ASPECTS OF THE BIOLOGY OF TWO INSHORE SPARID FISHES (*DIPLODUS SARGUS CAPENSIS* AND *DIPLODUS CERVINUS HOTTENTOTUS*) OFF THE SOUTH-EAST COAST OF SOUTH AFRICA

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ABSTRACT

The blacktail, *Diplodus sargus capensis* and the zebra, *Diplodus cervinus hottentotus*, sparid fishes endemic to South Africa, are important components of the recreational shore-fishery. To provide a basis for the management of these fish, aspects of the biology of both species were investigated in the Tsitsikamma National Park (TNP). In particular, the role of the TNP was evaluated as a management option for the conservation of both species.

Examination of stomach contents showed that juveniles of both species fed predominantly on amphipods, polychaetes and harpacticoid copepods. Adult *D. sargus* were omnivorous and fed opportunistically on a wide variety of reef associated invertebrates and algae including echinoids, polychaetes, anthozoans, ascidians and rhodophytes. The diet of adult *D. cervinus* was more specialized with a preference shown for polychaetes and amphipods. Seasonal differences were apparent in the diets of both species where considerably more amphipods were consumed in winter than in summer.

Feeding requirements of both species were reflected in their habitat preferences. Visual underwater assessment revealed that both species were most abundant on turbulent inshore reefs (1-10m). *D. sargus* were observed over a wide variety of reef associated habitats. In the literature they have also been recorded in the surf zone of sandy beaches and in the lower reaches of estuaries. *D. cervinus*, on the other hand, were more specific in their habitat requirements and were observed in greatest abundance on inshore reefs, often in close association with caves or overhangs. A comparison between the relative abundance and size structure of both species in the TNP with that of an exploited area immediately adjacent to the reserve, showed no significant differences. This was attributed to the low level of exploitation by rock-and-surf anglers occurring in the exploited study area, as well as the possibility of seeding of eggs and larvae, or emigration of adults from the TNP.

An investigation of the reproductive biology of both fish showed that *D. sargus* had an extended summer spawning season while in *D. cervinus* it was more restricted. Detailed histological examination of gonadal development showed that *D. sargus* were dygynous with partial protandry occuring in the male population.

D. cervinus were shown to be rudimentary hermaphrodites. Size at 50% maturity in *D. sargus* and *D. cervinus* was determined at 225 and 285mm fork length respectively, corresponding to ages of 4 and 6 years.

An age and growth study based on the examination of sectioned otoliths showed that both species were slow growing capable of reaching ages in excess of 20 years. Growth in *D. sargus* and *D. cervinus* was described by the von Bertalanffy growth equations:

$L(t) = 309.44(1-e^{-0.247[t+1.048]})$ and

$L(t) = 396.85(1-e^{-0.146[t+2.148]})$ respectively.

Life history characteristics of *D. sargus* and *D. cervinus* including slow growth, late maturation and occupation of a localised, demersal habitat showed that both species were vulnerable to the effects of over-fishing. Due to the present increase in the number of participants and the decrease in catch per unit effort in the recreational shore-fishery, more stringent management recommendations were proposed to ensure the adequate protection of both species. These included an increased minimum size limit and a decreased bag limit for both species. Based on the residency shown by both species and their high relative abundance in the TNP, marine reserves were considered to be a valuable addition to the suite of management options available for the conservation of these species. In this respect the reserve provided both protection for the spawner stock as well as the potential to seed adjacent areas.

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CHAPTER 1 - GENERAL INTRODUCTION

> The miracle of life defies the universal law of degradation, creates highly complex organic molecules, organizes chaotic matter into incredibly well programmed structures made of trillions of cells. It is the contemplation of life that inspired Father Teilhard de Chardin to meditate on the three infinities: in addition to the infinitely big and to the infinitely small, Teilhard told us there also was the *infinitely complex*: **Life** (J.Y. Cousteau 1979).

The South African marine ichthyofauna has 41 species belonging to the family Sparidae, 25 of which (including Diplodus sargus capensis and D. cervinus hottentotus) are endemic (Smith & Heemstra 1986). Many of these species are abundant on shallow reef ecosystems and are consequently of great importance to the South African linefishery (Penney, Buxton, Garratt & Smale 1989). The multi-species nature of this fishery coupled with the diverse sexuality inherent in the family Sparidae (Atz 1964) have complicated attempts to manage this fishery (Penney et al. 1989). To this end the Marine Linefish Programme (Van der Elst 1990) outlined the importance of investigating the biology of key species with a view to providing a scientific basis for their optimal management. It was under these auspices that the present study was undertaken.

The blacktail, Diplodus sargus, is widely distributed in the Mediterranean, eastern Atlantic and western Indian Ocean (Bauchot, Hureau & Miquel 1981). The sub-species D. sargus capensis (Smith 1844) is restricted to the area from Angola to Mozambique and southern Madagascar (Smith & Heemstra 1986). It is an abundant inshore species which favours turbulent seas and rocky shores (Van der Elst 1981). The zebra, Diplodus cervinus has a more restricted distribution, being found from the southern Mediterranean, through the Straits of Gibraltar to Cape Verde. It also occurs off the coast of Angola and southern Africa (Bauchot et al. 1981). The sub-species D. cervinus hottentotus (Smith 1844) is found along the south-east coast of southern Africa from Cape Point to Sodwana Bay (Smith & Heemstra 1986), although it appears to be most abundant between Knysna and Cape Infanta (Whibley & Garratt 1989). This species also frequents rocky inshore areas but may be found on offshore reefs down to a depth of 60m (Van der Elst 1981).

D. sargus and D. cervinus are important to the South African recreational fishery, where they are caught primarily by rock-and-surf anglers (Coetzee & Baird 1981a; Coetzee, Baird & Tregoning 1989; Clarke & Buxton 1989) and in the case of D. cervinus, by spearfishermen (Clarke 1988). Although they do not reach a particularly large size, they are both regarded as fine sporting and table fish and are actively pursued by light-tackle enthusiasts (Van der Elst 1981; Schoeman & Schoeman 1990). Rock-and-surf angling is accessible to all sectors of the community and is an extremely popular pastime. Evidence of this popularity is shown by the number of rock-and-surf anglers residing in South Africa which was estimated at 288 000 in 1987 (Van der Elst 1989). In addition to this, it has been estimated that the number of marine sportfishermen in this country is increasing annually at a rate of approximately 6.5% (Van der Elst 1986). This steadily increasing pressure on our inshore fish resources has resulted in an overall decline in catch rates and a change in the composition of catches with elasmobranchs making up an increasingly larger proportion of the catch (Coetzee et al. 1989; Van der Elst 1989). Van der Elst (op. cit.) demonstrated a change in the species composition of Natal's top ten shore-caught linefish between the period 1956-1960 and 1978-1982. From these data it can be inferred that catches of D. sargus in Natal have declined substantially (R. Van der Elst, Oceanographic Research Institute, Durban, pers. comm.).

Although recreational fishing is less important than commercial fishing in terms of the actual value of the catch landed, it nevertheless provides an extremely valuable asset to the country both in terms of indirect financial benefit (tourism, tackle, bait and other support industries) as well as the psychological and sociological benefits to the public in general (Smale & Buxton 1985; Attwood & Bennett 1990; Buxton & Clarke 1992). In view of the importance of recreational fishing and the current trends in the status of the inshore fishery, an urgent need for scientifically based management of this fishery has been stressed (Wallace & Van der Elst 1983). Due to their relatively small size, both D. sargus and D. cervinus are not targetted by club anglers and were initially given a low research priority in the marine line fish programme (Wallace & Van der Elst op. cit.). However, evidence suggests that both species are fairly heavily exploited, particularly by non-club anglers (Van der Elst 1989; Clarke and Buxton 1989) and considering their probable importance to the ecology of shallow marine ecosystems (Coetzee et al.

1989), the importance of these species has been re-evaluated. D. sargus and D. cervinus have now been given a medium and high research priority respectively (Van der Elst & Adkin 1991).

Relatively little is known about D. cervinus, information on its biology being limited to general accounts of the ichthyofauna of southern Africa (Van der Elst 1981). Limited research has been carried out on the diet and distribution of juveniles (Christensen 1978; Beckley 1985; Bennett 1987). In contrast, considerable research has already been done on D. sargus with particular regard to its diet and distribution and abundance along the coast (inter alia Christensen 1978; Joubert 1981a; Joubert & Hanekom 1980; Beckley 1985; Coetzee 1986; Lasiak 1986; Bennett 1987). However, little attention has been given to specific management recommendations for these species.

The occurrence of both Diplodus species within the Tsitsikamma National Park (TNP), a large marine reserve situated on the south-eastern Cape coast, offered a unique opportunity to study the biology and ecology of both species in a relatively undisturbed habitat. In the light of continued human expansion, the importance of marine reserves, not only as a means of conserving biotic diversity (Hockey & Buxton 1989), but as an 'open-air laboratory' in which to study organisms in their natural environments, has become increasingly relevant (Salm & Clark 1984). Marine reserves cover some 625km or 21% of the South African coastline (Robinson 1989). While many of these reserves have been establised as refuges to protect vulnerable species, few studies have attempted to evaluate their effectiveness (Roberts & Polunin 1991). Buxton & Smale (1989) pioneered attempts to evaluate the effectiveness of the TNP in conserving vulnerable linefish species and Burger (1991) examined changes in the ichthyofaunal community structure between exploited and unexploited areas. Similarly Bennett (in prep.) has examined the changes occuring in catch per unit effort (CPUE) of important shore-angling species after the establishment of the De Hoop Marine Reserve. One of the aims of the present study was to contribute to this increasing body of knowledge by evaluating the role of the TNP as a viable management option for the conservation of both Diplodus species.

The primary objective of the study was to investigate various aspects of the biology of D. sargus and D. cervinus which influence their distribution and abundance in the TNP. Chapter 2 examines the feeding biology of both species and how this effects their habitat preferences. Chapter 3 deals with the distribution, relative abundance and population structure of both species in the TNP and compares this with their present status in an exploited area adjacent to the Park. Aspects of their reproductive biology including reproductive seasonality, sex ratio, size at sexual maturity and spawning behaviour are discussed in Chapter 4. This Chapter also gives a detailed description of gonadal development and gametogenesis in both species. Age and growth of both species is described in Chapter 5. Finally, Chapter 6 concludes with a summary of those life history characteristics of the two species considered important to their management and evaluates the the role of the TNP in their conservation.

Study area

The TNP is situated on the south-eastern coast of South Africa, from Oubosstrand to Natures Valley (Figure 1). It covers 65.7km of coastline and extends 5.6km offshore except for a short section on the western boundary which extends 0.8km offshore (Hockey & Buxton 1989). The TNP was proclaimed in 1964 (Robinson 1989) and no exploitation of the area has been allowed with the exception of a two kilometer stretch west of the rest camp which is open to recreational shore-angling. On the whole, however, the littoral ecosystem of this area is believed to have reached a pristine state (Buxton 1987).

The coastline of the TNP is characterised by steep cliffs which have resulted from the erosion of a sandstone syncline with an east-west axis (Toerien 1976). These cliffs plunge approximately 180m to the sea where relatively deep water is found close inshore. The area is subjected to considerable wave energy from large, unabated swells that originate across the expanses of the Southern and Indian Oceans. Subtidally, the sedimentary rock strata form reefs that consist of long-shore ridges interspersed by gullies filled with sand or water-worn boulders (Buxton & Smale 1984).

Fish for biological samples were speared or caught on rod and line from numerous inshore areas within the TNP and off Sout River, outside the western boundary of the Park (Figure 1). Additional samples were collected at two local spearfishing competitions, one held at Knysna (Inter-provincial Championships, 8th October 1989) and the other at Plettenberg Bay (Springbok Trials, 18th August 1990). Visual census work was carried out on various subtidal reef complexes within the TNP and for comparative purposes, on exploited reefs off Sout River.

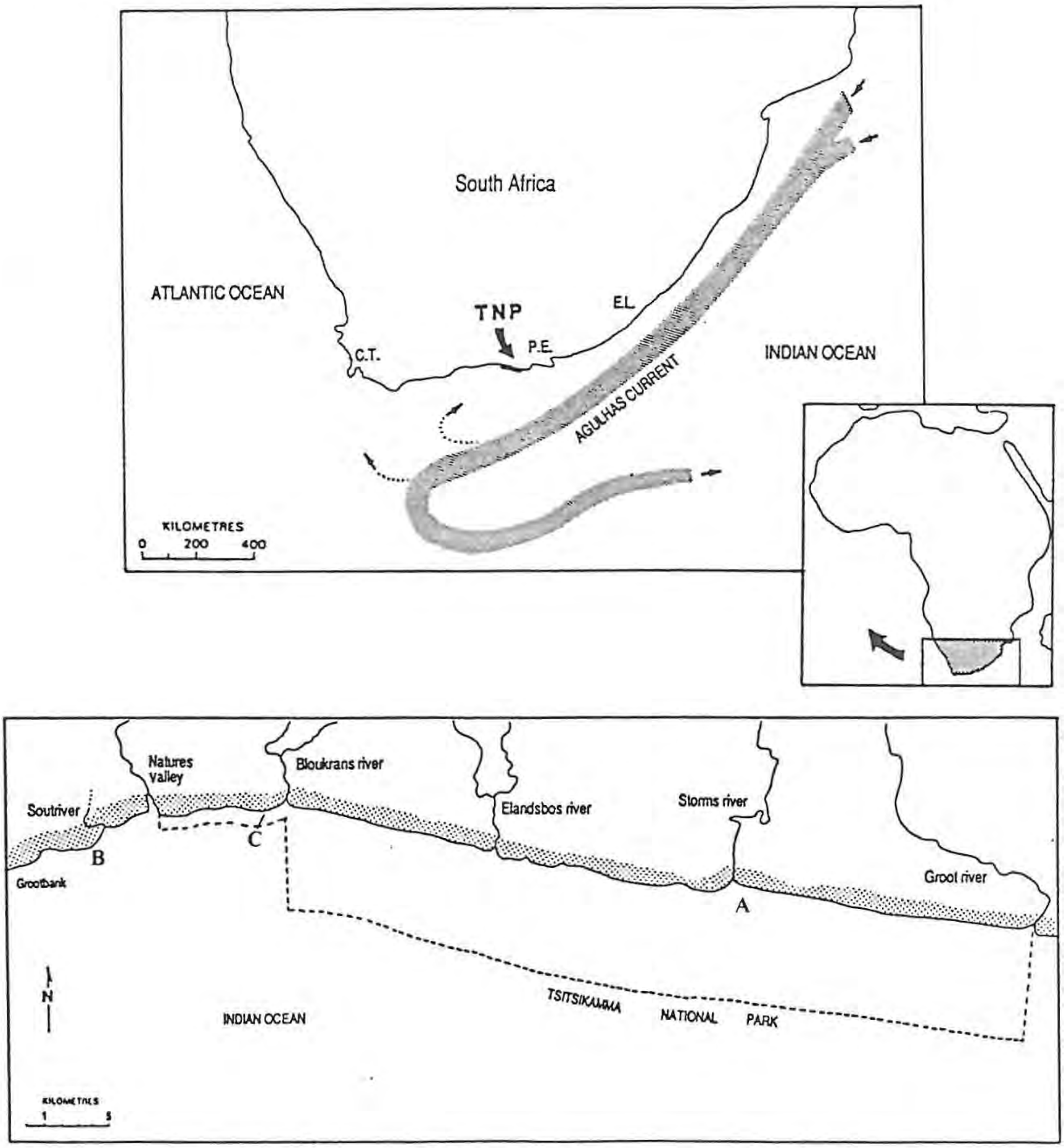


Figure 1. The position of the Tsitsikamma National Park on the south-eastern Cape coast (top) and the position of various subtidal reefs sampled both inside and outside the park. A = reefs around Storms River mouth; B = exploited reefs off Sout River; C = inshore reefs off the Bloukrans River mouth.

CHAPTER 2 - FEEDING

2.1 INTRODUCTION

Dietary studies provide valuable information on the ecology of fish species with respect to their nutritional status in the context of the ichthyofaunal community (Hyslop 1980). Although there has been a considerable amount of work published on the diet of D. sargus, much of this has focused on the diet of juveniles in the south-eastern Cape. These studies have shown that juvenile D. sargus feed predominantly on small crustaceans and chlorophytes in a variety of nursery habitats including intertidal rock pools (Christensen 1978), estuaries (Whitfield 1985) and the surf zone habitat (Lasiak 1986). The diets of larger D. sargus have been investigated in Natal (Joubert & Hanekom 1980) and off St Croix Island in Algoa Bay (Coetzee 1986). Both studies showed that larger D. sargus are omnivorous and ingest a wide variety of invertebrates and algae. Alternatively, the diet of D. cervinus has recieved little attention except by Christensen (1978) who found that juveniles, captured in rock pools in the eastern Cape, were carnivorous and fed on small crustaceans, chironomid larvae and polychaetes.

The present study was undertaken with the following objectives: 1) to describe and compare the food habits of these two morphologically similar species; 2) to investigate possible seasonal and size related differences in their food preferences and 3) to determine how feeding influences their habitat preference and distribution in the TNP.

2.2 METHODS

A total of 203 D. sargus and 189 D. cervinus were collected for stomach content analysis during the period April 1989 to December 1990. Most fish were caught by spear and line-fishing in the TNP but a small sample of juveniles (< 100mm FL) were collected from tidal rockpools and gullies using rotenone ichthyocide.

Total and gutted mass (grammes) and fork length (millimetres) were measured. Stomachs were removed by severing the oesophagus near to the buccal cavity and the intestine just anterior to the pyloric caecae and preserved in a buffered 10 percent formalin solution. To observe any changes in seasonal feeding intensity, stomach contents were weighed and an index of stomach fullness

(SFI) was calculated (Hyslop 1980).

$$SFI = \frac{\text{Stomach contents wt.}}{\text{Gutted fish wt.}} * 100$$

Stomach contents were then identified to the lowest possible taxon and, in smaller fish, assigned a visual percentage volume (Christensen 1978). In larger fish, where prey items were large enough to be weighed, volume was determined gravimetrically (Buxton & Clarke 1991). Percentage frequency of occurrence was also calculated to establish the relative amounts of each prey category consumed. Here the number of stomachs in which each food type occurred was expressed as a percentage of the total number of stomachs containing food (Hynes 1950). A ranking index (RI), the frequency of occurrence multiplied by the mean percentage volume/weight (Hobson 1974) was then computed for each prey group.

Changes in feeding with season were determined by comparing diets of fish caught during summer (October to March) with those caught during the winter months (April to September).

To determine whether there was a change in the diet of both Diplodus species with increasing size, fish were arbitarily divided into three size classes according to states of maturity: juveniles (32-150mm FL), sub-adults (151-225mm FL for D. sargus and 151-300mm FL for D. cervinus) and adults (D. sargus >225mm FL and D. cervinus >300mm FL).

Food overlap between the two species was calculated using the Spearman rank correlation coefficient (Fritz 1974).

$$r_s = \frac{\text{Sum } x^2 + \text{Sum } y^2 - \text{Sum } d^2}{2\ (\text{Sum } x^2)(\text{Sum } y^2)}$$

Where $\text{Sum } x^2 = \frac{N^3 - N}{12} - \text{Sum } Tx$ and $\text{Sum } y^2 = \frac{N^3 - N}{12} - \text{Sum } Ty$

Where r_s = Spearman rank correlation coefficient, N = number of ranks, d = difference between ranks and Sum Tx and Sum Ty are the number of tied observations for the x and y variables respectively.

2.3 RESULTS

Spear and line-fishing in relatively shallow water (<15m) appeared to minimise the regurgitation of stomach contents resulting from barotrauma (Buxton 1984). Of the 203 D. sargus stomachs sampled 68.5% contained food as did 80% of the 189 D. cervinus stomachs sampled.

Stomach fullness

Calculation of a monthly stomach fullness index (SFI) showed little seasonal variation in the amount of food consumed by both species (Figures 2 & 3). D. sargus did however show a higher mean (SFI=0.435) for the summer months (October to March) as opposed to the winter mean of 0.298.

Feeding seasonality in D. sargus and D. cervinus

The major prey categories of D. sargus are shown in Figure 4. A clear shift in diet was apparent with amphipods making up 39.5% (RI) of their diet during the winter and only 8.7% (RI) in summer. During summer, anthozoans, ascidiaceans, gastropods and algae were more important in their diet. This difference was most noticeable in juvenile D. sargus in which amphipods made up a major proportion (93% RI) of their winter diet. In summer they were partially replaced by polychaetes, harpacticoid copepods and Telmatogeton larvae.

A similar trend was observed in D. cervinus (Figure 5). In winter amphipods constituted 30.2% (RI) of their diet decreasing to 17.4% (RI) during the summer months. The deficit was replaced by other prey, especially polychaetes and decapod crustaceans, during the summer months.

The amphipods preyed upon by D. sargus and D. cervinus consisted of a number of species the majority of which belonged to the families Eusiridae, Gammaridae and Caprellidae. The most important prey species were Paramoera capensis and Caprella spp. which are abundant epifaunal carnivores (Griffiths 1976) and may be found living in association with seaweeds on rocky shores (Branch & Branch 1981).

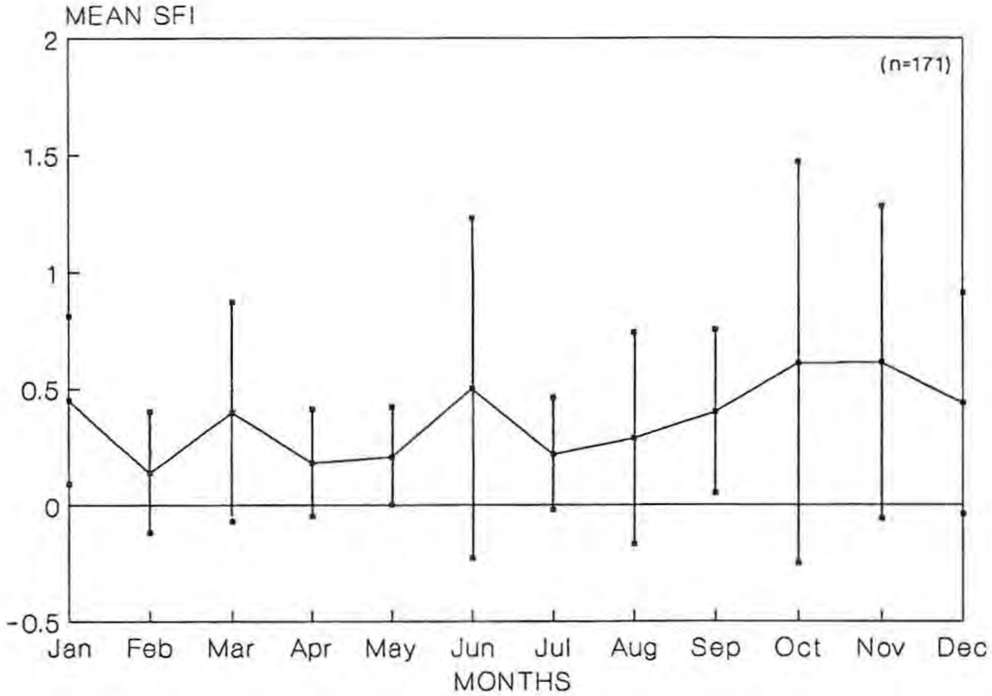


Figure 2. Mean monthly stomach fullness indices for <u>Diplodus sargus capensis</u>, sampled in the TNP from April 1989 to December 1990.

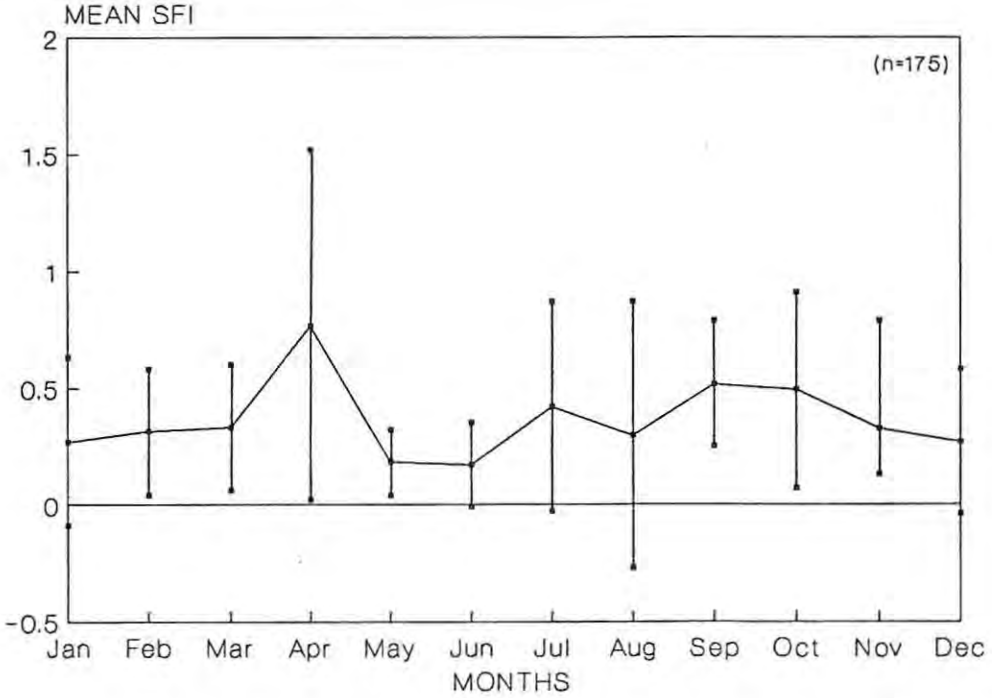


Figure 3. Mean monthly stomach fullness indices for <u>Diplodus cervinus hottentotus</u>, sampled in the TNP from April 1989 to December 1990.

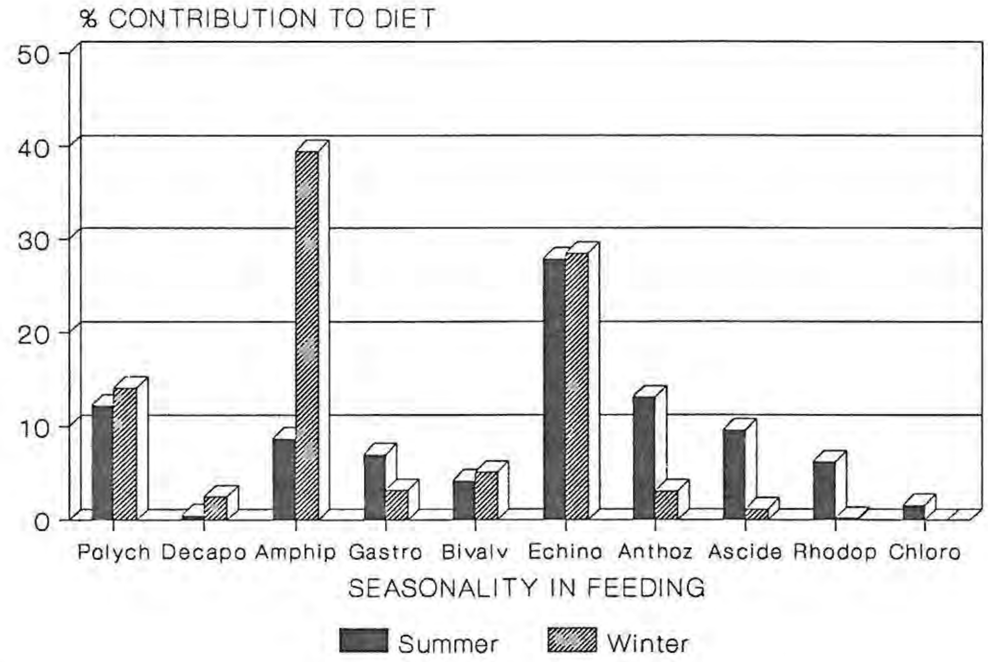


Figure 4. Seasonal changes in the major dietary items consumed by *Diplodus sargus capensis* in the TNP (n=138).

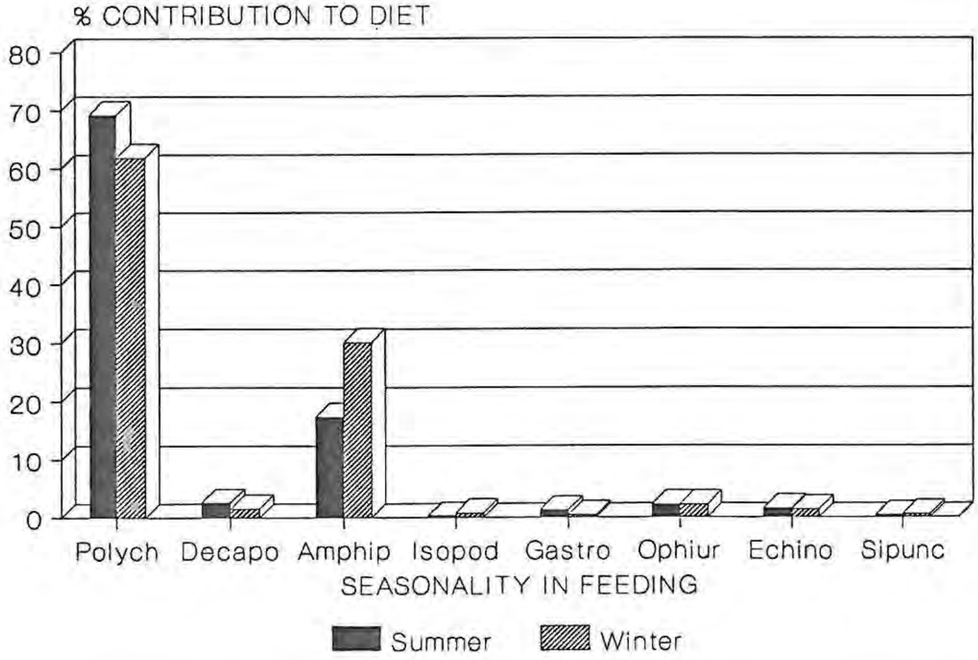


Figure 5. Seasonal changes in the major dietary items consumed by *Diplodus cervinus hottentotus* in the TNP (n=151).

Dietary composition of D. sargus of different size classes

A total of 34 juvenile D. sargus (41-150mm FL) were collected from intertidal rockpools and subtidal gullies. These fish were often found in large shoals where they appeared to feed on vertical surfaces of the substratum or in midwater away from cover. Amphipods, polychaetes, copepods and echinoids were the most important dietary components in juvenile D. sargus (Table 1). Gammarid and caprellid amphipods ranked as the most important prey items both in terms of frequency of occurrence (73.5%) and percentage volume (49.7%). Harpacticoid copepods appeared to be an important food source to only the smaller size classes of juvenile D. sargus (41-60mm FL). Amphipods and small polychaete worms became more important in the larger size classes (50-150mm FL). The occurrence of tube feet of the urchin Parachinus angulosus in the stomach contents of juvenile D. sargus showed evidence of a browsing habit (Hughes 1980), similar to that of juvenile Sparodon durbanensis (Buxton & Clarke 1991). In contrast to the findings of others (Christensen 1978; Whitfield 1985; Lasiak 1986), juvenile D. sargus in the TNP consumed very little green algae.

Sub-adult D. sargus (151-225mm FL) were found in shallow subtidal areas where they occurred in loose shoals of similarly sized individuals. They fed on a wide range of prey organisms associated with a rocky substratum. Echinoids, polychaetes, anthozoans, gastropods and bivalves were among the most important prey components (Table 2). Amphipods were less important in the diet of sub-adults which had a preference for slightly larger prey items. This diverse spectrum of prey organisms consumed by D. sargus was characteristic of the feeding behaviour of searchers (Hughes 1980).

Adult D. sargus (226-331mm FL) were also found to occur in aggregations of similarly sized individuals. They were found predominantly in the inshore zone and were seldom observed deeper than 15m. Little change in the diets between sub-adults and adults was observed except for an increase in the amount of the solitary ascidiacean, (Pyura stolonifera) (RI=2.44) and rhodophytes (RI=1.23) consumed (Table 3). Rhodophytes, consisting predominantly of coralline algae, were consumed fairly frequently (28.8% occurrence) but only constituted 4.25% of the diet by volume. This differed significantly from dietary studies of D. sargus in Natal (Joubert and Hanekom 1980) and off St Croix

Island near Port Elizabeth (Coetzee 1986) where algae was found to be an important dietary constituent.

Dietary composition of D. cervinus of different size classes

Juvenile D. cervinus normally occurred singularly and only seldom were more than 4 individuals found together. They were secretive in habit and often found near the bottom of rock pools or sublittoral areas in close association with cover. Amphipods (RI=27.22) and polychaete worms (RI=11.24) were the major prey items in the diet of the 23 juvenile D. cervinus (32-150mm FL) sampled (Table 4). Similar to the findings of Christensen (1978), smaller fish (32-50mm FL) fed mainly on chironomid larvae (Telmatogeton minor) and harpacticoid copepods. Amphipods and polychaetes then became successively more important in the diet of larger juveniles (51-150mm FL) which tend to be less secretive and forage as searchers (Hughes 1980).

Sub-adult D. cervinus (151-300mm FL) occurred on inshore reefs in a similar habitat to D. sargus and were often seen concurrently, however, they showed a greater selection for certain prey types. Together, polychaete worms and amphipods made up 94.7% (RI) of their diet (Table 5). This feeding specialization is reflected in their thick lips and fine incisiform teeth which enable them to grasp and manipulate prey such as the polychaete Lysidice natalensis which burrows under pods of Pyura stolonifera (Day 1974). Amphipods, particularly benthic gammarids such as Paramoera capensis and caprellids were also taken in large numbers.

Adult D. cervinus (301-440mm FL) normally occurred alone or in small aggregations of up to five individuals. They were furtive in habit and frequently observed in close association with caves or boulder strewn gullies on high relief reef down to about 25m. Although their diet consisted predominantly of polychaetes (RI=17.28) and amphipods (RI=18.2), a larger spectrum of prey organisms were consumed than in sub-adults (Table 6). Other important groups included decapod crustaceans (RI=8.98) such as the rock crab, Plagusia chabrus and ophiuroids (RI=6.38) such as Ophiothrix fragilis. The ingestion of these and other prey species such as urchins and gastropods suggest that adult D. cervinus have a greater ability than sub-adults to manipulate certain prey types both in terms of capture and mastication.

Dietary overlap between D. sargus and D. cervinus

A comparison of the diets in the three size classes of D. sargus and D. cervinus showed a significant overlap between juveniles (r_S=0.591) and sub-adults (r_S=0.593, $P<0.01$). The diets of adult D. sargus and D. cervinus showed no significant overlap (r_S=0.297, $P>0.05$).

TABLE 1. Stomach content analysis of juvenile Diplodus sargus capensis between 41mm and 150mm FL, sampled in rock pools and in shallow subtidal waters in the TNP from April 1989 to December 1990 (n=34).

Prey Species	% Freq.Occ.	Mean % Vol.	Rank
AMPHIPODA	73.52	49.69	36.53
Caprellidea	38.23		
Gammaridea	55.88		
POLYCHAETA	23.52	8.05	1.89
COPEPODA	8.82	7.20	0.63
Harpaticoidea	8.82		
ECHINOIDEA	8.82	5.44	0.48
Parechinus angulosus	8.82		
PISCES	11.76	3.44	0.40
Scales	11.76		
ANTHOZOA	14.70	2.64	0.38
INSECTA	14.70	2.50	0.36
Telmatogeton minor	14.70		
ISOPODA	14.70	2.26	0.33
GASTROPODA	11.76	2.79	0.32
BIVALVIA	5.88	3.82	0.22
CHLOROPHYTA	2.94	2.44	0.07
ASCIDIACEA	2.94	2.05	0.06
DECAPODA	2.94	0.44	0.01
MYSIDACEA	2.94	0.29	T
RHODOPHYTA	2.94	0.23	T
CIRRIPEDIA	2.94	0.14	T
TANAIDACEA	5.88	0.04	T
Apseudes digitalis	5.88		
UNIDENTIFIED	14.70	6.47	0.95

Trace (T) = Items with a rank of less than 0.01

TABLE 2. Stomach content analysis of sub-adult _Diplodus sargus capensis_ between 151mm and 225mm FL, sampled in the TNP from April 1989 to December 1990 (n=53).

Prey Species	% Freq.Occ.	Mean % Mass	Rank
ECHINOIDEA	47.16	22.97	10.83
Parechinus angulosus	47.16		
POLYCHAETA	35.84	10.52	3.77
Lysidice natalensis	3.70		
Lepidonotus semitectus	3.70		
Serpula vermicularis	3.70		
ANTHOZOA	33.96	8.96	3.04
Bunodactis reynaudi	9.25		
GASTROPODA	28.30	9.50	2.69
Patella spp.	11.11		
Fissurella mutabilis	3.70		
Amblychilepas scutellum	3.70		
Littorina spp.	3.70		
BIVALVIA	28.30	8.52	2.41
Perna perna	7.40		
Septifer bilocularis	3.70		
AMPHIPODA	26.41	5.84	1.54
Gammaridea	18.51		
Caprellidea	7.40		
ASCIDIACEA	16.98	7.81	1.32
Pyura stolonifera	5.55		
RHODOPHYTA	22.64	4.30	0.97
Duthiophycus setchelli	9.25		
DECAPODA	16.98	4.49	0.76
Cyclograpsus punctatus	1.85		
Plagusia chabrus	1.85		
OPHIUROIDEA	11.32	2.79	0.31
HOLOTHURIDAE	9.43	2.94	0.27
PORIFERA	11.32	1.83	0.20
BRYOZOA	13.20	0.78	0.10
SIPUNCULIDA	5.66	1.32	0.07
Phascolosoma spp.	5.66		
PISCES	3.77	1.96	0.07
CIRRIPEDIA	11.32	0.64	0.07
POLYPLACOPHORA	5.66	0.98	0.05
ISOPODA	3.77	0.41	0.01
Dynamenella huttoni	1.85		
ASTEROIDEA	1.88	0.56	0.01
HYDROZOA	7.54	0.11	T
CEPHALOPODA	1.88	0.37	T
PYCNOGONIDA	3.77	0.13	T
INSECTA	1.88	0.20	T
CHLOROPHYTA	1.88	0.18	T
TANAIDACEA	1.88	0.18	T
UNIDENTIFIED	9.43	1.60	0.15

Trace (T) = Items with a rank of less than 0.01

TABLE 3. Stomach content analysis of adult *Diplodus sargus capensis* between 226mm and 331mm FL, sampled in the TNP from April 1989 to December 1990 (n=52).

Prey Species	% Freq.Occ.	Mean % Mass	Rank
ECHINOIDEA	46.15	24.00	11.07
Parechinus angulosus	46.15		
POLYCHAETA	32.69	12.05	3.94
Lysidice natalensis	7.79		
Lepidonotus semitectus	5.76		
Pseudonereis variegata	3.84		
Cirriformia capensis	1.92		
Gunnarea capensis	1.92		
ASCIDIACEA	19.23	12.69	2.44
Pyura stolonifera	11.53		
ANTHOZOA	21.15	10.12	2.14
Bunodactis reynaudi	9.61		
Bunodosoma capensis	3.84		
RHODOPHYTA	28.84	4.25	1.22
Duthiophycus setchelli	9.61		
Polysiphonia sp.	5.76		
Arthrocardia sp.	5.76		
Hypnea spp.	3.84		
Amphiroa ephedraea	1.92		
Gelidium amansii	1.92		
Porphyra capensis	1.92		
Champia compressa	1.92		
Jania sp.	1.92		
Corallina sp.	1.92		
BIVALVIA	17.30	5.61	0.97
Perna perna	15.38		
GASTROPODA	19.23	4.88	0.93
Patella spp.	5.76		
Amblychilepas scutellum	3.84		
Gibbula zonata	1.92		
Fissurella mutabilis	1.92		
CEPHALOPODA	11.53	7.76	0.89
Octopus vulgaris	9.61		
CIRRIPEDIA	9.61	4.69	0.45
Balanus spp.	9.61		
AMPHIPODA	15.38	2.54	0.39
Gammaridea	11.53		
Caprellidea	1.92		
CHLOROPHYTA	19.23	1.88	0.36
Ulva spp.	13.46		
Bryopsis spp.	7.69		
DECAPODA	17.30	1.40	0.24
Plagusia chabrus	9.61		
BRYOZOA	15.38	0.51	0.07
INSECTA	3.84	0.78	0.03
ISOPODA	7.69	0.30	0.02

Table 3 cont/...

TABLE 3. continued

Prey Species	% Freq.Occ.	Mean % Mass	Rank
HOLOTHUROIDEA	5.76	0.38	0.02
Pentacucumis _spyridophora_	1.92		
ASTEROIDEA	1.92	0.59	0.01
Patiriella sp.	1.92		
PORIFERA	1.92	0.25	T
PISCES	1.92	0.25	T
OPHIUROIDEA	1.92	0.09	T
Ophionereis _porrecta_	1.92		
HYDROZOA	1.92	0.01	T
UNIDENTIFIED	13.46	4.86	0.65

Trace (T) = Items with a rank of less than 0.01

TABLE 4. Stomach content analysis of juvenile _Diplodus cervinus hottentotus_ between 32mm and 150mm FL, sampled by rotenone poisoning and spear in shallow subtidal waters in the TNP from April 1989 to December 1990 (n=23).

Prey Species	% Freq.Occ.	Mean % Vol.	Rank
AMPHIPODA	69.56	39.13	27.22
Gammaridea	69.56		
Caprellidea	13.04		
POLYCHAETA	39.13	28.73	11.24
Lysidice natalensis	8.69		
INSECTA	8.69	5.86	0.51
Telmatogeton minor	8.69		
BIVALVIA	8.69	4.56	0.39
ISOPODA	8.69	3.04	0.26
Dynamenella spp.	4.34		
COPEPODA	8.69	2.60	0.22
Harpacticoidea	8.69		
TANAIDACEA	13.04	0.86	0.11
Apseudes spp.	13.04		
DECAPODA	4.34	0.21	T
GASTROPODA	4.34	0.21	T
PISCES	4.34	0.17	T
Scales	4.34		
ANTHOZOA	4.34	0.15	T
OSTRACODA	4.34	0.04	T
BRYOZOA	4.34	0.04	T
MYSIDACEA	4.34	0.04	T
HYDROZOA	4.34	0.02	T
UNIDENTIFIED	30.43	13.82	4.20

Trace (T) = Items with a rank of less than 0.01

TABLE 5. Stomach content analysis of sub-adult *Diplodus cervinus hottentotus* between 151mm and 300mm FL, sampled in the TNP from April 1989 to December 1990 (n=91).

Prey Species	% Freq.Occ.	Mean % Mass	Rank
POLYCHAETA	82.41	61.22	50.46
Lysidice natalensis	27.47		
Sepula vermicularis	14.28		
Lepidonotus semitectus	13.18		
Cirriformia capensis	13.18		
Gunnarea capensis	7.69		
Euphrosine capensis	4.39		
Pista spp.	3.29		
Thelepus spp.	3.29		
Pseudonereis variegata	1.09		
AMPHIPODA	60.43	11.78	7.11
Gammaridea	54.94		
Paramoera capensis	13.18		
Ceradocus spp.	4.39		
Caprellidea	10.98		
ECHINOIDEA	17.58	4.17	0.73
Parechinus angulosus	17.58		
OPHIUROIDEA	17.58	3.50	0.61
Ophiocoma valenciae	2.19		
Ophiothrix fragilis	1.09		
SIPUNCULIDA	18.68	1.90	0.35
Phascolosoma japonicum	18.68		
DECAPODA	10.98	2.92	0.32
Plagusia chabrus	2.19		
GASTROPODA	14.28	2.06	0.29
Haliotis spadicea	3.29		
Fissurella mutabilis	3.29		
Littorina spp.	2.19		
Gibbula capensis	1.09		
ISOPODA	9.89	1.45	0.14
Dynamenella spp.	3.29		
Mesanthura catenula	2.19		
ASCIDIACEA	2.19	1.54	0.03
Pyura stolonifera	2.19		
HOLOTHURIDAE	4.39	0.60	0.02
CIRRIPEDIA	2.19	1.14	0.02
Balanus venustus	1.09		
BIVALVIA	5.49	0.24	0.01
Perna perna	2.19		
PISCES	4.39	0.27	0.01
Scales	4.39		
MYSIDACEA	3.29	0.27	T
Gastrosaccus?	2.19		
RHODOPHYTA	4.39	0.18	T
Acrosorium maculatum	1.09		
Plocamium rigidum	1.09		

Table 5 cont/...

TABLE 5. continued

Prey Species	% Freq.Occ	Mean % Mass	Rank
NEMATODA	1.09	0.38	T
HYDROZOA	2.19	0.04	T
ANTHOZOA	2.19	0.02	T
INSECTA	1.09	0.04	T
TANAIDACEA	1.09	0.02	T
POLYPLACOPHORA	1.09	0.01	T
UNIDENTIFIED	9.89	6.03	0.59

Trace (T) = Items with a rank less than 0.01

TABLE 6. Stomach content analysis of adult *Diplodus cervinus hottentotus* between 301mm and 440mm FL, sampled in the TNP and adjacent areas from April 1989 to December 1990 (n=36).

Prey Species	% Freq.Occ.	Mean % Mass	Rank
AMPHIPODA	83.33	21.84	18.20
Gammaridea	72.22		
Paramoera capensis	22.22		
Ceradocus spp.	5.55		
Caprellidea	22.22		
Caprella sp.	5.55		
POLYCHAETA	72.22	23.93	17.28
Lysidice natalensis	16.66		
Lepidonotus semitectus	11.11		
Euphrosine capensis	5.55		
Cirriformia capensis	5.55		
Eunice sp.	5.55		
Nereidae	5.55		
Serpula vermicularis	2.77		
Syllis sp.	2.77		
Nicolea macrobranchia	2.77		
Gunnarea capensis	2.77		
Loimia medusa	2.77		
DECAPODA	61.11	14.70	8.98
Plagusia chabrus	27.77		
Eriphia smithii	5.55		
Mursia cristimanus	2.77		
OPHIUROIDEA	52.77	12.09	6.38
Ophiothrix fragilis	8.33		
O. trigrochis	2.77		
ECHINOIDEA	38.88	6.45	2.51
Parechinus angulosus	38.88		
GASTROPODA	36.11	5.15	1.86
Fissurella mutabilis	22.22		
Gibbula zonata	16.66		
Haliotis spadicea	13.88		
Amblychilepas scutellum	8.33		
ISOPODA	33.33	2.56	0.85
Dynamenella spp.	22.22		
SIPUNCULIDA	19.44	2.02	0.39
Phascolosoma japonicum	19.44		
ASCIDIACEA	8.33	4.27	0.35
Pyura stolonifera	8.33		
CEPHALOPODA	8.33	3.05	0.25
Octopus vulgaris	5.55		
PISCES	11.11	0.50	0.05
Chorisochismus dentex	2.77		
HOLOTHURIDAE	5.55	0.52	0.02
Pentacta doliolum	2.77		
ANTHOZOA	11.11	0.25	0.02
Bunodactis reynaudi	5.55		

Table 6 cont/...

TABLE 6. continued

Prey Species	% Freq.Occ.	Mean % Mass	Rank
BIVALVIA	11.11	0.15	0.01
Perna perna	5.55		
PYCNOGONIDA	8.33	0.18	0.01
ASTEROIDEA	2.77	0.33	T
Patiriella exiqua	2.77		
POLYPLACOPHORA	5.55	0.12	T
Chiton tulipa	2.77		
RHODOPHYTA	5.55	0.04	T
Gelidium amansi	2.77		
Corallina sp.	2.77		
CIRRIPEDIA	5.55	0.02	T
BRYOZOA	2.77	0.01	T
UNIDENTIFIED	8.33	1.72	0.14

Trace (T) = Items with a rank of less than 0.01

2.4 DISCUSSION

Feeding studies on juvenile D. sargus from various coastal habitats (Christensen 1978; Joubert and Hanekom 1980; Whitfield 1985; Lasiak 1986) have shown that although a certain degree of trophic plasticity exists, major prey items are similar, namely small crustaceans (amphipods, harpaticoid copepods, isopods, cirripede nauplii, crab zoeae and ostracods), chlorophytes and polychaetes. Seaweeds found in rock pools and in shallow subtidal areas serve as micro-habitats for a diverse and abundant epifauna (Branch & Branch 1981) and are important foraging grounds for juvenile D. sargus. A change in foraging behaviour with increasing size was observed. Small, shoaling juveniles fed on planktonic crustaceans while larger juveniles and sub-adults browsed on benthic invertebrates and algae. This adoption of a benthic foraging habit occurs with the development of a more robust dentition and an increase in the number of molars on the upper and lower jaws (Christensen 1978).

Soon after their recruitment into nursery areas juvenile D. cervinus feed on harpacticoid copepods and chironomid larvae (Christensen 1978). Diving observations revealed that small juveniles (30-100mm FL) remained close to shelter, straying out periodically to feed on rhodophytan epifauna. Midwater feeding was not witnessed but occassionally single individuals were observed swimming with shoals of juvenile D. sargus of a similar size. The diet of larger juveniles (100-150mm FL) changed with an associated change in feeding behaviour. Fish of this size were not always found in the immediate vicinity of cover and tended to spend a large amount of time actively searching for amphipods and small polychaete worms which became major constituents in their diet. Although their dentition and short gut is similar to that of D. sargus and typical of an omnivore (Weatherly 1972), no algae were found in stomach contents of juvenile D. cervinus. This provides evidence that juvenile D. cervinus are carnivorous (Van der Elst 1981).

A significant dietary overlap was found in juvenile D. sargus and D. cervinus, both species feeding predominantly on gammarid and caprellid amphipods. Similarly, Christensen (1978) found considerable overlap in the diets of these species, particularly in the smaller size classes. Juvenile D. sargus were far more abundant in tidal rock pools and subtidal gullies than juvenile D. cervinus (Burger 1991) and observations showed that feeding behaviour differed between the two species. However, overlap measures are basically measures of similarity (Smith 1985) and the original interpretation of overlap as a measure of competition has been shown to be invalid (Hulbert 1978, Schoener 1983). Burger (1991) found that benthic amphipods were important to the diet of 18 other littoral fish species inhabiting tidal rock pools and subtidal gullies in the TNP. Since amphipods were not identified to species and the spacial and temporal aspects of the utilization of this resource were not investigated, dietary overlap between these co-habiting species should be seen as high usuage of a common food resource.

The importance of gammarid and caprellid amphipods as prey to both Diplodus species during winter, suggests that there is an increase in their abundance and/or availability. There is however, no record of seasonal fluctuation in the abundance of benthic amphipods along the coast of southern Africa (Prof. C.L. Griffiths, University of Cape Town, pers. comm.), and little is known about the biology of individual species.

Sub-adults of both D. sargus and D. cervinus are found over a wide range of habitat patches on shallow inshore reefs (0-15m). These habitats range from flat boulder beds interspersed with sand, to high relief reef with crests dominated by Pyura stolonifera. Observation showed that sub-adults of both species adopt a similar foraging strategy, during which an individual would swim just above the reef actively searching for prey. Fish using this type of foraging behaviour are known as searchers (Hughes 1980) and the time spent pursuing or handling prey is short relative to the time spent searching during a foraging period. Searchers are also characterized by having wide diets as prey are ingested opportunistically and all potential prey are consumed when encountered.

Although analysis showed significant dietary overlap between sub-adults of the two species, D. cervinus showed a clear preference for 'softer' prey, primarily polychaete worms and amphipods, which together make up 95% of their diet. D. cervinus are morphologically well adapted to feeding on polychaetes and amphipods because they have few molars and narrow incisors. This, together with their fleshy lips, assists them in capturing these invertebrates. D. sargus on the other hand have a more robust dentition, more molars and stronger incisors, typical of generalised invertebrate feeders. This feeding specialization would serve to fascilitate the co-existence between sub-adults of these two species which show spatial and dietary overlap.

Fishing and diving observations revealed that D. sargus fed diurnally with large specimens often being caught in shallow, turbulent gullies during high tide. From dietary analysis it was evident that sub-adult and adult D. sargus made excursions into these areas to feed on prey species such as brown mussels Perna perna, red-bait Pyura stolonifera, mussel worms Pseudonereis variegata and a variety of gastropod molluscs (Tables 2 & 3), which inhabit the lower balanoid intertidal zone (Branch & Branch 1981). Futhermore, it was apparent that D. sargus also fed actively at night. This was deduced from the high occurrence of small sea urchins Parechinus angulosus in their stomach contents. These organisms are common on shallow, inshore reefs but small specimens remain under rocks or stones during the day, only emerging at night to feed (Branch & Branch 1981). D. sargus only fed on small urchins which could be swallowed whole and it is suggested that feeding on these organisms took place at night. Schoeman & Schoeman (1990) report that D. sargus are frequently caught at night which provides further evidence of nocturnal feeding activity in this species.

Predation on sea urchins (P. angulosus) by D. sargus may form an important aspect of the trophic dynamics of shallow reef ecosystems. A number of workers (e.g. Hay 1984, McClanaghan & Shafir 1990) have noticed increases in numbers of urchins in heavily fished areas and have suggested this is a result of decreased predation by fish. Increased densities of urchins may cause decreases in algal cover thereby exerting an indirect influence on the distribution and abundance of juvenile D. sargus, which feed on the epifauna associated with these algae. A similar relationship was found between Chrysophrys auratus and Evechinus chloroticus in a shallow subtidal reef system in north-eastern New Zealand (Kingett & Choat 1981). It is suggested that dramatic increases in the number of urchins occuring in shallow reef ecosystems may be used as an indicator of environmental perturbations such as over-fishing. However, this aspect would require further detailed research.

Although D. sargus was found to be omnivorous, algae only made up 6.1% of their diet in the TNP and of this 97% was consumed during the summer months (see Figure 4). An analysis of the contents of the hindgut may have increased the apparent proportion of algae consumed, but hindguts were not analysed because differential retention times of undigestible material in the hindgut may bias results (Gannon 1976). In a study on the diet of D. sargus off St Croix Island in Algoa Bay, Coetzee (1986) found that algae made up 35% of the total dietary composition of fish between 210 - 420 mm TL. This increased to 50% if the whole alimentary tract was considered. Similarly, Joubert & Hanekom (1980) found algae, particularly Ulva species, to be important to the diet of D. sargus along the Natal coast. Both these studies showed that algae pass through the alimentary tract without being digested. Joubert & Hanekom (1980) showed evidence that seaweeds ingested by D. sargus act merely as a substrate for epiphytic diatoms which are digested.

There is no evidence to suggest that algae are limited along the Tsitsikamma coastline and calcareous algae, particularly Corallina spp. and Amphiroa ephedraea, dominate the benthos on subtidal reefs at depths of less than 10m (Buxton & Smale 1984). The increased importance of algae in the diet of adult D. sargus during the summer months may be due to the increased water temperature and photoperiod resulting in greater productivity and abundance of epiphytic diatoms. D. sargus showed selection for certain invertebrate prey over a wide range of available prey groups including algae. Ephytic diatoms digested by D. sargus probably constitute only a small proportion in relation to the animal food intake, and D. sargus may in fact be largely carnivorous (Joubert & Hanekom 1980).

The feeding specialization exhibited by sub-adult D. cervinus was also present in adult fish, in which polychaetes and amphipods made up 62% of their diet. Unlike the adults of other sympatric sparid species, such as Chrysoblephus laticeps (Buxton 1984) and Sparodon durbanensis (Buxton & Clarke 1991), D. cervinus fed predominantly on small prey. Although adult D. cervinus occasionally fed on relatively large prey such as rock crabs (Plagusia chabrus) and small octopus (Octopus vulgaris), particularly during the summer, the tendency to feed on large prey was not marked because benthic amphipods remained an important food scource in all size classes. Van der Elst (1981) stated that adult D. cervinus "change to a predominantly vegetarian diet" from being carnivorous as juveniles. This was not apparent in this study where algae constituted only trace amounts (RI<0.01) in the diet of adults. This shows that algae are ingested accidentally, probably while feeding on epifaunal amphipods, and that adult *D. cervinus* are carnivorous.

Polychaete worms ingested by *D. cervinus* included both active (Errantia) and sedentary forms (Sedentaria). The most important prey species (*Lysidice natalensis*, *Lepidonotus semitectus* and *Cirriformia capensis*) are commonly found living among red-bait pods (*Pyura stolonifera*) (Day 1967). Red-bait are filter feeders that thrive in areas where there is strong wave action or surge. Although normally associated with wave-beaten shores, Buxton & Smale (1984) recognised the importance of red-bait on subtidal reefs where they encrust reef crests at depths of up to 20m. Adult *D. cervinus* are powerful swimmers which enables them to feed on polychaete species associated with these red-bait colonies, both on turbulent inshore reefs and on deeper reefs.

Prey selected by adult *D. sargus* and *D. cervinus* showed no significant overlap. While they both consumed a wide range of prey organisms, the diet of *D. cervinus* was dominated by comparatively few prey groups. In addition, large *D. cervinus* were often encountered in discrete habitats in which they appear to be resident. This habitat selection may have been directly related to the availability of their preferred prey in these areas. Alternatively, adult *D. sargus* occurred in large numbers over a wide variety of inshore habitats. This lack of specialization in both habitat and prey selection was characteristic of the generalised, opportunistic nature of this species.

CHAPTER 3 - DISTRIBUTION AND ABUNDANCE

3.1 INTRODUCTION

One of the basic aims of ecology is to determine the causes underlying the distribution and abundance of organisms (Krebs 1985). Studying the ecology of marine organisms has lagged behind that of terrestrial animals due to the difficulties associated with working in the marine environment. The advent of SCUBA has greatly facilitated our ability to study marine organisms that occur in relatively shallow, nearshore environments (Buxton 1987). A variety of non-destructive, visual census techniques have been developed for estimating fish abundance (see review by Thresher & Gunn 1986), but these methods only provide an index of relative abundance, not an absolute measure of population size. However, they do provide an excellent method for determining depth and habitat preferences of fish and for comparing population structures between areas (Buxton & Smale 1989).

Although the establisment of marine reserves as a method of coastal resource management has increased dramatically over the past few years, there have been few attempts to evaluate their effectiveness (Roberts & Polunin 1991). The relatively pristine conditions occuring on subtidal reefs in the TNP offered a unique opportunity to study the depth and habitat preferences of both Diplodus species in their natural environment. Furthermore, by surveying an exploited area adjacent to the Park, which has been shown by Burger (1991) to have an altered community structure, an attempt was made to evaluate the role of the TNP in providing protection for these linefish species.

While D. cervinus are seldom seen or caught in great numbers (Schoeman & Schoeman 1990), D. sargus appears to be relatively abundant in many areas along the South African coast, even in areas subjected to relatively heavy fishing pressure such as the coast near Port Elizabeth (Clarke & Buxton 1989). These observations have led to speculation that this species is capable of colonizing exploited reef environments from which other, more specialized reef fish species have been removed. The reefs off Sout River provided an area adjacent to the TNP which is subjected to exploitation from ski-boat anglers, spear-fishermen, and to a limited extent, by rock-and-surf anglers. This area was used to compare the relative abundance and size structure of both species in an exploited area with that in the reserve.

The central objective of the study was to obtain estimates of relative abundance and size frequencies of Diplodus species in a variety of different reef habitats. The following questions were addressed: 1) Do different areas of the reef ecosystem support different population structures of Diplodus species? 2) What factors influence their distribution? 3) In similar habitats, does the relative abundance of Diplodus species differ inside and outside the marine reserve and, if so, are these differences attributable to exploitation?

The study of the distribution and abundance of fishes in a temperate marine environment is complicated by variables such as temperature changes, low visibility and habitat heterogeneity. With these inherent sources of variability, statistical analysis of the visual census data proved to be somewhat problematical, but perhaps a quote from Krebs (1985) will suffice to put this work into perspective, "...the problems of ecology are *biological* problems and will be solved not by mathematicians but by biologists."

3.2 METHODS

Sampling sites

Spatial variation in fish distribution within a temperate reef system may be high and related to specific features of the reef (Leum & Choat 1980; Kingett & Choat 1981). Buxton & Smale (1984) recognised that shallow reefs (<10m) along the Tsitsikamma coast were dominated by coralline algae, while on deeper reefs the algae were gradually replaced by filter feeding invertebrates. For the purposes of examining depth and habitat preferences of both Diplodus species in the TNP, six reef-associated habitats were recognised:

1) Sheltered inshore zones (1-10m) consisted of subtidal gullies and rocky bays sheltered from direct wave action. The seabed in these areas consisted of sand and water-worn boulders (10-100cm in diameter), while the benthos was dominated by coralline algae and sea urchins (Parechinus angulosus).

2) Exposed inshore zones (1-10m) consisted of shallow reefs within the breaker zone . This area was characterised by reef outcrops interspersed with sand and water-worn boulders (10-100cm

in diameter). Filter feeders such as mussels (Perna perna) and red-bait (Pyura stolonifera) dominated the reef outcrops, while rhodophytes (e.g. Plocamium corallorhiza), various species of coralline algae (e.g. Amphiroa ephedraea) and sea urchins (P. angulosus) were found on the less exposed parts of the reef. This habitat could only be sampled when exceptionally calm conditions prevailed.

3) Shallow high relief reefs (10-15m) consisted of ridges of reef running parallel to the shore interspersed by gullies containing sand and boulders. High relief was determined sujectively (sensu Buxton & Smale 1989) and generally consisted of reefs that rose sharply (>3m) from the surrounding area. The relief often incorporated caves, overhangs and crevices. Reef crests were covered by red-bait, while the slopes and gullies were dominated by coralline algae.

4) Deep high relief reefs (15-25m) consisted of similar reefs to those described above but were dominated by filter feeding organisms such as poriferans, ascidians, octocorals, soft corals, hydrozoans and encrusting bryozoans. Reef crests were still dominated by red-bait.

5) Shallow low relief reefs (10-15m) consisted of sandstone plateaus dominated by coralline algae (Amphiroa ephedraea and Lithothamnion spp.)

6) Deep low relief reefs (15-25m) consisted of similar reefs to those above but were dominated by filter feeders such as poriferans, ascidians and bryozoans. The invertebrate fauna was generally more sparse than that occuring on high relief reefs at the same depths.

Visual census method

The use of visual census techniques for assessing fish populations has been well documented (Kimmel 1985; Bohnsack & Bannerot 1986; Thresher & Gunn 1986; Sanderson & Solonsky 1986). Two basic techniques are recognised, namely, stationary point counts and transect counts. Stationary point counts can either take the form of instantaneous area counts (Bohnsack & Bannerot 1986) or set time counts where fish seen during a particular time interval are recorded (Kimmel 1985). Transect counts can either take the form of fixed width strip transects where divers swim along a line of set length and count each individual sighted within a set distance from the line (Thresher & Gunn 1986), or variable distance moving counts in which the distance of each fish observed from a set line is estimated (Sanderson & Solonsky 1986).

Fixed width strip transects have dominated in reef fish surveys on temperate rocky reefs (Leum & Choat 1980; Kingett & Choat 1981; Bell 1983; Buxton & Smale 1989). After experimenting with both point and strip transecting techniques, it was decided that a fixed width strip transecting technique would be most suitable for determining relative abundance and size structure of Diplodus species. The reasons for this choice were two-fold: 1) It provided a method whereby a quantitative estimate of relative abundance could be obtained for each habitat type (Sanderson & Solonsky 1986); 2) The distribution of both species was extremely 'patchy' and strip transecting provided a means whereby the greatest area of reef in each habitat type could be covered (Buxton 1987).

A multiple strip transecting technique was utilised as a large proportion of the visual census work was done in conjunction with a community level study on the Tsitsikamma littoral ichthyofauna (Burger 1991). By using multiple strip transects, all suprabenthic and semi-cryptic species observed could be enumerated. Each transect consisted of three 50m swims during which three different categories of fish species were enumerated. These included: 1) abundant species, shoals of suprabenthic species often attracted to divers e.g. Sarpa salpa, Boopsoidea inornata, Pachymetopon aeneum and Spondyliosoma emarginatum; 2) semi-cryptic species, such as the Cheilodactylids and Acanthistius sebastoides which are slow moving and difficult to observe; 3) other species including all suprabenthic species not included the above categories. Diplodus species were included under the 'other species' category.

On each dive a habitat type was selected, either from the shore or from a boat. In the inshore zone, divers swam from the shore along a 100m transect line marked off at 10m intervals. Offshore, depth and reef rugosity were determined using standard echo-sounding equipment on board a dive boat. Once the required depth was attained a shot line was dropped to mark the area and two divers descended to the reef, positioning the weighed end of the shot line on reef matching the required depth and habitat type.

One diver then swam out the 100m transect line after which the two divers swam independent 50m transects on either end of the line to minimize the effect of diver interference with fish. The number of D. sargus or D. cervinus seen in a corridor 2m on either side of the line were recorded and their sizes estimated to the nearest 50mm TL (Figure 6). Transecting was carried out at a steady, comfortable pace and after completion of two or three transects by each diver the line was moved if diving time at that depth allowed.

Assumptions

Rough seas, poor underwater visibility and various logistical difficulties associated with diving work in the TNP made it necessary to take full advantage of suitable diving conditions when they occurred. For this reason a number of assumptions, with regard to the relative abundance of Diplodus species, had to be made:

1) Temporal changes did not affect the relative abundance of either species in the particular habitats sampled (transecting was unavoidably carried out at different times of the day and during different seasons). Observations showed little indication that fish distribution changed according to the time of day and there was no evidence of seasonal spawning migrations occurring in either of the two study species. However, annual recruitment of juveniles into the shallow inshore areas, coinciding with their respective spawning seasons, significantly altered the relative abundance of fish in these inshore areas. For this reason and because juvenile D. sargus are found in large, monospecific shoals which greatly increase variability of counts (Thresher & Gunn 1986), juveniles of both species smaller than 100mm TL were excluded from the statistical analysis of their relative abundance.

2) Fish were not effected by the presence of divers. Underwater experience with these fish showed that they were generally skittish in the presence of divers, especially D. sargus. Smaller fish of both species appeared to be less disturbed by the presence of divers. Transect counts invariably under-estimate the actual number of fish present (Brock 1982; Thresher & Gunn 1986), but due to the consistency of the method used, the results were considered to be indicative of the relative abundances of fish in the different habitats sampled. More importantly, any

errors were assumed to be similar in all habitats sampled.

3) The relative abundance of Diplodus species was not affected by the range of temperatures at which sampling took place. Visual censusing was conducted at temperatures ranging from 15 to 21°C. Diplodus species are known to be tolerant of a fairly wide range of water temperatures (Van der Elst 1981; Schoeman & Schoeman 1990) and no apparent changes in abundance or behaviour were observed within this range. Considerable movement of both species were, however, recorded during periods of cold upwelling (rapid decline in water temperature) when temperatures dropped as low as 9°C. Transects done under these conditions were excluded from the analysis.

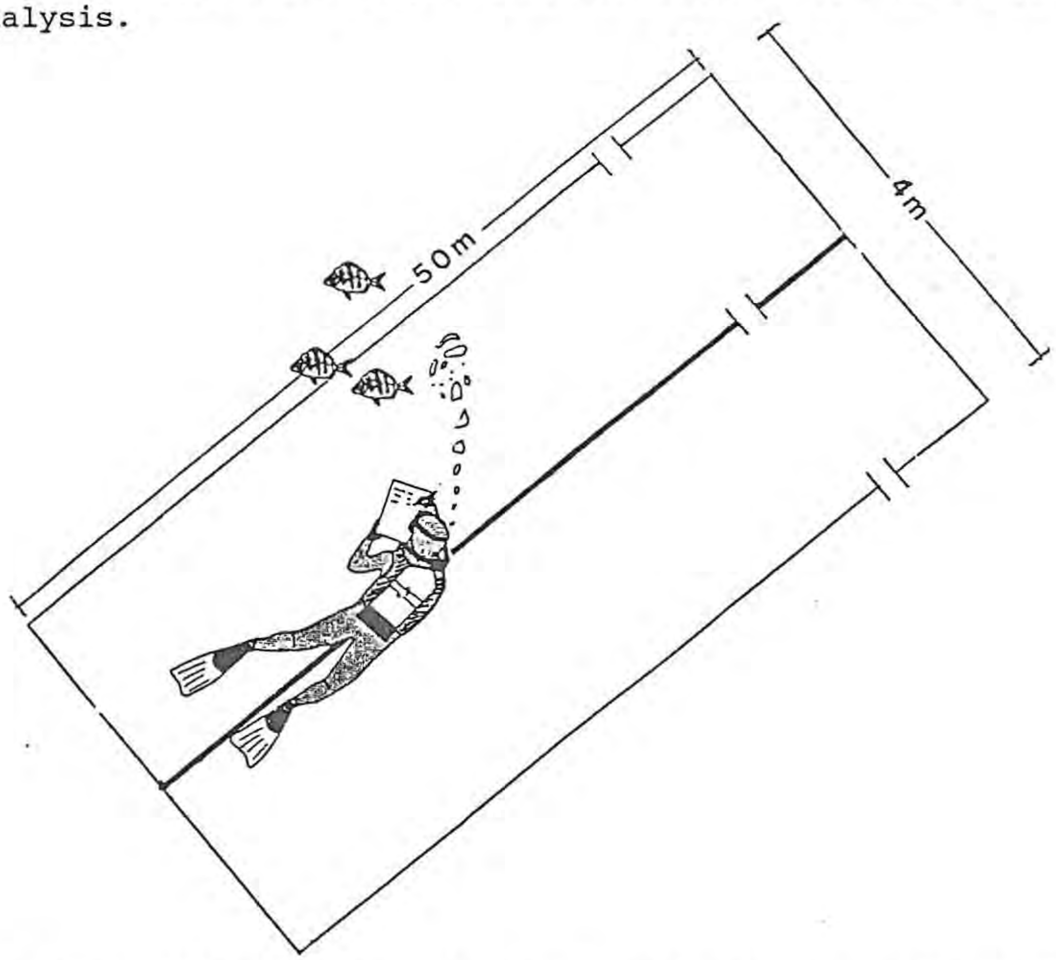


Figure 6. Illustration of the visual census method used during the study (adapted from Burger 1991)

3.3 RESULTS

Data analysis

The choice of each habitat type was subjective and in order to avoid the use of replicates that were not statistically independent (Hulbert 1984), data were collected from two or more sites representative of each of the described habitat types. Due to the 'patchy' distribution of both species and the high incidence of zero counts, count data were transformed (Log + 1) to reduce heterogeneity of variance (Kingett & Choat 1981). Transformed count data for each species from sites within each habitat type, were then compared using a one-way ANOVA and if no significant difference was found between sites, the data were pooled (Table 7 & 8). Data from all sites were pooled except for two offshore, low relief sites (10-15m) off Sout River, which showed significant differences in the number of D. sargus counted ($P<0.05$).

Comparison between the pooled data for each habitat type revealed that the relative abundance of both species was significantly higher in the inshore habitats ($P<0.05$). There were no significant differences observed between any of the offshore habitats sampled due to the low relative abundance (high incidence of zero counts) of both species on reefs deeper than 10m. However, trends in the data were apparent and these will be dicussed in more detail where relevant.

Depth and habitat preferences

The relative abundance of D. sargus and D. cervinus in the various habitat types sampled in the TNP are shown in Tables 9 & 10 respectively. Both species were found in greatest abundance on inshore reefs (1-10m), particularly those exposed to direct wave action (Figure 7). Offshore, D. sargus was seldom encountered on reefs deeper than 15m. By comparison, D. cervinus was observed, although in low numbers, on deeper reefs (15-25m), particularly in areas of high relief.

Small juveniles of both species (0-50mm TL) were found predominantly in the inshore habitats. D. sargus juveniles were common in both inshore habitats, where they comprised 74.6% and 44.9% of the population in the exposed and sheltered habitats respectively (Figure 8). Alternatively, D. cervinus juveniles were observed in greatest abundance in sheltered gullies and on low relief reefs (10-15m), where they made up 48.3% and 33.2% of the population in these two habitats respectively (Figure 9). Fish of both species larger than 50mm TL were found predominantly inshore. Those that were encountered in the offshore habitats exhibited a range of sizes (Figures 8 & 9), although only relatively large individuals (>150mm TL) were seen on reefs deeper than 15m.

Comparison between exploited and unexploited areas

A comparison between the relative abundance of D. sargus and D. cervinus in exploited and unexploited habitats is shown in Figures 10 & 11 respectively. Due to the logistical difficulties associated with working in the Sout River area (35km from launching site at Storms River), transecting was limited to three habitat types; an inshore exposed reef and two offshore low relief reefs at different depth ranges, 10-15m and 15-25m. The reefs selected were structurally similar to those of the same habitat type sampled within the TNP. No significant differences were found between the relative abundance of Diplodus species in exploited and unexploited habitats.

The higher relative abundance of D. sargus on the exploited inshore reefs (0.1577 fish m^{-2}) as compared to their abundance in the same habitat type inside the TNP (0.0452 fish m^{-2}) (Figure 10), resulted from the large number of small juveniles (0-50mm TL) counted in the exploited habitat. Of the D. sargus counted in this habitat, 83% were less than 50mm TL (Figure 12). Transecting on the exploited inshore reefs was carried out during December, shortly after the observed peak spawning season recorded for D. sargus (August to October). The large number of juveniles counted in this habitat was therefore, a result of their recent recruitment into the inshore zone.

Relative abundance of D. cervinus on inshore reefs was slightly higher in the TNP (0.0082 fish m^{-2}) than in exploited inshore reef areas (0.005 fish m^{-2}) (Figure 11). However, they were found in greater abundance on exploited offshore reefs, particularly at depths greater than 15m (0.0035 fish m^{-2}), when compared to their abundance on similar reefs inside the TNP (0.0008 fish m^{-2}). The size frequency distribution of D. cervinus from the three different habitats sampled off Sout River were similar, although the greatest size range was found inshore (Figure 13). A comparison between the overall population structure (combined size frequencies from all habitats) of D. cervinus from exploited and unexploited areas showed no significant differences (Figure 14). A simlilar comparison between the population structure of D. sargus also showed little difference in size structure of the populations between the two areas (Figure 15).

TABLE 7. Analysis of variance between counts of Diplodus sargus from sites sampled within each habitat type.

Habitat Type	Depth (m)	Number of Sites	Number of Transects	% Zero Counts	F-ratio	Sig. Level
a) TNP						
Inshore Exposed	1-10	2	63	49.2	1.181	0.2815
Inshore Sheltered	1-10	4	48	42.9	2.726	0.0554
Shallow Low Relief	10-15	2	71	63.4	0.275	0.6074
Shallow High Relief	10-15	2	54	66.7	0.059	0.8124
Deep Low Relief	15-25	2	62	98.4	0.937	0.3474
Deep High Relief	15-25	2	45	97.8	0.281	0.6044
b) Sout River						
Shallow Low Relief	10-15	2	49	57.1	11.239	0.0016*
Deep Low Relief	15-25	2	51	88.2	2.238	0.1411
Inshore Exposed	1-10	1	24	50.0	-	-

* Denotes a significant difference between sites

TABLE 8. Analysis of variance between counts of *Diplodus cervinus* from sites sampled within each habitat type.

Habitat Type	Depth (m)	Number of Sites	Number of Transects	% Zero Counts	F-ratio	Sig. Level
a) TNP						
Inshore Exposed	1-10	2	63	47.6	0.308	0.5870
Inshore Sheltered	1-10	4	48	51.8	1.587	0.2061
Shallow Low Relief	10-15	2	71	74.6	1.869	0.1760
Shallow High Relief	10-15	2	54	85.2	3.350	0.0729
Deep Low Relief	15-25	2	62	88.7	3.982	0.0505
Deep High Relief	15-25	2	45	86.7	1.378	0.2468
b) Sout River						
Shallow Low Relief	10-15	2	49	53.1	0.470	0.5037
Deep Low Relief	15-25	2	51	47.1	0.062	0.8077
Inshore Exposed	1-10	1	24	33.3	-	-

TABLE 9. The relative abundance (number of fish m^{-2}) of *Diplodus sargus* sampled in six different habitat types in the TNP.

Habitat Type	Depth (m)	Number of Transects	Total Number of Fish Seen	Mean ± S.D.	c.v.	Relative Abundance (Fish m^{-2})
Inshore Sheltered	1-10	56	309	5.52 ± 7.61	1.38	0.0266
Inshore Exposed	1-10	63	570	9.04 ±17.49	1.93	0.0452
Shallow Low Relief	10-15	71	76	1.06 ± 1.5	1.41	0.0049
Shallow High Relief	10-15	58	138	2.38 ± 7.05	2.96	0.0118
Deep Low Relief	15-25	62	2	0.03 ± 0.17	5.52	0.0001
Deep High Relief	15-25	45	10	0.22 ± 1.49	6.71	0.0011

TABLE 10. The relative abundance (number of fish m^{-2}) of *Diplodus cervinus* sampled in six different habitat types in the TNP.

Habitat Type	Depth (m)	Number of Transects	Total Number of Fish Seen	Mean ± S.D.	c.v.	Relative Abundance (Fish m^{-2})
Inshore Sheltered	1-10	56	58	1.03 ± 2.08	2.01	0.005
Inshore Exposed	1-10	63	104	1.65 ± 2.45	1.49	0.0082
Shallow Low Relief	10-15	71	34	0.47 ± 0.99	2.13	0.0021
Shallow High Relief	10-15	58	39	0.67 ± 1.83	2.72	0.0033
Deep Low Relief	15-25	62	10	0.15 ± 0.43	3.95	0.0008
Deep High Relief	15-25	45	19	0.42 ± 1.74	4.12	0.0021

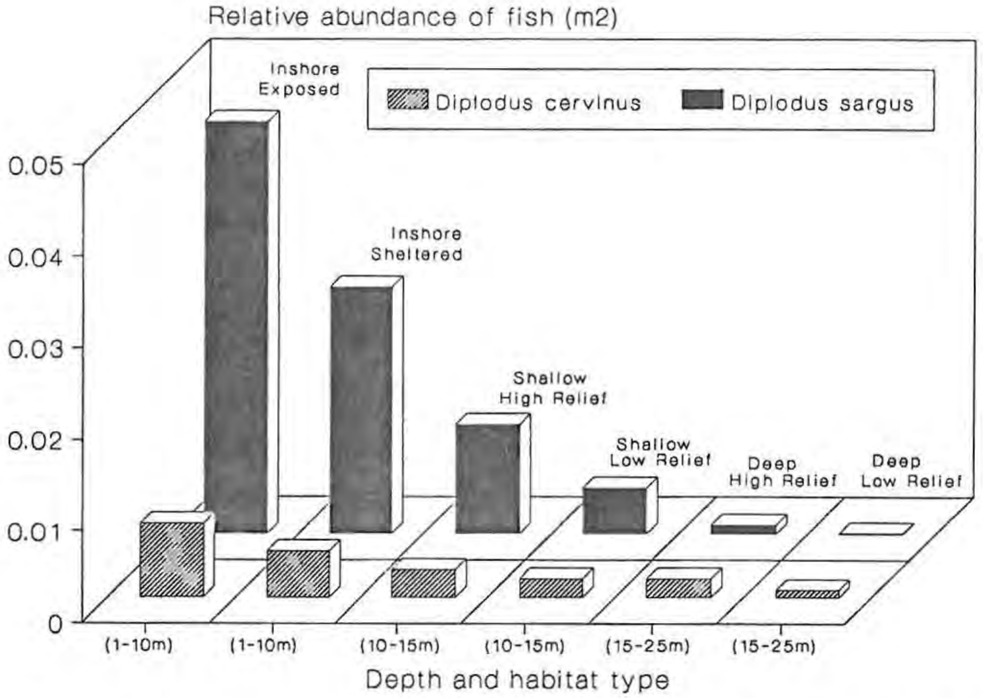


Figure 7. Depth and habitat preferences of <u>Diplodus</u> <u>sargus</u> <u>capensis</u> and <u>Diplodus</u> <u>cervinus</u> <u>hottentotus</u> sampled in the TNP.

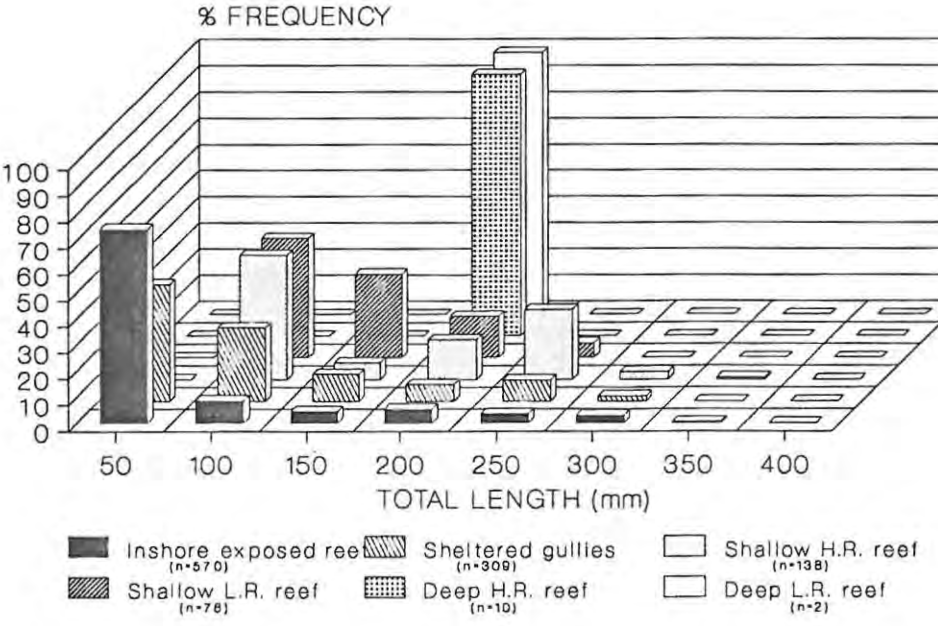


Figure 8. Length frequency distribution of <u>Diplodus</u> <u>sargus</u> <u>capensis</u> from six different habitat types sampled in the TNP.

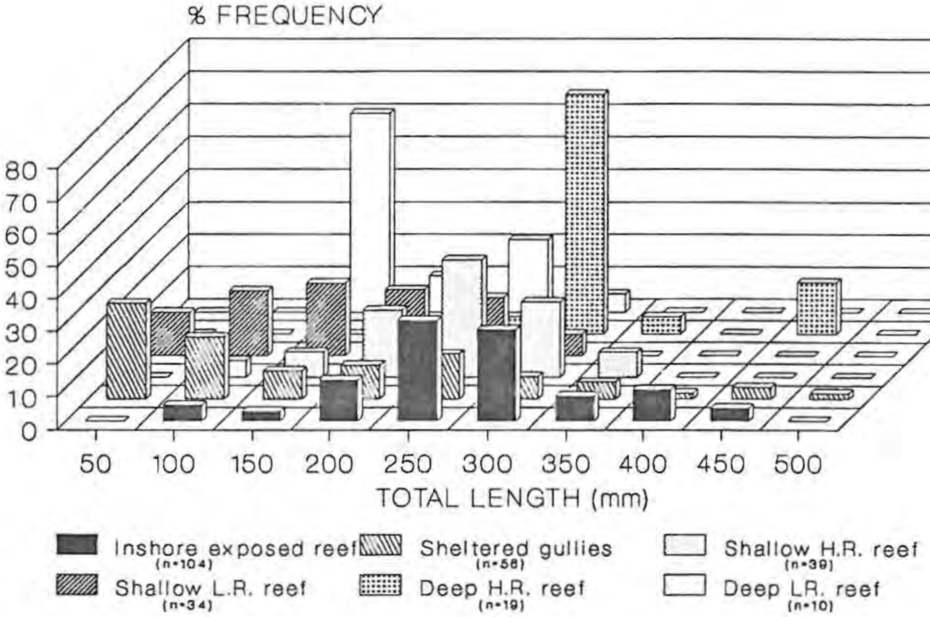


Figure 9. Length frequency distribution of <u>Diplodus cervinus hottentotus</u> from six different habitat types sampled in the TNP.

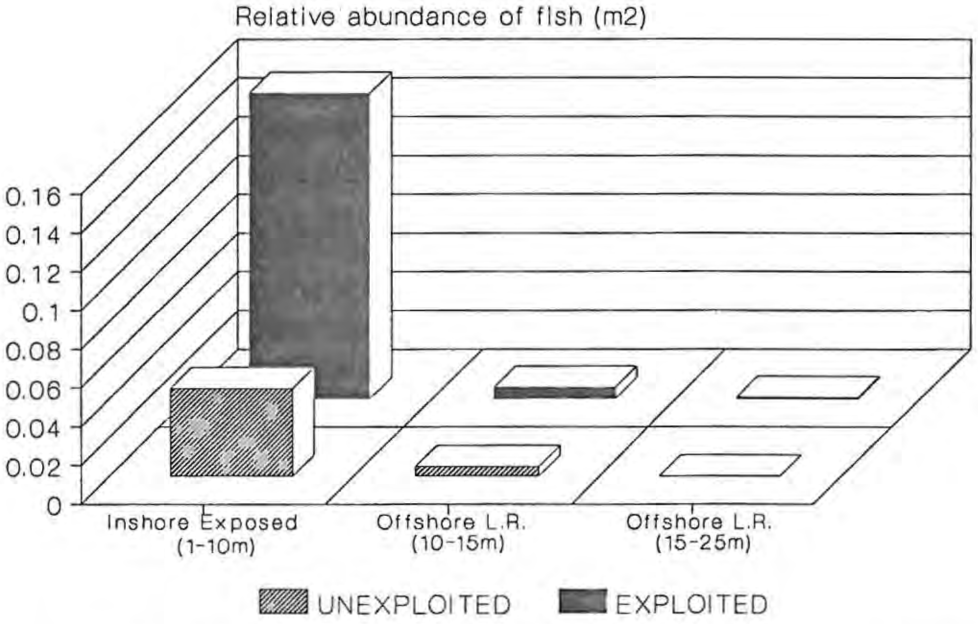


Figure 10. Relative abundance (fish m^{-2}) of <u>Diplodus sargus capensis</u> from exploited and unexploited habitats.

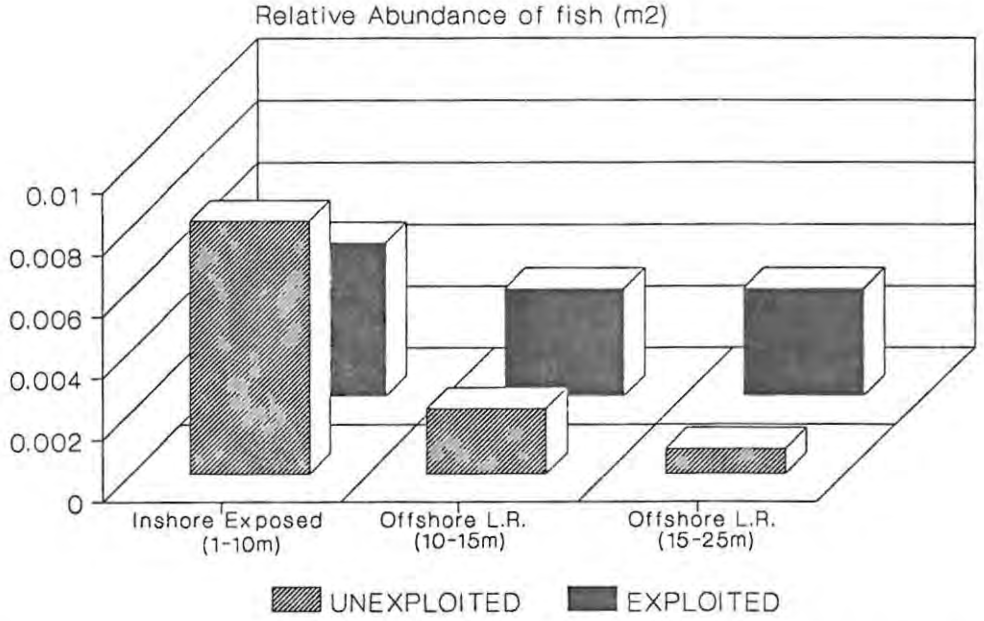


Figure 11. Relative abundance (fish m^{-2}) of Diplodus cervinus hottentotus from exploited and unexploited habitats.

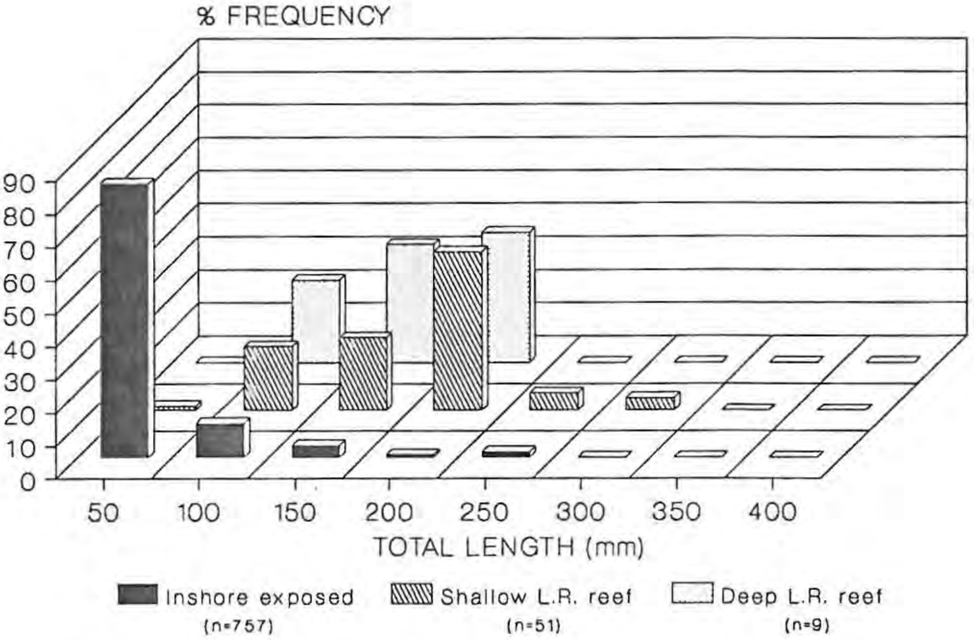


Figure 12. Length frequency distribution of Diplodus sargus capensis from three exploited habitats off Sout River.

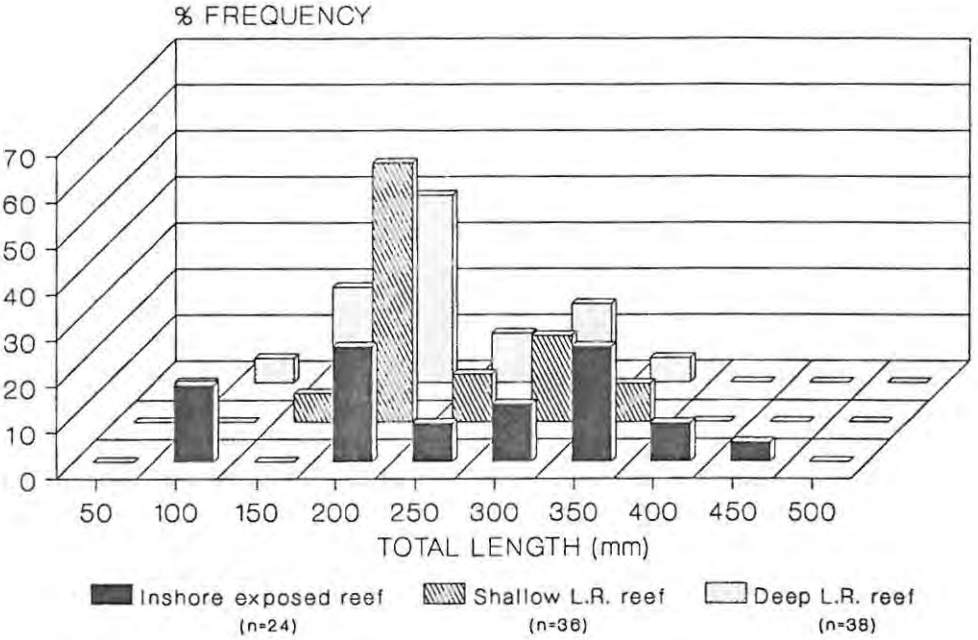


Figure 13. length frequency distribution of <u>Diplodus cervinus hottentotus</u> from three exploited habitats off Sout River.

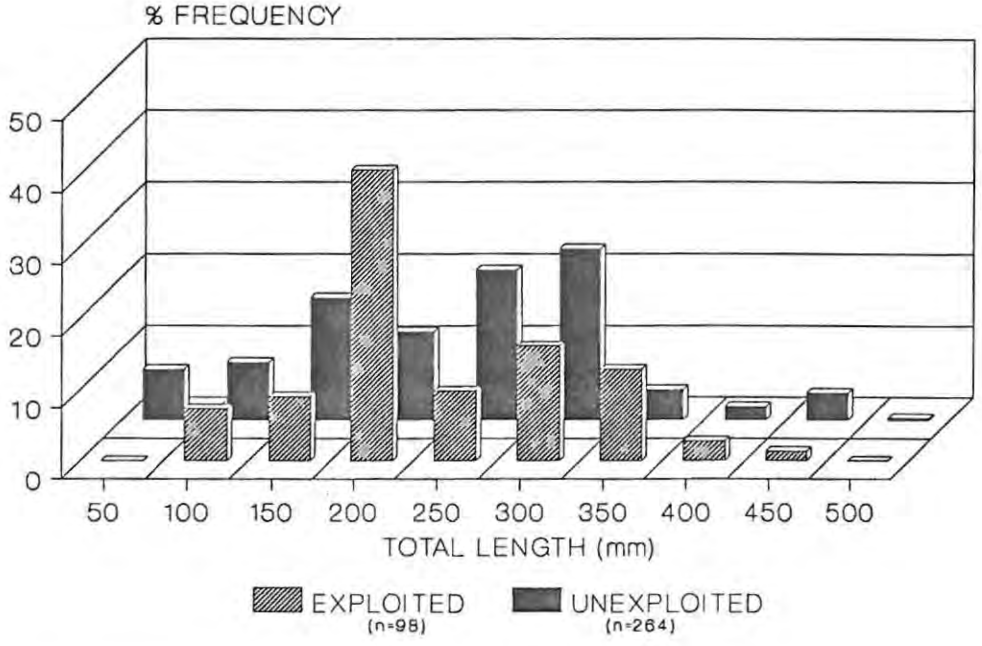


Figure 14. Combined length frequency data for <u>Diplodus cervinus hottentotus</u> from exploited and unexploited areas.

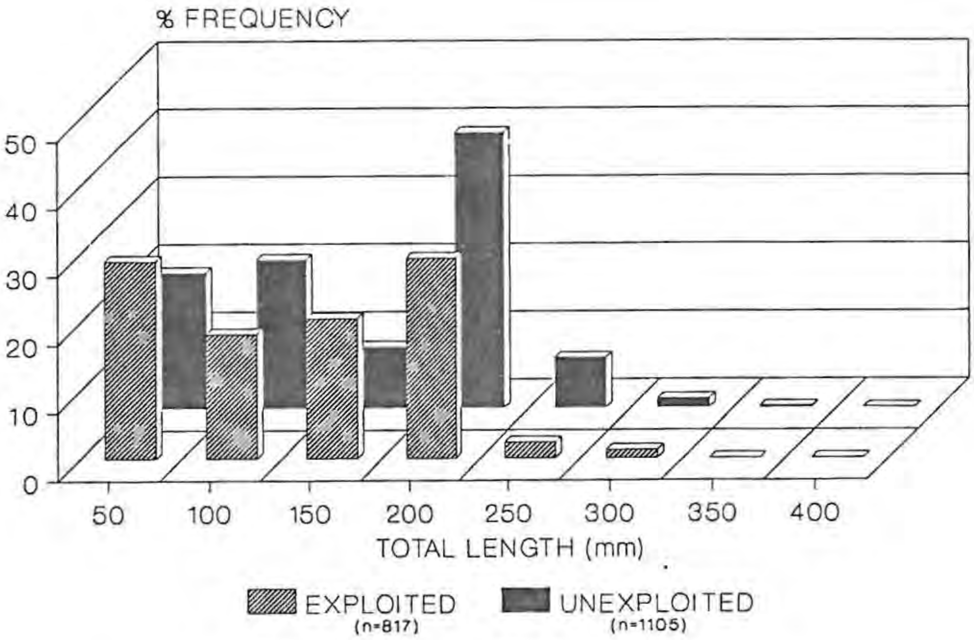


Figure 15. Combined length frequency data for Diplodus sargus capensis from exploited and unexploited areas.

3.4 DISCUSSION

Depth and habitat preferences

Visual assessment of the relative abundance of both Diplodus species in various habitats and at various depths, showed that both species were found primarily on inshore reefs (<10m), particularly those exposed to direct wave action. Similar observations on the inshore distribution of these species were made by Buxton & Smale (1984). Joubert & Hanekom (1980) described inshore reefs as those within the limits of influence of the surf zone which are consequently characterised by turbulent conditions. The occurrence of shallow reefs (<10m) exposed to an extensive surf zone are relatively scarce along the Tsitsikamma coastline. This is due to the nature of the coastline which is generally characterised by steep sandstone cliffs giving way to relatively deep water close inshore. Shore angling in many such areas produced relatively low catches of Diplodus species. Instead, many species normally associated with deeper, offshore reefs such as Boopsoidea inornata, Chrysoblephus laticeps, Cheimerius nufar and Petrus rupestris were captured fairly frequently while fishing off the rocks. For this reason a shallow reef area to the south of the Bloukrantz River mouth (Figure 1), with a continuous shallow surf zone (<10m in depth) extending approximately 200m from the shore, was chosen to be representative of an exposed inshore reef habitat.

Transecting in these inshore areas was at times extremely difficult because of water turbulence, reduced visibility and the 'shyness' of both species. The results shown are thus probably an under-estimate of the actual abundance of these species. While D. sargus was found almost exclusively at depths less than 15m, D. cervinus had a wider depth range and was encountered at depths of up to 25m, particularly on high relief reefs. Limited surveys on reefs deeper than 25m (restricted by safe no-decompression diving depths of <35m), showed no evidence of D. cervinus occuring at this depth (Buxton & Smale 1984, this study).

Of the various biotic and abiotic factors that are known to affect the distribution of fishes, food availability is one of the most important (Hobson 1974; Leum & Choat 1980; Kingett & Choat 1981; Bell 1983; Buxton & Smale 1989). Studies on the diet of D. sargus indicate that the abundance of this species in various reef associated habitats in the inshore zone may be directly related to their feeding requirements. Bell (1983) found that D. sargus off the French Mediterranean coast occurred in greater abundance on shallow reefs (7-10m) than on deeper reefs (15-20m) and suggested that this distribution was governed largely by the location of their preferred food items. Similarly, the feeding preferences of D. cervinus may also restrict their distribution to areas with an abundance of their preferred prey (see Chapter 2). The comparatively higher relative abundance of both species on high relief reefs, is thought to be related to food abundance. High relief areas have been shown to support a greater species diversity of preferred prey items (Hanekom & Coetzee in press).

Juvenile Diplodus species were restricted to inshore waters less than 10m deep. Large shoals of D. sargus (<50mm TL) were found both on exposed inshore reefs and in subtidal gullies and were also collected from tidal rock pools in the TNP (Burger 1991). Juveniles of this species have been recorded in a wide range of nursery habitats including the lower vegetated reaches of estuaries (Winter 1979; Beckley 1983), the sandy beach surf zone (Lasiak 1986; Bennett 1989), surf zone reefs (Berry, Van der Elst, Hanekom, Joubert & Smale 1982); subtidal reefs (Beckley &

Buxton 1989), subtidal gullies (Smale & Buxton 1989) and tidal rock pools (Christensen 1978; Christensen & Winterbottom 1981, Beckley 1985; Bennett 1987). It would appear, therefore, that juvenile D. sargus have the physiological capabilities to withstand a wide range of environmental conditions associated with these various nursery habitats (Bennett 1987). Juvenile D. cervinus (<50mm TL) were observed primarily in subtidal gullies although a few specimens were collected from tidal rock pools in the TNP (Burger 1991). The recorded distribution of D. cervinus juveniles is also confined to tidal rock pools (Christensen 1978; Beckley 1985) and shallow subtidal reefs and gullies (Bennett 1987; Beckley & Buxton 1989; Smale & Buxton 1989), suggesting that juveniles of this species are more specific in their habitat requirements.

The functioning of inshore habitats as nursery areas for juvenile marine fish are well known (Barnes & Hughes 1982). Suitable nursery areas must provide abundant food, some degree of protection from predators and the correct chemical and physical features for optimal growth (Joseph 1973). The distribution of juveniles of both species appeared to be closely related to the occurrence of coralline algae in the inshore zone. These algae are known to contain an abundant epifauna, including gammarid amphipods, which are important to the diet of both species (see Chapter 2). A similar relationship between the occurrence of coralline turf and the distribution of juvenile Chrysophrys auratus was shown by Kingett & Choat (1981).

There is little record of predation on juvenile Diplodus species in the literature but this aspect inevitably plays an important role in regulating their distribution (Huntsman 1979). The shoaling behaviour prevalent amongst juvenile D. sargus (<100mm TL) reflects synchronised co-operation to obtain food and to provide an element of protection from predation (Radakov 1973, Pitcher 1986). This type of behaviour may offer an explanation as to their occurrence in areas that lack physical shelter such as exposed inshore reefs. Juvenile D. cervinus were seldom seen in shoals comprising more than a few individuals and were often observed in close association with some form of physical shelter such as a small cave or overhang. The presence of piscivorous predators such as Pomatomus saltatrix, Cheimerius nufar and Petrus rupestris may, therefore, be an important factor in limiting the distribution of juveniles of both Diplodus species to tidal pools and shallow subtidal areas.

Visual census results revealed that exposed inshore reefs also provided an optimum habitat for Diplodus species larger than 100mm TL. Within this inshore habitat, adult D. sargus were frequently observed in loose aggregations ranging over a variety of habitat patches from flat boulder beds interspersed with sand to reef crests dominated by Pyura stolonifera. Adult D. cervinus appeared to be more specific in their habitat requirements and were often observed in close association with caves or overhangs on reef edges. Apart from having evolved in areas where the abundance of their preferred prey is greatest, other biotic factors such as resource partitioning and predation may influence the inshore distribution of adult Diplodus species. For instance, many of the suprabenthic fish species found on deeper reefs (>15m) have broadly similar dietary requirements to those of D. sargus and D. cervinus (Burger 1991). Although interspecific competition can only evolve if resources are lacking (Schoener 1974), the abundance of macrobenthic invertebrate feeders such as Chrysoblephus laticeps and C. cristiceps on deeper reefs in the TNP (Buxton & Smale 1989) may have an effect in limiting the distribution of both Diplodus species to shallow areas to which they are better adapted. In this regard however, the greater depth range observed in D. cervinus may be explained by their ability to specialize on eating polychaete worms (e.g. Lysidice natalensis) which are often found living between pods of Pyura stolonifera (Day 1967). P. stolonifera is abundant on reef crests at depths down to approximately 20m (Buxton & Smale 1984; pers. obs.).

Potential predators of adult D. sargus and D. cervinus include dolphins, seals, sharks and large predatory fish species. Remains of D. sargus have been found in the stomach contents of bottlenose dolphins (Tursiops aduncus) (Mr. V. Peddemors, Natal Sharks Board, Umhlanga Rocks, pers. comm.) and of red steenbras (Petrus rupestris) (Smale 1986). Whether these predators actually limit the depth distribution of adult Diplodus species is unknown as most of these predators can enter the inshore zone (pers. obs.). However, behaviourally speaking, the affiliation with caves and overhangs and the loose shoaling habit observed in adult D. cervinus and D. sargus respectively, may be in direct response to the threat of predation.

Physical factors such as wave action and water temperature were also considered to be important features influencing the distribution of Diplodus species in the TNP. Both species are deep bodied and laterally compressed, with well developed dorsal and anal fins which allow for a high degree of manoeuvrebility. These morphological features are essential adaptations for living in the turbulent conditions found within the inshore zone. Although this study did not specifically examine the influence of temperature on the distribution of Diplodus species, Buxton & Smale (1989) showed how ambient water temperature influenced the relative abundance of Chrysoblephus laticeps off the southern Cape coast. No apparent differences in behaviour, resulting from temperature induced changes in metabolic rate, were observed in either D. sargus or D. cervinus over the range of temperatures at which transecting took place (15-21°C). However, the Tsitsikamma coast is subject to periodic cold upwellings, particularly during the summer months after periods of strong easterly wind (Schumann, Perrins & Hunter 1982; Hanekom, Hutchings, Joubert & Van der Byl 1989). Observational dives carried out during periods of upwelling, when the water temperatures had dropped between 5-10°C overnight, showed that large shoals of reef fish, including both Diplodus species, accumulated in pockets of relatively warmer water such as those found in the Storms River mouth (Buxton 1988; Hanekom et al. 1989) and in sheltered gullies south of the Bloukrantz River mouth. Although poor visibility prevented quantification of these events, these observations suggest that the regional distribution of both Diplodus species is severely altered during periods of cold upwelling. Periodic fish kills of a number of species including D. sargus, have been recorded along the Tsitsikamma coast after severe cold upwellings, although Hanekom et al. (1989) observed that juveniles of this species were the most susceptable. The distributional range of both Diplodus species extends into the cooler waters of the Western Cape and it would seem that the rapidity of these temperature declines rather than the low temperatures *per se* were responsible for the observed mortalities (Hanekom et al. 1989).

Comparison between exploited and unexploited reef environments

The comparison between the exploited reefs off Sout River and those within the TNP showed no significant differences in relative abundance or size structure of Diplodus species. This suggests that exploitation off Sout River has had a negligible effect on stocks of Diplodus species. However, these results were based primarily on visual census work done offshore (10-25m) and only 24 transects were swum on inshore reefs (1-10m), which this study has shown to be the optimum habitat for both Diplodus species. These results should, therefore, be regarded with utmost caution and it is suggested that more work in the inshore zone is required before definite conclusions can be drawn.

Reasons for the observed similarity between the exploited and unexploited areas sampled may be a result of the close proximity of the reefs off Sout River to the boundary of the TNP at Groot River (approximately 5km). Bohnsack (1990) suggested that, amongst others, advantages of marine reserves may be to provide a recruitment source for surrounding areas and to supplement restocking of fished areas through emigration. Both Diplodus species have pelagic eggs and larvae (Brownell 1979) and eggs spawned within the TNP, even if retained in the regional circulation, could quite probably recruit on to inshore reefs off Sout River. Results from the ORI/SFW tagging programme (Van der Elst & Bullen 1991) showed that the average distance travelled by tagged and recaptured D. sargus (n=32) is 31km, over an average period of 84 days at liberty. Although Bennett & Attwood (in prep.) have shown that D. sargus are fairly resident in the De Hoop marine reserve, a combination of these results suggest that adult D. sargus are free ranging and are not necessarily resident to a particular reef complex. It is quite feasible therefore, that adult D. sargus may emigrate from the reserve and traverse the relatively short distance to the reefs off Sout River. Tag and recapture results of D. cervinus (Van der Elst & Bullen 1991) however, suggest that adults of this species are more resident (7 fish recaptured moved an average distance of 1.4 km over an average of 71 days at liberty) and may remain within the same area.

Exploitation of the inshore zone by rock-and-surf anglers in the Sout River area is thought to be relatively low due to the recent annexation of the De Vasselot Nature reserve (Hockey & Buxton 1989) which includes 8km of coastline extending from the western boundary of the TNP. Although this area only affords protection to the spring low water mark and fishing and bait collection is allowed, access to the area to the west of Sout River is difficult due to steep relief and the limited number of paths. Offshore, these reefs are fished fairly heavily by both recreational and commercial ski-boat anglers that launch from Plettenberg Bay. Burger (1991) showed that the relative abundance of the top reef predator Petrus rupestris was significantly lower on deep exploited reefs than on similar reefs within the TNP

(0.0005 fish m^{-2} and 0.0045 fisf m^{-2} respectively). Furthermore, the absence of larger individuals of this species in the exploited area was considered to be a classic example of the effects of fishing pressure (Weatherly 1972). There were no indications however, that D. sargus had been able to colonize these exploited reefs. Burger (1991) showed that a common deep reef species Boopsoidea inornata was significantly more abundant on deeper reefs off Sout River than was recorded on similar reefs in the TNP. From these results it is apparent that B. inornata was better adapted to colonizing the deeper reef environment than D. sargus. With respect to these observations, further work is necessary to explain whether D. sargus is capable of colonizing exploited, inshore areas along the South African coastline. It is suggested that an alternative site such as Cape St Francis, which is heavily exploited by rock-and-surf anglers, be used in comparison with the observed inshore abundance of D. sargus in the TNP.

Finally, although the differences observed were not significant, there did appear to be a greater relative abundance of adult D. cervinus on the deeper exploited reefs. This may be explained by some intrinsic difference in the deeper reefs off Sout River, with the area being more suitable to the habitat preferences of D. cervinus. No immediate differences in habitat between the reefs sampled in the TNP and off Sout River were apparent and it is possible that the higher abundance of D. cervinus was attributable to the effects of fishing. Burger (1991) found a lower diversity of fish species on the reefs off Sout River when compared to similar reefs in the TNP and attributed this "community disruption" to the effects of exploitation. D. cervinus are seldom caught from ski-boats in the south-east Cape as anglers tend to use relatively large hooks and target for redfish species such as Argyrozona argyrozona, Chrysoblephus laticeps, C. criticeps, C. gibbiceps and P. rupestris (Smale & Buxton 1985). With the exploitation of these redfish, some of which occupy similar niches to D. cervinus (e.g. C. laticeps and C. cristiceps), it is possible that D. cervinus has been able to successfully fill these unoccupied niches. Such suggestions however, remain purely speculative.

CHAPTER 4 - REPRODUCTION

4.1 INTRODUCTION

According to the theory of natural selection, life history characteristics of a species are selected in a way that maximizes the number of surviving offspring produced (Adams 1980). A sound knowledge of various aspects of the reproductive biology of both D. sargus and D. cervinus is therefore fundamental to an understanding of the life history of these fishes.

Sparid fishes exhibit a diverse sexuality (Atz 1964; Reinboth 1970; Thresher 1984) which may be expressed as sequential hermaphroditism (protandry or protogyny) or 'late' gonochorism (rudimentary hermaphroditism) (Buxton & Garratt 1990). The expression of this sexuality is very complex in many sparid species and its interpretation rather difficult (Matsuyama, Lara & Matsuura 1988). Nevertheless, interpretation of this sexuality forms an important factor in understanding the reproductive style exhibited. Reproductive studies done in South Africa on several important recreational and commercial sparid linefish have shown that the majority of these species are either protogynous or rudimentary hermaphrodites (Mehl 1973; Hecht & Baird 1977; Coetzee 1983; Garratt 1985b; Smale 1988; Buxton 1990; Buxton & Clarke 1991 & 1992), although there have been some unconfirmed reports of protandry (Lucks 1970; Coetzee 1986; P. Garratt, Oceanographic Research Institute, Durban, pers. comm.).

Work done on the reproductive biology of Diplodus species in South Africa has been concentrated on D. sargus capensis (Joubert 1981a; Coetzee 1986). Confusion surrounds the type of hermaphroditism exhibited by this species. It has been described as both a rudimentary hermaphrodite (Joubert 1981a) and a protandrous hermaphrodite exhibiting a special form of protandry (Coetzee 1986). Studies done on D. sargus sargus in the Mediterranean and D. sargus kotschyi in the Persian Gulf have described these subspecies as protandrous (Micale, Perdichizzi & Santangelo 1987; Abou-seedo, Wright & Clayton 1990) although rudimentary, non-functional hermaphrodites of the same subspecies have also been described (Reinboth 1962 & Lissia-Frau 1968 in Micale et al. 1987). Very little work has been done on the sexuality of D. cervinus hottentotus, although the spawning seasons of both species have been described (inter alia Christensen 1978; Brownell 1979; Beckley 1985).

To gain a better insight into the patterns of distribution and relative abundance of both species in the TNP and to comment on their management, various important aspects of their reproductive biology were investigated. These included determination of reproductive seasonality, length frequency distribution of sexes, sex ratios and size/age at sexual maturity. In addition to this, a detailed histological examination of gonadal development and gametogenesis in both species was undertaken as this is an indispensible pre-requisite for the diagnosis of hermaphroditism (Reinboth 1970).

4.2 METHODS

Monthly samples of D. sargus and D. cervinus from all size classes were collected by spearfishing and linefishing in the TNP between April 1989 and December 1990. A total of 382 D. sargus and 304 D. cervinus were sampled during this period. All fish were weighed (grammes), measured (millimeters fork length) and sexed macroscopically. Gonads were then dissected from the fish, weighed and visually assessed for their stage of maturation according to the criteria in Table 11. Macroscopic staging of gonads was later substantiated by histological examination.

To investigate the seasonality of spawning, a monthly gonado-somatic index (GSI) was calculated:

$$GSI = \frac{\text{Gonad mass (g)}}{\text{Eviscerated body mass (g)}} * 100$$

For histological examination, sub-samples of gonadal tissues were fixed in Bouin's solution for three days and then stored in 60% propyl alcohol. They were then embedded in paraffin wax, sectioned at 7um and stained using Gill's haematoxylin, OG 6 and EA 65 cytoplasmic stains. Sections were examined using light microscopy.

Sadovy & Shapiro (1987) recommend that in order to infer protandry the following steps be taken: 1) To hypothesize a sequence of development based on regular differences in gonadal histology of successive sizes. 2) To show evidence of intermediate individuals containing degenerating spermatogenic and developing ovarian tissue. 3) To induce sex change experimentally. Experimental induction of sex change was beyond the scope of this study but, in an attempt to resolve the type of hermaphroditism exhibited by D. sargus, the first two recommendations were incorporated into this study.

TABLE 11. Description of the macroscopic maturity stages in D. sargus and D. cervinus (from Buxton 1990).

1. Inactive/resting	Gonads small. Testes thin and transparent to off-white in colour. Ovaries long and thin, translucent orange in colour.
2. Developing	Gonads increase in size. Testes show some thickening and are white in colour. Sperm is visible if the testes are cut and gently squeezed. Ovaries become swollen and orange/yellow in colour. Eggs are visible to the naked eye.
3. Ripe	Testes very large and swollen. They are white in colour but often become pinkish as the breeding season progresses. Sperm is found in the testicular tissue and the yellow in colour. Translucent eggs are visible in the tissue and in the lumen.
4. Spent	Testes decreased in size and pinkish-grey in colour. Sperm may still be present in the main sperm duct. Ovaries are flaccid, bloodshot and reduced in size.

4.3 RESULTS

Reproductive seasonality

In D. sargus monthly gonado-somatic indices showed an extended spawning season, peaking in spring (August to October), but with relatively high GSI's being recorded throughout summer until March (Figure 16). This extended spawning season coupled with histological evidence of ripe ovaries containing oocytes in various stages of maturation suggest that oocyte development is asynchronous (Garratt 1985b). In teleosts with asynchronous ovaries the recruitment of oocytes is a continuous, ongoing process during the spawning season and the fish is capable of multiple spawns during this period (Wallace & Selman 1981). D. cervinus showed a more restricted spawning season with reproductive activity extending from August through to December with a peak in October (Figure 17).

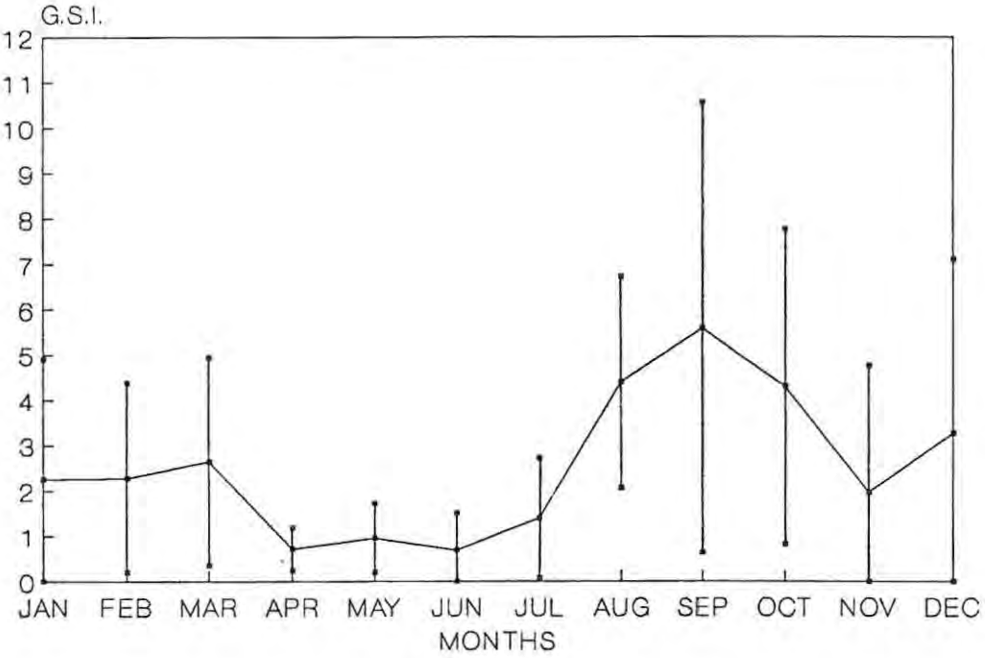


Figure 16. The mean monthly gonado-somatic indices for Diplodus sargus capensis sampled in the TNP from April 1989 to December 1990 (n=299).

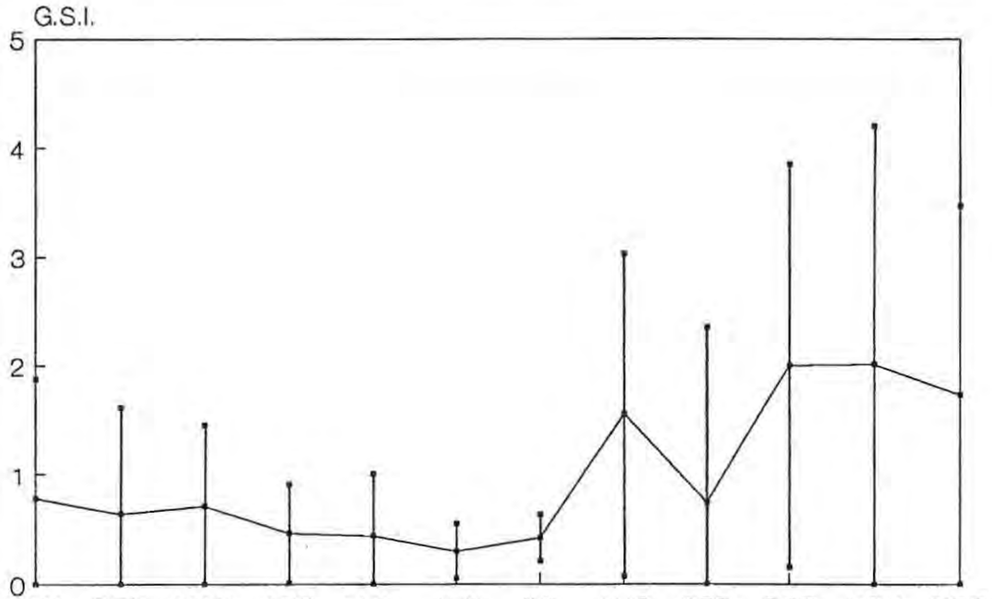


Figure 17. The mean monthly gonado-somatic indices for Diplodus cervinus hottentotus sampled in the TNP from April 1989 to December 1990 (n=244).

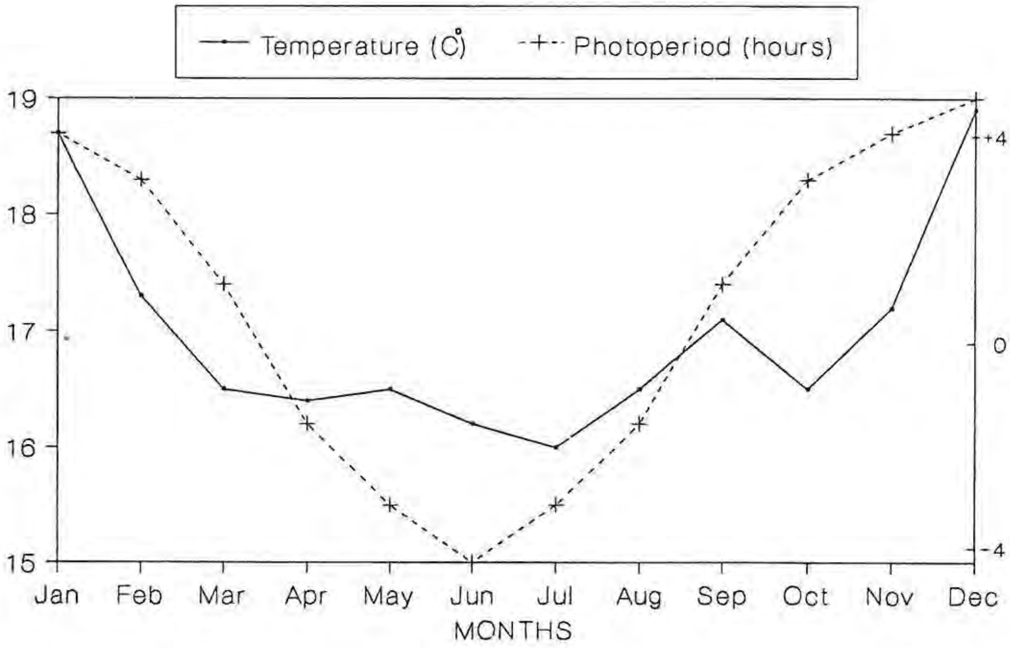


Figure 18. Mean monthly surface water temperatures and photoperiod recorded in the TNP between January 1989 and December 1990.

Oocyte development was similar to that of D. sargus suggesting that D. cervinus also undergoes multiple spawnings per spawning season. The spawning season in both species was correlated with photoperiod and surface water temperature (Figure 18). In both species, the gonado-somatic indices of male fish were found to be similar to those of females, during their respective spawning seasons.

Length frequencies, size at sexual maturity and sex ratios

1) D. sargus

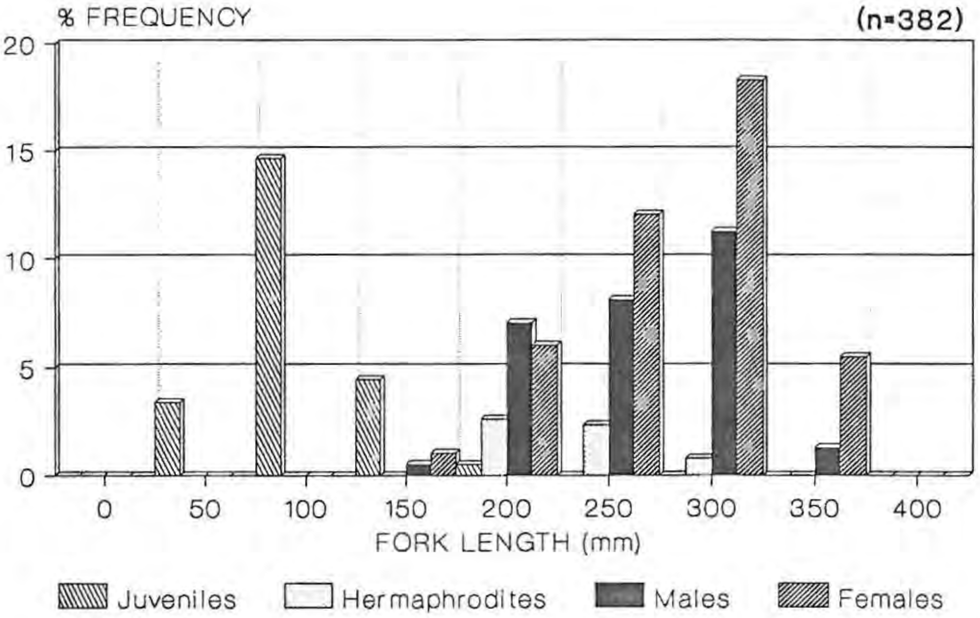
The length frequency distribution of D. sargus (Figure 19) showed that females dominated the larger size classes. Sexes were separated on a basis of macroscopic sex determination and where gonads were too small to sex, fish were classified as juveniles. Although many fish throughout the size range showed evidence of hermaphroditism, only intersexual gonads that were easily recognised macroscopically were included in the length frequency analysis. Intersexes were most frequently observed in the 150mm to 250mm FL size classes. Size at 50% sexual maturity was calculated at 225mm FL by graphing the proportion of active fish (developing, ripe or spent gonads), in each size class, during the breeding season (Figure 20). This size at 50% sexual maturity was equivalent to an age of 4 years. To avoid any bias from the inclusion of juvenile fish which are difficult to sex macroscopically (Smale 1988), an adult sex ratio was calculated at 1:0.1:1.98 (male:intersex:female, n = 188) using all fish greater than the size at 50% sexual maturity. A chi-square test calculated for males and females showed that there was a significant difference from a 1:1 sex ratio (X^2=19.78, P<0.001).

2) D. cervinus

Male and female D. cervinus showed similar length frequency distributions (Figure 21). Only four intersexual gonads were observed macroscopically between 150 and 250mm FL. Size at 50% sexual maturity was calculated at 285mm FL (Figure 22), which is equivalent to an age of 6 years. An adult sex ratio was calculated at 1.23:1 (male:female, n = 105) and a chi-square test showed no significant difference from a 1:1 sex ratio (X^2=1.15, P>0.05).

Gonadal development

The gonads of both species developed from an immature ovotestis in which the testicular and ovarian elements were clearly separated by connective tissue (Figure 23). The ovotestis consisted of an ovarian lobe in the dorso-lateral region of the abdominal cavity, the testicular lobe was ventro-lateral to the ovarian lobe. Posteriorly, the ovarian lobes fused to form a common oviduct, while folds of connective tissue formed a sperm duct which partially encircled the oviduct. This type of juvenile bisexuality is a common feature in the Sparidae (Buxton & Garratt 1990) and is associated with the fact that teleost gonads arise from a single primordium which initially lacks male and female elements (Atz 1964). Histological sex determination was only possible once the fish had reached approximately 100mm FL in D. sargus and 180mm FL in D. cervinus. In smaller fish the gonad consisted primarily of undifferentiated gonial cells (spermatogonia and/or oogonia) the sex of which could not be determined (Figure 24).



SEX RATIO 1:0.2:1.52 (M:H:F)

Figure 19. Length frequency analysis in Diplodus sargus capensis sampled in the TNP from April 1989 to December 1990.

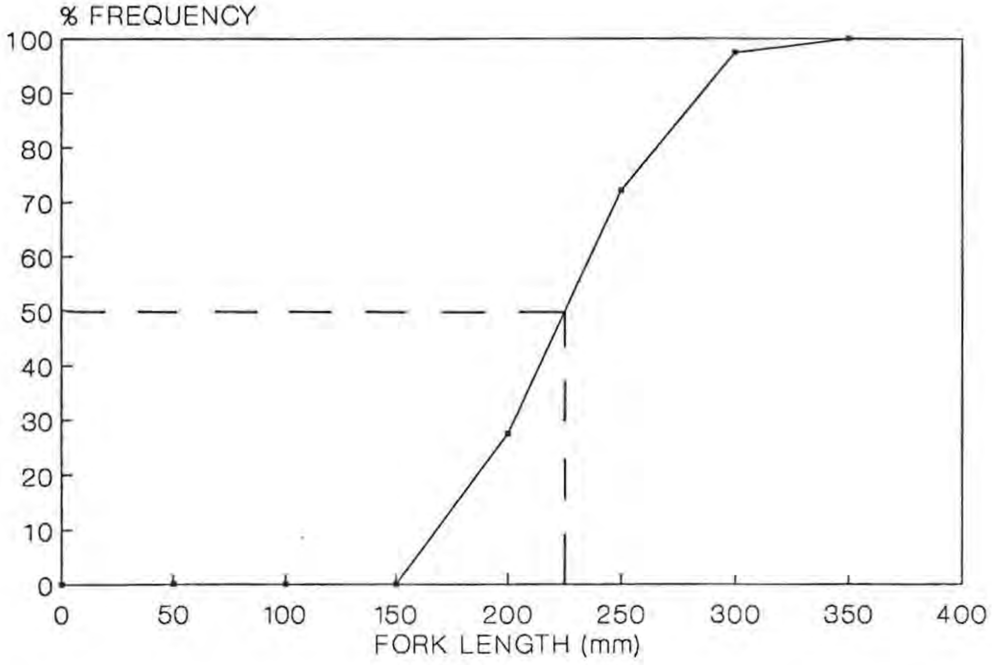
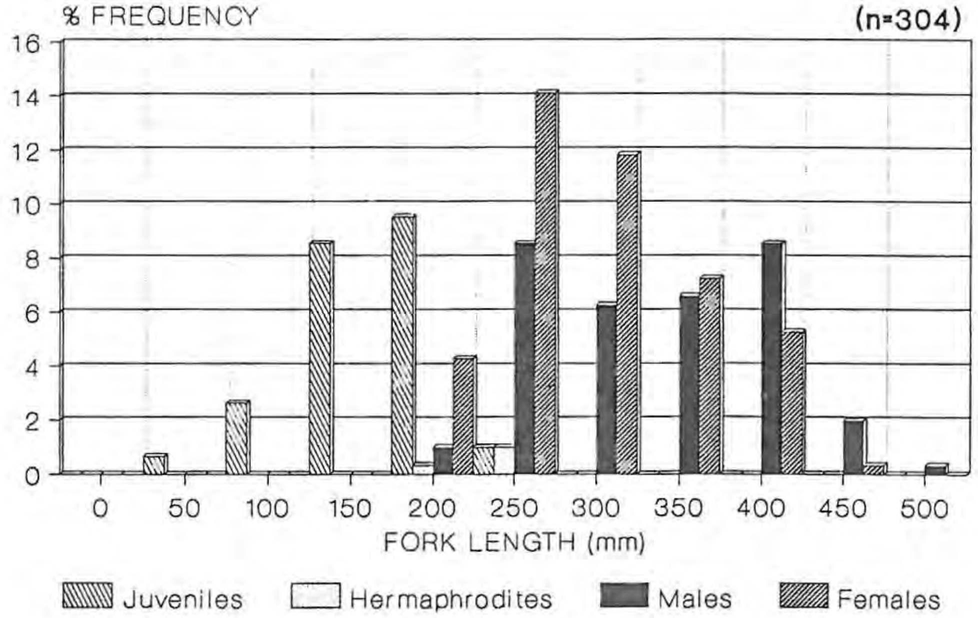


Figure 20. Length at 50% sexual maturity in Diplodus sargus capensis sampled in the TNP from April 1989 to December 1990 (n=218).



SEX RATIO 1:0.04:1.3 (M:H:F)

Figure 21. Length frequency analysis in Diplodus cervinus hottentotus sampled in the TNP from April 1989 to December 1990.

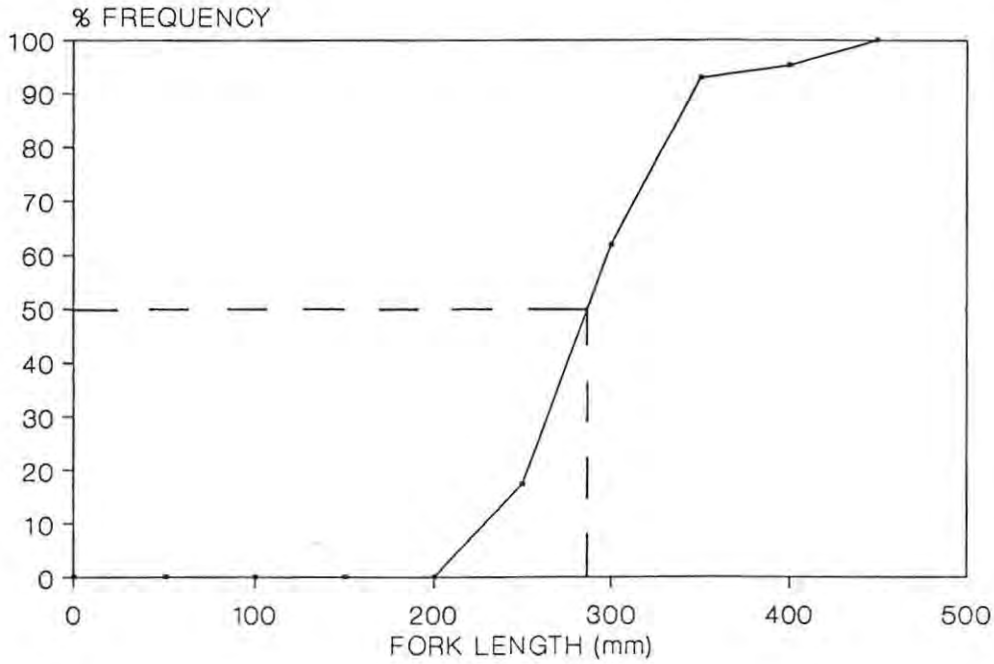


Figure 22. Length at 50% sexual maturity in Diplodus cervinus hottentotus sampled in the TNP from April 1989 to December 1990 (n=132).

1) D. sargus

To determine the pattern of gonadal development occuring in D. sargus, gonads from 164 fish of successive size classes were described on a basis of gross-anatomical and histological observations. Gonads were classified as one of four distinguishable types. A Type I gonad consisted of a non-functional ovotestis in which testicular and ovarian elements constituted similar proportions (Figure 25). A Type II gonad consisted of an ovotestis in which the testicular portion was dominant and was actively undergoing spermatogenesis. The ovarian portion remained intact and was only partially enclosed by the sperm duct (Figure 26). Oogenesis in the ovarian portion was curtailed at the late perinuclear stage whereafter oocytes underwent atresia similar to that described for pre-vitellogenic oocytes by Yamamoto (1956). Dormant oocytes of this nature have been described in protandrous sparid species (Reinboth 1970, Yeung & Chan 1987) but can also be found in the ovotestis of rudimentary hermaphrodites (Coetzee 1983; Smale 1988). A Type III gonad consisted of a dominant ovarian portion with a lateral flap of vestigial testicular tissue (Figure 27). In large females, particularly during the breeding season, the testicular flap was completely atrophied and no longer visible. A Type IV gonad consisted of a dominant, functional testis which had completely enveloped the ovarian portion (Figure 28). The latter consisted of a rudimentary oviduct containing a band of pre-vitellogenic oocytes. In most cases this rudimentary ovarian portion was not visible macroscopically.

The sequence of development of gonadal types in successive size classes is shown in Figure 29. Gonads of all fish developed from a non-functional, Type I ovotestes. In the 0-100mm size classes no fish had yet differentiated into a discernable sex. As the fish increased in size, either the ovarian or the testicular portion of the ovotestis became dominant. The size at which one sex became dominant did not appear to be fixed, with some individuals differentiating at a small size (130mm FL) while others retained a non-functional Type I ovotestis until shortly before sexual maturation (220mm FL). Males developed from the Type I gonad into either a Type IV male or an intermediate Type II gonadal condition which, although containing active spermatogenic tissue, still retained an inactive ovarian portion. A Type II gonad represents a bisexual functional male that retains the potential to develop into either a unisexual functional male (Type IV) or a unisexual functional female (Type III). Females (Type III gonad) either developed straight from the juvenile ovotestis (Type I) or from a Type II gonad which changed sex into a functional female. D. sargus could therefore be considered as a digynic species having both primary and secondary females in the population (Sadovy & Shapiro 1987; Buxton & Garratt 1990).

Examples of transitional gonads were found in fish measuring 223mm and 296mm FL. These gonads showed evidence of degenerating testicular tissue and developing ovarian tissue (Figure 30). They consisted of an ovarian portion undergoing normal oogenesis with some oocytes showing secondary yolk vesicle formation and a distinct follicular layer. Although the sperm duct still contained sperm from the previous breeding season, the testicular tissue showed definite signs of degeneration with spermatogonia being actively phagocytosed by leucocytes (Figure 31). Two other gonads were sectioned from fish of 255 and 256mm FL which showed degenerating testicular tissue and a developing ovary. In these individuals however, sex change into functional females was further developed with little trace of a functional sperm duct containing spermatozoa, remaining adjoined to the ovary (Figure 32). The occurrence of these transitional gonads provided evidence that some fish in the population undergo a facultative sex change from male to female. The potential of a Type II gonad to change sex into a functional female is probably dependent on social or environmental cues rather than being genetically predetermined (Reinboth 1988; Shapiro 1989). This would explain the variation in size of fish at sex change.

2) D. cervinus

The structure of the juvenile ovotestis in D. cervinus was similar to that described for D. sargus (Figure 33). Differentiation of the dominant sex took place well before sexual maturation. In developing males the ovarian portion degenerated until only a rudimentary oviduct, sometimes surrounded by a band of pre-vitellogenic oocytes, was still visible. The rudimentary oviduct was almost completely enveloped by the testis and developing sperm duct (Figure 34). The testicular tissue in differentiating males consisted predominantly of spermatogonia with a few isolated clumps of primary spermatocytes. In developing females the ovarian element became dominant while the testis was reduced to a thin, lateral flap of tissue (Figure 35). Of the 304 fish sampled only four intersexual gonads were recognised macroscopically. Histological examination of these ovotestes showed that they consisted of immature developing testes and a dormant ovarian portion which was probably representative of the retention of a non-functional, juvenile ovotestis. This type of development, where either the testis or the ovary matures after a stage of juvenile bisexuality, is typical of rudimentary hermaphrodites (Buxton & Garratt 1990) which mature as functional gonochorists.

Figure 23. Section of an immature ovotestis from Diplodus sargus capensis (130mm FL) in which the testicular (T) and ovarian (OV) elements are clearly separated by connective tissue (x20).

Figure 24. Section from an immature ovotestis from Diplodus sargus capensis (95mm FL) with undifferentiated gonial cells (UG) (x38).

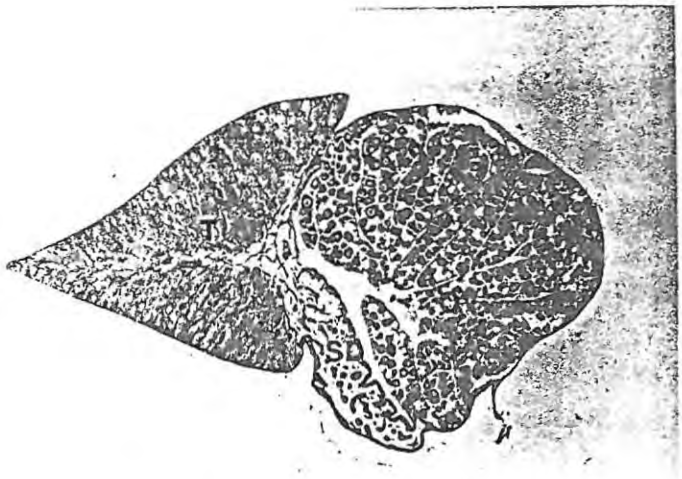


Figure 25. Section of a Type I gonad from Diplodus sargus capensis (164mm FL). T=Testis, OV=Ovary, SD=Sperm Duct (x12).

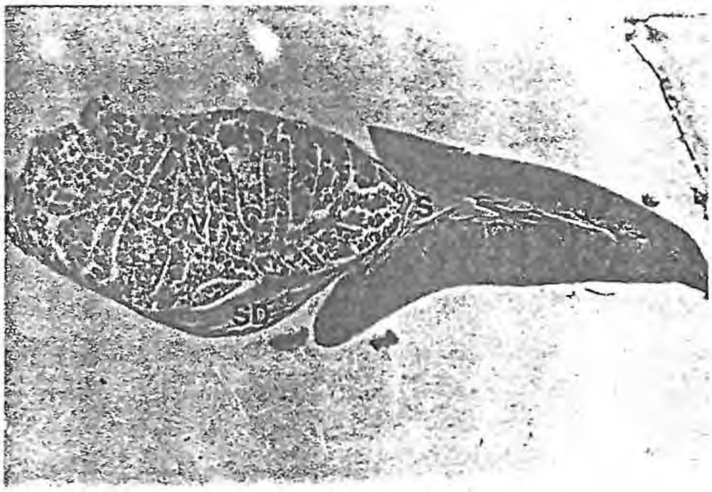


Figure 26. Section of a Type II gonad from Diplodus sargus capensis (203mm FL). T=Testis, OV=Ovary, SD=Sperm Duct, S=Spermatozoa (x13).

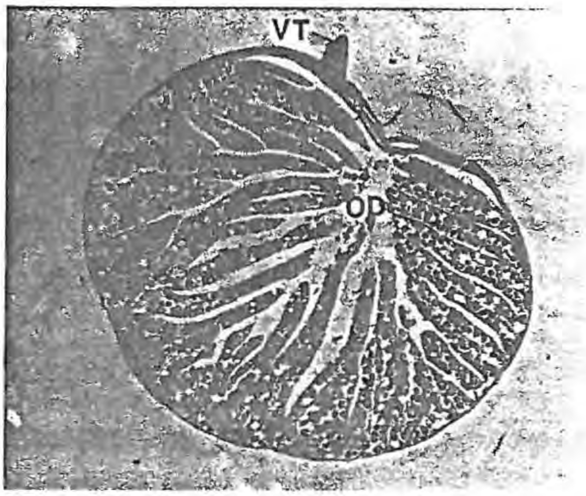


Figure 27. Section of a Type III gonad from Diplodus sargus capensis (188mm FL). VT=Vestigial Testis, OD=Oviduct (x10).

Figure 28. Section of a Type IV gonad from Diplodus sargus capensis (201mm FL). T=Testis, SD=Sperm Duct, RO=Rudimentary Oviduct (x17).

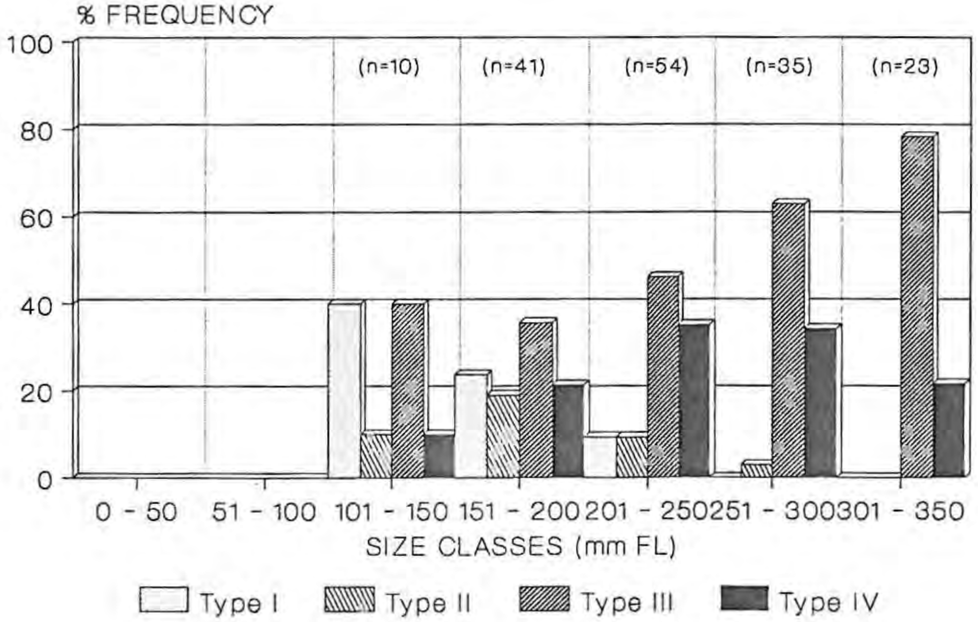


Figure 29. The developmental sequence of gonadal types in successive size classes of Diplodus sargus capensis from the TNP.

Figure 30. Section of a transitional gonad changing sex from male to female, from a Diplodus sargus capensis (297mm FL). DT=Degenerating Testis, SD=Sperm Duct (containing sperm), DO=Developing Ovary, 2° YVO=Secondary Yolk Vesicle Oocyte (x27).

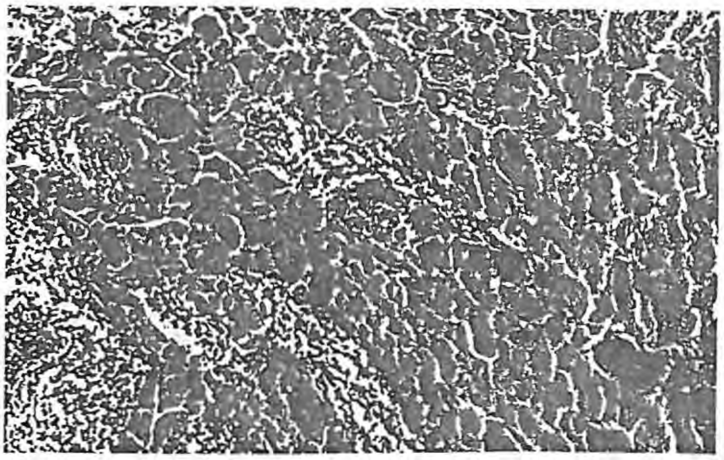


Figure 31. Section of degenerating testicular tissue from the above gonad shown under high magnification. S=Spermatozoa, DSG=Degenerating Spermatogonia (x200).

Figure 32. Section of a transitional gonad from Diplodus sargus capensis (256mm FL) in a later stage of sex change from male to female (note absence of the sperm duct). DO=Developing Ovary, DT=Degenerating Testis (x12).

Figure 33. Section of an immature ovotestis from Diplodus cervinus hottentotus (185mm FL). DT=Degenerating Testis, OV=Ovary (x32).

Figure 34. Section of a developing testis from Diplodus cervinus hottentotus (188mm FL). T=Testis, RO=Rudimentary Oviduct (x17).

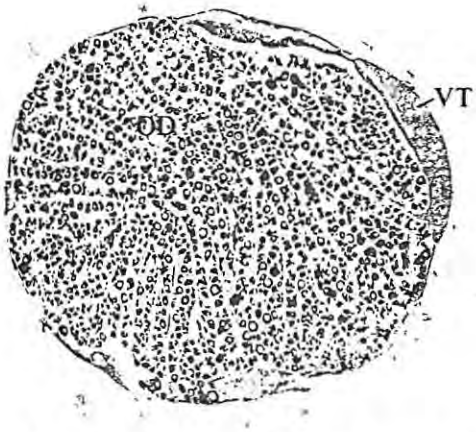


Figure 35. Section of a developing ovary from Diplodus cervinus hottentotus (197mm FL). VT=Vestigial Testis, OD=Oviduct (x15).

Gametogenesis

Gametogenesis was similar in both D. sargus and D. cervinus and unless indicated the following description applied to both species.

A) The ovary and oogenesis

The ovaries are paired structures that originate from the dorsolateral lining of the peritoneal cavity (Hoar 1969). They were located posteriorly attached to the dorsal wall of the peritoneal cavity by means of a thin layer of connective tissue, the mesovarium. Both ovaries were fused posteriorly by means of a short oviduct which emptied into the cloaca. The ovary itself was surrounded by a layer of connective tissue, the tunica albuginea. The tunica albuginea formed numerous ovigerous lamellae which projected into the ovocoele. The developing oocytes were found along the margins of these folds embedded in a loose connective tissue (Figure 36).

Oocyte development was classified using criteria taken from Yamamoto (1956), Coetzee (1983) and Buxton (1990). Oogenesis was described according to macroscopic staging which is an arbitary description of a continuous process with considerable variation in each developmental stage (Buxton 1990).

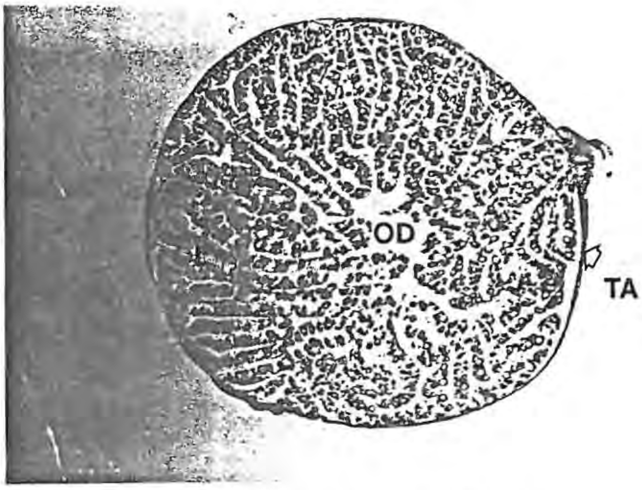


Figure 36. Transverse section of a Diplodus sargus capensis ovary showing the tunica albuginea (TA), oviduct (OD) and the ovigerous lamellae (OL) (x10).

Stage 1. Oogonia and pre-vitellogenic oocytes (Figure 37a)

Oogonia were observed in close association with the ovigerous lamellae. They consisted of small cells with a single large nucleus and a thin accumulation of slightly basophilic cytoplasm. Oogonia were most apparent in inactive\resting ovaries prior to sexual maturation or during the recovery period following spawning in mature ovaries. Pre-vitellogenic oocytes were found in ovaries at all stages of development but were most common in inactive/resting ovaries. Development through the pre-perinuclear, early perinuclear and late perinuclear stages (Coetzee 1983) was characterized by an increase in the number of nucleoli at the periphery of the nucleus and a slight decrease in the intensity of cytoplasmic staining from strongly basophilic in pre-perinuclear oocytes to faintly stained cytoplasm in late perinuclear oocytes.

Stage 2. Yolk vesicle formation and vitellogenesis (Figure 37b)

Developing ovaries were distinguished from inactive\resting ovaries by the presence of primary and secondary yolk vesicle oocytes (Yamamoto 1956). These oocytes exhibit a wide range of sizes depending on the stage of yolk vesicle formation. Primary 'yolk' vesicles, which are analogous to cortical granules (Wallace & Selman 1981), appear around the periphery of the cell and give rise to the cortical alveoli of larger eggs (Buxton 1990). The cortical alveoli fuse with the oolemma, releasing their contents into the perivitelline space at the time of fertilization (de Vlamming 1983). The primary 'yolk' vesicles should not be confused with the accumulation of enlarged lipid droplets in the nuclear region of the cytoplasm (Buxton 1990). The zona radiata is deposited between the cytoplasm and the follicle layer, the zona granulosa. Both of these layers become more distinct as development of the oocyte continues. In secondary yolk vesicle oocytes, acidophilic secondary yolk vesicles appear, initially at the periphery of the oocyte but later throughout the cytoplasm. At this stage nucleoli loose their peripheral arrangement and become randomly scattered throughout the nucleus.

Stage 3. Late vitellogenesis and maturing oocytes (Figure 37c)

Ripe ovaries were characterised by the presence of numerous large oocytes nearing maturation. These included oocytes in the tertiary yolk and migratory nucleus stages (Yamamoto 1956). The zona radiata becomes eosinophilic, increasing further in thickness and showing numerous radial striations. The cytoplasm is filled with eosinophilic secondary yolk globules except around the nucleus where lipid droplets begin to coalesce. These lipid droplets eventually displace the nucleus off-centre and form a single oil droplet which is characteristic of most known sparid eggs (Brownell 1979). Following the migratory nucleus stage, secondary yolk globules begin to coalesce to form a homogenous mass of yolk.

Although mature, hydrated oocytes were observed macroscopically in ripe ovaries, histological preparation was prevented due to the collapse of mature oocytes during the dehydration process (Coetzee 1983). The eggs of D. sargus measured 0.94 mm in diameter with a large oil droplet of 0.2 mm in diameter (Brownell 1979). The eggs of D. cervinus were similar in appearance being only marginally larger than those of D. sargus. The large oil droplet and small mature egg size are characteristic of pelagic eggs (Coetzee 1983; Thresher 1984; Buxton 1990).

Stage 4. Atretic oocytes (Figure 37d)

Normal atresia appeared both during and shortly after the spawning season. Atresia in pre-vitellogenic oocytes (stage 1) was characterised by a zoning of the cytoplasm which showed a distinct granular appearance. According to Yamamoto (1956) this zoning of the cytoplasm is a process of partial reabsorbtion of the oocyte whereafter it is rejuvenated into a smaller, healthy oocyte. Atresia in vitellogenic oocytes (stages 2 & 3) was recognised by a complete disruption in cellular organization. The nuclear membrane disintegrated and the cell took on an overall glandular appearance due to phagocytosis of the yolk by granulosa cells and leucocytes (Coetzee 1983; Buxton 1990).

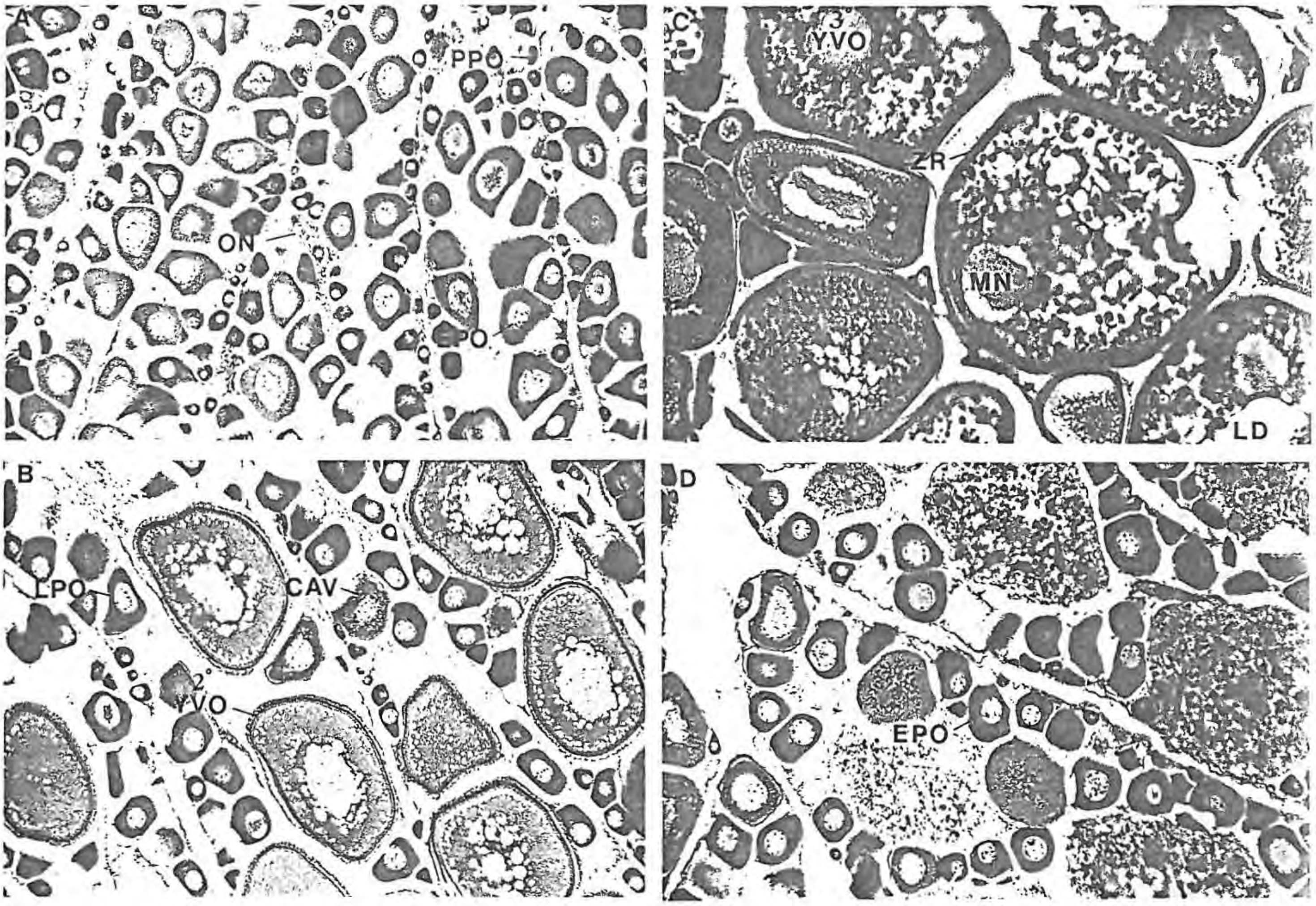


Figure 37. Oogenesis in *Diplodus sargus capensis* and *Diplodus cervinus hottentotus*. A) Section of an immature ovary (Stage 1) showing pre-vitelline oocyte development. ON=Oogonia, PPO=Pre-perinuclear Oocytes, EPO=Early Perinuclear Oocytes (x100). B) Section through a developing ovary (Stage 2) showing all stages of perinuclear oocytes and early vitellogenesis. LPO=Late Perinuclear Oocyte, CAV=Cortical Alveolar Stage, 2° YVO=Secondary Yolk Vesicle Oocyte (x100). C) Section through a ripe ovary (Stage 3) showing oocytes in the tertiary yolk vesicle stage (3° YVO) and migratory nucleus stage (MN). ZR=Zona Radiata, LD=Lipid Droplet (x100). D) Section through a spent ovary (Stage 4) showing atresia of vitellogenic oocytes. AF=Atretic Follicle, EPO=Early Perinuclear Oocyte (x100).

b) The testes and spermatogenesis

The testes were paired stuctures, triangular in section, contained within the tunica albuginea (Figure 38). The testicular tissue was proliferated by a mass of elongated lobules (analogous to seminiferous tubules) that formed a complex drainage system. These lobules drained into collecting ducts which finally opened into the two main sperm ducts. These fused posteriorly before emptying into the cloaca. Spermatogenesis was divided into four stages based on criteria from Hoar (1969), Coetzee (1983) and Buxton (1990).

Stage 1. Spermatogonia (Figure 39a)

Spermatogonia predominated in the testes, particularly towards the periphery of the organ. They were recognised by their relatively large size and lightly basophilic cytoplasm. In mature fish, sperm could still be present in the main sperm duct from the previous spawning season.

Stage 2. Spermatocyte and spermatid proliferation (Figure 39b)

Spermatogonia undergo a mitotic division to produce primary spermatocytes which are smaller in size, have reduced cytoplasm and are strongly basophilic. Primary spermatocytes then undergo a meiotic division to produce haploid secondary spermatocytes which then divide into spermatids. The latter were easily recognised by their exceptionally small size and visible lack of cytoplasm. Both spermatocytes and spermatids tended to proliferate towards the centre of the seminiferous lobules. At this stage there was no evidence of sperm in the main sperm duct.

Stage 3. Spermiogenesis and spermatozoa (Figure 39c)

Spermatids undergo metamorphosis into motile spermatozoa (spermiogenesis) which are characterized by their small size and densely stained nuclei. The lacunae of the seminiferous lobules become densely packed with spermatozoa which are conveyed via the collecting ducts to the main sperm duct. In the testes of ripe fish there was little evidence of spermatogonia although all other stages of spermatogenesis were visible.

Stage 4. Proliferation of spermatogonia (Figure 39d)

In spent testes spermatogonia appeared to proliferate at the periphery of the seminiferous lobules and although all stages of spermatogenesis were still visible, spermatocytes were reduced to isolated clusters. The main sperm duct still contained large amounts of sperm.

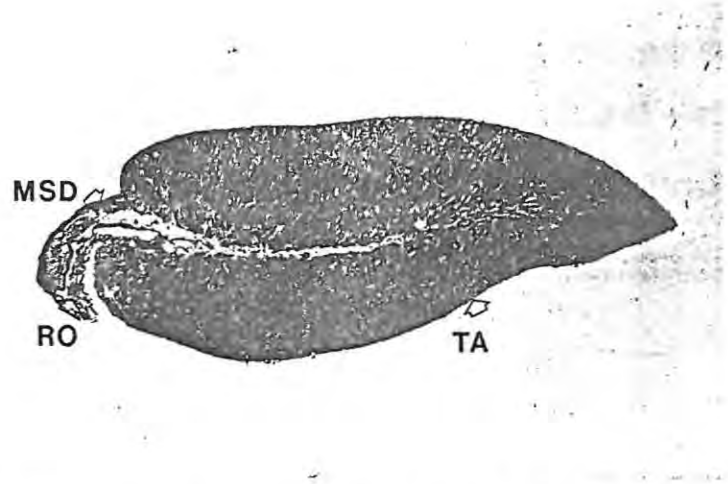


Figure 38. Transverse section of a Diplodus sargus capensis testis showing the tunica albuginea (TA), main sperm duct (MSD) and the rudimentary oviduct (RO) (x13).

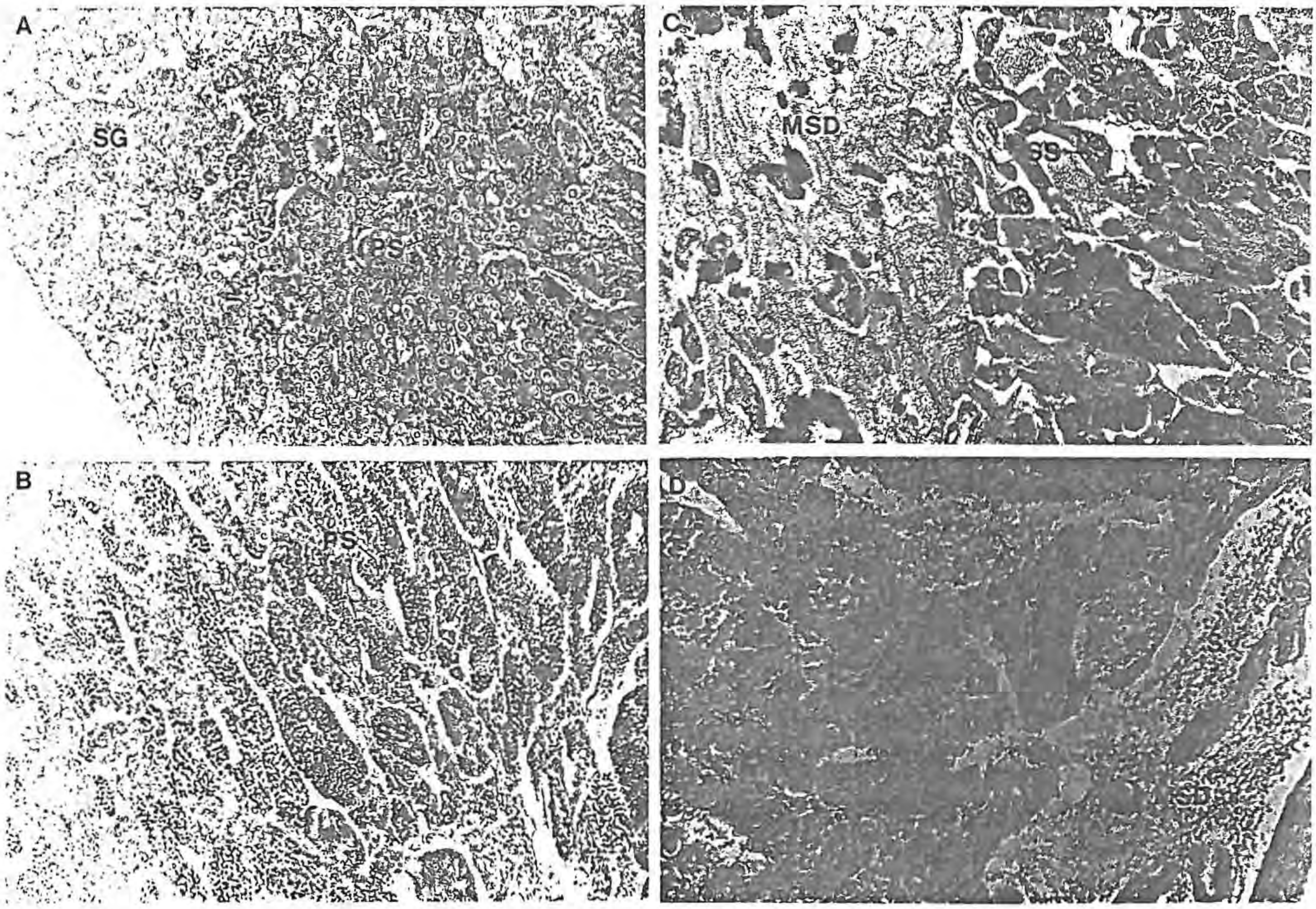


Figure 39. Spermatogenesis in Diplodus sargus capensis and Diplodus cervinus hottentotus. A) Section through an immature testis (Stage 1). SG=Spermatogonia, PS=Primary Spermatocytes (x200). B) Section through a developing testis (Stage 2) showing clusters of primary spermatocytes (PS) and secondary spermatocytes (SS) around the seminiferous lobules (x200). C) Section through a ripe testis (Stage 3) showing clusters of secondary spermatocytes (SS), spermatids (ST) and sperm in the main sperm duct (MSD) (x100). D) Transverse section through a spent testis (Stage 4) showing proliferation of spermatogonia (SG) while some sperm (S) is still remenant in the main sperm duct (MSD) (x200).

4.4 DISCUSSION

Reproductive seasonality

In *D. sargus* and *D. cervinus* the gonado-somatic indices showed that both species spawned during spring and summer, similar to many other South African sparid species (see review by Clarke 1988). The spawning seasons of both *Diplodus* species correlated well with the observed summer peak in abundance of their eggs off the south-western Cape coast (Brownell 1979). The extended spawning season of *D. sargus* (August to March) and the ability of individuals to spawn repeatedly ensured that "all their eggs were not in one basket", and the risk of catastrophic mortality of eggs and planktonic larvae was reduced (Thresher 1984). This spawning strategy also ensured that recruitment of juveniles into inshore nursery habitats was spread out over a period of time, thereby minimizing the possibility of inter and intraspecific competition for food and habitat space (Sale 1974; Johannes 1978; Christensen 1978). The more restricted spawning season of *D. cervinus* (August to December) was similar to that of a number of other sympatric sparid species including *Chrysoblephus laticeps* & *C. cristiceps* (Buxton 1990) and *Sparodon durbanensis* (Buxton & Clarke 1991). It appears that reproduction in all of these species is geared to take advantage of the beneficial conditions occurring during this time of year in order to ensure greatest survival of young.

Temperature and photoperiod appear to be the most important environmental factors influencing reproductive seasonality of fishes (de Vlaming 1972). Kadmon, Yaron & Gordin (1985) and Garratt (1985b) showed good correlation between increasing photoperiod and gonad maturation in *Sparus aurata* and *Chrysoblephus puniceus*. Increasing photoperiod and temperature was shown to influence gonad maturation in *Cheimerius nufar* (Coetzee 1983), *C. laticeps* and *C. cristiceps* (Buxton 1990) and *S. durbanensis* (Buxton & Clarke 1991). The present study showed that gonad maturation in both species correlated with increasing photoperiod and water temperature during July and August. Photoperiod is commonly temperature sensitive (de Vlaming 1972) and it is generally accepted that most fish species have a range of temperatures within which spawning can take place (Lagler, Bardach & Miller 1962). Inshore water temperatures along the south-eastern Cape coast show considerable fluctuation during the summer months due to the process of upwelling described in

Chapter 3. It is therefore probable that spawning, in both species, occurs when optimum, stable temperatures prevail after westerly winds cause a downwelling process and warmer water moves close inshore (Schumann et al. 1982).

It has been recognised that fish from tropical areas generally start spawning before those from more temperate areas (Coetzee 1983). In Natal D. sargus spawn between May and November (Joubert 1981a), while in the eastern Cape spawning occurs between June and December (Lasiak 1983; Beckley 1983; Coetzee 1986). This study showed that D. sargus in the TNP (south-eastern Cape) spawn between August and March with a peak recorded during spring. Bennett (1989) recorded an influx of small juvenile D. sargus (<25mm TL) into the surf zone in False Bay (southern Cape) between January and August. Daily increment analysis (Lang 1992), has shown that larval D. sargus take two to three months to become juveniles of the size recorded by Bennett (1989), which suggests that spawning in this region occurred during late summer. This evidence suggests that spawning in D. sargus, which occurs over their entire distribution, is strongly influenced by water temperature with spawning occuring during winter and spring in subtropical Natal waters and during spring and summer in the more temperate Cape waters. Correlation between months of peak spawning in D. sargus and mean monthly temperatures recorded along the South African coast (Bang & Pearce 1978; Shannon 1989; Hanekom et al. 1989) indicate that optimum spawning temperatures range from 17 to 20^{o}C.

Spawning in fish has been categorized into three groups according to the frequency of oocyte maturation: total synchronous spawners, group synchronous spawners and asynchronous spawners (Marza 1938 in Wallace & Selman 1981). Asynchronous spawners are characterised by having oocytes in all stages of development and having relatively protracted spawning seasons with multiple spawns per female (de Vlaming 1983). All stages of oogenesis were present in the ovaries of ripe D. sargus and D. cervinus and it is suggested that both species are asynchronous spawners, capable of multiple spawning bouts coinciding with favourable conditions during their respective spawning seasons. No attempt was made to estimate the fecundity of either species due to the problems associated with counting eggs of multiple spawners (Bagenal & Braum 1968; Garratt 1985b). However, judging from the small size of mature eggs (<1mm in diameter) and the high gonado-somatic indices recorded in ripe females (up to 25% of body weight), both species have relatively high fecundities, especially D. sargus where particularly high GSI's were noted (see Figure 16).

Population structure

1. D. sargus

Bimodal size frequencies with males occupying the smaller size classes and male biased sex ratios have often been used as diagnostic criteria for the occurrence of protandrous sex change in fishes (Sadovy & Shapiro 1987; Yeung & Chan 1987). By definition, protandrous hermaphrodites function first as males after which they change sex and function as females, with all females necessarily being derived from males (Buxton & Garratt 1990). The length frequency distribution of D. sargus showed that there was no clear separation in modal size between males and females, although females dominated the larger size classes. This was evident in an adult sex ratio significantly biased by females. Futhermore, the occurrence of primary females in the population suggested that D. sargus was not a protandrous hermaphrodite under the classical definition. Sadovy and Shapiro (1987) stipulate that neither the use of bimodal size (or age) frequency distributions nor biased sex ratios provide strong evidence for protandry. The reason for this is that there are various mechanisms that can produce bimodal size frequency distributions independently from hermaphroditism. These mechanisms include differential rates of growth and maturation, differential mortality, differential migration or spatial segregation by sex and selective trapping (Sadovy & Shapiro 1987).

Histological examination of gonadal development showed that D. sargus is a digynic species. Males and females both mature from a non-functional intersexual phase but some males retain the capability to change sex into secondary females. In order for this interpretation to be consistent with a definitive diagnosis of protandrous sex change and not to be confused with a prolonged juvenile bisexual phase (Sadovy & Shapiro 1987, Matsuyama et al. 1988) individuals must first be shown to have functioned as males before changing sex to female (Buxton & Garratt 1990). Mere evidence of sperm maturation occurring in the testicular region of an ovotestis is not sufficient to infer male functionality (Buxton & Clarke 1991). The occurrence of Type II gonads in fish larger than the size at 50% sexual maturity (>225mm FL), which possessed a functional sperm duct containing sperm during the spawning season, provided strong evidence that these fish were in fact functional males. Histological evidence of transitional Type II gonads was therefore, suggestive of protandric development amongst certain individuals in the population.

Work done on captive D. sargus sargus from the Mediterranean has shown that the majority of fish mature first as males with sex change occurring at different ages (Micale et al. 1987). The occurrence of a few individuals that mature as females has led to the usage of the term "unbalanced" hermaphroditism which is characterised by great variability in sexual phenotype (Micale et al. op. cit.). Similarly Abou-seedo et al. (1990) found that protandrous sex change took place in the majority of D. sargus kotschyi from Kuwait Bay during their second year of life but they also found that a number of fish in the population differentiated and functioned only as females. Although there is a lack of clarity in the terminology used, coupled in some instances with superficial observation, digyny does appear to be a common reproductive style in the various subspecies of D. sargus. Similar plasticity in the expression of the sexual phenotype has been described in other sparid species such as Acanthopagrus australis (Pollock 1985) where some females in the population are derived from protandric males while others differentiate straight from the bisexual juvenile condition. The assumption that sex change in fishes is genetically predetermined (Ghiselin 1969), is therefore, not sufficient to explain its intermittant occurrence amongst these species.

Any theory dealing with sex change must take into account the conditions under which an *individual* would most benefit from being a male or female relative to the rest of the breeding population (Warner 1978). Smith (1975 in Warner 1978) suggested that under conditions of lower mortality in larger individuals and where female fecundity increases greatly with age, protandry would increase zygote production. This explanation is however based on group selection and over-emphasizes the role females (Warner 1978). Following the theory of the size advantage model (Warner 1988a), sequential hermaphroditism would be advantageous where an individual reproduces best as one sex at a particular age or size and as the other when older and larger. Selection for protandry would then occur if females gained in reproductive ability with size or age faster than males (Warner 1988a). Implicit in this model however, is the suggestion that the proper age or size at which to change sex is genetically programmed (Buxton 1987). This was not apparent in D. sargus because it is characterised by variability in the size/age at sex change and because sex change itself appears to be an option to individual males rather than a genetically pre-determined requisite (Shapiro 1989).

2. D. cervinus

Similar size ranges for males and females and a sex ratio that does not differ significantly from unity are distictive features of gonochoristic species (Buxton & Garratt 1990). Histological examination of gonadal development in D. cervinus confirmed that this species is a rudimentary hermaphrodite where males and females develop from an immature bisexual gonad prior to sexual maturation. No evidence of sex change was found in mature individuals. Buxton & Garratt (1990) also refer to this group as 'late' gonochorists to distinguish them from 'true' gonochorists in which hermaphroditic tissue is not found. They suggest that all sparids previously classified as 'true' gonochorists should in fact be re-classified as rudimentary hermaphrodites owing to the occurrence of male and female elements in the early sparid gonad. Rudimentary hermaphroditism appears to be a common reproductive style amongst southern African sparids and has been reported in a number of species including Polysteganus undulosus (Ahrens 1964), Lithognathus lithognathus (Mehl 1973), C. nufar (Coetzee 1983, Garratt 1985b) Petrus rupestris (Smale 1988), S. durbanensis (Buxton and Clarke 1991) and Pachymetopon grande (Buxton & Clarke 1992).

Atz (1964), in a review of the intersexuality of fishes, suggested that rudimentary hermaphroditism in sparids strongly indicated a functional hermaphroditic ancestry. The selective advantage for the evolution of gonochorism over the apparent 'advantages' of being able to change sex are inevitably related to reproductive success of the individual. It has been speculated that if the energetic costs involved in changing sex are greater than the reproductive benefits derived then selection for sex change will be reduced (Shapiro 1987). In other words, if there is no significant difference between the rates of increase between male and female reproductive success, or if there is a substantial cost to changing sex that outweighs the advantages, then gonochorism would be favoured (Fischer & Petersen 1987).

Spawning behaviour

1. D. sargus

Evidence suggests that sex change in fish is initiated primarily by behavioural or demographic alterations within a fish's social system (Shapiro 1989). Of these alterations, the type of mating system employed appears to exert a major influence (Warner 1988b). No spawning behaviour was observed in D. sargus, however, various morphological and indirect behavioural characteristics were used to speculate on the type of mating system utilized. The most important of these characteristics included the similar size of functional males and females (monomorphism) and the large testis size in functional males. Similarity in the size of functional sexes suggests that reproductive success is not size related (Warner 1984; Buxton & Garratt 1990). Large size of one sex is important to mating success in species where the ability to control a territory or group of smaller individuals is a major determinant in mating frequency (Shapiro 1987; Buxton & Garratt 1990). Large testis size is seen as an advantage in terms of sperm competition where males compete with each other to fertilize eggs (Buxton & Garratt 1990). From these observations Buxton and Garratt (op. cit.) suggest that mating should take place in random pairs matched by size or in a group spawning sequence. Rare sightings of large, ripe-running males which appeared abnormally dark in colouration suggest that D. sargus may be sexually dichromic during spawning, a mate recognition feature common to many reef fish species (Thresher 1984). These colour differences between sexes suggests that spawning may occur in pairs, as has been found in other sexually dichromic species (Choat & Robertson 1975; Garratt 1991).

Considering the postulated scenario of random mating in pairs in D. sargus, what would be the selective advantage of having some males in the population capable of changing sex? The adult sex ratio of D. sargus was dominated by females (1:1.9) M:F. Let us assume that mating takes place in leks where males congregate to attract females (male dominance polygyny) (Emlen & Oring 1977). In a situation where male-male competition is strong (many Type IV males present) then selective pressure is placed on Type II males to change sex to female. However, if there are few Type IV males present, selective pressure for Type II males to change sex would be reduced. The apparent options to Type II males appears to be analogous to the situation in diandrous salmonids where two alternative life histories exist for the development of males (Gross 1985). No evidence is presented in support of these speculations and until spawning behaviour has been observed in D. sargus the reason for sex change in this species will remain an enigma.

2. D. cervinus

Large shoals of D. cervinus (up to 30 fish) were observed on two occasions during their spawning season and it is suggested that mating in this species takes place in a group spawning sequence. Monomorphism and large testis size in this species provides further evidence in support of group spawning behaviour (Buxton & Garratt 1990). In group spawners the potential for polygamy would be reduced and little sexual selection would occur (Buxton 1987). Monomorphism and a sex ratio close to unity as found in D. cervinus would therefore be expected (Buxton & Clarke 1991). This type of spawning behaviour has been postulated in other sparid species which are rudimentary hermaphrodites (Smale 1988; Buxton & Clarke 1991 & 1992).

Conclusion

D. sargus was found to have an extended spawning season while that of D. cervinus was more restricted. A detailed histological examination of gonadal development combined with length frequency analysis revealed that D. sargus are digynous with partial protandry occuring in some of the male population. Spawning is yet to be described in this species but is thought to involve a complex mating system. D. cervinus are rudimentary hermaphrodites with characteristics suggestive of group spawning behaviour.

In addition to their other life history characteristics, the different reproductive attributes shown by these two species are important considerations with respect to their management. Garratt (1985a) and Buxton (1987) discussed some of the problems associated with management of protogynous species in a size selective fishery. These include selective removal of bigger fish, mainly of one sex (males), from a population with the resultant imbalance in the sex ratio. Selective removal of larger D. sargus by recreational fishing may influence the adult sex ratio of this species. Joubert (1981a) found that the sex ratio of D. sargus in Natal was male-biased 1.3:1 (M:F), although females dominated the larger size classes. In addition, Joubert (op. cit.) found that 50% sexual maturity was reached between 150-160mm FL. This is different to the results presented in this study and it is suggested that the male-biased sex ratio and earlier size at sexual maturity of D. sargus in Natal may be in direct response to heavy fishing pressure. However, considering the ability of some males to change sex in response to changes in the social stucture of the population, the effects of fishing may be compensated to some extent. D. cervinus on the other hand are functional gonochorists and although the absence of sex change in this species provide fewer complications to their management, a combination of late maturation, slow growth and longevity (see Chapter 5) make this species particularly vulnerable to over-exploitation. These aspects are discussed in greater detail in Chapter 6.

CHAPTER 5 - AGE AND GROWTH

5.1 INTRODUCTION

The ability to determine the age of fish is an important tool in fishery biology (Bagenal 1974). Knowledge of the age of fish is essential for an understanding of various important life history parameters such as longevity, growth rate, age at maturity and mortality. Age in fishes is most frequently determined by interpreting and counting the growth zones that occur in various hard tissues such as otoliths, scales, dorsal fin spines, vertebrae and operculae (Weatherley & Gill 1987). These growth zones are generally laid down on an annual basis in response to various environmental and internal factors and are thought to represent alternate periods of fast and slow somatic growth.

Studies on various South African sparid species have shown that otoliths are the most suitable hard tissues for accurate age assessment (Nepgen 1977; Hecht & Baird 1977; Coetzee & Baird 1981b; Buxton & Clarke 1986; 1989; 1991; & 1992). Once the ages of fish from all size classes have been determined, these data can be applied to a growth model such as the von Bertalanffy equation to obtain the parameters K and $L\infty$, which are used to describe growth. This differential equation reflects the anabolic and catabolic contributions to the growth process in animals (Butterworth, Punt, Borchers, Pugh & Hughes 1989).

Information on the population dynamics of vulnerable linefish species is crucial for the establishment of a management programme to ensure their sustained utilization (Van der Elst & Adkin 1991). Considering the importance of both Diplodus species to the rock-and-surf fishery, the aim of this study was to estimate age and growth rates in both species in order to assist in their conservation and management.

5.2 METHODS

Total, fork and standard lengths of both species were measured in millimetres. Total body mass and evicerated mass were determined in grams. These parameters were expressed in the form of $y = ax+b$ for the length relationships and $y = ax^b$ for the length/weight relationship (Ricker 1975).

Otolith measurement, preperation and reading

An initial examination of scales from both species showed that although growth zones were distinguishable, they were difficult to enumerate, especially in older fish (cf. Beamish & McFarlane 1987). For this reason sectioned otoliths were used for age estimation. Sagittal otoliths were taken from 337 D. sargus and 292 D. cervinus sampled in the TNP and adjacent areas from April 1989 to December 1990. The otoliths were removed from the auditory bullae, cleaned and stored dry in paper envelopes. Otolith width and length, to the nearest 0.1mm, and otolith mass, to the nearest 0.001g were measured in order to determine the relationship between otolith growth and fish growth. Left otoliths were burned over a low intensity alcohol flame to enhance the optical clarity of the growth zones (Buxton & Clarke 1986). These otoliths were then embedded in casting resin and sectioned transversely through the nucleus using a twin-blade, diamond edged saw (Rauck 1976). The sections were mounted on glass slides using DPX mountant and examined under transmitted light using a low power dissecting microscope. Growth zones, each consisting of a wide hyaline zone and a narrow, darkly burnt opaque zone, were assumed to be representative of one years growth. Annual zones in each otolith section were counted four times, a fifth reading was then made concurrently by two readers and the best age estimate for each otolith was determined by consensus. Otoliths that had been badly sectioned or which were difficult to age (no consensus in age estimates) were rejected.

Using oxytetracycline labelling (Wild & Foreman 1980), daily growth increments in D. sargus and D. cervinus otoliths were studied by Lang (1992). Daily increment analysis was then used to validate the first annulus which was deposited at approximately 0.85mm from the otolith nucleus in D. sargus and 1.0mm in D. cervinus. The validation of the first annulus ensured that juvenile rings, apparent in some otoliths, were not confused with the first annual ring. This prevented possible over-estimation of age. The seasonality of zone deposition was determined by marginal zone analysis (Manooch 1982; Hecht & Smale 1986). The percentage frequency of hyaline and opaque zones on the margin of the otoliths were plotted on a monthly basis.

Growth calculations

The von Bertalanffy growth model was chosen to represent observed length-at-age data for D. sargus and D. cervinus as this model is generally regarded as the most suitable for expressing fish growth (Pauly 1979, Hughes 1986). The general form of the von Bertalanffy equation was used:

$$l(t) = L_\infty (1 - e^{-K[t - t_o]})$$

where l(t) is the length at age t, L_∞ is the theoretical maximum length according to the equation, K is the growth constant and t_o is the age at which, in terms of the model, the fish would commence growing from length l = 0 (Hughes 1986).

Parameter estimates for this equation were determined by iteration using the computer programme PC-YIELD (Hughes & Punt 1988). A test of the residual differences between the data and the fitted curve revealed that the absolute-error model provided the best fit to age-at-length data for both species (Hughes 1986).

5.3 RESULTS

The various length and length-mass relationships for D. sargus and D. cervinus are summarised in Tables 12 and 13 respectively. The exponent b in the length/weight relationship was >3 in both species. This value describes allometric growth in both species with fish becoming deeper bodied and heavier even after growth in length has slowed down (Tesch 1968). The relationships between otolith measurements (length, width and mass) and fork length for the two species (Tables 14 & 15) demonstrate the regional differences in otolith growth.

1. D. sargus

The relationship between otolith length and fork length was linear (Figure 40a), while otolith width increased asymtotically with increasing fish length (Figure 40b). These results indicated that most of the growth in D. sargus otoliths occured along the longitudinal axis, while growth along the lateral axis became slower with increased age. Otolith mass increased exponentially with fish length (Figure 40c), indicating that otoliths became substantially thicker and heavier even after increase in fish length had tapered off. This type of growth pattern in the otoliths of D. sargus resulted in a stacking of growth zones towards the periphery of otoliths from larger fish (Blacker

1974). Photomicrographs of sectioned otoliths from fish of three different sizes clearly showed the occurrence of stacking in larger fish (Figures 41a - c). Age estimation in older fish was extremely difficult due to this phenomenon. Stacking of growth zones has also been recorded in other sparid species including Cymatoceps nasutus (Buxton & Clarke 1989), Sparodon durbanensis (Buxton & Clarke 1991) and Pachymetopon grande (Buxton & Clarke 1992).

A total of 337 D. sargus otoliths were sectioned of which 19 (5.6%) were rejected as unreadable. The monthly frequency of occurrence of opaque and hyaline zones on the otolith margin showed no clear indication that these zones were deposited annually (Figure 42). Although it appeared as if two opaque zones are laid down per year it is suggested that this was simply a reflection of the small sample size of otoliths used for marginal zone analysis (n=270). Difficulty was experienced in determining whether the margin of the otolith was opaque or hyaline. For this reason only otoliths from fish aged at <10 years were used for marginal zone analysis as growth zones were clearer in otoliths from younger fish. Opaque growth on the otolith margin predominated during spring (August to October) co-inciding with peak spawning in D. sargus (see Chapter 4). Hyaline growth predominated for the rest of the year (November to July) except for a small peak in opaque growth recorded during April. In otoliths from older fish, which showed stacking of the growth zones, annual rings often appeared to split into two distinct rings towards the sulcal region of the sectioned otolith (Gauldie 1990). For this reason an attempt was made to make counts of annual rings away from the sulcal region, however, due to the occurrence of this phenomenon, the probability exists that age was over-estimated in some otoliths.

The absolute error model (Hughes 1986) gave the most appropriate fit to the length-at-age data for males, females (juveniles included with both sexes) and for the entire data set. This model assumed that variance was constant and normally distributed about the mean for each age class (Hughes 1986). Observed and expected mean length-at-age data are summarised in Table 16a. A Student's t-test showed no significant difference in the observed mean length-at-age data for males and females except in the age 4 size classes where mean length of males (218mm FL) was significantly lower than the mean length of females (230mm FL) (Table 16b). An index of growth *w* proposed by Gallucci & Quinn (1979), where

$w=(L\infty.K)$ was used to compare growth between sexes. The growth index w was similar in males (71.7) and females (77.2) suggesting that growth rates were similar in both sexes.

The von Bertalanffy growth curves for males, females and the entire data set are shown in Figures 43a - c respectively. Growth in D. sargus was relatively slow with the maximum age recorded at 21 years for a fish measuring 332mm FL. This is considerably slower than the estimated growth of D. sargus sargus in the Mediterranean which reaches approximately 8 years of age (Wassef 1985).

TABLE 12. Relationships between length and mass in Diplodus sargus capensis, sampled in the TNP from April 1989 to December 1990.

Equation	r^2	n
$TL(mm) = 1.162601\ FL(mm) + 2.553508$	0.999	119
$SL(mm) = 0.890571\ FL(mm) + 2.156629$	0.999	119
$Total\ Mass\ (g) = 0.0000074\ FL(mm)^{3.242}$	0.997	382

TABLE 13. Relationships between length and mass in Diplodus cervinus hottentotus, sampled in the TNP from April 1989 to December 1990.

Equation	r^2	n
$TL(mm) = 1.160665\ FL(mm) + 2.627736$	0.999	107
$SL(mm) = 0.893806\ FL(mm) + 2.551277$	0.998	107
$Total\ Mass\ (g) = 0.0000127\ FL(mm)^{3.141}$	0.995	304

TABLE 14. Relationships between otolith measurements (length, width and mass) and fork length in *Diplodus sargus capensis*, sampled in the TNP from April 1989 to December 1990.

Equation	r^2	n
$OL(mm) = 0.023691\ FL(mm) + 1.58207$	0.944	285
$OW(mm) = 0.114724\ FL(mm)^{0.628}$	0.902	185
$OM(g) = \exp(-6.19742 + 0.01115\ FL(mm))$	0.955	285

TABLE 15. Relationships between otolith measurements (length, width and mass) and fork length in *Diplodus cervinus hottentotus*, sampled in the TNP from April 1989 to December 1990.

Equation	r^2	n
$OL(mm) = 0.153755\ FL(mm)^{0.717}$	0.963	249
$OW(mm) = 0.113867\ FL(mm)^{0.658}$	0.838	184
$OM(g) = \exp(-5.55233 + 0.00921\ FL(mm))$	0.952	249

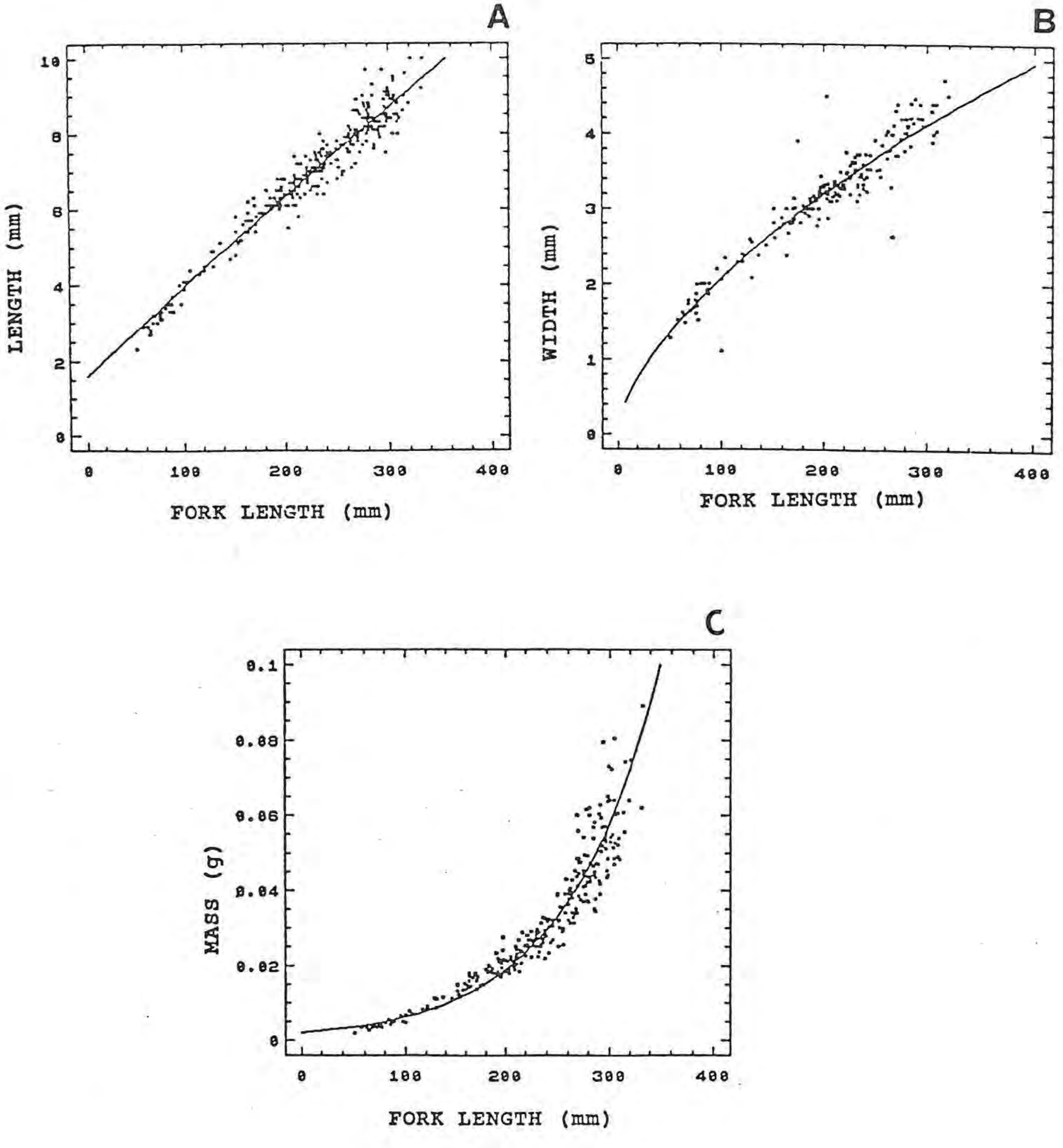


Figure 40. The relationship between otolith length and fork length (A), otolith width and fork length (B) and otolith mass and fork length (C) in Diplodus sargus capensis sampled in the TNP from April 1989 to December 1990.

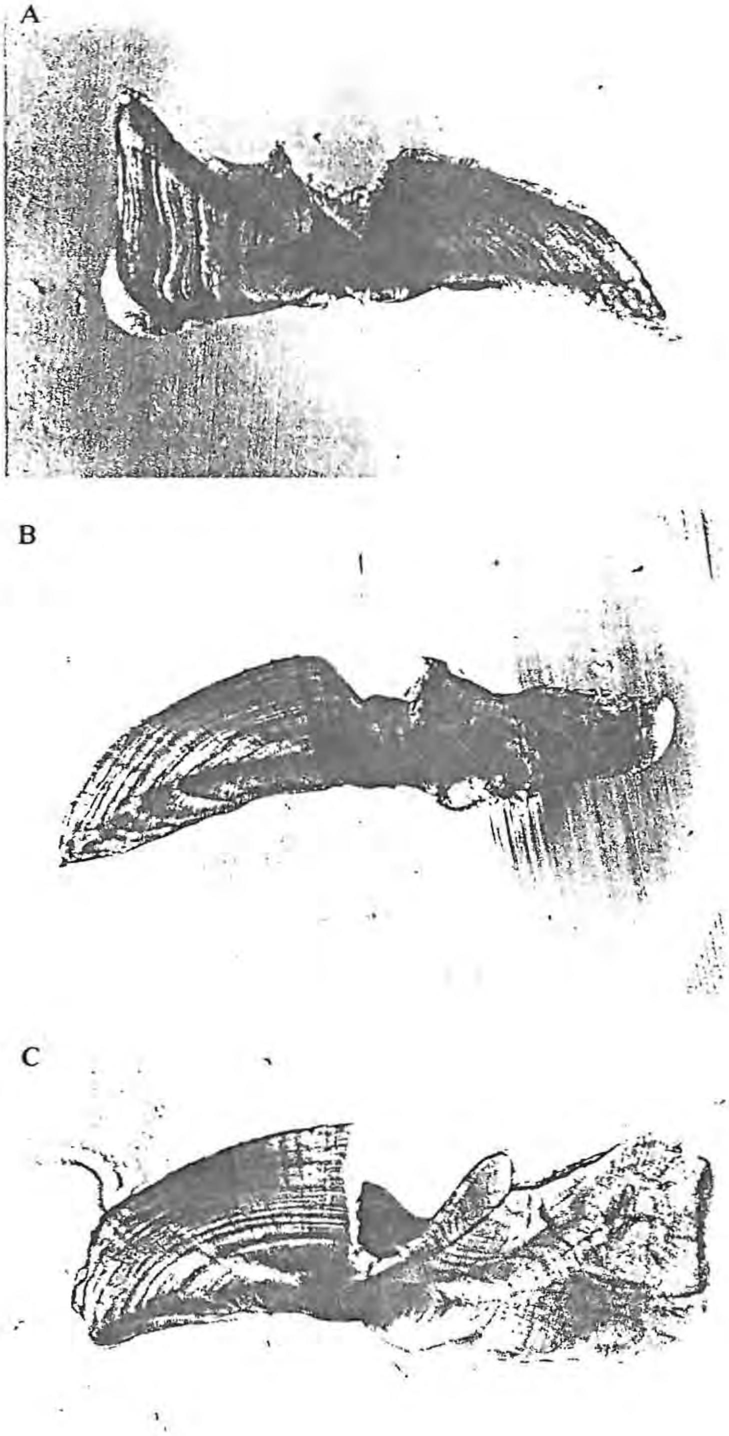


Figure 41. Photomicrographs of burnt and sectioned otoliths of Diplodus sargus capensis viewed under transmitted light (opaque zones are are marked in all three sections). A) D. sargus (195mm FL) 2 years old (x20). B) D. sargus (259mm FL) 6 years old (x14). C) D. sargus (299mm FL) 14 years old, note stacking of growth zones on the otolith margin (x13).

TABLE 16a. Observed mean length-at-age (mm FL) and expected mean length-at-age (from the von Bertalanffy growth curve) for *Diplodus sargus capensis*.

Age (Years)	Males			Females			All Fish		
	n	Observed mean length	Expected mean length	**n**	Observed mean length	Expected mean length	**n**	Observed mean length	Expected mean length
0	30	76	70	30	76	69	30	76	70
1	19	104	120	20	105	122	20	105	122
2	14	158	159	16	159	164	33	164	163
3	18	194	190	18	200	196	38	197	195
4	20	218	215	24	230	221	50	223	220
5	8	237	235	13	243	241	22	240	239
6	5	253	251	10	257	256	15	256	255
7	9	268	263	12	265	268	22	265	267
8	6	270	273	15	279	278	21	276	276
9	7	278	281	8	273	285	16	277	283
10	4	291	287	10	295	291	15	292	289
11	0	-	292	6	286	295	6	286	293
12	2	298	296	3	306	299	5	303	297
13	0	-	299	2	302	301	2	302	299
14	1	302	302	5	299	303	6	299	301
15	3	302	304	1	305	305	4	302	303
16	2	290	305	1	304	306	3	295	304
17	0	-	306	5	317	307	5	307	305
18	0	-	307	1	298	308	1	298	306
19	1	305	308	2	313	309	3	310	307
20	0	-	309	0	-	309	1	-	308
21	0	-	309	1	332	310	1	332	308

TABLE 16b. Test of significant difference between the observed mean length-at-age of male and female _Diplodus sargus capensis_ (P=0.05).

Age (Years)	Males Mean Length (mm)	Males ± Std. Dev.	n	Females Mean Length (mm)	Females ± Std. Dev.	n	d.f.	t
2	158	± 18.61	14	159	± 20.17	16	28	0.1667
3	194	± 12.99	18	200	± 17.80	18	34	1.2297
4	218	± 18.18	20	230	± 13.71	24	42	2.4246*
5	237	± 15.23	8	243	± 17.61	13	19	0.7604
6	253	± 11.80	5	257	± 23.25	10	13	0.3396
7	268	± 10.40	9	265	± 15.85	12	19	-0.4235
8	270	± 7.99	6	279	± 11.71	15	19	1.7992
9	278	± 6.73	7	273	± 11.59	8	13	-1.0687
10	291	± 22.55	4	295	± 9.39	10	12	0.4984
12	298	± 7.07	2	306	± 6.66	3	3	1.3964

* Denotes a significant difference

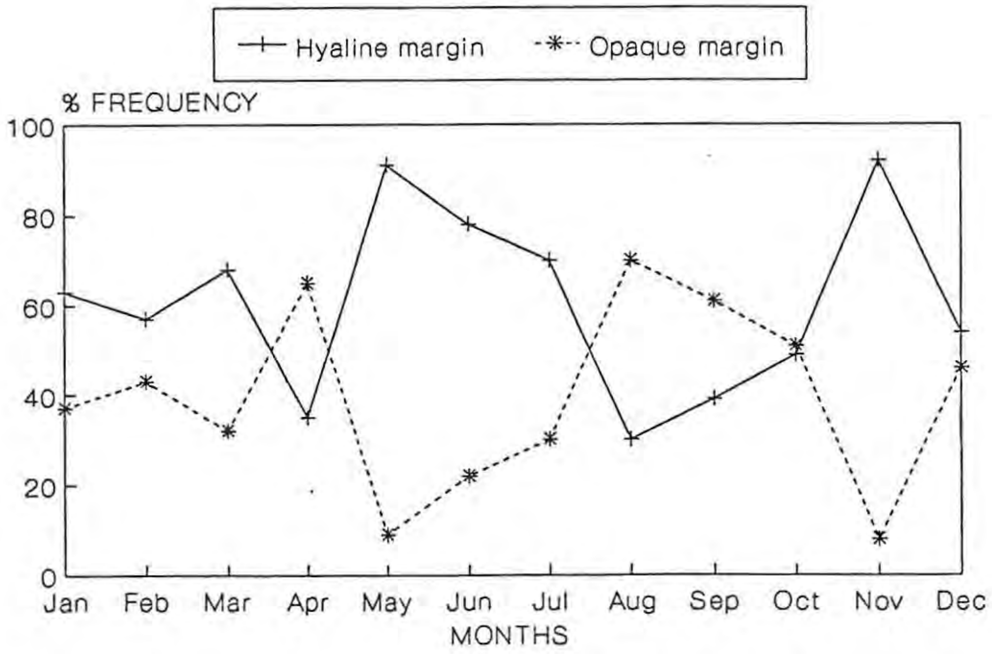


Figure 42. Temporal changes in the marginal zone of _Diplodus sargus capensis_ sampled in the TNP from April 1989 to December 1990 (n=270).

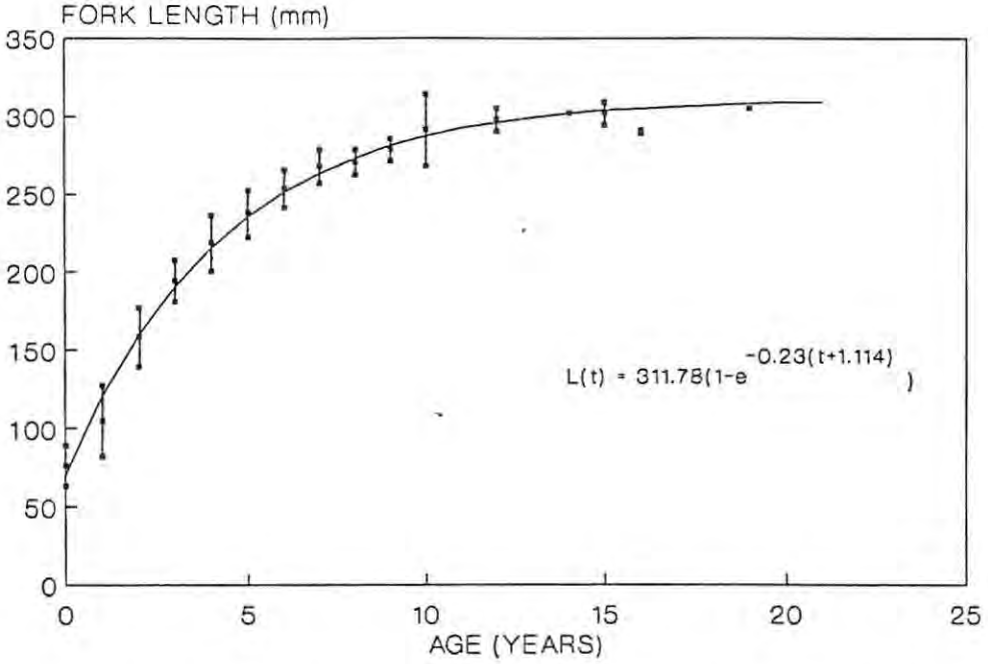


Figure 43a. The relationship between fork length and age in male Diplodus sargus capensis (juveniles included), sampled in the TNP from April 1989 to December 1990 (n=149).

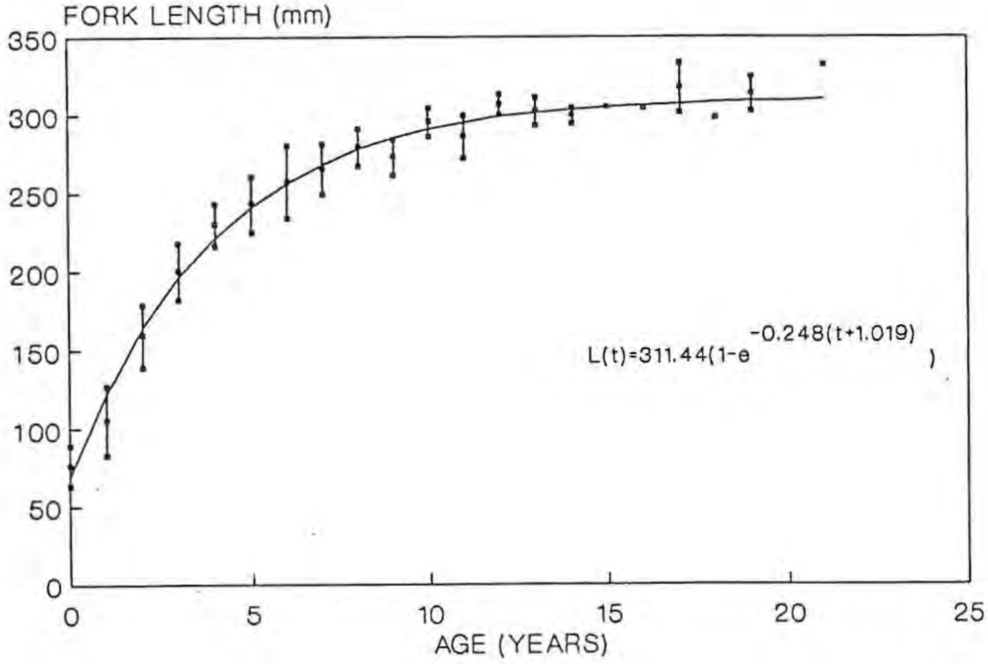


Figure 43b. The relationship between fork length and age in female Diplodus sargus capensis (juveniles included), sampled in the TNP from April 1989 to December 1990 (n=203).

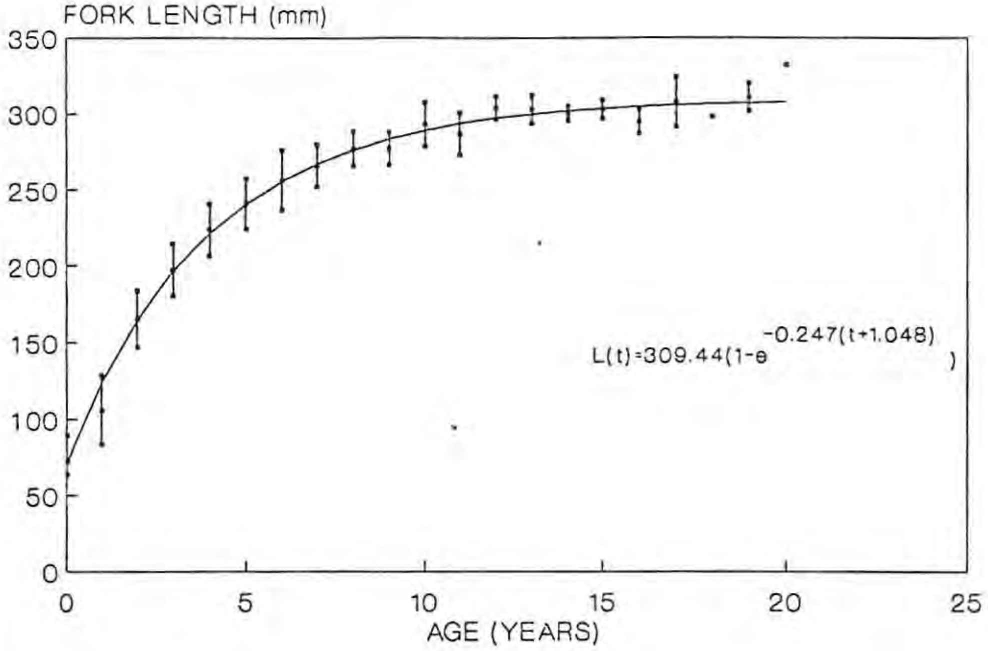


Figure 43c The relationship between fork length and age in Diplodus sargus capensis, sampled in the TNP from April 1989 to December 1990 (total data set, n=318).

2. D. cervinus

Otolith growth in D. cervinus was proportional in both length and width with increasing fish length (Figures 44a & b). The relationship between otolith mass and fork lenth was exponential (Figure 44c) indicating that, as with D. sargus, the otoliths continue to grow and become considerably thicker and heavier even after growth in fish length has reached an asymptote. Stacking of growth zones in otoliths from older fish (see Figures 45a - c) complicated age estimation in otoliths from larger fish.

A total of 292 otoliths were read of which 11 (3.8%) were rejected. The monthly percentage of opaque and hyaline zones on the otolith margin indicated that one opaque and one hyaline zone were deposited annually (Figure 46). The opaque zone was deposited during August to December co-inciding with the spawning season recorded in D. cervinus (see Chapter 4). The hyaline zone was deposited between January and July.

The absolute error model (Hughes 1986) gave the best fit to length-at-age data for males, females (juveniles included with both sexes) and for the total data set. Mean length-at-age data are summarized in Table 17a. A Student's t-test showed no significant difference between the observed mean length-at-age data for males and females (Table 17b). However, the presence of a few older males than females in the age and growth analysis and a higher calculated L_∞ for male D. cervinus may indicate greater longevity in males. Similarly, the growth index w (Galucci & Quinn 1979) was lower in males (56.5) than in females (69.5) indicating that growth rate was slower in males which take longer to reach an asymtote than females.

The von Bertalanffy growth curves for males, females and the total data set are presented in Figures 47a - c, respectively. Growth in D. cervinus was extremely slow with the maximum recorded age of 33 years for a fish of 480mm FL. The low L_∞ calculated for D. cervinus (396 mm FL) in comparison with the observed maximum length (480mm FL) can be attributed to the small sample of large fish combined with the rejection of some large otoliths due to reading difficulties. Split rings were also observed in the sulcal region of otoliths from D. cervinus.

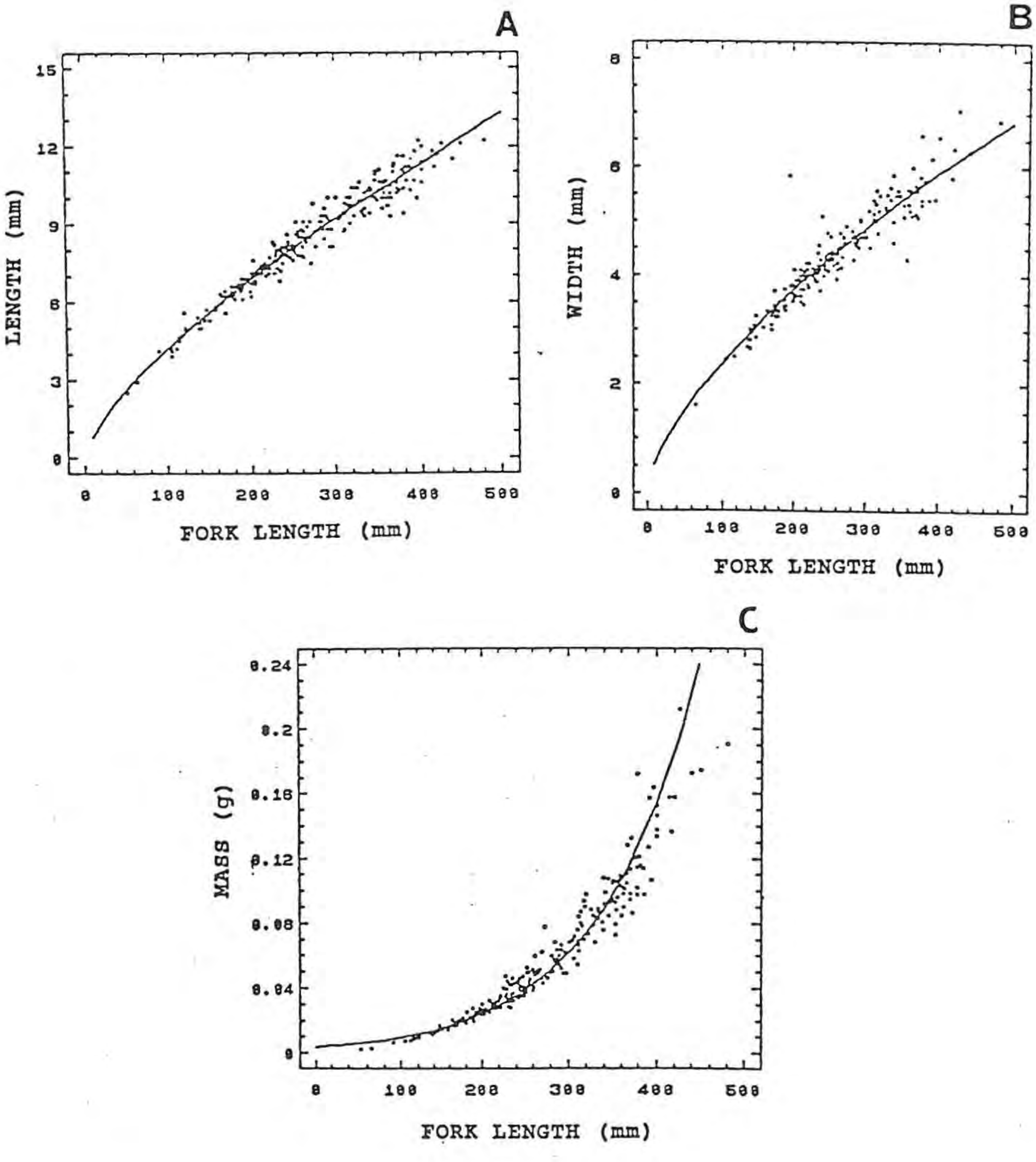


Figure 44. The relationship between otolith length and fork length (A), otolith width and fork length (B) and otolith mass and fork length (C) in Diplodus cervinus hottentotus sampled in the TNP from April 1989 to December 1990.

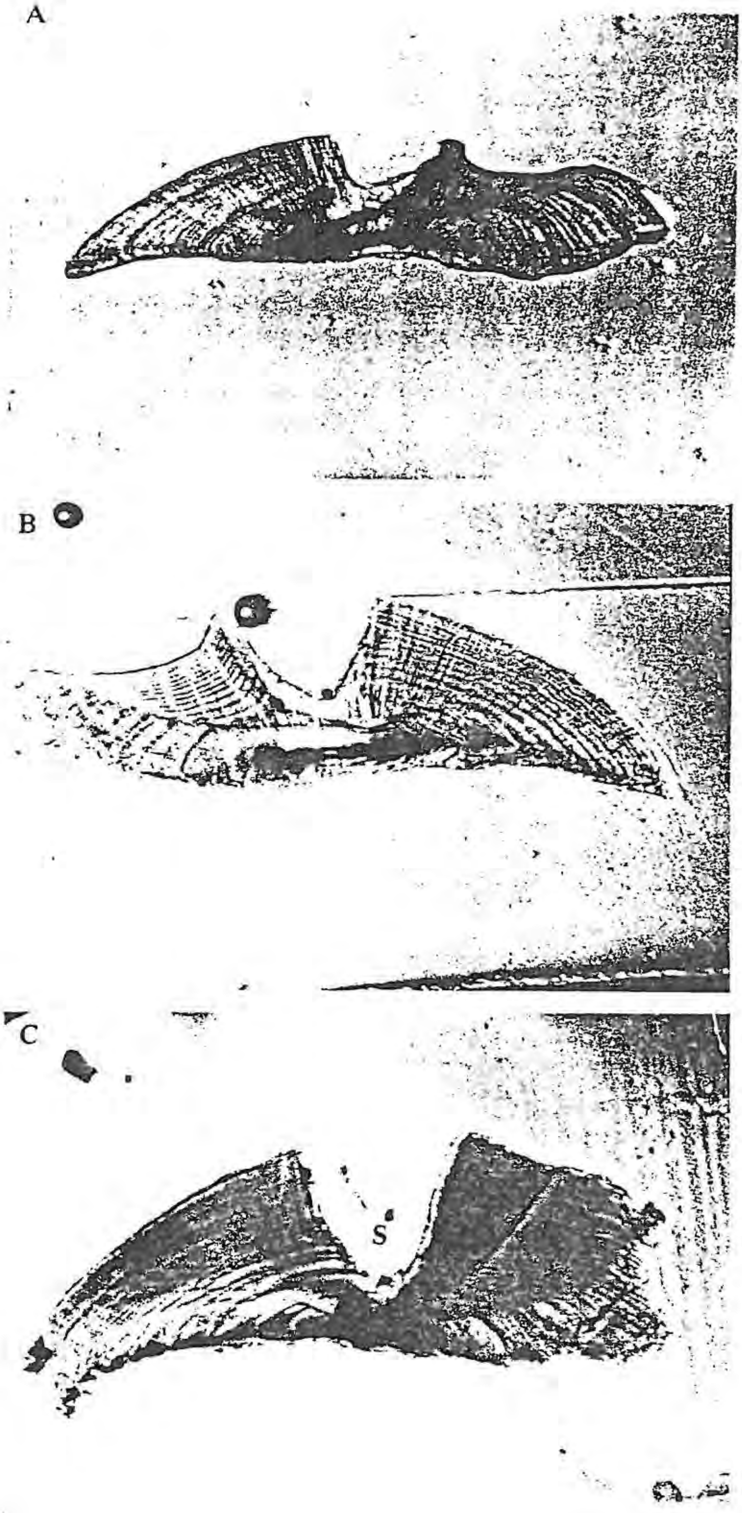


Figure 45. Photomicrographs of burnt and sectioned otoliths from Diplodus cervinus hottentotus viewed under transmitted light (opaque zones marked in A & B). A) D. cervinus (228mm FL) 3 years old (x14). B) D. cervinus (348mm FL) 12 years old (x12). C) D. cervinus (392mm FL) 27 years old, note stacking of growth zones and split rings towards the otolith sulcus (S) (x11).

TABLE 17a. Observed mean length-at-age (mm FL) and expected mean length-at-age (from the von Bertalanffy growth curve) for *Diplodus cervinus hottentotus*.

Age (Years)	Males			Females			All Fish		
	n	Observed mean length	Expected mean length	n	Observed mean length	Expected mean length	n	Observed mean length	Expected mean length
0	6	77	98	6	77	91	6	77	106
1	25	134	138	25	127	138	25	134	146
2	23	175	173	34	182	178	39	185	180
3	24	217	204	35	216	211	53	219	209
4	7	248	230	17	243	238	24	245	235
5	6	254	253	12	263	261	18	260	257
6	3	251	273	10	273	280	13	268	276
7	8	283	291	3	266	295	11	278	292
8	3	319	306	1	265	308	4	306	306
9	7	311	319	5	292	319	12	303	318
10	2	328	331	3	319	328	5	323	329
11	4	334	341	4	320	335	8	327	338
12	3	335	350	3	336	341	6	335	346
13	4	343	357	2	334	346	6	340	353
14	3	347	364	1	400	351	4	360	359
15	4	359	370	7	358	354	11	358	364
16	5	375	375	3	381	357	8	377	368
17	3	359	379	3	337	359	6	348	372
18	3	375	383	3	357	361	6	366	375
19	1	372	387	2	371	363	3	371	378
20	2	396	389	1	387	364	3	393	381
21	1	417	392	0	-	366	1	417	383
22	0	-	394	1	400	366	1	400	385
23	1	414	396	0	-	367	1	414	386
24	0	-	398	0	-	368	0	-	388
25	1	420	399	0	-	368	1	420	389
26	1	401	401	0	-	369	1	401	390
27	1	392	402	0	-	369	1	392	391
28	0	-	403	0	-	370	0	-	391
29	0	-	403	0	-	370	0	-	392
30	1	440	404	1	426	370	2	433	393
31	1	450	405	0	-	371	1	450	393
32	0	-	405	0	-	371	0	-	394
33	1	480	406	0	-	371	1	480	394

TABLE 17b. Test of significant difference between the observed mean length-at-age of male and female Diplodus cervinus hottentotus (P=0.05).

Age (Years)	Males			Females			d.f.	t
	Mean Length (mm)	± Std. Dev.	n	Mean Length (mm)	± Std. Dev.	n		
2	175	± 23.29	23	182	± 23.87	34	55	1.1125
3	217	± 21.63	24	216	± 22.15	35	57	-0.1613
4	248	± 19.65	7	243	± 19.08	17	22	-0.4903
5	254	± 9.05	6	263	± 21.28	12	16	1.0441
6	251	± 16.77	3	273	± 21.84	10	11	1.5881
7	283	± 29.04	8	266	± 4.00	3	9	-0.9920
9	311	± 25.25	7	292	± 32.21	5	10	-1.1091
10	328	± 23.33	2	319	± 13.20	3	3	-0.5819
11	334	± 26.81	4	320	± 16.23	4	6	-0.9253
12	335	± 17.56	3	336	± 11.14	3	4	0.0277
13	343	± 17.15	4	334	± 28.99	2	4	-0.4868
15	359	± 22.43	4	358	± 13.94	7	9	-0.0859
16	375	± 19.93	5	381	± 3.51	3	6	0.5065
17	359	± 19.60	3	337	± 17.21	3	4	-1.4605
18	375	± 14.01	3	357	± 17.79	3	4	-1.3514

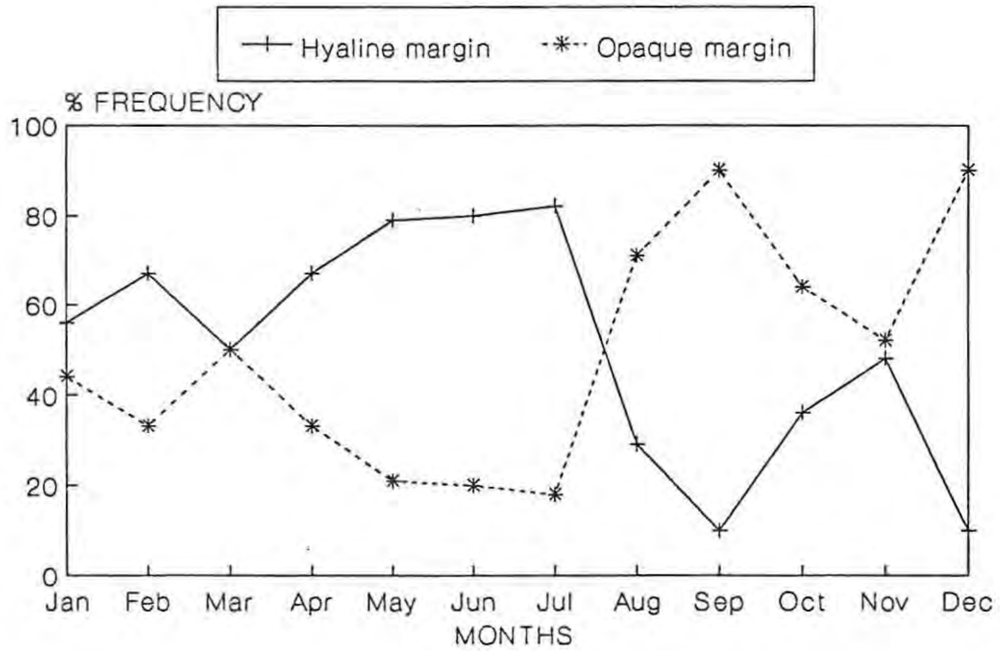


Figure 46. Temporal changes in the marginal zone of Diplodus cervinus hottentotus otoliths sampled in the TNP from April 1989 to December 1990 (n=235).

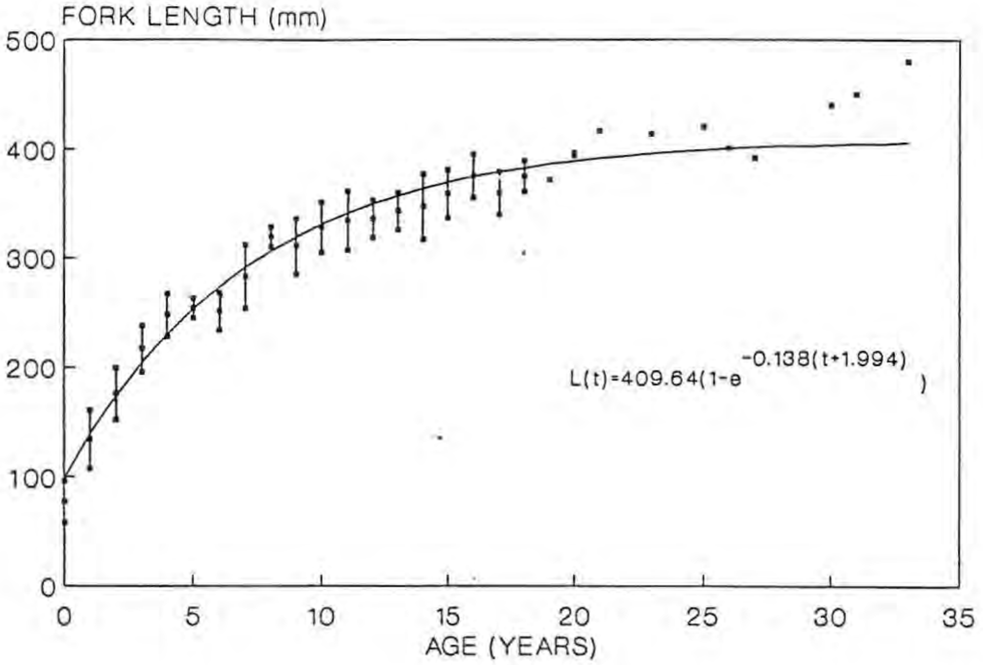


Figure 47a. The relationship between fork length and age in male Diplodus cervinus hottentotus (juveniles included), sampled in the TNP from April 1989 to December 1990 (n=154).

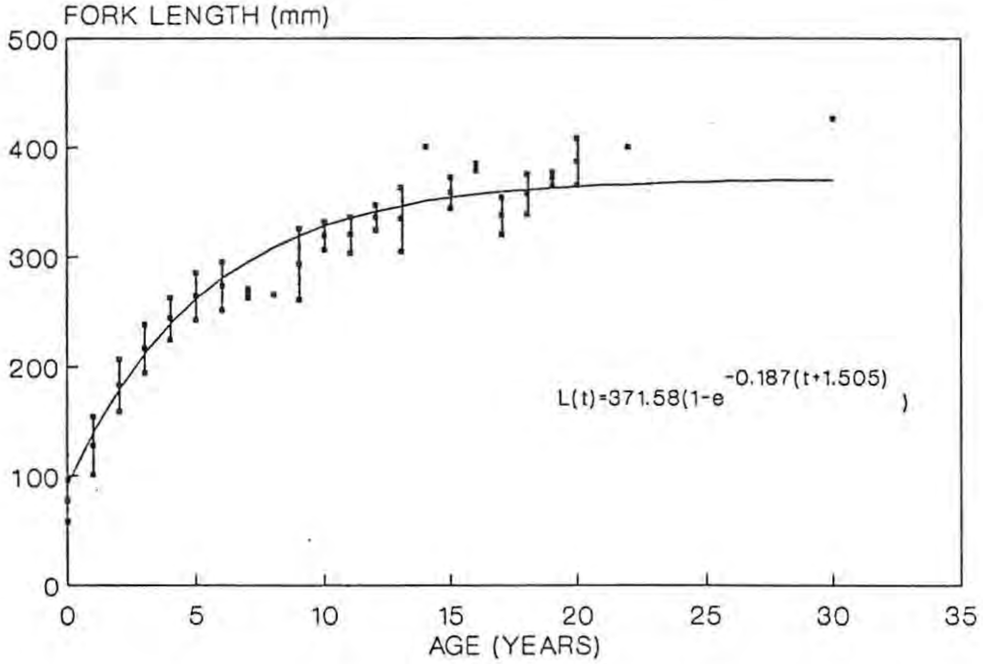


Figure 47b. The relationship between fork length and age in female Diplodus cervinus hottentotus (juveniles included), sampled in the TNP from April 1989 to December 1990 (n=182).

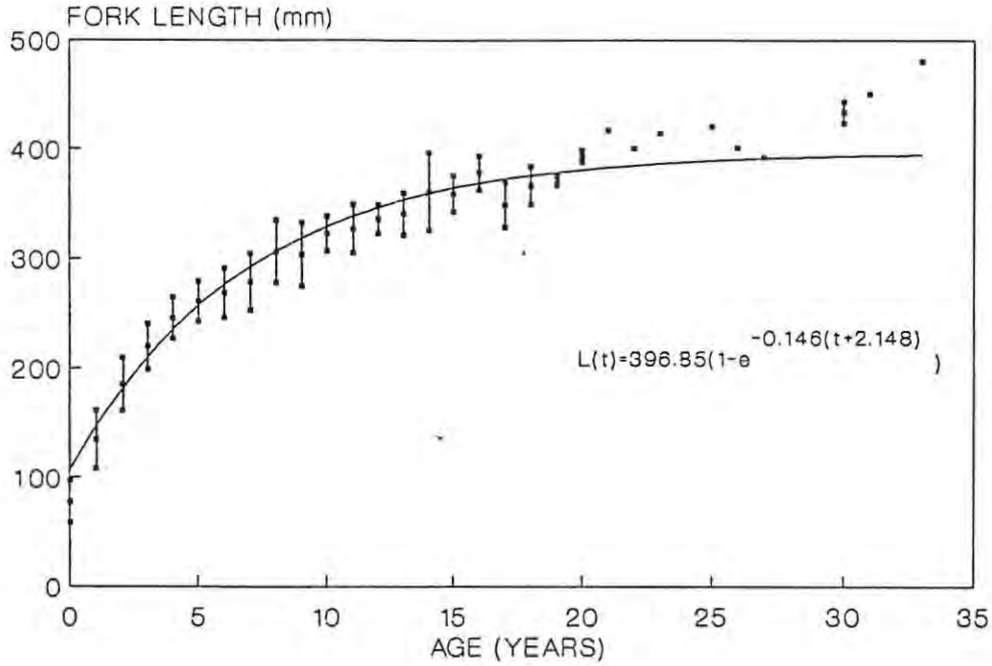


Figure 47c. The relationship between fork length and age in Diplodus cervinus hottentotus sampled in the TNP from April 1989 to December 1990 (total data set, n=281).

5.4 DISCUSSION

The realization that many fish species live for long periods, sometimes with minimal growth, has important implications to stock management and has stimulated a great deal of interest in the longevity of fishes (Beamish & McFarlane 1987). Unfortunately, with this surge of interest, a great deal of confusion has arisen in the terminology used to describe otolith structure in studies relating to the age and growth of fishes (Pannella 1974; Campana & Neilson 1985; Buxton & Clarke 1986; Buxton 1987; Lang 1992). In this study sectioned otoliths were viewed under transmitted light and the terms hyaline and opaque were used to describe zones that appeared optically clear and dense respectively.

The physiological processes governing zone formation in otoliths are not well understood (Blacker 1974). Reviewing the work done on otolith microstructure, Campana & Neilson (1985) suggest that growth in otoliths occurs through the differential deposition of calcium carbonate and protein during an endogenous circadian rhythm. Discontinuous growth is predominantly proteinaceous with opaque optical properties, while incremental growth appears translucent and is primarily inorganic. Thin opaque and wide hyaline zones were clearly discernable in otolith sections from both Diplodus species examined. The optical density of the opaque zones increased after heating the otolith over an alcohol flame suggesting protein dominance (Christensen 1964). Viewing sectioned otoliths from young (<2 years) D. sargus and D. cervinus using a scanning electron microscope, Lang (1992) showed that the opaque zones were composed of significantly narrower daily growth increments than those observed in the hyaline zones. This suggests that the opaque zones in otoliths of both species are representative of slower (discontinuous) growth, an observation consistent with the results of Campana & Neilson (1985). In both species peak opaque zonation occurred during spring and early summer co-inciding with the spawning season of both species. The energetic costs involved in spawning are high and Simkiss (1974) showed that less calcium is available for somatic growth during periods of high reproductive activity. From this evidence it would appear that the opaque zone in both Diplodus species is deposited during periods of high reproductive activity (slow somatic growth) and is composed predominantly of proteinaceous material. Alternatively, the wide hyaline zones are deposited during periods of 'normal' somatic growth during the rest of the year and are composed predominantly of calcium. This pattern of zone deposition has been observed in a number of other South African sparids (see review by Lang 1992).

Of fundamental importance to an age and growth study of this nature is the validation of the annual periodicity of growth zones (Panella 1974; Beamish & McFarlane 1983). Validation usually involves the use of indirect methods that help to corroborate the interpretation, rather than provide direct validation (Beamish & McFarlane 1983). These methods include cohort analysis (the annual progression of a strong year class through the population over a series of years can help verify that one annulus is deposited each year) or marginal zone analysis (Manooch 1982; Hecht & Smale 1986) as used in this study. The results obtained from the marginal zone analysis did not conclusively indicate that one hyaline and one opaque zone were deposited each year in either D. sargus or D. cervinus. Despite this result the growth zones were considered to be representative of annual increments and it is suggested that the relatively long spawning seasons in both these species, particularly D. sargus, may account for the observed discrepency in the time of opaque deposition. Futhermore, all other studies on South African sparids have shown growth zones to be annuli

(Nepgen 1977; Hecht & Baird 1977; Coetzee & Baird 1981b; Buxton & Clarke 1986, 1989, 1991 & 1992; Pulfrich & Griffiths 1988; Smale & Punt 1990; Buxton in press).

By enumeration of daily increments within the first annulus (approximately 360 from the otolith nucleus to the inner edge of the first opaque zone), Lang (1992) provided direct evidence of the annual periodicity of the first opaque and hyaline growth zones in otoliths taken from juveniles (<2 years old) of both *Diplodus* species. It should be pointed out however, that counts were only made on otoliths from young fish and that enumeration of daily increments in otoliths from older fish is considerably more difficult. Futhermore, counting of daily rings requires similar interpretive procedures to annual zone enumeration and is equally subjective (Campana & Neilson 1985). It is strongly recommended that, in order to confirm the annual periodicity of otolith growth zones in both *Diplodus* species, a tag and release project using an oxytetracycline (OTC) marker be undertaken in the TNP. An intramuscular injection of OTC provides a method of marking the otolith at the time of administration (Lang 1992). This will provide unequivocal evidence of the periodicity of zone deposition (Beamish & McFarlane 1987) and allow interpretation of the occurrence of depositional features such as 'split' rings in the otoliths of both species.

The von Bertalanffy parameter estimates derived for both *D. sargus* and *D. cervinus* showed that, similar to other sparid species, they were relatively slow growing, long lived species both capable of reaching ages in excess of 20 years. A comparison between the von Bertalanffy growth parameters, K, $L\infty$ and the growth index w are shown for a number of South African sparids in Table 18. Various workers have tried to compare the growth performances of fishes by referring to the values of $L\infty$ and K themselves. However, Moreau (1987) points out that population comparisons must use $L\infty$ and K together as they are correlated. Gallucci & Quinn (1979) suggested a new parameter $w=L\infty.K$ could be used for growth comparisons. According to Moreau (1987) w is only useful in comparing growth when t_0 values are the same for the compared fish populations and when their longevity is similar. It does however, allow a rough comparison of growth between species (Buxton in press). From Table 18 it is apparent that growth rates in South African sparids are fairly similar with the highest growth rate occuring in *Petrus rupestris* and the slowest in *Pachymetopon blochii*.

The growth index *w* calculated for D. sargus (76.3) was considerably higher than that of D. cervinus (57.9) indicating a faster growth rate in the former species. Futhermore, age at 50% sexual maturity was calculated at approximately 4 years for D. sargus and 6 years for D. cervinus. D. sargus could therefore be described as being more *r*-selected than D. cervinus in terms of its faster growth rate and earlier age at maturity (Adams 1980). These and other life history characteristics are discussed in relation to the management of both species in Chapter 6.

TABLE 18. A comparison of the von Bertalanffy growth parameters calculated for a number of South Africa sparids (modified from Buxton in press).

Species	Maximum Age (Years)	K	L_∞	ω	Reference
Argyrozona argyrozona	12	0.071	744	52.8	Nepgen (1977)
Pterogymnus laniarius	11	0.190	481	91.4	Hecht & Baird (1977)
Cheimerius nufar	22	0.065	953	61.9	Coetzee & Baird (1981b)
Pachymetopon aeneum	12	0.133	467	62.1	Buxton & Clarke (1986)
Pachymetopon blochii	12	0.097	538	52.2	Pulfrich & Griffiths (1988)
Cymatoceps nasutus	45	0.050	1089	54.5	Buxton & Clarke (1989)
Sparodon durbanensis	31	0.090	1021	91.9	Buxton & Clarke (1991)
Petrus rupestris	33	0.075	1383	103.7	Smale & Punt (1990)
Pachymetopon grande	38	0.153	461	70.5	Buxton & Clarke (1992)
Chrysoblephus laticeps	17	0.147	425	62.5	Buxton (in press)
Chrysoblephus cristiceps	22	0.081	655	53.1	Buxton (in press)
Diplodus sargus capensis	21	0.247	309	76.4	this study
Diplodus cervinus hottentotus	33	0.146	397	58.0	this study

CHAPTER 6 - GENERAL DISCUSSION AND MANAGEMENT CONSIDERATIONS

The management decisions applied to a species depend to a large extent on its life history characteristics. Those characteristics considered important with respect to management of D. sargus and D. cervinus included slow growth, longevity, relatively late maturation, habitat preference, iteroparity and sex change. Endemicity and a shallow depth distribution of both species were also considered important in this respect. Comparative studies of life history traits are of particular importance to fisheries biology. For example, Adams (1980) used the *r* and *K* continuum to characterize species for management purposes. *r*-Selected species were considered generalists having life history strategies focussed on productivity. The most well known marine examples are pelagic species which are characterized by early maturation, fast growth and a short life span (e.g. anchovies). On the other hand *K*-selected species are specialists, having life history strategies adapted for efficient exploitation of a specific limiting resource (Pianka 1974). Examples include fish species inhabiting specific niches within complex reef communities. These fish increase their individual fitness through competitive ability. In terms of commonly measured population parameters in fisheries biology, Adams (1980) suggested that a *K*-selected species would have a high age at first maturity, a low K value from the von Bertalanffy growth equation, a large $L\infty$ from the von Bertalanffy growth equation, a low rate of instantaneous natural mortality and a high maximum age.

Age determination from sectioned otoliths revealed that both D. sargus and D. cervinus were slow growing, long-lived species capable of reaching ages in excess of 20 years. Relative to fast growing, pelagic species found on the west coast, these species could be described as *K*-selected. They are similar to many other South African sparids (see Table 18), where relatively slow growth and longevity are the norm. Slow growth results in a lower yeild-per-unit stock, an older age at maturity and a slower recovery rate after over-exploitation than in fast growing species (Buxton & Clarke 1989). Fisheries based on slow growing species, such as those found in the South African linefishery, are extremely susceptable to overfishing and careful management of fish stocks is essential.

Although both Diplodus species can be considered to be relatively *K*-selected in terms of their growth characteristics, other life history traits exhibited by D. sargus show that this species is a generalist. D. sargus were shown to have a generalized niche requirement, both in terms of food and habitat. D. cervinus on the other hand had a specialized diet and fairly specific habitat requirements. In addition, D. sargus showed a relatively faster growth rate and an earlier at age at sexual maturity than D. cervinus. Similar to other sparids with pelagic eggs, both Diplodus species appeared to have a relatively high fecundity (small egg size and high GSI values) with multiple spawns per breeding season (iteroparity). These traits are typical of *r*-selected species. These observations illustrate that it is not easy to pigeon hole either of the study species as being *r* or *K* strategists. However, on the basis of habitat requirements, distribution and abundance, D. sargus is considered more of a generalist than D. cervinus.

A recreational fishery is typically biased towards the removal of the larger specimens from a population (Buxton 1987). Sequential hermaphrodites are therefore considered to be particularly vulnerable to over-exploitation because one sex is subject to greater fishing mortality than the other. For this reason intense fishing pressure may result in a significant alteration of the sex ratio which can seriously affect the reproductive potential of the population (Garratt 1985a; Buxton 1987). Although the factors influencing sex change in D. sargus are poorly understood, it is suggested that sex change occurs in response to various cues within the social system of this species. Sex change in D. sargus was observed at a variety of sizes/ages and appeared to be an 'option' to individual males rather than a genetically determined pre-requisite. For this reason it is postulated that selective removal of large individuals (predominantly females) by fishing, will be partially compensated by sex changing males and the sex ratio of the population will not be affected to the same extent as found in monandrous, protogynous species such as Chrysoblephus laticeps (Buxton in press). Although this postulation is based on speculation it is suggested that, from a management perspective, D. sargus should be considered no different to a gonochoristic species.

Further characteristics of D. sargus and D. cervinus considered important with respect to management included their inshore distribution and endemicity. Adults and juveniles of both species were shown to be most abundant on shallow inshore reefs (<10m). This localised distribution suggests that both species are vulnerable to stock depletion by shore-angling. However, considering that fish caught in shallow water (<10m) do not suffer from the effects of barotrauma, undersized fish can be successfully returned to the sea. Initial mark and recapture results (Van der Elst & Bullen 1991; Bennett & Attwood in prep.) suggest that both Diplodus species are fairly resident. Although more research on this aspect of their biology is required, if these species are shown to be sedentary then they will be particularly vulnerable to local extinctions due to over-fishing (Buxton 1987). Futhermore, due to the endemic distribution of the sub-species D. sargus capensis and D. cervinus hottentotus (Smith & Heemstra 1986), these species require careful management as recruitment from distant areas is not possible (Smale & Buxton 1985).

To summarise, the interaction of life history characteristics has a strong effect on the response of a species to fishing pressure (Adams 1980). It is clear that both Diplodus species are sensitive to the effects of over-fishing. Considering the present increase in participation and decrease in CPUE in the recreational shore-fishery (Van der Elst 1989) and the importance of both species to this fishery (Joubert 1981b; Coetzee et al. 1989; Clarke & Buxton 1989), careful management measures were deemed necessary to ensure their survival. Within the *r* and *K* continuum both Diplodus species were shown to be relatively *K*-selected, although D. sargus was shown to have a more generalized life history than D. cervinus. For this reason D. cervinus may be more vulnerable than D. sargus and may require more stringent conservation measures.

Management options

Many of the target species in the recreational rock-and-surf linefishery are also exploited by the recreational and commercial line-boat sectors (Clarke & Buxton 1989). Such multi-species, multi-user fisheries are generally difficult to manage (Smale & Buxton 1985; Clarke & Buxton 1989), especially when benefits derived from the resource differ among the users (e.g. economic, recreational, nutritional). A successful management strategy must therefore meet the criteria of being effective in terms of both the biology of the fish and its acceptance by the resource users (Attwood & Bennett 1990). For this reason, no single conservation measure can suffice in sustaining this complex fishery (Smale & Buxton 1985; Clarke & Buxton 1989).

Two basic options are utilized in the management of the South African linefishery, limitation of catch and limitation of effort (see reviews by Van der Elst 1985; Clarke 1988; Van der Elst 1989; Penney et al. 1989). Catch limitation is usually achieved through the imposition of size limits, bag limits (quotas) or gear restrictions, while effort is controlled by closed seasons and limited access. Of these options, limiting access of the number of recreational anglers or imposing gear restrictions such as control of hook size or the use of nylon line (Van der Elst 1985) would be detrimental to the recreational fishery in terms of the pleasure derived from the pursuit. It may also have a negative economic effect on industries related to the recreational fishery (Clarke 1988). These limitations are thus not considered to be practical management options.

In a multi-species fishery the implementation of species specific management regulations is compounded by factors such as the inability of anglers to direct fishing effort at a particular species or to return undersized fish to the sea due to barotrauma. However, because D. sargus and D. cervinus are exploited primarily by rock-and-surf anglers, undersized fish can easily be returned unharmed to the sea. For this reason species specific restrictions were considered to be a practical management strategy in the conservation of both Diplodus species.

Size limits

Size limits are generally set at the size at which a species reaches 50% sexual maturity. The rationale behind this choice is that it allows each fish an even chance to breed before being subjected to the risk of fishing mortality. However, as pointed out by Attwood & Bennett (1990), this limitation alone may not be sufficient to provide adequate protection to the breeding stock. The reason for this is that fecundity generally increases with fish size and protection of an adequate breeding stock may depend on the size-fecundity relationship in individual species (Roberts & Polunin 1991). Implementation of a maximum size limit has often been suggested as a possible solution to this problem. Unfortunately most recreational anglers find it very difficult to release the largest fish they capture because it is often the quality of the catch (e.g. trophy fish) which is more important than the actual quantity landed. For this reason maximum size limits are not popular. In the case of both Diplodus species which are relatively small and caught primarily by non-competitive, recreational anglers who generally catch fish for nutritional purposes, the implementation of a maximum size limit was not considered practical.

Present minimum size limits for D. sargus and D. cervinus are set at 200mm TL and 300mm TL respectively (Government Gazette, No. 13096, 28th March 1991). The size limit for D. sargus is considerably smaller than their size at 50% sexual maturity (264mm TL). However, in Natal 50% maturity in D. sargus has been calculated at approximately 180mm TL (Joubert 1981a). It is suggested that this earlier size at maturity may be in response to heavy fishing pressure along this coast. For this reason it is recommended that the minimum size limit for D. sargus be increased to at least 250mm TL which should ensure protection to a larger proportion of the breeding stock, particularly in Natal. Although the size limit for D. cervinus has been set at 300mm TL, their size at 50% maturity was calculated at 333mm TL. Considering the vulnerability of this species (slow growth, late maturation, longevity and fairly specific niche requirements) a further increase to 350mm TL is strongly recommended. This conservative size limit is considered practical from an enforcement point of view (i.e. same as Coracinus capensis) and should provide adequate protection to the spawning stock of this species. Due to the present 1kg size restriction in the Cape, this increase will not affect spearfishermen (1kg = 385mm TL).

Bag limits

Bag limits are an important component of the present fishing regulations (see Penney et al. 1989) which are aimed at optimal utilization of the South African marine linefish resource (Van der Elst 1985). Often bag limits are applied in the form of quotas which are aimed at maintaining the catch at a level offering adequate protection to the parent stock, thereby ensuring sufficient recruitment (Buxton 1987). Application of quotas requires a detailed knowledge of the relationships between egg production, stock density, growth and mortality for individual species. Information of this nature is costly to aquire and is not available for most South African linefish species. Furthermore, the open access nature of the recreational fishery precludes the formulation of a total allowable catch (TAC) at a sustainable yield for most species (Attwood & Bennett 1990). The rationale behind the imposition of bag limits in the

South African recreational fishery was therefore to direct effort away from reef species considered more vulnerable to the effects of over-fishing (Buxton 1987).

The ineffectiveness of present bag limits for certain recreational linefish species was pointed out by Buxton (1987) and Clarke (1988). They showed that the catch of the majority of recreational line-boat and shore-anglers in the Port Elizabeth area was substantially lower than that allowed by current legislation. *D. sargus* and *D. cervinus* are currently listed as restricted species and are both subject to bag limits of 10 fish/man/day. While catches of up to 10 *D. sargus* per angler in a days fishing are rare but still possible, it is an extremely unlikely occurrence to catch as many as 10 *D. cervinus* in a day (Schoeman & Schoeman 1990; pers. obs.). These observations suggest that present bag limits are providing little protection for these species.

Catch per unit effort (CPUE) data collected from various locations along the South African coast have shown that *D. sargus*, together with species such as *Pomatomus saltatrix* and *Sarpa salpa*, constitute one of the most important shore-angling species along the South African coast (Joubert 1981b; Coetzee & Baird 1981a; Buxton & Clarke 1989). In light of the considerable fishing pressure being placed on stocks of *D. sargus* and evidence that these stocks are declining in Natal (R. Van der Elst, Oceanographic Research Institute, Durban, pers. comm.), a more conservative bag limit for this species is strongly recommended. Due to its relatively slow growth, it is suggested that *D. sargus* be included with other protected species with a bag limit of 5 fish/man/day.

Available data suggests that *D. cervinus* make up a smaller proportion of shore-anglers catches than *D. sargus* (Coetzee *et al.* 1989; Clarke & Buxton 1989) and visual census data revealed that *D. cervinus* were less abundant within the inshore zone (1-10m) than *D. sargus*. Nevertheless, the importance of this species to the recreational shore-angling and spearfisheries should not be underestimated. Considering the more specialized life history of *D. cervinus* and their low relative abundance, this species was designated as being particularly vulnerable to the effects of over-fishing. For this reason a bag limit of 2 fish/man/day is recommended to assist in the conservation of this species. This bag limit should not be restrictive to the average angler as catches seldom exceed 2 fish/man/day (Coetzee et al. 1989; Clarke and Buxton 1989) but it should help to spread the catch more evenly between participants (i.e. reducing the bag of more successful anglers thereby increasing the availability of fish for less successful anglers).

Due to the annually increasing participation in the South African recreational shore-fishery (Van der Elst 1985), the importance of regular re-assessment of these bag limits by monitoring catches on a long term basis is stressed. Futhermore, effort should be made to promote a conservation ethic amongst recreational anglers and to encourage tagging of fish that are returned to the sea so that more information can be obtained on growth and movements of these species.

Closed seasons

Closed seasons, during which fishing is prohibited, are usually proclaimed over a period when a species is particularly susceptable to exploitation. For example, the period that coincides with the breeding season, when aggregations or migrations of fish may result in increased catches (Buxton 1987). The primary effect of closed seasons for most long-lived species is to reduce the total effort rather than to improve recruitment by protecting breeding fish, although the latter is a logical consequence (Buxton op. cit.).

Pomatomus saltatrix, Coracinus capensis and Petrus rupestris are presently the only species caught by rock-and-surf anglers that are protected by a closed season (although P. rupestris are seldom taken from the shore). A closed season, in addition to minimum size legislation and a bag limit of 5 fish/man/day, appears to have resulted in a considerable stock recovery in P. saltatrix (Van der Elst & Adkin 1991). The success of these restrictions may be explained by the fact that P. saltatrix are particularly vulnerable to fishing during their spawning season (September to December), when large shoals occur along the Natal coast (Van der Elst 1976). However, Attwood & Bennett (1990) have shown that the present closed season for Coracinus capensis (15th October to 28th February) is ineffective at improving catches. They suggest the reason for this is that the closed season coincides with the breeding season, when C. capensis are in poorest condition and when they are least catchable. Futhermore, the effect of the closed season is compromised by the additional effort attracted during the open season.

An important consequence of closed seasons for P. saltatrix and C. capensis is that they cause a re-direction of effort towards a number of other inshore species including D. sargus and D. cervinus. The spawning seasons of both Diplodus species overlap with the closed seasons of P. saltatrix and C. capensis. For this reason, any implementation of a closed season for either D. sargus or D. cervinus over their respective breeding seasons will probably result in a great deal of angler dissatisfaction. Furthermore, this period coincides with a large influx of anglers over the Christmas holidays. On these grounds, the implementation of a closed season is not recommended for either Diplodus species.

Closed areas

The fourth option used in management of the South African recreational fishery is that of areas closed to fishing. Although not implicit, this technique will be discussed under the role of marine reseves such as the TNP in conservation of both Diplodus species. One of the principal goals of the World Conservation Strategy is to ensure the sustainable utilization of species and ecosystems (IUCN 1980). It is within this context that the role of marine reserves in conserving vulnerable linefish species should be considered.

Marine reserves, in which fishing is prohibited, reduce total fishing effort and may serve as a means of conserving all species within the protected area. Classical methods of controlling catch and effort in a fishery, such as those discussed above, require large amounts of information about the status of the stocks and they are often complicated and expensive to enforce (Roberts & Polunin 1991). Protected areas are therefore often established either as an alternative, or in addition to other forms of fisheries management. In multi-species fisheries, marine reserves such as the TNP have been shown to be a viable management option for the protection of resident species with complex life histories (Buxton & Smale 1989).

Cessation of fishing within an area is likely to result in an increase in the abundance and average size of target species (Roberts & Polunin 1991). A comparison between the relative abundance and size structure of both Diplodus species in the TNP with that of an adjacent, exploited area showed no significant differences (see Chapter 3). Although these results suggested that the TNP was having little effect in protection of these species, a number of important considerations were emphasized: 1) The result was based on a comparatively few transects from the inshore zone (1-10m) of the exploited area, which was shown to be the optimum habitat for both species. 2) The exploited area off Sout River is fished predominantly by ski-boat fishermen and exploitation of the inshore zone by rock-and-surf anglers is believed to be limited. 3) The close proximity of the exploited area to the boundary of the TNP may result in restocking of the exploited populations through seeding and/or emigration. Clearly, further work is required before definite conclusions are drawn. Nevertheless, the fact that the TNP may be providing a source of recruitment and/or emigration of Diplodus species to exploited areas is considered important if marine reserves are to be used as an option to manage these species (Roberts & Polunin 1991).

Bennett (in prep.) showed that catches of both D. sargus and D. cervinus improved significantly after protection from exploitation in the De Hoop Marine Reserve. Tagging results from this area suggest that both species are strongly residential and Bennett & Attwood (in prep.) predict that it would take stocks of D. sargus and D. cervinus approximately 2.5 and 5-8 years respectively before they returned to a relatively pristine level after exploitation. Furthermore, Bell (1983) showed a significantly greater abundance and relative size of D. sargus and D. vulgaris inside as opposed to outside a marine reserve off the coast of France. He attributed these differences to the effects of exploitation. Based on this evidence it is suggested that both D. sargus and D. cervinus do recieve protection from the establishment of marine reserves.

Catch and effort data were recorded during the collection of biological samples while shore-fishing in the TNP. Methods used were similar to those of Bennett (in prep.) and all species caught that were not required for biological sampling were tagged and released. The results of these data (CPUE) can be used as an additional means of comparing the relative abundance of both Diplodus species. A total of 34 species were caught of which D. sargus and D. cervinus made up 19.1% and 4.2% of the total catch respectively. CPUE for D. sargus was calculated at 29.3 fish/angler/100hrs (17.5kg/angler/100hrs) while that for D.

cervinus was 6.5 fish/angler/100hrs (6.7 kg/angler/100hrs). This catch rate is considerably higher than the CPUE estimated for D. sargus (1.9kg/angler/100hrs) and D. cervinus (0.3kg/angler/100hrs) in the recreational rock-angling fishery at Port Elizabeth (Clarke & Buxton 1989). Although these catch rates must be compared with caution (CPUE may be effected by a wide variety of factors unrelated to fish abundance), it does suggest that protection is being afforded to both species in the TNP.

From the above discussion it is clear that marine reserves such as the TNP do provide protection for inshore reef species such as D. sargus and D. cervinus. Considering that South Africa has a coastline of approximately 3000km and adequate enforcement of species specific catch restrictions is difficult, marine reserves are considered to be a valuble management option in conserving these species.

Finally, it is important to point out that the establishment of marine reserves such as the TNP must be considered in a broader context than simply as an option for fisheries managers. The principal goal of area protection is conservation (Robinson 1989). In this respect the World Conservation Strategy outlined two other main objectives in addition to ensuring the sustainable utilization of species and ecosystems. These included: 1) "to maintain essential ecological processes and life-support systems" and 2) "to preserve genetic diversity" (IUCN 1980). Coastal ecosystems include both land and water components where ecological processes occur at high rates (Ray 1984). The ecological linkage between marine and terrestrial realms in coastal habitats precludes the effective management of one independent from the other (Salm & Clark 1984). In addition to providing protection to vulnerable fish species, the TNP has achieved the goal of conserving a rich diversity of marine and terrestrial flora and fauna along the Cape coastline.

Recommendations for future work:

1) Establishment of a mark-recapture programme in the TNP using an oxytetracycline marker to validate age determination in both Diplodus species. This can be done in conjunction with long-term catch data collection for comparison with other areas.

2) Visual assessment of the relative abundance of Diplodus species should be carried out in a comparable but heavily

exploited area such as Cape St Francis to allow a better examination of the effects of fishing on the size structure and abundance of these species.

3) An attempt should be made to observe and describe spawning behaviour and the mating system of both Diplodus species. This would allow a better understanding of the reproductive style of these species and the reasons for the occurrence of partial protandry in D. sargus.

REFERENCES:

ABOU-SEEDO, F., WRIGHT, J.M. & CLAYTON, D.A. 1990. Aspects of the biology of Diplodus sargus kotschyi (Sparidae) from Kuwait Bay. Cybium 14: 217-223.

ADAMS, P.B. 1980. Life history patterns in marine fishes and their consequences for fisheries management. Fish. Bull. U.S. 78: 1-12.

AHRENS, R.L. 1964. A preliminary report on the biology of the Seventy Four Polysteganus undulosus (Regan) in Natal waters. Unpubl. MSc. thesis, University of Natal.

ATTWOOD, C.G. & BENNETT, B.A. 1990. A simulation model of the sport-fishery for galjoen Coracinus capensis: an evaluation of minimum size limit and closed season. S. Afr. J. mar. Sci. 9: 359-369.

ATZ, J.W. 1964. Intersexuality in fishes. In: Intersexuality in vertebrates including man. (eds.) Armstrong, C.N. & Marshall. A.J. Academic Press, London. 145-232.

BAGENAL, T.B. & BRAUM, E. 1968. Eggs and early life history. In: Fish production in Fresh Waters. (ed.) Ricker, W.E. IBP Handbook No. 3: 519-181.

BAGENAL, T.B. 1974. The ageing of fishes. Unwin Brothers, England. 234pp.

BANG, N.D. & PEARCE, A.F. 1978. Physical oceanography. In: Ecology of the Agulhas Current region: an assessment of the biological responses to environmental parameters in the South West Indian Ocean. (ed.) Heydorn, A.E.F. Trans. Roy. Soc. S. Afr. 43: 156-162.

BARNES, R.S.K. & HUGHES, R.N. 1982. An introduction to Marine Ecology. Blackwell Scientific Publications.

BAUCHOT, M.L., HUREAU, J.C. & MIQUEL, J.C. 1981. Sparidae. In: FAO species identification sheets for fishery purposes (eds) Fischer, W., Bianchi, G. & Scott, W.B. Eastern Central Atlantic; fishing areas 34 & 47 (in part). Department of Fisheries and Oceans Canada, by arrangement with the Food and Agriculture Organization of the United Nations, vol. 4.

BEAMISH, R.J. & MCFARLANE, G.A. 1983. The forgotten requirement for age validation in fisheries biology. Trans. Am. Fish. Soc. 112: 735-743.

BEAMISH, R.J. & MCFARLANE, G.A. 1987. Current trends in age determination methodology. In: Age and growth of fish, (eds.) Summerfelt, R.C. & Hall, G.E., Iowa State Univ., Iowa. 15-42.

BECKLEY, L.E. 1983. The ichthyofauna associated with Zostera capensis Setchell in the Swartkops estuary, South Africa. S. Afr. J. Zool. 18: 15-24.

BECKLEY, L.E. 1985. The fish community of East Cape tidal pools and an assessment of the nusery function of this habitat. S. Afr. J. Zool. 20: 21-27.

BECKLEY, L.E. & BUXTON, C.D. 1989. Underwater observations of reef fish in and around Algoa Bay, South Africa. Trans. Roy. Soc. S. Afr. (47): 29-38.

BELL, J.D. 1983. Effects of depth and marine reserve fishing restrictions on the structure of a rocky reef fish assemblage in the north-western Mediterranean sea. J. Appl. Ecol. 20: 357-369.

BENNETT, B. 1987. The rock-pool fish community of Koppie Alleen and an assessment of the importance of Cape rock-pools as nurseries for juvenile fish. S. Afr. J. Zool. 19: 97-104.

BENNETT, B.A. 1989. The fish community of a moderately exposed beach on the southwestern Cape coast and an assessment of this habitat as a nursery for juvenile fish. Est. Coastal & Shelf Sci. 28: 293-305.

BENNETT, B.A. In press. Long-term changes in the catches of shore anglers in False Bay. Trans. Roy. Soc. S. Afr.

BENNETT, B.A. In prep. The effects of a new marine reserve on rock and surf angling fish. (to be submitted to S. Afr. J. mar. Sci.)

BENNETT, B.A. & ATTWOOD, C. In prep. Some predictions of the benefits to shore anglers of a marine reserve. (to be submitted to Biol. Conserv.)

BERRY, P.F., VAN DER ELST, R.P., HANEKOM, P., JOUBERT, C.S.W. & SMALE, M.J. 1982. Density and biomass of the icthyofauna of a Natal littoral reef. Mar. Ecol. Prog. Ser. 10: 49-55.

BLACKER, R.W. 1974. Recent advances in otolith studies. In: Sea Fisheries Research. (ed.) Harden-Jones, F.R., Elek Science, London. 67-90.

BOHNSACK, J.A. 1990. The potential of marine fishery reserves for reef fish management in the U.S. southern Atlantic, Miami. NOAA tech. Memo. NMFS-SEFC-261. 40pp.

BOHNSACK, J.A. & BANNEROT, S.P. 1986. A stationary visual census technique for quantitatively assessing community structure of coral reef fishes. NOAA Tech. Rep. NMFS 41: 1-15.

BRANCH, G. & BRANCH, M. 1981. The living shores of Southern Africa. Struik, Cape Town. 272 pp.

BROCK, R.E. 1982. A critique of the visual census method for assessing coral reef fish populations. *Bull. Mar. Sci.* 32 (1): 269-276.

BROWNELL, C.L. 1979. Stages in the development of 40 marine fish species with pelagic eggs from the Cape of Good Hope. *Ichthyol. Bull. Rhodes Univ.* 40: 84pp.

BURGER, L.F. 1991. The distribution patterns and community structure of the Tsitsikamma rocky littoral ichthyofauna. Unpubl. M.Sc. thesis, Rhodes University.

BUTTERWORTH, D.S, PUNT, A.E., BORCHERS, D.L, PUGH, J.B. & HUGHES, G.S. 1989. A manual of mathematical techniques for linefish assessment. *S. Afr. Nat. Scient. Prog. Rep.* 160: 1-83.

BUXTON, C.D. 1984. Feeding biology of the Roman *Chrysoblephus laticeps* (Pisces: Sparidae). *S. Afr. J. Mar. Sci.* 2: 33-42.

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

BUXTON, C.D. 1988. An unforgettable two days in the Tsitsikamma. *Ichthos* (Newsletter - J.L.B. Smith Institute of Ichthyology) 19: 12.

BUXTON, C.D. 1990. The reproductive biology of *Chrysoblephus laticeps* and *C. cristiceps* (Teleostei: Sparidae) *J. Zool., Lond.* 220: 497-511.

BUXTON, C.D. In press. Life-history changes in exploited reef fishes on the east coast of South Africa. (Submitted to *Env. Biol. Fish.*)

BUXTON, C.D. & CLARKE, J.R. 1986. Age, growth and feeding of the blue hottentot *Pachymetopon aeneum* (Pisces: Sparidae) with notes on reproductive biology. *S. Afr. J. Zool.* 21: 33-38.

BUXTON, C.D. & CLARKE, J.R. 1989. The growth of *Cymatoceps nasutus* (Teleostei: Sparidae). with comments on diet and reproduction. *S. Afr. J. mar. Sci.* 8: 57-65.

BUXTON, C.D. & CLARKE, J.R. 1991. The biology of the white musselcracker *Sparodon durbanensis* (Pisces: Sparidae) on the Eastern Cape coast, South Africa. *S. Afr. J. mar. Sci.* 10: 285-296.

BUXTON C.D. & CLARKE, J.R. 1992. The biology of the bronze bream, *Pachymetopon grande* (Teleostei: Sparidae) from the southeast Cape coast. *S. Afr. J. Zool.* (In press).

BUXTON, C.D. & GARRATT, P.A. 1990. Alternative reproductive styles in seabreams (Pisces: Sparidae). *Env. Biol. Fish.* 28: 113-124.

BUXTON, C.D. & SMALE, M.J. 1984. A preliminary investigation of the marine ichthyofauna in the Tsitsikamma Coastal National Park. Koedoe 27: 13-24.

BUXTON, C.D. & SMALE, M.J. 1989. Abundance and distribution patterns of three temperate marine reef fish (Teleostei: Sparidae) in exploited and unexploited areas off the southern Cape coast. J. App. Ecol. 26: 441-451.

CAMPANA, S.E. & NEILSON, J.D. 1985. Microstructure of fish otoliths. Can. J. Fish. Aquat. Sci. 42: 1014-1032.

CHOAT, J.H. & ROBERTSON, D.R. 1975. Protogynous hermaphroditism in fishes of the family Scaridae. In: Intersexuality in the Animal Kingdom. (ed.) Reinboth, R.R., Springer-verlag, Heidelberg. 263-283.

CHRISTENSEN, M.S. 1978. Trophic relationships in juveniles of three species of sparid fishes in the South African marine littoral. Fish. Bull. 76(2): 389-401.

CHRISTENSEN, M.S. & WINTERBOTTOM, R. 1981. A correction factor for, and its application to, visual censuses of littoral fish. S. Afr. J. Zool. 16: 73-79.

CHRISTENSEN, J.M. 1964. Burning of otoliths, a technique for age determination of soles and other fish. J. Cons. perm. int. Explor. Mer. 29:73-81.

CLARKE, J.R. 1988. Aspects of the biology of the musselcracker, Sparodon durbanensis, and the bronze bream Pachymetopon grande, (Pisces: Sparidae), with notes on the Eastern Cape recreational rock-angling and spear fisheries. Unpubl. M.Sc. thesis, Rhodes University.

CLARKE. J.R. & BUXTON, C.D. 1989. A survey of the recreational rock-angling fishery at Port Elizabeth, on the south-east coast of South Africa. S. Afr. J. mar. Sci. 8: 183-194.

COETZEE, P.S. 1983. Seasonal histological and macroscopic changes in the gonads of Cheimerius nufar (Ehrenberg, 1980) (Pisces: Sparidae). S. Afr. J. Zool. 18: 76-88.

COETZEE, P.S. 1986. Diet composition and breeding cycle of blacktail, Diplodus sargus capensis (Pisces: Sparidae), caught off St Croix Island, Algoa Bay, South Africa. S. Afr. J. Zool. 21: 237-243.

COETZEE, P.S. & BAIRD, D. 1981a. Catch composition and catch per unit effort of angler's catches off St Croix Island, Algoa Bay. S. Afr. J. Zool. 16: 137-143.

COETZEE, P.S. & BAIRD, D. 1981b. Age, growth and food of Cheimerius nufar (Ehrenberg, 1920) (Sparidae), collected off St. Croix Island, Algoa Bay. S. Afr. J. Zool. 16: 137-143.

COETZEE, P.S., BAIRD, D. & TREGONING, C. 1989. Catch statistics and trends in the shore angling fishery of the east coast, South Africa, for the period 1959-1982. S. Afr. J. mar. Sci. 8: 155-171.

COUSTEAU, J.Y. 1979. The Ocean World. World Publishers, New York. 446pp.

DAY, J.H. 1967. Polychaetes of Southern Africa Vol. 1 & 2. Trustees of the British Museum, London.

DAY, J.H. 1974. A guide to the marine life on South African shores. A.A. Balkema, Cape Town.

DE VLAMMING, V.L. 1972. Environmental control of teleost reproductive cycles: a brief review. J. Fish Biol. 4: 131-140.

DE VLAMMING, V.L. 1983. Oocyte development patterns and hormonal involvements among teleosts. In: Control Processes in Fish Physiology. (eds.) Rankin, J.C. Pitcher, T.J. & Duggan, R.T. Croom-Helm, London. 176-199.

EMLEN, S.T. & ORING, L.W. 1977. Ecology, sexual selection, and the evolution of mating systems. Science 197: 215-223.

FISCHER, E.A. & PETERSEN, C.W. 1987. The evolution of sexual patterns in the seabasses. BioScience 37: 482-489.

FRITZ, E.S. 1974. Total diet comparison in fishes by Spearman rank correlation coefficients. Copeia (1): 210-215.

GALLUCCI, V.F. & QUINN, T.J. 1979. Reparameterising, fitting and testing a simple linear growth model. Trans. Am. Fish. Soc. 108: 14-25.

GARRATT, P.A. 1985a. The offshore linefishery of Natal. I: Exploited population structures of the sparids Chrysoblephus puniceus and Cheimerius nufar. Investl. Rep. Oceanogr. Res. Inst., Durban 62: 18pp.

GARRATT, P.A. 1985b. The offshore linefishery of Natal. II: Reproductive biology of the sparids Chrysoblephus puniceus and Cheimerius nufar. Investl. Rep. Oceanogr. Res. Inst., Durban 63: 21pp.

GARRATT, P.A. 1991. Spawning behaviour of Cheimerius nufar in captivity. Env. Biol. Fish. 31: 345-353.

GANNON, J.E. 1976. The effects of differential digestion rates of zooplankton by alewife, Alosa pseudoharengus, on determinations of selective feeding. Trans. Am. Fish. Soc. 105:89-95.

GAULDIE, R.W. 1990. Phase differences between check ring locations in the orange roughy otolith (Hoplostethus atlanticus). Can. J. Fish. Aquat. Sci. 47: 760-765.

GHISELIN, M.T. 1969. The evolution of hermaphroditism among animals. Q. Rev. Biol. 44: 189-208.

GRIFFITHS, C.L. 1976. Guide to the benthic marine amphipods of southern Africa. Rustica press, Wynberg. 106 pp.

GROSS, M.R. 1985. Disruptive selection for alternative life histories in salmon. Nature 313: 47-48.

HANEKOM, N., HUTCHINGS, L., JOUBERT, P.A. VAN DER BYL, P.C.N. 1989. Sea temperature variations in the Tsitsikamma Coastal National Park, South Africa, with notes on the effect of cold conditions on some fish populations. S. Afr. J. mar. Sci. 8: 145-153.

HANEKOM, N. & COETZEE, P. In press. The benthic zonation on subtidal reefs within the Tsitsikamma National Park.

HAY, M.E. 1984. Patterns of fish and urchin grazing on Caribbean coral reefs: are previous results typical? Ecology 65: 446-454.

HECHT, T. & BAIRD, D. 1977. Contribution to the biology of the panga, Pterogymnus laniarius (Pisces: Sparidae): Age, growth and reproduction. Zool. Afr. 12: 363-372.

HECHT, T. & SMALE, M. 1986. Proceedings of a workshop on age determination and growth modelling of South African marine linefish. Investl. Rep. JLB Smith Inst. Ichthyology 21: 1-40.

HOAR, W.S. 1969. Reproduction. In: Fish Physiology. (eds.) Hoar, W.S. & Randall, D.J., Academic Press, New York. 1-72.

HOBSON, E.S. 1974. Feeding relationships of teleostean fishes on coral reefs in Kona, Hawaii. Fish. Bull. 72: 915-1032.

HOCKEY, P.A.R. & BUXTON, C.D. 1989. Conserving biotic diversity on southern Africa's coastline. In: Biotic diversity in southern Africa, concepts and conservation. (ed.). Huntley, B.J. pp. 298-309. Oxford University Press, Cape Town.

HUGHES, G. 1986. Examining methods of fitting age/length data to the von Bertalanffy growth curve with a view to applying a simplified version of the Beverton and Holt yield per recruit model. Unpubl. manuscript, Department of Applied Mathematics, University of Cape Town, South Africa. 70pp.

HUGHES, G.S. & PUNT, A.E. 1988. PC-YEILD user manual. Internal SANCOR line-fish Programme Document. 50pp.

HUGHES, R.N. 1980. Optimal foraging theory in the marine context. Oceanogr. Mar. Biol. Ann. Rev. 18: 423-481.

HULBERT, S.H. 1978. The measurement of niche overlap and some relatives. Ecology 59:67-77.

HULBERT, S.T. 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs 54: 187-211.

HUNTSMAN, G.R. 1979. Predation's role in structuring reef fish communities. Int. Symp. on Predator-Prey systems in fish communities and their role in fisheries management., Atlanta, Ga. 103-108.

HYNES, H.B.N. 1950. The food of fresh-water sticklebacks (Gasterosteus aculeatus and Pygosteus pungitius), with a review of methods used in studies of the food of fishes. J. Anim. Ecol. 19(1): 36-58.

HYSLOP, E.J. 1980. Stomach content analysis - a review of methods and their application. J. Fish. Biol. 17: 387-407.

IUCN 1980. The World Conservation Strategy. IUCN, Gland.

JOHANNES, R.E. 1978. Reproductive strategies of coastal marine fishes in the tropics. Env. Biol. Fish. 3: 65-84.

JOSEPH, E.B. 1973. Analysis of a nusery ground. In: Proceedings of a workshop on egg, larval and juvenile stages of fish in Atlantic coast estuaries. (ed.) Pacheco, A.C., pp. 118-121. Middle Atlantic Coastal Fisheries Centre Tech. Publ. No.1.

JOUBERT, C.S.W. 1981a. Aspects of the biolofy of five species of inshore reef fishes on the Natal Coast, South Africa. Invest. Rep. Oceanogr. Res. Inst. Durban 51: 1-16.

JOUBERT, C.S.W. 1981b. A survey of shore anglers catches at selected sites on the Natal Coast, South Africa. Invest. Rep. Oceanogr. Res. Inst. Durban 52: 1-13.

JOUBERT, C.S.W. & HANEKOM, P.B. 1980. A study of feeding in some inshore reef fish off the Natal coast, South Africa. S. Afr. J. Zool. 15: 262-274.

KADMON, G. YARON, Z. & GORDIN, H. 1985. Sequence of gonadal events and oestradiol levels in Sparus aurata(L.) under two photoperiod regimes. J. Fish Biol. 26: 609-620.

KIMMELL, J.J. 1985. A new species-time method for visual assessment of fishes and its comparison with established methods. Env. Biol. Fish. 12: 23-32.

KINGETT, P.D. & CHOAT, J.H. 1981. Analysis of density and distribution patterns in Chrysophrys auratus (Pisces: Sparidae) within a reef environment: an experimental approach. Mar. Ecol. Prog. Ser. 5: 283-290.

KREBS, C.J. 1985. Ecology. (3rd Ed.) Harper & Row, New York. 800pp.

LAGLER, K.F., BARDACH, J.E. & MILLER, R.R. 1962. Ichthyology. John Wiley & Sons, Inc. New York. 545pp.

LANG. J.B. 1992. The growth characteristics of sparid otoliths. Unpubl. MSc. thesis, Rhodes University.

LASIAK, T.A. 1983. Recruitment and growth patterns of juvenile marine teleosts caught at King's Beach, Algoa Bay. S. Afr. J. Zool. 18: 25-30.

LASIAK, T.H. 1986. Juveniles, food and the surf zone habitat: implications for teleost nusery areas. S. Afr. J. Zool. 21: 51-56.

LEUM, L.L. & CHOAT, J.H. 1980. Density and distribution patterns of the temperate marine fish Cheilodactylus spectabilis (Cheilodactylidae) in a reef environment. Mar. Biol. 57: 327-337.

LUCKS, D.K. 1970. Aspekte van die biologie van die witsteenbras (Lithognathus aureti Smith 1962) in die Sandwich hawe-Strandmeer. Unpubl. MSc. thesis, University of Stellenbosch.

MANOOCH, C.S. 1982. Ageing of reef fishes in the Southeast Fisheries Center. In: Proceedings of a workshop held October 7-10, 1980 at St. Thomas, Virgin Islands of the United States, (eds.) Huntsman, G.R., Nicholson, W.R. & Fox, W.W. Jr., NOAA Technical Memorandum NMFS-SEFC-80: 24-43.

MATSUYAMA, M., LARA, R.T., & MATSUURA, S. 1988. Juvenile bisexuality in the red sea bream, Pagrus major. Env. Biol. Fish. 21: 27-36.

McCLANAHAN, T.R. & SHAFIR, S.H. 1990. Causes and consequences of sea urchin abundance and diversity in Kenyan coral reef lagoons. Oecologia 83: 362-370.

MEHL, J.A.P. 1973. Ecology, osmoregulation and reproductive biology of the white steenbras, Lithognathus lithognathus (Teleostei: Sparidae). Zool. Afr. 8: 157-230.

MICALE, V., PERDICHIZZI, F. & SANTANGELO, G. 1987. The gonadal cycle of captive white bream, Diplodus sargus (L.). J. Fish Biol. 31: 435-440.

MOREAU, J. 1987. Mathematical and biological expression of growth in fishes: Recent trends and further developments. In: Age and growth of fish, (eds.) Summerfelt, R.C. & Hall, G.E., Iowa State Univ., Iowa. 81-113.

NEPGEN, C.S.DE.V. 1977. Biology of the hottentot *Pachymetopon blochii* (Val.) and the silverfish *Argyrozona argyrozona* (Val.) along the Cape southwest coast. *Investl. Rep. Div. Sea Fish. S. Afr.* 105: 1-35.

PANNELLA, G. 1974. Otolith growth patterns: an aid in age determination in temperate tropical fishes. In: The Ageing of Fishes. (ed.) Bagenal, T.B., Unwin Brothers, London. 28-39.

PAULY, D. 1979. Gill size and temperature as governing factors in fish growth: a genralization of von Bertalanffy's growth formula. *Ber. Inst. Meereskd. Christian-Albrechts Univ. Kiel* 63: 156pp.

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

PIANKA, E.R. 1974. Evolutionary Ecology. Harper & Row, New York. 356pp.

PITCHER, T.J. 1986. The behaviour of teleost fishes. Croom Helm Ltd., London. 553pp.

POLLOCK, B.R. 1985. The reproductive cycle of the yellowfin bream, *Acanthopagrus australis* (Gunther), with particular reference to protandrous sex inversion. *J. Fish. Biol.* 26: 301-311.

PULFRICH, A. & GRIFFITHS, C.L. 1988. Growth, sexual maturity and reproduction in the hottentot *Pachymetopon blochii* (Val.) *S. Afr. J. mar. Sci.* 7: 25-36.

RADAKOV, D.V. 1973. Schooling in the ecology of fish. J. Wiley & Sons, Ltd. Chichester. 173pp.

RAUCK, G. 1976. A technique of sawing thin slices out of otoliths. *Ber. Dt. wiss. Kommn. Meeresforsch.* 24: 339-341.

RAY, G.C. 1984. Conservation of marine habitats and their biota. *S. Afr. Nat. Sci. Prog. Rep.* 92: 109-134.

REINBOTH, R. 1970. Intersexuality in fishes. *Mem. Soc. Endocr.* 18: 515-543.

REINBOTH, R. 1988. Physiological problems of teleost ambisexuality. *Env. Biol. Fish.* 22: 249-259.

RICKER, W.E. 1975. Growth in length and in weight. In: Computation and interpretation of biological statistics of fish populations. *Bull. Fish. Res. Bd. Can.* 191: 203-233.

ROBERTS, C.M. & POULININ, N.V.C. 1991. Are marine reserves effective in management of reef fisheries? *Rev. Fish. Biol. & Fish.* 1: 65-91.

ROBINSON, G.A. 1989. Marine Reserves. In: Oceans of Life off Southern Africa. (eds.) Payne, A.I.L. & Crawford, R.J.M., Vlaeberg Publishers, South Africa. 339-346.

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

SALE, P.F. 1974. Mechanics of co-existence in a guild of territorial fishes at Heron Island. Proc. 2nd Internat. Symp. Coral Reefs 1: 193-206.

SALM, R.V. & CLARKE, J.R. 1984. Marine and coastal protected areas: a guide for planners and managers. IUCN, Gland, 302pp.

SANDERSON, S.L. & SOLONSKY, A.C. 1986. Comparison of a rapid visual and a strip transect technique for censusing reef fish assemblages. Bull. Mar. Sci. 39: 119-129.

SCHOEMAN, F. & SCHOEMAN, S. 1990. Strike! Strike Publications and Promotions, Somerset West. 616pp.

SCHOENER, T.W. 1974. Resource partitioning in ecological communities. Science 185: 27-38.

SCHOENER, T.W. 1983. The controversy over interspecific competition. American Scientist 70: 586-595.

SCHUMANN, E.H., PERRINS, L.A. & HUNTER, I.T. 1982. Upwelling along the South Coast of the Cape Province, South Africa. S. Afr. J. Sci. 78: 238-242.

SHANNON, L.V. 1989. The physical environment. In: Oceans of Life off Southern Africa. (eds.) Payne, A.I.L. & Crawford, R.J.M., Vlaeberg Publishers, South Africa. 12-27.

SHAPIRO, D.Y. 1987. Differentiation and evolution of sex change in fishes. BioScience 37: 490-497.

SHAPIRO, D.Y. 1989. Sex change as an alternative life-history style. In: Alternative life-history styles of animals. (ed.) Bruton, M.N., Kluwer Academic Publ., Dordrecht. 177-195.

SIMKISS, K. 1974. Calcium metabolism of fish in relation to ageing. In: Ageing of Fish. (ed.) Bagenal, T.B., Unwin Brothers, London. 1-12.

SMALE, M.J. 1986. The feeding habits of six pelagic and predatory teleosts in eastern Cape coastal waters (South Africa). J. Zool., Lond. 1: 357-409.

SMALE, M.J. 1988. Distribution and reproduction of the reef fish Petrus rupestris (Pisces: Sparidae) off the coast of South Africa. S. Afr. J. Zool. 23: 272-287.

SMALE, M.J. & BUXTON, C.D. 1985. Aspects of the recreational ski-boat fishery off the Eastern Cape, South Africa. *S. Afr. J. mar. Sci.* 3: 131-144.

SMALE, M.J. & BUXTON, C.D. 1989. The subtidal gully fish community of the Eastern Cape and the role of this habitat as a nursery area. *S. Afr. J. Zool.* 24(1): 58-67.

SMALE, M.J. & PUNT, A.E. 1990. Age and growth of the red steenbras *Petrus rupestris* (Pisces: Sparidae) on the southeast coast of South Africa. *S. Afr. J. mar. Sci.* 10: 131-139.

SMITH, E.P. 1985. Statistical comparison of weighted overlap measures. *Trans. Am. Fish. Soc.* 114:250-257.

SMITH, M.M. & HEEMSTRA, P.C. 1986. Smiths' Sea Fishes. Macmillan, South Africa. 1047 pp.

TESCH, F.W. 1968. Age and growth. In: Fish Production in Fresh Waters. (ed.) Ricker, W.E., IBP Handbook No. 3: 93-123.

THRESHER, R.E. 1984. Reproduction in reef fishes. T.F.H. Publ., U.S.A. 343-399.

THRESHER, R.E. & GUNN, J.S. 1986. Comparative analysis of visual census techniques for highly mobile, reef associated piscivores (Carangidae). *Env. Biol. Fish.* 17: 93-116.

TOEREIN, D.K. 1976. Geologie van die Tsitsikammakusstrook. *Koedoe* 19: 31-41.

VAN DER ELST, R.P. 1976. Game fish of the east coast of southern Africa: 1. The biology of the elf *Pomatomus saltatrix*. (Linneaus). in the coastal waters of Natal. *Invest. Rep. Oceanogr. Res. Inst., Durban* 44: 1-59.

VAN DER ELST, R.P. 1981. A guide to the common sea fishes of southern Africa. C. Struik, Cape Town. 367 pp.

VAN DER ELST, R.P. 1985. An appraisal of the new fishing laws. *Ski-Scene* S. Afr. 9: 26-32.

VAN DER ELST, R.P. 1986. Seehengel se toekoms onseker. *Trim en Sport* 10:7.

VAN DER ELST, R.P. 1989. Marine recretional angling in South Africa. In: Oceans of Life off Southern Africa. (eds.) Payne, A.I.L. & Crawford, R.J.M., Vlaeberg Publishers, South Africa. 164-176.

VAN DER ELST, R.P. 1990. Marine recreational fishing: Resource usage, management and research. *S. Afr. Nat. Scient. Prog. Rep.*: 167.

VAN DER ELST, R.P. & BULLEN, E. 1991. Editorial. Tagging News, Oceanogr. Res. Inst., Durban , 7: 5.

VAN DER ELST, R.P. & ADKIN, F. 1991. Marine linefish: Priority species and research objectives in Southern Africa. Oceanogr. Res. Inst., Durban, Special Pub. 1:1-131.

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

WALLACE, J.H. & VAN DER ELST, R.P. 1983. Marine linefish programme priority list. SANCOR, CSIR, Pretoria 70: 103pp.

WARNER, R.R. 1978. The evolution of hermaphroditism and unisexuality in aquatic and terrestrial vertebrates. In: Contrasts in Behaviour. (eds.) Reese, E.S. & Lighter, J., Wiley & Sons. 77-101.

WARNER, R.R. 1984. Mating behaviour and hermaphroditism in coral reef fishes. Am. Scientist 72: 128-136.

WARNER, R.R. 1988a. Sex change and the size-advantage model. TREE 3: 133-136.

WARNER, R.R. 1988b. Sex change in fishes: hypotheses, evidence, and objections. Env. Biol. Fish. 22: 81-90.

WASSEF, E.A. 1985. Comparative biological studies of four Diplodus species (Pisces: Sparidae). Cybium 9: 203-215.

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

WEATHERLY, A.H. & GILL, H.S. 1987. The biology of fish growth. Academic Press, New York. 443pp.

WHIBLEY, I. & GARRATT, P.A. 1989. The South African Fisherman. Struik Timmins, Cape Town. 220pp.

WHITFIELD, A.K. 1985. The role of zooplankton in the feeding ecology of fish fry from southern African estuaries. S. Afr. J. Zool. 20: 166-171.

WILD, A. & FOREMAN, T.J. 1980. The relationship between otolith increments and time for yellowfin and skipjack tuna marked with tetracycline. Inter. Am. Tropical Tuna Comm. Bull. 17: 509-541.

WINTER, P.E.D. 1979. Studies on the distribution, seasonal abundance and diversity of the Swartkops estuary ichthyofauna. Unpubl. M.Sc. thesis, University of Port Elizabeth.

YAMAMOTO, K. 1956. Studies on the formation of fish eggs. I. Annual cycle in the development of ovarian eggs in the Flounder, Liopsetta obscura. J. Fac. Sci. Hokkaido Univ. Ser. VI. 12: 362-373.

YEUNG, W.S.B. & CHAN, S.T.H. 1987. The gonadal anatomy and sexual pattern of the protandrous sex-reversing fish, *Rhabdosargus sarba* (Teleostei: Sparidae). *J. Zool., Lond.* 212: 521-532.