SPATIAL AND TEMPORAL DYNAMICS OF AN EXPLOITED REEF-FISH POPULATION

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DECLARATION

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Jean Glazer, of the Department of Environmental Affairs and Tourism, coded the general linear model described in Chapter 3.

This thesis is presented for examination for the degree of Doctor of Philosophy.

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CONTENTS

ABSTRACT

The successful management of the fishery for galjoen *Dichistius capensis* depends on an understanding of its spatial and temporal dynamics. This thesis investigates the movement of galjoen and its fishery parameters, and evaluates the role of marine protected areas (MPAs) and alternative assessment strategies.

A review of the literature shows that there are examples of resident behaviour, territoriality, nomadism and migration among fish. Combinations of the above may exist within a stock. Fish movement behaviour may be plastic, but never random. Planktonic stages are capable of influencing their destination and settlement.

Movement behaviour was studied by tagging galjoen at four sites in South Africa, three of them in MPAs. The majority of recaptured fish were caught at the release site, but the remainder moved throughout the range. Galjoen typically hold home-ranges. Movement was not linked to season, age or sex. Two models are advanced to explain movement. The polymorphic model is a balance of resident and nomadic behaviour displayed by different individuals. The tourist model, does not differentiate between fish. Each fish moves between a small number of distant sites as conditions dictate.

Mortality was greatest at the exploited site. The protected sites yielded the first direct estimates of natural mortality-rate, density and catchability of galjoen. Fishing mortality-rates were very high, whether inferred from size-distributions or from the product of effort and catchability, and can be sustained only through the existence of refuges. Spatial variation in fishery parameters and the high variance in CPUE suggest that monitoring must be intensive to detect trends.

An individual-based model (IBM) was developed to simulate the galjoen fishery of the twentieth century. Spatial-structure was incorporated by splitting the range into 100-m cells. Habitat-type, derived from geophysical data, determined the probability that galjoen occupied a cell, and the probability that the cell was exploited. The spatial and temporal effort distribution was based on trends in the coastal human population and an effort survey. Twelve model variations included combinations of two spawner-biomass *vs* recruitment relationships, three degrees of larval dispersal and two adult movement patterns. Effort increased on average at 3.5% p.a. By the end of the century the stock was invariably over-exploited. The shape of the spawner-biomass *vs*

recruitment curve was more important than larval dispersal or adult movement in determining population size and yield. Even small natural refuges and MPAs supported more fish than exploited areas, despite the action of larval dispersal and adult movement.

The IBM was used to compare the outcomes of three movement-models: random movement, tourist behaviour and polymorphism. A tagging model was embedded in the IBM to simulate the tagging experiment. Random movement failed to match the data, as it could not account for the high incidence of recaptures at the release sites and the frequency of displacements beyond 500 km. The tourist and polymorphic models both provided a reasonable match, after adjusting catchability, but only the tourist model could account for the lack of correlation between the proportion of 'zero-displacement' recaptures and time-free. The best-fit tourist model apportioned >90% of a galjoen's time to its natal home-range. Home-range size was accurately modelled by assuming that fish require a fixed area of appropriate habitat. Variability in home-range size resulted from the habitat distribution.

The effect of six MPAs of various sizes on the galjoen fishery was investigated with the IBM. By 2000, the MPAs improved the size of the stock by between 25 and 46%, relative to a scenario in which there were no MPAs. In no MPA did the density recover completely. Edge-effects were limited to within 2.5 km of MPA boundaries. MPA size was the strongest determinant of galjoen density within MPAs. All MPAs immediately decreased yield locally, but prevented further declines. MPAs increased future potential yield.

The IBM compared the reliability of spawner-biomass-per-recruit (SB/R) and CPUE-based assessment strategies. Catch-at-age data severely under-estimated mortality-rate, due to rapid increases and spatial differences in fishing mortality, and SB/R could not provide a meaningful index. The relative state of the stock could be approximated by regressing CPUE against effort or by measuring CPUE in exploited areas and large MPAs. Although both CPUE methods were also biased, the first could be corrected by applying a model suited to a fishery not in equilibrium, whereas the second could be avoided by comparing CPUE between similar habitats. For a declining stock, CPUE provides a better means of assessing stock size than SB/R, and it should be cheaper and faster to collect the data.

ACKNOWLEDGEMENTS

I am thankful to George Branch and Coleen Moloney, the two meticulous, hawk-eyed scientists who supervised this thesis. They provided excellent guidance and encouragement throughout.

This field-study would not have been possible without the voluntary assistance of a great number of anglers. More than one hundred of these participated in a fish-tagging programme that took place over a period of 15 years, which provided the basis of the study. The following anglers are specifically mentioned, for they provided the bulk of the assistance which amounted to 35 000 hours of fishing and bait-collecting, much of which took place under uncomfortable conditions: Simon Walker, Wynne de Wet, Mike de Wet, John Maasch, Clifford Hart, Deon Kotze, Stefan Swanson, Steve Lamberth, and Gavin Ritchie. There were also many other anglers who took the trouble to report tags and other information that was used in the study.

I took over the running of the tagging programme from Bruce Bennett in 1994, who laid down an excellent foundation for a long-term monitoring programme at De Hoop. Bruce and I had worked together, prior to his departure from Cape Town, and many of the ideas and theories tested in this thesis arose from that period. Bruce contributed massively to the tagging, and much of what I know about the biology of galjoen can be attributed to his work and observations.

While I was the nominal head of the programme, the actual work was undertaken efficiently and professionally by Lieze Swart. Lieze managed everything: bait-collecting, paper-work, logistics, catering and data-capture. Under strict instruction never to touch a fishing-rod herself, for my fear of corrupting a useful technician, Lieze had to endure thousands of hours of watching people catch fish. Fishing can never be described as a spectator sport.

Cape Nature Conservation supported the De Hoop programme enthusiastically from its inception, and has often gone beyond the call of duty when providing assistance. Usually this involved replacing a broken freezer, finding additional fuel, relaying telephone calls on foot etc. Ruloph Jalving, in particular, took great interest in the work. Sadly, his only attempt to participate actively in the programme was abruptly terminated by a broken ankle.

Apart from De Hoop, data were also obtained from two other sites, namely Tsitsikamma and Cape Point, for which I have to thank Paul Cowley and Simon Walker, respectively. These projects were supported by the South African National Parks.

Fish tagging in South Africa was introduced by the Oceanographic Research Institute (O.R.I.), under the guidance of Rudy van der Elst. To this day O.R.I. runs the tagging database from Durban and has supplied equipment, sought sponsorship for the programme and co-opted the public. Without their work the study of fish movement would not have been possible. For all this time, Elinore Bullen has done outstanding work by keeping her taggers 'in line'.

Vincent Taylor, himself a scientist, but more notably a fine angler and proponent of the sport, promoted the De Hoop project in angling circles. I do not under-estimate his efforts for a moment. Without the support of the organised-angling community, this project would likely not have survived. Vincent organised the sponsorship of jackets and windbreakers from Stellenbosch Farmer's Winery for the project. Other sponsorships included hooks, from Mustad, and a fishing rod from Basil Mannings.

Amina Mohamed of SA Statistics (Cape Town) provided the census data that form the basis of the model developed in Chapter 4. Never before have I had such rapid service from a Government Department.

I was employed by the Department of Environmental Affairs and Tourism throughout this study and they also covered my tuition fees in full, for which I am grateful. The department's librarians, Ben Wessels and Adrienne Melzer, were extremely helpful gatherers of literature, some of which was quite obscure.

This work was strengthened by discussions with many other scientists and colleagues who shaped my ideas over the years. These include in no particular order Steve Lamberth, Marc Griffiths, Paul Cowley, Bruce Mann, Trevor Willis, Hugh Dingle, Jean Glazer, Larry Hutchings, Tony Starfield, Phil Hockey, Robin Leslie, Joshua Sladek Nowlis and Mike Bergh. Special mention must go to Larry Hutchings who not only tagged fish and took a huge interest in the work (even agreeing to read a chapter), but also provided unyielding encouragement to get the thesis finished. Among his tactics were a temporary confiscation of my favourite fishing-rod, buying me a laptop computer, referring to all my colleagues as *doctor* X, and bluntly telling my wife to delay child-bearing until the thesis was submitted. This latter instruction had no impact.

Finally, I received the greatest support from my wife, Claire, who is a trained and experienced editor. After getting half-way through chapter one, Claire gave up editing the thesis with the words: 'I don't know what you are on about'. Claire reduced my domestic duties for a period of three years so that I might concentrate more fully on the thesis. I abused this offer by fishing more often.

This thesis is dedicated to those who taught me how to catch fish, knowingly or otherwise.

INTRODUCTION

There are many species of temperate reef-fish that are endemic to the southern African region, 'sandwiched' between the tropical zones of western and eastern Africa. During the last 100 years, fishing in South Africa has reduced the abundance of these fish substantially, as has happened to reef-fishes in coastal waters throughout the world. Whereas in general South Africa has a good record of managing fisheries, the linefishery (including almost 200 species caught by hook and line, and covering all reef-fishes) has performed poorly. Indeed, in 2000 the Minister of Environmental Affairs and Tourism declared a state of emergency in the linefishery, which paved the way for dramatic cuts in fishing effort in the commercial sector.

There are several technical reasons for the poor management of the linefishery, but economics played a pivotal role. With so many species in a fishery of comparatively modest value, the government cannot afford to invest in monitoring and assessment programmes for each species at the same level as it does for the few super-abundant demersal and pelagic species. The management strategies applied to the linefishery have been rudimentary and ineffective. Although strong arguments can be made to increase the level of investment in this sector, linefish management techniques will always have to be simple, robust and cheap. This thesis concentrates on one reef-fish species, galjoen (*Dichistius capensis*), and investigates two components of the management of the fishery that could meet these criteria, namely marine protected areas (MPAs) and fishery-dependent monitoring. It is an applied study.

Unlike demersal and pelagic fish, which are fairly evenly distributed, and which move widely over large areas of the continental shelf, reef-fishes are clumped and most appear not to be wide-ranging. Spatial dynamics could play a very important role in linefish management. The state of the stock may vary substantially across its range, thus complicating attempts at stock assessment. The rate at which fish replenish areas where there has been excessive fishing effort is critical to the impact that MPAs will have on the fishery, in terms of conservation and the maintenance of fishery yield.

An important part of this work is an investigation into the movement behaviour of galjoen, a surf-zone species that feeds on rock-dwelling, sedentary invertebrates. A previous study of galjoen yielded inconclusive answers about its movements (Attwood and Bennett 1994). Since that attempt, the data set has grown, and can be supplemented with data from other areas. A fresh attempt is made to develop a model of galjoen movement. The field studies also provide information that is crucial for modeling the fishery, and for evaluating candidate management and assessment strategies.

Before launching into an analysis of tag-and-recapture data, it was necessary to gain a comprehensive overview of fish movement behaviour, to assist with the development of hypotheses to explain galjoen movement. Chapter 1 is a review of empirical and theoretical studies of fish movement, drawing on examples from marine and freshwater environments, and from other branches of the animal kingdom. Can the movements of reef-fish be described by a model, or are they entirely unstructured, varying between individuals and over time in a chaotic way? Are the various terms used to describe animal movement, including resident behaviour, territoriality, migration and nomadism, applicable to fish, and are there environmental correlates that might indicate which pattern is most likely to apply to a specific environment or niche? From previous investigations into galjoen it was apparent that intra-specific variation could play an important role in behaviour of galjoen. Is fish behaviour genetic or learned, and how responsive is it to selection pressures, such as fishing mortality?

Chapter 2 presents and analyses tag-and-recapture data for the sole purpose of describing the movement patterns of galjoen. The pattern of tag recovery was not simple and the investigation had to focus at an intensive and an extensive scale. Although it was recognised that the use of passive, coded tags was not ideal for the purpose of investigating home-range behaviour, the high-energy environment that galjoen occupy precluded other methods. The study benefited from a large sample size. Two hypotheses are advanced in Chapter 2 to explain the recapture distributions, but the final choice is left to a modelling study in Chapter 5.

Chapter 3 investigates various aspects of the fishery for galjoen, and provides critical estimates of the natural mortality-rate, fish density and catchability. An important component of this work for later investigations was the variability of estimates between habitats, and between areas of differing fishing intensity. The study benefited from the presence of two MPAs. Parameters estimated in Chapters 2 and 3 are used to support the modelling exercises that form the remainder of this thesis.

A comprehensive model of the galjoen fishery is developed in Chapter 4. It is a spatially-structured, individual-based model (IBM) that retrospectively simulates the development of the fishery over the twentieth century. The movement and fate of all individual post-recruit galjoen are modelled explicitly. This type of model proved necessary to simulate one of the competing movement patterns, in which fish retain a memory of sites that they visit. No analytical or population model could adequately simulate this process, nor could such models realistically accomplish an equivalent level of spatial resolution in the habitat and effort domains. The model is developed using geographical data for habitat type and time-dependent, fishing intensity. Twelve variations of the model were developed that included two movement models, two spawner-biomass-recruitment relationships and three degrees of larval dispersal. The model was used to test competing movement hypotheses (Chapter 5), investigate the role of MPAs in the fishery (Chapter 6) and evaluate alternative assessment strategies (Chapter 7).

The tag-and-recapture data are embedded in a complex *milieu* of fishery interactions and cannot be considered separately. The competing movement models are simple, but to provide predictions comparable to the observations, they have to be embedded in a realistic model of the fishery. The IBM provides such a tool, but the model cannot be fitted to data by using a single objective function and a minimisation routine. Instead, pre-determined combinations of parameter values are used to compare the likelihood of both movement hypotheses. The statistical evidence is discussed in relation to the biology of the species.

South African coastal waters are endowed with several MPAs, in which fishing has been eliminated. With few exceptions, the effects of these closures on fisheries have not been investigated. Chapter 6 uses the IBM to replicate the effect of the introduction of six existing MPAs on the galjoen fishery. Because of the great resolution and flexibility of the model, the MPA dynamics could be studied in great detail. The model not only assesses the role of the MPAs, in terms of conservation and yield, but also describes the mechanisms of fish exchange between protected and unprotected areas, in relation to uncertainties about recruitment relative to spawner-biomass and the extent of larval dispersal.

The question of which assessment strategy to use for a reef-fishery in which there is great spatial and temporal variation in parameters is evaluated for the galjoen fishery. Most commonly-used assessment methods are discarded on the grounds that their data requirements are prohibitively expensive, or simply impossible to match. The evaluation is ultimately a decision between analyses of catch-per-unit-effort and size-structure data. The IBM simulates the true fishery dynamics and the predictions generated by each assessment method. By comparing the predictions to the 'true' situation, the bias of each method is calculated and the causes examined. The model analysis is augmented by considering the practicality and economy of data collection, based on data provided in Chapter 3. Finally the present assessment strategy for the linefishery is re-evaluated, and recommendations for practical steps put forward.

CHAPTER 1

FISH MOVEMENT BEHAVIOUR: OBSERVATION AND THEORY

ABSTRACT

Fish movements can be classified according to the same schemes that apply to terrestrial animals. Fish are capable of long distance migration and navigation in the absence of visual cues. Their movements are never random. An element of randomness may be evident during the dispersal of planktonic eggs and larvae, but recent studies point to great control of position and settlement. Common patterns of movement among post-recruit fish include:

1. The triangle pattern, in which fish migrate between recruiting, feeding and spawning areas;
2. Foraging within a home-range, and possibly defending it from others;
3. Commuting between day- and night-time areas; and
4. Ranging, by which fish are continuously moving in search of food.

Combinations of the above may exist within a stock as a mixed evolutionary stable strategy, and it is common for a population to include strays, which do not abide by the normal pattern. In an evolutionary sense, straying may be adaptive or maladaptive. Fish often move in shoals, as this confers benefits in terms of protection, feeding and energetics.

Optimal foraging theory and the ideal free distribution are models of movement and distribution that are based on the rate of food uptake. Notwithstanding some successful applications of these models, their simplistic assumptions generally ignore reproduction and predation. Natal-homing is a strategy that ensures the best chance of successful reproduction. More sophisticated models such as life history theory and game theory consider movement along with other life-history 'choices' in relation to the environment and the state of the animal.

INTRODUCTION

This thesis describes the movement patterns of an exploited fish, the galjoen *Dichistius capensis*, for the purpose of developing a spatial fishery model. A previous attempt at classifying the movement of galjoen yielded inconclusive answers (Attwood and Bennett 1994). Although a considerable body of data was available for this task, its interpretation was equivocal. It is clear that any further attempt to describe the movement pattern of galjoen should be prefaced by a thorough investigation into fish movement behaviour. Such an investigation is undertaken here. This study is not an end in itself, nor is it a critical review of fish movement studies, but it does provide a conceptual framework against which data can be interpreted.

The first task of this investigation is to provide some robust definitions of common fish movement patterns at the individual and population levels. Scientists studying fish movement frequently refer to, among others, residency, territoriality, dispersal, migration and emigration, although some of these terms are not applied consistently. Secondly, I will provide a brief synopsis of the capacity of fish to move and navigate, to ensure that a model of fish movement is developed within plausible limits. When considering movement rules for individual-based models of fish, Tyler and Rose (1994) drew a distinction between pattern-matching rules and process-matching rules. The third section of this chapter reviews observations of fish movement behaviour and groups these into convenient models. This will provide a basis for selecting pattern-matching rules. The fourth section considers the 'ultimate' causes of movement behaviour, by reviewing theory and experiment – this will provide the basis for process-matching rules.

An understanding of ultimate causes may assist in choosing between alternative movement models, if sufficient ecological information is available. It should also give an insight into the long-term effects of fishing on movement behaviour. Modern fishing practises are massive ecological manipulations, with selection so strong that the annual probability of survival can be less than 0.5 for an adult of a targeted species. Under these conditions, movement and other behavioural patterns are likely to exhibit extreme plasticity within and between generations. In particular, it is necessary to review studies of fish that display inter- and intra-population variability in movement behaviour. The contribution of conditional (environmental) and unconditional (inherited) factors to this variation is important. These contributions will be enhanced if the conditional variation is in any way density-dependant or if the unconditional variants are exposed to differential fishing mortality.

Although this review is selective in that it examines animal movement processes that may be relevant to the problems at hand (namely fishery management and assessment procedures), it is not limited to studies of fish. There is a considerable body of literature that examines similar problems among other taxa, particularly those in the terrestrial environment, where observation and telemetry is simpler than for marine fish. Much can be said about the differences between aquatic and terrestrial systems, but the fauna in each environment shares common problems in the struggle for survival (feeding, predator avoidance and reproduction).

Fish movement patterns that have been studied extensively are often dramatic, large scale or predictable migrations. Examples include vertical migration (typical of myctophids), catadromy (typical of anguilids), anadromy (typical of salmonids) and transoceanic migrations (typical of scombrids). The movement patterns of most commercially important bottom-dwelling fish with body lengths between 0.1 and 1 m are less well studied, largely because of the difficulty of observing movements that are wide–ranging and poorly co-ordinated at the population level.

CLASSIFICATION OF FISH MOVEMENT

Among the vast array of fish behavioural patterns that result in the relocation of a fish, it should be possible to identify some general patterns, and to define the terms that are used to describe them. I specifically exclude from this discussion those movements that are mere body movements and rotations. Nonetheless, it is appropriate to begin with the term that causes least confusion, namely *sedentary* behaviour, which describes the behaviour of an animal that is in contact with the substratum and does not shift its position. Problems arise when classifying non-sedentary behaviour, which includes the behaviour of all fish species. There is no shortage of literature that presents such classifications and definitions, and there is much inconsistency among authors with regard to terminology. Some classifications have been based on physical descriptions of the movement (e.g. distance, consistency in direction, repetition etc), while others have been based on biological events (e.g. feeding, spawning, home-range relocation etc.).

The next step from sedentary is *resident*. Resident animals move freely in a confined area. The emphasis of the definition rests on the confined area, commonly termed the *home-range*. Are there limits to the size of a home-range? Does the home-range extend to include diel movements? If so, does it also include seasonal movements? Nobody would argue with the description of a rock-pool as the home-range of an inter-tidal goby, this being the area in which it forages. But is the South Atlantic the home-range of tuna, which may display similar movements, but on a different scale? Can tuna, the widest ranging of all fish, be classed as resident, the class that is usually associated with the least mobile? This is one of the continuums in animal movement behaviour that a classification scheme should attempt to separate.

Of all the attempts to unravel these problems, Dingle (1996) provides one of the tidiest classifications (TABLE 1.1), although it must be accepted that some overlap and ambiguity is unavoidable. I have adopted this classification and summarise it below with reference to fish, but also refer to alternative perspectives.

Station-keeping includes those behavioural acts that keep an animal in a home-range. The simplest of these is *kinesis*, the control of position by varying speed and direction. An example among fish is the varied rates of turning of the planktivore *Chromis chrysurus* between good and bad foraging areas that were observed by Noda *et al.* (1994). *Foraging* is the movement in search of food within a home-range or habitat patch.

TABLE I: Dingle's (1996) classification of animal movement behaviour.

Movement type	Characteristics
Station-keeping:	
Kinesis	Movements that serve to keep an animal stationary
Foraging	Movements within a home-range
Commuting	Diel movements between day & night locations
Territoriality	Territorial defence & aggression, non-overlapping home-ranges
Ranging	Exploratory movements over wide areas in search of resources
Migration	Persistent, directed, non-exploratory, predictable, physiological adaptation

Definitions of the home-range are not always practical. The home-range is: the area in which an animal normally lives (Smith 1980); the area that an animal occupies exclusive of long-range migrations and erratic wanderings (Mace *et al.* 1984); a specific area that is repeatedly used in the course of an animal's activities; a relatively circumscribed area over which an organism travels to acquire resources it needs for survival and reproduction (Dingle 1996). What is meant by 'normally' and 'most', and what are the definitions of long-range migrations and erratic wanderings? Do all animals have a home-range?

Anderson (1982) proposed a statistical definition, based on the probability of finding an animal at a particular location. Accordingly, the home-range is specified by the area within the 'space-utilisation' contour that encompasses a fixed percentage of an animal's time (e.g. 95%). Within broad taxonomic groups, body-size and home-range size are correlated logarithmically. Chapman and Kramer (1999) provide such a relationship for fish. The size of a home-range may be correlated with the food requirements of the animal (Mace *et al.* 1984).

It would seem correct to say that a home-range is an extremely limited portion of potentially good habitat that is used habitually by an animal. In contrast, an animal does not hold a home-range if it moves freely throughout potentially good habitat. Home-range boundaries are thus not necessarily physically demarcated, and they may be invisible to human observers. An exception occurs when boundaries are defended and can be demarcated by observing and mapping aggressive displays. A territory is any defended area (Nice 1941). *Territoriality* is the aggressive defence of a disproportionate share of resources (Morrissey and Gruber 1993). Many of the territorial animals' movements are devoted to boundary patrols and defence. While home-ranges may overlap, in principle territories do not, although defence is never absolute.

Another type of station-keeping is *commuting* which includes regular movements between resources in a home-range. Marine examples include the diel movement of the epipsammic feeder *Mulloides flavolineatus* between day-time and night-time areas (Holland *et al.* 1993). Similarly, vertically migrating myctophids can be classed as commuters that remain within certain habitat boundaries, if not a home-range.

I next have to consider those movements that do not respect a home-range, including predictable migrations and erratic wanderings. Sinclair (1984) uses three terms to describe one-way movements: *emigration*, by which the animal moves along a predetermined direction; *dispersal*, by which the animal moves in an unpredictable direction; and *nomadism*, by which the animal moves with no consistent direction. Harden Jones (1968) draws a similarity between wanderings and dispersal, both of which describe widespread movements of fish away from the breeding area in search of food. Shields (1984) defines *dispersal* as the movement of an animal away from its site of origin to a new area, or succession of areas.

Dingle's (1996) *ranging* is perhaps similar to Sinclair's (1984) nomadism and Shields' (1984) dispersal. The animal moves in search of suitable resources and stops once these have been located. Ranging involves exploration for new resources, and perhaps for a new home-range. Dingle (1996) notes that there will remain confusion between foraging and ranging and between ranging and migration, largely because specific distinctions have not been looked for. *Natal ranging* and *reproductive ranging* describe the search for new home-ranges by juveniles and adults respectively.

Dingle (1996) is clear on the terms dispersal and emigration. Dispersal is a process whereby a population or a group of conspecifics increases the mean distance between the animals. In other words, they spread out. It is the opposite of aggregation. A single animal cannot disperse or aggregate. Emigration should simply refer to the start of *migration*, which, if viewed from the other side, is immigration. Nonetheless, some authors still prefer to see migration and emigration as fundamentally different processes when applied to fish, the latter being a one-way ticket (Fréon and Misund 1999).

Migration is the final term that needs defining, and one that has proved to be the most elusive. One thinks of migration as a movement that is spatially and temporally predictable, and the inclusion of a return journey is seen by many as a prerequisite. Harden Jones (1968) for example, defines migration as '*the class of movement which impels the migrants to return to the region from where they have migrated*'. Similarly, according to Sinclair (1984), migration is defined as a regular, round-trip within the life-span of an animal. Sinclair (1984) prefers not to use Baker's (1978) definition of migration that includes all forms of movement involving geographical relocation. Indeed, there is a widely held distinction between 'trivial' movements and migrations (Johnson 1969), notwithstanding the conceptual difficulty of separating the vast continuum of animal movements.

According to Dingle (1996), migration should not be defined in terms of the movement, but rather in terms of the mover. Migration need not be predictable or involve a round trip. He adopts a modification of Kennedy's (1985) definition: *Migratory behaviour is persistent and straightened-out movement effected by the animal's own locomotory exertions or by its active embarkation on a vehicle. It depends on some temporary inhibition of station-keeping responses, but promotes their eventual disinhibition and recurrence*. According to this definition, migration involves five attributes that distinguish it from other movement types:

i. The animal displays persistent motion that takes it beyond the home-range.
ii. The movement is direct, and not erratic in direction.
iii. The animal passes suitable resources that would otherwise not be overlooked.

iv. The animal engages in specific departure and arrival behaviour.

v. Physiological adjustments are made to reserve energy for a long journey.

Migrants commonly depart before existing resources are depleted. Ultimately, migration places the animal among favourable resources, thus avoiding the possibility of it being marooned in a degrading environment with insufficient resources or reserves for a long trek. Migration is a syndrome, or a way of life, that includes several accompanying behavioural and physiological adaptations. Dingle's (1996) definition is broad in terms of the movement, but specific in terms of behaviour.

THE CAPACITY OF FISH TO MOVE AND NAVIGATE

What are the inherent constraints to fish movement behaviour? There are obvious physical limits to swimming speed and migration distances. Another issue concerns the array of information that a fish can detect and process for the purpose of navigation. It is worth establishing what mechanisms fish use to orientate and locate themselves. We may wish to know if it is possible for fish to maintain small home-ranges in apparently featureless or changing environments. Likewise, with what accuracy and efficiency can fish navigate across open water to specific targets? Finally, we need to know something about the mechanisms of the development of movement behaviour – is it inherited or is it learned?

Swimming speeds

Fish can swim at speeds not exceeding three body lengths per second using aerobic respiration (Harden Jones 1968, Wardle 1975). Their endurance is virtually unlimited, provided that metabolites and oxygen are continuously replaced (Wardle 1993). Higher velocities of up to ten body lengths per second are attainable by using anaerobic respiration. Such velocities cannot be maintained for a long time, and soon the fish will be forced to rest while its glycogen stores are rebuilt (Wardle 1993). Swimming speeds are dependent on body shape and tail design. Thick-set ambush predators such as serranids with truncate tails are capable of slower cruising speeds than 'carangiform' streamlined, stiff-bodied pelagic fish with lunate tails, such as jacks and tunas. These differences can be enhanced by physiological characteristics, such as a large proportion of large red-muscle fibres. Species that lack a swim bladder may have a minimum swimming speed that is dictated by the need to provide hydrodynamic lift (Blaxter and Tytler 1978).

Fish clearly use currents to substantially increase their speed over ground. Telemetric observations on cod *Gadus morhua* in the English Channel showed that fish swim in mid-water when the tidal current enhances their progress, but rest on the bottom when the tide switches (Arnold *et al.* 1994). In some instances, cod were observed to take shelter in the lee of sand ripples when faced with a strong opposing tide. Not surprisingly, migration routes are strongly influenced by current patterns (Harden Jones 1968).

Scaled to size, larval fish are relatively faster than adults. Stobutzki and Bellwood (1994) and Leis *et al.* (1996) measured velocities of between 15 and 40 body lengths per second for coral reef fish larvae.

Navigation mechanisms

Spectacular migrations of some species over vast distances to specific target sites (particularly by salmon) have led to studies in two areas: how are fish guided and how is the target recognised (Leggett 1977)? There are three broadly recognised models of navigation (Dodson 1988, Dingle 1996). In the first model, called piloting, the fish uses a sequence of signals to reach the target, for example, a set of familiar landmarks that must be passed in the correct order. The fish may possess a mental map of the area that will allow it to choose between alternative routes. The second model is compass orientation, whereby the fish chooses the direction that will take it to the goal, without reference to landmarks. In these models, the fish is in familiar territory, within range of the appropriate landmarks, or from where the appropriate compass direction is known. The third model is true navigation, whereby the fish can orientate towards the goal in unfamiliar territory by using information at the point of departure. These fish will require a mental map and must be able to fix position.

Fish, like many other vertebrates, can detect a variety of physical signals, and some of these are commonly used for orientation (Dingle 1996). Gerkin (1959) reviewed several experiments that proved that fish use visual cues to keep their position within a home-range. Familiarity with immediate surroundings may be achieved by visually building a mental map of the area. The goby *Bathygobia soporator* possesses such a map of its inter-tidal habitat (Dodson 1988). When harassed at low tide, gobies jumped out of their tidal pools into adjacent, isolated pools. In this case, experiments proved that familiarity with the topography was achieved by reconnaissance at high tide, although it is unknown if fish orientate relative to topographic features or to a compass direction (Dodson 1988). Diurnal movements of tropical reef fish from several families are repeated with meter-accuracy, despite covering apparently featureless sand flats and seagrass beds in some cases (Ogden and Buckan 1973; Ogden and Quinn 1984; Holland *et al.* 1993; 1996). Presumably, these movements are achieved by the recognition of topographical features and the ability to orientate to a compass bearing.

Compass orientation can be based on magnetic or celestial stimuli, and fish are capable of using both signals (Leggett 1977, Ogden and Quinn 1984, Dodson 1988, Dingle 1996). The celestial cue is the time-compensated direction to the sun. There is also evidence that fish can detect polarised light and orientate to this field (Dodson 1988). Fish that live in deep water cannot use celestial information, and in the case of midwater species, there is no contact with geo-stationary features either. Cod *Gadus morhua* can maintain a constant direction in mid-water, without visual contact with the bottom for many hours (Arnold *et al.* 1994). This ability to maintain direction in the apparent absence of visual stimuli, which is widespread among oceanic species (Arnold *et al.* 1994 list another seven examples), points to either a magnetic compass or inertial guidance. Fish that can remember the number of left and right hand turns can use this information to hold direction. Goldfish *Carassius auratus* can maintain a balance of left and right hand turns over a 60 h period, in the absence of external cues (Kleerekopper *et al.* 1970).

There is considerable debate about which model of navigation is used by fish, and in particular the degree of navigational accuracy. Although fish use celestial information, it is unlikely that they can rely on it to fix position with any accuracy. Harden Jones (1968) provided a sobering calculation. '*An experienced navigator with a sextant (accurate to ±10 seconds of arc), a chronometer (accurate to ±0.5 seconds of time), and an almanac, can do little better than to fix his ship within ±800 m. It is unreasonable to expect a fish to improve on this...*'.

For transoceanic movements, during which fish lose contact with landmarks, navigation is not particularly accurate. Although the centre of distribution of moving plaice *Pleuronectes platessa* is highly consistent between years, the paths of individual fish are quite erratic (Leggett 1977). Routes taken by homing salmon, for example, are not always direct (Leggett 1977). Indeed, there is a high degree of inappropriate orientation. Many fish also go astray and do not reach their home river, but another river instead. There is, however, some debate as to whether straying is adaptive or maladaptive (Leggett 1977, Dingle 1996). In any event, it appears as if true navigation, the third model, is not used by fish, but that a combination of random search, piloting and compass orientation is sufficient to bring the vast majority of fish to their target eventually, if not directly (Harden Jones 1968, Leggett 1977, De Angelis and Yeh 1984).

Orientation experiments are always characterised by '*considerable scatter*' (Dingle 1996). Perhaps as a hedge against the possibility of straying, fish such as plaice and French grunts *Haemulon flavolineatum* have an estimate of the distance of the route, which they do not exceed if they are lost, but turn back instead (Dodson 1988). In the case of grunts, experimentally displaced fish follow a course appropriate for their original site but turn back after having covered a distance that corresponds to the route that should have been followed.

Fish may also respond to temperature gradients and be guided by oceanic fronts towards a target, as is the case for the American shad *Alosa sapidissima* (Neves and Depres

1979). Fish can detect temperature gradients as small as 0.1 °C, or even less (Frëon and Misund 1999). Chemical cues may also provide important signals, particularly for fish that enter rivers, as each river has a chemical signature. There is some evidence that salmonids home in on their target by using not one chemical cue, but rather a series of chemical cues, consistent with the first model of navigation (Leggett 1977). The chemicals that need to be followed when homing on natal sites are recorded by imprinting during the early life of the salmon (Dingle 1996). South African estuarine fish larvae that hatch at sea accumulate offshore of estuaries in the hope of being sucked into the river by the rising tide (Whitfield 1998). Presumably they use chemical signals to home in on these estuaries, although this has not been proven.

Fish may move in response to numerous physical signals, but these are not necessarily navigation cues. In many cases, fish move simply to maintain position in a favourable body of water. Thermal fronts, thermoclines, low oxygen water and salinity gradients may serve as impenetrable barriers that may restrict, chase or entrap fish (Frëon and Misund 1999).

Larval fish are capable of some surprising navigational feats. Leis *et al.* (1996) found that coral reef fish larvae, 10 – 20 mm in length, are able to detect and swim towards a reef, more than 1 km away, after being captured by a net and experimentally displaced. The mechanism for such orientation is not known, but there was considerable variation among individuals, despite the overall significant trend. The ability of larvae to navigate is one of the great unknowns in fish movement behaviour.

Acquisition of movement behaviour and routes

Behaviour may be controlled by 'closed' or 'open' programmes (Mayr 1982). Both types have a genetic basis, but the open programmes are flexible, allowing for learning and experience to guide responses to variable physical and biological environments. The distinction between 'deterministic' genetic control and adaptive behaviour based on experience and learning is important when investigating the plasticity of movement behaviour. Can movement behaviour alter only through natural selection, a process that might take a few generations?

Two anadromous species, namely sockeye salmon *Onchorhynchus nerka* and stickleback *Gasterosteus aculeatus*, are split into migrating and resident morphs, which are genetically determined (Dingle 1996). This type of genetic influence on movement behaviour is common throughout the animal kingdom, and likely to be widespread among fish.

For some species of birds the migration route (the direction taken) is genetically determined, but there is no similar example known among fish. Most studies of this aspect of long distance migrations have been performed on salmonids. Among sockeye salmon populations from different lakes, captured juveniles orientated in directions appropriate for their lake when placed in captivity (Ogden and Quinn 1984). However, Dodson (1988) notes that the juveniles had the chance to learn their routes prior to capture, and that their responses were very flexible. Other experiments on juvenile salmonids showed movement in compass directions in captivity that were either inconsistent or inappropriate for their migration route (Dodson 1988). Learning and experience are therefore likely to play an important role in the selection of migratory routes among salmonids, although the propensity for migration appears to be under genetic control.

Dodson (1988) reviewed evidence that suggests that fish learn how to orientate themselves in their immediate surroundings with respect to shorelines, compass bearings, bathymetry, shelter, predators etc. Moving a fish from its native area to an unfamiliar area results in it learning the new environment. Helfman and Schultz (1984) performed some transplant experiments on tropical French grunts, which proved that the routes between day- and night-time feeding sites were passed on socially from one fish to another (older to younger).

The routes fish use in their daily routines and long distance migrations appear to be controlled by open programmes. This observation is based on evidence from the few species that have been studied. However, the mere act of migration is likely to be controlled genetically.

COMMON PATTERNS OF FISH MOVEMENT

The classical triangle

The basic plan of a fish's migration is a triangle (Harden Jones 1968). The free-floating egg is spawned at point A, whereupon it drifts with the current and develops into a larval stage. The larval stage reaches a nursery ground, B, where it develops into a juvenile fish that ultimately recruits to the feeding ground, C. The adult fish migrates from C to A to spawn, an act that it may do once only, as is the case for eels, or repeatedly, over several years, as is the case for plaice. The most favoured explanation for such a pattern is that the spawning ground must be upstream of a favourable nursery ground. The adults must undertake a compensatory upstream migration. Of course, there are all types of variations on this theme. Spawning and feeding grounds may coincide. The adults need not migrate upstream, but may find a compensatory current, perhaps deeper down, to facilitate their migration.

This plan was recognised many decades ago on the strength of observations of large North Atlantic commercial marine fisheries: cod, salmon, eel, plaice and herring. This is a truly migratory lifestyle. Movements of fish are predictable on the basis of age and season. Spawning takes place in an area that is small compared to the range of the population). The South African pilchard *Sardinops sagax* provides an excellent example. The adults spawn on the western Agulhas Bank during spring and summer, the larvae drift onto the west coast where they recruit and the older fish migrate to the eastern Agulhas Bank during autumn and winter (Beckley and Van der Lingen 1999).

Spawning may take place in a river, in the case of anadromous fish, or the feeding ground may be in a river, in the case of catadromous fish. The important feature is that the stock is separated on the basis of age, which may relieve intra-specific competition (Harden Jones 1968). However, for many species the eggs and larvae may not be free-floating, in which case the triangle model is not an appropriate model. It also is not appropriate for the many species that spawn throughout their range, and it makes no attempt to explain movements within spawning, nursery and feeding grounds.

Tropical examples of fish migration are difficult to find. Eels are known to migrate into tropical rivers, as they do in most parts of the world, and coral trout *Plectropomus leopardus*, despite their home-range fidelity, undertake large synchronised movements for the purpose of spawning (Zeller 1997, Zeller and Russ 1998).

Diffusion and random-walk

Skellam (1951) and Okubo (1980) have laid a thorough foundation for the study of 'biodiffusion'. While aware of the danger of using the analogy of particle movement to describe animal movement, they saw great potential for ecological study in a family of mathematical models that describe diffusion and random-walk processes.

The well-known diffusion equation predicts that randomly moving particles will spread, such that the variance of the distances between the particles and their points of origin increases linearly over time. The predictions should also hold for any ensemble of individuals that move by taking small steps in directions that are not correlated over time or with other individuals (random-walk). Unchecked, such a process will ultimately spread particles infinitely widely, which is the process of dispersal. Diffusion is an irreversible and disorganising process, and would immediately seem at odds with life-giving processes that are organising and goal-directed (in a teleomatic sense).

Nonetheless, there are cases where aquatic animal movements are small compared to the turbulent (diffusive) length scales of their liquid medium. In such cases, the time-dependant distributions could be described by Fick's equation,

$$\partial N / \partial t = - D \partial N / \partial x \qquad \text{eq. 1.1}$$

(where N is the number of animals, t time, x distance and D the diffusion coefficient) over short periods, after allowing for the effects of advection and barriers. The most obvious application is the planktonic dispersal of passively drifting eggs and larvae. In this case, the animals take on the dispersal behaviour of their medium. (Such 'passive' transport of larval stages is discussed later.)

There is often an unpredictable element to the active movements of individual animals, such that diffusion models may describe active animal dispersal. Diffusion was used to describe the spread from the point of introduction of Muskrat in Europe, and nine-banded armadillo and larch casebearer in North America (Okubo 1980). These are atypical cases, however, as the multiplication of the introduced species is not necessarily checked by predators or competitors, and separating the effects of diffusivity and growth coefficients in the model were problematic.

The assumptions of diffusion are seldom met by animal populations. All animal populations are geographically bounded. The directions of animal movements are not isotropic (equal probability of moving in any direction), nor of infinitely short duration. The animal's environment is not uniform, nor obstacle free. However, most of these deviations from the assumptions can be accommodated by extending the model. A boundary can be imposed. Step size need not be infinitely small, provided that it is small in relation to the total length scale of movement. The persistence of diffusion and random-walk models in ecological studies can be attributed to extensions that introduce these non-random components. Okubo (1980) explores several extensions to random walk models that include, among others, serial correlation in steps, central bias in movement and homing behaviour. The dispersal of natural populations of herbivorous insects very often do not differ significantly from predictions of the diffusion model, but improved fits can be obtained by varying diffusivities with respect to time, spatial position, age and weather (Kareiva 1983).

De Angelis and Yeh (1984) developed *biased* random-walk models of fish movements that simulate some very simple turning and step behaviour, referred to as orthokinesis (where step length is a function of stimulus intensity), klinokinesis (where the frequency of turning is a function of stimulus intensity) and topotaxis (where movement has a directional bias along a stimulus gradient). These models show that directional movements over large space and time scales, such as transoceanic salmon migrations, can be reproduced from these simple micro-scale fish movements. Although stimulus gradients (temperature or chemical substance) are needed to effect homing behaviour, the models allow for a large amount of random behaviour. Some of these models are also able to reproduce aggregatory behaviour. One suspects that populations, such as plaice, which show great variability between individuals, but whose aggregates are stable and repeatable (Dodson 1988), may be described by some form of biased random-walk.

Diffusion models have been applied to two fisheries, one pelagic and the other benthic.

Yellowfin tuna *Thunnus albacares*: Mullen (1989) picked up on the basic problem of diffusion models: '*Any single value for* a^2 [diffusion coefficient] *estimated from tagging experiments predicts an almost homogeneous distribution*'. He overcame this problem by assigning different diffusion coefficients to different areas, such that tuna became more 'viscous' around areas of high production. The results of his variable diffusivity model reflected the observed magnitude of spatial variation in catch rates.

Lingcod *Ophiodon elongatus*: Numerous scientists had noted that this species does not migrate as there is no consistent movement in any direction. Male lingcod guard nests for six weeks of the year, such that there is a high propensity of resident behaviour, at least among the males. Smith *et al.* (1990) developed a diffusion model to estimate the movement of tagged lingcod in the Strait of Georgia. This was not a simple task, given the numerous islands and irregular shape of the Strait. They therefore numerically simulated the spread of diffusing fish from nine 'statistical' areas with a variety of diffusivities, and selected the value that produced results that were closest to those observed. Males and females moved such that 95% of their numbers remained within a radius of 17 and 34 km respectively. Notwithstanding the reasonably tight confidence intervals about their estimates of diffusivity, they did not provide any measure of goodness-of-fit. They did note that for every tagging study on this species there were recoveries made at considerable distances from the release location. When this is coupled with nest-guarding behaviour, one suspects that the data are over-dispersed with respect to the diffusion model. This combination of extreme resident behaviour and extreme mobility is characteristic of a number of species, and is discussed later in more detail.

Metapopulation dynamics

Another kind of model describes the case of a patchy environment in which the population (a *metapopulation*) is separated into several spatially discrete sub-populations, each with their own internal dynamics. Whereas diffusion describes population spread, metapopulations occupy fixed areas, with movement between them, in a patchy environment. The metapopulation concept, developed in the late 1960's (Hanski and Gilpin 1991), has been used to describe genetic divergence among fish (eg Riddle *et al.* 1998) and fish stock dynamics (Cooper and Mangel 1999).

Fish species that form metapopulations have presented severe difficulties for fisheries management, as there is usually a poor understanding of the connections between the sub-populations. If managed as a single, homogeneous stock, a metapopulation suffers severe local over-fishing, local extinction and loss of genetic diversity (Cooper and Mangel 1999).

Man *et al.* (1995) used a metapopulation model to evaluate the effect of marine protected areas on a fishery and assumed that sub-populations were connected by the dispersal of larvae. Sub-populations of marine invertebrates are typically linked by larval dispersal

(Shepherd and Brown 1993, Botsford *et al.* 1998). Sub-populations of surgeonfish *Acanthurus triostegus* show a significant correlation between genetic divergence and isolation within an archipelago (Planes *et al.* 1996). Between archipelagos, there is no such correlation, implying that distant migratory events are sporadic. It is conceivable that exchange between nearby islands is largely due to larval transfer, which is limited predictably by distance, whereas adults are responsible for the erratic, long-distance movements. For metapopulations that do not have broadcast larvae, like some salmonid species, neighbouring sub-populations may be sufficiently isolated to necessitate their treatment as separate evolutionary units (Fontaine *et al.* 1997, Riddle *et al.* 1998, Small *et al.* 1998).

McQuinn (1997) has used the metapopulation model to reconcile two very divergent views about stocks of the North Atlantic herring *Clupea harengus*, each view being partially supported by observations. One view considers the stocks to be separate genetic units, and another considers these stocks to be temporary manifestations of a very dynamic single stock that exhibits environmental pheno-plasticity. The metapopulation model reconciles all these observations, namely the repeatability in the place and timing of spawning by sub-populations (homing), morphometric dissimilarities between sub-populations, straying between sub-populations, persistence of sub-populations over ecological (but not evolutionary) time-scales, and the lack of genetic differentiation between sub-populations. An important component of this model is that strays may be adopted by non-natal sub-populations - a single-species version of Bakun and Cury's (1999) 'school trap' hypothesis.

A number of theoretical models have considered the effects of movement behaviour on the stability of metapopulations, with clear applications for fishery management and conservation. Crowley (1981) showed that high rates of dispersal between patches leads to synchrony between sub-populations, while at low rates the sub-populations act independently (Hanski and Gilpin 1991). The most stable situation arises from intermediate dispersal rates. More complex patterns can be obtained if other factors such as density-dependent recruitment are introduced (Botsford *et al.* 1994)

Fryxell and Lundberg (1993) further explored metapopulation dynamics of a (purely theoretical) Lotka-Voltera predator-prey system (fixed r, variable K, logistic model) under various types of predator movement behaviour. The density of prey, which was defined as having a sedentary nature, was strongly affected by predation. *Adaptive dispersal* described the situation whereby a predator moves if prey density falls below the average prey density, after an adjustment to account for the loss of energy that such a movement would incur. *Fixed dispersal* described the situation whereby a fixed proportion of animals in each patch move per unit time, irrespective of prey density. *Local dispersal* implied that the predator moves to one of the adjacent sub-populations, whereas *global dispersal* implied that the predator has an equal chance of moving to any sub-population. The combination of *adaptive* and *local* dispersal resulted in the greatest average and most stable predator population size, whereas other combinations yielded results that were highly variable at the population level, and cyclical at the local level. A criticism of this type of model is that it assumes an all-or-nothing dispersal process, whereas it is more probable that predators will vary with respect to tolerance to low prey density, thereby damping out much of the serial correlation and cyclicity observed in model results.

Tyler and Rose (1994) review theoretical studies that suggest that feeding behaviour may also affect the stability of metapopulations. Scramble competition for food results in boom and bust population cycles, whereas hierarchical access to resources by way of interference competition (territoriality) uncouples predator and prey populations.

An important lesson from metapopulation models is that simplistic predictions of single stock models are not justified if there are spatially separated sub-stocks.

Home-range

It has been known for a long time that fish species commonly display restricted movement. Gerkin (1959) listed thirty-four examples. Many of these were based on tag recoveries, for which it was assumed that multiple captures of the same fish in the same place pointed to restricted movement. He deduced that fish hold home-ranges, and today we know from telemetry that this is the case.

Are certain habitats, or certain food types, associated with the tendency of fish to maintain a home-range more frequently than others? The answer in both cases is no. Fish with home-ranges are commonly found in rivers (Pellett *et al.* 1998), streams (Bridcutt and Giller 1993), lakes (Minns 1995), reservoirs (Chilton and Poarch 1997), estuaries (Sheaves 1993), coral reefs (Zeller 1997), temperate reefs (Barrett 1995, Willis *et al.* 2001), soft sediments (Ohnishi *et al.* 1997), mangroves (Morrisey and Gruber 1993), kelp beds (Hartney 1996) and inter-tidal pools (Gibson 1993). It is only the pelagic environment that does not lend itself to the establishment of home-ranges. Piscivores (Holland *et al.* 1996), planktivores (Noda *et al.* 1994), insectivores (Bridcutt and Giller 1993), herbivores (Chilton and Poarch) and epipsammic feeders (Ohnishi *et al.* 1997) maintain home-ranges.

How big is a home-range? There are power relationships between body size and home-range for virtually all the major taxonomic groups (Mace *et al.* 1984). These relationships are driven by the food requirements of the animal. Kramer and Chapman (1999) established the following relationship for marine fish:

$$\text{Home-range length (m)} = 0.000178\ (\text{fork length (mm)})^{2.35}. \qquad \text{eq. 1.2}$$

Body length explained 73% of the variation of home-range size. Their data (n=24 species) included a range of fish sizes from 20 to 500 mm F.L., but were biased towards tropical species. Zeller and Russ (1998) showed by telemetry that coral trout typically have a home-range, which averages between 178 and 200 m in linear extent, depending on the type of reef. As part of the same study, mark-recovery results showed a mean displacement of only 95 m. The discrepancy is to be expected, because the tagging technique randomly selects two positions within the ambit of a fish, which can only be closer than the full extent of the home-range. Long term studies suggest that home-ranges can be stable over successive years (Barrett 1995, Pellet *et al.* 1998).

How do fish move within a home-range? Using the random walk model as a basis for 'wandering', Okubo (1980) showed how alternative formulations of a central tendency random-walk can describe (i) a case in which animals are bounded within an area or (ii) another case in which animals are attracted to a central point, but unbounded. The area-bound model predicts that the animal is repelled by the boundary. The central point model results in a high probability of the animal remaining close to the centre, but allows for occasional wanders for which the probability of return decreases with distance. Observations show that neither of Okubo's (1980) within-range models are particularly realistic.

Animals do not 'random-walk', but are likely to continue on a course that they have embarked upon, if only for a short distance. Fish also spend a disproportionate amount of time in some areas, and tend to repeat routes when moving between them. The planktivorous *Chromis chrysurus* identifies good feeding sites within its home-range and moves between these areas every one to three hours (Noda *et al.* 1994). Coral trout *Plectropomus leopardus* tend to move back and forth over the same area, and show high rates of revisitation to some areas (Zeller 1997). They may also spend extended periods at a single location. Repeated use of some areas may be an adaptation to avoid predators or to gain easy access to known resources.

The picture differs slightly among lemon sharks *Negaprion brevirostris*. They show a high degree of spatial and temporal repetition of activities, but re-use about 40% of the area used on the previous day (Morrissey and Gruber 1993). Only about 50% of their home-range is used on any day, and they shift their feeding areas from one day to the next. This suggests that the home-range is exploited in such a manner that preferred resources have sufficient time to recover from predation (Morrissey and Gruber 1993).

Home-ranges often overlap, particularly among fish that are social or form feeding aggregations (Helfman *et al.* 1989, Morrissey and Gruber 1993, Barrett 1995). Only where individuals are territorial do home-ranges not overlap. As a result, territories are usually smaller than home-ranges (Gibson 1993). Territories may be held by one

(Ohnishi *et al.* 1997) or both (Zeller 1997) sexes. Nest-guarding is a specialised form of territoriality that involves defensive vigilance, rather than aggressive behaviour.

Daily commuting

Telemetry has aided the study of short-term fish movement patterns, providing information that neither tagging nor direct observations can. Holland *et al.* (1993, 1996) used this method to follow individual goatfish *Mulloides flavolineatus* and blue trevally *Caranx melampygus* around a tropical Hawaiian island. Despite the different nature of their prey (epipsammic invertebrates vs. small fish) and habitat (sand flats vs. coral reef), both species showed similar patterns of movement that may be described as daily commuting. Both had separate day-time and night-time areas. Goatfish aggregated in medium to large schools during the day, but, as darkness set in, the schools broke up and the animals dispersed to night-time foraging areas on sand flats. Just before dawn the animals retraced their steps to assemble in schools. Movement between schools was very rare, and the tracks taken by the fish at dawn and dusk were highly repeatable, with one animal departing from the same few meters of reef edge at almost exactly the same time (within minutes) on three successive nights.

The blue trevally each patrolled a separate section of reef edge, but moved to a common area at night during which time their activity level dropped by 50%. As with goatfish, the tracks followed by blue trevally were repeated with great precision, with one fish arriving in a pool within a minute or two of 06h15 on five consecutive mornings.

A number of other species, including grunts (family Haemulidae) and wrasse (family Labridae) show similar repeatable migrations (Ogden and Quinn 1984). Some populations of bluehead wrasse *Thalassoma bifasciatum* undertake a daily spawning 'migration' (Tecumseh *et al.* 1990). In the tropics, the daily commuting habit appears widespread and cuts across species and families of a variety of feeding types. Californian temperate reef fish in kelp forests also undertake diel movements, but less commonly, and the timing of these movements is not as repeatable as those of tropical fishes

(Helfman 1993). At twilight, walleye surfperch *Hyperprosopon argenteum* and *Xenistius californiensis* were found to move distances of 1 600 m and 400 m respectively (Ebeling and Bray 1976, Hobson *et al.* 1981). On the basis of these kelp forest observations, Helfman (1993) noted that the sharp transition from day-time to night-time activity found in coral reef communities is lacking in temperate zones, where there is high variance in change-over times and where fish feed day and night. The reason for the difference between temperate and tropical diel patterns is ascribed to the length of the twilight period, which is shortest on the equator, and reduced crepuscular predation in temperate zones. One also suspects that a certain degree of stability in the environment is a prerequisite for such behaviour. Commuting routes of tropical French grunts *Haemulon flavolineatum* are maintained for periods of at least three years (Helfman *et al.* 1982).

The extent to which the commuting habit is common in temperate habitats is not known as there have not been many intensive movement studies on temperate species. Observations and telemetry are constrained respectively by low visibility and strong seas.

'Straying'

The earliest studies of home-range behaviour of fishes recognised that some individuals deviated from the normal pattern. Funk (1957) distinguished between a sedentary and a mobile group in the same population, and drew attention to the strays. Gerkin (1959) noted that among fish species the fraction of fish leaving the homing range varies between one third and none.

Fish can stray well beyond their home-range. Less than 10% of lemon sharks' positions are well beyond their home-range, and then usually in a different habitat (Morrisey and Gruber 1993). A small proportion of tagged lingcod move 'considerable' distances (Smith *et al.* 1990). Forty percent of channel catfish are 'strays' (Pellett *et al.* 1998). Holland *et al.* (1996) describe how 75% of recaptured blue trevally were caught within 500 m of their release position, but 4 fish had moved more than 15 km away. A small minority of coral trout *Plectropomus leopardus* moved after being tagged off the Great

Barrier Reef, whereas the vast majority appeared to be resident (Roberts and Polunin 1991). On a temperate Tasmanian reef, the monacanthid species *Penicipelta vittiger* is resident, with 79% of recoveries taken within 0.25 ha of the release position, but two fish crossed open stretches of sand to be caught 1.5 and 4.5 km away (Barrett 1995). Within the confines of a small tropical estuary, Sheaves (1993) recaptured the vast majority of tagged fish of two serranid and one lutjanid species within 40 m of the release site, but a few were recovered more than 2 km away.

These deviations from station-keeping may be caused by a number of adaptive or maladaptive processes. Fish may simply get lost. This is a possibility for migrants that attempt to return to a home-range. All straying that results from a fish being lost must be maladaptive. Resident fish can only lose their way if they are physically displaced from their home-range, for example, by a spate, or by the intrusion of low oxygen water. Fish that are experimentally displaced from their home-range normally show a remarkable ability to relocate it (Gerkin 1959, Thompson 1983, Hartney 1996). However, channel catfish that were experimentally displaced upstream failed to relocate their home-range, but then what natural event would displace a fish upstream (Pellett *et al.* 1998)? It is unlikely therefore that strays from a population of station keepers are lost, but their behaviour can still be maladaptive.

Among those populations that are territorial, some fish will not be able to maintain a territory and might be forced to adopt ranging tactics. This is the case among red-spotted masu salmon *Oncorhynchus masou ishikawai*, which have a clear linear social hierarchy in stream pools (Nakano 1995). Dominant animals aggressively defend optimal habitats, e.g. stream inlet points, whereas subordinates are non-territorial, often moving below dominants in the bottom layer and between pools. These subordinates adopt a sub-optimal strategy 'to make the best of a bad job' (Nakano 1995).

Large channel catfish are more likely to have an established home-range than smaller ones (Pellett *et al.* 1998). Presumably the young fish do not have the experience to choose a good home-range the first time round and have to select another area later. Alternatively, they are not sufficiently aggressive to defend a territory.

Many species show no correlation between straying and fish size, or, indeed, between straying and any obvious external character. These strays may be exhibiting an adaptive strategy. Either resident fish make occasional forays to distant areas from which they return, such as lemon shark, or they move house (home-range relocation), as displayed by some mature fish that colonise new artificial reefs (Kramer and Chapman 1999), or the population is split with respect to movement behaviour (see Mixed Strategies below).

Ranging

Tagging studies sometimes reveal very little structure in the recovery distribution. Some of these may indicate ranging, a nomadic existence where the fish are in search of resources, and may involve an exploratory component. Because of the inconsistencies of terminology, many of these movements were not explicitly identified as ranging.

It is necessary to regard ranging as a movement strategy in its own right, rather than to lump it with diffusion models. Nomadism could appear to be a diffusive process, but the movements of individual animals are often quite consistent over time. The wandering albatross, which was named after its apparent nomadic behaviour, provides a good example. The adults, which breed on Southern Ocean islands, disperse to cover the entire southern ocean during the non-breeding season. However, individual albatross fitted with geo-locating photometers, showed that individuals have preferred foraging areas, and do not wander randomly around the globe (Weimerskirch and Wilson 2000). The sympatric royal albatross circles the globe. They leave their islands off New Zealand to feed off South America, and later continue eastwards, downwind to return to New Zealand (Ryan 2000). If ranging is a genuine feeding strategy that is adaptive, then older fish should be more proficient at moving than younger ones, which is the opposite of station-keeping, according to which the young move prior to establishing a home-range or territory.

McPhee *et al.* (1999) invoked ranging to explain the tag recovery distribution of the swallowtail dart *Trachinotus coppingeri*, a surf-zone carangid in tropical Australia. About half of the tagged darts were recovered within 4 km of the release site, with increasing displacements achieved by progressively fewer fish. Only 2.7 % of the displacements exceeded 100 km. Direction of movement showed no discernible pattern, but displacement was positively correlated with fish size. However, some small fish did move large distances, thereby obscuring any distinction based on size. Displacement was positively correlated with time-at-liberty.

White shark *Charcharadon charcharias* are abundant in temperate coastal waters, such as the Agulhas Bank and the Californian upwelling region where they feed on seals. Infrequently, white sharks appear at oceanic islands in the tropics (Cliff *et al.* 2000). These encounters indicate that a small proportion of white sharks are ranging, as only very large adults and no juveniles or sub-adults have been found at these unusual locations (Cliff *et al.* 2000).

Of the six estuarine species studied by Sheaves (1993), five were resident, but the tetraodontid *Arothron manilensis,* in total contrast, showed no site-fidelity. Repeated captures of the same individuals within 30 days were all at different sites, some upstream and some downstream.

Sablefish *Anoplopoma fimbria* were recovered up to 2000 km from their release point, but the majority remained within a 50 km release area (Beamish and McFarlane 1987). Sablefish may be rangers, on the strength of the observation that the longer the fish were at large, the smaller the likelihood that they remained in the release area.

Mixed strategies

Mixed behavioural strategies are common within species and populations (Swingland 1984) and can easily confuse the study of fish movement. Movement behaviour is rarely consistent throughout a species, as most species show qualitative (i.e. type of movement) and quantitative (extent, routes, timing etc.) variation (Dingle 1996). Nowhere is this variation more apparent than among salmonids. The distinction between sea trout and lake trout is merely a behavioural distinction, either within or between populations. The proportion of migrants in salmonid populations varies between 50 and 94% (Jonsonn and Jonsonn 1993). Migration in salmonids is associated with a number of other behavioural and physiological phenomena that serve to further distinguish the morphs. The migration option involves a few trade-offs. Migrants have access to a marine food supply and grow faster, and as a result are more fecund. They also run a higher mortality risk on their seaward journey, and they start breeding one or two years later than resident salmonids. Furthermore, migrant males defend spawning territories and are the principal spawners. Smaller, resident males are satellites, and spawn by sneaking (Jonsson and Jonsson 1993). Similarly, sticklebacks *Gasterosteus aculeatus* may be resident in a river, or may migrate to the estuary to over-winter. The migrant form grows faster and matures later (Dingle 1996).

The various forms among salmonids actually look different (in size, colour and shape), but among other species external differences between migrants and residents are not obvious. Japanese sardines *Sardinops melanosticus* can be split into two groups (Fréon and Misund 1999). A coastal group that lives in bays has a limited migration range. An oceanic group displays extended seasonal migrations. This species shows a correlation between growth and migration range. Cod *Gadus morhua* are split into a coastal resident form and an offshore migratory form (Nikolskii 1969).

Off New Zealand, the movement pattern of hapuku *Polyprion oxygeneios*, a shelf-dwelling serranid, is more difficult to identify. One adult hapuku was caught three times in exactly the same place, over a period of five years, suggesting strong resident tendencies. Many tagged hapuku showed no displacement and most were recaught within 50 km, but approximately 20% moved more widely (Beentjes and Francis 1999). Large fish moved more frequently than small fish in the extreme south, the cut-off being approximately the size at maturity, although some small fish did move. There is some evidence in the seasonality of catches on certain grounds, and from tags returns, that a southern stock off South Island aggregates in Cook Strait to spawn annually, but not all fish follow the pattern – some moved in the wrong direction. There is no evidence of a spawning migration for the apparently separate stock off North Island, where the movements were small (maximum 51 km) and not correlated with age, but too large for station-keeping. The pattern for hapuku appears to be a complex mix of station-keeping and ranging, combined with migratory spawning for at least the southern stock.

The above examples are from temperate waters, and most of the fish in question are caught extensively by commercial fisheries. Long distance migrations among tropical fish appear to be rare (in contrast to tropical birds), but this may be an artifact of sampling. Studies of tropical fish movement seldom enjoy the benefits of an extensive recovery effort (from commercial fishers) for tagged fish. Tropical studies tend to be intensive, with a focus on movements within the home-range. Deviations that involve long distance movements are either unnoticed or their significance is not investigated (e.g. Holland *et al.* 1996). Tropical species are also less abundant than temperate species. It is, for example, unlikely that the tagging of 72 735 sablefish (Beamish and McFarlane 1988) can be matched for any tropical species. Rare, long-distance events are thus likely to be missed in the tropics.

Shoaling

Fish shoaling behaviour is usually studied for its effect on predator-prey dynamics and fish stock assessment, but it is also likely to have consequences for movement studies. In particular, the spatial distribution of fish, and population synchrony with respect to departure times and destinations, will be influenced by the tendency to aggregate and to travel in schools. In this regard, the following observations can be extracted from reviews of fish shoaling behaviour provided by Helfman (1984), Pitcher and Parrish (1993) and Fréon and Misund (1999):

i. Groups of fish that remain together are termed shoals. A school is a special type of shoal in which the fish are polarised and practise synchronised swimming.

ii. Approximately 80% of teleosts form shoals during at least one stage of their life-cycle.

iii. There is a proven genetic basis for shoaling in fish and there is substantial variation in shoaling behaviour within some species and populations.

iv. Schooling may reduce the probability of predator attacks per individual by a 'dilution' effect, increased vigilance by a shoal, and prey 'confusion' tactics.

v. Schooling may also aid migration by allowing greater navigational accuracy (more heads are better than one) and a hydrodynamic advantage, while shoals in general may facilitate the social transmission of information pertinent to routes and destinations.

vi. Shoaling may facilitate feeding by increasing the likelihood of an individual finding prey (particularly if they are patchy, or shoaling themselves), increase the amount of time available for feeding by reducing time spent by the individual on vigilance, and by the social transfer of information.

vii. Shoaling circumvents the problem of mate-finding.

viii. Shoal sizes within a population show variation that may cover four orders of magnitude. Fish may aggregate and disaggregate on a diurnal time scale, in relation to spawning cycles, or as dictated by predator avoidance responses or feeding requirements.

ix. Whereas a shoal can be regarded as a functional unit, individuals are not necessarily faithful to a shoal. Shoal fidelity is quite variable among fish species, as the following examples show. Repeated associations between individual yellow perch in shoals are entirely random. Helfman (1984) proposed a *leapfrog* mechanism for yellow perch, whereby individuals join the shoal as it approaches the home-range and then leave when the shoal passes. Fidelity is low, or sometimes non-existent, in loose feeding aggregations of the pomacentrid *Chromis chrysurus* (Noda *et al.* 1994). It has been calculated from tagging data that individual skipjack tuna *Katsuwonus pelamis* switch schools at a rate of between 16 and 63% per day (Hilborn 1991). Hilborn (1991) suggested that what might appear to be a single school of tuna could consist of smaller, more stable sub-units. Among juvenile grunts on coral reefs, fidelity is higher than expected from random associations (McFarland and Hillis 1982).

Larval 'dispersal'

Larval behaviour is likely to be as diverse as that of the adult stages, but comparatively little of it can be described, despite its importance for fishery management. Most fish species have a bipartite life cycle, including a morphologically distinct larval pelagic stage. It has been a widely accepted paradigm that the broadcast spawning strategy results in a wide spread of progeny. Fishery models with spatial dimensions usually draw recruitment from a common pool (eg, Polacheck 1990, Man *et al.* 1995). Unfortunately, theory in this field has overtaken observations (Warner *et al.* 2000).

The most important finding to emerge from recent investigations into larval dispersal is that the dispersal is often not nearly as random and pervasive as once accepted. For example, larval stages of inter-tidal rocky-shore fish along the north-eastern Pacific coast are able to resist offshore and longshore dispersal (Marliave 1986). Larvae of all stages were concentrated inshore, and occurred more frequently adjacent to rocky shores than sandy shores. In southern African near-shore temperate waters, the larvae of cryptic reef fish were located consistently over reefs, as opposed to sand, despite unusually strong prevailing currents averaging 0.5 $m.s^{-1}$ (Tilney *et al.* 1996). In contrast, this same survey found that the larvae of pelagic engraulids were evenly distributed over reef and sand.

Warner *et al.* (2000) reviewed several other studies, which showed that the larvae of reef-fish accumulate in certain areas and show a remarkable degree of retention. Accumulation is evident from settlement batches that include a variety of age-classes. Larvae apparently remain in 'holding areas' to recruit under favourable conditions. Caselle and Warner (1996) found seasonal variation, but no inter-annual variation, in the spatial structure of recruitment to a coral-reef fish community, suggesting the presence of a consistent and non-random element in dispersal. There is circumstantial evidence that physical and behavioural mechanisms facilitate larval retention near source populations

(Leis 1994, Swearer *et al.*, 1999, Warner *et al.*, 2000). These findings imply a far greater separation of sub-stocks within metapopulations.

What is surprising is not why larvae of benthic fish show retention and non-random distribution, but rather how a 20 mm fish can achieve the necessary control. There is obviously a selective advantage in being able to place progeny accurately, rather than randomly. Larvae are surprisingly fast, capable of velocities up to 30 cm.s^{-1} (Leis *et al.* 1996), and thus should be able to overcome typical near-shore currents. However, rather than fight currents, larvae more often exploit them, either to reach a distant target (e.g. Cowen *et al.* 1993, Shanks 1985 - who studied crab larvae), or to remain in a confined areas (Black *et al.* 1991, Breitburg *et al.* 1995).

In the above cases, the larvae make differential use of currents, perhaps by vertical positioning. There are many examples of larvae that make non-differential use of currents. For example, eels spawn in the Sargasso Sea and have larvae that reach both sides of the north Atlantic. In this case, it is the adults that choose the correct currents, as outlined in the *triangle model.*

Extensive and co-ordinated spawning migrations by adults may indicate that larvae disperse from a common pool to replenish large areas. In contrast, spawning *in situ* may indicate less dispersal and more retention.

ULTIMATE MODELS OF MOVEMENT

The previous section reviewed a number of kinds of movement patterns that are commonly observed among fish. These patterns are not always distinct, and quite often combinations of them are needed to describe the complexity of movement patterns that are observed within a population over large space and time scales, and as affected by environmental conditions and ontogeny. A theoretical framework is required to analyse and predict such patterns, and there are a number of models that attempt this by seeking the most basic level of explanation of animal behaviour (Giske *et al.* 1998). These models solve optimisation-functions that maximise reproductive output (e.g. Life history theory), or they consider the ultimate evolutionary consequences of individual actions (e.g. Game theory). An understanding of the ultimate causes of movement gives the population-modeler a theoretical basis to develop movement rules.

The study of animal movement looks at three decisions an animal makes repeatedly: when to move; where to move; and how to move (Pyke 1984). The last of these applies largely to terrestrial animals that have various gaits or modes of locomotion (e.g. walking, galloping, flying), and can be ignored in the study of fish. There is an enormous body of literature that has treated the theory of animal movement from an evolutionary and ecological perspective, from which a number of hypotheses and models have emerged. Some of these have direct relevance to the study of the movement of marine fish populations, and may be useful where direct observations are scarce or limited to certain situations, or where the behavioural pattern is obviously dynamic.

Optimal foraging

Optimal foraging theory assumes that natural selection favours those strategies that maximise food intake per unit time. Fitness is often correlated with energy intake in fish (Hart 1993). Under the umbrella of the optimal foraging theory, the *marginal value theorem* states that an animal will remain in a patch until the rate of energy gain falls below the rate achievable elsewhere (Charnov 1976). There are some practical inconsistencies that arise from the simplicity of the prediction. For example, an animal is unlikely to know the instantaneous feeding rate across all patches, and hence does not have the information needed to make the necessary assessments. Decisions about departure from a patch must be based on information that is accessible to the animal, which can be of three types, (i) time elapsed since entering patch, (ii) accumulated reward (prey capture) since arriving in the patch, and (iii) present rate of energy gain (Iwasa *et al.* 1981). Three corresponding movement rules would be: (i) leave after a 'fixed' residence-time, (ii) leave after a certain quantity of prey has been caught and (iii) leave if the time since the last capture exceeds a threshold time (or give-up time). Iwasa *et al.* (1981) calculated that the distribution of prey should determine which rule is used.

The results of experiments to verify these predictions are not always conclusive. Two laboratory studies by Marschall (1989) and De Vries *et al.* (1989) on sunfish *Lepomis macrochirus* showed that the search pattern within a patch is random (as opposed to systematic), but their results differed on departure rules: Marschall *et al.* found that sunfish behaviour is most consistent with the constant residence-time rule, whereas De Vries *et al.* found greater agreement with the give-up time rule. The difference may be a result of their differing experimental designs (de Vries *et al.* 1989).

The degree to which generalisations can be made from such experiments is limited, as the selection pressures wild fish face include much more than feeding efficiency. One of these considers competition from conspecifics.

Ideal Free distribution

Net food intake depends not only on the density of prey in a patch, but also on the degree of competition for that food. Among the many factors that may motivate an animal to move and influence the direction and the extent of that movement, is the density of the population in its immediate vicinity. The theory of density-dependent habitat selection has been developed as the *Ideal Free Distribution*, so called as it assumes that all animals are ideal (i.e. equal in competitive ability) and free to move to any patch in the range. The theory, developed by Fretwell and Lucas (1970), states that animals will preferentially seek the highest quality habitat, but will spread out among habitat of variable 'quality' as a trade-off between competition and habitat quality, such that all individuals possess the same 'fitness'. The terms 'habitat quality' and 'fitness' refer to complex entities that include energy-intake, survivorship and contributions to future gene pools. Usually models of the ideal free distribution are based on food resources.

Perhaps the most complete application of the ideal free distribution to fish population dynamics is the *basin model* developed by MacCall (1990). By including a spatial structure and some elementary ecological concepts, this model offers explanations for several phenomena that conventional fishery models are not able to address. A summary of the basin model is given here, because it touches on many aspects of fish distribution and movement.

The basin refers to a hypothetical surface joining points whose height represents the inverse of habitat suitability. The best habitat is therefore at the lowest trough on the surface. According to the ideal free distribution, fish will occupy progressively worse habitats as the population expands. The fish population is thus analogous to a liquid in the basin, under a gravitational force, whereby:

- the surface of the liquid is approximately level;
- the volume of the liquid represents the population size;
- the depth of the liquid at any point is a measure of the fish density, and hence habitat suitability, at that point; and
- the 'shore' of the liquid links habitat of equal suitability.

The prediction of the ideal free distribution, that productive habitat holds more fish than sub-optimal habitat, is difficult to test in the marine environment where feeding rates and food availability are not easily measured. The most frequent measure of habitat quality is the density of fish that occupy it, which leads to circular reasoning. It follows that fish need not be most dense in the geographical centre of the range, as the suitability of habitat can be highly fragmented with two or several disjunct maxima.

A testable aspect of the model is that the geographic range of the population will shrink as the population size decreases, and vice-versa. Linked to this process are predictions of movement. MacCall notes that marine fish can achieve an ideal free distribution in a dynamic environment by the movement of individuals to marginal habitat as the population increases, or by the differential rates of population growth (or decline) in different areas. In the former case, it is assumed that '*the habitat is sufficiently fine-*

grained that individuals are able to respond to large scale gradients of habitat suitability that tend to be detectable at the scale of short-term ambits' (p.17). The model assumes that habitats are spatially continuous rather than discrete, to facilitate an analytical treatment. Population change ΔN at any point is described by the equation:

$$\Delta N = G - M + D + (I - E) \qquad \text{eq. 1.3,}$$

where G is population growth, M mortality, D diffusion , I immigration and E emigration. Movement is partitioned into a diffusion and an advection component. The former process arises from random movements, while the latter is a direct response to gradients in habitat quality. The growth model is:

$$dN/dt = rN\,(1 - bN) \qquad \text{eq. 1.4,}$$

where r is the per capita growth rate and b is the density-dependent per capita decrement in growth rate.

Diffusion, which is not related to habitat quality or population density, results in a net movement away from areas of high density. As the highest densities are presumably in the best habitat, diffusion will take animals away from such areas towards peripheral, marginal habitat (which is not consistent with the ideal free distribution). But as more animals 'diffuse' away from high-density areas, the gradient of net habitat suitability slopes inwards towards the best habitats as marginal habitats become over-utilised and the best habitats become under-populated. The fish show a compensatory advection back towards habitat of high suitability. The assumptions of the ideal free distribution can be approximated if the rate of diffusion is low relative to the rate of advection. The resulting surface of the liquid is quasi-flat, with a slight depression at the centre.

MacCall (1990) notes that from an evolutionary perspective, diffusion towards marginal habitat is maladaptive in terms of the ideal free distribution, but may have benefits that are not included in the model, such as the colonisation of unoccupied sites. The colonisation of new habitat is facilitated by diffusion. MacCall overcomes the practical difficulty of separating advective from diffusive movement, by applying the model to fish species for which a larval phase undergoes diffusive dispersal, while the adults are capable of active, directional movement.

Carrying capacity (K) and growth rate (r) vary between habitats (following from eq. 1.4),

$K = r/b.$ eq. 1.5

MacCall argues convincingly that such a 'constant slope' model (the slope of per-capita growth rate vs. population size is constant between habitats) is consistent with the ideal free distribution. In contrast, two commonly used variants, in which (1) carrying capacity varies between habitats whereas the habitat suitability remains constant or in which (2) habitat suitability varies whereas carrying capacity remains constant, are at odds with the ideal free distribution. The fixed r, variable K model predicts that all habitat will be colonised at low population size, with no further colonisation of new habitat as the population grows in proportion to K. The fixed K, variable r model predicts that the best habitat will be occupied most rapidly, but that all habitats can ultimately hold the same number of fish.

An important variation of the basin model is the inclusion of a despotic fish distribution (or territorial behaviour), which results in a strongly density-regulated distribution that forces additional population growth into sub-marginal habitat.

MacCall explores the implication of the model for fisheries management, by developing a simple 19-cell model with two possible kinds of movement behaviour (no advection, moderate diffusion and moderate advection, low diffusion) and two possible harvesting strategies (free 'spatial' access for harvesters to all areas or restricted access selected for optimal yield). For both movement scenarios, free access rapidly results in a population extinction at high fishing mortality-rates, whereas the restricted access strategy is able to achieve an asymptotic catch rate at infinitely high fishing mortality-rates. This is achieved by preventing fishing in areas of high habitat suitability, thus maintaining the source of recruits. Below a maximum sustainable yield, there is no difference between the harvesting strategies. The same result has been achieved by a variety of other models, which show that harvest refugia are able to improve yield, provided that the stock is below the MSY level (Polacheck 1990, Quinn *et al.* 1993, Attwood and Bennett 1994). According to the ideal free distribution, the successful strategy for a high fishing mortality-rate would seem to be to exploit a 'hole' in the marginal habitat and then to harvest the immigrants.

MacCall notes that there are two key considerations to a spatial approach to fishery modelling:

- Is the population mobile such that it mixes on short time-scales and approaches homogeneity?
- Is recruitment diffusive and is it subject to directional drift?

Direct tests of the ideal free distribution among fish populations have been restricted to laboratory experiments, and the results have been somewhat equivocal. Typically, captive fish are offered the choice of two or more feeding sites that vary with respect to food delivery rate. The resulting distribution of fish across these sites is then compared to the predictions of the ideal free distribution.

Milinski (1988) showed that laboratory experiments corroborate the ideal free distribution, despite the fact that the assumptions of the model are not met entirely (fish differ with respect to competitive ability and interference). If the experimental sites differ with respect to food delivery with a ratio of 2:1, then laboratory-held fish should attend those sites in the same ratio. Variations in the ratio of food delivery during the experiment drew a rapid response from the fish, which changed their distribution accordingly.

Kennedy and Gray (1993) challenged the experimental designs of many of the laboratory experiments quoted by Milinski (1988) and refuted his conclusions. By using the matching rule (a statistical procedure that compares the logarithm of the ratios of density and ratios of food delivery between sites), they re-analysed the experimental data and showed that the distribution of fish mostly under-matched the distribution of resources. In other words, there were fewer fish than predicted at the best sites, and more than predicted at the poor sites. This discrepancy is ascribed to a number of unrealistic assumptions in the ideal free distribution, namely imperfect knowledge of feeding conditions at all sites, travel costs and competitive interference. Where suitable sites are separated by vast distances, it is inconceivable that fish will have perfect knowledge of food availability at all sites.

Extensions to 'fitness-models'

McNamara and Houston (1985) addressed the 'knowledge' problem by developing a model of habitat choice, whereby the individual moved if the current patch was less rewarding than the average of all patches previously experienced by that animal. Energy costs of feeding and travelling have been built into models of habitat choice (Hill and Grossman 1993, Tyler and Rose 1994), thereby equating fitness to *net*, rather than *gross* energy intake.

Interference is defined as the interaction between conspecifics that decreases feeding efficiency. It is distinct from the effect of direct depletion of resources. Sutherland (1983) argued that the spatial distribution of predators and prey will fit the function

$$b_i = c\ a_i^{\ 1/m} \qquad \text{eq. 1.6,}$$

where b_i is proportion of predators in the i^{th} patch, a_i the proportion of prey in the i^{th} patch, m the rate of interference and c a constant, such that the b_i values sum to one. Observed values of m range between 0 and 1.3 (Sutherland 1983). At a value of 1.0, the model predicts that predator distribution will mirror prey distribution because eq. 4 becomes linear. For values less than one, disproportionately high aggregations of predators are predicted in areas of high prey density. One of the limitations of this model is that decreased efficiency is assumed to be the same for invaders as for territory holders, which is not realistic.

A more general criticism of the ideal free distribution and optimal foraging models is the fact that processes other than feeding may affect reproductive success, such as predation and reproduction. Fitness cannot simply be equated to food intake rate, notwithstanding some experimental results that seem to confirm such a simple formulation. Fitness comprises many elements that interact in a complicated and seemingly intractable manner.

Reproduction constraints

Tyler and Rose (1994) presented several examples of extensions to 'fitness' models that incorporate reproduction. But with a totally new approach, Cury (1994) considered the constraints imposed by successful reproduction. He coined the term *obstinate nature*, which he used to describe the natal-site fidelity in spawning fish (and other marine species). Instead of fish selecting optimal environments, they merely return to their natal-site to spawn. The mechanism for such homing is imprinting. Adults return to natal sites to spawn irrespective of environmental change (the effects of which are likely to be unpredictable to an animal), because that strategy is likely to be most beneficial (in fitness terms) in the face of environmental uncertainty. An important corollary of the theory is that a small percentage of individuals can be expected to be strays. Cury backed up his theory with many examples among teleost fish, including the occurrence of sub-stocks within populations that were thought to be panmictic.

Life history theory, game theory and beyond

The evolution of life history traits, particularly those associated with reproduction, is the subject of intense ecological study. Certain life history traits are more likely to persist for given biotic and abiotic environments than others. There is also great phenotypic plasticity in behaviour (open programmes) and the ability of animals to make choices is regarded as a vital component of its 'fitness'. The choices may be influenced by the age or state of the animal and the state of the environment. *Life history theory* presents numerous predictions on the age at maturity, the frequency of spawning and clutch size, based on the state of the environment (Stearns 1976). For many years biologists used deterministic models to evaluate those reproductive tactics that are difficult to manipulate experimentally. *Stochastic dynamic programming* is a more powerful technique that can incorporate a variety of trade-offs in a fluctuating environment to assess the best strategy (Tyler and Rose 1994, Giske *et al.* 1998). A complicating refinement in these models is the use of state-dependence, instead of age-dependence, as it recognized that animals of similar age, but different histories (e.g. size, fat reserves, previous reproductive success, etc.), may best employ very different tactics (MacNamara and Houston 1996).

Game theory has been applied to finding evolutionary stable strategies (ESS) in natural populations. What strategy will persist in the long-term? A strategy is an ESS if, once established, no individual with a different strategy can successfully invade the population (Giske *et al.* 1998). A mixed ESS describes those situations where the success of a strategy is frequency-dependent, being favoured at low frequencies, but selected against at high frequencies. In populations with a mixed ESS, there is a dynamic balance between two strategies. Another class of model, stochastic-dynamic game theory, incorporates the dynamic influences of density-dependent processes on life-history tactics, at the expense of an enormous computational load (Mangel and Clark 1988).

The search for the best strategy gradually takes the researcher away from simple predictive models to complex modeling procedures that can evaluate countless trade-offs over large time periods. This is simulation of evolution itself, as is evident with the adaptive approaches discussed by Giske *et al.* (1998), in which genetic algorithms and neural networks (artificial intelligence) are used to search for persistent patterns in behaviour, and other processes in given environments. Such computationally intense procedures may well provide 'solutions', but the investigator is no closer to finding a simplifying theory that can be applied generally. At the leading edge of these investigations into fitness-related problems, analysis gives way to computer simulation in which the fitness 'function' is lost. There has been some question as to whether fitness-functions are appropriate at all (Hart 1993).

CONCLUSIONS

There are consistent and repeatable patterns of movement behaviour within and between fish populations. Fish movement patterns are similar to those of terrestrial animals, and fish can be described within the same classification scheme that is used for other animals. Such patterns have characteristic hallmarks that can be used to distinguish them from other patterns, either qualitatively or statistically.

Fish are capable of long distance migration and navigation, and their movements are not random or chaotic. An element of randomness may be evident during the dispersal of free-floating eggs and planktonic larvae, but recent studies are increasingly pointing to great control of position and settlement by larvae.

Fidelity to a home-range is widespread among fish species from a variety of habitats and ecological niches, and could be regarded as the most common behaviour among fish. Investigators have been quick to point to the advantages of familiarity with a territory. The homing response of <10 cm inter-tidal triplefins *Forsterygion varium*, experimentally displaced 700 m from their home-range (Thompson 1983), is testimony not only to its ability to navigate over unfamiliar territory, but also to the strong advantages to remaining in a home-range. Cury's (1994) hypothesis, which states that fish obstinately return to natal ground, was applied to reproduction, but the principle behind this behaviour could apply to other facets of the life-cycle as well. The repetitiveness of movements of coral reef fish of several species and families suggests that alterations to daily movement patterns are also not advantageous.

During stable environmental conditions, as commonly experienced in the tropics, the undisturbed fish is a creature of habit. However, such consistency and repetition does not imply that behaviour is 'fixed'. On the contrary, the balance of studies in this regard points to flexible behavioural programmes. Fish are capable of learning, and are able to adapt to changing circumstances in experiments, and their behaviour must be regarded as plastic. There are variations to all patterns, even within a population. Such variations may be due to the effect of a social hierarchy, genetic differences within a populations, or responses to different environments. Frèon and Misund (1999) point to the changes in movement and distribution of North Atlantic herring that were at least partially induced by a catastrophic collapse caused by over-fishing. Where possible, learning and genetic mechanisms should be built into fishery models, lending support to the approaches pioneered by Giske *et al.* (1998).

Models derived from optimal foraging theory suggest that flexibility of habitat-use in spatially and temporally variable environments is a distinct advantage. The ideal-free distribution predicts that fish will always search for 'optimal' feeding conditions, and it has some experimental support. However, this prediction appears to be at odds with commonly observed patterns in the field. As an example, fish have been known to stick to home-ranges despite violent upheavals in the environment (Gerkin 1957). The development of theory is hampered by the difficulty of incorporating more than a few factors that affect an animal's reproductive success.

Shoaling behaviour is very common among fish, yet most predictions based on optimal foraging theory do not consider the processes that favour such behaviour. The shoaling instinct is so strong in some species, that individual fish may forgo optimal feeding conditions in favour of remaining in a multi-species school that could take them to unfavourable environments (Bakun and Cury 1999).

The study of fish movement has a strong practical application in fisheries management. Fishery management demands a far greater understanding of fish movement behaviour than is usually available. Fishing effort is never applied uniformly in space. Certain parts of the fishes' range are exploited before others, and then often to a greater extent. Fish habitat, carrying capacity and production are also not uniform. A juxtaposition of the patterns of fish production and fishing mortality for any one species calls for a spatial component in fishery models.

The way in which fish move about will affect the supply of fish to fishing areas, and the density of fish in less exploited areas. Not only is fishing effort applied unevenly, but *marine protected areas*, in which fishing is not practiced, are now advocated worldwide as the most promising means for the recovery of over-exploited stocks and for placing harvesting practices on a sustainable basis (Guenette *et al.* 1999). Some studies have already attempted to predict the effect of MPAs across a broad range of fish movement patterns (Polacheck 1990, De Martini 1993, Attwood and Bennett 1994, Man *et al.* 1995, Sladek Nowlis and Roberts 1999a), but these models have been over-simplified in their portrayal of spatial structure.

Fishery models have usually accounted for fish movement in a simplistic manner, either because of the lack of detailed information or for the sake of convenient mathematical formulation. The most common procedure has been to assume a linear transfer rate between areas (Hilborn 1990, Polacheck 1990), or subpopulations (Man *et al.* 1995). These models can be grouped with random walk and diffusion models, as they all share the characteristic of fish moving down a density gradient. The stock is thus regarded as 'fluid'.

While it is possible that some form of fluid dynamics may adequately represent the movement patterns of many fish species, two important observations suggest that it is highly unlikely that this can be the case. Firstly, the physical environment is not uniform spatially. Often, suitable habitat for a species is distinctly patchy and not continuous. Secondly, fish are products of natural selection, which is a self-organising process that is unlikely to endow an animal with a survival strategy that is purely random with respect to movement or any other behaviour. Fish are goal directed, in a teleomatic sense. There are no examples among fish to support simple diffusion as a model of fish movement.

Only rarely have more realistic models, based on ecological theory and behavioural observations, been applied to describe fish populations, incorporating processes such as density-dependant dispersal (MacCall 1990), obstinate behaviour (Cury 1994) or individual variability in movement (Tyler and Rose 1994, Giske *et al.* 1998). There is clearly great scope for describing and including such processes in fishery models.

CHAPTER 2

A TAG-AND-RECAPTURE STUDY OF THE MOVEMENT PATTERNS OF GALJOEN *(DICHISTIUS CAPENSIS)*

ABSTRACT

The movement behaviour of post-recruit galjoen *Dichistius capensis* was studied by using a mark and recapture technique. 25191 Galjoen were tagged at four sites in South Africa. Three were in fully protected reserves (two in the De Hoop Marine Protected Area, one in the Tsitsikamma National Park), whereas the fourth was at the Cape Peninsula where recreational fishing was allowed. 2174 Fish were recaptured, some of them several times. The vast majority of fish were caught at the site of release. After correcting for differences in recovery effort between the release sites and other areas, it was estimated that the probability of encountering a tagged fish at the release site was 0.95. The remaining fish moved throughout the South African range of galjoen, which is disjunct to the Namibian range. There was no evidence to suggest that movement is linked to season, age or sex. Although not territorial, galjoen do hold home ranges, which were estimated to be no larger than 1.38 km in extent, but probably much smaller. Two likely models are advanced to explain the movement pattern. The polymorphic model is a combination of two movement patterns, one resident and another nomadic. The balance between the two may represent a mixed evolutionary stable strategy. The tourist model does not differentiate between fish. Each fish spends its time at a small number of widely-separated sites, moving between them as conditions dictate. The data presented here do not favour one model above the other unequivocally.

INTRODUCTION

Galjoen *Dichistius capensis* and banded galjoen *Dichistius multifasciatus* are the sole members of family Dichistiidae, and both are endemic to the southern African surf-zone. *Dichistius capensis* are among the most frequently caught fish by the recreational shore-fishery in South Africa and Namibia. Its distribution is bimodal, stretching from Durban to the Cunene River mouth, but remarkably few are caught in the area between Lamberts Bay and Luderitz where upwelling and the occurrence of cold, low-oxygen water is a frequent event. Galjoen eggs do not hatch below 14°C (Van der Lingen 1994). Nonetheless, galjoen are known to migrate across this area (Anon. 1984), thereby maintaining a link between the stocks. The banded galjoen *D. multifasciatus* has a sub-tropical distribution, stretching from Cape Agulhas to northern Mozambique, which overlaps partly with that of galjoen. It is a species of lesser importance to the fishery.

Galjoen have been well studied when compared to other species targeted by recreational shore-anglers. It is a medium-sized fish, which attains a maximum mass of 6 kg. Galjoen are found along turbulent, wave-exposed shores where they feed on epilithic invertebrates, and are less frequently found beyond the surf zone on shallow reefs and wrecks, and then often in large shoals (Bennett and Griffiths 1986, Rust and Rust 2000).

Galjoen eggs float and hatch within a day into larvae with limited endogenous food supplies (Van der Lingen 1994). The fish must feed within the first week, an act that necessitates at least a weak swimming capacity. During this time, there is tremendous scope for dispersal. Van der Lingen (1994) calculated that typical inshore currents could transport the young galjoen 240 km before feeding, but queried whether such a linear extrapolation is valid. The coast consists of a series of bays and capes, which would cause current retention. It is not uncommon for the larvae of reef-fish to show strong positioning capabilities (see review in Chapter 1), and it is quite likely that larval dispersal of galjoen is restricted. Nothing more can be added to this discussion of larval dispersal; galjoen larvae have yet to be found at sea.

The movement pattern of adult galjoen has not been explained satisfactorily, despite an earlier attempt at doing so (Attwood and Bennett 1994). Galjoen are known to swim in small groups and large shoals (Rust and Rust 2000), to display resident behaviour and undertake massive, unpredictable migrations (Attwood and Bennett 1994). There appears to be no clear support for accepting any of the conventional fish-movement models to explain the movement pattern of galjoen.

The study of movement behaviour of fish has a strong applied value as such behaviour will influence the effectiveness of marine protected areas as a mechanism of fish conservation, and it may affect the design of fishery monitoring programmes. This study is a detailed examination of tag-recapture information for galjoen from four sites (Fig. 2.1): two in the De Hoop Marine Protected Area, one in the Tsitsikamma National Park, and one along the Cape Peninsula. The first three of these sites fall within areas that are protected from fishing. The fishery-independent research that was undertaken at these sites benefited from the complete control that could be exerted on the tagging experiment in the absence of a conventional fishery. The aim of the study was to develop a model of galjoen movement patterns.

METHODS

Study areas

De Hoop Marine Protected Area

De Hoop is centrally situated along the warm temperate south coast (Fig. 2.1). The 51-km marine protected area (MPA) was proclaimed in 1984 and took effect from 1985, excluding all forms of fishing within a distance of three nautical miles from the shore. Fish were sampled in the MPA at two 3.4 km-long sites, Koppie Alleen (S 34°28.65`; E 020°30.70`) and Lekkerwater (S 34°26.92`; E 020°39.15`), which are 11 km apart. At De Hoop sea temperatures range between 12 and 20° C.

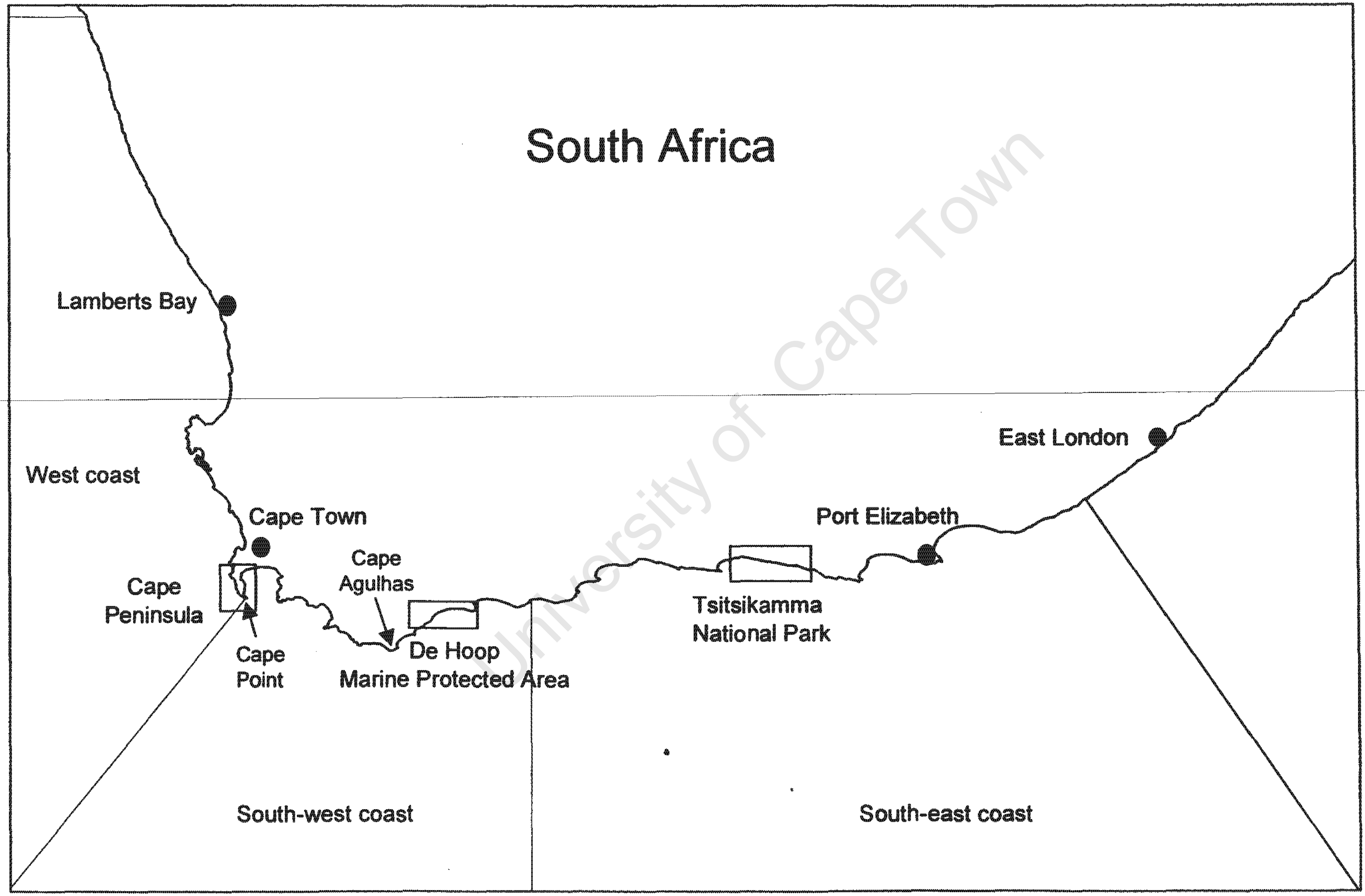


Figure 2.1 Locations of research sites and places mentioned in the text.

At both sites the shore is a mixture of exposed sandy beach and aeolianite rock platforms, or fossil dunes. These platforms have been eroded, leaving a mosaic of reef in the surf zone. The reefs occur exclusively at depths less than 6 m and are all within the surf zone, which extends to a distance of 200 m from the shore. Strong winds and high wave exposure cause the sand to be extremely mobile, covering and uncovering reefs on spatial scales of metres to hundreds of metres, and on temporal scales from hours to years. The beach at Koppie Alleen is a shifting dune system, in which sand is clearly transported back and forth between the land and the sea over great distances. The dunes here are sparsely vegetated. At Lekkerwater, the dunes have more vegetation, but are nonetheless unstable. The most notable qualitative difference between the sites is that the western two-thirds of the Koppie Alleen site has few reefs and constitutes a high-energy sandy beach, which extends a further 15 km westwards beyond the site.

The two sites have different exploitation histories. Prior to 1984, Koppie Alleen was heavily exploited by recreational anglers. Lekkerwater, where the shore was once privately owned, was lightly exploited. It was estimated that the Koppie Alleen site was fished for 31 179 angler-hours per year, prior to 1984, whereas the effort at Lekkerwater was only three percent of this estimate (Bennett and Attwood 1991). By 1991, the Koppie Alleen population recovered to a density that was indistinguishable on the basis of fishery-independent catch-per-unit-effort from that at Lekkerwater (Bennett and Attwood 1991).

Tsitsikamma National Park

Tsitsikamma is the eastern-most of the three research sites (Fig. 2.1). The shore here is made of steep sandstone headlands that are exposed to strong seas. Pocket beaches are rare, but sand does fill the bottom of many sub-tidal gulleys. Water temperatures are warmer than at the other sites, but less stable (range: 10°C to 24°C). Upwelling frequently causes sea surface temperature to drop sharply over a few hours. These events mask a small seasonal trend in temperature (Tilney *et al.* 1996).

Tsitsikamma was declared a National Park in 1964, when it became one of the largest 'no-take' marine protected areas in the world. The 58-km coastline was protected from shore-angling, with the exception of a 3-km stretch of coast in the centre, which was kept open for visitors who stay at the only lodge in the entire Park, where access to the coast is easy. Apart from being restricted by law, access to the remaining areas is physically demanding, involving a ca. 180 m cliff descent. Despite these challenges, poaching has been a problem at times. Nonetheless, fishing effort must be very low, when considering the inaccessible nature of the coast and the fact that regular law enforcement patrols seldom encounter poachers (J. Allen, Tsitsikamma National Park, pers. comm.).

The research site lies on the western side of Tsitsikamma and is split into four areas, namely Lottering, Bloukrans Mouth, Clintons Bank and Kliprivier. The last three areas form a continuous stretch of coast whereas Lottering is separated by a 3-km stretch of inaccessible coast. In total, the areas cover about 4 km of coastline.

Cape Peninsula

The Cape Peninsula (S 34°20`; E 018°24`) marks the border between the warm-temperate and cool-temperate zones (Fig. 2.1). The western shore of the peninsula is exposed, whereas the eastern shore ranges from low to moderate exposure. Sea surface temperature varies greatly across the Peninsula, being influenced by cool upwelling water on the western side (temperature range 9 - 16°C) and sun-warmed False Bay water on the eastern side (temperature range 12 - 20°C). The shores on both sides are formed by quartzitic sandstone rocks and platforms, interspersed with small pocket beaches and boulder beaches. The inshore reefs support kelp forests that form extensive canopies from the low-tide mark to 15-m depth contour. Heavy kelp wracks fuel a rich decomposer community in the inter-tidal zone. The physical habitat is fairly stable here by comparison to De Hoop, with only small changes caused by sand movements.

Parts of the western and eastern shore of the Peninsula are marine protected areas, but all fishing was undertaken in areas that were exploited by recreational shore-anglers, and to a lesser extent by spear-fishermen. Access to the southern-most part of the Peninsula was controlled by permit. Permit sales indicate that there were, on average, 2 800 visits by galjoen anglers to this area annually (Q. Vaughan, Cape Peninsula National Park, pers. comm.). This amounts to approximately 12 anglers per day over the 7.5 month season. There is approximately 10 km of fishable coastline in this area, which gives a rough effort estimate of 1.2 anglers per km per day.

Fishing and Tagging

De Hoop

A controlled shore-angling programme was initiated at Koppie Alleen to study galjoen in 1984, one year before the De Hoop MPA was proclaimed. Thereafter, the programme was allowed to continue as a fishery-independent survey, but all other fishing was stopped. Initially the programme involved fishing by a small group of anglers during monthly trips at Koppie Alleen, which lasted for 4 or 5 days each. Prior to 1987, 959 galjoen were killed for a biological study (Bennett 1988). From 1987 onwards all fish were tagged and returned to the sea, and the trips alternated between Koppie Alleen and Lekkerwater. From 1995 onwards the trips were reduced to six a year (three at each site), each lasting five days (Table 2.1).

A small number of volunteer anglers assisted the author and two other fishery scientists in the capture and tagging of fish. The composition of the volunteer angling team was kept as constant as possible. Although, in total, use was made of 86 anglers during 126 trips, most effort was accounted for by only eight anglers.

All fish caught were measured to the nearest mm in total length. Galjoen were tagged if they were larger than 250 mm, using plastic dart tags, 89 mm long and 1.4 mm diameter (manufactured by Hallprint, Australia). Inscribed on each tag was a unique alpha-numerical code and the postal address of the Oceanographic Research Institute in Durban. The fish handling procedure was gradually improved during the course of the programme. In the beginning, fish were measured with tape measures. These were replaced by rigid measuring-boards. In later years, a special sling with a central rigid baton and tape measure was used to land, tag, carry and measure fish with the minimum of human contact (Attwood 1998). Measurement error amounted to 3.2 mm standard deviation of total length (Attwood and Swart 2000). Timed tagging trials show that the average capture and tagging procedure kept the fish out of water for 1 minute and 20 seconds.

TABLE 2.1: Details of fishing trips. Only one angler fished at the Cape Peninsula.

Year	*Koppie Alleen*	*Lekkerwater*	*Tsitsikamma*	*Cape Peninsula*
	Number of trips per year			**Days fished**
1987	4			29
1988	6	5		18
1989	6	5		62
1990	6	5		39
1991	6	5		75
1992	6	5		59
1993	6	5		63
1994	3	3		71
1995	2	3	11	60
1996	3	3	12	62
1997	3	3	6	44
1998	3	3	6	38
1999	3	3	6	5
2000	1		1	

Fish caught by the public were reported to the Oceanographic Research Institute, where the position of the recapture was recorded as the coastline distance from the northern Mozambique border, measured in km (called the ORI locality code). The greatest drawback of this study is that the public was relied upon to return tags from fish recaptured outside the protected study sites. Although this did happen frequently, it was clear that a substantial fraction of tags was never reported. Lamberth (1997) estimated that only 58% of recaptured fish were successfully reported. Obviously those recaptured at the protected research sites were all recorded.

From 1998 onwards, both De Hoop sites were marked at 100-m intervals along the beach by boards with a number ranging from 1 to 35; anglers operated within the 3.4-km stretch. The position at which each fish was released or recaptured was recorded by the angler as the marker closest to the point where the fish was hooked. All recaptured fish were again returned to the water once the tag was cleaned of encrusting growth. In rare cases, the fish was sacrificed if the tag could not be read without being removed. In total, the percentage of galjoen that was sacrificed (either to read the tag, or because of a 'gill-hook') never exceeded one percent of the fish caught.

Tsitsikamma

A research programme was initiated here in 1995, based on a similar design to the De Hoop programme (Table 2.1). Fishing trips were scheduled monthly or bimonthly. A small number of volunteer anglers assisted a scientist from the Department of Ichthyology and Fisheries Science, Rhodes University, Grahamstown. Fish were caught and tagged in the same way as at De Hoop. Being in a MPA, the only fishing undertaken at the research site was by the research team, although there was concern that a small amount of poaching occurred. All fishing spots were named and identified on a 1:10 000 orthophoto chart so that distances could be calculated accurately.

Cape Peninsula

The Cape Peninsula data did not result from a designed experiment. One of the anglers who participated in the tagging studies at De Hoop, also fished regularly at Cape Peninsula. He caught, tagged and recorded fish in the same way as described for De Hoop and maintained complete records of every fishing trip. His fishing days were randomly distributed throughout the 7.5 month recreational season. Each fishing spot was named, and the distance between fishing spots was measured with a GPS unit. Records were maintained from 1987 to the present (Table 2.1).

Statistical methods

There were two biases that masked the true recapture distribution, and they acted in opposite directions. On the one hand, there was a greater recapture effort applied outside the protected research sites by recreational anglers than applied at the research site by the research team. On the other hand, not all of the recaptures outside of the protected sites were reported. Correction factors were calculated as the ratio of effort applied inside the protected release site to that applied in each of three broad recapture regions, divided by the rate of reporting (Table 2.2). The observed frequency of recaptures in each region was multiplied by the correction factors appropriate for the release site to estimate a recapture frequency that was comparable to that observed inside the protected sites, where recapture effort and recaptures were all recorded. Estimates of recreational effort per recapture region were taken from Brouwer *et al.* (1997), and a constant reporting ratio (58%) was applied to all areas (Lamberth 1997).

TABLE 2.2: Correction factors applied to the observed number of recaptures outside of the research sites in each of three broad recapture regions (Fig. 2.1). The factors differed between the four release sites.

Recapture Regions	*Koppie Alleen*	*Lekkerwater*	*Tsitsikamma*	*Cape Peninsula*
West coast	0.34	0.39	0.73	1.00
South-west coast	0.11	0.12	0.23	0.31
South-east coast	0.35	0.40	0.75	1.03

The data on the movement of fish within the release sites was used to estimate home-range size and the use of space within the home-range. The displacement of each recapture taken at the release site was calculated as the distance between the release and recapture position, in increments of 100 m. Each data set (one from each site at De Hoop) was summarised as a set of frequencies of occurrence of each displacement increment.

For example, if seven fish were re-caught in exactly the same place, then $\Delta x = 0$ and $f_{(\Delta x = 0)} = 7$. If three fish moved 200 m (irrespective of direction) then $f_{(\Delta x = 0.2)} = 3$. The frequencies of all Δx values, from $\Delta x=0$ to $\Delta x=2.5$, hold information about home-range size and the use of space within that range.

Various probability distributions were used to model the use of space by fish within the home-range. Each distribution gave the probability that a fish occupied position *x* at a random capture time. To compare the models to the displacement frequency data described above, theoretical displacement distributions were generated by randomly drawing two positions from the probability distribution – those two positions represented the release and recapture positions – and then calculating the difference between them. These differences were rounded-off to the nearest 100 m, so that the theoretical displacement distributions had the same resolution as the data. Fishing effort was effectively constant within the research sites, and there was no need to correct for differential application of effort.

Three probability distributions were developed: (i) the flat distribution (i.e. fish spend an equal amount of time at all areas within the home-range), (ii) the normal distribution (i.e. fish spend most time in the centre of the home-range) and (iii) the gamma distribution (i.e. as above, but the distribution of frequency of occupancy of sites within the home-range is either leptokurtic or platykurtic).

Uniform: $p(x) = 1/v$ Eq. 2.1

Normal: $p(x) = \dfrac{1}{\sigma\sqrt{2\pi}} e^{-(x^2/2\sigma^2)}$ Eq. 2.2

Gamma: $p(x) = \dfrac{x^{\alpha-1}}{\beta^{\alpha}\Gamma(\alpha)} e^{(-x/\beta)^{\alpha}}$ Eq. 2.3

The corresponding theoretical displacement distributions are referred to as the difference of flat deviates (DFD), the difference of normal deviates (DND) and the difference of gamma deviates (DGD).

Whereas the first two distributions require little explanation, the gamma distribution is not used frequently in behavioural studies. The generalised gamma distribution is an extremely adaptable distribution, which, it has been claimed (Taylor 1980), can fit dispersal data of any organism including humans! The probability density function, with two parameters was used. The factor $\Gamma(\alpha)$ is the gamma function (Press *et al.* 1986).

The parameters of the models were total home-range size (v) in the case of DFD, the standard deviation (σ) in the case of the DND, and α and β in the case of DGD. The resulting probability distributions of differences were calculated analytically, in the case of the DFD, and numerically, in the case of DND and DGD. Numerical solutions used 10 000 iterations to get a smooth curve. These probabilities, which represent multinomial coefficients, were referenced as $p(\Delta x)$. Multinomial coefficients were used to compute the log-likelihood (LLH) of the set of displacement frequencies given any of the three models (Lebreton *et al.* 1992):

$$LLH(v \text{ } or \text{ } \sigma \text{ } or \text{ } \alpha, \beta) = \sum_{\Delta x=0}^{34} f(\Delta x) \ln p(\Delta x) \qquad \text{Eq. 2.4}$$

Each model was fitted to the data for both release sites. The log-likelihood was maximised by adjusting the relevant parameters (v, σ or α and β).

The DFD model gave a direct estimate of v. The DND model used the relation $v \approx 4\sigma$ (i.e. two standard deviations either side of the mean) based on the convention that the home-range includes 95% of the animal's activity (Anderson 1992). No simple relation could be found in terms of α and β in this context. Instead, for the DGD model, the gamma distribution was used to calculate the length that corresponded to the 0.95 cumulative probability.

RESULTS

Sample size

This study is based on information derived from the capture of 27 606 galjoen from four research sites from 1987 to 2000 (Table 2.3). Most effort was expended at the two De Hoop sites, Koppie Alleen and Lekkerwater, and the majority of the sample came from here. The third largest contribution came from the Cape Peninsula, where the data spanned a similar period. Sampling at Tsitsikamma covered a shorter period from 1995 to 2000.

Tagged fish were recaptured at the experimental sites and elsewhere. Recapture rates varied between 0.12 (Koppie Alleen releases) and 0.043 (Tsitsikamma releases). Included in these rates are those fish that were recaptured more than once and those that were caught outside of the study site. Recapture records were complete at De Hoop and Tsitsikamma, but there were unknown losses due to non-reporting outside of these areas, including the Cape Peninsula site.

TABLE 2.3: Number of galjoen that were captured, tagged and recaptured n-times, and the recapture rate (all recapture events divided by first releases).

	Koppie Alleen	*Lekkerwater*	*Cape Peninsula*	*Tsitsikamma*
Captured	9322	14823	2590	871
Tagged	8310	13686	2360	835
Recaptured once only	763	964	218	32
Recaptured twice only	76	70	9	2
Recaptured >twice	28	11	1	0
Recapture rate	0.12	0.083	0.10	0.043

Size distributions

Captured galjoen ranged in size from 110 to 604 mm. Average sizes differed significantly among sites (one-way ANOVA, F = 665.1, d.f. = 27387, $p<0.05$) (Table 2.4). The average size of fish at Cape Peninsula was smaller than at the other sites, which may be attributed to the fact that the fish were exploited here. There was very little difference between the size distributions at the two De Hoop sites, but proportionately there were more large fish at Tsitsikamma as suggested by the 95 percentile. All sites had similar values for the fifth percentile, indicating similar proportions of small fish.

Adult fish may behave differently from immature fish with respect to feeding behaviour and migration. Such differences may be linked to the breeding cycle. If this was the case then the ratio of mature to immature fish in the samples might differ between months at each site. Accordingly, the following hypothesis was tested for each of the four sites, using a Chi-square contingency table. H_0: There is no difference in the relative numbers of mature and immature galjoen between months. A mature fish was classed as any galjoen larger than 349 mm TL.

TABLE 2.4. A comparison of the total length (mm) distributions of captured galjoen from the four research sites. n = sample size, Min. = smallest fish, Max. = largest fish, 5%ile = length of the fifth percentile, 95% = length of the ninety-fifth percentile. * Unprotected site.

Site	*n*	*Min.*	*Max.*	*5 %ile*	*95 %ile*	*Mean*	*St. dev.*
Koppie Alleen	10200	122	604	265	475	362.1	72.9
Lekkerwater	13907	110	595	275	475	359.7	63.4
Cape Peninsula*	2447	177	514	277	373	327.6	31.0
Tsitsikamma	834	187	588	283	502	380.6	64.0

The null hypothesis was rejected for the two De Hoop samples and for the Tsitsikamma sample (Table 2.5). In these cases, the percentage of mature fish (≥ 350 mm T.L.) peaked between July and November (Fig. 2.2). The fact that the period when the relative number

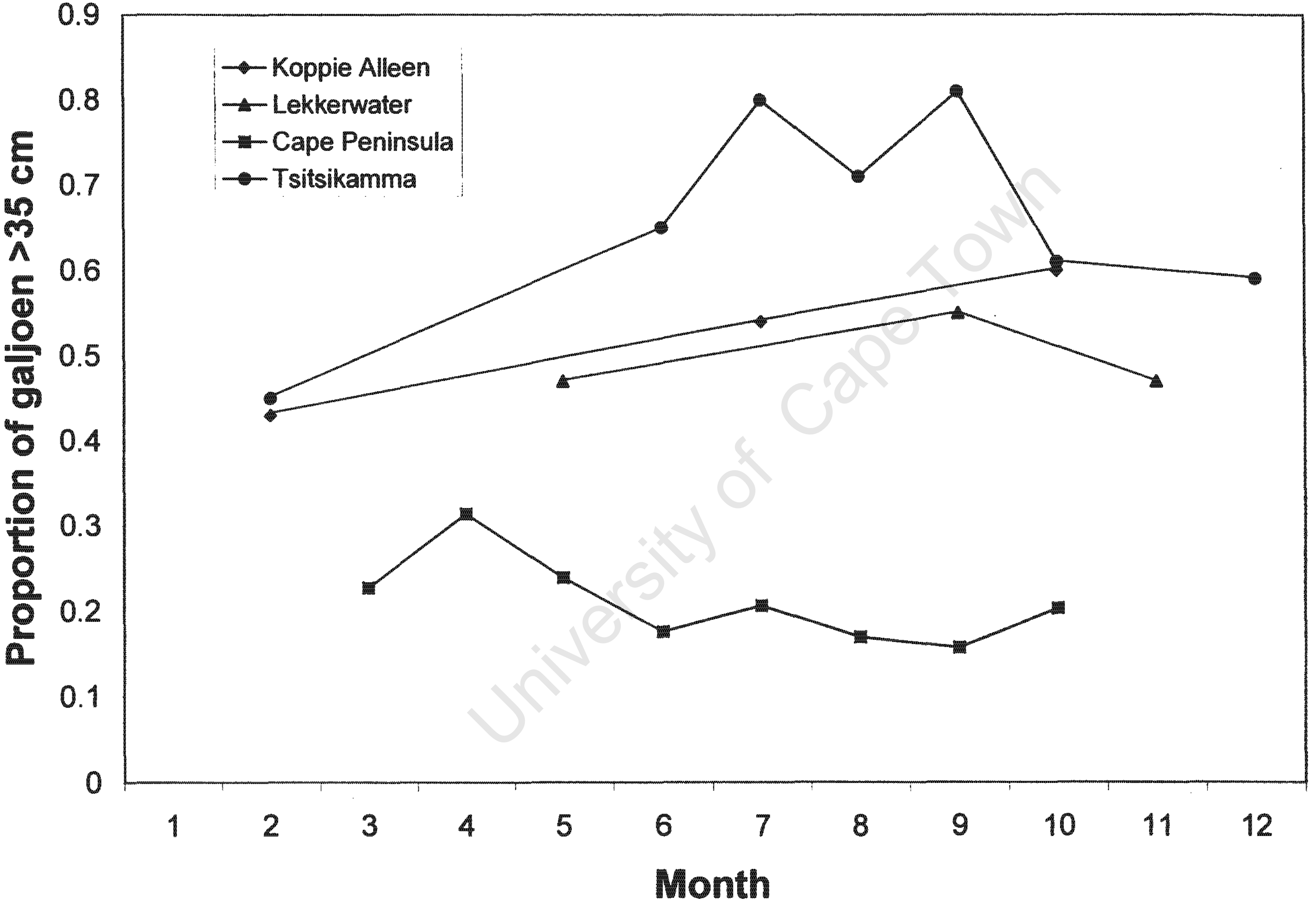


Figure 2.2 The proportion of mature galjoen (>350 cm) in monthly samples taken at four research sites.

of mature fish is at its lowest corresponds with the period of lowest CPUE (winter/spring) suggests that it is the availability of mature fish, and not immature fish, that varies seasonally (CPUE data are presented in chapter 3). The monthly differences in the Cape Peninsula sample were not significant at the 0.05 level. A trend at Cape Peninsula may have been masked by the effects of fishing, as suggested by the low overall percentage of mature fish. There is no evidence to suggest that adults migrate to a spawning site that occupies only a small part of the range. The timing of peaks in abundance of adults does not differ between sites.

TABLE 2.5. Proportions of samples that were larger than 349 mm (% Mature), and the results of a chi-square test on the differences in frequency of mature (≥350 mm) and immature (<350 mm) fish in monthly samples. DF = degrees of freedom, p=probability of H_0 being correct.

	n	*% Mature*	*Chi-square*	*DF*	*p*
Koppie Alleen	10200	54.6	86.1	2	<0.05
Lekkerwater	13907	50.6	64.8	2	<0.05
Cape Peninsula	2477	19.3	15.02	8	<0.10
Tsitsikamma	834	66.8	46.1	11	<0.05

Tag recapture data

A substantial fraction of tagged galjoen moved great distances, but most were recaptured at the release site (Fig. 2.3 and Table 2.6). The movements covered the entire South African range. Several of the De Hoop releases were recaptured north of Cape Point and east of East London, with the maximum displacement being over 1 000 km. The furthest distance moved by a Cape Peninsula fish was 1 300 km, covering almost the entire range. Only two fish from Tsitsikamma were recaptured outside of that study site, one of which covered 750 km westwards. The other was discovered in a fresh state in the stomach of a large sciaenid (*Argyrosomus japonicus*) in the Gamtoos estuary to the east of Tsitsikamma, and it was assumed that the fish was eaten in that vicinity. At the De Hoop

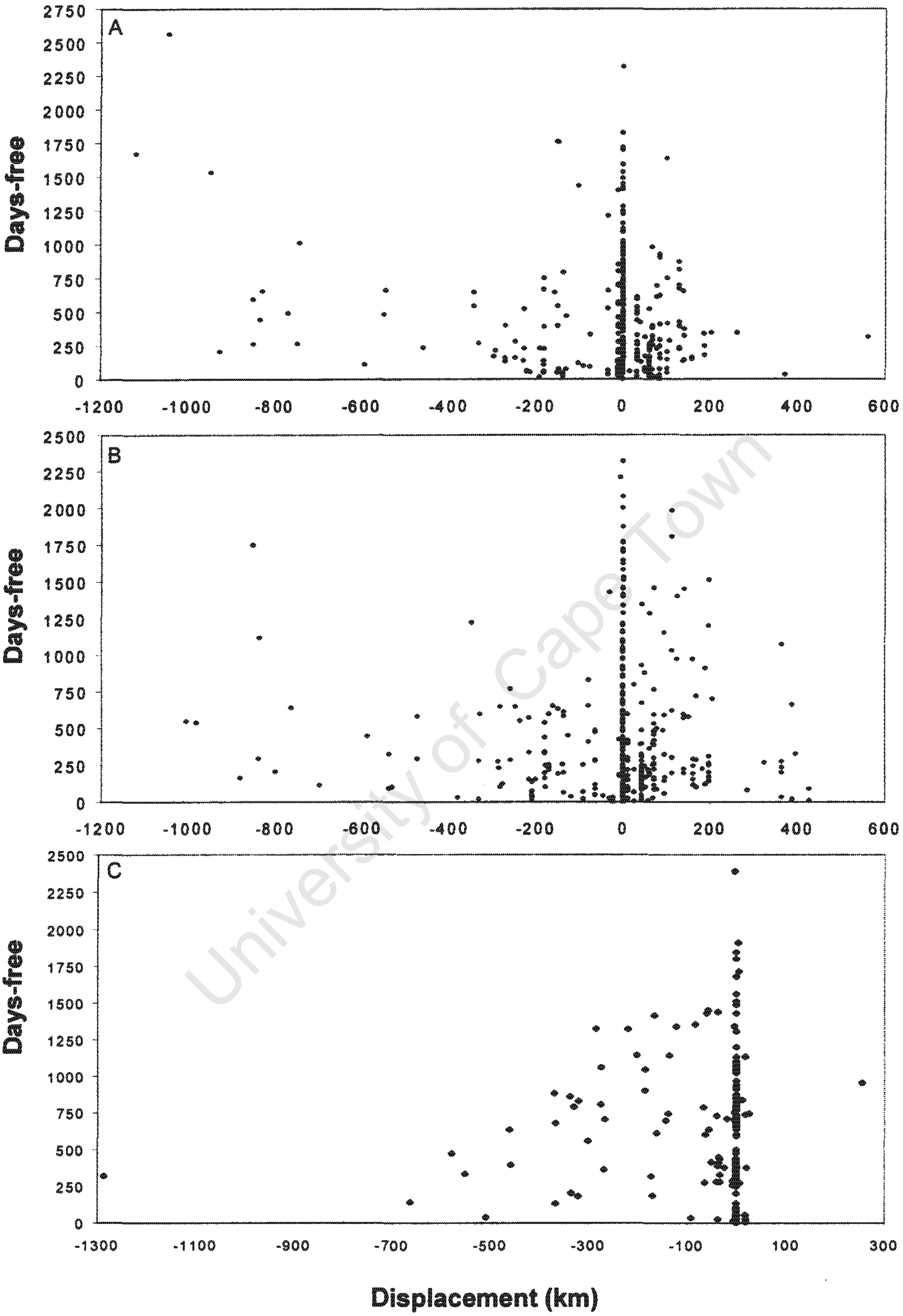


Figure 2.3 A scattergram of days-free against distance moved by galjoen (west positive). (a) Koppie Alleen, (b) Lekkerwater, (c) Cape Peninsula. The x-axes indicate relative distance.

and Cape Peninsula sites, both lying slightly on the western side of the range, most of the 'movers' went to the east.

The frequency of recaptures decreased with the absolute displacement distance (Fig. 2.4). This distribution has a long tail. The most notable feature of these data is that the vast majority of recaptures (approximately 80%) were made at the release site. After correcting for the effort and reporting biases, the fraction that was recaptured at the release site was even greater (Table 2.6). These corrected frequencies are a more reliable indication of the true movement patterns, despite the crude calculation of 'correction' factors. The effort estimates provided by Brouwer *et al.* (1997) were averages over large areas taken during a two-year period. The recaptures reported here were taken over a considerably longer period than that. Likewise, the estimate of the reporting rate, which was based on a questionnaire survey, was a once-off estimate with no indication of its accuracy. Despite these uncertainties, it is a reasonable assumption that the ratio of effort applied inside vs. outside the study sites was less than the reporting rate, and therefore the observed recapture frequencies outside of the research sites were adjusted downwards.

TABLE 2.6: The actual frequency and corrected relative frequency (based on correction factors applied to recapture regions listed in Table 2.2) of tagged fish that were recaptured to the west of the release site, at the release site, and to the east of the release site. Because the Cape Peninsula site was very large, only fish that moved less than 2 km were considered to have been recaught at the 'same site'.

	Koppie Alleen	*Lekkerwater*	*Cape Peninsula*	*Tsitsikamma*
	Actual frequencies			
West	103	91	12	1
Same site	811	901	153	32
East	96	145	64	1
	Corrected relative frequencies			
West	0.013	0.016	0.065	0.021
Same site	0.96	0.95	0.828	0.957
East	0.027	0.038	0.107	0.022

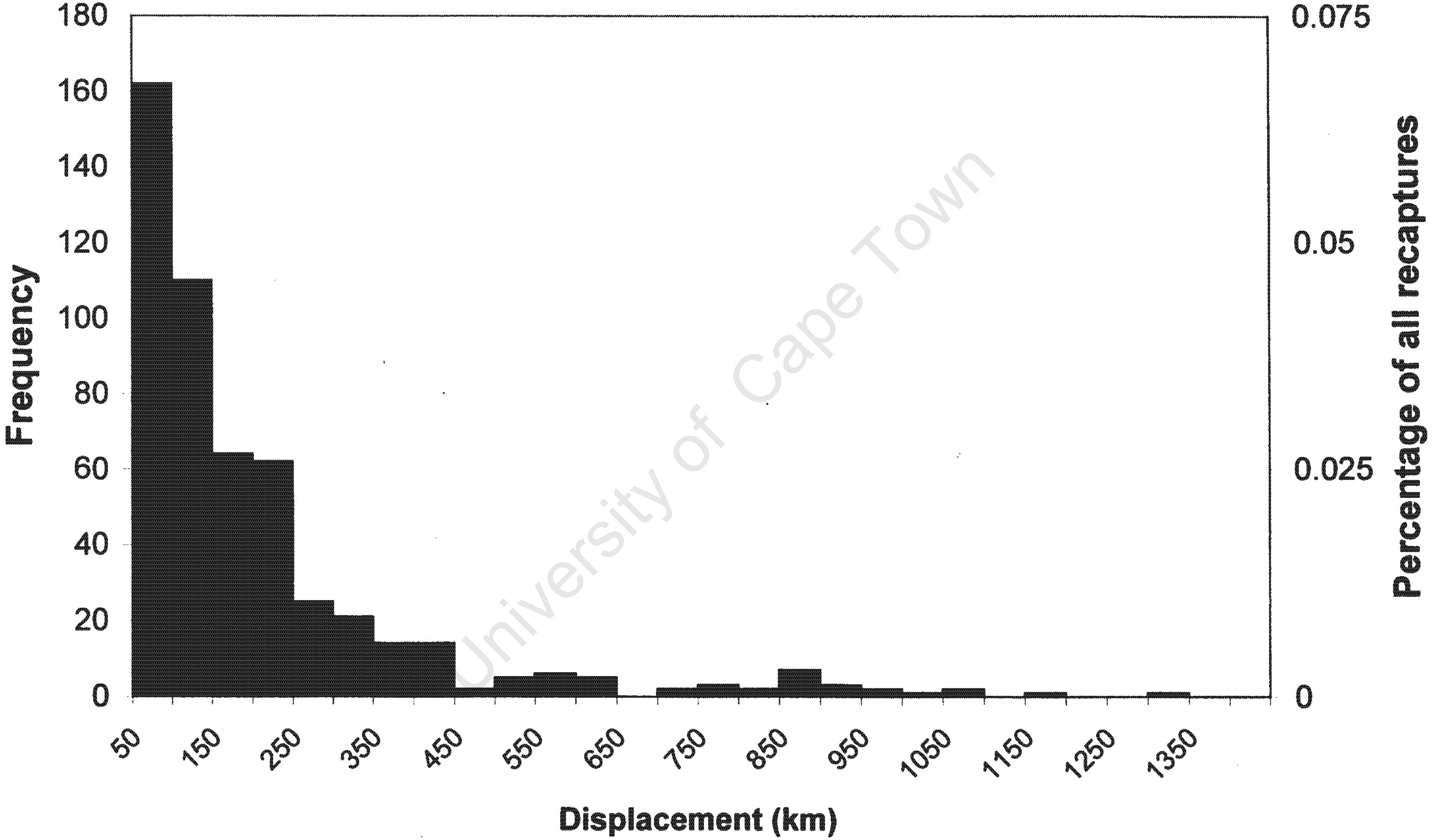


Figure 2.4 A frequency histogram of distance moved by galjoen tagged at all sites. The 0-50 km bin is excluded, because its frequency (1907) vastly exceeds those in all other bins combined.

After correction, the proportion of recaptures taken at the release site was similar for the two De Hoop sites and Tsitsikamma (approximately 95%), but smaller for the Cape Peninsula (83%).

A number of hypotheses can be tested in the search for a unifying theory for these distributions. The first of these is that the movement can be described by a diffusion process, whereby small, random movements of individuals cause the population to spread out according to Fick's equation (Okubo 1980). According to this equation, the variance in displacement (distance moved) increases linearly over time, by the rate D (the diffusion parameter), and the spatial distribution would be normal for tagged fish that have been free for any given time-since-release. Direct tests of these predictions are not possible, because the biases introduced by non-reporting and unequal effort distributions will mask any prediction cast in terms of absolute frequencies. Furthermore, it would be incorrect to dismiss diffusion simply because the variance does not increase linearly over time. The range of galjoen is limited, and it is clear that a maximum variance will be reached as fish reach the ends of the distribution. Judging from the recapture distribution (Fig. 2.3), this could happen quite quickly.

The most basic prediction of diffusion is that particles spread out over time, as the net movement of individuals at any point opposes the concentration gradient. Diffusion would predict that the proportion of fish remaining within close proximity of the point of origin will decrease over time. In this case, the proportion of recaptures made at the release site should decrease with increasing time-since-release. This can be tested with the available data because it is a prediction of temporal change that is unaffected by spatial biases in the recapture frequencies.

The following null hypothesis was tested with a chi-square test: The proportion of recaptures taken at the release site is independent of time-since-release. For data from each site (except for Tsitsikamma which had too few data for this test), a contingency table was constructed with the absolute frequency of zero and non-zero displacements against time-since-release categories. There were sufficient data for seven time-since-release categories for the De Hoop sites, but only five for the Cape Peninsula site. The proportion of zero displacements show no discernible trend over time-since-release, with perhaps the exception of the Cape Peninsula recaptures (Fig. 2.5). The null hypothesis was accepted at the 5% level in the case of Koppie Alleen and Cape Peninsula (Table 2.7).

Even the significant difference in proportions between time-free categories at Lekkerwater does not support the diffusion hypothesis, because the result was driven by low proportions in just one category (201-300 d). This was confirmed by a one-tailed Spearman's rank correlation test on the percentages versus the time-since-release categories shown in Fig. 2.5 ($r = -0.46$, $p>0.1$). Diffusion alone does not appear to explain the recapture pattern. If diffusion does play a role, it is well masked by other processes, which may involve seasonal or sex-related behaviours.

TABLE 2.7: Results of Chi square tests on the frequency of zero and non-zero displacements from recaptures that were grouped by time-since-release.

	Degrees of freedom	*Chi-square*	*p*
Koppie Alleen	6	10.87	0.092
Lekkerwater	6	45.51	<0.001
Cape Peninsula	4	6.15	0.187

The micro-scale, within-site, movements shed more light on the movement behaviour. Those recaptures taken at the protected research sites, for which exact locations were recorded for release and recapture events, can be used to estimate home-range size, provided that the home-range is substantially smaller than the study sites. The displacement data (Fig. 2.6) confirm that the three protected sites (smallest = 3.4 km) were large enough to contain home-ranges. The rationale for omitting those fish that left the study site in the calculation of home-range size is that they must have abandoned the home-range. For galjoen ($l_\infty \approx 670$ mm) the maximum predicted home-range size is 700 m, based on the allometric relationships reported by Kramer and Chapman (1999) for tropical reef-fish.

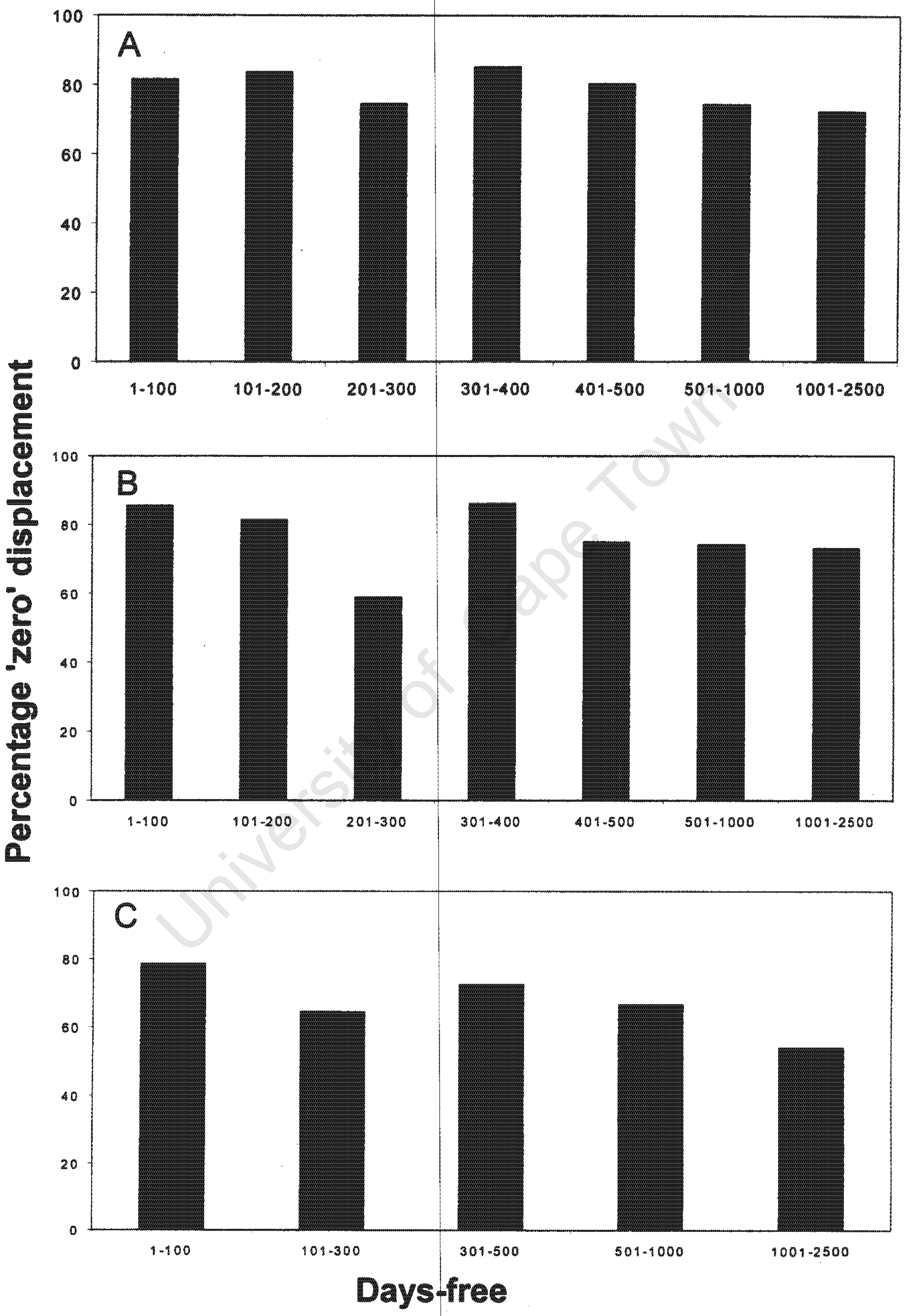


Figure 2.5 The percentage of recaptures that were taken at the release site in a range of time-free bins. (a) Koppie Alleen, (b) Lekkerwater, (c) Cape Peninsula.

At De Hoop and Tsitsikamma it is clear that galjoen show a high degree of site-fidelity, with 60% of the within-site recaptures having been taken within 200 m of the release position (Fig. 2.6). At the Cape Peninsula the site-fidelity is more extreme. Of the 31 recaptures at Cape Peninsula for which positions were accurately recorded, 24 were displaced by less than 100 m. However, these data were not used to estimate home-range size because they were biased by the fact that the fishing effort was not concentrated in a small area, but rather at nodes distributed over a large area. Some of these nodes were isolated from others by distances that varied between 0.2 and 2 km, which reduces the frequency of recaptures with displacements in this interval. As a result, home-range size would have been under-estimated at Cape Peninsula.

The Cape Peninsula data were useful in that they showed a continuum in the spatial recapture distribution from 2 km to 1300 km. In other words, those fish that abandoned their home-range moved to sites anywhere within this range of distances from the original home-range. This fact could not be established at the protected sites because the reserves prevented recaptures from large areas either side of the study sites. (The study site measures 3.4 km, but the MPA is much larger, at 51 km.)

The DFD, DND and DGD models represent different types of space-use within the home-range. The model that provides the best fit is the one that should be used to estimate the home-range size. For each of the three study sites, the DFD and DND models did not fit the data satisfactorily (Fig. 2.6). The discrepancy in each case was the same – the observed frequencies for small Δx values were too high, indicating a high degree of central tendency.

The DFD model estimated v to lie between 200 m (at Tsitsikamma) and 1400 m (at Lekkerwater). The σ parameter of the DND model could not be estimated using the likelihood method, because the best fit (when gauged by eye) produced zero $p(\Delta x)$ values at the high end of the Δx range. Zero $p(\Delta x)$ values required the calculation of the logarithm of zero, which causes a mathematical error. Very low likelihood values could have been assigned to such cases, but that would have biased the fit to an unknown

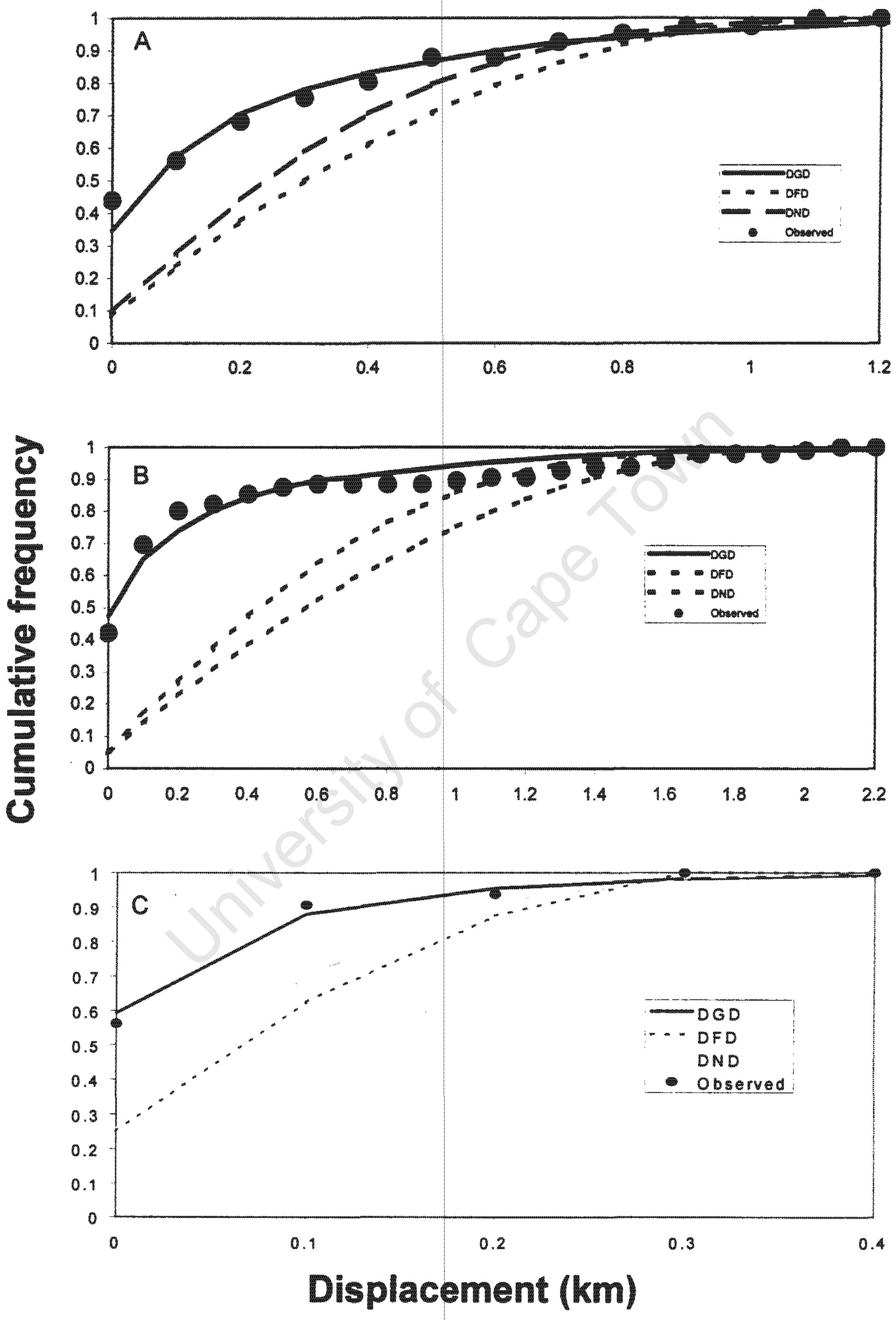


Figure 2.6 The cumulative proportion of recaptures taken at the release site at increasing distances from the point of release. Three model predictions are shown for comparison. (a) Koppie Alleen, (b) Lekkerwater, (c) Tsitsikamma.

extent. No attempt was made to use another method of fitting (e.g. sum-of-squares) as the model was obviously inappropriate. The DND curves illustrated in Fig. 2.6 were based on σ values of one-quarter of the estimate of v provided by the DFD model.

It is not surprising that the DGD model fitted the data best. With two free parameters it is considerably more flexible than either of the others. Based on these fits, home-ranges were estimated to lie between 340 m (Tsitsikamma) and 1380 m (Lekkerwater) (Table 2.8).

TABLE 2.8. Home-range size estimates based on the *difference of flat deviates* (DFD) and the *difference of gamma deviates* (DGD) models. The DGD model gave the best fit in every case, and its parameters are listed. The Kramer and Chapman (1999) predictions for the home-range based on fish size are listed for comparison

	n	*DFD*	*DGD*	α	β	*K&C prediction*
Koppie Alleen	41	800 m	1180 m	0.27	4.8	76 – 572 m
Lekkerwater	82	1400 m	1380 m	0.17	7.5	76 – 400 m
Tsitsikamma	32	200 m	340 m	0.42	0.95	76 – 373 m

The calculation of these home-range estimates is based on a sample that comprised a range of fish sizes from 250 mm to 588 mm. Home-range size varies allometrically, in accordance with the animals' resource requirements. Over this size range, home-ranges of tropical reef-fish were predicted to lie between 76 m and 572 m (Kramer and Chapman 1999). If the same pattern were true for galjoen, it would skew the distribution of displacement probabilities, and in so doing mask the true pattern of space-use. On the other hand, small fish may struggle to maintain a home-range, and may be forced to shift it over the course of a few months, thereby creating the impression of a larger home-range. When the data were split by size (less than 350 mm and greater than 350 mm), there was no evidence to support any of these size-based differences. Small fish and large fish showed the same distribution of space-use within the home-range (Fig. 2.7).

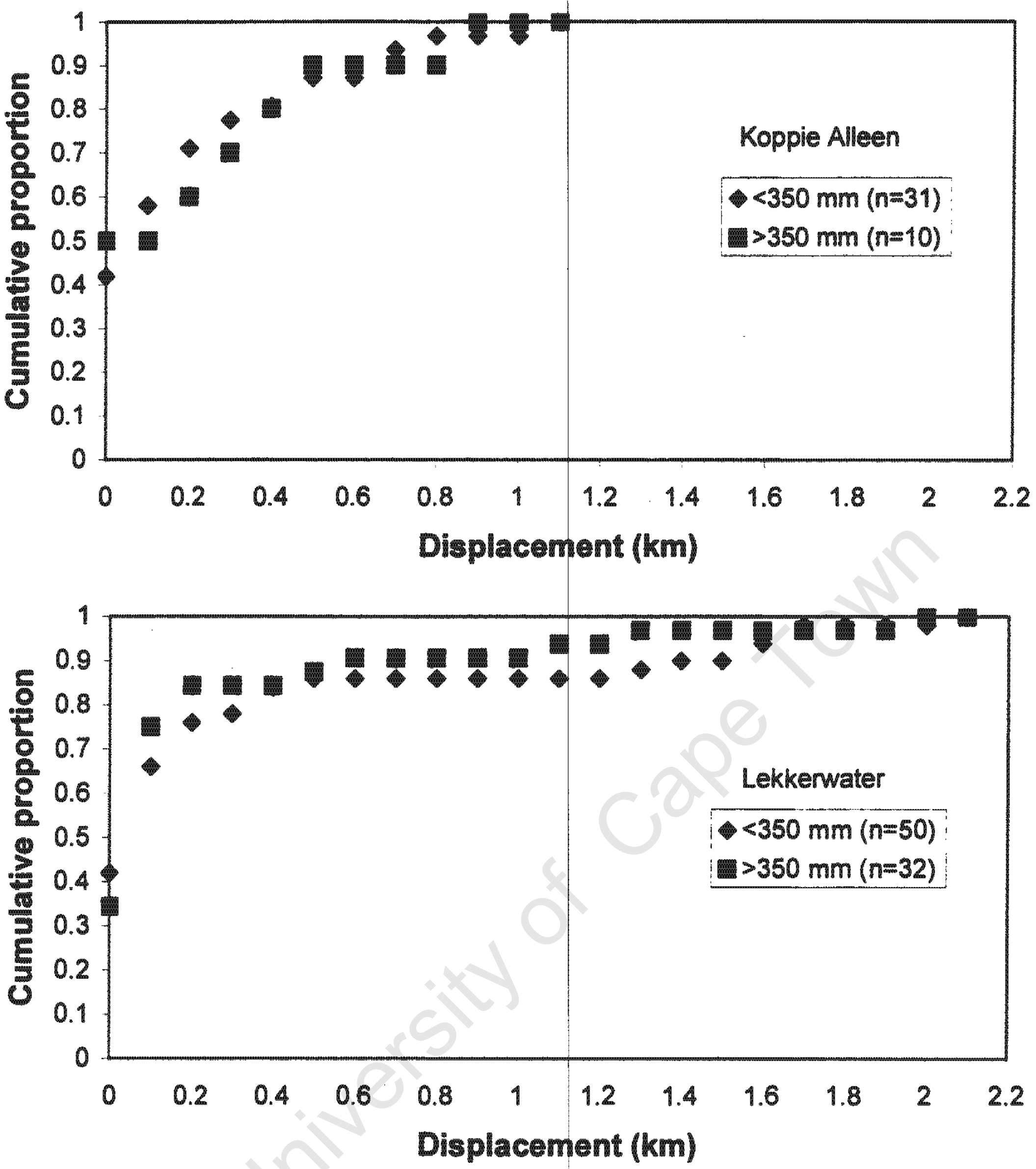


Figure 2.7 The cumulative proportion of recaptures taken at the Koppie Alleen and Lekkerwater release sites at increasing distances from the point of release for two size classes.

If it is accepted that at least some galjoen (perhaps most) hold home-ranges for at least some of the time (perhaps most), what causes fish to abandon the home-range and undertake long-distance movements? Such movements could be related to season or spawning. It has already been established that there are differences in the availability of mature fish within sites between months. The peaks in availability occur during winter/spring *at all sites*, which rules out a seasonal long-shore mass-migration. However, galjoen could still be more prone to leave the home-range at certain times of the year (e.g. non-breeding season), without participating in a mass-migration or going in a predictable direction. Home-range behaviour could be seasonal. To investigate this possibility, it was necessary to look at those recaptures with a short time-since-release and ask if the proportion of recaptures that were taken at the release site varied with release month.

A time-since-release period of three months was considered sufficiently small to detect seasonal effects, yet not so small as to exclude too much data. All recaptures that were free for longer than three months were excluded from this analysis. Those that were recaptured beyond the home-range were classed as 'movers' (i.e. displacement exceeded 2 km). At De Hoop the percentage of recaptures that were taken at the release site did not show a consistent trend with month (Fig. 2.8). This finding argues against any seasonal effect. There were insufficient data to test this hypothesis at the other sites.

Are fish equally likely to be found away from the release site, irrespective of size? It would be better to ask this question in terms of age, but the practical problem of assigning ages to unsexed galjoen prevents this approach. (Male and female galjoen grow at different rates [Bennett and Griffiths 1986].) At the two De Hoop sites, the size of fish differed between those that were recaptured at the release site, those that were recaptured to the east and those that were recaptured to the west (Table 2.9). The equivalent size differences at the Cape Peninsula site were not significant. At each site, the fish that moved were larger, but the differences were by no means clear-cut as the overlap in ranges between samples indicates. Many large fish were recaptured at the release site, whereas many small fish moved.

The multiple recaptures provide perhaps the best evidence for site-fidelity and home-range behaviour. The vast majority of multiple recaptures were at the release site (Table 2.10). Many fish were encountered several times at the same site, with two being caught seven times. The next most common patterns were those that included two identical sites, and a third distant site, once again suggesting a degree of site-fidelity.

TABLE 2.10. The frequency of different patterns of multiple recapture records. Each letter refers to a capture event, e.g. A-A-A indicates that the fish was caught three times. Identical letters imply that the captures were made at the same site, and different letters at different sites.

	A-A-A	*A-A-B*	*A-B-B*	*A-B-A*	*A-B-C*	*A-A-A-A-.. up to 7*
Koppie Alleen	65	4	5	1	1	29
Lekkerwater	46	13	4	1	1	11
Cape Peninsula	7	2	0	0	0	1
Tsitsikamma	2	0	0	0	0	0
Total	120	19	9	2	2	41

Clarification is required on what is meant by the 'same site'. At the De Hoop sites, the 'same site' means anywhere within the 3.4-km research site. The data shown in Fig. 2.6, based on recaptures taken from 1998 onwards, suggest that most recaptures would have remained in a much smaller area. At Tsitsikamma and Cape Peninsula, the 'same site' means within 200 m. The A-B-B (Table 2.10) pattern indicates that the fish was caught once at the research site, and then twice at another site. In this case, the fish were reported as having been caught twice in the same area (i.e. with a common ORI locality code). This reporting system is in practice not accurate to within 1 km – in some cases it may be out by as much as 5 km. Whereas it is assumed, on the strength of the data from the research sites, that two recaptures of the same fish, both recorded against a common ORI locality code, were caught within a distance corresponding to a typical home-range, this may not have been the case.

At both De Hoop sites, there was one record of a fish that moved and then returned to the site of original capture, and one fish that moved between three separate sites. These last two patterns were obviously biased against, because of the small probability that a fish caught outside of the release sites was both reported and returned to the sea alive. The best a researcher can hope for is to have a recapture reported, in which case the angler would normally take the fish home to report the tag.

DISCUSSION

Tag recapture data do not provide much information on fish movement behaviour. Each record gives only two positions (rarely more than two) that a fish occupied at specific times in its life. The most frustrating problem with tag recapture data is not knowing what the fish did between captures. Numerous records are needed to elucidate persistent patterns. Telemetry is a superior means of studying home-range behaviour, but not extensive movements. To follow a galjoen that does migrate would be very difficult, given the extent and pace of some movements. The most rapid displacement recorded was 83 km in three days, and the actual movement could have been faster still! Acoustic reception in the high-energy surf zone may prove to be a further difficulty with telemetry in the case of galjoen. For these reasons, the movements of galjoen are most practically studied with the use of visible coded tags, each bearing a postal address.

Galjoen appear to be robust fish. They live in a turbulent environment and do not shed scales except during severe abrasion. They also remain calm when out of water, which facilitates tagging, but they return to the water with much vigour. This behaviour may be attributed to their habit of feeding in shallow water, which occasionally leaves them stranded between successive waves. Galjoen are probably adapted behaviourally and anatomically to short periods of exposure and tolerate rough handling. These characteristics give the impression that post-tagging survival is high for galjoen. By contrast, other species are difficult to restrain when out of water, some shed scales easily and a few require a period of 'resuscitation' before they swim away. Nonetheless, it is obvious that tagging does affect the growth rate of galjoen, as it does for many other species (Attwood and Swart 2000). Other possible effects cannot be discounted.

The tag-recapture data from widely separated sites were remarkably consistent. In each case the vast majority of galjoen were recaptured in the immediate vicinity of the release site. Those fish that were recaptured away from the release site provided evidence of extensive movements throughout the range. Given that some fish have been known to move from Namibia to South Africa (Anon. 1984; but no evidence of the reverse movement), it is likely that the entire species is represented by one stock.

Galjoen probably spawn throughout their range. There is no evidence to suggest the contrary. Bennett and Griffiths (1986) found ripe females throughout their study area (Cape Infanta to Lamberts Bay). The paucity of fish in the area between Lamberts Bay and Lüderitz is most likely due to the failure of eggs to hatch in these cold waters.

The most appealing means of explaining the recapture distribution is that galjoen follow a random-walk, and that their movements can be described by a modified diffusion model. This type of model has been widely applied to animal movement behaviours (Okubo 1980, Kareiva 1983), but it fails to explain an intriguing feature that recurs in all the galjoen data sets. The probability of a tagged fish being found at the release-site is less than one, but that probability does not decrease with time-since-release (Fig. 2.5). This is a unique feature for which no analogue could be found in the literature on fish, or any other species. It suggests that galjoen may abandon their home-ranges, but without a gradual 'leakage' of tagged galjoen from the release site.

A logical step was to search for some factor that differentiated those fish that had moved from those that were recaptured at the release site, but none could be found. There is no apparent differentiation on the basis of size, sex or season, notwithstanding the slight trend of larger fish to move more frequently (Table 2.9). All fish over 470 mm were female (Bennett and Griffiths 1986) and fish of this size were recaptured both at the release sites, as well as away from them. Consequently, it is assumed that sex is not the differentiating factor. The ratios between those that were recaptured at the release sites and those that were not, were very skewed, which also argues against a sexual distinction in movement behaviour.

Why did a minority leave? It is possible that the distinction between those that moved and those that were recaptured at the release site may be spurious, because some of those that were recaptured at the release site may have moved and returned during their time free. Arguably, the most significant insight into their behaviour is the fact that galjoen hold home-ranges, and any movement beyond home-ranges should be regarded as infrequent deviations from this behaviour.

Home-range behaviour

There is clear evidence of site-fidelity and home-range behaviour among galjoen. The evidence is not direct, but rather statistical. When so many fish are each found to be in the same location at two randomly chosen times, then one can infer that they spend much time at that location (Fig.'s 2.4 and 2.6). The multiple recapture patterns provide additional confirmation of home-range behaviour (Table 2.10). Even among those fish that did leave the release site, the most common pattern still included two captures at the same site. Some fish that appear to have kept a home-range (two captures in the same place) later abandoned it (a third capture elsewhere), or fish that moved from a site established a home-range elsewhere (two recaptures at a common, distant site).

On the issue of home-range size, the four data sets were not in agreement. Recapture records from the two De Hoop sites pointed to larger home-ranges than those from the other sites, irrespective of the estimation method used (Table 2.8). The De Hoop estimates also exceeded the predictions based on the allometric relationship presented by Kramer and Chapman (1999), whereas the Tsitsikamma estimates were consistent with these predictions. The Cape Peninsula estimates were smaller, but these data were disqualified, *a priori*, due to the uneven recapture effort distribution, which served to under-estimate home-range size.

Those studies that have focussed intensively on short-term fish movements have shown that shallow-water species typically follow the same paths in their daily routine and spend disproportionate amounts of time in certain areas (see Chapter 1 for a review). Even within the home-range, the use of resources is spatially structured. The same may be true of galjoen, as there was a high degree of central tendency in the displacement data, as confirmed by the fitted DGD model (which was leptokurtic), and the failures of the DFD and DND models (Fig. 2.6). This distribution could not be explained on the basis of fish size (Fig. 2.7), despite the fact that home-range is in part a function of fish size (Kramer and Chapman 1999).

Galjoen do not, for most of the time at least, show signs of being territorial, as many fish of all sizes are simultaneously encountered in very confined areas, and they are known to swim in shoals. This interpretation is confirmed by the data that showed that large fish move more frequently than small fish, which is the opposite of the pattern found among territorial animals. Captive, ripe females have been known to display aggression towards other fish (van der Lingen, pers. comm.), but this behaviour is linked to either spawning or captivity.

The larger De Hoop estimates of home-range size could be explained by the habitat at those sites, which is unstable. The shifting sand dunes at De Hoop may cause fish to move their ranges either east or west over long periods of time. The Kramer and Chapman (1999) prediction was based on short-term observations in the tropics, whereby the movements of fish were mapped by divers or by telemetry. In contrast, the tag-recapture study used displacements over long periods, often exceeding a year, to estimate home-ranges. During such long periods home-ranges may shift location slightly, thereby giving the impression of large home-ranges, whereas fish use smaller areas during the short-term. If this is the case, then the home-range sizes for De Hoop presented in Table 2.8 are over-estimated and the true home-range size here would be closer to the tropical predictions.

Polymorphic model

The hypothesis that was developed by Attwood and Bennett (1994) that the galjoen population may be differentiated on the basis of movement behaviour, with a large part of the population being resident, while the remainder is nomadic, is still valid as a possible explanation of the recapture distribution. This is termed the *polymorphic* model and the results presented here do not contradict its predictions. Fish that display nomadic behaviour move continuously, such that if one of them is tagged, it will depart the release site shortly. The polymorphic model therefore explains why the fraction of tagged fish found away from the release site is independent of time-free.

There are many examples throughout the animal kingdom of similar differentiations with respect to movement behaviour. These differences may be genetic or conditional on some environmental factor (Swingland 1984, Dingle 1996).

The tourist model

Another model could also explain the existence of 'migrants and 'non-migrants', but without invoking any differentiation within the stock. According to the *tourist* model, a term that I borrowed from Craig and Hulley (1994) who used it to describe sunbird movements, galjoen may simply be moving between two or a small number of sites, where they may establish home-ranges. If tagged fish abandon home-ranges regularly to visit other sites, from which they later return, then the relative frequency of 'zero displacements' will remain approximately constant over time-since-release, as was observed. The ratio of 'zero' to 'non-zero' displacements will be a reflection of the relative amount of time spent in the home-range at the release site, as opposed to other sites, but will also be influenced by recovery effort. The tourist model predicts that fish will temporarily abandon the home-range to feed elsewhere. The data dispel any thoughts that such movements may be linked to spawning (Fig. 2.8, Table 2.9).

There are no clear analogues of the tourist model among fish, although it is appealing on the grounds of parsimony. Why invoke a split in the stock if another model can explain the data simply on the basis of time-partitioning?

Comparison of the two models

The polymorphic and the tourist models are fundamentally different in terms of their ethological mechanisms, but they are very difficult to distinguish on the basis of the data presented here. Following Dingle's classification scheme (1996), the behaviour of the movers should differ in terms of the two models. According to the polymorphic model, those fish that moved would be following a nomadic existence, continuously in search of new resources. According to the tourist model, the movers are migrants, abandoning their home-range temporarily for an alternative site. As migrants, the tourist fish will move rapidly and directly to the new site, probably without feeding along the way. Records of very rapid movements, together with occasional records of galjoen taken in deep water by trawlers suggest that migration is outside the surf zone, where they do not feed. (Of the 3 600 survey trawls undertaken by the government research vessel, '*R.S. Africana*', on the Agulhas Bank between 1982 and 1999, only two captured galjoen, one off Danger Point and one off Mossel Bay.)

Telemetry data on galjoen are needed to effectively discriminate between these hypotheses, but their small size and turbulent environment preclude the use of archival tags and acoustic tracking methods. The tagging method used provides only two positions occupied by a fish at specific times in its life. Only occasionally are tagged fish re-caught more than once.

Of the multiple recaptures, only two fish were recaptured at three separate sites (A-B-C), whereas two moved and then returned to the original site (A-B-A) (Table 2.10). Had there been a distinct bias in the relative frequencies of these patterns, it would have pointed to one model in favour of the other. Nonetheless, some of the multiple recaptures were difficult to reconcile with the polymorphic model (according to which fish are either resident or nomadic), which should result in a prevalence of the A-A-A and A-B-C patterns. Those fish that were captured three times with only two captures at the same site (i.e. A-A-B, A-B-B and A-B-A), indicated that a single fish could display both types of behaviour, i.e. resident behaviour followed by a migration or vice-versa. Such an interpretation is not necessarily correct, because a truly nomadic fish could visit the same site twice, resulting in patterns that could be mistaken for site-fidelity. However, the proportion of three-time captures that followed these patterns was reasonably high. There were 152 three-time captures in total, and the A-A-B, A-B-B and A-B-A patterns together accounted for 19% of these (Table 2.10). Of these three patterns, the recaptures taken outside of the study sites (i.e. the B's) accounted for 12.8% of the recapture events of the three-time captures. (There were 304 recaptures [152 x 2], the A-A-B pattern had 19 occurring at B, the A-B-B had 18 occurring at B and the A-B-A had 2 occurring at B. Therefore, [19+18+2]/304 = 0.128.) Based on the two-time captures, which were far more numerous than the three-time captures, the percentage of recaptures taken outside the study site was 21% (Table 2.6). It follows therefore that the majority of fish that moved from the release sites displayed the A-A-B, A-B-B and A-B-A patterns (12.8% of 21%). The discrepancy between these percentages is likely due to the fact that most fish that were recaptured at B did not survive, and hence could not be re-caught, thereby under-representing the A-B-A and A-B-C patterns. The proportions of the different patterns indicate that even the majority of fish that move display resident behaviour at some stage, which is at odds with the polymorphic model.

The long-distance movements of fish are almost certainly an adaptive strategy, because fish of all sizes abandoned the home-range. If such movements were maladaptive, there would have been a prevalence of small fish moving most frequently, either because they could not maintain a home-range (e.g. Pellett *et al.* 1998) or because they were sub-dominants (e.g. Nakano 1995). The trend of larger galjoen moving more frequently is perhaps a reflection of the reduced cost of movement with increasing size. It may also indicate that fish with greater knowledge of their environment (age = experience) are likely to move more regularly as they have more options.

The distinction between the models is not merely of academic interest – it will have important implications for fisheries management. Mixed evolutionary stable strategies explain the persistence of two (or more) genetically-based behavioural patterns within a population, if the selective advantage of each is frequency-dependent (Swingland 1984). If the polymorphic model has a genetic basis, then the resident morph will be selected against outside of refugia, while the nomadic morph will be selected against inside refugia. (Such an outcome would not favour the use of marine protected areas for fisheries management.) Is the higher proportion of migrants from the Cape Peninsula, the only exploited site that was studied, an indication of such an effect? Approximately 5% of the fish tagged at the protected sites moved, whereas the fraction in the Cape Peninsula sample was 17%. This discrepancy is more easily explained in terms of the polymorphic model than the tourist model.

In terms of the polymorphic model, a conditional response, for example, a response to deteriorating feeding conditions, is unlikely. If fish abandon a home-range because of a conditional response that may occur at any time, then the relative frequency of 'zero displacements' should gradually decrease with time-since-release. Such a decrease was not observed. It could be argued that some factor could condition fish early in life (i.e. before the age at which they were tagged) to either a nomadic or a resident existence, but it is not clear what such a factor might be.

For those who support the use of refugia for fisheries management, the tourist model is more promising. Tourists will be protected in a refuge, but will occasionally leave and become available for capture elsewhere. The large ratio of 'zero' to 'non-zero' displacements suggests that such exchange will not ‘drain’ the protected stock, while it may provide modest replenishments of adult fish to exploited areas, in addition to any additional supply of recruitment.

Dispersal, relative to within-patch movements, is an under-studied process (Travis and French 2000). The factors that cause animals to move and that determine the distance that they move and the site that they eventually choose remain elusive. Among trout, which is generally considered to be resident species, it is now known that fish occasionally and unpredictably undertake large migrations (Gowan and Faush 1996). Such movement may be an attempt by the fish to escape unfavourable conditions or reconnoitre their environment for the purpose of selecting new sites (Railsback *et al.* 1999).

Travis and French (2000) argue that most spatial models that incorporate animal movement are 'generally misleading' because they treat animal dispersal simplistically. Dispersal is usually modelled as either a move to a neighbouring patch, or a 'global' move that could take it to any patch (e.g. Fryxell and Lundberg 1993). In reality, animal dispersal lies between these extremes, tempered by such factors as density, cost of movement and familiarity with the environment. For galjoen, the distribution of distance moved, while very wide and occupying almost the entire range, is strongly leptokurtic. It is clear that 'spill-over' (Russ and Alcala 1996b, Jennings 2001) occurs among galjoen, but it is not a local phenomenon, detectable at reserve boundaries by a linefishery. (In contrast, a gill net-fishery would catch migrants at the reserve boundary.) Those that abandon the home-range move widely, so that if a fishery enhancement occurs immediately adjacent to a marine protected area, the mechanism is more likely to be larval dispersal than adult movement.

This interpretation is not at odds with the situation described by Alcala and Russ (1990) at Sumilon Island. They found that fish yields on the coral atoll were enhanced by the proximity of a small reserve, which they ascribe to adult fish moving (*migrating*, by their terminology) from the protected area to the fished area. Because of the small areas involved (the size of the reserve was 0.5 km^2) these fish movements were most likely not migrations or ranging movements, but rather movements within a home-range that straddled the reserve boundaries.

Divers report a variety of behavioural types with regard to shoaling and aggregation of galjoen (Rust and Rust 2000). Large shoals of similar sized fish are usually encountered outside of the surf zone on shallow reefs and particularly on wrecks. These fish do not appear to be feeding. In the surf zone, galjoen of all sizes may aggregate in large feeding shoals, or they may be encountered in small groups of less than ten. Galjoen are known to travel in schools, and may suddenly 'appear' in an area in large numbers. Shoaling behaviour could be explained by the polymorphic or the tourist model.

Home-range behaviour is very common among reef-fish, and indeed among fish from all habitats (Chapter 1). Studies of departures from the home-range, despite being a common behaviour, have been very few, largely because of the difficulty of studying fish movement intensively (to establish the home-range pattern) and extensively (to follow large-scale movements). The swallowtail dart *Trachinotus botla* shows an over-dispersed spatial recapture distribution (McPhee *et al.* 1999). Like galjoen, there is a trend of large fish moving more frequently; but unlike galjoen, the mean displacement distance was positively correlated with time-since-release. Movements of swallowtail dart are more reminiscent of ranging behaviour, whereby each fish has the potential to move widely. However, there was no evidence to suggest that swallowtail dart return to home-ranges, or that they hold home-ranges at all. The sablefish *A. fimbria* shows the same pattern, but on a much larger scale, with some movements exceeding 2 000 km (Beamish and McFarlane 1988). There is also no indication that sablefish hold home-ranges.

Off New Zealand, the hapuku *Polyprion oxygeneios* displays a mix of station-keeping, ranging and spawning migrations (Beentjes and Francis 1999). Some fish moved widely, and others were caught in exactly the same place over a period of five years. The galjoen recapture pattern therefore is not unusual. Many fish species display a curious mix of station keeping and migration (see Chapter 1), but for most there has not been much interest in the pattern, or any explanation why fish should abandon a home-range. It may be necessary to concede a substantial degree of plasticity in movement-behaviour of fish.

Theoretical considerations

Are there any theoretical considerations that might point to one model instead of the other? Cury's (1994) discussion of obstinate behaviour argues strongly for site-fidelity, particularly when it comes to spawning. The most successful strategy in the face of environmental uncertainty is simply to use the same area as your parents, who must have bred successfully. He does point to the occasional strays that '*are essential for long-term dynamics by exploring and fixing new environmental solutions that later become possible for the species*'. By this he implies that straying is adaptive. His arguments, and others along these lines, might be interpreted to favour the polymorphic model.

Another hypothesis is the ideal free distribution, which states that animals will be distributed in such a manner that each individual experiences the same food availability. Notwithstanding some problem assumptions, the model predicts that the distribution of animals will match the distribution of food. The process of distribution can include active movement, or selective mortality and reproduction rates that ultimately lead to different densities in different areas. MacCall (1990) developed a fish movement model on the assumptions of the ideal free distribution. That model predicted a gradual diffusion away from highly productive areas, due to larval drift, and a subsequent return towards productive areas by adults. Whether or not such a process occurs among galjoen cannot be established, largely because of the difficulty of determining where the productive areas are, other than by measuring adult density. Galjoen may frequently abandon home-ranges to sample areas elsewhere, and in that way routinely establish if their home-ranges offer the best feeding environment. Such a pattern is consistent with the tourist model. Travis and French (2000) term this 'intelligent-dispersal'. Some form of reconnaissance and information sharing between fish will make such migrations less risky.

Chitty's model, which was based on voles, predicts that cycles of population abundance are caused by density-dependent changes in the selection of behaviour. High densities favour aggression and migration, whereas low densities favour high reproductive potential and resident behaviour (Krebs *et al.* 1973). Chitty's hypothesis has a direct bearing on a common debate on the effect of marine protected areas in fisheries. If fish reach carrying capacity in a refuge, will there be a greater tendency for emigration? In other words, is the frequency of movement density-dependent? Fish may leave the home-range more frequently if density or intra-specific competition for resources is high. Not all observations of density-dependent migration support such a model (Travis and French

2000). Galjoen appeared to have the greatest frequency of residency in protected areas, where density was greatest (see following chapter), whereas those at the exploited site showed the greatest frequency of movement. There is no evidence that increased galjoen density promoted dispersal. Doherty and Williams (1988) found little evidence for resource-saturation among natural populations of coral reef-fish. The concept of local adult 'spill-over' from populations near carrying capacity in protected areas has little supporting evidence.

The choice of model is not made easier by the fact that they are not mutually exclusive. Many fish may remain resident their entire lives, while others display tourist-type behaviour. At this stage both models are regarded as possibilities, but the investigation will be pursued further in Chapter 5, by way of an individual-based model that can simulate the frequencies of recapture patterns for comparison.

CONCLUSIONS

Galjoen are principally resident fish with no set migration routes. They breed throughout their range, but the low survivorship of eggs below 15°C is likely to be the cause of the paucity of galjoen in the strong upwelling area between South Africa and Namibia. Egg dispersal is unlikely to be widespread in view of the fact that neither galjoen eggs nor larvae have ever been found at sea, despite extensive surveys that have detected eggs and larvae of hundreds of other species within the range occupied by galjoen (Beckley 1986, 1993, Buxton and Smale 1984, Tilney et al. 1996). There is sufficient evidence of long-range adult movement to suggest that the Namibian and South African stocks are part of the same population.

The size of the home-range is possibly larger than the allometric prediction of Kramer and Chapman (1999) based on an analysis of tropical reef-fish. The difference may be attributable to home-range shifts forced by a dynamic dune system at De Hoop, or because of differences in the way that the home-range was estimated.

Whether all fish follow the same strategy, which entails visiting a small number of sites, or whether a small fraction of the stock display a distinct nomadic type behaviour, while the remainder hold home-ranges is unclear. An examination of the relative frequencies of multiple recapture patterns suggested that individual fish may display resident and migratory behaviour, but the evidence is far from conclusive. A careful consideration of fitness-enhancing fish-movement rules, such as that undertaken by Railsback *et al.* (1999) for stream fish, may be necessary to resolve this issue.

Fish movement behaviour will have consequences for fisheries management. The stock is obviously not well mixed on the short time-scales that are relevant to fisheries management, which implies that the galjoen stock should be assessed at lightly and heavily exploited areas. Galjoen found in unexploited areas will be predominantly resident, whereas those found in heavily exploited areas will be either nomadic or recent arrivals. The fact that large fish move more frequently suggests that catch-at-size distributions derived from fishery data in areas where there has been a recruitment failure will be positively skewed due to the scarcity of young fish, compared to old fish that are replenished from elsewhere. Such a bias in catch-at-age analyses could have serious consequences for stock assessment.

The results obtained by this study indicate that any model of galjoen movement that is based on diffusion or constant transfer rates, as has been commonly applied to other species (see generic model of Hilborn 1990), will provide erroneous results. This conclusion is shared by Travis and French (2000). Galjoen movements are clearly structured, and any model that successfully reproduces observed patterns will have to account for individual variability and behavioural plasticity.

CHAPTER 3

ESTIMATING PARAMETERS OF THE GALJOEN *(DICHISTIUS CAPENSIS)* FISHERY

ABSTRACT

The dynamics of the fishery for galjoen *Dichistius capensis* were investigated at four sites in South Africa from 1987 to 2000. At three sites, which were protected from fishing, namely Koppie Alleen, Lekkerwater (both in the De Hoop Marine Protected Area) and Tsitsikamma, fishery-independent surveys were conducted. Data for the Cape Peninsula were obtained from records kept by a recreational angler. Catch-per-unit-effort (CPUE) was highest at De Hoop and lowest at Tsitsikamma. At De Hoop, CPUE varied significantly among anglers, months, years and gear-type. The mortality-rate was greater at the exploited site than at protected sites, where mortality-rates were taken as estimates of natural mortality. Tag and recovery data were used to estimate density and catchability. Fishing mortality-rates were very high, whether inferred from size-distributions, or from the product of effort counts and the catchability coefficient. Such high rates can be sustained only through the existence of refuges. Variation in fishery parameters among habitats and the high variance in CPUE data suggest that an effective monitoring programme will need to be intensive. To provide adequate stock assessments, fishery-dependent surveys should be augmented by studies in marine protected areas.

INTRODUCTION

Like so many of South Africa's linefish species, the galjoen *Dichistius capensis* has been heavily exploited. Prior to World War II it was reported that the numbers of galjoen were in decline in certain areas (Smith 1935). By 1973 galjoen were considered to be in serious trouble and a size limit was introduced. In 1984 the restrictions were revised again to further curb fishing mortality by adding a closed season and a bag limit. The first study of galjoen was undertaken by Bennett and Griffiths (1986) who worded their assessment of the stock carefully: '*Hard evidence to substantiate the contention that the numbers of galjoen are decreasing is difficult to find, …*'

Hard evidence is unnecessary for experienced fishermen - they know that the resource is severely depleted. A recent compilation of articles and quotes about galjoen (Rust and Rust 2000) leaves no doubt in the reader's mind that what was once an extremely abundant catch is now comparatively scarce. Bennett and Griffiths (1986) were referring to the frustration of not having accurate catch statistics to measure the decline in abundance. The only means of assessment was a per-recruit analysis, which Bennett (1988) based on the female stock. Only 16% of the original spawner-biomass-per-recruit remained. That classes galjoen as a collapsed fishery (Griffiths 1997).

The management of the galjoen fishery, and of most other South African linefish, is far from satisfactory. Since the 1973 regulations were promulgated, there has been no attempt to ascertain whether they have been successful in recovering the stock. The need to monitor the stock on a regular basis is now being addressed in a nationwide programme to improve linefish management (Griffiths 1997), but the design of an effective monitoring strategy will depend on a better understanding of galjoen fishery dynamics than we have at present. In particular, we need to know how much monitoring is required to estimate the chosen indicators with sufficient accuracy to be useful for assessment. The error in the indicator sets the limit for detection of change.

Most assessments of South African linefish stocks have been based on per-recruit models, but these give no indication in absolute numbers of population size, density, or depletion due to fishing. Another difficulty with the per-recruit calculations is the estimation of the natural mortality-rate. In South Africa, catch-at-age data are used to estimate the total mortality-rate, from which the natural mortality-rate is subtracted, leaving a remainder that is attributed to fishing. Bennett (1988) chose a value that was derived from a statistical analysis of natural mortality-rates and water temperature combinations across many species. While these two variables are positively related, there is considerable scatter about the regression, which clearly calls for a direct assessment of the natural mortality-rate of galjoen.

In theory, because galjoen are largely resident, mortality-rates and catch-per-unit-effort rates (CPUE) should vary between protected and exploited areas. This study compares data from fishery-independent surveys undertaken in three protected areas and one exploited area to provide a fresh analysis of the impact of fishing on the stock. The surveys made use of tag and recovery data, which presented the opportunity to estimate population density and catchability. The assessments are then used as a basis to plan a monitoring programme.

METHODS

Study areas

Fishery surveys were undertaken at Koppie Alleen and Lekkerwater (both in the De Hoop Marine Protected Area), Tsitsikamma National Park and Cape Peninsula. These sites and the details of the tagging procedures are described in Chapter 2. Additional detail relevant to the calculation of CPUE is provided below.

Catch-per-unit-effort

De Hoop

A small number of volunteer anglers assisted the author and two other fishery scientists in the capture and tagging of fish. The composition of the volunteer angling team was kept as constant as possible. Although, in total, use was made of 86 anglers during 126 trips (Table 2.1), most effort was accounted for by ten anglers. On each day of each trip anglers fished continuously, starting usually an hour after sunrise and finishing at sunset. The number of hours fished per angler was recorded. Prior to 1995, there were 11 field-trips per year, each held in a different moth, but thereafter the frequency was reduced to six per year. Apart from this change, sampling trips were undertaken in the same months of each year. No other fishing took place within De Hoop MPA.

Prior to 1995 the anglers kept to a single standard technique. They used 3 to 4 m fishing rods, with multiplier reels loaded with 10-15 kg breaking strain nylon. Lead sinkers weighing between 100 and 150g were used to cast bait on or near reefs in broken surf. The bait was limited to white mussels *Donax serra*, red-bait *Pyura stolonifera* and wonderworm *Marphysa* sp. Mustad 92570 hooks were used, ranging in size from #1 to #2/0. This technique, which targeted small epilithic feeders, was called the small-fish technique or *SFT*.

From 1995 onwards, a second fishing technique was introduced to target larger piscivorous fish, for which additional information was needed. Heavier tackle was used: sinkers weighed between 150 and 200 g, hook size varied from #3/0 to #10/0 and bait included bloodworm *Arenicola loveni*, pilchard *Sardinops sajax*, and chokka squid *Loligo vulgaris*. These baits were cast further into deep, unbroken surf, where the larger species were encountered more frequently. This technique was referred to as the big-fish technique or *BFT*. Anglers were instructed to use one or the other technique, which was recorded against that angler's catch. Both techniques caught galjoen, although galjoen were not a target of the BFT.

A third technique that was introduced to target elasmobranch species never caught galjoen and therefore does not contribute to this study. The combination of the three techniques cover the complete spectrum of methods used by shore-anglers in the Western and Eastern Cape. Spear-fishing is the only other technique that is used to catch galjoen legally, although there are reliable reports of localised illegal gill-net fishing for galjoen (Hutchings 2000).

Tsitsikamma

A research programme was initiated here in 1995, based on a similar design to the De Hoop programme (Table 2.1). A fishing trip was conducted every month, in which a small number of volunteer anglers assisted a scientist from the Department of Ichthyology and Fisheries Science in Grahamstown. Fish were caught, tagged and released using the *SFT*. Being in a reserve, the only fishing undertaken at this research site was by the research team, although there was concern that a small amount of poaching occurred.

Cape Peninsula

One of the anglers who participated in the tagging studies at De Hoop, also fished regularly at Cape Peninsula. He caught and tagged fish using the SFT, in the same way as described for De Hoop, and maintained complete records of every fishing trip. Fishing days were evenly distributed throughout the 7.5-month recreational season, which runs from the first of March to the fifteenth of October. Records were maintained from 1987 to the present (Table 2.1).

Statistical methods

Symbols that are routinely used in the text are explained with a listing of their units in Table 3.1.

1. Linear modelling of catch-per-unit-effort (CPUE) at De Hoop

CPUE rates are frequently used as a relative measure of fish density, but are likely to be influenced by a number of factors other than fish density. Ideally, these influences need to be factored-out before CPUE is used as an indicator of density between years and months. To examine the extent of these influences, a log-linear model was used to model the effect of angler, month and year and the interactions between them on the CPUE rates. This exercise was performed on the De Hoop surveys only, for the following reasons: (i) CPUE was very low and insufficient effort was applied at Tsitsikamma to get meaningful results, and (ii) at Cape Peninsula, only one angler and one fishing technique was used, and the CPUE was strongly affected by the fishery at that site.

TABLE 3.1: Definitions and units of mathematical symbols used in the text.

Symbol	*Definition*	*Unit*
C_i	i^{th} record of the number of fish caught by one angler in one day	fish
E_i	i^{th} record of the number of hours fished by one angler in one day	hours
$G_{a,k}$	Number of fish caught at site a, during trip k	fish
$T_{a,k}$	Number of fish tagged at site a, during trip k	fish
$R_{a,k}$	Number of fish recaptured at site a, during trip k	fish
$S_{a,k}$	Number of tagged fish still at large at site a, during trip k	fish
$N_{a,k}$	Number of fish at site a, during trip k	fish
H_k	Total effort applied during trip k	hours
n_{ik}	Number of times fish i was recaptured during trip k	captures
t_k	Date in the middle of trip k	Julian-day
L_i	Total length of fish i	mm
F	Instantaneous per-capita fishing mortality-rate	y^{-1}
M	Instantaneous per-capita natural mortality-rate	y^{-1}
Z	Instantaneous per-capita total mortality-rate	y^{-1}
β	Instantaneous per-capita tag-mortality-rate	y^{-1}
θ	Migrating fraction	ratio
q	Catchability	$km.h^{-1}$
r	Recatchability	$captures.h^{-1}$
ω	Proportion of fish that are male at recruitment	ratio

CPUE was expressed as a discrete count, C_i (number of fish caught by an angler during one day) for which the errors were assumed to follow a Poisson distribution (McCullagh & Nelder 1989). The model was,

$$\log(C_i) + error_i = \log(\lambda_{amys}) = \mu + \mu_a + \mu_m + \mu_y + \mu_s + \mu_{(m*y)} + \mu_{(a*s)} + \log(E_i), \qquad \text{eq. 3.1}$$

where λ_{amys} is the predicted catch rate, μ are the factors and the subscripts a, m, y and s refer to angler, month, year and technique (SFT or BFT), respectively.

CPUE records from the two De Hoop sites were modelled separately, for the years 1993 to 1999 (consistent use of anglers was made during this period). Although it was possible to lump these two sets together and then add *area* as another explanatory variable, the *month* and *area* factors would have been confused as different months were sampled in different areas according to a schedule that did not change between years. Two interaction terms were deemed meaningful as explanatory variables, namely [month x year], which accounts for variability at the trip level, and [angler x technique], which accounts for variability associated with the individual angler's use of different gear-types. Catch was assumed to be proportional to effort, measured in hours.

The model was fitted using the SAS (version 6.12) macro GENMOD (SAS Institute Inc. 1993), which employs a maximum likelihood method. The likelihood is the product of the Poisson probabilities of observing each C_i count, given the λ_{amys} values as calculated from the terms in equation 3.1. An algorithm evaluates different sets of values for these terms until it finds the one that results in the greatest likelihood value. GENMOD then evaluates the fit by calculating the deviance as an inverse measure of the fit. The deviance is twice the difference between the maximum attainable log-likelihood and the log-likelihood of the model under consideration.

The variance equation was adjusted by a factor related to the deviance (GENMOD DSCALE option) to allow for an error distribution that was over-dispersed with respect to the Poisson distribution. Over-dispersion could indicate an inappropriate choice of model. In this case, over-dispersion was expected, given a large daily variation in catch-rates that was more likely to reflect changes in fish-feeding conditions than changes in local fish abundance or angler performance. The Poisson distribution accounted for the error associated with the random chance of an angler catching a fish. The additional error attributable to daily variations in weather and water conditions lead to over-dispersion. Daily variation could not be factored out. The over-dispersion factor does not affect the parameter estimates, only the associated errors and significance tests.

The GENMOD TYPE 1 ANALYSIS was used to test the significance of each of the terms in equation 3.1. It starts by fitting the most basic version of equation 3.1, i.e. $\log(C_i) + \text{error}_i = \mu$, for which it calculates the deviance. It then progressively adds the remaining terms, each time calculating the deviance and testing whether the additional term provided a significant improvement in the explanation of the variance about C_i. To do so it uses the F-statistic, calculated from the difference in the deviance caused by the additional term. A large F-statistic translates into a small probability that the reduction of the deviance was due to chance. If that probability was less than 5%, then the term was regarded as significant.

2. Mortality rate

Mortality rates of exploited fish can be calculated from the declining frequency of catch-at-age (Butterworth *et al.* 1989), but it requires converting catch-at-size to catch-at-age data. This procedure is difficult to apply to galjoen, because the males and females grow at different rates (Bennett and Griffiths 1986). Fish were not sexed at any of the sites during the tagging experiment because galjoen could not be sexed without killing the fish. Using blood samples, Van der Lingen (1990) was able to identify the sex of most mature females for a few months prior to and during the breeding season, but immature fish and fish outside of the breeding season could not be sexed in this way.

In theory, given that males and females grow at different rates, a large enough random sample of fish lengths should hold information about the total mortality-rate and the relative proportion of each sex. A likelihood function was developed, to estimate both of these parameters from catch-at-length data.

The probability of selecting a fish of age t is

$$p(t) = Z\, e^{-Zt} \qquad \text{eq. 3.2}$$

and the probability of selecting a fish of length L is

$$p(L) = Z\, e^{-Zt(L)}\, \partial t / \partial L\,, \qquad \text{eq. 3.3}$$

where t(L) is the age of a length L fish and ∂t/∂L is the rate of change of age with length. A galjoen of length L could be either age $t_m(L)$ or $t_f(L)$, depending on its sex. These deterministic age-length functions are given by Bennett and Griffiths (1986). The probability of drawing a galjoen of length L from a population which experiences a constant mortality-rate can be formulated as follows:

$$p(L_i) = \omega Z e^{-Zt_m(L_i)} \, \partial t_m / \partial L + (1-\omega) Z e^{-Zt_f(L_i)} \, \partial t_f / \partial L \qquad \text{eq. 3.4}$$

In equation 3.4, ω is the proportion of newborn fish that are male.

However, the full size range of fish is never available from any one sampling technique. In the case of angling, the sample is truncated, eliminating all L < 325 mm, which is approximately the size at full selectivity, i.e. the length category with the highest frequency in the catch. To account for truncation, equation 3.4 was modified as follows:

$$p(L_i) = \omega Z e^{-Z(t_m(L_i)-t_m(325))} \, \partial t_m / \partial L + (1-\omega) Z e^{-Z(t_f(L_i)-t_f(325))} \, \partial t_f / \partial L \qquad \text{eq. 3.5}$$

In equation 3.5, ω is the proportion of males at recruitment, L = 325 mm. If a fish exceeded the maximum length for a male galjoen, then the first term in equation 3.5 was dropped. The log-likelihood function that was minimised with respect to Z and ω is:

$$LLH(L \mid Z,\omega) = \sum_i \ln p(L_i) \qquad \text{eq. 3.6}$$

Given the catch-at-length data set L, the values of Z and ω that yielded the lowest LLH were taken as the best estimates. The variances of these estimates were computed using information contained in the likelihood surface. The inverse of the second partial derivatives of the likelihood along the Z and ω axes (known as the Hessian matrix) are estimates of the variance and co-variance of the parameter estimates (Lebreton *et al.* 1992). The second derivative was calculated using a fourth order finite-difference method, and its square-root yielded the standard error.

The confidence intervals on these estimates were also calculated using the likelihood profiling method, which is regarded as more accurate for parameters that occur near a natural boundary (e.g. zero) (Lebreton *et al.* 1992).

To test the estimation procedure, a random number generator was used to produce synthetic data sets of catch-at-length, using a variety of Z and ω values. The sex of each artificial fish was determined randomly (with mean ω), and its life-span was drawn randomly from a negative exponential distribution (with slope $-Z$). Bennett and Griffith's (1986) age-length functions were used to convert age to length. Data sets of two sizes were generated for a variety of sex-ratios and mortality-rates, and the estimator (equation 3.6) was tested once on each data set. The estimates were compared to the Z and ω that were used to generate the data-sets.

For sample sizes of 10^3 and 10^4, the 95% confidence interval (calculated by the likelihood profile method) included the true values for each simulation (Table 3.2). However, it is apparent that the length-data hold little information on the sex ratio, particularly for high mortality-rates. High mortality-rates reduce the number of old fish, whose lengths carry most of the sex information. (The size difference between the sexes increases with age.) As a result, the confidence intervals on ω-estimates were considerably narrower for small Z-values. Because there was co-variance between the two parameters, the same was true of the confidence intervals about the Z-estimates. The second partial derivative of the likelihood surface ($\partial LLH^2/\partial Z\partial\omega$) was always strongly negative, which indicates that estimates of Z and ω are negatively correlated, i.e. an underestimate of ω would be accompanied by an over-estimate of Z.

A similar procedure was used to investigate the dependence of standard errors on sample size. Data sets of various sizes were generated for two parameter sets, namely {ω=0.5 and Z=0.4 y^{-1}} and {ω=0.5 and Z=2.0 y^{-1}}. Standard errors, which were calculated using the inverse Hessian method described above, decrease abruptly with sample size initially, but gradually flatten out at a sample size of about 8000 (Fig. 3.1).

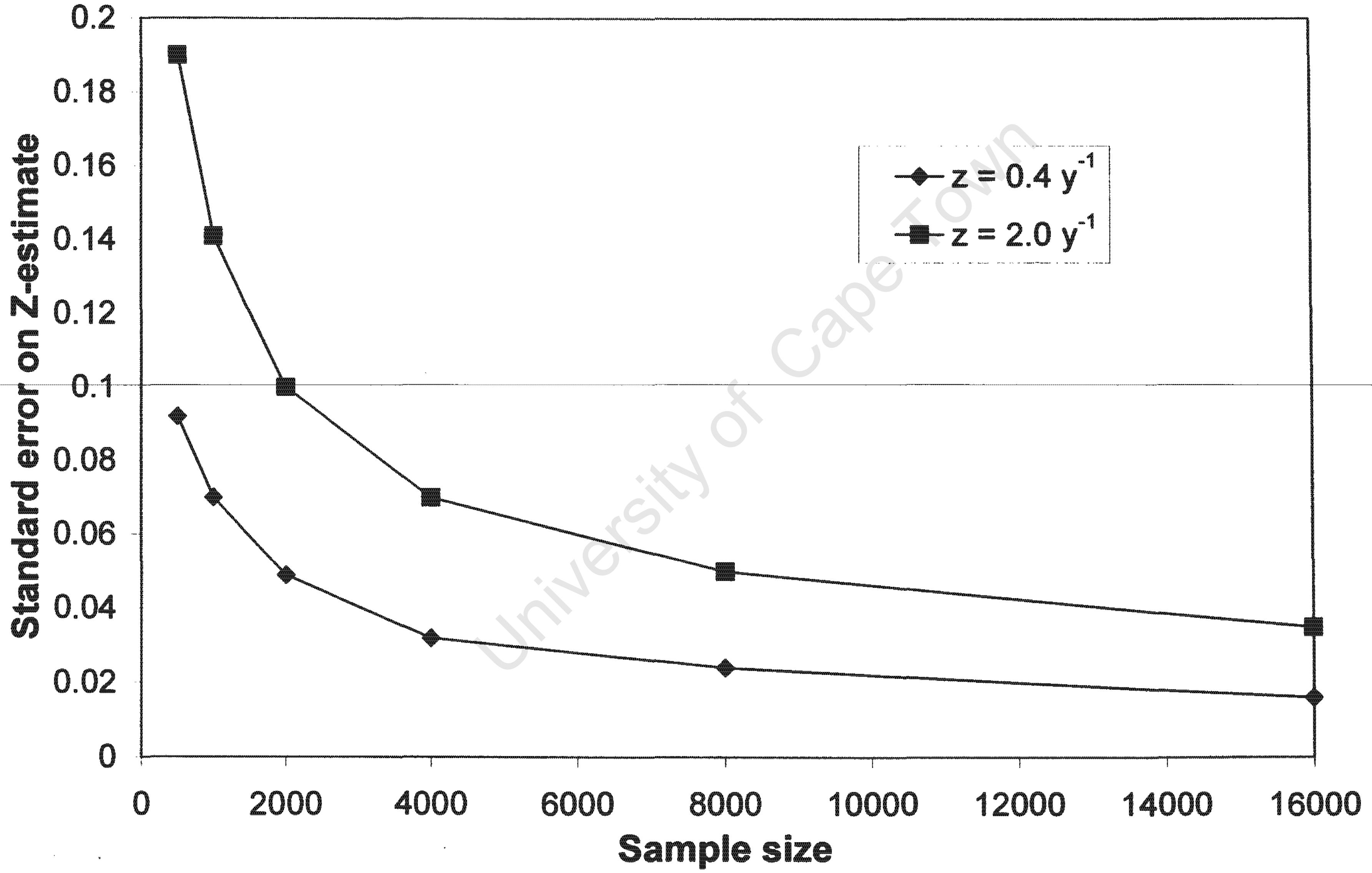


Figure 3.1 The relationship between the standard error of the estimate of mortality-rate based on catch-at-age data and sample size.

3. Tag-mortality-rate

The rate at which tagged fish are lost is the sum of the rates of natural mortality, fishing mortality, tag-induced mortality, and tag shedding. From tag-recapture data alone it is not possible to estimate the relative contributions of these processes, unless a double tagging procedure is used to quantify the tag-shedding component.

TABLE 3.2: Results of trials of the mortality-rate estimation procedure with simulated data sets of two sizes. True values of the male proportion [p(M)] and mortality-rate (Z) are given in the left-most column. The lower (L) and upper (U) 95% confidence limits are listed for each trial.

True value		Trials with n=1000				Trials with n=10000			
p(M)	Z	p(M)		Z		P(M)		Z	
		L	U	L	U	L	U	L	U
0.25	0.2	0.08	0.29	0.19	0.26	0.21	0.31	0.18	0.21
0.25	0.4	0.15	0.48	0.32	0.43	0.00	0.45	0.34	0.46
0.25	0.6	0.0	0.31	0.56	0.70	0.00	0.38	0.55	0.66
0.25	0.8	0.0	0.57	0.73	0.98	0.00	0.65	0.66	0.91
0.50	0.2	0.47	0.65	0.18	0.23	0.46	0.55	0.19	0.22
0.50	0.4	0.28	0.60	0.37	0.47	0.39	0.60	0.37	0.43
0.50	0.6	0.39	0.76	0.49	0.63	0.28	0.65	0.55	0.68
0.50	0.8	0.0	0.85	0.63	1.04	0.14	0.64	0.74	0.91
0.75	0.2	0.72	0.82	0.17	0.20	0.72	0.80	0.18	0.21
0.75	0.4	0.61	0.82	0.37	0.44	0.69	0.80	0.38	0.43
0.75	0.6	0.37	0.82	0.55	0.72	0.69	0.82	0.56	0.62
0.75	0.8	0.39	0.92	0.70	0.94	0.46	0.88	0.75	0.92

The tag-mortality rate can be estimated from the distribution of time-free measurements for all recaptured fish. The number of recaptures should follow an exponential distribution with respect to time-free. The tag-mortality-rate equals the inverse of the average time-free for all recaptured fish. The proof for this equality is given by Butterworth *et al.* (1989).

Such a simple procedure could not be used in this study because fish were tagged over a long period of time, and the time available for recapture was greater for those fish tagged in the early stages of the experiment and less for those tagged towards the end. Furthermore, recapture effort was not evenly distributed over time. At the protected sites, all fishing was restricted to three short fishing trips that were distributed unevenly during the year. At Cape Peninsula, the amount of recapture fishing effort was unknown, and it was limited to only 7.5 months of the year. Asymmetry in the recapture distribution could bias the simple estimation procedure based on average time-free.

Another procedure was devised that evaluated the likelihood of the observed temporal distribution of recapture frequencies. If fish i was released during trip j and recaptured three times, twice during trip k=j+2 and once during trip k=j+4, then its recapture record over the next 10 trips would be [0,2,0,1,0,0,0,0,0,0]. Each element in this vector is notated n_{ik}. The probability of recapturing a specific tagged fish during trip k depends on the amount of effort applied during the kth trip, and the probability of the fish being alive at the release site with its tag during trip k. Therefore, each trip has a unique expected frequency of recapture for each tagged fish, and the likelihood of the observed counts can be related to these expected frequencies using the Poisson distribution. This distribution is appropriate because of the random element associated with capturing a tagged fish and the very low observed recapture frequencies for individual fish. The likelihood of a single recapture record is the product of these probabilities over all trips subsequent to release, and the likelihood of the entire data set is the product of the likelihood of each recapture record of every released fish.

Two parameters are required to compute the expected mean recapture frequency, namely tag-mortality-rate and recatchability. In reality, there are more than two processes involved, but some of these become confounded, as discussed above, and cannot be identified separately. For example, the probability of a fish being present with its tag during trip k is the combined probability of it not having emigrated, died or lost its tag. The last two of these at least are confounded, and tag-mortality-rate (β) is assumed to be the rate at which tagged fish disappear, covering the different processes mentioned above.

The recatchability parameter (r) is the average number of times a specific fish will be caught with one unit of effort. Recatchability (units = captures per hour) includes catchability (q), but the two should not be confused. Using standard fisheries notation, where C is catch, E effort, and N population size, C = qEN. If N = 1 (the one tagged fish), then [qN] is the parameter referred to here as recatchability. Unfortunately, because of confounding, the effects of emigration are mixed in the estimate of r. Because the net movement of tagged galjoen from the release area was rapid, and not a gradual leakage (chapter 2), emigration was more likely to be confounded with recatchability than tag-mortality. For this reason, it was preferable to keep recatchability separate from catchability, which is to be estimated in another way.

The mean Poisson frequency (ϕ_{ik}) of recapture of fish i, which was tagged during trip j, during trip k is

$$\phi_{ik} = r\,H_k \exp^{-\beta(t_k - t_j)} . \qquad \text{eq. 3.7}$$

The probability (p_{ik}) of recapturing fish i, n_{ik} times during trip k is

$$p_{ik} = \frac{e^{-\phi_{ik}}\ \phi_{ik}^{\ n_{ik}}}{n_{ik}!} . \qquad \text{eq. 3.8}$$

The negative log-likelihood of the entire data set is therefore

$$LLH = -\sum_i \sum_k \log(p_{ik}) . \qquad \text{eq. 3.9}$$

The best estimates of r and β were obtained by minimising LLH. The confidence intervals were calculated using the likelihood profiling method, as described above for the mortality-rate procedure.

This model is of the general form described by Lebreton *et al.* (1992) to estimate survival rate, but in contrast to their examples, it has only two estimated parameters. Lebreton *et al.* (1992) show that time-dependent survival rates can be calculated for each period between release-recapture events. In general, one can estimate $(k-1)^2$ time-dependent survival rates and capture probabilities, given k sampling events. In this case, there were certainly enough data to attempt such a multi-parameter model. However, in the interest of accuracy and because the relevance of time-dependent changes in tag-mortality-rate to this study is questionable, a single mortality-rate was estimated. This model extends the basic Lebreton *et al.* (1992) model by specifically incorporating time and capture effort, thereby reducing the need to estimate each capture probability separately. It also uses the log-link, instead of the logit-link, as there is no need to constrain the predicted mean value between zero and one.

4. Galjoen density at De Hoop

The results of the controlled tagging experiment at the two De Hoop sites were used to estimate the average number of fish at those sites during all trips. A multiple mark-recapture method, which accounted for tag-mortality and emigration, was developed. The rationale of the method is that the ratio of the number of recaptures to the total number of fish caught during a trip is equal to the ratio of the total number of tagged fish alive at that site to the total number of fish at that site. The total number of fish tagged and recaptured at the release sites was perfectly known (but not at Cape Point, where density could thus not be assessed). Estimates were available of the tag-mortality-rate and the emigration rate.

An important condition for this method to yield an unbiased estimate is that each fish has an equal chance of capture. The tagging study showed that galjoen were not well mixed, but that they held home-ranges (Chapter 2). This was not a problem, provided that fish were caught throughout the site and not just at one or a few points. If, for example, there were gaps in the effort distribution exceeding the home range size, then clearly some fish would never have been available for capture, thus negatively biasing the estimate.

Anglers at De Hoop were free to move throughout the study sites and did not follow any pre-determined pattern. This strategy allowed effort to track abundance and presumably resulted in the highest catch-rates. Although galjoen were caught at every

100-m interval at the release sites, the effort distribution was not perfectly flat. However, the distribution of captures within the release-sites showed irregularities that had a smaller length scale than the home range size (<400 m). From this it was assumed that the entire population at each site was accessible to shore-anglers and that no fish were 'hidden'. The Tsitsikamma data were disqualified for this reason – there was a 3-km stretch within the site where no sampling occurred.

Another bias could result if some fish were more 'catchable' than others (a.k.a. the trap-happy effect). If this was the case, then the percentage of released fish that were recaptured should be exceeded by the percentage of re-released fish that were recaptured a second time. The results presented in Chapter 2 show that these rates were not different, and that all galjoen were thus equally catchable.

The number of tagged fish available for capture at site a, at time t, is a function of the sum of all the fish tagged at that site over all prior trips. Tag-mortality is an exponential loss, whereas migration was a once-off loss occurring shortly after tagging, with very small net losses thereafter (Fig. 2.5). The number of tagged fish available at site a, during trip *k*, was estimated sequentially:

$$S_{ak} = [S_{ak-1} + (T_{ak-1} - \theta)]\, e^{-\beta(t_k - t_{k-1})} \qquad \text{eq. 3.10}$$

The number of recaptures made at site a, during trip k, could then be predicted by

$$\hat{R}_{ak} = \frac{G_{ak}\, S_{ak}}{N_{ak}} \quad . \qquad \text{eq. 3.11}$$

A single estimate N_a was used to represent a mean of all N_{ak} values. The value of N_a, which minimised the sum of squares,

$$SS = \sum_k (R_{ak} - \hat{R}_{ak})^2 \,, \qquad \text{eq. 3.12}$$

was chosen as the best estimate of the average population size at site *a* during all trips. Sum-of-squares was used as a measure of discrepancy instead of a likelihood procedure based on the Poisson distribution, because the numbers of recaptures per trip were never small. The Poisson distribution becomes symmetrical for large mean values (McCullagh & Nelder 1989), hence the more convenient, symmetrical measure of discrepancy could be used.

The error on the density estimate was calculated using the bootstrap method (Press *et al.* 1986). Trip records were sampled randomly with replacement, i.e. equation 3.11 was evaluated repeatedly on a random selection of trip records, including duplications.

Each site at De Hoop covered 3.4 km of shoreline. Therefore, the average density of galjoen at each site was calculated by dividing the estimates of N_a by this length, to express density per metre of shoreline, as is the convention with sandy beach ecology (Brown and McLachlan 1990). This linear approach assumes that galjoen are limited to the surf-zone. It is a reasonable assumption at De Hoop where there is an absence of reefs beyond the surf-zone at both sites. Baits could be positioned up to 150 m from the high-water mark, thereby covering all potential galjoen habitat.

RESULTS

Sample size

This study is based on information derived from the capture of 27 606 galjoen from four research sites from 1987 to 2000 (Table 3.3). Most effort was expended at the two De Hoop sites, Koppie Alleen and Lekkerwater, and most of the fish came from here. The third largest contribution came from the Cape Peninsula, where the data spanned a similar period. Sampling at Tsitsikamma covered a shorter period from 1995 to 2000.

Tagged fish were recaptured at the research sites and elsewhere. Recapture rates varied between 0.12 at Koppie Alleen and 0.043 at Tsitsikamma. Included in these rates are those fish that were recaptured more than once and those that were caught outside the study site. All recaptures at De Hoop and Tsitsikamma were recorded, but there was a loss of data due to non-reporting outside of these areas, including the Cape Peninsula site.

TABLE 3.3: Number of galjoen that were captured, tagged and recaptured 'n'-times, and the recapture rate (all recapture events divided by first releases).

	Koppie Alleen	*Lekkerwater*	*Cape Peninsula*	*Tsitsikamma*
Captured	9322	14823	2590	871
Tagged	8310	13686	2360	835
Recaptured once only	763	964	218	32
Recaptured twice only	76	70	9	2
Recaptured >twice	28	11	1	0
Recapture rate	0.12	0.083	0.10	0.043

Catch-per-unit-effort (CPUE)

CPUE values were greatest at the De Hoop sites, followed by Cape Peninsula and Tsitsikamma (Table 3.4), and these differences were statistically significant at the 5% level (one-way ANOVA, F = 356.4, d.f. = 4296, p<0.01). If the *SFT* component of the De Hoop data is examined separately to make it more comparable to the other sites where only the *SFT* was employed, then the CPUE was even greater at De Hoop, averaging double the Cape Peninsula rate and more than ten times the Tsitsikamma rate (Table 3.4). The *SFT* CPUE was at least five times greater than that of the *BFT* at De Hoop. Smaller mean values were associated with relatively greater variation.

TABLE 3.4: Average catch per unit effort (fish per angler per hour) and associated standard error.

	Koppie Alleen	*Lekkerwater*	*Cape Peninsula*	*Tsitsikamma*
CPUE Total	0.92	1.23	0.64	0.10
s.d.	0.91	1.04	0.67	0.31
CPUE SFT	1.19	1.49	0.64	0.10
s.d.	0.90	1.01	0.67	0.31
CPUE BFT	0.16	0.33		
s.d.	0.32	0.47		

The four factors, fishing technique, month, year, and angler, and the two interaction terms: year x month and angler x technique, all significantly affected CPUE at the 0.05 significance level at both sites (Table 3.5). The 'technique' parameter had the greatest explanatory power, showing that anglers in the multi-species fishery are able to successfully target galjoen. Year and month also accounted for substantial variance.

TABLE 3.5: Results of the GLM applied to CPUE data for the De Hoop sites, giving the deviance and likelihood ratio statistics calculated by the progressive inclusion of additional parameters in the model in the order listed. '$p > F$' is the probability that the F value could be exceeded by chance.

Parameter	Deviance	DF	F	p > F
	Koppie Alleen			
Intercept	3895	0		
Year	3276	6	44	0.0001
Month	3036	2	51	0.0001
Angler	2833	10	9	0.0001
Technique	1038	1	767	0.0001
Month x Year	971	8	4	0.0004
Angler x Technique	874	10	4	0.0001
	Lekkerwater			
Intercept	4725	0		
Year	4607	6	6	0.0001
Month	4537	2	11	0.0001
Angler	3925	11	18	0.0001
Technique	1800	1	700	0.0001
Month x Year	1563	11	7	0.0001
Angler x Technique	1488	11	2	0.0109

There were 5.5 and 2.6-fold variations in CPUE that could be attributed to inter-annual difference at Koppie Alleen and Lekkerwater respectively (Table 3.6). There was not much agreement in the ranking of years at the two sites according to CPUE. At both sites 1998 and 1999 emerged as the weakest years, but for other years there was no agreement.

TABLE 3.6: CPUE factors associated with each year at the two De Hoop sites. The years are ranked in descending order. The factors, which are log-transformed, are not comparable between sites.

Koppie Alleen		*Lekkerwater*	
Year	Factor	Year	Factor
1993	1.18	1994	1.0
1995	1.15	1995	0.72
1997	1.12	1996	0.41
1996	1.08	1993	0.40
1994	0.94	1997	0.34
1998	0.31	1998	0.19
1999	0.00	1999	0.00

The seasonal picture was consistent between sites. In both cases, the CPUE appeared to peak between July and September, with a minimum in mid-summer (Table 3.7). The total extent of the seasonal effect on CPUE cannot be calculated because only the same three months per year were sampled at each site, and those months differed between sites. The first of the interaction terms (Table 3.5) accounts for variability associated with short-term changes by assigning a separate factor to each trip (five consecutive days). There was a considerable amount of variation at the daily level, which this model would not have been able to take into account. As a result, the fit was over-dispersed. To overcome this problem, it would have been necessary to include a three-way interaction term (day x month x year), but such an inclusion was deemed impractical, in view of the large number of days fished, and it would not provide useful information.

Angler performance is a nuisance parameter when it comes to designing CPUE monitoring programmes. Can random ensembles of CPUE records be analysed without attention to the performance of individual anglers? The fact that the angler factor was significant at both sites suggests that angler skill will affect the interpretation of CPUE data if the number of anglers in the sample is small. The total amount of variation explained by angler-differences was consistent between sites: 3.3-fold and 3.4-fold variation between the smallest and largest factors for Koppie Alleen and Lekkerwater respectively.

TABLE 3.7: CPUE factors associated with each month at the two De Hoop sites. The months are ranked in descending order. The factors, which are log-transformed, are not comparable between sites.

Koppie Alleen		*Lekkerwater*	
Month	Factor	Month	Factor
July	0.27	September	0.12
October	0.00	May	0.03
February	-0.37	November	0.00

The influence of angler-skill is diminished by the fact that the ranking of anglers by performance was not consistent between sites. The correlation of angler factors between sites was tested statistically. Spearman's rank correlation coefficient for these data is 0.42 (n=11), which corresponds to a p-value of 0.1 for a one-way test (Zar 1984). In other words, there is some doubt as to whether the performance of individual anglers across sites was correlated. Some anglers who performed consistently well (relative to others) at one site, performed consistently poorly at the other, which suggests an interaction between site and angler performance. The second interaction term, between angler and technique, shows that an angler's performance is dependent not only on the site, but also on the technique used. These results suggest that CPUE should be calculated from a large ensemble of anglers covering a variety of areas to ensure that the 'law of averages' reduces the influence of individual variation and the influences of targeting on the CPUE statistic.

Size distributions

The size distributions of fish taken at each site are reported in Chapter 2, under the same heading. These data were used here to calculate mortality-rates, which were ascribed to natural mortality in the protected sites, but which included fishing mortality at the Cape Peninsula.

To estimate the natural mortality-rate at De Hoop, only fish caught from 1995 onwards were analysed. It was necessary to omit the earlier samples, because the marine protected area came into effect at the beginning of 1985. Galjoen live to a maximum age of at least 13 years, and the age at first capture is 4 years (Bennett and

Griffiths 1986). Assuming that recruitment was constant, ten years had to pass before the age-structure of the protected fish lost the effect of the earlier fishing (i.e. the 3-year old cohort in 1985 would be the 13 year-old cohort in 1995). Such an omission of data was not necessary at Tsitsikamma, where protection took effect from 1964.

TABLE 3.8: Total mortality-rate estimated from galjoen size distributions (total length ≥ 325 mm) at four sites. n = sample size, Z = instantaneous total mortality-rate (y^{-1}), C. I. = 95% confidence interval, ω = male fraction at recruitment, -LLH = negative log-likelihood. * Unprotected site.

	n	*Z*	*C. I.*	ω	*C. I.*	*-LLH*
Koppie Alleen	2269	0.42	0.32-0.48	0.58	0.38-0.73	11826
Lekkerwater	3504	0.61	0.51-0.77	0.17	0.00-0.52	17796
Cape Peninsula*	1297	2.01	1.88-2.34	0.69	0.21-0.85	5227
Tsitsikamma	686	0.43	0.36-0.54	0.32	0.00-0.53	3603

The size distributions of galjoen that were caught translate into instantaneous mortality-rates (Z) between 0.32 and 2.34 y^{-1}, depending on the site (Table 3.8). The best estimates in the protected sites ranged from 0.42 to 0.61 y^{-1}, whereas the best estimate for the unprotected site was 2.01 y^{-1}. The Lekkerwater site had the highest Z-estimate of the three protected sites, but this was associated with a low estimate of the male-fraction. It is difficult to explain why the sex-ratio estimate at Lekkerwater is skewed, although the confidence interval included 0.5. Because the male-fraction and Z-estimates are negatively correlated by the assessment procedure (see explanation in methods), a more even sex-ratio should be associated with a lower Z-estimate, which would be closer to estimates at the other protected sites. The confidence intervals of the Z-estimates did not overlap between the two De Hoop sites, indicating a difference in size distributions. The Koppie Alleen and Tsitsikamma estimates were not significantly different.

Tag-mortality-rate

The estimated tag-mortality-rates were similar at the two De Hoop sites, but much lower at Tsitsikamma (Table 3.9). The very small recapture rate at Tsitsikamma and the small sample size (Table 3.3) produced a very wide confidence interval on the tag-mortality estimate and these should be treated as less reliable than the other estimates.

Indeed, the tag-mortality estimate is lower than the mortality estimate, which, in theory, should not be possible. The very low recatchability could have masked the decline of recapture frequency over time at this site. If the average time-free method is used (Butterworth *et al.* 1989), then tag-mortality estimate for Tsitsikamma is estimated as 1.16 y^{-1} (with a confidence interval of 0.5 – 1.8 y^{-1}), which is in agreement with the De Hoop estimates. The tag-mortality-rates at De Hoop translate into a tag-survivorship of approximately 32% per annum.

TABLE 3.9: Estimated instantaneous tag-mortality-rate (y^{-1}), the associated 95% confidence interval (Con. Int.) and estimated recatchability. n = sample size.

	n	*Tag-mortality (y^{-1})*	*Con. Int.*	*Recatchability (captures per hour)*
Koppie Alleen	8311	1.15	1.05 – 1.23	1.84×10^{-4}
Lekkerwater	13687	0.99	0.91 – 1.07	0.83×10^{-4}
Tsitsikamma	34	0.17	0.0 – 0.35	0.12×10^{-4}

Tag-mortality-rate was estimated in conjunction with a recatchability rate. The recatchability, which accounts for catchability and for losses to emigration, was smallest at Tsitsikamma and greatest at Koppie Alleen. Given the fact that the rates of emigration from these sites were similar (Chapter 2), these estimates should reflect differences in catchability.

Density at De Hoop sites

The average number of galjoen (larger than 250 mm) present during all sampling trips was estimated to be significantly greater at Lekkerwater than at Koppie Alleen (Table 3.10). The coefficient of variation on these estimates is in the order of 7%. Based on a sex-ratio of 1:1 and mortality-rates as reported in Table 3.8, the average galjoen at Koppie Alleen and Lekkerwater respectively weighs 818 g and 583 g, which translates into biomass values of 1.49 $kg.m^{-1}$ and 2.87 $kg.m^{-1}$ respectively.

TABLE 3.10: The estimated average density of galjoen (in numbers per km), and standard errors. The model fit is indicated by sum-of-squares.

	N (trips)	*Mean density*	*Standard error*	*S-o-S*
Koppie Alleen	57	1829	102	1740
Lekkerwater	49	4924	386	1671

Catchability

Catchability (q) is the impact that a unit of effort has on the stock. In this case, it is calculated on a beach-length basis, with units in km.h^{-1}. The equation of catchability of galjoen is F = qE, where E is effort measured in units of h.km^{-1}.y^{-1}, and F is the ratio of the instantaneous catch-rate to the population size, in units of y^{-1}. Furthermore, F = C/N, where C is the instantaneous catch-rate measured in fish.km^{-1}.y^{-1}, and N is the fish density measured in fish.km^{-1}. The fish density estimates, together with the catch records from the De Hoop data, give the opportunity to calculate F, the fishing mortality-rate potentially caused by the research sampling. (The qualifier 'potentially' is used because the fish were returned and not killed, but this does not affect the calculation.) From the recorded annual catch (fish.km^{-1}.y^{-1}), and population density (fish.km^{-1}), F at the two De Hoop sites is calculated to be in the order of 0.1 y^{-1}. Despite the higher CPUE at Lekkerwater, the catchability of galjoen there is lower than at Koppie Alleen (Table 3.11).

TABLE 3.11: Estimates of 'potential' F and catchability of galjoen at De Hoop.

	Catch (fish.km^{-1}.y^{-1})	*F(y^{-1})*	*E(hours.km^{-1}.y^{-1})*	*q (km.hour^{-1})*
Koppie Alleen	182	0.100	150	6.7×10^{-4}
Lekkerwater	345	0.073	240	3.2×10^{-4}

The catchability and recatchability estimates (Table 3.9) were calculated differently and they have different units, but they should still be numerically comparable. At both sites catchability exceeded recatchability by a factor of 3.8. This difference can partly be ascribed to the fact that the recatchability estimate included the effects of emigration as well as catchability. More significant is the fact that the ratios of these parameters between sites were remarkably consistent. The ratio between the q-estimates at Koppie Alleen and Lekkerwater is 2.19, whereas the ratio of r-estimates

(Table 3.9) between these sites is 2.21. This information allows q to be estimated for Tsitsikamma. The ratio of the r-estimates between Koppie Alleen and Tsitsikamma is 15.3, which means that the q-estimate at Tsitsikamma should be 4.6×10^{-5} km.h^{-1}.

DISCUSSION

Natural mortality-rate

The total mortality-rate of galjoen at the protected research sites should equal the natural mortality-rate (M). Galjoen were protected at those sites for periods that allowed at least one cohort to reach its maximum age without losses to fishing. The estimate of 0.43 y^{-1} is the median of the three estimates, and also the one that came from the oldest marine protected area, namely Tsitsikamma National Park. The age distribution is probably most stable at this site, as the population could be growing at the De Hoop sites after the reserve was brought into effect in 1985. A growing population would skew the age distribution in favour of young fish, and mortality would be over-estimated as a result.

By comparison, the models used by Bennett (1988) to estimate M, namely those of Pauly (1980) and Rikhter and Efanov (1977), yielded estimates that were approximately 0.1 y^{-1} lower (0.38 y^{-1} for males and 0.32 y^{-1} for females). It should be preferable to adopt the measured rate reported here, instead of extrapolating a value from models based on studies of other species. However, the galjoen population structure at protected sites could have been impacted by fishing in other areas, because of a small amount of exchange of adult fish.

Galjoen at De Hoop were estimated to exchange with those from exploited areas at a rate of approximately 5% (Chapter 2). It is difficult to put a time dimension to this estimate, because of the difficulty of deciding on the appropriate movement model. Either 5% of the fish exchange freely with those from outside areas, or fish spend 5% of their time in other areas. In either case, the number of adult galjoen entering the protected area would be fewer than the number leaving by a factor of at least e^{-F}. Assuming F in adjacent exploited areas to be 1.0 y^{-1}, the net loss from the protected sites caused by fishing in other areas is $0.05(1-e^{-F})$, or ≈ 0.03 y^{-1}. (The MPA loses 0.05 of its density through emigration, but gains only $0.05e^{-F}$ by immigration from exploited areas.) The total mortality-rate estimated for protected sites should therefore be decreased by this amount to represent the true natural mortality-rate, i.e. 0.43 - 0.03 = 0.4. This adjustment is conservative as it does not account for possible recruitment failures in exploited areas, which could have reduced density by more than e^{-F} in such cases.

The marine protected areas thus provided the first direct, albeit not unbiased, measurement of the natural mortality-rate of galjoen.

Impact of fishing

The tag and recapture information led to an estimate of galjoen density at two protected sites. With records of total catch and effort, it was then possible to estimate the impact of a unit of effort. The F-estimates in Table 3.11 are not dependent on estimates of M, which is a weakness of assessments based solely on catch-at-age data. The estimates of F and q were based on 13-year times-series, and therefore averaged out much of the inter-annual variation. The experimental fishing at De Hoop could potentially have reduced the local galjoen density at an instantaneous F-rate of approximately 0.1 y^{-1}, if the fish had been removed. All available estimates of Z from the fishing grounds range between 0.23 y^{-1} and 2.34 y^{-1} (Table 3.12). These estimates were based on catch-at-length data that were sampled at various locations and dates.

Corresponding estimates of effort are patchy and in some cases unreliable, particularly when instantaneous counts were extrapolated to estimate the total effort expended in a day. In addition, not all anglers target galjoen and it is difficult to allocate the amount of effort that was directed at galjoen. Brouwer *et al.* (1997) estimated from a questionnaire study that only 30% of anglers targeted galjoen, a figure that is likely to vary spatially and seasonally. The GLM model of CPUE shows that such targeting strongly affects the CPUE statistic. Consequently, there is considerable variation among the estimates of effort that are available (Table 3.13). I regard the values from Cape Peninsula and Koppie Alleen (prior to the reserve) as reliable estimates, as the vast majority of anglers there were fishing for galjoen, using the small-fish technique described here. Typical effort counts are in the region of 2 500 h $km^{-1}y^{-1}$. The estimate of 7449 h km^{-1} y^{-1} by Brouwer *et al.* (1997) should be reduced to 30%, the percentage of that sample that targeted galjoen. If 2 500 h $km^{-1}y^{-1}$ is multiplied by the q-estimates in Table 3.11, the predicted F-values lie between 0.8 and 1.75 y^{-1}. These estimates are within the range of those calculated from catch-at-length data (Table 3.12), after correcting for natural mortality. Without a size limit, such high fishing mortality-rates translate into reductions of potential female spawner-biomass-per-recruit of 98.4% and 99.4%, respectively. Such reductions guarantee extinction.

TABLE 3.12: Instantaneous per-capita mortality-rates estimated from catch-at-age (C@A) and catch-at-length (C@L) data. Ninety-five percent confidence intervals are given. Only point estimates were available from Bennett's (1988) study.

Area	Period(s)	Sex	Data	Z	Source
Lamberts Bay to Cape Infanta	1938-1986	Male	C@A	0.91	Bennett 1988
Lamberts Bay to Cape Infanta	1938-1986	Female	C@A	1.40	Bennett 1988
Cape Hangklip to Walker Bay	1995-1996	Both	C@L	0.56-1.06	Attwood and Farquhar 1999
Cape Point to Arniston	1995-1996	Both	C@L	0.66-1.2	Brouwer *et al.* 1997
Still Bay	August '95, '96	Both	C@L	0.23-0.68	Records of Galjoen Derby
Cape Peninsula	1987-2000	Both	C@L	1.88-2.34	This study

Galjoen should not be able to sustain the present harvest rate, as predicted by dynamic models with stock recruit relationships (Attwood and Bennett 1990, Attwood and Bennett 1995). However, the galjoen catch makes a substantial contribution to the shore-fishery in the south-western Cape (Brouwer *et al.* 1997), and the stock is clearly not close to extinction, even in areas that are heavily exploited. How can this discrepancy be explained?

The F- and q-values estimated for De Hoop depend linearly on the density estimate. There is no reason to suspect a bias in the density calculations. Good estimates of tag-mortality and emigration were obtained, and the fish were sampled throughout the study sites, thereby overcoming the mixing problem. As a check, these estimates can be compared to the results of studies of biomass of sandy-beach and rocky-shore ecosystems. Total macro-faunal biomass on a South African warm-temperate, high-energy, sandy beach is in the vicinity of 500 g C. m^{-1}, of which 130 g C.m^{-1} is due to fish (McLachlan and Bate 1984). Using their conversion from wet mass to carbon, the De Hoop galjoen densities amount to 192 and 370 $gC.m^{-1}$ for Koppie Alleen and Lekkerwater respectively. This comparison serves to show that the galjoen biomass estimate is near the average biomass for all fish combined on a sandy beach. The biomass of about another 40 species at De Hoop has still to be added. If the De Hoop density estimates are in error, they cannot be much higher. As a result, the q-estimates (and hence F-estimates) in Table 3.11 are not likely to be over-estimates.

TABLE 3.13: Estimates of shore-angling effort. AP = access point count, RC = roving creel count.

Area	Period	Method	$h.km^{-1}\ y^{-1}$	Source
Port Elizabeth	08/1985-08/1986	RC	1604	Clarke & Buxton 1989
SW Cape	not specified	RC	2299	Bennett 1993
Koppie Alleen	1984-1985	AP	2227	Bennett and Attwood 1991
Cape Peninsula to Arniston	1995-1996	RC	7449	Brouwer *et al.* 1997
Cape Peninsula	06/1999-05/2000	AP	2689	Gate records

Two other ways of explaining the discrepancy are possible. The first is that the stock is on its way to extinction; the catch-rates of today may not be sustainable. A counter-argument is that the CPUE over the decade prior to 1992 did not show a sustained decrease (Bennett *et al.* 1994). On the other hand, constant improvements in fishing technology (particularly the introduction of carbon-fibre rods, aerodynamic grab sinkers, chemically-sharpened hook, and dyneema fishing lines) and the sharing of information (cellular phones and fishing magazines) could be increasing catchability, thereby masking the effect of a declining stock on CPUE.

The second possibility is that the fishing mortality is applied unevenly, leaving many areas unexploited as natural refuges, while the remaining areas take the majority of the fishing effort. In this case, the natural refuges could be acting as a source of recruitment to other areas where exploitation is very heavy (i.e. greater than the average). Small natural refuges, provided that their size exceeds the home-range of the fish, could provide a vital source of protection. A high F-value, which would otherwise cause extinction, can be sustained provided that it is not applied throughout the stock. This has been shown to be possible in theory (Polachek 1990, DeMartini 1993, Quinn *et al.* 1993, Attwood and Bennett 1995), and it serves as a strong argument for supporting marine protected areas as a strategy for the conservation of fish.

Habitat effects

A weakness in the above extrapolation of natural mortality-rates and catchability is that the estimates are not necessarily transferable from one area to another. Indeed, these estimates differed among the De Hoop and Tsitsikamma sites, which were all protected from fishing. Spatial differences in population parameters are likely, due to habitat type differences (Table 3.14).

The exploited site did not have the lowest CPUE, but mortality there was the highest. The Cape Peninsula has always been known as a productive area for galjoen (Biden 1930). The carrying capacity of galjoen must be high there to sustain a moderate CPUE after many years of intense exploitation, as suggested by the high effort (Table 3.13) and mortality estimates (Table 3.8).

TABLE 3.14: Qualitative estimates of population and fishery parameters among the four study sites. Z is the total mortality-rate estimated from size distributions. F is measured as the difference between Z and M at the Cape Peninsula.

	Koppie Alleen	*Lekkerwater*	*Cape Peninsula*	*Tsitsikamma*
Habitat	Broken sandstone & sandy beach	Broken sandstone	Rocky shore & kelp forest	Exposed headland
Fish density	Low	High		
Catchability	High	Intermediate		Low
Recatchability	High	Intermediate		Low
Z	Low	Intermediate	High	Low
F	Zero	Zero	High	Zero
CPUE	High	Very High	Intermediate	Low

The low CPUE at the protected Tsitsikamma site suggests that either there are few fish there, or they are very difficult to catch. The low catchability estimate suggests the latter explanation, but the carrying capacity there could be lower than at De Hoop.

Tsitsikamma is at the eastern side of the range, where galjoen have never been a dominant part of the catch. Galjoen contribute only 2% to shore anglers' catches in the eastern Cape (Clarke and Buxton 1989). Rocky headlands are also not regarded as prime habitat for this species.

The differences in density, CPUE and catchability between the two De Hoop sites (Table 3.14), could be explained by the relative proportion of mixed rock and sand versus pure sandy beach. Mixed rock and sandy shores are where most galjoen are usually encountered. Approximately two thirds of the Koppie Alleen site comprises a pure sandy beach, where galjoen are caught in lesser quantities than on mixed rock and sandy shores. Accordingly, density is higher at Lekkerwater (Table 3.10), whereas catchability is higher at Koppie Alleen (Table 3.11). Again, this could be explained by the difficulty of catching galjoen among rocks, of which there are fewer at Koppie Alleen. Therefore, the ratio of CPUE between these two sites is not as skewed as would be predicted from the ratio of densities.

The above comparisons serve to illustrate that any assessment of the stock of galjoen should take habitat and location into account. Extensive use was made of protected areas for this study. Without them, the study as a whole would not have been possible. More specifically, this study constitutes the first attempt at quantifying the density of any South African linefish, and this was only possible because of the availability of an undisturbed research site. It follows that such sites have tremendous value for fishery assessment and that they should be distributed across all biogeographic regions and habitats for optimal effect for conservation and fishery assessment.

The great degree of patchiness also serves a warning to those who study the effects of fishing by comparing exploited and unexploited sites. No two sites are identical, stressing the need for adequate replication of both protected area and such studies.

Information content of catch data

Galjoen confound most standard attempts at quantifying fish. They live in a high-energy environment where diving is physically impossible and visibility is reduced to arm's length. Even under good conditions, diver counts of fish are notoriously variable and often biased (Lincoln Smith 1989). Underwater video techniques overcome many of these problems (Willis *et al.* 2000) but the habitat of galjoen will not allow this technique either. Whereas pelagic shoaling fish can be counted with acoustic methods, catch data are all that can be used to assess benthic stocks in remote or turbulent environments. Catch data permit only indirect or relative assessments.

Three types of data are available to researchers, namely tag and recapture data, catch-rate and catch-at-length frequencies. The last two of these could be derived from fishery-independent or fishery-dependent surveys. This study has made use of all three types in a fishery-independent survey, and some insights have been gained on the usefulness and costs of collection of each with respect to the galjoen fishery.

(i) Tag and recapture data. This type of catch data is a luxury for fishery researchers. Tag and recapture data provide information on movement and density that is not available from any other method. In the present case, the data led to the calculation of catchability. However, the data provide no real-time estimates. A ten-year data set provides estimates of parameters that are averages over that period. Large sample sizes are also required. In this study, data from >27 000 tagged fish yielded density estimates with a 95% confidence interval of ±15%.

Another drawback is the fact that tag and recapture data can only be put to optimal use in a marine protected area, where the experiment will not be disturbed. Such data could provide a useful monitoring function, especially as CPUE data will be generated as a by-product, but will not provide any information on the state of the fishery *per se*. Additional surveys, as described for other types of data, will be required.

Tag and recapture data are expensive in terms of labour and equipment, and the collection is time-consuming. To illustrate these costs, the De Hoop tagging study required an average of 170 man-days per year (or R40 000), and the equipment and data handling costs amounted to approximately R80 000 per year at current rates. This investment has to be maintained for at least five years. The entire exercise should be conducted at a few sites across the range of the species and habitat types. Taking three sites as a minimum, this amounts to R360 000 per annum. Mitigating some of these costs is the possibility of attracting volunteer assistance, as was done in this case, as part of a fishery extension project. Of concern is the effect of tags on the fish. Apart from mortality, it is strongly suspected that tags affect galjoen growth (Attwood and Swart 2000).

(ii) Catch rate. The catch by anglers can be monitored to provide two useful indices, namely average CPUE and total catch. The same measurements are taken in both cases (i.e. the number of fish caught by an angler) but the statistical treatment differs between the two.

CPUE provides a reliable, but relative measure of reef fish density (Willis 2000) and has been used to infer spatial and temporal differences in density (e.g. Bennett and Attwood 1991, Rakitin and Kramer 1996, Millar and Willis 1999). CPUE is a real-time measure, in contrast to catch-at-length or tag and recapture data that reflect processes that occur over several years. The major difficulty with CPUE as an index of abundance is the dependence on gear-type and angler. Not only is CPUE affected by the type of gear used (or targeting), but it is also increased by technological improvements. The effect of changes in gear type is difficult to quantify, but records of such changes should be kept. The influence of the variability due to anglers should disappear with large sample sizes that include many anglers.

Catch-at-length

At present, catch-at-length (-age) is the most commonly used variable for linefish assessment. A random sample of fish lengths caught by a particular gear-type is converted to catch-at-age data. Catch-at-age data are then used to estimate the mortality rate, which feeds into per-recruit models. Spawner-biomass-per-recruit can be used to assess the status of the stock, and to make adjustments to fishing regulations (Clark 1991, Punt 1993, Mace 1994). The common practice in South Africa has been to use one global estimate of mortality-rate to estimate the remaining percentage of unfished spawner-biomass per recruit (e.g. Bennett 1988, 1993, Buxton 1992, Van der Walt and Govender 1996). The reliability of this technique depends on several unrealistic assumptions, some of which have come to light from this study.

Firstly, per-recruit models assume that recruitment is constant. In fisheries that are expanding or shrinking (due to restrictions), this assumption is incorrect. In the galjoen example both scenarios could apply. Anglers are accessing remote areas more frequently, thereby reducing recruitment there. Additional restrictions in the form of closed areas could have the opposite effect. Measures of fishing effort and mortality estimates based on catch-at-length of galjoen do not correlate (Fig. 3.2). At Lekkerwater, where fish have been protected for 16 years, the mortality-rate is apparently higher than at Still Bay, a holiday resort that has expanded greatly over the last decade. A likely explanation of this discrepancy is that recruitment is increasing at Lekkerwater since protection took effect, thereby giving an over-estimate of mortality, whereas recruitment at Still Bay is collapsing, thereby giving an under-estimate of mortality.

Secondly, catch-at-length sampled from the fishery biases the estimates of fishing mortality-rate towards the rates at exploited areas. Natural refuges, or protected areas, where fish are not caught or are caught less frequently, are under-represented in samples, thereby providing a pessimistic overall estimate of mortality. Although a fishery-independent survey could be designed to derive estimates uniformly across all areas, some natural refuges are simply impossible to sample.

Thirdly, per-recruit models depend on the availability of reliable estimates of the natural mortality-rate. Estimating the natural mortality-rate in an established fishery will always be a problem. The estimate provided here for galjoen depended on the existence of a marine protected area and a fishery-independent survey. Natural mortality is likely to vary across the animal's range, implying that several such protected research sites are needed.

Fourthly, a problem not mentioned thus far, is that catch-at-length data can only be translated into mortality with reliable length-age relationships. It is, for example, worrying that growth rate estimates for galjoen and white steenbras *Lithognathus lithognathus* based on tagging and otolith readings do not concur (Attwood and Swart 2000). Age-length relationships are also known to change over time, perhaps partly as a result of exploitation (Law 2000), requiring frequent re-assessment.

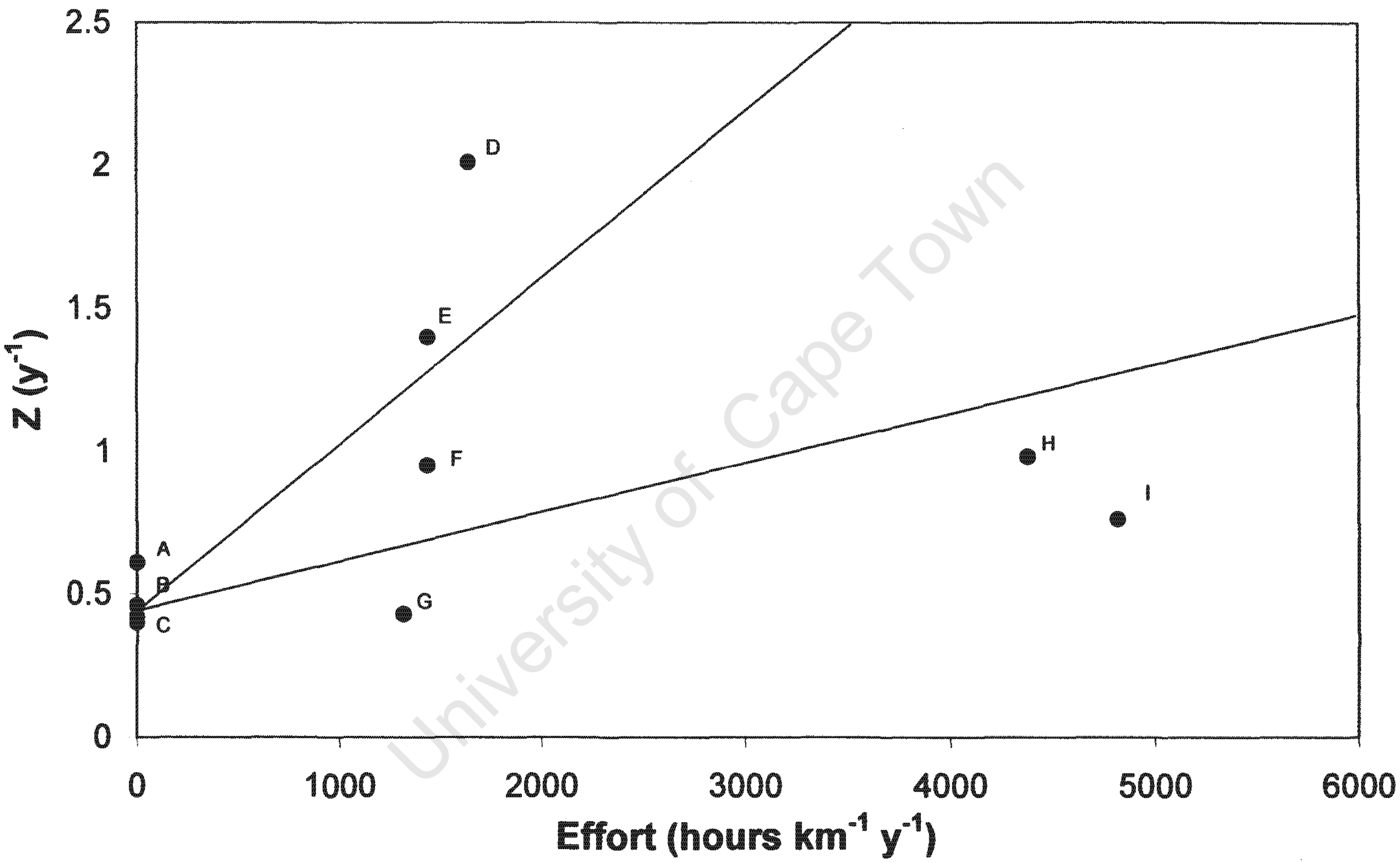


Figure 3.2 A scattergram of total mortality-rate estimates (Table 3.12) and effort counts (Table 3.13). A = Lekkerwater, B = Tsitsikamma, C = Koppie Alleen, D = Cape Peninsula, E = S.W. Cape females, F = S.W. Cape males, G = Still Bay, H = Hermanus, I = Southern Cape. The effort for samples H and I are over-estimates as they include targeting on many other species besides galjoen. The straight lines represent the upper and lower estimates of catchability, with a natural mortality-rate of 0.4 y^{-1}.

Finally, per-recruit models that use estimates of mortality derived from catch-at-length data do not allow for pro-active management. The effect of excessive harvest can only be detected a few years after the effect has been etched on the age structure. At that point it is difficult to reverse the trend. For this reason alone, CPUE monitoring is preferable to catch-at-length methods.

Monitoring requirements

The relationship between the standard deviation (sd) of a sample and the standard error (se) of the mean of that sample, $sd^2 = n\ (se^2)$, can be used to roughly scale the monitoring requirements in the galjoen fishery. The observed variability in catch-rates and mortality-rates based on catch-at-length indicates that exploited areas will have greater sampling requirements than lightly exploited areas if the same relative precision is desired everywhere (Table 3.15). In the case of catch-at-length data, more fish measurements are required from those areas where less fish are available, thereby presenting an even greater burden on the assessment of stocks in heavily exploited areas.

Because of the variability observed between habitats and between geographical locations, it will be necessary to estimate these parameters separately along discrete lengths of coastline, separated on the basis of habitat type. An area such as False Bay will require at least three estimates, one for the western rocky shore (34 km), one for the northern sandy shore (60 km), and another for the eastern rocky shore (33 km).

TABLE 3.15: The number of CPUE observations and fish measurements that must be made to estimate CPUE and Z respectively, to within the given accuracies in exploited and unexploited areas. Calculations were based on data from Koppie Alleen (as a protected area) and Cape Peninsula (as an exploited area).

	CPUE within 5%	Z within 0.1 y^{-1}	CPUE within 10%	Z within 0.2 y^{-1}
Exploited areas	1754	8000	438	2000
Protected Area	915	2000	229	400

Using a realistic target of achieving a confidence of 10%, and taking the average assessment area to be 50 km of exploited coast, approximately 17 500 CPUE measurements and 16 000 fish measurements will be needed for the entire 2 000 km range. Again, using a typical effort count (2 500 $h.km^{-1}.y^{-1}$ or 500 angler-days.$km^{-1}.y^{-1}$) and catch-rate (0.1 fish.h^{-1}), these demands will require a roving creel census covering approximately 13 000 km.days per year for CPUE and 117 000 km.days per year for size measurement. Of these two the catch-rate requirements are lower (and realistic). Fortunately, catch-rate is the better parameter to measure.

At a cost of R100 000 per observer per annum (including running expenses), and with a modest target of 1 200 km.days per observer per year (5 km per day for 238 working days), the annual cost of an effective catch-rate monitoring programme is just over R1 million. That cost could be recovered by charging anglers R1.00 per fishing-trip, which is negligible in relation to their total costs (McGrath *et al.* 1997). The current annual fee is R35 per angler.

CONCLUSION

The natural mortality-rate of galjoen is slightly higher than the estimate used by Bennett (1988) for his per-recruit analysis. The estimate presented here may still be biased by errors in the length-age relationship of galjoen, and by the possibility that the protected stocks that were analyses were either shrinking or expanding.

Galjoen density and population structure has been heavily impacted by fishing, where fishing effort has been high. However, the impact remains localised, and protected sites differ from exploited sites with respect to CPUE and age-structure.

Fishing mortality-rates as estimated from fishery dependent data are higher than can be sustained. Two possible explanations of the persistence of the fishery are that (a) technological improvements are masking the effect on CPUE of a continued downward trend in density or (b) the high fishing mortality is not applied evenly, leaving many pockets of fish that are sufficiently protected to act as a source of recruitment to exploited areas. The continuation of the fishery may depend on the existence of natural refuges or the provision of marine protected areas where those natural refuges have broken down.

Patchiness in habitat suitability results in spatial variations in carrying capacity. A heavily exploited but productive site, such as the Cape Peninsula, could hold more fish than a protected but unproductive site, such as Tsitsikamma. In these two examples the observed size-structures confirm that galjoen at the less productive site have a greater life-expectancy. The scale of spatial patchiness can be very small, as shown by the large differences in density between the two nearby De Hoop sites. The implication for monitoring is to maintain spatial consistency in sampling for the detection of inter-annual changes. The implication for stock assessment is to develop a comprehensive sampling strategy covering all habitat types throughout the range.

Further considerations for the design of a fishery-dependent survey are the need to cover the season systematically, because of strong seasonal effects in CPUE and catch-at-length, and the need to record ancillary information such as gear type and targeting. The strong effect of angler on catch data can be overcome by sampling large numbers of anglers.

The rough scaling exercise undertaken on the basis of measured variability in CPUE suggests that a comprehensive monitoring programme for stock assessment of galjoen is economically viable. As the galjoen forms part of a multispecies fishery, the requirements for monitoring the catch of other species should be assessed in a similar way, as one monitoring programme will have to cater for the entire fishery. It is clear, however, that fishery-independent studies using marine protected areas are required to provide information that cannot be obtained from fishery-dependent surveys.

CHAPTER 4

A SPATIALLY-STRUCTURED INDIVIDUAL-BASED MODEL OF THE GALJOEN FISHERY

ABSTRACT

An individual-based model was developed to simulate the growth of the South African galjoen fishery during the twentieth century. Spatial structure was incorporated by splitting the surf-zone habitat into 100-m cells and using geophysical data to assign a habitat type to each. Habitat type was used to determine the probability that galjoen occupy a cell, and the probability that the cell was accessible to anglers. The spatial and temporal effort distribution was modelled using the coastal human population as a proxy, while matching the absolute level of effort in the later part of the century to survey data. Twelve model variations covered the combinations of two spawner-biomass vs. recruitment curves, three larval dispersal scenarios and two adult movement patterns. Effort increased at an average annual rate of 3.5% and caused fish population size to decrease steadily for all model variations. By the end of the century the stock was invariably over-exploited. The shape of the spawner-biomass vs. recruitment curve was more important than larval dispersal or adult movement in determining population size and yield. The population was patchy, but it cannot be described as a meta-population. Even small natural refuges and marine protected areas support more fish than exploited areas, despite the action of larval dispersal and adult movement. Indices based on catch-data were biased by not representing unexploited areas.

INTRODUCTION

The galjoen fishery presents a number of management problems that are typical of reef-fisheries and recreational fisheries world-wide. The clumped distribution of both fish and fishermen implies that fishing mortality is likely to vary substantially across the range of the fish, and on a fine-scale. How does a manager assess such a stock accurately, particularly if catch-data are the only source of information? Linked to the problem of patchiness is the movement pattern of the fish and their larvae. The majority of studies on reef-fish suggest a high degree of residency and that larval dispersal is not as widespread as once thought (see review in Chapter 1), which can only serve to promote patchiness.

Rather than ignore patchiness, fishery managers are advocating MPAs to recover stocks and to sustain fisheries (Guenette *et al.* 1998). Spatial differences in fishing mortality-rates will further exacerbate patchiness. Typical scales of MPAs are between 0.1 and 10 km^2, although much larger areas have been proclaimed (Halpern in press).

Realistic spatial detail is required in models of reef-fisheries to gain an understanding of the interaction of processes that act at different scales. The galjoen fishery is a convenient example to model because its range can be represented by a one-dimensional array of habitat types along a 'quasi'-linear coastline, and because the movement pattern of the adults is well described (Chapter 2). Galjoen move in a patchy environment and are subject to spatially-variable fishing mortality. A complicating factor is that individual galjoen may differ with respect to movement behaviour.

What kind of model is most suited to elucidate the spatial structure of a reef-fishery? Despite their wide application in fisheries, standard production models (e.g. Schaefer and Fox models) are unsuitable, as it is essential that age-structure be incorporated. Movement behaviour may be age-dependent and reef-fisheries are often assessed from catch-at-age data. Age-structured population models could suffice for most applications, however, in the case of galjoen, they may not be able to reproduce the movement pattern of adults. It is postulated that individual galjoen could move between a small number of specific sites during their life (Chapter 2). This would imply that the probability of movement and the likely destinations are unique for each fish, even among those that find themselves at a common site. Only an individual-based model can replicate such a movement pattern. A population model would assign to each fish an equal probability of transfer between areas (e.g. Lindholm *et al.* 2001), which may be unrealistic in the case of galjoen.

Individual-based models (IBMs) are a popular method of modelling ecological processes, including the population dynamics that emerge from the fitness-maximising behaviour and selective mortality of individuals (Lomnicki 1999, and see Martínez-Garmendia 1998 and Railsback 1999 for applications to fish populations). IBMs have also been used more generally to study processes that emerge from individual variability (Van Winkle *et al.* 1993, Hinckley *et al.* 1996), or to study individual behaviour that leads to certain population responses (e.g. Walter *et al.* 1997). Technology has provided the processing power to turn such models into practical tools.

This chapter describes a retrospective IBM of the galjoen fishery and presents general results of the model. In subsequent chapters the IBM is used to further investigate the movement pattern of galjoen (chapter 5), to describe the likely effect of marine protected areas on the fishery (chapter 6) and to test the effectiveness of various monitoring and assessment techniques (chapter 7).

METHODS

All symbols used in the description of the model are listed in Appendix 1.

Model scope

The IBM simulates the development of the galjoen fishery in South Africa over the course of the twentieth century with realistic spatial structure and effort values. The spatial dimension stretches from Lamberts Bay in the west to Port Shepstone in the east, representing a coastline distance of approximately 2 000 km (Fig. 4.1). In South Africa, galjoen are rarely found outside this range. The time dimension covers 100 years, starting with the advent of substantive shore-angling in South Africa in 1900. Galjoen were caught by beach-seine nets prior to 1900, but such catches were very localised. The model therefore begins with a theoretically unexploited galjoen population, and then simulates the growth of the fishery and the change in the population up to the end of 2000.

Galjoen recruit into the fishery at age four, and only post-recruits were modelled as individuals. The quantity of recruits to each area was calculated according to a conventional spawner-biomass-recruitment relationship and a larval dispersal function. Four years after spawning, new recruits were given identity. During those four years the area-specific spawner-biomass was held in memory.

Model resolution

To simulate fish movements and spatial heterogeneity in habitat realistically, a fine spatial and temporal resolution is required. The 1 918-km range was split into 100-m cells, because the home-range of a galjoen is smaller than 1 km, but larger than 100 m (Chapter 2). Ideally, a daily time-step should update movement and mortality, but the computational load associated with daily updates was so great that a coarser time-step of one week was used instead.

Keeping records of individual fish

Computer memory was assigned to individual fish at recruitment to record the following data: date of birth, sex, status (alive or dead), and location (cell number). Additional variables were appended according to specific versions of the model. For example, the polymorphic model classes each fish as a resident or a nomad; the tourist model keeps record of the few locations that a fish visits throughout is life; the tagging model assigns

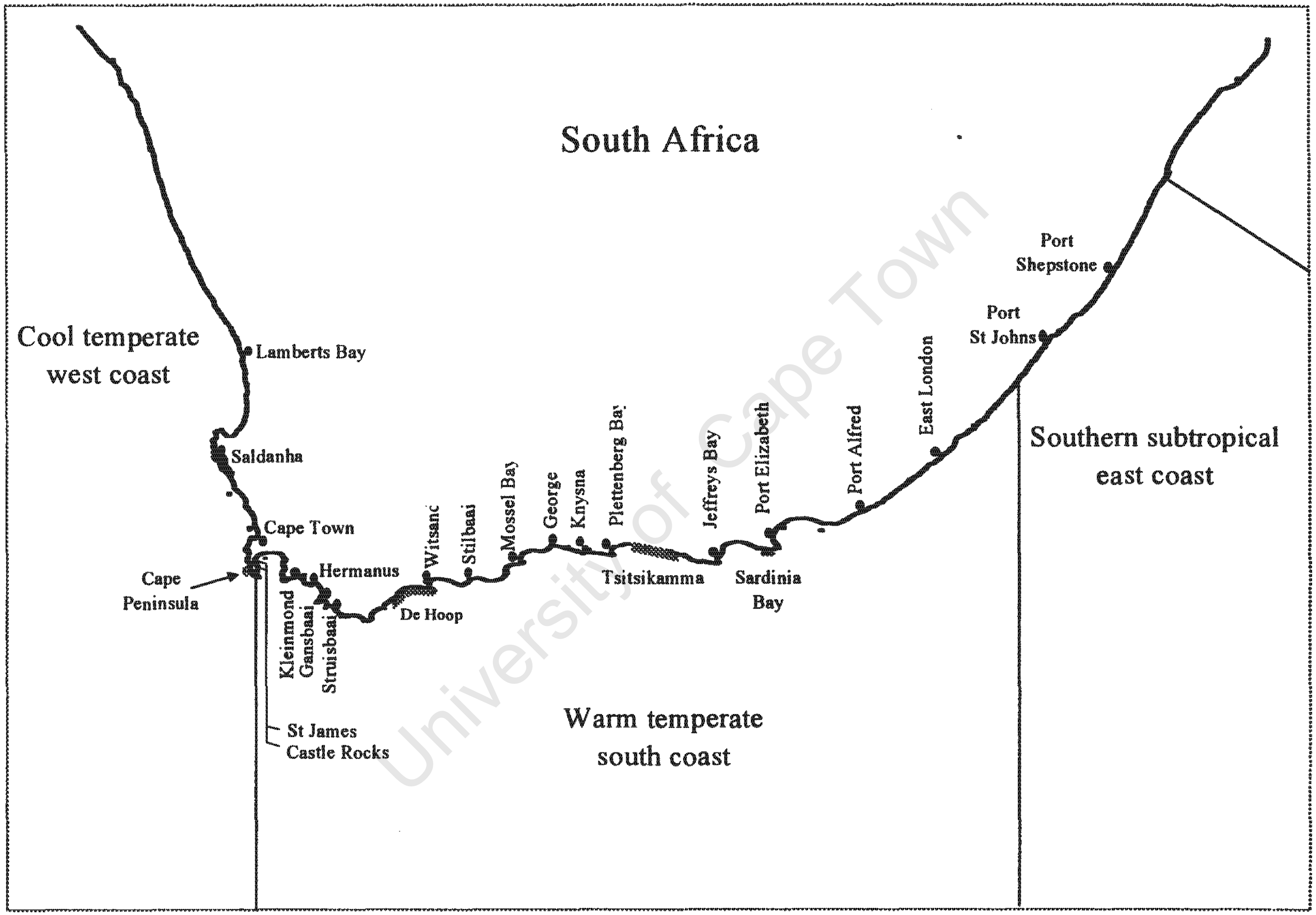


Figure 4.1 A map of South Africa's coastline showing places mentioned in the text. Shaded grey areas and sites labelled St James and Castle Rocks are marine protected areas.

tag numbers to certain fish to simulate the tag and recovery data set described in earlier chapters.

The entire population was represented by an array of size $N_{max} \times v$, where N_{max} is the maximum number of fish that could be alive at any one time and v is the number of variables recorded. With more than a million fish alive at any one time, frequent de-allocation of memory occupied by dead fish was necessary to free space and avoid processing data associated with dead fish. The process of weeding out dead fish and re-ordering the array to make space for new recruits was also time-consuming. The optimal trade-off between execution time and storage was an annual de-allocation of memory.

At the end of each model year, the living fish were summed per cell and age-class and written to a file for later analysis. Each record in that file comprised the integer numbers of fish per age-class alive in a particular cell at the end of a particular year. The catch of galjoen in each cell and each age-class was totalled throughout the year and written to a file at the end of each year, in the same format.

The spawner-biomass was totalled for each cell at the end of each model year, and stored in a one-dimensional array with A elements (A is the total number of active cells). These spawner-biomass totals were used to calculate recruitment four years later.

Habitat distribution and carrying capacity

The presence of galjoen and their carrying capacity in a cell depends on the habitat type and the geographical position of the cell. It is the distribution of habitat type that determines the patchiness of galjoen on a small scale. For simplicity a presence/absence system was used – either the cell contained the correct habitat and it supported galjoen, or the habitat was unsuitable and no galjoen occurred there. A cell was termed *active* if it was occupied by galjoen.

Each cell was assigned a particular habitat type, which was derived from a detailed geophysical map of the coast (Jackson and Lipschitz 1984). Six coastal (inter-tidal and immediate sub-tidal) habitats were recognised, namely: rocky headlands, wave-cut platforms, sandy beaches, boulder beaches, kelp beds and estuaries.

Galjoen feed primarily on rocky substrata and prefer unstable environments, presumably because instability favours pioneer algal turfs that are inhabited by the invertebrate species preferred by galjoen (Bennett and Griffiths 1986, Bennett and Attwood 1991). These conditions are provided most consistently at wave-cut platforms where broken rock is interspersed by shifting sand, and in kelp beds where dislodged holdfasts create new space. In addition, kelp wracks support large densities of decomposer amphipods and isopods, which are regularly seen in galjoen diets on the west coast (Bennett and Griffiths 1986). Boulder beaches are also unstable but rarely yield the high catch-rates associated with rocky platforms and kelp beds. Rocky headlands lead to deep water, where rocky invertebrate communities are more stable and, hence, where the optimal habitat for galjoen is found less often. Sandy beaches are occasionally interspersed with rock, too small or invisible for the area to be classed as a rocky shore. Sandy beaches are thus in-frequently inhabited by galjoen.

The assignment of occupational probabilities (the probability that a cell is active) to habitat types followed the ranking described above, although the probability values were subjectively chosen (Table 4.1). A random number generator was used to decide which cells were occupied by galjoen, according to the probabilities listed in Table 4.1.

In South Africa, galjoen are spread over three biogeographic provinces: the cool-temperate west coast, the warm-temperate south coast and the southern subtropical east coast (Emanual *et al.* 1992, Fig. 4.1). Not surprisingly, the highest abundance is found in the central of these provinces (see catch-data provided by Brouwer *et al.* 1997). It is postulated that the large-scale variability in galjoen density follows the primary productivity in the surf-zone, which decreases from west to east, but that it is limited by intense, cold upwelling events that occur frequently on the west coast. Galjoen eggs do not hatch below 14°C (Van der Lingen 1994), thus explaining the break in continuity of galjoen between South Africa and Namibia, in the region where upwelling is most intense. A three-stage function that reflects this broad pattern was used to model the carrying capacity in active cells: (i) a sharp increase from Lamberts Bay to Cape Point, (ii) an area of uniform carrying capacity from Cape Point to Still Bay and (iii) a gradual decrease from Still Bay to Port Shepstone (Fig. 4.2).

TABLE 4.1. Assumed percentage of cells that are occupied by galjoen (termed active cells), and the percentage that are accessible to shore-anglers, by habitat type.

Habitat type	% active	% accessible
Rocky platform	80	80
Kelp forest	60	50
Boulder beach	40	100
Rocky headland	20	60
Fine-grained sandy beach	10	100
Course-grained sandy beach	0	100
Estuary	0	100

Calculation of recruitment

The spawner-biomass recruitment relationship is unknown for this fishery, but the standard density-dependence argument can be applied. Eventually, populations must be limited by resources as fish densities are typically maintained within fairly narrow limits (Cushing 1988, Hilborn and Walters 1992). Density-dependent larval survivorship ensures above-average recruitment per spawner when density is low, and a maximum value for recruitment that caps population size. A Beverton and Holt function was used to model density-dependence in recruitment:

$$R_{ct} = \frac{S_{ct-4}}{\frac{1}{\mu} + \frac{S_{ct-4}}{K_c}} \quad , \qquad \text{Eq. 4.1}$$

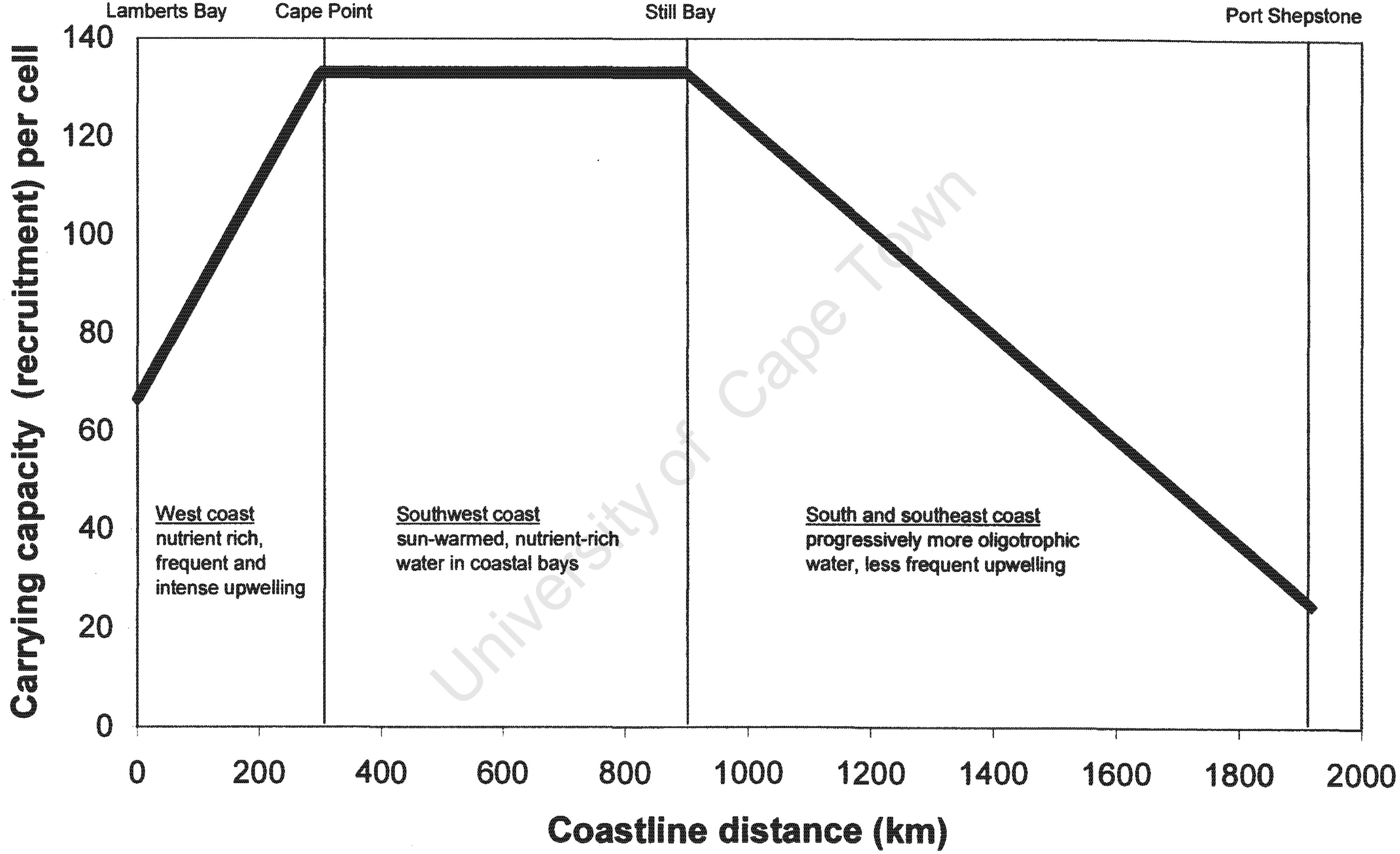


Figure 4.2 The spatial variation in carrying capacity of galjoen used in the model. The range, measured in km, extends from Lamberts Bay eastwards to Port Shepstone.

↓ fish

where R_{ct} is the recruitment strength per cell at the start of year t, S_{ct} is the spawner-biomass per cell at the end of year t, μ is the initial slope of the recruitment curve (i.e. when S is very small), and K_c is the recruitment at carrying capacity in cell c. The density dependence of this recruitment function can be viewed in two ways: either (i) adult spawning is density-dependent, with individual contributions per spawning-fish decreasing with increasing spawner-biomass or (ii) the survivorship of pre-recruits is density-dependent. Equilibrium occurs at the intersection of the spawner-biomass recruitment curve and the replacement line (Fig. 4.3). The population cannot sustain itself if the replacement line is steeper than the initial slope of the recruitment curve.

Larval dispersal was modelled by averaging the R_{ct} values over D active cells on either side of cell c (where D is the dispersal parameter), and then applying that value to cell c. Inactive cells do not contribute to recruitment and recruits are never assigned to inactive cells, therefore the averaging is calculated over the nearest (2D+1) active cells. The relationship between D and true coastline distance will vary according to the density of active cells.

$$\text{Recruitment to active cell i in year t} = \frac{\sum_{c=i-D}^{i+D} R_{ct}}{2D+1} \qquad \text{Eq. 4.2}$$

A high value of D corresponds to wide dispersal. The averaged recruitment value calculated by equation 4.2 is converted to an integer, which is the number of fish that assume identity and recruit to the cell.

Effort distribution

The distribution of fishing has varied over the course of the century and it peaked near densely-populated areas. Van der Elst (1993) estimated that recreational fishing effort in KwaZulu-Natal was increasing at a rate of 6% p.a. in the 1970s. During the 1990s McGrath *et al.* (1997) estimated an increase of 2% p.a. for the entire South African recreational fishery. Absolute levels of recreational shore-angling effort for the late 1990s

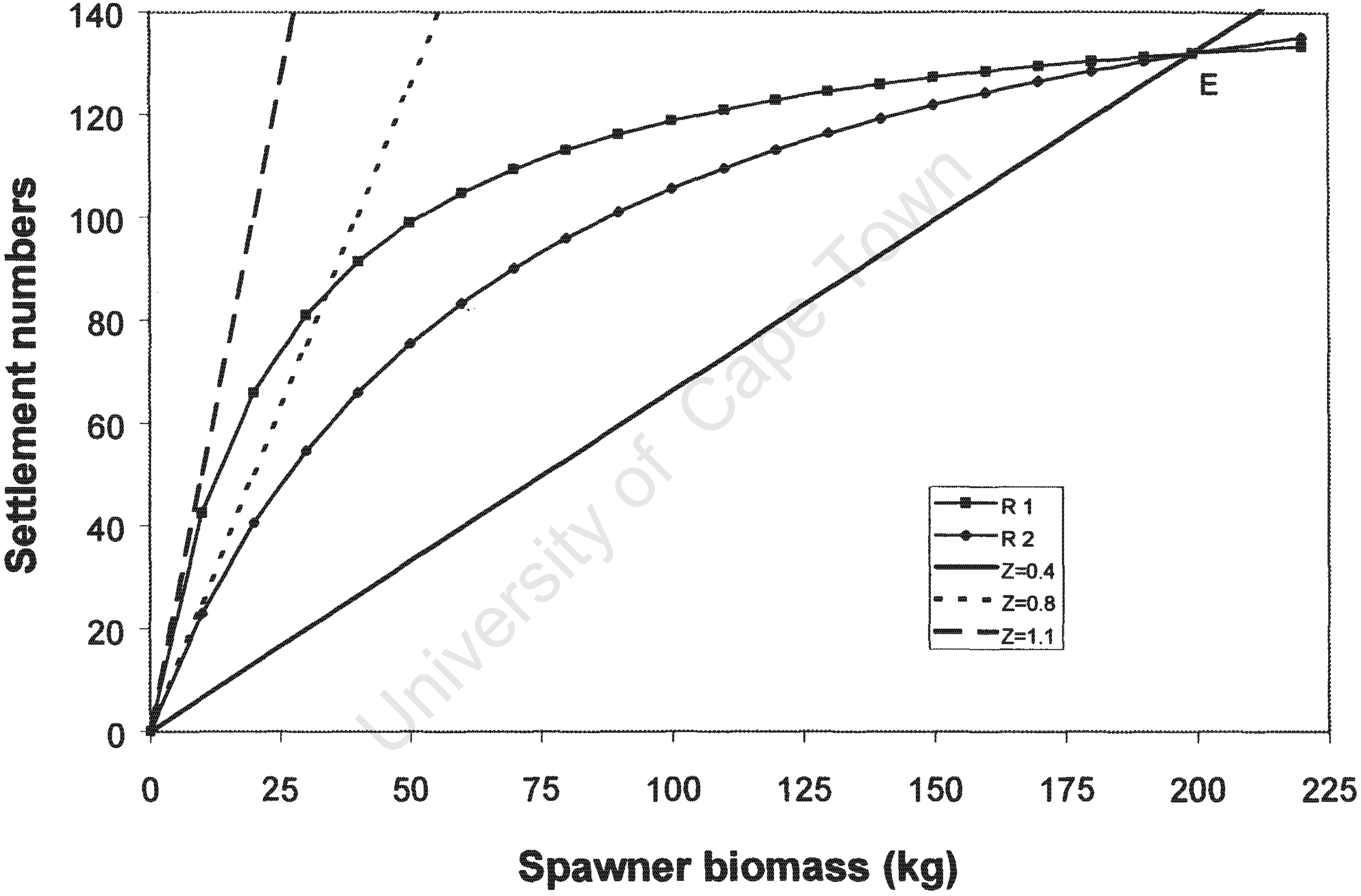


Figure 4.3 Two functions used for the spawner-biomass recruitment relationship (R1 and R2), and replacement lines for three total mortality-rates (Z=0.4, 0.8 and 1.1 y^{-1}).

were provided by Brouwer *et al.* (1997), but figures for the earlier parts of the century are not available, with the exception of a few localised survey results.

The spatial and temporal distribution of fishing effort was modelled on the assumption that the number of fishermen followed a similar distribution in time and space to the number of people living on (or near) the coast. Census data were obtained from *S.A. Statistics* (a branch of the Department of Commerce). These data cover the 20 major coastal towns over the range included in the model. Population censuses were taken 11 times during the twentieth century (Table 4.2).

For the between-census years, the historical populations of each town were assumed to increase linearly. The effort value for each cell is a function of its distance from each town and the population size of that town at the time. A normal distribution was used to spread the fishermen from each town, as most fishermen will prefer to fish close to home, but a small proportion are prepared to travel. A nationwide linefishery survey during 1995 and 1996 found that shore-anglers travelled a mean distance of 154 km from their home to the fishing destination (S. Lamberth, Marine and Coastal Management, unpublished survey data). A diffusion parameter was calculated to correspond to this statistic. An added refinement is that the diffusion parameter varied over time, increasing over the course of the century because of the increasing mobility of fishermen. For the start of the 20th century, when most fishermen would have walked or travelled by horse, the diffusion parameter was set at 5 km (i.e. 67% of fishermen remain within this distance of the town). This figure increased to 110 km for the end of the century, when high rates of car ownership and a well-developed road system made the coast much more accessible.

The absolute value of effort was adjusted to equate the mean effort value during 1996 to the mean value that was observed during the nationwide survey of that year (Brouwer *et al.* 1997). The relationship between population size and total effort was kept constant throughout the century.

TABLE 4.2. Census data for the major coastal towns. These figures must be multiplied by ten to arrive at the actual population counts. For the purpose of distributing fishing effort realistically, the greater Cape Town metropolis was split into a Table Bay and a False Bay component in a manner that reflects the position of residents relative to the coast. N/A = not available.

Coastal town	*1904*	*1911*	*1921*	*1936*	*1946*	*1951*	*1960*	*1970*	*1980*	*1985*	*1991*	*1996*
Lamberts Bay	0	0	13	59	88	162	124	103	405	360	450	626
Saldanha Bay	0	0	10	20	66	76	90	145	N/A	N/A	N/A	1972
Table Bay	4403	3063	9767	13518	15360	14114	12155	12596	N/A	N/A	N/A	51546
False Bay	232	161	1085	3379	6583	9409	12155	18895	N/A	N/A	N/A	206184
Kleinmond	0	0	1	13	26	39	31	50	158	219	285	384
Hermanus	0	63	90	137	335	362	327	341	477	571	661	2151
Gansbaai	0	0	2	75	90	108	98	104	165	192	284	360
Struisbaai	0	0	16	23	29	37	40	41	82	99	138	234
Witsands	0	0	0	0	0	6	3	0	14	23	38	20
Still Bay	0	0	0	0	18	16	17	25	63	196	265	677
Mossel Bay	169	194	270	345	377	442	614	776	1857	2040	3337	8828
George	1050	1914	1952	3371	4626	5926	7812	10554	6224	7281	9560	12504
Knysna	475	550	621	820	1020	1046	1098	1266	3641	3974	5042	11764
Plettenberg Bay	0	0	1	1	36	37	43	90	338	546	795	2187
Jeffreys Bay	0	0	6	20	34	32	45	74	262	416	630	1131
Port Elizabeth	3528	2980	4239	9409	12881	9613	23929	31661	54679	52288	67065	60138
Port Alfred	146	163	395	634	884	944	983	1258	1800	2500	3000	3500
East London	4702	4487	5863	8915	11247	12625	16415	15094	17053	16799	24047	23953
Port St Johns	35	64	39	57	85	87	100	161	N/A	N/A	N/A	7346
Port Shepstone	0	0	14	168	219	410	421	545	N/A	N/A	N/A	12157

Habitat affects accessibility to anglers. Shore-anglers can reach any part of a sandy beach, whereas rocky headlands, kelp forests and rocky platforms have restricted access, either because of the steepness and exposure of the intertidal zone, or because dense kelp cover prevents anglers from presenting bait in the water. Instead of attempting to assess whether each cell corresponds to physically accessible coast, each habitat was assigned an accessibility index, the fraction of cells that anglers can access (Table 4.1). A random number generator was used to decide which cells in each habitat were inaccessible to anglers, according to these indices. Those cells that were classed as inaccessible would not have been fished at all.

The effort in each cell for each year was calculated as follows:

$$E_{ct} = \alpha \; \Delta_c \sum_{town=1}^{town=20} (P_{town,t} \frac{1}{\sigma_t \sqrt{2\pi}} e^{-\frac{(c-c_{town})^2}{2\sigma_t^2}}) \quad , \qquad \text{Eq. 4.3}$$

where α is a constant used to equate population size to effort, Δ_c is a step function (either 1 or 0) used to denote physical accessibility of the cell to anglers, c is the cell number, t is the year, c_{town} is the cell number nearest to the centre of *town*, $P_{town,t}$ is the population in *town* in year *t*, and σ_t is the diffusion parameter that determines the spread of effort from each town in year t.

Apart from natural refuges, there were six marine protected areas that took effect at various times in the fishery (Table 4.3, Fig 4.1). Effort in these cells were set to zero from the years indicated.

TABLE 4.3: Year of establishment and number of coastline cells within six marine protected areas in which galjoen are fully protected by law. Each cell is 100 m in length.

Marine protected area	Date established	Number of cells
Cape Peninsula	1979	120
Millers Point	1990	40
St James	1990	20
De Hoop	1985	510
Tsitsikamma	1964	580
Sardinia Bay	1990	80

Fishing mortality

The effort value for each cell and year (E_{ct}) was converted into a fishing mortality-rate (F_{ct}) by multiplying it by the catchability factor, q. Catch-data from the De Hoop MPA were used to estimate how fishing selectivity varied with age. Full selectivity applies to age 5 onwards, whereas approximately 50% of full selectivity applies to the age 4 fish (the recruits). The recruits were therefore fished at half the rate of the older fish. By law, a size limit of 35 cm (age 5 for female, age 6 for male) did apply to the capture of galjoen from 1974 onwards, but there was little compliance with this regulation. Attwood and Farquhar (1999) found that 32% of the galjoen kept by anglers between Hangklip and Hermanus during 1995 and 1996 were under-sized. For this reason the model does not simulate the size limit, although it could easily be included.

Movement behaviour

Two movement models were developed to correspond to the tourist and polymorphic hypotheses described in chapter 2.

Tourist model: Each fish has a home-range that includes three cells - the cell to which it recruited and the nearest active cell on either side. It spends most of its time in that home-range, but occasionally leaves for another destination, where it also holds another home-range of three active cells. Three parameters describe this pattern. β is the probability of a fish leaving its natal home-range during a single time step (one week), and χ is the probability of it returning to that range. If χ exceeds β, then the fish spends most time in the natal home-range, on average. The third parameter is δ, a diffusion parameter used to select the location of a new home-range according to a normal distribution centred on the natal home-range.

Polymorphic model: Two kinds of fish exist, residents and nomads. Fish are assigned one or the other type of behaviour at recruitment in the ratio $\phi : (1-\phi)$, for residents and nomads respectively. In the absence of any genetic evidence, and for simplicity, it is assumed that this condition is not inherited, i.e. the ratio among recruits remains constant, irrespective of the relative frequency of movement types among the local spawning stock. Resident fish never leave the home-range, which includes three cells - the cell to which it recruited and the nearest active cell on either side. The nomadic fish move continuously, selecting a new cell each time step. The location of the new cell is drawn from a normal distribution, with a diffusion parameter γ, centred on its current cell location.

The model has closed boundaries. No fish or larvae cross the model outer boundaries and none enters.

Parameter values and model variations

The biological parameters (e.g. growth, spawning) were taken from Bennett and Griffiths (1986). The growth model is a Von Bertalanffy function, and egg production is a linear function of mass. Other fishery parameters (natural mortality-rate, age-at first capture and catchability) were estimated from data presented in Chapters 2 and 3. Point estimates were used for the natural mortality-rate and catchability.

Two values of the slope of the Beverton and Holt recruitment curve were selected for *high* and *low* resilience, while keeping the equilibrium values constant (Fig. 4.3). It is desirable to keep constant equilibrium values for the purpose of comparing results among simulations. If the equilibrium values are identical, any differences between simulations with different spawner-biomass-recruitment relationships can be ascribed to the degree of resilience. An additional complication is that the carrying capacity (equilibrium at Z=M) varies along the range of galjoen (Fig. 4.2), and hence the Beverton and Holt parameters were varied proportionately to keep the same shape curve for all cells, despite variations in the absolute quantities across the range.

Two parameters that are commonly used to describe the shape of a recruitment curve are (i) the maximum reproductive rate at low population size, a unitless ratio (Myers *et. al.* 1999) and (ii) z, the percentage of maximum recruitment realised at a spawner-biomass of 20% of carrying capacity (Hilborn and Walters 1992). The high resilience model corresponds to a z-value of 69% (or max. rep. rate of 5.4). The low resilience model corresponds to a z-value of 50% (or max. rep. rate of 2.4). Mortality-rates (fishing + natural) of 1.1 and 0.8 y^{-1} (Fig. 4.3) are required to collapse a stock with these respective spawner-biomass recruitment relationships. To put these curves into perspective, Myers *et al.* (1999) found that the maximum reproductive rate of 50 teleost species ranged between one and seven, while z ranged between 34% and 95%.

The absolute value of carrying capacity was set to equal the abundance of galjoen at De Hoop Marine Protected Area at the centre of the range of galjoen, where density estimates were obtained from two sites (Chapter 3). The higher of these were chosen (that corresponding to the Lekkerwater site), as it was assumed that all cells at this site were active whereas only a fraction of those at Koppie Alleen were active, due to habitat differences, as discussed in Chapter 3.

Three degrees of larval dispersal were considered: restricted (D=5 active cells or ±1.7 km in total), local (D=50 active cells or ±17 km) and regional (D=500 active cells or ±170 km). The conversion from active cells to absolute distance varies with the density of active cells. Global dispersal (i.e. all cells contribute to recruitment in all other cells equally) is not considered a realistic possibility. Current-closure systems (Nelson and Hutchings 1987) and prominent capes (such as Mossel Bay and Cape St Francis) cause localised meso- and micro-scale circulation (Tilney *et al.* 1996). Invertebrate larval dispersal off California, where there is a comparable upwelling system to the Benguela, is constrained to the distances between major promontories or capes, in that case 100 – 200 km (Botsford *et al.* 1998). Off South Africa those distances are similar. The D=500 scale was thus chosen as an upper limit. Most recent findings point to local retention of larvae of reef-fish (Warner *et al.* 2000), suggesting that an even smaller scale, linked to reef patterns, may be appropriate (Hence D=50). The restricted scale (D=5) might seem unrealistic for a species that produces floating eggs, but it was included to cover a possible natal-homing response that may be achieved at a later pre-recruit stage (fish only recruit at age 4).

The parameters of the polymorphic and tourist movement models were varied in an attempt to 'fit' the model to observation in the following chapter. In this chapter, values were selected on the basis that they appear to be consistent with results presented in Chapter 2. For the tourist model, the data shown in Figure 2.4 were used to estimate the value of δ, while β and χ were set at 0.01 and 0.25 per week respectively. For the polymorphic model, ϕ was estimated at 0.95 (Table 2.6), and the value of γ was initially set to 15 km^2 per week, which corresponds to an average displacement velocity of approximately 1.7 $km.d^{-1}$.

With two spawner-biomass recruitment functions, three larval dispersal possibilities and two movement models, there were twelve model variations. The name of each variation and the parameter values used are listed in Table 4.4. This notation is kept throughout subsequent chapters.

An attempt was made to describe realistic spatial structure and effort profiles without physically re-surveying the coast. These input parameters were regarded as fixed data and no variations were considered here. Further refinements to the model may include a revision of habitat types, but this will involve extensive field surveys, as the type of information required to improve on this model is not available from maps.

Table 4.4. The name of each model variation and the associated parameter values. The spawner-biomass recruitment parameters listed are those which produce the maximum carrying capacity within the range. μ and K_c are reduced proportionately to simulate lower carrying capacities (Fig. 4.2).

Model name	Type of movement	Stock-recruit parameters	Larval dispersal
T/SR1/LD5	Tourist model β= 300 km^2 χ=0.01 δ=0.25	Resilient model μ=5.9374 recruits/kg K_c=148.581 kg	D=5 active cells
T/SR1/LD50			D=50 active cells
T/SR1/LD500			D=500 active cells
T/SR2/LD5		Vulnerable model μ=2.6374 recruits/kg K_c=176.29 kg	D=5 active cells
T/SR2/LD50			D=50 active cells
T/SR2/LD500			D=500 active cells
P/SR1/LD5	Polymorphic model ϕ=0.95 γ=15 km^2	Resilient model μ=5.9374 recruits/kg K_c=148.581 kg	D=5 active cells
P/SR1/LD50			D=50 active cells
P/SR1/LD500			D=500 active cells
P/SR2/LD5		Vulnerable model μ=2.6374 recruits/kg K_c=176.29 kg	D=5 active cells
P/SR2/LD50			D=50 active cells
P/SR2/LD500			D=500 active cells

Random numbers were used in the simulations, but the model is not stochastic. The large number of individual fish together with fixed parameters for any one run means that results between runs with different random number sequences were almost identical. Stochasticity can only be achieved by varying parameter values, which is not feasible at present, particularly as prior distributions of many parameters are ill-defined. The present application of the model aims to investigate spatially-linked processes, for which stochastic simulations are not essential, rather than make probabilistic predictions, which will require a consideration of parameter uncertainty.

Execution

The model was initialised by setting the recruitment to each active cell to a value that corresponded to the equilibrium value for that cell for the first 12 years. Thereafter, the spawner-biomass was sufficiently high to continue maintaining recruitment at the equilibrium value.

?

A multiplicative, congruential algorithm called RAN0 (Press *et al.* 1992) supplied random numbers. Press *et al.* (1992) call this the 'minimum standard', sufficient for the majority of applications. Its only known flaw is that extremely small numbers (which are called with an equally small frequency) will be followed by a number smaller than 0.1. This failing might be problematic in applications that involve extremely rare events, such as atomic fission. RAN1, which does not have this failing, has a period of only 10^8, i.e. after 10^8 calls the sequence begins again. RAN0 is better in this respect with a period of 10^9, but both these generators will provide a sequence that has to be re-used, as the model calls for approximately 10^{11} random numbers. The seed number used for the first call merely establishes where the sequence will begin. The RAN0 sequence will be re-used approximately one hundred times, and RAN1 a thousand times. The ideal generator would be RAN2, but it takes twice as long to execute as RAN0. In the interests of minimising execution time, RAN0 was used. It is difficult to think of a reason not to re-use a sequence of 10^9 in this application, as there is no precise match between this period and cycles within the model (e.g. the number of calls per year or month).

The model was coded in FORTRAN 90 and executed on a Pentium III processor. Execution time was just short of an hour.

RESULTS

Spatial structure

The exact length of coastline that was modelled is 1918 km, and it was split into 19180 cells. The dominant habitat is fine-grained sandy beach, which covers about 43% of all cells (Table 4.4). Rocky headlands and rocky platforms contribute almost equal fractions, and together they account for another 41%. Most of the remainder consists of kelp forests. The habitat is not evenly distributed within the range. All kelp forests are in the west, whereas sandy beaches are more dominant in the east. Coastline habitats are also fragmented. Some habitat types may be continuous for 10 km and more, but the average run of cells of identical habitat is considerably less (Table 4.5).

Among 10-km segments of coastline, the modelled carrying-capacity of galjoen was highly variable (Fig. 4.4), although the basic underlying trend in carrying capacity was evident (as depicted in Fig. 4.2). Recruitment density peaked near the centre of the range, at approximately 1 000 recruits per km.

Overall, 30 percent of the cells were active, and 75% of those were accessible to anglers (Table 4.5). Whereas there was no fishing effort in 1295 active cells, not all of these were natural refuges. A natural refuge must consist of at least three adjacent active cells in which there is no fishing, due to the home-range behaviour that allows a fish to visit three adjacent cells. Overall, there were only 358 natural refuges of at least three active cells, not including the MPAs.

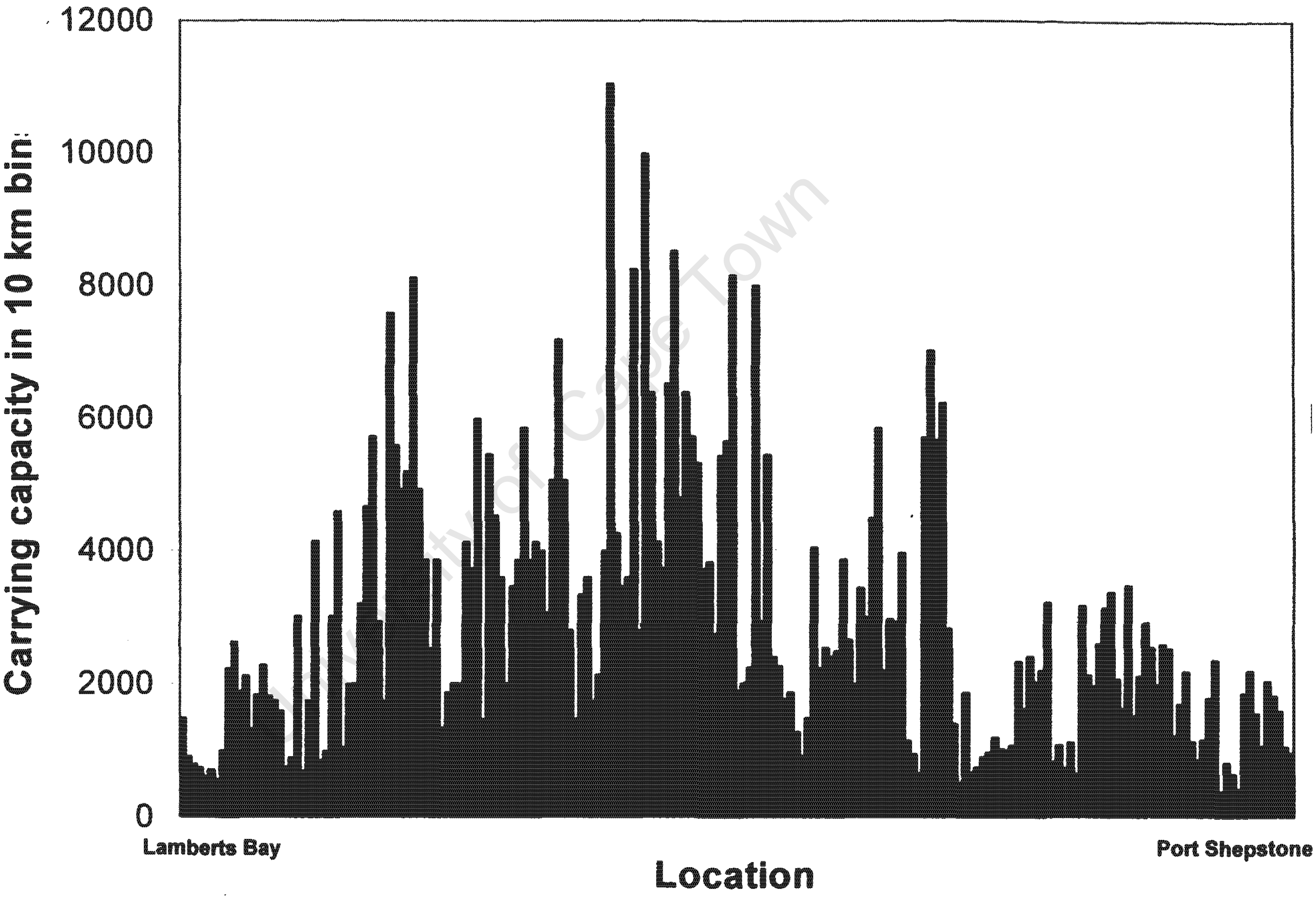


Figure 4.4 The modelled carrying capacity of galjoen in 10-km sections of coast. The carrying capacity is expressed as the recruitment strength (number of fish) at equilibrium without fishing mortality.

TABLE 4.5: Summary of the habitat field used in the IBM. RH = Rocky headland, RP = Rocky platform, KF = Kelp Forest, BB = Boulder beach, FSB = Fine-grained sandy beach, CSB = Coarse-grained sandy beach, E=Estuary. Each cell represents 100 m of coastline.

	RH	RP	KF	BB	FSB	CSB+E	Total
Cells	4002	3851	1515	347	8343	1122	19180
Cells (%)	20.9	20.0	7.9	1.8	43.5	5.8	
Average unbroken run (cells)	2.4	15	14	7	21	4	
Active cells	825	3064	911	133	825	0	5758
Accessible active cells	515	2441	430	133	825	0	4344

Effort and fishing mortality profiles

The coastal population increased at a mean annual rate of 3.5%, although the fitted exponential curve does not emulate the sharp rise in the coastal population from 1980 onwards (Fig. 4.5). Accordingly, the intensity of fishing increased steadily up to 1980, but then more than doubled in the last 20 years, despite the introduction of a few marine protected areas in the last few decades (Fig. 4.6).

The two recruitment curves in the model had initial slopes that corresponded to total mortality-rates of 0.8 and 1.1 y^{-1} (Fig. 4.3). At these mortality-rates the galjoen population will tend towards a zero equilibrium value. Averaging over all cells, these total mortality-rates (natural + fishing) were reached in 1974 and 1986, respectively (Fig. 4.6).

Fishing effort was dominated by four metropolitan areas in the early part of the century, but that influence was later spread over wider areas (Fig. 4.7). The longest gap between these occurs between False Bay and George, where approximately 400 km of coast received little effort in 1940, although later this area came within reach of city-based anglers. The slight eastward shift in the peak at Cape Town between 1940 and 1975 reflects the eastward spread of the metropolis and the opening of the False Bay coast.

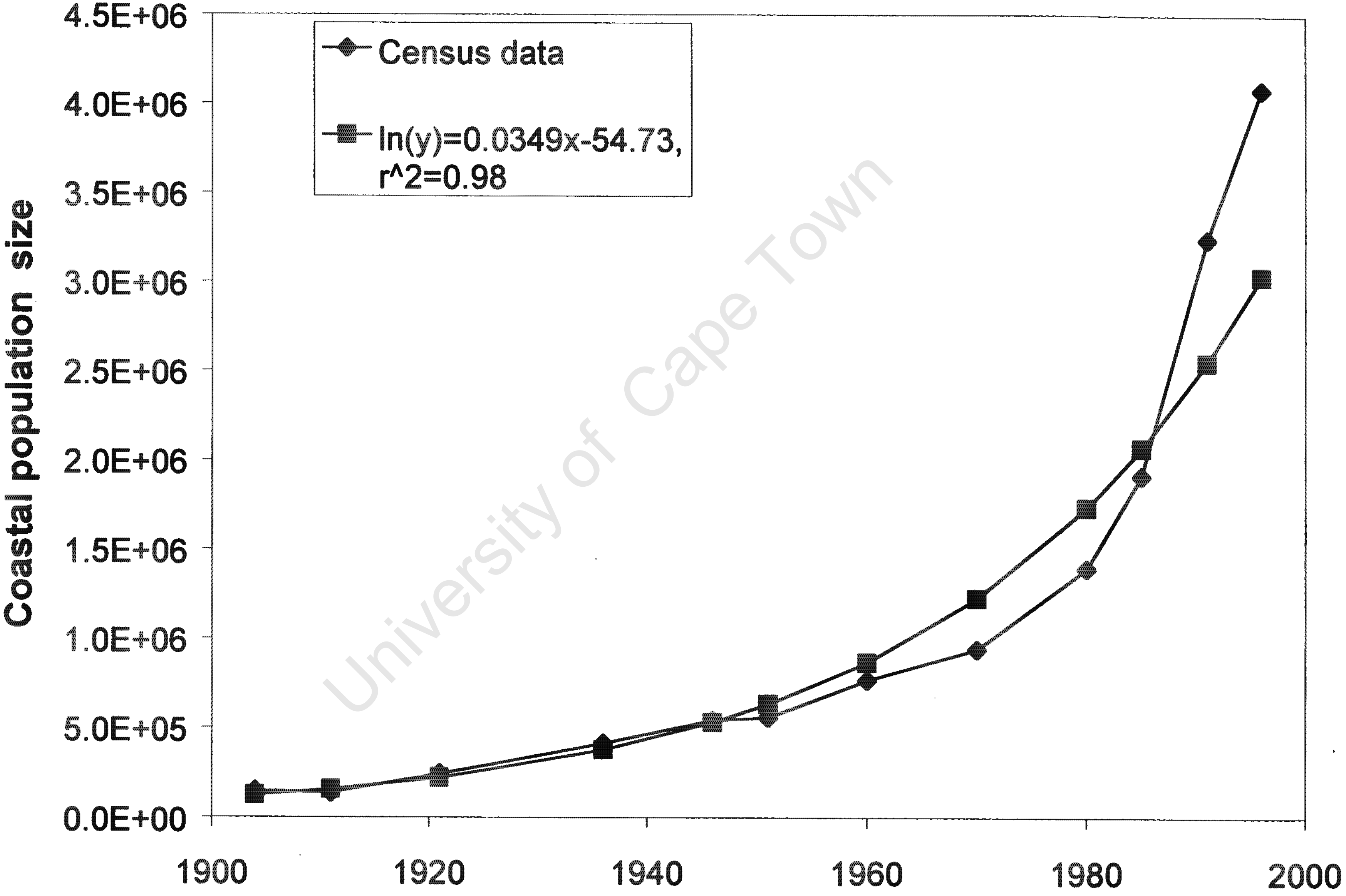


Figure 4.5 The combined population size of coastal towns from Lamberts Bay to Port Shepstone over the 20th C. The fitted exponential model suggests an average increase of 3.5% p.a.

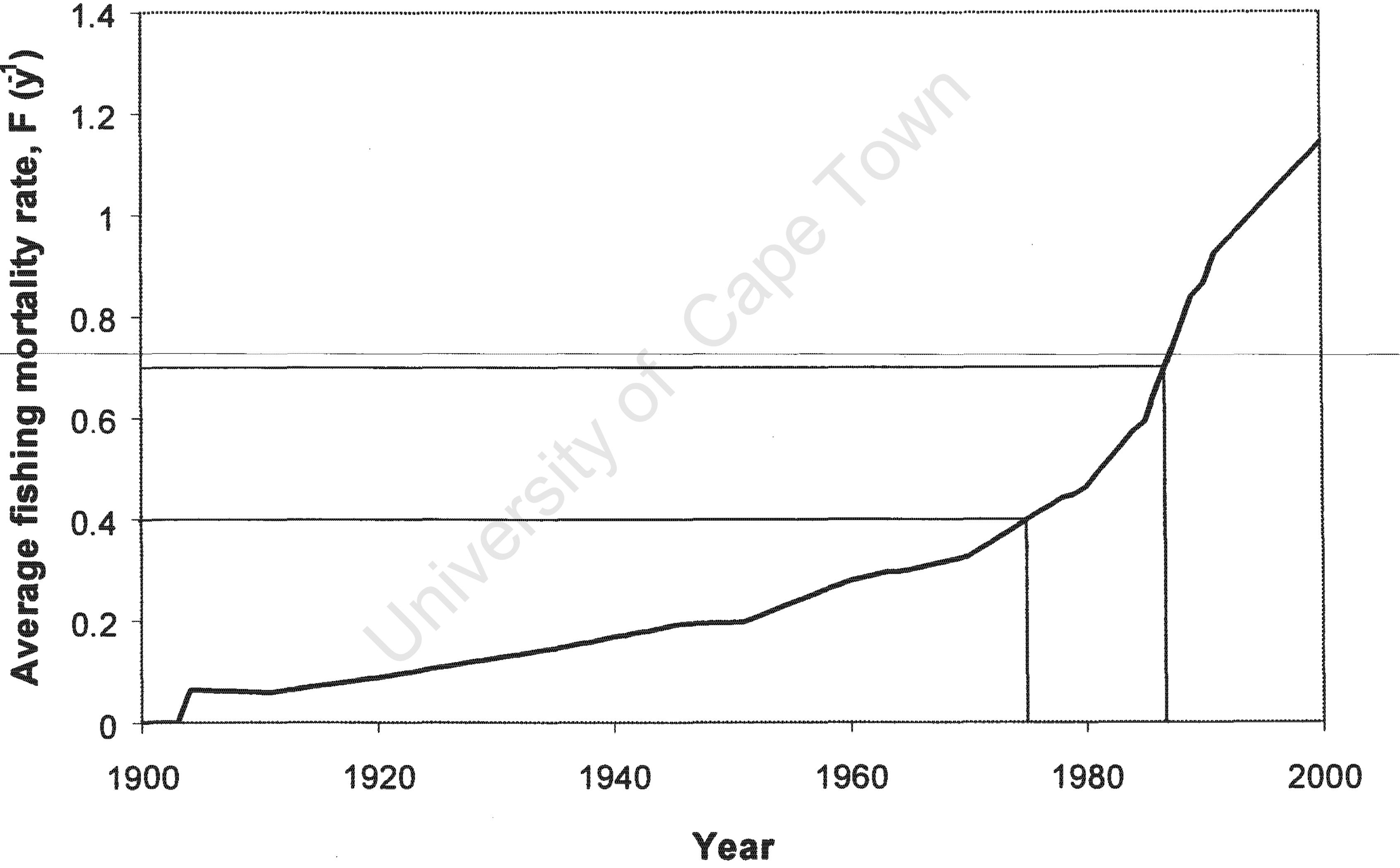


Figure 4.6 The average fishing mortality-rate across all cells was determined from census data and a model of angler distribution.

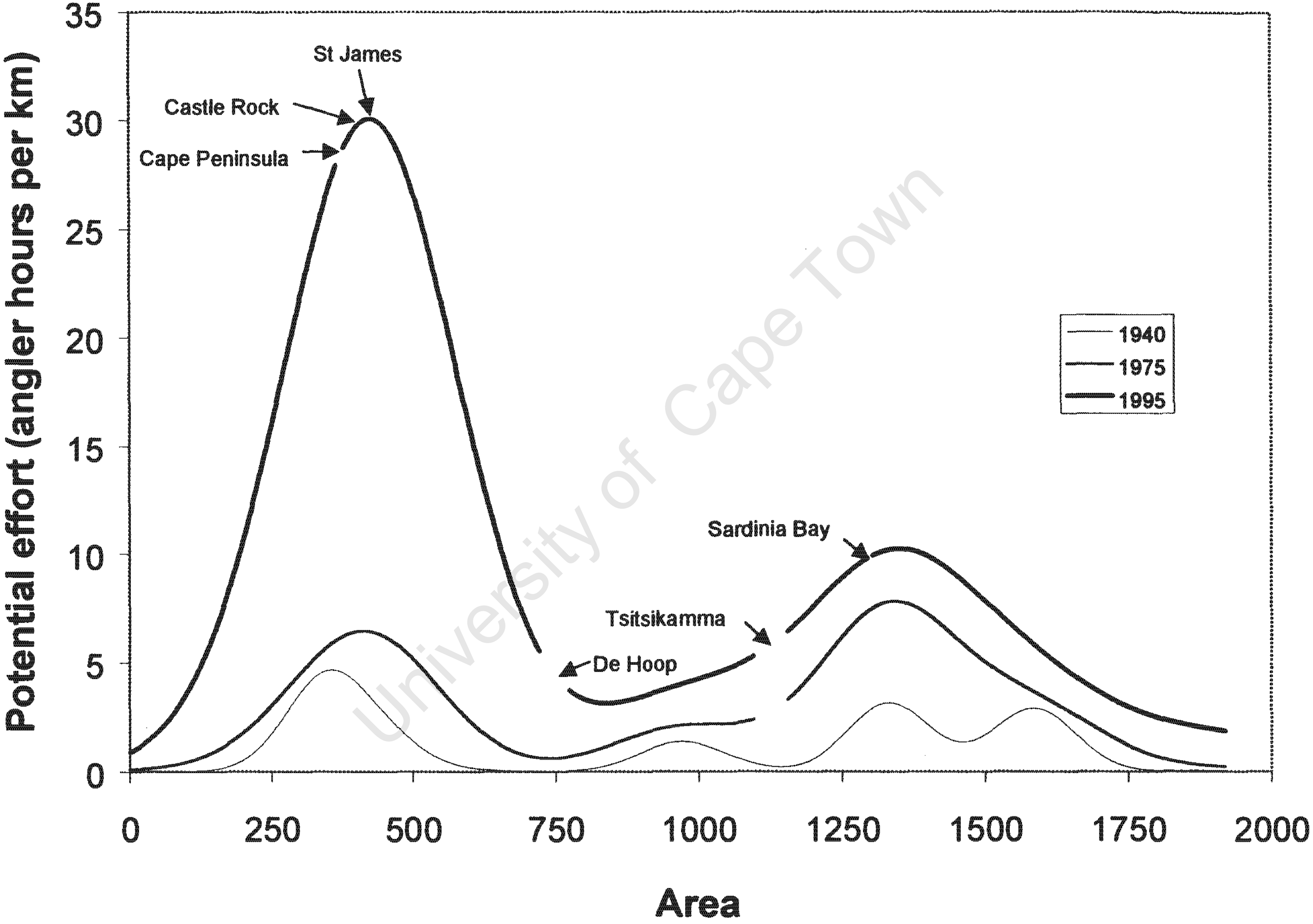


Figure 4.7 The modelled distribution of potential effort along the coast during three selected years. The qualifier 'potential' is used as not all cells are accessible to anglers. Discontinuities in the 1975 and 1995 lines represent no-take MPAs.

The resulting frequency distribution of fishing mortality-rate is positively skewed within all years (Fig. 4.8). Proportionately few cells have a large fishing mortality-rate, whereas many cells are not fished. Overall fishing effort is reduced because of inaccessibility to these cells, according to the proportions listed in Table 4.4. During 1995 some cells experienced phenomenally high fishing mortality-rates – up to 5.5 y^{-1}. Partly offsetting these were an increased number of cells in marine protected areas that were not fished at all during the most recent period.

Galjoen population trajectories

When the model was run without any fishing mortality, the start-of-year population stabilised after year 20 around a value of 1 666 000 fish. The coefficient of inter-annual variation was consistent between 0.0002 and 0.0004, and was not affected by the choice of movement model, spawner-biomass-recruitment relationship or the extent of larval dispersal. The end of year total population size was 1116500, after being reduced by natural mortality, which was constant throughout all cells and age-classes.

high & low resilience

When fishing mortality was applied, steady declines in the galjoen population occurred for every simulation (Fig. 4.9). The trajectories fell into two distinct groups according to the spawner-biomass recruitment parameters. There were only small differences between population trajectories that used the same spawner-biomass-recruitment relationship.

Models with the resilient spawner-biomass-recruitment relationship had higher population sizes in 2000 and higher overall catches than those with the less resilient function (Table 4.6). The population in 2000 was reduced to approximately 39% of the maximum for the resilient spawner-biomass-recruitment relationship and 30% for the less resilient relationship.

The polymorphic models had marginally greater final population sizes but smaller overall catches than their tourist counterparts (Table 4.6). Changes in the extent of larval dispersal by two orders of magnitude had comparatively little effect on the total

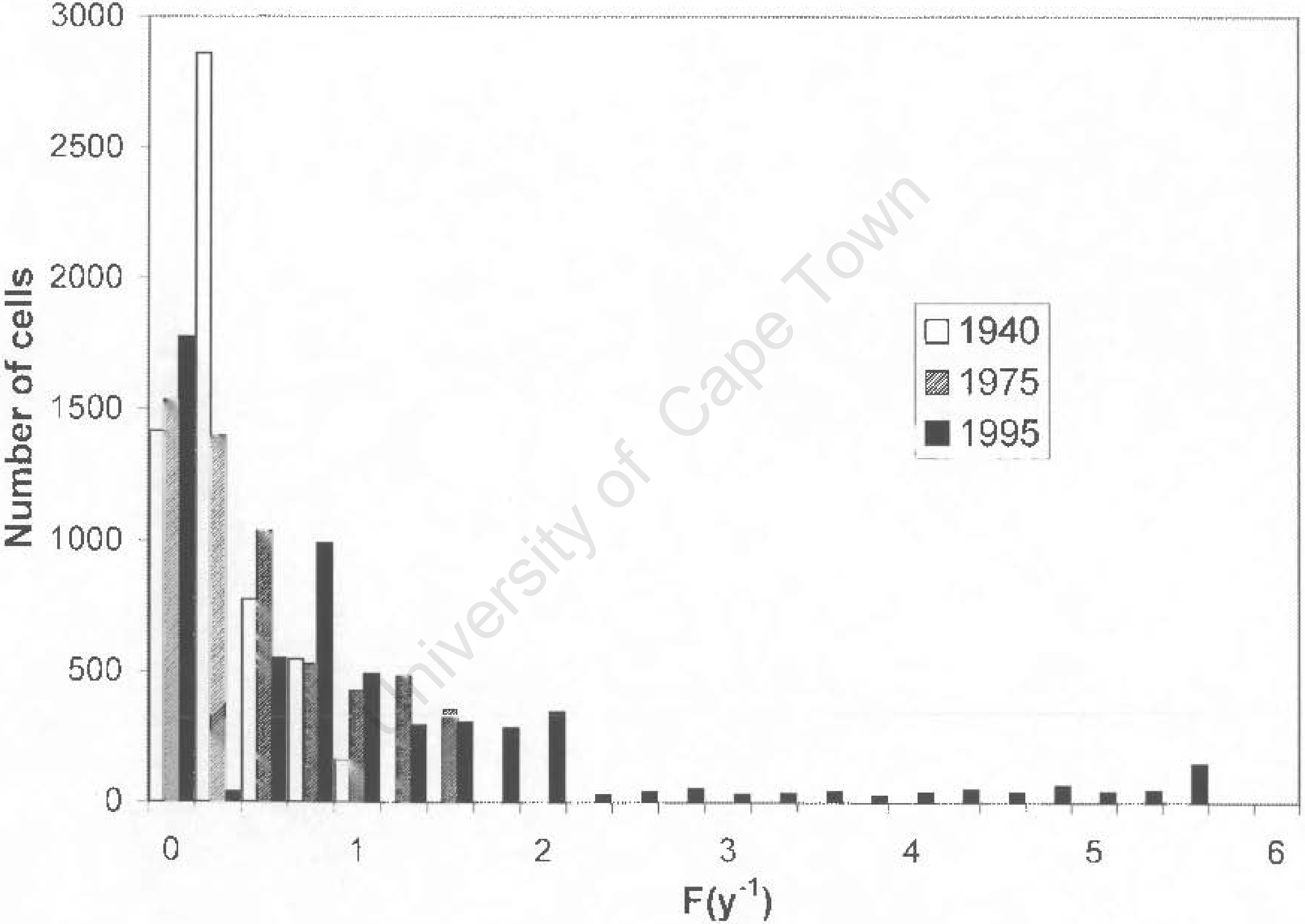


Figure 4.8 A frequency distribution of the fishing mortality-rate applied in cells during three selected years. The increasing frequency of 'zero' fishing mortality over time reflects the progressive introduction of marine protected areas.

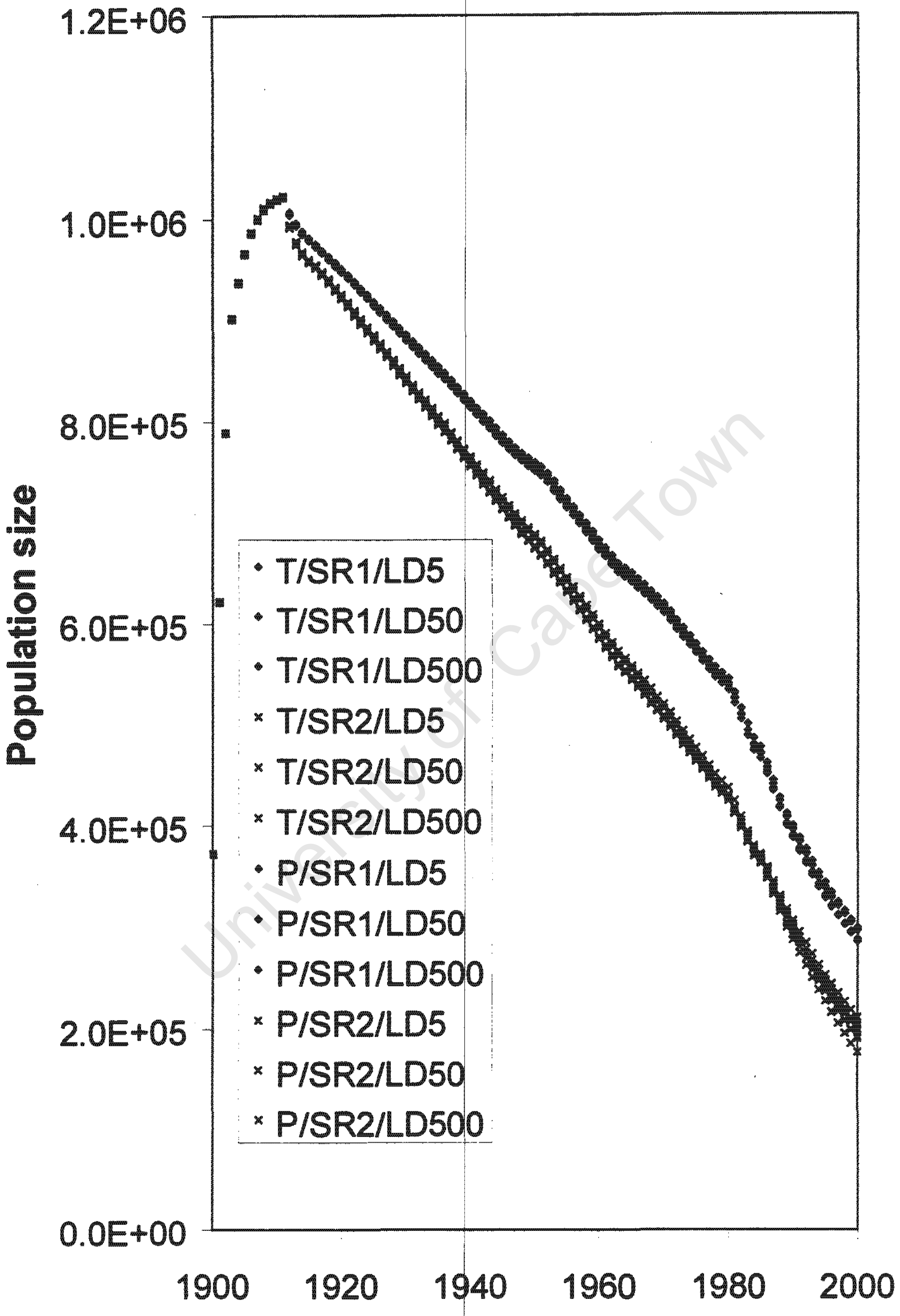


Figure 4.9 The trajectory of the end-of-year galjoen population size for 12 model variations. The initial 20 years were disregarded because they represent a stabilisation period after initiation.

population size, although this effect was consistent. Less dispersal resulted in larger final population sizes but smaller catches (Table 4.6).

TABLE 4.6: Relative population size by 2000 (relative to carrying capacity) and total catch over the 100-year simulation period.

Simulation	Population depletion	Total catch (x 10^6)
T/SR1/LD5	0.387	11.0
T/SR1/LD50	0.384	11.3
T/SR1/LD500	0.379	12.0
T/SR2/LD5	0.299	8.0
T/SR2/LD50	0.288	8.2
T/SR2/LD500	0.261	9.4
P/SR1/LD5	0.399	10.8
P/SR1/LD50	0.397	11.1
P/SR1/LD500	0.397	11.9
P/SR2/LD5	0.317	7.8
P/SR2/LD50	0.303	8.0
P/SR2/LD500	0.280	9.3

Catch trajectories

Total annual catches in terms of numbers peaked consistently between 1987 and 1991 (Fig. 4.10). These peaks occurred a few years after the average fishing mortality-rate exceeded the threshold values for the two spawner-biomass-recruitment curves (Fig. 4.6). Maximum annual catches ranged from 108 000 to 210 000 fish. The subsequent declines were greatest for those models with limited larval dispersal, but relatively slight for those with extensive larval dispersal. Larval dispersal and spawner-biomass-recruitment relationships were the major factors influencing catch. By contrast, the adult movement pattern had little effect.

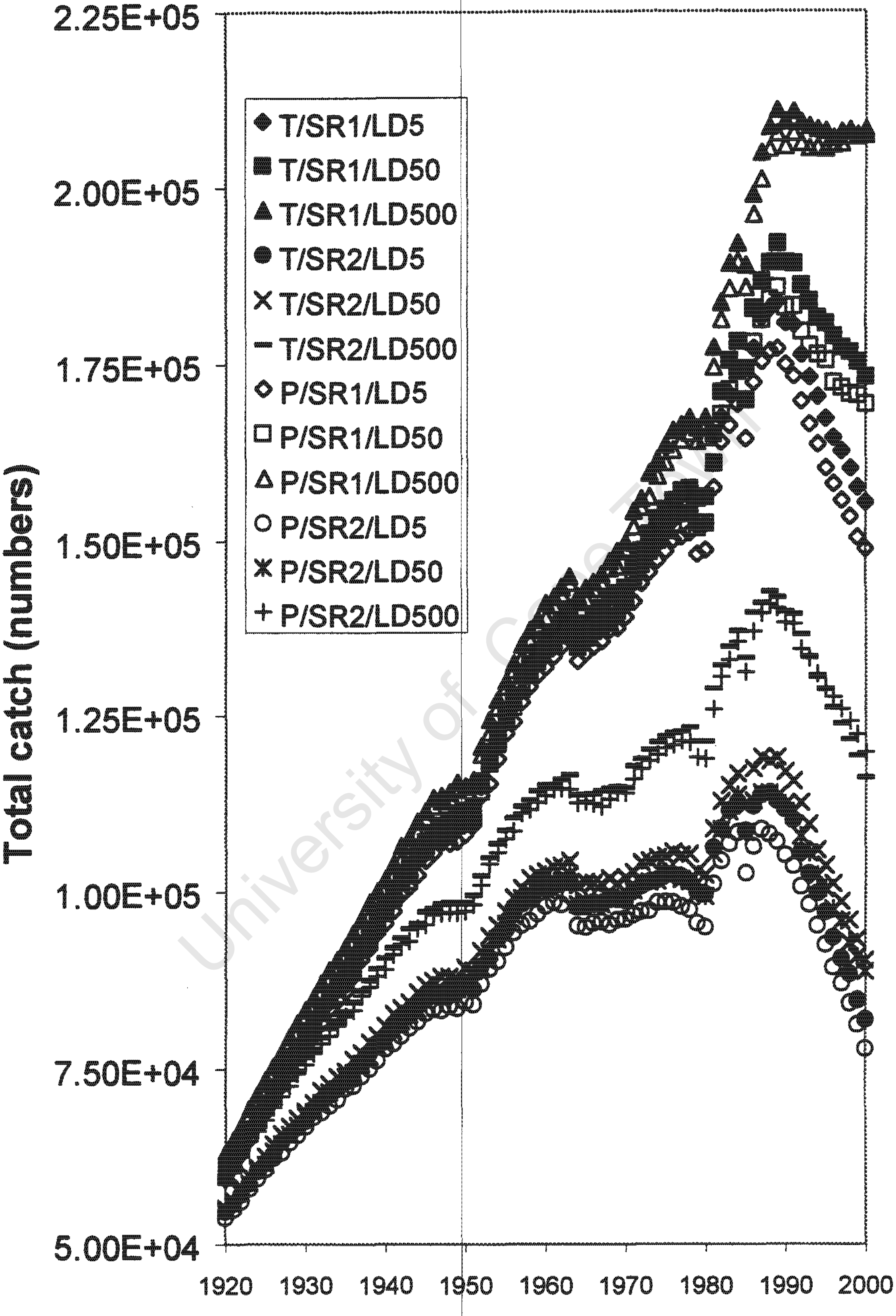


Figure 4.10 The trajectory of the catch of galjoen over time for each of the 12 model variations.

Catch per unit effort and abundance

The initial overall CPUE (total catch divided by total effort) was 0.6 fish per hour. This value declined according to local abundance, declining faster for those simulations that used the less resilient spawner-biomass-recruitment function. In a spatially-dimensionless environment, a constant catchability-value will cause CPUE to change in proportion to changes in abundance. However, in this spatially-structured model the two variables were not perfectly proportional (Fig. 4.11). At high densities, CPUE was proportional to abundance. At a population size of about 800 000, a small increase in CPUE relative to abundance around 1950 reflected the spreading of fishing effort to east of Cape Point, where fish densities were high. However, at low fish densities, CPUE declined more rapidly than abundance, as unfished cells supported high fish densities that were not reflected in the CPUE statistic.

Spatial variations in fish density and catch

Three scales of variation in density were evident (Plates 1-12). Large-scale variation results from the gradual changes in carrying capacity, which peaks in the centre of the range. At smaller scales, density variation is due to the application of variable fishing mortality-rates. The evolution of the fishery was characterised by local depletions that gradually spread from metropolitan areas. At the smallest scale, there is variation due to habitat type and natural refuges, which is evident at all degrees of larval dispersal (compare the inset in Plate 1 to that in Plate 3). Recoveries in density occurred in all marine protected areas for most simulations. Possible exceptions include the smallest MPA (St James) under conditions of wide larval dispersal and low resilience, when the recovery after ten years was not noticeable on the colour plot (Plates 6 and 12).

In 1930 the density of fish in approximately 80% of active cells was more than 75% of the carrying capacity, subject to variations in the spawner-biomass-recruitment relationship and larval dispersal. By 2000 the same density was found in less than 10% of active cells (Fig. 4.12). Despite widespread declines in abundance a few cells maintained

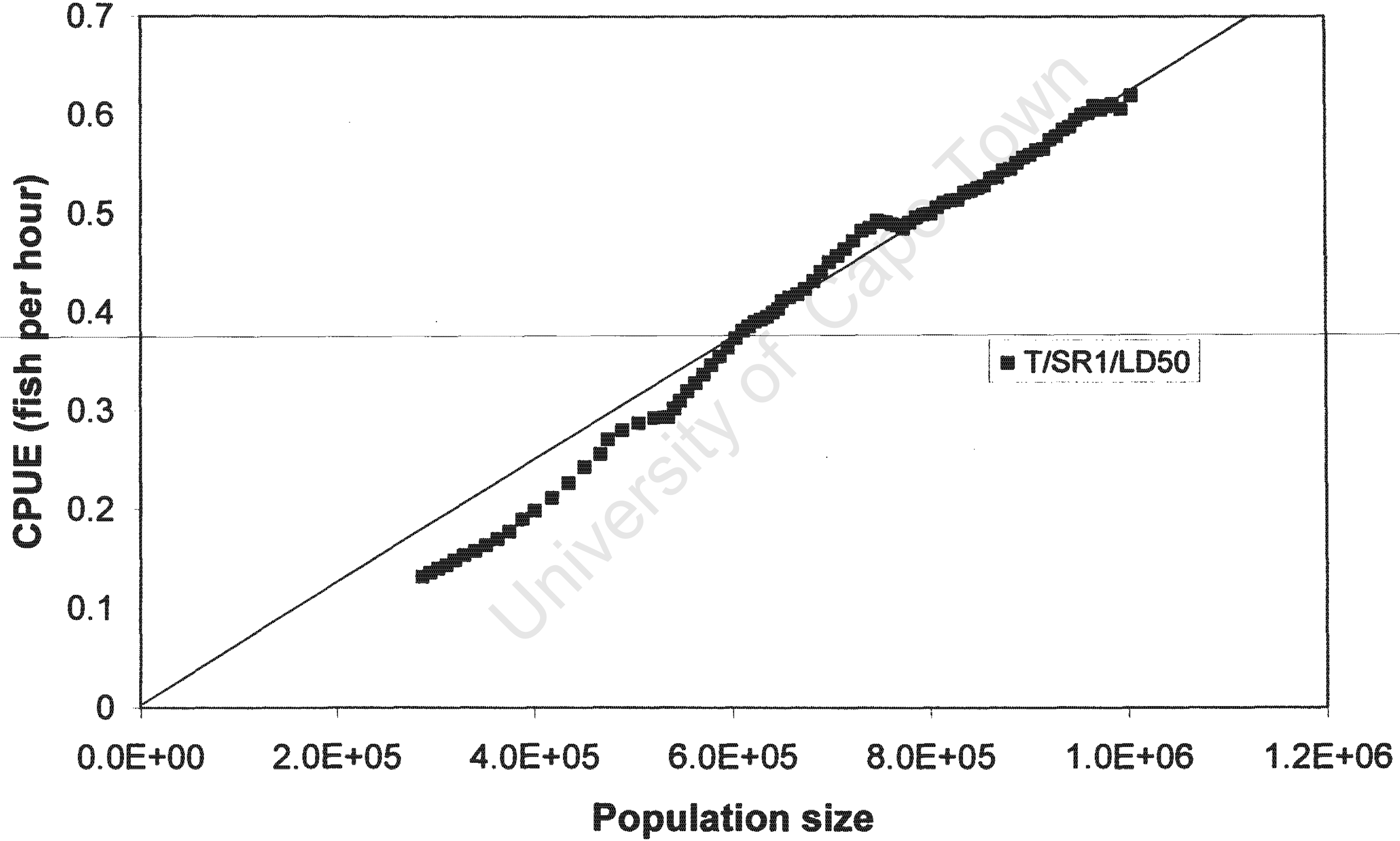


Figure 4.11 Total CPUE plotted against total population size for model T/SR1/LD50.

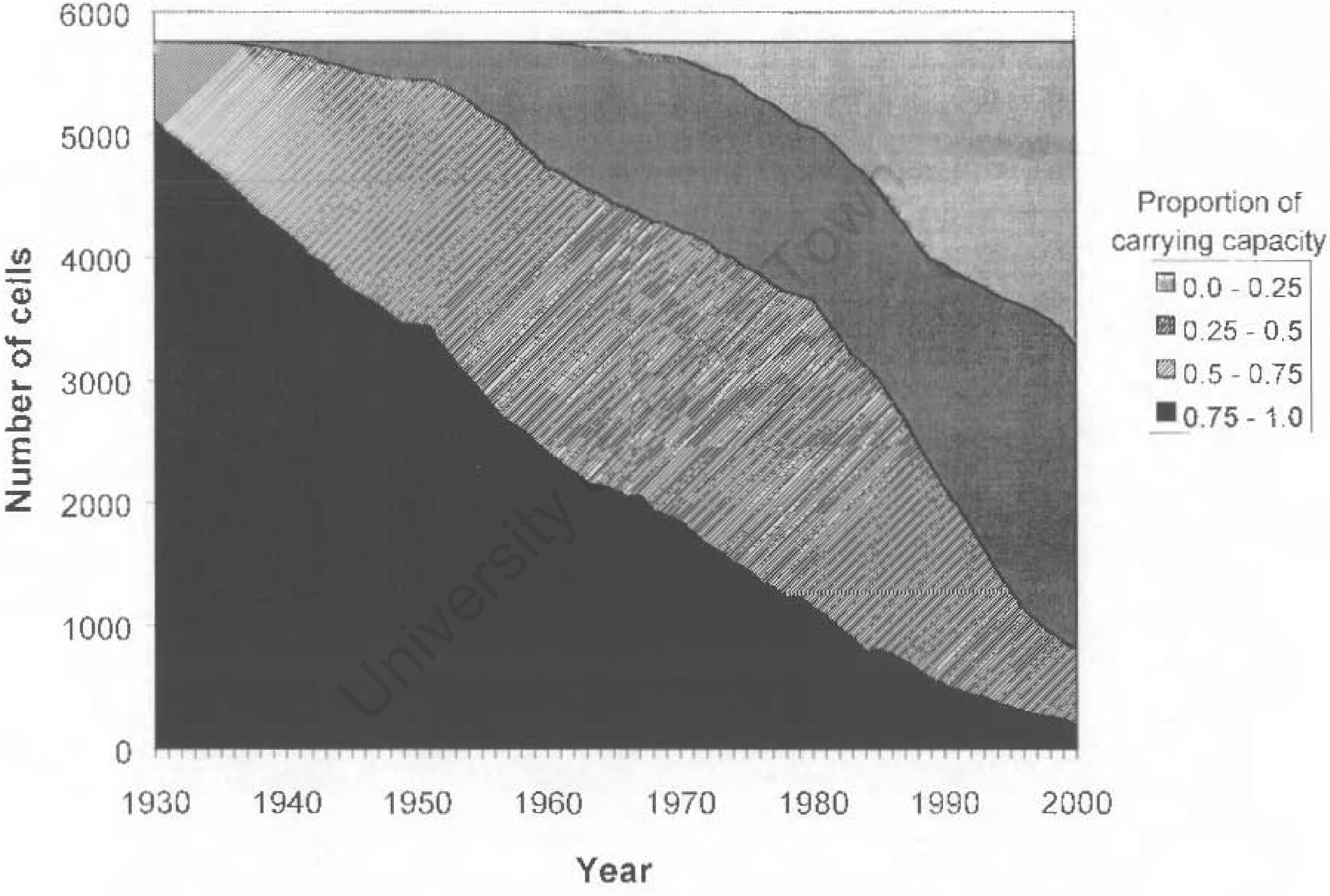


Figure 4.12 The change in the frequency distribution of galjoen density (expressed as a proportion of carrying capacity of active cells) during the course of the fishery, for model T/SR1/LD50.

high densities, even under the most extensive larval dispersal. The greatest variation in density between cells occurred in the mid-1970s, when approximately equal numbers of cells had very high and very low densities.

Variability caused by random numbers

Because all catch events and movements were determined in a probabilistic manner from the value of randomly generated numbers, model results depend on where in the sequence of random numbers the simulation begins. However, differences in aggregates (total population and total catch) between different simulations of the same model were negligible (Table 4.7). Even when summed over regions of approximately 50 km, the variation between simulations was small. Differences only became noticeable within a cell, and then only at high age-classes, where the quantities of fish are smaller than 10. The co-efficient of variation for recruitment in a cell was only 14%.

TABLE 4.7: Averages and coefficients of variation of results across six simulations of Model T/SR1/LD50. Each simulation used the same finite sequence of random numbers, but the sequence commenced in different places. Five model outputs were chosen to show the change in variability at different scales. The location of the output variable (year, cell, age) in the population and catch matrices is described in the top row.

	Year 60 Cell 500 Recruitment	Year 60 Cell 500 Age 4	Year 75 Cell 750 All Ages	Year 80 Sum cell 800 to cell 900	Year 90 All cells
Average live fish	101	8	131	8582	388508
C.V. live fish (%)	13.62	47.43	3.68	1.54	0.10
Average catch	N/A	5	107	5167	189116
C.V. catch (%)	N/A	43.84	9.30	0.77	0.18

DISCUSSION

Critical assumptions and simplifications

The sex, position and movement of adults vary at the level of the individual in this model. The movement parameters were based on measurements and hypotheses described in Chapter 2. In all other aspects (e.g. growth, egg-production, natural mortality) the model fish were identical. The parameters that describe growth and longevity were derived from comprehensive studies of their biology and fishery dynamics. However, it was necessary to rely on a number of assumptions about the fishery, either because certain information was lacking or because it was necessary to simplify certain processes for coding the model.

The first assumption, which is typical of most fishery models, is that recruitment is density-dependent. The initial slopes of the two curves chosen for this study lay within the bounds reported by Myers *et al.* (in press) for a wide selection of teleost species, yet they are sufficiently different to represent two vastly contrasting reproductive capacities. Given the dispersed nature of the fishery and local variations in abundance it is unlikely that the parameters of the spawner-biomass-recruitment curve can be estimated for galjoen.

The steady downward trend in population size for each simulation rests on the assumption that effort increased over the century. Although there are numerous 'snapshot' data sets that support this contention, there are no comprehensive data covering the entire spatial and temporal domain. It was assumed that recreational fishing effort was proportional to the human population at the coast. There is nothing to suggest that this frequency might have varied over the course of the century – consistency is thus the simplest assumption. The rate of population increase, as calculated from the census data (Fig. 4.5), lay between the estimates provided by Van der Elst (1993) and McGrath *et al.* (1997) for specific areas and time periods. Whereas the absolute effort values for the last decade were based on a nation-wide survey, the earlier values were reconstructed from census data. Most of the spatial analyses were performed on the final period of the model, at a time when the estimated fishing effort is most reliable. However, a mis-representation of the earlier fishing effort could produce an incorrect run-up to the final setting. It is unlikely that these past estimates could be improved, other than by conducting extensive research into past human settlements and the changing per-capita involvement in recreational fishing.

The choice of allocating unchanging carrying capacities for active cells, while leaving others empty is a massive over-simplification. There is no alternative to a finite subdivision of areas in a model that computes density. It is only the size of such areas (or cells) that is in question. The choice of a small cell size follows the thinking of Sale (1998) who maintains that in a spatial hierarchy, processes at one scale affect those at larger scales, but not the other way around, and that there are no 'emergent properties' at higher scales. The choice here was 100-m stretches of coast, in order to model at the smallest scale of galjoen movements. The presence/absence representation at this level leads to more continuous variations at larger scales (Fig. 4.4). One could argue that 100 m is not small enough as the distribution of galjoen and the rocks they feed on are patchy on a scale of less than 10 m, but obtaining data at this level of resolution is not feasible. A second reason for not choosing a finer scale than 100 m is that it would necessitate treating the surf zone as a two-dimensional habitat. The surf-zone is typically between 50 and 200 m wide, which means that each cell is approximately square.

Being a spatially-structured model, additional data were required to establish the distribution of fish. The available data were not suitable for this purpose. Although Attwood and Farquhar (1999) found that galjoen were never caught in three out of 20 small areas between Hermanus and Hangklip, catch-data cannot be used to infer distribution as they reflect the combined presence of fish and fishermen, and not the presence of fish alone. Instead, the following reasoning process was used. Firstly, from diet information, galjoen are known to be rock feeders and to prefer specific types of reef communities (shallow, unstable). Secondly, geophysical information provided the distribution of habitat types. Thirdly, the geophysical habitat type was matched to the presence of galjoen in a probabilistic manner. Although the ranking of habitat types according to galjoen preferences was based on reasoned arguments, a certain measure of subjectivity in the proportion of occupancy per habitat could not be avoided. Alternative habitat allocations, within the limits set by the geophysical data and the ranking of habitat type, would alter the density of fish as it is depicted in Figure 4.4 and the absolute magnitude of the fish population, but the processes under investigation should not be affected qualitatively.

The important qualitative results to emerge from this model stem from the fact that not all areas where galjoen occur are exploited. Again, reasoned arguments were used to rank habitat types according to accessibility, and some measure of subjectivity was used to fix the exact proportions. Detailed surveys might improve these estimates. The effect of such an alteration on the model would be to alter the magnitude of the natural refuge effect, but the effect would still be there.

Whereas there may be considerable latitude to adjust carrying-capacity figures, presence/absence arrays and the accessibility estimates, there can be little argument that both fish and fishermen are patchily distributed at varying scales and for different reasons, such that the distributions are independent of one another. It is the mismatch in such distributions that creates the phenomena known as natural refuges, which may have profound implications for fishery dynamics and assessment that have hitherto been largely ignored in this fishery, and most others. The primary effects of these refuges are the *pro-rata* reduction in fishing mortality (Fig. 4.8) and the increased resilience of the stock, but they will also influence the measurement of fishing mortality and population size. Fish density varies widely between 100-m cells, despite them having the same carrying capacity (Fig. 4.12).

Limitations of model with a large execution time

An often-cited drawback of IBMs is their enormous computational load, although it should be noted that the computational load of this model will not be much greater than an age-structured population model which reproduces the same spatial-structure. With 20 age-classes and 20 000 cells, the population model will require 4 x 10^5 state variables, with linkages between them for movement. In Hilborn's (1990) movement model, there were only seven areas, but these called for 25 movement parameters to apportion fish between contiguous areas. Such an approach is simply not feasible with 20 000 areas, where fish can move directly from one area to any other. The 11 x 16 grid population model developed by Lindholm *et al.* (2001) escaped this problem by allowing fish to move in a 'rook' pattern, i.e. they move one block at a time: north, south, east or west, but not diagonally.

Any model that provides fine resolution over a large area will be slow in execution. With long execution times, iterative model-fitting procedures, and stochastic simulations are impractical.

The inability to fit models of population and catch trajectories to data is of little concern in investigations into the South African linefishery at present, as there are few reliable and comprehensive catch and effort data sets available. Those data sets that are available provide snapshots, for small areas and short time periods. It is precisely because of the current reliance on fishery-dependent catch-data in a patchy environment that a detailed, process-orientated model could prove useful in the investigation of appropriate monitoring and assessment techniques.

Despite the model result being the collective realisation of millions of random events, the model is not stochastic. There may be a need to incorporate stochastic elements in the model. Stochastic simulations replicate important processes in fisheries (such as fluctuations in recruitment or errors in assessment) that have a strong bearing on fishery dynamics. For a resident, reef-fish stock, stochasticity and spatial structure are linked, particularly if larval dispersal is limited. It is unlikely that major causes of stochasticity (e.g. predation, disease, water temperature, reef quality) will vary in synchrony across the population (Sale 1998). Stochastic models without spatial structure are therefore unlikely to provide accurate representation of stock dynamics. In order to understand the fishery, it is of greatest importance to get the spatial context correct. In this respect, a spatially-structured IBM should be an improvement over models that include a single recruitment pool when investigating the effects of marine protected areas on reef-fisheries (Warner *et al.* 2000).

Scales of processes

No single spatial scale adequately defines the use of habitat by all stages of a reef-fish population (Sale 1998). The larval dispersal phase and the reef-associated adult phase may differ in scale by between two to five orders of magnitude. A fishery is a predator-prey system, and the scales at which predators operate are as relevant as those of the fish. In this model of the galjoen fishery the following processes influence the consideration of scale:

Range

Many marine species in southern Africa have bimodal distributions e.g. pilchard and abalone. Likewise, the galjoen population of South Africa is detached from the Namibian stock, although transfer between these stocks does occur. The South African range is approximately 2 000 km long, and within that range abundance peaks slightly to the west of centre.

Larval dispersal

This is a notoriously difficult scale to estimate, but some facts constrain the range of choices. Whereas galjoen eggs are known to float for a few days, and then to pass through a phase with weak swimming capacity, these young stages have never been found at sea, despite extensive sampling. In fact, the whereabouts of galjoen younger than age two remains a mystery. The strong affiliation of adults with shallow, surf-zone reefs, suggests that the young remain in this habitat too. Pre-recruits have occasionally been found in inter-tidal rock-pools, but nowhere else despite extensive sampling in surf, subtidal reef, soft-bottom bays and estuaries. Galjoen breed throughout their range, which implies that unidirectional dispersal is unlikely.

To cater for the uncertainty, three scales of larval dispersal covering two orders of magnitude were considered by the model. The largest of these covered 1 000 active cells, which translates on average to 330 km, or one-sixth of the South African range. Based on the findings of the invertebrate larval dispersal studies by Botsford *et al.* (1998) in the Californian upwelling system, it is unlikely that larvae will disperse more than 200 km. The smallest scale chosen for the model was 3.3 km. The model variations therefore adequately covered the range of reasonable possibilities.

Returning to the study by Botsford *et al*. (1998) it is apparent that the galjoen model may have misrepresented the larval dispersal process by dispersing larvae equal distances east and west. Instead, there may be distinct circulations patterns that trap larvae in particular areas, which will serve to fragment the stock to greater degree than predicted by the galjoen model.

Home-range behaviour

Home-ranges, estimated from tagging data, cover a maximum of 1.5 km, and probably much less over short time periods (Chapter 2). The model used proximate adjacent active cells for a home-range, which translates to approximately 0.7 km on average, or 0.04% of the range.

Home-range relocation

When (tourist) galjoen abandon the home-range, they can move to any position within the range, although most movements cover only a small portion of it (Chapter 2). The dispersal parameter used for this scaling was ~300 km, or 15% of the range.

Habitat patchiness

The average continuous run of habitat varies between 0.4 and 2.4 km, although stretches of over 20 km are present. Like all species, galjoen show affinities to certain physical habitat types. Such habitat types might not correspond exactly to any one of the types classified in this model. It is, however, assumed that the frequency of encountering galjoen correlates with these classifications. The presence of anglers on the coast is also linked to habitat type, as certain habitats are very difficult, if not impossible, to access. The scale of these sources of variation is in the order of 1% of the range.

Angler nodes

Recreational anglers are mostly part-time operators who are attached by way of a residence and business to a town. Towns are therefore nodes of predation in the fishery. Distances between towns are approximately 5% of the range. Throughout the course of the fishery, the effect of these becomes more diffuse as anglers gain access to better transport systems (vehicles and roads). The peaks in 1940 that corresponded to George-Knysna and East London were later overtaken, or merged, with the two large metropolitan areas of Cape Town and Port Elizabeth (Fig. 4.7).

Temporal scales: Fish generation time

The longevity of fish is often used as a measure of the resilience of fisheries. From fertilisation to recruitment into the fishery takes fours years for a galjoen. Another year will pass before first spawning. Minimum generation time is therefore five years. However, the peak spawning age is a trade-off between fecundity (related directly to mass) and numbers (these drop off exponentially with age), which determines the average generation time in accordance with the mortality-rate. The oldest known galjoen age is 21 years (the next was 14), but the average age in the catch is about six years. Generation time will lie between these ages, but closest to the average.

Temporal scales: Angler density

Throughout the model period (100 y), fishing increased at the average rate of 3.5% p.a. The only relaxing of fishing effort may have occurred when each of the six marine protected areas took effect, although it is more likely that MPAs displace effort (Chapter 6). The rate of fish recovery in these areas should be measured against the generation time of the fish.

Another factor likely to influence the temporal distribution of effort is the abundance of fish or expected catch rate (Attwood and Bennett 1990). Gillis *et al.* (1993) showed that commercial fishing effort could be predicted using the ideal free distribution, and Martel *et al.* (2000) modelled effort on the basis of catch-rates. No such relationship was included in this model of the galjoen recreational fishery for three reasons: (1) being a recreational fishery, expected catch rate is not the overriding determinant of effort, (2) fishermen do not have free access to all areas, and (3) it is a multi-species fishery.

Spatial structure in model results

Which of the scales described above are noticeable in the model results? Patchiness in the results at certain scales is built directly into the model, namely the fine-scale, habitat-linked presence/absence of fish and range-wide variation in carrying capacity. Variation at intermediate scales is less predictable. The interaction of realistic variations in fishing (spatial and temporal), larval dispersal, home-range behaviour and home-range relocation produces an almost intractable problem for the analytical modeller. The individual-based modeller, on the other hand, easily obtains a result, albeit one that can be difficult to interpret.

The primary effect of the habitat distribution is an apparently unstructured variation in density at the 10-km scale (Fig 4.4). Within some regions at least, the coastline shows a repeatable pattern of habitat type. The south coast, between Struisbaai and Tsitsikamma, consists of a series of half-moon bays, each protected by a rocky headland in the west, and to the east of that a long high-energy sandy beach (usually with an estuary) and then a broken rocky shoreline extending to the next headland. However, no dominant frequencies in variations of galjoen density could be detected in the model results. The model does indicate that, if the definition of habitat preference is reasonable, the galjoen population cannot be considered to be a meta-population. All 10-km bins are occupied. Larval dispersal and adult movement would have to be extremely localised to isolate sub-stocks on a scale smaller than 10 km. When the recovery data presented in Chapter 2

(Fig. 2.3) are lumped together it is clear that the areas where fish have been caught are continuous, thus supporting this interpretation.

An important feature of the model is that adult dispersal is wider than larval dispersal under all reasonable scenarios. It is possible that larvae are trapped in meso-scale circulation patterns, but the possibility of a strong meta-population structure is reduced by extensive adult dispersal.

Larval dispersal and adult movements serve to counteract the localised nature of the depletion caused by fishing, by spreading recruitment and fish among cells. Even under extensive larval dispersal, strong spatial variation caused by the angler-nodes (scale of 100 km), by natural refuges (scale of 300m) and by marine protected areas (various scales) is evident (Plates 1-12, Fig 4.12). The persistence of fishing-induced variation indicates that the action of fish movement and larval dispersal is comparatively weak. Accordingly, differences in population size and yield between different movement patterns and larval dispersal scenarios are small (Table 4.5), but predictable. Yield correlates positively with larval dispersal. Population size correlates negatively with larval dispersal. The interaction between larval dispersal, adult movement and refuge size, including reserve size, is investigated thoroughly in Chapter 6.

Temporal variation in model results

The continuous decline in abundance for every simulation is consistent with the opinions and assessments expressed previously on the galjoen fishery (Bennett 1988). The rate of decline does not accelerate in accordance with the increase in effort, although declines do hasten slightly near the end when effort climbs sharply (Fig. 4.9). Catches rise and then fall, clearly indicating classic over-exploitation (Fig. 4.10). These results are presented in terms of numbers. In terms of mass, the effect of over-fishing is more dramatic as mass reflects the stunted age-distribution under high fishing mortality-rates. The over-exploitation is a result of recruitment over-fishing, as the average fishing mortality-rate for all simulations corresponds to a halving of the recruitment production (Fig. 4.6).

The most important conclusion to be drawn from the continuous decline in abundance is that per-recruit models have never been appropriate for assessment. With ever increasing fishing mortality, the age-structure of the population would reflect a combination of mortality and declining recruitment, which would under-estimate mortality. This bias acts in opposition to another: because catch-data are derived from fished areas only, the per-recruit analysis will be pessimistic. The same bias applies to catch-per-unit-effort (CPUE) as an index of abundance – it over-estimates population decline, because of selective sampling (Fig. 4.11). The counter-action of these effects is explored further in Chapter 7.

Absolute values

The model yields a total carrying capacity within the modelled range of 1.6 million fish of age four onwards. Is this estimate realistic? The figure is based on the population density measured at two sites within a MPA averaged over thirteen years (Chapter 3), and assumptions about the distribution on galjoen habitat and carrying capacity. The average mass of galjoen above age 4 is slightly less than 1 kg, which means that the corresponding biomass estimate is about 1000 tonnes at carrying capacity. There are no stock estimates for comparison. The total yield according to the model is in the region of 150 000 fish at the close of the century, or about 90 ton (average mass of a landed galjoen is 600 g). For comparison, there are three shallow reef-fish species that are of a similar size to galjoen and which cover a similar range to that of galjoen, namely roman *Chrysoblephus laticeps*, red stumpnose *Chrysoblephus gibbiceps* and dageraad *Chrysoblephus cristiceps*. The total reported commercial catch of these species was 46.8, 6.7 and 23.8 tonnes during 1999, respectively. These figures can be scaled up by a factor of at least 1.25 to account for the recreational harvest and other unreported catches (Griffiths and Lamberth in press).

Under high fishing mortality (i.e. the final decade) CPUE values predicted by the model were of the same order as those measured in heavily exploited areas (Fig. 4.11). Attwood and Farquhar (1999) found that CPUE rates for 20 small areas near Hermanus ranged between zero and 0.18 fish per angler hour. CPUE predictions could be used to evaluate the use of certain CPUE rates as indicators or thresholds (Bennett 1998), but on their own they provide no potential for validating absolute population size.

Testing management strategies

The model is intended for use in understanding spatial processes, but it can be projected into the future to evaluate different management options, provided that effort trajectories can be anticipated on the appropriate scales. The model can simulate the effects of closed seasons, size limits and marine protected areas. Bag limits are not amenable to testing without substantial alterations to the model that will treat fish *and* anglers on an individual basis.

CONCLUSIONS

The homogeneous stock and the meta-population are mathematically tractable models. Unfortunately, neither are appropriate descriptions of the galjoen stock, which lies somewhere between these extremes. The distribution of fish is patchy on various scales, but the exchanges between the patches are such that no patch is isolated from neighbouring patches, yet on larger scales the dynamics become increasingly detached. Routinely used assessment models cannot describe such a stock.

The individual-based model provides a flexible framework for investigating the effects of spatial variability and the effect of processes that act at various spatial scales in the fishery. There is a heavy data-requirement for this model, which would preclude its use for most fisheries in South Africa at present. However, with the rapid development of geographical information system data-bases and extensive tag and recovery data sets, the spatial approach should be more practical in the near future.

Despite the action of larval dispersal and adult movement, natural refuges and marine protected areas are able to maintain higher fish densities than exploited areas across a wide range of uncertainties. Initial model results suggest that assessment procedures that do not take account of spatial processes are biased. Any assessment based on catch-data will overlook the potentially substantial proportion of a resident stock that is not available to the fishery, because of natural refuges and marine protected areas. The primary assumption of the per-recruit models, that the population is stable, is not valid for the galjoen fishery over the period of interest, and looking at the effort profiles for other fisheries (e.g. numbers of vessels) it is likely that the same problem applies to all reef-fisheries in South Africa.

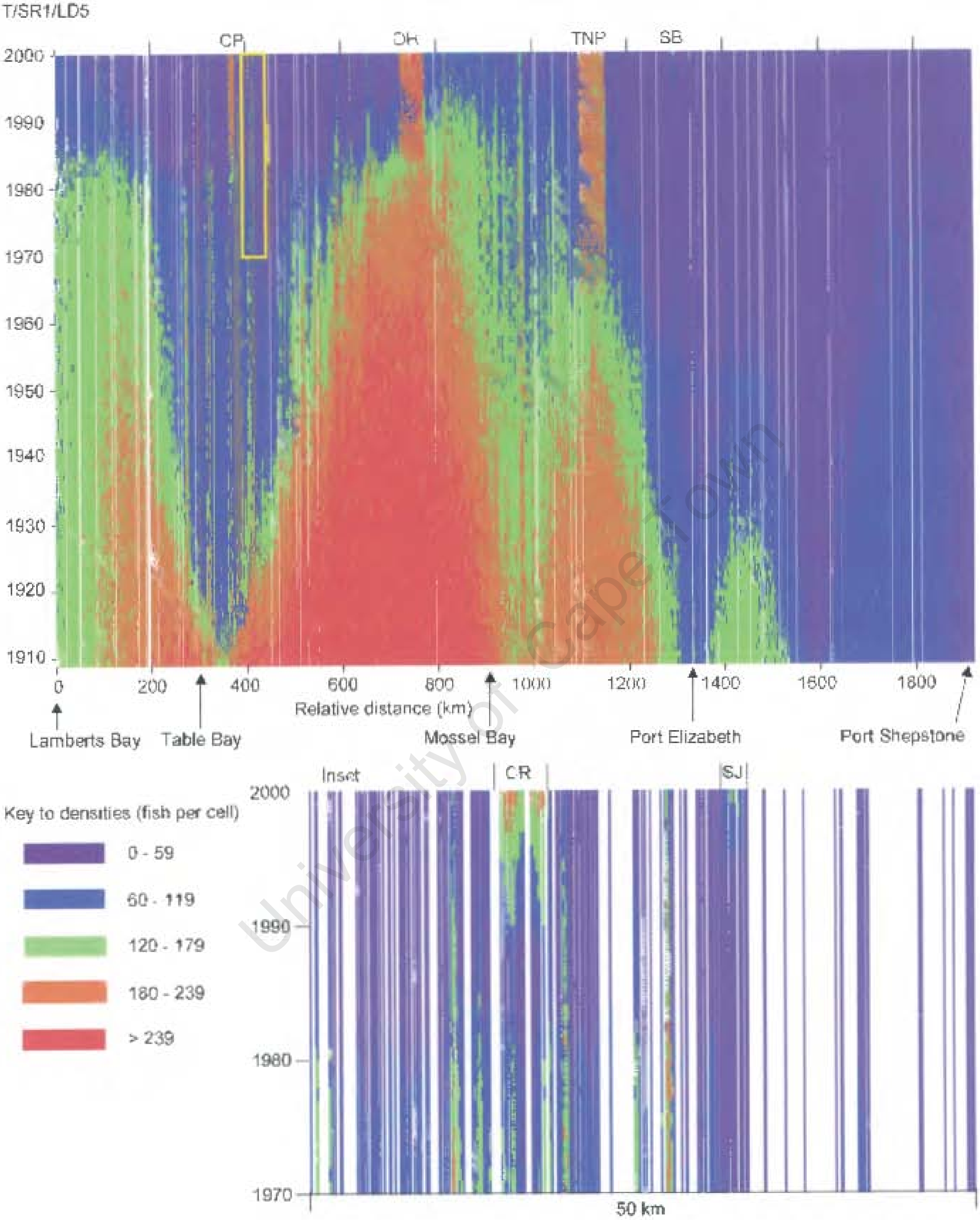
Appendix 1

Definition of symbols used in the description of the individual-based model.

Symbol	Definition	Units
N_{max}	Maximum number of fish alive at any time	fish
v	Number of variables held in memory for each fish	
A	Total number of active cells	
c	cell address, ranging from 1 to 19180	100-m stretches
K_c	Maximum recruitment in cell c	fish
μ	Initial slope of spawner-biomass-recruit curve	recruits/kg
E_{ct}	Effort in cell c during year t	$h.km^{-1}.y^{-1}$
F_{ct}	Fishing mortality-rate in cell c during year t	y^{-1}
R_{ct}	Recruitment to cell c at the start of year t	fish
S_{ct}	Spawner-biomass in cell c at the end of year t	kg
P_{town}	Human population at *town* in year *t*	people
c_{town}	Cell address of *town,* starting at Lamberts Bay	10-m stretches
σ_τ	Diffusion parameter for the distribution of anglers in year t	km^2
Δ_c	Accessibility parameter for cell c (either 1 or 0)	
q	catchability	$km.h^{-1}$
α	adjustable parameter used to equate population size to effort	$h.km^{-1}.y^{-1}. person^{-1}$
β	probability of a galjoen leaving its natal home-range	w^{-1}
χ	probability of a galjoen returning to its natal home-range	w^{-1}
δ	Diffusion parameter used to allocate alternative home-range sites	km^2
ϕ	Proportion of polymorphic fish that are resident	
γ	Diffusion parameter used to allocate polymorphic movement	$km^2.w^{-1}$
D	Larval dispersal parameter	Active cells

LEGEND TO PLATES 1 - 12

Each plate is a colour-coded representation of galjoen density over time (years 1910-2000) and space (1918 km of coastline) for each of the model variations, identified in the top left. The top panel shows the entire range, whereas the portion enclosed in the yellow block is expanded below. Most of the range is not inhabited by galjoen and should appear blank (white), but the printer overwrites all but the most extensive blank areas in colour, because of a lack of resolution. The expanded panel shows blank areas more realistically. For reference, the position of towns is given below the main panel, and the position of reserves is given above both panels. CP=Cape Peninsula MPA, CR=Caste Rocks MPA, SJ=St James MPA, DH=De Hoop MPA, TNP = Tsitsikamma National Park, SB=Sardinia Bay MPA.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Relative distance (km)
Lamberts Bay
Table Bay
Mossel Bay
Port Elizabeth
Port Shepstone
Key to densities (fish per cell)
0 - 59
60 - 119
120 - 179
180 - 239
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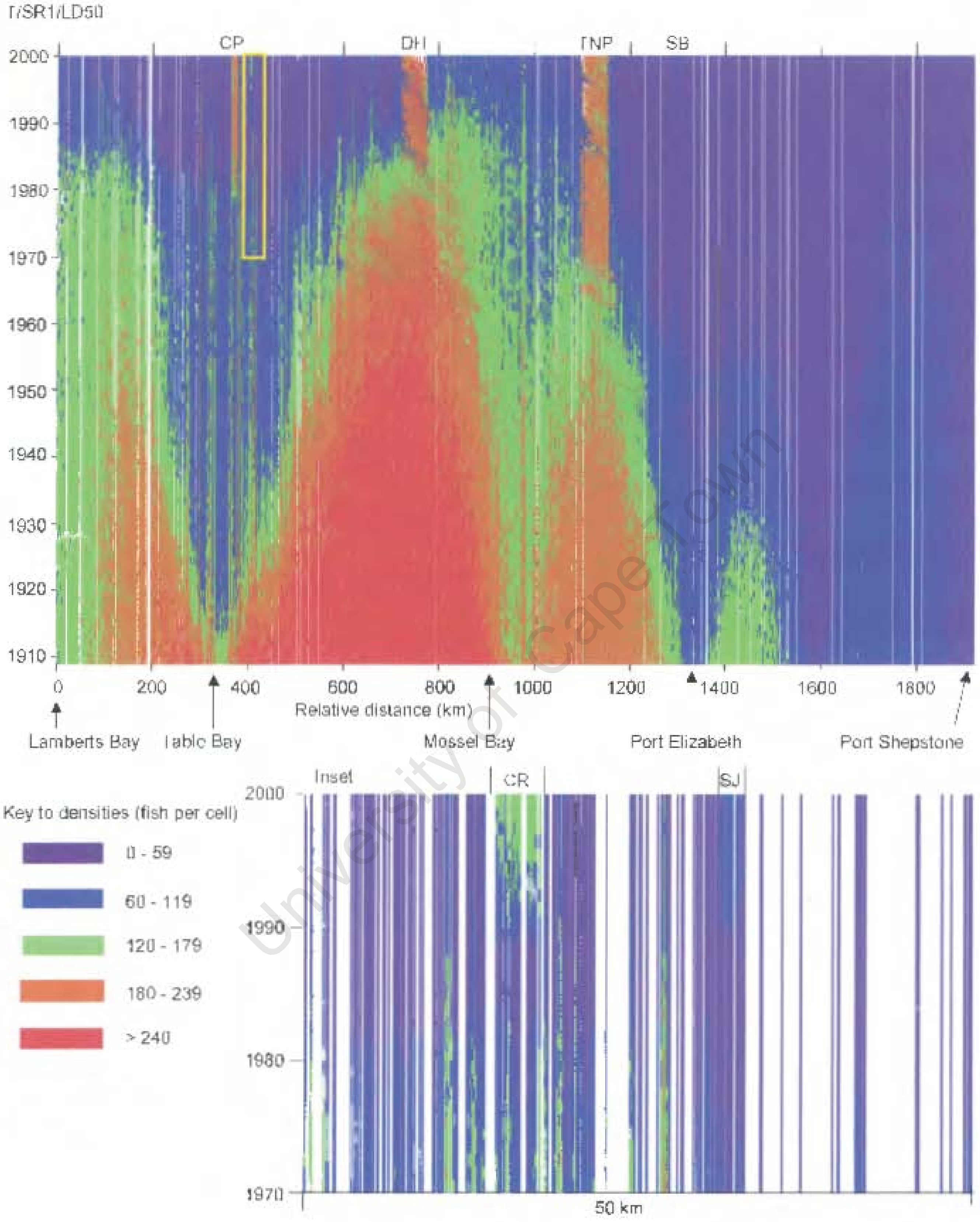
Plate 1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Key to densities (fish per cell)
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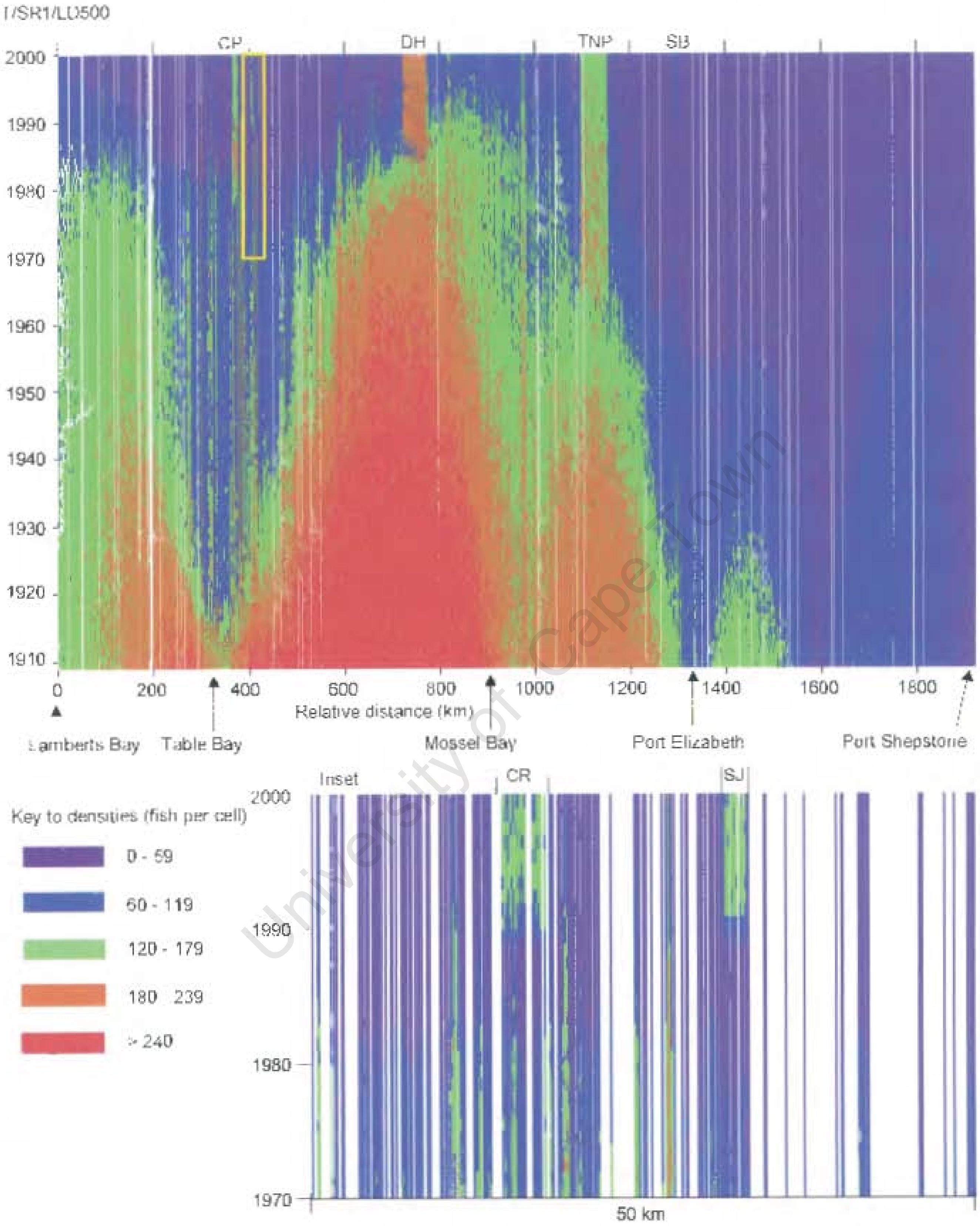
Plate 2



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Key to densities (fish per cell)
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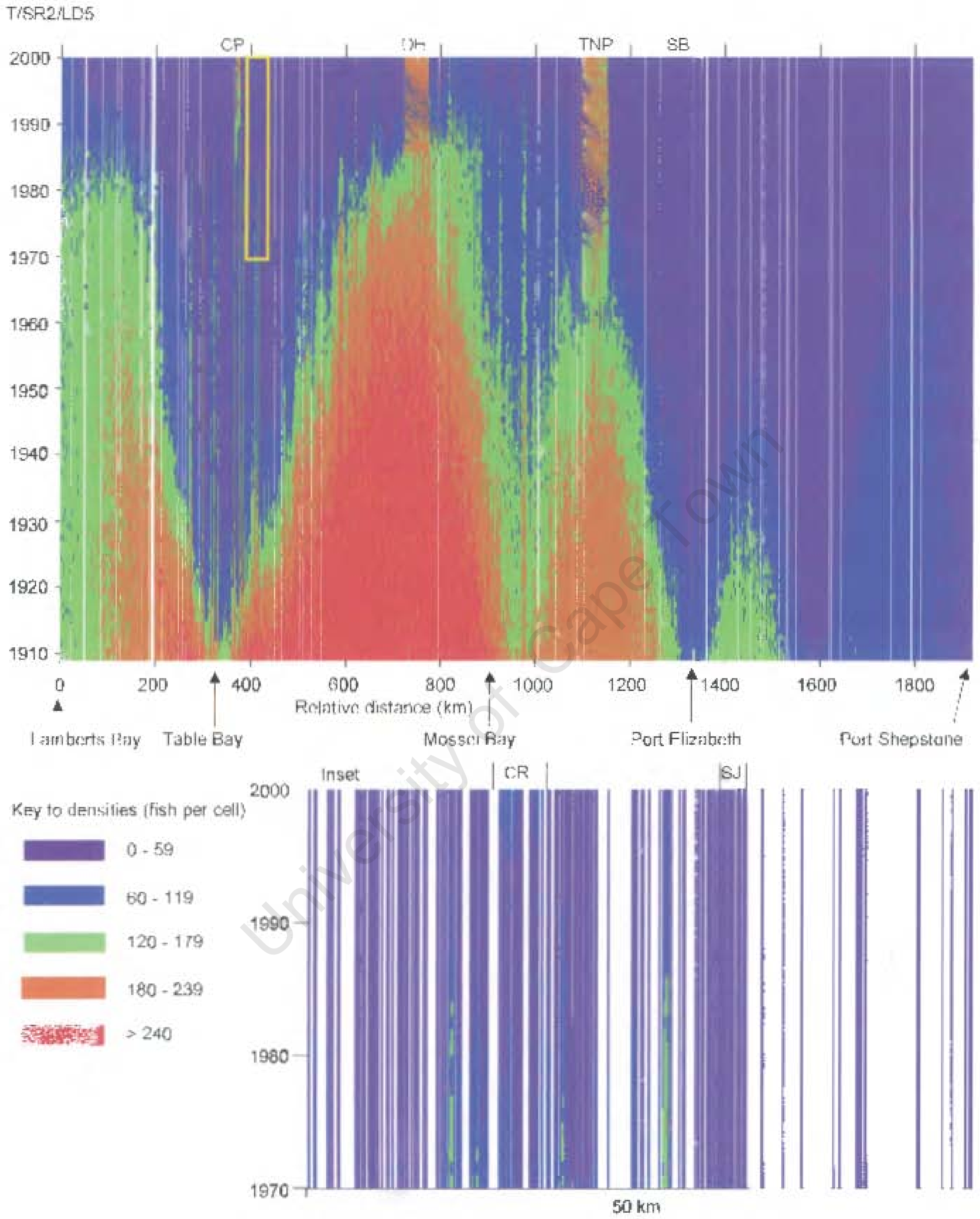
Plate 3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Relative distance (km)
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Port Shepstone
Key to densities (fish per cell)
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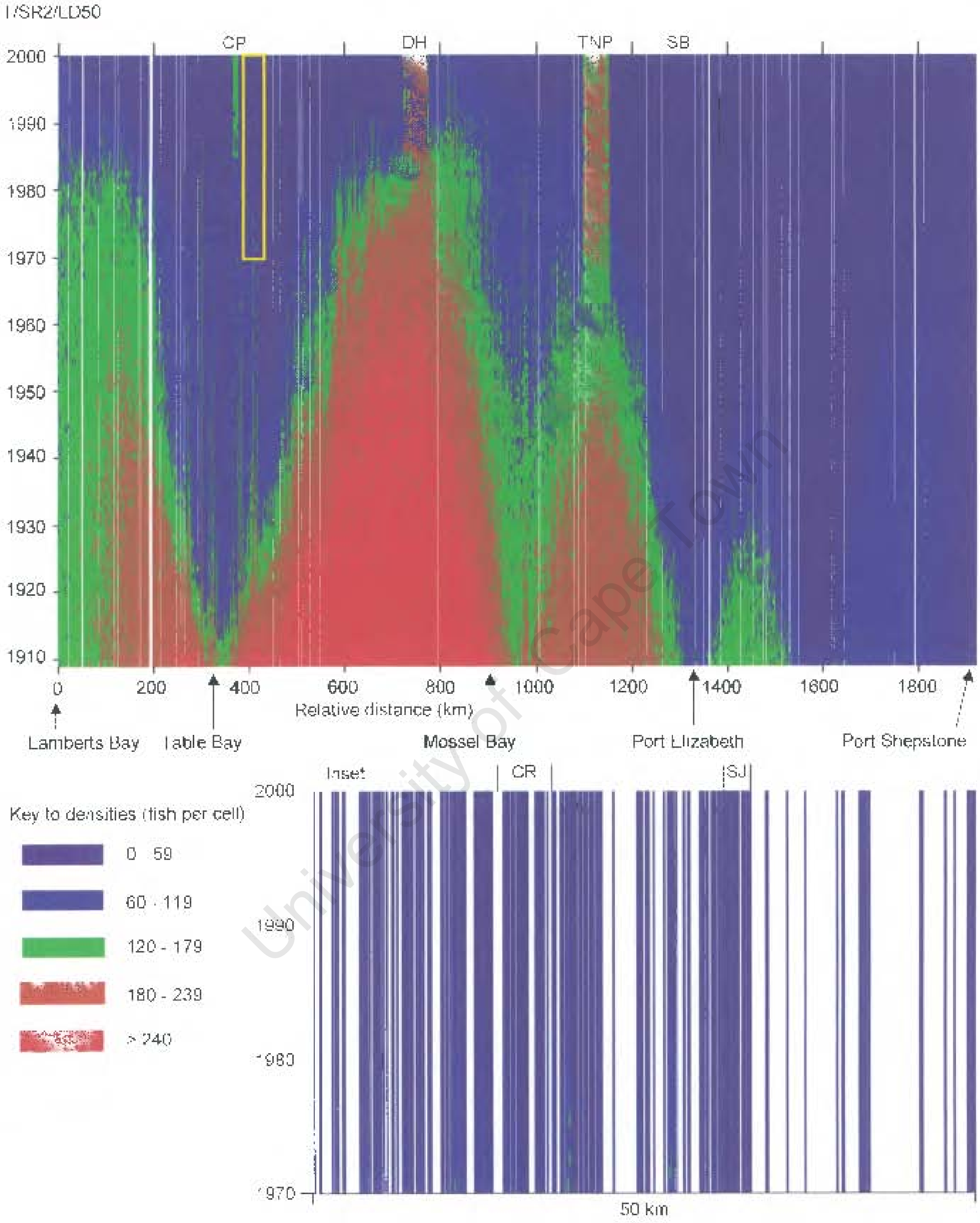
Plate 4



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Relative distance (km)
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Key to densities (fish per cell)
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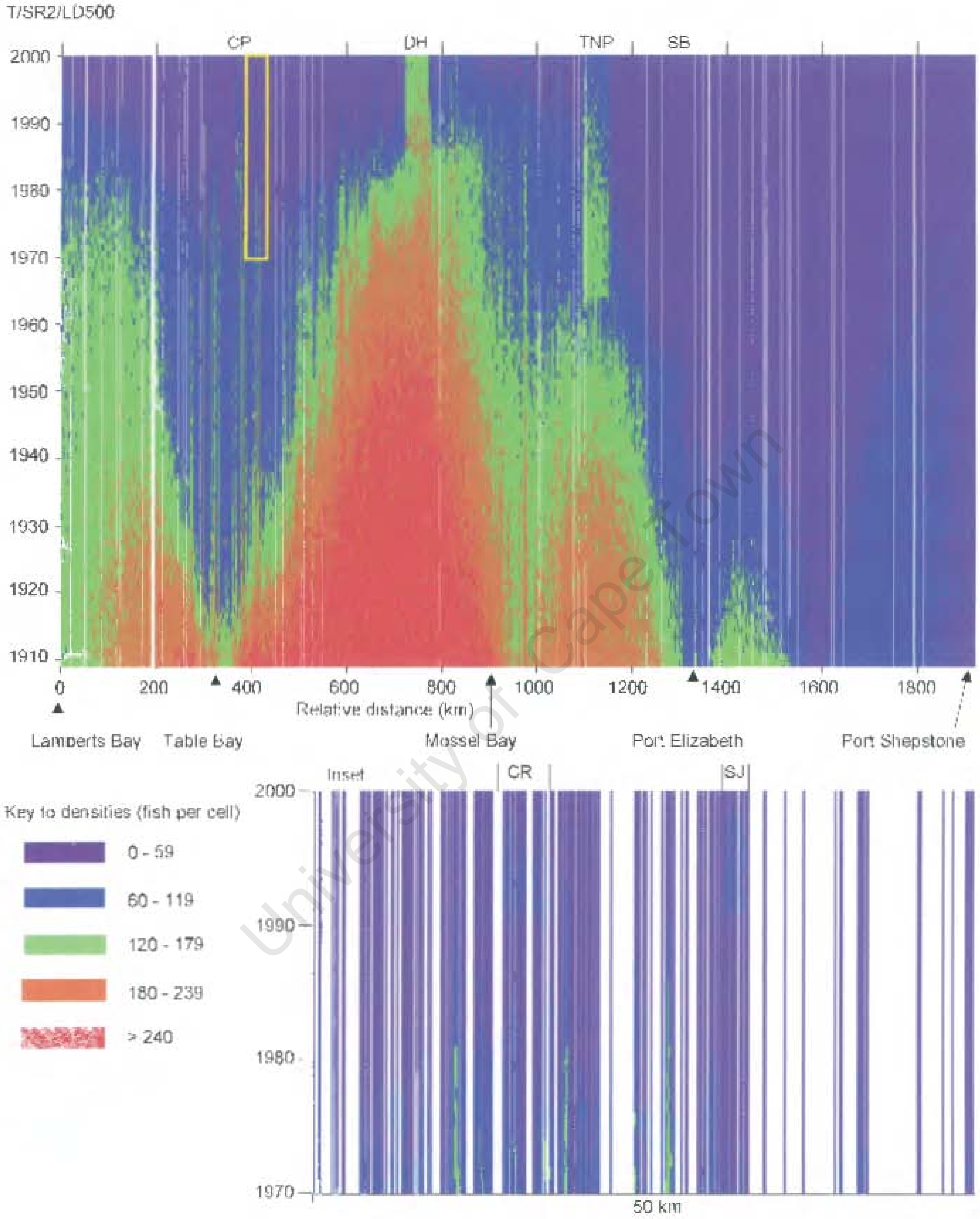
Plate 5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Relative distance (km)
Lamberts Bay
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Mossel Bay
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Key to densities (fish per cell)
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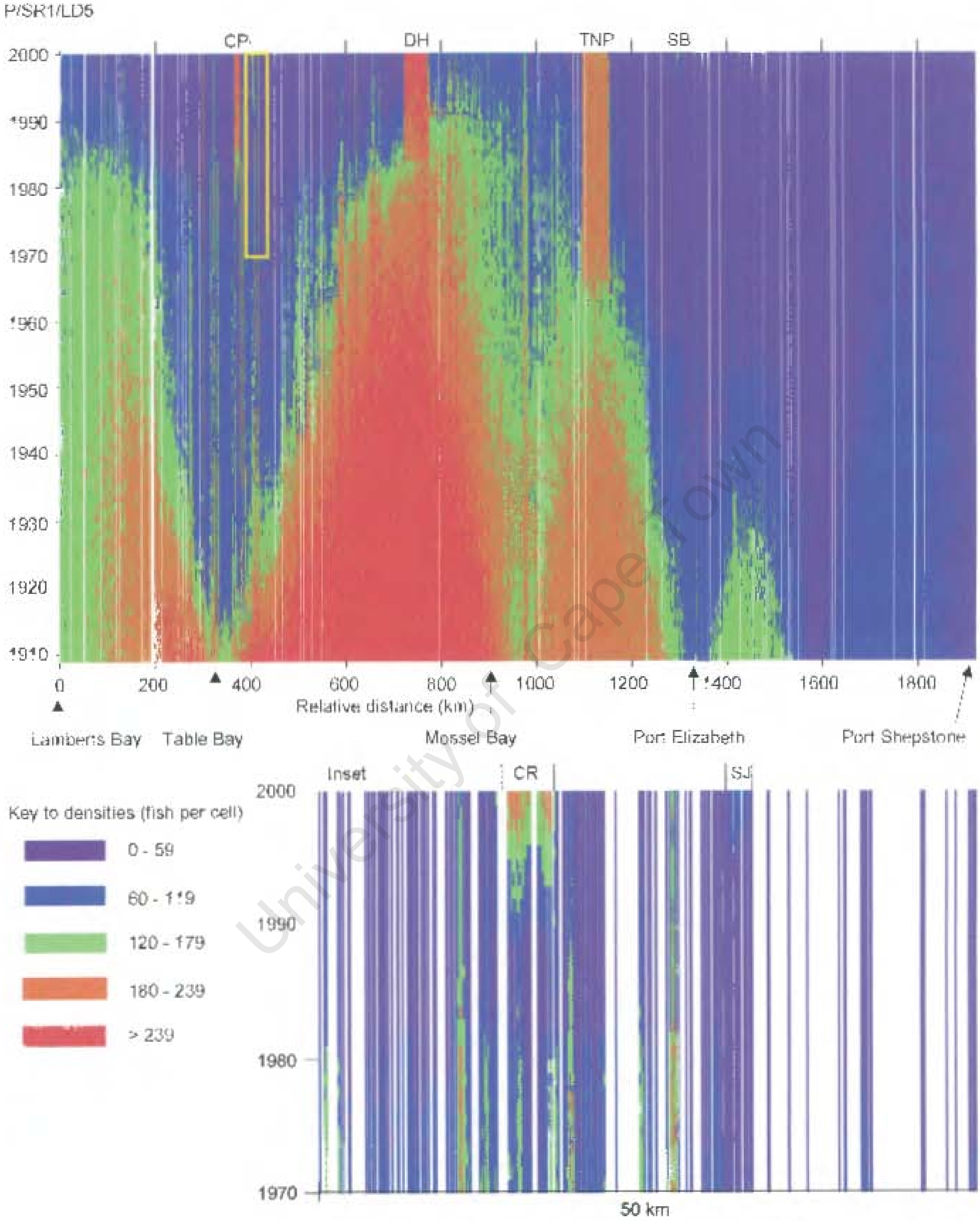
Plate 6



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Relative distance (km)
Lamberts Bay
Table Bay
Mossel Bay
Port Elizabeth
Port Shepstone
Key to densities (fish per cell)
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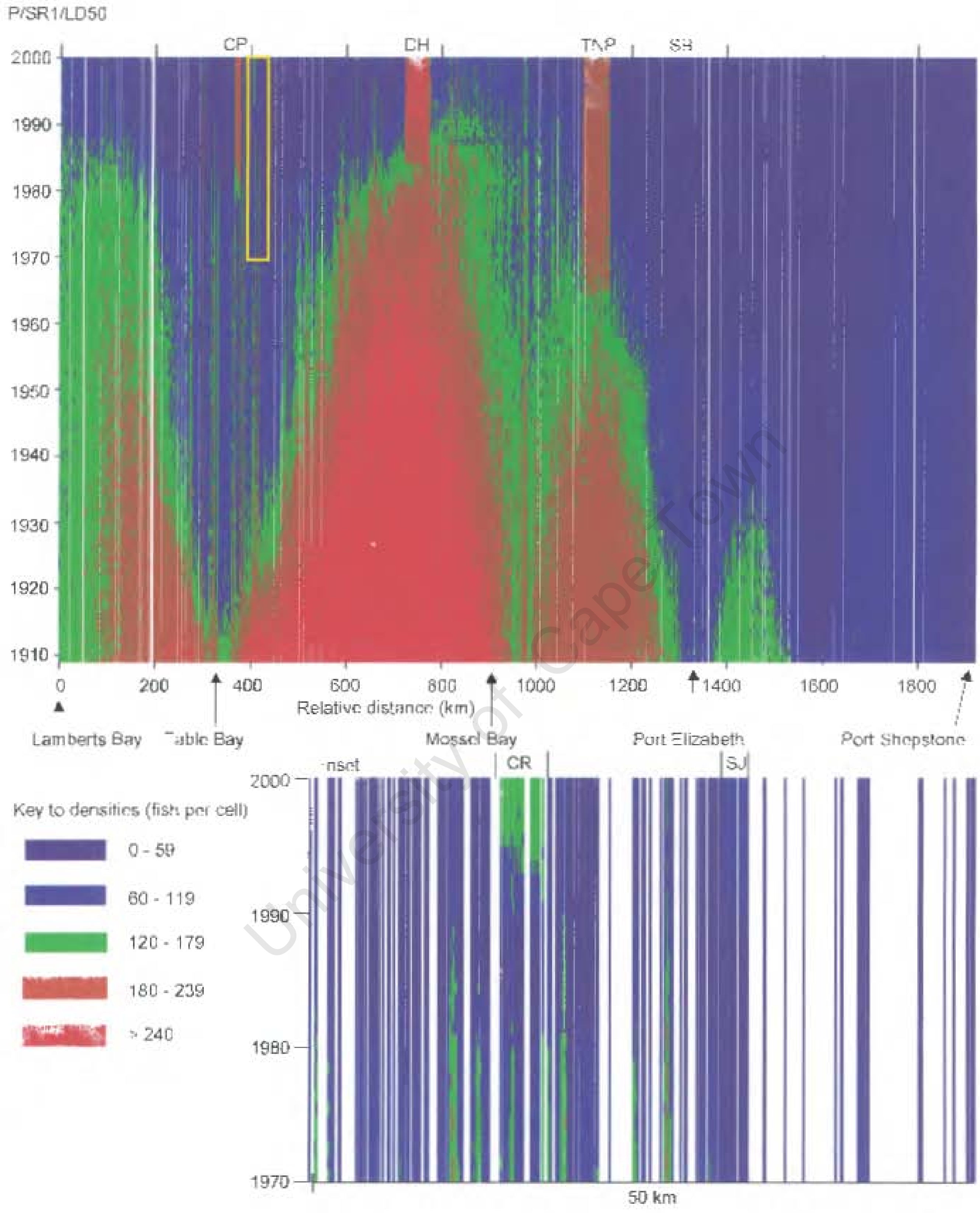
Plate 7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Relative distance (km)
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Mossel Bay
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Port Shepstone
Key to densities (fish per cell)
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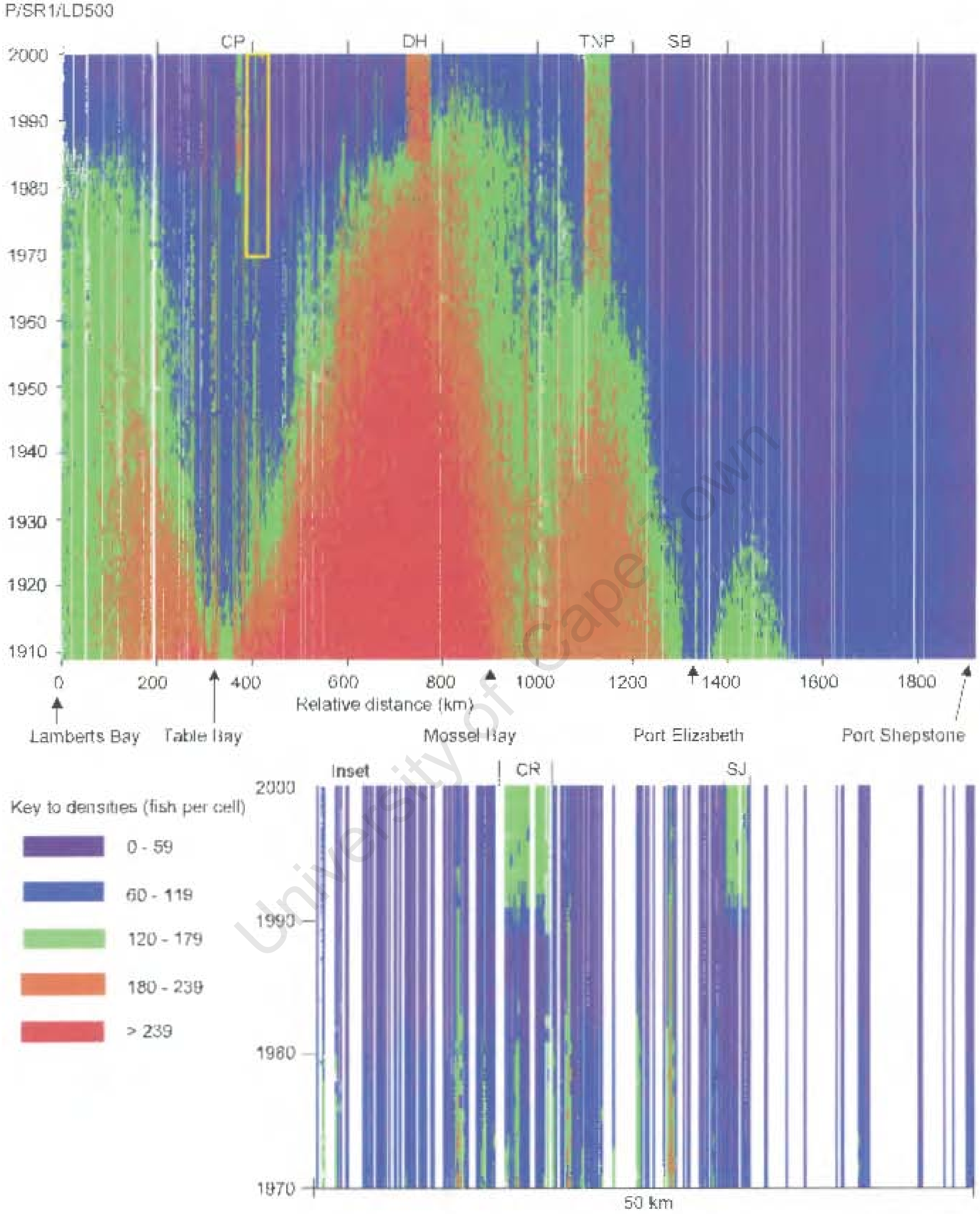
Plate 8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Relative distance (km)
Lamberts Bay
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Mossel Bay
Port Elizabeth
Port Shepstone
Key to densities (fish per cell)
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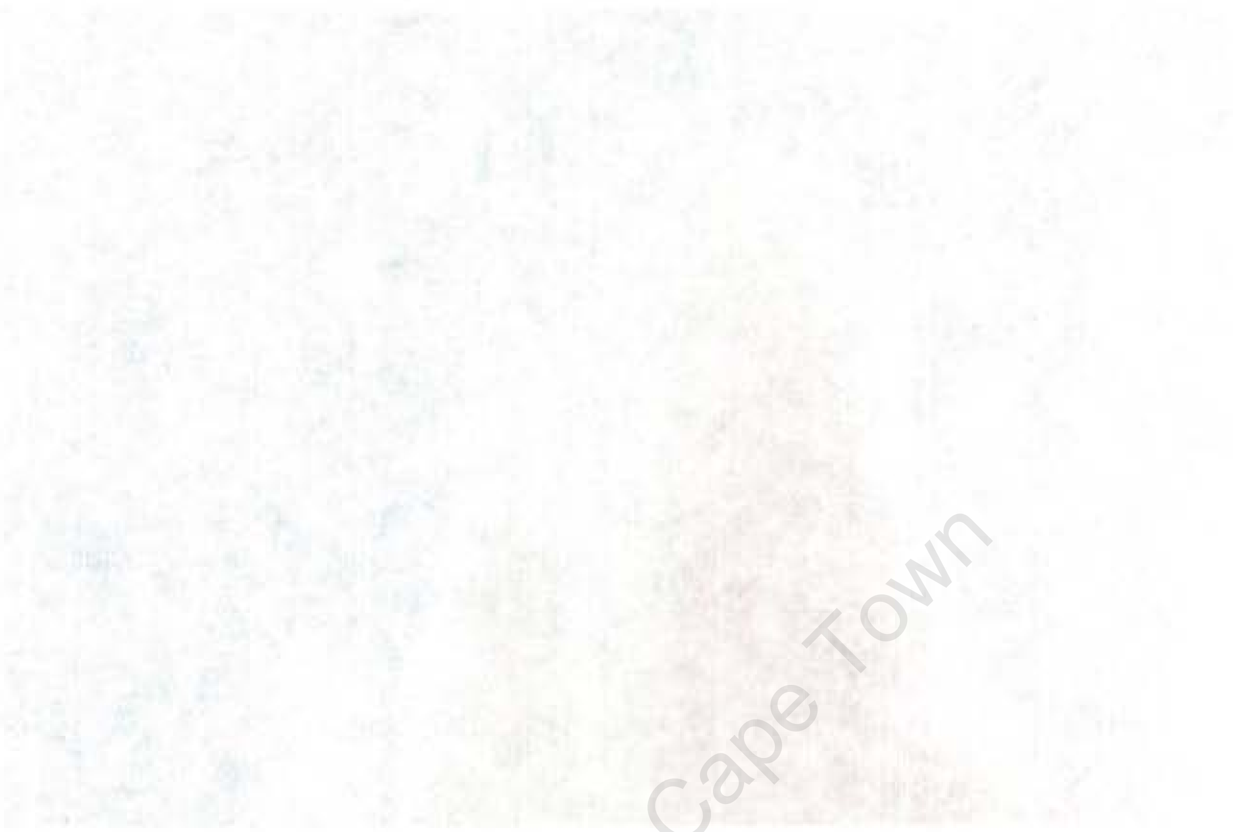
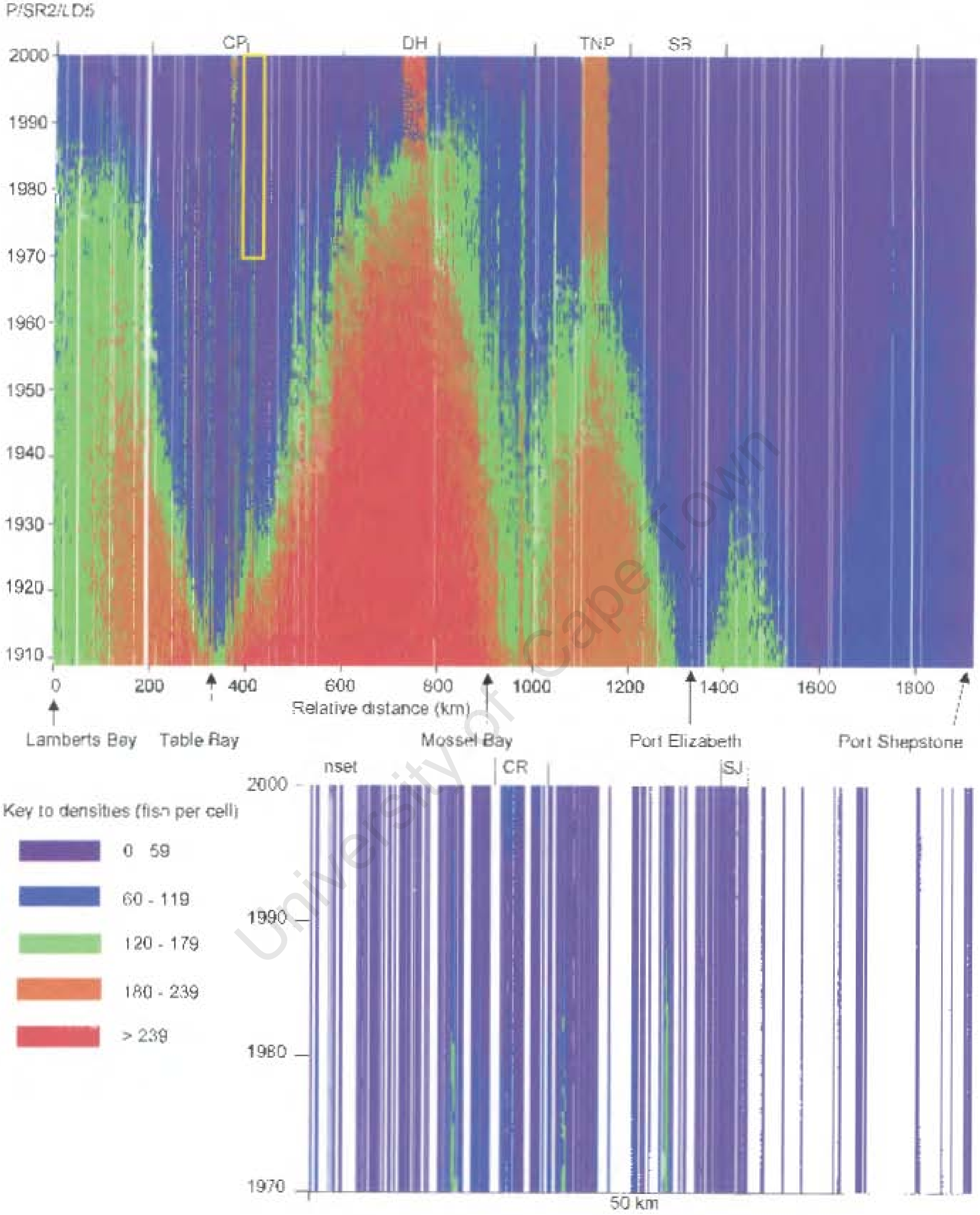
Plate 9

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Relative distance (km)
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Table Bay
Mossel Bay
Port Elizabeth
Port Shepstone
Key to densities (fish per cell)
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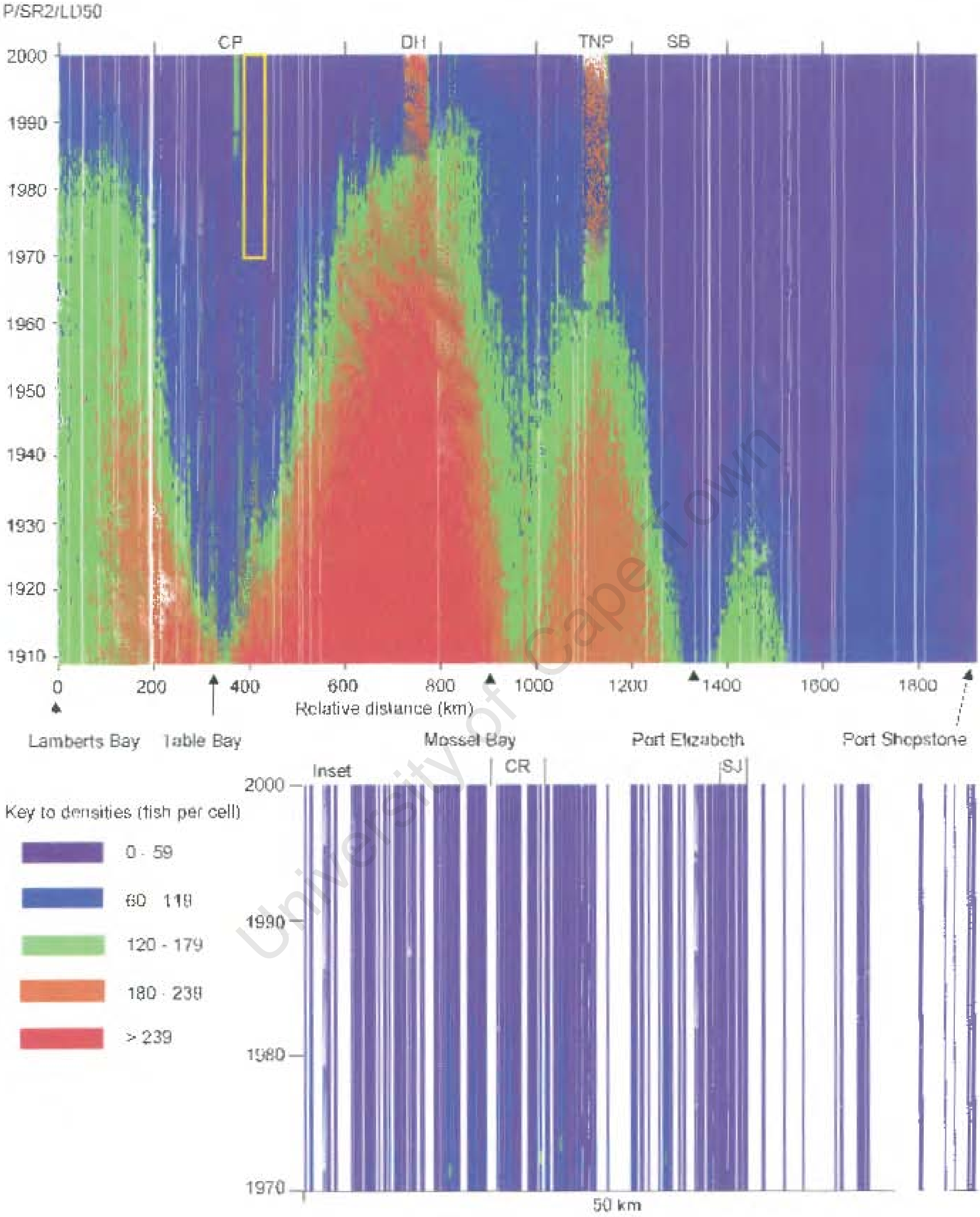
Plate 10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Relative distance (km)
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Table Bay
Mossel Bay
Port Elizabeth
Port Shepstone
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Key to densities (fish per cell)
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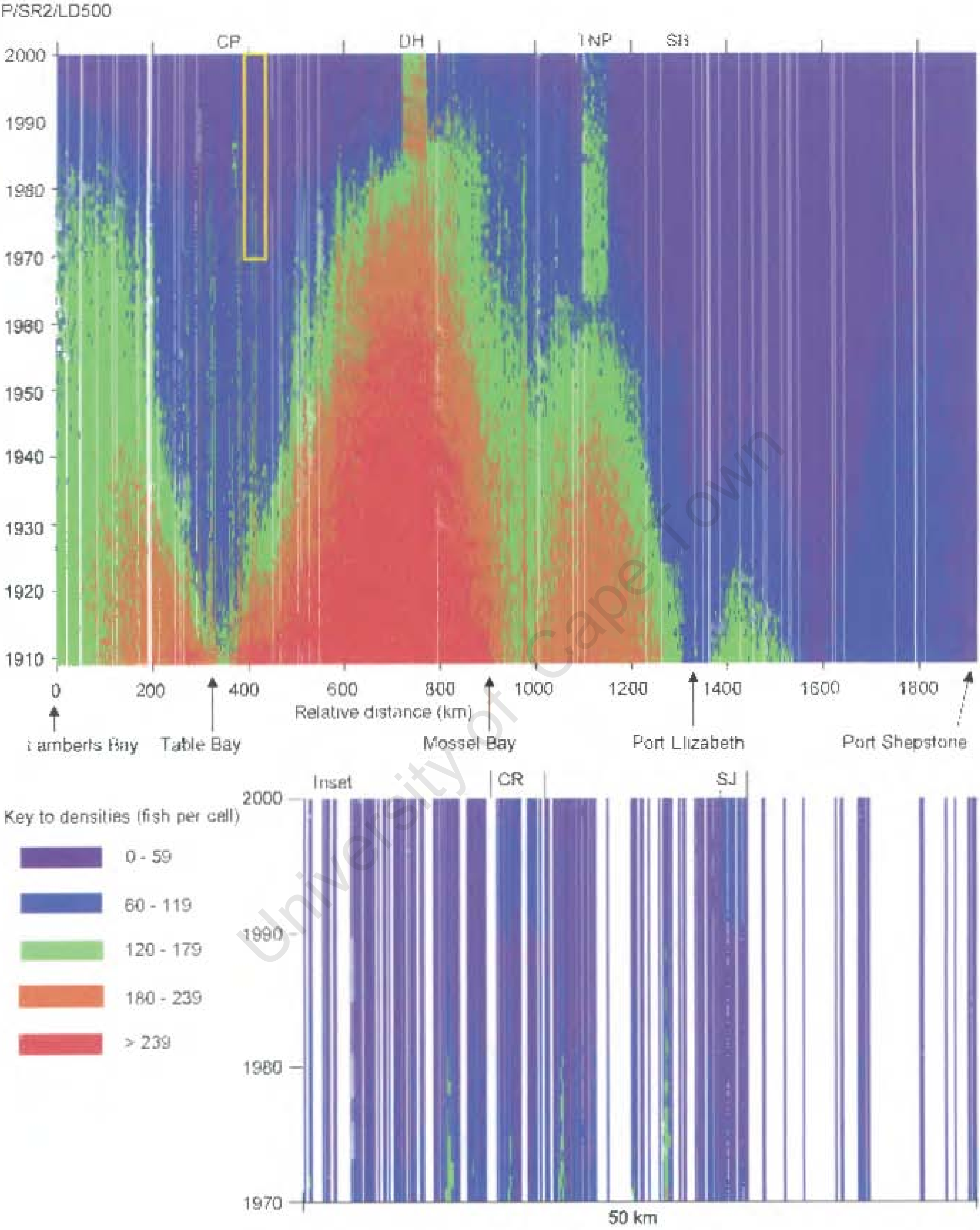
120 - 179
180 - 239
> 239

Plate 11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Relative distance (km)
Lamberts Bay
Table Bay
Mossel Bay
Port Elizabeth
Port Shepstone
Key to densities (fish per cell)
0 - 59
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120 - 179
180 - 239
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Plate 12

CHAPTER 5

SELECTION OF A LIKELY MODEL OF THE MOVEMENT PATTERN OF GALJOEN

ABSTRACT

An individual-based model was used to compare the outcomes of three movement-patterns: random movement, tourist behaviour (fish occasionally leave their home-range) and polymorphism (some are resident, others not). A tagging model was embedded in the individual-based model to simulate the tagging experiments at Lekkerwater, described in Chapter 2. The model was expected to replicate successfully several aspects of the tag and recapture data. The random movement pattern failed to match the data, as it could not account for the high frequency of recaptures at the release site while still allowing for some fish to travel in excess of 500 km. The tourist and polymorphic patterns were able to provide a reasonable match, after allowing for small adjustments in catchability, but only the tourist pattern could account for the lack of a correlation between the proportion of 'zero-displacement' recaptures and time-free. In addition, the high dispersal rate of the best-fit polymorphic pattern suggested that this model was less likely. The best-fit tourist pattern apportioned more than 90% of a galjoen's time to its natal home-range. Home-range size was accurately modelled by assuming that fish require a fixed area of good-quality habitat, and that variability in home-range size was a result of the spatial distribution of such habitat.

INTRODUCTION

Based on the results of a tagging study at four sites in South Africa it was concluded that galjoen are predominantly resident fish that remain within small home-ranges (Chapter 2). However, recoveries of tagged fish also indicated that galjoen can move extensively within their South African range of ±2 000 km. While constituting a minor proportion of the population, galjoen that display extensive movements beyond a home-range have important implications for the ability of a stock to colonise uninhabited areas, and to repopulate areas that have been depleted. From the point of view of a fishery manager, such movements affect the efficacy of marine protected areas and the interpretation of stock assessments.

From the data presented in Chapter 2 it was not possible to discriminate between two competing hypotheses about galjoen movement. Whereas random movements and age- and sex-related movement were not supported by the data, there was no indication whether a small percentage of galjoen are predisposed to movement (*polymorphic model*), or if all galjoen abandon their home-range temporarily and infrequently (*tourist model*). The individual-based model (IBM) developed in Chapter 4 indicated that these two movement patterns result in different dynamics for the fishery of galjoen, in particular the way in which refuges supply fish to depleted areas, although the effect of this uncertainty is less than that of other processes (such as the spawner-biomass-recruitment function and larval dispersal). Of particular interest is the question of selection against migratory behaviour, where spatial disparities in fishing mortality might favour resident fish in refuges.

In this chapter the IBM is used to examine the movement models in detail. The IBM can advance the analysis undertaken in Chapter 2 because it takes into account spatially varying fishing mortality rates and the uneven distribution of habitat, something that is impossible to do with an analytical model. The similarity between the model results and the data is the primary criterion for selecting the most likely model, but the parameter values should also be biologically plausible.

METHODS

Simulation of the tag experiment

The tagging experiment conducted at Lekkerwater (a site within the De Hoop Marine Protected Area) was simulated for the years from 1988 to 1999, using the spatially-structured, individual-based model described in Chapter 4. In the model, fish were 'tagged' during the weeks and years that corresponded to the tagging trips described in Chapter 2. Model fish were 'tagged' in the 34 cells that corresponded to the Lekkerwater research site. Fishing effort at the release site and the catchability value, which together determine the tagging rate, were taken from the data presented in Table 3.11.

A model fish was 'tagged' by simply assigning to it a unique number, which was immediately written to a file, along with the cell number and date. If that fish was caught again (in the protected areas or in the fished area) then the position and date of the subsequent capture was also written to the file. A file of 'pseudo' tag and recovery data was generated for each model variation.

Movement models

The symbols referred to below are defined in Appendix 1.

1. Random movement

This model described purely random movement, a possibility that was discarded in Chapter 2 as an unlikely explanation of the data. Its inclusion in this analysis serves mostly to confirm the inappropriateness of the diffusion model, and to serve as a baseline. At every time-step, all fish move to a new cell. The distance of the move (in cells) is drawn from a normal distribution, of adjustable width (γ).

2. Tourist model

The tourist model consists of identically behaving fish that split their time between two separate home-ranges. The two sites are referred to as the natal home-range (the one to which the fish recruits) and the alternate home-range. Movement from one to the other is timed stochastically, and is supposed to reflect unpredictable changes in environmental conditions that might trigger such a move. The respective probabilities (β or χ) of emigrating from either home-range are adjustable, and may result in one site being utilised substantially more than the other. The absolute magnitudes of β and χ were not that important, it was their relative magnitudes that determined the likelihood of a fish being caught twice in the same place, as opposed to different places. For this reason the relative use of home-ranges was conveniently summarised by the home-range-ratio (χ:β), or HRR. The smaller the HRR, the lower the probability of finding the fish in its natal home-range.

The distance between the two home-ranges was drawn from a negative-exponential distribution of adjustable slope (δ). Whereas a normal distribution was used for the initial testing of the model in Chapter 4, a negative-exponential distribution provided a better fit to the data. An initial estimate of the slope was obtained by fitting an exponential function to the displacement data illustrated in Fig. 2.4. The tourist model was therefore specified by two parameters: HRR and δ.

3. Polymorpic model

The polymorphic model consists of resident fish, which never leave a home-range, and nomadic fish, which move continuously in a random fashion. The relative proportion of residents and nomads at recruitment is adjustable (ϕ is the resident fraction), as is the dispersal rate of nomads (γ). The polymorphic model is thus also specified by two parameters. (The random model is a special case of the polymorphic model in which all fish are nomadic – there is no resident component, and no home-range behaviour. The random model is therefore a nested model with only one adjustable parameter.)

Comparison of model results and data

There were a number of tag and recapture results, reported in Chapters 2 and 3, that should be reproduced by the successful model (Table 5.1). But, because of certain key uncertainties in the model, not all of these could be used, and some need to be adjusted to account for potential bias in the data. The spawner-biomass-recruitment relationship, which sets the carrying capacity and the resilience of the stock to fishing, determines to a large part the size of the population and the catch (Chapter 4). When simulating the tag and recapture experiment, the number of fish tagged is affected directly by the choice of spawner-biomass-recruitment relationship. To eliminate the effect of the uncertainty in the spawner-biomass-recruitment relationship, the number of fish tagged is not used as a criterion for selecting the movement pattern. The tag and recapture statistics listed in Table 5.1 are unaffected by the abundance of fish. These include the recapture rate and the distribution of displacements, because they are relative measures – relative to either the total number of fish tagged or the total number of recaptures. The model does not include density-dependent effects in the movement or catchability components, and the abundance of fish at any site does not affect the passage of any fish or its susceptibility to capture. Therefore, apart from the actual number of fish tagged, the effect of the spawner-biomass-recruitment relationship can be ignored in comparisons of recapture rates and displacement distributions between the model and the data set.

Another great uncertainty in the fishery is the extent of larval dispersal, which, when varied over two orders of magnitude, affected trajectories of population size and catches. Predictably, density in protected areas was greater when larval dispersal was localised, and the reverse occurred in areas that were exploited (Chapter 4). For the same reason mentioned in the previous paragraph, larval dispersal will affect the number of fish tagged in the protected area (again causing the number of tagged fish to be unreliable as a criterion for judging movement patterns), but not the recapture rate or the relative distribution of recaptures.

Uncertainty in the catchability factor cannot be disregarded either. The catchability, which translates directly into the fishing rate, determines the number of fish that will be tagged *and* the recapture rate. No attempt was made to vary this rate in the comparisons that follow. Where the model result differed from the data, by having too low a recapture rate and resident recapture rate, it was possible to calculate the adjustment in catchability that was necessary to rectify the discrepancy, without actually re-running the model, because of the linear relationship between catch-rate and catchability. However, a successful model should not require a massive adjustment in catchability, because the catchability value that was used was based on several years of precise catch and effort data and density estimates. The coefficient of variation on the density estimate was 7% (Table 3.10). Therefore, the error in catchability should be of the same order. Catchability cannot be adjusted to alter the distribution of displacements, as a single catchability rate was used across all areas, and its adjustment will affect catch rates equally in all areas.

Non-reporting of tagged fish caught outside the protected area means that the recapture rate there could be substantially greater than reported. The only estimate of the rate of non-reporting is 42% (Chapter 2). This bias pushes the recapture rate from 0.083 to almost 0.1. (Non-reporting only affects the fraction of fish caught outside the protected area.) As a means of judging model results, any value that fell between the measured (but biased) rate and a corrected rate for 50% non-reporting was deemed acceptable. The same bias obviously impacts on the distribution of displacements, for which ranges are also given, but not on the resident recapture rate, for which all recaptures were recorded (Table 5.1).

The only other important uncertainty for comparisons is the fishing effort distribution. It is assumed that the model effort distribution that was fitted to the 1995/1996 survey data is a reasonable reflection of the actual effort values.

As explained in Chapter 4, it was not practical to fit the model to data using standard iterative fitting procedures, due to the time required for model execution. In addition, several criteria were used to evaluate the models, making it difficult to define a single objective function. Some adjustment of parameter values described in Chapter 4 (movement parameters and catchability) was necessary to achieve a match. A search for the appropriate combination of movement parameters (maximum of two for any model) was done by selecting values from a one- or two-dimensional grid, and determining from the responses of the recapture statistics, the direction in which to move. Grid values were as follows:

Random model: $\phi = 0$, $\gamma = [0.5, 2.5, 5.0]\ \mathrm{km^2.d^{-1}}$;

Tourist model: HRR = [2, 5, 10, 15, 20], $\delta = [0.5, 0.55, 0.6, 0.65, 0.7] \times 10^{-2}\ \mathrm{km^{-1}}$,

Polymorphic model: $\phi = [0.7, 0.75, 0.8, 0.85, 0.9, 0.95]$, $\gamma = [2, 3, 4, 5, 6, 7, 8]\ \mathrm{km^{-1}}$.

No attempt was made to improve the fit of any model by choosing smaller grid-spacings.

TABLE 5.1: Measurements and observations from tag recapture experiments that should be reproduced by a successful movement-model of galjoen. Recapture rates are expressed as a fraction of the total number of tagged fish.

Measurement/observation	Value/Range	Comment
Recapture rate	0.083 – 0.11	The observed rate of 0.083 is a minimum, as allowance should be made for non-reporting of tags. The given range accounts for a possible non-reporting rate of 50% (see chapter 2) in fished areas.
Recapture rate at release site (resident recapture rate)	0.066	Because all recaptures at the release site were reported, this measurement is reliable.
Proportion of < 2 km displacements	0.65 - 0.79	The measured proportion was 0.79, but allowance is made for a 50% rate of non-reporting outside of the protected area. 2 km is used as a cut-off to distinguish between within and across home-range movements.
Proportion of > 500 km displacements	0.012 – 0.024	The measured proportion was 0.012, but allowance is made for a 50% non-reporting rate.

RESULTS

Random model

The random movement model has only one adjustable parameter: the dispersal parameter, γ. Three values of this parameter were used in otherwise identical simulations. The number of fish tagged decreased with increasing dispersal as a result of improved protection of fish in the MPA at low dispersal (Table 5.2). This conclusion is supported by results that showed that the recapture rate improved with increasing dispersal as more fish moved to heavily exploited areas outside the MPA and that the resident recapture rate declined.

The random model failed because none of the dispersal values could reproduce all the basic tag and recapture statistics. A value of γ of less than 0.5 km^2.d^{-1} was required for the correct resident recapture rate, a value between 0.5 and 2.5 km^2.d^{-1} was required for the correct recapture rate; whereas a value between 2.5 and 5.0 km^2.d^{-1} was required to push enough fish beyond the 500-km displacement threshold. Adjusting the parameter either up or down corrects one or the other bias, but not all. Such inflexibility suggests that an extra adjustable parameter is required.

TABLE 5.2: Results of the random movement model for three values of dispersal. The values listed in Table 5.1 are repeated for comparison, but the number of fish tagged was not used as a criterion for judging movement patterns. Recapture rate and resident recapture rate are expressed as the proportion of the total number of fish tagged, whereas the two displacement categories are expressed as proportions of the total number of recaptures.

Variable	$\gamma = 0.5$ km^{2}d^{-1}	$\gamma = 2.5$ km^{2}d^{-1}	$\gamma = 5.0$ km^{2}d^{-1}	Measured
Number of fish tagged	9378	5930	4175	13686
Recapture rate	0.039	0.175	0.235	0.083-0.11
Resident recapture rate	0.014	0.002	0.001	0.066
<2-km displacements	0.365	0.012	0.006	0.65-0.79
>500-km displacements	0.000	0.006	0.024	0.012-0.024

Tourist model

Comparing across three home-range-ratios, it is apparent that the less time fish spend at their natal home-range (i.e. small HRR values), the fewer the fish in the protected area, and the greater the recapture rate (Table 5.3). Predictably, the resident recapture rate shows the opposite trend to the total recapture rate. These trends are due to an increase in the availability of 'protected' fish (fish whose natal home-range falls within the protected area) to the fishery. The opposing trends of the recapture rate and the resident recapture rate constrain the choice of HRR between 10 and 20. However, a value slightly in excess of 15 increases the fraction of recaptures that were caught at the release site and reduces the fraction that passed the 500-km mark beyond the measured ranges. The fraction of recaptures that passed 500-km can be increased by decreasing δ, but this parameter has no impact on any of the other results listed in Table 5.3, and therefore does not affect the choice of HRR. HRR=15 was chosen because it required the smallest adjustment in q to meet all the criteria. A δ value of 0.006 km^{-1} corresponds to a mean distance between alternate home-ranges of 167 km.

TABLE 5.3: Results of the tourist movement model for $\delta = 0.006$ km^{-1} and three HRR values. The measured values listed in Table 5.1 are repeated for comparison, but the number of fish tagged was not used as a criterion for judging movement patterns. The recapture rate and resident recapture rate are expressed as proportions of the total number of fish tagged, whereas the displacement categories are expressed as proportions of the total number of recaptures. The q-adjustment is the percentage shift in catchability required to increase the resident recapture rate to within 5% of the measured value and the recapture rate to within the range 0.083-0.11.

Variable	HRR = 5	HRR = 10	HRR= 15	Measured
# Tagged	10704	11569	12153	13686
Recapture rate	0.084	0.078	0.077	0.083-0.11
Resident recapture rate	0.050	0.057	0.062	0.066
<2-km displacements	0.599	0.732	0.789	0.65-0.79
>500-km displacements	0.038	0.026	0.016	0.012-0.024
Minimum q-adjustment	26%	10%	2%	

Polymorphic model

Increasing the nomadic fraction predictably increases the recapture rate and decreases the resident recapture rate and the proportion of <2-km displacements (Table 5.4). Again, the trade-off in these results constrains the choice of parameters. With a dispersal rate of 7 $km^2.d^{-1}$, the value of ϕ lies between 0.75 and 0.85. Changing the dispersal rate does alter the optimum ϕ value. Higher dispersal rates favour higher ϕ values and *vice versa*, but the results shown Table 5.4 provide a match with the smallest adjustment of catchability of any dispersal rate.

TABLE 5.4: Results of the conditional polymorphic movement model, with three (fixed) percentages of nomadic fish at recruitment, and $\gamma = 7$ $km^2.d^{-1}$. The measured values listed in Table 5.1 are repeated for comparison. Recapture rate and resident recapture rate are expressed as proportion of total number of fish tagged, whereas the displacement categories are expressed as proportions of the total number of recaptures. The q-adjustment is the percentage shift in catchability required to increase the resident recapture rate to within 5% of the measured value and the recapture rate to within the range 0.083-0.11.

Variable	$\phi = 0.75$	$\phi = 80\%$	$\phi = 85\%$	Measured
# Tagged	10587	11168	11719	13686
Recapture rate	0.088	0.083	0.075	0.083-0.11
Resident recapture rate	0.061	0.062	0.064	0.066
<2-km displacements	0.694	0.755	0.814	0.65-0.79
>500-km displacements	0.026	0.016	0.011	0.012-0.024
Minimum q-adjustment	3%	2%	11%	

Tourist vs polymorphic model

A consistent difference between the two movement models lies in the relative frequency of <2-km displacements when time-free is large. In Chapter 2 it was evident that there was no significant difference in the proportion of <2-km displacements across time-free categories (Fig. 2.5). It was argued that this ruled out the random model, as constant dispersal from the tagging site would result in an ever-decreasing proportion of <2-km displacements as time-free increased.

The tourist model showed no trend in the frequency of <2-km displacements, whereas the polymorphic model showed an increase as time-free increased (Fig. 5.1). All polymorphic recaptures after 2.5 years (30 months) of time-free showed <2-km displacements, which is not consistent with the data from Lekkerwater or any of the other sites (see Fig. 2.5). The increasing trend in the polymorphic model is explained by the high fishing rate outside the protected area, which quickly truncated the life-span of nomadic fish. Resident, tagged fish in the protected area persisted for longer.

Within-site recapture distributions

The model developed in Chapter 4 used a simple random approach to apportion a fish's time equally between three proximate 'active' cells. Active cells were outnumbered by inactive cells in the ratio of approximately 2.3:1, which means that the average home-range will be larger than 300 m. Home-ranges in the model varied in size between 300 m and 3.3 km, depending on the density of active cells (Fig. 5.2). The average home-range size was 770 m. The model therefore predicts that variation in home-range size is caused by the habitat distribution. The model provided the opportunity to test the accuracy of using tag and recapture data to estimate home-range size, as was done in Chapter 2.

One thousand 'resident' fish in the polymorphic model, randomly chosen from throughout the range, were 'recaptured' one week later to generate a cumulative displacement distribution (Fig. 5.3). The resulting distribution compared favourably with those reported in Chapter 2 (Fig. 2.6), with the ninety percent cut-off (one of the criteria used to estimate home-range size) corresponding to 550 m. The true average home-range size of 770 m corresponded to a cut-off in the cumulative displacement distribution of 94%.

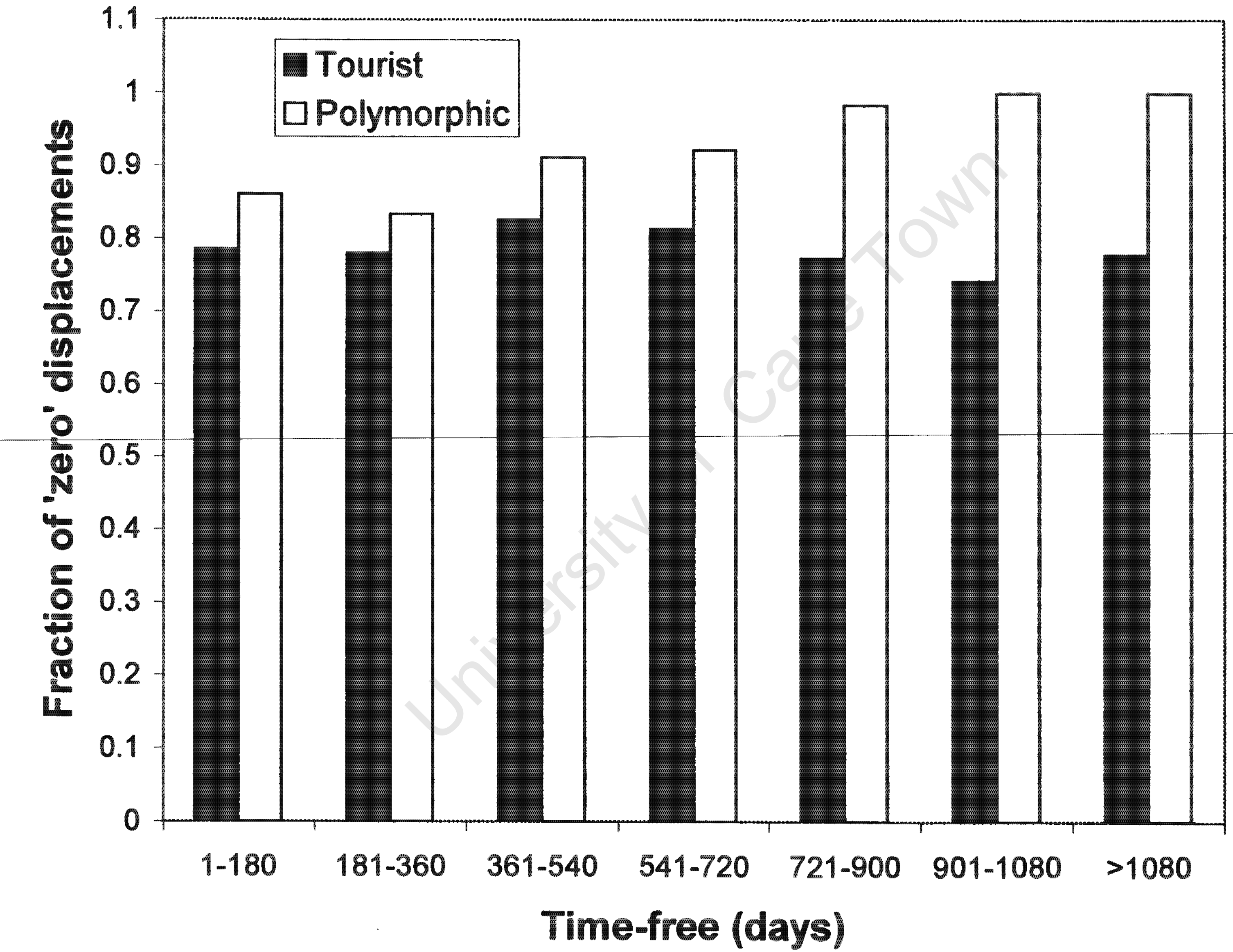


Figure 5.1. The fraction of 'zero' displacements (those that did not exceed 2 km) during seven time-free periods for the best-fit tourist and polymorphic models.

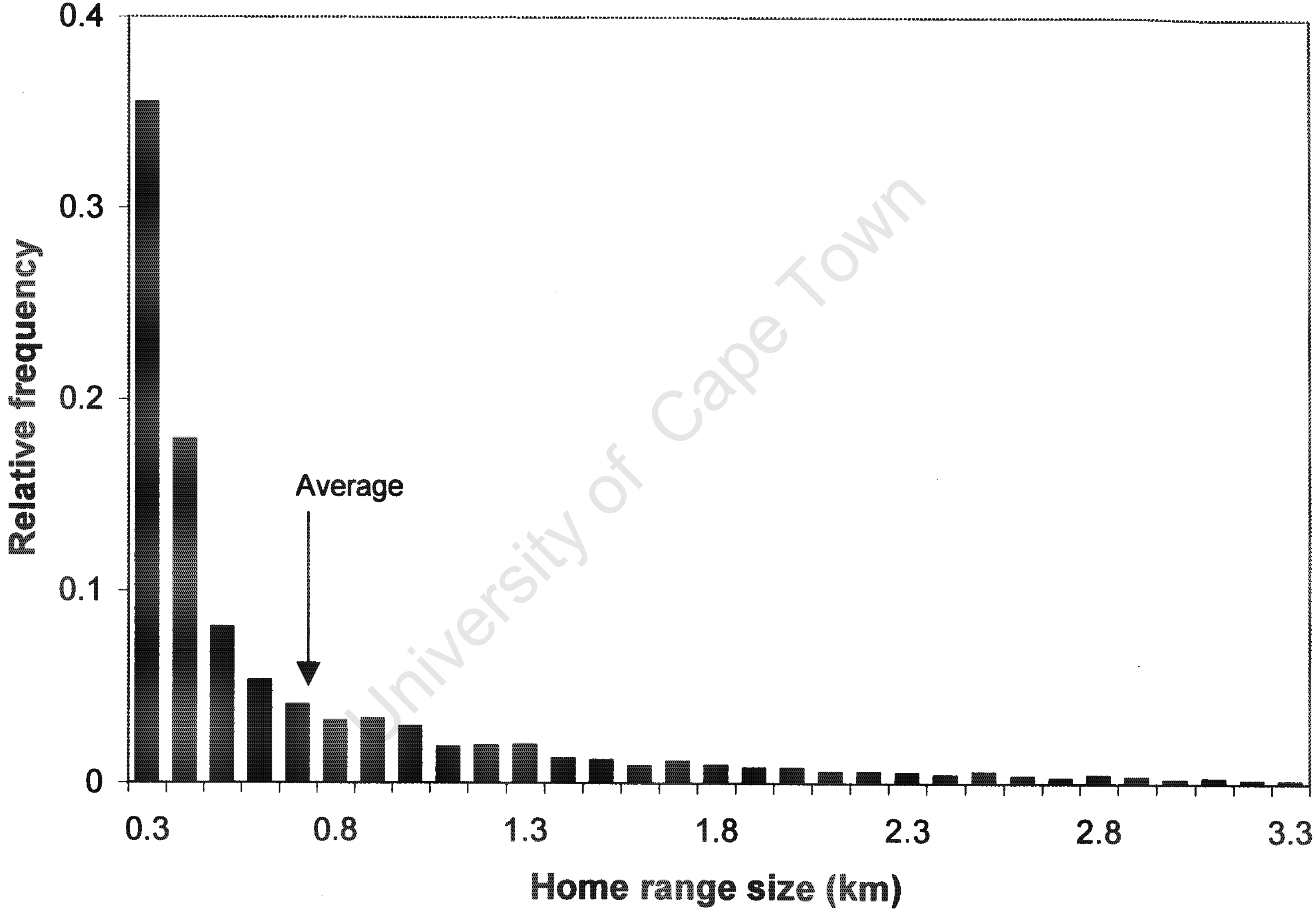


Figure 5.2. The relative distribution of home-range size predicted for fish that require three consecutive 'active' cells. The distances covered by all consecutive combinations of three active cells were used to calculate this distribution.

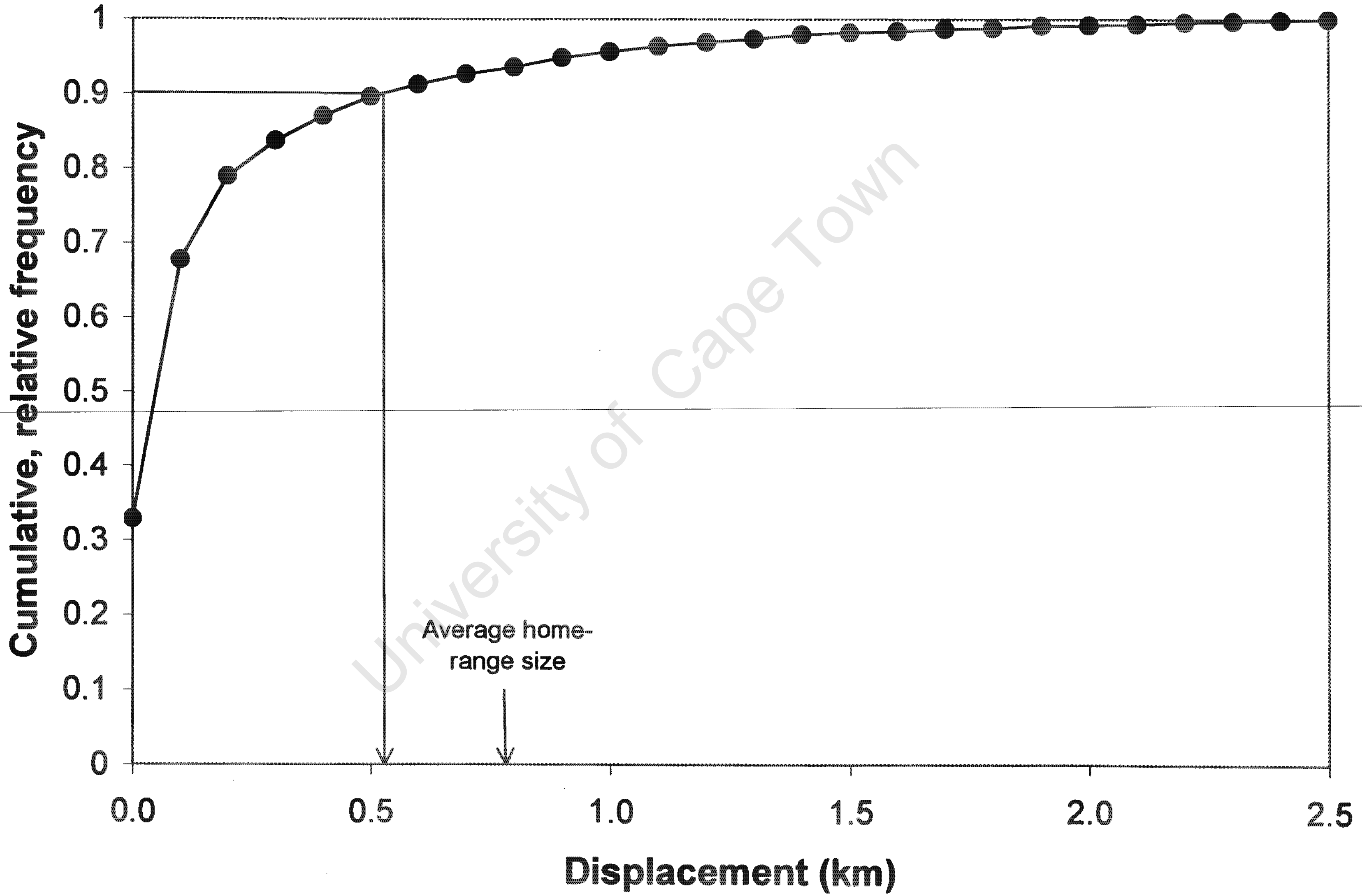


Figure 5.3. The cumulative, relative distribution of displacement of resident fish (n=10881). The arrows show the average home-range size and the prediction based on the 90% cut-off rule.

DISCUSSION

Using an IBM of the galjoen fishery with realistic spatial structure it was possible to consider the effects of hypothetical movement patterns on the outcome of a tagging experiment. At face value, the data presented in Chapter 2 provided no reliable means to discriminate between the tourist and polymorphic models. Although the multiple recapture patterns favoured the tourist model, it could not rule out the polymorphic model on statistical grounds. Because of spatially and temporally varying fishing mortality rates and the unpredictable distribution of suitable habitat, a simulation model was required to compute the progress and fate of tagged fish. The tourist and polymorphic models were able to simulate the observed capture and recapture rates, and spatial distribution, after some adjustment in catchability. However, only the tourist model correctly simulated the time-dependent pattern of recaptures (Fig. 5.4).

The distinction between the models rests on the exact mechanism of movement. In the polymorphic model, the nomadic fish move continuously. Tagged nomadic fish therefore disperse from the tagging site almost immediately. In contrast, tagged tourist fish do not relocate immediately; some may remain there for several years. Those that do move are likely to return, thereby ensuring a presence of tagged fish at the release site and a continuous supply of tagged fish to exploited areas for years after the tagging event. The data support the tourist model.

The objective of this work should be to select a pattern that is not only statistically consistent with data, but one that is also biologically plausible. There was nothing in the biology of galjoen, nor comparable examples, that clearly favoured one movement type above the other (Chapter 2). With the hindsight of simulations, it is clear that some subtleties in the tag and recapture data point towards the tourist model, i.e. a model in which all fish share a similar movement strategy that involves the possibility of infrequent and temporary migrations to a site (or sites) other than their natal home-range. The polymorphic model required a very high rate of dispersal among nomadic fish to match all aspects of the recapture data. The 'optimal' dispersal parameter of 7 $km^2.day^{-1}$

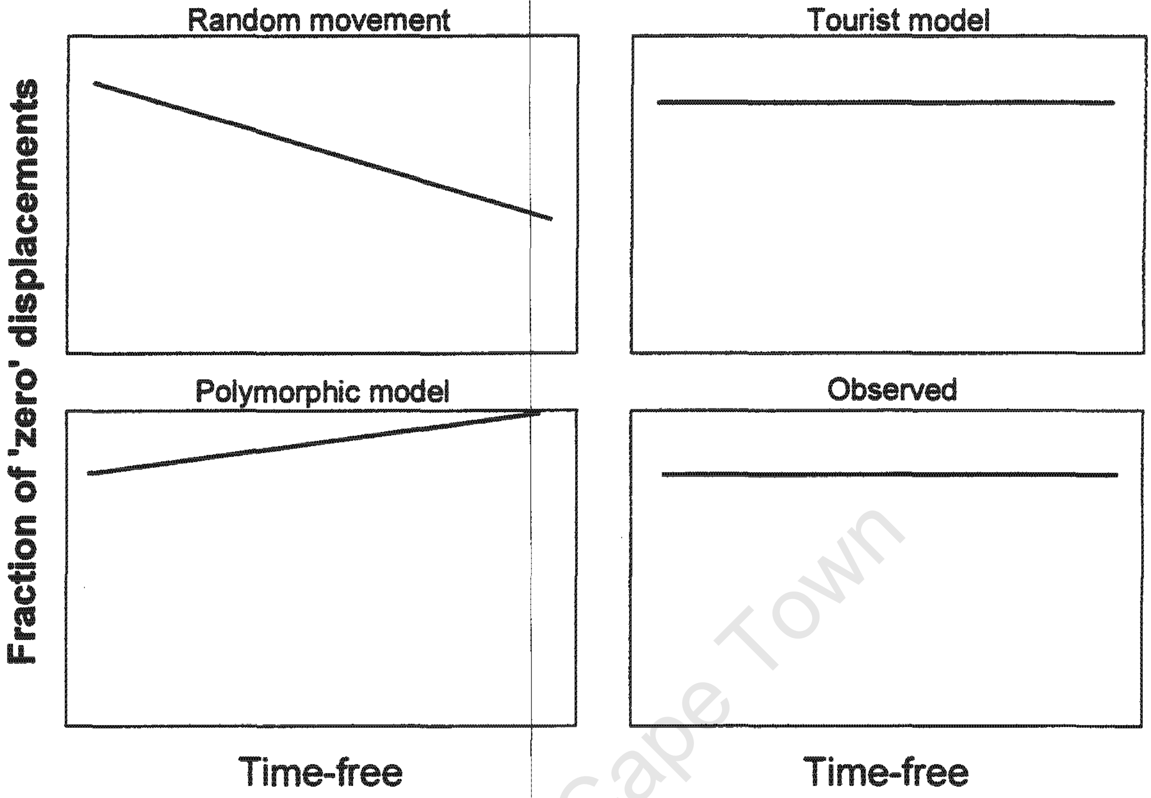


Figure 5.4. A schematic representation of the relationship between the fraction of 'zero', displacements and 'time-free' for three competing models of galjoen movement and the data presented in Chapter 2.

predicts velocities that are within the continuous swimming-speed capability of galjoen. However, it seems unlikely that such constant and rapid to-and-fro movements of a fish can result in an evolutionary competitive alternative to resident behaviour. Rapid displacements (> 20 km.d^{-1}) have been measured, but such movements are not compatible with feeding on sessile organisms, implying that they are more likely to be migrations than a foraging strategy. By contrast the tourist model requires extensive, but infrequent movements of all fish to reproduce the observed tag and recapture data.

The tourist model raises some obvious questions, for which only speculative answers can be offered:

Q: Why would galjoen leave a home-range occasionally?
A: Living in a physically dynamic environment, and being dependent on a benthic community in an early stage of ecological succession, galjoen may be forced to seek alternative feeding sites if feeding conditions deteriorate. They do so reluctantly, because of the cost associated with travel, and the risk of not finding a better environment.
Q: Why would galjoen return after a short interval?
A: Galjoen may retain a link to their natal site, preferring to spawn in an area in which they recruited (See obstinate behaviour [Cury 1994] described in Chapter 1). This may encourage a galjoen to return to its natal site repeatedly. Because the galjoen's feeding environment is dynamic, there is a reasonable chance that conditions will be favourable upon return. If a site is a productive galjoen area, consistently producing many recruits, the odds are good that conditions will be favourable. Faced with the dilemma of where to go when the alternative site fails to produce good feeding conditions, the fish's best choice is to return to its natal site, rather than head for another area of unknown quality and danger.
Q: Why do some galjoen travel so far (median movement was 167 km) to seek an alternative site?
A: Extensive upwelling of cold water is an example of an unfavourable event that covers a large length of coast, forcing a fish to move beyond it. The cost of long-distance travel may be mitigated to some extent by travelling in currents, or counter-currents, that run

parallel to the shore. There are occasional sightings of large aggregations of galjoen at offshore reefs and wrecks, which could serve as stop-over points along well travelled routes.

Q: Why are relatively more young fish recaught at the release site than at alternate sites?

A: It could be speculated that older fish will move between alternate sites with greater regularity than young fish, because their experience reduces the costs and risks involved in such a move and because larger fish are more efficient travellers. No age-based variation in movement behaviour was included in the model, although it is recognised that this omission could provide misleading results, particularly when investigating reserve effects.

Q: Do galjoen migrate?

A: Galjoen move rapidly, probably using offshore routes. Tag and recapture data provide minimum estimates of velocity between capture events. Velocities of over 20 $km.d^{-1}$ have been recorded in this way, indicating that they do not feed *en route*. Galjoen can be classed as migrants, provided that they know where they are going (first-time migrants could follow or receive instruction from experienced individuals) and that they leave before it is absolutely necessary to do so. If these conditions are not met, relocating galjoen could be classed as nomads or refugees (Dingle 1996). In any case, home-range relocation is a convenient term that describes the process behind the tourist model (Kramer and Chapman 1999).

Q: How does the tourist model account for shoaling behaviour?

A: Small groups (<10) are usually formed when feeding in broken surf, but larger schools form when not feeding, in calm or deep water (Rust and Rust 2000). The largest schools are found offshore. These observations suggest that school fidelity is low, and that schooling is used primarily for long-distance travel and protection. Schooling habits and social transmission of migration patterns is not sufficiently understood for inclusion in the model. The model assumes that fish act as individuals.

Parsimony in the tourist model

The tourist model is simple, including a measure of skewness of home-range use, and a negative-exponential function that determines distance between alternate sites. It is quite possible (even likely) that individual galjoen have more than two regularly used home-ranges, but that would make very little qualitative difference to the model outcome, provided that the natal home-range is vastly preferred above the others. The choice of only two home-ranges facilitates computation.

Railsback *et al.* (1999) have stated that simple movement rules should be able to explain complex behaviour and that the complexity should not be built into the rules. Chapter 2 showed that a model of home-range behaviour in which the fish used all parts of the range equally did not explain the recapture data. Instead, a two-parameter gamma distribution was needed to fit the data. From the IBM it was evident that the use of a biologically-meaningless gamma function was not necessary. It was possible to adequately replicate the within-site recapture data by assuming that fish used good patches with equal frequency (the simplest assumption) and that the variation in home-range size between fish was a result of the distribution of patches. These simple assumptions can describe quite complex patterns. Again, this reiterates the importance of spatial structure, if home-range size depends on the patchiness of the environment. Home-range size estimates differed between Cape Peninsula, Koppie Alleen and Lekkerwater (Chapter 2).

Resident fish have a certain dietary requirement that presumably translates directly into area of good quality habitat (Mace *et al.* 1984, Kramer and Chapman 1999). It was arbitrarily assumed that a galjoen needs three active cells for a home-range, but the choice of cell size was, by itself, a simplification with no ecological or geographical basis. The absolute density of active cells per habitat type was also chosen in the absence of comparable data (Table 4.1). The chosen combination of cell size, active cell requirements and active cell density provided a result that was consistent with the recapture data, but other combinations may also have worked. For the purpose of the investigations that follow, provided that the distribution of actual home-range size is correct, the choice of cell size, active cell requirements and active cell density is not critical. In contrast, the habitat distribution is consequential as it sets the broad framework for patchiness. The IBM has a realistic basis in the geographical data used to assign habitat type.

Development of the theory

A troublesome aspect of this work is the manner in which the movement hypotheses were developed and tested. It certainly did not follow the classic hypothetico-deductive method of first speculating and then building hypotheses and then testing by experiment. In reality, the tagging experiment was initiated to answer a simple question: how far do the fish move? No clear hypothesis influenced the design of the experiment. As data accumulated steadily, they pointed to certain possibilities and not to others, whereupon hypotheses were formed. Looking back, there was a distinct progression of hypotheses, one replacing the next. This progression was based more on the strengthening and expansion of the data set, rather than on new experiments providing definitive rejection.

The progression started with the (reasonable) idea that the everyday movements of fish along the shore, linked to tidal-cycles and patterns of sand movement, could be described as Brownian movement. An analytical model readily explained how fish were captured at the release site and, less frequently, at great distances away, without any seasonal component (Bennett *et al.* 1989). The famous work of Okubo (1980) provided some respectability for this hypothesis.

However, the weight of evidence outgrew the diffusion theory – as sample size increased there was not sufficient uncertainty in the results to accommodate the model. It eventually became obvious that the simple model was wrong. A new theory was needed and it was developed. The polymorphic model was fitted to the data (Attwood and Bennett 1994), and clearly provided a statistically better fit than the previous model, which was refuted.

However, the theories were not mutually exclusive. The polymorphic model allowed for the possibility that not all fish behave as Brownian particles, though some do. This is not a clear application of the Popper's method – the model was merely modified to accommodate an emerging feature of the data. Again, credibility was added by the literature, which cited numerous examples of populations that displayed such a split in behaviour, some even showing morphological differences that accompany a dichotomy in the need to travel (see review in chapter 1).

The tourist model did not emerge out of dissatisfaction with the polymorphic model, but was inspired by a seldom-quoted investigation into sunbirds (Craig and Hulley 1994). It became clear that another theory could explain the data. As a result of the modelling in this chapter, I accept the tourist model as a more likely explanation than the polymorhic model, because the IBM showed that its predictions were (marginally) more consistent with the data. There is the possibility that the polymorphic and tourist models are not mutually exclusive and that some blending of components might provide a better fit, but the available data are not sufficient to test this.

Some explanation of the model selection/rejection process is needed. The nature of the proof being sought here is primarily statistical: a comparison of rates, proportions and distributions. A problem is that the observations (data) are embedded in a large and complex *milieu* of fishery interactions and cannot be considered separately. (A field-study involving direct underwater observations would not confront this problem.) The competing movement models are simple, but to provide predictions comparable to the observations, they have to be embedded in a large and unwieldy, though simplified, model of the fishery. Here the question is, does the polymorphic model not fit the data because the hypothesis is wrong, or because the model of the fishery is inaccurate in a way that would affect the comparison of movement hypotheses? Every reasonable effort was made to ensure that the model was accurate and realistic.

According to Mayr (1982), the '*working scientist is a pragmatist*', '*science is based on probabilistic interpretation of scientific conclusions*', and it is '*inappropriate to speak of proof as absolute*'. Furthermore, he tells us that, '*accepting great flexibility is one of the attributes of scientific theories, the scientist is willing to test numerous theories, to combine elements of different theories, and sometimes even to consider several alternate theories simultaneously, while in search of evidence to adopt one in preference of the others.*'

The rejection of the polymorphic model is contingent on the realisation that, in its present formulation, the predictions did not match the data in every respect, whereas the tourist model provided an acceptable match.

CONCLUSION

Galjoen are resident fish that display home-range behaviour, frequenting areas that are large enough to include sufficient good-quality habitat. Occasionally, and unpredictably, galjoen leave their home-range in favour of another site (or sites), which could be a great distance away. The median distance between sites is approximately 167 km. A likely pattern results in fish spending more than 90% of their life in a home-range at the natal site. Protected areas should reduce the fishing mortality on fish by approximately this percentage, as the remaining time may be spent in wide-ranging exploited areas.

CHAPTER 6

A MODEL OF THE RECOVERY OF GALJOEN IN PROTECTED AREAS AND ASSOCIATED CHANGES IN YIELD

ABSTRACT

The effect of six marine protected areas (MPAs) on the galjoen fishery during the twentieth century was investigated with a spatially-structured, individual-based model. The MPAs, which covered a range of sizes from 2 to 58 km, were introduced at various stages into the fishery. By 2000, the MPAs had improved the size of the stock by between 25 and 46%, relative to a hypothetical scenario in which there were no MPAs. Density increased in all MPAs, except in the smallest MPAs under conditions of low stock productivity. In no MPA did the density recover to carrying capacity. Edge-effects, which were due to movements within the home-range, were limited to within 2.5 km of MPA boundaries, a result that was robust over a variation of two orders of magnitude in larval dispersal. The size of the MPA was the strongest determinant of galjoen density within MPAs. The recovery in MPAs was affected by the proximity of other MPAs, under certain conditions. The total catch in 2000 was probably not affected to a great extent by the introduction of MPAs. All MPAs immediately decreased yield locally, and later stabilised it. In areas where galjoen were heavily depleted, the introduction of a MPA improved yield locally, but the same was not true when MPAs were introduced to areas that were not heavily depleted. On balance, the MPAs had a positive effect, by leaving the stock in a better condition, and increasing the potential yield for the future.

INTRODUCTION

Because conventional, single-species approaches to management have generally failed to sustain fisheries, marine protected areas (MPAs) have been advocated as a means to protect exploited fish species, to recover their density and to improve yield (Ballantine 1991, Roberts and Polunin 1993, Clark 1996, Rose 1997, Roberts 1997b, Roberts and Hawkins 2000). There is a substantial body of information that suggests that fish in MPAs are more abundant and of greater mean age than their conspecifics in exploited areas (see reviews by Roberts and Polunin 1991, Rowley 1994, Attwood *et al.* 1997a, Jennings 2001). However, in the strictest scientific sense, it is rarely possible to ascribe differences in fish abundance across a MPA boundary to the effects of fishing with absolute certainty, because the experimental designs are almost always inadequately replicated (Roberts and Polunin 1991, Crowder *et al.* 2000, Willis *et al.* in press). In the temporal dimension, a time-series of fish catches can rarely be repeated experimentally. In the spatial dimension, areas that are compared are never identical and no two areas will have the identical carrying capacity of fish. Sufficiently large sample sizes will always show significant differences between two areas (Edgar and Barrett 1999).

Despite universal weaknesses in experimental designs, the observed differences across the boundaries of MPAs are almost certainly indicative of the direct effects of fishing, because this interpretation tallies well with three other observations: (1) fishing impacts heavily on fish abundance (Boehlert 1996), (2) bottom-feeding fish species are typically resident during some stage of their life (Chapter 1), and (3) cessation of fishing leads to recovery of stocks (Russ and Alcala 1996a, Bennett and Attwood 1991).

Using CPUE as a measure, the density of galjoen (*Dichistius capensis*) was found to increase in the De Hoop MPA after its creation in 1985 (Bennett and Attwood 1991) and it was subsequently greater there than in adjacent exploited areas (Bennett and Attwood 1993). Galjoen were more abundant and of greater average size in the Cape Peninsula MPA, than in immediately adjacent exploited areas (Naidoo and Verheye 2001). These results are consistent with our understanding of the fishery. Recent fishing pressure has been sufficient to reduce pristine spawner-biomass-per-recruit by 90 percent (Bennett 1988). Although not much is known of the extent to which galjoen larvae disperse, the adults are predominantly resident. Those that recruit in MPAs should have their life expectancy increased because of the absence of fishing.

The claim that fishery yield will improve once a suitable area is protected is contentious, and empirical support is rare (Crowder *et al.* 2000). Again, experimental difficulties include the collection of reliable catch statistics before and after the establishment of a reserve, the control of fishing effort and the lack of suitable control sites. Theoretical studies suggest that yield enhancements should occur under certain circumstances (Guenette *et al.* 1998), particularly for reef-fisheries that are severely over-exploited (Sladek Nowlis 2000, Dahlgren and Sobel 2000). For the galjoen fishery this question has not been answered by experiment or observation, and a modelling approach is still the only option available.

Six MPAs of various lengths (2 km – 58 km) took effect within the South African range of galjoen during the late stages of the twentieth century. The approach taken here was to consider retrospectively the role that the MPAs had on the galjoen fishery, and to draw some conclusions about the particular pattern of protected areas in relation to effort and habitat. Such an approach is as useful as a forecasting exercise, which would, in addition to past uncertainties, require the extrapolation of the fishery into an uncertain future. The MPAs within the range of galjoen include various designs that offer the opportunity to consider several inter-connected processes. These include size, spacing, position, effort displacement, timing, fish depletion and habitat quality.

METHODS

The individual-based model described in Chapter 4, including the tourist movement model described in Chapter 5, was used to examine the role of the six MPAs in the galjoen fishery. Six model variations included three larval dispersal scales (1.7, 17.0 and

170 km, equivalent to 5, 50 and 500 active cells) and two spawner-biomass-recruitment relationships (maximum reproductive rates being defined as in Myers *et al.* [1999] and set at 5.4 and 2.4). See Table 4.4 for model notation.

The effect of imposing MPAs was evaluated by comparing results of a particular model variation, against the results of another run in which the MPAs were all omitted. This approach is potentially flawed if effort is not kept constant (Crowder *et al.* 2000). Establishing a MPA may eliminate a certain amount of effort, but in general it will displace effort, thereby increasing effort in adjacent areas.

To avoid confounding the effects of effort reduction and protection, the models that introduced MPAs displaced all the effort that would have been applied in those areas. The effort model described in Chapter 4 was modified to redistribute the fishing effort that would have been applied in the MPAs to either side of the MPA, using two halves of the normal distribution with standard deviation σ_τ (Fig. 6.1). The time-dependent value of σ_τ was the same as that used to distribute effort from coastal towns (Chapter 4, equation 3), as the choice of alternative sites by anglers was presumably limited by the same constraints on angler-mobility. All model variations had the identical amount of effort applied – they differed only in the distribution of effort. The effect of MPAs was thus synonymous with the effect of displacing effort.

The initial effect of effort displacement is a reduction of yield. Later, however, catches in areas adjacent to MPAs may increase, which leads to the question: Is the loss of an area to fishermen offset by increased catches in adjacent areas? To answer this question, the catches in an area including the site of each MPA and a buffer zone of 25 km on either side were summed during simulations. These catches were compared between simulations with MPAs and those without.

Because three MPAs were very close (closer than 25 km) only four areas (and not six) were chosen for catch evaluations. The first of these included the three MPAs that were close together. The areas were: (i) a 107 km stretch from 25 km to the west of the Cape

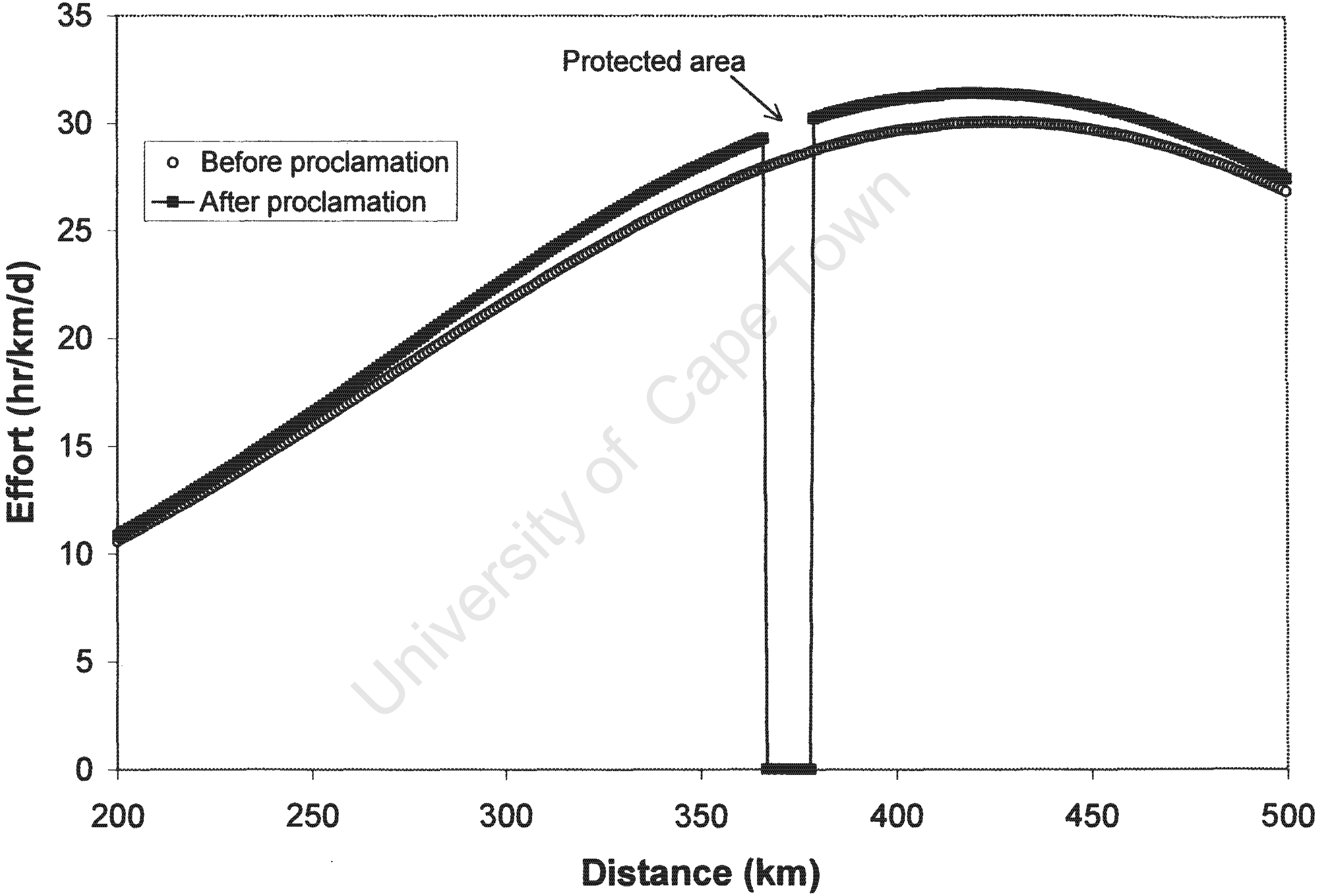


Figure 6.1. Redistribution of effort displaced from a marine protected area. The total effort across all areas remains unchanged. The underlying curvature was derived from the model based on coastal population statistics.

Peninsula MPA to 25 km east of the St James MPA, including both these MPAs and the Castle Rocks MPA; (ii) a 101-km stretch including the De Hoop MPA and 25 km on either side, (iii) a 108 km stretch encompassing Tsitsikamma MPA and 25 km on either side, and (iv) a 58 km stretch encompassing Sardinia Bay MPA and 25 km on either side. The choice of 25 km was arbitrary; a smaller area would exacerbate the effect of the MPA on catches, while a larger area would diminish the effect.

RESULTS

The six MPAs covered 7% of the range of galjoen, but included a slightly greater percentage of the habitat and carrying capacity. All, except the Tsitsikamma MPA, had a disproportionately greater share of galjoen habitat than predicted on the basis of their size (Table I). MPAs in South Africa under-represent sandy-shores (Attwood *et al.* 1997b), which is not a preferred habitat of galjoen. Furthermore, none of the MPAs existed on the extremes of the range of galjoen, where carrying capacity was low, and that further contributed to a disproportionate share of carrying capacity in each.

Table I. Descriptive statistics of the six areas in which fish were legally protected from capture. Here 'habitat' refers to areas that support galjoen, '% of carrying capacity' refers to the relative maximum contribution from that area to the whole population, and 'date' refers to the year in which protection (or displacement) commenced.

Protected area	Length km	% of range	% of habitat	% of carrying capacity	Date
Cape Peninsula	12	0.63	1.02	1.41	1979
Castle Rocks	4	0.21	0.40	0.55	1990
St James	2	0.10	0.28	0.38	1990
De Hoop	51	2.66	3.39	4.66	1985
Tsitsikamma	58	3.02	2.76	3.11	1964
Sardinia Bay	8	0.42	0.96	0.90	1990
Total	135	7.04	8.81	11.01	

Of equal relevance was the amount of fishing effort that each MPA displaced, but these statistics were complicated by the time-dependent nature of effort in the model (Fig. 6.2). The two largest MPAs displaced a disproportionately small share of the total effort. For example, De Hoop, covered 2.66% of the range and contributed 4.66 % of the carrying

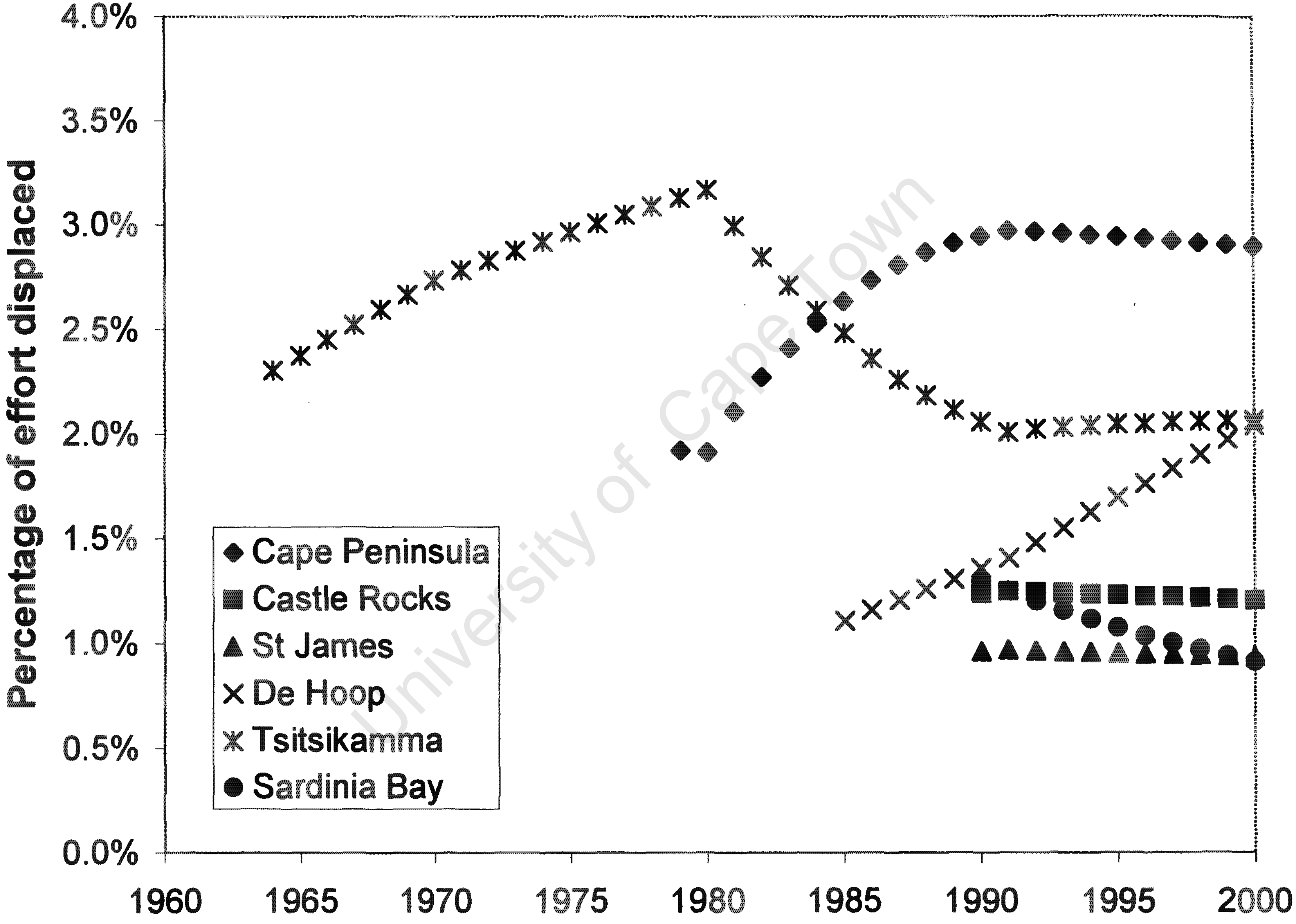


Figure 6.2. The percentage of galjoen-directed effort that was displaced from each marine protected area. The percentages changed with time, as the effort increased unevenly across the range of galjoen.

capacity but displaced only 1.1% of the effort when it was introduced. This proportion rose to 2.0% in 2000, because of a disproportionate increase in the human population along this coast. The MPAs near the Cape Town metropolitan area each displaced a disproportionately large amount of effort compared to their size by a factor between four and ten. Only for the Sardinia Bay MPA was the effort displacement consistent with the size of the area. During the period 1980 to 1990, the greater expansion of Cape Town than Port Elizabeth meant that the MPAs in the west gradually displaced a greater proportion of the effort than those in the east, which explains why the relative displacement from Tsitsikamma declines during this period.

Overall impact of protected areas

In the hypothetical situation of no MPAs, the galjoen population size declined continuously from 1910 to 2000, and yield peaked between 1986 and 1991 (Fig. 4.10). By comparison, when the MPAs were included (by displacing effort) the total population size at the end of 2000 was between 25 and 46% greater (Table 6.2). The effect on yield in the same year was less dramatic and inconsistent. Considering protection, productivity (spawner-biomass-recruitment function) and larval dispersal together, it was clear that there were strong individual effects and interactions, which can be summarised as follows:

1. The abundance was greater with MPAs than without.
2. The abundance was greater under the most productive spawner-biomass-recruitment function (SR1), than under the least productive function (SR2).
3. The abundance was greatest when larvae were not widely dispersed.
4. The abundance with MPAs relative to the abundance without MPAs increased with decreasing productivity. (The effects of effort displacement were most dramatic when the stock was most over-fished.)
5. The abundance with MPAs relative to the abundance without MPAs increased with decreasing larval dispersal. (The effects of effort displacement were partly negated by strong mixing of recruitment.)

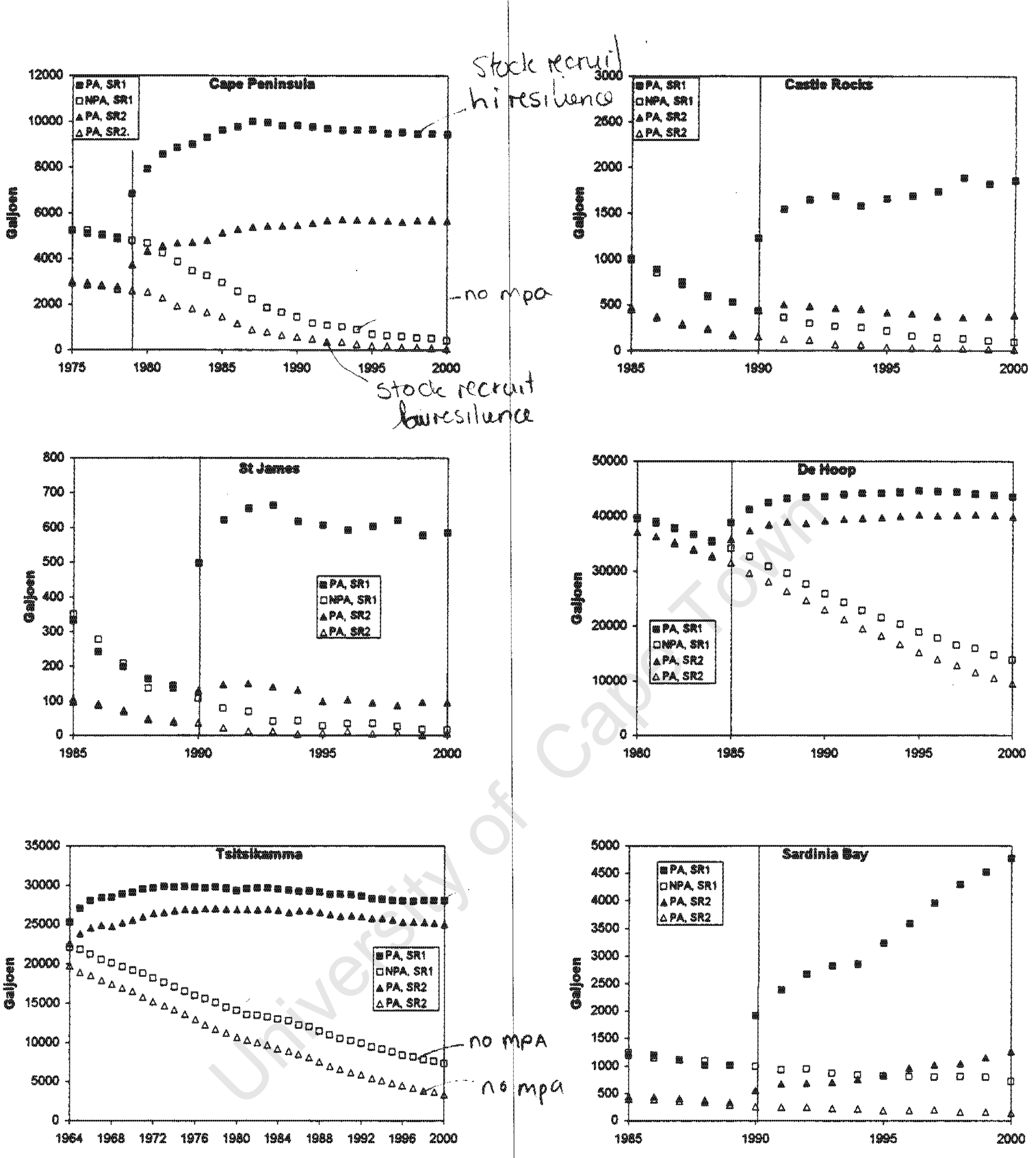
6. The yield in 2000 was greater under the most productive spawner-biomass-recruitment function, than under the least productive function (Fig. 4.10).
7. The yield in 2000 was greatest when larvae were widely dispersed.
8. The yield in 2000 with MPAs relative to the yield without MPAs increased with increasing larval dispersal.
9. The relative improvement in yield caused by protection was similar irrespective of productivity.

Table 6.2. The effect of the displacement of effort from the six marine protected areas on the total population size of galjoen and on the total catch, for two spawner-biomass-recruitment functions (SR1 and SR2) and three larval dispersal scenarios (LD5, LD50 and LD500 active cells in the model). Results are expressed relative to the case in which there was no displacement of effort (i.e. a value of 1.0 indicates no change). The total effort was identical for all simulations.

Change in population size (end of 2000)			
	LD=5	LD=50	LD=500
Stock-recruit 1	1.28	1.28	1.25
Stock-recruit 2	1.46	1.45	1.32
Change in total catch (2000)			
	LD=5	LD=50	LD=500
Stock-recruit 1	0.92	0.96	1.03
Stock-recruit 2	0.90	0.96	1.09

Density changes in protected areas

At the time of establishment of the MPAs, galjoen densities in the two largest MPAs were not heavily depleted (Table 6.3). The effort displacement was high at Tsitsikamma but low at De Hoop (Fig. 6.2). After ten years the density of galjoen increased slightly at both sites, but did not fully recover, remaining between 59 and 86% of the carrying capacity, depending on the combination of productivity and larval dispersal (Fig 6.3 and 6.4). Without protection, the density in these areas dropped to comparatively low levels (Fig. 6.3). The simulations show that protecting these two large sites resulted in the year-2000 density at these sites being three to four times greater than if no MPAs were introduced (Table 6.3). Because of the large size of these areas, they contributed massively towards the overall improvement in population size reported in Table 6.2.



stock recruit hi resilience

no mpa

stock recruit lowresilience

no mPA

no mpa

Figure 6.3. Projections of galjoen abundance in protected areas (PA), and in the same areas without protection (NPA), for two levels of stock productivity (SR1 and 2). Results of only the intermediate degree of larval dispersal are shown (LD50).

The results were more complicated for the three MPAs near Cape Town (Cape Peninsula, Castle Rocks and St James). These areas were heavily exploited prior to protection (Table 6.3). The initial relative density (relative to carrying capacity) was least for restricted larval dispersal, and greatest for extensive dispersal. This trend was most evident in the small St James MPA, and least evident in the larger Cape Peninsula MPA.

Table 6.3. The density of galjoen relative to carrying capacity immediately before each protected area was established (*Initial density*) and again ten years later (*Density after 10 y*) for three larval dispersal scenarios (LD=5, 50 and 500 active cells). The effect of the protected area can be gauged by the improvement of galjoen density relative to the situation in which there were no protected areas in 2000 (*Relative improvement*). According to this scale, a value of 1.0 indicates no change.

Protected area	Population statistic	LD=5	LD=50	LD=500
Cape Peninsula 12 km	Initial density (%)	43.5	45.7	46.2
	Density after 10 y (%)	68.8	65.4	55.6
	Relative improvement	17.5	23.3	9.6
Castle Rocks 4 km	Initial density (%)	18.1	20.5	24.5
	Density after 10 y (%)	48.1	30.9	29.5
	Relative improvement	31.0	20.6	11.9
St James 2 km	Initial density (%)	7.8	11.8	19.1
	Density after 10 y (%)	24.0	13.9	27.9
	Relative improvement	168.3	36.6	41.8
De Hoop 51 km	Initial density (%)	74.6	74.8	72.6
	Density after 10 y (%)	86.1	86.0	76.1
	Relative improvement	3.1	3.1	2.8
Tsitsikamma 58 km	Initial density (%)	71.6	72.1	68.1
	Density after 10 y (%)	86.2	84.8	76.4
	Relative improvement	4.0	3.8	3.0
Sardinia Bay 8 km	Initial density (%)	19.4	18.9	25.5
	Density after 10 y (%)	55.1	47.2	41.5
	Relative improvement	7.2	6.6	4.5

Density recovered to between 31 and 69% of carrying capacity in the Cape Peninsula MPA after ten years (Fig. 6.4) and stabilised at those levels (Fig. 6.3). Larval dispersal retarded the recovery. By 2000, the density was greater than what it would have been without protection by a factor ranging between 10 and 24. This measure of improvement was unstable, because the density in the unprotected case was very small (less than 20 fish in total) and subject to great stochastic variations (see discussion in Chapter 4 on

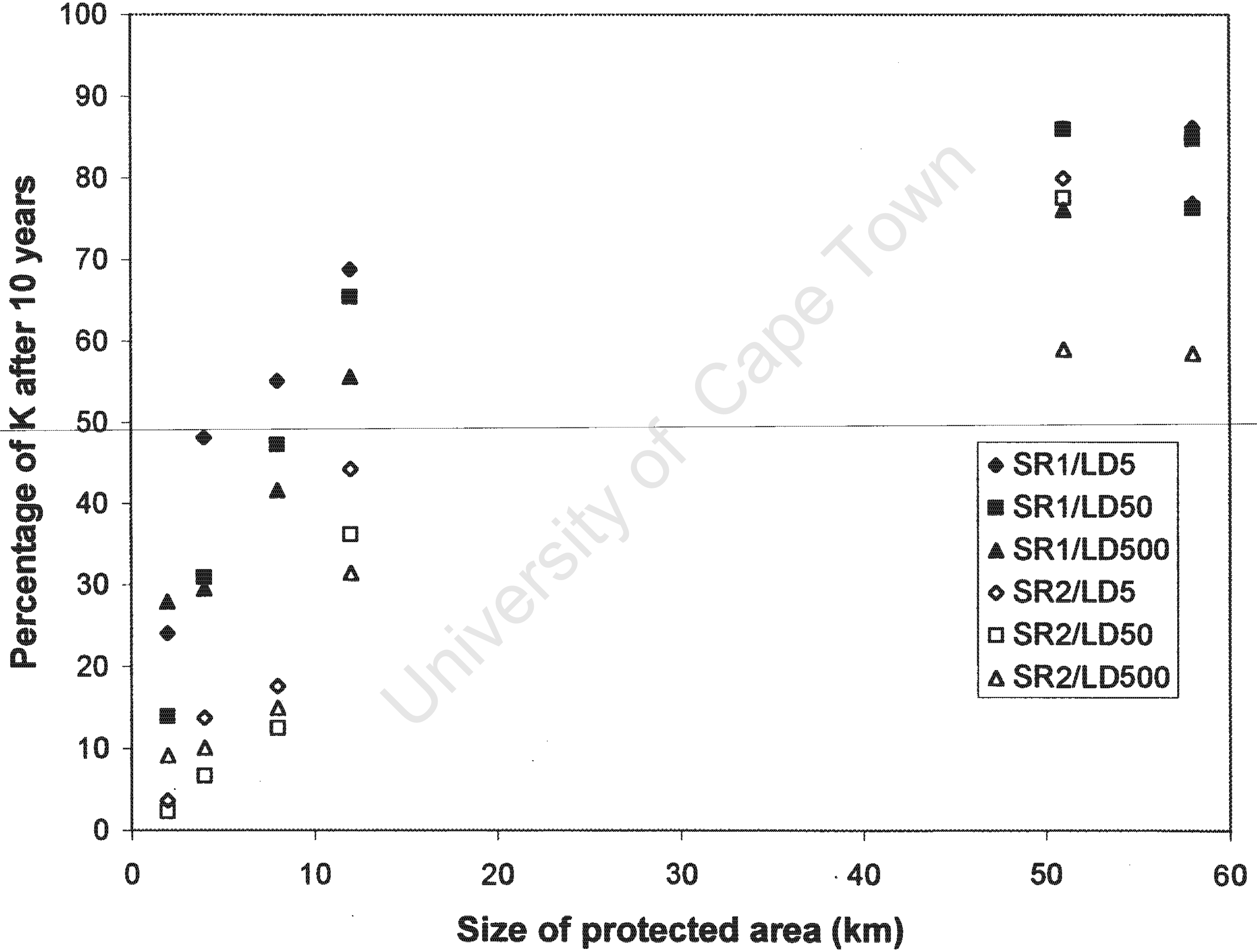


Figure 6.4. Effect of the size of a protected area on the recovery of galjoen after ten years in relation to the carrying capacity, for all combinations of productivity (SR1 and SR2) and larval dispersal (LD5, 50 and 500).

stochasticity). Hence, the trends in relative improvement with larval dispersal were highly variable for this and other small, heavily depleted MPAs.

The smaller Castle Rocks and St James MPAs saved galjoen from extirpation in these areas (Fig. 6.3). Relative improvements in density ranged up to 168 times (Table 6.3), despite their small area. These two MPAs were introduced in 1990 and only had ten years to show a recovery. For the less productive spawner-biomass-recruitment relationship, the absolute recovery was negligible, with insufficient recruitment from within or elsewhere to seed a recovery. The larger MPAs were to a great extent self-seeding, and did not experience this problem.

An exception to the general trend of suppressed recovery with increasing larval dispersal occurred in the St James MPA, which posted the highest recovery under maximum larval dispersal (Table 6.3). This anomaly is also evident from a comparison of plates 1-3 and 4-6. The intermediate larval dispersal resulted in the lowest recovery, whereas highly restricted and highly extensive dispersal resulted in more rapid recoveries. A likely explanation is that restricted dispersal resulted in a high-degree of self-seeding, whereas the extensive dispersal allowed seeding from a nearby MPA (Castle Rocks) or natural refuge. The intermediate dispersal achieved neither. Extensive larval dispersal effectively 'connected' St James to Castle Rocks (14 km apart) and Cape Peninsula (53 km away), thereby mutually increasing recruitment at both sites. The same effect is noticeable at Castle Rocks under the least productive spawner-biomass-recruitment function (Fig. 6.4), whereas under the more productive spawner-biomass-recruitment function the intermediate and highest larval dispersal produced almost identical results. The dependence on outside sources of recruitment was thus stronger with the least productive spawner-biomass-recruitment function.

The intermediate-sized Sardinia Bay MPA was also heavily depleted initially, but showed a recovery to between 12 and 55% of carrying capacity after ten years (Fig. 6.4). The recovery and relative improvement responded negatively to increased larval dispersal under the most productive spawner-biomass-recruitment function. Recoveries were slow with the least productive spawner-biomass-recruitment function (Fig. 6.3), but the extensive larval dispersal outperformed the intermediate case by a small margin (Fig. 6.4). Again, the likely explanation is the proximity of Tsitsikamma MPA, a strong source of recruitment, which would only just be 'connected' under the most extensive larval dispersal. The distance between Sardinia Bay and Tsitsikamma was 141 km and the larvae were dispersed on average 165 km in the most extensive dispersal scenario. As in the case of Castle Rocks, the fact that this effect was not evident under the more productive spawner-biomass-recruitment function was possibly because the population was less depleted and better able to seed itself, thereby being influenced less by outside contributions.

The purpose of illustrating subtle differences in the relative performance of MPAs under different degrees of larval dispersal is its potential relevance to fisheries that are heavily exploited, and in which MPAs (existing or planned) are typically small. It is clear that the reversal of the effect of larval dispersal in the presence of other MPAs only occurs when the stock is heavily depleted and for small MPAs (i.e. the bottom, left-hand corner of Fig. 6.4).

The recovery of galjoen after ten years was largely a function of the size of the MPA (Fig. 6.4). The variation attributed to the spawner-biomass-recruitment function and larval dispersal was small by comparison.

Density changes across protected areas

It may be more useful to look at recoveries spatially, rather than temporally, as this provides a result that can be compared to present-day sampling data. The temporal perspective requires measurements prior to the MPA being implemented, but these are rarely available, and predictions between 'protected' and 'unprotected' scenarios for the same area are not testable. Substantial improvements in densities in MPAs relative to those in the immediately adjacent areas were evident for all MPAs and for all larval dispersal scenarios (Fig. 6.5). The relative differences were greatest for the less productive spawner-biomass-recruitment function (not shown).

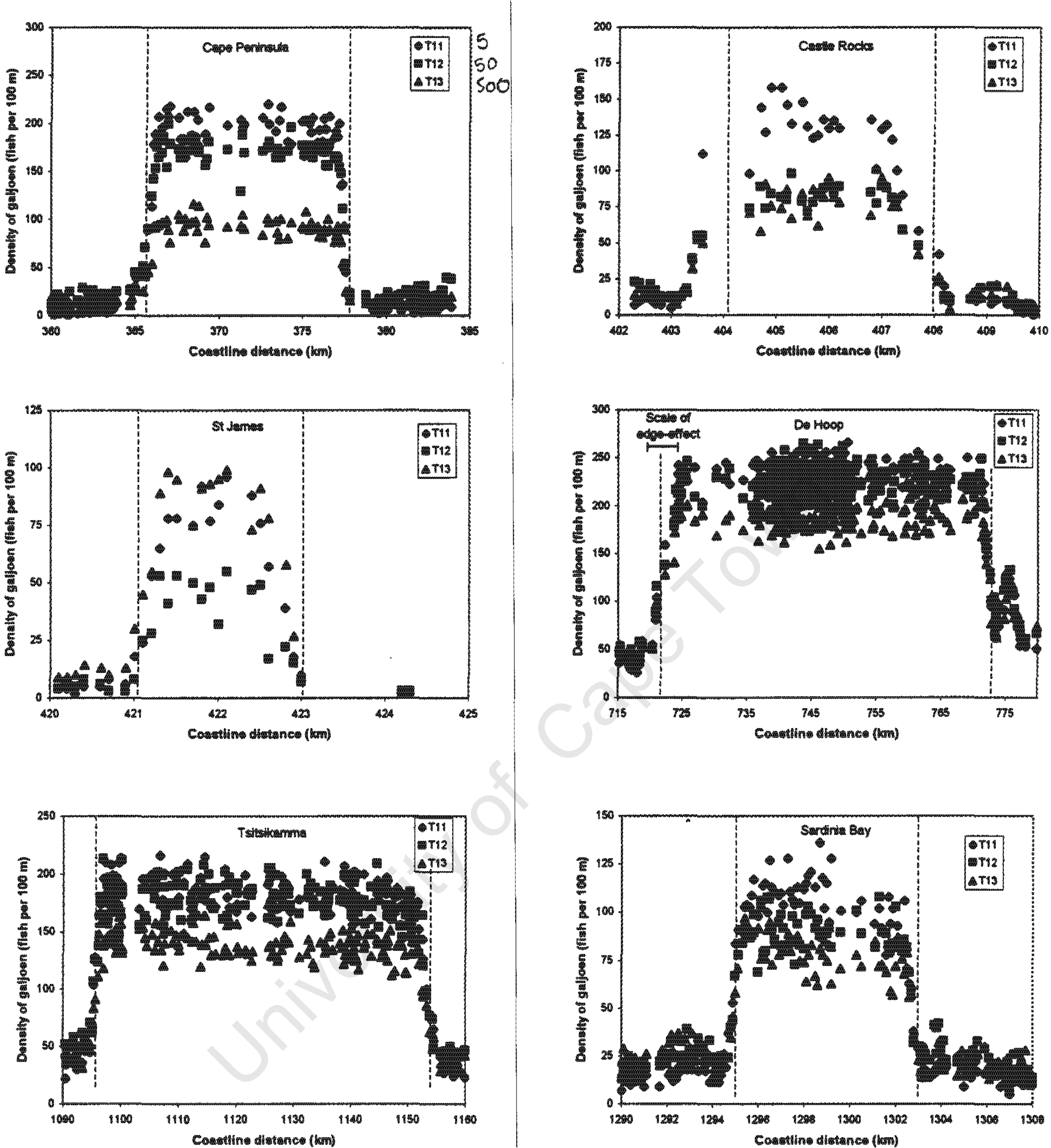
The abrupt change at the boundaries under all larval dispersal scenarios, shows that the 'edge-effects' are limited in extent. The transition from low to high density was completed within 5 km in the largest MPAs, which implies that the outermost 2.5 km of each MPA was affected by adjacent harvesting. The density profiles are more akin to the so-called 'bath-tub' curve (steep sides and flat on top) than to the 'dome-shaped' curve, with the exception of the two smallest MPAs. St James and Castle Rocks were not large enough to include home-ranges that were at least 2.5 km away from their boundaries, and hence the edge-effect dominated the entire MPAs.

Yield adjacent to protected areas

The intermediate larval dispersal model was used to investigate the effects of effort displacement from MPAs on local yield (Fig. 6.6). The improvements in yield were increased or decreased if larval dispersal was higher or lower, respectively, in accordance with the relative magnitude of effects shown in Table 6.2 .

In the Cape Peninsula area that encompassed Cape Peninsula, Castle Rocks and St James MPAs, the catch declined sharply from 1982 to 2000 due to over-exploitation, when the MPAs were not applied. With MPAs the catch dropped sharply twice, first due to the introduction of the Cape Peninsula MPA (1979), and then later because of the Castle Rocks and St James closures (1990). The decline, which started in 1982, was arrested by 1994, whereafter the MPAs resulted in a greater catch in the exploited zones than was achieved in the entire area without protection. By 2000, the trend suggested that the fishery would collapse locally without MPAs. The MPAs stabilised the catch at a level of approximately half the maximum yield that was achieved in 1982.

De Hoop was introduced at a time when the catch in that area was on the increase, due to increasing effort. Without the MPA, the catch peaked in 1991, whereafter it declined. The



5
50
500

Figure 6.5. Profiles of galjoen density across six marine protected areas. Results of the most productive stock-recruit relationship (SR1) are shown for three degrees of larval dispersal.

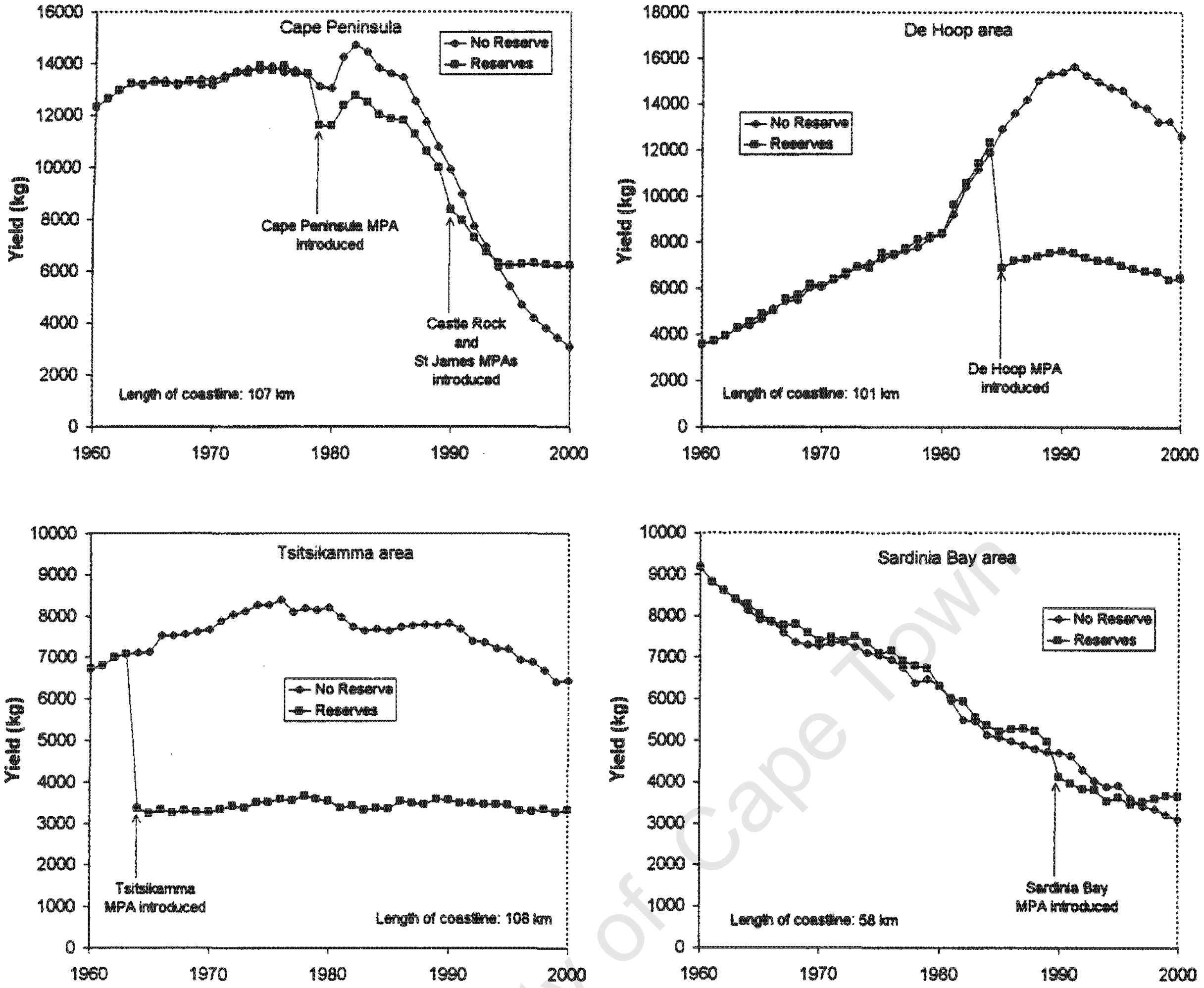


Figure 6.6. Annual yield in four areas that include MPAs, and in the same areas without protection. The first area included three MPAs. Only the results of model T/SR1/LD50 are shown.

MPA immediately dropped the local yield by almost 50%, whereafter it increased slightly up until 1990. This subsequent decline was slower than for the unprotected case. This large MPA reduced the catch substantially, although a linear extrapolation of the trends after 2000 suggests that the situation could reverse after two decades.

Had Tsitsikamma not been protected since 1964, catches would still have increased in that area for another 13 years as the effort increased. The decline thereafter was gradual. Compared to De Hoop, the rise in effort at Tsitskamma when unprotected was slower, and it was spread over a slightly larger area (Fig. 6.2), although it was still sufficient to cause a decline in yield after 1976. The MPA arrested the decline, albeit at a catch of approximately 40% of the maximum achieved without protection. However, the reduced catch was sustainable.

The catches at Sardinia Bay declined consistently over the period 1964 to 2000. The slight mismatch between the simulations prior to 1990, may be due partly to the excess effort that was displaced from the Tsitsikamma MPA in 1964 in the simulation with MPAs. The distance between these two MPAs is 141 km. The creation of the MPA at Sardinia Bay initially reduced the catch, but thereafter it stabilised and exceeded the catch of the unprotected scenario, which continued to decline. The model did not run for long enough to evaluate whether the catch rate would be sustainable.

DISCUSSION

The vast majority of reef-fishes in South Africa, including galjoen, are over-exploited, and their yields are declining (Penney *et al.* 1997, Griffiths 2000). The question posed by a study such as this should read: *Is a fishery likely to be sustainable if effort is restricted to certain areas?* What is being tested is the strategic concentration of fishing in certain zones, while reserving others. The investigation concerns not so much MPAs, but rather zonation. Zonation could be viewed as a new experiment in fishery management, one that offers an alternative to the '*limited catch, unlimited area*' approach. Some modelling studies have suggested that MPAs will need to cover more than half of the range of reef-fish to optimise long-term sustainable yields (Sladek Nowlis and Roberts 1999a, Walters 2000, Dahlgren and Sobel 2000, Mangel 2000a). Indeed, Walters (1998) is of the opinion that fishing should be the exception, and protection the rule. Most empirical studies have been based on relatively small MPAs, which are not likely to deliver the benefits that these models predict.

What should be measured?

In addition to their role as a means of conservation, the benefits of MPAs include their role in the management of fisheries. Hockey and Branch (1997) listed five that fall into this category:

- Protection of exploited species;
- Protection of spawning-stock;
- Protection of nursery areas;
- Improvement of yield in adjacent areas;
- Provision of undisturbed sites for research and base-line monitoring.

Fish abundance

Success at attaining the first three of these objectives can be measured in terms of fish abundance in the MPA. There are two instances when the trend in abundance may be indicative of success. The first of these occurs when it is specifically intended to recover a depleted stock, and, in the second, to arrest a sustained decline. In either case, an assessment within the MPA is required.

The objective of improving yield is more complicated as it involves an undisclosed time period. Usually one looks for sustainability, but for practical reasons a finite time-horizon must be chosen. In the spatial dimension, it may be more useful to consider catch over small areas that are meaningful to individual fishermen whose support or objections may have a strong bearing on the implementation of a MPA, rather than to consider the overall catch. This was the approach taken here when looking at areas that included a 25-km margin around MPAs.

The next problem is choosing a baseline for measurement. Does one literally interpret the yield objective and expect an increase? In the example of galjoen, which is typical of a fishery in the late stages of expansion, it is unrealistic to expect an increase in yield when (i) past catch rates were high but unsustainable and (ii) effort increased with no end sight. A more realistic interpretation of the objective might be to stabilise catch. Arguably, stability has become a more important criterion than absolute yield in defining the success of fishery management (Mangel 2000b). Here, the approach was to consider the yield and abundance objectives together. A practical criterion would be to maximise catch while leaving the final population size in a condition that is the same, or better, than some previous condition. Such a rule can be applied over short time-horizons, thereby avoiding uncertain extrapolations towards infinity.

Another way of evaluating the yield objective is by asking: *Do fishermen benefit?* This question is commonly asked, but it has to be phrased more specifically. Does one consider the individual fishermen (in which case CPUE is critical) or the entire fishing community (in which case total catch is relevant) or an economic indicator (which includes running costs and discounted value)? In this case, because total effort was kept constant between comparisons, the CPUE and total catch evaluations were effectively the same, but no attempt was made to consider socio-economic indicators. There is a massive cost associated with the displacement of effort. In an equilibrium situation, a zoned fishery may outperform one in which effort is applied homogeneously. However, the problems in implementing a zoned fishery stem from the transition from an unrestrained distribution of effort to a zoned distribution. The social and economic costs of relocating effort may take years to be recovered, and those that suffer the losses may not be the ones who later reap the benefits. The demonstration that a zoned fishery is more successful is therefore not always influential in decision-making. Although the valley on the other side of the mountain is known to be greener, the cost (political and economic) of getting there may be too high. This model looks at such a transition in simplistic terms of total population size and catch.

The final objective of MPAs should not be underplayed. MPAs can give important insights into the biology and ecology of fish and on the functioning of ecosystems undisturbed by human extractive activities: information that is vital for managing fisheries. The present study is a case in point, with many critical estimates having been derived from research into what was assumed to be pristine stocks. However, the model suggested that they were not in fact pristine.

Modelling approach

A wide variety of models has been used to test the performance of fisheries with MPAs and the effects of MPAs on fish abundance, each with its own objectives and limitations. These include conceptual models (Bohnsack and Ault 1996), logistic models (Quinn *et al.* 1993), per-recruit models (Polacheck 1990), statistical models (Edgar and Barrett 1999), stochastic models (Mangel 2000a), simulation models (Attwood and Bennett 1995), age-structured models (Holland and Brazee 1996), size-structured models (Sladek Nowlis and Roberts 1999a), metapopulation models (Man *et al.* 1995) and multi-species models (Pitcher *et al.* 2000). With the exception of a few statistical models, which were based directly on data that compared protected and unprotected areas, and one spatially-explicit model (Stockshausen *et al.* 2000), most of these have described fishery conditions in a static and symmetrical way. For example, many models assume homogeneous habitat (e.g. Attwood and Bennett 1995), almost all have a constant fishing mortality rate, and may lack a time dimension (e.g. Dahlgren and Sobel 2000) or even a spatial dimension (most of the analytical models). Sometimes these simplifications indicate a paucity of data, but often they are deliberate attempts to examine a particular effect (e.g. size or spacing) without complicating it with real variation. For statistical reasons, Ludwig (1995) argued that effective management models cannot be realistic!

The model used here aimed to mimic the real spatial structure as closely as possible. It reconstructed the effects of the haphazardly phased introduction of unplanned MPAs into a growing fishery. Although this model also made many simplifying assumptions (it is after all a model) and may be inaccurate in many respects, there is a 'real-life' component to it that most others have lacked, or deliberately omitted. The drawback is that the model combines processes, and their effects cannot be isolated clearly. The model does not provide a controlled environment for analyses, and it is not practical to consider a variety of alternative combinations of size or spacing, as has been done with simpler models. For this reason only two scenarios were considered: the existing situation (with MPAs) and a hypothetical, unmanaged fishery (without MPAs).

One advantage to including as much real variability as possible is that it discourages naïve projections. Most MPA models show substantial benefits in terms of yield (Guénette *et al.* 1998). The galjoen fishery shares characteristics with many of the reef-fisheries for which MPAs have been predicted to show an increase in yield, yet increases in galjoen yield were not always predicted. The reasons for the discrepancy include such real-life processes as:

- *Strong spatial variation in effort*. This may nullify some of the predictions based on symmetrical assumptions;
- *Temporal variation in effort*. In Africa the human population is growing fast. Effort increases must be considered;
- *Presence of natural refuges*. Some MPAs may have been naturally protected, such that additional legal protection produced a less-than-expected improvement. Because of its inaccessibility, Tsitsikamma was naturally protected to some extent;
- *Vast variation in the size of MPAs*. Rational planning has seldom played a strong role in conservation. In this case, some areas were very big, others very small, with nothing in the middle;
- *Reserves being declared in the most productive and least depleted part of the fishery*. Few fishery managers would be able to consider such an option realistically. The two large MPAs in question were not motivated on fishery terms; and
- *Transition from an un-managed fishery to one with MPAs at a time of peak production*. Few fishery managers would be able to consider such an option realistically, either.

Most of the models used to advocate the use of MPAs in a fishery seldom include these processes, and then certainly not all at once. An exception is the model of the Caribbean spiny rock lobster *Panulirus argus* developed by Stockshausen *et al.* (2000), which used realistic current patterns. They showed that the position of a MPA is as critical is its size.

The individual-based model with realistic spatial structure avoids obviously incorrect assumptions. These typically include:

- *Pooling recruitment across all areas.* This simplification produces unrealistic spatial uniformity and causes depleted areas to be replenished too rapidly;
- *Constant transfer rates for post-recruit fish between areas.* Whereas a fish may move from one area to another, constant transfer rates make it possible for fish to move consecutively across many areas, which is unlikely for bottom-associated species. Again, this error reduces spatial structure (e.g. Walters 2000);
- *Homogeneity across large areas.* Density gradients can be very sharp and natural refuges can play an important role. The dramatic impacts of new technology, such as fish-finders and the improved control of trawl nets over rocky ground, are testimony to the important role of natural refuges;
- *Treating the introduction of a MPA and the overall reduction of effort as synonymous in a dimensionless model* (e.g. Mangel 2000a). A MPA that includes 20% of the fishes' range has a very different effect to reducing fishing mortality by 20%.

Fish abundance

Most studies of reef-fish density across the boundaries of MPAs have found higher densities in the MPA (Halpern in press). Galjoen density has been demonstrated to have recovered in De Hoop MPA once it was protected (Bennett and Attwood 1991) and density in De Hoop and Cape Peninsula MPAs was greater than in the respective adjacent areas (Bennett and Attwood 1993, Naidoo and Verheye 2001). The model confirmed that such increases should have occurred in MPAs, except the smallest MPA under conditions of low productivity. However, no MPA was able to recover the density of galjoen within it to 100% of the carrying capacity, even under the most restricted scale of larval dispersal. If a 58-km MPA cannot achieve full recovery, then it must be conceded that full recovery will never be achieved practically. Parrish (1999) predicted that complete recovery of fish density would not be possible in MPAs.

The maximum density in the large MPA was 86% of carrying capacity (Table 6.3). Where did the losses occur? The 'bath-tub' curves (Fig. 6.5) predict that density will not peak in the centre of the large MPAs. The losses were therefore not entirely due to edge-effects. The fact that recovery was correlated with larval dispersal (Table 6.3) in large MPAs pointed to high larval dispersal as a substantial source of loss. Even the largest MPA did not harbour a 'closed' stock.

Under the most restrictive larval dispersal, the ceiling to recovery (86%) was set by adult migration (or home-range relocation). Apart from the losses at the edges, the data presented in previous chapters suggest that galjoen spend between 6 and 7% of their time at alternative sites (occupancy ratio = 15). The protection accorded by these MPAs would be reduced by this amount if there were heavy losses at the alternate sites. Even substantial increases in MPA size will not prevent these losses. Complete protection will only be achieved by containing adult movements, which according to the data presented in Chapter 2, would require at least a 1000-km MPA. Unlike the tropical fisheries modelled by Sladek Nowlis and Roberts (1999a), in this model adult galjoen movement covered vastly greater distances than the extent of larval dispersal. None of the three larval dispersal scales covered the entire range, which was an assumption based on local oceanographic patterns, and recent studies that suggest reef-fish larvae do not disperse widely and may be capable of positional control (Leis 1994, Botsford *et al.* 1998, Swearer *et al.* 1999, Warner *et al.* 2000, Stobutzki 2001).

In the interests of accuracy, the entire modelling exercise should be repeated, using an upwardly adjusted carrying capacity. In Chapter 3, the carrying capacity was estimated at the De Hoop sites and those estimates were used to set the carrying capacity in the model. The model now suggests that the density in the De Hoop MPA was below the real carrying capacity, perhaps by as much as 40% (Fig. 6.4). In other words, the model should be using a higher carrying capacity than what was measured at De Hoop. Such an adjustment should not affect the processes under discussion here, though absolute comparisons would be difficult. The same argument does not apply to the natural mortality estimate, which was also based on studies of the protected stocks, because a small correction was made for emigration (Chapter 3).

In De Hoop and Tsitsikamma density was not heavily depleted when these areas were introduced, and hence there was little scope for recovery. The success of these areas in terms of protection is best judged by the state the stock would have been in after 10 or 20 years without that protection. In both these cases, the model indicated a large difference. These MPAs simply maintained the status quo, or yielded slight improvements. Overall, the total density in 2000 was improved by between 20 and 44% (relative to the unprotected scenario) by the six MPAs that were implemented, and most of this improvement could be attributed to the two biggest areas.

With the exception of the smallest MPAs under conditions of low productivity, the remaining MPAs showed partial recoveries of galjoen density in the time available. In all cases, density would have declined, sometimes to very low levels, had that protection not been in place.

Size of protected area

An interesting dichotomy has emerged between empirical and theoretical studies of MPA design for fisheries. Modellers predict that, where fishing mortality is far above the optimal sustainable rate, in excess of 50% of the range should be protected for optimal fishery performance (e.g. Sladek Nowlis and Roberts 1999a, Mangel 2000a). Those models that take the actual size of the MPA into account suggest that the MPA should be large (e.g. Walters 2000). On the other hand, field biologists have shown that incredibly small (< 1 km) MPAs can effectively increase biomass (e.g. Russ and Alcala 1996a, Roberts and Hawkins 1997). Halpern (2000) found that, on average, 71 studies of fish showed increased density, biomass, size and diversity in MPAs, irrespective of the size of the MPA. Some of these MPAs were smaller than 0.1 km^2. Taken together these results can be confusing.

Halpern's (in press) results may be misleading because the study looked at improvements relative to an unprotected situation, and not in relation to maximum carrying capacity. The 168-fold improvement at St James belied the fact that density recovered to only 24% of what it was historically (Table 6.3, Fig. 6.5). It would be incorrect to regard this MPA as effective for galjoen, and its small size is the main reason for this.

Therefore, an important issue that emerged from the model was the appropriate standard for evaluating MPA effectiveness. A ten-fold improvement of density in a MPA may not be impressive if the historical density (or carrying capacity) was 50-fold greater. For galjoen, protecting a minimum area of 8 km was needed to recover density to more than 50% of the carrying capacity but, depending on productivity and larval dispersal, a much larger area may be needed to achieve this level of recovery (Fig. 6.4). The density in the large De Hoop and Tsitsikamma MPAs recovered to in excess of 50% under all the scenarios considered, but in those MPAs smaller than 10 km density usually did not attain this target.

how much is
caught + how
much left in
see
= carrying
capacity

The trouble with the 'carrying capacity' measure for field studies is that there is no real reason to think that it exists (Wolda 1989), and it is difficult to determine. Dahlgren and Sobel (2000), for example, developed a model to estimate the optimal size of MPAs, which required an estimate of unexploited stock size. For most of the species they considered, they had to estimate these values from 'accepted guidelines and theoretical models'. The scarcity of appropriate empirical data undermines efforts to develop such methods.

The strong effect of the size of an MPA (Fig. 6.4) is primarily due to the scale of home-range size. The simple model developed by Kramer and Chapman (1999) predicted this effect. A 'protected' fish that lives within a home-range length of the border will be susceptible to capture, although less frequently than one living well outside a MPA.

Based on tag–recovery data, the model used a home-range size distribution that had an average of 770 m and a maximum of 3.3 km (Chapter 5).

An abrupt change in density across MPA boundaries is expected for a resident fish species that is susceptible to a fishery (Ratikin and Kramer 1996, Kramer and Chapman 1999). Kramer and Chapman (1999) studied the changes in fish parameters across the boundary of the Barbados Marine Reserve (size 2.2 km). They found slight differences in density and stronger differences in mean size that were consistent with the fishing effect. These differences were not the result of settlement, which was actually greater in the fished area. Their result is not dissimilar to the predicted profile of galjoen density across the small St James MPA (2 km), which clearly succumbed to an edge-effect (Fig. 6.5).

Willis *et al.* (2000) assessed the density of snapper *Pagrus auratus* at ten sites across a MPA of 5 km length, such that two sites were outside the protected area at either end, and six were in the MPA. The profiles of density were distinctly dome-shaped, peaking in the centre of the MPA, with an edge-effect possibly as large as 5 km. Parsons *et al.* (2002) estimated by telemetry that the home-range size of *P. auratus* did not exceed 540 m, which they noted was too small to explain the edge-effect. They explained the discrepancy as being due to home-range shifts, as was observed with one fish that shifted the centre of its home-range by 300 m over the course of a few months. The same explanation was used in Chapter 2 to explain why the home-ranges calculated for galjoen from tag and recapture data were larger than predicted from short-term observations on similar-size tropical fish.

For galjoen it was predicted that the change in density across a boundary would be complete within 5 km, irrespective of the extent of larval dispersal, which was varied over two orders of magnitude. A MPA should be larger than this length so as to keep some fish from straying across the boundaries during their daily movements.

For galjoen, the reserve 'edge-effect' is not due to migration. Post-recruit galjoen do migrate, by abandoning their home-range, but because such migrations involve large distances and are direct (i.e. overlooking resources on the way), they will not contribute to an edge-effect in a line-fishery (by contrast, gill-nets may show an edge effect). Spill-over (Russ and Alcala 1996b, Jennings 2001) of galjoen is spread so widely that its impact, although potentially substantial, will not be detected spatially.

Alcala and Russ (1990) and Russ and Alcala (1996b) found evidence for enhanced catches near the boundary of a MPA, and suggested that migration of adult fish from the MPA was the mechanism behind the enhancement. Alcala and Russ (1990) acknowledged that there was no evidence for such migrations among tropical reef-fish. What would appear to be more likely is that the enhanced catches were due to an edge-effect caused by large home-range sizes (relative to the size of the MPA, which was smaller than 1 km in length), or even infrequent home-range shifts.

It is evident therefore, that spill-over can occur at two scales, one that is very localised (consistent with within home-range movements) and another that is very wide (consistent with migration). The latter will be more important as the reserve size increases. Most of the field studies to date have been on very small reserves, for which the 'home-range' spill-over would dominate. MPAs feed adjacent areas through the migration of adults, larval dispersal and movement within a home-range. Field studies have often detected the latter, but this is likely to be the least significant of the three, especially for large MPAs.

Yield

The introduction of MPAs in a fishery can be viewed either as a *pro rata* reduction in fishing mortality effected spatially, or as a means of effort displacement. It seems to be a matter of choice among modellers. The real situation in the galjoen fishery is probably somewhere between these extremes. Recreational anglers are not compelled to fish in the same way that commercial fishermen are, and a large MPA may well reduce the effort of those recreational anglers that reside adjacent to it. In the case of Tsitsikamma, this almost certainly happened. Land at De Hoop was expropriated, and residents were forced to reside elsewhere and some of those might not have fished again. In recent years, however, with the improvement of road access and the popularity of off-road vehicles, it is difficult to imagine that a MPA, particularly a small one, would affect an angler's participation in the fishery. Most anglers operate over large areas. On balance therefore, it is probably correct to assume that all effort is displaced and that none is lost (for a similar point of view read Crowder *et al.* 2000). Moreover, when comparing protected and unprotected scenarios, it is essential to take this point of view. Although in reality they may be mixed, the effects of reducing and displacing effort must be separated in an investigation into fishery dynamics. Effort displacement is the most frequent counter-argument to any projection that suggests a MPA might be beneficial, either in terms of yield or protection.

Overall it does not appear that the six MPAs had a huge effect on the total yield in year 2000 and the direction of the effect was either up or down. The cumulative catch up to 2000 would almost certainly have been depressed by the MPAs, as the result of the immediate losses of fishing grounds, prior to the build-up of additional stock. This effect has been explored by Sladek Nowlis and Roberts (1997b), who found that a phased introduction of MPAs reduced the extent of the initial losses. Later such losses were reversed by substantial gains in yield. Immediately after Tsitsikamma and De Hoop, the yield losses in the galjoen fishery must have been large.

Tsitsikamma and De Hoop are large MPAs that were introduced when catches in those areas were increasing (Fig. 6.6). If the galjoen fishery was the only consideration, were these MPAs introduced too early? No model predicts that MPAs will improve yield unless the fishery has been over-exploited (Rodwell and Roberts 2000, NRC 2001). At Tsitsikamma and De Hoop, however, the catch rate was too high to be sustained and a decline was inevitable, as predicted in the situation without protection. Between the time when these MPAs were introduced (1964 for Tsitsikamma and 1985 for De Hoop) and the time when the respective maximum yields were attained without protection (1976 and 1991 respectively) the density in these areas would have declined by approximately one-third (Fig. 6.3) and effort increased by a further 15% (Fig. 4.6). The MPAs immediately reduced the annual catch by approximately half within an area extending 25 km on either side of the MPAs. Delaying protection would have substantially compromised the ability of the stock to recover. The MPAs stabilised the catch, and left the stock in a better condition by 2000. The benefits of these large areas in terms of yield are projected to occur much later, at a time when the fishery would otherwise have been in a severely depleted state, but resource-protection benefits started almost immediately.

The smaller MPAs at Cape Town and Port Elizabeth were introduced later in heavily exploited areas. They were able to arrest a decline in yield in an area that extended 25 km past their boundaries. In terms of short-term yield alone, these MPAs were a success. It took some time to arrest the decline in the Cape Peninsula area, which was the most heavily exploited area of all, and it required three MPAs within the space of 100 km.

Connectivity

An unsuspected result, though minor in magnitude, pointed to an important process that has often been alluded to by those who advocate the use of MPAs (Ballantine 1996, Roberts 1997b). In theory, *connectivity* will be an important process that should define the zonation structure, but it has only been described in terms of conceptual models explicitly developed to demonstrate its importance. This model showed that the dynamics in a MPA are affected by the presence of another MPA, and that the usual inverse relationship between protection and larval dispersal does not hold when the stock is heavily depleted and reserves are tiny. In this respect, the lack of information on larval dispersal is a critical obstacle for planning an effective zonation system (Stockshausen *et al.* 2000, Stobutzki 2001).

'Open' MPAs will obviously offer less protection than one that is 'closed' (Stobutzki 2001), but for a MPA to be entirely self-seeding is not always an advantage, particularly if it begins with low densities, or if the densities fall dangerously low due to a catastrophic or natural event.

Position (hotspots, sources and sinks)

A popular line of argument is that MPAs should be sited at 'hot-spots', while fishing should proceed in 'marginal' areas, where the damage to the productivity of the stock will be limited (Jennings 2001). This concept is based on the 'ideal free distribution' (IFD), as applied by MacCall (1990) to fisheries, and by Kramer and Chapman (1999) to MPAs (Chapter 1).

Hot spots can be viewed in two ways. In terms of the IFD, a hot spot is an area of *better* habitat, and an area to which fish will move when the population declines. Alternatively, it can be an area with a high density of *suitable* habitat, an area that holds more fish because there is more *suitable* habitat. The subtleties in the words *better* and *suitable* are significant. According to the IFD, fish will preferentially seek certain areas, which will always be fully occupied. They will retreat to marginal areas only when competition at the preferred sites makes the marginal areas more profitable.

Crowder *et al.* (2000) followed essentially the same argument, when they based their source-sink model on Pulliam's (1988) BIDE (birth, immigration, death, emigration) model. Because of varying habitat quality, fish in certain areas were more productive, and those areas produced an excess of larvae, some of which helped to seed stocks in sink areas, which on their own were not sustainable. It follows that the source areas must be protected. Their model hinged on habitat *quality*.

On a local scale, the galjoen model has taken an alternative approach, which assumes that habitat quality can be measured as the frequency of *suitable* habitat. Two areas will differ in carrying capacity, not because the reefs are *better* in one than the other, but rather because it has more suitable reef. In practical terms, this is how habitat quality would be measured. The model was split so finely (100-m cells) that it was possible to take this approach. The home-range model (Chapter 5) assumed that fish adjust their home-range size to ensure that it includes sufficient suitable reef. As a result, all fish were equally productive (fecund), but their density varied between areas. Obviously if home-ranges were of a constant size among areas of varying density of correct habitat, then some fish would have been more productive than others.

It follows that the areas of high carrying capacity did not *attract* fish from elsewhere when the population declined. For reasons discussed in Chapter 2, the IFD does not apply to galjoen. Fish in hotspots were as prone to depletion as those in marginal areas. However, it is correct that a hotspot will produce more larvae than an equivalent sized area with less suitable habitat. This model, which was based on a survey of habitat type, showed that the existing MPAs included a higher proportion of galjoen habitat than exploited areas (Table I). In a sense, therefore, MPAs were located in hot-spots and their impact must have been larger than would have been predicted on the basis of absolute size alone.

Because galjoen adjust their home-range size to match the density of habitat, the length scale of edge-effects will be smaller for MPAs in hot-spots. MPAs for galjoen should be located in hot-spots, but the benefits of doing so will not be as strong as predicted by the IFD.

On a larger scale, there were changes in carrying capacity, which were reflected in the spawner-biomas-recruitment parameters (Chapter 4). Carrying capacity peaked in the centre. The reasons for this change had less to do with reef 'quality' than with water temperature, currents and biogeography, which would affect the success of spawning, hatching and recruiting. Again, the MPAs were situated near the centre of the range, which was also beneficial.

What about the possibility of certain areas being preferred sources of recruitment, by virtue of current patterns and distinct spawning sites? Roberts (1998) explained the logic of identifying and protecting sources of recruitment. Many fish species fit the so-called triangle model, which has separate areas for spawning, recruiting and feeding (Chapter 1). Galjoen spawn and recruit throughout their range. However, it is true that some areas are known for producing big fish, while others produce immature fish. Indeed, galjoen anglers occasionally refer to a reef as a 'nursery', and avoid such places. The scale of this variation is very small and may simply be a reflection of micro-habitat preferences imposed by body-size. It is also possible that galjoen have preferred sites for spawning, but again these choices are probably made at the micro-scale level. An example of this is the bluehead wrasse *Thalassoma bifasciatum,* which undertakes a daily spawning 'migration' to the outer edge of a coral reef (Tecumseh *et al.* 1990). The important implication of this uncertainty is to err on the side of larger MPAs, which should encompass all micro-scale habitats used during the life-cycle.

Testing model predictions

The individual-based model is not easily fitted to data, because it takes too long to execute (Chapter 4). Comparing most of the model predictions to data is also not particularly helpful, because of the huge uncertainty brought about by ignorance of recruitment productivity and larval dispersal.

Nonetheless, two data sets are available for comparison. CPUE data collected simultaneously at the 12-km Cape Point MPA and in the two 12-km areas immediately adjacent to it during the period 1999-2001 (Naidoo and Verheye 2001) should mirror the profile shown in Fig. 6.5. These data show significant differences in CPUE, with the MPA CPUE being 1.5 and 1.9 times greater than the CPUE outside the MPA on the southern and northern sides respectively. Qualitatively, the comparison is good, but the difference is not as great as predicted (Fig. 6.5). On the other hand the CPUE at Koppie Alleen in De Hoop improved four-fold in the 2.5 years following closure in 1985 (Bennett and Attwood 1991). This difference was larger than predicted (Fig. 6.3). Koppie Alleen was much more heavily exploited than other areas in De Hoop prior to 1984, because it was one of the few areas that had public road access. This model could not account for such anomalies. A quantitative comparison is therefore not meaningful, but again it is qualitatively correct.

Predictions that should be amenable to testing include the length scale of edge-effects and the qualitative trends of population density in MPAs and of yield adjacent to it, relative to MPA size. Some of these predictions were robust to uncertainty in recruitment productivity and larval dispersal, and are important results for fishery managers. Future monitoring (of effort and CPUE or fish size) should be accurately geo-referenced.

CONCLUSION

It has to be asked how useful investigations such as this are to conservation-planners. Decision-making processes have a poor record of assimilating scientific advice. MPAs in South Africa were usually guided by considerations that had little to do with fisheries, a situation that is prevalent everywhere (Roberts 1998, Simberloff 2000). The situation is made worse by large margins of uncertainty in results. Furthermore, galjoen is one of several sympatric fishes exploited in the surf-zone, some of which are more depleted than galjoen. The results obtained for galjoen cannot be expected to hold for species with vastly different characteristics.

A more positive viewpoint is that the fishing community is now more likely to embrace MPAs than before, as it has become clear that past practices have not been sustainable, and that fishery agencies are unable to police bag and size limits. The model has clarified the importance of spatial processes, and does give clear guidance for zoning the fishery.

This model included three fish-movement processes: larval dispersal, home-range shuffle and home-range relocation. The minimum effective size of the MPA depended on the home-range size, whereas the extent of recovery in the MPA depended on the extent of larval dispersal and the frequency of home-range relocation. The most important contribution of this study is the identification of a minimum effective size (~5 km). Whereas others have demonstrated that much smaller MPAs can result in recoveries (Roberts and Hawkins [1997] provides an extreme case), this model suggests that for galjoen the absolute recoveries in small MPAs will be severely limited, and that their impacts on the fishery will be insignificant unless they are linked to several other MPAs in close proximity.

As a summary of the development of the galjoen fishery, the model suggests that the introduction of the MPAs was a positive development. Although the catch in 2000 was probably not affected overall, the conservation status of the stock was substantially improved. Hence, the prospect of a sustainable fishery is now greater. The cost of this improvement was an initial drop in catches, which must have been substantial on a local scale. As others have demonstrated, whereas a system of zonation is optimal for heavily subscribed fisheries, the transition from an unmanaged fishery to one with MPAs is troublesome for a manager. For this reason, protection of smaller areas with heavily depleted stocks will probably find greatest acceptance. Such a policy may run counter to other objectives, which may seek to protect pristine environments. Ultimately the choice is not a scientific one.

Even with 8.8% of galjoen's habitat under protection from fishing, the total catch is probably still declining because effort is increasing. The fishery must be managed more effectively. Appropriate bag and size limits, if properly enforced and coupled with MPAs, should arrest the decline.

CHAPTER 7

EVALUATION OF ASSESSMENT STRATEGIES FOR THE GALJOEN FISHERY

ABSTRACT

The galjoen *Dichistius capensis*, which forms part of the multi-species linefishery, has been poorly managed in South Africa. A spatially-structured, individual-based model was used to compare the reliability and practicality of spawner-biomass-per-recruit (SB/R) and CPUE indices as assessment tools in the galjoen fishery. Other assessment methods were not deemed practical or economically viable. Catch-at-age data severely under-estimated the mortality-rate, because of (i) progressive recruitment failure, (ii) increasing fishing effort, (iii) adult fish movement between areas of high and low effort, and (iv) systematic sampling error. Because of the long-term trend in recruitment, SB/R, even when based on accurate mortality-rate estimates, could not provide a meaningful index of the state of the stock. The relative state of the stock could be approximated by regressing CPUE against effort or by measuring CPUE in exploited areas and large marine protected areas (MPAs). Although both CPUE methods were also biased, the first could be corrected by applying a model suited to a fishery that is not in equilibrium, whereas bias in the second could be avoided by comparing CPUE between similar habitats only. For a declining stock, such as galjoen, CPUE provides a better means of assessing stock size than SB/R, and it should be cheaper and faster to collect the data for CPUE analyses than for SB/R.

State of the stocks
fishery dependant CPUE CAL
independant survey

INTRODUCTION

Compared to other South African fisheries, the management of the multi-species linefishery has fared badly (Payne 2000). Galjoen are classed as a recreational (as opposed to commercial) linefish species, but the signs suggest that its fishery is presently not sustainable. The spawner-biomass-per-recruit (SB/R) index was found to be far below acceptable thresholds (Bennett 1988) and the model developed in Chapter 4 suggested that catches have been declining since 1990.

Several methods are used to assess South African fisheries. Overall, there is a similar reliance on fishery-dependent (catch-per-unit-effort, catch-at-size) and fishery-independent (survey) data, but not all fisheries use both types (Table 7.1). The linefishery is the only major South African fishery that is not assessed regularly. Indeed, for almost all species in the linefishery, only a single assessment has been done, sometimes drawing on data that covered more than one year. There are several possible reasons for this poor record:

Table 7.1: Data and models used to assess the abundance of South African marine species. '1' indicates the primary data source, '2' the secondary. CPUE=catch-per-unit-effort, C@size=catch-at-size, PM=production model, ASPM=age-structured production model, SSPM= size-structured production model, IA=integrated analysis, VPA=virtual population analysis, SB/R= spawner-biomass-per-recruit, AC=aerial census.

Species	Data type				Model
	CPUE	C@size	Recruit Survey	Biomass Survey	
Hake, Kingklip	1			2	ASPM
Sole	2	1		2	VPA
Horse mackerel	2	2		1	ASPM
Tuna	1	2			VPA + ASPM
Small pelagics		1	1	1	IA
Linefish		1			SB/R
Abalone	1	2		2	SSPM
South coast rock lobster	1				SSPM
West coast rock lobster	1			2	SSPM
Squid	1			2	PM
Kelp, Seals, Sea birds				1	AC

- The cost of assessment is large relative to the value of the fishery. Because there are so many species that contribute to a modest fishery, no one species will warrant the expense of the management strategies used on the valuable pelagic and demersal stocks.
- The fishery is disaggregated. Catches are channelled through hundreds (in the case of the boat-based fishery) or thousands (in the case of the shore-based fishery) of access points in very small quantities. Obtaining sizeable samples of the catch is thus not feasible economically.
- The effort in the linefishery cannot be separated on a species basis, although targeting definitely occurs.

To date, the linefishery has relied almost entirely on SB/R as an assessment method, but this index provides only a relative measure of the spawning potential of the average recruit at the prevailing rates of mortality. SB/R depends on accurate estimates of the mortality-rate. Typically, catch-at-size data are converted to catch-at-age data, from which the mortality estimates are made. By this method, the component of total mortality attributable to fishing is calculated by subtracting the natural mortality component, but deriving an estimate of natural mortality has always been problematic. The method in Chapter 3 was to use a marine protected area (MPA) to estimate the natural mortality-rate. This approach has never been taken before in South Africa, but it has been used in Namibia (Beyer *et al.* 1999). Butterworth *et al.* (1989) suggested the use of multi-species regressions of natural mortality vs body size, age at maturity or ambient sea temperature as a predictor. These methods are not ideal, because of inconsistencies in the individual species assessments that provided the data for the regressions, and the low precision of the regressions.

AL - CAA - SB/R
mortality
Total mort - SB/R
= M - F

use MPA to
get natural
mort rate

Other routinely used models (Table 7.1) have not been used to assess linefish species because of the difficulty of meeting the data requirements. Although catch-per-unit-effort (CPUE) data have been available for the linefishery, their poor quality has limited their usefulness for assessments up until now (Penney *et al.* 1997). A new monitoring programme is presently being implemented for the fishery, including an observer programme, which should result in vastly improved data quality. Therefore, the opportunity exists to consider assessment procedures based on CPUE.

Fishery-independent surveys of biomass or recruitment remain an unrealistic option for the linefishery. The patchy distribution of linefish, coupled with the complexity of their habitat, prevents direct assessments of biomass or recruitment in most cases. The only fishery-independent data that could prove useful, and feasible to collect, is CPUE within MPAs, where the fishery is excluded. The tag-recovery method described in chapter 3 is also not a realistic option for general application to linefish, given the lengthy time required to get an assessment, interference by the fishery, the cost of tags and the possible impact of the tag on the fish. There is great resistance to using tags on penguins, for example, because of the negative physiological effect on the birds, which may further endanger their status (Jackson and Wilson, in press). Galjoen suffer from reduced growth when tagged and their reproduction may also be affected (Attwood and Swart 2000).

These constraints therefore severely limit the choice of assessment models. Models that are fitted to time-series of abundance indices require annual monitoring going back several years. Virtual population analysis requires a relatively short series of size-(convertible to age) structured catch-data (as many consecutive years as there are cohorts), but it needs additional information in the form of fishing mortality-rates or absolute cohort strength for the terminal year. These requirements almost certainly preclude its use in the linefishery, although an attempt was made to use it for elf (*Pomatomus saltatrix*) with crude assumptions (Butterworth *et al.* 1989).

The options for the linefishery narrow down to SB/R (with additional information on natural mortality-rate), and CPUE as a relative index of abundance (with additional information on pre-exploitation abundance). Yield-per-recruit (Y/R) indices measure the life-time contribution of the average recruit to fishery yield under the prevailing mortality-rate. Y/R may form the basis of management strategies, such as $F_{0.1}$ (Pauly 1984), but it is not a stock-assessment method, because it provides no information on the size of the stock.

In this chapter a spatially-structured, individual-based model of the fishery is used to investigate the reliability and practicality of SB/R and CPUE indices as assessment tools in the galjoen fishery.

METHODS

SB/R = Beverton & H
Mort rates = VonBert

The reliability of indices of stock size was investigated by using a spatially-structured, individual-based model of the galjoen fishery (described in Chapters 4 and 5). The model represented the growth of the galjoen fishery in South Africa during the twentieth century, and included realistic spatial variations in habitat and effort, including six MPAs. The model represented the 'true' situation. The indices were calculated from the catch-data generated by the model and then compared to the 'true' situation.

Spawner-biomass-per-recruit (SB/R)

Total - M

SB/R → Mort rate → CAA → CAL

Before the SB/R index was calculated it was necessary to estimate the mortality-rate. By estimating the mortality-rate directly from the entire catch-at-age output from the model, a short-cut was taken, which avoided several steps that may have biased the estimate in reality. For example, it is typical that sub-samples of catch-at-size would be taken, which would introduce a degree of random sampling error, and further errors when translating from size to age. Additional systematic errors would be introduced if samples do not represent the entire range over which fishing takes place, as not all areas are exploited at the same rate. The SB/R method depends critically on estimates of the fishing mortality-rate, which is derived from catch-at-age data with additional information on the natural mortality-rate. The model assessments used the precise natural mortality-rate, but in reality there would be great uncertainty about this estimate too.

Another convenience provided by the model's catch-at-age data, was that the ages of fish were known with an accuracy of one week. This permitted estimating the total mortality-rate as the inverse of the average time that each fish lived beyond the age of full recruitment (age 5). This method is precise, but in practice it would rarely be used because of the large uncertainties in the ageing of galjoen. In practice, statistical approximations based on age-data with a one-year resolution, derived from age-length keys, have been used. Two such methods include calculating the slope of the descending limb of the catch curve and Chapman and Robson (1960) approximation (Butterworth *et al.* 1989). The Chapman and Robson approximation was found to yield identical answers to the 'inverse' method used here, whereas the 'slope' method performed badly for high total mortality-rates.

In the model, natural mortality-rates were subtracted from total mortality-rates to give fishing mortality-rates. The natural mortality-rate of galjoen was estimated at 0.4 y^{-1} from the catch-at-age-distribution at De Hoop MPA (Chapter 3). The SB/R index was calculated using the Beverton and Holt equations (Butterworth *et al.* 1989), which use natural and fishing mortality-rates and Von Bertalanffy growth parameters (Bennett 1988).

Catch per unit effort (CPUE)

The CPUE calculations avoided random sampling error by using the entire catch-data set, a luxury that would never be possible in practice. Systematic sampling error was minimised by calculating the ratio of the annual catch and effort for each individual spatial cell (including those in which galjoen did not occur, but in which fishing did occur), and then comparing the average ratio to the population size. Averaging over all cells (as opposed to only active cells) ensured that total effort was considered, as in practice there could be no differentiation between effort directed at galjoen and effort directed at other species. If this strategy was not followed, then a systematic sampling bias could be expected, as the estimate would be weighted by the most productive areas. Those cells that were not fished did not contribute to the average CPUE, which was an unavoidable source of bias.

The population size in the middle of each year was used for comparison, because the end-of-year population size was always substantially smaller than that at the start, and CPUE was calculated from catch-data generated throughout the year. To further mimic reality, it was assumed that only a short time-series was available, beginning when the fishery was already at an advanced stage, without any data covering the initial years.

Part of the investigation into CPUE made use of CPUE data generated in a MPA, to serve as a reference for the unexploited stock size in 2000. To simulate the collection of CPUE data in a MPA, the experimental fishing programme described and modelled in Chapter 5, was repeated at both research sites (Koppie Alleen and Lekkerwater), which are each 3.4-km in length. Experimental fishing occurred during three, equally-spaced weeks at each site in 2000. CPUE was calculated at these sites as the ratio of catch and effort over all cells in which effort was applied, including those in which galjoen did not occur. Therefore, similar biases in the CPUE data potentially applied in the MPA as elsewhere, with the exception of sampling error. Because the two research sites were small, there was a good chance that they were not representative of the habitat found elsewhere in exploited areas.

Sensitivity

Six model variations were considered. Two stock-recruit relationships, with maximum reproductive rates, as defined by Myers *et al.* (1999), of 5.4 (model SR1) and 2.4 (model SR2) were combined with three levels of larval dispersal: 1.7, 16.5 and 165 km. Only the tourist-movement model was used, as this was found to provide the best approximation of the tag and recovery data (Chapter 5). No variations in effort were considered.

RESULTS

Spawner-biomass-per-recruit (SB/R)

Even after circumventing the biases associated with sampling and data conversion that would be faced in reality, catch-at-age data over-estimated the fishing mortality rate in the early stages and then subsequently under-estimated the fishing mortality-rate used in the model (Fig. 7.1). By 2000, the under-estimate was in the order of 50%, and was greatest for the less productive spawner-biomass-recruitment function. The estimation of total mortality from catch-at-age data was thus asymptotically biased.

The initial over-estimation was caused by catch-data coming from only the small part of the range where fishing occurred, i.e. the absence of data from un-fished areas positively skewed the estimate. In later years, as effort spread more widely, this effect was swamped by four processes that greatly under-estimated the fishing mortality-rate:

(i) Progressive recruitment failure resulted in successive year-classes being weaker than those before. It was possible to calculate the minimum extent of the bias, knowing the spawner-biomass-recruitment function and the extent of the depletion of the stock. By 1990, the spawning-stock had been depleted to approximately 18% and 15% of carrying capacity for the productive and unproductive spawner-biomass-recruitment functions respectively, and at that time the spawning stock was being reduced at a rate of approximately 1% of carrying capacity per annum (Fig. 7.2). At this level of spawner-biomass and rate of depletion, recruitment declined by respectively 2.3% and 3.7% per annum on average across all areas (Fig. 7.2). In exploited areas, where catch-at-size data originated, the rates of decline were higher than the average rate, and therefore the bias was greater than this simple calculation suggests. The result of this progressive failure is that successive year-classes were weakened by these extents, and hence mortality was under-estimated. The faster the rate of decline in recruitment, the greater the discrepancy, which implies that higher fishing mortality-rates will be under-estimated to a greater extent.

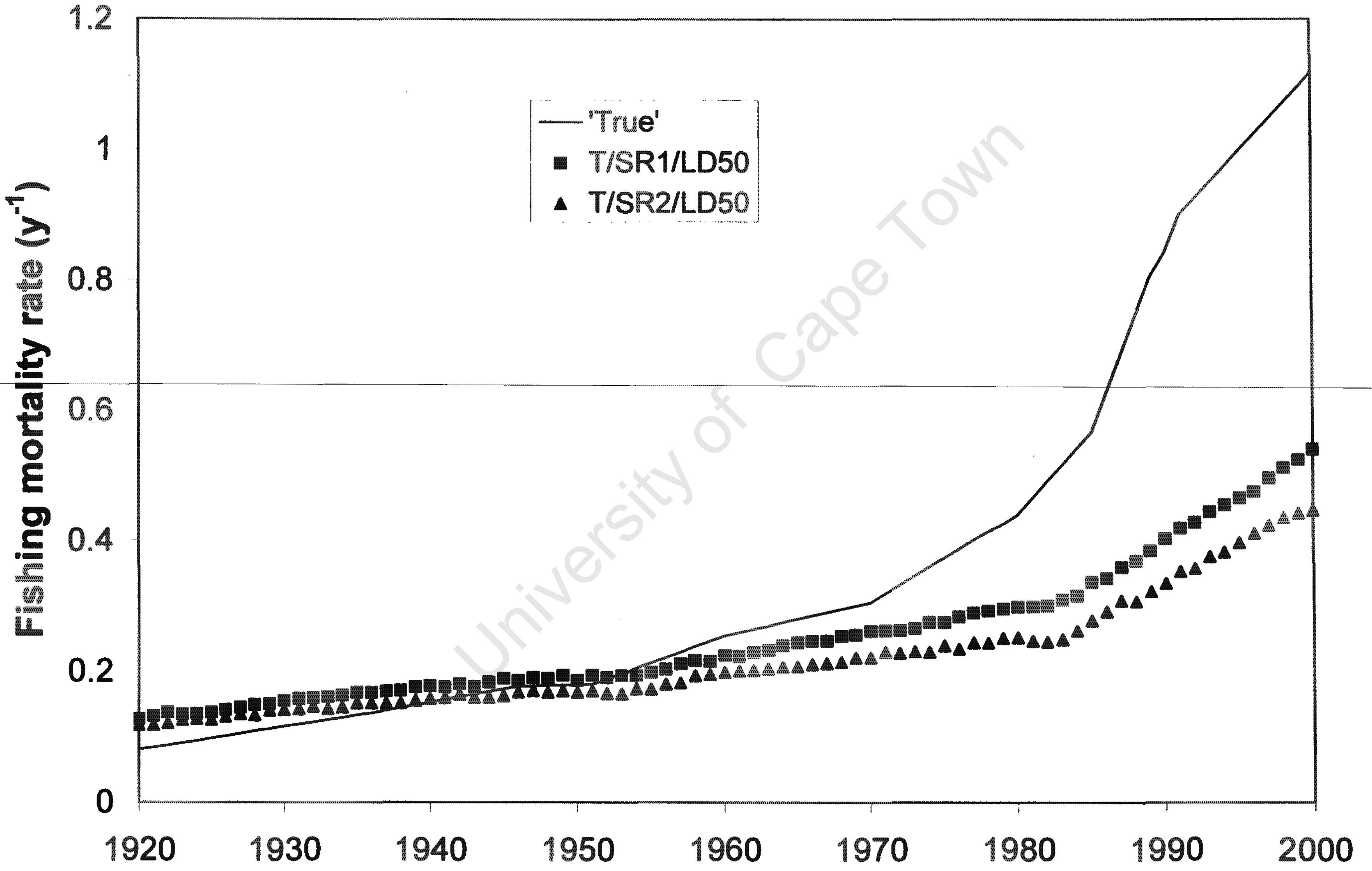


Fig. 7.1. The average fishing mortality-rate used in the model ('True') compared to the fishing mortality-rates estimated from catch-at-age data generated by models T/SR1/LD50 and T/SR2/LD50.

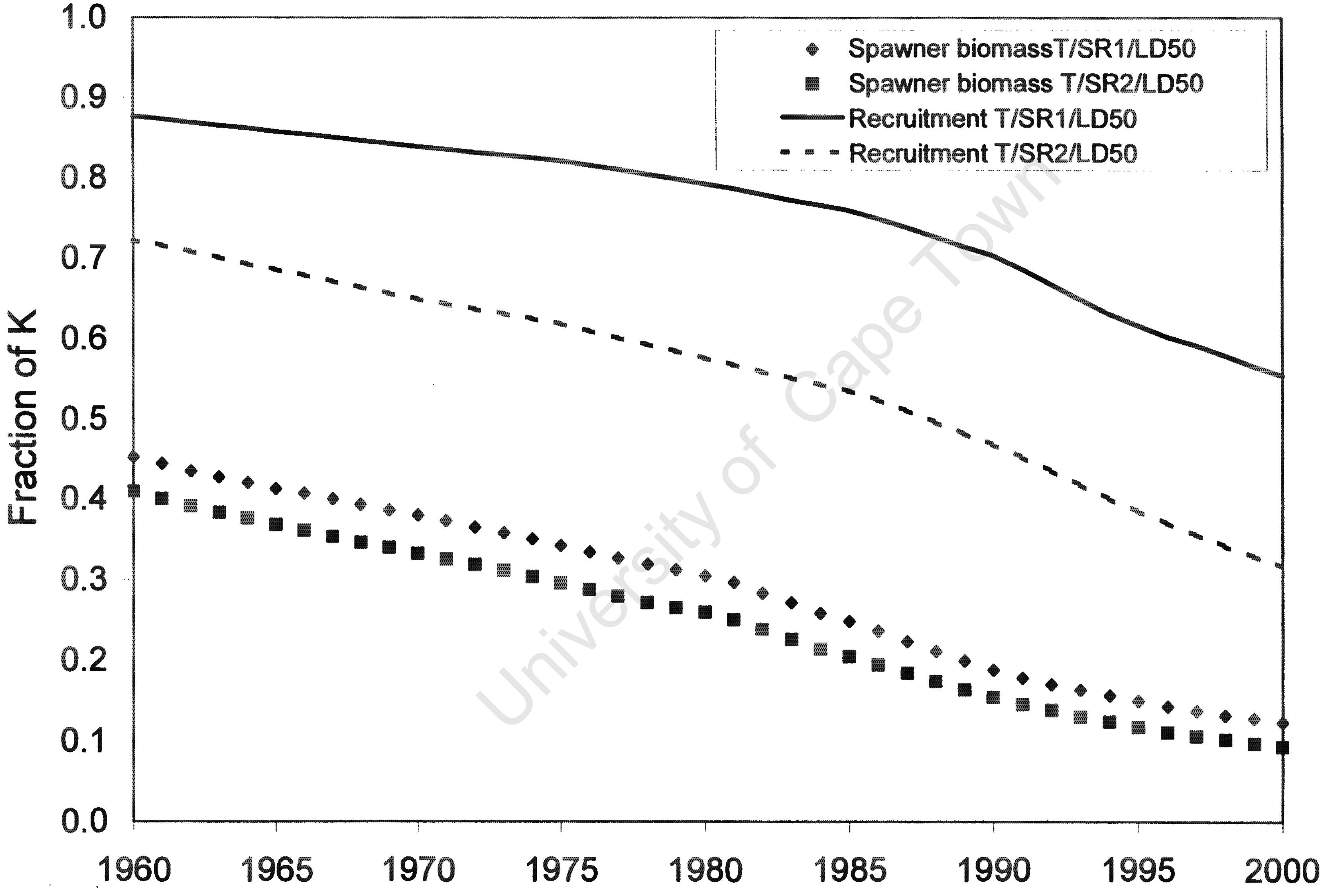


Fig. 7.2. Modelled time-series of relative spawning stock and recruitment, for models T/SR1/LD50 and T/SR2/LD50.

Further bias was caused by continuous increases in effort, and therefore mortality. As a result, successive year-classes were further weakened, and the age-distribution provided an estimate of the average mortality-rate that applied over the previous t_{max} years. (t_{max} is the maximum age of the fish. For galjoen it is realistically 14 years.) By 1990, the fishing mortality-rate was rising at 8% per annum (Fig. 7.1). Because of the sharp rise in fishing mortality-rate, its average value over the period 1986-2000 was considerably lower than it was in 2000. This effect was independent of the shape of the spawner-biomass-recruitment function.

(ii) In the model, the movement of post-recruit fish was not related to age. Old and young fish moved between areas with equal frequency (Chapter 5). The result of this pattern was that heavily-exploited areas were supplemented with fish from protected areas, natural refuges and lightly-exploited areas. Fish immigrating to heavily-exploited areas had an age-distribution that corresponded to a low exploitation rate. Because there were more fish moving from un- or lightly-exploited areas to heavily-exploited areas than the other way around, there was a negative bias on the mortality estimate. In areas that were heavily exploited, the arrival of a few old fish could strongly affect the estimate. Lightly-exploited areas, in relative terms, received almost no fish from heavily exploited areas. There was no way of estimating the magnitude of this bias, other than by comparing mortality estimates between simulations with and without adult movement. Such comparisons show a small bias of -0.05 and -0.08 y^{-1} for the two stock-recruit curves in 2000. The stronger effect in the case of the unproductive spawner-biomass-recruitment function is due to the greater impact of immigrant fish on depleted stocks.

(iii) Another bias that was difficult to quantify was the collapse of stocks in heavily exploited areas. When fishing mortality was low and limited to certain areas, catch-data emanated entirely from those areas, because there was so little fishing elsewhere. This bias accounts for the original over-estimation of fishing mortality (Fig. 7.1). In later years, when fishing mortality increased and spread, catch-data came from a much greater part of the range, but this time the relatively lightly-exploited areas made more substantial contributions to the catch-data because they were not over-exploited. In contrast, heavily-exploited areas delivered very little catch, and these areas were thus under-represented in catch-data, leading to an under-estimate of mortality. This bias could be overcome if the fishing mortality-rate was calculated from the age-distribution in the catch for each cell and then averaged across all cells to obtain a 'global' fishing mortality-rate. When this procedure was done at the level of the cell, the bias was reduced slightly (Table 7.2), indicating that the pooling of catch-data biases the estimate towards the mortality-rates in the areas with the most fish.

Table 7.2: Estimates of fishing mortality-rate in year 2000 calculated (i) from catch-at-age data that were pooled from all areas, and (ii) by averaging the fishing mortality-rates estimated from catch-at-age data in each area, in comparison to the true average fishing mortality-rate for two models with different stock-recruit curves.

Model	'Pooled'	'Averaged'	True
T/SR1/LD50	0.54 y^{-1}	0.66 y^{-1}	1.12 y^{-1}
T/SR2/LD50	0.45 y^{-1}	0.65 y^{-1}	1.12 y^{-1}

The combination of progressively reduced recruitment, increasing effort and adult movement resulted in a catch-at-age-distribution that was not log-linear (Fig. 7.3). The curve described by these data in any one year reflected the stronger cohorts of the preceding twenty years and caused mortality to be under-estimated. These results were unaffected by the extent of larval dispersal, which played no appreciable role in determining the spatial variation of the age-distribution.

With such heavily-biased estimates of the mortality-rate, there was little merit in considering the SB/R method further. Even if the result did give a fair reflection of the state of the stock (or spawning stock), that result would be coincidental, since without accurate mortality estimates and with a consistent trend in recruitment, the SB/R index is surely meaningless.

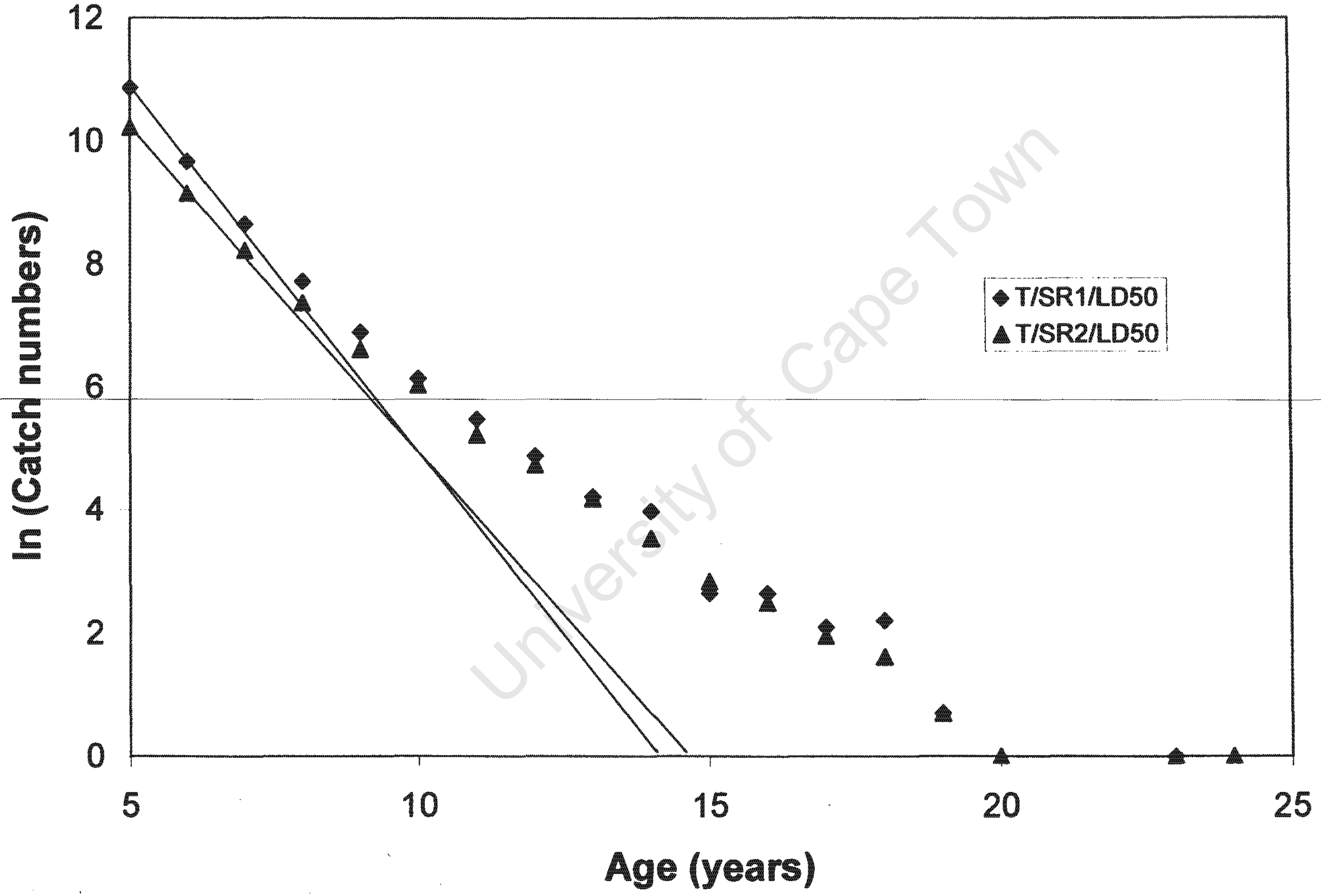


Fig. 7.3. Log-transformed catch-at-age data produced by models T/SR1/LD50 and T/SR2/LD50. The straight lines are drawn through the first two values of each series to illustrate the curvature of the log-transformed plots.

Catch per unit effort (CPUE)

There was an almost perfect linear correlation between CPUE and total population size for the years 1980 to 2000 (Fig. 7.4). An extrapolation of the trend shows that zero CPUE should be measured before extinction. This slight offset was probably the result of a failure to obtain data from MPAs and natural refuges. In reality, catchability (the slope of the line) would not be known with sufficient accuracy to draw a direct comparison between CPUE and absolute abundance. The result is that there is no way of knowing the extent of stock depletion without additional information on the size of the unexploited stock. Two sources of information may help to complete the assessment, namely effort trends and fish density in MPAs.

1. Effort trends: A plot of CPUE against some measure of effort (it would not have to be absolute) should yield a relationship, which, if extrapolated back to zero effort, should predict the CPUE for the unexploited stock size. Unfortunately, this method will only be accurate under conditions of equilibrium when the population size has had the chance to equilibrate to changes in effort (Butterworth *et al.* 1989). Rapid increases in effort will probably cause an under-estimate of the unexploited stock size. The model predicted a linear relationship between CPUE and effort (Fig. 7.5), and the ratio between the CPUE value in 2000 and the intercept of the linear regression predicted the relative stock size (relative to the unexploited stock size). However, for every model variation, this method produced an over-estimate of the exploited stock size, as predicted for an expanding fishery (Fig. 7.6). //
2. Density (CPUE) in MPAs: Experimental fishing in a MPA, in which fish have been protected for a sufficient period to stabilise, should yield CPUE values that are proportional to the unexploited stock size. There are a number of problems to this approach, and it is not a simple matter of comparing CPUE inside and outside a MPA. Because of the gradual changes in carrying capacity across the range of the species, comparisons can only be made locally. The CPUE measured in a MPA cannot be compared to the CPUE averaged across the range of the species. Accordingly, the CPUE in De Hoop sites was compared to the average CPUE over

the two 100-km areas on either side of the MPA. The second problem is that no MPA supports fish density at 100% of carrying capacity. For De Hoop, the estimates range between 59% and 86% depending on which model is used. This short-fall means that the stock size should be over-estimated. Contrary to this expectation, CPUE comparisons between the MPA and the adjacent areas under-estimated the size of the stock (Fig. 7.7). Habitat differences were the cause of the under-estimation. Koppie Alleen and Lekkerwater were selected as research sites because they included a high percentage of good habitat for galjoen. In the model, 52% of the cells that represented these sites were 'active'. By comparison, the adjacent area included a variety of habitats, in which the percentage of active cells was only 30%. Therefore, the carrying capacity of galjoen in the research sites was higher than in the exploited areas.

DISCUSSION

None of the assessment procedures considered was unbiased. The task that remains is to decide which is least biased, which biases can be corrected and which procedure is the cheapest and most practical.

In a fishery with great spatial variation in fishing effort, it would be expected that any assessment based on catch-data would under-estimate the state of the stock because of the failure to collect data from MPAs and natural refuges. Such a bias was evident in the estimation of the mortality-rate and in the relationship between CPUE and stock size, but there were far greater problems. Generally, these related to the rapid expansion in effort and habitat variation between areas.

Apart from the difficulties of collecting representative catch-at-size data and then translating these to catch-at-age data, catch-at-age data are likely to provide a severely biased estimate of the total mortality-rate. The model showed that increasing effort and decreasing recruitment were the largest sources of error, but these were exacerbated by adult fish movements between exploited and unexploited areas and the under-sampling of

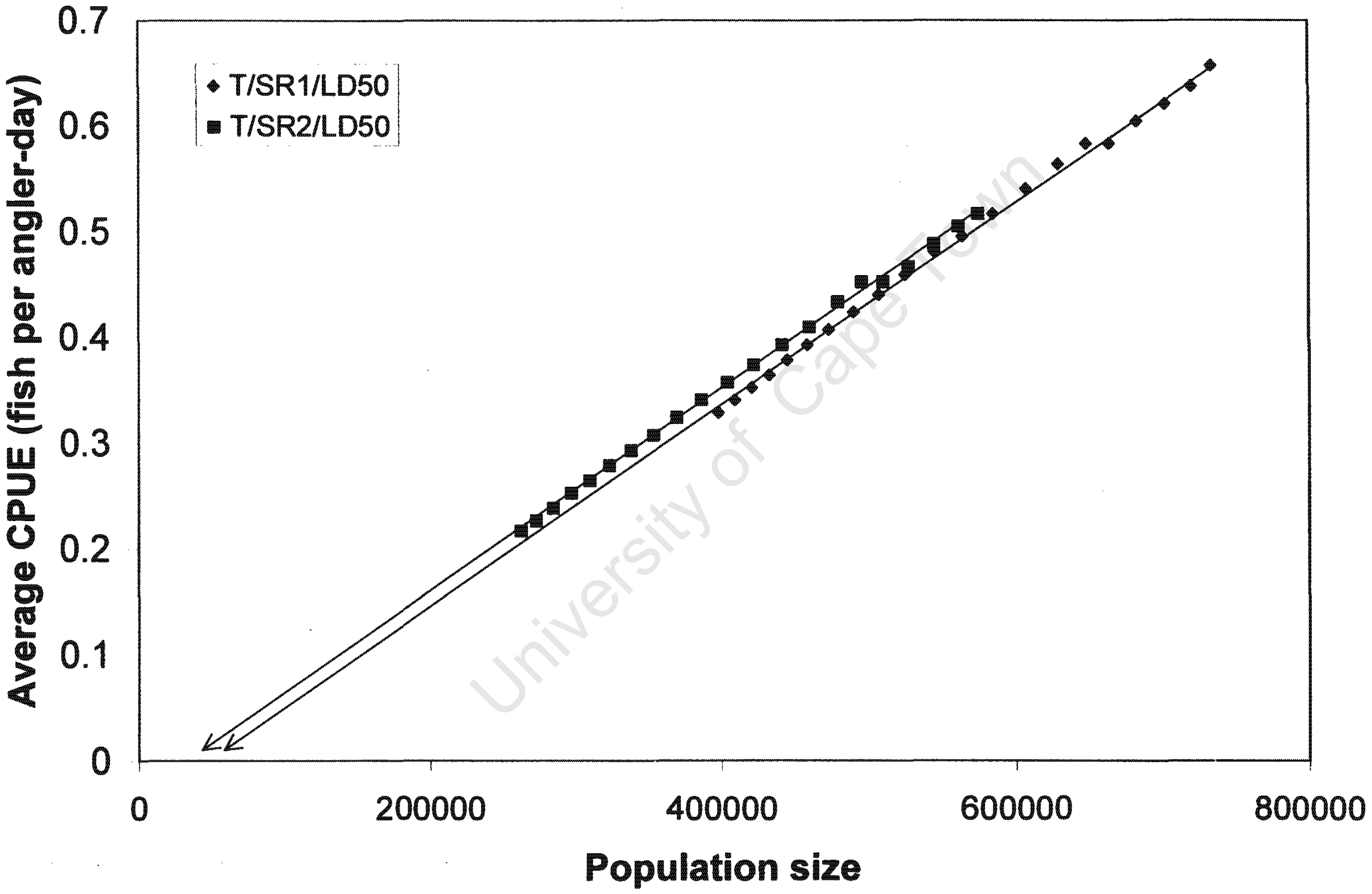


Fig. 7.4. Relationship between catch-per-unit-effort and population size generated by models T/SR1/LD50 and T/SR2/LD50 for the years 1980 to 2000.

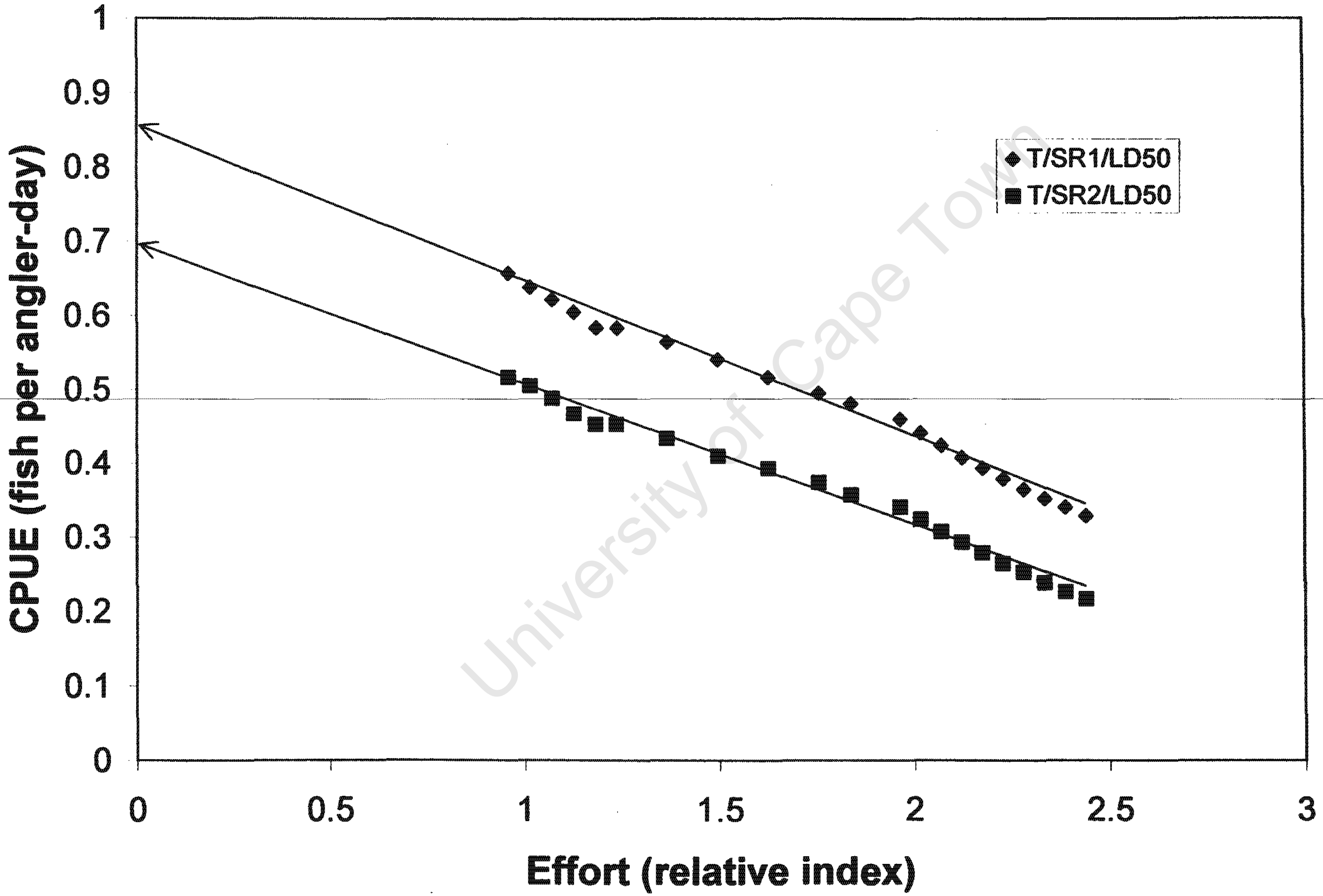


Fig. 7.5. Catch-per-unit-effort (CPUE) plotted against effort for models T/SR1/LD50 and T/SR2/LD50. The intercepts give an estimate of the CPUE for the unexploited stock size.

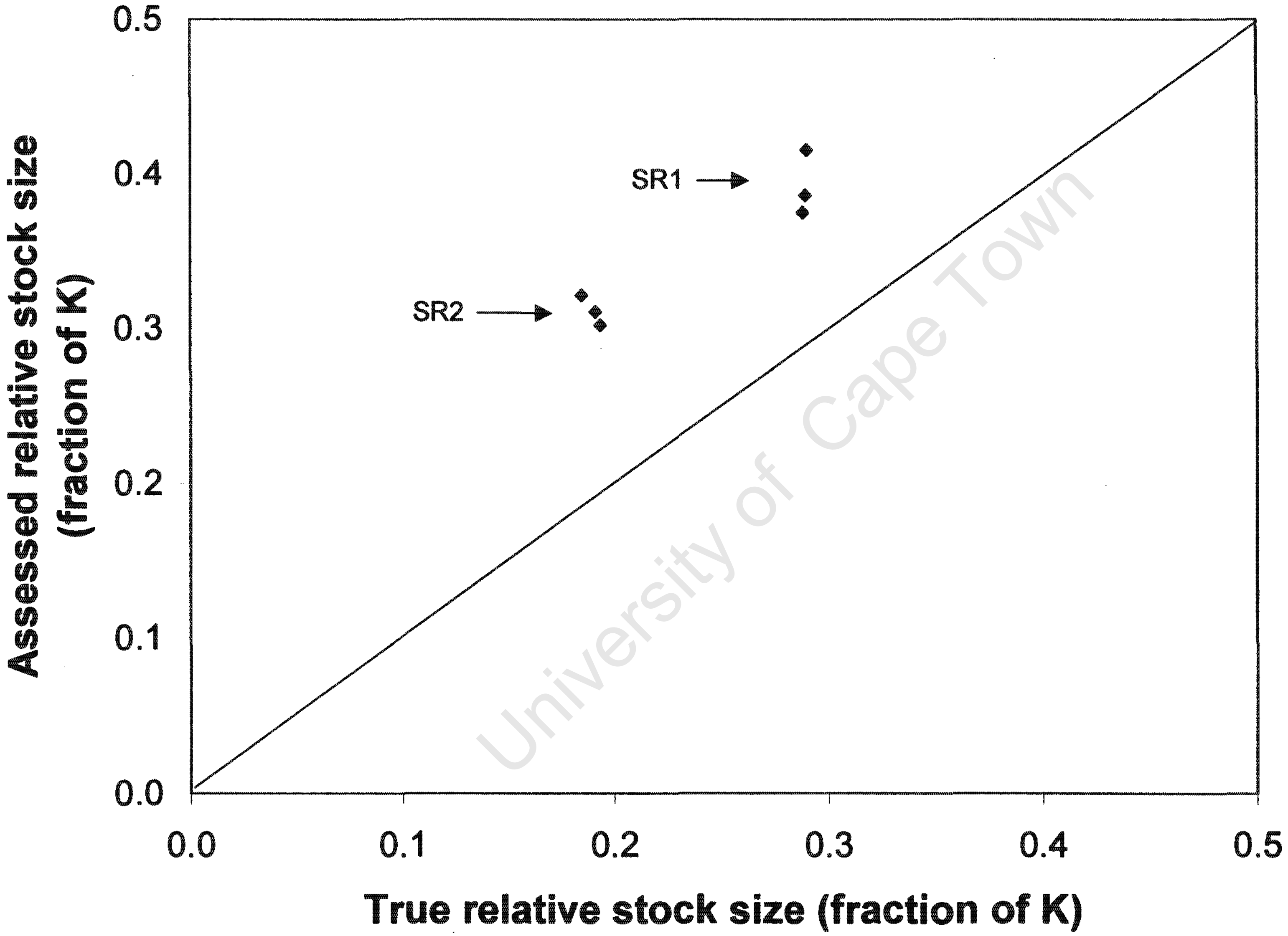


Fig. 7.6. Relative stock size assessed from regressions of CPUE vs effort compared to the 'true' stock size, for all six model variations. Results are grouped according to the stock recruit relationships SR1 and SR2.

very heavily-exploited areas. None of these problems can be overcome easily. The sampling bias could be overcome by sampling systematically in all areas but, as pointed out in Chapter 3, such a strategy would be economically unviable. A considerable amount of sampling effort is required in areas where CPUE is low to obtain a minimum, statistically-useful sample size of catch-at-size data.

The shape of the catch-curve, which was distinctly non-linear, may serve as an indication in other fisheries that effort has been increasing and/or recruitment has been decreasing. A similar shaped catch curve may be taken as evidence that large fish experience a lower natural mortality-rate than small fish (e.g. Beyer *et al.* 1999). Whereas it is quite feasible that large fish are less susceptible to predators, sustained increases in effort can produce the same effect.

Although the SB/R method is a common assessment strategy in the linefishery (Griffiths 1999), its use in the recreational fishery is questionable, owing to the difficulty of obtaining reliable mortality estimates and the strong possibility that there has been a sustained downward trend in recruitment. Apart from the reliability of the mortality estimate, the SB/R statistic itself is only meaningful if recruitment is constant. The cost and delays in establishing reliable age-length keys must also count against this method.

As a relative measure, the CPUE-based method is considerably less biased than the per-recruit methods. The greatest difficulty with this technique is to find a reliable measure of the absolute extent of stock depletion. The 'effort' method over-estimated stock size because the stock was not in equilibrium. This problem can be overcome by applying more sophisticated modelling techniques that take into account the longevity of the fish and the onset of maturity (Pauly 1984, Walters 1986). In contrast, the MPA technique under-estimated stock size. Again, precaution against this bias can be taken by comparing CPUE between similar habitats, which will require a high degree of spatial resolution in the data-collection procedure, and a good understanding of what is meant by effective habitat. Used in conjunction, these 'corrected' methods could provide a useful assessment.

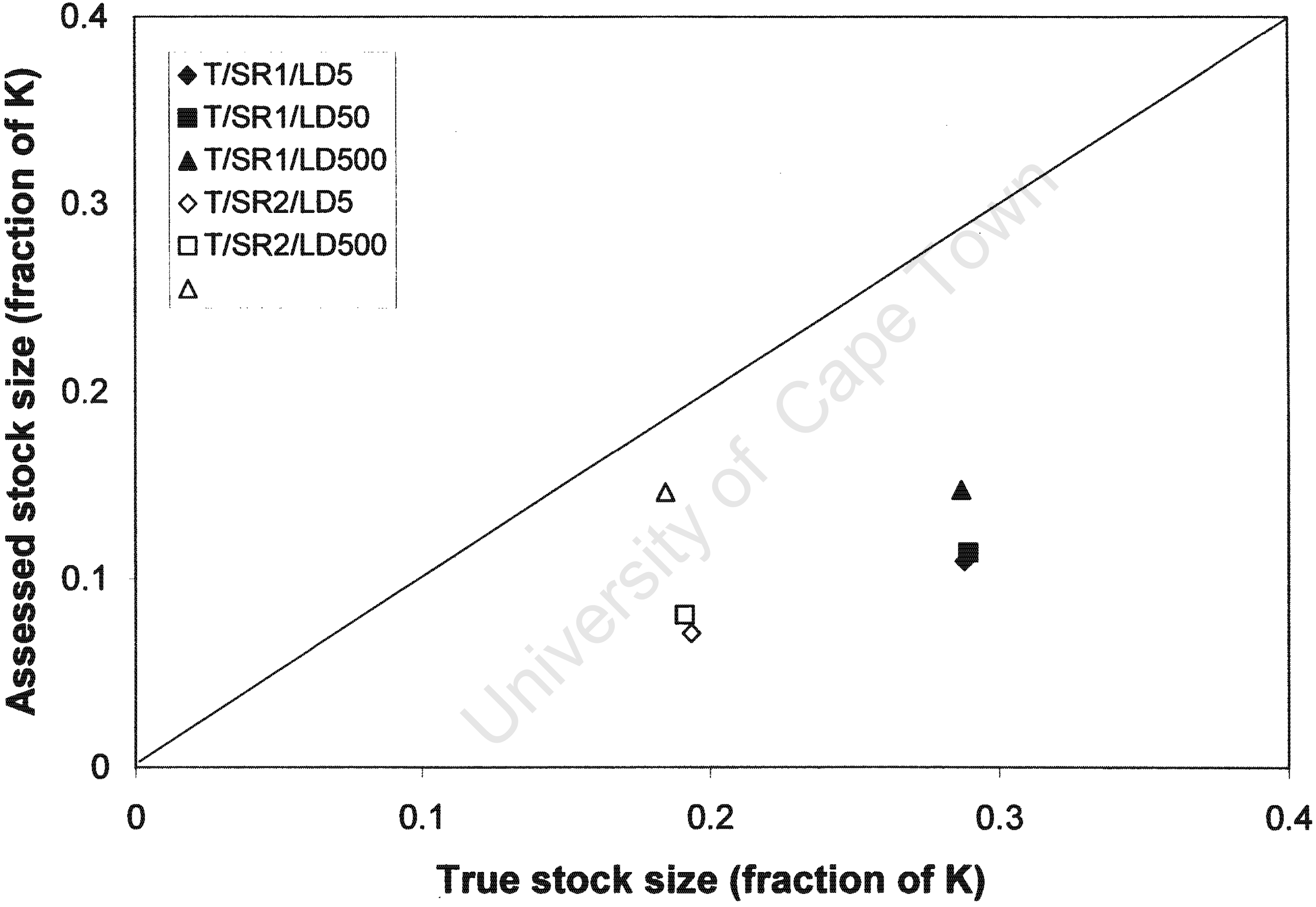


Fig. 7.7 The assessed relative size of the galjoen stock, based on a comparison of CPUE between a MPA and adjacent exploited areas, plotted against the 'true' relative size of the stock for six model variations.

A linear relationship is assumed to exist between CPUE and population size. This relationship will only break down when catchability is altered, either because of environmental conditions or changes in gear efficiency (Butterworth *et al.* 1989). It is probable that fishing gear has become more efficient over the course of the century (see discussion in Chapter 3), but no attempt has been made to investigate the impacts associated with new technology or practices. CPUE estimates that are widely spaced in time are probably not comparable. Such a comparison would serve to over-estimate the most recent population size where there have been significant changes in technology. A comparison of CPUE across MPA boundaries can provide an assessment with only one year's worth of data, and it would not be affected by catchability shifts. In contrast, the regression of CPUE against effort will require a time-series spanning at least ten years.

CPUE data are cheaper to collect than catch-at-age data. To obtain approximately similar levels of confidence in estimates (e.g. CPUE to within 5% and total mortality-rate to within 0.1 y^{-1}), less monitoring time is needed to collect CPUE data than catch-at-size data. For example, in an area of low fish density, equivalent to a CPUE rate of 0.1 fish per man per day, 1754 CPUE records are needed to achieve an estimate with 5% accuracy. However, at this CPUE rate, 1754 observations will generate 175 fish length records, whereas 8000 length records are needed to estimate mortality-rate to within 0.1 y^{-1} (Table 3.15).

CPUE monitoring is less prone to systematic sampling error than catch-at-size monitoring. Because the coefficient of variation of CPUE decreases with increasing fish density, twice as much sampling is required at low density to achieve the same level of confidence as at high density (Table 3.15). When estimating mortality-rates from catch-at-size data, the difference is more stark: between four and five times as many samples are required under low density than high density to achieve the same level of confidence in the mortality estimate. The CPUE method is thus more practical, as both high- and low-density areas can be sampled with similar monitoring effort. Catch-at-size monitors, on the other hand, will soon give up trying to obtain sufficient length measurements in a heavily exploited area.

On balance it would appear that the CPUE method is a better option than catch-at-age. However, the balance may shift if fishery conditions change. As a generalisation, it could be said that, for a fishery in strong decline, the CPUE method will be superior to SB/R, because (i) this condition renders SB/R unreliable and (ii) strong inter-annual changes in stock size will result in a good inter-annual CPUE signal. On the other hand, if the stock shows long-term stability, then SB/R might be preferred. Stability (equilibrium) is an assumption of the SB/R method, and it is also necessary for the estimation of the fishing mortality-rate, whereas inter-annual stability will not provide any signal in the CPUE series.

The indications are that the linefishery has declined sharply during the late twentieth century, and unless strong regulatory action is taken, such declines will continue. Presently, CPUE seems to be a more sensible assessment strategy than SB/R.

Whether SB/R or CPUE methods are used, there is clearly a strong argument to maintain one or more large MPAs, either as a means to estimate the natural mortality-rate, or to serve as a reference against which CPUE measurements can be compared. The possibility of using MPAs for these purposes have been mentioned in fishery text-books (e.g. Pauly 1984), but it is rare to see these methods being used in practice, probably because large MPAs are rarely available.

CONCLUSION

Biases in the assessment of the galjoen fishery are caused primarily by spatial and temporal inconsistencies that nullify various underlying assumptions in the models employed. Temporal changes in recruitment and fishing mortality are the primary causes of the failure of the SB/R method. Although the CPUE method is also biased, these biases can cause an over-estimate of the stock size (when extrapolating a time-series of CPUE vs. effort) or an under-estimate (when comparing CPUE across the boundary of an MPA). The biases in CPUE methods can be corrected, whereas the biases in mortality-rate estimation cannot be corrected without additional knowledge of effort trends and recruitment strength. The CPUE method is cost-effective and practical for collecting sufficient, representative data. Presently, the CPUE method is preferable to the SB/R method as an assessment strategy for the galjoen fishery. This conclusion is contingent on the assumption that the stock is in long-term decline. For a stable fishery, the SB/R technique may prove to be a superior assessment tool. Both the CPUE and the SB/R method will require the existence of a large MPA, either as a reference for the unexploited stock size or as a means to measure the natural mortality-rate, particularly if an assessment needs to be performed in only one year.

CHAPTER 8

CONCLUSIONS

This thesis grew out of a general dissatisfaction with the way reef-fish species are managed and assessed in South Africa. In the past, there has been an almost complete disregard of the spatial dimension. Stocks have been treated as homogeneous entities, for which parameters such as mortality rate, spawner-biomass-per-recruit and the state of the stock can be conveniently summarised by a single estimate. Such an approach is greatly at odds with any interpretation of catch-data or divers' observations, which can show large differences between nearby areas. The deliberate use of protected areas in the management will require not only an understanding of spatial processes, but also the development of procedures to incorporate the effects of protected areas into stock assessments.

Fish movement

The first part of this thesis is an investigation into the patterns of fish movement. The primary basis for fish distribution is the geography of the habitat and fishing effort but, within these confines, the spatial structure of the fish stock is determined by the pattern of fish movements. Purely random movement will break down patterns that may result from a spatially-variable application of fishing effort. Chapter 1 reviews fish movement patterns and concludes that these are highly structured, and that true random movement is seldom if ever observed. Fish movements can be quite complex, often involving different patterns within a stock, apportioned on the basis of age, sex, location or genetics. Nevertheless, a very common strategy among fish from all habitats is resident behaviour. Many fish species adopt home-ranges, and some may even defend territories. Another important lesson from the review is that fish behaviour can be plastic, responding to changing circumstances.

There are well-documented advantages for fish that choose not to move indiscriminately. Familiarity with food sources and predators, immunity against local diseases and reduced energy expenditure are primary reasons for a resident life, and natal-homing is a good response to environmental uncertainty. On average, those who remain in a proven area face fewer risks. Even the dispersal of larvae, once thought to be a predominantly passive process, is goal-directed, with larvae having at least some control over their final destination and timing of settlement.

Fitness-maximising models predict that it is beneficial for an animal to move under certain conditions. Most of these models have been necessarily simplistic, and can never incorporate the full suite of challenges that an animal has to overcome. As a result, their assumptions are crude and have to be examined critically.

Galjoen can be classed as a resident species, which holds home-ranges. Left as such, however, the classification would overlook an important and very noticeable component of the life-history of galjoen. Infrequently, individuals move vast distances that can span the entire range of the stock. These movements appear to be uncorrelated with age, sex or season. Although they are undoubtedly triggered by a cue, from the point of the human observer the departures are not predictable, nor explainable. The stock, or any substantial part of its, does not move as a cohesive unit.

Two competing hypotheses were advanced to explain the tag-recovery pattern in Chapter 2. According to the tourist model fish migrate between a small number of sites throughout their life. According to the polymorphic model some fish migrate, but most are resident. With the help of an individual-based model of the galjoen fishery, it was concluded in Chapter 5 that the tourist model provides the most likely explanation of the data. On average, galjoen spend more than 90% of their life in one location. The movements are thus a small part of the pattern, but they become noticeable, even dominant, in areas where galjoen have been heavily reduced in number, when the arrival of fish from more densely populated areas form a substantial addition to the local stock. It is perhaps this phenomenon that has lead many fishermen to believe that galjoen are principally migratory. In an area that is fully-protected, galjoen are predominantly resident, and large fluctuations in density are uncommon. In exploited areas, the resident fish diminish, and the contribution of immigrants to the local catch is much greater, and the catch rate itself fluctuates with new arrivals. In Chapter 3 it was shown that the coefficient of variation in catch-per-unit-effort (CPUE) diminished as its average value increased.

It is the resident nature of galjoen that ensures their protection in areas where fishing has been eliminated. No fixed home-range size can be given, as there seems to be large variation, between and within sites, but the dimension would seem to be smaller than one kilometre on average. In Chapter 2 it was suggested that the dynamic nature of coastal dune systems would cause shifts in home-ranges and in Chapter 5 it was argued that the patchy distribution of habitat would account for intra-specific differences in home-range size, if home-range size is determined by feeding requirements. The tag-recovery method is perhaps not the ideal way of measuring home-range size, because this technique cannot separate movements within the home range from small home-range shifts, and hence it over-estimates home-range size. Unfortunately, for species that live in the high-energy surf zone, underwater observation is not practical.

It is difficult to say if the tourist model holds for other reef-fish species, despite the apparent similarity in tag-and-recapture data for galjoen and other reef fish (Griffiths and Wilke, in press). The discrimination between the tourist model and the polymorphic model was entirely statistical, and relied on a large sample size, which is not available for other, less abundant species. Nevertheless, the co-existence of resident and migratory behaviour within a population is common, having been documented for numerous species around the world. Within populations of anadromous salmonids, individual fish take on either one or the other behaviour, whereas among galjoen it would appear that every fish has the potential to move when conditions dictate, but individuals appear to faithfully return to a site. More detailed studies on other reef-fish species, particularly those for which underwater observation is possible, may indicate if this movement pattern is more widespread.

Stock assessment

The tag-and-recapture data were used to estimate the density of galjoen at two research sites: Lekkerwater and Koppie Alleen – both lying in De Hoop Marine Reserve where no fishing is permitted. This was the first estimate of absolute density of a reef-fish species in South Africa. Although underwater assessments have been made of other reef fish species, these must be regarded as relative. Unfortunately, the tag-and-recapture method is not suitable for regular assessments (a fifteen year time-series was needed for the present assessments), or for assessments outside MPAs, where fishers would recapture, but not necessarily report, many tagged fish.

Although both research sites were equally protected and only 14 km apart, the density estimates differed vastly. Habitat could explain the differences, as there are more rocky platforms at Lekkerwater than at Koppie Alleen. Differences in habitat would have affected not only the density, but also the catchability. Convoluted rocky-shores make it more difficult for anglers to access fish than from a sandy beach. Some coastal habitats are so isolated or physically extreme that they cannot be accessed by anglers. If large enough, such areas may constitute natural refuges.

MPAs in fishery management

As a means for conserving the stock in face of exponentially increasing effort, MPAs, by displacing effort, appear to be remarkably successful for galjoen (Chapter 6). The resident nature of the fish and the fact it does not aggregate to spawn, means that the stock can be effectively protected, provided that the MPAs are large enough to overcome losses at the edges due to movements within the home-range. The estimate of home-range size suggests that a buffer of 2.5 km is needed at either edge of a MPA to ensure that those fish that recruit in the centre are protected. Even this precaution does not totally eliminate the effects of the fishery on fish in the MPA. The habit of galjoen of relocating over large distances implies there will be a loss from an MPA of any size, as those fish that leave will not be balanced by those arriving. Extensive larval dispersal provides another source of loss, which can be acute when outside areas have been totally depleted of spawning fish. Although large MPAs are preferable for aiding the assessment procedure, where these are not possible, because of the short-term costs to the fishery, small MPAs should be spaced closer than the scale of larval dispersal.

MPAs are likely to improve yield where the stock has been heavily depleted, after some delay during which the density in the MPA recovers. MPAs feed adjacent areas through the migration of adults, larval dispersal and movement within a home-range. Most field studies have detected the latter, often termed 'spill-over', but this is likely to be the least significant of the three processes, especially for large MPAs. Although the ultimate outcome of MPAs is improved and sustained yield, the difficulty in this strategy is where and when to implement MPAs to reduce short-term losses. The short-term costs to the fishery will be smallest for MPAs that are either small or introduced when the stock is very depleted, but these may not be the best option to provide long-term improvements.

Ongoing monitoring

The susceptibility of the spawner-biomass-per-recruit (SB/R) index to bias caused by recruitment failure has been well known, but there has never been a quantitative estimate of the bias for any species in the South African linefishery. On the basis of the rise in effort inferred from changes in the demography of coastal towns, the model suggests that the bias was so great that the method is not useful at all (Chapter 7). The problem concerns not so much the index itself, which takes no account of recruitment, but rather the problem of estimating the mortality rates needed to calculate the index. The errors are caused mainly by increasing mortality rates, and decreasing recruitment, but spatial variations in the mortality rate also played a role.

Methods based on CPUE are also beset with problems. But there is a good chance that these can be overcome by applying appropriate models to correct for non-equilibrium situations, or by careful attention to sampling of equivalent habitats. An important part of the choice of assessment methods rests with the practicality and cost of obtaining data for assessment. Here again, the CPUE method is superior to SB/R indices.

Fishery management

The most important contribution of this work is its addition to a growing body of studies, which indicate that spatial structure cannot be ignored in fisheries management. Indeed, such structure could be used to great advantage for conservation and assessment. Of equal importance are the temporal trends in effort, both past and projected, for they will determine which assessment techniques are most appropriate, and will help in deciding whether and where to place additional MPAs.

Clearly, the reliance on the SB/R method by the South African linefishery should be re-evaluated. Galjoen is only one of more than one-hundred species in this fishery, but all share similar characteristics (long-lived, late-maturing) and are targeted by the same effort. Therefore the characteristics of the galjoen fishery that caused the SB/R method to fail is likely to apply to many, if not most of the other species in the fishery. Although the commercial fishery has been capped by effort limitation, the species it targets are shared by the recreational fishery, which has not been capped.

Most of what has been learned about galjoen can be attributed to the De Hoop MPA. Without that protection there would never have arisen the opportunity to systematically study galjoen under natural conditions. Right now the same can be said of other MPAs and many other species, some of which are exceedingly scarce in exploited areas. MPAs make a double contribution to fish conservation, by reserving portions of the stock from fishermen, and by providing the necessary information to manage fisheries on a sustainable basis.

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