ASSESSMENT OF THE EFFECT OF GOUKAMMA MARINE PROTECTED AREA ON COMMUNITY STRUCTURE AND FISHERY DYNAMICS

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ABSTRACT

This study presents a detailed investigation into size, density and community structure of temperate marine reef fish in the medium-sized Goukamma Marine Protected Area (Goukamma MPA) and adjacent fishing grounds on the south coast of South Africa. The oceanographic conditions, the spatial distribution of the benthic community and the prevailing fishing effort are also described. Life history traits and per-recruit (*PR*) models for the principle target species, roman (*Crysoblephus laticeps*) are compared between the protected and exploited area. From the study results, various strategies are proposed for the use of MPAs in the conservation and management of linefish species along South Africa's south coast.

The distribution and topography of reefs in the protected and exploited sections of the study area were found to be comparable. Atmospheric pressure ranged from 992 to 1,032 mb, being significantly lower in summer. Wind speeds ranged from 0.7 to 71.3 km/h. Water temperatures ranged between 9.0 and 22.2 ºC and turbidity between 0.3 and 45.8 NTU. Water temperature and clarity were uniformly low in winter. In summer the water was generally warm, clear and stratified, with a thermocline at around 20 m, although intermittent upwelling events caused water temperature to decrease and clarity to deteriorate. Current speeds ranged between 0.11 and 2.59 km/h and were significantly higher in spring and autumn. Easterly currents prevailed in spring, summer and autumn and westerly and southerly currents in winter.

Hake (*Merluccius capensis*), various resident reef fish and kob (*Argyrosomus japonicus*) were most frequently targeted by the local linefishery. A significant amount of illegal fishing was found to occur in the protected area. Fishing effort was found to be highest around the border of the MPA (2.7 boats/km^2) and lowest in the core of the MPA (0.2 boats/km^2). If law enforcement remains poor it may be necessary to adapt the management strategy to extend the reserve, thereby mitigating against illegal fishing and ensuring a core area of no exploitation. Various other alternatives were investigated and it was demonstrated that the amount of fish caught of legal size could be increased by about 23% and post-release mortality of undersized fish reduced by 50% through the introduction of a suit of restrictive measures.

Randomly stratified underwater visual census (UVC) and controlled fishing were used to investigate the ichthyofauna and benthic community at protected and exploited sites in the study area. Resulting density and size data from 273 fishing sites and 177 point counts were analyzed using generalized linear models (GLMs). Fish communities were found to vary significantly, depending on the level of exploitation. Roman, the principle reef fish species targeted by the fishery had significantly higher densities within the protected parts of the study area (CPUE: 4.3 fish/anglerhour; UVC: 2.2 fish/point-count) as compared to the exploited part (CPUE: 3.4 fish/anglerhour; UVC: 1.8 fish/point-count), correlating strongly with the observed fishing effort. Also mean sizes were significantly higher in the protected area (299 mm from fishing survey and 233 mm from diving estimates) as compared to the exploited section (283 mm from fishing survey and 198 mm from diving estimates). Although other fish species also had significantly higher mean sizes at protected sites in most cases their densities were significantly lower. This suggests a top-down control of the fish community by the dominant predator (roman).

The results of the UVC showed the diversity of the ichthyofauna to be significantly higher inside the protected area. Interestingly this did not apply to the results of the controlled fishing experiment where the diversity of fish in the catch was lower in the protected area - a result that may be explained by the selectivity of fishing for the most aggressive species – and a reminder of the limitations of controlled fishing experiments. Possibly the most important finding of the study revolved around the benthic community. These were significantly different at exploited and protected sites, with algae and crinoids more abundant at exploited sites. Crinoids are the principle food of roman and were low in abundance where roman abundances were high, suggesting that the dominant top predator reduced crinoids. Furthermore, it substantiates the correlation of roman abundance with fishing effort, since habitat preferences can be ruled out by the observed causal predator-prey distribution pattern. Low algae abundances at protected sites correlated with high strepie (*Sarpa salpa*) frequencies within the fish communities encountered there. Strepie, a shoaling and abundant benthic grazer, does not compete for food with roman, suggesting a high potential for coexistence of the two species.

As expected, and found by other studies, life history traits of roman differed between protected and exploited sample-sites. With a significantly lower age-at-maturity and age-at-sex-change, the exploited population showed a typical response to fishing effort. The sex ratio of this protogynous hermaphrodite was found to be sustained at healthy levels by phenotypic plasticity. However, one important additional factor was highlighted by the study; the average condition factor of the protected population was significantly lower (0.0283 g/cm^3) compared to the exploited population (0.0295 g/cm^3). This was probably due to the higher intra-specific competition for lower food abundance in the protected area.

Interestingly the diving and fishing survey methods yielded similar mortality results for roman. Total mortality rate estimates derived from length frequency analysis from the diving and fishing survey were not different (0.32 and 0.29 y^{-1}, respectively) as were natural mortality rate estimates (0.24 and 0.19 y^{-1}, respectively). Natural mortality rate (M) estimates indicated by Pauly's and Hoenig's relationship were similar (0.25 and 0.23 y^{-1}, respectively).

Detailed yield-per-recruit (Y/R) and spawner biomass-per-recruit (SB/R) analyses were presented for different levels of M, varying age-at-recruitment (t_R) and fishing mortality (F). Current t_R (7.60 y) and F (0.16 and 0.25 y^{-1}, from the diving and fishing dataset, respectively) suggests an optimal exploitation of the population in the exploited part of the study area. However, a separate SB/R analysis of the male part of the population showed their vulnerability to over-exploitation, even at reduced age-at-sex-change from fishing. There therefore remains a high risk of recruitment failure for the roman population.

Of course MPAs can be used to measure stock status directly if the influence of factors such as cachability, habitat and sampling method on CPUE assessments can be limited or reduced. The experimental design in this study allowed for contemporary CPUE comparisons across the border of the Goukamma MPA. Results were similar to those obtained by the SB/R analyses. CPUE extrapolations therefore, using small MPAs, can provide reliable and consistent estimates, and offer a practical alternative to conventional assessment strategies.

This study has highlighted the importance of ensuring a well structured and comprehensive survey design when undertaking a comparison of protected and exploited marine areas. The results provide a comprehensive framework for future management of the Goukamma MPA and other protected areas along the temperate coastline of South Africa.

KEY WORDS: marine reserve · MPA · fishing effects · stock assessment · fishery management · marine conservation · reef community · life history · *Chrysoblephus laticeps* · Sparidae · Goukamma Marine Protected Area · South Africa

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TABLE OF CONTENTS

1 GENERAL INTRODUCTION

1.1 GLOBAL FISHERIES PESSIMISM

The world's fisheries are a major employer and an important source of food for an exponentially increasing population. Within the last decade the number of people working in fisheries has increased from 28 million to 38 million, of which 75% are working in the marine and inland capture fishery. In particular for developing nations, the sector's importance in income generation, employment and food security can't be overemphasized (Garibaldi *et al.* 2004).

A glance at a selection of scientific and popular articles on fishing reveals a general atmosphere of pessimism on the state of fisheries in every quarter of the globe. Resource declines due to overfishing have precipitated crisis for conservation and coastal economics.

By the early 1960s it was recognized that the scale of man's activities and technological advancements posed an ever increasing threat to the oceans, particularly its coastal waters (Björklund 1974). Today there is little left in the oceans that can be considered unaltered by humans (Roberts 2003), with changes in water chemistry, physical structure and biological functioning of the marine environment caused by a variety of human activities (Lubchenco *et al.* 2003). Natural patterns in terms of ecosystems, populations, species and genetic variation (Meffe and Carroll 1997) as well as underlying processes that maintain and interlink these natural patterns are being altered or destroyed worldwide.

Today, many marine stocks have collapsed or are locally extinct (Roberts 1997). Stocks of seven of the top ten species that contributed about 30% to the total world marine catch in 2003 are considered to be fully exploited or overexploited (Garibaldi *et al.* 2004).

As a result, fisheries yield has passed the turning point and global catches have begun to decline (Attwood *et al.* 1997a). After averaging 77 million tons in the preceding decade, world marine landings increased to an average of 84 million tons in the 1990s. In 2000, annual landings reached a high of 87 million tons, but decreased to around 84 million tons in 2001 and remained at that level in 2002. In reality, however, the total annual landings of the traditional marine target species have, since the early 1990s, fallen by several million tons. For a number of years total landings were maintained by a shift to new target species and better bycatch utilization through no-discard policies and improved technology (Garibaldi *et al.* 2004).

Since the oceans cover more than two thirds of the surface of the planet and more than 95% of the volume of the biosphere, they have historically been considered to be a boundless resource (Angel 1993). Compared to terrestrial systems, the marine environment has received little attention from conservationists and politicians (Roberts 2003). As many marine species have extremely high fecundities, their populations have been assumed to be more resilient to disturbance or exploitation than terrestrial populations (Roberts 2003).

There are numerous environmental pressures on the marine environment but the impact of fishing exceeds all others (Jackson *et al.* 2001, Carr *et al.* 2003). Fishing has reduced stocks to well below the level of maximum productivity (Huntsman 1994)

In order to develop an effective and practical management strategy for the future it is crucial to reflect on the performance of single species approaches.

1.2 FAILURE OF CONVENTIONAL MANAGEMENT

Single species approaches assume that production is a quantifiable function of biomass. Regulations are typically achieved by gear restrictions, but the application of total allowable catch (TAC), total allowable effort (TAE), closed seasons, bag and size limits are also common. Recommendations are based on production models and virtual population analysis, derivations thereof, or in few cases, spawner biomass-per-recruit (*SB/R*) and yield-per-recruit (*Y/R*) models.

However, today there are widespread concerns over the ability of these approaches to manage fisheries sustainably and conserve biodiversity (Bohnsack 1993, Ludwig *et al.* 1993). The collapse of the Peruvian anchoveta and the North Sea herring fisheries in the 1950s and 1960s illustrates some of the major problems in fisheries stock assessment. It is usually not possible to detect overfishing until it has already become quite severe (Hutchings 2000), and it is difficult to effectively reduce fishing effort, even after recognizing that it is necessary. Furthermore, over-exploited fisheries rarely recover after collapse (Hilborn and Walters 1992). This is particularly true for reef fish species, as they possess life history traits that commonly inhibit population recovery once overfishing occurs (Pinnegar *et al.* 2000).

Traditional single species and multi-species management require reliable information on biological reference points and inter-specific relationships. However, these parameters are often difficult to quantify (Attwood *et al.* 1997a). Unfortunately, even if reliable information could be obtained, the worldwide decline of large predators has induced potentially serious changes in ecosystems through top-down, trophic cascades (Pinnegar *et al.* 2000). As a result, management based on recent data alone will be misleading due to a 'missing baseline' (Myers and Worm 2003).

Several practical problems are related to the enforcement of conventional regulations. Access to many coastal fisheries is difficult to control and a high level of policing is necessary to enforce regulations such as bag and size limits. Also, there are difficulties in identifying, measuring and weighing fish in multi-species fisheries (Attwood *et al.* 1997a). Other practical difficulties are related to the common methods of fishing: while fisheries regulations are quite specific, fishing hardware like longlines, handlines and nets cannot deliver the required selectivity towards species, quantities and sizes without a substantial bycatch (Roberts 1997). Alverson *et al.* (1994) estimated that 26% of all fish caught are discarded at sea and landed bycatch is often not reported (Attwood *et al.* 1997a). Unfortunately, in most cases unintentional catches cannot be returned alive and the survival rate of returned fish is usually poor. Some fish suffer barotrauma and others die from injuries sustained in nets and during handling (Attwood *et al.* 1997a).

Finally, there are a couple of inherent problems when fishing effort is applied equally throughout the range of a population. Fisheries generally select large fish, creating a selection pressure favouring smaller fish size and slower growth (Ricker 1981), which in turn affects future yields. Larger individuals are usually the most fecund (Brosseau and Armstrong 1987) and their removal from the population will increase the risk of subsequent recruitment failure. Fishing methods generally select larger fish and select against aggressiveness in populations, which can alter migration patterns (Boehlert 1996), reduce genetic diversity (Ricker 1981, Roberts and Polunin 1991) and make individuals less catchable (Nuhfer and Alexander 1994). Large predators may disappear even under light fishing effort, and this in turn can induce severe changes in the whole ecosystem (Boehlert 1996).

The widespread failure of conventional management measures in the past has lead to intensive investigations into conceptually different strategies. As an alternative, an ecosystem approach advocates reliance on natural processes to restore and sustain biodiversity and fisheries resources by closing an area to exploitation.

1.3 MPAS AS MANAGEMENT ALTERNATIVE

MPAs have long been advocated as a viable alternative to single species protection in marine conservation, and recently, as an effective tool for fisheries management. Today, MPAs are regarded as a central component of precautionary fishery management and conservation of marine biodiversity by many authors (Bohnsack and Ault 1996, Clark 1996, Roberts 1997, Guénette and Pitcher 1999, Gell and Roberts 2003).

Complete information about complex ecosystem interactions is not essential for MPAs since they can provide protection for a representative portion of an ecosystem. MPAs should therefore aim to protect the habitat of a group, or guild of species which share a similar habitat within a biogeographic zone. The principle of habitat protection rather than single-species protection (Buxton 1987) also makes them the only means of protecting marine biodiversity comprehensively (Gubbay 1995). In this respect, MPAs are superior to many traditional catch restrictions in the conservation of marine biodiversity (Attwood *et al.* 1997a). Furthermore, MPAs, if large enough and established in relatively pristine areas, can counteract the 'missing baseline' problem. This potential is essential to fishery management as scientists can learn by comparing the effects of fishing effort on undisturbed ecosystems, which act as controls to evaluate natural variability (Roberts 1997).

MPAs may also be the key to enhancing fishery yield, where spatially homogenous management strategies have failed (Roberts 1997, Clark 1996). Fisheries yield will increase as a result of the proximity of an MPA, if there is substantial spill-over in the form of larvae, pre-recruits or adults. This increase in yield can be sufficient to offset the loss of fishing ground to a MPA (Roberts *et al.* 2000).

Mosqueira *et al.* (2000) and Halpern (2003) reviewed the effects of MPAs on marine populations and consistently found that mean density and size of exploited fishes within protected areas exceeded that of fished areas. At this stage the weight of the evidence suggest that no-take MPAs of appropriate size do have positive effects on fisheries and biodiversity. When added to conventional management methods, MPAs can be seen as insurance policy for fisheries by making it less likely that any failure of traditional management measures will lead to stock collapse (Attwood *et al.* 1997a).

Design implications of MPAs and MPA networks

Social, economic, ecological and pragmatic criteria are used throughout the world to decide on the location of MPAs (Salm and Price 1995). Systematic methods to evaluate these criteria include scoring and ranking methods (Hockey and Branch 1997), analyses of biogeographic distributions (Turpie *et al.* 2000), application of site-selection algorithms (Leslie *et al.* 2003), and definition and selection of hotspots in terms of species richness and endemism (Berger *et al.* 2003).

The roles of MPAs to conserve biodiversity and protect source stocks of exploited species seem to be at cross purposes, as MPAs implemented for the conservation of biodiversity are designed to increase the area of the MPA and reduce the lengths of boundaries to minimize export from the MPA whereas fisheries management requires larger boundary lengths to maximize the export of adults and larvae to increase fishing yields (Hastings and Botsford 2003).

There are several advantages of keeping MPAs rather small. Small MPAs enjoy local public support, which may indirectly assist in their management. Small MPAs are also easy to establish and enforce by the authorities. Furthermore, opportunities for comparative studies should be greater with small MPAs as a number of small MPAs and small adjacent zones will experience different levels of exploitation and protection (Beuttler 1994). Finally, they enjoy a higher acceptance by the fishing industry (McCay 1988) who, as a rule, are threatened by large MPAs, which appear to be designed to force them out of the business (Rigney 1990).
On the other hand, larger MPAs also bear some inherent advantages. DeMartini (1993) estimates that the overall contribution of multiple small closures will be less than that of one closure of equal total size, as they are more likely to hold viable populations of threatened species. A single large MPA will be easier to manage than several small MPAs of equivalent total size (Attwood *et al.* 1997a). Large MPAs can be zoned to accommodate a variety of uses (Kelleher and Kenchington 1992) and have a good buffering capacity towards the detrimental effects of pollutants or poaching.

A solution to this problem could be a combination of large MPAs for the conservation of biodiversity and small MPAs for more focused fisheries objectives providing for the optimum level of protection and resource use (Hockey and Branch 1994). By placing the larger MPAs in the centre of a biogeographic zone, aspects of representivity and diversity are covered and climate change, forcing species distribution either way, is counteracted (Hockey and Branch 1994).

Where the objective of the MPA is to protect a population or to improve the fishery for a species, the site-selection process will require a detailed knowledge of the life history of the species and of the local oceanography (Attwood *et al.* 1997a). MPAs for fishery enhancement should be scaled according to the movements of the targeted species (Griffiths and Wilke 2002) and be located where the stock to be protected is particularly vulnerable to capture (Gell and Roberts 2003).

Location and orientation of an MPA to ocean current patterns is crucial for its design, when taking into account aspects as spawning grounds and direction of larval dispersion (Carr and Reed 1993). A large MPA perimeter perpendicular to the current will allow for greater permeability than if it were parallel to the current (Rowley 1994).

It seems advisable, however, to concentrate on design principles for a network rather than individual MPAs because in practice, sophisticated concepts on the design of an individual MPA are rarely implementable (Ballantine 1997). The establishment of MPA networks can overcome some of the design problems attached to single, isolated MPAs. No detailed knowledge of the transport of propagules and population dynamics is needed to set up an effective network, provided that the principles of representativity, replication and size are fulfilled.

Species with a high dispersal potential will benefit from MPA networks stretching over correspondingly large ranges as they could be buffered from threats that might otherwise eliminate species with narrower ranges. In contrast, some species have limited dispersal due to retention by local currents and behavioural mechanisms, in which case a MPA network would have to consist of numerous broadly distributed MPAs to protect small populations, key source populations as well as genetic heterogeneity across species' ranges (Hastings and Botsford 2003, Palumbi 2003).

It is evident from the above section that more research is needed to prove the effectiveness of MPAs as fisheries management tools. In particular direct evidence of a net-spill-over from MPAs to exploited areas, is needed to strengthen MPAs as viable alternative. To achieve this, several research methods have to be combined and standardized consistently over a sufficient area and time interval (Willis *et al.* 2003).

South Africa has a relatively large number of MPAs and is therefore well positioned to play an important role in MPA research.

1.4 A CRITICAL REVIEW OF LINEFISH MANAGEMENT IN SOUTH AFRICA

Linefishing in South Africa is defined as the capture of fish with a hook and line, but excludes the use of longlines (Mann 2000). Together, the three sectors of the linefishery, namely, commercial, recreational and subsistence, target between 95 (Hutton *et al.* 2001) and 120 of the country's 2,200 marine teleost species (Penney *et al.* 1999).

The commercial sector is exclusively boat-based. From the descriptions provided by Sauer *et al.* (2003a), we learn that the total number of registered vessels operating in the commercial linefishing sector was estimated at 700 in the late 1990s, which accounted for 37% of all boats operating in marine fisheries in South Africa. Commercial linefishing is a low-earning, labour-intensive industry, important from a human livelihood point of view. Employing an estimated 4,500 fishers (27% of all fishers), it has the lowest average employment income compared to all South African fisheries. Linefishermen earn R 21,000 per year, whereas the industry average is R 37,000. The commercial linefishery has the largest fleet, however, due to a low vessel market value it contributes only 6% of the total estimated value of R 2 billion of all marine fisheries. The linefishery lands the third-largest catch (16956.1 tons) of all fisheries and has the third-largest total employment income of R 65 million, 15% of the total employment income of all fisheries.

The recreational boat-based sector expanded rapidly after the introduction of the trailable ski-boat in the 1970s and, with an estimated minimum of 4000 vessels (Hutton *et al.* 2001), has surpassed commercial vessels numbers (Penney *et al.* 1999, Hutton *et al.* 2001). Brouwer and Buxton (2002) estimated the total recreational effort at more than 24,000 fisher-days/year along the South African Eastern Cape coast. Off KwaZulu-Natal (KZN) recreational vessels were estimated to fish for about 35,000 boat-days/year (Penney *et al.* 1999).

There is an estimated 400,000 participants in the recreational shore-angling sector (McGrath *et al.* 1997). Brouwer *et al.* (1997) estimated that the total effort in this sector is 3.2 million angler-days/year, and the total catch 3,000 tons/year.

The subsistence category was legally created in 1998 to recognize those fishers who depend on the resource for food directly – usually poverty stricken communities or those using traditional methods. According to Clark *et al.* (2002), there are almost 30,000 subsistence fishers active along the South African coastline and 85% of them harvest fish.

Management history

The first attempts at managing linefish resources were marked by the introduction of minimum size limits for selected species in 1940. In the absence of life history information, these regulations were determined on a rather arbitrary basis and in the 1960s biological studies on a few important species were initiated (Sauer *et al.* 2003b). In the 1970s the Sea Fisheries Research Institute in Cape Town and the Oceanographic Research Institute in Durban independently started to collect data on the commercial and recreational linefishery, respectively. The two dataset were later merged into the National Marine Linefish System (NMLS) developed by the Sea Fisheries Research Institute in 1982 (Sauer *et al.* 1997).

The Minister of Environmental Affairs appointed a National Marine Linefish Committee (NMLC) in 1984 to develop management proposals for the South African linefishery (Penney *et al.* 1999). The management framework included revised minimum size limits, daily bag limits, closed seasons, commercial ban for some species, and the freezing of the commercial effort at the 1984 level (Sauer *et al.* 2003b). Although the basic life histories of some important species had been studied, most were unknown. At the time of their implementation, there was little scientific basis to determine bag or size limits correctly. As a result many bag limits were too large and size limits too low to offer any real protection (Attwood and Bennett 1995b). Furthermore, little information was available on the size and rate of growth of linefisheries in South Africa (Penney *et al.* 1999, Britz *et al.* 2001).

To compound this ignorance, the existence of strong lobby groups resulted in considerable compromise between managers and fishers (Sauer *et al.* 2003b), which, resulted in ineffective protection of linefish species. Due to the different management measures between the commercial and recreational sectors, controversy in the NMLC resulted in the establishment of the independent South African Marine Linefish Management Association (SAMLMA) in 1990. By providing a channel for negotiation between the representatives of all sectors, management measures implemented were again a compromise between conflicting views of the sectors. This lead to widespread dissatisfaction among fishers from all sectors. Scientists concluded that the fishery regulations had not been successful in limiting fishing mortality to sustainable rates (Penney *et al.* 1999).

Upon scientific advice the Minister of Environmental Affairs and Tourism in 2000 declared an emergency in the traditional linefishing sector, in terms of a provision in the Marine Living Resources Act (1998). This step provided the Minister with extraordinary powers to regulate the fishery. A Linefish Management Protocol (LMP) was drafted to define the procedures of monitoring, assessment and regulation, with the specific objective of rebuilding depleted stocks (Griffiths 2000). In terms of the emergency, the number of commercial linefish permits were reduced by 75% in 2003.

The state of all South African fisheries was summarized by Payne (2000), who concluded that all fisheries were well managed with the exception of abalone and linefish. At a mean value of R 300 per kg (50 US$) landed mass of abalone, its not difficult to understand the problems experienced in this shell-fishery. But, why should the linefishery have fared so badly?

Effort escalation

Although effort was nominally capped at the 1984 level, inadequate regulations and poor enforcement (Sauer *et al.* 2003b) effectively meant that effort in the commercial fishery continued to escalate. The subsistence sector was legally introduced in 2000, adding additional pressure. At the same time, access to the recreational fishery was not regulated and effort continued to increase there too (Penney *et al.* 1999). Compliance with conventional management regulations has been poor, mainly due to inadequate enforcement effort. Most shore-anglers chose to ignore regulations (Brouwer *et al.* 1997, Attwood and Farquhar 1999).

Apart from socio-economic factors that lead to an increase in effort, a number of technical factors increased the efficiency of linefishing steadily over the course of the 20th century. Major advances were associated with the introduction of motorized vessel (1930s), monofilament line (1950s), ski-boats (1960s), radios (1970s), eco-sounders (1970s), off-road vehicles (1970s), Global Positioning System (1990s) and cellular phones (1990s). Other improvements were thinner, stronger and less transparent lines, graphite rods and reels and chemically sharpened hooks.

Linefish species

South Africa's rich biodiversity is attributed to the confluence of two contrasting water masses (Branch and Branch 1981a). Four coastal biogeographic zones are recognized, a cold Namaqua Bioregion, a cool-temperate South-western Cape Bioregion, a warm-temperate Agulhas Bioregion and a subtropical Natal Bioregion (Driver *et al.* 2005). Sink *et al.* (2005) recognise an additional biogeographic break in northern KwaZulu-Natal, distinguishing a Delagoa Province (from about Cape Vidal up to Mozambique), which is distinct from the Natal Province (southwards of there to central Transkei). Collectively, they support a rich ichthyofauna of 2,200 species, of which 13% are endemic to South Africa; a proportion similar to those of more isolated regions such as the Red Sea and the Mediterranean, which have 14% and 15%, respectively (Van Der Elst 1993b). Two families, the Sparidae (seabreams) and the Clinidae (klipfishes), dominate the endemic fish species (Turpie *et al.* 2000). At least 41 of the 112 species of seabreams that occur worldwide can be found in southern African waters, of which 25 species are known to be endemic to the region (Smith and Smith 2003).

Griffiths (2000) examined long-term catch-per-unit-effort (CPUE) data for the commercial linefishery between the Orange River and the Kei River. He estimated that present catches are less than 10% of those reported during the first third of the 20th century. Stock assessments conducted since the mid-1990s revealed that most commercially exploited linefish populations were at severely depleted levels (Sauer *et al.* 2003b).

Seabreams feature most strongly in the list of depleted species. The failure of these species to sustain catches is commonly attributed to a combination of traits that increase their vulnerability to capture and reduction of spawning capacity at the population level. Resident behaviour has been indicated for most seabreams (Mann 2000). Furthermore, seabreams are long-lived, late maturing species. Under even moderate fishing effort, few are expected to reach maturity and the replacement of losses due to fishing is slow. Adding to these problems is the habit of changing sex, which is common amongst seabreams. Fishing mortality is often more heavily felt by one sex than the other, resulting in skewed sex ratios, and thereby reducing spawning potential to a greater extend than would have been predicted from a reduction in longevity alone (Penney *et al.* 1989, Buxton 1993).

Seabreams have declined severely in numbers and average size (Griffiths 2000, Brouwer and Buxton 2002). Of 17 of the most important linefish species assessed in 1990, populations of 12 were found to have collapsed. Half of these collapsed stocks were of seabream species (Sauer *et al.* 2003b). Since many seabream species are important reef predators, their declining numbers also have potential impacts on reef community structure (Griffiths 2000).

Problems with current assessments

Attwood (2002) evaluated the use of available assessment models in the South African linefishery. Despite their wide application in fisheries, standard production models are unsuitable for linefish assessments, as it is essential that age-structure and year-to-year recruitment are incorporated. Models that are fitted to time-series of abundance indices require annual monitoring going back several years. Virtual population analysis requires a relatively short series of age-structured catch-data, but it needs additional information in the form of fishing mortality-rates or absolute cohort strength for the terminal year. These requirements are costly and practically preclude the use of this model for the linefishery, as there are many species in a fishery of comparatively modest value: the government cannot afford monitoring and assessment programmes for each species as it does for the few highly abundant demersal and pelagic species.

Moreover, the linefishery is disaggregated - catches are landed at hundreds of access points in very small quantities. Hence, obtaining sizeable samples of the catch is expensive and time consuming. Also, the effort attached to catch data cannot be separated on a species basis, as it is a multi-species fishery (Attwood 2002).

The options for the linefishery narrow down to trends in catch composition data, SB/R and CPUE as a relative index of abundance. Attached to each method are a variety of inherent difficulties, assumptions and biases that cast doubts on the reliability of the assessments (Penney *et al.* 1999).

Trends in catch composition have been used broadly to indicate the collapse of some species relative to others. However, they can be highly misleading, as there is usually no record of effort attached to the dataset. For example, if the total catch in a multi-species fishery is decreasing, an increasing relative frequency of any one species in that catch is not a reliable indication of stock increase as it is measured relative to an unstable reference. The applications of catch composition data in fishery management are therefore limited - they might indicate the relative performance of a species, but are of little use as an assessment method, despite being used by some authors (Coetzee 1978, Van Der Walt and Govender 1996, Attwood and Farquhar 1999, Penney *et al.* 1999, Griffiths 2000).

Per-recruit (*PR*) models let us scale age-at-recruitment (t_R) in relation to fishing mortality (F). They are useful for planning fishery regulations aimed at maintaining potential yield or *SB/R*. *PR* models are based on the assumption that recruitment is constant, or more correctly, they do not consider the effects of recruitment variation (Butterworth *et al.* 1989). *PR* models have been extensively used in the linefishery, in particular *SB/R*, which has provided a more useful indicator of population vulnerability to fishing effort. Although the model itself is independent of recruitment variation, the *SB/R* result indicates the effect of exploitation rate on the life-time contribution of a single fish to future recruitment. This effect has been modelled explicitly with stochastic age-structured production models, which related *SB/R* to the likelihood of spawning failure for a variety of life history patterns (Sissenwine and Daan 1991, Punt 1993, Mace 1994). From these results critical and threshold *SB/R* levels have been identified for use in data-poor fisheries. Where it is impractical to obtain sufficient data to model populations explicitly, *SB/R* could be used as a substitute to scale F such that it prevents recruitment failure.

Unfortunately, *SB/R* models have been used in South Africa as a means to assess the condition of a stock, a function for which they are totally unsuitable. Being independent of recruitment, the *SB/R* result bears no relation to either the absolute or the relative size of the stock when based on measured or estimated mortality rates. Ignoring this, scientists have frequently estimated mortality and used SB/R models to report on the condition of the stock (Buxton 1992, Bennett 1993a, Punt *et al.* 1993, van der Walt and Govender 1996, Booth and Buxton 1997b, Chale-Matsau *et al.* 2001, Hutton *et al.* 2001). These assessments are flawed for reasons described below.

Mortality rates are measured by the declining frequency of catch-at-age in random fish samples. Such measurements are biased by long-term trends in recruitment, which were likely to be negative for most of the 20th century if a stock-recruitment relationship is assumed, and fishing mortality, the product of effort (*E*) and catchability (*q*), which certainly increased throughout that period. These trends would have resulted in the underestimation of mortality rates by elevating the frequency of older age groups relative to younger age groups.

The estimation of *F* is seldom satisfactory. Whereas total mortality (*Z*) and its error are easily, but not reliably, measured, its partitioning into *F* and natural mortality (*M*) terms is difficult to achieve. Almost all SB/R 'assessments' have relied upon an empirical relationship between *M*, mean sea temperature and growth parameters based on a multiple regression of 175 fish stocks, non of which were sparids (Pauly 1980). Whereas the model was significant, very few assessments have considered the implication of this model's error, which has a coefficient of variation (*cv*) in the order of 200% of an absolute value. Although some authors considered different levels of *M*, the range of estimates applied only account for a *cv* less than 80% (Smale and Punt 1991, Buxton 1992, Bennett 1993b, Punt *et al.* 1993, Van Der Walt and Govender 1996, Booth and Buxton 1997b). The consequent uncertainty in the *SB/R* results are so great as to render them practically useless.

Despite these weaknesses, *SB/R* was advocated as the preferred assessment model for the linefishery: "Without long time-series of catch data and information on the spawner biomass recruit relationship, yield per-recruit (*Y/R*) and spawner biomass per-recruit (*SB/R*) models represent the most appropriate stock assessment methods available" (Penney *et al.* 1997). Not only do these models fail to reflect stock size, the estimates upon which they are based are systematically biased and inaccurate.

The obvious alternative to *P/*R methods is CPUE data, but this information has some serious problems of its own. CPUE is generally accepted to be proportional to the number of fish available. CPUE based assessments therefore do take the relative size of a stock into account. Relative measures may be useful for monitoring inter-annual change, but provide no information on the status of the stock, for which some absolute measure is required. To achieve an absolute measure, CPUE records have to be compared with data from the start of the fishery, when the stock was at or close to pre-exploitation levels. Unfortunately such data are not available for the South African linefishery and typically are lacking for fisheries worldwide. The inability to determine the departure of a stock from pristine conditions is generally referred to as ‘missing baseline’ (B_0) problem (Butterworth *et al.* 1989).

Furthermore, CPUE data recorded in the past history of the fishery are subject to bias as linefishing methods have become more effective over time. F is defined as the product of q and E. Changes in q, however, are not easily quantifiable. This so called ‘technology creep’ results in considerable doubt in the comparability of CPUE datasets that are widely separated in time.

Moreover, available datasets derived from different methods of data recording, are therefore not standardised and great care needs to be exercised when comparing such records. For example, E has been recorded as catch-weight/fisher/year (Griffiths 2000), fish/fisher/day (Attwood and Bennett 1995b, Van Der Walt and Govender 1996, Brouwer *et al.* 1997, Attwood and Farquhar 1999), fish/fisher/hour (Smale and Buxton 1985, Griffiths 2000), catch-weight/fisher/hour (Fennessy *et al.* 2003), catch-weight/fisher/outing (Griffiths 2000), catch-weight/fisher/day (Hecht and Tilney 1989, Brouwer *et al.* 1997, Attwood and Farquhar 1999), total annual catch-weight/access-point (Hecht and Tilney 1989), total annual catch/area (Bennett 1993b) or as annual mean catch-weight/boat/year (Griffiths 2000, Fennessy *et al.* 2003), without taking the number of actual outings into account (Griffiths 2000). Fish were either counted or, more often, batch weighed and their numbers back-calculated, without sufficient knowledge of size frequencies of catches, which over the past decades have undergone considerable change (Penney *et al.* 1999).

Linefish assessments in South Africa experienced difficulties described above, in relation to the design of data collection procedures, the standardization of such procedures and the inappropriate use of models. Detection of the current crisis in the management of the linefishery was based on a number of assessments that indicated stock collapses, but as the following examples illustrate, these assessment are unreliable.

Griffiths and Hecht (1995) sampled geelbek (*Atractoscion aequidens*) for per-recruit assessments. The stock, however, is disaggregated by age, with different age-classes found in different areas. The length frequencies, derived from these separate samples, cannot be considered as representative of the stock. The low *SB/*R value was interpreted as a sign of collapse, which was corroborated by low CPUE values in relation to CPUE records from the late 19th century. Unfortunately, this CPUE comparison suffered from the lack of standardization of units and no attempt to quantify the effects of technology creep associated with the transition from rowing boats to powered ski-boats.

White steenbras (*Lithognathus lithognathus*), examined by Bennett (1993b), is caught with different gear types, dependent on the size of the fish. Per-recruit assessments for this species were troubled by the inability to calculate *F* from discontinuous size frequencies. Therefore, only size frequencies obtained from recreational anglers were used to estimate *Z*, which cannot be considered representative for the variety of methods used to exploit the stocks. Long-term trends in CPUE were determined from voluntary and compulsory commercial catch records, club records and research angling. Catches were noted in different units and highly variable over time. Clear trends were hardly detected.

The stock status of red steenbras (*Petrus rupestris*) was investigated by Smale and Punt (1991) using *SB/R* assessments. Adults migrate to spawn off the Pondoland coast while recruits are found on the broad Agulhas Bank. Due to the age disaggregated stock, *F* could not be determined and age at first capture estimates had to be obtained from that geographical area in which exploitation of the youngest individuals occurred. Trends in CPUE where unequivocal (Penney and Wilke 1993). Although CPUE decreased inshore, an increase was recorded offshore on the Agulhas Bank, probably due to improved targeting.

The fishery for the seventy-four (*Polysteganus undulosus*) collapsed in the late 1960s prior to any stock assessment. Chale-Matsau *et al.* (2001) performed stock assessment from accessioned samples collected in the early 1960s. Finally, recruitment is likely to have collapsed on a spatially large scale which prevents the use of the models in the first place. These results are not even suitable to plan a possible fishery for seventy-four in the future. Due to the collapse of the stock, genetic diversity might be reduced to such an extend that the growth rate of the remaining population has changed and age-at-maturity is likely to be reduced due to extensive fishing effort in the past.

SB/R assessments of red roman (*Chrysoblephus laticeps*) and dageraad (*Chrysoblephus cristiceps*) stocks were conducted by Buxton (1987) in the Tsitsikamma National Park (Tsitsikamma NP) and the Port Elizabeth area. Samples obtained from research fishing in the Tsitsikamma NP revealed a higher estimate of total mortality (*Z*) than those from recreational catches in the Port Elizabeth area. The author concedes that the samples were not necessarily representative of the true population in the areas, resulting from incomparable sampling procedures during research fishing and fishery dependent sampling.

Attwood (2003a) investigated the dynamics of the fishery for galjoen (*Dichistius capensis*) using CPUE data from inside and outside the De Hoop MPA. Unfortunately, data from the protected sites were obtained from fishery-independent surveys and therefore not comparable to fishery data. The author concluded that adequate stock assessments have to make use of fishery-independent CPUE data only, which may ensure reliable comparisons across MPA boundaries.

Apart from these examples, similar problems could be identified in almost every other assessment. Moreover, stock assessments of many other exploited sparids have never been attempted, namely, red stumpnose (*Chrysoblephus gibbiceps*), white stumpnose (*Rhabdosargus globiceps*), cape stumpnose (*R. holubi*), poenskop (*Cymatoceps nasutus*), fransmadam (*Boobsoidea inornata*), zebra (*Diplodus cervinus hottentotus*), blacktail (*D. sargus capensis*), steentjie (*Spondyliosoma emarginatum*), blue hottentot (*Pachymetopon aeneum*), bronze bream (*P. grande*), sand soldier (*Pagellus pellottii natalensis*), santer (*Cheimerius nufar*) and musselcracker (*Sparodon durbanensis*) (Mann 2000).

The most common biases in the assessments are all positive, i.e., we tend to over-estimate the state of a stock (technology creep, declining recruitment and increasing effort). Other problems, such as lack of standardization, could cause a bias in either direction. One could argue that the conclusion that linefish stocks are over-exploited is justified by the fact that so many assessments point to collapse and that the most common biases under-estimate the extent of depletion. However, the scientific community has to concede that the assessments are poor, and can be contested almost without exception, and that a fundamental revision of stock assessment procedures is required.

Potential role of MPAs

Contemporary CPUE comparisons across MPA borders offer a practical alternative as they conveniently overcome the inherent difficulties of the assessment strategies described above (Attwood 2003a). However, MPAs have their own biases. Efficacy of enforcement, duration of protection and lack of equivalence of habitats will all introduce biases to assessments based on MPAs. A careful experimental design can limit or reduce the influence of factors such as catchability, long-term environmental change and sampling method on the assessments. In this way, CPUE could be used to measure stock status directly.

This rationale is at the basis of this study, which attempts to obtain an estimate of the effect of fishing on a reef fish population. A closer look at available MPAs, their suitability for this task and the quality and results of previous MPA assessments in South Africa is appropriate at this point. One of the reasons that this method has not been used or tested, relates to the lack of suitable MPAs that are representative of habitat found in fishing grounds. Indeed, MPAs are a rather belated addition to conservation programmes of most countries. In 2005, South Africa had 19 MPAs, which offered the opportunity to test this new assessment method, and to further comment on the role of MPAs in marine conservation.

1.5 MPAS IN SOUTH AFRICA

Although MPAs in South Africa have mainly been established for conservation of marine biodiversity, their benefits for fisheries management soon became evident (Cowley *et al.* 2002, Attwood 2003b). Additional ‘no take’ areas should be considered to protect seabream species in particular (Griffiths 2000), given the problems of slow growth rates, sex-change, barotrauma, strong inter-sector competition, difficulty in achieving substantial reduction in effort and ineffectiveness of the current bag limits. It is likely that the maintenance of a number of adequately large, suitably situated MPAs offers one of the few practicable alternatives in the conservation and management of endemic reef fish stocks (Penney *et al.* 1999).

Under the current Marine Living Resources Act (18 of 1998), the Minister of Environmental Affairs and Tourism has the power to declare MPAs or areas dedicated for specific fishing regulations. The Minister may proclaim these areas for the conservation of biodiversity, the management of fisheries (to rebuild stocks, enhance the abundance of stocks and to provide areas for research) or to reduce any conflict that might arise in an area due to competing fishing activities (Bause 2004).

With the establishment of the Tsitsikamma NP in 1964, South Africa became one of the first countries in the world to implement no-take MPAs. Currently, 5% of the South African coastline is protected by no-take MPAs, while 18% is protected by some form of conservation (Attwood *et al.* 1997b).

Amongst the MPAs, shoreline lengths vary from 800 metres in Haarder Bay to 145 km in the contiguous St Lucia and Maputaland MPAs. Other large MPAs are the Tsitsikamma NP and the De Hoop MPA with about 50 km of coastline each. However, the average length of MPAs is 16 km (Attwood *et al.* 1997b) due to the high number of small protected sites. Goukamma MPA, with 18 km of coastline, is the only MPA that can be considered as medium-sized by South African standards.

South African MPAs – case studies

Many studies on South Africa's large 'no-take' MPAs have served to demonstrate the potentially positive effects of marine protection on heavily exploited reef fish species (Attwood *et al.* 1997a): Research in the De Hoop MPA indicated that large MPAs can provide effective refuges for reef-dwelling seabream species (Bennett and Attwood 1993). After introduction of the MPA, six out of ten fish species recovered within six years of no fishing (Bennett and Attwood 1991). Conducting a tag and recapture study in the centre of the 50 km De Hoop MPA, Attwood and Bennett (1994) showed that the export loss of adult galjoen (*D. capensis*) sustained a fishery in adjacent areas that previously was rapidly declining (Attwood 2003b).

Studies around the 50-km Tsitsikamma NP yielded similar results: comparing the CPUE of research fishing in the Park (P. Cowley, Rhodes University, unpublished data) with the average CPUE found by Brouwer *et al.* (1997) at exploited sites in the region showed a higher CPUE for the protected site. Tagging studies on seabream species showed that 96% of recaptures were made close to the site of release, indicating that individuals of these species were resident inside the park for long periods (Cowley *et al.* 2002). The park proved to be particularly effective in protecting long-lived, slow-growing, resident teleosts (Buxton 1993): as indicated by diving and fishing surveys. Seabreams were found to be larger and more abundant in the park as compared to exploited areas (Buxton 1987), and had a healthier sex ratio (Buxton and Smale 1989). Tilney *et al.* (1996) concluded from an analysis of current-meter records that there was likely to be substantial export of seabream larvae to adjacent exploited areas.

Comparing the CPUE of the linefishery along the north and south coast of KZN, Penney *et al.* (1999) concluded that the large St. Lucia and Maputaland MPAs on the north coast have sustained catches in adjacent areas, particularly reef fish.

Until recently, MPA research focused on large MPAs, established several decades ago, e.g. the Tsitsikamma NP (Buxton 1987, Burger 1990, Tilney *et al.* 1996, Brouwer *et al.* 2003, Smith 2005) and the De Hoop MPA (Bennett and Attwood 1991 & 1993, Attwood and Bennett 1994 & 1995a, Penney 2001). Additionally, evaluations were either incomplete or of questionable design, as they did not investigate offshore environments, were insufficiently stratified over space and time, lacked standardization of data collection at non-MPA sites, or were biased due to low comparability of sampled sites.

Bennett and Attwood (1993) conducted an extensive scientific angling program in the De Hoop MPA. However, the data for comparison from exploited sites came from recreational catch reports and no offshore component was included. Burger (1990) assessed the sub-tidal ichthyofauna of the Tsitsikamma NP, providing a detailed inventory of the ichthyofauna. Unfortunately, only one reef outside the MPA was sampled for comparison and no experimental fishing or collection of samples for life history investigations were conducted to substantiate the findings. Buxton (1987) presented the most comprehensive study to date, using UVC, fishing data and life history parameters to compare several sites inside and outside the Tsitsikamma NP. Unfortunately, fishery-dependent length frequencies of only two species were obtained and UVC was conducted during a total period of only ten month. Moreover, MPA and control sites were more than 200 km apart, raising doubts about their biogeographical comparability.

Examples of studies of areas in South Africa that may experience little exploitation because of their inaccessibility, are sparse. Clarke and Buxton (1989) recorded a considerably lower catch rate of shore-anglers close to the large metropolitan area of Port Elizabeth than recorded by Coetzee and Baird (1981b) around the nearby St. Croix Island. They concluded that the difficult access to the island had kept exploitation levels low, resulting in higher densities of reef fish species. The only other examples come from marine invertebrate species (Sauer 1995, Clark *et al.* 1996, Lasiak 1998, Mayfield *et al.* 2001).

Philosophy of MPA studies

A philosophical issue in all of these studies is whether the MPA is the subject or the method of study. Many scientists have attempted to answer the question ‘Do MPAs support higher abundances of target species than exploited areas?’ (Mosqueira *et al.* 2000). Another approach is to use MPAs as a *fishermen exclusion device*, to assess the impacts of fishing, in the same way that an experimental ecologist excludes predators. Many papers cite one of the objectives of MPAs as the provision of an ecological benchmark (Kelleher and Kenchington 1992, Agardy 1994, Gubbay 1995, Roberts and Hawkins 2000).

Some care needs to be taken when using the results from one approach to answer questions raised by the other to avoid circular reasoning. If a MPA is found to have little impact, does that mean that exploited fish populations respond poorly to protection, that fish were not exploited to any significant extent or is it the result of a badly implemented MPA (i.e. poor compliance, wrong habitat, or inappropriate size)? On the other hand, if a significant difference is detected, can one conclude that it represents the impact of exploitation, or protection, if the suitability of the MPA for comparison was not investigated *a priori*.

This study uses a MPA to assess the effects of fishing, however, prior to embarking on the investigation, it was necessary to evaluate the effectiveness of the MPA *for this purpose* by investigating the nature of habitat, the degree of compliance by fishers and appropriate spatial scales when selecting comparable sites. Having ensured that the MPA can serve as an effective experimental method, i.e. an ecological benchmark, results of the comparisons can be attributed to fishing effects after isolating the effects of all other known and measurable influences. The measured impacts can be used to support statements about the impact of fishing, or conversely, about the likely impact of protection by MPAs of similar design in similar ecological settings.

1.6 KEY QUESTIONS AND RESEARCH PLAN

The goal of this study was to evaluate the medium-sized Goukamma MPA as a strategy to protect reef fish and the reef community in general and to investigate likely impact on the fishery in adjacent waters.

In order to assess the potential of Goukamma MPA in the conservation and management of reef fish species, the following key questions were formulated:

- What oceanographic and meteorological conditions prevail in the study area?
- What reef habitats are present and how are they distributed in the study area?
- What is the relative composition of fish and benthic taxa on reefs inside and outside the Goukamma MPA?
- What is the relative density and average size of reef fish species inside and outside the Goukamma MPA?
- What is the relative density of benthic taxa on reefs inside and outside the Goukamma MPA?
- What are the relative levels of fishing effort and how are they distributed inside and outside the Goukamma MPA?
- Can the relative differences (if any) in fish and benthic taxa densities/compositions and fish sizes be ascribed to fishing effort and/or physical/biotic factors?
- What are the differences (if any) in life history traits of targeted species inside and outside the Goukamma MPA?

A comprehensive description of the oceanographic and meteorological conditions in the study area was required for a comparison of fish survey results with other sites in South Africa, and globally. Therefore, a weather station, recording wind speed, direction and atmospheric pressure, was erected at the beginning of the study. Water temperature, turbidity and currents were regularly monitored throughout the study at fixed positions. On days with favourable sea conditions the seafloor in the MPA and the adjacent areas were mapped using global positioning system (GPS) and sonar. The initial mapping study was used to identify suitable research sites but was continued throughout the study to improve resolution and confidence in spatial patterns (chapter 2).

In chapter 3, results from the survey of the local boat-based linefishery are presented. Fishing boats were counted, positions recorded with GPS and skippers interviewed to identify targeted species. Positions of reefs and fishing boats were entered into a GIS database and the resulting maps of reefs and zones of differential fishing effort were used to randomly stratify the site selection for biological data collection.

Over the study period of more than three years, biological and physical data were collected at identified research sites in the study area. By means of controlled fishing and standardized point assessments using SCUBA, the density and size of fishes and the abundance of benthic taxa were recorded. Multivariate analysis and generalized linear models were used to determine factors influencing reef community structure and evaluate the effect of exploitation (chapter 4).

Chapter 5 describes the influence of exploitation on life history and population structure. Representative samples of target species were collected at the end of the study, so as not to influence the results of surveys mentioned above. Two geographically separated samples (inside and outside the MPA) were obtained by means of line- and spear-fishing during the spawning season to obtain growth and length information on the target species under protected and exploited conditions.

In conclusion (chapter 6) the role of the Goukamma MPA in the conservation and management of commercially important linefish species is evaluated. Potential dispersal distances of larvae and eggs are projected and implications for a MPA network along the south coast are discussed.

2 DESCRIPTION OF THE PHYSICAL ENVIRONMENT OF THE GOUKAMMA MPA AND ITS USEFULNESS FOR COMPARATIVE REEF FISH ASSESSMENTS

2.1 INTRODUCTION

Although there are now several papers and text books on the subject of marine protected area (MPAs) design, it is quite unusual to find examples of MPAs that have been properly ‘designed’ to meet stated objectives. This is particularly true of older MPAs, which are the ones that scientists are most inclined to use for benchmark studies, on the assumption that they contain stable communities. However, scientists now realize that climate change does not allow stable communities, except for a brief period spanning less than a decade (Soto 2002). Often, detailed studies of the environment encompassing a MPA, and of the suitability of the choice for meeting specific objectives, have not been undertaken, or certain objectives have been added later. In the worst cases, the objectives of MPAs were never clearly articulated or understood at the time of their proclamation (Pressey and Tully 1994). Even where studies have been available, MPA design has been constrained by social, economic and political considerations (Margules and Pressey 2000). Frequently, therefore, MPAs are evaluated only after their designation.

It is now widely recognized that MPAs can provide examples of undisturbed marine communities which can serve as benchmarks for ecological impact studies. Unfortunately, this objective conflicts with another frequently cited objective. MPAs are often implemented to protect unique features of an area, which inadvertently limits their value for comparative studies.

Goukamma is an example of a MPA that was established in 1990 for the broad objective of conserving marine life (Hiseman 1998). Its boundaries coincided with a terrestrial reserve to take advantage of existing conservation staff and structures. In retrospect, it is expected that Goukamma protects examples of south coast temperate reef communities, but this has never been demonstrated. Goukamma was never purposely designed to serve as a benchmark for ecological studies; this specific objective was added later (Attwood *et al.* 1997b).

The study of topography and local oceanographic conditions is of particular importance when considering the effectiveness of MPAs. For conservation of depleted fishery resources it is essential to know that the site includes appropriate habitat (Attwood 2002). For the export of fish larvae and eggs to boost recruitment in adjacent fisheries, some understanding of currents is required (Gaines *et al.* 2003). Here we need to establish if the MPA can be used as a benchmark to evaluate the effect of fishing. Comparisons between exploited and unexploited areas can be confounded by local habitat differences (Willis *et al.* 2003).

Goukamma is situated along the South African south coast and falls centrally within the warm temperate biogeography zone (Emanuel *et al.* 1992, Turpie *et al.* 2000). On the basis of its geography, Goukamma would appear to be representative of a large inshore zone, but this area is oceanographically complex, being subjected to warm water intrusions from the Agulhas Current and wind-induced upwelling of cold South Indian/Atlantic Central Water (Harris 1978). Whereas the Agulhas Bank has been well studied, we are comparatively ignorant of the oceanography of the immediate inshore zone where reef fish are very abundant. It is possible that the oceanographic conditions at Goukamma do not provide ideal habitats for commercially important reef fish or that the design of the MPA does not provide comparable reefs for assessing reef fishes. In particular, oceanographic events may not effect the MPA and adjacent sites equally, causing differences between sites that are not related to fishing.

This chapter provides a physical and oceanographic description of the Goukamma MPA and its immediate environments. This information is used to assess Goukamma as a site representative of the south coast, to consider its value for benchmark studies and to qualify ecological comparisons with other reef fish studies in the south coast temperate zone.

2.2 MATERIAL AND METHODS

Study area

Goukamma MPA is situated on the Southern Cape coast in the heart of the Garden Route between Gerrickes Point (34°02`S, 22°45`E) and Buffels Bay (34°04`S, 23°00`E). The study area stretches about 27 km along the coast and extends 5 km offshore, incorporating an area of about 150 km^2. Goukamma MPA is a medium size MPA, protected from boat-based line-fishing since 1990. The Goukamma Nature Reserve occupies the adjacent land and has been protected since 1974. The length of the Goukamma MPA shoreline is about 18 km with a total area of approximately 40 km^2 (Figure 2.1). It includes rocky platforms, sandy beaches, an estuary (Goukamma River), sub-tidal rocky reefs of aeolianite or sandstone origin (Flemming *et al.* 1983), and sub-tidal sandy and muddy substrates (Zoutendyk and Duvenage 1989).

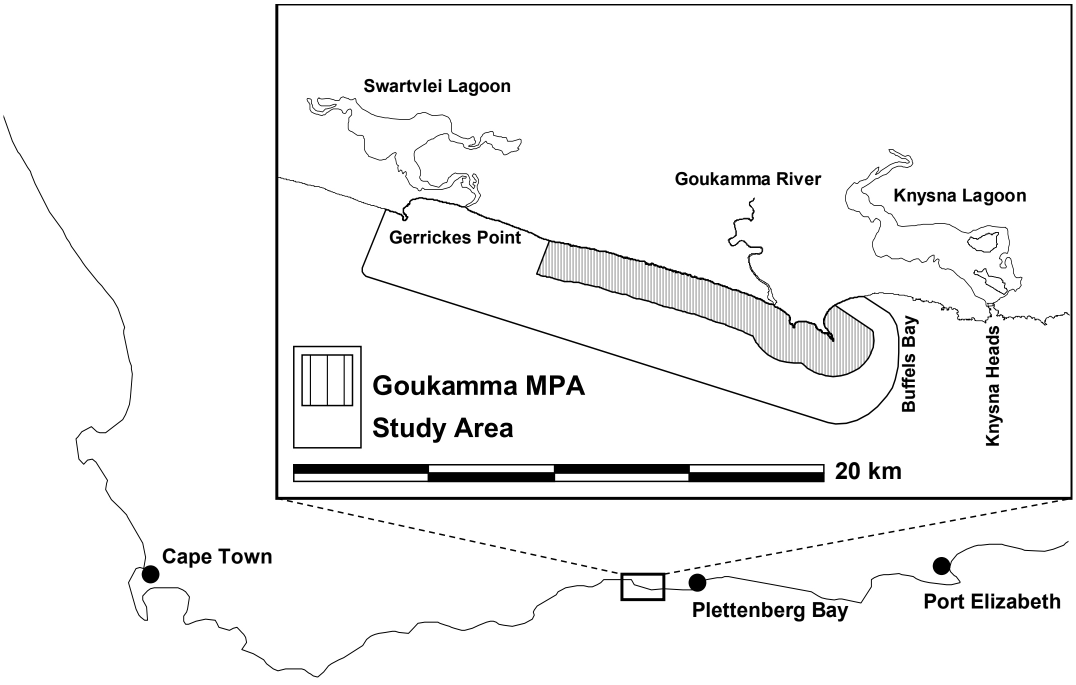


Figure 2.1: Map of the Study Area with the Goukamma MPA

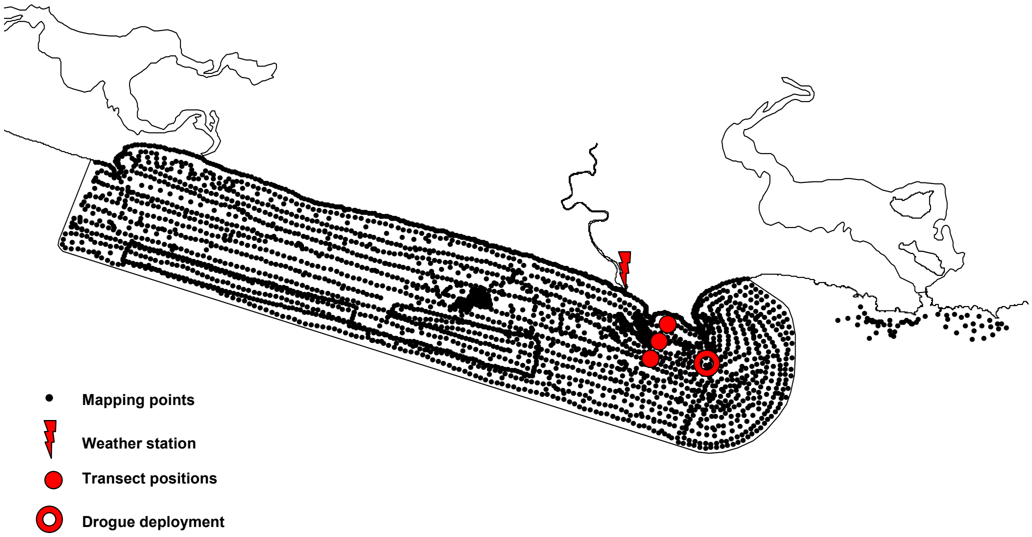


Figure 2.2: Study area with locations of oceanographic and meteorological data recordings

Topography

GPS accuracy was determined on two separate occasions with a GPS receiver (Garmin GPS 45 Personal Navigator), on 28.06.01 and 14.09.03. The receiver was held stationary in the Goukamma Nature Reserve and set to record position once every minute for 24 hours. These data were used to calculate the standard deviation from the average position. The 99% confidence interval (i.e. three standard deviations) was used as an indication of GPS positioning accuracy.

During favourable sea conditions the area from Gerrickes Point in the West to Buffels Bay in the East (Figure 2.2; see figure 2.1 for localities mentioned in the text) was topographically surveyed. In addition, the reefs near the mouth of the Knysna Lagoon were also surveyed with the aim of evaluating this site as a potential area for comparison with the MPA. The boat-based GPS receiver (Furuno Colour GPS Plotter GP-1610C) and echo sounder (Furuno

Colour LCD Sounder FCV-600L) were linked electronically by writing data, in NMEA (Nautical Marine Electronics Association) strings, to a laptop during the survey. The GPS antenna was mounted directly above the echo sounder transducer at the stern of the vessel. Survey speed was kept below five knots to reduce GPS error.

Additional information on bottom profile (rock or sand) was assessed by interpretation of the echo sounder's colour display. Red coloured profiles were interpreted as hard substrata, yellow as soft substrata. The accuracy of depth soundings and bottom type interpretations was verified during SCUBA dives.

The topographic data were imported into ArcView (Version 3.2a, Environmental Systems Research Institute) to display mapping points spatially and outliers were corrected. Mapping points were then interpolated using different methods in Spatial Analyst (Version 2.0a, Environmental Systems Research Institute) to produce continuous seafloor maps. Shaded reliefs and contour lines were superimposed. The four methods of spatial data interpolation offered by the software were used for comparison, namely, 'triangulated irregular network' (TIN), 'inverse distance weighted' (IDW), spline regularized and spline tension. The TIN and IDW interpolation methods produced maps with realistic depths but were lacking a smooth surface. The regularized spline method produced smooth surfaces but unrealistic depth interpolations. The tension spline method produced the smoothest and most realistic seafloor map by fitting a minimum-curvature surface through the mapping points including more points in the calculation at the costs of extended computational time (Environmental Systems Research Institute Inc 1996). Descriptions and maps of all interpolation methods can be reviewed in the appendix (Figure 8.1).

Information on substrate type (rock/sand) was displayed spatially and the reefs in the area were digitized by hand using Edit Tools (Version 3.5 for ArcView).

Meteorology

A weather station was erected alongside the Goukamma River estuary. The instruments were fixed to a six-meter wooden pole, stabilized by steel cable stays. Wind speed (MCS 177-3 Wind Speed Sensor), direction (MCS 177-3 Wind Speed Sensor) and atmospheric pressure (MCS 157 Barometer) were recorded hourly by an internal data logger (MCS 120-02EX Data Logger).

Weather data were downloaded monthly, over a period of 29 months, using Memory Module (Version 1.2.30, MC Systems Ltd.). Data were checked for outliers and stored in an ACCESS (Microsoft® Corp. 2002) database. A non-parametric statistical test (Kruskal-Wallis) was conducted to compare median wind speed and atmospheric pressure between seasons if assumptions of normality (using chi-square test) and homogeneity of variances (using Hartley F-max and Levene's test) were not met. Otherwise mean speeds were compared using parametric one-way ANOVA and results were compared by means of Tukey's test. All statistical tests were conducted in STATISTICA (Version 6.1, StatSoft Inc.). Wind speeds and atmospheric pressures were tested for normality of distribution (chi-square test) within each season and homogeneity of variances (Hartley F-max and Levene's test). SigmaPlot (Version 8.02, SPSS Inc.) was used for graphical presentation of circular data.

Temperature and turbidity

Temperature and turbidity were measured at three fixed positions on a transect line leading from inshore-shallow to offshore-deep water. The inshore position was 0.5 km from shore in 12 m of water depth, the second position was 1.0 km offshore in 24 m depth and the offshore position was 1.8 km in 36 m depth. A bathy-turbidity-thermograph (Bathy-thermograph BT2000 and Global Water WQ770 Turbidity Meter) was lowered manually to measure water temperature and turbidity for each meter throughout the water column.

Prior to deployment, the turbidity meter was calibrated from 0 to 1000 Nephelometric Turbidity Units (NTU) using Formazin solutions of different concentrations (250, 125, 62.5, 31.3, 15.7 and 0 NTU).

Temperature and turbidity data of individual transects were downloaded into EXCEL (Microsoft® Corp. 2002) using Mirror (Version bt2000, Marine and Coastal Management, South Africa). Data were then plotted vs. depth and checked for outliers. As determined in several in situ experiments the measurements of the turbidity meter were influenced by sunlight and sediment. Depending on water clarity and weather conditions, sunlight could enter the lateral openings of the sensor in the upper layer of the water column leading to increased light intensities reaching the backscatter unit of the turbidity meter. Sediments stirred up when the unit hit the bottom artificially increased turbidity measurements.

Temperature and turbidity monthly means as well as frequencies were calculated from the combined data from all stations. In all, 150 transects were conducted. Equal numbers of transects were undertaken each season, covering a 22 month period. Graphical presentation was done in EXCEL, Surfer (Version 8.00, Golden Software Inc.) and SigmaPlot.

Currents

Currents were measured with a surface drogue, instead of a conventional, moored current meter, as this approach is superior for describing water tracks, and specifically for the detection of areas of water retention that may effect supply and settlement of biota. Furthermore, the extrapolation of currents, measured by moored instruments in the vicinity of complex bottom topography could be systematically biased by topographically-induced eddies and current rectification. Of course using drogues also has some drawbacks; eggs and larvae are roughly 1-2mm long and so subject to microscale turbulence and differential flows separated by the thermocline, and therefore may have quite different trajectories compared with large drogues.

A holey-sock drogue equipped with a GPS unit (Niiler *et al.* 1995) was released regularly at a fixed position about 1 km offshore. The position of the drogue was tracked by the GPS receiver (Garmin GPS 45 Personal Navigator); positions were recorded every minute. The design of the drogue ensured that wind and waves had a negligible effect on its travel and the 6 m sock is assumed to track the surface water in the range 2-8m (see Figure 8.2 a in the appendix for illustrations). To facilitate the recovery of the drogue the buoy was fitted with a radio transmitter (Novatech DR-400). A direction finding radio receiver was used to locate the drogue. Equal numbers of drogue trials were undertaken each season, covering a 40 month period. After each trial, the GPS data were downloaded onto a PC and imported into ACCESS. ArcView was used to display and check drogue tracks for outliers. The cleaned data were then imported into EXCEL to calculate the drogue's speed and direction.

A non-parametric test (Kruskal-Wallis) was conducted to compare median speeds of currents between seasons if assumptions of normality (using chi-square test) and homogeneity of variances (using Hartley F-max and Levene's test) were not met. Otherwise, mean speeds were compared using parametric one-way ANOVA and results were compared by means of Tukey's test. All statistical tests were conducted in STATISTICA. Differences in current directions between quadrants were tested with the Kolmogorov-Smirnov contingency tables. Rayleight`s test was used to determine mean angles, mean angular deviation and uniformity of circular distribution of current directions. The parametric Watson-Williams multi-sample test was employed to compare differences in mean directions between datasets (all in EXCEL). SigmaPlot was used for graphical presentation of circular data.

2.3 RESULTS

2.3.1 Topographic mapping

GPS accuracy

The two GPS positioning experiments yielded 1413 and 1406 positions respectively. The GPS accuracy was determined to be 5.1 and 6.1 m, respectively. This degree of accuracy, in relation to the length of the boat (5.45 m) and the mean water depth (±15 m), was sufficient for topographical mapping of the study area.

Mapping

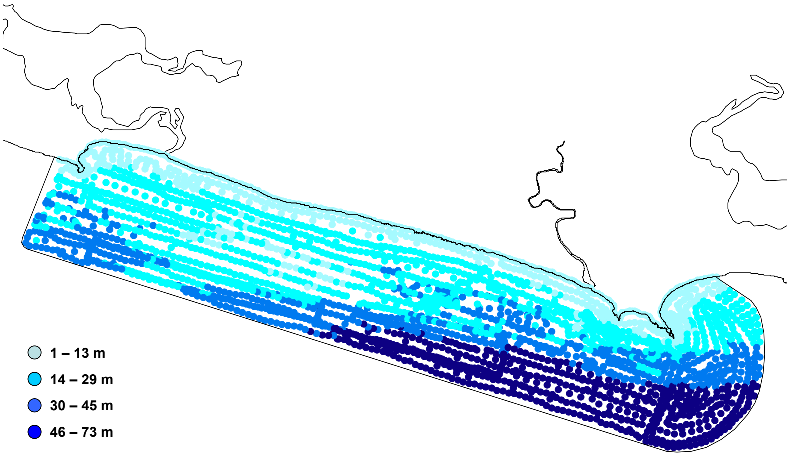


Figure 2.3: Study area with 3521 depth readings

Depth soundings between 1 to 73 m were recorded in the study area (Figure 2.3). The study area (149.6 km^2) includes 43.8 km^2 of reef and 105.8 km^2 of sand flats. A number of reef types were encountered (Figure 2.5); a large rocky foul area (31.0 km^2), three medium-sized inshore reefs with a total area of 7.5 km^2 and numerous smaller reefs inshore and offshore with a total area of 5.3 km^2.

The reefs near the mouth of the Knysna Lagoon were substantially different to those found in the Goukamma MPA because they were shallow, inshore reefs connected to the headland that flanks the lagoon mouth (Knysna Heads). Furthermore, the proximity of a large permanently open lagoon may affect the comparability of these reefs with those of Goukamma. Therefore, the Knysna Heads reefs were not considered for any further sampling effort.

Soundings were interpolated to produce a seafloor map (Figure 2.4). Reef profile was highly variable, but high and low profiles were equally distributed throughout the reef complex of the study area.

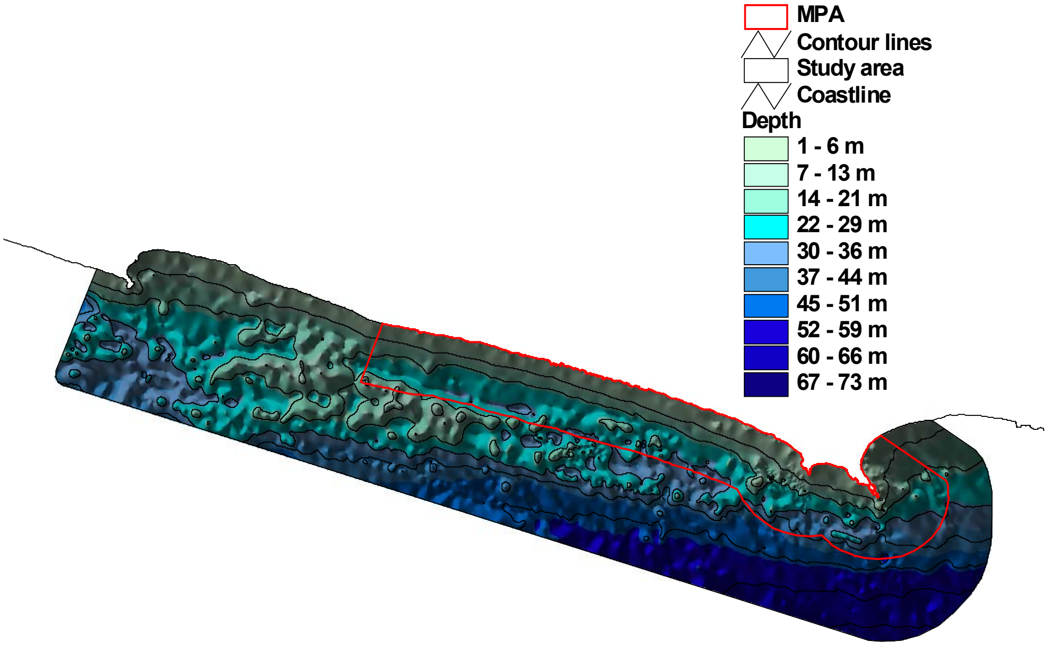


Figure 2.4: Continuous seafloor map of study area generated by using spline tension interpolation

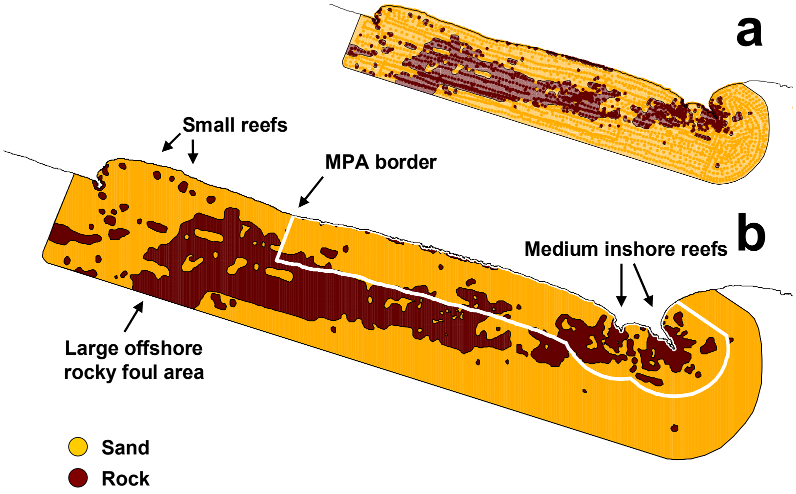


Figure 2.5: The colour echo-sounder differentiated between soundings over rock and sand (a) thereafter interpolated to show the reef complexes (b)

The distribution of rocky and sandy substrates mapped - 1454 points were identified as rock and 2067 as sand (Figure 2.5).

Reefs inside and outside the MPA were comparable in depth (Figure 2.4) and size with a large rocky foul area ensuring continuity of reef habitat across the border (Figure 2.5).

Accuracy of echo sounder readings

Substrate interpretations and depth readings were confirmed during 58 survey dives. In only two areas were corrections needed where sand was mistaken as rock. In both cases, the mistaken patches were small and isolated. Depths recorded during survey dives were on average 1.7 m deeper than those from echo-sounder readings. The greatest inaccuracies occurred when surveying high profile reefs.

2.3.2 Meteorology and Oceanography

Meteorological measurements

Between March 2001 and August 2003, 14169 measurements of atmospheric pressure, wind speed and direction were recorded.

Atmospheric pressure and wind speed

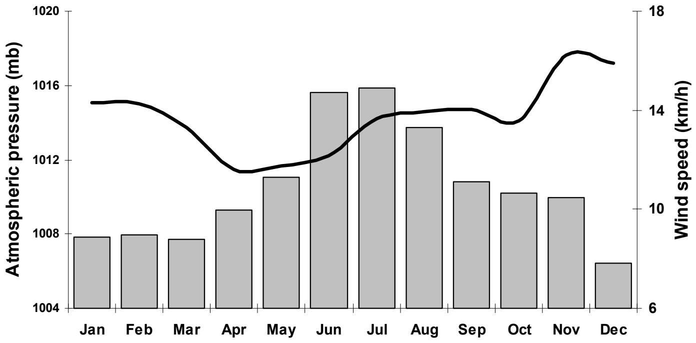


Figure 2.6: Mean atmospheric pressure (bars) and wind speed (line) for each month

Atmospheric pressure was highest in winter and lowest in summer (Figure 2.6). Wind speeds ranged from 0.7 to 71.3 km/h with an annual mean of 13.3 km/h. Wind speed was tested for differences between seasons. Due to the very large dataset, neither normality ($p < 0.001$) nor homogeneity of variances ($p < 0.001$) was detected after log-transformation and non-parametric Kruskal-Wallis ANOVA was applied. It is understood that non-parametric tests do assume homogeneous variances (Underwood 1997) and strictly speaking, the approach is not statistically valid. Results in figure 2.7 are therefore only used for their descriptive value.

Wind speed differed between seasons, being highest in summer and lowest in autumn (p-values between 0.001 and 0.002, Figure 2.7).

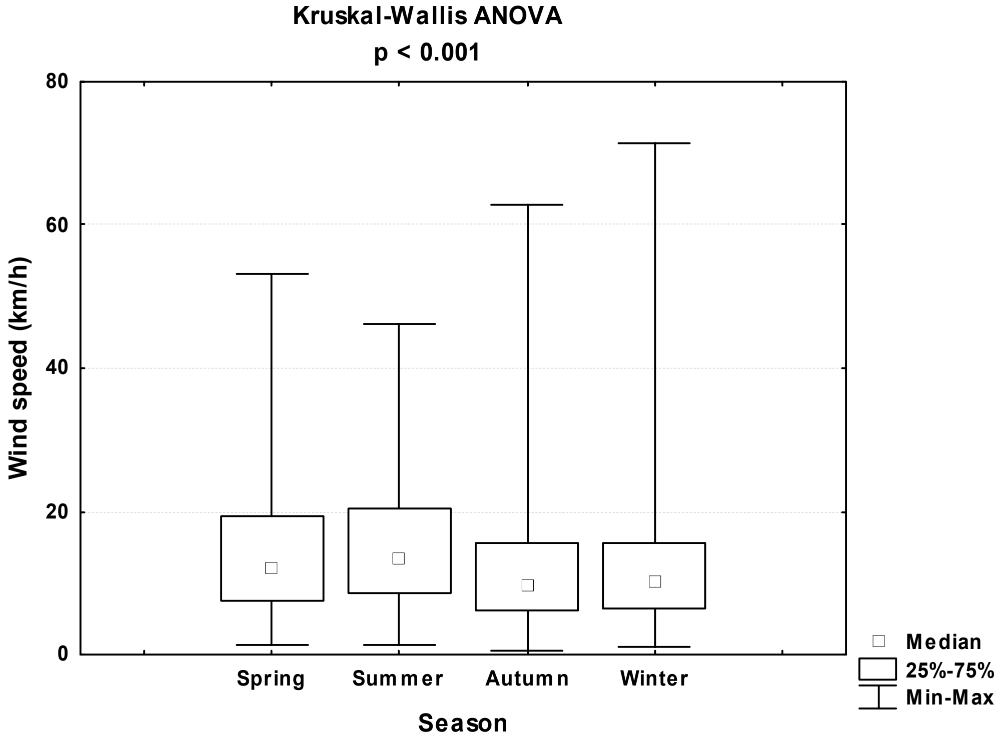


Figure 2.7: Median wind speed compared over season

Overall, southerly and westerly winds were most frequent (Figure 2.8 a) and SW and NE winds had the greatest velocity (Figure 2.8 b). Seasonal differences in directional frequency and wind velocity were not marked, but winter month were characterized by a stronger westerly component (see appendix, figure 8.3 and figure 8.4, respectively).

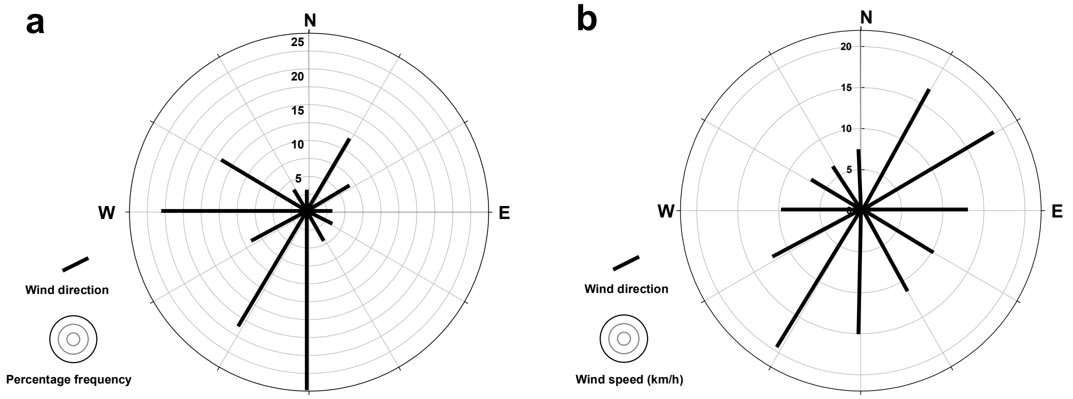


Figure 2.8: Percentage frequency (a) and median wind speed (b) for yearly wind directions. The highest frequency is 26% (southerly)

Sample size and stratification of temperature and turbidity measurements

Between November 2001 and September 2003 the offshore transect with three stations was sampled 50 times.

Monthly mean temperature and turbidity

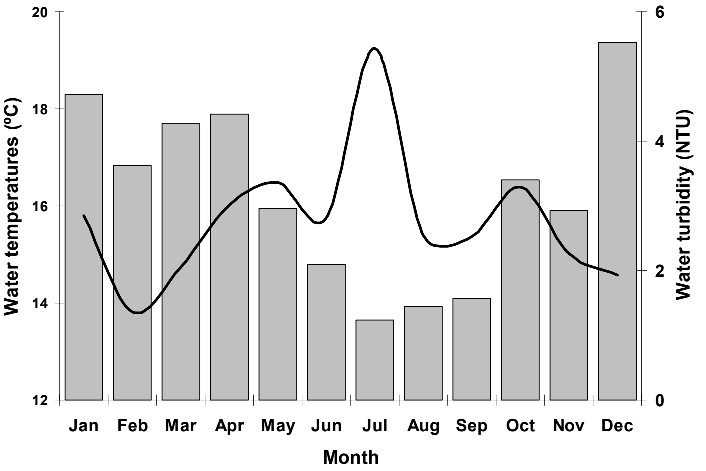


Figure 2.9: Mean water temperatures (bars) and turbidities (line) per month

Sea temperatures, averaged through the water column and across all three stations, ranged between 9.0 and 22.2 ºC. Monthly mean temperatures were higher and more variable in summer (Figure 2.9). Seawater turbidity, averaged through the water column and across all three stations, ranged between and 0.3 and 45.8 NTU. High turbid waters generally coincided with low water temperatures, but this apparent correlation does not imply that cold waters are turbid. Rather, it is understood that turbid waters are caused by strong seas, which prevail in winter (Zoutendyk and Duvenage 1989). Also, turbidity measurements are assumed to be biased towards calmer sea conditions, as it was impossible to sample from a small skiboat in rough seas.

Temperatures fell into four broad groups, indicating separate water masses. The coldest (average 9.5 ºC) is typical of newly upwelled South Atlantic/Indian Central Waters (Schumann *et al.* 1988), mostly prevalent in summer below the thermocline. The warmest water mass averaged 19.5 ºC also prevailed in summer, but above the thermocline. The 16.5 ºC water mass prevailed in autumn below the thermocline once upwelling had ceased. The 14.0 ºC water mass is the result of complete winter breakdown of the thermocline and a well mixed water column (Figure 2.10).

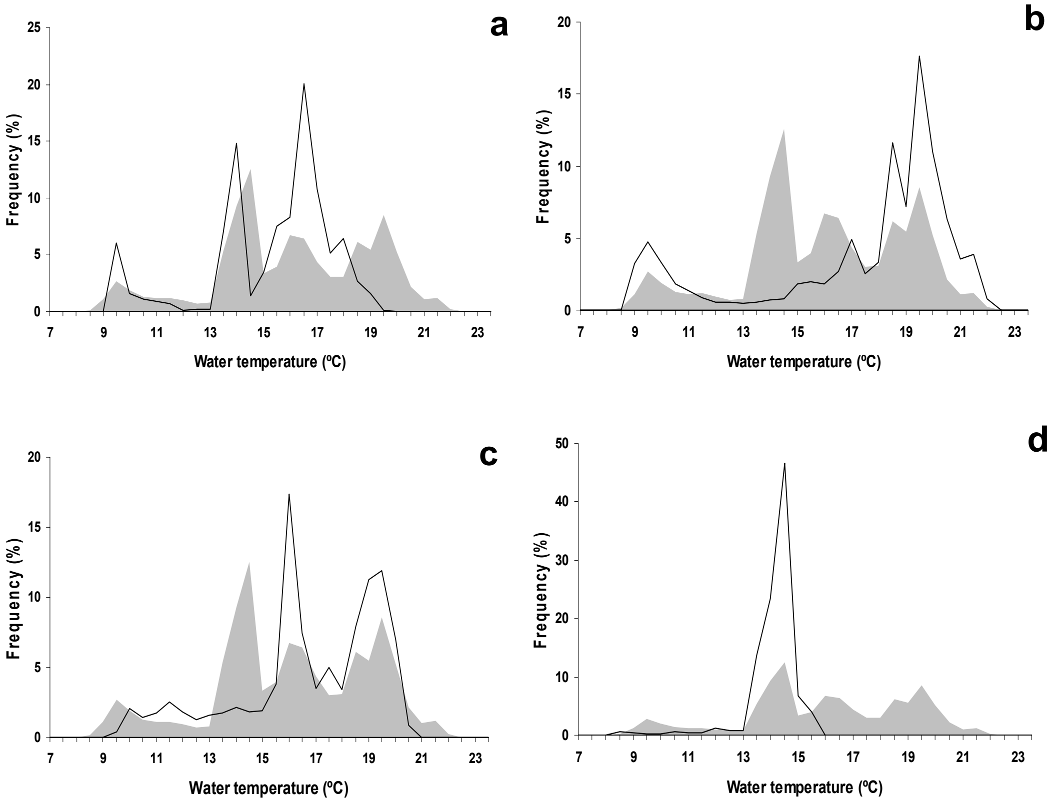


Figure 2.10: Seasonal (line) frequencies of water temperature measurments taken in Goukamma; spring (a), summer (b), autumn (c) and winter (d). Annual frequencies (shaded grey) are shown in each graph for comparison

Water column structure

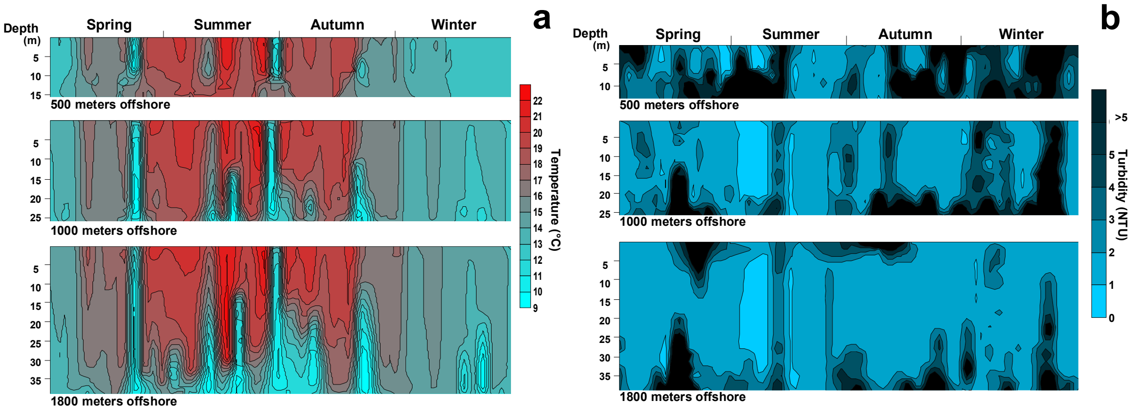


Figure 2.11: Temperature (a) and turbidity (b) contours interpolated over season at three positions

Temperatures were uniformly low throughout the water column from the beginning of winter to early spring at all three transect positions (Figure 2.11 a). From mid-spring onwards the water column stratified, with warmer water on the surface and colder layers at the bottom. By end of summer this stratification was most pronounced at the offshore position breaking down towards shore. During active upwelling brought on by prolonged easterly winds, cold water displaced the thermocline upwards and intensified the temperature gradient (Figure 2.12 b). Cold water intrusions decreased water temperatures from over 21 °C at the surface to less than 9 °C at the bottom. On occasion, upwelled water reached the surface. No major upwelling events were recorded throughout winter. Water stratification deteriorated during autumn and disappeared by the beginning of winter (Figure 2.11 a).

Generally, water turbidity was higher inshore than offshore and near the sea floor (Figure 2.11 b). Less often, turbid waters were also measured at the surface. Turbid bottom water often associated with cold upwelling events (see Figure 2.11). Typically, water turbidity was highly stratified, changing suddenly within a few meters in the water column (Figure 2.12 c).

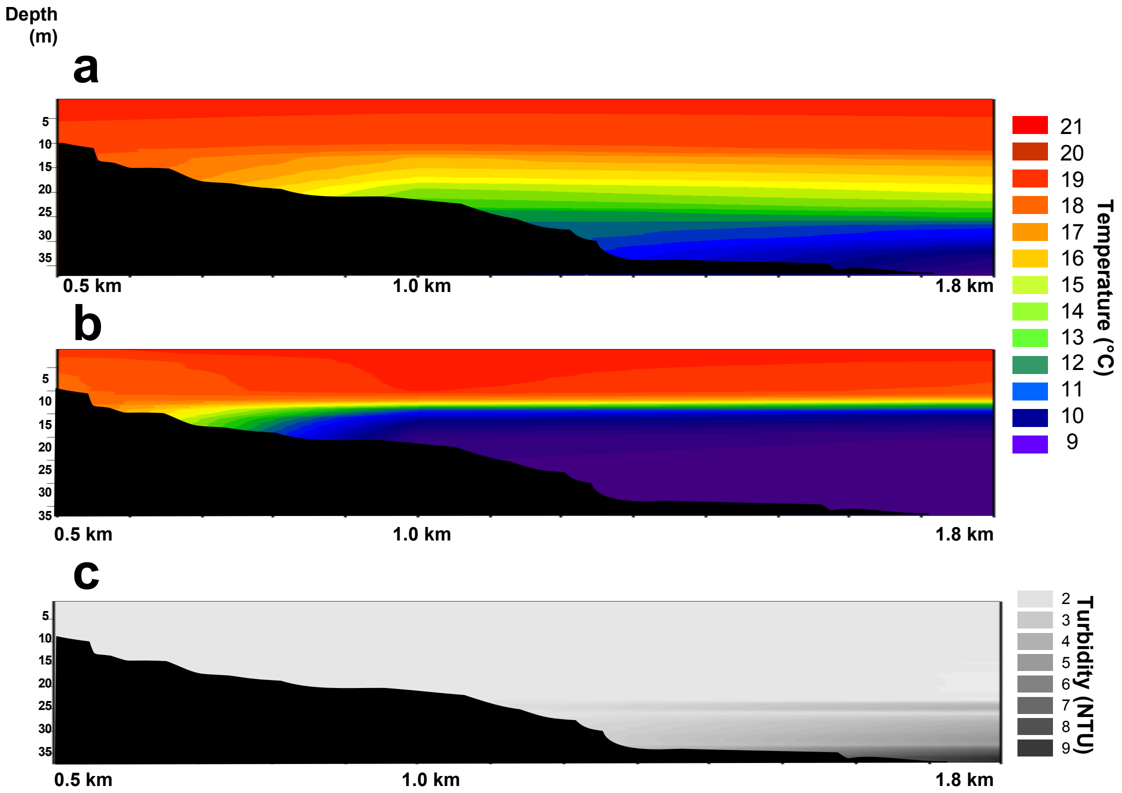


Figure 2.12: Temperature and turbidity sections during stratification of sea water in summer (a), cold upwelling (b) and formation of a nephelometric layer (c)

Sample size of current measurements

Between May 2001 and September 2004, 29 drogue trials were conducted. In all, 2669 individual position recordings were downloaded. Deployments lasted between 35 minutes to over 4 hours. Displacement distances between 167 and 8551 m were recorded. There were 8 trials in spring (Sep-Nov), 6 in summer (Dec—Feb), 6 in autumn (Mar-May) and 9 in winter (Jun-Aug). Individual tracks of all trials separated by season are shown in Figure 2.13.

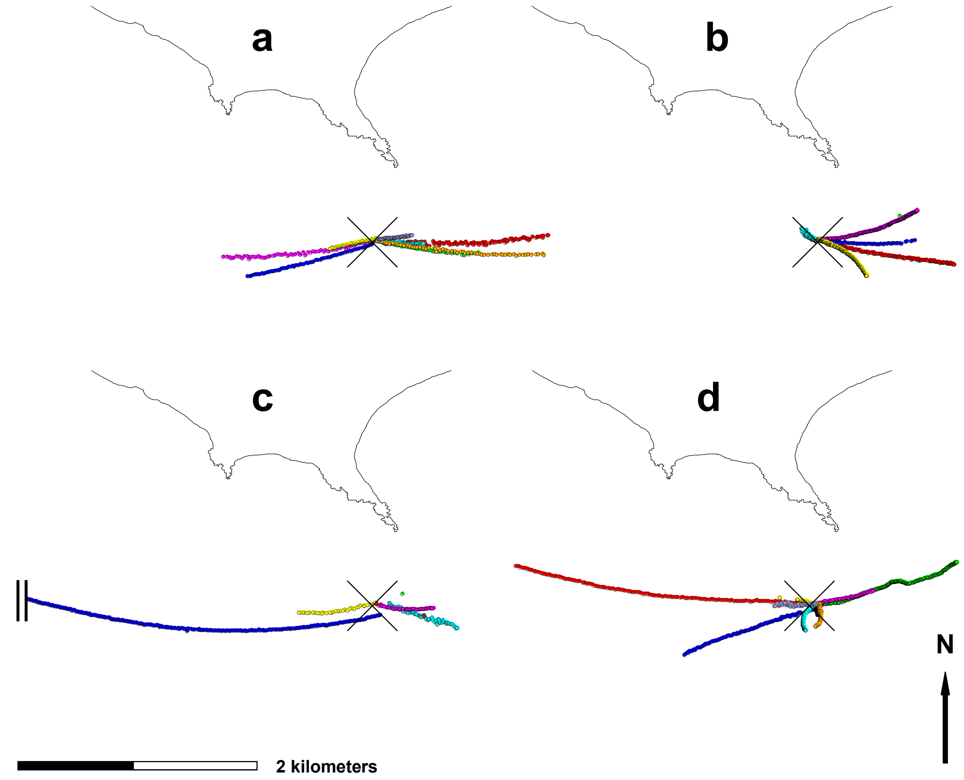


Figure 2.13: Drogue tracks recorded for spring (a), summer (b), autumn (c) and winter (d). Crosses denote point of release

Season and current speed

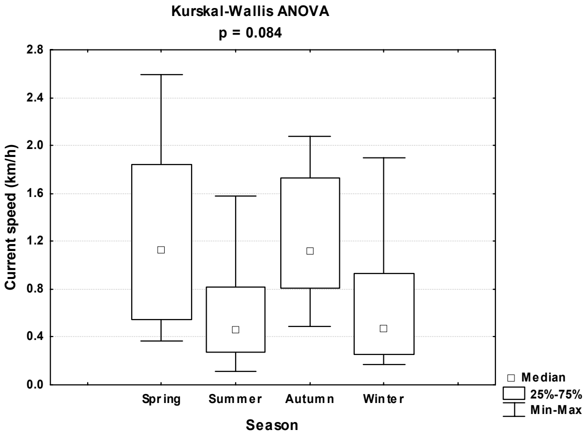


Figure 2.14: Effect of season on current speed tested with non-parametric Kruskal-Wallis ANOVA

Current speeds ranged between 0.11 and 2.59 km/h with a mean of 0.93 km/h. Mean speeds were higher in spring and autumn with 1.25 and 1.22 km/h and lower in summer and winter with 0.62 and 0.66 km/h respectively.

Although variances were homogeneous (p > 0.620), distributions of seasonal current speed frequencies were non-normal. Therefore, non-parametric Kruskal-Wallis ANOVA was used to confirm the results from parametric one-way ANOVA (Figure 2.14). Differences in current speed over season were not significant for both tests (parametric $p < 0.071$; non-parametric $p < 0.084$)

Current direction

The angular distribution is mainly bimodal with high frequencies of occurrence in westerly and easterly direction, with a bimodal distribution axis orientated at 63º (E-W) but three distinct current groups were observed (Figure 2.15). The mean directions of these groups were 92º E, 187º S and 272º W.

With 17 and 9 occurrences, respectively, currents in easterly and westerly direction were significantly more common ($p < 0.05$) than those in southerly directions (3 occurrences).

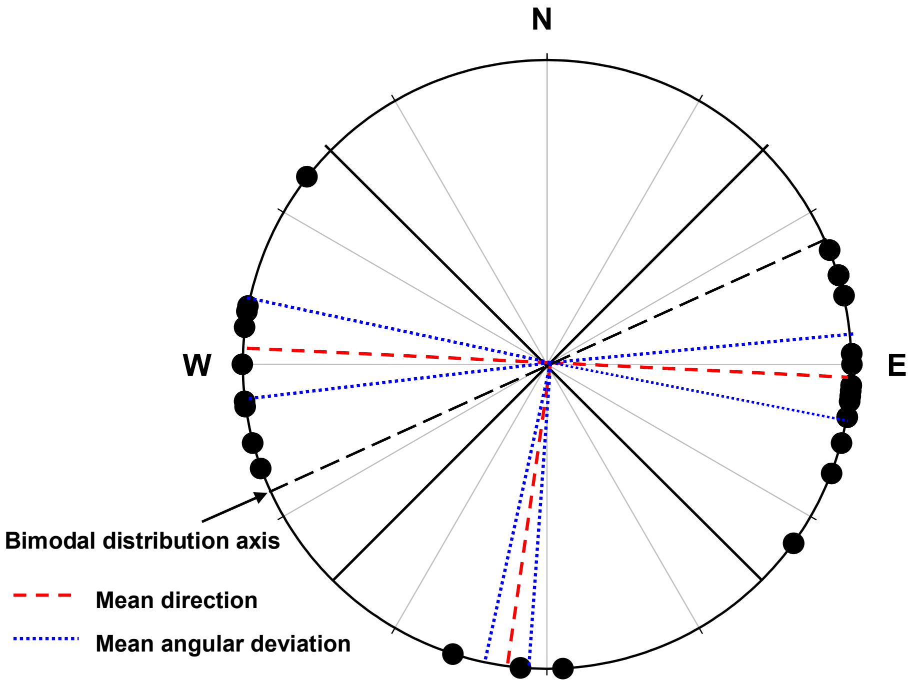


Figure 2.15: Angular distribution of current directions with mean direction and mean angular deviation for the eastern, western and southern quadrant. Bimodal distribution axis is indicated.

Current direction and speed

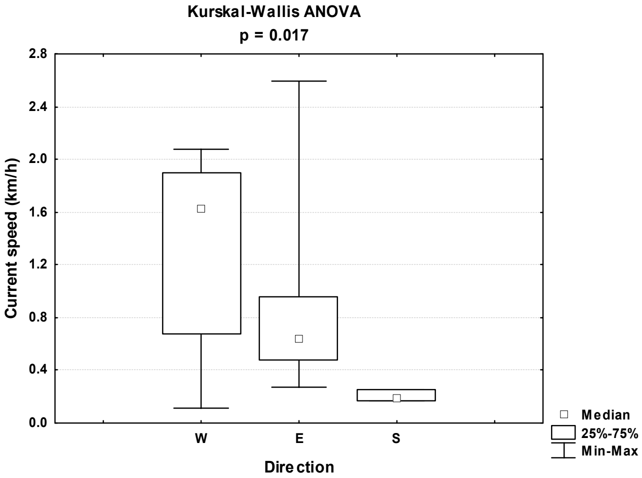


Figure 2.16: Median of current speed in three different quadrants tested with nonparametric Kurskal-Wallis ANOVA

Due to the very large dataset, neither normality (p < 0.001) nor homogeneity of variances (p = 0.039) was detected after log-transformation. Therefore, non-parametric Kruskal-Wallis ANOVA was applied. Current speeds between the three quadrants (east, west and south) were significantly different (p < 0.017; figure 2.16). Currents in southerly direction were slowest with a median of 0.19 km/h. Westward currents, with a median of 1.62 km/h, were the fastest of all quadrants. Eastward currents had a median of 0.64 km/h, but reached peaks of up to 2.59 km/h (Figure 2.17).

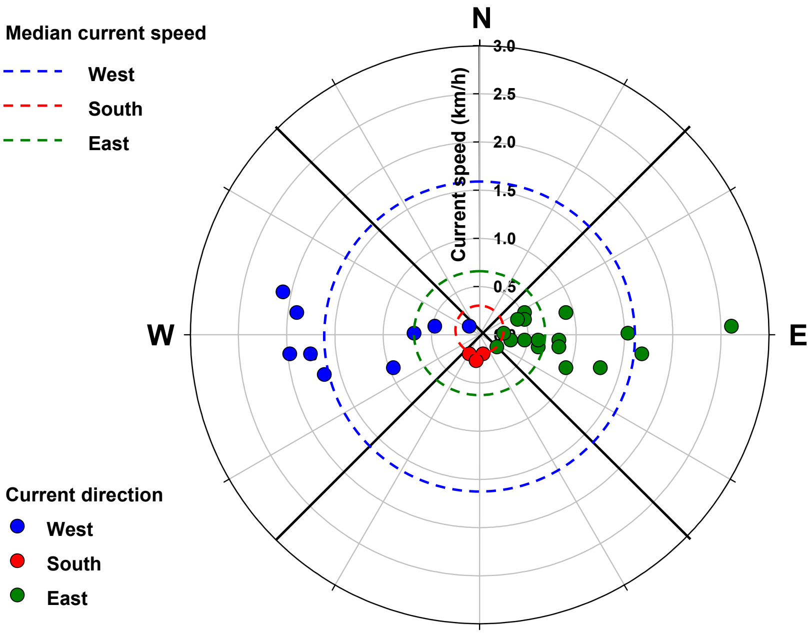


Figure 2.17: Directions and speed of individual current measurements. Median current speeds for the different quadrants are indicated

Season and current direction

Season	East	West	South	North	Total
Spring	6	2	0	0	8
Summer	5	1	0	0	6
Autumn	4	2	0	0	6
Winter	2	4	3	0	9
Total	17	9	3	0	29

Table 2.1: Season and current direction

No difference in distribution of current directions between seasons could be detected ($p > 0.1$). However, in summer, spring and autumn, eastward currents were dominant ($p < 0.01$, 0.025 and 0.05, respectively). This dominance of eastward currents built up in spring, reached a peak in summer and then declined in autumn. No southward or northward currents were encountered during the sampling interval for these seasons (Table 2.1).

2.4 DISCUSSION

Benthic habitat

The Goukamma shoreline lies on the eastern end of a geological formation known as the Wilderness Dune Cordons, the structure and formation of which is described by Illenberger (1996). Several dunes running parallel to the shore and reaching thicknesses of 200 m had their origin during high sea-levels of the Pleistocene inter-glacial periods. During the complex sea-level history of the last million years, there have been several phases of dune building followed by coastal erosion. Aeolonite sandstone that developed from coalesced dune deposits became eroded with recent sea-level rise, and now forms the inter-tidal and sub-tidal reefs in the Goukamma region.

Sub-tidal reef extends to 37 m depth and approximately two miles offshore. Beyond that lies soft sediment which forms part of the south coast trawlable ground. Overall, the study area consists of 29% reef, the remainder being sediment. In the Goukamma MPA itself, reef accounts for only 25%. In total, the Goukamma MPA includes only 10.4 km^2 of reef. Reef occurs mostly in the eastern end of the MPA, where the Walkers Pt headland extends into the sea, but a rocky foul area runs along the entire southern boundary, occupying substantial sections on the seaward limit of the MPA in two places, in the centre and the west. The bulk of this rocky foul area lies outside the MPA, but it is continuous across the border.

Comparability of reef habitat across the MPA boundary

The bathymetry of the study area does not show a steady increase in depth with distance offshore. The bulk of the reef complex lies between 14 and 29 m, but it does not shelf into deep water. The relative uniformity of depth of the reef complex is probably explained by its origin at the base of high coastal dunes. Rising sea-levels would have eroded the dune and exposed and submerged a flat expanse of coalesced dune, or sandstone. Indeed, one of the shallowest points of the reef complex is found on the south-western corner of the MPA, one nautical mile offshore. No discernable differences in reef structure, in terms of profile or rugosity, were noted across the entire reef complex (Figure 2.4).

These results indicated that there was sufficient scope for selecting sites for ecological comparison across the MPA boundary without looking further afield. Surveys around the Knysna Heads revealed reefs of a different character, and which are subjected to substantial estuarine output and fluvial deposit. Although originally it was envisaged to compare reef communities in Goukamma MPA with those of the exploited reefs near Knysna, the physical survey suggested that a comparison within the same reef complex at Goukamma would be more appropriate than a comparison between disjoint and dissimilar reefs. Moreover, the original concern that comparisons across the Goukamma MPA boundary would be confounded by dissimilar depths, because of the inshore position of the MPA, was not substantiated. There were vast areas of reef of similar profile and depth within the same complex on either side of the boundary. Selecting sites for comparison in close proximity is preferable, for eliminating unknown or indiscernible biogeographic influences (Booth 2004, Tobler 1970).

Difference in water temperature and turbidity measured between the fixed stations along the transect were depth related. As shown by measurements during biological sampling (described in a later chapter) throughout the study area, shallow stations, irrespective of their distance offshore, generally had higher bottom temperatures and turbidities than deeper stations. These difference are depth related and do not indicate consistent differences between sites of similar depth across the MPA boundary. Higher bottom temperatures in shallow water can be explained by the position of the thermocline, which was usually deeper than the depth of the innermost fixed sampling station, inside the MPA. The higher bottom turbidity in shallow water, on the other hand, is likely to be caused by wave action re-suspending bottom sediments in shallow areas (Zoutendyk and Duvenage 1989).

Surface currents were strong, but no particular current direction prevailed even within a season. Measured currents in the study area would serve to exchange dissolved nutrients, suspended organic matter, plankton, including fish spawning products, freely throughout the study area. The lack of any obvious consistent current direction, or areas of water retention, suggests that there are no systematic differences in food supply or fish recruitment over the reef complex. Conversely, the strength of the currents and the lack of consistent direction suggests a potential for widespread export of spawning products of reef organisms in all directions.

Conventional current measurements by moored instruments have been useful for studying oceanographic processes because they provide continuous, geo-referenced data (Roberts and Van Den Berg 2002), however, they fail to explicitly demonstrate diffusive processes in the vicinity of complex inshore topography. The only other study of inshore currents with a surface drogue along the Cape south coast (Attwood *et al.* 2002) indicated very similar current patterns to those found in Goukamma including onshore and offshore advection associated with downwelling and upwelling, respectively.

In their appraisal of MPA fishery studies, Gell and Roberts (2003) raised the difficulty of selecting appropriate control sites. Good control sites need to satisfy two conflicting conditions, namely, that they need to be close together so as not to represent divergent ecosystems, but that they also need to be far apart such that the sites do not effect one another, specifically by the way of recruitment of pelagic larvae. Practically, meeting both these criteria is impossible, as fish larvae can be transported over hundreds of kilometres by ocean currents, distances which may also encompass substantial ecosystem change. In this study, physical adjacency of control sites is not problematic, as it is understood that the larvae of the reef fish (Sparidae) have long planktonic life spans and are so widely distributed that micro-scale variations in recruitment are unlikely. This study is in fact not a direct study of MPA effectiveness, but rather an intensive assessment of fishing effects on post-recruit survivorship, population structure and community structure.

Is Goukamma representative of warm temperate south coast habitat?

The geological formations of Goukamma are found repeated throughout the south coast. Unstable sand dunes and wave cut aeolonite sandstone platforms with associated offshore reefs can be found in False Bay, Walker Bay, De Hoop MPA and St Sebastians Bay, the Riversdale coast, Vleesbaai, Mossel Bay (east), Wilderness, Oyster Bay, Jeffreys Bay, Sardinia Bay and Schoenmarkerskop. The various coastal habitats have been mapped in preparation for South Africa's Oil Contingency Plan (Jackson and Lipschitz 1984), but also provides a convenient basis for calculating approximate distribution and extend of habitat types. Three broad coastal habitat types can be recognized, namely, pure sandy beaches, sand dunes with wave cut aeolonite sandstone platforms and steep, rocky headlands. Pure sandy beaches such as Van Staadens are characterized by an absence of hard substrata. Steep, rocky headlands, such as Tsitsikamma, Harkerville and the Rooiels coastlines, are geologically stable coastlines that have not shifted with rising sea-levels, nor given rise to extensive shallow sub-tidal reef during periods of sea-level rise. In contrast, the wave cut platforms of Goukamma and other similar sites are part of extensive reef complexes that have been covered and uncovered by changing sea-levels during past glaciation-cycles. Using coastline length as a measure of inshore habitat, submerged sandstone platforms such as those found at Goukamma, account for approximately 30% of the coastline between Cape Point and Port Elizabeth.

Water temperature and turbidity can influence distribution and movement behaviour of fish (Hanekom *et al.* 1989, Kerwath 2005) and reproductive success of populations (Sauer *et al.* 1992). Wind-induced upwelling and ocean currents play a major role in the dispersal of eggs and larvae that effects the recruitment of reef dwelling organisms (Tilney *et al.* 1996, Roberts and Van Den Berg 2002).

An important consideration when planning this study was the extent to which the findings could be extrapolated to fisheries throughout the warm temperate south coast. Three biogeographic regions can be distinguished in southern Africa (Emanuel *et al.* 1992, Turpie *et al.* 2000): one of these, the warm temperate south coast, extends from Cape Point to Port Alfred. Goukamma lies centrally in this zone.

Nearshore seawater along the south coast is characterized by uniform temperatures in winter and stratification in summer intensifies by intermittent upwelling events (Harris 1978, Schumann 1999). The Agulhas Bank is fed by frequent intrusions of warm Agulhas Current water, which in summer lies on top of a sharp thermocline. Prevailing westerly winds result in strong mixing to depths of 80 to 90 m in winter (Swart and Largier 1987). Wind-induced upwelling of cold water, although most extensive on the west coast, occurs with less frequency and intensity throughout the south coast including the Port Alfred area in the east (Schumann *et al.* 1982). Seasonality of upwelling events, position of the thermocline and temperatures throughout the water column during summer stratification and uniform winter water were very similar in this study and in Algoa Bay (Schumann *et al.* 1988) and the Tsitsikamma NP (Hanekom *et al.* 1989).

Another feature of Goukamma that was not unique was the occasional intrusion of a highly turbid, nepheloid layer, which is known to influence certain species (Sauer *et al.* 1992). High light penetration in surface water layers and nutrient-rich water after upwelling events result in higher turbidity levels through increased plankton density (Fonds and Eisma 1967, Nybakken 1993, Pérez *et al.* 2005) and the formation of marine snow below the thermocline (Ransom *et al.* 1998). Higher turbidity is also present in the bottom mixed layer in which mud deposits are continuously re-suspended (Phillips and Scholz 1982) and where the aggregation of marine snow adds to the formation of a bottom nepheloid layer (Ransom *et al.* 1998). Bottom nepheloid layers, which are a feature of the south coast mud belt of the inner Agulhas Bank between Mossel Bay and Port Elizabeth, were also present in the Goukamma study area (Zoutendyk and Duvenage 1989). Higher turbidity, generally, in winter is due to more wave action and the break-down of the thermocline, which facilitates the mixing of turbid bottom waters with surface layers (Zoutendyk and Duvenage 1989).

Most of the energy in Agulhas Bank shelf water is in the form of coastal trapped waves, generated by synoptic weather patterns. Atmospheric pressure variations, therefore, produce current speeds an order of magnitude greater than tidal waves (Tilney *et al.* 1996). Yearly mean atmospheric pressures recorded in the study area, follow the same pattern as described by Van Zyl (2003) for the entire south coast. In winter, atmospheric pressure along the south coast is dictated by the subtropical high pressure belt around 30° South. In summer, however, intense warming of the land creates a shallow low pressure system.

Throughout the year westerly and easterly winds are dominant along the south coast (Goschen and Schumann 1988, Schumann *et al.* 1988, Hanekom *et al.* 1989, Jury 1994). The prevailing westerlies at 30º S and cyclonic low pressure systems (Ahrens 1999) are the reason for the high frequencies of westerly winds, in particular in winter (Jury 1994). This was closely matched by the measured wind frequencies in the study area. Westerly winds were frequent throughout the year, in particular in winter. 'Easterly' is the general wind direction along the south coast describing onshore winds (Harris 1978) caused by the warming of the land (Van Zyl 2003) and a prevailing anticyclonic high pressure system at sea (Jury 1994). These onshore winds are strongest and most frequent in summer (Harris 1978, Schumann *et al.* 1988, Jury 1994). In the study area, however, southerly and south-westerly winds were common throughout the year. This was also found for the Cape Agulhas region (Harris 1978) and could be explained by the direction of the local coastline running from north-west to south-east in both regions. This difference from the general pattern for the south coast is small and does not change oceanographically important events such as upwelling and current patterns (see below).

Near-shore current patterns have been investigated along the south coast in general (Shannon 1967, Harris 1978) and for Algoa Bay (Goschen and Schumann 1988) and the Tsitsikamma NP (Tilney *et al.* 1996, Attwood *et al.* 2002) in particular. Currents are mainly alongshore; eastward, as a result of Agulhas counter currents and westward, driven by the prevailing easterly winds. With increasing distance from the Agulhas Current, wind-driven currents become dominant. Harris (1978) analyzed wind subtracted ships drift between Plettenberg Bay and Mossel Bay and found highest frequencies for eastward followed by westward currents with few southward currents. These frequencies were closely matched in this study, however, median current velocities differed, probably due to the different methods applied. Attwood *et al.* (2002), using the exact same holey-sock drogue for trials, also noted east and westward currents as most frequent. Current velocities were higher for westward than for eastward currents and modal current velocity was 0.83 km/h compared to a mean of 0.93 km/h in this study.

Despite its shallow depth and inshore position, the physical environment in Goukamma is subjected to the same oceanographic processes as found over the broader Agulhas Bank.

Comparison with other MPAs

Topographic surveys of reefs along the south coast were conducted at Castle Rock MPA (Kerwath 2005), De Hoop MPA (Penney 2001) and the Tsitsikamma NP (Buxton 1987). Although reefs were also found further offshore in deeper water (De Hoop MPA and Tsitsikamma NP), inshore reefs were comparable in terms of depth range and structure with those described in this study.

Despite the similarity of habitat, Goukamma MPA provided the best representative study site on the basis of its size and location. Castle Rock MPA and Sardinia Bay MPA are situated at the western and eastern end of the warm temperate south coast biogeographic zone, respectively. Choosing such geographic extremes as study areas may limit the value of the findings as generalization of the south coast conditions, particularly in respect of the study of community effects of fishing. Whereas fish population dynamics may be similar across vast areas, there is a gradual shift in species composition along the east-west axis of the south coast biogeographic zone.

On the other hand, the reefs in the Tsitsikamma NP and De Hoop MPA are centrally situated but these are large MPAs which extend well seawards of reefs. In these cases, only comparisons with disjointed and remote sites have been possible. For example, Buxton's (1992) study of reef fish in the Tsitsikamma NP compared populations that were separated by hundreds of kilometres.

Conclusions

Goukamma MPA provides an excellent site for comparative reef fish studies between exploited and unexploited areas. It is representative of the warm temperate south coast, which has a high degree of ichthyofaunal endemism and a large number of overexploited reef fish species. Furthermore, the size and design of Goukamma MPA and the structure of its inshore reefs conveniently provide areas for comparative study which are similar in respect of habitat quality and oceanographic conditions. Among the seven MPAs between Cape Point and Port Elizabeth, Goukamma MPA provided the best possibility for an intensive study of the community effects of reef fishing.

3 ASSESSMENT OF THE FISHERY IN THE STUDY AREA AND IMPLICATIONS FOR MANAGEMENT

3.1 INTRODUCTION

The detection of fishing effects on the reef fish communities by way of comparison depends on the presence of a strong fishing effort differential between comparable habitats. It is crucial that at least one fish species that is reef-dwelling and resident is targeted by the fishery, as highly mobile fish are unlikely to exhibit differences in biological indicators across the border of a medium-sized MPA (Botsford *et al.* 2003).

A review of fisheries data, providing information on past fishing activities in the area, is important, as fisheries often change target species and past impacts have lasting effects where slow-growing species are an integral part of the exploited fish community (Pauly *et al.* 1998).

According to the National Marine Linefish System (2001), 23 tons of linefish were caught by a commercial fleet of 30 boats exerting a total effort of about 11,500 man-hours between Knysna and Gerrickes Point in the 1980s. The main target species were kob (*Argyrosomus japonicus*; 11 tons), roman (*Chrysoblephus laticeps*; 2 tons), hake (*Merluccius capensis*; 1.8 tons) and santer (*Cheimerius nufar*; 1.4 tons). In the 1990s, ever decreasing catches of kob, roman and santer and an increasing demand for hake for overseas markets (Europe), changed the spectrum of species targeted by the commercial linefishery. In 2000, the total effort and CPUE had doubled to about 20,000 man-hours and 3.3 fish/hour, increasing the total catch to 82 tons. This was possible by commercial operators abandoning traditional species like roman and santer and targeting species that had previously been underexploited. Today, almost 90% of the catch is hake and shark catches have increased tenfold. Catches of kob, roman and santer have decreased to about 15% of their 1980s levels.

Reef fish are now mainly targeted by the recreational sector during the holiday seasons, however, on days when sea conditions are unfavourable for catching hake (warm, clear water), commercial boats do target the inshore reefs (pers. obs.).

To ascertain the current fishing effort in the study area it was necessary to survey the positions of fishing boats and record their catch. Commonly used survey techniques include access point and aerial surveys and are described by Pollock *et al.* (1994) and Brouwer and Buxton (2002). A general problem with techniques that rely on information supplied by fishers is that they do not supply accurate information on catch position or catches. Aerial surveys suffer the same problem. More reliable information can be obtained through a roving creel survey, where positions of vessels can be mapped at sea using GPS. When working at sea, this method does have the disadvantage of often not being able to get an accurate number or weight of fish caught but does provide information on species composition of the catch and targeting.

The controlled fishing survey in this study that was required for a subsequent community structure analysis, also allowed me to gain baseline information on the linefishing method itself and to identify implications for conventional management.

A large problem with management measures like size limits and species restrictions is the lack of selectivity produced by the fishing gear (Roberts 1997). This leads to sometimes high proportions of unwanted or protected species (bycatch) and undersized fish that have to be returned (Alverson *et al.* 1994). The survival rate of returned fish can be very low (Attwood *et al.* 1997a, Diggles and Ernst 1997, Domeier *et al.* 2003) and many reef-dwelling sparids are known to die during handling or after release. It is therefore desirable to identify traditional management measures that reduce bycatch, the proportion of undersized fish in the catch and post-release mortality rates.

The influence of hook size and bait type on catch rates, bycatch reduction and size selectivity has been documented for various line fisheries (Punt *et al.* 1996, Erzini *et al.* 1998, Sousa *et al.* 1999, Woll *et al.* 2001). The influence of hook size, bait type and other environmental factors on composition of catch and post-release mortality has not been studied in the South African linefishery.

The main objectives of this chapter are to:

- Provide a map of the study area with zones of different fishing effort by recording the positions of boats at sea using GPS.
- Identify target species of the local linefishery by interviewing fishers at sea.
- Identify management measures that will reduce post-release mortality of undersized fish and bycatch in the area by evaluating linefishing methods.

3.2 MATERIAL AND METHODS

Boat counts

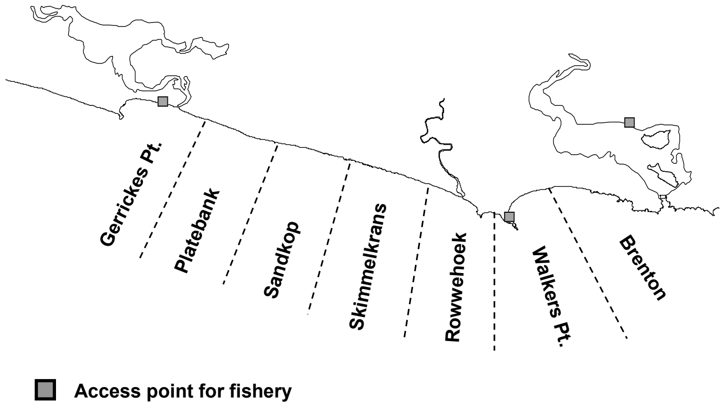


Figure 3.1: Study area showing access points for the local fishery and zones of systematic boat counts

Due to the unpredictable weather patterns of the study area boat counts and interviews were conducted at sea on a random basis. The study area was divided into seven similar-sized zones stretching from Brenton in the east to Gerrickes Point in the west (Figure 3.1). All zones were easily recognizable at sea by identification of characteristic coastal features such as settlements, headlands or rock faces. All fishing boats visible (with the aid of binoculars) were counted while travelling along the MPA's seaward border. Counts therefore always covered the first two zones closest to the access point (Brenton and Walkers Pt.) and additional zones to the west if biological research was scheduled in those zones. Boat counts were influenced by surface visibility and swell height. Counts were stratified by season during a period of 23 months. The allocation of sampling events and boats counted per season and zone were tested for randomness with chi-square contingency tables. All statistical analyses were conducted with EXCEL routines.

Boat checks

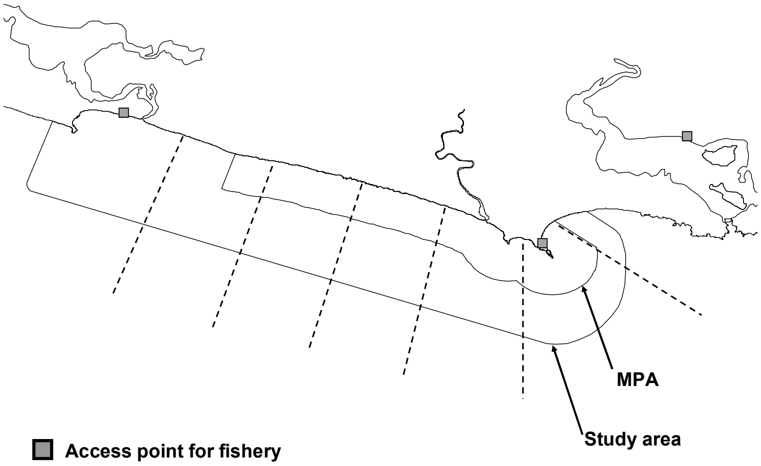


Figure 3.2: Study area showing the design of systematic boat checks

Boats were approached at sea to check position and catch. Due to time limitations, not all boats within a zone were approached individually. Boats outside the study area were not checked (Figure 3.2), but were included in the counts. During boat checks, boat position, water depth and bottom type (sand/rock) were recorded using the boat-based GPS receiver and echo-sounder. The boat's name, registration number and number of crew were noted and the skipper was interviewed to get information on catch and species targeted. Checks were stratified over season during a period of 34 months. Vessel positions were subsequently plotted in GIS using ArcView.

Controlled fishing method

Circle hooks (VMC Sport Circle) of five different sizes were used (*1/0* to *5/0*) exclusively. The barbs of the hooks were clipped to avoid unnecessary injuries to the fish and to allow hooks to be removed rapidly. Two hooks of the same size were used per set of fishing tackle. Redbait (*Pyura stolonifera*), pilchard (*Sardinops sagax*) or squid (*Loligo vulgaris*) were used as bait. The same bait was used on both hooks.

The standard fishing time per fishing session was one angler-hour, but at least ten minutes, if more than three anglers participated. In total only ten different fishers, all trained in scientific sampling, participated in the survey.

Water depth and temperature were measured with the average temperature of the bottom four meters, recorded as the relevant temperature for the reef being fished.

The captured fish were measured to the nearest millimetre and hook size and bait used were recorded along with the fork length. The way the fish were hooked was noted as lip (hooked in the mouth area) or gut (hook swallowed). All fish were released after checking for barotrauma and deflated using a surgical needle (Rumo Spinal Needle, 18-G by 3.5″: 1.20 ∅ by 90 mm). A record was kept of capture mortality.

Hook sizes and bait types were stratified over season and zones to achieve comparable sample sizes. Analysis on hook size and bait type preferences were based on comparisons of catches of individual species with the total catch, using chi-square contingency tables in EXCEL. Recording the individual soak times of hook and bait types would have allowed us to directly analyse gear type success on one species. This, however, was not practical.

To investigate the influence of hook size and bait type on the length of fish caught and capture mortality, generalized linear models (GLMs) were applied. To find the optimal combination of parameters, the fit of the different models (200 different combinations of parameters) were assessed using the Akaike information criterion (AIC). The AIC is a combination of negative log-likelihood, which measures the lack of model fit to the observed data, and a bias correction factor, which increases as a function of the number of model parameters and is defined as:

$$AIC = -2\ln\left[L\left(\theta_p \middle| y\right)\right] + 2p, \tag{3.1}$$

where p is the number of free parameters and $L(\theta_p|y)$ is the likelihood of model parameters given the data y (Johnson and Omland 2004).

The influence of hook size and bait type on fork length was only analyzed for roman as it was the only species with sufficient data to generate the sample size necessary for a GLM. Since the response code in this model was continuous (measured fork length of roman caught) a normal distribution was assumed. The commonly used link function for this distribution is the identity link described as (McCullagh and Nelder 1995d):

$$f(z) = z \tag{3.2}$$

Hook sizes *1/0-3/0* and *4/0-5/0* were pooled and analyzed as 'small' and 'large', respectively, along with bait type and other relevant parameters (factors). As shown in chapter 4, depth and level of exploitation (location of the sampled fish inside or outside the MPA) had a significant effect on roman size and were therefore included in the GLM of the form:

$$\begin{aligned} Forklength = \beta_0 + \beta_1(Depth) + \beta_2(\mathrm{Re}\,serve/Outside) + \beta_3(Bait-type) \\ + \beta_4(Hooksize) + \varepsilon \end{aligned}, \tag{3.3}$$

where $\beta_{0\text{-}I}$ are the estimated predictor variables and ε the error (McCullagh and Nelder 1995b). Before modelling main effects, second degree interactions between main effects (factors) were modelled and significant results were noted. The model was coded in STATISTICA.

The influence of body area hooked, season, depth, temperature and fork length on mortality was only analyzed for roman as it was the only species sufficiently available to generate the sample size necessary for a GLM. The effect of hook size, fork length and bait type on the way the fish were hooked, were analyzed for roman and fransmadam (*Boobsoidea inornata*). The response code for mortality (yes/no) or the method of hooking a fish (lip/gut or lip/body) was a binary variable. Therefore, the distributions were assumed to be binomial. The commonly used link function for the binomial distribution is the logit link described as (McCullagh and Nelder 1995a):

$$f(p) = \log(p/(1-p)), \tag{3.4}$$

where p is the underlying continuous probability of the binary dependent variable, ranging from 0 to 1. In the logit regression model, the predicted values for the dependent variable will never be less than (or equal to) 0, or greater than (or equal to) 1, regardless of the values of the independent variables. To model the influence of relevant recorded parameters (factors) on mortality and hooking method, GLMs of the form:

$$\begin{aligned}\log\big(p(Mortality))/\big(1-p(Mortality)\big) &= \beta_0 + \beta_1\big(Depth\big) + \beta_2\big(Season\big) \\ &+ \beta_3\big(Hooked\big) + \beta_4\big(Forklength\big) + \beta_5\big(Temperature\big) + \varepsilon\end{aligned} \tag{3.5}$$

and

$$\begin{aligned}\log\big(p(Hooked)/\big(1-p(Hooked)\big)\big) &= \beta_0 + \beta_1\big(Hooksize\big) + \beta_2\big(Forklength\big) \\ &+ \beta_3\big(Bait-type\big) + \varepsilon\end{aligned} \tag{3.6}$$

were applied. Here, $\beta_{0\text{-}I}$ are the estimated predictor variables and ε the error (McCullagh and Nelder 1995b). Before modelling main effects, second degree interactions between main effects (factors) were modelled and significant results were noted. The models were coded in STATISTICA.

Differences in mortality rates of individual species were investigated, using EXCEL chi-square contingency tables. Factors were tested using one-way ANOVAs in STATISTICA.

The frequencies and mean fork lengths of species caught during fishing sessions were correlated with succession (position caught) using STATISTICA.

Implications for management

The results of the section on the influence of gear and bait type on linefishing catches were used to evaluate their implications for management. Applied to the dataset from the exploited part of the population, selectivity for roman, length frequencies, biomass and mortality rates were calculated for the current linefishing method ($\text{LFM}_{\text{current}}$) and a proposed linefishing method ($\text{LFM}_{\text{proposed}}$). $\text{LFM}_{\text{current}}$ used all hook sizes and bait types over all reefs during fishing sessions of varying length. $\text{LFM}_{\text{proposed}}$ used only *4/0* and *5/0* hooks and pilchard or squid as bait over reefs shallower than 20 m during fishing sessions of more than one hour.

3.3 RESULTS

Sample size of boat counts

Over the period March 2002 to April 2004, 76 systematic boat counts were conducted and 352 fishing boats encountered.

Boat counts and zones

Zone	Brenton	Walkers Pt.	Rowwehoek	Skimmelkrans	Sandkop	Platebank	Gerrickes Pt.	All
Visits	75	76	75	48	32	18	10	334
Total # boats	16	188	85	38	13	9	3	352
Boats/visit	**0.21**	**2.47**	**1.13**	**0.79**	**0.41**	**0.50**	**0.30**	**1.05**

Table 3.1: Summary of ski-boat counts in the different zones

The average number of boats counted per zone was just slightly greater than one, but ranged between 0.21 off Brenton and 2.47 off Walkers Point (Table 3.1). Boats counted per visit were significantly different among zones ($p < 0.001$).

Boat counts and season

Season	Spring	Summer	Autumn	Winter
Outings	16	20	26	14
Total # boats	64	43	165	80
Boats/outing	**4.0**	**2.2**	**6.3**	**5.7**

Table 3.2: Summery of ski-boat counts in different seasons

Fishing boats counted per outing varied between 2.2 in summer and 6.3 in autumn (Table 3.2). The number of boats counted per outing were significantly different among season ($p < 0.01$).

Sample size and stratification of boat checks

Over the period June 2001 to April 2004, 154 boats were checked and interviews conducted at sea.

Vessels and catch

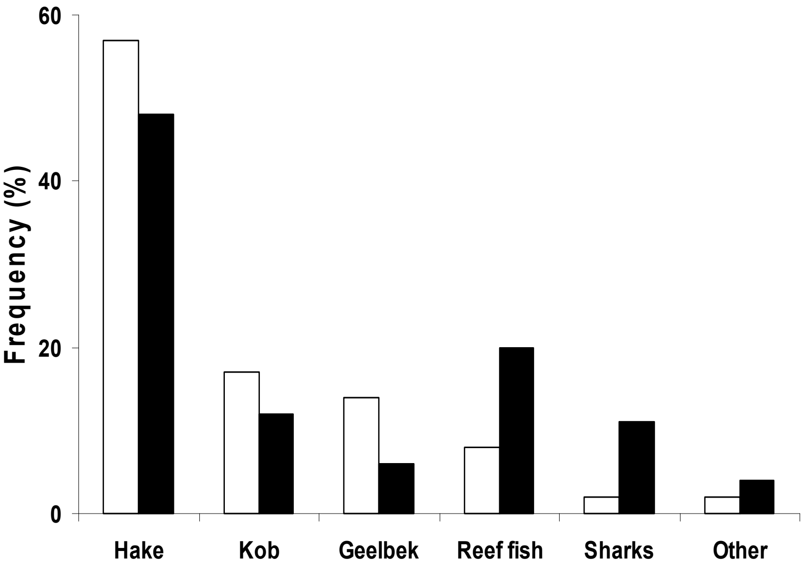


Figure 3.3: Percentage frequency of boats targeting (white bars) and catching (dark bars) different fish species or groups

The number of fishers working on the fishing boats varied between one and ten with a median of four. Of all vessels checked 63% were fishing on sand whilst 37% were fishing on rocky substrata. Almost 70% of the boats in the area were targeting hake. Kob and geelbek (*Atractoscion aequidens*) were targeted by 20% and 16% of the boats, respectively (Figure 3.3). Only 10% of all boats claimed to target reef fish and 2% were also targeting sharks. In terms of fish caught, numbers did not reflect species targeted with catches of hake, kob and geelbek of 50%, 12% and 6%, respectively. Although seldom targeted reef fish and sharks made up a substantial portion of the catch.

Season and catch

The targeting of the different fish species and the catch composition varied seasonally. Hake were neither targeted nor caught in summer while kob were targeted by about 20% of the boats throughout the year. Geelbek on the other hand were targeted predominantly in summer (60% of the boats). This was similar to reef fish and sharks when catch frequencies were high; 50 and 25% of all boats caught reef fish and sharks respectively during the summer months (Figure 3.4).

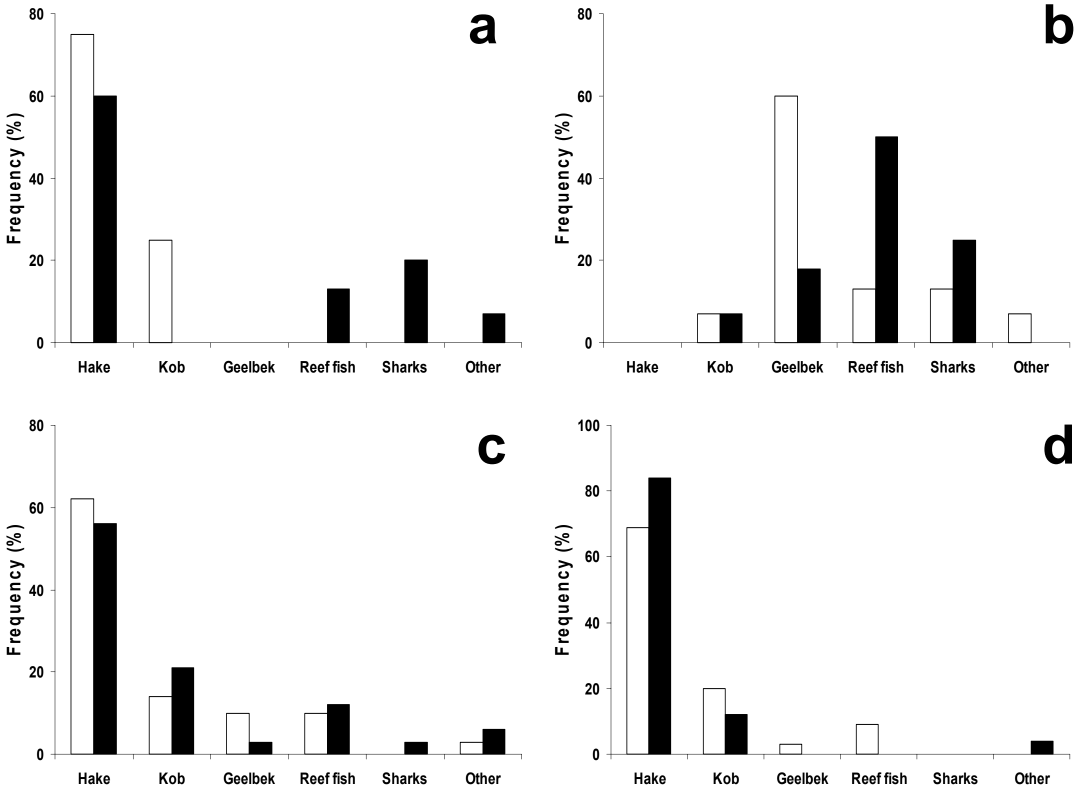


Figure 3.4: Fish species and groups targeted (white bars) and caught (dark bars) in percentage frequency for spring (a), summer (b), autumn (c) and winter (d).

Positions of boats

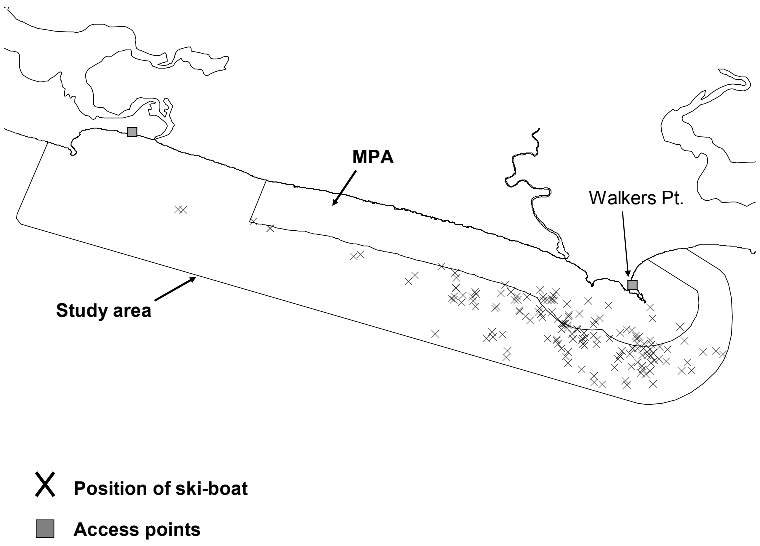


Figure 3.5: Map of the study area with positions of 154 checked fishing boats. Border of the MPA is indicated

The fishing effort in the study area was found to concentrate along the MPA's border with 36 boats (30%) encountered inside the borders of the MPA (Figure 3.5). For reasons mentioned in the methods more boats were recorded close to the Walkers Pt. launch site and less in the western part of the study area. To describe the effect of the MPA on fishing patterns, zones stretching parallel to the MPA's boarder were created, and the relative effort per zone was mapped.

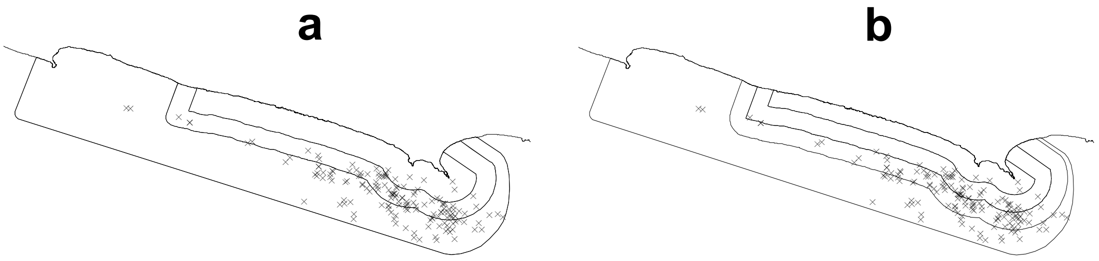


Figure 3.6: Study area with a three-zone (a) and a four-zone (b) pattern. Fishing effort indicated by crosses

The first zoning pattern is the MPA within the study area - a two-zone pattern (see Figure 3.5) - the boundary buffered one nautical mile (1.852 km) off the shore line (these two zones were named '**Reserve**' and '**Outside**'). The second pattern, originating from an initial stratification effort for biological assessments (see chapter 4), includes three zones (Figure 3.6 a), with two internal boundaries buffered 500 m off the MPA's boundary (these three zones were named '**Core**', '**Trans**' and '**Out**'). Two four-zone patterns were created according to the level of fishing effort in the study area of which one is shown in figure 3.6 b. Both patterns include a narrow inshore zone buffered just 900 m off the shore line, where fishing effort was lowest ('**$L_{0.9}$**'). Then follows a 1000/1200 m wide zone with medium fishing effort buffered from the first zone offshore ('**$M_{1.0}$**'/'**$M_{1.2}$**'). The highest fishing effort was determined for the third zone, which is 1000/800 m wide ('**$H_{1.0}$**'/'**$H_{0.8}$**'). Finally, the remaining offshore part of the study area, named '**Off**'.

To calculate the relative fishing effort among zones, the number of boats recorded within each zone was divided by its area (Table 3.3). Due to the violations of the MPA's boundaries, the relative fishing effort inside the MPA was almost as high as it is for the outside area. The **Core**/**Trans**/**Out** pattern reveals how the fishing effort concentrates around the MPA's border, 2.7 boats/km^2 were recorded in the '**Trans**' zone, a value four and seven times higher than in the '**Core**' and '**Out**' zones, respectively. The four-zone zoning patterns reveal areas of very low and high exploitation, namely, 0.2 and 2.8 boats/km^2, a difference in relative fishing effort spanning factor 14.

Pattern	Zone	Area (km^2)	Boats (N)	Boats/km^2
Reserve/Outside	Reserve	40	36	**0.9**
	Outside	109	118	**1.1**
Core/Trans/Out	Core	27	10	**0.4**
	Trans	27	74	**2.7**
	Out	95	70	**0.7**
$L_{0.9}/M_{1.0}/H_{1.0}$/Off	$L_{0.9}$	18	4	**0.2**
	$M_{1.0}$	24	37	**1.6**
	$H_{1.0}$	28	77	**2.8**
	Off	80	36	**0.5**
$L_{0.9}/M_{1.2}/H_{0.8}$/Off	$L_{0.9}$	18	4	**0.2**
	$M_{1.2}$	29	56	**1.9**
	$H_{0.8}$	23	58	**2.6**
	Off	80	36	**0.5**
Core/TransOut	Core	27	10	**0.4**
	TransOut	122	144	**1.2**
$L_{0.9}/M_{1.0}/H_{1.0}$Off	$L_{0.9}$	18	4	**0.2**
	$M_{1.0}$	24	37	**1.5**
	$H_{1.0}$Off	108	113	**1.0**
$L_{0.9}/M_{1.2}/H_{0.8}$Off	$L_{0.9}$	18	4	**0.2**
	$M_{1.2}$	29	56	**1.9**
	$H_{0.8}$Off	103	94	**0.9**

Table 3.3: Area, number of boats and relative fishing effort for the different zoning patterns and their zones. Fusion of zones were used to produce new patterns (Core/TransOut, $L_{0.9}/M_{1.0}/H_{1.0}$Off and $L_{0.9}/M_{1.2}/H_{0.8}$Off)

Although more boats per area were recorded in the eastern part of the study area, zones stretching parallel to the MPA's border were chosen to describe the fishing effort spatially. This method appears to bias fishing effort towards higher levels in the western part of the study area. However, more than 70% of all boats were targeting hake and not reef or reef associated fish. This was confirmed by identification of soft substrate on the echo-sounder whenever the GPS positions of boats targeting hake were recorded. These hake-boats were found mainly in the eastern offshore part of the study area, where the substrate was almost exclusively sand (compare Figures 2.5 and 3.5). Boats in the western part of the study area were mainly encountered on the large rocky foul area and claimed to target reef or reef associated fish. Fishing pressure, targeting the reef fish species relevant in this study, was therefore uniformly distributed in east west direction. Nevertheless, all recorded boats were used to calculate the relative index of exploitation among zones as they do reflect a general attitude of fishermen towards the reserves boarder, irrespective of the fish species targeted.

Hook, bait and catch

From September 2000 to October 2003, 2406 fish were caught. Significantly more roman were caught with larger hooks (*4/0-5/0*) as compared to smaller hooks (*1/0-3/0*). However, there was no significant preference for any of the used bait types (Table 3.4). Fransmadam (*Boobsoidea inornata*) and steentjie (*Spondyliosom emarginatum*) were caught significantly more often when using small hooks and had a preference for red bait and squid, respectively. Although not significant due to the small sample size, there was a trend towards higher catch rates for blue hottentot (*Pachymetopon aeneum*) when using squid or pilchard as bait. Santer (*Cheimerius nufar*) showed a clear preference for pilchard followed by squid – only three out of 83 fish were caught with red bait. However, a clear trend for more fish of this species being caught with larger hooks did not turn out to be significant due to the small sample size.

Species	**N**	Percentage of all caught fish with				
		Hook size		**Bait type**		
		small	**large**	**red bait**	**squid**	**pilchard**
Roman	**1089**	39.2	50.6	45.2	43.0	44.7
p-value		**< 0.001**		> 0.1		
Fransmadam	**687**	31.3	21.6	38.8	26.4	23.3
p-value		**< 0.001**		**< 0.001**		
Steentjie	**201**	9.5	5.8	6.4	9.3	4.7
p-value		**< 0.01**		**< 0.01**		
Blue hottentot	**89**	3.7	3.3	2.0	3.9	3.4
p-value		> 0.1		> 0.1		
Santer	**83**	2.8	4.2	0.9	3.0	6.4
p-value		> 0.05		**< 0.001**		

Table 3.4: Influence of hook size and bait type on the number of various species caught, expressed as percentage of all caught fish using a particular gear. Differences from expected frequencies are indicated by respective p-values.

Hook, bait and size

Predicted mean fork length of roman was significantly higher inside the MPA than outside ($p < 0.001$) and at shallower sites as compared to deeper sites ($p < 0.001$). With predicted mean fork lengths of 285 and 294 mm respectively, fish caught on small hooks (*1/0-3/0*) were significantly smaller ($p = 0.005$, figure 3.7) than those caught on large hooks (*4/0-5/0*). Bait type had a significant influence ($p = 0.031$) on fork length. Roman caught with red bait were smaller (predicted mean: 281 mm) than those caught with squid or pilchard (predicted means: 292 and 295 mm respectively). No significant interactions between main effects were detected.

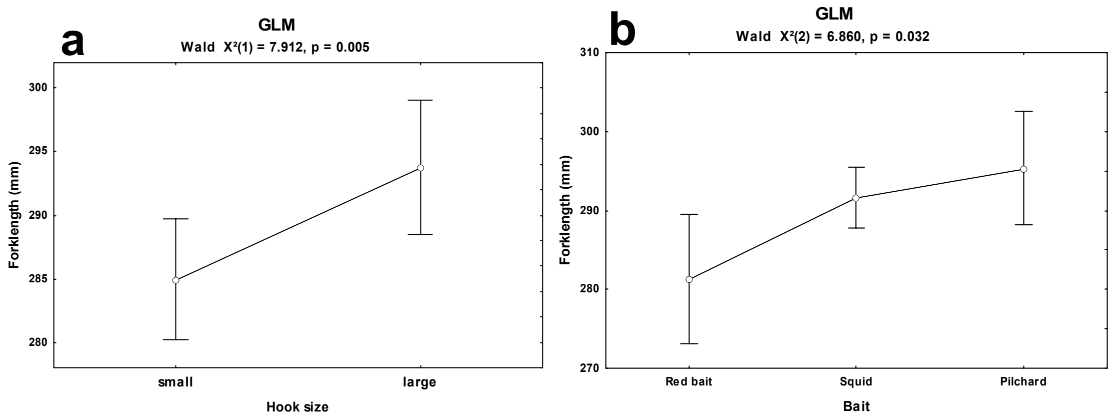


Figure 3.7: Influence of hook size (a) and bait type (b) on the mean fork length of caught roman as predicted by a GLM. Vertical bars denote 95% confidence interval

Capture mortality

The mortality rate for the entire catch was 4.8% (Table 3.5). The highest species specific mortality rate was recorded for dageraad (*Chrysoblephus cristiceps*). With 22.5%, it was significantly higher than the overall mortality rate. Roman as well had a significantly higher mortality rate of 7.6%. Blue hottentot, santer and steentjie had average mortality rates between 4.5 and 2.5%, statistically not differing from the overall mortality rate. The only abundant species with a significantly lower mortality rate of 1.3% was fransmadam.

Species	Survivors/Mortalities (N)	Mortality rate (%)
Dageraad	31/9	22.5**
Roman	952/78	7.6**
Blue hottentot	84/4	4.5
Santer	69/2	2.8
Steentjie	196/5	2.5
Fransmadam	665/9	1.3**
All	2290/116	4.8

Table 3.5: Capture mortality rates of various fish species. ** indicates mortality rates significantly different from the mortality rate for all species (4.8%) at $p < 0.01$.

Possible factors influencing mortality rate were modelled for roman. Of the potential factors, season, temperature and fork length did not influence mortality. However, capture depth and the way the fish were hooked had a significant effect (p-values of 0.033 and 0.001 respectively). Higher mortalities occurred with fish caught from deeper reefs. The way the fish were hooked had the strongest influence, with gut-hooked fish resulting in higher mortality rates than body- or lip-hooked fish. No significant interactions between main effects were detected.

Although data was not sufficient to apply GLMs, this was also apparent for some of the other species. Of the remaining five most abundant species, all showed a trend towards higher mortalities at deeper sites with mortalities of dageraad and fransmadam being caught at significantly deeper sites as shown by a parametric ANOVA test ($p = 0.013$ and 0.009, respectively).

Species	**Percentage hooked**			**Percentage mortality hooked**		
	gut	**lip**	**body**	**gut**	**lip**	**body**
Dageraad (N=42)	37.5	62.5	0**	53.3	4.0	-**
Roman (N=1089)	12.3	87.2	0.5**	27.6	4.8	0**
Santer (N=83)	8.5	90.1	1.4	33.3	0	0**
Blue hottentot (N=89)	2.3	86.4	11.3**	0	5.3	0
Fransmadam (N=687)	1.0	94.4	4.6**	0	1.1	6.4*
Steentjie (N=201)	0	86.6	13.4**	-	1.21	11.1*
All	**7.3**	**89.4**	**3.3**	**28.4**	**2.8**	**7.6**

Table 3.6: Frequencies of various fish species being hooked in the lip, the outer surface (body) or the gut and mortality rates coinciding with the different hooking methods. Frequency distributions or mortality rates of a species differing significantly from those observed for all fish are indicated by *($p < 0.05$) or **($p < 0.01$).

To investigate factors influencing the manner in which the fish were hooked (gut-, lip- or body-hooked), hook size, fork length and bait type were modelled for roman and fransmadam. Only the fork length of caught fish had a significant effect ($p < 0.001$ and 0.025, respectively). The predicted mean fork lengths of lip- and gut-hooked roman were 288 and 309 mm and of lip- and body-hooked fransmadam 224 and 216 mm, respectively. In other words, larger roman were significantly more often gut-hooked and smaller fransmadam body-hooked irrespective of hook size or bait type (Table 3.6).

Catch sequence

The catch frequencies of the four most abundant species roman, fransmadam, steentjie and blue hottentot were correlated with their positions in the catch sequence during a fishing session (Figure 3.8). Catch frequencies of roman decreased during fishing sessions from more than 50% at the start of the catch sequence to below 30% by the end (r = -0.83). Fransmadam, steentjie and blue hottentot showed the opposite pattern with catch frequencies increasing during fishing sessions (r-values of 0.66, 0.72 and 0.82, respectively). Insufficient data were available for similar analysis for other species.

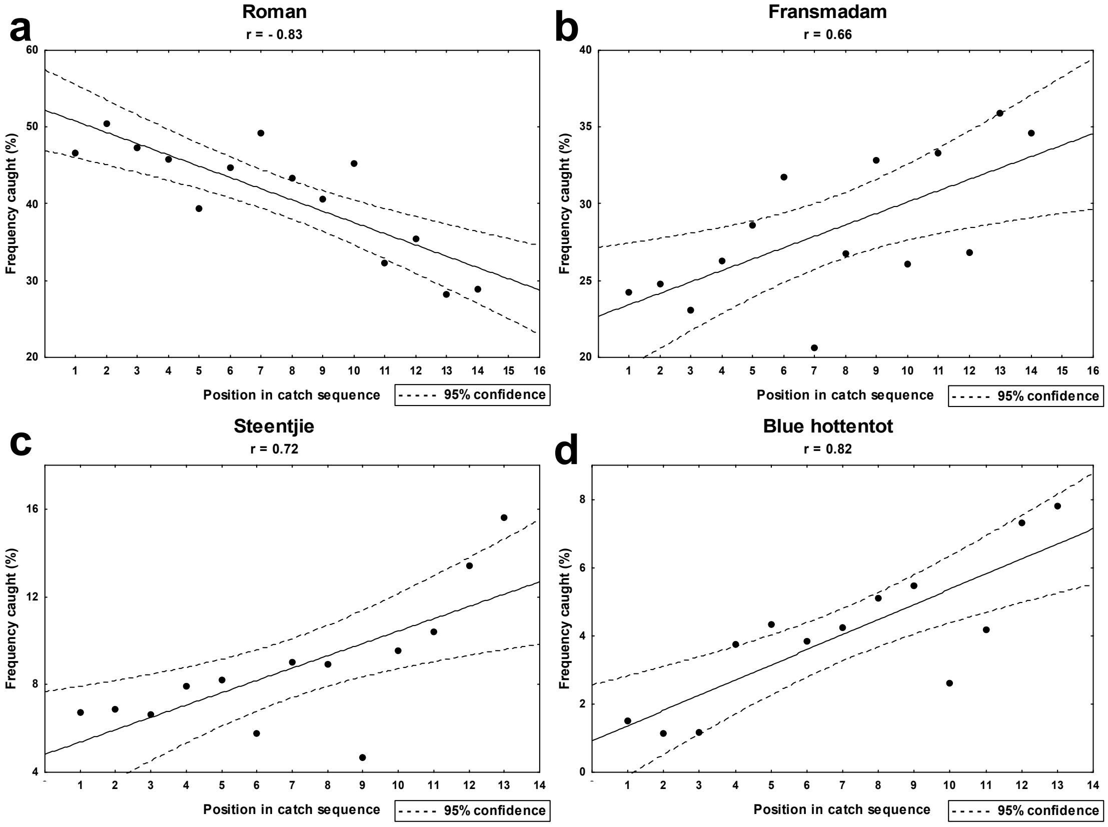


Figure 3.8: Correlations between the frequency and position in catch sequence of roman (a), fransmadam (b), steentjie (c) and blue hottentot (d) caught during fishing sessions.

The correlation of mean fork lengths with positions in the catch sequence was only investigated for the two most abundant species due to otherwise insufficient sample sizes. Fisheries are typically selective towards more aggressive individuals (Ricker 1981). These are usually the larger size classes of a species. Therefore, mean fork lengths of caught fransmadam decreased during fishing sessions (Figure 3.9 b). However, mean fork lengths of caught roman increased during fishing sessions (Figure 3.9 a).

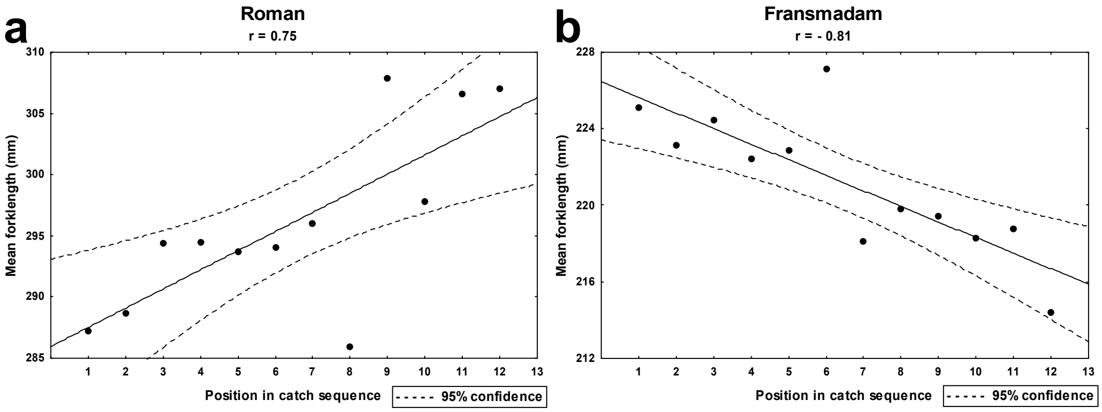


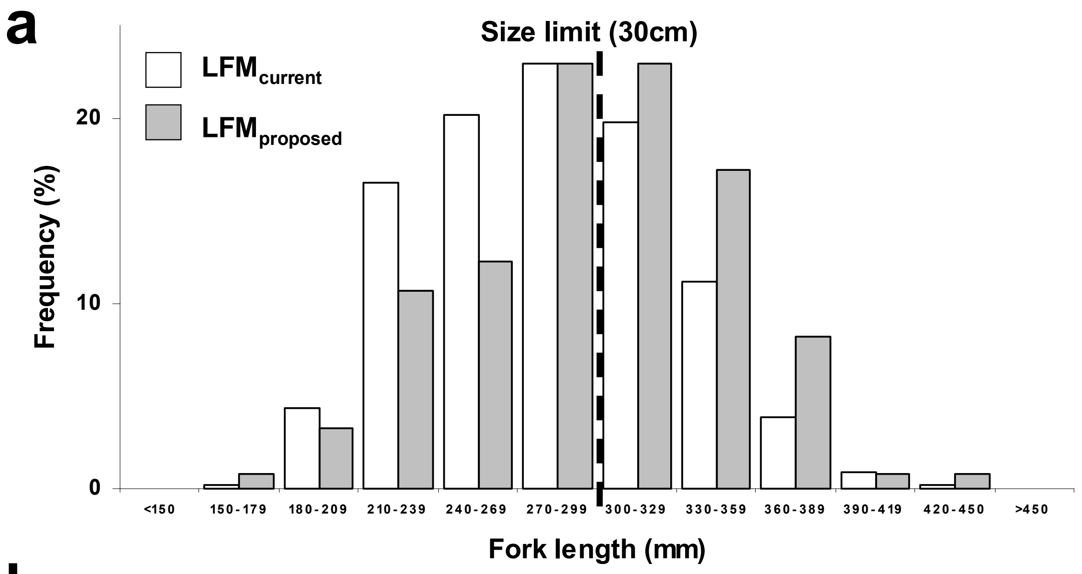
Figure 3.9: Correlation between mean fork length and position in catch sequence of roman (a) and fransmadam (b) caught during fishing sessions.

Implications for management

From the results above, using current linefishing method ($LFM_{current}$), the loss of roman in terms of numbers and biomass, due to immediate post-release mortality of undersized fish, is at least 4.9 and 3.4%, respectively (Figure 3.10).

Following the proposed linefishing method ($LFM_{proposed}$) is likely to increase catch rates of legally sized (> 30 cm) roman and decrease post-release mortality rates of undersized roman. The use of large hooks (*4/0-5/0*) and pilchard or squid as bait over shallow reefs (water depth < 20 m) during long fishing sessions (> one hour) should increase the selectivity for legally sized fish and fishing on shallow reefs will decrease post-release mortality rates of undersized fish.

When these management regulations are applied to the dataset, the number and biomass of legally sized roman increase by 39 and 23%, respectively. Furthermore, mortality rates of fish caught drop from 7.6 to 5.5%. As a result, the loss of undersized fish due to immediate post-release mortality decreases in terms of numbers and biomass by 43 and 50%, respectively (Figure 3.10).



b

	Legally sized roman as % of total catch in numbers(weight)	Increase in % from Regulation 1 to 2 in numbers(weight)	Mortality as % of total catch	Mortality of undersized roman as % of total catch in numbers(weight)	Decrease in % from Regulation 1 to 2 in numbers(weight)
LFM$_{current}$	36(56)	39(23)	7.6	4.9(3.4)	43(50)
LFM$_{proposed}$	50(69)		5.5	2.8(1.7)	

Figure 3.10: Expected length frequencies (a) and catch rates (b) of roman for the current linefishing method (LFM$_{current}$) and the proposed linefishing method (LFM$_{proposed}$)

3.4 DISCUSSION

Relative fishing effort in the study area

The spatial analysis of fishing effort in the study area revealed zones with highly different fishing effort. In the $\mathbf{H_{1.0}}$ zone just outside the MPA, relative effort was 14 times higher than in the narrow $\mathbf{L_{0.9}}$ zone inside the MPA. Although protection was not absolute, this differential was sufficient for the purpose of studying fishing effects. A relative difference of one to seven, half the value found in this study, was sufficient to produce significant changes in abundance, size and assemblage of eight species of parrotfish in the Caribbean (Hawkins and Roberts 2003). The distribution of fishing effort in this study is likely to induce detectable differences in the reef community.

The few boats encountered in the C**ore** zone comprised entirely of recreational visiting fishermen during the holiday season, who were unaware of MPA regulations. Higher fishing effort around the border might be a result of increasing distance of areas further offshore from access points. This relationship is reflected in the boat counts, generally decreasing alongshore with increasing distance from access points. Also, higher catch rates close to the MPA, experienced or assumed, might have lead fishermen to choose sites as close as possible to the MPA's border. This was also found to be common around the Hol Chan Marine Reserve off Belize (Polunin and Roberts 1993) and the Anse Chastanet Marine Reserve off St Lucia (Roberts and Hawkins 1997). Fishermen inside, but close to the border of the Goukamma MPA, were usually aware of their vicinity to the border but claimed to have different GPS marks.

Target species of the local linefishery

Fish species caught by fishermen in the study area matched well with the catch reports in the National Marine Linefish System (2001) summarized in the introduction of this chapter. Hake was the most sought after species due to its high market value and catchability. Although catches of kob and geelbek have consistently declined in the past decade, their high market value makes them a preferred target of the linefishery. The strong declines in CPUEs of reef fish in the last decade (Griffiths 2000) has made fishing for these species less profitable.

However, the fishery survey in this study confirms that reef fish are still caught in relatively large numbers with more than 20% of the boats catching reef fish. This is largely due to the targeting of reefs by commercial fishers when hake are unavailable and the high recreational effort during holiday periods. When fishing on reefs, roman make up for about half of the catch of the local fishing boats as shown by catch reports of three commercial boats fishing in the study area over a period of ten years.

The same result was found by Griffiths (2000) who analyzed survey data for the southern Cape. These high catches of roman, in particular in the decades before 1990, their slow growth (Buxton 1987) and high level of residency (Kerwath 2005) make them a promising indicator species for examining fishing effects (Leaman 1991).

Catch sequence

Catch sequence frequencies can only change if the caught fish are either kept or remain less catchable for the rest of the fishing session after release. It is therefore assumed that the fish, released during a controlled fishing session, temporarily change their behaviour towards baited hooks, such as they are unlikely to be caught again in that same fishing session. This may be explained by the fact that sparid reef fish suffer from barotrauma during capture (Booth and Buxton 1997b, Penney *et al.* 1999) and are likely to memorize the cause of traumatic events (Portavella *et al.* 2003, Yue *et al.* 2004, Broglio *et al.* 2005), or temporarily leave the area of capture (Kerwath 2005).

The high frequency of roman caught in the beginning of fishing sessions may be a result of high aggressiveness and dominance of roman over other fish species in the ecosystem (Penrith 1972). However, this does not explain the higher frequency of smaller roman in the beginning of fishing sessions. A possible explanation may be that larger fish, which are male, are less likely to encounter the bait than females. Kerwath (2005) described the movement behaviour of roman in the Goukamma and Castle Rock MPAs using sonar tags. He found that males occupied smaller territories than the smaller females during the spawning season. As a result, the calculated activity index (distance moved per time interval) for females was higher than for males. Considering that the spawning season lasts for four months per year (Buxton 1990), females, on average, should be more likely to encounter a bait than males.

On the other hand, smaller, female roman should have higher energy demands than larger, male fish as they are in a stage of faster growth (Buxton 1993, chapter 5 in this thesis), have a higher activity index (Kerwath 2005) and develop heavier gonads relative to their body weight (Buxton 1990) than males. Therefore, feeding behaviour should be more motivated in females resulting in higher catch frequencies early in fishing sessions.

During experimental underwater linefishing using SCUBA, larger fish were observed to be more cautious whereas their smaller counterparts would readily take the bait. This was also observed by Penrith (1972) during behavioural studies on roman in the field. Only after many of the smaller, female individuals have been caught, larger, more cautious fish will have a chance to examine and eventually take the bait, resulting in increased average fork length of fish caught later in fishing sessions.

These size-dependent behavioural differences have implications for management. Longer fishing sessions will increase the frequency of legally sized roman in the catch, but at the same time increase bycatch and post-release mortality of unwanted species. Therefore, recommendations concerning the length of fishing sessions are difficult to evaluate as they are a trade off between species and size selectiveness.

This kind of dilemma is inherent in many traditional management measures. Size-limits aim to increase *SB/R*, but, at the same time, remove the largest individuals from the population which are usually the most fecund (Brosseau and Armstrong 1987). Larger hooks and more effective bait select against aggressiveness in populations, which can alter migration patterns (Boehlert 1996), reduce genetic diversity and make individuals less catchable (Nuhfer and Alexander 1994).

Implications for management

The results of the study reveal some interesting trends in terms of the use of selected fishing gear and baits. Although these simulations do reveal a number of alternate management methods for the linefishery it must be recognized that the introduction of regulations governing hook sizes, area fished and bait-use would be difficult to enforce. Also, reefs shallower than 20 m are rare along the south coast and overall CPUE would be likely to drop if fishing effort was restricted to a few spots. Moreover, selective exploitation of shallow ecosystems might lead to changes in fish behaviour towards habitat selection, further reducing CPUE and productivity of the ecosystem. The use of MPAs, therefore, still appears the best option by reducing mortality to zero in carefully selected areas.

4 ASSESSMENT OF THE EFFECTS OF FISHING ON THE COMMUNITY STRUCTURE

4.1 INTRODUCTION

Of all anthropogenic activities, fishing has the greatest impact on temperate reef ecosystems (Jackson *et al.* 2001). Changes in mean size and density of targeted species are the most noticeable effects of fishing (McClanahan *et al.* 1999) and serve as a good indicator of the rate of exploitation (Leaman 1991). The fish species most targeted by hook and line fisheries are usually predators high up in the trophic web (Pauly *et al.* 1998) and even if only one apex predator population is targeted by the fishery, densities of other fish in the ecosystem can change, due to a shift in top-down control (Boehlert 1996, Pinnegar *et al.* 2000).

Numerous studies have described the effect of fishing on size and abundance of targeted reef fish species world wide (Mosqueira *et al.* 2000). Fewer studies have investigated the influence of exploitation on the whole sub-tidal reef community, including invertebrates and algae (Pinnegar *et al.* 2000). Studies investigating this issue in temperate reef ecosystems have been conducted outside South Africa (Cole *et al.* 1990, Sala 1996, Babcock *et al.* 1999, Edgar and Barrett 1999, Tegner and Dayton 2000, Macpherson *et al.* 2002, Shears and Babcock 2003).

Where targeted fish species are omnivorous, dietary overlap can change fish densities throughout all trophic guilds and directly or indirectly change invertebrate and algal cover on temperate (Sala 1996) and tropical reefs (McClanahan and Muthiga 1989). This in turn can lead to a decreased overall productivity of the ecosystem (McClanahan and Sala 1997).

One of the arguments in favour of MPAs is their potential role in maintaining productivity of reefs by conserving natural ecosystem control (Tegner and Dayton 2000). However, decreased abundance of top-predators may have complex effects on fish communities through top-down control (Pinnegar *et al.* 2004). Although the removal of large predators by fishing should increase the abundance of smaller prey specimens which in turn might increase overall productivity, such a change is not necessarily useful to man.

Theoretical models (Shin and Cury 2001, Hastings and Botsford 2003) as well as field studies (Alcala and Russ 1990, Garcia-Rubies and Zabala 1990, Jennings *et al.* 1996, Russ and Alcala 1996) have shown how diversity of reef fish can be reduced by fishing, but a decrease of fish diversity under exploitation was not always detected (Jennings and Polunin 1996, Edgar and Barrett 1999). Smith (2005) recorded an increase of temperate reef fish diversity inside the Tsitsikamma NP as compared to adjacent exploited areas during UVC surveys. Controlled fishing surveys conducted by Smith (2005) at the same sites indicated the opposite, indicating potential bias associated with one or both methods.

The presented study is the first to investigate the impact of fishing on the community of temperate marine reef fish and food web structure in South Africa, using a medium-sized MPA. The study was designed to overcome common experimental problems found in field studies on community effects (Willis *et al.* 2003), namely:

- Insufficient stratification over space and time
- Lack of standardization of sampling procedures
- Bias due to low comparability of sampling sites
- Application of only one method for sampling and analysis

The main objectives of this chapter are to:

- Determine relative density and average size of reef fish species inside and outside the Goukamma MPA using controlled fishing and UVC.
- Determine the relative density of benthic invertebrates and algae on reefs inside and outside the Goukamma MPA.
- Examine the influence of fishing effort and physical/biotic factors on fish and benthic community structure using multivariate analysis.
- Examine the influence of fishing effort and physical/biotic factors on fish and benthic taxa densities and fish size and diversity using generalized linear models and multivariate analysis.

4.2 MATERIAL AND METHODS

Design - stratification, randomness and standardization

Two methods were used to assess differences in the ichthyofaunal community between the MPA and the exploited area: controlled fishing and UVC using SCUBA.

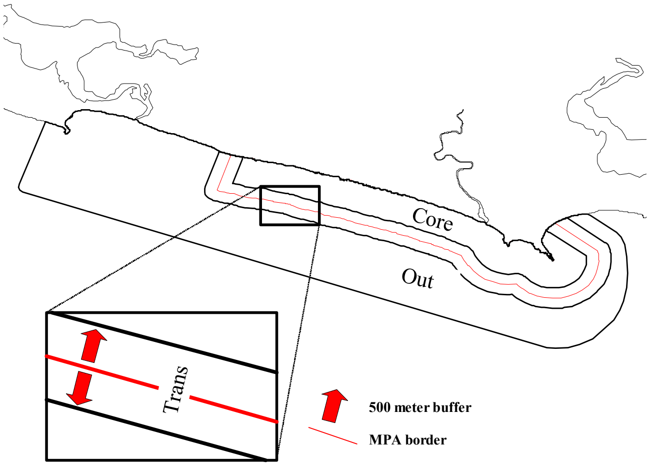


Figure 4.1: Creation of the transitional (Trans) zone

Sampling was designed using fixed-effects and random-effects (Zahr 1999). Sampling sites were stratified over zone, season and time of day (fixed-effects) to ensure equal numbers of samples for statistical analysis. Other factors like depth, temperature and turbidity were treated as random-effects, as stratification of sampling sites over these factors would have been impractical or impossible. Fishing surveys were stratified over season (spring/summer/autumn/winter) and time of day (morning/afternoon). Diving surveys were restricted to the summer months and therefore only stratified over time of day (morning/afternoon). Three research zones were outlined in ArcView at the beginning of all surveys and the controlled fishing and UVC effort was stratified evenly among these zones. Figure 4.1 shows these zones, namely, the core zone (or '**Core**'), transitional zone (or '**Trans**') and outside zone (or '**Out**'). The Trans zone was created by shifting the MPA's border 500 m towards inshore and offshore, using the 'buffer-function' in ArcView.

To increase the spatial resolution of the ichthyofaunal community and to relate these differences to fishing effort, patterns derived from the analysis of the fishery survey (chapter 3) were included in the stratification of surveys. In all, seven differently zoned patterns were used (Figure 4.2) to cater for varying spatial effects of fishing on the numerous fish species examined. The 'colour-coding' of zones will be used in subsequent chapters to facilitate graphic recognition.

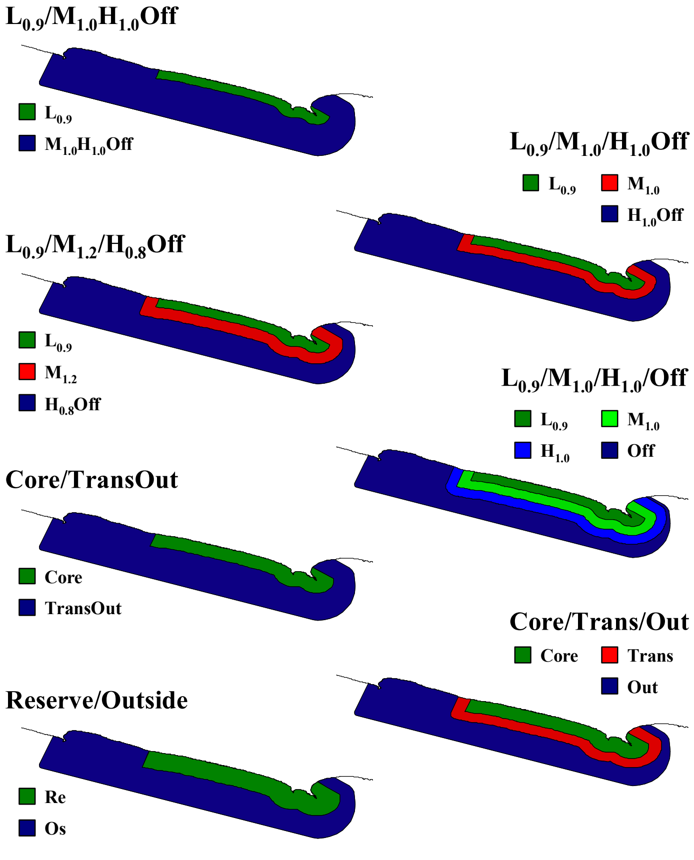


Figure 4.2: Study area showing the seven zoning patterns used to stratify sampling sites

CPUE and UVC surveys are known for their relatively high variance (Brock 1982, Willis *et al.* 2000), therefore every effort was made to maintain consistency in these methods. Whenever possible, surveys were conducted in at least two different zones on the same research-day in order to apply the same error to the compared zones. Fishermen and divers followed strict protocols and the research teams were kept as constant as possible to minimize effects of different skills. To avoid bias in site selection, the anchor or diving buoy was deployed randomly after rocky substrate was identified (chapter 2) in the designated research zone.

Biological sampling for the fishing and diving survey started on the 29th of September 2000 and was finished on the 18th of January 2004 - a sampling period of more than three years and four months. The stratification effort of benthic assessments (filming sites), controlled fishing (fishing sites) and UVC (point counts) were successfully accomplished, except for the stratification of point counts over time ($p < 0.05$, table 4.1). Too many point counts were conducted in the morning, due to better diving conditions.

Factor	Code	Filming sites	Fishing sites	Point counts
Time	**Morning**	32	129	120*
	Afternoon	16	144	57*
Season	**Spring**	N/A	64	N/A
	Summer		63	
	Autumn		76	
	Winter		70	
Reserve/Outside	**Reserve**	21	145	79
	Outside	27	128	98
Core/Trans/Out	**Core**	17	111	63
	Trans	14	80	55
	Out	17	82	59
Core/TransOut	**Core**	17	111*	63*
	TransOut	31	162*	114*
$L_{0.9}/M_{1.0}/H_{1.0}$/Off	**$L_{0.9}$**	13	87	47
	$M_{1.0}$	11	65	43
	$H_{1.0}$	13	61	48
	Off	11	60	39
$L_{0.9}/M_{1.0}/H_{1.0}$Off	**$L_{0.9}$**	13	87*	47
	$M_{1.0}$	11	65*	43
	$H_{1.0}$Off	24	121*	87
$L_{0.9}/M_{1.2}/H_{0.8}$Off	**$L_{0.9}$**	13	87	47
	$M_{1.2}$	15	88	59
	$H_{0.8}$Off	20	98	71
$L_{0.9}/M_{1.0}H_{1.0}$Off	**$L_{0.9}$**	13*	87*	47*
	$M_{1.0}H_{1.0}$Off	35*	186*	130*
Total effort		**48**	**273**	**177**

Table 4.1: Stratification of sampling units over season, time of day and zones. * indicates failed stratifications as shown with Kolmogorov-Smirnoff contingency tables ($p < 0.05$).

Positioning at fishing sites

Before any data recording, it was insured that the anchor had a firm grip and that the boat had settled. The GPS receiver monitored position during each fishing session. The boats ‘track’ was usually an arc when on anchor, due to the swinging action downwind of the anchor. Extended downwind track indicated anchor drift, which terminated further sampling. If the fishing session had not exceeded the minimum time interval of ten minutes it was declared invalid and no data were recorded. A new station was immediately selected in the same zone.

GPS coordinates were taken at the end of each fishing session as the average of the positions recorded during the fishing station.

Positioning at diving sites

The GPS position in degrees and decimal seconds was taken directly at the diving buoy using the boat-based GPS receiver. The shot-line of the diving buoy (five kilogram danford anchor, three meter anchor chain, 20 and 10 m polypropylene shot-line ∅ 14 mm connectable by fixed eyes and stainless steel clips; Scanmarin 40″buoy) was kept as straight as possible, to improve the accuracy of the position reading. For safety reasons, minimum and maximum diving depths were set to 10 and 30 m respectively. Therefore, a 20-m shot-line was used for dives between 10 and 20 m of water depth and a 30 m shot-line for water depths between 20 and 30 m.

Boat-based recordings

The depth measured by the echo-sounder during surveys was subjected to some variation resulting from the swing of the boat on anchor and the action of swells. Depth readings on the echo sounder's display were monitored throughout the survey and an estimate of the mean water depth was recorded. At the end of surveys, temperature and turbidity were recorded. Data were downloaded, 'cleaned' and the average temperature and turbidity over the bottom four meters were recorded. Light conditions during each survey were classified as fine (sun visible at all times) or cloudy (sun partly or completely obscured by clouds). Furthermore, the height of the swell during each survey was estimated by averaging the lift of the boat in meters caused by the passing swell as shown on the echo sounder's display and recorded as small (less than two meters) or high (more than two meters).

Controlled fishing

Material and methods were described earlier (chapter 3).

Underwater recordings

Diving surveys were conducted by at least two divers at a time. The following habitat characteristics were estimated by all divers in the team and pooled directly after the dive. The bottom was classified as 'rock' or 'sand' if one substratum type was clearly dominant, 'rock-sand' if the bottom was mainly comprised of rocky substratum interspersed by a few sandy patches or 'sand-rock' if mainly sandy substratum with some erratic rocks were present. In cases where only sandy substrate was encountered at a dive site no biological data were recorded, but depth and bottom type were noted for topographic uses. The horizontal water movement (surge) above the reef, caused by wave action was described as weak or strong. Dominant fish species and benthic taxa were recorded in order of decreasing abundance and a list of all fish species seen during the dive was compiled. The rugosity of the rocky substratum was described as 'low' if the rock face was generally smooth with a few holes and crevices or 'high' if the rock face was rugged with many holes, crevices and caves.

Before point counts were conducted, the horizontal visibility was measured by the diver using a Secchi-disc (black and white aluminium disc ∅ 25 cm, with two kilogram lead weight), attached to the anchor chain of the shot-line, as visual reference. The diver swam away from the disc, unreeling a scaled nylon line and recording the distance from the disappearing disc in meters. The depths of individual point counts, recorded by the diver's pressure gauge (Aqua-Lung Monitor 2) were noted and the mean depth was determined as general site-depth. The profile (or relief) of the reef within the dive site was calculated as the difference between the shallowest and deepest point count depth in meters.

A second diver recorded digital footage (Sony Digital Video Camera Recorder DCR-PC1, Sea&Sea halogen spot CL-20D, Sea&Sea U/W Digital Video Housing VX-1D) of the benthic organisms throughout the dive. To get a representative overview of the patchily distributed benthos, footage was taken at different locations during the dive. To keep findings comparable to point count results, filming was restricted to the same circular area, with a maximum radius of 15 m from the shot-line (Figure 4.3).

Index	Description
1	present
2	rare
3	frequent
4	common
5	abundant
6	dominant

Table 4.2: Abundance indices used in the quantitative analysis of digital underwater video footage

After a dive, the digital footage was downloaded onto PC and edited using Movie Maker (Version 5.1 for Windows®, Microsoft® Corp.). At the end of biological data collection, the downloaded footage of all dives was analyzed comparatively. A relative index of abundance was used to quantitatively analyze benthic taxa (Table 4.2). The seven benthic taxa used were algae (Alg), Gorgonaria (Gor), Ascidiacea (Asc), Bryozoa (Bry), Crinoidea (Cri), Hydrozoa (Hyd) and Porifera (Por).

It is understood that this division of benthic taxa is considerably coarse and does not necessarily represent functional groups. This is particularly true for the species aggregation 'algae' as it covers a huge range of functional groups (encrusting corallines, articulated corallines, corticated algae, ephemerals and kelps). Although more useful, a finer classification would have been beyond the scope of this study. Echinoids were extremely low in (visible) abundance on reefs deeper than ten meters, and could not be evaluated using underwater footage.

Standardized UVC of fish

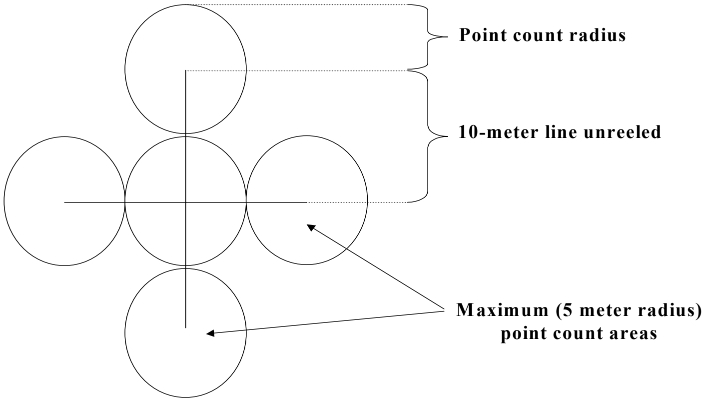


Figure 4.3: Design of underwater point counts. Five point counts with a radius of five meters are shown (maximum survey area)

Between three and five point counts were conducted per dive within 15 m of the shot-line, if the horizontal visibility was three meters or greater (Figure 4.3). The first count was done by swimming away from the shot-line in a random direction, unreeling a ten-meter line (plastic reel with 10 m parachute cord - ∅ 3.5 mm, one meter scaling) clipped to the fixed eye of the shot-line. The count was done at the end of the ten-meter line, surveying an area with a radius of not more than five meters (see Figure 4.3). This procedure was repeated at least twice by unreeling the line in a direction 90° from the preceding point count, using a diving compass as reference. If time was sufficient, a fifth count was taken at the shot-line. Depths at all point counts were recorded, measured by means of a pressure gauge (Aqua-Lung Monitor 2).

The individual point counts were of the type ‘instantaneous area count’ (Thresher and Gunn 1986). The method assumes that all fish in a known area are counted at one point in time. In this study, the area was a circle, the radius depending on the horizontal visibility. Visibilities below three meters made species identification during counts increasingly difficult. Therefore, the minimum radius for counts was set to three meters. To avoid survey area overlap among counts, the maximum radius was set to five meters, using the scaled ten-meter line as reference. Point counts were done with the diver standing over the centre of the circular survey area. Each point count consisted of several, consecutive 360°-rotations. Only individuals of one species were counted per 360°-rotation. Each rotation started with the diver looking up from the reef in a horizontal direction starting to rotate slowly. The first (new) species that was seen was chosen for the count and the 360°-rotation started earlier was completed, counting all detectable fish of that species. Species were counted separately to improve precision of counts (Smith 1989). If no new species were detected after a 360°-rotation the point count was terminated.

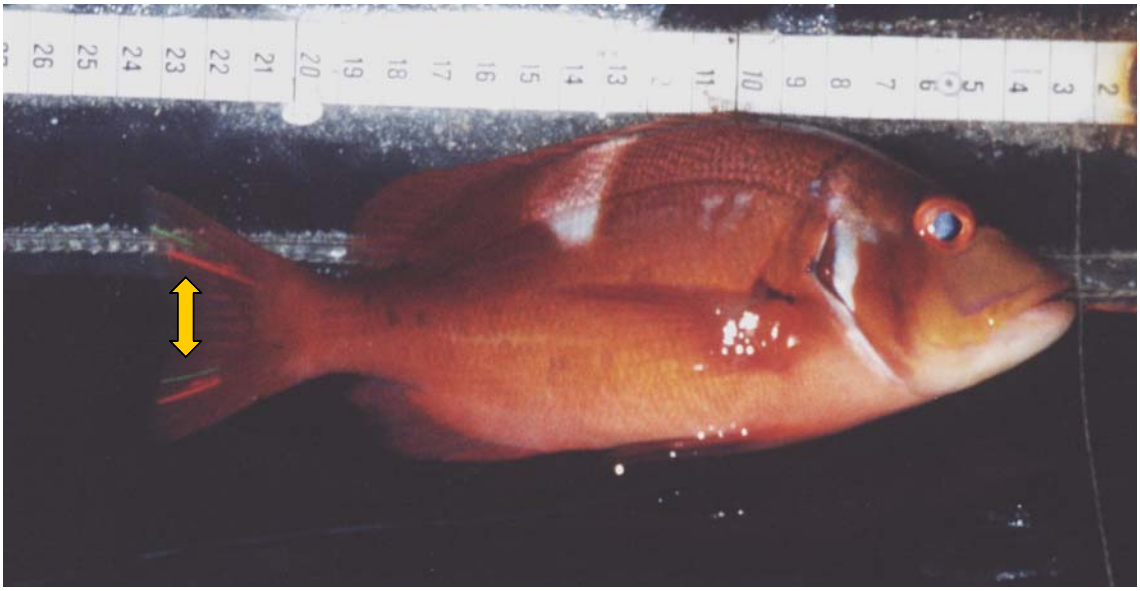


Figure 4.4: Roman carrying four VIE tags in the caudal fin (see yellow up-down arrow). The tag code of this individual was green-red-green-red

After the point count, a slow 360°-rotation was conducted and the sizes of roman were estimated in 5-cm classes. A scaling on the diving slate (perspex slates - 20×30cm, covered with marine paper fixed by plastic number plate screws) was used as reference.

In an initial experiment, size estimates were exercised using a tagging method for confirmation. About 100 roman were caught by rod and line, measured to the nearest millimetre and tagged using Visible Implant fluorescent Elastomer (VIE) tags (Northwest Marine Technology Inc. VIE Hand Injection Master Kit). These tags are comprised of a coloured elastomer and a resin, which get mixed just before tag application. The mixture was injected with a syringe into the caudal fin, between fin rays and the epidermis where it hardens and forms a coloured tag. Like this, four tags were injected per caudal fin, forming a colour-code that can be recognized under water during scuba surveys (Figure 4.4). All fish were released in a confined area of reef and scuba surveys were conducted within one week after tagging. The size of all fish carrying a tag was estimated and recorded along with the tag code of the fish. Size estimates were compared with the measured sizes of the individual fish at the time of tag application.

Density and size analysis

The densities of the eight most abundant fish species were calculated as CPUE (catch-per-unit-effort) for the dataset from fishing surveys and as number-per-point-count for the dataset from diving surveys. These abundance indices and the abundances from the assessment of the seven most important benthic taxa were plotted in GIS using ArcView for visualization of the spatial distribution of densities. The measured fork lengths of the eight most abundant fish species in the fishing survey dataset and the estimated fork lengths of roman in the diving survey dataset were averaged for each fishing and diving site. The values were also plotted in GIS using ArcView.

It is understood that the spatial vicinity of point counts conducted at each site increased the likelihood of auto-correlation. Therefore, using individual point counts as independent samples, rather than pooling data of all point counts during each dive, highlighted the dangers of pseudo-replication during analysis. However, GLM analysis of diving survey data would not have been possible using count data at site level due to small sample numbers. Also to avoid statistical over-fitting, the GLMs were run with a reduced number of factors. Therefore, although it is recognised that results should be viewed with some caution, the analysis was done to attempt to separate the effects of environmental factors from the effect of exploitation. To provide further independent evidence for the results, selected zoning patterns were analysed using the pooled point count data per dive site.

To separate the effects of factors on the density and size of fish species and benthic taxa generalized linear models (GLMs) were coded in STATISTICA. As opposed to general linear models, the distribution of the response variable *Y* in a generalized linear model can be non-normal and does not have to be continuous. Furthermore, the response variable can be nonlinearly related to the predictor variables $\beta_{0\text{-}i}$. Therefore, the linear combination of the predictor variables is ‘connected’ to the response variable via a link function of the form:

$$f(Y) = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_i x_i + \varepsilon \,, \tag{4.1}$$

where $f(\mathrm{K})$ is a link function, $\beta_{0\text{-}I}$ the estimated predictor variables and ε the error (McCullagh and Nelder 1995b). Distribution of residuals for selected model runs can be reviewed in the appendix (Figure 8.5 and 8.6). To find the optimal combination of parameters the fit of the different models (200 different combinations of parameters) were assessed using AIC in STATISTICA (see equation 3.1). Before modelling main effects, second degree interactions between main effects (factors) were modelled. Due to the large number of interaction-terms GLMs based on small sample sizes were compromised by statistical over-fitting. Therefore, only combinations of main effects with zoning patterns were modelled and consistent results are discussed.

In this study, the response variables in the applied GLMs were of different nature and distribution, depending on the survey method.

Benthic survey

The response codes in the benthic survey were of categorical nature (abundance categories). Due to the small sample size, missing cell values resulted while combining parameters (factors) with categories during the computations of GLMs. Therefore, abundance categories were reduced from 1 – 3 to ‘rare’ and from 4 – 6 to ‘abundant’ and a binomial distribution was chosen. The commonly used link function for the binomial distribution is the logit link described as (McCullagh and Nelder 1995a):

$$f(p) = \log\left(p/(1-p)\right), \tag{4.2}$$

where p is the underlying continuous probability of the binary dependent variable, ranging from 0 to 1. In the logit regression model, the predicted values for the dependent variable will never be less than (or equal to) 0, or greater than (or equal to) 1, regardless of the values of the independent variables. To model the influence of relevant recorded parameters (factors) on abundance, GLMs of the form:

$$\begin{aligned}\log\left(p(Abundance)/\left(1-p(Abundance)\right)\right) &= \beta_0 + \beta_1(Depth) + \beta_2(\mathrm{Pr}\,ofile) \\ &\quad + \beta_3(Rugosity) + \beta_4(Zoning - pattern) + \varepsilon\end{aligned} \tag{4.3}$$

were applied. The seven investigated benthic taxa were combined with the seven zoning patterns resulting in the computation of 49 GLMs.

Fishing survey

The response codes in the fishing survey were continuous or count variables (measured fork length or number of fish caught). The distributions of these variables are commonly assumed to be normal or poisson, respectively. The commonly used link function for the poisson distribution is the log link (McCullagh and Nelder 1995c):

$$f(z) = \log(z) \tag{4.4}$$

To model the abundance of fish species in the study area the relevant recorded parameters (factors) were included in a GLM of the form:

$$\begin{aligned}\log(Abundance) = \beta_0 + \beta_1(Depth) + \beta_2(Temperature) + \beta_3(Turbidity) \\ + \beta_4(Season) + \beta_5(Time) + \beta_6(Weather) \\ + \beta_7(Swell) + \beta_8(Zoning - pattern) + \varepsilon\end{aligned} \tag{4.5}$$

The response variables (CPUE) was combined with the eight most abundant fish species and the seven zoning patterns resulting in the computation of 56 GLMs.

The commonly used link function for the normal distribution is the identity link (Equation 3.2). To model the size of fish species in the study area the relevant recorded parameters (factors) were included in a GLM of the form:

$$\begin{aligned}Forklength = \beta_0 + \beta_1(Depth) + \beta_2(Temperature) + \beta_3(Turbidity) + \beta_4(Season) \\ + \beta_5(Time) + \beta_6(Weather) + \beta_7(Swell) + \beta_8(Zoning - pattern) + \varepsilon\end{aligned} \tag{4.6}$$

The response variable (fork length) was combined with the eight most abundant fish species and the seven zoning patterns resulting in the computation of 56 GLMs.

Diving survey

The response codes in the diving survey were continuous or count variables as well (estimated fork length or number of fish counted). The commonly used link function for the poisson distribution is the log link (Equation 4.4). To model the abundance of fish species in the study area the relevant recorded parameters (factors) were included in a GLM of the form:

$$\begin{aligned}\log(Abundance) = \beta_0 + \beta_1(Depth) + \beta_2(Temperature) + \beta_3(Turbidity) \\ + \beta_4(\Pr ofile) + \beta_5(Visibility) + \beta_6(Time) + \beta_7(Bottom) \\ + \beta_8(Rugosity) + \beta_9(Zoning - pattern) + \varepsilon\end{aligned} \qquad (4.7)$$

The response variable (fish counts of the eight most abundant fish species) was combined with the seven zoning patterns resulting in the computation of 56 GLMs.

The commonly used link function for the normal distribution is the identity link (Equation 3.2). To model the size of fish species in the study area the relevant recorded parameters (factors) were included in a GLM of the form:

$$\begin{aligned}Length - estimate = \beta_0 + \beta_1(Depth) + \beta_2(Temperature) + \beta_3(Turbidity) \\ + \beta_4(\Pr ofile) + \beta_5(Visibility) + \beta_6(Time) + \beta_7(Bottom) \\ + \beta_8(Rugosity) + \beta_9(Zoning - pattern) + \varepsilon\end{aligned} \qquad (4.8)$$

The response variable (size estimates for roman) was combined with the seven zoning patterns resulting in the computation of seven GLMs.

Community analysis

Benthic and fish community data from fishing and diving surveys were analyzed using non-parametric multivariate analyses from the PRIMER package (Version 5.2.2, Plymouth Marine Laboratories). Bray-Curtis Similarity matrices were calculated for abundance data of benthos and fish as described by Bray and Curtis (1957).

Data from controlled fishing and UVC were standardized and root and root-root transformed, respectively, before calculation of the Bray-Curtis similarity matrices. A higher transformation was chosen for the abundance data from UVC due to the higher variance of counts. This is desirable to prevent the results being biased by the counts of a few very abundant species (Clarke and Warwick 1994f).

Tree diagrams (dendograms) were produced using a group average hierarchical sorting strategy according to Cormack (1971).

Additionally, non-metric multidimensional scaling (MDS) algorithms described by Clarke and Warwick (1994c) were employed.

The BIOENV procedure was used to relate continuous factors to community structure (Clarke and Warwick 1994b).

Analysis of similarity (ANOSIM) was carried out among levels of categorical factors and zones of zoning patterns to determine if their communities differed significantly (Clarke and Warwick 1994e).

The SIMPER routine determined the relative contribution of individual species to the similarities and differences among groups (Clarke and Warwick 1994d).

Ranked species abundance (dominance) curves were produced from benthic and fish abundance data for the different levels of categorical factors and zones to visualize differences in community structure. On the *y*-axis taxa were ranked in decreasing order of abundance expressed as a percentage of the total abundance of all taxa. Log transformation of the *x*-axis enabled a better visualization of the commoner species (Clarke and Warwick 1994a).

Additionally, the influence of factors on community type were analyzed using non-parametric Kruskal-Wallis ANOVA or parametric one-way ANOVA, if assumptions of normality and homogeneity were met. Analysis was carried out in STATISTICA. Distribution of community types were mapped using ArcView and tested for randomness using chi-square contingency tables in EXCEL.

To separate the effects of factors on the community types generalized linear models (GLMs) were coded in STATISTICA. The response codes in these GLMs were of categorical nature (three types of communities). Therefore, a multinomial distribution had to be chosen (McCullagh and Nelder 1995e). A link function is used to model the response code when the dependent variable is assumed to be nonlinearly related to the factors. The commonly used link function for the multinomial distribution is the generalized logit link (Equation 4.2). To model the distribution of benthic community types in the study area the relevant recorded parameters (factors) were included in a GLM of the form:

$$\log\left(p(Communitytype)/\left(1-p(Communitytype)\right)\right)=\beta_0+\beta_1\left(Depth\right)+\beta_2\left(\mathrm{Pr}\,ofile\right) \\ +\beta_3\left(Rugosity\right)+\beta_4\left(Zoning-pattern\right)+\varepsilon \tag{4.9}$$

To model the distribution of the fish community types from fishing surveys in the study area the relevant recorded parameters (factors) were included in a GLM of the form:

$$\log\left(p(Communitytype)/\left(1-p(Communitytype)\right)\right)=\beta_0+\beta_1\left(Depth\right) \\ +\beta_2\left(Temperature\right)+\beta_3\left(Turbidity\right)+\beta_4\left(Season\right) \\ +\beta_5\left(Time\right)+\beta_6\left(Weather\right)+\beta_7\left(Swell\right) \\ +\beta_8\left(Zoning-pattern\right)+\varepsilon \tag{4.10}$$

The low number of samples (44 sites) in the diving survey did not allow the computation of GLMs to model fish community types. The community types from the benthic and fishing surveys were combined with the seven zoning patterns resulting in 14 GLMs. All GLMs were coded in STATISTICA. To find the optimal combination of parameters the fit of the different models (200 different combinations of parameters) were assessed using AIC in STATISTICA (see equation 3.1). Before modelling main effects, second degree interactions between main effects (factors) were modelled. Due to the large number of interaction-terms the GLMs were compromised by statistical over-fitting. Therefore, only combinations of main effects with zoning patterns were modelled.

Diversity analysis

The richness and diversity of the fish communities in each zone were expressed using Margalef's richness index, the Shannon-Wiener diversity index and the taxonomic diversity index, respectively. Calculations were conducted using PRIMER.

Margalef's richness index expresses how many individuals are in the sample relative to the total number of species in that sample by calculating:

$$d=(S-1)/\log N\,, \tag{4.11}$$

where d is Margalef's index, S is the number of species and N is the number of individuals (Clarke and Warwick 1994a).

The Shannon-Wiener diversity index uses the principles of information theory. It gives a better assessment of composition diversity by indicating if a community is dominated by one or few species:

$$H' = -\sum p_i(\log p_i)\,, \tag{4.12}$$

where H' is the Shannon-Wiener diversity index, i is the sample number and p_i is the proportion of the total count represented by the ith species (Clarke and Warwick 1994a).

The taxonomic diversity index incorporates taxonomic (or phylogenetic) information and expresses an average taxonomic 'distance' between two organisms randomly chosen from a sample (Clarke and Warwick 1994a):

$$\Delta = \left(\sum\sum\nolimits_{i<j} \omega_{ij} x_i x_j\right) \Big/ \left(n[n-1]/2\right), \tag{4.13}$$

where x_i is the abundance of the ith species, n is the total number of individuals in the sample and ω_{ij} is the 'distinctness weight' denoted to the path length connecting species i and j within their hierarchical, taxonomic classification.

Indices of zones were tested for normality of distribution and homogeneity of variances using chi-square, Hartley F-max and Levene's test. If the assumptions were not met, the indices were log-transformed. If the assumptions were not met after transformation, a non-parametric Mann-Whitney U test or a non-parametric Kruskal-Wallis ANOVA was conducted to compare median indices of zones within zoning patterns. Otherwise, mean indices were compared using parametric Students t-test or one-way ANOVA and results were compared by means of Tukey's test. All statistical tests were conducted in STATISTICA.

4.3 RESULTS

In all, 48 sites were assessed using digital underwater video, 273 sites were fished and 177 point counts were conducted at 44 dive sites. During fishing and diving surveys, 47 species of fish were identified. In all, 7452 fish of 34 species were counted during diving surveys and 2496 fish of 37 species were caught during fishing surveys. A detailed list of species and numbers recorded using these two different methods is provided in table 4.3.

UVC

Species	**Number**
Fransmadam (*Boobsoidea inornata*)	2499
Steentjie (*Spondyliosoma emarginatum*)	2073
Blue hottentot (*Pachymetopon aeneum*)	863
Roman (*Chrysoblephus laticeps*)	496
Strepie (*Sarpa salpa*)	459
Two-tone fingerfin (*Chirodactylus brachydactylus*)	192
Cape knifejaw (*Oplegnathus conwayi*)	187
Blacktail (*Diplodus sargus capensis*)	162
Zebra (*Diplodus cervinus capensis*)	124
Piggy (*Pomadasys olivaceum*)	96
Janbruin (*Gymnocrotaphus curvidens*)	84
Santer (*Cheimerius nufar*)	50
Cape stumpnose (*Rhabdosargus holubi*)	39
Redfingers (*Cheilodactylus fasciatus*)	22
Red stumpnose (*Chrysoblephus gibbiceps*)	19
Barred fingerfin (*Cheilodactylus pixi*)	18
Red steenbras (*Petrus rupestris*)	15
Bronze bream (*Pachymetopon grande*)	14
Doublesash butterflyfish (*Chaetodon marleyi*)	11
Jutjaw (*Parascorpis typus*)	8
Spotted ragged-tooth (*Eugomphodus taurus*)	3
Sand steenbras (*Lithognathus mormyrus*)	3
Hottentot (*Pachymetopon blochii*)	3
White musselcracker (*Sparodon durbanensis*)	3
Koester (*Acanthistius sebastoides*)	2
Galjoen (*Coracinus capensis*)	2
Striped catshark (*Poroderma africanum*)	2
Black musselcracker (*Cymatoceps nasutus*)	1
Puffadder shyshark (*Haploblepharus edwardsii*)	1
Panga (*Pterogymnus laniarius*)	1
White seacatfish (*Galeichthyes feliceps*)	*
Leopard catshark (*Poroderma pantherinum*)	*
Bronze whaler (*Carcharhinus brachyurus*)	*
Giant yellowtail (*Seriola lalandi*)	*
Total	**7452**

Controlled fishing

Species	**Number**
Roman (*Chrysoblephus laticeps*)	1089
Fransmadam (*Boobsoidea inornata*)	687
Steentjie (*Spondyliosoma emarginatum*)	201
Blue hottentot (*Pachymetopon aeneum*)	89
Santer (*Cheimerius nufar*)	83
Sand soldier (*Pagellus natalensis*)	47
Dageraad (*Chrysoblephus cristiceps*)	42
White seacatfish (*Galeichthyes feliceps*)	41
Koester (*Acanthistius sebastoides*)	29
Striped catshark (*Poroderma africanum*)	27
Piggy (*Pomadasys olivaceum*)	18
Mackerel (*Scomber japonicus*)	16
Leopard catshark (*Poroderma pantherinum*)	15
Smoothhound (*Mustelus mustelus)*	13
Dusky kob (*Argyrosomus japonicus*)	12
Red stumpnose (*Chrysoblephus gibbiceps*)	12
Panga (*Pterogymnus laniarius*)	11
Blacktail (*Diplodus sargus capensis*)	9
Puffadder shyshark (*Haploblepharus edwardsii*)	9
Red steenbras (*Petrus rupestris*)	9
Geelbek (*Atractoscion aequidens*)	6
Sooth hammerhead shark (*Sphyrna zygaena*)	6
Bronze bream (*Pachymetopon blochii*)	3
Strepie (*Sarpa salpa*)	3
Dusky shark (*Carcharhinus obscurus*)	2
Zebra (*Diplodus cervinus capensis*)	2
Janbruin (*Gymnocrotaphus curvidens*)	2
Elf (*Pomatomus saltatrix*)	2
Spotted gullyshark (*Triakis megalopterus*)	2
Maasbanker (*Trachurus trachurus*)	2
Carpenter (*Argyrozona argyrozona*)	1
Bronze whaler (*Carcharhinus brachyurus*)	1
Black musselcracker (*Cymatoceps nasutus*)	1
Hottentot (*Pachymetopon blochii*)	1
Jutjaw (*Parascorpis typus*)	1
Cape stumpnose (*Rhabdosargus holubi*)	1
Bluntnose spiny dogfish (*Squalus megalops*)	1
Total	**2496**

Table 4.3: Number of species recorded during UVC and controlled fishing. Grey fields indicate species exclusively recorded using respective method. *species observed during dives but never included in point counts

4.3.1 Benthic community

The community of the study area

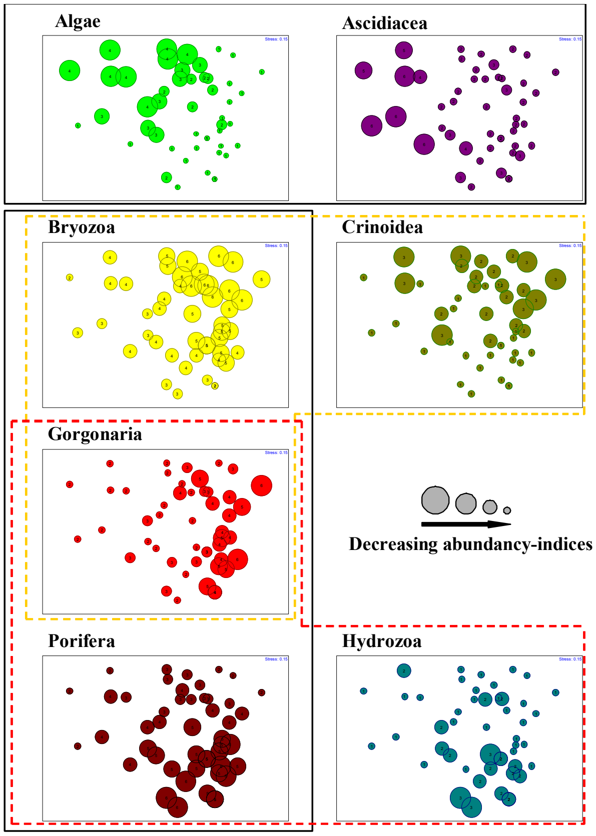


Figure 4.5: MDS plots of 48 sites with superimposed abundances of seven benthic taxa. The size of circles indicate relative abundance for that particular taxon, but are not comparable between taxa

Differences in community structures are based on differences in abundances of functional groups. Figure 4.5 shows MDS plots of 48 sites with abundance-indices of the seven investigated benthic taxa superimposed. In these MDS plots, similar sites (in terms of community structure) are plotted closer together. In all seven plots, higher abundances, as indicated by larger bubbles, are found at more similar sites. This suggests, that the benthic communities are markedly different and that all seven taxa contribute to these differences.

Algae and ascidians (upper solid block in figure 4.5) were more abundant at similar sites, found in the left and upper left corner of the MDS plot. These taxa were characteristic of one community type. On the other hand, Bryozoa, Gorgonaria and Porifera (left solid block in figure 4.5) were more abundant at sites found in the right half of the MDS plot. A closer look reveals that Bryozoa and Gorgonaria overlap in the upper right and Porifera and Gorgonaria in the lower right corners of the MDS plot. Additionally, Crinoidea and Hydrozoa, found in the upper and lower half of the MDS plot respectively, seem to exclude each other. This pattern suggests two further community types, one with high occurrences of Bryozoa, Gorgonaria and Crinoidea (yellow dotted block in figure 4.5) and another where Porifera, Gorgonaria and Hydrozoa are abundant (red dotted block in figure 4.5).

A cluster dendrogram based on Bray-Curtis similarities in percent for the 48 sites is shown in figure 4.6. At a cut-off-level of 80%, three principal groups can be identified. Group B and C are more similar in community structure to each other than to group A.

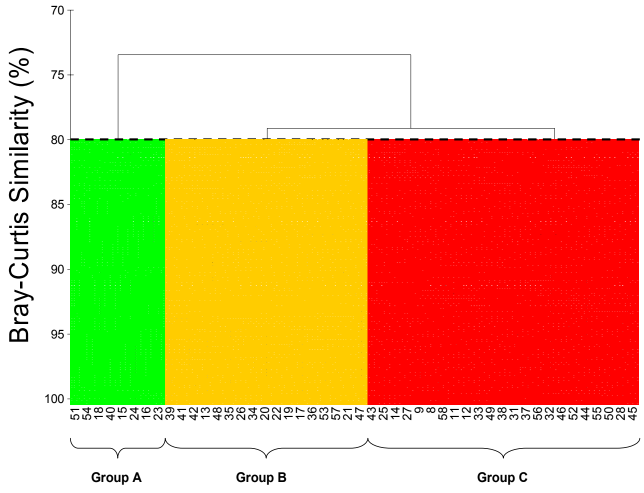


Figure 4.6: Cluster dendrogram indicating the similarities of 48 sites

A dominance plot, as shown in figure 4.7, provides an indication of underlying differences in abundances of individual taxa within each group. Table b in figure 4.7 summarizes the frequencies of the different taxa throughout the study area. Generally, Bryozoa was the most abundant benthic taxon closely followed by Porifera. Markedly lower in abundance were Gorgonaria and Ascidiacea, followed by algae, being less than half as abundant as Bryozoa. And finally crinoids and Hydrozoa constituted less than 10% of the overall occurrence each.

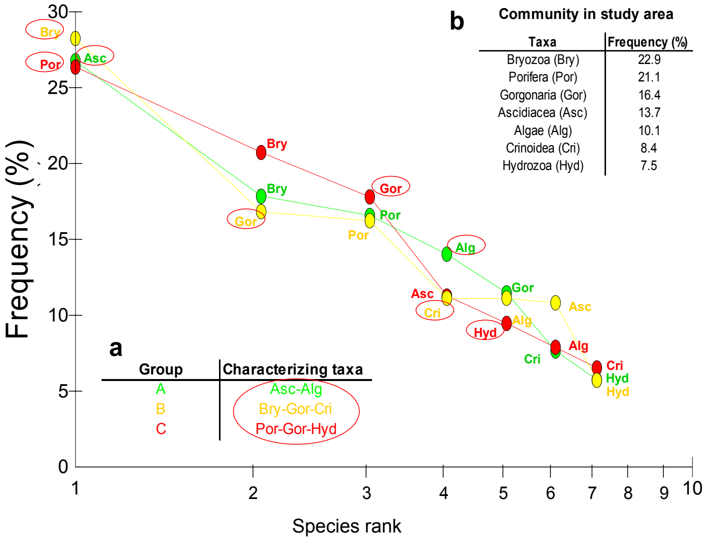


Figure 4.7: Dominance plots of the three benthic groups (a) and table indicating frequencies of benthic taxa in the whole study area

Group A (green line in figure 4.7) differs from this general abundance pattern. Ascidians become the dominant taxon almost doubling in frequency of occurrence and algae increase by 50%. Therefore, group A was identified as an Ascidiacea-Algae community (Asc-Alg). In group B (yellow line in figure 4.7) Bryozoa have the highest frequency of occurrence (28.2%) of all taxa in all groups. Gorgonaria move into second position and crinoids occur almost twice as often when compared to groups A and C. Group B was identified as the Bryozoa-Gorgonaria-Crinoidea (Bry-Gor-Cri) community. Finally, group C (red line in figure 4.7) was dominated by Porifera, but Gorgonaria occurred more frequently here than in all the other groups, and Hydrozoa were almost twice as abundant when compared to the other two groups. Therefore, group C was characterized by a Porifera-Gorgonaria-Hydrozoa dominance (Por-Gor-Hyd).

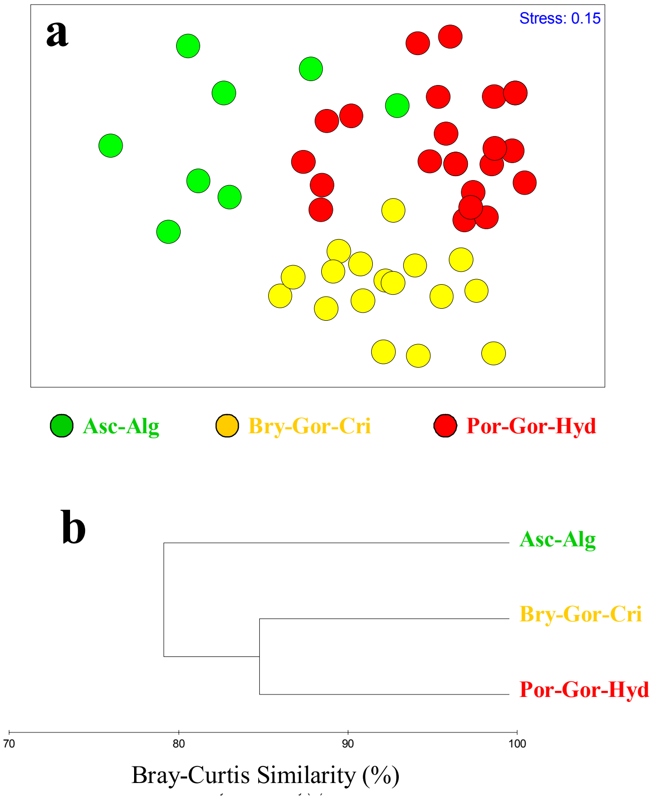
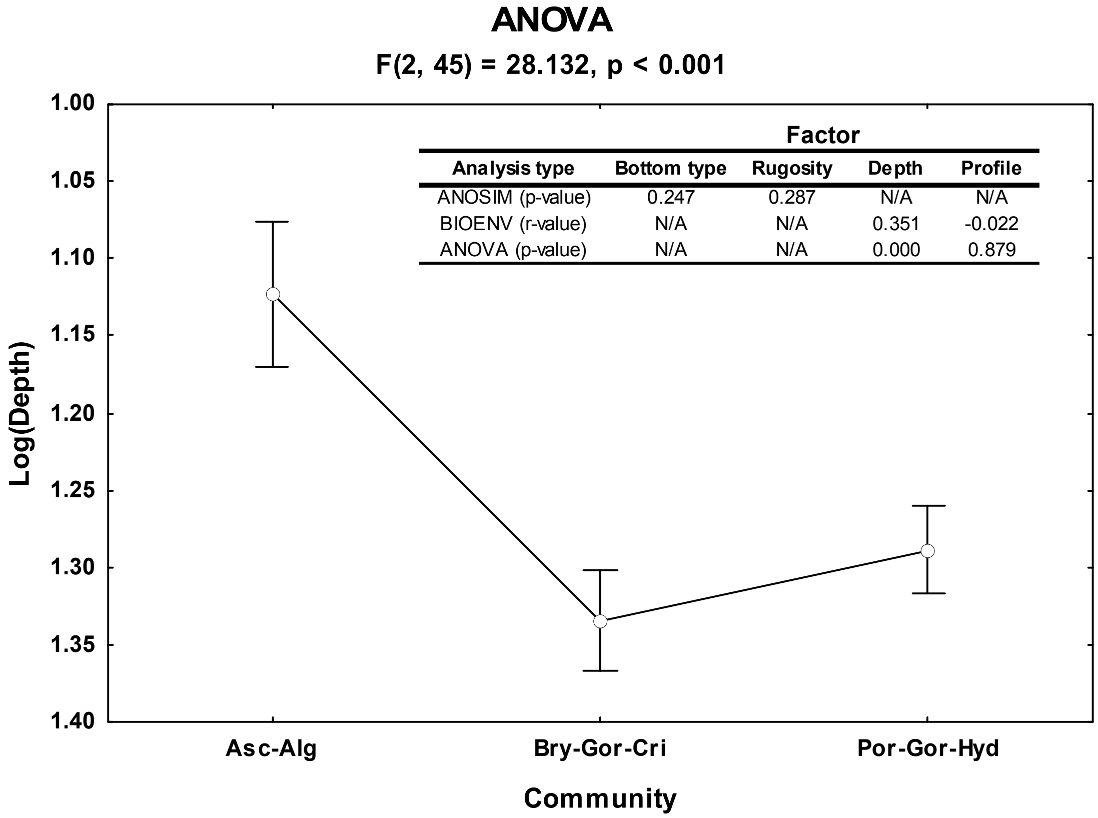


Figure 4.8: MDS plot (a) and cluster dendrogram (b) of the three benthic groups

The three different communities, separated clearly into three different corners of an MDS plot area (Figure 4.8 a). Underlying similarity percentages in the cluster dendrogram in figure 4.8 b were 77.5 between the Asc-Alg and Por-Gor-Hyd communities, 80.8 between the Asc-Alg and Bry-Gor-Cri communities and 84.8 between the Por-Gor-Hyd and Bry-Gor-Cri communities.

This pattern was reconfirmed by a SIMPER procedure, where percentage contribution of individual taxa to similarities within groups and dissimilarities among groups were calculated. The lowest average dissimilarity occurred between the Por-Gor-Hyd and Bry-Gor-Cri communities (20.9%). Both communities had a higher average dissimilarity with the Asc-Alg community (ranging from 26.4 – 26.7%). In other words, the Asc-Alg community is the most different of the three communities.

The reasons for these differences can be investigated by analysis of the potentially relevant factors. These were reef type (described by bottom type, reef profile and rugosity), vertical (depth) and spatial (zoning patterns) distribution. Figure 4.9 summarizes the influence of factors on community structure using various tests.

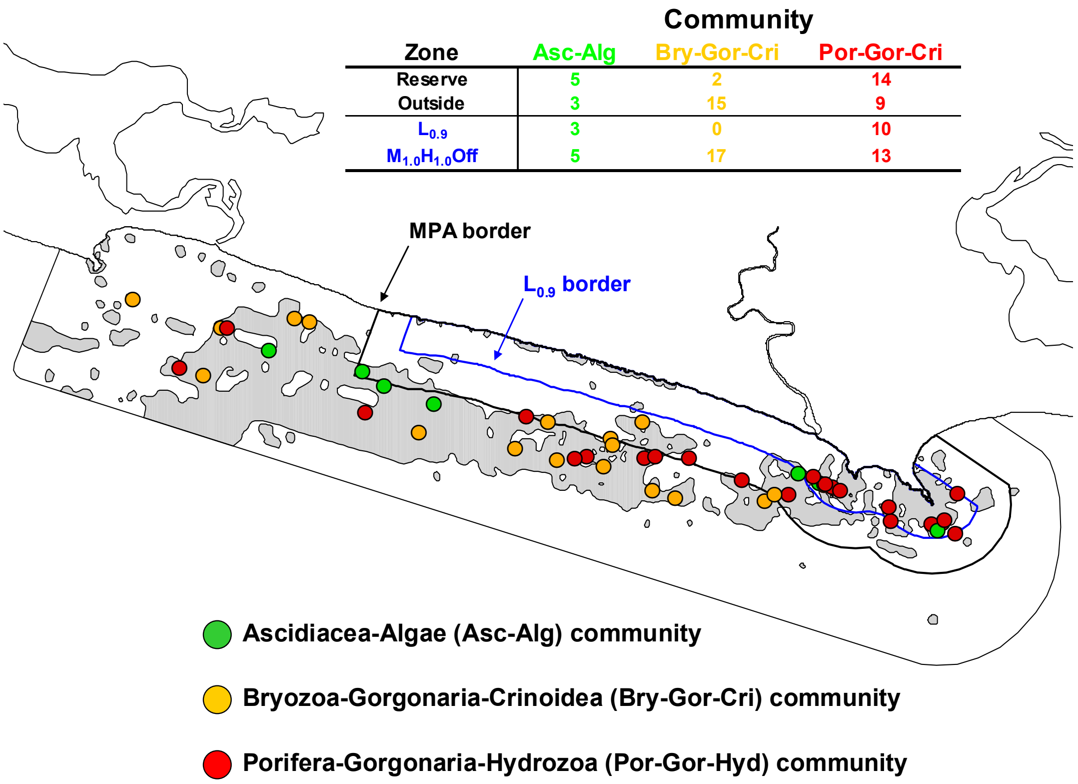


	Factor			
Analysis type	Bottom type	Rugosity	Depth	Profile
ANOSIM (p-value)	0.247	0.287	N/A	N/A
BIOENV (r-value)	N/A	N/A	0.351	-0.022
ANOVA (p-value)	N/A	N/A	0.000	0.879

Figure 4.9: Influence of factors on the three benthic communities using ANOVA, ANOSIM and BIOENV tests. Vertical bars denote the 95% confidence intervals

Bottom type and rugosity did not have an influence on community structure ($p = 0.247$ and 0.287, respectively). Reef profile did not correlate with community structure ($r = -0.022$) and was not different among the three communities ($p = 0.879$). However, depth showed a weak correlation with community structure ($r = 0.351$). This was clarified by an ANOVA test, revealing significantly shallower sites with Asc-Alg communities. Distribution of Log-transformed depths was normal ($p = 0.375$) and variances homogeneous ($p = 0.388$).

The effect of spatial patterns on the occurrence of benthic communities was investigated using chi-square contingency tables (Figure 4.10). An unequal distribution of benthic communities over space can be clearly seen and was tested to be significant ($p < 0.001$) for the **Reserve/Outside** and **L$_{0.9}$/M$_{1.0}$H$_{1.0}$Off** zones.



	Community		
Zone	Asc-Alg	Bry-Gor-Cri	Por-Gor-Cri
Reserve	5	2	14
Outside	3	15	9
L$_{0.9}$	3	0	10
M$_{1.0}$H$_{1.0}$Off	5	17	13

Figure 4.10: Map of the study area with distribution of the three benthic communities within two zoning patterns

The occurrence of Bry-Gor-Cri communities is reduced within the protected inshore zones and replaced by the Por-Gor-Hyd community (see table in figure 4.10).

In order to separate the effects of depth and zones on the distribution of the two identified communities, a GLM was applied. All seven zones were combined with the factors, resulting in seven individual GLMs. However, due to the small sample size, GLMs of only three zoning patterns could be calculated. Bottom type, rugosity, and reef profile did not have an influence on benthic community as predicted using conventional tests (p-values between 0.103 and 0.799). Depth showed a potential influence at p-values between 0.064 and 0.072. Of the three investigated zones, **Core/TransOut** and **Reserve/Outside** had p-values of 0.066 and 0.047, strongly suggesting an influence of zones on the benthic community. No significant interactions between main effects were detected for the three analysed zoning patterns.

In summary, the distribution of the three identified principle communities were influenced by depth and zones. Depth had a strong influence on the distribution of the Asc-Alg community, with shallow reefs supporting higher occurrences. Zones seem to have a strong influence on the distribution of Bry-Gor-Cri and Por-Gor-Hyd communities. However, after separating the effects of depth and zones using a GLM, these effects were significant for only one of the zoning patterns modelled as the GLM was compromised by a small sample size. The influence of factors and zones on the benthic community can be clarified with a more detailed look at density patterns of individual taxa.

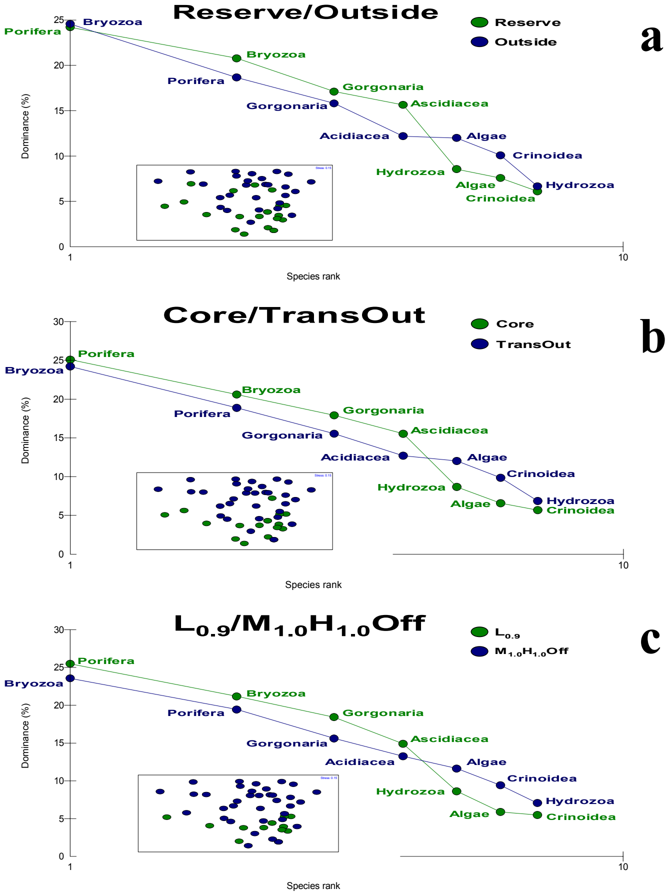


Figure 4.11: Dominance and MDS plots of benthic taxa for the Reserve/Outside (a), the Core/TransOut (b) and the $L_{0.9}$/$M_{1.0}H_{1.0}$Off (c) zoning patterns

Dominance- and MDS plots for the three two-zone zones, **Reserve/Outside**, **Core/TransOut** and **$L_{0.9}$/$M_{1.0}H_{1.0}$Off** are presented in figure 4.11 a, b and c, respectively. In all three MDS plots, the protected inshore zones can be found in the lower part of the plot area, considerably dissimilarity from the exploited offshore areas. In terms of dominance, all protected inshore and exploited offshore zones reveal the same pattern. The protected inshore **Reserve**, **Core** and **$L_{0.9}$** zones are dominated by Porifera with low abundances of algae and Crinoidea. The exploited offshore zones **Outside**, **TransOut** and **$M_{1.0}H_{1.0}$Off** are dominated by Bryozoa with high abundances of algae and Crinoidea. Communities of protected inshore zones when compared to their respective exploited offshore zones were significantly different as indicated by ANOSIM tests (p-values between 0.001 and 0.048).

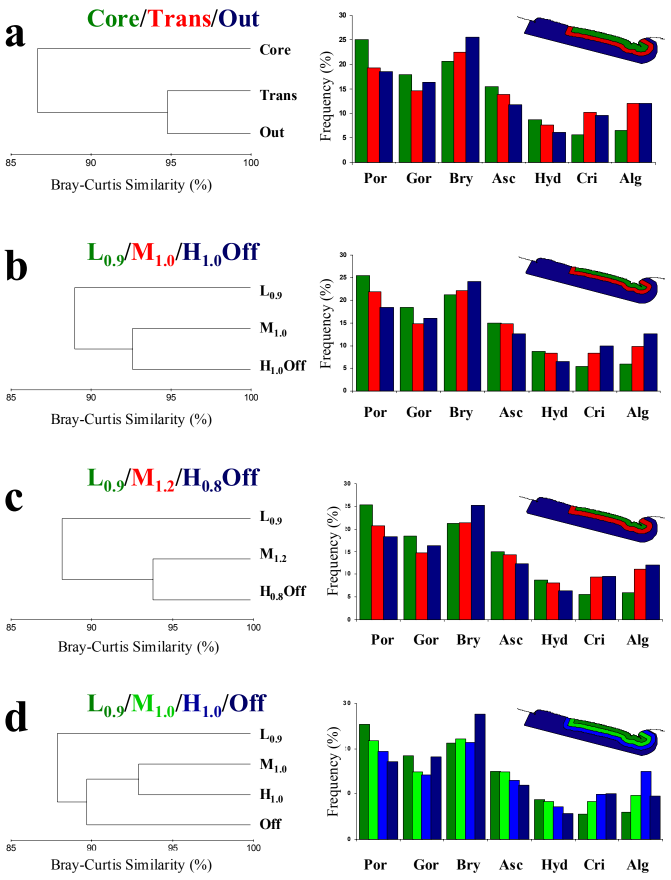


Figure 4.12: Cluster dendrograms and frequency plots of benthic taxa for the Core/Trans/Out (a), the $L_{0.9}$/$M_{1.0}$/$H_{1.0}$Off (b), the $L_{0.9}$/$M_{1.2}$/$H_{0.8}$Off (c) and the $L_{0.9}$/$M_{1.0}$/$H_{1.0}$/Off (d) zoning patterns

Cluster dendrograms and frequency graphs of individual benthic taxa for the three three-zone zones **Core/Trans/Out**, **$L_{0.9}$/$M_{1.0}$/$H_{1.0}$Off** and **$L_{0.9}$/$M_{1.2}$/$H_{0.8}$Off** and the one four-zone zone **$L_{0.9}$/$M_{1.0}$/$H_{1.0}$/Off** are presented in figure 4.12 a, b, c and d, respectively. Similarities decrease consistently when comparing the protected inshore zones with their respective exploited offshore zones. For example, similarity between **Trans** and **Core** is 88% but then drops to 85% between **Core** and **Out**. Analogously, similarities among **$L_{0.9}$** and the **$M_{1.0}$** and **$M_{1.2}$** are 91 and 92% respectively, but then drop to 86% for **$L_{0.9}$** compared to **$H_{1.0}$Off** and **$H_{0.8}$Off**. Eventually, when comparing the **$L_{0.9}$** with **Off**, similarity drops even further to 85%. This gradual change in community structure when moving from the protected inshore towards the exploited offshore zones is also evident in the frequency plots in figure 4.12. Generally, poriferan, ascidian and hydrozoan abundances dropped and bryozoan, crinoid and algal abundances rose when moving from protected inshore to exploited offshore zones, explaining this gradual change.

The community in **Core** was significantly different from the communities in **Trans** and **Out** as shown by ANOSIM tests (p-values of 0.002 and 0.001, respectively). However, communities in **Trans** and **Out** were not different (p = 0.265). Analogously, **$L_{0.9}$** was significantly different to **$M_{1.0}$** and **$M_{1.2}$**, and **$H_{1.0}$Off** and **$H_{0.8}$Off** (p-values of 0.021 and 0.020, and 0.002 and 0.001, respectively). However, **$M_{1.0}$** and **$H_{1.0}$Off** and **$M_{1.2}$** and **$H_{0.8}$Off** were not significantly different (p-values of 0.119 and 0.086, respectively).

The density of benthic taxa

In all seven zoning patterns, depth had a significant influence on algal distribution, with shallower reefs showing higher algae abundances (p-values between 0.035 and 0.050, figure 4.13). Additionally, all zones had a significant influence on algal distribution (p-values between 0.007 and 0.026). Algal abundances were generally low in the **$L_{0.9}$**, **Core** and **Reserve** zones, increasing across the border of the MPA to highest levels in the **$H_{1.0}$** zone and eventually slightly decreasing in the **Off** zone. Other measured factors did not have a significant influence on the algal distribution in the area. No significant interactions between main effects were detected.

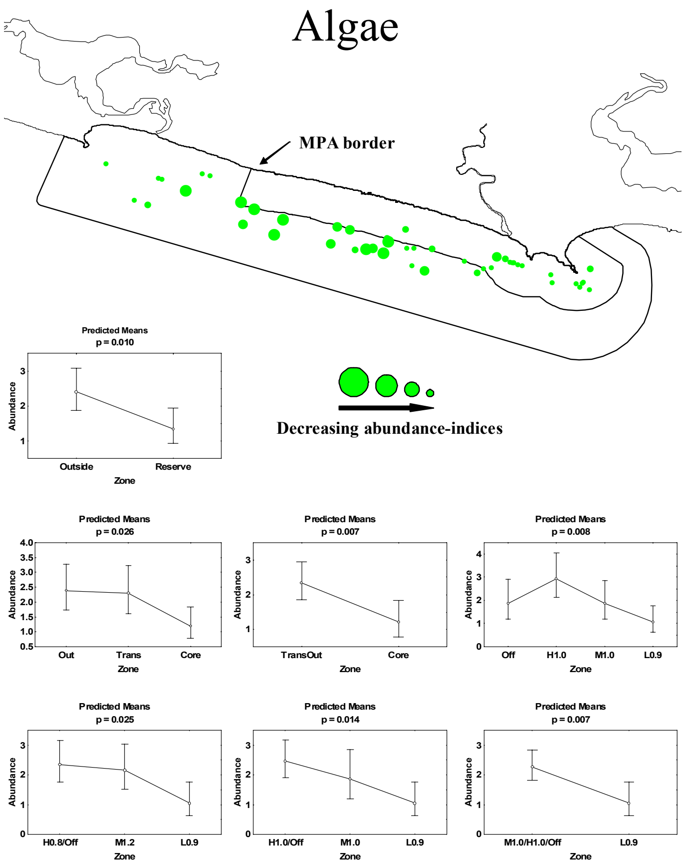


Figure 4.13: Abundance of algae in the study area at 48 sites with results for the seven zoning patterns using a GLM. Vertical bars denote 95% confidence intervals

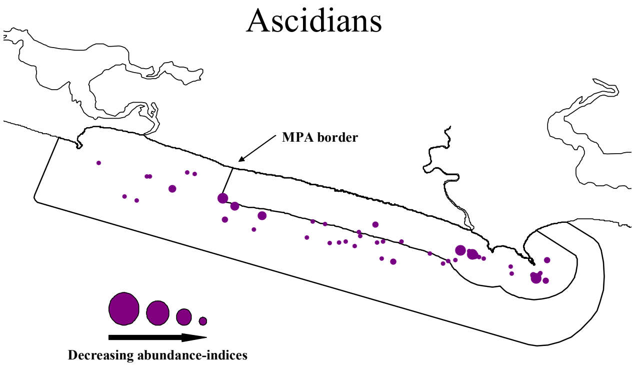


Figure 4.14: Abundance of ascidians in the study area at 48 sites

Only depth had an influence on ascidian distribution, with shallow reefs accommodating high ascidian abundances (Figure 4.14). This effect was highly significant in all seven zoning patterns ($p < 0.001$). A significant ($p = 0.041$) interaction between zoning patterns and reef profile was noted. Higher ascidian abundances occurred on high profile reefs under exploitation.

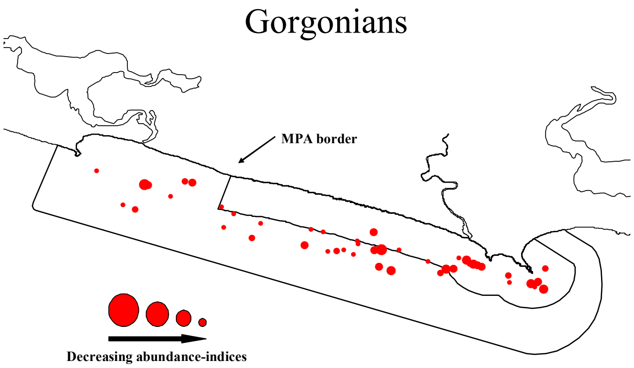


Figure 4.15: Abundance of gorgonians in the study area at 48 sites

None of the measured factors or zones had an effect on gorgonian distribution (Figure 4.15). No significant interactions between main effects were detected.

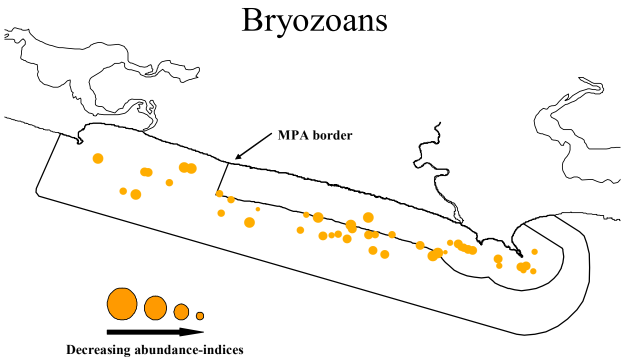


Figure 4.16: Abundance of bryozoans in the study area at 48 sites

None of the measured factors or zones had an effect on bryozoan distribution (Figure 4.16). No significant interactions between main effects were detected.

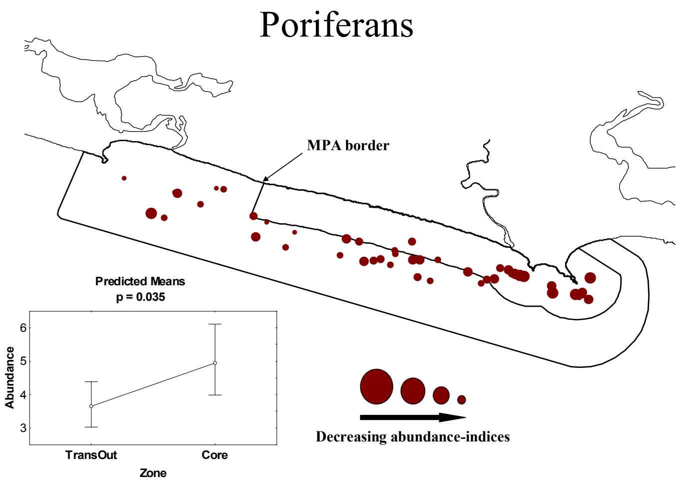


Figure 4.17: Abundance of poriferans in the study area at 48 sites. Vertical bars denote 95% confidence intervals

None of the measured factors had a significant effect on poriferan distribution. (Figure 4.17). Of the various zones, only **Core/TransOut** revealed a significant effect towards higher poriferan abundances in the **Core** zone (p = 0.035). The remaining zones indicated this effect at p-values between 0.067 and 0.117. No significant interactions between main effects were detected.

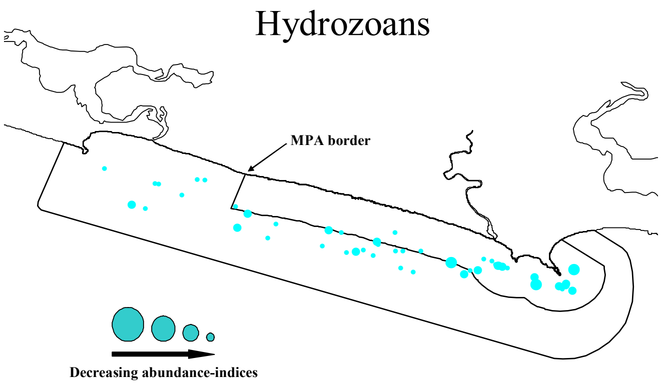


Figure 4.18: Abundance of hydrozoans in the study area at 48 sites

Neither factors nor zones had any influence on abundances of hydrozoans (Figure 4.18). No significant interactions between main effects were detected.

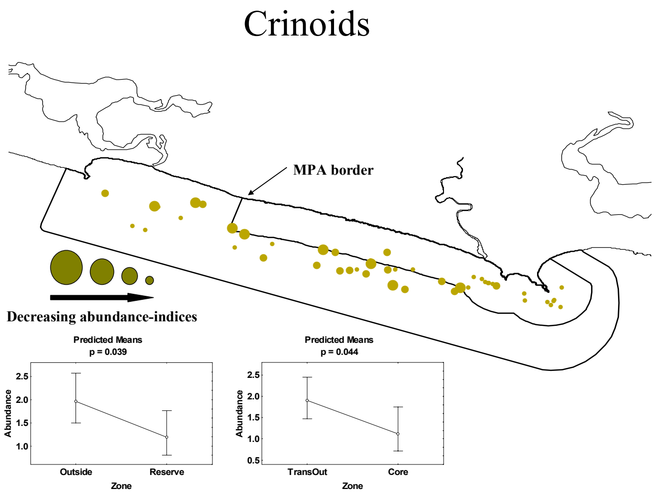


Figure 4.19: Abundance of crinoids in the study area at 48 sites. Vertical bars denote 95% confidence intervals

Abundances of crinoids were lower in the **Reserve** and **Core** zones with p-values of 0.039 and 0.044, respectively (Figure 4.19). The remaining zoning patterns indicated this trend with p-values between 0.073 and 0.167. Other factors were not influential. No significant interactions between main effects were detected.

In summary, the distribution of Hydrozoa, Bryozoa and Gorgonaria were not determined by any measured factors or zoning patterns. Ascidians and algae were more abundant at shallower sites. Taxa influenced by zoning patterns were Porifera, Crinoidea and algae. Porifera were more abundant in the protected inshore zones, whilst Crinoidea and algae were more abundant in the exploited offshore zones of the area (Table 4.4).

	Factor			
Taxa	**Zone**	**Depth**	**Profile**	**Rugosity**
Algae	Outside	shallow	-	-
Ascidiacea	-	shallow	-	-
Gorgonaria	-	-	-	-
Bryozoa	-	-	-	-
Porifera	Inside	-	-	-
Hydrozoa	-	-	-	-
Crinoidea	Outside	-	-	-

Table 4.4: Influence of factors on the abundance of the seven most abundant benthic taxa in the study area. Factor codes indicate significantly higher abundances

4.3.2 Ichthyofauna from controlled fishing

The community of the study area

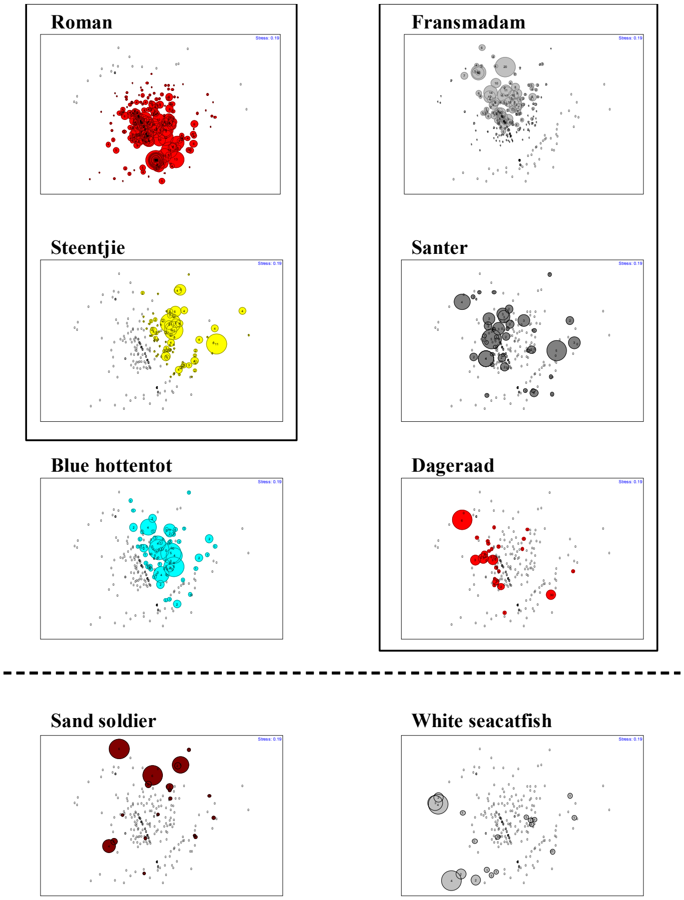


Figure 4.20: MDS plots of 273 sites with superimposed abundances of eight fish species. The size of circles indicate relative abundance for that particular species, but are not comparable between species

Differences in community structures are based on differences in abundances of functional groups. The clustering of stations on the basis of similarity of controlled fishing catch composition is primarily driven by the abundances of roman and fransmadam. These two numerically dominant species cause a separation in MDS plots into a roman-dominated community (bottom right in figure 4.20) and a fransmadam-dominated community (top left in figure 4.20). Santer and dageraad were abundant where roman was scarce but show considerable overlap with fransmadam, suggesting high occurrences of these species in communities where roman is low and fransmadam is high in abundance (right solid block in figure 4.20). Steentjie has more overlap with roman than with fransmadam, suggesting higher abundances of this species in roman-dominated communities (left solid block in figure 4.20). Blue hottentot seems to have considerable overlap with all major species and can therefore be expected to be present in all communities. Finally, sand soldier and white seacatfish show very little overlap with any major species in the MDS plot (below dotted line in figure 4.20).

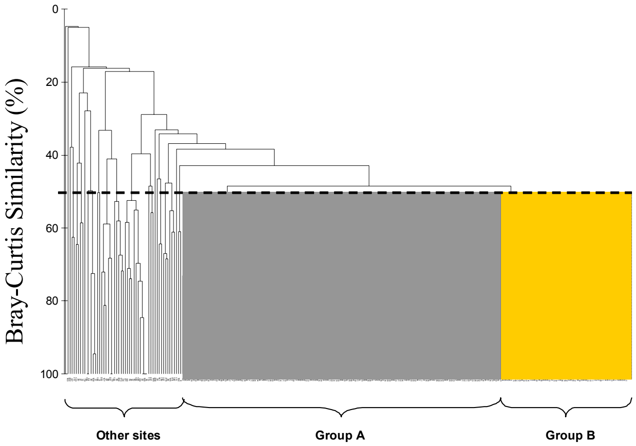
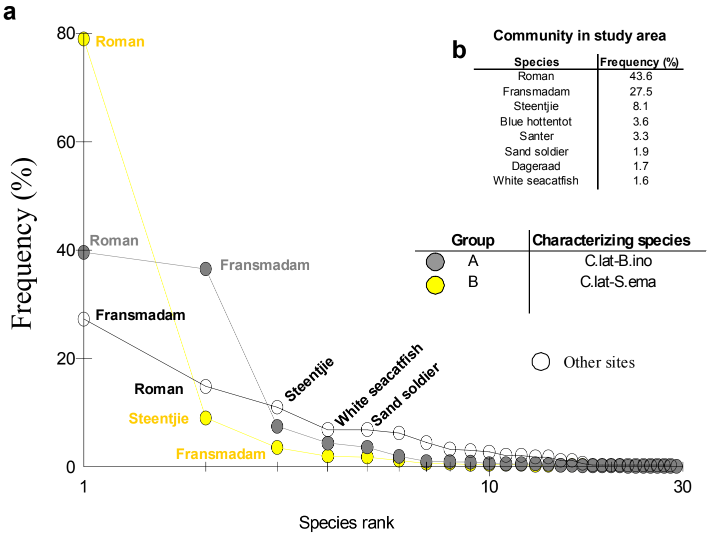


Figure 4.21: Cluster dendrogram indicating similarities of 273 sites

A cluster dendrogram, based on Bray-Curtis similarities in percent calculated for the 273 sites is presented in figure 4.21. At a cut-off-level of 50%, two principal groups can be identified. Group A and B are more similar in community structure to each other than to the remaining sites, which are heterogeneous due to low within-similarities (Figure 4.21).



Community in study area

Species	Frequency (%)
Roman	43.6
Fransmadam	27.5
Steentjie	8.1
Blue hottentot	3.6
Santer	3.3
Sand soldier	1.9
Dageraad	1.7
White seacatfish	1.6

Group	Characterizing species
● A	C.lat-B.ino
● B	C.lat-S.ema

○ Other sites

Figure 4.22: Dominance plots of the two identified groups of fish and the remaining sites (a) and table indicating frequencies in the whole study area (b)

Roman was by far the most abundant fish species with almost 50% frequency of occurrence, followed by fransmadam, with more than a quarter of all fish caught (Figure 4.22 b). Markedly lower in abundance was steentjie with less then 10% frequency of occurrence. Then, less than half as abundant were blue hottentot and santer, and finally sand soldier, dageraad and white seacatfish.

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The fish community at the ‘other sites’ (black line in figure 4.22 a) differ from the general abundance pattern. Roman drop dramatically in abundance to less than one third of its overall occurrence. Additionally, abundances of sand soldier and white seacatfish are greater by a factor of four and five, respectively. However, these fish communities are heterogeneous and the differences in abundances of individual species should not be generalized. Group A (grey line in figure 4.22 a) follows the general abundance pattern except for roman being slightly decreased and fransmadam slightly increased in abundance. Group A was identified as the *C. laticeps* - *B. inornata* (C.lat-B.ino) dominated community. Finally, group B (yellow line in figure 4.22 a) is strongly dominated by roman with almost 80% frequency of occurrence and fransmadam abundance decreases eightfold. Therefore, group C is characterized by a *C. laticeps* – *S. emarginatum* dominance (C.lat-S.ema).

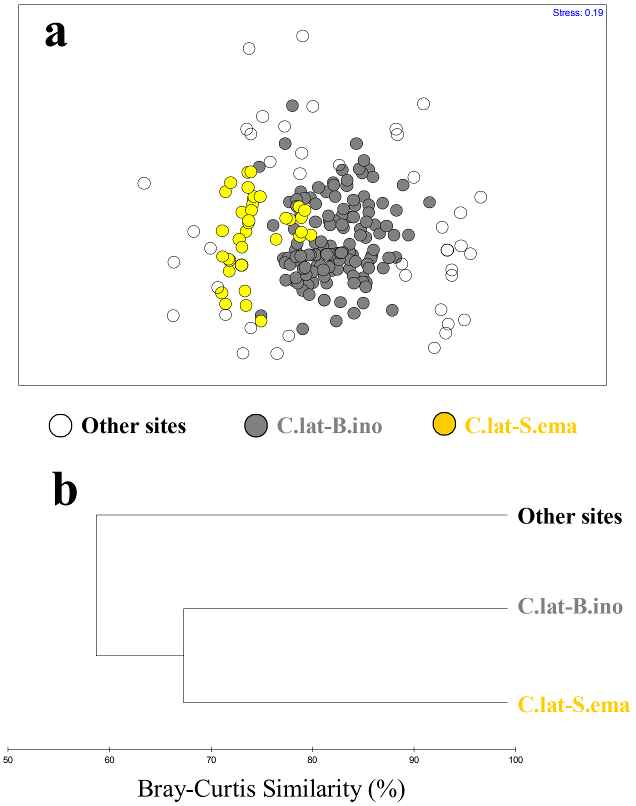


Figure 4.23: MDS plot (a) and cluster dendrogram (b) of the three groups of fish communities

These differences are illustrated and quantified in figure 4.23. An MDS plot of the two different communities (Figure 4.23 a), clearly separates the C.lat-B.ino and the C.lat-S.ema communities into two different corners of the plot area.

A SIMPER test confirmed the dominant role of roman in the C.lat-S.ema community. Roman contributed 95.3% to the within similarity of this group. In the C.lat-B.ino group roman and fransmadam cumulatively contributed 94.6% to the within similarity of this group.

Underlying similarity percentages in the cluster dendrogram in figure 4.23 b were 51.2 between the C.lat-S.ema community and the ‘other sites’, 66.2 between the C.lat-B.ino community and the ‘other sites’ and 67.3 between the C.lat-S.ema and the C.lat-B.ino communities. In other words, the ‘other sites’ are the least similar to the two grouped communities.

The reasons for these differences can be investigated by analysis of the potentially relevant factors. These were weather, time of day, season, temperature, turbidity, depth and spatial distribution (zoning patterns). Table 4.5 summarizes the influence of factors on community structure using various tests.

	Factor					
Analysis type	**Weather**	**Season**	**Time**	**Depth**	**Temperature**	**Turbidity**
ANOSIM (p-value)	0.903	0.004*	0.358	N/A	N/A	N/A
BIOENV (r-value)	N/A	N/A	N/A	0.066	-0.016	0.067
Kruskal-Wallis (p-value)	N/A	N/A	N/A	0.417	0.856	0.526
ANOVA (p-value)	N/A	N/A	N/A	0.224	0.73	0.002*

Table 4.5: Influence of factors on community structure using ANOVA, ANOSIM, BIOENV and Kruskal-Wallis test. * indicates significant p-value < 0.01

Weather and time of day did not have an influence on community structure ($p = 0.903$ and 0.358, respectively). Season, however, had a significant influence on community structure ($p = 0.004$). Depth, temperature and turbidity did not correlate with community structure (r – values between -0.016 and 0.067) and were not different among the two grouped communities and the ‘other sites’as shown by nonparametric tests (p-values between 0.417 and 0.856). Turbidity was significantly different between the grouped communities and the ‘other sites’ when using parametric ANOVA. However, the distributions of log-transformed turbidities were not normal ($p < 0.001$) nor were variances homogeneous ($p < 0.001$).

Mean turbidity was higher at the ‘other sites’ (Figure 4.24 b). Of the seasons, only spring and autumn samples proved to be significantly different in community structure. In spring, higher catches of roman and santer were recorded. In contrast to that, catches of roman dropped in autumn whereas those of fransmadam and steentjie increased.

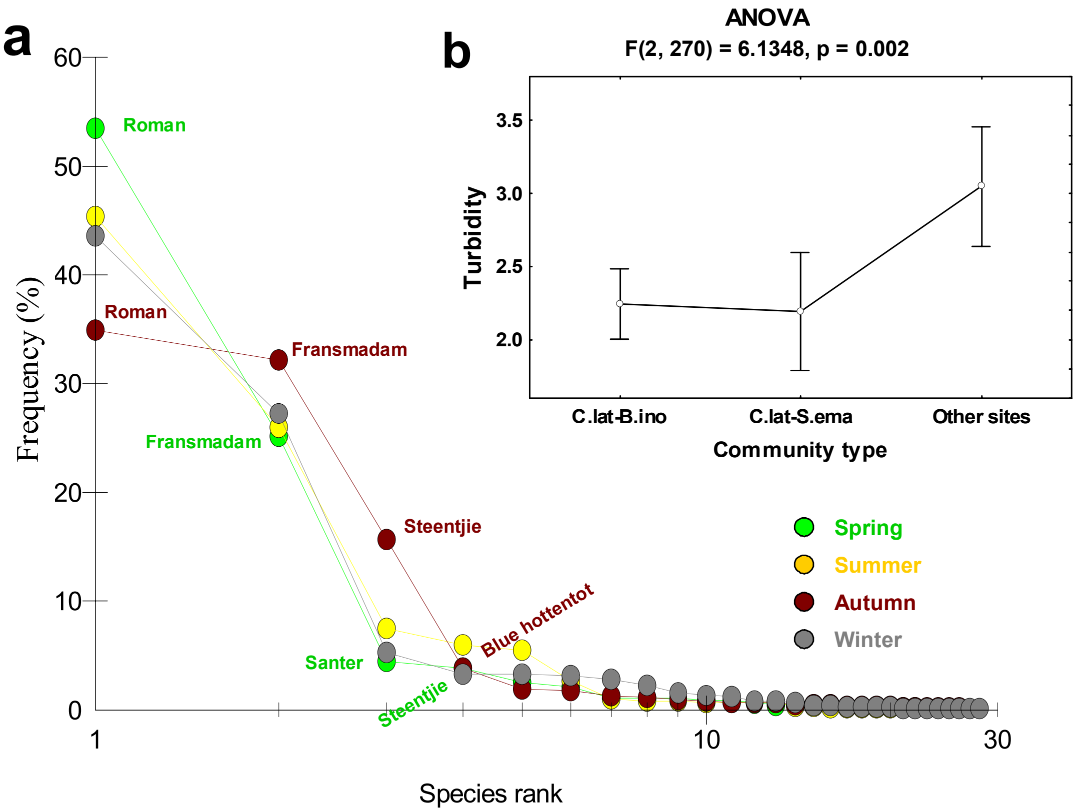
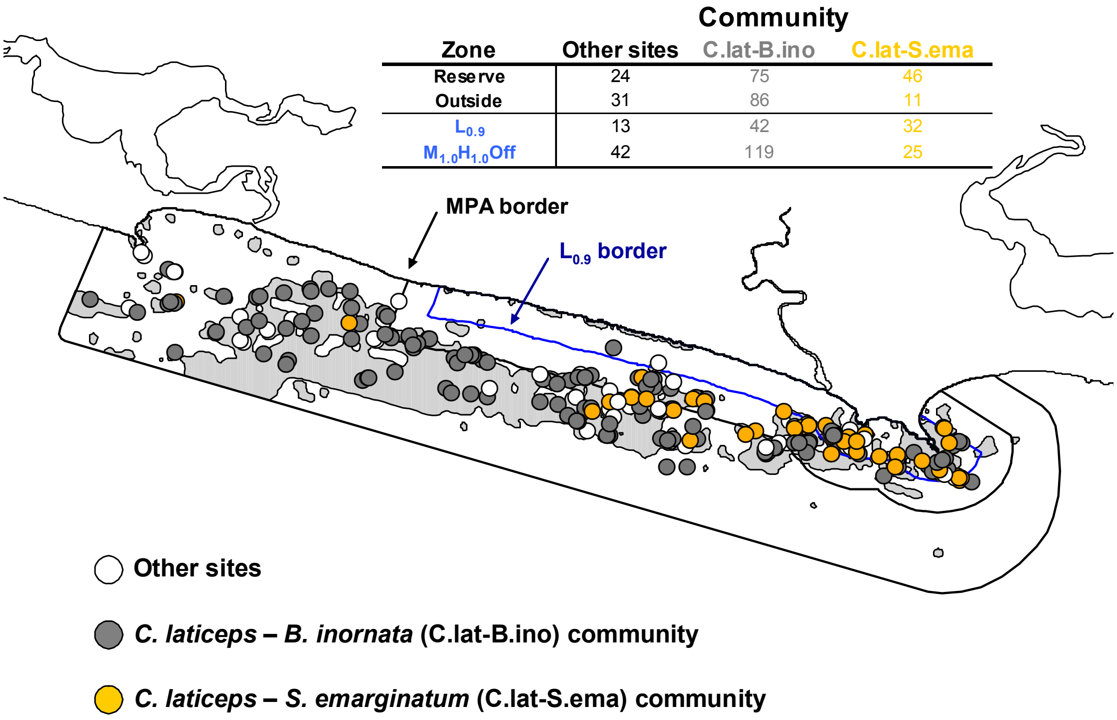


Figure 4.24: Influence of season (a) and turbidity (b) on the fish community using dominance plot and ANOVA test. Vertical bars denote 95% confidence intervals

The effect of spatial patterns on the occurrence of fish communities was investigated using chi-square contingency tables (Figure 4.25). An unequal distribution of fish communities over space can be clearly seen and was tested to be significant ($p < 0.001$) for the **Reserve/Outside** and **$L_{0.9}$/$M_{1.0}H_{1.0}$Off** zones.

The occurrence of C.lat-B.ino communities is reduced within the protected inshore zones and replaced by the C.lat-S.ema community. Distribution of the 'other sites' is random (Figure 4.25).



	Community		
Zone	Other sites	C.lat-B.ino	C.lat-S.ema
Reserve	24	75	46
Outside	31	86	11
$L_{0.9}$	13	42	32
$M_{1.0}H_{1.0}Off$	42	119	25

Figure 4.25: Map of the study area with distribution of the two groups of fish communities and the 'other sites' within two zoning patterns

GLMs were used to separate the effects of factors and zoning patterns on the distribution of the two grouped communities and the 'other sites'. All seven zoning patterns were combined with the factors, resulting in seven individual GLMs. In all seven models, turbidity (p-values between 0.007 and 0.019) and zone (all p-values smaller 0.001) had a significant effect on community type. Season was influential in five of the seven models with p-values between 0.032 and 0.071. Due to the high number of factors, GLMs of only five zoning patterns could be calculated using interaction terms. However, no significant interactions were detected for these five analysed zoning patterns.

In summary, the distribution of the two identified principle communities and the 'other sites' are influenced by turbidity, season and zones. Turbidity was higher at sites that had high dissimilarities in fish community structure ('other sites'). Spring and autumn had different community structures with higher levels of top-predators in spring. The occurrence of C.lat-S.ema communities was gradually reduced and replaced by C.lat-B.ino communities when moving from protected inshore to exploited offshore zones. The influence of factors and zones on the fish community can be clarified with a more detailed look at density patterns of individual species (see '***Densities of fish species***').

The diversity of the study area

To estimate the diversity within the study area, the Margalef richness, Shannon-Wiener diversity and the taxonomic diversity indices were calculated for the 273 sites. The influence of continuous factors like depth, temperature and turbidity were investigated by correlation (Table 4.6).

	Factor		
Index	**Depth**	**Temperature**	**Turbidity**
Margalef	0.290	N/A	0.204
Shannon-Weaver	0.208	N/A	N/A
Taxonomic diversity	0.331	-0.131	0.277

Table 4.6: Correlation coefficients among three physical factors and three richness and diversity indices. Correlations were significant at $p < 0.05$

Only weak and very weak correlations resulted with higher diversities in cold, turbid and deeper waters. The influence of categorical factors were investigated using parametric and non-parametric tests. Neither weather (p-values between 0.334 and 0.957) nor time of day (p-values between 0.231 and 0.982) had a significant effect on the three investigated diversity indices.

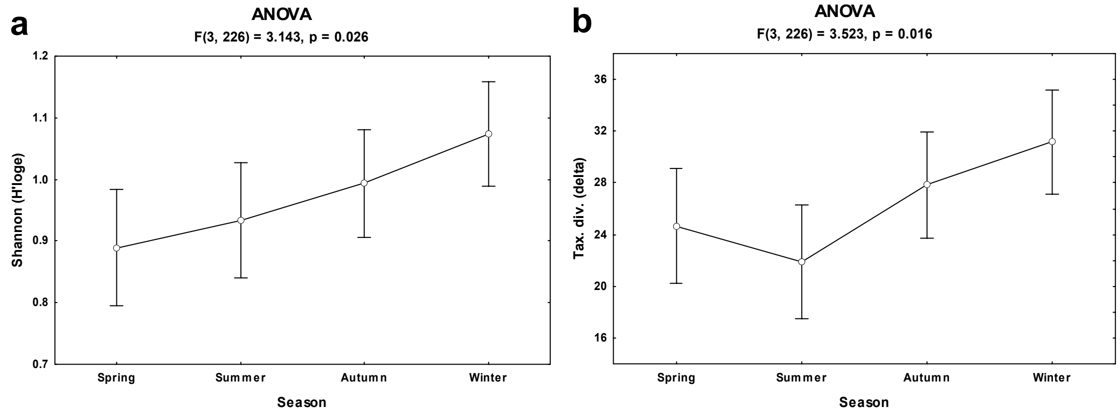


Figure 4.26: Influence of season on the Shannon-Wiener (a) and taxonomic (b) diversity index using ANOVA tests. Vertical bars denote the 95% confidence intervals

The Shannon-Wiener index increases consistently throughout the year, being lowest in spring and eventually significantly higher in winter (p = 0.026, figure 4.26 a). The distribution of indices was normal for all seasons and variances homogeneous. The taxonomic diversity index (delta) was lowest in summer and highest in winter, again being significantly different (p = 0.016, figure 4.26 b). Variances were homogeneous, however, the distribution of indices was not normal. A nonparametric test reconfirmed this result at a p-level of 0.009. The Margalef richness index showed the same pattern over season as the taxonomic diversity index when using parametric tests (p = 0.041). However, normality and homogeneity of variances could not be established after log-transformation and a nonparametric test did not confirm the result at this significance level.

The community of zones

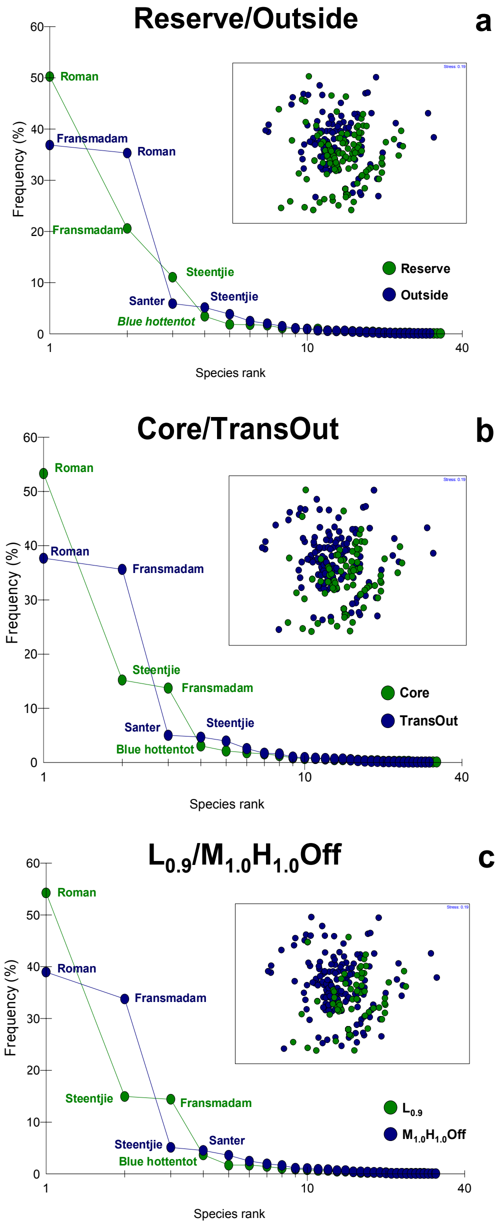


Figure 4.27: Dominance and MDS plots of fish species for the Reserve/Outside (a), the Core/TransOut (b) and the L$_{0.9}$/M$_{1.0}$H$_{1.0}$Off (c) zoning patterns

Irrespective of zoning patterns, the zones separate weakly in MDS plots, with the protected inshore zone dominating bottom right and exploited offshore zone top left (Figure 4.27). In terms of absolute dominance, the protected inshore and exploited offshore zones reveal similar patterns. In the protected inshore **Reserve**, **Core** and **L$_{0.9}$** zones roman-dominated and steentjie abundance was higher than usual. Abundances of fransmadam as well as of top-predators like santer and dageraad were decreased. This pattern becomes more obvious as the protected inshore zones get narrower (from **Reserve** towards **L$_{0.9}$**) with roman abundance increasing further and steentjie becoming the second most abundant species. The exploited offshore zones **Outside**, **TransOut** and **M$_{1.0}$H$_{1.0}$Off** are characterized by equal dominance of roman and fransmadam, resulting from a decrease and increase of abundances, respectively. Additionally, steentjie abundance was decreased and top-predators like santer and dageraad were increased in abundance. As the exploited offshore zones get broader, reaching further into protected inshore areas (from **Outside** towards **M$_{1.0}$H$_{1.0}$Off**) roman and steentjie abundances increased gradually. Communities of protected inshore zones as compared to their respective exploited offshore zones were significantly different as indicated by ANOSIM tests for all zoning patterns (p-values between 0.001 and 0.012).

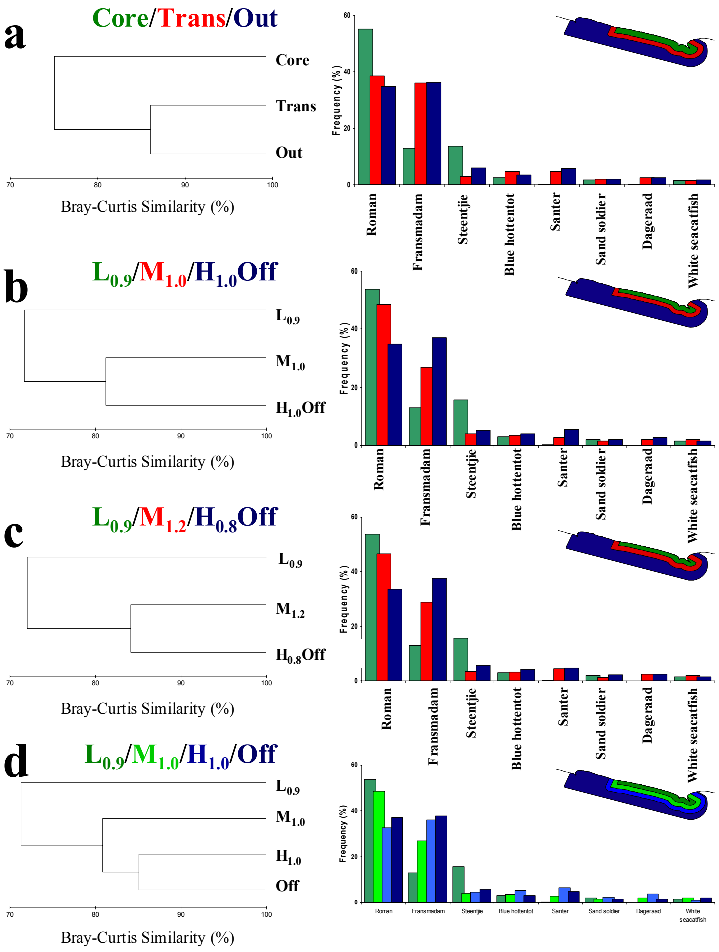


Figure 4.28: Cluster dendrograms and frequency graph of fish species for the Core/Trans/Out (a), the $L_{0.9}$/$M_{1.0}$/$H_{1.0}$Off (b), the $L_{0.9}$/$M_{1.2}$/$H_{0.8}$Off (c) and the $L_{0.9}$/$M_{1.0}$/$H_{1.0}$/Off (d) zoning patterns

Cluster dendrograms and frequency graphs of fish species for the three three-zone patterns **Core/Trans/Out**, **$L_{0.9}$/$M_{1.0}$/$H_{1.0}$Off** and **$L_{0.9}$/$M_{1.2}$/$H_{0.8}$Off** and the one four-zone pattern **$L_{0.9}$/$M_{1.0}$/$H_{1.0}$/Off** are shown in figure 4.28 a, b, c and d, respectively. Within each zoning pattern, similarities decrease consistently when comparing the protected inshore zones with their respective exploited offshore zones. This gradual change in community structure when moving from the protected inshore towards the exploited offshore zones is also evident in the frequency plots in figure 4.28. Generally, roman and steentjie frequencies decrease when moving from protected inshore to exploited offshore zones, with a slight increase of roman frequency in the **Off** zone and steentjie frequency in the outermost zones off each pattern. Frequencies of fransmadam, blue hottentot, santer and dageraad generally increase when moving from protected inshore to exploited offshore zones, with a slight decrease of blue hottentot frequency in the **Out** zone and blue hottentot, santer and dageraad frequencies in the **Off** zone.

The community of the **Core** zone was significantly different from the communities of the **Trans** and **Out** zones ($p < 0.001$) as shown by an ANOSIM test. However, communities of the **Trans** and **Out** zones were not different ($p = 0.250$). Analogously, the **L$_{0.9}$** zone was significantly different to the **M$_{1.0}$** and **M$_{1.2}$** zones, and the **H$_{1.0}$Off** and **H$_{0.8}$Off** zones (p-values of 0.020 and 0.016, and 0.001 and 0.001, respectively). The **M$_{1.0}$** and **H$_{1.0}$Off** as well as the **H$_{1.0}$** and **Off** zones were not significantly different ($p = 0.252$ and 0.787, respectively), however, the **M$_{1.2}$** and **H$_{0.8}$Off** zones were significantly different ($p = 0.005$).

The diversity of zones

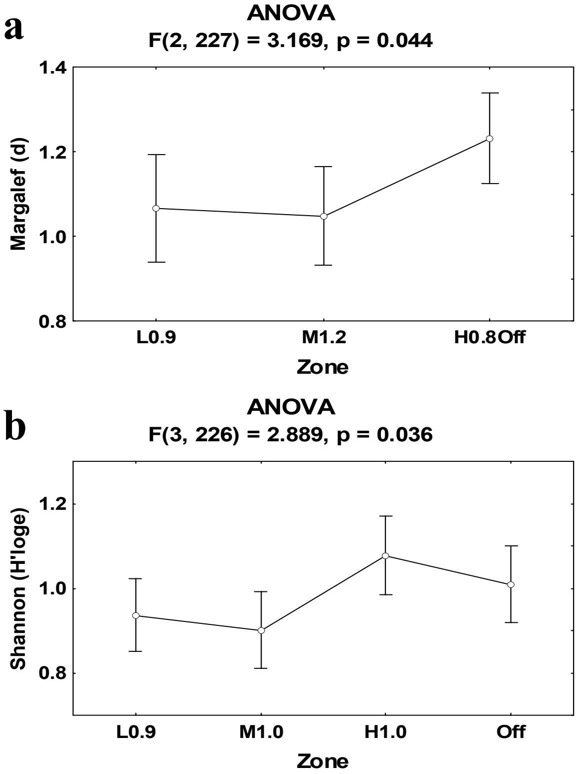
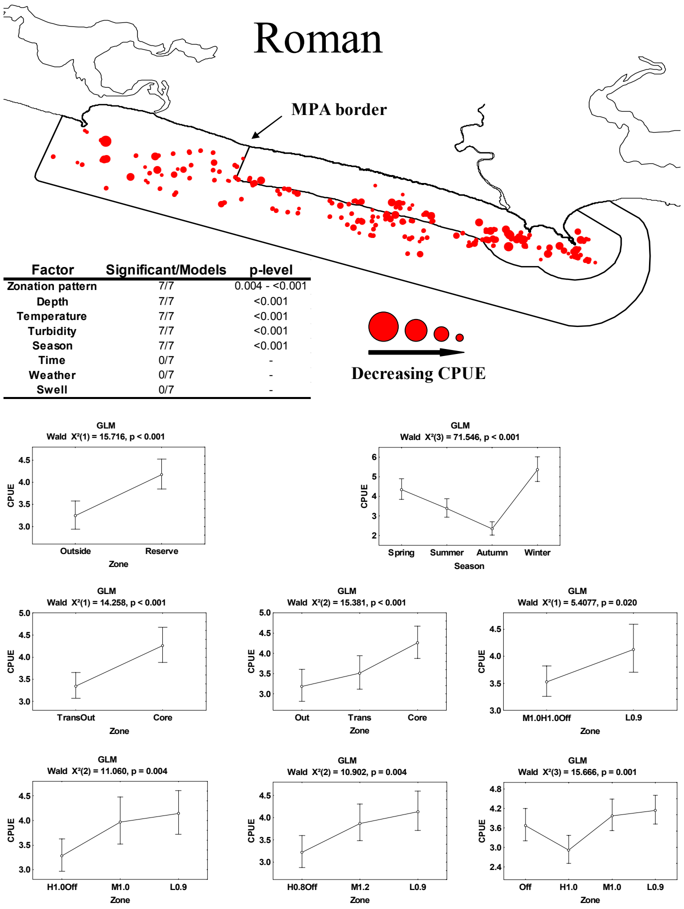


Figure 4.29: Difference of Margalef (a) and Shannon-Wiener diversity index (b) within two different zoning patterns, tested with ANOVA. Vertical bars denote 95% confidence intervals

To estimate the diversity within zoning patterns, the Margalef, Shannon-Wiener and the taxonomic diversity indices were calculated for the individual zones. In general, diversity indices tended to be lower in the protected inshore zones typically increasing across the MPA's borders to higher levels in the exploited offshore zones. This pattern was weakest in the taxonomic diversity index, where differences were small and never significant (p-values between 0.297 and 0.972) but more established in the Margalef diversity index with a significant difference ($p = 0.044$) in the **L$_{0.9}$/M$_{1.2}$/H$_{0.8}$Off** pattern (Figure 4.29 a). Otherwise p-values were between 0.141 and 0.455. The Shannon-Wiener diversity index was more sensitive and showed significant differences in three of the seven zoning patterns, with p-values of 0.004, 0.024 and 0.036 for the

$L_{0.9}$/$M_{1.2}$/$H_{0.8}$Off, **$L_{0.9}$/$M_{1.0}$/$H_{1.0}$Off** and **$L_{0.9}$/$M_{1.0}$/$H_{1.0}$/Off** patterns, respectively. Otherwise p-values were between 0.069 and 0.284. Figure 4.29 b shows the result for the **$L_{0.9}$/$M_{1.0}$/$H_{1.0}$/Off** pattern.

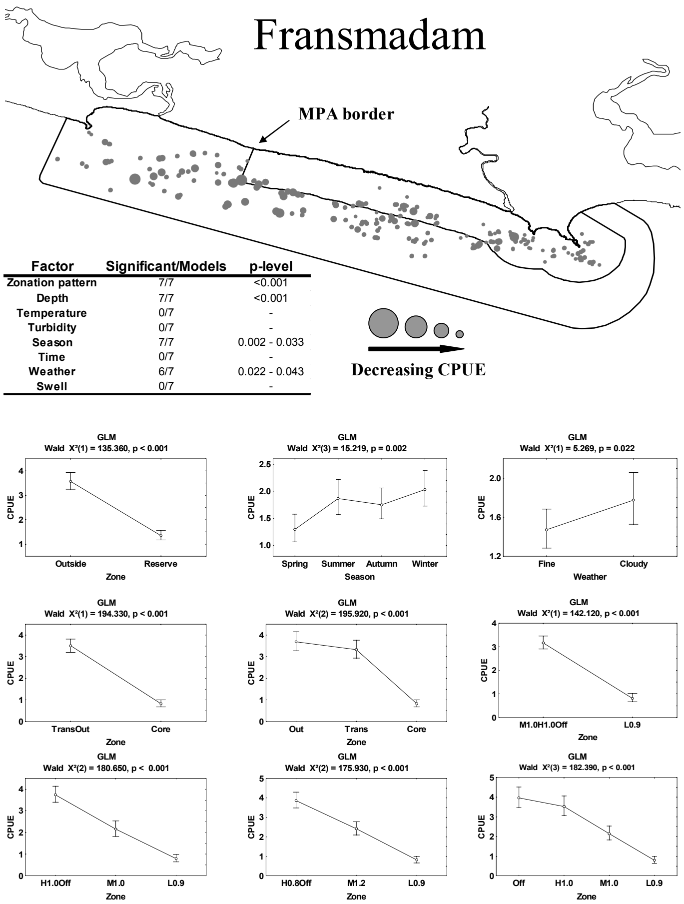
Densities of fish species



Factor	Significant/Models	p-level
Zonation pattern	7/7	0.004 - <0.001
Depth	7/7	<0.001
Temperature	7/7	<0.001
Turbidity	7/7	<0.001
Season	7/7	<0.001
Time	0/7	-
Weather	0/7	-
Swell	0/7	-

Figure 4.30: Abundance of roman (N = 1089) in the study area at 273 sites with results for the seven zoning patterns using GLMs. Vertical bars denote 95% confidence intervals

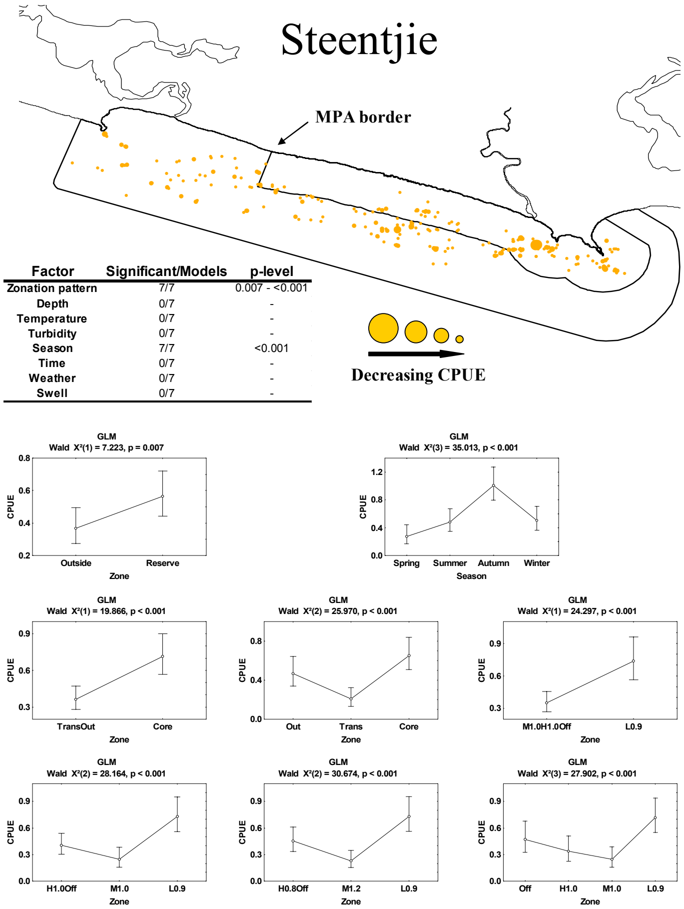
In all seven models depth, temperature and turbidity had a highly significant influence on roman CPUE ($p < 0.001$), with shallow reefs, low turbidity and warm water conditions supporting a higher CPUE (Figure 4.30). Season, as well, had a highly significant effect in all seven models ($p < 0.001$). CPUE was highest in winter and then consistently decreased throughout the year to less than half its initial value in autumn. Additionally, zone, irrespective of zoning pattern had a highly significant influence on CPUE (p-values between 0.004 and <0.001). Roman CPUE was high in the **$L_{0.9}$**, **Core** and **Reserve** zones, decreasing across the border of the MPA to lowest levels in the **$H_{1.0}$** zone, eventually slightly increasing in the **Off** zone (Figure 4.30). Interaction terms in GLMs of all zoning patterns could be calculated. Only season interacted consistently in all models (p-values between 0.046 and <0.001). The combination of protection and spring or summer yielded higher roman catches during controlled fishing.



Factor	Significant/Models	p-level
Zonation pattern	7/7	<0.001
Depth	7/7	<0.001
Temperature	0/7	-
Turbidity	0/7	-
Season	7/7	0.002 - 0.033
Time	0/7	-
Weather	6/7	0.022 - 0.043
Swell	0/7	-

Figure 4.31: Abundance of fransmadam (N = 687) in the study area at 273 sites with results for the seven zoning patterns using GLMs. Vertical bars denote 95% confidence intervals

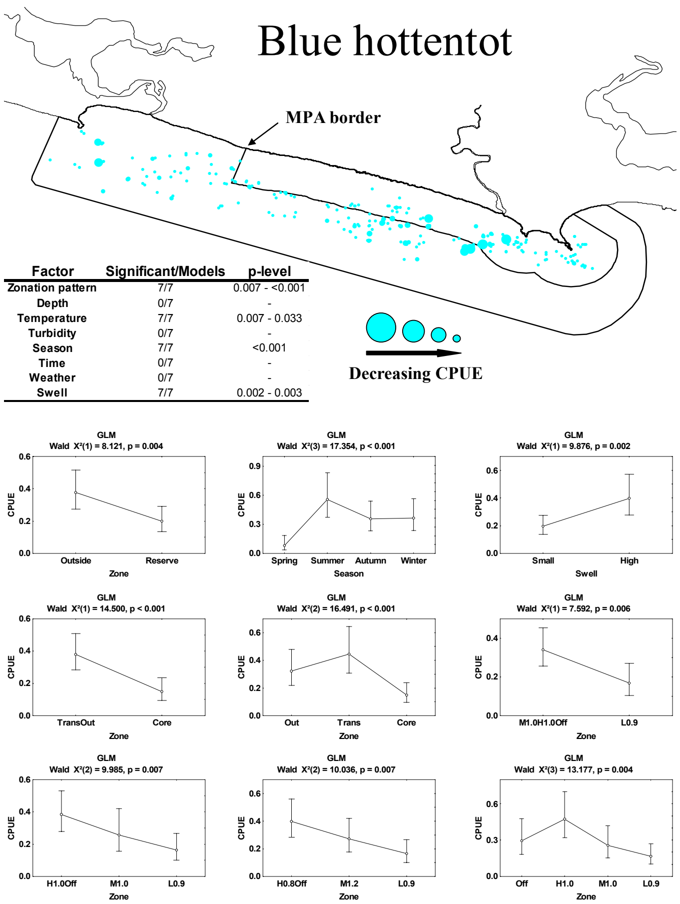
In all seven models depth had a highly significant influence on fransmadam CPUE ($p < 0.001$), with shallow reefs supporting a higher CPUE (Figure 4.31). Season, as well, had a significant effect in all seven models (p-values between 0.033 and 0.0023). CPUE was lowest in spring and increased towards summer. Weather had significant effect in six out of the seven models with p-values between 0.043 and 0.022. The CPUE was higher during cloudy conditions. Additionally, all zones, irrespective of zoning patterns, had a highly significant influence on CPUE ($p < 0.001$). Fransmadam CPUE was generally low in the **L$_{0.9}$**, **Core** and **Reserve** zones, increasing across the border of the MPA to highest levels in the **Off** zone (see graphs in figure 4.31). Other factors like time of day, temperature, turbidity or swell did not influence fransmadam CPUE. Of the main effects, only time of day interacted consistently in models. Six out of seven zoning pattern interacted strongly with time of day (p-values <0.001). The combination of exploitation and afternoon resulted in higher fransmadam catches.



Factor	Significant/Models	p-level
Zonation pattern	7/7	0.007 - <0.001
Depth	0/7	-
Temperature	0/7	-
Turbidity	0/7	-
Season	7/7	<0.001
Time	0/7	-
Weather	0/7	-
Swell	0/7	-

Figure 4.32: Abundance of steentjie (N = 201) in the study area at 273 sites with results for the seven zoning patterns using GLMs. Vertical bars denote 95% confidence intervals

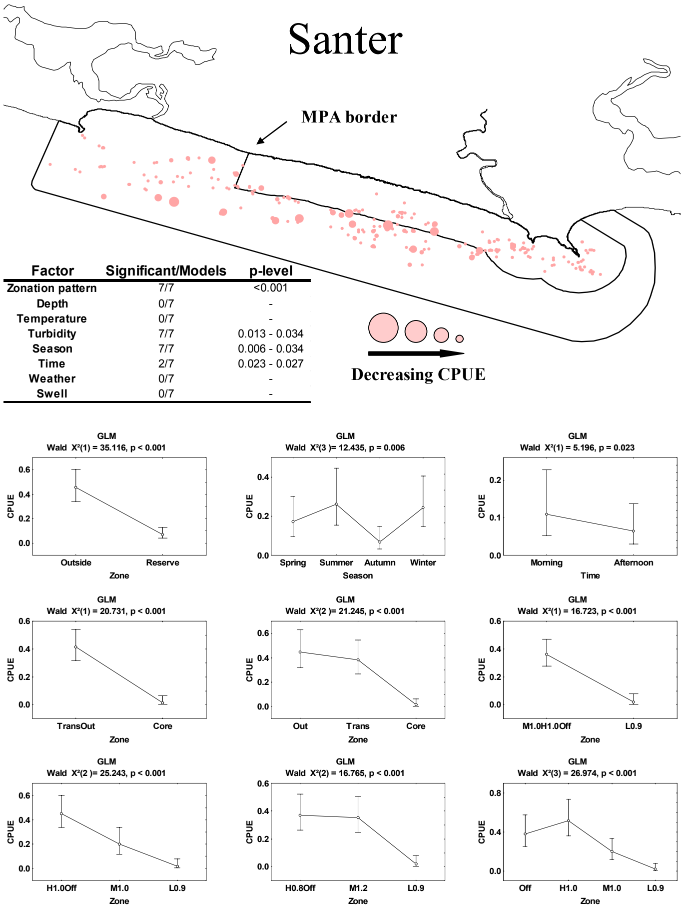
Season had a highly significant influence on steentjie CPUE ($p < 0.001$) in all seven models (Figure 4.32). CPUE was lowest in spring, increases over summer and reaches a maximum in autumn, being more than three times as high as in spring. Then, CPUE dropped to summer levels in winter. Additionally, all zones, irrespective of zoning patterns, had a highly significant influence on CPUE (p-values between 0.007 and <0.001). Steentjie CPUEs were generally high in the $\mathbf{L_{0.9}}$, **Core** and **Reserve** zones, decreasing fast across the border of the MPA to about half the initial level in the **Trans**, $\mathbf{M_{1.0}}$ and $\mathbf{M_{1.2}}$ zones then increasing slowly across the $\mathbf{H_{1.0}}$ zone to a mid-level CPUE in the **Off** zone (see graphs in figure 4.32). Other factors like time of day, depth, temperature, turbidity, weather or swell did not influence steentjie CPUE. Season interacted significantly in all zoning patterns (p-values <0.001). Steentjie CPUE was higher at protected sites during autumn.



Factor	Significant/Models	p-level
Zonation pattern	7/7	0.007 - <0.001
Depth	0/7	-
Temperature	7/7	0.007 - 0.033
Turbidity	0/7	-
Season	7/7	<0.001
Time	0/7	-
Weather	0/7	-
Swell	7/7	0.002 - 0.003

Figure 4.33: Abundance of blue hottentot (N = 89) in the study area at 273 sites with results for the seven zoning patterns using GLMs. Vertical bars denote 95% confidence intervals

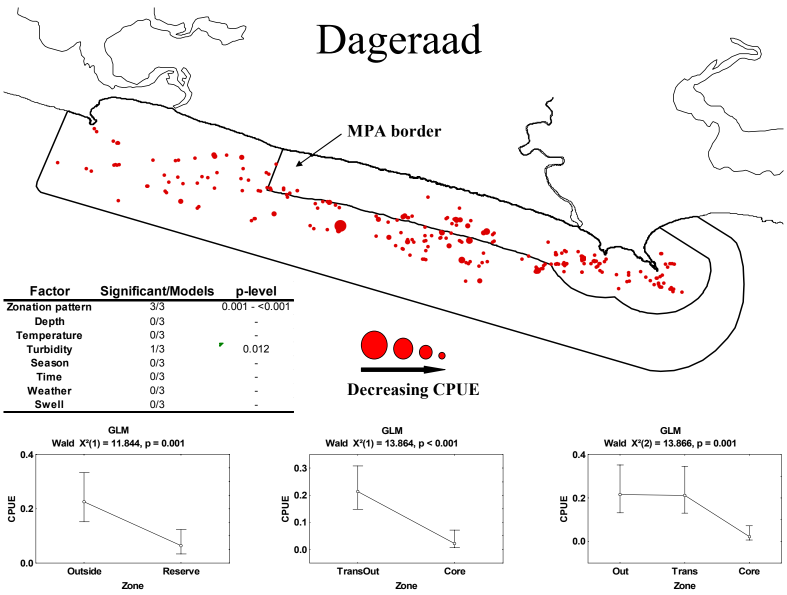
In all seven models season had a highly significant influence on blue hottentot CPUE ($p < 0.001$, figure 4.33). CPUE was lowest in spring reaching a maximum in summer, being more than five times as high as in spring. CPUE then dropped to mid-levels in autumn and winter. Swell height had a significant influence on CPUE as well, with higher swells supporting higher CPUE (p-values between 0.003 and 0.002). Higher seawater temperatures as well resulted in a higher CPUE for blue hottentot in all seven models (p-values between 0.033 and 0.007). Additionally, all zones, irrespective of zoning patterns, had a highly significant influence on CPUE (p-values between 0.007 and <0.001). Blue hottentot CPUE was generally low in the **$L_{0.9}$**, **Core** and **Reserve** zones, increasing moderately across the border of the MPA in the **$M_{1.0}$** and **$M_{1.2}$** zones and eventually reaching a maximum in the **$H_{1.0}$** and **Trans** zones with twice to three times the initial level. CPUE dropped slightly in the **Out** and **Off** zones (see figure 4.33). Due to missing cell values, GLMs of only four zoning patterns could be calculated using interaction terms. Of the main effects, only depth interacted consistently in models. (p-values between 0.009 and 0.002). During controlled fishing deeper reefs that were exploited yielded a higher blue hottentot CPUE.



Factor	Significant/Models	p-level
Zonation pattern	7/7	<0.001
Depth	0/7	-
Temperature	0/7	-
Turbidity	7/7	0.013 - 0.034
Season	7/7	0.006 - 0.034
Time	2/7	0.023 - 0.027
Weather	0/7	-
Swell	0/7	-

Figure 4.34: Abundance of santer (N = 83) in the study area at 273 sites with results for the seven zoning patterns using GLMs. Vertical bars denote 95% confidence intervals

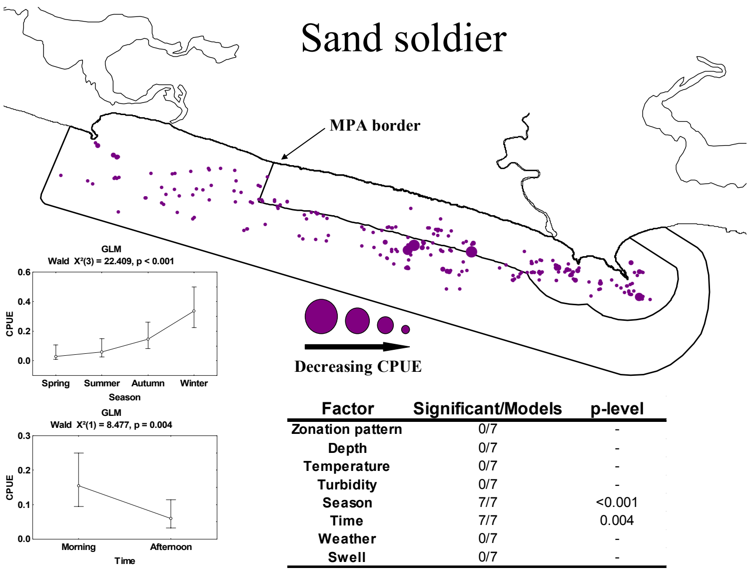
Season had a highly significant influence on santer CPUE in all seven models (p-values between 0.006 and 0.034, figure 4.34). CPUE was low in spring reaching a maximum in summer, dropping to its lowest level in autumn and rising again towards winter. Time had a significant influence on CPUE in two of the seven models, with higher CPUE in the morning (p-values between 0.023 and 0.027). Higher seawater turbidities resulted in a significant decrease in CPUE for santer in all seven models (p-values between 0.013 and 0.034). Additionally, all zones, irrespective of zoning patterns, had a highly significant influence on CPUE ($p < 0.001$). Santer CPUE was generally low in the $\mathbf{L_{0.9}}$, **Core** and **Reserve** zones increasing moderately towards the $\mathbf{M_{1.0}}$ zone but faster in the $\mathbf{M_{1.2}}$, $\mathbf{H_{1.0}}$ and **Trans** zones with many times the initial level. Maximum levels were reached in the $\mathbf{H_{1.0}}$, **Out**, $\mathbf{H_{0.8}Off}$ and $\mathbf{H_{1.2}Off}$ zones. CPUE dropped slightly in the **Off** zone (see figure 4.34). Due to the small sample size, GLMs for interaction terms could not be calculated.



Factor	Significant/Models	p-level
Zonation pattern	3/3	0.001 - <0.001
Depth	0/3	-
Temperature	0/3	-
Turbidity	1/3	0.012
Season	0/3	-
Time	0/3	-
Weather	0/3	-
Swell	0/3	-

Figure 4.35: Abundance of dageraad (N = 42) in the study area at 273 sites with results for the seven zoning patterns using GLMs. Vertical bars denote 95% confidence intervals

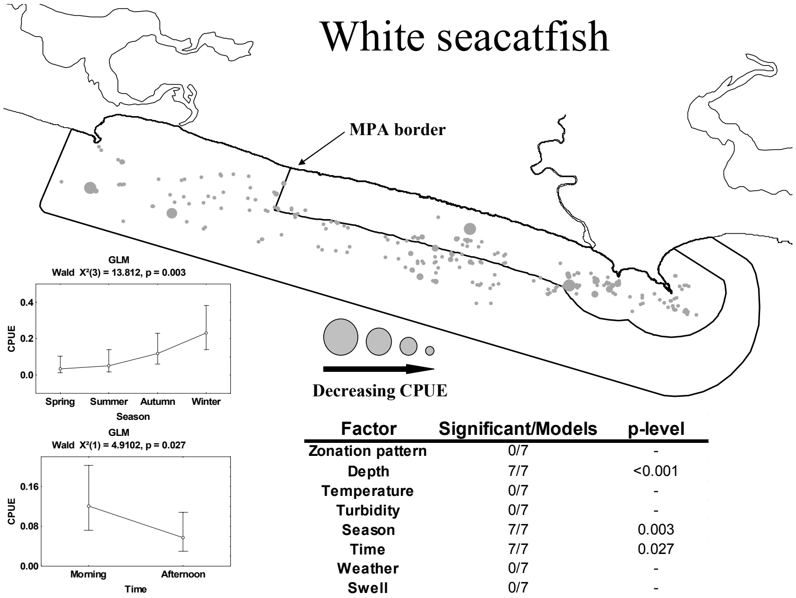
Due to the small sample size, missing cell values only allowed the computation of three models (Figure 4.35). In only one of the three models turbidity had a significant influence on dageraad CPUE (p = 0.012). Higher seawater turbidities resulted in a significant decrease in CPUE. Zones, using three computable zoning patterns, had a highly significant influence on CPUE (p-values between 0.001 and <0.001). Dageraad CPUE was very low in the **Core** and **Reserve** zones increasing more than fivefold towards the **Trans**, **TransOut** and **Outside** zones (see graphs in figure 4.35). Other factors like depth, temperature, swell, time of day, season or weather did not influence dageraad CPUE. GLMs using interaction terms were compromised by the small sample size and only one zoning patterns could be calculated. None of the main effects interacted with the analysed zoning pattern.



Factor	Significant/Models	p-level
Zonation pattern	0/7	-
Depth	0/7	-
Temperature	0/7	-
Turbidity	0/7	-
Season	7/7	<0.001
Time	7/7	0.004
Weather	0/7	-
Swell	0/7	-

Figure 4.36: Abundance of sand soldier (N = 47) in the study area at 273 sites with results for the seven zoning patterns using GLMs. Vertical bars denote 95% confidence intervals

In all seven models season had a highly significant influence on sand soldier CPUE ($p < 0.001$, figure 4.36). CPUE was lowest in spring, increasing consistently throughout the year and reaching highest levels in winter, with more than tenfold the original level. Additionally, time of day had a highly significant ($p = 0.004$) influence on CPUE in all seven models. Sand soldier CPUE was higher in the morning (see figure 4.36). Other factors like depth, temperature, turbidity, swell and weather as well as all of the zones did not have an influence on sand soldier CPUE. Due to missing cell values, GLMs of only three zoning patterns could be calculated using interaction terms. Of the main effects, only swell interacted consistently in the three computable models. (p-values between 0.034 and 0.005). The combination of exploitation and small swells resulted in higher steentjie CPUE.



Factor	Significant/Models	p-level
Zonation pattern	0/7	-
Depth	7/7	<0.001
Temperature	0/7	-
Turbidity	0/7	-
Season	7/7	0.003
Time	7/7	0.027
Weather	0/7	-
Swell	0/7	-

Figure 4.37: Abundance of white seacatfish (N = 41) in the study area at 273 sites with results for the seven zoning patterns using GLMs. Vertical bars denote 95% confidence intervals

A highly significant influence of season on white seacatfish CPUE was recorded in all seven models (p = 0.003, figure 4.37). CPUE was lowest in spring, increasing consistently throughout the year and reaching highest levels in winter, with more than tenfold the original level. Additionally, time of day and depth had a significant (p = 0.027 and <0.001, respectively) influence on CPUE in all seven models. White seacatfish CPUE was higher in the morning and at deeper sites (see figure 4.37). No influence of zones on white seacatfish CPUE was detected. Due to the small sample size, GLMs of only two zoning patterns could be calculated using interaction terms. None of the main effects interacted consistently in the two computable models.

In summary, abundances of sand soldier and white seacatfish were not influenced by zones. Abundances of roman and steentjie were generally high at protected inshore sites and low at exploited offshore sites, with a slight decrease in the **Off** zone. Abundances of fransmadam, blue hottentot, santer and dageraad showed the opposite pattern, with low CPUE at protected inshore sites and high CPUE at exploited offshore sites. The CPUE for roman and fransmadam was higher at shallower sites but lower for white seacatfish. Higher temperatures resulted in an increase in CPUE for roman and blue hottentot. Turbid seawater resulted in a decrease of abundance for roman, santer and dageraad. Season had an influence on CPUE for all species but dageraad with lowest levels in spring. Maximum CPUE was reached in winter except for steentjie and blue hottentot, where highest levels were attained during autumn and summer, respectively (Table 4.7).

	Factor							
Species	**Zone**	**Season**	**Time**	**Depth**	**Temperature**	**Turbidity**	**Weather**	**Swell**
Roman	Inshore	Winter	-	shallow	high	low	-	-
Fransmadam	Offshore	Winter	-	shallow	-	-	cloudy	-
Steentjie	Inshore	Autumn	-	-	-	-	-	-
Blue hottentot	Offshore	Summer	-	-	high	-	-	high
Santer	Offshore	Winter	morning	-	-	low	-	-
Dageraad	Offshore	-	-	-	-	low	-	-
Sand soldier	-	Winter	morning	-	-	-	-	-
White seacatfish	-	Winter	morning	deep	-	-	-	-
All	Offshore	Winter	-	shallow	high	low	-	-

Table 4.7: Influence of factors on the CPUE of the eight most abundant and all 37 species caught in the study area. Factor codes indicate significantly higher CPUE ($p < 0.05$)

4.3.3 Ichthyofauna from UVC

The community of the study area

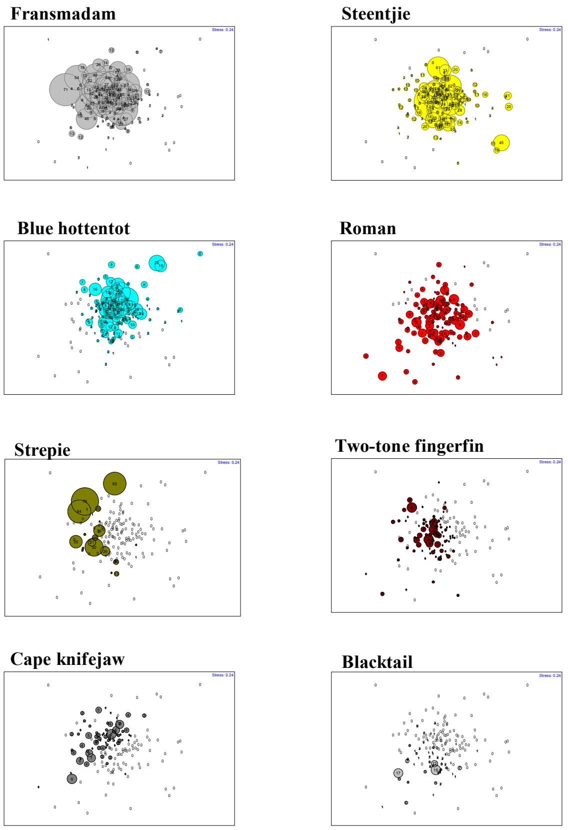


Figure 4.38: MDS plots of 177 point counts with superimposed abundances of eight fish species. The size of circles indicate relative abundance for that particular species, but are not comparable between species

In all eight MDS plots, higher counts, as indicated by larger bubbles, were found at similar sites, indicating the presence of different communities (Figure 4.38). However, highest counts for most species were found in the centre of the MDS plot and the total abundances of the eighth most abundant species varied largely, from 2499 for fransmadam to 162 for blacktail. This makes it difficult to group species into communities using this type of analysis. However, the high abundance of fransmadam and steentjie, with more than twice and three times the number of the next most abundant species, respectively, indicates their potential for dominating fish communities. Additionally, fransmadam is found in the centre-left part and steentjie in the centre-right part of the MDS plot, illustrating a possible dominance of each fish species in different fish communities. Finally, high numbers of strepie found in an area of the MDS plot underlines some importance of this fish species in the characterization of the fish community (see figure 4.38). However, only seven sites had high abundances, and they were interspersed with large numbers of low density sites.

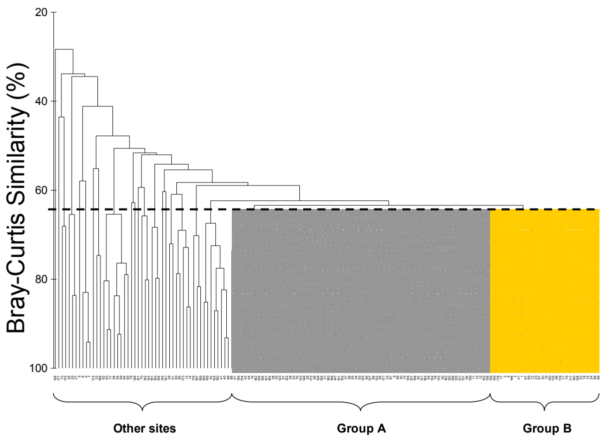
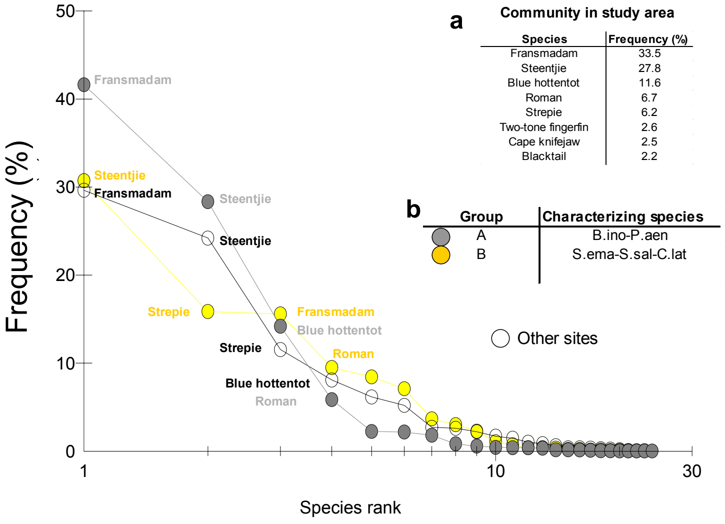


Figure 4.39: Cluster dendrogram indicating similarities of 177 point counts



a Community in study area

Species	Frequency (%)
Fransmadam	33.5
Steentjie	27.8
Blue hottentot	11.6
Roman	6.7
Strepie	6.2
Two-tone fingerfin	2.6
Cape knifejaw	2.5
Blacktail	2.2

b

Group	Characterizing species
● A	B.ino-P.aen
● B	S.ema-S.sal-C.lat

○ Other sites

Figure 4.40: Dominance plots of the three identified groups of fish (a) and table summarizing frequencies in the whole study area (b)

A cluster dendrogram based on Bray-Curtis similarities in percent calculated for the 177 point counts is shown in figure 4.39. At a cut-off-level of 65%, two principal groups can be identified. A SIMPER test revealed that similarities within group A and B were equally high, with 51.4 and 52.3%, respectively.

Fransmadam and steentjie are by far the most abundant species with more than 60% frequency of occurrence combined, followed by blue hottentot with only one tenth of all fish caught (Figure 4.40 a). Then follow roman and strepie with about half that frequency of occurrence and eventually two-tone fingerfin, cape knifejaw and blacktail.

Group B (yellow line in figure 4.40 b) differs from the general abundance pattern. Fransmadam drops in abundance to about half of its overall occurrence. Abundance of steentjie increases to become the dominant species of this group and strepie more than doubles in frequency of occurrence. Roman reaches its highest frequency of occurrence in this group. Therefore, group B was identified as *S. emarginatum – S. salpa - C.*

laticeps (S.ema-S.sal-C.lat) community. Group A (grey line in figure 4.40 b) follows the general abundance pattern of the community in the study area (figure 4.40 a). However, the abundance of fransmadam and blue hottentot are increased by about one third and abundance of strepie dramatically decreases to less than one tenth of its overall frequency. Group B was identified as the *B. inornata* – *P. aeneum* (B.ino-P.aen) community. The 'other sites' (black line in figure 4.40 b) also follow the general abundance pattern of the community in the study area. But here, the abundances of the first three species are decreased considerably and strepie abundance is twice as high. However, these fish communities are heterogeneous and the differences in abundances of individual species should not be generalized.

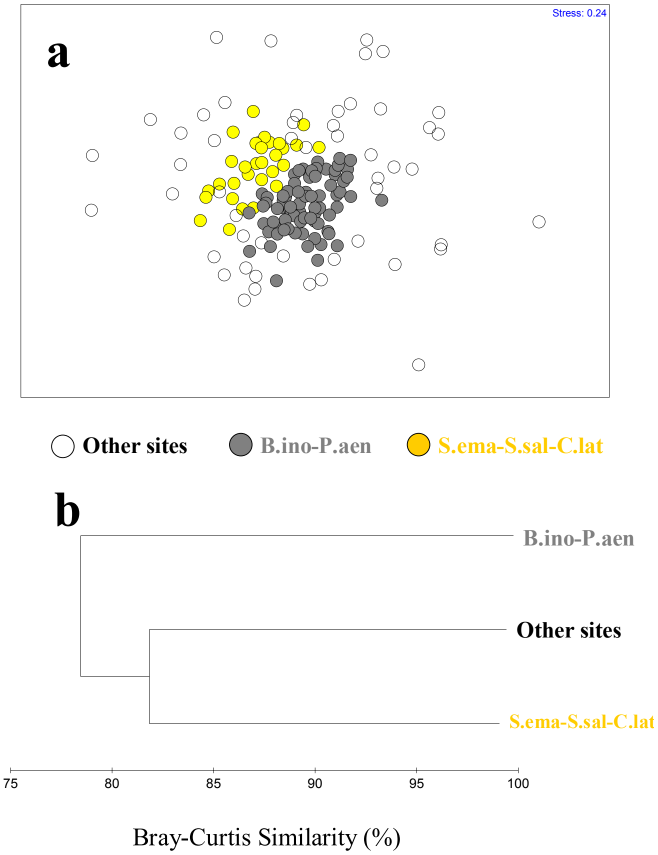


Figure 4.41: MDS plot (a) and cluster dendrogram (b) of the three groups of fish communities

An MDS plot of the two identified communities, clearly separates the B.ino-P.aen and the S.ema-S.sal-C.lat communities into two different corners of the plot area, but the 'other sites' are not an homogeneous grouping (Figure 4.41 a). Underlying similarity percentages in the cluster dendrogram in figure 4.41 b were 76.5 between the B.ino-P.aen and the S.ema-S.sal-C.lat communities, 80.4 between the B.ino-P.aen community and the 'other sites' and 81.8 between the 'other sites' and the S.ema-S.sal-C.lat community.

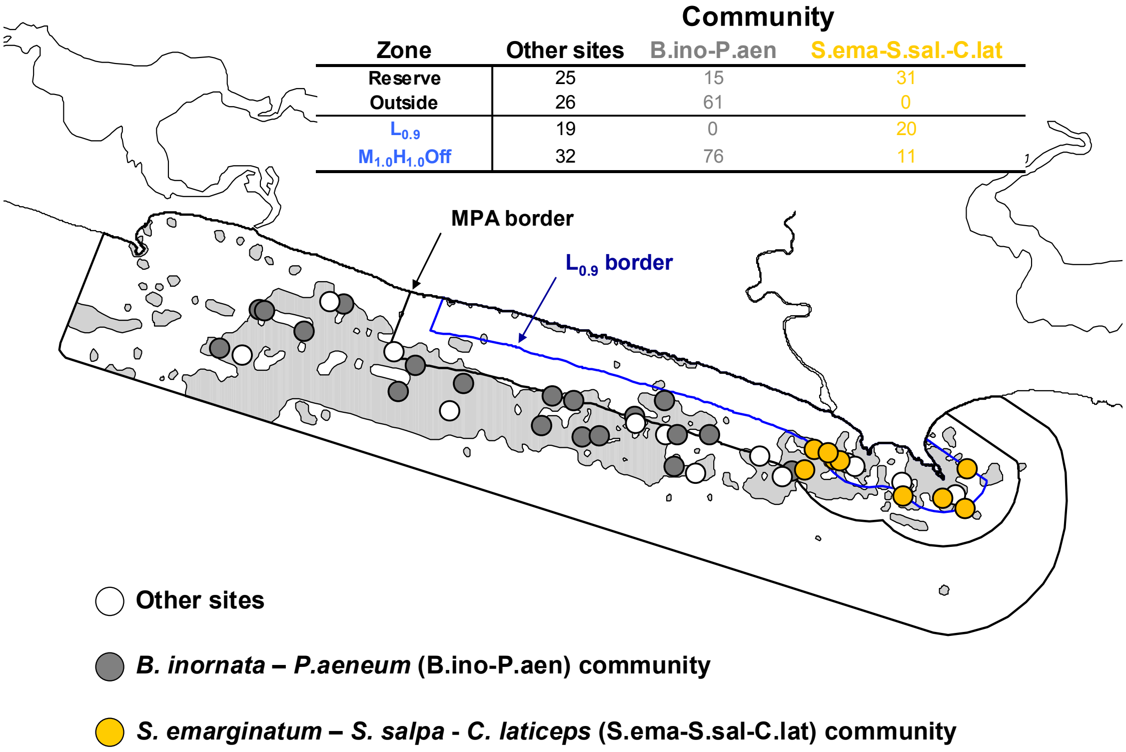
The reasons for these differences can be investigated by analysis of the potentially relevant factors. These were time of day, benthos, bottom, rugosity, surge, temperature, turbidity, depth, visibility, profile and spatial distribution (zoning patterns). The influence of factors on community structure, tested with ANOSIM and BIOENV (Table 4.8).

	Analysis type	
Factor	ANOSIM (p-value)	BIOENV (r-value)
Time	0.085	N/A
Benthos	0.744	N/A
Bottom	0.063	N/A
Rugosity	0.896	N/A
Surge	0.136	N/A
Temperature	N/A	0.239
Turbidity		
Visibility		

Table 4.8: Influence of factors on community structure using ANOSIM and BIOENV

None of the categorical factors had a significant influence on community structure with p-values between 0.063 and 0.896. Of the continuous factors, the combination of temperature, turbidity and visibility correlated strongest of all possible selections with community structure. However, with an r-value of 0.239, this correlation was only weak.

The effect of spatial patterns on the occurrence of fish communities was investigated using chi-square contingency tables. An unequal distribution of fish communities over space can be clearly seen and was tested to be significant for the investigated **Reserve/Outside** and **$L_{0.9}$/$M_{1.0}H_{1.0}$Off** zones ($p < 0.001$, figure 4.42). The occurrence of the B.ino-P.aen community is reduced within the protected inshore zones and replaced by the S.ema-S.sal.-C.lat community. Distribution of the ‘other sites’ is random (see figure 4.42).



	Community		
Zone	Other sites	B.ino-P.aen	S.ema-S.sal.-C.lat
Reserve	25	15	31
Outside	26	61	0
$L_{0.9}$	19	0	20
$M_{1.0}H_{1.0}$Off	32	76	11

Figure 4.42: Map of the study area with distribution of the three groups of fish communities within two zoning patterns

In summary, the distribution of the three identified principle communities are only influenced by zones. The influence of factors and zones on the fish community can be clarified with a more detailed look at density patterns of individual species (see '***Densities of fish species***').

The diversity of the study area

To estimate the diversity within the study area, the Margalef richness, Shannon-Wiener and the taxonomic diversity indices were calculated for the 177 point counts. The influence of continuous factors like depth, temperature, turbidity, profile, and visibility were investigated by correlation (Table 4.9).

	Factor				
Index	**Depth**	**Temperature**	**Turbidity**	**Profile**	**Visibility**
Margalef	-0.210	0.392	N/A	0.200	0.181
Shannon-Weaver	N/A	0.387	N/A	0.294	N/A
Taxonomic diversity	N/A	0.301	N/A	0.209	N/A

Table 4.9: Correlation coefficients among five physical factors and three richness and diversity indices. Correlations were significant at $p < 0.05$

Only weak and very weak correlations resulted with higher diversities in shallower, warmer waters and high profile reefs. The influence of categorical factors were investigated using parametric and non-parametric tests. Neither rugosity (p-values between 0.687 and 0.991) nor surge (p-values between 0.280 and 0.962) had a significant effect on the three investigated diversity indices. Although the Margalef richness and taxonomic diversity indices were not influenced by time of day or bottom type (p-values 0.174 / 0.297 and 0.071 / 0.290, respectively), the Shannon-Wiener diversity index showed to be significantly different (p-values of 0.025 and 0.015, respectively) with higher diversities of fish observed in the morning and on rocky substrate (Figure 4.43 a and b, respectively).

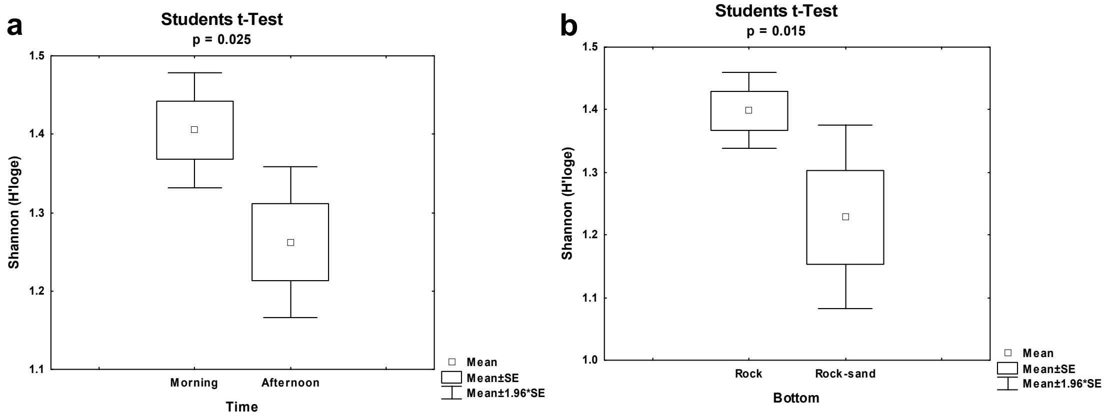


Figure 4.43: Influence of time of day and bottom on the Shannon-Wiener diversity and Margalef's richness index

The community of zones

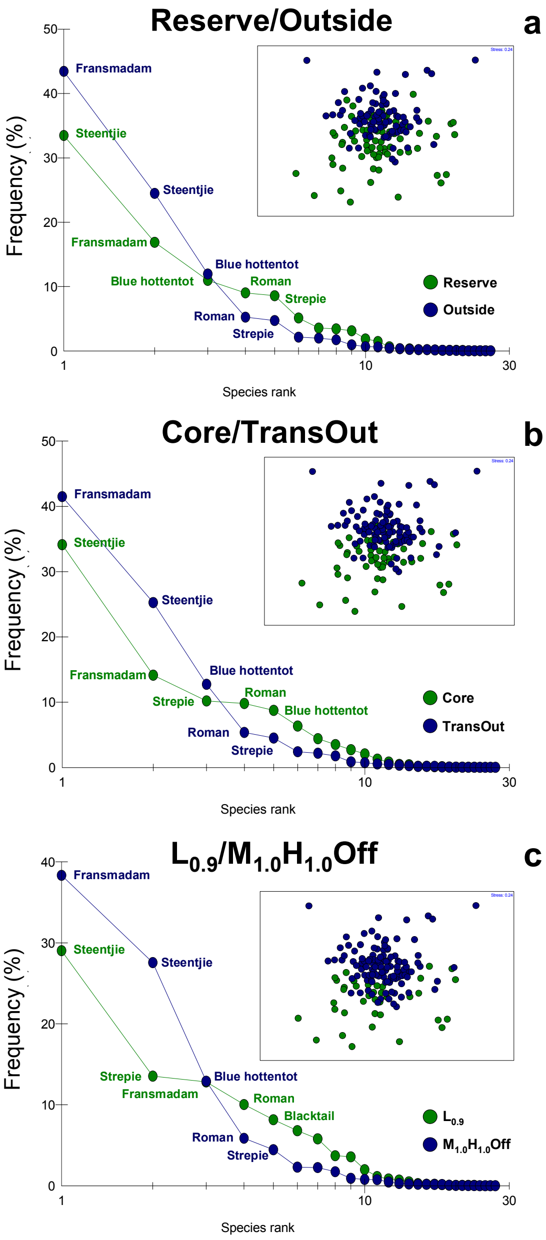


Figure 4.44: Dominance and MDS plots of fish species for the Re/Os (a), the Core/TransOut (b) and the $L_{0.9}/M_{1.0}H_{1.0}$Off (c) zoning patterns

In all three MDS pots, the protected inshore zones can be found in the lower part of the plot area, considerably separated in similarity from the exploited offshore zones (Figure 4.44). In terms of absolute dominance, the protected inshore and exploited offshore zones reveal similar patterns. The protected inshore **Reserve**, **Core** and **$L_{0.9}$** zones are characterized by higher abundances of steentjie, strepie, roman and blacktail. This pattern becomes more obvious as the protected inshore zones get narrower (from **Reserve** towards **$L_{0.9}$**) with roman abundance increasing further and strepie becoming the second most abundant species. In the narrow **$L_{0.9}$** zone, the protected inshore species blacktail surpasses blue hottentot in abundance. The exploited offshore zones **Outside**, **TransOut** and **$M_{1.0}H_{1.0}$Off** are characterized by a dominance of fransmadam and an increase of blue hottentot abundance. Communities of protected inshore zones compared to exploited offshore zones were significantly different as indicated by ANOSIM tests ($p < 0.001$) for all zoning patterns.

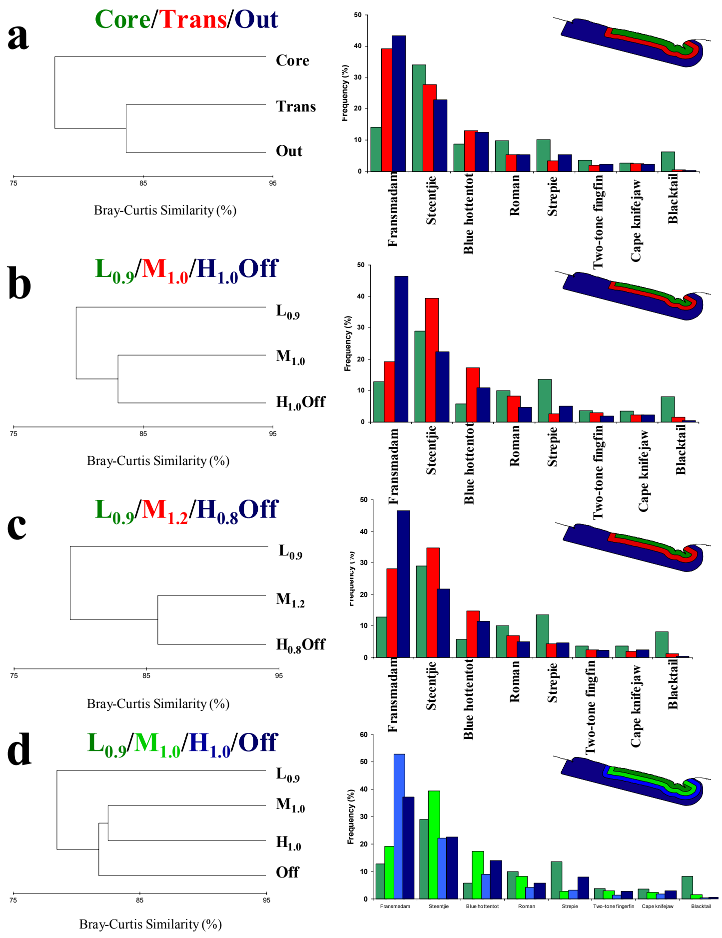


Figure 4.45: Cluster dendrograms and frequency graph of fish species for the Core/Trans/Out (a), the $L_{0.9}$/$M_{1.0}$/$H_{1.0}$Off (b), the $L_{0.9}$/$M_{1.2}$/$H_{0.8}$Off (c) and the $L_{0.9}$/$M_{1.0}$/$H_{1.0}$/Off (d) zoning patterns

Cluster dendrograms and frequency graphs of fish species for the three three-zone patterns **Core/Trans/Out**, **$L_{0.9}$/$M_{1.0}$/$H_{1.0}$Off** and **$L_{0.9}$/$M_{1.2}$/$H_{0.8}$Off** and the one four-zone pattern **$L_{0.9}$/$M_{1.0}$/$H_{1.0}$/Off** are presented in figure 4.45 a, b, c and d, respectively. Within each zoning pattern, similarities decrease consistently when comparing the protected inshore zones with their respective exploited offshore zones. The **Off** zone, however, is more similar to the **$L_{0.9}$** zone. This gradual change in community structure when moving from the protected inshore towards the exploited offshore zones with the exception of the **Off** zone is also evident in the frequency plots in figure 4.45. Generally, roman and steentjie frequencies decreased when moving from protected inshore to exploited offshore zones, with a slight increase of roman frequency in the **Off** and steentjie frequency in the **$M_{1.0}$** and **$M_{1.2}$** zones. Frequencies of fransmadam and blue hottentot generally increased when moving from protected inshore to exploited offshore zones, with a slight increase of blue hottentot frequency in the **$M_{1.0}$** and **$M_{1.2}$** zones.

The community of the **Core** zone was significantly different from the communities of the **Trans** and **Out** zones ($p < 0.001$) as shown by an ANOSIM test. However, communities of the **Trans** and **Out** zones were not different ($p = 0.184$). Analogously, the **$L_{0.9}$** zone was significantly different to the **$M_{1.0}$** zone and the **$H_{1.0}$Off** zone ($p < 0.001$). The **$M_{1.0}$** and **$H_{1.0}$Off** zones were not significantly different ($p = 0.063$). The communities of all zones in the **$L_{0.9}$/$M_{1.2}$/$H_{0.8}$Off** and the **$L_{0.9}$/$M_{1.0}$/$H_{1.0}$/Off** patterns were significantly different from each other with p-values between 0.045 and <0.001.

The diversity of zones

To estimate the diversity of zones, the Margalef richness, Shannon-Wiener and the taxonomic diversity indices were calculated for the individual zones. In general, diversity and richness indices tended to be higher in the protected inshore zones typically decreasing across the MPA's borders to lower levels in the exploited offshore zones. This pattern was weakest in the Margalef richness index, where differences were small and never significant (p-values between 0.109 and 0.426) but more established in the Shannon-Wiener diversity index with five significant results from the seven zoning patterns (p-values between 0.004 and 0.040). The taxonomic diversity index was more sensitive and showed significant differences in all of the seven zoning patterns, with p-values between 0.010 and <0.001. Figure 4.46 visualizes these trends for the Margalef richness index and the significant differences for the Shannon-Wiener and taxonomic diversity indices using the most detailed zoning pattern (**$L_{0.9}$/$M_{1.0}$/$H_{1.0}$/Off**).

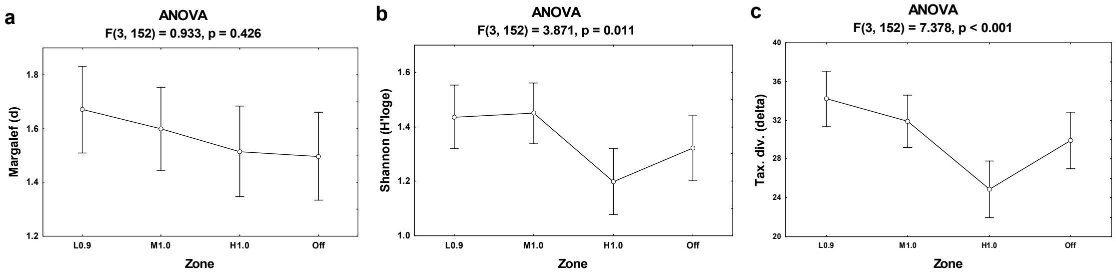
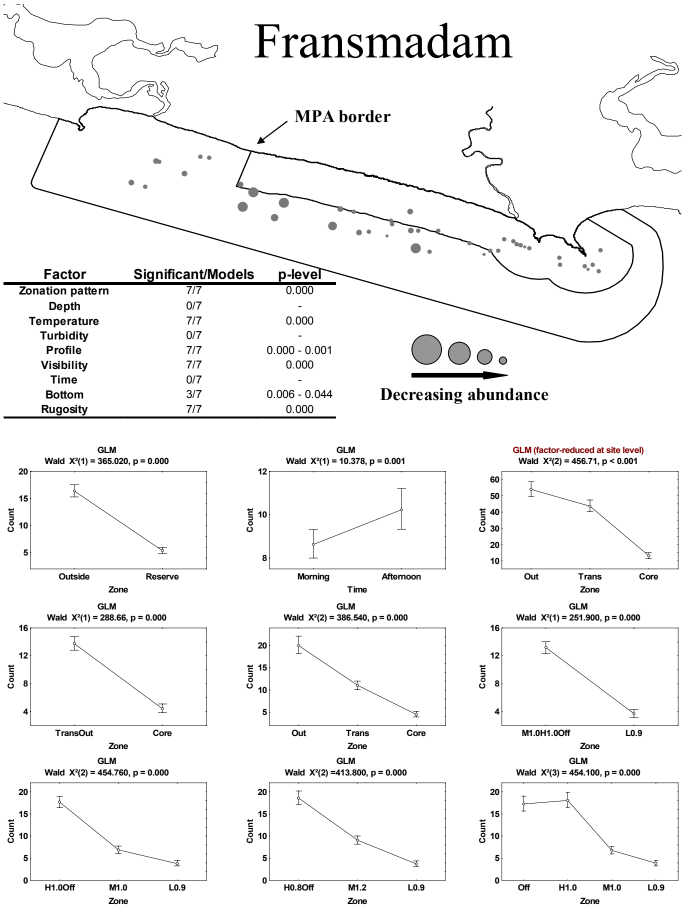


Figure 4.46: Difference of Margalef's richness (a), Shannon-Wiener (b) and taxonomic diversity index (c) within the $L_{0.9}$/$M_{1.0}$/$H_{1.0}$/Off zoning pattern, tested with ANOVA. Vertical bars denote 95% confidence intervals

Densities of fish species

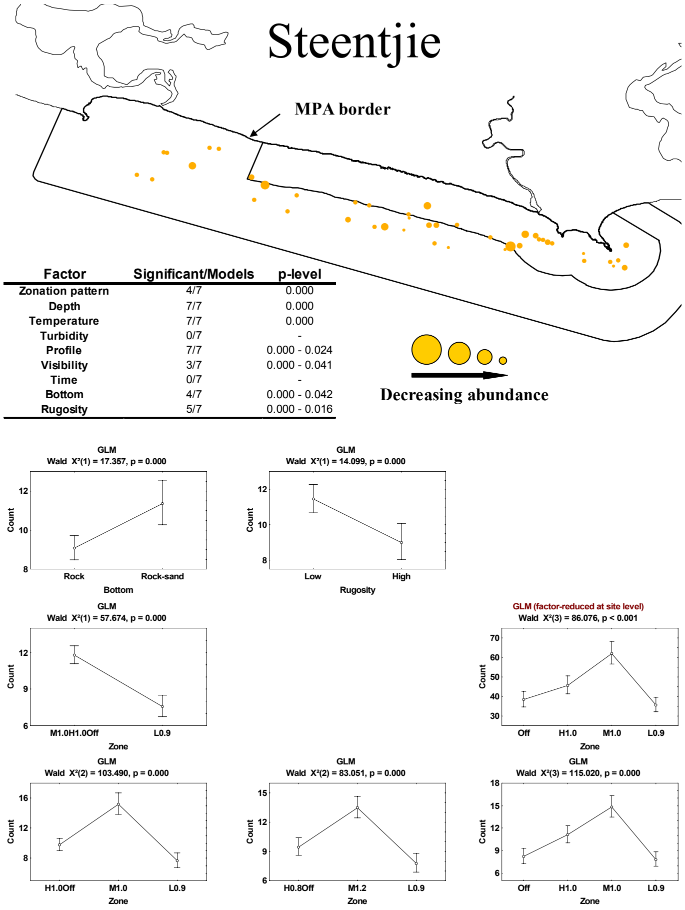


Factor	Significant/Models	p-level
Zonation pattern	7/7	0.000
Depth	0/7	-
Temperature	7/7	0.000
Turbidity	0/7	-
Profile	7/7	0.000 - 0.001
Visibility	7/7	0.000
Time	0/7	-
Bottom	3/7	0.006 - 0.044
Rugosity	7/7	0.000

Figure 4.47: Average abundance of fransmadam (N = 2499) in the study area for 177 point counts at 44 sites with results for the seven zoning patterns using GLMs. Vertical bars denote 95% confidence intervals

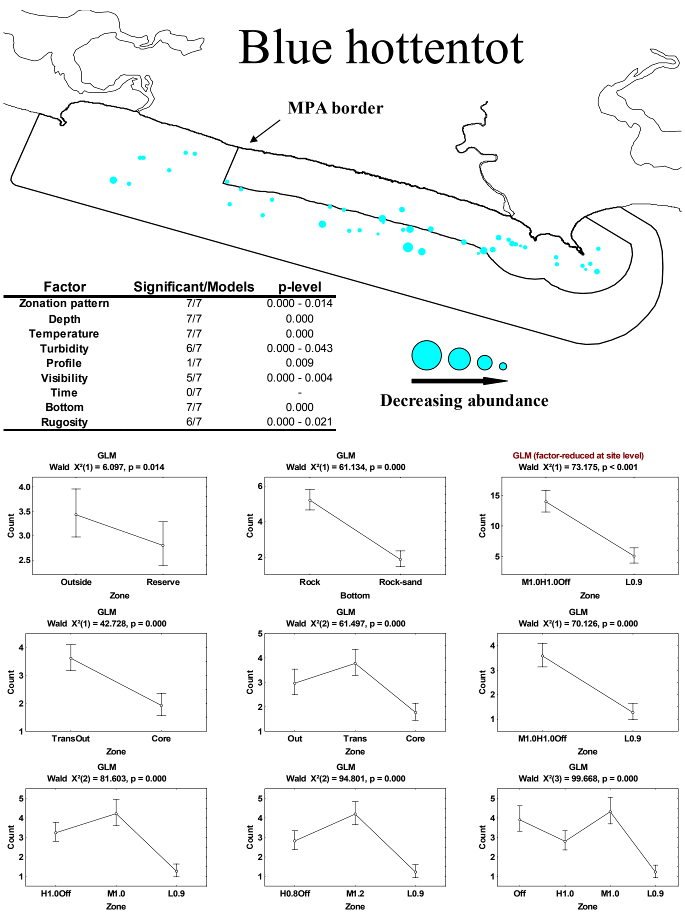
In all seven models water temperature and visibility as well as reef profile, rugosity and benthic community had a highly significant influence on fransmadam abundance (p-values between 0.001 and 0.001, figure 4.47). Higher abundance of fransmadam was observed over high profile – high rugosity reefs in warm and clear water. Bottom had a significant influence on abundance in three of the seven models (p-values between 0.006 and 0.044). Rocky bottom resulted in higher abundances. Additionally, all zones, irrespective of zoning patterns, had a highly significant influence on abundance ($p < 0.001$). Fransmadam abundance was low in the $\mathbf{L_{0.9}}$, **Core** and **Reserve** zones, increasing across the border of the MPA to highest levels in the $\mathbf{H_{1.0}}$ zone and eventually slightly decreasing in the **Off** zone (see figure 4.47). None of the main factors interacted consistently with the seven zoning patterns.

In all seven models water depth, temperature and reef profile had a significant influence on steentjie abundance (p-values between 0.001 and 0.024, figure 4.48). Higher abundances of steentjie were observed over shallow, high profile reefs in warm water. Visibility, bottom and rugosity had a significant influence on abundance in three, four, five and six of the seven models, respectively (p-values between 0.001 and 0.042). Higher visibilities, rocky bottom with sandy patches and low rugosity resulted in higher abundances. Additionally, zone had a highly significant influence on abundance in four of the seven zoning patterns ($p < 0.001$). Steentjie abundance was highest in the **$M_{1.0}$** and **$M_{1.2}$** zones, decreasing towards the **$L_{0.9}$** and **Off** zone (see figure 4.48). Bottom type interacted significantly in six of the seven zoning patterns (p-values between 0.028 – <0.001). More steentjie were observed over protected reefs interspersed with sandy patches.



Factor	Significant/Models	p-level
Zonation pattern	4/7	0.000
Depth	7/7	0.000
Temperature	7/7	0.000
Turbidity	0/7	-
Profile	7/7	0.000 - 0.024
Visibility	3/7	0.000 - 0.041
Time	0/7	-
Bottom	4/7	0.000 - 0.042
Rugosity	5/7	0.000 - 0.016

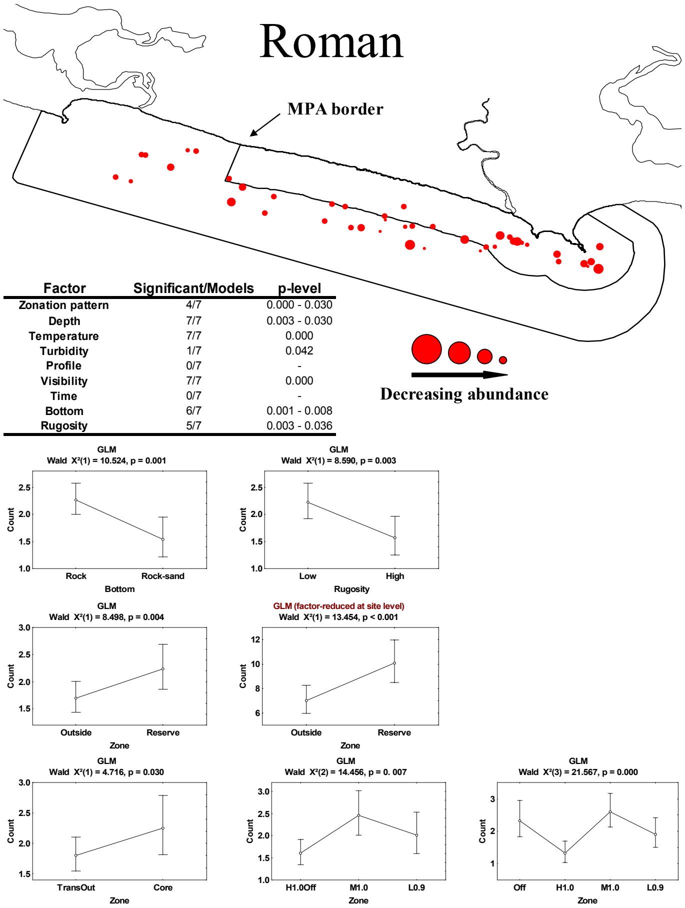
Figure 4.48: Average abundance of steentjie (N = 2073) in the study area for 177 point counts at 44 sites with results for the seven zoning patterns using GLMs. Vertical bars denote 95% confidence intervals



Factor	Significant/Models	p-level
Zonation pattern	7/7	0.000 - 0.014
Depth	7/7	0.000
Temperature	7/7	0.000
Turbidity	6/7	0.000 - 0.043
Profile	1/7	0.009
Visibility	5/7	0.000 - 0.004
Time	0/7	-
Bottom	7/7	0.000
Rugosity	6/7	0.000 - 0.021

Figure 4.49: Average abundance of blue hottentot (N = 863) in the study area for 177 point counts at 44 sites with results for the seven zoning patterns using GLMs. Vertical bars denote 95% confidence intervals

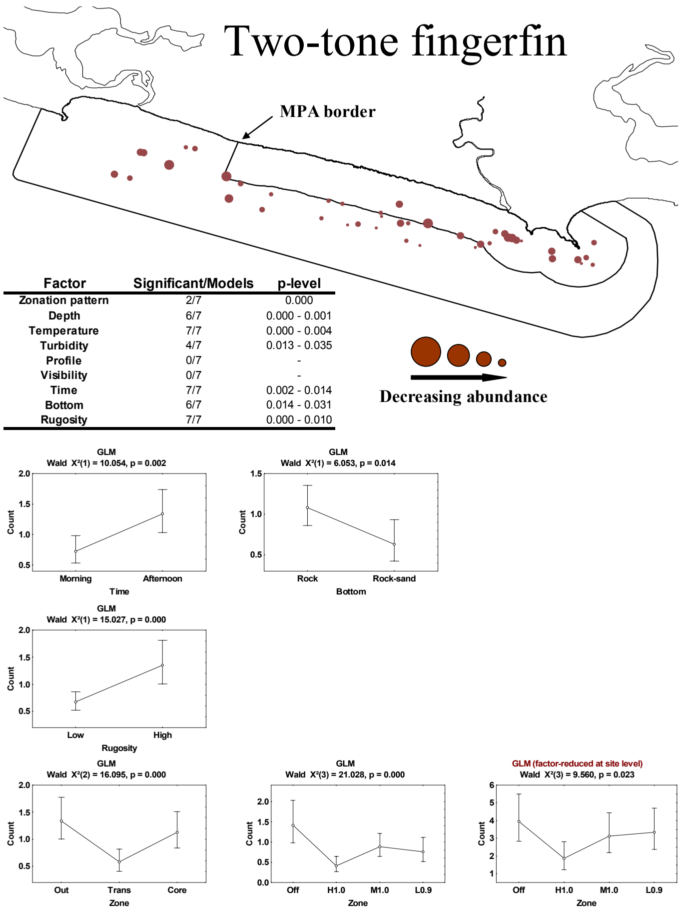
In all seven models water depth, temperature and bottom type had a significant influence on blue hottentot abundance ($p < 0.001$, figure 4.49). Higher abundance of blue hottentot was observed over deeper reefs, rocky bottom and in warm water. Turbidity and rugosity had a significant influence on abundance in six of the seven models (p-values between 0.001 and 0.043). Lower turbidities and high rugosity reefs resulted in higher abundance. Profile and visibility as well had an influence on abundance in one and five of the seven models, respectively (p-values between 0.001 and 0.009). Abundance was reduced over low profile reefs in low water visibility. Additionally, all zones, irrespective of zoning patterns, had a highly significant influence on abundance (p-values between 0.001 and 0.014). Blue hottentot abundance was low in the **$L_{0.9}$**, **Core** and **Reserve** zones, increasing towards the border of the MPA to highest levels in the **Trans**, **$M_{1.0}$** and **$M_{1.2}$** zones. Abundance decreases towards the **$H_{0.8}$Off**, **$H_{1.0}$Off**, **$H_{1.0}$** and **Out** zones, but increases slightly in the **Off** zone (see figure 4.49). None of the main factors interacted consistently with the seven zoning patterns.



Factor	Significant/Models	p-level
Zonation pattern	4/7	0.000 - 0.030
Depth	7/7	0.003 - 0.030
Temperature	7/7	0.000
Turbidity	1/7	0.042
Profile	0/7	-
Visibility	7/7	0.000
Time	0/7	-
Bottom	6/7	0.001 - 0.008
Rugosity	5/7	0.003 - 0.036

Figure 4.50: Average abundance of roman (N = 496) in the study area for 177 point counts at 44 sites with results for the seven zoning patterns using GLMs. Vertical bars denote 95% confidence intervals

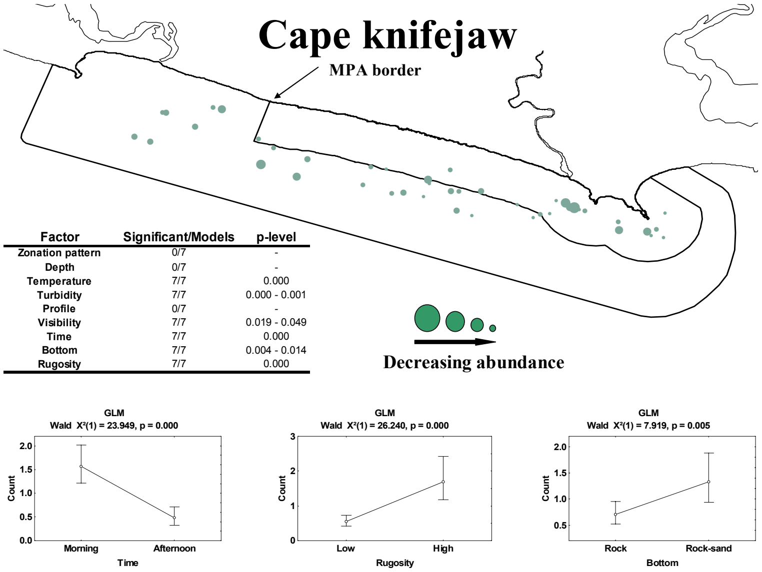
In all seven models water depth, temperature and visibility had a significant influence on roman abundance (p-values between 0.001 and 0.030, Figure). Higher abundance of roman was observed over shallower reefs and in clear and warm water. Rugosity and bottom type had a significant influence on abundance in five and six of the seven model, respectively (p-values between 0.001 and 0.036). Low rugosity reefs and rocky bottoms resulted in higher abundances. Turbidity as well had an influence on abundance (p = 0.042) in one of the seven models. Abundance was reduced in low water turbidity. Additionally, zone had a significant influence on abundance in four of the seven zoning patterns (p-values between 0.001 and 0.030). Roman abundance was low in the **Outside**, **TransOut** and **$H_{1.0}$Off** zones with an increase in the **Off** zone. High abundance was observed in the **Reserve**, **Core** and **$M_{1.0}$** zones with a slight decrease in the **$L_{0.9}$** zone (see Figure). None of the main factors interacted consistently with the seven zoning patterns.



Factor	Significant/Models	p-level
Zonation pattern	2/7	0.000
Depth	6/7	0.000 - 0.001
Temperature	7/7	0.000 - 0.004
Turbidity	4/7	0.013 - 0.035
Profile	0/7	-
Visibility	0/7	-
Time	7/7	0.002 - 0.014
Bottom	6/7	0.014 - 0.031
Rugosity	7/7	0.000 - 0.010

Figure 4.51: Average abundance of two-tone fingerfin (N = 192) in the study area for 177 point counts at 44 sites with results for the seven zoning patterns using GLMs. Vertical bars denote 95% confidence intervals

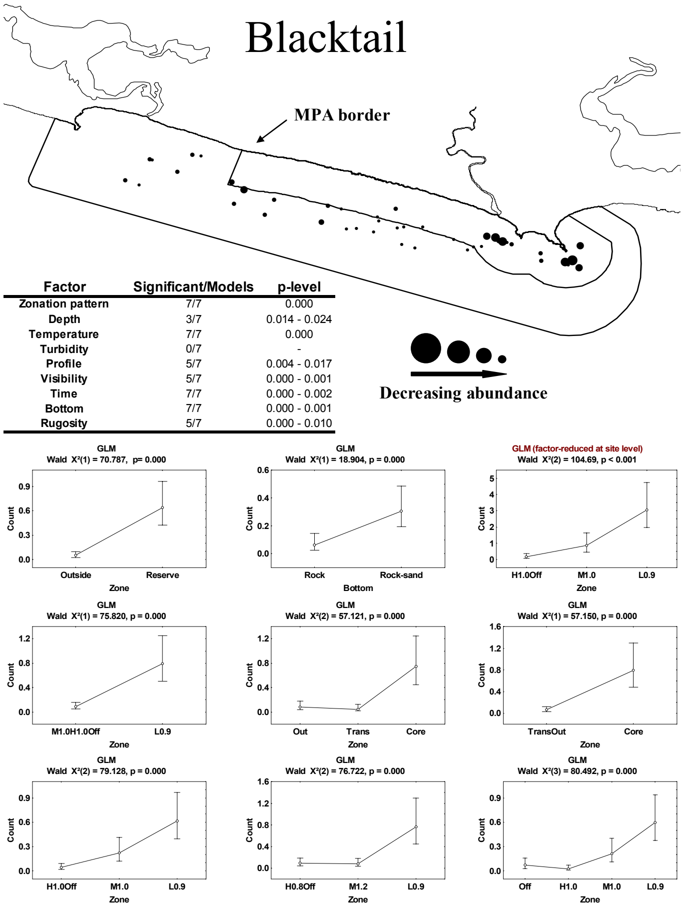
In all seven models water temperature, time of day and rugosity had a significant influence on two-tone fingerfin abundance (p-values between 0.001 and 0.014, figure 4.51). Higher abundance of two-tone fingerfin was observed in warm water conditions, over high rugosity reefs and in the afternoon. Depth and bottom type had a significant influence on abundance in six of the seven model (p-values between 0.001 and 0.031). Shallow reefs and rocky bottoms resulted in higher abundance. Turbidity as well had an influence on abundance in four of the seven models (p-values between 0.013 and 0.035). Higher abundance was recorded in low water turbidity. Additionally, zone had a significant influence on abundance in two of the seven zoning patterns ($p < 0.001$). Two-tone fingerfin abundance was highest in the **Out** and **Off** zones and lowest in **Trans** and $\mathbf{H_{1.0}}$, increasing again towards the Core and $\mathbf{M_{1.0}}$ zones with a slight decrease in the $\mathbf{L_{0.9}}$ zone (see figure 4.51). Due to the low number of two-tone fingerfin counted, GLMs of only three zoning patterns could be computed using interaction terms. None of the main factors interacted consistently with the seven zoning patterns.



Factor	Significant/Models	p-level
Zonation pattern	0/7	-
Depth	0/7	-
Temperature	7/7	0.000
Turbidity	7/7	0.000 - 0.001
Profile	0/7	-
Visibility	7/7	0.019 - 0.049
Time	7/7	0.000
Bottom	7/7	0.004 - 0.014
Rugosity	7/7	0.000

Figure 4.52: Average abundance of cape knifejaw (N = 187) in the study area for 177 point counts at 44 sites with results for the seven zoning patterns using GLMs. Vertical bars denote 95% confidence intervals

In all seven models water temperature, turbidity, rugosity and time of day had a highly significant influence on cape knifejaw abundance (p-values between 0.001 and 0.001, figure 4.52). Higher abundance of cape knifejaw was observed in warm water, low water turbidity, in the morning and over low rugosity reefs. Bottom type and visibility had a significant influence on abundance in all seven models as well (p-values between 0.004 and 0.049). High visibility and rocky bottoms with sandy patches resulted in higher abundance (see figure 4.52). Zones did not influence cape knifejaw abundance. Due to the low number of cape knifejaw counted, GLMs of only two zoning patterns could be computed using interaction terms. None of the main factors interacted with the seven zoning patterns.



Factor	Significant/Models	p-level
Zonation pattern	7/7	0.000
Depth	3/7	0.014 - 0.024
Temperature	7/7	0.000
Turbidity	0/7	-
Profile	5/7	0.004 - 0.017
Visibility	5/7	0.000 - 0.001
Time	7/7	0.000 - 0.002
Bottom	7/7	0.000 - 0.001
Rugosity	5/7	0.000 - 0.010

Figure 4.53: Average abundance of blacktail (N = 162) in the study area for 177 point counts at 44 sites with results for the seven zoning patterns using GLMs. Vertical bars denote 95% confidence intervals

In all seven models water temperature, time of day and bottom type had a highly significant influence on blacktail abundance (p-values between 0.001 and 0.002, figure 4.53). Higher abundance of blacktail was observed in warm water, in the morning and over rocky reefs with sandy patches. Visibility, reef profile and rugosity had a significant influence on abundance in five of the seven models (p-values between 0.001 and 0.017). High visibility, high profile and low rugosity reefs resulted in higher abundance of blacktail. Furthermore, depth influenced abundance as well in three of the seven models, with shallow reefs supporting higher blacktail abundance (p-values between 0.014 and 0.024). All zones, irrespective of zoning patterns, had an effect at high p-values (0.001). Abundance was high in the **$L_{0.9}$**, **Core** and **Reserve** zones, decreasing consistently across the border of the MPA. A very slight increase was recorded in the **$H_{0.8}$Off**, **Out** and **Off** zones (see figure 4.53). Due to the low number of blacktail counted, GLMs of only two zoning patterns could be computed using interaction terms. None of the main factors interacted with the seven zoning patterns.

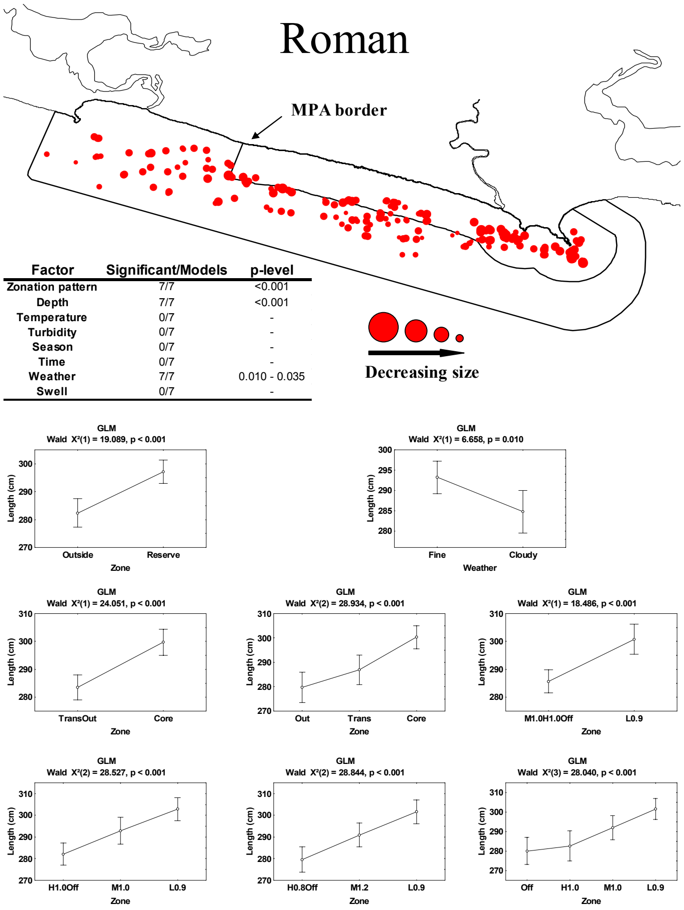
In summary, the abundance of only cape knifejaw was not influenced by zones. Abundances of roman and blacktail were generally high at protected inshore sites and low at exploited offshore sites, with a slight increase in the **Off** zone. The abundance of steentjie was highest around the border of the MPA. Fransmadam, blue hottentot and two-tone fingerfin were most abundant in the exploited offshore sites. Generally, high water temperatures and visibilities as well as high profile reefs increased the number of observed fish and with the exception of fransmadam lower turbidities had the same effect. Fish abundances were generally higher over shallower reefs with the exception of blue hottentot. The effects of other factors were less consistent (Table 4.10).

	Factor								
Species	**Zone**	**Depth**	**Temperature**	**Turbidity**	**Profile**	**Visibility**	**Time**	**Bottom**	**Rugosity**
Fransmadam	Offshore	-	high	high	high	high	afternoon	rock	high
Steentjie	between	shallow	high	-	high	high	-	rock-sand	low
Blue hottentot	Offshore	deep	high	low	high	high	-	rock	high
Roman	Inshore	shallow	high	low	-	high	-	rock	low
Strepie	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
Cape knifejaw	-	-	high	low	-	high	morning	rock-sand	low
Two-tone fingerfin	Offshore	shallow	high	low	-	high	afternoon	rock	high
Blacktail	Inshore	shallow	high	-	high	high	morning	rock-sand	low
All	Offshore	-	high	-	-	high	morning	-	high

Table 4.10: Influence of factors on the abundance of the eight most abundant and all 34 species observed in the study area. Factor codes indicate significantly higher abundances

4.3.4 Sizes of fish species

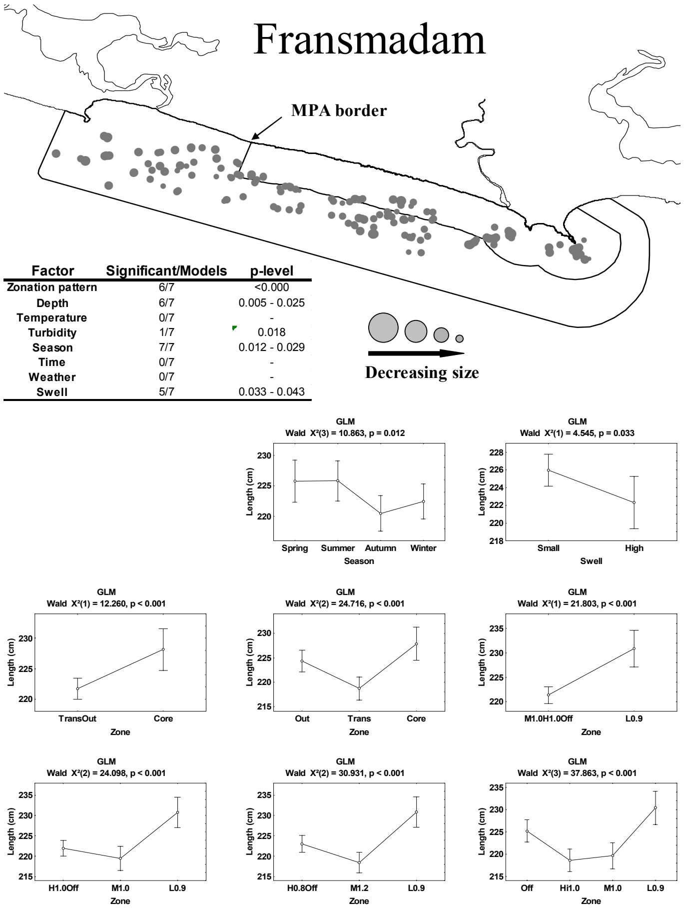
Controlled fishing



Factor	Significant/Models	p-level
Zonation pattern	7/7	<0.001
Depth	7/7	<0.001
Temperature	0/7	-
Turbidity	0/7	-
Season	0/7	-
Time	0/7	-
Weather	7/7	0.010 - 0.035
Swell	0/7	-

Figure 4.54: Average fork lengths of roman (N = 1089) in the study area at 230 sites with results for the seven zoning patterns using GLMs. Vertical bars denote 95% confidence intervals

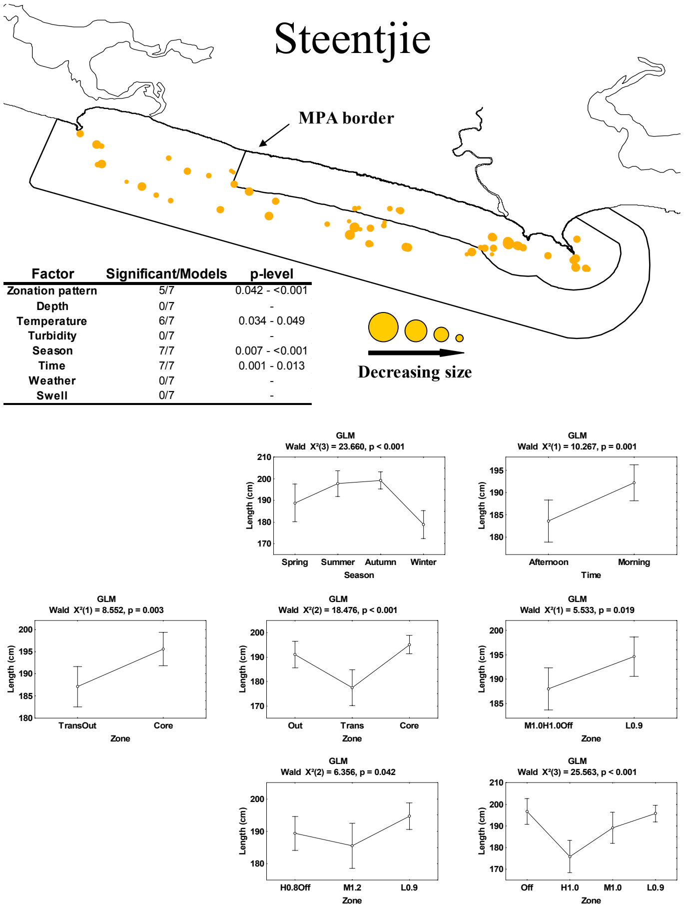
Depth had a highly significant effect on the size of roman, with larger fish caught at shallower sites in all seven models ($p < 0.001$, figure 4.54). Furthermore, weather had a significant influence on size in all seven models (p-values between 0.008 and 0.048). Larger fish were caught during fine weather conditions. Zones, irrespective of zoning patterns, had an effect on roman size in all seven models at low p-values ($p < 0.001$). Fish were significantly larger in the protected inshore zones and sizes were decreasing consistently towards the exploited offshore zones (see graphs in figure 4.54). Also, larger fish were caught in fine weather conditions as indicated in four models (p-values between 0.010 and 0.035). Other factors like temperature, turbidity, season, time of day or swell did not influence roman size. Time of day interacted significantly in all zoning patterns (p-values between 0.004 – 0.012). Larger roman were caught in the morning at protected sites.



Factor	Significant/Models	p-level
Zonation pattern	6/7	<0.000
Depth	6/7	0.005 - 0.025
Temperature	0/7	-
Turbidity	1/7	0.018
Season	7/7	0.012 - 0.029
Time	0/7	-
Weather	0/7	-
Swell	5/7	0.033 - 0.043

Figure 4.55: Average fork lengths of fransmadam (N = 687) in the study area at 181 sites with results for the seven zoning patterns using GLMs. Vertical bars denote 95% confidence intervals

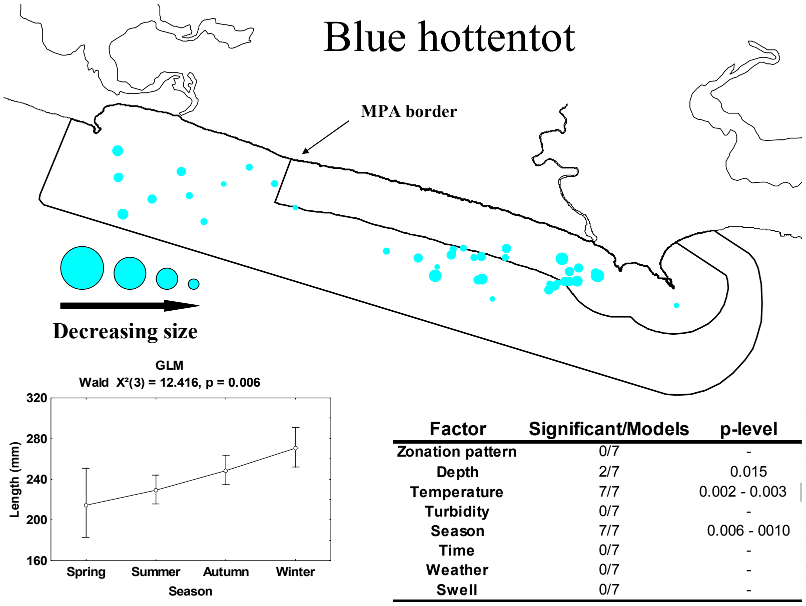
In six of the seven models, depth had a significant effect on the size of fransmadam, with larger fish caught at deeper sites (p-values between 0.005 and 0.025, figure 4.55). In one of the seven models turbidity had an effect, with larger fish being caught in high water turbidity ($p = 0.018$). Furthermore, swell had a significant influence on size in five of the seven models (p-values between 0.033 and 0.043). Larger fransmadam were caught during small swells. Season had an influence in all seven models with p-values between 0.013 and 0.031. Smaller fish were caught in autumn and winter. Zones had an effect on fransmadam size in six of the seven models at low p-values ($p < 0.001$). Fish were larger in the protected inshore zones. Sizes decreased across the MPA's border, reaching a minimum in the **Trans**, **$M_{1.0}$**, **$M_{1.2}$**, and **$H_{1.0}$** zones. Then, sizes increased again in the **Out**, **$H_{0.8}$Off**, **$H_{1.0}$Off** and **Off** zones (see figure 4.55). Other factors like temperature, turbidity, time of day or weather did not have an effect on fransmadam size. In all seven GLMs no main factor interacted consistently with zoning pattern.



Factor	Significant/Models	p-level
Zonation pattern	5/7	0.042 - <0.001
Depth	0/7	-
Temperature	6/7	0.034 - 0.049
Turbidity	0/7	-
Season	7/7	0.007 - <0.001
Time	7/7	0.001 - 0.013
Weather	0/7	-
Swell	0/7	-

In six of the seven models, temperature had a significant effect on the size of steentjie, with larger fish caught at sites with higher seawater temperatures (p-values between 0.034 and 0.049, figure 4.56). Furthermore, time of day had a significant influence on size in all seven models (p-values between 0.001 and 0.013). Larger steentjie were caught in the morning. Season as well had an influence in all seven models with p-values between 0.007 and <0.001. The fork length of fish caught increased consistently from winter towards autumn. Zones influenced steentjie size in five of the seven models at p-values values between 0.042 and <0.001. Fish were larger in the protected inshore zones. Sizes decreased across the MPA's border, reaching a minimum in the **Trans**, **M$_{1.2}$**, and **H$_{1.0}$** zones. Then, sizes increased again in the **Out**, **H$_{0.8}$Off** and **Off** zones (see figure 4.56). Other factors like depth, turbidity, weather or swell did not have an effect on steentjie size. Weather interacted significantly in all zoning patterns (p-values between 0.035 and <0.001). At exploited sites larger steentjie were caught during cloudy weather condition.

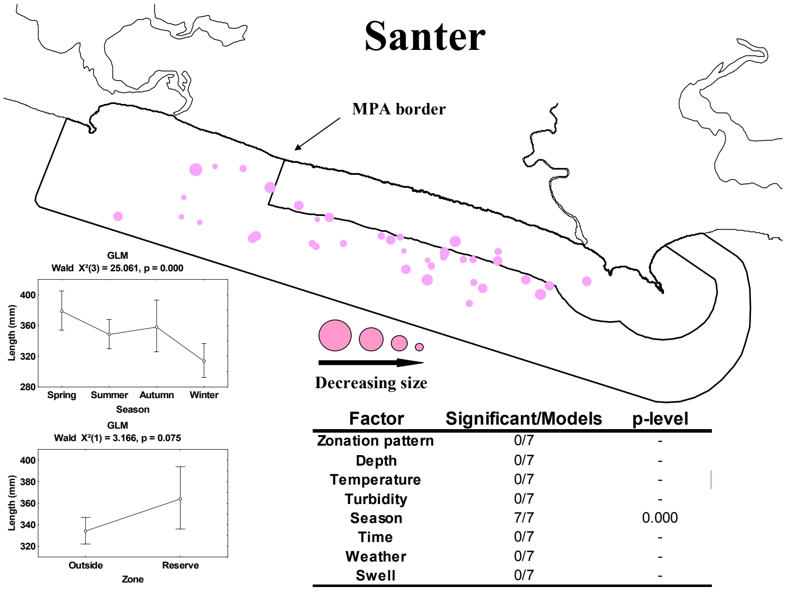
Figure 4.56: Average fork lengths of steentjie (N = 201) in the study area at 84 sites with results for the seven zoning patterns using GLMs. Vertical bars denote 95% confidence intervals



Factor	Significant/Models	p-level
Zonation pattern	0/7	-
Depth	2/7	0.015
Temperature	7/7	0.002 - 0.003
Turbidity	0/7	-
Season	7/7	0.006 - 0010
Time	0/7	-
Weather	0/7	-
Swell	0/7	-

Figure 4.57: Average fork lengths of blue hottentot (N = 89) in the study area at 52 sites with results for the seven zoning patterns using GLMs. Vertical bars denote 95% confidence intervals

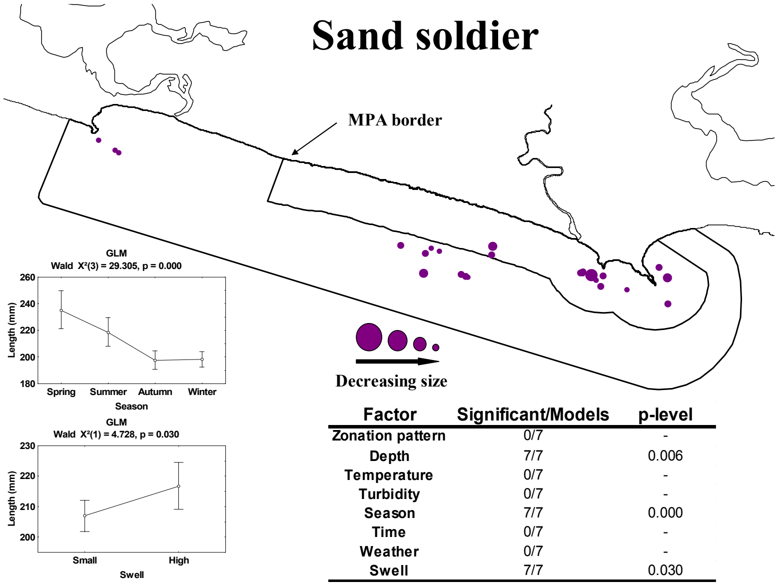
In all seven models, temperature had a significant effect on the size of blue hottentot, with larger fish caught at sites during higher seawater temperatures (p-values between 0.002 and 0.003, figure 4.57). Furthermore, depth had a significant influence on size in two of the seven models (p-values between 0.002 and 0.018). Larger blue hottentots were caught at deeper sites. Season had an influence in all seven models with p-values between 0.006 and 0.010. The fork length of fish caught increased consistently from spring towards winter (see figure 4.57). Zones did not have an effect on blue hottentot size. The low sample size compromised the computation of GLMs using interaction terms.



Factor	Significant/Models	p-level
Zonation pattern	0/7	-
Depth	0/7	-
Temperature	0/7	-
Turbidity	0/7	-
Season	7/7	0.000
Time	0/7	-
Weather	0/7	-
Swell	0/7	-

Figure 4.58: Average fork lengths of santer (N = 83) in the study area at 42 sites with results for the seven zoning patterns using GLMs. Vertical bars denote 95% confidence intervals

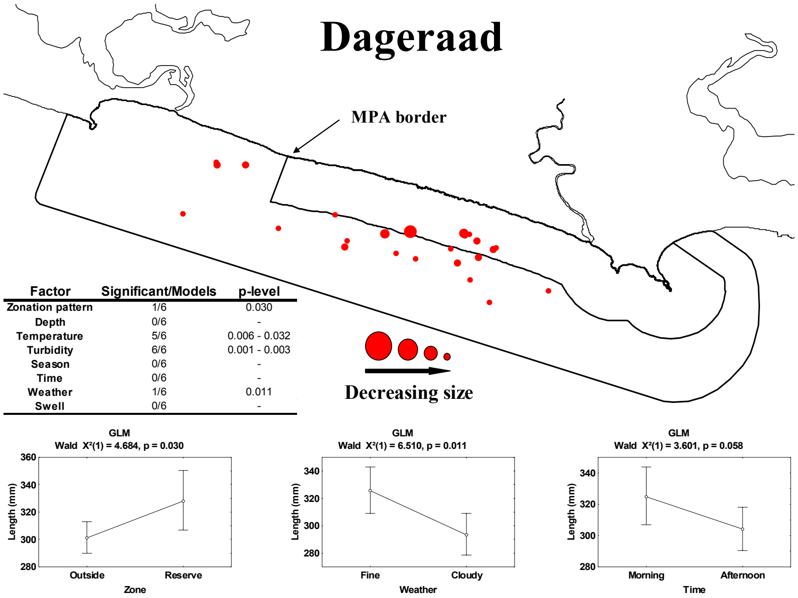
Season had an influence in all seven models with a p-value of 0.001 (Figure 4.58). The fork length of caught fish decreased from spring towards winter. Other factors like zones, depth, temperature, turbidity, time of day, weather or swell did not influence santer size. However, due to the absence of santer in most of the protected inshore zones, only one of the zoning patterns (**Reserve/Outside**) had enough data within the protected inshore zone (**Reserve**) to allow the computation of a GLM (see distribution map in figure 4.58). Therefore, it is worthwhile mentioning that the trend for larger fish within the protected inshore zones was detected for santer as well at a p-value of 0.075 (see graph in figure 4.58). The low sample size compromised the computation of GLMs using interaction terms.



Factor	Significant/Models	p-level
Zonation pattern	0/7	-
Depth	7/7	0.006
Temperature	0/7	-
Turbidity	0/7	-
Season	7/7	0.000
Time	0/7	-
Weather	0/7	-
Swell	7/7	0.030

Figure 4.59: Average fork lengths of sand soldier (N = 47) in the study area at 25 sites with results for the seven zoning patterns using GLMs. Vertical bars denote 95% confidence intervals

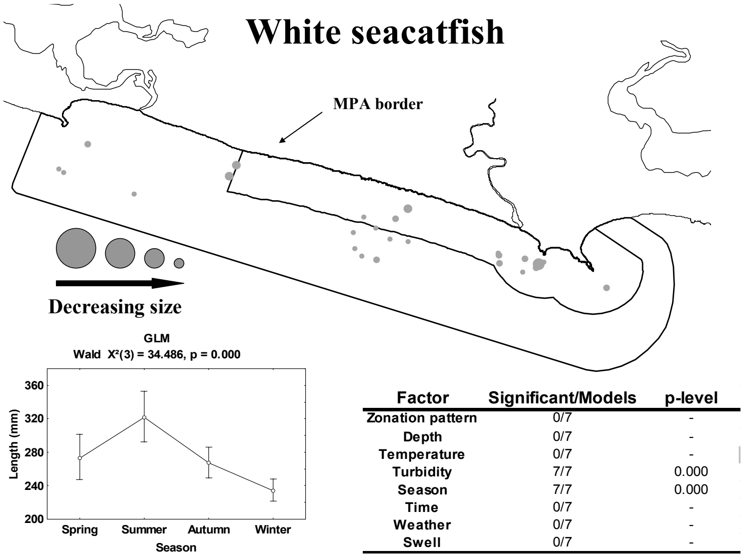
Season had an influence in all seven models ($p < 0.001$, figure 4.59). Sizes of sand soldier decreased consistently from spring towards winter. Additionally, swell had a significant influence in all seven models, with larger fish being caught in high swells (see Figure). Depth as well was significant in all seven models ($p = 0.006$) – larger fish were caught at deeper sites. The remaining factors zone, temperature, turbidity, time of day and weather did not influence sand soldier size. The low sample size compromised the computation of GLMs using interaction terms.



Factor	Significant/Models	p-level
Zonation pattern	1/6	0.030
Depth	0/6	-
Temperature	5/6	0.006 - 0.032
Turbidity	6/6	0.001 - 0.003
Season	0/6	-
Time	0/6	-
Weather	1/6	0.011
Swell	0/6	-

Figure 4.60: Average fork lengths of dageraad (N = 42) in the study area at 26 sites with results for the seven zoning patterns using GLMs. Vertical bars denote 95% confidence intervals

No dageraad were caught in the narrower protected inshore zones of most zoning patterns (see distribution map in figure 4.60). Therefore, in only one model, zone had a significant influence on dageraad size with larger fish recorded in the **Reserve** zone (p < 0.030). Weather had a significant influence on size in one of the six models – larger dageraad were caught during fine weather conditions. Temperature and turbidity had a significant influence on fish size in five and six models with p-values of 0.006 – 0.032 and 0.001 – 0.003, respectively. Larger fish were caught in colder and more turbid water. Although other factors did not have an effect on dageraad size, it is worthwhile mentioning that the trend for larger fish caught in the morning was also detected for dageraad at a p-value of 0.075 (Figure 4.60). The low sample size compromised the computation of GLMs using interaction terms.



Factor	Significant/Models	p-level
Zonation pattern	0/7	-
Depth	0/7	-
Temperature	0/7	-
Turbidity	7/7	0.000
Season	7/7	0.000
Time	0/7	-
Weather	0/7	-
Swell	0/7	-

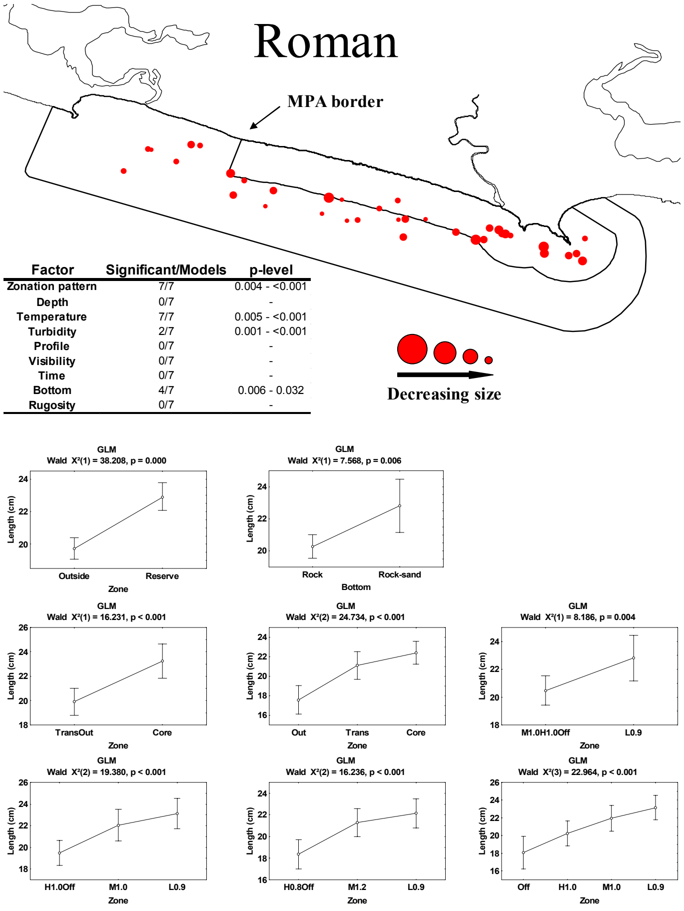
Figure 4.61: Average fork lengths of white seacatfish (N = 41) in the study area at 25 sites with results for the seven zoning patterns using GLMs. Vertical bars denote 95% confidence intervals

Season and turbidity had a highly significant effect on fish size in all seven models ($p < 0.001$, figure 4.61). Higher water turbidity resulted in larger white seacatfish caught at respective sites. Larger fish were caught in summer, decreasing towards winter and slightly increasing in spring (see figure 4.61). The low sample size compromised the computation of GLMs using interaction terms.

In summary, fork lengths were higher in protected inshore zones and lower at exploited offshore zones, except for blue hottentot, sand soldier and white seacatfish, for which no zone effect was detected. Season had an effect on fish size in all species but dageraad, with sizes peaking mainly in summer and spring. Larger roman were caught at shallower sites as opposed to fransmadam, blue hottentot and sand soldier, where larger individuals were caught in deeper waters. Whenever relevant, time of day, turbidity and weather produced larger fish during morning, low turbidity or fine weather conditions, respectively (Table 4.11).

	Factor							
Species	**Zone**	**Season**	**Time**	**Depth**	**Temperature**	**Turbidity**	**Weather**	**Swell**
Roman	Inshore	-	-	shallow	-	-	fine	-
Fransmadam	Inshore	Summer	-	deep	-	low	-	small
Steentjie	Inshore	Autumn	morning	-	high	-	-	-
Blue hottentot	-	Winter	-	deep	high	-	-	-
Santer	(Inshore)	Spring	-	-	-	-	-	-
Dageraad	Inshore	-	(morning)	-	low	low	fine	-
Sand soldier	-	Spring	-	deep	-	-	-	high
White seacatfish	-	Summer	-	-	-	low	-	-

Table 4.11: Influence of factors on fork length of the eight most abundant fish species in the study area. Factor codes indicate significantly higher fork lengths. Factor codes in brackets indicate higher fork lengths at p-values between 0.1 and 0.05.



Factor	Significant/Models	p-level
Zonation pattern	7/7	0.004 - <0.001
Depth	0/7	-
Temperature	7/7	0.005 - <0.001
Turbidity	2/7	0.001 - <0.001
Profile	0/7	-
Visibility	0/7	-
Time	0/7	-
Bottom	4/7	0.006 - 0.032
Rugosity	0/7	-

Figure 4.62: Average fork lengths of roman (N = 539) in the study area for 177 point counts at 44 sites with results for the seven zoning patterns using GLMs. Vertical bars denote 95% confidence intervals

In all seven models, temperature had a highly significant effect on the size of roman, with larger roman observed in warm water (p-values between 0.005 and <0.001, figure 4.62). Furthermore, bottom had a significant influence on size in four of seven models (p-values between 0.006 and 0.032). Larger fish were observed over rocky substrate with sandy patches. Turbidity had an influence on size in two of the seven models (p-values of 0.001 and <0.001). Larger roman were recorded in low water turbidity. Zone had a highly significant effect on roman size irrespective of zoning patterns (p-values between 0.004 and <0.001). Fish were larger in the protected inshore zones and sizes were decreasing consistently towards the exploited offshore zones (see figure 4.62). Other factors like depth, profile, visibility, time of day or rugosity did not influence roman size. Due to the large number of factors, GLMs of only two zoning patterns could be computed using interaction terms. Here, rugosity interacted significantly with the two zoning patterns (p-values of 0.010 and 0.004). Larger roman were observed on low rugosity reefs under protection.

4.4 DISCUSSION

The influence of the various abiotic factors and fishing on benthic distribution, fish abundance and fish size are discussed separately. Due to the large number of taxa investigated, effects are generalized. Special attention is directed at results that were common across methods. An attempt is made to identify trophic relationships among taxa and to propose a food-web for the reef community based on these results.

Season

The higher CPUE in the winter months overall, and in particular for roman, santer, sand soldier, fransmadam and steentjie, might be caused by spawning related feeding patterns. Fransmadam and steentjie spawn between spring and summer (Van Der Elst 1993a). The spawning of roman and santer is correlated with the peak of seawater temperatures and day length in summer (Coetzee 1983, Buxton 1987), typical for many sparids in southern waters (Brownell 1979a, Brouwer and Griffiths 2005). The lower summer CPUE might be a result of less time spent on feeding during the spawning season (Wootton 1999b). The opposite was only found for blue hottentot where feeding activity and spawning season coincided in summer (Buxton and Clarke 1985). Seasonal migrations as a reason for variations in CPUE of these species is unlikely, as such behaviour has never been reported in the literature and authors generally consider these reef fish as resident (Buxton 1987, Van Der Elst 1993a, Branch *et al.* 1999b, Kerwath 2005).

The influence of season on fish size of fransmadam, blue hottentot, santer, sand soldier and white seacatfish consistently pointed towards higher mean sizes during seasons where lower CPUE values were recorded. It appears that smaller fish reduce feeding more than larger fish during the spawning season (see above), implying that they allocate more time to spawning. A reason for this, however, could be extracted neither from the data in this study nor from the literature.

Time of day

Diurnal variability in reef fish abundance indices has often been reported (Helfman 1986). Decreased abundance of reef fish in the afternoon is most likely due to a lower visibility during UVC (Fautin and Allen 1992, Thompson and Mapstone 2002). Another explanation is that increased feeding activity in the morning hours causes higher activity levels of territorial fishes defending their resources hence increasing their 'visibility' (Polunin and Klump 1989).

At Goukamma, reef fish were generally more active in the morning hours as indicated by higher counts and CPUE, suggesting a diurnal feeding pattern. Stomach and intestine content analysis of roman and dageraad by Buxton (1987) revealed a diurnal pattern in feeding for roman and dageraad with higher feeding activities just after sunrise. Although the same result was found for roman in this study, no pattern was detected for dageraad, possibly due to a small sample size.

It can be argued that the strong effect of season (see above), in particular for small immature individuals, is not so much related to spawning as to satiation. Species that feed primarily after sunrise might reduce feeding activity as they become satiated. Thus during winter when day length is shorter, fish might spend longer daylight periods feeding. However, CPUE surveys were conducted between sunrise and sunset, thus starting earlier in summer and later in winter, according to day length. Therefore, possible diurnal feeding patterns of fish should be covered equally between seasons. The GLM analysis then separated the effects of season and time of day on CPUE.

Depth

The influence of depth on abundance of benthic organisms at Goukamma is similar to what has been found at other sites in South Africa. Buxton (1987) described higher abundances of algae on shallow reefs but more filter-feeders such as gorgonians on deeper reefs in the Tsitsikamma NP. Burger (1990), studying the same area, generally confirmed these results but added that ascidians like red bait (*Pyura stolonifera*) frequently dominated shallow reef crests, whereas bryozoans and poriferans were typically more abundant on deeper reefs. Branch *et al.* (1999c) described the most common ascidian, red bait, as very common along the South African coasts, forming extensive coverage from low tide to about ten meters deep. The largest and most conspicuous poriferans on reefs, the orange wall-sponge (*Spirastrella* *spinispirulifer*) (Branch *et al.* 1999d) and the common sinuous and palmate sea fans (*Eunicella tricoronata* and *Leptogorgia palma*) (Branch *et al.* 1999a) which can form dense underwater forests, were found in deeper waters between 10 and 100 m.

The lower abundance of algae on deeper reefs at Goukamma is likely to be caused by the generally high turbidity of the seawater attenuating light penetration. The feeding of ascidians is facilitated by strong water movement (Branch and Branch 1981b), which is found on reef crests in shallower water.

An influence of depth on reef fish abundance has been reported from tropical areas (Bell 1983, Shpigel and Fishelson 1989) and from the warm temperate South African coast (Buxton and Smale 1989, Burger 1990). Using UVC, Lechanteur (2004) determined that fish species generally preferred shallower reefs around the Cape Peninsula. The same was found in this study as indicated by a higher overall CPUE over shallower sites. As opposed to other studies, this was also determined for roman, using both survey methods. Buxton (1987), Burger (1990) and Lechanteur (2004) recorded lower densities of roman on shallower reefs during UVC surveys in the Tsitsikamma NP and around the Cape Peninsula. A closer look, however, reveals that in these studies, shallower reefs were sites below ten meters of water depth. In this study, no sites shallower than eight meters were investigated. Lechanteur (2004) divided the deeper sites further and recorded higher densities of roman between 8-15 m than between 15-25 m, which is similar to the zoning pattern used in this study.

A possible explanation for the higher roman abundance on shallower reefs could be related to the higher standing biomass of algae and grazers such as crinoids (Fina 2004). Feather stars and urchins are the main prey of roman. Larger roman were found over shallower reefs.

The higher productivity of shallow reefs might also explain why fransmadam, steentjie, two-tone fingerfin and blacktail were found to be more abundant over shallow reefs at Goukamma and elsewhere (Buxton 1987, Burger 1990, Mann and Buxton 1992, Van Der Elst 1993a, Branch *et al.* 1999b). Although GLM results for strepie were not significant due to high variability (shoaling behaviour, resulting in extreme patchiness of distribution), this herbivorous species was more abundant on shallow, turbulent reefs. This tendency has been reported elsewhere (Buxton 1987, Burger 1990, Van Der Elst 1993a).

In contrast to these findings blue hottentot were more abundant over deeper reefs, confirming findings of Burger (1990) and Branch *et al.* (1999b). Blue hottentot is the only sparid that feeds mainly on hydrozoans (Buxton and Clarke 1985), which might allow them to penetrate deeper reefs more successfully than other species that directly or indirectly rely on algal productivity in shallower waters.

Depth also had an influence on mean sizes of some fish species. Except for roman (see above), fish like fransmadam, blue hottentot and sand soldier were generally larger over deeper reefs, confirming findings of Buxton (1987), Burger (1990), Van Der Elst (1993a) and Branch *et al.* (1999b). Variation across depths might be a result of ontogenetic change in diet found in many sparid fish, where shallower reefs are used as nursery areas for juveniles and sub-adults (Christensen 1978).

Temperature

Temperature can have an important influence on temperate reef fish distribution (Stephens *et al.* 1984). In this study, higher temperatures generally increased CPUE and the number of fish counted during UVC. This relationship of low fish densities during UVC in low water temperatures was also found by Buxton (1987) in the Tsitsikamma NP generally, and in particular for roman. He concluded that, with a lower metabolic rate during cold upwelling, a higher proportion of the fish may be ‘hold up’ in shelter areas or might follow pockets of warm water. Conversely, under warm water conditions, the fish are more active.

Kerwath (2005) recorded the same paucity of fish during diving counts in cold water in the Castle Rock MPA. Subsequent sonar tracking experiments, however, revealed that roman were hiding in crevices and caves together with other fish species and were not leaving the area. Cold upwelling events can have detrimental effects on the fish community as they can lead to fish mortality in extreme cases (Hanekom *et al.* 1989).

Although the results may at first glance appear contradictory, the lower CPUE recorded for most fish species during Summer (see above) does not contradict the lower CPUE recorded during lower water temperatures. Although water temperatures were on average higher in Summer, frequent cold upwelling events during this period resulted in numerous measurements of a low catch at temperatures below the average temperature during winter.

Turbidity and visibility

Significantly higher turbidities were measured at sites that were heterogeneous concerning their fish communities (‘other sites’). These heterogeneous communities should therefore not be discussed as an entity. However, there were some sites with very high abundances of white seacatfish and sand soldier. Both species are found predominantly over sandy bottoms (Tilney and Hecht 1990, Van Der Elst 1993a, Branch *et al.* 1999b) and it is probable that some of the fishing sites where these species were caught were conducted close to or partly on sand, which would explain the high bottom turbidity in combination with increased abundances of these sand-dwelling bottom fish.

Low turbidity and/or high visibility consistently resulted in higher CPUE, UVC counts and mean fish sizes of individual species during controlled fishing and UVC. Due to their large eyes, feeding and predator avoidance of sparids should be generally more successful in clearer water (Bruton 1985, Gregory 1993). Turbid water on the other hand favours sharks (Kajiura 2001), which are important predators of reef sparids since the fishing-induced disappearance of top predators such as red steenbras and seventy-four from inshore reef ecosystems (Smale *et al.* 1994, Smale and Goosen 1999). During conditions of high water turbidity at Goukamma, it has been observed that reef sparids are feeding less actively, stay low above the reef and even tend to hide. This predator avoidance should be more frequent among larger individuals of a species as they are less in need of energy (see chapter 3). This may explain why fish caught and observed were smaller during low visibility/high turbidity.

Higher UVC counts are expected in clear water, as fish are easier to identify and more visible at distance. Larger roman have been observed to be more cautious than smaller roman during underwater fishing experiments (Kerwath 2005) and point counts, keeping a larger distance from the observer. This might also lead to lower size estimates of roman during UVC.

Weather

Fransmadam were caught more often during cloudy weather. Cloudy weather conditions reduce underwater visibility, with the potential to reduce detectability of bait. Although no drop in overall CPUE was recorded during cloudy weather conditions, the particularly large eyes of fransmadam might put this species at a competitive advantage relative to other smaller-eyed species to spot bait more readily under such conditions, resulting in an increased CPUE for this species.

The mean size of caught roman and dageraad were higher during fine weather conditions. The activity of otherwise cautious, larger fish (see chapter 3) should increase under such favourable conditions.

Reef profile, rugosity and bottom type

The importance of reef profile to fish has been demonstrated by several authors (Gascon and Miller 1982, Shpigel and Fishelson 1989, West *et al.* 1994). A high reef profile and rugosity generally resulted in higher abundances of fish during UVC in this study, in the Tsitsikamma NP (Buxton and Smale 1989) and around the Cape Peninsula (Lechanteur 2004). Higher fish densities should be supported by the larger surface of high profile reefs, providing a higher standing biomass of benthic organisms. Furthermore, a higher habitat complexity should make this reef type preferable to a larger variety of fish species (Buxton 1987, Lechanteur 2004).

However, reef profile did not have any effect on roman and two-tone fingerfin abundance in this study. This is believed to be a result of an underestimation of cryptic reef fish in the case of two-tone fingerfin on complex reefs (Smith 1989, Willis 2001). Roman, on the other hand, should have less possibilities to hide where reef profile and rugosity is lower. Difficulties in spotting the fishes due to the high complexity of the habitat (Harmelin-Vivien *et al.* 1985) and their tendency to hide in caves and crevices (Kerwath 2005) might have cancelled out the otherwise favourable effect of high profile/rugosity environments.

Only three fish species were more abundant on rocky reefs interspersed with sandy patches. Steentjie build nests in sand during spawning (Van Bruggen 1965) and are known to graze on algae at times (Burger 1990, Van Der Elst 1993a), as well as, the predominantly herbivorous species cape knifejaw (Van Der Elst 1993a, Branch *et al.* 1999b) and blacktail (Joubert and Hanekom 1980, Coetzee 1986). Vicinity to sandy substrate often causes siltation of reefs which can be tolerated by species that are colonizers of newly exposed, or disturbed habitat such as algae.

Effects of fishing on fish size

The effect of fishing is usually reflected by a decrease of fish sizes at fished sites, compared to protected sites (Leaman 1991). It is understood, however, that for a large dataset, the detection of significant differences in fish sizes is a likely result, due to natural variability (Edgar and Barrett 1999). More important, therefore, is the consistency with which the results point in the same direction. In this study, differences in fish sizes were either not detected or pointed towards lower fish sizes under exploitation. Significantly lower mean sizes outside the Goukamma MPA were recorded for roman, fransmadam, steentjie and dageraad. There were too few santer in the samples to confirm any trend ($p = 0.075$), but average size was again longer inside the MPA. Underwater size estimates confirmed this result for roman. Mean sizes of species generally correlated well with the level of relative fishing effort in the different zones. Roman, santer and dageraad are sought-after target species in the South African linefishery (Buxton 1993, Coetzee and Baird 1981a). Fransmadam and steentjie make excellent bait (Van Der Elst 1993a, Smith and Smith 2003) and are often kept when caught (Smith 2005) and are prone to post-release mortality. These results clearly document the effect of fishing on exploited reef fish species.

Higher mean sizes of roman and other frequently-caught fish species were also measured by Buxton (1987) and Smith (2005) inside the Tsitsikamma NP, compared to fished sites off Port Elizabeth and Plettenberg Bay, respectively. When considering mean sizes of roman, some explanation is offered by exploitation history and MPA size. A high mean size of roman (313 mm) was found in the old and large Tsitsikamma NP (25 years, 250 km^2) where poaching is reduced to zero. A mean size of 302 mm was recorded in the younger and smaller Goukamma MPA (10 years, 40 km^2), where frequent poaching was reported. Due to higher fishing effort mean size was lower outside the Goukamma MPA (279 mm). Finally, in the heavily exploited Plettenberg Bay, a mean sizes of 263 mm was recorded.

However, levels of exploitation between those areas are difficult to compare as the fisheries were surveyed by different methods. A comparison of the size of the human population closest to the nearest access point and accessibility of fishing grounds might give some indication on fishing effort (Jennings and Polunin 1996). Population sizes and accessibility increase from Buffels Bay (<1,000; exposed coastline) to Plettenberg Bay (50,000; sheltered bay), correlating with decreasing target fish sizes.

Burger's (1990) failure to detect any differences in fish sizes other than for red steenbras between the Tsitsikamma NP and a directly adjacent area is most likely attributed to inadequate experimental design. Only one exploited site was investigated for comparison and no quantitative information on the level of fishing effort was obtained.

Effects of fishing on fish and benthic density

Fishing effort was the single most important factor determining fish abundance at Goukamma. Lower roman density under exploitation was also recorded by Buxton and Smale (1989), Burger (1990), Lechanteur (2004) and Smith (2005) for various locations along the South African south coast. The result at Goukamma was expected, given the high proportion of roman in the linefish catch in the study area in combination with a sufficiently high difference in fishing effort among the different zones. Hawkins and Roberts (2003) summarize several studies that show similar fishing-induced effects. As predicted, roman densities correlated negatively with fishing effort ($R^2 = -0.95$; $p = 0.023$; figure 4.63).

a

Study area	TNP	GMPA	GMPA (Outside)	PBB
CPUE	4.6	4.3	3.4	1.3

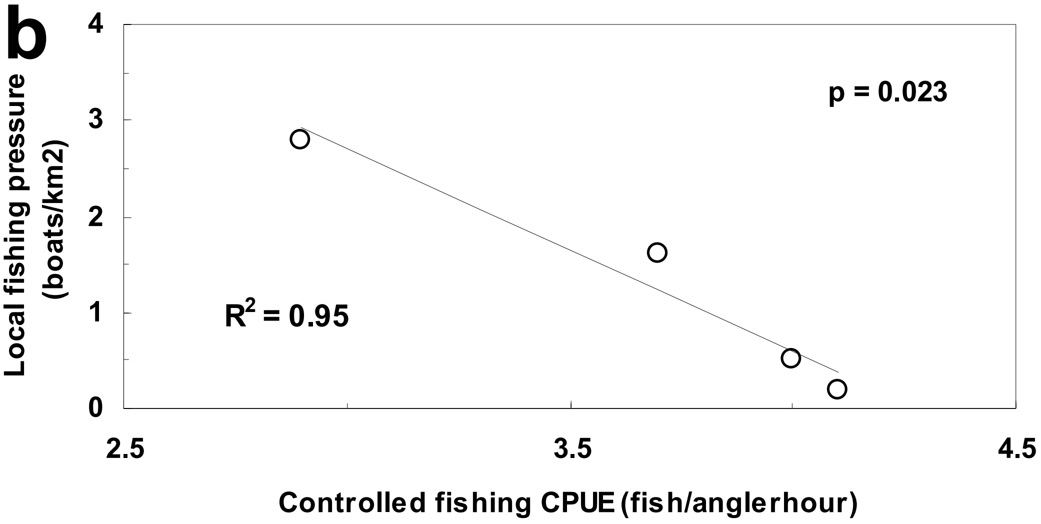


Figure 4.63: Median CPUE of roman recorded by Smith (2005) in the Tsitsikamma NP (TNP), Plettenberg Bay (PBB) and at Goukamma MPA (GMPA) (a) and in the different zones in and around the Goukamma MPA (b) using controlled fishing

The higher numbers of roman inside the MPA are also likely to be the reason for decreased crinoid densities, as they are the main food source for this species (Buxton 1984, Van Der Elst 1993a). The distribution of other fish species in the community is more difficult to interpret. Apart from steentjie, blacktail and strepie, all other species were more abundant under exploitation, although their vulnerability to linefishing was indicated by generally lower mean sizes (see above). It is therefore most likely that the abundance of those fish species are controlled by inter-specific competition, exerted by roman, the most dominant and exploited species in the community.

‘Top-down effects’ in temperate marine ecosystems have been demonstrated by a number of authors and are reviewed by Shears and Babcock (2002). The removal of top-predators by fishing typically resulted in an increase of prey and/or competing species within the ecosystem.

Except for the herbivorous strepie (Van Der Elst 1993a, Antolié *et al.* 1994, Havelange *et al.* 1997, Branch *et al.* 1999b), all investigated species show dietary overlap of varying extend with roman. Santer (Coetzee and Baird 1981a, Smale 1986), dageraad (Buxton 1987), fransmadam (Burger 1990) and blue hottentot (Buxton and Clarke 1985) are omnivorous species like roman (Buxton 1984), possibly resulting in competition for food. On the other hand, the virtual absence of algae in the diet of roman, might be the reason for the increased abundances of strepie, blacktail and steentjie inside the MPA, as steentjie (Burger 1990, Van Der Elst 1993a) and blacktail (Joubert and Hanekom 1980, Coetzee 1986, Mann and Buxton 1992) partly rely on algal grazing. These differences in feeding strategies might allow these species to coexist with roman more easily. Lower densities of algae inside the MPA compared to outside suggest that habitat preference can not be the reason for the observed distribution patterns.

Analogously, competition outside the MPA seems to be reduced by the preference of fransmadam and blue hottentot for different depth ranges. The higher abundance of blue hottentot outside the MPA is also consistent with lower hydrozoan densities, the main food of this species (Buxton and Clarke 1985). Although low in dietary importance for fransmadam, poriferans were only found to be taken by this species (Burger 1990). High fransmadam density outside the MPA (more than 50% of the catch) might, amongst other unknown factors, contribute to the reduced poriferan densities.

Effects of fishing on the fish and benthic community

Fishing-induced changes of reef community structure have been shown in many studies worldwide (e.g. Russ and Alcala 1989, Alcala and Russ 1990, Garcia-Rubies and Zabala 1990, Jennings and Polunin 1996, Wantiez *et al.* 1997, Babcock *et al.* 1999, Edgar and Barrett 1999, McClanahan *et al.* 1999, Shears and Babcock 2003).

Multivariate analysis of the fish and benthic communities at Goukamma confirmed the single species/taxa results discussed above. Fishing was the only factor that consistently explained the different communities found during controlled fishing and UVC.

The results of this study give some insight into trophic and competitive relationships within the reef community under protection (Figure 4.64 a) and exploitation (Figure 4.64 b). It should be noted that the following statements are speculative, but provide a platform for further studies. The high abundance of roman, when fishing effort is low, reduces the abundance of prey (crinoids) and competitors (omnivorous fish). Abundance of those species that can (alternatively) feed on algae, such as steentjie, blacktail and strepie, might be less affected. This, in turn, might also result in low algal density. Reduced numbers of roman due to fishing, reduces inter-specific competition with omnivorous fish such as santer, dageraad, fransmadam and blue hottentot. The highly abundant fransmadam and blue hottentot (comprising up to 60% of the fish counted over reefs) may coexist more easily through depth separation of their habitats, they might, however, reduce steentjie, blacktail and strepie densities through competition for food and space lower down in the dominance hierarchy. As a result, crinoid and algal densities should be higher outside the MPA.

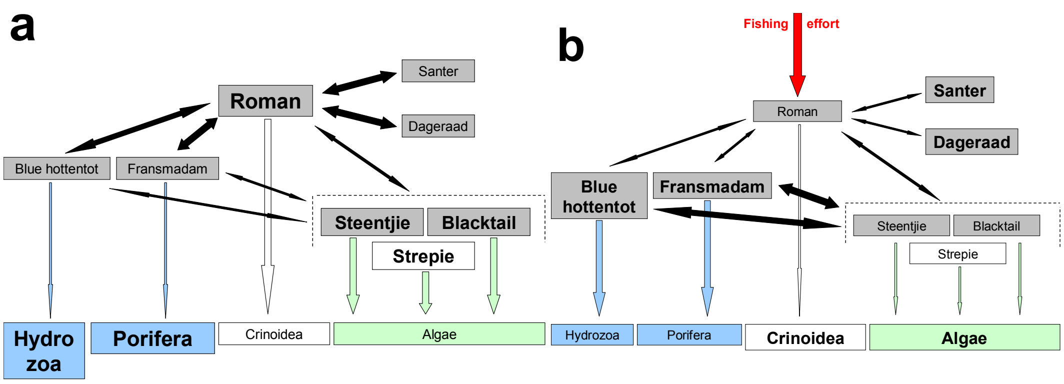


Figure 4.64: Possible food-web of the reef community explaining the observed abundances of taxa under protection (a) and exploitation (b). Grey boxes = species with dietary overlap with roman; black arrows = inter-specific competition; blue objects= part of diet, rarely taken by roman; green objects = part of diet, never taken by roman. Thicker arrows and bold text indicate stronger interactions and higher abundances, respectively

Unfortunately, the information available on feeding of fransmadam and steentjie, comprising up to 70% of the fish counted over reefs, were based on only a few specimens reported in the literature. For a better understanding of food webs on temperate marine reefs in South Africa, further study of feeding habits and diet composition of fish are necessary.

Effects of factors on reef fish diversity

The lower diversity of fish species under exploitation found at Goukamma is similar to trends found in tropical and temperate areas that were studied by UVC (Alcala and Russ 1990, Burger 1990, Garcia-Rubies and Zabala 1990, Jennings et al. 1996, Russ and Alcala 1996, Wantiez *et al.* 1997).

Burger (1990) determined reef fish diversity inside the Tsitsikamma NP and adjacent exploited sites. Absolute values of Margalef's richness and the Shannon-Wiener indices decreased under exploitation and were comparable to this study, when taking into account that the ln- instead of the log-transformation was used. Jennings and Polunin (1996) investigated species richness in relation to exploitation levels of coral reef fish communities at multiple, far apart sites in Fiji. No influence of fishing effort on fish diversity was detected. The authors concluded that the structure of coral reef fish communities is not governed by a single dominant process, but by a range of processes that operate on different scales in different circumstances. Since almost 150 different fish species were considered during UVC surveys, rather complex ecosystem control mechanisms should be expected.

Temperate marine communities, on the other hand, are often more simple in this respect (Nybakken 1993) and few studies have not found differences in fish diversity under different levels of exploitation. The failure of Edgar and Barrett (1999) to detect any difference in fish diversity between Tasmanian MPAs and associated unprotected reference sites could be due to the recent establishment of these MPAs (6 years earlier), or the low power of the statistical tests used, as acknowledged by the authors.

In contrast to UVC, controlled fishing indicated a lower diversity inside the Goukamma MPA, also found by Smith (2005) under similar conditions in the Tsitsikamma NP. In both studies, roman was the most abundant top-predator and main target species of the fishery. High numbers of roman inside these MPAs and the selectivity of fishing towards aggressive top-predators (Ricker 1981), might have obscured the higher species diversity. On the other hand, reduced abundance of roman under exploitation should increase chances of other fish species to be selected by this method, thereby increasing diversity of caught fish at exploited reference sites. The consistency with which the two methods (UVC and controlled fishing) yielded opposite results strengthens this conclusion. Warm and clear water over shallow reefs yielded higher diversities during UVC – cold and turbid water over deep reefs produced higher diversities during controlled fishing surveys. As evident from the single-species analysis using GLMs, roman is less abundant in cold water and over deep reefs, allowing other species to be selected by fishing. As shown in sonar tracking experiments (Kerwath 2005), roman cease feeding and hide in crevices and caves during cold water conditions. Warm water conditions on the other hand increase the diversity of fish, as warm water species protrude further south in summer (Van Der Elst 1993a), but coinciding higher activities of roman obscure this increase as indicated by lower diversities during controlled fishing surveys in summer. Unfortunately, a seasonal comparison of UVC was not possible due to logistic limitations.

Rocky, high-profile reefs and morning hours also supported higher fish diversities during UVC. Many reef fish species are more active in the morning (Buxton 1987, overall CPUE in this study) and rocky high profile reefs should provide more habitat types and niches for a larger variety of fish species than low profile areas with sandy patches.

Conclusions

Goukamma MPA showed substantial differences in diversity, density, size and composition of reef organisms compared to nearby fishing grounds. These differences are most likely a result of protection despite the small size and recent establishment of the MPA.

The systematic design of the experiment facilitated the separation of effects on fish density, size and benthic structure. Whereas it is usually reported that fishing causes changes in fish density and fish size, this study was able to place the relative effects into perspective. Direct comparisons among areas with different fishing mortality could easily be misleading if environmental influences are not taken into account.

Fish and benthic densities across the MPA boundary relate well with results of diet studies but further work in this area is required.

5 EFFECTS OF FISHING ON THE LIFE HISTORY AND POPULATION STRUCTURE OF ROMAN

5.1 INTRODUCTION

Many MPAs have been implemented to protect stocks of reef fish, which are typically slow-growing and sex-changing (Buxton 1993). Studies on the effect of MPAs have mainly focused on abundance and size of fishes between protected and exploited areas (Roberts and Polunin 1991). However, fishing can also change important life history traits of targeted species (Geisel 1976). Few studies have tried to quantify the effects of fishing on life history characteristics of long-lived reef fish (Leaman 1991), and these studies often suffered from a lack of a detailed experimental design. For example, Hawkins and Roberts (2003) found significant differences in the sex ratio of protogynous parrotfish under different rates of exploitation in the Caribbean. Unfortunately, fish sizes were only estimated and sex determined during UVC, and no biological samples were used. In South Africa the effects of exploitation on life history traits of two sparid reef fish were examined by Buxton (1993). Samples were obtained from the comparably large Tsitsikamma NP (250 km^2), the first marine park to be established in the country some 25 years earlier, and the Port Elizabeth area, 200 km away. On this geographic scale, genetic and environmental differences between populations cannot be ruled out as reason for the different life history traits observed.

Apart from food and habitat availability (Lloret and Planes 2003) exploitation may influence fish condition by altering the intensity of competition. Hence, if all other factors are equal, the condition of an exploited fish population should be lower where fishing effort is reduced. Many studies on the condition of reef fish have focused on the importance of habitat quality for marine fish physiology (Kerrigan 1994, Francis 1997, Berumen *et al.* 2005). Few studies have aimed to assess the effect of exploitation on the condition of fish. Lloret and Planes (2003) determined the condition of white seabream (*Diplodus sargus*), a sparid reef fish in the Mediterranean, in relation to habitat quality and exploitation. The fish in the protected area were in better condition. The effect of fishing on fish condition was uncertain due to better habitat quality within the MPA.

In this study the Goukamma MPA and adjacent areas were used to investigate the effect of fishing on the life history of temperate marine fish under different rates of exploitation. Immediately adjacent sites were chosen to eliminate uncertainty caused by environmental and genetic variations. The study species chosen was the roman, a sex-changing sparid. Roman is the main target species of the reef fishery at Goukamma, and stocks of this species are particularly vulnerable to recruitment failure due to increased mortality of larger, male individuals (Buxton 1993). This chapter therefore examines growth, age-at-maturity and sex-change and condition of the protected and exploited part of the roman population. The data was then used to assess the status of the stock through the use of appropriate mathematical models. Age structured population models require reliable estimates for fishery parameters such as catch-at-age, catch rate and the relationship of stock size to recruitment (Butterworth *et al.* 1989). These data are usually not available in the study of reef fisheries (Huntsman *et al.* 1983) and per-recruit (*P/R*) models, which are simplified versions of the full dynamic pool model, are more commonly used in the planning of reef fisheries (Huntsman *et al.* 1983, Manooch and Mason 1984, Buxton 1993). A similar constraint applied to the current study and data were only sufficient for the use of *Y/R* and *SB/R* models. Finally the results are used to examine different management recommendations based on these models, with particular reference to sex-change and phenotypic plasticity of life history traits of this species.

5.2 MATERIAL AND METHODS

Target species

Samples of fish, stratified across size and zone, were retained for biological examination to test for differences in life history parameters that may be related to fishing. Only roman was caught in sufficient numbers over a wide size range to allow sufficient stratification across factors.

Sampling interval and site selection

To retain the pristine nature of the population structure of roman inside the MPA for the duration of the study, samples for biological examination were taken at the end of the study period. Sampling was conducted over a ten day period at the end of January 2004, the middle of the spawning season for this species.

Two geographically separated samples were collected (Figure 5.1). The sample representing a population in undisturbed conditions (hereafter referred to as 'inside-sample') was taken within the area $\mathbf{L_{0.9}}$ (see chapter 3) inside the MPA, which had the lowest fishing effort. The second sample, representing an exploited population (hereafter referred to as 'outside-sample') was taken offshore of this area, where the fishing effort was highest. The relative difference in fishing effort between these two sampling areas was one to 14.

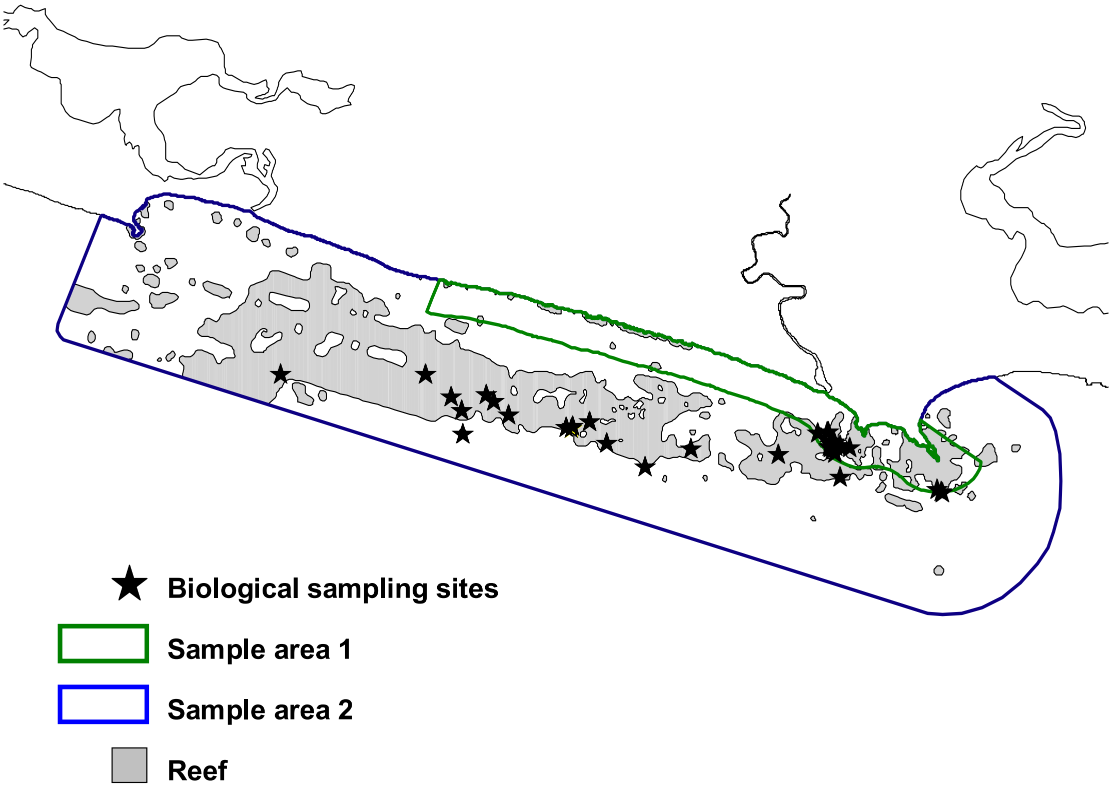


Figure 5.1: Study area showing the positions of 39 sampling sites. Sample area 1 corresponds to $L_{0.9}$, which was an unexploited area. Sample area 2 was exploited.

Sampling design and procedure in the field

The target sample size for each area (exploited and unexploited) was set at 150 fish. Each sample consisted of ten 20-mm size classes with ten fish collected for every 20-mm size class, ranging from 140 to 420 mm. Fish in the range 140-200 mm and 360-420 mm were generally under-represented in the catch and were obtained by spear-fishing using SCUBA. Each fish was measured (fork length – one millimetre) and weighed to the nearest gram (Electronic Balance, Adam Equipment MW 5000 – Capacity: 5000 × one gram). Sagittal otoliths were removed, cleaned and stored dry for later age determination. The gonads were sexed, removed and staged according to their development using visual criteria (Table 5.1), and subsequently stored in 70% ethanol for later weight determination to the nearest 0.1 g.

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

Table 5.1: Classification of maturity stages in roman modified from Buxton (1987)

Preparation and reading of otoliths in the laboratory

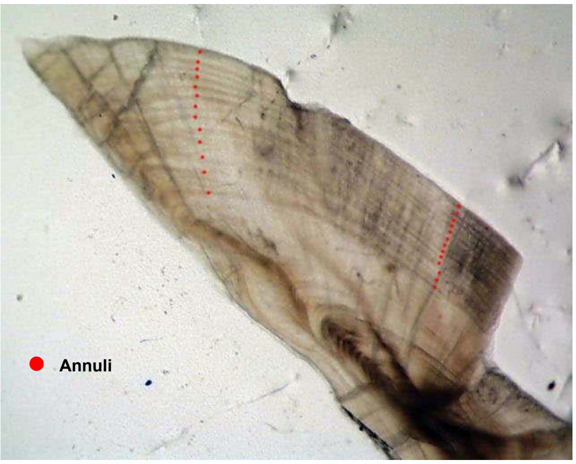


Figure 5.2: Photomicrograph of sectioned sagittal otolith of a 13 year old roman

Sagittal otoliths were embedded in clear casting resin, sectioned to 0.2 - 0.5 mm through the nucleus using a diamond-edged, double bladed saw, and mounted on slides with DPX mountant (Mixture of distyrene, plasticizer: tricresyl phosphate and xylene). Alternating opaque and hyaline zones were separated and counted with each otolith being read at least twice under transmitted and reflected light (see figure 5.2) using a dissecting microscope (Kyowa FIBRE OPTIC FL-150 with 44 mm lens). Readings were undertaken at a weekly interval without knowledge of fish lengths. If the two readings did not agree, a third was taken. If the three readings differed by only two years the median age estimate was taken, otherwise the otolith was rejected (Buxton 1993).

Age and growth calculations

The von Bertalanffy growth equation was used to model length-at-age:

$$L_t = L_\infty (1 - e^{-K(t-t_0)}), \tag{5.1}$$

where L_t is length at time t, L_∞ is the theoretical asymptotic length, K is the body growth coefficient that determines the rate at which L_∞ is attained, and t_0 the age of fish with zero length. Generalized non-linear least squares procedures were used to estimate growth parameters. Parameter variance was calculated using parametric bootstrap by resampling 500 bootstrap replicates. The first-order bias-corrected percentile method (Efron and Tibshirani 1993) provided confidence intervals from the sorted bootstrap data.

To determine whether the von Bertalanffy or the Schnute growth equation modelled growth more realistically, the same non-linear least squares procedure was fitted to the age-length samples using the Schnute growth equation. Model fit was compared using a likelihood ratio test. Calculations were conducted for the whole sample as well as for the 'inside-' and 'outside-sample' separately. Differences in growth parameters estimated from the samples from each zone were tested using a likelihood ratio test. All calculations were done using macros in EXCEL.

Determination of age-at-maturity and sex-change

The age-at-sexual maturity was determined by fitting a logistic ogive to the proportion of reproductively active female fish sampled during the spawning season (Booth and Buxton 1997a). The two-parameter logistic ogive was fitted using the non-linear least squares procedure (Booth and Buxton 1997b, Welcomme 2001):

$$P_a = (1 - e^{-(a - a_{50} / \delta)})^{-1} \tag{5.2}$$

where P_a is the percentage of mature fish at age a, a_{50} is the age at 50% maturity and δ is the rate with which sexual maturity is attained. Parameter variance was calculated using parametric bootstrap by resampling 250 bootstrap replicates. The first-order bias-corrected percentile method (Efron and Tibshirani 1993) provided confidence intervals from the sorted bootstrap data.. Age-at-50 % sex-change was determined analogously, by fitting the logistic ogive to the proportion of reproductively active male fish. Calculations were conducted for the entire sample as well as for the 'inside-' and 'outside-sample' separately. Differences in a_{50} and δ estimated from these samples were tested using a likelihood ratio test. Using the same methods, length-at-50% maturity and length-at-50% sex-change was determined. All calculations were done in EXCEL.

Determination of sex ratio

The entire datasets from the fishing survey (1089 specimens) and diving survey (539 length estimates) were used to construct a sex-at-length key and transform length frequencies into sex ratios within the different sampling areas. Differences in sex ratios among sampling areas were then investigated using chi-square contingency tables in EXCEL.

Condition factor

The condition factor (*K*) describes the relationship between length and weight of a fish and is calculated from Weatherley (1972):

$$K = W / L^3, \qquad (5.3)$$

where *W* and *L* are the observed weight and length.

Condition factors were calculated for the entire dataset and separately for the inside- and outside-samples. Differences in condition factors were tested using parametric Students t-test if assumptions of normality and homogeneity were met. If assumptions were not fulfilled after log-transformation of the data, a non-parametric Mann-Whitney U test was applied. Comparisons were also carried out within each sample between mature and immature fish of similar size classes and between samples using only mature fish of similar size classes. This was done to avoid bias in condition factor calculations due to earlier maturation of fish within the outside-sample and differences in length frequency distributions between the inside- and outside-sample. All calculations were conducted in STATISTICA.

Mortality estimates

Annual mortality for roman in the study area was estimated using direct and indirect methods. Direct estimates were obtained through catch curve analysis (Ricker 1975) of the entire dataset from the fishing survey (1089 specimens). An independent direct estimate was obtained by analysis of 539 length frequency estimates from the diving survey (Buxton 1987). An age-length key, constructed from length-at-age data was used to transform length frequency distributions to age frequency distributions (Butterworth *et al.* 1989). The slope of a straight line fitted to points on the descending limb provides an estimate of total mortality (Z).

All calculations were conducted for the inside- and outside-samples separately as well as for the combined datasets. Mortality estimates from the catch and diving survey length frequency data were tested for differences using the homogeneity-of-slopes model. The total annual mortality calculated for the inside-sample was used as an estimate of M. Additionally, two indirect methods were used to estimate natural mortality (M).

Pauly (1987):

$$\log(M) = -0.0066 - 0.279\log(L_\infty) + 0.6543\log(K) + 0.4634\log(T)\,, \qquad (5.4)$$

where T is the mean annual water temperature (°C) of the species' environment and L_∞ and K are von Bertalanffy parameters.

Hoenig (1983):

$$\ln(M) = 0.941 - 0.873\ln(t_{\max})\,, \qquad (5.5)$$

where $t_{\max}$ is the age of the oldest fish in the sample.

Fishing mortality ($F = Z - M$) is obtained by substitution (Gulland 1985). Calculations were done in EXCEL and STATISTICA.

Yield-per-recruit (Y/R) and spawner biomass-per-recruit (SB/R) analysis

Fishing mortality varies with age, due to hook selectivity of the fish. In this per-recruit (*PR*) analysis, age-specific selectivity was modelled using the logistic model (Butterworth *et al.* 1989) described as:

$$S_t = (1 + e^{-(t - t_{50} / \delta)})^{-1} \tag{5.6}$$

where S_t is the selectivity of the gear on a fish of age t, t_{50} is the age-at-50% selectivity, and δ is the rate of change. The total biological dataset from the fishing survey (1089 specimens) was used to construct an age-length key and transform length frequency to age frequency.
Y/R was calculated as (Chen and Gordon 1997):

$$Y / R = \sum_{t_R}^{t_{\max}} C_t W_t \tag{5.7}$$

where C_t is the catch of the tth age class, W_t is the average weight of fish of the tth age class, t_R is the age of recruitment and t_{max} is the age of the oldest fish in the fishery.

Using the exponential survival function and the catch equation (Ricker 1975), the model becomes:

$$Y / R = \sum_{t_R}^{t_{\max}} \left[W_t S_t F \frac{1 - e^{-S_t F - M_t}}{S_t F + M_t} e^{-\sum_{k=t_R}^{t-1} (S_k F + M_k)} \right] \tag{5.8}$$

where S_t is the selectivity coefficient for fish of the age t, F is the fishing mortality rate, and M_t is the natural mortality rate at age t.

SB/*R* was described as a function of F (Kanyerere 2003):

$$SB / R = \sum_{t_R}^{t_{\max}} \left[W_t \Psi_t e^{-\sum_{k=t_R}^{t-1} (S_k F + M_t)} \right] \tag{5.9}$$

where Ψ_t is the proportion of fish at age t that are mature. W_t is the begin-year mass of a fish at age t and is defined as (Wootton 1999a):

$$W_t = a(L_t)^b \text{, with } L_t = L_\infty\left(1 - e^{-K(t-t_0)}\right) \tag{5.10}$$

where L_∞, K and t_0 are the von Bertalanffy growth parameters and a and b are the parameters of the mass-length relationship.

The values of F_n were obtained by solving the equation (Punt 1997):

$$\left.\frac{d(Y/R)}{dF}\right|_{F=F_n} = n\left.\frac{d(Y/R)}{dF}\right|_{F=0}, \tag{5.11}$$

where $F_{0.1}$ and F_{max} correspond to a slope of 10% and 0%, respectively.

Fishing mortality corresponding to the quantity $F_{SB(x)}$ was obtained by solving the equation:

$$F_{SB(x)} = F_{SB(F=0)} \times x \tag{5.12}$$

where $F_{SB(x)}$ is the fishing mortality that reduces SB/R to x% of the pristine $(SB/R)_{F=0}$.

All computations were conducted using macros in EXCEL and isopleths were calculated using the bivariate interpolation method for irregular grids in SigmaPlot. Calculations were conducted for the combined datasets as well as for the inside- and outside-sample separately for the two estimates of M (calculated with the fishing and diving data).

5.3 RESULTS

Stratification and sample size

Using a combination of linefishing and SCUBA, 168 roman were obtained for the 'inside-sample' and 119 for the 'outside-sample' (Figure 5.4). It was not possible to obtain ten fish for the largest size-classes.

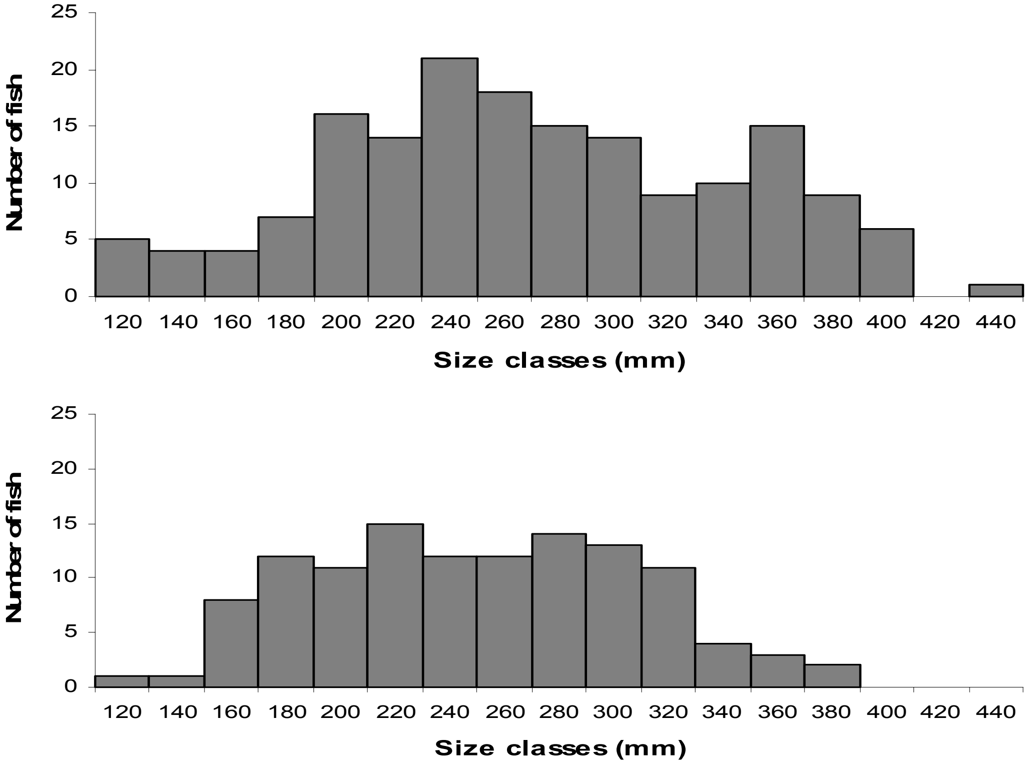


Figure 5.4: Number of samples obtained for the inside- (a) and outside- sample (b)

Age and growth

The otoliths of 250 fish were readable and used for age and growth calculations. Ages ranged from two to 19 years. The fit of the von Bertalanffy and Schnute growth models were not significantly different (p = 0.570; likelihood ratio test). Growth parameters were not different between samples (Table 5.2).

	Sample area			
Parameter	**combined**	**inside**	**outside**	**p-value (inside-outside)**
L_∞	512.86 mm (FL)	504.07 mm (FL)	510.77 mm (FL)	0.93
K	0.086 year^{-1}	0.091 year^{-1}	0.084 year^{-1}	0.79
t_0	-1.77 year	-1.50 year	-2.02 year	0.52

Table 5.2: Parameter estimates for length-at-age data fitted using the von Bertalanffy model for the whole dataset, the inside-sample and the outside-sample. p-values derived from likelihood ratio tests for differences among parameters of different samples are indicated

The observed and expected mean lengths-at-age for the entire dataset and the length-at-age von Bertalanffy growth curves for the three different datasets can be reviewed in the appendix (Table 8.1 and figure 8.7, respectively).

Age at maturity and sex-change

Age- and length-at-50% maturity and sex-change were significantly lower in the outside-sample (Table 5.3).

	Sample area			
Parameter	**combined**	**inside**	**outside**	**p-value**
Age-at-50% maturity (t_{M50})	3.49 y	4.27 y	2.97 y	0.026*
Logistic delta (δ_{tM50})	1.67	1.22	1.13	0.353
Length-at-50% maturity (l_{M50})	183.59 mm (FL)	202.83 mm (FL)	167.43 mm (FL)	0.002**
Logistic delta (δ_{lM50})	43.12	27.50	33.61	0.636
Age-at-50% sex-change (t_{SC50})	9.14 y	10.25 y	7.99 y	<0.001**
Logistic delta (δ_{tSC50})	1.10	0.93	0.89	0.853
Length-at-50% sex-change (l_{SC50})	310.47 mm (FL)	330.2 mm (FL)	289.91 mm (FL)	<0.001**
Logistic delta (δ_{lSC50})	14.44	10.78	7.68	0.310

Table 5.3: Summary of parameter estimates for age- and length-at-50% maturity and sex-change for the complete dataset, the inside-sample and the outside-sample. p-values derived from tests for differences among parameters of the inside- and outside-sample are shown. * indicates significant p-value < 0.05. ** indicates significant p-value < 0.01

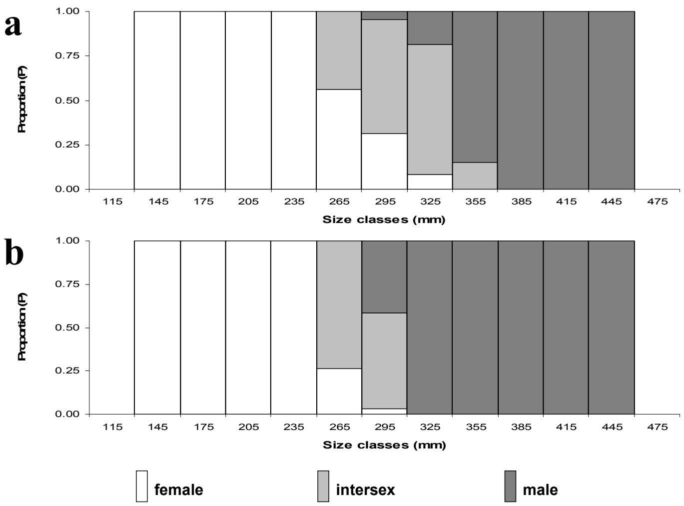


Figure 5.5: Proportion of males, intersexes and females within each size class in the inside-sample (a) and outside-sample (b)

The shift of sex-change to smaller size-classes within the outside-sample can be clearly illustrated with a sex-separated length frequency diagram (Figure 5.5).

Logistic ogives illustrating the relationship between sexual maturity, sex-change and age or length can be reviewed in the appendix (Figure 8.8).

Sex ratio

Sex ratios were calculated using the entire dataset from the fishing and diving surveys using a sex-at-length key (Table 5.4). Female proportions were significantly lower for the fishing survey dataset ($p < 0.01$), as compared to the diving survey dataset.

To demonstrate the effect of reduced size-at-maturity and sex-change on sex ratios, parameters obtained from the inside-sample were applied to the outside-sample. This skews the sex ratios towards higher female proportions in the outside-sample. The decreased size-at-maturity and sex-change actually observed in the outside-sample compensates for the relative scarcity of larger (male) individuals, resulting in sex ratios skewed towards higher male proportions.

(Dataset)	**Observed sex ratio**			**Sex ratio assuming equal size at maturity&sex change**		
Sample area	**female**	**intersex**	**male**	**female**	**intersex**	**male**
(Fishing survey)						
Inside	1.5	0.4	1.0	1.5	0.4	1.0
Outside	1.0	0.2	1.0	4.0	1.0	1.0
p-value		**< 0.01***			**< 0.01***	
(Diving survey)						
Inside	4.9	0.5	1.0	4.9	0.5	1.0
Outside	4.1	0.3	1.0	11.3	0.8	1.0
p-value		**> 0.1**			**< 0.05***	

Table 5.4: Comparison of sex ratios between the inside- and outside-sample from the fishing- and diving survey dataset. Expected sex ratios for equal size-at-maturity and sex-change for both sample areas as well as p-values from comparative tests are indicated. * indicates significant p-value

Mortality estimates

The instantaneous annual mortality rate was estimated by catch-curve analysis applied to the fishing and diving data within the two sampling areas (Figure 5.6). The mortality estimates determined from the inside-samples are assumed to be an estimate of *M*, due to the lack of fishing effort in combination with the restricted movement of roman (Kerwath 2005). Mortality rate estimates did not differ between sampling methods (controlled fishing- and UVC survey length frequencies), however, there was a highly significant difference among mortality rates estimated from the inside- and outside-samples (Table 5.5).

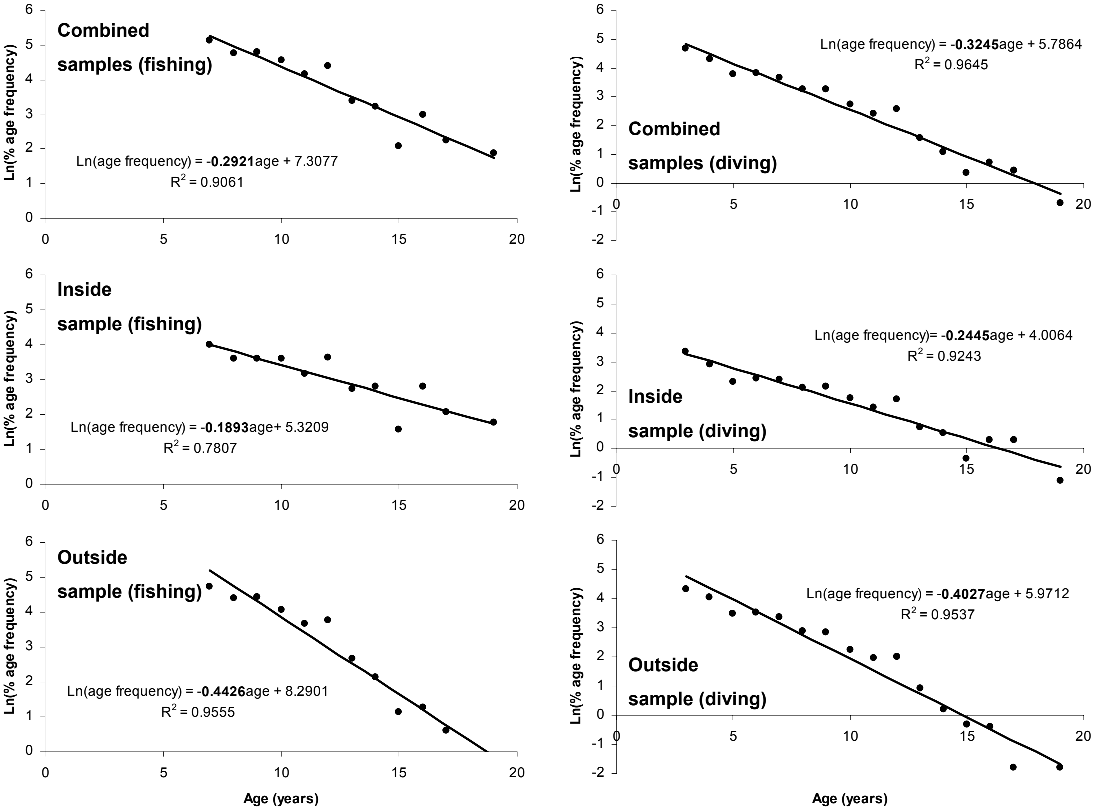


Figure 5.6: Mortality rates estimated from the descending limbs of catch curves using data derived from controlled fishing- and diving surveys, for all areas (combined) and inside and outside the unexploited zone

	Sample area			
Dataset	**combined (*Z*)**	**inside (*M*)**	**outside (*Z*)**	**p-value (inside-outside)**
Fishing survey	0.29 y^{-1}	0.19 y^{-1}	0.44 y^{-1}	<0.001*
Diving survey	0.32 y^{-1}	0.24 y^{-1}	0.40 y^{-1}	<0.001*
p-value	0.85	0.14	0.33	

Table 5.5: p-values from comparative tests among mortality estimates derived from different datasets and sample areas. * indicates significant p-value < 0.001

In addition to direct methods, the indirect methods of Pauly and Hoenig were applied to obtain an estimate of *M* from the controlled fishing survey dataset (Table 5.6). *F* was calculated by subtraction (i.e. *F* = *Z* - *M*).

Sample area	**Catch curve analysis**			**Pauly's estimates**		**Hoenig's estimates**	
Fishing survey	***Z***	***M***	***F***	***M***	***F***	***M***	***F***
Combined	0.29	0.19	0.10	0.25	0.04	0.23	0.06
Inside	0.19	0.19	0.00	0.26	-0.07	0.23	-0.04
Outside	0.44	0.19	0.25	0.25	0.20	0.32	0.16
Diving survey							
Combined	0.32	0.24	0.08	0.25	0.08	0.23	0.09
Inside	0.24	0.24	0.00	0.26	-0.02	0.23	0.01
Outside	0.40	0.24	0.16	0.25	0.16	0.32	0.09

Table 5.6: Summary of all calculated mortality estimates using direct and indirect methods. *F* is determined by subtracting estimates of *M* from *Z*. Three methods of estimating *M* were used (catch curve analysis in MPA, Pauly's and Hoenig's relationships) and each yielded a different estimate of *F*

Condition factor (K)

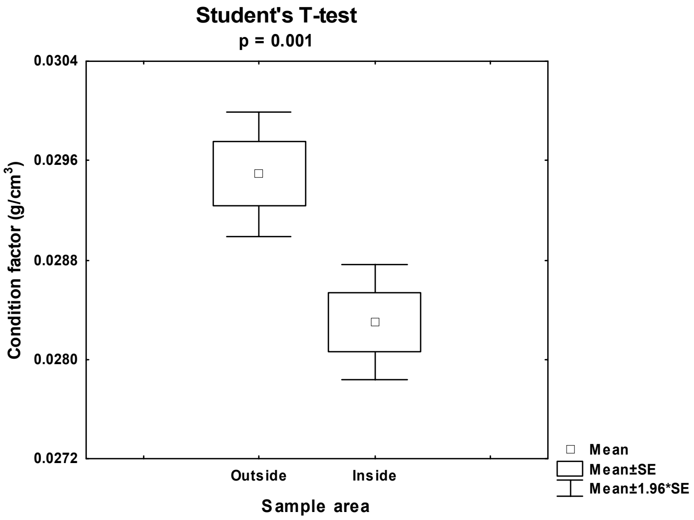


Figure 5.7: Comparison of mean condition factors of mature roman between 200 and 300 mm sampled in the inside- and outside area

Due to limited availability of larger size classes in the outside area, the mean length of the inside-sample (278.6 mm) was significantly higher (p = 0.012) than the mean length of the outside sample (258.5 mm). There was no difference in mean condition factors between mature and immature roman within size-classes and within sample areas (p = 0.905 / p = 0.917).

Differences in mean condition factor between the inside- and outside-sample were tested using mature individuals between 200 and 300 mm. Condition factors were normally distributed (p = 0.316 / p = 0.299; inside- and outside-sample, respectively) and the variances comparable (p = 0.824). The mean condition factor of fish outside the protected zone was significantly higher (p = 0.001) than of fish inside the protected zone (Figure 5.7). Gonad weights of these samples were not different (tested using parametric ANOVA).

Per-recruit analysis

Coefficients in the mass-length relationships for the combined sample and for the two different areas were determined as 0.00102 for ‘a’ and between 3.0681 and 3.0918 for ‘b’, indicating allometric growth for fish in all sample areas (Figure 5.8).

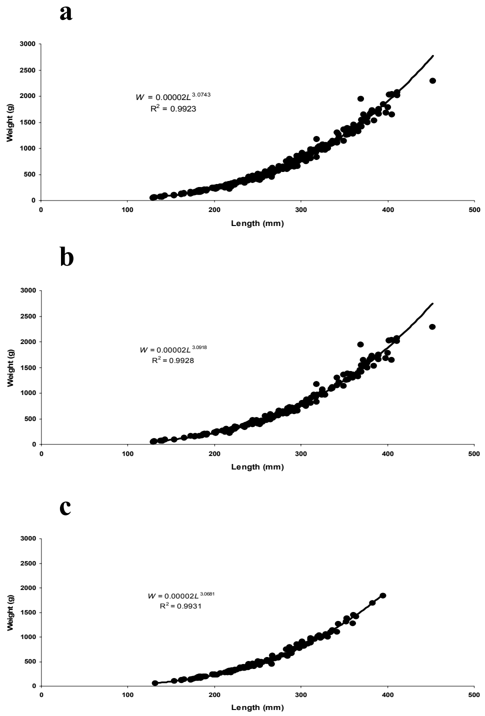


Figure 5.8: Mass-length relationship for roman sampled in the whole study area (a), the inside-area (b) and the outside area (c)

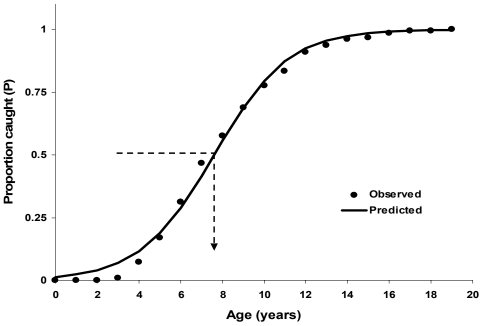


Figure 5.9: Selection ogive for roman in the line-fishery (n = 1082)

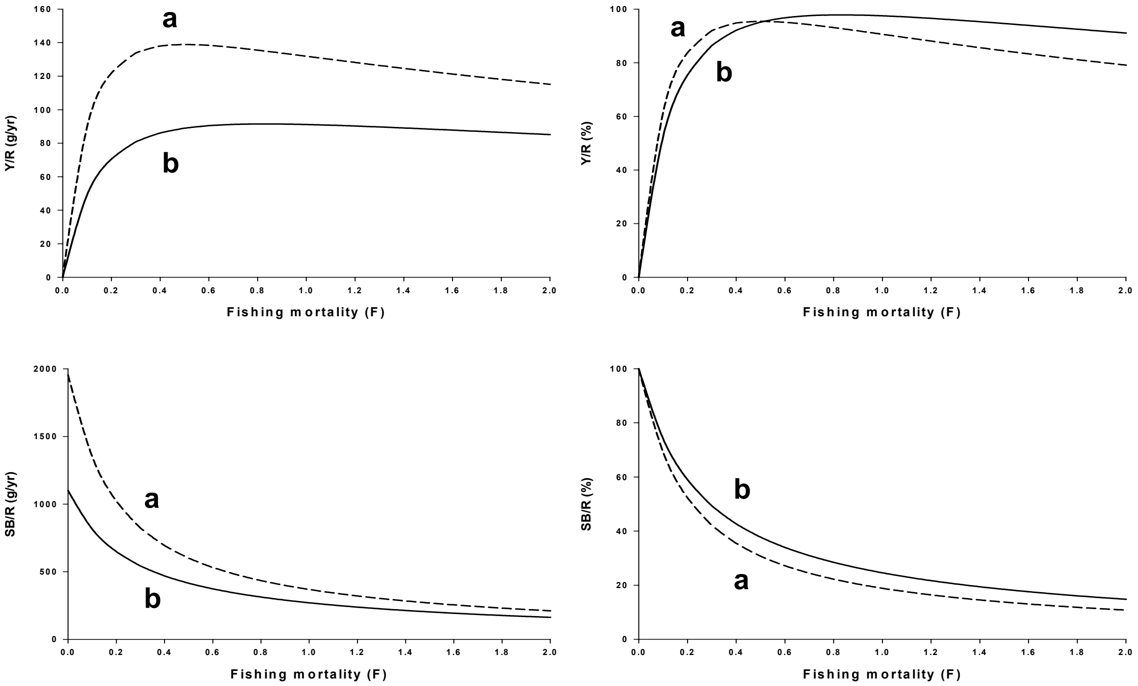
Age-at-50% selectivity for the line-fishery was estimated at 7.60 y with a rate of change (δ) of 1.77 y^{-1} (Figure 5.9). Additional parameters for the *Y/R* analysis were obtained from the age and growth analysis (Table 5.7). Due to uncertainty associated with estimates of *M*, both the estimates derived from the controlled fishing and UVC survey datasets were used.

	Value per sample area		
Parameter	**combined**	**inside**	**outside**
L_{∞}	512.86 mm (FL)	504.07 mm (FL)	510.77 mm (FL)
K	0.086 y^{-1}	0.091 y^{-1}	0.084 y^{-1}
t_0	-1.77 y	-1.50 y	-2.02 y
M (fishing / diving survey dataset)	0.19 / 0.24	0.19 / 0.24	0.19 / 0.24
a (mass-length relationship)	0.00002	0.00002	0.00002
b (mass-length relationship)	3.0743	3.0918	3.0681
t_{M50}	3.49 y	4.27 y	2.97 y
δ_{tM50}	1.67 y^{-1}	1.22 y^{-1}	1.13 y^{-1}
t_{SC50}	9.14 y	10.25 y	7.99 y
δ_{tSC50}	1.1 y^{-1}	0.93 y^{-1}	0.89 y^{-1}
Age-at-(50%)- recruitment (t_R)	7.6 y	7.6 y	7.6 y
Logistic delta (δ_{tR})	1.77 y^{-1}	1.77 y^{-1}	1.77 y^{-1}
t_{max}	19 y	19 y	14 y

Table 5.7: Summary of parameters used in the per-recruit analyses for the entire data set, the inside-sample and the outside-sample

Y/R and *SB/R* curves for roman at the current t_R (7.60 y) and for the two estimates of *M* are shown in figure 5.10. As mentioned previously estimates of *M* derived from the fishing- and diving survey data (0.19 and 0.24 y^{-1}, respectively) were applied when calculating *Y/R* and *SB/R*. The biological reference points F_{max} and $F_{0.1}$ ranged between 0.23 - 0.30 and 0.50 - 0.83 y^{-1}, respectively, for the lower *M* value. Current fishing effort (F_{cur}) derived from catch curve analysis using the fishing survey data was estimated at 0.25 y^{-1}, being just above the biological reference points $F_{0.1}$ (0.23 y^{-1}). This suggests an optimal exploitation by the fishery. However, F_{cur} estimated analogously from the diving survey data (0.16 y^{-1}) suggests an under exploitation of the resource, with an $F_{0.1}$-value of 0.30 y^{-1}.

SB/R declines rapidly with an increase in *M* (Figure 5.10). Values of F_{SB50}, F_{SB40} and F_{SB25} were 0.22, 0.33 and 0.68 y^{-1} for the lower estimate of *M* (0.19 y^{-1}) and 0.29, 0.45 and 0.97 y^{-1} for the higher estimate of *M* (0.24 y^{-1}). *SB/R* as a percentage of the pristine unfished condition for the biological reference points of F_{max} and $F_{0.1}$ are 31 and 49% for the lower *M* (0.19 y^{-1}) and 28% and 49% for the higher *M* (0.24 y^{-1}), respectively. This suggests that $F_{0.1}$ acts as a conservative biological reference point for the investigated population for both estimates of *M*, with the current fishing effort of 0.25 y^{-1} optimally exploiting the resource at a *SB/R* value of 47%. However, for the second estimate of current fishing effort (0.16 y^{-1}) the resource appears under exploited with a *SB/R* value of 64%.



	M	$F_{0.1}$	$F_{\max}$	F_{SB50}	F_{SB40}	F_{SB25}	$F_{current}$
a	0.19	0.23	0.50	0.22	0.33	0.68	0.25
b	0.24	0.30	0.83	0.29	0.45	0. 97	0.16

Figure 5.10: *Y/R* and *SB/R* as functions of *F* (with biological reference points) for roman in the entire study area for two estimates of *M* (a = 0.19 y^{-1}, b = 0.24 y^{-1}) and a t_R value of 7.60 y. Curves are presented in g/year and as a percentage of the maximum expected *SB/R* of an unfished year class ($SB/R_{\max}$)

Y/R expressed as a percentage of the maximum expected *Y/R* decreases more slowly after reaching the maximum in the case of the population with the higher *M* (Figure 5.10). The same is true for *SB/R* expressed as percentage of the maximum expected *SB/R* of an unfished year class.

Isopleths illustrating the response of *Y/R* to different values of *F* and t_R for roman for the two estimates of *M* were calculated (Figure 5.11). Biological reference points, current *F* and current t_R are indicated. Yield increases rapidly at low values of *F* over most of the range of t_R. For low t_R, maximum possible yield is reached at considerably low values of *F*, than yield decreases slowly but steadily at higher values of *F*. At t_R values around 8 y for the higher value of *M* and around 6 y for the lower value of *M*, maximum yield reaches a plateau at an *F* value of about 0.30 y^{-1}. However, the maximum possible yield is only reached at 0.50 and 0.83 y^{-1} for the lower and higher *M* values, respectively. Beyond those ages-at-recruitment, maximum yield is not attained irrespective of the value of *F*. It is obvious from figure 5.11 that $F_{0.1}$ and F_{cur} never reach this plateau of maximum yield irrespective of t_R. For the current t_R, an increase in current *F* to 0.33 and 0.45 y^{-1} for the *M* values of 0.19 and 0.24 y^{-1} respectively, will elevate yields onto this plateau coinciding with the biological reference point F_{SB40}.

Plots of expected biomass-per-recruit against age for fished and unfished populations were calculated for the two estimates of natural mortality (Figure 5.12) Expected *SB/R* is generally lower for the higher *M*. Fishing reduces male biomass to more than half the unexploited biomass, unfished levels, at all biological reference points. In particular for high *M* (Figure 5.12 b), $F_{\max}$ and F_{SB25} reduce the male biomass to dramatically low levels. However, current *F* (0.25 and 0.16 y^{-1}) preserves comparably high levels of male biomass.

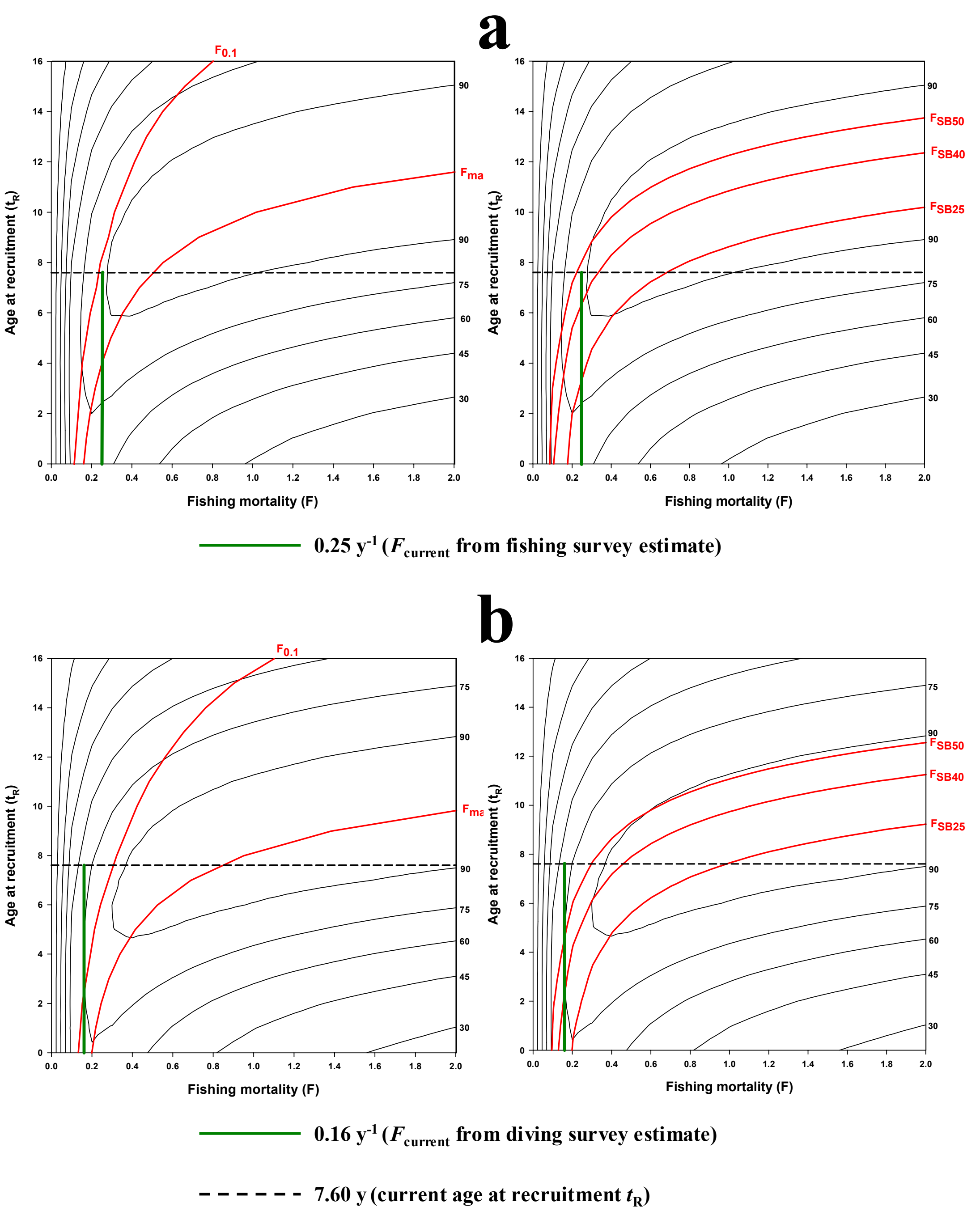


Figure 5.11: *Y/R* isopleths expressed as a percentage of the maximum expected *Y/R* (Y/R_{max} at F_{max}) for roman at a *M* of 0.19 y^{-1} (a) and 0.24 y^{-1} (b). Biological reference points, current *F* and current t_R are indicated

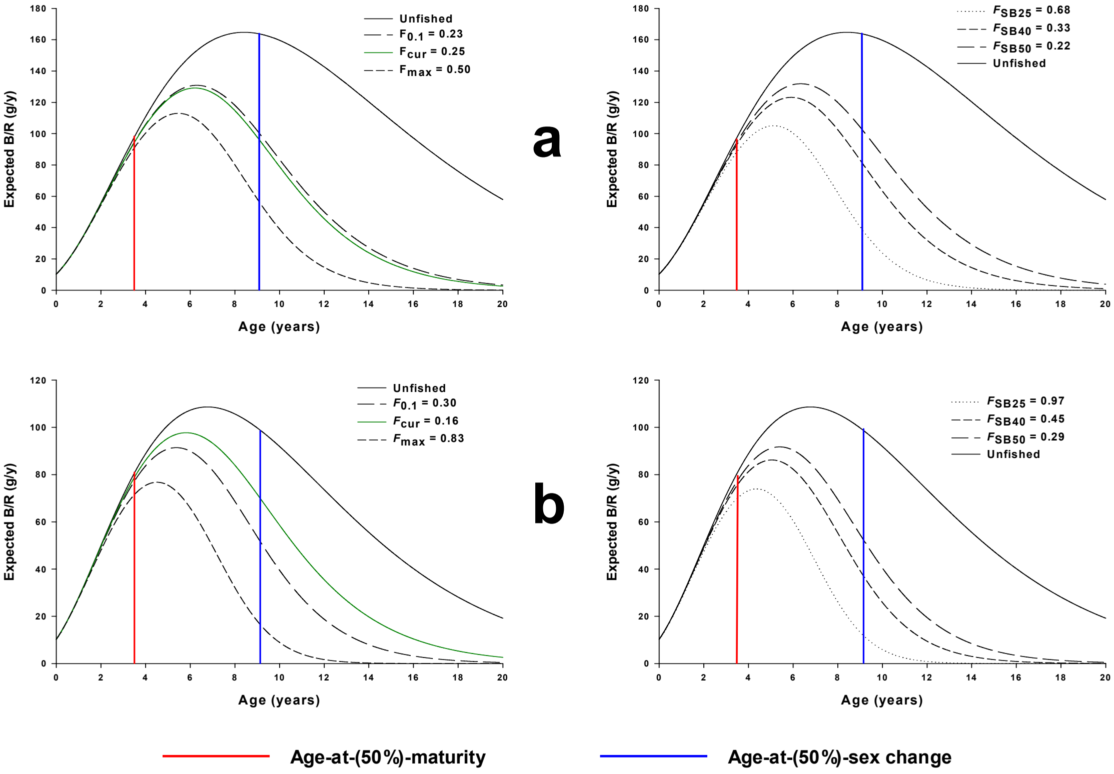


Figure 5.12: Expected biomass-per-recruit (*B/R*) for fished and unfished populations of roman at the current t_R of 7.60 y and M values of 0.19 y^{-1} (a) and 0.24 y^{-1} (b). Biological reference points, current F and age-at-50% maturity and sex-change are indicated

The effect of fishing on roman population structure is better illustrated by looking at changes of expected male and female *SB/R* with increasing *F* (Figure 5.13 a). For both estimates of *M*, the initially higher male spawner biomass drops below female spawner biomass at low *F*. Female spawner biomass is generally less affected by fishing effort. Again, when looking at relative decrease of spawner biomass as a percentage of the unfished spawner biomass, populations at higher *M* are slightly less affected by fishing effort.

Lower values of age-at-50% maturity and at sex-change have the effect of maintaining overall *SB/R* at a higher value for all values of *F*. If the parameter values found in the unexploited population are used, *SB/R* is strongly reduced by fishing (Figure 5.13 b).

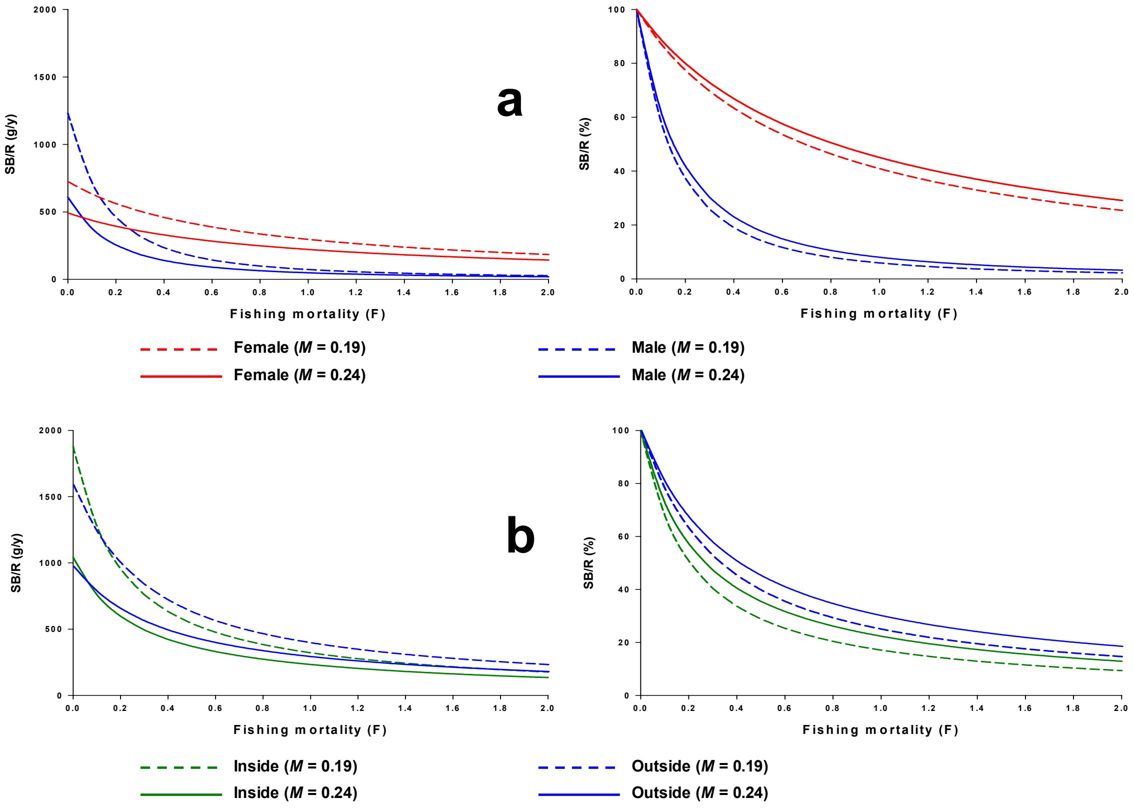


Figure 5.13: *SB/R* as functions of *F* for roman for males and females (a) and (b) the inside- and outside-sample separately at different levels of *M* and current t_R of 7.60 y. Curves are presented in g/y and as a percentage of $SB/R_{\max}$

This relationship holds true over the whole range of t_R (Figure 5.14). Spawner biomass is well protected at current fishing efforts and t_R in the inside- and outside population due to decreased age-at-maturity.

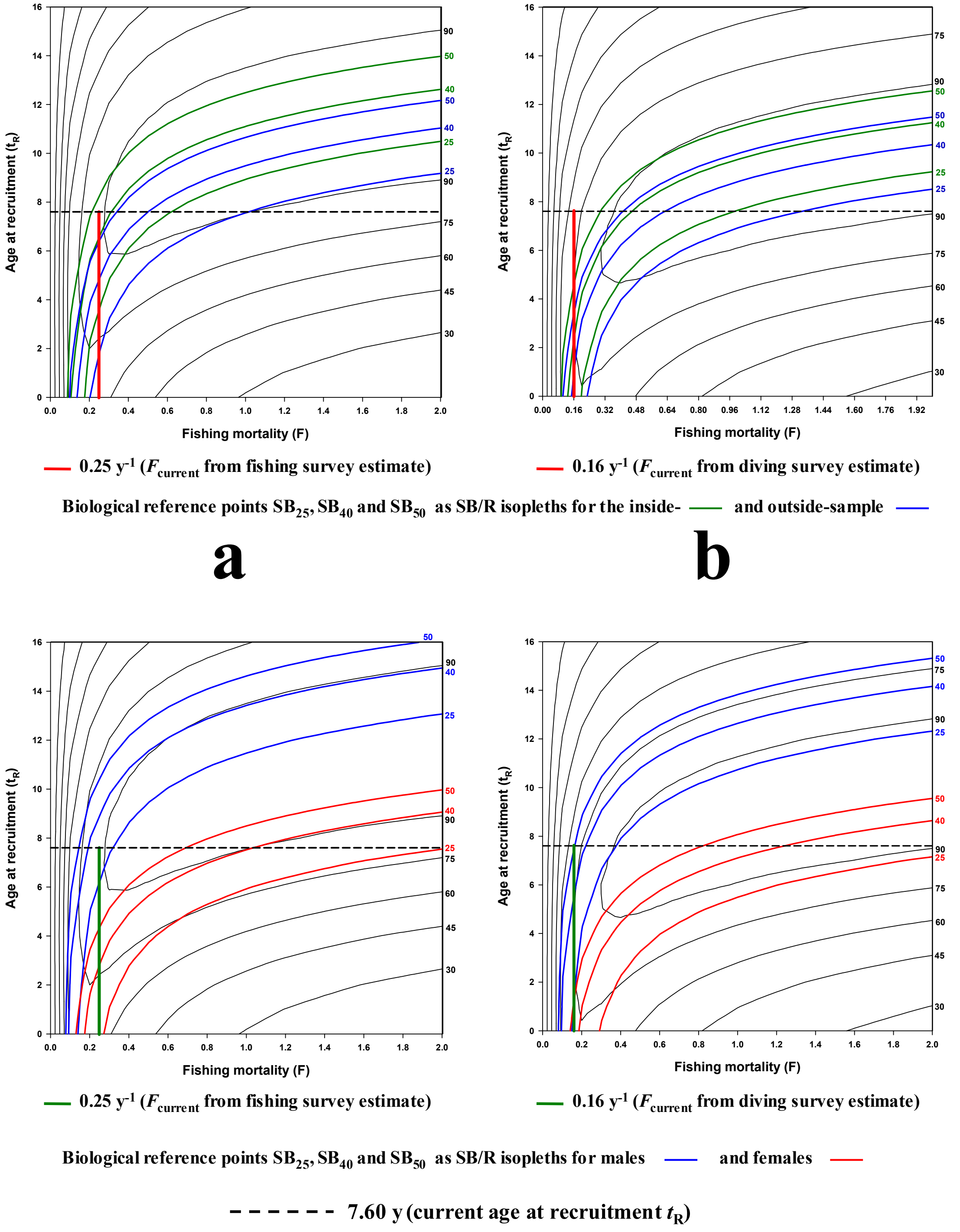


Figure 5.14: *Y/R* isopleths expressed as a percentage of *Y/R*$_{max}$ for roman at a *M* of 0.19 y^{-1} (a) and 0.24 y^{-1} (b). Biological reference points as *SB/R* isopleths for the inside- and outside-sample, and males and females separately, are superimposed. Current *F* and current t_R are indicated

Current F (0.25 and 0.16 y^{-1}) at current t_R can be increased to obtain maximum Y/R (0.30 and 0.45 y^{-1}, respectively) while protecting a minimum of 40% of the SB/R (at both rates of M and for the inside and outside parameters). However, when looking at males and females separately, an increase of F in this manner would lead to a reduced male spawner biomass below 25% of the unfished population. The plateau of maximum Y/R cannot be realised by any combination of t_R and F without reducing the male SB/R below 40% (Figure 5.14).

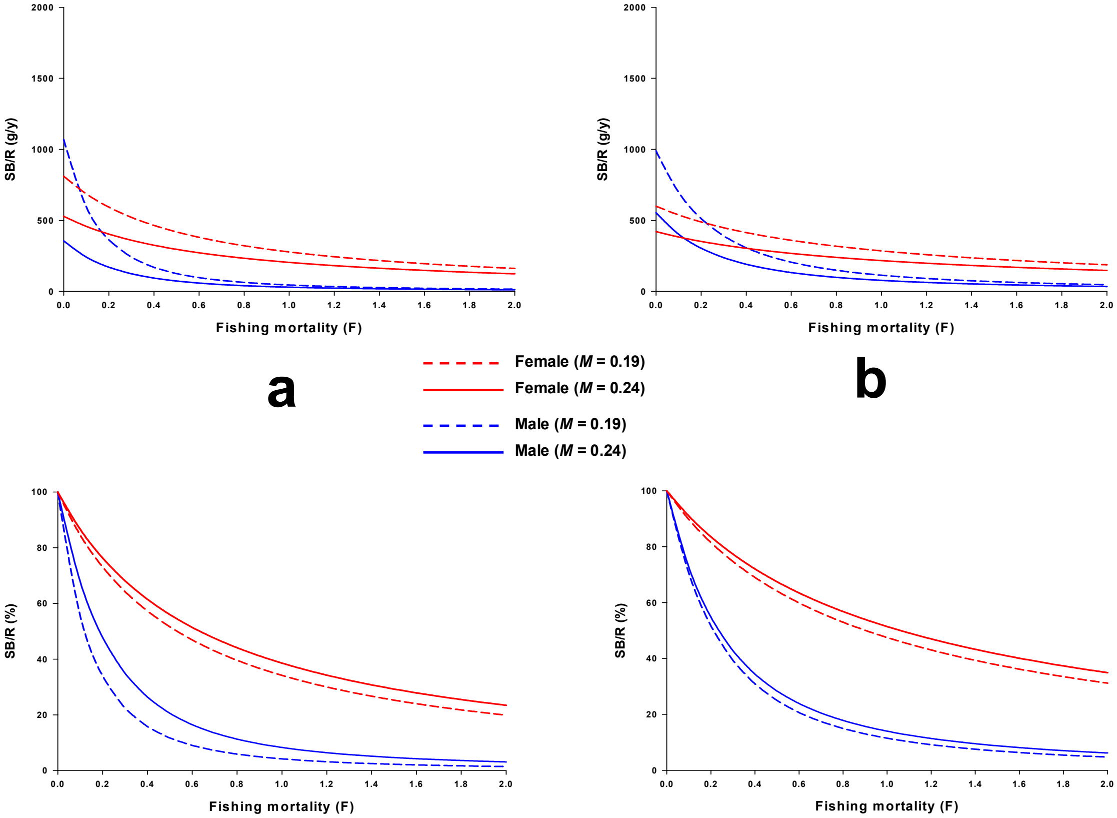


Figure 5.15: SB/R as functions of F for roman for males and females within the inside- (a) and outside-sample (b) separately. Curves are presented in g/y and as a percentage of $SB/R_{\max}$ and at different levels of M and current t_R of 7.60 y

Recognising the sensitivity of SB/R of the inside population, and males in particular, towards increasing F, it is appropriate to examine male (and female) SB/R both for the inside and outside population. Male SB/R is lower in the inside population (Figure 5.15 a) than in the outside population (Figure 5.15 b) at high F and at both estimates of M.

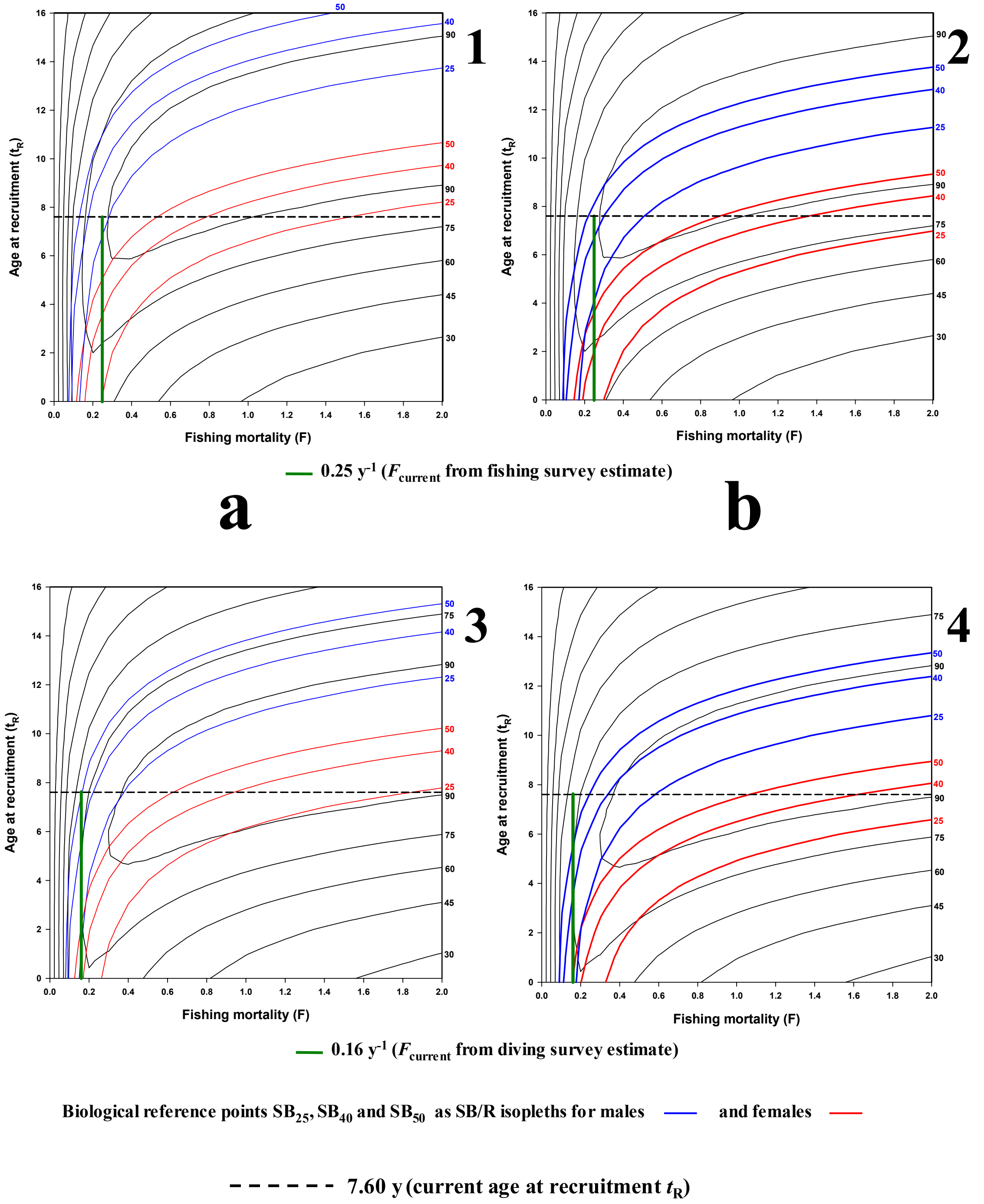


Figure 5.16: ***Y/R*** **isopleths expressed as a percentage of** ***Y/R*****$_{max}$ for roman at low (1 and 2) and high (3 and 4) levels of** ***M*****. Biological reference points as** ***SB/R*** **isopleths for the inside- (a) and outside-sample (b) and males and females separately are superimposed. Current** ***F*** **and current** ***t_R*** **are indicated**

Figure 5.16 extends this view through varying t_R, with figure 5.16 a representing the inside and figure 5.16 b the outside population at low (Figure 5.16 - 1 and 2) and high (Figure 5.16 3 - and 4) levels of *M*. As expected, the combination of low *M* and decreased ages-at-maturity and sex-change (Figure 5.16 b 2) results in the most desirable situation for the fishery. If one then applies *F* and t_R in combinations that lead to exploitation on the maximum yield plateau, *SB/R* values for the female part of the population drops just below 50% and male *SB/R* values of over 50% can still be attained for a large range of combinations.

5.4 DISCUSSION

Age and growth

The parameters of the growth curve and length-weight relationship for roman at Goukamma are very similar to those found by Buxton (1987). The predicted L_∞ of 513 mm fork length matches the South African angling record of 512 mm (Buxton 1987). The longest roman at Goukamma recorded in this study was 462 mm fork length.

Differences in growth rates as a response of populations to exploitation have been demonstrated by Ricker (1981) and Godø and Moksness (1987) for salmon (*Oncorhynchus* spp.) and cod (*Gadus morhua*), respectively. Faster growth under exploitation could be explained by reduced competition for food (Craig 1985). On the contrary, slower growth could be caused by size-selective fishing gear imposing high mortality in fast-growing individuals (Ricker 1969). In this study, there was no difference in growth parameters between the protected and the exploited part of the roman population. Similarly Buxton (1987) found no difference in the growth of roman between the Tsitsikamma NP and the Port Elizabeth area. However, he found reduced growth rates for dageraad at the exploited site. This sparid fish is generally slower growing and longer lived than roman and was subjected to a significantly higher fishing effort than roman (Buxton 1993). As fishing mortality for roman at Goukamma was estimated to be three to four times lower than that estimated for dageraad in the Port Elizabeth area (Buxton 1993), it is possible that higher rates of fishing mortality may have reduced the growth rate of roman in other areas along the South African coastline.

Sex ratio, age-at-maturity and sex-change

Fishing was found to be the most likely cause of decreasing the age at sexual maturity for North Sea plaice *Pleuronectes platessa* (Rijnsdorp 1989), Northeast Arctic cod *Gadus morhua* (Jørgensen 1990) and Norwegian herring *Clupea harengus* (Toresen 1986). Among sequential protogynous hermaphrodites fishing reduces the proportion of males in the population. In compensation age-at-sex-change may also be reduced (Buxton 1993, Coleman *et al.* 1996, McGovern *et al.* 1998, Hawkins and Roberts 2003). The age-at-sex-change is likely to be controlled by behavioural interactions between males and females (Robertson 1972, Shapiro 1980).

At Goukamma, fishing mortality was found to reduce the frequency of larger size-classes in the sample collected outside the MPA. This reduction of males most likely induced the noted reduction in age and size at maturation and sex-change. The net result was that sex ratio in the exploited part of the population remained almost unaltered. Decreased age-at-sex-change maintained the high proportion of males in the exploited part of the population.

My study shows how phenotypic plasticity in the processes of maturation and sex-change can maintain a healthy sex ratio in a population of sequential hermaphroditic fish. In other studies, skewed sex ratios did or did not lead to earlier sex-change, however, no other study has found that earlier sex-change could maintain sex ratios. A possible explanation for the maintenance of sex ratio at Goukamma in contrast to the skewed sex ratios found by Buxton's comparison may relate to the difference in fishing pressure in the exploited area. A higher fishing mortality possibly reduced the male component to an extent that could not be fully compensated by a shift in age-at-sex-change. In the study of Buxton (1993) the exploited area was close to Port Elizabeth, a large coastal urban area with 1.1 million people, with larger numbers of recreational and commercial linefishers than in the Goukamma area (Buxton 1987). Although there was no marked difference in the calculations of fishing mortality between the studies (see next paragraph), this may be due to the sampling design in the study by Buxton (1993). Where comparative samples are obtained from distant sites, as was the case in Buxton's comparison, intrinsic differences in growth rates, patterns of maturation and sex-change due to the different populations sampled might complicate interpretations of the results.

Mortality estimates

The total mortality rate of roman at Goukamma (0.3 y^{-1}) compared favourably with other estimates for reef fish (Huntsman *et al.* 1983, Hughes 1986, Buxton 1993, South African Association for Marine Biological Research 2000). Estimates of natural mortality rate from controlled fishing (0.19 y^{-1}) and UVC (0.24 y^{-1}) inside the MPA were similar and matched well with Pauly's and Hoenig's estimates of 0.25 and 0.23 y^{-1}, respectively.

Using UVC, Buxton (1987) estimated the fishing mortality rate for roman in the Port Elizabeth area to be 0.15 y^{-1}, at a natural mortality rate of 0.20 y^{-1}, derived from Pauly's relationship. Both values are very close to those determined in this study, 0.25 and 0.16 y^{-1}, from controlled fishing and UVC, respectively. However, total mortality estimates derived from catch curve analysis were higher inside the Tsitsikamma NP then off Port Elizabeth. Considering that the samples were taken from the core area of a large and well established MPA this was an unexpected result. The author concedes that the estimates might have been based on different populations and/or samples were not necessarily representative of the true population in the areas. This can be a common error where procedures for collecting samples derived from research fishing within a MPA and fisheries landings in an exploited area are not standardized.

Condition factor

From the results of chapter 4 it was not surprising that a higher condition factor was found for roman outside of the Goukamma MPA. The higher condition factor of roman outside the Goukamma MPA can be explained by reduced competition for food due to a lower density of roman there. As reported earlier, the higher abundance of crinoids, the principle prey of roman, outside of the MPA, was likely to have been a result of reduced predation pressure, as other factors were discounted by the GLM analysis. Surprisingly, fish with higher condition factors did not allocate additional metabolic products into fecundity, as gonad weights of mature fish of the same size-class did not differ during the spawning season.

In contrast, and as mentioned earlier, a study on white seabream (*Diplodus sargus*) in the Mediterranean found that fish condition was greater inside a MPA then outside (Lloret and Planes 2003). In that case, however, habitat quality was found to be the most important factor influencing fish condition and protection did not have a clear effect. Habitat quality was higher inside the protected areas, which were therefore not comparable to the exploited sites.

Per-recruit analysis

The response to different fishing mortality rates, ages-at-recruitment and natural mortality rates were comparable to other yield-per-recruit assessments conducted for a variety of reef fish (Huntsman *et al.* 1983, Buxton 1992, Punt *et al.* 1996). Results in this study are compared in more detail to those found by Buxton (1987, 1992) obtained for roman in South

Africa. Buxton (1992) used the same natural mortality rates to model yield-per-recruit as in this study. The $F_{0.1}$ values of 0.26 and 0.32 y^{-1} (at $M = 0.19$ and 0.24 y^{-1}) obtained in my study were similar to the values found in Buxton's study for $F_{0.1}$ (0.23 and 0.30 y^{-1}) because he used similar growth rates. However, $F_{\max}$ and absolute values for yield-per-recruit in grams were considerably lower in my study. The higher age-at-recruitment (7.6 as compared to 6.0 y) obtained and used for yield-per-recruit estimates of roman in my study is responsible for this difference. In both studies, yield-per-recruit isopleths reached a plateau at an age-at-recruitment of about seven years and a fishing mortality rate of 0.4 y^{-1} when a natural mortality rate of around 0.2 y^{-1} was applied. These results suggest that in both studies roman populations seem to be slightly under-exploited or optimally exploited. When applying the higher natural mortality rate of 0.24 y^{-1}, derived from UVC, to the yield-per-recruit isopleths, a plateau is reached at an age-at-recruitment of about 5.5 y and a fishing mortality rate of 0.4 y^{-1}. At the corresponding F_{current} of 0.16 y^{-1} and age-at-recruitment of 7.6 y, the yield-per-recruit results indicate under-exploitation of the resource.

Spawner biomass-per-recruit analysis yielded similar predictions in both studies. Spawner biomass-per-recruit was around 1,500 g in the unfished population for the estimates of natural mortality rates, with higher spawner biomass-per-recruit at the lower natural mortality rate. When considering a SB_{40} as a safe biological reference point, it certainly appears that one could accept an increase in the rate of fishing mortality at current age-at-recruitment to 0.33 or 0.45 y^{-1}, depending of course on the applicable natural mortality rate.

As found by Buxton (1992) and in this study, the sex-changing nature of roman complicates any predictions. Ages-at-maturity and sex-change respond to fishing mortality, but these changes are difficult to model in a continuous manner, as per-recruit models do not take account of shifts in critical ages. Male spawner biomass drops rapidly with an increasing fishing mortality rate and decreasing age-at-recruitment. Maximum yield-per-recruit at male SB_{40} could theoretically only be reached at a decreased age-at-maturity and sex-change induced by exploitation. At natural mortality rates of 0.19 or 0.24 y^{-1} and reduced age-at-maturity and sex-change, an age-at-recruitment of about 9 y and fishing mortality rate of 0.5 y^{-1} would result in maximum yield-per-recruit with a low risk of recruitment failure. To achieve male SB_{40} in conjunction with maximum yield-per-recruit, the fishing mortality rate and age-at-recruitment would have to be monitored constantly and failure to do so would lead to a very high risks of recruitment failure. To increase age-at-recruitment, the gear restrictions recommended in chapter 3 could be applied. However, enforcement of these restrictions are costly and impractical.

The results of this study further substantiate the call for caution when managing slow-growing and sex-changing reef fish (Buxton 1992). Fishing induces skewed sex ratios that can only be compensated through phenotypic plasticity if fishing mortality is moderate. Probably due to the higher intra-specific competition for (fewer) food, the average condition factor of the protected population was significantly lower compared to the exploited population. Maximum yield-per-recruit at low risk is not necessarily achievable and probably impossible to control, given the inherent problems in converting and enforcing the recommended fishing effort and gear restrictions. The additional use of MPAs is a practical way of ensuring the fishery against recruitment failure and has been advocated for sex-changing reef fish in South Africa (Buxton 1992, Penney *et al.* 1999, Cowley *et al.* 2002) and worldwide (Roberts *et al.* 2000, Hawkins and Roberts 2003).

6 CONCLUSIONS

General

The questions that have been addressed in this thesis are not new. Several other studies have focused on the effect of MPAs on reef fish, and roman has been one of the more intensively studied reef fish in South Africa.

What is new is the approach to the experimental design, such as the use of complementary methods of assessment, standardisation of methods and descriptions of physical habitat and benthic community structure. These methods have gone a long way to reduce many of the uncertainties that have plagued MPA studies. Problems such as the unknown extent of poaching, the influence of habitat type and geographic separation, and selective and inconsistent sampling methods raise doubts about the conclusions of most MPA studies.

By accounting for environmental influence, this study was able to place the relative effects of fishing on a reef fish population into perspective. Using a small MPA, it could be shown that a moderate rate of fishing mortality can decrease density and size of roman. This moderate fishing mortality allowed the population of sequential hermaphroditic roman to maintain a healthy sex ratio outside the MPA through phenotypic plasticity. Probably due to the magnitude of fishing mortality rate, other studies failed to document this mechanism. The systematic design of the experiment allowed one to separate the influence of habitat quality, and for the first time, the effect of intra-specific competition on reef fish condition could be measured accurately. Higher densities inside the MPA led to higher competition for food among roman, resulting in a decreased average condition factor of the protected population compared to the exploited population.

Fishing had an influence beyond the main target species of the fishery. Fishing reduced the diversity of the reef fish community and the size of reef fish generally. Although affected by fishing, some reef fish species occurred in higher abundances, which is most likely due to reduced inter-specific competition with roman. This top-down effect of roman might also have changed the composition of invertebrate prey organisms and algae.

The consistency of the results achieved, using different methods of assessment and analysis, underlines the potential of the experimental design to detect relatively small differences in biological indicators. This high-resolution approach is of particular importance when investigating the effectiveness of small MPAs and could therefore be used as a guideline for similar research efforts. As in most studies the present research did have some limitations. For example it can be argued that the results in this study are confounded by spatial differences between sites inside and outside the MPA that pre-existed MPA declaration. Although information on the 'before' state are very useful, their comparability to a 'later' state of a MPA can be in turn confounded. The impact of fishing on long-lived, slow-growing reef fish will be more detectable the longer the time interval between MPA declaration and MPA re-evaluation. This should be in particularly true when considering fishing induced changes in fish physiology (e.g. changes in condition factor and age-at-maturity) and population parameters (e.g. changes in growth rate and sex ratio). Unfortunately, comparisons of a same reef area after longer time intervals might be biased due to climate change (Soto 2002), variations in recruitment and the general problem of replicating the exact same evaluation methods in the face of technological research advances (see Introduction in this thesis).

As mentioned in the introduction, MPAs can be used to measure stock status directly if the influence of factors such as catchability, habitat and sampling method on CPUE assessments can be limited or reduced. The experimental design in this study allowed for contemporary CPUE comparisons across the border of the Goukamma MPA to assess the status of the roman stock in the area.

Stock assessment

As no detailed historic data on CPUE of reef fish are available for South Africa the difference in biomass, caused by reduced recruitment over time, cannot be determined. Large MPAs could be used to obtain an estimate of CPUE in a contemporary unexploited population. Due to their large size, however, control sites are inherently incomparable to exploited sites. On the other hand, CPUE rates in small MPAs are likely to be reduced through poaching and spill-over effects (Figure 6.1).

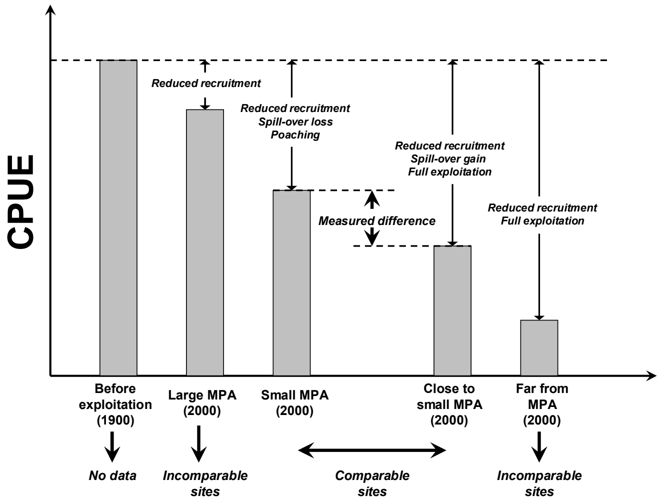


Figure 6.1: Hypothetical rates of CPUE at sites with different rates of exploitation and their usefulness for stock assessment

In the case of the fishery for roman, the effects of adult spill-over are negligible due to the small home range of this species (Kerwath 2005). Therefore, only the relative level of poaching within the Goukamma MPA in relation to the level of exploitation in directly adjacent fishing grounds has to be known for stock assessment purposes (Figure 6.1).

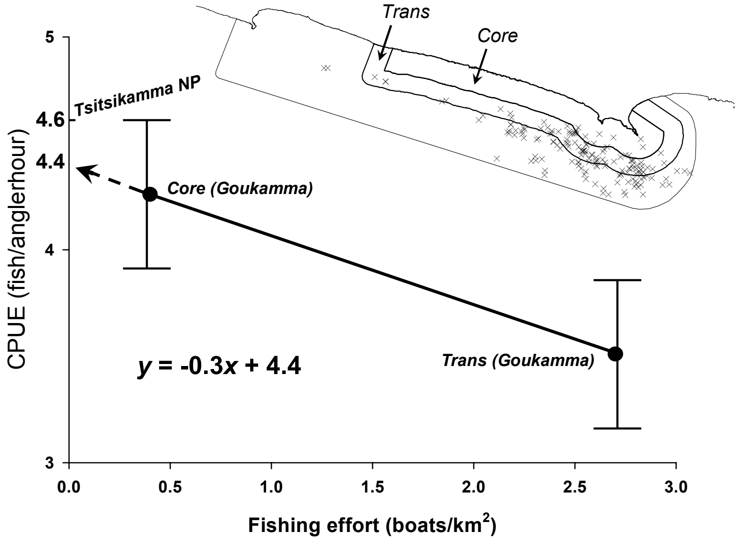


Figure 6.2: Extrapolation of research CPUE and fishing effort measured in the Core and Trans zones to obtain an estimate of the CPUE under unexploited condition

The stock status of roman in the fishing grounds of the area can be estimated by extrapolation, using research CPUE and fishing effort data measured in the **Core** zone and the directly adjacent **Trans** zone (Figure 6.2). The CPUE measured in the **Core** zone would have been reduced by some poaching (measured). Assuming that density of roman is linearly related to measured fishing effort ($C = B \times q \times E$), it is possible to extrapolate CPUE to reflect an unexploited stock. The value so attained is 4.4 fish per hour.

During the Goukamma MPA sampling period, Smith (2005) measured the CPUE for roman in the Tsitsikamma NP, using the exact same material (research vessel and equipment) and methods (sampling procedure). The measured CPUE of 4.6 fish per hour in the Tsitsikamma NP for roman is close to the calculated CPUE rate at zero fishing effort in this study. The small difference in CPUE of 0.2 fish per hour might be due to habitat differences, variation in recruitment or a combination of both. Smith (2005) also measured the roman CPUE in the Plettenberg Bay area. At a value of 1.3 fish per hour, a stock reduction to less than 30% of the pristine stock can be inferred. The reef systems in Plettenberg Bay, however, are more accessible to a larger fishing community, leading to a considerably high fishing effort (Smith 2005).

In chapter 5, per-recruit models were used to assess the biomass per-recruit for roman inside and outside the Goukamma MPA, under the assumption that recruitment is identical for the MPA and adjacent areas. To compare these results on stock status to the CPUE extrapolation results above, the number of fish caught per unit of effort has to be transformed into biomass caught per unit effort (BPUE):

$$BPUE = \left(\frac{\sum_{i}^{N} weight_i[g]}{N} \right) \times CPUE\,, \qquad (6.1)$$

where *N* is the number of fish in the sample. The weight is calculated from the length of all fish in the sample, using the length-weight relationship determined for the roman population.

Due to the significant difference in mean size of roman, the mean weight per fish caught in the **Trans** zone is lower (775 g) then in the **Core** zone (977 g). The biomass caught per unit effort for roman caught in the **Trans** and **Core** zones is therefore 2713 and 4162 g/hour, respectively. By extrapolation, the biomass caught per unit effort at zero fishing effort is 4414 g/hour. Therefore, in terms of biomass, the stock of roman has been reduced to **61%** in the exploited area.

Interestingly this estimate lies midway between the biomass reduction estimated by the two biomass per-recruit models in chapter 5. Predicted from the datasets obtained during controlled fishing and UVC, the biomass of the roman population under current levels of exploitation is reduced to **52** and **69%**, respectively (Figure 6.3).

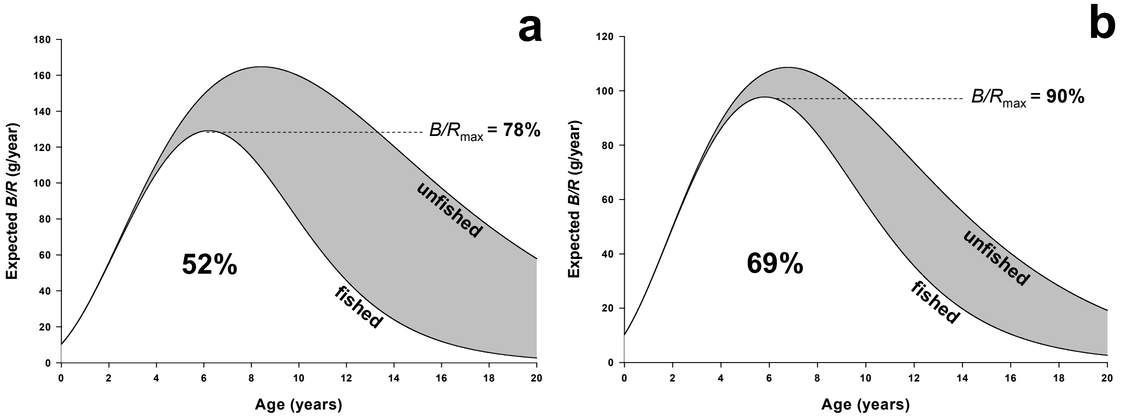


Figure 6.3: Expected *B/R* for roman, calculated from the controlled fishing (a) and UVC (b) dataset. Biomass for the unfished (grey shaded area) and fished (white area) populations at *F* = 0.25 (a) and 0.16 (b) are presented. Biomass indicated as a percentage of unexploited stock

The above result is an important one as it shows that contemporary CPUE extrapolations, using small MPAs can be very useful to assess the stock status of resident reef fish populations. If designed carefully, they deliver reliable and consistent estimates, and offer a practical alternative to conventional assessment strategies.

Potential to improve recruitment and conserve biodiversity along the south coast

As mentioned in the introduction, the approach taken here is to treat the MPA as part of an experiment to examine the effects of fishing on a reef fish population and reef community. But clearly the results are also useful from the perspective of MPA design and advocacy.

A number of theoretical models have shown the potential of MPAs to enhance fisheries by supplying recruits to exploited areas (DeMartini 1993, Attwood and Bennett 1994). Recently, the role of larval dispersal in the design of MPA networks has been emphasised (Palumbi 2003, Shanks et al. 2003). Not only should the MPA seed other areas, but the MPA itself needs to be seeded. These recruits could come from other MPAs or from the site of production through local retention currents (Gaines *et al.* 2003).

As sex-changing reef fish are particularly vulnerable to over-exploitation through recruitment failure, MPAs are promising tools in the conservation of sparid reef fish stocks in South Africa (Buxton 1987). The distribution of fish larvae is strongly affected by currents (Leis and Goldman 1983). Current patterns and their implications for the dispersal of sparid larvae in and from the Tsitsikamma NP have been studied by Tilney *et al.* (1996), Attwood *et al.* (2002) and Brouwer *et al.* (2003). The homogeneous distribution of sparid larvae suggested passive mechanisms of dispersal and projections of dispersal distances were based on current patterns determined from drogues and fixed instruments. All authors concluded that export of larvae and eggs from the Tsitsikamma NP was very likely.

From the range of current speeds recorded in this study, transport of passive biota from the centre of the Goukamma MPA across its borders would be achieved in time intervals from three hours to three days. Taking into account that sparid larvae require about 30 days before they can actively settle (Brownell 1979b, Brouwer *et al.* 2003), export of larvae is possibly the rule rather than the exception.

A projection of larval dispersal over larger scales may help to identify potential sink areas for recruits exported from the Goukamma MPA, and evaluate the extent of connectivity to other MPAs and the potential for self-seeding by local retention currents. Current velocities and directional frequencies in this study closely matched those found by Attwood *et al.* (2002), using holey-sock drogues in the Tsitsikamma NP.

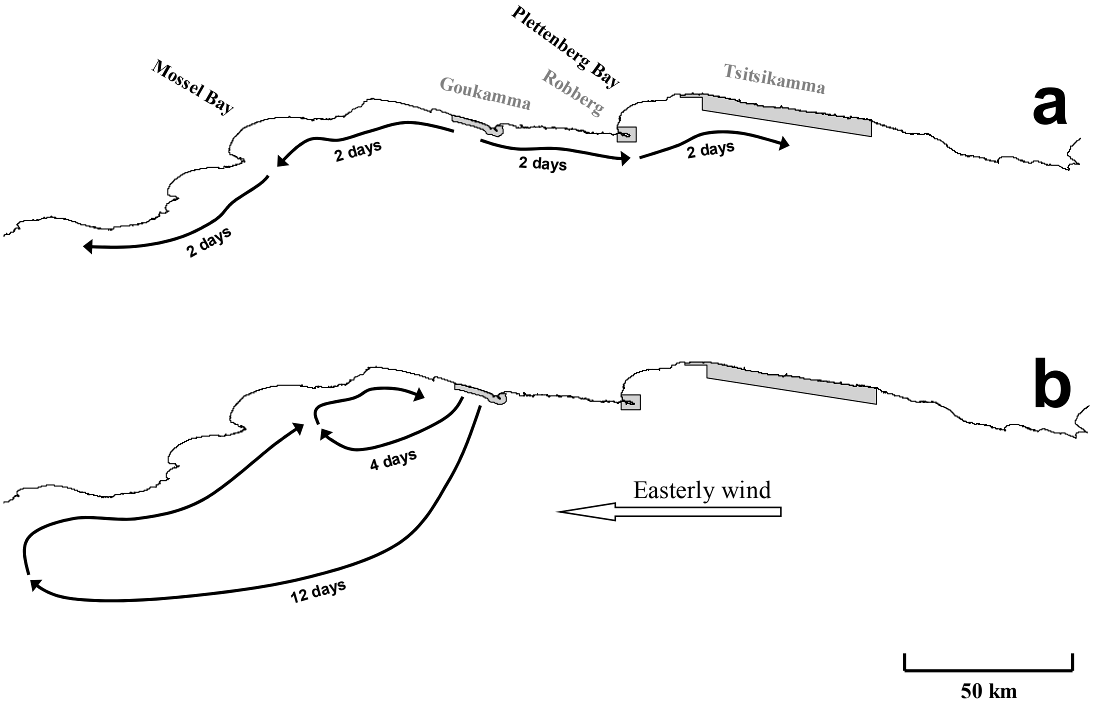


Figure 6.4: Projected distances of larval dispersal from the Goukamma MPA into surrounding areas using large scale current patterns suggested by Tilney (1996) and mean current velocities measured in the Goukamma MPA. Arrows indicate potential larval dispersal during long-shore oscillation (a) and upwelling events (b)

Using continuous long-term current measurements from a bottom moored electromagnetic current meter and infrared satellite imagery, Tilney *et al.* (1996) identified two distinct current patterns characterizing the area between Mossel Bay and Algoa Bay. A fairly regular long-shore current oscillation was recorded mainly in winter, caused by east-moving cyclones. They generate barotrophic waves with periods of two to four days. Using the mean current velocities for eastward and westward currents measured in the Goukamma MPA long-shore larval dispersal for periods of two to four days can be projected. Connectivity to the Robberg MPA and the Tsitsikamma NP in the east and reefs in the Mossel Bay and Stillbaai area to the west is possible (Figure 6.4 a).

Another current pattern was recorded during strong easterly winds most frequently occurring in summer, caused by shallow low pressure systems on land. They cause upwelling events, lasting for periods between 4 and 12 days. The mean current velocity for south-ward directions in Goukamma suggests that offshore water movements of between 20 and 60 km are probable. As revealed from infrared satellite imagery, prevailing easterly winds push the cold water between 50 and 250 km westwards. Then, westerly winds drive the water eastwards and inshore with downwelling occurring along the coast. As a result, larvae could be transported up to 60 km offshore, 250 km eastward and back to the Goukamma MPA possibly re-seeding the area (Figure 6.4 b).

In summary, Goukamma MPA is highly likely to improve conservation of biodiversity through connectivity to other MPAs in addition to self-seeding. The long planktonic life-span of reef fish larvae, the strength of the currents and the lack of consistently prevailing ocean circulation patterns, suggest little spatial variation in recruitment along the south coast. Therefore, MPAs such as Goukamma should have a good potential to improve recruitment in exploited areas along the south coast.

Management recommendations for the Goukamma MPA

Insufficient funds lead to poor enforcement (Pritchard 1993) and sometimes uncontrolled poaching, which can render MPAs ineffective as management tools (Klima *et al.* 1986, Jennings *et al.* 1996, Maliao *et al.* 2004). South Africa's MPAs are troubled by poor resources and poaching (Lemm and Attwood 2003). Unless the compliance problems are addressed adequately, future MPA initiatives should take into account the possibility of designing a buffer zone where some infringement of the regulations will be inevitable.

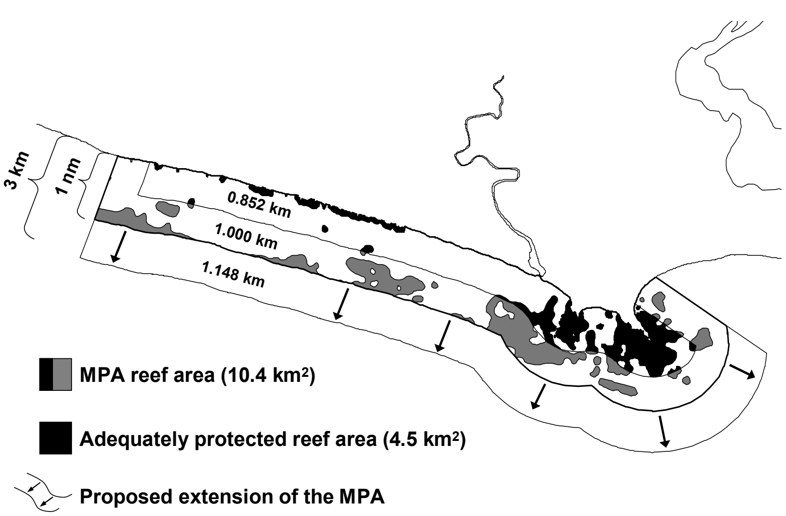


Figure 6.5: Reef area inside the Goukamma MPA (grey and dark area), reef area adequately protected (dark area) and proposed seaward extension

In this study, relative fishing effort inside the MPA was only slightly lower than outside. Only within the **Core** zone, half the size of the designated MPA, was the fishing effort at acceptably low levels. This suggests that MPAs in general should be designed larger than the targeted area for protection, especially where enforcement or management is poor.

The spatial fishery survey in the study area revealed a high rate of poaching inside the Goukamma MPA, effectively reducing the protected reef area to 4.5 km^2 (Figure 6.5). Considering the vulnerability of reef fish to exploitation and the small area of adequately protected reef, insufficient enforcement will compromise the functioning of the MPA. Enlarging the effectively protected reef area will increase the ecosystem's buffering capacity and can be achieved in two ways. Firstly, effective enforcement of the current MPA borders increases the protected reef area from 4.5 to 10.4 km^2 (Figure 6.5).

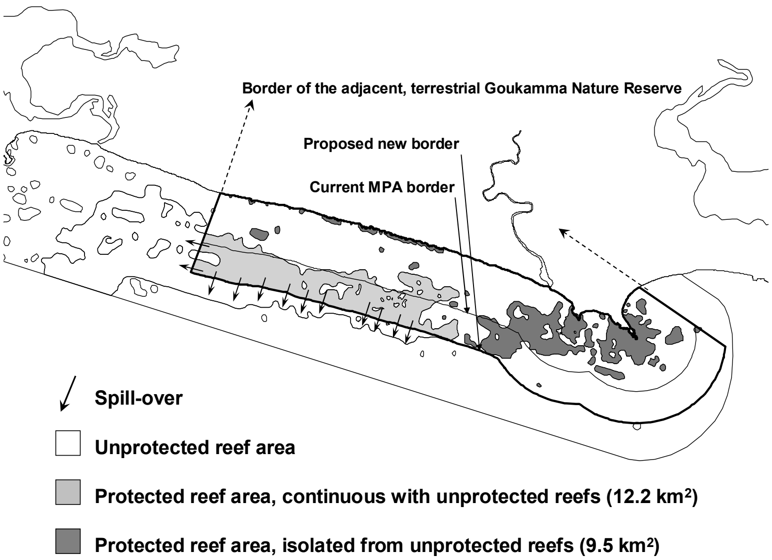


Figure 6.6: Extension of the Goukamma MPA including a continuous reef for fisheries enhancement and isolated reefs to boost recruitment

Alternatively, extending the current border of the MPA about one kilometre seawards should have a similar effect, as poaching was found to be most severe within this distance of the border. To facilitate reference for fishers and MPA staff, buffering should extend the border 1.148 km seawards, placing the new border exactly three kilometres off the coastline. Along-shore extension is not advisable as this would overshoot the border of the adjacent, terrestrial Goukamma Nature Reserve (Figure 6.6). Apart from increasing the buffering capacity, the proposed MPA dimensions would more effectively achieve two other goals: the conservation of biodiversity and enhancement of directly adjacent fisheries through spill-over and export of fish eggs and larvae. This would result from the fact that the two larger, inshore reefs in the east would be entirely included in the MPA (Figure 6.6). These reefs and a number of smaller reefs, making up a total area of 9.5 km^2, would be isolated from unprotected reefs by sandy flats. This makes spill-over of adult roman unlikely (Kerwath 2005) and the protected reefs would provide fairly pristine ecosystems for a more efficient conservation of biodiversity. A higher abundance, particularly of larger, more fecund roman, would increase spawning success and export of products.

The new MPA would also include more suitable reef habitat across the border in the west (Figure 6.6). This should increase its potential to enhance directly adjacent fisheries through spill-over (Kerwath 2005). A larger part of the continuous reef system would be included in the MPA (12.2 km^2), further increasing the potential spill-over through improved buffering capacity and higher overall productivity.

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8 APPENDIX

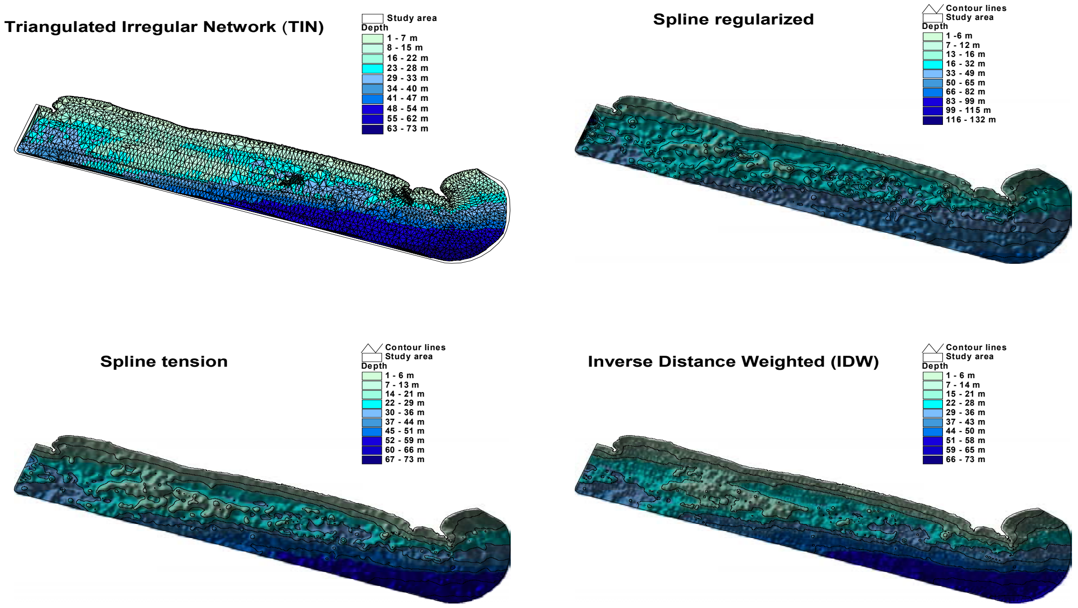


Figure 8.1: Continuous seafloor maps of study area generated by using four different methods of interpolation. TIN describes a surface as a set of non-overlapping triangles. Heights between triangle corners can be interpolated, allowing for the definition of a continuous surface. The IDW interpolation method assumes that each mapping point has a local influence that decreases with distance. It weights the points closer to the processing cell greater than those farther away. The regularized spline incorporates three derivatives into its minimization calculations. The tension spline includes only the first two derivatives, however, it includes more points in the spline calculation and produces smoother surfaces at the costs of extended computational time (Environmental Systems Research Institute Inc 1996)

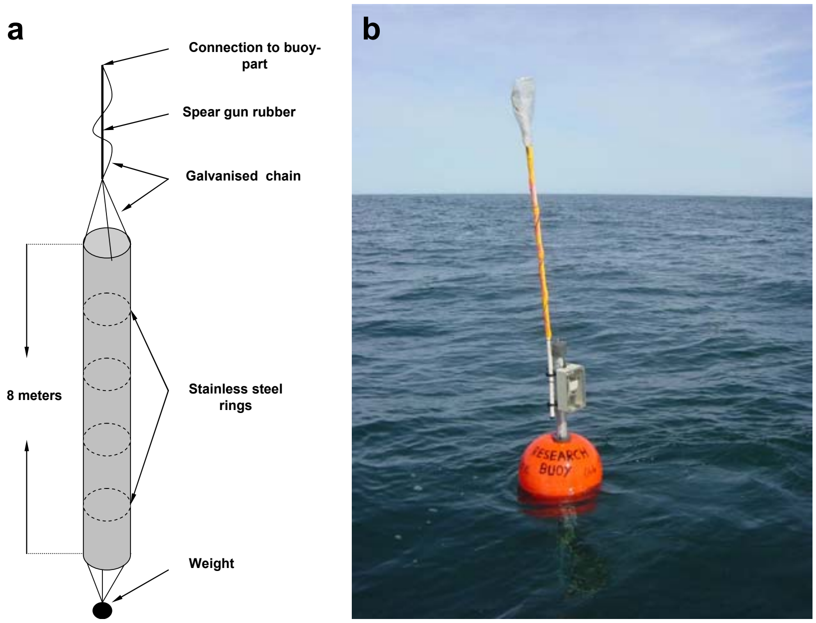


Figure 8.2: Holey-sock (a) and buoy-part of drogue after deployment (b). Note GPS receiver in splash-water proof box and GPS antenna extension

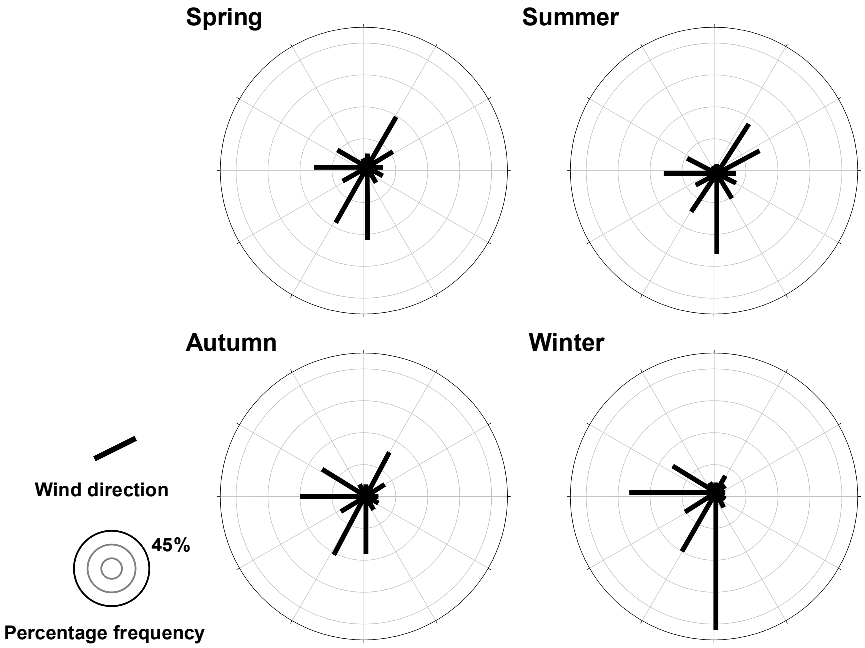


Figure 8.3: Wind roses for different seasons. Radial gridlines are 10%-steps apart ending at a maximum of 45% in all four plots

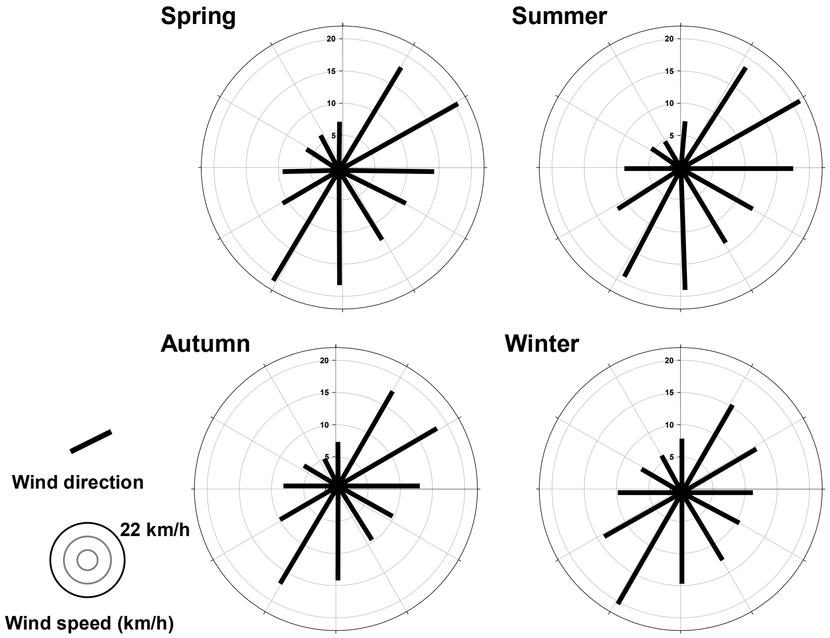


Figure 8.4: Median wind velocities in km/h for different wind directions by season. Radial gridlines are 5 km/h-steps apart ending at a maximum of 22 km/h in all four plots

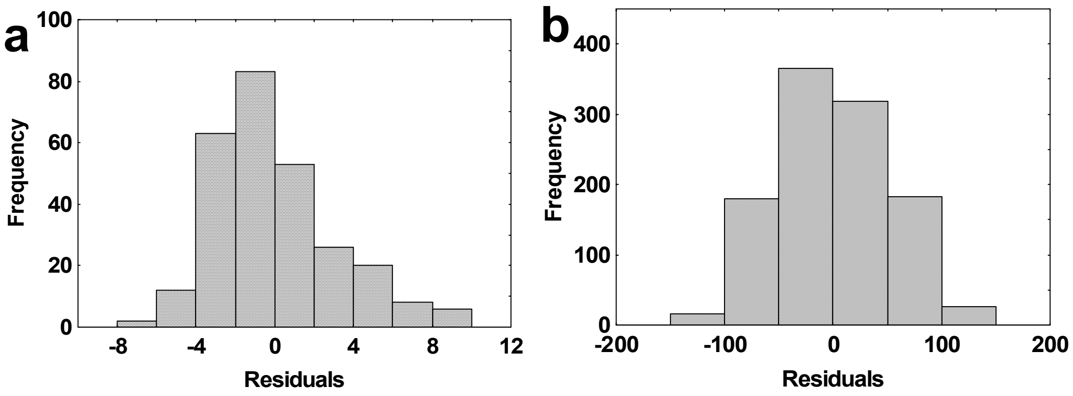


Figure 8.5: Distribution of residuals in GLM analysis for roman abundance (a) and size (b) using controlled angling

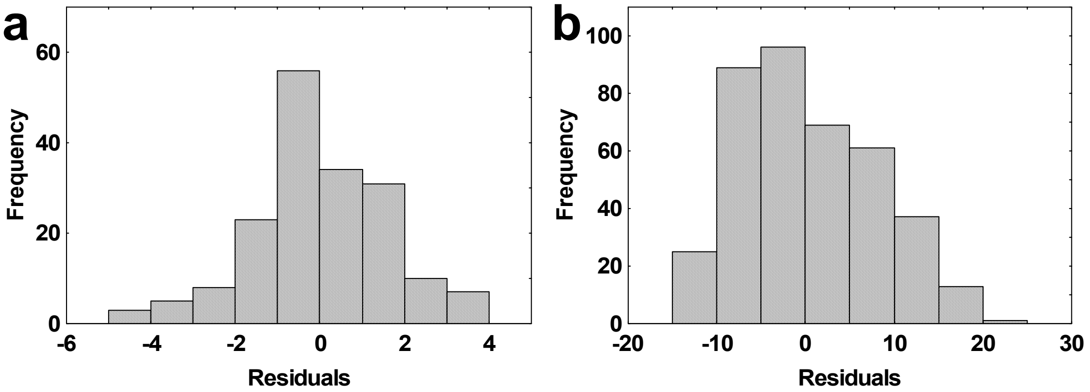


Figure 8.6: Distribution of residuals in GLM analysis for roman abundance (a) and size (b) using UVC

Age (years)	n	Range (FL mm)	Mean observed length ± SD (FL mm)	Expected length (FL mm)
2	6	129-183	142.5±20.5	141.3
3	21	131-190	168.0±18.4	171.8
4	32	165-239	203.8±19.0	199.7
5	26	198-265	225.0±17.3	225.4
6	32	209-295	248.6±21.9	249.0
7	31	230-312	269.4±18.2	270.6
8	20	251-311	289.0±15.0	290.5
9	21	267-335	308.2±18.2	308.7
10	15	270-381	330.9±30.6	325.5
11	11	301-366	334.8±21.5	340.8
12	15	305-395	355.9±24.9	354.9
13	6	358-390	372.0±11.1	367.9
14	5	358-411	384.8±19.0	379.8
15	2	370-380	375.0±7.1	390.7
16	4	390-402	397.5±5.3	400.7
17	2	405-452	428.5±33.2	409.9
18	0			418.4
19	1	405-405	405.0	426.1

Table 8.1: Sample size, range (FL, mm), observed (FL ± standard deviation) and expected lengths-at-age determined from the full dataset for roman

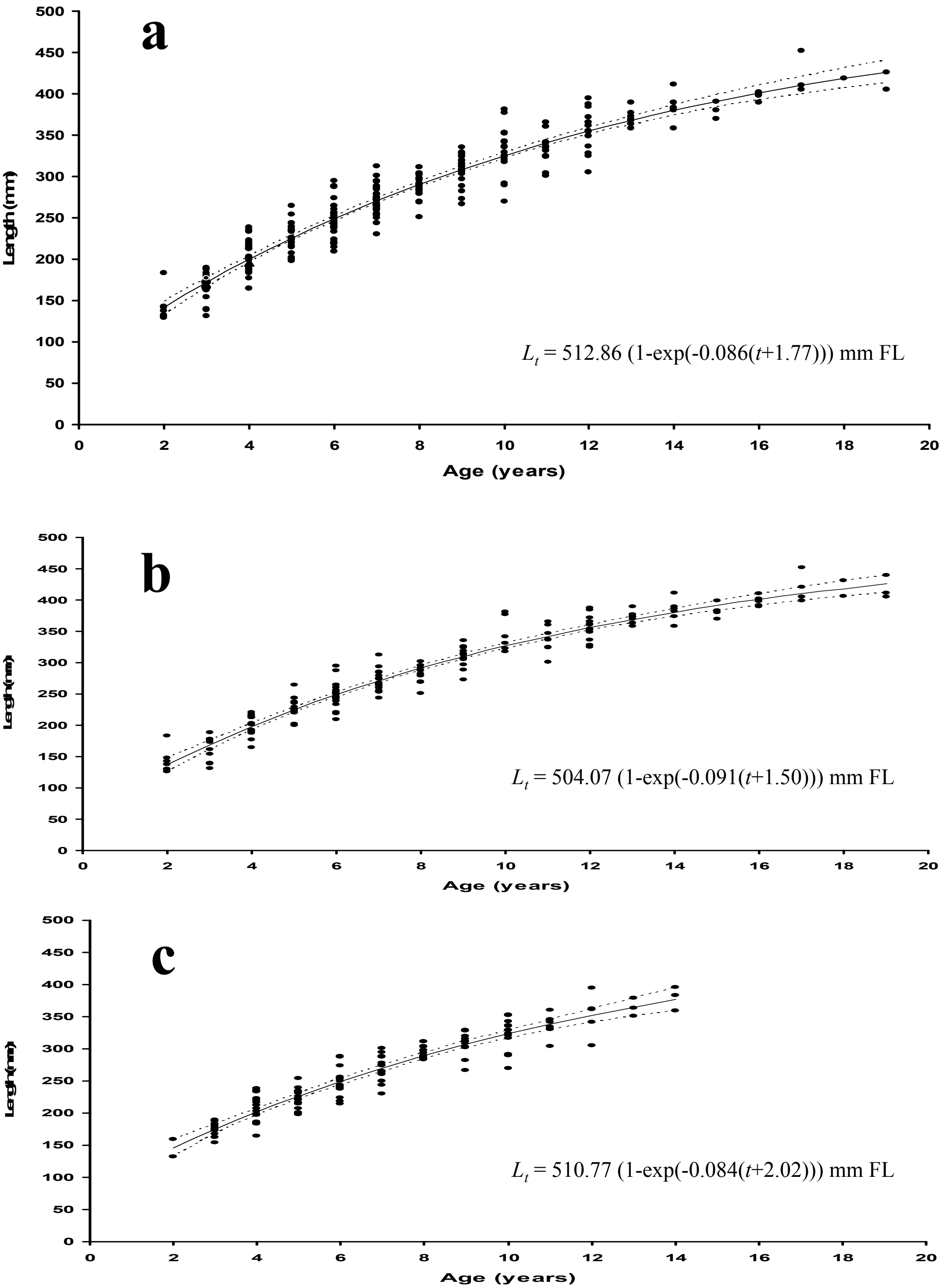
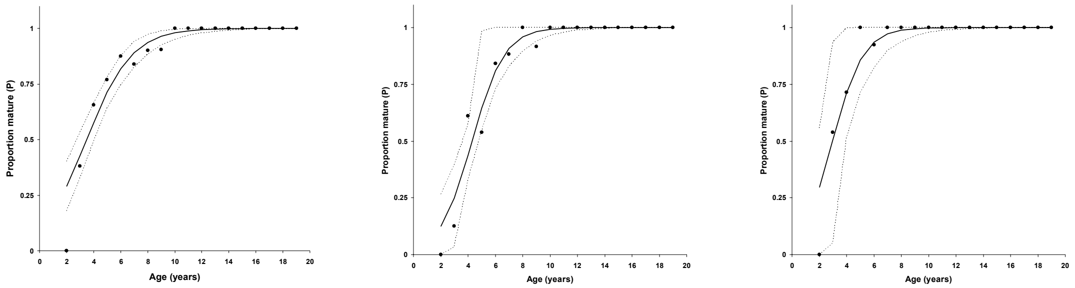


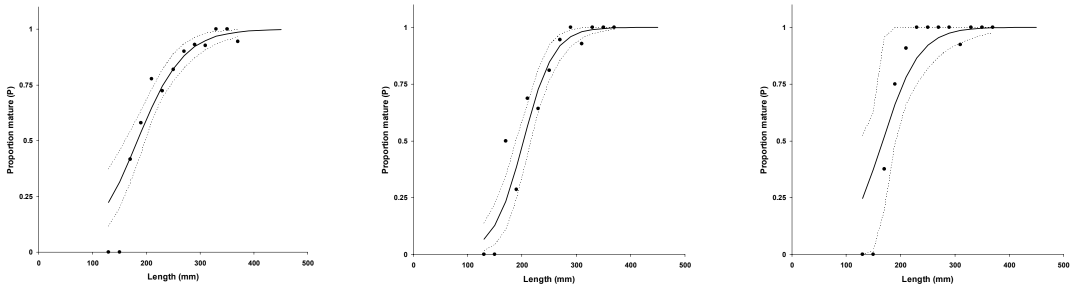
Figure 8.7: Observed individual lengths-at-age and the expected von Bertalanffy growth curve with associated 95 % confidence intervals calculated from 500 bootstraps for the whole dataset (a), the inside-sample (b) and the outside-sample (c)

a **b** **c**

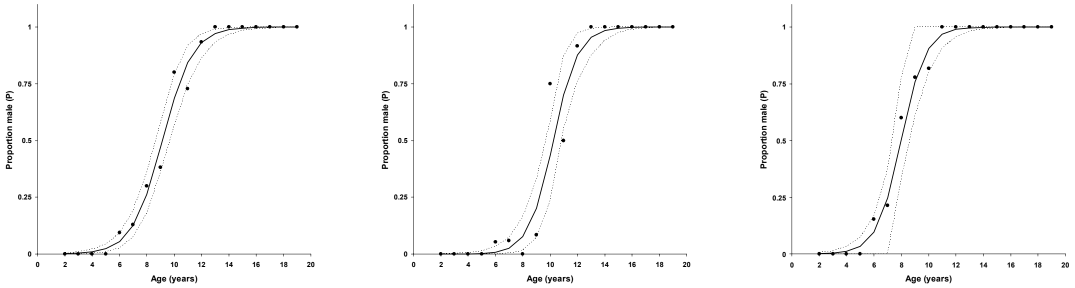
Age-at-50% maturity



Length-at-50% maturity



Age-at-50% sex change



Length-at-50% sex change

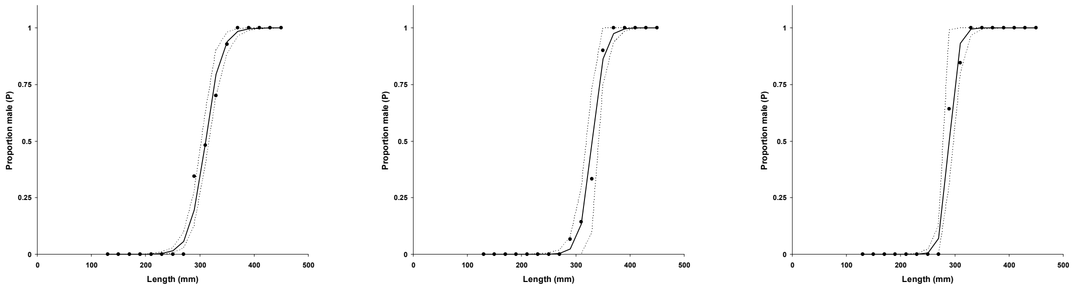


Figure 8.8: Age- and length-at-50% maturity and sex-change with associated 95 % confidence intervals calculated from 250 bootstraps for the whole dataset (a), the inside-sample (b) and the outside-sample (c)