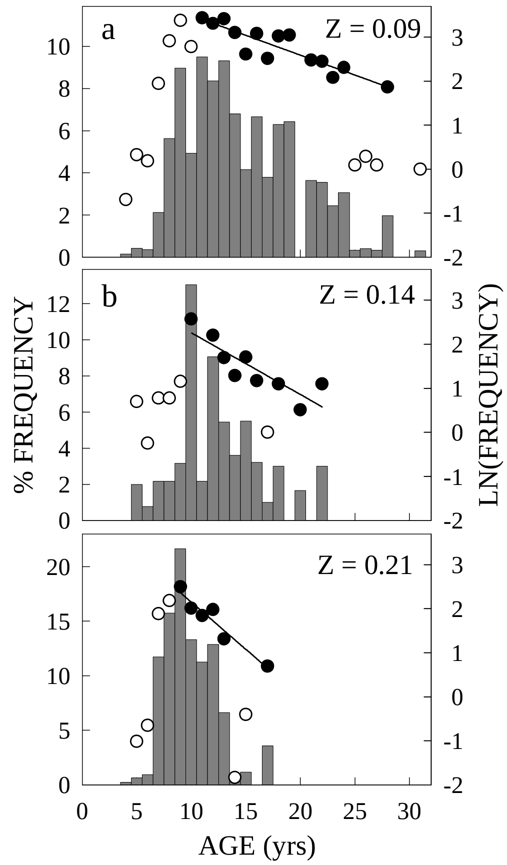

Figure 6.1: Total mortality rate (*Z*) estimates derived from the regression based catch curve analysis for *Diplodus capensis* in southern Angola. Estimates are presented for females (a) and males (b) in the unexploited area and females (c) in the exploited area. Small sample size prevented the calculation of *Z* for males in the exploited area. Filled circles indicate points that were used in the analysis and open circles indicate points that were excluded from the analysis.

SBR and BR input parameters

While the female L_∞ was considerably smaller in the exploited area than in the unexploited area, the K was much greater (Table 6.1). The weight-at-age (W_t) of fish in the exploited area was therefore considerably lower (Figure 6.2). The age-at-50% maturity (ψ_t) was similar for both areas; however, the width of the ogive ($\delta\psi_t$) was greater for the unexploited area (Table 6.1). Age-at-50% selection (S_t) for the subsistence fishery was calculated as 6.1 years (see Chapter 5) (Figure 6.2). The relative numbers-at-age ($\tilde{N}_t$) in the exploited area was greatly reduced at zero F compared to the unexploited area (Figure 6.2). When the M estimate for fish in the unexploited area was incorporated along with the exploited area information, the

$\tilde{N}_t$ mirrored that of the unexploited area. However, when the actual F estimate was included, a rapid depletion in the relative number of fish was observed with increasing age (Figure 6.2).

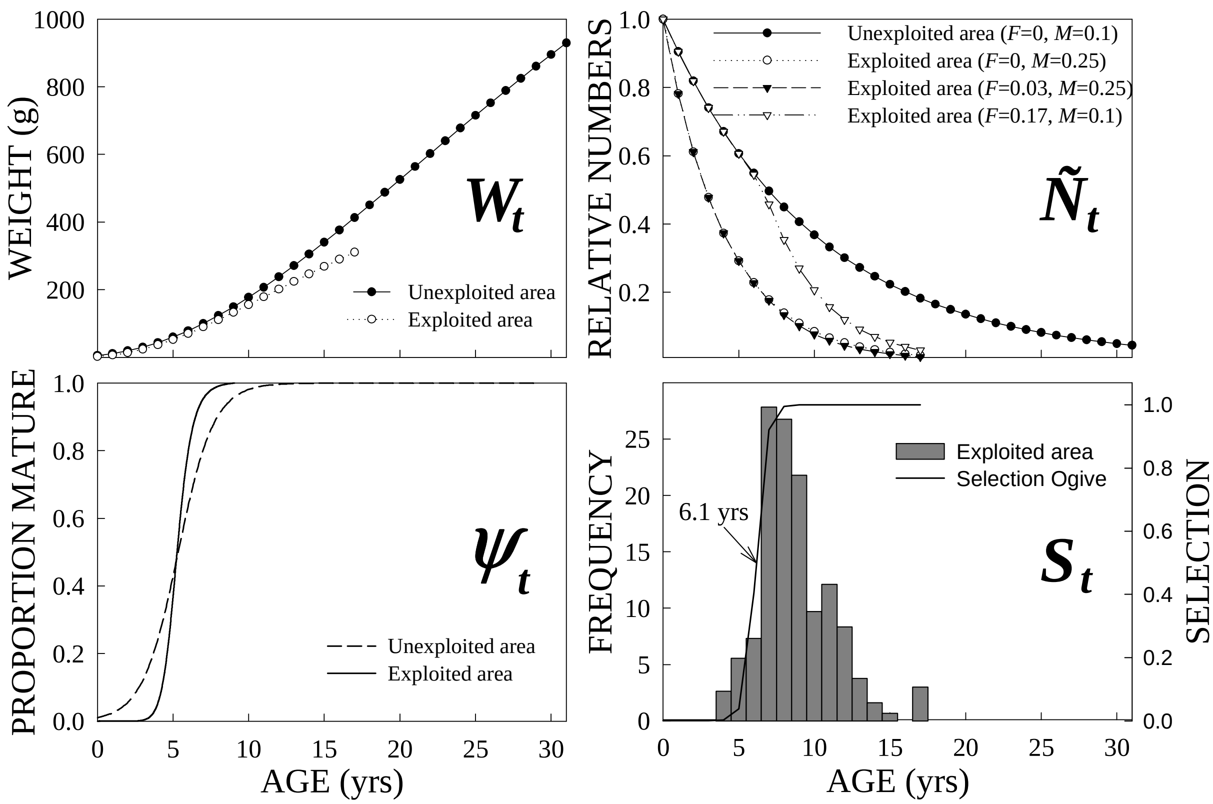

Figure 6.2: Graphical representation of the input parameters (W_t = weight-at-age, $\tilde{N}_t$ = Numbers-at-age, ψ_t = age-at-50% maturity, S_t = age-at-50% selection) obtained for the application of per-recruit models to *Diplodus capensis* in an exploited and unexploited area in southern Angola.

SBR and BR analyses

1. *Basic model - Analysis of the stock using data from the exploited area only*

Due to the disagreement between the two Z estimates and the two M estimates in the exploited area, these values could not be averaged in order to calculate F (average values would have resulted in M exceeding Z). Therefore, the highest Z estimate [0.27 y^{-1} (Chapman and Robson 1960)] and lowest M estimate [0.25 y^{-1} (Hoenig 1983)] were used and F was calculated to be 0.03 y^{-1}. The per-recruit analysis estimated the SBR and BR at 90% and 93% of pristine levels, respectively (Figure 6.3).

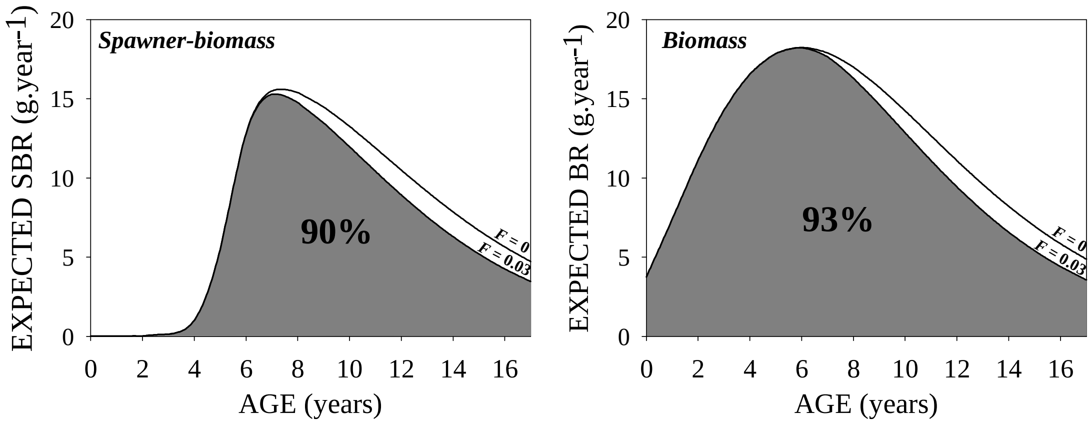

Figure 6.3: Results of the "basic model" analysis showing spawner biomass- (SBR) and biomass-per-recruit (BR) as a function of age for female *Diplodus capensis* in southern Angola. Life-history parameters and estimates of mortality were obtained from the exploited area only.

2. *Sensitivity of the SBR model to M*

Using the average of the two catch-curve estimates as the best estimate of M (0.1 y^{-1}) from the unexploited area, F was calculated as 0.17 y^{-1}. The per-recruit analysis estimated the SBR and BR at 48% and 55% of pristine levels, respectively (Figure 6.4).

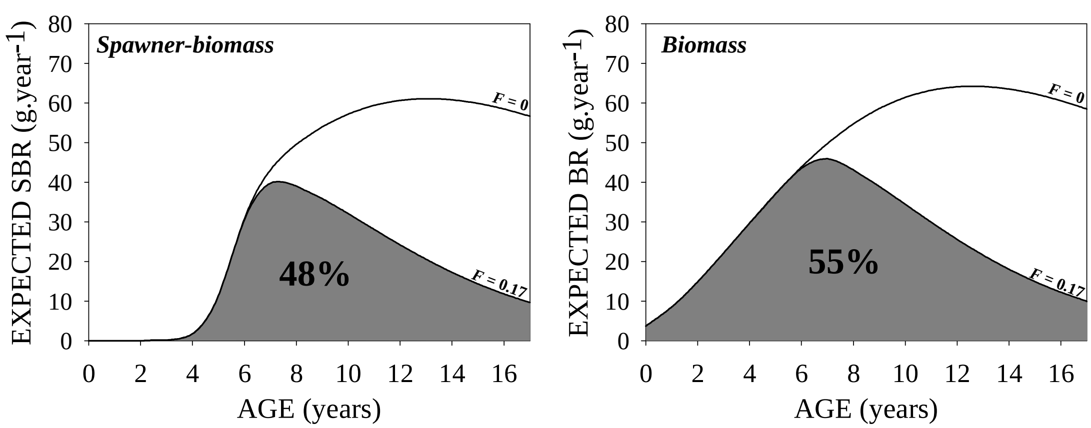

Figure 6.4: Results of the "sensitivity of the SBR model to *M*" analysis showing spawner biomass- (SBR) and biomass-per-recruit (BR) as a function of age for female *Diplodus capensis* in southern Angola. Life-history parameters were used from the exploited area information and the estimate of F was obtained using the unexploited area estimate of M = 0.1 y^{-1}.

3. Estimation of pristine levels using information from the unexploited area

Using the life-history parameters and estimate of *M* from the unexploited area, a true level of SBR_0 and BR_0 was estimated. Using the SBR and BR values from the exploited area in analysis 2, the per-recruit analysis estimated the SBR and BR at 20% and 25% of pristine levels, respectively (Figure 6.5).

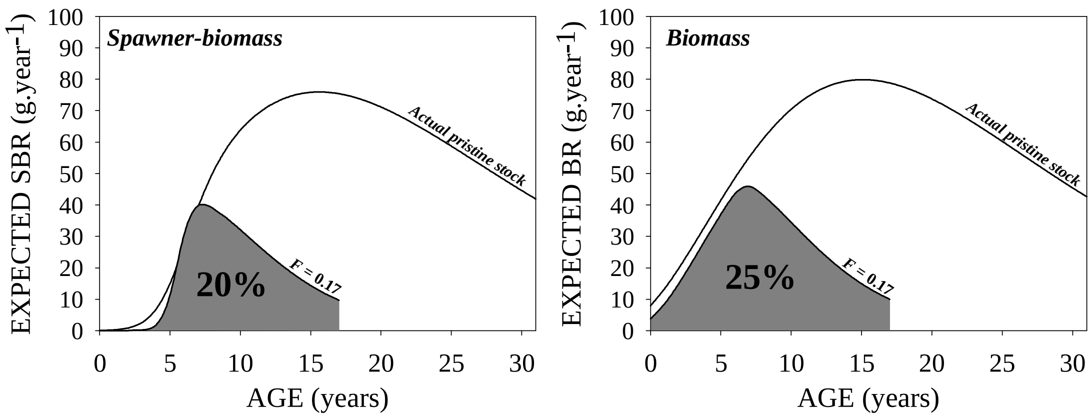

Figure 6.5: Results of the "estimation o pristine levels" analysis showing spawner biomass- (SBR) and biomass-per-recruit (BR) as a function of age for female *Diplodus capensis* in southern Angola. Life-history parameters and mortality estimates were used from the unexploited area information to estimate the "actual pristine" stock and this mortality estimate was used to calculate *F* for the exploited area.

4. "Shifting baseline" analysis

Four different estimates of "pristine" levels were obtained using the available life-history parameters and mortality rate estimates (Figure 6.6). The best estimate of "pristine" level was assumed to be obtained when the life-history parameters and *M* estimate from the unexploited area were used in the per-recruit analysis. When the longevity estimate for the exploited area was incorporated, the estimates of SBR_0 and BR_0 were reduced 48% and 54% of the baseline, respectively. When the life-history parameters from the exploited area were incorporated, SBR_0 and BR_0 were reduced by a further 7% and 10%, respectively. Finally, when the empirical *M* value from the exploited area [Hoenig's (1983) estimate of 0.25 y^{-1}] was applied, a further underestimate of 33% and 32% for the SBR_0 and BR_0 was observed, respectively. Therefore, the cumulative reduction in the "pristine" level estimate of the SBR and BR due to the fishery induced changes in longevity, life-history parameters, and *M* estimates, was 92% and 88%, respectively.

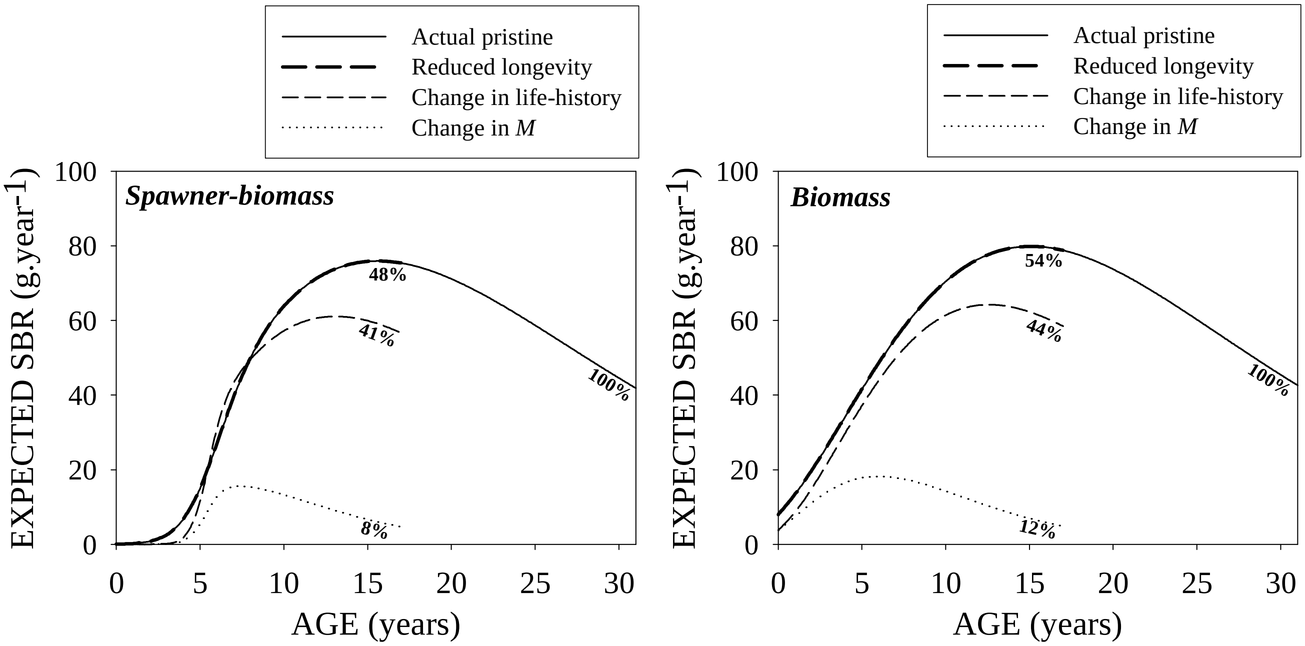

Figure 6.6: Results of the "shifting baseline" analysis showing spawner biomass- (SBR) and biomass-per-recruit (BR) as a function of age for female *Diplodus capensis* in southern Angola. SBR and BR were calculated at zero *F* under different life-history and *M* scenarios. Percentages below the lines represent the percent of the actual pristine stock estimate which was set as a baseline.

Discussion

The analysis that incorporated the life-history parameters and *M* estimate of the fish in the unexploited area (analysis 3) was considered to represent the best estimate of what pristine levels are and therefore can be considered the best possible assessment of this fishery with the information available. It was concluded that SBR and BR are currently at 20% and 25% of pristine levels, respectively.

This assessment suggests that the *D. capensis* fishery is depleted, which is unsurprising given the life-history characteristics of this species (slow growth, high longevity and late maturation) in southern Angola. Furthermore, it is now widely accepted that a low level of small-scale fishing can have a big impact on target fish populations (Jennings et al. 1995, Jennings and Polunin 1996, Russ and Alcala 1996, Pinnegar and Engelhard 2008). A SBR level of 20% of pristine suggests that the current level of fishing is not sustainable. In fact, it is surprising that the stock is able to replace itself under the current fishing conditions with such a depleted SBR. Even more surprising is the relatively high CPUE (mean = 3.03 fish.fisher.hour^{-1}) for this species in the exploited area. The most likely reason for this is that there are vast (on a scale of 10's of kilometres) unexploited areas in southern Angola that essentially play the role of MPA's and provide a refuge for large mature fishes. These fishes almost certainly provide a source of recruitment for the exploited area investigated in this study. Therefore, if the fishing effort spreads and reduces the extent of the unexploited areas in the future, it is likely that the *D. capensis* resource will collapse due to recruitment overfishing. This has important management implications, which will be discussed in the following chapter.

The use of a particular stock assessment model is often dictated by the information that can be collected with the available financial and human resources. In Angola, the total lack of any historical (or current) catch data precluded the use of any of the full dynamic pool models. Therefore, the per-recruit assessment approach was adopted to assess this fishery. If the quality of the input data is improved, it is likely to improve the reliability of the assessment. In the current study, there was the unusual existence of a truly unexploited area from which life-history information could be collected. By incorporating this information into a series of SBR and BR analyses, this study has shown that the results of a SBR and BR assessment can be highly influenced by fishery induced changes in population longevity, change in life-history parameters and natural mortality rate estimates. These changes affected both the estimates of "pristine" levels and the normal stock assessment results. It was shown that SBR_0 and BR_0 were underestimated by up to 92% and 88%, respectively, while the current SBR and BR levels were overestimated by up to 70% and 68%, respectively. This discrepancy not only highlights the importance of obtaining reliable estimates of mortality, but also the importance of obtaining life-history parameters from unexploited populations. Although in the case of *D. capensis* in southern Angola, the difference in the growth parameter estimates was an artifact of fishing rather than a physiological response to exploitation; these results challenge the validity of the per-recruit approach to assessing already exploited fish stocks.

The basic model SBR and BR analyses simulated the way that most present day stock assessments are conducted by only using information collected from exploited fish stocks. The uncertainty associated with the empirical estimates of M was immediately seen when the average of the two M estimates exceeded the average of the two Z estimates. This is impossible and therefore in order to maintain biological realism, the highest *Z* estimate and the lowest *M* estimate had to be accepted for the application of the SBR and BR analyses. Fishing mortality was therefore estimated as 0.03 y^{-1} and the current SBR and BR were estimated to be at 90% and 93% of pristine levels, respectively. In this case, a fisheries manager would mistakenly assume that the current level of fishing activity in the exploited area is negligible and recommend that fishing pressure could be greatly increased without an increased risk of recruitment overfishing.

The second analysis was conducted to investigate the extent to which the traditional empirical estimates of *M* influence the model outputs. In this analysis, *F* was calculated as 0.17 y^{-1} and the current SBR and BR were estimated to be 42% and 38% lower than the initial assessment, respectively. This clearly illustrates the importance of obtaining reliable estimates of natural mortality. However, achieving this is inherently difficult for many fish stocks (Vetter 1988, Hilborn and Walters 1992, Bohnsack 1993, Ludwig et al. 1993, Pascual and Iribarne 1993, Hutchings 2000). Despite this, almost all mathematical models of fish stock dynamics (with the exception of simple surplus production models) require *M* as an input parameter (Vetter 1988) and therefore the use of empirical equations to obtain an estimate of *M* has become common practice in fisheries science. While these models (e.g. Pauly 1980, Hoenig 1983) have the advantage of requiring minimal input data, they do not necessarily produce reliable estimates of *M* (Vetter 1988) due to the inherent variation among the fish stocks upon which they are based. In this study the empirical equation estimate of Hoenig (1983) (0.13 y^{-1}) and Pauly (1980) (0.18 y^{-1}) overestimated *M* when compared to the more reliable catch curve methods (0.10 y^{-1}). Hoenig's (1983) equation is based on the idea that the longevity and *M* of a species are inversely related since animals from a population with a high mortality rate would not survive long enough to reach an old age. This implies that, irrespective of any other characteristic of the fish, if it lives up to the same age as another species of fish, their *M* will be the same. For example, a bronze bream (*Pachymetopon grande*) should die at roughly the same rate as a black musselcracker (*Cymatoceps nasutus*), or a yellowfin tuna (*Thunnus albacares*) should die at roughly the same rate as a salema (*Sarpa salpa*). Although a relationship between longevity and mortality rate is intuitive, there are many other ecological factors that can influence a fish's rate of natural mortality, such as its position in the food web. The use of this equation on exploited populations (for which it is designed) may produce inaccurate estimates since the older fish in the population are typically removed first. Furthermore, the difficulty associated with ageing older fishes casts further doubt on the accuracy of these estimates. Pauly's (1980) method provided a greater overestimate of the rate of natural mortality than Hoenig's (1983) method. This is unsurprising as none of the 175 fish stocks considered while formulating this relationship were sparids, and as Götz (2005) states, very few assessments have considered the implication of this model's error, which has a coefficient of variation (CV) in order of 200%. Butterworth et al. (1989) state that the 95% confidence intervals for the Pauly (1980) estimates span a range of about a third to three times the value obtained. For this reason, the per-recruit analysis should be repeated using different values of M ($M \pm 0.1$) in order to assess the sensitivity of the results to this potential inaccuracy (Butterworth et al. 1989). Nevertheless, empirical equations are useful since they allow us to inexpensively reduce the uncertainty about a stock's mortality rate from the region of all possible values, to the region of more likely values (Pascual and Iribarne 1993). However, the discrepancy in the results of this study demonstrated that estimates obtained from empirical equations should be treated with caution and that catch curve based methods are favourable when information can be collected from unexploited populations.

Götz et al. (2008a) used two catch-curve methods and three empirical equations to estimate M for *D. capensis* in the TNP. The estimates ranged from 0.12 y^{-1} to 0.63 y^{-1}. Unlike this study, the two catch-curve estimates [0.52 y^{-1} (Ricker 1975) and 0.63 y^{-1} (Pauly 1984)] were much greater than the empirical equation estimates [0.12 y^{-1} (Butterworth et al. 1989), 0.18 y^{-1} (Hoenig 1983) and 0.31 y^{-1} (Pauly 1980)]. Assuming that these estimates are reliable, the fact that the catch-curve estimates were considerably higher than the empirical equation estimates provides evidence of fishing mortality in the TNP. While poaching does take place in the reserve (P.D. Cowley pers. comm.), there is no published information to quantify the amount. Despite this, the high catchability of *D. capensis* (highest CPUE) in the TNP, and the conclusion of Götz et al. (2008a) that this species was the best indicator species to assess the level of exploitation, suggests there is significant illegal fishing effort in the research fishing area. In their analyses, Götz et al. (2008a) assumed that the impact of sampling and poaching was insignificant ($Z = M$). They suggested that the variability in mortality estimates may be due to temporally segregated sampling periods; sampling of different populations; the residual effects of exploitation before closure of the MPA; incorrect growth estimates in previous studies; and gear bias between studies.

Natural mortality refers to all possible causes of death except fishing (Pauly 1980) and can therefore only be directly measured on completely unfished stocks. Once fishing occurs, scientists are dependent on the empirical equations discussed above. These equations are based on life-history parameters of unexploited or lightly exploited fish stocks. Therefore, if fisheries induced alterations (not necessarily responses) in the life-history parameters occur, accuracy of the estimates will be affected. This was evident from the exploited area estimates of *M* in the current study, where a change in the growth parameters and maximum age was observed. The resulting *M* estimates were much higher [0.31 y^{-1} and 0.25 y^{-1} for Pauly's (1980) and Hoenig's (1983) equations, respectively] than those from the unexploited area. This type of overestimation has serious implications for stock assessment and highlights the value of having pre-exploitation life-history information for the direct estimation of *M.* Such a situation may only be afforded by conducting research in MPA's or in uninhabited coastal environments, since most exploitable fish stocks are already exploited.

The second analysis (sensitivity of the SBR model to *M*) estimated the SBR and BR of *D. capensis* at 48% and 55% of pristine levels, respectively. It is generally accepted that the risk of recruitment overfishing is greatly increased at SBR levels below 25% of pristine (limit reference point), and that fisheries are aimed to be managed at SBR levels of above 35% of pristine (target reference point) (Butterworth et al. 1989, Clark 1991, Clark 1993, Punt et al. 1993, Booth 2004, Hilborn 2010). A fisheries manager who is faced by the results of this assessment would conclude that the stock falls within the "safe" limits of pristine SBR and BR and would be largely unconcerned with the stock status. However these values were calculated as a percentage of the back-calculated pristine levels from the exploited area life-history information. As discussed above, the third analysis is considered to represent the most reliable assessment of this fishery based on the available information. This analysis showed that the current SBR and BR levels estimated using the standard analysis (analysis 1) overestimated the current SBR and BR by 70% and 68%, respectively. The disparity between the results of the first three analyses is largely affected by the estimate of "pristine" levels.

The "shifting baseline" analysis exemplified how the shifting baseline syndrome (Pauly 1995, Pinnegar and Engelhard 2008) can influence the per-recruit assessment. In this situation, a fisheries scientist working in the exploited area would assume that the oldest fish sampled provides a reliable estimate of longevity for this species in the area. This immediately shifts the baseline and in the case of *D. capensis* resulted in a 52% and 46% underestimate of SBR_0 and BR_0, respectively. This underestimation was further exacerbated by the difference in life-history parameters between the two areas and resulted in a further 7% and 10% reduction in the SBR_0 and BR_0 estimate. Furthermore, when the unreliable *M* estimates were incorporated into the analysis, a further reduction of 33% and 32% was observed in the SBR_0 and BR_0, respectively. Although the order in which these analyses were conducted was irrelevant, the most important result from the "shifting baseline" analysis is that the cumulative loss in what we perceive as being pristine levels due to a reduction in longevity, change in life-history and an unreliable *M* estimate was 92% and 88% for SBR and BR, respectively.

Although the results of this study suggest that the SBR approach is not suitable as an assessment tool, it still has its place in fisheries management today. It is, however, crucial that the limitations of this model are well understood and that input parameters are obtained from unexploited populations wherever possible. The quality and reliability of the input parameters used is of paramount importance. Possibly the most crucial parameter that needs to be estimated accurately is *M*. If the accurate estimation of *M* is precluded then the SBR assessment results are likely to have very little meaning. As mentioned above, the only way to accurately estimate *M* is from observed catch-at-age data from an unexploited population. This is often not possible and may only be achieved in MPA's. However, a biological fish sampling study in an MPA flouts the very point of this invaluable management tool. Other means of increasing the reliability of the *M* would be to use the Hoenigs (1983) longevity based estimate but use the oldest recorded specimen for the species under study (not necessarily the oldest specimen from the study). Any pre-fishery or earlier fishery life-history parameter estimates should also be incorporated into the analysis in the estimation of pristine levels.

Conclusion

This study showed that a combination of an underestimate of longevity, different estimates of the Von Bertalanffy growth parameters and overestimates of the natural mortality rate in the exploited population resulted in a 92% underestimate of the pristine SBR value. The assessment based on the actual pristine SBR estimate from the unexploited area revealed that the subsistence fishery had reduced *D. capensis* to 20% of its pristine SBR levels and highlighted the value of pre-exploitation life-history information for the application of per-recruit models.

CHAPTER 7

General discussion with considerations for management and future research priorities

The fishery system is comprised of three interacting systems: (1) the resource; (2) the resource users; and (3) the resource managers (McClanahan and Castilla 2007). There are many factors within each system that add to the complexity of effective fishery management and each fishery is different from the next.

The *D. capensis* resource in southern Angola

In Chapter 2 the taxonomic status of *D. capensis* was confirmed in southern Angola. Although there is not sufficient morphological evidence to differentiate the South African and Angolan populations as separate species, there is sufficient evidence to conclude that they represent discreet stocks. Therefore, management strategies should be based on information gathered for this species in southern Angola and not simply transferred from South Africa.

Knowledge of the biology and life-history characteristics of a species is crucial for the successful management of its fisheries. These aspects were investigated for *D. capensis* in Chapter 3 - 5. Along with its high abundance in the inshore zone, the omnivorous diet of this species indicates that it is an important component of the inshore food web of southern Angola. Therefore, its exploitation may have irreversible cascading effects on the community (Steneck 1998), which is important to consider when adopting an ecosystem approach to fisheries management. *Diplodus capensis* displays life-history traits that are common amongst other sparid fishes and include slow growth, high longevity and relatively late maturation. These characteristics render a species particularly susceptible to overexploitation

(Acosta and Appeldoorn 1992, Chale-Matsau et al. 2001) and are therefore important to consider for the management of its fisheries.

The susceptibility of this species to fishing was shown in Chapter five where, even at low levels of subsistence fishing, there is convincing evidence for localised depletion based on the truncation of the size and age structure of the population, reduced longevity and an overall reduction in the proportion of females. The spawner biomass-per-recruit (SBR) analysis in Chapter 6 supported this evidence by concluding that SBR in the subsistence fishing area is currently at 20% of pristine levels. This is below the target reference point of 35%, which is generally accepted to represent safe SBR levels (Butterworth et al. 1989, Clark 1991, Clark 1993, Punt et al. 1993, Booth 2004, Hilborn 2010), and therefore there is a clear requirement for management of this species in southern Angola.

The *D. capensis* resource users

There is anecdotal evidence to suggest that there has been a recent increase in the amount of fishing effort in the inshore zone of southern Angola which is likely to place increased pressure on these fish stocks. This was seen in three fishing sectors over the course of the study period. Firstly, recreational fishing is becoming increasingly popular. Angolans are starting to invest in more sophisticated tackle (technology creep) and are travelling greater distances in 4X4 vehicles in order to fish. Secondly, subsistence fishers are willing to walk longer distances in order to find larger fish and some of them own motorcycles, which allow them to travel larger distances when the tide is low. Thirdly, in the artisanal sector, which has traditionally targeted deeper water species (e.g. *Dentex macropthamus* and *Atractoscion aequidens*), fishers appear to be incorporating shallower waters into their fishing grounds. Furthermore, the illegal gillnet fishery appears to be expanding into the inshore zone and there is also evidence for an expansion in the range of “float boats” which previously only fished around the coastal villages. These boats are typically less than 2m in length and are constructed from foam floats covered with plastic grain bags. The foam floats that are used are collected from flotsam on the beach and fishers paddle these cost effective vessels with plastic plates. Recently, in a new development, groups (up to 15) of these fishers are transported daily on motorized vessels, where they exploit previously unexploited inshore fishing grounds. Although this evidence is purely qualitative and based on personal observations, *D. capensis* is likely to be affected by the expansion of all three of the above mentioned sectors due to its high abundance and catchability in the inshore zone.

The *D. capensis* resource managers

The main goal of the fishing policy in Angola is to maximise the benefit to the Angolan population of the long term sustainable exploitation of marine resources in the Economic Exclusive Zone (EEZ) (Duarte et al. 2005). The commercial fishing sector is currently managed on a total allowable catch (TAC) basis, with a proportion (150 000 t/annum) of the total TAC being allocated to the artisanal/small scale sector. There are no regulations governing subsistence fishing in Angola. Current fishing policy dictates that controls on fishing in the artisanal sector in terms of catch and effort will only be imposed on the fishery if the TAC of 150 000 t/annum is exceeded. Fisheries data indicate that the artisanal fishery has never reached this TAC and therefore management authorities believe that there is no cause for concern (Duarte et al. 2005). Therefore, the Institute for the Development of Artisanal Fisheries (IPA) in Angola has focused on developing the artisanal fishery with no attention being paid to its management and control. Concomitantly, the subsistence sector has been largely ignored.

There are currently no restrictions on the harvesting of *D. capensis* and other similar reef associated species and the facilities and infrastructure needed to support a progressive coastal fisheries sector are either completely inadequate or in a severely degraded state (Duarte et al. 2005). To this end, Duarte et al. (2005) suggested that one of the most urgent requirements of the fisheries sector in Angola is to institute fishery controls on the capture of largely resident reef fish. Without such controls, the goal of long term sustainability is unlikely to be achievable and there is a critical need to increase the quality of both the fishery regulations and MCS (Monitoring, Surveillance and Compliance).

Management options for the *D. capensis* resource in southern Angola

Conventional fisheries management tools

Among the conventional tools available for fishery management are size limits, bag limits, gear restrictions, closed seasons and restricted access (McClanahan and Castilla 2007). These tools are widely used but there is growing concern as to the efficacy of these approaches in achieving sustainability and conserving biodiversity (Bohnsack 1993, Ludwig et al. 1993, Bohnsack and Ault 1996, Stergiou 2002). Reasons for their failure include the high mortality of released fish, the inability of the enforcement agencies to control fishing effort, poor compliance by all sectors, a general lack of education amongst resource users, the conflict between regulations and strong cultural traditions, and the implementation of unenforced or unenforceable regulations (Bohnsack and Ault 1996).

Size limits are typically set at the length at which the fish matures in order to allow individuals the chance to reproduce at least once before becoming vulnerable to capture. For *D. capensis* in southern Angola this would equate to a length of 150mm FL. The length at 50% selection of the subsistence fishery is 170mm FL (Chapter 5). Therefore, although size limits are not necessarily effective at providing adequate protection to the breeding stock (Attwood and Bennett 1990) due to fecundity generally increasing with fish size (Roberts and Poulinin 1991), the gear utilised in the subsistence fishery is providing inherent protection to the entire juvenile population (since the length at selection is greater than the length at 100% maturity). If a gear restriction was imposed it would involve setting a minimum hook size that the fishers are allowed to use. However, this would be to increase the size at selection, which is clearly not necessary. It is, however, necessary to maintain the current hook size in the fishery and not to allow fishers to start using smaller hooks.

Daily bag limits are typically set in order to allow adequate protection to the parent stock and therefore reduce the risk of recruitment overfishing. Ideally, in order to set bag limits that are effective at reducing mortality, a time series of abundance data (such as CPUE) is needed (Attwood and Bennett 1995b). Such information is not available for the *D. capensis* subsistence fishery in southern Angola and therefore precludes the effective use of this method. Although an arbitrary daily bag limit could be set for this fishery, there are other complicating factors that inhibit the use of this tool. For example, as fish population size declines, and as effort increases, the daily bag limit should be reduced to remain effective (Attwood and Bennett 1995b).

Although the rationale behind size limits, bag limits, closed seasons and restricted access is valid, they are not considered to be appropriate management tools for a subsistence fishery such as this one. It is unrealistic to expect impoverished, subsistence resource users to release small fish or return fish after they have exceeded their bag limit. If such restrictions are imposed on these fishers, compliance is likely to be very low, unless there is intensive MCS. However, because the *D. capensis* resource is of very little economic value, the Angolan government is unlikely to dedicate funding to the MCS of this fishery. Furthermore, it is unlikely that a court of law would uphold a fine issued to an individual who is breaking the regulations to feed his family a low value, highly abundant fish species.

This raises the question of whether it is worth implementing the above conventional effort or catch controls in order to actively manage the *D. capensis* stock in southern Angola. Although there is evidence of local depletion in the fished area, the large expanses of unexploited areas appear to be providing a source of recruitment and are re-seeding the fished area. Furthermore, the subsistence fishers catch large numbers of fish in this area and based on the current catches, this resource is still providing a valuable source of food security for the people that utilise it. Therefore, implementing any form of control is likely to reduce the benefits to the fishers and is unlikely to be effective due to compliance issues. Furthermore the implementation of catch or gear restrictions will probably cause conflict between the resource managers and the resource users. Therefore, it is concluded that conventional management measures are not an appropriate method of managing this resource. However, if the current fishing effort spreads into the currently unexploited areas, their spillover and re-seeding function will be removed and there is likely to be a large-scale collapse of the fishery due to the removal of the primary source of recruitment.

What can be learned from the management of D. capensis in South Africa?

In South Africa, *D. capensis* forms an important part of the recreational linefishery (Brouwer et al. 1997, Brouwer and Buxton 2002). A stock assessment has never been carried out for this species (Mann 2000), however a decreasing trend in catch per unit effort (CPUE) has been documented in certain areas (Joubert 1981a, Clarke and Buxton 1989, Brouwer 1997, Mann et al. 1997). Under South African legislation, this species is a no-sale species and may not be commercially harvested and sold. The current management regulations in place for the recreational fishery for *D. capensis* in South Africa are size (200mm TL) and bag (5 $person^{-1}$. day^{-1}) limits (DEAT 2009). The bag limit is however rarely reached by the average angler and is therefore not an effective management tool (Cowley et al. 2002). Due to its life-history characteristics and resident behaviour, MPA's have been suggested as, and shown to be, useful management tools for this species (Bennett and Attwood 1991, Cowley et al. 2002). The abundance of *D. capensis* was shown to have increased four to five fold in two years in the De Hoop MPA after the proclamation of the reserve (Bennett and Attwood 1991), and in the TNP the abundance of *D. capensis* was over five times higher than in the open access areas in the south-eastern Cape (Cowley et al. 2002). Clearly MPA's are invaluable management tools for this species.

Marine protected areas as a management tool for D. capensis in southern Angola

There are currently no MPA's in Angola, however, MPA's are gaining widespread attention as tools for conserving biodiversity while maintaining healthy sustainable fisheries (Bohnsack 1993, Bohnsack and Ault 1996, Clark 1996, Roberts 1997, Roberts and Hawkins 2000, Roberts et al. 2001, Sobel and Dahlgren 2004). Bohnsack (1990) gives a comprehensive list of the potential benefits that may be expected from the establishment of MPA's, including (1) protection of spawner biomass, (2) providing a recruitment source for surrounding areas, (3) supplemental restocking of fished areas through emigration, (4) maintenance of natural population age structure, (5) maintenance of areas of undisturbed habitat, and (6) insurance against management failures in fished areas.

There is unquestionable evidence to suggest that protecting areas from fishing leads to increases in abundance, average body size, and biomass of exploited fish populations (Roberts and Hawkins 2000). For example, the positive effects of MPA's have been well documented in Tasmania with the use of multiple reserves as replicates and unprotected areas as reference sites (Edgar and Barrett 1997, 1999, Barrett et al. 2007). Collectively, these studies have found statistically significant increases in the number, density and mean size of marine algae, invertebrates and fishes within MPA's over both short and long time scales.

Given the life-history characteristics of *D. capensis*, the physical environment in southern Angola and the current fisheries management situation in the country, MPA's are considered to be the most applicable management tool for this species. However, due to the small size of the fishery and its low economic importance, it would be difficult to motivate the proclamation of an MPA for this species alone. However, MPA's are not single species management tools, but rather form an excellent ecosystem based management tool. Other reef fish species that are caught in the subsistence, recreational and artisanal fisheries in southern Angola would also be afforded protection through inshore MPA's. These include zebra seabream *Diplodus hottentotus*, dusky grouper *Epinephelus marginatus*, golden grouper *Epinephelus costae*, bluespotted seabass *Cephalopholis taeniops,* rubberlip grunt *Plectorhinchus mediterraneus*, Steindachner's drum *Umbrina steindachneri*, Barnard's dentex *Dentex barnardii*, pink dentex *Dentex gibbosus*, red pandora *Pagellus bellottii*, red banded seabream *Pagrus auriga*, sand steenbras *Lithognathus mormyrus*, and salema *Sarpa salpa*. MPA's would also provide temporary refuge for migratory species such as west coast dusky kob *Argyrosomus coronus* [whose juveniles appear to be highly resident (Potts et al. 2010)], leerfish *Lichia amia* and bluefish *Pomatomus saltatrix*.

Despite there being substantial evidence that MPA's increase abundance, biomass, and species diversity, it will be a long time, if ever, before anyone can conclusively prove that marine reserves improve catches of fisheries (Sobel and Dahlgren 2004). However, this should not prevent them from being used, especially in developing countries. The approach of fishery managers to conservation and management in developing countries is often driven by the perceived need for stock assessment, rather than by the need to implement the most effective management regime possible (Mahon 1997). Stock assessment tools have been devised by scientists in developed countries working on large fish stocks with huge economic value. Developing countries then tend to base their approach to fisheries assessment and management on these concepts and techniques, often without adaptation and without thought to what is feasible and affordable given the nature of the fishery and the human resources available (Mahon 1997). Wilson et al. (1994) contend that the biological aspects of a fishery are too complicated and chaotic to be accurately described by numerical models and proposed that fisheries management should rather focus on controlling how, when and where to fish, rather than trying to control how much or how many fish can be caught. Caddy (1999) agreed with this view and sees the success of future inshore fisheries management to rely on the refugium approach (MPA's) and that conventional direct catch and effort controls will become redundant for inshore fisheries. The complexity and chaos contention of Wilson et al. (1994) seems particularly applicable to the current Angolan situation and MPA's offer an alternative means of fisheries management to the data and personnel intensive stock assessment based management approach.

The major factors affecting the design and performance of MPA's are not biological or physical but rather social, cultural, political and economic variables (Sobel and Dahlgren 2004). Such variables are critical to take into account when implementing an MPA and the success or failure of an MPA largely depends on these social factors. However, in southern Angola, these variables could be largely ignored for the implementation of MPA's since there are large areas of the coastline which currently receive little or no human activity. The population is centred in the two towns of Namibe and Tombua and travel along the coastline is only possible by foot, boat or 4X4 vehicle. Therefore, MPA's could be proclaimed without affecting established coastal communities. However, as outlined above, there is anecdotal evidence for expansion in the ranges of the recreational, subsistence and artisanal fisheries. Consequently, the need to implement MPA's is a matter of urgency.

The concept of integrated coastal management (ICM) is increasingly seen as holding many of the potential solutions to existing problems associated with the establishment of MPA's (Laffoley 1995). One facet of ICM is zoning, which has been used successfully in the implementation of MPA's worldwide (Day 2002, Villa et al. 2002, Friedlander et al. 2003, Klein et al. 2008). The principle objectives of zoning are (1) to provide protection for critical habitats, ecosystems and ecological processes, (2) to separate conflicting human activities, (3) to protect the natural and/or cultural qualities of the MPA whilst allowing a spectrum of reasonable human uses, (4) to reserve suitable areas for particular human uses, whilst minimizing the effects of those uses on the MPA, and (5) to preserve some areas of the MPA in their natural state undisturbed by humans for the purposes of scientific research or education (Laffoley 1995). In the coastal zone of southern Angola, there is little overlap in the areas that the different resource users utilise. The major sectors utilizing the coastal zone are subsistence and recreational. The subsistence fishers are bound by transportation constraints and, as a result, their fishing activity is focused around the coastal towns.

Recreational fishers generally have access to 4X4 transportation which allows them to travel to specific areas that they wish to fish. However, at present, the majority of the recreational fishing in the area is centred around Flamingo Lodge. Therefore an opportunity exists to zone these areas for recreational and subsistence use, respectively, with a strictly no-take MPA between them. An MPA situated between a recreational and subsistence fishing area would potentially be effective at maintaining the biomass of reef associated fishes and would continue to seed the surrounding areas through spillover of eggs, larvae and adults. Such an MPA would potentially cover a substantial area since the subsistence and recreational fishing areas are roughly 15km apart. However, a large MPA is not necessarily more effective than many small ones (Roberts and Hawkins 2000) and, in fact, it has been shown that the relative benefits from reserves are similar irrespective of reserve size (Halpern 2003). Having said this, it remains critical that reserves are large enough to protect areas of habitat that will be viable over the long term and that will support ecologically viable populations (Roberts and Hawkins 2000). From the viewpoint of fisheries, many small reserves in southern Angola may be better than a few large reserves because large reserves are often more difficult to implement and enforce and many small reserves will act as a more effective buffer against catastrophic disturbances (Roberts and Hawkins 2000).

Future assessment and monitoring

The collection of suitable catch, effort and biological information used in typical fisheries assessment models is costly and time consuming, especially in developing countries. The per-recruit assessment approach that was adopted during this study has given a good “snapshot” of the current status of the *D. capensis* subsistence fishery and has highlighted the potential danger of recruitment overfishing. Since this study made use of an unexploited area, the estimate of pristine levels can be considered relatively accurate. Therefore, the SBR approach can be used as a future assessment tool for this fishery. An assessment could be carried out every 5-10 years based on biological information collected from the catches of the fishers. However, it is important to note that the SBR approach is not a “stock assessment” tool per se because it tells us nothing about the actual size of the stock (Attwood 2003). It is essentially a life-history tool that informs us about how the life-time spawning potential of an average recruit will be affected at a given level of fishing mortality. Therefore, the SBR approach is perhaps not an appropriate “assessment” tool for this fishery. Furthermore, since this species is highly resident it is susceptible to local depletion and therefore age-based sampling would have to be conducted in each specific area that *D. capensis* is exploited in order to gain an accurate assessment of each population. Due to the current lack of capacity in the Angolan fisheries department (Duarte et al. 2005) and the general neglect of the subsistence fishing sector, this approach is not suggested as a future assessment or monitoring tool.

Alternatives to age-based models are therefore required in order to assess and monitor the *D. capensis* resource in the future. It is proposed that these include simple indicators that can be used to assess the level of exploitation on the resource. The data requirements for such a monitoring protocol will allow for the following management measures to be obtained (the significance of which is also described):

1) Distribution and amount of effort: a major concern of the recreational and subsistence fisheries is the potential spread and increase in effort. This is important to quantify in order to gain an understanding of the amount of natural refuges available to *D. capensis* and other reef fishes.
2) Gear characteristics: it is important to monitor the method of capture and the gear characteristics of the fishers. A smaller hook size will render a greater proportion of the population susceptible to capture, which could increase the risk of growth overfishing.
3) Fate of catch: it is important to monitor whether the catch of the fishers is being used as a source of food or whether they are selling their catch as a source of income. If fishers start selling their catch, there will be an incentive to increase their investment into gear which could lead to further overexploitation.
4) Mean size of fish: one of the immediate and most obvious effect of fishing is a reduction in the mean size of fish in the population (Jennings et al. 1999). Therefore, the mean size of fish caught in the fishery can give an indication of the level of exploitation when compared to other fished and unfished areas.
5) Population length structure: similar to point four, a truncation of the length structure of the population is another conspicuous effect of fishing (Haedrich and Barnes 1997, Goñi 1998, Jennings et al. 1999, Hutchings 2005). Therefore, by comparing the length structure of the fished population to the unexploited one, an indication of the level of exploitation in the fishery can be obtained.

6) Index of abundance: CPUE data can provide an accurate measure of reef fish density (Willis et al. 2000) and has been used to assess spatial and temporal differences in density (e.g. Bennett and Attwood 1991, Millar and Willis 1999). The collection of CPUE data can therefore be used to compare different exploited sites with the unexploited area investigated in this study.
7) Sex ratio: in Chapter five it was shown that the sex ratio was less female biased in the exploited area than in the unexploited area because the larger fish (predominantly females) are preferentially removed by fishing. Therefore, the sex ratio could be used as an indication of the level of exploitation for this species.

These data requirements can be satisfied by collecting simple information from fishers through analysis of their catch and interviews (Figure 7.1) and can be collected by fishery personnel with limited training through access point and/or roving creel surveys. It is envisaged that each of these points be used as an indicator of the level of exploitation and incorporated into a framework such as a Traffic Light Precautionary Management Framework (TLPMF) (Caddy 2002, Potts et al. 2008). Baseline estimates of these indicators in their pre-fishing state have been collected from the unexploited area investigated during this study, which is central to the success of such an approach (Potts et al. 2008). Once cut-off values are determined, the TLPMF incorporates information from each indicator and allows the fishery manager to assess the level of exploitation from an holistic perspective.

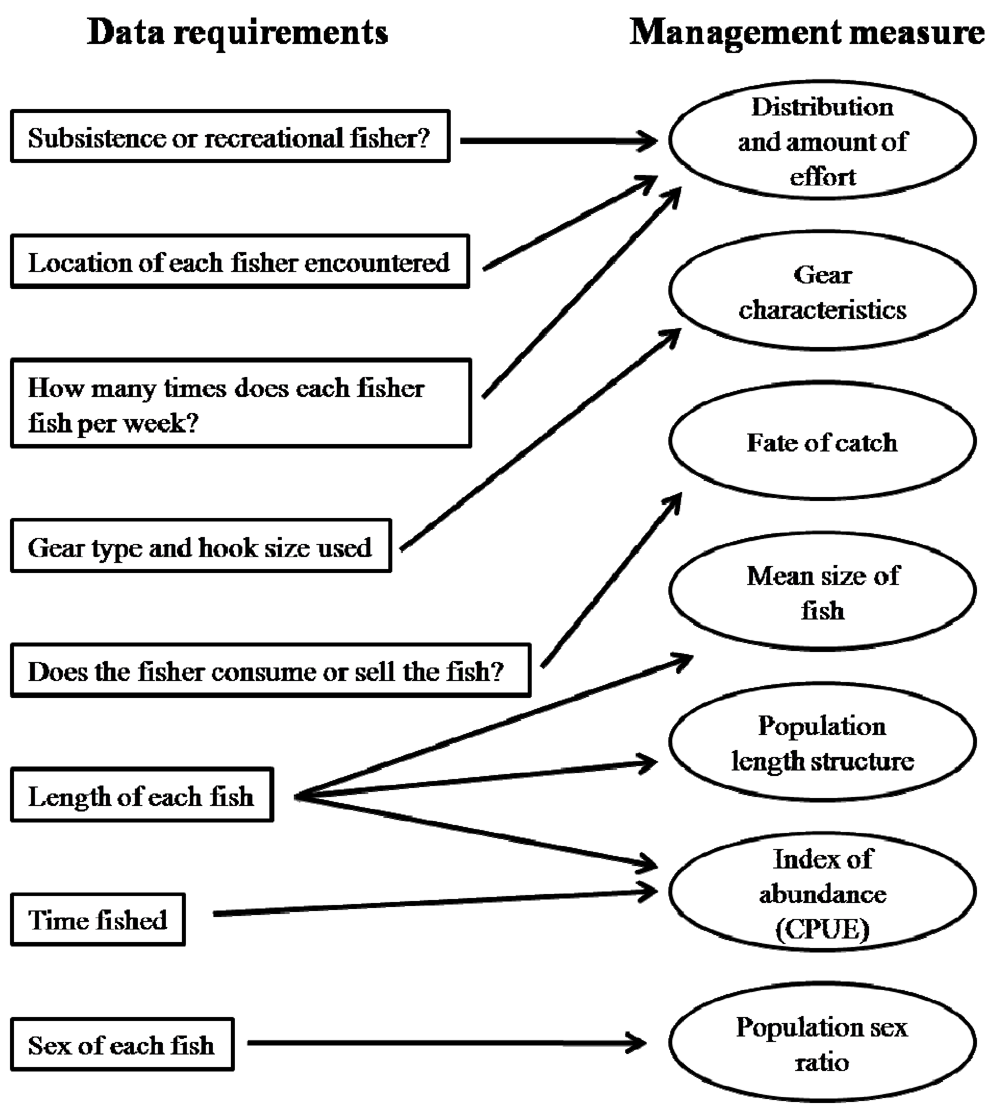

Figure 7.1: Data requirements and their associated management measures for a simple, cost-effective monitoring protocol proposed for the *Diplodus capensis* fishery in southern Angola.

Future research priorities

Based on the results of this study, the following are identified as priority research needs in southern Angola:

1) The most critical research need in southern Angola is to investigate the appropriate size and location of MPA's and their combination into networks. This should include the quantification of various designs on the protected habitat distribution, potential

egg and larval dispersal, and the change in the extent of fishing pressure of the protected populations (e.g. Kaplan et al. 2009).

2) This study has provided the very rare opportunity to collect pre-exploitation biological information for a resident reef fish population. Future work should focus on the collection of biological information of other reef associated fishes in order to obtain an accurate baseline to which exploited populations can be compared. With the observed increase in fishing pressure and the extending distribution of the fishing grounds, this should be conducted as a matter of urgency.

3) The untouched marine areas still present in southern Angola provide an opportunity to document the ecosystem structure in this region before heavy inshore exploitation occurs. This will be invaluable when adopting an ecosystem approach to fisheries management because it will provide a baseline to which exploited areas can be compared. Such research will be most effectively conducted using underwater visual census.

4) With the imminent threat of global climate change to world fisheries, the potential effects of changing sea water temperatures should be investigated for the important fishery species. Physiological studies to determine the critical thermal minimum and maximum temperatures and the tolerance of various life-stages of a species could provide a good starting point to predict future distribution shifts in marine species.

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