Empirical studies of fish movement behaviour and their application in spatially explicit models for marine conservation

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Table of contents

Abstract

This thesis investigates the movement behaviour of South African two coastal fish species and evaluates the effectiveness of marine protected areas (MPAs) in their protection and management. Its primary focus is on resolving the movement patterns of roman *Chrysoblephus laticeps* (Sparidae) in and around the Goukamma and Castle Rock MPAs in the Western Cape province of South Africa. A pilot study of the methodology investigated the movement behaviour of spotted grunter *Pomadasys commersonnii* (Haemulidae) in the sheltered East Kleinmonde Estuary in the Eastern Cape province.

The application of different tagging methods was tested in a controlled tank experiment. Tagged roman were monitored over a 198-day period. Barbed dart, t-bar anchor and Visible Implanted Fluorescent Elastomer (VIFE) tags were compared. Application techniques and underwater visibility of VIFE tags were tested on roman and on fransmadam *Boobsoidia inornata* in a pilot study. Needles of gauge 25 were found to be optimal for VIFE tag application. Whereas VIFE tagging caused fin rot in fransmadam, it had no negative effect on roman. VIFE tagged fish could be identified by divers from a distance of three metres under ambient light in an observation tank in five metres water depth. There was no significant difference in growth rate between groups of roman with different tags and controls after 198 days. High tag loss rates were experienced for barbed dart and t-bar anchor tags, although barbed dart tags performed better than t-bar anchor tags. Although some of the VIFE marks had deteriorated, all VIFE tagged fish were individually recognised at the end of the study. Conventional dart and VIFE tags are feasible methods to tag roman. However, the

high tag loss rate of conventional tags must be taken into account in the design of a tagging study.

Previous mark and recapture studies on roman are beset with a number of problems. Poor experimental design and low precision of capture positions resulted in equivocal results of limited value. A tagging experiment was designed to eliminate ambiguity in data interpretation and to produce a dataset that could be used to model roman residency and dispersal. A combination of conventional barbed dart tags and Visible Implanted Fluorescent Elastomer tags was used to tag roman in the Goukamma Marine Protected Area (GMPA) on the temperate South African south coast. Sixty one percent of roman were recaptured within 50 m of the tagging position. A small proportion moved considerable distances of up to four kilometres. The extent of these movements was not dependent on fish size or sex. Data from this experiment and from a previous tagging study in the Tsitsikamma National Park (TNP) were used to model the resident behaviour of roman. The model suggests a probability of 91% (GMPA) and 94% (TNP) of residency within a 10000 m^2 cell. This result suggests that individual roman will benefit from protection in small MPAs.

A different experimental approach was required to investigate the exact home range of this species. Firstly the feasibility of using acoustic telemetry to study the movement of coastal fish in South Africa was investigated. The telemetry equipment comprised two VEMCO V8 transmitters and a VEMCO VR60 receiver linked to a directional hydrophone. A tank experiment was conducted to examine the effects of the transmitter implantation. A tracking experiment was conducted on spotted grunter *Pomadasys commersonnii* in the East Kleinmonde Estuary. Operated fish recovered quickly and, with respect to swimming behaviour and growth rates, no differences

were found between fish with implants and controls. The maximum detection range in the estuary was 400 m. Interference between different transmitter frequencies was negligible. Transmitter location recordings were found to be accurate within five metres. Two fish were tracked over a seven-day period. The fish preferred the lower reaches of the estuary where they made repeated and prolonged use of specific areas.

The success of the initial experiments allowed this method to be used to investigate the spatial utilisation and activity patterns of roman *Chrysoblephus laticeps*. Surgically implanted VEMCO V8, V13 and V16 transmitters were used to track 13 roman inside the Castle Rock MPA in False Bay. Transmitters implanted into *C. laticeps* in tanks had no apparent effects on growth and physiology. Manual boat- and diver-based tracking experiments covered a 17-month period. A VEMCO VRAP radio acoustic positioning system was used over two one-month periods during and after the spawning season of roman. Analysis of data using a 95% fixed kernel algorithm suggests that roman are resident throughout their adult life, occupying home ranges between 1000 and 3000 m^2. Activity was lower at night. During periods of cold-water upwelling, fish retreated into caves. During the spawning season, females extended their home ranges, possibly to mate with different males. These results confirm that this species is well suited for protection and management with small MPAs.

The effect of two MPAs on the South African south coast on the population of *C. laticeps* was simulated with a spatially explicit individual based model (IBM). Life history parameters determined in recent studies and the effect of fishing on the size of sex change was taken into account. Fish densities and size frequencies were based on recent underwater visual census. The distribution of suitable habitat in the study areas

was also incorporated. The results show a rapid recovery of the fish size frequency spectrum and sex ratio to pre-exploitation levels inside both MPAs. Little 'spillover' of fish into the fished areas occurred resulting in negligible improvement of catches. The results suggest that for resident species like roman, even small MPAs offer sufficient protection.

I thank the almighty God of philosophers, knowledge seekers and free spirits for giving me the courage to leave the sheltered environment of my Bavarian hometown and travel to foreign countries to study and explore. It has been an amazing journey.

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This work is dedicated to my late parents,

Helga Kerwath and Dr. Wolf-Rüdiger Kerwath.

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Chapter I: General introduction

Like terrestrial animals, fishes exhibit an astonishing variety of movement behaviour, with vast differences in magnitude and speed. Fish movement has been classified in terms of time (i.e. seasonal, diel), direction (i.e. vertical, horizontal, catadromous, anadromous), magnitude (i.e. sedentary, trans-oceanic) and purpose (i.e. spawning migration, exploratory, predator avoidance, commuting between habitats favourable for different life history stages).

This thesis is concerned with the consequences of fish movement for conservation and management strategies. In the context of this work, movement shall be defined as change of location over time; motions of body parts or stationary body shifts like rotations are excluded. Although estuarine fish are the subject of investigation in one of the chapters, the focus is on movement patterns of an exploited reef fish species and their effect on the role of Marine Protected Areas (MPAs) in the conservation of this species.

Whereas the theory of underlying causes and the classification of fish movement behaviour have been intensively discussed elsewhere (Attwood 2002; Dingle 1996, Harden Jones 1968), this is an applied study that focuses on the practical aspects of studying fish movement and its consequences for fisheries management.

The movement pattern of a fish species often affects both the fishery and its markets. Large-scale migrations, as exhibited by many anadromous salmonids, catadromous anguilids and pelagic engraulids (*inter alia* Beckley and van der Lingen 1999; Brege *et al.* 1996; Dare and Potter 2003), are usually undertaken by the entire stock. They represent more or less predictable movements, facilitating market stability as fish

become periodically available to localised fisheries at certain times of the year. Movements of nomadic species like Atlantic bluefin tuna *Thunnus thynnus* (Block *et al.* 2004; Fromentin *et al.* 2004), yellowtail *Seriola lalandi* (*Gillanders et al.* 2001) or snoek *Thyrsites atun* (Griffiths 2002; Nepgen 1979) are less predictable and include only a part of the stock. Patterns are irregular and are typically related to factors such as prey abundance or water temperature (Davis and Stanley 2002). Fishermen are aware of these factors and use cues such as increased sea temperature or feeding seabirds to maximise the chances of an encounter with the moving stock. However, as availability of fish and size of catch fluctuate (Ravier *et al.* 2001), markets for some of these species can be unstable, often preventing the development of large scale industrial fishing operations, which in turn makes these species less vulnerable to overfishing.

Many demersal fish species, reef associated fishes in particular, utilise a confined area of suitable habitat for extended periods of time (*inter alia* Griffiths and Wilke 2002; Matthews *et al.* 1990; Zeller 1997). Once fishermen discover a particular area, the fishes are often exploited until the stock is locally depleted. This particular pattern of space utilisation can be detrimental to an exploited population, but it can also facilitate its conservation, as one simply has to close an area of suitable habitat to fishing to prevent parts of the stock from overexploitation. The creation of these areas, hereafter referred to as marine protected areas (MPAs), should not only benefit the stock in the protected zone, but - in theory - also help to replenish fish in fishing areas, if a part of the spawning population is protected (*inter alia* Bohnsack 1996; Corless *et al.* 1997; Gell and Roberts 2003; Gell *et al.* 2005; Holland and Brazee 1996; Roberts *et al.* 2001; Russ *et al.* 2003). Many reef fishes are broadcast spawners; their planktonic eggs and larvae typically drift for several weeks before settling on a reef

16

(Brouwer *et al.* 2004; Hickford and Schiel 2003; Tilney *et al.* 1996) theoretically allowing even distant fishing areas to be replenished with recruits. In addition, as the fish population in the protected area and therefore the competition for available resources increases, adult fish might be forced to leave the area, resulting in a 'spillover' of fishes into the fished areas (Barrett *et al.* 2004; Botsford *et al.* 2004; Gell and Roberts 2003; Kaundra-Arara *et al.* 2004; Maypa *et al.* 2004).

Those who advocate the virtues of MPAs often simplify this concept. Mixed behavioural strategies within species and populations (Dingle 1996), selection pressure imposed by fishing (Law 2000), and differences in habitat suitability and oceanographic conditions result in large variations in the area that is used by the individual fish. Detailed knowledge of the movement behaviour of a fish species is required to decide which proportion of suitable habitat needs to be protected to positively affect the exploited stock and to quantify this effect to provide a convincing argument for the closure of an area to fishing.

Unfortunately, such detailed information is seldom available. One reason for this can be found in the nature of the habitat: the aquatic environment makes the study of fish movement behaviour difficult. Unaided direct visual observation of fish is limited to clear shallow waters or to rather rare instances when fishes are close to the surface. Underwater observations are typically limited to short time intervals (e.g. SCUBA diving) or require expensive technology (e.g. submersibles). In many cases, direct observation is simply not possible due to the speed, agility and endurance of fish.

Large-scale migrations of fish can simply be concluded from catch frequency patterns (*inter alia* Francis 2001; Griffiths *et al.* 2002; Hartgers and Buijse 2002; McBride *et*

al. 2001; Nielsen *et al.* 2001). The majority of studies of fish movement however rely on methods that involve tagging the fish with a marker (dye, plastic tag, visible implant, passive integrated transponder etc.) that allows the identification of the fish either visually or with the aid of a detection device (*inter alia* Appeldoorn 1997; Brouwer *et al.* 2004; Jimenez and Fernandez 2001; Matthews and Reavis 1990; Munro 2000; Patterson *et al.* 2001; Zerbi *et al.* 1999); or attaching a transmitter capable of emitting an electro- magnetic or acoustic signal that can be received with a radio, a satellite or an acoustic receiver (*inter alia* Almeida *et al.* 1999; Bagley *et al.* 1994; Block *et al.* 2004; Bolden 2002; Connolly *et al.* 2002; Ledgerwood *et al.* 1999; Matthews 1992; Matthews *et al.* 1990; Thorstad *et al.* 2001a; Thorstad *et al.* 2002; Zeller and Russ 1998).

Whereas all the methods above have been used to study aspects of fish movement behaviour, each individual method has its shortcomings with regard to the study of reef fish movement patterns in the context of MPA design.

Direct underwater observation is advantageous to study the interactions between fishes and their environment in detail because it yields valuable information on the causes of certain movement patterns like territorial behaviour, spawning aggregations, the use of shelter etc. (Brannan *et al.* 2003; Ide *et al.* 2000; Soares *et al.* 2002). However, as a standalone method, underwater observation is not suitable to quantify space used by individual fish. As observations are limited by dive time, light and sea conditions, they typically cover only a small part of the animal's lifetime resulting in an underestimate of the utilised area.

Mark and recapture experiments are beneficial to gain understanding of general patterns of space utilisation. Mark and recapture is widely used in the study of

dramatic large-scale, including transoceanic, movement patterns of commercially valuable species. However, mark and recapture data are of limited value when used to predict home range behaviour, as they typically contain only two positions occupied during the life of a fish, and the spatial resolution in such studies is often too coarse to quantify the use of space accurately. Commercial recapture data are often beset with non- or false reporting of recaptures, which results in high degrees of uncertainty in the quantification of movement.

Telemetry studies are becoming widely used in fisheries research and are most suited to study the small-scale spatial utilisation patterns of individual fish. The ability to track fish continuously over extended periods provides a distinct advantage over other techniques. The biggest drawback of telemetry studies is their manpower- and technology-intensive nature and the resulting limits in sample size and duration. Other shortcomings of telemetry include the accuracy of the position recordings when remote systems are used, and the lack of verification of the natural behaviour of animals with transmitter attachments or implants.

None of the observation methods introduced above is - when applied individually – capable of providing the information required to gain a full understanding of the movement behaviour of a fish species. Fish conservation requires knowledge of intensive (e.g. home range) and extensive (e.g. ranging) movements, which can only be studied effectively by combining the available methods.

To quantify the effect of an MPA on a species whose movement behaviour is known, this information needs to be incorporated in a spatially explicit model. When movement information is used in fisheries models, spatial dynamics are often oversimplified; patchiness of suitable habitat and changes in behaviour during the life

history of a fish are seldom considered (Bentley *et al.* 2004). To be useful for decision-making, models have to incorporate a realistic understanding of fish behaviour and biology (Guénette *et al.* 1998).

Numerical population models (Polacheck 1990; DeMartini *et al* 1993; Attwood and Bennett 1995; Sladek-Nowlis and Roberts 1999; Guénette *et al.* 2000; Parrish 1999) have often been used to predict MPA effects, although they, like general stock assessment models, are beset with a number of problems. High degrees of uncertainty, generalisation, simplification, difficult parameterisation and untested assumptions can limit their predictive power (Parrish 1999 and Hastings and Botsford 1999). Individual-based simulation models (IBMs) have the advantage that they can incorporate differences in parameters related to life history or behaviour of individual fish in relation to differences in external parameters (i.e. fishing mortality rate, distribution of suitable habitat), thereby facilitating a more realistic simulation of population behaviour (*inter alia* Alonzo and Mangel 2004; Barot *et al.* 2004; Bertolo *et al.* 2004).

The aim of this work was to combine a range of techniques to gain a comprehensive understanding of fish movement behaviour and to use this information in an individual based model to simulate the effect of MPA implementation on a fished population. There are three aspects to this work:

1. Many of the methods have not previously been used in the South African marine environment, which is very exposed, and others have not been properly assessed, hence methodology and experimental design had to be rigorously tested in pilot experiments.

2. The assessment of extensive (ranging) and intensive (home range) fish movement requires different experimental approaches. Therefore, these aspects were investigated in separate field studies employing different experimental designs.

3. Data from movement studies are valuable for fisheries management and conservation only if they result in a quantitative measure of fish movement, which can then be used to assess the effect of a particular management option. Thus, data from the field studies were used in an individual based modelling approach to predict the effects of MPAs.

This thesis is structured as a progression of independent studies, followed by a general conclusion. As these units form the basis for manuscripts in preparation, submitted or in press for scientific publication, a limited degree of repetition in the introductions, materials and methods of the individual chapters was unavoidable.

Apart from Chapter IV, this thesis focuses on one particular species. Roman is a member of the family Sparidae or sea breams, a group of typically reef associated temperate marine fish. Roman is one of many sparids that are endemic to southern Africa. Several reasons favoured the selection of roman as the main study species: traditionally, roman is a component of the South African hand-line fishery and ranks amongst the top ten commercially important linefish species. Its life history is well studied (Buxton 1984; Buxton 1987; Buxton 1989; Buxton 1992; Buxton 1993; Buxton and Allen 1989; Buxton and Garratt 1990). Roman is a benthic omnivore; its indiscriminate feeding behaviour does not only make it an easy catch, it also facilitates tank experiments. Roman is a robust species that responds well to stress associated with handling and manipulation like tagging or transmitter implantation.

Although the population is severely over-exploited (Griffiths 2000), roman continues to be targeted by the commercial and recreational line fishery. As traditional management approaches like bag and size limits are unsuitable for this species and failed to protect the stock from collapse (Lamberth 1997), there is a need for an alternative strategy. Previous mark and recapture studies found that roman show a high level of residency (Buxton and Allen 1989; Griffiths and Wilke 2002; Mann 1999), therefore making it a promising candidate for protection in MPAs. This was further substantiated by studies that found differences in size and densities of roman between MPAs and fished areas (Buxton 1987).

There are important considerations that should precede any movement study: does the chosen method affect the behaviour of the study fish? Is the method feasible to gain the required information? A tank experiment described in Chapter II investigates the effects of traditionally used barbed dart and t-bar anchor tagging on roman and introduces Visible Implanted Fluorescent Elastomer (VIFE) tagging, a method new to South Africa.

In Chapter III, two tagging methods are taken into the field. Dart tags are used in combination with VIFE tags in a boat-based mark and recapture study to determine the general movement pattern of roman in the Goukamma MPA. Patterns of tag recovery were compared with the results of previous studies and used in combination with tag loss rates and roman densities to model roman dispersal.

Chapter VI introduces the use of telemetry equipment to study fish movement in South Africa. Because of the difficult working conditions in the rough waters along the South African south coast, it was decided to launch the telemetry work in the sheltered estuarine environment to facilitate testing of equipment and gain experience

in the methodology. As roman do not occur in estuaries, spotted grunter *Pomadasys commersonnii*, another locally important exploited temperate fish (Baird and Pradervand 2002), was selected for this part of the study. Transmitter implant techniques were tested; effects on mobility, growth and survival of the study species were investigated in a tank experiment. Range of the reception and precision of the position recordings were determined and, finally, the feasibility of recording accurate and frequent positions of fishes with transmitters from a small boat was explored in a field experiment on the East Kleinmonde Estuary.

The experience gained during the pilot study on the estuary was then used in a telemetry study on roman in the Castle Rock MPA, described in Chapter IV. After confirming the feasibility of the transmitter implantation for roman in a tank study, and determining the range of the equipment and accuracy of the position records in the marine environment, manual boat-based and underwater tracking was combined with remote positioning to investigate the small-scale movement patterns of roman, and the effect of biological and abiotic factors on their home range behaviour.

The information on the degree of residency (Chapter III) and the space utilisation patterns (Chapter V) was then used in Chapter VI to develop an individual-based model that simulates the fate of post-recruit roman around two South African MPAs. The incorporation of detailed information on movement behaviour, life history patterns such as density-dependent sex change and fisheries parameters, the distribution of suitable habitat and observed fish densities and size frequencies allowed for a realistic simulation of the effect of the MPAs on the roman stock around the reserve areas under different fishing scenarios.

Finally, the findings of this study are synthesized and conclusions for fisheries management are drawn with recommendations for further investigations.

Chapter II: A comparative study to evaluate methods to tag South African reef fishes.

Abstract

The application of different tagging methods was tested in a controlled tank experiment. Tag loss and effects of tagging on growth rate and mortality on roman *Chrysoblephus laticeps* (Sparidae) were monitored over a period of 198 days. The study tested the commonly used barbed dart and t-bar anchor tags as well as Visible Implanted Fluorescent Elastomer (VIFE) tags, a tag type not previously used in South Africa. Application technique and underwater visibility of VIFE tags were tested on roman and on fransmadam *Boobsoidia inornata* in a preliminary experiment. The use of 25- gauge needles improved VIFE tag application. Whereas VIFE tagging caused fin rot in fransmadam, it had no negative effect on roman. VIFE tagged fish could be identified by a diver in an observation tank five metres in depth from a distance of three metres under ambient light. There was no significant difference in growth rates among groups of roman with different tags and controls, but high tag loss rates for barbed dart (53%) and t-bar anchor tags (73%). Although some of the VIFE marks were incomplete, all VIFE tagged fish were individually recognised at the end of the study. The results highlight the need to take cognisance of the high tag loss rate of conventional tags during the design of mark and recapture studies.

Introduction

Mark and recapture studies are commonly used to determine aspects of the biology, migration patterns and stock parameters of marine fishes (Emery and Wydoski 1987 listed 1400 studies).

For the majority of these applications it is necessary to distinguish individuals over long periods of time. Although increasingly replaced by more sophisticated systems such as Passive Integrated Transponder (PIT) (Prentice *et al.* 1990a; Prentice *et al.* 1990b), Visible Implanted Fluorescent Elastomer (VIFE) (Willis and Babcock 1998, Bailey *et al.* 1998, Beukers *et al.* 1995), and coded wire tags (Bergman *et al.* 1992, Haw *et al.* 1990), the different types of traditional barbed dart and t-bar anchor tags are still commonly used all over the world (Carstens *et al.* 2003; Laurenson *et al.* 2005; Ortiz *et al.* 2003). In South Africa, these tags have been applied in large-scale tagging studies on commercially important linefish species (Griffiths and Wilke 2002; Mann 1999). Analysis and interpretation of data generated from these studies can have a strong influence on fisheries management decisions. However, the validity of the conclusions relies on the following assumptions (Buckley and Blankenship 1990):

- Tagging does not affect the normal biological functions of the fish, i.e. movement behaviour, growth, reproduction, mortality and predation.

- The tags remain on the animals for the duration of the study, or their loss rate can be described by a mathematical function with known parameters.

In the case of traditional tags, evidence for a breach of these assumptions is mounting. Attwood and Swart (2000) report on a slower growth rate of tagged galjoen *Dichistius capensis* and white steenbras *Lithognathus lithognathus*. Similar results were found

for carpenter *Argyrozona argyrozona* (Brouwer and Griffiths 2004). Fouling adds drag (Hedgepeth *et al.* 1978) and may affect the swimming performance (Serafy *et al.* 1995). The sinus created by the internal anchor makes the fish vulnerable to infections (Roberts *et al.* 1973a; Roberts *et al.* 1973b). Tag shedding rates differ between tag types and species (Baglin *et al.* 1980a; Baglin *et al.* 1980b; Davis *et al.* 1982; McFarlane and Beamish 1986; McGlennon and Partington 1997; Xiao *et al.* 1999). Few studies adequately validate the use of the tag of choice in relation to the underlying assumptions. Buckley and Blankenship (1990) state that in many cases it appears that the choice or acceptability of tags is related more to historic use than to proven reliability. Furthermore, Bergman *et al.* (1992), Haw *et al.* (1990) and McFarlane *et al.* (1990) all point out that the credibility of tagging studies rests on demonstrating that assumptions about tag effects are correct.

This study was therefore initiated to provide a comparative assessment of tagging methods on roman, *Chrysoblephus laticeps*, a temperate sparid fish that is endemic to South Africa and represents an important component of the line fishery. Although the subject of numerous tagging studies with barbed dart and t-bar tags (Buxton and Allen 1989; Bullen and Mann 2004; Griffiths and Wilke 2002), the effects of the tags on this species have never been tested in a controlled experiment.

The objectives of the study were:

- To validate the use of traditional barbed dart and t-bar anchor tags.

- To test the feasibility of an alternative tag, the Visible Implant Fluorescent Elastomer (VIFE).

VIFE tagging has not been used previously in the tagging of South African marine fishes. It has been developed for batch tagging of juvenile fishes (Bonneau *et al.* 1995) and has been successfully applied to mark individual fishes in various studies (Parsons *et al.* 2000; Willis and Babcock 1998). The VIFE tags comprise a viscous liquid elastomer that is injected into translucent tissue where it sets to form a permanent biocompatible mark that is fluorescent under UV-light. Potential advantages of the VIFE system are the reduced effects on growth and mortality (Dewey and Zigler 1996) and possible underwater recognition of individual fish by SCUBA divers.

A controlled tank experiment was conducted to compare the tag loss rates and the effects on the fish of the three tag types, namely barbed dart tag, t-bar anchor tag and VIFE tag, when applied to roman *Chrysoblephus laticeps*. A second species, fransmadam *Boobsoidia inornata* was included in the pilot experiment to evaluate the visibility of tags on a species with a different colouration to that of *C. laticeps*.

Materials and Methods

Pilot experiment to test the feasibility of Visible Implanted Fluorescent Elastomer Tagging

Seven *C. laticeps* and nine *B. inornata* were caught by hook and line in False Bay, South Africa and transferred to two holding tanks (7500 l; Ø 2 m; H 1,2 m; open circulating seawater system; covered with shade cloth) at the Sea Fisheries Research Aquarium, Cape Town. Fishes were randomly placed in the two tanks and kept for an acclimatisation period of five days to minimize stress prior to tagging.

The fish were sequentially anaesthetised with a 2-phenoxy ethanol solution (0.25 ml/l; 80 l container), then placed on a wet plastic covered foam cushion and measured to the nearest millimetre fork length. Gloves were worn during handling to avoid epidermal damage and infections. The elastomer fluid (VIE Four Colour Kit; Northwest Marine Technology, Inc., Shaw island, Washington, USA) was then injected into the tissue between the fin rays. A maximum of five marks per fish were attempted, depending on the speed of the application. All the available colours (green, orange, red and yellow) were used and marks were attempted on dorsal, anal and caudal fins. Two methods were used to apply the Elastomer; the supplied tag applicator and a syringe with a 25-gauge needle. After the tagging was completed, the fish were carefully released back into the holding tanks. After a holding period of 17 days on a diet of squid (*Loligo vulgaris reynauldii*) white mussel (*Donax serra*) and red bait (*Pyura stolonifera*), all fish were examined to assess their general health and the condition and visibility of the tags. One fish of each species was released into a large observation tank (60000 l, Ø 4 m; H 4.8 m) where they were observed by a

SCUBA diver and filmed with an underwater digital video camera under ambient light, camera strobe light and UV-light.

Effect of different tag types on tag retention, growth and survival of roman *C. laticeps*

A total of 100 roman was caught with hook and line in False Bay, Western Cape Province. After deflation of the swim bladder with a hypodermic needle, the fish were retained in portable tanks, transferred to the Sea Fisheries Aquarium and released in three holding tanks (7500 l; Ø 2 m; H 1,2 m; open circulating sea water supply).

After an acclimation period of five months, four groups of 15 healthy fish of comparable size frequency were selected for the experiment. The fish were weighed to the nearest gram and measured to the nearest millimetre fork length. A digital photo was taken of each fish for individual recognition, and fin or scale damage was noted.

The first group was tagged with barbed plastic dart tags (89 mm, Ø 1,4 mm; Hallprint Pty Ltd; South Australia). The tag was inserted on the left hand side of the animal into the musculature below the posterior third of the dorsal fin, ensuring that the barb hooked in the pterygophores. The second group was tagged at the same position with t-bar anchor dart tags (Hallprint Pty Ltd; South Australia). The tag was inserted in the musculature with a commercial tagging gun (Banok 203 L series; Banok company Ltd; Japan). The third group was marked with VIFE tags, as described earlier, using a 25-gauge needle. Four individual VIFE marks were placed into the caudal fin. The last group was not tagged and served as a control. All fish were released back into the holding tanks with five differently sized fish of each group in every tank to ensure standard conditions amongst groups, to minimise the risk of technical failures or disease and to facilitate recognition of individuals that experienced tag loss.

The fish were fed to saturation two to three times a week with pilchard (*Sardinops sagax*), squid (*Loligo vulgaris reynaudii*) and white mussel (*Donax serra*). Tank temperature and water conditions were documented during feeding. Notes were made on abnormal behaviour, signs of infections and status of the tags. The fish were captured with a dip net after 40 and 198 days and their condition reassessed. Wet mass, fork length, tag-condition and fish condition were recorded during the assessments and digital photos of each fish were taken to facilitate individual recognition of fishes. Tag scars were photographed separately. VIFE tag condition was described using four categories:

1. Complete (C): Tag was fully intact.

2. Partially lost (P): Parts of the tag material were lost; but the tag was presumably still visible to a diver.

3. Incomplete (I): The tag was barely detectable under normal light.

4. Lost (L): The tag could not be detected, even after dissection of the fin.

Growth data analysis

To allow comparisons between growth rates of fish of different initial length, relative length increments *RLI* were calculated as

$$RLI = \frac{\Delta L}{L_{\text{inf}} - L_i} \,, \qquad\qquad \textbf{Equation II-1}$$

where ΔL is the length increase over the observation period, L_{inf} the theoretical maximum length of the von Bertalanffy growth curve for roman (Götz in prep.) and L_i the initial length. Weight increments were compared directly, as an index similar to

the *RLI* does not correct for different initial weights. After testing for homogeneity of variance (F-test), differences between the groups were tested with a one way-ANOVA.

Results

Pilot experiment

<u>Tagging procedure</u>

Although bigger fish took longer to be sedated, all the fish were motionless after five minutes in the anaesthetic bath. VIFE tags were initially applied to dorsal, anal and caudal fins but it soon became evident that the caudal fin is the most suitable fin for tag application, because it does not collapse but remains rigid. Furthermore, the rays are closely spaced and less material is needed to make a mark of suitable size. The tag application proved to be difficult, especially on smaller individuals. The needle had to be inserted into the thin tissue between the fin rays without piercing through the tissue. Care had to be taken not to withdraw the needle too quickly; otherwise fluid oozed out of the entry wound and the mark was lost. Application times per mark varied between 20 seconds and 1.5 minutes. The small needles that were provided with the tagging kit were unsuitable as needles quickly clogged and a lot of material was wasted. Tagging time was unnecessarily prolonged because of the slow flow of material through the narrow gauge needles. The larger 25-gauge needles on 1-ccl syringes worked more efficiently on both small and large fish.

<u>Survival and conditions during the observation period</u>

All fish started swimming upright less than five minutes after release into the holding tanks. No fish died during the tagging procedure. Whereas all roman resumed feeding the following day, fransmadam only started feeding five days after the treatment. Tag loss, survival and loss of individual marks are summarised in

33

Table II-I.

After two days, five fransmadam showed signs of fin rot. After 10 days five fransmadam had lost their caudal fin completely and died; only two of the remaining four appeared healthy. Two more fransmadam died with fin rot at day 15 and only two appeared healthy after the 17-day experimental period.

All roman survived the 17-day period and none showed signs of fin rot or fungal infections. One animal showed a mild distension of the left eye, a condition further referred to as "pop eye" disease. This condition is presumably caused during the rapid ascent of a fish during its capture and the resulting barotrauma. Gas permeates into the tissues in the eye socket causing increased pressure and inflammation. Typically, the eye becomes distended and is eventually lost.

<u>Tag loss</u>

All tags inserted in fins other than the caudal fin were lost after 17 days. Five fransmadam lost their tags due to fin rot. All marks applied to the roman caudal fins remained visible, although some material was lost. Marks that were made with the larger 25-gauge needle were still completely intact after 17 days.

Table II-I: Summary of tag loss and fish conditions for VIFE tagged *C. laticeps* and *B. inornata* after 17 days.

Species	Condition			Retention of complete individual marks on surviving fish
	healthy	signs of ill-health	dead	
B. inornata	2	0	7	60%
C. laticeps	6	1	0	73%

Underwater detectablity

Although the water in the observation tank was turbid on the day of the assessment (visibility ca. 4 m), marks were visible under ambient light from 3 m distance. The diver reported no difference in general detection of the marks between the two species. The ability to identify the different colours varied with the light conditions. Under natural light with low intensity, orange and green were easily confused with red and yellow respectively, especially on the larger roman, where a thick layer of tissue covered the tag. UV-light improved tag visibility and identification, but only with the diver in close proximity to the fish (<1.5 m). Direct artificial light (underwater camera strobe) made it more difficult to approach the fish and did not improve tag recognition.

Main experiment

General conditions

All tanks were connected to an open seawater flow system; therefore the temperature and the water conditions reflected those experienced in the ocean directly adjacent to the aquarium. The temperature varied between 12 °C and 16 °C with a mean of 14.3

°C. The turbidity of the water varied with the sea conditions around the water intake of the aquarium. During several periods with rough sea conditions, the bottom of the tanks was not visible. The initial size and weight composition of fish was not significantly different among the different treatment groups (Figure II-1 and Figure II-2). (ANOVA; F = 0.20 p=0.90 (length) and F = 0.09, p=0.97 (weight)).
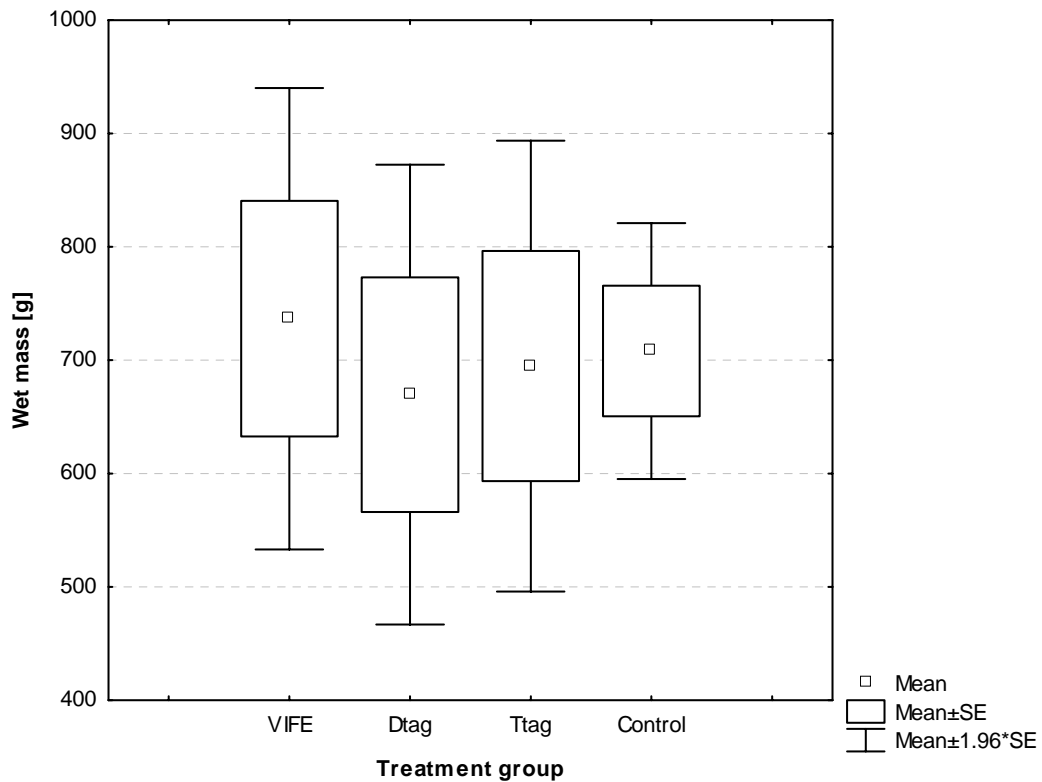
Figure II-1: Comparison between mean wet weight of the treatment groups at the beginning of the 198-day tank experiment.
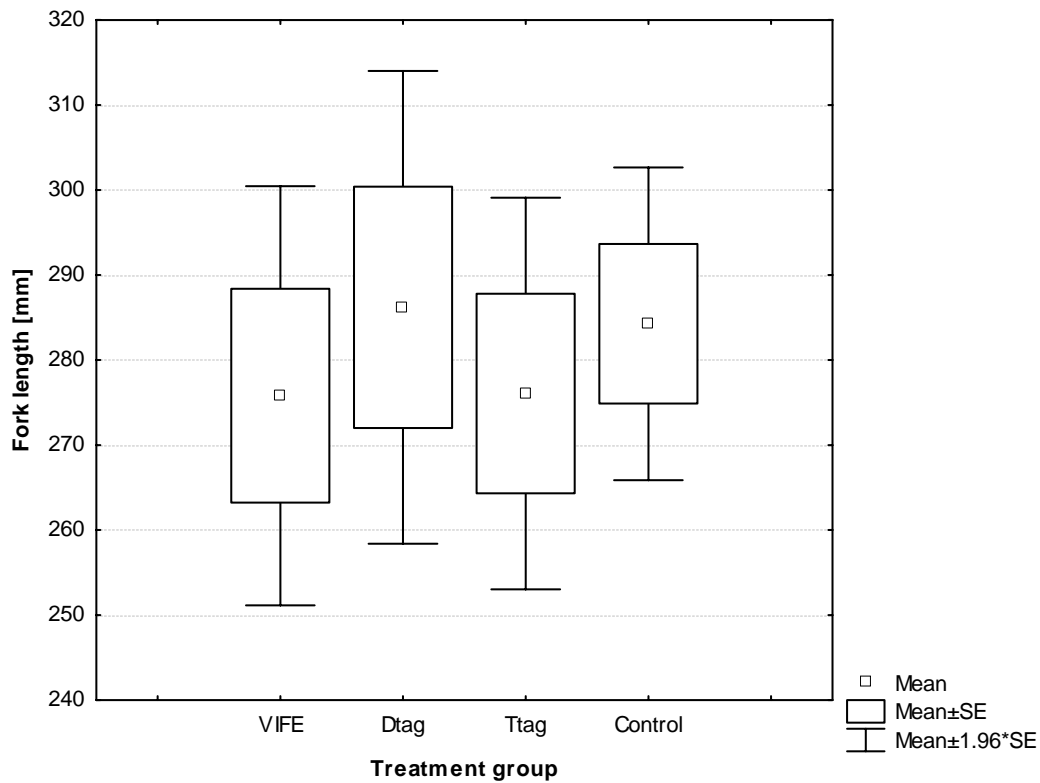
Figure II-2: Comparison between mean fork length of fish between treatment groups at the beginning of the 198-day tank experiment.

Observations after release and during feeding

All fish survived the tagging procedure. Tagged fish accepted food one hour after being returned to the tanks. None of the fish behaved abnormally the day after the tagging. Some dart and t-bar tagged animals developed a bruise around the tag with ca. 5 – 7 mm diameter. During feeding, fish with external tags showed no signs of restricted mobility and their behaviour could not be distinguished from untagged fish.

40 day assessment

The majority of the fish, independent of treatment or tank, showed no visible signs of distress after 40 days. Seven fish had minor abrasions of the upper caudal lobe and

two fish had minor canine damage, presumably caused by bumping into the tank wall during capture attempts or during flight reactions when disturbed by aquarium personnel. Two dart tags and one t-bar tag were shed during the first 40 days. The cross pieces of the t-bar tag were broken off at one end. Twelve t-bar tags had exposed filaments and two dart tags stood out further than normal and had contact with the dorsal and caudal fins of their respective fishes. This had caused obvious fin degradation at the contact point. In addition, one individual suffered from minor "pop-eye" disease of the left eye. All VIFE tagged fish could be individually identified, although a number of VIFE tags were partially lost or incomplete. Changes in VIFE tag condition are summarized in Table II-II.

There was no significant difference in weight increase among the different tag types and the control group after 40 days (ANOVA; $F = 0.99$; $p=0.40$). Only fish that retained their tags were included in the analysis. Weight increments after 40 days are shown in Figure II-3. Relative length increment was not analysed after 40 days because of the high measurement error of length measurements in relation to the slow growth rate.
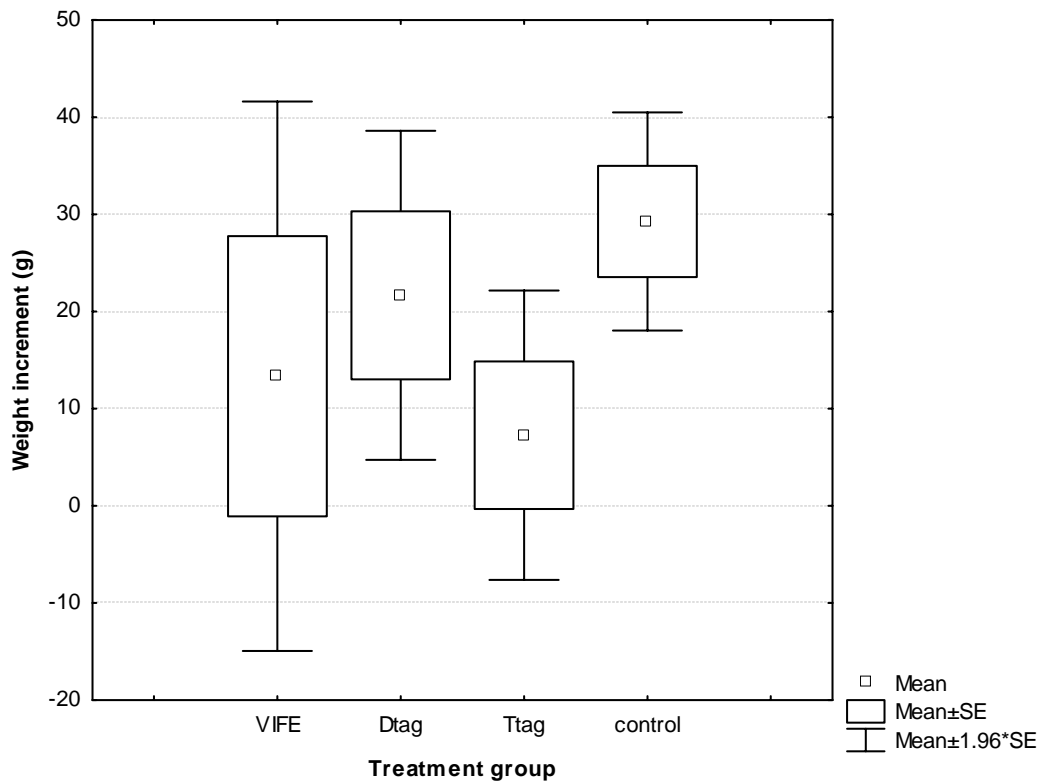
Figure II-3: Comparison of relative weight increments among different treatment groups after 40 days.

198 day (final) assessment

After 198 days, one dart-tagged fish and two control fish from different tanks had died. Two of them had developed "pop eye" disease; one appeared to have an inflated intestine and was unable to control its buoyancy. Three of the remaining fish of different tanks (T-bar tag, dart tag and control) had developed mild "pop-eye" disease on one side. The condition of the remaining 54 fishes had not changed since day 40. All VIFE tagged fish could be individually identified, although several tags had been partially lost or were notably incomplete (Table II-II). Due to the careful selection of clearly distinguishable fish within treatment groups and the photo identification, all fish without tags were individually identified after 198 days. Fish that had lost their

dart or t-bar tag revealed greyish tag scars of 3 to 7 mm diameter regardless of tag type.

Eleven T-bar tags and 8 dart tags were lost during the study period, representing 73% and 53% of the initial tags, respectively. Five T-bar tags and one dart tag were lost without being detected and had presumably been lost in the drainage system. The other shed tags were all recovered on the day of tag loss. The filaments of six t-bar tags had split and the barbs of 4 dart tags were missing. A thin layer of algal growth covered tags shed after day 100. No indentations or abrasions caused by teeth marks were evident on any shed tag. The shedding of dart tags can be described as a constant rate independent of time at liberty (Figure II-4). Instantaneous tag loss rate of 0.0028 day^{-1} (linear regression; R^2= 0.85).

Table II-II: Summary of tag status of VIFE tagged *C. laticeps*.

VIFE retention	40 days	198 days
Complete	42%	25%
Partially lost	33%	37%
Incomplete	25%	38%

The chart shows Percentage tag loss (y-axis, 0% to 60%) plotted against Days (x-axis, 0 to 250).

y = 0.0028x

$R^2 = 0.854$
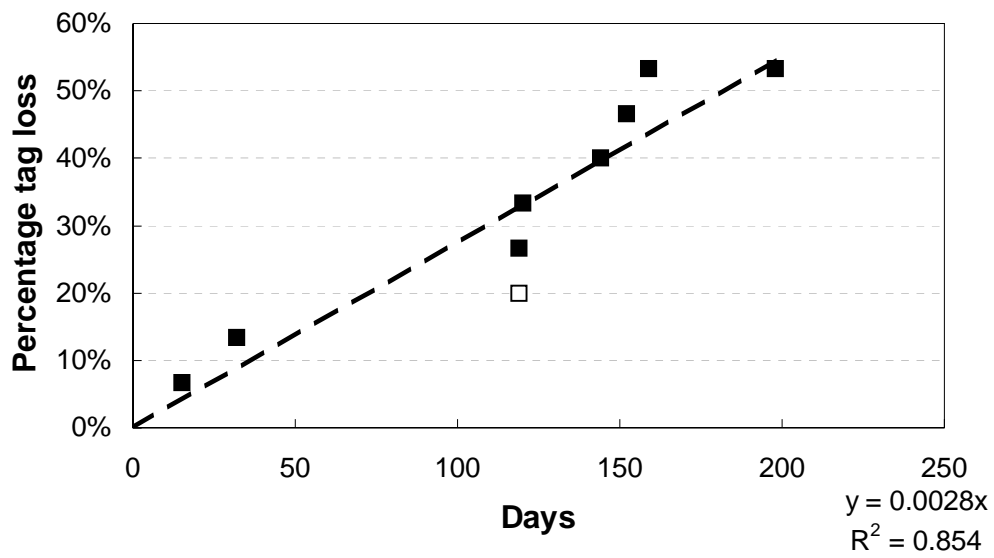
Figure II-4: The percentage of lost dart tags is plotted against the study days. The tag loss date of one missing tag was plotted as if it occurred halfway between the two assessments and is indicated by the white markerbox.

41
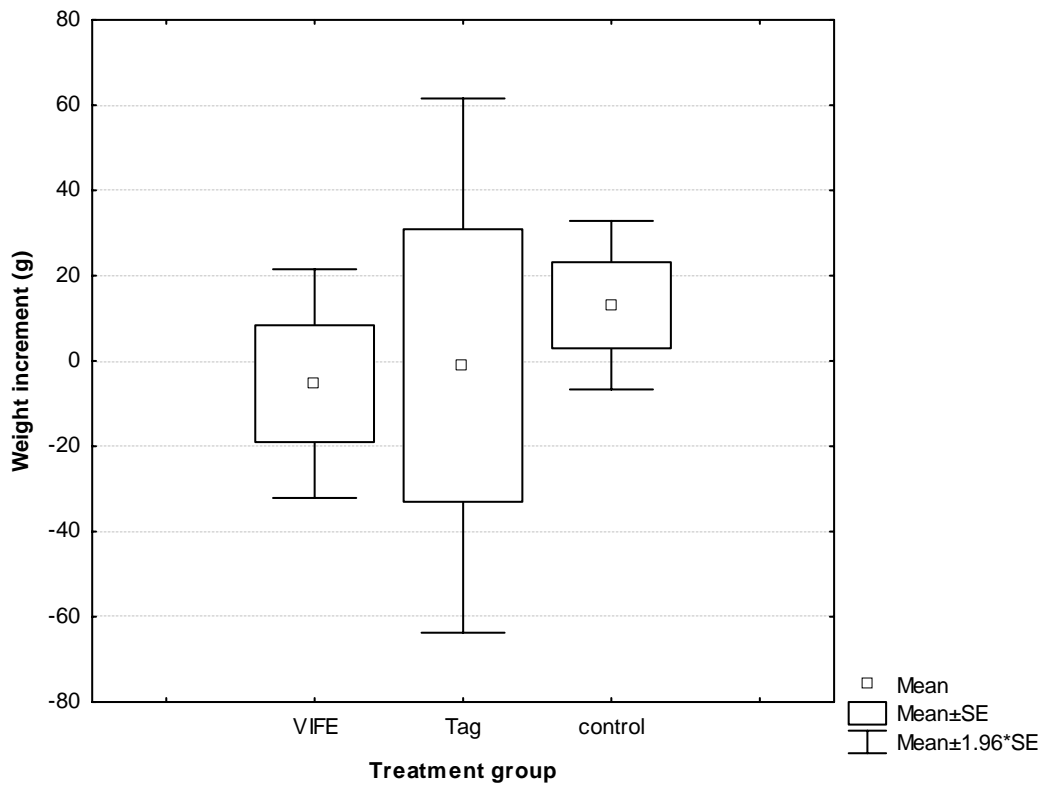
Figure II-5: Comparison of weight increments between different treatment groups after 198 days. Data for dart and t-bar tags are pooled.
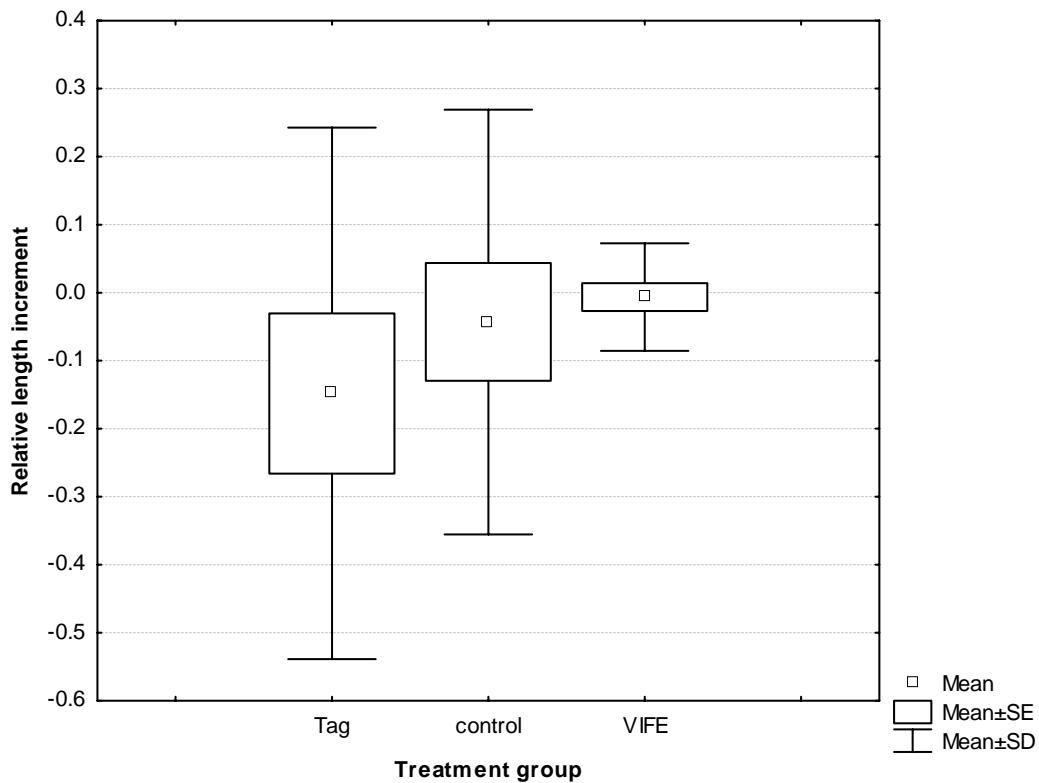
Figure II-6: Comparison of relative length increments between different treatment group after 198 days. Data for dart and t-bar tags are pooled.

Results from the 12 fish that retained a t-bar or a dart tag at the end of the study period were pooled to achieve a meaningful sample size. There was no significant difference in growth among the VIFE tagged fish, the remaining t-bar- and dart tagged fish and the control group at end of the experimental period (ANOVA; $F = 0.85$; $p = 0.43$ for relative length increments (Figure II-6) and $F = 0.26$; $p = 0.76$ for weight increments (Figure II-5)).

Discussion

General

It is critical for the correct interpretation of mark and recapture results to test the effect of tags on growth and mortality of the study species and to assess the rate of tag loss. In this study, the growth of roman after 198 days in captivity was lower than for wild populations (Mann and Kistnasamy 2000). The low mortality rate of 3%, the fact that the fish were feeding normally and the healthy condition of most of the animals at the end of the study period suggest that stress from captivity is unlikely to be a causal factor. High stocking densities of captive fish may inhibit growth (*inter alia* Ekanem 2004; Essa 1996). It is also possible that the slow growth might be attributed to the diet of mainly pilchard, which differs from the invertebrate-dominated diet in the natural environment. The fact that there was no difference in mortality or growth rate between tagged groups and control fish suggests that these fish are suitable for tagging studies irrespective of the type of tag used. The performance of the different tags appears to be the major deciding factor when planning such a study.

Tag application

VIFE tags have not been used on South African marine fishes, but previous studies indicate that they have a better retention rate and are less intrusive than traditional tags (Willis and Babcock 1998). A clear result from this study is that VIFE tagging, if carried out correctly, is an effective method to individually mark roman. The technique is more complicated than traditional tagging and requires more experience. The small needles provided with the tagging kit did not work well for fishes of the size of roman and should be replaced by 25-gauge needles, which facilitate speedy tag application. Individual VIFE tagging is limited by positions for marks on the fish. In

roman only the caudal fin proved to be suitable. With the four different fluorescent colours available and two positions in the upper and two in the lower lobe of the caudal fin, it is possible to mark 256 individual fish. The alphanumerical code of traditional tags allows for an almost unlimited number of combinations, but it cannot be recognised by SCUBA divers.

The turbid conditions of the temperate South African south coast were simulated in the observation tank as it was connected to the sea via an open flow system and hence experienced a similar degree of turbidity. Despite the turbid water on the day of the SCUBA assessment, the tags were clearly visible and all individual marks were discerned over a distance of three metres. The recognition of the individual marks requires experience, especially as the combinations red-orange and yellow-green are easily confused. A powerful waterproof UV-strobe would facilitate the SCUBA identification of individual marks and the detection of red marks, which might be difficult to see in greater depths due to the greater scatter of light with short wave lengths.

Tagging effects

Tagging may negatively affect growth, and increase mortality rate. Because VIFE tags are situated inside the fin tissue, potential problems associated with conventional tags (fouling, infections) are eliminated once the material is cured and the small puncture wound is closed. T-bar and dart tags on the other hand might affect the growth rate of a fish in two ways: the fish has to expend more energy to overcome the additional drag of the tag (Serafy *et al.* 1995) and the fish uses more resources to fight infections caused by the tag (Roberts *et al.* 1973b).

In a tank experiment, food is readily available and the effects of additional drag on the energy expenditure of the fish might differ from *in situ* experiments. Roman is a resident benthic omnivore, feeding mainly on echinoderms and crustaceans (Buxton 1984). Its movement is restricted to small home ranges (Chapter IV) and hunting success does not depend on speed or prolonged swimming, therefore effects of drag are probably negligible.

Fin degradation and infections are mainly caused by tag contact with the fin during movement. This is frequently the case when the tag gets heavier with the increase of biological fouling. Little biological fouling occurred during this study, which may be due to the filter system of the water supply. *In situ*, tags on roman recovered after the same period of time show a high degree of biological fouling (pers. obs.); therefore, an increased infection rate *in vivo* may apply.

Due to the anaesthetisation and the longer handling time, VIFE tagging could potentially cause higher mortality immediately after tagging, however this study has shown this not to be the case for roman irrespective of the type of tag used. What is clear, however, is that VIFE tag mortality varies from species to species. *B. inornata* developed severe fin rot soon after VIFE tagging, causing mortality within 5 days. Willis and Babcock (1998) detected fin rot in 47% of VIFE tagged *Pagrus auratus*, a temperate sparid fish from New Zealand, but did not attribute it directly to tagging. The present study serves to emphasise that tagging methods need to be tested across species and that results cannot be generalized.

Tag loss

One of the main drawbacks in mark and recapture studies is the uncertainty in estimating tag loss. As is evident in this study, tag type and placement has a major

effect on tag loss. Most notable in this study was the high shedding rate of barbed dart and t-bar anchor tags. Scientists with extensive tagging experience carried out the tagging. None of the tags had bite marks and picking on tags by other fish was never observed. Improper tagging and effects of overcrowding can therefore be excluded and it can be assumed that the tag loss rates are equally high for *in vivo* experiments. Dart tags performed better than t-bar tags, probably because they are anchored between the pterygophores and their filaments are more rigid. Whether shedding is caused by a biological reaction (Bergman *et al.* 1992) remains to be established. Instantaneous tag loss rates for dart tagged *P. auratus* were shown to be much lower (McGlennon and Partington 1997) than the tag loss experienced in this study, emphasizing that tag loss rates vary between similar species.

The high short-term tag loss of VIFE tags in the pilot study was likely due to tagging technique, as correct application is critical to retention rate (Willis and Babcock 1998). Care has to be taken not to allow Elastomer material to flow out of the entry wound; otherwise much of the mark is lost before the material is cured.

If properly inserted, VIFE tags show a much lower tag loss rate than traditional tags. All individual fish were recognised after 198 days, although some of the material was lost. In field studies, all VIFE tagged fish were individually identified after more than two years at liberty (Chapter III).

Conclusions

T- bar and dart tagging methods traditionally used in many tagging programmes, have a number of disadvantages that are highlighted in this study. The extent of the negative effects on the biology of the fish depend on the life style of the study species and need to be individually tested prior to field studies to avoid invalid conclusions being drawn from the data. For roman, the traditional tags did not seem to have a negative effect on growth and survival, but the high tag loss rate will make long term studies inefficient. The feasibility of tagging programmes needs to be revised through rigorous testing of the effects of tags and tag loss rates for all species. VIFE tagging can pose an effective alternative in intensive, small scale scientific tagging programmes, especially in ecological studies that examine juvenile dispersal (Buckley and Blankenship 1990) and assess of site fidelity (Willis *et al.* 2001, Chapter III).

Chapter III: Movement patterns of roman *Chrysoblephus laticeps* derived from mark and recapture data

Abstract

The movement behaviour of adult roman *Chrysoblephus laticeps* (sparidae) was investigated using mark and recapture techniques. The accuracy and precision of data from previous mark and recapture programmes featuring this species were limited. A mark and recapture study was designed around the available information on roman movement behaviour and carried out in the Goukamma Marine Protected Area (GMPA) on the South African temperate south coast. A combination of conventional barbed dart tags and Visible Implanted Fluorescent Elastomer tags were used to tag roman from a skiboat. Datasets from this experiment and from a previous tagging study in the Tsitsikamma National Park (TNP) were used to model the degree of residency. Sixty one percent of the recaptures occurred within 50 m of the tagging position, suggesting that roman are highly resident. A small proportion of fish, independent of size and sex, moved distances of up to 4 km. Taking tag loss, mortality and effort distribution into account, a probability of 91% (GMPA) and 94% (TNP) was calculated for roman to be resident within a 100m by 100m cell, suggesting that individual roman will benefit from small MPAs.

Introduction

For many reef-associated fishes, the application of conventional fisheries management strategies (bag limits, size limits, restricted access) has failed (Griffiths 2000). The majority of once abundant fish stocks have been heavily depleted (Griffiths 2000, Penney *et al.* 1999) or fished to commercial extinction (Chale-Matsau *et al.* 2001).

Marine protected areas (MPAs) have been identified as an alternative measure to conserve fish (Attwood *et al.* 1997, Bohnsack 1996, Griffiths 2000, Polacheck 1990). There is widespread evidence that MPAs can protect resident fish against overfishing (Buxton and Smale 1989, Roberts and Polunin 1991). Populations within MPAs have been shown to build up rapidly (Russ and Alcala 1989) and potential benefits for the adjacent fishery in the form of 'spillover' of migrating adults and larval dispersal have been shown in a number of studies (Alcala and Russ 1990, Attwood 2002, Sladek-Nowlis and Roberts 1999). These processes will occur only if the MPA is big enough in relation to the area utilised by the individual fish (Attwood and Bennett 1994, Kramer and Chapman 1999). Therefore, detailed information on the movement patterns is needed to design and evaluate MPAs.

This chapter describes the movement patterns of roman *Chrysoblephus laticeps* using mark and recapture techniques. Roman, a reef-associated sparid is endemic to the South African warm temperate coast. It is frequently caught by shore and skiboat anglers from Port Edward to Cape Point and can be found amongst the ten most important species in the traditional hand-line fishery (Lamberth 1997).

Roman is a typical example of an over-exploited line-fish. Its opportunistic feeding behaviour (Buxton 1984) makes it vulnerable to capture by line-fishermen, and effort has increased markedly during the last 100 years, placing the stock under great

pressure (Griffiths 2000). The combination of its high longevity and its sex changing habit have added to the vulnerability of the stock (Buxton 1989, Buxton 1993), now regarded as collapsed (Griffiths 2000). Conventional management regulations, i.e. bag limits and size limits, are unlikely to result in the rebuilding of the stock. Roman are susceptible to barotrauma and ruptured swimbladders (as a result of the expanding gas in their peritoneal cavities) when brought to the surface. Captured fish are often unable to return to the reef when released.

Information on movement patterns of roman

The movement patterns of roman have received considerable research attention (Table III-I). Buxton and Allen (1989) concluded that roman in the Tsitsikamma Marine Park are sedentary and do not migrate over large distances. Griffiths and Wilke (2002) studied movement patterns of roman and other linefish on the Agulhas Bank. They described roman as being station keeping, with a certain proportion moving farther a-field.

Additional data are available from a long term tagging programme, the Sedgwick's/ORI/WWF Tagging Programme, which uses volunteer anglers to tag and release fish in South African and Namibian waters. Several intensive mark and recapture studies in MPAs run by scientific organisations, like the Tsitsikamma National Marine Park tagging programme, are nested within this programme. Data from these programmes suggest that roman are predominantly resident throughout their adult life.

Table III-I: Summary of available information on roman movement from mark and recapture projects (Peer reviewed publications are indicated by asterisk*). a Buxton 1989, b Griffiths 2002, c ORI total, d ORI Tsitsikamma subset.

Source	Study area	Period	Method	Source of recaptures	Accuracy	Fishing effort	Tags	Recaptures	Maximum displacement	Displacement >1 km (%)
a*	Tsitsikamma MPA	1985-86	Skiboat angling	Scientific personnel, Recreational shore-anglers	not specified	unknown	379	11	2 km	n/a
b*	Agulhas bank	1987-93	Skiboat/ship angling	Commercial fishermen	1 km	unknown	4083	240	39 km	25%
c	South Africa	ongoing	Shore and skiboat angling	Recreational anglers	1km	unknown	2958	138	247 km	13%
d	Tsitsikamma MPA	ongoing	Shore angling	Scientific personnel	100m	known	460	81	0.5 km	0%

Limitations of existing data

Although previous studies and the ongoing programmes give an indication of the general movement pattern of roman, there are several limitations in the experimental design that diminish the information content of the data. These include:

- Reliance on recaptures from fishermen (sources b,c)

  Recapture data submitted by commercial and recreational fishermen can be flawed in several ways. Recapture positions are falsely reported or not reported to protect favourable fishing grounds or to hide illegal fishing activities e.g. fishing inside MPAs. As it is impossible to quantify this effect, it

leads to bias in the estimation of percentage of moving fish and distance of movement.

- Spatially limited effort (sources a,c)

  If recovery effort is limited to an area much smaller than the maximum range of the species, the data will be biased, as emigrating fish are simply not recaptured. This is the case for shore angling, as only alongshore movement can be detected.

- Unknown fishing effort, catchability (sources a,b,c)

  Recapture rates will depend partly on the recovery effort. In many cases the tagging sites are subjected to higher effort than elsewhere. This effect can be quantified only if the fishing rate and the catchability of the species are known.

- Limited precision of mark and recapture positions (sources a,b,c)

  If the resolution of the tagging and/or recapture positions is coarse, as is the case with most recapture data collated from the fishery, small-scale movements, which can be crucial for the protection of resident species in small MPAs, cannot be detected.

These limitations cast some doubt on the reliability of the findings reported above, and may go some way to explain the variation in the observations listed in Table III-I.

The aim of this study was therefore (i) to re-evaluate previous findings of roman movement studies, (ii) to carry out a new tagging experiment that would generate a reliable dataset, eliminating the uncertainties of previous studies, (iii) to use these data

in an individual based simulation model to quantify roman residency, taking the distribution of fishing effort, tag loss and mortality rates into account and (iv) to apply the model to another recent dataset from the Tsitsikamma tagging programme (Cowley 1999, Cowley 2000, Potts and Cowley 2002) to compare and verify results.

Study site

The tagging experiment was carried out in the Goukamma Marine Protected Area (GMPA), which is situated along South Africa's warm temperate south coast between Sedgefield in the west and Buffalo Bay in the east [34.04˚S; 22.83˚E - 34.07˚S; 22.98˚E] (Figure III-1). The GMPA was proclaimed in 1990. It includes approximately 16 km of coastline and extends one nautical mile seawards from the high water mark covering an area of 43 km^2.
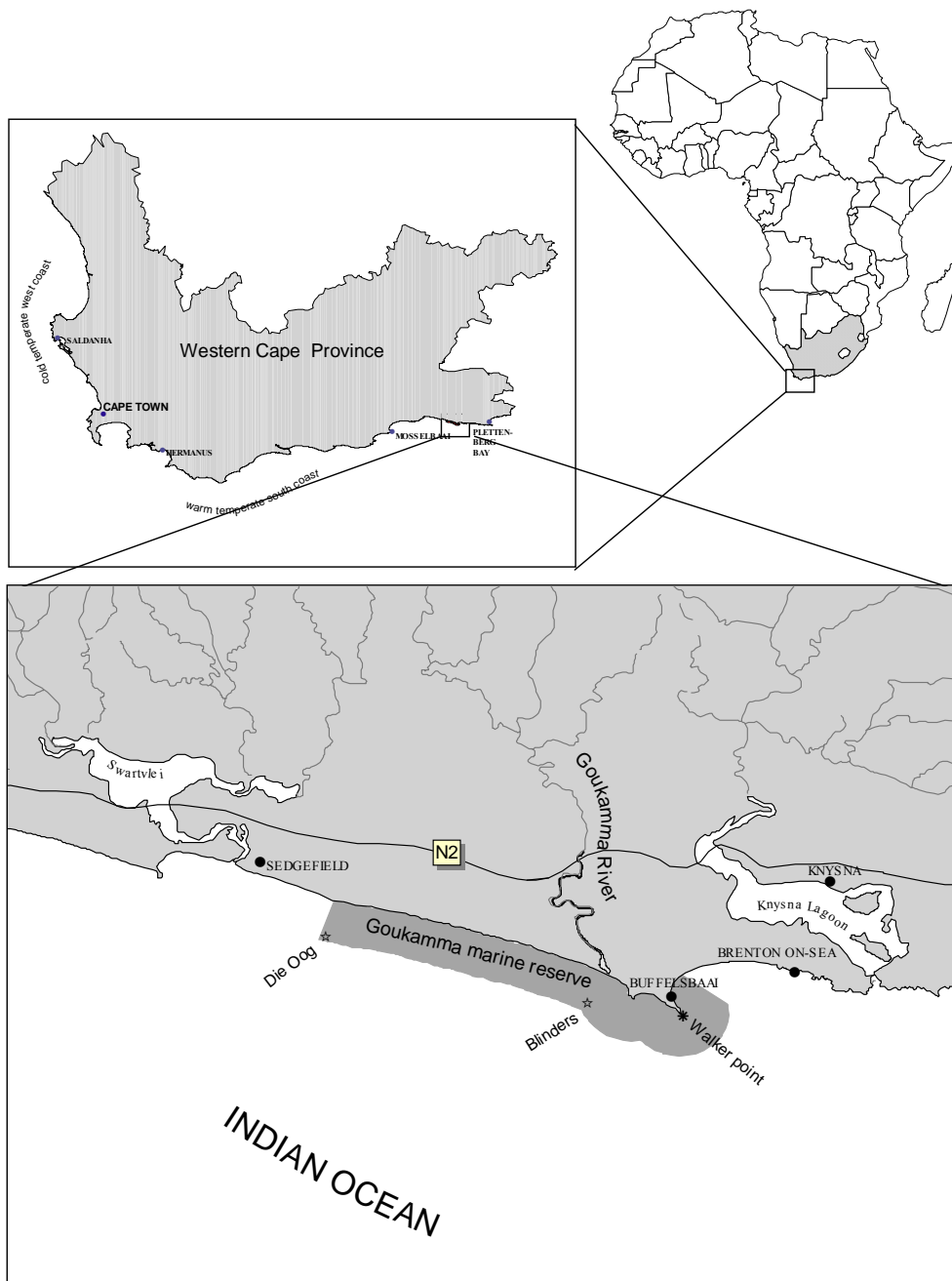
Figure III-1: Africa with inserts of the Western Cape Province of South Africa and the Goukamma Marine Protected Area.

The subtidal habitat features a number of reefs formed by submerged aeolonite dune cordons parallel to the shoreline separated by flat sandy or muddy substrate. The

maximum depth of the protected zone is 36 m with most of the area shallower than 30 m.

The Goukamma area has a long history of human utilisation. Shore fishing and collection of intertidal organisms started with the indigenous Khoi-San populations. At the turn of the 20th century, a recreational and a commercial fishery had developed. The post colonial period saw the introduction of boats, fishing lines and more sophisticated gear. First recorded catches were landed at Gerrickes Point, west of Sedgefield (Gilchrist 1924). Today, the area is heavily utilised by shore anglers and recreational and commercial skiboat fishermen. At present, commercial skiboats operating from Knysna are mostly targeting hake *Merluccius capensis* stocks in the area. Reef- associated fishes, such as roman, are mainly caught by commercial boats in the summer months, in periods when hake are scarce, and by an increasing fleet of recreational skiboat and shore anglers during the holiday season in December (Götz 2005).

Materials and Methods

Standardised fishing

Tagging was carried out from May 2001 to September 2003 from a 5.5m semi-rigid inflatable boat. Research angling sites were selected according to a random-stratified design, ensuring the effort was evenly distributed with respect to depth and pre-selected zones within each season. After the pre-selection of a general area, the actual anchoring positions were randomly selected from suitable rocky substrate detected on an echo sounder.

Position recording

The geographic coordinates of each fishing site were determined with a GPS (Furuno Colour GPS Plotter GP-1610C) after the boat had settled on its anchor position. To maximise the accuracy of the position recordings, the anchor rope was kept as short as possible allowing a maximum angle of 45° between anchor rope and the seafloor. The position of the boat was monitored with the tracking function of the GPS receiver. If the boat shifted during the fishing session due to changes in current or wind direction, the position was recorded as the centre of the GPS track. In these cases the maximum inaccuracy of the position equalled the water depth plus GPS error (5 m), which was approximately 30 m. Usually, wind and current held the boat in a stable position, resulting in an accuracy equivalent to the GPS error.

The fishing team was kept as consistent as possible. Only ten people participated in fishing activities during the programme. Fish were captured with rod and line. Barbless circular hooks (VMC sport circles) with clipped barbs were used to ensure minimum damage to the fish and to reduce the frequency of gut or gill hooking.

Captured fish were placed on a wet plastic stretcher on which the fork length (FL) was measured to the nearest millimetre. The swim bladder was deflated with an 18-gauge hypodermic needle if necessary.

Tagging

Two types of tag were used: Barbed dart tags (d-tag; 89 mm, Ø 1,4 mm; Hallprint Pty Ltd; South Australia) and Visible Implanted Fluorescent Elastomer (VIFE) tags (Northwest Marine Technology Inc., Shaw Island, Washington, USA). Whereas dart-tagging effort was randomly spread over the entire study area, VIFE tags were used to mark fish at one selected reef in the core area of the MPA, an area of approximately 200×200 m. This was done in an attempt to saturate a particular area with VIFE tagged fish to maximise the chance of multiple re-sightings during SCUBA assessments.

Dart tags were inserted on the left side of the animal into the musculature below the posterior third of the dorsal fin until the barb hooked one of the pterygophores. Tagged fish were then released immediately. For the VIFE tagging, the fish were tranquillised in an 80 l tank containing a2-phenoxy ethanol seawater solution ($0.25 ml \cdot l^{-1}$). After the fish were completely motionless, they were measured and their swimbladders deflated. The fish were then placed on a wet plastic-covered foam cushion and four implants were inserted into the membranes between the rays of the caudal fin with a 25-gauge needle. A combination of four different colours (green, red, orange and yellow) at 4 different positions (two on the upper and two on the lower fin-lobe) was used to create individual codes. The size of the implants varied between 1 mm× 10 mm and 2 mm × 30 mm dependent on the size of the fish. The code was recorded in dorso- ventral direction e.g. RRYG for red-red-yellow-green.

58

After tagging, the fishes were kept in an 80 l seawater container until they recovered from the effects of the anaesthetic. Once the fish was able to swim upright and manoeuvre properly it was released.

Recapture

All recaptures were made by the research team during the main study period from May 2001 to October 2003 and during a research survey onboard the *RV Sardinops* in January 2004, which terminated the tagging study (Table III-II). During the main study period, recaptured fish were released again. Dart tags were cleaned from excessive biological fouling before the fish was released. During the *RV Sardinops* survey, the fish were sacrificed for biological analysis. The GPS position of the recapture was taken with a handheld GPS receiver (Garmin GPS 45 personal navigator) at the position of the angler on the gunwale.

Underwater re-sightings were attempted during SCUBA assessments of the fish density in the area. The GPS position was then taken at the dive buoy.

Table III-II: Angling and diving effort during the Goukamma tagging programme.

Study period	Vessel	Angling days	Angling stations	Dives
May 01-Oct 03	Skiboat	88	273	53
Jan-04	RV Sardinops	11	36	5

The Tsitsikamma tagging programme

The Tsitsikamma tagging programme is part of a long-term shore-angling based project to monitor the line-fish stocks in the Tsitsikamma Marine Park (Cowley 1999, Cowley 2000, Potts and Cowley 2002). A subset of the mark and recapture data from this programme, collected in a period of 6 years from a 2.8 km stretch of coast in the centre of the park with accuracy of the angler positions and spatial resolution of mark and recapture data similar to the Goukamma study, was selected to run the model with another data source.

Table III-III: Summary of the Tsitsikamma shore-angling dataset used in the model.

Study period	No of angling sessions	No of tags	1st recaptures	2nd recaptures	Total	Recapture rate [%]
Feb 98-Jun 04	158	261	49	7	56	21

Modelling framework

A model was developed to estimate the extent of residency among roman. The model was applied to the data resulting from the Goukamma study and, in a slightly modified version, to the subset of the data from the Tsitsikamma shore-angling programme (Table III-III). The general framework follows Hilborn's (1990) approach by calculating expected recapture rates and comparing these to the observed recapture rates. The procedure involved linking five models:

1. A fish position model calculated the chance of each individual tagged fish being alive and retaining its tag at every fishing day.

2. A recapture model specified the probability of each individual fish being caught during each fishing session.

3. A Poisson distribution was used to calculate the likelihood of each individual recapture. These likelihoods were multiplied together, to specify the overall likelihood of the dataset.

4. A non- linear minimisation routine called Amoeba (Press et al. 1986) was then used to find a set of parameter values that minimize the negative log-likelihood.

5. Finally, likelihood profiles and the likelihood ratio test were used to determine confidence intervals for each individual parameter.

Table III-IV: Definitions, units and origin of mathematical symbols used in the model.

Symbol	Parameter	Unit	Source
M	Natural mortality rate	day^{-1}	Estimated variable
T	Tag loss rate (dart tags only)	day^{-1}	Estimated variable
N	Total number of fish per cell	fish	UW-counts (Buxton 1987, Götz 2005)
Q	Number of suitable cells within the range of the fish	cells	Estimates from sea floor maps, tested
t	Time since release	days	Calculated: $d-a_f$
a_f	Day of release of fish f	Julian day	Dataset
d	Angling day	Julian day	Dataset
C_d	Number of fish caught in a particular fishing session on day d	fish	Dataset
p	Probability of fish caught in release cell		Estimated variable
P_{ft}	Probability of fish f being alive and bearing its tag at time t		Calculated
$\hat{R}_{ft}$	Predicted probability of recapturing fish f at time t		Calculated
R_{ft}	Observed recapture of fish f at time t		Dataset

Fish position model

The geographical domain, which includes the entire Goukamma study area (Figure III-1), was divided into 100 by 100 m cells. Roman movement was simplified by considering only two conditions: the tagged fish remained in the tagging cell, or moved to another cell with suitable habitat within the domain. A binary approach was taken to model habitat suitability, either a cell held suitable roman habitat or not.

Movement beyond the domain was not considered. The movement model therefore specifies the chance of the tagged fish being alive and retaining its tag on fishing days subsequent to its tagging, and whether or not it is located in the tagging cell. The chance of the fish being alive and retaining is tag is a function of the natural mortality rate (M) and the tag loss rate (T). As the there was no tag loss considered for VIFE tags, these two parameters were estimated separately.

The probability of a fish being alive and still bearing its tag in the tagging cell is

$$P_{ft} = pe^{(-M-T)t}$$
Equation III-1

with $t = d - a_f$
Equation III-2

and for all other cells

$$P_{ft} = \frac{(1-p)}{Q-1} e^{(-M-T)t}$$
Equation III-3

The last equation spreads the probability of locating a "non-resident" fish among all other Q-1 cells. The number of suitable cells in the range of the fish (Q) depends on the maximum displacement distance, the topography of the study area and the location of the tagging cell within the domain. Assuming a maximum displacement distance of 4 km for Goukamma (Table III-VI), the area where the fish could have been located is roughly $5 \cdot 10^7$ m^2 or 5000 cells. However, movement was constrained by land and by the availability of suitable habitat within the range of the fish. Accordingly, Q was estimated to be in the order of 1000. Because of uncertainty in this estimate, values

from 100 to 10000 were used to test the influence of Q on the estimated parameters (Table III-VIII).

Recapture Model

It was assumed that all cells with suitable habitat host equal numbers of roman (N). The probability of recapturing a specific individual in a cell is given by the number of fish caught during a specific fishing session (C_d) divided by the total number of roman in a cell (N), assuming all roman in a cell stand an equal chance of being captured, regardless of sex or size.

The probability of recapturing individual roman is

$$\hat{R}_{ft} = \frac{P_{ft} C_d}{N}$$

Equation III-4

Likelihood model

The recapture model calculates the probability of recapture, which is expected to follow a Poisson distribution, because the probability of recapturing a fish is small, the capture events are discrete and capture events are random.

The likelihood of the recapture data set given any particular combination of p, M and T is

$$L(R \mid p, M, T) = \prod_f \prod_d \frac{e^{-\hat{R}_{ft}} \hat{R}_{ft}^{R_{ft}}}{R_{ft}!}$$

Equation III-5

The values of p, M and T that resulted in the maximum likelihood were taken to be the best estimates. For computational convenience, equation III-5 was log transformed and multiplied by –1.

$$LL = -\log L$$ **Equation III-6**

Minimisation routine

A non-linear minimisation routine called "Amoeba" (downhill simplex method of Nelder and Mead, Press *et al.* 1986) was used to minimise the negative log likelihood *LL*. The routine required the estimation of initial values of p, M and T, which were bounded between 0 and 1. Different initial values within these plausible boundaries were tried. Tolerance levels were set to 5 E –07 and the maximum number of iterations was constrained to 500.

Confidence intervals

The likelihood profiling method was used to determine the 95% confidence intervals of the estimated parameters. Profile likelihood intervals are based on the relationship between –2 ln(L) and the X^2-distribution (Lebreton *et al.* 1992). The 95% confidence interval includes all parameter values that satisfy the inequality:

$$\ln(L) \geq \ln(L_{min}) + \frac{3.8416}{2}$$ **Equation III-7**

The number 3.8416 represents the upper 95% point of the X^2-distribution on one degree of freedom.

Modifications for the Tsitsikamma shore angling dataset

To cater for the different tagging domains, the model had to be modified slightly. As only dart tags were used during the Tsitsikamma study, no distinction between different tag types had to be made. A fishing session was equivalent to a shore-angling session spent in a particular cell on a particular day. Q was estimated the same way as for Goukamma. Values between 100 and 10000 were tested (Appendix, Table III-VIII), based on the maximum movement distance of 4 km as found for the Goukamma study. The Goukamma value was adopted here, because recaptures derived from shore angling studies are unlikely to provide a realistic value for the maximum displacement of fish as offshore recaptures are not possible.

Results

Recaptures in Goukamma

490 Roman were tagged in the GMPA; 394 with dart tags and 96 with VIFE tags. The tagged fish ranged from 220 to 475 mm fork length (Table III-VI). Roman start becoming sexually mature at 170 mm, therefore the sample is unlikely to include juvenile fish. Forty-two fish were recaptured during the study, including multiple recaptures. VIFE tags accounted for 28 of the recaptures, representing almost a third of the released fish tagged with this method (Table III-V). Seven fish were recaptured twice and one fish was caught three times. None of the recaptured fish had crossed the boundary of the GMPA. All of the VIFE tagged fish could be identified, although some of the marks were incomplete.
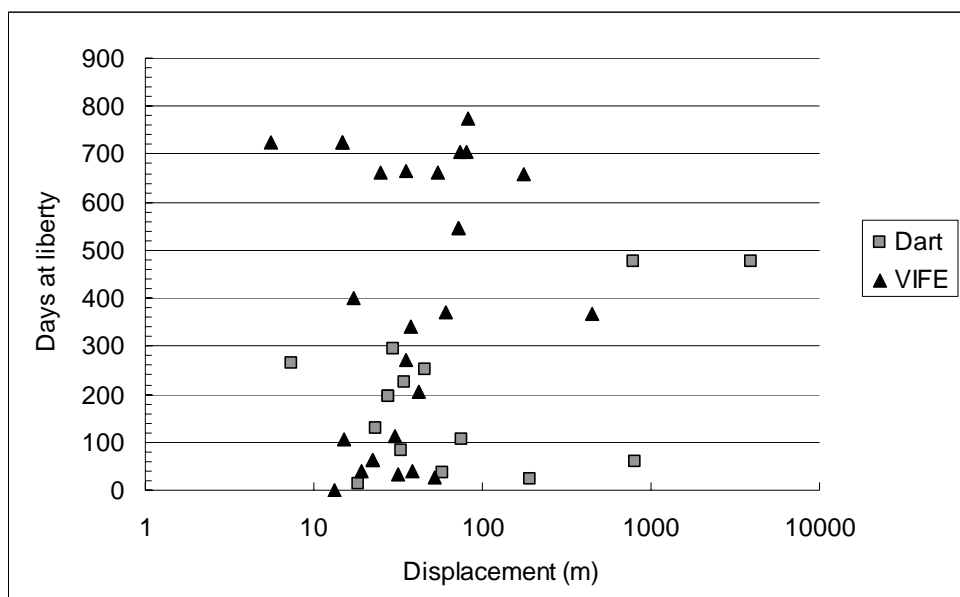
Figure III-2: Displacement (log scale) of recaptured roman in the Goukamma area, plotted against days at liberty.
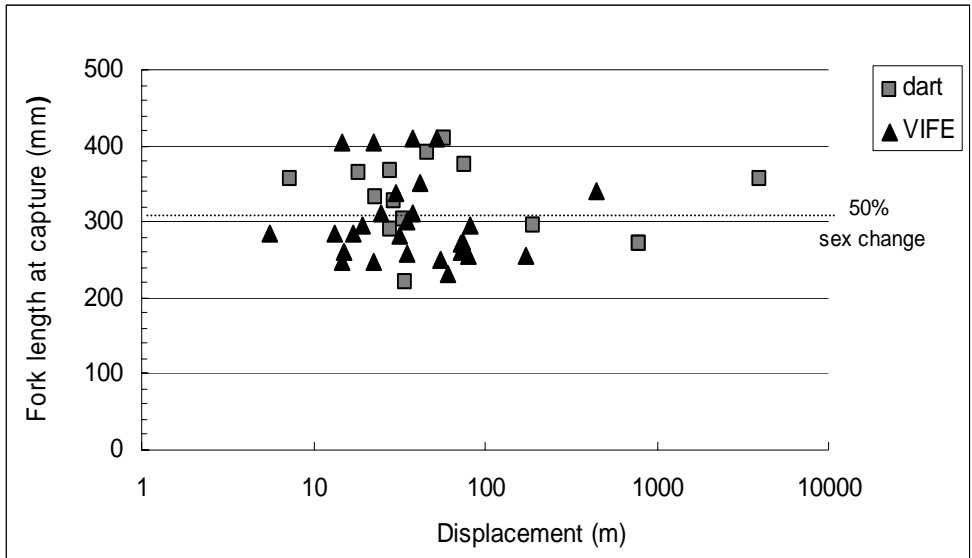
Figure III-3: Roman fork length at time of capture in the Goukamma area, plotted against displacement (log scale). The size of 50% sex change is indicated by the dotted line.
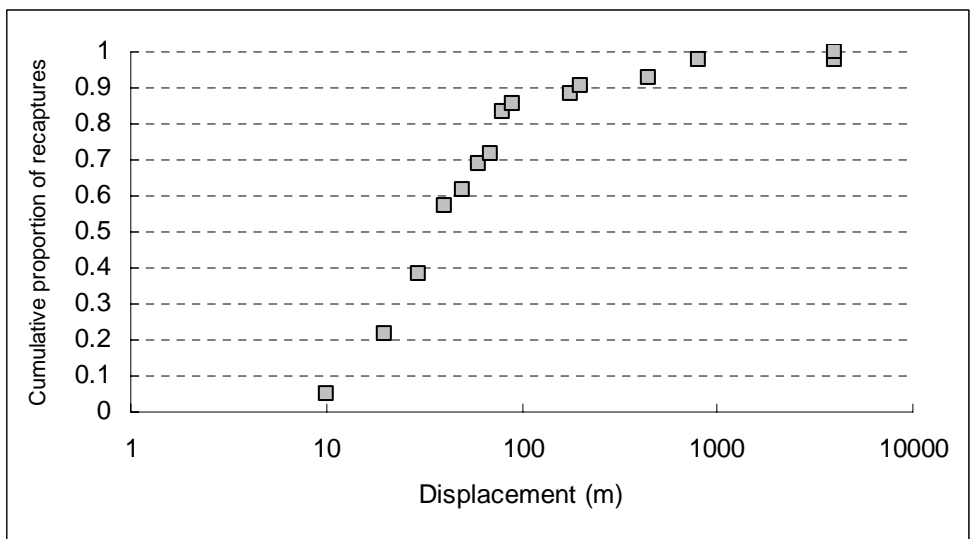
Figure III-4: Cumulative proportion of recaptures in the Goukamma area at increasing distances from the tagging point (log scale).

Most fish were recaptured close to the release point. 85% of the fish were recaptured within 100 m, 61% within 50 m of the capture position. The remaining individuals moved between 180 m and 4 km. These recaptures showed no correlation between

distance moved and time at liberty (Figure III-2). There is no evidence for a size or gender related change in residency from the data (Figure III-3). The fish that travelled the furthest measured 271 mm and 357 mm, respectively and represented different sexes.

Table III-V: Number of recaptures of roman in the Goukamma area between May 2001 and January 2004.

Tag type	Number	1st recaptures	2nd recaptures	3rd recaptures	Total	Recapture rate
Dart	394	13	2	0	15	0.04
VIFE	96	21	5	1	27	0.29
Total	490	34	7	1	42	0.09

Table III-VI: Summary of roman recaptures in the Goukamma area between May 2001 and January 2004.

Tag type	Initial FL [mm]		Days at liberty		Recapture distance [m]	
	min	max	min	max	min	max
Dart	220	441	13	475	7	3968
VIFE	221	435	0	774	6	100

Underwater re-sightings

Re-sightings of VIFE tagged fish underwater occurred exclusively in the VIFE tagging area. Generally, low visibility and incomplete marks made the recognition of the tag code underwater impossible. However, several fish with VIFE marks were sighted; four during underwater fish counts on the reef in 2002 and ten during the RV Sardinops survey in January 2004. The latter were re-sighted during two dives in the centre of the VIFE tagging area. Given the extent of the reef of less than 4 ha, it can be safely assumed that the maximum displacement distance for these fish was less than 100 m.

Model results

The probability p of recapturing a fish in its tagging cell was 51% for the Goukamma and 94% for the Tsitsikamma data (Table III-VII). Likelihood profiles for p for both datasets showed well-defined minima of the negative log-likelihoods (Figure III-5, Figure III-6). The estimated values of the parameters M and T differed by two orders of magnitude between the two datasets. Likelihood profiling of M and T produced flat curves with a broad range of values within the confidence intervals for both datasets and no local minima for the Goukamma data (Table III-VII, Figure III-5, Figure III-6). Estimates of the parameters M and T are in fact additive for the Tsitsikamma dataset and could have been estimated as a single parameter. As this did not affect the value of p, the parameters were estimated separately because of programming convenience. A test run with a combined parameter M+T did not result in different values of p.

Table III-VII: Estimates and confidence intervals of probability of recapturing a fish in its tagging cell p, the mortality rate M and the tag loss rate T. Results are shown for the Goukamma and the Tsitsikamma dataset.

Parameter	Goukamma		Tsitsikamma	
	Value	CI (95%)	Value	CI (95%)
P	0.51	0.37 - 0.66	0.94	0.78 - 1
M	-1.00 E-06	-3.40E-04 - 0	-2.42E-04	-9.00E-04 - 0
T	-2.8 E-06	-1.00E-03 - 0	-2.07E-04	-9.50E-04 - 0

Running the model with the different values of Q did not change the p value (Table III-VIII). A value of 1000 was accepted as being assumed most realistic for both studies.

Discussion

General movement pattern

This study was designed to eliminate uncertainties and flaws in the experimental design of earlier studies on the movement of roman. The general movement pattern of roman emerging from this study is in agreement with earlier findings for this species and is commonly found across a wide range of reef-associated fishes (*inter alia*, Attwood and Bennett 1994, Buxton and Allen 1989, Holland *et al.* 1996, Smith *et al.* 1989). The majority of the adult population permanently resides in a confined area, whereas a proportion of fish exhibit movements that are in the order of two to three orders of magnitude greater then the extent of the home range.

In the case of roman, the pattern can be described as 'straying' (Attwood 2002). Roman of all sizes are caught throughout the species distributional range, which excludes the possibility of a directed migration as is exhibited by other species (Brouwer 2002, Griffiths and Hecht 1995). None of the results of the studies conducted so far indicate a relationship between time at liberty and distance moved. In all studies, fish have been recorded to travel distances of several kilometres in a few days. One fish from this study was recaptured after 8 months virtually on its tagging spot. Seven months later, the fish had moved to another site four kilometres from its tagging position.

Movement is not related to spawning, immature fish also do move (Griffiths and Wilke 2002) and movement occurs throughout the year. Similar recapture results have been found in all the tagging programmes, in different areas. Whether this movement pattern is universal in adult roman, or if the population is polymorphic in terms of movement behaviour (Attwood and Bennett 1994) cannot be answered from the

existing data and requires a genetic analysis in conjunction with mark and recapture data.

Movement of adult roman does not seem to be gender related. In this study, the two fish with the largest displacement were dissected and found to be of opposite sexes. The size range at which sexual transition takes place is variable between different areas (Buxton 1993, Götz 2005). As sex cannot be determined externally, gender related movement could therefore not be studied without obtaining and dissecting the recaptured specimen. However, Griffiths and Wilke (2002) recaptured fish several kilometres from their tagging point that were smaller than 200 mm and larger than 400 mm, beyond the size range of sexual transition.

Why do individuals leave their home range? Straying might be an adaptive strategy; a response triggered by one or a combination of factors (i.e. predator density, prey density, population density, sex ratio, environmental change) declining below or raising above a threshold level. Mark and recapture data contain too little information about the point in time when a fish actually moves and are therefore unsuitable to give a satisfactory answer.

Home range size

The extent of the home range of individual fishes is important for their effective protection inside MPAs. The high resolution of the mark and recapture positions in this study showed that the majority of roman exhibit strong site fidelity. Half of the recaptures occurred within 50m of the release position. The multiple recaptures provide further evidence for strong site fidelity. Five fish were captured twice within less than 40 m of the release site and one fish was caught three times within 20 m of its tagging position over a period of two years.

In previous studies the majority of fishes were recaptured in proximity to their release position, even after periods of more then 5 years (Griffiths and Wilke 2002). While this seems to be in agreement with the findings of this study, the results have to be viewed in the context of the resolution of the position recording in the different datasets. A resident animal's movement is confined within the limits of its home range. Mark and recapture information is typically limited to two positions in time, which will most likely be much smaller than the maximum extent of an animal's home range. With a resolution of 1 km, Griffiths and Wilke's "station keeping" animals might have a home range with an extent of 2 km, equalling the maximum displacement distance found in Buxton's study.

Based on the results of this study (Figure III-4), the linear extent of this home range seems to be less then 100 m. Kramer and Chapman (1999) predict home range size of marine fish with a power relationship based on mean fork length (Appendix). Assuming an average roman size of 300 mm FL for Goukamma (Götz 2005), a home range of 118 m maximum linear extent was calculated, corresponding well with the range found in this study. However, telemetry experiments are needed to provide a more reliable estimate.

Maximum dispersal

Although there is concurrence in the general movement pattern found by mark and recapture studies , large differences can be found in the extent of the movements. The maximum movement of roman reported to date was 247 km. However, this distance given by the ORI tagging programme was in fact the result of a misidentification of fish by the angler. The second biggest movement (54 km) was in the same order as Griffiths' maximum distance estimate (39 km). Yet, less than 5% of the fish of these

two sources were recaptured further than 13 km from their tagging spot. While these distances are plausible, they stem from recapture reports from commercial and recreational fishermen and may therefore be unreliable. There are cases of recaptured fish in the Plettenberg Bay area that have in fact been caught in the Tsitsikamma National Park, resulting in displacement distances of 10 - 50 km (Cowley pers. com.). The maximum movement distance of 4 km found in this study agrees with the maximum distance from Buxton's study (2km) and the mode of the displaced fish from Griffiths' study (6km). The flattening of the cumulative curve in Figure III-4 supports the use of 4 km as a reasonable upper limit for modelling.

Methodology

In this study, VIFE tagging was used to complement traditionally used dart tags. Prevailing high turbidity in the study area (Zoutendyk and Duvenage 1989) and the resulting low visibility in combination with the fading of individual marks precluded underwater recognition of the tag codes. While the underwater recognition of individuals was not successful, the VIFE codes of fish captured by rod and line were all recognised, confirming the high retention rate of this tag type (Chapter I, Bailey *et al.* 1998, Willis and Babcock 1998).

The difference in recapture rates (Table III-V) between the two different tag types demonstrates a general bias of mark and recapture data: The VIFE tags were applied in a small area, which was visited regularly during the study period, resulting in a greater chance of recapturing resident fish. The dart tagging effort on the other hand was spread randomly over the entire study area. Recapture rates of predominantly resident fish therefore depend on incidental fishing in tagging cells and on fish that

left their home cell. Considering the extent of the study area, the chances of recapture are small, as reflected by the dart tag recapture rate.

To give an indication of maximum dispersal, mark and recapture studies have to cover an area the size of the maximum distance travelled by the fish. Which size of area should have been covered? The Goukamma tagging programme covered an area of ca. 25 km alongshore and up to 5 km offshore with little suitable habitat in close proximity to the study area. Maximum displacement distance might be dependent on the distribution of suitable habitat in the study area and the fish's ability to navigate over areas of unsuitable substrate (Appeldoorn 1997). Roman is a benthic omnivore, strongly associated with reefs and reliant on caves and crevices for shelter during the night and during sudden sea-temperature drops (Chapter IV). Therefore, it seems unlikely that individual fish would cross extensive areas of sandy or muddy sea floor. Roman were never seen during dive surveys in Tsitsikamma on egg beds of chokka squid *Loligo vulgaris reynaudii* close to reef, although the spawning squid and eggs represent a potential food source, utilised by other sparids. From these deliberations it can be assumed, that the studied area was in the order of the plausible maximum distance for roman.

Is the movement an artefact of the tagging process? In most experiments, fish are tagged and released at the surface. Removing the animal from its natural environment, handling and tagging put it under stress. Once returned into the water, a disoriented fish, which had build up high levels of lactic acid has to navigate back to its original position on the reef, sometimes against strong surface currents. During this process, some fish might simply get lost and have to re-settle in a new area. However, the observed movement pattern is universal across a broad range of families and habitats

including robust surf zone species like galjoen *Dichistius capensis* (Attwood 2002, Attwood and Bennett 1994) and species from shallow tropical reefs like coral trout (Zeller 1997, Zeller 1998), where currents and water depth should not affect the fish. While tagging effects cannot be entirely excluded, it can be assumed that the observed movement pattern is natural.

Modelling the rate of dispersal

One of the most important aspects for managing fish species in MPAs is the rate of dispersal, as it will determine the rate of exchange of adult fish between the MPA and the fishing area. In this regard, results from existing studies are somewhat equivocal, considering the biases mentioned earlier. The model developed in this study provides an estimate of the residency of individual roman.

With only 51% probability of individual roman being recaptured within their home cells, this estimate seems low compared to other studies. However, the following has to be considered: Assuming a circular home range with a radius of 50m (a reasonable assumption in light of the recapture pattern, confirmed by telemetry experiments (Chapter IV)) only a fish that has the centre of its range exactly in the centre of the cell would spend 100% of its time in its assigned home cell. A fish that was caught and tagged at the edge of its home range however might only spend a certain percentage of its time in its tagging cell, whereas most of the time it would be located in a neighbouring cell, making it an emigrant according to the model definitions. For the Goukamma study, it was possible to calculate the expected percentage of recaptures in the tagging cell (Appendix IV). Even if no fish had left its home range of 50 m radius, only 60% would have been recaptured in the tagging cell. As the model

suggests a 51% chance of recapture in the tagging cell, the difference (9%) represents the chance of a genuine emigration, resulting in a 91% chance of residency.

For the Tsitsikamma study, the rugged shoreline in the study area has many gullies and blinders, confining the home range of the fish. As fish were caught by shore angling, it was likely that the majority of fish were in fact tagged within 10 to 50 m from the shore, as casts farther than 50 m are rare (Cowley pers. comm.). Hence, the 100 by 100 m cell was not fully utilised. Therefore, the percentage of residency of 94% can be accepted for the Tsitsikamma data.

Model mechanics and sources of uncertainty

To avoid parameters related to catchability and fishing, which are difficult to estimate, a new approach was followed in the recapture model: the chances of catching an individual tagged roman depends on the ratio between the number of roman caught and the number of roman available, provided that no individual is caught twice during a fishing session. This approach had a number of advantages: nuisance parameters typical for angling data like angler performance (Attwood 2002) fell away. Furthermore, the method is independent of angling-time and species composition of the catch.

The model presented here was developed to avoid the biases of earlier studies, taking into account the distribution of fishing effort, tag loss and mortality rate.

According to Box and Jenkins (Lebreton *et al.* 1992), model selection must be guided primarily by the knowledge of the biology of the studied species. Therefore, the model was developed based on considerations on the movement pattern of roman:

undirected movements not related to sex and size, within a maximum distance, independent of time at liberty.

One assumption of the model is that the number of fish in a fished cell is known and is constant. Although good estimates of average roman densities for the Goukamma (Götz 2005) and the Tsitsikamma site (Buxton 1987) are available from underwater point counts and line transects, the data indicate variations in absolute densities between the assessment sites. However, to a degree, these variations might be attributed to differences in underwater visibility and fish activity due to differences in season, temperature or individual behaviour (Götz 2005). Differences in the micro-habitat (caves, crevices) are also responsible for variations in fish densities between different point counts, but will play less of a role in the differences between the model cells due to their larger size.

Tag loss and natural mortality are a function of time. The model estimates these two parameters, assuming constant rates. A tank experiment (Chapter I) showed, that dart tag loss is appreciably linear over time. Values of M as estimated in the model are low compared to mortality estimates from underwater counts during the study period ($M = -0.24$ y^{-1} (Götz 2005)). This is to be expected, as the mortality is given as a yearly rate from size class frequencies, whereas most recaptures occurred within a few months. Furthermore, the broad confidence intervals indicate that there is not enough information in the data for a precise estimate of M. This is even more evident for the tag loss rate T, as this estimate largely depends on the few recaptures of dart tagged fish.

Conclusions

The results of this study confirm that adult roman are predominantly resident. A small proportion of fish, however, leave their home range and travel considerable distances. This movement is not related to size, age or sex and there is no evidence for a directed migration related to spawning or feeding patterns. The extent of the home range of resident roman is smaller than anticipated from earlier results, suggesting that even small MPAs can be beneficial for their protection. However, telemetry experiments are required to confirm the size of roman home ranges and to investigate factors determining their extent.

The percentage of moving fish and the distances moved are important factors that have to be taken into account in the planning of MPAs. Mark and recapture data have to be analysed carefully to avoid erroneous results.

The low dispersal rate of roman further supports the prospect of protecting this species in small MPAs, lowering the possibility of draining the MPA through large degrees of exchange across its boundaries. Nevertheless, to quantify the effect of a specific MPA, the distribution of suitable habitat, the fishing effort beyond its boundaries and the particular life history of the study species has to be taken into consideration.

Appendix

(I) Chapman's and Kramer's relationship between body size and home range length was determined with a linear regression using data from 29 species of coral reef fishes. It is given by the equation

$$\text{Homerange}\,[\text{m}] = 0.000178 \times (\text{fork length}\,[\text{mm}])^{2.35} \qquad \textbf{Equation III-8}$$

(II) Changes in the number of cells in the considered domain had a negligible effect on the parameter estimates.

Table III-VIII: Model behaviour with different values of Q. Example from the Tsitsikamma shore-angling dataset.

Q	p	M	T	L
100	0.94	-0.00025	-2E-07	173.63
1000	0.94	-0.00024	-2E-07	175.90
10000	0.94	-0.00024	-2E-07	178.19

(III) Likelihood profiling showed well-defined minima for the probability of recapturing a roman in its tagging cell.
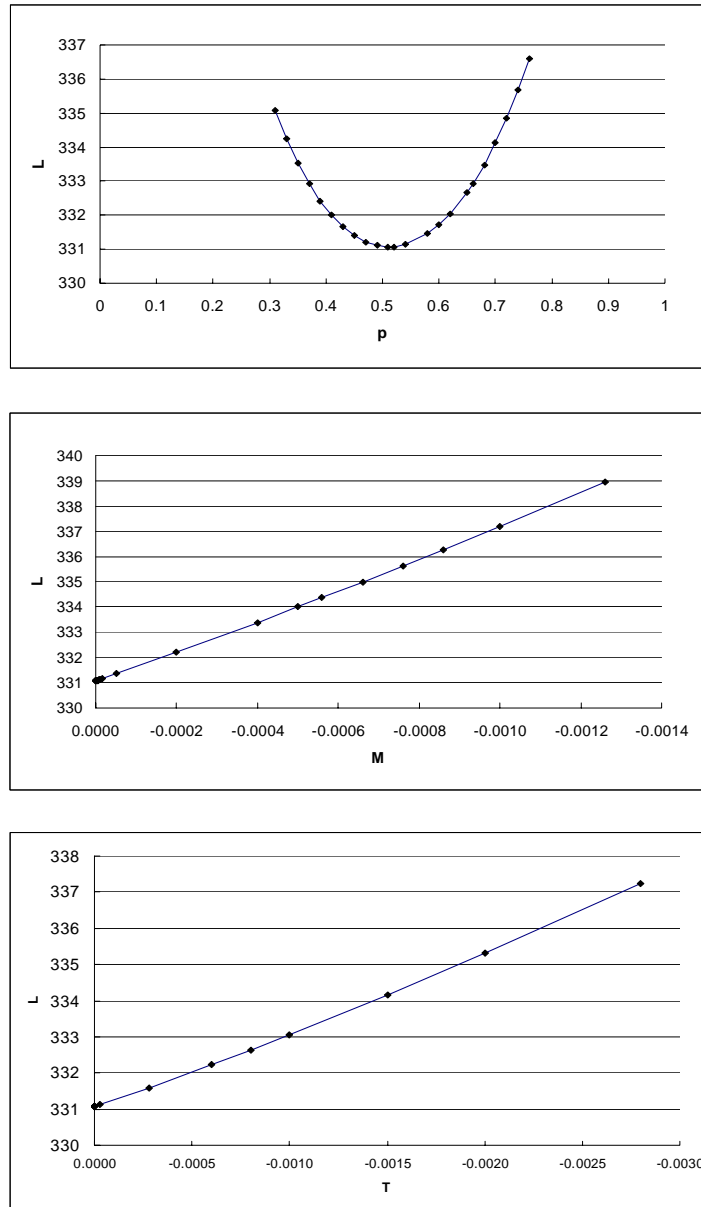
Figure III-5: Likelihood [L] profiles for the parameters p, M and T for the Goukamma (skiboat angling) dataset.
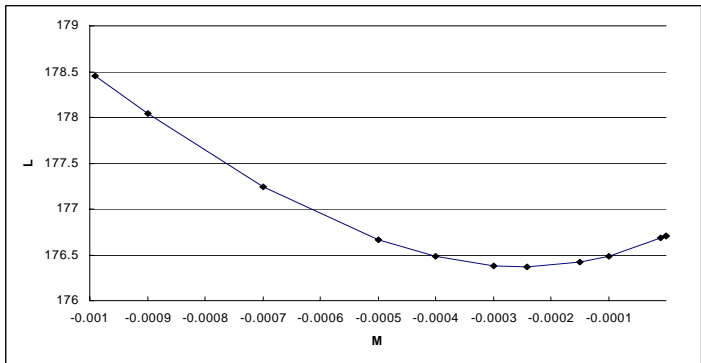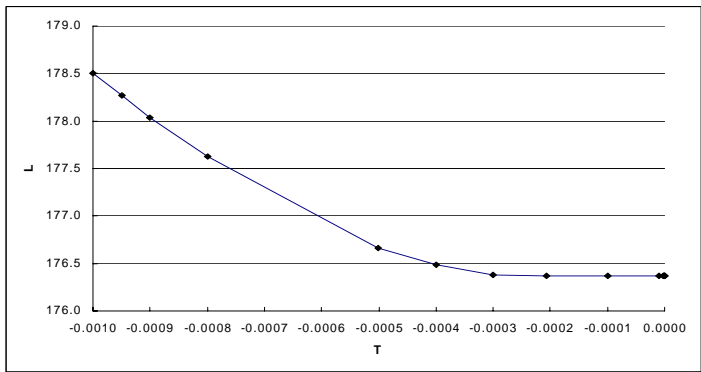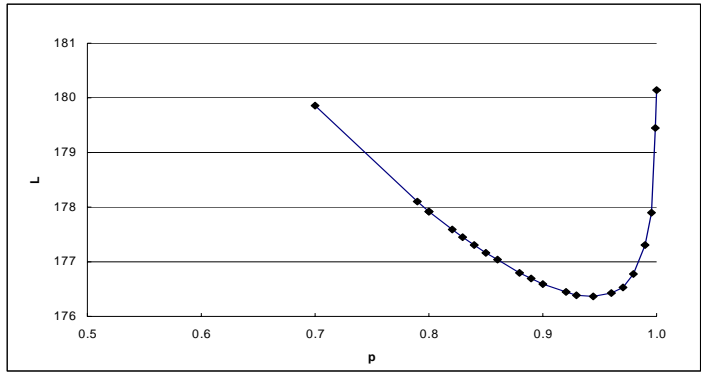
Figure III-6: Likelihood [L] profiles for the parameters p, M and T for the Tsitsikamma (shore angling) dataset.

(IV) The chances of recapturing a fish tagged at a random position within its home range cell were determined with the following procedure. First, a random tagging position within the tagging cell was selected. As the centre of the circular home range of the fish can be anywhere within 50 m of this tagging position, this centre position was determined by taking a random bearing and a random distance < 50 m from the tagging position.   A recapture position was then established by taking a random bearing and a random distance < 50 m from the centre point. Two scenarios were possible: (1) The recapture position was within home range cell, or (2) the recapture position was outside the home range cell. This procedure was repeated. The chances of recapturing a fish in its home cell were given by the number of times the recapture position fell inside the home cell divided by the total number of repetitions (0.6 after 10000 repetitions).

Chapter IV: Telemetry experiment on spotted grunter *Pomadasys commersonnii,* in an African estuary

Abstract

The feasibility of using acoustic telemetry to study the movements of coastal fish in South Africa was investigated. The telemetry equipment comprised of two VEMCO V8 continuous transmitters and a VEMCO VR60 receiver linked to a directional hydrophone. Field experiments demonstrated that the equipment's maximum detection range was 400 m. The transmitters were set to neighbouring frequencies, but interference between these was found to be negligible. The accuracy of locating the transmitter equalled the previously determined Global Positioning System (Garmin GPS 12) accuracy of approximately 5 m. A tank experiment was conducted to examine the effects of the transmitter implantation. Fish recovered quickly after the surgical procedure and, with respect to swimming behaviour and growth rates, no differences were found between fish with implants and controls. A tracking experiment was conducted on spotted grunter *Pomadasys commersonnii* in the East Kleinemonde Estuary. Two fish were tracked over a seven-day period. The fish preferred the lower reaches of the estuary where they made repeated and prolonged use of distinct areas.

Introduction

It is of critical importance that fish movements and migrations are considered in the development of fishery management plans. To date, two experimental approaches to study fish movement have been used. These are tagging studies using external passive tags (e.g. dart tags) and telemetric investigations. Studies with passive numbered tags provide a cheap and convenient method to detect general patterns of residency and migration. In addition, for certain species they can be used to evaluate stock status (Wootton 1999). Unfortunately, they cannot reveal details of the movement of the fish between tagging and recapture events (Attwood 2002). In contrast, telemetry enables short-term, high-resolution movement data of individual fish to be collected and correlated with ambient conditions. However, telemetry experiments are usually confined to small sample sizes and are run for limited periods.

Telemetry has been successfully used to study the movement patterns of a range of fish species (and sizes) inhabiting freshwater rivers, lakes, estuaries, inshore coral reefs as well as offshore benthic and pelagic marine environments (*inter alia* Bagley *et al.* 1994, Block *et al.* 2004, Holland *et al.* 1985, Holland *et al.* 1996, Matthews 1992, Matthews *et al.* 1990, Meyer *et al.* 2000, Miller and Menzel 1986, Okland *et al.* 2003, Solomon *et al.* 1999, Zeller 1997, Zeller 1999). The present study was initiated to investigate the feasibility of using this technique for spotted grunter (*Pomadasys commersonnii*) in a closed estuary. Interest in this species stems from its importance in the estuarine dependent fisheries of South Africa. Throughout its distributional range, it is well represented in the catches of estuarine recreational and subsistence fishers (Baird and Pradervand 2002). It is also caught in the KwaZulu-Natal subsistence trap and net fisheries and in the south-east coast net fishery (Lamberth 1997). Furthermore, in the inshore prawn trawl fishery in KwaZulu-Natal, spotted

grunter is a common bycatch species. In recent years, this has precipitated user conflicts and now requires management intervention. Although much is known about the biology and ecology of this species (Beckley *et al.* 2002, Fennessy 2000), reliable data on their movement within estuaries and possible migrations into the marine environment is lacking. Such information is crucial to the development of an appropriate management strategy for this species.

The objective of this study was to address issues that may influence the experimental design and feasibility for further more detailed studies on spotted grunter and other coastal fish in South Africa. The secondary objectives were (i) to evaluate the effect of the transmitter implantation on fish survivorship and mobility; (ii) to determine the range of the receiver, the interference between tags transmitting on different frequencies, and the precision with which the transmitter could be located in the field and (iii) to assess the feasibility of recovering accurate and frequent positions of fish with surgically implanted transmitters.

Study site

The study was undertaken in the predominantly closed East Kleinemonde Estuary (Eastern Cape Province, South Africa) approximately 15 km North-East of Port Alfred (33° 32' S, 27° 03' E; Figure IV-1). At the time of this study (January 2002) the mouth was closed. Consequently, field trials during this study were conducted in a body of water not subject to tidal currents (water movement), current reversals and exposed intertidal areas that are usually associated with permanently open estuaries. The water level was approximately 0.7 m below the maximum-recorded level (recorded from marks on a road bridge). Mean surface and bottom water temperatures

and salinities during the study period were 26.0 °C and 25.5 °C and 12.4 ‰ and 13.9 ‰ respectively.
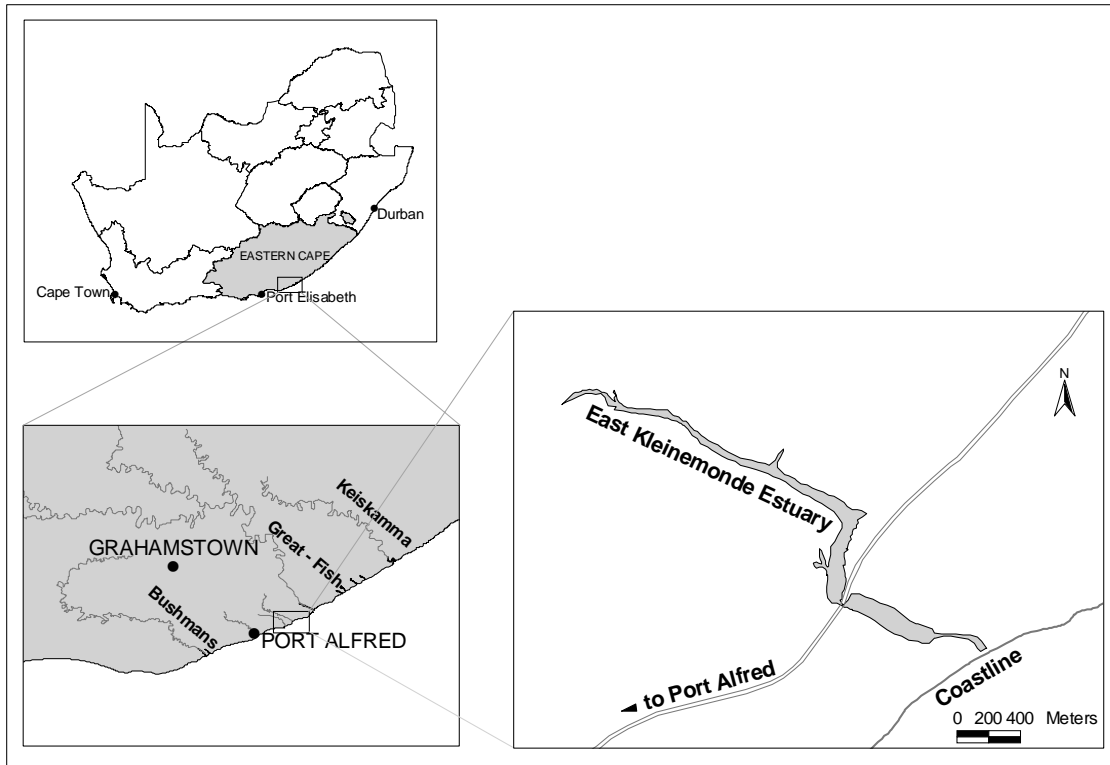
Figure IV-1: Map of South Africa with inserts of the Grahamstown area in the Eastern Cape Province and the study site near Port Alfred in the Eastern Cape Province, South Africa.

Materials and Methods

Fish capture and tank experiment

On two consecutive days, a total of five fish were captured using seine nets and rod-and-line from the lower reaches of the estuary. The fish were kept in a 1000 l holding tank containing estuarine water (11 ‰; 22 °C). The fish were held in the system for a period that did not exceed 3 days. The tank water was changed daily and aerated with a small aquarium pump. The fish were then transferred to a 4000 l holding tank. The tank was linked to a partially recirculating seawater system (35 ‰; 20 °C; natural light) at the Rhodes University laboratory facilities in Port Alfred. The acclimation to the higher salinity was undertaken over a minimum three-hour period.

On the following day, the fish were anaesthetised in a 70 l container filled with seawater (35 ‰; 20 °C) using 2-phenoxy ethanol (0.25 ml/l). The anaesthetised fish were weighed to the nearest gram and measured to the nearest millimetre. "Dummy tags" - nylon cylinders with dimensions equal to the transmitters used in the field experiment (Vemco V8; length $\times$ diameter = 35 $\times$ 9 mm; mass = 5.3 g) – were implanted in the peritoneal cavity of randomly two selected fish. The remaining three control fish (without implants) were released directly into the 4000 l holding tank. The fish subjected to surgery were placed with their ventral body surface upwards in the groove of a v-shaped, plastic-covered foam cushion in a small container with oxygenated water. During the operation, the fish's gills were kept underwater at all times. A small incision was made along the ventral midline (approximately 3 cm anterior of the anal fin) and the dummy tag was inserted into the body cavity. The incision was closed with 2-3 sutures of surgical thread; both nylon and catgut threads were tested. The fish were then injected with Oxy-tetracycline (0.1 ml per 1000 g

body weight), and released into the holding tank. They were observed daily with respect to swimming performance, feeding and possible behavioural abnormalities. After 100 days, they were sacrificed and examined.

Telemetry system

The telemetry system that was used in this study was manufactured by VEMCO Ltd. (Halifax, Canada). It consisted of (i) a portable receiver unit (VR 60) with a directional hydrophone capable of receiving signals from various transmitter types and frequencies, and (ii) two V8 transmitters (continuous transmission pinger-type) with frequencies of 65.536 and 69.000 Hz respectively. Both transmitters were factory preset to transmit signals on a 12 hr on-off cycle. The transmission was initialised by the connection of two wires, which was done at 08:00. Consequently, for the duration of the study, the tags transmitted a daily signal from 08:00 until 20:00.

The detection range of the equipment was determined by dropping a transmitter attached to a weight marked with a buoy line at a fixed location in the estuary. The boat (with the VR 60 receiver) would then move away until the signal could no longer be received. The boat was turned and approached the transmitter until the signal was detected again. The procedure was repeated with the transmitter placed at different depths. Geographic coordinates (Garmin GPS 12; accuracy: ± 5 m) were taken to determine the distance between the boat and transmitter.

To test the accuracy of locating the position of the transmitter, it was placed at a spot unknown to the boat operator. The operator then manoeuvred the boat to the hypothetical position of the transmitter. The position of the boat was then compared to the actual position of the transmitter.

To test for interference between the two transmitters (preset at different frequencies),

one   trans

mitter was submerged close to the hydrophone, while the receiver was selected to pick up the signal of a second transmitter located farther away. Signal reception was monitored on each of the predetermined dedicated frequency channels.

Field tracking experiment

Two fish were fitted with the V8 transmitters using the same methodology described for those fish fitted with dummy tags during the tank experiment. Following surgery, the fish were kept in captivity (1000 l holding tank), and released at the same spot where they had previously been caught (exactly 48 hours after capture). For a period of seven days, positional fixes for each fish were taken hourly (when possible) between 8:00 and 20:00. The fish were followed with a small boat powered by an electric outboard motor.

Environmental data

At each recorded fish position, water depth was measured to the nearest 10 cm, salinity was recorded using an ATAGO handheld refractometer, and the temperature was measured to the nearest 0.5 °C. In the deeper channels, surface and bottom temperature and salinity readings were taken.

Results

Table IV-I: Length and weight increase of 5 spotted grunter during the 100-day tank experiment.

Treatment	Initial length (mm)	Initial weight (g)	Length increase (mm)	Length increase (%)	Weight increase (g)	Weight increase (%)
Implant	451	1020	36	8	760	75
Implant	545	1700	11	2	700	41
Control	370	600	47	13	580	97
Control	420	880	45	11	800	91
Control	460	1200	26	6	580	48

Dummy tag experiment

The duration of the surgical procedure (measured as the time the fish left the anaesthetic bath to being released into the holding tank) varied between five and seven minutes. All the fish recovered within five minutes of being released into the holding tank, and started swimming upright without obvious signs of stress. No behavioural difference between the controls and the fish with the dummy tags was observed during the 100-day tank experiment. The fish started feeding within two days after the treatment, and were fed sardines (*Sardinops sagax*) or sand prawns (*Callianassa krausi*) every morning for the duration of the experiment. After the

observation period, all the fish had grown substantially. Their weights increased between 45 and 97% and their lengths between 2 and 13% (Table I). The incisions had healed completely in both fish with dummy transmitters, and the operation scars were barely visible. The catgut sutures had dissolved completely and there was no wounding around the indissoluble nylon sutures. Fish dissections revealed that the dummy tags were embedded in a layer of fatty tissue, and had not moved from the site where they had been originally placed. In addition, there were no signs of infection or haemorrhaging.

Range of reception

The maximum detection range of the transmitter signal was 400 m. The water depth and the depth at which the transmitter was placed did not have an effect on the range of the signal - as long as there was no solid obstacle in the line between the transmitter and receiver. Furthermore, underwater vegetation such as the *Ruppia cirrhosa* beds in the littoral zone of the estuary did not affect the range of the signal.

Accuracy of the location recording

The estimation of the position proved to be very accurate. By following the signal with the directional hydrophone - until the signal was equally strong in all directions at the lowest gain of the receiver - the boat skipper was able to manoeuvre the boat directly above the submerged transmitter. Hence, the accuracy of the position was limited to the accuracy of the GPS instrument (5 m).

Interference between the transmitters was negligible. Only at a high gain (with the receiver set on a neighbouring channel) and the hydrophone in close proximity to the transmitter was a very weak signal audible. The signal was easily recognised as interference as its strength hardly changed when the hydrophone was rotated. The

signal from the distant transmitter (with receiver on its dedicated frequency channel) faded when the hydrophone was turned slightly away from its known direction.

Tracking experiment
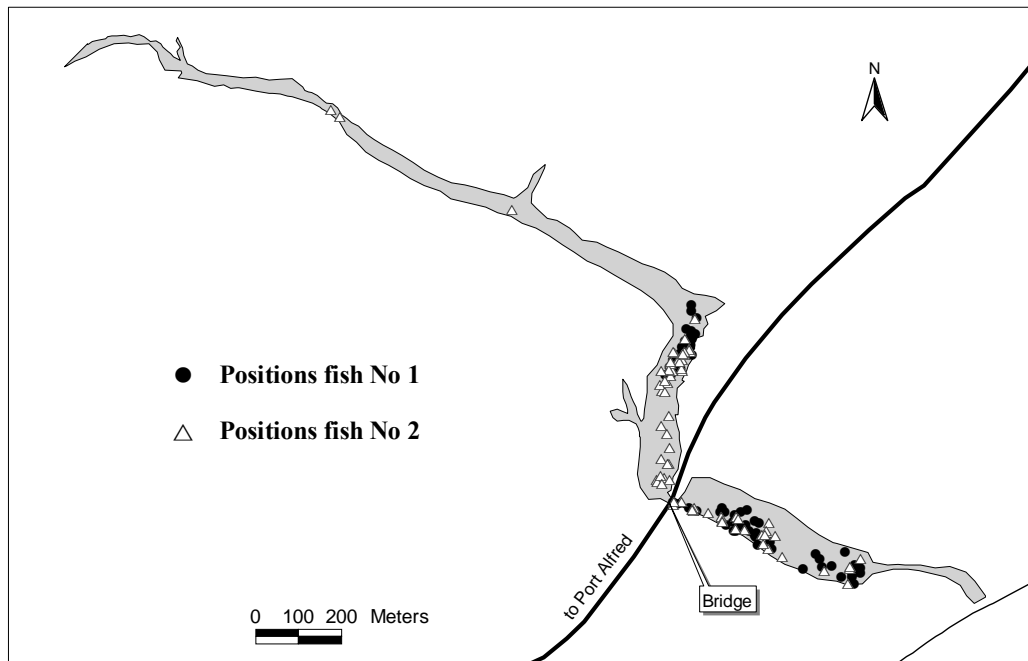
Figure IV-2: Map of the East Kleinemonde estuary with all recorded positions.

Fish 1:

The first grunter (540 mm; 1700 g) was released on the 12th of January 2002 at 15:00 from the eastern bank in the lower reaches of the estuary, approximately 400 m away from the closed estuary mouth (i.e. at the site where it was captured 48 hrs earlier). It stayed close to the release site until about 17:00, when it moved upstream along the western bank and up to the bridge. Just prior to the transmitter being switched off at 20:00, it turned back, and was located near the western bank about 200 m below the bridge.

On the following morning, it was once more found close to the release site, it then again patrolled the western bank up to the bridge until 10:00, turned back and remained almost stationary for the rest of the day - about 200-300 m below the bridge.

The next day, the fish was located 400 m beyond the bridge on the eastern bank. The fish remained in this general region for the following three days. On day six (17th January), it was once again located at the release site in the lower reaches of the estuary. It occupied this area again in the late afternoon of the 18th, the early afternoon of the 19th and the morning of the 20th (**Figure IV-2**).

Fish 2:

The second fish (532 mm; 1800 g) was released on the 13th of January 2002 at 09:00. The release site (i.e. initial capture site) was also in the lower reaches close to the mouth of the estuary. Following release, the fish moved slowly upstream to the area just above the bridge (11:00), where it stayed until the early afternoon (15:00). For the rest of that day it patrolled the eastern bank between the bridge and a location 400 m upstream.

On the 14th of January it was located at 09:30 for the first time. The fish was found in the middle reaches of the estuary close to a small inlet (tributary) approximately 1 km upstream of the bridge. It then moved further upstream (09:30 – 11:30) into the upper reaches of the estuary. The signal was lost and only recovered in the late afternoon. The fish had moved back to the release site in the lower reaches. It then moved along the western bank, and was finally recorded halfway between the bridge and the release spot. On the 15th and the morning of the 16th of January, the fish remained in the same area as fish No 1, approximately 400 m beyond the bridge. In the afternoon it moved downstream and was last recorded in the area halfway between the bridge

and the release site. In the late afternoon of the 18th, the early afternoon of the 19th and the morning of the 20th of January, it swam along the western bank of the lower reaches, between the bridge and the release site (**Figure IV-2**).

Table IV-II: Maximum and minimum recorded distance moved by the two spotted grunter during the 7 day experiment.

Distance (m) between recorded positions	Fish No. 1	Fish No. 2
Maximum per day	430	1900
Minimum per day	150	240
Maximum overall	910	1900

The maximum distance between positions recorded during one day was 1900 m (Fish No 2; January 14th). This also represents the maximum range during the whole observation period. The minimum distance between recorded points on a single day was 150 m (Fish No 1; January 15th). Fish No 2 was generally more mobile than Fish No 1 (Table IV-II). Both fish spent extended periods at fixed locations.
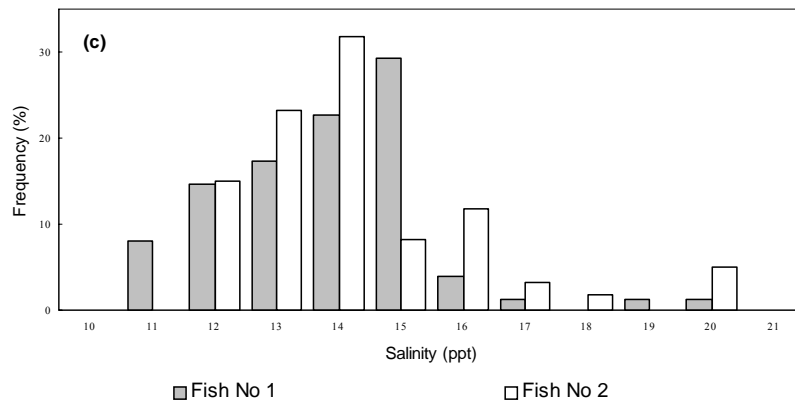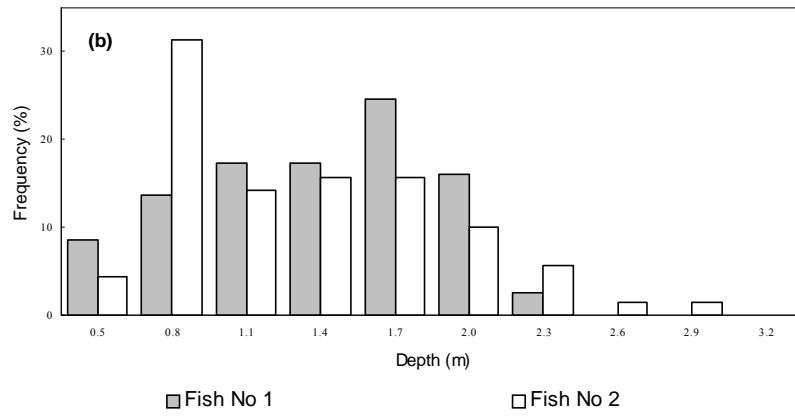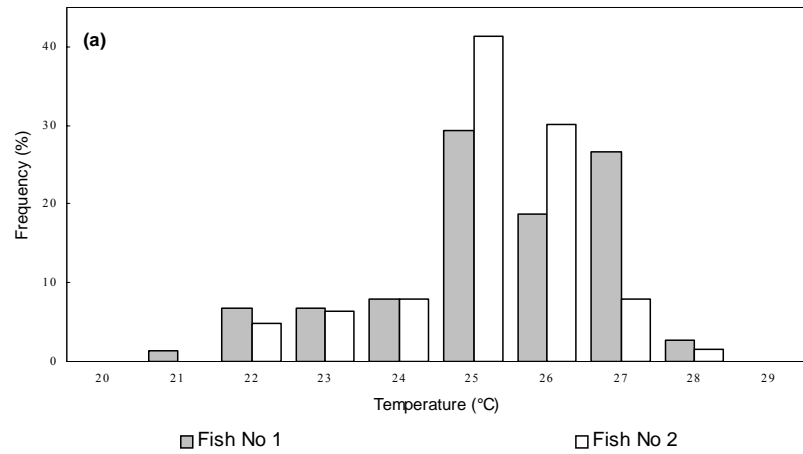
Figure IV-3 Frequency plot of (a) bottom temperature, (b) water depth and (c) salinity at the recorded positions for fish No 1 and 2.

Over the observation period, the bottom temperatures (as measured at the observation points) varied between 21 °C and 29 °C. The majority of the measurements were between 25 °C and 28 °C. Fish No 1 stayed within a slightly broader temperature range than fish No 2 (**Figure IV-3**).

The depths measured at the recorded positions represent the whole depth regime of the estuary. The fish were found in water as shallow as 0.5 meters - where their characteristic "tailing behaviour" during feeding on infaunal organisms (e.g. *Callianassa kraussi*) was observed. They were also recorded in the channel under the bridge (maximum depth: 3.2 m). Fish No 2 utilised a wider range of water depths than fish No 1 (**Figure IV-3**), and was more often found in shallow water.

During the observation period, the salinity at the different locations varied between 11 and 20 ‰. (**Figure IV-3**).

Discussion

Dummy tag experiment

The capture, handling, 20 km road transfer to the Port Alfred tanks (with higher salinity) and surgery did not appear to adversely affect the health or behaviour of the fish. Rearing experiments on spotted grunter have shown that the species is robust and tolerant of handling and disturbance (Deacon and Hecht 1996). All fish started feeding 48 hours after the surgery. Within this period, post operation stress levels in other species are reported to decrease to normal (Jepsen *et al.* 2001).

Investigations into the metabolic response of juvenile spotted grunter to chase and capture behaviour revealed that normal pre-stress metabolic rates are re-established after a period of about 1.5 hrs (Radull *et al.* 2002). As an estuarine-dependent species, spotted grunter tolerates rapid changes in environmental conditions. No behavioural differences between the tagged fish and the controls could be observed, suggesting that the implants did not affect the swimming performance of the fish. The surgical procedure proved to be uncomplicated, and can be undertaken in the field, and if necessary, on a vessel. This would ensure the rapid release of the fish, and thus minimise the stresses caused by handling and captivity and reduce the possibility of the fishes territory being occupied during its absence. Nevertheless, releasing the fish shortly after surgery may increase the risk of predation. However, roman (*Chrysoblephus laticeps*) that were released immediately after implantation showed no signs of restricted mobility, and there was no bleeding from the incision that would attract potential predators (pers. obs.). Catgut is preferable to nylon for the sutures though it is slightly more difficult to handle. It dissolves completely and therefore minimises the risks for infection or biological fouling.

While the small sample size precluded a statistical comparison between the tagged fish and the controls, the weight and length increases of all the fish were well within the normal growth parameters of the fish under comparable experimental rearing conditions (Bacela 1997). This is contrary to the results reported from similar studies investigating other species, in which slower or even negative growth rates were recorded (Eveson and Welch 1999, Martinelli *et al.* 1998). The complete healing of the incisions and the fact that the tag had not moved within the body cavity further indicates that this method is suitable for this species. Furthermore, it is not unreasonable to assume, that, on release, the fish should resume normal behaviour.

Equipment

The combination of the VR 60 receiver and the V8 transmitters proved to be suitable for intensive studies of fish movement. The small size of the receiver unit makes it possible to use on virtually any kind of boat. The signal could be accurately located at any time during the transmitting period - provided it was within the range of reception. Contrary to previous experiments (e.g. Matthews *et al.* 1990), the interference between transmitters emitting different frequencies was negligible.

It has been reported (Matthews *et al.* 1990) that dense underwater vegetation such as kelp negatively affects the range of the signal. However, the *Ruppia cirrhosa* beds that form bands on the banks of the estuary did not seem to have an effect. Solid obstructions like rocks impede the reception of the signal (Matthews *et al.* 1990). This did not pose a problem in this study as there were no such obstructions in the study area.

Tracking experiment

The tracking experiment was designed as a preliminary study to test the feasibility of the methods. The limitations of this study included: (i) the low sample size of only two fish, (ii) no night-time data, because the transmitters were pre-set to only transmit signals for 12 hours (08h00 to 20h00), and (iii) a short observation period of seven days. Consequently, the observations were based on limited data and trends in relation to space utilisation and ambient conditions are not conclusive. The positive results of the tank experiment and the observation of the "tailing" behaviour make it reasonable to conclude that the two fish resumed with their natural behaviour after they were released. The positions that were recorded with the GPS can be assumed to be within 20 m of the actual positions of the fish. When the fish stayed in the deeper waters, the skipper was often able to position the boat above the fish so that the signal was equally strong in all directions when the receiver was set on the lowest gain. In such cases, the fish did not appear to be disturbed by the boat, because it often stayed at the same spot for several hours. In the shallow areas and close to the banks this was often not possible because of motor disturbance. In such cases, the closest possible position was taken. Sometimes the signal weakened during the approach, suggesting that the fish was moving away from the boat.

Both fish seemed to prefer the lower reaches of the estuary. This may be attributed to the biotic and abiotic characteristics of the estuary and / or physiological responses to the fore mentioned factors. Spotted grunter can tolerate a wide range of salinities (Deacon and Hecht 1999), however, rearing experiments have shown higher mortality rates at lower salinities. Deacon (1997) showed no negative differences in growth, food conversion and protein ratios in spotted grunter maintained at salinities over 12 ‰. This corresponds with the salinities measured at the positions where the fish were

encountered. Only once did a fish (No 2 on 14 January 2002) enter a portion of the estuary where salinity values were < 10 ‰. Throughout the study, salinity was >12 ‰ where the fish were recorded. Mass mortalities of this species have been recorded in the Kosi and St Lucia estuarine systems when salinities fell below 5 ‰ (Blaber *et al.* 1976). Similar observations were made in the East Kleinemonde Estuary in May 2000 following a prolonged period of freshwater dominance (< 5 ‰) in conjunction with a sudden drop in water temperature (Cowley pers. obs.). It is hypothesized that the regular presence of both spotted grunter in the shallow sandy lower reaches is associated with feeding. The observation of "tailing" behaviour of one of the tracked fish provides supportive evidence.

Conclusions

The results of this preliminary study show that telemetry is a useful tool to study movement of estuarine fishes. It could be further applied to gain high- resolution data on (i) migration patterns, (ii) estuarine dependency and (iii) vulnerability to exploitation, information pertinent towards effective fisheries management.

Chapter V: Spatial utilisation and activity patterns of roman *Chrysoblephus laticeps* in a small South African marine protected area

Abstract

Spatial utilisation and activity patterns of roman *Chrysoblephus laticeps* were investigated by telemetry. Surgically implanted VEMCO V8, V13 and V16 transmitters were used to track 13 roman inside the Castle Rock Marine Protected Area on the South African temperate south coast. Transmitters implanted into *C. laticeps* in tanks had no apparent effects on growth and physiology. Manual boat- and diver-based tracking experiments commenced over a 17-month period. A VEMCO radio acoustic positioning system (VRAP) was used to record fish positions approximately every 8 minutes over two 1-month periods during and after the spawning season of roman. Analysis of movements using a 95% fixed kernel algorithm suggests that roman occupy small home ranges between 1000 and 3000 m^2. Activity was lower at night. During periods of cold-water upwelling, fish retreated into caves. During the spawning season, females extended their home ranges, possibly to mate with different males. These results confirm that this species is well suited for protection and management with marine protected areas.

Introduction

It has become widely accepted that marine protected areas (MPAs) should play a strategic role in sustainable management of fishery resources (Guénette *et al.* 1998, Parsons *et al.* 2000, Zeller 1997). Fishery enhancement is based on the protection of fish inside MPAs and the resulting increase in fish density outside MPAs because of the export of larvae and post-recruit fish (Roberts *et al.* 2003).

There are a number of studies (Gell and Roberts 2003, Gell *et al.* 2005) that suggest that fish are successfully protected in MPAs. In South Africa, Bennett *et al.* (1991) reported a recovery of surf-zone fish species following the establishment of the De Hoop MPA. Buxton (1993) and Götz (2005) found higher fish densities and larger size classes in areas closed to fishing, in comparison with fishing sites. However, these examples are from large MPAs (>40 km^2). The degree of protection offered by an MPA ultimately depends on how much of the space that a fish utilises is protected from fishing.

Space utilisation is likely to depend on a variety of factors relating to the life history of the species (maturity, size, gender) and to the environment (distribution of suitable habitat, food availability, season and oceanographic conditions). Whereas large-scale movements (migrations, ranging and nomadism) are best studied with mark and recapture techniques, questions related to small-scale movements and home range behaviour cannot be adequately resolved by mark and recapture, which typically provides only two positions that a fish occupies in its entire life. Acoustic telemetry techniques offer a better alternative for studying small-scale movements of marine fishes. Although technologically and logistically challenging, telemetry allows continuous tracking of marine animals for extended time periods.

Two different methods are commonly used in telemetry studies. Manual tracking involves following the animal with a boat or by diving with a mobile hydrophone (*inter alia* Bolden 2002, Connolly *et al.* 2002, Holland *et al.* 1985, Holland *et al* 1996, Matthews *et al.* 1990, Matthews *et al.* 1992, Zeller 1997). Remote positioning involves the automatic recording of a fish's position by stationary hydrophones. (Thorstad *et al.* 2003). The most advanced remote system, radio-acoustic-positioning (RAP), calculates the position of the study animal by triangulation of the source of the sonic pulse. These data are transmitted in real-time to an onshore base-station (Parsons *et al.* 2000, Ralston and Horn 1986, Sarno *et al.* 1994).

Each method has its merits. Whereas manual tracking is theoretically not constrained to a certain area, it is labour intensive (Holland *et al.* 1985) and it does not allow simultaneous tracking of different individuals. Remote positioning allows collection of high-resolution data quasi-simultaneously from different individuals but is confined to the detection range of the array. Furthermore, it is logistically demanding and prone to equipment failure.

In this study, telemetry was used to investigate the movement patterns of roman *Chrysoblephus laticeps*, (Sparidae) in the Castle Rock MPA in False Bay, South Africa. With an extent of only 6 km^2 and adjacent areas that are heavily utilised by commercial linefishermen, shore anglers and spearfishermen (Lechanteur 1999), even movements in the order of a few hundred meters would make the population of roman inside the reserve vulnerable to fishing. Mark and recapture studies indicate that this species exhibits a high degree of residency during most of its adult life (Chapter III; Bullen and Mann 2004, Buxton and Allen 1989, Griffiths and Wilke 2002). This is supported by anecdotal re-sightings of recognisable individuals by spearfishermen and

observations during SCUBA dives (Penrith 1972). However, the extent of the area that roman utilise during resident periods of their life history remains uncertain, although this information is crucial for the design of MPAs that aim to protect this species.

A combination of manual tracking and remote positioning was used in conjunction with underwater observations to investigate area utilisation of adult roman and to determine the effects of biological (sex, size, spawning) and abiotic factors (habitat, season, time of day, temperature) on their movement. As this is the first telemetry study on a South African temperate marine fish, emphasis was placed on methodology and experimental design to provide guidelines for similar studies along the exposed South African coast. Transmitter implantation methods that were successfully applied on spotted grunter *P.commersonnii* (Chapter VI) were adopted for this study and the long-term effect of the procedure on behaviour, growth and survival of roman was investigated in a tank experiment.

Study site

Figure V-1: The Castle Rock Marine Protected Area in False Bay, Western Cape, South Africa.

The Castle Rock MPA in False Bay was established in 1979 on recommendation from a committee appointed by the Minister of Economic Affairs to preserve "its particularly rich and unique marine life". It extends three kilometres along the shore from Bakoven Rock to Bobbejaanklip [34.23ºS 18.47ºE – S 34.25ºS 18.47ºE] (Figure

V-1). Originally defined as an area one nautical mile seaward from the high water mark, its easterly boundary was changed for convenience to a straight longitudinal line [18.495ºE]. The shoreline is characterised by granite boulder fields that extend well into the subtidal zone where they represent the main reef substrate. The reserve contains numerous exposed rocks and blinders. Seals "haul out" on the large exposed rocks in the southern part of the reserve. Dense kelp beds can be found mainly along the coastline in water shallower than 15 m. The seafloor slopes gently to a maximum depth of 45 m at the seaward boundary of the reserve with soft substratum as the dominant habitat.

While the exploitation of the marine resources of False Bay can be traced back to the Khoi-San hunters and gatherers, the commercial beach seine and the line fishery in the area started with the arrival of European settlers (Penrith 1972). Notable decline of catches was recorded at the beginning of the 20th century, but the bay continues to be heavily utilized by commercial and recreational fishermen (Lechanteur 1999). Castle Rock MPA was originally proclaimed as a no take zone. However, since 1988 commercial fishing for snoek *Thyrsites atun* (pelagic species) has been allowed inside the reserve.

Materials and Methods

Tank experiment to test the effect of transmitter implantation on roman

Eight roman were caught with rod and line from the *RV Sardinops* in False Bay, east of Seal Island. Their swimbladders were deflated with a hypodermic needle. The fish were then anaesthetised in an 80 l container filled with a 2-phenoxy ethanol ($0.25 ml \cdot l^{-1}$) seawater solution in preparation for surgery. The anaesthetised fish were placed with their ventral body surface facing upwards in the groove of a v-shaped, plastic-covered foam cushion in a small container filled with oxygenated water. During the entire operation, the fish's gills were kept underwater. A small incision was made along the ventral midline (approximately 2 cm anterior of the anal fin) and a dummy transmitter (nylon cylinder with dimensions equal to the Vemco V8 transmitters used in the field experiment) was carefully inserted into the peritoneal cavity. The incision was closed with 2-3 sutures of cromic catgut (Clinigut 24 mm, 3/8 circle; Sasurel Pty Ltd; South Africa). Finally, the fish received an Oxytetracycline injection (0.1 ml per 1000 g body weight), and were released into the holding tank.

Surgical gloves were worn throughout the procedure to minimise the risk of infection. Afterwards the fish were released into portable tanks on board the ship (2000 l, open seawater circulation). Five additional fish were caught and kept as controls. On the following day, all the fish were transferred to the Sea Fisheries Research Aquarium, Sea Point, Cape Town, were they were weighed to the nearest gram, measured to the nearest millimetre fork length and released into a holding tank (7500 l; Ø 2 m; H 1,2 m) with open circulating sea water supply.

The fish were fed to saturation two to three times a week with pilchard (*Sardinops sagax*), squid (*Loligo vulgaris reynauldii*) and white mussel (*Donax serra*). Abnormal behaviour, signs of infections and abnormal tag conditions were noted. The fish were reassessed after 40 and 198 days. Weight, fork length, fish condition and the state of the incision scar were noted during the assessments. Digital photos of each individual fish and their incision scars were taken. After the second assessment, the fish were sacrificed and dissected.

Growth data analysis

To allow comparisons between growth rates of fish of different initial sizes, relative length increments (RLI) were calculated as

$$RLI = \frac{\Delta L}{L_{inf} - L_i}$$ **Equation V-1**

with ΔL= absolute length increase, L_{inf} the theoretical the von Bertalanffy maximum length for roman (Götz 2005) and L_i the initial length. Weight increments were compared as absolute values.

After testing for normality and homogeneity of variance (F-test), differences between the treatments were tested with t-tests.

Field study

Overview

Table V-I: Experimental details of roman tracking and remote positioning experiment.

Fish No.	Fork length [mm]	Functional sex	Gonad stage at catch	Transmitter type	Frequency [khz]	Capture method	Release method	Tracking method (manual, remote)	Release-date	End-date	Tracking-period [d]	Days with valid positions	No. of valid positions
1	393	male		V16-4L	60	SCUBA angling	by diver	m	18-Sep-02	7-Nov-03	415	41	151
2	385	male		V16-4L	54	Boat angling	by diver	m	25-Sep-02	27-Sep-02	3	3	-
3	400	male		V16-4L	54	SCUBA angling	surface	m	28-Sep-02	29-Sep-02	2	2	-
4	285	female		V8SC-2L	84	Boat angling	by diver	m	19-Feb-03	6-Nov-03	261	19	80
5	248	female		V8SC-2H	78	Boat angling	surface	m	13-Jul-03	18-Jul-03	6	6	16
6	397	male		V8SC-2H	63	Boat angling	surface	r,m	28-Oct-03	1-Dec-03	35	35	3347
7	273	female	ripe	V8SC-2H	72	Boat angling	surface	r,m	29-Oct-03	1-Dec-03	34	24	185
8	354	?		V8SC-2H	66	Boat angling	surface	r,m	29-Oct-03	1-Dec-03	34	26	408
9	264	female	running	V8SC-2H	75	Boat angling	surface	r,m	31-Oct-03	1-Dec-03	32	19	485
10	227	female		V13-1H	84	Boat angling	surface	r,m	03-Mar-04	4-Mar-04	2	2	41
11	282	female		V13-1H	57	Boat angling	surface	r,m	04-Mar-04	24-Mar-04	21	21	531
12	335	?		V8SC-2H	54	Boat angling	surface	r,m	03-Mar-04	24-Mar-04	22	22	1473
13	338	male		V8SC-2H	69	Boat angling	surface	r,m	04-Mar-04	24-Mar-04	21	21	3303

Thirteen roman were tracked during the period of September 2002 and March 2004. It was impossible to implement a strict tracking protocol, as tracking time per individual

was dependent on battery life of the transmitter, sea conditions and availability of personnel and equipment. Three different types of transmitters with different battery life spans were used during the study (Vemco Ltd, Nova Scotia, Canada; Table V-II). Details on the study animals capture, release and tracking methods and individual tracking times are summarised in Table V-I.

Three different tracking methods were used, boat-based manual tracking, manual underwater tracking on SCUBA gear and remote positioning with a VEMCO radio acoustic positioning system (VRAP; Vemco Ltd., Nova Scotia, Canada). Boat-based manual tracking was carried out mainly during 5 two-week blocks and opportunistically during day trips from September 2002 to March 2004. The VRAP system was deployed from the 28th of October to 1st of December 2003 and from the 3rd to the 28th of March 2004, periods during and after the spawning season of roman. SCUBA tracking was done opportunistically during the entire study period, depending on weather and oceanographic conditions.

Capture and surgery

Fish were caught either with rod and line from an anchored skiboat or by SCUBA divers using small fishing rods, with 50 cm of fixed line. The latter method was used in an attempt to minimize barotrauma and to target individuals of certain sizes. The fish were brought to the surface slowly and handed over to the surgery team on the boat. Circle hooks (VMC sport circles 1/0-5/0) were used to minimise gut and gill hooking.

After carefully removing the hook, the fish were measured to the nearest millimetre on a wet plastic stretcher and the swim bladder was deflated with a hypodermic needle. The fish were then anaesthetised and transmitters were surgically implanted as

117

described for the tank experiment. The fish were placed in an 80 l container with oxygenated seawater immediately after the operation. Once they resumed swimming normally they were either released from the skiboat or put in a seawater filled plastic bag and returned to the place of capture on the reef by a diver.

Manual boat-based tracking

A directional hydrophone (VEMCO; V-10) attached to a two-metre aluminium pole was mounted amidships on the gunwale of a 6 m skiboat, allowing 360° rotation. When lowered in tracking position, the pole extended below the hull of the boat.

The hydrophone was connected to a VEMCO VR-60 receiver, which converted the signal into visible needle deflection on a volt metre and audible pulses. Gain, volume and frequency were adjustable.

Tracking procedure

Tracking was carried out by a three-man team; a tracker, a data recorder and a skipper. The tracker operated the hydrophone and the receiver. He rotated the hydrophone to find the direction to the fish. Once signals were received, the boat was steered in the direction of the strongest signal. A position was recorded only when the signal was equally strong in all directions when the receiver was set to the lowest possible gain. The data capturer would note geographic coordinates (GP1850WDF GPS receiver; Furuno; USA), time, water depth and comments on the signal strength (weak vs strong) and regularity (regular vs irregular). Habitat was classified as 'rock', 'sand' or 'mix' as determined from the display on the echo sounder. The accuracy of these classifications were verified during SCUBA dives. Tracking was initiated immediately after fish were released.

In the first few hours, positions were typically recorded every 15 minutes depending on the activity of the fish. Once the fish had settled, positions were taken at hourly intervals. If a fish could not be located, a search in the form of an outward spiral from the last known position was undertaken. If the signal could not be detected within a kilometre from the last known position, that search was abandoned. When time permitted, all reefs in the entire study area were scanned for lost fish.

Accuracy and maximum range of the manual tracking

To determine the accuracy of the manual tracking method, simulation tests were conducted. A SCUBA diver carrying a transmitter was deployed in the study area. The diver descended directly to the sea floor in a vertical line and maintained his position for the duration of the test. The geographic position was taken at the dive site. The boat then retreated beyond the detection range of the transmitter. The tracker, who was unaware of the position of the diver, had to detect the signal and direct the skipper to obtain a position of the diver. The geographic positions were then compared. The procedure was repeated three times with approaches from different directions.

Manual underwater tracking

Underwater tracking was done by SCUBA divers with an underwater hand-held unit (DPL-275 underwater pinger receiver; Datasonics). This unit is comprised of a directional hydrophone, a receiver that converts the signal into audible pulses and an underwater headphone. Frequency and sensitivity were adjustable.

Underwater tracking sessions were used to assess the condition of the fish with implants and to record their behaviour. Behavioural observations of the study animals

and their con-specifics were made during 23 SCUBA dives. Observations were recorded on underwater slates and on digital video.

Remote positioning

Position data were automatically calculated with the VRAP system. The system comprised of an array of three surface buoys, a base station and a personal computer. Each buoy contained an omni-directional hydrophone, an ultrasonic receiver, a two-way radio link, a microprocessor controller, and a re-chargeable battery. The base station included a two-way radio, timing circuitry and a PC serial data link. The buoys were moored in the configuration of an equilateral triangle. The signals from the transmitters were radioed to the base station ashore. When all three buoys received pulses, the computer software calculated the position of the transmitter by comparing the respective arrival times of signals at each hydrophone. The system was set up to cycle through the frequencies of the different transmitters. Depending on how many transmitters were deployed, each frequency was scanned at least every 8 minutes. The scanning time per tag was set to one minute. Data were uploaded to the base station every 12 seconds to reduce data loss due to poor radio communications. The automatic calibration of the buoy positions was repeated every four hours to maximise the position accuracy.

Moorings

To accommodate rough sea conditions in the study area, the mooring system had to be strengthened. Each buoy was moored with three anchors: A main anchor consisting of a steel-cable attached to five railway bars (60 kg, 80 cm) and two side anchors each made from polypropylene rope attached to two railway bars (60 kg, 80 cm). The side anchors were laid out in the main wave direction. On each side anchor rope, a surface

buoy was attached at a distance of ca. two metres from the VRAP buoy to preclude it from touching the hydrophone during foul weather (Figure V-2).
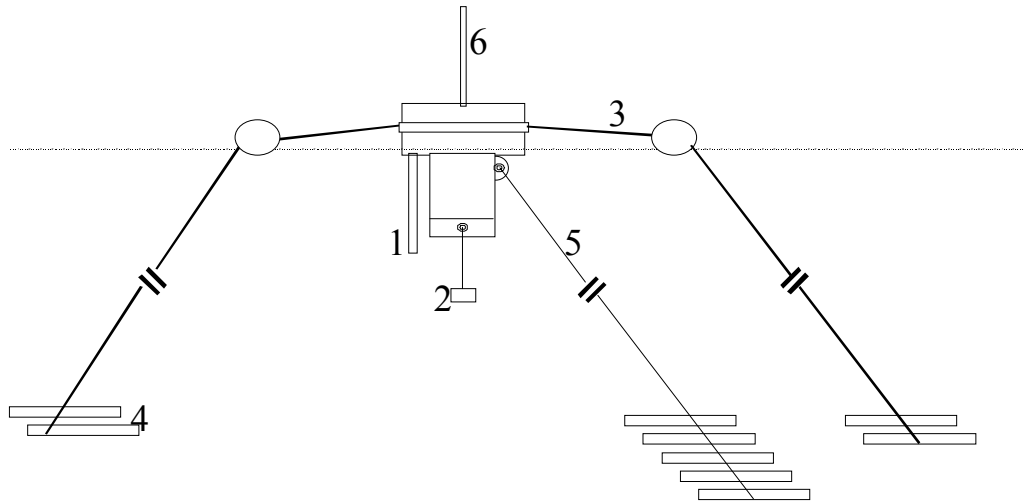
Figure V-2: Schematic diagram of the mooring setup of one VRAP–buoy: 1 Hydrophone, 2 Counter-weight, 3 Side anchor rope with surface buoy, 4 Railway bars, 5 Main anchor (steel cable), 6 Antenna.

Accuracy and maximum range of the remote positioning

Erroneous position estimates may have resulted from background noise, signal reflection and turbulence. The maximum range of the system was determined during regular manual tracking of animals whose pulses were not received by all three hydrophones and whose positions were therefore not plotted by the system. Two test transmitters were deployed to determine the accuracy of the position recordings. One transmitter was placed in the centre of the triangle, the other one in a shallow area with high profile reef, outside the triangle ca. 40 m north of the north-eastern buoy. The latter position was selected to determine the maximum deviation, as the shallow reef was likely to cause high noise levels and signal shadowing; and the position

outside the triangle in proximity of one buoy was expected to be unfavourable for the triangulation of the position.

Data analysis

The "position- average" algorithm from the VRAP5 software (Version 5.1.2; Vemco Ltd) was selected to calculate all positional fixes. All data points were transferred to a Microsoft Access database and processed in Microsoft Excel. A data cleaning routine in Microsoft Visual Basic was developed to remove spurious position estimates. Firstly, any positions that were more than 150 m from the centre of the triangle were deemed unrealistic as they exceeded the maximum range of the system. Secondly, a data point was regarded as an outlier if the speed necessary to cover the distance between consecutive positions exceeded the plausible maximum speed of roman. The plausible maximum speed of roman was determined from data within the triangle during five days of favourable sea conditions and therefore reliable recordings. This speed was calculated as the maximum velocity between consecutive points, assuming the animals travelled in a straight line.

Thirdly, after tests runs with different distances, any position resulting from a movement greater than 10 times the distance between the previous and the following positions in a time interval of less than 30 min was considered a "flier" and removed from the data set.

Minimum convex polygon (MCP) and fixed kernel home ranges were calculated in ArcView (Version 3.2, Environmental Systems Research Institute inc, Redlands, California) GIS software with the Animal Movement extension (Hooge *et al.* 2001). The smoothing factor (h) was determined with the least square cross validation

method available in the programme. T-tests and Kruskal-Wallis tests were executed in Excel (Microsoft corporation) and Statistica (Version 6.1, StatSoft Inc.).

<u>Auxiliary data</u>

Temperature profiles were obtained with a bathythermograph deployed at a fixed GPS position on every outing. A permanent underwater temperature logger was installed by SCUBA divers in a cave at the centre of the study area from February 2003 until the end of the study. Temperature was recorded every hour.

Table V-II: Transmitter specifications.

Transmitter type	Expected battery life [d]	Dimensions (mm) (Ø; length)	Weight in water [g]
V 16-4L	365	16; 65	12
V 13-1H	37	13; 36	6
V 8-SC-2H	25	9; 30	3.1
V 8-SC-2L	102	9; 28	2.8

Results

Tank experiment

The surgical procedure proved to be difficult on the ship, which was rolling in the rough conditions, resulting in prolonged surgery times (measured as the time the fish left the anaesthetic bath to being released into the holding tank) of 8 to 12 minutes. Three fish died during surgery or immediately after release into the holding tank. The remaining five individuals recovered within 10 minutes of being released into the holding tank and they could not be distinguished from the control fish by their swimming motions. All fish started feeding after two days of being transferred to the holding tank in the aquarium.
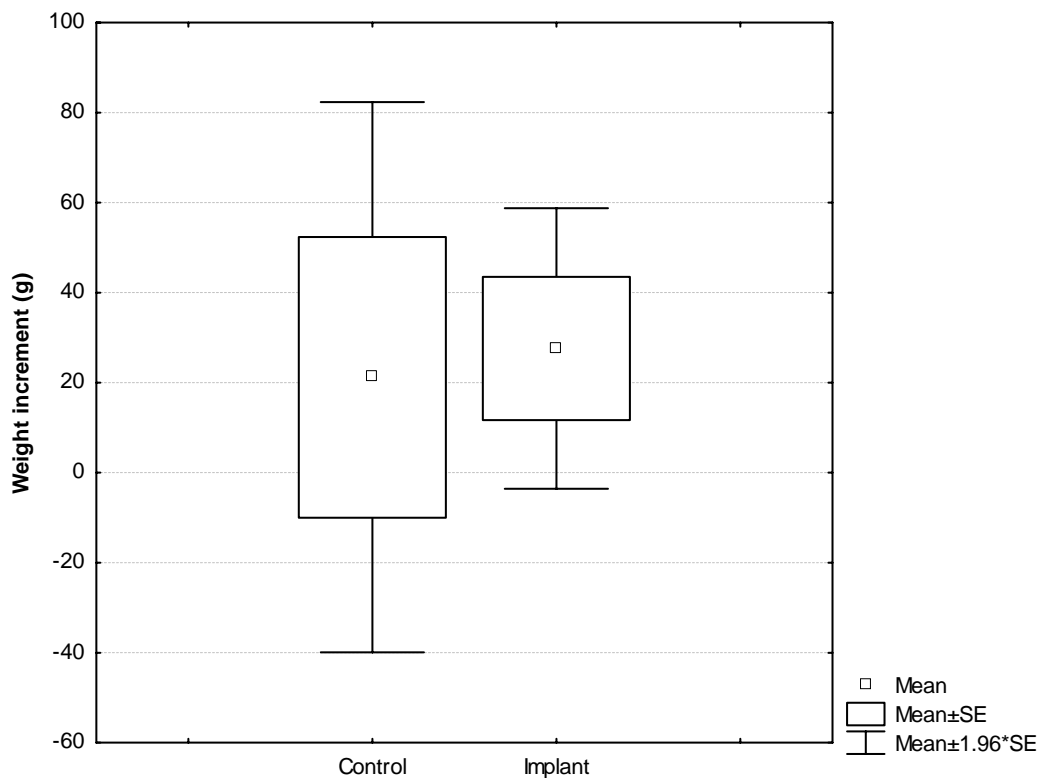
Figure V-3: Box and whisker plot of weight increments 40 days after the treatment.

After 40 days, all fish were shown to be in a healthy condition. The sutures had dissolved completely and the scales had grown back so that the incision scar was barely visible. There was no significant difference in weight increment between treated fish and the control group (t-test; $F = 3.84$; $p = 0.22$, Figure V-3). Length increments were not analysed after 40 days because the error of length measurements was of similar magnitude to the growth during such a short interval. At the final assessment after 198 days, all fish were healthy and could be individually identified with the aid of the digital photos. There was no difference in growth rate between fish with implanted dummy transmitters and controls (t-test; $F = 1.96$; $p = 0.52$ for length; and $F = 1.02$; $p = 0.98$ for weight increments, respectively (Figure V-4,Figure V-5). The incision scars had disappeared apart from a slight discolouration in the area where the scales had grown back. No haemorrhaging of organs or infections were observed and the dummy transmitters were embedded in mesenterial tissue.
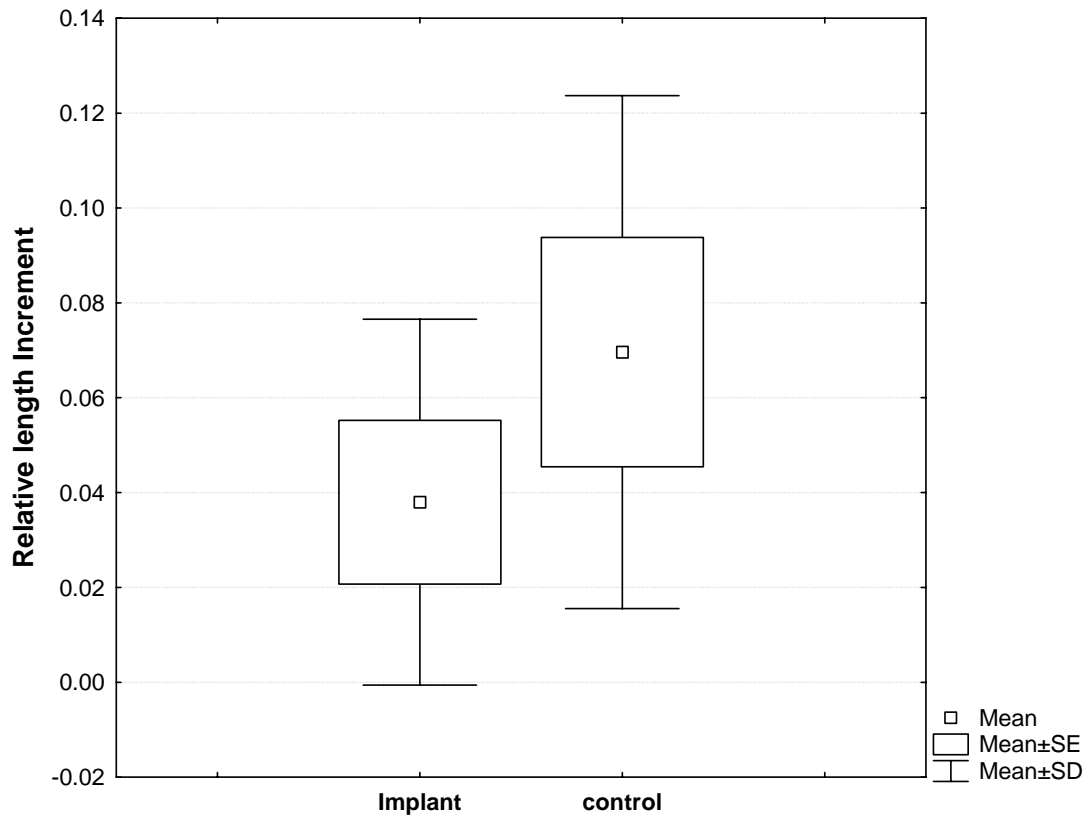
Figure V-4: Box and whisker plot of length increments 198 days after the treatment.
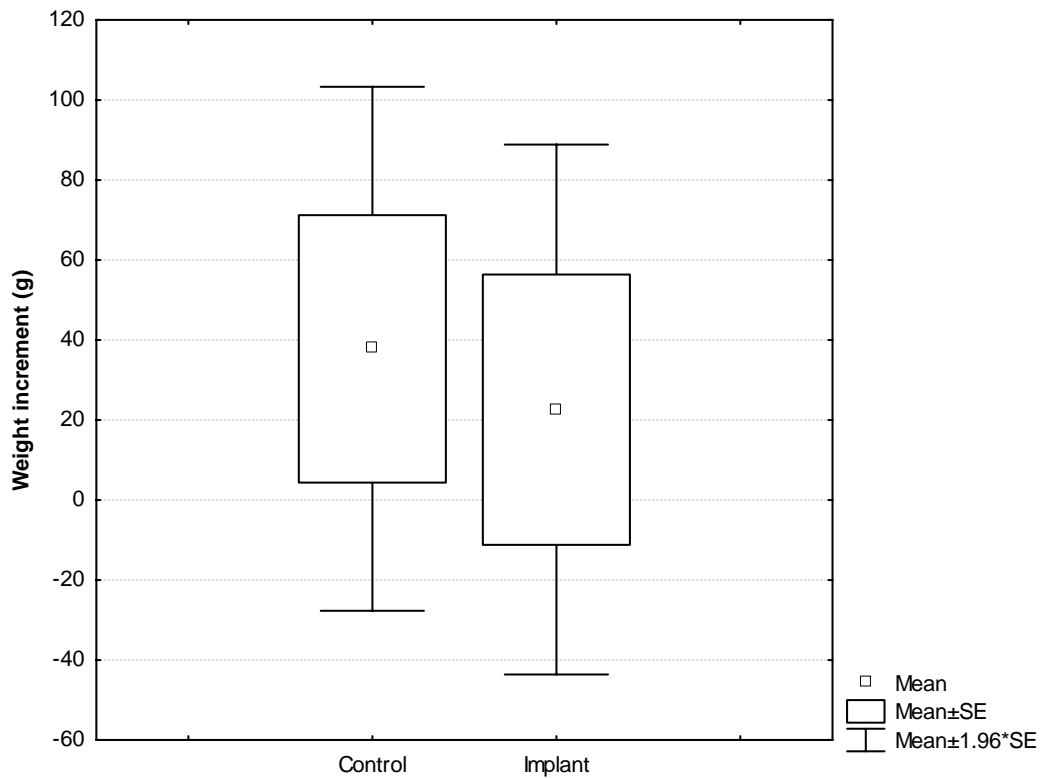
Figure V-5: Box and whisker plot of weight increments 198 days after the treatment.

Field study

<u>Range and accuracy of manual tracking</u>

The three trials resulted in deviations of 7, 9 and 12 m between the positional fix of the tracker and the GPS position of the diver. The signal was first received by the tracker at a distance of 180, 150 and 200 m respectively from the diver's position. However, during cold-water events (upwelling), the detection-range frequently decreased to less than 50 m. The signal became irregular and the determination of the exact location was difficult. However, SCUBA tracking verified the accuracy of the surface tracking. In most instances, divers were able to locate the fish immediately when they descended at the positions identified by surface tracking.

Range and accuracy of remote positioning

Due to the high wave energy environment and the high profile topography of the reefs in the study area, the receptive field of the VRAP system was smaller than anticipated. To achieve a satisfactory reception rate of pulses, the distance between the buoys had to be reduced from 300 m as recommended from the VRAP hardware manual to ca. 70 m. The buoy system was set up over a reef area known from manual tracking sessions with a maximum depth of 15 m. During poor sea conditions the radio communications between the buoys and the base station failed frequently, resulting in the loss of data. During stormy periods, the system frequently failed to record pulses, due to radio download failures and high noise levels underwater.
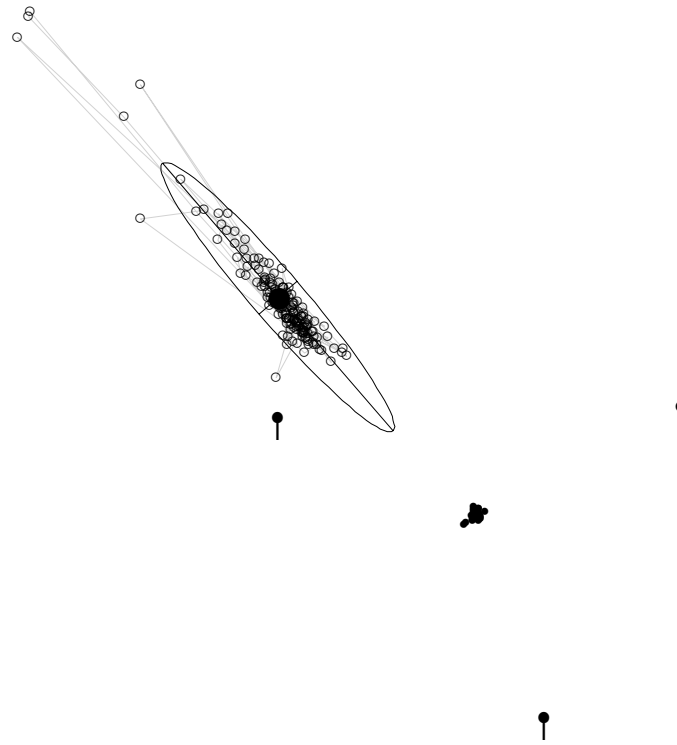
Figure V-6: Plot of positional fixes of two stationary test transmitters (open circles and black dots) during a day with unfavourable sea conditions. The position of the VRAP array is indicated by the buoy symbols. The ellipsoid represents 95% of the points received from the transmitter outside the buoy triangle, assuming a bivariate normal distribution of deviation.

The accuracy of the positions in the centre of the triangle was high even during unfavourable conditions. Ninety-five percent of the recordings of the test transmitter position fell within 2.2 m. The accuracy of the positions and the frequency of recordings were deteriorating outside the triangle, especially around buoys and in high relief reef areas. The data of the test transmitter outside the triangle had numerous outliers. Most of the deviations occurred along the axis from the centre of the triangle

129

to the transmitter position, as described in the VRAP manual (Figure V-6). Assuming a bivariate normally distributed deviation, a Jenrich-Turner ellipsoid (bivariate normal method of Jenrich and Turner in Hooge *et al.* 2001) was used to describe the deviation. A subset of the data taken from the day with the worst deviations was chosen for the analysis to determine the maximum deviation. 95% of the points along the main axis of deviation were within 33 m of the centre, along the short axis of the ellipsoid, 95% of positions were within less than 5 m.

The maximum speed of roman was determined as 0.69 ms^{-1}, comparing favourably with theoretical maximum swimming speed of 3 body lengths per second. Ninety-nine percent of values were less than 0.37 ms^{-1}. Mean speed was 0.049 m/s (StD 0.11 ms^{-1}). The data cleaning routine removed 10% of positional fixes, resulting in a final dataset of 9724 positions. 128 points were out of the range of the system, 723 positions were removed because the roman speed limit was exceeded and 165 positions were removed as "fliers".

Capture, transmitter implantation and post-surgery effects

Barotrauma was found to occur in all fish caught regardless of the capture method and swimbladders of all fish needed to be deflated prior to surgery. All thirteen fish recovered from the surgical procedure and displayed normal swimming motions in the recovery bin within 10 minutes after surgery. The behaviour of 12 of the fish was observed during SCUBA tracking sessions.

Immediate post release observations were made of the three fish that were returned to their capture location on the reef by SCUBA divers (Table V-I). Fish 1 retreated immediately into a large cave (Figure V-7), where the divers relocated it in the afternoon of the same day. Fish 2 slowly retreated from the divers but remained in

close proximity to the release spot. Fish 4 swam in a south-easterly direction to a position 100 m from the original capture site (Figure V-7), but returned to its original position in the afternoon, where it was seen foraging on reef invertebrates at a position within 10 m of the original site of release. The fish appeared very active, moving continuously inside a small area, acting aggressively towards roman of similar size while foraging.

Whereas the majority of fish were not discernable from their untreated con-specifics by their behaviour, two fish displayed abnormal swimming motions. Fish 2 showed restricted mobility after one day. After two days, its condition deteriorated and it was swimming head up in an unnatural manner, being caught by a diver with a hand net. The dissection revealed that the tag had shifted to the front between the liver and the stomach. Bruises of the peritoneal cavity lining and the liver lobe were evident. One the release day, fish 3 seemed less agile than other roman and swam with the head slightly elevated. During resting phases it was lying on its side and made no attempt to escape when examined by a diver. There was no visible infection of the incision.

Two fish (fish 3 and fish 10) disappeared one day after surgery and their signals could no longer be detected in the study area during several searches. Fish 10 disappeared from the receptive field of the VRAP system 3 hours after release and its condition could not be verified by underwater tracking. It was manually tracked the next day in the morning ca. 100 m north-east of the buoy triangle, after which it disappeared.
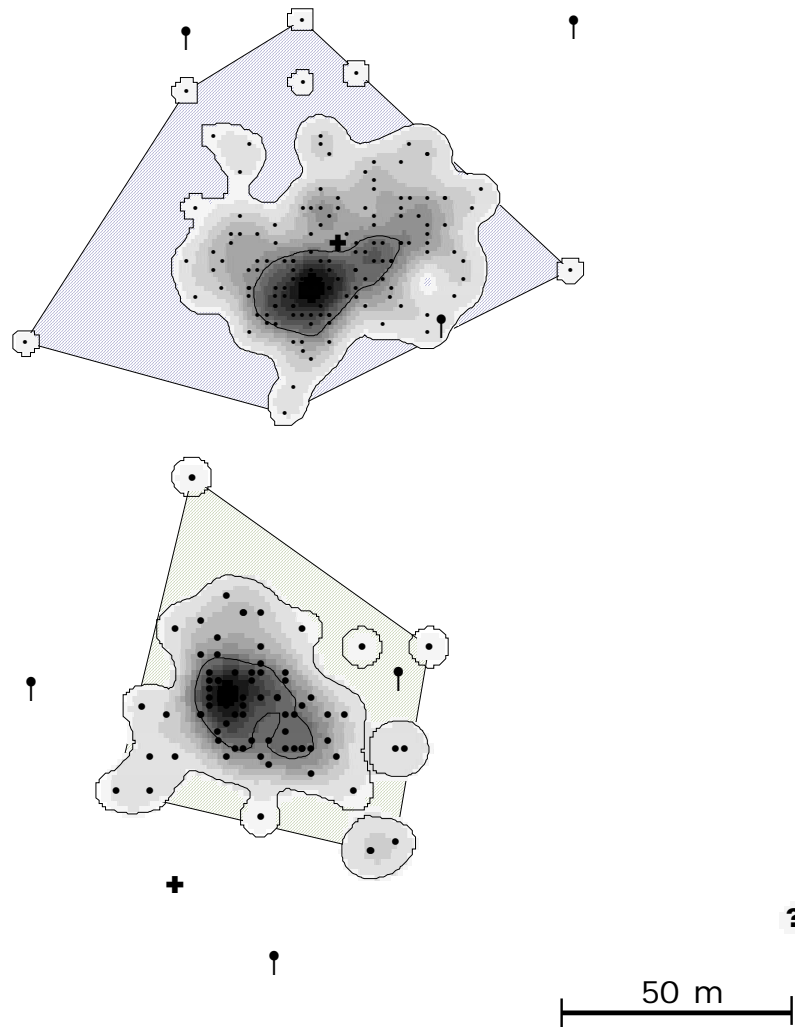
Figure V-7: Minimum convex polygon and kernel home range plot of fish 1 and 4 derived from manual tracking. Shading indicates the differences in utilisation density in 5% increments. Ninety-five percent and 50% kernel home ranges are emphasised with black lines, MCP home range areas are hatched. The position of the VRAP array is indicated by the buoy symbols. The cross marks the northern entrance of a cave utilised by fish 1. The question mark indicates the first position of fish 4 after the surgery. It was not included in the home range analysis.

Table V-III: Summary of home range area and average speed of roman in the Castle Rock MPA.

Fish No	Tracking method	Greatest distance between two positions [m]	MCP area [m^2]	50% Kernel home range [m^2]	95% Kernel home range [m^2]	Average speed [ms^{-1}]
1		95	9612	362	2760	-
2		-	-	-	-	-
3	Manual	-	-	-	-	-
4		145	3524	447	2783	-
5		52	883	227	1278	-
6		204	9218	250	1087	0.112
7	Remote/Manual	317	19167	2864	11561	0.126
8	(Spawning season)	336	36134	1052	7927	0.148
9		328	24280	2225	10631	0.160
10		-	-	-	-	-
11	Remote/Manual	150	9612	195	924	0.118
12	(After spawning season)	154	11924	169	1304	0.141
13		142	12594	243	1562	0.154

Home range patterns

The ten remaining fish were resident within small home ranges during their individual tracking periods. In case of fish 1 and 4, the fish with the longest observation times, all positions were within 55 m of the original capture location during their respective tracking periods of 14 and 8 months. (The first position of fish 4 was attributed to

post-capture stress and therefore not included in home range analysis). These fish were found during every tracking attempt, close to the position of original capture, even after periods of up to three months without tracking.

A researcher caught fish 4 incidentally 8 months after its release, less then 30 m from the original capture site. It appeared in good condition with a length increase of 8 mm since capture. It had ripe ovaries with no visible testicular tissue. The internal organs appeared healthy, no fat was found in the body cavity, as expected during spawning season. The tag was embedded in mesenterial tissue, no haemorrhaging was found at the surrounding tissues. The fish tasted excellent (Attwood pers. com.).

A similar home range extent was found from the remote positioning of fish 6 during the spawning season and fish 11-13 after the spawning season (Figure V-8, Figure V-9). Ninety-nine percent of recorded positions were within a distance of less than 50 m of the release site. All four fish were logged by the system every day of the tracking period. Fish 5 was only observed over a period of 6 days and unfavourable sea conditions precluded frequent position recording. However, the fish was resident in a small home range during this period and was found in a crevice close to its capture spot during two underwater tracking sessions.

Fish 6
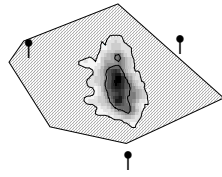
Fish 7
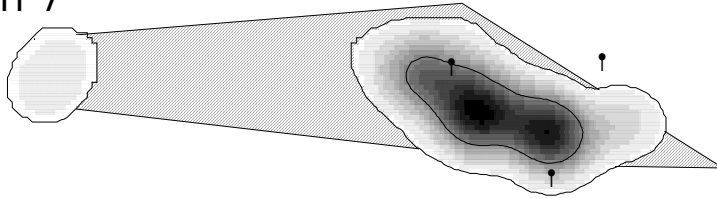
Fish 8
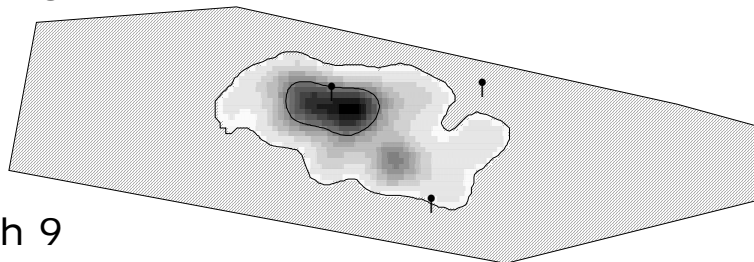
Fish 9
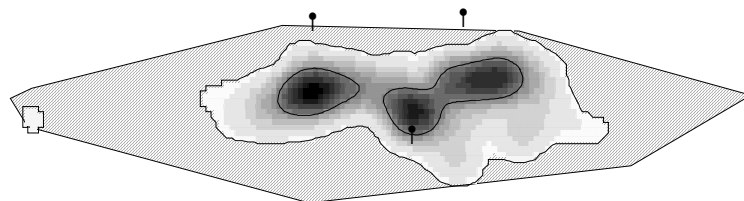
100 m

Figure V-8: Minimum convex polygon and kernel home range plot of fish during the spawning season. Manual tracking and remote positioning data were combined for the home range calculations. Shading indicates the differences in utilisation density in 5% increments. Ninety-five percent and 50% kernel home ranges are emphasised with black lines, MCP home range areas are hatched. The position of the VRAP array is indicated by the buoy symbols.

Fish 11

Fish 12

Fish 13

100 m
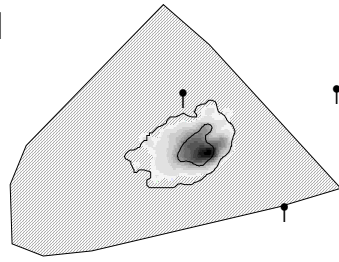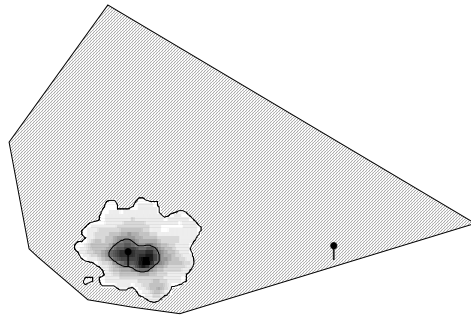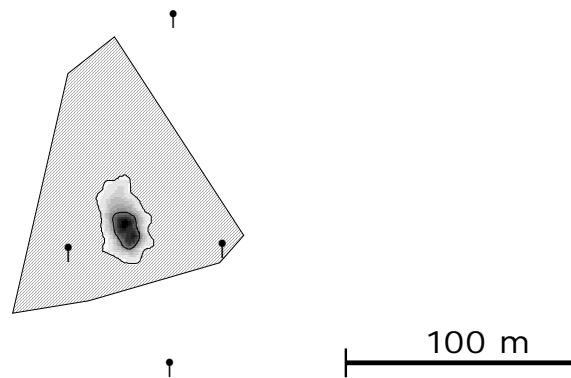
Figure V-9: Minimum convex polygon and kernel home range plot of fish after the end of the spawning season. Manual tracking and remote positioning data were combined for the home range calculations. Shading indicates the differences in utilisation density in 5% increments. Ninety-five percent and 50% kernel home ranges are emphasised with black lines, MCP home range areas are hatched. The position of the VRAP array is indicated by the buoy symbols.

Three fish, all tracked during the spawning season, showed similar activity patterns, dissimilar to all other fish. Fish 7 and 9, two female fish with ripe ovaries and fish 8, whose sex could not be visually determined, appeared to be more active, covering larger distances within short periods (Figure V-8). Although they frequented the buoy triangle during most of the study period, the system frequently failed to calculate their positions for periods of several hours or even days. However, the signal was received by at least one of the buoys, indicating the presence of the fish in the area, just outside the receptive field of one of the buoys. Manual tracking revealed that the fish had moved inshore during those periods, to areas with dense kelp. The same locations were frequented a number of times during these outings, the fish were always found at their preferred locations with all manual position records within a 30 m diameter. There seemed to be no temporal pattern for the commuting between locations within the buoy triangle and the kelp areas, the fish were found in the kelp and in the triangle during similar times of the day. Few positions were recorded on the sandy areas between the triangle and the kelp.

SCUBA tracking during two dives on the afternoon of the 6th November in the kelp and in the triangle and a dive in the triangle in the afternoon of the following day resulted in the observation of spawning related behaviour at both localities: fish swam parallel to each other in close proximity. One fish would then tilt away from the other exposing its white abdominal area. If the other fish did not withdraw, it was attacked. Only female fish with an estimated fork length between 20 and 30 cm, including the two study animals clearly identified as females, exhibited this behaviour. Large fish (males) did not engage in aggressive displays. Fish 6, a male, was observed during the same dive but did not exhibit any of the behaviour described above.

A clear habitat preference was distinguished from the echo-sounder recordings during manual tracking. Ninety-eight percent of the recorded positions were over clearly discernable rocky substratum or over areas of rock sand interface. Only 2% of the positions were taken over sand. During SCUBA tracking, the animals were never encountered in sand dominated areas although the remotely recorded positions of fish 7-9 indicated that the fish traversed sandy areas between two reef complexes during the spawning season.

Although all the fish were strongly reef-associated, there was a clear difference between habitats occupied by individual fish. Fish 1 resided in a high relief reef area with diverse invertebrate communities, dominated by large boulders with numerous caves and crevices. The frequent withdrawal of the fish into a large cave resulted in a week and irregular signal on the VR- 60 receiver on the boat, where pulses were received only from certain directions close to the actual position of the cave. Ninety seven percent of the manual tracking positions were taken over rock and none over sand. The area occupied by fish 4 on the other hand was dominated by low relief reef surrounded by sand with strong siltation at the edges of the gently sloping rocky areas. This was reflected in its position recordings, with 74% noted as 'mix' and 6% as 'sand'.
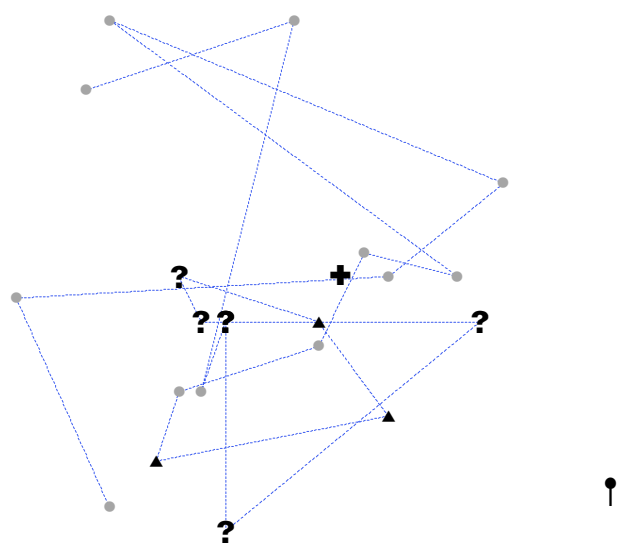
Figure V-10: Manual-tracking positions of fish 1 from the morning of the 25th to the evening of the 26th of September 2002. Grey circles indicate daytime positions, night positions are indicated by black triangles. Question marks represent positions with weak and irregular signal during the night. The position of the VRAP array is indicated by the buoy symbols.
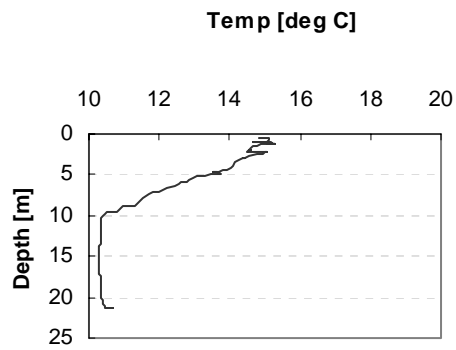
Figure V-11: Temperature profile from the morning of the 11th of December 2004, the day with the coldest temperature during the study period, caused by upwelling conditions.
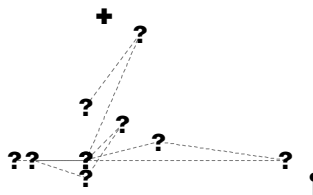
Figure V-12: Manual-tracking positions of fish 1 from the morning of the 11th to the evening of the 13th of December 2002. Question marks represent positions with weak and irregular signal. The position of the VRAP array is indicated by the buoy symbols.

140

Table V-IV: Average speed of fish 6 during different time periods.

Time period	speed average [ms^{-1}]	St dev
Total	0.113	0.16
0:00 h -4:00 h	0.058	0.10
4:00 h -8:00 h	0.111	0.15
8:00 h -12:00 h	0.128	0.18
12:00 h -16:00 h	0.139	0.17
16:00 h -20:00 h	0.125	0.16
20:00 h –0:00 h	0.089	0.14

Activity patterns

The average speed of the remotely tracked fish was between 0.11 and 0.16 ms^{-1} (Table V-III). Fish 6 was selected to investigate changes in activity patterns, because its home range was inside the triangle and the positioning therefore frequent and accurate. There was a highly significant difference between average swimming speeds for the different periods of the day (Kruskal–Wallis test, H = 35.44, p = 0.000). The period with the lowest activity was between 0:00 h and 4:00 h, while the fish was most active between 12:00 h and 16:00 h (Table V-IV).

At night between 20:00h and 4:00 h no positions were logged by the VRAP system for fish 7, 9 and 11. However, the first and the last recorded positions in the morning and evening were well in the detection range of the system and there was no track indicating movement out of the receptive field.

Fish 1 was manually tracked during three nights (Figure V-10). While positions were easily obtained until dusk, the signal became week and irregular after dark with positions around the location of the cave, which was marked by a reference buoy. Fish 4 was tracked during one night. All the positions were within 30 m of each other. The signal on the surface unit was clear during the night, indicating that the fish was not in a cave.

Fish 1 was tracked during a period of cold water between the 11th and the 13h December 2002 (Figure V-12). The signal received from the surface unit became weak and irregular in the same manner as described for nocturnal periods with all positions around the cave area. Diver tracking confirmed that the fish had retreated into the cave. During the 11th, bottom temperatures declined to 10.3 °C, the lowest recorded temperature thus far (Figure V-11). Divers reported that no fish were found in the open and the signal was difficult to detect with the handheld underwater unit. The divers found fish 1 in a small crevice at the back of the cave together with two other roman of similar size and a hottentot *Pachymetopon blochii*. The divers tracked the fish to the same location inside the cave on the following day.

Discussion

Methodology

Although acoustic telemetry is the only feasible method for studying home range behaviour of temperate reef fish intensively over meaningful time periods, its application for roman in the Castle Rock MPA posed a number of problems.

Perhaps the greatest limiting factor for this study was the nature of the habitat. The high relief reef in the study area caused frequent shadowing and reflection of the acoustic pulse, resulting in reduced reception and irregular signals during manual tracking. Kelp cover, on the other hand, did not seem to have an influence on the signal strength. Matthews *et al.* (1990) reported similar findings for a tracking experiment on Quillback rockfish *Sebastes maligner* in Washington State, although their maximum detection range of 1 km was much higher.

In addition to the problem of signal attenuation by high relief reef habitat, the high wave energy environment created difficulties for the use of moored instruments. The enhanced mooring system helped to keep the VRAP buoys steady even during 70 km h^{-1} wind and waves over 2.5 m. However, bad sea conditions resulted in a high number of outliers and in the loss of data due to radio failure.

As roman are generally resident and do not display rapid movements, the reduced detection range did not pose a problem. However, the accuracy of the position recordings is very important to study movement patterns of highly resident species. The small deviations in the simulation trials verified the good accuracy of boat based tracking position recordings (Chapter VI). Differences in signal appearance gave clues

to whereabouts of the fish. If the signal became weak and irregular, the divers would find the fish had withdrawn into a crevice.

Apart from sea condition, the accuracy of the remotely recorded positions depended on numerous factors, including distance of the fish from the centre of the system, position over the reef in relation to the system and topography of the area. Therefore, *de facto* outliers could not be discerned from real positions and removal of outliers according to strict mathematical rules based on position in relation to the triangle was impossible. However, the data cleaning routine presented here represents an improvement to the procedure used by Parsons *et al.* (2000), as it incorporated the maximum detection range of the system and plausible speed of the study species.

Capture, transmitter implantation and post-surgery effects

As with any intrusive experiment, the effects of the methods on the phenomenon under investigation have to be considered. An important question for fish tracking experiments is if and how quickly the fish resume their natural behaviour after release.

Hooking, capture, handling and exposure to air has a negative effect on the condition of fish in catch and release experiments (Thorstad *et al.* 2001b). Most 'tagging-induced' mortalities occur within the first 24 h after release (Finstad *et al.* 2003). In this study, the high mortality rate during and immediately after the surgery in preparation for the tank experiment can be attributed to the unfavourable sea-conditions on the particular day, which resulted in difficulties during surgery, long handling times and rough handling, caused by the rolling of the ship.

During the field study, when the surgery was carried out on a skiboat, no mortalities occurred during or immediately after the treatment. An additional factor that negatively affected this species is the rupture of the swimbladder (pers. obs.), caused by the rapidly expanding gas when the fish is pulled to the surface. Over-inflation of the swim-bladder might be caused just by handling (Keniry *et al.* 1996) and could not be avoided by capturing fish on SCUBA gear and slowly bringing them to the surface. Over-inflation and rupture of the swimbladder can result in impaired buoyancy control and increases the chance of predation and it is possible that this may have been the cause of the disappearance of the two fish. Zeller (1999) reports on two coral trouts that were eaten by a white tip reef shark shortly after post-surgical release. He recommends keeping the animals for periods of two weeks after surgery. However, other authors have successfully released fish shortly after surgery (Parsons *et al.* 2000, Thorstad *et al.* 2001a).

The possibility of decreased survival of a fish released directly after surgery has to be weighed carefully against possible alteration of its space utilisation behaviour due to prolonged *ex-situ* captivity. Removing potentially territorial species for long periods could cause changes in territories and social hierarchies, where they exist.

The long- term effects of transmitter implantation are highly variable (*inter alia* Jadot 2003, Lefrancois *et al.* 2001, Martinelli *et al.* 1998, Thorstad *et al.* 2000, 2001b) and depend on the specific method of attachment as well as on the physiology of the study species. The method similar to the one described here was successfully applied on other sparids (Chapter III, Jadot 2003, Parsons *et al.* 2000). The results from the tank experiment indicate that for Roman there are no long-term effects that can be directly

attributed to the implant procedure. The healthy condition and the normal gonad development of fish 4 eight months after release support these findings.

Did the treated fish resume natural behaviour? Although all the fish in the tank experiment resumed their natural behaviour, two fish in the field study showed severe effects as a result of the treatment. This highlights the importance of the underwater verification of the state of the treated fish. (i.e. Bolden 2002, Matthews *et al.* 1990). Surface tracking did not indicate any abnormal behaviour (long stationary periods or increased movement). Fish 4 displayed increased swimming activity immediately after release. This effect has been observed in other studies (i.e. Connolly *et al.* 2002). It might have been a flight reaction after being released by the diver, or the result of capture-stress.

Home range patterns

The results of this study confirm that adult roman utilise confined areas for prolonged periods. A high degree of site fidelity in this species has been suggested for some time: Penrith (1972) reported on a large roman, which 'inhabited the same deep cave for a minimum of 25 months'. Reports by divers and spear-fishermen on large roman with characteristic scars, that are repeatedly found at the same rock or in the same crevice are common (J.Allen, S.Brouwer pers. com.). Although long distance movements in the order of several kilometres have been reported occasionally (Bullen and Mann 2004, Griffiths and Wilke 2002), they are not considered here, as they can be more effectively studied with mark and recapture telemetry techniques (Chapter III).

A home range is an analytical construct, that has biological meaning only when the assumptions of the individual home range model are met and the limitations of the model understood (White and Garrot; see Hooge *et al.* 2001). To use a human analogy, the home range could be equivalent to the house where a person lives, the neighbourhood, the town where he works, shops or goes out, the places were he spends his holidays etc.

As this study is concerned with the protection of fish in the context of MPA design, the imperative question would be what size of an area needs to be closed to include a certain percentage of area utilised by the fish. Although Penrith's observations aptly describe roman behaviour (Penrith 1972), the sizes of the areas utilised by the fish (15 m^2) are based on continuous observational times of typically less then 1 h during SCUBA dives and therefore not meaningful in the context of conservation.

In this study four different measures of the extent of this area were provided, each for the entire observational period of the individual fish: Maximum distance between two positions, Minimum Convex polygon (MCP) and 50% and 95% fixed kernel home ranges (Table V-III). Each method has its merits (*inter alia* Anderson 1982, Hooge *et al.* 2001, Seaman and Powell 1996, Worton 1989).

The maximum distance between two recorded positions does not provide information on home range area, as it is confined to one dimension much like mark and recapture. Calculating a home range area with this distance as diameter would produce an over estimate, as home ranges are never completely circular. Furthermore, this method as well as the MCP is prone to sample size effects and errors caused by outliers.

147

Kernel estimators describe home ranges in a probabilistic sense. They estimate the distribution of an animal's position (utilisation distribution) in a nonparametric manner. Seaman and Powell (1996) found that the cross-validated fixed kernel estimator provided the best area estimates in simulations with known utilisation density distributions. However, the smoothing factor and therefore the area estimate depends on sample size and data structure.

In this study, less frequent manually recorded positions, where the fish left the receptive field during spawning season, had to be combined with the remotely recorded positions. Although this might result in an underestimate of the 50% kernel areas, it is unlikely to have an effect on the 95% kernel home rage.

The differences between home ranges calculated by the different methods for the same dataset are very clearly illustrated in the results of this study. The 95% kernel home range for fish 6 was 4 times the size of the 50% kernel home range and the MCP is 9 times the size of the 95% kernel.

In the context of MPA design, the results of this study lead to the following considerations: To offer 100% protection to an individual fish over a period of several years without taking the possibility of long distance movement into account, an area of ca. 40000 m^2 would have to be closed to fishing. To protect 95% of its utilised area, only a quarter of this zone has to be closed. This area could be further reduced to 3000 m^2 for most of the year outside the spawning season from March to November.

Is home range size a function of fish size? From the 6 fish with reliable home range estimates outside the spawning season, neither 50% kernels nor 95% kernels showed a correlation with fish size, although the dataset is too small for meaningful statistical testing. Mark and recapture studies on roman (Chapter III, Bullen and Mann 2004,

Griffiths and Wilke 2002) also found no relation between size and movement distance. Zeller (1997) found no relation between fish and home range-size for tracked Coral Trout. There seem to be positive correlations for *Thalassoma bifasciatum* (Tecumseh *et al.* 1990), Lemon sharks (Morrissey *et al.* 1993) and negative correlations for Saithe (Sarno *et al.* 1994).

Is the home range size a function of the availability of suitable habitat? Home range size might depend on the availability of resources inside the home range. Two scenarios are plausible: Either fish in sub-optimal habitat have larger home ranges or fish density decreases in sub-optimal areas. The results of this study supported the latter: Roman were found to be strongly reef associated, as 98% of all positions were recorded on rocky substrate. The home ranges of fish 1 and 4 had a similar extent although the area utilised by fish 4 was notably different and included patchy low relief reef with low rugosity, therefore effectively including fewer resources (food and shelter). Home ranges of the three fish tracked after the spawning season also had home ranges of similar size despite the patchy distribution of reef inside their home ranges.

Other authors described a significant influence of reef profile and rugosity on roman abundance (Buxton 1987, Götz 2005). Although the conclusions here are based on a small sample and the underwater description of the habitat is somewhat subjective, the results point towards a constant home range size and a habitat dependent variation in fish density. As sandy areas were traversed by fish during this study, these findings indicate the possibility of a 'spill over' of fish to other reef complexes outside the protected zone, as fish density inside the protected area increases.

Spawning related behaviour

Whereas fish 1 and 6, both large males, did not show changes in movement patterns during the spawning season, both ripe females exhibited a pattern significantly different from the males. The area utilised by these two fish was two to five times the area of fish at other times. Within this extended range, the fish commuted between several core areas, where they remained stationary for prolonged periods. While these observations are far from conclusive due to the small sample size and the failure to determine the sex of fish 8, it points towards gender-specific change in activity pattern during the spawning season. The female fish were observed engaging in behaviour related to courtship (Buxton 1987) at different core areas. Contrary to Buxton's reports on rushing and lateral display for fish of all sizes, observations of this behaviour during this study were limited to small fish (females), whereas large males in the vicinity remained inactive.

Roman are serial spawners. The observed pattern might be an evolutionary adaptation to increase mating and spawning success, where males remain site-attached and females compete to mate with different males over a wider reef area. This would result in a selective process for stronger females as they get to mate more often with different males. More observations are required to verify this hypothesis.

Activity patterns

Outside the spawning season, all the fish had a focal point within their home ranges that was disproportionately utilised, marked by the 50% kernel area. This pattern is commonly found in reef-associated fish (see Zeller 1997). From the manual tracking results and the underwater observations of fish 1, it becomes evident that the location of the focal point is associated with a shelter site. In the case of roman, the use of

shelters may be an adaptation to decrease predation. During a sudden drop in temperature due to upwelling, fish 1 remained inside or within 10 m of its shelter for three days. As poilikothermic animals, rapid temperature changes will affect the metabolism of the fish, as blood oxygen affinity, haemoglobin oxygen saturation and digestive enzymes often perform optimally in a narrow temperature range (Moyle and Cech 2000). This will result in the fish becoming lethargic (Smith and Heemstra 1986). Withdrawal into crevices might protect them from predators like Great White Sharks *Carcharodon carcharias* and Cape Fur Seals *Arctocephalus pusillus,* species that are not affected by temperature changes.

Roman seem to exhibit a diurnal activity pattern: The area utilised by fish 1 and 4 decreased during the manual tracking sessions over night and there was a significant decrease in swimming speed of fish 6. As pointed out in the results, the failure of the position recordings for fish 7,9 and 11 and the weak and irregular signals for fish 1 suggest, that the animals withdrew into their shelters at least for parts of the nocturnal period. Ebeling and Bray (1976) proposed, that temperate diurnal fish become inactive at night and seek shelter. Saithe *Pollachius virens* and Pollack *Pollachius pollachius* decrease their speed and range of movement at night (Sarno *et al.* 1994). Many invertebrate feeders are diurnal (Buxton 1987) but unlike in many tropical species, there is no sharp transition between day and night time activities, maybe due to the longer crepuscular period in temperate regions.

Are roman territorial? Any area that is defended against intruders is called a *territory.* (Nice, in Attwood 2002). An animal defends an area to sequester resources therein, which may be food, shelter, favourable nesting or spawning sites or a combination thereof (Wootton 1999). As all the home ranges of the fish tracked in this study

overlapped and fish of all sizes are frequently found within a small area during underwater assessments (pers. obs.; Götz 2005) it can be reasoned that roman are not territorial regarding their home range.

Anecdotal diver observations indicate that large roman are territorial regarding their shelter site (Lechanteur 1999, Penrith 1972). This finding could not be supported during this study. Several large males were frequently observed inside the cave inhabited by fish 1 and during the cold water period described above, two large fish were found side by side in the same crevice.

Territorial behaviour can change in relation to the presence of conspecifics and the availability of food (Dill, in Wootton 1999). In this study fish 4 showed aggression towards other roman during foraging. As fish 4 inhabited an area of low relief reef, the food availability might be limited hence the benefits from defending a food source might outweigh the costs. Territorial behaviour among roman has also been observed in tank experiments, where the availability of food was spatially limited (pers. obs.). No aggression was found when food supply was saturated (Chapter II). Similar results have been found for *Orysias latipes* (Magnuson 1962, in Wootton 1999).

Conclusions

Despite a number of logistical problems it can be concluded that telemetry is suitable to study temperate reef fish in a high-energy environment and similar experiments to the one described here could yield important information on a number of temperate marine fish species in South Africa and elsewhere.

The verification of the accuracy of the remote positioning could be improved by setting up more test transmitters in different directions from the triangle and by continuous logging of oceanic conditions affecting the system (wind, waves, temperature, turbidity etc.). However, deviation caused by the position of the fish on the reef is an unavoidable source of error. Using remote positioning in combination with manual tracking has several advantages: The accuracy of the remotely recorded positions can be validated and an area beyond the detection range of the system can be scanned for fish that are not recorded by the remote positioning system.

Whereas the transmitter implantation technique presented here worked well on the robust study species, it is important to examine the effects of the treatment in pilot experiments for every new species, as it might react differently to the treatment. Tracking the study fish underwater added value to this study, as the condition of the study animals were verified and important behavioural observations that helped to interpret the surface tracking and remote positioning data were made.

The findings of this study confirm what has been indicated by anecdotal observations and mark and recapture studies: Post-recruit roman are resident and hold small home ranges. This study was concerned with the home range behaviour of roman, however long distance movements occur infrequently and form a component of the life history of this species that needs to be considered in its management.

While mark and recapture studies merely provided an indication of the linear extent of fish movement, the use of telemetry made it possible for the first time to estimate the area utilised by individual adult roman. Accepting the 95% fixed kernel as the most reliable estimate, the size of this area is in the order of $1000 - 3000$ m^2, independent of habitat and fish size. However, female fish seem to extend their range during the spawning season. The observations of aggressive behaviour between females, possibly in competition to mate with different males, contradict the current theories of resource -and female defence polygyny (Buxton 1987). Larger sample sizes and more observational time underwater are necessary to achieve a better understanding of the mating system of roman.

The small extent of the area utilised by individual roman make this species a prime candidate for successful protection inside small MPAs. The extended movement of females during the spawning season has important implications for the management of roman with small MPAs as fish are likely to 'spill over' into fished areas. Spill over might also be a result of increased density inside the reserve. If one accepts the finding that home range size is constant for adult roman, an increased fish density would lead to increased home range relocation if the carrying capacity of the reserve were reached. Both effects would be beneficial to the fishery, but the extent of these benefits can be quantified only if these findings are incorporated in a model that simulates these effects for different MPAs under different levels of fishing pressure.

Chapter VI: An individual based model of roman, *Chrysoblephus laticeps,* populations around two marine protected areas.

Abstract

Individual based models (IBMs) are advantageous over population models as they account for the effect of differences in life histories of individual fish depending on their use of space. The effect of two MPAs on the South African temperate south coast on the population of *C. laticeps* was simulated with a spatially explicit IBM. Recently determined life history parameters including the effect of fishing on the size of sex change was taken into account. Fish densities and size frequencies were based on recent underwater visual census data. The distribution of suitable habitat in the study areas was incorporated. The results show a quick recovery of the fish size frequency and sex ratio to pre-exploitation levels inside both MPAs. The results suggest that for resident species like roman, even small MPAs offer sufficient protection. Little 'spillover' of fish into the fished areas resulted in negligible improvement of catches. The effect of these MPAs is the protection of a healthy spawning population that will improve recruitment by exporting larvae into fished areas rather than enhancing the catches through export of adult fish. Results show that the incorporation of behavioural data into spatially explicit individual based models can provide realistic simulations of MPA effects, thus providing a powerful tool to the management of commercially important fish species.

Introduction

The evaluation of marine protected areas (MPAs) for the purpose of fisheries management is the focus of a growing body of literature. There is general consensus that MPAs can offer protection to exploited marine fish and invertebrates (Gell and Roberts 2003). Most of the evidence is derived from comparative underwater visual assessment (UVC) or fishing surveys between fished and non-fished areas. In the face of the large variability of fish densities and fishing effort in space and time (Garcia-Charton and Perez-Ruzafa 1999, Guénette *et al.* 1998, Guidetti 2002), few studies (Götz 2005, Russ and Alcala 1989) can unequivocally attribute differences between fished and non-fished areas to protection. On the other hand, failure to prove differences in fish density or catch per unit effort (CPUE) between sampling stations within and immediately outside an MPA does not necessarily imply that the MPA is not functional. It might be simply the result of an exchange across the MPAs boundaries (Walters 2000).

On the level of the individual, the protection offered by an MPA is a function of the time the fish spends inside the MPA. As this depends on the space utilisation pattern of the species, a number of studies have attempted to assess protection offered by MPAs by determining movement patterns of adults through mark and recapture (Munro 2000, Russ *et al.* 2003) and telemetry (Zeller and Russ 1998) and thereby assessing the potential for 'spillover' or, from a conservation perspective, 'drainage' of the reserve. Whereas these studies are useful in assessing the potential of MPAs for protection (Attwood and Bennett 1994, Roberts and Polunin 1991, Zeller 1997), in terms of fisheries management, the reserve effect needs to be quantified, under different levels of fishing pressure and with different MPA sizes. Numerical population models that incorporate spatial components (e.g. Attwood and Bennett

1995, DeMartini and Edward. 1993, Guénette *et al.* 2000, Parrish 1999, Polacheck 1990, Sladek-Nowlis and Roberts 1999) have been used to predict reserve effectiveness under different management scenarios. However, these models suffer the same problems as general stock assessment models (Babcock *et al.* 1999, Murray *et al.* 1999). High degrees of uncertainty, generalisation, simplification, difficult parameterisation and untested assumptions can limit their predictive power and might lead to equivocal results, e.g. a comparison of Parrish (1999Parrish (1999) and Hastings and Botsford (1999Hastings and Botsford (1999). Murray *et al.* (1999) advocates greater attention to develop successful models. Models should reflect a realistic understanding of fish behaviour and biology to be useful for decision-making (Guénette *et al.* 1998). Model selection should be guided primarily by an understanding of the biology of the studied species (Lebreton *et al.* 1992).

As individual fish of the same cohort exhibit different biological and behavioural traits depending on their environment and their genes, using average values of parameters may result in bias and misrepresentation of population behaviour. Individual-based simulation models (IBMs) facilitate a more realistic simulation of population behaviour by accounting for variability with respect to gender, age, life history strategies, habitat food availability and mortality (*inter alia* Alonzo and Mangel 2004, Barot *et al.* 2004, Bertolo *et al.* 2004). Rapid increases in computing power have made IBMs a viable tool in ecology, and they have become widespread in the analysis of fish populations in marine ecosystems (Megrey *et al.* 2002). In the context of MPA evaluation, IBMs have been used successfully to simulate the protective effect of MPAs (Attwood 2002).

This study presents the application of an individual based model to test the effect of MPA protection on roman, *Chrysoblephus laticeps* (Sparidae). Roman is among the ten most important species of the traditional hand-line fishery in South Africa, however the stock has been in decline since the beginning of the 20th century and is now regarded as collapsed (Griffiths 2000). The model simulates post-recruitment survival of roman inside and immediately outside two MPA's, Goukamma and Castle Rock, a medium sized (42 km^2) and a small (6 km^2) MPA on the South African temperate South Coast. The model explores the impact of different rates of fishing pressure on the catch rate, size distribution and sex ratio, taking into consideration the unique life history and behavioural patterns of this species such as density-dependent sex change and gender-dependent area utilisation. The distribution of suitable habitat in the study area and the observed fish density and size distribution are incorporated in the model to provide realistic predictions of the impact of spatial management strategies on roman.

Material and Methods

Study species

The biology and ecology of roman is well studied Buxton 1984, Buxton 1987, Buxton 1989, Buxton 1993, Penrith 1972). Recent studies on this species investigated density, age and growth, size composition, fisheries parameters, habitat selection and movement behaviour (Götz 2005, Chapter III,V). Roman are protogynous hermaphrodites found on temperate reefs from Cape Point to Port Edward (Smith and Heemstra 1986). Mark and recapture experiments show a high degree of residency of adult fish with only a small proportion of recaptures further than 100 m from the tagging location (Chapter III). Telemetry experiments indicate that adult roman typically utilise a confined home range over extended periods (Chapter V). However, there is evidence that female fish increase their home range during the spawning season in summer and utilize different locations on the reef, possibly to mate with different males. (Chapter V). It also has been demonstrated that fishing alters the age of sexual maturity and sex change of this species (Götz 2005).

Model description

Model scope

The IBM preserves the habitat distribution of the study area and is geographically correct with respect to MPA boundaries. The model was applied separately to the Goukamma MPA and Castle Rock MPA. Parameters values and origin are described in Table VI-I. The model domains were rectangular, representing areas that were topographically surveyed during the field studies (Chapter III, IV) according to the

methodology described by Götz (2005) for the Goukamma area. These domains included the MPAs and adjacent fishing areas (Figure VI-1 and Figure VI-2)).

Table VI-I: Description of parameters used in the model.

Parameter	Baseline value	Description and source
sp	0.33 y	Length of spawning season. Baseline value chosen from Buxton (1987)
l_{qt}	330 mm	Length of 50% sex change for 'pristine' population (Götz 2005)
δ	9.23	Steepness of sex change curve (Götz 2005)
l_{rec}	200 mm	Length at first capture. Value chosen from the data attained on a sampling trip with the RV Sardinops off Goukamma (see Chapter III)
a	2.0 E -05	Intercept of length-weight relationship (Götz 2005)
b	3.07	Slope of length-weight relationship (Götz 2005)
T_{max}	19 y	Maximum age (Götz 2005)
N	346 fish per cell	Determined during underwater visual census (Kerwath, Götz, unpublished data)
p	0.09	Probability of fish leaving its home cell. (Chapter III)
D_{max}	40 cells	Maximum movement distance (Chapter III)
A	25 cells	Measure for expanded home range of females during spawning season. (Chapter IV)
M	0.24 y^{-1}	Natural mortality based on underwater visual census (Götz 2005)
F	0.2 y^{-1} 0.16 y^{-1}	Instantaneous fishing mortality. First value was estimated for the Castle Rock area, from Lechanteur (1999) and Marine and Coastal Management unpublished data. The second value for Goukamma area was taken from Götz (2005)

<u>Model resolution</u>

The domains were divided into 100 m × 100 m cells. These cells were given properties that denote habitat (land, sand, rock) and position (x, y) and status (reserve/ fishing area).
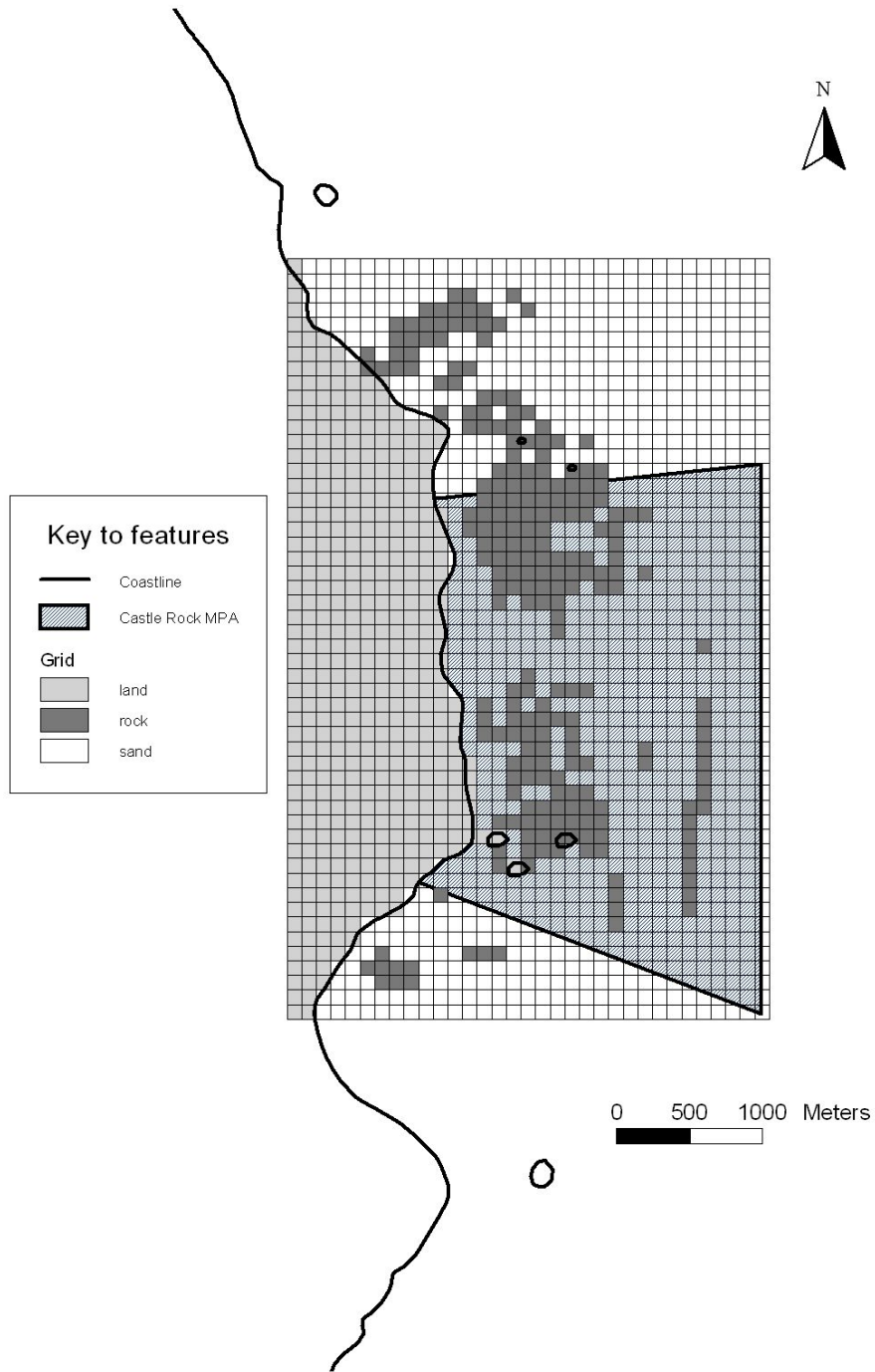
Figure VI-1: Map of the Castle Rock MPA domain. The modelled domain contained 237 suitable cells in total, of which 155 (65%) fell within the MPA boundaries.
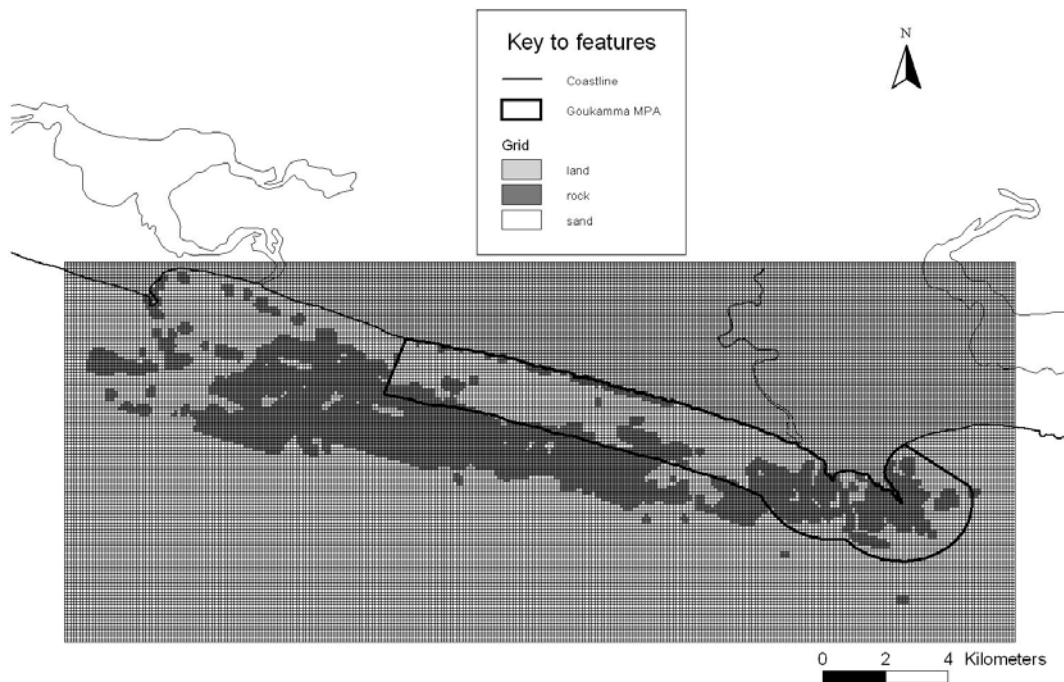
Figure VI-2: Map of the Goukamma MPA domain. The modelled domain contained 5533 suitable cells in total, of which 1612 (29%) fell within the MPA boundaries.

Initialisation of the model

Estimates of roman density and length frequency distribution were derived from underwater point counts (Götz 2005). Fish were randomly assigned to the cells with suitable habitat (rock). Each 100 m × 100 m cell initially received equal numbers of fish according to the observed mean fish density. The fish were then assigned to 50 mm length classes starting from the 101 mm – 150 mm class according to the observed length frequency distribution. Each fish was randomly allocated an exact length within its class. The sex of each fish was derived from its length. Parameters

determined by Götz (2005) were used to determine the probability for a fish of length l, being either female or male.

$$P_l = (1 + e^{-(l-l_{50}/\delta)})^{-1}$$

Equation VI-1

P_l is the probability of a fish being male at length l, l_{50} is the length at 50% sex change and δ is the rate with which sex change is attained. Age -at -maturity was not considered in the model. All fish were initially female. Initial age of each fish was derived from an age -length key (Appendix, after Götz 2005).

Running the model

Once initialised, the simulation progressed in one-year intervals. The probability of each fish surviving the year was calculated on the basis of its mortality risk. Surviving fish advanced to the next age class. Their new length was determined from the age-length data derived from Götz (2005). It was calculated by randomly assigning a value within two standard deviations of the mean length using a gauss normal random algorithm (Press *et al.* 1986). The probability of fish changing sex was calculated based on their individual length as well as on the sex ratio in the cell. Surviving fish could leave their home cell with a fixed probability at the end of each year and relocate to other cells with suitable habitat within their maximum movement distance. The procedures for updating sex, position and probability of survival are described separately below.

Mortality

Mortality rate in cells within the reserve was set to the instantaneous natural mortality rate *M*. This rate was determined by transforming the length frequency distributions from underwater counts to age frequency distributions according to the age -length

key (Butterworth *et al.* 1989). The slope of a straight line fitted to points on the descending limb provides an estimate of *M*. For the cells in fishing areas, an instantaneous fishing mortality rate *F* was added. The mortality risk of male fish was dependent only on the status (MPA, fished area) of its home- cell. After each simulation year *t* the probability of survival of male fish Pm_t was calculated as

$$Pm_t = e^{-M}$$

Equation VI-2

in MPA cells and

$$Pm_t = e^{-M-F_t}$$
Equation VI-3

in cells in the fished area, where *M* is the natural mortality rate, *F* is the fishing mortality rate in the simulation year *t*.

The increased home range of females during the spawning season was simulated in the following manner: The linear displacement of females during the spawning season was measured as 200 m from the centre of the range (Chapter V). Therefore an area

$$A_{sp} = (2 \cdot 200m + 100m)^2$$
Equation VI-4

was chosen to represent the area covered by females at this time. This area equated to 25 cells. This cell is referred to as spawning area and is referenced by the home cell *q* in its centre.

The ratio of suitable cells that are fished to the total number of suitable cells was determined for all spawning areas around each cell in the domain and incorporated into the stochastic determination of female survival. For female fish, the probability

Pf_{tq} of surviving the simulation year t in the home cell q depended on the ratio r_q of suitable fished cells to suitable cells in the spawning area around the home cell q. Pf_{tq} was calculated as

$$Pf_{tq} = e^{-M - (F \cdot sp \cdot r_q)}$$ **Equation VI-5**

if q was in an MPA, and

$$Pf_{tq} = e^{-M - (F \cdot sp \cdot r_q) - (F \cdot (1-sp))}$$ **Equation VI-6**

if q was in a fished area, where M is the natural mortality rate, F the fishing mortality rate, t the simulation year, r_q the cell specific fishing ratio during the spawning season and sp proportion of the year occupied by the spawning season.

Sex change

The probability that a female fish of length l in cell q will change sex at the end of simulation year t was given by

$$P_{lqt} = (1 + e^{-(l - lqt_{50} / \delta)})^{-1},$$ **Equation VI-7**

where δ is the rate of sex change and lqt_{50} the length of 50% sex change in cell q at the end of simulation year t. The term δ depended on the ratio of male to female fish in the cell at the end of the simulation year and was given by the linear relationship

$$lqt_{50} = -2.06 \cdot \frac{Nf_{qt}}{Nm_{qt}} - 346.8,$$ **Equation VI-8**

where Nf_{qt} is the number of females in cell q after simulation year t and Nm_{qt} is the number of males, respectively. This relationship was determined by using data from a biological assessment of the roman population in the Goukamma area (Götz 2005). The sex ratio inside the core area of the Goukamma MPA and the corresponding length of 50% sex change were considered as the set of values for a pristine population. The sex ratio and the length of 50% sex change observed in the fishing area provided a second set of values. The linear relationship in equation VI-8 was then derived from the two sets of values. A threshold value for lqt_{50} was introduced to avoid an unrealistic shift of lqt_{50} towards immature size classes. The chosen value of 260 mm FL corresponds with the size of the smallest hermaphrodite found in the Goukamma sample (Götz unpublished data).

Movement

The probability p of fish emigrating from their home cells was estimated for the Goukamma area (Chapter III). Fish that left their home cell could, in accordance with the model of roman dispersal (Chapter III), settle in any suitable cell within the maximum movement distance. In the simulation, distance and direction of movement were determined stochastically. Distance D was determined as a random number within the maximum movement distance of 40 cells (4 km). Direction was determined as a random angle γ. The new destination cell coordinates (x, y) were then calculated with

$$x = D \cdot \cos \gamma \qquad\qquad\qquad \textbf{Equation VI-9}$$

and

$$y = D \cdot \sin \gamma \text{ ,} \qquad\qquad\qquad \textbf{Equation VI-10}$$

respectively by rounding to integer value. If the destination cell coordinates exceeded the boundaries of the domain, fish were noted as emigrated. As one would assume that the population outside the domain is fished, emigrants were replaced in their original home cell with fish identical to the population in the fished area to simulate immigration from outside the domain. This was done to preclude a closed or reflective boundary effect that would bias the results when the MPA area was big in relation to the total domain.

If the destination cell fell within the domain, the fish was randomly assigned to a suitable cell within the rectangular area determined by the original home cell and the destination cell. If no suitable habitat existed in this area, a new destination cell was stochastically determined and the procedure was repeated.

Recruitment

Recruitment into the model was constant, as the processes that influence recruitment are beyond the limited geographical scope of the modelled domains. The recruitment level was set to replace the number of fish that died naturally in MPA cells before fishing started. Fish were recruited into the model at age two; their size frequency distribution was determined according to an age-length key (Götz 2005). Recruitment took place at the end of each simulation year. Recruited fish were assigned randomly to cells with suitable habitat.

Recruitment into the fishery was assumed to be knife-edged. The value for fish in the model to enter the fishery was set to 200 mm, the smallest fish size caught during experimental angling, assuming that all fish that were captured died.

Catch

The weight W (g) of the individual fish were calculated from their length l (mm) *as:*

$$W = a(l)^b$$
Equation VI-11

where a and b are the parameters of the length-weight relationship determined for the Goukamma area (Götz 2005). Catch was calculated from the sum of the weight of captured fish per year and expressed as an average value per cell per year to allow comparison between fishing areas with differing sizes before and after MPA implementation.

Fecundity

Ovary mass was calculated as an index for fecundity. The mass was determined according to a linear relationship between body length and ovary mass from a sample of 46 female roman with stage IV gonads (pre-spawning, staged after Griffiths 1997),

$$W_o = 0.0108 \cdot W + 1.9045$$
Equation VI-12

where W_o is the gonad weight in grams and W is the fish weight in grams ($R^2 = 0.61$).

Similar to the catch, the fecundity index was expressed as average ovary mass per cell per year to allow comparison of MPA and outside areas.

Model output

The program produced primary output in tabular format: Three tables revealed the progression of size frequencies of fish in the MPA cells, the fishing cells and the catch, respectively. A summary table showed the progression of fish numbers split into males and females, the sex ratio, the average catch-weight per cell, the average fecundity per cell for the MPA and the fished areas, and movement and immigration from the MPA and fished areas. A graphical output was available in the form of an GIS plot that depicted the fish density per suitable cell (Figure VI-3-Figure VI-8). Initial analysis revealed that a stable output is typically achieved within one modelled fish generation (18 years, as the fish are entered at age 2). A simulation run was therefore set to a period of 54 years. For the first 18 simulation years fishing mortality was set to zero to allow the simulation to stabilize. In years 19-36 the entire domain was fished with the fishing mortality rate chosen for the respective area (Table VI-I). The MPA was implemented in years 37-54 assuming a constant F for the fished areas, set at the same value prior to the MPA implementation.

Results

The usefulness of individual-based simulation models is often negated by the difficulty in digesting and analysing their voluminous and complicated output (Megrey *et al.* 2002). To overcome this, the results of the simulation in the present study were summarised to address three key issues in assessing the impact of MPAs:

1. Status of the adult fish population in comparison to pre-MPA levels, status of the adult fish population in the closed area in comparison to the adjacent fished area after the MPA implementation, and the exchange of fish between the MPA and the fished area ('spillover').

2. Consequences of MPA protection for the reproductive capacity of the stock and the potential role of MPAs in seeding adjacent areas.

3. Consequences of MPA protection for the fishery, typically in form of effort displacement as a result of area closure and potential catch enhancement in the fishing area.

To compare the status of the adult fish population in the closed area to pre-exploitation levels, male and female fish density per cell was plotted in Arcview 3.2 for the year 18 (pre-exploitation), year 36 (last year of exploitation of MPA area) and 54 (protected). To show recovery, size frequency distribution in the MPA and the adjacent area were plotted for the years 18, 36 and 54. 'Spillover' was expressed in form of immigration from the domain and net exchange between the MPA and the adjacent fishing area. Fecundity was expressed as a combination of sex ratio and ovary mass per cell. Both values were plotted for the years 18 to 54. Catch was expressed as average catch per cell and plotted as a fraction of the

initial catch for the years 19 (first year of exploitation) to 54. The relative catch-at-

size frequencies were plotted for the years 19, 36 and 54.

Figure VI-3: GIS plot of total fish density per cell in a section of the Goukamma area. (a) before exploitation (b) after 18 years of exploitation without the MPA (c) after a further 18 years of exploitation with the MPA.

173
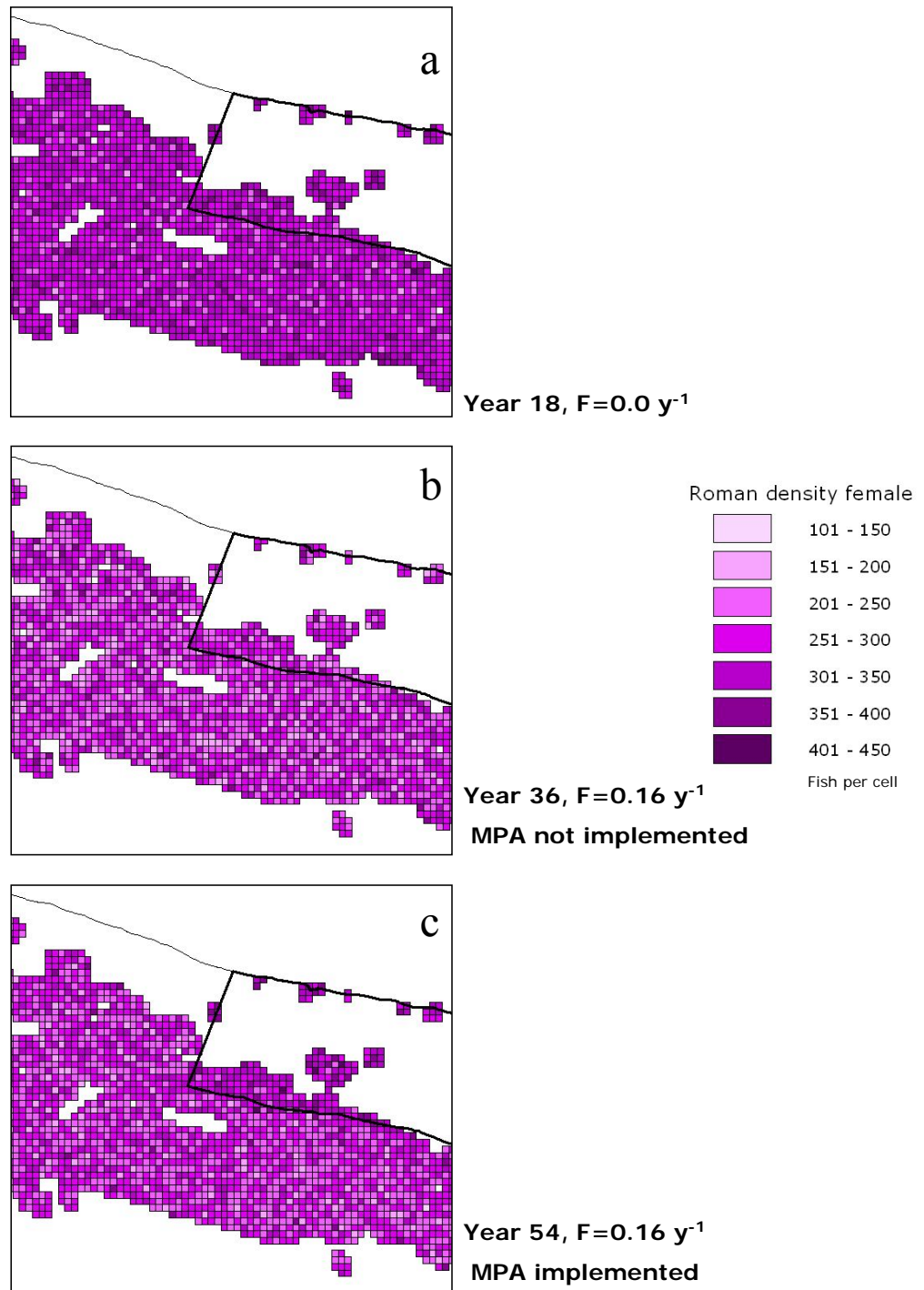
Figure VI-4: GIS plot of female fish density per cell in a section of the Goukamma area. (a) before exploitation (b) after 18 years of exploitation without the MPA (c) after a further 18 years of exploitation with the MPA.

174
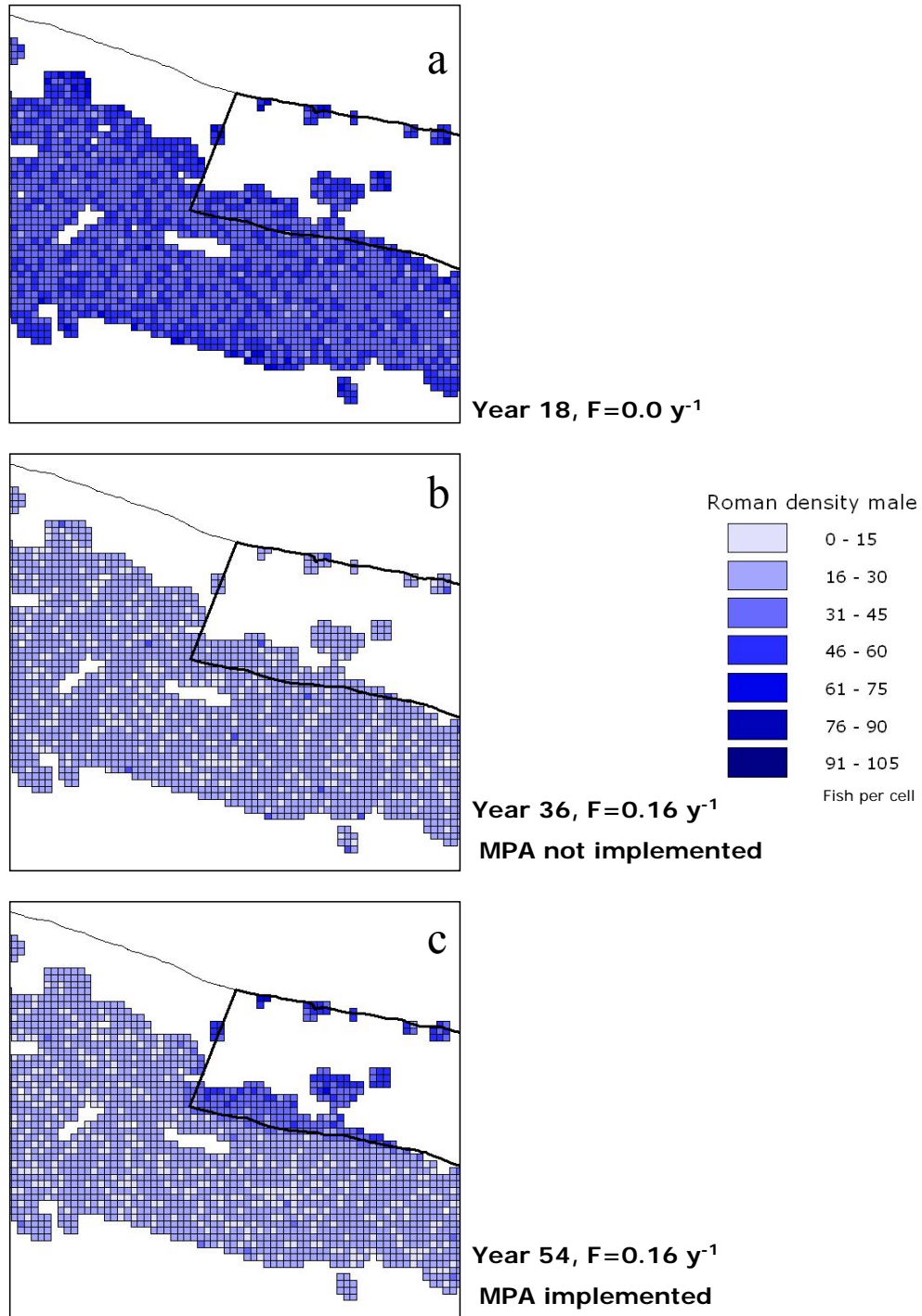
Figure VI-5: GIS plot of male fish density per cell in a section of the Goukamma area. (a) before exploitation (b) after 18 years of exploitation without the MPA (c) after a further 18 years of exploitation with the MPA.

Year 18, F=0.0 y^{-1}

Year 36, F=0.20 y^{-1}

MPA not implemented

Year 54, F=0.20 y^{-1}

MPA implemented

Roman density total

	101 - 150
	151 - 200
	201 - 250
	251 - 300
	301 - 350
	351 - 400
	401 - 450
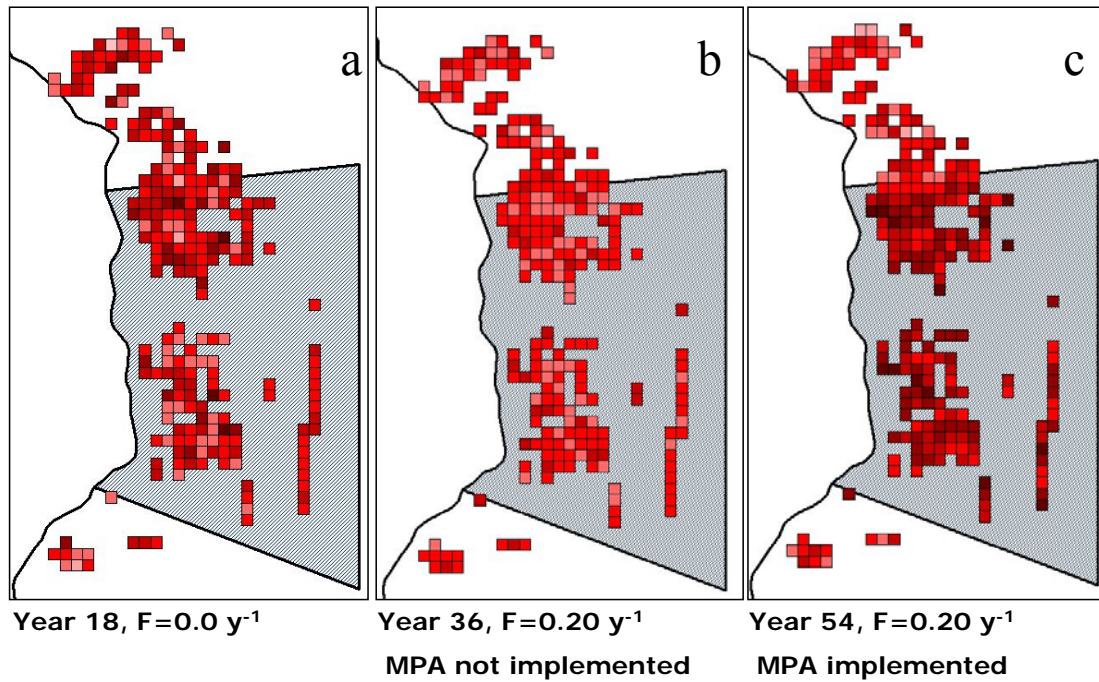
Fish per cell

Figure VI-6: GIS plot of total fish density per cell in the Castle Rock area.

(a) before exploitation (b) after 18 years of exploitation without the MPA

(c) after a further 18 years of exploitation with the MPA.
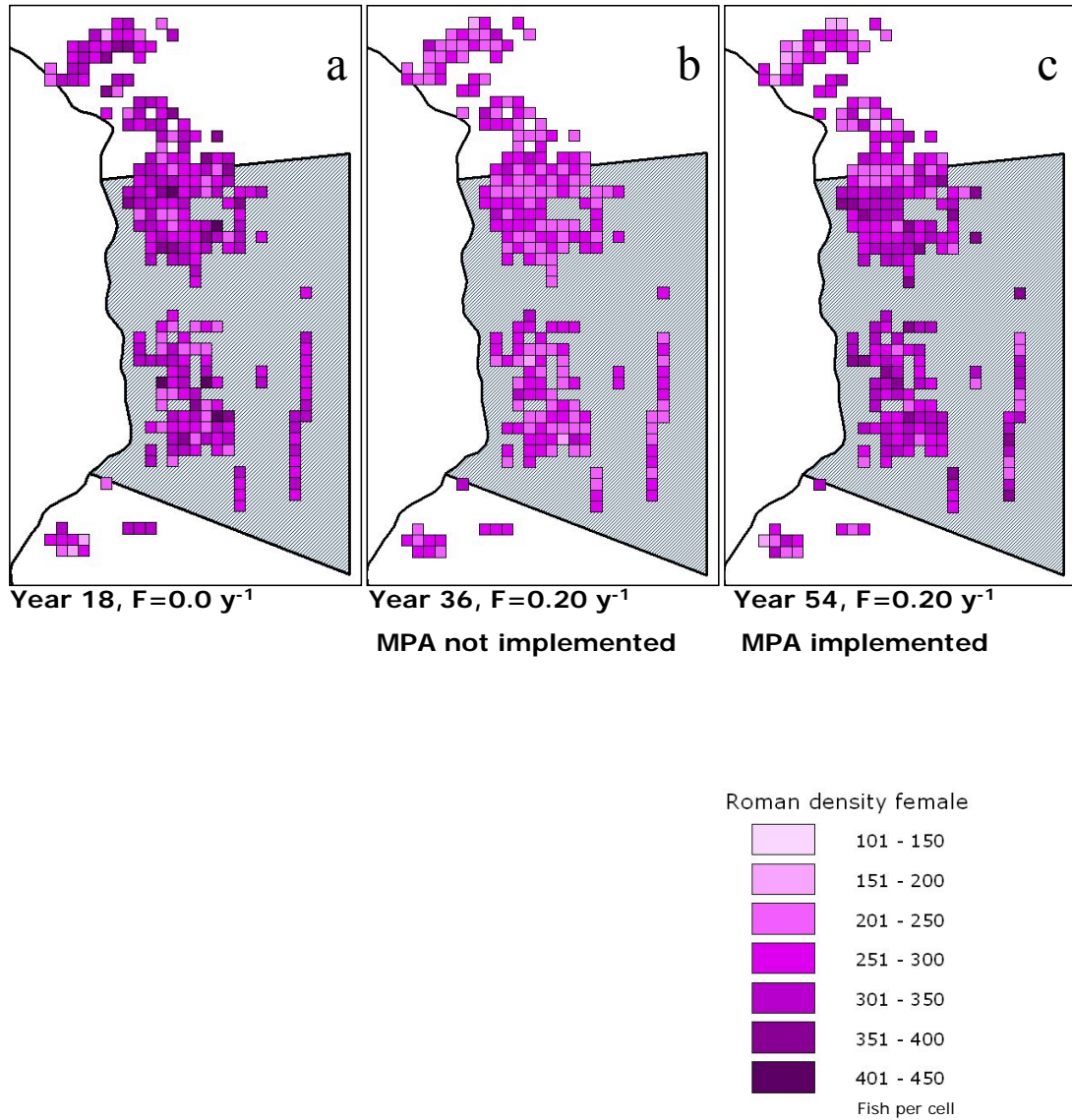
Figure VI-7: GIS plot of female fish density per cell in the Castle Rock area. (a) before exploitation (b) after 18 years of exploitation without the MPA (c) after a further 18 years of exploitation with the MPA.

Year 18, F=0.0 y⁻¹

Year 36, F=0.20 y⁻¹

MPA not implemented

Year 54, F=0.20 y⁻¹

MPA implemented

Roman density male

	0 - 15
	16 - 30
	31 - 45
	46 - 60
	61 - 75
	76 - 90
	91 - 105
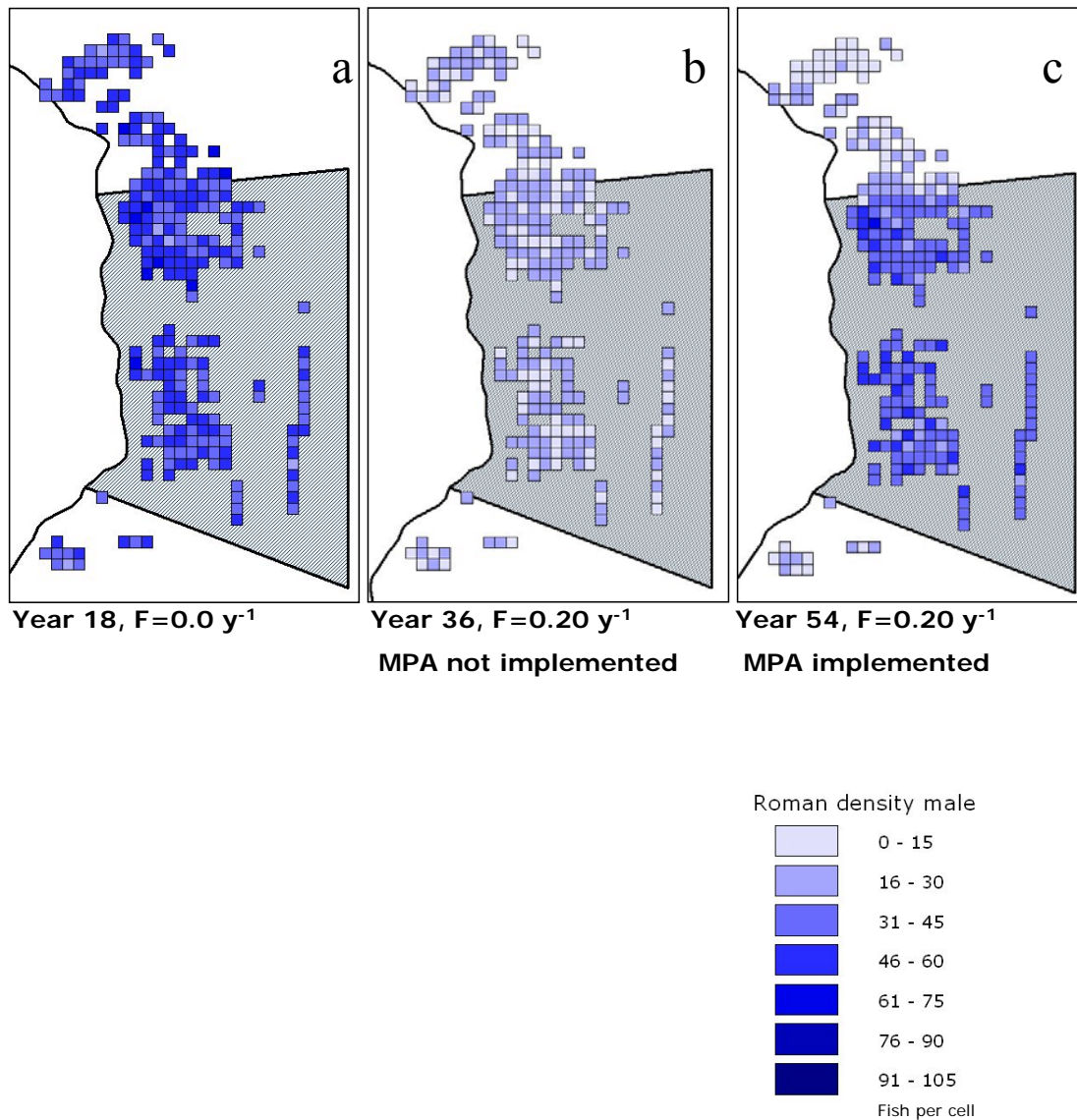
Fish per cell

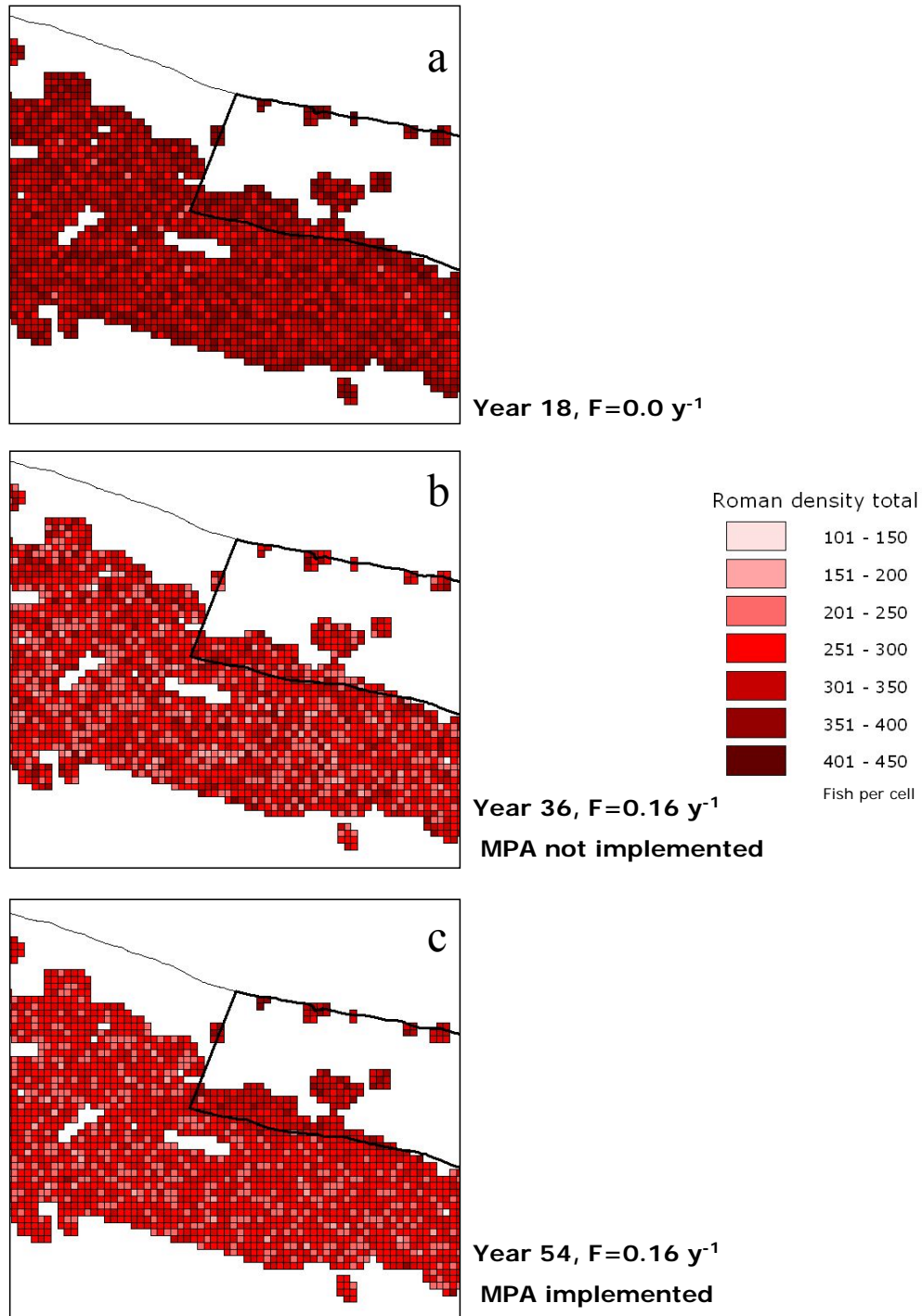**Figure VI-8: GIS plot of male fish density per cell in the Castle Rock area.**

(a) before exploitation (b) after 18 years of exploitation without the MPA

(c) after a further 18 years of exploitation with the MPA.

Goukamma   Castle Rock
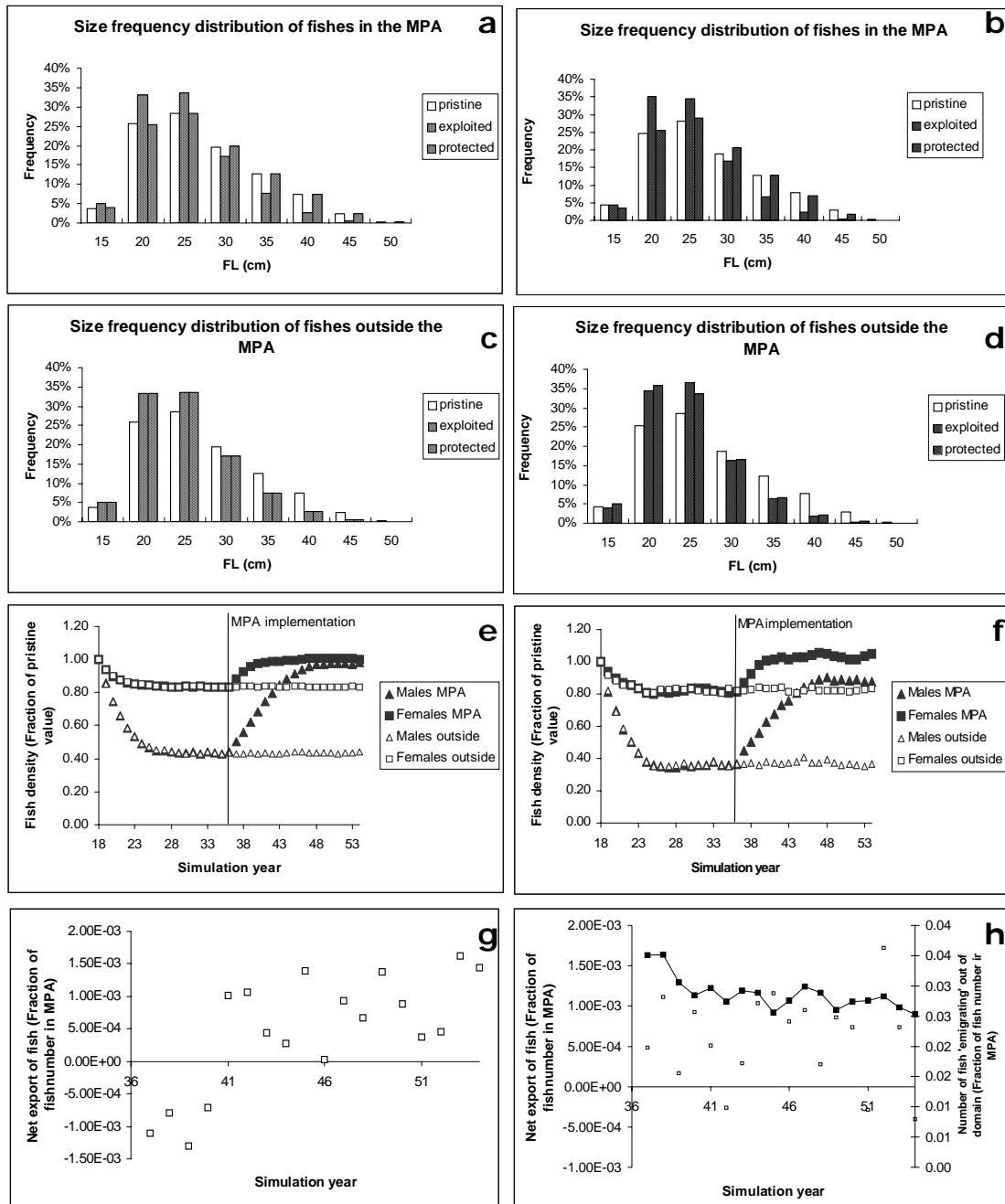
Figure VI-9: Fish population dynamics in the two MPAs and their adjacent areas. Changes in size frequency distribution for the years 18(pristine), 36(exploited) and 54 (18 years after the MPA implementation) (a-d). Progression of male and female fish density (e, f). Net relative export of fish by number in the Goukamma area (g) and net export- and emigration rate (line) in the Castle rock area (h). Emigration from the Goukamma domain was negligible.

Goukamma

Castle Rock
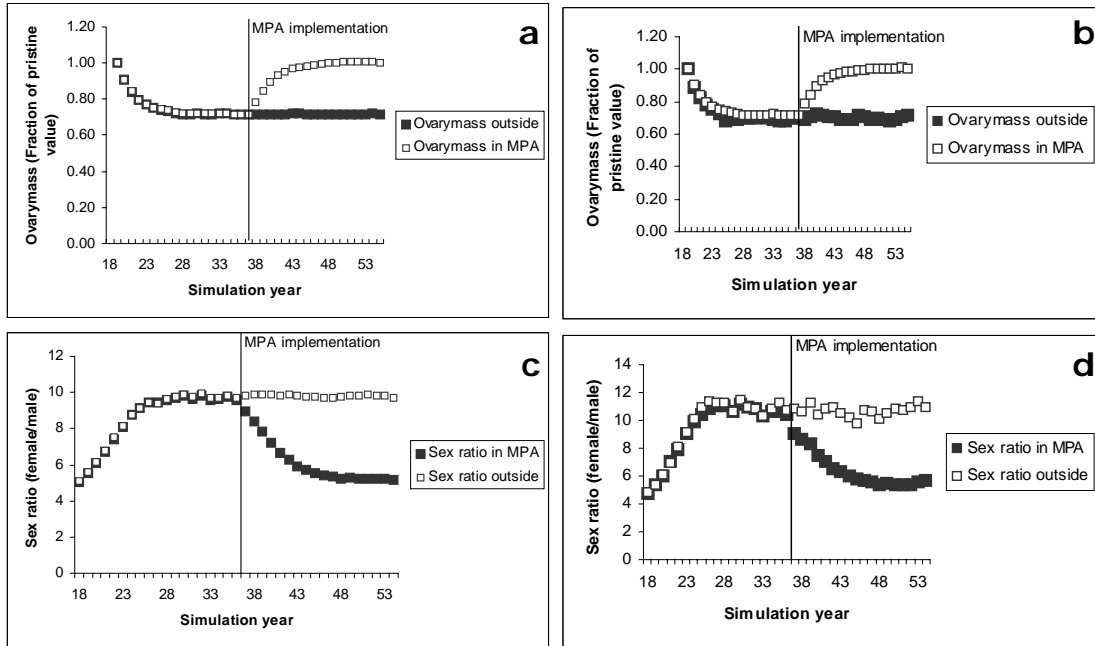
Figure VI-10: Progression of ovary mass (a, b) and sex ratio (c, d) for the Goukamma and Castle rock MPAs.

Goukamma

Castle Rock
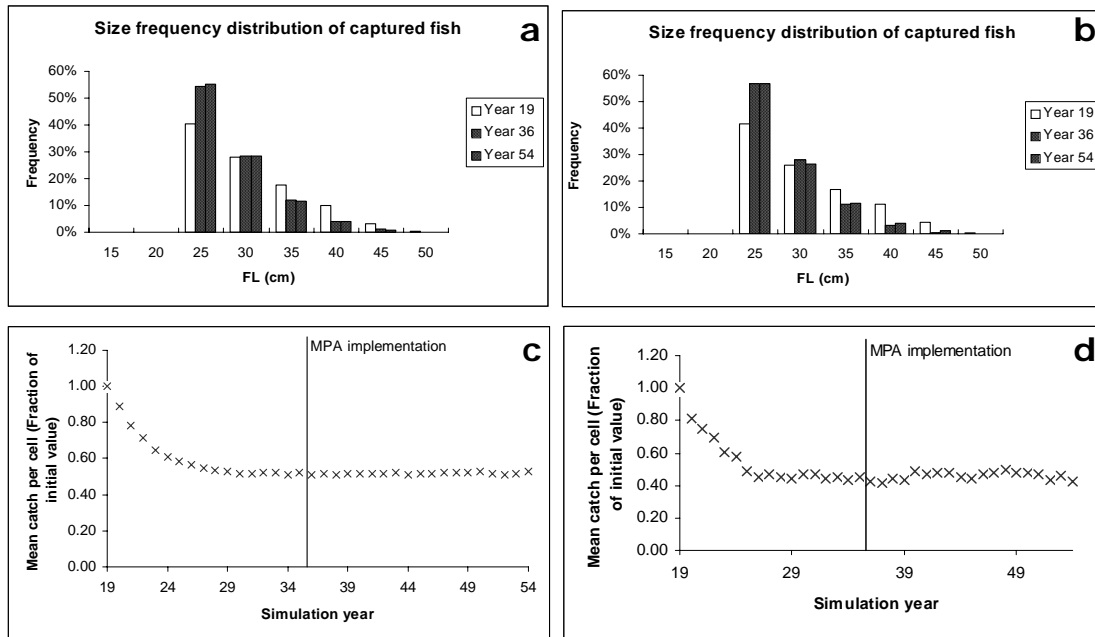
Figure VI-11: Progression of size frequency distribution (a, b) and mean catch per cell (c, d) in the fishing areas adjacent to Goukamma and Castle Rock MPA.

Effect on adult fish population

In both areas the onset of fishing resulted in a rapid decline of the adult fish population. After 8 years the decline had stabilised, characterized by a shift towards smaller fish (Figure VI-9 a, b) and a disproportionate decline of male density (Figure VI-9 e, f). This decline was more pronounced in the Castle Rock domain: Male fish density declined to levels under 34% of their original value, whereas in Goukamma, the value remained above 45%. After MPA implementation, fish densities and size frequency increased rapidly in both MPA areas. Female fish density reached a pristine value within 5 years of the MPA implementation. The density of male fish recovered more slowly, with the male population inside the Goukamma MPA regaining pristine status

by the end of the simulation period. For the Castle Rock MPA, recovery stagnated after 10 years at 90% of pristine values. (Figure VI-9 e, f). The fish density plots (Figure VI-3-Figure VI-8) reveal a sharp transition between the MPA and the adjacent areas. This was more pronounced for the Goukamma area. While the transition between high and low densities falls onto the MPA boundary for male fish in both domains, there appeared to be a narrow area of low female densities along the inside of the northern border of the Castle Rock MPA (Figure VI-7).

Although net export of fish from the MPAs to the adjacent areas within the domain increased in the Goukamma area towards the end of the simulation, the numbers were negligible in both cases (Figure VI-9 g, h). Exchange between the MPA and the area 'outside' the domain (immigration) was negligible in the case of Goukamma, but amounted to a maximum of 4% of protected fish in the Castle Rock MPA (Figure VI-9 h).

Fecundity and sex ratio

For both areas ovary mass per cell declined rapidly and remained at values around 72% until the onset of protection. With MPA implementation the ovary mass recovered to its pristine level after 10 years within the MPAs, but remained at exploited levels in the adjacent areas (Figure VI-10 a,b).

After the start of exploitation sex-ratios shifted rapidly towards females and peaked just under 10:1 in Goukamma and over 11:1 in Castle Rock. Whereas the ratio returned to pristine value inside the Goukamma MPA by the end of the simulation period, the pristine value of 4.8:1 was not reached inside the Castle Rock MPA (Figure VI-10 d). Sex ratios outside the MPAs showed no sign of recovery after MPA implementation.

Catch

The average catch per cell declined steadily for seven years after the onset of fishing and stabilised at values of approximately 52% and 45% of the first year of catch for Goukamma and Castle Rock, respectively (Figure VI-11 c,d). Whereas this value did not change in Goukamma after the area closure, catches experienced a slight improvement of around 1% in the areas adjacent to Castle Rock. Mean differences between the exploited (plateau) values and the values after both MPA implementations approached statistical significance at the 95% confidence interval (paired t-test, p= 0.07). This improvement was also evident in the size frequency distribution of the catch (Figure VI-11 b), which shifted slightly towards larger size classes.

Sensitivity

Because the model includes a number of stochastic elements, ten simulations were run on the Castle Rock domain with equal parameter values to test for variation. The variation around the key output values (number of fish per size class and per sex, catch) was less than 1% and therefore negligible.

The Castle Rock domain was also used to test the influence of the input parameters fishing mortality, movement rate and density-dependent sex change. In the sensitivity analysis, the values of these parameters were set to baseline values, values at the 95% confidence limits and values exceeding the boundaries of certainty.

Higher rates of fishing mortality alone did not change the fish density inside the MPA, however, the density in the adjacent area declined significantly. Although higher movement rates somewhat balanced the two areas they did not profoundly affect the general trend (Table VI-II).

Higher fishing rates exacerbated the shift towards female fish and prevented the MPA area from recovering to pristine sex-ratio values. Higher movement rates had a balancing effect with higher female – male sex ratios inside the MPA. Interestingly fixing the length of 50% sex change led to unrealistic sex-ratio values in the outside area for F=0.7 (Table VI-III).

Table VI-II: Sensitivity to varying levels of fishing mortality F and movement rate p. Predicted fish density in the MPA and the adjacent fishing areas (simulation year 54), expressed as a fraction of the pristine value. Results are presented for year 54.

Fish movement rate	F=0.2 y^{-1}		F=0.4 y^{-1}		F=0.7 y^{-1}	
	MPA	Outside	MPA	Outside	MPA	Outside
p=0.09	1.02	0.75	1.01	0.62	0.99	0.56
p=0.23	0.99	0.74				
p=0.49	0.97	0.78			0.95	0.60

Table VI-III: Sensitivity of sex-ratio (female to male) to varying rates of fishing mortality F and movement rates p (simulation year 54) with both density dependent- and fixed length of 50% sex change l_q. Results presented for year 54.

Sex ratio (female:male)	F=0.2 y^{-1}		F=0.7 y^{-1}	
	MPA	Outside	MPA	Outside
p=0.09	5.7	10.9	6.1	17.7
p=0.09, fixed l_q	5.4	14.8	6.4	102.2
p=0.49	7.3	10	9.2	16.6
p=0.49,fixed l_q	8.4	14.4	14.2	61.1

Discussion

The use of MPAs in fisheries management necessitates an understanding of habitat requirements, life history, fish movement and fish behaviour (Guénette *et al.* 1998). The study presented aimed to incorporate these factors in a realistic manner, using a comprehensive dataset from recent field studies in an individual based model. Incorporating a realistic habitat distribution and a realistic home range and movement pattern dependent on the life history of the individual fish profoundly affected the outcome of the modelling exercise. Contradicting earlier findings (Griffiths and Wilke 2002), the results demonstrate that even small MPAs such as Castle Rock have the potential to rebuild a healthy spawning population of roman inside their borders, with fish densities, fish size structures and sex ratios close to pre-exploited levels.

Although crucial for a realistic simulation, very few models incorporate the distribution of suitable habitat (Attwood 2002, Guénette *et al.* 1998), mostly because the required data are seldom available. For this study, the resolution of (100 x 100) m^2 cells was chosen to represent the smallest scale of roman movement, corresponding with the findings from mark and recapture and telemetry studies (Chapters II and IV). The importance of the incorporation of a realistic habitat distribution becomes clear when the Goukamma MPA domain is considered (Figure VI-2). Only 40% of the MPA area comprises of suitable reef. Reef areas are concentrated in the eastern part of the reserve, whereas in the fishing area the biggest reef complex is adjacent to the western part of the reserve. This habitat distribution pattern is detrimental to the exchange of adult fish across the reserve boundaries and might be a reason for the little 'spillover' observed in the simulation (Figure VI-9).

186

Exchange of fish between a MPA and an adjacent area is a function of both habitat distribution and fish movement behaviour. For this study fish movement was simulated in two ways: Firstly, a size- and sex-independent component which allowed for relocation to another home range; and secondly a sex-dependent component which allowed for an increased home range of female fish during the spawning season. Because of the limited area utilised by this species (a maximum movement distance of 4 km and a home range increase to 500 m linear extent for females), these movements are unlikely to have an effect on roman populations protected in large MPAs like the Tsitsikamma National Park (alongshore extent 75 km). However, particularly for small MPAs like Castle Rock, these movements are crucial because they will result in a considerable exchange of individuals between the MPA and the fished area, which might drain the MPA if the fishing mortality adjacent to the MPA is high.

Incorporation of density-dependent sex change has not been attempted previously. Götz (2005) found a significant difference of size at 50% sex change between samples from the MPA and from the adjacent fishing area that could be directly attributed to exploitation, as other factors were eliminated using General(ised) Linear Modelling. This substantiates the earlier findings of Buxton (1987Buxton (1987). Nothing is known about the underlying mechanism for the shift in length of sex change in roman. The little work that has been conducted on other reef fish species that live in social groups (Ross 1990) suggests a socially controlled mechanism, where females change sex after the assessment of their social environment (i.e. sex-ratio, size ratio-threshold Lutnesky 1989, Ross 1990, Ross *et al.* 1990). Possible mechanisms include those that rely on visual and chemical stimuli to suppress sex change, as postulated by Lutnesky (1989Lutnesky (1989).

In this simulation, sex change of the individual fish was a function of both its size and of the sex ratio in its resident cell. This pattern was chosen to simulate a biologically plausible mechanism, effectively creating a linear relationship between the sex ratio in a cell and the size at sex change of the female fish in that cell, until the threshold level is reached. Although an attempt was made to calibrate the model by using the Goukamma data (Götz 2005), a direct comparison of the model result with the real values was impossible because juvenile fish were lumped with females in the simulation and a shift in the size at 50% maturity (Götz 2005) was not considered.

Ignoring the timing of sex change can lead to inaccurate and unrealistic results. This became clear in the sensitivity analysis (Table VI-III) where high fishing rates led to unrealistic sex-ratio values, synonymous with population collapse due to sperm limitation (Alonzo and Mangel 2004). Therefore, although direct comparison with real datasets are not possible, the compensatory effect of the decreased size of sex change, as seen in the model results, does reflect empirical findings (Buxton 1987, Götz 2005).

Effect of MPAs on the adult fish population structure

Typically, theoretical studies of MPA effects predict a larger population inside the MPA boundaries with an increased longevity of individuals and a shift to larger size classes (Bohnsack 1996). This prediction is increasingly supported by empirical evidence, although in many cases the quality of the research and the validity of the results are vigorously debated (Gell and Roberts 2003). The results from this study match this prediction. In both simulations, the population inside the MPA increased rapidly, with a shift to larger size classes. Interestingly, this also held true for the much smaller Castle Rock MPA. Contrary to the conclusions from a mark and

recapture programme in the Agulhas area (Griffiths and Wilke 2002), discussed in Chapter III), a reserve as small as Castle Rock appears to offer sufficient protection to allow the recovery of a roman population within its boundaries. Moreover, its small size in relation to the maximum movement distance of roman that relocate their home range resulted in a measurable amount of adult 'spill over'. Although home range relocation is the main factor responsible for this phenomenon, the area of decreased female density along the northern boundary of the MPA indicates that the increased female home range during the spawning season also plays a contributing role. The spill over rate in similar sized MPAs can therefore be expected to be higher where more suitable habitat exists across its boundaries.

An encouraging result is the speed of the recovery of the population inside the MPAs. Similar rates of recovery were found in empirical studies for many resident fish and invertebrate species (Russ and Alcala 1996, Roberts *et al.* 2001, Gell and Roberts 2003). The delayed recovery of male fish inside the MPAs is a result of the increase of the size at 50% sex change to pre–exploitation levels. As the slope of the regression line, which controls the change of the size at 50% sex change, was rather arbitrary, this delay might not necessarily be found in real populations. However, the fact that the male population inside the Castle Rock MPA does not return to pre- exploited levels is likely to be a realistic scenario, as a percentage of males are likely to 'spill over' to the adjacent fishing area.

Consequences for population fecundity

Even the moderate fishing mortality rates of 0.2 y^{-1} and 0.16 y^{-1} used in the simulations resulted in a drop in ovary mass to levels of around 72% of pre exploitation levels. With a concomitant shift to the lower size classes, this means the

population now consists of higher proportions of small, less fecund females. Smaller females spawn less often and their eggs have higher mortality rates due to smaller oil globules (Chapman *et al.* 2004). The additional negative shift in size at sex change further exacerbates this loss of reproductive capacity. The skewed sex ratio indicates that the population is not able to compensate for the loss of males by accelerated sex change of females. This phenomenon has been confirmed by field studies on roman (Buxton 1993), and slinger (*Chrysoblephus puniceus*), a congeneric species where sex ratios of 18:1 (female to male) have been found in exploited populations (Lichucha *et al.* 2001). Heavily skewed sex ratios will result in the limited availability of sperm and hence further decrease effective reproduction of the population.

In both MPAs, ovary mass, sex-ratio and size frequency of the population had nearly returned to pre-exploitation levels 10 years into MPA protection. This result is particularly encouraging for Castle Rock, suggesting that even a small MPA can host a healthy spawning population of roman. A more difficult question is to what extent the spawning population inside the MPAs contribute to the total roman population through larval export. Given the complex current patterns in False Bay (*inter alia* Wainman *et al.* 1987), and the fact that in some cases a small fraction of the spawning population can be responsible for the spawning success of an entire fish stock (Larson and Julian 1999), it is possible that Castle Rock MPA could be responsible for sustaining roman populations on a large proportion of reefs in False Bay. In the case of the Goukamma MPA, the fast alongshore currents in the area (Brouwer *et al.* 2004, Götz 2005) could enable pre-flexion larvae to drift to areas more than 200 km to the east and to the west.

Consequences for the fishery

The question of MPA effectiveness through 'spillover' into the fishing area is one of the most controversial topics in MPA research. For this study the average catch weight per cell dropped by half in both simulation scenarios as a result of exploitation. This decline was connected with a shift towards smaller average fish size, as larger fish became unavailable. As weight decreases exponentially with size, it effectively means that to catch the same amount of fish, a larger number of smaller fish need to be caught to make up for their smaller weight. In both scenarios, MPA protection did not significantly improve the catch in the adjacent areas, although there seemed to be a slight shift towards larger size classes in the Castle Rock simulation. As the only means of improving the catch in the simulation was adult 'spillover', it can be concluded that this process is too weak to make a difference to the catch, even to moderately fished populations.

There are empirical examples in recent literature that demonstrate improved catch rates in areas adjacent to reserves (Galal *et al.* 2002, Roberts *et al.* 2001). However, most of these examples are from fish species with home ranges an order of magnitude larger than that of roman. The small home ranges effectively preclude boundary effects, which would otherwise lead to enhanced catches in the areas directly adjacent to the reserve. The unfavourable clustering of reef habitat in both areas, with little cross boundary reef, adds to the limited adult exchange across the MPA borders.

Sources of uncertainty

Whereas much emphasis was put on the realistic simulation of life history traits and behaviour of the adult fish population, fluctuations in fishing mortality rates over time and size specific fishing mortality rates were not considered. Other limitations include

the disregard of a stock-recruitment relationship and a simplified derivation of ovary mass as a measure of fecundity.

There are several reasons for not incorporating a recruitment function into the simulation, and relying on a constant recruitment scenario. The scope of the model domains is limited in relation to the distribution range of the population. Roman occur along approximately1700 km of coastline and can be found on reefs on the Agulhas bank 130 km offshore (Griffiths and Wilke 2002). Therefore processes within the model domain should not substantially affect the reproductive capacity of the entire population. Moreover, recruitment of roman is influenced by highly complex, poorly understood environmental and biological processes, which cannot be convincingly simulated with any confidence.

Although the programme allows the adjustment of fishing mortality on an annual basis, it was decided to keep the values constant during the simulation exercise. The estimate of F used for Goukamma was derived from data from underwater visual census (Götz 2005), provided a realistic estimate of the current fishing mortality outside the MPA. It was not possible to project the likely changes in effort in the next two decades with any certainty, as targeting roman in the Goukamma area dropped substantially when shallow-water cape hake *Merluccius capensis* became the primary target of the commercial line fishery in the area in the early 1990's (pers. obs.). It is possible that this may change in the future. The recreational fishing sector may also become more important as the numbers of recreational fishers are presently not limited.

Forecasts of fishing effort for the area around the Castle Rock MPA are even more uncertain. Reef-associated fish in the area are mainly targeted by commercial

fishermen, when the key targeted species such as Snoek *Thyrsites atun,* Geelbek *Atractoscion aequidens* and Yellowtail *Seriola lalandi* are unavailable. This results in large fluctuations of fishing pressure. A validation of the fishing mortality rate of roman via underwater visual census, as done for Goukamma (Götz 2005), would provide a more reliable estimate. However, even very high fishing mortality rates do not profoundly change the general trend of the simulation results.

The question of estimating fecundity is particularly challenging. For this model ovary mass was used as a proxy for fecundity which is an over-simplification of a very complex biological process. Whereas individual ovary mass increased linearly with fish weight in the simulation, in reality fecundity will probably increase exponentially, as there is evidence for other closely related sparids (Garratt 1986) that larger females have larger eggs and spawn more frequently during one season. In addition, in terms of intra-specific female competition, (Chapter IV), larger females dominate smaller females and might therefore contribute even more to the population fecundity. Further studies on the reproductive biology and the spawning behaviour of roman are needed to resolve this question.

Conclusions

As opportunities for empirical studies of this nature are rare, the individual based simulation model presented here makes it possible to conduct a virtual 'before- after- control- impact analysis' as advocated by Russ *et al.* (2003). The results, in relation to empirical evidence from field studies, indicate that the model is able to provide a good approximation of the *in situ* processes regarding the development of post-recruit roman populations through MPA protection. As computational speed is increasing and fine scale geographical information on the near shore habitats are fast becoming

available in digital format, simulations like the one presented here will become more

and more useful in the management of existing and in the planning of new MPAs.

Table VI-IV: Normalised age-length key derived from underwater visual census and biological sampling in the core area of the Goukamma MPA in January 2004.

Size class (mm FL)	Frequency of occurrence	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
											Age									
101-150	0.306		0.0805	0.1931	0.0322															
151-200	0.257		0.0046	0.0413	0.1238	0.0596	0.0275													
201-250	0.181				0.0085	0.0367	0.0622	0.0565	0.0085	0.0057	0.0028									
251-300	0.161						0.0115	0.0316	0.0488	0.0430	0.0143	0.0086	0.0029							
301-350	0.074									0.0082	0.0143	0.0164	0.0225	0.0082	0.0020	0.0020				
351-400	0.020										0.0022	0.0000	0.0033	0.0022	0.0045	0.0011	0.0045	0.0011		0.0011
401-450	0.002																0.0022			
451-500	0.000																			
Age frequency		0.0000	0.0851	0.2344	0.1644	0.0963	0.1011	0.0881	0.0573	0.0569	0.0337	0.0250	0.0287	0.0104	0.0065	0.0032	0.0045	0.0033	0.0000	0.0011

Chapter VII: General synthesis and conclusions

The general aim of this work was to study the movement behaviour of fish and its influence on management of the fishery with MPAs. Prior to this work, fish movement behaviour in South Africa had been studied only with mark and recapture techniques. The widespread use of dart and t-bar tags has been used to support conclusions on the habits of numerous coastal species. This method is perhaps still the only practical means to study extensive fish movements, although it requires large sample sizes, and is quite inappropriate for elucidating short-term behaviour and home ranges. A general criticism of mark and recapture studies is the failure to study the effect of the tags on the fish and to quantify tag loss. Many studies have also failed to determine the accuracy of catch and recapture position data or to consider the distribution of the recovery effort. These problems were addressed in chapters II and III, culminating in a quantitative assessment of the site-fidelity of roman.

Although roman can be described as a resident species, there is a component of the population, independent of size or sex, which moves considerable distances. Largely ignored by fisheries managers, these intra-specific differences in movement behaviour are very important in the way a stock responds to a particular fisheries management strategy. The effectiveness of MPAs will largely depend on the ratio of resident and non-resident fish within the populations they aim to protect. Therefore, this ratio needs to be quantified for all commercially important species. Useful application of mark and recapture data are possible only when positions are accurately and reliably reported, the tag-loss and the mortality rate for each species has been established and the spatial distribution of the fishing and hence the recapture effort is known and covers the maximum movement distance of the species.

There can be no doubt that current mark and recapture programmes in South Africa need to be revised. The tag loss rates and tagging effects need to be tested on all the tagged species. To answer specific questions, mark and recapture effort should be directed at a few species at a time, and the fishing effort directed at these species should be simultaneously assessed. The accuracy and reliability of the recapture information should also be improved, possibly through the deployment of observers on vessels and at access points during the study.

Besides the ratio of resident versus non-resident fish, the extent of the home range of resident individuals will influence the effectiveness of MPAs. Acoustic telemetry was used in this study to answer questions about the site fidelity. The testing of the equipment and principle methods in the estuarine environment was a valuable exercise and did not only provide the necessary experience needed for the challenging study in the marine environment, but sparked a number of broader studies of spotted grunter *Pomadasys commersonnii* and dusky kob *Argyrosomus japonicus* movement in South African estuaries. The telemetry equipment and the methodology also proved feasible to study small-scale movements of fishes in the South African marine environment. Again, knowledge of the effect of the tags on the behaviour and health of fish is critically important and the transmitter attachment or implantation method needs to be verified for every species studied. Similarly the performance of the technology in the field needs to be tested in each environment under all conditions.

In the case of roman, the telemetry experiments revealed a complex pattern of home range behaviour dependent on environmental conditions and biological factors, making it impossible to put home range size into a single figure. However, even if the maximum extent of the home range of the studied animals is considered, the results

indicate that resident individuals can be fully protected by even the smallest South African MPAs. A similar result may well hold true for a number of related temperate reef fishes, all targeted by the South African linefishery (e.g. *Chrysoblephus cristiceps*, *Chrysoblephus gibbiceps*, *Cheimerius nufar*, *Cymatoceps nasutus, Pachymetopon sp.*). Telemetry studies are required to confirm these patterns.

This study produced a good understanding of movement behaviour of post-recruit roman. The modelling approach has removed many uncertainties from the analysis of mark and recapture data and could be applied to future studies on fish movement in South Africa and elsewhere. The individual based model approach (IBM) made it possible to consider many important factors in the simulation of the MPA effects, by not ignoring important structures and processes through the use of 'average values'. The complex nature of sparid life history calls for IBMs. Efforts have been made to incorporate sex-changing behaviour in growth and population models, but these attempts are at the limits of mathematical tractability. IBMs accomplish complex calculation easier by taking advantage of computing power. The spatial IBM is very flexible and can be easily extended to the entire distributional range of roman or transferred to other species, but it is 'data hungry'. The extension of this model will require studies on larval survival, dispersal and settlement.

From a fisheries perspective, MPAs can only be considered a valid management option if they aid the recovery of the fish-stocks outside their boundaries without a large decrease in fishing area. In this regard, the total area unavailable to the fishery is as important as the size of the individual MPA units. The total size of the area that should be closed to fishing will require additional spatial modelling, using spatial

IBMs but incorporating knowledge of stock recruit relationships and distribution of habitat.

For the size of the individual MPAs however, it appears that many small MPAs are of greater benefit to the fishery than a few large ones. Given that spawning home ranges of individual fish are fully included, there would be little difference in the overall spawning capacity between many small and few large MPAs. The potential of 'spillover' of adult fish from many small MPAs however was shown to be higher and the potential of equally seeding all fished areas through larval drift seems greater.

Because MPAs have multi-species objectives, the generality of the results presented here will be strengthened by the number of species that can be modelled with reliable and detailed information. Repeating the methods employed here on other species is important to support the design of a MPA-network along South Africa's coast that aims to recover reef fish populations.

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