# BIOLOGY, POPULATION DYNAMICS AND MANAGEMENT OF CARPENTER (*ARGYROZONA ARGYROZONA*), AN ENDEMIC SOUTH AFRICAN REEF FISH.

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# BIOLOGY, POPULATION DYNAMICS AND MANAGEMENT OF CARPENTER (*ARGYROZONA ARGYROZONA*), AN ENDEMIC SOUTH AFRICAN REEF FISH.

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By

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Dedicated to my parents

*Argyrozona argyrozona* (Valenciennes, 1830)
**Photographed by the author in the Tsitsikamma National Park at a depth of 36m**

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# PREFACE

This thesis is submitted as a collection of six papers (each as a separate chapter), preceded by an introduction and followed by a general discussion. A degree of repetition in the introductions (and to some extent the discussions) from each of the papers was therefore unavoidable. Where dual authorships are concerned (see Appendix I), the senior author was responsible for all data collection, data analysis, concepts, hypotheses and conclusions.

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# ABSTRACT

Carpenter, *Argyrozona argyrozona* (Valenciennes, 1830), is an endemic South African sparid fish. They form an important component of the commercial linefishery on the South African east coast, where they are the third most important species landed. Recent investigations revealed that the catch per unit effort (*cpue*) of this species has declined markedly since the early 1900's. Despite these declines and the importance of this resource, remarkably little biological information on this species exists for providing management advice. This thesis investigates the life history of carpenter, particularly those aspects that are used for management. This includes an investigation into the stock distribution and identification of nursery areas, and an assessment of age, growth, reproduction and movement patterns.

Age and growth was assessed using methods based on both otoliths and mark-recapture. Transverse sagittal sections from the Tsitsikamma National Park showed clear opaque and translucent growth increments. Marginal growth zone analysis and mark-recapture of chemically tagged fish (Oxytetracycline) revealed that these were deposited on an annual basis: opaque in summer and translucent in winter. *A. argyrozona* were found to be long lived (up to 27 years) and slow growing. Within reader (between counts) and between readers average percent error (APE) was 5.3 and 1.8, respectively, showing that readability of carpenter otoliths is high. Comparison between whole and sectioned otoliths showed that the former significantly under-estimated the age of fish older than 10 years ($p<0.01$).

A large proportion (68%) of the individual growth rates derived from mark-recapture data were below those predicted by the otolith based von Bertalanffy growth model ($p<0.01$). This was attributed to the negative influence of external tags, as hydroids, frequently occurring on the tags of recaptured fish, were observed to cause severe lesions and in some cases, extensive fin damage. This brings into question the use of mark-recapture studies to calculate growth of some species.

The effects of sampling design and sample size on age and growth estimation were assessed. The minimum sample size required to accurately estimate growth and mortality, and the effects of using either random or stratified sampling procedures were tested. Decimal and integer ageing both produced similar estimates of von Bertalanffy growth parameters, growth curves, spawner biomass-per-recruit (*SB/R*) and fishing mortality (*F*) estimates. Sampling monthly throughout the year and collecting data in a single large sample provided similar growth curves, von Bertalanffy, *F* and *SB/R* estimates. The data showed that estimates based on less than 300 random samples were unreliable. However, accurate growth parameter estimates were achievable with less than 200 samples if the sample was stratified with 10 or more samples per 2 cm size class.

An investigation into the reproductive biology of *A. argyrozona* within the Tsitsikamma National Park revealed that they were serial spawning late gonochorists. The size at 50% maturity ($L_{50}$) was estimated at 292 and 297 mm FL for females and males, respectively. Both monthly gonadosomatic indices and macroscopically determined ovarian stages strongly suggest that *A. argyrozona* within the Tsitsikamma National Park spawn in the austral summer between November and April. The presence of post-ovulatory follicles (POF's) confirmed the six month spawning season, while monthly proportions of early (0-6 hour old) POF's showed that spawning frequency was highest (once every 1-2 days) from December to March. Although spawning season was more highly correlated to photoperiod (r = 0.859) than temperature (r = -0.161), the daily proportion of spawning fish was strongly correlated (r = 0.93) to ambient temperature over the range 9-22$^{o}$C. Both spawning frequency and season increased with fish length. As a result of the allometric relationship between annual fecundity and fish mass a 3 kg fish was calculated to produce 5 fold more eggs per kilogram of body weight than a fish of 1 kg. In addition to producing more eggs per unit weight each year, larger fish also produce significantly larger eggs.

Adult emigration and larval dispersal of *A. argyrozona* from the Tsitsikamma National Park (TNP), South Africa, were investigated using mark-recapture data and Acoustic Doppler Current Profiler measurements of currents. Tagging data showed that adult carpenter were mainly resident, with a small proportion (7%) leaving the TNP in both easterly and westerly directions. No relationship was found between fish movement patterns and fish size or time-at-liberty. Current patterns suggest that eggs and larvae spawned within the TNP are mainly transported eastwards towards established nursery grounds; the median estimated distance moved was 299 km (range 42-561 km) in 30 days (time to flexion). Given this pattern of ichthyoplankton dispersal together with the fact that adult carpenter within the TNP display a high degree of residency and that they are

much more abundant than in adjacent fishing grounds (*cpue* = 23 times greater), it appears that the TNP protects a viable carpenter spawner population capable of seeding adjacent fishing grounds.

Fishery independent biomass surveys and commercial linefish catch returns were used to elucidate the spatial patterns of *A. argyrozona* distributed along the South African continental shelf. Two distinct areas of abundance were determined, one on the central and the other on the eastern Agulhas Bank. Tagging studies revealed little exchange between them. Two distinct nursery areas were identified. These data suggest that in each area juvenile *A. argyrozona* settle and move inshore, and then move offshore as they grow. Otolith readability and growth rates varied between regions, with fish from the Eastern Cape having the lowest average percentage error and the slowest growth rates, readability decreased westward. $L_{50}$ varied between the central and eastern Agulhas Bank as did mass at length. Based on the distribution of carpenter, variability in otolith readability, mass at length, variation in growth and size at maturity, it is concluded that carpenter exist as two separate stocks, one on the central Agulhas Bank and the other on the eastern Agulhas Bank.

*SB/R*, fecundity-per-recruit (*Egg/R*) and yield-per-recruit (*Y/R*) models were used to model both South African carpenter stocks. Owing to the allometric relationship between annual fecundity and individual size, *Egg/R* ratios were between 40 and 74% of *SB/R* at equivalent *F*. *Egg/R* ratios account for allometric increases in fecundity with size/age, and are therefore regarded as more accurate estimates of reproductive potential, and

biological reference points for per-recruit analysis should wherever possible be based on this quantum. It is shown that the current length at first capture ($l_c$) (250 mm TL) and $F$ (at $M = 0.1$) will reduce $Egg/R$ to 6.41% of the pristine value in the Eastern Cape and between 6.06 and 14.15% on the central Agulhas Bank, indicating that both stocks are heavily over exploited. An increase in $l_c$ from 250 to 350 mm TL and a 70% reduction in commercial fishing effort is recommended to attain a target reference point of 40% $Egg/R_{F=0}$. Bag frequency analysis indicates that a reduction in daily bag limit from 10 to 4 fish.person$^{-1}$.day$^{-1}$ would effect an equivalent reduction in recreational $F$. The trawl bycatch of carpenter is only 3% of the reported line catch, consequently restrictions to this fishery are not recommended.

# - Chapter 1 -

# Introduction

# - Chapter 1 -

## Introduction

Fisheries management has failed globally. This is evidenced by the many stocks that are overfished despite over 100 years of management attempts (Hart and Reynolds 2002; Smith 2002). Over subscription of effort due to severe global overcapacity and our inability to manage single species in complex systems are probably the main reasons (Garcia and Newton 1997; Buckworth 2002; Reynolds *et al*. 2002). In order to halt these declines, single species management has been attempted, but more recently an ecosystem approach to management has been advocated (Bohnsak 1998; Cochrane and Payne 1998; Pitcher and Pauly 1998; Pauly and Christensen 2002; Anon 2002; FAO 2003). South African fisheries management has had varying levels of success with some stocks optimally utilised (Payne and Bannister 2003), but many are severely overexploited (Griffiths 2000; Tarr 2000).

In South Africa, prior to 1994 access to marine resources was largely in the hands of the white minority and there were no clearly stated objectives for marine exploitation. With democratisation in 1994 the focus of fisheries management was restated to include transformation of the fishing industry to increase access for historically disadvantaged population groups and also to manage and control the rights holders for the sustainable utilisation of marine resources (Cochrane and Payne 1998). To achieve this goal a rights allocation process was undertaken and the Marine Living Resources Act (Act number 18 of 1998; Government Gazette No. 18930) was developed. The general principles of this Act state that the South African marine resources must be managed for the long-term sustainable utilisation of the resources with an ecosystem approach to management. Of primary importance to achieving these goals is information on fish stocks, without which there can be no credible management (Haggan 1998).

Fishing by hook and line (linefishing) is certainly one of the oldest forms of human exploitive activity in the marine environment. With the development of small motor powered boats after World War II boat based linefishing expanded worldwide. As technology improved, the area available to fishing became larger and currently most, if not all, shelf environments are fishable with hook and line gear. Globally increasing effort now means that many fish stocks are exploited over their entire distribution range and, in many cases, across most life-history stages. Although some stocks were thought to have shown signs of overexploitation prior to World War II, the increase in post-war fishing effort caused changes to the species composition of the catch (Garcia and Newton 1997) and led to the collapse of many linefish stocks worldwide (Garcia and Newton 1997; Jennings and Kaiser 1998). These declines have been noted in fish stocks from Canada (Parsons and Beckett 1997), the United States of America (Ault *et al*. 1998; Vaughn and Prager 2002), New Zealand (Harley et al 2000a; Paul 1974; Zeldis and Francis 1998), Australia (Samoilys 1997) and the tropics (Grandcourt 2003; Pauly 1997a, b). In order to halt these declines different management strategies have been used in the various regions. While in some areas such as New Zealand linefish stocks are managed by allocating a Total Allowable Catch (TAC) (Annala 1996), most linefish catch is controlled by size limits, bag limits and closed seasons (Coutin *et al*. 2003; Richards and Rago 1999; Vaughn and Prager 2002).

Most linefisheries in temperate and tropical environments are multispecies in nature, thereby requiring a large suite of regulations, which confuses the users. To further complicate the issues many of the species are caught in more than one fishery or by more than one user group (Coutin *et al*. 2003), which causes conflict (either real or perceived) between groups (Ault *et al*. 1998; Brouwer *et al.* 1997; Sauer *et al.* 1997; Mann *et al.* 1997; Mann *et al.* 2003). Finally, a large policing organisation is required to enforce the regulations in a fishery where the catch is landed at numerous small ports. To address the multi-species/multi-user complexities Caddy and Cochrane (2001) note that an "ecosystem management" approach could address some of these problems. One such approach is the use of Marine Protected Areas (MPA), where many species and their associated habitats could be protected simultaneously (Bohnsack 1998). The use of MPAs represents a holistic approach to managing a wide variety of species simultaneously. According to Pauly (1997b) MPAs are essential in order to guard against stock collapse, even under conditions of low fishing mortality.

The South African linefishery consists of over 200 species (Mann 2000) and is the 3rd most economically valuable fishery in South Africa (Cochrane and Payne 1998). While access to the recreational fishery is unlimited, the commercial fishery was, at the onset of this work, limited to 2998 commercial permits and many of these permit holders had dual permits with linefishing and squid, lobster or pelagic permits. Despite declines in catches of South African linefish species and the long history of fishing in South Africa (Ahrens 1964; Chale-Matsau *et al*. 2001; Griffiths 2000), attempts to manage the resource have only been recently undertaken. With the exception of a closed season for two species shad (*Pomatomus saltatrix*) and snoek (*Thyrsites atun*) and a few arbitrarily chosen size limits that were instituted in 1940, few other efforts to manage the resource were made. A comprehensive management plan designed to regulate both recreational and commercial linefishing was only implemented in December 1984 (Government gazette no. 9543 of 1984). However, in most instances the measures imposed were implemented only after serious declines were experienced (Attwood and Farquhar 1999; Griffiths 2000).

Despite the implementation of this management plan stocks continued to decline, as most of the bag limits were based on intuition rather than scientific data and as a result they did not limit catch sufficiently and therefore failed to provide efficient resource protection (Attwood and Bennett 1995; Brouwer *et al.* 1997; Griffiths 1997a; Sauer *et al.* 1997; Cowley *et al.* 2002). Where scientific data were available, minimum sizes were based on the length at 50% maturity. However, this is not always suitable as the length at 50% maturity makes the minimum size limit unacceptably large for some species (Griffiths 1996a). In addition, it is not always clear where to set a size limit for sex changing species (Buxton 1992) and in some instances size limits at this level do not provide the species with adequate protection to prevent stock collapse (Griffiths 1997a). To address these issues a linefish management protocol was developed for the South African linefishery, which proposed that regulations be based on clearly defined objectives and quantifiable reference points (Griffiths *et al*. 1999).

South Africa is the world "hot spot" for sparids with 41 species, of which 25 (61%) are endemic (Smith and Heemstra 1986), and this is the most important group in the South African commercial ski-boat (as defined on page 10) linefishery after snoek (Brouwer and Buxton 2002; Spencer Jones 2002). Although many sparids in South Africa have been extensively studied (Booth and Buxton 1997; Booth and Hecht

1997; Buxton 1989, 1990, 1993; Buxton and Garratt 1990; Chale-Matsau *et al*. 2001; Garratt 1985, 1986, 1988; Griffiths *et al*. 2002; Mann and Buxton 1998; Radebe *et al*. 2002; Smale 1988) little is known about several important species (van der Elst and Adkin 1991; Mann 2000). In many instances our understanding of the biology of the species already investigated is inadequate (Nepgen 1977), or is in need of re-assessment (Ahrens 1964). In addition, there is a paucity of data on how fishing dynamics affect age, growth and reproduction of many of these species.

Carpenter *Argyrozona argyrozona* (Valenciennes, 1830) is an endemic South African sparid that occurs from St Helena Bay to KwaZulu-Natal (Fig. 1). They inhabit low to high relief rocky areas to depths of 200 m (Nepgen 1977; Buxton and Smale 1984; Smith and Heemstra 1986; Smale and Badenhorst 1991). This slender sparid reaches a maximum size of approximately 700 mm total length (TL) and 3.5 kg. Like most heavily exploited South African sparids, catches of carpenter have declined markedly from historic maxima (Hecht and Tilney 1989; Griffiths 2000; Brouwer and Buxton 2002). Carpenter are targeted by commercial ski-boat operators and to a lesser extent recreational users (Brouwer and Buxton 2002). Although carpenter are caught in summer they are primarily targeted in winter when more valuable species such as kob (*Argyrosomus inodorus*) become less available.

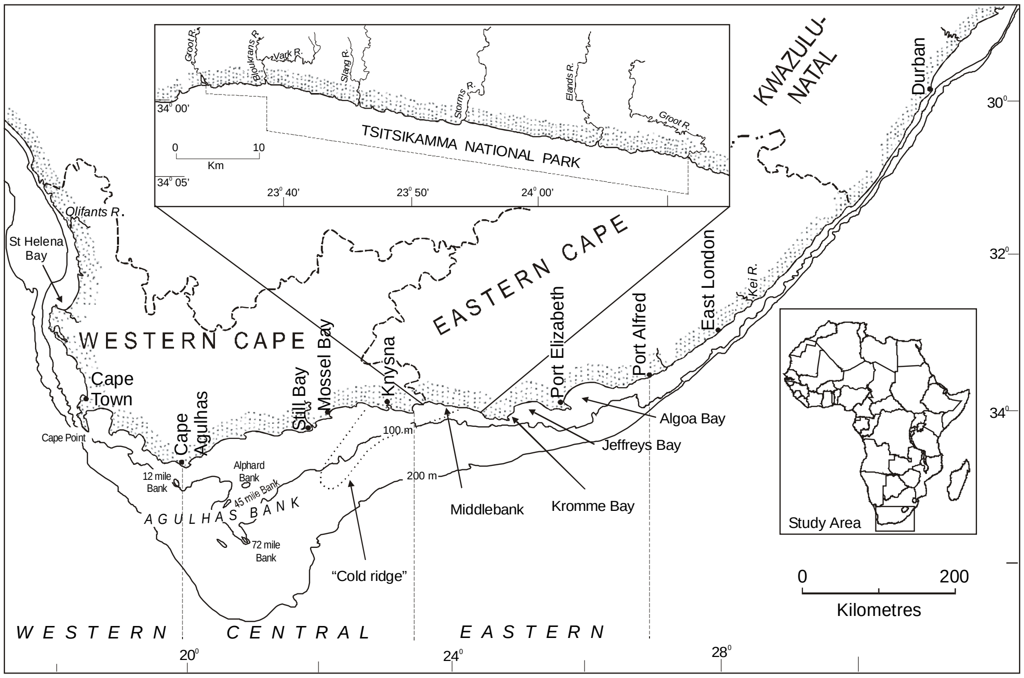

Figure 1: Locator map showing the study area and places mentioned in the text.

The total annual carpenter catch in the commercial linefishery is currently around 561 tons (Spencer Jones 2002), making it the third most important linefish species in South Africa and the most important sparid species in the linefish catch. Small numbers (11 tons per annum) are landed as by-catch by the inshore trawl industry (Spencer Jones 2002) where it is estimated that an additional 1.1 tons are discarded annually (Walmsley, Rhodes University, unpublished data) and approximately 3 tons are landed by the longline fishery (Spencer Jones 2002). Catch per unit effort (*cpue*) of line-caught carpenter peaked at approximately 17 tons.boat$^{-1}$.year$^{-1}$ in the early 1900's, but catch rates have declined by 95% since that time (Griffiths 2000). Trawl *cpue* of this species was highest in the late 1940's at approximately 19 tons.boat$^{-1}$.year$^{-1}$ and have also declined by approximately 95% since then (Griffiths 2000). Historical data indicate that carpenter catches have declined dramatically in areas such as Port Alfred and Port Elizabeth (Hecht and Tilney 1989; Brouwer and Buxton 2002), indicating that this species may be subject to local depletion. Despite these declines, catches of carpenter have escalated in recent years as a result of targeting by line-boats on the central Agulhas Bank, particularly around the 45 and 72-mile banks (Fig. 1). This has been facilitated by the introduction of large decked boats with blast freezers that are capable of travelling long distances and remaining at sea for up to one month.

To date no attempt has been made to determine the stock status of this important resource or to establish biological reference points for its management. Owing to the lack of any accurate long-term abundance index, per-recruit modelling represents the most suitable method of stock assessment for the majority of our linefish species (Griffiths *et al.*1999), and requires accurate estimates of biological parameters such as age-at-maturity, growth and mortality. Life history information is also important for the formulation of management strategies such as size and bag limits, closed seasons and MPA size and placing. Recent research on the silver kob, *Argyrosomus inodorus* (Griffiths 1997a) revealed that the current management approach (setting minimum size limits according to sizes at 50% maturity and arbitrarily determining bag limits according to perceived vulnerability or resilience) does not provide adequate protection for some species. As a result more appropriate management measures are needed and should in future include a holistic approach to management using MPAs and strictly enforced regulations based on per-recruit models.

As with many South African sparids, carpenter biology is not well understood and the information that does exist is outdated. To date, the only study on the biology of the carpenter was based on specimens collected at the western extreme of their distribution range (Cape Point to Danger Point) in the late 1960's (Nepgen 1977; Nepgen 1982). Most of the fish examined during Nepgen's (1977) study were inactive, suggesting that spawning occurs further to the east. Spawning seasonality, therefore, was not accurately delineated and sizes at 50% maturity were not calculated. In addition, fish were aged using whole otoliths, which generally results in under-ageing in older sparids (Buxton and Clark 1991).

When the present study was initiated the fishery regulations of South Africa listed carpenter as a commercially exploitable species. This means that commercially licensed fishers could catch unlimited numbers and recreational anglers were restricted to catching 10 fish.person$^{-1}$.day$^{-1}$. The size limit for carpenter, for all sectors, is 250 mm total length (TL). There is no closed season and no dedicated Marine Protected Area (MPA) for this species. However, they are abundant in the Tsitsikamma National Park (TNP), a 75 km long MPA that has been closed to fishing since 1964.

In the study area (Cape Point to Kei River) (Fig. 1) approximately 1431 commercial and 454 recreational vessels operated in 1997 (Sauer *et al.* 1997). The boat based commercial and recreational linefisheries exploit the inshore areas of the Agulhas Bank (Fig. 1) from ski-boats. These are small (4-12 m) vessels with a small crew (2-12 people) that put to sea for an average of 8 hours daily (Brouwer and Buxton 2002). They fish using hook and line in a radius of ± 40 km from each port. Decked boats from which fish are caught using hook and line exploit the offshore areas. These boats are larger (±20 m) than the ski-boats and remain at sea for up to one month. They have up to 20 crewmembers and are fitted with blast freezers. The catch is frozen at sea.

The objectives of the present study were as follows:

- To study the life history and population dynamics (growth rate, size at maturity, mortality rates, movement patterns and diet) of *A. argyrozona* throughout its distribution, and to determine its responses to exploitation and therefore the degree of plasticity in life history.
- To assess movement patterns and to establish the effectiveness of the Tsitsikamma National Park, and therefore by implication, other large Marine Protected Areas as important management tools for *A. argyrozona*.
- To determine the stock status of *A. argyrozona* on major fishing grounds.
- To develop a management plan for *A. argyrozona*, in order to ensure the optimal utilisation of this resource.

There are two main themes: firstly a base-line study was conducted in the TNP to assess seasonal trends in growth and reproduction, as well as movement patterns within the Park and export of fish from it (Chapters 2-4). Secondly, samples were collected through the distribution range of the species to delineate stocks, to determine the position of the spawning areas, assess regional variation in growth and reproduction and to assess biological responses to exploitation, as fishing mortality was expected to vary regionally (Chapters 5-8).

This thesis is written as a collection of papers. Chapter 2 describes the age and growth of carpenter in the TNP, where an evaluation of methods based on whole and sectioned otoliths and mark recapture data are investigated. Chapter 3 describes the reproduction of this species in the TNP, to establish seasonal trends, size at maturity, fecundity and spawning frequency. Chapter 4 describes the adult movement patterns of this species and larval dispersal from the TNP, using tag and release and current movement data. Chapter 5 compares the effects of sample size and sampling techniques used for age and growth data collection on the von Bertalanffy parameters and Spawner Biomass-per-Recruit (*SB/R*) estimates. Using fishery independent data, commercial linefish catches and tag and release data, Chapter 6 describes the stock distribution and changes in distribution patterns with growth. Life history parameters are compared throughout the distribution range. Using the parameters determined in previous Chapters carpenter stocks are assessed using *SB/R* and fecundity-per-recruit (*Egg/R*) models in Chapter 7. Finally, recommendations regarding the management of the resource are discussed in Chapter 8 and a new management plan is proposed.

## Study area

The study area extended from Cape Point to the Kei River, which is where carpenter occur in commercially available densities, and included the TNP. The TNP was selected as a sample site where a theoretically pristine population could be studied and an accurate estimate of natural mortality could be obtained. The TNP is a MPA that is closed to all forms of fishing. The Park is a 75 km stretch coast between the Groot River (east) ($30^o$04’S, $24^o$12’E) and the Groot River (west) ($33^o$59’S, $23^o$34’E) (Hanekom *et al.* 1997) (Fig. 1). It extends 5.56 km offshore and includes reefs from the shore to depths of up to 100 m. The Park was first proclaimed in 1964 and included coastal forest and the sea from the low water mark to 0.8 km offshore (Government Gazette No. 936 of December 1964). In 1983 the seaward boundary was extended to 5.56 km from the low water mark (Government Gazette No. 4237 of March 1974). Finally in 1996 the offshore section of the MPA was extended to include 0.8 km from the low water mark offshore along the Nature’s Valley coast up to Grootbank (23° 30’E) (Government Gazette No. 17070 of April 1996).

The oceanography of this area has been thoroughly researched and is thought to play a role in stock separation of some South African linefish species (Griffiths *et al*. 2002). A discussion of the study area’s oceanography is therefore relevant at this stage. The continental shelf along the northeastern seaboard of South Africa is narrow, extending to less than 15 km offshore in certain areas (Beckley and van Ballegooyen 1992). The shelf moves offshore between East London and Port Elizabeth, becoming increasingly wider towards the central Agulhas Bank. The Agulhas Bank is a roughly triangular extension of the continental shelf off southern Africa (Fig. 1). The western Agulhas Bank is considered to be part of the Benguela ecosystem and is characterised by cold, nutrient rich upwelled waters (Lutjeharms *et al*. 1996). The Agulhas Current, which is warm and nutrient deficient, directly influences the eastern margin (Lutjeharms *et al*. 1996). The inshore coastal areas are subject to strong seasonal wind-induced upwelling (Schumann *et al*. 1988).

The central Agulhas Bank possesses primary shelf characteristics (Schumann and Beekman 1984). It is subject to seasonal fluctuation in the thermocline structure where summer is characterised by a strong thermocline, which is eroded during winter storms by strong westerly winds, at which time warm surface water penetrates deep into the water column (Schumann and Beekman 1984). The Agulhas Current, which flows along the east coast of South Africa following the edge of the continental shelf, carrying warm tropical waters southwestwards, is the most prominent oceanographic feature of the region (Beckley and van Ballegooyen 1992). Water surface temperature in the core of the current averages around 22$^{o}$C in August and 27$^{o}$C in March (Illgner 1996). Inshore of the Agulhas current the temperature is lower than in the core of the current, averaging 18$^{o}$C (Greenwood and Clarke 1994), and the water movements are characterised by circulations and counter currents (Hutchings 1994). Wind has a strong effect on the inshore oceanography of the region, with frequent wind-induced upwelling events in summer. Upwelling in the area is also caused by divergence of the Agulhas current between East London and Port Elizabeth (Hutchings 1994).

One feature of the Agulhas Bank that has been speculated to affect fish distribution is the semi-prominent “cold ridge” that extends from Knysna to the mid-shelf south off

Still Bay (Fig. 1) (Boyd and Shillington 1994; Roberts and van den Berg 2002). Boyd and Shillington (1994) speculate that this “cold ridge” is maintained by an upwelling of the thermocline in the shelf interior, resulting from cyclonic circulation that has been generated by the widening of the shelf in this area that forces the Agulhas Current offshore. This ridge is thought to be a barrier to the movement of warm-temperate demersal species and has been shown to divide stocks of some linefish species (Griffiths 1997a; Griffiths *et al*. 2002).

The topography of the Agulhas Bank is variable with extensive areas of high and low profile reef separated by soft sand and mud sediments (Smale and Badenhorst 1991). The shelf itself is generally smooth because of erosion during sea-level regression and transgression with most bathymetric disturbances consisting of aeolianites and igneous protrusions (Schumann and Beekman 1984).

The TNP is situated on the eastern Agulhas Bank (Fig. 1) and the oceanographic environment is dominated by coastal waters. The inshore currents are variable and have been the focus of recent research activities (Tilney *et al*. 1996; Attwood *et al*. 2002; Roberts and van den Berg in press). This combined work shows that the inshore currents (up to 5 km offshore) of the region appear to flow predominantly in an east-west direction. With periods of sustained high velocity (24 $cm.s^{-1}$) more common in an easterly direction (Roberts and van den Berg in press). Currents are strongest at the surface. Only slight onshore/offshore currents are experienced and are thought to be associated with the tidal flux (Roberts and van den Berg in press). Although displacement of water occurs predominantly in an easterly direction from the TNP, strong displacement to the west is also known to occur, but for shorter durations

(Roberts and van den Berg in press). The system is strongly influenced by wind-driven upwelling in the region (Schuuman *et al*. 1988; Attwood *et al*. 2002; Roberts and van den Berg in press). Easterly winds cause upwelling by producing offshore transport of water in the upper layers that is replaced with cooler water from the deep (Schumann *et al*. 1982). Large thermocline displacements can occur within hours of the onset of a strong wind with an easterly component, and once established, the upwelling may take several days to dissipate (Schumann *et al.* 1982). Sudden changes in temperature are experienced during these events and temperature may drop by 10$^{o}$C or more in a few hours (Schumann *et al.* 1988; Roberts 1999). Generally the upward motion of the thermocline is confined to a coastal band a few tens of kilometres wide (Schumann *et al*. 1982). Winds with an easterly component are more common in summer, while westerly and southwesterly winds, which form the greatest portion of the annual wind force, are frequent in winter (Ross 1988).

# - Chapter 2 -

# Age and growth of *Argyrozona argyrozona* (Pisces: Sparidae) in a Marine Protected Area: an evaluation of methods based on whole otoliths, sectioned otoliths and mark recapture [1]

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[1] Brouwer, S.L. and Griffiths, M.H. 2004. Age and growth of *Argyrozona argyrozona* (Pisces: Sparidae) in a Marine Protected Area: an evaluation of methods based on whole otoliths, sectioned otoliths and mark recapture. Fish. Res. 67: 1-12.

# Age and growth of *Argyrozona argyrozona* (Pisces: Sparidae) in a Marine Protected Area: an evaluation of methods based on whole otoliths, sectioned otoliths and mark recapture

## ABSTRACT

*Argyrozona argyrozona* is an important component of the South African commercial linefishery. The purpose of this study was to develop a reliable protocol for estimating age and calculating growth. Methods based on both otoliths and mark-recapture data were investigated. Transverse sagittal sections from the Tsitsikamma National Park showed clear opaque and translucent growth increments. Marginal growth zone analysis and mark-recapture of chemically tagged fish (Oxytetracycline) revealed that these were deposited on an annual basis: opaque in summer and translucent in winter. The first translucent check was shown by daily increment counts to mark the completion of the first annulus (i.e. not a juvenile/false check). Within reader (between counts) and between readers average percent error (APE) was 5.3 and 1.8, respectively showing that readability of carpenter otoliths is high. Comparison between whole and sectioned otoliths showed that the former significantly under-estimated the age of fish older than 10 years (p<0.01). The maximum age obtained from whole otoliths was 16 years while that obtained from otolith sections was 27 years. Based on realistic $L_\infty$ estimate and the distribution of residuals, the three parameter von Bertalanffy growth function adequately fitted the observed length-at-age data derived from otolith sections. Growth rates did not differ significantly between sexes (f = 2.217; p = 0.09). Growth of carpenter in the Tsitsikamma National Park is described by the following equation:

$$L_t = 623\ mmFL\ \ (1 - e^{-0.08\,/\,yr\,(t-1.96\,yrs\,)})$$

A large proportion (68%) of the individual growth rates derived from mark-recapture data were below those predicted by the otolith based von Bertalanffy growth model (p<0.01). This was attributed to the negative influence of external tags, as hydroids, frequently occurring on the tags of recaptured fish, were observed to cause severe lesions and in some cases, extensive fin damage. This brings into question the use of mark-recapture studies to calculate growth of some species.

**Key Words**: Otolith sections, whole otoliths, mark-recapture, daily increments, chemical marking.

## INTRODUCTION

Carpenter *Argyrozona argyrozona* is a medium-sized reef-fish (attaining 3.5kg) that is endemic to the warm-temperate waters of South Africa. Although an important target species of the commercial handline fishery operating between Cape Point and the Kei

River (Griffiths 2000; Brouwer and Buxton 2002), little is known of the life history or population dynamics of this predatory sparid fish.

Nepgen (1977) estimated the growth rate of carpenter based on whole otoliths but, owing to higher opacity, was unable to read the sagittae of larger individuals. In addition to this other studies have shown that annuli tend to stack on the medial surface of sparid otoliths, with the result that whole otoliths generally underestimate age (Buxton and Clarke 1991; Francis *et al*. 1992). Embedding, sectioning and mounting otolith sections is nevertheless labour intensive, and is only prudent where age estimates are significantly improved. Although mark-recapture provides a cost-effective alternative for measuring growth rate, a recent study suggests that in some species external tags may retard growth (Attwood and Swart 2000).

The primary objective of the present study was to establish a reliable protocol for age determination and growth estimation in carpenter. Annulus formation in otolith sections was validated using three methods – daily growth increments, chemical marking and marginal growth zone analysis - and the counts of growth zones in sectioned and whole otoliths were compared. Growth rate derived from sectioned otoliths was also compared with that calculated from mark-recapture data.

It is well established that fishing may cause changes in population parameters (Buxton 1993, Harris and McGovern 1997). Therefore in addition to the main objective, sampling in a large no-take marine reserve was intended to provide base-line information that could be used to evaluate the impact of fishing on life history of carpenter in exploited areas.

## MATERIAL AND METHODS

A total of 2328 carpenter (259-572 mm FL), was collected (March 1996 – June 1999), with hook and line in the Tsitsikamma National Park (TNP) (Fig. 1). To enable the comparison of whole and sectioned otoliths over a wider size range (153 - 572 mm FL) an additional 477 fish were collected off Struis Bay (Fig. 1), on the central Agulhas Bank (April 2000). In each case total length (mm), fork length (mm), whole mass (g), gutted mass (g) and sex were recorded and sagittal otoliths were removed, cleaned and stored dry. For the purpose of age validation 921 live carpenter from the TNP were measured (mm FL) injected with oxytetracycline (OTC) (0.5 ml/kg), then tagged (Hallprint, D-dart tag) and released. Where necessary the gas bladder was bled with a hypodermic needle prior to release.

The left otolith from each pair was embedded in clear casting resin and sectioned (0.5mm) through the core, using a rotating diamond blade. Using a random number selector in Microsoft Excel (Microsoft corp., 2000) a sub-sample of 945 TNP otoliths was selected for this analysis. The sections were mounted on glass slides with DPX mountant and viewed at 10-20 x magnification with transmitted light. Whole right otoliths were soaked in methyl salicylate for 3-5 minutes and examined under a binocular stereo microscope at 10 x magnification with reflected light. Without prior knowledge of fish size, each of the whole and sectioned otoliths were read twice, a minimum of three weeks between readings. When counts did not agree, a third reading was taken, the two concurrent readings being accepted as the age of the fish. When all three counts differed the otolith was rejected from further analysis. A sub sample of 407 sectioned otoliths was read by a second reader, following the above procedure to assess the reproducibility of the results. Whole and sectioned counts were compared using a paired t-test and the following section-based age categories: 2-5; 6-10; 11-15 and 16+.

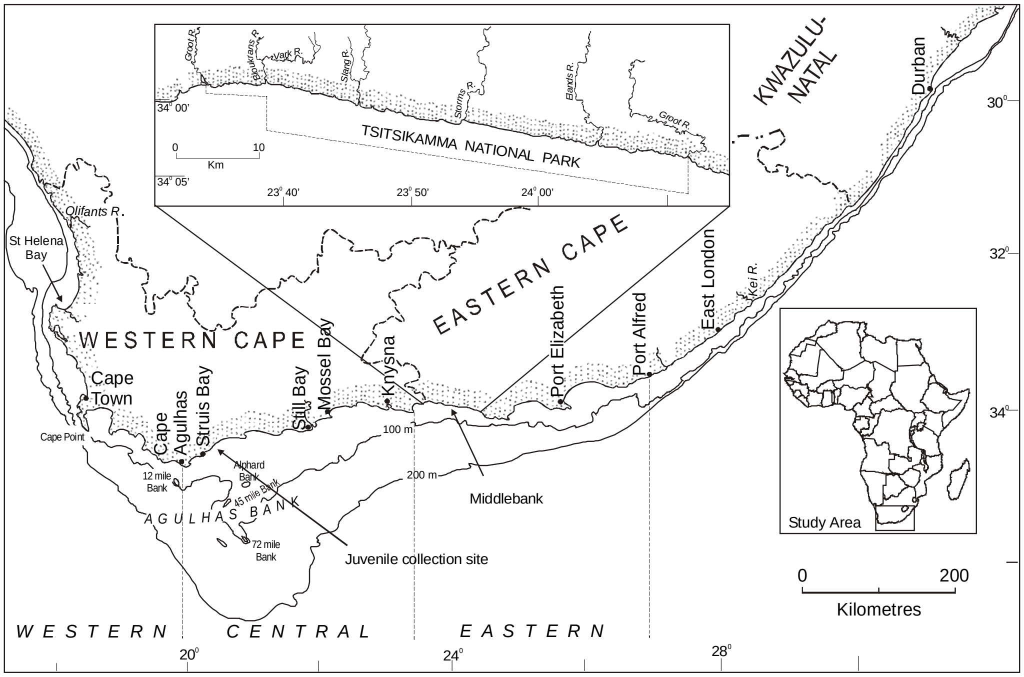


Figure 1: Map of the study area showing the position of the Tsitsikamma National Park on the eastern seaboard of South Africa, the 100 m and 200 m isobaths, and places mentioned in the text.

To determine the periodicity of growth zone formation, the proportion of opaque and hyaline margins was calculated on a monthly basis. The outer ring was considered to be either opaque or translucent only when the entire edge demonstrated this characteristic. If only a partial ring was formed the preceding layer was taken. Otoliths of recaptured fish were sectioned and photographed under ultraviolet light and then white light in order to determine the position of the OTC band and the number of opaque and translucent bands deposited during the time at liberty. To avoid problems with edge interpretation only complete growth bands in the otolith were considered to represent a year's growth, and incomplete bands were not counted. However, as the growth bands are formed over a period of time the resolution is expected to be only within approximately 3 months.

As some sparid fishes lay down juvenile rings (Griffiths *et al*. 2002) it was necessary to validate the first annulus. To this end a sample of 6 otoliths containing one opaque and one translucent zone was polished on the proximal surface until the nucleus was visible. These were examined under oil immersion at 400 x magnification and daily growth increments were enumerated between the nucleus and the margin. Although daily increments were not validated they appeared to be similar as those validated by Lang and Buxton (1993) for another South African sparid *Diplodus cervinus hottentotus*. As young fish do not occur in the TNP, but move in from nearby nursery areas (Brouwer *et al*. 2003) the otoliths of fish < 250 mm FL were obtained from small individuals collected inshore on the central Agulhas Bank.

The 3-parameter von Bertalanffy growth model was fitted to the observed length-at-age data for TNP fish older then 5 years using an iterative least squares procedure (Microsoft EXCEL (Microsoft corp., 2000) SOLVER routine with Newton algorithm option). Data for the male and female fish were pooled as a likelihood ratio test revealed that there was no significant difference between their growth ($f = 2.217$; $p = 0.09$). As a result of size related dispersal into the TNP (Brouwer *et al*. 2003), age classes below 6 years were poorly represented and are moreover thought to consist of the faster growing individuals in each age category. The data were modelled using only ages 6 and above. Likelihood ratio tests were used to compare male and female growth (Punt 1992).

Growth rates determined from tagged fish were compared to the growth rates evaluated from otolith ring counts using the methods described by Attwood and Swart (2000). Growth rate of tagged fish was calculated as follows:

$$G_i = 365\left(\frac{FL_{i\,rec} - FL_{i\,rel}}{dt}\right)$$

where $FL_{i\ rel}$ and $FL_{i\ rec}$ are the lengths (FL mm) at release and recapture respectively and *dt* is the number of days at liberty. Note only fish free for >1 year were used for this analysis. The otolith-derived von Bertalanffy growth function, is transformed to compare length-based growth rates as follows:

$$\frac{dFL}{dt} = L_\infty \times k\left(1 - \frac{FL}{L_\infty}\right)$$

where $L_\infty$ and *k* are parameters from the von Bertalanffy growth equation and FL is the fish length at recapture (FL mm). $G_i$ and *d*FL/*dt* values were compared graphically and by a paired t-test. The regression formulae to convert fork length to total length appear in Appendix II.

Estimates of ageing precision were determined using three methods: average percentage error (APE) (Beamish and Fournier 1981), coefficient of variation (CV) and index of precision (D) (Chang 1982). Between-reader differences were compared using APE. Even though CV is statistically more robust (Campana 2001), APE has been more widely used and was included for comparative purposes.

Temperature data were collected at the sampling site using a Seamon Mini recorder (Hugrun, Iceland) stationed in the TNP at 35m. A thermistor array consisting of four underwater temperature recorders (UTR's) at depths of 12m, 19m, 27m and 35m recorded the temperature every minute and stored an hourly average, which was later downloaded (Roberts 1999). Photoperiod data were downloaded from the South African Astronomical Observatory database (www.saao.ac.za).

## RESULTS

Sectioned carpenter otoliths consisted of clearly discernible opaque and translucent growth zones (Fig. 2a). Chemical marking confirmed that one opaque and one translucent zone were deposited each year (Fig 2b), which comprised an annulus. Nine fish that were recaptured during this study had otoliths that were marked with OTC (Table I) including one that was injected and recaptured twice. The number of annuli observed was highly correlated with the number of years free (Pearson Rank Correlation, r = 0.95). Marginal growth zone analysis indicated that the opaque zone is deposited during summer (November to March) (Fig. 3) spawning season (Chapter 3).

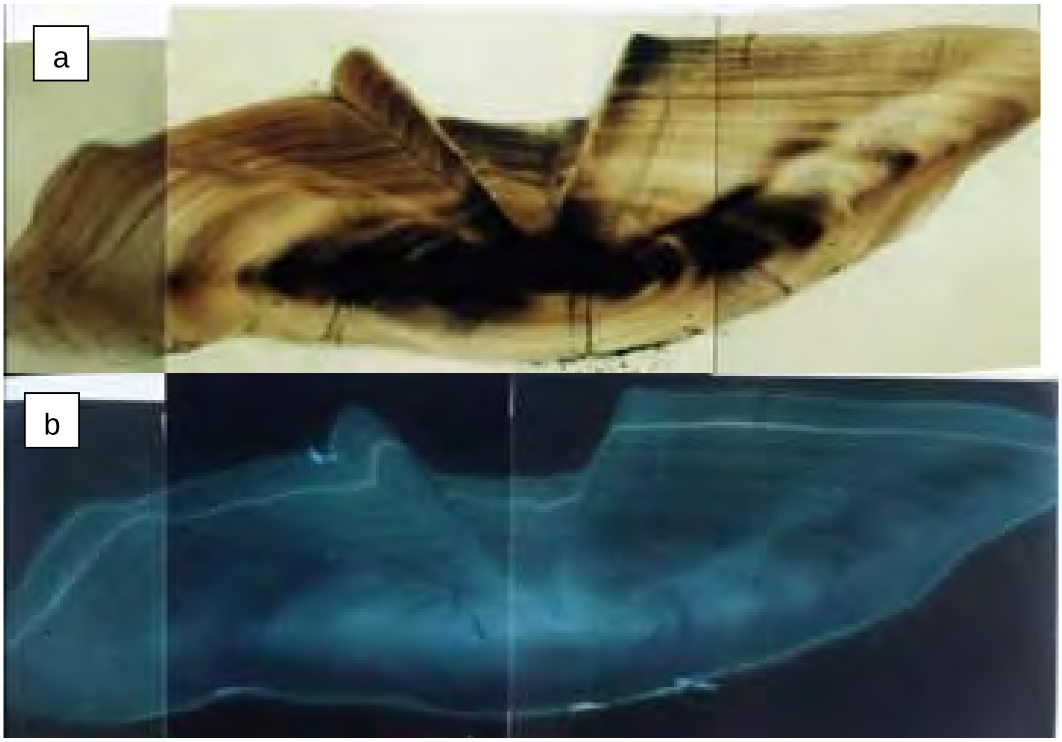


Figure 2: Photomicrograph of an OTC marked otolith under (a) white light and (b) ultraviolet light. The 11-year old fish was free for 1219 days (3 years) after OTC injection and as is evident 3 annuli (each comprising one translucent and one opaque zone) were deposited during this time.

Table I: Results of the chemical marking experiment including time between marking and death, in days, the decimal years and the number of annuli (one opaque and one translucent zone) deposited during this period. * = Results from a single fish which was injected with OTC twice (at day 0 and 230). 770 days passed between the second recapture and the final capture.

| **Days Free** | **Years free** | **Annuli from OTC mark** |
|---|---|---|
| 1219 | 3.34 | 3.5 |
| 722 | 1.98 | 2 |
| 718 | 1.97 | 2 |
| 715 | 1.96 | 2 |
| 230* | 0.63 | 0.5 |
| 770* | 2.11 | 2 |
| 1000* | 2.74 | 2.5 |
| 1470 | 4.03 | 4 |
| 1027 | 2.81 | 2 |

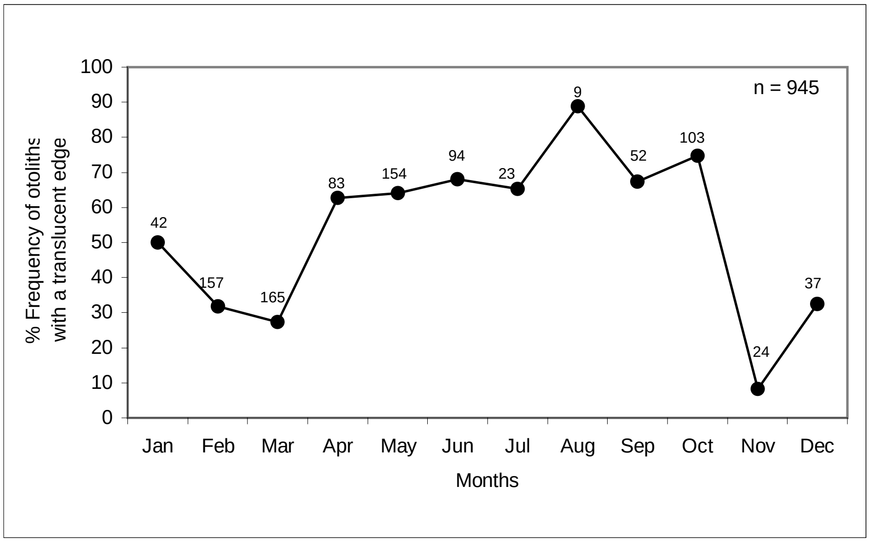


Figure 3: The temporal changes in the proportion of *A. argyrozona* otoliths from the Tsitsikamma National Park with translucent margins. Point values = n.

The six otoliths with one hyaline zone were analysed for daily growth, and had between 319 and 426 daily growth rings (average 353 days ± 39.7). This indicates that the first hyaline zone marks the end of the first annulus and that it is not a juvenile check. In addition the data indicated that these individuals were spawned between November and April the peak spawning time for this species (Chapter 3).

The within reader APE (5.3), CV (7.9) and D (4.6) were all low, as was the between-reader APE (1.8), indicating that readability of the otoliths was high.

Comparison of whole and sectioned otoliths revealed that the former underestimated the age of fish older than 10 years (Fig. 4). The maximum estimated ages were 16 and 27 years for whole and sectioned otoliths respectively. Matched pairs t-test revealed that differences between ages determined using whole and sectioned otoliths were not significant for section-based age classes 2-5 and 6-10 ($p>0.1$) but that these differences were highly significant ($p<0.01$) for section based age classes 11-15 and

16+. Furthermore, comparing the size classes showed that there was no significant difference for those below 300 mm FL ($p>0.1$) while those above this size ages based on whole and sectioned otoliths were significantly different ($p<0.001$).

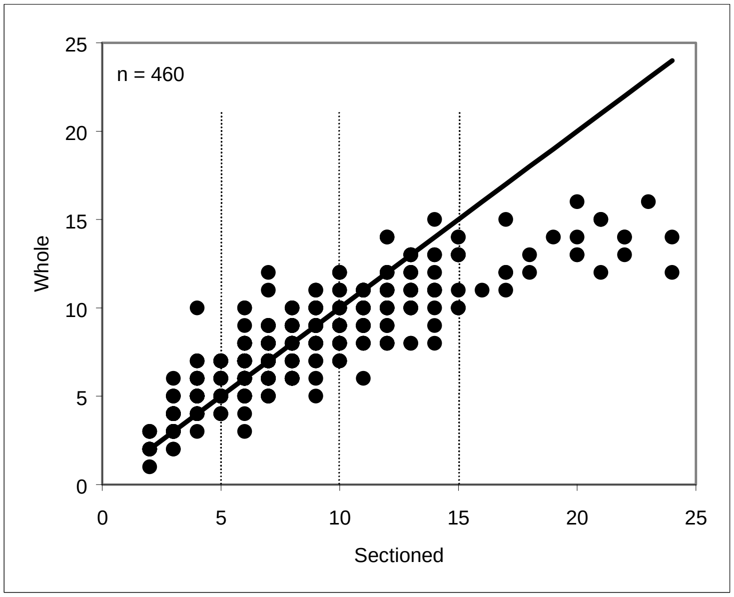


Figure 4: The relationship between ages determined from whole and sectioned sagittal otoliths of identical fish. Deviation from the 1:1 line shows the extent of the ageing bias. Dotted vertical lines show section based age categories used in the statistical comparisons (pared t-test).

The 3-parameter von Bertalanffy model gave a realistic $L_\infty$ estimate that was similar to the size of the largest fish sampled (Fig. 5) (Table II and III) and was used for additional calculations.

Most (68%) individual growth rates estimated from tag and release data were lower than those predicted for fish of equivalent length by the otolith derived model (Fig. 6). Paired t-test revealed that this difference was highly significant ($p<0.01$)

The relationship between the time at which the opaque zone was deposited and photoperiod, temperature and Gonadosomatic index (GSI) was compared using a Pearson correlation. This showed that there was little correlation between opaque zone deposition and temperature (r = -0.076), but good correlation was found with both photoperiod (r = 0.668) and GSI (r = 0.787).

## DISCUSSION

On reviewing no less than 372 papers Campana (2001) concluded that most (65%) age and growth studies did not provide estimates of ageing precision. Of those that did, CV was by far the most common (57%); the median of 117 studies being 7.6. CV calculated for carpenter during the present study was 7.9. A review of 33 papers on sparid age and growth revealed that only 4 (12%) provided indices of precision. APE ranged from 3.9 in *Sarpa salpa* (van der Walt and Beckley 1997) to 4.7 in *Rhabdosargus sarba* (Radebe *et al*. 2002), both of which are short-lived species, reaching 6 and 16 years respectively.

Table II: Parameter estimates of length-at-age (FL mm) data modelled using the von Bertalanffy growth model for *A. argyrozona* sampled in the Tsitsikamma National Park. Values in parenthesis are standard errors.

| **Parameter** | **Estimate** |
|---|---|
| 3-parameter von Bertalanffy model | |
| $L_\infty$ | 623 (10.77) |
| $k$ | 0.08 (0.007) |
| $t_0$ | -1.96 (0.12) |

Table III: Observed and expected mean length at age (mm FL) derived from the von Bertalanffy growth curve for *A. argyrozona* in the Tsitsikamma National Park.

| **Age (years)** | **Mean observed length-at-age (± SD)** | **Expected length-at-age** | **n** |
|---|---|---|---|
| 1 | 147 (±24.2) | 166.6 | 6 |
| 2 | - | - | 0 |
| 3 | 289 (±42.43) | 236.4 | 2 |
| 4 | 280 (±16.34) | 263.9 | 9 |
| 5 | 303 (±19.10) | 289.7 | 23 |
| 6 | 309 (±24.61) | 313.9 | 65 |
| 7 | 334 (±27.44) | 336.7 | 92 |
| 8 | 357 (±27.30) | 358.0 | 118 |
| 9 | 375 (±32.45) | 378.1 | 141 |
| 10 | 400 (±30.36) | 396.9 | 115 |
| 11 | 409 (±34.03) | 414.5 | 85 |
| 12 | 432 (±36.13) | 431.1 | 61 |
| 13 | 458 (±38.69) | 446.7 | 35 |
| 14 | 467 (±38.70) | 461.3 | 24 |
| 15 | 491 (±34.82) | 475 | 11 |
| 16 | 497 (±27.70) | 487.8 | 6 |
| 17 | 520 | 499.9 | 1 |
| 18 | 537 (±23.33) | 511.3 | 2 |
| 19 | 526 (±13.44) | 521.9 | 2 |
| 20 | 572 | 531.9 | 1 |
| 21 | 567 | 541.3 | 1 |
| 22 | 516 (±15.56) | 550.1 | 2 |
| 23 | 519 (±42.48) | 558.3 | 4 |
| 24 | - | 566.1 | 0 |
| 25 | - | 573.4 | 0 |
| 26 | - | 580.2 | 0 |
| 27 | 525 | 586.6 | 1 |

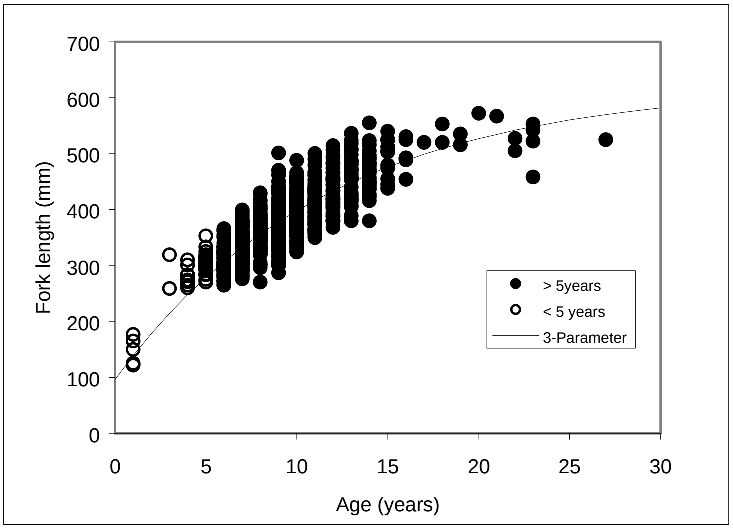


Figure 5: The calculated von Bertalanffy growth curve and observed lengths at age for *A. argyrozona* using sectioned sagittal otoliths sampled in the Tsitsikamma National Park between March 1996 and July 1999. Age group 1 fish were determined from the nursery areas of the Agulhas Bank. The growth curves were fitted to the 6+ year age classes n = 801.

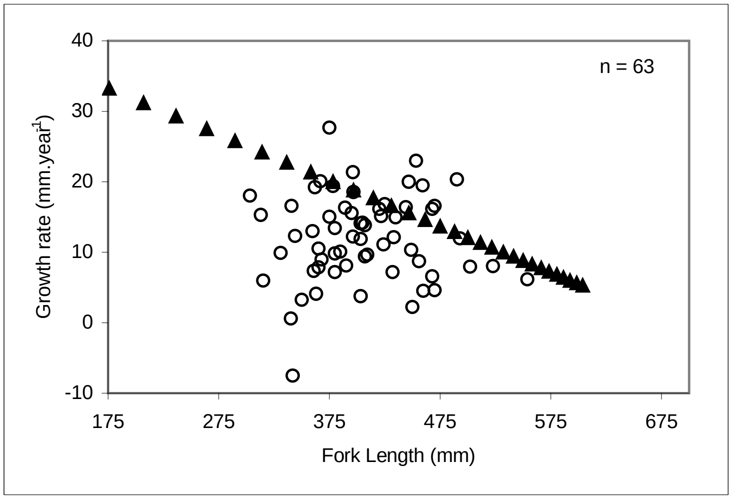


Figure 6: The predicted growth rate of *A. argyrozona* in the Tsitsikamma National Park from otoliths (triangles) and the calculated growth rate from tag recoveries (circles).

Another long-lived species *Polysteganus undulosus* showed poor precision with an APE of 18.23 (Chale-Matsau et al 2001). While marginally higher than that for short-lived sparids, the APE for carpenter in the TNP (5.3) was substantially lower than that of *P. undulosus*.

Fluorochrome marking, generally held to be the most reliable method of age validation, has been successfully used for a wide range of fishes including sciaenids (Murphy *et al*. 1998), sparids (Francis *et al*. 1992; Lang and Buxton 1993), serranids (Ferreira and Russ 1993), lutjanids (Cappo *et al*. 2000) and polyprionids (Francis *et al*. 1999). The OTC marking from this study provided irrefutable evidence that one annulus (comprised of 1 opaque and 1 translucent zone) is deposited annually in carpenter.

Although receiving considerable attention, the formation of growth zones in fishes' otoliths remains unclear. In a review including 94 species in 36 families Beckman and Wilson (1995) found little correlation between opaque zone deposition in the otoliths and spawning season (only 19%), leading them to conclude that opaque zone deposition is partially related to local increases in temperature, but that the controlling factors are a combination of environmental and endogenous factors. The marginal zone analysis revealed that carpenter deposit opaque zones during summer (November to March) when GSI's are highest (Chapter 3). This was supported by OTC marking, as all fish injected during summer had the OTC mark in the opaque zone of the otolith. A review of 21 other sparid studies showed that, in 71% opaque zone deposition coincided with the spawning season, 12% coincided partially and 17% showed no overlap (Table IV). Of the sparid species reviewed here, 55% produced the opaque zone in summer but temperature data were not provided. In the case of carpenter, however, there was little correlation between temperature and opaque zone deposition ($r = -0.076$), but good correlation was found with photoperiod ($r = 0.668$) and GSI ($r = 0.787$). Although photoperiod is believed to trigger gonad development in carpenter (Chapter 3), higher correlation between opaque zone deposition and GSI would suggest that endogenous rhythms play a significant role in annulus formation in carpenter.

This study showed that, as with other species (Buxton and Clarke 1989, 1991; Hyndes *et al*. 1992; Horn and Sutton 1996), whole otoliths underestimate the age of older fish. Beamish and McFarlane (1995) noted that erroneous predictions of growth can result in a fishing strategy that will result in overfishing of the stock. Fecundity per recruit (*Egg/R*) analysis using the von Bertalanffy growth model based on the whole and sectioned otoliths and size at maturity of 278 mm FL (Chapter 3), showed that fishing mortality (*F*) required to achieve the target reference point of $Egg/R = 40\%\ Egg/R_{F=0}$ (Griffiths *et al*. 1999) was 0.151 for whole- and 0.09 for sectioned-based models. According to the section-based model, $F = 0.151$ would result in an *Egg/R* ratio of 18% of pristine which is equivalent to half of the target *F* and well below the 25% threshold. This illustrates the danger of using age estimates based on whole otoliths for the management of carpenter and other long-lived species.

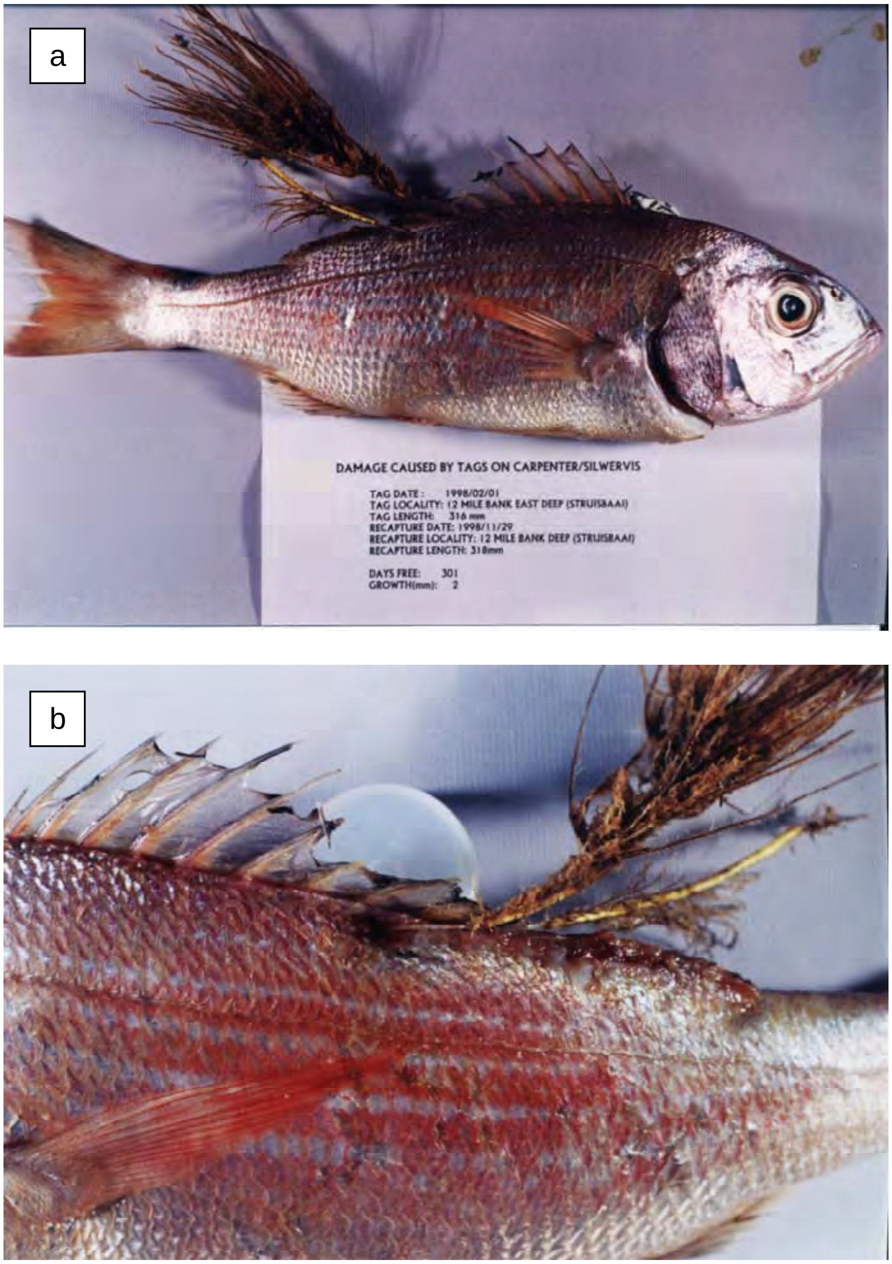
Table IV: A summary of 23 studies on sparid growth and reproduction showing the timing of spawning and opaque zone deposition in the otoliths. * = Northern Hemisphere species, s = spawning season, o = opaque zone deposition.

| Species | Jan | Feb | Mar | Apr | May | Jun | Jul | Aug | Sep | Oct | Nov | Dec | Reference |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Chrysoblephus cristiceps* | s | | | | | | | | | | s | s | Buxton (1993) |
| | o | o | | | | | | | o | o | o | o | |
| *Chrysoblephus laticeps* | s | | | | | | | | | s | s | s | Buxton (1993) |
| | o | o | | | | | | | o | o | o | o | |
| *Diplodus cervinus hottentotus* | | | | | | | | s | s | s | s | s | Mann and Buxton (1997; 1998) |
| | | | | | | | | o | o | o | o | | |
| *Diplodus sargus capensis* | s | s | s | | | | | s | s | s | s | s | Mann and Buxton (1997; 1998) |
| | | | o | | o | o | o | | | o | o | o | |
| *Pachymetopon grande* | s | s | s | s | s | s | | | | | | | Buxton and Clarke (1992) |
| | | | | | | o | o | o | o | o | o | | |
| *Pachymetopon blochii* | s | | | | | | | | | | s | s | Pulfrich and Griffiths (1988) |
| | o | o | | | | | | | | o | o | o | |
| *Pachymetopon aeneum* | s | s | s | | | | | | s | s | s | s | Buxton and Clarke (1986) |
| | o | o | | | | | | | o | o | o | o | |
| *Sparodon durbanensis* | s | | | | | | | s | s | s | s | s | Buxton and Clarke (1991) |
| | | | | | | o | o | o | o | | | | |
| *Cymatoceps nasutus* | | | | | | | | | | s | s | s | Buxton and Clarke (1989) |
| | | | | | o | o | o | o | o | o | | | |
| *Cheimerius nufar* | | | | | | | | s | s | s | s | | Garratt (1985) |
| | | | | | | | | | | | | | |
| *Cheimerius nufar* | | | | | | | | | | | s | s | Coetzee and Baird (1981) |
| | o | o | | | | | o | o | o | o | o | o | |
| *Chrysoblephus puniceus* | | | | | | s | s | s | s | s | s | | Garratt (1985) |
| | | | | | | | | | | | | | |
| *Pterogymnus laniarius* | s | s | s | s | s | | | | s | s | s | s | Hecht and Baird (1977) |
| | o | o | o | o | o | | | o | o | o | o | o | |
| *Pterogymnus laniarius* | s | s | s | s | s | s | s | s | s | s | s | s | Booth and Buxton (1997) |
| | | | | | | o | o | o | o | | | | |
| *Argyrozona argyrozona* | s | | | | | | | | | s | s | s | Nepgen (1977) |
| | o | o | | | | | | | | | o | o | |
| *Argyrozona argyrozona* | s | s | s | | | | | | | | s | s | This study |
| | o | o | o | | | | | | | | o | o | |
| *Lithognathus lithognathus* | | | | | | o | o | o | o | o | | | Bennett (1993) |
| | | | | s | s | s | s | s | | | | | |
| *Dentex gibbous** | | | | | | s | s | s | | | | | Pajuelo and Lorenzo (1995) |
| | | | | | | o | o | o | o | o | | | |
| *Pagellus erothrinus** | | | | | s | s | s | s | | | | | Pajuelo and Lorenzo (1998) |
| | | | o | o | o | o | o | o | o | | | | |
| *Pagrus pagrus** | s | s | s | s | | | | | | | | | Pajuelo and Lorenzo (1996) |
| | | | | | | o | o | o | o | o | | | |
| *Dentex dentex** | | | | s | s | s | | | | | | | Morales-Nin and Moranta (1997) |
| | | | | | | | o | o | o | | | | |

Although the 3-parameter von Bertalanffy growth model provided a realistic estimate of $L_\infty$ and was used to model the length-at-age, in the TNP, fish younger than 6 years old were poorly represented. The reason for this is that juveniles are mostly found in bays outside the Park (Brouwer *et al.* 2003). Consequently, fish below 6 years old sampled in the TNP, were thought to be the larger individuals of these age classes due to size specific movement into the TNP (Brouwer *et al*. 2003). It is, therefore, not surprising that lengths-at-age for 3-5 year old fish were larger than those predicted by the von Bertalanffy growth function.

Growth rates derived from mark-recapture were mostly (68%) lower than those derived from otoliths for fish of equal length. On obtaining similar results for *Lithognathus lithognathus* (Sparidae) and *Dichistius capensis* (Dichistidae) Attwood and Swart (2000) concluded that either otoliths provided inaccurate estimates of age for these two species (growth zone deposition was not directly validated), or that tagging negatively affected growth. In the case of carpenter, however, direct validation and low CV confirm that ageing is accurate, thereby suggesting that external tags depress growth rate. Many of the recaptured fish displayed lesions caused by hydroids that were growing on the tags and in severe cases fin rays of the second dorsal fin were almost completely destroyed (Fig. 7).

The findings of this chapter emphesises this typt of st that mark-recapture data should be used with caution when estimating growth in fishes….



DAMAGE CAUSED BY TAGS ON CARPENTER/SILWERVIS

TAG DATE : 1998/02/01
TAG LOCALITY: 12 MILE BANK EAST DEEP (STRUISBAAI)
TAG LENGTH: 316 mm
RECAPTURE DATE: 1998/11/29
RECAPTURE LOCALITY: 12 MILE BANK DEEP (STRUISBAAI)
RECAPTURE LENGTH: 318mm

DAYS FREE: 301
GROWTH(mm): 2

Figure 7: Damage to the fin rays of *A. argyrozona* caused by hydroids growing on a tag (a), and a close up showing that the fin rays have been completely eroded by the tag and hydroids (b).

# - Chapter 3 -

## Reproductive biology of *Argyrozona argyrozona* (Pisces: Sparidae) in a Marine Protected Area[2]

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[2] Brouwer, S.L. and Griffiths, M.H. in press. Reproductive biology of *Argyrozona argyrozona* (Pisces: Sparidae) in a Marine Protected Area. Fish. Bull.

# Chapter 3

# Reproductive biology of *Argyrozona argyrozona* (Pisces: Sparidae) in a Marine Protected Area

## ABSTRACT

*Argyrozona argyrozona* an endemic South African sparid comprises an important component of the handline fishery. A three-year study (1998-2000) into its reproductive biology within the Tsitsikamma National Park revealed that they were serial spawning late gonochorists. The size at 50% maturity ($L_{50}$) was estimated at 292 and 297 mm FL for females and males, respectively. A likelihood ratio test revealed that there was no significant difference between male and female $L_{50}$ ($p>0.5$), the combined $L_{50}$ was estimated at 295 mm FL. Both monthly gonadosomatic indices and macroscopically determined ovarian stages strongly suggest that *A. argyrozona* within the Tsitsikamma National Park spawn in the austral summer between November and April. The presence of post-ovulatory follicles (POFs) confirmed the six month spawning season, while monthly proportions of early (0-6 hour old) POFs showed that spawning frequency was highest (once every 1-2 days) from December to March. Although spawning season was more highly correlated to photoperiod ($r = 0.859$) than temperature ($r = -0.161$), the daily proportion of spawning fish was strongly correlated ($r = 0.93$) to ambient temperature over the range 9-22$^{o}$C. These results suggest that short-term upwelling events, a strong feature in the Tsitsikamma National Park during summer, would negatively affect reproductive output. Both spawning frequency and season increased with fish length. As a result of the allometric relationship between annual fecundity and fish mass a 3 kg fish was calculated to produce 5 fold more eggs per kilogram of body weight than one of 1 kg. In addition to producing more eggs per unit weight each year, larger fish also produce significantly larger eggs.

**Key Words:** Spawning season, size at maturity, batch fecundity, spawning frequency.

## INTRODUCTION

Carpenter, *Argyrozona argyrozona*, is an endemic South African sparid found between St Helena Bay and KwaZulu-Natal (Fig.1) (Smith and Heemstra 1986). Even though carpenter are the third most important species in the linefishery in terms of landed mass, catch per unit effort (*cpue*) on traditional fishing grounds declined by 95% during the 20th century (Griffiths 2000). The only previous study on the reproductive biology of carpenter was based on specimens collected towards the western extreme of the distribution range (west of Cape Agulhas), where most of the fish examined were inactive (Nepgen 1977). As a result spawning seasonality was not accurately delineated and sizes at 50% maturity were not calculated. Assuming carpenter to be determinate spawners Nepgen (1977) overestimated batch fecundity by conducting immature oocyte counts.

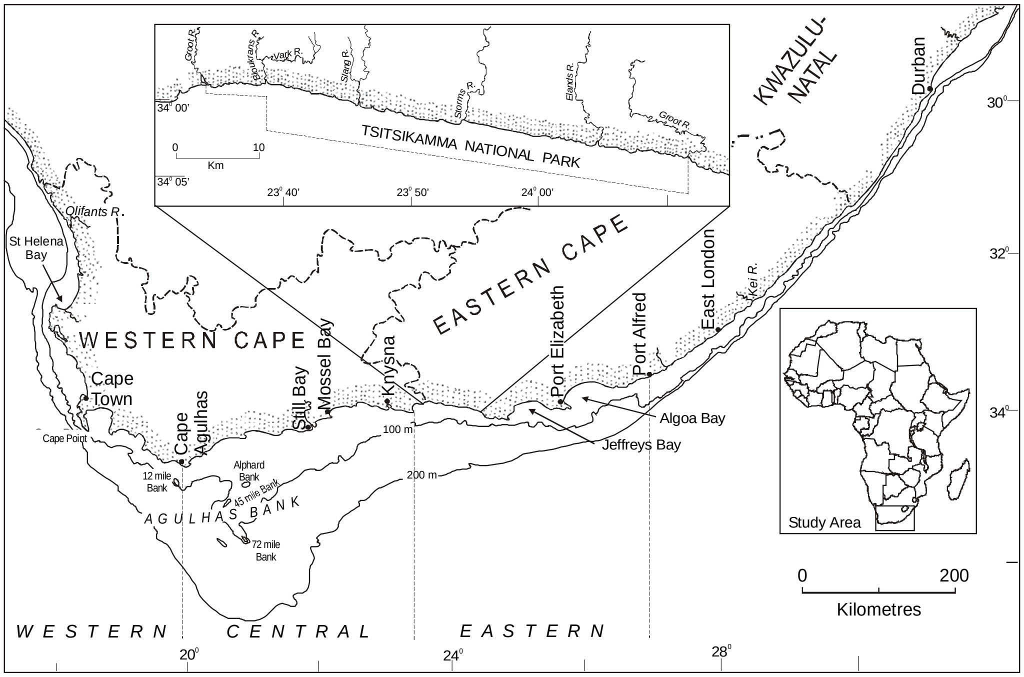


Figure 1: Map of the study area showing the position of the Agulhas Bank, Tsitsikamma National Park, 100 and 200m isobaths and the places mentioned in the text.

The objective of the present study was to provide information on spawning seasonality, size at maturity and annual fecundity of carpenter in the Tsitsikamma National Park (TNP), a 75 km no-take Marine Protected Area (MPA) that has existed since 1964 (Fig. 1). It was envisaged that in conjunction with other studies on carpenter (Chapter 6) in exploited areas this information would assist in determining the impacts of fishing on the life history of carpenter.

## MATERIAL AND METHODS

Fish were caught from a research vessel at depths between 20 and 90 m using baited hook (2/o - 6/o) and line. An attempt was made to biologically sample 60 fish per month between March 1996 and June 1999, although weather conditions did not always allow for this. Sampling involved measuring total and fork length (FL) (mm), whole mass (g), gutted mass (g), sexing the fish and removing the gonads. Gonads were staged macroscopically according to a seven-stage maturity index (Table I), and weighed to the nearest 0.1g. The whole gonads were preserved in 10% neutrally buffered formalin or alternatively fixed in Bouin’s solution for 48 hours and then stored in 60% ethanol. Preserved samples were processed for histological analysis as per the techniques described by Hunter *et al*. (1985) and Osborne *et al*. (1999).

Length at maturity was modelled using a 2-parameter logistic ogive according to King (1995) of the form:

$$p_i = \frac{1}{1 + \exp^{-(L_i - L_{50})/a}}$$

where $p_i$ is the proportion of mature fish in size class *i*, sampled during the spawning season (November to April), $L_i$ mid-length of size class *i*, $L_{50}$ is the length at which 50% of the fish are sexually mature (stage 4+) and *a* is the width of the ogive. The ogive was fitted by minimising the negative log-likelihood. Differences in male and female $L_{50}$ and *a* were tested by calculating the negative log-likelihood as follows:

$$-L=-\sum_{i=1}^{n}\left[m_i\times\lambda n\left(\frac{p_i}{1-p_i}\right)+n_i\times\lambda n(1-p_i)+\lambda n\begin{pmatrix}n_i\\m_i\end{pmatrix}\right]$$

where $n_i$ is the number of samples in size class *i*, and $m_i$ is the number of mature fish in size class *i*.

Spawning frequency was estimated using daily proportions of ovaries containing early post-ovulatory follicles (POFs), hereafter referred to as the spawning fraction (Hunter and Macewicz 1985). POFs were aged by comparing them with known age POFs from spawning females under captive conditions. Female carpenter, held in a flow through system at ambient sea temperature (mean 16$^{o}$C, range 9.5-20$^{o}$C) in 5000 l circular tanks, were stimulated to ovulate with a commercially available GnRH-analogue (Davis 1996). Three fish were sacrificed immediately after ovulation and then three fish every six hours over the following 48-hour period. Although POFs deteriorate along a continuum, histological analysis of ovaries revealed three clearly defined POF stages (Fig. 2). The proportions of wild caught fish with Stage 1 POFs, the spawning fraction, was inverted to produce an estimate of spawning frequency (Wilson and Nieland 1994). The proportions of wild caught fish with Stage 1 POFs was used to assess spawning time.

Batch fecundity was estimated from counts of hydrated oocytes from ovaries without POFs or atretic oocytes (Hunter and Macewicz 1985). A ± 1.00g section was removed from the middle of the right ovary. This was weighed to the nearest 0.01g and the hydrated oocytes separated according to the method described by Lowerre-Barbieri and Barbieri (1993). Hydrated oocytes were suspended in water and counted at 8-10 times magnification in a Bokkeroff tray, and measured to 0.1mm with an ocular micrometer along the longest diameter.

Annual fecundity was calculated as follows:

$$Af_t = \left( \frac{ls_j}{sf_j} \right) \times fb_t$$

where $Af_t$ is the annual fecundity for fish $t$, $ls_j$ is the length of the spawning season (days) for fish of size class $j$, $sf_j$ is the spawning frequency (days) for fish of size class $j$ (all months combined) and $fb_t$ is the batch fecundity of fish $t$.

Spawning season was established by calculating the monthly proportions of macroscopic gonad stages and mean monthly gonadosomatic index (GSI) (Buxton 1990) for fish larger than $L_{50}$:

$$GSI = \left( \frac{m_g}{m_s} \right) \times 100$$

Where $m_g$ is the gonad mass (g) and $m_s$ is the somatic mass (g) (minus gonad and stomach mass).

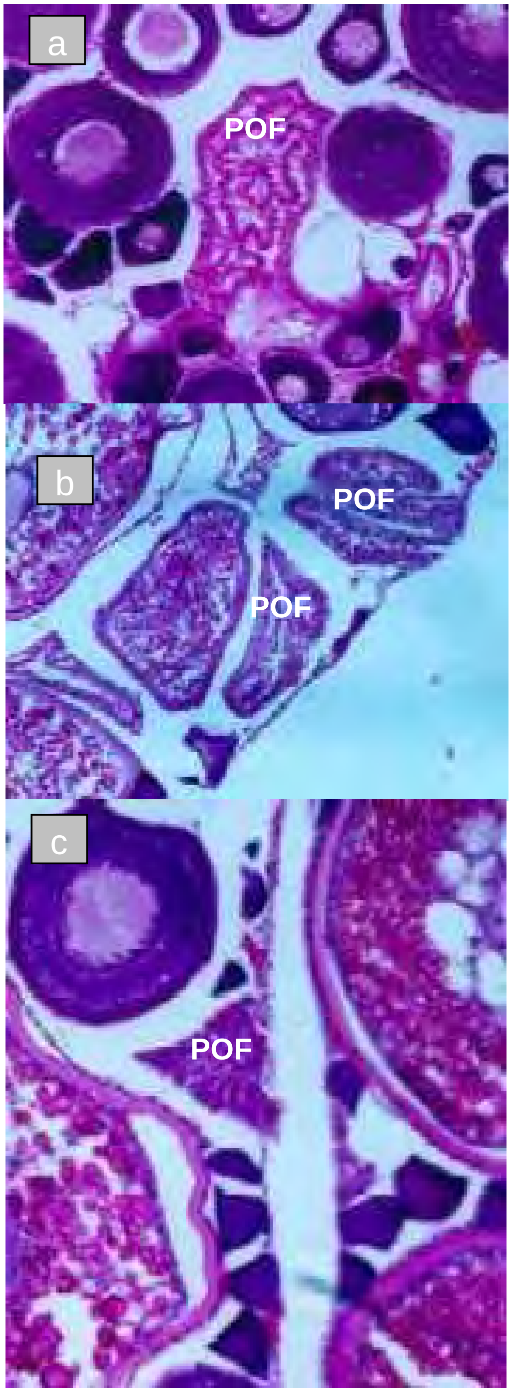


Figure 2: Post ovulatory follicle (POF) stages, photographed at 200x magnification, determined from fish chemically induced to spawn in an open circulating system housed at the Tsitsikamma National Park. a = stage 1 (0-6 hours), b = stage 2 (7-24) hours and c = stage 3 (25-48) hours.

Table I: Classification and descriptions of macroscopic and microscopic ovary and testis stages of *A. argyrozona* sampled in the Tsitsikamma National Park.

| Stage | Macroscopic | Microscopic |
|---|---|---|
| 1 – Juvenile female | Ovo-testis appears as thin transparent vessel. | Both ovarian and testicular tissue present in equal proportions, however in the later stages ovarian tissue becomes dominant. |
| 1 – Juvenile male | Ovo-testis appears as thin transparent vessel. | Both ovarian and testicular tissues are present in equal proportions, however in the later stages testicular tissue becomes dominant. |
| 2 – Immature/ resting female | Translucent orange tubes, no eggs visible to naked eye. | Cells in the perinucleolus stage with a large nucleus containing 8-15 nucleoli located along the periphery of the nucleus. There may be remnants of the testes on the periphery of the ovary. |
| 2 – Immature/ resting male | Thin white and flaccid but larger than those in stage 1, no sperm in tissue. | No sperm cells are noticeable and the seminiferous tubules appear to be empty. Remnants of ovarian tissue may be present in the centre of the testes. |
| 3 – Active female | Oocytes visible to naked eye as tiny granules in gelatinous orange matrix, little increase in diameter of ovary. | Vitellogenesis begins in the oocytes, which become more rounded and begin to accumulate yolk (yolk vesicles). Yolk appears as a narrow ring of small yolk vesicles in the periphery of the cytoplasm. |
| 3 – Active male | Wider and triangular in cross section. | The seminal vesicles expand and become filled with spermatogonia. |
| 4 – Developing female | Gonad larger and orange/yellow in colour. Eggs clearly discernible. Veins and arteries large and plentiful. | Yolk vesicles are common and primary yolk oocytes begin to appear, which are characterised by the formation of small spherical yolk granules. |
| 4 – Developing male | Testes wider and deeper, creamy white in colour, obvious presence of sperm in main sperm duct. | The seminiferous tubules of the testes are filled with spermatozoa, which are also present in the primary sperm duct. |
| 5 – Ripe female | Ovaries are large in diameter, may be a few hydrated eggs. Yellow oocytes take up all the space. Veins and arteries large and plentiful. | Tertiary yolk oocytes, characterised by large yolk plates, appear along with primary yolk and yolk vesicles. The nucleus becomes irregular in shape and smaller in size. The nucleus migrates to the animal pole of the cell after which hydration begins, resulting in increased transparency of the cells and an increase in cell size. |

| | | |
|---|---|---|
| 5 – Ripe male | Sperm present in main sperm duct and in tissue. Gonad soft and breaks when lightly pinched. | The seminiferous tubules expand with copious amounts of spermatozoa that fill the lumen of the primary sperm duct. |
| 6 – Ripe running female | Amber in colour. Large with substantial proportion of gonad with hydrated eggs, which fill the lumen. Veins and arteries large and plentiful. | Filled with hydrated oocytes. Due to dehydration during the histological preparation, these oocytes appear as collapsed bags. Hydrated oocytes may squash and re-shape the immature oocytes that surround them. |
| 6 – Ripe running male | Free flowing sperm extruded from fish when the abdomen is lightly squeezed. Testes very delicate and break easily when handled. Copious amounts of sperm present in main sperm duct and in tissue. | The seminiferous tubules of the testes appear distended and are filled with mature spermatozoa, as is the lumen of the primary sperm duct. |
| 7 – Spent female | Ovary reduced in size similar to stage 2 flaccid. Few yolked oocytes remaining. Ovary bloodshot. | Cells in various stages of atresia, and some hydrated and mature oocytes may be present in the tissue. |
| 7 – Spent male | Testes small shrivelled and bloodshot, white in colour. | The seminiferous tubules are no longer distended and have thicker walls than stage 6. They contain few spermatozoa, which are present in the lumen of the primary sperm duct. Large blood vessels are apparent in the tissue. |

In order to investigate the relationship between spawning and temperature, temperature data were collected at the sampling site using a Seamon Mini recorder (Hugrun, Iceland) stationed at 35 m depth on the reef from which the biological samples were collected. A thermistor array consisting of four underwater temperature recorders (UTR's) at depths of 12 m, 19 m, 27 m and 35 m recorded the temperature every minute and stored an hourly average, which was later downloaded (Roberts 1999). Photoperiod data were downloaded from the South African Astronomical Observatory database (www.saao.ac.za). Pearson Rank correlation was used to measure the correlation between GSI and temperature, and GSI and photoperiod trends.

# RESULTS

Histological examination of the gonads revealed that although juveniles possess both testicular and ovarian tissue simultaneously (i.e. an intersex) they mature as either a male or female (Table I), and are therefore late gonochorists (rudimentary hermaphrodites). Gametogenesis was similar to that described for other late gonochoristic sparids e.g. *Pterogymnus laniarius* (Booth and Hecht 1997). The size at 50% maturity was estimated at 292 (±1.77) and 297 (±2.1) mm FL for females (n = 778) and males (n = 998) respectively (Fig. 3), and in both cases is equivalent to an age of *c.* 5 years (Brouwer and Griffiths 2004). A likelihood ratio test revealed that there was no significant difference between male and female $L_{50}$ ($p>0.5$) or $a$ ($p>0.1$). The combined size at 50% maturity was estimated at 295 mm FL. Complete (100 %) maturity for both sexes occurred at 480 mm FL, an age of *c.* 15 years (Brouwer and Griffiths 2004). The sex ratio was 1F:1.3M (n = 1776). A chi-square test with Yates' correction factor applied revealed that this was a significant difference from unity ($p<0.01$).

Three age-related POF stages were identified within the ovaries of captive spawned carpenter (Fig. 2). Stage 1 POFs (0-6 hours) are very loosely arranged and appear as a long convoluted string with a large clearly defined lumen. The granulosa cells are clearly determinable and widely spaced, with clearly visible nuclei (Melo 1994). Stage 2 POFs (7-24 hours) are smaller and more densely packed but still have a determinable lumen. The granulosa cells are closely packed and dense. Stage 3 POFs (25-48 hours) are small and densely packed. There is no lumen and the granulosa cells are closely arranged and no longer distinguishable from one another. After 48 hours at 16°C POFs were no longer detectable.

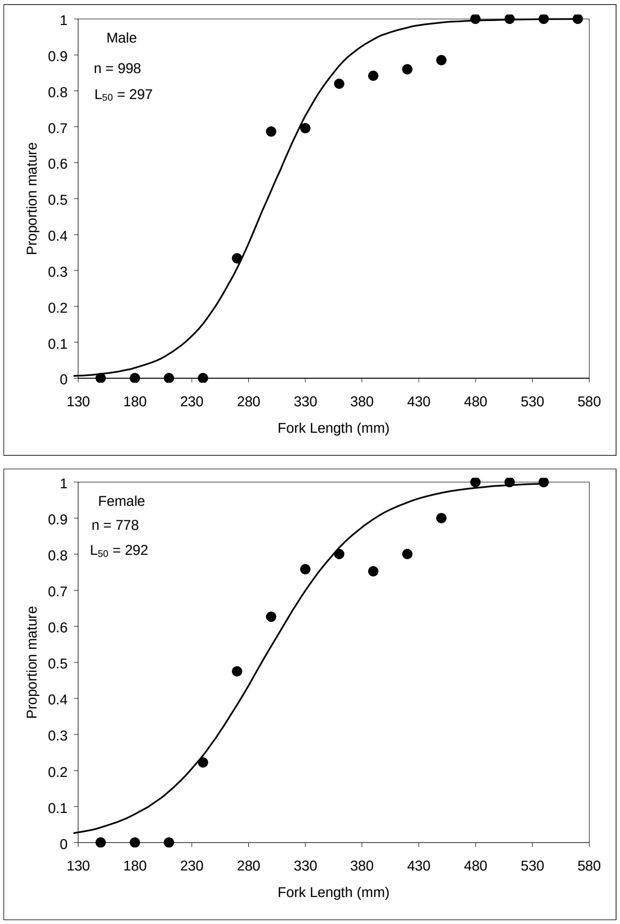


Figure 3: The proportion of mature *A. argyrozona* in the different length classes sampled in the Tsitsikamma National Park. The curves are 2-parameter logistic ogive and are fitted using a maximum likelihood approach.

Mean GSI and the proportions of ripe (stage 5) and ripe running (stage 6) fish increased in November and remained high until April (Figs. 4 and 5), indicating that carpenter are summer spawners. The presence of early POFs from November to March (sample numbers being too low for April) supports the macroscopically determined spawning season. The monthly spawning fraction did, however, reveal that spawning frequency was highest in January and February, when the fish spawned at two day intervals and lowest in November and April when they were found to spawn every 2-3 days (Table II).

Batch fecundity was positively correlated with both fish mass ($r = 0.71$; $p<0.01$) and fork length ($r = 0.71$; $p<0.01$). No correlation was found between fish length and relative batch fecundity (eggs.fish somatic mass$^{-1}$) (Fig. 6). The proportion of fish with stage 1 POFs revealed that spawning frequency and season increased with fish length (Table III). Accounting for size related patterns in spawning season (Fig. 7) and frequency, annual fecundity increased allometrically with mass (Fig. 8) and age (Table IV). Hydrated egg size was significantly smaller and more variable (average 1.0 mm ± 0.16) in fish below the length at 100% maturity (480 mm FL) than those above this length (1.1 mm ± 0.09) (t-test, $p<0.005$).

A positive relationship between temperature at the time of spawning (back-calculated from stage 1 POFs, assuming a delay of 6 hours) and the proportion of ovaries with stage 1 POFs indicated that spawning events were positively correlated to temperature ($r = 0.93$; $p<0.01$) over the range 9°C and 22°C (Fig. 9). Temperature and photoperiod varied seasonally (Fig. 10). GSI was however strongly correlated ($r = 0.86$) with photoperiod, but exhibited a weak negative relationship with seasonal temperature. An analysis of stage 1 POFs revealed that spawning occurred in the early morning (Fig. 11).

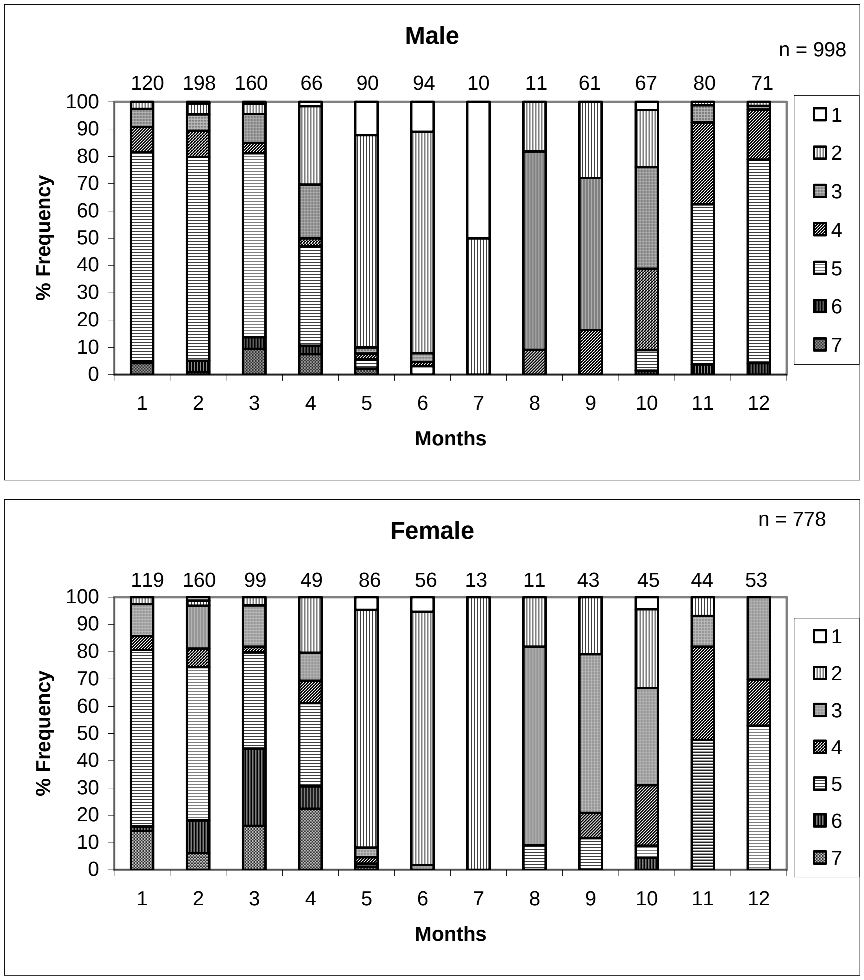


Figure 4: Monthly variation in the proportion of macroscopic gonad stages of *A. argyrozona* > $l_{50}$ caught in the Tsitsikamma National Park (March 1996 – July 1999). Numbers in the legend refer to the gonad stages in Table I. 1 = Juvenile, 2 = Immature, 3 = Active, 4 = Developing, 5= Ripe, 6 = Ripe running and 7 = Spent.

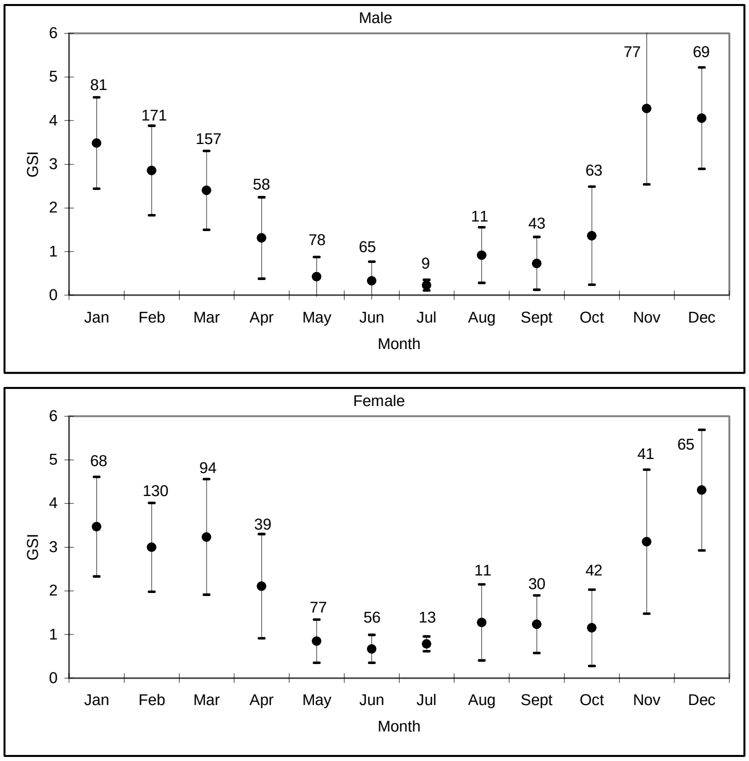


Figure 5: Seasonal variation of the standard deviation in the gonadosomatic index (GSI) and mean values (•) for male and female *A. argyrozona* sampled in the Tsitsikamma National Park. Values = n.

## DISCUSSION

Late gonochorism, protandry, protogyny and hermaphroditism are the recognised reproductive styles of sparids (Smale 1988; Buxton and Garratt 1990). Although carpenter were previously described as gonochoristic (Nepgen 1977), microscopic examination of the gonads revealed that they are late gonochorists. The sex ratio calculated during this study (1 female: 1.3 male) was typical for those observed for other late gonochorists (Griffiths *et al*. 2002).

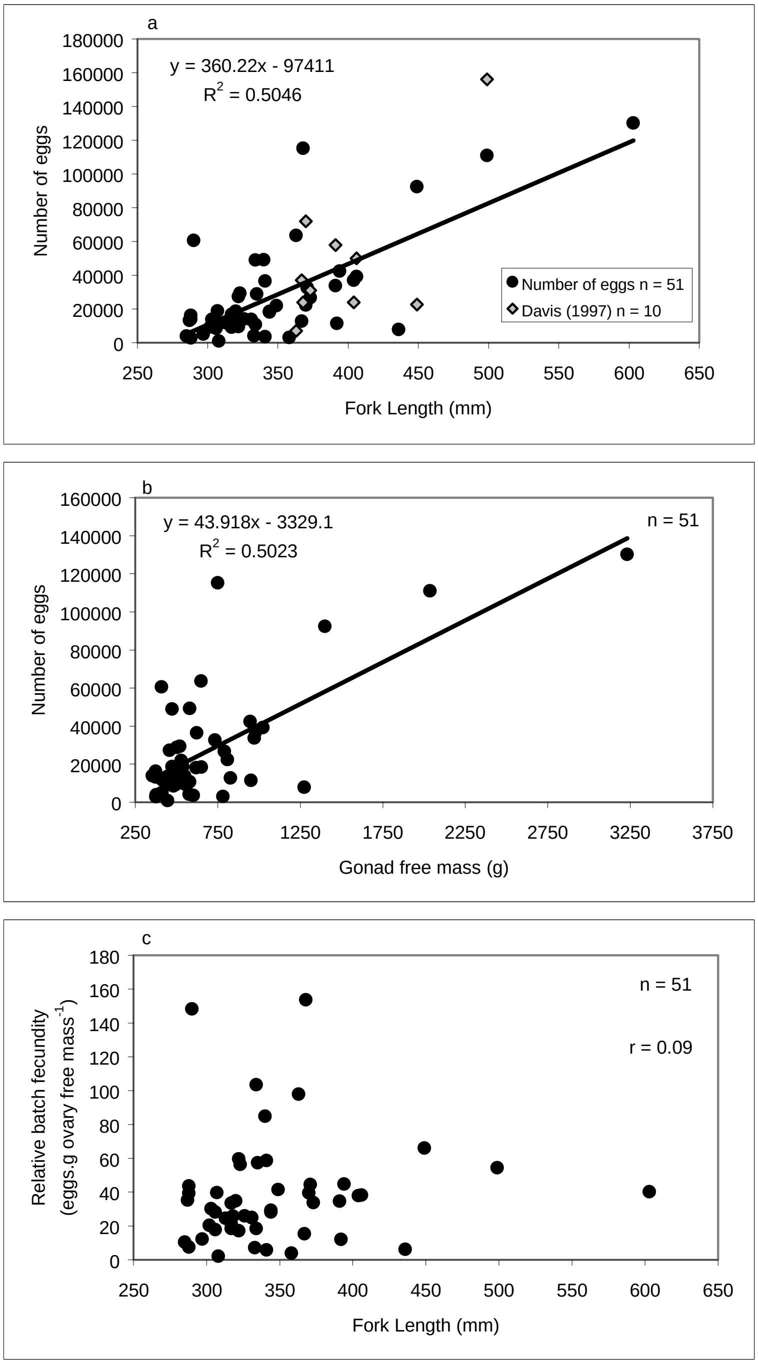


Figure 6: The relationships for *A. argyrozona* between a – fish length and batch fecundity including data from fish spawned artificially in a previous study (Davis 1996), b – fish mass and batch fecundity and c – fish length and relative batch fecundity.

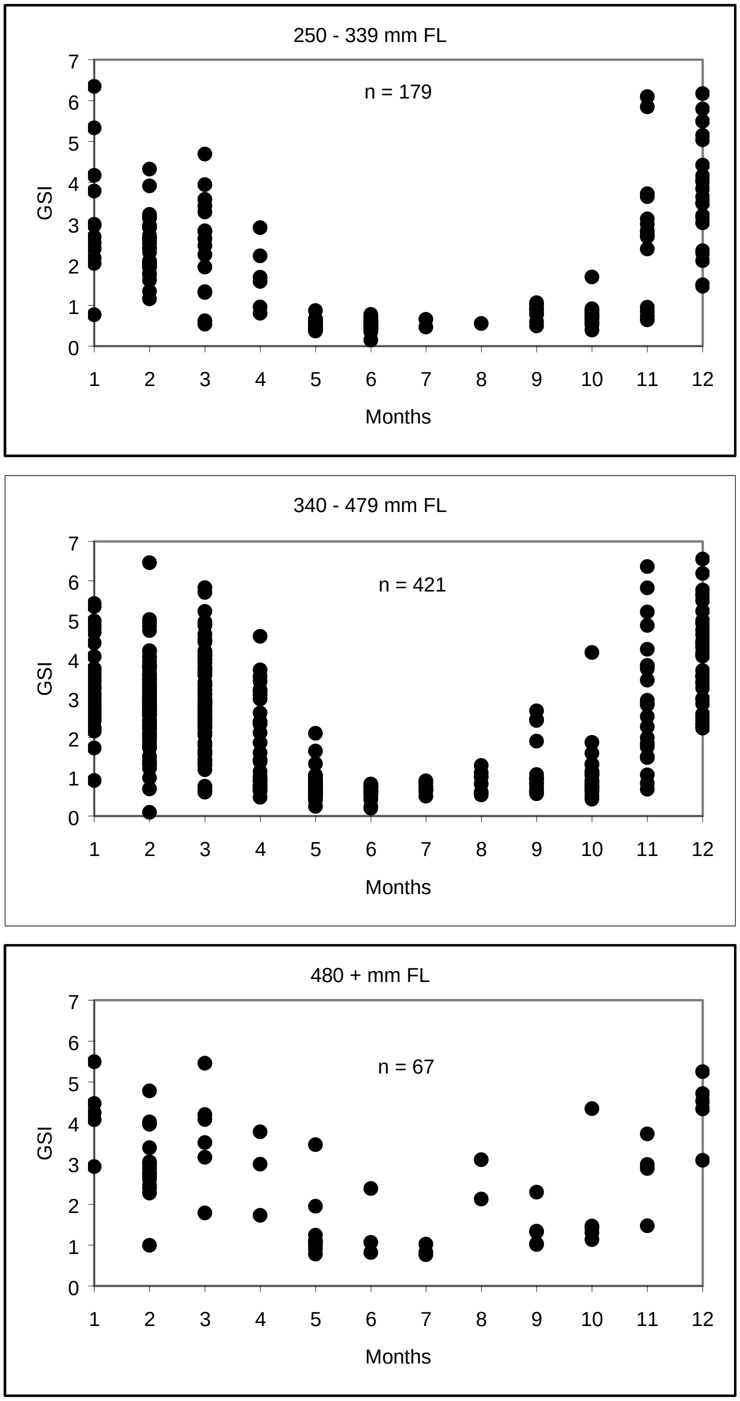


Figure 7: Seasonal variation of the gonadosomatic index (GSI) for female *A. argyrozona* from three size classes sampled in the Tsitsikamma National Park.

Table II: Spawning frequency determined from the proportion of ovaries with stage 1 POFs or macroscopically determined hydrated oocytes for *A. argyrozona*. * In these months there were not enough ovaries containing POFs to make any valid estimation.

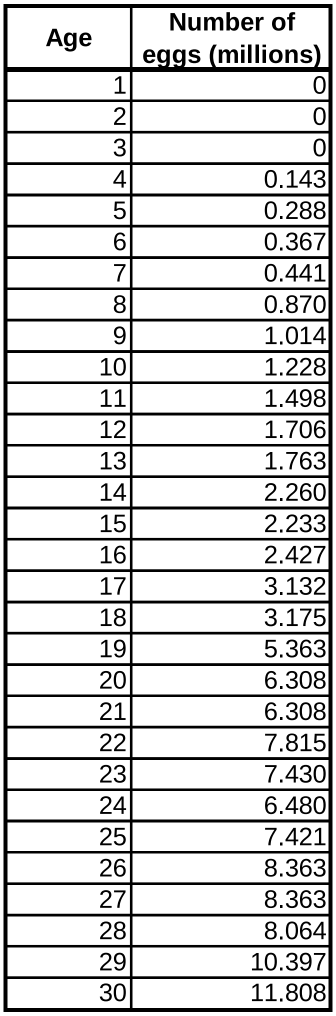
| Month | Spawning frequency days (n) | | % with hydrated oocytes | % ovaries with stage 1 POFs |
|---|---|---|---|---|
| | Macroscopic | POFs | | |
| November | 2.1 (44) | 4.6 (23) | 48 | 22 |
| December | 1.9 (53) | 3.5 (21) | 53 | 28 |
| January | 1.5 (119) | 1.6 (5) | 66 | 60 |
| February | 1.5 (160) | 1.5 (35) | 68 | 66 |
| March | 1.6 (99) | - | 64 | Not enough data* |
| April | 2.6 (49) | - | 39 | Not enough data* |

Upon reviewing 90 species of reef fish, Sadovy (1996) concluded that although GSI’s reflect the gonad maturity patterns for a species they are poor indicators of peak spawning times. By way of example, in the red hind grouper *Epinephelus guttatus* yolked oocytes are present in the ovaries for four months of the year, but actual spawning is limited to a period of 10 days (Sadovy 1996). In the case of carpenter, however, the presence of POFs from November to April supports the six month spawning season suggested by macroscopic methods, although in some larger individuals (> 480 mm FL) hydrated oocytes and POFs were found from October to May. Monthly spawning fraction and percentage of ovaries with hydrated oocytes, nevertheless, reached a peak during January and February, which was not detected in the monthly GSI's. But given that monthly proportions of macroscopically determined hydrated ovaries closely tracked trends in proportions with POFs (Table II), it was concluded that expensive and time consuming histological analysis is not necessary for determining spawning peaks in this species.

Table III: Spawning frequency (averaged over all months) and length of the spawning season calculated from the presence of stage 1 POFs in *A. argyrozona* ovaries in three size classes.

| Size class (mm) | Average spawning frequency (Days) | Spawning season (Months) |
|---|---|---|
| 250 – 339 | 9 | 6 |
| 340 – 479 | 4 | 7 |
| 480 + | 3.9 | 9 |

Table IV: Individual age based annual fecundity of *A. argyrozona* in the Tsitsikamma National Park.



| **Age** | **Number of eggs (millions)** |
|---:|---:|
| 1 | 0 |
| 2 | 0 |
| 3 | 0 |
| 4 | 0.143 |
| 5 | 0.288 |
| 6 | 0.367 |
| 7 | 0.441 |
| 8 | 0.870 |
| 9 | 1.014 |
| 10 | 1.228 |
| 11 | 1.498 |
| 12 | 1.706 |
| 13 | 1.763 |
| 14 | 2.260 |
| 15 | 2.233 |
| 16 | 2.427 |
| 17 | 3.132 |
| 18 | 3.175 |
| 19 | 5.363 |
| 20 | 6.308 |
| 21 | 6.308 |
| 22 | 7.815 |
| 23 | 7.430 |
| 24 | 6.480 |
| 25 | 7.421 |
| 26 | 8.363 |
| 27 | 8.363 |
| 28 | 8.064 |
| 29 | 10.397 |
| 30 | 11.808 |

Apart from being indicators of spawning seasonality GSI trends can provide insight into the mating patterns of a species (Sadovy 1996). Pair spawning sparids such as

*Chrysoblephus laticeps* have low male GSI (±10% of female) relative to female GSI during the spawning season (Buxton 1990). Although the spawning behaviour of carpenter has not been documented, the GSI of males (average 3.0 ± 1.4) was similar to that of females (average 3.3 ± 1.4) during the spawning season. The large testes size suggests that they are group spawners and that sperm competition is high (Sadovy 1996). Further evidence for group spawning is that carpenter do not demonstrate sexual dimorphism (Smale 1988; Mann and Buxton 1998; Griffiths *et al*. 2002).

Like many other South African sparids carpenter are summer spawners (Buxton and Clarke 1986; Buxton and Clarke 1991; Buxton 1993). While various environmental cues have been suggested for this, it is probably a combination of events that leads to gonad maturation and spawning. Smale (1988) and Garratt (1985) attributed increases in gonad activity of *Petrus rupestris* and *Chrysoblephus puniceus* to an increase in photoperiod and water temperature, respectively, and Scott and Pankhurst (1992) showed that seasonal temperature regulated gonad development for *Pagrus aratus*. Based on the data collected during this study, photoperiod appears to be responsible for the onset of gonad maturation in carpenter, as the gonads begin to develop in September and October when day length increases, but water temperature is variable (Fig. 10). Photoperiod was also highly correlated with GSI (r = 0.86) while temperature shows a weakly negative relationship (r = -0.16).

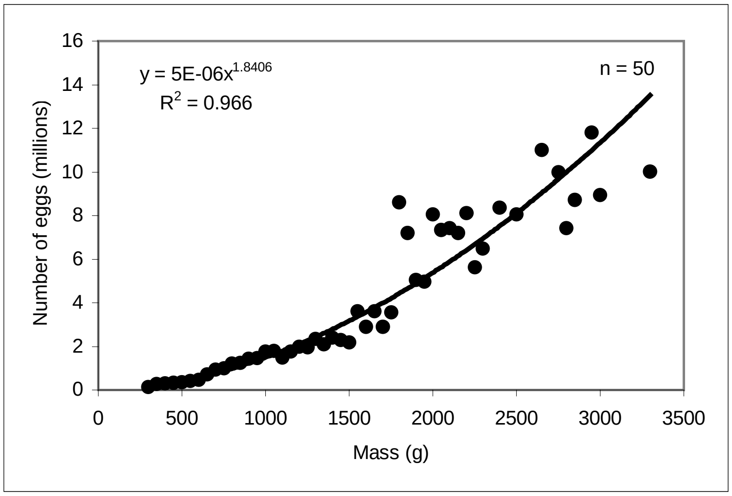


Figure 8: The relationship between annual fecundity and fish weight for *A. argyrozona* in the Tsitsikamma National Park.

Nepgen (1977) calculated spawning frequency for this species based on oocyte size frequency analysis of inactive females. Finding only one peak in the oocyte size frequency distribution, he assumed that carpenter spawned only once a year. In the present study POFs and various yolk stage oocytes were found to occur simultaneously, proving that carpenter are serial spawners. Taking into account monthly trends in spawning frequency and the length of the spawning season, Tsitsikamma carpenter are estimated to spawn at least 30 times per year. This is similar to other predatory reef fishes e.g. *Mycteroperca microlepis* (30-40 times per year) (Collins *et al*. 1998). Nevertheless, as with other species (Danilowicz 1995) spawning fraction in carpenter during the spawning season was highly correlated with water temperature (r = 0.931) suggesting that short term cold water upwellings, a common feature of the TNP during summer (Schumann *et al*. 1982), may negatively impact annual reproductive output in this area.

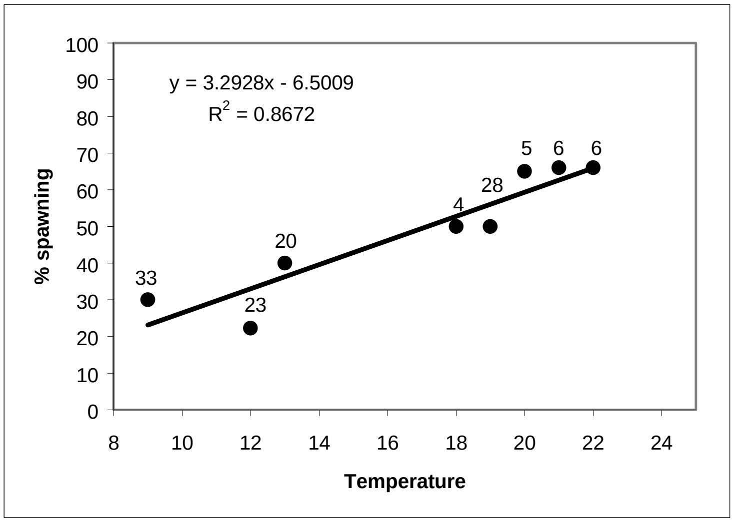


Figure 9: The relationship between proportion of *A. argyrozona* spawning (back calculated from stage 1 POFs, 0-6 hours) and sea water temperature in the Tsitsikamma National Park. Numbers above symbols refer to number of fish sampled with POFs.

Although reproductive output in fishes is highly variable between individuals (Sadovy 1996), absolute fecundity increases with size (Hunter *et al*. 1985; Davis and West 1993; Wilson and Nieland 1994; Collins *et al*. 1998). In this study, absolute annual fecundity increased markedly with fish size and spawning season was longer for large fish. The positive correlation of batch fecundity and fish size (r = 0.71) coupled with the increased length of the spawning season for the older fish, greatly increases larger fishes' absolute annual fecundity. Sadovy (1996) notes that for red snapper *Lutjanus compechanus* one large female (601 mm FL) will produce as many eggs as 212 small (420 mm FL) females. Similarly, one large female carpenter of 3.3 kg will produce as many eggs as 72 small ones of 0.3 kg. In addition to higher reproductive output, the larger fish produce significantly bigger eggs and thus are likely to produce more viable larvae (Ojanguren *et al*. 1996; Pepin and Anderson 1997).

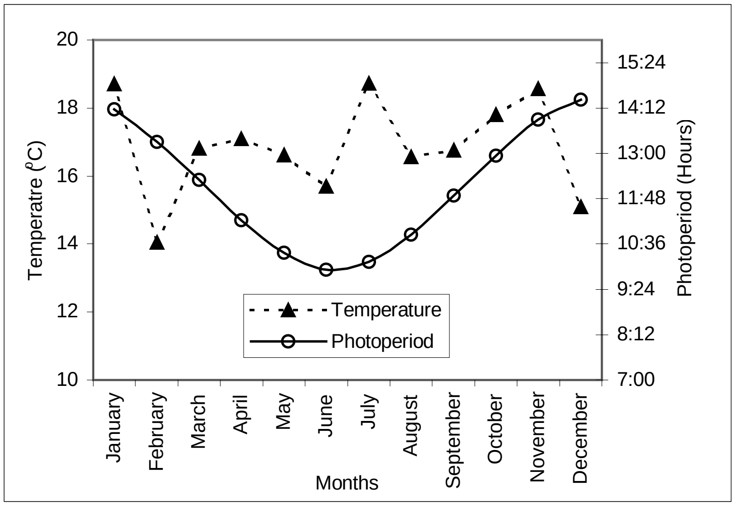


Figure 10: Monthly average temperature and photoperiod for the Tsitsikamma National Park.

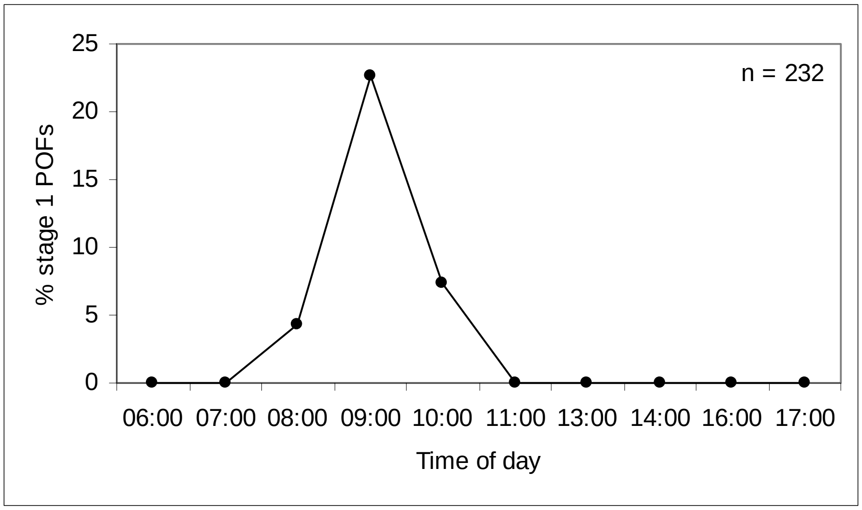


Figure 11: The daily proportion of stage 1 POFs found in the ovaries of *A. argyrozona* sampled in the Tsitsikamma National Park.

Exploited populations were traditionally managed to maximise growth (Griffiths 1997b). However, it is imperative to maintain sufficient numbers of reproductive adults to ensure egg production and avoid recruitment failure. To address this, linefish management in South Africa is based on spawner biomass per recruit models

(Griffiths 1997c). One assumption of this approach is that reproductive output is linearly related to spawner biomass, regardless of individual size (Buxton 1992). Since this study has shown that reproductive output in carpenter is allometrically related to individual mass, fecundity-per-recruit models would be more appropriate for future stock assessment of this species.

# - Chapter 4 -

## Adult movement and larval dispersal of A*rgyrozona argyrozona* (Pisces: Sparidae) from a temperate marine protected area [3]

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[3] Brouwer, S.L., Griffiths, M.H. and Roberts, M.J. 2003. Adult movement and larval dispersal of A*rgyrozona argyrozona* (Pisces: Sparidae) from a temperate marine protected area. *Afr. J. mar. Sci*. **25**: 395-402.

# - Chapter 4 -

# Adult movement and larval dispersal of A*rgyrozona argyrozona* (Pisces: Sparidae) from a temperate marine protected area

## Abstract

Adult emigration and larval dispersal of carpenter *Argyrozona argyrozona* from the Tsitsikamma National Park (TNP), South Africa, were investigated using mark-recapture data and Acoustic Doppler Current Profiler measurements of currents. Tagging data showed that adult carpenter were mainly resident, with a small proportion (7%) leaving the TNP in both easterly and westerly directions. No relationship was found between fish movement patterns and fish size or time-at-liberty. Current patterns suggest that eggs and larvae spawned within the TNP are mainly transported eastwards towards established nursery grounds; the median estimated distance moved was 299 km (range 42-561 km) in 30 days (time to flexion). Given this pattern of ichthyoplankton dispersal together with the fact that adult carpenter within the TNP display a high degree of residency and that they are much more abundant than in adjacent fishing grounds (*cpue* = 23 times greater), it appears that the TNP protects a viable carpenter spawner population capable of seeding adjacent fishing grounds.

**Key words**: currents, dispersal, eggs, larvae, mark-recapture, movement patterns, Sparidae, transport

## INTRODUCTION

Carpenter *Argyrozona argyrozona* is an important component of the South African commercial linefishery (Brouwer and Buxton 2002). However, like many other reef fish, the catch per unit effort (*cpue*) of this species has declined markedly since the early 1900s (Griffiths 2000). It is a slow-growing, long-lived species, having two distinct areas of abundance; one over the central Agulhas Bank and the other over the eastern Bank (Griffiths and Wilke 2002). Tagging studies suggest that exchange between these two populations is limited (Griffiths and Wilke 2002).

Given the limitations of conventional management tools such as bag and size limits, marine protected areas (MPAs) have been advocated as an effective strategy for the conservation of reef fish (Bohnsack 1998). Of central importance to this hypothesis is the ability of MPAs to supply recruits to adjacent fishing areas in sufficient numbers to maintain catches at predetermined levels (Carr and Reed 1993). In theory, MPAs benefit adjacent fisheries through both adult movement and larval seeding. However, supportive empirical evidence remains sparse. Because most no-take MPAs that protect reef fish are small, populations are impacted by fishing through edge effects, whereby fish move to and fro across reserve boundaries (Griffiths and Wilke 2002). Also, most MPAs are relatively new and the fish populations have not as yet recovered to pristine levels of abundance (Bohnsack 1998). By contrast, the Tsitsikamma National Park (TNP) on the south-east coast of South Africa is a well-established (since 1964), no-take MPA that covers a relatively long coastline of approximately 75 km. It is the only MPA in South Africa that is perceived to be large enough (i.e. >50 km) to effectively provide complete protection for warm temperate sparids in the region (Griffiths and Wilke 2002).

The objective of this study was to establish whether the TNP seeds adjacent fisheries with adult and/or larval carpenter.

# MATERIAL AND METHODS

The Tsitsikamma National Park extends between the Groot River (East; 30$^{o}$04´S, 24$^{o}$12´E) and the Groot River (West; 33$^{o}$59´S, 23$^{o}$34´E; Fig. 1). It extends 5.6 km offshore with reefs ranging in depth from shallow to c. 100 m (Tilney *et al.* 1996). This habitat and depth range is ideally suited to carpenter (Smith and Heemstra 1986, Smale and Badenhorst 1991).

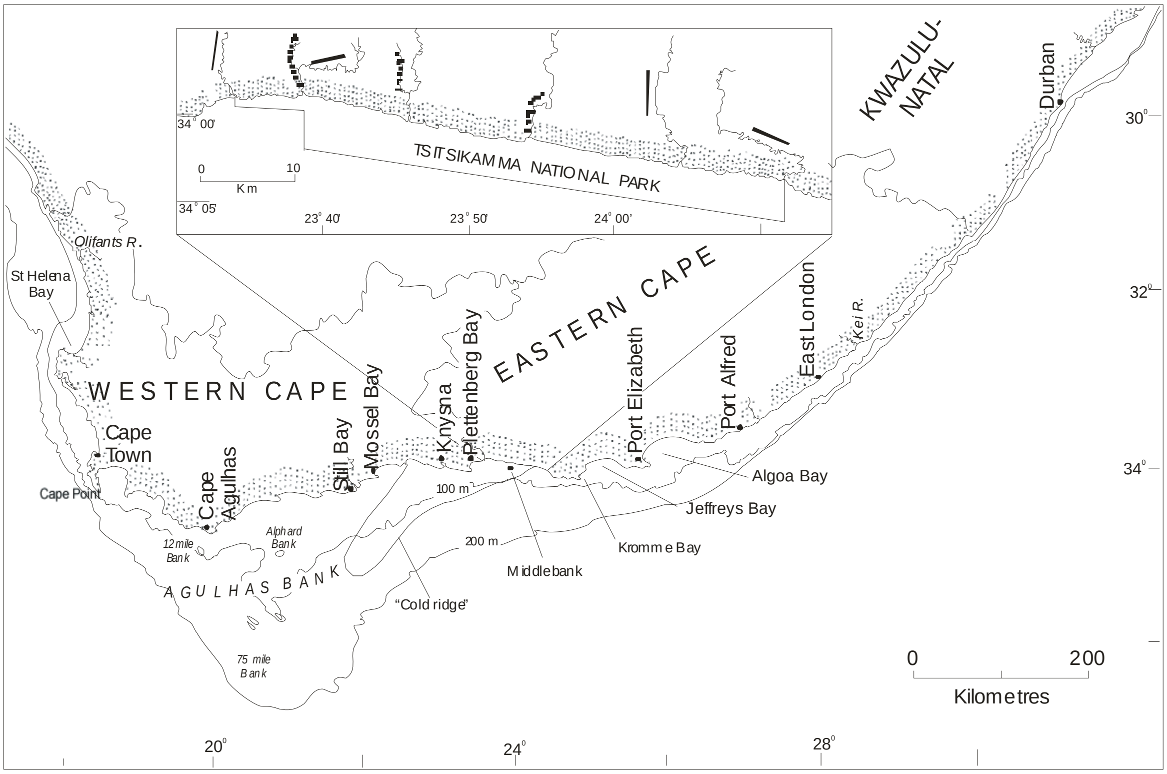

Figure 1: Map of the study area showing the position of the Tsitsikamma National Park on the eastern seaboard of South Africa, the 100 m and 200 m isobaths, and places mentioned in the text.

Carpenter were caught from a skiboat using handline over a prominent reef (Middlebank; 34°02.72´S, 23°52.51´E), situated 1 n. mile from the coast and in 36 m of water, near the centre of the TNP (Fig. 1). Fish were measured (mm, *FL*) and tagged on the left side with a dart D-tag (Hallprint, Australia), and when necessary the gas bladder was deflated using a hypodermic needle. Tags were individually coded and marked with a return address to the Oceanographic Research Institute (ORI), Durban. Number of fishers, fishing time, depth and location were recorded for each fishing trip. Recaptures within the TNP were made during scientific fishing operations between January 1997 and December 2000, whereas fish caught outside the park were reported to ORI by commercial and recreational fishers.

Fish were sacrificed during the spawning season and gonads preserved for histological analysis in order to identify spawning events (See Chapter 3 for details). The presence of post-ovulatory follicles, confirmed that carpenter spawn in the TNP at the study site (Chapter 3). To determine the fate of eggs and larvae spawned there, currents were measured using a 300 kHz Acoustic Doppler Current Profiler (ADCP). The instrument was deployed on Middlebank, an established spawning site for carpenter, between July 1998 and December 2002. Current direction and speed (cm $s^{-1}$) were recorded every 30 minutes at 2 m depth intervals between 3 and 31 m.

To establish likely settlement areas for carpenter larvae spawned on Middlebank, passive egg and larval drift were inferred using progressive vector plots calculated for 30 days after an established spawning event. Because carpenter eggs are buoyant (Davis and Buxton 1996), and are generally found near the surface (Wood 1998), movement within the upper 11 m was used in this analysis. Spawning times were back-calculated according to the presence of early post-ovulatory follicles in histological ovary sections from fish collected on Middlebank. Histological analysis of capture-spawned carpenter revealed that early post-ovulatory follicles were present for up to 6 hours after a spawning event (Chapter 3).

Spatial patterns in the distribution of juvenile carpenter were determined using data collected from research demersal biomass surveys carried out by Marine and Coastal Management between 1986 and 2001, using the swept area method (detailed in Badenhorst and Smale 1991). These data were converted to geo-referenced catch per unit effort (*cpue*; number of fish trawl$^{-1}$ minute$^{-1}$) estimates. Distribution maps of *cpue* were obtained by means of Kriging (*SURFER*®; Golden Software, Inc., USA).

## RESULTS

In all, 2 338 carpenter were tagged (range = 227 - 658 mm; FL mean = 376mm FL). Of these, 114 (5%) were recaptured, all of which were larger than size-at-50% ($L_{50}$) maturity. The average time-at-liberty for these fish was 526 days (range 9-1 691 days). Carpenter were found to be largely resident, 90.3% being recaptured at the site of release (<0.5 km from the site of release); 2.7% were recaptured within the TNP away from the point of release, and 7.1% were caught outside the reserve. The eight fish recaptured outside travelled distances of between 36 and 290 km, in an easterly (75%) and westerly (25%) direction (Fig. 2). There was no evidence to suggest that fish at liberty for longer periods moved greater distances long shore (Fig. 3), but carpenter seemed to move into deeper water with increasing time-at-liberty (Fig. 4). *Cpue* was on average 5.39 fish person$^{-1}$ hour$^{-1}$.

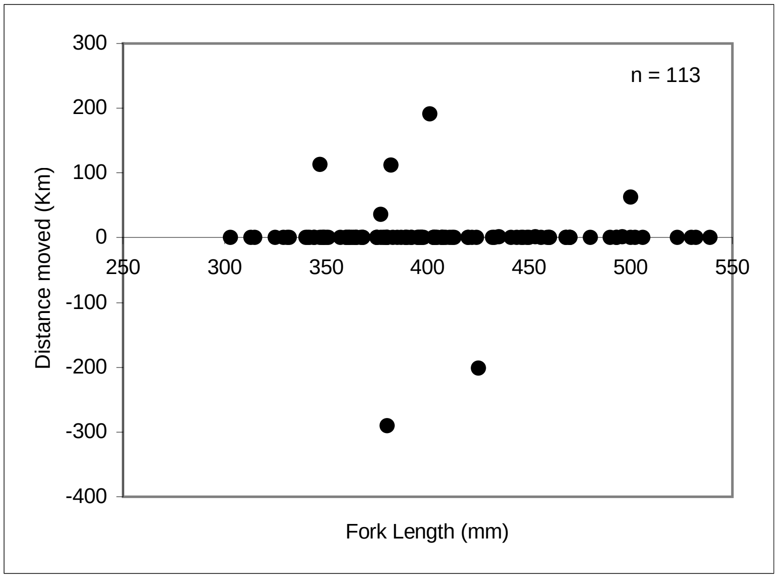

Figure 2: The distance moved by *A. argyrozona* from various size classes tagged and released in the Tsitsikamma National Park. Positive movement indicates movement to the east and negative movement indicates westward movement.

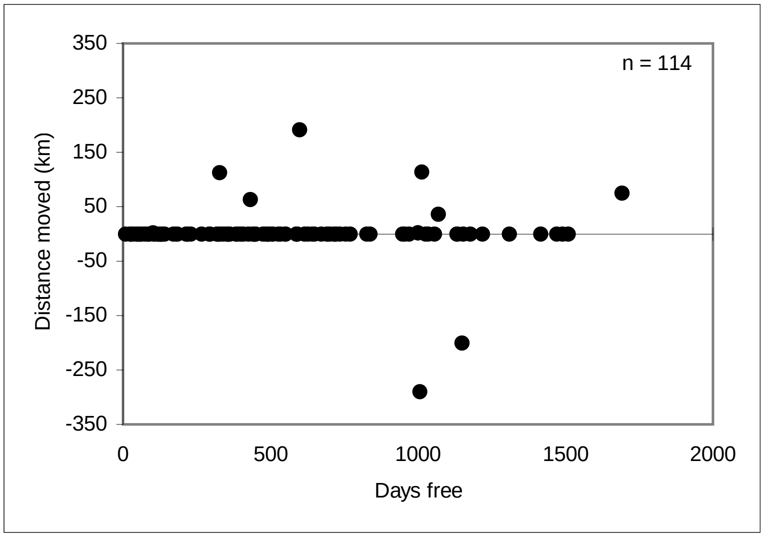

Figure 3: The time related distance moved by *A. argyrozona* tagged and released in the Tsitsikamma National Park. Positive movement indicates movement to the east and negative movement indicates westward movement.

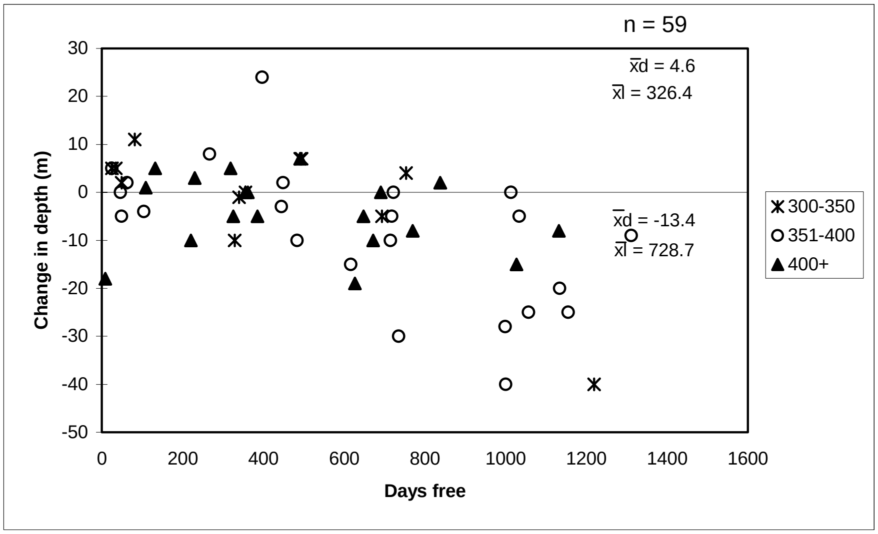

Figure 4: The change in depth between the area at release and recapture for *A. argyrozona* tagged and released in the Tsitsikamma National Park. Showing the mean change in depth ($\overline{xd}$) and time at liberty ($\overline{xl}$) for fish above and below the zero change line. Negative values indicate movement into deeper water.

Data from the demersal biomass surveys revealed two areas of abundance of juvenile carpenter. Smallest fish (50-100 mm *TL*) were most prevalent over the eastern Agulhas Bank between Jeffrey’s Bay and Algoa Bay, and east of Cape Agulhas near the Alphard Banks (Fig. 5a). Larger fish (101-200 mm *TL*) were concentrated inshore between Algoa Bay and Plettenberg Bay, and at Cape Agulhas (Fig. 5b).

During the study period, currents moved in different directions and at varying velocities, with depth (Table I). The median distance moved by the surface layer (0-11m) during the 30-day period, following six spawning events, was 299 km eastwards (range 42-583 km).

Progressive vectors for these six periods are shown in Figure 6, which shows that larvae were potentially transported eastwards and parallel to the 100m isobath (Fig. 7).

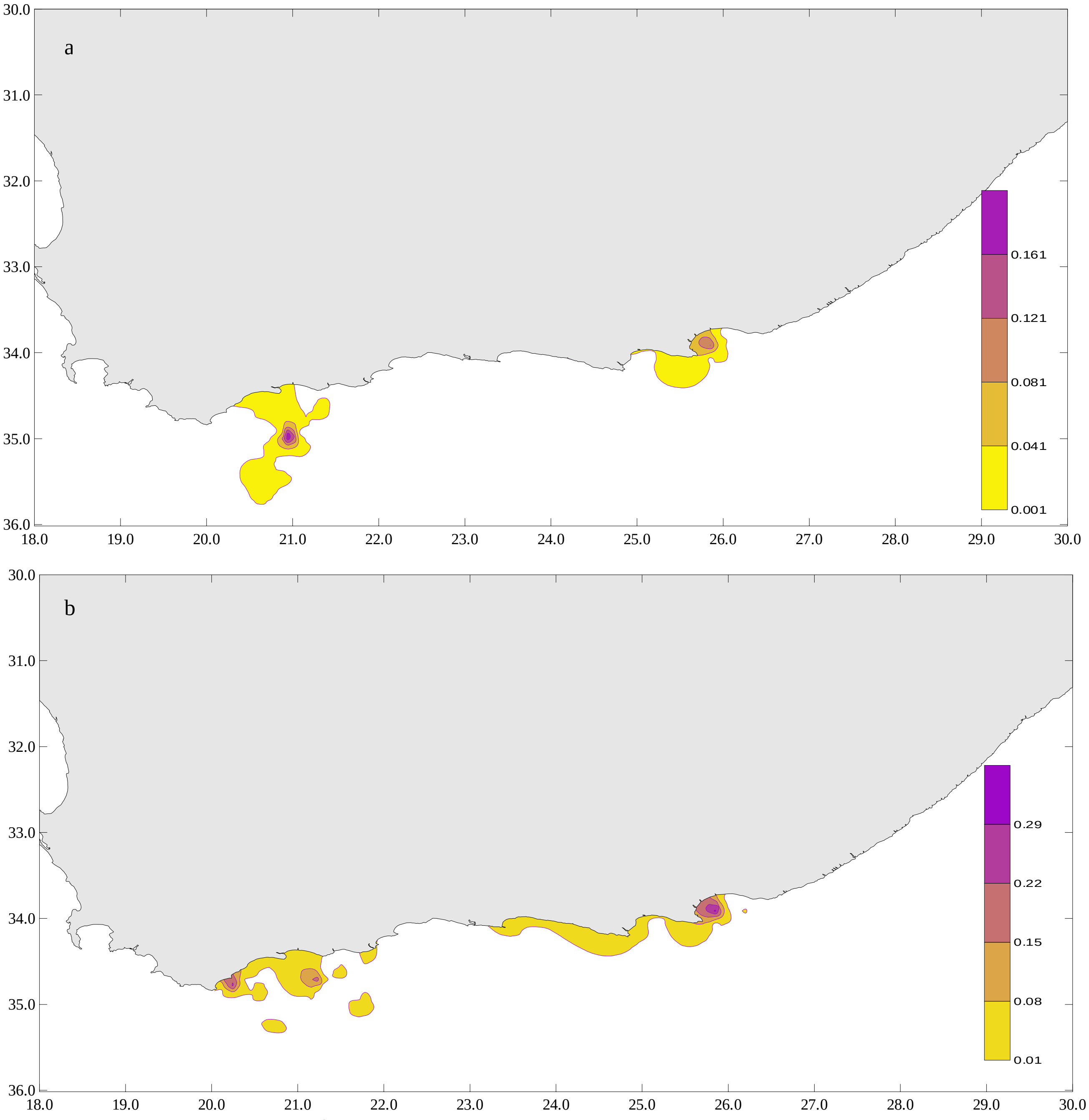

Figure 5: Distribution of a) 50-100 mm TL and b) 101-200 mm TL *A. argyrozona* based on *cpue* (fish.trawl$^{-1}$) from 3725 demersal trawls conducted between 1986 and 2001.

# DISCUSSION

Adult carpenter are clearly resident within the TNP, with only a small proportion of the population moving out of the reserve. This pattern is similar to that described for carpenter on the central Agulhas Bank (Griffiths and Wilke 2002), where most fish are resident and few are migratory. No attempt was made in the present study to quantify the potential number of individuals exported from the TNP, because of the limitation rendered by an under-reporting rate of 60% of recaptured tagged fish in the South African commercial linefishery (Brouwer 1997), as well as the effort differential (about 500 vessels in the fishing fleet in adjacent areas and 1 research vessel in the TNP). However, given the effort differential and the fact that only 7% of recaptures were made outside the TNP, adult emigration is expected to be low. The concept of a resident adult population within the TNP is further supported by an average *cpue* that was 23-fold higher than that recorded on the adjacent fishing grounds (Brouwer and Buxton 2002).

Griffiths and Wilke (2002) found that carpenter on the central Agulhas Bank move into deeper water as they grow. This also seems to be the case in the TNP, where depth of recapture increased with time-at-liberty. However, it is important to note that these movements took place on the same reef system, over horizontal distances of 20- 2 000 m. No depth data were recorded for fish caught outside the TNP.

Currents remain the major determinant of pelagic larval dispersal (Leis and Goldman 1983), but larval behaviour is often more complex than have been described in the literature (Stobutzki 2001). Postflexion larvae of some teleosts can swim and orientate themselves towards physical cues in the current, thereby controlling their dispersal (Richards and Lindeman 1987, Leis 1991). Therefore, only dispersal of preflexion larvae was considered here. Carpenter are pelagic spawners and their eggs float close to the water surface. Experimentally, it has been estimated that eggs of carpenter hatch after 26-30 h at 19$^{o}$C, and that larvae undergo flexion after approximately 24 days (Davis and Buxton 1996). Eggs and preflexion larvae of carpenter were found mainly in the upper 12 m in the TNP by Wood (1998).

Table I: Potential transport of larvae at four depths, for six consecutive months. Trajectories were calculated for 30 days using data collected by an ADCP moored at Middlebank in the Tsitsikamma National Park.

| Date of spawning | Depth (m) | Longshore movement (km) | On/off-shore movement (km) | Net direction (degrees) | Compass direction |
|---|---|---|---|---|---|
| 15-Oct-98 | 5 | 352 | 8 | 94 | ESE |
| | 11 | 352 | 30 | 110 | SE |
| | 21 | 408 | 12 | 97 | ESE |
| | 31 | 248 | 23 | 70 | NE |
| 23-Nov-98 | 5 | 360 | 23 | 75 | NE |
| | 11 | 352 | 12 | 97 | ESE |
| | 21 | 248 | 4 | 86 | ENE |
| | 31 | 16 | 10 | 35 | NE |
| 14-Dec-98 | 5 | 583 | 38 | 70 | NE |
| | 11 | 561 | 12 | 86 | ENE |
| | 21 | 446 | 36 | 73 | NE |
| | 31 | 104 | 36 | 65 | NE |
| 14-Jan-99 | 5 | 114 | 10 | 105 | ESE |
| | 11 | 144 | 18 | 110 | SE |
| | 21 | 90 | 22 | 125 | SE |
| | 31 | 59 | 3 | 276 | WNW |
| 16-Feb-99 | 5 | 233 | 12 | 108 | ESE |
| | 11 | 245 | 10 | 96 | ESE |
| | 21 | 114 | 4 | 84 | ENE |
| | 31 | 6 | 14 | 23 | NNE |
| 15-Mar-99 | 5 | 44 | 36 | 128 | SE |
| | 11 | 42 | 63 | 212 | SW |
| | 21 | 234 | 108 | 247 | SW |
| | 31 | 189 | 60 | 253 | SW |

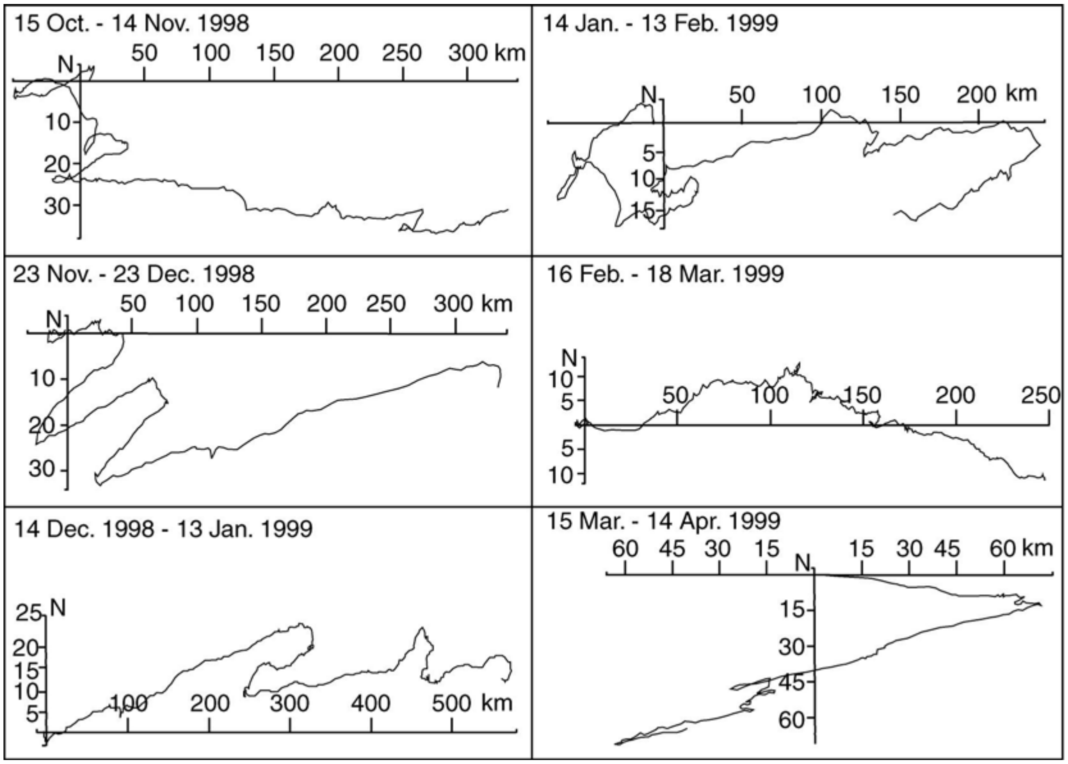

Figure 6: The plots of six progressive vector tracks at 11 m depth showing the potential trajectory of neutrally buoyant biological material from the Tsitsikamma National Park. The start of each track corresponds to confirmed spawning events.

Several attempts have been made to assess larval export of teleosts and chokka squid *Loligo vulgaris reynaudii* para-larvae from the TNP by studying current patterns. Tilney *et al*. (1996) used a bottom-moored (at 40 m deep) electromagnetic current meter and Attwood *et al*. (2002) tracked surface currents using short-period (6-24h) drogue releases. This study used an ADCP that tracked currents continuously at discrete depths throughout the water column over a period of one year. Tilney and Buxton (1994) and Tilney *et al*. (1996) speculated that local inshore hydrography in the TNP could retain larvae in the reserve, but farther offshore, larvae could be transported up to 250 km westwards. However, Tilney *et al*. (1996) probably underestimated current speeds, because only bottom currents were considered in their study. Attwood *et al*. (2002), on the other hand, measured surface currents of short duration and suggested that dispersal was in both an easterly and westerly direction. Long-term current monitoring has nevertheless shown that the movement of the surface layer is mainly eastwards, with potential maximum distances exceeding 580 km in 30 days.

Unlike the abovementioned studies, this study has linked water movement to observed spawning events, and both were measured simultaneously. The ADCP data indicated that the median distance moved by the surface water from the spawning location was 299 km east (range 42 - 583 km) in 30 days. The average current speed from this study (24 cm $s^{-1}$) suggests that larvae could be transported from the TNP to Algoa Bay within 30 days.

The spawner biomass surveys showed that small (50–100 mm *TL*) carpenter were most dense in the Algoa Bay region, suggesting that the larvae settle and spend the first few months of their lives in this embayment. Larger juveniles (101-200 mm *TL*) were most abundant between Algoa Bay and Plettenberg Bay, indicating that they move in a westerly direction as they grow. In support of this theory, Wallace *et al* (1984), who conducted trawl surveys of the inshore bays between Mossel Bay and Algoa Bay, found juvenile carpenter (75-200 mm *TL*) only in Algoa Bay, Jeffrey's Bay and Plettenberg Bay. Semi-closed anticyclonic circulation patterns were found in Kromme Bay by Roberts and van den Berg (in press), which are assumed to be typical of other log-spiral shaped bays of the Eastern Cape (Roberts 1990), and therefore should theoretically retain larvae.

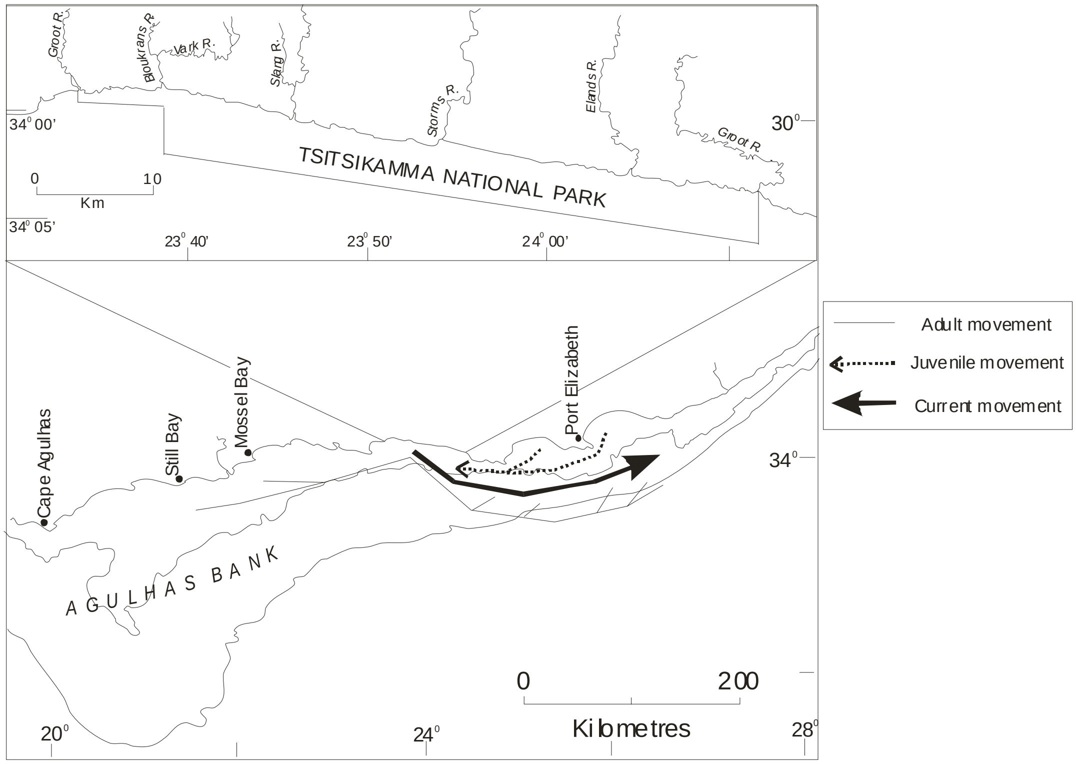

Figure 7: Summary map showing potential larval drift of *A. argyrozona* from the average current movement over 30 days, adult movement from the Tsitsikamma National Park and the predicted juvenile movement back to the Tsitsikamma National Park.

Given that juvenile carpenter > 200 mm FL are not found in the TNP and, assuming that juveniles disperse westwards as they grow, fish in the TNP probably recruit from the Algoa Bay nursery ground. They are unlikely to originate from the more distant central Agulhas Bank nursery, because the "cold ridge", which lies between Knysna and offshore of Still Bay (Fig. 1; Boyd and Shillington 1994), is believed to be a physical barrier to many warm, temperate demersal species (Griffiths 1997, Griffiths and Wilke 2002, Griffiths *et al*. 2002). Given the abundance of carpenter >250 mm *FL* off Port Alfred, the Algoa Bay nursery is also assumed to seed fishing grounds to the east.

It is likely that the TNP is an effective source of carpenter larvae. Its biomass within the reserve is probably dependant on recruitment of juveniles from nursery areas on the fishing grounds. Spatially structured models are therefore necessary to gain a better understanding of the role of the TNP in enhancing stocks of important reef fish.

# - Chapter 5 -

## Influence of sample design on estimates of growth and mortality in *Argyrozona argyrozona* (Pisces: Sparidae)

## - Chapter 5 -

# Influence of sample design on estimates of growth and mortality in *Argyrozona argyrozona* (Pisces: Sparidae)

## ABSTRACT

In order to determine the minimum sample size required to accurately estimate growth and mortality, and to assess the effects of using either random or stratified sampling procedures, a large sample of *A. argyrozona* (n = 618) was collected during February and March 1999 from the central Agulhas Bank. In the Tsitsikamma National Park monthly samples were collected for a period of one year and a single large sample was collected during February and March 1999. Decimal and integer ageing both produced similar estimates of von Bertalanffy growth parameters and growth curves, and there was no difference in the spawner biomass-per-recruit (*SB/R*) and fishing mortality (*F*) estimates. Sampling monthly throughout the year and collecting data in a single large sample provided similar growth curves, von Bertalanffy, *F* and *SB/R* estimates. Assessing the number of data points in a randomly collected data set used to estimate the von Bertalanffy and other fishery parameters showed that estimates based on less than 300 random data points were unreliable. However, accurate parameter estimates based on less than 200 data points were achieved when the sample was stratified with 10 or more samples per 2 cm size class.

**Key Words:** Age and growth, sample design, sample size, integer ageing, decimal ageing, random sample, stratified sample.

## INTRODUCTION

During the last two decades there has been considerable focus on age validation and estimation. But there has been little empirical research into the effect of sample design on estimation of growth and mortality. Samples for age and growth assessment are usually collected monthly so that marginal zone analysis can be undertaken for age validation purposes (Campana 2001). Monthly sampling is also used to establish seasonal trends in reproduction (Sadovy 1996) and feeding (Cortes 1997). However, monthly sampling is costly and not always possible to undertake throughout the entire distribution range of a species. This may occur due to the complex nature of species distribution (Kritzer *et al*. 2001), the cost of sampling or inclement weather during some seasons. In addition, large consistently collected samples are not always possible for species that are only caught sporadically or that have been heavily depleted. For these populations, knowing the effects of the sampling design on the model outputs and knowing how many samples would make a meaningful data set, becomes essential.

The precision and accuracy of a parameter estimate for a fish population is a function of not only the biological characteristics of the population, but also sampling gear, sampling design and the number of samples collected (Kritzer *et al*. 2001). Sampling of fish species for biological research is varied and often relies on opportunistic samples collected incidentally during other research projects (Buxton 1993; Allen and Winter 2002; Mann *et al*. 2002). Other studies, however, have more focused collection methods aimed specifically at biological research, such as a stratified sampling technique (Griffiths 1996b). Otoliths are generally considered to be the most reliable structures to age long-lived species, but collection and processing of otoliths is costly and time consuming. Therefore, reducing the number of samples that need to be processed is important. Furthermore, in some instances minimising sample size may be a stated research goal in order to reduce the impacts of the sampling programme, such as in Marine Protected Areas (MPAs) or when sampling rare species. Despite these varied methods, remarkably few examples exist of studies that attempt to assess the effects of sample size and design on model outputs and those experiments that have been conducted use computer simulations to create populations (Goodyear 1995; Jensen 1996; Coggins and Quinn 1998).

The objective of this Chapter is to assess the effects, based on empirical data, of how sampling regime and sample size influence the parameter estimation for age and growth studies and to assess how integer (aged as a whole number) and decimal age (aged as a number plus a fraction of a year) estimates affect these parameters.

## MATERIAL AND METHODS

### Monthly *v*. Single Large Sample

A total of 300 carpenter (259-572 mm FL), were collected monthly (January 1998 – December 1998), with hook and line in the Tsitsikamma National Park (TNP). In addition, a "once off" single large sample of 301 fish was collected from the TNP in February and March 1998. To determine the effects of sample size on the parameter estimates, additional samples of 618 fish (125-595 mm FL) were collected between December 1997 and May 1998 from the central Agulhas Bank. In each case total length (mm), fork length (mm), whole mass (g), gutted mass (g) and sex were recorded and sagittal otoliths were removed, cleaned and stored dry. The left otolith from each pair was processed as per Brouwer and Griffiths (2004).

The von Bertalanffy parameters of the above integer-aged samples were compared using a likelihood ratio test to minimise the log-likelihood of the form (after Hilborne and Mangel 1997):

$$\lambda nL = \frac{n}{2} \times \lambda n\left(\frac{\sigma^2}{n}\right) + \frac{n}{2}$$

where $n$ is the number of samples and $\sigma^2$ is the variance.

### Random *v.* Stratified Sample and Sample size

To determine the effects of sample size on length-at-age estimates for integer aged otoliths, the Agulhas Bank data were used, as this sample has a wider size range than the TNP. For this a random sub-set of 100, 200, 300, 400, 500 and 600 fish were used. Although theses data are not independent, to overcome this, a much larger sample would be required.

To test the effect of random versus stratified sampling on length-at-age estimates, individuals were selected from the Agulhas Bank data set, using 5, 10 or 15 samples from each 2 cm size class.

For each of the above data sets the von Bertalanffy model was fitted to the observed length-at-age data using an iterative least squares procedure (Microsoft EXCEL (Microsoft corp., 2000) SOLVER routine with Newton algorithm option). Total mortality ($Z$) and fishing mortality ($F$) at natural mortality ($M$) = 0.1 were then estimated (Chapter 7), as well as spawner biomass-per-recruit ($SB/R$), based on biological reference points ($40\%SB/R_{F=0}$ and $25\%SB/R_{F=0}$).

Upper and lower confidence intervals for the von Bertalanffy parameters were generated using parametric bootstrapping by generating a pseudodataset from the maximum likelihood estimate with a normal error structure.

### Integer *v.* Decimal Aging

Monthly length-at-age samples from the TNP were assessed in two ways; firstly using integer ages and secondly using decimal ages. Decimal ages were determined by assuming $1^{st}$ February to be the birth date (as this is the approximate date at the middle of the spawning season) and for each month thereafter the age was taken as:

$$Age = CR + \frac{M}{12}$$

where $CR$ is the number of completed hyaline rings and $M$ is the number of months after February that the fish was sampled. The von Bertalanffy parameters were estimated and compared using the methods above.

## RESULTS

### Monthly *v.* Single Large Sample

Monthly data and the single large sample produced similar estimates of $L_\infty$, $k$ and $t_o$ (Fig. 1) (Table I). Likelihood ratio tests showed that there was no significant difference between the estimates of $L_\infty$, $k$ and $t_o$, where $p>0.5$, $p>0.5$, $p>0.05$ for each of the parameters respectively. Each data set produced similar growth curves through all age classes (Fig. 2) and the residual spread of the data was even for both data sets (Fig. 3). The sum of squares of the monthly and single large sample was 30229.2 and 301984.4 respectively. Both techniques produced similar estimates of $F$ (0.19 and 0.20) and $SB/R_{current}$ (21.7 and 22.9%) (Table II).

### Random *v.* Stratified Sample and Sample size

Random samples of increasing size indicated that samples of > 200 fish were consistent but in those with 200 or less, older and younger fish are poorly represented (Fig. 4). Estimates of $SB/R$ based on catch curves and on von Bertalanffy growth parameters tended to stabilize with random samples >300 ($F$ = 0.13-0.14; $SB/B_{current}$ = 30-34%), whereas estimates of total mortality $Z$ stabilize with samples >200 (Table

II). All the data sets provided an even residual data spread with no apparent trend (Fig. 5). However, samples with 300, 400, 500 and 600 data points provided consistent von Bertalanffy parameter estimates (Table I). Growth curves derived from samples with 100-600 data points varied. All were relatively similar from ages 3-16 but differed above and below this range with the 300+ data sets providing the most consistent results (Fig .6). The maximum likelihood estimates for the von Bertalanffy growth parameters showed that the confidence intervals (CI) improved as the number of samples increased, but stabilised and remained relatively consistent for samples with 300 or more data points (Fig. 7).

Stratified sampling resulted in fairly low sample numbers (101, 193 and 250 fish for the 5, 10 and 15 samples per 2 cm size class respectively), but a relatively even spread of the data over the age range (Figs. 8 & 9) (Table I). Stratified samples provided a more even spread of the data than random samples, which had few young (<3 years) and very old (>16 years) fish (Figs. 10 & 11). Stratified sampling at 10 and 15 fish per 2 cm size class produced almost identical growth curves throughout the age range of this species, which were not different from 5 fish per class nor from the growth curves generated from the entire data set (i.e. the sample with 600 data points) (Fig. 12) (Table III). The von Bertalanffy parameters varied (Table I) which affected the *SB/R* estimates.

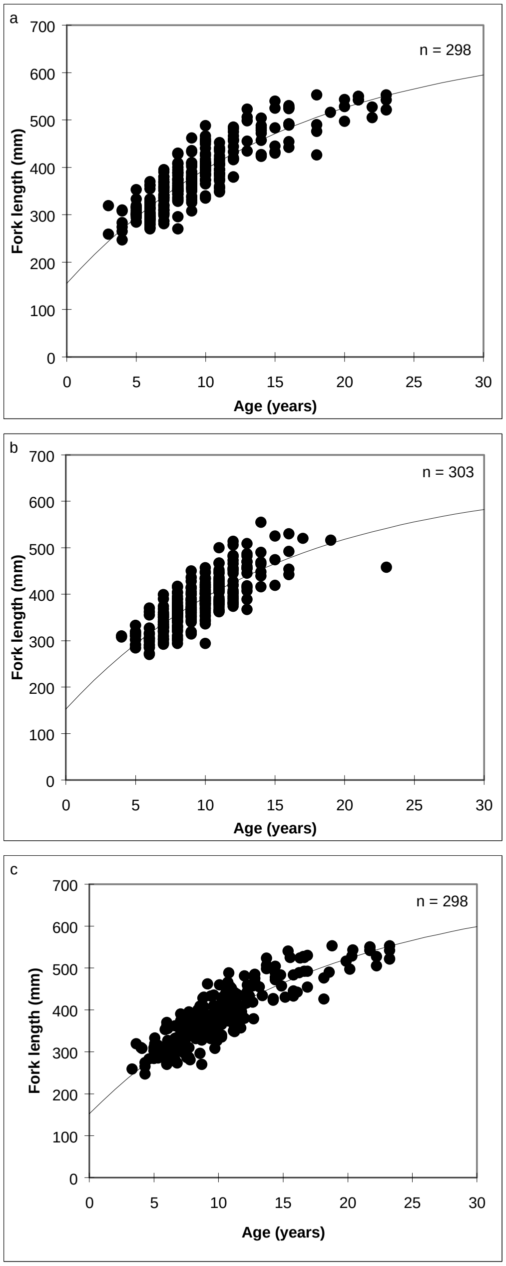

Figure 1: The calculated von Bertalanffy growth curves and observed lengths at age for *A. argyrozona* based on sectioned sagittal otoliths collected in the Tsitsikamma National Park a) on a monthly basis (January to December 1998) and aged using whole numbers (intercepts), b) as a single large sample aged using whole numbers (intercepts) (February 1998) and c) as in a) but aged on a decimal system.

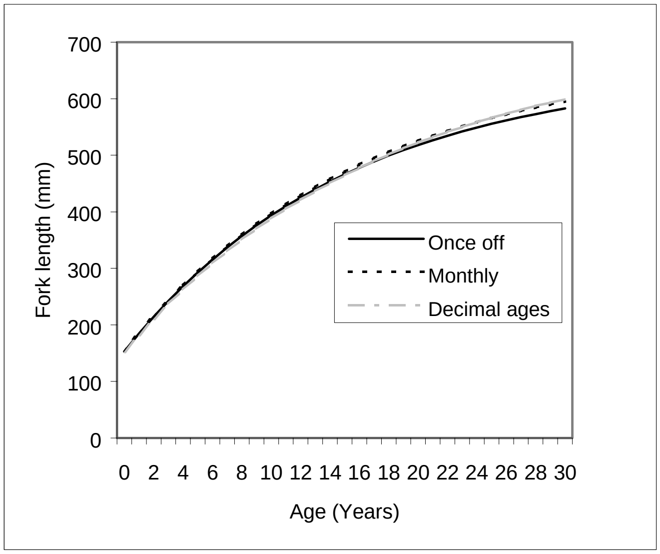

Figure 2: The calculated von Bertalanffy growth curves for *A. argyrozona* using sectioned sagittal otoliths sampled in the Tsitsikamma National Park between January and December 1998.

Assessing *F* and *SB/R* estimates derived from all of the above sampling strategies revealed that, for carpenter, integer and decimal ageing provided almost identical estimates of $SB/R_{current}$ (Table II). Monthly sampling and a single large sample provided similar estimates of $SB/R_{current}$ (21.7 *v.* 22.9). Randomly collected samples with <300 data points provided inconsistent estimates of $SB/R_{current}$ (27.5 *v.* 43.3) but those with >300 data points all provided similar estimates of $SB/R_{current}$ (30 *v.* 33.9) (Table II). Although stratified sampling resulted in few data being collected, this method provided consistent results for 10 and 15 samples per 2 cm size class ($F$ = 0.13; $SB/R_{current}$ = 34.6-34.4), but $SB/R_{current}$ was higher for the 5 samples per 2 cm size class at 44.8% (Table II).

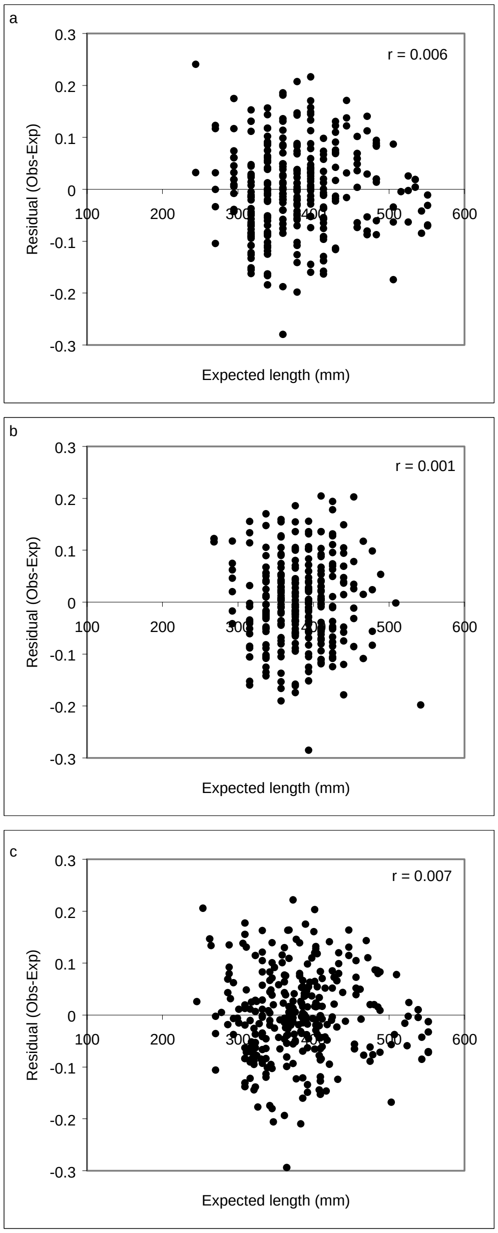

Figure 3: The residual plots for the fits to the von Bertalanffy growth model for the observed lengths at age for a) samples collected monthly and aged using whole numbers, b) samples collected in a single large sample and aged using whole numbers and c) samples collected monthly but aged using decimal ageing for *A. argyrozona* using sectioned sagittal otoliths sampled in the Tsitsikamma National Park between January and December 1998.

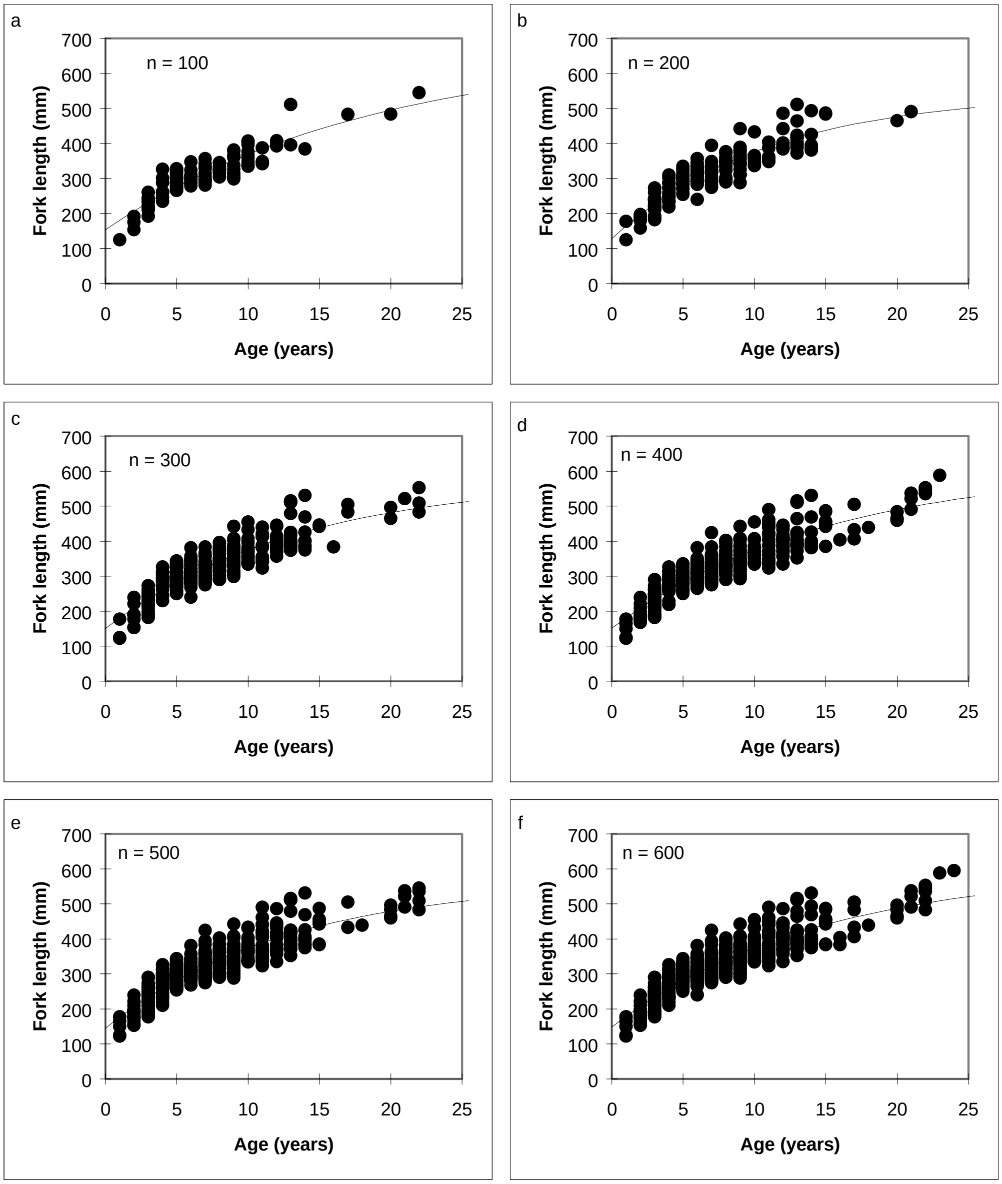

Figure 4: The calculated von Bertalanffy growth curves and observed lengths at age for *A. argyrozona* using integer aged sectioned sagittal otoliths sampled on the Agulhas Bank between December 1997 and May 1998.

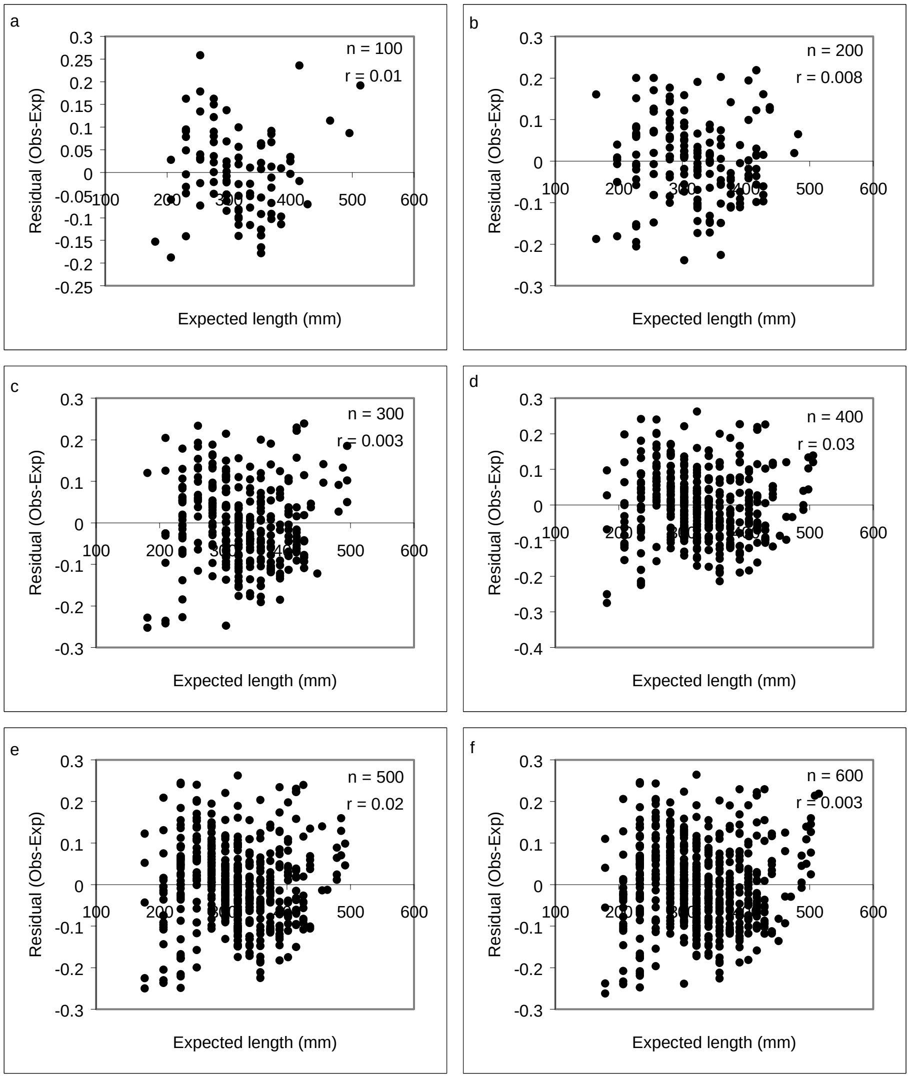

Figure 5: The residual plots for the fits to the von Bertalanffy growth model for the observed lengths at age for *A. argyrozona* using integer aged sectioned sagittal otoliths sampled on the Agulhas Bank between December 1997 and May 1998.

Table I: Parameter estimates of length-at-age (FL mm) data modelled using the von Bertalanffy growth model for *A. argyrozona* sampled in the various regions and various methods.

| **Tsitsikamma National Park samples** | | | | |
|---|---|---|---|---|
| **Sample** | $k$ | $L_\infty$ | $t_0$ | **n** |
| Monthly | 0.06 (0.002) | 674 (5.7) | -4.2 (7.7) | 298 |
| Single large | 0.06 (0.001) | 651 (13.2) | -4.0 (18.4) | 303 |
| Decimal | 0.06 (0.001) | 700 (14.8) | -4.3 (19.6) | 298 |
| **Agulhas Bank samples** | | | | |
| | **Random samples** | | | |
| 100 | 0.05 (0.07) | 674 (151) | -4.9 (12.3) | 100 |
| 200 | 0.09 (0.17) | 544 (129.2) | -3.0 (17.3) | 200 |
| 300 | 0.07 (0.17) | 577 (73.6) | -4.0 (17.4) | 300 |
| 400 | 0.07 (0.001) | 612 (17.0) | -4.3 (16.6) | 400 |
| 500 | 0.08 (0.001) | 567 (25.5) | -3.8 (25.2) | 500 |
| 600 | 0.07 (0.001) | 600 (11.6) | -4.1 (13.3) | 600 |
| | **Stratified Samples** | | | |
| 5 per class | 0.09 (0.05) | 584 (46.7) | -1.9 (12.2) | 101 |
| 10 per class | 0.09 (0.08) | 589 (68.4) | -2.4 (9.2) | 193 |
| 15 per class | 0.09 (0.08) | 576 (36.1) | -2.3 (6.9) | 250 |

## Integer *v*. Decimal Aging

Decimal age estimates produced similar growth curves to integer age estimates (Figs. 1-3) and similar estimates of $L_\infty$, $k$ and $t_o$ (Table I). Likelihood ratio tests showed that there was no significant difference between the estimates of $L_\infty$, $k$ and $t_o$, where in all cases p>0.5. Decimal ageing reduced the sum of squares by only 3.3% from 302292.7 to 292288.2. Decimal and integer ageing resulted in the same $F$ (0.12) and $SB/R_{current}$ (21.8% and 21.7% respectively) estimates (Table II).

Table II: Comparisons of the biological reference points derived from the various sampling strategies, $F_{current}$ and $SB/R_{current}$ are expressed as a percentage of $F$ = 0 at $M$ = 0.1.

| **Tsitsikamma National Park samples** | | | | | | |
|---|---|---|---|---|---|---|
| **Sample (n)** | **Maximum age** | $Z$ | $F_{current}$ | $SB/R_{current}$ | $40\%SB/R_{F=0}$ | $25\%SB/R_{F=0}$ |
| Monthly (298) | 23 | 0.29 | 0.19 | 21.7 | 0.1 | 0.2 |
| Single large (303) | 23 | 0.30 | 0.20 | 22.9 | 0.1 | 0.2 |
| Decimal (298) | 23 | 0.29 | 0.19 | 21.8 | 0.1 | 0.2 |
| **Agulhas Bank samples** | | | | | | |
| **Random samples** | | | | | | |
| 100 | 22 | 0.26 | 0.16 | 27.5 | 0.1 | 0.15 |
| 200 | 21 | 0.23 | 0.13 | 43.3 | 0.1 | 0.2 |
| 300 | 22 | 0.22 | 0.12 | 32.4 | 0.1 | 0.2 |
| 400 | 23 | 0.21 | 0.11 | 33.4 | 0.15 | 0.25 |
| 500 | 22 | 0.20 | 0.10 | 33.9 | 0.1 | 0.25 |
| 600 | 24 | 0.23 | 0.13 | 30.0 | 0.1 | 0.2 |
| **Stratified Samples** | | | | | | |
| 5 per class (102) | 24 | 0.19 | 0.09 | 44.8 | 0.15 | 0.25 |
| 10 per class (193) | 24 | 0.23 | 0.13 | 34.6 | 0.15 | 0.25 |
| 15 per class (250) | 24 | 0.23 | 0.13 | 34.4 | 0.1 | 0.25 |

## DISCUSSION

Age and growth studies have been conducted on species where as few as 15 (Chater *et al*. 1995) to over 4500 (Harris and McGovern 1997) individual fish were aged. This study shows that the number of samples analysed is important, especially for randomly collected data. Many fisheries organisations employ randomised opportunistic sampling to collect routine data and when sampling rare species. In these instances less than 300 randomly collected data points appear to be insufficient for an accurate assessment of a long-lived species (>20 years). Although growth curves can be generated, the effects on age based modelling are profound (see below).

This seems to be a result of increased sampling the middle size classes and few sampled from the old (very large) and young (very small) groups. In a review of 58 studies on 26 families of fishes from 124 populations, the modal number of samples used was 120 (range 15 - 4503), of which only 56% were based on sample sizes over 200, and only 34% had more than 300 data points. This variation suggests that there is a need to determine "how many data points are enough"? If only small samples sizes can be collected or processed, how should the sampling programme be conducted? But the number of samples required will depend on the number of age classes. More empirical studies are required to determine the number of samples required for different groups of fish.

By truncating the age estimate to the nearest integer, the problem associated with determining the birth date of long-lived fish with a protracted spawning season is overcome. Of the 58 studies above only 2.4% used decimal ageing techniques. This study showed that decimal ageing did not improve the age estimates or the model outcomes for this species. Furthermore, decimal ageing only decreased the residual sum of squares by 3.3%, and is therefore not thought to be necessary for this species.

Table III: The results of a pairwise comparison between the random and stratified samples showing the p values.

| | **Stratified 5** | **Stratified 10** | **Stratified 15** | **Random** |
|---|---|---|---|---|
| **Stratified 5** | 0 | >0.1 | <0.1 | <0.001 |
| **Stratified 10** | | 0 | >0.1 | <0.01 |
| **Stratified 15** | | | 0 | >0.1 |
| **Random** | | | | 0 |

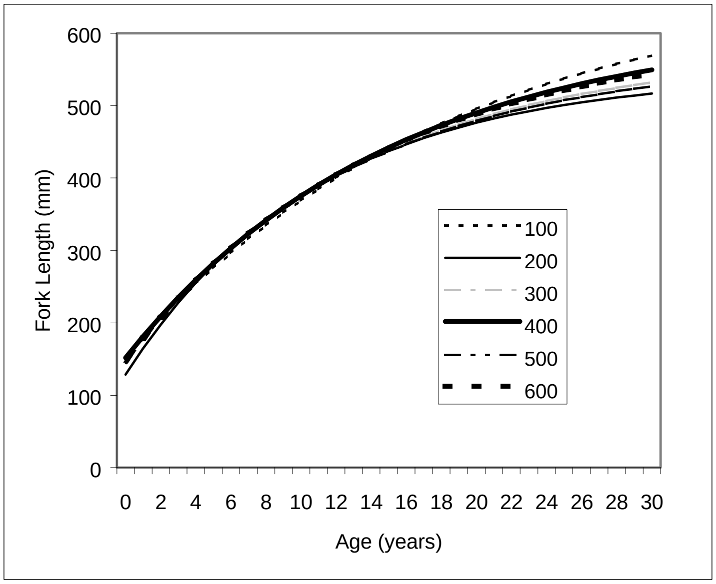

Figure 6: The calculated von Bertalanffy growth curves for *A. argyrozona* using integer aged sectioned sagittal otoliths sampled on the Agulhas Bank between December 1997 and May 1998.

To overcome the biases associated with over-sampling certain age/size groups, Tesch (1968; in Goodyear 1995) suggested that a stratified sampling design be employed. In this study stratifying the sample provided consistent results with 10 or more samples per 2 cm size class, and provided similar results to the random samples with 300+ data points. It would, therefore, appear that by stratifying the sample accurate results could be achieved with approximately 200 samples. This conclusion is supported by Kritzer *et al*. (2001), who found through computer simulation, that for a fish with a maximum age of 30, 210-300 samples should be sufficient to estimate age and growth parameters i.e. 7-10 samples per age class.

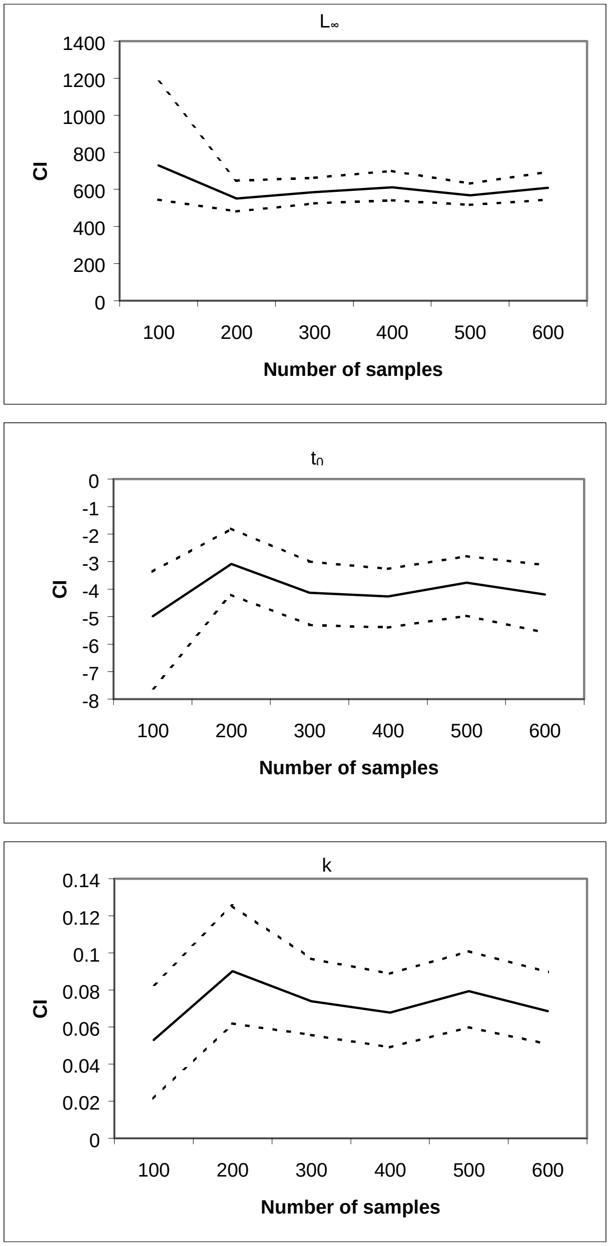

Figure 7: Upper and lower confidence intervals (CI) (estimated using the bootstrapping method) for the von Bertalanffy growth parameters for increasing random samples of *A. argyrozona* from the Agulhas Bank. Samples were aged using integer aged sectioned sagittal otoliths collected between December 1997 and May 1998.

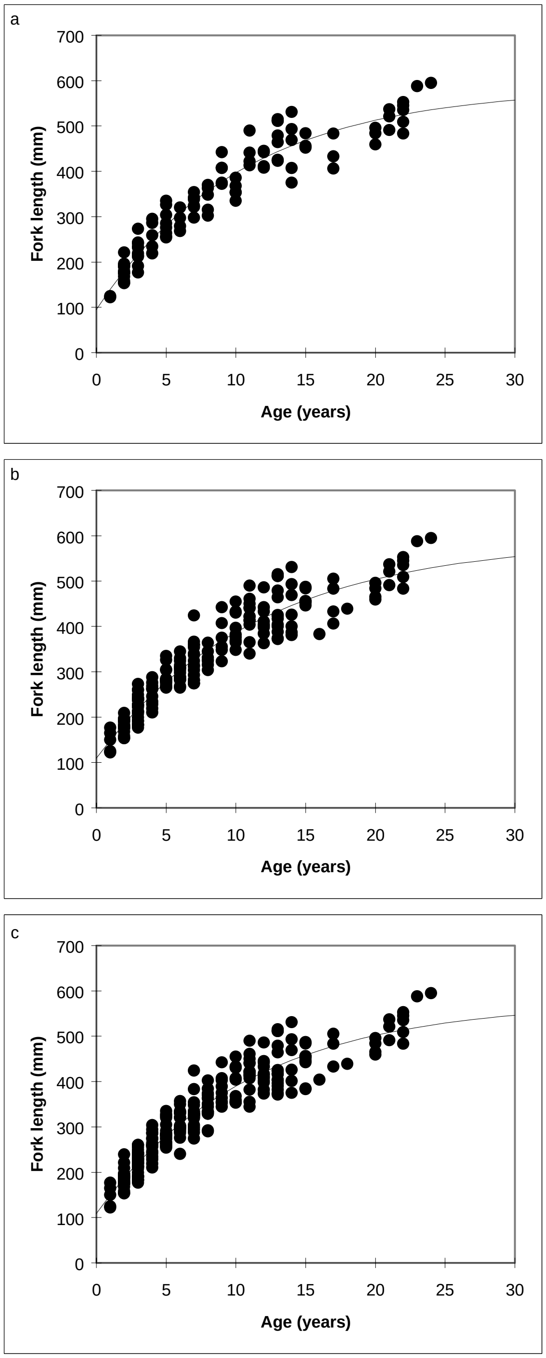

Figure 8: The calculated von Bertalanffy growth curves and observed lengths at age for *A. argyrozona*, using integer aged sectioned sagittal otoliths collected on the Agulhas Bank between December 1997 and May 1998. Samples were stratified using a) five fish per 2 cm size class, b) 10 fish per 2 cm size class and c) 15 fish per 2 cm size class.

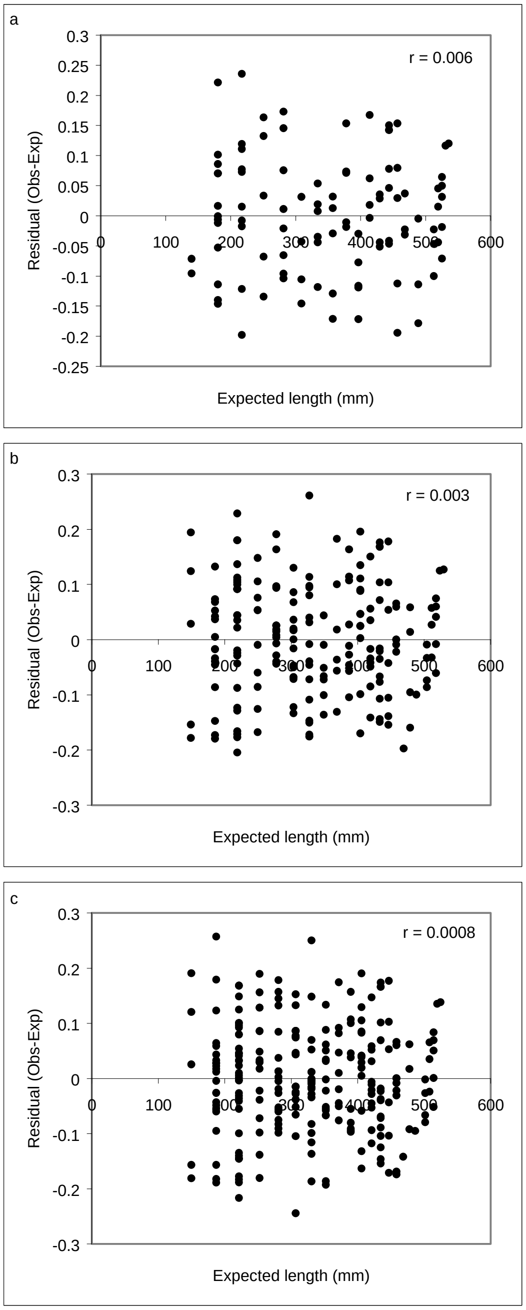

Figure 9: The residual data spread for the observed lengths at age for *A. argyrozona*, using integer aged sectioned sagittal otoliths collected on the Agulhas Bank between December 1997 and May 1998. Samples were stratified using a) five fish per 2 cm size class, b) 10 fish per 2 cm size class and c) 15 fish per 2 cm size class.

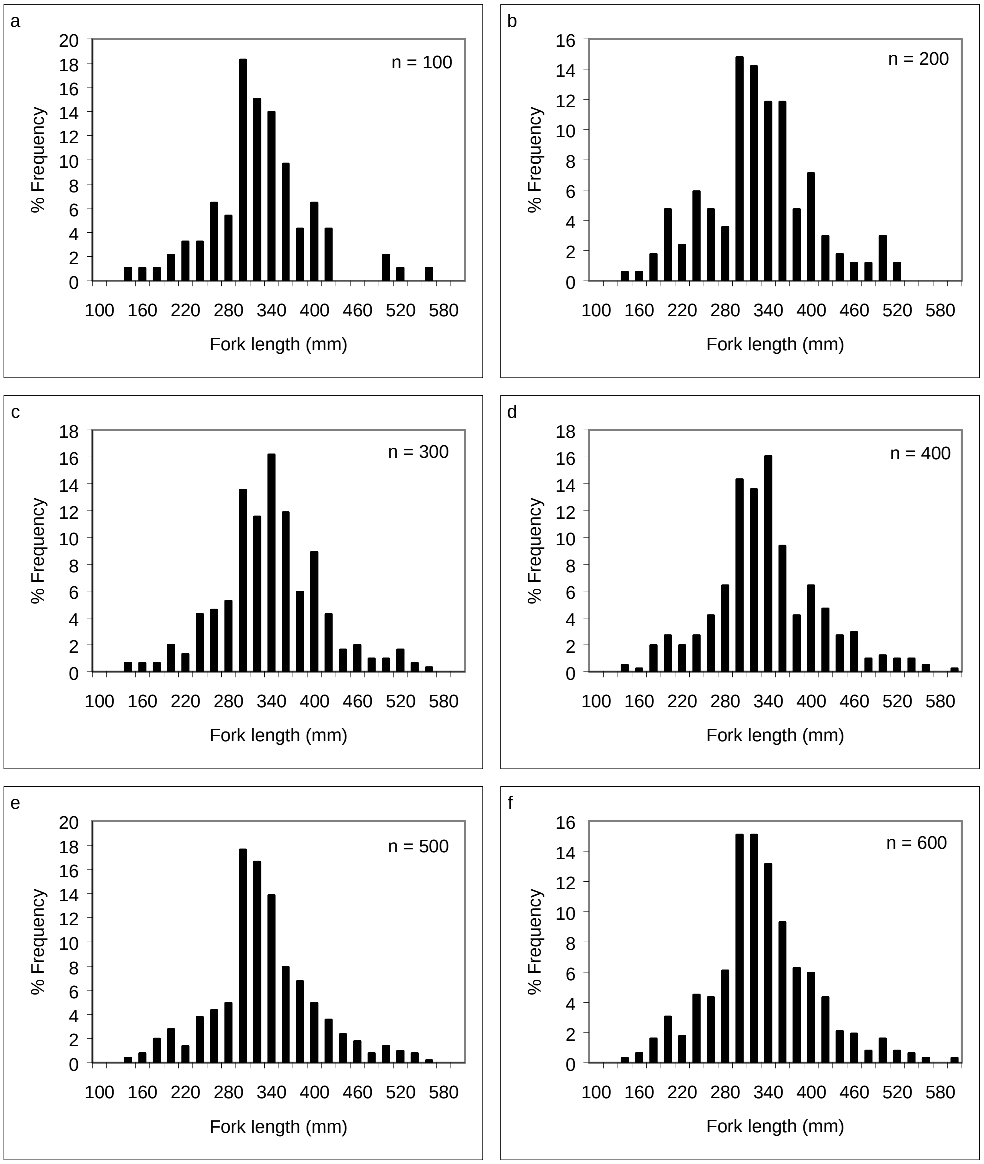

Figure 10: Length frequency distributions of randomly sampled *A. argyrozona* used for the age and growth analysis.

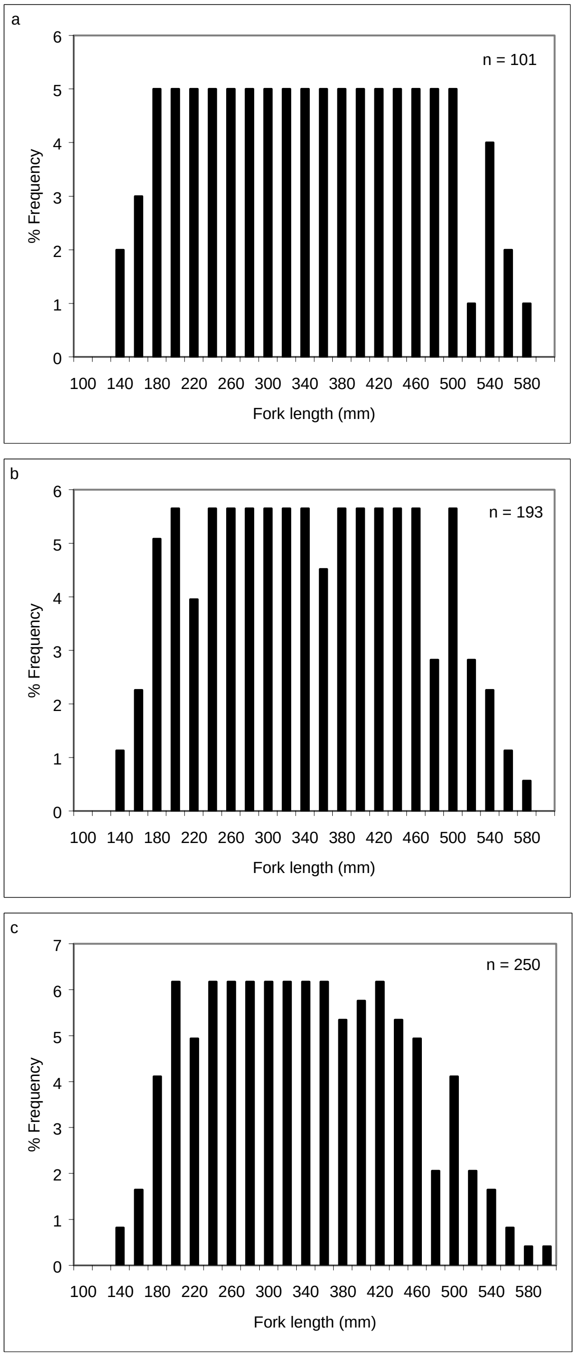

Figure 11: Length frequency distributions of *A. argyrozona* sampled for use in the age and growth analysis with a stratified sampling procedure a) 5 per size class, b) 10 per size class c) 15 per size class.

The implications of the above data become obvious when they are used to model the fishery for management purposes. $F_{current}$ and $SB/R_{current}$ values were all similar at approximately 0.2 and 22% respectively for the TNP samples, irrespective of whether the samples were collected annually or in a single large sample, or whether they were aged using integer or decimal ageing techniques. This demonstrates that the annual sampling strategy will not bias age-based models for long-lived slow growing sparids. However, sample size for randomly collected samples had a large effect on $SB/R_{current}$ outcomes, but appeared to stabilize at 300+ samples. However, accuracy can be achieved with small numbers of samples by stratifying the sample and having 10 or more data points per 2 cm size class. Kritzer *et al*. (2001) noted that for most parameters they tested, relative improvements in the quality of the data above a sample size of 300 were negligible, unless the sample size was increased by the order of several hundreds. This is supported by the empirical data of the present study, which showed that parameter estimates stabilized at 300 and remained relatively stable between 300 and 600.

These data suggest that for long-lived slow growing species such as carpenter, the annual sampling strategy does not affect age and growth or $SB/R_{current}$ estimates. This suggests that annual sampling can be conducted in one area, and a single large sample can be collected in other areas where monthly sampling is not possible, without compromising the integrity of the data nor the comparability of the two datasets, provided that the full species size range is available at all times. Sample size, however, does affect these estimates and large samples (300+) are required to improve precision when data are randomly collected. If only small samples (<300) can be collected, a stratified sampling design with 10+ fish per 2 cm size class should be undertaken. Goodyear (1995) noted that in computer simulated populations, strong year classes can bias stratified samples, but this could be overcome by stratifying the samples by age class. However, to do this a large age sample would be required. Since the objective is to reduce the number of otoliths that need to be processed, stratifying by age class is inappropriate.

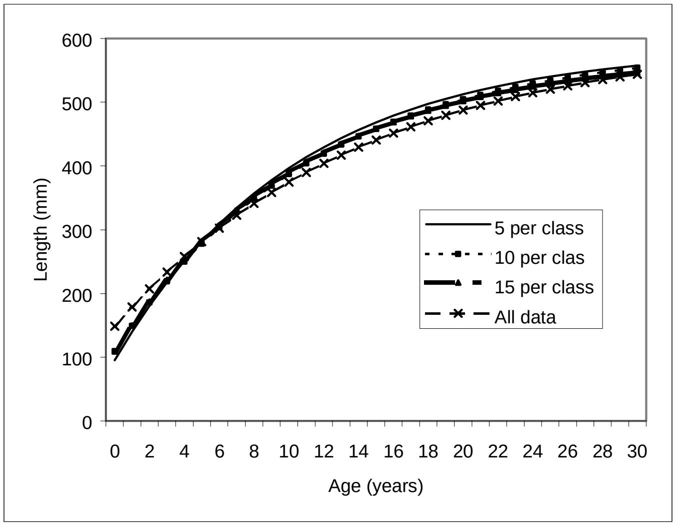

Figure 12: The calculated von Bertalanffy growth curves for *A. argyrozona* using integer aged sectioned sagittal otoliths sampled on the Agulhas Bank between December 1997 and May 1998. Samples were stratified using five fish per 2 cm size class, 10 fish per 2 cm size class, 15 fish per 2 cm size class and compared to the entire data set of 600 randomly collected samples.

# - Chapter 6 -

## Stock separation and life history of *Argyrozona argyrozona* (Pisces: Sparidae) on the South African east coast

# - Chapter 6 -

## Stock separation and life history of *Argyrozona argyrozona* (Pisces: Sparidae) on the South African east coast

### ABSTRACT

Fishery independent biomass surveys and commercial linefish catch returns were used to elucidate the spatial patterns of *A. argyrozona* distributed along the South African continental shelf. Two distinct areas of abundance were determined, one on the central and the other on the eastern Agulhas Bank. Tagging studies revealed little exchange between them. Juveniles < 100 mm TL were found on the Alphard Bank and in Algoa Bay. Juveniles of 101-200 mm TL were found in the inshore waters between Algoa Bay and Plettenberg Bay in the east and in the inshore waters at Cape Agulhas in the west. Fish > 200 mm TL were found offshore of Algoa Bay and across the central Agulhas Bank. These data suggest that juvenile *A. argyrozona* settle and move inshore, and then move offshore as they grow.

Otolith readability and growth rates varied between regions, with fish from the Eastern Cape having the lowest average percentage error (4.82 *v.* 5.33 and 7.03) and the slowest growth rates; readability decreased westward. Size at sexual maturity ($L_{50}$) varied regionally with female fish in the Eastern Cape maturing at a smaller size ($L_{50}$ = 206 mm FL) than other populations (TNP = 292, Agulhas Bank = 267). Mass at length varied between regions with carpenter on the Agulhas Bank having the highest mass at length and those in the Eastern Cape having the lowest. Fish in the Eastern Cape and inshore Agulhas Bank fed primarily on pelagic teleosts while those on the offshore Agulhas Bank fed on *Pyrosoma* spp. a gelatinous pelagic ascidian. Based on the distribution of carpenter, variability in otolith readability, mass at length, variation in growth and size at maturity it is concluded that carpenter exist as two separate stocks and should be managed accordingly.

**Key words**: Life history, age and growth, age at maturity, size at maturity, diet, stock separation.

### INTRODUCTION

Knowledge of the distribution, integrity and separation of stocks is fundamental to effective long and short-term management (Pawson and Jennings 1996). There are many methods that have been used to attempt to separate marine fish stocks, including species distribution and abundance, tags (natural or artificial), morphometrics and meristics, calcified structures, genetics and life-history parameters (Japp 1990; Pawson and Jennings 1996; Griffiths 1997a).

Distribution patterns provide a broad ecological context for investigations into stock delineation of commercially important species. The distribution of carpenter, *Argyrozona argyrozona* is not well understood. Smith and Heemstra (1986) note that they occur from Cape Point to KwaZulu-Natal, and catches are also made in the commercial linefishery west to St Helena Bay (Spencer Jones 2002). Smale and Badenhorst (1991) note that they are caught over the entire Agulhas Bank from Cape Agulhas to Port Alfred to depths of 162 m. However, carpenter are not evenly distributed across the Bank and based on limited survey data (i.e. 5 surveys prior to this study), the South African carpenter population appears to have two distinct areas of abundance, one on the eastern and one on the central Agulhas Bank (Fig. 1) (Smale and Badenhorst 1991). A tagging study on the central Agulhas Bank (Griffiths and Wilke 2002) suggests that exchange between the central and eastern Agulhas Bank is limited.

Like most South African sparids (Buxton and Garratt 1990) carpenter are slow growing, long-lived (max. age = 30) and late to mature (100 % maturity = 15 years old) with a high degree of site fidelity (Griffiths and Wilke 2002; Brouwer *et al*. 2003; Brouwer and Griffiths 2004; Chapter3). These factors make this species vulnerable to over exploitation. The inshore carpenter population(s) of the eastern (Port Elizabeth and Port Alfred) and central Agulhas Bank have been heavily fished for more than a century. The offshore spawning grounds of the central Agulhas Bank became vulnerable to the fishery in the mid 1980’s through improvements in fishing vessels, freezing equipment, electronic navigation global positioning systems (GPS) and echo sounder technology (Griffiths 2000). This long history of intensive fishing has negatively affected the carpenter populations, which have shown substantial declines in catch rates (Hecht and Tilney 1989; Griffiths 2000; Brouwer and Buxton 2002) and fecundity-per-recruit (Chapter 7).

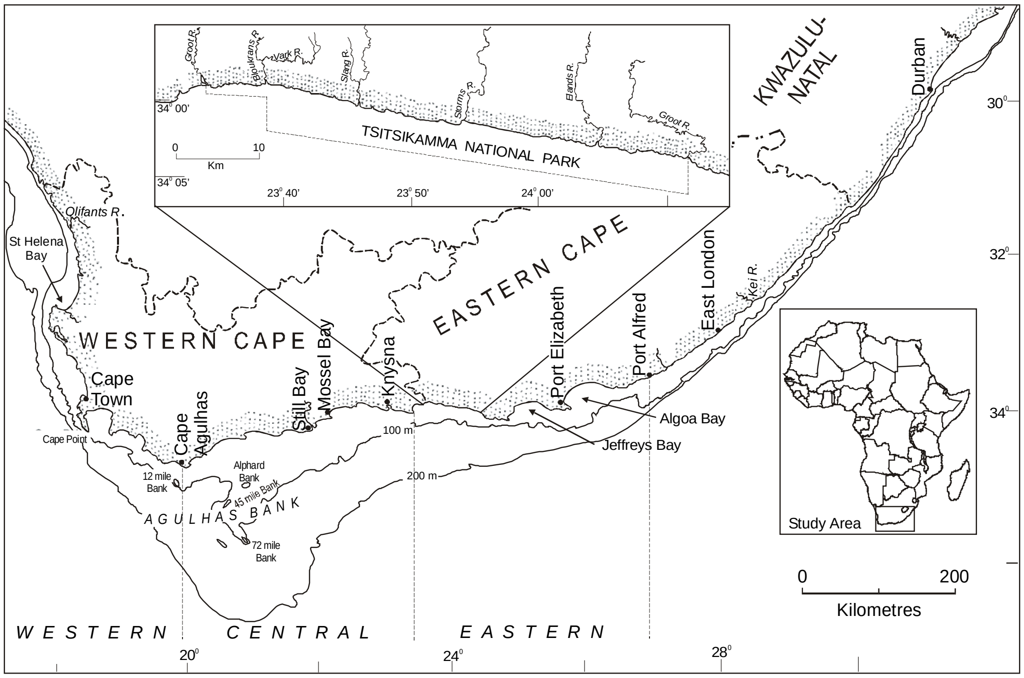

Figure 1: Map of the study area showing the regions of the Agulhas Bank and the Tsitsikamma National Park on the eastern seaboard of South Africa, the 100 m and 200 m isobaths, and places mentioned in the text.

Knowledge of life history is essential for successful stock identification and is necessary for the formulation of management strategies (Griffiths 1997a). Despite the economic importance of carpenter to fishing communities along the South African seaboard and the recorded declines in catch per unit effort (*cpue*) of > 95% (Griffiths 2000), very little is known about the life history of this species.

The objectives of this Chapter are:

1. To elucidate the spatial distribution patterns of both adult and juvenile carpenter over the Agulhas Bank.
2. To test the hypothesis of multiple stocks or management units using fishery dependent, fishery independent, mark recapture and biological data.
3. To provide information on the life history of carpenter, throughout its distribution range, necessary for management.

## MATERIAL AND METHODS

### Spatial patterns of abundance

Patterns of spatial distribution were investigated using catch returns from commercial linefishers and data collected by swept area demersal biomass surveys. To determine the biomass and distribution of commercially important trawl caught species, a series of cruises beginning in 1986 was conducted biannually by the department of Marine and Coastal Management (MCM) (Badenhorst and Smale 1991). The survey area is extensive (Fig. 2) and extends seawards to depths of 500 m. This area is divided into four depth zones (0-50, 51-100, 101-200 and 201-500), each of which is further divided into 5 x 5 mile blocks. Blocks are selected semi-randomly according to the ratio of blocks per stratum. A 180-foot German trawl is used with a 25 mm mesh liner attached to the cod end. Trawls are limited to 30 minutes. As part of the sampling procedure fish are identified, weighed and measured (see Badenhorst and Smale (1991) for details). Owing to some variation in trawl time, catch data were standardized to fish.trawl minute$^{-1}$. The data for carpenter were extracted from the trawl database at MCM and converted to geo-referenced *cpue* (number of fish.trawl minute$^{-1}$) data for three size classes (50-100, 101-200, 201+ mm TL). Distribution maps of *cpue* were obtained by means of Kriging (*SURFER*®; Golden Software, Inc., USA).

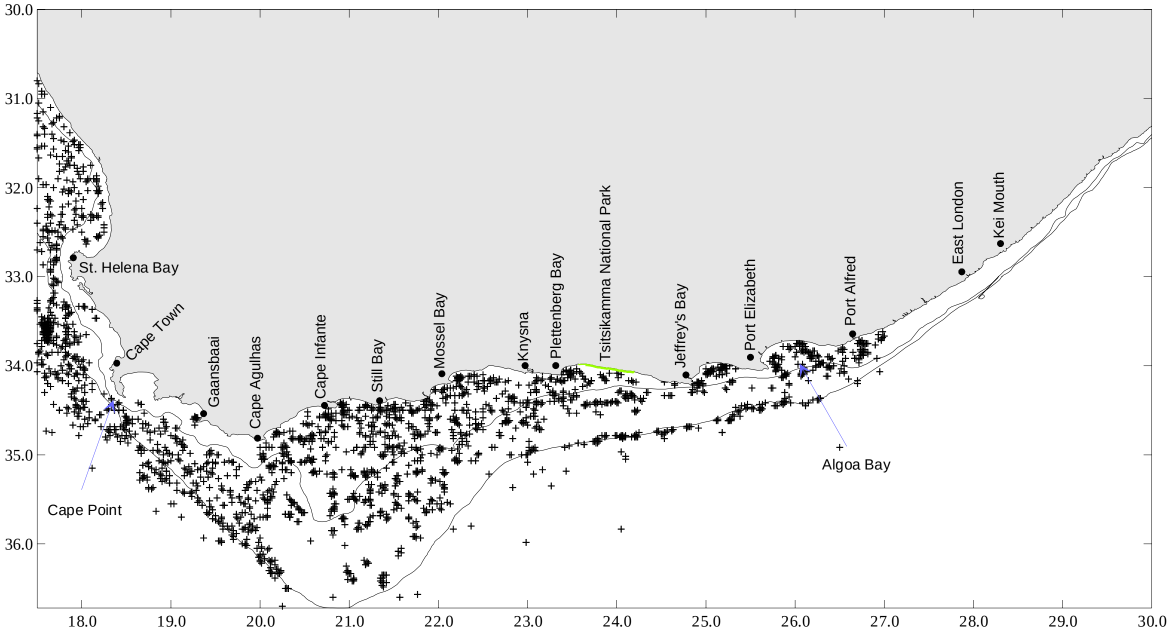

Figure 2: Map of South Africa showing the position of each trawl conducted by the *FRV Africana* (1986-2002), 100 m and 200 m depth contours and the places mentioned in the text.

The commercial linefish data were extracted from the National Marine Linefish System (NMLS) at MCM, which has recorded catch and effort in the linefishery since 1984. Each location along the South African coast is coded in 1 km intervals from east to west. Catch and effort data are linked to the closest location code. The coastline was divided into 40 areas of approximately equal distance (±75 km). Due to the varying widths of the continental shelf from west to east the locations were separated into offshore (>60 m depth) and inshore (< 60 m depth) sections and linked to the closest coastline location. Mean annual catch and effort values for each of the 40 areas were plotted on a linear representation of the coastline.

Carpenter, collected during research linefishing trips and at selected sites on the eastern and central Agulhas Bank (Fig. 3), were measured (mm fork length [FL]) and tagged on the left side with individually coded dart D-tag (Hallprint, Australia) and released.

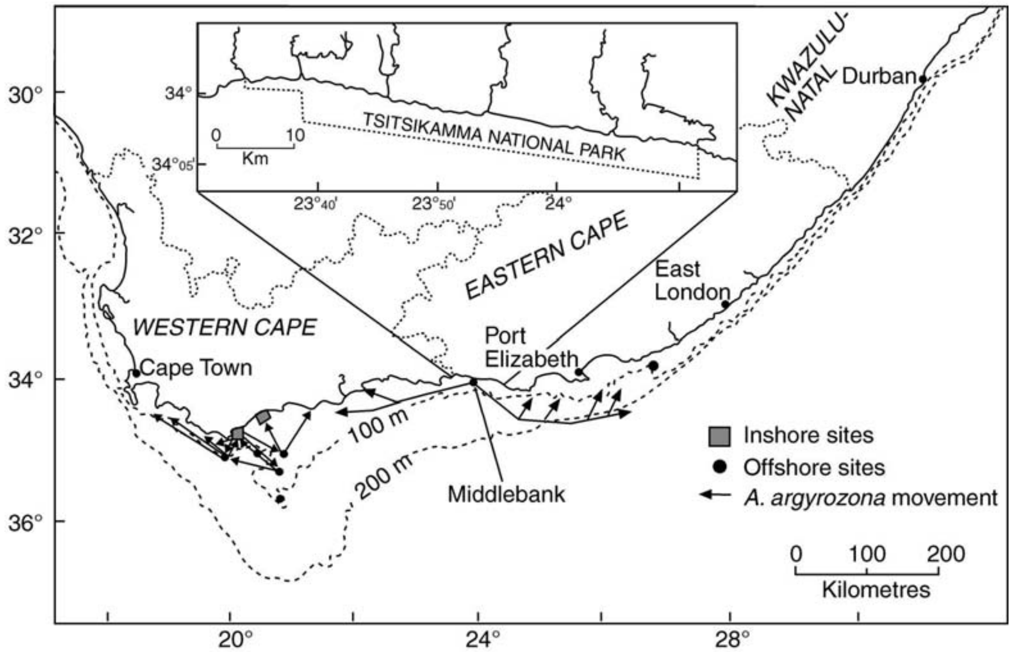

Figure 3: Map showing the tagging sites, and the shortest straight-line distance moved by *A. argyrozona* tagged and released (Modified from Griffiths and Wilke 2002; Chapter 5).

## Biological data

To assess regional variability in the biological parameters of carpenter four areas were compared: 1) the Tsitsikamma National Park (TNP), which is a Marine Protected Area (MPA) on the eastern Agulhas Bank that has been closed to exploitation since 1964; 2) the Eastern Cape between Port Alfred and Port Elizabeth, a heavily fished area on the eastern Agulhas Bank (Fig. 1); 3) the central Agulhas Bank which was divided into two areas separated by depth; the inshore area (<60 m depth) that has been heavily fished for over 100 years and; 4) the offshore area (>60 m depth), which has been exploited since the mid 1980's. The TNP was selected as it was hoped that this would allow carpenter to be studied in a pristine population, in order to accurately calculate natural mortality (*M*) and to permit the life history of the species to be assessed under conditions where fishing mortality was zero, as has been done was done for other sparids (Buxton 1993).

At each site fish were sampled, total and fork length (mm), whole mass and gutted mass (g) were measured; the fish were sexed and otoliths removed. Gonads were removed, weighed to within 0.1 g and assigned a visual index of maturity (Chapter 3). The gonads were preserved in neutrally buffered formalin for histological analysis as per Chapter 3. The otoliths were cleaned and stored dry in paper envelopes and prepared and aged as per Brouwer and Griffiths (2004). Stomach contents were identified to the lowest possible taxon and weighed to within 0.1 g.

A previous study of the reproductive biology of carpenter in the TNP (Chapter 3) revealed that they spawn from October to April. In order to compare the regional life history parameters, carpenter were simultaneously sampled during the spawning season (December – March of 1998 and 1999) across the Agulhas Bank from Port Alfred in the East to the 12-mile bank in the West (Fig. 1). Samples collected at Port Alfred and Port Elizabeth were pooled and are referred to as the Eastern Cape sample. The central Agulhas Bank data were separated by depth as above. It was assumed that during the spawning season fish condition would be similar and growth would be negligible, enabling valid comparisons to be made (Chapters 2, 3 and 5).

The size and age at maturity, spawning frequency, batch fecundity and annual fecundity by age class were calculated for each sampling area according to the methods described in Chapter 3. The 3-parameter von Bertalanffy growth model was fitted to the observed length-at-age data (Brouwer and Griffiths 2004) for each population, using an iterative non-linear minimisation routine (Microsoft EXCEL (Microsoft corp., 2000) SOLVER routine with Newton algorithm option), and the ogives were calculated as per Chapter 3. Within population male to female sex ratios were compared using a Chi-square test with Yates' correction factor applied.

The overall size frequency of the central Agulhas Bank population was estimated by weighting offshore and inshore samples according to the relative biomasses estimated during the fishery independent surveys. Raising factors (*RF*) for each area (*i*) were calculated as follows:

$$RF_i = \frac{\overline{B_i}}{tM_i}$$

where $\overline{B_i}$ is the mean biomass estimated from the demersal biomass surveys in area *i* (1990-1999) and $tM_i$ is the mass of fish measured during the demersal biomass surveys during that period in area *i*. Numbers measured in each size class, both inshore and offshore, were raised by area specific factors, which were then combined to produce an overall size frequency estimate for the central Agulhas Bank. Although the demersal biomass surveys miss a portion of the population that occurs over high profile reef, it is assumed that this bias is equal for the offshore and inshore areas and that demersal biomass surveys provide an index of relative abundance in each area.

Given that carpenter on the central Agulhas Bank move offshore as they mature, accurate size-at-maturity estimates could not be directly determined. Inshore and offshore proportions of mature fish in each 1 cm size class were therefore weighted according to the relative abundance in each of these areas. Mature fractions in each size class of the central Agulhas Bank population were calculated as follows:

$$Pmat_i = \frac{P_{iinshore} N_{iinshore} + P_{ioffshore} N_{ioffshore}}{N_{iinshore} + N_{ioffshore}}$$

where $Pmat_i$ is the proportion mature in size class $i$ in the population, $P_{iinshore}$ is the proportion mature inshore in size class $i$, $P_{ioffshore}$ is the proportion mature offshore in size class $i$, and $N_{iinshore}$ and $N_{ioffshore}$ are the relative number of fish in size class $i$ from the inshore and offshore areas respectively. The raised number of fish and the total number mature were then used to estimate the size at 50% maturity ($L_{50}$) according to the methods described in Chapter 3.

The von Bertalanffy parameters were compared using a likelihood ratio test to minimise the negative log-likelihood of the form (after Hilborne and Mangel 1997):

$$\lambda nL = \frac{n}{2} \times \lambda n\left(\frac{\sigma^2}{n}\right) + \frac{n}{2}$$

where $n$ is the number of samples and $\sigma^2$ is the variance. Ogives were compared using a likelihood ratio test, which minimises the negative log likelihood as per Chapter 3.

Indices of relative reproductive output (*RRO*) were calculated for each area using the trawl and linefishery data separately as follows:

$$RRO = Fb \times B$$

$$Fb = \sum_{i=1}^{n} Fa_i \times p_i$$

where $B$ is a biomass index, $Fb$ is the reproductive potential, $Fa_i$ is annual fecundity at age $i$ and $p_i$ is the proportion of fish in age class $i$ determined from the length frequency distribution in each area.

$B$ for the trawl data was calculated as follows

$$B = \overline{d_i} \times A_i$$

$$\overline{d_i} = \frac{\sum_{j=1}^{n_i} d_{ij}}{n_i}$$

where $\overline{d_i}$ is the mean density (t) in stratum $i$, $A_i$ is the area ($nm^2$) of stratum $i$, $d_{ij}$ is the density of carpenter (t) in trawl $j$ in stratum $i$ and $n_i$ is the number of trawls in stratum $i$. $B$ for the line data was simply expressed as:

$$B = cpue_i \times A_i$$

where $cpue_i$ is the average *cpue* (kg.fisher.$^{-1}$day$^{-1}$) in stratum $i$.

The *RRO* for each area was then expressed as a percentage of the total *RRO* for all areas, this was done for the trawl and line data separately.

The relationship between fork length and mass (minus gonad and stomach mass) was determined for carpenter at each of the sample sites, the data were log transformed for linearity and the slopes and intercepts were tested for significant differences (Zar 1999).

## RESULTS

### Spatial patterns of abundance

Although carpenter occur from St. Helena Bay to KwaZulu-Natal they are available in commercially exploitable densities mainly between Cape Agulhas and East London (Fig. 4). Both the commercial linefishery and fishery independent trawl data show that the carpenter population is unevenly distributed across the Agulhas Bank with two areas of abundance, one on the eastern Agulhas Bank between Port Elizabeth and Port Alfred and the other on the central Agulhas Bank (Fig. 4 & 5). Early juveniles (50-100 mm TL), although caught in low numbers (0.27 fish.minute$^{-1}$), are found predominantly in Algoa Bay and on the Alphard Banks off Cape Infanta on the central Agulhas Bank (Fig. 6a). Juvenile fish in the 101-200 mm TL size class are most abundant in the inshore waters from Algoa Bay to Plettenberg Bay in the east and in the inshore areas at Cape Agulhas in the west (Fig. 6b). All size classes > 200 mm TL showed similar distribution patterns, enabling the data to be pooled. Fish in this size class were most abundant offshore on the central Agulhas Bank, and between Algoa Bay and Port Alfred on the eastern Agulhas Bank (Fig. 6c). Length frequency distributions of line caught fish show that on the central Agulhas Bank smaller fish (<200 mm FL) live in shallower water than the larger individuals (Fig. 7).

In all, 2 338 carpenter were tagged in the TNP, 401 and 2496 in the inshore and offshore Agulhas Bank respectively and 11 at Port Alfred. Of these, 316 were recaptured, 114 (5%) from the TNP, 44 (11%) inshore Agulhas Bank and 158 (6%) offshore Agulhas Bank. Carpenter were found to be largely resident: 90%, 68% and 84% being recaptured at the site of release from the TNP, inshore Agulhas Bank and offshore Agulhas Bank, respectively. Of those tagged in the TNP 7.1 % were caught outside the reserve (Fig. 3). The eight fish recaptured outside travelled distances of between 36 and 290 km, in an easterly (75%) and westerly (25%) direction (Fig. 3). No carpenter tagged on the central Agulhas Bank were recaptured east of Still Bay and none tagged in the TNP or at Port Alfred were caught west of Still Bay (Fig. 3).

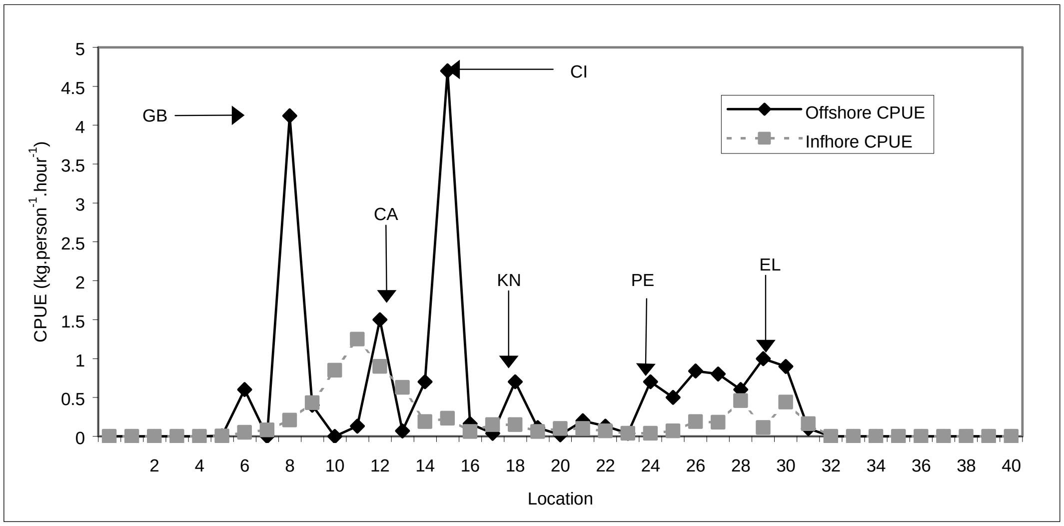

Figure 4: Catch per unit effort of *A. argyrozona* landed by the linefishery in each port throughout the distribution range of *A. argyrozona*. GB = Gaansbaai, CA = Cape Agulhas, CI = Cape Infanta, KN = Knysna, PE = Port Elizabeth, EL = East London.

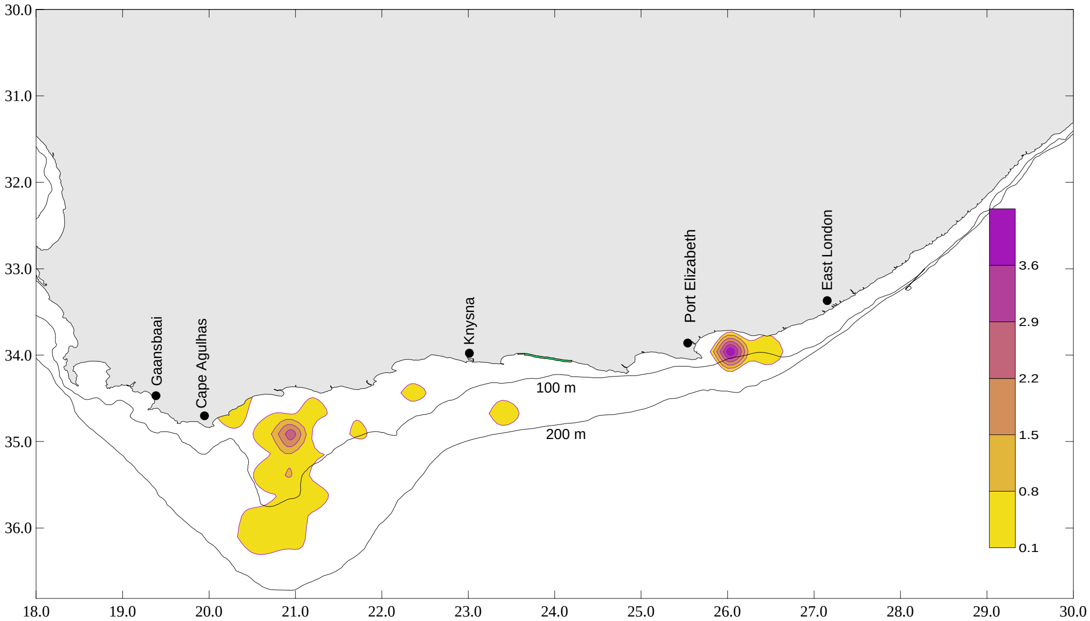

Figure 5: Distribution of all size classes of *A. argyrozona* determined from *cpue* (fish. trawl minute$^{-1}$) from demersal biomass surveys.

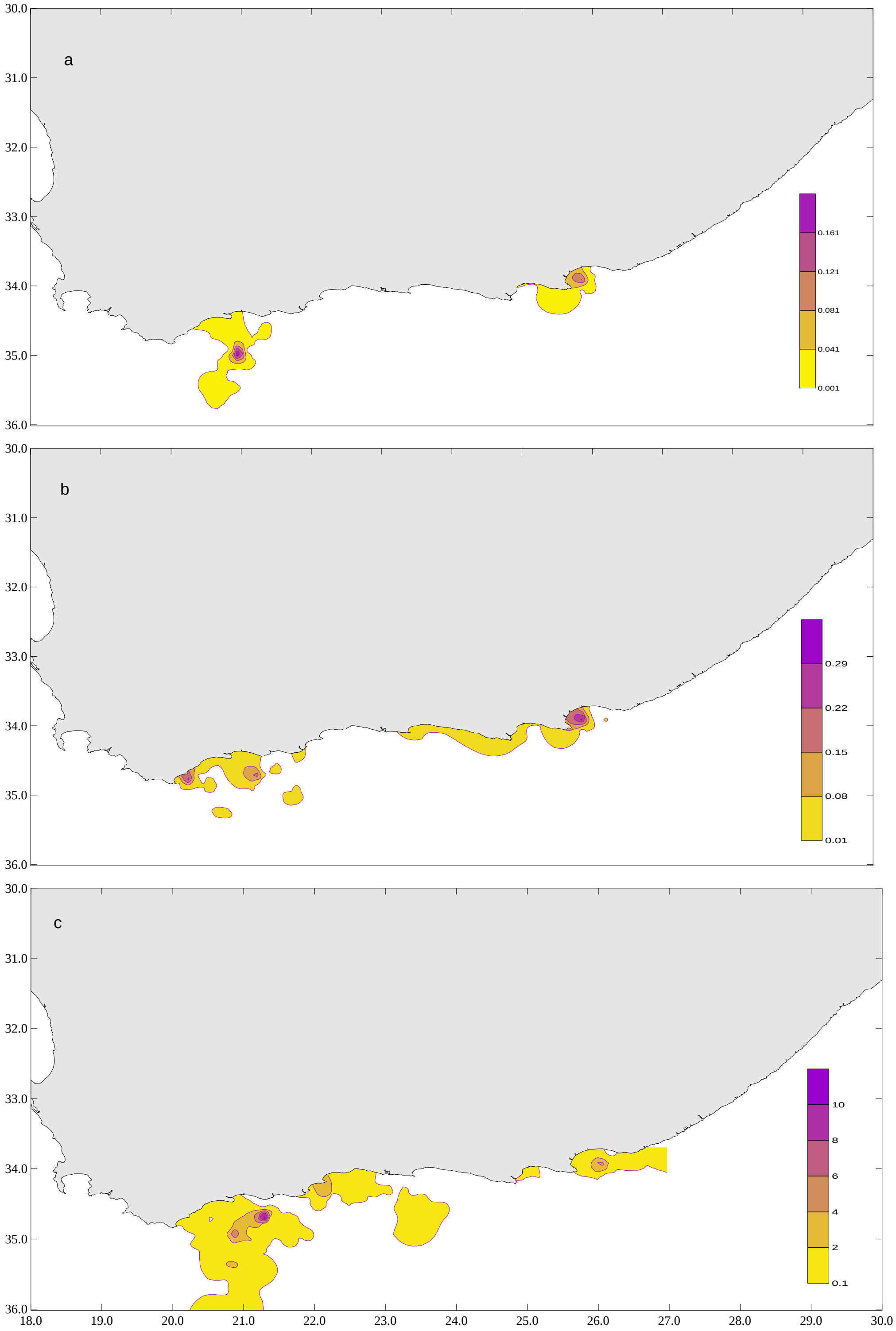

Figure 6: Distribution of a) 50-100 mm TL, b) 101-200 mm TL and c) 200+ mm TL *A. argyrozona* based on *cpue* (fish. trawl minute$^{-1}$) from demersal biomass surveys.

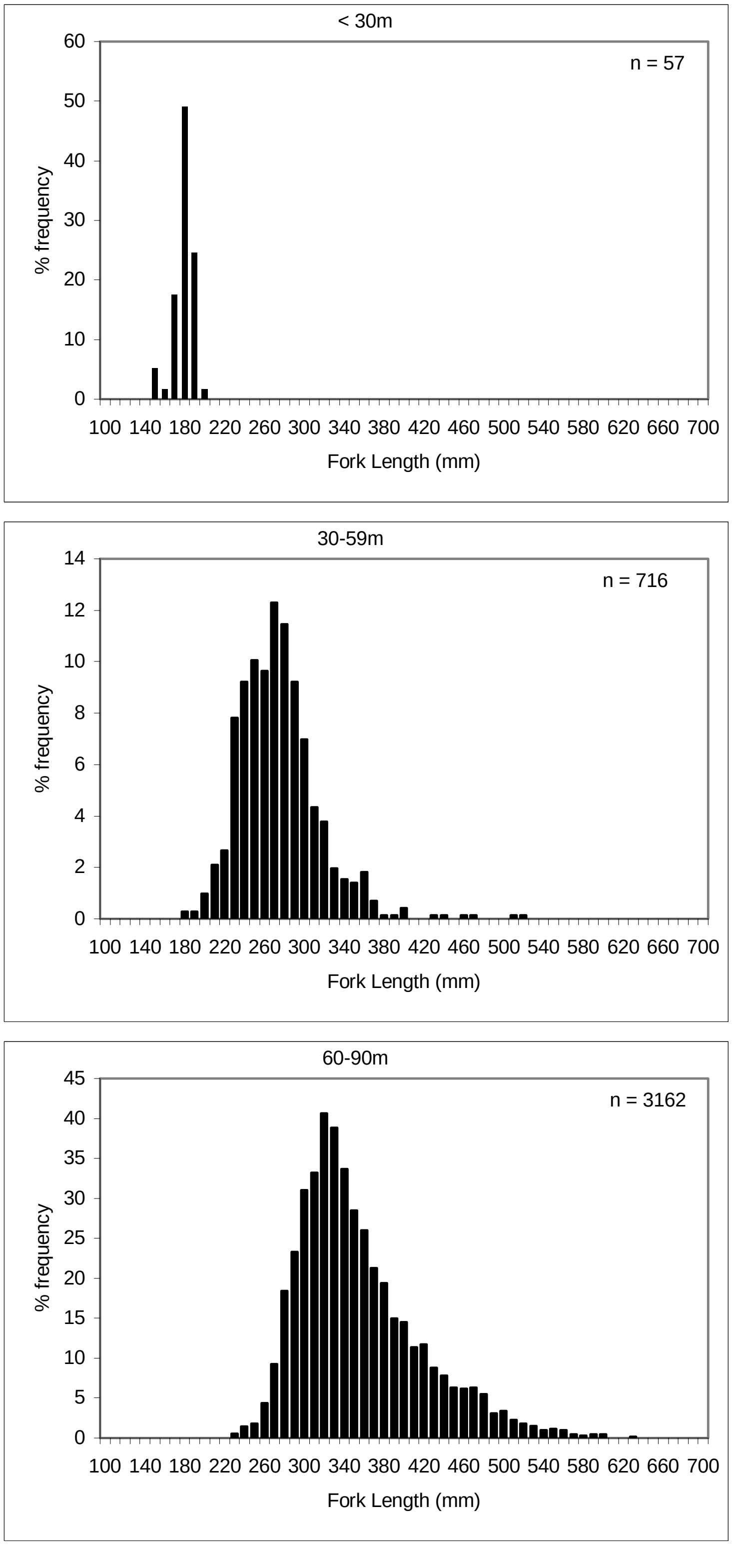

Figure 7: Length distribution for *A. argyrozona* caught by hook and line on the central Agulhas Bank (1997-1999) at different depths (Griffiths and Wilke 2002).

**Biological data**

Otolith readability varied across the Agulhas Bank with average percentage error (APE), coefficient of variation (CV) and index of precision (D) being lowest in the east and highest in the west (Table I). The growth curve was steepest (Fig. 8) and $L_\infty$ highest in the TNP. $L_\infty$ was lowest in the Eastern Cape (Table II). Likelihood ratio tests revealed that overall differences in growth curves were highly significant in terms of $L_\infty$ (p=0.05), *k* (p=0.01) and $t_0$ (p<0.001) (Table II).

Table I: Regional variation in the readability of the otoliths, mean age and length for *A. argyrozona*. APE = Average Percentage Error, CV = Coefficient of variation and D = Index of Precision.

| Area | APE | CV | D | Mean age | Mean length |
|---|---|---|---|---|---|
| Eastern Cape | 4.82 | 6.34 | 3.66 | 7.4 (±4.15) | 314 (±67.4) |
| TNP | 5.33 | 7.90 | 4.56 | 9.5 (±2.8) | 382 (±59) |
| Agulhas Bank | 7.03 | 10.06 | 5.81 | 7.5 (±3.9) | 324 (±72.4) |

In the TNP female carpenter $L_{50}$ was estimated at 5 years and 297 mm FL, in the Eastern Cape $L_{50}$ is reached at 206 mm FL and at 2 years old. For the inshore and offshore central Agulhas Bank respectively (Table III) female $L_{50}$ was estimated at 272 mm FL (5 years old) and at 235 mm FL (3 years old). The combined central Agulhas Bank $L_{50}$ was 267 mm FL (4 years old) (Fig. 9). The proportions of mature female fish in spawning condition (stage 5 and 6) were: 54% in the Eastern Cape, 77% in the TNP, 64% in the inshore Agulhas Bank and 81% in the offshore Agulhas Bank (Fig. 10). Spawning seasonality was similar for all areas, but spawning on the central Agulhas Bank appeared to start one month later than the eastern Agulhas Bank (October *v.* November) and was extended into May (Fig. 11) with the result that the spawning seasons were of a similar length. The batch fecundity at size (Table IV) showed no significant difference between regions and spawning frequency was similar at 2.9, 2.2 and 2.3 days for the Agulhas Bank, TNP and Eastern Cape respectively. Size specific annual fecundity was therefore similar in all areas. However, the size structure of the populations (Fig. 12) (Table V & VI) with more large fish present in the offshore Agulhas Bank, combined with the large size of this area, indicates that the offshore central Agulhas Bank has more reproductive potential than the eastern Agulhas Bank and inshore central Agulhas Bank. Both the trawl and line data provided similar estimates of relative reproductive output (Table VII). The offshore central Agulhas Bank accounts for most (88-93%) of the relative reproductive output or egg production (Table VII). The eastern Agulhas Bank accounts for only 6.4% of the egg production, but 29-37% of this comes from the TNP.

Table II: Regional variation in the von Bertalanffy growth parameters for *A. argyrozona* and the results of a likelihood ratio test to determine where significant differences occur, - = no significant difference, * = $p<0.05$, ** = $p<0.01$, *** = $p<0.0001$.

| Area | $k$ | $L_\infty$ | $t_o$ |
|---|---|---|---|
| Eastern Cape | 0.08 | 524 | -3.9 |
| TNP | 0.06 | 684 | -3.6 |
| Agulhas Bank | 0.06 | 619 | -4.5 |
| ***k*** | | | |
| | TNP | Agulhas Bank | Eastern Cape |
| TNP | - | - | * |
| Agulhas Bank | - | - | ** |
| Eastern Cape | * | ** | - |
| **$L_\infty$** | | | |
| | TNP | Agulhas Bank | Eastern Cape |
| TNP | - | * | - |
| Agulhas Bank | * | - | *** |
| Eastern Cape | - | *** | - |
| **$t_o$** | | | |
| | TNP | Agulhas Bank | Eastern Cape |
| TNP | - | - | *** |
| Agulhas Bank | - | - | *** |
| Eastern Cape | *** | *** | - |

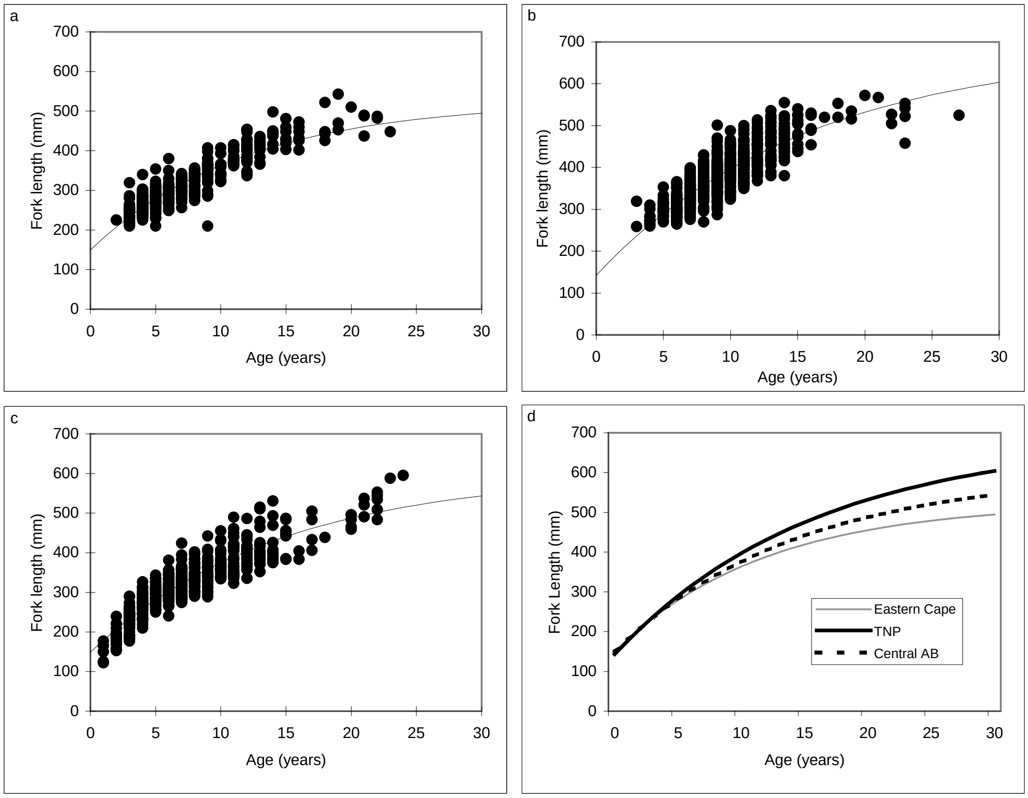

Figure 8: The observed length-at-age data of *A. argyrozona* from a) the Eastern Cape, b) the TNP, c) the central Agulhas Bank and d) the special von Bertalanffy growth model fitted to the observed data from each region.

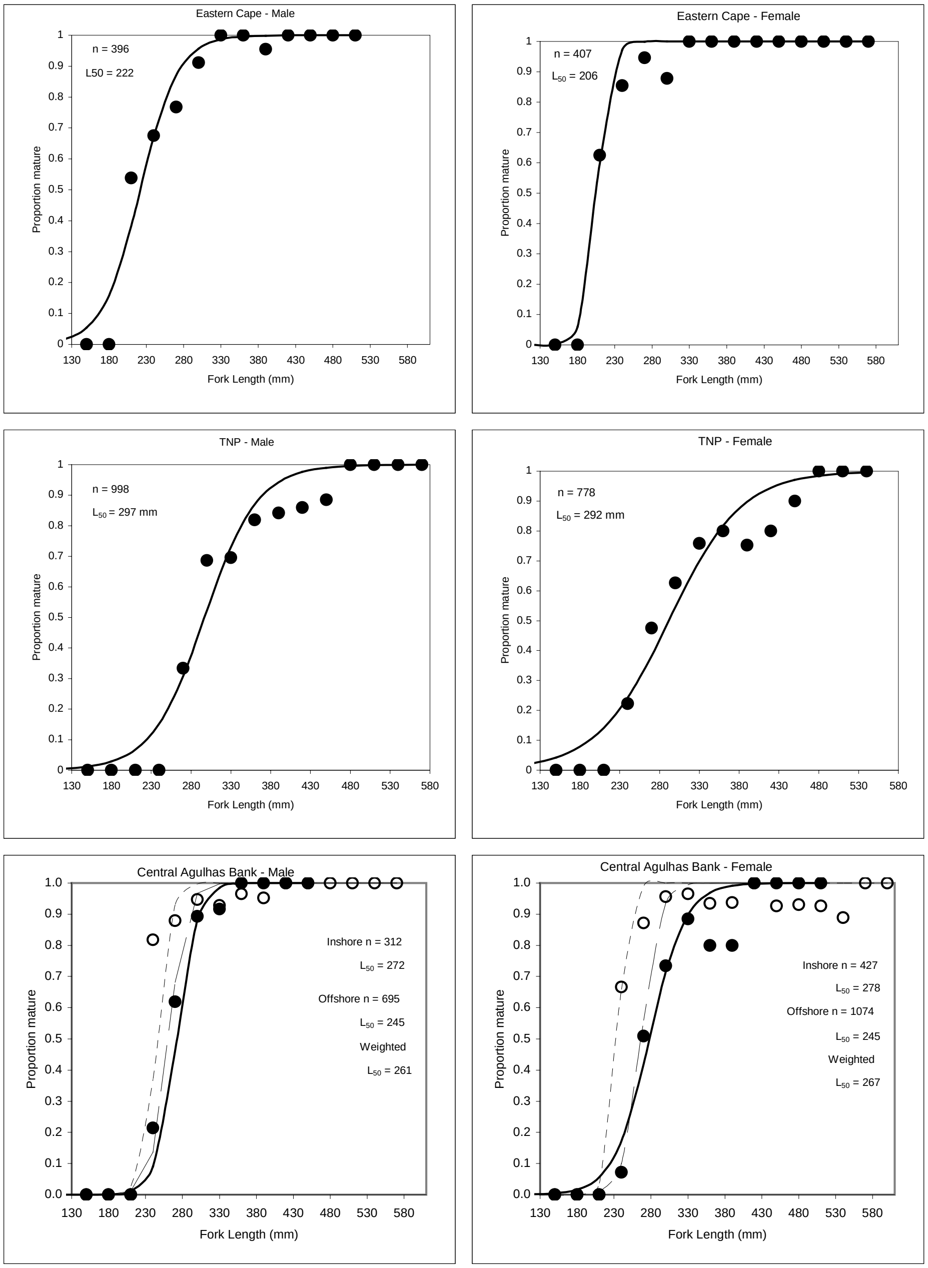

Figure 9: The proportion of mature *A. argyrozona* in the different length classes sampled in the various locations. The curves were fitted using a 2-parameter logistic ogive. The inshore areas of the central Agulhas Bank are represented by closed circles ( • ) and solid line (–), the offshore areas are represented by open circles (o) and a broken line (---). The long dashed line (—) represents the pooled and weighted central Agulhas Bank estimates.

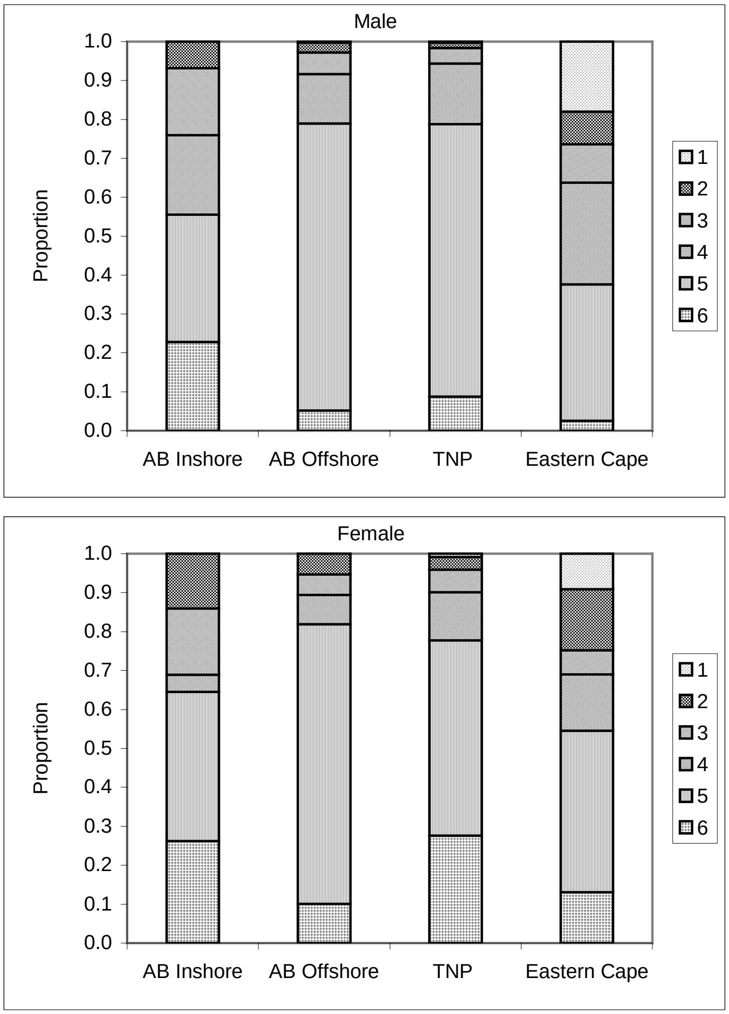

Figure 10: Maturity stages of *A. argyrozona* >$L_{50}$ sampled in the major sampling regions during the spawning season (November - April). 1 = Juvenile, 2 = Immature, 3 = Resting, 4 = Developing, 5 = Ripe and 6 = Ripe running. AB = Agulhas Bank.

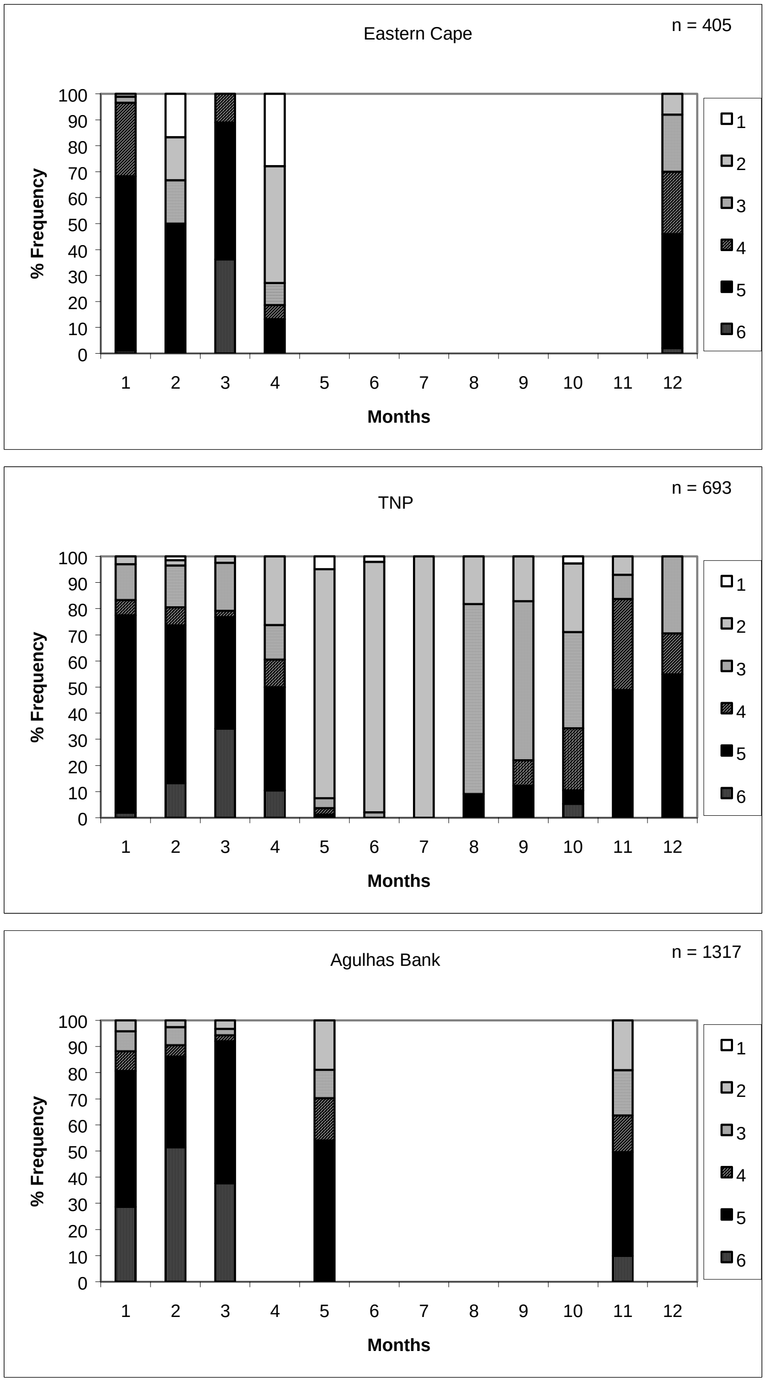

Figure 11: Monthly macroscopic stages for female gonads of *A. argyrozona* $>L_{50}$ from the Eastern Cape, TNP and Agulhas Bank. 1 = Juvenile, 2 = Immature, 3 = Resting, 4 = Developing, 5= Ripe and 6 = Ripe running.

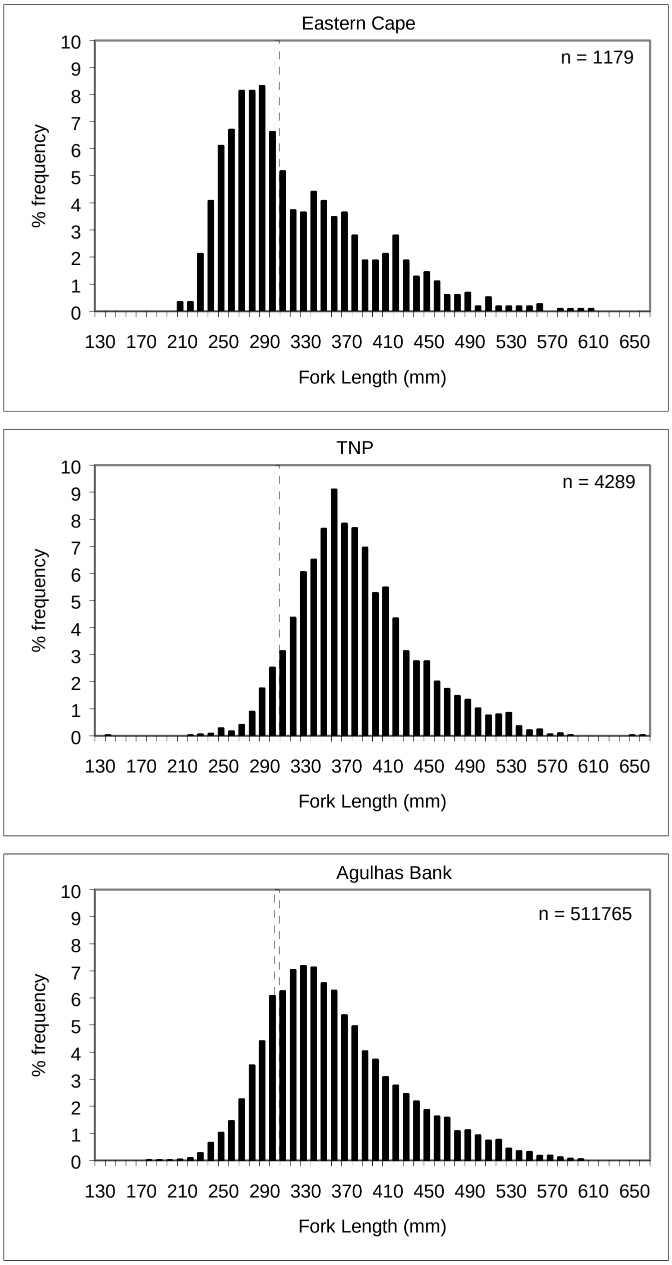

Figure 12: Length frequencies of *A. argyrozona* sampled in the various regions of the South African seaboard (Agulhas Bank = offshore and inshore areas combined), showing the size distribution and the proposed size limit ($l_c$) (---) (300 mm FL).

In all regions the sex ratio varied between size classes (Table VIII). The central Agulhas Bank population, both inshore and offshore, had a slight female bias in all size classes, the Eastern Cape population had a female bias in the small (<300 mm FL) and large (500+ mm FL) size class and the TNP population had a male bias in all size classes >300 mm FL.

Table III: Regional variation in the size and age at 50 % maturity of *A. argyrozona* sampled across the Agulhas Bank during the spawning season. $L_{50}$ = size (mm) at 50 % maturity $t_{50}$ = age (years) at $L_{50}$.

| Area | Sex | $L_{50}$ | $t_{50}$ | % Immature |
|---|---|---|---|---|
| Eastern Cape | Male | 222 | 2 | 22 |
| | Female | 206 | 2 | 24 |
| TNP | Male | 297 | 5 | 13 |
| | Female | 292 | 5 | 7 |
| Agulhas Bank – inshore | Male | 272 | 5 | 55 |
| | Female | 278 | 5 | 63 |
| Agulhas Bank – offshore | Male | 245 | 4 | 6 |
| | Female | 235 | 3 | 6 |
| Agulhas Bank pooled data | Male | 261 | 4 | - |
| | Female | 267 | 4 | - |

Comparison of mass at length during the spawning season revealed that male carpenter were significantly heavier at length than females ($p<0.05$), and that the central Agulhas Bank, TNP and Eastern Cape all had significantly different mass at length (Table IX), with fish in the TNP being heaviest (Fig. 13).

Carpenter are pelagic predators feeding on a wide variety of species, but diet varied between the populations on the central and eastern Agulhas Bank (Fig. 14 and 15). Fish on the eastern Agulhas Bank (TNP and Eastern Cape combined) utilised a wide variety of species in the diet, particularly teleosts, but diet changed with fish size. Fish below 280 mm FL fed primarily on small pelagic teleosts and numerous other small species such as *Sepia* spp. and euphausids. Medium sized fish fed mostly on teleosts, *Sepia* spp. and mycids. Those in the largest size class (355 + mm FL) fed mostly on pelagic teleosts. The central Agulhas Bank population fed primarily on *Pyrosoma* spp. a pelagic colonial ascidian and pelagic teleosts, but diet varied inshore and offshore. The inshore populations utilised a wide variety of pelagic teleosts (Fig. 15). In the offshore regions diet was dominated by *Pyrosoma* spp. (Fig 15).

## DISCUSSION

### Stock differentiation

Despite the limitations of the trawl surveys, the data does reveal two separate areas of abundance, one on the eastern Agulhas Bank and the other on the western Agulhas Bank. This is corroborated by commercial linefish catches, where geographically related *cpue* trends consist of two modal groups, as well as the tagging studies that show little movement between the western and eastern Agulhas Bank. More importantly the data revealed that Algoa Bay and the inshore areas off Cape Agulhas are nursery areas for this species. Although no research trawl data are available for areas north east of Port Alfred, catches of carpenter from the linefishery north east of East London were low and contributed little to catches (Brouwer 1997; Fennessy *et al*. 2003). It is therefore assumed that the bulk of the stock lies on the Agulhas Bank and that there are two distinct management units (stocks).

Table IV: Comparison of mean batch fecundity at size (±SD) from the various regions and from an independent study on *A. argyrozona* artificially induced to spawn conducted in the TNP by Davis 1996.

| FL (mm) | TNP | Agulhas Bank | Eastern Cape | Davis (1996) |
|---|---|---|---|---|
| 260 | | 5963 (±1291) | | |
| 270 | 8040 | 7692 (±3404) | | |
| 280 | | 12573 (±4776) | | |
| 290 | 10260 (±4284) | 12668 (±3940) | 17888 | |
| 300 | 14040 (±3931) | 13916 (±6260) | | |
| 310 | 17105 (±9072) | 15550 (±5778) | 15093 (±8696) | |
| 320 | 15878 (±5729) | 17540 (±6365) | 19751 (±2327) | |
| 330 | 19100 (±7945) | 19920 (±6365) | 16770 (±3764) | |
| 340 | 23415 (±7102) | 22199 (±6823) | 22653 (±254) | |
| 350 | 21725 (±10257) | 28277 (±8989) | 26800 (±3450) | |
| 360 | 23940 (±7731) | 30823 (±10413) | 27200 (±3020) | |
| 370 | 28166 (±11534) | 354613 (±11638) | 22800 | 34983 (±27558) |
| 380 | 29760 (±9172) | 43269 (±11618) | 28400 (±8845) | 44383 (±18975) |
| 390 | 37066 (±10777) | 45623 (±16151) | 30300 (±3965) | |
| 400 | 44854 (±29804) | 49786 (±18614) | | |
| 410 | 43532 (±14021) | 45213 (±12498) | 42600 (±849) | 37000 (±18385) |
| 420 | 38547 (±12005) | 57640 (±10363) | 51000 (±7637) | |
| 430 | 45140 (±12174) | 62706 (±14012) | 52400 (±14316) | |
| 440 | 70860 (±17779) | 64460 (±19379) | 67200 | |
| 450 | 70955 (±21772) | 65651 (±19417) | | |
| 460 | 56028 (±9410) | 87497 (±21292) | | |
| 470 | 72660 (±25507) | 90564 (±2464) | | |
| 480 | 79950 (±31055) | 117150 (±22984) | | |
| 490 | 66394 (±20851) | 101333 (±49605) | | |
| 500 | 58440 (±7976) | 124560 (±36144) | | 89317 (±94304) |
| 510 | 90024 (±20453) | 115423 (±20815) | | |
| 520 | 83606 (±17865) | 126240 (±39821) | | |
| 530 | 78600 | 156000 | | |
| 540 | 116400 (±36826) | 128580 (±8231) | | |
| 550 | 226800 | 183600 (±106915) | | |
| 560 | 116400 | 152200 (±37722) | | |
| 570 | | 196800 | | |
| 580 | | 148800 | | |
| 600 | | 166890 (±26537) | | |

Table V: Comparison of the length-at-age between the inshore and offshore central Agulhas Bank population. Values in parentheses refer to n ±SD. Significant differences are indicated as follows * = p<0.1, ** = p<0.01, *** = p<0.001.

| Age | Inshore | Offshore |
|---|---|---|
| 1 | 148 (5±24.18) | |
| 2 | 186 (23±19.82) | |
| 3 | 233 (62±27.22) | |
| 4 | 275 (59±28.75) | 284 (2±5.66) |
| 5 | 292 (57±23.54) | 302 (22±16) ** |
| 6 | 312 (44±24.29) | 302 (55±24.71) * |
| 7 | 323 (37±30.32) | 315 (62±27.63) |
| 8 | 333 (18±33.13) | 336 (38±25.66) |
| 9 | 372 (8±43.56) | 340 (33±29.89)* |
| 10 | 381 (13±45.04) | 373 (13±26.34) |
| 11 | 392 (6±53.32) | 387 (23±43.86) |
| 12 | 371 (2±19.09) | 399 (20±33.28) |
| 13 | 420 (3±84.63) | 407 (16±37.04) |
| 14 | 407 (1) | 419 (12±51) |
| 15 | 455 (2±3.54) | 449 (10±46.55) |
| 16 | | 415 (3±39.25) |
| 17 | 445 (1) | 487 (6±58.55) |
| 18 | | 437 (2±2.83) |
| 19 | | 469 (1) |
| 20 | | 482 (3±15.63) |
| 21 | | 516 (3±23.35) |
| 22 | | 525 (5±28.74) |
| 23 | | 588 (1) |
| 24 | | 573 (2±31.82) |

Carpenter of the smallest size class (50 –100 mm TL) were found in two discrete areas, with highest densities in Algoa Bay and further offshore on the central Agulhas Bank, particularly around the Alphard Bank. This suggests that juvenile carpenter settle and spend their first few months in these areas. Juvenile carpenter on the central Agulhas Bank appear to move inshore towards Cape Agulhas as they grow. In Algoa Bay, however, juveniles seem to move coastwise with growth, expanding the distribution of 101-200 mm TL juveniles westwards.

These results therefore indicate that there are two primary nursery grounds for carpenter, supporting the two stock hypothesis. These data are supported by an inshore trawl survey conducted in 1980 that sampled the inshore bays between Mossel Bay and Algoa Bay (Wallace *et al*. 1984, Buxton *et al*. 1984), which recorded carpenter of 97-107 mm TL only in Algoa Bay and Jeffrey's Bay in shallow waters (<30 m). In both areas the large individuals (200+ mm TL) then appear to move offshore with growth. These data are supported by observations that no carpenter below 200 mm FL were sampled in the TNP (Fig. 8), suggesting that they move in from the east. Size at age comparisons revealed that the movement patterns in this area are size based, as TNP fish have a greater length at age than those further to the east (Table VI). Recruitment of newly settled juveniles to both nursery areas is affected by different physical forces. On the eastern Agulhas Bank, eggs and larvae are exposed to very strong currents that transport them towards Algoa Bay (Brouwer *et al*. 2003). The situation on the central Agulhas Bank is more complex and not easy to explain. Boyd and Shillington (1994) suggested that, in summer, both surface and bottom currents around the 45 and 72 mile banks are weak, but could result in some inshore flow towards the Alphard Bank area, a suggestion supported by Huggett *et al.* (2003).

Table VI: Comparison of the length-at-age between the eastern Agulhas Bank population. Values in parentheses refer to n ±SD. Significant differences are indicated as follows * = p<0.1, ** = p<0.01, *** = p<0.001.

| Age | TNP | Eastern Cape |
|---|---|---|
| 1 | | |
| 2 | | 225 (1) |
| 3 | 289 (3±42.43) | 246 (37±21.56) |
| 4 | 280 (9±16.34) | 264 (168±17.87)*** |
| 5 | 303 (23±19.10) | 276 (122±22.39) *** |
| 6 | 309 (45±24.61) | 290 (88±23.95) *** |
| 7 | 334 (92±27.44) | 305 (51±22.96) *** |
| 8 | 357 (118±27.30) | 324 (51±31.38) *** |
| 9 | 375 (141±32.45) | 340 (54±33.22) ** |
| 10 | 400 (115±30.36) | 350 (29±30.96) *** |
| 11 | 409 (85±34.03) | 377 (23±22.41) ** |
| 12 | 432 (61±36.13) | 401 (33±33.85) |
| 13 | 458 (35±38.69) | 407 (23±21.36) *** |
| 14 | 467 (24±38.70) | 429 (12±29.30) * |
| 15 | 491 (11±34.82) | 442 (9±24.29) *** |
| 16 | 497 (6±27.70) | 438 (7±23.75) *** |
| 17 | 520 (1) | 461 (3±44.77) |
| 18 | 537 (2±23.33) | 456 (6±33.48) |
| 19 | 526 (2±13.44) | 485 (4±39.82) |
| 20 | 572 (1) | 510 (1) |
| 21 | 567 (1) | 501 (6±38.90) |
| 22 | 516 (2±15.56) | 504 (6±42.98) |
| 23 | 519 (4±42.48) | 502 (2±76.37) |
| 24 | | 496 (1) |
| 25 | | 587 (1) |
| 26 | | |
| 27 | 525 (1) | 606 (1) |

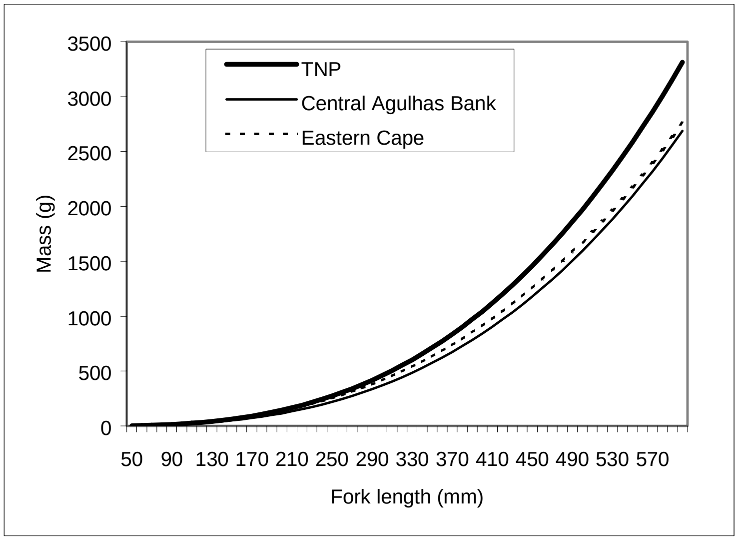

Figure 13: Mass at length of *A. argyrozona* sampled at various locations on the Agulhas Bank South Africa.

Depth related length frequencies and demersal biomass survey distributions show that carpenter of the larger size classes move offshore towards the 100 m depth contour as they grow. However, due to the narrow continental shelf in the eastern Agulhas Bank the fish move offshore and long-shore mostly (71%) in an easterly direction back towards Algoa Bay. Given that they congregate around rocky reef areas, trawling can miss areas of greatest density. As Smale and Badenhorst (1991) note, carpenter are most abundant in trawl catches when the nets were torn by rock or contained sponges and soft corals. However, it should be noted that high profile reefs at the 72 mile and 45 mile banks are areas where large (> 350 mm) carpenter shoal, and as a result these are under represented in the trawl catch. Small juveniles (<100 mm) do not shoal and are not found on high profile reefs (C. G. Wilke, during diving observations in nursery areas, MCM inshore resources, pers. comm.) with the result that their distribution patterns are probably more accurately depicted by the trawl catch.

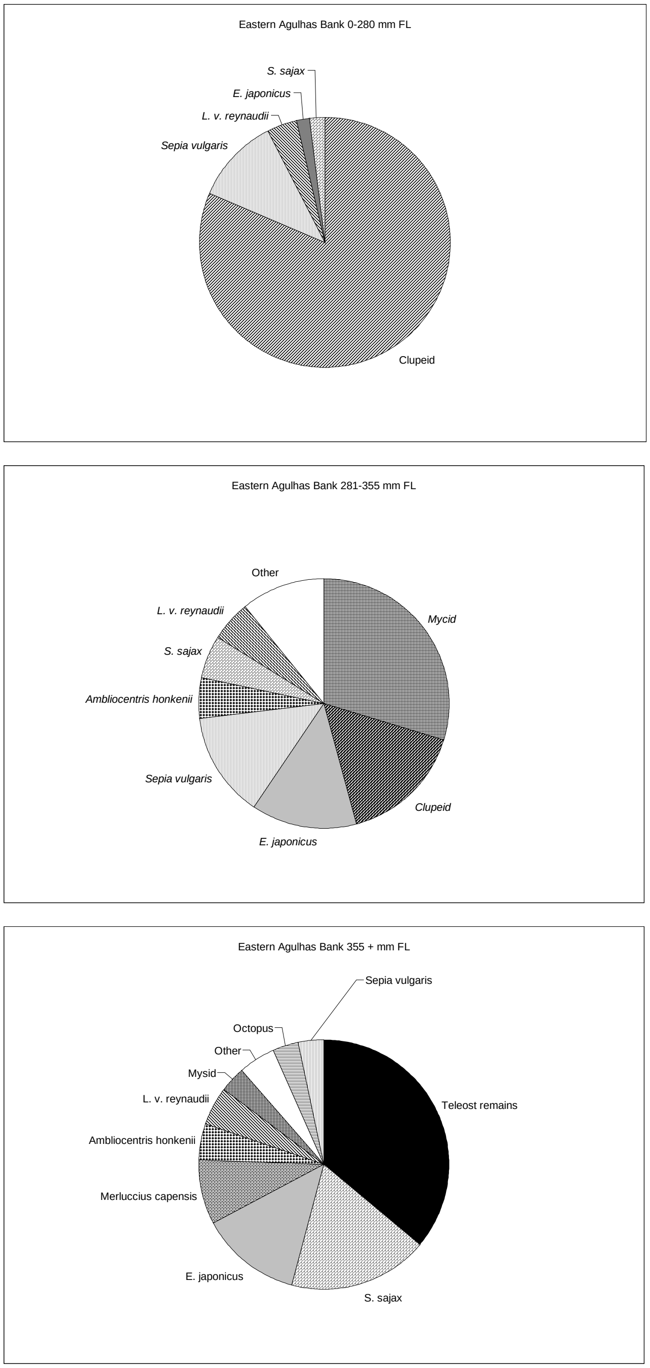

Figure 14: Variation in the diet (% mass) of *A. argyrozona* sampled on the eastern Agulhas Bank. Eastern Agulhas Bank refers to the combined data from the TNP and the Eastern Cape samples.

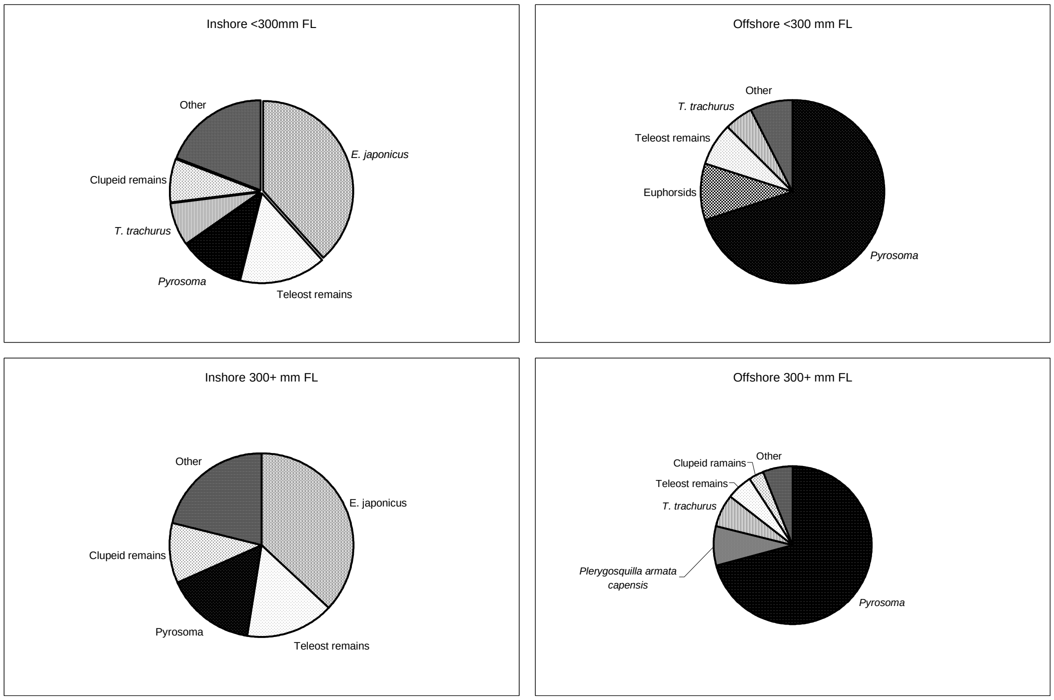

Figure 15: Stomach contents (% mass) of *A. argyrozona* sampled from the central Agulhas Bank.

Table VII: Percentage relative reproductive output of *A. argyrozona* estimated from swept area trawl and from *cpue* line data for the Agulhas Bank.

| Area | Trawl estimates | Line estimates |
|---|---|---|
| Inshore Agulhas Bank | 0.5% | 0.2% |
| Offshore Agulhas Bank | 87.5% | 93.4% |
| TNP | 3.5% | 2.4% |
| Eastern Cape | 8.8% | 4% |

Table VIII: Sex ratios of *A. argyrozona* from the four regions sampled along the South African coast. * = significant difference at <0.05

| Length (mm FL) | F:M | n | $\chi^2$ |
|---|---|---|---|
| TNP | | | |
| 200-299 | 1:0.96 | 96 | 0.05 |
| 300-399 | 1:1.32 * | 1033 | 19.80 |
| 400-499 | 1:1.31 * | 564 | 10.24 |
| 500+ | 1:1.08 | 83 | 0.12 |
| All | 1:1.25 * | 1797 | 22.9 |
| Eastern Cape | | | |
| 200-299 | 1:0.91 | 499 | 1.06 |
| 300-399 | 1:1.27 * | 1293 | 18.11 |
| 400-499 | 1:1.30 * | 687 | 11.53 |
| 500+ | 1:0.58 * | 87 | 6.09 |
| All | 1:0.98 | 878 | 0.07 |
| Inshore Agulhas Bank | | | |
| 200-299 | 1:0.85 | 433 | 2.83 |
| 300-399 | 1:0.61 * | 193 | 11.45 |
| 400+ | 1:0.50 | 6 | 0.67 |
| All | 1:0.73 | 739 | 17.89 |
| Offshore Agulhas Bank | | | |
| 200-299 | 1:0.78 | 233 | 3.61 |
| 300-399 | 1:0.65 * | 1193 | 52.81 |
| 400-499 | 1:0.65 * | 274 | 12.28 |
| 500+ | 1:0.25 * | 69 | 24.38 |
| All | 1:0.65 * | 1769 | 81.20 |

Note: In the inshore Agulhas Bank sample 400+ size classes were combined due to small sample size.

## Life history comparison

In order to effectively assess the parameters used for stock separation it is important to determine how external factors such as fishing mortality affect them. Fisheries are by their nature selective and are thought to place selective pressure on species, that may cause changes in life history parameters such as growth and maturity (Beacham 1983; Leaman 1991; McAllister *et al.* 1992; Buxton 1993; Taniuchi *et al.* 1993; Rijnsdorp 1993; Newman *et al.* 1996). These changes can manifest themselves as either a competitive release where growth increases (DeMartini *et al.* 2003) or a genetic selection for slower growing individuals which mature earlier in life, when the faster growing later maturing individuals are removed from the population, prior to reproduction (Roff 1984). This affects long term fishery yields, because slow growing, early maturing, individuals reduce productivity of the population, thereby reducing the overall potential yield (Buxton 1993).

Maximising lifetime fecundity is a central feature of life history optimisation. Hence, exponentially increasing fecundity with age confers little benefit to the individual when mortality rates preclude significant survival of older age classes (Leaman 1991). Due to the mass/fecundity relationship (Chapter 3), as the size structure of the population decreases, the overall reproductive output of the population will decrease, unless size at maturity decreases to compensate for this. As a result, changes to the age at maturity are important when considering a population's reproductive potential. Size and age at maturity link individual growth and reproductive potential of a population, and therefore are of prime concern to population dynamics studies (Beacham 1983). Temporal and geographic variation in these parameters have been documented for sciaenids (Griffiths 1997a, b, c), sparids (Buxton 1993), lutjanids (Newman *et al*. 1996), pleuronectids (Brodziak and Mikus 2000) and squalids (Taniuchi *et al*. 1993) and appear to be related to mortality.

Table IX: Comparisons of mass at length for *A. argyrozona* across the Agulhas Bank taken from fish sampled in the same months (November – April) and over the same size range (200-600 mm FL). Significant differences are represented as follows * = p<0.01, ** = p<0.001.

| Area | TNP | Central Agulhas Bank | Eastern Cape |
|---|---|---|---|
| TNP | - | ** | ** |
| Central Agulhas Bank | ** | - | * |
| Eastern Cape | ** | * | - |

In order to maximise the individual's potential lifetime fecundity, life-history theory proposes that altered mortality schedules for strongly iteroparous species will be compensated through alterations in the age specific allocations of the reproductive effort. Under unfished conditions, in a strongly iteroparous species such as carpenter, mortality will be highest in pre-reproductive individuals and delayed maturity and increased lifespan will be adaptive. Therefore, in heavily exploited stocks, the higher mortality rate of adults caused by size selective fishing, confers a selective advantage on greater reproductive energy expenditure earlier in life (Leaman 1991). If the species exhibit some form of life history plasticity, increased mortality of adults should lead to a lowered age at first maturity and increased reproductive effort prior to ages where mortality occurs (Leaman 1991). In carpenter there is a lower growth rate in the Eastern Cape, which has a higher $F$ than the pooled Agulhas Bank data and a corresponding decrease in the size at maturity (Table X). Size at maturity affects growth, because the onset of maturity results in more resources being allocated to reproduction and less are available for growth. Therefore, a decrease in the size at maturity causes a decrease in the growth rate. These data therefore support Leaman's (1991) hypothesis and help to explain the decrease in the size at maturity in exploited carpenter populations.

Table X: A comparison of exploitation rates, growth rate, age ($t_{50}$) and size ($L_{50}$) at female 50% maturity and predicted size at maturity (values in parentheses are the actual $L_{50}$/Roff $L_{50}$ x100) for *A. argyrozona* sampled in various regions of their distribution.

| Area | $F$ | $k$ | Female $t_{50}$ | Female $L_{50}$ | Predicted $L_{50}$ (Roff 1992) |
|---|---|---|---|---|---|
| Pooled Agulhas Bank | 0.144 | 0.06 | 4 | 267 | 398 (67) |
| Eastern Cape | 0.22 | 0.08 | 2 | 206 | 388 (53) |

Decreased size at maturity could be a result of a genetic shift or phenotypic plasticity, but in this case it is unclear what the mechanism is. As this species has a complex movement pattern, size/age at maturity comparisons of heavily exploited *v.* non-exploited areas are difficult. In both stocks fish move from heavily exploited areas to less or un-exploited areas as they grow and mature. Age at maturity estimates are biased on the central Agulhas Bank, as young mature fish move offshore, hence decreasing the age at maturity estimates offshore and increasing the estimates inshore. Therefore, the true age/size at maturity was estimated from the weighted data at 267 mm FL or 4 years old. In the Eastern Cape carpenter move long-shore as they grow. This is evident as carpenter are significantly larger at age in the TNP than in the Eastern Cape. Therefore, large faster growing fish arrive in the TNP and remain there for a number of years. As a result of this few immature fish live in the TNP and the age at maturity estimates have a positive bias. These data suggest that both fish movement patterns and exploitation rate affect the size and age at sexual maturity estimates for carpenter.

Roff (1992) developed a method to predict the optimal size and age at maturity based on $L_\infty$ and *k*. Using the predicted *v.* actual length at maturity, the length at maturity for all carpenter populations was well below (53-67%) that predicted by Roffs (1992) method, suggesting that some compensation is taking place. It is, therefore, likely that, in both the Eastern Cape and central Agulhas Bank, a high $F_{current}$ combined with a long history of exploitation lower the size at maturity and growth rate of carpenter.

Investigations into the sex ratios showed that there were overall more females than males in the central Agulhas Bank and Eastern Cape populations, but more males in the TNP population. Gonochoristic and late gonochoristic species (i.e. carpenter) should tend towards a 1:1 sex ratio. The deviation from this sex ratio in carpenter populations is therefore unexpected and difficult to explain. Griffiths (1997a) hypothesized that observed deviations from the 1:1 sex ratio could occur for the following reasons: 1) more individuals of one or other sex are produced; 2) sampling methods actively select one sex over the other; and 3) equal numbers of both sexes are produced, but one sex is diminished at a faster rate through emigration or mortality. In all carpenter populations there was no significant deviation from the 1:1 sex ratio for the size classes up to the size at 50% maturity (i.e. <300 mm FL), which effectively excludes hypothesis one.

Regarding hypothesis two, the sampling methodologies were the same throughout the study and relatively similar numbers of males and females were caught < 300 mm FL, so the hypothesis can be excluded. Hypothesis three is therefore a possibility. On the eastern Agulhas Bank (i.e. TNP and Eastern Cape populations) 300-499 mm FL size classes became skewed in favour of males. Above this size class the TNP population returns to a 1:1 ratio. However, in the Eastern Cape population the 500+ size class has a female bias. In the central Agulhas Bank population all size classes from 300+ mm FL were skewed in favour of females. This suggests that male carpenter are more prone to mortality in heavily fished areas, but the reason for this is unclear. Additional research is required before the mechanism driving the skewed sex ratios can be elucidated. The skewed sex ratios, however, do suggest an explanation for the high mass at length for the TNP population, which is male biased and male carpenter are heavier at length than females.

For exploited stocks increased food availability associated with decreased density of predators can cause an increase in growth rate (Leaman 1991; DeMartini *et al*. 2003). However, the Eastern Cape has the highest *F* and lowest growth rate suggesting that this is not the case for the South African carpenter stocks. Nevertheless, variation in a species diet should not be ignored. Anecdotal evidence from the fishing industry in the Eastern Cape suggests that small pelagic teleosts, such as *Sardinops sagax*, which are the primary diet of carpenter, are unpredictable and have a patchy distribution in time and space. Moreover Barange and Hampton (1997) and Barange *et al*. (1999) showed that *S. sagax* and *Engraulis japonicus* were more consistently present over time on the central than on the eastern Agulhas Bank. As a result reduced food availability on the eastern Agulhas Bank could depress growth. In addition, on the offshore central Agulhas Bank, *Pyrosoma* spp. appear to be relatively consistent throughout the area and was present during all seasons sampled. They are utilised not only by carpenter, but also other species in this area such as sperm whales *Physeter macrocephalus* (Best 1999) and swordfish *Xiphias gladius* (C. Smith, Marine and Coastal Management, unpublished data). However, no data on the calorific values of either the teleosts or *Pyrosoma* spp. were available nor are data on carpenter consumption rates as, when caught, even in shallow water, they regurgitate their food in an attempt to dislodge the hook. When caught in deep water barotrauma forces the stomach out of the fish's mouth, limiting further investigation.

The effects of exploitation on the size at maturity and growth rate should be considered in the development of management models. This study shows that factors driving the size at maturity are difficult to predict for this species, which can complicate management. MPAs can offset these trends by protecting the reproductive capacity of the population. The primary advantage of this strategy is that spawning biomass would be protected, thereby providing a source of recruits for the surrounding areas (Brouwer *et al*. 2003). Consequently, the potential for an offshore MPA on the offshore areas of the central Agulhas Bank, where 88-93% of the reproductive potential exists should be investigated.

# - Chapter 7 -

## Management of *Argyrozona argyrozona* (Pisces: Sparidae) based on per-recruit models

## - Chapter 7 -

# Management of *Argyrozona argyrozona* (Pisces: Sparidae) based on per-recruit models

## ABSTRACT

Carpenter *Argyrozona argyrozona* is an endemic sparid that constitutes an important component of the South African linefishery between Cape Agulhas and Port Alfred. The South African carpenter population is divided into two stocks one on the central Agulhas Bank and the other on the eastern Agulhas Bank. Spawner biomass-per-recruit (*SB/R*), fecundity-per-recruit (*Egg/R*) and yield-per-recruit (*Y/R*) models were used to model both South African carpenter stocks. Owing to the allometric relationship between annual fecundity and individual size, *Egg/R* ratios were between 40 and 74% of *SB/R* at equivalent fishing mortality (*F*). *Egg/R* ratios account for allometric increases in fecundity with size/age, and are therefore regarded as more accurate estimates of reproductive potential. Hence, biological reference points for per-recruit analysis should wherever possible be based on this quantum. It is shown that the current length at first capture ($l_c$) (250 mm TL) and *F* (at $M = 0.1$) will reduce *Egg/R* to 6.41% of the pristine value in the Eastern Cape population and between 6.06 and 14.15% on the central Agulhas Bank, indicating that both stocks are heavily over exploited. An increase in $l_c$ from 250 to 350 mm TL and a 70% reduction in commercial fishing effort is recommended to attain a target reference point of 40% $Egg/R_{F=0}$. Bag frequencies indicate that a reduction in daily bag limit from 10 to 4 fish.person$^{-1}$.day$^{-1}$ would effect an equivalent reduction in recreational *F*. The trawl bycatch of carpenter is only 3% of the reported line catch, consequently restrictions to this fishery are not recommended.

**Key Words:** Spawner biomass-per-recruit, fecundity-per-recruit, yield-per-recruit, bag limit, size limit, Sparidae, management.

## INTRODUCTION

Carpenter *Argyrozona argyrozona* is a medium sized sparid (reaching 3.5 kg and 700 mm TL) endemic to the southeast coast of South Africa (Smith and Heemstra 1986). The carpenter resource consists of two separate stocks (Chapter 6): one on the central Agulhas Bank (Fig. 1), where juvenile fish live inshore and migrate offshore as they grow and the second on the eastern Agulhas Bank (Fig. 1), where they are confined to the inshore regions (<150 m depth) due to the narrow continental shelf. Carpenter in the Eastern Cape and inshore central Agulhas Bank have been targeted by the linefishery for over 100 years. The offshore regions of the central Agulhas Bank have been exploited since the mid 1980's following the introduction of modern freezer vessels (Griffiths 2000). Both stocks have demonstrated declines in catch per unit effort (*cpue*) of over 95% during the 20th century (Griffiths 2000). Despite these declines carpenter are still heavily targeted in both regions and remain an important component of the commercial linefishery (Sauer *et al*. 1997; Brouwer and Buxton 2002). In December 1985, a recreational daily bag limit of 10 fish.person.day$^{-1}$ and a size limit for both commercial and recreational sectors of 250 mm TL (=200 mm FL) were legislated. Owing to a lack of life history information or an operational management plan, the regulations were based on intuition rather than quantitative analysis. Despite catch restrictions the stock has continued to decline (Hecht and Tilney 1989; Griffiths 2000; Brouwer and Buxton 2002) suggesting that these management decisions have been ineffective. This emphasises the need for a formal stock assessment upon which quantitative regulations may be based.

Although some catch and effort data exist for the carpenter fishery, like many linefisheries worldwide they are sparse and unevenly distributed through time (Huntsman *et al*. 1983; Buxton 1992; Griffiths 1997a). Per-recruit models therefore represent the most appropriate stock assessment method (Griffiths 1997a; Griffiths *et al*. 1999). The accepted target reference point for the South African linefishery is 40% of pristine ($F$ = 0) spawner biomass-per-recruit ($SB/\mathrm{R}$) ($F_{SB40}$) and the threshold reference point is 25% $SB/R_{F=0}$ ($F_{SB25}$) (Griffiths *et al*. 1999).

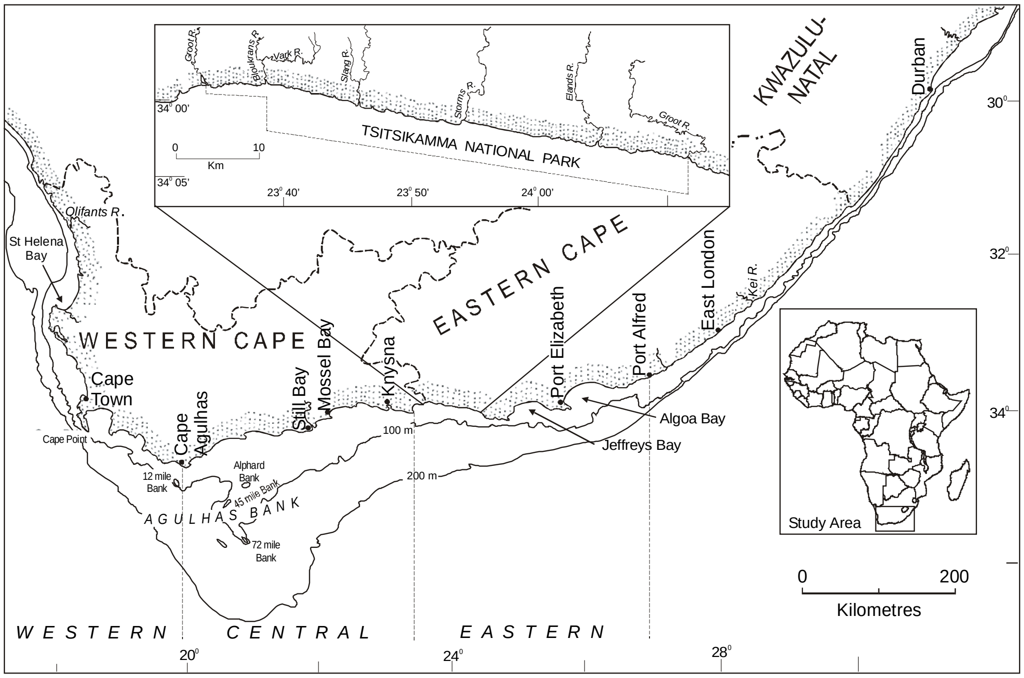

Figure 1: The study area showing the positions of the western, central and eastern Agulhas Bank, Tsitsikamma National Park, the 100 m and 200 m isobaths, and places mentioned in the text.

The primary objectives of this study were to determine the optimal levels of fishing mortality (*F*) and the length at first capture ($l_c$) for the South African carpenter stocks using per-recruit models, and to make recommendations for the management of the resource. One important assumption of the *SB/R* approach is that the relative fecundity or eggs per unit biomass is the same for small and large adults, which it is not (Chapter 4). A comparison of *SB/R* and fecundity-per-recruit (*Egg/R*) reference points is therefore included.

## MATERIAL AND METHODS

### Data sources

The basic data used for the per-recruit analysis were:

i) Random fork length measurements (mm) of fish caught by commercial and recreational linefishers from all major fishing grounds of the offshore and inshore central Agulhas Bank and the eastern Agulhas Bank during the years 1986-2001. These data were collected from the following sites: Port Alfred, Port Elizabeth, Still Bay, Cape Agulhas, Alphard Bank and 12, 45 and 72 mile banks (Fig. 1) by onboard and shore based observers, appointed by Marine and Coastal Management (MCM) (National Marine Linefish System, MCM, Cape Town). Size composition data in the Tsitsikamma National Park (TNP), a Marine Protected Area (MPA) on the eastern Agulhas Bank, were obtained from research fishing operations using gear identical to that used by the commercial fleet.

ii) Length data from swept area (bottom trawl) demersal biomass surveys conducted by MCM (Chapter 6) across the entire Agulhas Bank between Cape Town and Port Alfred (Badenhorst and Smale 1991).

iii) The age length key, length mass relationship and the special von Bertalanffy growth parameters derived in Brouwer and Griffiths (2004) from fish collected from both the Eastern Cape and the central Agulhas Bank populations (Fig. 1) during the years 1997-2000.

iv) The size at maturity information from both stocks during the period 1997-2000 (Chapter 4).

v) Age based fecundity estimates were determined from both stocks during the period 1997-2000 (Chapter 4).

The central Agulhas Bank samples were separated by depth into inshore (< 60m depth) and offshore (> 60m depth) areas (Fig. 1), as carpenter move offshore as they grow (Chapter 6) and effort directed at carpenter is much higher on inshore grounds (10261 *v*. 5084 fisher days.year$^{-1}$) (Griffiths and Wilke 2002).

## Mortality estimation

Total annual mortality ($Z$) was estimated from data collected in all areas using two methods, catch-curve analysis (Ricker 1975) and the following equation (Butterworth *et al*. 1989):

$$Z = \lambda n[1 + \frac{1}{a_m - a_f}]$$

Where $a_f$ is the age at full recruitment and $a_m$ is the mean age of all fully recruited fish sampled.

Natural mortality ($M$) was estimated using Pauly's (1980) empirical equation and Roff's (1984) method:

$$\log M = \log 3 + \log L_\infty + \log k + \log\left[1 - \frac{L_T}{L_\infty}\right] - \log L_T$$

Where $L_\infty$ and $k$ are derived from the von Bertalanffy equation and $L_T$ is the length at maturity. This method potentially provides more accurate results and is considered to be superior to Pauly's (1980) model, which is entirely empirical (Roff 1984). Roff (1984) compared both methods and showed that his method predicted a value of $M$ closer to the observed value than Pauly's (1980) method for 9 of 17 species.

Having estimated $Z$ (by averaging the results from the two methods above) and $M$ (the median of the results from the two methods above for both stocks), $F$ was then obtained by substitution ($F = Z-M$). Mortality rates were estimated separately for each area (Fig. 1), and in the TNP, a large (75km) MPA that has been closed to fishing since 1964 and $Z$ was expected to approximate $M$.

**Per-recruit analysis**

Yield-per-recruit (*Y/R*), spawner biomass-per-recruit (*SB/R*) and fecundity-per-recruit (*Egg/R*) were calculated according to the following equations where the number of recruits was set to 1:

$$Y/R=\sum_{t=0}^{30}\frac{(FS_t)}{(FS_t+M)}(e^{-\sum_{i=0}^{t-1}FS_i+M})(1-e^{-FS_i-M})W_t$$

$$SB/R_t=B_t(e^{-\sum_{i=0}^{t-1}(F_iS_i+M)})W_t$$

$$SB/R=\sum_{t=0}^{30}SB/R_t$$

$$Egg/R_t=B_t(e^{-\sum_{i=0}^{t-1}(F_iS_i+M)})E_t$$

$$Egg/R=\sum_{t=0}^{30}Egg/R_t$$

Where:

$F$ = the instantaneous fishing mortality,

$S_t$ = the proportion of fish at age $t$ larger than the $l_c$ (see Table I),

$W_t$ = the estimated individual mass at age $t$,

$E_t$ = the estimated individual fecundity of fish age $t$ (note that this refers to females only, therefore annual fecundity at age is divided by 2) and

$B_t$ = the proportion of mature females at age $t$ (see Table I).

Table I: The proportion-at-age (where 1 refers to 100%) on the central Agulhas Bank of mature female *A. argyrozona* and fish larger than each of three alternative minimum size limits ($l_c$) that were modelled in this study (mm FL). Proportion mature was determined by transformation using proportions of mature fish per length-class.

| Age | Proportion mature | Proportion of fish larger than the size limit | | |
|---|---|---|---|---|
| | | 200 | 300 | 400 |
| 1 | 0 | 0 | 0 | 0 |
| 2 | 0 | 1 | 0 | 0 |
| 3 | 0.1 | 1 | 0.03 | 0 |
| 4 | 0.5 | 1 | 0.04 | 0 |
| 5 | 0.7 | 1 | 0.2 | 0 |
| 6 | 0.8 | 1 | 0.4 | 0 |
| 7 | 0.8 | 1 | 0.75 | 0 |
| 8 | 0.9 | 1 | 0.82 | 0 |
| 9 | 0.91 | 1 | 0.9 | 0.05 |
| 10 | 0.96 | 1 | 1 | 0.07 |
| 11 | 0.96 | 1 | 1 | 0.4 |
| 12 | 0.96 | 1 | 1 | 0.6 |
| 13 | 0.96 | 1 | 1 | 0.8 |
| 14 | 0.97 | 1 | 1 | 1 |
| 15 | 1 | 1 | 1 | 1 |
| 30 | 1 | 1 | 1 | 1 |

Selectivity for each age class was calculated from the age-length key by dividing the number of fish within each age class above the minimum size limit ($l_c$) being tested, by the total number of fish within that age class. Due to the difficulties in obtaining accurate estimates of $M$ for exploited populations, the sensitivity of the per-recruit models was tested by varying $M$ by plus or minus 50% centred around the median $M$ = 0.1 (i.e. 0.05, 0.1 and 0.15).

## RESULTS

### Mortality estimates

The age distributions and the corresponding catch curves for the Eastern Cape, TNP and inshore and offshore Agulhas Bank are shown in Fig. 2. It is evident that fish sampled on the inshore Agulhas Bank and the Eastern Cape regions consist of younger age classes than those on the offshore Agulhas Bank or TNP. These trends were further supported by data derived from research trawl catch (Fig. 3) from the inshore and offshore central Agulhas Bank. Estimates of $Z$ varied between regions (0.22-0.4) but both catch-curve and Butterworth *et al.* (1989) methods provided similar results within each region (Tables II and III). Estimates of $Z$ calculated using line and trawled length frequencies were also similar within each region, suggesting that gear selectivity did not bias the results (Tables II and III). Estimates of $M$ were similar (Table IV) with a median value of 0.1.

Table II: Total mortality ($Z$) estimates from two models for *A. argyrozona* sampled in the linefishery from various regions.

| Method | Eastern Cape | TNP | Agulhas Bank inshore | Agulhas Bank offshore |
|---|---|---|---|---|
| Butterworth *et al.* (1989) | 0.23 | 0.39 | 0.4 | 0.25 |
| Catch-curve (Ricker 1975) | 0.32 | 0.31 | 0.38 | 0.22 |
| Average | 0.28 | 0.35 | 0.39 | 0.24 |

Table III: Total mortality ($Z$) estimates from two models for *A. argyrozona* sampled from research trawling from various regions.

| Method | Agulhas Bank inshore | Agulhas Bank offshore | Agulhas Bank all data |
|---|---|---|---|
| Butterworth *et al.* (1989) | 0.32 | 0.25 | 0.29 |
| Catch-curve (Ricker 1975) | 0.41 | 0.26 | 0.26 |
| Average | 0.37 | 0.26 | 0.28 |

### Per-recruit analysis

*SB/R*, *Egg/R* and *Y/R* curves for South African carpenter at the current minimum size limit (200 mm FL) and at two alternatives (300 and 400 mm FL) are shown in Figures 4, 5 and 6. *SB/R* and *Egg/R* declined rapidly with increasing $F$. Despite the fact that

$F_{current}$ varied with changes in $M$, both $SB/R_{current}$ and $Egg/R_{current}$ ratios revealed that the fishery is overexploited, where most current per-recruit estimates are well below the target reference point ($F_{SB40}$) (Table V). At $M$ = 0.1 the $Egg/R_{current}$ varied regionally from 14.15 to 6.06 %, while the $SB/R_{current}$ ranged from 22.44 to 11.99 % (Table V).

The inshore areas of the Agulhas Bank have a larger $F$ (0.2-0.3 *v*. 0.1-0.2) and a correspondingly lower $Egg/R_{current}$ (3.75-12.97 *v*. 10.24-30.26) than the offshore regions. The Eastern Cape has a larger $F$ (0.17-0.27 *v*. 0.16-0.26) and a correspondingly lower $Egg/R_{current}$ (4.24-9.58 *v*. 9.85-18.24) than the TNP. The data showed that $Egg/R$ was 40-74% of $SB/R$ at all levels of $M$. At the current $l_c$ (200 mm FL) $F$ is required to be at 0.05 on both the Agulhas Bank and Eastern Cape to achieve the target reference point of $F_{Egg/R40}$ (Table VI). $Y/R$ at the current $l_c$ (and $M$ = 0.1) peaked at $F$ = 0.1 for both the Agulhas Bank and Eastern Cape areas, which is considerably higher than $F$ required to attain 40% $Egg/R_{F=0}$. Assuming $M$ = 0.1, $F_{current}$ was estimated at 0.22, 0.25 and 0.15 for the Eastern Cape, inshore and offshore Agulhas Bank areas respectively (Table V).

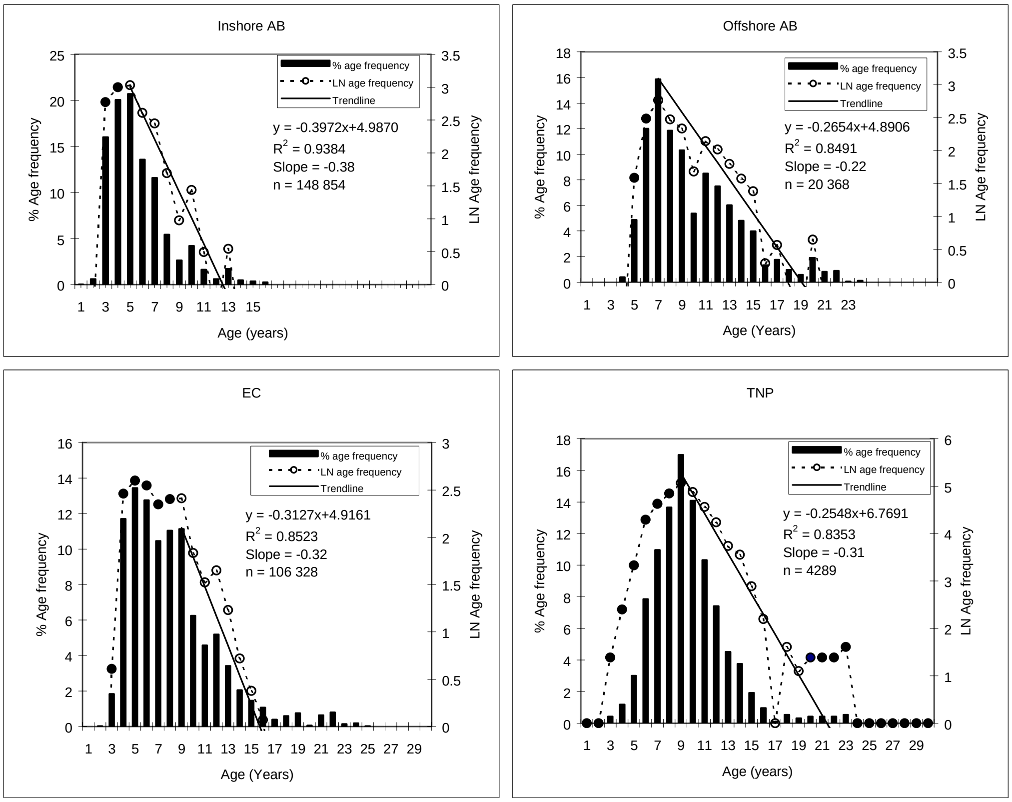

Figure 2: The age distributions (bars) and catch-curves (circles) of *A. argyrozona* caught by the linefishery (and research fishing in the TNP) in the various regions. Total mortality (*Z*) was determined from the slope of the declining limb of the catch-curve. Open circles represent the data points that were used to calculate the slope. AB = Agulhas Bank, EC = Eastern Cape.

Table IV: Natural mortality (*M*) estimates from two models for *A. argyrozona* sampled in the various regions.

| Method | Eastern Cape | TNP | Agulhas Bank inshore | Agulhas Bank offshore |
|---|---|---|---|---|
| Pauly (1980) | 0.09 | 0.1 | 0.17 | 0.1 |
| Roff (1984) | 0.1 | 0.15 | 0.1 | 0.1 |

Table V: Comparison of biological reference points in the various regions, $F_{current}$, spawner biomass-per-recruit (*SB/R*) and fecundity-per-recruit (*Egg/R*) expressed as a percentage of $F = 0$ for each level of natural mortality (*M*). Percent expressed as $(Egg/R_{current}) / (SB/R_{current})$ x 100.

| **Inshore Agulhas Bank line caught** | | | | |
|---|---|---|---|---|
| *M* | $F_{\text{current}}$ | $SB/R_{current}$ | $Egg/R_{current}$ | Percent |
| 0.05 | 0.30 | 7.80 | 3.75 | 48 |
| 0.10 | 0.25 | 11.99 | 6.06 | 51 |
| 0.15 | 0.20 | 21.81 | 12.97 | 59 |
| **Offshore Agulhas Bank line caught** | | | | |
| *M* | $F_{\text{current}}$ | $SB/R_{current}$ | $Egg/R_{current}$ | Percent |
| 0.05 | 0.20 | 16.41 | 10.24 | 62 |
| 0.10 | 0.15 | 22.44 | 14.15 | 63 |
| 0.15 | 0.11 | 40.80 | 30.26 | 74 |
| **Inshore Agulhas Bank trawl caught** | | | | |
| *M* | $F_{\text{current}}$ | $SB/R_{current}$ | $Egg/R_{current}$ | Percent |
| 0.05 | 0.36 | 4.56 | 1.82 | 40 |
| 0.10 | 0.31 | 9.34 | 4.34 | 47 |
| 0.15 | 0.26 | 16.99 | 9.28 | 55 |
| **Offshore Agulhas Bank trawl caught** | | | | |
| *M* | $F_{\text{current}}$ | $SB/R_{current}$ | $Egg/R_{current}$ | Percent |
| 0.05 | 0.21 | 10.94 | 5.93 | 54 |
| 0.10 | 0.16 | 22.44 | 14.15 | 63 |
| 0.15 | 0.11 | 40.80 | 30.27 | 74 |
| **Eastern Cape** | | | | |
| *M* | $F_{\text{current}}$ | $SB/R_{current}$ | $Egg/R_{current}$ | Percent |
| 0.05 | 0.27 | 8.45 | 4.24 | 50 |
| 0.10 | 0.22 | 13.00 | 6.41 | 49 |
| 0.15 | 0.17 | 18.70 | 9.58 | 51 |
| **Tsitsikamma National Park** | | | | |
| *M* | $F_{\text{current}}$ | $SB/R_{current}$ | $Egg/R_{current}$ | Percent |
| 0.05 | 0.26 | 16.15 | 9.85 | 61 |
| 0.10 | 0.21 | 22.44 | 13.50 | 60 |
| 0.15 | 0.16 | 29.74 | 18.24 | 61 |

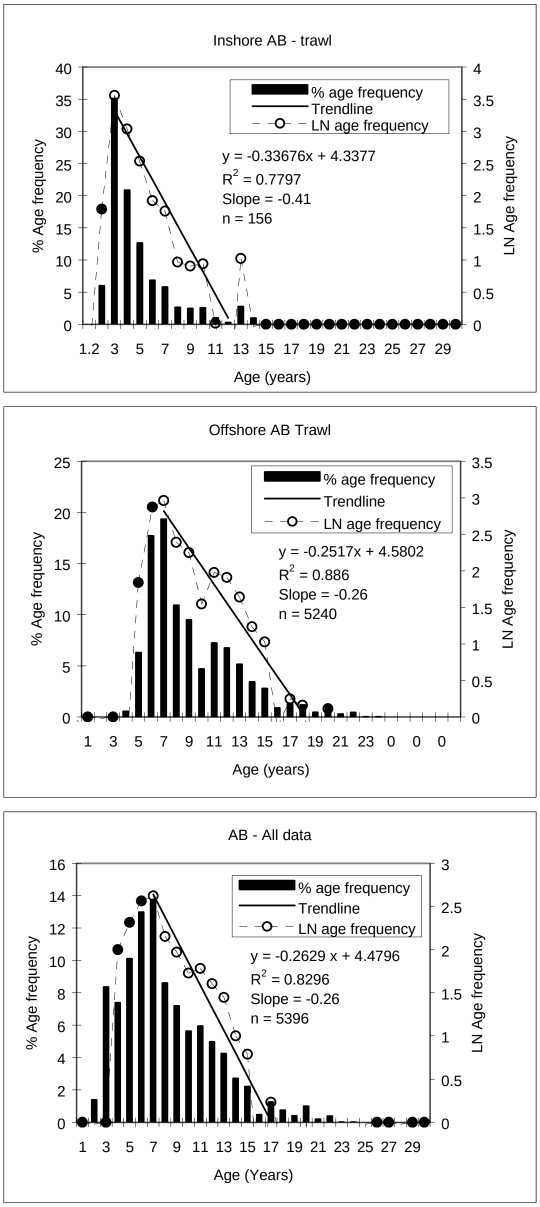

Figure 3: The age distributions (bars) and catch-curves (circles) of *A. argyrozona* caught on the central Agulhas Bank (AB) by the trawl biomass survey. Total mortality (*Z*) was determined from the slope of the declining limb of the catch-curve. Open circles represent the data points that were used to calculate the slope.

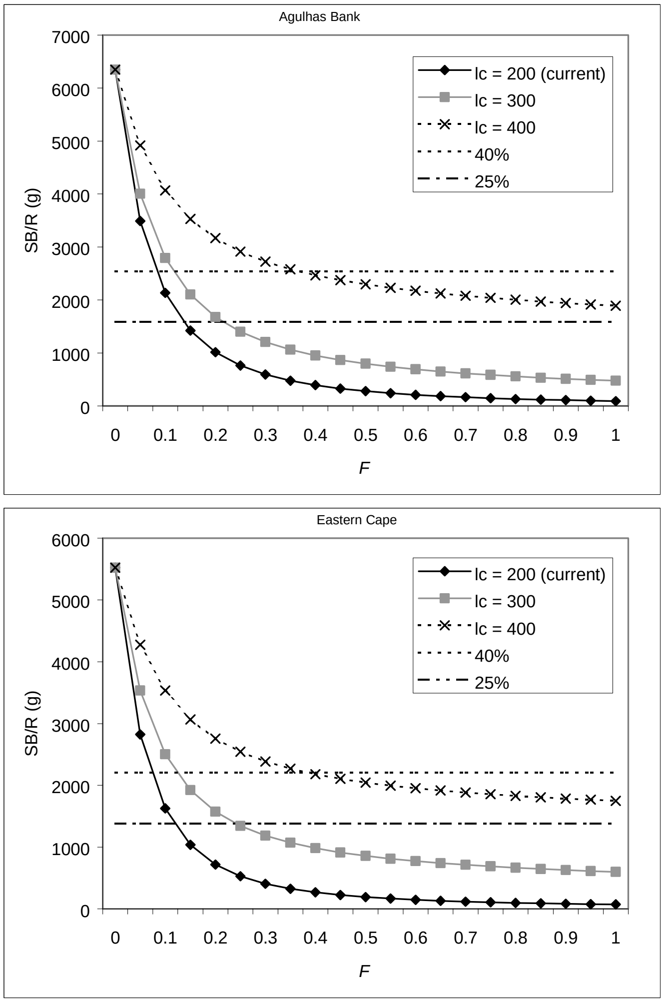

Figure 4: The relationship between spawner biomass-per-recruit (*SB/R*) and instantaneous fishing mortality in the Eastern Cape and the central Agulhas Bank for alternative minimum sizes (mm FL) at first capture ($l_c$). The 25% $SB/R_{F=0}$ and 40% $SB/R_{F=0}$ levels were calculated at $M$= 0.1.year$^{-1}$.

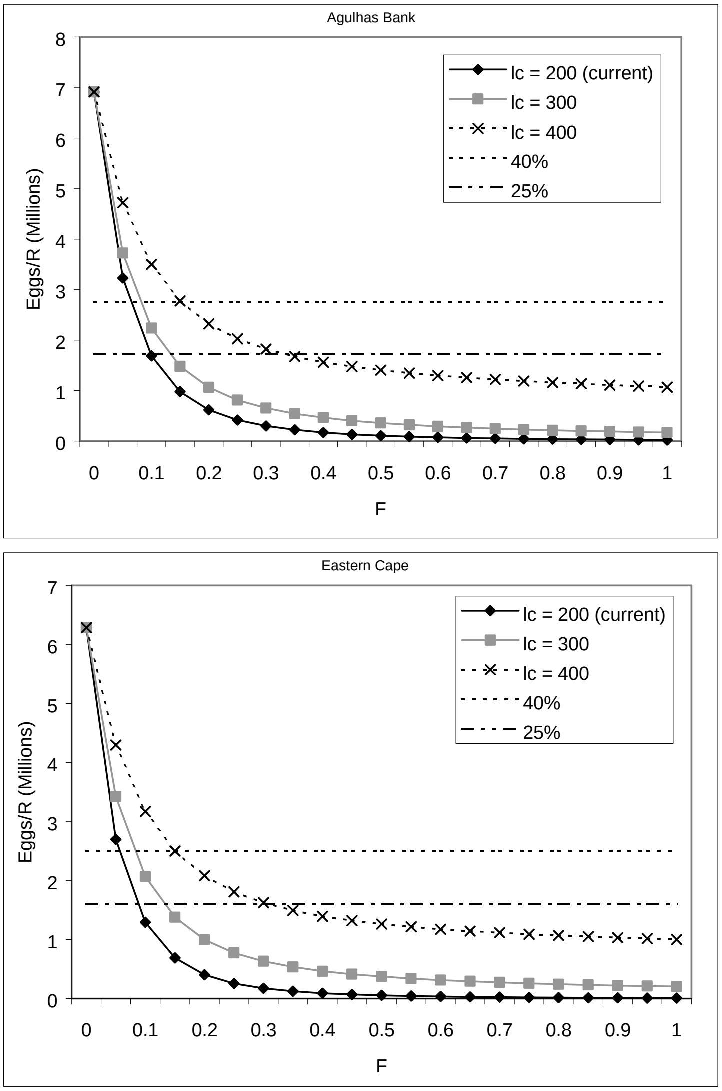

Figure 5: The relationship between fecundity-per-recruit (*Egg/R*) and instantaneous fishing mortality in the Eastern Cape and the central Agulhas Bank for alternative minimum sizes (mm FL) at first capture ($l_c$). The 25% $Egg/R_{F=0}$ and 40% $Egg/R_{F=0}$ levels were based on the $Egg/R_{F=0}$ calculated at $M$= 0.1.year$^{-1}$.

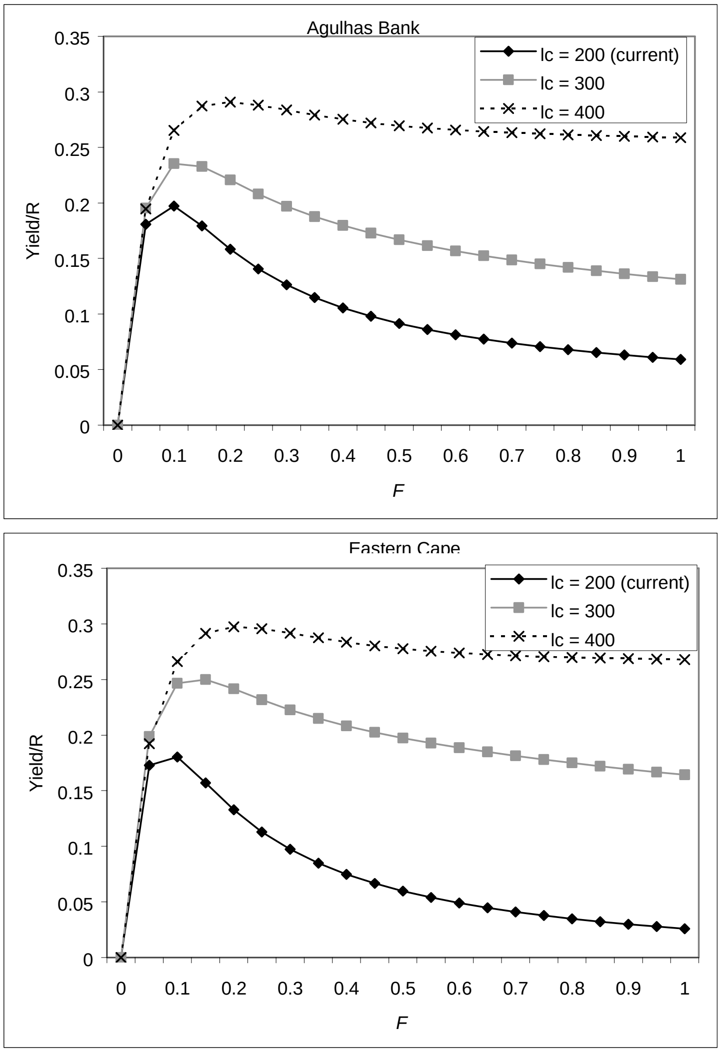

Figure 6: The relationship between yield-per-recruit (*Y/R*) (kg) in the Eastern Cape and the central Agulhas Bank for alternative minimum sizes (mm FL) at first capture ($l_c$) calculated at $M$ = 0.1.year$^{-1}$.

Table VI: $Egg/R_{current}$ as a percentage of $Egg/R_{F=0}$ for three levels of $M$ at $l_c$ current (200 mm FL) calculated over a range of $F$ values.

| $F$ | $M$ = 0.05 | $M$ = 0.1 | $M$ = 0.15 |
|---|---|---|---|
| **Eastern Cape** | | | |
| 0.05 | 38.76 | 42.91 | 47.88 |
| 0.1 | 16.63 | 20.45 | 25.51 |
| 0.15 | 7.96 | 10.95 | 14.95 |
| 0.2 | 4.24 | 6.42 | 9.48 |
| 0.25 | 2.49 | 4.07 | 6.39 |
| 0.3 | 1.58 | 2.74 | 4.52 |
| 0.35 | 1.06 | 1.94 | 3.31 |
| 0.4 | 0.75 | 1.42 | 2.50 |
| 0.45 | 0.55 | 1.07 | 1.93 |
| 0.5 | 0.42 | 0.83 | 1.52 |
| 0.55 | 0.32 | 0.65 | 1.22 |
| 0.6 | 0.25 | 0.52 | 0.99 |
| 0.65 | 0.2 | 0.42 | 0.81 |
| 0.7 | 0.16 | 0.35 | 0.67 |
| 0.75 | 0.14 | 0.29 | 0.56 |
| 0.8 | 0.11 | 0.24 | 0.47 |
| 0.85 | 0.09 | 0.20 | 0.4 |
| 0.9 | 0.08 | 0.17 | 0.34 |
| 0.95 | 0.07 | 0.15 | 0.29 |
| 1 | 0.06 | 0.13 | 0.25 |
| **Agulhas Bank** | | | |
| 0.05 | 41.94 | 46.74 | 52.25 |
| 0.1 | 19.60 | 24.42 | 30.27 |
| 0.15 | 10.24 | 14.15 | 19.14 |
| 0.2 | 5.93 | 8.94 | 12.97 |
| 0.25 | 3.75 | 6.06 | 9.28 |
| 0.3 | 2.54 | 4.34 | 6.92 |
| 0.35 | 1.82 | 3.23 | 5.32 |
| 0.4 | 1.36 | 2.49 | 4.20 |
| 0.45 | 1.04 | 1.96 | 3.39 |
| 0.5 | 0.82 | 1.58 | 2.78 |
| 0.55 | 0.66 | 1.30 | 2.32 |
| 0.6 | 0.55 | 1.08 | 1.95 |
| 0.65 | 0.45 | 0.91 | 1.66 |
| 0.7 | 0.38 | 0.78 | 1.43 |
| 0.75 | 0.33 | 0.67 | 1.24 |
| 0.8 | 0.28 | 0.58 | 1.09 |
| 0.85 | 0.24 | 0.51 | 0.96 |
| 0.9 | 0.21 | 0.45 | 0.85 |
| 0.95 | 0.19 | 0.40 | 0.75 |
| 1 | 0.17 | 0.35 | 0.67 |

# DISCUSSION

The estimates of *M* obtained from both methods used in this study were fairly consistent, suggesting that a high degree of confidence can be placed in the estimate of $M = 0.1$. Estimates of $M<0.2$ are considered low (Buxton 1992; Pauly 1997b), which is expected for carpenter as they are long lived and slow growing. A review of the diets of 19 sympatric piscivorous predators revealed no evidence of carpenter remains in the stomachs of cetaceans, elasmobranchs or large teleosts and only small numbers (0.05% - 0.7% of total mass of diet) in seals *Arctocephalus pusillus pusillus* (David 1987; Castley *et al*. 1991), supports the low *M* value.

The high *F* values for the Eastern Cape and inshore Agulhas Bank areas can be attributed to the fact that carpenter are highly accessible in these areas and commercial linefishing effort is high (Sauer *et al*. 1997; Brouwer and Buxton 2002). The high *Z* estimate in the TNP was an unexpected result, as the TNP is a large reserve (75 km long) that has been closed to fishing for since 1964, and *Z* was expected to approximate *M*. The high *Z* in the TNP is probably a result of emigration of the older fish (13+ years) from the park, as these age classes were poorly represented there. Tagging data showed that while most fish appear to be resident, a small proportion of carpenter do leave the TNP (Brouwer *et al*. 2003), and anecdotal evidence from the squid fishery reveals that large carpenter are caught offshore (± 10 nm offshore) of the TNP, supporting this hypothesis. This highlights the problem in accurately determining *Z* from a catch curve or Butterworth *et al*.'s (1989) equation for populations with size specific dispersal.

Without a long time series of accurate catch and effort data or information on the spawning stock and recruitment relationship, *Y/*R and *SB/*R are the most appropriate stock assessment methods available (Appledoorn 1996; Griffiths *et al*. 1999). *SB/R* levels of 40% and 25% of pristine are accepted as default target and threshold reference points for South African linefish species, as they are robust to a wide range of life history strategies and spawner-recruit relationships (Clarke 1993; Punt 1993; Mace 1994; Griffiths *et al*. 1999). $SB/R_{current}$ was consistently higher (40-74% at $M$ = 0.1) than $Egg/R_{current}$ in each area whether line or trawl data were used. This is due to the allometric increase in fecundity with individual mass observed for carpenter. For example, a single 3 kg fish produces 5 fold more eggs per kilogram of body weight than a 1 kg fish (Chapter 3). Accounting for age specific fecundity, *Egg/R* is a more appropriate estimate of the spawning potential for the carpenter resource than *SB/R*. It is therefore, recommended that target and threshold reference points of 40% $Egg/R_{F=0}$ and 25% $Egg/R_{F=0}$ respectively be incorporated into the management plan for this species.

The results of this study show that the current $l_c$ and calculated $F$ have the potential to reduce the reproductive potential of carpenter to between 6.06 and 14.15% of pristine on the central Agulhas Bank and 6.41% in the Eastern Cape. Although it is uncertain as to whether the population is in equilibrium or not, trawl and line caught *cpue* of carpenter have declined by more than 95% in both stocks (Griffiths 2000), indicating that the stocks are heavily depleted and that reproductive potential is severely depressed. Mortality would, however, be overestimated if fish migrate from the sample area (Appledoorn 1996), as occurs on the inshore Agulhas Bank and Eastern Cape. Similarly mortality will be underestimated by migration into an area, a situation in the offshore Agulhas Bank and TNP. As a result the $Egg/R_{current}$ in the central Agulhas Bank stock is probably somewhere between 6.06 and 14.15%. The data derived from the trawl survey, which is a random survey of the entire central Agulhas Bank ($Egg/R_{current}$ = 14.15%), gives similar estimates to the line caught data, providing additional confidence in the calculated per-recruit ratios for this stock.

Although trawling is often blamed for declines in linefish catch (Sauer *et al.* 1997), owing to the small trawl catch (<3% of line catch) of carpenter (Table VII), trawling including discards is not thought to have had a major impact on this resource. The reason being that adult carpenter populations occur largely over high profile reef and are thus not available to the South African trawl fleet. Given that the recreational sector lands <5% of the total carpenter catch (Brouwer and Buxton 2002), future management for the South African carpenter resource should focus on reducing commercial line catch.

One of the goals of the South African Marine Living Resources Act (Act 18 of 1998) is to utilize stocks optimally and at sustainable levels, and to rebuild depleted stocks. It is therefore assumed that the primary objective of carpenter management should be to implement regulations that would provide for an $Egg/R$ ratio of 40% $Egg/R_{F=0}$.

In order to reduce $F$ and achieve the target reference point of 40% $Egg/R_{F=0}$ the following options are available:

1. Current $l_c$ (200 mm FL) and an effort reduction of 85, 65 and 84% in the inshore and offshore Agulhas Bank and Eastern Cape respectively (Table VIII).

2. Increasing $l_c$ to $L_{50}$ (300 mm FL) and an effort reduction of 71, 64 and 52% in the inshore and offshore Agulhas Bank and Eastern Cape respectively.
3. Increase $l_c$ to 400 mm FL with an effort reduction of 27% in the inshore Agulhas Bank and no effort reduction in the offshore Agulhas Bank or the Eastern Cape.

Table VII: Historic line, trawl and longline catch (tons) of *A. argyrozona* and the percentage of trawl catch.

| Year | Linefishery | Trawl fishery | Hake longline | Trawl % of total |
|---|---|---|---|---|
| 1988 | 939 | 28 | - | 2.9 |
| 1989 | 755 | 31 | - | 3.9 |
| 1990 | 1197 | 23 | - | 1.9 |
| 1991 | 1204 | 14 | - | 1.1 |
| 1992 | 872 | 8 | - | 0.9 |
| 1993 | 684 | 10 | - | 1.4 |
| 1994 | 615 | 16 | - | 2.5 |
| 1995 | 747 | 22 | - | 2.9 |
| 1996 | 830 | 15 | 6 | 1.8 |
| 1997 | 800 | 21 | 11 | 2.5 |
| 1998 | 482 | 23 | 9 | 4.5 |
| 1999 | 561 | 11 | 11 | 1.9 |

A new fishing rights allocation process is currently underway in South Africa and, based on the stock assessment results of other species, aims to reduce the current effort in the commercial linefishery by approximately 70 % (Government Gazette No. 21949). It would therefore be prudent to pursue option 2 (above), which requires a decrease in $F$ of 52-71 % and an increase in the minimum size limit from 200 mm FL to 300 mm FL (350 mm TL) (see Appendix II for regression equation). Estimated $Y/R$ ratios under this scenario revealed that on the central Agulhas Bank yield from each cohort would decrease by only 1 %, but in the Eastern Cape yield would increase by 10%. However, owing to limitations of $Y/R$ analysis, where increases in recruitment anticipated from a larger spawner biomass are not accounted for, and should substantially increase total yield.

Table VIII: Percentage effort reduction required to achieve $F_{Egg/R25\%}$ and $F_{Egg/R40\%}$ at current $l_c$ (250mm TL) values in parentheses refer to ($F_{SB25\%}$ and $F_{SB40\%}$).

| Area | Effort reduction to $F_{Egg/R25\%}$ ($F_{SB25\%}$) | Effort reduction to $F_{Egg/R40\%}$ ($F_{SB40\%}$) |
|---|---|---|
| Inshore Agulhas Bank | 76 (52) | 85 (70) |
| Offshore Agulhas Bank | 43 (10) | 65 (44) |
| Eastern Cape | 74 (48) | 84 (68) |

Fishers participating in the South African commercial linefishery express concern that changes to fishery regulations will negatively affect their economic returns (Brouwer 1997). Although initially short term losses can be expected due to the increased $l_c$, the analysis of yield shown above reveals that total catch will decline by a negligible margin (1%) in the inshore Agulhas Bank area, and increase by 10% in the Eastern Cape. This suggests that the socio-economic concerns expressed by fishers remaining in the fishery are unjustified and that those in the Eastern Cape will potentially show positive economic benefits in the long term. Furthermore, it should be noted that an increase in spawner biomass should increase recruitment to the fishery and total yield should increase in the long term. In addition, the additional yield will be shared by fewer fishers thereby substantially increasing economic returns. One of the current management objectives for the linefishery is the social upliftment of fishing communities dependent on the resource. The current analysis indicates that this will be achieved by the proposed management strategy.

Those individuals that lose their commercial rights (i.e. the “part time” commercial fishers) could continue to fish as recreational anglers. Consequently this sector will show a large and sudden increase in effort after the allocation process is complete. As a result of this, the recreational sector's effort on this species should be reduced by a similar proportion. Using daily bag limits to effect an equivalent reduction in recreational $F$ is therefore essential. Currently the recreational fishers have a daily bag limit of 10 fish.person$^{-1}$.day$^{-1}$. Bag frequency analysis from an access point survey between Kei Mouth and Still Bay (Brouwer and Buxton 2002) was used to determine the potential reduction in catch associated with a particular daily bag limit. This was determined by the fraction of the surveyed catch that the daily bag limit would have prevented (Attwood and Bennett 1995). The daily bag frequencies of carpenter and the potential reduction in $F$ resulting from the enforcement of various bag limits are given in Table IX. These data revealed that a reduction in the current bag limit from 10 fish.person$^{-1}$.day$^{-1}$ to 5 fish.person$^{-1}$.day$^{-1}$ would reduce the recreational catch by 63% and to achieve a 71% effort reduction, a daily bag limit of 4 fish.person$^{-1}$.day$^{-1}$ would be required.

Setting minimum size limits to equal the length at 50% maturity ($L_{50}$) is a strategy often adopted for linefisheries (Griffiths 1997a). This study revealed that under current $F$, an increase in the size limit to 350 mm TL (i.e. $L_{50}$) would result in an *Egg/R* ratio of 11.8, 21.4 and 15.88% for the inshore and offshore Agulhas Bank and Eastern Cape, respectively, and would thus not prevent stock depletion. Griffiths (1997a) reported similar results for *Argyrosomus inodorus*, a sciaenid exploited by South African linefishers. Such results indicate that $l_c = L_{50}$ does not provide stocks with adequate protection and should therefore be used with caution.

There is some resistance from users to the regulations (Brouwer 1997), because many species affected by barotrauma die when released and high mortality rates of released fish will decrease the effectiveness of a size or bag limit (Harley *et al*. 2000 a, b). This could potentially cause problems, as an increase in the size limit is proposed here as part of the management plan. However, observations made during the tagging study revealed that only a small proportion of carpenter needed treatment to relieve the symptoms of barotrauma, even those caught at depths down to 90 m. The recapture rate of 5-7% suggests that the survival rate of released fish is sufficient. This increases the likelihood that size and bag limits collectively will be effective management tools for this species.

Table IX: Observed recreational bag frequencies of *A. argyrozona* sampled during an access point survey between 1994 and 1996 in the southeastern Cape (Brouwer and Buxton 2002) and the potential percentage reduction in fishing mortality resulting from the enforcement of various daily bag limits for *A. argyrozona*.

| Daily bag limit | Frequency | % Reduction in *F* |
|---|---|---|
| 0 | 74 | 100 |
| 1 | 10 | 89 |
| 2 | 4 | 81 |
| 3 | 2 | 75 |
| 4 | 1 | 71 |
| 5 | 1.5 | 63 |
| 6 | 1 | 55 |
| 7 | 0.25 | 53 |
| 8 | 0.5 | 49 |
| 9 | 0.25 | 47 |
| 10 | 0.25 | 41 |

Previous studies have focused on inshore linefish populations (*e.g.* Penny *et al*. 1999). This study shows that the offshore component of linefish stocks can also be depleted. Furthermore, a change in the current management of carpenter is required to rebuild the stocks to the target reference point. In order to assess any changes in the stock as a result of the amendments to the regulations re-assessments are necessary. Therefore, *F* should be estimated on a regular basis (Chapter 8) to assess the performance of the management plan. Owing to the costs of reproductive studies, estimates of fecundity will not be available for all species. Nevertheless, biological reference points calculated from *SB/R* models should be regarded as conservative when determining stock status and appropriate regulations.

# - Chapter 8 -

# General Discussion

## - Chapter 8 -

## General Discussion

Linefish stocks around the world are usually managed by limiting commercial effort and/or using size limits, bag limits and closed seasons for both commercial and recreational users. More recently Marine Protected Areas (MPAs) have been proclaimed to protect species, using a whole ecosystem approach (Bohnsak 1998). While some linefish stocks are managed by allocating a Total Allowable Catch (TAC) (Annala 1996; Harley *et al*. 2000), most have historically been managed using size limits, bag limits and closed seasons (Richards and Rago 1999; Vaughn and Prager 2002), which have met with limited success. The reasons for this lack of success are many, including: lack of compliance (Brouwer *et al*. 1997; Sauer *et al*. 1997); bag limits that were set too high and therefore failed to constrain catch; the complex nature of the biology, where sex change, residency and slow growth are common biological traits (Brule' *et al*. 2003; Buxton 1990; Buxton and Garratt 1990; McGlennon *et al*. 2000; Richards and Rago 1999) and ineffective size limits. Size limits are often set too low to provide adequate protection (Griffiths 1996a) and those that are set at the length at 50% maturity ($l_c$) are not always suitable, as $l_c$ makes the minimum size limit unacceptably large for some species (Griffiths 1996a). It is not always clear where to set a size limit for sex changing species (Buxton 1992) and in some instances size limits at $l_c$ do not provide adequate protection to prevent stock collapse (Griffiths 1997a; Chapter 7). In addition, barotrauma affects many species and impacts on the survival rates of released fish (Collins *et al*. 1999).

Richards and Rago (1999) showed that strict management based on good science and with both political and user support can result in the successful long term recovery of heavily depleted fish stocks. In South Africa, a linefish management plan was instituted in 1986, and despite almost two decades developing a negotiated a suite of management measures, there is little evidence to suggest that any reversal of linefish stock depletion has been achieved. This suggests that for some of these stocks, including carpenter, the management plan has failed. The reason for this is unclear, but in many instances the regulations were based on inadequate information or intuition rather than scientific data.

### Scientific knowledge limitations for management

The assessment of linefish stocks is complicated by the lack of long term data (Griffiths 2000) and the change in fishing practices. Catch per unit effort (*cpue*) rates can be used as a measure of relative fish abundance (Gulland 1983), provided that the fishing methods remain consistent through time (Attwood and Farquhar 1999). In South Africa, linefishing methods have changed considerably over the last 100 years due to technological advances. Therefore, long-term *cpue* trends could understate population trends, suggesting that the 95% decline in the carpenter, *Argyrozona argyrozona*, population calculated by Griffiths (2000) could be an underestimate.

### Actions to rebuild stocks to the target reference points

The data presented in this thesis showed that carpenter is a long-lived (maximum age 30), late maturing (± 5 years) species and consists of two stocks, both of which are heavily overexploited (fecundity per-recruit (*Egg/R*) is 6-14% of pristine on the central Agulhas Bank and 6-13% on the eastern Agulhas Bank). Furthermore, exploitation has affected the life history of the species and size at maturity appears to have declined in response to high levels of fishing mortality ($F$). These facts indicate that strict management is needed to re-build the carpenter stocks. Using the data presented in this thesis, a management plan was formulated for carpenter (Appendix II). The purpose of a management action is to control fishing mortality such that populations are maintained at levels corresponding to target reference points (Griffiths *et al*. 1999). The proposed plan for carpenter was tabled at the South African Marine Linefish Management Association (SAMLMA), which is a forum consisting of scientists, managers and user group representatives. At this forum the size limit was increased from 250 to 350 mm TL and the recreational bag limit was decreased from 10 to 4 fish.person$^{-1}$.day$^{-1}$, as recommended.

The proposed carpenter management plan along with a suite of new linefish recommendations are currently moving through the management review process (Fig. 1). This process has now reached the legal advisory stage and will hopefully be referred for public comment shortly (C. Wilke pers. comm. Marine and Coastal Management linefish section). In addition, the allocation process has had the effect of excluding the participation of freezer capacity vessels greater than 12m from the linefishery (see below) on the offshore regions of the central Agulhas Bank. Furthermore, in August 2003 the linefish rights allocation process was completed and the commercial effort was reduced from 2998 to 759 commercially registered linefish boats.

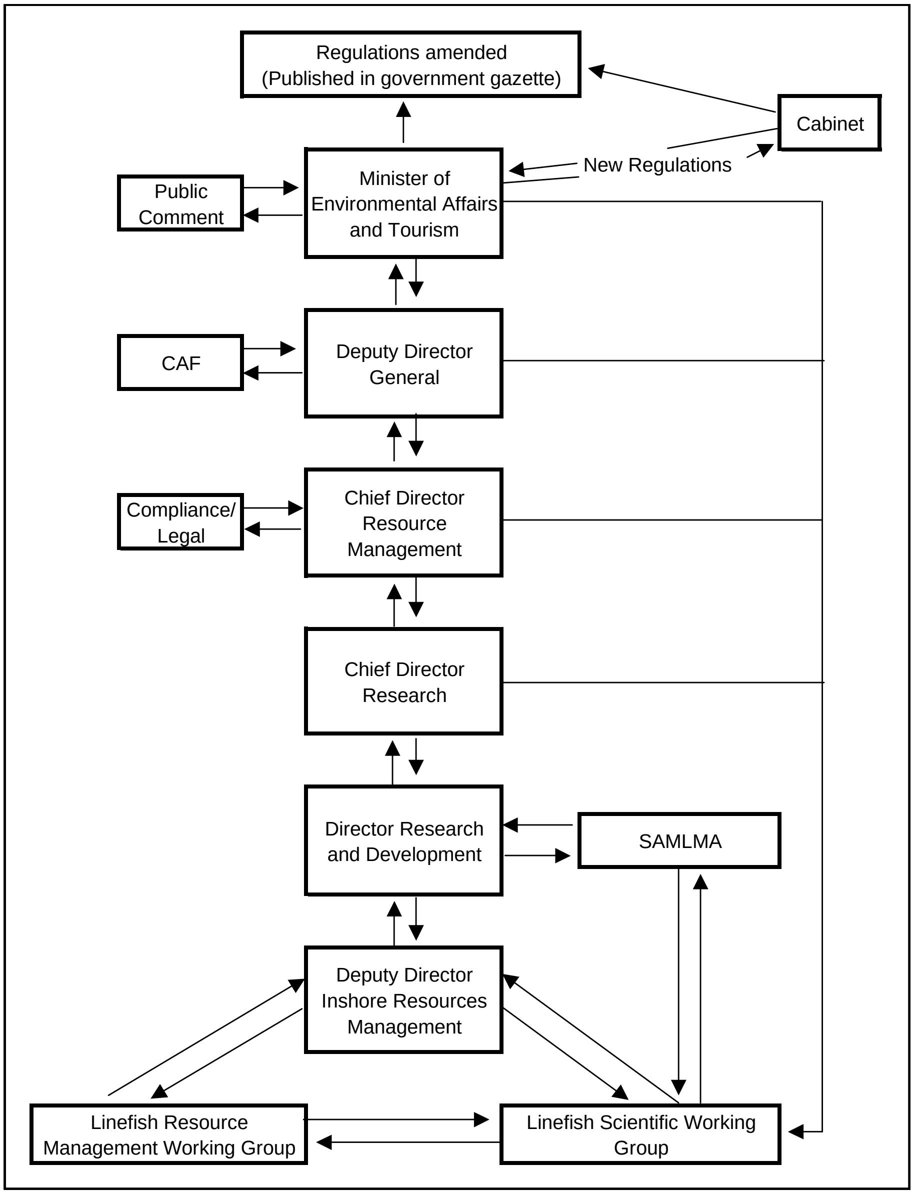

Figure 1: Flow chart representing the sequence of events and group/personal interactions involved in the South African marine linefish management review process. [1]CAF = Consultative Advisory Forum, SAMLMA = South African Marine Linefish Management Association.

Uncertainty in the dynamic nature of marine ecosystems is, according to Sumaila (1998), one of the biggest obstacles to providing effective management. The behaviour of fishers and decision makers' actions must therefore be precautionary

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[1] A forum consisting of at least 5 members appointed by the Minister of Environmental Affairs and Tourism to provide the Minister with advice on management and related legislation. As set out in the Marine living Resources act (Act 18 of 1998).

(Buckworth 1998; Hart and Reynolds 2002). According to Penny (1997), species with slow growth and limited distribution that are caught in multispecies, multi-user fisheries are likely to remain susceptible to overexploitation even with strictly enforced management plans, as they are prone to rapid stock depletion. Pauly (1997b), supports this argument, and advocates the use of MPAs as an additional measure to guard against stock collapse. MPAs represent a holistic approach to management of marine systems where whole ecosystems can be protected, and essential ecological processes can be maintained undisturbed. MPAs provide a refuge for overexploited resident species (Buxton and Smale 1989; Russ and Alcala 1989; Bohnsak 1998) and the TNP has been shown to house healthy populations of large individuals of many South African linefish species (Brouwer 2002; Cowley *et al*. 2002).

This form of management falls within the scope of the guidelines set out in the South African Marine Living Resources Act (Act 18 of 1998), which advocates the use of an ecosystem approach to management. Furthermore, the use of MPAs as a management tool is inline with Pitcher and Pauly's (1998) belief that rebuilding ecosystems should be the ultimate goal of fisheries management. The high *cpue* (23 times greater than the adjacent fishery) and relative reproductive output in the TNP carpenter population shows that this MPA provides effective protection for adult carpenter and that adjacent stocks can benefit from recruits from that area. The TNP therefore should be maintained as a closed area MPA.

### Ongoing assessment and compliance needs

Carpenter are well below the threshold reference point, therefore the populations' response to the newly implemented management plan must be closely monitored to check for possible stock recovery and to consider whether additional restrictions will be required. As carpenter consists of two stocks, which are separated more or less around the political boundary between the Western and Eastern Cape, managing the carpenter resource differently in each province is possible. However, a management regime that discriminates between users of the same sector in different areas increases interregional user conflict that can decrease compliance (Sauer *et al*. 1997). Despite this, the varying effort levels and varying degrees of regional law enforcement may mean that one stock may recover faster than the other. In the future, different management policies for each stock may become necessary, therefore separate regional assessments of this resource are appropriate. Restricting user movement between areas could facilitate regional management, increase co-operation among fishing communities, instil a sense of ownership (Attwood and Farquhar 1999) and improve compliance as well as reduce inter-regional conflict.

Low levels of user compliance with the fishery regulations are experienced in the South African commercial linefishery (Sauer *et al*. 1997). This compliance problem needs to be tackled as a matter of urgency. If the newly proposed management plan is to be successful increased compliance is essential. In order to increase compliance an enlarged body of fishery control officers is required. Currently the South African fisheries inspectorate is understaffed and therefore unable to effectively police the entire fishery (Brouwer *et al*. 1997; Sauer *et al*. 1997). A landings monitoring programme, however, would free the current inspectorate for increased enforcement work. In the past most of the inspectorate was involved in monitoring landings for TAC purposes for other fisheries such as West Coast rock lobster (*Jasus lalandii*), and currently most are involved in policing of high profile resources such as abalone

(*Haliotis midae*). Scientifically trained monitors used to collect fishery information are being increasingly used internationally (Davis and Reynolds 2003). A programme of coastal monitors at access points, which has been proposed for the South African linefishery, would be essential to monitor changes in catch trends such as length frequency, *cpue*, and bag frequencies. This programme is critically important so that the impacts of management measures can be assessed.

Users in both the commercial and recreational sectors are not familiar with the fishery regulations. Consequently, even though there is general support for the regulations they are not always adhered to, rendering them ineffective (Brouwer *et al*. 1997; Mann *et al*. 1997; Sauer *et al*. 1997). Improvements in fisher knowledge of the regulations will hopefully result from the fact that the new permits for all linefish species have a list of the regulations attached. Nevertheless, an effective policing body will still be essential, as a high proportion of fishers in all linefish sectors (32, 26 and 28% in the ski-boat, rock and surf and spear fisheries, respectively) have admitted to knowingly ignoring fishery regulations at some time in their lives (Brouwer *et al*. 1997; Mann *et al*. 1997; Sauer *et al*. 1997).

Continuous re-assessment of the resource is vital, so that the response of the stock to the management actions can be monitored. This can be done through numerous methods, but most important would be a continuous assessment of the *cpue*, length frequency and bag frequency trends collected continuously by shore monitors, followed by updated stock assessments using *Egg/R* methods with an updated age length key. These data can be collected as per the methods outlined in Chapter 5, where a single large sample is collected from each stock using a stratified sampling design. Age validation would not be necessary as the growth zones have been validated as annuli (Brouwer and Griffiths 2004), and fecundity at size is unlikely to change. Age and length at maturity (and fecundity at age if needed) can also be obtained from a single large sample, if it is conducted during the spawning season. For carpenter December to February would be the most appropriate time for collecting this sample (Chapters 3 and 6). Stock assessments would need to be carried out at frequencies appropriate to the generation time of the species i.e. at half the maximum age of the species (Griffiths 1997d), which in the case of carpenter would be once every 15 years. However, as carpenter is important to the fishery it may be prudent to assess the fishery at more regular intervals such as every 10 years. $F$, however, should be calculated more regularly such as every 5 years (Griffiths 1997d).

One of the objectives of sampling in the TNP was to obtain an accurate estimate of $M$. It was believed that $Z$ in the TNP would approximate $M$ as $F = 0$. However, as juveniles only begin to enter the park at ±200 mm FL and, in all likelihood, adults leave the park later in life, calculating an accurate estimate of $Z$ in that area was not possible. Hence, for this species $M$ must be calculated using other methods, such as that proposed by Roff (1984). Although $F$ can be estimated from tag and release data, the difference in effort inside and outside the Tsitsikamma National Park made this method unreliable for this study. Estimates of $Z$ and $M$ are needed to calculate $F$, and these data can be obtained from various methods such as catch curves and tag and release data (Griffiths 1997d). Catch curves allow accurate estimates of $Z$, but only after several years of exposure to a specific level of exploitation. Tag and release methods, however, can yield estimates of mortality in only 1 year. In South Africa, tag and release methods have limited application as an estimated 60% of fish recaptured by the South African commercial linefishery go unreported (Brouwer 1997). However, if the access point monitoring programme (see above) is implemented, accurate *cpue* and catch data will be obtained and age structured production models could be employed, particularly if the data reveal strong signals. In addition, the presence of shore-based monitors will increase the tag recapture reporting rate.

There is some resistance from users to the regulations (Brouwer 1997), because many species affected by barotrauma die when released and high mortality rates of released fish will decrease the effectiveness of a size or bag limit (Harley *et al*. 2000 a, b). This could potentially cause problems, as an increase in the size limit is proposed here as part of the management plan (Chapter 7; Appendix II). However, observations made during the tagging study revealed that only a small proportion of carpenter needed treatment to relieve the symptoms of barotrauma, even those caught at depths down to 90 m. The recapture rate of 5-7% suggests that the survival rate of released fish is sufficient. This increases the likelihood that size and bag limits collectively will be effective management tools for this species. Increasing the size limit will have other benefits. Fish movement into the TNP is size related, and the increased size limit will ensure that more carpenter will be able to avoid capture and move into the TNP. This will increase the spawner biomass in the TNP (assuming that the carrying capacity has not yet been reached), which in turn could increase recruitment to the fishery (Brouwer *et al*. 2003).

The primary concern of fishers to a change in the regulations is the direct negative effect that it will have on their catch (Brouwer 1997). With the change in regulations the estimated short term losses in catch are likely to be a concern for commercial linefishers. However, increases in *cpue* as the stock recovers, and thus financial gains should ensure not only sustainability of the resource, but also long-term financial security for participants. Furthermore, as there are fewer participants competing for the resource each fisher could potentially experience higher catch rates.  A matter of concern, however, is that those commercial fishers who have lost their commercial licence can theoretically remain active in the fishery as recreational users. As a result the recreational sector is expected to undergo a sudden increase in effort. While the management plan takes recreational use into account, effective fishery control to ensure compliance with the regulations is essential to restrict the recreational catch.

### Future directions for research and management

As valuable information can be obtained from commercial fishers (Grandcourt 2003), fishery dependent data is often sought after by fisheries managers. A problem that may be experienced by future programmes aimed at collecting biological information from fishery dependent sources, is that fisher co-operation may decline. This occurs when fishers begin to realise that biological research on species such as kob (*Argyrosomus* spp.), geelbek (*Atractoscion aequidens*) and carpenter has resulted in increased size limits and decreased bag limits. Fishery dependent biological data may then become more difficult to obtain (pers. obs.). In order to negate this effect, when stocks improve as a result of effective management, bag limits will increase and more commercial entrants may be allowed. When this occurs advertisement initiatives should focus on successes to promote the value of fisheries management to the public.

The TNP has been shown to protect carpenter and other linefish populations and to seed adjacent areas with recruits. Therefore, by implication, other large appropriately placed MPAs should offer this species protection from fishing pressure. A MPA aimed at protecting linefish species, including carpenter, from overfishing would need to be large. Griffiths and Wilke (2002) suggest that, based on carpenter movement data, a MPA of >147 km long would be needed to effectively protect carpenter. A MPA of this size would be difficult to create, as it would include large areas that are currently fished by many different sectors. However, offshore on the central Agulhas Bank a MPA centred around the 45 mile bank is a possibility. Firstly, this area consists of high profile reef and is therefore avoided by the demersal trawl fleet. Secondly, it contains not only carpenter but also mature reproductively active individuals of many other severely depleted reef associated linefish species, such as red steenbras *Petrus rupestris* and red stumpnose *Chrysoblephus gibbiceps* (Smale and Badenhorst 1991; Griffiths and Wilke 2002). Thirdly, through the Vessel Monitoring System (VMS) that is being phased in at present, it will be possible to restrict access to an offshore MPA in South Africa, as all vessel movements will be monitored by MCM. Finally, due to the collapsed state of many of the South African linefish species, it is policy to limit participation in the linefishery to those who rely on these resources as primary income.

As a result of this, rights holders in the commercial linefish sector may not possess rights to other marine fisheries (Government Gazette no. 21949). The net effect of this is that large vessels used mostly for squid, *Loligo vulgaris reynaudii*, swordfish *Xiphias gladius* and tuna, *Thunnus* spp., which are attracted to the offshore regions by these lucrative fisheries, and fish part time for linefish, no longer have access to that resource. Therefore, the linefish effort on the offshore Agulhas Bank is expected to drop markedly. As a result, proclaiming an offshore MPA where no vessels are fishing will potentially receive little resistance from the user groups. The creation of an offshore MPA may, perhaps, appear to be an unnecessary exercise, but as fish stocks in the area increase, it may become financially viable for fishers to invest in large vessels with the aim of targeting linefish offshore. This situation is to some extent already becoming apparent. An MPA in this area would therefore guard against 1) effort creep. Although the technology exists to fish in this area, it is not currently financially viable to do so exclusively for linefish. However, it was noted by both Buckman (1998) and Smith (2002) that it is usually in the best interests of individual fishers to increase their harvesting power; 2) future exploitation of this portion of these spawner stocks, thereby creating more stability in inshore linefish stocks that are dependent on recruitment from this area. A large offshore MPA on the central Agulhas Bank should be seen as a holistic approach to managing a suite of South African linefish species. This would therefore be highly beneficial to carpenter and other stocks and should be investigated as a matter of urgency, and if implemented should be monitored for signs of recovery through a scientifically run fishery independent monitoring programme (using *cpue* at 1 to 3 year intervals).

This proposal to include an offshore MPA in South Africa’s MPA network falls in line with international trends, where an ecosystem approach to management is advocated. Furthermore, it follows the South African Marine Living Resources Act (Act 18 of 1998), which identifies the need to protect ecosystems as a whole.

An ecosystem approach to management requires the protection of whole ecosystems such as the TNP. Nevertheless, conservative management outside of these areas is still required. This work focused on biology and biological management of the carpenter resource and the management plan presented here (Appendix II) deals exclusively with these aspects of the management process. It does not take into account the economic implications to the state of appointing coastal monitors or the short term economic implications to the users of the effects of reduced carpenter catch. To successfully manage this and other linefish species, user acceptance of the management process is essential and the effects of the management plan on users should therefore be assessed. The economic and socio-economic implications of the management plan, both in the short and long term for both users and management agencies should therefore be investigated as a matter of urgency.

# REFERENCES

AHRENS, R.L. 1964. A preliminary report on the biology of the seventyfour, *Polysteganus undulosus* (Regan 1908), in Natal waters. M.Sc. thesis. University of Natal, Durban: 77pp.

ALLEN, B.R. and WINTER, S.P. 2002. Age and growth of the spinner shark *Carcharhinus brevipinna* (Muller and Henle, 1839) of the Kwa-Zulu Natal coast, South Africa. *S. Afr. J. mar. Sci.* **24**: 1-8.

ANNALA, J.H. 1996. New Zealand's ITQ system; have the first eight years been a success or a failure? *Rev. Fish Biol*. **6**: 43-62.

ANON. 2002. Plan of Implementation. World Summit on Sustainable Development; Unpublished document. Department of Environmental Affairs and Tourism. South Africa. 54pp.

APPLEDOORN, R.S. 1996. Model and method in reef fishery assessment. In *Reef fisheries*. Polunin, N.V.C. and Roberts, C.M. (Eds.). Chapman and Hall, London: 219-248.

ATTWOOD, C.G. and BENNETT, B.A. 1995. A procedure for setting daily bag limits on the recreational shore-fishery of the south-western Cape, South Africa. *S. Afr. J. mar. Sci*. **15**: 241-251.

ATTWOOD, C.G. and FARQUHAR, M. 1999. Collapse of linefish stocks between Cape Hangklip and Walker Bay, South Africa. *S. Afr. J. mar. Sci*. **21**: 415-432.

ATTWOOD, C.G. and SWART, L. 2000. Discrepancy between otolith and tag-recovery estimates of growth for two South African surf-zone teleost species. *S. Afr. J. mar. Sci*. **22**: 9-15.

ATTWOOD, C.G., ALLEN, J.C. and P.J. CLAASSEN. 2002. Nearshore surface current patterns in the Tsitsikamma national Park, South Africa. *S. Afr. J. mar. Sci*: **24**: 151-160.

AULT, J.S., BOHNSAK, J.A. and MEESER, G.A. 1998. A retrospective (1979-1996) multispecies assessment of coral reef fish stocks in the Florida Keys. *Fish. Bull., Wash*. **96** (3): 395-414.

BADENHORST, A. and M.J. SMALE. 1991. The distribution and abundance of linefish and secondary trawlfish on the Cape south coast of South Africa, 1986-1990. *S. Afr. J. mar. Sci.* **11**: 395-407.

BARANGE, M. and HAMPTON, I. 1997. Spatial structure of co-occurring anchovy and sardine populations form acoustic data: implications for survey design. *Fish. Oceanogr*. **6** (2): 94-108.

BARANGE, M., HAMPTON, I. and ROEL, B.A. 1999. Trends in the abundance and distribution of anchovy and sardine on the South African continental shelf in the 1990s, deduced from acoustic surveys. *S. Afr. J. mar. Sci*. **21**: 367-391.

BEACHAM, T.D. 1983. Variability in median size and age at sexual maturity of Atlantic cod, *Gadus morhua*, on the Scotian shelf in the northwest Atlantic ocean. *Fish. Bull., Wash*. **81**: 303-321.

BEAMISH, R.J and FOURNIER, D.A. 1981. A method for comparing the precision of a set of age determinations. *Can. J. Fish. Aquat. Sci.* **38**: 982-983.

BEAMISH, R.J and MCFARLANE, G.A. 1995. A discussion of the importance of ageing errors, and an application to walleye pollock: the worlds largest fishery. In: *Recent developments in fish otolith research*. D.H. Secor, J.M. Dean and S.E. Campana (Eds.). University of South Carolina press: 545-565 pp.

BECKLEY, L.E. and VAN BALLEGOOYEN, R.C. 1992. Oceanographic conditions during three ichthyolpankton surveys of the Agulhas current in 1990/91. *S. Afr. J. mar. Sci*. **12**: 83-93.

BECKMAN, D.W. and WILSON, C.A. 1995. Seasonal timing of opaque zone formation in fish otoliths. In *Recent developments in fish otolith research*. Sector, D.H., Dean, J.M., and Campana, S.E. (Eds.). Columbia; University of South Carolina press: 27-43 pp.

BENNETT, B.A. 1993. Aspects of the biology and life history of white steenbras *Lithognathus lithognathus* in southern Africa. *S. Afr. J. mar. Sci*. **13**: 83-96.

BEST, P.B. 1999. Food and feeding of sperm whales *Physeter macrocephalus* off the west coast of South Africa. *S. Afr. J. mar. Sci*. **21**: 393-413.

BOHNSACK, J.A. 1998. Application of marine reserves to reef fisheries management. *Aust. J. Ecol*. **23**: 298-304.

BOOTH, A.J and BUXTON, C.D. 1997. The biology of the panga, *Pterogymnus laniarius* (Teleostei: Sparidae), on the Agulhas Bank, South Africa. *Env. Biol. Fish*. **49**: 207-226.

BOOTH, A.J and T. HECHT. 1997. A description of gametogenesis in the panga *Pterogymnus laniarius* (Pisces: Sparidae) with comments on changes in maturity patterns over the past two decades. *S. Afr. J. Zool*. **32**(2). 49-53.

BOYD, A.J. and F. SHILLINGTON. 1994. Physical forcing and circulation patterns on the Agulhas Bank. *S. Afr. J. Sci*. **90**: 114-122.

BRODZIAK, J and MIKUS, R. 2000. Variation in life history parameters of Dover sole, *Microstomus pacificus*, off the coasts of Washington, Oregon and northern California. *Fish. Bull., Wash*. **98**: 661-673.

BROUWER, S.L. 1997. An assessment of the South African East Coast linefishery from Kei Mouth to Stil Bay. M.Sc. thesis, Rhodes University: 124pp.

BROUWER, S.L. 2002. Movement patterns of red steenbras *Petrus rupestris* tagged and released in the Tsitsikamma National Park, South Africa. *S. Afr. J. mar. Sci*. **24**: 375-378.

BROUWER, S.L. and C.D. BUXTON. 2002. Catch and effort of the shore and ski-boat linefisheries along the South African Eastern Cape coast. *S. Afr. J. Mar. Sci*. **24**: 341-354

BROUWER, S.L. and M.H. GRIFFITHS. 2004. Age and growth of *Argyrozona argyrozona* (Pisces: Sparidae) in a Marine Protected Area: an evaluation of methods based on whole otoliths, sectioned otoliths and mark recapture. *Fish. Res*. **67**: 1-12.

BROUWER, S.L., MANN, B.Q., LAMBERTH, S.J. SAUER, W.H.H. and ERASMUS, C. 1997. A survey of the South African shore angling fishery. *S. Afr. J. mar. Sci*. **18**: 165-177.

BROUWER, S.L., GRIFFITHS, M.H. and ROBERTS, M.J. 2003. Adult movement and larval dispersal of *Argyrozona argyrozona* (Pisces: Sparidae) from a temperate marine protected area. *Afr. J. mar. Sci*. **25**: 395-402.

BRULE', T., RENAN, X., COLAS-MARRUFO, HAUYON, Y., TUZ-SULUB, A.N. and DENIEL, C. 2003. Reproduction in protogynous black grouper (*Micteroperca bonaci* (Poey)) from the southern Gulf of Mexico. *Fish. Bull., Wash*. **101**: 463-475.

BUCKWORTH, R.C. 1998. World fisheries are in a crisis? We must respond. In: *Reinventing fisheries management.* Pitcher, T.J., Hart, P.J.B. and Pauly, D. (EDS.). Kluwer Academic Publishers, London. 1-17.

BUTTERWORTH, D. S., PUNT, A.E, BORCHERS, D.L., PUGH, J.B. and HUGHES, G. [S]. 1989. *A manual of mathematical techniques for linefish assessment*. Rep. S. Afr. Nat. scient. Progms. **160**: [i] + 83 pp.

BUXTON, C.D. 1989. Protogynous hermaphroditism in *Chrysoblephus laticeps* (Cuvier) and *C. cristiceps* (Cuvier) (Teleostei: Sparidae). *S. Afr. J. Zool*. **24**: 212-216.

BUXTON, C.D. 1990. The reproductive biology of *Chrysoblephus laticeps* and *C. cristiceps* (Teleostei: Sparidae). *J. Zool. Lond*. **220**: 497-511.

BUXTON, C.D. 1992. The application of yield-per-recruit models to two South African sparid reef species, with special consideration to sex change. *Fish. Res.* **15**: 1-16.

BUXTON, C.D. 1993. Life-history changes in exploited reef fishes on the east coast of South Africa. *Env. Biol. Fish*. **36**: 47-63.

BUXTON, C.D. and CLARKE, J.R. 1986. Age growth and feeding of the blue hottentot *Pachymetopon aeneum* (Teleostei: Sparidae) with notes on reproductive biology. *S. Afr. J. Zool.* **21**: 33-38.

BUXTON, C.D. and CLARKE, J.R. 1989. The growth of *Cymatoceps nasutus* (Teleostei: Sparidae), with comments on diet and reproduction. *S. Afr. J. mar. Sci.* **8**: 57-65.

BUXTON, C.D. and CLARKE, J.R. 1991. The biology of the white musselcracker *Sparodon durbanensis* (Pisces: Sparidae) on the Eastern Cape coast, South Africa. *S. Afr. J. mar. Sci.* **10:** 285-296.

BUXTON, C.D. and CLARKE, J.R. 1992. The biology of the bronze bream, *Pachymetopon grande* (Teleostei: Sparidae) from the south-east Cape coast, South Africa. *S. Afr. J. Zool.* **27** (1): 21-32.

BUXTON, C.D. and GARRATT, P.A. 1990. Alternative reproductive styles in seabreams (Pisces: Sparidae). *Env. Biol. Fish.* **28**: 113-124.

BUXTON, C.D. and SMALE, M.J. 1984. A preliminary investigation into the ichthyofauna of the Tsitsikamma Coastal National Park. *Koedoe*. **27**: 13-24.

BUXTON, C.D. and SMALE, M.J. 1989. Abundance and distribution patterns of three temperate marine fish (Teleostei: Sparidae) in exploited and unexploited areas off the southern Cape coast. *J. Appl. Ecol.* **26**: 441-451.

BUXTON, C.D., SMALE, M.J., WALLACE, J.H., and COCKCROFT, V.G. 1984. Inshore small-mesh trawling survey of the Cape south coast. Part 4. Contributions to the biology of some Teleostei and Chondrichthyes. *S. Afr. J. Zool*. 19(3): 180-188.

CADDY, J.F. and COCHRANE, K.L. 2001. A review of fisheries management past and present and some future perspectives for the third millennium. *Ocean coast. Mgmt* **44**: 653-582.

CAMPANA, S.E. 2001. Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation. *J. Fish. Res*. **59**: 197-242.

CAPPO, M., EDEN, P., NEWMAN, S.J. and ROBERTSON, S. 2000. A new approach to validation of periodicity and timing of opaque zone formation in the otoliths of eleven species of *Lutjanus* from the central Great Barrier Reef. *Fish. Bull., Wash*. **98**: 474-488.

CARR, M.H. and D.C. REED. 1993. Conceptual issues relevant to marine harvest refuges: examples from temperate reef fishes. *Can. J. Fish. Aquat. Sci*. **50**: 2019-2028.

CASTLEY, J.G, COCKCROFT, V.G and KERLEY, G.I.H. 1991. A note on the stomach contents of fur seals *Arctocephalus pusillus pusillus* beached on the south-east coast of South Africa. *S. Afr. J. mar. Sci.* **11**: 573-578.

CHALE-MATSAU, J.R., GOVENDER, A. and BECKLEY, L.E. 2001. Age, growth and retrospective stock assessment of an economically extinct sparid fish, *Polysteganus undulosus*, from South Africa. *Fish. Res*. **51**: 87-92.

CHANG, W.Y.B. 1982. A statistical method for evaluating the reproducibility of age determination. *Can. J. Fish. Aquat. Sci*. **39**: 1208-1210.

CHATER, S.A., FERGUSON, R. VAN DER ELST, R.P. GOVENDER, A. and BECKLEY, L.E. 1995. Catch statistics and notes on the biology of two knifejaw species (Teleostei: Oplegnathidae) from Natal, South Africa. *Lammergeyer*. **43**:6-14.

CLARKE, W.G. 1993. The effect of recruitment variability on the choice of a target level of spawning biomass per recruit. In *Proceedings of the international symposium on management strategies for exploited fish populations, Anchorage, Alaska. October 1992.* Kurse, G., Eggers, D.M., Marasco, R.J., Pautzke, C and Quinn, T.J. (Eds.). Alaska Sea Grant Rep. **93-02**: 233-246.

COCHRANE, K.L. and PAYNE, A.I.L. 1998. People, purses and power: developing fisheries policy for the new South Africa. In: *Reinventing fisheries management.* Pitcher, T.J., Hart, P.J.B. and Pauly, D. (EDS.). Kluwer Academic Publishers, London. 73-99.

COETZEE, P.S. and BAIRD, D. Age, growth and food of *Chimerius nufar* (Ehrenberg, 1920) (Sparidae), collected off St. Croix Island, Algoa Bay. *S. Afr. J. Zool*. **16** (3): 137-143.

COGGINS Jr., L.G. and QUINN, T.J. 1998. A simulation study of the effects of aging error and sample size on sustained yield estimates. *Fishery stock assessment models, Alaska sea grant program*. **AK-SG-98-01**: 55-975.

COLLINS, L.A., A.G. JOHNSON, C.C. KOENIG and M.S. BAKER. 1998. Reproductive patterns, sex ratio, and fecundity in gag, *Mycteroperca microlepis* (Serranidae), a protogynous grouper from the northeastern Gulf of Mexico. *Fish. Bull., Wash.* **96**: 415-427.

COLLINS, M.R., MCGOVERN, J.C., SEEDBERRY, G.R., MEISTER, H.S. and PARDIECK, R. 1999. Swim bladder deflation in black sea bass and vermilion snapper: potential for increasing post release survival. *N. Am. J. Fish. Mgmt*. **19**: 828-832.

CORTES, E. 1997. A critical review of methods of studying fish feeding based on analysis of stomach contents: application to elasmobranch fishes. *Can. J. fish. Aquat. Sci*. **54**: 726-738.

COUTIN, P.C., CASHMORE, S. and SIVAKUMURAN, K.P. 2003. *Assessment of the snapper fishery in Victoria. Final Rep.* **97/128**. Victoria, Australia; Marine and Freshwater Resources Institute: 205pp.

COWLEY. P.D., BROUWER, S.L. and TILNEY, R.L. 2002. The role of the Tsitsikamma National Park in the management of four shore-angling fish along the south-eastern Cape coast of South Africa. *S. Afr. J. mar. Sci*. **24**: 27-35.

DANILOWICZ, B.S. 1995. The role of temperature in spawning of damselfish *Dascyllus albisella*. *Bull. Mar. Sci*. **57** (3): 624-636.

DAVID, J.H.M. 1987. Diet of the South African fur seal (1974-1985) and an assessment of competition with fisheries in southern Africa. *S. Afr. J. mar. Sci*. **5**: 693-713.

DAVIS, J.A. 1996. Investigations into the larval rearing of two South African sparid species. M.Sc. thesis. Rhodes University: 138pp.

DAVIS, J.A. and C.D. BUXTON. 1996. Larval development of laboratory-reared carpenter, *Argyrozona argyrozona* (Pisces: Sparidae). *S. Afr. J. Zool*. **31** (1): 10-14.

DAVIS, S.I. and REYNOLDS, J.E. 2003. Guidelines for developing an at-sea fishery observer programme. *FAO Fish. Tech. Pap*. **414**: 116pp.

DAVIS, T.L.O. and G.J. WEST. 1993. Maturation, reproductive seasonality, fecundity, and spawning frequency in *Lutjanus vittus* (Quoy and Gaimard) form the North West shelf of Australia. *Fish. Bull., Wash*. **91**: 224-236.

DEMARTINI, E.E., DINARDO, G.T. and WILLIAMS, H.A. 2003. Temporal changes in population density, fecundity and egg size of Hawaiian spiny lobster (*Panulirus marginatus*) at Necker Bank, northwestern Hawaiian Islands. *Fish Bull., Wash*. **101**: 22-31.

FAO. 2003. Implementation of ecosystem approach to fisheries management to achieve responsible fisheries and to restore fisheries resources and marine environments. Committee on Fisheries, 25th Session. Rome, Italy. 6pp.

FENNESSY, S.T., MCDONALD, A.M., MANN, B.Q. and EVERETT, B.I. 2003. An assessment of the recreational and commercial ski-boat fishery in the Transkei. *Afr. J. mar. Sci*. **25**: 61-78.

FERREIRA, B.P. and RUSS, G.R. 1993. Age validation and estimation of growth rate of coral trout, *Plectropomus leopardus*, (Lacepede 1802) from Lizard Island, Northern Great Barrier Reef. *Fish. Bull., Wash*. **92**: 46-57.

FRANCIS, M.P., MULLIGAN, K.P., DAVIES, N.M. and BEENTJES, M.P. 1999. Age and growth estimates for New Zealand hapuku, *Polyprion oxygeneios*. *Fish. Bull., Wash*. **97**: 227-242.

FRANCIS, R.I.C.C., PAUL, L.J. and MULLIGAN, K.P. 1992. Ageing of adult snapper (*Pagrus auratus*) from otolith annual ring counts: validation by tagging and oxytetracycline injection. *Aust. J. Mar. Freshwater Res*. **43**: 1069 –1089.

GARCIA, S.M. and NEWTON, C. 1997. Current situation, trends and prospects in world capture fisheries. In *Global trends: fisheries management*. Pikitch, E.K., Huppert, D.D and Sissenwine, M.P. (Eds.). American Fisheries Society Symposium, 20. Bethesda, Maryland: 2-27.

GARRATT, P.A. 1985. The offshore linefishery of Natal: II: Reproductive biology of the sparids *Chrysoblephus puniceus* and *Cheimerius nufar*. *Oceanogr. Res. Inst. Invest. Rep*. **63**: 1-21.

GARRATT, P.A. 1986. Protogynous hermaphroditism in slinger *Chrysoblephus puniceus* (Gilchrist and Thompson, 1971) (Teleostei: Sparidae). *J. Fish Biol*. **28** (3): 297-306.

GARRATT, P.A. 1988. Notes on seasonal abundance and spawning of some important offshore linefish in Natal and Transkei waters, southern Africa. *S. Afr. J. mar. Sci*. **7**: 1-8.

GODINHO, A.L. 1997. Weight-length relationship and condition of the characiform *Triportheus guentheri*. *Env. Biol. Fish*. **50**: 319-330.

GOODYEAR, C.P. 1995. Mean size at age: an evaluation of sampling strategies with simulated red grouper data. *Trans. Am. Fish. Soc*. **124**: 746-755.

GRANDCOURT, E.M. 2003. The effects of intensive line fishing on the virgin biomass of a tropical deepwater snapper, the crimson jobfish (*Pristipomoides filamentosus*). *Fish. Bull., Wash*. **101**: 305-311.

GREENWOOD, C. and CLARKE, D.I. 1994. Time series of monthly mean sea temperature around the South African coast. Internal report Sea Fisheries Research Institute. **124**: 36pp.

GRIFFITHS, M.H. 1996a. Life history of the dusky kob *Argyrosomus japonicus* (Sciaenidae) off the east coast of South Africa. *S. Afr. J. mar. Sci*. **17**: 135-154.

GRIFFITHS, M.H. 1996b. Age and growth of South African silver kob *Argyrosomus inodorus* (Sciaenidae) with evidence for separate stocks. *S. Afr. J. mar. Sci*. **17**: 37-48.

GRIFFITHS, M.H. 1997a. The application of per-recruit models to *Argyrosomus inodorus,* an important South African sciaenid fish. *Fish. Res*. **30**: 103-115.

GRIFFITHS, M.H. 1997b. The life history and stock separation of silver kob, *Argyrosomus inodorus,* in South African waters. *Fish. Bull., Wash.* **95** (1): 47-67.

GRIFFITHS, M.H. 1997c. Management of the South African dusky kob *Argyrosomus japonicus* (Sciaenidae) based on per recruit models. *S. Afr. J. mar. Sci*. **18**: 213-228.

GRIFFITHS, M.H. 1997d. Towards a management plan for the South African linefishery; objectives and strategies. In *Management and monitoring of the South African marine linefishery*. SANCOR Occ. Res. Rep. **3**: 3-14.

GRIFFITHS, M.H. 2000. Long-term trends in the catch and effort of commercial linefish off South Africa's Cape Province: Snapshots of the 20th century. *S. Afr. J. mar. Sci*. **22**: 81-110.

GRIFFITHS, M.H. and HECHT, T. 1995. On the life history of *Atractoscion aequidens*, a migratory sciaenid off the east coast of southern Africa. *J. Fish Biol*. **47**: 962-985.

GRIFFITHS, M.H. and WILKE, C.G. 2002. Long term movement patterns of five temperate-reef fishes (Pisces: Sparidae): implications for marine reserves. *Mar. Freshwater Res*. **53**: 1-12.

GRIFFITHS, M.H., ATTWOOD, C. and THOMPSON R. 1999. New management protocol for the South African linefishery. In *Proceedings of the third southern African marine linefish symposium, Arniston, 28 April – 1 May 1999*. SANCOR Occ. Rep. **5**: 145-156.

GRIFFITHS, M.H., WILKE, C. PENNY, A.J. and Y. MELO. 2002. Life history of white stumpnose *Rhabdosargus globiceps* (Pisces: Sparidae) off South Africa. *S. Afr. J. mar. Sci*. **24**: 281-300

GULLAND, J.A. 1983. Fish stock assessment. A manual of basic methods. *FAO/ Wiley Series on Food and Agriculture*. **1**: 223pp.

HAGGAN, N. 1998. Reinventing the tree: reflections on the organic growth and creative pruning of fisheries management structures. In: *Reinventing fisheries management.* Pitcher, T.J., Hart, P.J.B. and Pauly, D. (EDS.). Kluwer Academic Publishers, London. 19-30.

HANEKOM, N., MANN-LANG, J.B., MANN, B.Q. and T.V.Z. CARINUS. 1997. Shore angling catches in the Tsitsikamma National Park, 1989-1995. *Koedoe.* **40** (2): 37-56.

HARLEY, S.J., MILLAR, R.B. and MCARDLE, B.H. 2000a. Examining the effects of changes in the minimum legal size used in Hauraki Gulf snapper (*Pagrus aratus*) fishery in New Zealand. *Fish. Res*. **45**: 179-187.

HARLEY, S.J., MILLAR, R.B. and MCARDLE, B.H. 2000b. Estimating unaccounted fishing mortality using selectivity data: an application in the Hauraki Gulf snapper (*Pagrus auratus*) fishery in New Zealand. *Fish. Res*. **45**: 167-178.

HARRIS, P.J. and MCGOVERN, J.C. 1997. Changes in the life history of red porgy, *Pagrus pagrus*, from the southeastern United States, 1972-1994. *Fish. Bull., Wash*. **95**: 732-747.

HART, P.J.B. and REYNOLDS, J.D. 2002. Banishing ignorance: underpinning fisheries with basic biology. In: *Handbook of fish biology and fisheries, Volume 1, Fish Biology.* Hart, P.J.B and Reynolds, J.D. (EDS.). Blackwell publishing, Cornwall. 1-11.

HECHT, T. and BAIRD, D. 1997. Contributions to the biology of the panga *Pterogymnus laniarius* (Pisces: Sparidae): Age growth and reproduction. *Zool. Afr*. **12**: 363-372.

HECHT, T. and TILNEY, R.L. 1989. The Port Alfred fishery; a description and preliminary evaluation of a commercial linefishery on the South African east coast. *S. Afr. J. mar. Sci*. **8**: 103-117.

HILBORNE, R and MANGEL, M. 1997. The ecological detective: confronting models with data. Monographs in population biology No. 28. Princeton; Princeton University Press: 315pp.

HORN, P.L. and SUTTON, C.P. 1996. Validated ages, growth and productivity parameters for silver warehou (*Seriolella punctata*) off the south and east coasts of South Island, New Zealand. *N.Z. Jl. mar. and Freshwater Res*. **30**: 301-312.

HUGGETT, J., FREON, P. MULLON, C. and PENVEN, P. 2003. Modelling the transport success of anchovy *Engraulis encrasicolus* eggs and larvae in the southern Benguela: the effects of spatio-temporal spawning patterns. *Mar. Ecol. Prog. Ser*. 250: 247-262.

HUNTER, J.R. and B.J. MACEWICZ. 1985. Rates of atresia in the ovary of captive and wild northern anchovy *Engraulis mordax Fish. Bull., Wash*. **83** (2): 119-136.

HUNTER, J.R., N.C.H. LO, and R.J.H. LEONG. 1985. Batch fecundity and multiple spawning in fishes. In *An egg production method for estimating spawner biomass of pelagic fish: Application to the northern anchovy, Engraulis mordax*. Lasker, R. (Ed.). NOAA Tech. Rep. NMFS. **36**: 67-77.

HUNTSMAN, G.R., MANOOCH, G.S. and GRIMES, C.B. 1983. Yield per recruit models of some reef fishes of the U.S. south Atlantic Bight. *Fish. Bull., Wash.* **81**: 679-695.

HUTCHINGS, L. 1994. The Agulhas Bank: a synthesis of available information and a brief comparison with other east-coast shelf regions. *A. Afr. J. Sci.* 90: 179-185.

HUTCHINGS, J.A. 2002. Life histories of fish. In *Handbook of fish biology and fisheries, volume 1, Fish Biology*. Hart, P.J.B and Reynolds, J.D. (Eds.). Oxford; Blackwell publishing: 149-174.

HYNDES, G.A., LONERAGAN and POTTER, I.C. 1992. Influence of sectioning otoliths on marginal increment trends and age and growth estimates for the flathead *Platycephalus speculator*. *Fish. Bull., Wash.* **90**:276-284.

ILLGNER, P.M. 1996. Coastal Features. In *The geomorphology of the Eastern Cape*. Lewis, G.A. (Ed.). Grahamstown, Grocott and Sherry, South Africa: 52-71.

JAPP, D.W. 1990. A new study on age and growth of kingklip *Genypterus capensis* off the south and west coasts of South Africa, with comments on its use for stock identification. *S. Afr. J. mar. Sci.* 9: 223-237.

JENNINGS, S. and KAISER, M.J. 1998. Effects of fishing on marine ecosystems. *Adv. Mar. Biol*. **34**: 201-352.

JENNINGS, S., REYNOLDS, J.D. and POLUNIN, N.C.V. 1999. Predicting and vulnerability of tropical reef fishes to exploitation with phylogenies and life histories. *Cons. Biol*. **13** (6): 1466-1473.

JENSEN, A.L. 1996. Ratio estimation of mortality using catch curves. *Fish. Bull., Wash*. **27**: 61-67.

King, M. 1995. Fisheries biology, assessment and management. 341pp. Blackwell, London.

KRITZER, J.P., DAVIES, C.R. and MAPSTONE, B.D. 2001. Characterizing fish populations: effects of sample size and population structure on precision of demographic parameter estimates. *Can. J. Fish. Aquat. Sci.* **25**: 1557-1568.

LANG, J.B. and BUXTON, C.D. 1993. Validation of age estimates in sparid fish using fluorochrome marking. *S. Afr. J. mar. Sci.* **13**: 195-203.

LEAMAN, B.M. 1991. Reproductive styles and life history variables relative to exploitation and management of *Sebastes* stocks. *Env. Biol. Fish*. **30**: 253-271.

LEIS, J.M. 1991: The pelagic stage of reef fishes: The larval biology of coral reef fishes. In *The ecology of fishes on Coral Reefs*. Sale. P.F. (Ed.). New York; Academic Press: 182-230.

LEIS, J.M. and B. GOLDMAN. 1983. Studies on the biology of larval fishes in the Lizard Island area, Northern Great Barrier Reef. In *Proceedings: Inaugural Great Barrier Reef Conference*. Baker, T.J., Carter, R.M., Sammarco, P.W. and Stark, K.P. (Eds.). Townsville; James Cooke University Press: 221-225.

LOWERRE-BARBIERI, S.K. and L.R. BARBIERI. 1993. A new method of oocyte separation and preservation for fish reproduction studies. *Fish. Bull., Wash*. **91**: 165-170.

LUTJEHARMS, J.R.E, MEYER, A.A., ANSORGE, I.J., EAGLE, G.A. and ORREN, M.J. 1996. The nutrient characteristics of the Agulhas Bank. *S. Afr. J. mar. Sci*. **17**: 253-274.

MACE, P.M. 1994. Relationships between common biological reference points used as thresholds and targets of fisheries management strategies. *Can. J. Fish. aquat. Sci*. **51**: 110-122.

MANN, B.Q. 2000. Southern African marine linefish status reports. *Oceo. Res. Inst. Spec. Pbl.* **7**: 257pp.

MANN, B.Q. and BUXTON, C.D. 1997. Age and growth of *Diplodus sargus capensis* and *D. cervinus hottentus* (Sparidae) on the Tsitsikamma coast, South Africa. *Cybium*. **21** (2): 135-147.

MANN, B.Q. and BUXTON, C.D. 1998. The reproductive biology of *Diplodus sargus capensis* and *D. cervinus hottentus* (Sparidae) off the south-east Cape coast, South Africa. *Cybium*. **22** (1): 31-47.

MANN, B.Q., FENNESSY, S.T., GOVENDER, A. and VAN DER WALT, B. 2002. Age and growth and preliminary stock assessment of Stonebream *Neoscorpis lithophilus* (Pisces: Sparidae) along the Kwa-Zulu Natal coast, South Africa. *Mar. Freshwater Res.* **53**: 131-138.

MANN, B.Q., MCDONALD, A.M. SAUER, W.H.H. and HECHT, T. 2003. Evaluation of participation and management of the Transkei shore linefishery. *Afr. J. mar. Sci*. **25**: 79-97.

MANN, B.Q., SCOTT, G.M. MANN-LANG, J.B. BROUWER, S.L., LAMBERTH, S.J., SAUER, W.H.H. and ERASMUS, C. 1997. An evaluation of the participation and management of the South African spearfishery. *S. Afr. J. mar. Sci*. **18**: 179-193.

MCALLISTER, M.K., PETERMAN, R.M and GILLIS, D.M. 1992. Statistical evaluation of a large-scale fishing experiment designed to test for a genetic effect of size-selective fishing on British Columbia pink salmon (*Oncorhynchus gornuscha*). *Can. J. Fish. Aquat. Sci.* **49**: 1294-1304.

MCGLENNON, D., JONES, G.K., BAKER, J., JACKSON, W.B and KINLOCH, M.A. 2000. Ageing, catch-at-age and relative year-class strength for snapper (*Pagrus auratus*) in northern Spencer Gulf, South Australia. *Mar. Freshwater Res*. **21**: 669-677.

MELO, Y.C. 1994. Spawning frequency of the anchovy *Engraulis capensis*. *S. Afr. J. mar. Sci.* **14**: 321-331.

Microsoft Corporation. 2000. Excel. Microsoft Corporation, Seattle, WA.

MORALES-NIN, B. and MORANTA, J. 1997. Life history and fishery of the common dentex (*Dentex dentex*) in Mollorca (Balearic Islands, western Mediterranean). *Fish. Res.* **30**: 67-76.

MURPHY, M.D., ADAMS, D.H., TERMAIN, D.M. and WINNER, B.L. 1998. Direct validation of ages determined for adult black drum, *Pogonias cromis*, in east-central Florida, with notes on black drum migration. *Fish. Bull., Wash.* **96**: 382-387.

NEPGEN, C.S.V. 1977. The biology of the hottentot *Pachymetopon blochii* (Val.) and the silverfish *Argyrozona argyrozona* (Val.) along the cape south-west coast. *Investl. Rep. Div. Sea Fish. Rep. S. Afr*. **105**: 1-35.

NEPGEN, C.S. DE V. 1982. Diet of predatory and reef fish in False Bay and possible effects of pelagic purse-seining on the food supply. *Fish. Bull. S. Afr*. **16**: 75-93.

NEWMAN, S.J., WILLIAMS, D.McB. and RUSS, G.R. 1996. Variability in the population structure of *Lutjanus adetii* (Castelnau, 1873) and *L. quinquelineatus* (Bloch,

1790) among reefs in the central Great Barrier Reef, Australia. *Fish. Bull., Wash*. **94**: 313-329.

OJANGUREN, A.F., REYES-GAVILAN, F.G. and BRANA, F.. 1996. Effects of egg size on offspring development and fitness in brown trout, *Salmo trutta* L. *Aquaculture*. **147** (1-2): 9-20.

OSBORNE, R.F., Y.C. MELO, M.D. HOFMEYER and D.W. JAPP. 1999. Serial spawning and batch fecundity of *Merluccius capensis* and *M. paradoxus*. *S. Afr. J. mar. Sci*. **21**: 211-216.

PAJUELO, J.G. and LORENZO, J.M. 1995. Biological parameters reflecting the current state of exploited pink dentex *Dentex gibbosus* (Pisces: Sparidae) population off the Canary Islands. *S. Afr. J. mar. Sci*. **16**: 311-319.

PAJUELO, J.G. and LORENZO, J.M. 1996. Life history of the red porgy *Pagrus pagrus* (Teleostei: Sparidae) off the Canary Islands, central Atlantic. *Fish. Res*. **28**: 163-177.

PAJUELO, J.G. and LORENZO, J.M. 1998. Population biology of the common pandora *Pagellus erythrinus* (Pisces: Sparidae) off the Canary Islands. *Fish. Res*. **36**: 75-86.

PARSONS, L.S. and BECKETT, J.S. 1997. Fisheries management in Canada: the case of Atlantic groundfish. In *Global trends: fisheries management*. Pikitch, E.K., Huppert, D.D and Sissenwine, M.P. (Eds.). American Fisheries Society Symposium, 20. Bethesda, Maryland: 73-79.

PAUL, L.J. 1974. Hauraki gulf snapper fishery, 1972 and 1973: some evidence for a declining catch-rate. *N.Z. Jl. mar. Freshwater Res*. **8** (4): 569-587.

PAULY, D. 1980. On the interrelationships between natural mortality, growth parameters and mean environmental temperature in 175 fish stocks. *J. Cos. int. Explor. Mer*. **39**: 175-192.

PAULY, D. 1997a. Points of view – Putting fisheries management back in places. *Rev. Fish Biol. Fish*. **7**: 125-127.

PAULY, D. 1997b. Small-scale fisheries in the tropics: Marginality, marginalization, and some implications for fisheries management. In *Global trends: fisheries management*. Pikitch, E.K., Huppert, D.D and Sissenwine, M.P. (Eds.). American Fisheries Society Symposium, 20. Bethesda, Maryland: 40-49.

PAULY, D. and CHRISTENSEN, V. 2002. Ecosystem models. In: *Handbook of fish biology and fisheries, Volume 2, Fisheries*. Hart, P.J.B and Reynolds J.D. (Eds.). Blackwell publishing. Cornwall. 211-227.

PAWSON, M.G. and JENNINGS, S. 1996. A critique of methods for stock identification in marine capture fisheries. *Fish. Res*. 25: 204-217.

PAYNE, A.I.L. and BANNISTER, R.C.A. 2003. Science and fisheries management in southern Africa and Europe. *Afr. J. mar. Sci*. 25: 1-23.

PENNY, A.J. 1997. Discussion session. In *Management and monitoring of the South African marine linefishery*. SANCOR Occ. Res. Rep. **3**: 15-22.

PENNY, A.J., MANN-LANG, J.B., VAN DER ELST, R.P. and WILKE, C.G. 1999. Long-term trends in catch and effort in the KwaZulu-Natal nearshore linefisheries. *S. Afr. J. Mar. Sci*. 21: 51-76.

PEPIN, D.C. Orr. and ANDERSON, J.T. 1997. Time to hatch and larval size in relation to temperature and egg size in Atlantic cod (*Gadus morhua*). *Can. J. Fish. Aquat. Sci.* **54** (Suppl. 1): 2-10.

PITCHER, T.J. and PAULY, D. 1998. Rebuilding ecosystems, not sustainability, as the proper goal of fisheries management. In: *Reinventing fisheries management.* Pitcher, T.J., Hart, P.J.B. and Pauly, D. (Eds.). Kluwer Academic Publishers, London. 311-329.

PULFRICH, A. and GRIFFITHS, C.L. 1988. Growth, sexual maturity and reproduction in the hottentot *Pachymetopon blochii* (Val.). *S. Afr. J. mar. Sci*. **7**: 25-36.

PUNT, A.E. 1992. *PC-Yield II users guide (Version 2.2)*. Rep. Benguela Ecol. Prog. S. Afr. **26**: 1-36.

PUNT, A.E. 1993. Use of spawner-biomass-per-recruit in the management of linefisheries. In *Fish, Fishers and Fisheries. Proceedings of the second South African marine linefish symposium, Durban, October 1992*. Beckley, L.E and van der Elst R.P. (Eds). Spec. Publ. Oceanogr. Res. Inst. S. Afr. **2**: 80-89.

RADEBE, P.V., MANN, B.Q., BECKLEY, L.E. and GOVENDER, A. 2002. Age and growth of *Rhabdosargus sarba* (Pisces: Sparidae) from KwaZulu-Natal, South Africa. *Fish. Res*. **58**: 193-201.

REYNOLDS, J.D., DULVY, N.K. and ROBERTS, C.M. 2002. Exploitation and other threats to fish conservation. In: *Handbook of fish biology and fisheries, Volume 2, Fisheries*. Hart, P.J.B and Reynolds J.D. (Eds.). Blackwell publishing. Cornwall. 319-341.

RICHARDS, C.M. and K.C. LINDEMAN. 1987. Recruitment dynamics of reef fishes: planktonic processes, settlement and demersal ecologies, and fishery analysis. *Bull. Mar. Sci.* **41** (2): 392-410.

RICHARDS, R.A. and RAGO, P.J. 1999. A case history of effective fishery management: Chesapeake Bay striped bass. *N. Am. J. Fish. Mgmt*. **19**: 365-375.

RICKER, W.E. 1975. Computation and interpretation of biological statistics of fish populations. *Bull. Fish. Res. Bd. Can*. **191**: 1-382.

RIJNSDORP, A.D. 1993. Fisheries as a large-scale experiment on life-history evolution: disentangling phenotypic and genetic effects in changes in maturation and reproduction of North Sea plaice, *Pleuronectes platessa* L. *Oecologia*. **96**: 391-401.

ROBERTS, M.J. 1990. Dispersion of a buoyant effluent discharged into the nearshore waters of Algoa Bay. M.Sc. thesis. University of Port Elizabeth.

ROBERTS, M.J. 1999. CD-ROM Tsitsikamma National Park Oceanographic Data, version 1.0. Marine and Coastal Management. Cape Town. South Africa.

ROBERTS, M.J. and M. VAN DEN BERG. 2002. Recruitment variability of chokka squid (*Loligo vulgaris reynaudii*) – role of currents on the Agulhas Bank (South Africa) in paralarvae distribution and food abundance. *Bull. Mar. Sci*. **71** (2): 691-710.

ROBERTS, M.J. and M. VAN DEN BERG. In press. ADCP measured currents along the Tsitsikamma coast (South Africa) and potential transport of Squid paralarvae and ichthyoplankton. *Afr. J. mar. Sci*. **26**:

ROFF, D.A. 1984. The evolution of life history parameters in teleosts. *Can. J. Fish. Aquat. Sci*. **41**: 989-1000.

ROFF, D.A. 1992. *The evolution of life histories theory and analysis*. Chapman and Hall. New York. 535pp.

ROSS, G.J.B. 1988. Coastal hydrography. In *A field guide to the Eastern Cape*. Lubke, R.A.. Guess, F.W. and Bruton, M.N. (Eds.). Wildlife society of southern Africa: 31-32.

RUSS, G.R. and ALCALA, A.C. 1989. Effects of intense fishing pressure on an assemblage of coral reefs. *Mar. Ecol. Prog. Ser*. **56**: 13-17.

SADOVY, Y.J. 1996. Reproduction of reef fish species. In *Reef fisheries*. Polunin, N.V.C. and Roberts, C.M. (Eds.). London, Chapman and Hall: 15-59.

SAMOILYS, M.A. 1997. Periodicity of spawning aggregations of coral trout *Plectropomus leopardus* (Pisces: Serranidae) and the northern Great Barrier Reef. *Mar. Ecol. Prog. Ser*. **160**: 149-159.

SAUER, W.H.H., PENNY, A.J., ERASMUS, C., MANN, B.Q., BROUWER, S.L., LAMBERTH, S.J. and STEWART, T.J. 1997. An evaluation of attitudes and responses to monitoring and management measures for the South African boat-based linefishery. *S. Afr. J. mar. Sci.* **17**: 147-164.

SCHUMANN, E. H. and BEEKMAN, L.J. 1984. Ocean temperature structures on the Agulhas Bank. *Trans. R. Soc. S. Afr*. **45** (2): 191-203.

SCHUMANN, E.H., L.-A. PERRINS and I.T. HUNTER. 1982. Upwelling along the South Coast of the Cape province, South Africa. *S. Afr. J. Sci.* **78**: 238-242.

SCHUMANN, E.H., ROSS, G.J.B. and GOSHEN, W.S. 1988. Cold water events in Algoa Bay and along the Cape couth coast South Africa, in March/April 1987. *S. Afr. J. Sci*. **84**: 579-584.

SCOTT, S.G. and N.W. PANKHURST. 1992. Interannual variation in the reproductive cycle of the New Zealand snapper *Pagrus aratus* (Bloch & Schneider) (Sparidae). *J. Fish Biol*. **41**: 685-696.

SMALE, M. J. 1988. Distribution and reproduction of the reef fish *Petrus rupestris* (Pisces: Sparidae) off the coast of South Africa. *Afr. J. Zool*. **23** (4): 272-287.

SMALE, M.J. and A. BADENHORST. 1991. The distribution and abundance of linefish and secondary trawlfish on the Cape south coast of South Africa, 1986-1990. *S. Afr. J. mar. Sci.* **11**: 395-407.

SMITH, T. 2002. A history of fisheries and their science and management. In: *Handbook of fish biology and fisheries, Volume 2, Fisheries*. Hart, P.J.B and Reynolds J.D. (Eds.). Blackwell publishing. Cornwall. 61-83.

SMITH, M.M. and P.C. HEEMSTRA. 1986. *Smiths Sea Fishes*. Southern Book Publishers, Johannesburg; Macmillan: xx + 1047 pp.

SPENCER JONES, J. 2002. *Fishing industry handbook, South Africa, Namibia and Mozambique*. Cape Town; George Warman Publications: 464 pp.

STOBUTZSKI, I.C. 2001. Marine reserves and the complexity of larval dispersal. *Rev. Fish Biol. Fish.* **10**: 515-518.

SUMAILA, U.R. 1998. Protected marine reserves as hedges against uncertainty: an economist's perspective. In: *Reinventing fisheries management.* Pitcher, T.J., Hart, P.J.B. and Pauly, D. (Eds.). Kluwer Academic Publishers, London. 301-309.

TANIUCHI, T. TACHIKAWA, H, SHIMIZU, M and NOSE, Y. 1993. Geographical variations in reproductive parameters of shortspine spurdog in the north Pacific. *Nippon Suisan Gakkaishi (Bull. japan. Soc. scient. Fish.)*. **59** (1): 45-51.

TARR, R.J.Q. 2000. The South African abalone (*Haliotis midae*) fishery: a decade of challenges and change. In: *Workshop on rebuilding abalone stocks in British Columbia*. (Ed.) Campbell, A. *Can. Spec. Publ. Fish. aquat. Sci.* 32-40.

TILNEY, R.L. and C.D. BUXTON. 1994. A preliminary ichthyoplankton survey of the Tsitsikamma National Park. *S. Afr. J. Zool*. **29** (3): 204-211.

TILNEY, R.L., NELSON, G., RADLOFF, S.E. and C.D. BUXTON. 1996. Ichthyoplankton distribution and dispersal in the Tsitsikamma National Park marine reserve, South Africa. *S. Afr. J. mar. Sci*. **17**: 1-14.

VAN DER ELST, R.P. and ADKIN, F. 1991. Marine linefish priority species and research objectives in southern Africa. *Oceanogr. Res. Inst. (Durban) Spec. Publ.* **1**: 132 pp.

VAN DER WALT, B.A. and BECKLEY, L. E. 1997. Age and growth of *Sarpa salpa* (Pisces: Sparidae) off the east coast of South Africa. *Fish. Res*. **31**: 241-248.

VAUGHN, D.S. and PRAGER, M.H. 2002. Severe decline in abundance of red porgy (*Pagrus pagrus*) populations off the southeastern United States. *Fish. Bull., Wash*. **100**: 351-375.

WALLACE, J.H., KOK, H.M., BUXTON, C.D. and B. BENNETT. 1984. Inshore small-mesh trawling survey of the Cape south coast. Part 1. Introduction, methods, stations and catches. *S. Afr. J. Zool*. **19** (3): 154-164.

WILSON, C.A. and D.L. NIELAND. 1994. Reproductive biology of red drum, *Sciaenops ocellatus*, from the neritic waters of the northern Gulf of Mexico. *Fish. Bull*. **92**: 841-850.

WOOD, A.D. 1998. Contributions towards the taxonomy of the ichthyoplankton species composition and an understanding of its dynamics along the south east coast of South Africa. PhD thesis, Rhodes University. 338 pp.

ZAR, J.H. 1999. *Biostatistical analysis*. New Jersey, Prentice Hall. 663 pp.

ZELDIS, J.R. and FRANCIS, R.I.C.C. 1998. A daily egg production method estimate of snapper biomass in Hauraki Gulf, New Zealand. *ICES J. Mar. Sci*. **55**: 522-534.

# APPENDIX I

## Papers emanating from this thesis

BROUWER, S.L., GRIFFITHS, M.H. and M. ROBERTS. 2003. Adult movement and larval dispersal of *Argyrozona argyrozona* (Pisces Sparidae) from a temperate Marine Protected Area. *Afr. J. mar. Sci.* **25**: 395-402.

BROUWER, S.L. and GRIFFITHS, M.H. 2004. Age and growth of *Argyrozona argyrozona* (Pisces Sparidae) in a Marine Protected Area: an evaluation of methods based on whole otoliths, sectioned otoliths and mark recapture. *Fish. Res*. 67: 1-12.

BROUWER, S.L. and GRIFFITHS, M.H. in press a. Reproductive biology of *Argyrozona argyrozona* (Pisces Sparidae) in a temperate Marine Protected Area. *Fish. Bull*.

BROUWER, S.L. and GRIFFITHS, M.H. in prep b. Influence of sample design on estimates of growth and mortality in *Argyrozona argyrozona* (Pisces: Sparidae).

BROUWER, S.L. and GRIFFITHS, M.H. in prep c. Stock separation and life history of A*rgyrozona argyrozona* (Pisces: Sparidae) on the South African east coast.

BROUWER, S.L. and GRIFFITHS, M.H. in prep d. Management of *Argyrozona argyrozona* (Pisces: Sparidae) based on per-recruit models.

# Appendix II

## BIOLOGICAL CONSIDERATIONS FOR THE CARPENTER MANAGEMENT PLAN

**Compiler**: S.L. Brouwer (MCM)

**Fishery importance:**
Carpenter *Argyrozona argyrozona* is an important component of the commercial linefishery between the Kei River and Cape Point. Annual average reported catch (1985-2001) is 704 tons making them the third most important species in the commercial linefishery in this region. The recreational sector catches are approximately 5% of the commercial catch. Approximately 23 tons are caught annually in the demersal trawl fishery and an additional 1.2 tons are discarded.

**Stock Structure:**
Carpenter comprise two separate stocks one on the central Agulhas Bank and one on the eastern Agulhas Bank.

**Life history and Population Dynamics:**
See Chapters 2-7.

**Assessment:**
Model: Fecundity per recruit (*Egg/R*)
Target Reference Point: 40%$Egg/R_{F=0}$
Threshold Reference Point: 25%$Egg/R_{F=0}$
Frequency of review: 15 years (i.e. half of maximum age)
Date of last assessment: 2003

**Data requirements:**
Model: Age-at-maturity, fecundity, fecundity-at-age, growth curve, length-weight relationship, age at first capture.
Mortality: Age/length key, size composition of catch.

**Additional Monitoring:**
Method: Observer based catch and effort data (landing site/access point surveys/onboard monitors).
Frequency: Annually.
Date of last survey: 1995 (access point survey).

**Stock status**: *Collapsed*.
*Egg/R* was 6.06% (inshore Agulhas Bank), 14.15% (offshore Agulhas Bank) and 6.41% (Eastern Cape) at the time of assessment. Current *cpue* is 4.6% of historic values.

**Management objectives:**
To rebuild fecundity per recruit ratio to the Target Reference Point.

**History of regulations:**
A size limit of 25 cm TL was imposed on all sectors in 1985 and recreational fishers were limited to 10 fish.person$^{-1}$.day$^{-1}$. Commercial fishers have no bag limits.

**Recommendations:**
The minimum size limit should increase to 35 cm TL, the recreational bag limit should be reduced to 4 fish.person$^{-1}$.day$^{-1}$ and the commercial effort reduced by 70%.

Table 1: Morphometric relationships for *A. argyrozona* sampled in the Tsitsikamma National Park.

| **Relationship** | | **n** | **$r^2$** |
|---|---|---|---|
| Total mass (g) | = 1.0158 eviscerated mass (g)$^{1.0125}$ | 883 | 0.9979 |
| Fork length (mm) | = 0.8455 total length (mm)$^{1.0143}$ | 3920 | 0.9983 |
| Fork length (g) | = 37.055 mass (mm)$^{0.3446}$ | 4266 | 0.9825 |
| Total length (mm) | = 1.1914 fork length (mm)$^{0.9843}$ | 3920 | 0.9983 |
| Total mass (g) | = 4.00x10$^{-5}$ fork length (mm) $^{2.8553}$ | 4256 | 0.9848 |
| Fork length (mm) | = 13.866 otolith length (mm)$^{1.2174}$ | 434 | 0.9266 |