LIFE HISTORY CHANGES OF TWO REEF FISH SPECIES IN EXPLOITED AND UNEXPLOITED MARINE ENVIRONMENTS IN SOUTH AFRICA.

Submitted in Fulfilment of the Requirements
for the Degree of
DOCTOR OF PHILOSOPHY
of
Rhodes University

by
COLIN DAVID BUXTON
October 1987

TABLE OF CONTENTS

<u>Chrysoblephus</u> <u>cristiceps</u>

3.6 - Reproduction

3.6.1 - Protogynous Hermaphroditism

Results

3.6.2 - The Reproductive Cycle

Results

3.6.3 - The Reproductive Cycle of Exploited Populations

CHAPTER 4. EXPLOITATION AND CONSERVATION

4.2 - Yield per Recruit Estimation

4.3 - Conservation

ACKNOWLEDGEMENTS

This study was funded jointly by the South African Committee for Oceanographic Research and the Cape Department of Nature Conservation. It was made possible through the co-operation of the National Parks Board who supported the study in the Tsitsikamma Coastal National Park.

I would like to thank my supervisors Professors Tom Hecht and Mike Bruton for their help and encouragement throughout the study. Many others in the Department of Ichthyology and Fisheries Science and the J.L.B Smith Institute helped during the study, to all I am grateful. In particular, I would like to thank Dr. Tony Ribbink for stimulating discussions, Andy Scholtz for assistance with the yield per recruit analysis and Rob Stobbs for the otolith photography.

I would also like to thank the staff of the Port Elizabeth Museum for their support during the study; Dr. John Wallace for initiating the Deep Reef Programme; Dr. Malcolm Smale for all of his assistance throughout the study, both on land and underwater, and for collecting most of the material from East London; Dr. Bill Branch for stimulating discussion; Winston Mahola for assistance in the laboratory and last but not least Merle du Plessis, my laboratory assistant, for typing, drawing proofreading, scribing, reference management and the many other tasks she performed so efficiently.

A very special word of thanks must go to John Clarke, my colleague in the Deep Reef Programme, for his enthusiasm and support in all aspects of field and laboratory work. John provided a much needed attentive ear during the formulation of the ideas presented here and critically proofread much of the thesis.

I am grateful to Denis Bouwer and his staff at the Tsitsikamma Coastal National Park for their help and assistance during my field trips to the Park. John Allen, Peet Joubert and Sarel Yssel gave freely of their time to assist with diving and field work. In particular, I would like to thank John and his wife Jean for their warm hospitality on these occasions.

The study would not have been possible without the support of the ski-boat angling fraternity between Mossel Bay and East London. It is difficult to single out any of the fishermen but to Trevor Moldenhauer, Ricky Cooper, Stan McCarthy, Johnny Engelbrecht, Ginkle Venter, Bobby Bush, Geoff Clarke and Mike Burger a special word of thanks for always going out of their way to help. I would also like to thank Walter Whittal for allowing me to examine fish at Walmer Fisheries.

Many people assisted with prey identification, Dr. Naomi Millard with

hydroids, Dr. Brian Kensley with crustacea, Professor John Day with polychaetes, Phil Coetzee with polychaetes and hydroids and Billy Liltved with molluscs. To all I am grateful.

I thank Dr. Doug Butterworth and Andre Punt for providing computer assistance and statistical advice with the age analysis.

Finally, I would like to thank my wife Lynne and daughter Samantha-Anne for coping throughout, especially during the writeup. For Lynne's patience, encouragement and assistance with typing and proof-reading I am greatly indebted. I dedicate this thesis to them.

ABSTRACT

A detailed investigation into the life histories of Chrysoblephus laticeps and C. cristiceps in exploited and unexploited marine environments on the south-east coast of southern Africa is presented. The study provided information necessary for the evaluation of marine reserves as a management option for these and similar reef species.

Visual underwater assessments showed a clear spatial separation between adults and juveniles of both species, suggesting a recruitment of juveniles into shallow water followed by a gradual outward migration into deeper water with age. Density estimates of C. laticeps in the Noordhoek (0.0064 fish/m^2) and Tsitsikamma (0.0254 fish/m^2) areas were significantly different and were attributed to exploitation. Within area differences in density were also significantly correlated with temperature, depth and substratum relief. Similar comparisons for C. cristiceps were not possible because these fish shied away from divers.

Habitat preferences were mirrored in the diets of both species which fed on a wide variety of reef associated benthic animals. Size of prey appeared to be gape limited, only larger fish being able to manipulate prey. Quantitative differences between the diets of fish sampled in different areas were a reflection of differences in available prey and not related to the relative density of predators. The dietary characteristics recorded in these fish were typical of search hunters.

An age and growth study based on the examination of sectioned otoliths showed that both species were slow growing and long lived. Maximum recorded ages were 18 and 22 years for C. laticeps and C. cristiceps respectively. Growth rates in exploited and unexploited areas were not significantly different although there was an indication that growth was slower in the exploited areas for C. cristiceps.

Several inconsistencies in otolith interpretation and terminology were evaluated. Contrary to other South African studies the results suggested that somatic growth was fastest just after spawning. This coincided with the winter months and was reflected by the deposition of a hyaline zone in the otolith.

Two independent estimates, the Pauli derivation and visually assessed length frequency analysis, produced the same value for total mortality of C. laticeps in the Tsitsikamma area (0.2). This result, together with a significant difference in the rate of fishing mortality at different areas along the coast suggested that the populations sampled were discrete and supported the postulate that both species were sedentary. Further support was obtained from a mark-recapture study. Although sample numbers were low the results showed no evidence of large scale migratory patterns in these fish.

An investigation of the reproductive biology of both fish showed that they were protogynous hermaphrodites, all males being derived from females with no evidence for polyandry. Males were shown to be capable of mating with a number of females and this, together with monandry, monochromatism and a small testis size, suggested a polygynous mating system in both species. Observations of the courtship behaviour in captive C. laticeps also supported polygyny.

A significant difference in the mean size at sex reversal between unexploited and exploited populations supported the postulate that sex reversal was independent of the size or age of the animal. The size at which sex reversal occurred appeared to be dependent on sex ratio.

A detailed yield per recruit analysis of the response of the population to different levels of fishing mortality and size at recruitment (t_R), showed that sex reversing species were particularly vulnerable to overfishing. This was due to a dramatic decline in the number of surviving individuals past t_R which resulted in a skewing of the sex ratio towards females. Evidence is presented to show that current legislation is inadequately protecting the spawner stock of both species.

In conclusion it is shown that longevity, sex reversal, restricted movements and the occupation of a demersal habitat make these species particularly vulnerable to overexploitation in a size-selective fishery. The sustained yield in the linefishery is suggested to be a result of distant recruitment from relatively unexploited populations rather than the adequacy of current conservation measures. The need to protect the spawner stock is emphasised and the use of marine reserves as an additional protection for sedentary reef-dwelling species is therefore advocated.

CHAPTER 1 - INTRODUCTION

> Conservation's concern for maintenance and sustainability is a rational response to the nature of living resources......and also an ethical imperative, expressed in the belief that we have not inherited the earth from our parents, we have borrowed it from our children (IUCN 1980).

Proclamation of reserves in the marine environment has lagged behind that of terrestrial systems (Davis 1981). Bjorklund (1974) listed a little over 180 marine reserves worldwide under national jurisdiction, many of which have been poorly enforced (Randall 1982). Yet between 50 and 70 percent of the world's population live in the coastal zone, arguably making it simultaneously the most populated, productive, polluted and perturbed biome on earth (Ray 1984). Ehlrich (1974), reviewing human population growth and the problems it posed for the environment, noted that the time for research as a major approach to the world's problems was long past. Reviewing the critical status of habitat destruction in general, Frankel & Soule (1981) stated "Conservationists cannot afford the luxury of methodological elegance.....it is our tenet that crude initiatives based on rough guidelines are better than the paralysis of procrastination induced in some scientists by the fear of inadequate data". This sort of concern has led to an explosive increase in coastal conservation and in the ten years following Bjorklund's report the number of coastal reserves and parks rose to an estimated 1200 (Salm & Clarke 1984). An ever increasing literature is now available that sets out the requirements and planning of coastal resource management (e.g. Siegfried & Davies 1982; Ray 1984; Sorensen, McCreary & Hershman 1984; Salm & Clarke 1984; Snedaker & Getter 1985; Clarke 1985).

One of the stated objectives of the World Conservation Strategy is sustainable utilisation of species and ecosystems (IUCN 1980). As well as maintaining essential ecological processes and preserving genetic diversity, marine reserves are considered an integral part of the management strategy for marine fisheries. Scientific evaluation of this objective has however, not kept pace with the proclamation of marine reserves and the technology for exploitation has developed faster than the understanding of the requirements for the rational use and sustained yield of the sea's resources (Ray 1968).

The central hypothesis of this study was therefore to evaluate whether reserves were a viable option for the conservation and management of exploited marine reef fishes, by comparing fish populations in exploited and unexploited environments. Of particular interest were the reef fishes exploited by commercial and recreational linefishermen.

South Africa has a marine coastline of approximately 3000km encompassing a diversity of ecosystems ranging from the sub-tropical in Natal to cold temperate in the Western Cape. Excluding lagoons and the island groups proclaimed for the protection of seabirds and seals, there are 28 mainland reserves or sanctuaries which either include intertidal areas or extend into the sea. Of these, 19 probably hold little benefit for linefish species either because fishing is allowed throughout the sanctuary or because only narrow intertidal areas are protected. The remaining reserves which are likely to be of direct benefit to linefishes include Castle Rocks, Betty's Bay, Sardinia Bay, three areas near East London, De Hoop, Tsitsikamma and the St. Lucia/Maputoland reserves (Fig. 1). Although these areas cover only 11 percent of the coastline considerable advances have been made beyond the realisation that it is necessary to protect more of the coastline. Recently the Council for the Environment set out proposals for an extensive system of marine conservation areas that encompass the needs of both conservation and recreation in the coastal zone (Robinson, Siegfried & Visser 1985).

In South Africa the exploitation of reef fishes forms part of a multi-user, multi-species linefishery which is poorly understood. Studies on its dynamics are few and in the Eastern Cape include an analysis of commercial redfish catches (Crawford & Crous 1982), a study of recreational shore angling in Algoa Bay (Coetzee & Baird 1981a) and an investigation of aspects of the recreational ski-boat fishery including catch, effort and economics (Smale & Buxton 1985). Smale & Buxton (1985) show that fishes of the family Sparidae dominate reef fish catches, but despite these studies very little is known about the contribution of individual species to the overall linefish catch. Assessing the effects of exploitation and evaluating conservation options without this knowledge is therefore difficult.

Prior to the initiation of this study very little had been published on the biology of South African linefish species and only six of the 79 species recorded in the Eastern Cape recreational fishery had been studied. These included Argyrosomus hololepidotus, Pomadasys commersonni (Wallace & Schleyer 1979), Argyrozona argyrozona (Nepgen 1977), Cheimerius nufar (Coetzee 1983), Polysteganus undulosus (Ahrens 1964) and Pterogymnus laniarius (Hecht & Baird 1977). With the exception of C. nufar and P. laniarius these studies were not in the Eastern Cape.

A review of the literature showed that much of the published research on marine reserves or parks deals with the needs, requirements and planning of these areas (see reviews listed above). Although not entirely restricted to marine reserves a lot of the published research has examined community structure. Coral reefs have been well studied (for reviews see Sale 1980; Thresher 1983; Bohnsack 1983; Alevizon, Richardson, Pitts & Serviss 1985; Walsh 1985), although temperate reefs have also received some attention (Leum & Choat 1980; Gillian 1980; Kingett & Choat 1981). Much of the legislation prohibiting activities in marine reserves has been designed to allow fish populations to recover or remain at natural levels. Despite this there have been few attempts to evaluate the effects of these restrictions on fish community structure (Bell 1983). Bell suggested that the lack of comparative studies probably reflected a difficulty in quantifying the composition and size structure of reef fish assemblages without adversely affecting the fauna. This underlines the importance of this study as a contribution to the understanding of the effects of marine reserves.

The Tsitsikamma Coastal National Park, a large marine reserve situated on the southern Cape coast of South Africa, provided a unique opportunity to evaluate the usefulness of marine reserves as a management option for certain species of reef fish. Fishing within this area has been prohibited since 1965 and because of its size and relative inaccessability the populations of reef species resident in the Park are thought to have attained natural levels. An understanding of the biology of these populations therefore provides a baseline from which to compare exploited populations.

Two species, the Roman Chrysoblephus laticeps and dageraad Chysoblephus cristiceps, were selected for study. These fish were important components of both commercial and recreational catches (Crawford & Crous 1982; Smale & Buxton 1985), but little was known of their biology. Apart from taxonomic studies, published information included distributional records (Smith 1965), accounts of protogynous hermaphroditism in both C. laticeps (Penrith 1972a) and C. cristiceps (Robinson 1976), notes on behaviour of these and other related sparids (Penrith 1972b) and popular accounts by Biden (1930) and van der Elst (1981) on angling in South Africa that included notes on the biology of both species.

To properly evaluate the above hypothesis a thorough understanding of the life histories of the two study species was necessary, and a detailed investigation of their biology is presented in Chapter 3. The first section deals with habitat preferences and the species associations found in inshore waters down to approximately 30m. From the outset it must be pointed out that the depth of the study was limited by safe diving depth (50m) although this does not represent the depth limitation for either species. This was followed by a detailed examination of relative abundance determined by visual assessment and a comparison of density in representative exploited and unexploited areas. A preliminary evaluation of the degree of residency of the fish was determined by tagging in the Park. Finally the population structure of fish caught by linefishermen is compared to that obtained in the Park.

Subsequent sections deal with the basic biology of the fish including age and growth, mortality, feeding and reproduction. In each case a full description is followed by a comparison of exploited and unexploited populations.

In Chapter 4 the importance of these species to the linefishery is evaluated, and yield models (Beverton & Holt 1957) are derived using growth and mortality parameters obtained in this study. The differential effects of exploitation on protogynous and gonochoristic species are also modelled. Conservation options for these and other reef species are then considered and in the general discussion conservation options are evaluated. Special consideration is given to important life-history characteristics of these fish and the applicability of island biogeographic theory to marine reserves is also discussed.

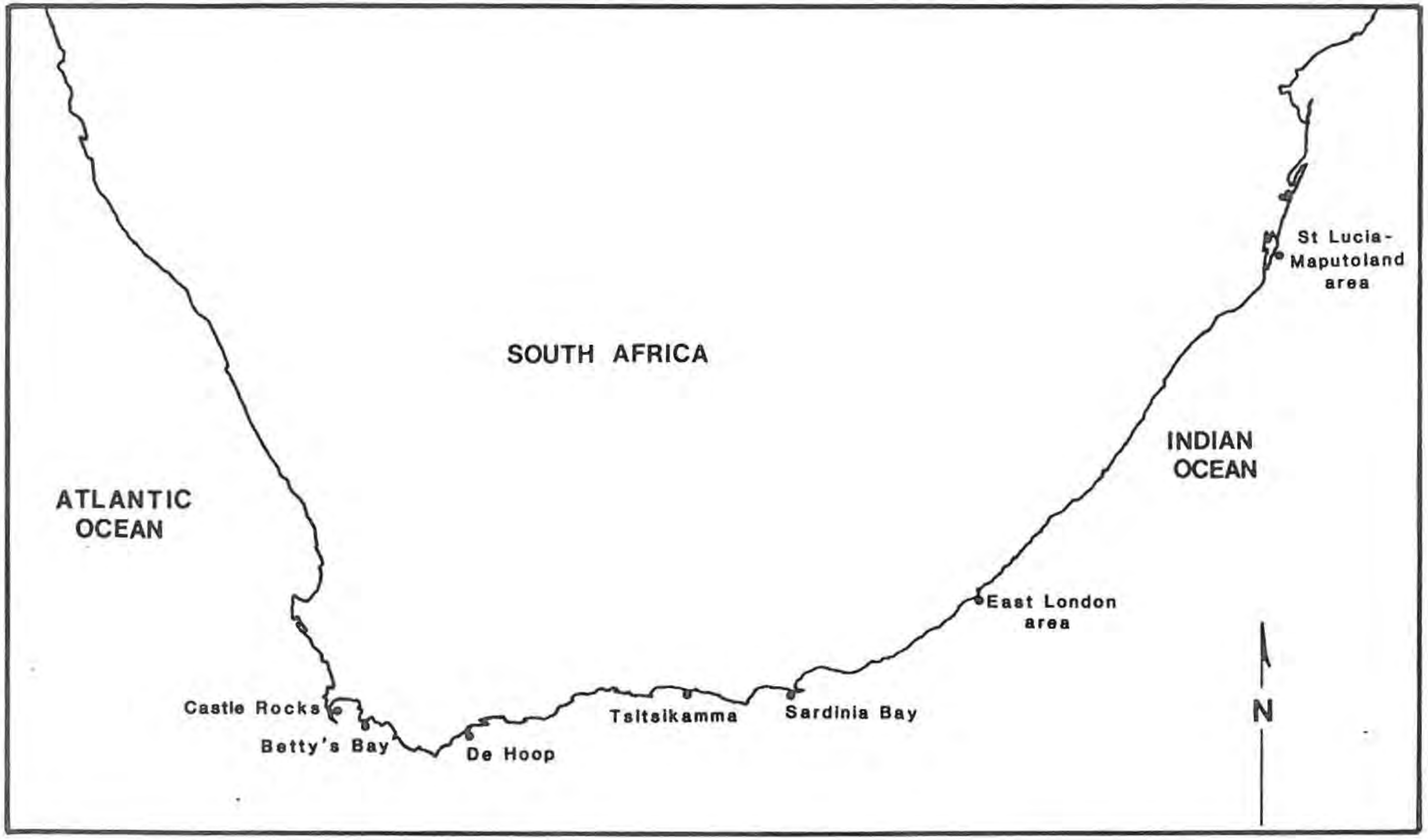


Figure 1. Map of South Africa showing existing marine reserves affording protection to linefish species.

CHAPTER 2 - STUDY AREAS

Recreational ski-boat catches were sampled at eleven launching sites between Mossel Bay (34°10'S,22°08'E) and Kei River Mouth (32°41'S,28°23'E) along the south-east coast of South Africa (Fig. 2). Throughout the study, unless stated, samples from these areas were lumped as follows (sample frequency is given in parenthesis):

1. Mossel Bay - Buffalo Bay - Knysna (every two months)
2. Cape St. Francis - Jeffreys Bay (monthly)
3. Sardinia Bay - Noordhoek (weekly)
4. Algoa Bay (weekly)
5. East London - Gonubie - Kei River Mouth (every two months)

In addition samples were obtained from research fishing in the Tsitsikamma Coastal National Park on a monthly basis. Sampling periods are given in the appropriate sections of the text.

Two core sites were intensively studied, the Tsitsikamma Coastal National Park and the Port Elizabeth environs from Sardinia Bay to Woody Cape. The extent of hard substrata in these two areas was mapped using side-scan sonar with a 50kH towfish. In the Tsitsikamma area this work was completed in two stages, an offshore survey between 800m and 5km from the coast (Flemming , Eagle, Fricke, Hunter, Martin, Schumann, Swart & Zoutendyk 1983), and an inshore survey from 800m to the intertidal. The two surveys were done from the R.V. <u>Meiring Naude</u> and the Port Elizabeth Museum ski-boat <u>Delphinus</u> respectively. All of the area surveyed off Port Elizabeth was done using <u>Delphinus</u>. The method used was to tow the sonar fish along surveyed lines such that they provided 100% overlap when operating on a 200m sonar range (Flemming <u>et al</u>.) 1983. All of the surveying was completed with the assistance of the National Research Institute of Oceanology.

The Tsitsikamma Coastal National Park situated on the southern Cape coast between Nature's Valley and Oubosstrand, covers approximately 60km of coastline. The marine sanctuary extends 5.6km offshore except for a short section on the western boundary which extends 0.8km offshore. The geology of the area is characterised by a large sandstone syncline with an east-west axis. Steeply dipping beds in the southern limb of this fold have produced the cliffs characteristic of the shoreline (Toerien 1976) while subtidally they provide a series of reefs separated by sand-filled valleys. A detailed side-scan sonar survey of the park showed that most of the reefs were of sandstone origin with the exception of a series of reefs on the eastern border. These may be aeolianite deposits similar to the paleo-dunes found in the Wilderness area further west along the coast (Flemming <u>et al</u>. 1983; B.W. Flemming, National

Research Institute of Oceanology, pers. comm.) (Fig. 3).

Biological information was collected from four areas in close proximity to the Storms River Mouth (Fig. 4). The faunal characteristics of these reefs are summarised in Chapter 3.1.

Ski-boat sampling stations in the Port Elizabeth area are illustrated in Figure 5 and a side-scan survey of the substrata around Cape Recife (34°02'S,25°42'E) is shown in Figure 6. The reefs in this area were very similar to those encountered in the Tsitsikamma area i.e. sandstones of the Table Mountain series with an east-west strike. The faunal characteristics of these reefs are also described in Chapter 3.1.

Circulation patterns on the southeast coast of Southern Africa are dominated by the southward flowing Agulhas current which roughly follows the margin of the continental shelf (Fig. 2). Harris (1978) notes that where the continental shelf is narrow the coastal waters move in sympathy with the current and where the coastline and current paths diverge eddies are induced. Cyclonic vortices, induced by a shear zone between the current and the coast, also lead to counter currents near the coast. Both of these effects appear to be intermittent and depend on meanders in the current as well as the influence of weather patterns, particularly pressure and wind, on the sea surface. The Agulhas current separates from the coast at Cape Morgan and west of this the frequency of eastward counter currents increase. In the area between the Great Fish Point and Cape St Francis the frequency of east-flowing currents is higher than the west-flowing currents.

Both of the core areas studied may be considered high energy environments and are subjected to considerable wave action. During the winter months when the entire coast is subjected to storms with a 5-8 day cycle, anti-cyclonic cells of low pressure move along the coast in an easterly direction producing rainy conditions with strong westerly winds. During these storms swells are normally greater than 1-2m, the water is turbulent and visibility is very low (<2m) due to suspended sediments. In summer the wind direction is predominantly easterly and wave height is much less.

Specific references to other aspects of the physical environment including sea temperatures and photoperiod, wind direction and wind induced cold upwelling are made where appropriate in the text.

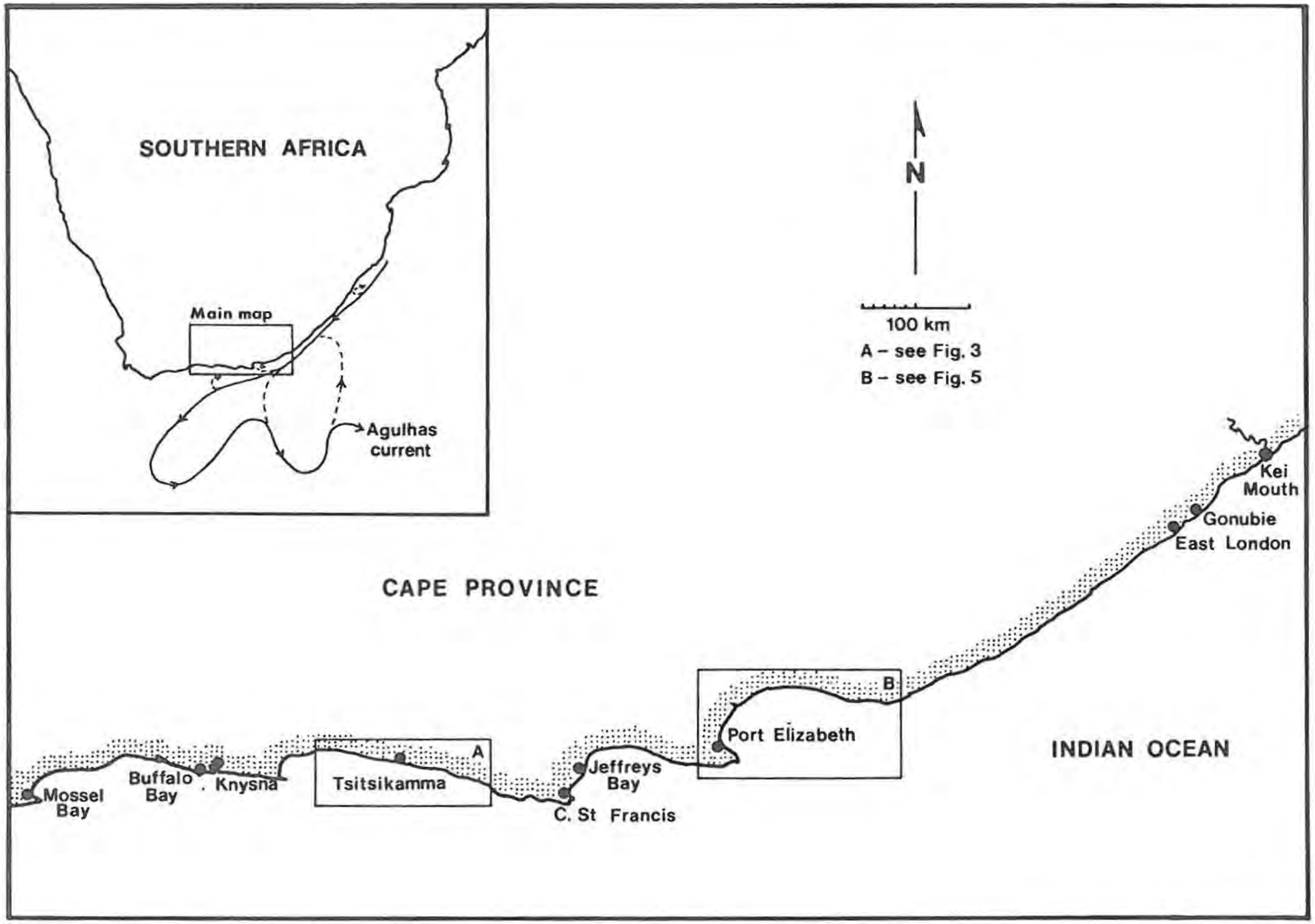


Figure 2. Map of the overall study area in southern Africa showing the sampling sites. Inset: Map of southern Africa showing the position of the Agulhas current (Harris 1977).

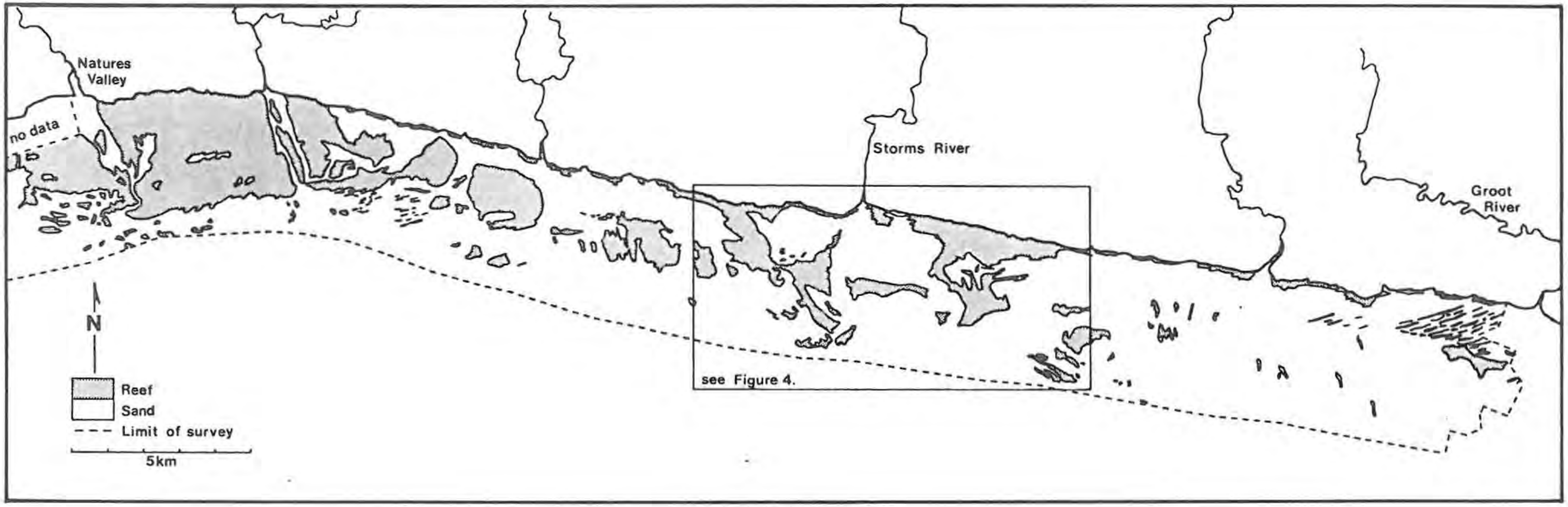


Figure 3. Extent of reef and sand substrata in the Tsitsikamma Coastal National Park obtained using side-scan sonar. The limit of the survey is also the approximate seaward boundary of the park, which extends from Natures Valley to the Groot river.

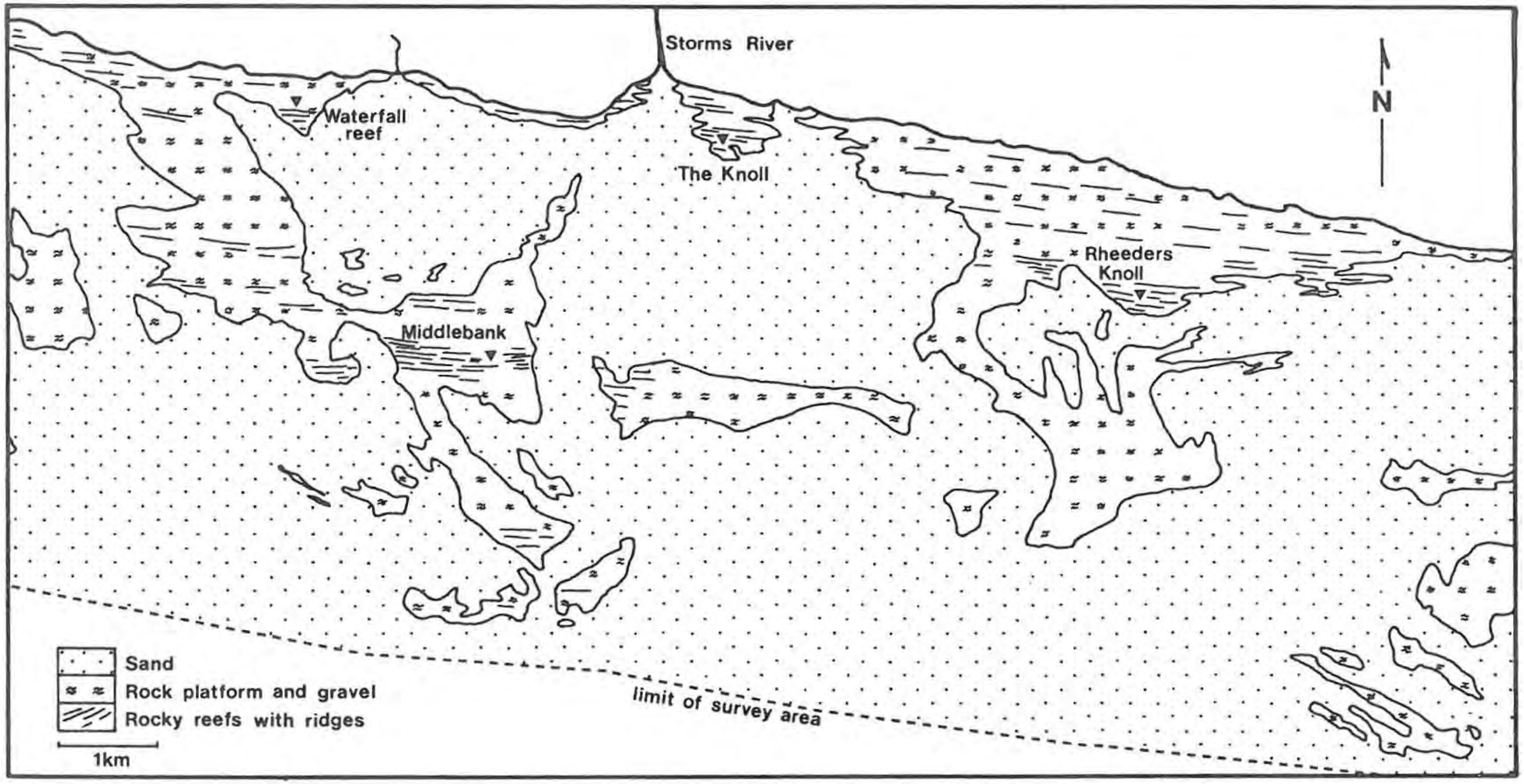


Figure 4. Side-scan sonar survey of the main sampling area in the Tsitsikamma Coastal National Park, showing the substratum characteristics and the areas sampled (▼).

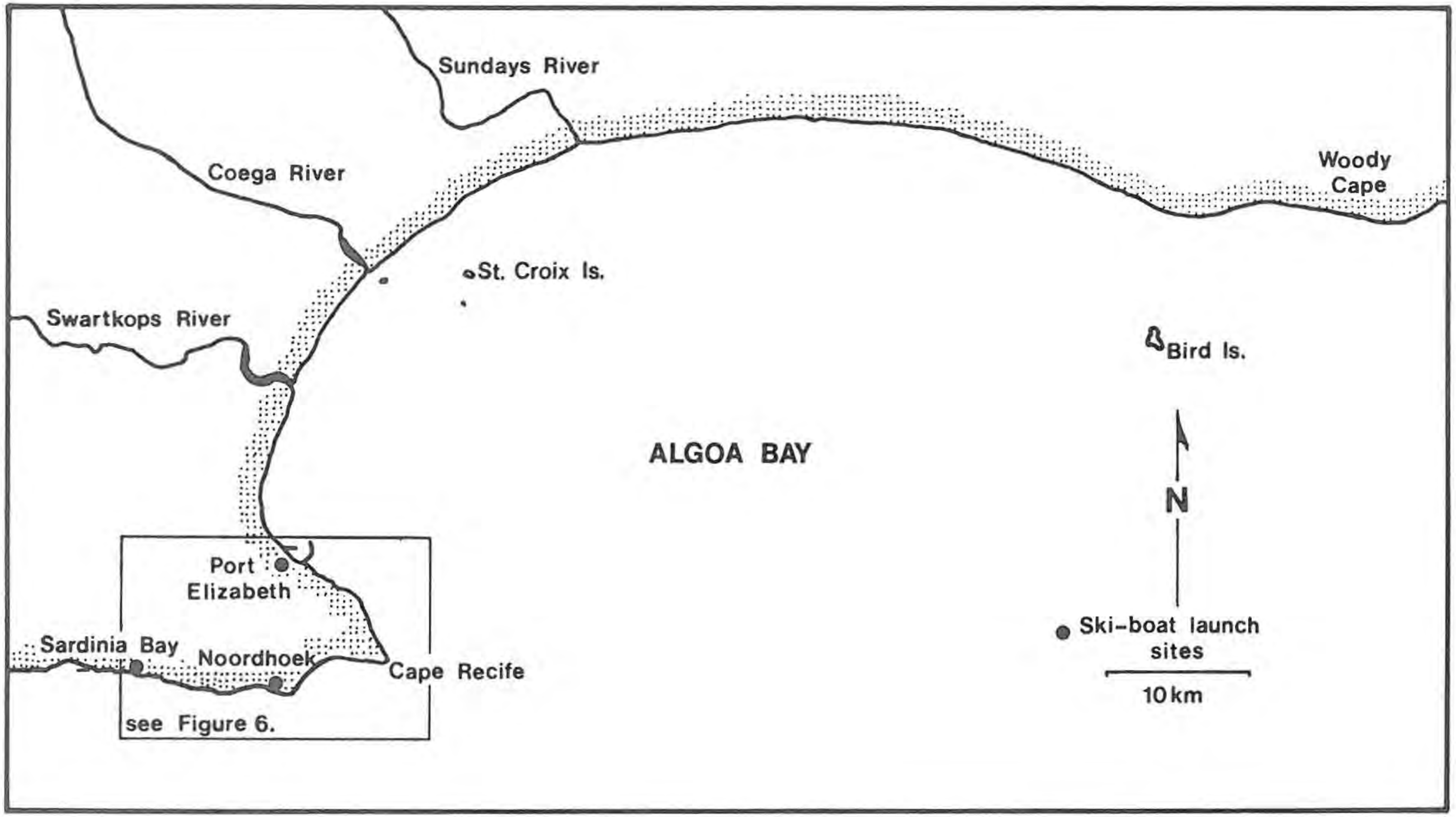


Figure 5. Map of Algoa Bay environs showing ski-boat launch sites and fishing areas referred to in the text.

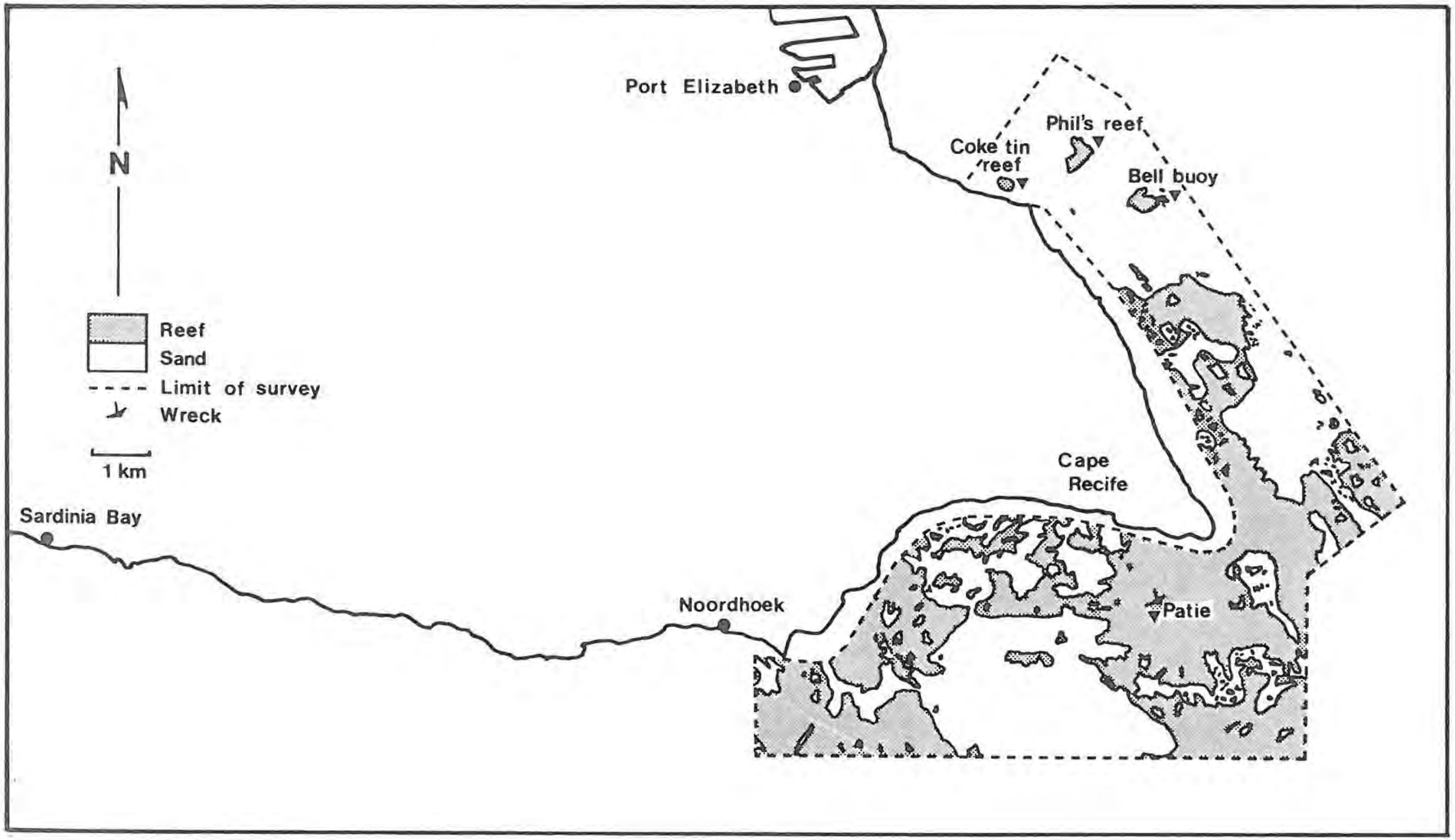


Figure 6. Side-scan sonar survey of reef and sand substrata in the Port Elizabeth area. The main dive areas are marked (▼).

CHAPTER 3 - DEMOGRAPHY AND GENERAL BIOLOGY

3.1 - HABITAT PREFERENCES AND ESTIMATION OF FISH DENSITY

INTRODUCTION

The importance of obtaining an estimate of population size and distribution in ecological studies has led to an extensive literature on the methodology and problems associated with estimating density (for reviews see Cochran 1953; Stuart 1962; Seber 1973; Ricker 1975; Caughley 1977). The choice of technique depends on whether the population being investigated is open or closed (Seber 1973) and on whether absolute or relative density is required. Three different techniques may be applied to reef fishes : 1) destructive sampling; 2) tag-and-recapture studies and 3) visual census.

Destructive sampling methods include ichthyocides (Randall 1963; Smith & Tyler 1972; Smith 1973) and explosives (Talbot 1965; Talbot & Goldman 1974). While both may provide fairly quantitative samples, particularly of cryptic species, they are non-selective (Brock 1982), less effective for highly mobile species (Smith & Tyler 1973a), do not enable successive estimates of abundance (Russel, Talbot, Anderson & Goldman 1978) and are unsuitable in marine parks where it is undesirable to adversely affect the fauna (Bell 1983). In addition, explosives are not very effective for fishes with poorly developed or absent swim bladders (Talbot 1965).

Tag-and-recapture studies designed to estimate abundance assume equal catchability, closed populations and unrestricted mobility (Seber 1979). These are unrealistic for reef fish populations and hence the method is unlikely to provide convincing results for these animals (Thresher & Gunn 1986). This technique has however been used to evaluate population mobility (Bardach 1958, Randall 1961; Leum & Choat 1980) and was used successfully in this study to evaluate the movements of C. laticeps and C. cristiceps in the Tsitsikamma area (see below).

The advent of SCUBA has seen an explosion of studies designed to estimate species diversity and abundance using visual assessment techniques. Pioneered by Brock (1954) and Bardach (1959) the method provides a non-destructive means of assessing fish abundance, and can be divided into three classes: spot mapping, point counts and transects. Spot mapping, widely used by ornithologists (Shields 1979; Riper 1981), involves the mapping of territories and home ranges of individuals at randomly chosen points within the area of interest but has not been used in the study of reef fish populations (Thresher & Gunn 1986).

Point counts involve the enumeration of animals by a stationary observer (Thompson & Schmidt 1977; Jones & Thompson 1978; Bohnsack & Bannerot 1982; Kimmel 1985). They may be either interval counts made for a specified time assuming no recounts and similar mobility between species, or 'instantaneous' counts where all species are recognised and their average size recorded in as short a time as possible. The technique is particularly useful for estimating species diversity and assessing highly mobile species (Thresher & Gunn 1986).

Transects involve an observer traversing a measured path and counting all individuals within a fixed distance of the path. It is the method most frequently used to estimate the density of reef fish in spite of a number of problems associated with observer error (Sale 1974; Alevizon & Brooks 1975; Russell et al. 1978; Robertson & Lassig 1980; Anderson, Ehrich, Roughgarden, Russell & Talbot 1982; Gladfelter & Johnson 1983; Thresher & Gunn 1986). Transects generally provide an under-estimate of density (Seber 1979) which, in fish surveys, is compounded by difficulty in detecting both cryptic species as well as 'alert' or 'shy' species that may avoid divers (Brock 1954; Sale & Douglas 1981; Brock 1982). Reviewing the literature Thresher & Gunn (1986) show that most studies using visual assessment of fish abundance have not attempted to validate the precision or accuracy of the technique used and suggest that at best will only provide an index of relative abundance and not a measure of the absolute population size.

This section of the study has been divided into two parts. The aim of the first part was a qualitative assessment of the preferred habitats of the two study species, particularly with respect to differences in the distribution of adults and juveniles. The overall suprabenthic ichthyofauna in the two areas was also compared. The second part deals quantitatively with differences between the relative densities of adult and sub-adult C. laticeps and C. cristiceps in both exploited and unexploited areas. Answers to the following questions were sought: 1) Do different areas of the reef ecosystem support different densities of fish? 2) What factors influence their distribution? 3) Are the populations found at Noordhoek different to those found at Tsitsikamma? and 4) Are differences observed between localities attributable to fishing?

METHODS

Of the methods available, line transects were chosen because they covered a greater area than other techniques, only two species were being surveyed and because the species studied were thought to be fairly sedentary. Estimates of density were obtained from visual counts made by a single diver swimming along a 120m x 10m transect recording fish lengths on a frosted perspex sheet. Depth, time and a description of the topography and substratum characteristics were also recorded. A constant swimming speed was maintained as far as possible to prevent the re-counting of fish and each 30m section was completed in 2-5 minutes. To correlate estimated and observed length, fish were occasionally speared and estimated length was found to be accurate within ten percent.

Each transect consisted of a 60m weighted nylon line, the ends of which were bouyed at the surface, and a 30m free floating nylon line attached to the centre of the fixed line (Fig. 7). The diver first swam the 60m line followed by two 30m sections in opposite directions to the fixed line using the free floating line as a guide. Bright yellow markers were fixed to the transect lines every 10m which served to orientate the diver on the transect and to provide an estimate of visibility. Experience showed that a lower limit of approximately 5-10m visibility was necessary for successful transecting. Within the constraint of pre-selecting the depth using an echosounder, transects were considered random because the lines were deployed from a surface boat.

ASSUMPTIONS

A combination of poor diving conditions (bad weather, large swell, poor visibility, upwelling) and manpower limitations made it necessary to accept a number of basic assumptions. The first assumption was that the diver did not influence the density of fish seen on the transect (cf. Bohnsack & Bannerot 1982; Thresher & Gunn 1986). Observations of C. laticeps suggested that they were relatively unperturbed by the presence of SCUBA divers as they did not retreat from or appear to follow divers. They were however sensitive to any disturbance of the benthos, presumably to obtain food, and would approach divers under these circumstances. C. cristiceps on the other hand were very shy and were seen in very low numbers on transects. If surprised underwater, e.g. by a diver swimming over a reef crest, they would rapidly retreat from the divers' presence. Also the number of fish seen was always far lower than would be expected from fishing results on the same day in the same area. Although difficult to quantify it appeared that the smaller size classes of this species (less than approximately 250mm fork length) were less disturbed by the presence of SCUBA divers.

The second assumption was relevant to the width of the strip chosen. Past experience in both areas showed that visibility was seldom greater than 10m and a strip width of 5m would compromise acceptable visibility and maximum area covered. This assumed that detectability of fish remained constant with increasing distance from the line. Sale & Sharp (1983) showed that density was inversely related to strip width but that the effect differed between species.

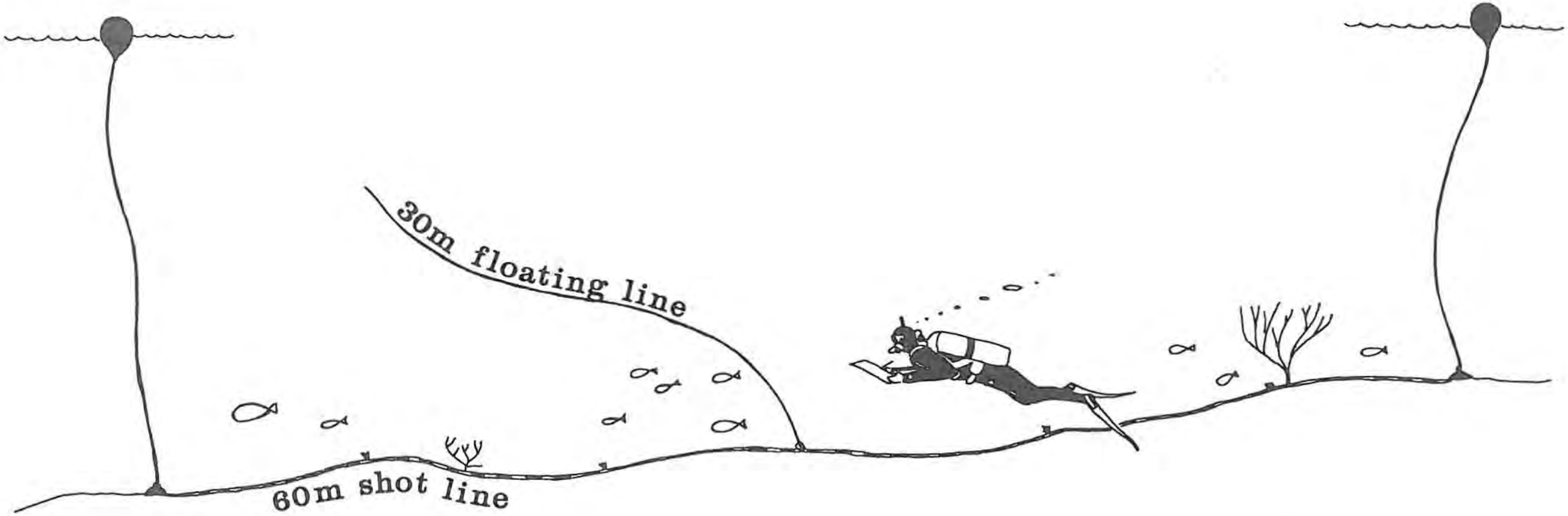


Figure 7. Illustration of the line transect method of visual assessment used during the study.

The third assumption was that the numbers of fish in a particular area did not vary diurnally. Localised movements of the two study species, e.g. dawn or dusk feeding and breeding migrations, were not observed but to minimise possible errors, all of the assessments were done at least an hour after or before dawn and dusk respectively.

RESULTS

Habitat survey

The reef ecosystem in the Tsitsikamma area was divided into three types. The first, a shallow inshore zone extending subtidally from the coastline to about 10m, consisted of low relief reefs interspersed by extensive sandy flats (Fig. 8). The reefs were dominated by calcareous algae with few octocorals, poriferans, ascidians and other filter-feeders present. The second reef type found in water between 10 and 25m was characterised by a rugged relief (Fig. 9). Macroalgal cover typical of TYPE 1 reef was absent but microalgae were present (N. Jarman, Sea Fisheries Research Institute, pers. comm.). The benthic fauna was rich in ascidians (particularly the redbait Pyura stolonifera on the reef crests), poriferans, octocorals, echinoderms and reef-building and encrusting bryozoans. The relief incorporated overhangs, holes and cracks providing shelter for associated fish species. A third reef type was found in water below 25m. Similar in appearance to the TYPE 2 reef, but not as rugged, it differed mainly in depth, the absence of Pyura and the presence of large stands of kelp Ecklonia bisperforata (Fig. 10).

Extensive surveys were also conducted on the reefs surrounding the Port Elizabeth area. The benthos did not differ macroscopically from that found in Tsitsikamma, particularly with respect to the gradation from an algal dominated inshore zone to a filter-feeder dominated offshore zone, but no reef comparable to the TYPE 3 reef in Tsitsikamma was found in this area.

A summary of species recorded in the shallow subtidal in Tsitsikamma and Port Elizabeth is given in Table 1. For each species a semi-quantitative assessment of abundance and the approximate size of small fish is shown. A summary of species seen on transects over type 2 and type 3 reefs in the Tsitsikamma is given in Table 2 and a semi-quantitative assessment of the species found on reef between 10 and 30m in the Port Elizabeth area is given in Table 3.

Estimation of fish density

Tsitsikamma Coastal National Park (TCNP)

Figure 8. Shallow inshore zone dominated by coralline algae.

Figure 9. Reef between 10 and 25m dominated by filter feeders.

Figure 10. Deep reef below 25m showing dense stands of kelp.

TABLE 1. Visual assessment of species found in shallow subtidal areas in the Tsitsikamma and Port Elizabeth areas. (xxx - abundant, xx - common, x - uncommon). Approximate sizes (total length in mm) of small fish are given and species important to the South African line - fishery are asterisked.

SPECIES	RELATIVE ABUNDANCE					
	Tsitsikamma			Port Elizabeth Environs		
	small		large	small		large
Boopsoidea inornata	xxx	<50	x	xxx	<50	xx
Chaetodon marleyi	x	<50	x	x	<50	x
Cheilodactylus fasciatus	xxx	<50	xxx	xx	<50	xx
Cheilodactylus pixii	x	<50	x			x
Chirodactylus brachydactylus	xxx	<75	xxx	xxx	<75	xxx
*_Chrysoblephus cristiceps_	x	<100		x	<150	
*_Chrysoblephus laticeps_	xx	<75	x	xx	<100	
*_Cymatoceps nasutus_	x	<100		xx	<150	x
Diplodus cervinus	xxx	<75	xx	xxx	<50	xx
*_Diplodus sargus_	xxx	<75	xx	xxx	<50	xx
Gymnocrotaphus curvidens			x			x
Lithognathus lithognathus	x	<75	x			
Lithognathus mormyrus	x	<50	xx			x
Monodactylus falciformis			x			
Mugil spp.	xx	<100	xxx	xx	<100	xxx
Oplegnathus conwayi	x	<100	xx	x	<100	x
*_Pachymetopon aeneum_	x	<50				
*_Pachymetopon grande_			x	xxx	<75	x
Pagellus natalensis			x			
*_Petrus rupestris_	x	<300		x	<250	
Pomadasys olivaceum			xx			
Rhabdosargus holubi			xx	x	<50	xx
Rhonciscus striatus			x			
Sarpa salpa	xxx	<100	xxx	xx	<50	xx
*_Sparodon durbanensis_	xx	<150	x	x	<100	
Spondyliosoma emarginatum	x	<75		x	<50	xx

Total observation time = 460 minutes.

TABLE 2. Percentage contribution of species to all fish observed on underwater transects and approximate total length ranges of fish observed on reef types 2 and 3. Species important to the South African line-fishery are asterisked.

SPECIES	TYPE 2 REEF		TYPE 3 REEF	
	Contribution (%)	Length (mm)	Contribution (%)	Length (mm)
Acanthistius sebastoides	0,05	125-200		
*_Argyrozona argyrozona_			13,82	275-400
Boopsoidea inornata	31,02	75-250	27,28	175-200
Chaetodon marleyi	0,01	75-100		
Cheilodactylus fasciatus	0,34	75-300	0,38	225-250
Cheilodactylus pixii	0,24	75-150	0,03	100-125
Cheimerius nufar	0,03	200-250		
Chirodactylus brachydactylus	1,05	125-350	0,06	225-250
Chirodactylus grandis	0,02	650-700		
*_Chrysoblephus cristiceps_	0,43	125-550		
*_Chrysoblephus gibbiceps_	0,05	75-350	0,55	225-450
*_Chrysoblephus laticeps_	1,95	75-400	1,12	125-350
Coracinus capensis	0,04	275-300		
*_Cymatoceps nasutus_	0,01	650-700		
Diplodus cervinus	0,34	125-350		
*_Diplodus sargus_	0,25	125-300		
*_Epinephelus guaza_	0,04	275-450	0,06	300-400
Gymnocrotaphus curvidens	0,44	125-350	0,19	275-300
Oplegnathus conwayi	0,77	75-550		
*_Pachymetopon aeneum_	17,44	75-350	15,84	125-300
*_Pachymetopon grande_	0,03	300-350		
Pagellus natalensis	0,02	150-175		
*_Petrus rupestris_	0,88	175-700	0,27	225-900
Rhabdosargus holubi	0,57	75-300	0,06	200-250
Rhonsiscus striatus	0,01	75-100		
Sarpa salpa	32,88	75-150		
Scombrops dubius			16,38	150-200
*_Sparodon durbanensis_	0,13	250-450		
Spondyliosoma emarginatum	10,86	75-200	23,99	125-200
Sharks	0,11		0,03	
Number of transects	20		4	
Total number of fish	10378		3669	

TABLE 3. Visual assessment of species found in the Noorhoek and Port Elizabeth areas (xxx-abundant, xx-common, x-uncommon). Total length and range are expressed in mm. Species important to the South African line-fishery are asterisked.

SPECIES	RELATIVE ABUNDANCE						
	Noordhoek				Algoa Bay		
	small		large	range	small		large
Acanthistius sebastoides			x	100-250			
Boopsoidea inornata	xx	<50	xxx	50-225	xxx	<50	xxx
Chaetodon marleyi			x	75-125	x	<50	x
Cheilodactylus fasciatus			x	75-250	xxx	<50	xxx
Cheilodactylus pixi	xx		xx	100-150	x	<50	x
*_Cheimerius nufar_	x	<100	x	50-275			x
Chirodactylus brachydactylus	xx	<75	xxx	50-350	xx	<100	xx
*_Chrysoblephus cristiceps_			x	200-300	xx	<150	xx
*_Chrysoblephus gibbiceps_			x	200-300			x
*_Chrysoblephus laticeps_	x	<50	x	100-350	xx	<150	xx
*_Chrysoblephus puniceus_							x
Diplodus cervinus			x	150-300	x	<100	xx
*_Diplodus sargus_			x	100-250	xx	<150	xx
*_Epinephelus guaza_			x	200			x
Gymnocrotaphus curvidens			x	200-300			x
Oplegnathus conwayi	x	<100	x	50-450	x	<100	x
*_Pachymetopon aeneum_	xxx	<100	xxx	50-350	xxx	<50	xxx
*_Pachymetopon grande_							x
Pagellus natalensis							x
*_Petrus rupestris_			x	200-300			
Polysteganus praeorbitalis			x	150-250			
*_Porcostoma dentata_			x	150-200			
Rhabdosargus holubi			x				x
Rhonsiscus striatus							x
Sarpa salpa	x	<100	xx	75-150			
*_Sparodon durbanensis_							x
Spondyliosoma emarginatum	x	<100	x	75-200	xxx	<50	xxx

Data for the Tsitsikamma area were collected between November 1984 and August 1985 from three sites; Waterfall, the Knoll and Rheeders (see Fig. 4). With the exception of an area of aeolionite ridges on the eastern boundary of the Tsitsikamma Park these areas were considered to include all of the reef types typically found between 5 and 30m (Buxton & Smale 1984).

Chrysoblephus laticeps

The frequency distribution of individual estimates is given in Figure 11. Goodness of fit testing showed that the sample was not normally (X^2=42.6, v=4) or randomly (X^2=40.24, v=4) distributed about the mean. For this reason transformation of the data (Kingett & Choat 1981) to reduce heterogeneity of variance was not possible.

A summary of the 76 individual line transects (Table 4) produced an overall mean density of 0.0254±0.0143 fish/m^2 equal to one fish/39m^2 with a co-efficient of variation of 0.56. This high variance was found to be a combination of three factors; depth, temperature and relief, all of which influenced the numbers of fish counted (Table 5). Density obtained over the same temperature (16°C), depth (15-25m) and relief (high relief) conditions showed that the three sites were not significantly different (Kruskal-Wallis test, Hc=1.65, $P<0.05$, v=3). The data were therefore pooled to test the effect of temperature on density.

Mean density at 16° C for high relief reef between 15 and 25m was significantly lower than the density obtained at 18-20°C (Mann-Whitney U test using normal approximation, Z=3.67, $P<0.05$, df=31,25). These temperature differences were closely related to season, 16°C data being obtained between August and November (late winter-early summer) and the 18-20°C data between January and March (summer-early autumn).

The effect of depth on density was compared at the Knoll where, at constant temperature (16° C) and relief (high relief) the density of C. laticeps between 6-11m was significantly lower than that at 15-25m (Mann-Whitney U test, U=68.5, $P<0.05$, df=6.13).

Finally, the effect of reef type was compared in the Waterfall area. Numbers of C. laticeps were significantly higher on high relief reefs than those obtained on low relief reefs (Mann-Whitney U test, U=138, $P<0.05$, df=17,10).

Chrysoblephus cristiceps

A summary of the 69 line transects in the Tsitsikamma area on which C. cristiceps were counted is given in Table 6. The overall mean density for the three study sites combined was 0.0028±0.0054 fish/m^2 (n=69, cv=1.92) or roughly one fish/357m^2. Differences between the Rheeders, Knoll and Waterfall areas were difficult to evaluate because of a high incidence of zero-counts in the sample (42%).

TABLE 4. *Chrysoblephus laticeps*. Summary of density estimates in the Tsitsikamma Coastal National Park.

AREA	PERIOD	TEMPERATURE	n	DENSITY (no.m^{-2})
	(mth/yr)	(mean ^{0}C)		$\overline{x}$ s
Rheeders	08/85	16	9	0.0157 ± 0.0075
Knoll	08/85	16	12	0.0199 ± 0.0069
Waterfall	08/85	16	8	0.0327 ± 0.0180
Waterfall	11/84	16	16	0.0184 ± 0.0107
Rheeders	03/85	17	3	0.0461 ± 0.0121
Waterfall	08/85	17	3	0.0156 ± 0.0096
Waterfall	01/85	18	3	0.0333 ± 0.0242
Waterfall	03/85	18	3	0.0433 ± 0.0085
Knoll	03/85	19	4	0.0267 ± 0.0000
Rheeders	01/85	20	3	0.0200 ± 0.0203
Knoll	01/85	21	3	0.0289 ± 0.0222
Waterfall	01/85	21	3	0.0294 ± 0.0025
Waterfall	01/85	22	4	0.0371 ± 0.0070

TABLE 5. *Chrysoblephus laticeps*. Analysis of variance of density at three sites in the Tsistikamma (variable - density: factors - area, depth, rugosity).

FACTOR	LOCALITY	CONDITIONS	DENSITY (no.m^{-2})	cv	n	
Area	Waterfall	16^{0}C, hr, 15-25m	0.0241 ± 0.0093	0.38	15	ns
	Knoll	16^{0}C, hr, 15-25m	0.0228 ± 0.0041	0.18	9	
	Rheeders	16^{0}C, hr, 15-25m	0.0233 ± 0.0160	0.69	12	
Temperature	All areas	16^{0}C, hr, 15-25m	0.0232 ± 0.0126	0.54	31	***
	All areas	18-20^{0}C, hr, 15-25m	0.0354 ± 0.0131	0.37	25	
Depth	Knoll	16^{0}C, hr, 6-11m	0.0159 ± 0.0069	0.43	6	**
	Knoll	16^{0}C, hr, 15-25m	0.0259 ± 0.0097	0.37	13	
Rugosity	Waterfall	16^{0}C, hr, 15-25m	0.0265 ± 0.0150	0.56	17	*
	Waterfall	16^{0}C, lr, 15-25m	0.0138 ± 0.0102	0.74	10	

hr = high relief, lr = low relief, cv = co-efficient variation,
*** = $P<0.001$, ** = $P<0.01$, * = $P<0.05$, ns = not significant.

Mean density at each area was a function of the proportion of zero-counts and at Rheeders where this value was only 28%, the mean density was significantly higher than at Waterfall (Mann-Whitney U test, U =380.5, P<0.05, df=14,37). This difference was thought to relate more to chance effects associated with diver avoidance rather than to a real difference in relative density because the areas were very similar in other respects. The difference between Rheeders and the Knoll was not significant (Mann-Whitney U test, U=398.5, P<0.05, df=18,37).

Fish were only seen at the Knoll on three of the 18 transects, all of which were below 15m. Not discounting the reservations expressed above, this result may suggest a depth preference in the species. Excluding these shallow tansects from the overall analysis a density of 0.00355±0.00592 fish/m^2 (n=54, cv=1.66) was obtained.

Density estimation in the Noordhoek area

Estimates of abundance in this area were obtained from 33 individual strip counts between November 1984 and April 1985, and a further 5 in April 1986 (Table 7). All of the counts were done in roughly the same area off the Patie, Noordhoek (see Fig. 6) between 12 and 27m depth and between 16 and 20^{0}C. Low numbers and a high incidence of zero-counts (26% and 66% for C. laticeps and C. cristiceps respectively) prevented a comparison of depth, temperature and relief in this area.

Individual estimates of C. laticeps in the Noordhoek area,which were obviously not normally distributed (Fig. 12), were also not randomly distributed about the mean (X^2=44.18, v=5). The estimates could therefore not be transformed to reduce heterogeneity of variance. The pooled data produced an overall mean density of 0.0064 ± 0.007 fish/m^2(n=38, cv=1.09) for C. laticeps which was significantly lower than the mean density recorded at Tsitsikamma (Mann-Whitney U test using normal approximation, Z=6.27, P<0.01, df=76,38).

The mean density of C. cristiceps at Noordhoek of 0.0031±0.0063 fish/m^2(n=58, cv=2.04) was not significantly different from the mean density recorded at Tsitsikamma (Mann-Whitney U test using normal approximation (Z=0.428, P<0.05, df=69,38).

Finally the length frequencies of fish recorded on transects in the Tsitsikamma and Noordhoek areas are compared with length frequencies of fish caught on handline in the same areas (Fig. 13).

DISCUSSION

The results of the habitat survey showed depth related changes in both species composition and size of fish. In the shallow subtidal areas of the Tsitsikamma, fish were separated into small and large sizes with the inference that small fish represented juveniles, although size at sexual

TABLE 6. *Chrysoblephus cristiceps*. Summary of density in the Tsitsikamma Coastal National Park.

AREA	PERIOD (mth/yr)	TEMPERATURE (mean ^{0}C)	n	% ZERO COUNTS	DENSITY (no.m^{-2}) $\bar{x}$	s
Waterfall	11/84	16	16	81	0.000521	± 0.001173
Rheeders	08/85	16	9	44	0.004629	± 0.007536
Waterfall	08/85	16	8	63	0.001875	± 0.002429
Knoll	08/85	16	16	100	no fish seen	
Rheeders	03/85	17	2	0	0.022500	± 0.010607
Waterfall	08/85	17	3	33	0.001944	± 0.001735
Waterfall	01/85	18	3	66	0.000926	± 0.001603
Knoll	03/85	19	3	0	0.008889	± 0.001925
Rheeders	01/85	20	3	0	0.008333	± 0.007265
Knoll	01/85	21	3	100	no fish seen	
Waterfall	01/85	21	3	0	0.003333	± 0.000000
Waterfall	01/85	22	4	25	0.002916	± 0.002846

TABLE 7. Summary of density estimates in the Noordhoek area.

	PERIOD (mth/yr)	TEMPERATURE (mean^{0}C)	n	ZERO COUNTS (%)	DENSITY (no.m^{-2}) $\bar{x}$	s
C. laticeps						
	10/84	16	7	29	0.005194	± 0.006114
	03/85	16	3	67	0.002777	± 0.000000
	03/85	17	6	40	0.004166	± 0.003402
	04/85	17	3	33	0.003333	± 0.003402
	02/85	18	4	0	0.019097	± 0.007206
	12/84	19	4	50	0.004166	± 0.001964
	04/86	19	5	0	0.012000	± 0.008367
	03/85	20	6	17	0.004167	± 0.003291
C. cristiceps						
	10/84	16	7	100	no fish seen	
	03/85	16	3	67	0.005555	± 0.000000
	03/85	17	6	60	0.002222	± 0.002324
	04/85	17	3	33	0.007777	± 0.005092
	02/85	18	4	25	0.015972	± 0.012081
	12/84	19	4	75	0.005555	± 0.000000
	04/86	19	5	100	no fish seen	
	03/85	20	6	67	0.001389	± 0.002670

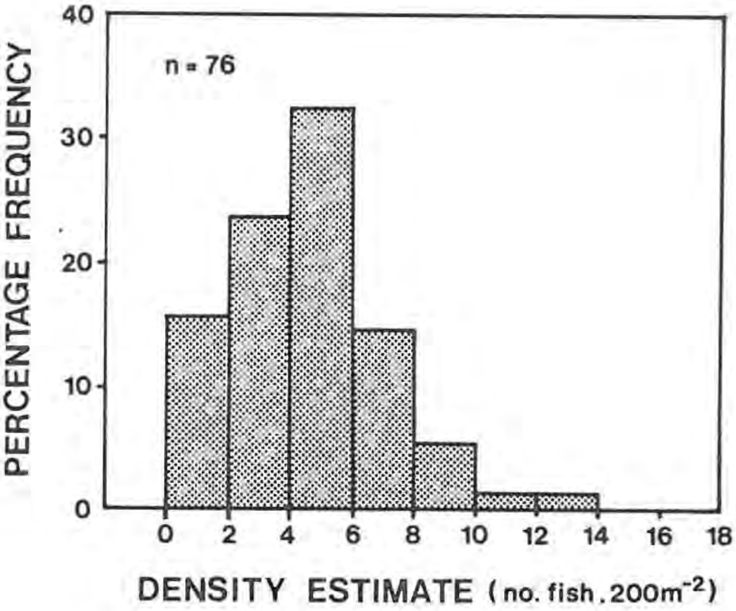


Figure 11. Frequency distribution of individual density estimates of visually assessed Chrysoblephus laticeps in the Tsitsikamma area.

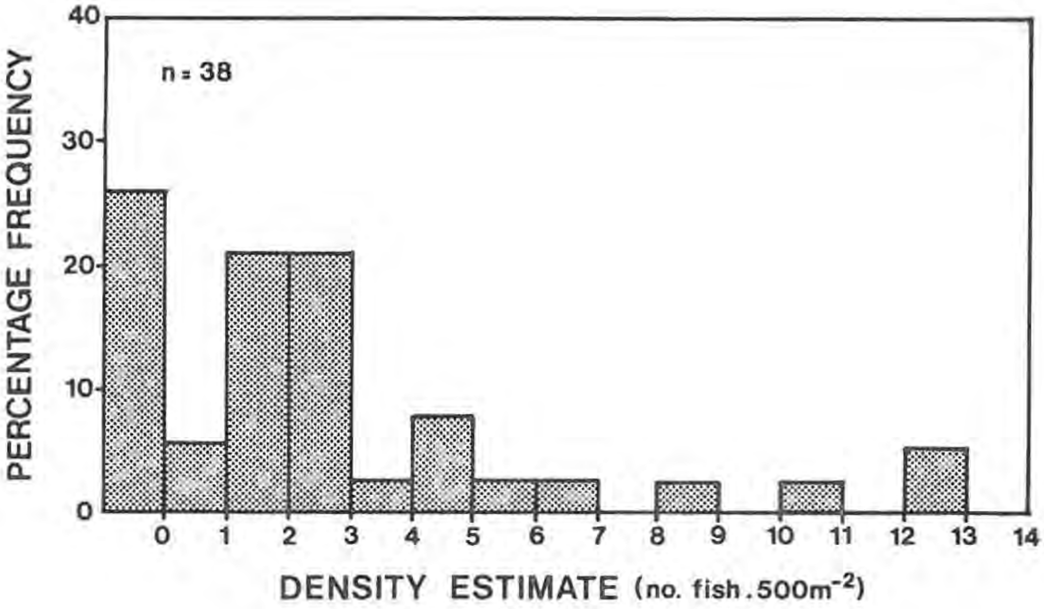


Figure 12. Frequency distribution of individual density estimates of visually assessed Chrysoblephus laticeps in the Noordhoek area.

maturity for most species was unknown. The area supported three distinct groups of fish. The first, typically shallow water species, included zebra Diplodus cervinus, blacktail Diplodus sargus, mullet species, bronze bream Pachymetopon grande, Cape stumpnose Rhabdosargus holubi, strepie Sarpa salpa and musselcracker Sparodon durbanensis. Both large and small specimens were present. Studies on these fish suggest that their distribution may be attributed to feeding preferences (Christensen 1978; Blaber 1974; Joubert 1981; Lasiak 1982; Buxton & Kok 1983). The second group were represented mainly by juveniles of species more common in deeper water including Fransmadam Boopsoidea inornata, dageraad Chrysoblephus cristiceps, Roman C. laticeps, poenskop Cymatoceps nasutus, blue hottentot Pachymepon aeneum, red steenbras Petrus rupestris and steentjie Spondyliosoma emarginatum. These fish were only present between December and April suggesting an influx of recruits over a short period of time and hence a restricted breeding season for the species. The third group including white and sand steenbras Lithognathus lithognathus and L. mormyrus, moony Monodactylus falciformis, red tjor-tjor Pagellus natalensis and piggy Pomadasys olivaceum are species associated with sandy substrates (Mehl 1973; Joubert & Hanekom 1980; Buxton, Smale, Wallace & Cockcroft 1984).

The composition of suprabenthic species found on reefs at depths between 10 and 25m showed that S. salpa, B. inornata, P. aeneum and S. emarginatum were the most numerous of the species recorded. Although many of the species found on type 1 and type 2 reefs were similar, observations showed that fewer juveniles were present on the deeper reefs. This was particularly true for important linefish species with the exception of P. rupestris, juveniles of which were more common in this depth range. Of the 29 species recorded 59 percent were from the family Sparidae, many of which are important to the line fishery. This domination by a single family differs considerably from the diversity found on tropical reefs (Risk 1972; Alevizon & Brooks 1975; Brock, Lewis & Wass 1979; Bohnsack & Talbot 1980).

Depth, bottom time and poor visibility imposed severe restrictions on the visual assessment of deep reefs in the Tsitsikamma area (type 3) and as a result only four transects were successfully completed during the study period. Combining these results with incidental observations showed a lower suprabenthic species diversity than shallower reefs. B. inornata, S. emarginatum and P. aeneum were still numerically important whereas S. salpa were not recorded at all. Silverfish Argyrozona argyrozona and gnomefish Scombrops dubius, species not recorded on shallower reefs, were important whereas red stumpnose Chrysoblephus gibbiceps were seen in greater numbers on these reefs compared to the shallower study sites.

A comparison of the suprabenthic species diversity in Tsitsikamma and Port Elizabeth showed that the two areas were very similar, only

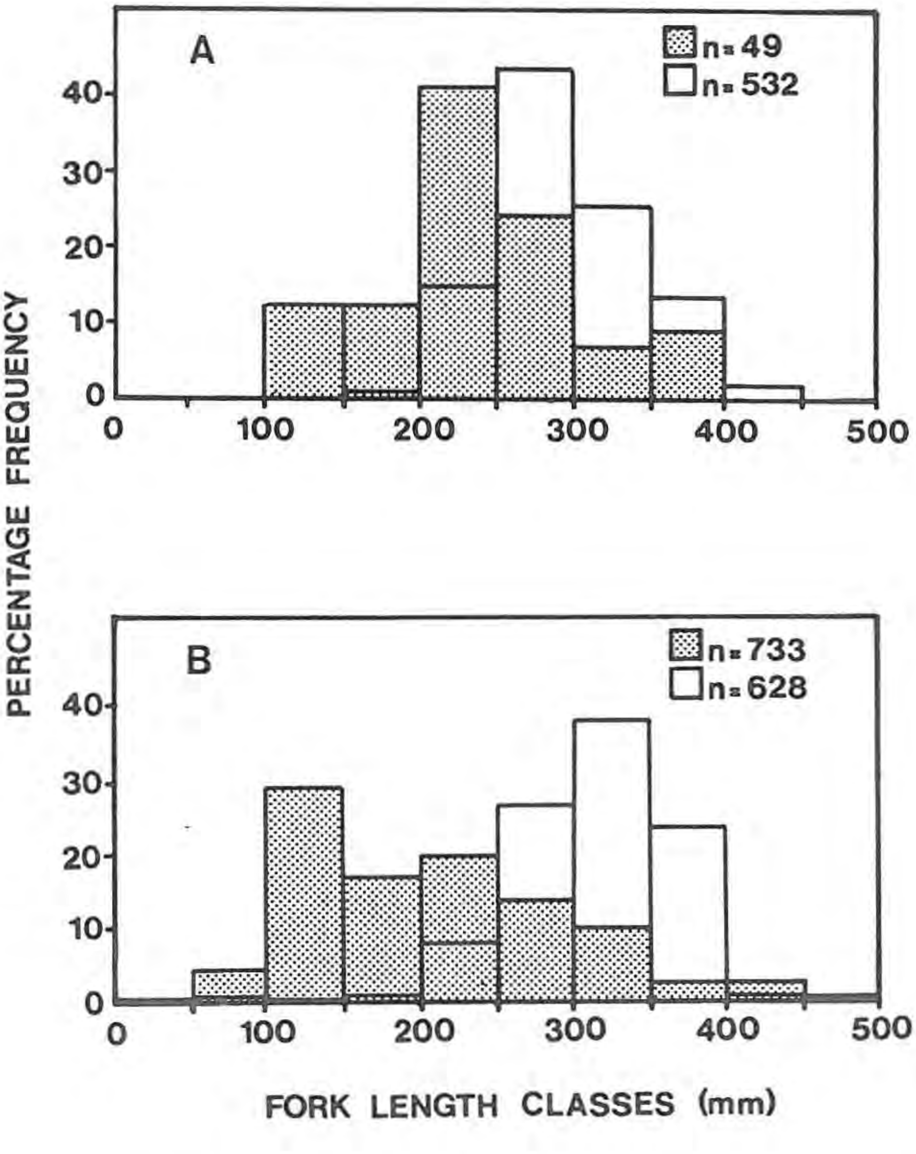


Figure 13. A comparison of the length frequency distributions of Chrysoblephus laticeps caught on handline (open) and those visually assessed (shaded) in the Noordhoek (A) and Tsitsikamma (B) areas.

Chirodactylus grande, *Chrysoblephus puniceus*, *Polysteganus praeorbitalis* and *Porcostoma dentata* were not found in both areas. Depth preferences of different size classes and species were also similar in the two areas.

Juveniles of both *C. laticeps* and *C. cristiceps* were most common in shallow water down to approximately 10m where they seemed to prefer the rock-sand interface. Beckley (1985) did not record these species in a tide pool survey in the Port Elizabeth area. Rotenone collections in the Tsitsikamma between 10 and 30m did not record any juveniles of these species either (Buxton & Smale 1984). These data suggest that recruitment occurs in shallow water followed by a gradual outward migration with increasing size. This distribution may be associated with feeding preferences as well as some protection from predators, both of which will be more fully discussed in later sections.

Visual assessments of fish using SCUBA are also restricted by practical no-decompression working depths of less than 35m. For this reason it was not possible to evaluate the importance of deeper reefs to the population dynamics of both of the study species. Limited surveys of reefs deeper than 25m showed that *C. laticeps* were common at this depth but *C. cristiceps* were not seen. Although the absence of many species may be explained by their preference for shallower water, the lack of *C. cristiceps* was unexpected as they are caught on line at this depth. This may be attributed to a tendency to avoid divers, aggravated by poor visibility. This behaviour is also thought to bias the shallow water results as the ratio of *C. cristiceps* to *C. laticeps* is far greater in line catches than in the visual assessments.

Three factors, depth, relief and temperature were found to influence the within area estimates of *C. laticeps* density. The comparison between the shallow (6-11m) and deep (15-25m) stations substantiated the qualitative assessment that adults preferred the deeper reefs. Depth *per se* was probably not the cause of this observed distribution but rather an effect brought about by availability of preferred prey at the deeper sites. The shallower stations had a greater proportion of algae whereas the deep stations were dominated by filter feeders and associated benthic fauna. The change in diet observed between juveniles and adults, described later, also appears to influence the distribution of juveniles, these being more abundant close inshore.

The second influence was relief. The results at Waterfall showed that fish were more abundant on the high relief reefs and two factors probably influenced this distribution. Food availability was probably important because high relief reefs appeared to support both a greater diversity and abundance of preferred prey items such as echinoids, crustaceans and molluscs, which are associated with the benthic filter feeding community. Low relief reefs were by comparison fairly depauperate, an effect thought to be associated with the scouring influence of sand, many being covered and uncovered by shifting sand during storms. Secondly, C. laticeps appeared to be most abundant in areas that afforded shelter in the form of cracks, overhangs and shallow caves. Penrith (1972b) reported that large C. laticeps were restricted to caves and suggested that this was to avoid predators. However, they have not been recorded in the diet of piscivorous predators including dolphins (G. Ross & V. Cockcroft, Port Elizabeth Museum, pers. comm.) and seals (J. David, Sea Fisheries Research Institute, pers. comm.) and are of minor importance to the diet of sharks and fish (M. Smale, Port Elizabeth Museum, pers. comm.). In this study no evidence was found to support Penrith's observation that large C. laticeps were restricted to caves, as both large and small fish ranged freely over the reef in the areas studied.

Finally there was a significant difference in the density recorded at low and high ambient water temperatures, more fish being seen when the water was warm. This result was particularly difficult to understand because much of the data presented further on in this study suggests that C. laticeps are fairly sedentary.

On a number of occasions diving was done during cold upwelling conditions when temperatures had dropped to approximately 5-10°C. Under these conditions the suprabenthic species were conspicuous by their absence and careful searches of shelter sites revealed very few fish, suggesting that they had moved out of the area perhaps following pockets of warmer water. No such concentrations of fish or warm water were ever encountered although it is common spearfishing practice in the study area to look for fish around pinnacles above the thermocline during upwelling conditions. This behaviour, an acute response to decreased water temperature, must not be confused with the acclimated tolerance to lower water temperatures and does not explain the decrease in density during winter. It is well known that populations of a single species can have different eco-phenotypes, with different thermal preferences, based on different thermal histories. However, in the Western Cape these fish are common in areas where the water temperatures are permanently colder than in the Tsitsikamma area, demonstrating their ability to acclimate to colder water conditions.

The ability of a diver to detect fish in cold water may decrease because the fish are less mobile. With a lower metabolic rate a higher proportion of the fish may be 'holed up' in shelter areas. Conversely in summer under warmer water conditions the fish are more active and conspicuous especially during the reproductive season. The efficiency of divers doing visual assessments under different temperature regimes has never been tested and is probably worthy of some attention.

The comparison between Noordhoek and Tsitsikamma showed a highly significant difference in the density of C. laticeps, the exploited site having far fewer fish per unit area. Size frequency distributions of C.

laticeps in these two areas also showed a decrease in the proportion of larger fish (cf. change in sex ratio, Chapter 3.6). Both of these effects may have resulted from exploitation (Weatherley 1972) but Leum & Choat (1980) caution against this conclusion arguing that variable recruitment patterns and bottom topography could give similar results.

Because of the problems associated with the visual assessment of C. cristiceps, a 'shy' species, no conclusions could be drawn from the finding that densities of this species in the exploited and unexploited areas were similar. Linefish catch data provided evidence that these two populations are indeed very different and the visual assessment results for this species are therefore regarded with extreme caution.

Before accepting that exploitation is the cause of the lower density of C. laticeps at the exploited site further examination of the problem is necessary and subsequent chapters in this study will present further evidence to substantiate this hypothesis.

3.2 MARK AND RECAPTURE STUDY

INTRODUCTION

During 1985-86 an intensive tagging programme was carried out in the Tsitsikamma area with a two-fold objective. The first was to study the movements of C. laticeps and C. cristiceps so that the degree of residency in these species could be established. The second objective was to validate age and growth studies by marking fish with oxytetracycline. When taken up in the otolith this chemical provides a mark from which subsequent growth over a known time period can be evaluated (Wild & Foreman 1980).

Tag and recapture studies may also be used to estimate population density (Seber 1973; Laird & Stott 1978), but the necessary assumptions of closed populations, unrestricted mobility and particularly equal catchability are thought to be unrealistic in a size selective fishery (Thresher & Gunn 1986). For this reason density estimates were not considered.

Only one previous attempt to tag reef fish in South Africa has been published (Stander & Nepgen 1968). This study was designed to evaluate the movements of a number of species in the False Bay area. In 1985 a National Tagging Programme was started by the Oceanographic Research Institute in Durban which includes all recreational angling species, but results from this study have not yet been published.

METHODS

Techniques available to mark fishes are variable and the choice of method depends on several considerations (Laird & Stott 1978). Time constraints prevented both a systematic testing of the various techniques available and a study of tag retention. Short experimental trials were run to test the most suitable tag location and the suitability of different length tags. Anchor tags (FD67C Floy Tag Manufacturing Co. Seattle, Wash.) were chosen because individual identification was necessary, the tags were easily identified upon recapture and other workers have found them to be suitable for a wide range of reef species (Stander & Nepgen 1968; Shaw, Nagtegaal, Archibald & Leaman 1981; Davis & Reid 1982).

Specimens were caught on handline using 4/0 barbless hooks, placed on a foam rubber mat to minimise injury and the fork length was measured to the nearest millimetre. The swimbladder was deflated using a hypodermic needle and the tag injected below the second dorsal spine taking care to anchore the tag in the pterygiophores. The fish were given an intraperitoneal injection of oxytetracycline (OTC), called Terramycin, at a dcsage of approximately 50mg/kg body weight (Shaw et al. 1981) and returned to the water immediately. OTC is a calcium specific antibiotic incorporated in the growing periphery of the otolith (Wild &

Foreman 1980) that shows up as a mark under ultra violet illumination (Casselman 1974).

Tags carried an identification number, the Port Elizabeth Museum address and the word 'Reward'. Notices advertising the project were widely distributed in the area between Mossel Bay and East London and in the local press (Fig. 14). A reward was offered for the return of the whole tagged fish. For each returned tag the following information was recorded from the finder; date and place of capture, fork length and if possible the whole fish or the head was obtained for the extraction of otoliths.

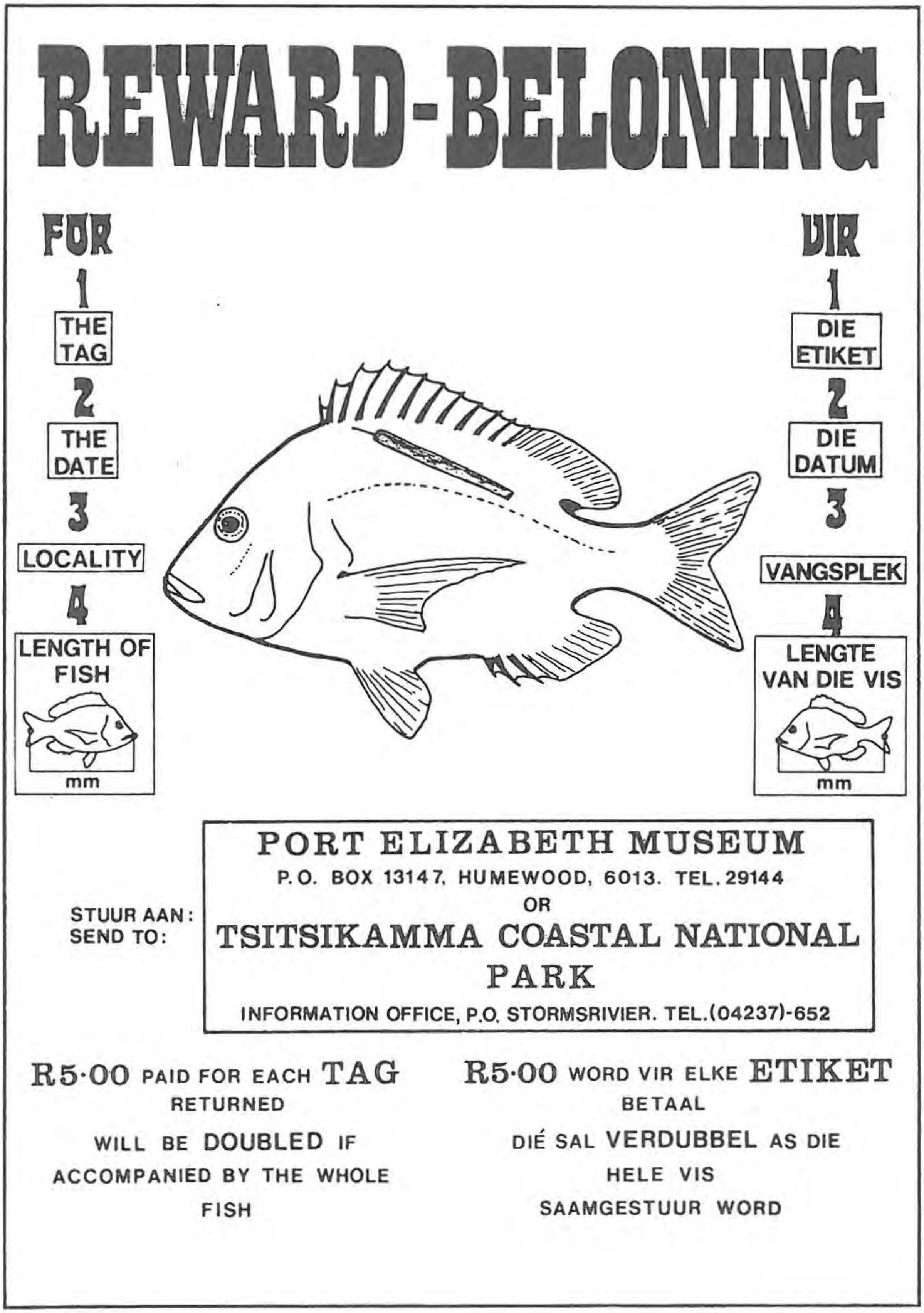
RESULTS

Thirteen *C. laticeps*, 13 *C. cristiceps*, two *Pachymetopon aeneum* and one *C. gibbiceps* were tagged and kept in a 16m diameter circular aquarium for 1-5 months. Half of the *C. cristiceps* were tagged with short tags (±20mm) and half with tags between 50-100mm. The shorter tags were observed to spin and cause a severe lesion around the tag site after a few days. All of the other fish including those recaptured from the sea showed no signs of discomfort from the longer tags. Three of the *C. laticeps* were tagged in the operculum. This appeared to cause some irritation to the fish as they were observed to repeatedly brush the substrate in an obvious attempt to dislodge the tag. All of these tags fell off after less than two weeks.

The length frequencies of all fish tagged during the study are shown in Figure 15. A total of 379 *C. laticeps* and 85 *C. cristiceps* were tagged from June 1985 to May 1986 in the area between the Knoll and Rheeders (Tables 8&9). The *C. laticeps* tagged ranged in length between 181mm and 436mm and *C. cristiceps* between 212mm and 608mm.

The mortalities of fish during tagging are also summarised in Tables 8 & 9. Pre-tagging mortality was the most significant contributor (96%) to total mortality and resulted from either severe barotrauma, where the gut protruded from the anus or the mouth, or from a swallowed hook that could not be removed without injury to the fish. Post-tagging mortality occurred infrequently (8%) and was defined as the inability to return a tagged fish to the sea. These fish either floated on the surface or sank without observable movement and although listed as dead the latter may have recovered.

Recaptures are summarised in Table 10. Eleven *C. laticeps* were recaptured, three by anglers and eight during tagging operations, and maximum time at liberty was 588 days. All were caught within 2km of the tag locality and six of the fish were caught on the same reef as the one on which they were tagged (Fig. 16). Only one *C. cristiceps* was recaptured after 265 days at liberty, also on the same reef as it was



REWARD-BELONING

FOR

1 THE TAG

2 THE DATE

3 LOCALITY

4 LENGTH OF FISH

mm

VIR

1 DIE ETIKET

2 DIE DATUM

3 VANGSPLEK

4 LENGTE VAN DIE VIS

mm

STUUR AAN:
SEND TO:

PORT ELIZABETH MUSEUM
P.O. BOX 13147, HUMEWOOD, 6013. TEL. 29144
OR
TSITSIKAMMA COASTAL NATIONAL PARK
INFORMATION OFFICE, P.O. STORMSRIVIER. TEL.(04237)-652

R5·00 PAID FOR EACH **TAG** RETURNED WILL BE **DOUBLED** IF ACCOMPANIED BY THE WHOLE FISH

R5·00 WORD VIR ELKE **ETIKET** BETAAL DIÉ SAL **VERDUBBEL** AS DIE HELE VIS SAAMGESTUUR WORD

Figure 14. Notice used to bring the tagging project to the attention of local anglers between Mossel Bay and Port Elizabeth.

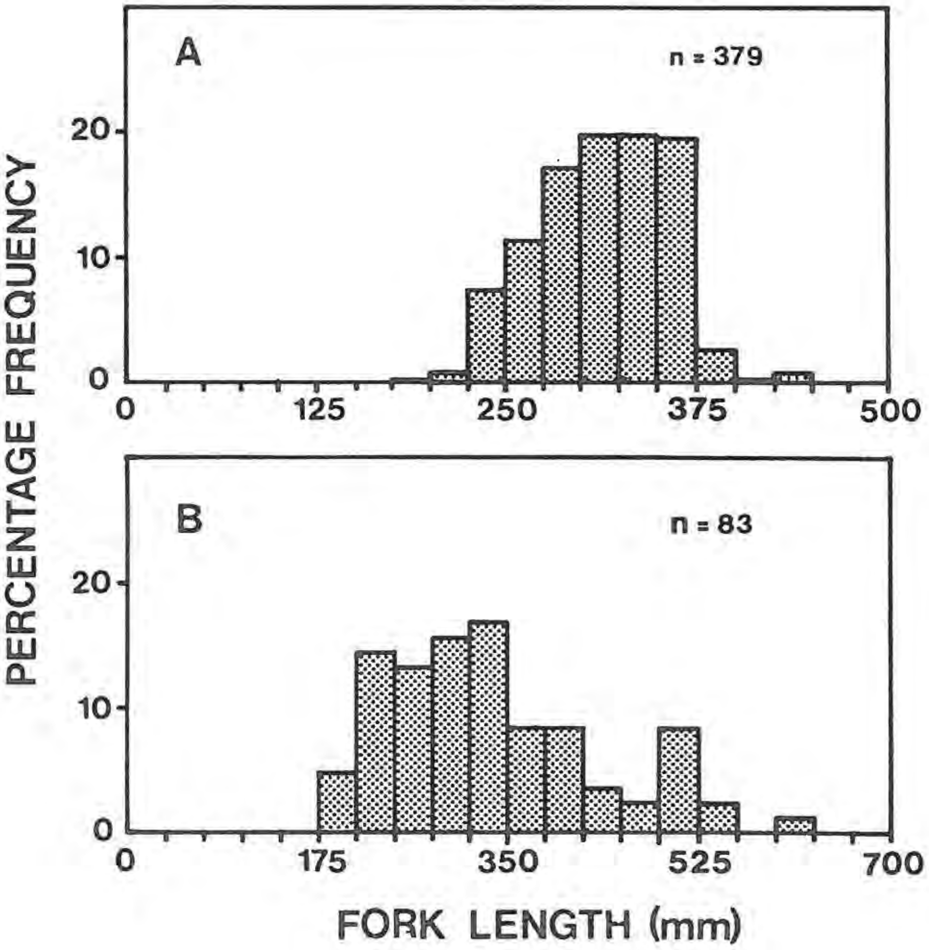


Figure 15. Length frequencies of all *Chrysoblephus laticeps* (A) and *C. cristiceps* (B) tagged in the Tsitsikamma area.

TABLE 8. <u>Chrysoblephus</u> <u>laticeps</u>. Summary of pre and post tagging mortalities,locality and date of tagging.

DATE	NO. TAGGED	LOCALITY	TAGGING MORTALITIES	
			Pre	Post
850618	10	Rheeders	0	0
850618	35	Rheeders	0	1
850620	37	Rheeders	16	4
850620	35	Rheeders	2	1
850621	60	Rheeders	{	
850621	33	Stielkop	14	1
850718	33	Rheeders	{	
850718	15	Stielkop	13	0
850816	5	Rheeders	10	0
850821	17	Stielkop	10	0
850828	7	Stielkop	4	0
860313	5	Stielkop	3	0
860313	2	Rheeders	1	0
860314	8	Knoll/S'kop	6	0
860519	21	Stielkop	7	0
860521	5	Waterfall	0	0
860521	12	Stielkop	{	
860521	12	Rheeders	{	
860521	27	Stielkop	9	1
Total	379		95	8

TABLE 9. <u>Chrysoblephus</u> <u>cristiceps</u>. Summary of pre and post tagging mortalities, locality and date of tagging.

DATE	NO. TAGGED	LOCALITY	TAGGING MORTALITIES	
			Pre	Post
850618	6	Rheeders	0	0
850618	14	Rheeders	3	0
850620	13	Rheeders	6	0
850620	7	Rheeders	2	0
850621	17	Rheeders	2	1
850718	7	Rheeders	2	0
850816	2	Rheeders	4	0
860313	3	Stielkop	2	1
860313	9	Rheeders	3	0
860314	2	Knoll/S'kop	0	0
860521	5	Stielkop	13	2
Total	85		37	4

tagged.

Two *C. laticeps*, of 305 and 371mm, had grown 27 and 25mm respectively during 18 months at liberty. The predicted growth rate for these fish, based on the age determination in Chapter 3.4 was 27.5 and 11mm respectively. The poor correlation between these rates for the larger of the two fish was thought to be a result of the difficulty in estimating the age of older fish. Overall the increment in lengths were small and in some cases negative during the time at liberty which supports the slow growth rate observed in both species (see Chapter 3.4).

TABLE 10. Recaptures of *Chrysoblephus laticeps* and *C. cristiceps* in the Tsitsikamma area.

SPECIES	TAGGED			RECAPTURE			DAYS AT	LENGTH
	Date	Area	FL	Date	Area	FL	LIBERTY	INCR.(mm)
C. laticeps	850618	Rh	362	850624	Sk	?	6	?
"	850620	Rh	292	850629	Sk	?	9	?
"	850620	Rh	307	850816	Rh	315	57	8
"	850621	Rh	315	850718	Rh	312	27	-3
"	850621	Rh	346	850718	Rh	348	27	2
"	850621	Rh	296	850718	Rh	299	27	3
"	850621	Sk	312	850624	Sk	?	3	?
"	850621	Sk	371	870107	Sk	396	565	25
"	850718	Sk	349	850821	Sk	350	34	1
"	850821	Sk	364	860423	Kn	370	245	6
"	850825	Kn	305	870409	Sk	332	588	27
C. cristiceps	850618	Rh	360	860311	Rh	357	265	-3

Sk = Stielkop, Rh = Rheeders, Kn = Knoll; FL = fork length

DISCUSSION

Unfortunately the otoliths of the fish that had been at liberty the longest were not obtained for age validation. It is hoped however that future samples will yield positive results from fish marked with OTC. Good correlation was obtained between observed and predicted growth in *C. laticeps* even though the sample size was small. No growth was measured from the single recaptured *C. cristiceps*. The negative growth measured in two of the recaptured fish was disturbing but may have been caused in two ways. Firstly by inaccurate measuring or recording of the fish length during tagging and secondly as a result of changes in the length of the fish after death. These changes, a result of rigor mortis and later relaxation of the musculature can result in consistent, measurable differences in length after death (Ricker 1975; A. Penney, Sea Fisheries

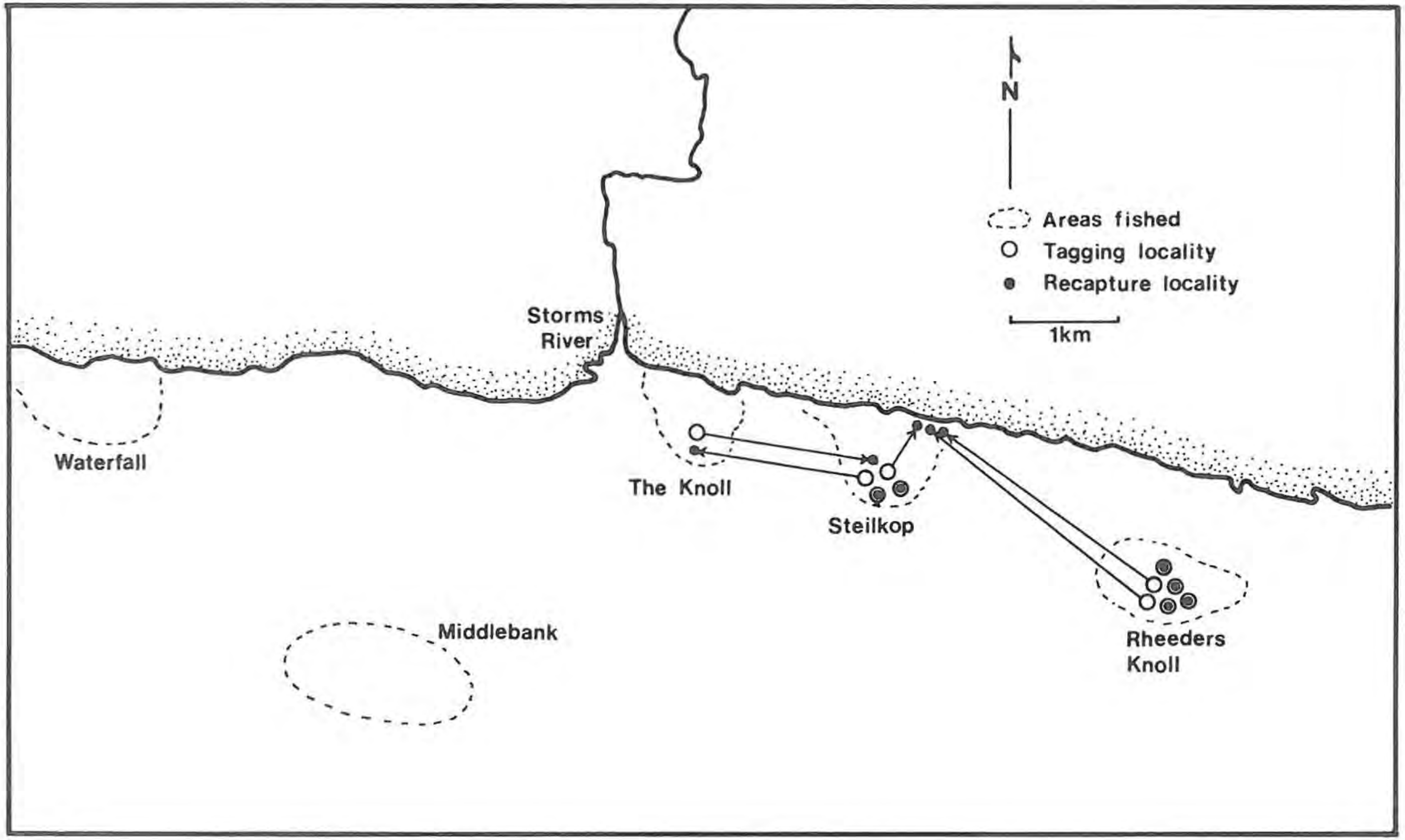


Figure 16. Map of the tagging and recapture localities in the Tsitsikamma Coastal National Park.

Research Institute Cape Town, pers. comm.).

A significant aspect of the study was that all recaptures were made very close to the area of tagging and no recaptures were reported from outside the Park. This would suggest that these species were highly resident, however before accepting this conclusion several limitations must be considered. Firstly, research fishing effort in the Park was limited to the area between the Knoll and Rheeders, consequently movements of fish outside this area but still within the Park would go undetected. Secondly, recaptures from areas outside the Park would come from anglers who are often suspicious of research activities (Randall 1961) and may resist reporting recaptures in spite of the reward offered. In addition poachers would not be expected to report recaptures. Thirdly, the percentage recaptures was low, 2.9% and 1.2% for C. laticeps and C. cristiceps respectively. This was indicative of the low numbers of fish tagged (Robson & Regier 1964), the probability of recapture decreasing proportionately with distance from the tagging locality.

Nevertheless, the recapture of most of the fish from the same reef as the one on which they were tagged together with further evidence presented below supports the hypothesis that adult C. laticeps and C. cristiceps are sedentary species that are resident within the Park.

3.3 - POPULATION STRUCTURE

INTRODUCTION

Part of the basic understanding of any fishery is a length frequency analysis of the fish caught. Together with some measure of effort this knowledge may provide a simple index of the abundance of the stock (Gulland 1975). This was the rationale behind an extensive programme to measure lengths of commercial and recreational linefish catches in South Africa (van der Elst & Adkin 1987) as well as a study on the Eastern Cape recreational ski-boat fishery (Smale & Buxton 1985), both of which are discussed in Chapter 4.1.

In this study length frequency data on *C. laticeps* and *C. cristiceps* were collected from ski-boat angler catches at localities between Mossel Bay and East London. Similar data were also collected in the Tsitsikamma area by research fishing. The objective of the analysis was to determine the range of sizes taken, the mean size of the catch and the size at recruitment to the fishery. Differences in these characteristics between the Tsitsikamma and the exploited areas were compared to determine whether they represented natural variation over geographical range or were due to exploitation.

METHODS

Most of the data were collected from weekend catches of ski-boaters operating from launch sites in the Port Elizabeth area including the Port Elizabeth Deep Sea Angling Club, Noordhoek Ski-Boat Club, Sardinia Bay Ski-Boat Club as well as boats operating from the Swartkops river mouth and Red Windmill (see Fig. 5). In addition periodic sampling was done at Mossel Bay, Buffalo Bay, Knysna, Jefferies Bay, East London, Gonubie and Kei river mouth (see Fig. 2).

The catch of each species was quantified by measuring either the caudal, fork or total length. Every effort was made to eliminate bias by working each boat in turn as it landed, and whenever possible all catches were monitored. However, when large numbers of boats were active on a particular day, only a sub-sample of the boats were worked.

In the Tsitsikamma all samples were obtained from research fishing by the Port Elizabeth Museum and Parks Board staff. Although techniques and hook sizes varied slightly between areas they were generally comparable and were not considered to bias the samples.

RESULTS

The overall length frequency distributions of all fish sampled between Mossel Bay and East London excluding those caught in the Tsitsikamma

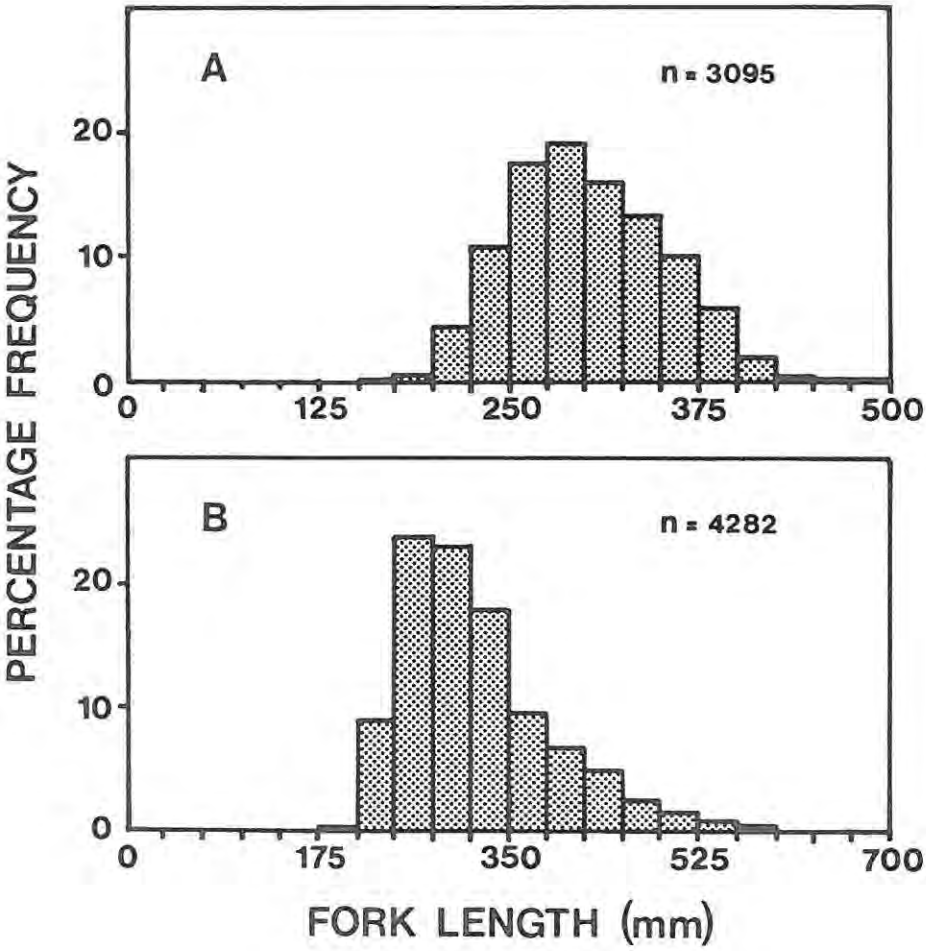


Figure 17. Combined length frequency analysis of all *Chrysoblephus laticeps* (A) and *C. cristiceps* (B) sampled at exploited sites between Mossel Bay and East London from 1978 to 1986.

area, are shown in Figure 17. *C. laticeps* ranged in size from 172mm to 476mm, had a mean length of 300mm with a mode centred on the 275-300mm size class and the size at recruitment to the fishery was 254mm fork length. Recruitment was assumed to be knife-edged and the method of calculation is shown in Appendix 2. Limitations of this assumption are discussed in Chapter 3.4. The mean length of *C. cristiceps* was 320mm with a mode centred on the 245mm-286mm size class. The fish ranged in length between 188mm and 610mm and size at recruitment to the fishery was 242mm. The structure of both of these exploited populations was unimodal and both had approximately the same size at recruitment to the fishery. They differed in the range of vulnerable lengths however, because *C. cristiceps* attained a larger maximum size than *C. laticeps*.

Length frequency distributions of *C. laticeps* from individual areas are shown in Figure 18 and size at recruitment to the fishery, mean size and range of lengths caught in each area are summarised in Table 11.

TABLE 11. Population structure of *C. laticeps* caught between Mossel Bay and Woody Cape.

AREA	SAMPLE PERIOD	MEAN SIZE $\bar{x} \pm s$	RANGE	SIZE AT RECRUITMENT	n
Woody Cape-St Croix Is.	1978-86	318 ± 45	192-350	278	741
St Croix-Cape Recife	1978-86	308 ± 45	217-454	260	292
Noorhoek-Sardinia Bay	1979-85	304 ± 48	175-449	258	1086
Jeffreys Bay	1986	279 ± 51	203-450	220	113
Knysna-Mossel Bay	1980-83	270 ± 47	172-398	212	334
Tsitsikamma	1980-86	317 ± 44	130-457	278	1077

The mean sizes of the fish caught in the exploited areas were significantly different (ANOVA $F=66.72$, $P<0.01$, $df=5,3642$) and increased along the coast between Mossel Bay (270±47mm) and Woody Cape (318±45mm). In the Tsitsikamma area the mean size of the catch was 317mm fork length. The proportion of large fish in the catch was also correlated with area, more of the larger size classes being caught in the Woody Cape and Tsitsikamma areas. Size at recruitment was well correlated with mean size, also increasing between Mossel Bay and Woody Cape.

A similar analysis for *C. cristiceps* is shown in Figure 19 and summarised in Table 12. Again a trend in the mean size of the catch in different areas along the coast was recorded. The highest value was recorded in the East London area (421mm), followed by St Croix to Woody Cape (326mm). In the exploited areas between St Croix and Mossel Bay mean catch size was lowest (284mm). Size at recruitment followed this trend. Mean size and size at recruitment of the fish caught in the

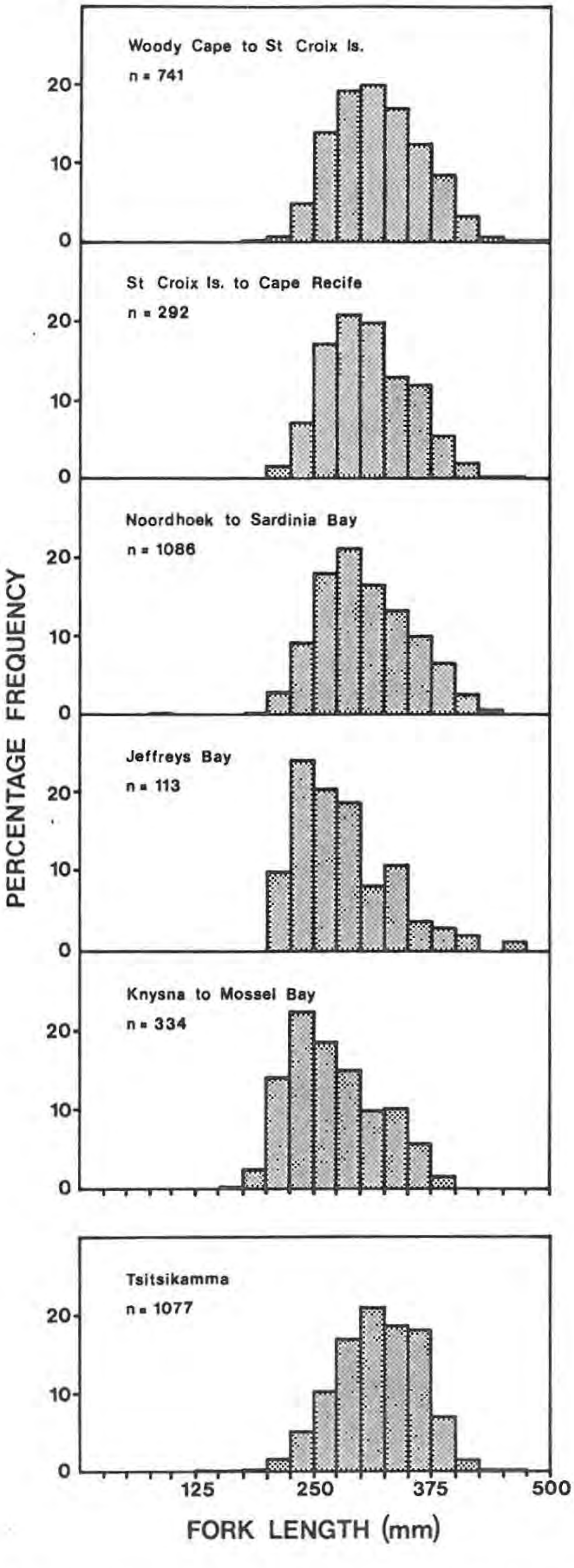


Figure 18. Length frequency analysis of Chrysoblephus laticeps sampled between Woody Cape and Mossel Bay. See Table 11 for the sampling period.

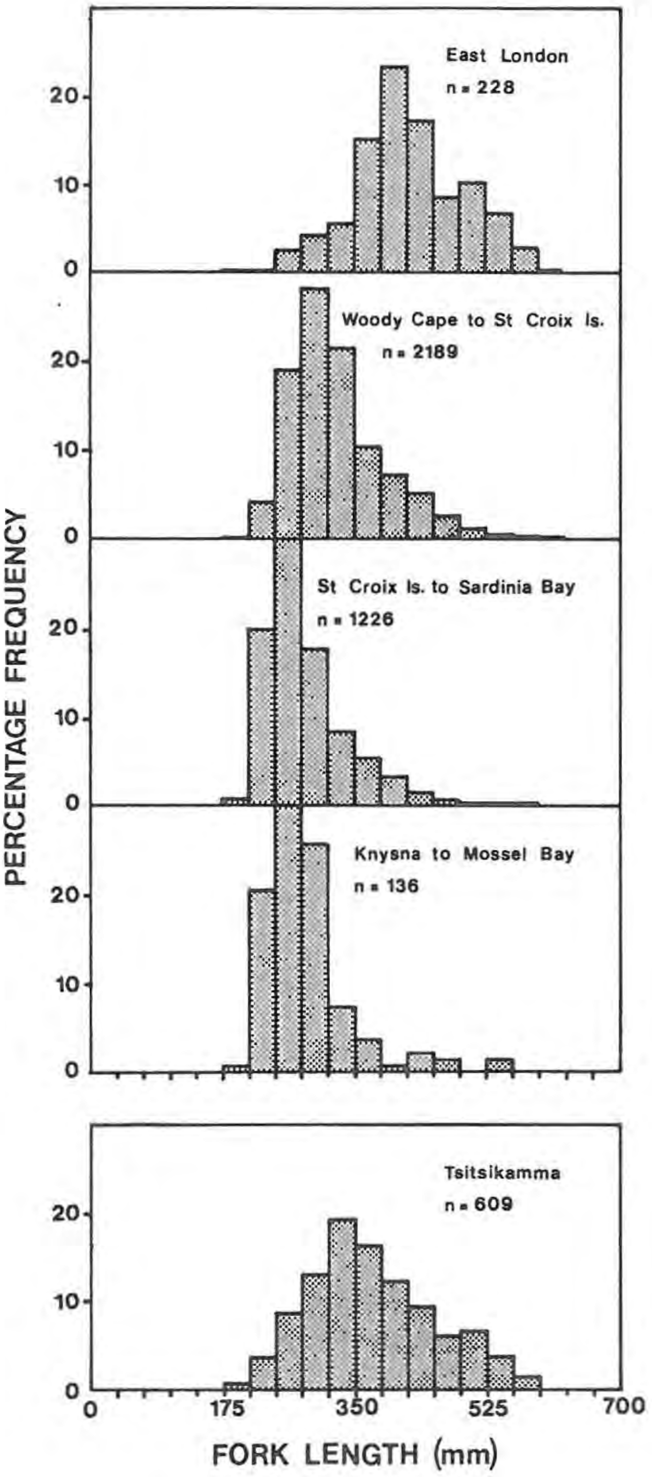


Figure 19. Length frequency analysis of Chrysoblephus cristiceps sampled between East London and Mossel Bay. See Table 11 for the sampling period.

Tsitsikamma were 370mm and 291mm respectively.

TABLE 12. Population structure of C. cristiceps caught between Mossel Bay and East London.

AREA	SAMPLE PERIOD	MEAN SIZE x ± s	RANGE	SIZE AT RECRUITMENT	n
East London	1984-86	421 ± 75	188-610	364	228
Woody Cape-St Croix Is.	1978-86	326 ± 63	209-602	266	2189
St Croix-Sardinia Bay	1978-86	284 ± 57	190-577	235	1226
Knysna-Mossel Bay	1980-83	284 ± 58	204-557	235	136
Tsitsikamma	1980-86	370 ± 83	200-586	291	609

Annual length frequency analysis of C. laticeps for three areas, Woody Cape to Cape Recife, Noordhoek to Sardinia Bay and Tsitsikamma are summarised in Figures 20-22. Analysis of variance showed that the mean size of the catch between years was not significantly different in the Tsitsikamma and Noordhoek areas (F=1.87, P<0.05, df=6,4136 & F=1.01, P<0.05, df=3,934 respectively). In the Port Elizabeth area mean size of catch was not different between 1978-1981 (F=1.88, P<0.05, df=3,1083) but inclusion of data between 1982-1986 produced a significant difference due to an increase in the mean size over these years (F=8.98, P<0.05, df=5,2151).

DISCUSSION

In a line-fishery the size of fish caught is thought to be a function of hook size but the relationship is not simple because for every hook size there are a range of fish sizes that may be caught. Effects such as the straightening of small hooks by big fish and differences in the expertise of the fishermen may confound the relationship. Studies on the influence of hook sizes on the size composition of the catch have produced conflicting evidence. A direct relationship between hook size and mean size of fish caught was found for Pachymetopon blochii (A. Pulfrich, University of Cape Town, pers. comm.) but not for C. puniceus in which the number of fish caught, not the size caught, appeared to be related to hook size (P. Garratt, Oceanographic Research Institute Durban, pers. comm.). This relationship has also been studied in a number of other species including Petrus rupestris, C. laticeps, Pachymetopon aeneum, Boopsoidea inornata and Spondyliosoma emarginatum (B. Bennett, University of Cape Town, pers. comm.), in which there appeared to be an optimum hook size that was related to the gape of the jaw of each species.

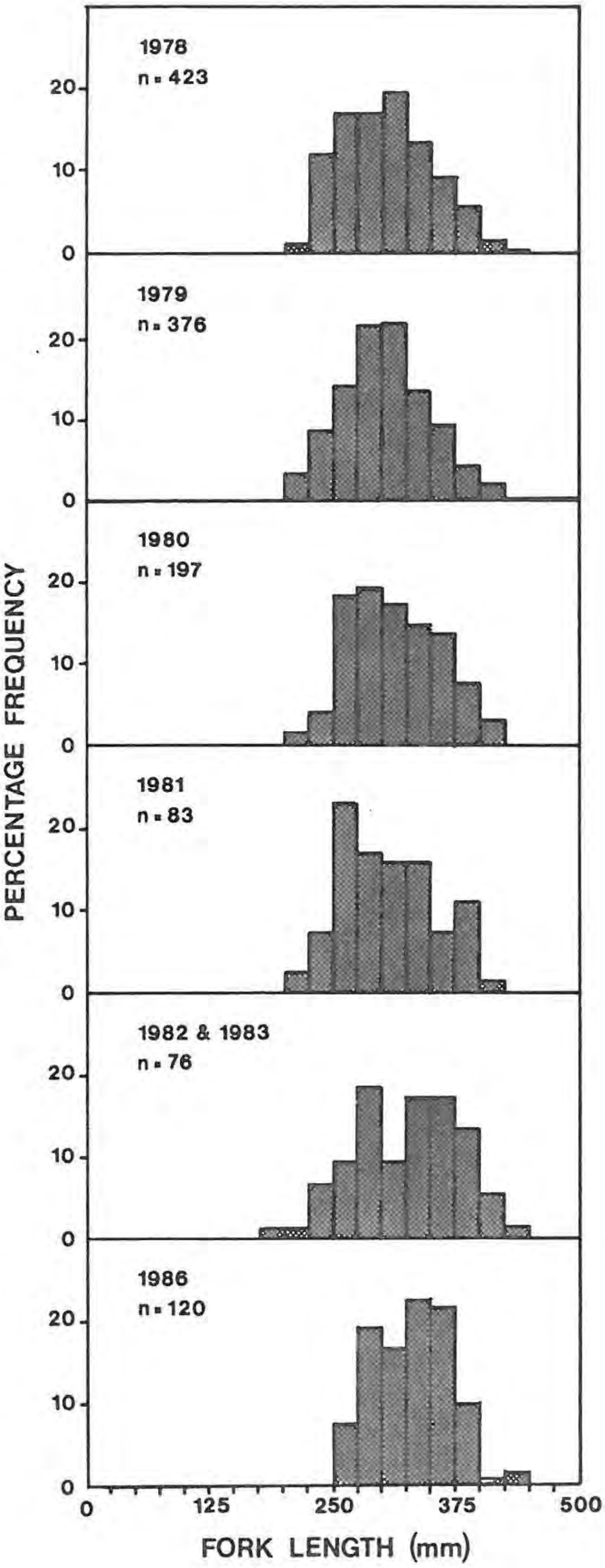


Figure 20. Annual length frequency analysis of <u>Chrysoblephus laticeps</u> sampled in the area between Woody Cape and Cape Recife.

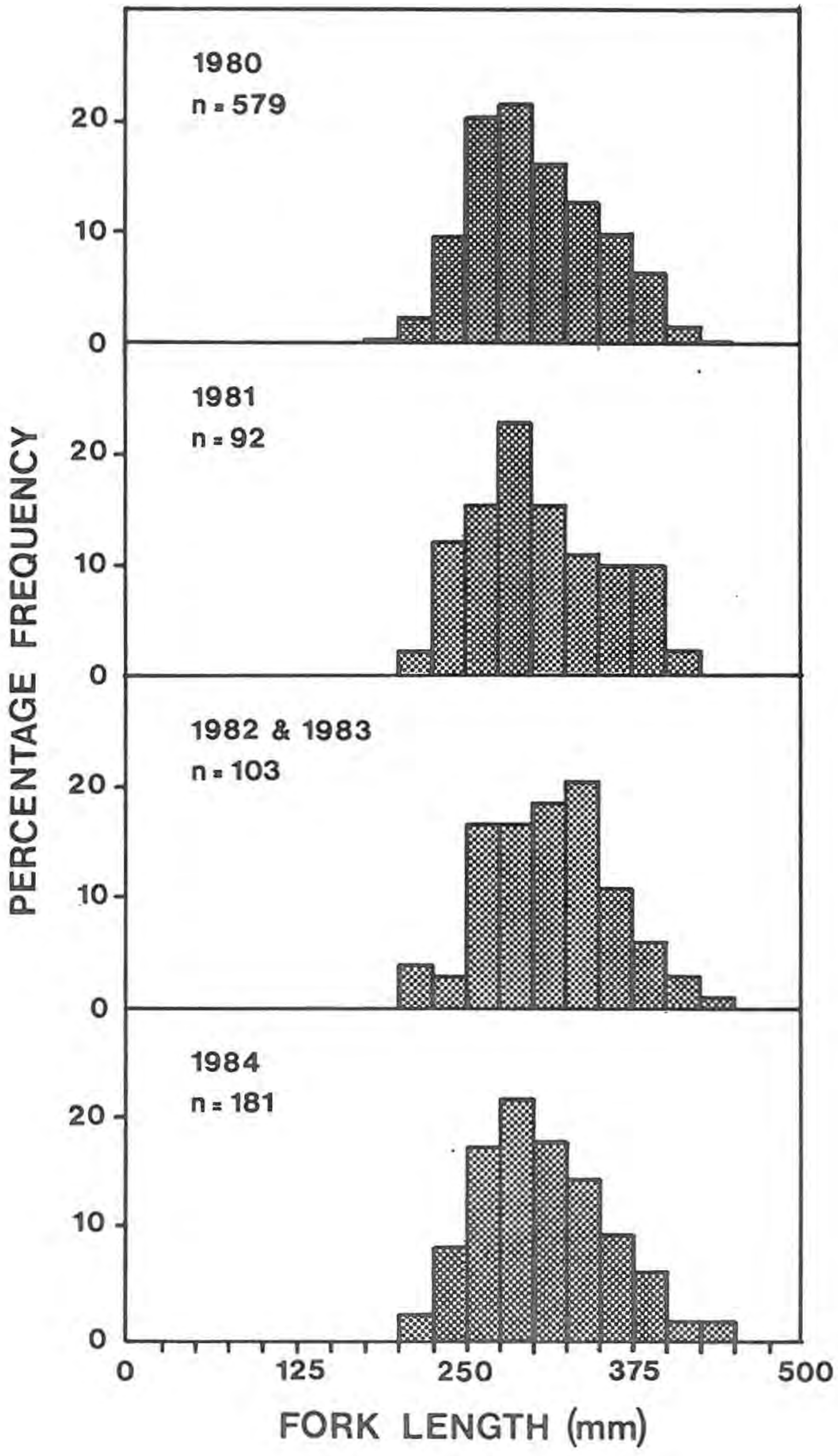


Figure 21. Annual length frequency analysis of <u>Chrysoblephus laticeps</u> sampled between Noordhoek and Sardinia Bay.

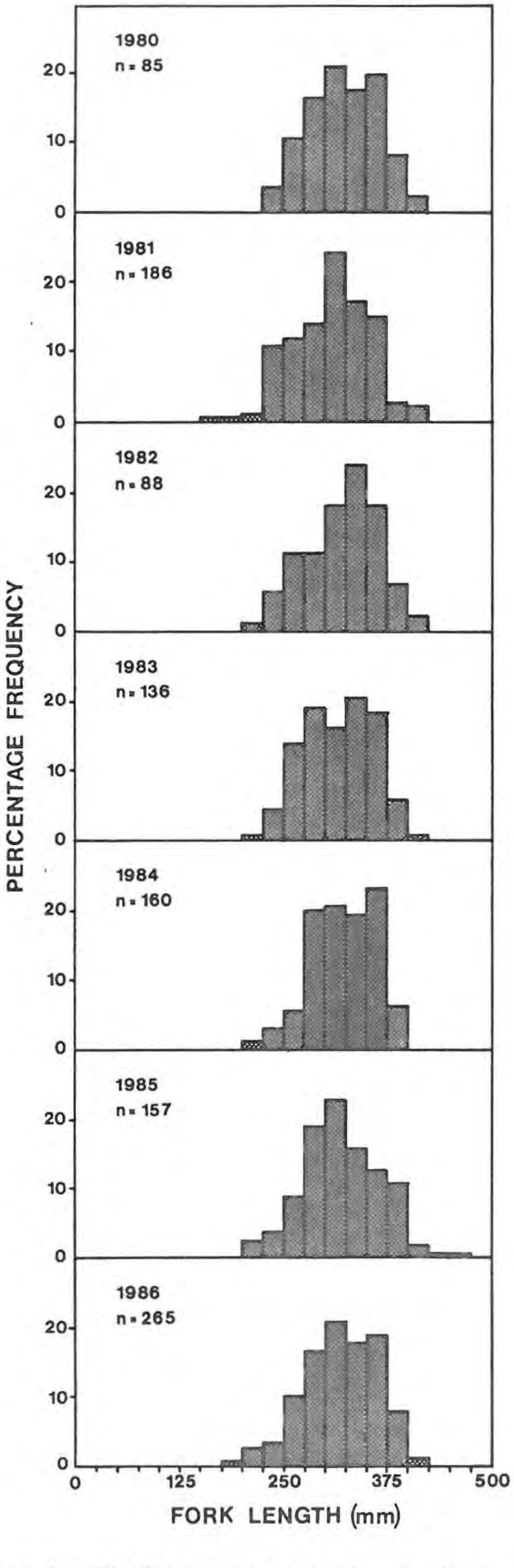


Figure 22. Annual length frequency analysis of <u>Chrysoblephus laticeps</u> sampled in Tsitsikamma.

Until 1985 minimum size restrictions were 200mm and 230mm total length for C. laticeps and C. cristiceps respectively. In 1985 these sizes were changed and a common minimum size restriction of 250mm total length was introduced for both species. Size at recruitment to the line-fishery was thought to be a combination of these restrictions and the motivations of individual fishermen, the choice of hook size being dependent on both factors. Trophy hunters would choose larger hooks than fishermen whose aim it was to catch as many fish as possible and for these reasons recruitment was not knife-edged. The theoretical size at recruitment was dependent on the range of hook sizes used in the fishery, but the actual size at recruitment based on the length frequency of landed fish was governed more by the minimum legal size limit of each species. Smaller size classes were presumably returned to the sea but whether these fish survived or not is crucial to the dynamics of the fishery and will be discussed below.

Comparing the length frequencies it was clear that both the size at recruitment and the proportion of large fish caught were different in the areas studied. Variation in the size at recruitment appeared to contradict the assumption that it was governed by legislation and two explanations were possible. Firstly, that the fishermen were selecting larger fish in some areas, either by targeting with different techniques (e.g. large hooks) or because they were for some reason returning smaller fish to the sea. Secondly, that the population structure in different areas was not the same.

Prior to January 1986 there were no restrictions on the number of fish taken by each fisherman and the size frequency of the catch, above the size at which fish were fully recruited to the fishery, was expected to be a function of the size frequency of the population. The first explanation was considered unlikely because no evidence was obtained to suggest that techniques varied along the coast. Particularly with respect to hook sizes, the range used within areas would obscure differences between areas. While catches of large fish were generally considered to be more attractive to most recreational fishermen, personal experience on fishing trips indicated that all fish above the legal size would be kept if caught.

Considering the second alternative it is logical to argue that the probability of catching large fish is greater in a pristine area than in one that has been extensively fished, because large fish are selectively removed by the linefishery and both species have a slow growth rate. The results of this study showed a direct relationship between mean size of the catch and recruitment size, indicating that as the population was skewed by the removal of the larger size classes so size at recruitment decreased until it approached the minimum legal limit. The greater proportion of large fish in catches taken from the Tsitsikamma for example, was considered a result of it being an unexploited area and suggests that mean size of catch is probably related to the level of exploitation.

This probability would also increase if larger fish were more successful in competing for a bait. Personal underwater observations support this idea. When a bait was lowered it was immediately seen to be swamped by small fish such as *B. inornata*, *S. emarginatum* and *P. aeneum* which were quickly chased away by the arrival of any large species such as *Petrus rupestris*, *C. laticeps* and *C. cristiceps*. Larger individuals of each species also chased smaller ones from the bait.

To summarise, the results presented in this study suggested that area differences between the mean size of the catch as well as the size at recruitment into the fishery were the result of different levels of exploitation. The greater vulnerability of larger fish, a consequence of size selectivity, legislation governing the fishery and longevity in the species studied, has resulted in a skewing of the population structure towards the smaller size classes. This has skewed the sex ratio towards the females because both species are protogynous hermaphrodites. In a comparable study of the Natal line-fishery, Garratt (1985b) also found a shift in the mean size and size at recruitment of *C. puniceus* when comparing Mozambique and Natal catches. He attributed this to the higher level of exploitation in Natal. Garratt suggested that this could have serious consequences for the fishery if the size at sex reversal was genetically fixed as this could reduce the breeding potential through a lack of males in the population. The effects of exploitation on the sex ratio and size at sex reversal in *C. laticeps* and *C. cristiceps* are discussed in Chapter 4.

3.4 - AGE, GROWTH AND MORTALITY

INTRODUCTION

Chrysoblephus laticeps and C. cristiceps are important components of the recreational and commercial line fisheries on the Cape south coast, yet nothing is known of their population characteristics. Smale & Buxton (1985) showed that these species were among the three most important reef species in the recreational fishery operating in the Port Elizabeth area. Unpublished commercial landings of C. laticeps and C. cristiceps in 1986 were 90 620kg and 14 500kg respectively, representing 9.7 and 1.5 percent of the total landed weight of deep reef species in the Southern Cape linefishery (A.J. Penney, Sea Fisheries Research Institute, Cape Town pers. comm.).

The objective of this study was to determine basic population parameters for unexploited stocks of C. laticeps and C. cristiceps in the Tsitsikamma Coastal National Park, which would then provide a baseline for the study of exploited populations between Mossel Bay and East London. Parameters included observed and theoretical lengths-at-age, age and size structure of the different populations, lengths at first capture and the range of ages present in the fishery, as well as both natural and fishing mortalities.

The use of analytical assessments in providing advice for the management of fish stocks requires data on the age structure of the stocks, and underlies the need for this study.

METHODS

Collection and preparation of otoliths

Data used in this section came from two sources, the recreational ski-boat fishery operating in the Port Elizabeth area and research fishing in the Tsitsikamma Park. Small specimens were obtained by spearfishing in both areas because the 4/0 to 6/0 hook sizes used in the fishery tended to exclude fish of below 200mm fork length from the catch.

Various structures were examined as to their suitability for determining the age of both species. Scales showed no identifiable patterns and in the larger fish showed signs of erosion and regrowth. Spines and rays were sectioned but also showed no clear growth patterns. Vertebrae and opercular bones were not considered because the fish had to be returned to the fishermen undamaged. Otoliths on the other hand were easily removed by breaking away the lower section of the skull, and showed a distinct growth pattern which was easily interpreted (Fig. 23).

A number of techniques were used in an attempt to enhance the readability of otoliths. These included examining them whole, longitudinally and transversely sectioned, burnt and unburnt, stained with ninhydrin (Schneppenheim & Freytag 1980) or methyl violet-B (Albrechtsen 1968) as well as emersing the whole otolith in various liquids including water, alcohol, saline, glycerol and xylene. Although whole otoliths of fish below 250mm were readable when viewed in water under transmitted light, best results were obtained by sectioning.

Both otoliths were removed, cleaned in fresh water and stored dry in manila envelopes. The left sagitta was burned over a low intensity spirit flame until it turned pale brown and care was taken not to char the otolith as this tended to obscure the internal structure, particularly at the margin. The otolith was then mounted in clear casting resin and sectioned to a thickness of 0.5mm using a double-bladed saw (Rauck 1976). Each section was mounted on a clear glass slide and viewed with a low power dissecting microscope under transmitted and reflected light.

The otoliths were read at least twice, approximately three weeks apart. If the readings did not agree the otolith was read a third time and two coincident readings accepted as the best estimate of age. If the three readings differed only slightly the mid reading was accepted but if they differed by more than three years the otolith was rejected.

Terminology

Three otoliths, the sagitta, astericus and lapillus are found in the auditory bulla of fishes (Hecht 1978). Of these the sagitta is usually used for ageing because it is the largest except in fishes of the order Cypriniformes and Siluriformes (Hecht 1979). They are composed of needle shaped aragonite crystals radiating in three dimensions from a central nucleus through an organic matrix which is not uniformly distributed throughout the whole otolith (Degens, Deuser & Haedrich 1969).

TABLE 13. Terminology of seasonal growth zones as used by different authors.

AUTHOR	TAXON	AREA	FAST GROWTH	SLOW GROWTH
Dannevig 1956	Gadus	Norway	Transparent	Opaque
Coetzee & Baird 1981	Cheimerius	S. Africa	Opaque	Hyaline
Irie 1960	Lateolabrax	Sea of Sato	Translucent	Opaque
Mugiya 1964	Salmo Kareius	Hokkaido	Opaque	Translucent
Pannella 1971	Merluccius	W. Atlantic	Fast	Slow
Buxton & Clarke 1986	Pachymetopon	S. Africa	Light	Dark

Interpretation of age is based on a regular pattern in the deposition of organic and inorganic material which forms recognisable zones in the otolith that may be related to time. Despite a long history of age determination, dating back to 1759 (Ricker 1975), there is still considerable confusion surrounding the terms used to describe these zones (Panella 1974; Buxton & Clarke 1986; ICSEAF 1986). The main source of this arises in part out of the use of a number of adjectives to describe the optical appearance of the growth zones, but also because the processes underlying zone formation are not fully understood. Table 13 lists examples of the inconsistent use of terms by different workers.

The appearance of the growth zones under different lighting conditions and the failure by many authors to describe clearly the technique used when viewing such tissue contribute to the problem. Under incident light a reflective zone (opaque) will appear white or lighter than zones absorbing light (hyaline), which are translucent and appear darker or black when viewed over a dark background. These optical characteristics are reversed under transmitted light (Fig. 23)

Casselman (1974) showed that the hyaline ring in pike cleithra contained more calcium than the opaque ring and Mugiya (1965) found that the opaque ring contained more protein than the hyaline ring. Differences between the relative proportions of protein in the rings become visible when the otolith is heated (Chugunova 1959). Dannevig (1956) showed that the opaque zone in cod otoliths turned black when charred and attributed this to the organic content. Christensen (1964) produced the same result but was uncertain about the locality of the proteinaceous material, suggesting that it was between the opaque and hyaline zones. She states however that "The fact that the otolith stops growing, or at least that its growth rate slows down considerably for several months each year, and the fact that the black ring is formed during these very months, makes it reasonable to regard the growth of the otolith as growth of inorganic matter which is interrupted by formation of membranes of organic matter" (Christensen 1964, p. 78).

Blacker (1969,1974) disputed Dannevig's interpretation stating that only the hyaline zone burns in cod otoliths. Photographic evidence to support this is however unconvincing (Blacker 1974, fig. 5&6), and he himself states that "If most of the organic matter really is in the opaque zones, then there must be a reason why the smaller amount of protein in the hyaline zones burns in preference to that in the opaque zones" (Blacker 1974, p. 76).

Inconsistencies also exist over which of the two zones represents the fast growth period (Table 13). Reviewing the literature on the microstructure of otoliths, Campana & Neilson (1985) present a considerable body of evidence to suggest that growth in otoliths occurs through differential deposition of calcium carbonate and protein during an endogenous circadian rhythm. Discontinuous growth is predominantly proteinaceous with opaque optical properties, while incremental growth is translucent and mostly inorganic.

South African studies on the growth of fish appear to be consistent with the opposite view, that the translucent zone (hyaline) is a slow growth period. This apparently originated from the work of Botha (1971) who stated that the narrow hyaline zones of hake burned black and represented slow growth. He quoted Blacker's (1969) work in support of this observation. Subsequent studies appear to have agreed with this interpretation (Geldenhuys 1973,1978; Nepgen 1977; Hecht & Baird 1977; Coetzee & Baird 1981b; Rossouw 1984; ICSEAF 1986). It is important to note however, that this interpretation does not invalidate the estimate of age in these studies as long as zone formation can be related to a time period.

Almost certainly this interpretation has resulted from the optical appearance of whole otoliths and to understand this apparent contradiction it is necessary to consider how growth zones are formed. Growth varies with temperature, food availability, reproductive output and any other physiological condition that lowers surplus energy (Newell 1977). During periods of slow growth the daily incremental phase will be less and the relative proportion of protein high (Campana & Neilson 1985). Because the discontinuous growth is opaque, increased incremental growth will result in decreased opacity.

These relationships are illustrated in Figures 23 and 24. In unburnt transverse sections the incremental growth is translucent (wide zones) and the discontinous growth appears as narrow white bands (Fig. 24b & d). The same relationship is also apparent in the whole otolith of small fish (Fig 24a) but not in larger whole otoliths (Fig 24c) because transparency is also a function of otolith thickness. Because the relative amount of protein in the incremental phase varies gradually, the incremental zone will only appear translucent when growth is maximal. Burning the otolith showed that the opaque zones turned brown (Fig 23d), a result consistent with the observations of Dannevig (1956), Christensen (1964) and Campana & Neilsen (1985).

Data analysis

To calculate length-weight and length conversion relationships fish were sub-sampled over a range of lengths. Length was expressed as a power function of mass and length relationships were described by least squares linear regression.

A Schnute analysis of length-at-age (Schnute 1981) was used to evaluate which of the available growth models would best fit the data. This showed that at the five percent level a generalised von Bertalanffy growth model could be used to describe the C. laticeps data but that the C. cristiceps data approximated region 3, an unbounded curve. This result most probably resulted from the higher variability in the age

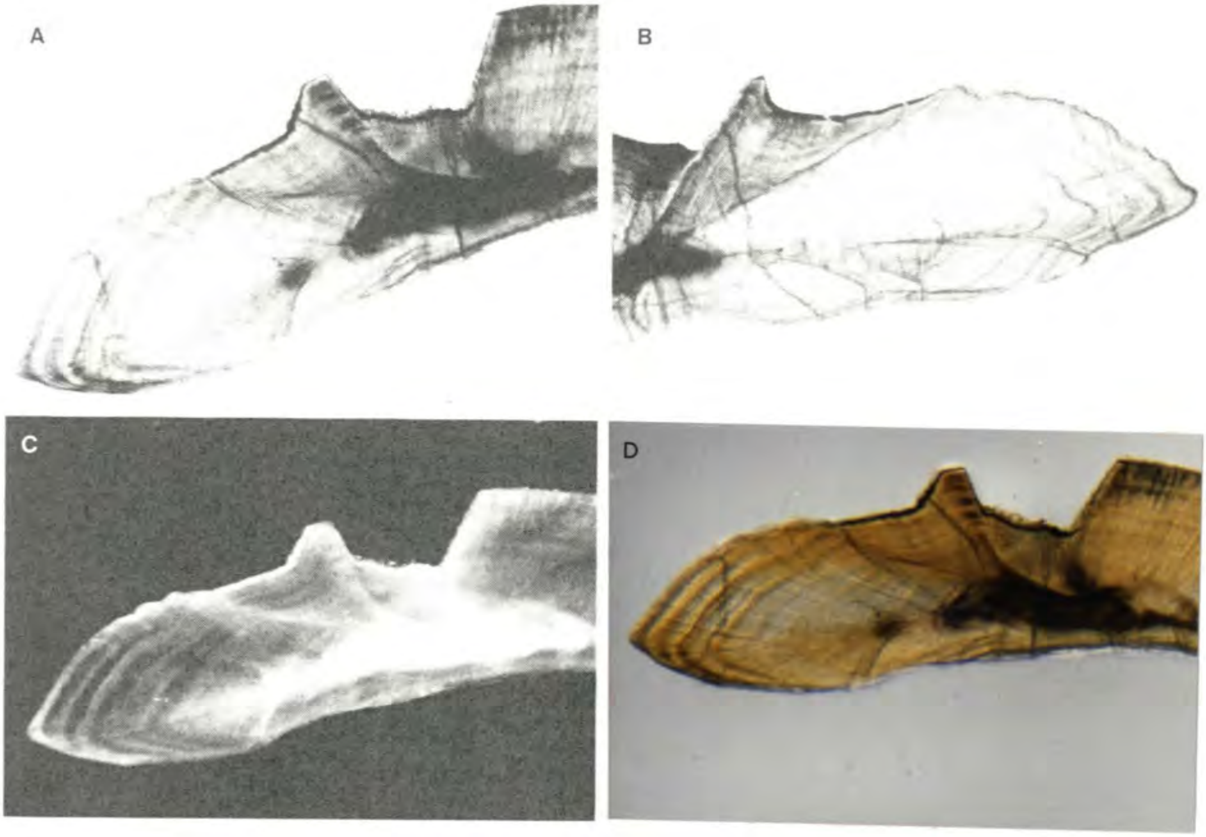


Figure 23. Otolith sections from Chrysoblephus laticeps and C. cristiceps viewed under different lighting conditions. (A). Otoliths from C. laticeps and (B) C. cristiceps under transmitted light. (C). The same otolith pictured in (A) but viewed under transmitted light and (D) after burning. Note that the opaque zones burned more intensely than the translucent zones due to higher relative amounts of protein.

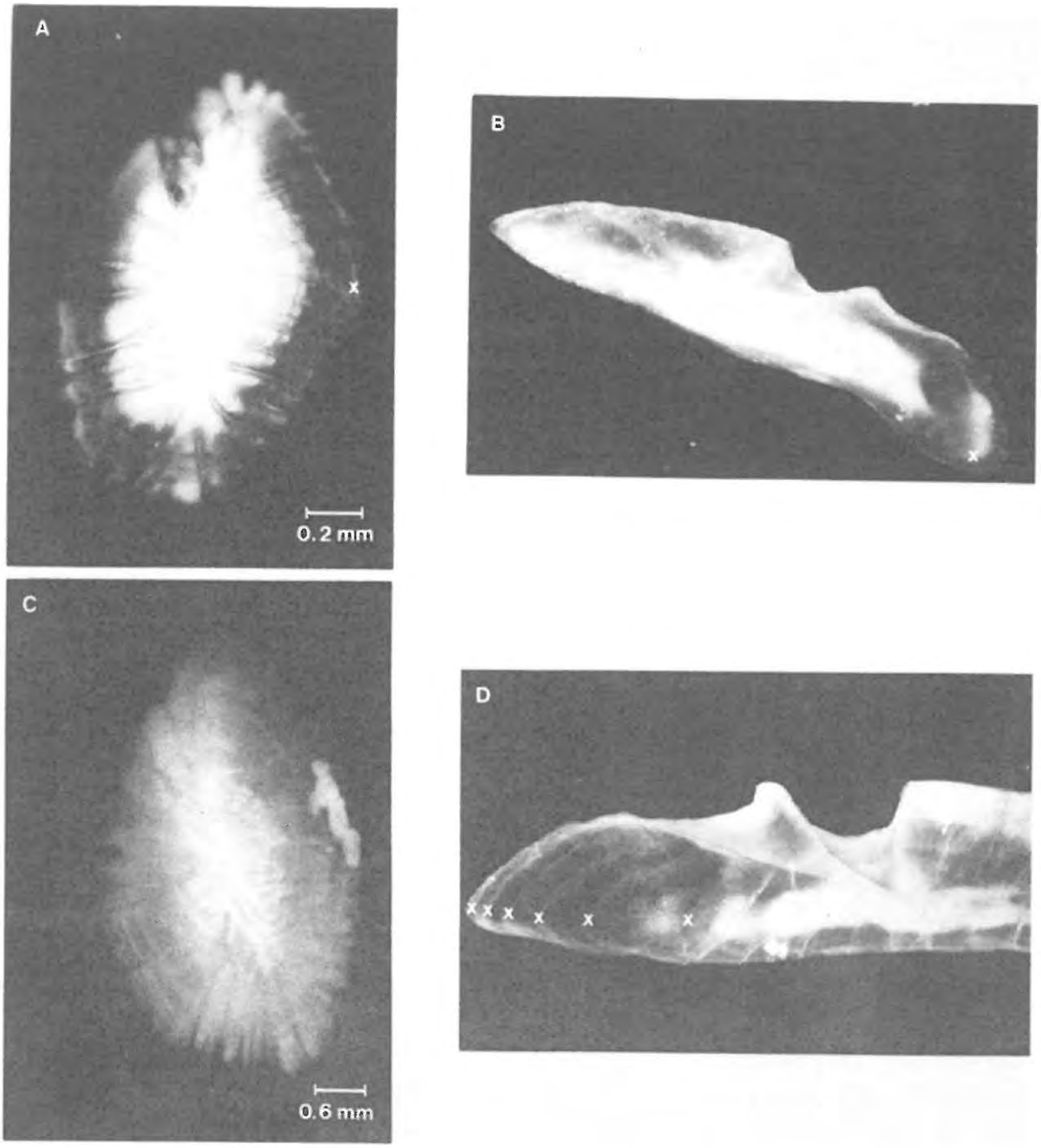


Figure 24. Photomicrographs of the otoliths of *Chrysoblephus laticeps* viewed in reflected light. Whole (A) and sectioned (B) otoliths from a one year old individual showing a single opaque annulus (x) near the margin of the otolith. Note the translucent appearance of the whole otolith. Whole (C) and sectioned (D) otoliths from a six year old individual. Note the overall opacity of the whole otolith.

estimates of the older fish and for this reason was ignored in favour of the von Bertalanffy model. A summary of the Schnute parameter estimates is given in Table 14.

The von Bertalanffy growth equation was used to describe growth as a function of age:

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

where L_t was fish length at age t and L_∞, K and t_0 were co-efficients characteristic of the stock in question. Although the von Bertalanffy growth model has been criticised (Knight 1968; Bayley 1977) it was chosen over other models because observed length-at-age suggested asymptotic growth and because it can readily be incorporated into stock assessment models (Vaughan & Kanciruk 1982).

The method of fitting the von Bertalanffy equation depends on the variance of the data (Hughes 1986) and in both species studied the relative error model was used because variance increased with age. Parameter estimates were obtained by non-linear minimization of the function:

$$SS_R = \sum_{\alpha=1}^{N}\left[(L^\alpha(t)-L_{VB}(t))/L_{VB}(t)\right]^2=\sum_{\alpha=1}^{N}(E_\alpha)^2 \qquad ..\text{Hughes(1986)}$$

where L(t) is the observed length of fish α at age t and $\alpha = 1...N$, N being the total number of fish in the sample. $L_{VB}(t)$ is the predicted length at age t according to the von Bertalanffy equation. This assumes that the relative error E_α is normally distributed.

Total annual mortality estimates were obtained from catch curves by plotting the natural logarithm of age frequency against age. The slope of a straight line fitted to points greater than the age of full recruitment to the fishery (t_R) provided an estimate of instantaneous total mortality (Z). Before constructing catch curves the age-length key of the aged subsample was normalised for each length class and combined with the total length frequency distribution of the whole catch to give the full catch age frequency distribution (Appendix 1).

Natural mortality (M) was obtained from the relationship (Pauly 1980):

$$\log M = -0.0066-0.279 \log L_\infty+0.6543 \log K+0.4634 \log T$$

where T is the mean annual water temperature (°C) of the species' environment and L_∞ and K are von Bertalanffy parameters. Fishing mortality (F) was obtained by substitution in the equation:

$$F = Z - M$$

TABLE 14. Schnute growth parameters for *C. laticeps* and *C. cristiceps*.

C. laticeps

AREA		Y(1)	Y(2)	a	b
Tsitsikamma		71.82	383.23	0.0884	1.5933
	s.e.	1.82	2.69	0.0162	0.1344
	c.v.	0.03	0.01	0.1828	0.0843
Noordhoek		196.60	429.31	-0.0059	2.242
	s.e.	3.46	11.22	0.1148	0.780
	c.v.	0.02	0.03	-19.4400	0.780

C. cristiceps

AREA		Y(1)	Y(2)	a	b
Tsitsikamma		186.99	512.24	0.0049	2.1177
	s.e.	3.82	3.26	0.0162	0.1869
	c.v.	0.02	0.01	3.2840	0.0882
Noordhoek		158.71	436.89	0.0171	1.4956
	s.e.	2.59	5.90	0.0389	0.3657
	c.v.	0.02	0.01	2.2770	0.2445

TABLE 15. Length-weight and length conversion relationships for *C. laticeps* and *C. cristiceps*.

C. laticeps

n = 242 $\quad Wt(g) = 0.000012\ FL(mm)^{3.154}$ $\quad r^2 = 0.99$
n = 104 $\quad TL(mm) = 1.1144\ FL(mm) - 2.855$ $\quad r^2 = 0.99$
n = 104 $\quad FL(mm) = 26.9071\ OL\ (mm) - 22.161$ $\quad r^2 = 0.96$

C. cristiceps

n = 159 $\quad Wt(g) = 0.000013\ FL(mm)^{3.151}$ $\quad r^2 = 0.99$
n = 57 $\quad TL(mm) = 1.1432\ FL\ (mm) - 3.6024$ $\quad r^2 = 0.99$
n = 41 $\quad FL(mm) = 30.3231\ OL\ (mm) - 68.3743$ $\quad r^2 = 0.95$

RESULTS

Morphometrics

Morphometric analysis of length and weight as well as the relationship between otolith diameter (measured on the long axis) and fork length are given in Table 15.

Validation of annuli

Validation of the zones as annuli was determined by marginal increment analysis (Manooch 1982). This was done by examining the monthly proportion of hyaline zones on the otolith margins for C. laticeps (Fig. 25) and C. cristiceps (Fig. 26). The results showed that one hyaline zone was formed each year in both species, in C. laticeps from April to August and in C. cristiceps from March to August. In both cases this coincided with cooler winter temperatures and was just after the breeding season.

For C. laticeps this conclusion was substantiated by monthly length frequency analysis of juvenile fish speared in shallow water (<10m) at Coke Tin Reef and Phil's Reef in Algoa Bay. Samples were considered random because every fish seen on a particular dive was shot. Figure 27 shows the modal progression of length over a period of 12 months together with the appearance of the otolith at different times of the year. Extrapolating backwards it was clear that the fish hatched sometime between November and January, well within the breeding season of the species. The first hyaline zone was observed to form 4-6 months after spawning at a length between 60 and 75mm. These results compared very well with the observed growth rate of C. laticeps in captivity (Brownell 1979), who recorded the length of an eight month old specimen as 66mm total length. This is very close to the predicted total length of 65-82mm (60-75mm fork length), for an eight month old fish sampled at Coke Tin Reef.

Age determination

A total of 471 C. laticeps otoliths were read of which 5.5% were rejected as unreadable. Of those remaining 132 were from fish sampled at Noordhoek and 313 from fish sampled in the Tsitsikamma. Separate observed length-at-age plots for the two areas are shown in Figures 28 and 29, and estimates of von Bertalanffy growth parameters are summarised in Table 16.

There were considerable differences in the von Bertalanffy parameter estimates between Noordhoek and Tsitsikamma but the calculated lengths-at-age over the range 3-14 years (area of most data points) were not significantly different (Table 17).

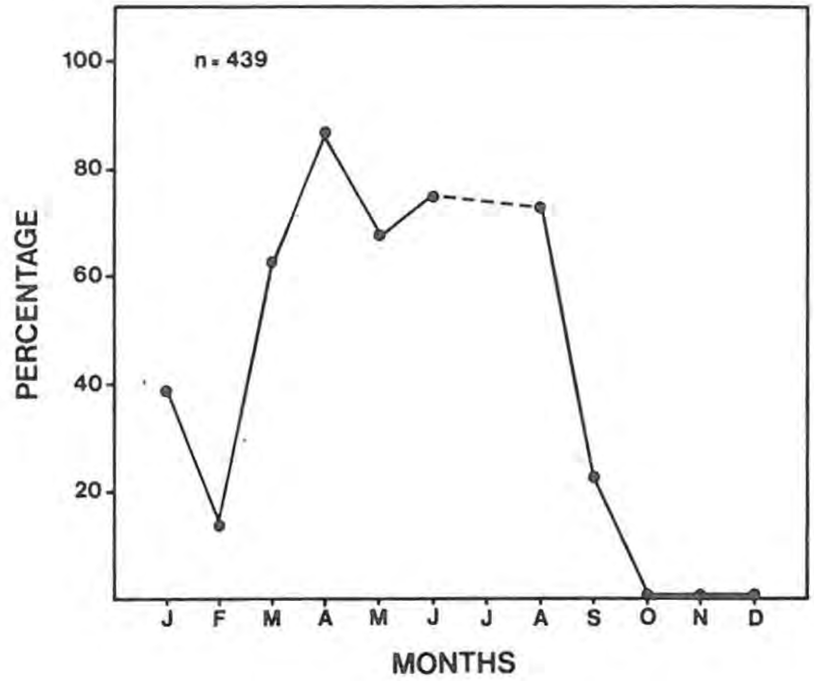


Figure 25. Marginal increment analysis of hyaline zones in the otoliths of Chrysoblephus laticeps sampled in the Tsitsikamma and Noordhoek areas between 1983 and 1986.

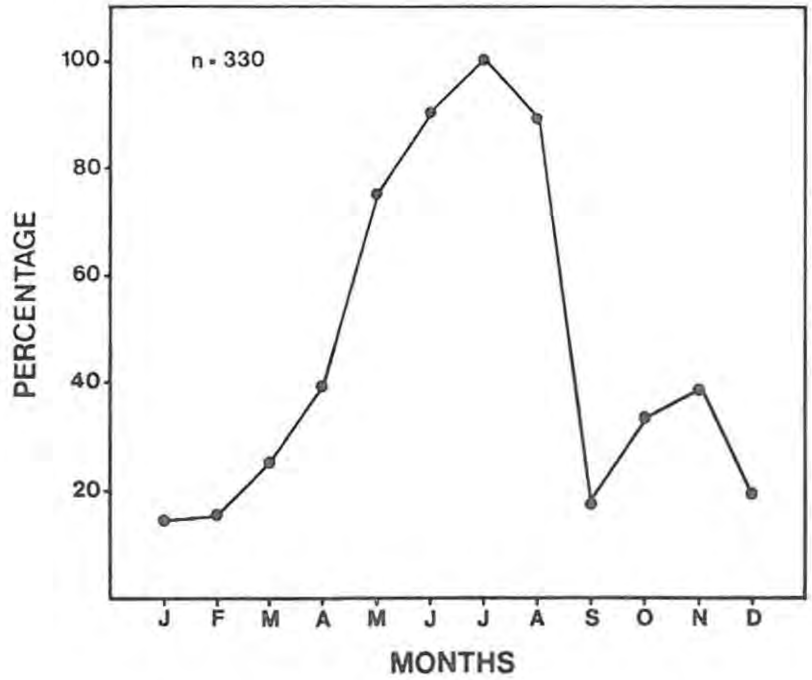


Figure 26. Marginal increment analysis of hyaline zones in the otoliths of Chrysoblephus cristiceps sampled in the Tsitsikamma and Port Elizabeth areas between 1983 and 1986.

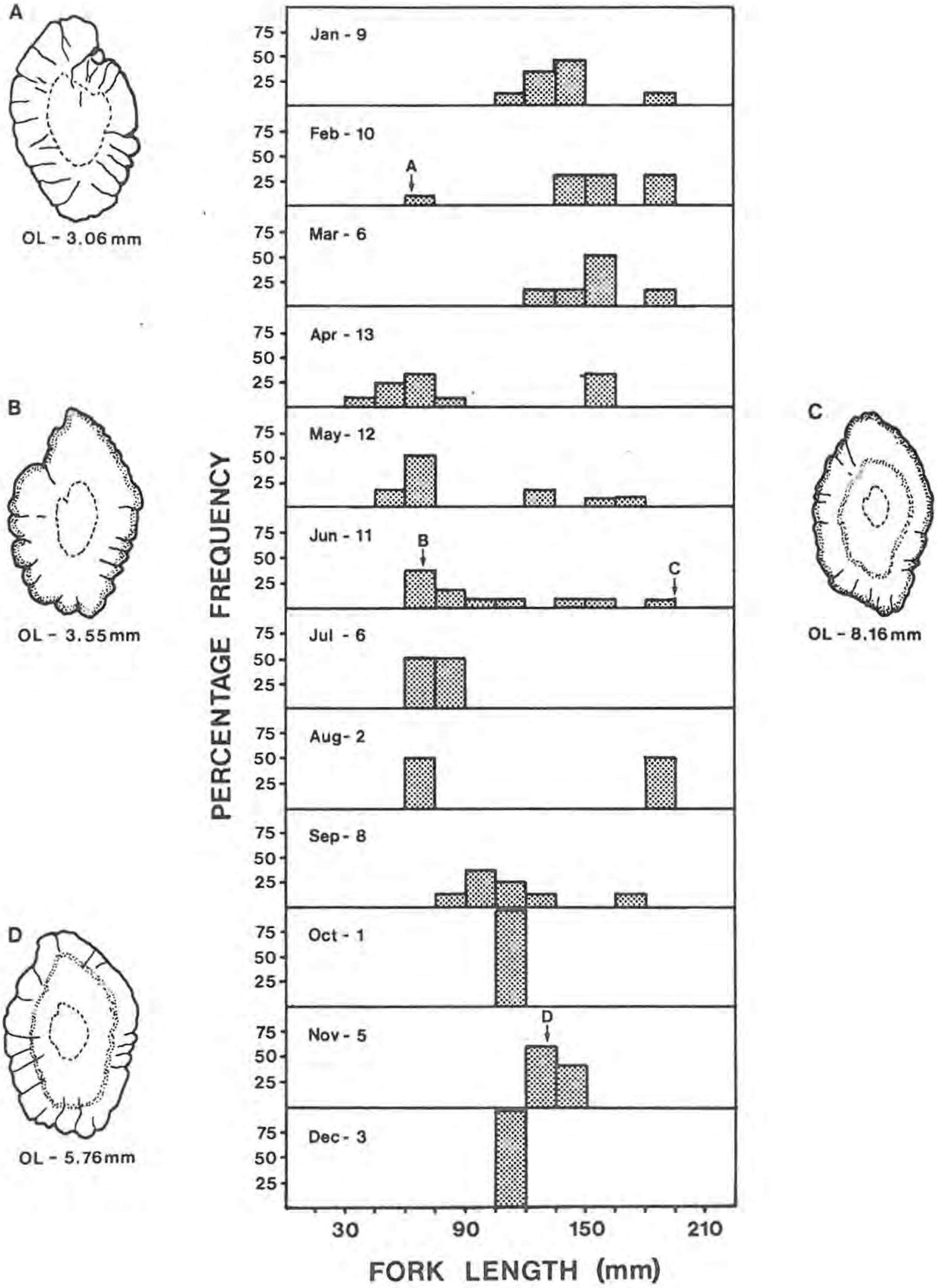


Figure 27. Length frequency analysis of 86 juvenile <u>Chrysoblephus laticeps</u> speared in Algoa Bay between September 1981 and August 1982. The illustrated otoliths show the position of the hyaline zones (shaded) at different times of the year. The nucleus is outlined by dashes.

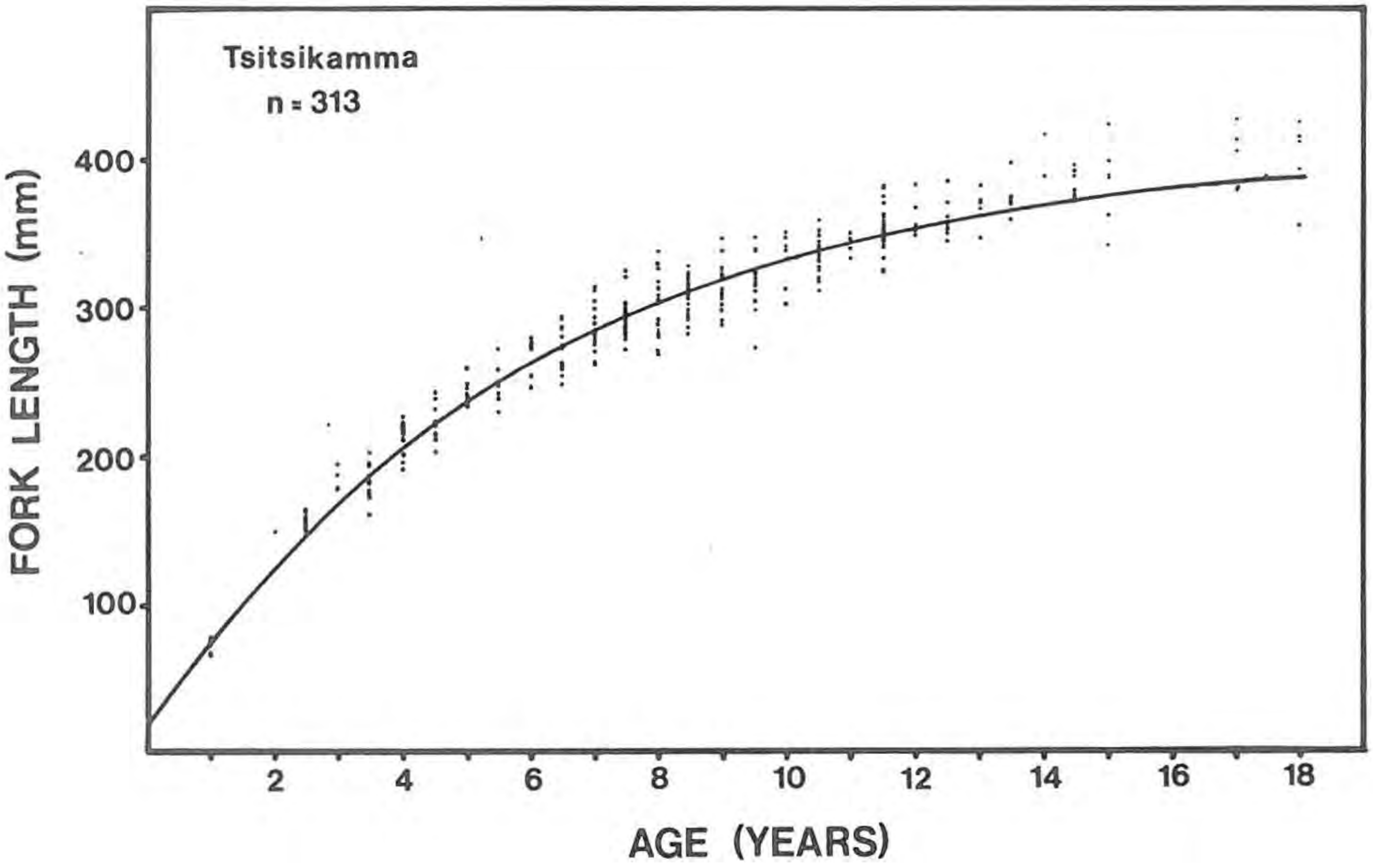


Figure 28. Observed length-at-age of Chrysoblephus laticeps sampled in the Tsitsikamma area between 1983 and 1986.

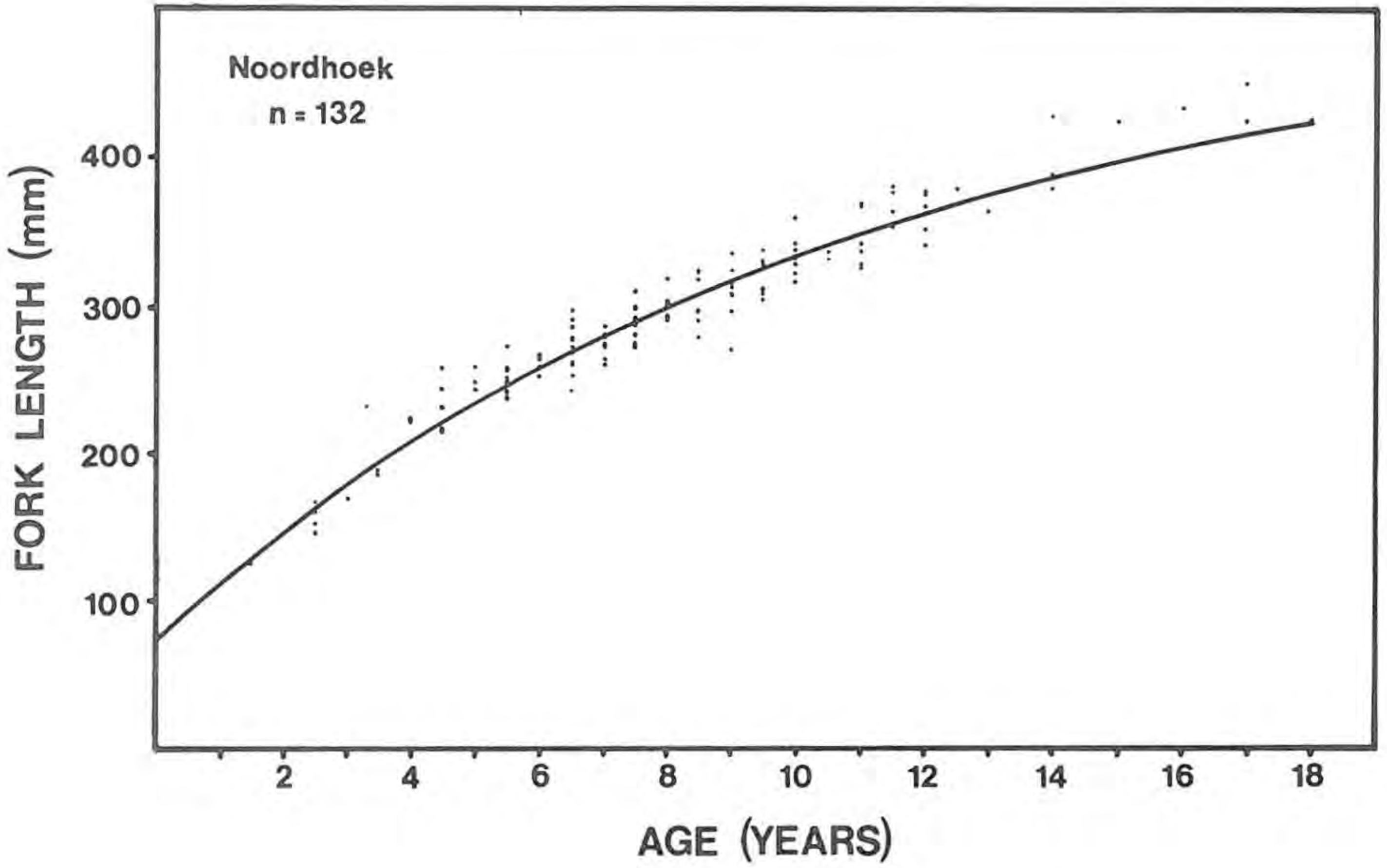


Figure 29. Observed length-at-age of Chrysoblephus laticeps sampled in the Noordhoek area between 1983 and 1986.

TABLE 16. Von Bertalanffy parameter estimates for *C. laticeps* sampled in Tsitsikamma and Noordhoek. Combining both areas produced the best fit.

AREA	AGE RANGE		L_∞	K	t_0
Tsitsikamma	1-18		409.93	0.1633	-0.2188
(n = 313)		s.e.	5.34	0.0057	0.0575
		c.v.	0.01	0.0349	0.2630
Tsitsikamma	2-18		435.64	0.1319	-0.8328
(n = 305)		s.e.	8.90	0.0078	0.1627
		c.v.	0.02	0.0590	-0.1953
Noordhoek	1-18		503.12	0.0940	-1.6480
(n = 132)		s.e.	25.99	0.0109	0.3075
		c.v.	0.05	0.1161	-0.1866
*Tsitsikamma and Noordhoek	1-18		415.44	0.1578	-0.2858
(n = 445)		s.e.	5.74	0.0059	0.0760
		c.v.	0.01	0.0377	-0.2660

s.e. = standard error
c.v. = co-efficient of variation
* = preferred fit

TABLE 17. Mean and standard error of observed and calculated lengths-at-age for *C. laticeps* sampled in Tsitsikamma (T) and Noordhoek (N). t = t-test statistic.

AGE	n	LENGTH-AT-AGE (T)		n	LENGTH-AT-AGE (N)		t
		Observed $\bar{x} \pm s$	Calculated $\bar{x} \pm s$		Observed $\bar{x} \pm s$	Calculated $\bar{x} \pm s$	
1	8	71.9 ± 1.7	74.0 ± 2.1	-	- -	111.0 ± 5.9	-
2	1	149.0 ± -	124.6 ± 1.4	1	126.0 -	146.2 ± 4.0	-
3	15	161.3 ± 4.1	167.6 ± 1.2	5	158.4 ± 4.4	178.2 ± 2.7	0.39
4	24	196.8 ± 4.1	204.1 ± 1.3	5	209.0 ± 9.2	207.4 ± 2.0	1.23
5	17	231.9 ± 3.7	235.1 ± 1.3	9	238.1 ± 5.3	233.9 ± 1.6	0.97
6	16	255.3 ± 3.7	261.5 ± 1.2	17	252.9 ± 2.5	258.1 ± 1.6	0.55
7	37	276.8 ± 2.6	283.9 ± 1.1	20	271.9 ± 2.9	280.1 ± 1.5	1.33
8	35	295.2 ± 2.9	302.9 ± 1.0	19	292.1 ± 2.7	300.1 ± 1.5	0.71
9	41	308.6 ± 2.3	319.0 ± 1.0	13	310.2 ± 5.0	318.4 ± 1.5	0.31
10	23	322.9 ± 4.2	332.7 ± 1.1	15	326.6 ± 3.7	334.9 ± 1.7	0.61
11	24	336.3 ± 2.5	344.3 ± 1.3	8	341.8 ± 5.8	350.0 ± 2.1	1.00
12	24	354.6 ± 3.6	354.2 ± 1.5	10	364.9 ± 4.2	363.5 ± 2.6	1.84
13	13	361.4 ± 3.6	362.6 ± 1.8	2	370.5 ± 7.6	376.3 ± 3.3	0.97
14	9	379.2 ± 6.5	369.7 ± 2.1	4	393.3 ±11.5	387.7 ± 4.0	1.14
15	13	383.1 ± 5.5	375.8 ± 2.4	1	424.0 -	398.0 ± 4.9	-
16	-	- -	380.9 ± 2.7	1	433.0 -	407.5 ± 5.7	-
17	5	396.6 ± 9.2	385.3 ± 2.9	2	435.5 ±13.6	416.1 ± 6.6	-
18	6	397.8 ±10.3	389.0 ± 3.2	1	422.0 -	423.9 ± 7.5	-

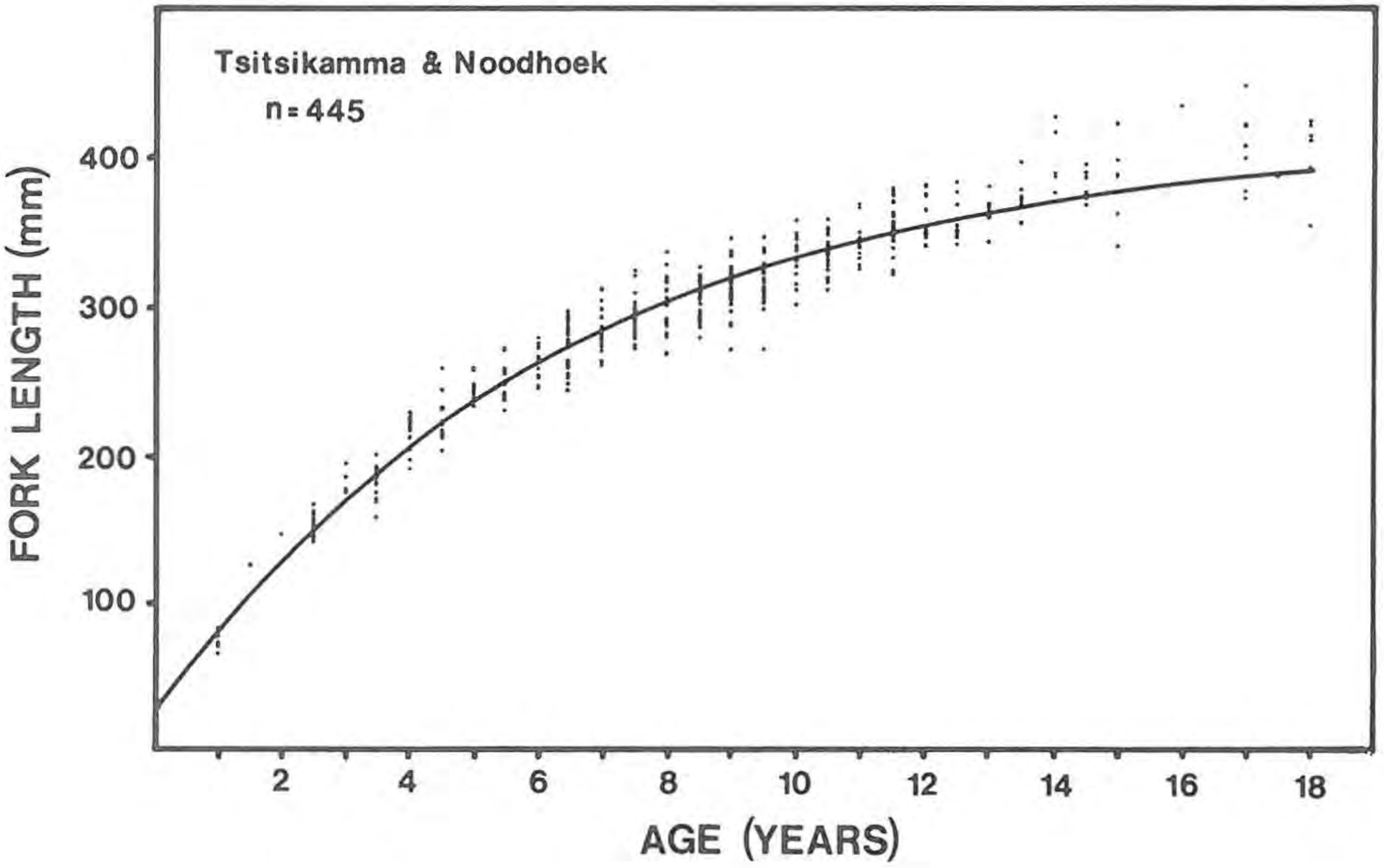


Figure 30. Observed length-at-age of *Chrysoblephus laticeps* sampled in the Tsitsikamma and Noordhoek areas combined, between 1983 and 1986.

The number of data points between 0-2 years and 15-18 years in the Noordhoek area were too low for statistical comparison. A runs test (Zar 1984) showed that the points above age 13 were not randomly distributed about the calculated age, effectively shifting the curve towards a higher L_∞. Approximation of the von Bertalanffy parameters after successive removal of data for ages 18 to 14 from the Noordhoek area increased the agreement between the two areas (Table 18). A likelihood-ratio test (Ratkowski 1983) showed that growth rates were not significantly different between the two areas ($P<0.05$, $x=3.306$). The data sets were therefore combined (Fig. 30) and the resultant parameter estimates are given in Table 19.

Otoliths used for growth analysis of *C. cristiceps* were obtained from two areas, Tsitsikamma (unexploited) and the Port Elizabeth area between Noordhoek and Bird Island (exploited). A total of 265 and 109 otoliths were examined from these areas respectively with a rejection rate of 14%. Separate observed length-at-age plots are given for these areas in Figures 31 and 32, and estimates of von Bertalanffy growth parameters are given in Table 20.

A comparison of mean observed length-at-age (Table 21) showed a significant difference between areas over the 5-13 year range. The growth rate in the exploited area was slower over this range but the estimated length-at-age converged again at age 16. As was the case for *C. laticeps*, the number of fish sampled above 11 years old was low in the Noordhoek area and a runs test indicated that the observations were not randomly distributed about the mean. This result, brought about by the increased difficulty in estimating the age of large fish, had the effect of increasing L_∞ to a level beyond that which was considered a realistic result. A consideration of ages 1-12 only indicated that slower growth rate in the exploited area was a real phenomenon. There is clearly a need for continued ageing of large fish to support this hypothesis.

The exponents of the length-weight relationship for the respective species were used to describe somatic growth (Table 22).

TABLE 22. Somatic growth equations for *C. laticeps* and *C. cristiceps* sampled in Tsitsikamma and Noordhoek. Weight exponents are those given in Table 15.

SPECIES	AREA	EQUATION
C. laticeps	All areas	$Lt = 415.4\left\{1-e^{-0.1578(t+0.2858)}\right\}^{3.154}$
C. cristiceps	Tsitsikamma	$Lt = 576.9\left\{1-e^{-0.1147(t+0.5296)}\right\}^{3.151}$
	Noordhoek	$Lt = 692.2\left\{1-e^{-0.06995(t+1.1931)}\right\}^{3.151}$

TABLE 18. Von Bertalanffy growth parameters for *C. laticeps* after successive removal of ages 18 to 14.

AGE RANGE	L_∞	K	t_0	n
2-17	503.92	0.0938	-1.6541	131
2-16	486.52	0.1008	-1.5193	129
2-15	475.03	0.1061	-1.4280	128
2-14	464.19	0.1114	-1.3401	127
2-13	447.76	0.1205	-1.2054	124

TABLE 19. Mean and standard error of observed and calculated lengths-at-age for *C. laticeps*, using data from both Tsitsikamma and Noordhoek.

AGE	n	LENGTH-AT-AGE	
		Observed	Calculated
		$\bar{x} \pm s$	$\bar{x} \pm s$
1	8	71.8 ± 1.7	76.3 ± 2.7
2	1	137.5 ± 11.5	125.8 ± 1.7
3	15	160.6 ± 3.2	168.1 ± 1.2
4	24	198.9 ± 3.8	204.2 ± 1.1
5	17	234.1 ± 3.0	235.1 ± 1.1
6	16	254.1 ± 2.2	261.4 ± 1.0
7	37	274.9 ± 1.9	283.9 ± 1.0
8	35	294.2 ± 2.1	303.1 ± 0.9
9	41	309.0 ± 2.1	319.5 ± 0.9
10	23	324.4 ± 2.9	333.5 ± 1.0
11	24	337.7 ± 2.3	345.5 ± 1.2
12	24	357.5 ± 2.7	355.7 ± 1.5
13	13	362.3 ± 3.0	364.4 ± 1.8
14	9	383.5 ± 5.8	371.9 ± 2.1
15	13	386.1 ± 5.9	378.2 ± 2.4
16	-	433.0 -	383.7 ± 2.7
17	5	407.7 ± 9.9	388.3 ± 3.0
18	6	401.3 ± 9.4	392.3 ± 3.2

TABLE 20. Von Bertalanffy parameters for C. cristiceps sampled in Tsitsikamma and Noordhoek.

AREA	AGE RANGE		L_∞	K	t_0
Tsitsikamma	1-22		576.89	0.1147	-0.5296
(n = 233)		s.e.	12.97	0.01	0.15
		c.v.	0.02	0.06	0.28
Noordhoek	2-19		692.20	0.0700	-1.1931
(n = 96)		s.e.	53.84	0.01	0.24
		c.v.	0.08	0.14	-0.20

s.e. = standard error
c.v. = co-efficient of variation

TABLE 21. Mean and standard error of observed and calculated lengths-at-age for C. cristiceps sampled at Tsitsikamma (T) and Sardinia Bay to Noordhoek (N&S). n = sample number, t = t-test statistic.

AGE	n	LENGTH-AT-AGE (T) Observed $\bar{x} \pm s$	Calculated $\bar{x} \pm s$	n	LENGTH-AT-AGE (N&S) Observed $\bar{x} \pm s$	Calculated $\bar{x} \pm s$	t
1	3	87.0 ± 1.2	92.9 ± 5.6	-	- -	111.0 ± 5.9	-
2	-	- -	145.4 ± 3.9	5	126.8 ± 7.7	146.2 ± 4.0	-
3	2	205.0 ± 0.0	192.1 ± 2.7	7	159.7 ± 5.4	178.2 ± 2.7	4.25*
4	4	231.8 ± 9.0	233.9 ± 2.1	5	209.4 ± 6.6	207.4 ± 2.0	2.52*
5	15	272.0 ± 4.5	271.0 ± 1.7	12	243.3 ± 5.1	233.9 ± 1.6	4.57*
6	25	296.8 ± 3.5	304.2 ± 1.7	18	264.5 ± 4.7	258.1 ± 1.6	5.67*
7	43	326.2 ± 3.2	333.8 ± 1.6	8	281.6 ± 8.5	280.1 ± 1.5	5.49*
8	23	344.5 ± 3.6	360.1 ± 1.5	9	319.3 ± 7.1	300.1 ± 1.5	3.48*
9	28	366.8 ± 3.8	383.6 ± 1.5	9	348.2 ± 7.4	318.4 ± 1.5	2.34*
10	17	390.4 ± 5.0	404.6 ± 1.5	5	349.8 ±10.0	334.9 ± 1.7	3.78*
11	13	413.3 ± 4.9	423.3 ± 1.6	3	411.7 ± 4.3	350.0 ± 2.1	0.15*
12	17	434.9 ± 5.0	439.9 ± 1.9	2	441.0 ± 2.0	363.8 ± 2.6	0.41*
13	9	446.9 ± 8.0	454.8 ± 2.2	1	459.0 -	376.3 ± 3.3	0.15*
14	10	459.3 ± 5.0	468.0 ± 2.7	1	452.0 -	387.7 ± 4.0	-
15	4	471.0 ±13.1	479.8 ± 3.1	2	468.0 ± 3.0	398.0 ± 4.9	-
16	6	508.5 ± 7.5	490.3 ± 3.6	-	- -	407.5 ± 5.7	-
17	5	501.6 ± 5.0	499.7 ± 4.1	-	- -	416.1 ± 6.6	-
18	3	518.6 ± 7.6	508.1 ± 4.7	1	525.0 ± -	423.9 ± 7.5	-
19	2	537.0 ± 4.0	515.5 ± 5.1	-	- -	431.0 ± 8.4	-
20	1	532.0 -	522.1 ± 5.6				
21	1	580.0 -	528.1 ± 6.3				
22	2	563.0 ±16.1	533.4 ± 7.0				
23	1	586.0 -	538.1 ± 7.8				

*Significant at $P<0.05$.

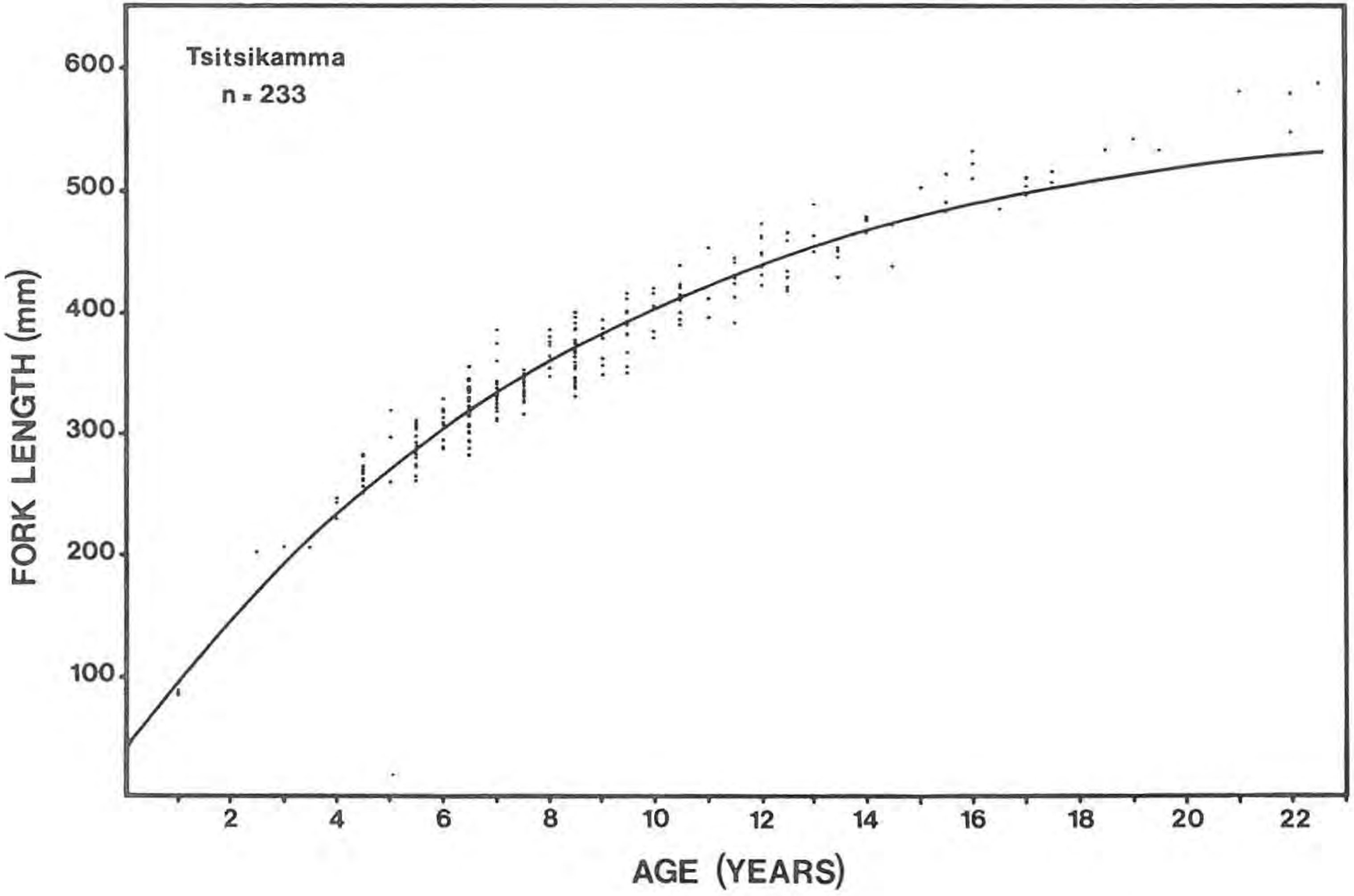


Figure 31. Observed length-at-age of Chrysoblephus cristiceps sampled in the Tsitsikamma area between 1983 and 1986.

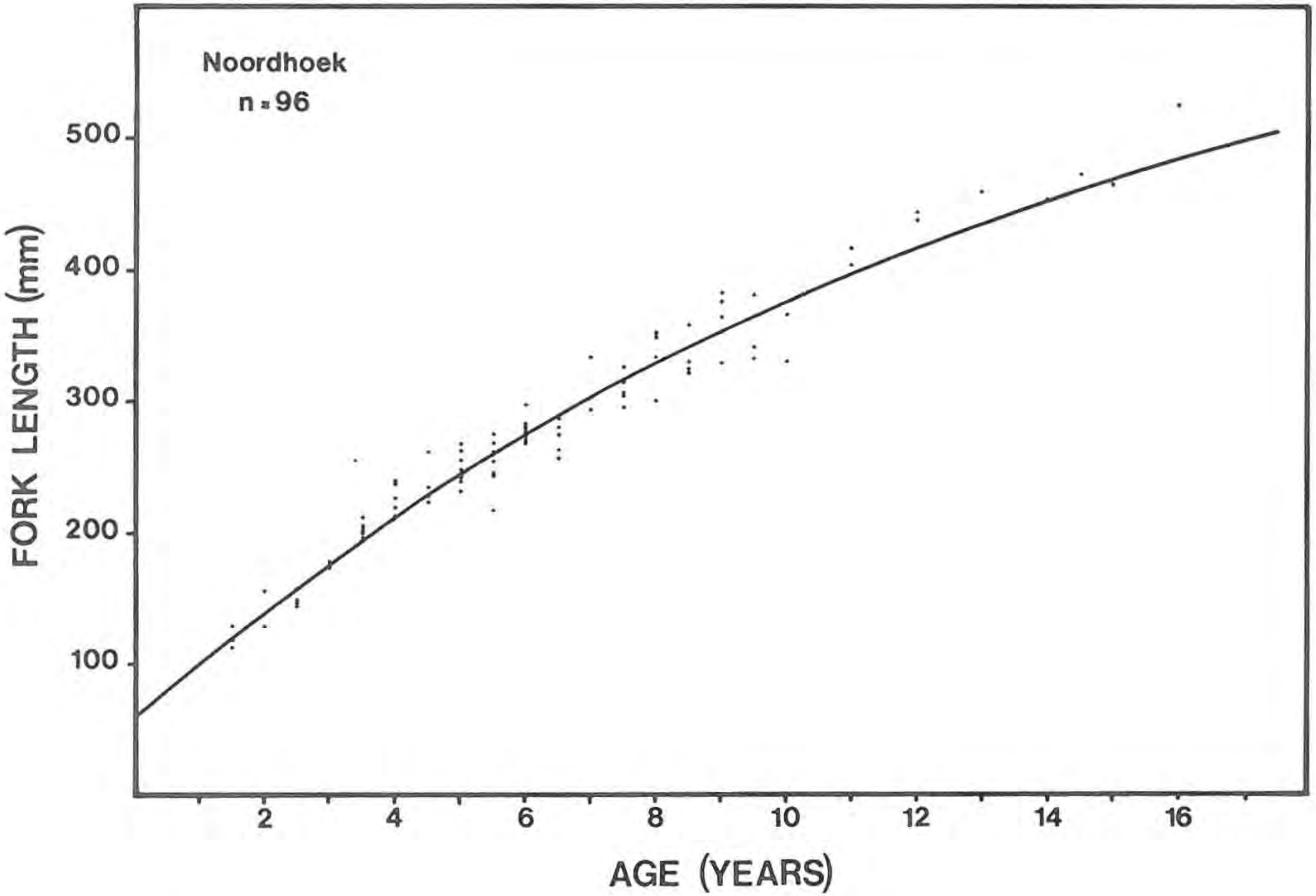


Figure 32. Observed length-at-age of Chrysoblephus cristiceps sampled in the Port Elizabeth area between 1983 and 1986.

Mortality estimation

Ricker (1975) states that, to construct an age-length key, the fish used for age determination must be taken from the same stock, during the same season and with the same gear used to take length frequency samples. Age-length keys must also only be applied to length samples from the same year. The reason for this is that year classes do not always have the same initial abundance and are infrequently subjected to exactly the same fishing pressure from one year to the next.

This ideal was not met in this study because time constraints prevented the ageing of fish from all areas sampled. Age analysis showed that growth rates from widely separated areas were comparable, particularly for C. laticeps. Furthermore slow growth rates probably smoothed the effects of variability in recruitment and, therefore, initial abundance in the fishery. For these reasons age-length keys were derived using the total number of fish sampled over the entire study period for each of the areas studied. The combined age analysis for C. laticeps (Noordhoek and Tsitsikamma) was used for all areas. Two separate age determinations were used for C. cristiceps, one for Tsitsikamma and the Port Elizabeth analysis for all exploited areas.

Age frequencies derived from normalized catch length frequency data for each of the areas sampled are summarised in Figure 33 for C. laticeps and Figure 34 for C. cristiceps. The corresponding catch curves for these areas are summarised in Figures 35 and 36 respectively.

An analysis of covariance of the data for C. laticeps showed that the slopes of these regressions were significantly different ($P<0.05$, $F=5.131$, $df=4$). Jeffreys Bay showed the highest rate of instantaneous total mortality (0.34) followed by Mossel Bay/Knysna (0.30), Tsitsikamma (0.27) and the areas surrounding Port Elizabeth (0.23, 0.25 and 0.21).

A similar result was also obtained for C. cristiceps, catch curves being significantly different in all of the areas sampled ($P<0.05$, $F=17.5$, $df=16$). Port Elizabeth and Noordhoek had the highest instantaneous total mortality rates (0.83) followed by Mossel Bay (0.62) and East London (0.59), while the rate in Tsitsikamma (0.27) was significantly lower than that of the exploited areas.

The influence of temperature on the Pauly derivation of M was not significant over the range of temperatures recorded at the different sampling sites. A mean annual temperature of $17^{0}C$ was chosen for the estimation of M based on thermoscript readings in the Tsitsikamma and bottom temperature records taken during visual assessments at Noordhoek. Total, natural and fishing mortalities are summarised in Table 23 .

Independent estimates of total mortality (Z) were obtained for the C. laticeps populations in Tsitsikamma and Noordhoek by constructing catch curves from age frequencies derived by visual assessment (Fig. 37).

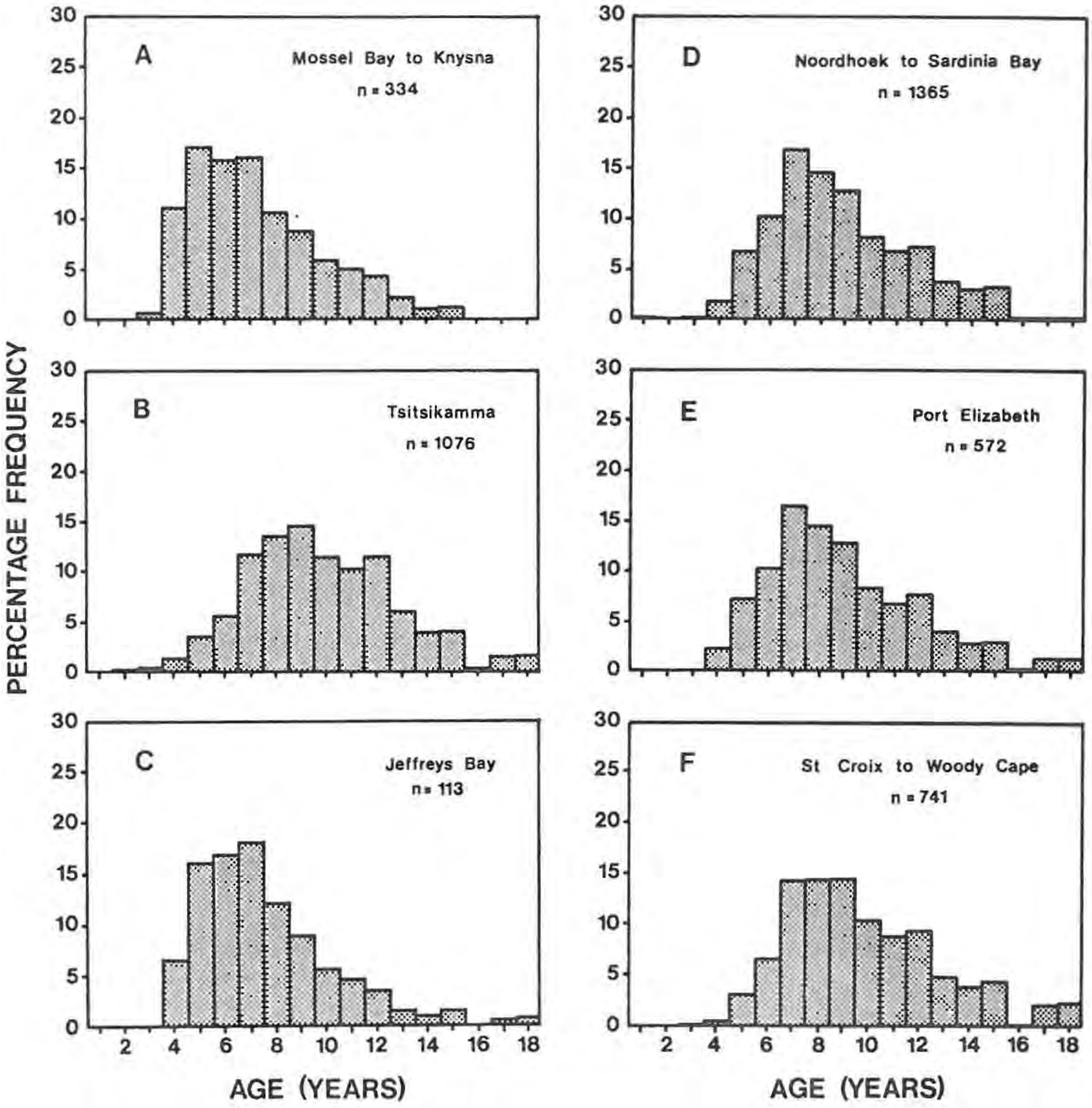


Figure 33. Age frequencies of <u>Chrysoblephus laticeps</u> sampled between Mossel Bay and Woody Cape. See Table 11 for the sampling period.

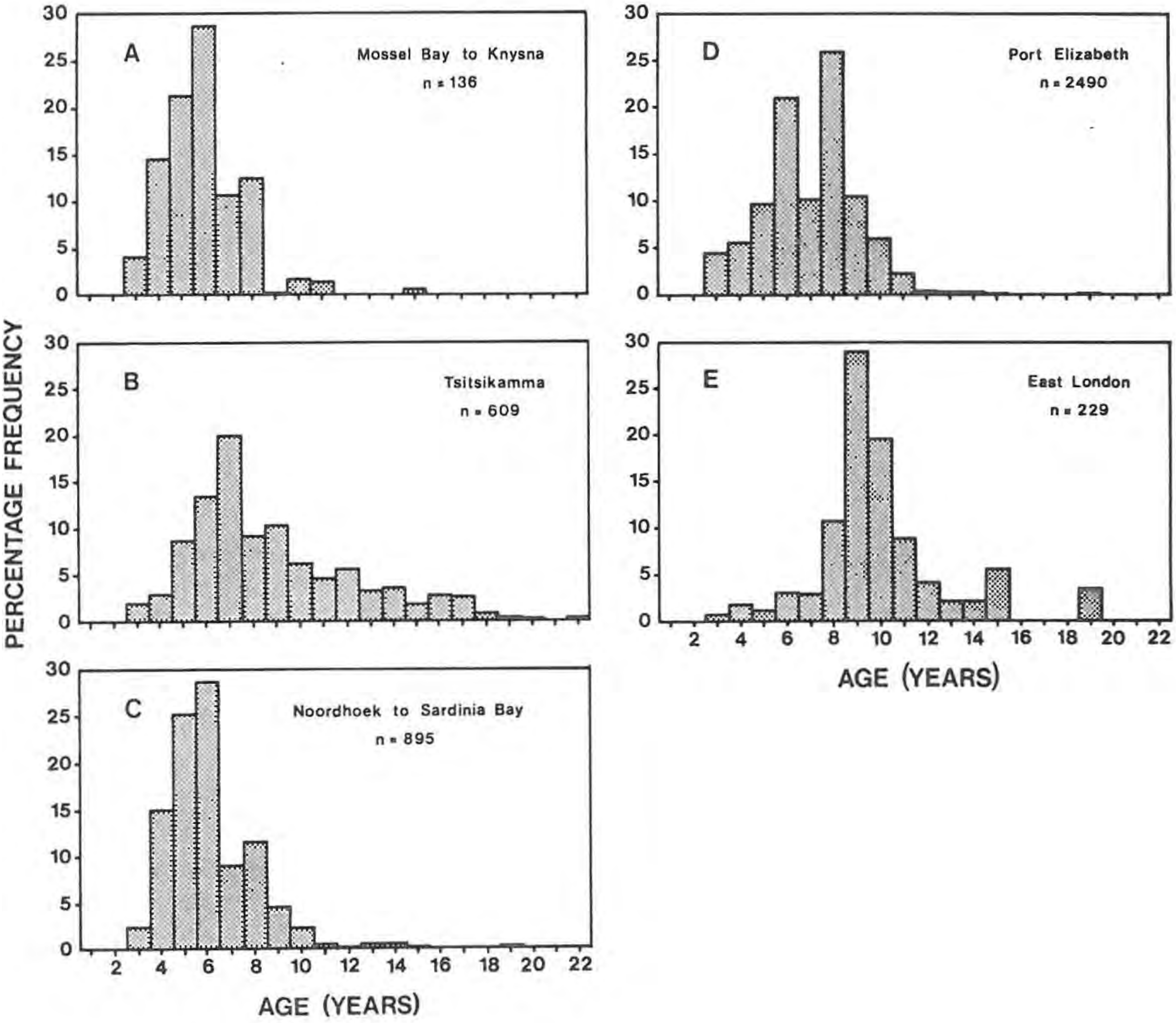


Figure 34. Age frequencies of <u>Chrysoblephus cristiceps</u> sampled between Mossel Bay and East London. See Table 11 for the sampling period.

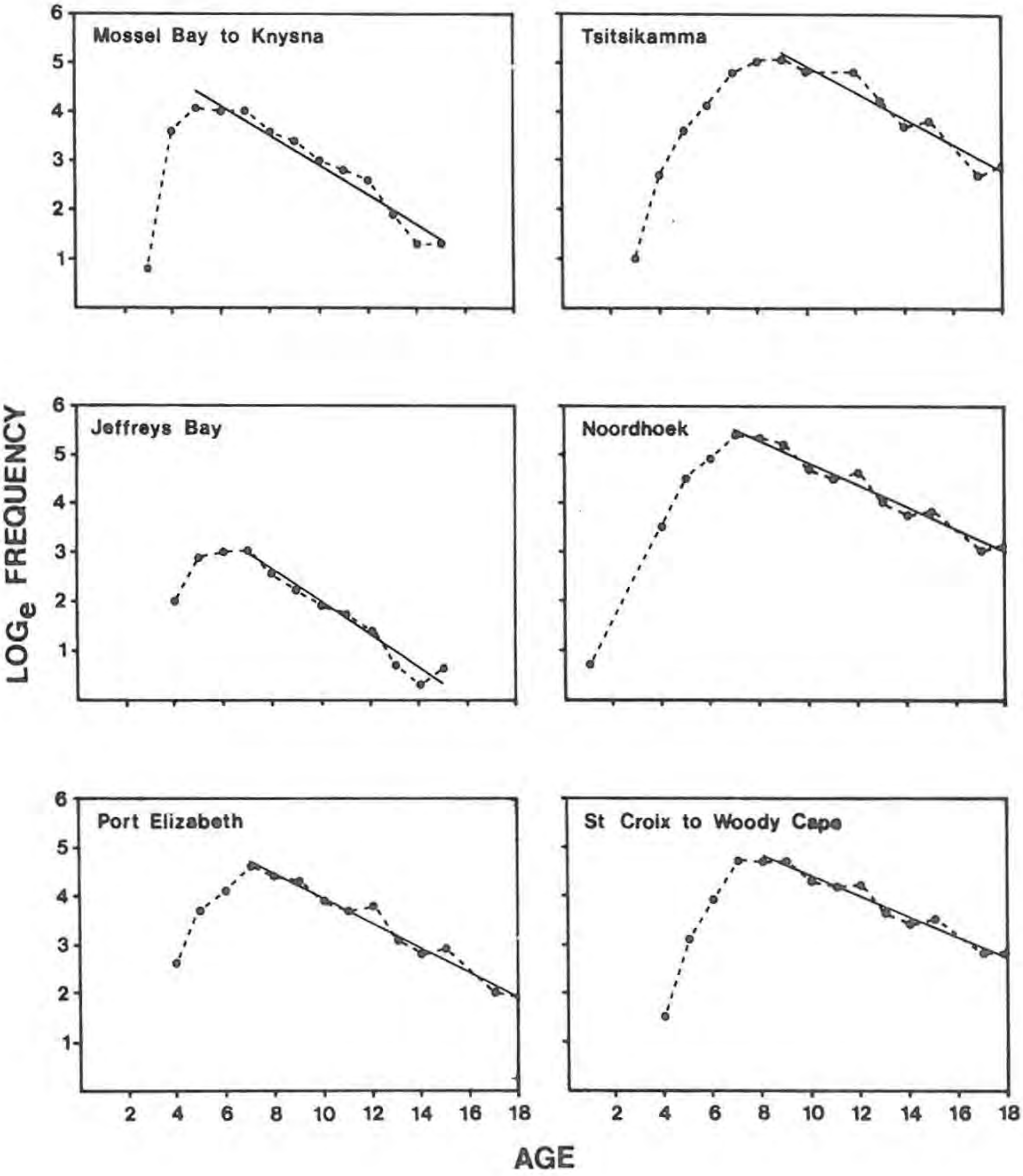


Figure 35. Catch curves for Chrysoblephus laticeps based on the age frequency analysis summarised in Figure 33. Regressions were fitted using least squares analysis.

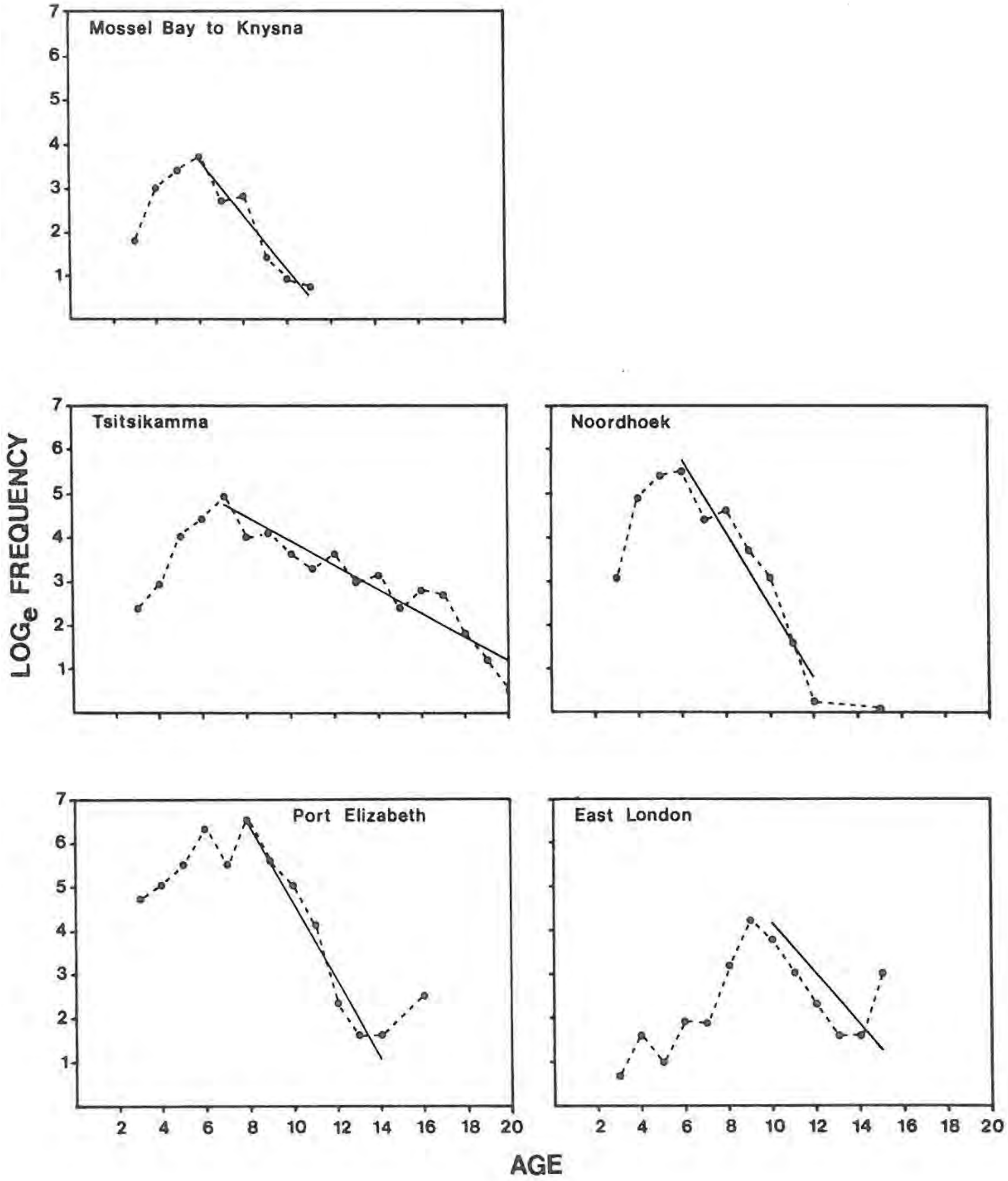


Figure 36. Catch curves for <u>Chrysoblephus cristiceps</u> based on the age frequency analysis summarised in Figure 34. Regressions were fitted using least squares analysis.

DISCUSSION

The von Bertalanffy parameter estimates derived for both C. laticeps and C. cristiceps showed that they were long lived and slow growing species. Combined age analysis of C. laticeps sampled at Noordhoek and Tsitsikamma gave an estimated L_∞ equal to 415mm fork length which was close to the observed maximum length recorded in the fishery (Lmax = 457mm fork length). Similarly values of L_∞ and Lmax for C. cristiceps were 576 and 586mm fork length in Tsitsikamma and 692 and 577mm in Noordhoek respectively. Knight (1968) pointed out that L_∞ was not usually equal to Lmax but was a theoretical length that would be achieved if growth continued indefinitely at rate K. Maximum known lengths of C. laticeps and C. cristiceps were 512 and 632mm respectively (Table 24), considerably larger than both the predicted and observed maximum lengths recorded in this study. Two factors may have contributed to this result. Firstly, maximum known lengths (S.A. records) could have been inaccurately reported while secondly, and perhaps more likely, smaller maximum sizes may reflect a general decline resulting from a steady increase in fishing pressure over the past 10-15 years (van der Elst 1982).

Few studies on the growth rate of South African sparids have been published (Table 24), but those available show that slow growth and longevity are the norm in this family. Most of these studies were done on a restricted size range taken from commercial and recreational fisheries. From the list of maximum known sizes it is clear that many of these species may achieve ages in excess of the reported maximum age. Sampled catches of A. argyrozona, for example, showed a Lmax of 720mm, considerably lower than the maximum recorded size of 790mm. This was also evident for both C. laticeps and C. cristiceps where fish larger than the Lmax were sampled but not aged because the otoliths were unreadable.

Ricker (1975) showed that the difference between the asymptotic size and actual size of a fish decreased exponentially at a rate K, known as the Brody growth co-efficient. Values of K for South African sparids were fairly similar and, as expected, species with the highest L_∞ values had the lowest values of K (Table 24).

Based on this reasoning the results obtained for C. cristiceps suggest that the growth rate in the Port Elizabeth area was slower than the growth rate in the Tsitsikamma area. Earlier in this chapter it was argued that the convergence of predicted lengths-at-age was probably an artifact due to low sample sizes combined with increased difficulty in ageing of older fish. Accepting the hypothesis that growth was slower in exploited populations it became necessary to examine what factors may contribute to this change.

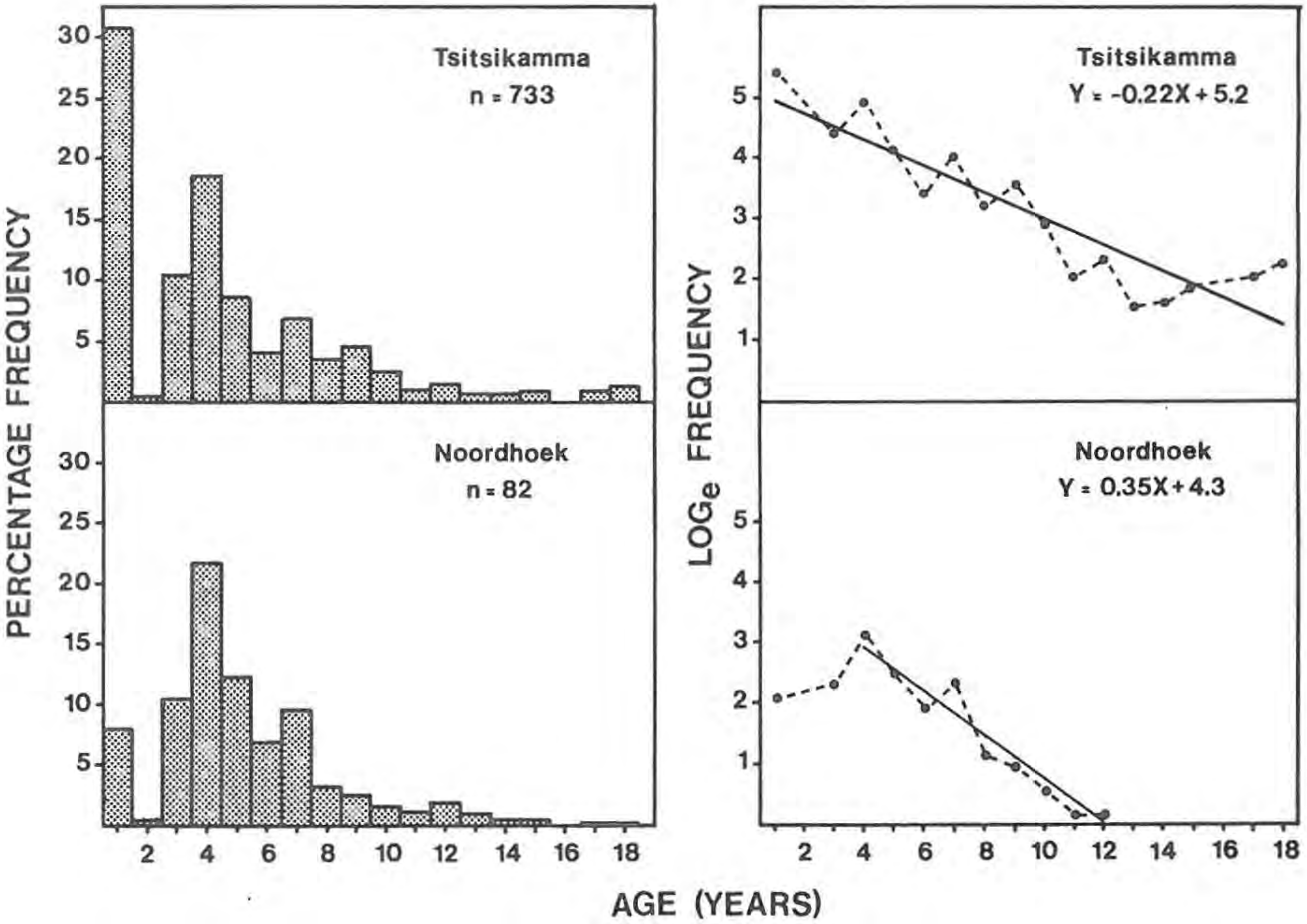


Figure 37. Age frequencies and catch curves of <u>Chrysoblephus laticeps</u> based on visual assessments of fish sampled in the Tsitsikamma and Noordhoek areas. Regressions were fitted using least squares analysis.

TABLE 23. Instantaneous total (Z) and fishing (F) mortality for *C. laticeps* and *C. cristiceps* sampled between Mossel Bay and East London during the study period.

SPECIES	AREA	MORTALITY ESTIMATE Z	F
C. laticeps	Mossel Bay/Knysna	0.3007	0.0946
	Tsitsikamma	0.2731	0.0670
	Jeffreys Bay	0.3375	0.1314
	Noordhoek/Sardinia Bay	0.2320	0.0259
	Port Elizabeth	0.2540	0.0479
	St Croix/Woody Cape	0.2082	0.0021
C. cristiceps	Mossel Bay/Knysna	0.6203	0.4676
	Tsitsikamma	0.2653	0.1126
	Noordhoek/Sardinia Bay	0.8296	0.6769
	Port Elizabeth	0.8319	0.7455
	East London	0.5883	0.4356

TABLE 24. Summary of published age and growth analyses of South African sparids.

SPECIES	SOURCE	K	AGE obs.	LENGTH obs.	max.
Pterogymnous laniarius	Hecht & Baird (1977)	0.19	11	*422	*450
Pachymetopon blochii	Nepgen (1977)	0.14	9	400	423
	Hughes (1986)	0.14	8		
Argyrozona argyrozona	Nepgen (1977)	0.07	12	720	790
Pachymetopon aeneum	Buxton & Clarke (1985)	0.13	12	400	433
Cheimerius nufar	Coetzee & Baird (1981b)	0.07	22	*705	*750
Cymatoceps nasutus	Buxton & Clarke(unpub.)	0.05	45	1099	1161
Pachymetopon grande	**Clarke & Buxton(unpub.)	0.15	38	532	572
Sparodon durbanensis	**Clarke & Buxton(unpub.)	0.09	31	959	1029
Chrysoblephus laticeps	This study	0.16	18	449	462
Chrysoblephus cristiceps	This study				
(Tsitsikamma)		0.11	22	602	664
(Port Elizabeth)		0.07	19		

obs.- observed maximum age and fork length.
max.- maximum known length (Smith and Heemstra 1986; van der Elst 1981).
*Measurements refer to total length
**J.R. Clarke, Port Elizabeth Museum

A number of studies have found variations in biological functions such as growth, mortality and fecundity (Craig 1985). Healey (1980) suggests that these responses may be attributed to natural population regulating mechanisms. Crowding, for example, can result in reduced growth rate, late maturity, decreased fecundity and increased longevity (Craig 1985). Food shortage is usually invoked to explain these responses but other factors such as pheromones (Pfuderer & Francis 1972) and social interactions (Hoffman 1985) may be responsible. Growth rate may be expected to increase in a fished population because of reduced competitive interactions present under climax conditions. Examples would be the ability to obtain a greater share of preferred food items and less energy spent on resource defence e.g. mating sites.

Conversely it may be argued that in a size selective fishery fast-growing individuals become vulnerable to fishing earlier and have higher mortality rates than their slow growing counterparts. Because growth rate is a heritable trait (Favro, Kuo & McDonald 1979) fast growth would be selected against under sustained fishing pressure and growth rate would decrease relative to the undisturbed population. This is in effect the same process that produces "Rosa Lee's phenomenon" (Ricker 1969) where back-calculated lengths are smaller than the true average size at the age in question because of selective mortality in a size selective fishery. Unfortunately back-calculation was not possible in this study because of the irregular outline of the otolith and difficulty in sectioning the otolith exactly through the nucleus.

A third possibility that may not be discounted is that the two populations might represent different stocks with inherent differences in growth rate and clearly a closer examination of age structure particularly over the larger size range in the exploited population is necessary before this problem can be resolved.

In both C. laticeps and C. cristiceps the fast growth period (hyaline zone) was recorded in the winter months, after the breeding season. Others who have studied growth in South African fish have also recorded the hyaline zone in the winter months but have considered this as a slow growth period (Botha 1971; Geldenhuys 1973; Hecht & Baird 1977; Buxton & Clarke 1985; Thomas 1983,1985).

Botha (1971), in a study of the growth of Cape hakes, showed that the hyaline zone was formed just after peak spawning and that the opaque zone was formed at the same time that fat reserves were being accumulated (see his Fig. 5, p. 10). He considered the opaque zone to represent fast growth between spawning seasons and the hyaline zone to be a period of slow growth immediately after spawning. A re-evaluation of this evidence using the interpretations of this study suggests a number of subtle differences. Firstly the slowest growth period would be at the end of Botha's opaque zone at a time when fat deposition was greatest and prior to spawning. Secondly, that the period of most rapid growth would occur immediately after spawning, in Botha's hyaline zone. This interpretation agrees with Botha's statement that peak feeding takes place immediately after spawning. Thirdly it seems logical that peak somatic growth would occur prior to the accumulation of fat reserves.

Thomas (1983) showed a close correlation between the hyaline formation and cold upwelling suggesting that this was a period of slow growth. In the Benguella upwelling system one would expect cold periods to be associated with nutrient enrichment and an abundance of food. Interpreting the hyaline zone as a fast growth period would therefore be more plausible.

In general, somatic growth will be expected to be greatest when other energy demanding processes are low, for example, gonadal investment. That this occurs in winter is irrelevant as can be shown by considering the balanced energy equation (Ricker 1978):

$$P = Gs + Gr = C - M$$

where production (P) consists of somatic growth (Gs) and reproductive growth (Gr), determined by ingested energy (C) less maintenance energy (M). Surplus energy, above the maintenance cost (M), may be higher in summer than in winter but because most is used for reproductive growth, somatic growth is low. In winter when reproductive growth is zero all surplus energy can be used for somatic growth.

From these examples and the results of this study, it would appear that the interpretaton of the hyaline zone as a period of fast growth is not inconsistent with observed data.

Estimates of total mortality based on catch curves are subject to the assumptions that: (1) recruitment and survival are constant in the population; (2) the sample is randomly taken from the age groups involved and; (3) fishing mortality has been constant over the time span represented by the oldest fish in the age series. Since survival is the complement of mortality, and is made up of fishing and natural mortality, assumption (1) implies that each of these in turn is also uniform (Ricker 1975).

Nothing is known about recruitment patterns in South African sparids but a number of observations made during this study were relevant to the first assumption. Firstly, both _C. laticeps_ and _C. cristiceps_ were batch spawners and fecundity was high. Secondly, based on the observation that the relative abundance of juveniles was low and restricted to a narrow inshore zone, that mortality of egg and larval stages was proportionately very high. Thirdly, studies of predator-prey relationships suggested that natural predators (apart from man) were few and the survival rate, once the fish are past the larval stage, was probably high. These factors, together with the observed slow growth rate, would smooth out the effects of strong or weak year classes so that by the time the fish were recruited to the fishery population numbers would be expected to be stable. The first assumption was therefore satisfied and variation in recruitment and survival was considered random.

All fishing gear is subject to a certain amount of selectivity e.g. mesh size, trawl depth and hook size. Factors affecting the composition of linefish catches include hook size, range of fish sizes available, expertise of individual fishermen and the ability of larger fish to compete more successfully for a bait. Underwater visual assessments in the different areas showed that all sizes were available to inshore recreational fishermen and differences between good and poor fishermen were assumed to even out in the combined catch.

The third assumption was considered least likely to be valid because van der Elst (1982) reported a steady increase in the number of participants in the recreational linefishery in South Africa. Smale & Buxton (1985) also showed an increase in the annual effort of the Port Elizabeth recreational ski-boat fishery between 1972 and 1985 with the implication that catch had also increased. CPUE over the same period was unknown.

Analysis of covariance showed that total mortality estimates in the areas studied were significantly different. Since the natural rate of mortality derived for C. laticeps was constant over the geographical range sampled, these differences were attributed to fishing mortality. The results summarised in Table 23 showed that F was low in all of the areas sampled. Reworking Nepgen's (1977) study on growth and mortality of two South African sparids, Hughes (1986) showed that Argyrozona argyrozona ($F = 0.34$) was moderately fished while Pachymetopon blochii ($F = 0.57$) was overfished. Although it is essential to relate the level of F to the size at recruitment to the fishery t_R before conclusions can be drawn regarding the level of exploitation in a fishery (Beverton & Holt 1957), these results suggested that C. laticeps was lightly exploited in the areas examined.

Visual assessment of C. laticeps populations in Tsitsikamma provided an independent estimate of $Z = 0.22$. Almost certainly a limited amount of poaching must occur in the park, particularly at the extremities which are close to recreational ski-boat and commercial fisheries operating from Plettenberg Bay and Cape St Francis respectively. This effect together with research fishing was considered negligible, particularly in the centre of the park where most of the samples were taken. Z in this area is therefore equal to M because F is zero. Although the estimate obtained from visual assessment was not significantly different from that obtained by fishing ($Z = 0.27$) ($P<0.05$, $t=0.8$, $df=21$) it more closely approximated the Pauly estimate of $M = 0.20$.

A similar comparison in Noordhoek showed that the estimate of total mortality from linefishing ($Z=0.23$) was significantly different from visual assessment ($Z=0.35$) ($P<0.05$, $t=2.79$, $df=16$). Using the latter estimate the value of F for this area became 0.15, which would still be relatively low but closer to the result expected from an area so easily accessible to recreational fishermen. The difference between the two estimates was puzzling, particularly because the Tsitsikamma result seemed to suggest that linefish catches were random samples of the true population.

Two explanations were possible; firstly that the estimates were based on different populations and secondly that the catch was not representative of the true population in the area. In the Tsitsikamma region all of the research fishing was done over the same reefs that were visually assessed. The same was not true for the Noordhoek area because for practical reasons all of the areas used by the fishermen could not be surveyed. More importantly, the catch in the Noordhoek area was taken in both shallow and deep water, whereas no visual assessment was done at depths greater than 30m. Obviously if the deep water population structure differed from that between 0-30m, it would influence the total catch frequency.

The second possibility arises if fish are disproportionately represented in the catch. Lower values of Z effectively mean that the catch is biased towards the larger fish, which could result for example if they were more successful at competing for a bait. The results in the two areas would appear to contradict each other in this respect.

From the age length frequencies it is clear that C. cristiceps became vulnerable to the recreational linefishery at an earlier age in the exploited areas except in East London where the recruitment age was greater than in Tsitsikamma. The range of ages caught at exploited sites was also lower than that in the Tsitsikamma. Few fish older than 14 years were caught between Port Elizabeth and East London while at Mossel Bay and Knysna the maximum age class recorded was 11 years.

Some evidence has been presented in this study that suggests that adult C. cristiceps, like C. laticeps, may be a fairly resident species (see Chapter 3.2). This was supported by the lower Z values obtained in the Tsitsikamma area. If C. cristiceps were migratory then the Park would afford little protection from fishing predation and Z would be much higher. The estimate of Z obtained from the linefishing catch curve may therefore be considered an approximation of M. This value (0.27) was higher than the Pauly derivation (0.15), possible reasons for which have been mentioned above in the discussion on natural mortality in C. laticeps.

Differences in Z between areas were also attributed to fishing because M was considered to be the same over the geographical range sampled. The results summarised in Table 23 show that F ranged between 0.4 and 0.7 in the exploited areas suggesting that these populations were more heavily exploited than *C. laticeps*.

3.5 - FEEDING

INTRODUCTION

Studies of the diet of animals based on the analysis of gut contents are fundamental to the understanding of growth, production, abundance, distribution and the ecological role of the individuals in the community (Hickey 1975; Windell & Bowen 1978). The where, when and what of dietary choice is the subject of a vast literature on feeding (Hughes 1980) and, based on the optimal foraging theory of MacArthur & Pianka (1966), much of this attempts to predict how animals will feed most efficiently when faced with a prey choice in the presence of competition. Recently the concept of resource utilisation as a mechanism to effect co-existence has been criticised (Ebeling & Laur 1982; Grossman 1982).

The objectives of dietary studies range from simple documentation of what a species may eat (Druzhinin 1975; Frogolia 1977) to more complex studies investigating community structure and resource partitioning (Smith & Tyler 1973b; Cross 1982; Gladfelter & Johnson, 1983). A second major field of study is concerned with the physiology of feeding (Hyslop 1980).

Most studies on the feeding biology of South African marine teleosts have been limited to descriptive analyses of dietary composition (Davies 1949; Talbot 1955; Blaber 1974; van der Elst 1976; Nepgen 1977, 1982; Baird 1978; Joubert & Hanekom 1980; Coetzee & Baird 1981b; Cyrus & Blaber 1983; Buxton & Kok 1983; Clarke & Buxton 1985; Smale & Bruton 1985; Buxton & Clarke 1986; Garratt 1986b), although Christensen (1978), Lasiak (1986) and Smale (1986) have investigated aspects of community structure with respect to resource partitioning.

With the exception of a preliminary investigation of the diet of a number of teleosts in False Bay including _C. laticeps_ (Nepgen 1982) nothing has previously been published on the diet of either _C. laticeps_ or _C. cristiceps_.

This study presents quantitative information on the feeding habits of both species in two spatially separated areas on the south-east coast of South Africa, Algoa Bay and Tsitsikamma. Changes in diet related to fish size and area are discussed and the possible effects of decreased density on the diet of fish in exploited areas are considered. For reasons described below more detailed aspects of the feeding ecology of _C. laticeps_ were examined including feeding periodicity, feeding selectivity and feeding behaviour.

METHODS

Approximately 2000 C. laticeps and 3300 C. cristiceps obtained from ski-boat catches in the Port Elizabeth area were examined for stomach contents. Almost all of these fish were longer than 200-250mm fork length, the legislated minimum size in both species, and because of stomach eversion and regurgitation only 3.0 and 2.1 percent respectively contained food. Additional samples, particularly of smaller fish, were speared by SCUBA divers. Fewer regurgitations occurred in speared fish, and observations of fish activity and substratum type were made before sampling. C. cristiceps were difficult to spear because they tend to shy away from divers and for this reason the sample sizes in some of the study areas were low. In comparison C. laticeps were easily speared and at two localities, Algoa Bay and the Knoll, all of the fish examined for gut contents were speared.

The mass of each fish was determined in grammes, and the fork length measured to the nearest millimetre. If the stomach was not everted it was removed with the hindgut and each was preserved separately in a buffered 10 percent formalin solution. Gut contents were identified to the lowest possible taxon and assigned a visual percentage volume (Christensen 1978). Numerical percentage contribution (Pillay 1952), percentage frequency of occurrence (Hynes 1950), and a ranking index, the frequency of occurrence multiplied by the mean percentage volume (Hobson 1974), were calculated for each prey group.

Prey were identified using the following reference material; Hydrozoa - Millard (1975), Polychaeta - Day (1967 a,b), Isopoda - Kensley (1978), Decapoda - Barnard (1950) & Kensley (1981), Mollusca - Kilburn (1982) and Echinodermata - Clarke & Courtmann-Stock (1980).

Potentially available prey items on Phil's reef, Algoa Bay were collected in $0,25\text{m}^2$ quadrats using an airlift suction sampler (Chess 1979). Feeding selectivity was determined using the formula of Berg (1979),

$$\text{Sel} = \log_{10} x \; \frac{\%N_i \text{ in the ingested food}}{\%N_i \text{ in the potentially available food}}$$

where Sel = feeding selectivity for a prey item i and $\%N_i$ = numerical percentage of prey item i.

Feeding periodicity was examined by dividing the gut into five areas; the stomach and four equal quarters of the hindgut. The presence or absence of food items in these areas was noted over three periods during the day; sunrise ± 1hr, sunset ± 1hr and the period in between.

RESULTS

Chrysoblephus laticeps

Comparison of stomach and hindgut contents

Regurgitation of stomach contents by fish taken in deep water may limit the value of feeding studies (Randall 1967). The alternative of examining hindguts is often considered undesirable because of the advanced stage of digestion normally found there. This may render prey unrecognisable or, if identifiable by special techniques (Feller et al. 1979), difficult to quantify because of differential retention times in the gut. In particular, hard skeletal components may be concentrated in the hindgut (Laevastu 1965, Froglia 1977).

Preliminary comparisons of the contents of the stomach and the hindgut of C. laticeps suggested that there was little difference in their prey composition. Consequently, it was considered valid to compare and list as prey items any species found in either part of the gut. For the purposes of this comparison only, 50 stomachs and 48 hindguts taken from separate fish between 229 and 384mm were analysed. All of these fish were caught on handline in the Noordhoek area. The results are summarised in Table 25.

An analysis of stomach contents showed that crinoids, decapods, ophiuroids, asteroids and anomurans respectively were the most important prey items in terms of numbers, frequency of occurrence and volume. Asteroids were more important than ophiuroids because of a greater mean percentage volume contribution. Overall, 47 different prey items were recorded from the stomachs.

By comparison hindgut analysis produced 49 different prey items, the relative importance of which were little different from those in stomachs. The rank order of importance between crinoids and decapods and between ophiuroids and anomurans switched, in both cases a relative increase in the importance of crustacean over echinoderm prey. Such a switch was, however, not apparent when considering percentage frequency of occurrence. The apparent increase in percentage volume estimates of crustacean over echinoderm prey could have resulted from the relatively unchanged state of crustacean exoskeletons in the hindgut. Echinoderms on the other hand were more rapidly broken up by mastication and digestion and occupied a smaller volume in the hindgut. Comparisons between stomach and hindgut based on mass would also be expected to differ. Despite the unchanged volume of crustacean material as it passed through the gut, there was a considerable reduction in mass per unit volume as a result of the digestion of soft tissue. This finding would hold true for a number of other prey types with hard exoskeletons.

TABLE 25. Prey groups represented in the stomachs (n=50) and hindguts (n=48) of Chrysoblephus laticeps sampled at Noordhoek in 1980. Fork length range = 229-384mm.

Prey species	% Numbers		% Freq occ		Mean % Vol		Rank	
	S	H	S	H	S	H	S	H
Crinoidea	19.8	16.8	62.0	56.3	29.3	26.8	18.1	15.1
Decapoda	21.4	24.6	56.0	68.0	26.6	34.4	14.9	23.4
Asteroidea	8.6	7.4	30.0	27.1	12.4	8.3	3.7	2.2
Ophiuroidea	12.8	10.8	32.0	25.0	8.9	3.7	2.9	0.9
Unidentified	-	-	38.0	43.8	6.2	7.7	2.4	3.4
Anomura	11.8	13.8	38.0	33.3	4.6	8.0	1.8	2.6
Polychaeta	4.8	1.5	18.0	6.3	2.2	1.6	0.4	0.1
Gastropoda	6.4	6.9	10.0	20.8	2.7	2.5	0.3	0.5
Pelecypoda	2.1	2.5	8.0	10.4	1.0	0.7	0.07	0.07
Amphineura	0.5	1.5	2.0	6.3	0.3	0.8	0.06	0.05
Echinoidea	3.2	1.5	6.0	6.3	0.9	0.7	0.05	0.05
Sipunculida	2.7	5.9	8.0	10.4	0.4	1.8	0.03	0.02
Cephalopoda	1.1	0.5	4.0	2.1	0.7	0.1	0.02	T
Isopoda	0.5	1.0	2.0	4.2	0.8	0.3	T	T
Cirripeda	0.5	-	2.0	-	3.0	-	T	-
Bryozoa	1.6	1.5	6.0	6.1	0.2	0.2	T	0.01
Cnidaria	1.6	1.5	6.0	6.3	0.1	0.2	T	0.01
Porifera	0.5	0.1	2.0	4.2	0.1	0.1	T	T
Algae	-	0.5	-	2.1	-	0.1	-	T

Trace (T) = Prey with a rank less than 0.01.

Considering the minor components of the diet it is clear that, although the relative importance of prey may vary between the stomach and the hindgut the overall composition of the diet is essentially similar. There is little evidence to suggest that the occurrence of hard tissues is unduly exaggerated in the hindgut of C. laticeps.

Comparison of the diet of small and large fish

A total of 37 small C. laticeps between 37 and 135mm long were speared on Coke tin reef during April 1982 and April 1983, of which 28 had stomach contents (Table 26). No C. laticeps larger than 135mm was seen on Coke-tin Reef or any other shallow reef in Algoa Bay during the study (personal observation). Polychaete worms ranked as the most important prey item in terms of frequency of occurrence (64.3%) and volume (40.2%), although the group was numerically inferior to crustaceans. Crustaceans included macrurans, mysids, brachyurans, amphipods, anomurans, tanaids, isopods, ostracods and cumaceans, all of which represented small specimens, and most of which were ingested whole. Apart from polychaetes the only non-arthropod group represented was the ophiuroid Amphiura capensis which was found in two stomachs.

A total of 82 fish between 101 and 334mm long were speared on Phil's Reef between September 1980 and January 1983. Of these, 50 had stomach contents, 23 had hindgut contents (stomach empty) and nine were completely empty. The animals were arbitrarily divided into two length classes, 100-200 and >200mm. There were 19 different prey items in the stomachs of the 37 fish in the 100-200mm size class (Table 27), and the importance of prey in terms of frequency of occurrence, numbers and rank was similar in all stomachs. Ophiuroids were the most important group, Ophiothrix fragilis, Ophiactus carnea and Amphipholis similis being identified. Decapod crustaceans occurred more frequently (43.2%), but they were ranked below polychaetes (35.1%) because of their lower mean volume contribution to the diet. As a group, crustaceans were more important in the diet than polychaetes. A number of prey items not found in the diet of small fish (<100mm) were recorded for this length class. These included cephalopods, nemerteans, fish, sipunculids, gastropods, pelecypods and the sea urchin Parechinus angulosus.

The diet of 13 large C. laticeps (>200mm) differed considerably from that of the smaller ones (Table 28). Cephalopods, which with one exception were absent in the diet of small fish, were the most important group, followed by crinoids, polychaetes and echinoids. The diet of large fish was characterised by low percentage numbers, but high percentage volume contributions of the important prey species. Smaller prey items such as ophiuroids and the small crustaceans were replaced by larger animals. This finding represented an apparent change in feeding

TABLE 26. Analysis of the stomachs of 28 juvenile *Chrysoblephus laticeps* (FL = 37-135mm) speared on Coke tin reef between April 1982 and April 1983.

Prey species	% Numbers	% Freq occ	Mean % Vol	Rank
Polychaeta				
Remains	15.5	64.3	40.2	25.8
Macrura	26.4	42.9	22.1	9.5
Remains	6.2	25.0	11.8	
Caridae	7.8	17.9	4.6	
Euphausidae	10.1	7.1	3.9	
Nouvelia natalensis	0.8	3.6	1.2	
Hippolyte kraussina	1.6	3.6	0.5	
Mysidacea	35.7	32.1	11.6	3.7
Remains	23.3	17.9	5.7	
Mesopodopsis slabberi	0.8	3.6	3.5	
Mysidopsis similis	11.6	10.7	2.3	
Brachyura	3.1	14.3	7.4	1.0
Dehaanius dentatus	0.8	3.6	3.4	
Macropodia falcifera	0.8	3.6	1.4	
Remains	0.8	3.6	1.4	
Megalopa	0.8	3.6	1.2	
Amphipoda	7.8	21.4	4.6	1.0
Remains	6.9	17.9	4.4	
Caprellidae	0.9	3.6	0.2	
Unidentified remains	-	7.1	4.6	0.3
Ophiuroidea				
Amphiura capensis	1.6	7.1	2.9	0.2
Anomura				
Galathea sp.	1.6	7.1	2.6	0.2
Tanaidacea	3.9	10.7	2.0	0.2
Pycnogonida	0.8	3.6	1.4	0.1
Isopoda	0.8	3.6	0.3	0.01
Ostracoda	0.8	3.6	0.1	T
Cumacea	0.8	3.6	0.1	T

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

TABLE 27. Analysis of the stomachs of 37 *Chrysoblephus laticeps* (FL = 100-200mm) speared on Phil's reef between September 1980 and January 1983.

Prey species	% Numbers	% Freq occ	Mean % Vol	Rank
Ophiuroidea	43.9	67.5	41.6	28.1
Ophiothrix fragilis	26.3	51.3	29.1	
Ophiactus carnea	4.4	8.1	2.9	
Amphioplus integer	1.1	2.7	2.7	
Unidentified	12.0	10.8	6.7	
Polychaeta	16.4	35.1	17.3	6.1
Decapoda	17.5	43.2	13.1	4.3
Brachyura	5.4	13.5	7.0	
Galathea sp.	5.4	13.5	1.4	
Paguridea	2.2	5.4	3.0	
Macrura	2.2	5.4	1.4	
Dehaanius dentatus	1.1	2.7	0.9	
Pseudodromia latens	1.1	2.7	0.8	
Isopoda	6.5	13.5	9.2	1.2
Crinoidea				
Tropiometra carinata	3.0	8.1	3.7	0.29
Mysidacea	1.1	2.7	2.7	0.07
Cephalopoda				
Sepia tuberculata	1.1	2.7	2.7	0.07
Sipunculida	2.2	5.4	1.5	0.08
Nemertea	1.1	2.7	2.0	0.06
Pisces	1.1	2.7	1.6	0.04
Gastropoda	1.1	2.7	1.4	0.04
Unidentified remains	-	5.4	0.8	0.04
Pelecypoda	1.1	2.7	1.1	0.03
Echinoidea				
Parechinus angulosus	3.3	8.1	0.2	0.01

TABLE 28. Analysis of the stomachs of 13 large *Chrysoblephus laticeps* (FL>200mm) speared on Phil's reef between September 1980 and January 1983.

Prey species	% Numbers	% Freq.occ	Mean % Vol	Rank
Cephalopoda	15.0	38.5	34.9	13.4
Octopus sp.	10.8	25.0	91.3	
Sepia sp.	5.4	16.6	90.0	
Crinoidea	15.0	46.2	13.3	6.1
Comanthus wahlbergi	2.5	7.7	7.3	
Tropiometra carinata	7.5	23.1	5.1	
Remains	5.0	15.4	0.9	
Polychaeta	10.8	30.8	11.3	3.5
Echinoidea				
Parechinus angulosus	7.5	23.1	10.4	2.4
Ophiuroidea	27.5	30.8	9.5	2.9
Ophiothrix fragilis	25.0	23.1	9.3	
Remains	2.5	7.7	0.2	
Decapoda	10.0	30.8	6.3	1.9
Unidentified	2.5	7.7	1.9	
Dromiacea	5.0	15.4	3.9	
Plagusia chabrus	2.5	7.7	0.6	
Sipunculida	5.0	15.4	6.9	1.0
Isopoda	5.0	15.4	1.9	0.3
Amphineura	2.5	7.7	3.9	0.3
Gastropoda				
Fissurellida	2.5	7.7	0.8	0.06
Unidentified remains	-	7.7	0.8	0.06

strategy, in which a meal consisted of a large prey item instead of a number of small prey items.

Daylight observations showed that C. laticeps usually swam close to the reef both as individuals and in loose groups. Feeding individuals hovered above the reef in a head down searching mode and attacked and rapidly consumed prey when found. A feature of the diet of smaller fish was the fact that most prey were ingested whole. This was only partially the case in larger fish, which were able to crush prey such as echinoids, crinoids and asteroids. These feeding habits are reflected in the jaws of juvenile and adult fish both of which are equipped with incisiform teeth specialised for grasping prey. Large fish also have well developed crushing teeth (Fig. 38).

Apparent feeding selectivity

Measures of overlap between the prey items found in the stomach and the available food may reveal the degree of specialisation in the diet of a predator (Frame 1974). The absolute availability of any particular prey item is difficult to quantify owing to effects such as accessibility, conspicuousness and activity, both on the part of the prey and the predator. An excess of a particular prey item in the stomach over its occurrence in the available food may thus be a combination of these effects as well as selectivity on the part of the predator (Jones 1952). Assuming that all prey items eaten are equally available, the apparent selectivity of the predator for a particular prey may be calculated from the selectivity index already described.

Numerical and mass percentages of potentially available prey are presented in Figure 39. Prey items not found in the diet of C. laticeps, including poriferans, octocorals, hydrozoans and ascidians were omitted. Differences between the apparent feeding selectivity of large and small C. laticeps are shown in Figure 40.

Fish in the 100-200mm size class fed non-selectively on polychaetes, isopods, crinoids, gastropods, bivalves and selectively on ophiuroids. Although Ophiothrix fragilis only constituted 28% of the available ophiuroid prey it formed 83% of the ophiuroids eaten. On the other hand Ophiactus carnea formed 60% of available and only 13% of ingested ophiuroids. Underwater observations showed that O. carnea remained sheltered on the reef, particularly amongst reef-building bryozoans, while O. fragilis was more often seen crawling over the bryozoans and may therefore have been exposed to predation. The larger size of O. fragilis may further increase its availability to predators. Groups apparently selected for included sipunculids, small echinoids (P. angulosus) and decapod crustaceans. With the exception of Inachus guentheri and Pinnotheres spp., all of the crab species found on the reef

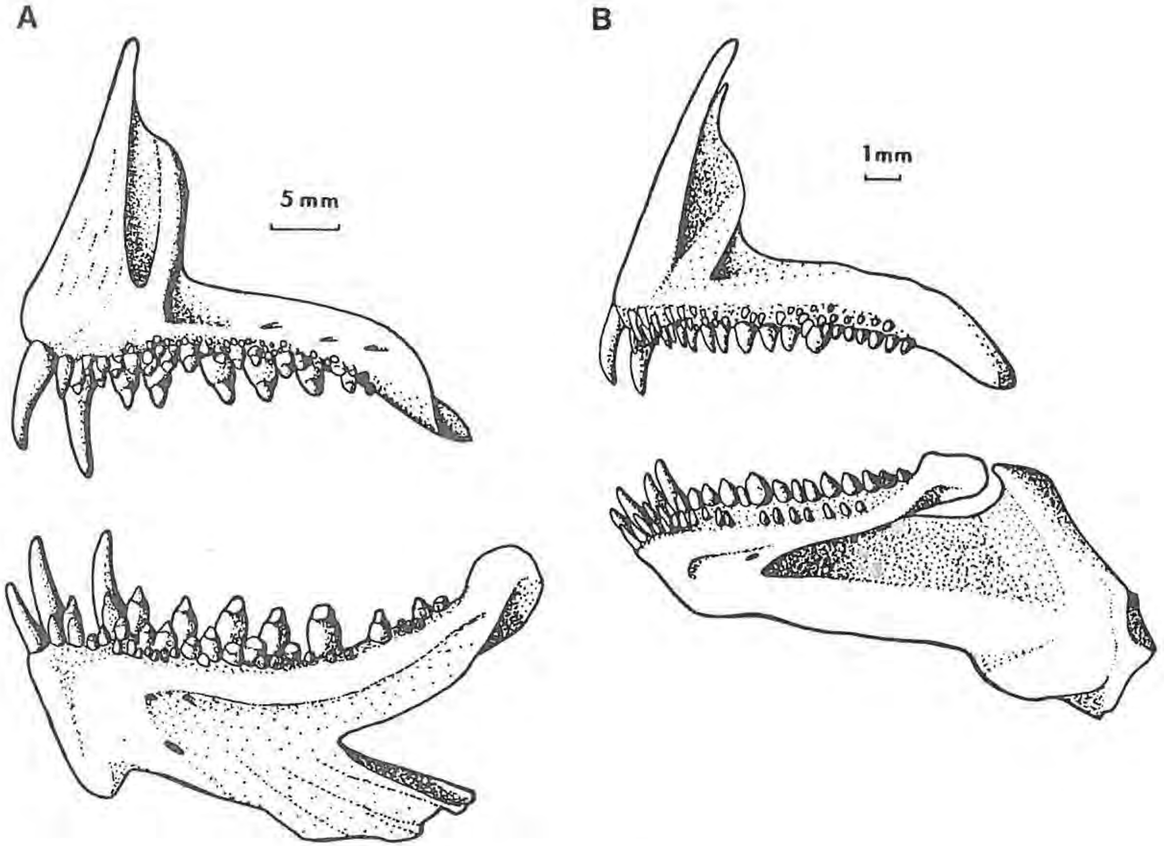


Figure 38. Medial lateral view of the jaws of *Chrysoblephus laticeps*. (a) fish >200mm, (b) fish 100mm.

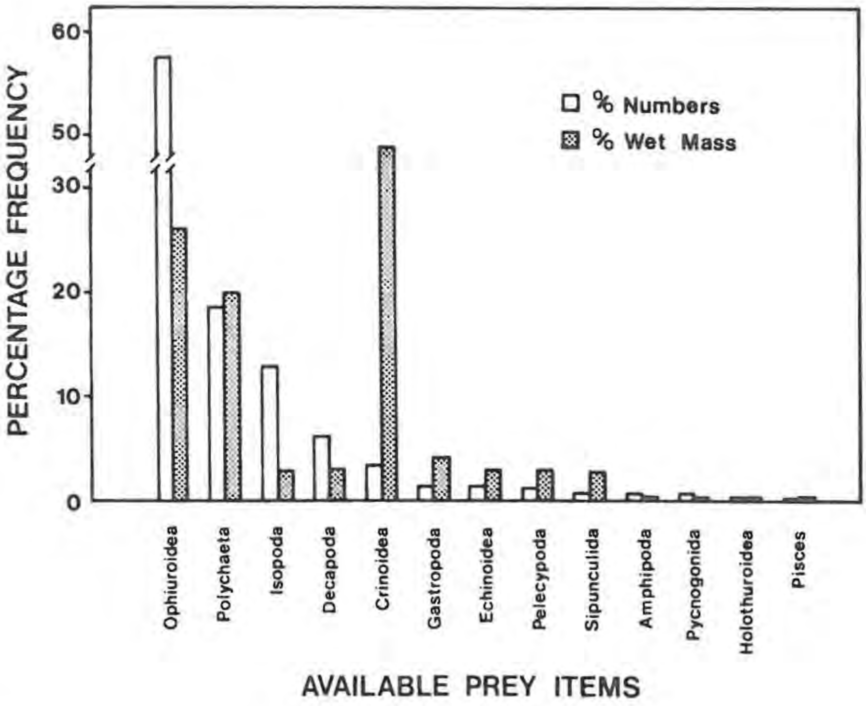


Figure 39. Numerical and mass percentages of potentially available prey found on Phil's Reef in 1982.

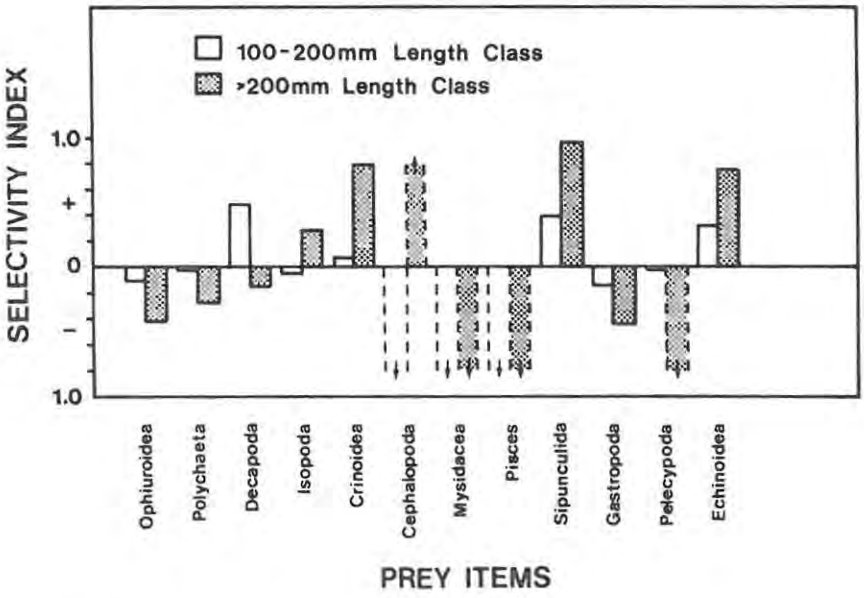


Figure 40. Apparent feeding selectivity of *Chrysoblephus laticeps* speared on Phil's Reef between 1980 and 1983. Inferred preferences (dashes) are explained in the text.

were represented in the stomachs of small C. laticeps. Of the more mobile prey, only one cephalopod, Sepia tuberculata, was found in the diet while Octopus spp. were completely absent.

In fish larger than 200mm small prey including ophiuroids, polychaetes and crustaceans were less important in the diet. This was reflected by negative selectivity indices, while crinoids, echinoids, sipunculids and to a lesser extent isopods were selected food items (Fig. 40). The inability to sample highly mobile prey species including cephalopods, mysids and fish presented a problem in assessing the apparent selectivity for these items in the diet. An ongoing benthic survey of this area suggests that cephalopods are not numerically important on Phil's reef (P.S. Coetzee, Port Elizabeth University, pers. comm.). Nevertheless, cephalopods (Sepia spp. and Octopus spp.) were the most important prey in the diet of large C. laticeps, suggesting considerable selectivity for these prey.

Analysis of diet in the Tsitsikamma area

The smallest fish sampled were speared in March 1983 at the Mooring Gulley, in water less than 10m deep. The stomach contents of eight fish between 69 and 79mm long are summarised in Table 29. Polychaete worms were the most important prey item in terms of rank (25.8), frequency of occurrence (62.5%) and volume (41.3%), although they were numerically inferior to crustaceans. These included amphipods, brachyurans, mysids and macrurans in order of importance. Small fish were found in the same habitat in both Tsitsikamma and Port Elizabeth, a reef-sand interface in shallow water. The diets of small fish were similar in the two areas, both in terms of prey type and range of prey eaten.

A total of 118 C. laticeps, between 143mm and 425mm long, were speared at the Knoll in the Tsitsikamma Park between March 1985 and October 1986. Of these, 68 had stomach contents, 44 had hindguts (stomach empty) and six were completely empty. Thirteen different prey groups were recorded in the stomachs of the 18 fish between 101 and 200mm fork length (Table 30). Compared to the smaller fish the diet was characterised by a greater range of prey items some of which had been broken up by chewing. Polychaetes ranked highest (21.7) and were more important in the diet than any other prey group in terms of numbers (27.5%), frequency of occurrence (55.6%) and volume (39.1%). They were followed by ophiuroids and brachyurans which ranked 3.5 and 3.1 respectively.

The diet of 50 large C. laticeps, between 201 and 425mm fork length, is summarised in Table 31. Twenty-eight different prey items were recorded of which Brachyura (10.0) ranked most important above gastropods (4.3), polychaetes (3.9) and Octopus sp. (2.3). Some of the prey items important in the diet of large fish but absent from the diet of small

TABLE 29. Analysis of the stomachs of 8 juvenile *Chrysoblephus laticeps* (FL = 69-79mm) speared in the Mooring Gulley in March 1983.

Prey species	% Numbers	% Freq.occ	Mean % Vol	Rank
Polychaeta	21.7	62.5	41.3	25.8
Unidentified remains	-	37.5	25.0	9.4
Amphipoda	34.8	25.0	5.6	1.4
Brachyura *Dehaanius dentatus*	4.4	12.5	11.3	1.4
Amphineura	4.4	12.5	6.3	0.8
Ophiuroidea	4.4	12.5	6.3	0.8
Mysidacea	8.7	12.5	1.3	0.2
Echinoidea *Parechinus angulosus*	4.4	12.5	1.3	0.2
Macrura Caridae	4.4	12.5	0.6	0.08

TABLE 30. Analysis of the stomachs of 18 Chrysoblephus laticeps (FL = 100-200mm) speared in the Knoll area between March 1985 and October 1986.

Prey species	% Numbers	% Freq.occ	Mean % Vol	Rank
Polychaeta	27.5	55.6	39.1	21.7
Ophiuroidea	25.0	27.8	12.4	3.5
Ophiothrix fragilis	20.0	16.7	5.1	
Remains	5.0	11.1	7.4	
Brachyura	12.5	27.8	11.1	3.1
Remains	5.0	11.1	8.5	
Dehaanius dentatus	7.5	16.7	2.6	
Cephalopoda				
Octopus sp.	5.0	11.1	5.6	0.6
Crinoidea				
Comanthus wahlbergi	5.0	11.1	5.2	0.6
Unidentified remains	-	5.6	5.6	0.3
Pisces	5.0	11.1	2.8	0.3
Gobiidae	2.5	5.6	2.8	
Apletodon pelligrini	2.5	5.6	0.1	
Echinoidea				
Parechinus angulosus	2.5	5.6	4.6	0.3
Sipunculida	10.0	5.6	1.9	0.1
Gastropoda				
Fissurellidae aperta	2.5	5.6	0.6	0.03
Asteroidea				
Marthasterius glacialis	2.5	5.6	0.1	0.01

TABLE 31. Analysis of the stomachs of 50 *Chrysoblephus laticeps* (FL = 201-425mm) speared in the Knoll area between March 1985 and October 1986.

Prey species	% Numbers	% Freq.occ	Mean % Vol	Rank
Brachyura	24.5	40.0	24.9	10.0
Plagusia chabrus	13.3	24.0	14.5	
Dehaanius dentatus	8.2	14.0	7.3	
Remains	3.1	4.0	3.2	
Gastropoda	14.3	26.0	16.6	4.3
Remains	5.1	10.0	7.8	
Haliotus parva	3.1	8.0	3.5	
Opercular remains	2.0	4.0	1.2	
Megatobennus africanus	1.0	2.0	2.0	
Haliotus sangineum	1.0	2.0	1.2	
Fissurellidae	1.0	2.0	0.5	
Amblichilepas scutella	1.0	2.0	0.3	
Polychaeta	14.3	30.0	13.1	3.9
Cephalopoda				
Octopus sp.	9.2	18.0	12.8	2.3
Echinoidea	9.2	18.0	10.5	1.9
Parechinus angulosus	8.1	16.0	8.8	
Echinocardium cordatum	1.0	2.0	1.7	
Crinoidea	7.1	16.0	7.8	1.2
Comanthus wahlbergi	4.1	8.0	5.1	
Tropiometra carinata	3.1	6.0	2.6	
Remains	-	2.0	0.1	
Ophiuroidea	6.1	12.0	2.5	0.3
Ophiothrix fragilis	5.1	8.0	2.5	
Remains	1.0	4.0	0.04	
Pisces	3.1	8.0	2.4	0.2
Clinidae	2.0	4.0	1.2	
Gobiidae	1.0	2.0	0.8	
Apletodon pelligrini	0.1	2.0	0.4	
Asteroidea	2.0	4.0	3.4	0.1
Marthasterius glacialis	1.0	2.0	2.0	
Remains	1.0	2.0	1.4	
Acidiacea				
Pyura sp.	2.0	4.0	1.5	0.06
Amphineura	2.0	4.0	1.5	0.06
Sipunculida	2.0	4.0	1.4	0.05
Unidentified remains	-	4.0	0.7	0.02

Table 31 cont/...

TABLE 31 continued

Prey species	% Numbers	%Freq occ	Mean%Vol	Rank
Macrura	1.0	2.0	0.6	0.01
Isopoda	1.0	2.0	0.3	T
Anomura	1.0	2.0	0.1	T

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

fish were considered 'difficult to handle' in the following terms. These included gastropods and amphineurans which are protected by hard exoskeletons, as well as keyhole limpets and Haliotidae which are difficult to remove from the substrate. Highly mobile species such as crabs and cephalopods were also more important in the diet. These inclusions suggest a greater ability to manipulate prey both in terms of capture and in dealing with protective armour.

The same general characteristics of the diet of C. laticeps sampled in Port Elizabeth were found in the fish sampled in Tsitsikamma. Small fish fed on small prey which were swallowed whole, and the diet was apparently gape limited. The increase in gape and the acquisition of more powerful jaws in larger fish enabled a proportionately higher degree of prey manipulation.

Changes in the diet with locality

Summary diagrams of the diets of large fish (>200mm) from the Noordhoek, Algoa Bay, Knoll and Rheeders areas are presented in Figure 41. A combined total of 56 prey species from 23 groups were identified in these areas but despite this wide variety of potential prey only eight groups were abundant in the diets. These included brachyurans, crinoids, cephalopods, asteroids, echinoids, gastropods, polychaetes and ophiuroids. The relative importance of each group was clearly different both between and within the geographical areas studied. These changes may have resulted from selection on the part of the predator or differences in the availabliliy of prey between areas.

Feeding periodicity

The presence of food in the guts of 117 fish speared at the Knoll at different times of the day is summarised in Figure 42. The proportion of stomachs containing food was fairly consistent thoughout the day, and at any time approximately half contained food. Most of the hindguts examined contained food, with a trend of increasing fullness towards the evening. Although not conclusive, these results suggest that C. laticeps are diurnal feeders, feeding intensively at first light. This was evident from the greater incidence of full stomachs in the early morning and a higher proportion of food in the first quarter of the hindgut at this time of the day. Feeding continues throughout the day and may peak again just before sunset. Passage rate through the hindgut appeared to be quite slow, as judged by the presence of food in the hindguts of all fish sampled very early in the morning. A more detailed study including fish sampled at night is necessary to confirm these observations.

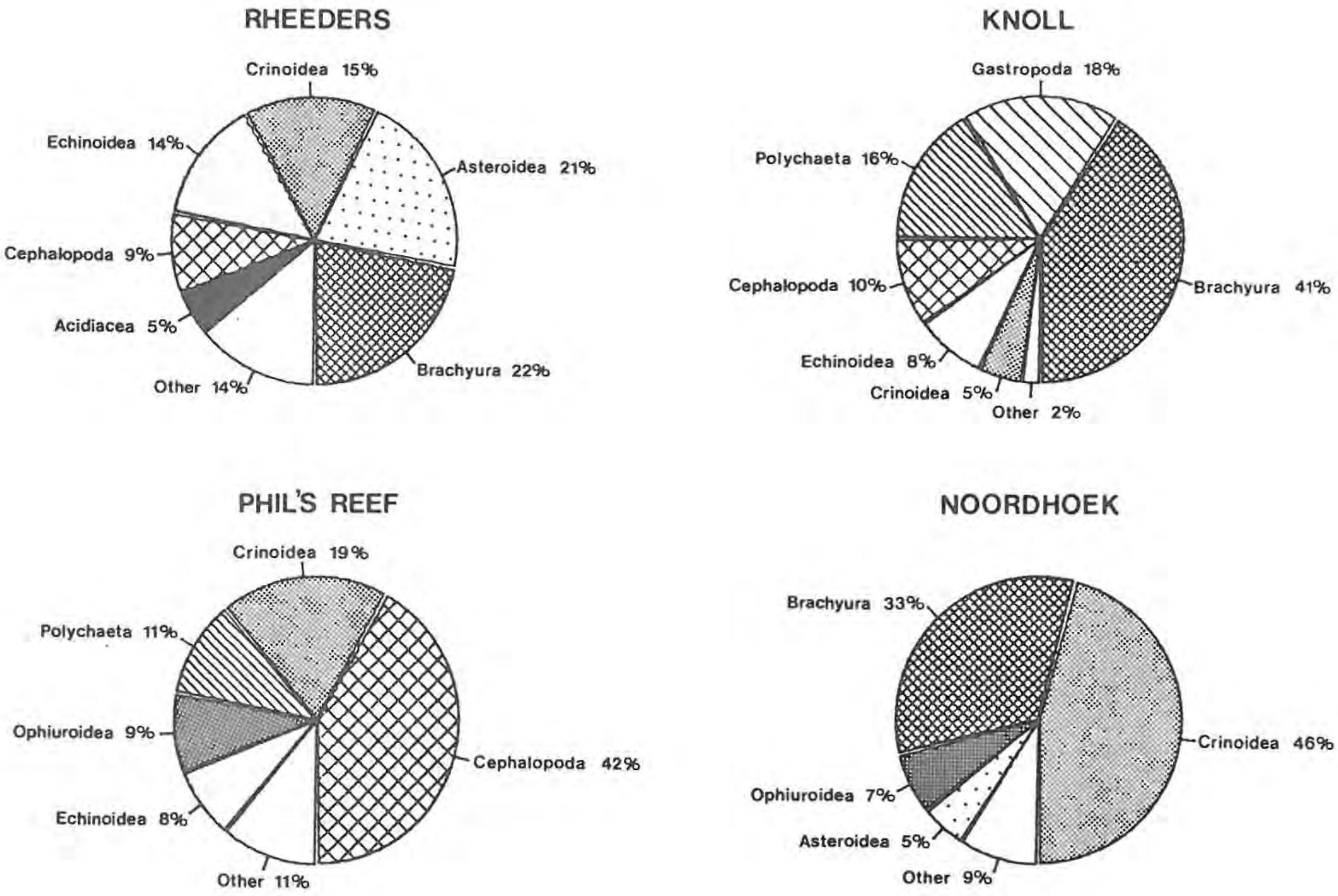


Figure 41. Comparison of the diet of *Chrysoblephus laticeps* from four areas on the Cape south coast, Rheeders and Knoll in the Tsitsikamma Park and Phil's Reef and Noordhoek in the Port Elizabeth area. Major prey groups are expressed as a percentage of the ranked index.

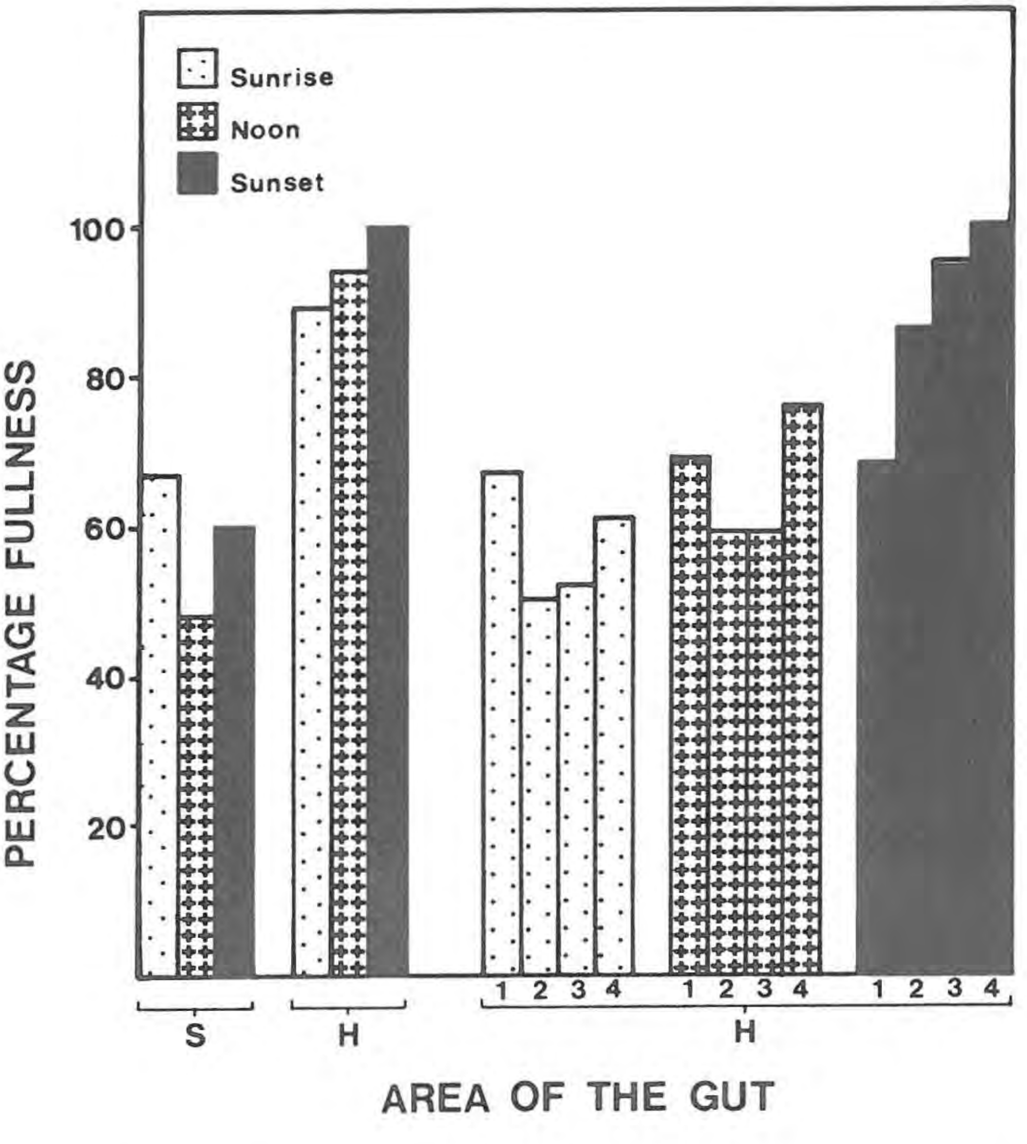


Figure 42. Percentage fullness of the stomachs (S) and hindguts (H) of 117 Chrysoblephus laticeps sampled at different times of the day. The hindgut was also separated into equal quarters (1-4), from the pylorus to the anus, to roughly determine passage rate of food. All fish were speared at the Knoll in Tsitsikamma between August 1985 and October 1986.

Chrysoblephus cristiceps

For this species the contents of both stomachs and hindguts were examined because sample sizes were small in some areas. Although the relative importance of major prey groups in both areas of the gut was similar, there were considerable differences between the number of species representing each prey group. The diversity found in the hindguts of sub-adult and adult C. cristiceps was greater than that found in stomachs, particularly of species belonging to echinoderm, brachyuran and molluscan groups. The reason for this was thought to be a combination of small sample sizes and large diet width, possibly compounded by longer retention times of hard exoskeletal material in the hindgut. Quantitative analyses of trends in the diet were limited to stomach contents and only when necessary was specific reference made to hindgut contents.

Analysis of the diet in the Port Elizabeth area

Twenty-seven different prey items, representing 18 prey groups, were recognised in the stomachs of the 41 juvenile C. cristiceps speared at Phil's reef (Table 32). These fish sampled between June 1981 and May 1982 ranged in length between 99 and 225mm fork length. Although this represented a high diversity of prey, only four groups, ophiuroids, brachyurans, polychaetes and anomurans, contributed significantly to the diet. Ophiuroids were considerably more important than the other three in terms of frequency of occurrence (62.9%), volume (36,9%), numbers (32,5%) and rank (22.0) and Ophiothrix fragilis was the most common of the brittle-stars eaten. Next most important were brachyurans, which had lower individual contributions than polychaetes and anomurans but were ranked higher as a group because they were represented by more species. Those identified included the small seaweed crab Dehaanius dentatus, Plagusia chabrus, Parapilumnous sp. and numerous sponge crab species (Dromiidae). With the exception of the crabs and the two crinoid species, Tropiometra carinata and Comanthus wahlbergi, prey items taken by juvenile C. cristiceps were small and the size of prey items eaten was related to the size of the fish.

The diet of 86 sub-adult C. cristiceps between 226 and 335mm fork length is summarised in Table 33. These fish, caught between February 1980 and March 1982, included both speared and line-caught fish in the area between Sardinia Bay and Woody Cape. Ranked in order of importance the three major prey groups eaten were crinoids (14.2), brachyurans (13.7) and ophiuroids (4.6). Again the stomachs contained a high diversity of prey representing at least 30 species from 18 groups. By including prey found in the hindguts this number increased to 48 species. Next to the crinoid T. carinata (2.87) the ophiuroid O. fragilis (1.5) was the most

TABLE 32. Prey recorded in the stomachs (n=35) and hindguts (n=11) of *Chrysoblephus cristiceps* (FL=99-226mm) sampled at Phil's reef between 1981 and 1982.

Prey Species	Numbers (%)		Frequency occ. (%)		Mean volume (%)		Rank	
	S	H	S	H	S	H	S	H
Ophiuroidea	32.5	20.8	62.9	72.7	35.0	44.2	22.0	32.1
Ophiothrix fragilis	21.7	10.4	48.7	36.4	27.4	26.4		
Remains	3.6	10.4	8.6	36.4	3.6	17.8		
Ophiactus carinea	6.0	-	8.6	-	3.4	-		
Amphiura capensis	1.2	-	2.9	-	0.6	-		
Brachyura	12.1	14.6	28.6	45.4	17.0	9.3	4.9	4.1
Remains	6.0	2.1	14.3	9.1	7.6	0.2		
Dehaanius dentatus	2.4	2.1	5.7	9.1	1.7	0.9		
Plagusia chabrus	1.2	2.1	2.9	9.1	2.9	0.9		
Dromiidae	1.2	8.3	2.9	18.2	2.9	7.3		
Parapilumnus sp.	1.2	-	2.9	-	2.0	-		
Polychaeta	13.3	8.3	31.4	27.3	10.2	9.6	3.2	2.6
Remains	-	4.2	-	18.2	-	5.0		
Eunice sp.	-	4.2	-	9.1	-	4.6		
Anomura	15.7	14.6	28.6	27.3	10.7	9.5	3.1	2.6
Galathea sp.	9.6	12.5	20.0	18.2	6.9	9.0		
Paguridae	6.0	2.1	8.6	9.1	3.9	0.5		
Cephalopoda	2.4	2.1	5.7	9.1	4.3	0.5	0.3	0.04
Sepia sp.	1.2	-	2.9	-	2.3	-		
Octopus sp.	1.2	-	2.9	-	2.0	-		
Egg mass	-	2.1	-	9.1	-	0.5		
Pisces	2.4	-	5.7	-	4.3	-	0.3	-
Mysidacea	1.2	-	5.7	-	4.0	-	0.2	-
Siriella sp.	1.2	-	2.9	-	2.9	-		
Remains	1.2	-	2.9	-	1.1	-		
Crinoidea	3.6	16.7	8.6	18.2	2.6	5.5	0.2	0.9
Tropiometra carinata	2.4	2.1	5.7	9.1	2.0	2.7		
Comanthus wahlbergi	1.2	-	2.9	-	0.6	-		
Remains	-	14.6	-	18.2	-	2.7		
Macrura	3.6	2.1	5.7	9.2	3.4	0.1	0.2	0.3
Hippolyte kraussina	3.6	-	5.7	-	3.4	-		
Remains	-	2.1	-	9.1	-	0.1		
Pycnogonida	1.2	2.1	2.9	9.1	2.9	0.1	0.08	0.08
Isopoda	2.4	2.1	2.9	9.1	1.4	3.6	0.04	0.3
Holothuroidea	1.2	-	2.9	-	1.4	-	0.04	-
Unidentified Remains	-	-	5.7	27.3	0.7	13.2	0.04	3.6

Table 32 cont/...

TABLE 32 continued.

Prey Species	Numbers (%)		Frequency occ. (%)		Mean volume (%)		Rank	
	S	H	S	H	S	H	S	H
Gastropoda	2.4	6.3	5.7	18.2	0.6	1.6	0.04	0.3
Megatobennus africanus	1.2	-	2.9	-	0.6	-		
Remains	1.2	4.2	2.9	18.2	0.6	0.8		
Fissurella scutella	-	2.1	-	9.1	-	0.8		
Pelecypoda	1.2	4.2	2.9	18.3	0.6	0.8	0.02	0.1
Chlamus tinctus	-	2.1	-	9.1	-	0.7		
Remains	-	2.1	-	9.1	-	0.2		
Echinoidea								
Parechinus angulosus	1.2	2.1	2.9	9.1	0.1	0.1	T	T
Sipunculida	1.2	-	2.9	-	0.6	-	0.0	-
Amphineura								
Chiton tulipa	-	2.1	-	9.1	-	0.9	-	0.1
Porifera	-	2.1	-	9.1	-	0.5	-	T

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

TABLE 33. Prey recorded in the stomachs (n=43) and hindguts (n=56) of *Chrysoblephus cristceps* (FL=226-335mm) sampled between Sardinia Bay and Woody Cape from 1980-1982.

Prey Species	Numbers (%)		Frequency occ. (%)		Mean volume (%)		Rank	
	S	H	S	H	S	H	S	H
Crinoidea	16.1	11.4	55.8	66.1	25.5	24.4	14.2	16.1
Tropiometra carinata	4.9	2.6	25.6	14.3	11.2	7.4		
Comanthus wahlbergi	6.6	2.6	16.3	17.9	6.2	5.3		
Unidentified	4.5	6.2	16.3	35.7	8.1	11.7		
Brachyura	27.3	26.6	58.1	73.2	23.5	31.5	13.7	23.1
Unidentified	12.8	6.9	32.6	30.4	11.3	11.1		
Plagusia chabrus	3.3	2.9	16.3	19.6	7.4	5.7		
Dehaanius dentatus	7.8	11.9	11.6	33.9	3.3	10.1		
Dromiidae	2.4	1.0	11.6	7.1	1.4	1.8		
Inachus guntheri	0.4	0.7	2.3	1.8	0.1	0.1		
Mursia cristimanus	0.4	-	2.3	-	0.1	-		
Macropodia falcifera	-	1.4	-	10.7	-	1.4		
Pseudodromia rotunda	-	1.2	-	7.4	-	0.9		
Pseudodromia sp.	-	0.2	-	1.8	-	0.2		
Ophiuroidea	12.4	6.4	34.9	30.4	12.8	4.5	4.5	1.4
Ophiothrix fragilis	4.5	0.2	20.9	1.8	7.3	0.1		
Unidentified	7.0	5.9	11.6	26.8	4.6	4.3		
Ophionereis porrecta	0.8	-	4.7	-	0.9	-		
Ophiarachnella capensis	-	0.2	-	1.8	-	0.1		
Unidentified remains	-	-	34.9	71.4	6.1	17.5	2.1	12.5
Gastropoda	2.4	19.7	25.6	42.9	6.8	4.5	1.7	1.9
Haliotus parva	1.6	2.4	9.3	7.1	3.3	0.7		
Amblichilepus scutella	0.8	0.2	4.7	1.8	2.3	1.3		
Shell fragments	4.9	9.7	4.7	21.4	0.3	1.5		
Haliotus sangineum	1.2	0.2	2.3	1.8	0.6	0.0		
Phallium labiatum	2.0	-	2.3	-	0.1	-		
Opercular remains	0.4	1.0	2.3	5.4	0.1	0.2		
Marginella sp.	0.8	-	2.3	-	0.0	-		
Unidentified Remains	0.4	4.0	2.3	8.9	0.0	0.5		
Oxystele sp.	-	0.5	-	1.8	-	0.2		
Megatobennus africanus	-	0.2	-	1.8	-	0.1		
Fissurella mutabilis	-	0.2	-	1.8	-	0.1		
Gibbula sp.	-	0.5	-	1.8	-	T		
Nassarius sp.	-	0.2	-	1.8	-	T		
Fissurellidae	-	0.5	-	1.8	-	T		
Anomura	9.5	14.0	20.9	44.6	8.3	7.6	1.7	3.4
Unidentified	7.0	6.9	11.6	26.8	4.9	4.2		
Paguridae	2.4	5.0	9.3	14.2	3.4	2.4		
Galathea sp.		2.1		5.4		1.1		

Table 33 cont/...

TABLE 33 continued

Prey Species	Numbers (%)		Frequency occ. (%)		Mean volume (%)		Rank	
	S	H	S	H	S	H	S	H
Cephalopoda	2.4	1.2	14.0	5.4	11.3	1.7	1.6	0.1
Octopus sp. (?vulgaris)	2.0	-	11.6	-	9.9	-		
Sepia sp.	0.4	1.0	2.3	3.6	1.4	1.7		
Loligo sp. (?reynaudi)	-	0.2	-	1.8	-	0.1		
Polychaeta	3.3	1.9	16.3	12.5	3.1	1.2	0.5	0.2
Unidentified	2.4	1.0	11.6	7.1	2.2	0.2		
Eunice sp.	0.4	1.0	2.3	5.4	0.5	0.9		
Thelepus pequenianus	0.4	-	2.3	-	0.5	-		
Asteroidea	1.2	0.5	7.0	3.6	1.4	0.4	0.1	1.5
Marthasterius glacialis	1.2	-	7.0	-	1.4	-		
Unidentified	-	0.5	-	3.5	-	0.4		
Echinoidea								
Parechinus angulosus	5.3	3.3	18.6	17.9	0.4	0.6	0.2	0.1
Pelecypoda	0.8	3.3	4.7	19.6	0.1	0.8	0.01	0.2
Chlamys tinctus	0.8	2.8	4.7	12.5	0.1	0.6		
Unidentified	-	0.7	-	5.4	-	0.1		
Limaria rotundata	-	0.2	-	1.8	-	0.1		
Amphineura	1.2	5.0	4.7	19.6	0.1	2.1	0.01	0.4
Unidentified	1.2	0.7	4.7	5.4	0.1	0.9		
Chaetopleura pertusa	-	2.4	-	3.6	-	0.7		
Chiton crawfordi	-	1.0	-	7.1	-	0.3		
Dinoplax gigas	-	0.2	-	1.8	-	0.1		
Notoplax productus	-	0.5	-	3.6	-	0.1		
Chiton tulipa	-	0.2	-	1.8	-	0.1		
Sipunculida	0.8	0.2	2.3	1.8	0.2	T	T	T
Isopoda	2.0	1.4	2.3	10.7	0.1	0.7	T	0.07
Amphipoda	2.9	0.2	2.3	1.8	0.1	0.2	T	T
Pycnogonida	0.4	0.5	2.3	3.6	0.1	0.3	T	0.01
Cnidaria	0.4	0.7	2.3	5.4	0.1	0.1	T	T
Algae	0.4	0.5	2.3	3.6	0.1	T	T	T
Bryozoa	0.4	0.7	2.3	5.4	T	0.1	T	T
Porifera	-	1.2	-	8.9	-	0.4	-	0.03
Pisces	-	0.5	-	3.6	-	0.3	-	0.01

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

important prey species consumed, followed by P. chabrus (1.9), Octopus sp. (1.14) and a second crinoid C. wahlbergi (1.10). As a group brachyurans ranked higher than ophiuroids because they were represented by more species. With an increase in size C. cristiceps were able to prey on animals that were more mobile (large crabs and octopus), protected by hard exoskeletons (large gastropods and amphineurans) and firmly attached to the substratum (limpets and Haliotidae). This trend, also observed in C. laticeps, indicated a greater ability to manipulate prey.

A total of 76 fish between 340 and 604mm fork length were sampled in the Port Elizabeth area, of which only 20 had food in their stomachs (Table 34). Crinoids (rank = 20.3) were the most important prey consumed, with T. carinata and C. wahlbergi being equally represented. Ophiothrix fragilis was the third most important species consumed but as a group ophiuroids were less important than both gastropods and brachyurans. The greatest differences between stomach and hindgut contents were observed in adult C. cristiceps. A combined total of 68 species were recorded in the diet of these fish of which only 26 were present in the stomach contents. In particular the number of brachyuran species recorded in the hindgut was significantly higher than the number found in the stomach. Brachyurans were also found in a higher percentage of the hindguts examined where they also averaged a higher mean percentage volume than in the stomachs. If this was not a result of the concentration of hard exoskeletal material in the hindguts, the contribution of brachyurans to the diet of adult C. cristiceps could be greater than suggested by stomach analysis. A similar argument holds for asteroid species which, although a minor component in the hindgut, were completely absent in the stomachs examined. The most probable explanation for these discrepancies was the low number of adult C. cristiceps stomachs available for analysis.

Analysis of the diet in the Tsitsikamma area

Only five small C. cristiceps were sampled in this area. They ranged in size between 73 and 89mm fork length and were all speared in the Mooring Gulley in March 1983. Analysis of stomachs only (Table 35), showed that ophiuroids (32.0) ranked highest in the diet followed by crinoids (12.3) and sipunculids (7.6). Although this sample was very small it compared well with the Port Elizabeth data and emphasised the importance of ophiuroids in the diet of small fish.

The narrower diet width observed in Tsitsikamma could simply be related to the sample size but may also be due to a size related change in diet. All of the Tsitsikamma fish were below 100mm fork length while the Port Elizabeth fish were all above this length. Obviously these differences could also be related to differences in prey availability in

TABLE 34. Prey recorded in the stomachs (n=20) and hindguts (n=66) of *Chrysoblephus cristiceps* (FL=337-602mm) sampled between Woody Cape and Sardinia Bay from 1980-1982.

Prey Species	Numbers (%)		Frequency occ. (%)		Mean volume (%)		Rank	
	S	H	S	H	S	H	S	H
Crinoidea	18.3	13.3	55.0	75.8	36.9	31.2	20.3	23.7
Tropiometra carinata	5.4	4.3	25.0	24.2	19.0	10.5		
Comanthus wahlbergi	11.8	5.0	25.0	25.8	12.9	10.8		
Unidentified	1.1	4.0	5.0	25.8	5.0	10.0		
Gastropoda	15.1	22.7	40.0	62.1	15.1	3.0	6.0	1.9
Remains	4.3	1.6	20.0	6.1	3.5	0.4		
Shell fragments	4.3	12.3	10.0	39.4	3.1	1.4		
Amblichilepas scutella	1.1	-	5.0	-	5.0	-		
Opercular remains	1.1	1.1	5.0	9.1	2.0	0.1		
Fissurellidea aperta	1.1	-	5.0	-	1.0	-		
Calliostoma africana	2.2	1.1	5.0	3.0	0.4	0.1		
Clavatula sp.	1.1	-	5.0	-	0.3	-		
Haliotus parva	-	0.5	-	4.6	-	0.3		
Fissurellidae	-	0.3	-	3.0	-	0.2		
Marginella piperata	-	1.3	-	1.5	-	0.1		
Haliotus sangineum	-	0.2	-	1.5	-	0.1		
Calliostoma ornata	-	0.8	-	1.5	-	0.1		
Crepidula sp.	-	0.2	-	1.5	-	0.1		
Fusinus sp.	-	2.2	-	1.5	-	0.1		
Oxystele sp.	-	0.3	-	1.5	-	0.0		
Trochidae	-	0.2	-	1.5	-	0.0		
Turitella carinifera	-	0.2	-	1.5	-	0.0		
Natica sp.	-	0.3	-	1.5	-	0.0		
Fissurella mutabilis	-	0.2	-	1.5	-	0.0		
Brachyura	9.7	19.0	25.0	80.3	11.0	26.6	2.7	21.4
Plagusia chabrus	1.1	2.9	5.0	16.7	5.0	4.0		
Eudromidia frontalis	2.2	0.2	10.0	1.5	1.7	0.3		
Dehaanius dentatus	2.2	3.0	10.0	18.2	1.4	1.7		
Unidentified	3.2	5.0	5.0	34.9	2.2	7.9		
Dromiidae	1.1	1.0	5.0	7.6	0.8	2.2		
Mursia cristimanus	-	3.8	-	16.7	-	5.8		
Macropodia falcifera	-	1.1	-	9.1	-	1.1		
Inachus guntheri	-	0.8	-	6.1	-	1.4		
Goneplax angulata	-	0.2	-	1.5	-	0.8		
Atelecyclus septemdentatus	-	0.2	-	1.5	-	0.5		
Pseudodromia latens	-	0.3	-	3.0	-	0.2		
Pseudodromia rotunda	-	0.2	-	1.5	-	0.3		
Philyra punctata	-	0.2	-	1.5	-	0.2		
Pseudodromia sp.	-	0.2	-	1.5	-	0.2		
Unidentified remains	2.2	0.8	30.0	74.2	8.0	14.8	2.4	11.0

Table 34 cont/...

TABLE 34 continued

Prey Species	Numbers (%)		Frequency occ. (%)		Mean volume (%)		Rank	
	S	H	S	H	S	H	S	H
Ophiuroidea	23.7	6.6	35.0	28.8	5.2	2.1	1.8	6.0
Ophiothrix fragilis	16.1	3.5	35.0	9.1	3.5	0.4		
Amphiura capensis	6.5	0.2	5.0	1.5	1.5	0.0		
Unidentified	1.0	1.9	5.0	15.2	0.2	1.2		
Amphipholis strata	-	0.8	-	4.6	-	0.3		
Astrocladus euryale	-	0.2	-	1.5	-	0.1		
Echinoidea	-	3.7	-	24.2	-	2.0	-	0.5
Echinocardium cordatum	2.2	0.5	10.0	4.6	7.0	0.6	0.7	
Parechinus angulosus	-	3.0	-	18.2	-	1.3		
Anomura	9.7	12.8	20.0	53.0	2.9	7.5	0.6	4.0
Unidentified	4.3	8.6	10.0	31.8	2.2	3.5		
Pylopagurus liochele	4.3	-	5.0	-	0.7	-		
Paguridae	1.1	2.7	5.0	16.7	0.1	2.9		
Galathea sp.	-	1.4	-	6.6	-	1.1		
Cephalopoda	2.2	0.1	10.0	7.6	5.1	0.3	0.5	2.1
Loligo sp. (?reynaudi)	1.1	0.5	5.0	4.6	5.0	0.2		
Octopus sp. (?vulgaris)	1.1	-	5.0	-	0.1	-		
Unidentified	-	0.2	-	1.5	-	0.0		
Sepia sp.	-	0.2	-	1.5	-	0.0		
Polychaeta	2.2	1.8	5.0	15.2	5.0	0.5	0.3	0.1
Eunicidae	2.2	0.2	5.0	1.5	5.0	0.1		
Unidentified	-	1.6	-	16.7	-	0.5		
Pelecypoda	8.6	5.0	20.0	31.8	1.1	1.8	0.2	0.6
Chlamys tinctus	4.3	1.6	15.0	9.1	0.4	0.6		
Venus sp.	1.1	0.2	5.0	1.5	0.4	0.0		
Donax sp.	1.1	-	5.0	-	0.2	-		
Solen sp.	1.1	-	5.0	-	0.1	-		
Unidentified	1.1	1.3	5.0	10.6	0.1	0.3		
Limaria rotundata	-	1.3	-	10.6	-	0.7		
Parvicardium sp.	-	0.5	-	3.0	-	0.1		
Musculus cuneatus	-	0.2	-	1.5	-	0.0		
Macrura	1.1	0.8	5.0	7.6	1.5	1.3	0.08	0.1
Pisces	1.1	0.5	5.0	4.6	1.5	0.2	0.08	0.01
Hydrozoa	1.1	0.5	5.0	4.6	0.3	0.2	0.01	0.01
Bryozoa	2.2	2.1	10.0	19.7	0.1	0.4	0.01	0.08
Porifera	1.1	1.4	5.0	12.1	0.1	2.0	T	0.2

Table 34 cont/...

TABLE 34 continued

Prey Species	Numbers (%)		Frequency occ. (%)		Mean volume (%)		Rank	
	S	H	S	H	S	H	S	H
Asteroidea	-	2.9	-	25.8	-	5.1	-	1.3
Marthasterius glacialis	-	1.4	-	12.1	-	2.9		
Unidentified	-	0.5	-	4.6	-	1.1		
Astropecten irregulatis	-	0.3	-	3.0	-	0.9		
Patriella exugia	-	0.6	-	6.1	-	0.3		
Amphineura	-	0.6	-	6.1	-	0.8	-	0.05
Chaetopleura pertusa	-	0.3	-	3.0	-	0.6		
Unidentified	-	0.3	-	3.0	-	0.2		
Sipunculida	-	1.1	-	7.6	-	0.3	-	0.01
Amphipoda	-	1.4	-	6.1	-	0.2	-	T
Pycnogonida	-	0.4	-	3.0	-	0.2	-	T
Isopoda	-	0.2	-	1.5	-	0.1	-	T
Algae	-	0.3	-	3.0	-	T	-	T

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

Table 35. Analysis of the stomachs of five juvenile *Chrysoblephus cristiceps* (FL = 73-89 mm) speared in the Mooring Gulley during March 1983.

Prey species	% Numbers	% Freq.occ	Mean % Vol	Rank
Ophiuroidea	33.3	80.0	40.0	32.0
Ophiactus carinea	6.7	20.0	19.0	
Amphiura capensis	13.3	20.0	8.0	
Remains	6.7	20.0	7.0	
Ophiothrix fragilis	6.7	20.0	6.0	
Crinoidea	26.7	80.0	15.4	12.3
Comanthus wahlbergi	13.3	40.0	8.0	
Tropiometra carinata	6.7	20.0	0.4	
Sipunculida	13.3	40.0	19.0	7.6
Unidentified	-	40.0	12.0	4.8
Amphipoda	6.7	20.0	13.6	2.7
Brachyura	6.7	20.0	0.2	0.4

the two areas.

The Tsitsikamma fish were sampled in the same area as the smallest C. laticeps. Interestingly the diets of the two species overlap, but the dominant prey organisms were different. Juvenile C. laticeps fed mostly on polychaetes while C. cristiceps concentrated on ophiuroids and crinoids. Feeding stategies of the two species were also different in that C. cristiceps did not ingest all prey items whole, nipping pieces of both crinoid and ophiuroid arms.

Too few fish between 226 and 335mm fork length were sampled to provide any meaningful comparison with the Port Elizabeth data. The results summarised in Table 36 did however, indicate that crinoids are the most important prey in this area as well, occurring in all three of the fish sampled.

A total of 33 prey species were recorded in the guts of 20 large C. cristiceps sampled in the Tsitsikamma area between December 1980 and September 1981 (Table 37). The large starfish Marthasterius glacialis was the most important prey species in the diet, followed by crinoids and brachyurans with ranks of 11.6, 5.5 and 4.4 respectively. Octopus sp. ?vulgaris, P. chabrus and C. wahlbergi were important prey species.

These results compared well with the Port Elizabeth study, crinoids and brachyurans being important in the diets in both areas. As was the case with C. laticeps, differences between the relative importance of prey items in the areas studied may have been the result of selection on the part of the predator or differences in the availability of certain prey over the geographical range. In C. cristiceps the most obvious difference in the diets between the areas studied was the importance of M. glacialis in the diet of adult C. cristiceps sampled in Tsitsikamma. Detailed benthic studies are needed to explain these observations.

Comparing the three size classes of fish it was clear that with an increase in the size of the predator there was a change in the relative importance of certain key prey groups. Ophiuroids, the most important prey of juvenile fish, showed a steady decline in abundance with an increase in fish size while crinoids and gastropods showed the opposite trend (Figure 43). Brachyurans were important in the diet of sub-adult fish and less important in both the juvenile and adult diets.

DISCUSSION

Analysis of the diets of C. laticeps and C. cristiceps showed that both species fed on a wide variety of reef associated benthic animals. In addition juveniles also fed on supra-benthic crustaceans such as mysids which occur over reef and sandy substrata. Much of the diet, particularly in the smaller fish consisted of small prey items and

TABLE 36. Analysis of the stomachs and hindguts of 3 sub-adult *Chrysoblephus cristiceps* (FL = 226-335 mm) speared in the Tsitsikamma area during 1981.

Prey species	% Numbers		% Freq Occur		Mean % Vol		Rank	
	S	H	S	H	S	H	S	H
Crinoidea	6.4	8.3	100.0	100.0	30.3	35.0	30.3	35.0
Comanthus wahlbergi	6.4	4.2	100.0	50.0	30.3	25.0		
Remains	-	4.2	-	50.0	-	10.0		
Unidentified	-	-		50.0	16.7	20.0	11.1	10.0
Asteroidea								
Marthasterius glacialis	2.1	4.2	33.3	50.0	20.0	10.0	6.7	5.0
Anomura	38.3	12.5	33.3	50.0	16.7	10.0	5.5	5.0
Amphineura								
Notoplax productus	2.1	-	33.3	-	6.7	-	2.2	
Chiton crawfordi	-	4.2	-	50.0	-	1.0		5.0
Gastropoda	38.3	33.3	33.3	100.0	6.0	3.5	2.0	3.5
Haliotus parva	-	4.2	-	50.0	-	1.5		
Opercular remains	-	8.3	-	50.0	-	0.5		
Shell fragments	-	20.8	-	50.0	-	1.5		
Brachyura	2.1	4.2	33.3	50.0	1.7	12.0	0.6	6.0
Ophiuroidea								
Ophionereis porrecta	4.3	-	33.3	-	1.0	-	0.3	-
Pelecypoda								
Chlamus tinctus	2.1	-	33.3	-	0.7	-	0.2	-
Echinoidea								
Parechinus angulosus	2.1	16.7	33.3	50.0	0.3	8.5	0.1	4.3
Isopoda	-	4.2	-	50.0	-	0.5	-	0.3
Amphipoda	-	8.3	-	50.0	-	0.5	-	0.3
Algae	-	-	-	50.0	-	0.5	-	0.3

TABLE 37. Analysis of the stomachs and handguts of 20 adult *Chrysoblephus cristiceps* (FL>336 mm) sampled in the Tsitsikamma area between December 1980 and September 1981.

Prey Species	% Numbers		%Freq. Occur		Mean % Vol		Rank	
	S	H	S	H	S	H	S	H
Asteroidea								
Marthasterius glacialis	4.9	1.1	42.9	35.7	27.1	5.6	11.6	2.0
Crinoidea	4.9	4.2	28.6	92.9	19.3	23.8	5.5	22.1
Comanthus wahlbergi	1.6	3.9	14.3	78.6	12.8	21.5		
Remains	3.3	0.2	14.3	7.1	6.4	1.2		
Tropiometra carinata	-	0.2	-	7.1	-	1.1		
Brachyura	9.8	9.4	28.6	85.7	15.4	21.6	4.4	18.6
Plagusia chabrus	1.6	1.5	14.3	28.6	14.1	6.7		
Dehaanius dentatus	6.6	3.3	14.3	35.7	1.1	5.6		
Remains	1.6	4.0	14.3	42.9	0.1	8.7		
Macropodia falicifera	-	0.2	-	7.1	-	0.4		
Xanthidae	-	0.4	-	7.1	-	0.1		
Dromiidae	-	0.2	-	7.1	-	0.1		
Cephalopoda	1.6	0.4	14.3	14.3	14.3	1.2	2.0	2.0
Octopus sp.	1.6	0.2	14.3	7.1	14.3	0.1		
Loligo sp.	-	0.2	-	7.1	-	1.1		
Unidentified	-	-	28.6	100.0	7.1	20.4	2.0	20.4
Gastropoda	37.7	34.0	42.9	85.7	4.6	7.1	2.0	6.1
Shell fragments	36.1	28.9	42.9	64.3	4.3	4.5		
Amblichilepas scutella	1.6	0.2	14.9	7.1	0.3	0.1		
Remains	-	1.1	-	28.6	-	1.0		
Oxystelle sp.	-	0.2	-	7.1	-	0.7		
Opercular remains	-	2.8	-	21.4	-	0.2		
Marginella cylindrica	-	0.6	-	7.1	-	0.4		
Calliostoma ornata	-	0.2	-	7.1	-	0.1		
Gibbula sp.	-	0.2	-	7.1	-	0.1		
Anomura	34.4	32.7	28.6	71.4	2.4	9.1	0.7	6.5
Polychaeta	1.6	0.6	14.3	14.3	4.3	0.7	0.6	0.1
Porifera	1.6	0.4	14.3	14.3	2.9	0.2	0.4	0.03
Echinoidea	1.6	6.6	14.3	78.6	0.7	7.0	0.1	5.5
Parechinus angulosus	-	5.3	-	64.3	-	2.2		
Echinocardium cordatum	-	1.1	-	14.3	-	4.6		
Remains	-	0.2	-	7.1	-	0.1		
Amphineura	1.6	0.2	14.3	7.1	0.3	0.1	0.04	0.01
Chaetopleura pertusa	1.6	-	14.3	-	0.3	-		

Table 37 cont/...

TABLE 37 continued

Prey Species	% Numbers		%Freq Occur		Mean % Vol		Rank	
	S	H	S	H	S	H	S	H
Ophiuroidea	-	4.8	-	50.0	-	2.2	-	1.1
Ophiothrix fragilis	-	3.9	-	28.6	-	1.2		
Ophiarachnella capensis	-	0.2	-	7.1	-	0.6		
Remains	-	0.6	-	14.3	-	0.3		
Astrocladus euryale	-	0.2	-	7.1	-	0.1		
Bryozoa	-	0.7	-	35.7	-	2.1	-	0.7
Pynogonida								
Pallenopsis intermedia	1.1	-	28.	-	0.6	-	0.2	
Isopoda	-	1.7	-	21.4	-	0.5	-	0.1
Algae	-	0.4	-	14.3	-	0.3	-	0.4
Pelecypoda	-	0.7	-	14.3	-	0.1	-	0.02
Cirripeda	-	0.2	-	7.1	-	0.1	-	T
Amphipoda	-	0.2	-	7.1	-	0.1	-	T
Tanaidacea	-	0.4	-	7.1	-	0.1	-	T
Ascidiacea								
Pyura stolonifera	-	0.2	-	7.1	-	0.1	-	T
Pisces	-	0.2	-	7.1	-	0.1	-	T

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

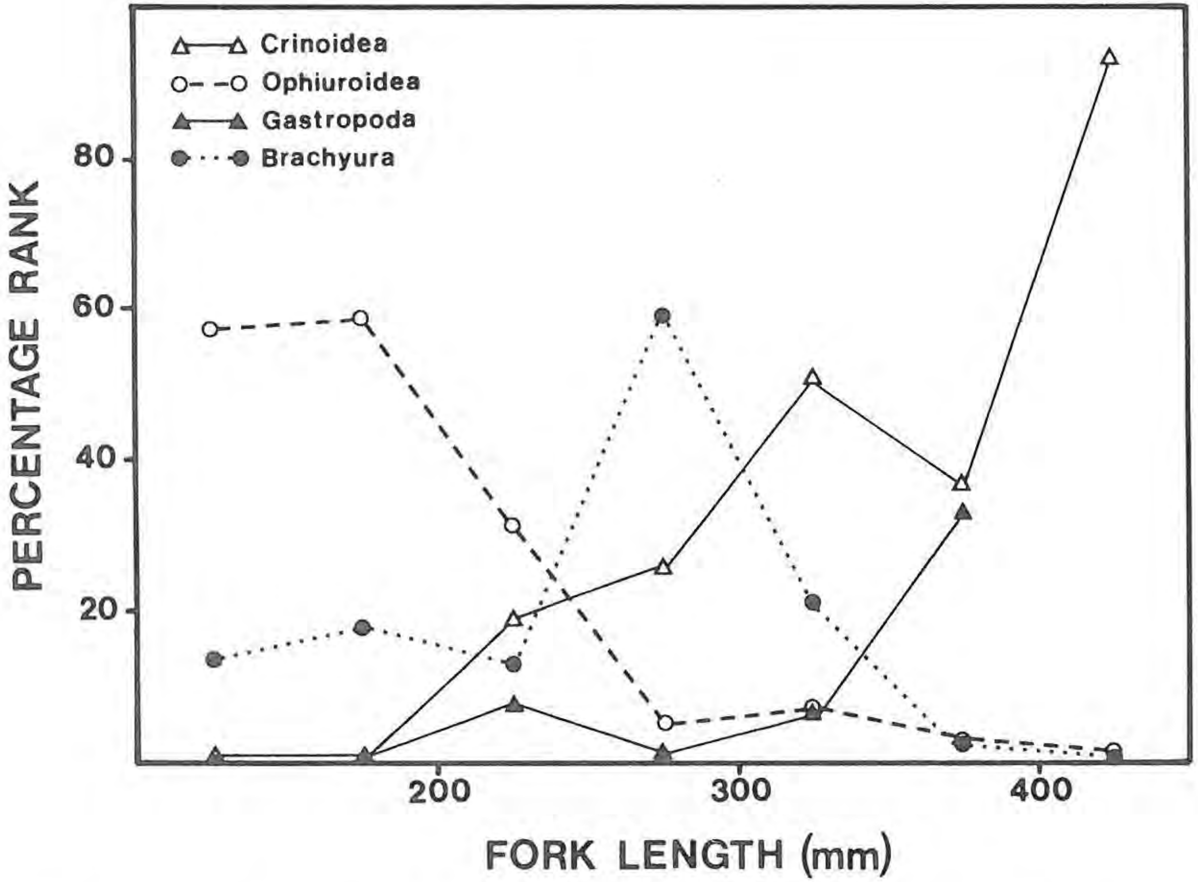


Figure 43. Size related changes in the importance of certain key prey groups in the diet of *Chrysoblephus laticeps* sampled in the Sardinia Bay to Woody Cape area between 1980 and 1982.

appeared to be gape limited although large fish were capable of a certain amount of prey manipulation. This included the removal of firmly attached prey from the substratum, crushing of hard shelled prey and pursuit of highly mobile prey. These characteristics of the diet were typical of search-hunters (Hughes 1980), which do not normally spend much time pursuing or handling prey relative to the amount of time spent searching during a foraging bout. Searchers also typically have wide diets because prey are ingested opportunistically and all potential prey are consumed when encountered.

Optimal foraging theory predicts that particular prey may be eaten selectively when the relative value of prey items differ in terms of assimilated energy (Hughes 1980). While the range of prey consumed by both C. laticeps and C. cristiceps was large, diet was always dominated by comparatively few prey groups. This indicated that the fish were either selecting their prey or that some prey items were encountered more frequently than others. A comparison between potentially available prey and the diet of large C. laticeps in Algoa Bay showed that dietary composition was not always a simple function of the numerical abundance. Larger fish in particular fed selectively on a few large prey species while smaller fish were less selective in their prey choice and had a wider diet. A correlation between the size of predator and prey has been found in many studies (Leviten 1976; Menge & Menge 1974) and is consistent with the optimal diet model (Hughes 1980).

Comparisons of the dietary composition in spatially separate areas showed that the relative importance of prey groups was different. This indicated that although capable of selective feeding over a wide range of prey items, prey choice was limited by availability and abundance. Intra-specific competition may also influence the diet (Hughes 1980; Ralston 1981), lower predator densities providing a better environment in terms of optimal foraging theory (Hughes 1980). This theory predicts that in a less competitive environment (lower density) an animal would choose a more optimal diet and that diet width may decrease. The selectivity shown in the diet of fish sampled at Phil's Reef showed that the potential for intra-specific competition could exist if prey were limited, and would most likely be related to predator density. Since predator density was much lower in the Port Elizabeth area, differences in the diet between Port Elizabeth and Tsitsikamma could have resulted from both a change in the competitive environment and differences in the benthic faunal characteristics of each area.

If different dietary compositions were only a result of a change in predator density then similar results from the two reefs in the Tsitsikamma would be expected. Also, the expected diet width in the exploited areas should have been narrower than the Tsitsikamma diet. In fact neither of these predictions were valid, suggesting that differences in the observed diet were due to differences in available prey. Ideally quantitative analysis of prey abundance in all of the areas studied together with empirical evidence on prey choice and optimal diet would be necessary to evaluate the observed differences in the diet, but this was beyond the scope of this study.

3.6 - REPRODUCTION

GENERAL INTRODUCTION

This account of the reproductive biology of *C. laticeps* and *C. cristiceps* has been divided into three parts. The first investigates protogynous hermaphroditism in the two species, elaborating on the work of Penrith (1972a) and Robinson (1976) who first described sex reversal in these fish. A detailed histological description of changes in the gonad during the life of an individual is given and selective advantages of this type of reproduction are considered. The second part deals with the reproductive characteristics of the two species including oogenesis, spermatogenesis, reproductive seasonality and a description of the mating behaviour of *C. laticeps*. Both of these parts deal with the unexploited populations sampled in the Tsitsikamma area.

The final part describes aspects of the reproductive biology of exploited populations sampled between Mossel Bay and East London, concentrating on the Port Elizabeth area. These included reproductive seasonality, sex ratio, size at sex reversal and size at maturity. Differences between areas were attributed to exploitation, the effects of which were different in the two species, and reasons for this are discussed.

3.6.1 - PROTOGYNOUS HERMAPHRODITISM

INTRODUCTION

The occurrence of hermaphroditism in fishes is well documented and may have arisen independently in as many as 10 lineages (Reinboth 1970; Smith 1975; Warner 1978). New accounts are continually being reported and in certain families hermaphroditism is the rule rather than the exception e.g. Sparidae, Scaridae and Serranidae. Its most complex expression is found in the Sparidae (sea-breams or porgies), which exhibit protogyny, protandry, rudimentary hermaphroditism and true gonochorism (Atz 1964; Alexseev 1982). Two general patterns of sexual ontogeny may be recognised. The gonad may differentiate and function first as one sex and then the other (protogyny and protandry), otherwise maturation of either the testis or the ovary follows a stage of juvenile intersexuality where non-functional elements of both sexes are recognisable (rudimentary hermaphroditism). Most of the species studied so far appear to be sequential hermaphrodites. Central to the study of reproduction in the sparids are the questions: which of the two, hermaphroditism or gonochorism, was ancestral and is rudimentary hermaphroditism derived from sequential hermaphroditism or is it an intermediate between gonochorism and sequential hermaphroditism?

The object of this section was to examine in detail the development of the reproductive organs from the juvenile state, through the female phase, sex reversal and finally to the male condition. The applicability of current theories proposed to explain the occurrence of hermaphroditism in fish are evaluated and possible advantages afforded to these species are discussed.

METHODS

Data were collected between June 1984 and May 1986 in the Tsitsikamma area. Most specimens were obtained by handline fishing and a few, particularly the smaller fish, were speared. Fish were weighed, measured and sexed using visual criteria (Table 38) before the gonads were removed and weighed. All weights were in grammes. Monthly samples of gonadal tissues were fixed in Bouin's solution for three days and stored in 50% propyl-alcohol. They were then embedded in wax, sectioned at 7µ and stained with Harris' haematoxylin and Eosin-Y for histological examination.

TABLE 38. Classification of maturity stages in _C. laticeps_ and _C. cristiceps_ (modified from Buxton & Clarke 1986).

1. Virgin and resting	Sexual organs small. Testis thin and transparent to greyish white. Ovary long and thin, pink in colour with no visible eggs.
2. Developing	Both male and female tissues increase in size. Testis shows a lateral thickening, a marginal increase in length and is coloured a greyish white. Sperm visible in the main sperm duct if cut and gently squeezed. The ovary increases in size particularly on the long axis to half or more of the visceral cavity length. Colour changes from pink to reddish orange and eggs are visible to the naked eye.
3. Active	Testis greyish white with sperm present in the main duct and the tissue. As the breeding season progresses the testis becomes more pinkish. Ovary is swollen and yellow-orange in colour. Translucent eggs are visible in the tissue and in the lumen. May be slightly flaccid and bloodshot if some spawning has taken place.
4. Post spawning	Testis decreases marginally in size, is reddish-grey in colour with no sperm in the tissue but present in the main sperm duct. Ovary decreases considerably in size, is flaccid and has a large empty lumen. Reddish-orange colour with very few clear eggs visible.

RESULTS

Length frequency and sex ratio

The length frequencies of all C. laticeps sampled are shown in Figure 44a. Sexes were separated on the basis of macroscopic sex determination and the ratio of male:hermaphrodite:female was 1:0.58:1.11. Hermaphroditic fish were recorded between 250 and 425mm fork length with a mean of 321±29mm.

A similar plot for C. cristiceps is shown in Figure 44b. The ratio of male:hermaphrodite:female was 1:1:4.22 and the mean size of hermaphrodites was 418±45mm, ranging between 280 and 525mm fork length.

Reproductive cycle

The development of the gonad from immaturity, through the ovarian cycle, sex inversion and finally to the male phase was so similar that the following description applies to both species unless specifically stated.

The ovaries are paired structures fusing posteriorly and emptying into a single short oviduct. They are suspended in the body cavity by a thin layer of peritoneum, the mesovarium, beneath which is the tunica albuginea. The composition of the tunica albuginea is fairly uniform in most teleosts, consisting of smooth muscle layers, connective tissue and blood vessels (van der Horst 1976). Ovigerous lamellae project from the tunica albuginea and fill the ovary except for a central ovocoel which is continuous with the oviduct (Fig. 45a). Serial sections of the ovaries showed no evidence of differentiated male tissue but the work of D'Ancona (1949) and Alexseev (1982) suggests that a testicular primordium forms in the early stages of gonadal development in sparids. During the breeding season there was a marked increase in the size of the ovary which, when ripe, occupied approximately two thirds of the body cavity. Following spawning the ovary either regressed to a resting stage or another batch of eggs were ripened and spawned. The first appearance of differentiated testicular tissue occurred at the posterior ventral surface of the ovary, where it formed a thin sheet (Fig. 45b). This occurred at approximately 250mm fork length in C. laticeps and 280mm fork length in C. cristiceps. During the initial phase of testicular development the ovary remained functional (Fig. 45c) but immediately following spawning development of the testis accelerated with a corresponding degeneration of the ovary. Similar to other reports on hermaphroditic sparids (Atz 1964; Coetzee 1983), the ovary and the testis were separated by a connective tissue layer, the oviduct and main sperm duct remaining functionally separate throughout development. This differs from sex change in serranids, where the ovary is invaded by testicular elements (Smith 1965).

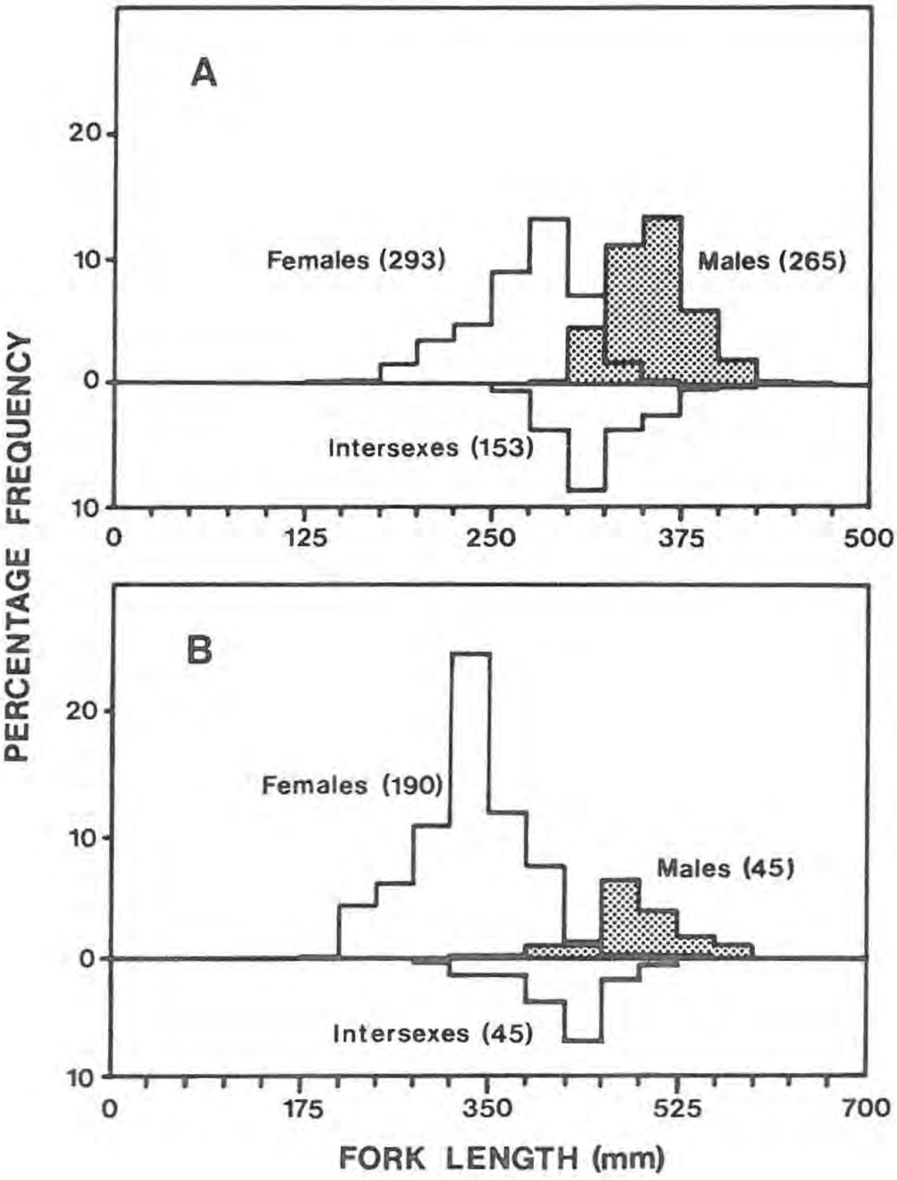


Figure 44. Sex separated length frequency analysis of Chrysoblephus laticeps (A) and C. cristiceps (B) sampled in the Tsitsikamma area between 1984 and 1986. Males are shaded and sample sizes are given in parenthesis.

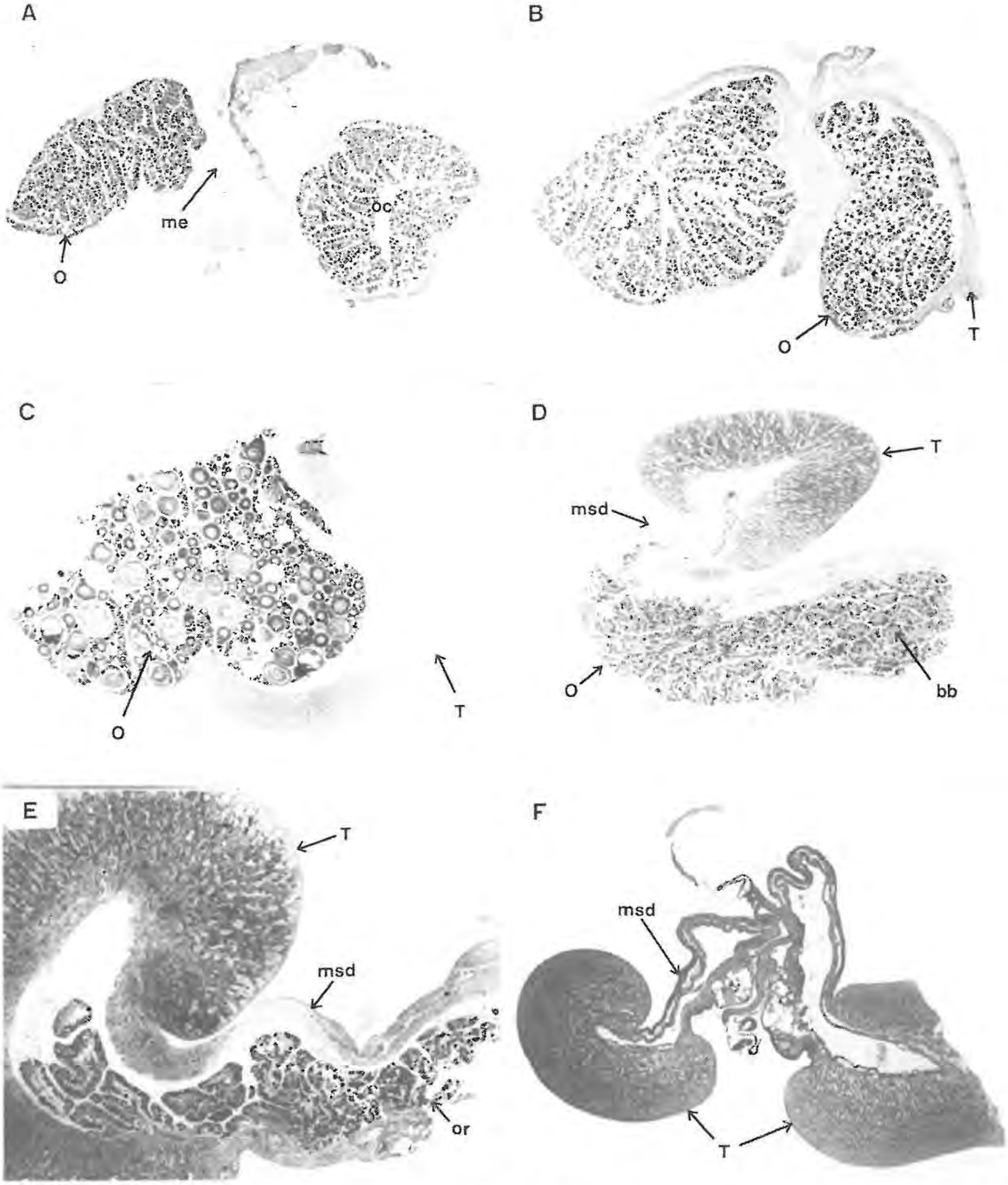


Figure 45. Development of the gonad in Chrysoblephus laticeps and C. cristiceps. A. Transverse section through inactive ovaries (x11.0). B. Transverse section through the ovo-testis of an inactive functional female showing eary development of the testis (x13.0). C. Transverse section through the ovo-testis of a functional female showing an active ovary and an inactive testis (x12.5). D. Transverse section through the ovo-testis of an inactive functional male showing a developing testis and degenerating ovary with numerous brown bodies (x6.5). E. Transverse section through the ovo-testis of a functional male showing degenerate female tissue and a mature testis with sperm in the main sperm duct (x20.0). F. Transverse section through the testes of a functional male. Ovarian history only evident by a few small brown bodies in the mesentary (x10.0). me - mesentary, O - ovary, T - testis, msd - main sperm duct, or - ovarian remains.

Sex inverting individuals were recorded throughout the year. Most hermaphrodites examined were either functional females showing early testicular development or functional males with a degenerating ovary and only 1.5 percent of them had an ovo-testis with an equal development of the two sexes. This suggested that sex reversal was a fairly rapid process (cf. Alexseev 1982). Once sperm production began there was no evidence of continued ovarian activity and ultimately the ovary degenerated to a connective tissue mass containing a number of 'brown bodies' (Figs. 45d & 50d) characteristic of the degeneration of ovarian tissue (Smith 1965; Young & Martin 1982). Ovarian rudiments, particularly of the oviduct, were evident throughout testicular development.

The testes were paired structures, triangular in section and consisted of a number of seminiferous tubules leading into secondary sperm ducts. Posteriorly these ducts joined to form a common main sperm duct. Each testis was surrounded by a tunica albuginea of connective tissue and collagen which appeared to be continuous with the seminiferous tubules (Fig. 45e).

DISCUSSION

The separation of the modal size of females and males has been regarded as evidence for sex inversion in a number of species including C. laticeps and C. cristiceps (Penrith 1972a; Robinson 1976). This alone does not provide absolute evidence of sequential hermaphroditism (Sadovy & Shapiro 1987) as size segregation may result from differential growth and mortality between the sexes. Differential growth would however, not explain the absence of males in the smaller size classes of protogynous species (Shapiro 1981) or the observation that sex inverting individuals occurred over a narrow size range between males and females. Reinboth (1970) stated that conclusive evidence for protogyny can be obtained only by careful histological examination of all stages in the reproductive cycle. This study showed that in both C. laticeps and C. cristiceps all individuals functioned first as females before undergoing sex inversion, with no evidence of simultaneous hermaphroditism.

A number of theories have been proposed to explain the occurrence of hermaphroditism in vertebrates (Ghiselin 1969; Warner 1978). Initial attempts to explain sequential hermaphroditism were based on group advantages such as maximising (Smith 1967) or optimising (Smith 1975) the population zygote production. Liem (1968) considered sex change as a means of overcoming the absence of a particular sex during periods of very low density (see also Smith 1975).

More recent theories explain selection for sequential hermaphroditism in terms of an increase in the reproductive potential of an individual during its lifetime. Based on the size advantage model of Ghiselin (1969) these theories state that sequential hermaphroditism would be advantageous where an individual reproduces best as one sex at a particular size or age and as the other when larger or older. Selection for protogyny exists where large males obtain a disproportionate share of reproductive success (Robertson & Choat 1974; Warner 1975; Warner, Robertson & Leigh 1975.) Implicit in these models is the suggestion that the proper age or size at which to change sex is genetically programmed.

Shapiro (1984) provides evidence that the size/age at which sex reversal takes place is extremely variable within species and therefore doubts the importance of size or age *per se* in the model. He prefers to regard behavioural induction of sex reversal as a means for providing improved reproductive success whenever circumstances allow, regardless of the point in life at which these circumstances occur. In other words relative size is more important than absolute size in the determination of when an animal changes sex in a population.

The population structure of protogynous parrot fishes and wrasses found on tropical reefs has been well studied (e.g. Choat & Robertson 1975; Robertson & Warner 1978; Warner & Robertson 1978; Robertson, Reinboth & Bruce 1982). Two distinct reproductive patterns have been observed which relate to the sexual ontogeny of the males of the species studied. The first, monandry, prevails when all males are derived from sex inverting females. Mating takes place between large, territorial males and a size ordered harem of females, smaller males being aggressively excluded from mating by the large dominant males. The second type, diandry, includes males born as such (primary) as well as those that result from sex change (secondary). The most obvious characteristic of these species is colour dimorphism, large secondary males being brightly coloured while females and primary males are drab (colour dimorphism is uncommon in monandric species). Secondary males monopolize the breeding by occupying preferred mating territories and mating sequentially with a number of females. Preferred sites are down-current areas on the edge of the coral reef so that gametes are carried away from reef predators. Primary males are aggressively excluded from most of the breeding but succeed either by interfering with the mating activities of larger males (joining a spawning couple at the moment of gamete release) or by occupying a spawning site *en masse* and group spawning with the females that appear there. In the latter many males mate with a single female.

Primary males were not observed in *C. laticeps* and *C. cristiceps* either macroscopically or histologically and all males were thought to be derived from functional females. This result differs slightly from the findings of a study on the congeneric *C. puniceus* found off Natal, South

Africa. Garratt (1986a) suggested that observed small males could be regarded as primary males (i.e direct development) and that large males were derived from females by sex reversal, but no histological evidence was provided to confirm this observation. Considering the phenotypic plasticity exhibited by fish, evidenced by a change in the size of sex reversal in different populations (Shapiro 1981), the occurrence of primary males in protogynous members of the genus Chrysoblephus remains uncertain.

Many similarities were found between the reproductive characteristics of tropical labroids and the temperate sparids of this study. As well as being monandric, both C. laticeps and C. cristiceps were monochromatic species with a clear separation between the size of males and females. Reproductively active males of both species had small testes and gonado-somatic indices remained relatively low throughout the year, suggesting a much lower investment in male gamete production by these fish than that of many closely related sparids which have a large testis during the breeding season. Examples include Cheimerius nufar (Coetzee 1983), Chrysoblephus gibbiceps, Pachymetopon grande and Sparodon durbanensis (J.R. Clarke and C.D. Buxton, Port Elizabeth Museum unpublished results) and Petrus rupestris (M.J. Smale, Port Elizabeth Museum, pers. comm.).

In dichromatic labroids the relative size of the testis was much greater in primary males (initial colour phase) than in secondary males (terminal phase) (Roede 1972; Choat & Robertson 1975) because in multi-male/single female groups the potential number of eggs fertilised by an individual male was a function of the number of sperm released. The basic difference in the spawning strategy of the two male types was thought to favour the development of a large testis in group spawners because of sperm competition (Warner & Robertson, 1978).

Assuming that similar selective pressures have resulted in parallel evolution of these characters in labroids and sparids, the existence of monandry, monochromatism and small testis size are evidence of a mating system in which large males control breeding by resource defence. This postulate was supported by laboratory observations of the mating behaviour of C. laticeps (see chapter 3.6.2), as well as field observations. C. laticeps were frequently seen in groups consisting of one large individual (presumably male) and a number of smaller individuals (presumably female). In one area of the Tsitsikamma, the Mooring Gulley, the same large fish (identified by a black scar on the caudal peduncle) was repeatedly observed with 3-5 smaller fish over three successive months.

In conclusion the results of this study show that both C. laticeps and C. cristiceps are protogynous hermaphrodites and all males are derived from functional females. Similarities between these species and tropical labroids suggest a parallel evolution of reproductive traits such as monochromatism, small testis size and monandry. These characters provide circumstantial evidence of a polygynous mating system in the study species which is discussed in the next section of this chapter.

3.6.2 - THE REPRODUCTIVE CYCLE

INTRODUCTION

The South African ichthyofauna has 41 species belonging to the family Sparidae, 25 of which are endemic (Smith & Smith 1986). Most of the species are important to the recreational and commercial line fisheries (Smale & Buxton 1985; Garratt 1986b). Detailed studies of the reproductive biology of these fish are few, and include research on Cheimerius nufar (Coetzee 1983; Garratt 1986a), Chrysoblephus puniceus (Garratt 1986a), Lithognathus lithognathus (Mehl 1973) and Pterogymnus laniarius (Hecht 1976). Most appear to be either protogynous or rudimentary hermaphrodites (Garratt 1986a). Protogynous hermaphroditism presents special management problems because in a size selective fishery, such as the recreational linefishery in South Africa, large fish (mostly males) are selectively removed from the population with a resultant imbalance in sex ratio.

This section describes the reproductive cycle of C. laticeps and C. cristiceps. It includes a histological study of both oogenesis and spermatogenesis, notes on the spawning behaviour of C. laticeps and evaluates mating systems that may exist in these two species. Information presented here represents a baseline from which the effects of exploitation on the reproductive biology of these two species may be examined.

METHODS

Sampling procedures and techniques for the preparaton of histological material were described in Part 1. Mean sizes of the various egg classes, measured using an eyepiece micrometer, were not corrected for shrinkage during dehydration. Maturity values for fish caught during the breeding season were determined by expressing the frequency of reproductively active animals (stage 2-4) as a percentage of the total in each size class. Courtship behaviour of a pair of C. laticeps was monitored in the main tank of the Port Elizabeth Oceanarium which is 20m in diameter and 2m deep. Daily observations were made for a three-week period during October-November 1986, after which the fish were sacrificed to confirm their sex and to determine the stage of development of the gonads.

RESULTS

Size at maturity and gonado-somatic index

The size frequencies of female and male fish sampled are shown in Figure 46, together with percentage maturity values. These maturity values obviously only apply to female fish because all males are reproductively active after sex reversal. In C. laticeps fifty percent maturity was attained at approximately 190mm fork length and all females above 225mm fork length were reproductively mature. In C. cristiceps these values were attained at 355 and 420mm fork length respectively.

Individual gonado-somatic indices for female C. cristiceps and C. laticeps are shown in Figure 47. Peak gonadal activity was recorded between November and January in C. cristiceps and between October and late January - early February in C. laticeps. Both breeding seasons were fairly restricted, gonadal recrudescence beginning as photoperiod increased and spawning taking place at peak photoperiod (maximum daylength). Spawning was also well correlated with peak sea water temperatures and gonadal regression began with falling temperatures. Male gonado-somatic indices are summarised in Figure 48. In both species there was only a slight increase in the gonado-somatic index during the breeding season, suggesting a much lower investment in gamete production by males than either females of the same species or males of many other local sparids that have large testes.

Ovarian cycle

Various classifications of oocyte maturation in teleosts are found in the literature (Yamamoto 1956; Braekefelt & McMillan 1967; de Vlamming 1972a; Wallace & Selman 1981; Bouain & Siau 1983; Coetzee 1983). They differ primarily in the number of developmental stages, from only two (Bouain & Siau 1983) to 12 (Yamamoto 1956) but the actual processes appear to be similar, even in widely separated groups of fish. Two major oocyte growth phases exist: pre-vitellogenesis, involving the transformation of oogonia to oocytes and their development to the end of the perinuclear stage, and vitellogenesis, including all stages of yolk formation from the cortical alveolar stage to maturation. The ovarian and testicular cycles of the two species were found to be so similar that the following description applies to both species.

The different stages in the development of the eggs of C. laticeps and C. cristiceps are summarised in Tables 39 and 40 respectively. These stages are fairly arbitrary because oocyte growth is a continuous process. For this reason considerable variation is found in each developmental stage. Despite this, there was a good correlation between

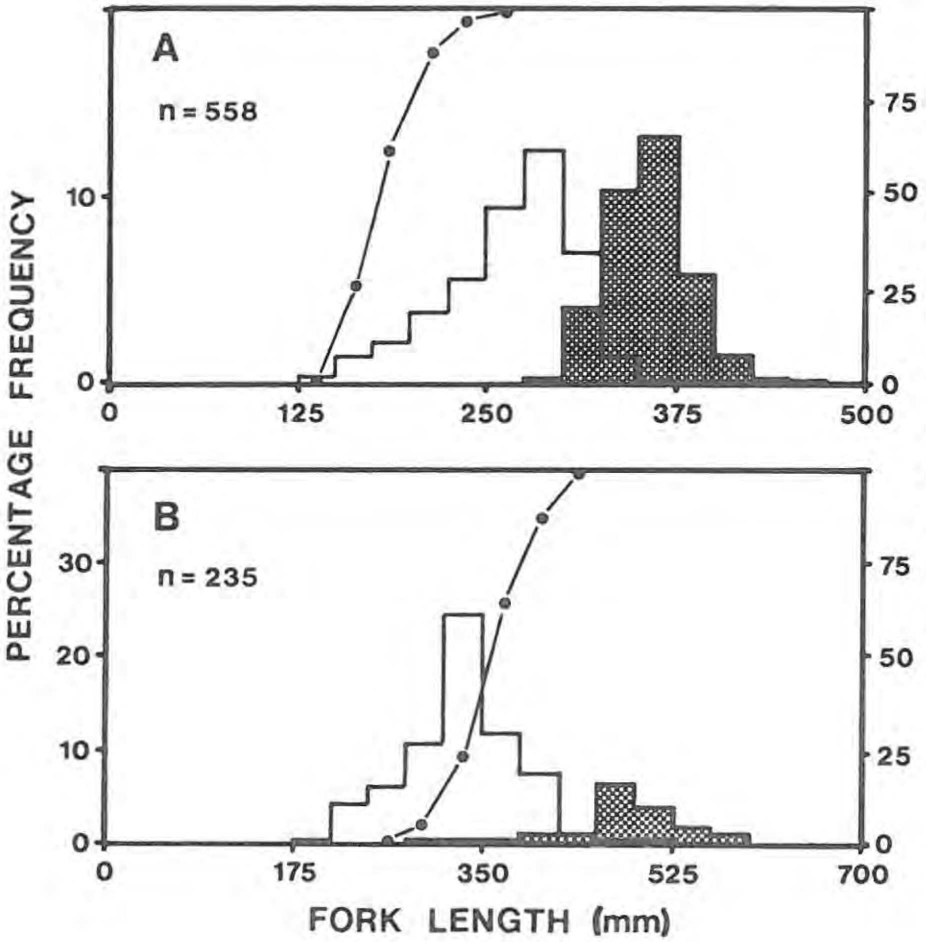


Figure 46. Length frequency analysis and percentage maturity of Chrysoblephus laticeps (A) and C. cristiceps (B) sampled in the Tsitsikamma area between 1984 and 1986. Males are shaded.

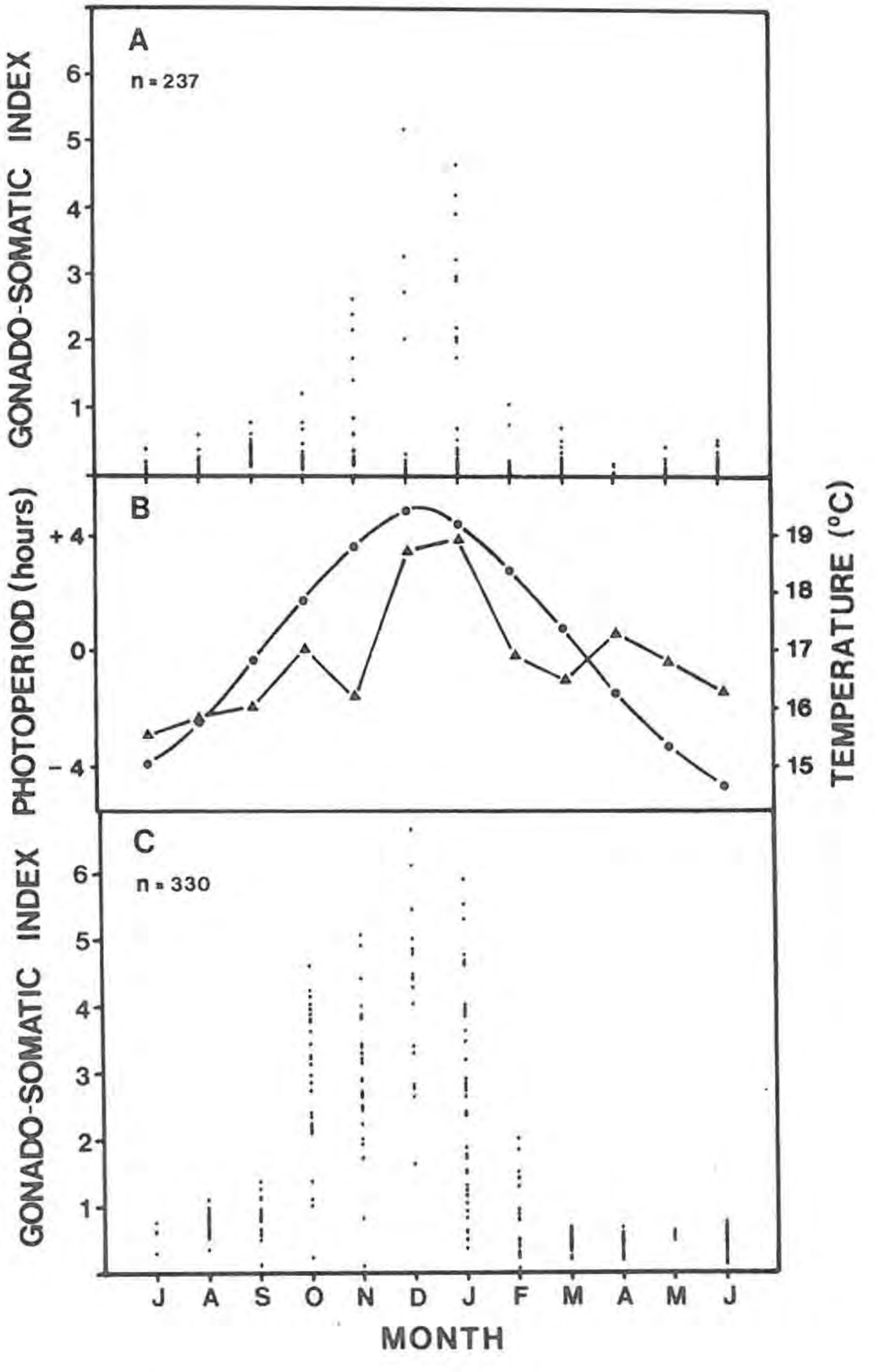


Figure 47. Seasonal variation in gonado-somatic index of female *Chrysoblephus cristiceps* (A) and *C. laticeps* (C) sampled in the Tsitsikamma area between 1984 and 1986. Mean monthly sea temperatures (▲) and photoperiod (●) for 1986 are also given.

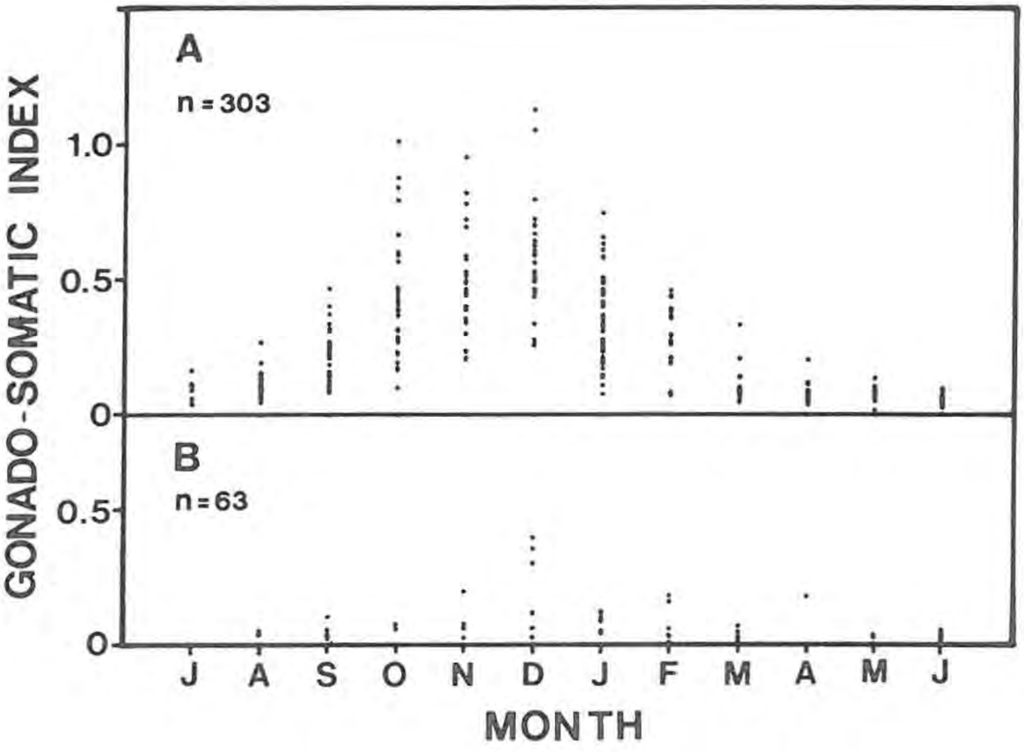


Figure 48. Seasonal variation in gonado-somatic index of male Chrysoblephus laticeps (A) and C. cristiceps (B) sampled in the Tsitsikamma area between 1984 and 1986.

TABLE 39. Microscopic oocyte stages observed in Chrysoblephus laticeps sampled at Tsitsikamma. All measurements in are in µ, x = mean, s = standard deviation.

STAGE	NAME	CELL DIAMETER			NUCLEUS DIAMETER			NUCLEOLUS DIAMETER	NO. of NUCLEOLI		CA DIAMETER		YG DIAMETER		ZR THICKNESS		ZG THICKNESS		Pre-dep zone		n
		x	s	range	x	s	range	range	x	range	x	range	x	range	x	range	x	range	x	range	
1	Oogonia	12.1	1.6	7.2- 20.4	6.9	1.7	4.8- 9.6	-	-	-	-	-	-	-	-	-	-	-	-	-	19
2	Perinuclear oocytes																				
	a) Pre-	35.7	9.8	28.8- 57.1	17.2	1.7	9.6- 25.9	1.2- 9.6	6	1-13	-	-	-	-	-	-	-	-	-	-	43
	b) Early-	60.2	12.5	36.0- 85.2	30.6	6.4	18.0- 40.8	1.2-12.0	11	7-23	-	-	-	-	-	-	-	-	-	-	45
	c) Late-	101.0	15.2	76.8-138.0	56.1	9.0	42.0- 78.0	1.2- 9.6	16	8-25	-	-	-	-	2.3	0.6-2.4	1.4	0.6-2.4	-	-	40
3	Primary vesicle oocytes	142.1	14.0	114.0-172.8	69.9	11.2	45.6-109.4	1.2-14.4	25	21-27	4.8	3.6- 7.2	-	-	2.1	0.6-3.6	2.6	2.4-3.6	-	-	35
4	Secondary yolk vesicle oocytes																				
	a) Early	202.7	21.4	148.8-242.4	92.8	9.5	72.0-106.8	1.2- 9.6	23	19-28	6.8	4.8- 9.6	4.4	2.4- 4.8	4.8	3.0-6.0	3.8	2.4-7.2	-	-	41
	b) Late	279.1	24.7	225.0-333.0	100.7	13.9	73.2-127.2	1.2-14.4	23	12-36	21.3	16.8- 26.4	12.3	8.4-19.2	6.4	4.8-8.4	4.0	2.4-4.8	-	-	33
5	Tertiary yolk oocytes (incl. migratory nucleus)	356.6	20.3	306.0-408.0	122.1	14.4	97.2-156.0	1.2-12.0	15	8-28	87.5	45.6-148.0	Coalesced		9.2	8.4-9.6	3.2	2.4-6.0	-	-	35
6	Mature eggs (fresh)	500+																			

CA = cortical alveolar, YG = yolk globule, ZR&G = zona radiata & granulosa

TABLE 40. Microscopic oocyte stages observed in *Chrysoblephus cristiceps* sampled at Tsitsikamma. All measurements in are in µ, x = mean, s = standard deviation.

STAGE	NAME	CELL DIAMETER			NUCLEUS DIAMETER			NUCLEOLUS DIAMETER	NO. of NUCLEOLI		CA DIAMETER		YG DIAMETER		ZR THICKNESS		ZG THICKNESS		PRE-DEP ZONE		n
		x	s	range	x	s	range	range	x	range	x	range	x	range	x	range	x	range	x	range	
1	Oogonia	13.4	2.3	8.4- 19.2	8.1	0.7	6.0- 14.4	-	-	-	-	-	-	-	-	-	-	-	-	-	68
2	Perinuclear oocytes																				
	a) Pre-	36.6	8.6	28.8- 56.4	16.5	4.7	7.2- 24.0	3.6-12.0	5	1-13	-	-	-	-	-	-	-	-	-	-	43
	b) Early-	59.5	10.5	40.8- 80.4	28.4	4.2	19.2- 32.2	4.8- 9.6	10	5-20	-	-	-	-	-	-	-	-	-	-	48
	c) Late-	88.8	14.4	68.4-151.2	46.9	9.8	31.2- 88.8	1.2-12.0	15	7-22	-	-	-	-	1.6	1.2-2.4	-	-	-	-	50
3	Primary vesicle oocytes	158.1	24.5	105.6-216.0	75.0	10.8	54.0- 96.0	2.4- 9.6	25	18-30	6.6	1.2- 9.6	-	-	2.6	1.2-2.4	1.5	1.2-2.4	1.5	1.2-2.4	41
4	Secondary yolk vesicle oocytes																				
	a) Early	213.8	21.4	181.2-261.6	93.4	15.1	72.0-132.0	4.8-12.0	18	10-25	8.3	4.8- 12.0	3.6	1.2- 7.2	2.4	1.2-4.8	3.7	2.4-4.8	3.7	3.6-4.8	37
	b) Late	312.3	36.2	255.0-373.0	109.6	14.8	73.2-135.6	3.6-12.0	25	12-40	15.1	12.0- 31.2	13.5	7.4-24.0	6.0	2.4-9.6	4.4	3.6-7.4	4.7	3.6-9.6	38
5	Tertiary yolk oocytes (incl. migratory nucleus)	379.3	25.4	309.0-459.0	120.0	19.9	85.2-151.2	2.4-12.0	18	10-31	45.8	16.8-160.8	Coalesced		7.6	4.8-12.0	4.1	2.4-9.6	-	-	79

CA = cortical alveolar, YG = yolk globule, ZR&G = zona radiata & granulosa the two species. The large oil globule and small size of the mature eggs were typical of pelagic spawners and compared well with a similar study on C. nufar (Coetzee 1983), although more recently Craik & Harvey (1987) suggest that most of the bouyancy in pelagic eggs results from their high aqueous content rather than from lipids.

Oocytes developed from the small oogonia found in the germinal epithelium. They were characterised by a high nucleus to cytoplasm ratio and were found in the peripheral regions of the ovigerous lamellae, both as nests and individually (Fig. 49a). Oocytes predominated immediately after the breeding season. This suggests a peak of activity associated with the recruitment of a new batch of eggs for the next breeding season.

With further growth there was an increase in the relative volume of the cytoplasm which also became strongly basophilic. Each cell was surrounded by a theca within which the blood vessels supplying the follicle were found. Pre-perinuclear oocytes were polygonal in shape with a deeply basophilic cytoplasm and were found closest to the germinal epithelium (Fig. 49b). The nucleus at this stage contained one or two large nucleoli and often a number of smaller ones. Early and late perinuclear oocytes were more ovoid in shape, had a less basophilic cytoplasm and nuclear development was characterised by a proliferation of nucleoli in the peripheral regions of the nucleus (Fig. 49b&c). In late perinuclear oocytes the nucleoplasm had a granular appearance and the nucleoli became flattened against the nuclear membrane. At this stage the follicle was surrounded by a layer of cells forming the zona granulosa. A light margin was also apparent immediately below the zona granulosa which Yamamoto (1956) suggested was a pre-deposit zone associated with the formation of the zona radiata.

The formation of the zona granulosa marked the end of the primary growth phase and was followed by the appearance of primary 'yolk' vesicles (Yamamoto 1956) in the ooplasm (Fig. 49c). According to de Vlaming (1983) these give rise to the cortical alveoli which accumulate in the peripheral regions of the cell, fuse with the oolema and release their contents into the perivitelline space at fertilisation. The term 'yolk vesicle' appears to be misleading as cortical alveoli have also been confused with the accumulation of oil droplets in the nuclear region of the cytoplasm (Braekefelt & McMillan 1967; van der Horst 1976; Coetzee 1983).

The zona radiata which developed between the cytoplasm and the zona granulosa, marked the beginning of the formation of yolk. Acidophilic 'secondary yolk' globules first appeared in the region of the cortical alveoli but later also developed as extra vesicular yolk throughout the cytoplasm. Yolk accumulation continued until it obscured the cortical alveoli, and in the tertiary yolk vesicle stage entirely filled the cytoplasm (Fig. 49d).

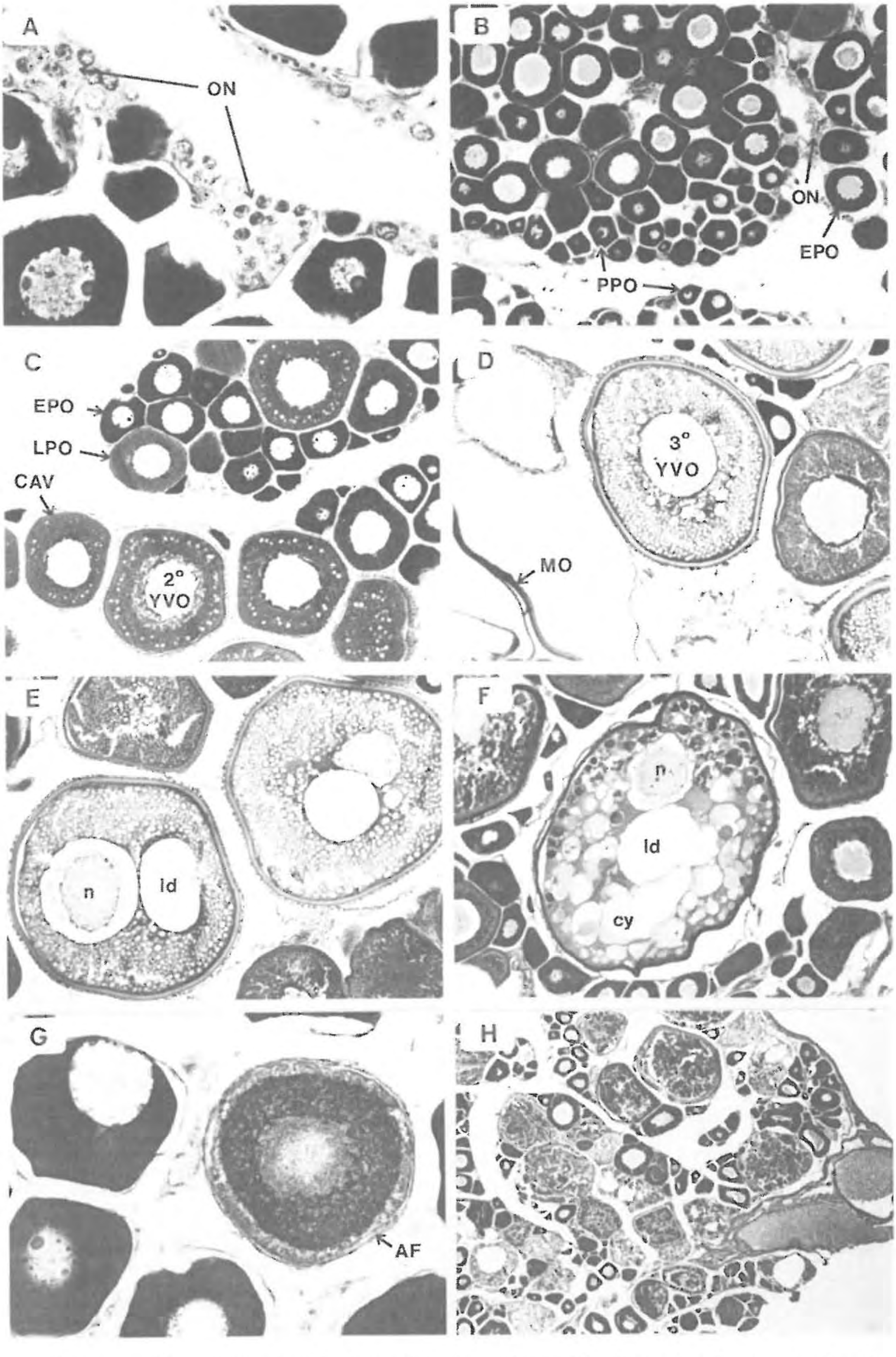


Figure 49. Oocyte development in Chrysoblephus laticeps and C. cristiceps. For explanation see facing page.

During vitellogenesis the zona granulosa and the zona radiata increased in thickness, pore canals developed in the zona radiata and nucleoli proliferated. Towards the end of development the nucleus began migrating towards the periphery of the cell (Fig. 49e). This was followed by a degeneration of the nuclear membrane, formation of the oil drop and yolk coalescense (Fig. 49f).

Two distinct atretic events were recognised in the ovaries of C. laticeps and C. cristiceps. The first was a resorption of yolked oocytes during normal ovarian cycling. This process was observed throughout the breeding season but was most common immediately after spawning. The second was a condition associated with sex inversion and included degeneration of all oocyte stages and the progressive absorption of the entire ovary.

Atresia was characterised by hypertrophy of the follicle granulosa, disappearance of the zona radiata and disintegration of both the nuclear membrane and the nucleus (Fig. 49g&h). Phagocytosis of the yolk by both leucocytes and the granulosa cells resulted in an overall glandular appearance typical of teleost atresia (Barr 1963; van der Horst 1976; Crossland 1977; Cyrus & Blaber 1984). In spite of this appearance there is no evidence of a corpora lutea-like function of these cells in teleosts (de Vlaming 1972a).

Testicular cycle

The testes were paired structures, triangular in section and consisted of a number of seminiferous tubules leading into secondary sperm ducts. Posteriorly these ducts joined to form a common main sperm duct. Each testis was surrounded by a tunica albuginea of connective tissue and collagen fibres which appeared to be continuous with the seminiferous tubules.

In the pre-spawning condition the seminiferous tubules contained a mass of spermatogonia characterised by a lightly stained basophilic cytoplasm and a large nucleus (Fig. 50a). These gave rise by mitotic division to cysts of secondary spermatogonia which had smaller nuclei (van der Horst 1976). Each cyst was surrounded by a distinct membrane and all cells in a cyst formed a clone at the same stage of development (Fig. 50b). Further division produced a number of spermatocyte stages with the more advanced stages being closer to the lumen of the tubule The final stage of development within the cyst was the formation of spermatids following which the cyst ruptured. This released the spermatids into the lumen where final maturation into spermatogonia took place (Fig. 50c). This process was similar to spermatogenesis observed in other teleosts (Ruby & McMillan 1970; van der Horst 1976; de Vlamming 1972a; Coetzee 1983).

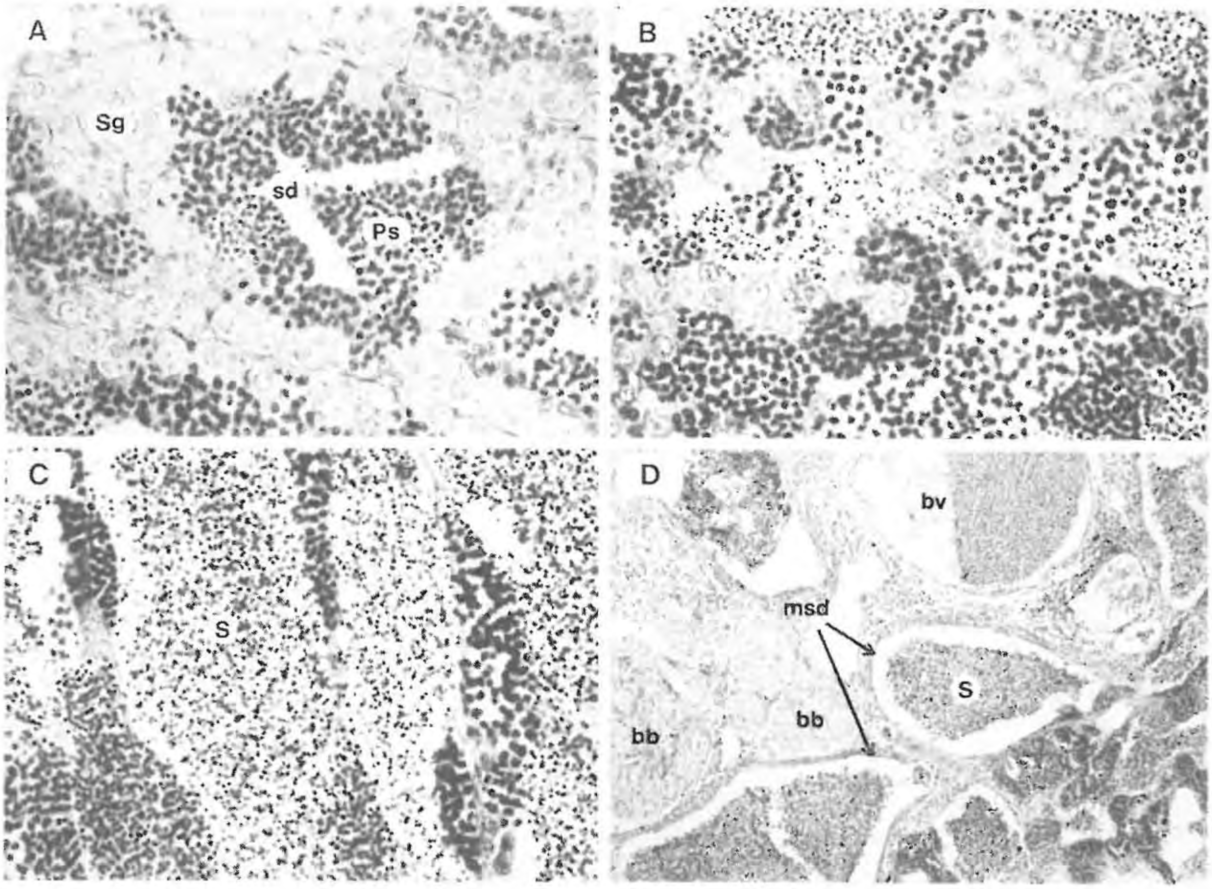


Figure 50. Spermatogenesis in Chrysoblephus laticeps and C. cristiceps. A. Transverse section through the testis during early development showing spermatogonia (Sg) and primary spermatocytes (Ps) around an empty lobule (sd) (x450). B. Transverse section through the testis showing clones of spermatocytes at different stages of development (x450). C. Longitudinal section through a mature testis showing sperm in the lobules (x450). D. Transverse section through the testis of a ripe male showing sperm in the main sperm duct (msd) and two 'brown bodies' (bb). bv - blood vessel (x105).

There was no relationship between the occurrence of sperm in the main sperm duct and the time of year although spermatogenesis appeared to be restricted to the breeding season. The presence of sperm in the testis in the non-breeding season was therefore considered to be a remnant of the previous breeding cycle (van der Horst 1976) and was taken into account when evaluating reproductive activity macroscopically.

Courtship behaviour in C. laticeps

Courtship behaviour always took place in the same area of the aquarium, fairly close to a number of artificial reefs (rising 1-2m above the bottom) and adjacent to the main water inlet. During the day the fish spent most of their time in the vicinity of these reefs. Interaction between them at this time was limited to occasional rushing and chasing. At the same time the male did not pay any attention to other species, which contrasted with his behaviour during courtship. In addition to obvious behavioural changes, the onset of courtship was marked by a distinct change in colouration of both fish. The belly region lost its normal dull pink colouration, becoming completely white. The two white flashes, on the dorsal surface and the cheek, also intensified in appearance.

Five separate behavioural patterns were recognised during the courtship sequence: (a) rushing (b) mouth bumping, (c) circling, (d) nuzzling and spawning ascent and (e) spawning (Fig. 51). Courtship began in the late afternoon and increased in frequency and intensity over a 30-45 minute period. Rushing was defined as any rapid swimming by either partner towards the other which usually resulted in a flashing of the belly by the 'rusher' in passing. This behaviour occurred throughout the day but with increased frequency during the late afternoon. The male appeared to initiate rushes more frequently than the female. Rushing was often seen in the wild, where it occurred between fish of all sizes. Behaviour of this nature is common in polygamous species and serves to maintain the social organisation of the group (Moyer & Nakazono 1978; Shapiro 1981; Hoffman 1985). Once courtship began the male often chased other species that entered the general spawning area, particularly reef sparids with a reddish colouration.

During courtship most approaches proceeded to circling, in which the pair swam around each other in a horizontal attitude. The orientation of male to female during circling was any combination of dorsal to ventral but was most frequently ventral to ventral. Mouth bumping was deliberate contact which lasted for more than a couple of seconds. During this behaviour the fish often moved slowly upwards in the water column and frequently proceeded directly to nuzzling and a spawning ascent. No sequence was found between circling and mouth bumping, either behaviour could occur first or be left out of the courtship routine.

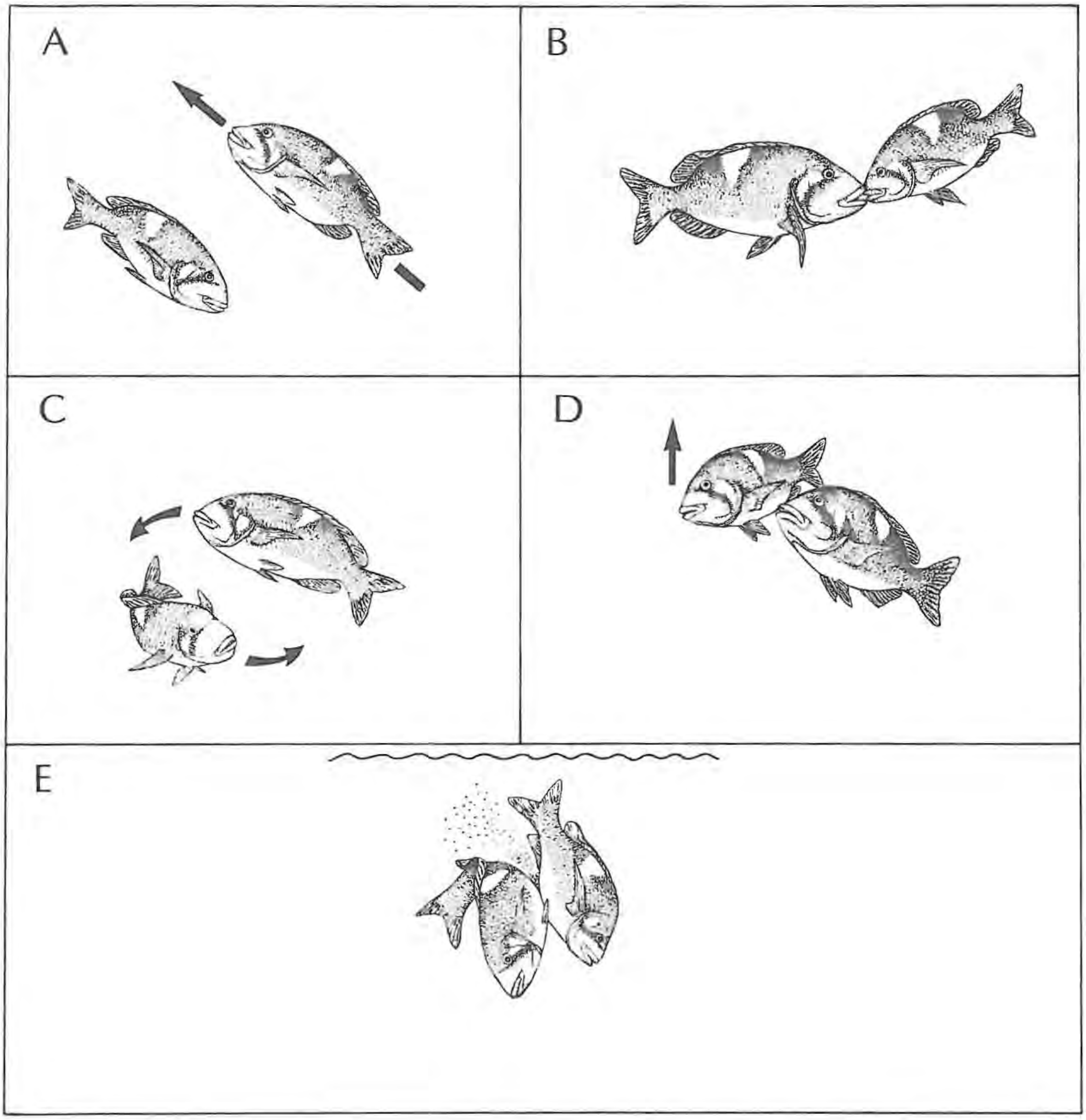


Figure 51. Courtship behaviour in *Chrysoblephus laticeps*. (A) rushing, (B) mouth bumping, (C) circling, (D) nuzzling with spawning ascent and (E) spawning.

Nuzzling was interpreted as a tactile stimulation of the female by the male during which he continually nudged her vent with a rapid opening and closing of his mouth. This behaviour is almost universal in fishes and is thought to either physically stimulate the movement of eggs or induce muscle contractions (Thresher 1984). Nuzzling was always performed in conjunction with the spawning ascent during which the pair slowly moved up in the water column, the female remaining motionless and the male pushing her towards the surface. The spawning ascent probably evolved as a means of minimizing egg predation by filter feeding organisms on the reef (Johannes 1978), and is a common behaviour pattern in the courtship of many pelagic spawning reef fish.

The spawning ascent was frequently interrupted by either the presence of other fish swimming in close proximity (particularly larger species) or perhaps by the incomplete readiness on the part of the female to spawn. Interruption caused a momentary loss of the white belly colouration, which resumed a more dull red colour. At the moment of spawning the male orientated himself head to tail with the female so that their vents were almost touching during the mutual release of gametes. This was followed by a rapid swim towards the substrate and a complete loss of the white belly colouration.

DISCUSSION

The gonado-somatic index showed that the spawning season in both C. laticeps and C. cristiceps was fairly restricted. In C. laticeps spawning began in October and ended in January while in C. cristiceps the season was slightly shorter, beginning in November and ending in January. Gonad development, based on size, peaked in December for both species. These results compared well with a study of the seasonal occurrence of sparid eggs and larvae in the waters off the south-western Cape coast (Brownell 1979), which indicated that many South African sparids spawned in summer.

Of the environmental factors that may influence the reproductive seasonality of fishes, temperature and photoperiod appear to be the most important (de Vlaming 1972b). This relationship has been demonstrated in a number of South African sparids including C. nufar (Coetzee 1983; Garratt 1986a), C. puniceus (Garratt 1986a) as well as for the species in this study. The longer breeding seasons of sparid populations found in the warmer sub-tropical waters off Natal, South Africa (Garratt 1986a) suggest that while photoperiod may be an important cue influencing the neuro-endocrine centres that control gonadotropic secretion in teleosts (de Vlaming 1972b), temperature may be a more important determinant of the length of the breeding season. Reviewing the reproductive biology of lutjanoid-like fishes in general, Thresher (1984) noted that most temperate sparids spawn in spring and summer, and have a shorter breeding season than their tropical counterparts. The results presented here were consistent with these views, showing that *C. laticeps* and *C. cristiceps* have well defined breeding seasons that are closely correlated with both photoperiod and temperature.

In both species the gonado-somatic indices of male fish were found to be considerably lower than those of females during the breeding season. Although the number of gametes produced need not necessarily be a function of the size of the gonad (e.g. multiple spawners), this indicated that the energy invested in gamete production by males was less than that of females.

It is generally accepted that the cost of producing sperm is less than that of eggs, even though the latter may vary tremendously in size (Baylis 1981). This rather simplistic view is, however, complicated by considerable sperm wastage during spawning which may make the cost of producing a zygote more equitable to both parents (Williams 1966).

In many fishes the size of the gonad, and hence the gonado-somatic index, in the male and female are comparable. This is also true of a number of South African sparids including *C. gibbiceps*, *S. durbanensis*, *P. grande* and *P. rupestris* (personal observations). Presumably sperm production in these species is far greater than that found in *C. laticeps* and *C. cristiceps* and may reflect a difference in the mating systems of the two groups. Field observations showed that *C. laticeps* frequently occur in groups of one or a few large individuals (males) together with numerous smaller fish (females) and that these groups were fairly stable over time (see chapter 3.6.1).

The spawning behaviour in *C. laticeps*, protogyny and the relatively small testis size all point to both species being polygynous, with large males spawning with a number of females. Conversely large testis size is probably indicative of group spawning, in which a large testis is advantageous under conditions of intense sperm competition.

Emlen and Oring (1977) outlined two pre-conditions for the evolution of polygamy. Firstly, that multiple mates, or resources sufficient to attract multiple mates, must be energetically defendable by individuals. The degree to which these resources are dispersed usually defines the degree to which they are able to be defended and is related directly to clumping of the resource. The second prerequisite is an ability to utilize the potential for polygamy. This is most frequently related to the degree of parental care required for the successful rearing of young. Regardless of the ability to defend resources, polygamy can only develop if one or both parents are freed from having to rear their young.

The results presented here showed that *C. laticeps* were pelagic spawners, producing small eggs (approx. 500µm diameter) with a large oil droplet. Courtship behaviour showed that gametes were released well above the substrate, following which the fish returned to the reef. They are therefore particularly well disposed to polygamy because neither parent is restricted by the need to protect their offspring.

Accepting this postulate, that C. laticeps is polygynous, it is necessary to examine the factors, environmental and behavioural, that maintain the aggregation of females. Following Emlen and Oring (1977) two mating strategies are possible. The first, resource defence polygyny, exists when males have access to numerous females indirectly by defending critical resources. The second, female (or harem) defence polygyny, is found when males have direct access to many females as a result of female gregariousness.

Resource defence polygyny

For many pelagic spawning reef fish, optimal spawning sites are defined by the need to protect the gametes from immediate predation by filter feeders and planktivores (Thresher 1984). This is achieved by spawning in areas where currents quickly remove the fertilised eggs from the reef (Warner 1984). Where optimal spawning sites are sufficiently patchy, large male fish are able to occupy these sites and monopolise spawning by aggressive exclusion of smaller males. Observations of C. laticeps in the aquarium showed that these fish always spawned in the same area. It is significant that the spawning site chosen was immediately downstream of the main inlet, i.e. where the current was strongest. The benefits derived from resource defence lie in an increased probability of mate attraction. The male is effectively increasing his genetic fitness above that of the other individuals in the population by mating with a large number of females on a daily basis. Fitness in this sense is defined as a measure of the reproductive success of an individual relative to that of other individuals in the same population (Emlen & Oring 1977). The magnitude of the benefit is influenced by the temporal pattern of availability in sexually receptive partners. If all of the females were sexually receptive at exactly the same time then the potential for males to monopolise mating is reduced. Two possibilities are immediately apparent. In the protogynous Anthias squamipinnis, Shapiro (1981) showed that sex reversal was behaviourally induced primarily by female-female interaction. It is possible that a similar interaction may prime females on a sequential basis to mate with the male. In other words the absence of the dominant female during mating could result in a priming effect on the next female in the hierarchy. The advantages to the female in waiting to pair with the dominant male will be discussed below.

Female defence polygyny

The basic assumption in the above model is that resources are sufficiently clumped to be economically defendable. If they are not, then the ability for monopolisation of the resource is reduced. An alternate explanation for the aggregation of females then becomes necessary. One such possibility is the concept of a limited spawning period (Thresher 1984). Many pelagic spawning reef species restrict their spawning activities to narrow 'launch windows'. During these periods the immediate chance of survival of offspring is greater for reasons such as reduced predator activity and favourable tidal or current conditions. In C. laticeps spawning was diurnal and was restricted to a short period in the late afternoon. Under these conditions it would be advantageous for the female to reduce the time spent searching for a mate by waiting to spawn with the dominant male.

Similar observations on the behaviour of C. cristiceps in the field were not possible because they tend to shy away from divers. However, based on similarities such as small testis size and protogyny it is possible that the above arguments apply equally well to this species.

To summarise, the study has shown that the understanding of the mating systems of C. laticeps, and particularly of C. cristiceps, is far from complete. Both species have a restricted breeding season which is correlated with both temperature and photoperiod. Protogynous hermaphroditism and pelagic spawning provide both species with the potential for the development of a polygynous mating system. Behavioural observations on C. laticeps suggest that large males are able to mate with a number of females by either monopolising critical resources such as spawning sites or by taking advantage of female gregariousness.

3.6.3 - THE REPRODUCTIVE CYCLE OF EXPLOITED POPULATIONS

INTRODUCTION

Typically a recreational linefishery is biased towards the removal of the larger specimens from a population. Protogynous species are thought to be particularly vulnerable to over-exploitation under these conditions because males are subject to a greater fishing mortality than females (Smale & Buxton 1985; Buxton & Clarke 1986). Intense fishing pressure may result in a significant alteration of the sex ratio which can seriously affect the reproductive potential of the population (Smith 1982; Garratt 1985b).

This section examines the reproductive biology of C. laticeps and C. cristiceps from five exploited localities on the southern Cape coast between Mossel Bay and the Kei River mouth (see Fig. 2). Specific characters such as size at maturity, sex ratio and size at sex reversal in these areas were compared to the results obtained in the Tsitsikamma Coastal National Park. Although the Park lay close to the midpoint of the geographical range of both species it did not follow that the area was an optimum environment for the species or that population parameters measured there represented the normal sexual dynamics of the species under unexploited conditions. In spite of this possible limitation the characteristics of the Tsitsikamma population were considered to be a baseline from which to compare exploited populations.

Observed differences between areas were thought to result from either natural variation over a geographical range or from different levels of exploitation. These possibilities are investigated for both species. Differences in the reproductive characters were greatest in C. cristiceps and reasons for this are examined.

METHODS

Most of the sampling effort was concentrated on the recreational ski-boat fisheries operating in the Port Elizabeth area between Woody Cape and Sardinia Bay but additional information was collected from the fisheries operating in the Mossel Bay to Knysna area, Jeffreys Bay and the East London to Kei River mouth area. Detailed sampling procedures are described in the first part of this chapter. Fish smaller than 200mm fork length were not landed in the recreational ski-boat fishery due to minimum size regulations, so percentage maturity was only determined in the Port Elizabeth area where small fish were speared.

RESULTS

Gonado-somatic indices for female C. laticeps and C. cristiceps are shown in Figure 52. The breeding season in C. laticeps stretched from September to March with a peak in December. This result was similar to the result obtained in Tsitsikamma, the apparently longer season in Port Elizabeth resulting from a bigger sample size with a more normal distribution. In C. cristiceps peak reproductive activity was recorded in November, one month earlier than the result obtained in Tsitsikamma although the length of the breeding season was the same in the two areas. Because very few ripe females were sampled in either area the difference was thought to result from low samples and not a real difference in the breeding season in the two areas. Gonadal recrudescence in both species was again well correlated with both photoperiod and temperature, the significance of which is discussed elsewhere. Male gonado-somatic indices are summarised in Figure 53. The relative increase in the size of the testis of C. laticeps was low but activity coincided with that of the ovary. An increase in the size of the testis was not observed in C. cristiceps. Based on the presence of sperm in the tissue (macroscopic and histological examination) many of these fish were sexually active. This observation showed that the gonado-somatic index was a poor indicator of spawning season in these fish and confirmed the result observed in Tsitsikamma that male investment in gamete production was low, particularly in C. cristiceps.

Percentage length frequencies of C. laticeps sampled between Mossel Bay and Port Elizabeth are shown in Figure 54. Males, females and hermaphrodites are plotted separately for each area except in Mossel Bay-Knysna where hermaphrodites were not recorded separately. A summary of the mean size of the total catch and different sexes as well as the size class of sex reversal, 50% maturity and sex ratio for each area is given in Table 41.

The size class with the highest frequency of hermaphroditic fish was similar in all areas studied. There appeared to be a trend in the mean size of hermaphrodites which increased along the coast between Mossel Bay and Port Elizabeth, but ANOVA showed that these differences were insignificant ($F=2.4$, $P<0.05$, df=3.237). Sex ratios recorded in the exploited areas showed that females were more abundant than males in the catches (Table 41).

Combined spearfishing and ski-boat catches for the area between Sardinia Bay and St Croix Island are shown in Figure 55. The percentage maturity determined for this area (172mm fork length) was slightly lower than the value obtained in Tsitsikamma (180mm fork length see Fig. 46).

Length frequency analyses of C. cristiceps caught by recreational ski-boat fishermen at localities between Mossel Bay and East London are

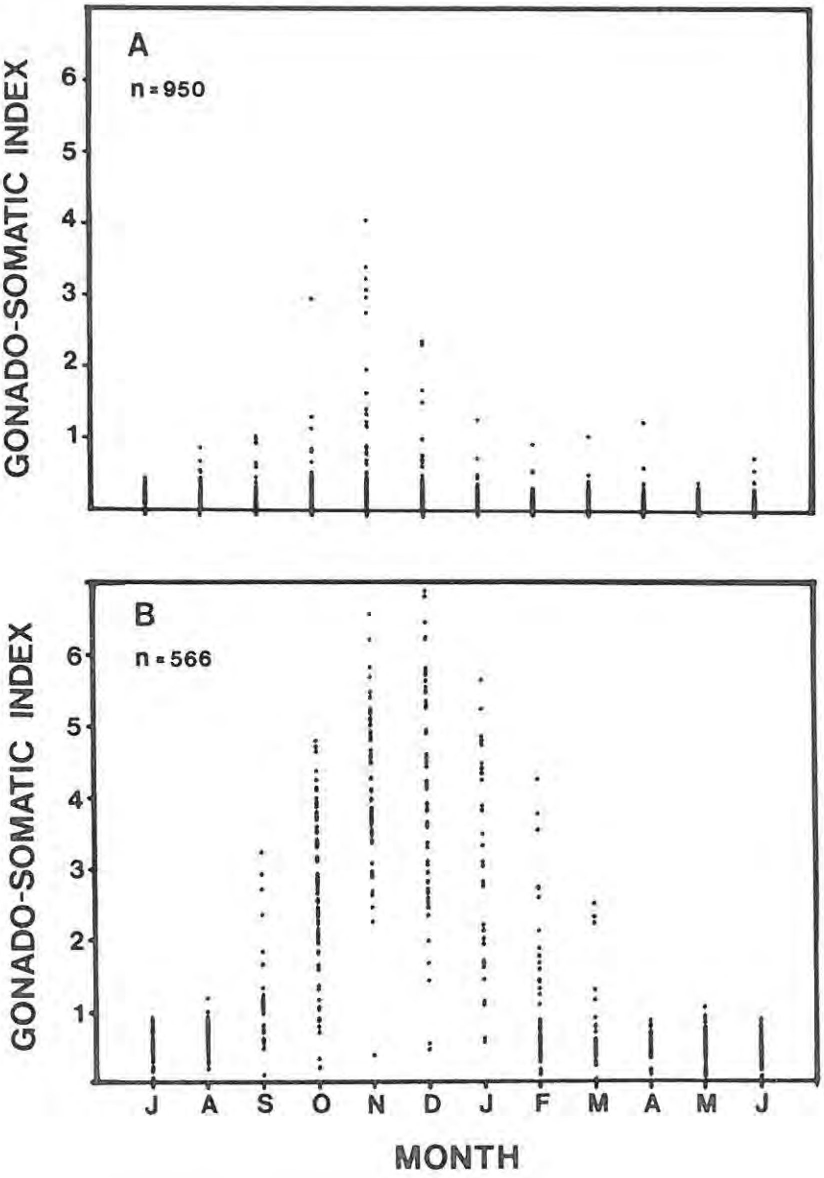


Figure 52. Seasonal variation in gonado-somatic index of female *Chrysoblephus cristiceps* (A) and *C. laticeps* (B) sampled in the Port Elizabeth area between 1984 and 1986.

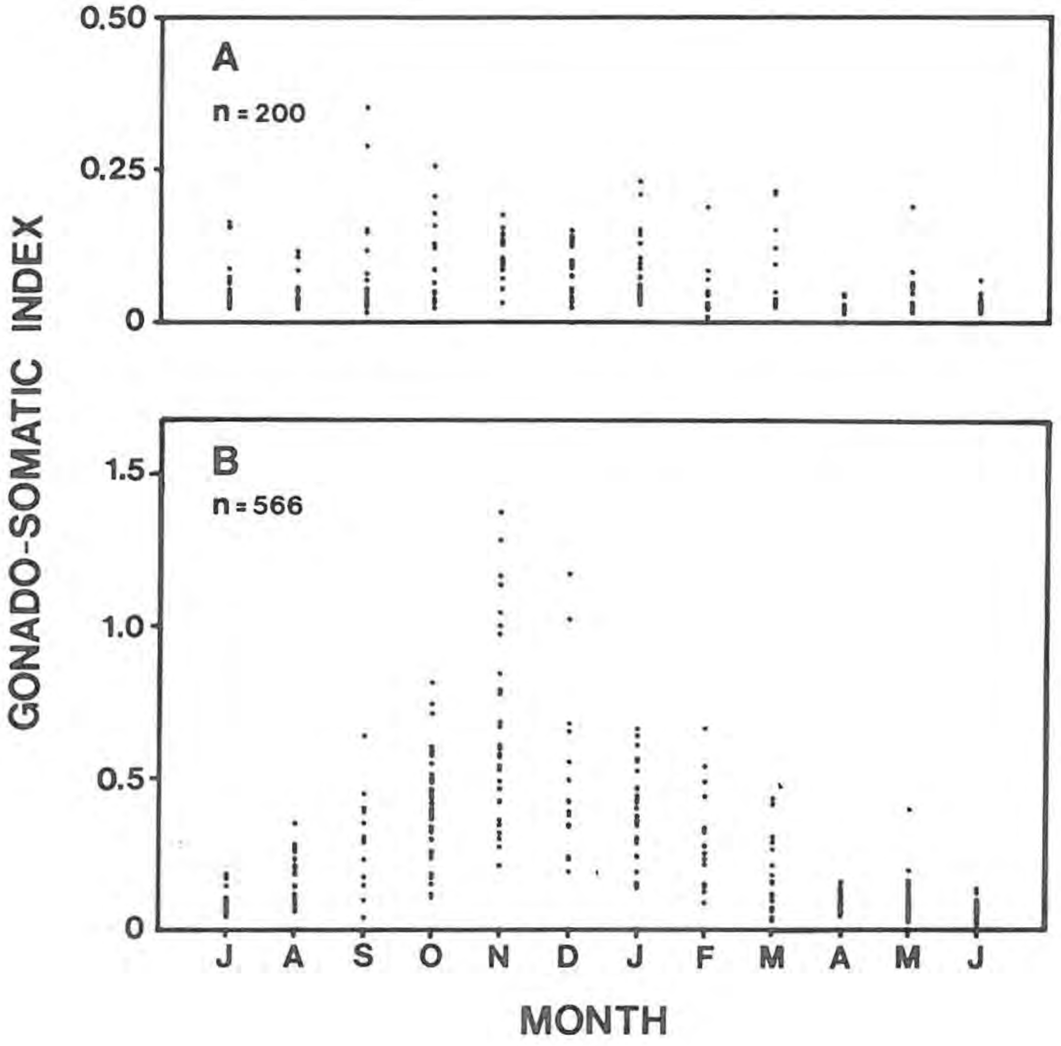


Figure 53. Seasonal variation in gonado-somatic index of male Chrysoblephus cristiceps (A) and C. laticeps (B) sampled in the Port Elizabeth area between 1984 and 1986.

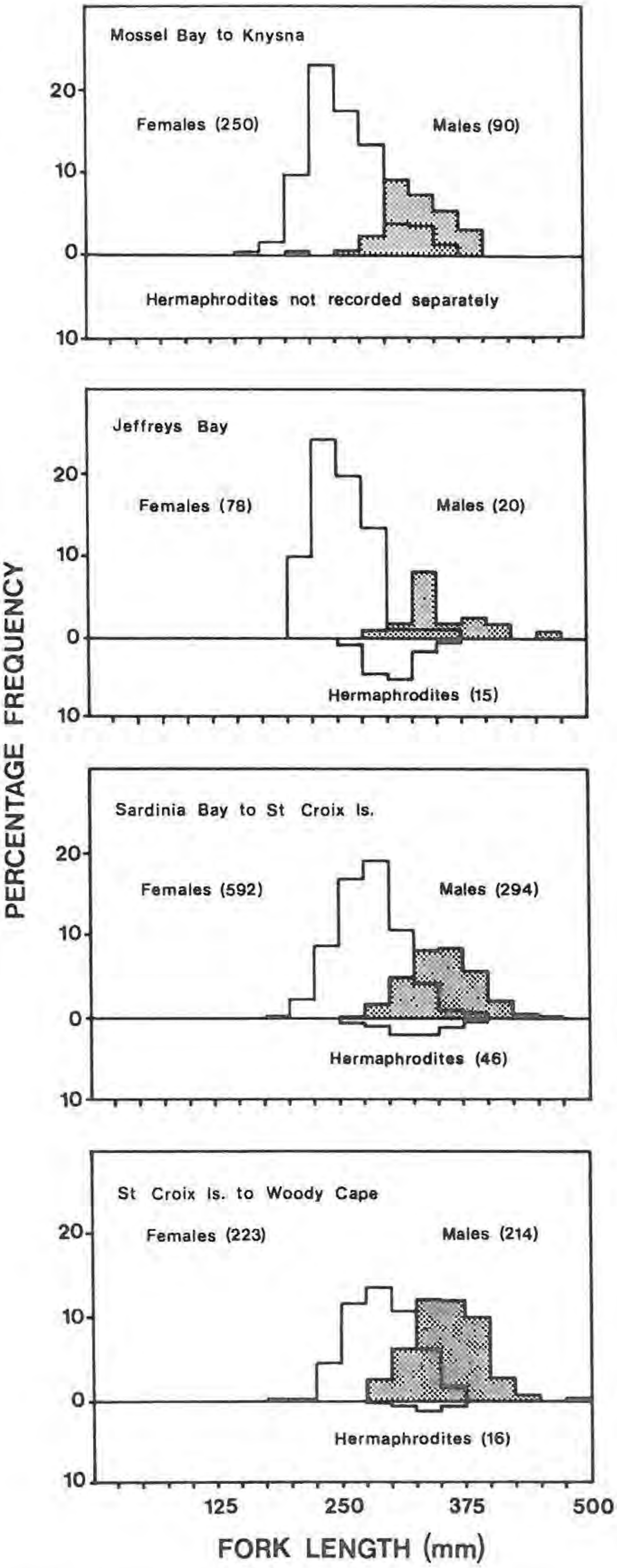


Figure 54. Length frequency analysis of Chrysoblephus laticeps sampled between Mossel Bay and Woody Cape from 1980 and 1986. Males are shaded and sample numbers are given in parenthesis.

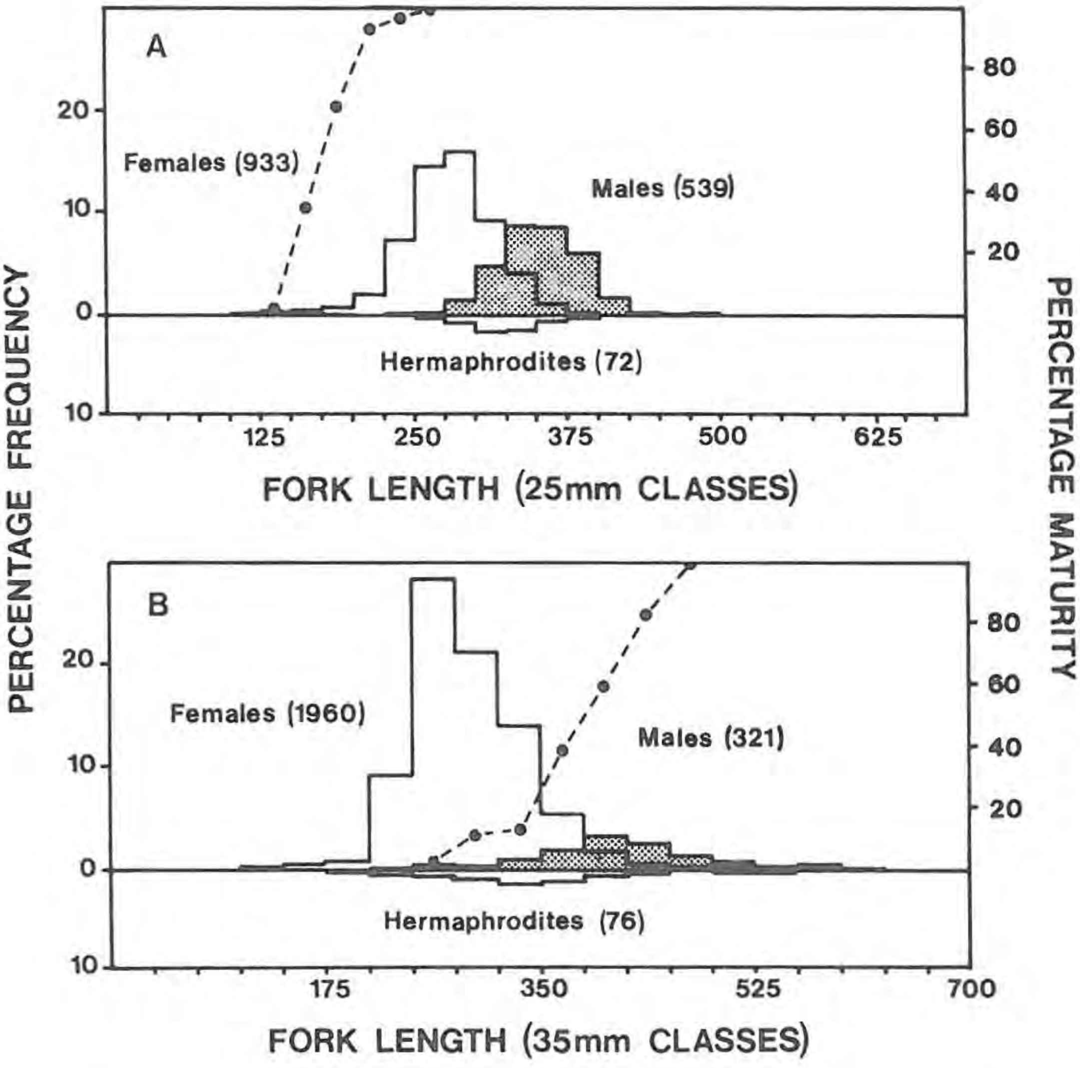


Figure 55. Length frequency analysis and percentage maturity in <u>Chrysoblephus laticeps</u> (A) and <u>C. cristiceps</u> (B) sampled between St Croix Island and Sardinia Bay from 1984 and 1986. Males are shaded and sample numbers are given in parenthesis.

TABLE 41. Mean and standard deviation of the catch composition, and reproduction characteristics of _C. laticeps_ caught in exploited and unexploited areas on the southern Cape coast between 1980 and 1986. All lengths are fork length (mm).

	K&MB	JB	SB-StC	StC-WC	TSI
Total Catch	277±48	280±51	305±47	322±46	317±44
Males	331±30	388±40	351±34	354±34	350±26
Females	257±36	254±29	281±33	290±32	277±31
Hermaphrodites	-	309±21	323±29	332±21	318±28
Sample number	340	113	933	453	997
Sex reversal	300-325	300-325	300-350	325-350	300-325
50% maturity	-	-	ca. 172		ca. 180
Sex ratio (♂:⚥:♀)	1:-:2.78	1:0.75:3.9	1:0.16:2.01	1:0.07:1.04	1:0.36:0.83

K&MB - Mossel Bay to Knysna; JB - Jeffreys Bay; SB-StC - Sardinia Bay to St Croix Island; StC-WC - St Croix Island to Woody Cape; TSI - Tsitsikamma.

TABLE 42. Mean and standard deviation of the catch composition, and reproductive characteristics of _C. cristiceps_ caught in exploited and unexploited areas on the southern Cape coast between 1980 and 1986. All lenght are fork length (mm).

	K&MB	SB-StC	StC-WC	EL	TSI
Total Catch	284±56	286±59	326±67	393±85	372±82
Males	398±135	400±95	425±59	468±91	494±48
Females	279±46	277±45	302±43	360±59	333±54
Hermaphrodites	-	295±56	368±54	402±41	416±47
Sample number	98	859	1438	151	534
Sex reversal	315-350?	245-280	315-350	385-420	420-455
50% maturity	-	ca. 375		-	ca. 365
Sex ratio (♂:⚥:♀)	1:-:23.5	1:0.44:13.05	1:0.19:4.43	1:0.15:2.27	1:0.64:3.79

K&MB - Mossel Bay to Knysna; SB-StC - Sardinia Bay to St Croix Island; StC-WC - St Croix Island to Woody Cape; EL - East London; TSI - Tsitsikamma.

given in Figure 56 and the reproductive characteristics of these populations are summarised in Table 42. The mean size of hermaphrodites showed a trend similar to that found in C. laticeps, increasing along the coast between Mossel Bay and East London. All were lower than the size recorded in Tsitsikamma and ANOVA showed that the difference between the means was highly significant ($F=34.9$, $P<<0.01$, df=3.141).

This trend was also apparent in the sex ratio. Both the proportion of females in each population and the mean size at sex reversal were well correlated with area. In the Mossel Bay-Knysna and Sardinia Bay-St Croix Island areas, the proportion of females in the catches was considerably greater than in the other areas. Sex ratios were similar in the St Croix to Woody Cape and the Tsitsikamma areas and in East London the proportion of females was lowest.

Estimating the size at maturity was difficult in this species because few reproductively active females were sampled during the study. This resulted mainly from a seasonality in catches, poorest catches occurring over the breeding season, and the difficulty in obtaining speared samples because the fish avoid divers. Fifty percent maturity was estimated by combining ski-boat and spearfishing catches in the area between Sardinia Bay and Woody Cape. This produced a value of 375mm fork length (Fig. 55) which was higher than the value of 365mm fork length obtained in the Tsitsikamma.

DISCUSSION

The reproductive characteristics of a population evolve together as inter-related traits and are determined by the demographic environment (Williams 1966; Stearns & Crandall 1984). Mean values of these characters are determined by the relative fitness of all individuals in the population, fitness measured as the lifetime reproductive contribution of the individual, and should be constant under a given set of stable conditions. Changes in the environment may induce changes in the characters along a 'plastic trajectory' (Stearns & Crandall 1984) and a change in one trait may result in compensatory changes in another (Stearns 1976). Data presented here showed that aspects of the reproductive biology differed in the areas studied and that effects were not random but appeared to follow trends between Mossel Bay and East London.

The most obvious difference between the populations sampled was a change in sex ratio, the proportion of males being lower in the exploited areas even though the range of sizes taken was similar. This decrease, observed on both sides of the Tsitsikamma, suggested that differences in sex ratio were not the result of a trend over the species' range. Alternatively, exploited populations of these fish would be expected to have fewer males because of the selective removal of larger fish in the line-fishery. A comparison between the catch composition in the Sardinia

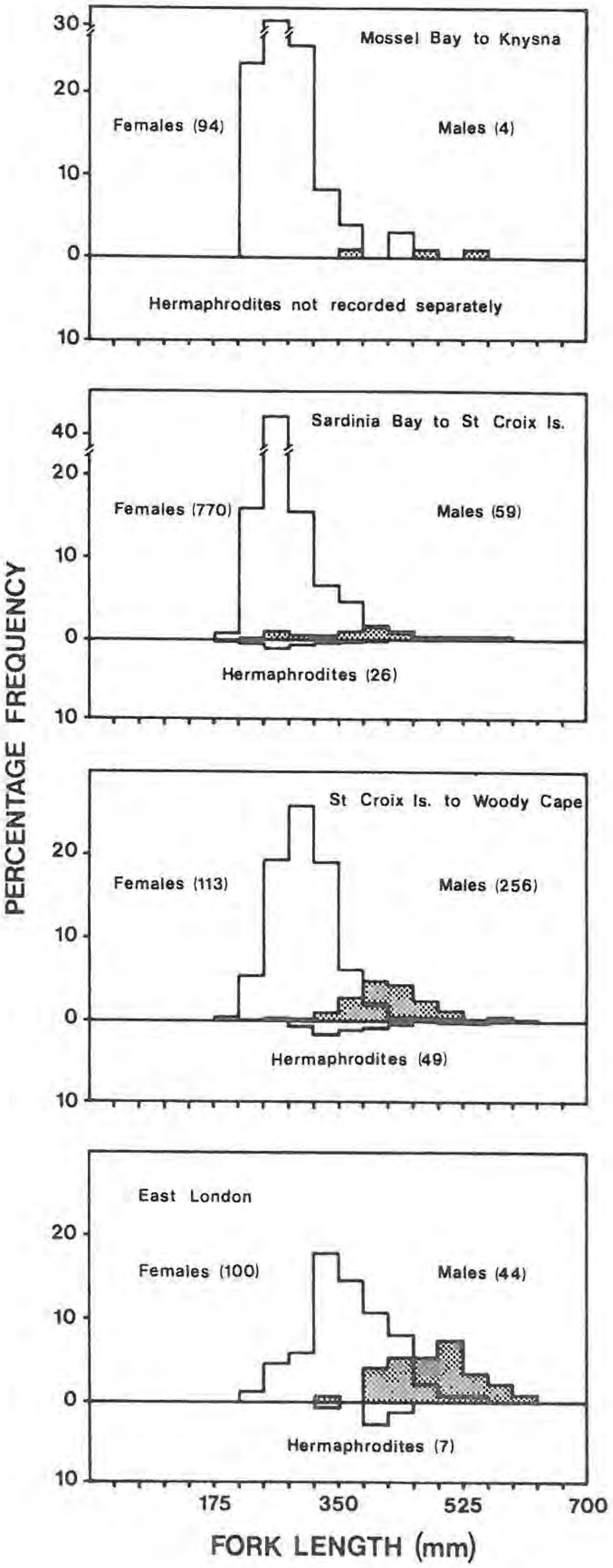


Figure 56. Length frequency analysis of <u>Chrysoblephus cristiceps</u> sampled between Mossel Bay and East London from 1980 and 1986. Males are shaded and sample numbers are given in parenthesis.

Bay-St Croix and St Croix-Woody Cape areas indicated that the intensity of fishing had a direct effect on the proportion of males in the population. Most of the effort in the recreational ski-boat fishery in this area was concentrated within 15km of the launching sites (Smale & Buxton 1985). It followed that the Sardinia Bay-St Croix population would be more heavily exploited because of its proximity to the launch areas and as expected was found to have a lower percentage of males. Garratt (1986a), in a study of *C. puniceus* off Natal, found that populations on the south coast had fewer males than those further north and also attributed the differences to exploitation.

Mean size at sex reversal appeared to be directly related to sex ratio. This effect was most noticeable in populations of *C. cristiceps*, areas with a low proportion of males having a significantly lower size at sex reversal. Other studies have shown that sex reversal may be induced by the removal of males (Fishelson 1970; Robertson 1972) and Shapiro (1980) suggested that sex reversal was controlled by behavioural interaction between males as well as females.

In *C. laticeps* size at maturity was slightly lower in the Port Elizabeth area than in Tsitsikamma while the reverse held for *C. cristiceps*. Since growth rates of these species were not significantly different in these areas size at maturity was expected to be fairly constant. This follows the reasoning of Stearns & Crandall (1984), who suggested that age at maturity should change in response to a change in growth induced by environmental stress.

The results presented here supported the concept of inter-related traits, a change in sex ratio in both species being related to corresponding effects in the size at sex reversal. If these differences were related to exploitation the question arises: Why were the effects apparently more severe in *C. cristiceps*? Factors that may contribute to these differences include the proportion of females in the catch, size at sexual maturity, size at recruitment to the fishery, sex ratio threshold and different levels of fishing pressure between the species, and are discussed below.

Size at recruitment varied slightly between areas and species but was effectively set by minimum size regulations in the linefishery. It is important to note here that the minimum size was the same for both fish (250mm total length). Relating the number of females in the catch, size at recruitment and size at maturity (Fig. 57), it is shown that a greater proportion of large female *C. cristiceps* were being caught, many of which are not sexually mature. By comparison all of the *C. laticeps* taken in the fishery were mature and many of the mature size classes were not recruited to the fishery.

Smith (1982) suggested that the reproductive value of age classes differed, younger females being more valuable than older females largely because of the limited life span of the older fish. Garratt (1985b)

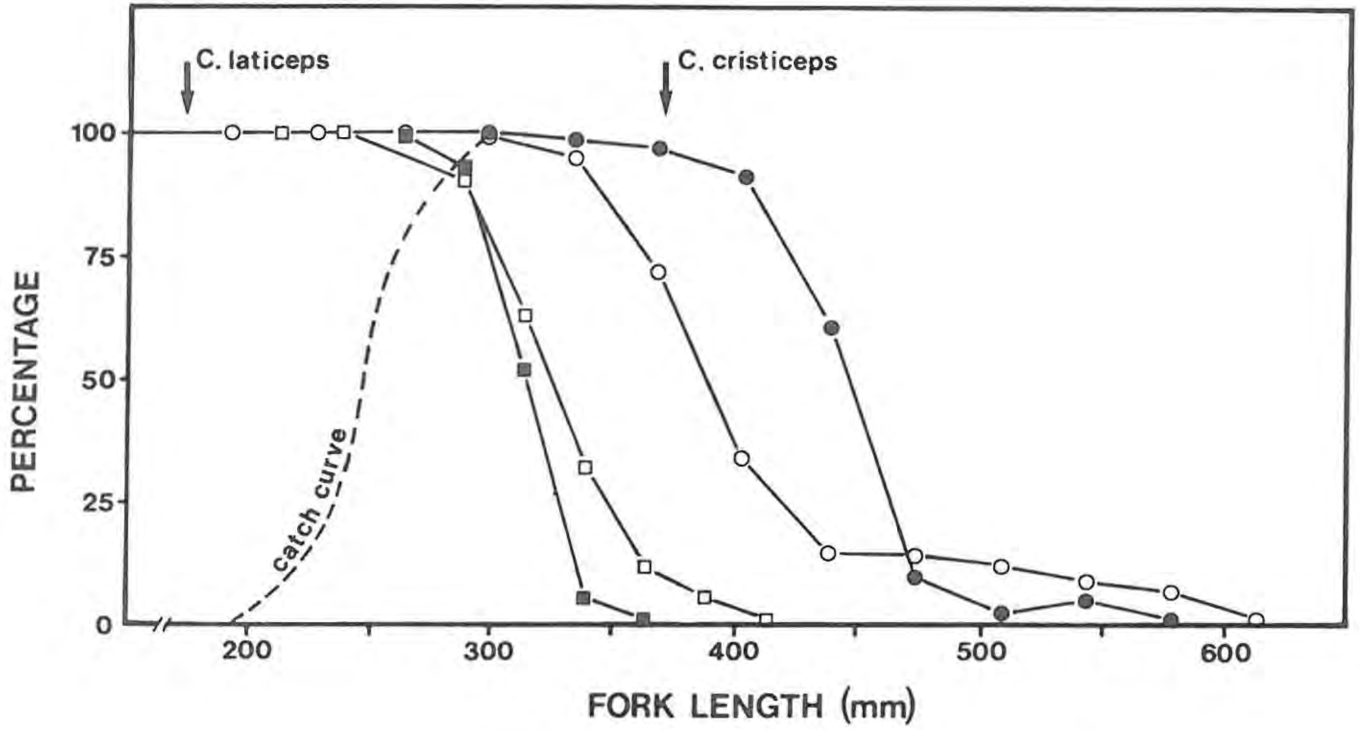


Figure 57. The effects of fishing on the populations of Chrysoblephus cristiceps (circles) and C. laticeps (squares) in Tsitsikamma (solid) and Noordhoek (open). Descending curves represent the percentage females in the population for different size classes and the ascending curve is the percentage of the population vulnerable to fishing. Arrows indicate the 50% maturity levels of the two species.

showed in C. puniceus that the highest contribution to population egg production was made by females just after they became sexually mature.

From Figure 57 it is apparent that more of the reproductively valuable females in the C. cristiceps population were vulnerable to fishing. Smith (1982) suggested that a change in the size at sex reversal would act as a compensatory mechanism to restore a desirable sex ratio. This hypothesis suggests that the organisms adjust size at sex reversal to maintain optimum population sex ratio. This implies group selection which may or may not occur in nature (Stearns 1976), but should only be invoked when individual selection cannot explain the observed effect (Williams 1966). A more simple explanation may be found by considering the reproductive strategy of the individual. Optimal strategy maximises reproductive value at all ages (Ware 1984) and advantages of reproducing as one sex when small and the other when large have been discussed elsewhere in this Chapter. Removal of the larger males provides the opportunity of sex reversal in the dominant females (see above). Shapiro (1979) showed that control of sex reversal was more complex than a simple dependence on the presence or absence of males and in social groups the removal of a male did not always result in the immediate reversal of a female. Shapiro (1981) introduced the concept of a sex ratio threshold which, when exceeded, would cause sex reversal of a dominant female. This could also explain why size at sex reversal in C. laticeps was not significantly different between areas. If the ratio of males to females had not surpassed the sex ratio threshold then size at sex reversal would remain unchanged. Removal of dominant females as well as males would provide a greater opportunity for sex reversal in progressively smaller females.

Finally, the differences observed between the two species may have resulted from a more intense fishing pressure on C. cristiceps. Smale & Buxton (1985) showed that the recreational ski-boat fishery in the Port Elizabeth area was a multispecies one and assumed that effort was divided equally amongst reef species. The validity of this may be questioned for some areas, for example, between St Croix Island and Woody Cape where C. cristiceps are abundant and few C. laticeps are caught. Based on commercial landings of the two species the opposite trend would be expected because annual landings of C. laticeps are greater.

In conclusion, the results of this section showed that breeding season and age at maturity in both species were the same in the Port Elizabeth and Tsitsikamma areas. Differences in the sex ratios of the populations between Mossel Bay and East London were attributed to exploitation and size at sex reversal was related to the proportion of females in the population.

CHAPTER 4 - EXPLOITATION AND CONSERVATION

4.1 THE FISHERY

Linefishing in South Africa may conveniently be divided into two sectors, commercial and recreational, although there is considerable overlap between the two in terms of the way in which the resource is utilised. Stander & Nepgen (1968) suggested that the importance of the linefishery lay not in the relative value of the catch but in the income it provided for a large number of individuals as a subsistence fishery. This reasoning may be extended to the recreational fishery as well. Its value as a recreational pursuit and the subsiduary industry that it supports may far exceed the landed value of the recreational catch (Charbonneau & Hay 1978).

An important aspect of the linefishery is that it is multi-faceted, both in terms of target species and participants. The commercial sector differs mainly in the scale of the operation which ranges from subsistence fishing from small craft to large company owned vessels that can remain at sea for long periods of time. While some of the participants are exclusively linefishermen others only operate during the seasonal availability of species such as snoek (Thyrsites atun), fishing other resources for the rest of the year e.g. crayfish. Target species in the commercial fishery vary with area as well as season.

In contrast, the recreational fishery may be divided into shore anglers (including estuarine, rock and surf) and boat anglers. This study deals mainly with the latter although there is naturally a great degree of overlap between the target species of commercial and recreational fishermen operating from boats.

Recreational boat anglers operate from craft known as ski-boats, which are relatively small (4,5-8m long) partly decked and powered by twin petrol-driven outboard motors or inboard engines with tilting propulsion gear. These boats are transported on trailers and manned by a skipper with as many as five crew. Because of their mobility they can be launched almost anywhere along the coast. Ski-boating commenced in South Africa in the 1940's, primarily as a recreational activity over weekends. Present motivations vary from that of pure sport to semi-commercialism in which fish are sold to recover the costs of the fishing trip or even to supplement the income of the participants (Smale & Buxton 1985).

Publications relating to the recreational aspect of the linefishery are few and deal with the biology of target species (reference to most of these has been made in the relevant preceding sections of this study). Most of these studies are fairly recent and have arisen out of an increased awareness of the importance of the linefishery in South Africa defined by the National Linefish Programme Committee (Anon. 1979; Wallace & van der Elst 1983). Only two studies relating to the dynamics of the fishery itself have been published. Smale & Buxton (1985) studied aspects of the fishery in the Eastern Cape including historical effort trends, catch and effort from one club over a two year period and a preliminary evaluation of the ski-boat fishery. Garratt (1985a) published an account of the exploited population structures of two linefish species caught on the Natal coast with brief reference to the fishery and special management problems. Also relevant however, is a study of historical catch trends in the commercial fishery between the Cape Peninsula and Port Alfred (Crawford & Crous 1982), because of the overlap in target species between this and the recreational sector. In addition, there is an extensive 'grey' literature that is found in internal and annual reports of various institutions which summarise the annual catches of linefish and the status of the fishery in general.

This literature is reviewed with respect to *C. laticeps* and *C. cristiceps* to place the exploitation of these two species and the overall linefishery in perspective.

C. laticeps are caught by both sectors of the fishery between Cape Point and East London, although occasional catches may be taken further east. Their range is thought to extend further north to Mozambique and Mauritius (Smith & Heemstra 1986). *C. cristiceps* are less common in catches west of St Sebastian Bay although they are caught as far east as Port Durnford on the northern Natal coast. Their range does not extend further north than Natal (Smith & Heemstra 1986). Attempts to quantify the annual landings of these and other linefish species are difficult because species are lumped into categories such as redfish or silvers and in earlier records identifications were uncertain (Ahrens 1964).

In spite of these problems Crawford & Crous (1982) have attempted to analyse trends in the commercial catches of redfish on the Cape south coast. This analysis provides a number of useful insights although the increasing importance of certain species as a consequence of a long term change in environmental temperatures appears dubious based on the presented evidence. Despite their conclusions to the contrary the importance of *C. laticeps* to the catch in the areas studied remains unclear because they are lumped with two other species (see their Fig. 5). The same may be said for *C. cristiceps*. Their inference that *C. laticeps* (including *Chrysoblephus gibbiceps* and *Cheimerius nufar*) and *Petrus rupestris* (including *Polysteganus undulosus* and *Chrysoblephus cristiceps*) are the most important components of the redfish catch in Algoa Bay differs considerably from the result obtained by Smale & Buxton (1985) for the recreational fishery over the same period. In the latter study where species were not lumped, the most important redfish in the Algoa Bay area were *C. nufar* and *C. cristiceps*, followed by *C. laticeps*. The others *P. rupestris*, *C. gibbiceps* and *P. undulosus* were only minor components of the catch.

Crawford & Crous (1982) also attempt to demonstrate a relationship between the level of exploitation and the percentage contribution of *C. cristiceps* to the combined redfish catch. They suggest that the higher proportions of *C. cristiceps* in East London and Tsitsikamma are related to a lower level of exploitation. (see their Fig. 10). Ignoring the fact that lumped catches make such a comparison extremely difficult the following points need to be examined. The first is that in the Tsitsikamma area all research fishing was done over reef where *C. cristiceps* and *C. laticeps* predominate. Catches of the other redfish species (*C. gibbiceps*, *C. nufar*, *P. undulosus*) on these reefs, with the exception of *P. rupestris*, are rare because they are found in different habitats (Buxton & Smale 1984). Secondly, east of Port Elizabeth catches of *C. laticeps* and *C. gibbiceps* decline due to the limits of their distributional ranges. Taking these points into consideration the relationship between the level of exploitation and the percentage contribution of *C. cristiceps* in the combined redfish catch appears to be non-existent.

Table 43 summarises the estimated Cape landings of redfish species by both commercial and recreational fishermen between 1981 and 1985. These data were extracted from the annual reports of the Sea Fisheries Research Institute (Anon. 1983, 1984, 1985). Two groups are distiguished, 'Roman' which includes *C. laticeps*, *C. gibbiceps* and *C. nufar* as well as 'steenbras', which includes *P. rupestris*, *P. undulosus* and *C. cristiceps*. A number of trends are apparent in three arbitrarily chosen sites along the Cape coast (Fig. 58). In all three areas the catches of the Roman group showed an increasing trend (Fig. 58a) while catches of the steenbras group remained fairly constant despite considerable annual fluctuations (Fig. 58b). The increase in catches of Roman in these areas was not apparent elsewhere as the overall Roman catches along the entire Cape coast averaged between 200 and 300 tonnes (Fig. 58c). The total catch of all linefish species remained fairly constant over the same period. Apart from a peak in 1981 catches have varied between 6 and 7 thousand tonnes with a very slight downward trend. It is important to note here that fluctuations in the catches do not necessarily imply changes in the actual fish populations as they could equally result from differential targeting of effort. These results are similar to those of Crawford & Crous (1982) who showed that although there were peaks and troughs in the annual catch, there was no evidence of either a declining or increasing trend in the redfish fishery in Struis Bay or Gans Bay between 1968 and 1980. Together these observations are important as they show that the linefishery in the Cape is relatively stable. Peaks and troughs in the reported catches of most reef species appear to be related to the availability of preferred schooling species such as yellowtail (*Seriola lalandi*), geelbek (*Atractoscion aequidens*) and kob (*Argyrosomus hololepidotus*), and provide no evidence of a significant change in the

TABLE 43. Summary of the estimated Cape landings of Roman and Steenbras by both commercial and recreational anglers between 1981-1985. Percentage of total catch in parenthesis.

YEAR	AREA	CATCH (kg) Roman	Steenbras	All species
1981	Struis Bay	14 896	5 442	407 256
	Port Elizabeth	23 605	33 024	509 810
	East London	4 298	17 166	39 559
	All Areas	300 304(2.9)	108 738(1.1)	10 117 641
1982	Struis Bay	13 481	26 033	442 747
	Port Elizabeth	8 767	8 937	405 248
	East London	3 622	14 989	26 919
	All Areas	210 809(2.8)	91 518(1.2)	7 609 673
1983	Struis Bay	64 372	20 753	304 058
	Port Elizabeth	11 098	37 064	453 367
	East London	1 783	8 894	17 267
	All Areas	333 170(4.6)	117 333(1.6)	7 219 822
1984	Struis Bay	43 940	7 049	563 280
	Port Elizabeth	45 150	27 638	475 882
	East London	4 668	19 613	31 383
	All Areas	268 702(4.1)	167 522(2.5)	6 593 373
1985	Struis Bay	62 500	7 100	689 300
	Port Elizabeth	65 200	13 700	441 100
	East London	11 900	27 700	66 100
	All Areas	335 300(4.9)	74 900(1.1)	6 781 300

TABLE 44. Summary of the contribution of redfish to the total linefish catch during 1986 as determined by commercial catch returns. Data obtained from the National Marine Linefish database, Sea Fisheries Research Institute.

SPECIES	CATCH (kg)	PERCENTAGE (R)	(T)	*ADJUSTED CATCH(kg)	PERCENTAGE (T)
C. laticeps	135 243	38.0	0.107	221 208	0.174
C. cristiceps	25 878	7.0	0.020	42 315	0.033
C. gibbiceps	22 472	6.0	0.017	36 745	0.029
P. rupestris	74 017	21.0	0.058	121 033	0.096
C. nufar	98 533	28.0	0.078	161 122	0.128
Total redfish (R)	356 143		0.281	582 366	0.459
Unsp. redfish (U)	226 226				
Total (T)	126 874 157				

T = Total linefish catch less squid.
U = Unspecified redfish i.e. proportion of the redfish catch not separated into species, includes above species and A. argyrozona
* Catch adjusted using proportions of (U).

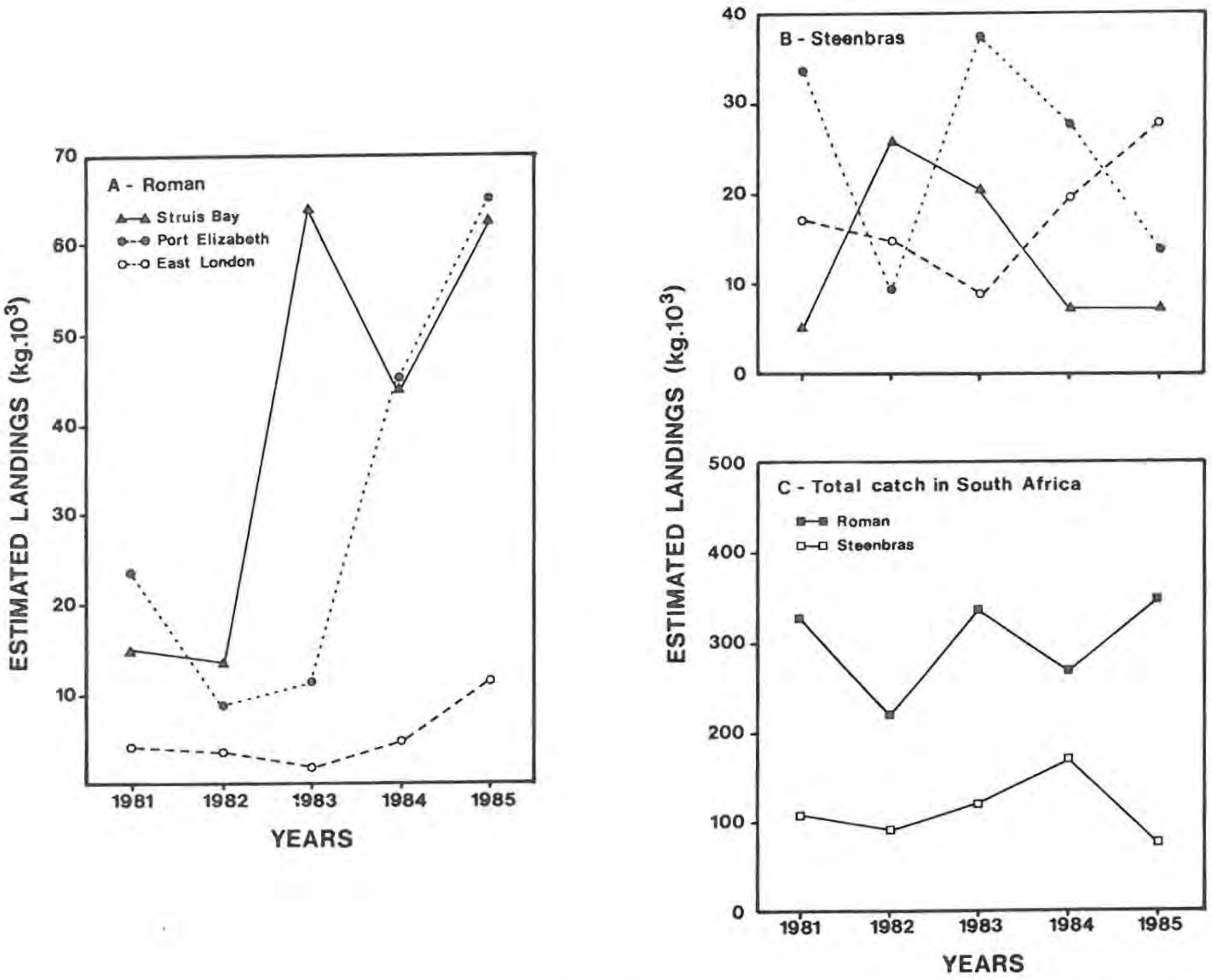


Figure 58. Trends in the Cape landings of linefish between 1981 and 1985 at three localities: Struis Bay, Port Elizabeth and East London. (A) Roman (including C. laticeps, C. nufar and C. gibbiceps) (B) Steenbras (including P. rupestris, C. cristiceps and P. undulosus). (C) All linefish species. Data summarised from annual reports of the Sea Fisheries Research Institute (Anon 1983, 1984, 1985).

numbers of the former.

The individual importance of C. laticeps and C. cristiceps to the linefishery remains unclear. In the commercial sector, however, better information is available for 1986. Table 44 summarises the reported catches of specified redfish, unspecified redfish and the total linefish catch for 1986. These results show that both species are relatively small components of the overall catch, although they may be more important in localised areas. Still a problem with this data is the portion of the catch lumped as unspecified reds, which increases the total linefish catch by 61%. In addition, although these returns are considered to be fairly accurate (A.J. Penney, Sea Fisheries Research Institute pers. comm.), a substantial amount of fish, kept by the fishermen to take home, is not reported. Estimates from one area alone, Struis Bay, are put as high as 20 000kg per annum and are thought to be mostly redfish (A.J. Penney pers. comm.).

The only published information on the contribution of C. laticeps and C. cristiceps to the recreational fishery is that of Smale & Buxton (1985) who show that C. cristiceps and C. laticeps are the second and third most important reef species caught in the Algoa Bay area. Overall they ranked fourth and fifth in importance to this fishery. Comparative data is not available for other areas but more recent observations in some areas suggest that this importance is decreasing because fishermen are targeting for species not subject to bag limits e.g. A. argyrozona and M. capensis. (pers. obs.). The impact of recent fishing legislation on this trend is discussed more fully below. Smale & Buxton (1985) also show that seasonality in catches of redfish species is a result of targeting of effort rather than availability.

To summarise, this information shows that while the value of the landed catch of linefish in South Africa is low (20.384 million Rands Fresh on Board (FOB) in 1985, Anon. 1985b), the activity is important as a subsistence fishery in many areas of the commercial sector and supports a large subsiduary industry with respect to both commercial and recreational fishing. Its value as a recreational pursuit is urgently in need of quantification. Reported landings do not show that catches are declining and the contributions of individual species are, at present, difficult to quantify.

4.2 - YIELD PER RECRUIT ANALYSIS

INTRODUCTION

The goal of most studies on the growth and mortality of fish populations is to estimate the potential yield of the stock at different levels of exploitation (Ricker 1975). Methods available for such assessments are varied (Cushing 1983) but Huntsman, Manooch & Grimes (1983) point out that neither the dynamic pool (Beverton & Holt 1957) nor the surplus yield (Schaefer 1957) population models are useful in the study of most reef fisheries. The reason for this is that the necessary data, including the relationship of stock size to recruitment, a long time series of catch and effort as well as the dynamic interplay between and among species, are not usually available.

An abbreviated version of the full dynamic pool model, the yield per recruit model (Beverton & Holt 1956,1957), has been used in a number of studies on reef fish (Huntsman & Manooch 1978; Manooch & Matheson 1981; Huntsman et al. 1983; Manooch & Mason 1984; Mason & Manooch 1985). This model predicts the ratio of the number or weight of fish caught during the life span of a cohort to the initial abundance of that cohort when it entered the fishing grounds. Beverton & Holt (1957) showed that the total annual yield of the population was the same as the lifetime yield of a single year class assuming that recruitment was constant from year to year. Instantaneous rates of growth and mortality are also assumed to be constant.

Parameter estimate requirements for the model are minimal yet it allows an analysis of the relationship between fishing mortality, recruitment age and equilibrium yield per recruit. The former may also be varied to determine effects on yield per recruit.

The aim of management in using this model is therefore to find the optimum combination of age at recruitment and fishing pressure that will produce the greatest yield (Pitcher & Hart 1982). By constructing a curve of yield per recruit against increasing fishing pressure a maximum value may be obtained. This represents the Beverton & Holt prediction of maximum sustainable yield (MSY) for a particular combination of recruitment age and fishing mortality.

MSY has however, been severely criticised (Larkin 1977; Gulland 1978) and, if it exists at all, it is doubtful that it provides a useful conceptual basis for management (Pitcher & Hart 1982). Much of this criticism is based on the observation that populations are not at equilibrium and that the effects of competition and the relationships between species are not taken into account in predicting MSY.

While the yield per recruit model has also been criticised because recruitment is variable (Cushing 1983), Huntsman et al. (1983) point out that it is probably appropriate for most reef fisheries because carrying capacity and growth, rather than recruitment, are most often limiting factors. Because larval stages are pelagic and long lived (Thresher 1984; Brownell 1979), recruitment is probably sufficient to replace losses from mortality via a pool of juveniles living in marginal habitats (see also Sale 1975,1978). Inclusion of recruitment in the model (Pitcher & Hart 1982; Beddington & Cook 1983) was not possible because the stock-recruitment relationship for these fish is unknown.

The objective of this study was to determine the effects of fishing mortality (F) and size at recruitment (t_R) on the yield per recruit and spawner per recruit, particularly in relation to the age at sex reversal. The current status of the fishery was examined by comparing the fishing mortality at maximum yield per recruit (F_{MSY}) against the marginal yield ($F_{0.1}$) defined by Gulland (1968) and Gulland & Boerema (1973).

METHODS

A computer programme was used to perform the yield per recruit analysis using the microcomputer package LOTUS 1-2-3 (Sluczanowski 1985). This derived yield per recruit as a percentage of Bmax:

$$\begin{aligned} Y/R = 100\, W_\infty\, F \exp(Ft_R) \Big[& (\exp(-Zt_R) - \exp(-Zt_M))/Z \\ & + 3 \exp(Kt_0)\, (\exp(-(Z+K)t_M) - \exp(-(Z+K)t_R))/(Z+K) \\ & - 3 \exp(2Kt_0)\, (\exp(-(Z+2K)t_M) - \exp(-(Z+2K)t_R))/(Z+2K) \\ & + \exp(3Kt_0)\, (\exp(-(Z+3K)t_M) - \exp(-(Z+3K)t_R))/(Z+3K) \Big] / \mathrm{Bmax} \end{aligned}$$

where W_∞ = asymptotic weight of a fish

F = instantaneous rate of fishing mortality

t_R = age at recruitment to the fishery

t_M = maximum age of the fishery

t_0 = theoretical age at length '0'

Z = instantaneous rate of total mortality (F+M)

M = instantaneous rate of natural mortality

K = growth co-efficient from the von Bertalanffy growth equation for length.

Bmax = the maximum expected biomass per recruit of an unfished year class.

Y/R = yield per recruit

The model assumes that recruitment to the fishery with respect to age (t_R) is knife-edged. Knife-edge recruitment implies that all fish of a given age become vulnerable to fishing at a particular time in a given year (Ricker 1975). This is not apparent in the linefishery because of variability in both the length at age and the probability of capture using different sized hooks (see chapter 3.3). Specification of the age at recruitment is critical to the determination and has been interpreted in a number of ways (Lenarz, Fox, Sakagawa & Rothschild 1974; Ricker 1975; Huntsman et al. 1983; Hughes 1986). In this study t_R was approximated by obtaining the length at 50% of the cumulative length frequency distribution (l_t) and then converting age using the von Bertalanffy equation (Hughes 1986). This method is shown in Appendix 2.

Yield per recruit isopleths were constructed by plotting the yield per recruit for various levels of F and t_R and then drawing the isopleths by hand.

RESULTS

Isopleths describing the response of yield per recruit to different values of F and t_R are shown in Figures 59 and 60 for C. laticeps and C. cristiceps respectively. Both responses were similar and showed that yield per recruit increased rapidly at low values of F over most of the range of t_R. At low values of t_R maximum yield was attained at correspondingly low values of F, after which yield decreased fairly rapidly. At recruitment ages slightly less than the median value, maximum yield reached a plateau at an F of approximately 0.6 in both species and, at higher recruitment ages maximum yield was not attained irrespective of the level of F.

Plots of expected biomass per recruit against age for fished and unfished populations as well as yield per recruit against F at observed t_R and half t_R are shown in Figures 61-65. These plots summarise observed responses for both species in Tsitsikamma and the Port Elizabeth and Noordhoek areas. Parameters used to construct these curves as well as values of F_{MSY} and $F_{0.1}$ values are summarised in Table 45.

TABLE 45. Summary of the parameters used to construct Y/R models for Chrysoblephus laticeps and C. cristiceps.

SPECIES	AREA	M	Bmax @ AGE	F	t_R	$F_{0.1}$	F_{MSY}	FIG.
C. laticeps	Tsi	0.206	0.164@ 7.27	0.067	6.5	0.256	2.426	61
C. laticeps	Noord	0.206	0.164@ 7.27	0.026	5.5	0.226	0.965	62
C. cristiceps	Tsi	0.153	0.488@ 9.76	0.113	5.0	0.132	0.300	63
C. cristiceps	Noord	0.153	0.488@ 9.76	0.677	4.5	0.124	0.260	64
C. cristiceps	Noord	0.105	0.694@14.78	0.677	4.5	0.069	0.173	65
C. laticeps	Tsi	0.1	0.164@ 7.27	0.067	6.5	0.569	10.000	66a
C. laticeps	Tsi	0.4	0.164@ 7.27	0.067	6.5	0.119	0.173	66b

Tsi = Tsitsikamma, Noord = Noordhoek, Bmax = maximum biomass-at-age per recruit and the age at which this is attained.

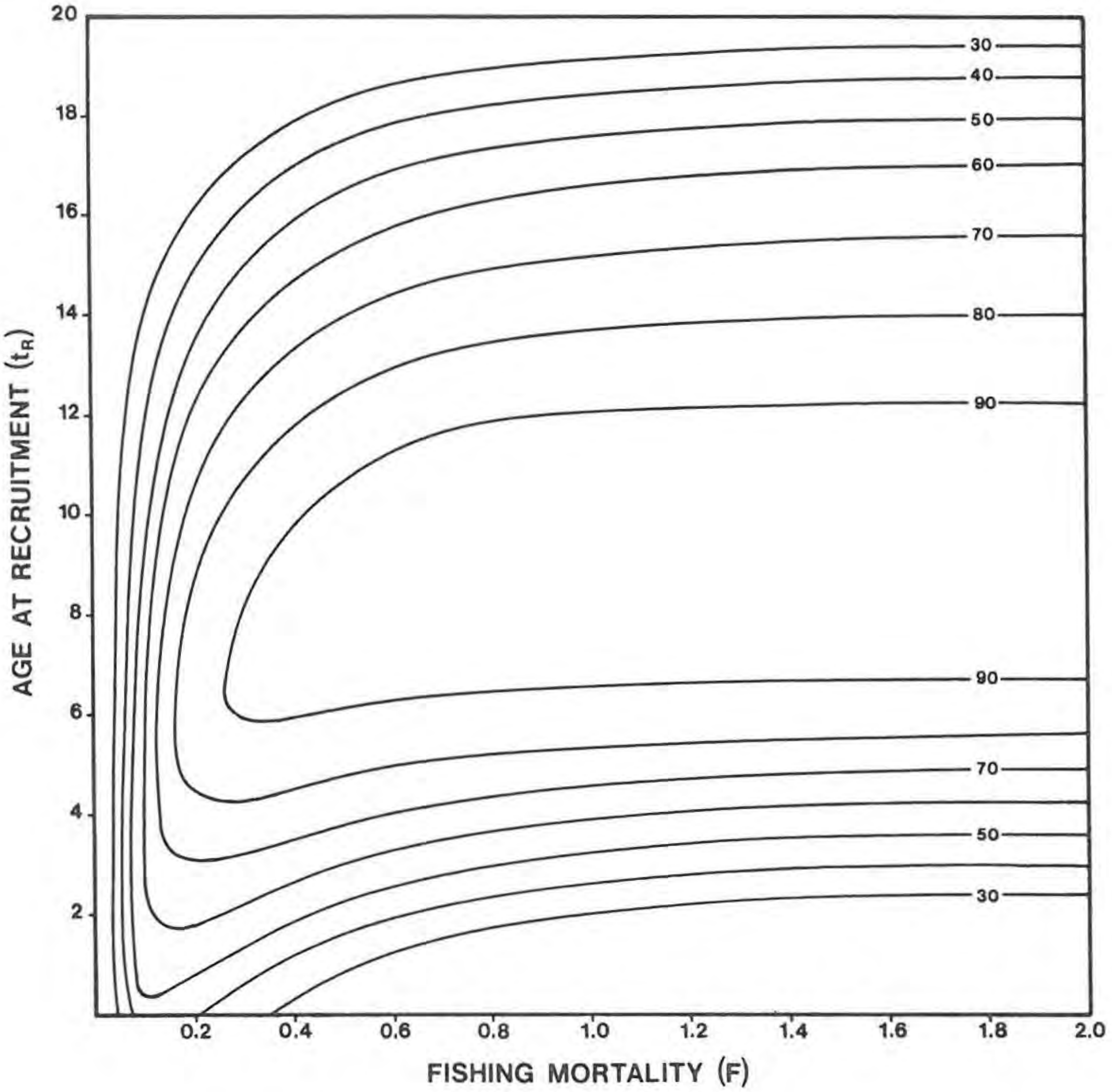


Figure 59. Yield per recruit isopleths expressed as a percentage of Bmax for Chrysoblephus laticeps. This analysis was based on growth parameters determined for the Tsitsikamma population.

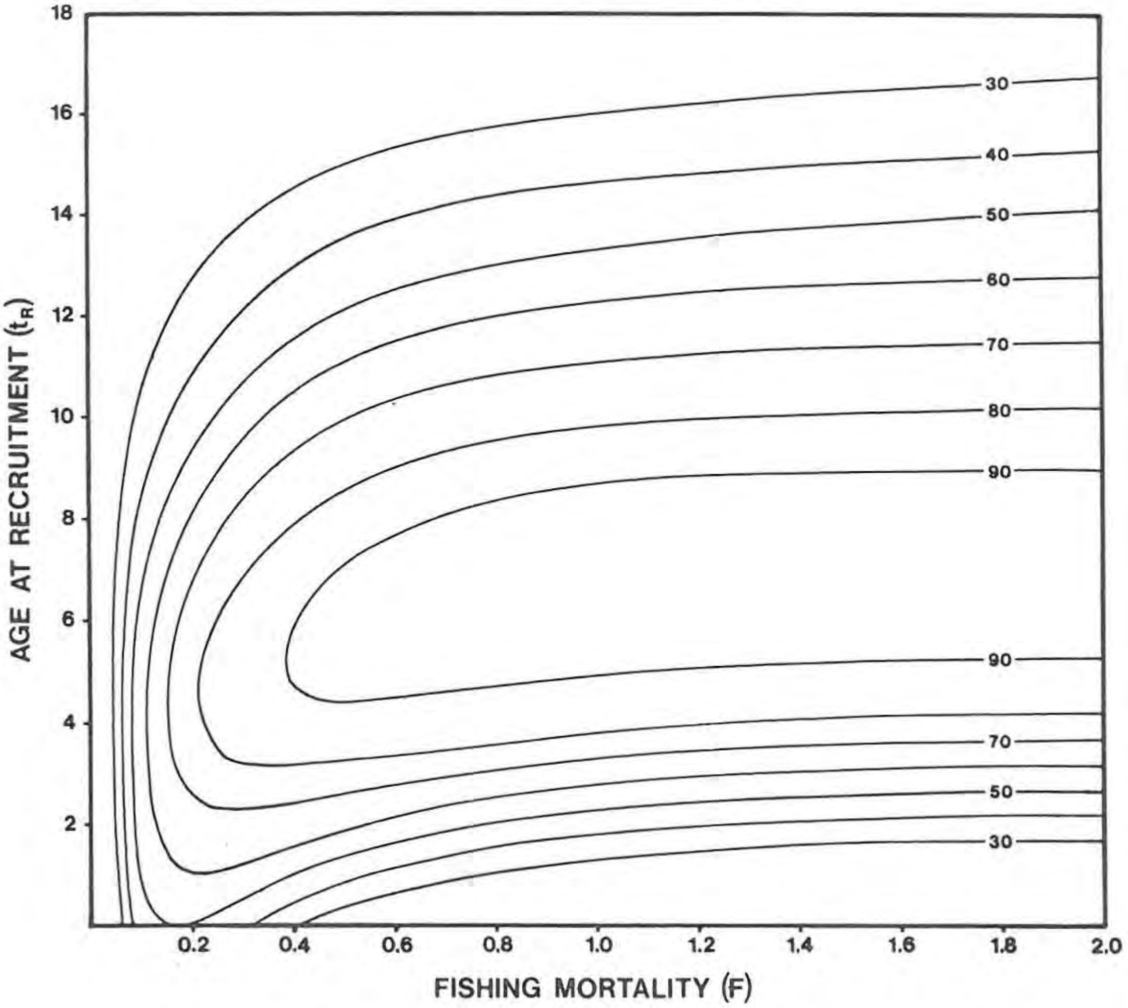


Figure 60. Yield per recruit isopleths expressed as a percentage of Bmax for Chrysoblephus cristiceps. This analysis was based on growth parameters determined for the Tsitsikamma population.

For C. laticeps in both Tsitsikamma (Fig. 61) and Noordhoek (Fig. 62), the effect of fishing on the expected biomass at age was only slight because F was low in both areas. The yield per recruit curve in both areas was almost asymptotic and F_{MSY} was relatively high. $F_{0.1}$ was considerably lower than F_{MSY} but in both areas was higher than the current levels of F in the fishery. On the Cape south coast fishing mortality varied from a high of 0.06 in Jeffreys Bay to a low of 0.01 at Woody Cape (see Table 23). In both areas decreasing t_R resulted in a lower F_{MSY} but, more importantly, showed that beyond a certain level of F yield would decline.

Similar plots for C. cristiceps are shown in Figure 63 for Tsitsikamma and Figures 64 and 65 for Port Elizabeth. The expected biomass curve for the Tsitsikamma showed a substantial decline as a result of fishing, the effect probably being more due to a relatively low t_R rather than F which was only moderate. The yield per recruit curve reached its maximum at a relatively low F value, decreasing gradually at higher levels. $F_{MSY}>F_{0.1}>$observed F of 0.11 and the response to decreasing t_R was the same as for C. laticeps. In the Port Elizabeth area two curves were constructed, one using growth parameters determined for the Tsitsikamma population (Fig. 64) and the other using parameters determined for the Port Elizabeth population (Fig. 65). The results were considerably different. Growth rate determined in the Port Elizabeth population was slower and as a result maximum expected biomass was achieved at a higher age (Fig. 65a). In both cases the effect of fishing was dramatic, radically altering the biomass curve beyond t_R. This effect was a combination of a high level of F (0.67) and a relatively low t_R, The effect being greater when growth was lower because t_R was proportionately lower than the maximum age (Fig. 65a).

In both cases the yield per recruit curves showed that $F>F_{MSY}>F_{0.1}$ suggesting that the population was overfished. The effect was even more acute in the slower growing case (Fig. 65b). Once again a decrease in t_R worsened the situation, lowering the level of F at which F_{MSY} was reached.

The effect of mortality on the yield per recruit prediction was investigated by changing the value of M determined for the C. laticeps population. M was increased to 0.4 in Figure 66a and decreased to 0.1 in Figure 66b. These results can be compared with those summarised in Figure 61. At a lower M the model showed that F_{MSY} would only be reached at an unrealistically high F (10.0), and a current yield at F of 0.07 was well below marginal and sustainable yield. Increasing M resulted in a lowering of both marginal and sustainable yield values but these were still higher than the observed levels of F in the fishery.

The influence of varying F and t_R on the expected biomass at age for C. laticeps is summarised in Figures 67 and 68. In each plot the proportion

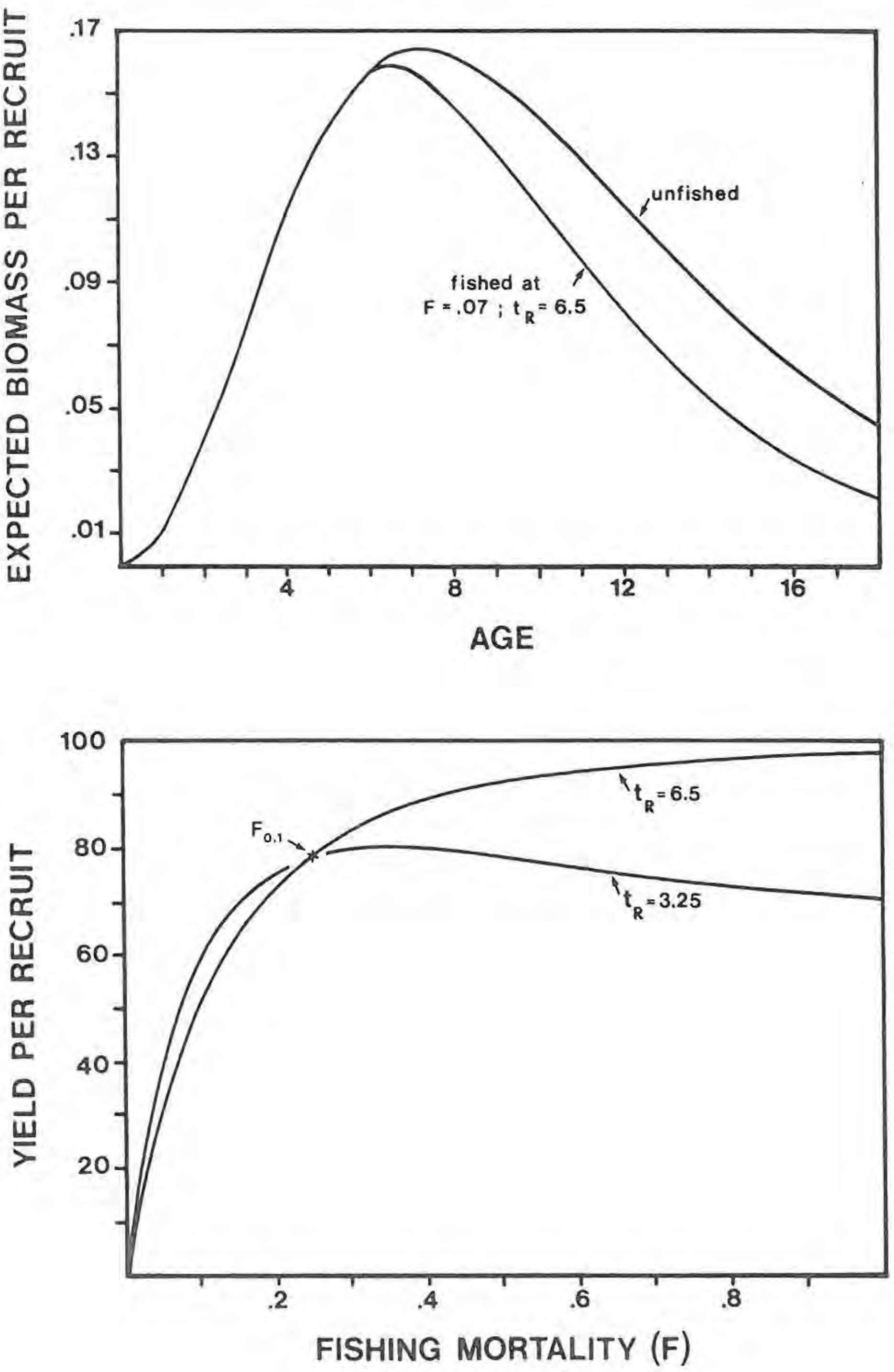


Figure 61. (A) Expected biomass for a fished and unfished population and (B) yield per recruit as a function of increasing fishing pressure for <u>Chrysoblephus laticeps</u> sampled in Tsitsikamma.

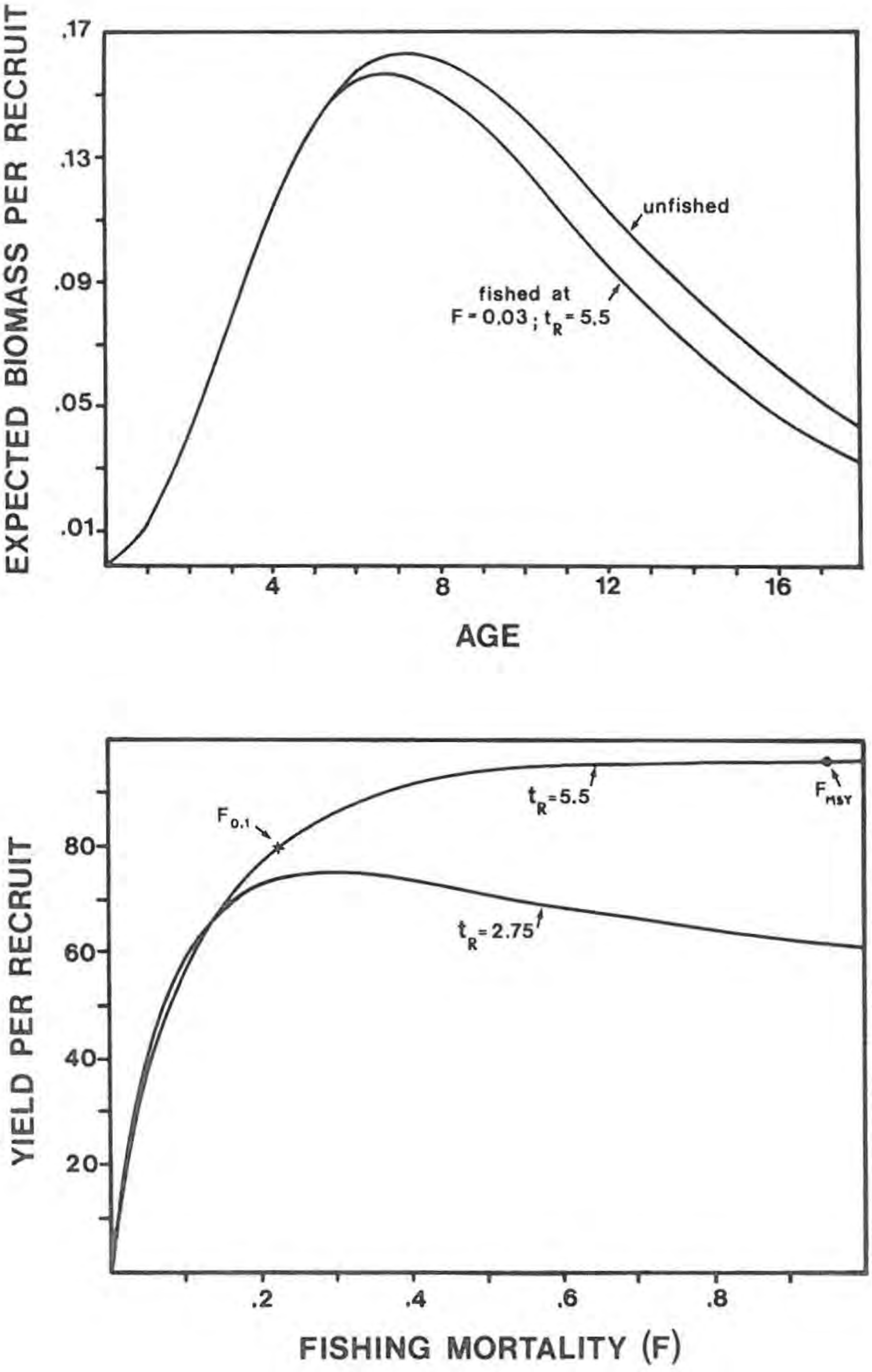


Figure 62. (A) Expected biomass for a fished and unfished population and (B) yield per recruit as a function of increasing fishing pressure for *Chrysoblephus laticeps* sampled at Noordhoek.

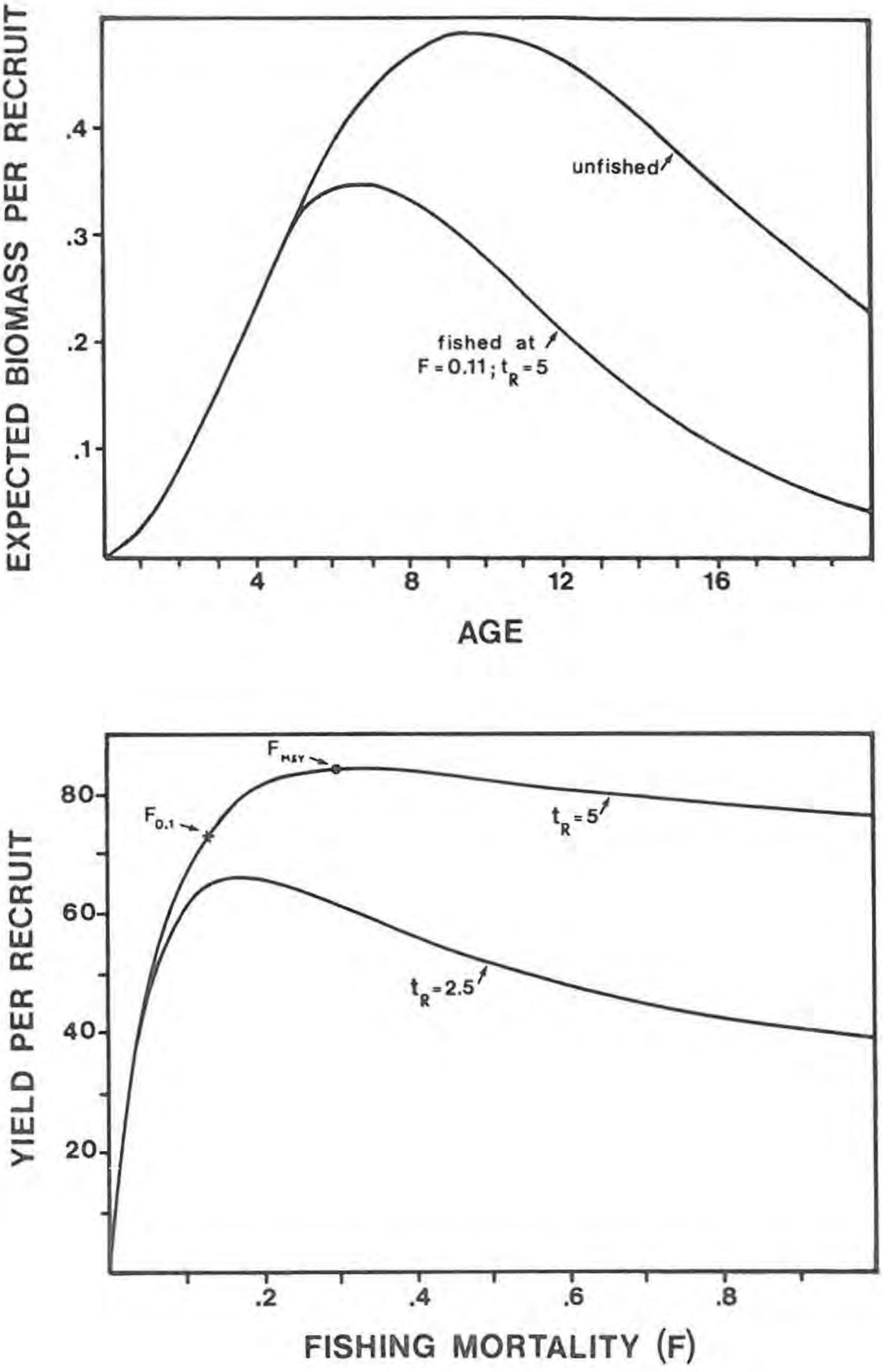


Figure 63. (A) Expected biomass for a fished and unfished population and (B) yield per recruit as a function of increasing fishing pressure for <u>Chrysoblephus cristiceps</u> sampled in Tsitsikamma.

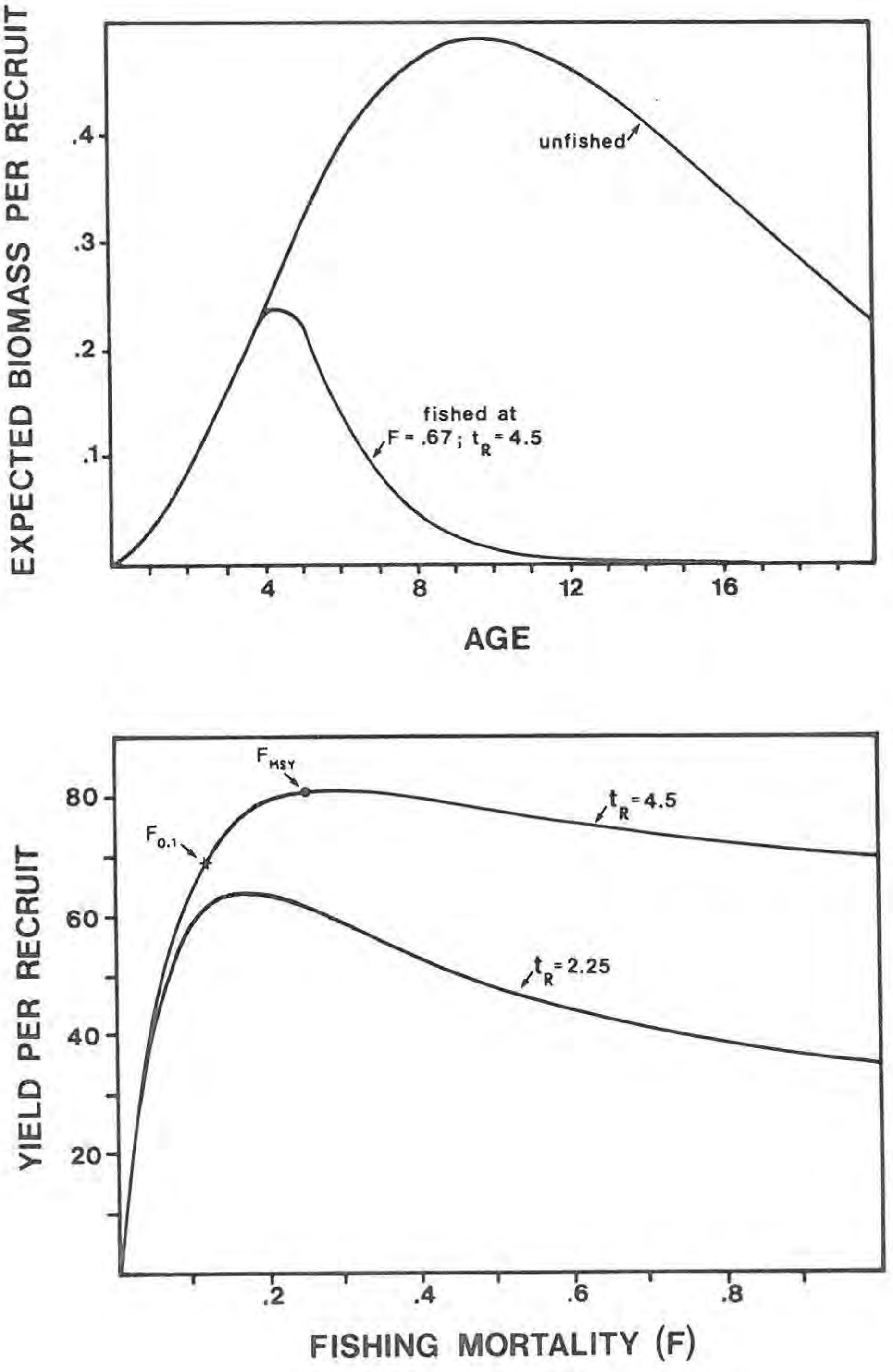


Figure 64. (A) Expected biomass for a fished and unfished population and (B) yield per recruit as a function of increasing fishing pressure for Chrysoblephus cristiceps sampled at Noordhoek but using growth parameters determined for the Tsitsikamma population.

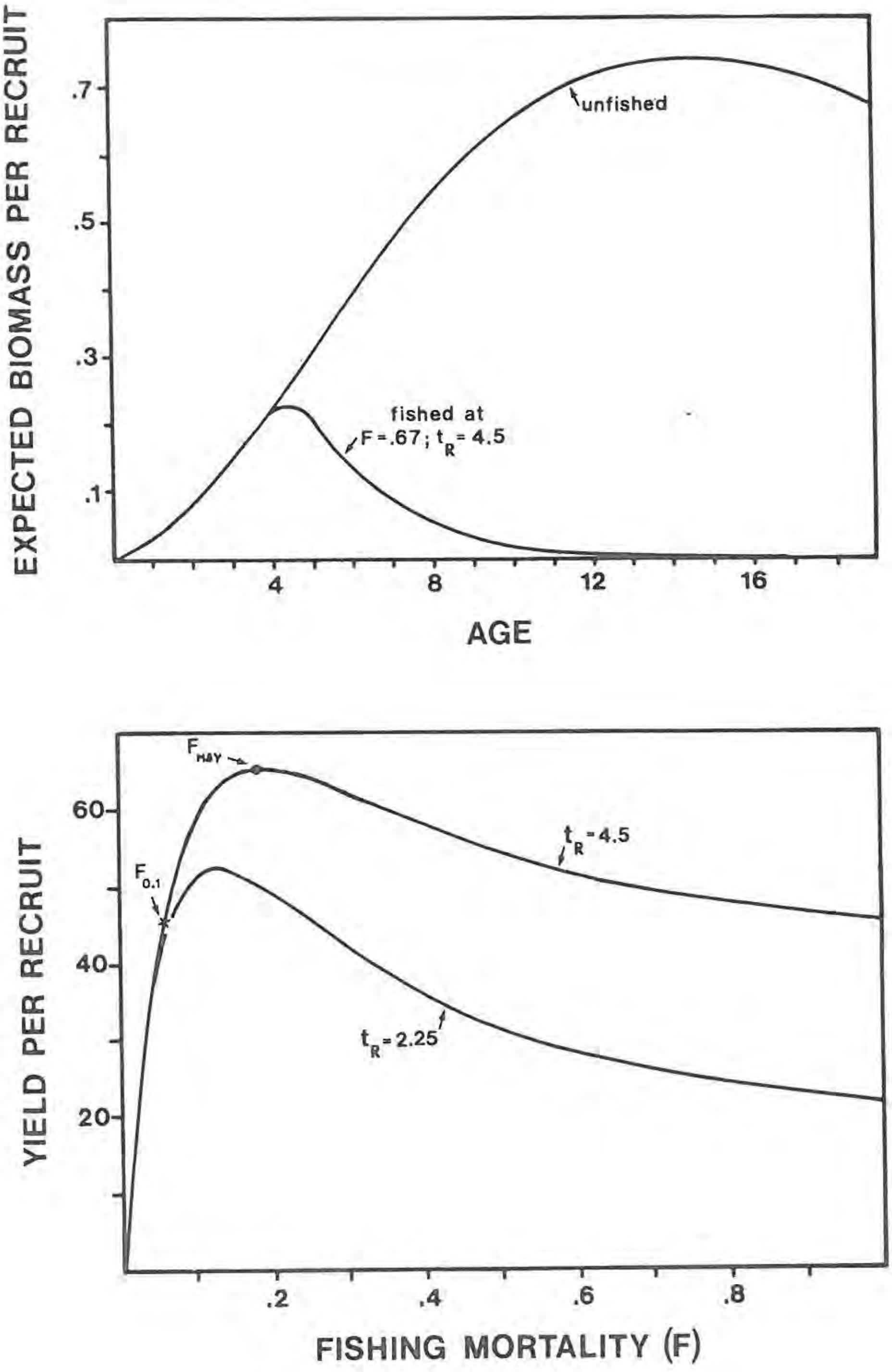


Figure 65. (A) Expected biomass for a fished and unfished population and (B) yield per recruit as a function of increasing fishing pressure for Chrysoblephus cristiceps sampled in the Port Elizabeth area using growth parameters determined for the Port Elizabeth population.

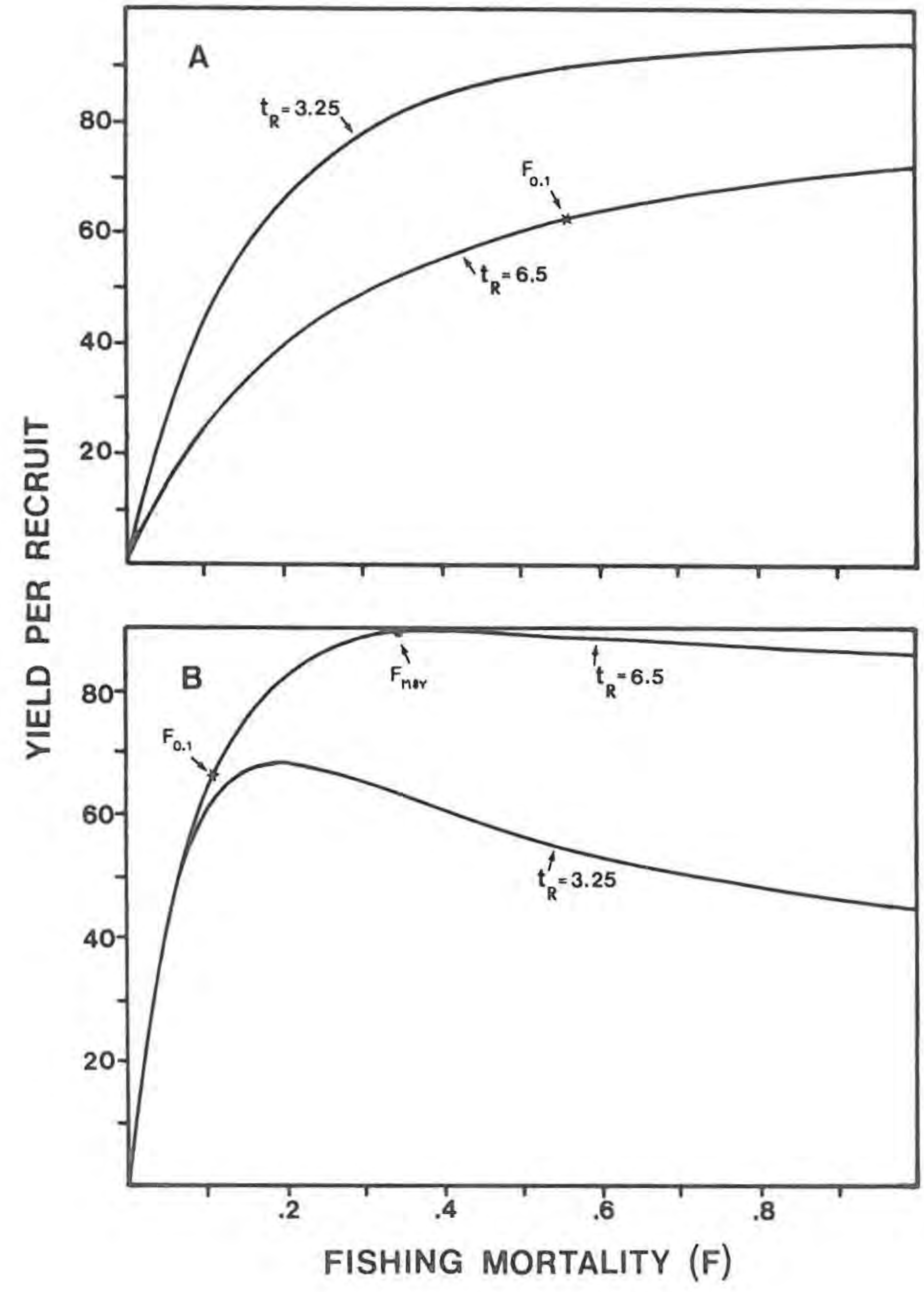


Figure 66. Yield per recruit as a function of increasing fishing pressure for *Chrysoblephus laticeps* sampled in Tsitsikamma. (A) Natural mortality set at 0.1 and (B) natural mortality set at 0.4.

of males present in a fished population has been shaded. Keeping the age at recruitment constant at 3yrs old and increasing F from 0.03 to 0.25, there was a marked decline in biomass of males remaining in the population (Figure 67). At higher levels of F (>0.5) the biomass of fish surviving past t_R drops off sharply (compare Fig. 67c & 68a). Keeping F constant and varying t_R produced a similar result, with a decline in the proportion of males present in the population as t_R is decreased. Conversely, if F is low t_R can be reduced to correspondingly low levels without substantially altering the number of survivors in each age class and hence the sex ratio (compare Fig. 67a & 68c).

DISCUSSION

The responses to differing levels of F and t_R for both species were fairly typical and were similar to the results obtained for a number of reef species studied in the South Atlantic Bight (Huntsman _et al_. 1983). As was the case for these fishes the maximum yield was attained at a very high F relative to the level needed to achieve 80 to 90% of the maximum. At low values of F the models predicted that maximum yield would be sustained over a wide range of recruitment ages. Conversely it appeared that beyond a certain recruitment age (>7 and >9 for _C. laticeps_ and _C. cristiceps_ respectively), maximum yield could not be obtained irrespective of the level of exploitation. Superficially this result suggested that beyond a certain level of t_R the population could never be overfished in the classical sense where the recruitment potential was reduced by overfishing the breeding stock.

However to understand the special case presented by a species that changes sex, effects of varying F and t_R on the number of surviving fish relative to critical ages of maturity and sex reversal were examined. These results showed that except at low levels of F, the number or biomass surviving past t_R declined rapidly, a peculiarity of long lived species (Ricker 1963). Comparing the males and females in an unfished population it was clear that the ratio was skewed towards females and was shown to be dramatically increased even by relatively moderate levels of F.

The model predicts therefore that sex ratio in a sex reversing species may be drastically altered at moderate levels of F, even if t_R is kept high. This has very special implications for the linefishery on the South African coastline and may be illustrated by an example.

A combination of relatively low levels of F and a recruitment age (t_R), well above the age at maturity in females, suggested that the _C. laticeps_ stocks were relatively 'healthy'. They showed no classical indications of overfishing, such as a change in growth rate, a change in the size at which females mature or a change in the size at sex reversal.

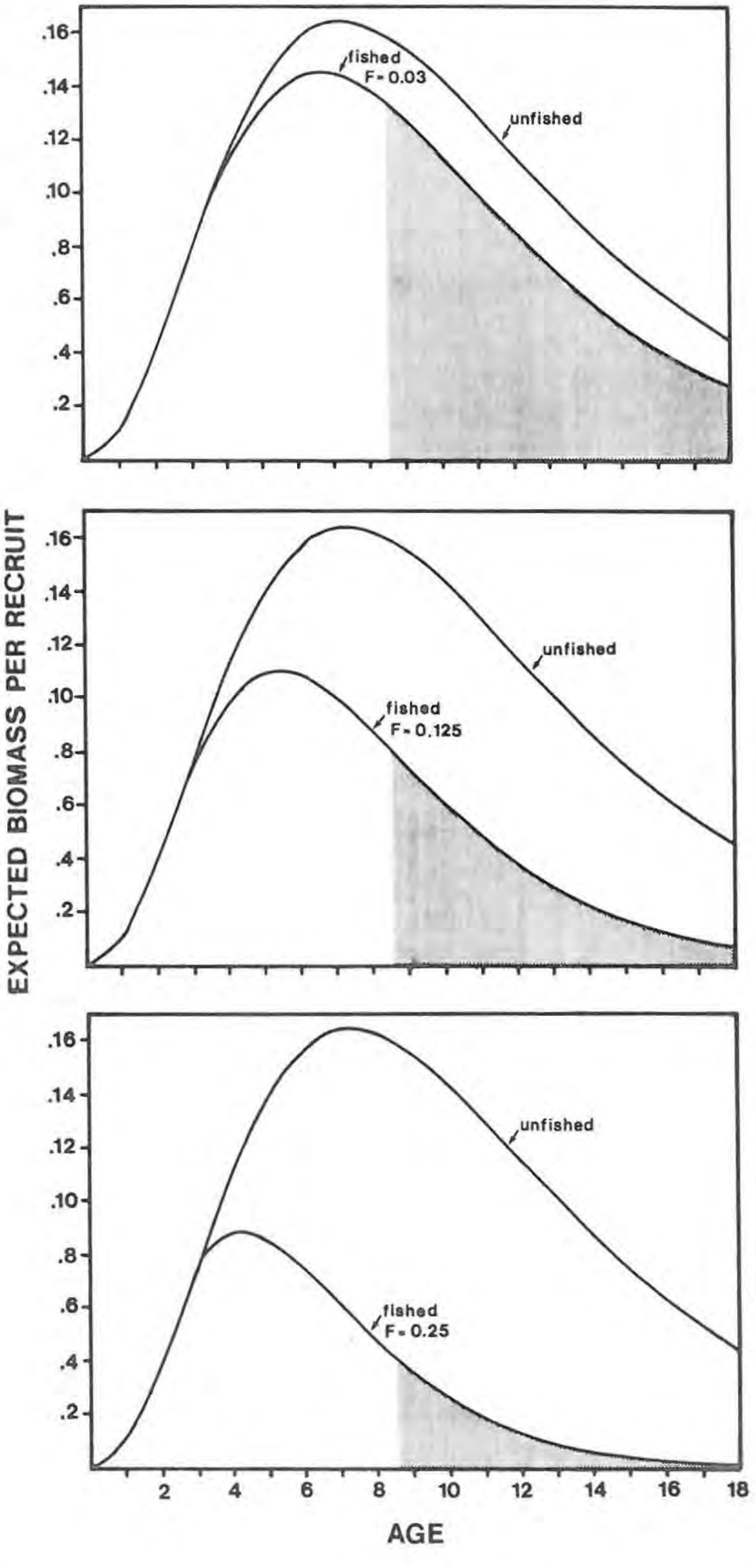


Figure 67. Expected biomass per recruit for Chrysoblephus laticeps under constant t_R (3 years) and variable F. Males are shaded.

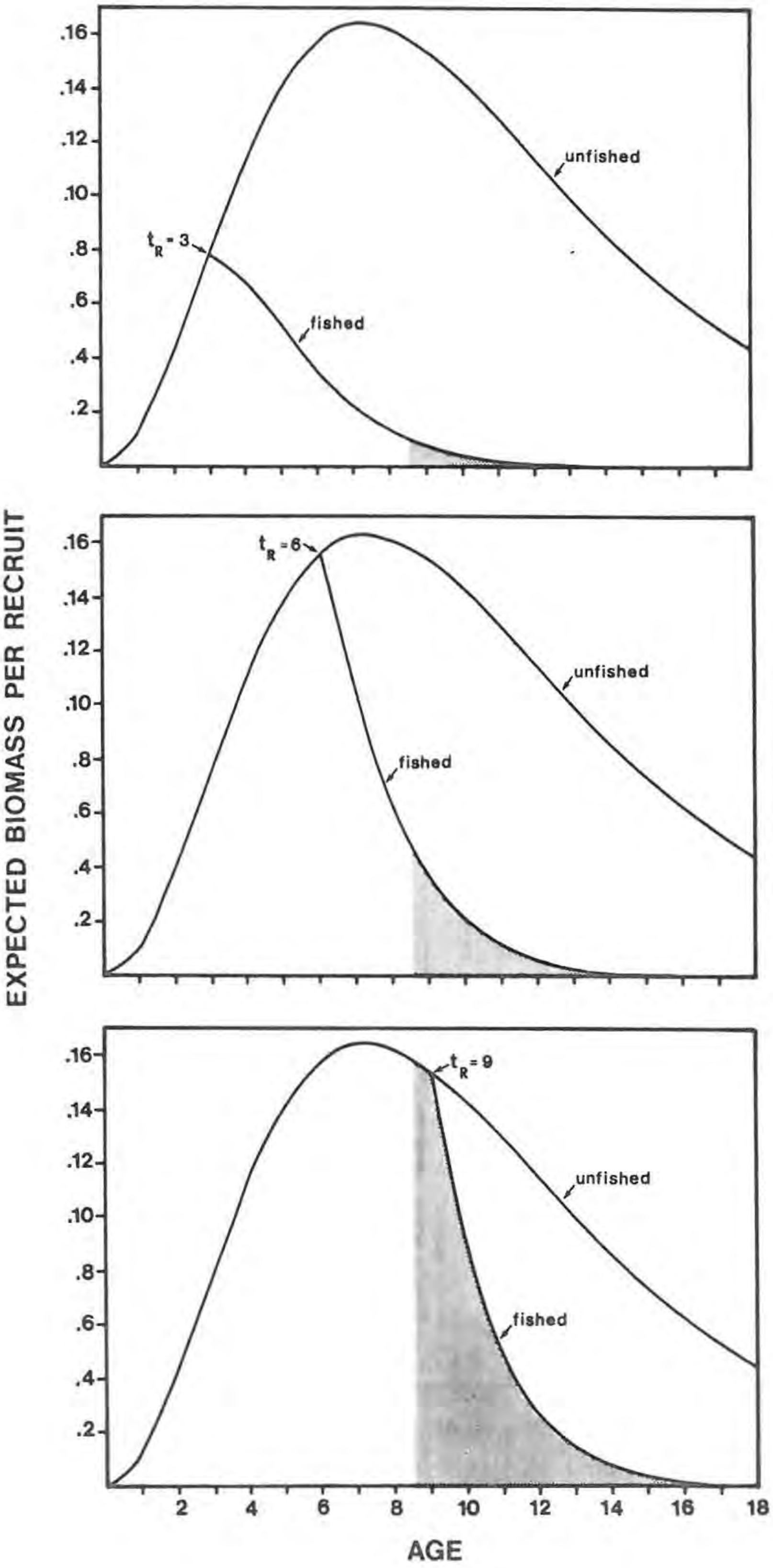


Figure 68. Expected biomass per recruit for Chrysoblephus laticeps under constant F (0.5) and variable t_R. Males are shaded.

In protogynous species the latter effects may be expected as a result of a decrease in male density. C. cristiceps on the other hand was shown to have a lower size at maturity and sex reversal in the exploited areas. This was almost certainly due to the fact that even though F was moderate, t_R was too small and resulted in a critical imbalance in the ratio of males to females. Slower growth in the Noordhoek population appeared to make the model predictions even more acute because both maximum yield per recruit and marginal yield per recruit were decreased. Reservations have however been expressed as to the validity of the difference in growth due to low sample sizes.

Comparing these results with the information presented above on the state of the fishery, there appeared to be an obvious anomaly. The fishery clearly did not show any significant decline in overall catch of redfish species, yet the model predicted that even low levels of F would produce an appreciable change in the population structure and a corresponding decrease in reproductive potential. How then was the fishery being sustained?

Perhaps the most significant implication of this study is that it is conceivable that a high yield could be sustained in certain areas despite high levels of F and a low t_R, provided that recruitment was maintained by seeding from a parent stock elsewhere. Because reef populations are probably limited by carrying capacity and most produce large numbers of offspring which are well dispersed, recruits are probably not limiting. A serious imbalance in the sex ratio as shown in the model would be of little consequence under these conditions. The sustained yield of the C. cristiceps fishery in areas where the proportion of mature fish has been significanty reduced (Fig. 64a) is most likely due to distant recruitment. This could also explain the sustained yield of the slinger C. puniceus in Natal despite obviously high levels of F and low t_R (Garratt 1985b). Garratt argued that the reproductive potential of this species had been lowered due to a significant change in the sex ratio and was puzzled by the lack of 'response' to this imbalance. It is possible that the presence of an apparently unexploited stock further north in northern Natal-Mozambique could be maintaining the southern Natal yield by distant recruitment.

This argument provides support for efforts to protect these breeding populations if the fishery further south is to be maintained and presents a case for the similar protection of entire spawning stocks of other species along the coast. An important condition of the argument is that the spawning stock is fairly resident and, if met, applies equally well to gonochoristic species.

4.3 - CONSERVATION OPTIONS

A number of options are available for the protection of species in a line fishery, the four main ones being size limits, bag limits, closed seasons and closed areas. The management of the South African linefishery is particularly problematical because it is a multi-species fishery and is utilised by both the commercial and recreational sectors. These factors have led to a suite of conservation options including all of the above measures and in the following sections each of these techniques is reviewed.

Size limits

Current legislation in South Africa (Anon 1984b) imposes a minimum size limit on most of the important linefish species, notable exceptions being Pachymetopon aeneum, P. grande and Diplodus cervinus (Appendix 3). The minimum size for C. laticeps and C. cristiceps is 250mm total length.

Minimum sizes have been law in some countries for at least 200 years and there are two main reasons for which they may be imposed (Allen 1954). The first is the maintenance of an adequate breeding stock. Embodied in this is the principle that a fish should be given a chance to spawn at least once before it is caught. Clearly this fails for many species, e.g. semelparous salmon that breed once and then die. In sex reversing species, a maximum size based on this premise would have to be larger than the size at sex reversal to protect both sexes. The second reason is to promote a maximum yield of that kind of catch which is regarded as most desirable. This requirement may differ in the commercial and recreational sectors. In the former it may simply be the greatest quantity of marketable sized fish while in the latter the best catch will vary with the motivations of the angler. Some fishermen will opt for a large bag and others for trophy specimens.

Bag limits

A limit on the number of fish taken by an angler per unit time (usually one day) is also a common method of controlling the exploitation of recreational species. The restriction was introduced into the South African recreational fishery in 1984. Current legislation provides a maximum bag limit of 10 fish/man/day with a further limit of only 5/man/day of the species contained in the protected list. The rationale behind the imposition of these limits was to direct effort away from reef species which were considered more vulnerable to overfishing (J.H. Wallace, Port Elizabeth Museum, pers. comm.).

Bag limits in the form of quotas are the most widely used method of managing commercial fisheries where both catch and effort may be accurately monitored. The desired effect of bag limits is usually to maintain the catch at a level where sustained yield is ensured through the protection of the parent stock. In this way adequate recruitment is maintained. The method requires a detailed knowledge of the relationships between egg production, stock density, growth and mortality. An indirect effect of the method is the equalisation of catches, achieved by reducing the bag taken by the more successful anglers, thereby making more fish available for the less successful anglers. This can also produce an important negative effect. In a stock where abundance fluctuates the stabilising influence may be detrimental under conditions of low density because the same fishing pressure will have a greater impact on the population (Allen 1955). Under such conditions it becomes important to adjust the bag limit with stock density.

The effect produced by a bag limit for a particular species will depend on the relationship between bag sizes before and after legislation. Figure 69 summarises the bag sizes taken by recreational anglers at the Port Elizabeth Deep-sea Angling Club during 1980. Of 116 fishing trips only 9.2 percent of the anglers had more than 5 fish/man/day of the protected species and only 15.4 percent of the trips yielded more than 10 fish/man/day. Furthermore, a considerable number of the fish caught on any outing, particularly when catches were good, were species on the open list. These results suggest that the imposition of bag limits has probably done little to change the fishing habits in this area and is unlikely to improve the state of the reef stocks.

Closed seasons

Closed seasons, during which fishing is prohibited, are usually proclaimed to protect a species over a particularly vulnerable period of the life cycle. This period frequently coincides with spawning, when aggregation and migration of many species leads to the so called 'runs' in the fishery. Catches of many species under these conditions e.g. Polysteganus undulosus, Lithognathus lithognathus and Pomatomus saltatrix are good. It is important to note that the primary effect of this measure for most reef species is to reduce total effort rather than to improve recruitment by protecting breeding fish, although the latter is a logical consequence. The reason for this is that most of the reef species appear to be long-lived. This may be illustrated by a hypothetical example. Consider a species that lives for three years, breeds once and is fished in its third year. Preventing exploitation until after breeding will obviously improve recruitment, and after spawning, this year class may be heavily fished without affecting recruitment. In long lived species spawning occurs in successive

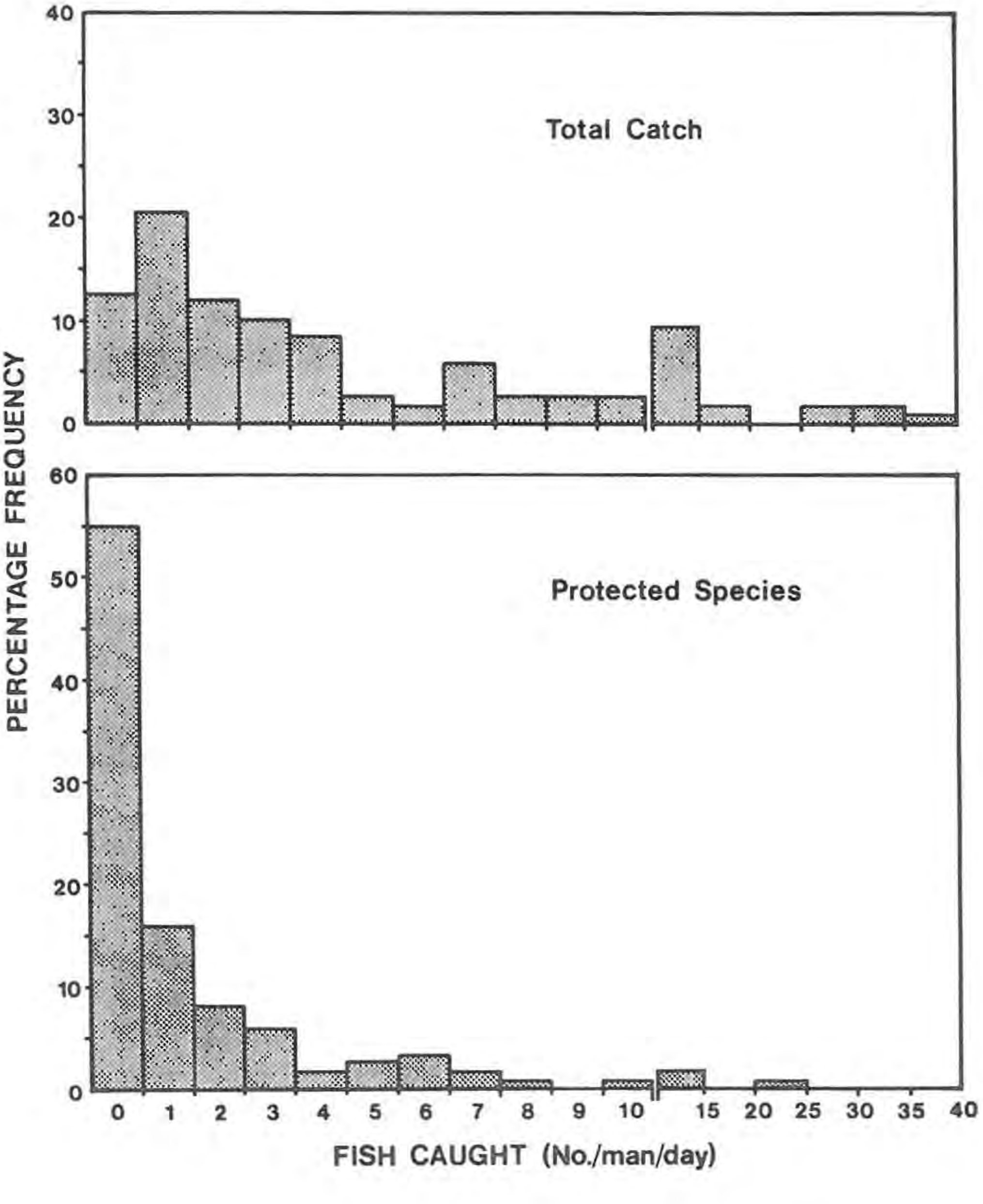


Figure 69. The percentage frequency of individual bag sizes taken from ski-boat fishermen of the Port Elizabeth Deep Sea Angling Club in 1980. The area fished was between Bird Island and Noordhoek.

breeding seasons and the maintenance of a viable spawning stock is independent of the season in which the fish are caught. Clearly the advantage for the long-lived species is a reduction in total catch at a time when the fish are particularly vulnerable.

Only three South African reef species are protected in this way at present, *P. undulosus*, *P. rupestris* and *Coracinus capensis*. *P. undulosus* has been shown to be particularly vulnerable to fishing during the breeding season when it aggregates in large shoals in the Natal region (Ahrens 1964). Fishing pressure on these shoals has almost certainly produced a reduction in the spawning stock of this species and has led to a general decline in catches of the species (Crawford & Crous 1982). On the other hand very little is known about the migratory patterns and spawning behaviour of *P. rupestris* and the usefulness of the closed season for this fish has still to be demonstrated.

Closed areas

The fourth option is to close an area to fishing. Although not implicit this technique will be discussed in the context of marine reserves in the following section.

4.4 - GENERAL DISCUSSION AND MANAGEMENT CONSIDERATIONS

The most important characteristics of the South African linefishery from a management perspective are the high diversity of species taken and its multi-user nature. While all of the species studied so far are relatively long-lived, they differ in that they may be resident or migratory, pelagic or demersal, gonochoristic or sex-reversing and geographically widespread or endemic. Clearly, no single conservation strategy will be sufficient to protect species with such diverse characteristics and the need for a suite of management options has been recognised (Smale & Buxton 1985).

This discussion concentrates on evaluating conservation options applicable to Chrysoblephus laticeps and C. cristiceps and those species that have similar life history characteristics. Life history characteristics that are considered important are longevity, sex reversal, restricted movement and the occupation of a demersal habitat with a relatively shallow depth distribution. Following a discussion of these special considerations, current legislation will be evaluated and possible alternatives examined, including the role of marine reserves as a management option. The applicability of island biogeographic theory to marine reserves is discussed in detail and finally, priorities for future research are proposed.

Life history characteristics of C. laticeps and C. cristiceps

Age determination by otolith analysis showed that C. laticeps and C. cristiceps were long-lived and slow-growing species, capable of achieving ages in excess of 20 years. Comparative studies on other South African reef species (Nepgen 1977; Hecht & Baird 1977; Coetzee & Baird 1981b; Buxton & Clarke 1985) suggest that slow growth and longevity are probably the norm in this group of fish. Slow growth has important consequences for the fishery potential and management of these species, including a lower yield per unit stock (because of a lower production/biomass ratio), an older age at maturity (approximately 4 and 8 years old for C. laticeps and C. cristiceps respectively) and a slower recovery rate after heavy exploitation.

The observed longevity and apparently low incidence of predation on C. laticeps and C. cristiceps indicated that adult survivorship was high. Conversely survival during the early ontogeny was considered to be very low. This was apparent from the low density of juveniles on shallow reefs in spite of an obviously high fecundity (evidenced by many small eggs and multiple spawning). The possibility that juveniles occupied deeper reefs that were not surveyed, although not ruled out, was considered unlikely.

The combination of longevity, late maturation and high adult survivorship is typical of K-selected (MacArthur & Wilson 1967; Pianka 1970, 1972; Gadgil & Solbrig 1972 and others) or precocial (Balon 1979a,b, 1981, 1983; Noakes & Balon 1982) species. These species are characterised by a prolonged growth interval and later maturation, lower fecundity, greater parental investment per young and longevity (see Stearns 1976; Noakes & Balon 1982 for reviews of these characters). On the other hand the apparently high fecundity and low parental investment per young are more consistent with the typically r-selected or altricial species. These in turn are characterised by a life history pattern including a short growth interval and early maturation, high fecundity, low parental investment per individual young and a shorter life span.

Graham (1977) points out that high fecundity does not necessarily imply a high reproductive allocation because, relative to brood care, the cost of producing many small eggs may be low. Gadgil & Solbrig (1972) also stressed the need to view life history characters in a comparative way, "an organism is more or less of an r-strategist only in comparison with another organism" (Gadgil & Solbrig *op. cit.*, p14). If reproductive allocation can be quantified in terms of gonad mass relative to body mass (cf. Stearns 1983), it is clear that both *C. laticeps* and *C. cristiceps* invest less in gamete production than sparids that are rudimentary hermaphrodites e.g. *Chrysoblephus gibbiceps* (own observations), *Sparodon durbanensis*, and *Pachymetopon grande* (J.R. Clarke, Port Elizabeth Museum, pers. comm.).

Little is known about the spawning behaviour of sparid fishes, but in general they appear to be iteroparous, pelagic spawners that exibit no parental care (Thresher 1984). There are, however, exceptions e.g. *Spondyliosoma emarginatum*, a South African nest-building species (van Bruggen 1965). This observation, of little parental investment in individual offspring, appears to contradict the prediction of altricial-precocial life history theory, that precocial species should exibit relatively more parental care per individual offspring. Considering the reproductive patterns of temperate reef fish in general (Thresher 1984), it appears that the predictions of bet-hedging (Shaffer 1974; Murphy 1968 in Stearns 1976) more adequately explain the observations. Bet-hedging theory suggests that in a fluctuating environment that affects juvenile mortality, selection will favour reduced reproductive effort and longevity. Many more studies on southern African temperate marine species are necessary to evaluate the general applicability of these life history models (which were developed to a large extent on northern hemisphere species).

One aspect of altricial-precocial life history theory that deserves mention is the suggestion that the early life history will be of critical importance and be a primary determining influence on the future life history of the organism (Noakes & Balon 1982). Clearly man-induced perturbations that affect the early ontogeny of an animal will be of importance to the later development (Bruton 1986), and may be relevant to the management of the species.

The next important life history characteristic relevant to management is sex reversal. Both C. laticeps and C. cristiceps were shown to be protogynous hermaphrodites, all males being derived from functional females. Based on courtship behaviour, protogyny and the relatively small size of the testes, C. laticeps were also shown to be polygamous, and although mating was not observed in C. cristiceps, it is suggested that a similar pattern occurs in this species.

Advantages and disadvantages of this reproductive strategy have been discussed in detail above (Chapter 3.6). In general these arguments are based on the size advantage model of Ghiselin (1969) and propose that sex reversal may be selected if animals are able to reproduce more successfully as one sex when small and the other when large. The size advantage model has been refined by several others (Smith 1975; Warner 1975; Warner et al. 1975; Jones 1980) but appears to suffer from a major shortcoming. Shapiro (1984) points out that the model generally assumes that individuals are genetically predetermined to change sex at a particular size or age. This has not, however, been demonstrated for any species, rather, sex change has been found to occur at almost any mature size provided the appropriate stimulus is present (Shapiro 1984). Observations during this study support Shapiro's objections. Sex reversal in C. laticeps and C. cristiceps appeared to be correlated to sex ratio, individuals in exploited areas changing sex at a smaller size probably in response to behavioural cues which are influenced by sex ratio. Aldenhoven (1984) also provided evidence that is inconsistent with the size advantage model, that sex change is related to social interactions within a harem. The implications of this reproductive strategy for management are discussed below.

Clearly the underlying processes of sex reversal are far from resolved and much exciting work on sex reversal lies ahead. Further studies on exploited South African sparids will contribute to this field, particularly with respect to the inter-relationship between sex ratio and sex reversal.

Three other life history characteristics require further comment particularly with respect to their implications for management. These relate to the distribution of the species and include demersal habitat, restricted movement and endemism. Both C. laticeps and C. cristiceps were shown to be demersal predators, and diving observations showed that they remained close to the substratum at all times. This is also apparent from the way in which they are caught in the local linefishery, referred to as 'bottom fishing'. Evidence was also presented that showed a separation in the depth distribution of adults and juveniles, the latter preferring shallow subtidal areas while adults were most abundant on reefs deeper than 10m. The lower distributional depth was not determined but they are both caught from at least 50m. The management problem associated with this depth distribution is referred to as barotrauma, resulting from the expansion of the swim-bladder when the fish are brought to the surface. Effects vary, but in severe cases the stomach may be everted and forced out of the mouth and/or the intestine forced out of the anus. Rapid deflation of the swim-bladder with a hypodermic needle relieved the symptoms in many cases (see Chapter 3.2) but this is not considered a practical procedure in the fishery and many of the fish returned to the sea would probably not survive. Eye embolisms, which occurred less frequently, could not be relieved.

Mark and recapture studies provided strong evidence that C. laticeps is a sedentary species, all recaptures being made within 2km of the area of tagging. Further evidence was obtained from the mating behaviour of these fish. These observations suggested that males are polygamous and are able to mate with a number of females by either monopolising preferred spawning areas or taking advantage of female gregariousness. Either event implies a site affinity at least during the breeding season. Once again the same observations were not made for C. cristiceps but were implied from similar reproductive characteristics such as testis size and protogyny. Fewer C. cristiceps were marked but the single recapture was taken from the same site at which the animal was tagged.

The results on the movement patterns of these species are far from complete. If these fish are shown to be sedentary then they will be particularly vulnerable to local extinctions due to over-fishing. On a broader scale the problem is equally serious because there is a high degree of endemism in South African reef species (Smith & Heemstra 1986). Smale & Buxton (1985) point out that South African reef fish species need careful management because in many cases their distributional range is very limited and recruitment from distant areas is not possible.

Conservation

The preceding discussion has examined important life history characteristics that are relevant to the conservation of these and other reef fish species. What follows is an examination of current management practices and problems as well as possible alternatives. A review of the available literature showed that both C. laticeps and C. cristiceps were of localised importance to the linefishery, but that in both the recreational and commercial sectors they were relatively minor components of the total catch. Of the reef species they were among the most important caught in the area between Cape Point and East London. The number of species involved in the linefishery and to a lesser extent problems in their identification have led to the practice of lumping the catches. This has resulted in a serious shortcoming in the information available on the quantity of each species removed from its population. This problem is particularly evident in the commercial sector where fish are grouped according to how they are marketed. In the recreational sector the same problem has arisen out of a general apathy on the part of the participants to provide reliable catch information on a voluntary basis (R.P. van der Elst, Oceanographic Research Institute, Durban pers. comm.).

At present these and other reef sparids are subject to a minimum size restriction of 250mm TL and a bag limit restricting the daily catch of recreational fishermen to a maximum individual catch of 5 fish from the protected list per day (Appendix 3). Two separate motivations are proposed for these measures. Minimum sizes were set at a level aimed at protecting the reproductive potential of the stock. Bag limits on the other hand, were introduced to limit effort and particularly for the 'barotrauma species' to direct effort away from species that were considered vulnerable (van der Elst 1985). In this light we may ask, how effective are the measures?

A major shortcoming in the provisions of the minimim size regulation is adequate protection of males in sex reversing species. For both C. laticeps and C. cristiceps (and others e.g. C. puniceus) the minimum size is set well below the observed mean size at sex reversal. Equally serious is the observation that for C. cristiceps the minimum size regulation is below the level of 50% maturity, therefore casting doubt on whether there is adequate protection even for females. Certainly this limit is totally inadequate for large species such as Petrus rupestris, and Cymatoceps nasutus. Criticism may also be levelled at the bag limit. Evidence presented from this study area clearly showed that bag limits will have had little effect on the fishing habits or catches taken by recreational fishermen. A study of this relationship in other areas will provide useful insights into the overall effectiveness of bag limits as a protective measure.

Yield per recruit analysis showed that at present levels of recruitment to the fishery (t_R), moderate levels of exploitation would be sufficient to significantly reduce the number of individuals surviving past t_R. In a protogynous species this has the effect of skewing the sex ratio towards females, and the effect is inversely proportional to t_R. Length frequency distributions of both species in exploited areas confirmed this, the ratio of males to females being significantly less than that found in unexploited areas. Both the results of this study and those of Garratt (1985a), who worked on C. puniceus in Natal, suggested that the sex ratio of the unexploited fish should have reached a stage where reproductive potential would be impaired.

The examination of catch statistics, although based on lumped catches, did not provide support for this argument. Contrary to the predictions of the yield per recruit model and the intuitive expectations of the effects of exploitation on recruitment, catches in some areas were shown to increase. An important observation related to the Natal catch is that quality has decreased (measured by the mean size of the fish caught), but quantity has not declined substantially (P.A. Garratt, Oceanographic Research Institute, Durban, pers. comm.). Since serious shortcomings are evident in the current protective measures we must ask, how is the fishery being sustained at its present level?

Examining the South African coastline and the distribution of relatively unexploited areas it becomes immediately apparent that present fisheries could be sustained by distant recruitment. This is illustrated in Figure 70. Examples of relatively unexploited areas include the St Lucia/Mozambique area for C. puniceus, Transkei for P. rupestris and the Woody Cape and Tsitsikamma areas for C. laticeps and C. cristiceps. An important feature of this distribution is the relationship between the position of the unexploited areas, the fisheries they support and the direction of the major current movements.

Marine reserves

Since one of the primary objectives of the study was to evaluate the effectiveness of marine reserves as a conservation option, it is relevant to briefly review the concepts embodied in the formation of nature reserves.

Modern wildlife management addresses the problem of preserving biological interaction instead of individual species because without these interactions a species cannot exist (Siegfried & Davies 1982). The need to save as much biological diversity as possible has resulted in considerable effort to identify representative areas and to implement their preservation (see Grindley, Cooper & Hall 1976 and Robinson, Siegfried & Visser 1985 for South African examples). In South Africa the National Parks Board have adopted the International Union for the Conservation of Nature and Natural Resources (IUCN) definition of the term conservation as "...the management of human use of the biosphere so that it may yield greatest sustained benefit to present generations while maintaining its potential to meet the needs and aspirations of future generations." (Anon 1987). The three primary objectives of this process as defined by the IUCN (1980) are:

1. Maintenance of essential ecological processes and life-support systems.

2. Maintenance of biotic diversity.
3. Sustainable utilisation of valuable species and ecosystems.

The third of the above objectives is of particular relevance to the use of marine reserves as an option for the maintenance of yield in a fishery. In this context the role of the reserve is to maintain a breeding stock sufficient to seed adjacent areas that have become incapable of doing so themselves as a result of the exploitation of adult fishes. Simultaneously, preservation of the entire community results in the maintenance of the interactive environment necessary for the preservation of the species. Fundamental to the understanding of such processes is a thorough knowledge of the early ontogeny of the species concerned, particularly with respect to its dispersive ability and its life history in response to environmental change e.g. the age and size at first maturity.

The preservation of marine areas of beauty or of special significance has been slow to develop, reasons for which are twofold (Randall 1982). Only recently has man entered the sea with diving gear to appreciate its beauty and there has long been the belief that its resources were inexhaustible, making conservation unnecessary. This thought process has led to uncontrolled pollution of the sea and a rapid depletion of many important fish stocks.

Ray (1984) points out that because the large expanses of the seas are so ecologically interdependent it is difficult to identify critical habitats. These he defines as identifiable areas vital to the survival of a species at some point in its life cycle because of the processes that occur within it. Because critical habitats may be very large and manageable sanctuaries small, other devices may be more useful in marine conservation e.g. control of human interference through pollution and fisheries.

A significant difference between marine and terrestrial reserves is the ability of the terrestrial manager to provide an environment relatively free of human perturbations. An obvious exception is the direct ability to control acid rain. In the same way that acid rain can be carried into terrestrial reserves by winds, so too can various pollutants be carried into most marine reserves by currents, the marine 'winds' (Salm & Clarke 1984). This property, while providing a major management difficulty, also provides the reason why marine reserves may be a successful management option and will be discussed more fully below.

The classic theory of island biogeography developed by MacArthur & Wilson (1967), explained the number of species on oceanic islands in terms of an equilibrium between the immigration rate of colonists and the extinction rate of inhabitants. The model has been extended to explain species diversity in a number of other situations e.g. birds in patches of isolated vegetation (Vuilleumier 1970), small mammals on mountain peaks that are isolated by desert (Brown 1971), cave faunas (Vuilleumier 1973), fish species in lakes (Barbour & Brown 1974), freshwater mussels in rivers (Sepkoski & Rex 1974) and weeds in vacant city plots (Crowe 1979). Immigration rate was found to vary inversely with distance from the source and extinction rate varied inversely with the size of the island.

Many of the problems peculiar to islands were also thought to be relevant to the management of reserves because these are natural habitats isolated in a sea of man-modified ecosystems (Diamond 1975; Diamond & May 1976; Wilson & Willis 1975; Goeden 1979). It is therefore necessary to examine the model and to ask the questions: do marine reserves behave like islands? and what aspects of island biogeographical theory will be relevant to marine reserves?

A marine reserve will only behave like an island when, in terms of the movement of species between areas, it is isolated from similar habitats elsewhere. In this respect the dynamics of island biogeography have been shown to differ between groups, based on their relative dispersive ability e.g. birds and mammals (Diamond & May 1976).

It is thus difficult to visualise a marine reserve functioning as an island because of the dispersive ability of fish, both as adults and larvae. Goeden (1979) points out however, that many adult fish (on coral reefs) lead sessile lives, limited in terms of dispersal by territories or home ranges. In addition, reef species may be reluctant to traverse large expanses of sand, a behavioural barrier to dispersion (Diamond 1982).

An important aspect of island biogeography that is relevant to conservation practice is the relationship between area and species diversity. Many studies have shown that as a rough general rule a 10-fold increase in area produces a 2-fold increase in species diversity (Diamond 1973; Wilson & Willis 1975). For this reason it was advocated that reserves be as large as possible (Diamond 1975; Wilson & Willis 1975), although for a contrary view see Simberloff & Abele (1976). It follows from the species-area relationship that excessive ecosystem fragmentation will result in fewer species. Wilson & Willis (1975) also emphasise ecological truncation as a consequence of habitat reduction. This is the early loss of specialist and large species due mainly to the fact that they occur at low densities or require large areas for sustenance, or both. The loss of species in this way may lead to a wave of decline or extinctions in associated species, known as trophic cascades (Diamond 1982). Alternatively there may be a 'density compensation', an increase in numbers of generalised of 'weedy species' which in turn could seriously affect the composition of the community. Thresher, Sainsbury, Gunn & Whitelaw (1986) showed a steady increase in the number of larvae in demersal trawl catches off the northwest shelf of Australia which they attributed to a decline in natural predators through overfishing. They suggest that the explosion of lizard fishes, themselves larval predators, could seriously affect the recruitment of more desirable food fishes.

The relationship between species diversity on islands and distance from the source habitat is also relevant to the reserve situation. Studies have shown (e.g. Diamond 1973), that diversity is inversely related to distance from the source, once again being dependent on dispersive ability. For some groups this relationship is effectively non-existent e.g. pteridophytes, which are very good dispersers (Williamson 1981). Clearly a marine reserve will only succeed from a fishery perspective if it is able to seed adjacent areas by juvenile and/or adult migration, egg and larval dispersion, or both. To fully understand this relationship, a study of these movements is essential.

The implications of island biogeographic theory have also been used to suggest the best design principles for reserves (Wilson & Willis 1975; Diamond 1975). The best reserves are considered to be large, circular and as little fragmented as possible. Although objections to these design criteria have been put forward (size by Abele & Connor 1979, shape by Game 1980 and configuration by Simberloff & Abele 1976; Higgs & Usher 1980), these only apply to special circumstances and the overall principles still apply (Diamond 1976; Terborgh 1976; Whitcomb, Lynch, Opler & Robbins 1976; Gilpin & Diamond 1980). Problems associated with dispersion in the reserve (Diamond 1975) and peninsular effects (MacArthur & Wilson 1967) are probably less important in the marine context because of the dispersive ability of eggs and larvae.

As already mentioned above, modern wildlife management addresses the problem of preserving biological interaction instead of individual species. To protect desired species such as those important to the linefishery it becomes necessary to protect the entire reef community associated with the fish. Logically a thorough knowledge of the entire ecosystem including predator-prey, competitive and mutualistic interactions, nutrient cycling and energy flow will be necessary to determine the minimum size requirement of the reserve.

The observation that the existing level of exploitation in the South African reef fishery could possibly be explained by distant recruitment, the predictions of the yield per recruit model, sex reversal, longevity and limited distribution all provide strong support for the use of marine reserves in the management of these species. In particular, the predictions of the yield per recruit model suggest that it is essential to protect the breeding populations, a requirement that current legislation is unable to do.

Two alternatives are possible:

1. to increase the minimum size (t_R) to a level above the size at sex reversal in sex reversing species and above the size at maturity in gonochoristic species.

2. to identify and proclaim as reserves areas large enough to protect the breeding populations of resident species. Minimum size levels can then be set suitable to particular needs e.g. trophy size for anglers and marketable size for commercial species. It is important to note that once recruitment is assured through the protection of a parent stock, minimum sizes are only necessary to achieve a sustained yield of the desired size. Under these conditions bag limits will only act as a quota system, spreading the catch more equitably between the participants. Bag limits will not effect further conservation of the resource per se.

Both of the above methods are based on ensuring adequate recruitment through protection of the breeding population. The marine reserve option has the added attraction that it embodies the concepts of IUCN, to preserve entire communities rather than individual species.

This study would not be complete without some mention of important future research requirements. Perhaps the two most obvious gaps in our knowledge are in the understanding of the early ontogeny of most of the important linefish species and the movements of adults as well as the egg and larval stages. Both of these aspects are crucial to our understanding of the life-histories of the fish and the effectiveness of marine reserves as a management technique. Studies of the early ontogeny are necessary to test current thought on the relevance of early life history in the later development of the organism and to evaluate the influence of man-induced changes on this development. Knowledge of egg and larval distribution will determine how effective the reserve is in seeding adjacent areas, while a better understanding of adult movement will establish whether the reserve is protecting the spawner stock. A considerable amount of work needs to be done on the composition of sub-tidal benthic community of the South African coast, not only in marine reserves. This area of research (including taxonomy and species biology) is an important gap in our understanding of community processes, which are particularly important in the consideration of suitable areas for marine reserves.

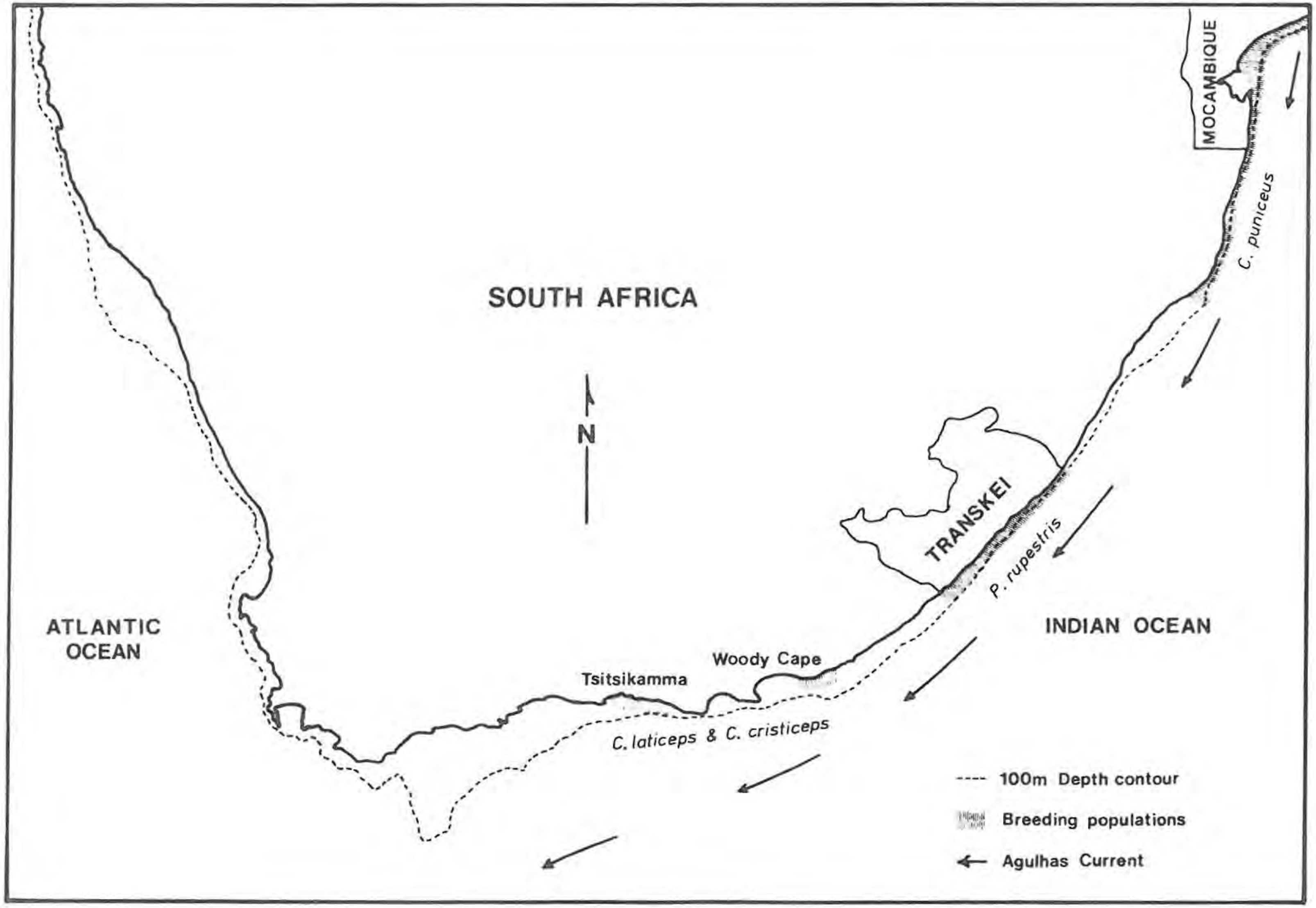


Figure 70. Approximate localities of relatively unexploited populations of important linefish species capable of seeding adjacent areas, particularly those downstream of the Agulhas current.

REFERENCES

ABELE, L.G. & CONNOR, E.F. 1979. Application of island biogeography theory to refuge design: making the right decision for the wrong reason. Proc. 1st Conf. on Sci. Res. in the Nat. Parks 1: 89-94.

AHRENS, R.L. 1964. A preliminary report on the biology of the seventy four Polysteganus undulosus (Regan) in Natal waters. MSc thesis, University of Natal, South Africa: 77pp.

ALBRECHTSEN, K. 1968. A dyeing technique for otolith age reading. J. Cons. perm. int. Explor. Mer 32: 278-280.

ALDENHOVEN, J.M. 1986. Different reproductive strategies in a sex changing coral reef fish Centropyge bicolor (Pomacanthidae). Aust. J. Mar. Freshw. Res. 37: 353-360.

ALEKSEEV, F.E. 1982. Hermaphroditism in sparid fishes (Perciformes, Sparidae). 1. Protogyny in porgies, Pagrus pagrus, P. orphus, P. ehrenbergi and P. auriga, from West Africa. J. Ichthyol. 22: 85-94.

ALEVIZON, W.S. & BROOKS, M.G. 1975. The comparative structure of two western Atlantic reef-fish assemblages. Bull. Mar. Sci. 25: 482-490.

ALEVIZON, W.S., RICHARDSON, R., PITTS, P. & SERVISS, G. 1985. Coral zonation and patterns of community structure in Bahamian reef fishes. Bull. Mar. Sci. 36: 304-316.

ALLEN, K.R. 1954. Factors affecting the efficiency of restrictive regulations in fisheries management. 1. Size limits. N.Z. J. Sci. Technol. Sec. B 35: 498-529.

ALLEN, K.R. 1955. Factors affecting the efficiency of restrictive regulations in fisheries management. 2. Bag limits. N.Z. J. Sci. Technol. Sec. B 36: 305-334.

ANDERSON, G.R.V., EHRICH, A.H., ROUGHGARDEN, J.D., RUSSELL, B.C. & TALBOT, F.H. 1982. The community structure of coral reef fishes. Am. Nat. 117: 476-495.

ANON 1979. Marine line fish research programme. S.A. Nat. Sci. Prog. Rep. 37: 1-17.

ANON 1983. Report. Rep. mar. Dev. Brch S. Afr. 51: 13-16.

ANON 1984. Report. Rep. mar. Dev. Brch S. Afr. 52: 13-17.

ANON 1984b. Government Notice. S.Afr. Government Gazette 234: 6pp.

ANON 1985a. Report. Rep. mar. Dev. Brch S. Afr. 53: 17-20.

ANON 1985b. South African fishing industry handbook and buyers guide 1987. 18th Edition. Ed. H. Engelhart. Bowford Publ. Cape Town. 226pp.

ANON 1987. National Parks in South Africa. Rep. Nat. Parks Bd. S.Afr.: 1-12.

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

BAIRD, D. 1978. Food of the mackerel Scomber japonicus from western Cape waters. Fishery Bull. S. Afr. 10: 62-68.

BALON, E.K. 1979a. The theory of saltation and its application in the ontogeny of fishes: steps and thresholds Env. Biol. Fish. 4: 97-101.

BALON, E.K. 1979b. The juvenilization process in phylogeny and the altricial to precocial forms in the ontogeny of fishes. Env. Biol. Fish. 4: 193-198.

BALON, E.K. 1981. About the processes which cause the evolution of guilds and species. Env. Biol. Fish. 6: 129-138.

BALON, E.K. 1983. Epigenetic mechanisms: reflections on evolutionary processes. Can. J. Fish. Aquat. Sci. 40: 2045-2058.

BARBOUR, C.D. & BROWN, J.H. 1974. Fish species diversity in lakes. Am. Nat. 108: 473-489.

BARDACH, J.E. 1958. On the movements of certain Bermuda reef fishes. Ecology 39: 139-146.

BARDACH, J.E. 1959. The summer standing crop of fish on a shallow Bermuda reef. Limnol. Oceanogr. 4: 77-85.

BARNARD, K.H. 1950. Descriptive catalogue of South African decapod crustacea (crabs and shrimps) Ann. S Afr. Mus. 38: 1-837.

BARR, W.A. 1963. The endocrine control of the sexual cycle in the plaice, Pleuronectes platessa (L.). I. Cyclical changes in the normal ovary. Gen. Comp. Endocrinol. 3: 197-204.

BAYLEY, P.B. 1977. A method for finding the limits of application of the von Bertalanffy growth model and statistical estimates of the parameters. J. Fish. Res. Bd Can. 34: 1079-1084

BAYLIS, J.R. 1981. The evolution of parental care in fishes, with reference to Darwin's rule of male sexual selection. Env. Biol. Fish. 6: 223-251.

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

BEDDINGTON, J.R. & COOKE, J.G. 1983. The potential yield of fish stocks. FAO Fish. Tech. Pap. 242: 1-47.

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.

BERG, J. 1979. Discussion of methods of investigating the food of fishes, with reference to a preliminary study of the prey of Gobiusculus flavescens (Gobiidae). Mar. Biol. 50: 263-273.

BEVERTON, R.J.H. & HOLT, S.J. 1956. The theory of fishing. *In*: Sea Fisheries: their investigation in the United Kingdom. M. Graham (ed.). Arnold, London: 372-441.

BEVERTON, R.J.H. & HOLT, S.J. 1957. On the dynamics of exploited fish populations. *Fishery Invest. series II, Lond.* 19: 1-533.

BIDEN, C.L. 1930. Sea-angling fishes of the Cape (South Africa). Oxford Univ. press. Lond. 304pp.

BJORKLUND, M.I. 1974. Achievements in marine conservation, I. Marine parks. *Environ. Cons.* 1: 205-223.

BLABER, S.J.M. 1974. Field studies of the diet of *Rhabdosargus holubi* (Pisces : Teleostei : Sparidae). *J. Zool. Lond.* 173: 407-417.

BLACKER, R.W. 1969. Chemical composition of the zones in cod (*Gadus morhua* L.) otoliths. *J. Cons. perm. int. Explor. Mer* 33: 107-108.

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

BOHNSACK, J.A. 1983. Species turnover and the order versus chaos controversy concerning reef fish community structure. *Coral Reefs* 1: 223-228.

BOHNSACK, J.A. & BANNEROT, S.P. 1982. A random point census technique for visually assessing coral reef fishes. *In*: The Visual Assessment of Fish Populations in the Southeastern United States: 1982 Workshop. South Carolina Sea Grant Technical Report 1: 5-7.

BOHNSACK, J.A. & TALBOT, F.H. 1980. Species-packing by reef fishes on Australian and Caribbean reefs: an experimental approach. *Bull. Mar. Sci.* 30: 710-722.

BOTHA, L. 1971. Growth and otolith morphology of the Cape hakes *Merluccius capensis* Cast. and *M. paradoxus* Franca. *Investl Rep. Div. Sea Fish. S. Afr.* 97: 1-32.

BOUAIN, A. & SIAU, Y. 1983. Observations on the female reproductive cycle and fecundity of 3 species of groupers (*Epinephelus*) from the southeast Tunisian seashores. *Mar. Biol.* 73: 211-220.

BRAEKEVELT, C.R. & McMILLAN, D.B. 1967. Cyclic changes in the ovary of the brook stickleback *Eucalia inconstans* (Kirtland). *J. Morph.* 123: 373-396.

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

BROCK, R.E., LEWIS, C. & WASS, R.C. 1979. Stability and structure of a fish community on a coral reef in Hawaii. *Mar. Biol.* 54: 281-292.

BROCK, V.E. 1954. A preliminary report on a method of estimating reef fish populations. *J. Wildl. Mgmt* 18: 297-308.

BROWN, J.H. 1971. Mammals on mountaintops: Non-equilibrium insular biogeography. Am. Nat. 105: 467-478.

BROWNELL, C.L. 1979. Stages in the early development of 40 marine fish species with pelagic eggs from the Cape of Good Hope. Ichthyol. Bull. Rhodes Univ. 40: 1-84.

BRUTON, M.N. 1986. Life history styles of invasive fishes in southern Africa. In: The ecology and management of biological invasions in southern Africa. IWA Macdonald, F.J. Kruger and A.A. Ferrar (eds). Oxford University Press Cape Town. pp 201-208.

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. & KOK, H.M. 1983. Notes on the diet of Rhabdosargus holubi (Steindachner) and Rhabdosargus globiceps (Cuvier) in the marine environment. S. Afr. J. Zool. 18: 406-408.

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., WALLACE, J.H. & COCKCROFT, V.G. 1984. Inshore small-mesh trawling survey of the Cape south coast. Part 4. Contributions to the biology of some Teleostei and Chondrichthyes. S. Afr. J. Zool. 19: 180-188.

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

CASSELMAN, J.M. 1974. Analysis of hard tissue of pike Esox lucius L. with special reference to age and growth. In: Ageing of fish. T.B. Bagenal (ed.). Unwin Brothers, England: 13-27.

CAUGHLEY, G. 1977. Analysis of vertebrate populations. Wiley, London: 234pp.

CHARBONNEAU, J.J. & HAY, M.J. 1978. Determinants and economic values of hunting and fishing. Forty-third North American Wildlife Conference: 391-403.

CHESS, J.R. 1979. Some procedures for assessing organisms associated with rocky substrata. In: Gutshop '78. Fish Food Habit Studies. Proceedings of the Second Pacific Northwest Technical Workshop. S.J. Lipovsky and C.A. Simenstad (eds). Univ. Washington, Seattle: 25-28.

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

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

CHRISTENSEN, M.S. 1978. Trophic relationships in juveniles of three species of sparid fishes in the South African marine littoral. Fishery

Bull. U. S. 76: 389-401.

CHUGUNOVA, N.I. 1959. Age and growth studies in fish. National Science Foundation, Washington: 132pp.

CLARKE, A.M. & COURTMAN-STOCK, J. 1976. The echinoderms of southern Africa. Brit. Mus. Nat. Hist. Lond. 277pp.

CLARKE, J.R. 1985. Coastal resources management: Development case studies. Renewable resour. inf. Ser. III: 1-749.

CLARKE, J.R. & BUXTON, C.D. 1985. Notes on the diet of Pterogymnus laniarius (Cuvier) (Pisces : Sparidae). S. Afr. J. Zool. 20: 68-71.

COCHRAN, W.G. 1953. Sampling techniques. Wiley, New York: 330pp.

COETZEE, P.S. 1983. Seasonal histological and macroscopic changes in the gonads of Cheimerius nufar (Ehrenberg, 1820) (Sparidae : Pisces). S. Afr. J. Zool. 18: 76-88.

COETZEE, P.S. & BAIRD, D. 1981a. Catch composition and catch per unit effort of anglers' catches off St. Croix Island, Algoa Bay. S. Afr. J. Wildl. Res. 11: 14-20.

COETZEE, P.S. & BAIRD, D. 1981b. Age, growth and food of Cheimerius nufar (Ehrenberg, 1820)(Sparidae), collected off St Croix Island, Algoa Bay. S. Afr. J. Zool. 16: 137-143.

CRAIG, J.F. 1985. Aging in fish. Can. J. Zool. 63: 1-8.

CRAIK, J.C.A. & HARVEY, S.M. 1987. The causes of buoyancy in eggs of marine teleosts. J. mar. biol. Ass. U.K. 67: 169-182.

CRAWFORD, R.J.M. & CROUS, H.B. 1982. Trends in commercial handline catches of redfishes along the Southern Cape coasts, Republic of South Africa. Koedoe 25: 13-31.

CROSS, J.N. 1982. Resource partitioning in three rocky intertidal fish assemblages. In: Gutshop '81. Fish Food Habit Studies. Proceedings of the Third Pacific Workshop. G.M. Cailliet and C.A. Simenstad (eds). Univ. Washington Seattle: 142-150.

CROSSLAND, J. 1977. Seasonal reproductive cycle of snapper Chrysophrys auratus (Forster) in the Hauraki Gulf. N. Z. J. Mar. Freshwat. Res. 11: 37-60.

CROW, T.M. 1979. Lots of weeds: insular phytogeography of vacant urban lots. J. Biogeog. 6: 169-181.

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

CYRUS, D.P. & BLABER, S.J.M. 1983. The food and feeding ecology of Gerreidae, Bleeker 1859, in the estuaries of Natal. J. Fish Biol. 22: 373-393.

CYRUS, D.P. & BLABER, S.J.M. 1984. The reproductive biology of Gerres in Natal estuaries. J. Fish Biol. 24: 491-504.

D'ANCONA, U. 1949. Ermafroditismo ed intersessualita nei Teleostei. *Experientia* 5: 381-389.

DANNEVIG, E.H. 1956. Chemical composition of the zones in cod otoliths. *J. Cons. perm. int. Explor. Mer* 21: 156-159.

DAVIES, D.H. 1949. Preliminary investigations on the foods of South African fishes with notes on the general fauna of the area. *Investl Rep. Div. Sea Fish. S. Afr.* 11: 1-36.

DAVIS, G.E. 1981. On the role of underwater parks and sanctuaries in the management of coastal resources in the southeastern United States. *Environ. Cons.* 8: 67-70.

DAVIS, T.L.O. & REID, D.D. 1982. Estimates of tag shedding rates for Floy FT-2 Dart and FD-67 Anchor Tags in Barramundi, *Lates calcarifer* (Bloch). *Aust. J. mar. Freshwat. Res.* 33: 1113-1117.

DAY, J.H. 1967a. A monograph of the Polychaeta of southern Africa: part 1. errantia. *Brit. Mus. Nat. Hist. Lond.* 458pp.

DAY, J.H. 1967b. A monograph of the Polychaeta of southern Africa: part 2. sedentaria. *Brit. Mus. Nat. Hist. Lond.* 878pp.

DEGENS, E.T., DEUSER, W.G. & HAEDRICH, R.L. 1969. Molecular structure and composition of fish otoliths. *Mar. Biol.* 2: 105-113.

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

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

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

DIAMOND, J.M. 1973. Distributional ecology of New Guinea birds. *Science*. N.Y. 179: 759-769.

DIAMOND, J.M. 1975. The island dilemma: lessons of modern biogeographic studies for the design of natural reserves. *Biol. Conserv.* 7: 129-146.

DIAMOND, J.M. 1976. Island biogeography and conservation: strategy and limitations. *Science* N.Y. 193: 1027-1029.

DIAMOND, J.M. 1982. Implications of island biogeography for ecosystem conservation. *S. Afr. Nat. Sci. Prog. Rep.* 61: 46-60.

DIAMOND, J.M. & MAY, R.M. 1976. Island biogeography and the design of natural reserves. *In*: Theoretical ecology. Principles and applications. R.M. May (ed). Blackwell Scientific Publications, Oxford: p 163-186.

DRUZHININ, A.D. 1975. Some data on sparid fishes (Family Sparidae) of the Gulf of Aden Region. *J. Ichthyol.* 15: 531-541.

EBELING, A.W. & LAUR, D.R. 1982. Does resource partitioning have a descriptive null hypothesis? In: Gutshop '81. Fish Food Habit Studies. Proceedings of the Third Pacific Workshop. G.M. Cailliet and C.A. Simenstad (eds). Univ. Washington, Seattle: 158-165.

EHLRICH, P.R. 1974. Human population and environmental problems. Environ. Cons. 1: 15-20.

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

FAVRO, L.D., KUO, P.K. & McDONALD, J.F. 1979. Population-genetic study of the effects of selective fishing on the growth rate of trout. J. Fish. Res. Bd Can. 36: 552-561.

FELLER, R., TAGHON, G.L. & JUMARS, P.A.1979. Analysis of 'GORP'. In: Gutshop '78. Fish Food Habit Studies. Proceedings of the Second Pacific Northwest Technical Workshop. S.J. Lipovsky and C.A. Simenstad (eds). Univ. Washington, Seattle: 1-4.

FISHELSON, L. 1970. Protogynous sex reversal in the fish Anthias squamipinnis (Teleostei, Anthiidae) regulated by the presence or absence of male fish. Nature, Lond. 227: 90-91.

FLEMMING, B.W., EAGLE, G.A., FRICKE, A.H., HUNTER, I.T., MARTIN, A.K., SCHUMANN, E.H., SWART, V.P. & ZOUTENDYK, P. 1983. Agulhas bank studies report II - Proceedings of the seventh workshop held at Stellenbosch. NRIO Memo. 8319. Stellenbosch, South Africa.

FRAME, D.W. 1974. Feeding habits of young winter flounder (Pseudopleuronectes americanus): prey availability and diversity. Trans. Am. Fish. Soc. 103: 261-269.

FRANKEL, O.H. & SOULE, M.E. 1981. Conservation and evolution. Camb. Univ. press. 327pp.

FROGLIA, C. 1977. Feeding of Lithognathus mormyrus (L.) in Central Adriatic Sea (Pisces, Sparidae). Rapp. Comm. int. Mer Medit. 24: 95-97.

GADGIL, M. & SOLBRIG, O.T. 1972. The concept of r- and K-selection: evidence from wild flowers and some theoretical considerations. Am. Nat. 106: 14-31.

GAME, M. 1980. Best shape for nature reserves. Nature 287: 630-631.

GARRATT, P.A. 1985a. The offshore linefishery of Natal: I: Exploited population structures of the sparids Chrysoblephus puniceus and Cheimerius nufar. Invest. Rep. Oceanogr. Res. Inst., Durban 62: 1-18.

GARRATT, P.A. 1985b. The offshore linefishery of Natal: II: Reproductive biology of the sparids Chrysoblephus puniceus and Cheimerius nufar. Invest. Rep. Oceanogr. Res. Inst., Durban 63: 1-21.

GARRATT, P.A. 1986a. Protogynous hermaphroditism in the slinger, Chrysoblephus puniceus (Gilchrist & Thompson, 1908) (Teleostei:Sparidae). J. Fish Biol. 28: 297-306.

GARRATT, P.A. 1986b. The offshore linefishery of Natal: III: Food and feeding of the sparids *Chrysoblephus puniceus* and *Cheimerius nufar*. *Invest. Rep. Oceanogr. Res. Inst., Durban* 64: 1-17.

GELDENHUYS, N.D. 1973. Growth of the South African maasbanker *Trachurus trachurus* Linnaeus and age composition of the catches, 1950-1971. *Investl Rep. Div. Sea Fish. S. Afr.* 101: 1-24.

GELDENHUYS, N.D. 1978. Age determination of the South African round herring *Etrumeus micropus* and length and age composition of the commercial catches, 1965-1973. *Investl Rep. Div. Sea Fish. S. Afr.* 115: 1-16.

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

GILLIAN, M.R. 1980. Beta diversity of a gulf of California rocky shore community. *Env. Biol. Fish.* 5: 109-116.

GILPIN, M.E. & DIAMOND, J.M. 1980. Subdivision of nature reserves and the maintenance of species diversity. *Nature* 285: 567-568.

GLADFELTER, W.B. & JOHNSON, W.S. 1983. Feeding niche separation in a guild of tropical reef fishes (Holocentridae). *Ecology* 64: 552-563.

GOEDEN, G.B. 1979. Biogeographic theory as a management tool. *Environ. Cons.* 6: 27-32.

GRAHAM, J. 1977. Reproductive effort and r- and K-selection in two species of *Lacuna* (Gastropoda:Prosobranchia). *Mar. Biol.* 40: 217-224.

GRINDLEY, J.R., COOPER, K.H. & HALL, A.V. 1976. Proposals for marine nature reserves for South Africa. *Rep. Coun. Habitat Wildl. Soc. S. Afr.*: 16pp.

GROSSMAN, G.D. 1982. Community regulation and patterns of resource partitioning. *In*: Gutshop '81. Fish Food Habits Studies. Proceedings of the Third Pacific Workshop. G.M. Cailliet and C.A. Simenstad (eds). Univ. Washington,Seattle: 166-177.

GULLAND, J.A. 1968. The concept of the marginal yield from exploited fish stocks. *J. Cons. int. Explor. Mer* 32: 256-261.

GULLAND, J.A. 1975. Manual of sampling and statistical methods for fisheries biology. Part 1. Sampling methods. *FAO Man. Fish. Sci.* 3: 87pp.

GULLAND, J.A. 1978. Fishery management: new strategies for new conditions. *Trans. Am. Fish. Soc.* 107: 1-11.

GULLAND J.A. & BOERMA, L.A. 1973. Scientific advice on catch levels. *Fish Bull.* U.S. 71: 325-335.

HARRIS, T.F.W. 1978. Review of coastal currents in southern African waters. *S. Afr. Nat. Sci. Prog. Rpt.* 30: 1-103.

HEALEY, M.C. 1980. Growth and recruitment in experimentally exploited lake whitefish (*Coregonus clupeaformis*) populations. *Can. J. Fish. Aquat. Sci.* 37: 255-267.

HECHT, T. 1976. The general biology of six major trawl fish species of the Eastern Cape coast of South Africa with notes on the demersal fishery, 1967-1975. PhD thesis, University of Port Elizabeth, South Africa: 384pp.

HECHT, T. 1978. A descriptive systematic study of the otoliths of the Neopterygean marine fishes of South Africa. Part 1. Introduction. *Trans. R. Soc. S. Afr.* 43: 191-197.

HECHT, T. 1979. The value of otoliths in fresh water fisheries biology and taxonomy. Department of Zoology and Biology, University of the North, Pietersburg, *Series* A19: 1-17.

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

HICKEY, C.R. Jr. 1975. Fish behaviour as revealed through stomach content analysis. *N.Y. Fish Game J.* 22(2): 149-155.

HIGGS, A.J. & USHER, M.B. 1980. Should nature reserves be large or small. *Nature* 285: 568-569.

HOBSON, E.S. 1974. Feeding relationships of teleostean fishes on coral reefs in Kona, Hawaii. *Fishery Bull. U. S.* 72: 915-1031.

HOFFMAN, S.G. 1985. Effects of size and sex on the social organization of reef-associated hogfishes, *Bodianus* spp. *Env. Biol. Fish.* 14: 185-197.

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

HUNTSMAN, G.R. & MANOOCH, C.S. III. 1978. Minimum size limits for reef fishes. *Proc. Ann. Conf. Southeast. Assoc. Fish Wildl. Agencies* 32: 509-513.

HUNTSMAN, G.R., MANOOCH, C.S. III & GRIMES, C.B. 1983. Yield per recruit models of some reef fishes of the U.S. South Atlantic Bight. *Fishery Bull. U.S.* 81: 679-695.

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

HYSLOP, E.J. 1980. Stomach contents analysis - a review of methods and their application. *J. Fish Biol.* 17: 411-429.

ICSEAF. 1986. ICSEAF otolith interpretation guide. No. 2 Cape horsemackerel. int. Commn SE. Atl. Fish Otol. interp. gde 2: 1-24.

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

IRIE, T. 1960. The growth of the fish otolith. J. Fac. Fish. Anim. Husb. Hiroshima Univ. 3: 203-221.

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

JONES, G.P. 1980. Contribution to the biology of redbanded perch Ellerkeldia huntii (Hector), with a discussion on hermaphroditism. J. Fish. Biol. 17: 197-207.

JONES, N.S. 1952. The bottom fauna and food of flatfish of the Cumberland coast. J. Anim. Ecol. 21: 182-205.

JONES, R.S. & THOMPSON, M.J. 1978. Comparison of Florida reef fish assemblages using a rapid visual technique. Bull. Mar. Sci. 28: 159-172.

JOUBERT, C.S.W. 1981. Aspects of the biology 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. & HANEKOM, P.B. 1980. A study of feeding in some inshore reef fish of the Natal Coast, South Africa. S. Afr. J. Zool. 15: 262-274.

KENSLEY, B. 1978. Guide to the marine isopods of southern Africa. Trustees s. Afr. mus. Cape Town. 173pp.

KENSLEY, B. 1981. On the zoogeography of southern African decapod crustacea, with a distributional checklist of the species. Smithson. Contr. Zool. 338: 1-64.

KILBURN, R. 1982. Sea shells of southern Africa. Macmillan, Johannesburg. 249pp.

KIMMEL, 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.

KNIGHT, W. 1968. Asymptotic growth: an example of nonsense disguised as mathematics. J. Fish. Res. Bd Can. 25: 1303-1307.

LAEVASTU, T. 1965. Manual of methods in fisheries biology. FAO Manual in Fisheries Science 9: 41-45.

LAIRD, L.M. & STOTT, B. 1978. Marking and Tagging. In: Methods for assessment of fish production in fresh waters. T. Bagenal (ed.). IBP Handbook No. 3. Blackwell Scientific Publications, Oxford: 84-100.

LARKIN, P. 1977. An epitaph for the concept of maximum sustainable yield. Trans. Am. Fish. Soc. 9: 26-32.

LASIAK, T.A. 1982. Structural and functional aspects of the surf-zone fish community in the eastern Cape. PhD thesis, University of Port Elizabeth, South Africa: 459pp.

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

LENARZ, W.H., FOX, W.W. Jr., SAKAGAWA, G.T. & ROTHSCHILD, B.J. 1974. An examination of the yield per recruit basis for a minimum size regulation for Atlantic yellowfin tuna, Thunnus albacares. Fishery Bull. U.S. 72: 37-61.

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

LEVITEN, P.J. 1976. The foraging strategy of vermivorous conid gastropods. Ecol. Monogr. 46: 157-178.

LIEM, K.F. 1968. Geographical and taxonomic variation in the pattern of normal sex reversal in the teleost fish order Synbranchiformes. J. Zool., Lond. 156: 225-238.

MACARTHUR, R.H. & PIANKA, E.R. 1966. On optimal use of a patchy environment. Am. Nat. 100: 603-609.

MACARTHUR, R.H. & WILSON, E.O. 1967. Theory of island biogeography. Princeton Univ. Press, New Jersey. 203pp.

MANOOCH, C.S. 1982. Aging 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. G.R. Huntsman, W.R. Nicholson and W.W. Fox, Jr. (eds). NOAA Technical Memorandum NMFS-SEFC-80: 24-43.

MANOOCH, C.S. III & MASON, D.L. 1984. Age, growth and mortality of lane snapper from Southern Florida. Northeast. Gulf Sci. 7: 109-115.

MANOOCH, C.S. III & MATHESON, R.H. III. 1981. Age, growth and mortality of gray snapper collected from Florida waters. Proc. Ann. Conf. Southeast. Assoc. Fish Wildl. Agencies 35: 331-344.

MASON, D.L. & MANOOCH, C.S. III. 1985. Age and growth of mutton snapper along the east coast of Florida. Fish. Res. 3: 93-104.

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

MENGE, J.L. & MENGE, B.A. 1974. Role of resource allocation, aggression and spatial heterogeneity in coexistence of two competing intertidal starfish. Ecol. Monogr. 44: 189-209.

MILLARD, N.A.H. 1975. Monograph on the Hydroida of southern Africa. Ann. S. Afr. Mus. 68: 1-513.

MOYER, J.T. & NAKAZONO, A. 1978. Population structure, reproductive behavior and protogynous hermaphroditism in the angelfish Centropyge interruptus at Miyake-jima, Japan. Jap. J. Ichthyol. 25(1): 25-39.

MUGIYA, Y. 1964. Calcification in fish and shell-fish. 3. Seasonal occurrence of a prealbumin fraction in the otolith fluid of some fish, corresponding to the period of opaque zone formation in the otolith. Bull. Jap. Soc. scient. Fish. 30: 955-961.

MUGIYA, Y. 1965. Calcification in fish and shell-fish. 4. The differences in nitrogen content between the translucent and opaque zones of otoliths in some fish. Bull. Jap. Soc. scient. Fish. 31: 896-901.

NEPGEN, C.S. DE V. 1977. The 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.

NEPGEN, C.S. DE V. 1982. Diet of predatory and reef fish in False Bay and possible effects of pelagic purse-seining on their food supply. Fishery Bull. S. Afr. 16: 75-93.

NEWELL, R.C. 1977. Biology of intertidal animals. Marine Ecological Surveys, Kent, United Kingdom: 1-781.

NOAKES, D.L.G. & BALON E.K. 1982. Life histories of tilapias: an evolutionary perspective. In. Biology and culture of tilapias. R.S.V. Pullen & R.H. Lowe-McConnell (eds). ICLARM, Manilla: 15-59.

PANNELLA, G. 1971. Fish otoliths: daily growth layers and periodical patterns. Science N.Y. 173: 1124.

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

PAULY, D. 1980. On the interrelationships between natural mortality, growth parameter, and mean environmental temperature in 175 fish stocks. J. Cons. perm. int. Explor. Mer 39: 175-192.

PENRITH, M.J. 1972a. Sex reversal in the sparid fish Chrysoblephus laticeps. Koedoe 15: 135-139.

PENRITH, M.J. 1972b. The behaviour of reef-dwelling sparid fishes. Zool Afr. 7: 43-49.

PFUDERER, P. & FRANCIS, A.A. 1972. Isolation of a new heart rate depressing pheromone from the water of crowded fish. Fedn Proc. Fedn Am. Socs exp. Biol. 31: 486.

PIANKA, E.R. 1970. On "r" and "K" selection. Am. Nat. 104: 592-597.

PIANKA, E.R 1972. "r" and "K" or "a" and "b" selection? Am. Nat. 106: 581-588.

PITCHER, T.J. & HART, P.J.B. 1982. Fisheries ecology. Croom Helm, Lond.: 414pp.

PILLAY, T.V.R. 1952. A critique of the methods of study of food of fishes. *J. zool. Soc. India* 4: 185-200.

RALSTON, S. 1981. Aspects of the reproductive biology and feeding ecology of *Chaetodon miliaris*, a Hawaiian endemic butterflyfish. *Env. Biol. Fish.* 6: 167-176.

RANDALL, J.E. 1961. Tagging reef fishes in the Virgin Islands. *Proc. Gulf Caribb. Fish. Inst.* 14: 201-241.

RANDALL, J.E. 1963. An analysis of the fish populations of artificial and natural reefs in the Virgin Islands. *Carib. J. Sci.* 3: 31-47.

RANDALL, J.E. 1967. Food habits of reef fishes of the West Indies. *Stud. Trop. Oceanogr.* 5: 665-847.

RANDALL, J.E. 1982. Tropical marine sanctuaries and their significance in reef fisheries research. *In*: Proceedings of a workshop held October 7-10, 1980 at St. Thomas, Virgin Islands of the United States. G.R. Huntsman, W.R. Nicholson and W.W. Fox, Jr. (eds). NOAA Technical Memorandum NMFS-SEFC-80: 167-178.

RATKOWSKI, D.A. 1983. Nonlinear regression modelling. Marcel Decker: 135-154.

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

RAY, G.C. 1968. Marine parks for Tanzania. Conservation foundation Wash. D.C.: 47pp.

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.

RICKER, W.E. 1963. Big effects from small causes: two examples from fish population dynamics. *J. Fish. Res. Bd. Can.* 20: 257-264.

RICKER, W.E. 1969. Effects of size-selective mortality and sampling bias on estimates of growth, mortality, production and yield. *J. Fish. Res. Bd Can.* 26: 479-541.

RICKER, W.E. 1975. Computation and interpretation of biological statistics of fish populations. *Bull. Fish. Res. Bd Can.* 191: 1-382.

RICKER, W.E. 1978. Introduction. *In*: Methods for assessment of fish production in fresh waters. T. Bagenal (ed.). IBP Handbook No. 3. Blackwell Scientific Publications, Oxford: 1-6.

RIPER, C. van, III. 1981. Summarizing remarks: comparison of methods. *In*: Estimating numbers of terrestrial birds, studies in avian biology 6. C.J. Ralph and J.M. Scott (eds). Allen Press, Lawrence: 217-218.

RISK, M.J. 1972. Fish diversity on a coral reef in the Virgin Islands.

Atoll Res. Bull. 153: 1-6.

ROBERTSON, D.R. 1972. Social control of sex reversal in a coral reef fish. Science 177: 1007-1009.

ROBERTSON, D.R. & CHOAT, H. 1974. Protogynous hermaphroditism and social systems in labrid fishes. Proc. 2nd Internat. Symp. Coral Reefs 1: 217-225.

ROBERTSON, D.R. & LASSIG, B. 1980. Spatial distribution patterns and coexistence of a group of territorial damselfishes from the Great Barrier Reef. Bull. Mar. Sci. 30: 187-203.

ROBERTSON, D.R., REINBOTH, R. & BRUCE, R.W. 1982. Gonochorism, protogynous sex-change and spawning in three sparisomatinine parrotfishes from the western Indian Ocean. Bull. mar. Sci. 32: 868-879.

ROBERTSON, D.R. & WARNER, R.R. 1978. Sexual patterns in the labroid fishes of the western Caribbean, II: The parrot fishes (Scaridae). Smithson. Contrib. Zool. 255: 1-26.

ROBINSON, G.A. 1976. Sex reversal in the dageraad Chrysoblephus cristiceps (Pisces, Sparidae). Koedoe 19: 43-48.

ROBINSON, G.A., SIEGFRIED, W.R. & VISSER, G.A. 1985. A plan for the protection of special natural features and systems in the South African Coastal zone. Unpubl. Rep. Coun. Env.: 1-18.

ROBSON, D.S. & REGIER, H.A. 1964. Sample size in Petersen mark-recapture experiments. Trans. Am. Fish. Soc. 93: 215-226.

ROEDE, M.J. 1972. Color as related to size, sex and behaviour in seven Caribbean labrid fish species (genera Thalassoma, Halichoeres and Hemipteronotus). Stud. Fauna Curacao 138: 1-264.

ROSSOUW, G.J. 1984. Age and growth of the sand shark, Rhinobatus annulatus, in Algoa Bay, South Africa. J. Fish Biol. 25: 213-222.

RUBY, S.M. & McMILLAN, D.B. 1970. Cyclic changes in the testis of the brook stickleback Eucalia inconstans (Kirtland). J. Morph. 131: 447-465.

RUSSELL, B.C., TALBOT, F.H., ANDERSON, G.R.V. & GOLDMAN, B. 1978. Collection and sampling of reef fishes. In: Coral Reefs: Research Methods. D.R. Stoddart and R.E. Johannes (eds). Monographs on Oceanographic Methodology 5. UNESCO, Norwich: 329-345.

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

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

SALE, P.F. 1975. Patterns of use of space in a guild of territorial reef fishes. Mar. Biol. 29: 89-97.

SALE, P.F. 1978. Co-existence of coral reef fishes - a lottery for living space. *Env*. *Biol*. *Fish*. 3: 85-102.

SALE, P.F. 1980. The ecology of fishes on coral reefs. *Oceanogr*. *Mar*. *Biol*. *Ann*. *Rev*. 18: 367-421.

SALE, P.F. & DOUGLAS, W.A. 1981. Precision and accuracy of visual census techniques for fish assemblages on coral patch reefs. *Env*. *Biol*. *Fish*. 6: 333-339.

SALE, P.F. & SHARP, B.J. 1983. Correction for bias in visual transect censuses of coral reef fishes. *Coral* *Reefs* 2: 37-42.

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

SCHAFFER, W.M. 1974. Optimal reproductive effort in fluctuating environments. *Am*. *Nat*. 108: 783-790.

SCHAEFER, M.B. 1957. A study of the dynamics of fishery for yellowfin tuna in the Eastern Tropical Pacific Ocean. *Bull*. *inter-Am*. *trop*. *Tuna* *Commn* 2: 247-285.

SCHNEPPENHEIM, R. & FREYTAG, G. 1980. Age determination by staining otoliths of *Notothenia* *rossii* *marmorata* with ninhydrin. *Cybium*, *3e* *Serie* 8: 13-15.

SCHNUTE, J. 1981. A versatile growth model with statistically stable parameters. *Can*. *J*. *Fish*. *Aquat*. *Sci*. 38: 1128-1140.

SEBER, G.A. 1973. The estimation of animal abundance and related parameters. Griffin, Lond.: 506pp.

SEBER, G.A. 1979. General mathematical principles and theory of fauna sampling. *In*: Aerial Surveys of Fauna Populations, Australian Nat. Parks Wildl. Serv., Spec. Publ. 1, Canberra: 1-7.

SEPKOWSKI, J.J. & REX, M.A. 1974. Distribution of freshwater mussels: coastal rivers as biogeographic islands. *Syst*. *Zool*. 23: 165-188.

SCHAFFER, W.M. 1974. Optimal reproduction in fluctuating environments. *Am*. *Nat*. 108: 783-790.

SHAPIRO, D.Y. 1979. Social behaviour, group structure, and the control of sex reversal in hermaphroditic fish. *Adv*. *Study* *Behav*. 10: 43-102.

SHAPIRO, D.Y. 1980. Serial female sex changes after simultaneous removal of males from social groups of a coral reef fish. *Science* 209: 1136-1137.

SHAPIRO, D.Y. 1981. Size, maturation and the social control of sex reversal in the coral reef fish *Anthias* *squamipinnis*. *J*. *Zool*., Lond. 193: 105-128.

SHAPIRO, D.Y. 1984. Sex reversal and sociodemographic processes in coral reef fishes. *In*: Fish Reproduction. G.N. Potts and R.J. Wooton (eds): 103-118.

SHAW, W., NAGTEGAAL, D.A., ARCHIBALD, C.P. & LEAMAN, B.M. 1981.

Rockfish tagging cruises off Southwest Vancouver Island (*M/V Ocean King*) and off Northwest Vancouver Island and in Queen Charlotte Sound (*M/V Blue Waters*) during 1980. *Can. Data Rep. Fish. Aquat. Sci.* 288: 133pp.

SHIELDS, W.M. 1979. Avian census techniques: an analytical review. *In:* The role of insectivorous birds in forest ecosystems. J.G. Dickson, R.N. Conner, R.R. Fleet, J.C. Kroll and J.A. Jackson (eds). Academic Press, New York: 23-51.

SIEGFRIED, W.R. & DAVIES, B.R. 1982. Conservation of Ecosystems: theory and practice. *S. Afr. Nat. Sci. Prog. Rep.* 61: 1-97.

SIMBERLOFF, D.S & ABELE, L.G. 1976. Island biogeography theory and conservation practice. *Science* N.Y. 191: 285-286.

SLUCZANOWSKI, P.R. 1985. The Beverton and Holt yield per recruit model using LOTUS 1-2-3. *Fish. Res. Paper, Dept. Fish. S. Australia* 13: 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. (B) 1: 357-409.

SMALE, M.J. & BRUTON, M.N. 1985. Predation and prey selectivity by *Argyrosomus hololepidotus* (Osteichthyes: Sciaenidae) in south-eastern Cape waters off South Africa. *S. Afr. J. Zool.* 20: 97-108.

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.

SMITH, C.L. 1965. The patterns of sexuality and the classification of serranid fishes. *Am. Mus. Novit.* 2207: 1-20.

SMITH, C.L. 1967. Contribution to the theory of hermaphroditism. *J. theor. Biol.* 17: 76-90.

SMITH, C.L. 1973. Small rotenone stations: a tool for studying coral reef fish communities. *Am. Mus. Novit.* 2512: 1-21.

SMITH, C.L. 1975. The evolution of hermaphroditism in fishes. *In:* Intersexuality in the animal kingdom. R. Reinboth (ed). Springer, New York: 295-310.

SMITH, C.L. 1982. Patterns of reproduction in coral reef fishes. *In:* Proceedings of a workshop held October 7-10, 1980 at St. Thomas, Virgin Islands of the United States. G.R. Huntsman, W.R. Nicholson and W.W. Fox, Jr. (eds). NOAA Technical Memorandum NMFS-SEFC-80: 49-66

SMITH, C.L. & TYLER, J.C. 1972. Space resource sharing in a coral reef fish community. *Los Ang. County nat. Hist. Mus. Sci. Bull.* 14: 125-170.

SMITH, C.L. & TYLER, J.C. 1973a. Population ecology of a Bahamian suprabenthic shore fish assemblage. *Am. Mus. Novit.* 2528: 1-38.

SMITH, C.L. & TYLER, J.C. 1973b. Direct observations of resource sharing in coral reef fish. *Helgol. Wiss. Meersunters.* 24: 264-275.

SMITH, J.L.B. & SMITH, M.M. 1986. Sparidae. *In*: Smith's Sea Fishes. M.M. Smith and P.C. Heemstra (eds). Macmillan, Johannesburg: 580-594.

SMITH, M.M. & HEEMSTRA, P.C. (eds). 1986. Smith's Sea Fishes. MacMillan, South Africa.

SNEDAKER, S.C. & GETTER, C.G. 1985. Coastal resources management guidelines. *Renewable resour. inf. ser.* II: 1-205.

SORENSEN, J.C., McCREARY, S.T. & HERSHMAN, M.J. 1984. Institutional arrangements for management of coastal resources. *Renewable resour. inf. ser.* I: 1-165.

STANDER, G.H. & NEPGEN, C.S. 1968. Some facts about linefish - with special reference to False Bay. *S. Afr. Shipp. News Fish. Ind. Rev.* 23: 108-111.

STEARNS, S.C. 1976. Life-history tactics: a review of the ideas. *Q. Rev. Biol.* 51: 3-45.

STEARNS, S.C. 1983. The evolution of life-history traits in mosquitofish since their introduction to Hawaii in 1905: Rates of evolution, heritabilities, and developmental plasticity. *Am. Zool.* 23: 65-75.

STEARNS, S.C. & CRANDALL, R.E. 1984. Plasticity for age and size at sexual maturity: a life-history response to unavoidable stress. *In*: Fish Reproduction: Strategies and Tactics. G.W. Potts and R.J. Wootton (eds). Academic Press, London: 13-33.

STUART, A. 1962. Basic ideas of scientific sampling. Griffin, London: 99pp.

TALBOT, F.H. 1955. Notes on the biology of the white stumpnose, *Rhabdosargus globiceps* (Cuvier), and on the fish fauna of the Klein River estuary. *Trans. R. Soc. S. Afr.* 34: 387-407.

TALBOT, F.H. 1965. A description of the coral structure of Tutia Reef (Tanganyika Territory, East Africa) and its fish fauna. *Proc. zool. Soc. Lond.* 145: 431-470.

TALBOT, F.H. & GOLDMAN, B. 1974. A preliminary report on the diversity and feeding relationships of the reef fishes at One Tree Island, Great Barrier Reef. *In*: *Proc. Symp. Corals and Coral Reefs, 1969, Mar. Biol. Assoc. India*: 425-444.

TERBORGH, J. 1976. Island biogeography and conservation: strategy and limitations. *Science* N.Y. 193: 1029-1030.

THOMAS, R.M. 1983. Back-calculation and time of hyaline ring formation in the otoliths of the pilchard off South West Africa. *S. Afr. J. Mar. Sci.* 1: 3-18.

THOMAS, R.M. 1985. Growth rate of the pilchard off South West Africa, 1971-1983. *Investl Rep. Sea Fish. Res. Inst. S. Afr.* 128: 1-41.

THOMPSON, M.J. & SCHMIDT, T.W. 1977. Validation of the species/time random count technique sampling fish assemblages at Dry Tortugas. *Proc. 3rd Internat. Symp Coral Reefs* 1: 283-288.

THRESHER, R.E. 1983. Environmental correlates of the distribution of planktivorous fishes in the One Tree Island lagoon. *Mar. Ecol. Prog. Ser.* 10: 137-145.

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.

THRESHER, R.E., SAINSBURY, K.J., GUNN, J.S. & WHITELAW, A.W. 1986. Life history strategies and recent changes in population structure in the lizardfish genus, *Saurida*, on the Australian Northwest Shelf. *Copeia* 1986: 876-885.

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

VAN BRUGGEN, A.C. 1965. Records and observations in the Port Elizabeth oceanarium in 1960. *Zool. Gart. Leipzig.* 34: 183-202.

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: 367pp.

VAN DER ELST, R.P. 1982. Did you have bumper catches in 1980? *Ski-Scene* - Jan/Feb.: 59-61.

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. & ADKIN, F. 1987. Marine linefish catch statistics : *Chrysoblephus cristiceps*. Oceanographic Res. Inst. Durban, Unpubl. Internal Report: 1-26.

VAN DER HORST, G. 1976. Aspects of the reproductive biology of *Liza dumerili* (Steindachner, 1869)(Teleostei: Mugilidae) with special reference to sperm including comparisons with *Xenopus laevis* (Daudin) sperm. PhD Thesis. University of Port Elizabeth. South Africa. 377pp.

VAUGHAN, D.S. & KANCIRUK, P. 1982. An empirical comparison of estimation procedures for the von Bertalanffy growth equation. *J. Cons. Ciem.* 40: 211-219.

VUILLEUMIER, F. 1970. Insular island biogeography in continental regions I. The northern Andes of South America. *Am. Nat.* 104: 373-388.

VUILLEUMIER, F. 1972. Insular island biogeography in continental regions II. Cave faunas of Tessin, southern Switzerland. *Syst. Zool.*

22: 64-76.

WALLACE, J.H. & SCHLEYER, M.H. 1979. Age determination in two important species of South African angling fishes, the kob (Argyrosomus hololepidotus Lacep.) and the spotted grunter (Pomadasys commersoni Lacep.) Trans. R. Soc. S. Afr. 44: 15-26.

WALLACE, J.H. & VAN DER ELST, R.P. 1983. Marine linefish programme priority species list. S. Afr.Nat. Sci. Prog. Rep. 70: 1-113.

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

WALSH, W.J. 1985. Reef fish community dynamics on small artificial reefs : The influence of isolation, habitat structure and biogeography. Bull. Mar. Sci. 36: 357-376.

WARE, D.M. 1984. Fitness of different reproductive strategies in teleost fishes. In: Fish Reproduction: Strategies and Tactics. G.W. Potts and R.J. Wootton (eds). Academic Press, London: 349-366.

WARNER, R.R. 1975. The adaptive significance of sequential hermaphroditism in animals. Am. Nat. 109: 61-82.

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

WARNER, R.R. 1984. Mating behaviour and hermaphroditism in coral reef fishes. Am. Sci. 72(2): 128-136.

WARNER, R.R. & ROBERTSON, D.R. 1978. Sexual patterns in the labroid fishes of the western Caribbean, I: The Wrasses (Labridae). Smithson. Contrib. Zool. 254: 1-27.

WARNER, R.R., ROBERTSON, D.R. & LEIGH, E.G., Jr. 1975. Sex change and sexual selection. Science 190: 633-638.

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

WHITCOMB, R.F., LYNCH, J.F., OPLER, P.A. & ROBBINS C.S. 1976. Island biogeography and conservation: strategy and limitations. Science N.Y. 193: 1030-1032.

WILD, A. & FOREMAN, T.J. 1980. The relationship between otolith increments and time for yellowfin and skipjack tuna marked with tetracycline. Bull. inter-Am. trop. Tuna Commn 17: 509-560.

WILLIAMS, G.C. 1966. Adaptation and natural selection. A critique of some current evolutionary thought. Princeton University Press, Princeton: 290pp.

WILLIAMSON, M. 1981. Island populations. Oxford Univ. press., London. 286pp.

WILSON, E.O. & WILLIS, E.O. 1975. Applied biogeography. In: Ecology and evolution of communities. M.L. Cody & J.M. Diamond (eds). Harvard

Univ. Press, Cambridge: p 522-534.

WINDELL, J.T. & BOWEN, S.H. 1978. Methods for study of fish diets based on analysis of stomach contents. *In*: Methods for assessment of fish production in fresh waters. T. Bagenal (ed.). IBP Handbook No. 3. Blackwell Scientific Publications, Oxford: 219-226.

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.

YOUNG, P.C. & MARTIN, R.B. 1982. Evidence for protogynous hermaphroditism in some lethrinid fishes. *J. Fish Biol.* 21: 475-484.

ZAR, J.H. 1984. Biostatistical analysis. Second edition. Prentice-Hall, Englewood Cliffs: 718pp.

APPENDIX 1

The method used to construct catch curves is outlined below and is illustrated by an example spreadsheet for Chrysoblephus laticeps sampled at Noordhoek in 1984 (cf. Fig. 29 and Table 17).

1. An age key was set out using 25mm size classes.

2. This key was normalised by dividing each age class by the age frequency for that size class (i.e. row division of age class by age frequency).

3. A normalised age-length key is then obtained by multiplying each row by the length frequency for that size class. From this the normalised age frequency, % age frequency, cumulative % age frequency and natural log of the age frequency were determined for each age class.

4. Regression of ln(age frequency) vs age was done using least squares analysis. Note that only values on the decending limb were included in the analysis.

1. Age key..../

1. Age key for C. <u>laticeps</u> sampled at Noordhoek

Size class	Age class																		Age frequency
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	
51-75	6.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6.0
76-100	2.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.0
101-125	1.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.0
126-150	-	2.0	6.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8.0
151-175	-	-	11.0	4.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	15.0
176-200	-	-	3.0	12.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	15.0
201-225	-	-	-	12.0	8.0	-	-	-	-	-	-	-	-	-	-	-	-	-	20.0
226-250	-	-	-	1.0	15.0	14.0	2.0	-	-	-	-	-	-	-	-	-	-	-	32.0
251-275	-	-	-	-	3.0	18.0	31.0	5.0	1.0	1.0	-	-	-	-	-	-	-	-	59.0
276-300	-	-	-	-	-	1.0	21.0	31.0	15.0	1.0	-	-	-	-	-	-	-	-	69.0
301-325	-	-	-	-	-	-	3.0	16.0	33.0	17.0	5.0	2.0	-	-	-	-	-	-	76.0
326-350	-	-	-	-	-	-	-	2.0	5.0	18.0	22.0	8.0	4.0	-	1.0	-	-	-	60.0
351-375	-	-	-	-	-	-	-	-	-	1.0	5.0	18.0	10.0	6.0	4.0	-	1.0	1.0	46.0
376-400	-	-	-	-	-	-	-	-	-	-	-	5.0	3.0	5.0	7.0	-	2.0	2.0	24.0
401-425	-	-	-	-	-	-	-	-	-	-	-	-	-	1.0	2.0	-	3.0	4.0	10.0
426-450	-	-	-	-	-	-	-	-	-	-	-	-	-	1.0	-	1.0	1.0	-	3.0

2. Normalised age key obtained from row division of age classes by age frequency

1.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
-	0.25	0.75	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
-	-	0.73	0.27	-	-	-	-	-	-	-	-	-	-	-	-	-	-
-	-	0.20	0.80	-	-	-	-	-	-	-	-	-	-	-	-	-	-
-	-	-	0.60	0.40	-	-	-	-	-	-	-	-	-	-	-	-	-
-	-	-	0.03	0.47	0.44	0.06	-	-	-	-	-	-	-	-	-	-	-
-	-	-	-	0.05	0.31	0.53	0.08	0.02	0.02	-	-	-	-	-	-	-	-
-	-	-	-	-	0.01	0.30	0.45	0.22	0.01	-	-	-	-	-	-	-	-
-	-	-	-	-	-	0.04	0.21	0.43	0.22	0.07	0.03	-	-	-	-	-	-
-	-	-	-	-	-	-	0.03	0.08	0.30	0.37	0.13	0.06	-	0.02	-	-	-
-	-	-	-	-	-	-	-	-	0.02	0.11	0.39	0.22	0.13	0.19	-	0.02	0.02
-	-	-	-	-	-	-	-	-	-	-	0.21	0.13	0.21	0.29	-	0.08	0.08
-	-	-	-	-	-	-	-	-	-	-	-	-	0.10	0.20	-	0.30	0.40
-	-	-	-	-	-	-	-	-	-	-	-	-	0.33	-	0.33	0.33	-

3. Normalised age-length key obtained from row multiplication of normalised age key by sample length frequency

Length Frequency	Normalized age-length frequency																	
0.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1.0	1.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2.0	-	-	0.4	1.6	-	-	-	-	-	-	-	-	-	-	-	-	-	-
43.0	-	-	-	25.8	17.2	-	-	-	-	-	-	-	-	-	-	-	-	-
138.0	-	-	-	4.3	64.7	60.4	8.6	-	-	-	-	-	-	-	-	-	-	-
246.0	-	-	-	-	12.5	75.1	129.3	20.8	4.2	4.2	-	-	-	-	-	-	-	-
281.0	-	-	-	-	-	4.1	85.5	126.2	61.1	4.1	-	-	-	-	-	-	-	-
217.0	-	-	-	-	-	-	8.6	45.7	94.2	48.5	14.3	5.7	-	-	-	-	-	-
177.0	-	-	-	-	-	-	-	5.9	14.8	53.1	64.9	23.6	11.8	-	3.0	-	-	-
138.0	-	-	-	-	-	-	-	-	-	3.0	15.0	54.0	30.0	18.0	12.0	-	3.0	3.0
86.0	-	-	-	-	-	-	-	-	-	-	-	17.9	10.8	17.9	25.1	-	7.2	7.2
28.0	-	-	-	-	-	-	-	-	-	-	-	-	-	2.8	5.6	-	8.4	11.2
7.0	-	-	-	-	-	-	-	-	-	-	-	-	-	2.3	-	2.3	2.3	-
Age Freq.	2.0	0.0	0.4	31.7	94.4	139.5	232.0	198.7	174.2	112.9	94.2	101.2	52.6	41.1	45.6	2.3	20.9	21.4
% Age Freq.	0.14	-	0.0	2.3	6.9	10.2	16.9	14.6	12.8	8.2	6.9	7.4	3.9	3.0	3.3	0.17	1.5	1.6
Cum. % Freq.	0.14	0.1	0.2	2.5	9.3	19.6	36.5	51.7	63.9	72.1	78.9	86.4	90.3	93.3	96.6	96.7	98.2	99.8
Ln Age Freq.	0.7	-	-0.9	3.5	4.5	4.9	5.4	5.3	5.2	4.7	4.5	4.6	4.0	3.7	3.8	0.8	3.0	3.1

4. Regression analysis

all data

Y obs	X	Y calc
5.4	7.0	5.6
5.3	8.0	5.3
5.2	9.0	5.1
4.7	10.0	4.8
4.5	11.0	4.5
4.6	12.0	4.2
4.0	13.0	3.9
3.7	14.0	3.6
3.8	15.0	3.3
0.8	16.0	3.0
3.0	17.0	2.7
3.1	18.0	2.4

Regression Output:

Constant	7.7068183675
Std Err of Y Est	0.7564462025
R Squared	0.685
No of Observation	12.0
Degrees of Freedom	10.0
X Coefficient	-0.2949881069
Std Err of C	0.063257

excluding age 16

Y obs	X	Y calc
5.4	7.0	5.5
5.3	8.0	5.3
5.2	9.0	5.0
4.7	10.0	4.8
4.5	11.0	4.6
4.6	12.0	4.4
4.0	13.0	4.1
3.7	14.0	3.9
3.8	15.0	3.7
3.0	17.0	3.2
3.1	18.0	3.0

Regression Output:

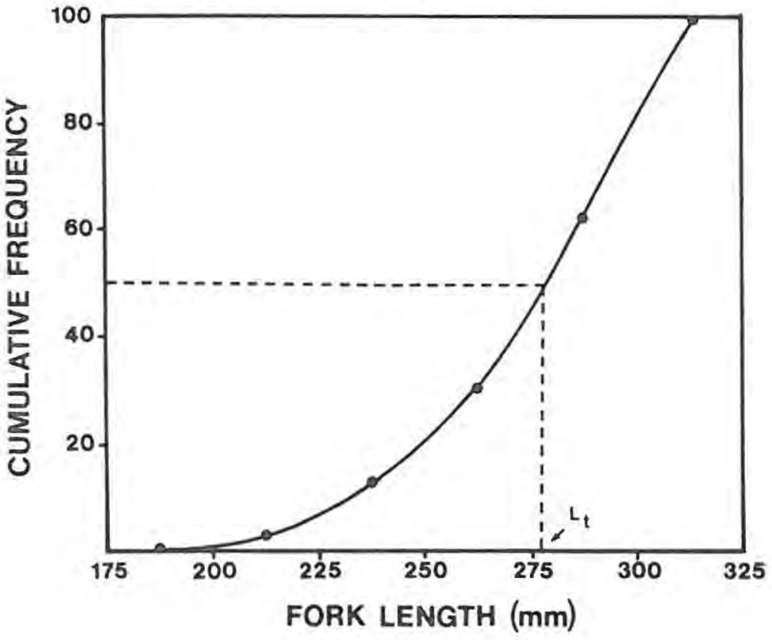
Constant	7.1336279577
Std Err of Y Est	0.1537179175
R Squared	0.970415
No of Observation	11.0
Degrees of Freedom	9.0
X Coefficient	-0.2319671718
Std Err of C	0.0135008488

APPENDIX 2

Method for calculation of t_R, the age at recruitment to the fishery. The example is calculated from the length frequency of Chrysoblephus laticeps sampled in Tsitsikamma (Fig. 18).

Size class	fish measured	% contri-bution	cumulative % frequency
176-200	3	0.5	0.5
201-226	17	3.0	3.5
226-250	54	9.0	12.5
251-275	110	18.5	31.0
276-300	182	31.0	62.0
301-325	225	38.0	100.0
Total	591	100.0	

Plotting cumulative % frequency against length:



From this l_t = 280mm FL and by substitution in the von Bertalanffy equation
t_R = 6.5yrs

APPENDIX 3

Summary of minimum size regulations and bag limits for marine linefish species set in December 1984 (Anon 1984b). Three classes of fishermen are recognised. A - class, fishermen deriving their entire income from linefishing. B - class, fishermen deriving part of their income from linefishing. C - class, recreational fishermen. All measurements are total length.

Minimum size limits

Size limit (cm)	Species (Old size limits in brackets)
15	Strepie - *Sarpa salpa* (10cm FL, Natal Ordinance)
20	Blacktail/Dassie - *Diplodus sargus* (15cm)
	Cape stumpnose - *Rhabdosargus holubi* (20cm)
	White stumpnose - *Rhabdosargus globiceps* (20cm)
22	Hottentot - *Pachymetopon blochii* (22cm)
25	River bream - *Acanthopagrus berda* (-)
	Natal stumpnose - *Rhabdosargus sarba* (20cm)
30	Elf/shad - *Pomatomus saltatrix* (30cm)
	Spotted rock cod - *Epinephelus andersoni* (30cm)
	Yellow-belly rock cod - *Epinephelus guaza* (30cm)
	White-edged rock cod - *Epinephelus albomarginatus* (30cm)
35	Galjoen - *Coracinus capensis* (20cm)
40	Spotted grunter - *Pomadasys commersonni* (30cm)
	White steenbras - *Lithognathus lithognathus* (30cm)
	Kob - *Argyrosomus hololepidotus* (40cm)
	Squaretail kob - *Argyrosomus thorpei* (40cm FL Natal Ord.)
	Geelbek - *Atractoscion aequidens* (40cm)
	Musselcracker - *Sparodon durbanensis* (-)
60	Snoek - *Thyrsites atun* (70cm)
70	Leervis/Garrick - *Lichia amia* (38cm)

Barotrauma/...

Barotrauma species list

A general size limit of 25cm is set for these species which all suffer from barotrauma (overinflated swimbladder) when brought to the surface

Red roman	*Chrysoblephus laticeps* (20cm)
Red stumpnose	*Chrysoblephus gibbiceps* (20cm)
Red steenbras	*Petrus rupestris* (30cm)
Dageraad	*Chrysoblephus cristiceps* (23cm)
Silverfish	*Argyrozona argyrozona* (25cm)
Seventy-four	*Polysteganus undulosus* (25cm)
Slinger	*Chrysoblephus puniceus* (23cm)
Soldier/Santer	*Cheimerius nufar* (23cm)
Scotsman	*Polysteganus praeorbitalis* (20cm)
Poenskop	*Cymatoceps nasutus* (-)

Protected species list

Class B and C fishermen are not permitted to catch more than a total bag of five of the protected species per man per day.

River bream	*Acanthopagrus berda*
Elf/Shad	*Pomatomus saltatrix*
Galjoen	*Coracinus capensis*
Leervis/Garrick	*Lichia amia*
Englishman	*Chrysoblephus anglicus*
Red roman	*Chrysoblephus laticeps*
Red stumpnose	*Chrysoblephus gibbiceps*
Red steenbras	*Petrus rupestris*
Dageraad	*Chrysoblephus cristiceps*
Seventy-four	*Polysteganus undulosus*
Slinger	*Chrysoblephus puniceus*
Soldier/Santer	*Cheimerius nufar*
Scotsman	*Polysteganus praeorbitalis*
Poenskop	*Cymatoceps nasutus*
Spotted rock cod	*Epinephelus andersoni*
White-edge rock cod	*Epinephelus albomarginatus*
Yellow-belly rock cod	*Epinephelus guaza*
Musselcracker	*Sparodon durbanensis*
John Brown	*Gymnocrotaphus curvidens*
Brown hottentot	*Pachymetopon grande*
Cape Knifejaw	*Oplegnathus conwayi*
Natal Knifejaw	*Oplegnathus robinsoni*
Milk fish	*Parascorpis typus*
Cape baardman	*Umbrina canariensis*
Natal baardman	*Umbrina ronchus*