THE DISTRIBUTION PATTERNS AND COMMUNITY STRUCTURE OF THE TSITSIKAMMA ROCKY LITTORAL ICHTHYOFAUNA.

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ABSTRACT

The results of a community survey of the rocky intertidal and subtidal reef ichthyofauna of the Tsitsikamma National Park and adjacent areas are presented. An updated species checklist is given, comprising 116 species of 46 families, including a new genus and species of Tripterygiid. Single species are shown to dominate, in terms of numbers, both the cryptic and subtidal components for all the areas sampled down the vertical profile. Species richness, evenness and diversity are found to increase with depth for both the cryptic and suprabenthic components.
A community level feeding study shows an increase in trophic specialisation with depth and food availability is found to be an important factor delimiting littoral fish vertical distribution. The nursery function of the Tsitsikamma rocky littoral area is assessed and it is shown that shallow littoral areas as a whole are more important than intertidal pools alone in functioning as nurseries. The results of the study are found to fit into the existing trend of an increase in species richness and diversity, from west to east, along the South African coast.
A significant difference is shown between the observed frequencies of species on exploited reefs outside the Park and unexploited reefs inside the Park. The density of the key reef predator *Petrus rupestris* is shown to be nine times more abundant on deep reef inside the park compared to deep reef outside the park (0.0045 fish/m^2 and 0.0005 fish/m^2 respectively) and a paucity of larger individuals of this species on exploited reefs is noted. Marked differences in the relative abundance of other species between exploited and unexploited reefs are evident and it is hypothesised that community disruption has occurred on exploited reefs, either directly or directly because of the removal of *P. rupestris*. These results are discussed in the context of marine reserves as a conservation strategy and a recommendation is made to extend the 5.6km seaward boundary of the Tsitsikamma National Park westwards to include the large concentration of presently exploited rocky reefs between the Blaaukrans river mouth and Natures Valley.

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CHAPTER 1. GENERAL INTRODUCTION.

The World Conservation Strategy outlines living resource conservation as having three objectives - (a) "to maintain essential ecological processes and life-support systems", (b) "to preserve genetic diversity" and (c) "to ensure the sustainable utilisation of species and ecosystems" (IUCN 1980). The sentiments of this document voiced the fundamental shift in conservation thinking that was taking place towards the end of the 1970's and has continued to take place during the last decade. The nature of this change lies in the adoption of an ecosystem approach rather than a single species approach to conservation. The primary tenet of ecology is the fact that all organisms interact - with each other, and with the environment. If we are to conserve ecosystems we must know more about their components, biotic and abiotic and how they interact. Conservationists now widely recognise that if ecosystems are to be maintained then the biodiversity of the ecosystem needs to be conserved first (Carleton Ray 1988). Biotic diversity has been defined as "The variety and variability of all living organisms, ...the diversity of the complexes of associated species and of their interactions ..." (Huntley 1989). Krebs (1985) points out that biodiversity is measured at the community level in ecosystems and it is for this reason that community level ecological studies have become increasingly important.

Marine reserves offer protection to the productive littoral (intertidal zone down to photic subtidal zone) ecosystems of the earths oceans (Randall 1980). The role of ichthyofauna within nearshore marine ecosystems is recognised as being extremely important not only because of their dominant role in the natural functioning of these ecosystems (Krebs 1985) but also because fish have great economic value to man. Because of the relative inaccessibility of the marine littoral realm, ecological studies in this zone are often difficult. Despite this difficulty a growing number of littoral fish studies within the Tsitsikamma National Park (TNP) have been undertaken.

The first ichthyological publication concerning the TNP was JLB and Margaret Smiths' *Fishes of the Tsitsikamma Coastal National Park* (Smith & Smith 1966). This book was not based on work done specifically within the park and is also dated, as many of the fishes names have changed in the interim. Since then several single species studies on fish have been conducted within the parks boundaries. Short notes on sex reversal in the Roman *Chrysoblephus laticeps* (Penrith 1972(a)) and the dageraad *Chrysoblephus cristiceps* (Robinson 1976) have been published. Crawford & Crous (1982) and Crawford (1982) examined hand-line and demersal catches in the southern Cape region as a whole. In the last decade valuable work, based in the TNP, on the biology and ecology of Roman (Buxton 1984, Buxton 1987, Buxton & Smale 1989), dageraad (Buxton 1987, Buxton & Smale 1989) and the red steenbras *Petrus rupestris* (Smale 1986, Smale 1988, Buxton & Allen 1989, Buxton & Smale 1989) has been published.

Buxton & Smale (1984) laid the foundation for ichthyofaunal community level studies within the TNP by publishing the findings of a preliminary investigation of the marine ichthyofauna in the park. This work was added to by Burger (1988) who showed the vertical distribution patterns of the rocky intertidal and cryptic subtidal reef components of the Tsitsikamma littoral zone. This study, however, did not look at the suprabenthic (fish that live in the water column above the reef) component of the reef ichthyofauna, and also had an inadequate data base for between area comparisons. It was in this light that the present study was initiated in 1989 with two principle aims:

1. To document the species diversity, relative abundance and community structure of the littoral ichthyofauna, from intertidal rock-pools down to deeper subtidal reefs within the TNP.
2. To investigate the possible effects of exploitation on unprotected reefs adjacent to the reserve, both in the form of differences in the density of species targeted for by fishermen, as well as community structure differences as a whole.

The role of rocky littoral areas as nursery areas for marine fish has received some attention in the South African literature (Beckley 1985(a), Bennett 1987, Smale and Buxton 1989). The nursery function of the Tsitsikamma intertidal zone is investigated in this study and the role of rocky littoral waters as a whole is discussed in Chapter 3.

Simply elucidating the community structure of an assemblage of fish does little to understand how they interact. In an attempt to further understand the dynamics of the Tsitsikamma littoral ichthyofauna, a community level feeding study was undertaken in Chapter 4. The results of stomach content analyses of the most important species is used, in conjunction with the results of previous feeding studies done along the South African coast, to examine the trophic structure of the littoral ichthyofaunal community.

Chapter 5 examines the results of this study in context with previous littoral ichthyofaunal surveys along the southern African coast to show the zoogeographical trends and affinities that exist for this coast. The evolutionary theory concerning the origins of southern Africa's littoral fish is also briefly discussed.

In the final chapter the factors delimiting the distribution of rocky littoral fish in the Tsitsikamma are discussed. The results of the comparison between exploited and unexploited reefs within the study area is assessed and recommendations aimed at conserving reef ecosystems on the south Cape coast are made.

CHAPTER 2. THE STUDY AREA.

2.1. The Tsitsikamma National Park.

The Tsitsikamma National Park is situated on the south coast of South Africa (Figure 1). The Park extends from Oubosstrand in the east to Nature's valley in the west, a distance of 65.75 km (Hockey & Buxton 1989). The Park was proclaimed in 1964 (Robinson 1989) and the littoral ecosystem afforded protection by it, is believed to have reached a pristine state (Buxton 1987). The park extends 5.6 km out to sea (Hockey & Buxton 1989), except for the section between Bloukrans river mouth and Natures Valley where it extends 0.8 km offshore (Buxton 1987). In January 1988 a further 8 km of coastline was added to the western end of the Park by the annexation of the De Vasselot Nature reserve (Hockey & Buxton 1989). This section, however, only offers protection to the marine ecosystem as far as the spring low water mark.

2.1.1. Sample Areas.

Intertidal collections were done at Steilkop and along the Otter trail, to the west of Stormsriver mouth (as indicated on Figure 1). Two subtidal reef complexes were sampled inside the park - namely Steilkop reef complex (3 km to the east of Stormsriver) and The Knoll (just to the east of Stormsriver). Outside the park a subtidal reef complex approximately 3 km to the west of Natures Valley was sampled. This reef was chosen because of it's similarity in terms of aspect, rugosity and substratum cover to the two reef areas sampled inside the park. The effects of fishing on the ichthyofaunal community structure could be investigated by sampling this reef, as both commercial and recreational boat fishermen, as well as spear-fishermen, are known to fish on these reefs.

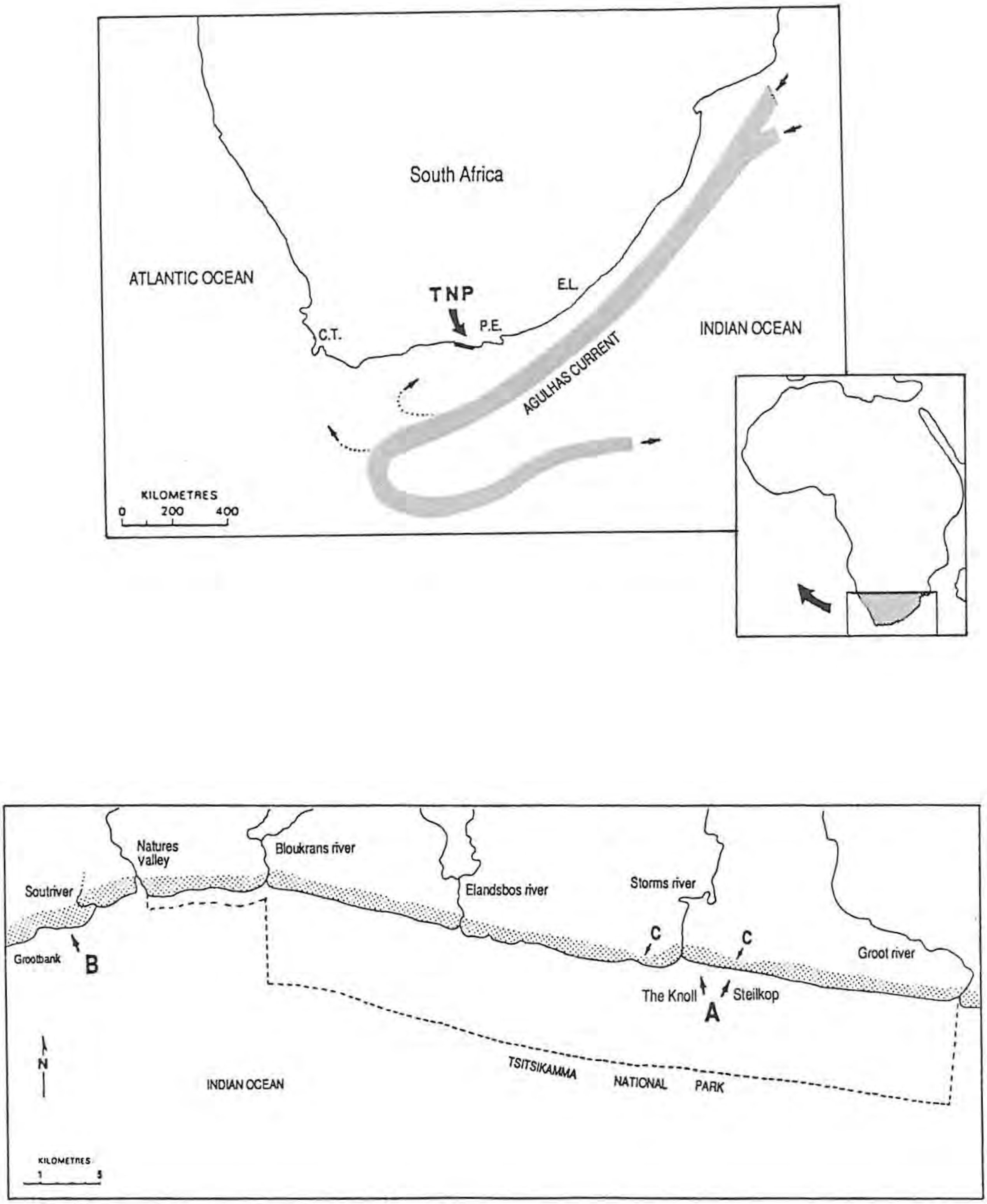


FIGURE 1: The position of the Tsitsikamma National Park on the southern Cape coast (top) and the position of the sample sites both inside and outside the TNP (bottom). A = position of The Knoll (closest to Stormsriver mouth) and Steilkop reef complexes. B = subtidal reef sampled outside the park. C = intertidal areas sampled.

2.2. The geology and benthic zonation of the Tsitsikamma littoral area.

The TNP lies within the Tsitsikamma coastal belt that is composed primarily of sedimentary sandstone formations of the Table Mountain group (Toerien 1976). Along the coast a steep escarpment drops from 180m down to a rocky coastline. Erosion by the sea in this latter area has left an intertidal zone that is narrow and characterised by sharp vertically lying sedimentary sandstone ridges and inter-lying troughs that run parallel to the coast. In places along the coast perpendicular faults have eroded to form subtidal gullies that often extend behind a higher seaward ridge and into the intertidal zone (see Figures 2 and 3).

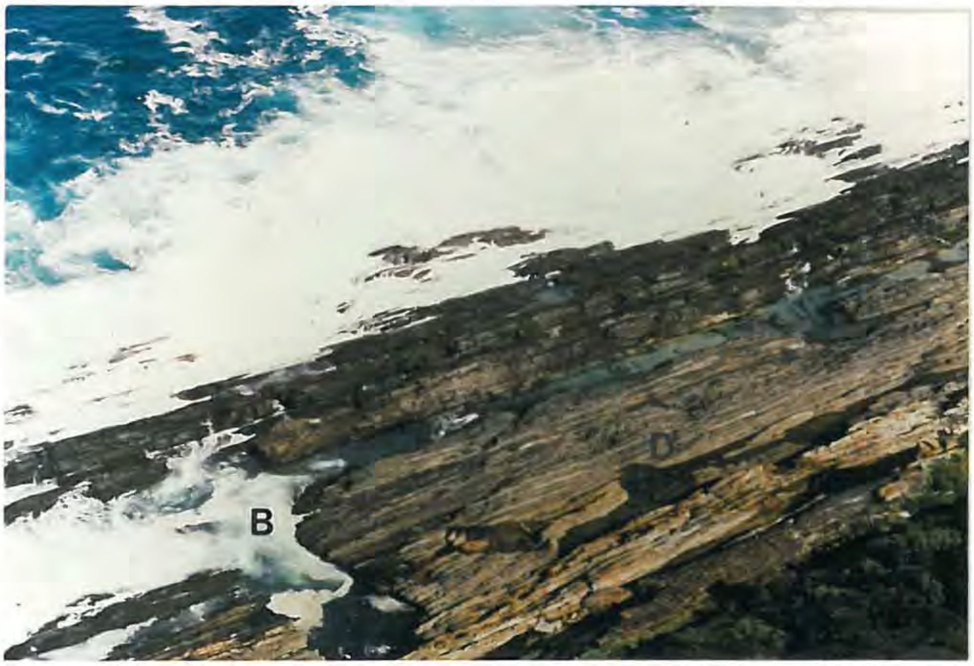


FIGURE 2: A view looking down on the intertidal area at Steilkop, showing the typical position of exposed rock-pools (A), subtidal gullies (B), sheltered rock-pools (C) and upper rock-pools (D) (see text for further explanation).

Subtidally the sedimentary rock strata provide reefs that consist of long-shore ridges with interlying sand and loose-rock filled gullies. Buxton & Smale (1984) recognised three distinct reef types within the Tsitsikamma subtidal zone. The first were reefs found in less than 10m of water and dominated by calcareous algae, particularly *Corallina* spp. and *Amphiroa ephedraea*. The second were reefs found between 10 and 25m depth of water and dominated by filter-feeding invertebrates such as ascidians, poriferans, octocorals and reef-building and encrusting bryozoans. A third reef type was recognised below 25m and was characterised by large stands of *Ecklonia bisperforata*.

Diving during the study period supported the existence of the first two reef types described above but not of the third. It was found that at depths of 25 to 35m, on both the Knoll and Steilkop reef complexes, filter-feeder dominated reef still predominated but that standing stocks of invertebrates were much lower than on shallower reefs. Bryozoans and sponges appeared to dominate these more barren areas. It is suggested that stands of *Ecklonia* are more sparse than previously thought and may in fact be restricted to isolated deeper reefs. In addition it was noted that filter-feeding invertebrates were common and often dominant on the steep, seaward facing slopes of shallow reefs, where light availability was insufficient to support algae growth. Buxton & Smale (1984) recognised the importance of the ascidian *Pyura stolonifera* (redbait) on deeper reefs, where they encrust the reef crests. It must be noted that this animal also dominates shallow reef crests.

Burger (1988) recognised a transition zone between shallow and deep reefs with a mixed substratum cover, with both algal and invertebrate components present. Gradation between ecotypes in nature is well documented (Barnes & Hughes 1982, Krebs 1985, Odum 1971). However I believe the classification of this transition zone as a separate ecotype is unjustified and the nature of this area should rather be regarded as ecotonal (Jones 1990) between the more clearly defined deeper and shallower reef types.

For the purposes of this study, for which comparison between areas was of primary importance, collection of data was restricted to areas that complied with the prerequisites outlined in Table 1.

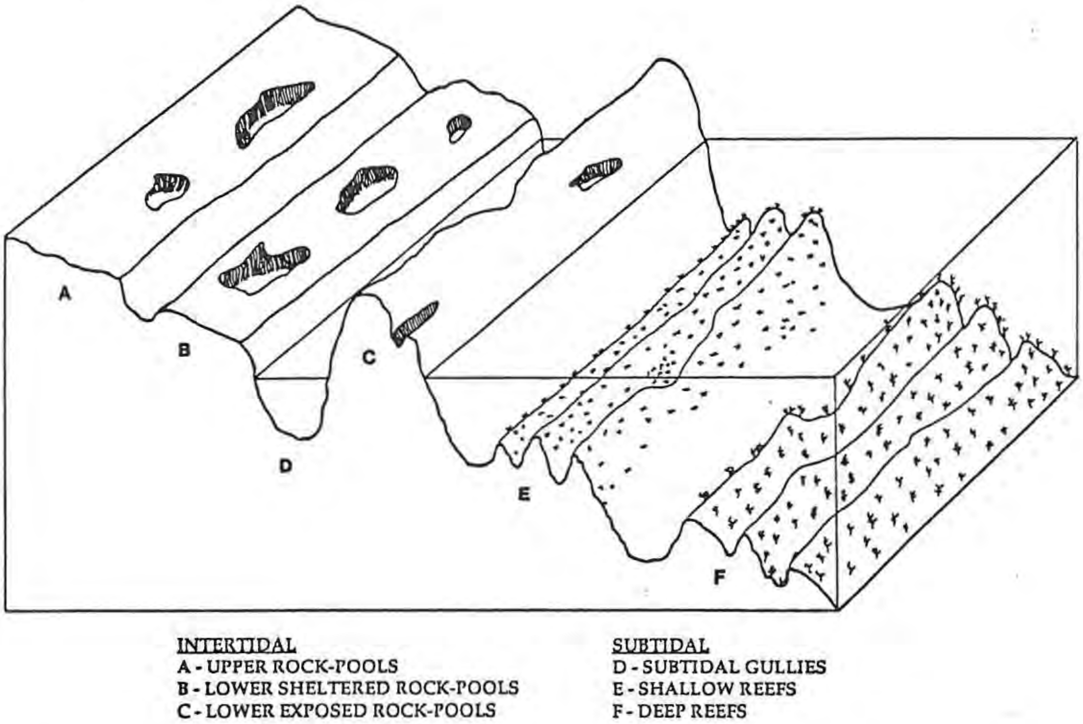


FIGURE 3: The six rocky littoral zones sampled during the study.

TABLE 1: Description of the six rocky littoral zones.

ZONE	DISTINGUISHING FEATURES
A: UPPER INTERTIDAL	Rock-pools located high on the shore. Generally shallow with little or no algae growth. Smooth rock sides with sand and rock bottoms. Completely exposed during all low tides. Wave action virtually non existent. Subjected to temperature and salinity extremes.
B: LOWER INTERTIDAL (SHELTERED)	Rock-pools located low on the shore. Separated from the sea only at spring low tides. Wave action minimal. Temperature and salinity matching that of the sea, with limited warming effects during spring tides. Fringing algae growth (dominant spp. *Sargassum heterophylum* and *Gelidium pristoides*). A range of invertebrates occur without clear dominance by any single group. Pool bottoms covered by sand and/or boulders and pebbles.
C: LOWER INTERTIDAL (EXPOSED)	Rock-pools on the seaward side of ridges. Wave action high to intense even at low tides. Exposed only at spring low tides with calm sea conditions. Substrate cover is similar to sheltered pools although pools are more scoured.
D: SUBTIDAL GULLIES	0 - 10m in depth. Sheltered. Coralline algae dominant substrate cover with some invertebrates including sessile filter-feeding organisms. Sand and rock bottoms.
E: SHALLOW REEFS	Coralline algae dominated reef sampled between 5 and 12m. As described by Buxton & Smale (1984) (see text).
F: DEEP REEFS	Filter-feeding invertebrate dominated reef sampled between 15 and 30m. As described by Buxton & Smale (1984) (see text).

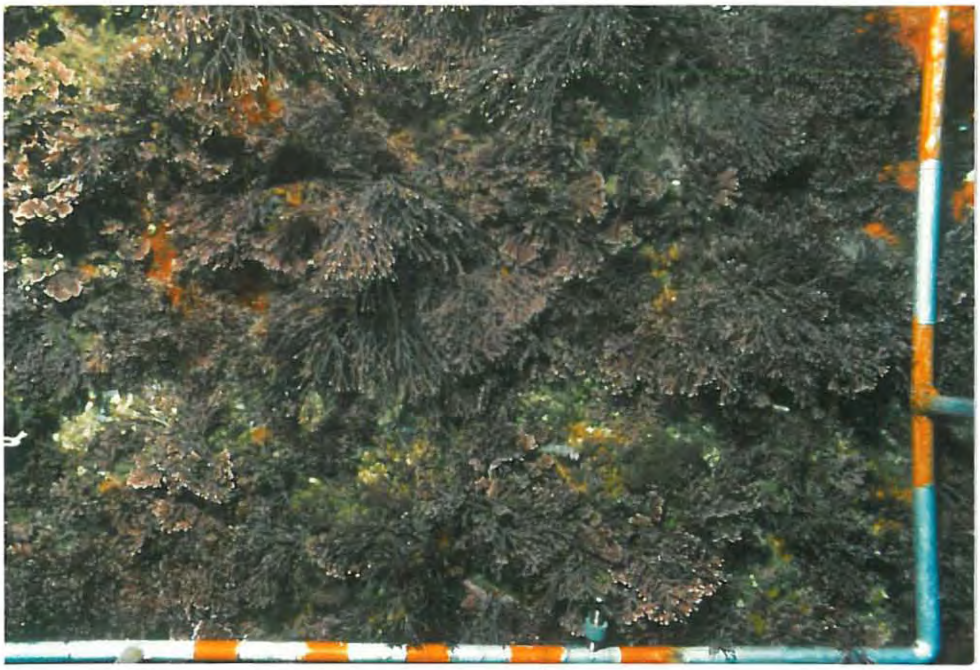


FIGURE 4: A close-up view of shallow reef covered with coralline algae. (Photo: P. Coetzee)

FIGURE 5: Typical deep filter-feeding invertebrate dominated reef. Two suprabenthic species are visible above the reef, Roman *Chrysoblephus laticeps* in the foreground and the Fransmadam *Boopsoidea inornata* in the background. (Photo: C. Buxton)

2.3. The physical properties of the sea in the Tsitsikamma.

The Tsitsikamma coastline is washed by waters that are a mixture of cool Atlantic ocean water and warm Indian ocean water (Harris 1978, Shannon 1970). The Agulhas Current, the major oceanic current along the east and south-east coast of southern Africa, follows the depth contours along the Agulhas Bank and is therefore forced away from the coast in the southern Cape region (Figure 1). This leaves a large area of water between Port Elizabeth and Cape Point without a dominant coastal current as such. Harris (1978) concludes that for the region between Cape St Francis and Cape Agulhas, in which the Tsitsikamma falls, wind induced near-shore currents are more important than oceanic currents. In this regard Hanekom et al. (1989) documented the often sharp seawater temperature declines that occur, following easterly (NE - SE) winds, in the area. This decline in near-shore seawater temperature is attributed to wind induced upwelling of deeper-lying colder water (Schumann et al. 1988). The mean seawater temperature of the region varies seasonally with a winter mean of between 16 - 17° C and a summer mean of between 20 - 21° C. (Schumann & Beekman 1984). The upwellings, which occur predominantly in summer (Hanekom et al. (1989) found that over a 7 year period 81% of the cold-water upwellings occurred between November and April) can result in severe drops in seawater temperature with deleterious effects to littoral fish (Buxton 1988, Hanekom et al. 1989).

Perhaps the most overriding physical attribute, however, of the sea along the Tsitsikamma coastline is its high energy nature. For much of the year large swells, emanating from the roaring forties along the Antarctic convergence, strike the unprotected Tsitsikamma coastline unabated. The littoral profile has a steep aspect which results in severe wave action in the near-shore region. In addition the steep aspect of the coastline results in retroflected water movement that causes strong surge on subtidal reefs.

CHAPTER 3. THE COMMUNITY STRUCTURE OF THE TSITSIKAMMA LITTORAL ICHTHYOFAUNA.

"Living organisms can be understood only
when they are considered as part of the system
within which they function" (Dubos 1981, p. 37).

3.1. Introduction.

A community of organisms comprises a typical species composition that has resulted from the interaction of populations, overseen by physical environmental factors, over time. It is not surprising therefore that Smith (1978) states that "almost any study of community ecology begins with a list of the species present." Whilst a community level ecological study may certainly start with such a list it cannot end there. In order to understand how the community is structured, the relative abundance and size distribution patterns of species need to be studied too. In addition, community level measures of species diversity, species richness and species evenness, concepts that go beyond pure species numbers, are needed to understand the dynamics of any community in order to best conserve it, which ultimately is the aim of any ecological study.

The fact that littoral fish are inextricably linked to their environment means that community structure will vary between areas that have different suites of environmental determinants. Littoral fish zonation can either be horizontal (along-shore) or vertical (down the littoral profile). The first is concerned mainly with coastal distribution patterns and the findings of this study are discussed, in relation to littoral fish distribution patterns along our coast, in the next chapter. Establishing the vertical distribution patterns of the Tsitsikamma rocky littoral ichthyofauna are central to this chapter.

The role of rocky intertidal and shallow subtidal areas as nursery areas for juvenile marine fish has been the subject of some debate in the South African literature (Beckley 1985(a), Bennett 1987, Smale and Buxton 1989). For this reason the nursery function of the Tsitsikamma littoral area is assessed in this chapter. Finally a comparison of subtidal reef fish community structure is made between exploited reefs outside the TNP and comparable reefs inside the TNP.

3.2. Methods.

Various methods have been used by ichthyologists to characterise intertidal and reef fish communities. These can be classed as either destructive (e.g. fishing, spearing, netting, poisoning or dynamiting) or non-destructive (visual censusing). Randall (1963), Russell et al. (1978) and Smith (1973) provide useful review papers on these methods. The overriding consideration for all methods is that they are selective and the method chosen should depend on the aims of the study.

The vast majority of previous studies that have looked at whole communities have used a combination of visual census techniques to characterise the more visible sector of the population and one or more destructive methods to survey the less-visible cryptic sector (e.g. Buxton & Smale 1984, Sale & Dybdahl 1978, Kingsford et al. 1989). Berry et al. (1982) used baited transects in order to census cryptic blennies but this method has inherent biases and is not suitable for whole community surveys.

In this study a combination of rotenone poisoning and visual censuses were chosen to characterise the Tsitsikammma littoral ichthyofauna. Rotenone was used to sample intertidal rock-pools and the cryptic subtidal component, whilst visual censuses were used to sample the suprabenthic subtidal component.

3.2.1. Rotenone Collection.

The use of rotenone as a method of collecting fish for research started in the mid - 1930's (Randall 1963). Since then it has been used extensively in both intertidal (Beckley 1985(a) & (b), Bennett 1987, Gibson 1972) and subtidal areas (Alevizon & Brooks

1975, Burger 1988, Sale & Dybdahl 1978, Smale & Buxton 1988, Yoshiyama 1981).
Rotenone, a biodegradable legume derivative, kills fish by blocking the respiratory sites on their gills (Randall 1963, Russell et al. 1978, Smith 1973). It's effect is virtually restricted to fish although some cephalopods, echinoderms and turbellarians were noticed to be affected, a fact documented by Randall (1963). The action of rotenone is affected by temperature (Randall 1963, Gilderhus et al 1986) becoming less effective at lower temperatures. It was noted during this study that subtidally rotenone had limited effect below 15 ^{0} C.
Whilst rotenone is highly effective in intertidal rock-pools because both the poison and the fish are trapped within the pools, it's use subtidally is hindered by rapid dispersal of the poison and by the escape of fish. For this reason it is ineffective against larger suprabenthic species. A further shortcoming noted during this study was that affected fish were also readily preyed upon by larger fish in the area (see also Randall 1963).

Dry rotenone powder was used in this study and was prepared for use by mixing it with seawater and detergent (which acts as a surfactant) in the ratio 1: 10: 0,25. *Pronoxfish*, a more effective commercially prepared rotenone mixture, was used together with rotenone for deeper collections and when water temperature was around 15° C.

Intertidal rock-pools were sampled at spring low tide by poisoning selected pools with rotenone. The rotenone was mixed into the pools and affected fish were caught with hand-nets. In deeper pools the bottoms were searched by snorkel divers.

Subtidally, mixed rotenone was conveyed down by SCUBA divers onto the reef in plastic squeeze bottles and plastic bags. The mixed rotenone was released close onto the reef in holes and crevices. The rotenone was always mixed with sea water, after trials showed that mixing it with fresh water caused the rotenone "cloud" (formed on release into the water column) to rise off the reef and disperse more easily. Dead fish were collected underwater by divers using hand-nets.

Once caught the fish were kept on ice to preserve their colour for photographic purposes. The fish were pinned out, and fins and rays were painted with 100% formalin to fix them in position for identification and photography. Fish were photographed in a glass cuvette and thereafter fixed in 10% buffered formaldehyde solution. After two weeks the specimens were transferred into 50% propyl alcohol for permanent preservation. The fish were identified using Smith & Heemstra (1986) and measured to the nearest mm (total length). The entire collection was accessioned into the J.L.B. Smith Institute of Ichthyology collection in Grahamstown.

3.2.2. **Visual Censusing.**

Two broad categories of visual census techniques are recognised namely stationary point counts and moving transect counts. Historically, moving transect counts were the first to be used to characterise visible reef fish (Brock 1954). Since then many variations of both stationary and moving transects have been developed.

Stationary point counts can either take the form of counts where fish seen during particular time intervals are recorded (Kimmel 1985, Jones & Thompson 1978) or instantaneous area counts, where a fixed area is censused as fast as possible (Bohnsack & Bannerot 1982, Bohnsack & Bannerot 1986, Schaap & Green 1988, Thresher & Gunn 1986).

Moving transect methods can either take the form of simple line swims, where divers swim along a line of a set length and count each individual sighted (Branden _et al._ in Schaap & Green 1988), fixed width strip transects (see below) or variable distance moving counts (Sanderson & Solonsky 1986, Thresher & Gunn 1986).

Fixed width strip transects have predominated in reef fish surveys in both tropical coral reef studies (Alevizon _et al_ 1985, Bell _et al_ 1985, Brock 1954 , Brock 1982, Colton & Alevizon 1981, Godwin & Kosaki 1989, Galzin & Legendre 1987, Kimmel 1985, Russ & Alcala 1989, Sale & Douglas 1981) and temperate rocky reef studies (Bell 1983, Buxton & Smale 1989, Kingsford _et al_ 1989, Leum & Choat 1980, Russell 1977, Stephens & Zerba 1981, Stephens et al 1984).

Combinations of instantaneous counts and strip transects have been used by some workers. Schaap & Green (1988) used a combination of fixed width strip transects and instantaneous point counts to characterise the reef fish community structure on reefs off the coast of Tasmania, Australia. They found the first method ideal for assessing the populations of the more cryptic species whilst the point counts gave better results when assessing more visible and motile species.

As no precedent for whole community reef fish censuses existed for South African temperate waters some time was spent in formulating a suitable censusing technique. Variations of both point and strip transecting techniques were tested. Instantaneous stationary point counts were rejected because they did not allow divers time to record all species present, especially the more cryptic individuals, let alone estimate lengths of all individuals seen. If longer times were used it was found that common species such as *Boopsoidea inornata* and *Pachymetopon aeneum* would aggregate around divers and such species would therefore be over-estimated. Buxton & Smale (1989) did use stationary point counts to effectively estimate densities of three *Chrysoblephus* species in the southern Cape. However the overriding aim of the present study was to characterise whole communities.

Using conventional fixed width strip transecting techniques, as first used in the TNP by Buxton & Smale (1989), it was found that divers had insufficient time to record all individuals of all species as well as record their lengths. Secondly it was realised that for the censusing of more cryptic species a narrower strip was needed.

The logical progression was to divide the population into sectors and census each sector separately for any one count. This has been done by previous workers. Berry et al. (1982) used separate swims to count the abundant species *Pomadasys olivaceum* on a shallow tropical rocky reef off Durban in Natal. Similarly Smith (1989) found that multi-species reef fish censuses were improved by counting different groups of species using different procedures. He placed fish into one of the following three groups; cryptic species, schooling fish and fishes encountered singly or in small groups, in order to survey a temperate reef fish assemblage near Sydney, Australia.

The visual census method used in the study.

The required depth was determined using sonar equipment aboard the dive boat. A shot line was then dropped onto the reef. Two divers descended to the reef and positioned the weighted end of a shot line on reef matching the required depth and habitat type (as outlined in Table 1). One diver then swam out 100m of line marked at 10m intervals as a means of reference. The two divers swam independent 50m transects on either end of the line to minimise the effect of diver interference with fish. A complete transect comprised three 50m swims recording the different components of the suprabenthic community as outlined in Table 2.

TABLE 2: The three species groups recorded independently for each complete transect.

GROUP	CRITERIA	SPECIES
1. ABUNDANT SPECIES.	Species attracted to SCUBA divers and/or species occurring in great numbers or in shoals.	*P. aeneum* (blue hottentot). *B. inornata* (fransmadam). *S. salpa* (strepie). *S. emarginatum* (steenjie).
2. GENERAL SPECIES.	Species that occur in small numbers on the reef. Includes all Chondrichthyes seen.	All suprabenthic species not mentioned in group 1 or 3.
3. SEMI-CRYPTIC SPECIES.	Serranids and Cheilodactylids which live close on the reef but are visible by divers.	*C. brachydactylus* (twotone fingerfin). *C. fasciatus* (redfingers). *C. pixi* (barred fingerfin). *A. sebastoides* (koester).

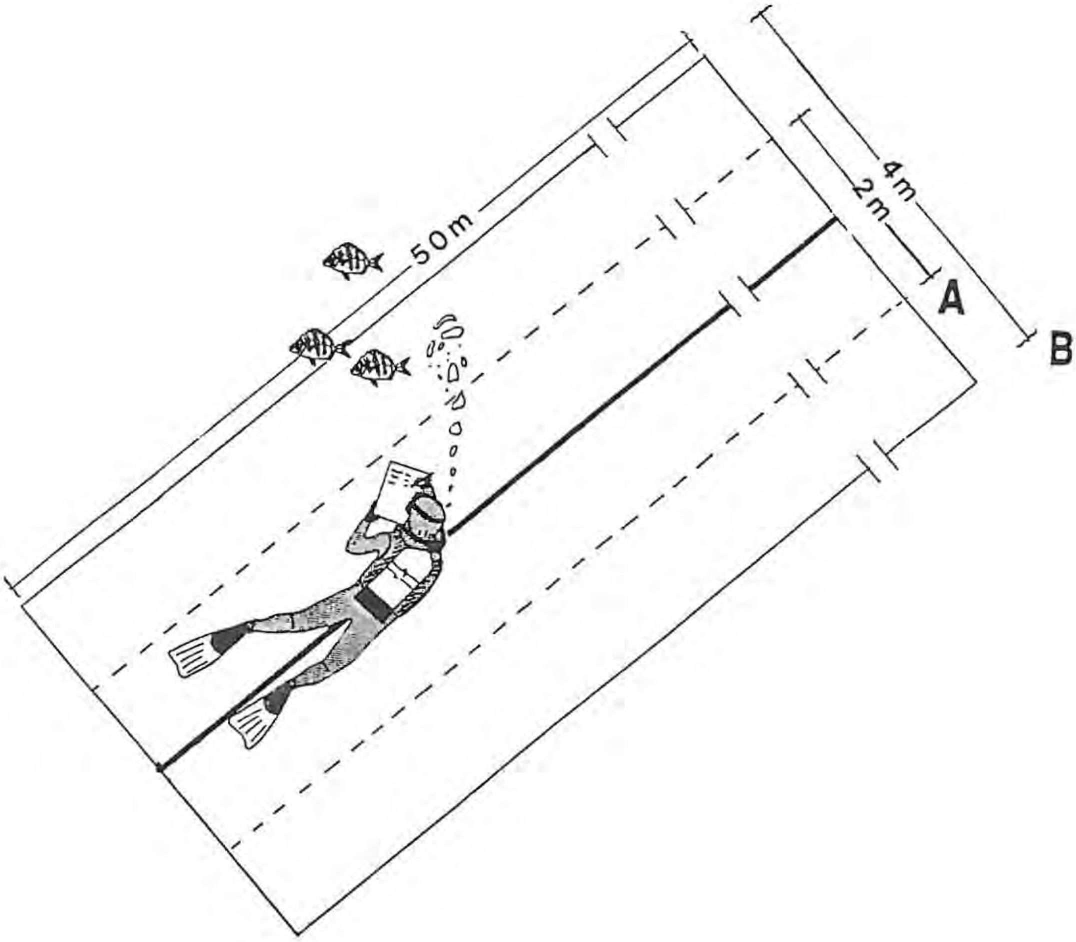


FIGURE 6: Illustration of the visual census method used during the study. A = Transect used for semi-cryptic species. B = Transect used for general and abundant groups of species.

Fish were only recorded when encountered whilst counting their group. The total lengths of individuals of species encountered in the transect were estimated and placed in 50mm size classes. The perspex slates used during the counts had size classes marked on the sides for quick reference underwater.

Fish were counted within 2m on either side of the line for groups 1 and 2, whilst a narrower (1m on either side of the line) transect width was used for the less visible semi-cryptic fish (group 3)(see Figure 6). These widths were visualised using the fact that the length of an outstretched adult arm is approximately 1m. Divers swam 1 to 2m above the line at a steady, comfortable pace. Two to three transects were done by each diver and the line was then moved if diving time at that depth allowed.

3.3. Data analysis.

(a) Replication.

Hurlbert (1984) warns against the practice of pseudoreplication in ecological field experiments. One of the sources of pseudoreplication is the use of replicates that are not statistically independent. Subtidal sampling introduces a number of variables which can affect the significance of the sample. These include variations in temperature, visibility, water movement, reef type, reef topography and collector effectiveness. In order to avoid pseudoreplication and to ensure that samples were truly representative of a particular reef type, samples were taken from similar subtidal zones on two different reef complexes within the TNP. The corresponding sets of data were then tested statistically to see if there was any significant difference between the two.

(b) Species diversity indices.

Species diversity, or species heterogeneity, is a characteristic unique to the community level of biological organisation (Krebs 1985), measuring the community structure of a population (Chou 1982). Species diversity measures are for this reason central to any community study.

Diversity indices go beyond straight forward species counts, referred to by some as taxonomic diversity (Smith 1978), by incorporating the number of species present as well as the total number of all individuals present in any community, and in certain indices the number of individuals of each species present as well.

In order to allow between - area comparisons to be made three commonly used community diversity indices were calculated for each area sampled.

For all three indices: N = Total number of individuals.

n_i = Total number of individuals of each species.

S = Total number of species.

1. The Margalef species richness index: $d = (S - 1)/\ln N$.
(after Pielou 1966, Peet 1974, Chou 1982)

Species richness, as measured by the Margelef index, is taken to be a measure of diversity without considering the relative proportion of each species (Krebs 1985).

2. The Shannon-Weaver index: $H = -\sum(n_i/N)\ln(n_i/N)$
(after Pielou 1966, Peet 1974, Chou 1982, Krebs 1985).

The Shannon - Weaver index, often referred to as the Shannon - Weaver overall index (e.g. Beckley 1985(a)), has the attribute of being influenced by both the number of species present and how evenly or unevenly the individuals are distributed among the constituent species (Chou 1882, Krebs 1985). This information function is sample size independent and thus samples of different sizes can be directly compared (Pielou 1966, Chou 1982).

3. The Pielou evenness index: $e = H/\ln S$
(after Pielou 1966, Chou 1982).

This index gives a measure of how evenly the individuals in a community are distributed among the constituent species.

3.4. Results

Four divers totally conversant with the suprabenthic ichthyofauna in the area conducted the visual censuses whilst a total of 22 divers helped with subtidal rotenone collections. An estimated total of 303 diver hours were spent sampling underwater to a maximum depth of 30m. Sampling on reef deeper than this was not attempted because of restricted no-decompression bottom time using standard SCUBA apparatus.

31 rock-pools were sampled within the TNP yielding 29 species of 12 families. Subtidally 58 rotenone samples and 230 visual censuses were completed on reef inside and outside the TNP. A total of 109 species of 45 families were found in this area.

3.4.1. Species checklist for the TNP.

A total of 116 species of 46 families were recorded for the Tsitsikamma littoral zone waters. This figure includes species caught by hook-and-line within the TNP, both from the shore and off the NPB ski-boat *Aonyx*, as well as species observed underwater but off the study areas.

Table 3 provides a species checklist of the fish positively recorded in the Tsitsikamma littoral zone. The work of Smith & Smith (1966) was not considered in this analysis as their list of species were not based on fish specifically sampled within the Tsitsikamma area. However, species recorded by Buxton & Smale (1984), but not in this study, were included.

TABLE 3: Fishes of the Tsitsikamma littoral zone.

I = Intertidal
S = Subtidal reef
P = Pelagic
* = Endemic to southern Africa (Namibia to Northern Natal)
\+ = Recorded only by Buxton & Smale (1984).

FAMILY/SPECIES	COMMON NAME	DISTRIBUTION	
CARCHARHINIDAE			
Carcharhinus brachyurus	copper shark	S	
Galeorhinus galeus	soupfin shark	S	
Mustelus	smooth-hound	S	
Triakis megalopterus	spotted gullyshark	S	*
SCYLIORHINIDAE			
Haploblepharus edwardsii	puffadder shyshark	S	*
Haploblepharus fuscus	brown shyshark	S	*
Haploblepharus pictus	dark shyshark	S	*
Poroderma africanum	striped catshark	S	*
Poroderma pantherinum	leopard catshark	S	*
SPHYRNIDAE			
Sphyrna sp.	hammerhead	P	
LAMNIDAE			
Carcharodon carcharias	great white shark	P	
ODONTASPIDIDAE			
Eugomphodus taurus	spotted ragged-tooth	S	
TORPEDINIDAE			
Torpedo fuscomaculata	blackspotted electric ray	S	
RHINOBATIDAE			
Rhinobatos annulatus	lesser guitarfish	S	*
MYLIOBATIDAE			
Myliobatis aquila	eagleray	S	*
DASYATIDAE			
Gymnura natalensis	backwater butterflyray	S	

FAMILY/SPECIES	COMMON NAME	DISTRIBUTION
CONGRIDAE		
Conger wilsoni	Cape conger	I,S
ARIIDAE		
Galeichthys ater	black seacatfish	I,S*
Galeichthys feliceps	white seacatfish	S *
GADIDAE		
Gaidropsarus capensis	Cape rockling	S *
BYTHITIDAE		
Bidenichthys capensis	freetail brotula	S *
Dermatopsoides talboti	lesser orange brotula	S *
Grammonoides opisthodon	bighead brotula	S
BATRACHOIDIDAE		
Batrichthys apiatus	snakehead toadfish	S *
Chatrabus hendersoni	chocolate toadfish	S *
GOBIESOCIDAE		
Apletodon pellegrini	chubby clingfish	I,S
Chorisochismus dentex	rocksucker	I,S*
BERYCIDAE		
Centroberyx spinosus	short alfonsino	S
SYGNATHIDAE		
Syngnathus acus	longsnout pipefish	S *
TETRAROGIDAE		
Coccotropsis gymnoderma	smoothskin scorpionfish	S *
CONGIOPODIDAE		
Congiopodus spinifer	spinenose horsefish	S *
TRIGLIDAE		
Chelidonichthys kumu	bluefin gurnard	S *
KUHLIIDAE		
Kuhlia mugil	barred flagtail	I,S
SERRANIDAE		
Acanthistius sebastoides	koester	S *
Epinephilus guaza	yellowbelly rockcod	I,S
Serranus cabrilla	comber	S
SCOMBROPIDAE		
Scombrops boops	gnomefish	S *
POMATOMIDAE		
Pomatomus saltatrix	elf	S,P*
HAEMULIDAE		
Pomadasys commersonnii	+ striped grunter	S
Pomadasys olivaceum	piggy	S
Pomadasys striatum	+ striped grunter	S
SPARIDAE		
Argyrozona	carpenter	S *
Boopsoidea inornata	fransmadam	S *
Cheimerius nufar	santer	S
Chrysoblephus cristiceps	dageraad	S *
Chrysoblephus gibbiceps	red stumpnose	S *
Chrysoblephus laticeps	Roman	S *
Cymatoceps nasutus	black musselcracker	S *
Diplodus cervinus hottentotus	Zebra	I,S
Diplodus sargus capensis	blacktail	I,S
Gymnocrotaphus curvidens	janbruin	S *
Lithognathus	white steenbras	S *
Lithognathus mormyrus	sand steenbras	S
Pachymetopon aeneum	blue hottentot	S *
Pachymetopon grande	bronze bream	S

FAMILY/SPECIES	COMMON NAME	DISTRIBUTION
Pagellus bellottii natalensis +	red tjor-tjor	S
Petrus rupestris	red steenbras	S *
Porcostoma dentata +	dane	S
Pterogymnus laniarius +	panga	S
Rhabdosargus globiceps	white stumpnose	S *
Rhabdosargus holubi	Cape stumpnose	I,S*
Sarpa salpa	strepie	I,S
Sparodon durbanensis	white musselcracker	I,S*
Spondyliosoma emarginatum	steentjie	S *
CENTRACANTHIDAE		
Spicara axillaris	windtoy	S *
CORACINIDAE		
Coracinus capensis	galjoen	S *
PARASCORPIDIDAE		
Parascorpis typus	jutjaw	S *
SCORPIDIDAE		
Neoscorpis lithophilus	stonebream	S *
MONODACTYLIDAE		
Monodactylus falciformes	Cape moony	S
MULLIDAE		
Paupeneus rubescens +	blacksaddle goatfish	S
SCIAENIDAE		
Argyrosomus hololepidotus	kob	S
Atractoscion aequidens +	geelbek	S,P
Umbrina canariensis	baardman	S
CHAETODONTIDAE		
Chaetodon marleyi	doublesash butterflyfish	S *
OPLEGNATHIDAE		
Oplegnathus conwayi	Cape knifejaw	S *
CARANGIDAE		
Lichia amia	garrick	S,P
Seriola lalandi	giant yellowtail	S,P
Trachurus	maasbanker	S,P*
CHEILODACTYLIDAE		
Cheilodactylus fasciatus	redfingers	I,S*
Cheilodactylus pixi	barred fingerfin	S *
Chirodactylus brachydactylus	twotone fingerfin	I,S*
Chirodactylus grandis	bank steenbras	S *
MUGILIDAE		
Liza richardsonii	southern mullet	I,S*
CONGROGADIDAE		
Halidesmus scapularis	snakelet	I,S*
BLENNIIDAE		
Chaloroderma ocellata	two-eyed blenny	I,S
Parablennius cornutus	horned blenny	I,S*
Parablennius pilicornis	ringneck blenny	I,S
Plagiotremus tapeinosoma	piano blenny	S
TRIPTERYGIIDAE		
Tripterygiidae gen. nov.	(new genus & species)	S *
Cremnochorites capensis	Cape triplefin	S *
CLINIDAE		
Blennioclinus brachycephalus	lace klipfish	I *
Blennioclinus stella	silverbubble klipfish	S *
Blennophis striatus	striped klipfish	S *
Cirrhibarbis capensis	barbelled klipfish	I,S*
Climacoporus navalis	fleet klipfish	I,S*

FAMILY/SPECIES	COMMON NAME	DISTRIBUTION
Clinus acuminatus	sad klipfish	S
Clinus agilis	agile klipfish	I *
Clinus berrisfordi	Onrust klipfish	S *
Clinus cottoides	bluntnose klipfish	I,S*
Clinus nematopterus	chinese klipfish	S *
Clinus robustus	robust klipfish	S *
Clinus superciliosus	super klipfish	I,S*
Clinus taurus	bull klipfish	S *
Clinus venustris	speckled klipfish	S *
Pavoclinus graminis	grass klipfish	I,S*
Pavoclinus pavo	peacock klipfish	I,S*
Pavoclinus profundus	deepwater klipfish	S *
Xenopoclinus kochi	platanna klipfish	S
Xenopoclinus leprosus	leprous platanna-klipfish	S
GOBIIDAE		
Caffrogobius agulhensis	Agulhas goby	S *
Caffrogobius caffer	banded goby	I,S*
Caffrogobius saldanha	commafin goby	S *
ZANCLIDAE		
Zanclus canescens	Moorish idol	S
SOLEIDAE		
Solea fulvomarginata	lemon sole	S *
TETRAODONTIDAE		
Amblyrhynchotes honckenii	evileye blaasop	S
MOLIDAE		
Mola mola	ocean sunfish	P

The majority of sharks recorded for the area were sampled using hook and line during tagging exercises or on chance observations (e.g. one positive sighting of a great white *Carcharodon carcharias* was made close inshore in the Steilkop area).

The cryptic longsnout pipefish *Sygnathus acus* was not recorded in rotenone collections but was observed in shallow water in the Stormsriver mouth area. Tropical vagrants *Plagiotremus tapeinosoma* (piano blenny) and *Zanclus canescens* (Moorish idol) were observed in this area as well. A single sighting of an ocean sunfish *Mola mola* was made offshore in 1988.

3.4.2. Statistical analysis of subtidal data collected within the TNP.

Rotenone sample data as well as visual census data for the two subtidal areas (The Knoll and Steilkop reef complexes) were tested statistically to see if there was any significant difference between the two sets of data. The frequencies of individuals of species sampled in each area was used to perform a standard Chi-square test and Table 4 summarises the results of this test.

TABLE 4: Summary of the Chi-square statistics for both rotenone and visual census samples for the two reef zones on The Knoll and Steilkop reef complexes.

ZONE/COLLECTION METHOD	X^2	D.F.	SIG. LEVEL
SHALLOW REEF - ROTENONE	15.9741	14	0.314961
SHALLOW REEF - VISUAL	24.2358	20	0.232243
DEEP REEF - ROTENONE	10.5340	14	0.722193
DEEP REEF - VISUAL	18.7202	19	0.474916

No significant differences were found between the two areas sampled for both rotenone collections and visual censuses ($p > 0.05$). As a result corresponding data sets were pooled for comparative analysis with exploited reef samples.

3.4.3. Distribution, relative abundance and community structure within the TNP littoral zone.

To facilitate comparisons down the profile, intertidal rotenone collections were split into cryptic and suprabenthic species and the results analysed separately. Tables 5 - 16 summarise the results of rotenone sampling and visual census counts for the six areas down the TNP littoral profile. For each Table the species collected are listed together with their respective families in taxonomic order. For intertidal and cryptic subtidal fish the number of fish sampled (n), the % contribution to the overall catch for that area (%N), the total length (TL) range and mean of each species as well as the population standard deviation (S.D.) are shown. For subtidal suprabenthic fish, sampled using visual transects, length ranges and means are not given as fish were placed in 50mm size classes. The average density and the population coefficient of variance (C.V.) pertaining to the density estimates is given for the suprabenthic component.

TABLE 5: Cryptic fish sampled with rotenone in upper intertidal rock-pools within the TNP between 1988 and 1990 (number of pools sampled = 9).

FAMILY/SPECIES	n	%N	T.L. (mm)		
			RANGE	MEAN	S.D.
GOBIESOCIDAE					
Chorisochismus dentex	26	4.8	63 - 184	103	29.5
CLINIDAE					
Cirrhibarbis capensis	4	0.7	67 - 106	92	18.2
Clinus cottoides	51	9.4	21 - 97	60.6	24.8
Clinus nematopterus	3	0.6	85 - 98	91	6.6
Clinus superciliosus	73	13.4	24 - 166	92.6	19.3
GOBIIDAE					
Caffrogobius caffer	386	71.1	30 - 150	79.7	26
	N = 543				

TABLE 6: Suprabenthic fish sampled with rotenone in upper intertidal rock-pools within the TNP between 1988 and 1990 (number of pools sampled = 9).

FAMILY/SPECIES	n	%N	T.L. (mm)		
			RANGE	MEAN	S.D.
SPARIDAE					
Diplodus sargus	3	3.8	49 - 65	56.3	8.1
Sparodon durbanensis	77	96.2	21 - 125	48.4	13.6
	N = 80				

TABLE 7: Cryptic fish sampled with rotenone in sheltered intertidal rock-pools within the TNP between 1988 and 1990 (number of pools sampled = 10).

FAMILY/SPECIES	n	%N	T.L. (mm)		
			RANGE	MEAN	S.D.
CONGRIDAE					
Conger wilsoni	1	0.1	505	505	---
ARIIDAE					
Galeichthys ater	3	0.4	68 - 92	81	12.1
GOBIESOCIDAE					
Chorisochismus dentex	20	2.4	75 - 95	85.7	8.5
Apletodon pellegrini	1	0.1	26	26	---
CONGROGADIDAE					
Halidesmus scapularis	5	0.6	50 - 125	55.6	53
BLENNIIDAE					
Parablennius pilicornis	1	0.1	34	34	---
CLINIDAE					
Cirrhibarbis capensis	11	1.4	20 - 110	42.5	33
Climacoporus navalis	1	0.1	30	30	---
Clinus cottoides	327	39.8	25 - 104	58.6	24.4
Clinus superciliosus	139	16.9	70 - 160	97.5	22.6
Pavoclinus graminis	4	0.5	49 - 70	48.5	14.8
Pavoclinus pavo	1	0.1	35	35	---
GOBIIDAE					
Caffrogobius caffer	308	37.5	30 - 150	73.9	28.3
	N = 822				

TABLE 8: Suprabenthic species sampled with rotenone in sheltered intertidal rock-pools within the TNP between 1988 and 1990 (number of pools sampled = 10).

FAMILY/SPECIES	n	%N	T.L. (mm)		
			RANGE	MEAN	S.D.
KUHLIIDAE					
Kuhlia mugil	1	0.3	32	32	---
SERRANIDAE					
Epinephilus guaza	1	0.3	140	140	---
HAEMULIDAE					
Pomodasys olivaceum	4	1	89 - 102	96.8	5.7
SPARIDAE					
Diplodus cervinus	3	0.8	45 - 192	103	78.2
Diplodus sargus	65	16.9	23 - 89	51.7	11.8
Lithognathus mormyrus	2	0.5	85 - 110	97.5	17.7
Rhabdosargus holubi	2	0.5	76 - 86	81	7.1
Rhabdosargus globiceps	2	0.5	75 - 80	77.5	3.5
Sarpa salpa	24	6.2	66 - 104	85.3	11.6
Sparodon durbanensis	220	57.1	18 - 155	60.5	19.2
MONODACTYLIDAE					
Monodactylus falciformes	10	2.6	47 - 79	60	9.2
CHEILODACTYLIDAE					
Chirodactylus brachydactylus	16	4.2	100 -252	134	46.1
MUGILIDAE					
Liza richardsoni	35	9.1	70 - 164	94.9	20.7
	N = 385				

TABLE 9: Cryptic fish sampled with rotenone in exposed lower intertidal rock-pools within the TNP between 1988 and 1990 (number of pools sampled = 10).

FAMILY/SPECIES	n	%N	T.L. (mm)		
			RANGE	MEAN	S.D.
GOBIESOCIDAE					
Chorisochismus dentex	74	15.3	17 - 203	67.8	43.5
BLENNIIDAE					
Parablennius cornutus	1	0.2	79	79	---
CLINIDAE					
Blennioclinus brachycephalus	5	1.1	56 - 110	89.8	22.7
Cirrhibarbis capensis	41	8.5	43 - 142	96.5	23.8
Climacoporus navalis	2	0.4	35 - 43	39	5.7
Clinus agilis	6	1.2	94 - 105	99.5	4.8
Clinus cottoides	282	58.4	30 - 135	68.6	25.5
Clinus superciliosus	63	13	71 - 220	123.7	38.9
Pavoclinus graminis	1	0.2	39	39	---
Pavoclinus pavo	8	1.7	60 - 94	79.4	10.1
	N = 483				

TABLE 10: Suprabenthic species sampled with rotenone in exposed lower intertidal rock-pools within the TNP between 1988 and 1990. Number of pools sampled = 10.

FAMILY/SPECIES	n	%N	T.L. (mm)		
			RANGE	MEAN	S.D.
SPARIDAE					
Sparodon durbanensis	2	28.6	130 - 153	141.5	11.5
CHEILODACTYLIDAE					
Cheilodactylus fasciatus	3	42.9	126 - 148	138.7	9.3
Chirodactylus brachydactylus	2	28.5	200 - 203	201.5	1.5
	N = 7				

TABLE 11: Cryptic fish sampled with rotenone in subtidal gullies within the TNP between 1988 and 1990 (number of samples = 4).

FAMILY/SPECIES	n	%N	T.L. (mm)		
			RANGE	MEAN	S.D.
CONGRIDAE					
Conger wilsoni	16	6.8	76 - 776	532.7	3.5
GOBIESOCIDAE					
Apletodon pellegrini	8	3.4	22 - 33	27.6	1.4
TETRAROGIDAE					
Coccotropsis gymnoderma	4	1.7	21 - 26	23.5	90.5
TRIGLIDAE					
Chelidonichthys kumu	1	0.4	85	85	---
CONGROGADIDAE					
Halidesmus scapularis	3	1.3	113 - 126	121	0.9
BLENNIIDAE					
Chalaroderma ocellata	21	8.9	32 - 108	74.4	28.9
Parablennius cornutus	7	3	42 - 105	78.9	25.2
TRIPTERYGIIDAE					
Cremnochorites capensis	14	6	35 - 75	56.4	23.6
CLINIDAE					
Blennioclinus stella	2	0.8	33 - 38	35.5	8.1
Blennophis striatus	1	0.4	83	83	24.9
Cirrhibarbis capensis	1	0.4	120	120	35.6
Climacoporus navalis	19	8	35 - 75	50.5	7.1
Clinus cottoides	91	38.6	23 - 113	53.7	19.8
Clinus robustus	2	0.8	28 - 30	29	---
Clinus superciliosus	12	5.1	52 - 160	97.1	---
Clinus taurus	1	0.4	82	82	2.1
Pavoclinus pavo	18	7.6	31 - 61	53	16.3
GOBIIDAE					
Caffrogobius caffer	8	3.4	49 - 156	79	6.8
Caffrogobius saldanha	7	3	106 - 118	111.6	38.5
	N = 236				

TABLE 12: Suprabenthic fish sampled using line transect visual censuses in subtidal gullies within the TNP between 1988 and 1990 (number of transects = 52).

FAMILY/SPECIES	n	%N	DENSITY (m/2)	C.V.
SCYLIORHINIDAE				
Poroderma africanum	2	0.06	0.0003	4
Poroderma pantherinum	1	0.03	0.00015	5.6
RHINOBATIDAE				
Rhinobatis annulatus	1	0.03	0.00015	5.6
SERRANIDAE				
Acanthistius sebastoides	1	0.03	0.00015	5.6
Epinephilus guaza	1	0.03	0.00015	5.6
POMATOMIDAE				
Pomatomus saltatrix	13	0.48	0.004	5.7
HAEMULIDAE				
Pomadasys olivaceum	1	0.03	0.00015	5.6
SPARIDAE				
Boopsoidea inornata	403	13.8	0.06	1.07
Cheimerius nufar	1	0.03	0.00015	5.6
Chrysoblephus laticeps	22	0.8	0.003	1.9
Diplodus cervinus	53	1.8	0.008	1.9
Diplodus sargus	376	13	0.056	1.6
Gymnocrotaphus curvidens	30	1	0.005	1.2
Lithognathus mormyrus	6	0.2	0.0009	2.9
Pachymetopon aeneum	25	0.9	0.004	2.1
Pachymetopon grande	22	0.8	0.003	1.9
Petrus rupestris	1	0.03	0.00015	5.6
Rhabdosargus holubi	61	2.1	0.009	2.3
Rhabdosargus globiceps	1	0.03	0.00015	5.6
Sarpa salpa	1318	45.4	0.2	0.9
Sparodon durbanensis	91	3	0.014	1.6
Spondyliosoma emarginatum	9	0.3	0.0014	2.3
CORACINIDAE				
Coracinus capensis	45	1.6	0.007	2.4
MONODACTYLIDAE				
Monodactylus falciformes	1	0.03	0.00015	5.6
CHAETODONTIDAE				
Chaetodon marleyi	1	0.03	0.00015	5.6
OPLEGNATHIDAE				
Oplegnathus conwayi	25	0.9	0.004	0.8
CHEILODACTYLIDAE				
Cheilodactylus fasciatus	27	0.9	0.008	1.6
Chirodactylus brachydactylus	255	8.8	0.08	0.5
MUGILIDAE				
Liza richardsonii	109	3.8	0.02	3.4
TETRAODONTIDAE				
Amblyrhynchotes honckenii	2	0.06	0.0003	4
	N = 2902			

TABLE 13: Cryptic fish sampled with rotenone on coralline algae dominated shallow reefs within the TNP between 1988 and 1990 (number of samples = 8).

FAMILY/SPECIES	n	%N	T.L. (mm)		
			RANGE	MEAN	S.D.
CONGRIDAE					
Conger wilsoni	2	0.3	105 - 145	125	28.3
ARIIDAE					
Galeichthys ater	4	0.6	110 - 330	233	91.5
GADIDAE					
Gaidropsarus capensis	2	0.3	61 - 161	111	70.7
BYTHITIDAE					
Bidenichthys capensis	19	2.8	32 - 76	60	13.4
Dermatopsoides talboti	2	0.3	35 - 57	46	15.6
BATRACHOIDIDAE					
Batrichthys apiatus	1	0.1	38	38	---
GOBIESOCIDAE					
Apletodon pellegrini	18	2.6	16 - 27	21.4	3.1
TETRAROGIDAE					
Coccotropsis gymnoderma	40	5.9	9 - 45	31.2	8.9
CONGROGADIDAE					
Halidesmus scapularis	32	4.7	38 - 123	73.6	26.8
BLENNIIDAE					
Parablennius cornutus	1	0.1	50	50	---
Parablennius pilicornis	15	2.2	30 - 74	50.3	14.8
Chalaroderma ocellata	8	1.2	68 - 85	73	6.2
TRIPTERYGIIDAE					
Cremnochorites capensis	217	32.1	17 - 79	48.8	15.3
CLINIDAE					
Blennioclinus stella	19	2.8	30 - 46	35	4.2
Blennophis striatus	4	0.6	115 - 174	141.5	24.4
Cirrhibarbis capensis	3	0.4	47 - 110	84	33
Climacoporus navalis	58	8.5	14 - 63	39.7	15.5
Clinus acuminatus	1	0.1	36	36	---
Clinus berrisfordi	3	0.4	39 - 45	42.7	3.2
Clinus cottoides	8	1.2	62 - 180	127.6	33.8
Clinus nematopterus	17	2.5	40 - 125	50.6	20.6
Clinus superciliosus	25	3.7	19 - 178	84.5	50
Clinus taurus	3	0.4	76 - 120	92	24.3
Clinus venustris	7	1	12 - 115	62	37.8
Pavoclinus graminis	15	2.2	36 - 120	90.6	25.4
Pavoclinus pavo	145	21.3	26 - 100	48.7	16.8
Xenopoclinus kochi	3	0.4	66 - 92	77.7	13.2
Xenopoclinus leprosus	1	0.1	64	64	---
GOBIIDAE					
Caffrogobius agulhensis	8	1.2	51 - 65	56.4	4.8
N = 681					

TABLE 14: Suprabenthic fish sampled using line transect visual censuses on coralline dominated reef within the TNP between 1988 and 1990 (number of transects = 61).

FAMILY/SPECIES	n	%N	DENSITY (m/2)	C.V.
CARCHARHINIDAE				
Carcharhinus brachyurus	1	0.02	0.00014	8.42
SCYLIORHINIDAE				
Poroderma africanum	9	0.17	0.00063	2.64
Poroderma pantherinum	2	0.04	0.00014	5.92
ODONTASPIDIDAE				
Eugomphodus taurus	1	0.02	0.00014	8.42
RHINOBATIDAE				
Rhinobatis annulatus	1	0.02	0.00014	8.42
MYLIOBATIDAE				
Myliobatis aquila	1	0.02	0.00014	8.42
SERRANIDAE				
Acanthistius sebastoides	1	0.02	0.00014	8.42
Epinephilus guaza	1	0.02	0.00014	8.42
HAEMULIDAE				
Pomadasys olivaceum	1	0.02	0.00014	8.42
SPARIDAE				
Boopsoidea inornata	1206	22.44	0.00014	0.84
Cheimerius nufar	1	0.02	0.00014	8.42
Chrysoblephus gibbiceps	5	0.09	0.00035	5.54
Chrysoblephus laticeps	133	2.47	0.0094	0.82
Cymatoceps nasutus	1	0.02	0.00014	8.42
Diplodus cervinus	34	0.63	0.0024	2.21
Diplodus sargus	76	1.41	0.0054	1.41
Gymnocrotaphus curvidens	138	2.57	0.0097	1.11
Lithognathus mormyurus	1	0.02	0.00014	8.42
Pachymetopon aeneum	175	3.26	0.013	1.42
Pachymetopon grande	15	0.28	0.0011	2.11
Petrus rupestris	4	0.07	0.00028	4.12
Rhabdosargus globiceps	1	0.02	0.00014	8.42
Rhabdosargus holubi	14	0.26	0.00098	2.21
Sarpa salpa	2622	48.76	0.185	1.38
Sparodon durbanensis	5	0.09	0.00035	6.92
Spondyliosoma emarginatum	56	1.04	0.0039	3.03
CORACINIDAE				
Coracinus capensis	1	0.02	0.00014	8.42
MONODACTYLIDAE				
Monodactylus falciformes	1	0.02	0.00014	8.42
CHAETODONTIDAE				
Chaetodon marleyi	3	0.06	0.00021	4.79
OPLEGNATHIDAE				
Oplegnathus conwayi	76	1.41	0.0054	0.66
CARANGIDAE				
Trachurus	1	0.02	0.00014	8.42
CHEILODACTYLIDAE				
Cheilodactylus fasciatus	57	1.06	0.0081	1.22
Cheilodactylus pixi	15	0.28	0.0021	2.39
Chirodactylus brachydactylus	715	13.31	0.11	1.02
TETRAODONTIDAE				
Amblyrhynchotes honckenii	1	0.02	0.00014	8.42

N = 5374

TABLE 15: Cryptic fish sampled with rotenone on filter-feeding invertebrate dominated deep reefs within the TNP between 1988 and 1990 (number of samples = 13).

FAMILY/SPECIES	n	%N	T.L. (mm)		
			RANGE	MEAN	S.D.
CONGRIDAE					
Conger wilsoni	1	0.1	178	178	11.6
ARIIDAE					
Galeichthys ater	3	0.3	200 - 280	231.6	42.5
GADIDAE					
Gaidropsarus capensis	34	3.3	51 - 195	103.1	97.6
BYTHITIDAE					
Bidenichthys capensis	40	3.9	25 - 70	53	11.2
Dermatopsoides talboti	5	0.5	51 - 66	59.8	6.8
Grammonoides opisthodon	3	0.3	16 - 50	31.3	46
BATRACHOIDIDAE					
Batrichthys apiatus	5	0.5	17 - 76	46	22.7
Chatrabus hendersoni	12	1.2	30 - 205	123.2	15
GOBIESOCIDAE					
Apletodon pellegrini	8	0.8	17 - 31	22.9	32.9
BERYCIDAE					
Centroberyx spinosus	1	0.1	15	15	7.7
TETRAROGIDAE					
Coccotropsis gymnoderma	277	28.6	13 - 47	30.3	9.3
CONGIOPODIDAE					
Congiopodus spinifer	1	0.1	42	42	8.1
CONGROGADIDAE					
Halidesmus scapularis	88	8.8	27 - 118	79.3	77.3
BLENNIIDAE					
Chalaroderma ocellata	85	8.7	22 - 72	42.1	45.5
Parablennius cornutus	3	0.3	42 - 58	49.7	42.5
Parablennius pilicornis	1	0.1	52	52	---
TRIPTERYGIIDAE					
Cremnochorites capensis	158	16.2	16 - 75	51.3	15
Tripterygidae gen. nov.	7	0.7	35 - 45	40.4	107
CLINIDAE					
Blennioclinus stella	3	0.3	33 - 51	39.1	34.2
Blennophis striatus	7	0.7	28 - 153	67	63.6
Climacoporus navalis	45	4.6	21 - 66	44.7	7.7
Clinus acuminatus	4	0.4	42 - 85	58	53.9
Clinus cottoides	2	0.2	86 - 111	93.2	41.3
Clinus nematopterus	6	0.6	35 - 49	41.5	18.9
Clinus superciliosus	5	0.5	20 - 130	74.2	8.3
Pavoclinus graminis	3	0.3	59 - 121	93	31.4
Pavoclinus pavo	25	2.6	18 - 54	42.4	73.1
Pavoclinus profundus	4	0.4	42 - 62	58	66.7
Xenopoclinus leprosus	1	0.1	54	54	---
GOBIIDAE					
Caffrogobius agulhensis	139	14.2	30 - 73	53.6	11.3
	N = 976				

TABLE 16: Suprabenthic fish sampled using line transect visual censuses on filter-feeding invertebrate dominated reef within the TNP between 1988 and 1990 (number of transects = 61).

FAMILY/SPECIES	n	%N	DENSITY (m/2)	C.V.
SCYLIORHINIDAE				
Poroderma africanum	22	0.64	0.0017	4.12
Poroderma pantherinum	4	0.12	0.0003	3.84
ODONTASPIDIDAE				
Eugomphodus taurus	1	0.03	< 0.0001	---
RHINOBATIDAE				
Rhinobatis annulatus	1	0.03	< 0.0001	---
MYLIOBATIDAE				
Myliobatis aquila	1	0.03	< 0.0001	---
DASYATIDAE				
Gymnura natalensis	1	0.03	< 0.0001	---
SERRANIDAE				
Acanthistius sebastoides	17	0.49	0.0027	1.89
Epinephelus guaza	1	0.03	< 0.0001	---
HAEMULIDAE				
Pomodasys olivaceum	35	1.01	0.0028	5.58
SPARIDAE				
Boopsoidea inornata	847	24.55	0.068	0.93
Cheimerius nufar	1	0.03	< 0.0001	---
Chrysoblephus cristiceps	2	0.06	0.0001	5.52
Chrysoblephus gibbiceps	4	0.12	0.0003	3.84
Chrysoblephus laticeps	259	7.51	0.021	0.49
Cymatoceps nasutus	1	0.03	< 0.0001	---
Diplodus cervinus	10	0.29	0.0008	3.21
Diplodus sargus	2	0.06	0.0001	5.52
Gymnocrotaphus curvidens	54	1.57	0.0043	1.05
Lithognathus mormyrus	1	0.03	< 0.0001	---
Pachymetopon aeneum	1068	30.96	0.086	0.98
Petrus rupestris	56	1.62	0.0045	0.71
Pachymetopon grande	7	0.21	0.0005	3.62
Rhabdosargus globiceps	1	0.03	< 0.0001	---
Rhabdosargus holubi	12	0.35	0.0009	3.95
Sarpa salpa	102	2.96	0.0082	5.05
Sparodon durbanensis	2	0.06	< 0.0001	---
Spondyliosoma emarginatum	351	10.17	0.028	2.05
CORACINIDAE				
Coracinus capensis	1	0.03	< 0.0001	---
PARASCORPIDIDAE				
Parascorpis typus	2	0.06	0.0001	5.52
MONODACTYLIDAE				
Monodactylus falciformes	1	0.03	< 0.0001	---
CHAETODONTIDAE				
Chaetodon marleyi	2	0.06	0.0001	5.52
OPLEGNATHIDAE				
Oplegnathus conwayi	89	2.58	0.0071	0.53
CARANGIDAE				
Trachurus trachurus	1	0.03	< 0.0001	---
CHEILODACTYLIDAE				
Cheilodactylus fasciatus	51	1.47	0.0082	1.31
Cheilodactylus pixi	179	5.2	0.029	0.77
Chirodactylus brachydactylus	263	7.5	0.042	0.68
Chirodactylus grandis	1	0.03	< 0.0001	---
N = 3453				

Relatively few species were found to make up large proportions of the samples in each area. Figures 7 and 8 below illustrate the percentage contribution of the most important species for the cryptic and suprabenthic components respectively, for the six sub-areas within the TNP littoral zone.

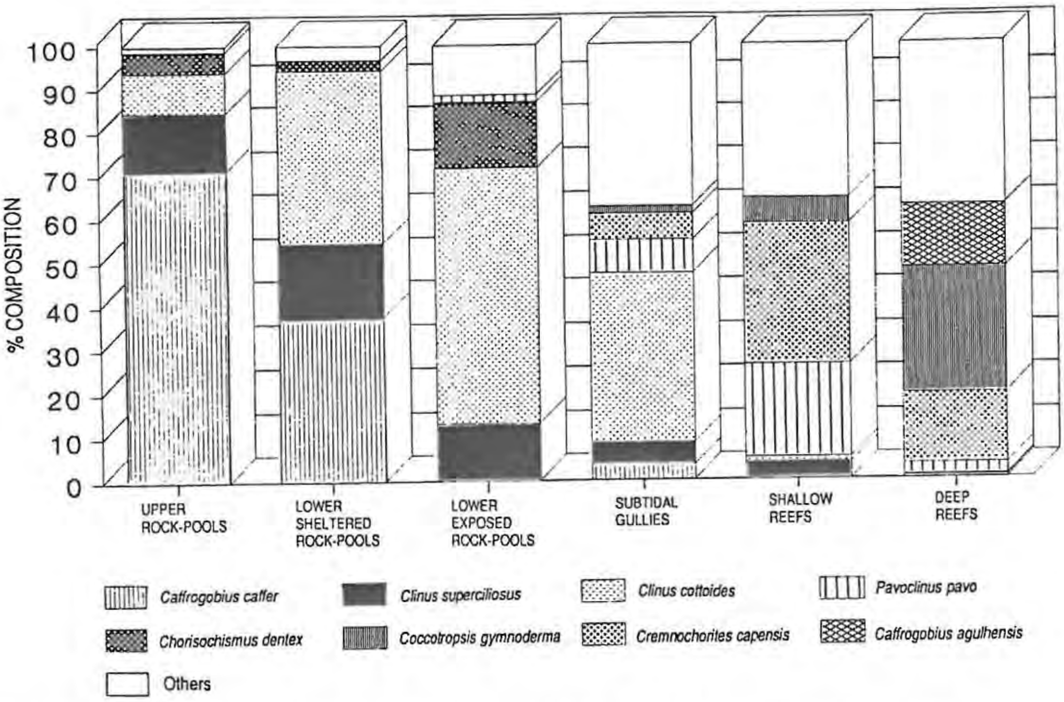


FIGURE 7: The percentage composition of the eight most abundant cryptic species for the six littoral areas within the TNP.

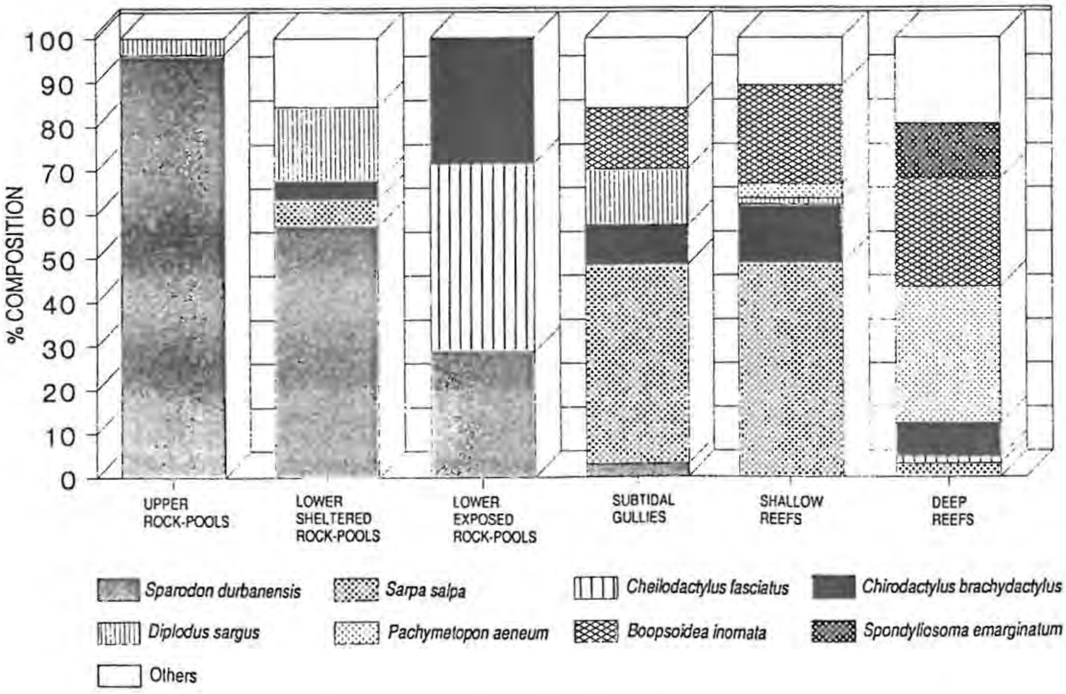


FIGURE 8: The percentage composition of the eight most abundant suprabenthic species for the six littoral areas within the TNP.

The size frequency distributions of the most important species were calculated for each area in which they were found. Figures 9 to 24 show the size frequencies of 16 abundant species found within the study area.

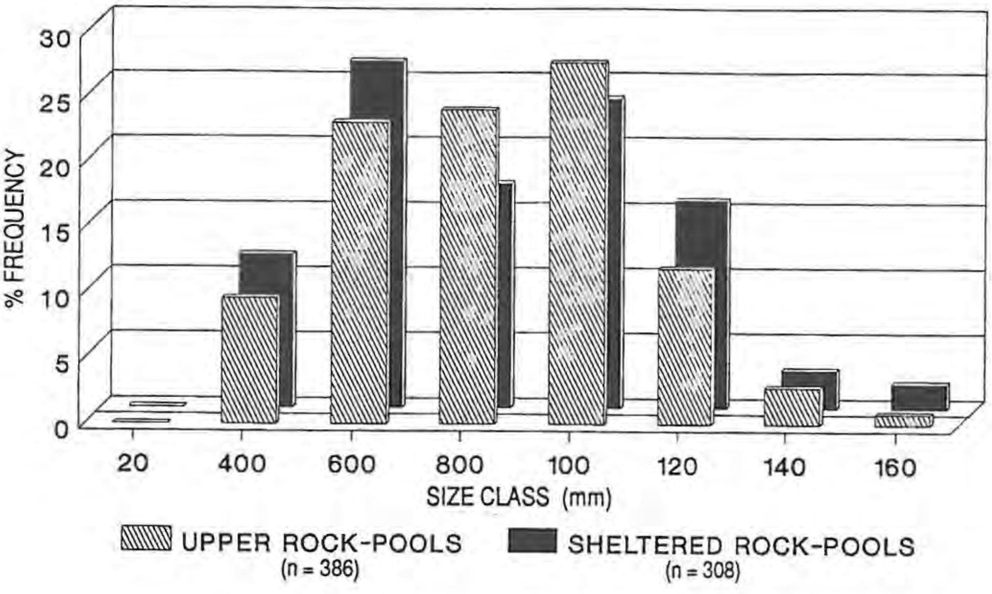


FIGURE 9: The length frequency distribution of *Caffrogobius caffer* in upper and sheltered lower intertidal rock-pools.

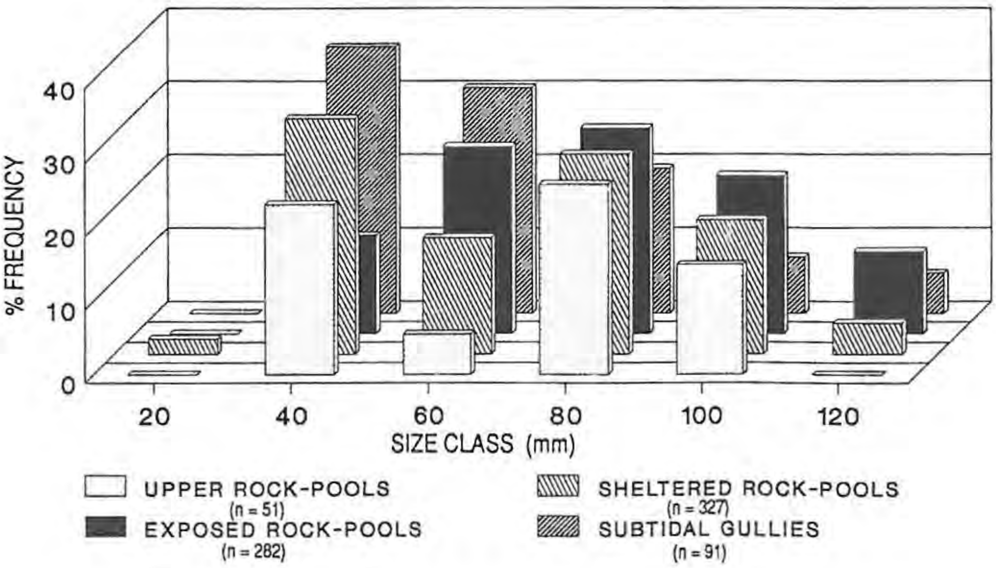


FIGURE 10: The length frequency distribution of *Clinus cottoides* in intertidal rock-pools and subtidal gullies.

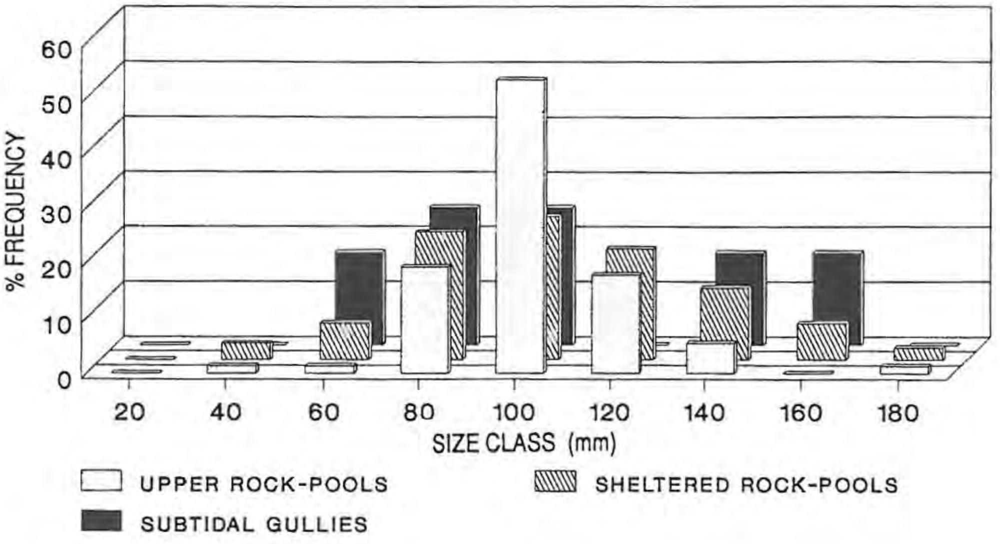


FIGURE 11: The length frequency distributions of *Clinus superciliosus* in upper pools, sheltered and exposed lower pools and subtidal gullies.

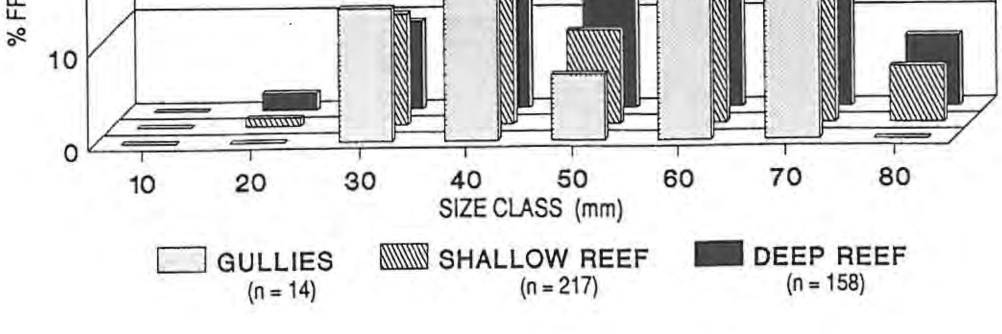


FIGURE 12: The length frequency distributions of *Cremnochorites capensis* in gullies and on shallow and deep subtidal reef.

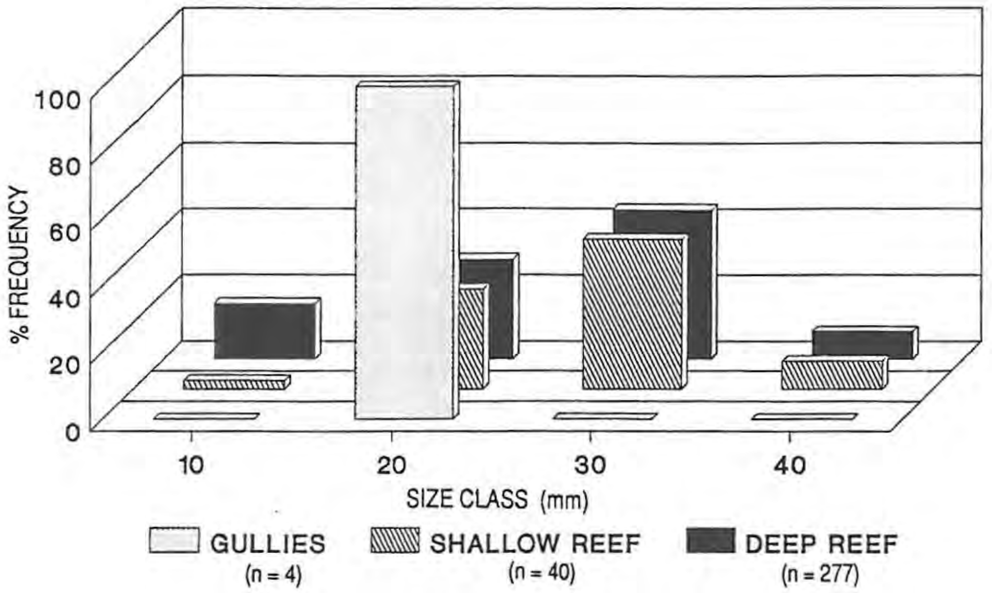


FIGURE 13: The length frequency distribution of *Coccotropsis gymnoderma* in gullies and on shallow and deep reef.

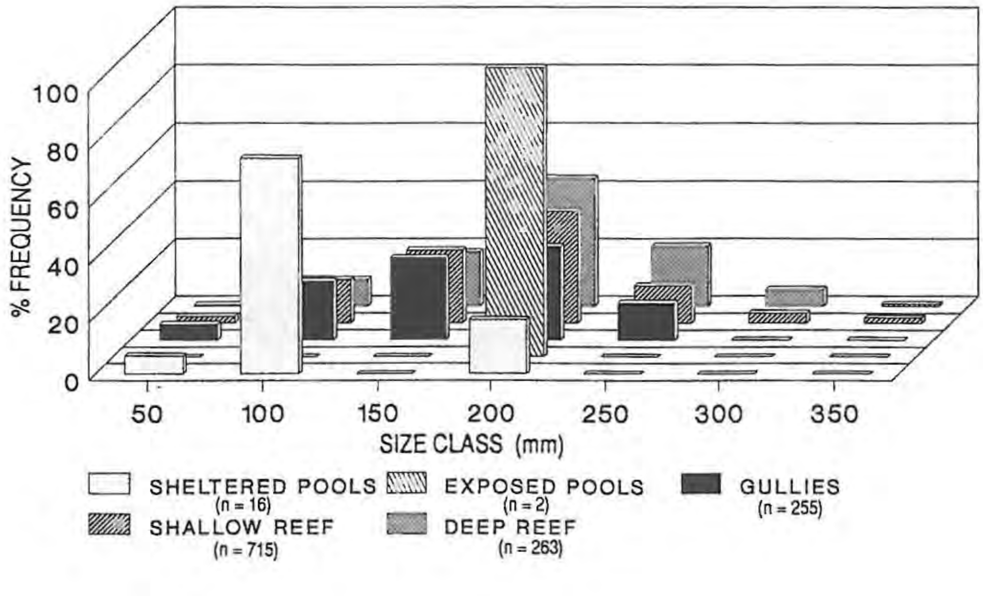


FIGURE 14: The length frequency distribution of *Chirodactylus brachydactylus* in sheltered and exposed pools, subtidal gullies and on shallow and deep reef.

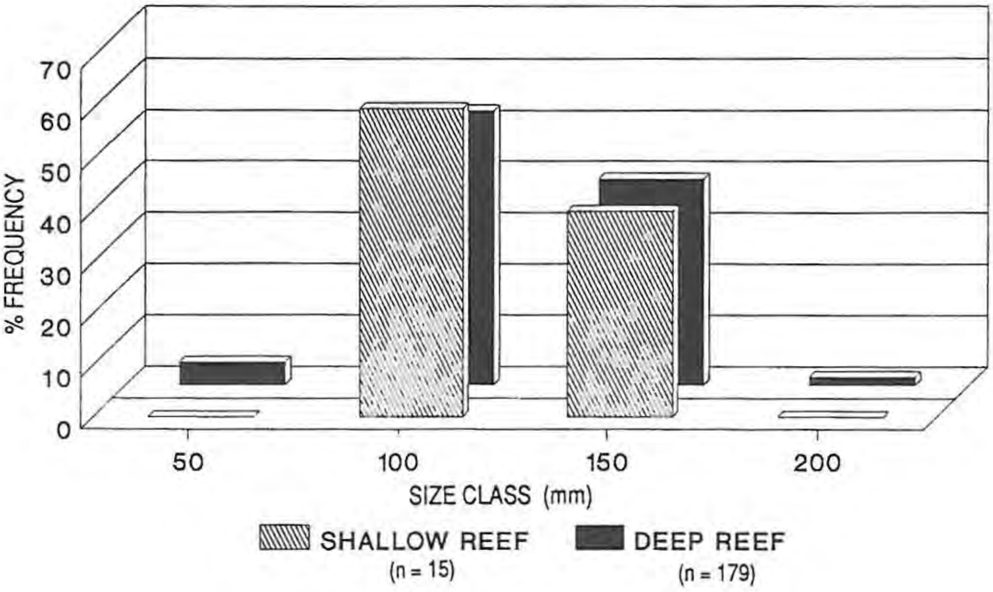


FIGURE 15: The length frequency distribution of *Cheilodactylus pixi* on shallow and deep subtidal reef.

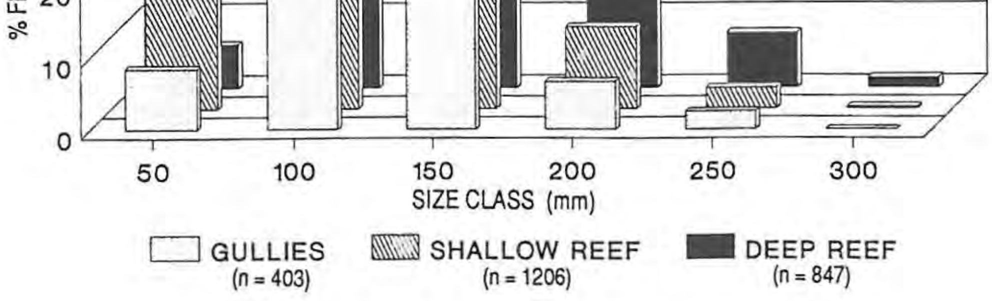


FIGURE 16: The length frequency distribution of *Boopsoidea inornata* in gullies and on shallow and deep reef.

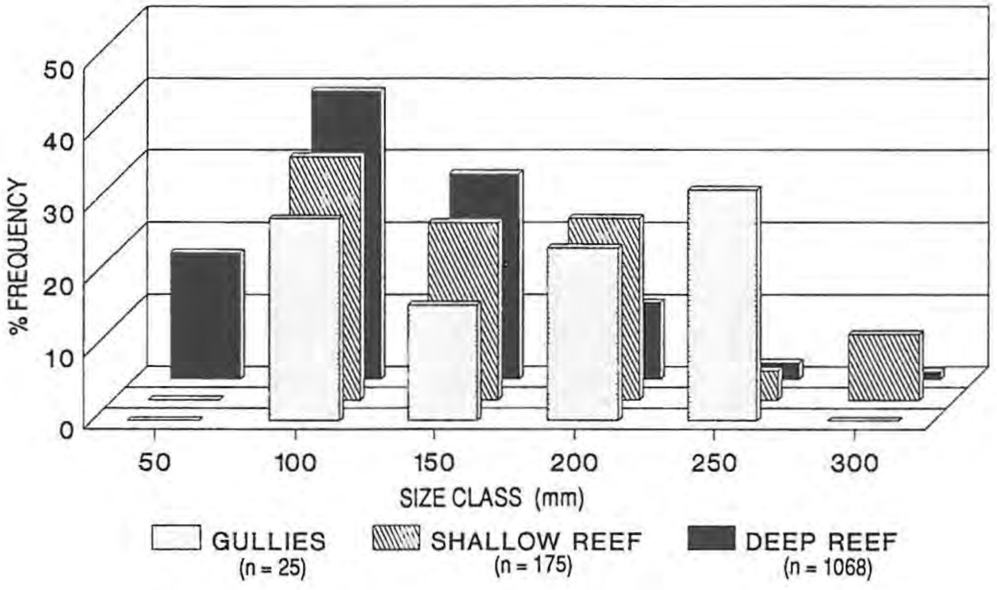


FIGURE 17: The length frequency distribution of *Pachymetopon aeneum* in gullies and on shallow and deep reef.

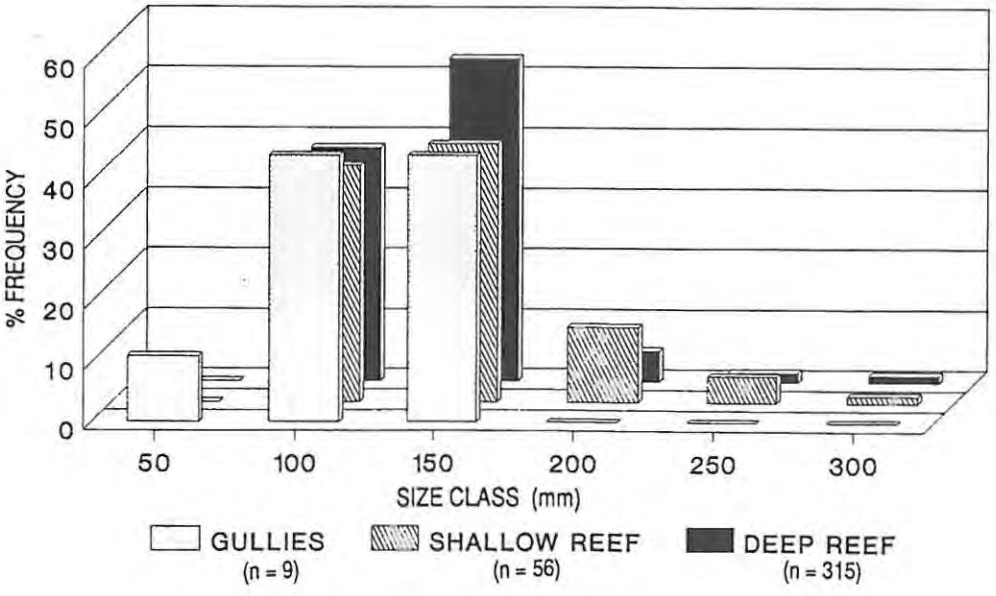


FIGURE 18: The length frequency distribution of *Spondyliosoma emarginatum* in gullies and on shallow and deep reef.

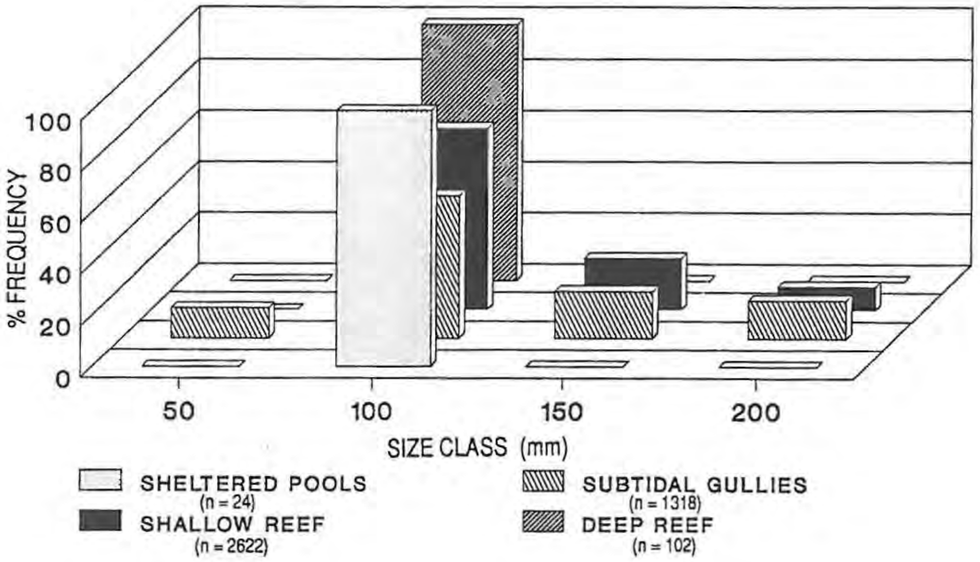


FIGURE 19: The length frequency distribution of *Sarpa salpa* in sheltered intertidal pools, subtidal gullies and on shallow and deep reef.

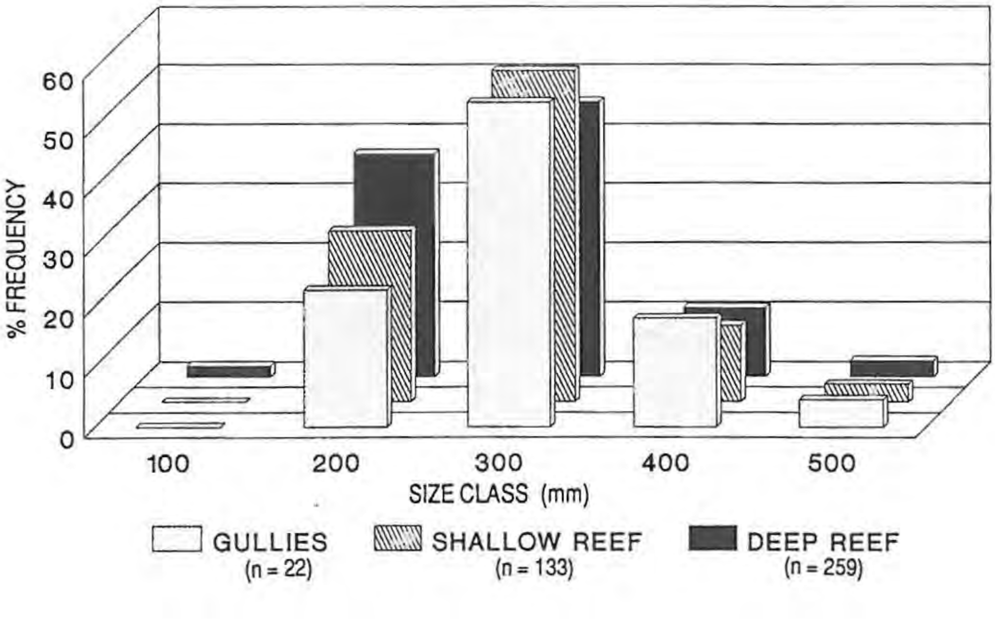


FIGURE 20: The length frequency distribution of *Chrysoblephus laticeps* in gullies and on shallow and deep reef.

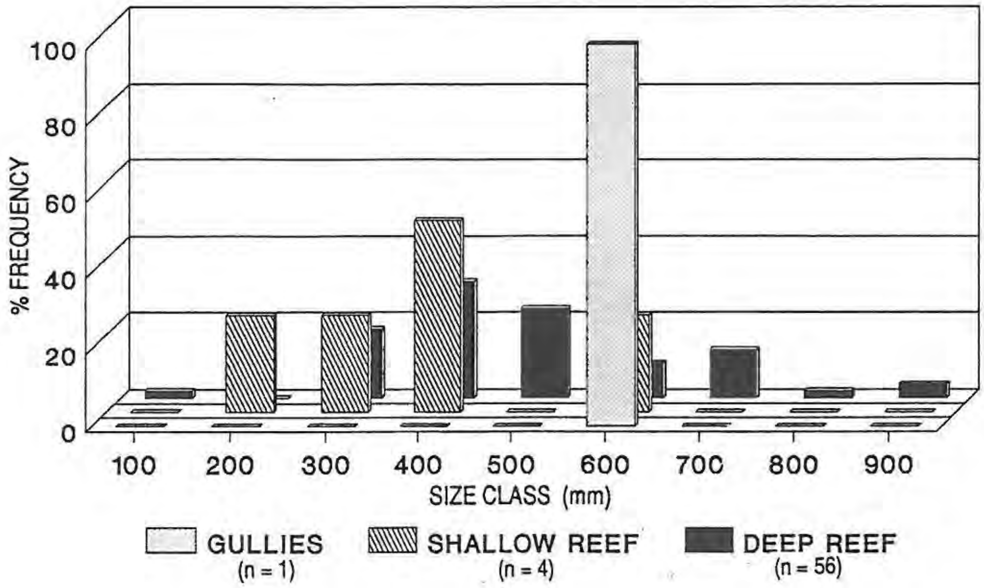


FIGURE 21: The length frequency distribution of *Petrus rupestris* in gullies and on shallow and deep reef.

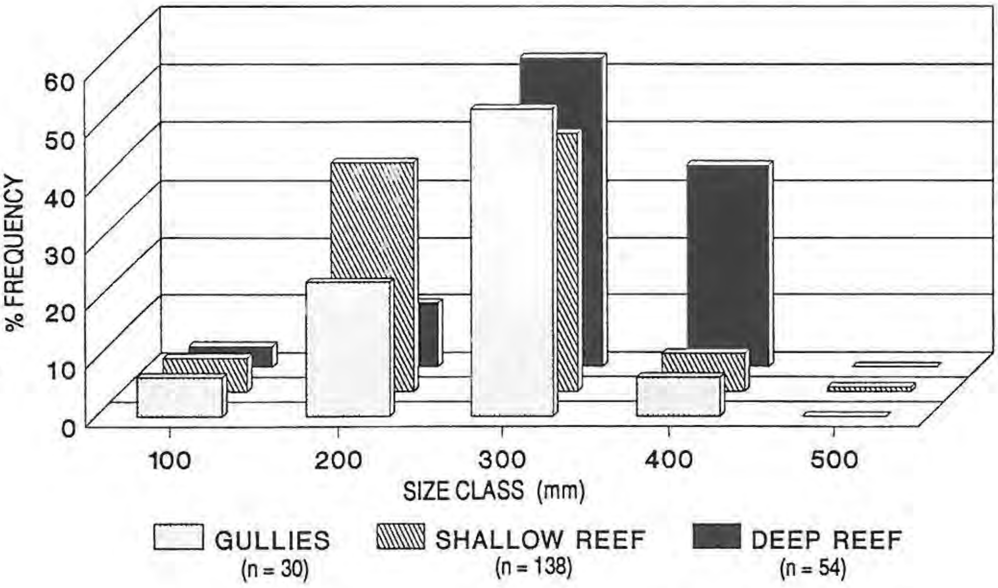


FIGURE 22: The length frequency distribution of *Gymnocrotaphus curvidens* in gullies and on shallow and deep reef.

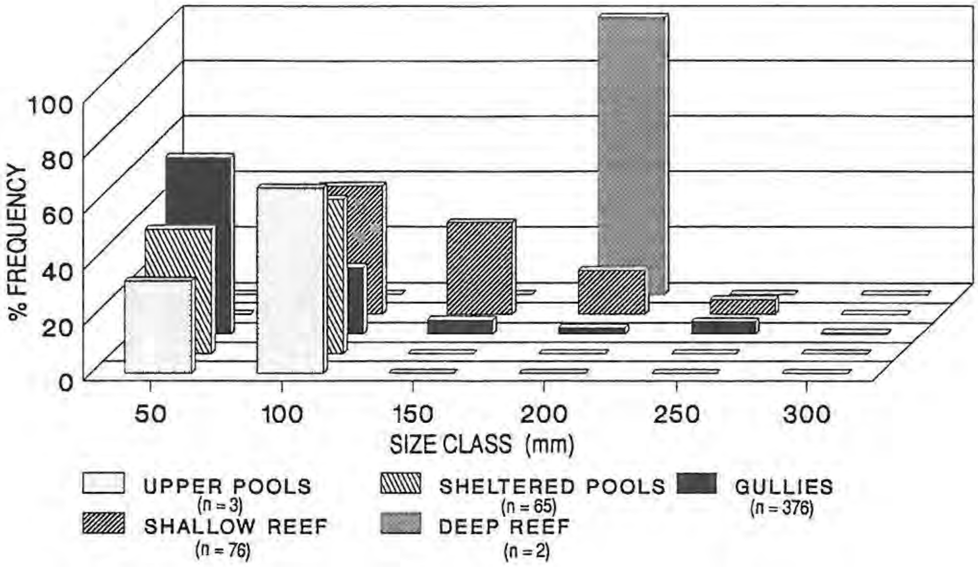


FIGURE 23: The length frequency distribution of *Diplodus sargus* in upper and sheltered lower intertidal pools, gullies and shallow and deep reef.

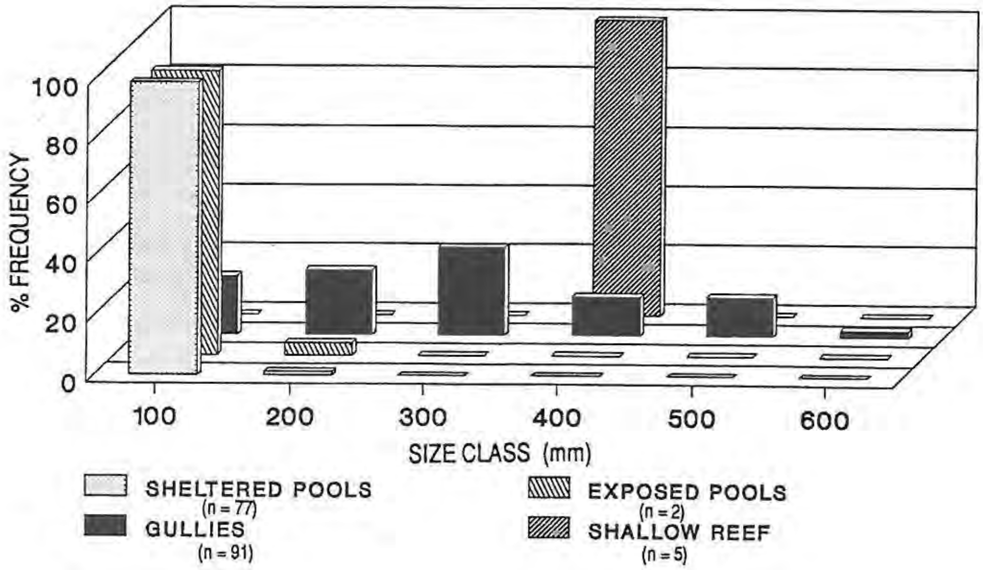
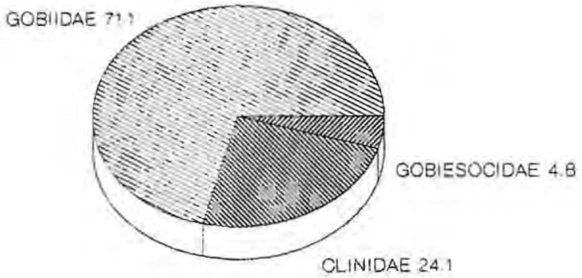


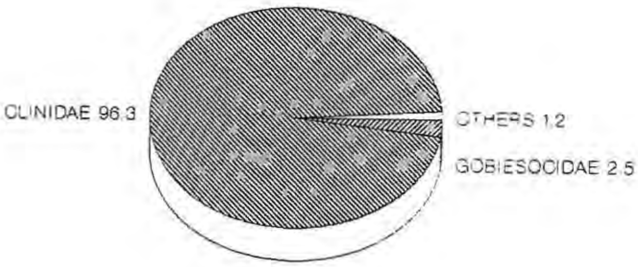
FIGURE 24: The length frequency distribution of *Sparodon durbanensis* in sheltered and exposed lower intertidal pools, gullies and on shallow reef.

The percentage composition of the families sampled in the six sub-areas within the TNP littoral zone were calculated. Figures 25(a) - (f) show the cryptic compositions and Figures 26(a) - (f) show the suprabenthic compositions.

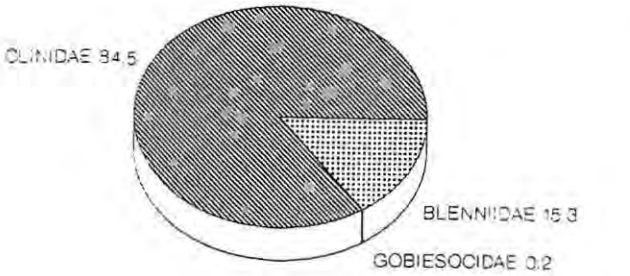
(a) Upper intertidal rock-pools.



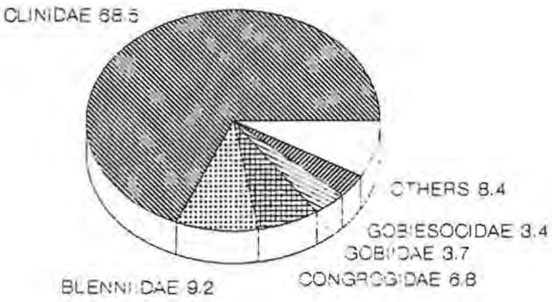
(b) Sheltered lower intertidal rock-pools.



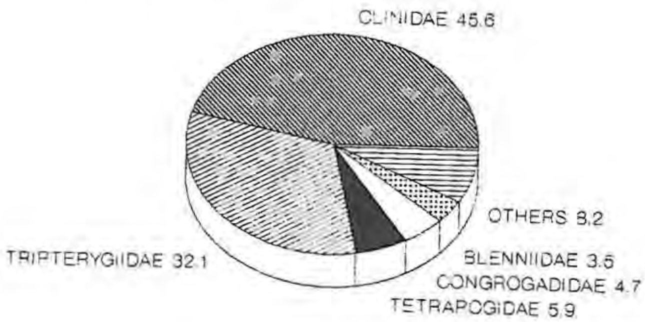
(c) Exposed lower intertidal rock-pools.



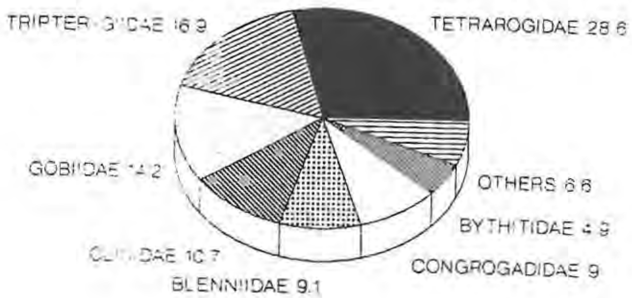
(d) Subtidal gullies.



(e) Shallow reef.

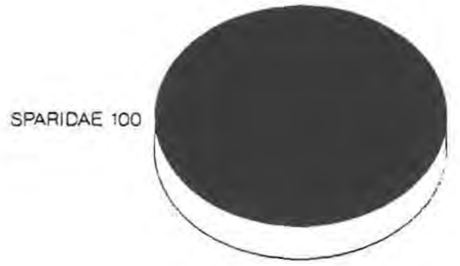


(f) Deep reef.

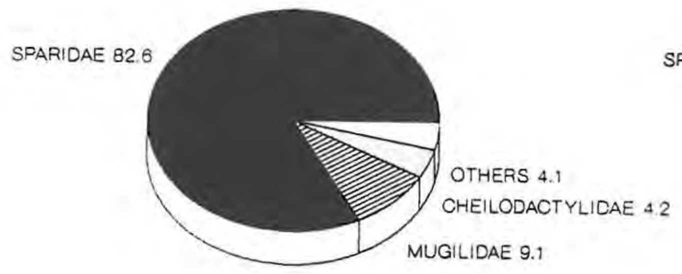


FIGURE'S 25 (a) - (f): Percentage composition of the constituent families of the cryptic ichthyofauna for the six sub-areas within the Tsitsikamma littoral zone.

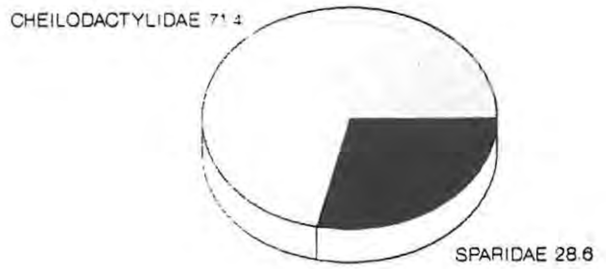
(a) Upper intertidal rock-pools.



(b) Sheltered lower intertidal rock-pools.



(c) Exposed lower intertidal rock-pools.



(d) Subtidal gullies.

(e) Shallow reef.

(f) Deep reef.

FIGURE'S 26 (a) - (f): Percentage composition of the constituent families of the suprabenthic ichthyofauna for the six sub-areas within the Tsitsikamma littoral zone.

3.4.4. Species diversity down the TNP littoral profile

The species richness (as measured by the Margalef index), the species diversity (as measured by the Shannon-weaver index) and the species evenness (as measured by the Pielou index) were calculated for both the cryptic and the suprabenthic components for the six sub-areas within the TNP littoral zone. Table 17 and Figures 27-29 summarise the results of these calculations.

TABLE 17: Species diversity measures as calculated for cryptic and suprabenthic littoral fish within the TNP.

(a): CRYPTIC FISH

AREA	SPECIES	SPECIES DIVERSITY MEASURE		
		MARGALEF	SHANNON	PIELOU
UPPER INTERTIDAL	6	0.79	0.94	0.15
SHELTERED INTERTIDAL	13	1.79	1.30	0.51
EXPOSED INTERTIDAL	10	1.46	1.29	0.56
SUBTIDAL GULLIES	19	3.30	2.21	0.75
SHALLOW REEF	29	4.30	2.34	0.70
DEEP REEF	31	4.36	2.37	0.67

(b): SUPRABENTHIC FISH.

AREA	SPECIES	SPECIES DIVERSITY MEASURE		
		MARGALEF	SHANNON	PIELOU
UPPER INTERTIDAL	2	0.23	0.16	0.23
SHELTERED INTERTIDAL	13	2.01	1.14	0.24
EXPOSED INTERTIDAL	3	1.03	1.08	0.99
SUBTIDAL GULLIES	28	3.39	1.43	0.43
SHALLOW REEF	35	3.84	1.17	0.33
DEEP REEF	37	4.18	1.77	0.50

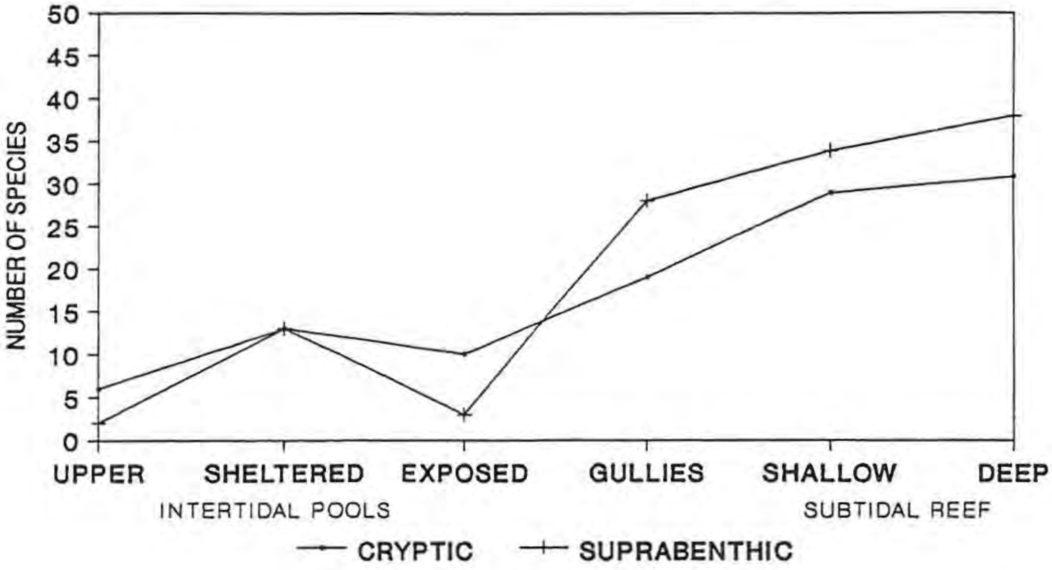


FIGURE 27: The number of cryptic and suprabenthic species recorded in each area down the littoral profile.

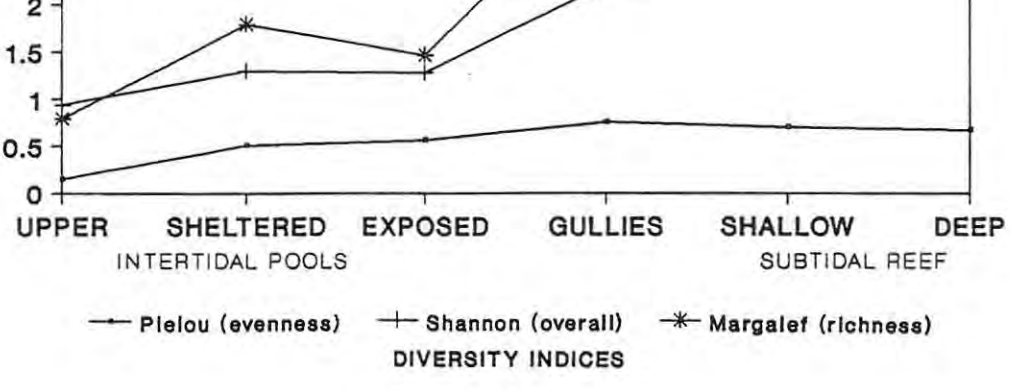


FIGURE 28: The three species diversity measures for the cryptic component of the Tsitsikamma littoral ichthyofauna, down the littoral profile.

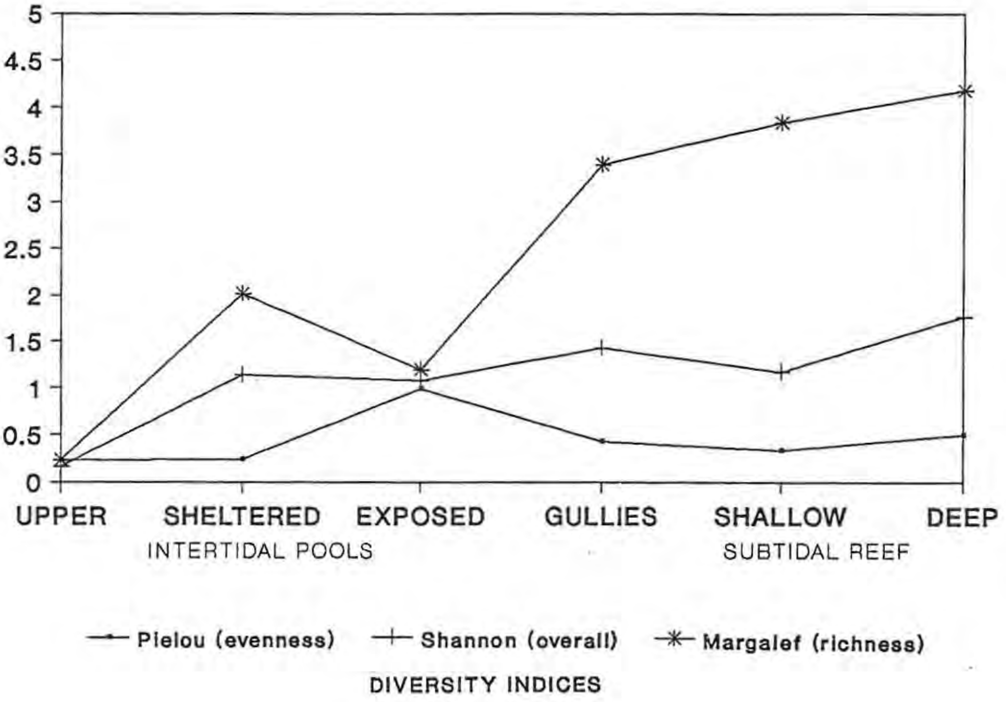


FIGURE 29: The three species diversity measures for the suprabenthic component of the Tsitsikamma littoral ichthyofauna, down the littoral profile.

3.4.5. Distribution, relative abundance and community structure on exploited reefs.

The results of rotenone collecting and visual censuses for shallow and deep reef types outside the park are shown in Tables 18 to 21.

TABLE 18: Cryptic fish sampled with rotenone on coralline algae dominated shallow reefs outside the TNP during 1990 (number of samples = 7).

FAMILY/SPECIES	n	%N	T.L. (mm)		
			RANGE	MEAN	S.D.
CONGRIDAE					
Conger wilsoni	1	0.4	105	105	---
ARIIDAE					
Galeichthys ater	2	0.7	111 - 335	223	34.2
GADIDAE					
Gaidropsarus capensis	1	0.4	145	145	---
BYTHITIDAE					
Bidenichthys capensis	7	2.6	48 - 75	61.4	9.9
BATRACHOIDIDAE					
Batrichthys apiatus	1	0.4	57	57	---
Chatrabus hendersoni	2	0.7	24 - 30	27	4.2
GOBIESOCIDAE					
Apletodon pellegrini	5	1.9	29 - 36	32	2.6
TERAROGIDAE					
Coccotropsis gymnoderma	6	2.2	22 - 43	31.7	8.3
CONGROGADIDAE					
Halidesmus scapularis	22	8.2	36 - 119	73.7	23.1
BLENNIIDAE					
Chalaroderma ocellata	6	2.2	40 - 62	52.3	8.2
TRIPTERYGIIDAE					
Cremnochorites capensis	191	71.3	29 - 80	47.9	13.8
CLINIDAE					
Blennophis striatus	1	0.4	56	56	---
Cirrhibarbis capensis	1	0.4	85	85	---
Climacoporus navalis	7	2.6	30 - 56	41	8.2
Clinus acuminatus	2	0.7	62 - 66	63.5	3.5
Clinus cottoides	1	0.4	125	125	---
Clinus superciliosus	3	1.1	88 - 122	106	17.2
Clinus venustris	2	0.7	102 - 106	104	2.8
Pavoclinus pavo	1	0.4	60	60	---
GOBIIDAE					
Caffrogobius agulhensis	4	1.5	34 - 52	43.5	8.4
Caffrogobius saldanha	1	0.4	66	66	---
N = 267					

TABLE 19: Suprabenthic fish sampled using line transect visual censuses on coralline algae dominated reef outside the TNP during 1990 (number of transects = 49).

FAMILY/SPECIES	n	%N	DENSITY (m/2)	C.V.
SCYLIORHINIDAE				
Poroderma africanum	14	0.4	0.0014	2.37
Poroderma pantherinum	2	0.06	0.0002	4.9
SERRANIDAE				
Acanthistius sebastoides	3	0.1	0.0006	4.12
SPARIDAE				
Boopsoidea inornata	918	28	0.09	0.71
Crysoblephus laticeps	127	3.9	0.013	0.75
Diplodus cervinus	36	1.1	0.0037	1.2
Diplodus sargus	51	1.6	0.0052	1.52
Gymnocrotaphus curvidens	122	3.7	0.012	0.77
Pachemetopon aeneum	122	3.7	0.012	1.72
Pachemetopon grande	6	0.2	0.0006	3.18
Rhabdosargus holubi	16	0.5	0.0016	1.92
Sarpa salpa	1342	41	0.14	1.78
Sparodon durbanensis	5	0.2	0.0005	4.12
Spondyliosoma emarginatum	170	5.2	0.017	1.51
CHAETODONTIDAE				
Chaetodon marleyi	3	0.1	0.0003	3.96
OPLEGNATHIDAE				
Oplegnathus conwayi	12	0.4	0.0012	3.18
CHEILODACTYLIDAE				
Cheilodactylus fasciatus	44	1.3	0.0089	0.54
Cheilodactylus pixi	7	0.2	0.0014	3.81
Chirodactylus brachydactylus	271	8.3	0.055	0.83
N = 3271				

TABLE 20: Cryptic fish sampled with rotenone on filter-feeding invertebrate dominated deep reefs outside the TNP during 1990 (number of samples = 6).

FAMILY/SPECIES	n	%N	T.L. (mm)		
			RANGE	MEAN	S.D.
ARIIDAE					
Galeichthys ater	1	0.4	120	120	---
GADIDAE					
Gaidropsarus capensis	3	1.1	102 - 155	133	27.6
BYTHITIDAE					
Bidenichthys capensis	1	0.4	45	45	---
Dermatopsoides talboti	2	0.8	25 - 40	32.5	10.6
BATRACHOIDIDAE					
Batrichthys apiatus	7	2.7	31 - 40	36	3
Chatrabus hendersoni	9	3.4	133 - 193	165	20
GOBIESOCIDAE					
Apletodon pellegrini	7	2.7	21 - 29	24.9	3.5
TETRAROGIDAE					
Coccotropsis gymnoderma	10	3.8	21 - 45	27.3	6.7
CONGROGADIDAE					
Halidesmus scapularis	26	10	40 - 129	79.9	21.7
BLENNIIDAE					
Chalaroderma ocellata	22	8.4	36 - 70	53.8	6.9
TRIPTERYGIIDAE					
Cremnochorites capensis	96	36.8	24 - 70	42.5	9.3
Tripterygiidae gen. nov.	1	0.4	35	35	---
CLINIDAE					
Blennophis striatus	1	0.4	105	105	---
Climacoporus navalis	9	3.4	35 - 56	46.1	9.4
Clinus cottoides	1	0.4	78	78	---
Clinus nematopterus	1	0.4	52	52	---
Clinus superciliosus	1	0.4	155	155	---
Pavoclinus pavo	28	10.7	30 - 62	44.9	9.4
Pavoclinus profundus	1	0.4	66	56	---
GOBIIDAE					
Caffrogobius agulhensis	34	13	29 - 65	42.5	10.1
N = 261					

TABLE 21: Suprabenthic fish sampled using line transect visual censuses on filter-feeding invertebrate dominated reef outside the TNP (number of transects = 50).

FAMILY/SPECIES	n	%N	DENSITY (m/2)	C.V.
CARCHARHINIDAE				
Carcharhinus brachyurus	1	0.04	<0.0001	5.62
SCYLIORHINIDAE				
Poroderma africanum	5	0.2	0.0005	3.06
Poroderma pantherinum	8	0.3	0.0008	4.83
ODONTASPIDIDAE				
Eugomphodus taurus	1	0.04	<0.0001	5.62
SERRANIDAE				
Acanthistius sebastoides	10	0.4	0.002	2.51
Epinephelus guaza	1	0.04	<0.0001	5.62
SPARIDAE				
Boopsoidea inornata	1166	41.1	0.1143	0.78
Cheimerius nufar	2	0.07	0.0002	2.51
Chrysoblephus cristiceps	2	0.07	0.0002	2.51
Chrysoblephus gibbiceps	19	0.7	0.0019	1.69
Chrysoblephus laticeps	167	5.9	0.0164	0.46
Diplodus cervinus	38	1.3	0.0037	1.19
Diplodus sargus	9	0.4	0.0009	2.71
Gymnocrotaphus curvidens	40	1.4	0.0039	1.64
Lithognathus mormyrus	1	0.04	<0.0001	5.62
Pachymetopon aeneum	688	24.3	0.0675	0.81
Pachymetopon grande	3	0.1	0.0003	4.04
Petrus rupestris	5	0.2	0.0005	3.06
Rhabdosargus holubi	7	0.2	0.0007	3.26
Sarpa salpa	100	3.5	0.0098	7.14
Spondyliosoma emarginatum	172	6.1	0.0169	1.55
SCORPIDIDAE				
Parascorpis typus	3	0.1	0.0003	4.04
MONODACTYLIDAE				
Monodactylus falciformes	1	0.04	<0.0001	5.62
CHAETODONTIDAE				
Chaetodon marleyi	2	0.07	0.0002	2.51
OPLEGNATHIDAE				
Oplegnathus conwayi	51	1.8	0.005	1.03
CHEILODACTYLIDAE				
Cheilodactylus fasciatus	37	1.3	0.0073	1.93
Cheilodactylus pixi	90	3.2	0.0176	1.04
Chirodactylus brachydactylus	207	7.3	0.0406	1.1
Chirodactylus grandis	1	0.04	<0.0001	5.62
N = 2837				

The results of both visual transects and rotenone collections on exploited areas outside the park and the same areas inside the park were tested statistically. Similarity between the observed frequencies of species found on shallow and deep reef in the two areas was tested using a Chi-square test and the results are summarised in Table 22 below.

TABLE 22: Summary of the Chi-square statistics for both rotenone and visual census samples for the two reef zones on exploited and unexploited reefs.

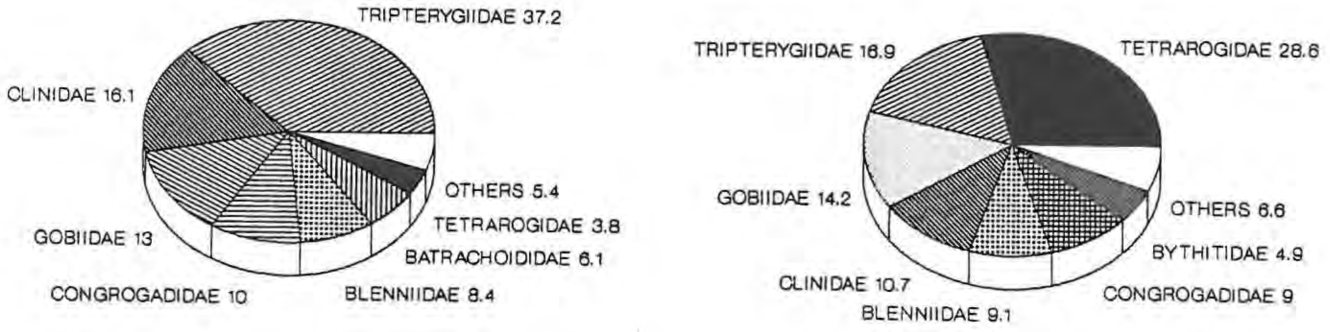
ZONE/COLLECTION METHOD	X^2	D.F.	SIG. LEVEL
SHALLOW REEF - ROTENONE	147.132	20	< 0.000005
SHALLOW REEF - VISUAL	297.703	18	< 0.000005
DEEP REEF - ROTENONE	162.345	19	< 0.000005
DEEP REEF - VISUAL	305.187	27	< 0.000005

Rotenone and visual census data for both shallow and deep reef samples were found to be significantly different. Visual census samples were found to be the most significantly different indicating large differences in the frequencies of suprabenthic species observed on exploited and unexploited reefs.

The percentage composition, by family, of the fish sampled on shallow and deep reef for both cryptic and suprabenthic species is shown in Figures 30 and 31. Corresponding pie charts for inside the park samples are included for comparison.

(a) Shallow exploited reef

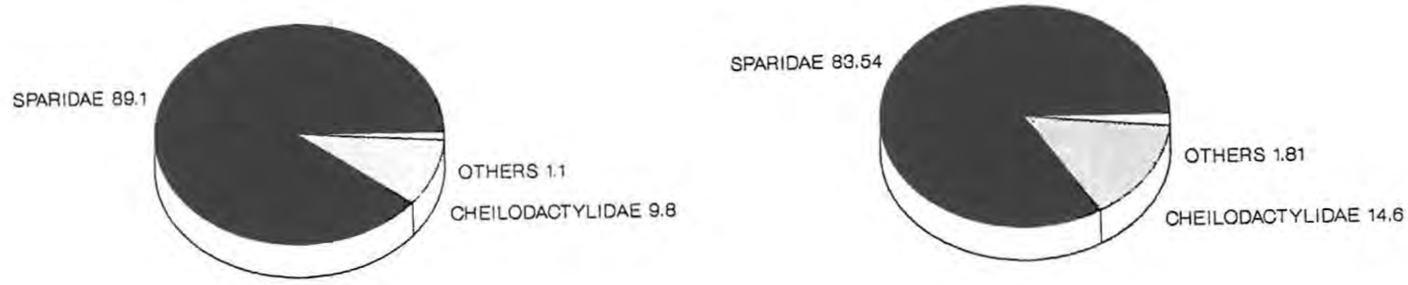
(b) Shallow unexploited reef.



(c) Deep exploited reef.

(d) Deep unexploted reef.

FIGURE'S 30 (a) - (d): Percentage composition of the constituent families of the cryptic ichthyofauna for the two reef types outside the park and the same reef types inside the park.



(a) Shallow exploited reef

(b) Shallow unexploited reef.

(c) Deep exploited reef.

(d) Deep unexploted reef.

FIGURE'S 31 (a) - (d): Percentage composition of the constituent families of the suprabenthic ichthyofauna for the two reef types outside the park and the same reef types inside the park.

The size class frequencies for the seven most important species (either because of their numerical abundance or in the case of *P. rupestris* because of their dominant position in the reef ecosystem) for both shallow and deep reefs outside the park were calculated and compared to the same reef type inside the park. Figures 32 - 44 show the results of this comparison.

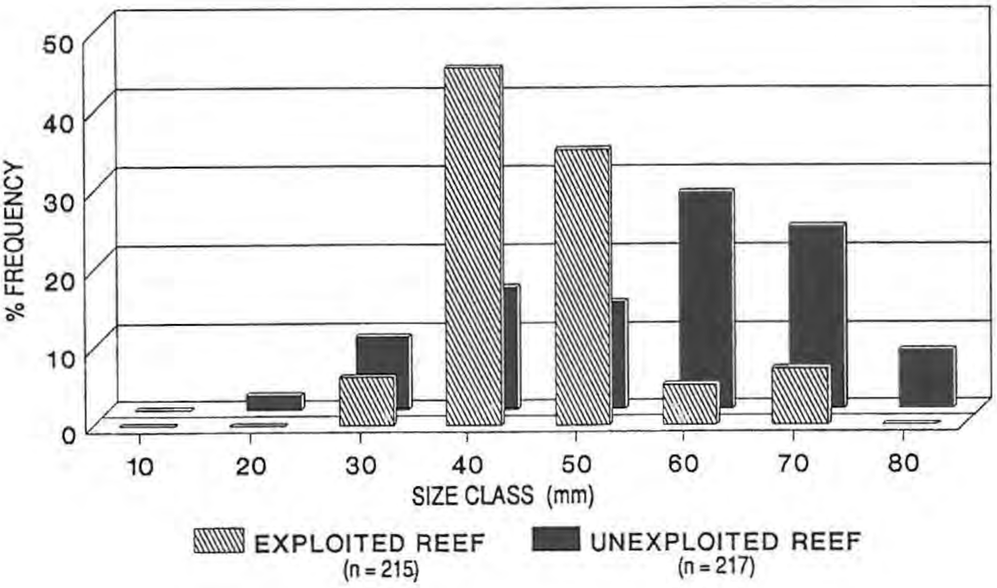


FIGURE 32: The length frequency distribution of *Cremnochorites capensis* on exploited and unexploited shallow reefs.

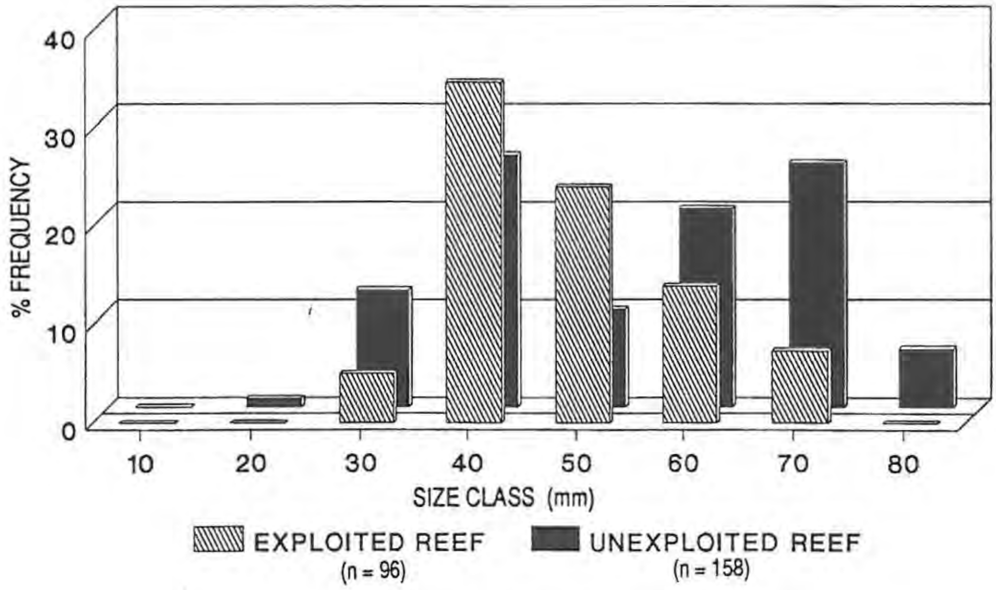


FIGURE 33: The length frequency distribution of *Cremnochorites capensis* on exploited and unexploited deep reefs.

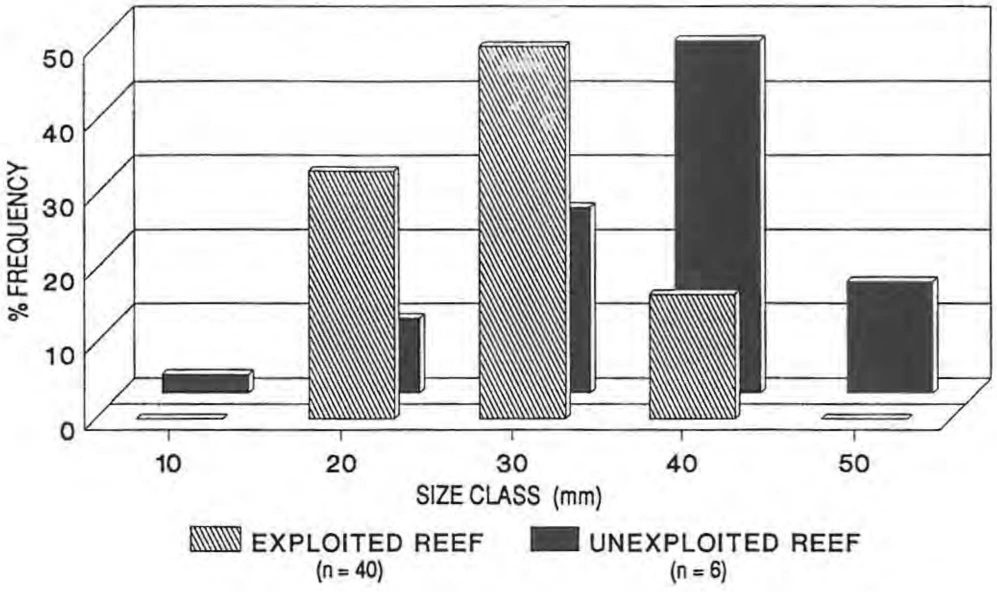


FIGURE 34: The length frequency distribution of *Coccotropsis gymnoderma* on exploited and unexploited shallow reefs.

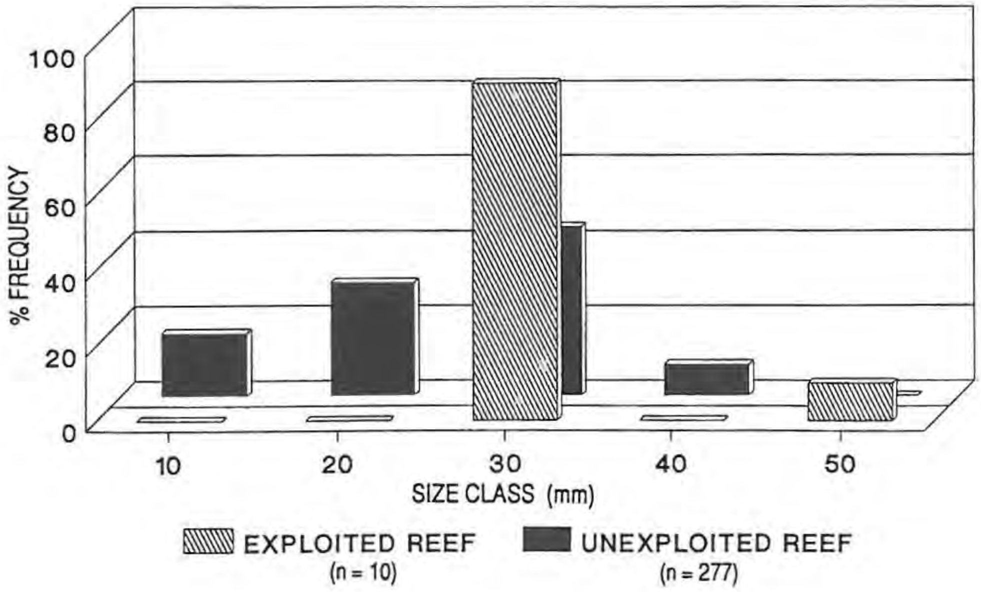


FIGURE 35: The length frequency distribution of *Coccotropsis gymnoderma* on exploited and unexploited deep reefs.

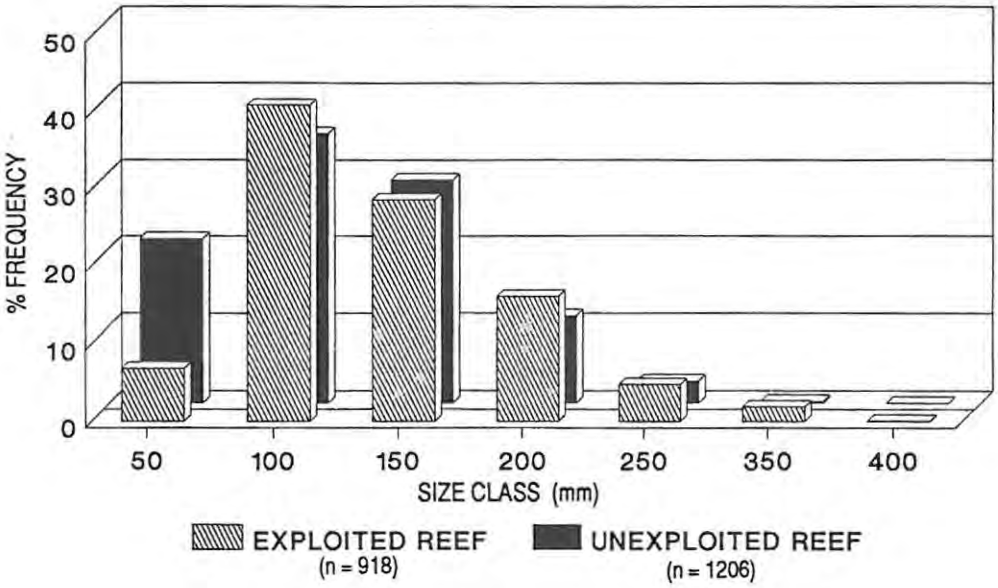


FIGURE 36: The length frequency distribution of *Boopsoidea inornata* on exploited and unexploited shallow reefs.

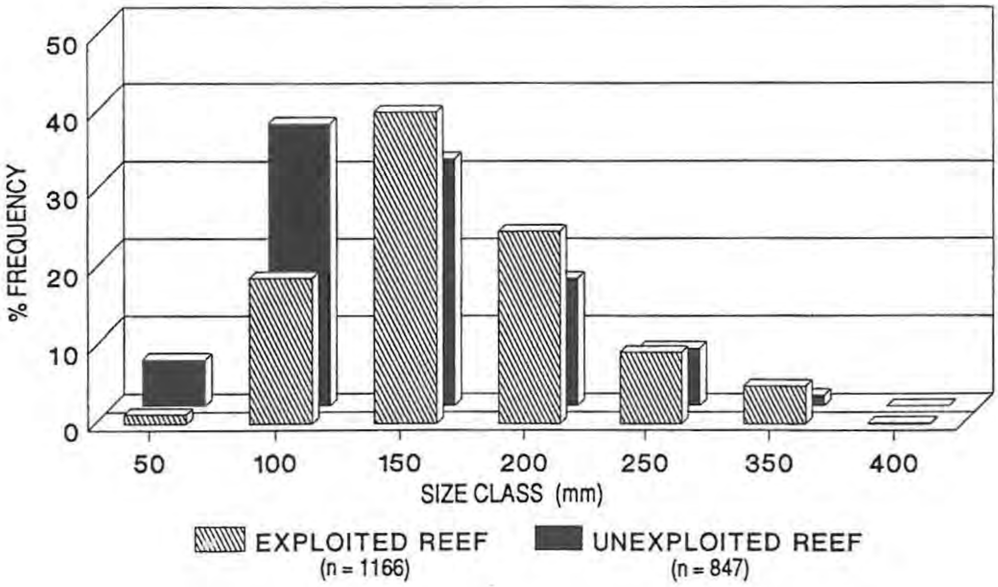


FIGURE 37: The length frequency distribution of *Boopsoidea inornata* on exploited and unexploited deep reefs.

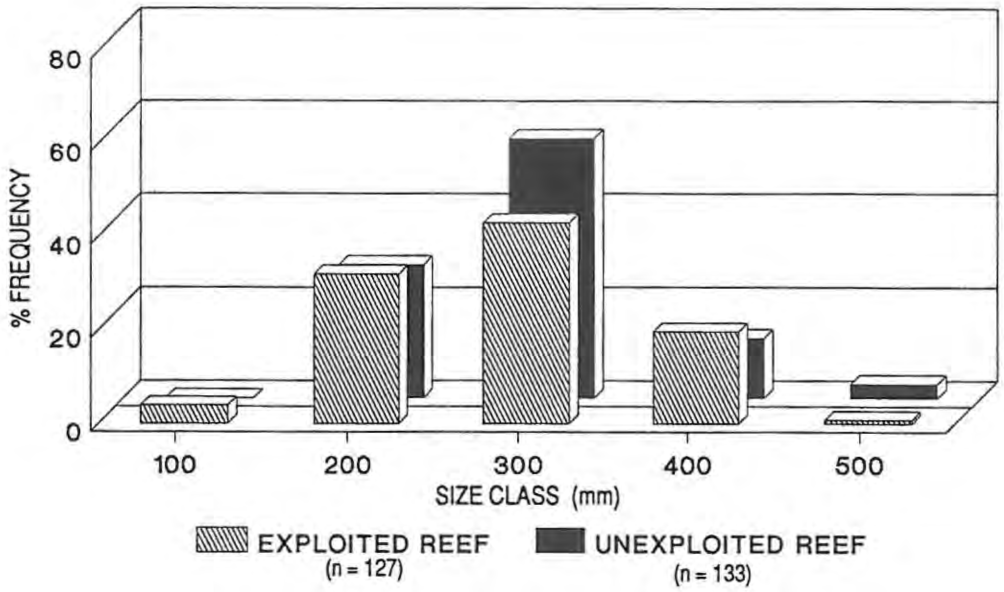


FIGURE 38: The length frequency distribution of *Chrysoblephus laticeps* on exploited and unexploited shallow reefs.

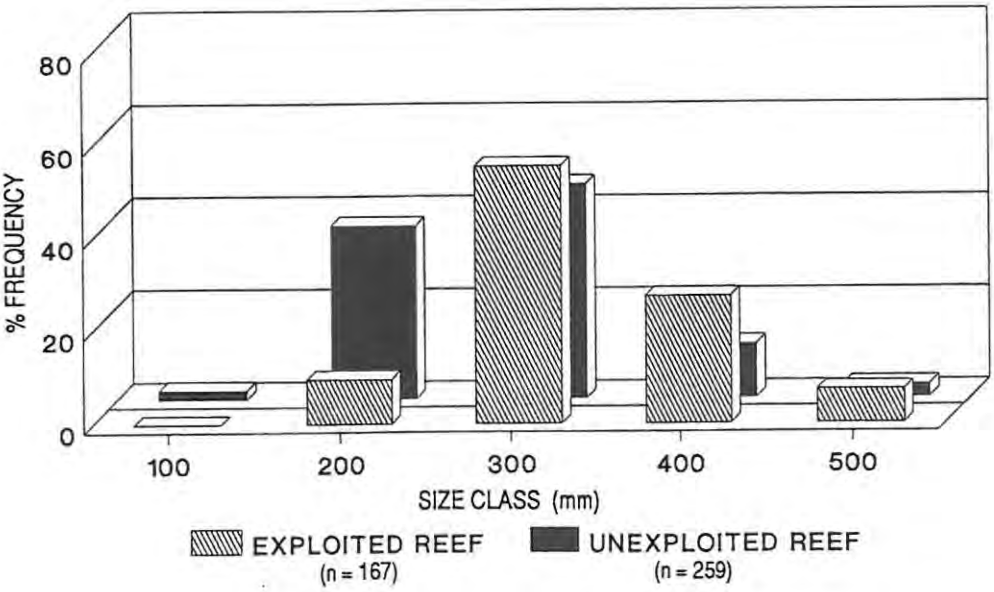


FIGURE 39: The length frequency distribution of *Chrysoblephus laticeps* on exploited and unexploited deep reefs.

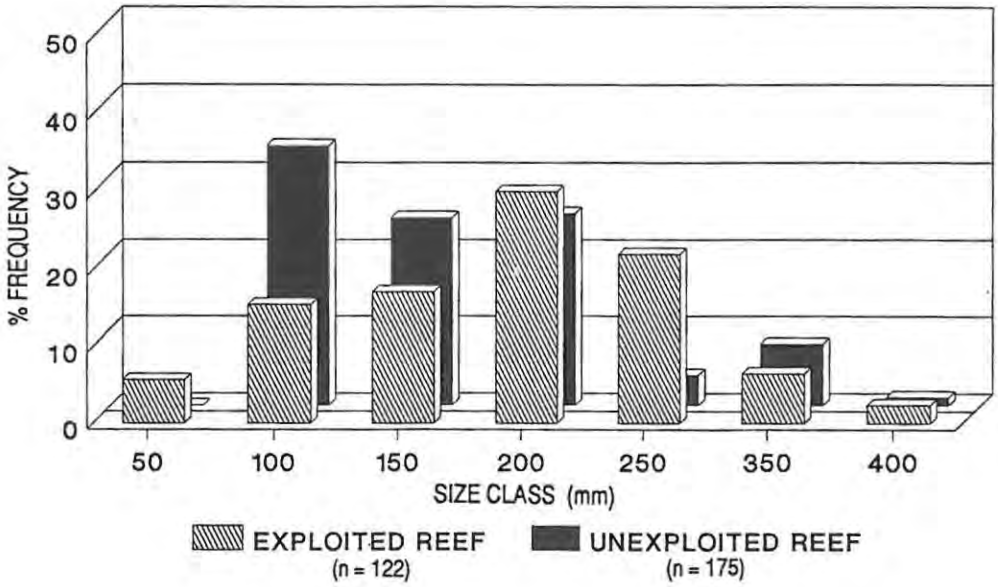


FIGURE 40: The length frequency distribution of *Pachymetopon aeneum* on exploited and unexploited shallow reefs.

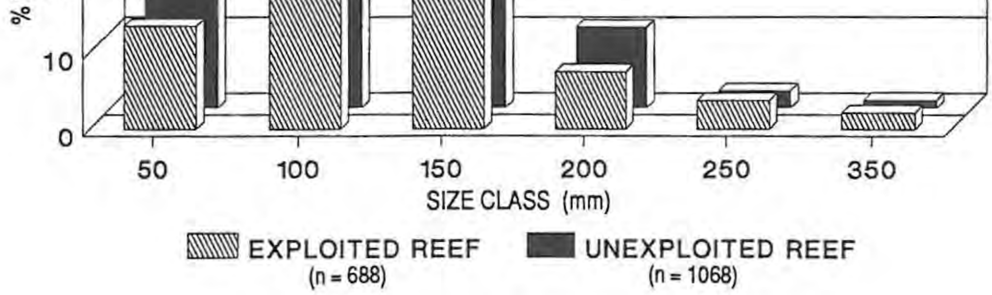


FIGURE 41: The length frequency distribution of *Pachymetopon aeneum* on exploited and unexploited deep reefs.

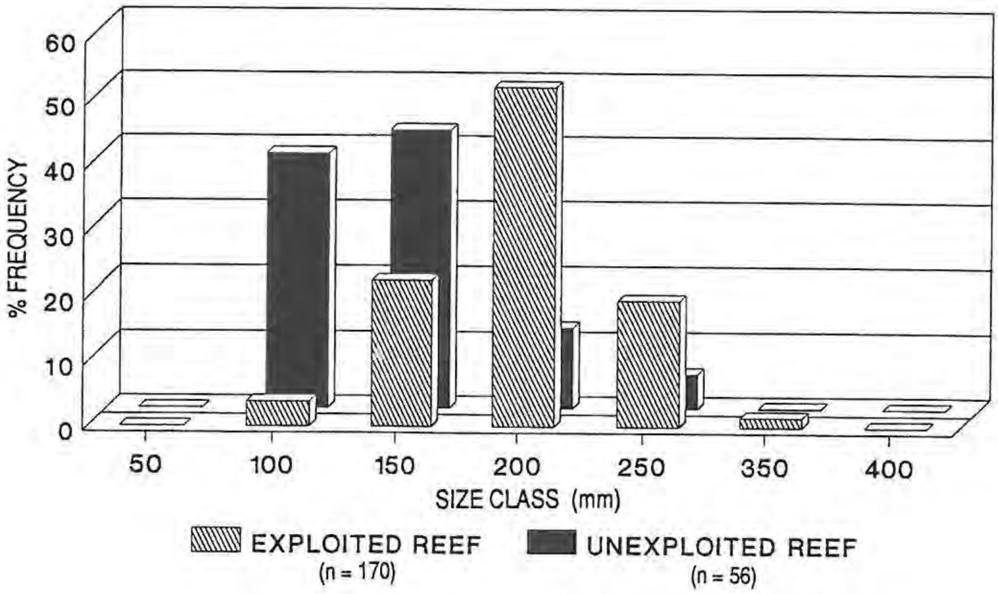


FIGURE 42: The length frequency distribution of *Spondyliosoma emarginatum* on exploited and unexploited shallow reefs.

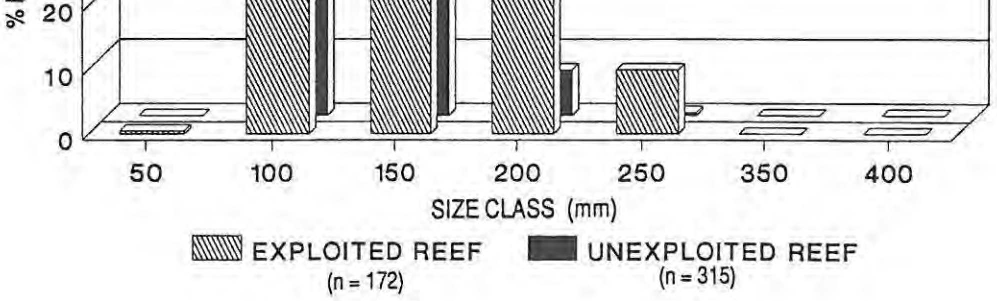


FIGURE 43: The length frequency distribution of *Spondyliosoma emarginatum* on exploited and unexploited deep reefs.

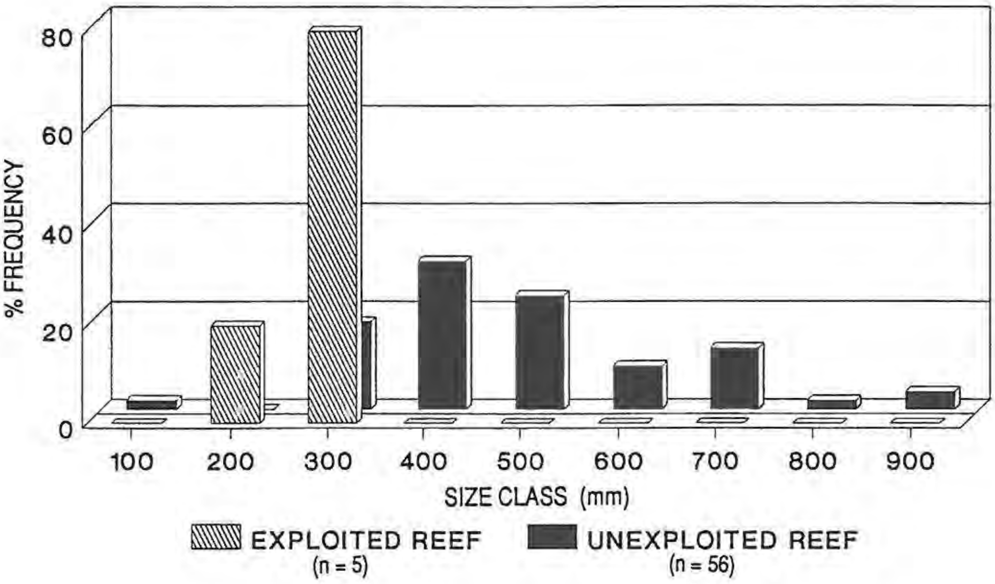


FIGURE 44: The length frequency distribution of *Petrus rupestris* on exploited and unexploited deep reefs.

3.4.6. Species diversity on exploited reefs.

The three diversity indices calculated for the cryptic and suprabenthic ichthyofaunal components on exploited reefs is shown in Table 23 below. The corresponding indices for unexploited reefs is given for comparison.

TABLE 23: Species diversity indices for cryptic and suprabenthic littoral fish on the two reef types on both exploited and unexploited reefs.

(a): CRYPTIC FISH

AREA	SPECIES	DIVERSITY MEASURE		
		MARGALEF	SHANNON	PIELOU
SHALLOW REEF - EXPLOITED	21	2.89	1.07	0.38
SHALLOW REEF - UNEXPLOITED	29	4.30	2.34	0.70
DEEP REEF - EXPLOITED	20	3.12	2.20	0.57
DEEP REEF - UNEXPLOITED	30	4.36	2.37	0.67

(b): SUPRABENTHIC FISH.

AREA	SPECIES	DIVERSITY MEASURE		
		MARGALEF	SHANNON	PIELOU
SHALLOW REEF - EXPLOITED	19	2.47	1.05	0.38
SHALLOW REEF - UNEXPLOITED	35	3.84	1.17	0.33
DEEP REEF - EXPLOITED	28	3.40	1.57	0.47
DEEP REEF - UNEXPLOITED	37	4.18	1.77	0.50

3.4.7. Intertidal seasonality.

In order to asses whether intertidal rock-pools were being utilised as nursery areas, summer and winter month intertidal samples were compared. The rationale being that the majority of sparids breed in spring - summer. The community structure as a whole for the three intertidal areas within the TNP for both summer and winter months is shown in tables 24 to 29 below.

TABLE 24: Upper intertidal rock-pools sampled with rotenone during summer between 1988 and 1990 (tansient species = T).

FAMILY/SPECIES	n	%N	T.L. (mm)		
			RANGE	MEAN	S.D.
GOBIESOCIDAE					
Chorisochismus dentex	18	5.8	63 - 180	108	27.2
SPARIDAE					
Diplodus sargus (T)	8	2.6	49 - 65	54.8	6.1
Sparodon durbanensis	66	21.1	21 - 62	45	8.2
CLINIDAE					
Cirrhibarbis capensis	2	0.6	102 - 106	104	2.8
Clinus cottoides	9	2.9	57 - 90	70.1	11.7
Clinus nematopterus	1	0.3	85	85	---
Clinus superciliosus	22	7	55 - 166	92.4	25.5
GOBIIDAE					
Caffrogobius caffer	187	59.7	25 - 150	73.9	29.3
N = 313					

TABLE 25: Upper intertidal rock-pools sampled with rotenone during winter between 1988 and 1990 (transient species = T).

FAMILY/SPECIES	n	%N	T.L. (mm)		
			RANGE	MEAN	S.D.
GOBIESOCIDAE					
Chorisochismus dentex	8	2.8	75 - 184	98.6	37
SPARIDAE					
Sparodon durbanensis (T)	11	3.8	49 - 125	69	20.7
CLINIDAE					
Cirrhibarbis capensis	3	1	67 - 105	87.3	19.1
Clinus cottoides	42	14.6	21 - 97	58.4	26.3
Clinus nematopterus	2	0.7	90 - 98	94	5.7
Clinus superciliosus	51	17.7	24 - 139	92.7	17.8
GOBIIDAE					
Caffrogobius caffer	171	59.4	35 - 135	77.5	21
N = 288					

TABLE 26: Sheltered lower intertidal rock-pools sampled with rotenone during summer between 1988 and 1990 (transient species = T).

FAMILY/SPECIES	n	%N	T.L. (mm)		
			RANGE	MEAN	S.D.
ARIIDAE					
Galeichthys ater	3	0.6	68 - 92	81	12.1
GOBIESOCIDAE					
Chorisochismus dentex	13	2.6	35 - 185	106	41.5
HAEMULIDAE					
Pomadasys olivaceum (T)	4	0.8	89 - 102	96.8	5.7
SPARIDAE					
Diplodus cervinus (T)	4	0.8	45 - 192	90.8	68.4
Diplodus sargus (T)	65	12.9	23 - 89	51.7	11.8
Lithognathus mormyrus (T)	2	0.4	85 - 110	97.5	17.6
Rhabdosargus globiceps (T)	2	0.4	75 - 80	77.5	3.5
Sarpa salpa (T)	24	4.7	66 - 104	85.3	11.6
Sparodon durbanensis (T)	185	36.5	18 - 122	58.7	17.2
CHEILODACTYLIDAE					
C. brachydactylus (T)	6	1.2	105 - 252	168	61.6
MUGILIDAE					
Liza richardsonii (T)	22	4.3	72 - 164	97.7	25.2
CONGROGADIDAE					
Halidesmus scapularis	3	0.6	20 - 42	34.3	12.4
CLINIDAE					
Cirrhibarbis capensis	11	2.2	20 - 110	42.5	33
Climacoporus navalis	1	0.2	30	30	---
Clinus cottoides	187	36.9	20 - 120	62.6	25.8
Clinus superciliosus	71	14	35 - 200	92.5	35.8
Pavoclinus graminis	2	0.4	35 - 40	37.5	3.5
Pavoclinus pavo	1	0.2	35	35	---
N = 606					

TABLE 27: Sheltered lower intertidal rock-pools sampled with rotenone during winter between 1988 and 1990 (transient species = T).

FAMILY/SPECIES	n	%N	T.L. (mm)		
			RANGE	MEAN	S.D.
CONGRIDAE					
Conger wilsoni	1	0.2	505	505	---
GOBIESOCIDAE					
Apletodon pellegrini	1	0.2	26	26	---
Chorisochismus dentex	7	1.3	75 - 95	85.7	8.5
KUHLIIDAE					
Kuhlia mugil (T)	1	0.2	32	32	---
SERRANIDAE					
Epinephilus guaza	1	0.2	140	140	---
SPARIDAE					
Rhabdosargus holubi (T)	2	0.4	76 - 86	81	7.1
Sparodon durbanensis (T)	35	7	36 - 155	71.4	25
MONODACTYLIDAE					
Monodactylus falciformes (T)	10	1.9	47 - 79	60	9.2
CHEILODACTYLIDAE					
Chirodactylus brachydactylus	10	1.9	100 - 142	113.4	12.5
MUGILIDAE					
Liza richardsoni (T)	13	2.5	70 - 102	90.2	7.7
CONGROGADIDAE					
Halidesmus scapularis	2	0.4	50 - 125	87.5	53
BLENNIIDAE					
Parablennius pilicornis	1	0.2	34	34	---
CLINIDAE					
Clinus cottoides	69	13	25 - 104	58.6	24.4
Clinus superciliosus	68	12.8	70 - 160	102.7	22.5
Pavoclinus graminis	2	0.4	49 - 70	59.5	14.8
GOBIIDAE					
Caffrogobius caffer	308	58	30 - 150	73.9	28.3
N = 531					

TABLE 28: Exposed lower intertidal rock-pools sampled with rotenone during summer between 1988 and 1990 (transient species = T).

FAMILY/SPECIES	n	%N	T.L. (mm)		
			RANGE	MEAN	S.D.
GOBIESOCIDAE					
Chorisochismus dentex	49	17.1	22 - 195	61.7	41.2
SPARIDAE					
Sparodon durbanensis (T)	2	0.7	130 - 153	141.5	11.5
CHEILODACTYLIDAE					
C. brachydactylus (T)	2	0.7	200 - 203	201.5	1.5
Cheilodactylus fasciatus (T)	3	1	126 - 148	138.7	9.3
CLINIDAE					
Blennioclinus brachycephalus	5	1.7	56 - 110	89.8	22.7
Cirrhibarbis capensis	16	5.6	43 - 130	88	30.3
Clinus cottoides	171	59.6	30 - 135	65.8	25.6
Clinus superciliosus	36	12.5	71 - 220	114.4	40.8
Climacoporus navalis	2	0.7	35 - 43	39	5.6
Pavoclinus graminis	1	0.4	39	39	---
N = 287					

TABLE 29: Exposed lower intertidal rock-pools sampled with rotenone during winter between 1988 and 1990 (transient species = T).

FAMILY/SPECIES	n	%N	T.L. (mm)		
			RANGE	MEAN	S.D.
GOBIESOCIDAE					
Chorisochismus dentex	25	12.3	17 - 203	79.8	46.3
BLENNIIDAE					
Parablennius cornutus	1	0.5	79	79	---
CLINIDAE					
Cirrhibarbis capensis	25	12.3	76 - 142	102	16.6
Clinus agilis	6	3	94 - 105	99.5	4.7
Clinus cottoides	111	54.7	34 - 124	76.5	19.5
Clinus superciliosus	27	13.3	92 - 196	136.1	33.1
Pavoclinus pavo	8	3.9	60 - 94	79.4	10.1
N = 203					

Differences between the observed frequencies of the constituent species found in summer and winter intertidal samples were tested statistically and the results are shown in Table 30.

TABLE 30: Summary of the Chi-square statistics for the three intertidal areas comparing summer and winter samples for each area.

ZONE	X^2	D.F.	SIG. LEVEL
UPPER ROCK-POOLS	84.3598	7	< 0.000005
SHELTERED ROCK-POOLS	466.748	8	< 0.000005
EXPOSED ROCK-POOLS	22.6444	8	< 0.000005

A significant difference was found between summer and winter samples for all three intertidal areas. Summer samples differed the most significantly to winter samples in sheltered intertidal rock-pools followed by upper rock-pools and exposed rock-pools. These differences were attributed to the observed increase in transient species during summer months (see Figure 45 below).

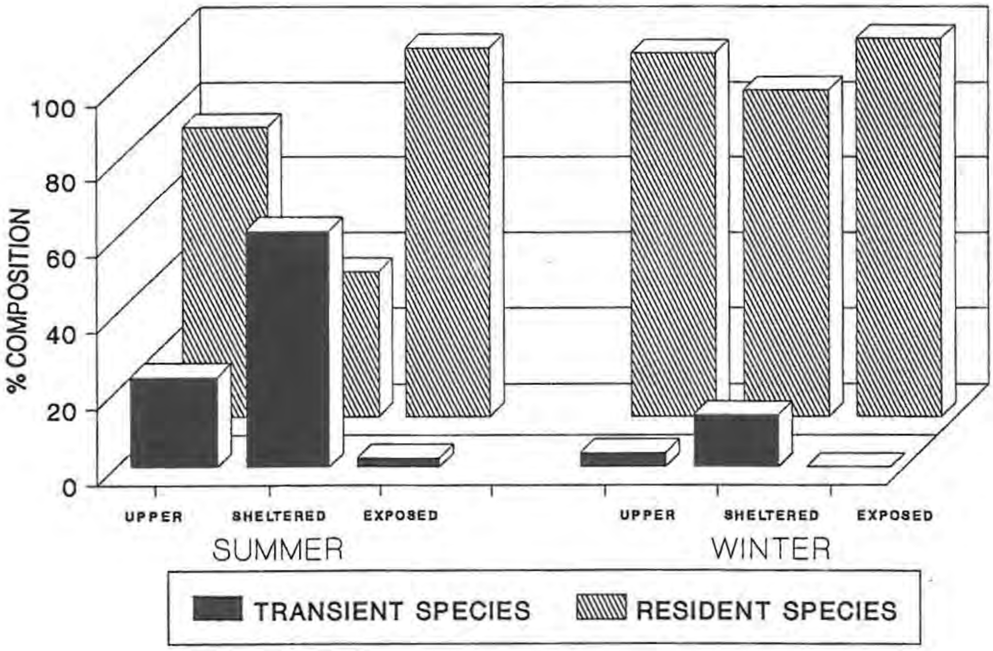


FIGURE 45: The percentage composition of transient species versus resident species in the three intertidal areas for both summer and winter months.

3.5. Discussion.

3.5.1. General distribution and relative abundance patterns of littoral fish within the TNP.

Distinct distribution patterns along the vertical littoral profile were exhibited by many species. In the following discussion cryptic families are treated first followed by the suprabenthic families.

Three gobies were recorded in the study area with quite different distribution patterns. *Caffrogobius caffer* was by far the most abundant of the three and occurred predominantly in upper intertidal rock-pools (making up 71.1% of the cryptic catch in this area), although it was found down to subtidal gullies (see Figure 25). Figure 9 shows it's length frequency distribution for upper and lower sheltered rock-pools. There appears to be no difference between the two areas. Bennett et al. (1984) also found that this species was more common higher up in the intertidal than in lower pools. The two other gobies that were recorded in the study area both had subtidal distribution ranges. The distribution of *Caffrogobius saldanha* was restricted to subtidal gullies whilst *Caffrogobius agulhensis* was found from shallow reefs down to deeper reefs. Gobies show a similar distribution pattern in the Port Elizabeth area. *C. caffer* was restricted to intertidal areas (Beckley 1985(a)) whilst Smale & Buxton (1989) recorded *C. saldanha* in subtidal gullies. *C. agulhensis* was absent from both of these areas. There would thus appear to be a definite zonation pattern amongst Gobies along the Cape coast, with the possibility that intra-specific competitive exclusion has taken place. Temperatures of 35° C (20° C higher than the sea temperature at the time) were recorded for upper intertidal rock-pools and the ability of *C. caffer* to withstand these high temperatures must play a role in it's ability to successfully inhabit this area.

Two species of clingfish were found in the study area with quite different distributions. *Chorisochismus dentex* was found intertidally where it was common in exposed rock-pools (15.3% of the catch). It's flattened morphology and it's ability to suck onto rock allows it to withstand the often severe wave action experienced in the region. The smaller *Apletodon pellegrini* was only found subtidally from gullies to deeper reefs. The marked difference in the diet and feeding behavious of the two species would preclude competition between them. *C. dentex* is a specialist feeder that has evolved a method of dislodging and feeding on flat molluscs (described by Stobbs 1980) whilst *A. pellegrini* is a more generalist feeder preying on small amphipods and isopods (see Chapter 4). *C. dentex* are common intertidally on the Cape Peninsula coast (Bennett & Griffiths 1984), the Cape Agulhas area (Bennett 1987) and in the Port Elizabeth area (Beckley 1985(a)). In addition Smale & Buxton (1989) recorded this species in great numbers in subtidal gullies in the Port Elizabeth area. The reason that *C. dentex* was not recorded subtidally in this study is puzzling.

Clinids were the most abundant group of cryptic fish. Eighteen species of the family Clinidae were collected in the study area, representing 47.4% of all South African clinids. Two clinids *Clinus cottoides* and *Clinus superciliosus* were found along the entire littoral profile, from upper intertidal rock-pools down to deeper reefs, although both showed a preference for intertidal rock-pools and subtidal gullies. The length frequency distributions of both species did not appear to differ between areas (see Figures 10 and 11). *C. cottoides* was common in all intertidal areas (see Figure 7) making up 9.4%, 39.8% and 58.4% in upper, lower sheltered and lower exposed pools respectively. This species was also common in subtidal gullies where it constituted 38.6% of the cryptic catch, but was poorly represented in shallow and deep reef collections. *C. superciliosus* showed a similar distributional pattern, making up 13.4%, 16.9% and 13% of the cryptic catch in upper, lower sheltered and lower exposed collections respectively (see Figure 7). This species was less abundant subtidally than *C. cottoides* comprising only 5.1%, 3.7% and 0.5% of the cryptic catch in gullies, shallow reefs and deep reefs respectively. Both *C. cottoides* and *C. superciliosus* have widespread coastal distributions, having been recorded along the entire Cape coast (Beckley 1985(a), Bennett & Griffiths 1984, Christensen & Winterbottom 1981, Smale & Buxton 1989). The remaining clinids were all present in small numbers in one or more of the six littoral zones. Only one clinid, *Blennioclinus brachycephalus* was restricted to the intertidal rock-pools where it was collected in exposed pools. In contrast, ten species of clinids had distributions that were restricted to subtidal areas. *Clinus robustus* was found only in subtidal gullies. *Clinus taurus* was found in gullies and on shallow reefs. *Clinus berrisfordi*, *Clinus venustris* and *Xenopoclinus kochi* were restricted to shallow reefs. *Clinus acuminatus* and *Xenopoclinus leprosus* were found on both shallow and deep reefs. *Pavoclinus profundus* (aptly named the deepwater klipfish) was collected only on deeper reefs.

Clinids are all viviparous (Smith & Heemstra 1986) and dissection of clinids during this study confirmed this and in addition revealed that differential development occurs. All clinid individuals of all species dissected had offspring in various stages of development from undeveloped eggs to well developed larvae. This prolonged breeding season together with the fact that young are born in an advanced stage of development would enhance the success of a cohort in the harsh littoral environment. A detailed study of the reproductive biology of this important littoral group would be extremely useful in helping to understand the high degree of endemism exhibited by this group as well as explaining their distribution patterns both vertically and horizontally along our coast.

Two triplefin species were collected in the study area, both with subtidal distributions. *Cremnochorites capensis* was found from subtidal gullies down to deeper reefs. It was the most common cryptic species on shallow reefs, making up 32.1% of the catch in this area. The length frequency distributions for this species showed a slight bimodal distribution, with modal peaks around 40mm and 60mm (Figure 12) for all three subtidal regions in which it was sampled. The nature of this size frequency distribution pattern is not understood, but may represent two cohorts of different ages. A second Tripterygiid was collected at Steilkop at 20m and at the same depth outside the park. This species has been found to be new to science and has been placed in a new genus (Holleman et al in press).

A single Tetrarogid species, *Coccotropsis gymnoderma*, was collected subtidally within the Tsitsikamma littoral zone. This species was the dominant cryptic fish collected on deeper reefs where it made up 28.6% of the collection. The size frequency distribution of this species showed a predominance of smaller individuals in subtidal gullies compared to the two reef areas (see Figure 13). However this may be an artifact of the low number of individuals sampled in gullies.

Two families dominated the suprabenthic component of the Tsitsikamma littoral ichthyofauna, namely the Cheilodactylids and the Sparids.

Cheilodactylus brachydactylus showed the widest distribution range and was the most abundant of the four Cheilodactylid species found within the Tsitsikamma littoral area. This species was found in all of the littoral areas, barring upper intertidal rock-pools. It was particularly abundant on coralline dominated shallow reefs where it made up 13.3% of the suprabenthic fish sampled in this area. Although this species constituted 28.5% of the suprabenthic fish collected in lower exposed rock-pools, only seven suprabenthic individuals in total (of all species) were collected from this area. More than 60% of this species sampled in sheltered pools were young fish <100mm in TL (see Figure 14). Exposed pools had larger individuals, with the majority falling into the 200mm size class (see Figure 14). There seemed to be no difference in the length frequency distributions between the individuals sampled in the three subtidal areas with a modal distribution, peaking in the 200mm size class, for all three areas. *Cheilodactylus fasciatus* was found subtidally from gullies down to deep reefs. The distribution of the closely related *Cheilodactylus pixi* was restricted largely to deeper reefs where it was relatively common (making up 5.2% of the sample). It was absent from gullies and made up only 0.3% of the shallow reef suprabenthic sample. No significant difference between the size frequency distribution of this species on shallow and deep reef areas was noted (see Figure 15). The fourth cheilodactylid found in the study area was *Chirodactylus grandis* which was only recorded on deep reefs. This species has an adult size that is much larger than the other three cheilodactylids (often reaching 1000mm in TL) and is more a free swimming species, roaming in mid-water above the reef (pers. obs.).

The most abundant suprabenthic group were the sparids, which as a family, were found in all six of the littoral zones. Only two sparid species were found in upper intertidal rock-pools, namely *D. sargus* and *S. durbanensis*. These two species also made up the majority of the sparids collected in lower sheltered pools (16.9% and 57.1% of the catch respectively) whilst *S. durbanensis* was the only sparid found in exposed pools. All of the above fish were juveniles (see Figures 23 and 24). Juveniles of *D. cervinus*, *Lithognathus mormyrus*, *Rhabdosargus holubi*, *Rhabdosargus globiceps* and *Sarpa salpa* were also collected in sheltered rock-pools although not in great numbers.

Four sparid species dominated the suprabenthic component in all three subtidal areas.

The herbivore *Sarpa salpa* was the most abundant suprabenthic species in subtidal gullies and on shallow reefs where it comprised 45.4% and 48.8% of the suprabenthic sample respectively. This species only constituted 3% of the suprabenthic fish censused on deeper reefs. The size frequency distributions for this species showed a predominance of individuals within the 100 mm size class, in all areas in which it was found (see Figure 19).

Boopsoidea inornata was abundant in all subtidal areas making up 13.8%, 22.4% and 24.6% of the suprabenthic fish sampled in gullies, shallow reefs and deep reefs respectively. Size frequency distributions for this species were similar for all three subtidal areas (see Figure 16).

Pachymetopon aeneum appeared to prefer deeper water where it was the most abundant suprabenthic species making up 31% of the sample. Although present on shallow reefs and in gullies this species only comprised 3.3% and 0.9% of the fish sampled in these areas, respectively. The apparent abundance of larger fish in subtidal gullies (see Figure 17) may also be an artifact of the low numbers censused in this area.

The fourth abundant sparid *Spondyliosoma emarginatum* also showed a preference for deeper reef where it made up 10.2% of the suprabenthic fish sampled in this area. It contributed only 1.04% to the shallow reef sample and 0.3% to subtidal gully censuses. The size frequency distribution of this species in the three subtidal areas was found to be similar with the majority of individuals being concentrated in the 100 and 150mm size classes (see Figure 18).

The three *Chrysoblephus* species that were recorded subtidally in the study area (*Chrysoblephus laticeps, Chrysoblephus gibbiceps* and *Chrysoblephus cristiceps*) all showed a deep reef preference. Density estimates for *C. laticeps* were 0.003 fish/m^2, , 0.0094 fish/m^2 and 0.021 fish/m^2 for gullies, shallow reef and deep reef respectively. These estimates compare favourably with previous work by Buxton and Smale (1989) within the TNP. They recorded density estimates of 0.023 fish/m^2 for the Knoll reef and 0.025 fish/m^2 for subtidal reefs within the TNP as a whole.
The size frequency distribution of this species was found to be similar for the three subtidal areas sampled (see Figure 18). Juvenile *C. laticeps* are known to occur in shallow subtidal areas (Buxton 1987 and pers. obs.) and it is suggested that the time of sampling would influence the observed frequency of juveniles. Juveniles are normally seen in gullies and on shallow reef towards the end of spring and through the early half of summer (pers. obs.). The other two *Chrysoblephus* species were less abundant. Both were absent from subtidal gully counts. Density estimates for *C. gibbiceps* were 0.00035 fish/m^2 and 0.0003 fish/m^2 for shallow and deep reef counts respectively. Buxton & Smale (1984), Buxton (1987) and Buxton & Smale (1989) have documented the fact that *C. cristiceps* avoids divers and this was confirmed during this study as well.

Another sparid that showed deep water preference was *Petrus rupestris*. Density estimates of *P. rupestris* were 0.00015 fish/m^2, 0.00028 fish/m^2 and 0.0045 fish/m^2 for subtidal gullies, shallow reefs and deep reefs respectively. Despite the higher density of this species on deeper reef it only made up 1.6% of the suprabenthic fish censused in this area. The density estimates obtained in this study compare favourably with those obtained by Buxton & Smale (1989). They recorded density estimates of 0.002 fish/m^2 for the Knoll reef at 20m depth and an overall density of 0.013 fish/m^2 for reefs between 12 and 27m within the TNP. Size frequency distributions for this species on shallow and deep reef showed a higher frequency of larger individuals on deep reef (see Figure 21).

Several suprabenthic species showed a preference for shallow water. Adult *Sparodon durbanensis* were common in subtidal gullies (making up 3% of the fish sampled in this area) with a density estimate of 0.014 fish/m^2 compared to 0.00035 fish/m^2 on shallow reefs and < 0.0001 fish/m^2 on deeper reefs.

Coracinus capensis, which is a well known shallow white-water angling species, showed a similar distribution pattern with a high density estimate for gullies (0.007 fish/m^2) and low estimates for shallow and deep reefs (0.00014 fish/m^2 and < 0.0001 fish/m^2 respectively).

Another species which showed a shallow water preference was *Pachymetopon grande*. Density estimates for this species in subtidal gullies and on shallow and deep reefs were 0.003 fish/m^2, 0.0011 fish/m^2 and 0.0005 fish/m^2 respectively.

The two *Diplodus* species found in the Tsitsikamma, *Diplodus cervinus* and *Diplodus sargus* were also more common in shallow water. As mentioned already juveniles of these species were found intertidally. *D. sargus* was found to be very common in subtidal gullies where it comprised 13% of the fish sampled, of which 63.5% were juveniles less than 50mm in total length (see Figure 23). Densities of this species were 0.056 fish/m^2, 0.0054 fish/m^2 and 0.0008 fish/m^2 for gullies, shallow reefs and deep reefs respectively. Densities of *D. cervinus* were 0.008 fish/m^2, 0.0024 fish/m^2 and 0.0001 fish/m^2 respectively.

Gymnocrotaphus curvidens was found in all three subtidal areas but was also more abundant on shallow reef where it contributed 2.57% to the total number of fish sampled in this area. The size frequency distributions of this species in the three subtidal areas shows a higher frequency of larger individuals (in the 400mm size class) on deep reef (see Figure 22).

3.5.2. Species diversity patterns.

The number of species recorded in each area for both the cryptic and the suprabenthic components increased down the littoral profile from upper intertidal rock-pools down to deeper reefs, with the exception of exposed rock-pools which did not fit this trend (see Figure 27). This anomaly may be explained by the fact that exposed pools are extremely harsh habitats being subjected to severe wave action for much of the time and would thus not support a great diversity of species. The high Pielou evenness index for suprabenthic species in exposed rock-pools area can be explained by the fact that only three suprabenthic species were collected in this zone with low numbers recorded for each species. Evenness for shallow and deep subtidal zones for the cryptic component of the littoral ichthyofauna were slightly lower than for subtidal gullies (see Figure 28). Krebs (1985) indicates that evenness will be lower if any species is dominant, in terms of numbers, in any community. The dominance of *Cremnochorites capensis* in shallow reef collections and *Coccotropsis gymnoderma* on deep reef collections would account for this slight drop in evenness. The fact that species richness and species evenness measures for suprabenthic species were slightly lower on shallow reefs than in subtidal gullies (Figure 29) may be explained by the fact that gullies are more protected than reefs. The dominance, in terms of numbers, of *B. inornata* on shallow reefs may have a lowering effect on these measures of diversity for shallow reefs as well.

3.5.3. Comparison of community structure between unexploited and exploited reefs.

Samples from exploited and unexploited reefs were to some extent similar in terms of the species that occurred in each. All the species sampled on exploited reefs were found on similar reef type inside the park, although the number of species recorded was higher for both shallow and deep unexploited reef (see Table 23). This difference in species composition together with great differences in the relative abundance of several species is thought to be the reason why the overall community structure was found to be significantly different. In addition the length frequency distributions differed for several species for the same reef types on exploited and unexploited areas.

Suprabenthic community structure at the family level appeared to be very similar in terms of percentage composition between exploited and unexploited reefs (see Figures 31(a) and (b)). However census data for both shallow and deep reefs outside the park was found to be significantly different to data for the same areas inside the park (see Table 22). Whilst relative abundance and density estimates for most species did not differ considerably between exploited and unexploited reefs, two species showed marked differences in relative abundance and density estimates. The most striking difference was the paucity of individuals of the top reef predator *Petrus rupestris* on exploited reefs compared to reefs inside the park. This species was not even seen on shallow reef outside the park during 49 visual transects, and it's density estimate for deep reef inside the park was nine times as high as on the same reef type outside the park (0.0045 fish/m^2 and 0.0005 fish/m^2 respectively). Furthermore the respective length frequency distributions for exploited and unexploited deep reef differed considerably. Figure 44 shows the absence of larger individuals of this species on exploited reef. In contrast the population sampled on unexploited reef shows an even size distribution with large individuals of up to 1000mm TL seen in this area.

The second major observed difference between exploited and unexploited suprabenthic samples was the increased abundance of *Boopsoidea inornata* on exploited reef compared to unexploited reef, especially on deep reef. Density estimates for this species were 0.1143 fish/m^2 on exploited deep reef and 0.068 fish/m^2 on unexploited deep reef. The size frequency distributions for this species did not differ considerably for shallow reef samples (see Figure 36), whilst deep samples showed a slight increase in the proportion of larger individuals on exploited reef (see Figure 37).

Of the three common suprabenthic species *P. aeneum, S. emarginatum* and *C. laticeps*, only *S. emarginatum* showed significant differences in length frequency distributions between exploited and unexploited areas (see Figures 42, 43). A higher frequency of larger individuals was recorded on shallow exploited reef than for shallow unexploited reef for this species.

The significant difference that was found between exploited and unexploited cryptic fish samples can also be explained by marked differences in the percentage contribution to the overall catch in each area shown by a small number of key species.

Cremnochorites capensis although being important on shallow reefs inside the park (where it made up 45.6% of the sample) was found to completely dominate the sample on shallow exposed reefs (making up 71.3% of the catch). This species was also the most dominant species on deep reef outside the park, where it made up 37.2% of the sample, compared to a 16.9% contribution to the sample on deep reef inside the park. Size frequency distribution comparisons between exploited and unexploited reefs revealed a higher frequency of smaller individuals on exploited reef, especially on shallow reef (see Figure 32).

The tetrarogid *Coccotropsis gymnoderma* that was the most dominant cryptic species on deep reef inside the park, where it made up 28.6% of the catch, was poorly represented in collections made on deep exploited reefs, only contributing 3.8% to the sample in this area. The clinid *Pavoclinus pavo* which was important in shallow samples inside the park, where it made up 21.3% of the catch, contributed only 0.4% to the sample collected on the same reef type outside the park.

It would thus appear that there has been a dramatic population increase by *Cremnochorites capensis* on subtidal reefs outside the park, to the detriment of the other cryptic species. Whether this has been as a direct result of the removal of the piscivore *Petrus rupestris* is unknown. *Cremnochorites capensis* is included in the diet of *P. rupestris* (Smale 1988) but it is not known to what extent this species is predated upon.

These observed differences between exploited and unexploited reef samples are discussed further, within the framework of previous work on the effects of the removal of top predators, in the final chapter.

3.5.4. Intertidal seasonality and the role of the Tsitsikamma rocky littoral zone as a nursery area for marine fish.

The importance of rocky intertidal and shallow subtidal areas along the South African coast as nursery grounds for juvenile marine fish has been discussed by Beckley (1985(a)), Bennett (1987) and Smale & Buxton (1989). Beckley (1985(a)) concluded that four species (*S. durbanensis, D. cervinus, C. fasciatus* and *C. brachydactylus*) may rely heavily or exclusively on tidal pools as nursery areas in the Port Elizabeth area. When assessing Cape rock-pools as nurseries for juvenile fish Bennett (1987) argued that when one considers the area of rock-pools available relative to the other habitats in which they occur, then rock-pools do not serve an important nursery function for juvenile marine fish.

In this study the frequencies of transient suprabenthic species were shown to be higher in summer samples than in winter samples from intertidal rock-pools. Sheltered rock-pools in particular showed a higher proportion of juvenile transient species in summer (62% of the fish sampled) than in winter (15% of the fish sampled) collections. Upper intertidal rock-pools had a limited nursery function and the role of lower exposed pools was negligable. However only two species - *S. durbanensis* and *D. sargus* appear to be utilising intertidal rock-pools as a nursery to any appreciable extent in the TNP (see Figure's 23 and 24). Based on the low numbers present in intertidal samples the other suprabenthic transient species do not appear to be utilising this area as nursery areas. In assessing the nursery role of the rocky littoral zone as a whole these results support Smale & Buxton (1989) who believe that the nursery function of intertidal rock-pools is possibly overstated and that they function together with shallow subtidal areas as "shallow-water nurseries". Further evidence for this was the occurrence of juvenile size fish for several species in subtidal areas. Appreciable proportions of juvenile fish (< 100mm TL) were recorded for three species in subtidal gully, shallow and deep reef samples respectively (shown as a percentage of the total number of individuals of that species recorded in each area) for the following species: *P. aeneum* (28%, 33.7% and 57.5%) , *B. inornata* (45.63%, 56.3% and 42.4%) and *S. emarginatum* (55.5%, 39.2% and 38.7%).

CHAPTER 4. THE TROPHIC DYNAMICS OF THE TSITSIKAMMA LITTORAL ZONE

4.1. Introduction.

The determination of community trophic composition is fundamental to the understanding of resource utilisation and resource partitioning. In addition community level feeding studies help explain fish distribution patterns and also how communities are likely to be affected by man-induced changes.

Most feeding studies on fish found in South African waters have concentrated on single species and while useful in autecological studies they have been of limited use in the understanding of the trophic dynamics of the whole community. The few multi-species feeding studies done along our coast include work by Christensen (1978) who studied the feeding habits of *Diplodus sargus, D. cervinus* and *Sarpa salpa* in the eastern Cape and showed how marked ecological separation occurred. Joubert & Hanekom (1980) conducted a detailed feeding study of seven important Natal inshore reef fish and provided qualitative information on the feeding of a further 23 species, combining these to characterise the trophic structure of the community as a whole. Bennett et al (1983) analysed the stomachs of 20 species of intertidal fish from the Cape Peninsula and examined the extent to which co-existing fish competed for the same food resource. Coral reef fish community feeding studies have predominated in the international literature (Hiatt & Strasburg 1960, Hobson 1974, Randall 1967, Williams & Hatcher 1983), with a few studies being done in temperate areas (Gibson 1968, Gibson & Ezzi 1987).

The trophic guild concept was first used by ichthyologists in the early 1960's working on coral reefs (for reviews see Smith 1978, Sale 1980). There seems to be no hard and fast rule in the criteria for defining trophic guilds. In the literature trophic groupings have ranged from broad categories of herbivores, omnivores and carnivores (Gibson 1968, Joubert & Hanekom 1980) to more defined aggregations often based on shared morphological feeding adaptations (e.g. Hiatt & Strasburg 1960, Hobson 1974, Randall 1967, Williams & Hatcher 1983). A combination of these two levels of trophic guild definitions was used in this study, similar to that of Williams & Hatcher (1983). For the purposes of this study a trophic guild is taken to be a group of fish whose diets overlap significantly or fish that are seen as utilising the same or closely related food resource.

4.2. Methods.

As the primary aim of this study was to compare the trophic structure of different areas within the Tsitsikamma littoral an exhaustive feeding study of every species was not attempted. Limited stomach contents analyses were used together with previous feeding studies to categorise species into the chosen trophic guilds. Of the 116 species recorded in the TNP, 46 were considered for this study. The remainder of the species are either (a) very rare (< 5 individuals collected), (b) tropical vagrants (e.g. Moorish idol, piano blenny) or (c) non-reef dwellers (e.g. predominantly white water spp. e.g. galjoen, sandy substratum dwellers e.g. *G. feliceps* or more pelagic fish e.g. Sciaenids).

Prey items were identified down to the lowest possible taxon, using Branch & Branch (1981), Day (1969), Griffiths (1976) and Kensley (1978). Frequency of occurrence, percentage volume and a ranking index combining these two parameters were used to analyse the contents. Frequency of occurrence was chosen for it's worth in comparing diets across the broad spectrum of feeders within the community, as it gives a quick and effective qualitative indication of diet (Hyslop 1980). To complement this and provide a measure of quantification the percentage volume method was used. A ranking method (after Hobson 1974) calculated as the frequency of occurrence multiplied by the mean percentage volume was computed for each prey category.

4.3. Results.

The stomach contents of 32 species were examined and the results of these are tabulated below in taxonomic order. The measurements in parentheses indicate the size range (total length) of the fish examined.

TABLE 31: The results of the stomach content analyses of 31 littoral fish examined from the TNP.

SPECIES / PREY ITEMS	%F	%V	RANK
Poroderma africanum (650 - 735mm) n = 4			
Brachyura	100	64	6400
Cephalopoda	75	35	2625
Poroderma pantherinum (560 - 600) n = 3			
Brachyura	100	100	10000
Gaidropsarus capensis (102 - 152mm) n = 7			
Amphipoda	86	76	6536
Brachyura	71	12	852
Macrura	14	12	168
Bidenichthys capensis (35 - 46mm) n = 6			
Amphipoda	83	72	5976
Mysidacea	33	28	924
Dermatopsoides talboti (52 - 56mm) n = 3			
Amphipoda	100	100	10000
Batrichthys apiatus (32 - 41mm) n = 3			
Amphipoda	100	65	6500
Isopoda	33	25	825
Mysidacea	33	10	330
Chatrabus hendersoni (155 - 176mm) n = 6			
Anomura	100	61	6100
Gastropoda	17	11	187
Brachyura	17	11	187
Isopoda	17	10	170
Pycnogonida	17	3.5	59.5
Macrura	17	3.5	59.5

SPECIES / PREY ITEMS	%F	%V	RANK
Apletodon pellegrini (21 - 25mm) n = 3.			
Amphipoda	100	100	10000
Chorisochismus dentex (131 - 182mm) n = 10.			
Gastropoda, *Helcion*	60	49	2940
Gastropoda, *Patella*	50	28	1400
Polyplacophora	40	15	600
Echinoidea	10	7	70
Macrura	10	1	10
Coccotropsis gymnoderma (29 - 42mm) n = 15			
Amphipoda, Gammaridea	73.3	66.7	4889
Amphipoda, Caprellidea	26.6	26	692
Macrura	13.3	7.3	97
Acanthistius sebastoides (110 - 262mm) n = 4			
Brachyura	75	57.5	4313
Ophiuroidea	50	30	1500
Isopoda	25	10	250
Crinoidea	25	2.5	62.5
Boopsoidea inornata (136 - 258mm) n = 7			
Polychaeta, Neridae	71.4	61.7	4405
Zoantharia	43	19.2	826
Gastropoda, *Helcion*	28.6	16.7	478
Porifera	14.3	1.7	24
Chlorophyta, *Ulva*	14.3	0.7	10
Chrysoblephus gibbiceps (392 - 587mm) n = 5			
Gastropoda	80	29	2320
Brachyura	40	29	1160
Sipunculida	40	17	680
Echinoidea, *Parechinus*	40	10	400
Polychaeta, Sedentaria	40	8	320
Holothuroidea	20	2	40
Amphineura, Polyplacophora	20	2	40

SPECIES / PREY ITEMS	%F	%V	RANK
Macrura, Caridea	20	2	40
Ophiuroidea	20	1	20
Gymnocrotaphus curvidens (291 - 289mm) n = 9			
Porifera	100	74.2	7420
Rhodophyta	66.7	15.8	1054
Unidentified animal	66.7	5.8	387
Bryozoa	33.3	1.7	56.6
Ascidia	33.3	1.7	56.6
Amphipoda, Caprellidea	33.3	0.8	27
Spondyliosoma emarginatum (195 - 250mm) n = 6			
Polychaeta, Surpulidae	50	33.3	1665
Amphipoda, Gammaridea	50	28.3	1415
Gastropoda	16.7	23	384
Unidentified animal	50	7	350
Rhodophyta	16.7	6	100
Amphipoda, Caprellidea	33.3	1.2	40
Macrura	33.3	1.2	40
Oplegnathus conwayi (153 - 582mm) n = 3			
Crinoidea	66.6	52	3463
Porifera	66.6	44.3	2950
Unidentified animal	33.3	3.7	123
Cheilodactylus fasciatus (88 - 170mm) n = 7			
Amphipoda, Gammaridae	86	56	4816
Amphipoda, Caprellidae	71.4	33	2356
Brachyura	71.4	8	571
Isopoda	43	3	129
Cheilodactylus pixi (90 - 157mm) n = 5			
Amphipoda, Gammaridae	80	52	4160
Brachyura	60	18	1080
Macrura, Penaeida	60	12	720
Isopoda	40	8	320

SPECIES / PREY ITEMS	%F	%V	RANK
Cirripedia	40	4	160
Echinoidea, *Parechinus*	20	3	60
Bivalvia	20	3	60
<u>*Chirodactylus brachydactylus*</u> <u>(156 - 300mm)</u> <u>n = 5</u>			
Amphipoda, Gammaridae	100	19	1900
Gastropoda	80	19	1520
Bivalvia	60	23	1380
Ophiuroidea	60	8.3	498
Echinoidea, *Parechinus*	40	7	280
Rhodophyta	40	5	200
Macrura, Caridea	40	5	200
Sand	20	3	60
<u>*Halidesmus scapularis*</u> <u>(89 - 123mm)</u> <u>n = 10</u>			
Amphipoda, Gammaridae	100	72	7200
Amphipoda, Caprellidae	100	28	2800
<u>*Chalaroderma ocellata*</u> <u>(26 - 35mm)</u> <u>n = 4</u>			
Amphipoda	75	50	3750
Bivalvia	50	27.5	1375
Rhodophyta	50	10	500
Gastropoda	25	12.5	313
<u>*Parablennius cornutus*</u> <u>(35 - 42mm)</u> <u>n = 3</u>			
Amphipoda	100	41.1	4110
Bivalvia	100	26.1	2610
Isopoda	100	6.1	610
Gastropoda	33.3	6.7	223
Rhodophyta	33.3	6.7	223
<u>*Cremnochorites capensis*</u> <u>(56 - 72mm)</u> <u>n =12</u>			
Amphipoda, Gammaridae	100	56.3	5630
Amphipoda, Caprellidae	80	23.7	1896
Isopoda	80	20	1600

SPECIES / PREY ITEMS	%F	%V	RANK
Blennioclinus stella (42 - 62mm) n = 3			
Amphipoda, Gammaridae	100	100	10000
Blennophis striatus (101 - 135mm) n = 4			
Amphipoda, Gammaridae	100	82	8200
Isopoda	100	18	1800
Cirrhibarbis capensis (123 - 151mm) n = 3			
Amphipoda, Gammaridae	100	100	10000
Climacoporus navalis (31 - 48mm) n = 9			
Amphipoda, Gammaridae	100	55.7	5570
Amphipoda, Caprellidae	66.6	22.5	1499
Isopoda	100	12	1200
Mysidacea	44.4	9.8	435
Clinus cottoides (62 - 89mm) n = 10			
Amphipoda, Gammaridae	80	58.3	4664
Amphipoda, Caprellidae	60	23.3	1398
Isopoda	50	18.3	915
Clinus nematopterus (41 - 86mm) n = 3			
Amphipoda	100	100	10000
Clinus superciliosus (86 - 163mm) n = 10			
Amphipoda, Gammaridae	80	65.8	5264
Isopoda	40	18.3	732
Bivalvia	40	13.3	532
Rhodophyta	20	2.6	52
Pavoclinus pavo (56 - 77mm) n = 5			
Amphipoda, Gammaridae	100	64	6400
Isopoda	100	36	3600

SPECIES / PREY ITEMS	%F	%V	RANK
Caffrogobius agulhensis (39 - 61mm) n = 6			
Amphipoda	100	41.6	4160
Chlorophyta	100	31.6	3160
Rhodophyta	66.6	26.6	1772
Caffrogobius caffer (79 - 123mm) n = 10			
Amphipoda	70	41.8	2926
Chlorophyta	70	33.3	2331
Isopoda	50	12.3	615
Copepoda	20	12.5	250

These results, together with the results of previous feeding studies, were used to place species into one of the trophic guilds outlined in Table 32.

TABLE 32: Trophic guilds of littoral fish found in the TNP.

GUILD	DEFINITION
1. HERBIVORES	Plant eaters
2. OMNIVORES	Plant/animal eaters
2.1. PLANKTIVORES	Zoo-/phytoplankton eaters
2.2. BENTHOS FEEDERS	Algae/invertebrate eaters
3. CARNIVORES	Animal eaters
3.1. MEIO-INVERTEBRATE FEEDERS	Motile meio-invertebrate feeders
3.2. MACRO-INVERTEBRATE FEEDERS	Motile/sessile macro-invertebrate feeders
3.3. PISCIVORES	Fish feeders

The herbivore group are fish that are browsers on epilithic algae. Planktivores were assumed to be omnivores as it is unlikely that fish specifically target for either phytoplankton or zooplankton whilst feeding in the water column (Williams & Hatcher 1983). The division between meio- and macro-invertebrate feeders is based on prey size and method of feeding. Meio-invertebrate feeders are those fish that prey mainly on crustaceans smaller than 10mm. Macro-invertebrate feeders are fish that feed on invertebrates larger than 10mm, both motile (mainly crustaceans and annelids that are taken whole) and sedentary (poriferans, ascidians and cnidarians that are often grazed upon).

A clearer break-down of the composition of feeding guilds is seen in Table 33. Only the important food categories are mentioned and it must be noted that many species have a wide range of prey items besides those mentioned.

TABLE 33: The species composition of the feeding guilds for the Tsitsikamma littoral zone.

GUILD/SPECIES	PRINCIPAL FOOD
<u>1. HERBIVORES:</u>	
Sarpa salpa	Chlorophyta, Rhodophyta (Christensen 1978)
<u>2. OMNIVORES - (a) PLANKTIVORES:</u>	
Parascorpis typus	Plankton
<u>2. OMNIVORES - (b) BENTHOS FEEDERS:</u>	
Pachymetopon grande	Algae, Hydrozoa, Octocorallia (Clarke 1988)
Caffrogobius agulhensis	Amphipoda, Chlorophyta
Caffrogobius caffer	Amphipoda, Chlorophyta, Isopoda
<u>3. CARNIVORES - (a) MEIO-INVERTEBRATE FEEDERS:</u>	
Gaidropsarus capensis	Amphipoda
Bidenichthys capensis	Amphipoda, Mysidacea
Dermatopsoides talboti	Amphipoda
Apletodon pellegrini	Amphipoda

GUILD/SPECIES	PRINCIPAL FOOD
3(a) MEIO-INVERTEBRATE FEEDERS cont.	
Coccotropsis gymnoderma	Amphipoda
Cheilodactylus fasciatus	Amphipoda, Brachyura
Cheilodactylus pixi	Amphipoda, Brachyura, Macrura
Chirodactylus brachydactylus	Amphipoda, Gastropoda, Bivalvia
Halidesmus scapularis	Amphipoda
Chalaroderma ocellata	Amphipoda, Bivalvia
Parablennius cornutus	Amphipoda, Bivalvia, Isopoda
Cremnochorites capensis	Amphipoda, Isopoda
Blennioclinus stella	Amphipoda
Blennophis striatus	Amphipoda, Isopoda
Cirrhibarbis capensis	Amphipoda
Climacoporus navalis	Amphipoda, Isopoda
Clinus cottoides	Amphipoda, Isopoda
Clinus nasatopterus	Amphipoda
Clinus superciliosus	Amphipoda, Isopoda, Bivalvia
Pavoclinus graminis	Amphipoda (Bennett et al. 1984)
Pavoclinus pavo	Amphipoda, Isopoda
3. CARNIVORES - (b) MACRO-INVERTEBRATE FEEDERS:	
Poroderma africanum	Brachyura, Cephalopoda
Poroderma pantherinum	Brachyura
Galeichthys ater	Brachyura, Isopoda, Cephalopoda (Tilney & Hecht 1990)
Batrichthys apiatus	Gastropoda, Bivalvia
Chatrabus hendersoni	Anomura
Chorisochismus dentex	Gastropoda, Polyplacophora
Acanthistius sebastoides	Brachyura, Ophiuroidea
Boopsoidea inornata	Polychaeta, Zoantharia, Gastropoda
Chrysoblephus cristiceps	Brachyura, Crinoidea (Buxton 1987)
Chrysoblephus gibbiceps	Brachyura, Gastropoda, Sipunculida
Chrysoblephus laticeps	Brachyura, Crinoidea, Cephalopoda (Buxton 1987)
Diplodus cervinus	Polychaeta, Amphipoda (Mann pers. comm.)*
Diplodus sargus	Echinoidea, Anthozoa, Gastropoda (Mann pers. comm.)*
Gymnocrotaphus curvidens	Porifera
Pachymetopon aeneum	Hydrozoa, Tunicata, Octocorallia (Buxton & Clarke 1986)
Rhabdosargus holubi	Crustacea, Echinoidea, Polychaeta (Buxton & Kok 1983)
Sparodon durbanensis	Gastropoda, Anomura (Clarke 1988)
Spondyliosoma emarginatum	Polychaeta, Amphipoda
Oplegnathus conwayi	Crinoidea, Porifera
3. CARNIVORES - (c) PISCIVORES:	
Petrus rupestris	Osteichthys, Cephalopoda (Smale 1986)

(* B.Q. Mann, Dept. Ichthyology & Fisheries Science, RU)

In order to compare the trophic structure of the six sub-areas outlined in Chapter 2 the relative proportion of individuals of all species belonging to a particular guild were computed for each area. Figure 46 illustrates the results of this comparison.

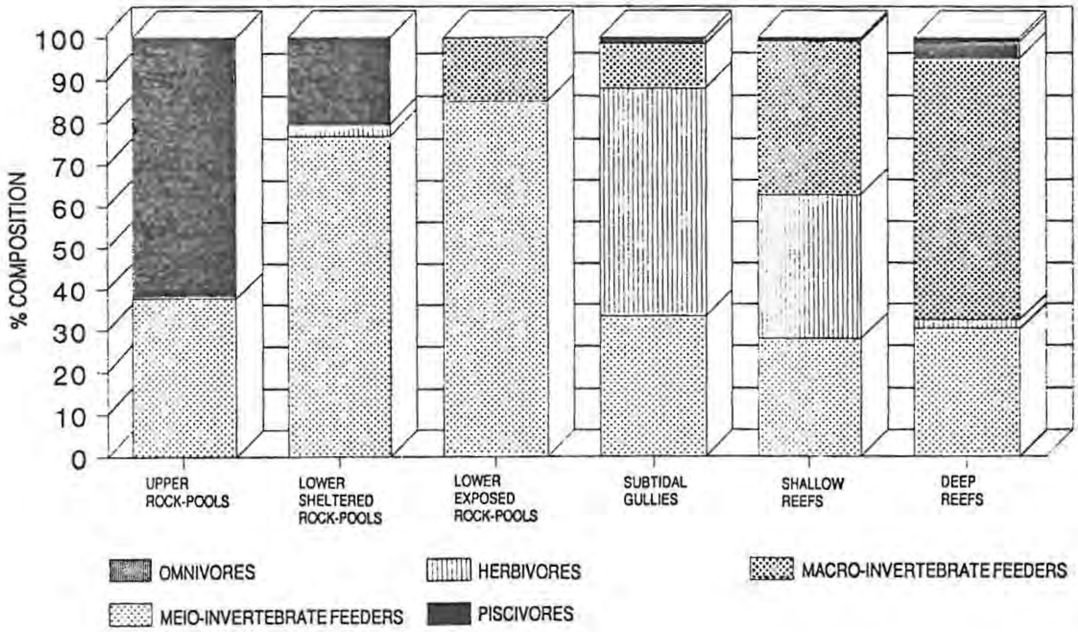


FIGURE 46: The trophic structure of the Tsitsikamma littoral ichthyofauna.

4.4. Discussion.

The trophic structure differed considerably between the six sub-areas within the Tsitsikamma rocky littoral zone. Numerical abundance of single species in each area affected the trophic structure considerably. Cousins (1987) warns against the use of simple, numerically based, trophic dynamics studies. This study does not investigate conversion rates or energy flow in any area and as a result is aimed purely at investigating broad differences in trophic structure between different areas.

Meio-invertebrate feeders were found to be an important group in all six littoral areas, explained possibly by the wide ranging distribution of amphipods. A range of littoral fish fell into this guild all of them cryptic or semi-cryptic (Cheilodactylids).

Macro-invertebrate feeders in contrast were largely restricted to subtidal areas, with the exception of the limpet and urchin feeder *Chorisochismus dentex* which made up the entire proportion of this guild in exposed intertidal rock-pools. Sparids, the most abundant subtidal suprabenthic group, accounted for the high proportion of macro-invertebrate feeders on shallow and deep reefs.

The herbivore guild was restricted to subtidal gullies and shallow reef. This limited distribution of the herbivore guild can be explained by the fact that algal growth is restricted to shallow subtidal areas which in turn limits the distribution of the single herbivore *Sarpa salpa*.

Trophic guild composition patterns cannot be explained by food availability alone as is illustrated by the high proportion of omnivores in upper intertidal rock-pools. The omnivore *Caffrogobius caffer* makes up more than 60% of the fish sampled in this area (see Figure 26). Macro-algal growth is extremely limited in this area and it is suggested that this species may be moving either diurnally or during high tides to feed in lower sheltered rock-pools where algal growth is more substantial. The high relative abundance of this species in upper intertidal rock-pools at low tides may be linked to it's high degree of temperature and/or salinity tolerance.

Whilst more detailed stomach content analyses may reveal targeting for specific prey species, there appeared to be a high degree of dietary overlap within trophic guilds, especially within the meio-invertebrate feeder group. Prey specialisation was observed in a few of the species studied. *G. curvidens* grazed almost entirely on sponges, it's prominent curved incisors allowing it to bite off small chunks of sponges. *Oplegnathus conwayi* also preyed heavily on sponges.
Several species appear to be utilising small crabs as a primary food source, including both *Poroderma* spp., *Acanthistius sebastoides* and *Chrysoblephus* spp., although none of these preyed entirely on crabs. *C. hendersoni* was found to target for anomurans. Both naked and shelled hermit crabs were found in their stomachs.

The fact that fish consume different prey at different times during their life is well documented in the literature (Bennett et al 1983, Buxton 1987, Cross 1981, Gibson & Ezzi 1987, Hobson 1974, Sale 1980). Bennett et al (1983) showed that 73% of the intertidal fish examined from the Cape peninsula showed changes in diet with increasing size and argued that prey selection depended on mouth size. Changes in diet with size have been demonstrated for many species found in the Tsitsikamma littoral area including *C. laticeps* and *C. cristiceps* (Buxton 1987), *S. durbanensis* (Beckley 1988, Clarke 1988), *P. rupestris* (Smale 1986), *C. dentex* Stobbs (1980), *S. salpa* (Christensen 1978), *D. sargus*, *D. cervinus* (Mann pers. comm.) and *A. sebastoides* (Smale 1986).

As several of these species are feeding on small crustaceans as juveniles (and are therefore meio-invertebrate feeders as juveniles) the chances of dietary overlap occuring within this guild are increased. Concurrent predation on any prey species may also be taking place at different times of the day thereby reducing overall competition for food. Bennett et al. (1983)

speculated that sub-division of the habitat may be occuring because of body shape. They point out that elongate species such as *H. scapularis* are able to gain access to considerably smaller holes and crevices than conventionally shaped species and therefore may exploit different food resources.

Finally an increase in the number of guilds with depth was noted in this study (see Figure 46). Related to this is the observed increase in trophic specialisation down the littoral profile. These trends are likely to be related to the documented increase in habitat heterogeneity, and benthos diversity with depth (Hanekom & Coetzee, in press). Whilst this study does not illustrate the point, it is possible that competition may be higher in intertidal areas where food is more of a limiting factor and that a higher level of resource partitioning is occuring in subtidal areas.

CHAPTER 5. THE ZOOGEOGRAPHICAL STATUS OF THE TSITSIKAMMA LITTORAL ICHTHYOFAUNA.

5.1. Introduction.

Attempts to divide the southern African coast into faunal regions or provinces started towards the end of the last century. Forbes (1856) and Woodward (1856) (in Briggs 1974) depicted a single "South African" province extending from about Bogenfels on the coast of South West Africa around the Cape to a point on the Natal coast just north of Durban. However it was the pioneering work of Stephenson (1939, 1944, 1947) on the rocky intertidal biota of southern Africa that really laid the foundation of South African marine zoogeography on which later workers have built. Stephenson (1947) proposed the subdivision of the coast into three major faunal provinces, a West Coast or Namaqua province, a South Coast or Agulhas province and a tropical East coast province. Tsitsikamma lies in the middle of the Agulhas province, which has been described as a warm temperate region (Briggs 1974).

Diversity patterns for different groups of organisms have been shown to correlate with these provinces including algae (Branch & Branch 1981), and invertebrates (Branch & Branch 1981, Brown & Jarman 1978). Although earlier ichthyological work by Hoese & Winterbottom (1979), Marsh et al (1978), Penrith (1970, 1972, 1976) and Winterbottom (1976(a), 1976(b), 1978) provided some insight into littoral ichthyofaunal distribution patterns, it is only in the last decade that thorough littoral ichthyofaunal surveys have been conducted along our coast.

5.2. Rocky littoral fish distribution patterns around the southern African coast.

More recent intertidal collections of rock-pools fish along our coast have revealed a distinct trend with an increase in the number of species, and a decrease in the proportion of endemics, as one moves from the western Cape, along the south coast and up the east coast (see Figure 47).

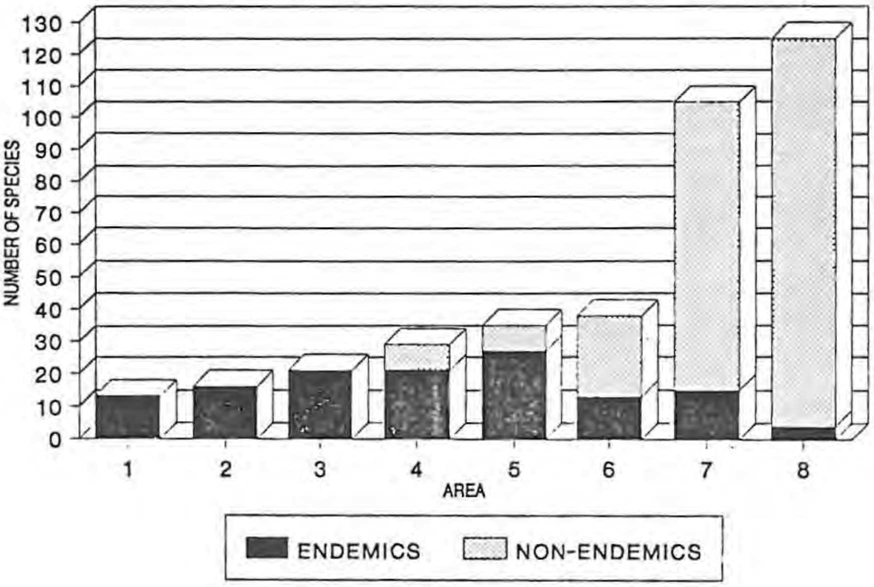


FIGURE 47: The relative proportion of endemic and non-endemic rocky intertidal fish along the South African coast for the following areas:

1. Cape Peninsula (Atlantic)	(Bennett & Griffiths 1984)
2. False Bay	(Bennett & Griffiths 1984)
3. Koppie Alleen	(Bennett 1987)
4. Tsitsikamma	**(This study)**
5. Port Elizabeth	(Beckley 1985(a))
6. Port Alfred	(Christensen & Winterbottom 1981)
7. Coffee Bay	(Walter 1988)
8. Sodwana Bay	(JLB Smith Inst. unpubl. data)

A similar trend in species diversity is illustrated in Figure 48. This can also be tied in with Stephenson's provinces and we can see that the diversity of intertidal fish is greatest within the tropical East Coast Province and least within the West Coast or Namaqua Province.

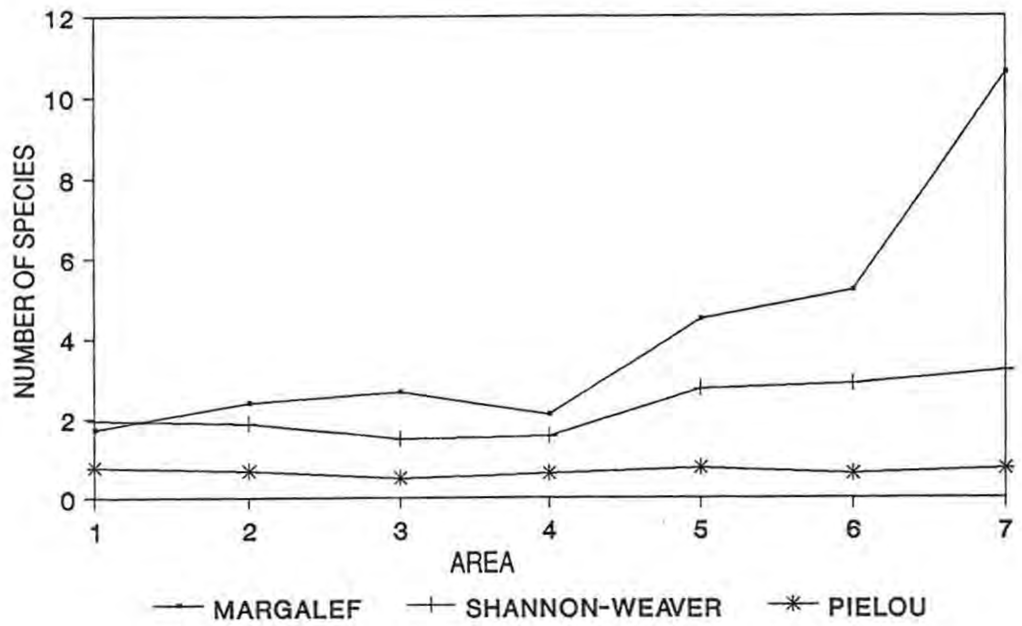


FIGURE 48: Species diversity trends in intertidal fish along the South African coast as measured by the Margalef species richness index, the Shannon-weaver overall index and the Pielou evenness index for the following places.

1. Cape Peninsula (Atlantic) (Bennett & Griffiths 1984)
2. False Bay (Bennett & Griffiths 1984)
3. Koppie Alleen (Bennett 1987)
4. Tsitsikamma **(This study)**
5. Port Elizabeth (Beckley 1985(a))
6. Port Alfred (Christensen & Winterbottom 1981)
7. Coffee Bay (Walter 1988)

Only three subtidal surveys other than this study have been conducted along the southern African coast. Burger (1988) sampled reefs in the TNP, Musson (1989) sampled a reef area off Port Alfred and Smale & Buxton (1989) documented the fish inhabiting subtidal gullies in Port Elizabeth. All of these studies, however, used only rotenone poisoning as a means of sampling and therefore excluded a large proportion of the total community (see Chapter 3). Total species counts and measures of species diversity are therefore incorrect for these areas. Attempts by Burger (1988) to compare subtidal survey findings are erroneous for this reason. There is thus insufficient data at present to provide a meaningful comparison of subtidal endemism and diversity.

5.3. Discussion.

The intertidal patterns outlined above can be better understood by considering the evolutionary theory concerning the origins of the Agulhas Province ichthyofauna.
There is general acceptance that the Indo-West-Pacific was the primary source for the majority of the world's marine fish fauna (Longhurst & Pauly 1987, Penrith 1976). In this area species evolved which were "slowly, surely, and conservatively selected for in a speciose and thus brutally competitive environment" (Mead 1970 in Penrith 1976). Penrith (1976) speculates that by the Pleistocene (1 million years ago) this fish fauna were "established, divergent, successful, but adapted to fairly restricted niches and in general had not penetrated much beyond the coral reef limit". The level of the sea at this time is thought to be about 100m higher than at present (Smith 1970). The low-lying areas of South Africa would have been submerged and warmer water would have flowed from the Indian Ocean to the Atlantic Ocean thus enabling fish of tropical Indo-West-Pacific origin to penetrate our waters. Penrith (1976) speculates that peripheral movements of less specialised forms of tropical species, which were "to a large extent adapted to reef conditions", would of occurred at this time. Perhaps the most important adaptation would of been the ability to utilize reef biota as a food source. Hobson (1974) notes that from early Mesozoic times the main line of actinopterygian evolution has progressed through a series of generalised carnivores feeding mainly on motile crustaceans and fish. The predominance of crustaceans as a food source for littoral fish was noted during this study and this may well have played an important role in the radiation of tropical ancestors into our waters.

Subsequent global cooling after the Pleistocene resulted in the retreat of the coastline and approximately 15 to 20 thousand years ago the sea level had dropped to around 130m below the present level (Smith 1970). This would of placed the southern edge of Africa some 150 km nearer the Antarctic than at present (Smith 1970) and would of formed quite a considerable barrier to further radiation of tropical fish species. Since then the sea has retreated once more to it's present day level. So it is therefore implied that the South African ichthyofaunal compliment evolved within the last million years and that the high level of endemicity in this area can be attributed to the unique set of events that have occurred around our coast during this time.

It is still unclear what events may have caused the geographic, reproductive or other form of isolation that would of been necessary for the speciation of southern African ichthyofauna, especially within the families Sparidae and Clinidae.
Further work that addresses the theory of zoogeographical distribution of littoral fish should concentrate on documenting the community structure in areas of faunal province overlap such as the Ciskei/Transkei region. The taxonomic as well as biological (reproductive and feeding) affinities of our temperate reef fish to coral reef assemblages, and in particular the western Indian ocean coral reef communities, should also be studied.

The fact that the inhospitable nature of our coastal waters foregoes regular subtidal sampling should not discourage field studies that could shed light on the origins of our littoral ichthyofauna and why such a high degree of endemism exists amongst out littoral fish.

CHAPTER 6. GENERAL DISCUSSION AND CONCLUSIONS.

6.1. Distribution patterns and factors affecting species distribution and community structure.

When trying to determine the factors which cause littoral fish distribution patterns it is important to remember that whilst certain factors, whether biotic or abiotic, might have more influence than others, all ecological elements work together in determining where certain fish are found. Firstly certain physical factors such as water temperature and wave action will have an overriding effect on littoral fish distribution patterns. Gibson (1969(a), 1982) points out the adaptations intertidal residents have evolved in order to withstand the severe wave action in this area. Gobies, gobiesocids and to a limited extent clinids and blennies, have modified pelvic fins which allow them to "suck" onto the substratum. Clingfish as their name implies are especially well adapted in this respect and this adaptation can be seen in *C. dentex*. This adaptation undoubtedly allows this species to successfully inhabit exposed rock-pools where they have evolved another special adaptation -- that of dislodging limpets and polyplacophorans (Stobbs 1980).

Temperature has been shown to influence littoral fish distribution patterns greatly. Gibson (1982) quotes a number of papers that have investigated the role of temperature in determining intertidal fish distributions. The ability of *C. caffer* to withstand the high temperatures experienced in upper intertidal rock-pools is believed to have allowed it to so successfully inhabit this region to the exclusion of other species. Stephens et al. (1984) showed how temperature gradients affected the distribution and abundance of temperate reef fish in California and illustrated how fish were found in areas of optimum temperature preference. Depth related subtidal temperature regimes have not been shown for the Tsitsikamma. Temperatures did not appear to differ significantly between shallow and deep samples for the same time of year. Cold-water upwellings have been discussed in Chapter 2 and it was noted during this study that thermoclines which had developed because of easterly winds often remained in place for some time after upwelling events at depths of around 12 to 20m. In other words deeper reefs may have lower temperature regimes which in turn could affect fish distribution and abundance patterns in this area. It would be a valuable exercise to monitor temperature fluctuations at various depths on subtidal reefs over time.

Odum (1971) points out that the more heterogeneous and complex the physical environment the more complex the plant and animal communities and the higher the species diversity. Habitat heterogeneity is measured at two levels. Macrospacial heterogeneity refers to topographic relief whilst microspacial heterogeneity refers to local scale relief (substratum cover) (Krebs 1985).

Both macrospacial and microspacial heterogeneity have been shown to increase with depth in the TNP (Buxton & Smale 1984, Hanekom & Coetzee in press). A benthic survey by Hanekom & Coetzee (in press) found that shallow, low relief reefs were species rich but had a low species diversity, and that medium to high relief deeper reef were species rich and had a high species diversity. This increase in benthic diversity with depth increases the habitat microspacial heterogeneity considerably because of the nature of the organisms involved. The proliferation of poriferans, ascidians, octocorals and bryozoans on deep reefs results in a marked increase in reef surface area. This increase in habitat heterogeneity has a twofold effect. Firstly available niches, purely in terms of space, are increased. Sale (1978) has indicated how important space is in reef ecology. This has profound implications for the diversity of cryptic species and it is not surprising that overall species richness of this component of the community increases appreciably with depth (see Figure 28). Secondly an increase in habitat heterogeneity will affect the trophic structure of the reef ecosystem as a whole by providing food for macro-invertebrate feeders that feed on sessile invertebrates themselves as well as providing niches for a greater diversity and biomass of smaller invertebrates which in turn will increase the diversity of cryptic fish (as shown by this study).

Food availability has been shown to be an important factor determining distribution of reef fish (e.g. Sale & Dybdahl 1978, Smith 1978, Talbot _et al._ 1978). Hobson (1974) considered trophic relationships to be the primary force in determining community organisation on coral reefs off Hawaii. Bell (1983) related the feeding requirements of reef fish in the Mediterranean to their observed distribution patterns. It was shown in this study that food availability plays a major role in determining species distributions. The widespread distribution of small crustaceans is believed to contribute to the observed abundance of meio-invertebrate feeders throughout the Tsitsikamma littoral zone. The availability of food is also thought to explain the distribution of herbivores and omnivores which are limited largely to shallow algae-rich areas. The distribution of many sparids that are macro-invertebrate feeders may also be linked to the increased biomass of sessile reef invertebrates on deeper reefs (Coetzee & Hanekom _in press_).

Whilst environmental factors and food availability may determine to a large extent what fish are found where, their success in that area is more closely linked to evolutionary responses to the environment such as reproductive strategy and behavioral peculiarities such as territoriality and competitiveness. The reproductive biology has only been studied in a few suprabenthic species found in the TNP and very little is known about the reproductive strategy of cryptic species. Elucidating reproductive rates, breeding behaviour, fecundity and method of dispersal amongst littoral ichthyofauna would provide valuable clues concerning observed distribution patterns.

Competition for food and space, the two most important resources for reef fish, is poorly understood, although it has been discussed at length in the literature (_inter alia_ Helfman 1978, Sale 1978, Sale 1980, Vandermeer 1972, Whittaker _et al._ 1973). Pianka (1974) notes that competition, in the sense of competing for identical resources, is only likely if such resources are in short supply. No evidence is available to assess whether food supply is scarce or abundant in the Tsitsikamma littoral zone. Gammarid amphipods, which were found to be the principal food item for a large number of meio-invertebrate feeders, are extremely abundant in the Tsitsikamma littoral especially on subtidal reefs where they are found in great numbers in amongst the reef benthos. It is therefore unlikely that food is a limiting resource within the TNP rocky littoral zone, especially on subtidal reefs. Similarly space is unlikely to be a limiting resource either, especially on deeper reefs which have been shown to have a high habitat heterogeneity.

It has been suggested that predation plays a major role in structuring reef fish communities (e.g. Huntsman 1979). Although several studies have compared exploited and unexploited areas (inter alia Bell 1983, Bohnsack 1981, Russ & Alcala 1989) and have shown clear community differences between these areas, no conclusive evidence exists that shows how top predators are regulating reef fish communities. Temperate reefs characteristically have large, often territorial, top predators belonging to a single species (Stephens & Zerba 1981, Stephens et al. 1984, this study). The extent to which these species are controlling the populations of reef fish is not known but the significantly larger populations of the abundant prey species *C. capensis* found on exploited reef in this study could be explained by the removal of the top predator *P. rupestris* from the same area.

The mobility of fish introduces another factor delimiting community structure. Gibson (1969(a), 1969(b), 1982, 1984) discusses the diurnal and tidal vertical migration patterns that are exhibited by intertidal fish, pointing out the difficulty (and often physical impossibility) of sampling intertidal areas during high tides.

As a result no quantitative field data exists that confirm such migrations. Endogenous rhythms of locomotory activity coinciding with tidal activity for two species of *Blennius* on the Mediterranean coast was shown experimentally by Gibson (1969(b)). Gibson (1982) points out that there are many examples of restricted movement on rocky shores. In this regard Marsh et al (1978) demonstrated that South African clinids moved between pools at high tide and that some individuals showed fidelity to particular pools over a 4-month period. Slow recolonisation rates of pools which have been experimentally depopulated have been attributed to the fidelity to a particular area and the restricted movement within it (e.g. Bussing 1972 in Gibson 1982). Beckley (1985(b)) found, however, that rapid recolonisation occurred with species of Clinidae, Gobiidae, Sparidae and

Cheilodactylidae in intertidal rock-pools in the Port Elizabeth area. She found that repopulation of pools was not exclusively by juvenile recruits and suggested that the larger recolonisers were fishes from adjacent pools whose home ranges overlapped, with the study pools. She did not, however, show that fishes home ranges extend beyond the limit of their immediate pool. Vertical feeding migration of the goby *Caffrogobius caffer* during high tides, from upper intertidal rock-pools where they are the most abundant cryptic species to lower to pools containing macro-algae, was suggested earlier in this study (see Chapter 4). The work of Butler (1982) in the eastern Cape suggests that this species does not undergo such migrations as he found that feeding was not influenced by tide phase, with peaks of feeding occurring during both high and low tides. It is possible that *C. caffer* does indeed undergo tidal feeding migrations within the Tsitsikamma intertidal zone where food may not be as plentiful as in other rocky intertidal areas along our coast.

Cryptic subtidal fish by their very nature would not benefit from substantial movement away from their protected reef environment. The life-history strategies of the majority of the cryptic subtidal species in the Tsitsikamma suggest a stenotopic life-style. As mentioned all the clinids are viviparous and their offspring are unlikely to brave the pelagic gauntlet and are more likely to undergo more localised dispersals. It is possible that "pregnant" females may undergo vertical movements before the offspring are born but no evidence for or against this exists. The other two abundant cryptic subtidal species *Coccotropsis gymnoderma* and *Cremnochorites capensis* were both found to have large adhesive eggs with a low fecundity. The two toadfish found subtidally (*Batrichthys apiatus* and *Chatrabus hendersoni*) were also found to have similar reproductive strategies. It is therefore unlikely that these cryptic subtidal species undergo great vertical migrations either for reproductive purposes or for feeding. Leum & Choat (1980) found that the semi-cryptic cheilodactylid *Cheilodactylus spectabilis* did not undergo diurnal feeding migrations on a temperate reef in New Zealand.

Even though suprabenthic species may, because of their free swimming behaviour, have a much greater capacity for vertical and horizontal migrations, indications are that large scale migrations of most suprabenthic species is not taking place. Tagging studies by Buxton (1987) of *Chrysoblephus laticeps* and *Chrysoblephus cristiceps* within the TNP showed a high degree of residency with tagged individuals being recaptured on the same reef up to 565 days later. Tagging studies on these and other species has been continued since then and are currently still being done. Tagged fish were observed underwater on numerous occasions during the study period on The Knoll, Steilkop and Waterfall reefs (to the west of Stormsriver mouth). One particular *Petrus rupestris* individual was observed on exactly the same part of the Steilkop reef during visual censusing in this area. It was easily identified because of it's large size and the exact position of it's tag. It was thought to be tagged some three months previous to this set of sightings.

Localised vertical migrations for reproduction, either for mating, spawning or both, cannot be ruled out for suprabenthic species, especially sparids. Buxton (1987) documented the spawning behaviour of *Chrysoblephus laticeps* which involved mid-water vertical migrations but there is no evidence for migration into shallower water *per se*. The peculiar nesting behaviour of *Spondyliosoma emarginatum* has been described by Bruggen (1965 in Penrith 1972(b)) and Penrith (1972(b)). A nesting aggregation of *Spondyliosoma emarginatum* as described by these authors was observed early in November 1990 in shallow water (10m) near the mooring gully in the Stormsriver mouth. Eight males that were dark in colour (almost black) with light vertical bars posteriorly were observed guarding nest sites approximately half a meter in diameter on sandy substrate. They actively chased other species away and swam up to the several lighter coloured females that were swimming around above the nests. The density of this species was found to be far greater on deep reefs than on shallow reefs (0.028 fish/m^2 and 0.0039 fish/m^2 respectively) and it is therefore possible that this species is migrating into shallow water to breed.

Whilst migrations may affect community structure the beforementioned factors of temperature, habitat heterogeneity, food availability, competition and reproductive strategy are more likely to be primary causal factors in delimiting littoral fish distributions and overall community structure.

6.2. The effect of the removal of top predators and the community structure of exploited reefs.

The results of the comparison of community structure between exploited reef outside the park and unexploited reefs inside the park supports the growing evidence in the literature that exploitation of top reef predators is having a marked effect on the community structure of reef fish communities (Bell 1983, Bohnsack 1981, Mclanahan & Muthiga 1989, Pimm & Hyman 1987, Russ & Alcala 1989, Schaap & Green 1988).

Both the low densities and the reduction in the proportion of larger size classes (see Figure 44) for *Petrus rupestris* are classic indications of over-fishing (Bell 1983, Russ & Alcala 1989, Schaap & Green 1988). Smale (1988) argues that *P. rupestris* may be less sensitive to heavy exploitation because of their high reproductive output. However he fails to include in his argument their slow growth rate and large age at maturity (which he showed to be 575mm FL). The extremely low number of individuals of breeding size on exploited reefs shown by this study further suggests that populations of this species have been adversely affected by exploitation.

The increased abundance of *Cremnochorites capensis* on exploited reefs may, or may not, be as a direct result of the removal of *P. rupestris*. Although this species is included in the diet of *P. rupestris* (Smale 1986) the extent or rate of predation is not yet known. The densities of three cheilodactylid species and the serranid *Acanthistius sebastoides* which Smale (1986) showed to be the favourite prey of *P. rupestris* were not found to be greatly different between exploited and unexploited reefs. Whilst an increase in prey densities was recorded for heavily fished areas by Russ & Alcala (1989), Bohnsack (1981) showed significant increases in the abundance of species (on exploited reefs) that were not being preyed on specifically by top predators. Therefore the removal of top reef predators may have indirect effects which allow one or more species to rapidly increase their populations to the detriment of co-existing species. The increase in the density of *Boopsoidea inornata* on exploited reefs outside the park compared to unexploited reefs inside the TNP may be explained in this way.

Bell (1983), Russ & Alcala (1989) and Schaap & Green (1988) all found significantly lower species diversity on exploited reefs compared to unexploited reefs. The observed difference in species diversity found in this study, with diversity lower on exploited reefs outside the park than for reefs inside the park, is further evidence of community disruption having occurred because of exploitation.

The underlying assumption that is being made in the above discussion is that temperate reef ecosystems are stable ecosystems in a state of equilibrium. Two schools of thought exist amongst biologists concerning the equilibrium status of reef fish communities and has resulted in the order versus chaos controversy (Bohnsack 1983). The order theory proposes that reef fish communities are constant, with relatively little change in composition through time (e.g. Smith 1978). The chaos theory in contrast has been supported by observations that reef fish composition is unpredictable with great variation from one census to the next (Sale 1978, Sale 1982, Sale & Dybdahl 1978, Talbot et al. 1978). Bohnsack (1983) showed how time intervals between samples had a pronounced effect on estimates of reef fish species turnover rates and argued that differences between the two schools of thought may have arisen as an artifact of the time interval between samples. Regardless of the turnover rates of the temperate species found on reefs off the Tsitsikamma, the observed differences between exploited and unexploited samples are so significantly different that they cannot be explained by the time interval between samples in the two areas.

Exploitation of the top reef predator *P. rupestris* on reefs outside the TNP has had a deleterious effect on the density and size distribution of this species. The fact that key species, within both the cryptic and suprabenthic components of the reef fish community, are significantly more abundant on reefs outside the park indicates either direct or indirect disruption of the reef fish community structure due to the removal of this top predator.

6.3. Conclusions and recommendations.

This study shows that the TNP offers protection to a diverse assemblage of littoral fish. In addition the position of the TNP on the south coast of southern Africa means that fish representative of the Agulhas Province littoral ichthyofauna are protected as a part of their pristine ecosystem.

The fact that ichthyofaunal species diversity increases with depth highlights the importance of the 5.6km seaward boundary of the TNP in protecting offshore reef ecosystems.

The results of the comparison between unexploited reefs within the TNP and exploited reefs outside the Park forms part of the growing evidence that marine reserves can and are playing a vital role in conserving our reef ecosystems in their entirety. It is suggested that further replication of data be carried out on exploited reef in the Natures Valley area. If further study supports the findings of this study then it is recommended that the 5.6km seaward boundary of the TNP be extended westwards to the De Vasselot area to offer protection to the large concentration of rocky reef that has been shown by side-scan sonar surveys (Buxton 1987) to exist in this area, particularly between the Groot River and the Bloukrans river mouths.

If long-term monitoring is carried out in such a newly proclaimed area, especially for key species such as *P. rupestris*, it would provide extremely valuable information concerning the rehabilitation of exploited environments that would in turn be of great use to marine ecosystem management along our coastline.

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