Mark-recapture models for determination of mortality, migration and growth in *Pomatomus saltatrix* (Teleostei)

by
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Preface

The work described in this thesis was carried out whilst employed at the Oceanographic Research Institute, Durban.

This study represents original work by the author and has not been submitted in any form to another University. Where use was made of the work or research samples of others it has been duly acknowledged in the text.

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Finally I would like to thank my wife Althea and my daughter Mallorie who sacrificed more for this research than I ever did. Thank you for being there.

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Abstract

This study primarily attempts to develop models to estimate population dynamic parameters from mark-recapture data. Model implementation is illustrated using data collected from the South African *Pomatomus saltatrix* fishery. The models developed allow for the estimation of mortality, survival and migration rates in exploited fish stocks. A growth model is also developed which simultaneously estimates growth parameters as well as validates the hard structure banding using age-length and mark-recapture data. There are number of advantages to these models. Given appropriate datasets the mark-recapture models developed in this study can be applied to others species of interest. The models can be modified easily e.g. the growth model can incorporate growth functions other than the von Bertalanffy model. The models can be programmed into a spreadsheet which facilitates the estimation of parameter variances using likelihood profile or bootstrapping methods and allows the testing of model assumptions based on simulations.

A general mortality model is developed and is illustrated with mark-recapture data from the *P. saltatrix* fishery. The model provides an estimate of the average fishing mortality for the Cape and KwaZulu-Natal and is then extended to include movement between the Cape and KwaZulu-Natal. It utilises mark-recapture data from the Sedgwick's-ORI Tagging Programme as well as effort and catch data from the National Marine Linefish System (NMLS). Estimates of annual fishing mortality rates in KwaZulu-Natal are derived from the model which takes into account immigration of *P. saltatrix* into KwaZulu-Natal from the Cape as well as emigration from KwaZulu-Natal to other areas including the Cape.

The average fishing mortality rate was estimated to be 0.27 year^{-1} between 1984 and 1993 in the Cape and KwaZulu-Natal combined. This is likely to be underestimated because of non-reporting of tags, shedding of tags and tag-induced mortality. The model is shown to be robust for estimating the average fishing mortality rate and exploitation rate only when annual variability in fishing mortality is small during the study period.

The second model to quantify migration into and out of KwaZulu-Natal waters suggested that the whole adult Cape stock migrates into KwaZulu-Natal during winter. Further, this whole stock is available to fishing in KwaZulu-Natal although there is probably large exchange between inshore and offshore areas and, in the latter zone, *P. saltatrix* is inaccessible to shore-based fishing. Large fishing mortality rates for the years 1987 to 1993 were estimated in KwaZulu-Natal. These large fishing mortality rates may prevent the return migration of *P. saltatrix* to the Cape and the model predicts that possibly less than 4% actually return to the Cape.

An age and growth study based on otolith readings was also undertaken. Validation of the growth banding as annual was confirmed by developing a model that estimated growth parameters using age-length data and simultaneously estimating times-at-liberty of tagged individuals based on arbitrarily chosen band deposition periodicities. It is shown that the assumption of annual banding led to the best prediction of periods of liberty of tagged individuals with small coefficients of variations in the parameter estimates. However, since only a few tagged animals were used in the analysis more research is needed to verify the robustness of this technique for use on other fish. The growth of *P. saltatrix* in the present study was found to be faster than that of a previous study in South Africa.

A modified delay-difference model was developed to estimate relative biomass and relative catch based on observed mean body weights and effort indices. For the period 1956 to 1972 the model predicts that there was a decline in *P. saltatrix* abundance with corresponding declines in mean weight of the catch. Although during this period there was a general decline in fishing mortality, the fishing mortality was sufficiently high for growth overfishing to occur. It was found that during the 17 year period there was a 44% reduction in biomass which is similar to an estimate in another study. Catch during the period was annually variable but generally declined with time especially in the later years. The decline in average weight harvested and the variable but lower catches during this period are consistent with observations by fishers.

An evaluation of the present closed season for *P. saltatrix* in conserving egg production was performed. It showed that better conservation of egg production is possible by shifting the present closed season (September to November) to extend over the October to December season but this may adversely affect the tourism industry in KwaZulu-Natal. Shortening the present closed season by one month (September) does not affect egg production but increases present yield levels. This study suggests that the closed season may not be useful in terms of reducing the fishing mortality rate on *P. saltatrix* as fishers may be encouraged to fish harder in the open season to make up for the lost yields of the closed season. Moreover, lengthy closed seasons may also increase fishing mortality because fishers tend to fish harder in the months open to fishing. Assuming no large annual recruitment variations the *P. saltatrix* stock is presently optimally exploited as current fishing mortality rates are just below the MSY or optimum yield levels.

Chapter One

INTRODUCTION

1.1 Biology of *Pomatomus saltatrix*

Pomatomus saltatrix, commonly known as the elf or shad in South Africa, is a moderately-sized coastal fish that can attain 120cm total length (TL measured from the tip of the snout to tip of the upper caudal fin lobe rotated down to the midline) or 14.4kg (Smith and Heemstra, 1986) and is widely distributed in warm and temperate waters of the world (van der Elst, 1988; van der Elst, 1976). Off South Africa, it is

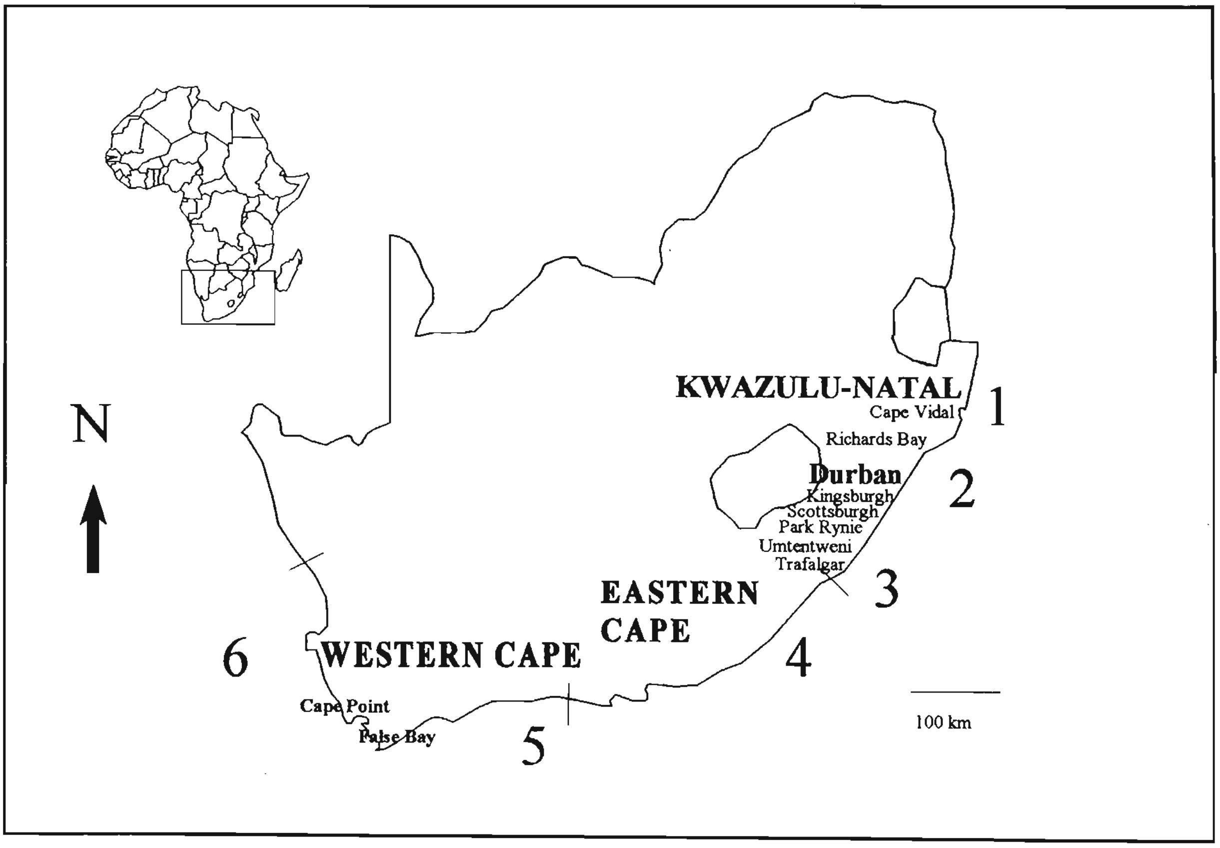

Figure 1.1 Map of South Africa showing areas mentioned in the text. Numbers indicate areas given in Table 1.3.

distributed along the west, south and east coasts and is particularly common from False Bay in the Western Cape, along the Eastern Cape coast to KwaZulu-Natal. Its most northern limit on the east coast is southern Mozambique (Figure 1.1). In this study Cape refers to both the Western Cape and Eastern Cape coasts.

In South Africa 50% maturity in females is reached at a total length of 25cm while 100% maturity is reached at a size of 33cm (TL) (van der Elst, 1976). These maturity sizes are similar to those reported from Australia (Bade, 1977). However, in southern Brazil a 50% maturity size of 35cm (TL) was recorded (Haimovici and Krug, 1992). In the South Atlantic Bight of the USA a large size-at-maturity was also recorded (45cm FL) (Oliver *et al.*,1989).

Spawning occurs off KwaZulu-Natal in early spring to summer (September to January with peak spawning in November) and is believed to occur continuously over this protracted spawning period (van der Elst, 1976). Continous spawning from late spring to summer has also been recorded in southern Brazil (Haimovici and Krug, 1992). Previously, on the eastern seaboard of the United States it was believed that there were two separate stocks of *P. saltatrix* with two distinct spawning periods: a spring spawning in the South Atlantic Bight and a summer spawning in the Middle Atlantic Bight (Kendall and Walford, 1979). Recent research, however, has concluded that *P. saltatrix* in these regions is a unit stock with a protracted continuous spawning period (Smith *et al.*, 1994).

It is believed that spawning occurs in relatively shallow water on the continental shelf of KwaZulu-Natal. Beckley (1993) collected *P. saltatrix* larvae in 50 to 100m of water during the months of October and February and found none in deeper water off the edge of the shelf in the Agulhas current (500-2000m). *Pomatomus saltatrix* eggs have been recorded regularly off Park Rynie south of Durban in 30 to 60m of water during the months of October to March (Beckley and Connell (in press)). On the east coast of the United States high concentrations of eggs and larvae have been sampled mainly from midshelf waters though moderate to high concentrations of eggs sometimes occurred within 10km of the shore (Smith *et al.,* 1994)

Pomatomus saltatrix is a voracious predator and adults feed almost exclusively on teleosts (van der Elst, 1976) while juvenile *P. saltatrix* (<20cm (TL)) largely consume crustaceans and some fish (Bennett 1989). Juanes and Conover (1994) found that 4-7cm (TL) *P. saltatrix* displayed a diet shift from planktivory to piscivory as they underwent a habitat shift from offshore waters to inshore nursery areas. They concluded that the rapid growth in young-of-year *P. saltatrix* in temperate regions is a result of the early shift in diet from zooplankton to a fish diet; a case of pursuing a tropical life-style in temperate waters.

In South Africa during winter, *P. saltatrix* undertakes a relatively extensive migration from the cooler Cape waters to the warmer KwaZulu-Natal waters (Figure 1.2). Van der Elst (1976) noted that angler catch rates of *P. saltatrix* along the south coast of

KwaZulu-Natal tend to peak in early winter, followed by increased catch rates on the north coast later in the season. In late summer the catch rate in the Cape increases. He interpreted this as a winter migration into KwaZulu-Natal followed by a return migration to the Cape. This migration is mainly spawning related, but, 0+ *P. saltatrix* also migrate, possibly to reach warmer waters and the greater availability of food off the KwaZulu-Natal coast. During this same period a prey species *Sardinops sagax* also migrates into KwaZulu-Natal waters.

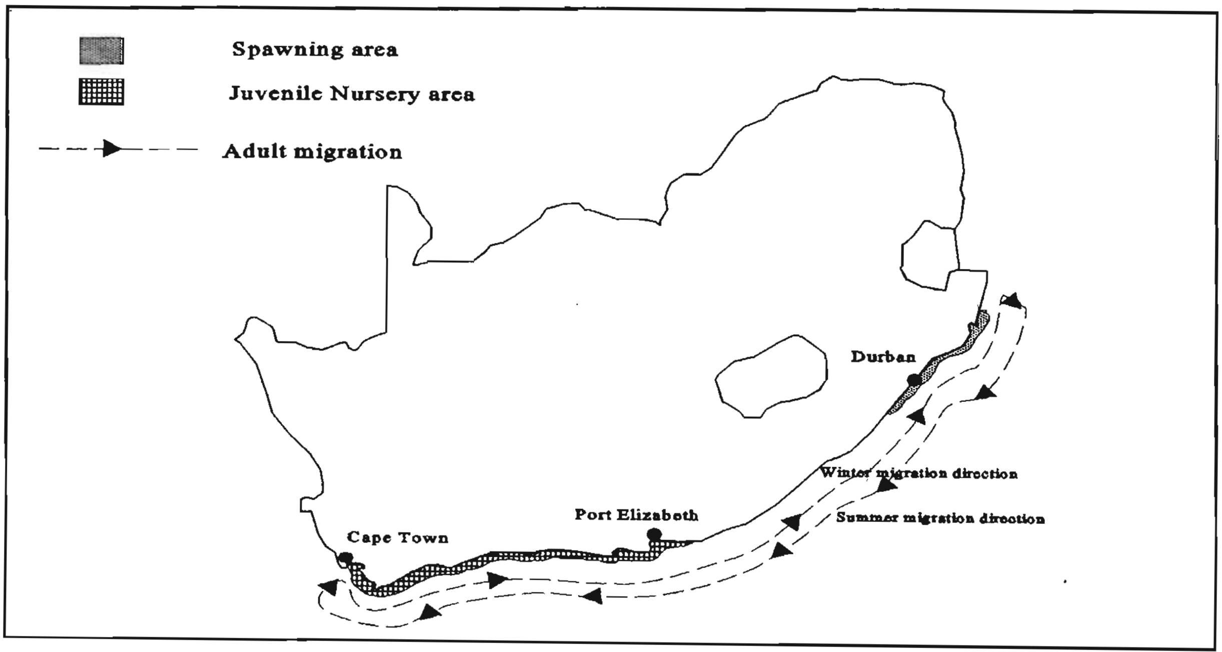

Figure 1.2 Migration route of adult *P. saltatrix* along the west, south and eastern coast of South Africa showing the known spawning area and the juvenile nursery area.

The migration of 0+juveniles appears to occur before the adult migration as early in the fishing season off KwaZulu-Natal small *P. saltatrix* are caught while later in the season larger *P. saltatrix* are caught. A similar migration of *P. saltatrix* occurs on the east coast of Australia where adult *P. saltatrix* migrate during winter from southern coastal areas to Fraser Island (Oueensland) to spawn in spring and early summer, after which they return south (Pollock (1984)cited in Morton *et al.*, 1993).

It was previously believed that after spawning the pelagic *P. saltatrix* larvae drifted passively from KwaZulu-Natal to Cape waters using the Agulhas current (van der Elst, 1988). The Agulhas current is the most important large scale oceanographic feature off the east coast of southern Africa and forms part of the warm, western boundary current in the south-western Indian Ocean (Heydorn *et al.*, 1978). The source of the Agulhas current is the waters from the Mozambique Channel and areas south of Madagascar. Off Durban the core of the current is found at the continental shelf break at a distance of some 40-60 km from the coast, while south of Durban to Port Alfred the Agulhas current can be as close to 10 km from the coast (Shillington 1993). At about 20°E off the south of the continent the Agulhas current retroflects and turns eastward (Schumann 1987). From recent research it appears that the larvae of many linefish species including *P. saltatrix* utilise the oceanographic features associated with the shoreward edge of the Agulhas current for dispersal to nursery areas in the Eastern Cape (Beckley, 1993). Juvenile *P. saltatrix* (between 10 to 20cm (FL)) are frequently encountered in sheltered bays in the Eastern Cape in shallow water less than 20m deep (Wallace *et al.*, 1984a; Wallace *et al.*, 1984b; Smale, 1984). These areas are considered to be *P. saltatrix* nursery areas. On the east coast of the United States similar transport occurs and processes such as filaments, meanders and eddies where there is exchange between shelf and Gulf stream waters help in the translocation of larvae towards the shore as well as advecting larvae northwards (Smith *et al.,* 1994). After spawning off Fraser Island in Australia *P. saltatrix* eggs drift southwards under the influence of the East Australian current (Hamon and Tranter, 1971 cited in Morton *et al.,* 1993).

1.2 The *Pomatomus saltatrix* fishery in South Africa

In the province of KwaZulu-Natal (Figure 1.1), *P. saltatrix* is the most sought after nearshore angling species (Joubert, 1981) and is harvested almost exclusively by rod and line by anglers fishing from the shore. Limited catches are harvested from ski-boats fishing further offshore.

No commercial exploitation of *P. saltatrix* is permitted in KwaZulu-Natal (Table 1.1) and in the current fisheries legislation (Sea Fisheries Act No. 12 of 1988) it is classified as a restricted species that may not be offered for sale in this region. The sale and commercial harvesting of *P. saltatrix* are, however, permitted in the Eastern and Western Cape (Figure 1.1).

Table 1.1. Management regulations for *P. saltatrix* in South Africa. Minimum size limits are expressed as total lengths and the fishing sector refers to the group of fishers that the regulations were aimed at. Cape includes Western Cape and Eastern Cape.

YEAR	REGULATIONS	FISHING SECTOR	AREA
1916-1959	Min.size (23cm)	Unknown	Unknown
1973	Min.size(31cm) Bag limit (10)	Recreational anglers	KwaZulu-Natal
1977	Min.size(31cm) Bag limit (2) Closed season (1 Sept-31 Dec) No sale of *P. saltatrix*	Recreational anglers	KwaZulu-Natal
1979	Min.size (30cm) Bag limit (4) Closed season (1 Sept-30 Nov) No sale of *P. saltatrix*	Recreational anglers	KwaZulu-Natal
1985	Min.size (30cm) Bag limit (5) Closed season (1 Sept-30 Nov) No sale of *P. saltatrix*	Recreational anglers Spearfishers	KwaZulu-Natal and Cape
1992	Min.size (30cm) Bag limit (5) Closed season (1 Sept-30 Nov) No sale of *P. saltatrix*	Recreational anglers Spearfishers Commercial fishers (KwaZulu-Natal only)	KwaZulu-Natal and Cape

This disparity in regulations between the Cape and KwaZulu-Natal has resulted in the development of a large illegal market in KwaZulu-Natal (pers. obs.). Presently, *P. saltatrix* fetches a minimum price of R14 (US$ 3.80) per fish (most are less than 1kg). These high market prices have resulted in Western Cape commercial fishers illegally selling their *P. saltatrix* catches to non-registered intermediaries in KwaZulu-Natal. These market forces have also provided a strong incentive for anglers in KwaZulu-Natal to poach (i.e. to exceed daily bag limits, retain undersize fish and to fish during the closed season). The control of such illegal activities is extremely difficult. In 1987 there were estimated to be 92 000 resident shore-anglers in KwaZulu-Natal and 288 000 anglers countrywide (van der Elst, 1989). However, from April 1993 to March 1994 Natal Parks Board conservation officers reported only 295 offences relating to *P. saltatrix* in KwaZulu-Natal (Anon., 1994).

The minimum size limit of 30cm(TL) which corresponds to the length at 100% maturity of female *P. saltatrix* (van der Elst, 1976) is set for both the Cape and KwaZulu-Natal waters and is applicable to both commercial fishers and recreational anglers. Most anglers in KwaZulu-Natal adhere to this regulation. In a shore-angling survey conducted in KwaZulu-Natal between April 1994 and August 1995 it was found that <6% of the *P. saltatrix* sampled were less than the minimum size limit (van der Walt, 1995). Recreational anglers in both the Cape and KwaZulu-Natal and commercial fishers in KwaZulu-Natal are restricted to a daily bag limit of five *P.*

saltatrix/angler/day. However, in the Western Cape, commercial harvesters have no daily bag limits nor any other catch restrictions such as total allowable catches.

A closed season during the spawning period extends from 1 September to the last day of November of each year. The closed season was set up to protect the spawning stock and to reduce effort in the fishery. Although, the closed season is applicable in both KwaZulu-Natal and Cape waters *P. saltatrix* does not spawn in the Cape (van der Elst, 1976). The closed season applies also to commercial harvesting in the Cape although in reality, few *P. saltatrix* are harvested during this time in the Cape (Lamberth *et al.*, 1995) and therefore the regulation has little effect on reducing effort in this region.

No netting of this species is permitted in KwaZulu-Natal. In the multi-species seine netting fishery of False Bay, netters can legally harvest *P. saltatrix* but only as a bycatch, i.e. it cannot be a target species. The netters may retain and sell those fish that are above the legal size limit (Lamberth *et al.*, 1995). Lamberth *et al.* (1994) monitored 31% of seine hauls in False Bay from January 1991 to December 1992 and found that during this period over 17 000 *P. saltatrix* were harvested and ranged in size from 5 to 85cm (TL). Fifty five percent were immature and below the minimum legal size and *P. saltatrix* occurred in 62% of the hauls monitored. In False Bay, from 1985 to 1992, *P. saltatrix* numerically constituted 10%, 48% and 42% of the beach-seine, commercial linefishery and recreational shore-angling mean annual catch, respectively (Lamberth *et al.*, 1994).

The *P. saltatrix* fishery in the Cape was only regulated from 1985 (Table 1.1). In KwaZulu-Natal stringent management measures were introduced in the late 1970s (Table 1.1) when a declining CPUE (van der Elst, 1976) led many to believe that there had been a reduction in the stock during the period 1956 to 1973. This was believed to be the result of possible growth and recruitment overfishing. As this was the first recreational angling species to be regulated in KwaZulu-Natal this sparked wide public debate. The Smith Commission of Enquiry was appointed to resolve the issue (Natal Provincial Administration, 1979a; Natal Provincial Administration, 1979b; Natal Provincial Administration, 1979c). The Smith Commission was mandated to examine the validity that the *P. saltatrix* population was declining in KwaZulu-Natal, to identify the causative factors and to recommend conservation measures (Smith *et al.*, 1979).

With representation from the angling public and scientists it was concluded that there was a decline in *P. saltatrix* abundance primarily because of overfishing. However, pollution, increases in abundance of inshore sharks predating on *P. saltatrix* and natural fluctuations in *P. saltatrix* abundance due to environmental effects were not ruled out. Management regulations, although very unpopular at the time, were re-evaluated and there was a reduction of the closed season by one month (i.e. the closed season now extended from the 1 September to the 30 November of each year). Previously, the closed season included the month of December but the Commission noted that this "holiday" month was important in terms of attracting angling tourists to

KwaZulu-Natal. Based on this economic reason and that the spawning of *P. saltatrix* was on the decline during this period it was recommended that harvesting of *P. saltatrix* be allowed in December. The Commission also recommended that the present minimum size (30cm TL) be retained, the daily bag limit be increased from 2 to 4 *P. saltatrix*/angler/day, the sale of *P. saltatrix* to be prohibited and that the restrictions be applied over the long-term and only be reviewed once new data or arguments became available.

Although not part of the Commission's terms of reference it was recommended that the relevant authorities along the rest of the South African coast also take appropriate management measures for the conservation of *P. saltatrix*. At that time, however, this recommendation was not heeded.

What is clear from the historical implementation of management regulations (Table 1.1) is that regulations have been drawn up in isolation in different parts of the country. In KwaZulu-Natal there has been a deliberate move by the provincial authorities to prohibit commercial exploitation of *P. saltatrix* while restricting the recreational harvest. In the rest of the country the management strategy, since 1985, has been to protect the commercial fishery and limit the recreational harvest. The only effective management regulation for commercial harvesting in the Cape is a minimum size limit as the closed season in the Cape co-incides with a period of low abundance of *P. saltatrix* in this region. Since 1985 the recreational fishing regulations in the rest of the country have been in keeping with the regulations in KwaZulu-Natal.

These regulations (Table 1.1) have resulted in user conflict between *P. saltatrix* harvesters in the Western Cape, Eastern Cape and KwaZulu-Natal. Many anglers in the latter two regions believe that sacrifices are being made simply to protect commercial harvesting in the Western Cape.

1.3 Stock assessment

The first attempt to assess the stock status of *P. saltatrix* was carried out by van der Elst (1976) and was based on CPUE data from fishing tournaments of the Natal Coast Anglers Union (NCAU), an angling union in KwaZulu-Natal to which many rock and surf angling clubs are affiliated. The tournaments occurred bi-monthly and regularly between the years 1956 and 1973. Although, the annual time series of CPUE was highly variable from year to year, a fitted regression line to the time series resulted in a negative slope indicating a possible decline in abundance over this time period. The major criticism of this analysis is that CPUE from angling tournaments is not necessarily an index of *P. saltatrix* abundance in KwaZulu-Natal. The reason being that competition anglers (whose angling success is judged on a points scale) usually target cartilaginous fishes because their large weights contribute more points. In a study of the catch of cartilaginous fish during competitions van der Elst (1979) found that CPUE of cartilaginous fish increased significantly between 1956 and 1976 with corresponding decreases in CPUE of teleosts. This could be a result of targetting preference for these large cartilaginous fishes. Competition anglers seldom target *P. saltatrix* because of the relatively small size of this species. Guastella and Nellmapius (1993) found that *P. saltatrix* comprised a mere 7% (by number) of catches of shore-anglers participating in competitions in KwaZulu-Natal . In the False Bay area of the Western Cape, Bennett (1991) also analysed shore-anglers' competition data and found that between 1938 and 1985 *P. saltatrix* comprised only 1.2% (by number) of the total catch of "edible" species (i.e. excluding elasmobranchs). In contrast to studies based on competition data, *P. saltatrix* forms at least 50% of non-competitive shore-anglers' catches in KwaZulu-Natal (Guastella and Nellmapius, 1993). In another similar study, based on limited data of a roving creel census (Natal Parks Board law enforcement shore-patrols) Govender *et al.* (1995) found that between June and September 1994 *P. saltatrix* constituted 71% (by number) of all species harvested by shore anglers from the inshore waters of KwaZulu-Natal. Another reason that cautions against the use of CPUE as as index of *P. saltatrix* abundance is that over the years species composition of shore-based catches has changed. For example, the bony fish component of shore-based anglers' catches decreased from 95% of the catch in the period 1956 to 1960 to under 50% during 1978 to 1982 (van der Elst, 1989).

Hughes (1986) using age data from van der Elst (1976) undertook a yield-per-recruit assessment of the KwaZulu-Natal *P. saltatrix* fishery. She re-estimated the von Bertalanffy growth parameters using a weighted non-linear technique. She estimated that $F_{0.1}$ for the *P. saltatrix* fishery lay in the region of 0.35 to 0.6 year^{-1} based on the assumption that the ages-at-capture ranged from 1 to 3 years and that the natural mortality rate ranged from 0.41 to 0.48 year^{-1}. She also concluded that an increase in the minimum size limit would not benefit the fishery in yield terms. Unfortunately, there was insufficient data for her to estimate the fishing mortality rate and hence, few conclusions on the stock status of *P. saltatrix* could be made.

Butterworth *et al.* (1989) utilising the CPUE series reported in van der Elst (1976) and extending it with new data for the period 1974 to 1976 fitted a surplus production model to the data. They concluded that there had been a 72% (s.e. 11%) reduction in CPUE since the start of the fishery. They also concluded that the biomass in 1976 was 0.28 *K* (± 0.11) and as this value was below *K*/2 they suggested that possible biological overexploitation of the resource had occurred (*K* is a parameter of the Schaefer Surplus Production Model and defines the carrying capacity of the stock). However, they pointed out that these conclusions were open to debate as they had assumed a linear relationship between CPUE and effort - an assumption that only holds for equilibrium conditions. In the case of the *P. saltatrix* fishery, the stock is unlikely to be in equilibrium.

Based on a VPA analysis of catch-at-age data from KwaZulu-Natal for the period 1956 to 1976, which is largely prior to the introduction of *P. saltatrix* fishing regulations, Butterworth *et al.* (1989) estimated fishing mortality rates between 0.7

and 1 $year^{-1}$ which suggested that the stock was heavily exploited. The observed catch-at-age data were acquired from van der Elst (unpublished data). A von Bertalanffy growth function (van der Elst, 1976) was used to assign ages to the observed weights. This method would have resulted in biased age estimates. Van der Elst (1976) estimated von Bertalanffy parameters using a Walford plot and the estimates were: L_∞ = 84cm (TL), k=0.1966 $year^{-1}$ and t_0=0.03 years. Hughes (1986) utilising the same age-length data and a Walford plot arrived at different parameter estimates. She only reported the L_∞ value which was equal to 76cm (TL). However, she does comment that the parameter estimates of van der Elst (1976) did not give a good fit to the observed length-at-age data. Furthermore, the growth curve of van der Elst (1976) was based on a small sample of scales from 116 fish in which age estimates were verified.

Butterworth *et al.* (1989) utilising tagging data (obtained during the period of *P. saltatrix* fishing regulations) estimated fishing mortality rates in the *P. saltatrix* fishery. The analysis was based on a model that related mean time-at-liberty (d) to the instantaneous total fishing mortality rate (Z) i.e. $d=1/Z$. They assumed a tag loss of 2.5 $year^{-1}$ for operculum tags, that the natural mortality rate equalled 0.4 $year^{-1}$ and that the emigration rate equalled 6.4 $year^{-1}$ and thus estimated that the fishing mortality rate in KwaZulu-Natal to be 0.14 $year^{-1}$ and 0.05 $year^{-1}$ in the Cape. This analysis suggested that stock was underexploited or possibly recovering as a result of the newly introduced fishing regulations.

Management regulations for the *P. saltatrix* fishery were largely based on biological knowledge and economic considerations. Despite the limitations of some of the stock assessment analyses, fisheries managers largely ignored conclusions drawn from these studies. For example, despite Butterworth *et al.* (1989) illustrating a decline in fishing mortality rate between 1959 and 1976 managers still assumed that the observed decline in CPUE of *P. saltatrix* during this period was largely due to overfishing. Furthermore, van der Elst (1979) argued that the observed decline in *P. saltatrix* CPUE could be attributed to an increase in abundance of small inshore sharks predating on *P. saltatrix* .

1.4 National databases for recreational linefisheries

In South Africa there are many national databases in which fisheries-related data are captured. The best and most extensive databases consists of catch, effort and biological data on the major commercial fisheries. These fisheries are largely centred in Western Cape waters and target mainly fish such as hake, rock lobster, pilchards and anchovies. The recreational fisheries of South Africa were perceived to be economically unimportant when compared to the commercial industrial fisheries of South Africa and as such very little effort was allocated to collecting information on recreational fisheries. Nevertheless, there are two national databases in South Africa that have been designed to specifically capture information on marine recreational linefisheries: the Sedgwick's-ORI tagging programme and the National Marine

Linefish System (NMLS). In this study, data on *P. saltatrix* from these two national programmes have been utilised and brief synopses of these programmes and the *P. saltatrix* data collected within them follow.

1.4.1 The Sedgwick's-ORI tagging programme in relation to *P. saltatrix*

The Sedgwick's-ORI tagging programme is a national marine fish tagging programme involving fisheries researchers, recreational and commercial harvesters, government management agencies as well as a major corporate sponsor. Volunteers (mainly recreational anglers) tag and release fish (bony and cartilaginous) in an effort to increase current scientific knowledge on these species. The programme was initated in 1984 and by 1995 nearly 100 000 fish of 305 different species had been tagged by over 3 000 taggers. The history and details of this programme are discussed in van der Elst (1990). From the programme's inception in 1984, *P. saltatrix* has been one of the most popular "tagging fish". Over the nine year period to January 1993 some 2 737 *P. saltatrix* had been tagged with 108 recaptures reported. This represents a return rate of 3.95%. Note that as the programme is continuously updated on a daily basis the actual numbers of fish that are tagged and recaptured also change daily. For example, information on fish that are tagged and released sometimes takes several months to be entered into the system because fishers usually do not post their tagging information back promptly. As a result, tagging information is largely dependent on when the feedback run was done and not on the time period for which data is requested.

Consequently, it will be noticed that in this study marking and recapture information are numerically different in the different chapters even though the period under review is the same. Generally, these differences were minor for *P. saltatrix* and do not affect the conclusions of this study.

P. saltatrix are usually tagged with a dart tag with an approximately 90mm plastic streamer (designated "A" tags). Although, some taggers sometimes use incorrect tags that are designed for other species, only *P. saltatrix* tagged with "A" tags have been recaptured. For this reason, only the tag dynamics of *P. saltatrix* marked with "A" tags were considered in this study. A summary of the overall tag type statistics for *P. saltatrix* are shown in Table 1.2.

The tagging of *P. saltatrix* in six broad geographical areas is summarised in Table 1.3. The six areas are indicated in Figure 1.1. The release of tagged *P. saltatrix* occurs along the entire South African coast although the majority occurs along the along the coast of KwaZulu-Natal and the Eastern Cape (Table 1.3). Few *P. saltatrix* are tagged in the waters of the Western Cape coast. In Figure 1.3 the numbers of *P. saltatrix* released in 100km sections of the coast are shown.

Table 1.2 Tag types used for tagging *P. saltatrix* in the Sedgwick's-ORI tagging programme from Jan 1984 to Jan 1993. Only *P. saltatrix* tagged with "A" tags were considered further in this study. This is an example of a typical feedback from the programme. The feedback summary was performed on 4 February 1993.

TAG TYPE	No. TAGGED
TOTAL RELEASED	2737
A TAGS USED	2537
B TAGS USED (for billfish)	15
C TAGS USED (for sharks)	4
D TAGS USED (for fish <1kg)	181

Table 1.3. Tagging statistics for *P. saltatrix* in the Sedgwick's-ORI tagging programme for six areas off the South African coast. Area 1 - Zululand coast, area 2 - north coast of KwaZulu-Natal, area 3 - south coast of KwaZulu-Natal, area 4 - Transkei coast, area 5 - south-eastern Cape coast up to Cape Point, area 6 - western Cape coast from Cape Point to South Africa/Namibia border.

	AREA 1	AREA 2	AREA 3	AREA 4	AREA 5	AREA 6
NO. TAGGED	832	249	345	318	969	20
A TAGS USED	727	245	336	287	934	4
B TAGS USED	0	1	0	14	0	0
C TAGS USED	1	0	1	0	2	0
D TAGS USED	104	3	8	17	33	16
NO. RECAPTURED ("A" tags).	26	5	14	14	49	0
% RECAPTURED	3.6	2.0	4.2	4.9	5.3	0

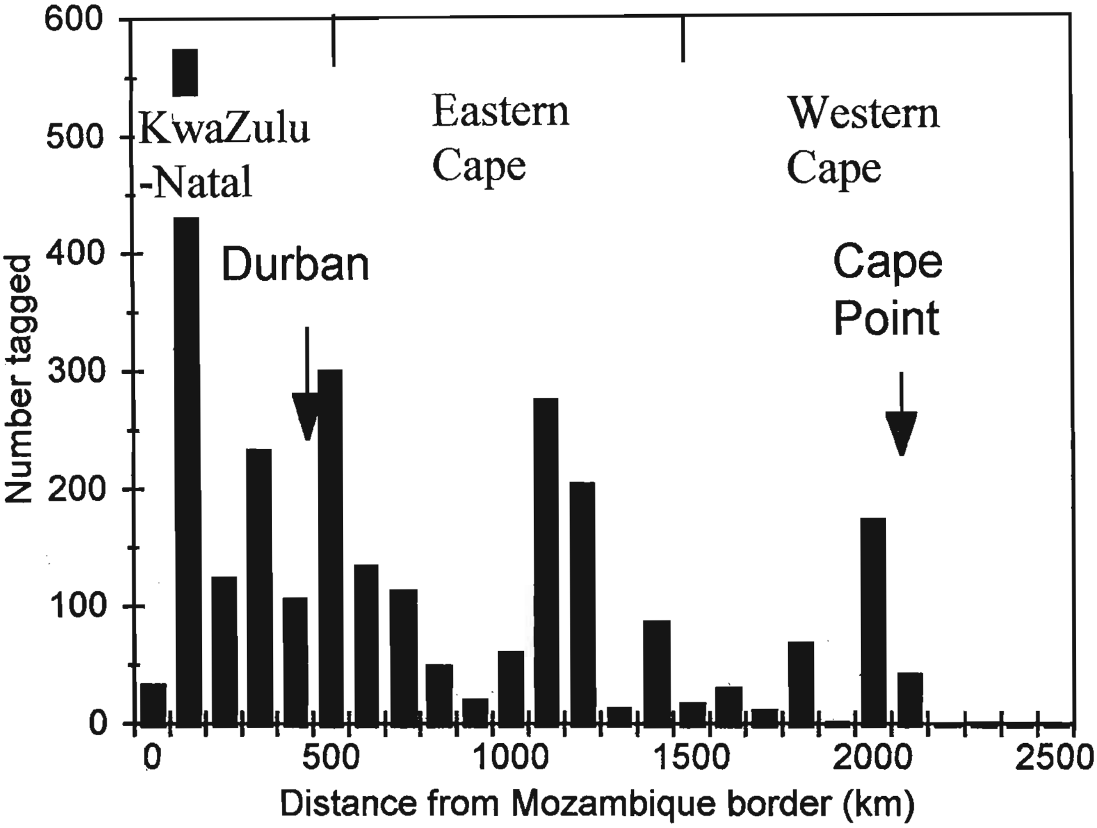

Figure 1.3 The number of *P. saltatrix* tagged along the Western Cape, Eastern Cape and KwaZulu-Natal coasts.

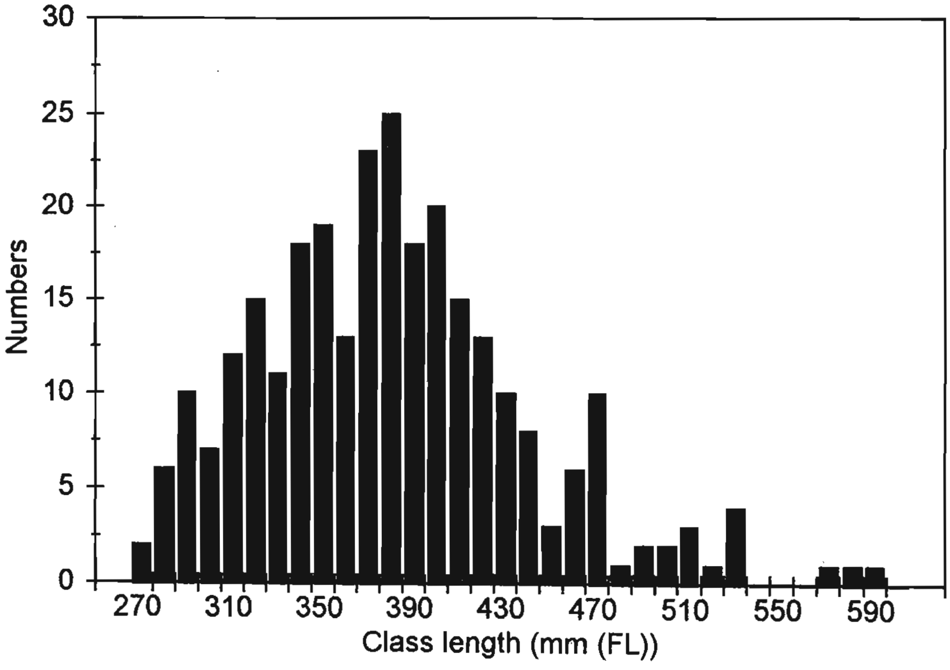

Figure 1.4 Length frequency distribution of *P. saltatrix* tagged along the Western Cape, Eastern Cape and KwaZulu-Natal coasts.

In Figure 1.4 the length frequencies of *P. saltatrix* tagged in KwaZulu-Natal and the Cape are shown. The tagged *P. saltatrix* ranged in size from 270 to 590 mm (FL) with an average size of 381 mm (S.D. = 59, *n* =280). The sample size of *P. saltatrix* tagged and with corresponding length measurements is very much smaller than the number tagged (2 537) because few anglers actually measure their tagged animals. As the fish were all larger than the length-at-50% maturity (230mm (FL), van der Elst, 1976), they were all assumed to be adult *P. saltatrix*.

Recaptured *P. saltatrix* travelled an average distance of 126km with one tagged individual covering a distance of 1 661km having being marked at Strandfontein in the Western Cape and recaptured at Amanzimtoti on the south coast of KwaZulu-Natal. It covered this distance in 82 days.

The average time-at-liberty was 54 days with the longest time being just over a year (374 days). The frequency distribution of the times-at-liberty of recaptured *P. saltatrix* is shown in Figure 1.5. The majority of *P. saltatrix* were recaught within two months of their release (Figure 1.5). Average speed of travel was 77 km.month^{-1} with a maximum speed of 938 km.month^{-1}

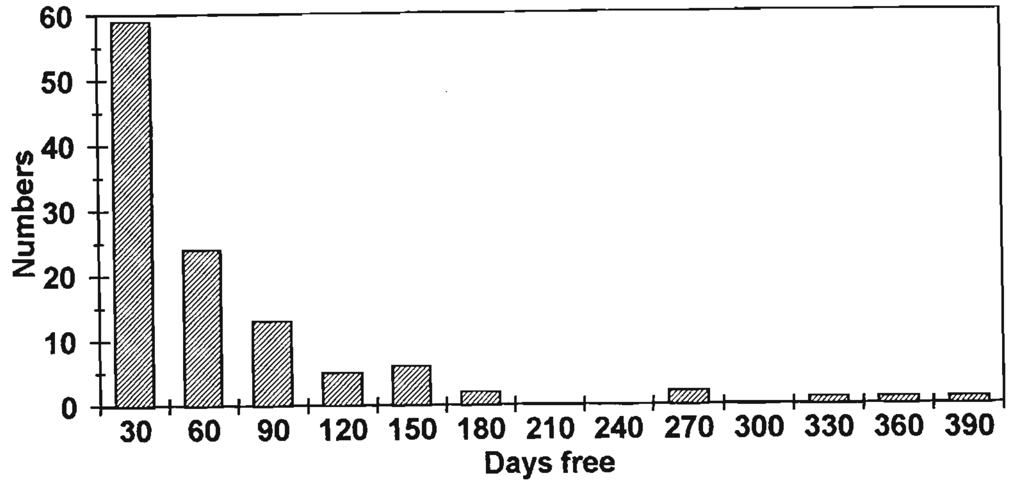

Figure 1.5 Frequency of times-at-liberty of recaptured *Pomatomus saltatrix*.

1.4.2 The National Marine Linefish System (NMLS) in relation to the *P. saltatrix* fishery

The NMLS is a national computerised catch and effort database in which data from South African commercial and recreational linefisheries are captured (Penney, 1993). Recreational catch and effort data are collected in the form of shore patrol records (a type of roving creel census associated with law enforcement patrols) of the Natal Parks Board, fishing competition results from shore, spear, light-tackle and ski-boat fishers, catch cards from controlled angling areas and voluntary daily catch cards from shore, spear, light-tackle and ski-boat fishers. Commercial catch and effort data are captured in the form of compulsory monthly catch returns from all registered linefishing vessels, landing reports from fisheries harbours and returns from major linefish dealers. At least 94% of commercial data emanates from the Western and Eastern Cape; the rest from KwaZulu-Natal. In contrast, 96% of recreational returns are received from KwaZulu-Natal compared to only 4% from the Western and Eastern Cape (Penney, 1993). The system has been in operation since 1985 and the number of commercial and recreational returns has increased steadly from 66 500 in 1985 to 127 000 in 1990 (Penney, 1993).

Mann (1995) has outlined various limitations to the recreational data captured in the NMLS. These include, in the case of voluntary catch cards, mis-identifications of fish species, incorrect weights, exaggeration and under-reporting of catch. The main drawback of angling competition data is that particular species are targetted and the NMLS, at present, does not take into account targetting preference. Data from the NPB shore-patrols is generally more accurate, although, until recently (1994) effort data were not recorded.

Only Guastella and Nellmapius (1993) and Govender *et al.* (1995) have specifically utilised *P. saltatrix* data captured in the NMLS. The study of Guastella and Nellmapius (1993) showed that, although *P. saltatrix* was the most important species in the shore-based fishery in KwaZulu-Natal, few shore-based competition anglers targetted *P. saltatrix* during tournaments. They also concluded that *P. saltatrix* was unimportant in the ski-boat linefishery, the spearfishery and the light-tackle fishery which operates mainly in estuaries.

In June 1994, the Natal Parks Board, in collaboration with the Oceanographic Research Institute, implemented a new shore-patrol data sheet for collection of shore angling data for the NMLS. The major differences between the old and new data sheets were that estimates of fishing effort and information on key fish species and invertebrates harvested were introduced. Govender *et al.* (1995) analysing 33% of the new shore-patrol forms submitted in 1994 found that in the 96 465 hours fished, 29 998 fish were caught of which 71% were *P. saltatrix*. In the Cape Vidal region which is situated on the Zululand coast of KwaZulu-Natal *P. saltatrix* formed 95% of the catch. This region also recorded the highest CPUE (1.15 *P. saltatrix*/angler hr). Other areas in KwaZulu-Natal in which *P. saltatrix* formed a significant proportion of the catch were Richards Bay (62%, CPUE=0.06 *P. saltatrix*/angler hr), Kingsburgh (70%, CPUE=0.1 *P. saltatrix*/angler hr), Scottsburgh (45%, CPUE=0.4 *P. saltatrix*/angler hr), Umtentweni (46%, CPUE=0.1 *P. saltatrix*/angler hr) and Trafalgar (91%, CPUE=0.2 *P. saltatrix*/angler hr) (Figure 1.1).

1.5 Objectives of this study

Mark-recapture methods that have been applied to fish populations traditionally, have been used to estimate population size (Lebreton *et al.*, 1992). However, tagging programmes can also contribute to understanding fish growth, survival and mortality rates, fish movement and migration rates, all of which can form some basic component of age-structured stock assessment models. This shift from the primary focus of estimating population size is reflected in recent research which has utilised data originating from the Sedgwick's-ORI tagging programme. For example, utilising mark-recapture data Govender (1994) had shown that the king mackerel *Scomberomorus commerson* deposited two opaque bands annually in the otolith. Attwood and Bennett (1994) have shown that galjoen *Dichistius capensis* tagged in the De Hoop Marine Reserve display either resident or nomadic behaviour in respect to movement out of the reserve thus benefitting adjacent exploited areas by restocking them with adult fish. From tagging data, Cliff *et al.* (in press) have estimated the population size of white sharks *Carcharodon carcharias* from Struis Bay to KwaZulu-Natal, as well as fishing and total mortality rates for this species. Their study provided evidence of the low stock size of white sharks along the southeastern coast justifying the protected status of this species in South Africa. In another study, Govender and Birnie (in press) estimated fishing and total mortality for juvenile dusky sharks *Carcharhinus obscurus* captured by recreational anglers and commercial fishers as well those harvested in shark meshing operations off the KwaZulu-Natal coast.

In all these studies, mark-recapture models were developed taking into account the unique nature of the Sedgwick's-ORI tagging programme. Many mark-recapture models have been developed for fish populations based on single batch release-multiple recapture studies (Hilborn, 1989; Kleiber *et al.*, 1987; Seber, 1982). Essentially, the Sedgwick's-ORI tagging programme is a multiple release-multiple recapture programme and thus makes the use of single batch release-multiple recapture models invalid (see section 1.6 below).

This study primarily attempts to address model development utilising mark-recapture data, for *P. saltatrix*, a species which is of major importance to the shore-based recreational linefishery of South Africa. It is important to note that the *P. saltatrix* data was merely used to illustrate the approach of models developed rather than to provide concrete management strategies for this species. In this study a general mortality model is intially developed and is then extended to include movement between two areas: the Cape (which combines the Eastern and Western Cape) and KwaZulu-Natal. It utilises mark-recapture data from the Sedgwick's-ORI tagging programme as well as effort and catch data from the National Marine Linefish System (NMLS). A simulation study is then undertaken to test the robustness of the mortality model in estimating an average fishing mortality rate given variable annual fishing mortality rates.

A stock assessment (using a delay-difference model) which is based on a time series of mean weights for *P. saltatrix* is then undertaken. The assessment provides estimates of relative annual biomass and catch. Necessary to this analysis is information on growth, hence an age and growth study based on otolith readings was also undertaken. The growth model incorporates mark-recapture data and size-at-age data. The tagging data were used to validate the assumption of annual periodicity in the deposition of seasonal bands in *P. saltatrix* otoliths.

Further, using a modified Beverton and Holt (1957) yield-per-recruit and eggs-per-recruit model, the present closed season for *P. saltatrix* was evaluated for its effectiveness in conserving egg production as well as reducing effort in this fishery. Alternative timing of the closed season as well as alternative closed season durations were also evaluated. The effectiveness of the closed season in reducing effort was examined by comparing fishing rates to harvest the same yield in closed versus continuous season scenarios. From this analysis recommendations in terms of closed season duration as well as timing thereof are made.

1.6 Introduction to recent multiple release- multiple recapture models developed for fish stocks

Following is a brief review of recent multiple release-multiple recapture models that have been developed for use in fish studies. Also, the similarities and differences between these recent models and the models developed in this study are discussed in general terms. In this study a multiple release-multiple recapture study is defined as one where fish are continuously marked and released throughout the study period (as opposed to a single batch release at the begining of the study period). The recapture of individuals also occurs throughout the study and recaptured animals are not returned alive to the tagged population sample.

In recent years, the development of multiple release-multiple recapture models for the estimation of survival rates in fish (and other animals), for example, has been facilitated, primarily, by advances in computer technology (Lebreton *et al.,* 1992). Seber (1982) provided the mathematical and statistical framework for the use of these models for estimating survival and population size parameters and drew on the work of researchers such as R. M Cormack, G.M. Jolly , B.F.J. Manly and M.J. Parr. The studies by Lebreton *et al.* (1992) and those of Burnham *et al.* (1987) provided a unified approach to model development, experiment design and maximum likelihood theory in multiple release- multiple recapture studies. All multiple release-mutiple recapture models have a common model structure which consists of two parts: a model that describes the survival of tagged animals over time and a model that predicts the rate of recapture of tagged animals. Table 1.4 gives an example matrix of expected survivors and recaptures for a three-year tagging and a four-year recovery study.

From the general multiple release-mutiple recapture matrix model depicted in Table 1.4 basic survival equations and recapture functions can then be specified depending on the fishery under study. For example in a closed exploited population (no immigration or emigration) the survival function S_i can be modelled as $S_i = \exp(-Z_i)$

where Z is the instantaneous total mortality rate and is equal to the sum of the instantaneous fishing mortality rate (F_i) in year i and the instantaneous natural mortality M (constant for each year) i.e. $Z_i = F_i + M$.

Table 1.4 Matrix of expected (a) survivors and (b) recaptures of a general multiple release-mutiple recapture model based on models of Seber (1982), Lebreton *et al.* (1992) and Burnham *et al.* (1987). The matrix is based on three tagging years and four recovery years. S_i is the annual survival function from year i to i+1, and f_i are the recapture rates in year i.

(a)

Year of tagging	**Numbers of fish tagged**	**Expected Survivors in year:**			
		1	2	3	4
1	N_1	N_1	N_1S_1	$N_1S_1S_2$	$N_1S_1S_2S_3$
2	N_2		N_2	N_2S_2	$N_2S_2S_3$
3	N_3			N_3	N_3S_3

(b)

Year of tagging	**Numbers of fish tagged**	**Expected Recaptures in year:**			
		1	2	3	4
1	N_1	N_1f_1	$N_1S_1f_2$	$N_1S_1S_2f_3$	$N_1S_1S_2S_3f_4$
2	N_2		N_2f_2	$N_2S_2f_3$	$N_2S_2S_3f_4$
3	N_3			N_3f_3	$N_3S_3f_4$

The recapture functions f_i can possibly written as the product of the exploitation rate (F_i/Z_i) and the tagged survivors in year i (e.g. N_1S_1 represents the number of fish tagged in year 1 that survive to year 2) and the death rate (1-exp(-Z_i(i))). For example, the recapture rate in year 2 can be written as

$$f_2 = \frac{F_2}{Z_2} N_1 S_1 (1 - e^{-Z_2})$$

In this example it is assumed that there is no tag loss and that all recaptured tags are reported. However, as would be seen in subsequent chapters these " tag errors" can be accounted for explicitly in multiple release-mutiple recapture models.

Note that the N_is in Table 1.4 can either be stratified in terms of age, sex or length class etc. or be unstratified, for example, representing a combination of age classes. The latter form was followed in this study as fishers seldom measured the length of their tagged fish, and hence, the tagged fish could not be assigned to either a length or age class.

Model parameters can then be estimated by minimising some objective function using maximum likelihood methods. For example Lebreton *et al.* (1992) and Burnham *et al.* (1987) assume that the tag recoveries can be approximated by multinomial distributions while other researchers have assumed Poisson distributions (Hilborn, 1989 and this study).

From Table 1.4 it can be seen that recoveries in each year have to be linked to the year in which they were tagged in order for the model to be implemented. In this study this linking was alleviated by developing a model in which recaptures in each year were derived from different years of tagging. This is shown in matrix form in Table 1.5 (using the general notation of Table 1.4)

Table 1.5 Matrix of expected (a) total annual survivors and (b) total annual recaptures of a multiple release-mutiple recapture model developed in this study. Notation used is defined as in table 1.4

(a)

Year of tagging	Numbers of fish tagged	Total Expected Survivors in each year from different tagging years			
		1	2	3	4
1	N_1	N_1			
2	N_2		$N_1S_1+N_2$		
3	N_3			$N_1S_1S_2+N_2S_2+N_3$	
4					$N_1S_1S_2S_3+N_2S_2S_3+N_3S_3$

(b)

Year of tagging	Numbers of fish tagged	Total Expected Recaptures in each year from different tagging years			
		1	2	3	4
1	N_1	N_1f_1			
2	N_2		$N_1S_1f_2+N_2f_2$		
3	N_3			$N_1S_1S_2f_3+N_2S_2f_3+N_3f_3$	
4					$N_1S_1S_2S_3f_4+N_2S_2S_3f_4+N_3S_3f_4$

The approach adopted in this study as outlined in Table 1.5 was adopted because of two practical reasons. Firstly, interrogation of the Sedgwick's-ORI tagging database for data required for the model outlined in Table 1.5 was much easier and shorter on computer time than compared to the data requirements for the model outlined in Table 1.4. Secondly, the spreadsheet programming of the model in Table 1.5 was easier to implement and debug than the model shown in Table 1.4. These cost savings in computer time are important when dealing with large databases such as the Sedgwick's-ORI tagging database.

Chapter Two

MORTALITY

2.1 Introduction

The principal aim of many studies of exploited fish populations is to investigate the decrease in abundance brought about by man on these populations i.e. to ascertain the mortality as a result of fishing. One way of estimating the fishing mortality rate is to tag and release a large number of fish and then recapture them. This can be illustrated as follows. If a known number of fish are tagged and released and it is assumed that this group of tagged fish decreases at a mortality rate (G), one may surmise that G comprises the sum of several independent components, namely, mortality that can be ascribed to man's fishing efforts (F) and losses due to other causes (X). The component (X) can include natural mortality (M), additional mortality as a result of tagging, errors because of the shedding of tags or the non-reporting of tags from captured animals and emigration of individuals from the areas of capture. In this, and subsequent chapters, some methods for the estimation of mortality rates for tagged *P. saltatrix* are explored taking these components into account. In this chapter, combined mortality rates for the Western Cape, Eastern Cape and KwaZulu-Natal are estimated.

2.2 The mortality model

A model was developed to estimate mortality rates for *P. saltatrix* and is based on two equations which are commonly applied in fisheries science, namely, the exponential survival equation and the Baranov catch equation (Ricker, 1975). The exponential survival equation describes the decline of a year class of fish with time and is expressed as

$$N_t = N_0 e^{-Zt} \qquad (2.1)$$

where

N_t = the number of *t*-aged fish,

N_0 = the number of recruits (0-aged fish), and

Z = the instantaneous total mortality rate.

Equation (2.1) can be modified to estimate Z using mark-recapture data. If N_0 now represents the number of fish marked at the beginning of time t=0, then N_t is the number of tagged fish that is alive at the beginning of time t.

The Baranov catch equation is usually used to estimate the catch-at-age t (C), given an estimate of the instantaneous fishing mortality rate (F) and is written as

$$C_t = N_t \frac{F}{Z}(1 - e^{-Zt}) \qquad (2.2)$$

By combining equation (2.1) with the Baranov catch equation (2.2) the number of tag returns (P) expected at beginning of time t can be estimated as

$$P_t = N_o \frac{F}{Z}(1 - e^{-Zt}) \tag{2.3}$$

given an estimate of Z, N_0 and F, the instantaneous fishing mortality rate.

2.2.1 A multiple release-multiple recapture model assuming constant mortality

Based on the above general equations (which assume a single batch release of tagged animals), the model was extended to include multiple releases and recaptures. It is assumed that tagging occurs at the beginning of a year while recaptures occur at the end. Assuming that T_t fish are tagged at the beginning of time interval t, then the total number of tagged fish that are at large at the beginning of the next time interval $t+1$ (N_{t+1}) is given by

$$N_{t+1} = T_t e^{-Z} \tag{2.4}$$

where Z is the total instantaneous mortality rate and is assumed to be constant. If T_t fish are tagged and some portion ($1-\alpha$) die from the tagging process or shed their tags immediately (type I losses) then αT_t are effectively tagged. Therefore, the number of tagged fish at large at the beginning of the $(t+1)$th period is

$$N_{t+1} = \alpha T_t e^{-Z} \tag{2.5}$$

If, at the beginning of the time interval $t+1$, a further T_{t+1} fish are marked and released then the number alive is expressed as

$$N_{t+1} = \alpha T_t e^{-Z} + \alpha T_{t+1} \tag{2.6}$$

The number of tagged fish surviving to the beginning of the next time interval $(t+2)$ can be written as

$$N_{t+2} = N_{t+1} e^{-Z} + \alpha T_{t+2} \tag{2.7}$$

where N_{t+1} is obtained from equation (2.6). In this way survivors from previous time intervals (multiple release tagging study) are accumulated in the function (2.7).

By applying the Baranov catch equation it can be shown that the number of tagged fish expected to be reported at the end of the $t+2$th time interval (R_{t+2}) is

$$R_{t+2} = \beta \frac{F N_{t+2}}{Z} (1 - e^{-Z}) \tag{2.8}$$

where β is a probability that an angler will report the tag from a recaptured fish in a usable form. It should be noted that in equation (2.8) the parameters α, β and F are confounded as a single parameter which is represented by their product ($\alpha\beta F$).

2.3 Model assumptions

The basic model assumptions are that marked and unmarked fish suffer the same mortality rate, that both groups are equally vulnerable to fishing and that the marked fish become randomly mixed with unmarked fish. It should be noted that these assumptions are not necessary for the application of the model developed because *only* marked animals are considered in the model. However, if comparisons are to be made between marked and unmarked animals based on the model, then these assumptions are necessary.

Depending on whether the population is closed or open the estimate of Z in the above model then represents fish losses as a result of the combined effects of natural mortality, fishing mortality, emigration, long-term tag shedding and tag-induced mortality (type II losses). In this study it was assumed that the population was open and therefore emigration of tagged *P. saltatrix* are acounted for in the model implicitly. The model assumption of constant mortality over the tagging study is probably unreasonable for *P. saltatrix*. Variable fishing mortality can be introduced into the model but this requires annual effort data or accurate estimates of catch and biomass, none of which are available for the whole *P. saltatrix* fishery. It should be noted that the fishing mortality rate estimated for the combined Eastern Cape, Western

Cape and for KwaZulu-Natal represents a mean estimate over the study period and variablity in the estimate will be reflected in the coefficient of variation. A low coefficient of variabilty would indicate that the assumption of constant mortality is a reasonable one (see simulation study).

2.4 Mark-recapture data

Mark-recapture data for *P. saltatrix* were obtained from the Sedgwick's-ORI tagging programme for the period 1984 to 1993. Only fish tagged with "A" tags were considered and only those marked fish released between January 1984 and December 1993 were considered in the mortality model. Over this time period, 2 640 *P. saltatrix* were tagged. *P. saltatrix* were tagged mainly along the Eastern Cape and KwaZulu-Natal coasts. The majority of *P. saltatrix* marking occurred during the months of the closed season (September to November) of each year. The mean number of *P. saltatrix* marked in each month was 21.6. A total of 113 was recaptured representing a return rate of 4.28%. The mean monthly recapture rate was 0.9. For this sample, the mean time-at-liberty was 52 days with a range from one to 374 days (see Figure 1.4, chapter one for the time-at-liberty frequency distribution). Based on 280 marked *P. saltatrix* in which the lengths were verified the following statistics were determined. *P. saltatrix* that were marked ranged in size from 270 to 590 mm (FL) and the average size was 381mm(FL) (see Figure 1.3, chapter one for size frequency distribution). Table 2.1 summarises the release and capture information for *P. saltatrix* which served as input to the mortality model.

Table 2.1. The number of *P. saltatrix* tagged and recaptured per year. Only *P. saltatrix* tagged with "A" tags were considered. *N* is the number marked while *O* is the observed number of recaptures.

YEAR	*N*	*O*
1984	58	3
1985	309	14
1986	282	11
1987	439	13
1988	288	10
1989	263	16
1990	281	12
1991	98	4
1992	333	14
1993	289	16

2.5 Estimating the parameters

Hilborn (1990) has shown that the sampling distribution of tag recoveries can be approximated by a Poisson distribution. The likelihood of the expected number of recoveries R_t for $t = 1 \ldots n$, given the observed number of tag recoveries O_t is

$$L(O_t|R_t) = \frac{e^{-R_t} R_t^{O_t}}{O_t!} \tag{2.9}$$

The total likelihood of observing all R_t given the corresponding O_t is the product of the individual likelihoods:

$$L(O|R) = \prod_{t=1}^{n} (e^{-R_t} R_t^{O_t} / O_t!) \qquad (2.10)$$

For computational convenience, the negative of the log-likelihood was calculated and forms the quantity to be minimised:

$$-\ln(L(\mathbf{P})) = -\sum_{t=1}^{n} \ln(e^{-R_t} R_t^{O_t} / O_t!) \qquad (2.11)$$

where **P** is a vector of the parameters of the model.

Given the number of *P. saltatrix* marked and the tag returns reported in each time interval, estimates of the parameters ($\alpha\beta F$ and Z) can be obtained by using a nonlinear minimisation routine that will find optimum parameter estimates that minimise the negative log-likelihood (equation 2.11).

Deviations of observed values from those estimated from the mortality model were examined using the "deviance" of McCullagh and Nelder (1983). The deviance is defined as

$$deviance_t = -2[L(O_t|R_t) - L(O_t|O_t)] \qquad (2.12)$$

where $L(x|y)$ is the log-likelihood of x given y. The deviance can be viewed as being analogous to residuals in least squares estimation. A large deviance value indicates a poor model fit to a particular pair of data points.

2.5.1 Precision of parameter estimates

Confidence bounds for the parameters of the mortality model were determined using the likelihood profile method (Schnute, 1989, Lebreton *et al.*, 1992) and a bootstrap technique (this method is discussed in detail in chapter four). For the likelihood profile method the 95% confidence interval for a parameter P_i of the vector **P** was determined by minimising the negative log-likelihood for a range of values of P_i with the remaining parameters being free. The 95% confidence point values of P_i are equal to the upper and lower boundary values of the range of P_i that satisfy the inequality

$$2[L(Y|\mathbf{P})-L(Y|\mathbf{P}_{best})]\leq 3.84 \qquad (2.13)$$

where $L(Y|\mathbf{P}_{best})$ is the negative log-likelihood of the best estimate of **P** and 3.84 is the value of the chi-squared distribution with 1df at confidence level 0.95.

Model parameter estimates and their precision for *P. saltatrix* were obtained by implementing the model in a QUATTRO PRO spreadsheet which was programmed with a function optimisation routine. To obtain an unconfounded estimate of F, independent estimates of the "nuisance" parameters α and β must be obtained. They are “nuisance” parameters as they cannot be estimated from the mark-recapture data alone.

2.6 Values for “nuisance” parameters

2.6.1 Reporting of recaptured tags - ß

Rudy van der Elst, Oceanographic Research Institute (pers. comm.) attempted to obtain an estimate of β, the probability of reporting, by inserting tags into known number of landed *P. saltatrix* without the knowledge of fishers and then noting the number of tags that were reported. This, however, proved unsuccessful. An estimate of non-reporting in the Sedgwick’s-ORI tagging programme was thus obtained by interviewing anglers at fishing tournaments and during field sampling by researchers of the Oceanographic Research Institute, Durban. An angler was asked if he or she at any time had landed a fish that had been marked with a tag. If the angler replied in the affirmative the interviewer then questioned the angler as to what he or she did subsequently with the tag. If the angler stated that he or she reported the tag to the address on the tag, the interviewer then verified this by asking about the type of feedback he or she received from the Tagging Programme Officer. From such data the β factor which is the number of usable returns to the total number of anglers interviewed that had caught a tagged fish was estimated. The fraction of anglers who do not report their tags (L) was expressed as

$$L = 1 - \beta = 1 - \frac{G}{I} \tag{2.14}$$

where

G = the number of interviewed anglers who had caught a tagged fish and reported it in a usable form,

I = the total number of interviewed anglers who had caught a tagged fish.

In this study it was assumed that all interviewed anglers who reported their tags did so in a usable form. This is a reasonable assumption since, for the recaptures to be usable, only the date and locality of the tagged recaptures are required and this information is usually provided by anglers (Elinor Bullen, Oceanographic Research Institute, pers. comm.). Data to estimate β were provided by Rudy van der Elst and Bruce Mann, both of the Oceanographic Research Institute, Durban. Of the 336 anglers interviewed 36 had caught a tagged fish. Of this figure 27 had returned the tag with usable information. This provides a β estimate of 0.75.

2.6.2 Estimating α - immediate tag shedding and tag-induced mortality

To provide an estimate of α, necessary data were obtained from a study of captive, chemically tagged *P. saltatrix* (Mann *et al.,* in prep.). A sample of 26 *P. saltatrix* ranging in size from 203 to 365mm (FL) were tagged with "A" tags and kept at Sea

World in a tank (34 000 *l*) with circulating sea-water. As part of the experiment, the tagged fish were injected with either oxytetracycline hydrochloride of concentration 15 mgl^{-1} at a dosage of 50 mg.kg^{-1} of fish or with corresponding dosages of saline solution. The *P. saltatrix* were monitored closely and those that died or shed their tags within 10 days of the initiation of the experiment were used to provide an estimate of α. The time period of 10 days was chosen because it was observed that after this period *P. saltatrix* usually did not display any ill-effects from the presence of a tag. The parameter α was calculated from the formula $\alpha = 1 - S$ where S is the number of *P. saltatrix* that either died or shed their tags within 10 days as a proportion of the total sample of fish tagged. In the study, two specimens died within 10 days. Both had also been chemically tagged with oxytetracycline hydochloride. No specimens shed their tags within 10 days. The parameter α was therefore estimated to be 0.92 i.e. type I losses equal 8%.

2.7 Simulation study

In the model it was assumed that the fishing mortality rate was constant. If the fishing rate varies from year to year then F provides an estimate of the average fishing mortality rate for the period under study. A Monte Carlo simulation was performed to test the robustness of the mortality model to this latter assumption. In Figure 2.1 a flowchart describes the steps undertaken during the simulation process.

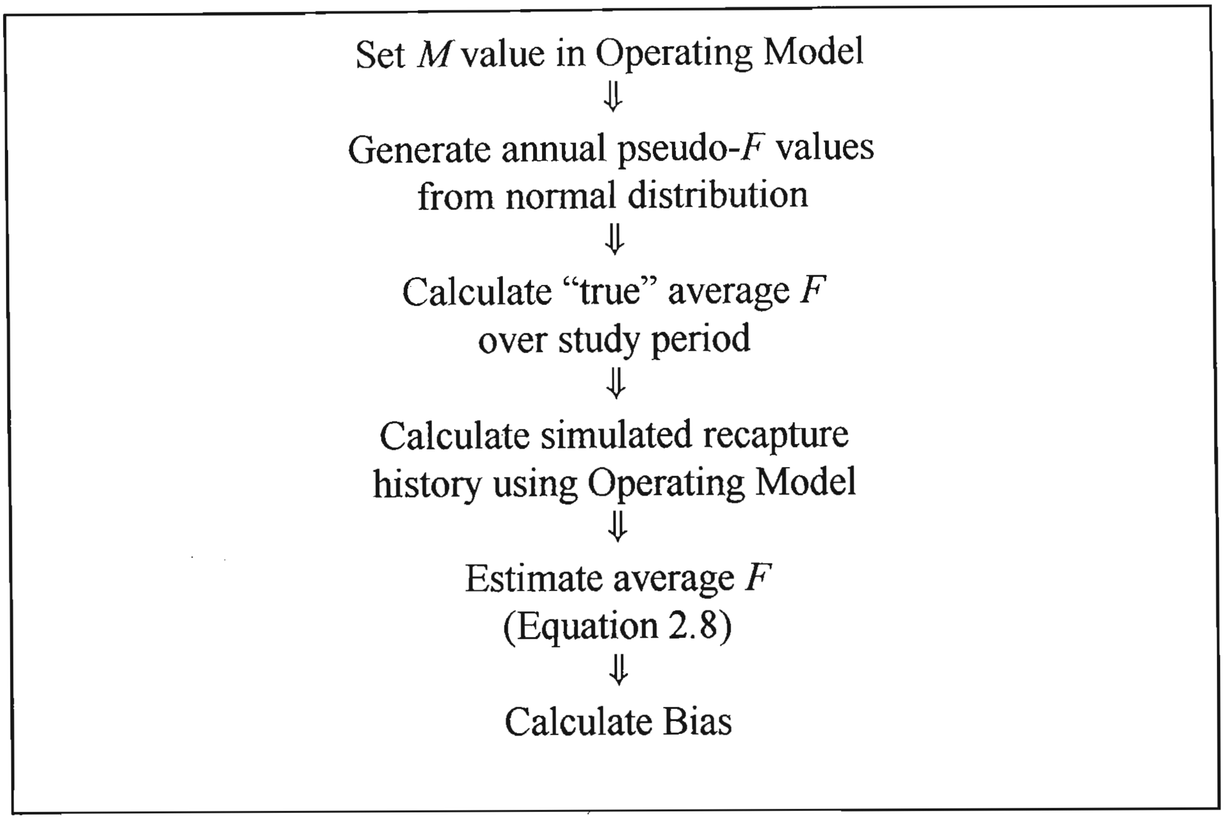

Figure 2.1 Flowchart of a single simulation run to test the robustness of the mortality model for estimating an average fishing mortality rate given annual variability in the fishing mortality rate.

2.7.1 Operating Model

An operating model was initially set up. Punt (1992) states that an operating model is a mathematical/statistical model of the fishery and in simulation studies is usually used to generate artificial data sets. In this study the operating model was used to generate the artificial recapture data sets and is illustrated as follows.

Pseudo-data sets of annual *F* estimates for the years 1984 to 1993 were randomly generated from a normal distribution. A normal distribution was chosen based on observed annual fishing mortalities estimated from a VPA study during the period

1956 to 1976 in KwaZulu-Natal (Butterworth *et al.* 1989) as well as fishing mortalities in KwaZulu-Natal from a mark-recapture study for the period 1987 to 1993 (see chapter three). In Figure 2.2 the observed fishing mortality frequencies for these periods are given as well as predicted frequencies (using the method described in Sokal and Rohlf (1995)) based on the observed mean fishing mortality of 1.03 year^{-1} (S.D.=0.657)).

The observed fishing mortality frequencies follow a normal distribution with a skewed right tail. It appears that the assumption of a normal distribution is valid as the observed mean *F* value (1.03 year^{-1}) corresponds closely to the observed median value (0.985 year^{-1}). In a true normal distribution both these measures of central tendency

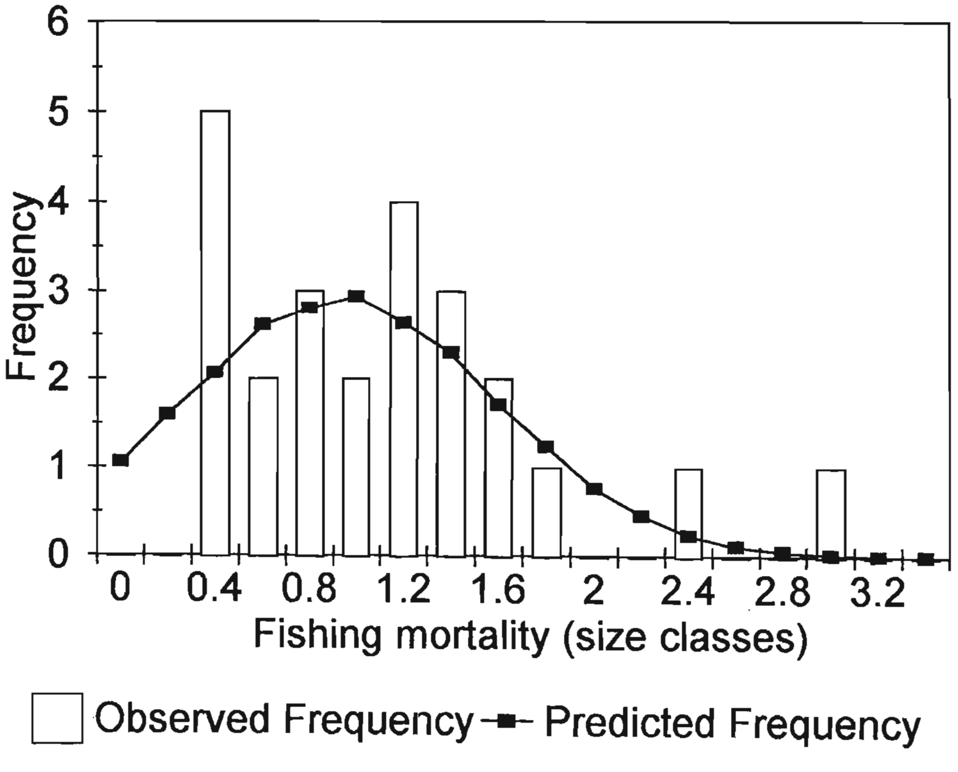

Figure 2.2 Observed and predicted fishing mortality frequencies for the period 1956 to 1976 (Butterworth *et al.* 1989) and for the period 1987 to 1993 (see chapter three). Predicted frequencies were drawn from a normal distribution with a mean fishing mortality of 1.03 year^{-1} and a standard deviation of 0.657 as calculated from the observed data.

are equal (Sokal and Rohlf 1995).

From these pseudo annual F estimates and using the observed number of annual taggings (Table 1.1) a pseudo-series of recapture histories were generated by re-arranging equation (2.8). For example the simulated recaptures in 1986 are obtained from the following equation

$$R^{p}_{1986}=\frac{F^{p}_{1986}N_{1986}}{F^{p}_{1986}+M}(1-e^{-F^{p}_{1986}-M})$$

where

R^{p}_{1986} = the pseudo number of recaptures for the year 1986,

F^{p}_{1986} = is the pseudo fishing mortality in year 1986 drawn randomly from the normal distribution,

N_{1986} = are the tagged survivors from previous years of tagging plus those newly tagged at the beginning of 1986; survivorship modelled as in equation (2.7), using the observed number of annual taggings

M = the instantaneous natural mortality rate assumed constant.

In order to simplify the study it was assumed that there was no shedding of tags, that all recaptured tags were reported, that there was no emigration and that the instantaneous natural mortality rate was constant and equalled 0.4 year^{-1} (sensitivity to this latter assumption was tested by setting the natural mortality rate to 0.3 and 0.5 year^{-1} and redoing the simulation for each M value).

The estimation procedure was then applied to each pseudo recapture data set to obtain parameter estimates of the average F. One hundred pseudo data sets were generated. This value of estimated average F was then compared to the "true" average F ("true" average F calculated from the pseudo annual F values generated from the normal distribution for the years 1984 to 1993) i.e.

$$\textit{true average } F = \frac{\sum_{1984}^{1993} F_i^p}{n}$$

where F_i^p is a pseudo generated fishing mortality in year i and n are the number of years.

The bias was expressed as

$$\textit{bias } (\%) = \frac{(\textit{estimated average } F - \textit{true average } F).100}{\textit{true average } F}$$

$$\textit{average bias} = \frac{\sum_{1}^{a} \textit{bias}}{a}$$

where a is the number simulations undertaken i.e. $a = 100$.

The average biases were expressed as both negative and positive biases. A negative bias indicates the degree of underestimation of the "true" value while a positive bias indicates the degree of overestimation.

The simulation was, therefore, used to test how effective the model was in estimating:

- the average fishing mortality rate over the study period (1984-1993) given annual variability in the fishing mortality
- the average exploitation rate ($F/(F+M)$) over the study period. The average exploitation rate is the ratio of the average fishing mortality to the average total mortality rate

Note that in both the above simulations the same data sets were used.

2.8 Results

Estimates of the model parameters and their precision are shown in Table 2.2. No right 95% confidence intervals could be reported for the likelihood profile method because the log-likelihood surface around the minimum was extremely flat especially on the right tail. This indicates that the point estimates of $\alpha\beta F$ and Z were estimated very poorly. This was confirmed using the bootstrap method which gave large CV values for the parameter estimates as well as wide confidence limits (Table 2.2).

Table 2.2. Parameter estimates of equation (2.7) and 95% confidence intervals for *P. saltatrix* mark-recapture data fitted to the model. In parenthesis are bootstrap estimates of the coefficients of variation and the 95% confidence intervals. Only the left 95% confidence intervals are reported for the likelihood profile method.

PARAMETER	ESTIMATE $year^{-1}$ (CV)	LEFT 95% C.I.	RIGHT 95% C.I.
$\alpha\beta F$	0.187 (422%)	0.043 (0.05)	- (0.70)
Z	4.37 (435%)	0.955 (1.34)	- (17.55)

In Table 2.3 observed and model-predicted recaptures are shown as well as their associated deviances. As indicated by the small deviance values there is close agreement between the observed number of recaptures and those predicted by the model (except for the years 1987 and 1989). Figure 2.3 shows the model fit to the observed data. In Table 2.4 the bias values are given for the simulation study.

Table 2.3. Observed and model-predicted recaptures and their associated deviance values for a *P. saltatrix* mark-recapture study.

Year	Observed Recaptures	Predicted Recaptures	Deviance
1984	3	2.45	0.113
1985	14	13.1	0.059
1986	11	12.1	0.103
1987	13	18.73	1.967
1988	10	12.43	0.508
1989	16	11.29	1.740
1990	12	12.04	0.000
1991	4	4.3	0.021
1992	14	14.15	0.002
1993	16	12.41	0.951

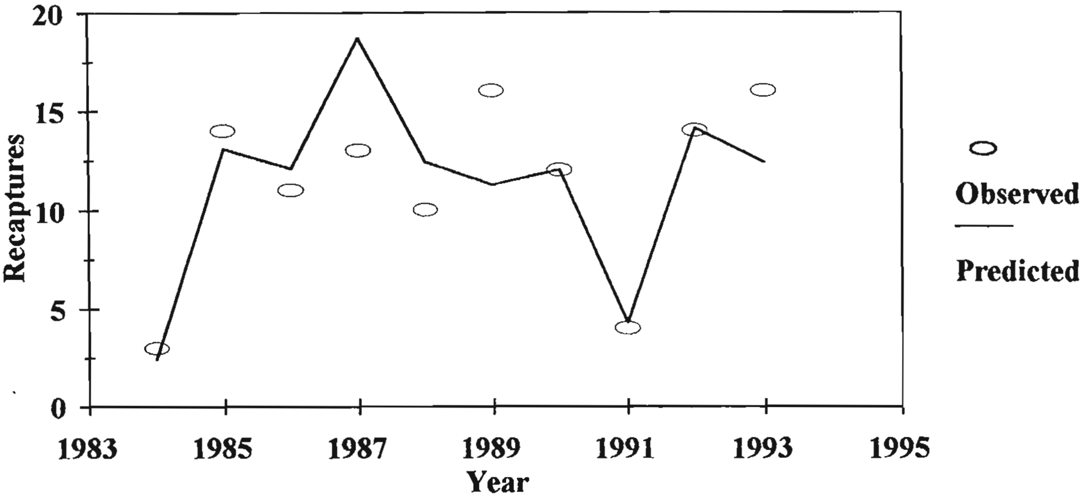

Figure 2.3 Observed and model predicted recaptures of *Pomatomus saltatrix* tagged along the Western Cape, Eastern Cape and KwaZulu-Natal coasts.

Table 2.4 Model bias values for the estimation of (a) the average fishing mortality rate for the years 1984 to 1993 as well as for (b) the exploitation rate for various values of natural mortality rates based on a Monte Carlo simulation.

(a) Average fishing mortality

	Average bias for 100 simulations (%)		
M	Positive	Negative	No. of positive bias
0.3	31	5	94
0.4	30	4.89	91
0.5	27	4.54	97

(b) Exploitation rate

	Average bias for 100 simulations (%)		
M	Positive	Negative	No. of positive bias
0.3	8.57	1.52	89
0.4	9.29	2.36	92
0.5	9.31	1.58	93

Overall, the mortality model overestimates the average fishing mortality rate by as much as 30%. However, better accuracy is obtained for the estimation of the exploitation rate with the positive bias usually less than 10% and the negative bias close to 2%. Generally the bias of the estimated parameters was not sensitive to the choice of natural mortality rate (Table 2.4). It is possible that the model overestimated the average fishing mortality with large bias because the sample size of annually tagged fish was too small or that the interannual variability in fishing mortality was too large. In an effort to determine which of these two factors resulted in an overestimate of the average fishing mortality rate with a large bias the simulation was re-run under two different scenarios:

1. The interannual variability in fishing mortality was reduced by setting a lower standard deviation (0.3) when drawing random annual fishing mortality rates from the fitted normal distribution
2. The number of annually tagged animals was arbitrarily increased by 20% annually

The results of this simulation are given in Table 2.5.From Table 2.5b it can be seen that increasing the sample size of animals tagged does not reduce the bias when estimating the average fishing mortality rate nor the exploitation rate. However, the bias in estimating the average fishing mortality rate and exploitation rate is substantially reduced when the interannual variability in fishing mortality rate is low

(Table 2.5a).

Table 2.5 Estimates of bias for the average fishing mortality rate and the exploitation rate for a model (a) that had low annual variability in fishing mortality and (b) when the observed number of annual tags released was increased by 20%. The base case values are from the simulation given in Table 2.4 and are shown in parenthesis. All simulations were run with $M = 0.4$ year^{-1}.

(a)

	Bias (%)		
	Positive	Negative	No. Of Positive Bias
Exploitation rate	2.58 (9.29)	0.8 (2.36)	79 (92)
average fishing mortality	10.3 (30)	4.16 (4.89)	75 (91)

(b)

	Bias (%)		
	Positive	Negative	No. Of Positive Bias
Exploitation rate	8.07 (9.29)	1.00 (2.36)	95 (92)
average fishing mortality	30 (30)	4.96 (4.89)	91 (91)

2.9 Discussion

In the simulation study for the range of natural mortality seeded (0.3 to 0.5 year^{-1}) it was found that the model overestimates the average fishing mortality rate and the exploitation rate. Generally, the average fishing mortality rate can be overestimated by 30% and the exploitation rate by 10%. The model, therefore, estimates the exploitation rate with greater accuracy than the average fishing mortality rate. The average fishing mortality bias is substantially reduced (by 20%) if the interannual variability in fishing mortality is low. It is therefore possible that the average fishing mortality rate estimated for *P. saltatrix* is probably overestimated by as much as 30% as the fishing mortality distribution for this species shows high annual variability (Figure 2.2). Based on the simulation study the exploitation rate for *P. saltatrix* estimated in this study is probably more accurate than the estimated average fishing mortality rate. Increasing the sample size of tagged animals does not reduce the bias when estimating either the average fishing mortality nor the exploitation rate. Therefore, it would seem that the model performs better if restricted to short-term tagging studies over which there is low variability in annual fishing mortality.

In the simulation it was assumed that there was no shedding of tags and that all recaptured tags were reported. Clearly this is unrealistic. However, since these two parameters cannot be estimated from the mark-recapture data and are confounded with the estimate of average *F*, the conclusions drawn from the simulation study are not affected by these assumptions.

The estimate of β which is the ratio of usable tag returns to the total number of tags captured was assumed to equal 0.75 for *P. saltatrix*. This implies that 25% of recaptured tags are not returned. Kleiber *et al.* (1987) estimated a best and a worst case β value of 0.87 and 0.47, respectively, in a study of Pacific skipjack tuna.

Although the sample size of anglers interviewed was small, it is believed that β equal to 0.75 may be a reasonable estimate for *P. saltatrix* recaptured in KwaZulu-Natal. In this region the Sedgwick's-ORI tagging programme is promoted more widely and the anglers interviewed in the survey where mainly from this region. Non-reporting in the rest of South Africa is probably higher than 25% as the programme is not actively promoted in this region and hence anglers may be complacent in returning tags. A nationwide study which will provide estimates of non-reporting of tags in KwaZulu-Natal and the rest of South Africa is presently underway (Bruce Mann, Oceanographic Research Institute, pers. comm.).

An α estimate of 0.92 could be too optimistic for *P. saltatrix* as the survival of tagged fish depends largely on the skill of the tagger (Hearn *et al.*, 1991) which, in the case of the experimental study, was probably higher than that for the average tagger. A further limit of this study is that no controls nor replicates were undertaken and this probably results in an overestimate of α. Furthermore, it cannot be shown conclusively that the *P. saltatrix* that died during the experiment died from the effects of the dart tag alone. Their death could have been as a result of the tetracycline injections. It is believed, however, that this is unlikely (Mann *et al.*, in prep.). The α estimate for *P. saltatrix* was, however, utilised in the analysis because it was similar to the value of 0.9 used by Kleiber *et al.* (1987) in their study of Pacific skipjack tuna. Furthermore, in an Australian study it was reported that the short-term mortality suffered by tagged *P. saltatrix* amounted to 10% which is similar to the value arrived at in this study

(Lenanton, 1995).

Given that the value of $\alpha\beta$ was estimated to be 0.69 for *P. saltatrix*, estimates of the instantaneous fishing mortality rate (F) can be obtained. The parameter F was estimated to be 0.27 year^{-1}. Table 2.4 gives estimates of fishing mortality for *P. saltatrix* for the years 1956 to 1973 (years prior to the introduction of fishing regulations) as well the period after the introduction of fishing regulations.

Table 2.4 Estimates of average fishing mortality rates for *P. saltatrix* for various years using different methods. The analyses were based on the assumption that $M = 0.4$ year^{-1}, and that the mean age-at-full recruitment and age-at-capture both equalled 3 years (Butterworth *et al.*, 1989).

METHOD	AREA	F (year^{-1})	STUDY PERIOD
VPA	KwaZulu-Natal	0.74	1956-1973
Catch Curve	KwaZulu-Natal	0.44	1956-1973
Catch-at-age (different to VPA)	KwaZulu-Natal	0.74	1956-1973
Tagging	KwaZulu-Natal	0.14	1981-1983
Tagging	Eastern & Western Cape	0.05	1981-1983

Butterworth *et al.* (1989) estimated F values for *P. saltatrix* ranging from 0.7 -1.0 year^{-1} based on a VPA analysis. Such high F values were probably a result of the fact that the VPA analysis was based on age data obtained prior to the period of fishing regulations currently imposed on *P. saltatrix*. During this period, fishing pressure on *P. saltatrix* was believed to be very high. However, estimates of F determined by

Butterworth *et al.* (1989) from a tagging study during the period of imposed fishing regulations in KwaZulu-Natal, indicated a decrease in fishing mortality when compared to the time period prior to fishing regulations (Table 2.4). Their estimate of *F*, in this case, was similar but lower than the estimate of *F* determined in this study. This decrease in average *F* cannot simply be ascribed to the positive effects of the fishing regulations because in the VPA analysis (which utilised catch-at-age data prior to any regulations), Butterworth *et al.* (1989) noted that from 1959 to 1972 there was a general decline in fishing mortality for *P. saltatrix*. The increase in the average *F* from the period of fishing regulations (as shown by the tagging study of Butterworth *et al.* (1989) and the present study) could be a result of the increase in numbers of anglers that enter the fishery annually. The number of fishers that entered the rock and surf fishery of KwaZulu-Natal nearly doubled from 1975 to 1987 (van der Elst, 1989).

The estimate of the total mortality rate (*Z*) for *P. saltatrix* is much larger than the estimate of *F*. The estimate of *Z* is 4.37 year^{-1}. Based on the mean time-at-liberty of tagged fish, Butterworth *et al.* (1989) derived a formula to estimate *Z* (see chapter one for equation), from which they estimated a total mortality rate of 10.1 year^{-1} for *P. saltatrix* based on their tagging data. Their estimate of *Z* is much higher than that estimated in this study. A possible reason is that tag shedding and tagging mortality were higher in their study as *P. saltatrix* were tagged with operculum tags. In a tank study it was found that these tags were not retained for long periods of time and there was high mortality that could be attributed to the presence of the tag (van der Elst, 1990).

The difference between *Z* and *F* provides an estimate of *X* which is the sum of the natural mortality rate, the emigration rate and long-term tag shedding and tag-induced mortality rates. For *P. saltatrix*, *X* was estimated to be 4.1 year^{-1}. If it is assumed that *M* for *P. saltatrix* ranges from 0.4 to 0.5 year^{-1} (Butterworth *et al.*, 1989; Hughes, 1986) and is reasonable for tagged *P. saltatrix* then the combined effects of emigration, long-term tag shedding and mortality as a result of tagging is exceedingly high in *P. saltatrix*. If we assume that the latter two effects are minimal as suggested by the study on captive, tagged *P. saltatrix* (Mann *et al.*, in prep.) it could be concluded that the *P. saltatrix* emigration rate is very high. This is to be expected in a highly migratory species such as *P. saltatrix* (Kendall and Walford, 1979; van der Elst, 1976).

In their analysis, Butterworth *et al.* (1989) assumed a *M* value equal to 0.4 year^{-1} while Hughes (1986) assumed an *M* range of 0.41 to 0.48 year^{-1} for *P. saltatrix* - all of which are higher than the value of *F* estimated in this study. The maintenance of a fishing mortality rate close to the natural mortality rate is often a management goal, based on the belief that maximum sustainable yield occurs at this point (Clark, 1991). Thus, it would appear that, at present, biological overexploitation is not occurring in the South African *P. saltatrix* fishery. However, taking into account recruitment fluctuations, Beddington and Cooke (1983) recommended maintaining *F* below 0.3*M* which would indicate possible biological overexploitation in the South African *P. saltatrix* fishery. In contrast, however, a number of stocks have been shown to have *F* values corresponding to maximum sustainable yields that are larger than the value of *M* estimated for these stocks (Caddy and Csirke, 1983). These studies, however, assume that the whole stock is available to fishing. A high emigration rate, as suggested by this study, would indicate that a large percentage of the population is not available to anglers. Note that in the model, recaptured fish that return to their place of tagging are not treated as fish that have emigrated. It is possible that a large portion of the stock is not available to fishing because the majority of *P. saltatrix* harvesting occurs from the shore using rod and line and those fish beyond casting distance will not be available to the angler. This migration aspect is explored in greater detail in the next chapter.

Chapter Three

MIGRATION

3.1 Introduction

Using CPUE data, van der Elst (1976) showed that *P. saltatrix* are seasonally abundant along the KwaZulu-Natal coast with abundance in any particular area related to movement of *P. saltatrix* shoals through the area. The primary stimulus for movement from the Western and Eastern Cape to KwaZulu-Natal during winter is believed to be related to spawning. However, the physiological need to move to warmer waters (*P. saltatrix* are infrequently caught below 15 °C) and the availability of prey such as *Sardinops sagax* along the KwaZulu-Natal coast during winter may also stimulate this migration (van der Elst, 1976). Seasonal migration has an important bearing on availability of *P. saltatrix* for harvesting by anglers and should therefore be accounted for in stock assessment analyses.

In this chapter the seasonal migration of *P. saltatrix* along the coast of South Africa is investigated. The movement of *P. saltatrix* in and out of the coastal waters of KwaZulu-Natal is quantified. The analysis is based on a modification of a model described by Hilborn (1990) which utilised mark-recapture data. The model simultaneously estimates *P. saltatrix* movement parameters, annual fishing mortalities in KwaZulu-Natal and the natural mortality rate.

3.2 The movement model

Hilborn's (1990) general movement model has been adapted for the available data on *P. saltatrix*. The model was modified to describe annual movement of *P. saltatrix* into and out of KwaZulu-Natal coastal waters and, unlike Hilborn's technique, provides estimates of instantaneous rates of mortality and migration. Tagging of *P. saltatrix* occurs in KwaZulu-Natal and the adjacent Eastern and Western Cape regions. Given estimates of fishing effort for *P. saltatrix* in KwaZulu-Natal, the model provides estimates of the proportion of the *P. saltatrix* stock moving into KwaZulu-Natal coastal waters from the rest of South Africa and the proportion of the *P. saltatrix* stock moving from KwaZulu-Natal to other regions. The model also provides estimates of fishing and natural mortality rates in KwaZulu-Natal. Note that since suitable fishing effort data are only available for KwaZulu-Natal, the model was modified to estimate fishing mortalities for KwaZulu-Natal alone. The model has three major components: (1) a population dynamics and movement model for marked *P. saltatrix*, (2) an observation model describing the capture of marked individuals, and (3) a model specifying the likelihood of recoveries of tagged *P. saltatrix*.

3.2.1 Population dynamics and movement model

This component of the model describes how a group of marked fish survive and move over a period of time. It is assumed that tagging of *P. saltatrix* occurs simultaneously at the beginning of the time period in both KwaZulu-Natal and the rest of South Africa (Eastern and Western Cape) and that there is movement between these areas. It is also assumed that survival of tagged *P. saltatrix* is not affected by movement and is a function of the instantaneous annual rate of fishing and natural mortality. Based on these assumptions the number of marked *P. saltatrix* alive in KwaZulu-Natal at the end of time period $t+1$ is described by

$$N_{(n,t+1)} = [N_{(n,t)} + T_{(n,t+1)}(1 - e^{-P_{no}}) + T_{(c,t+1)}\ e^{-P_{cn}}](e^{-F_{n,t+1} - M})$$

$$F_{n,t} = E_{n,t}q \qquad \textbf{(3.1)}$$

where

$n =$ index for KwaZulu-Natal,

$c =$ index for the Cape (Eastern & Western Cape),

$M =$ the instantaneous natural mortality rate (assumed to be constant),

$P_{no} =$ the instantaneous rate of emigration of *P. saltatrix* from KwaZulu-Natal to other areas (the Cape)(assumed to be constant for each year),

$P_{cn} =$ the instantaneous rate of immigration of *P. saltatrix* from the Cape to KwaZulu-Natal (assumed to be constant for each year),

$T_{(n,t+1)} =$ the number of *P. saltatrix* tagged in KwaZulu-Natal at the beginning of time $t+1$, and

$T_{(c,t+1)} =$ the number of *P. saltatrix* tagged in the Cape at the beginning of time $t+1$.

$F_{n,t}=$ the instantaneous fishing mortality rate at time t in KwaZulu-Natal,

$E_{n,t}=$ effort directed at *P. saltatrix* in KwaZulu-Natal at time t,

$q=$ the catchability co-efficient, assumed to be constant,

$N_{(n,t)}=$ are the numbers of tagged fish in KwaZulu-Natal that survive to the end of time period t. Note that this function accumulates the number of tagged survivors from previous time intervals (the survivors also include those that moved from the Cape to KwaZulu-Natal).

Taking into account immediate tag shedding and tag-induced mortality (see chapter two), equation (3.1) can be rewritten as

$$N_{(n,t+1)}=[N_{(n,t)}+\alpha T_{(n,t+1)}(1-e^{-P_{no}})+\alpha T_{(c,t+1)}\ e^{-P_{cn}})](e^{-F_{n,t+1}-M}) \tag{3.2}$$

where α is the proportion of *P. saltatrix* that survive type I mortalities.

3.2.2 Observation model

This component of the model is based on the Baranov catch equation (Ricker, 1975). It predicts the number of marked *P. saltatrix* that are recovered and reported and is based on the prediction of the number alive which is derived from equation (3.2). The expected number of tag recoveries reported in KwaZulu-Natal at end of time $t+1$ is thus

$$R_{(n,t+1)}=\beta\frac{F}{Z}[N_{(n,t)}+\alpha T_{(n,t+1)}(1-e^{-P_{no}})+\alpha T_{(c,t+1)}\ e^{-P_{cn}}](1-e^{-F_{n,t+1}-M}) \tag{3.3}$$

where β is the proportion of recovered tags that are reported to the management agency in a usable form. Estimates of α and β were the values used in chapter two.

3.2.2.1 Timing of migration

In equation (3.2) and (3.3) it is assumed that tagging and emigration occur instantaneously at the beginning of the year while recaptures occur at the end. In the following analysis it was assumed that emigration occurred 6 months after tagging i.e. tagging occurs at the beginning of the year, emigration in the middle of the year and recaptures at the end. To take this into account equation (3.2) is rewritten as

$$N_{(n,t+1)}=[N_{(n,t)}+\alpha T_{(n,t+1)}(1-e^{-P_{no}/2})+\alpha T_{(c,t+1)}\ e^{-P_{cn}/2}](e^{-F_{n,t+1}-M}) \tag{3.2.1}$$

while equation (3.3) is rewritten as

$$R_{(n,t+1)}=\beta\frac{F}{Z}[N_{(n,t)}+\alpha T_{(n,t+1)}(1-e^{-P_{no}/2})+\alpha T_{(c,t+1)}\ e^{-P_{cn}/2}](1-e^{-F_{n,t+1}-M}) \tag{3.3.1}$$

3.2.3 Likelihood for mark-recapture data

Hilborn (1990) has shown that the sampling distribution of tag recoveries can be approximated by a Poisson distribution. The third model component specifies the likelihood (*L*) of the number of recoveries being reported if the population dynamics and observation model are true. The likelihood of the expected number of recoveries $R_{n,t}$, t=1...*n*, given the observed number of tag recoveries $O_{(n,t)}$ is

$$L(O_{(n,t)}|R_{(n,t)}) = \frac{e^{-R_{(n,t)}}R_{(n,t)}^{O_{(n,t)}}}{O_{(n,t)}!} \tag{3.4}$$

The total likelihood of observing all $O_{(n,t)}$ given the corresponding $R_{n,t}$ is the product of the individual likelihoods:

$$L(O|R) = \prod_{t=1}^{n}(\frac{e^{-R_{(n,t)}}R_{(n,t)}^{O_{(n,t)}}}{O_{(n,t)}!}) \tag{3.5}$$

For computational convenience, the negative of the log-likelihood was calculated and this equation formed the quantity to be minimised:

$$L(P) = -\sum_{t=1}^{n}\ln(\frac{e^{-R_{(n,t)}}R_{(n,t)}^{O_{(n,t)}}}{O_{(n,t)}!}) \tag{3.6}$$

where *P* is a vector of the parameters of the model. The whole model was implemented in a QUATTRO PRO spreadsheet which was programmed with a function optimisation routine. Confidence intervals (95%) were calculated using the likelihood profile and the bootstrap methods (see chapter two and four, respectively, for the technique descriptions).

3.3 Mark-recapture and KwaZulu-Natal fishing effort data

The model requires as input, tagging and fishing effort data. Mark-recapture data for *P. saltatrix* for the period January 1987 to December 1993 were obtained from the Sedgwick's-ORI tagging programme (Table 3.1). The data were divided into the two areas where tagging of *P. saltatrix* occurred : KwaZulu-Natal and the Cape (Eastern and Western Cape).

Table 3.1 Annual mark-recapture and effort data for *P. saltatrix* which served as input to the movement model. Cape refers to the Eastern and Western Cape regions. Density of effort data from NPB shore-patrols/NMLS.

YEAR	NUMBER MARKED		KWAZULU-NATAL	
	KWAZULU-NATAL	CAPE	RECAPTURES	EFFORT (rods/km)
1987	212	242	8	3.32
1988	146	145	6	1.97
1989	93	201	4	1.52
1990	267	82	8	2.05
1991	64	58	1	2.21
1992	202	156	8	2.54
1993	127	189	11	4.18

Fishing effort density data for *P. saltatrix*, for the same period as the tagging study, are available for KwaZulu-Natal and were extracted from the Natal Parks Board (NPB) shore-patrol data within the National Marine Linefish System (NMLS) (Table 3.1). *Pomatomus saltatrix* is the primary target species for shore-based angling in KwaZulu-Natal and it constitutes nearly 50% (by number) of all species harvested annually from the shore (Guastella and Nellmapius, 1993). The number of fishing rods, recorded by NPB staff, per kilometre of coast was therefore regarded as a reliable index of total fishing effort in KwaZulu-Natal. The product of the total fishing effort and the proportion of *P. saltatrix* in the total number of fish sampled was assumed to be proportional to the fishing effort directed at *P. saltatrix* (Butterworth *et al.*, 1989). The annual fishing effort index (E_t) for *P. saltatrix* (Table 3.2) was calculated as

$$E_t = \frac{\textit{Annual rod count}}{\textit{total km patrolled}} \cdot \frac{\textit{Number of P. saltatrix counted}}{\textit{total fish counted}}$$

3.4 Results

Table 3.2 gives the results of the general movement direction and movement speed for *P. saltatrix* tagged in KwaZulu-Natal and the Cape during summer (November to April) and winter (May to October).

During winter 62% of *P. saltatrix* tagged in the Cape moved in a northeasterly direction towards KwaZulu-Natal at considerable speed (242 km.month^{-1}) while only 20% moved in the opposite direction at very low speeds (40 km.month^{-1})(Table 3.2). During the same time period a smaller percentage of *P. saltatrix* tagged in KwaZulu-Natal (30%) also moved in a northeasterly direction at a more moderate speed (88 km.month^{-1}). Some 53% of *P. saltatrix* tagged in KwaZulu-Natal during winter moved in a southwesterly direction at a moderate speed (69 km.month^{-1}). This suggests that the predominant movement during winter is in a northeasterly direction from the Cape to KwaZulu-Natal.

During summer some 33% of *P. saltatrix* tagged in KwaZulu-Natal moved in a southwesterly direction at a relatively fast speed (123 km.month^{-1}) while 50% moved in a northeastly direction at a low speed (50 km.month^{-1}). In the Cape 28% of *P. saltatrix* tagged in summer moved southwestward at a moderate speed (86 km.month^{-1}) while a slightly higher percentage (38%) moved northeastward at very low speed (27 km.month^{-1}). Generally, then, in summer *P. saltatrix* tagged along the Cape and KwaZulu-Natal coasts moved relatively fast in a southwesterly direction but in both areas a considerable percentage moved in the opposite direction at low to moderate speeds.

Of the 1 111 *P. saltatrix* marked in KwaZulu-Natal from 1987 to 1993, 4% were recaptured with all recaptures being taken in KwaZulu-Natal. However, of the 1 073 *P. saltatrix* marked during this same period in the Cape, 5% were recaptured in the

Cape and 1% recaptured in KwaZulu-Natal.

Table 3.2 Percentage of tagged *P. saltatrix* moving in a northeasterly (NE) or southwesterly (SW) direction along the eastern coast of South Africa. Speed of migration during summer (Nov to Apr) and winter (May to Oct) in KwaZulu-Natal and the Cape (Eastern and Western Cape) are indicated. The seasons are based on the time at tagging.

CAPE			
	DIRECTION	PERCENTAGE MOVING	AVERAGE SPEED ($km.month^{-1}$)
Summer	NE	38	27
	SW	28	86
Winter	NE	62	242
	SW	21	40
KWAZULU-NATAL			
Summer	NE	50	50
	SW	33	108
Winter	NE	30	88
	SW	53	69

Simultaneous estimation of the parameters q, P_{no}, P_{cn} and M was difficult as some of the parameters were confounded. It was therefore decided to fix M for a range of values and estimate the other free parameters. Table 3.3 gives the results of this analysis as well as the 95% confidence intervals. As there was no difference in the parameter estimates whether it was assumed that emigration occurred at the time of tagging or whether it occurred at the middle of the year parameter estimates and confidence bounds reported are the same for both models. The catchability coefficient (q), the instantaneous rate of immigration of *P. saltatrix* from the Cape to KwaZulu-

Natal (P_{cn}) and the instantaneous rate of emigration of *P. saltatrix* from KwaZulu-Natal (P_{no}) did not vary substantially for the range of M assumed (Table 3.3). The rate of immigration into KwaZulu-Natal from the Cape was much higher than the rate at which *P. saltatrix* emigrate from KwaZulu-Natal to other areas. The rate of emigration from KwaZulu-Natal into other areas (P_{no}) was directly related to the value of M assumed while the rate of immigration of *P. saltatrix* into KwaZulu-Natal from the Cape (P_{cn}) as well as the estimate of q was inversely related, being highest for low values of M (Table 3.3).

Table 3.3 Estimates of *P. saltatrix* emigration and catchability parameters for a range of assumed natural mortality (M) values. Values in parentheses are 95% confidence ranges estimated using the bootstrap technique. Values in square brackets are the instantaneous rates expressed as annual percentages. Parameter estimates and confidence bounds were the same whether it was assumed that emigration occurred at the time of tagging or whether it occurred in the middle of the year.

	M=0.5 yr^{-1}	M=0.4 yr^{-1}	M=0.3 yr^{-1}
P_{no} (yr^{-1})	0.0402 [4%] (0.0094-0.0784)	0.0364 [4%] (0.0117-0.077)	0.0333 [3.3%] (0.0111-0.0627)
P_{cn} (yr^{-1})	3.16 [96%] (2.51-4.32)	3.21 [96%] (2.55-5.073)	3.25 [96%] (2.56-4.39)
q(km/rods/yr)	0.62 (0.21-3.07)	0.68 (0.27-3.76)	0.76 (0.28-2.48)

Estimates of the 95% confidence intervals for the parameters using the likelihood profile method could not be attempted as the negative log-likelihood surface at the minimum was extremely flat and as a result large changes in the parameters yielded small changes in the log-likelihood. This shows that although the point parameter estimates are fairly well estimated they have extremely wide confidence ranges. This was confirmed by the bootstrap estimates of the 95% confidence ranges (Table 3.3).

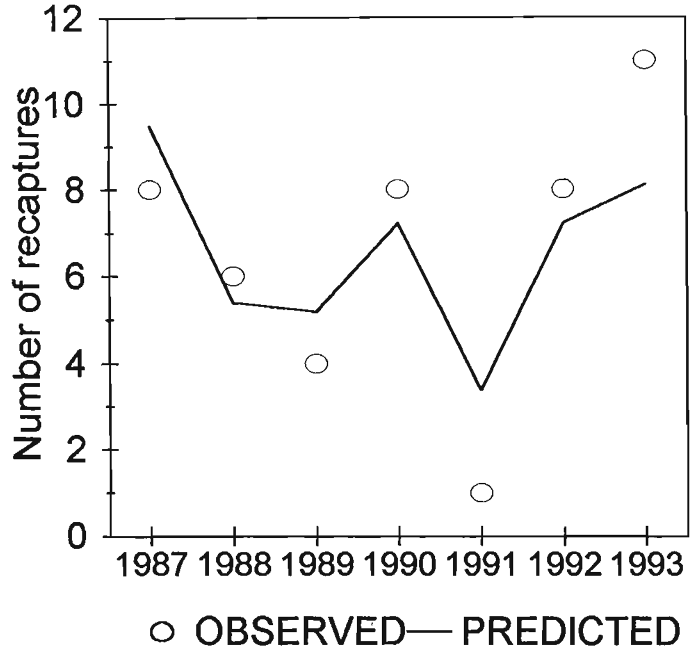

Figure 3.1 Observed and model predicted recaptures of *P. saltatrix* captured in KwaZulu-Natal taking into account migration. Parameter values are shown in Table 3.2 for $M = 0.4$ year^{-1}.

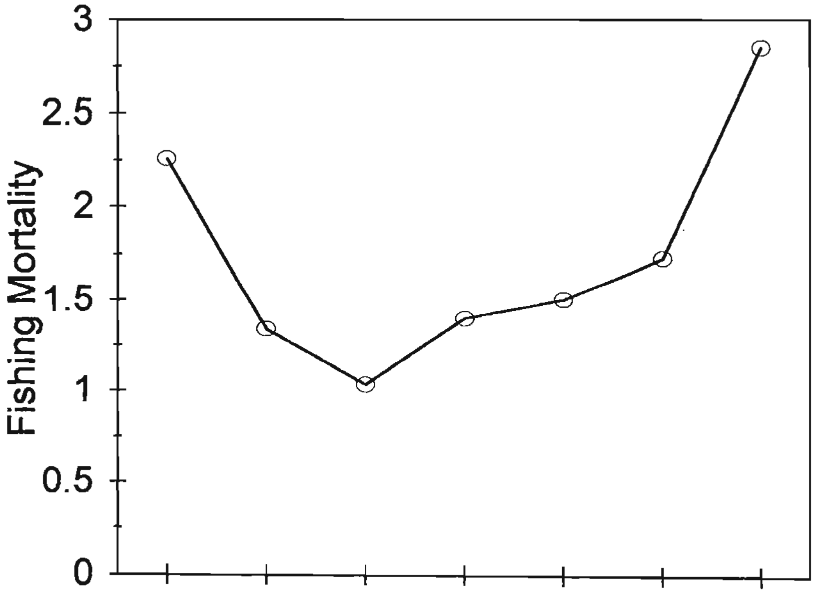

Figure 3.2 Estimated fishing mortality rates for *P. saltatrix* in KwaZulu-Natal taking migration into account. Parameter values are shown in Table 3.2 for $M = 0.4$ year^{-1}.

The parameter q was the most poorly estimated parameter.

Figure 3.1 shows the observed and model-predicted recaptures reported in KwaZulu-Natal taking migration into account. In Figure 3.2 estimated annual fishing mortalities off KwaZulu-Natal are shown. The fishing mortalities for KwaZulu-Natal for the years 1987 to 1993 ranged from 1.03 to 2.85 year^{-1} with a mean value during this time period equal to 1.66 year^{-1} (Figure 3.2).

3.5 Discussion

In this study it has been confirmed that during winter there is a migration of *P. saltatrix* from the Cape to KwaZulu-Natal as described by van der Elst (1976). From a limited tagging experiment off the east coast of Australia Bade (1977) concluded that there was a northward migration of *P. saltatrix* from New South Wales to Queensland during winter and spring which was possibly related to the need to move to warmer waters during winter. Similar migrations occur in the South Atlantic Bight in the USA (Oliver *et al.*, 1989). Lund and Maltezos (1970) showed from a tagging study in the USA that *P. saltatrix* movement around New York and southern New England was also related to changes in water temperature.

Surprisingly there is no difference in parameter estimates whether it is assumed that emigration occurs instantaneously at the beginning or the middle of the year. This would indicate that model is insensitive to this assumption.

The migration of *P. saltatrix* from Cape to KwaZulu-Natal waters is extensive as it appears that virtually the whole adult population (96%) moves during winter from the Cape to KwaZulu-Natal. However, the return migration in summer is not as extensive with possibly only 4% returning to the Cape. This indicates that the whole adult population is available for harvesting in KwaZulu-Natal. This winter migration into the KwaZulu-Natal from Cape waters by *P. saltatrix* is characterised by high speeds of migration. Note that the average speed estimated during this time period (242 km.month^{-1}) does not represent the exact speed of travel but rather the net resultant speed.

It has been suggested that during winter and especially in KwaZulu-Natal there is an inshore current that flows counter to the Agulhas current and may assist in the northward migration of certain unrelated species such as *P. saltatrix*, the pilchard *Sardinops sagax*, the sparids *Lithognathus lithognathus* and *Rhabdosarbus holubi*, the sciaenid *Argyrosomus hololepidotus* and the carangid *Lichia amia* (Heydorn *et al.*, 1978). Recent research, however, has shown no indication of the establishment of such a counter-current (Schumann 1987), although, there are sporadic current reversals which occur as a result of variations in wind forcing and which occur with greater frequency closer to the coast (Schumann 1987). Also, in the surf zone itself, wave action generates a long-shore drift which is known to move sediment northeastwards along the east coast of South Africa (Swart 1983). Although these currents probably assist in the northeastward migration of *P. saltatrix* during winter they are probably not as important for this powerful swimming fish as they would be for small pelagics such as *Sardinops sagax*. In laboratory studies where *P. saltatrix* were forced to swim against water currents, adults maintained speeds of 4 to 4.6 body lengths per second for at least 30 minutes (Oliver *et al.,* 1989). At intermediate and high swimming speeds *P. saltatrix* shift to ram gill ventilation, transferring the workload of ventilation from the branchial to the swimming musculature which results in significant metabolic savings during rapid swimming (Freadman, 1979). Ogilvy and Dubois (1981) determined that even the introduction of turbulence into a swimming chamber did not reduce the maximum swimming speed of *P. saltatrix*.

The return migration of *P. saltatrix* during summer is not as intensive as the northward winter migration. It is characterised by slower speeds of travel and a relatively smaller percentage of individuals returning. The predominate orientation coupled with high speeds of migration is in a southwesterly direction during the return migration in summer . The lower percentage of individuals returning to the Cape could possibly be a result of high fishing mortality rates on return migrants in KwaZulu-Natal (see discussion below). The slower speed of migration during summer would indicate that the Agulhas current is not used as a southward transporting mechanism for *P. saltatrix*. Schumann (1987) recorded daily speeds for the core of the Agulhas current ranging from 130 to 170 km/day which is very much higher than speeds recorded for

P. saltatrix during its southward migration. It must also be noted that the core of the Agulhas current is located off the edge of the continental shelf away from the habitat frequented by *P. saltatrix*.

The *P. saltatrix*-directed fishing effort for the years 1987 to 1993 is variable from year to year with an average annual fishing effort index of 2.5 rods/km (coefficient of variation = 36%) (Table 3.1). It is believed that these effort indices are valid for *P. saltatrix*. Joubert (1981), in a survey of shore-anglers' catches conducted between 1975 and 1977 found that, despite anglers being restricted to two *P. saltatrix*/person/day, it was still the dominant species in anglers' catches making up 22% of the harvest by number indicating the targetting preference of the anglers. From analysis of the NPB shore-patrol data and catch cards filled in by recreational anglers, Guastella and Nellmapius (1993) reported that *P. saltatrix* constituted at least 50% of shore-anglers' catches for the years 1986 to 1991. In both these studies the small sparid fish *Sarpa salpa* was the second most abundant species and numercially constituted about 20% of the catch. However, this species is not targetted by the majority of anglers. In another study, Govender *et al.* (1995) reported that in 96 465 hours fished along the KwaZulu-Natal coast during June to September 1994, shore-based anglers recorded a catch of 29 998 fish of which 71% were *P. saltatrix*.

In this study it has been shown that at least 96% of adult *P. saltatrix* annually migrate from Cape waters into KwaZulu-Natal during winter. It has been suggested that the primary stimulus for this extensive migration is spawning related (van der Elst, 1976). However, van der Elst (1976), sampling catches of shorebased-anglers in KwaZulu-Natal found few ripe-running and active *P. saltatrix* during the spawning season. He did encounter a fair proportion of fish with partially spawned and spent ovaries. He attributed the low numbers of ripe-running *P. saltatrix* to the possibility that the fish do not feed whilst actively spawning. However, even in seine net catches off beaches in KwaZulu-Natal he did not encounter ripe running *P. saltatrix* which casts some doubt on this hypothesis. It is possible that the surf zone along the KwaZulu-Natal coast is not the primary spawning area for *P. saltatrix.* Spawning must thus occur further offshore anywhere from beyond the surf zone to the edge of the continental shelf. Note that in KwaZulu-Natal little or no fishing for *P. saltatrix* occurs in the latter zone.

There are three possible scenarios which may be considered for local movement between inshore and offshore waters. Firstly, there could be a one-way movement from inshore waters to offshore waters with spawning occurring in the latter region. This will be reflected by a high P_{no} value as no fishing occurs in the offshore zone so the probabiltiy of a tagged *P. saltatrix* being recaught is low. The second type of movement could be categorised as movement from inshore areas to offshore areas followed by a return movement to inshore waters (following spawning in the offshore zone). The third type of inshore-offshore movement is such that there is free interchange between these two areas i.e. after spawning in the offshore zone *P.*

saltatrix may return to inshore waters and return later to spawn in offshore waters - this type of inshore-offshore movement may occur more than once. Both the second and third scenarios will result in a lower P_{no} value as tagged *P. saltatrix* can be recaught in the inshore area. Note that in this study, one cannot distinguish between the second and third scenarios because no tagging nor recaptures were performed in offshore waters.

In this study it was found that a mere 3.6% of *P. saltatrix* emigrate from KwaZulu-Natal inshore waters. This suggests that the second and third scenarios are more likely for *P. saltatrix*. Lund and Maltezos (1977) have recorded an inshore-offshore movement similar to the second scenario proposed in this study. *P. saltatrix* off the east coast of the USA display an offshore spawning followed by an inshore movement after spawning. Further, they have shown that the spawning occurs over a restricted time period. Possibly a similar inshore-offshore movement occurs for *P. saltatrix* in KwaZulu-Natal. However, the fact that continuous spawning occurs in KwaZulu-Natal favours the third scenario. Beckley and Connell (in press) recorded *P. saltatrix* eggs to be abundant throughout the summer in KwaZulu-Natal and it is possible that in KwaZulu-Natal local movement between inshore and offshore waters occurs continuously during the spawning season but with spawning restricted to the offshore areas.

In this study no *P. saltatrix* marked in KwaZulu-Natal were recaptured in the Cape.

This implies that either fishing mortality is so high in KwaZulu-Natal that it prevents the return migration into the Cape or that *P. saltatrix* emigrate to other areas where there is little fishing effort. The latter is unlikely as only a mere 3.6% of adult *P. saltatrix* emigrate from KwaZulu-Natal waters and this would be considered a negligible proportion of the stock if they migrate to other areas. During the years 1987 to 1993 the average fishing mortality rate on *P. saltatrix* in KwaZulu-Natal was 1.7 year^{-1} (Figure 3.2). This is much higher than than the overall fishing mortality rate estimated for KwaZulu-Natal and the Eastern and Western Cape combined (0.27year^{-1} - see previous chapter). It is therefore possible that the large fishing mortality on *P. saltatrix* in KwaZulu-Natal results in few *P. saltatrix* successfully migrating back to the Cape. Hughes (1986) estimated that $F_{0.1}$ for *P. saltatrix* was equal to 0.6 year^{-1}. The average fishing mortality during 1987 to 1993 was 1.7 year^{-1} which is more than double the optimum harvesting rate and would result in few returning *P. saltatrix* migrants surviving. The fishing mortality rates in KwaZulu-Natal were fairly high in 1987 and 1993 and lower and about constant in the years 1988 to 1992 (Figure 3.2). This trend is similar to that of the numerical abundance of *P. saltatrix* recorded by Natal Parks Board staff during shore-patrols (Guastella *et al.*, 1994; Beckley *et al.*, 1995) and indicates that the numbers of *P. saltatrix* recorded during NPB shore-patrols may provide a useful index of fishing effort for *P. saltatrix*.

Chapter Four

GROWTH

4.1 Introduction

The description of growth is fundamental to age-structured stock assessment models. Historically, age estimates for fish have been obtained from hard structures such as scales or otoliths by enumerating seasonally deposited opaque or translucent bands in the calcified tissue (Beamish and McFarlane, 1987). Such ageing methods are based on the assumption that the periodicity of band deposition is known or can be validated. To date, the only direct method of validation has been the use of chemical dyes such as tetracycline which chemically marks the hard structure. This fluorescent mark then serves as a reference point from which the periodicity of the seasonal bands can be deduced once sufficient somatic growth has accrued. Other indirect techniques for validation of hard structure banding include marginal increment analysis, back calculation methods and the analysis of modal progression of length frequency data in conjunction with age data (Hecht and Smale, 1986).

In this chapter, a growth model is developed that utilises mark-recapture data to validate the periodicity of opaque band deposition in the otoliths of *P. saltatrix*. The model is an extension of the method described by Govender (1994). The method is based on the assumption that if a growth curve (derived from size-at-age data and assuming an arbitrary periodicity of the banding in the hard structure) can reasonably predict the time-at-liberty of tagged individuals then the growth parameters and the periodicity assumed for the seasonal bands must be valid.

4.2 Materials And Methods

Age estimates for *P. saltatrix* were obtained from reading whole otoliths (n=340). Otoliths were collected on a irregular basis during the period 1992 to 1994 from various angling sites along the KwaZulu-Natal coast. Small specimens were sampled from seine netting catches and were generally smaller than the permitted minimum size. Most samples were obtained from illegally caught specimens that were confiscated by the Natal Parks Board and were representative of the size range of *P. saltatrix* caught along the KwaZulu-Natal coast. Otoliths were immersed in ethanol and were read against a black background under a low power dissecting microscope using reflected light. The number of opaque bands was counted from the nucleus to the outer margin of the otolith. Each otolith was read twice with a minimum of one month between readings. The second reading was performed without the reader consulting the previous reading. If both readings of the same otolith coincided this was taken as the age estimate. If the readings differed by one or more bands the otolith readings were rejected. This rejection criterion was used to improve the precision in age readings (precision is used to describe the reproducibility of age estimates and does not imply that the age estimates are accurate). For example, if 95% of age determinations between two readers agree within ± 1 year for *P. saltatrix*, this can be very poor precision since samples in this study contained only a few year classes. Similarily, if 95% of spiny dogfish (*Squalus acanthias*) age determinations agree within ± 5 years, this can represent very good precision since dogfish may be old as 60 years with approximately 30 age groups in the fishery (Beamish and McFarlane, 1987).

Mark-recapture data for *P. saltatrix* were obtained from the Sedgwick's-ORI tagging programme. Length data from only eight recaptured specimens could be verified and were used in the analysis. Unfortunately, many anglers do not measure the fish they tag whilst others merely guess the size. Those that do measure their catch sometimes fail to indicate if the lengths measured are fork or total lengths. In some cases, although length measurements were accurate, negative growth was recorded and these individuals were excluded from this analysis. Given that most animals were recaptured within two months of tagging (see chapter one) it is possible that tagging retarded growth during this short period.

4.3 Growth model incorporating mark-recapture data to validate age estimates

The model allows age estimates that have been derived from hard structures such as scales or otoliths to be validated using corresponding mark-recapture data for a given fish species. The model is based on the assumption that if a growth equation derived from size-at-age data reasonably predicts the growth increment during the time-at-liberty of tagged individuals then the estimated growth parameters and the assumed time period for deposition of the seasonal bands are appropriate. The model consists of two components. The first model component estimates growth parameters from size-at-age data based on different deposition periods of hard structure bands. The second model component then predicts times-at-liberty for recaptured tagged individuals using the growth parameters derived from the first model component i.e. the time required to achieve the observed growth increase is estimated. If the times-at-liberty are reasonably predicted then the assumption of periodicity in hard structure deposition is assumed to be valid.

4.3.1 First model component

For this study it was assumed that the von Bertalanffy growth function adequately describes the growth of *P. saltatrix*. This assumption could have been relaxed but was made to keep the number of model parameters to a minimum. Further, many other studies have assumed von Bertalanffy growth in *P. saltatrix* (van der Elst, 1976; Bade, 1977; Krug and Haimovici, 1989; Barger, 1990; Chiarella and Conover, 1990). The traditional parameterization of the von Bertalanffy function was discarded in favour of Schnute's (1981) parameterization of the von Bertalanffy growth function as some studies (Ratkowsky, 1986; Schnute, 1981) have shown that this parameterization results in statistically more stable parameter estimates. Schnute's parameterization of the von Bertalanffy growth function, which is also a three parameter model, is written as

$$Y(t)=Y(1)+[(Y(2)-Y(1)]\frac{[1-\exp(-a(t-T(1)))]}{[1-\exp(-a(T(2)-T(1)))]} \qquad 4.1$$

where

$Y(t)$ = size of a t aged fish,

$Y(1)$ = mean size of $T(1)$ aged fish,

$Y(2)$ = mean size of $T(2)$ aged fish,

a = constant (and $a \neq 0$) , and

$Y(2) > Y(1)$ and $T(2) > T(1)$.

In equation (4.1) the variable t is re-defined as

$$t_i=\frac{B_i}{P}$$

where

t_i = the age of fish i,

B_i = the number of otolith (or hard structure) bands counted for fish i, and

P = the periodicity of the otolith band assumed ($P > 0$ and is an integer)

If $P = 1$ then one hard structure band is deposited annually and if $P = 2$ then the periodicity is bi-annual.

The traditional von Bertalanffy parameters (L_∞, k and t_0) can be obtained from the parameters of equation (4.1) (Schnute 1981) i.e.

$$L_\infty = \frac{\exp[aT(2)]Y(2) - \exp[aT(1)]Y(1)}{\exp[aT(2)] - \exp[aT(1)]} \ ,$$

$$k = a \ ,$$

$$t_0 = T(1) + T(2) - \frac{1}{a}\ln\left[\frac{\exp[aT(2)]Y(2) - \exp[aT(1)]Y(1)}{Y(2) - Y(1)}\right]$$

Given a matched data set of otolith band readings and fish size measurements for a particular species and assuming a time period for otolith band deposition (e.g. $P = 1$ or 2), parameter values of equation (4.1) Y(1), Y(2) and a can be obtained by specifying the ages T(1) and T(2) and then minimising an appropriate objective function.

Two error structures are considered for model (4.1):

additive

$$Y(t)_{i,obs} = Y(t)_{i,pred} + \epsilon_i$$

and multiplicative

$$Y(t)_{i,obs} = Y(t)_{i,pred} \exp(\epsilon_i)$$

where $Y(t)_{i,obs}$ and $Y(t)_{i,pred}$ are the observed and predicted sizes of fish i aged t and ϵ_i are the "model errors". The error terms ϵ_i are assumed to be independent random variables following a normal distribution with mean= 0 and a variance σ^2. Given size-at-age data based on an assumed value for P, estimates of $Y(1)$, $Y(2)$ and a can be obtained by utilising a nonlinear minimisation routine that will find optimum parameter estimates that satisfy the minimisation criteria

$$SS = \sum_{i=1}^{n} (Y(t)_{i,obs} - Y(t)_{i,pred})^2$$

for the case of the additive model (n is the number of fish aged), and for the multiplicative model

$$SS = \sum_{i=1}^{n} (\ln(\frac{Y(t)_{i,obs}}{Y(t)_{i,pred}}))^2$$

4.3.2 Second model component

In the following section, equation (4.1) is transformed to predict the time-at-liberty of tagged individuals given parameter estimates obtained from the size-at-age data. To derive the mark-recapture model corresponding to equation (4.1), t is first made the subject of formula (4.1)

$$t = T(1) - (1/a)[1 - [1 - \exp(-a(T(2) - T(1)))]\frac{Y(t) - Y(1)}{Y(2) - Y(1)}] \quad (4.2)$$

If fish grow from size Y(m), when marked at age t(m), to size Y(r), when recaptured at age t(r) then, from equation (4.2), the predicted time-at-liberty, Δt, taken to achieve this growth increment can be written as

$$\Delta t = t(r) - t(m) = -(1/a)\ln\left[\frac{(Y(2)-Y(1))-(1-\exp(-a(T(2)-T(1))))(Y(r)-Y(1))}{(Y(2)-Y(1))-(1-\exp(-a(T(2)-T(1))))(Y(m)-Y(1))}\right] \quad \textbf{(4.3)}$$

Given parameter estimates of equation (4.1) (Y(1), Y(2) and a) derived from otolith banding-size data and for a range of P values assumed, the best estimates of P, Y(1), Y(2) and a are deemed those that minimise the criteria

$$SS_{tag} = \sum_{i=1}^{M} (\Delta t - \Delta g)^2 \quad \textbf{(4.4)}$$

where Δg is the observed time-at-liberty for fish i and M is the number of tagged fish for which mark-recapture data is obtained. Note that equation (4.4) is not minimised during the estimation process but is evaluated after estimates are obtained once the appropriate *SS* functions are minimised.

4.3.2.1 Comparing the fits between the additive and multiplicative models

All models were tested for randomness of the residuals using a runs test (Draper and Smith, 1966). If a model failed the test of randomness it was immediately rejected as an appropriate model. As the error structure for the additive and multiplicative error models are different in each case, direct comparisions, based on normal statistical tests such likelihood ratio tests, are not possible in these cases (Punt, 1992). This means that selection between the two models cannot be undertaken objectively. Punt (1992) therefore suggests an *ad hoc* rule that may be regarded as an attempt to select the model which minimises some expected discrepancy. The model that minimises the following equation was therefore selected as the one that best describes the age-length relationship for *P. saltatrix*.

$$Total_{CV} = CV(a)^2 + CV(Y(1))^2 + CV(Y(2))^2 + CV(SS_{tag})^2$$

where CV is the coefficient of variation as a percentage and the other parameters are defined as in equations (4.1) and (4.4). This method, therefore, requires estimates of standard errors for each parameter. Note that the von Bertalanffy parameters are ignored in the above equation because they are actually derived from estimates of the Schnute (1981) parameters.

4.4 Estimating standard errors using the "parametric" bootstrap technique

The "parametric" bootstrap technique (Efron, 1981; Punt and Butterworth, 1993) was used to calculate standard errors for the parameters Y(1), Y(2) and *a* of the Schnute growth curve as well as the derived quantities L_∞, k , t_0 and SS_{tag}. The "parametric" bootstrap technique was employed because besides estimating standard errors for the parameters of a model it also provides estimates of standard errors for quantities derived from these parameters (Punt, 1992). The standard error for a parameter ***K*** is estimated from a series of artificially generated data sets. As the method is computationally intensive, 100 pseudo-data sets were generated. Each data set (which has samples equal to that in the original dataset) is generated from the formula

$$Y(t)_{i,art} = Y(t)_{i,pred} + \epsilon_i$$

where $Y(t)_{i,art}$ and $Y(t)_{i,pred}$ are the artificially generated and original model predicted size-at-age, respectively, while ϵ_i is an artificially generated residual, selected at random for each $Y(t)_{i,pred}$. The residuals are generated from a normal distribution given the original mean residual value and standard deviation of the residuals. To each pseudo-data set or bootstrap a new set of parameter estimates is obtained by fitting the model to these bootstraps. The standard error of a parameter ***K*** is then obtained from

$$S.E.(K) = \sqrt{\sum_{1}^{100} \frac{(K^n - K_{mean})^2}{100-1}}$$

where K^n is the value of the ***K*** parameter from the *n*th artificially generated data set and K_{mean} is the average of the K^n values.

4.5 Results

In Table 4.1 the lengths at marking and recapture as well as the times-at-liberty of tagged *P. saltatrix* are given. Some lengths that were reported as total lengths were converted to fork lengths using the equation FL(mm)=TL(mm).0.885 + 1.19 ($r^2 = 0.99$; n = 55). At the time of marking the fish ranged in size from 270 to 370mm with times-at-liberty ranging from 49 days to 243 days (Table 4.1).

Of the 340 otoliths that were read, 256 age estimates co-incided for both readings and represents a 75% agreement between the two readings. The rest of the readings were excluded from further analysis. The Schnute and von Bertalanffy growth parameter estimates, their coefficient of variation as well as the estimates of SS_{tag} (equation 4.4) and $Total_{CV}$ are given in Table 4.2 for the various error models fitted.

Table 4.1 Fork lengths at marking and recapture as well as the times-at-liberty for eight tagged *P. saltatrix* obtained from the Sedgwick's-ORI tagging programme. Lengths marked with an asterisk were converted from total lengths using a fork length-total length conversion.

Fish No.	Fork length at marking (mm)	Fork length at recapture (mm)	Time-at-liberty (days)
1	355	380	49
2	270	286	66
3	370	388	67
4	380	420	88
5	280	320	101
6	364^*	390	116
7	320^*	346^*	146
8	370	393^*	243

Table 4.2 Schnute and von Bertalanffy growth parameter estimates derived from age-length data, their coefficient of variation as a percentage (in parenthesis) as well as the sums of squares of the observed and predicted times-at-liberty (SS_{tag}) and $Total_{CV}$ of tagged *P. saltatrix*. Note that the Schnute parameter *a* is equivalent to the parameter *k* in the von Bertalanffy growth function. * - indicates those models that passed the runs test for randomness of residuals.

Model	Periodicity	Parameter						
		a,k	Y(1)	Y(2)	L_∞	t_0	SS_{tag}	$Total_{CV}$
Additive	Annual*	0.094	222	663	1247	-2.09	0.29	659.4
CV		(25)	(2.9)	(4.3)	(86)	(8.7)	(2.74)	
	Biannual*	0.19	222	663	1247	-1.05	0.38	1794.2
CV		(42)	(3)	(3.8)	(98)	(13)	(2.59)	
Multiplicative	Annual*	0.43	190	525	552	-0.97	0.33	409.9
CV		(17)	(4)	(6)	(10.8)	(11)	(8.3)	
	Biannual*	0.86	190	525	552	-0.49	0.38	501.6
CV		(20.5)	(4.3)	(7)	(13)	(14)	(3.72)	

All models passed the runs test for randomness of residuals (Table 4.2) indicating there was no systematic trends in the residuals and hence all models adequately describe the observed data (Butterworth *et al.*, 1989).

For both the additive and multiplicative models the assumption of annual deposition of the otolith bands resulted in smaller residual sum of squares between the observed and predicted times-at-liberty (SS_{tag}) for the tagged *P. saltatrix* than that obtained under an assumption of biannual deposition (Table 4.2). However, the difference is very slight between the assumption of annual and biannual bands making the choice between models a difficult one. This slight difference between models is possibly due to the small sample size of tagged individuals available. Furthermore, the growth increments and the times-at-liberty for the tagged individuals are relatively small. Ideally the growth increments should span more than a year.

Generally, the additive model resulted in the parameters *a,k* and L_∞ having large CVs while for the multiplicative model only the *a,k* parameters were estimated with a large CV (although the CV was less than that of the additive model). The fairly large CV for the L_∞ and *a,k* parameters are a result of the fact that the age-length data for *P. saltatrix* is only slightly curvilinear (Figure 4.2) and hence the asymptotic length and the *a,k* parameters (which describes the "bend" in the curve) are poorly defined. The L_∞ is better estimated for the multiplicative model because the model explicitly takes into account that variance in length is greater at older ages while the additive model assumes that variance in lengths is constant for each age class which is not the case for *P. saltatrix* as it displays variable growth (see discussion).

The additive model assuming annual periodicity of the otolith banding produced the smallest SS_{tag} value with a low CV followed by the multiplicative model assuming the same banding periodicity but with a larger CV. However, the former model has a much larger $Total_{CV}$ value when compared to the latter model (Table 4.2). For this and other reasons (see discussion) the multiplicative model which assumes annual deposition was selected as the model that best describes the age-length data of *P. saltatrix*. Furthermore, the additive model predicts an L_∞ value very much larger than

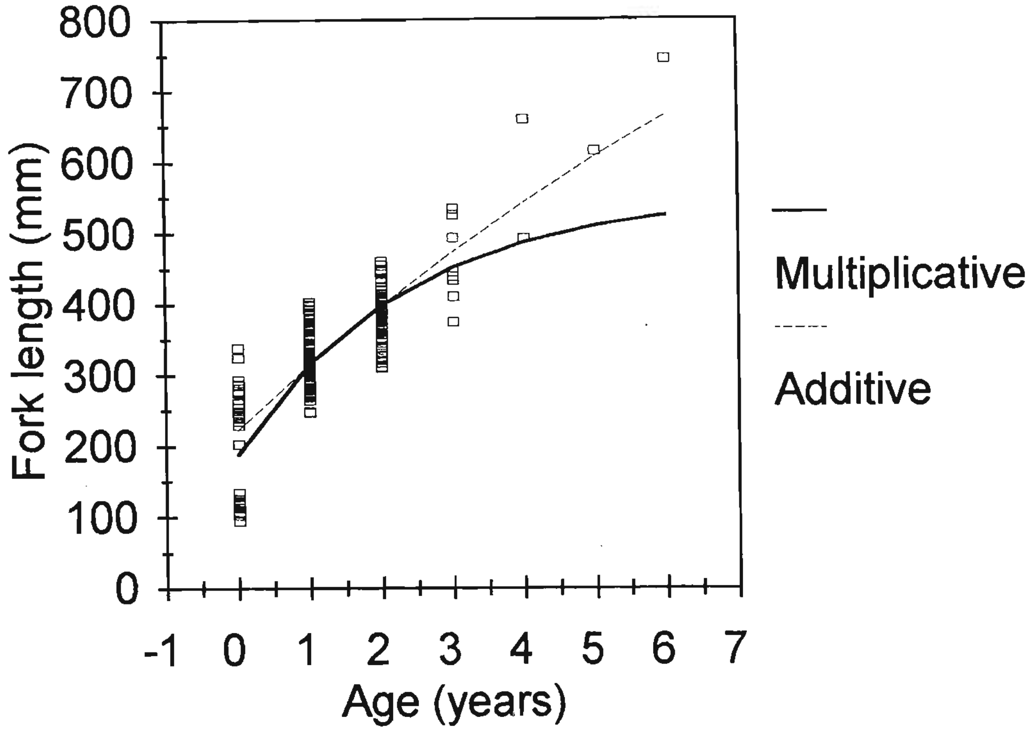

Figure 4.1 Age-length relationship for *P. saltatrix* for the additive and multiplicative models assuming annual periodicity of the otolith bands.

that which is observed in the catch while that of the multiplicative model is very similar to the sizes of large *P. saltatrix* taken along the KwaZulu-Natal and Cape coasts. In Figure 4.1 the age-length relationship for the multiplicative and additive model assuming annual periodicity of the otolith bands is shown. Note that up to three years of age there is very little difference in growth predicted by the two models. At higher ages the multiplicative model consistently underestimates the length of older fish. As these age classes seldom form part of the catch (van der Elst, 1976; Butterworth *et al.*, 1989; this study) this bias will not greaterly affect the predictions of stock assessment analyses using this growth curve (Butterworth *et al.*, 1989).

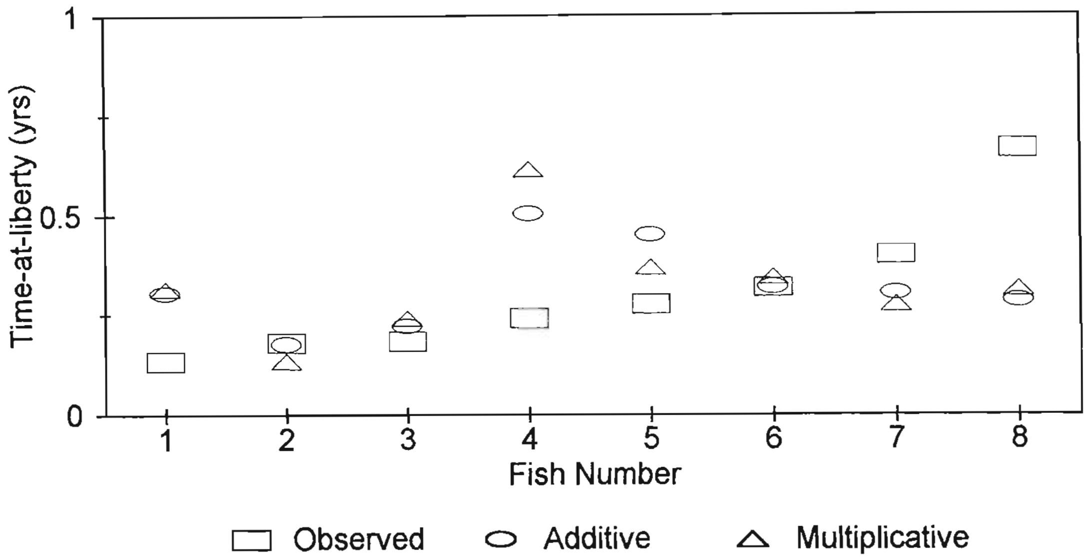

Figure 4.2 Observed and predicted times-at-liberty for tagged *P. saltatrix* based on the assumption of annual periodicity for two different model estimates of the growth parameters.

In Figure 4.2 the observed and predicted times-at-liberty for the tagged *P. saltatrix* for the both the additive and the multiplicative model are shown. Generally, the additive model provides better predictions of the time-at-liberty than the multiplicative model, however, the differences are slight as shown by the estimates of SS_{tag} which are similar for both models (Figure 4.2, Table 4.2).

4.6 Discussion

The combination of mark-recapture and age-length data to validate the periodicity of hard structure banding is a useful technique. However, in the case of *P. saltatrix* it cannot conclusively be deduced that periodicity of opaque band formation is annual. The method is useful in cases when ageing material cannot be obtained throughout the year i.e. when catches are seasonal or when the fishing season is restricted to only a part of the year. Indirect validation methods such as marginal increment analysis ideally require monthly samples of otoliths or scales which may not be possible to obtain if the fishery is a seasonal one or when fishing is restricted to outside a closed season, as in the case of *P. saltatrix* (Hecht and Smale, 1986).

The model developed can, with slight modification, accommodate other growth curves such as the logistic or Gompertz curves. It is possible that in the case of *P. saltatrix* the species undergoes seasonal growth with growth slowing or ceasing at low water temperatures and growth increasing with increases in water temperature (Weatherley, 1972). Such a seasonal model was not considered in this study because in order to fit such a growth curve age estimates have to be obtained at a higher resolution than annual estimates e.g. monthly age estimates. Such age estimates require expensive and sophisticated age determinations techniques such as reading daily rings (Beamish and McFarlane, 1987), a technique which is beyond the scope of this study.

Despite the statistical error model chosen (additive or multiplicative), the assumption of annual otolith bands resulted in growth parameter estimates that better fit the age-length data and at the same time reasonably predict the times-at-liberty of tagged *P. saltatrix* individuals than when compared to the assumption of biannual bands. The two statistical error models that were used to describe von Bertalanffy growth in *P. saltatrix* resulted in very different growth parameter estimates. The multiplicative model predicted a faster growth rate with a smaller asymptotic size while the additive model predicted a somewhat slower growth rate with a relatively higher asymptotic size. These differences can be attributed to the variation in length-at age modelled by the two error models. For the additive model it is assumed that there is constant variation in length-at age with increasing age. For the multiplicative model variation in length-at-age increases with age. Variation in length-at-age increasing with age is probably more realistic for *P. saltatrix* given the lengthy spawning period (van der Elst, 1976; Beckley and Connell (in press)) which results in individuals having different "birthdays" and consequently individual variation in growth (Mann *et al.*, in prep).

Overall, the multiplicative model resulted in smaller coefficients of variation in the parameter estimates than did the additive model. Based on this *ad hoc* criterion the multiplicative model assuming annual periodicity was chosen as the best model fit to the age-length data for *P. saltatrix*. The assumption, however, that band periodicity in *P. saltatrix* is annual was based not only on the conclusions of this study but on other age and growth studies carried out on *P. saltatrix* in South Africa. Van der Elst (1976) using age readings from scales validated the periodicity of the scale bands as annual by marginal increment analysis. He showed that the opaque zone of scales were deposited from July to September prior to the peak spawning period. In another study, Mann *et al.*, (in prep.) using tetracycline-marked *P. saltatrix* in a captive study also deduced that only one opaque band was deposited in the otolith annually. However, the time formation of the opaque zone was from October to January which coincides with the time of spawning. They also noted that the position of the fluorescent band varied between individuals resulting in differences in the timing of the opaque zone formation. This can be attributed to individual differences in growth and to the fact that *P. saltatrix* has a prolonged asynchronous spawning season (van der Elst, 1976). The individual variation in *P. saltatrix* growth (Table 4.4) as well as individual variation in the timing of opaque zonation formation (Mann *et al.,* in prep.) would contribute to the similar predictions of the time-at-liberty predicted by the annual and biannual band models. This is so, because the model implicitly assumes that the timing of zone formation is the same in all fish and that variability in individual growth is negligible.

The von Bertalanffy parameters estimated in this study differ from those reported by van der Elst (1976) (Table 4.3). Note that the growth values reported by van der Elst (1976) are incorrect. The correct values using his data and a Walford plot yields the values $L_\infty = 67$ cm (FL), $k = 0.18$ $year^{-1}$ and $t_0 = -1.23$ years indicating faster growth than initially reported by van der Elst (1976). Moreover, van der Elst's (1976) data also yields even faster growth if a nonlinear technique is used to estimate the parameters (Hughes, 1986). Hughes (1986) did not report the actual values but using the technique described by her they were calculated to be $L_\infty = 64$cm (FL), $k = 0.21$ $year^{-1}$ and $t_0 = -1.1$ years. Thus, the difference in *P. saltatrix* growth as observed by van der Elst (1976) and this study is due to the parameter estimation technique being different in each case i.e van der Elst (1976) used a Walford plot to estimate the von Bertalanffy parameters from mean length-at age data while in this study a nonlinear parameter estimation technique utilising all individually observed length-at-age data as well as a superior reparameterization of the von Bertalanffy growth function were used.

Table 4.3 Estimates of the von Bertalanffy growth parameters for both sexes of *P. saltatrix* from various studies in different regions. All lengths are fork lengths. *- values reported by van der Elst (1976) are incorrect. The correct values using his technique is $L_\infty = 67$ cm, $k = 0.18$ year^{-1} and $t_0 = -1.23$ years.

METHOD (REGION)	L_∞ (cm)	k (year^{-1})	t_0 (years)	SOURCE
Walford (South Africa)	75 (FL)*	0.1966*	0.03215*	van der Elst (1976)
Walford (Brazil)	58.7 (FL)	0.397	-0.321	Krug and Haimovici (1989)
Non-linear (Gulf of Mexico)	94.4 (FL)	0.18	-1.033	Barger (1990)
Non-linear (U.S.South Atlantic)	101.9 (FL)	0.096	-2.493	Barger (1990)
Walford (East Australia)	72.6 (FL)	0.3267	0.296	Bade (1977)
Walford (East Australia)	72.7 (FL)	0.163	-0.409	Bade (1977)
Non-linear (South Africa)	55.2 (FL)	0.43	-0.97	This study
Non-linear (New York Bight)	90.9 (FL)	0.22	-0.71	Chiarella and Conover (1990)

The growth of *P. saltatrix* worldwide is variable from region to region (Table 4.3). A possible reason for such variability is that the species occurs in both temperate as well as subtropical regions and that in the latter regions growth is generally faster than in colder waters (Weatherley, 1972). Areas where fast growth in *P. saltatrix* was recorded include Brazil (Krug and Haimovici, 1989), Gulf of Mexico (Barger, 1990), the east coast of Australia (Bade 1977) and KwaZulu-Natal, South Africa (this study). Slower growth in *P. saltatrix* has been recorded from the U.S. Atlantic coast (Barger, 1990; Chiarella and Conover 1990), KwaZulu-Natal, South Africa (van der Elst, 1976) and the east coast of Australia (Bade, 1977). It is clear that growth parameters estimated by van der Elst (1976) are generally in keeping with studies conducted in temperate regions while parameters estimated in this study are in keeping with estimates from more subtropical regions.

Moreover, there are differences in the mean length-at-age reported by van der Elst (1976) and those recorded in this study (Table 4.4). Van der Elst (1976) reported smaller mean lengths-at-age which indicates a slower growth rate. However, in his study as well as the present study there was large variability in mean length-at-age (large standard deviations). As a result there is overlap between the mean lengths-at-age reported in this study and that of van der Elst (1976) and hence a similarity in growth rates.

Table 4.4 Mean length-at-age for *Pomatomus saltatrix* estimated from scales (van der Elst, 1976) and otoliths (this study).

This Study				van der Elst (1976)		
Age	FL (mm)	S.D.	n	FL (mm)	S.D.	n
0+	203	79	31			
1+	325	36	129	226	46	11
2+	387	34	83	301	37	31
3+	448	59	9	372	27	28
4+	577	118	2	411	32	7
5+	615	-	1	461	44	4
6+	745	-	1			

Recent research has indicated that faster growth in *P. saltatrix* increases survival rate. Hare and Cowan (1995) have found that within a *P. saltatrix* cohort, faster growing individuals had a higher probability of survival suggesting that cohorts with higher growth rates have higher recruitment probabilities. Furthermore, juvenile *P. saltatrix* display a early diet shift from planktivory to piscivory which accounts for the rapid growth in young-of-year *P. saltatrix* (Juanes and Conover 1994). All these factors would contribute to rapid growth early in the life history of *P. saltatrix* thereby resulting in faster overall growth as observed in this study.

In conclusion, the model developed can be used in conjunction with traditional validation methods to validate periodicity in hard structure banding. It is useful in cases when age material cannot be obtained throughout the year a requirement for most indirect validation techniques. The model, with modification, can incorporate growth curves other than the von Bertalanffy growth function. Growth in *P. saltatrix* has been shown to be faster than a previous South African study and it is concluded that band formation in *P. saltatrix* otoliths occurs annually.

Chapter Five

BIOMASS

5.1 Introduction

In this chapter a modified delay-difference model is developed to estimate relative biomass based on mean body weights and effort indices reported by van der Elst (1976) for the years 1956 to 1972. The mean body weights and effort data for *P. saltatrix* were from fishing competition data recorded by angling clubs and are assumed to represent the mean catch weight and effort expended by all angling sectors. The model allows the examination of the effects of growth overfishing. For the period 1956 to 1972 no fishing regulations were imposed on the capture of *P. saltatrix.*

5.2 The model

The delay-difference models of Deriso (1980) and Schnute (1985) incorporate age-structured approaches with surplus production modelling based on certain assumptions e.g. that mean body weight can be described by the linear Ford-Walford plot. The conceptual advantage of these models is that simple equations can be used to model the total population biomass and total numbers in comparison to models such as yield-per-recruit which require many sub-equations and which model the entire population age structure (in reality it is a cohort's age structure over its fishable life history that is modelled in YPR analysis). Other advantages of the Deriso-Schnute models are that they are dynamic, they do not need the assumption of continuous equilibrium and various input data or auxillary data can quite easily be incorporated into the model when estimating the parameters of the model. The Deriso-Schnute model consists of two basic equations that describe the annual total biomass and annual total numbers of a fish population. The biomass of fully recruited fish (B) in year t can be described as

$$B_t = s_{t-1}\alpha N_{t-1} + s_{t-1}\rho B_{t-1} + w_k R_t \tag{5.1}$$

where α and ρ are the intercept and slope of a Ford-Walford plot, N and R are the total number of fish and total number of recruits, respectively, in year t, s is the fraction of survivors and w_k is the mean weight of a recruit at the age of full recruitment k. Note that equation 5.1 differs from the Deriso-Schnute equation. The Deriso-Schnute equation expresses biomass in any year as a function of the biomasses of previous years i.e. the numbers function is ignored (Deriso, 1980; Schnute, 1985; Hilborn and Walters, 1992 - see page 333 for the detailed derivation of equations 5.1 and 5.2). The equation describing the total numbers (N) in year t is

$$N_t = s_t N_{t-1} + R_t \tag{5.2}$$

Dividing equation 5.1 with 5.2, the mean body weight of the fish ($\bar{W}$) in the population can be estimated as

$$W_t = \frac{B_t}{N_t} \tag{5.3}$$

In this analysis of the *P. saltatrix* fishery the survival function s was modelled as

$$s_t = \exp(-M-F_t) \tag{5.4}$$

where F_t is the instantaneous fishing mortality rate in year t and M is the instantaneous natural mortality rate and is assumed to be time and age invariant. Note that emigration effects will be incorporated into the estimate of M.

The fishing mortality rate (F) in year t can be expressed as a function of fishing effort (f) by the following equation

$$F_t = f_t q \tag{5.5}$$

where q is the catchability coefficient i.e. the number of fish harvested when one unit of effort is expended. Note as the effort values used in this study are relative effort indices q actually represents the proportional coefficient between F_t and f_t.

The catch (C) in numbers is estimated from the following equation

$$C_t = \frac{f_t q}{f_t q + M} N_t (1 - \exp(-f_t q - M)) \tag{5.6}$$

5.3 Model input data

Input data for the delay-difference model for *P. saltatrix* and their source are given in Table 5.1

Table 5.1 Mean weight and relative fishing effort values (van der Elst, 1976) for *P. saltatrix* harvested during fishing tournaments in KwaZulu-Natal during 1956 to 1972.

Year	Mean Weight (g)	Effort Indices
1956	771.4	10.11
1957	101.9	15.57
1958	951.2	18.79
1959	881.0	50.90
1960	940.5	39.46
1961	90.3.6	20.76
1962	939.3	53.79
1963	857.1	13.48
1964	865.5	33.79
1965	775.0	10.11
1966	679.8	35.32
1967	767.9	13.34
1968	798.8	4.61
1969	682.1	3.95
1970	733.3	21.95
1971	760.7	19.65
1972	941.7	3.49

5.4 Estimating the model parameters

5.4.1 Growth parameters

The Ford-Walford growth parameters (α and ρ) were estimated using weight-age data (n=162) for *P. saltatrix* (see chapter four for description of age determination using otoliths). The growth equation used was the one proposed by Schnute (1985) and is written as

$$w_a=\alpha+\rho w_{a-1}=w_{k-1}+(w_k-w_{k-1})\frac{1-\rho^{1+a-k}}{1-\rho} \tag{5.6}$$

Estimates of the parameters w_k, w_{k-1} and ρ were obtained by minimising the residual sum of squares (SS_w) i.e.

$$SS_w=(w_a-e_a)^2$$

where e_a is the observed weight at age a. Confidence intervals were estimated using the bootstrap technique (see chapter four).

5.4.2 Other parameters

In the delay difference model the parameters to be estimated other than the growth parameters include M, the biomass in the year 1956 (B_{1956}), the catchability coefficient q and the average recruitment rate over the study period R_t. The parameter (R_t) was removed as a parameter by setting it to one (this was performed because the convergence processing time was greatly reduced from 3 hours to 2 hours on a 486 CPU with 8 Mb of RAM). However, this results in the estimates of biomass and catch being relative rather than absolute value estimates.

Therefore, three parameters are to be estimated: M, q and B_{1956}. Parameters were estimated by implementing the model in a QUATTRO PRO spreadsheet and minimising the following equation

$$SS = \sum_{1}^{n}(\ln\frac{W_t}{D_t})^2 \qquad (5.7)$$

where D_t is the observed mean weight and W_t predicted mean annual body weight. Equation (5.7) assumes lognormal errors which is an error structure suggested by Hilborn and Walters (1992) for delay difference models. Standard errors for the parameters were estimated using the "parametric" bootstrap technique (see chapter four). As the method was computationally expensive only 25 bootstraps were undertaken.

5.5 Results

Estimates of the Ford-Walford parameters using Schnute's (1985) equation were w_k = 452 g (CV=5.2%), w_{k-1} = 302 g (CV=12%) and ρ=1.66 (CV=3.8%) and were based on 162 data points. The curve was based on an age of full-recruitment of one year. The fit of equation 5.6 to the observed data is shown in Figure 5.1 and the residual plot in Figure 5.2. Estimates of the Deriso-Schnute parameters are given in Table 5.2.

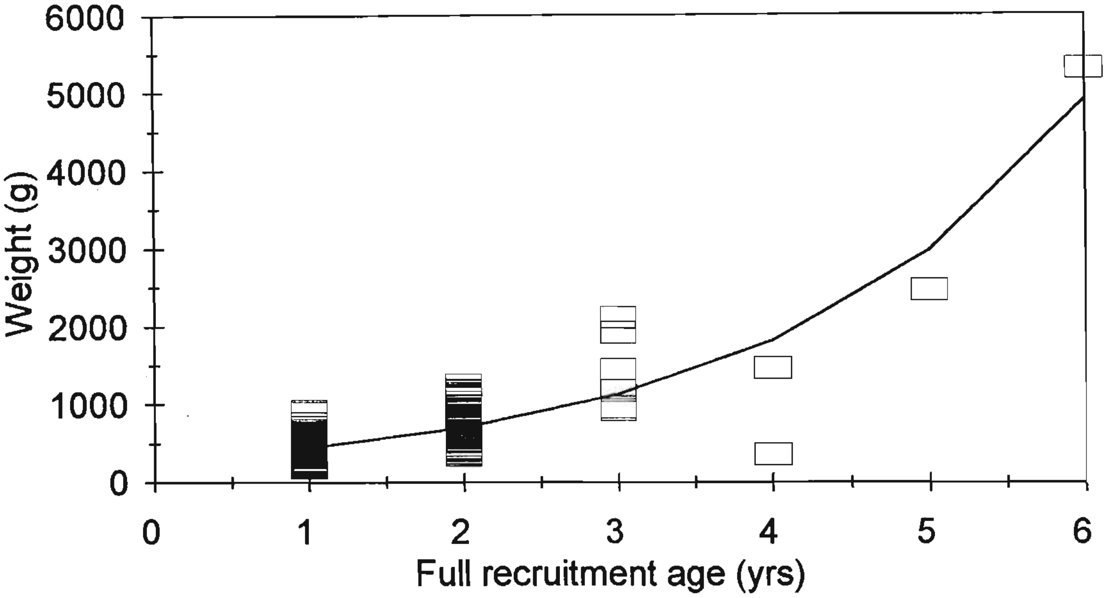

Figure 5.1 Weight-age relationship for fully recruited *P. saltatrix* based on equation 5.6.

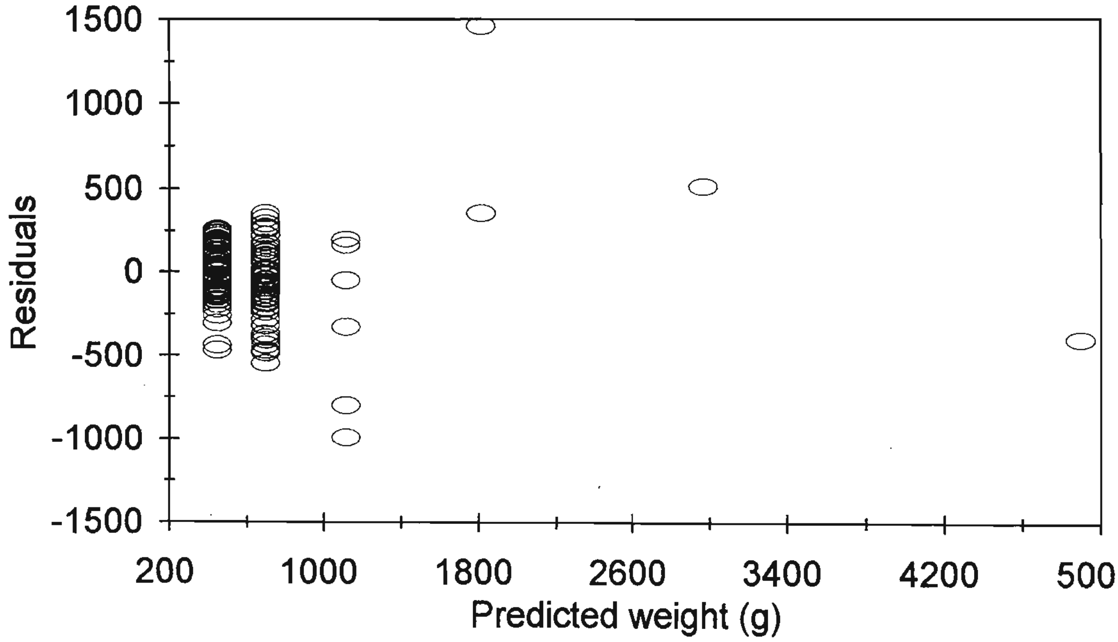

Figure 5.2 Residual plot versus predicted weight (n=162)

Table 5.2 Estimates of the Deriso-Schnute parameters from a time series (1956-1972) of mean weights for *Pomatomus saltatrix* captured during fishing competitions. The average recruitment rate parameter R was arbitarily set to one. Coefficients of variations were estimated using the "parametric" bootstrap technique.

	M (year^{-1})	q	B_{1956}
Estimate	0.895	9×10^{-9}	2961.9
CV (%)	2.1	900	3.6

The natural mortality rate was estimated to be 0.895 year^{-1} with a low CV. This estimate of M is includes an emigration component. The relative biomass estimate in year 1956 was also estimated with good precision (Table 5.2) however, the catchabiltity coefficient was estimated with very poor precision. As a result there is little confidence in the estimates of fishing mortality rates and catch in numbers estimated in this study.

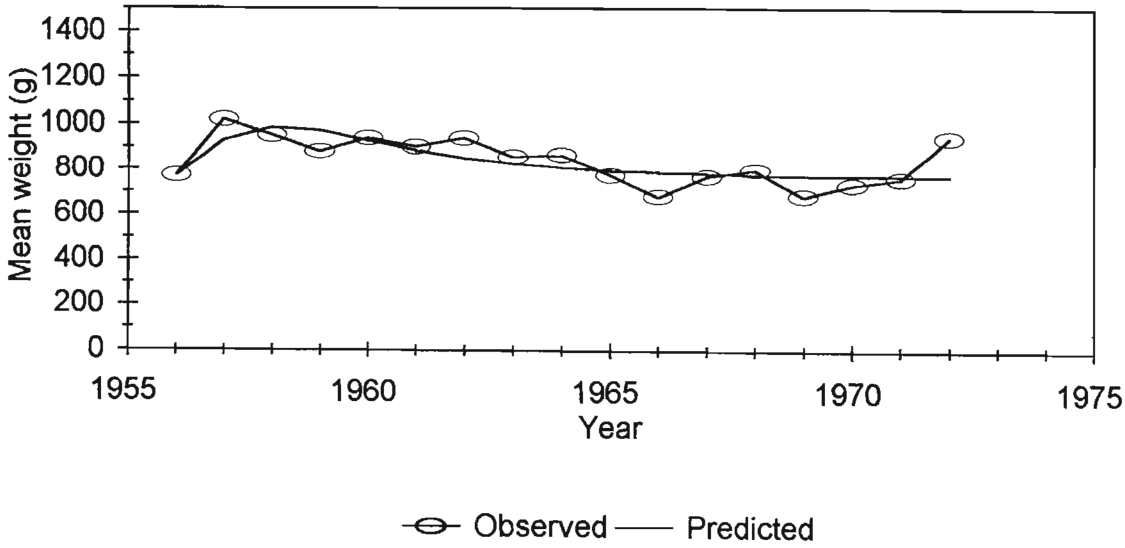

Figure 5.3 Observed and model predicted mean weights for *P. saltatrix*

In Figure 5.3 the observed time series as well as the predicted time series of mean weights are shown for the Deriso-Schnute parameter estimates. Generally, for the observed mean weights from 1956 to 1969 there has been a decline in mean weight with increases in mean weight thereafter (Figure 5.3). However, since no standard deviations were reported for these mean weights (van der Elst, 1976) it is not clear if this is a real trend. Generally, the predicted mean weight has a similar trajectory with a very good fit of the model to the observed weights. This is evident from the residual plot shown in Figure 5.4 which indicates that the residuals are normally distributed with no trends.

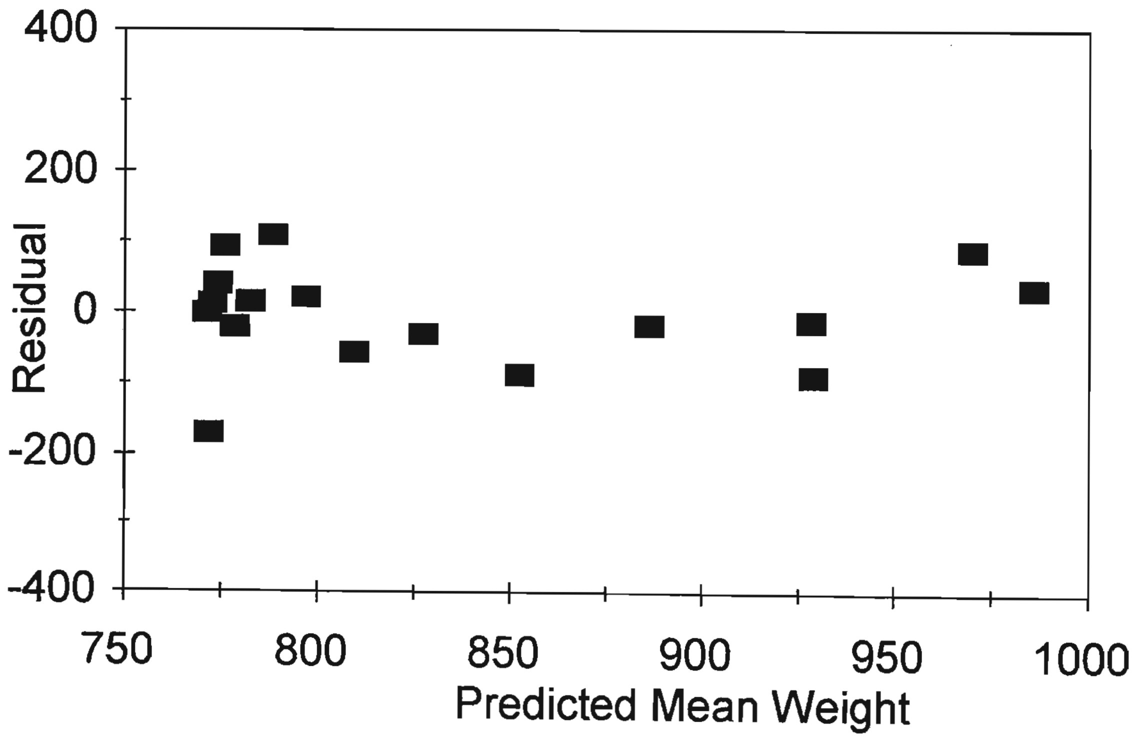

Figure 5.4 Residual plot versus predicted mean weight for *P. saltatrix*

In Figure 5.5 the predicted relative biomasses and catch are shown. During the 17 years there has been a dramatic decrease in relative biomass with stable biomasses after 1965. Predicted annual catches are variable, however, throughout the time series there has been a general decline in catch numbers. This is consistent with observations by fishers during this period who complained of declining catches and a reduction in average size of *P. saltatrix* harvested (Smith *et al.*, 1979; van der Elst, 1976).

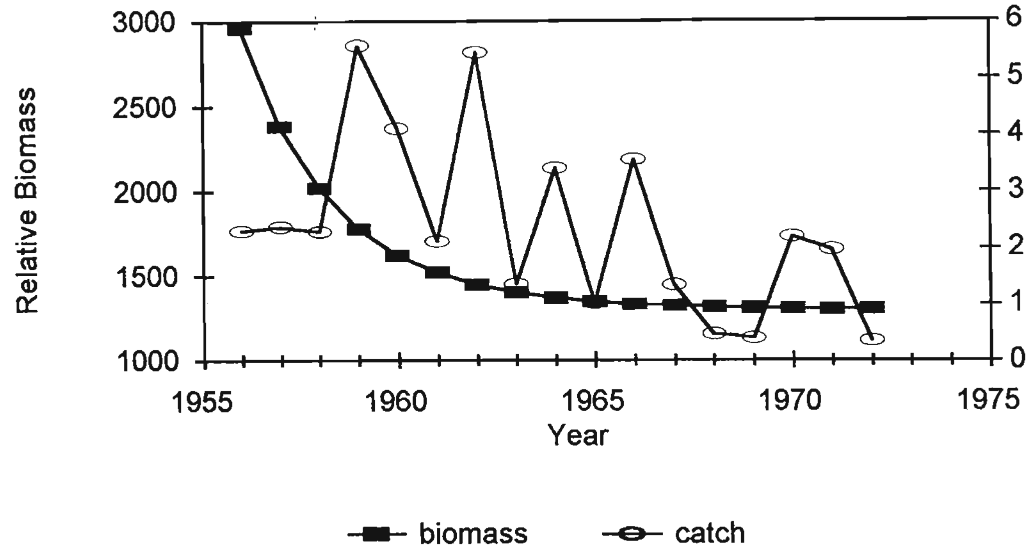

Figure 5.5 Model predicted estimates of relative biomass and catch for *P. saltatrix* for the years 1956 to 1972.

In Figure 5.6 estimates of relative fishing mortality rates are given. These fishing mortality rates are compared to estimates obtained from a VPA study by Butterworth *et al.* (1989). The trend in each data set is similar showing variable annual fishing mortality rates with a general decline in the latter part of the time series. The fact that q is estimated with high variance would indicate that the fishing mortality rates in this study would also be estimated with wide variances.

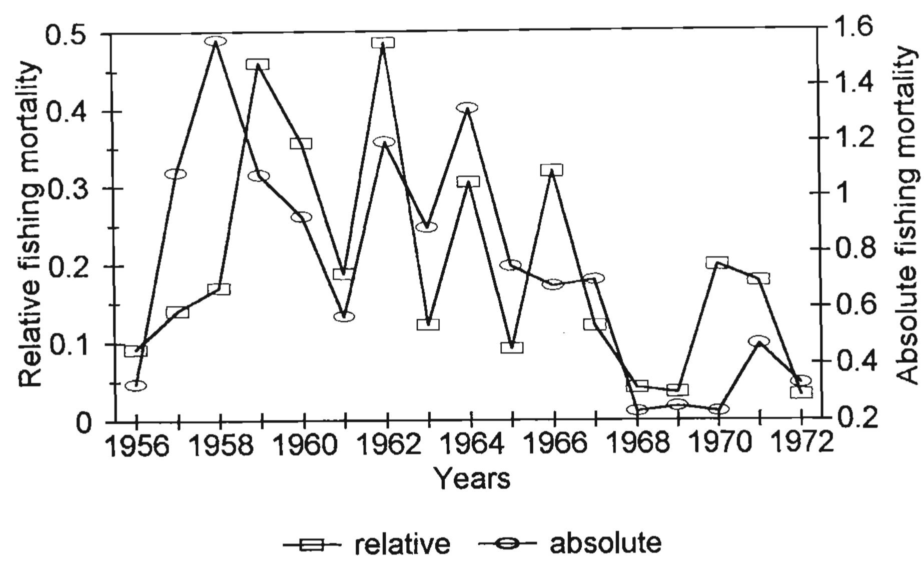

Figure 5.6 Relative fishing mortality rates estimated for *P. saltatrix* in this study compared to estimates of absolute fishing mortality estimated by Butterworth *et al.* (1979) from a VPA study during the same time period.

5.6 Discussion

The growth parameters were fairly well estimated (low CVs). In many fish species ρ lies between zero and one i.e. $0 < \rho < 1$ (Schnute 1985). This assumes an asymptotic relationship between the fully recruited ages and body weight. However, the estimate of ρ for *P. saltatrix*, estimated in this study, is greater than 1 because the weight at age relationship is an exponentially increasing relationship (Figure 5.1) rather than an asymptotic relationship. This is a result of the lack of older age classes in the catches. In the study of van der Elst (1976) he aged a few fish to at least 8 years while Butterworth *et al.* (1989) for their VPA analysis assumed ages up to 10 years. In this study, few fish sampled were older than 3 years. The lack of older fish in the catch could be a result of the higher fishing mortality rates recorded during this study. At high fishing mortality rates older fish become less abundant as they are usually the individuals that are initially fished out (Punt *et al.*, 1993).

In the model, it is assumed, that growth, natural mortality rate (plus an emigration factor) and average recruitment are constant throughtout the 17 years and that only the fishing mortality rates would result in biomass changes i.e.the Deriso-Schnute model, as implemented in this study, captures only the effects of growth overfishing (Hilborn and Walters, 1992) . It is clear that although the fishing mortality rate has been variable from year to year with a general decrease between 1964 to 1972 (Figure 5.6) the fishing mortality rates have been sufficiently high to reduce the biomass to relatively low but stable levels. The general decline in fishing mortality during the latter years of the time series is insufficient to allow re-building of biomass during this time. However, it is sufficient enough for the population biomass to stablise (Figure 5.5) indicating that equilibrium has been reached.

During the 17 years there has been approximately a 44% reduction in biomass. This percentage reduction has a small confidence range (40 to 45%) as the coefficient of variation for the B_{1956} parameter was very low (3.6%). This 44% reduction in biomass is in keeping with the findings of Butterworth *et al.* (1989) who estimated that during the same time period *P. saltatrix* abundance decreased by as much as 58% (ranging from 34 to 82%) based on an analysis of catch and effort data. Van der Elst (1976) also reported similar declines in CPUE for the same time period.

The natural mortality rate was well estimated and with a low CV (2.1%). However, this estimate in the case for *P. saltatrix* is probably too large to represent declines from natural mortality alone. It is therefore assumed that this estimate is confounded with emigration effects. If the natural mortality rate in *P. saltatrix* is in the region of 0.3 to 0.5 year^{-1} then it may be assumed that emigration is of a similar value and possibly ranges from from 0.4 to 0.6 year^{-1} for the whole *P. saltatrix* stock.

As the model fit to the observed data is a good fit it is presumed that the assumption of a constant level of average recruitment during the study period was a reasonable assumption. This would indicate that although biomass has declined during the study period the decline in parent stock was insufficient to affect the recruitment rate. It would therefore appear that recruitment is independent of a wide range of parent stock size except (obviously) at very low parent stock sizes. This would imply that a Beverton and Holt stock-recruitment curve might be a reasonable expression for the relationship between parent stock size and recruitment for *P. saltatrix*. It should, however, be borne in mind that in the case of *P. saltatrix* recruitment rates would be more greatly affected by physical and biological changes in the environment than just by changes in parent stock size. This is so because van der Elst (1976) showed that *P. saltatrix* abundance was directly related to changes in annual rainfall and changes in water temperature. Years of high mean water tempertaures (> 20°C) and low rainfall (< 1000mm) show relatively high abundances of *P. saltatrix*. It is therefore probable that in the case of *P. saltatrix* that annual abundance and hence recruitment can be largely dependent on environmental changes.

In conclusion, during the 1956 to 1972 period there was a decline in *P. saltatrix* abundance with corresponding declines in mean weight of the catch. Although during this period there was a general decline in fishing mortality, (this study, Butterworth *et al.* (1989)) the fishing mortality was sufficiently high for growth overfishing to occur i.e. removal of older animals which results in changes in mean size with time. It is therefore imperative that the mean size of *P. saltatrix* harvested be closely monitored as this may provide an indication of possible declines in future abundance. However, this easier said than done because the present regulations (minimum size limit, bag limit and closed season) would also affect the mean size of *P. saltatrix* harvested. In KwaZulu-Natal, van der Elst (1976) showed that the mean size of *P. saltatrix* harvested during the months of September to November (present closed season) was generally larger than that harvested outside this period. Furthermore, the mean size of *P. saltatrix* differs geographically. For example, van der Elst (1976) recorded a larger mean size for *P. saltatrix* harvested from the north coast of KwaZulu-Natal as compared to the south coast of KwaZulu-Natal. This is probably due to migration effects. During the fishing season the fish gradually move from the south to the north coasts over an approximately 6 month period. This would provide sufficient time for adequate increase in growth and hence a difference in mean size.

Chapter Six

EVALUATION OF CLOSED SEASON

6.1 Introduction

In recent years the restriction of fishing during certain parts of the year (closed season) has been used to manage some South African linefish resources. This management option is claimed to reduce total effort in the fishery and protect the fish stock during a vulnerable period of its life history (Buxton, 1990). For example, fish may aggregate for spawning and during this period may be susceptible to increased capture especially if it is easy for fishers to locate spawning shoals. In such an example it is intuitive that a closed season introduced during this vulnerable portion in the life history of a species would certainly conserve future spawning potential. However, it is not clear if a closed season can reduce overall effort on the species because fishers may simply fish more intensely in the open season to make up for lost yield during the closed season.

In the current South African legislation a closed season has been used to protect the following linefish species: *P. saltatrix*, seventyfour *Polysteganus undulosus* (Sparidae), red steenbras *Petrus rupestris* (Sparidae) and galjoen *Dichistius capensis* (Coracinidae). In the case of *P. saltatrix* the closed season for fishing extends from the first of September to the last day of November of each year. The regulation is applicable in the Eastern Cape, Western Cape and KwaZulu-Natal waters and is applicable to both commercial and recreational harvesting. This regulation has been in force since 1973 in KwaZulu-Natal and since 1985 in the Eastern and Western Cape. To date, there has been no evaluation of whether this managment regulation has achieved the desired objective of reducing effort on *P. saltatrix* and protecting the spawning stock of *P. saltatrix*. In fact, there has been no evaluation of the closed season for any of the linefish species so regulated.

In this chapter a modified yield-per-recruit model (Beverton and Holt, 1957) is used to test what effects the present closed season have on the amount of eggs produced and on yield harvested. Other closed season strategies such as alternative timing of the season and reduction in the closed season duration were also evaluated.

6.2 Yield-per-recruit model

In order to examine the effects of a closed season on egg production of *P. saltatrix* and on the yield harvested the Beverton and Holt (1957) yield-per-recruit model was modified. The major modification is that the time-step for the yield and egg estimates at various fishing mortality rates was set to one month (1/12 years) as opposed to the more traditonal time-step of one year.

The yield-per-recruit (YPR) is calculated as follows

$$YPR=\sum_{t=t_c}^{\max}\frac{F_t}{F_t S_t A_t+M}(N_t(1-e^{-(S_t A_t F_t)-M}).W_t.S_t.A_t \qquad \textbf{(6.1)}$$

where

t_c = mean age corresponding to the minimum size limit,

max = maximum observed age in the fishery,

F_t = instantaneous fishing mortality rate on t-aged fish and is assumed to be constant for each age class,

M= instantaneous natural mortality rate assumed to be constant,

N_t= the number of fish surviving to age t, such that

$$N_t=Re^{(-(S_t A_t F_t)-M)t} \qquad \textbf{(6.2)}$$

R= number of recruits and is set to one,

W_t= mean weight at age t, such that

$$W_t=a[L_\infty(1-\exp(-k(t-t_0))]^b \qquad \textbf{(6.3)}$$

a,b= length-weight parameters,

L_∞= asymptotic mean length,

k= growth constant,

t_0= theoretical age at zero length,

S_t= the selectivity function, such that

$$S_t = \begin{cases} 0 & \text{if } t<t_c \\ 1 & \text{if } t\geq t_c \end{cases}$$

$A_t=$ is a closed season function, such that

$$A_t = \begin{cases} 0 & \text{if the month is closed} \\ 1 & \text{if the month is open} \end{cases}$$

6.3 Eggs-per-recruit

Van der Elst (1976) determined that the mean fecundity (*fm*) of *P. saltatrix* increased exponentially with an increase in size and was described by the following formula

$$fm = 7.32 \times 10^{-8}(L_t)^{4.65}$$

Beckley and Connell (in press) reported mean monthly egg counts for *P. saltatrix* sampled off a station in KwaZulu-Natal. The samples were obtained from January 1987 to April 1995 and were expressed as the mean number of eggs per sample. In order to obtain a relative index of the amount of eggs produced in a month the following formula was used to standardise the mean number of eggs reported by Beckley and Connell (in press). The relative mean number of eggs produced each month (E_t) was calculated as

$$E_t = \frac{\text{mean number of eggs sampled in a month}}{\text{mean number of eggs sampled in the peak month}}$$

The number of eggs produced per recruit (EPR) was therefore, modelled from the following equation

$$EPR = \sum_{t=t_m}^{\max} (fm)_t . E_t . Re^{(-(S_t A_t F_t) - M)t} \tag{6.4}$$

where

$t_m =$ age-at-maturity

6.4 Mean weight of catch

The mean weight of the catch (W_{mean}) is calculated by the total yield-per-recruit in weight divided by the total yield-per-recruit in numbers i.e.

$$W_{mean} = \frac{\sum_{t=t_c}^{\max} \frac{F_t}{F_t S_t A_t + M} (N_t(1 - e^{-(S_t A_t F_t) - M}) . W_t . S_t . A_t}{\sum_{t=t_c}^{\max} \frac{F_t}{F_t S_t A_t + M} (N_t(1 - e^{-(S_t A_t F_t) - M}) S_t . A_t} \tag{6.5}$$

6.5 Model assumptions

In the model constant recruitment is assumed. This may not be a reasonable assumption for *P. saltatrix* but there is at present no information on a stock-recruitment relationship for this species. Both natural and fishing mortality have been assumed to be age-invariant for ages above t_c. Although not realistic, violations of this assumption will affect both yield as well as egg estimates. The magnitude of the bias will depend on the magnitude of the variability. It is also assumed that all age classes above the age corresponding to the minimum size limit are available for harvesting and that selectivity is a knife-edged function. This is probably true for ages 0 to 3. From the analysis of migration in chapter three and growth in chapter four it is clear that these age groups which are the age classes most often tagged and released are available to harvesting and that few migrate away from the areas of fishing. The unavailabilty of older age classes to harvesting will result in yield calculations that are overestimated in this model. However, the effects on egg production will not be affected. It is possible that larger and older individuals are not available to anglers fishing from the shore because of the large fishing mortality rate on this species in KwaZulu-Natal (see chapter three). Fishers, especially recreational anglers, usually target the larger individuals and, at high fishing rates, rapidly fish these individuals out. A similar situation has occurred in the sex-changing sparid *Chrysoblephus puniceus* (Punt *et al.,* 1993).

The natural mortality rate for *P. saltatrix* has been assumed to equal 0.4 year^{-1}. Butterworth *et al.* (1989) made the same assumption in their analysis of *P. saltatrix*. Hughes (1986) assumed that *M* ranged from 0.41 to 0.48 year^{-1} in her study of *P. saltatrix* whilst off the temperate east coast of the United States Terceiro *et al.* (1992) assumed an *M* value equal to 0.35 year^{-1} for this species. The assumption of *M* equal to 0.4 year^{-1} thus appears to be a reasonable assumption for *P. saltatrix* harvested in

South African waters.

Maturity has also been assumed to be a knife-edged function. This is a reasonable assumption as the age difference between the length-at-50% maturity and the length-at-100% maturity is 3 months (based on the growth curve estimated in chapter four). It is also assumed that the monthly egg production pattern does not change from year to year and is the same for each age class. Monthly gonadosomatic indices recorded for *P. saltatrix* in the 1976-1977 period (van der Elst, 1976) showed a similar trend to the monthly egg counts obtained from 1987 to 1993 (Beckley and Connell (in press)). Egg abundance did lag the GSI indices by one month i.e. GSI peaked in November while egg counts peaked in December. There is no information at present as to whether the monthly egg production pattern is the same for each age class.

6.6 Results

In Tables 6.1 and 6.2, data and parameter estimates that were used in the yield- and egg-per-recruit analyses are summarised as well as the data sources.

Table 6.1 Input data to the yield- and egg-per-recruit analyses.

PARAMETER	ESTIMATE	SOURCE
L_∞	552mm	this study
k	0.43 year^{-1}	this study
t_0	-0.97	this study
a	0.000015	van der Elst (1976)
b	2.97	van der Elst (1976)
t_c	0.7 years	this study
t_m	0.5 years	this study
M	0.4 year^{-1}	Butterworth *et al.* (1989)

Table 6.2 Relative egg counts recorded by Beckley and Connell (in press). The mean number of eggs recorded per sample in December was 16.7 eggs per sample.

MONTH	RELATIVE EGG COUNT	MONTH	RELATIVE EGG COUNT
Jan	0.59	July	0.03
Feb	0.28	Aug	0
Mar	0.35	Sep	0.015
Apr	0.023	Oct	0.28
May	0.023	Nov	0.8
Jun	0.023	Dec	1

6.6.1 Closed seasons versus fishing throughout the year

The effects on egg production and on the yield harvested were examined for the present closed season as well as for fishing throughout the year (this is referred to as a continuous season, in this study). In the case of a closed season the A_t values for the months of the closed season (e.g.September to November) where set to zero and the rest of the months to one.

The yield-per-recruit curves for *P. saltatrix* are dome-shaped with maximum sustainable yield occuring at high fishing mortality rates (Figure 6.1). The biological reference point F_{MSY} and $F_{0.1}$ are estimated for the various closed seasons and are given in Table 6.3. The average fishing mortality rate estimated for KwaZulu-Natal (1.7 year^{-1} - see chapter three) is lower than the fishing rates estimated at which MSY or optimal yield occurs irrespective of the timing of the closed season. It is obvious that an introduction of the present closed season has resulted in a decrease in yield but with corresponding increases in egg production (Figures 6.1 and 6.2).

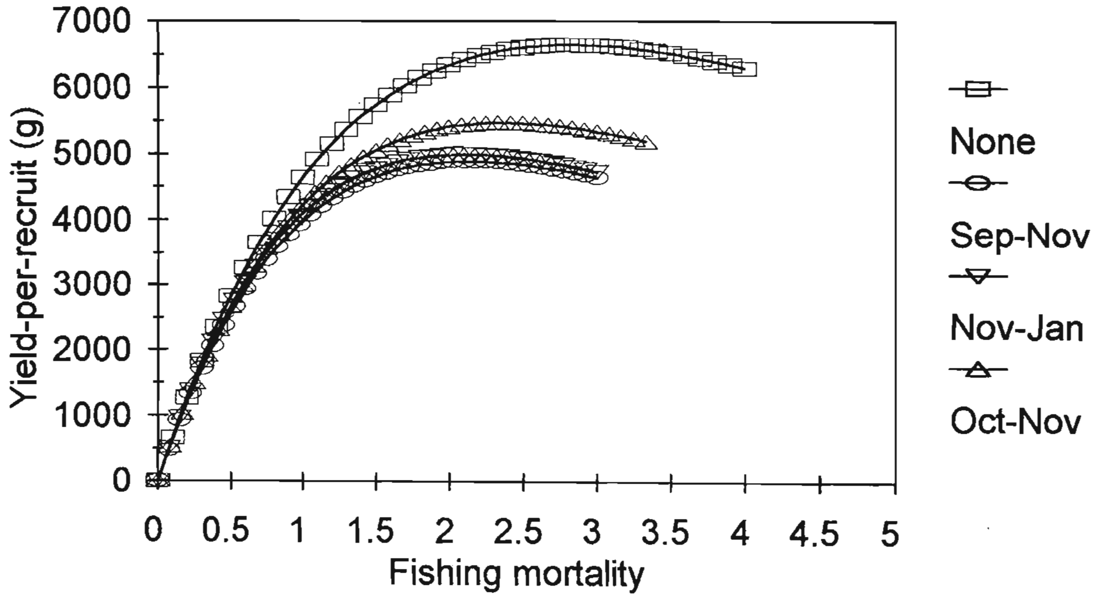

Figure 6.1 Yield-per-recruit estimates for the *P. saltatrix* fishery at various fishing mortality rates (year^{-1}) and for various closed seasons.

Table 6.3 Percentage of egg production in the *P. saltatrix* fishery compared to a pristine state for various closed season options at a fishing mortality rate of 1.7 year^{-1}. The fishing mortality rate is an average estimate for KwaZulu-Natal (see chapter three). F_{MSY} and $F_{0.1}$ estimates for various closed season options are also given.

CLOSED SEASON	EGG PRODUCTION (%)	F_{MSY} (year^{-1})	$F_{0.1}$ (year^{-1})
None	53	2.8	2.5
Sep-Nov (Current season)	67	2.1	1.9
Nov - Jan	83	2.1	1.9
Oct - Nov	65	2.3	2.1

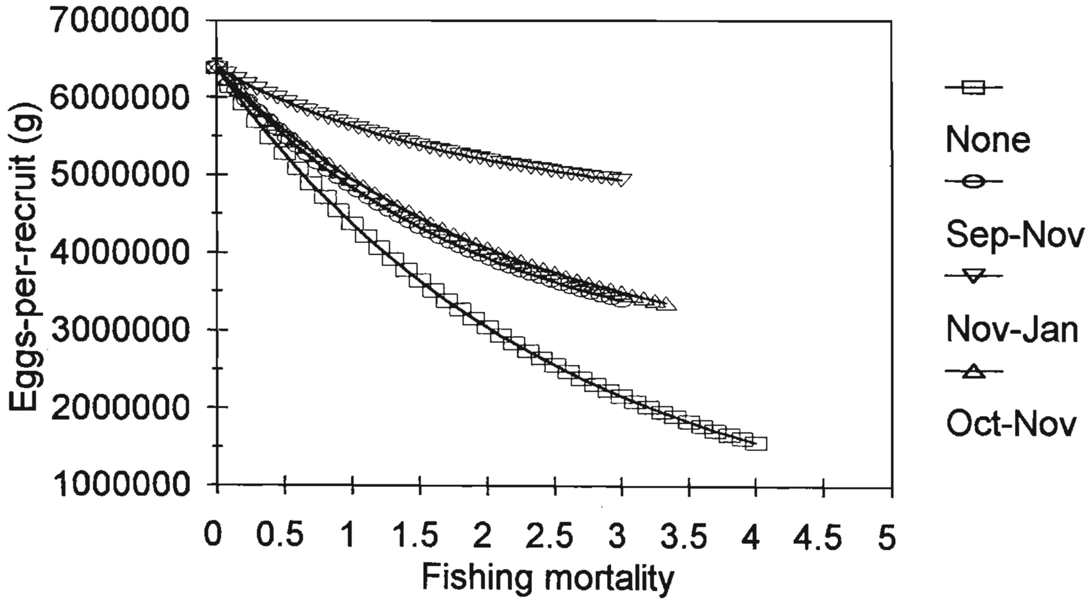

Figure 6.2 Eggs-per-recruit estimates for the *P. saltatrix* fishery at different fishing mortality rates (year^{-1}) and for various closed season options.

A reduction of the closed season by one month (September) results in an increase in yield but with no change in egg production (Figure 6.3). This is not surprising because the number of eggs produced in this month relative to the peak month of December is very low (Table 6.2). Shifting the closed season from the present September-

November to November to January which coincides with peak egg production does not alter yields harvested substantially but results in enormous conservation of egg production (Figure 6.3).

In Table 6.3 the percentage of egg production for the various closed season options compared to a pristine state is given for the current fishing mortality rate in KwaZulu-Natal. Egg production for the two month closed season from October to November is slightly lower than the present three month closed season (September to November).

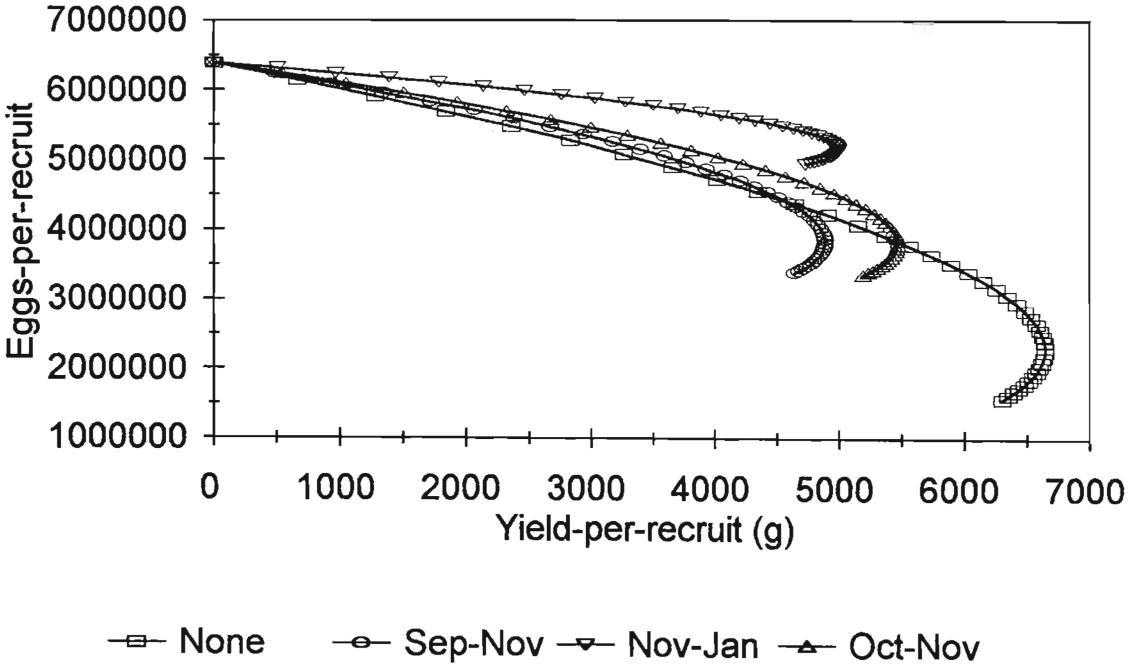

Figure 6.3 Eggs-per-recruit versus yield-per-recruit for the *P. saltatrix* fishery for various closed season options.

Although the present closed season and the other closed season options examined indicate that closed seasons increase egg production, keeping the fishery open throughout the year has very little effect on egg production provided that the fishing mortality rate is maintained at the present level.

In Figure 6.4 the mean size of the catch is shown for the various closed season options. Generally, there are only very minor differences in mean weight of the fish caught for the various closed season options. The introduction of a closed season does not alter the mean weight of fish caught substantially.

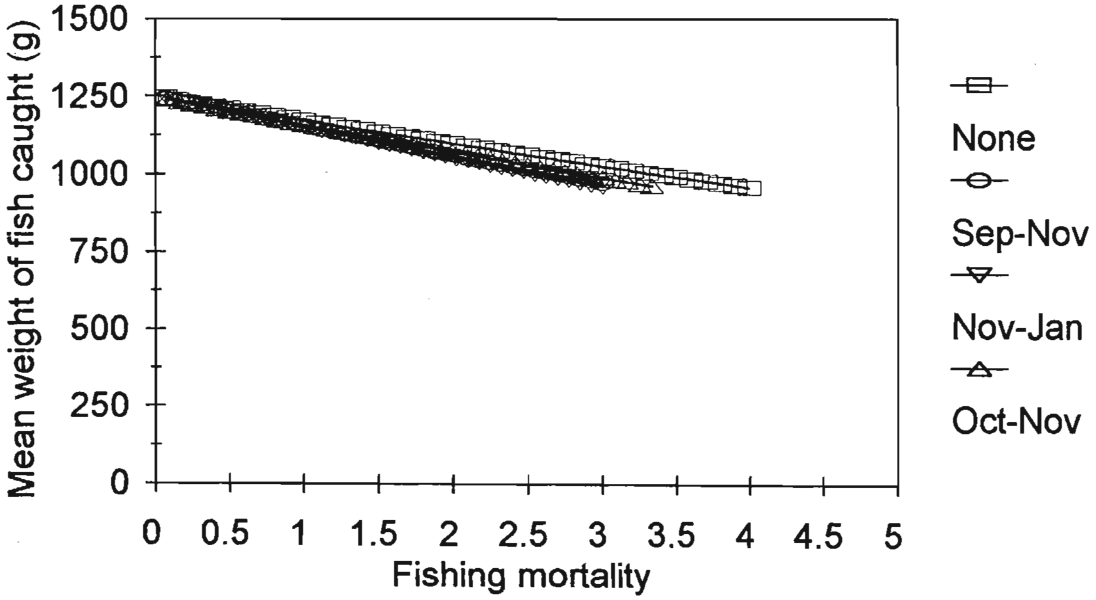

Figure 6.4 Mean catch weight in the *P. saltatrix* fishery at various fishing mortality rates (year^{-1}) and for various closed seasons.

One possible effect of this closed season management strategy is that fishers may tend to fish harder in the open season in order to compensate for lost yields in the closed season. For example, in a continuous fishing season to realise a yield-per-recruit of

4900 g a fishing mortality rate of approximately 1 year^{-1} needs to be exerted (Figure 6.1). To realise the same yield with the present closed season it would take a fishing mortality rate of nearly 2 year^{-1} which is double that if no closed season applied (Figure 6.1). Moreover, despite fishers "diverting" the fishing mortality from the closed season to other months of year it also possible that the length of the closed season could also affect the fishing mortality rate i.e. the longer the closed season the greater the fishing mortality in the months in which fishing is permitted. This is shown in Figure 6.4. For example, the two month closed season (Oct to November) results in

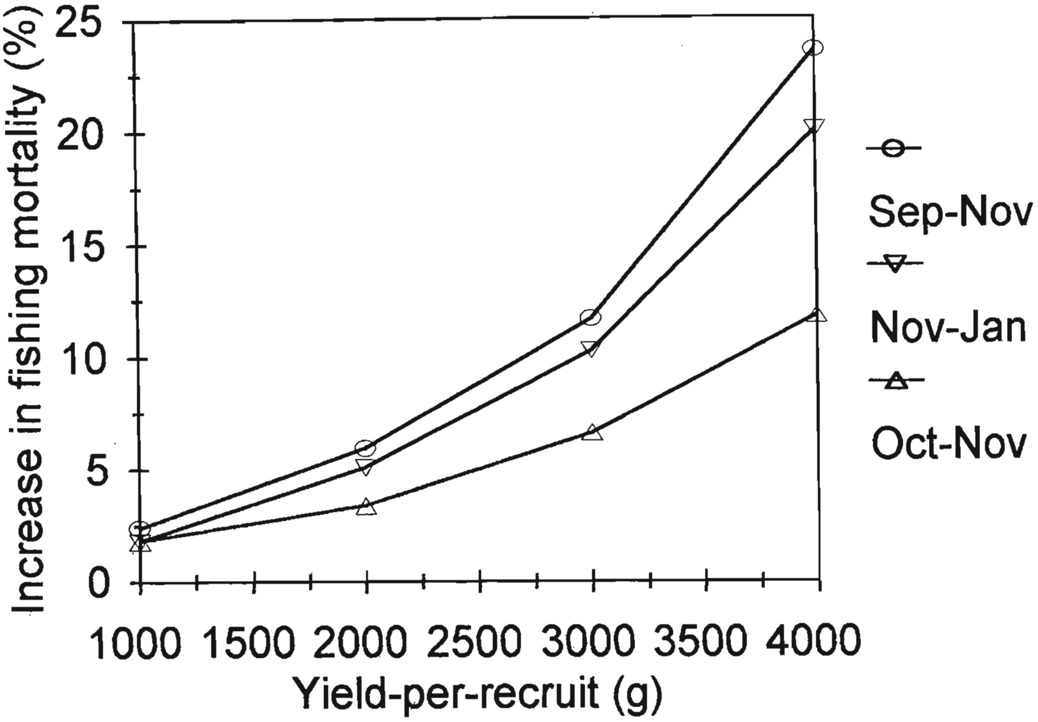

Figure 6.5 Increases in fishing mortality rate with implementation of various closed season options. Increases are compared to the base case or "continuous" season option for *P. saltatrix*.

smaller increases in fishing mortality when compared to a three month closed season. The increases in fishing mortality rate are compared to the base case or the continuous fishing season option.

6.7 Discussion

The implementation of the present closed season benefits the *P.saltatrix* fishery by conserving egg production in this species during the spawning period. Greater benefit in egg production conservation can be realised by shifting the present three month closed season to extend over the November-January period without loss in present yield levels. However, this period coincides with the influx of tourists to the coast of KwaZulu-Natal during the summer holiday season. Extending the closed season over this time period may adversely affect this tourist industry. In fact, the Smith Commission of enquiry in 1979 recognised this and recommended that December should not be included as a month closed to *P. saltatrix* fishing in KwaZulu-Natal (Smith *et al.*, 1979). However, the changing political climate in South Africa may require investigation into the claim that local sea-side resorts rely largely on the patronage of anglers.

Reducing the present closed season by one month (September) would increase yields in the fishery without having an adverse effect on egg production. In the study by Beckley and Connell (in press) it was found that relative to the peak month of spawning (December) relatively few eggs are spawned during September. In the study by van der Elst (1976) it was found that the gonadosomatic index during September was 55% of the GSI index for the peak month of November. These studies indicate that September is not a critical month for spawning. At present, closing this month to fishing has no beneficial effects in terms of conserving egg production.

The present level of exploitation appears to be sustainable for *P. saltatrix* as the current level of exploitation is below the levels of MSY or optimum yield. This coupled with the fact that egg production during a continuous fishing season results in an egg production level at just 50% of a pristine level would indicate that a minimum size limit and a daily bag limit presently offer sufficient protection to the *P. saltatrix* fishery (Butterworth *et al.*, 1989) provided that fishing mortality does not increase above sustainable levels.

The high fecundity of *P. saltatrix* (van der Elst, 1976; Bade, 1977) and its high rate of somatic growth (chapter four) are the dominant processes that afford *P. saltatrix* resilence to overfishing even at high fishing rates. The open access nature of this fishery and the fact the new entrants to this fishery increase at annual rate of 6% (van der Elst, 1989) would indicate that fishing mortality in this fishery is likely to increase substantially in the future. The high annual variability in catches in *P. saltatrix* fisheries is well documented (van der Elst, 1976; Bade, 1977; Krug and Haimovici, 1989) and indicates that, possibly, recruitment fluctuates annually and is enviromentally dependent. Variability in annual recruitment was not considered in the yield-per-recruit analyses because of a lack of knowledge of environmental conditions that directly affect recruitment.

Surprisingly, the introduction of a closed season has had little effect on the mean weight of catches even at high fishing rates. Since 1987, the mean weight of *P. saltatrix* recorded during fishing competitions has fluctuated between 690 to 864g which is lower than the values predicted by the per-recruit model (Figure 6.4). This is probably because of differential fishing mortality on age classes. In the per-recruit model it is assumed that all age classes experience the same fishing mortality rate. Butterworth *et al.* (1989) from a VPA analysis showed that fishing mortality is higher on younger *P. saltatrix* than on older individuals. Age-dependent fishing mortality rates which favour smaller-sized individuals would result in smaller mean sizes as observed in the KwaZulu-Natal fishery.

It is shown that the closed season does protect the spawning stock of *P. saltatrix* by conserving egg production, however, the closed season does not necessarily reduce effort in the fishery. This could be as a result of two reasons. Firstly, fishers may divert effort during those months open to fishing in order to compensate for yields lost during the closed season. Secondly, closed seasons that are too long may also promote greater effort since fishers may spend more time fishing during months open to fishing. Hence, this may result in greater fishing mortality rates when compared to closed seasons that are of shorter duration.

Chapter Seven

CONCLUSIONS

This study on developing mark-recapture models utilised data from the Sedgwick's-ORI tagging programme and the National Marine Linefish System. These data are derived from voluntary contributions by recreational anglers as well as from regional management officers as they undertake regular law enforcement shore-patrols and as a result, there are inherent biases and shortcomings in the data sets. In spite of these shortcomings, this study has shown that useful population dynamic parameters can be estimated from these data for the *P. saltatrix* fishery.

The models developed in this study allow for the estimation of mortality, survival and migration rates in exploited fish stocks. The growth model can be used to simultaneously estimate growth parameters as well as to validate the hard structure banding. The per-recruit model allows a fishery manager to objectively decide on the period and length of a closed season based on stated aims to be achieved in the fishery. There are number of advantages to these models. Given appropriate datasets the mark-recapture models developed in this study can be applied to others species of interest i.e. the models are general. With slight modification the models can also incorporate other datasets eg. mortality and survival rates can be estimated on a monthly basis if appropriate monthly fishing effort data are available. The models can easily be implemented in a spreadsheet and as a result does not require the reseacher to have extensive programming experience. The spreadsheet programming facilitates the estimation of parameter variances using likelihood profile or bootstrapping methods as well as allowing the testing of model assumptions based on simulations.

It is concluded that growth in *P. saltatrix* is much faster and more variable than was previously documented from South African waters. Fast growth in *P. saltatrix* offers some resilience to high fishing pressure as it results in maturity and recruitment to the fishery being attained at an earlier age. Fishing mortality is shown to be exceedingly high in KwaZulu-Natal with the present fishing regulations for *P. saltatrix* having little effect in reducing this mortality. It is concluded that immigration into KwaZulu-Natal from the Eastern and Western Cape is extensive with virtually the entire mature stock undertaking the migration. High fishing mortality rates affect the return migration of *P. saltatrix* from KwaZulu-Natal to the Eastern and Western Cape and also result in declines in *P. saltatrix* biomass. High fishing mortality rates result in minor changes in mean weight of *P. saltatrix* caught but these changes are large enough to be used as an index of biomass decline in the fishery as shown by the delay-difference model.

A framework for the objective evaluation of the effects of a closed season on egg production and yield harvested has been developed. It offers a scientifically defensible means of comparing alternative timing and duration of proposed closed seasons by testing the outcomes on egg production and yield harvested. It is shown that by reducing the present closed season by one month (September) the anglers' expectations of greater yield harvested and fisheries managers' goal of conserving spawning potential are jointly fulfilled. A closed season management strategy for *P. saltatrix* cannot guarantee reductions in fishing effort over the long-term.

There is a need to develop a defensible management plan for the utilisation of *P. saltatrix* in South Africa aimed at achieving established goals for the fishery. The plan

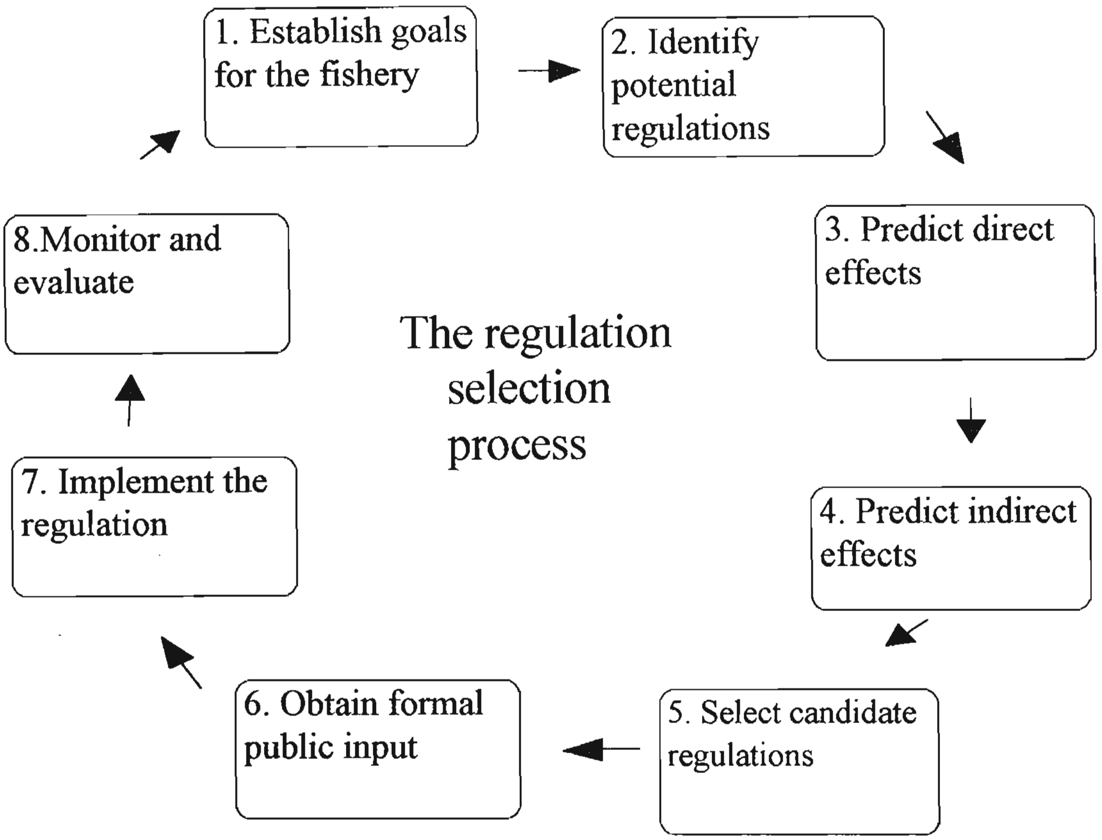

Figure 7.1 A strategy for the selection of a harvest regulation process for a recreational fishery (from Johnson and Martinez, 1995)

has to be developed jointly by national and regional management authorities, fisheries scientists, commercial and recreational harvesters as well as other stakeholders such as the tourist industry and the general public. Participation should be drawn from the Western Cape, Eastern Cape and KwaZulu-Natal provinces as the stock is shared between these regions.

A possible process for the selection of a management strategy for a recreational fishery has been proposed by Johnson and Martinez (1995) and is given in Figure 7.1.

In the context of the South African *P. saltatrix* fishery, fisheries managers have largely concentrated on identifying potential regulations and then implementing them. The present study on *P. saltatrix* contributes to the above process by predicting direct and indirect effects of regulations and hence selection of appropriate controls. Moreover, and most importantly, it has shown the role of quantitative modelling procedures using information from existing national databases to monitor and evaluate recreational fisheries such as the *P. saltatrix* fishery.

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