Age, growth, reproductive biology and diet of *Spondyliosoma emarginatum* (Cuvier 1830) in the West Coast National Park, South Africa

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In memory of Johnny and Walker my pups

DECLARATION

I hereby declare that all of the work presented in this thesis is my own, except where otherwise stated in the text. This thesis has not been submitted in whole or in part for a degree at any other university.

signature removed

Lucinda Fairhurst

24/11/05

Date

ABSTRACT

Comprehensive morphometric measurements and counts, external colouration, reproductive behaviour and diet of steentjies (*Spondyliosoma emarginatum*) in Langebaan Lagoon were recorded between September 2004 and February 2005. Sagittal otoliths were extracted and age estimates recorded from both whole and sectioned otoliths in order to estimate growth and mortality parameters. A total of 302 steentjies (139 – 312 mm fork length) was sampled of which 243 were females, 55 were males and four were individuals with hermaphroditic gonads. Macroscopic and microscopic examination of gonads and monthly gonadosomatic indices suggest a spring spawning season and that steentjies are protogynous hermaphrodites with males significantly larger than females ($t = 64.75$, $df = 301$, $p < 0.001$). During the reproductive season, males develop a blue colouration. All males with this colouration had testes classified as either active or ripe and had significantly larger gonad masses than those without mating colours ($U = 3.5$, $Z = 6.48$, $p < 0.001$).The length-at-50%-maturity for females was 171 mm (FL) and for males was 204 mm (FL). The size at 50% sex change was estimated as 250 mm (FL). Analysis of foregut contents showed steentjies to be opportunistic omnivores, changing from plant to animal food as they age. The average percent error and coefficient of variation values for whole otoliths were 4.59% and 6.00% respectively, and 10.89% and 14.53% for sectioned otoliths. Although the results of the whole otolith study provided more precise age estimates, there was a strong indication of bias so the sectioned otolith results were used for calculating the growth model. Growth (by sex) was modelled using a model developed for sex changing sparids that allows for accelerated growth after sex change. Steentjies appear to have shorter life spans than most sparids; the oldest individuals sampled attaining less than 7 years of age. Growth rates appear to be relatively high. The smallest, youngest fish were all female, with males only present in the larger size classes. The estimated mortality for steentjies was $0.7y^{-1}$. Such a high mortality rate implies that further increase in fishing pressure on this species may not be sustainable in Langebaan Lagoon.

INTRODUCTION

Seabreams (family: Sparidae) are found in almost all of the oceans of the world, but are most diverse in the waters around southern Africa (Garratt 1993). Forty one species occur in these waters, twenty-one of which are endemic (Smith & Heemstra 1986). Twenty-nine sparid species are important components of various line and net fisheries in South Africa leading to considerable research effort being directed at the family in recent years (Beckley 1983, Beckley 1984, Booth and Buxton 1997, Buxton and Garratt 1990, Garratt 1993, Griffiths 1997, Griffiths *et al.* 2002, Pajuelo and Lorenzo 2002 and Hesp *et al.* 2004).

The steentjie, *Spondyliosoma emarginatum* (Cuvier 1830), is a southern African reef-fish belonging to the family Sparidae. Its distribution stretches from Saldanha Bay to Mozambique, and includes a population off southern Madagascar (Smith and Heemstra 1986). Large shoals are found in the vicinity of reefs in coastal waters. Although considered to be intolerant of low salinities (van der Elst 1988), they have been observed feeding on small crustaceans and algae in estuaries in Mozambique (van Bruggen 1965) and there is evidence of juveniles occurring in the Swartkops and Sundays estuaries in the Eastern Cape (Beckley 1983 and Beckley 1984).

Steentjies are relatively small fish, but they are becoming important in the catches of recreational and commercial line fishermen as populations of larger reef-fish species have become depleted (Aitken and Mann 2000). The maximum total length attained by steentjies is documented as 45 cm, although few exceed 25 cm (Smith and Heemstra 1986, van der Elst 1988). According to these authors, steentjies are gonochoristic (separate sexes), reaching sexual maturity at approximately 22 cm. The reproductive season extends from September through to the end of February (during the austral spring and summer). Steentjie spawning behaviour has been observed in captivity (van Bruggen 1965 cited by Buxton and Garratt 1990). The male creates a shallow depression (nest) on a sandy bottom, where courtship and spawning takes place (Aitken and Mann 2000, van der Elst 1988). The territorial, intensely coloured males (van der Elst 1988) then mate with females above these depressions, and guard the benthic eggs until hatching (Beckley 1989). No other sparid in southern Africa has been reported to display similar behaviour.

The congeneric black sea bream (*Spondyliosoma cantharus*) in the North Atlantic displays similar spawning and nest guarding behaviour as has been documented for steentjies (Gonçalves and Erzini 2000). The spawning period of *S. cantharus* extends from February to April with a peak in March (boreal spring), and they also lay sticky eggs in shallow depressions (Gonçalves and Erzini 2000). These authors also described *S. cantharus* as hermaphroditic and potentially protogynic.

Steentjies are considered omnivorous. There are very few descriptions of the feeding behaviour and diet of steentjies. Van der Elst (1988) described their major food source as an ascidian known locally as 'redbait', supplemented by polychaete worms, small crabs and amphipods. Limited algal grazing may also occur (van der Elst 1988). A study carried out by Lechanteur and Griffiths (2003) resulted in the grouping of steentjies with other sparid species as a 'small-benthic-invertebrate predator'. Steentjies have also been described as predators of chokka squid (*Loligo vulgaris reynaudii*); they have been observed taking suspended particulate matter over the squid egg beds, biting at trailing tips of squid arms and chewing on the tips of squid egg capsules (Sauer and Smale 1993 cited by Smale *et al.* 2001). Steentjies have also been observed attacking female squid on their descent to lay eggs, although it is unclear whether they are in fact attempting to bite the squid (Smale *et al.* 2001).

A characteristic of sparids is rapid growth in the first few years of life, which slows dramatically with increasing age (Gonçalves *et al.* 2003, Griffiths *et al.* 2002). Age determination of many sparids has been used in conjunction with measures of sexual maturity to determine their age-at-maturity and their growth rates. Sparids found in South African waters have maximum ages ranging from 6 to 50+ years (Mann and Radebe 2000), with most species displaying relatively long life spans (Garratt 1993). Age determination studies have been conducted on several species of South African sparids (e.g. Pulfrich and Griffiths 1988, Bennett 1986b, Garratt *et al.* 1993, Griffiths *et al.* 2002, Pajuelo and Lorenzo 2002, Radebe *et al.* 2002). To date, no age data have been collected for steentjies.

There is little information available for the management of the steentjie fishery. The growth rates of steentjie populations have never been studied, yet this is one of the crucial life-history parameters required for fishery assessments and regulation. Apart from incidental observations listed above, no study of the reproductive biology has been made. Such information is now required at the West Coast National Park (WCNP), where steentjies occur at the western end of their range in Langebaan Lagoon. A rapidly expanding recreational fishery targets steentjies and other species, and there is concern that these fisheries are not sustainable. Anecdotal information suggests that steentjies at Langebaan are isolated from those found on the south coast of South Africa, and attain a larger size. This study aims to investigate the sexual biology, growth, diet and mortality rate of steentjies in the WCNP. This information will fill many of the gaps in knowledge of the basic biological and ecological characteristics of steentjies. The results of this study are intended to support conservation and management of the steentjie recreational fishery at Langebaan.

STUDY AREA

Langebaan Lagoon is a shallow, sun-warmed embayment, where numerous warm-water species find the only refuge along the otherwise cool-temperate west coast of South Africa (Fig. 1). The lagoon is productive because it is fed by nutrient rich upwelled water from the Benguela system and is documented as having a surface temperature of 15 °C during winter months and ranges from 14 to 24°C in the summer season (Shannon and Stander 1977). There are no rivers flowing into the lagoon; it was formed by the prehistoric rise and fall of the sea. Some fresh-water drains in from the surrounding 'supratidal' *Juncus krausii* marshes along the southern end of the lagoon (Christie and Moldan 1977, De Graaff and Hanekom 1995), but the salinity remains similar to that of seawater (35 ^{o}/oo).

With water depths ranging between 2 and 10 m, Langebaan is a shallow and large marine aquatic system (16 km in length and 2-3 km in width) with channels. There is strong tidal exchange with the open sea. Shannon and Stander (1977) reported that around 12 percent of the volume of the lagoon-bay system is exchanged during a spring tide with current speeds in the middle section of the lagoon of about 20 cm per second.

The soft substratum is mainly unvegetated and measurements have shown that the abundant phytoplankton densities in the rich upwelled waters of the west coast and Saldanha Bay drop dramatically in the lagoon (Boucher and Jarman, 1977). This is thought to be due to extensive beds of filter feeding white clams *Mactra glabrata* that siphon phytoplankton out of the water column. Large beds of the alga *Gracilaria verrucosa* lie in and near the mouth of the lagoon and extensive areas are covered by eelgrass (*Zostera capensis*) near the southern end of the lagoon. Saltmarshes and rooted plants such as the seagrasses and reeds take up nutrients from the water, making it difficult for phytoplankton to thrive in the lagoon (de Graaff and Hanekom 1995, Christie and Moldan 1977). Lagoon waters are therefore clear.

No comprehensive audit of Langebaan's ichthyofauna has been undertaken. It has been suggested (Prof. G. Branch, University of Cape Town pers. comm.) that the relatively few fish species (when compared to estuaries) may be a result of the clarity of the water, because estuarine fish prefer turbid waters to allow them to conceal themselves from predators. In contrast, hundreds of species of invertebrates inhabit the lagoon, almost double the number found in any other lagoon in South Africa. The intertidal sandflats are densely populated by four species of prawn including the sand prawn *Callianassa kraussi* (used by anglers in the lagoon) and the mud prawn *Upogebia africana* (Wynberg and Branch 1991). Large breeding colonies of piscivorous seabirds, which are endemic to the nearshore regions of South Africa and Namibia, occur on the four inshore islands near

Langebaan, and hundreds of waders gather together in summer at the salt marshes (de Graaff and Hanekom 1995).

The lagoon has been proclaimed a RAMSAR site of international conservation importance and is divided into three different utilization zones: sanctuary, restricted recreational zone and controlled, multi-purpose recreational zone (Fig. 1) (de Graaff and Hanekom 1995). The islands and the southern end of the lagoon are included in the sanctuary zone where no access is allowed. The middle section of the lagoon is the 'restricted recreational zone' where power boats and fishing are not allowed. The mouth of the lagoon is a multi-purpose recreational zone where power boats, yachts, waterskiers and fishers are permitted.

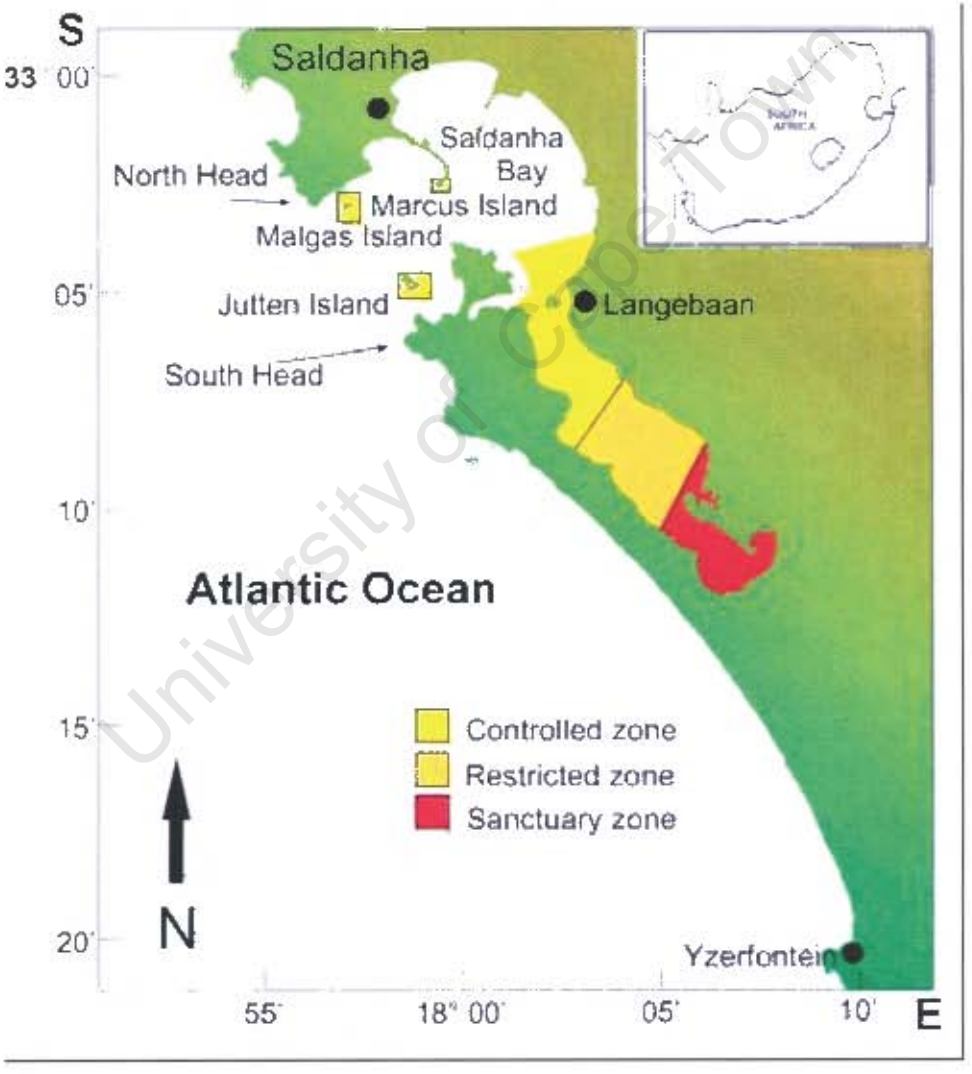

Fig. 1: The south-western Cape, showing the location of Langebaan Lagoon and Saldanha Bay and the three zones within Langebaan Lagoon.

MATERIALS AND METHODS

Steentjies (139–312 mm fork length, FL) were captured from the controlled and restricted zones (Fig. 1) by linefishing from boats using hook sizes between 1 and 4 (mustad) in Langebaan Lagoon between August 2004 and January 2005. For each fish, various morphometric measurements and observations of external colouration, sex, gonad stage and gut contents were recorded. The sagittal otoliths were then removed, cleaned, weighed and stored dry in paper envelopes for the purpose of age determination.

External colouration and morphometrics

Each fish was examined and external colouration and morphometrics were noted. Photographs of all fish (fresh where possible) were taken, because the bright blue and yellow mating colours faded soon after death. The morphometric measurements that were recorded were total length (TL, mm), fork length (FL, mm), body depth (mm), whole mass (g) and gutted mass (g). For the first 200 fish, fin counts were carried out on dorsal and anal spines and rays and pectoral rays. The first and second gill arches were removed from the left side of these fish and preserved in buffered 10% formalin. Thirty gill arches were randomly selected and the gill rakers on the first arch were counted using a dissecting microscope under low magnification.

Reproductive biology

The gonads of each fish were removed, weighed, visually assessed and classified according to macroscopic appearance (Fig. 2), before being preserved in buffered 10% formalin. The macroscopic stages were subsequently assessed by histological analysis (microscopically).

Macroscopic staging.

A description of the maturity stages for each sex is summarized in Table I. Gonadosomatic indices (GSI) were calculated by expressing gonad mass as a percentage of fish mass.

$$\text{GSI}\,(\%) = \frac{\text{gonad weight (g)}}{\text{fish weight (g)} - \text{gonad weight (g)}} \text{X}\,100 \qquad (1)$$

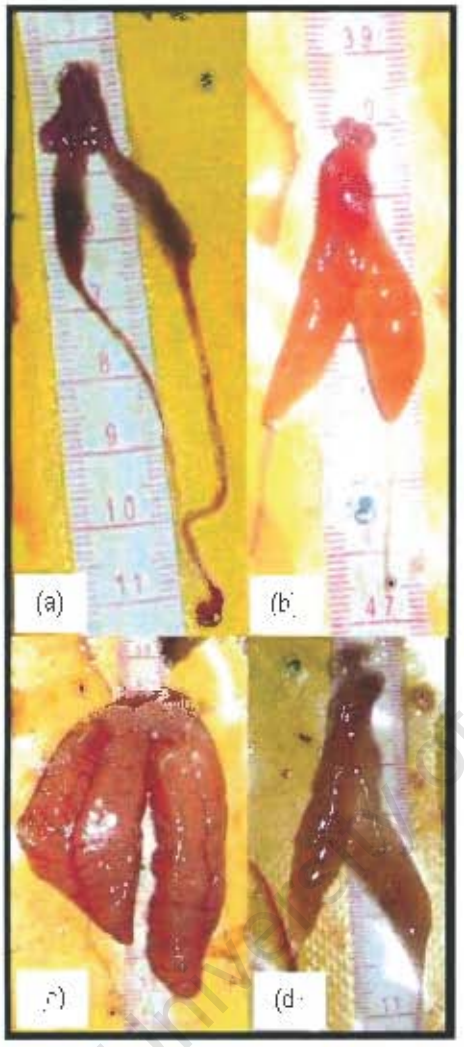

Fig. 2: Macroscopic view of female steentjie gonads: (a) juvenile, (b) active, (c) ripe and (d) spent ovaries that were removed from fish that were frozen after capture from Langebaan Lagoon.

Table I: Criteria used in the allocation of steentjie gonads to maturity stages (macroscopic stages based on Griffiths *et al.* (2001) and microscopic stages are being developed).

Stage		Macroscopic description	Microscopic description
1	Juvenile	Sexual organs small. Ovaries appear translucent or pinkish sacs with no visible eggs. No vascularisation. In either sex. Testis thin and flattened and transparent to pinkish white.	No or vestigial oocytes are present.
2	Active	Ovary swells and increases in length. Colour changes to yellow/orange sacs. Tiny orange/yellow pinprick eggs are just visible to the naked eye. Testes become thicker and grey/cream in colour. No spermatic fluid is visible when cutting through the testes. Some vascularisation is present.	No oocytes are visible in the ovaries (oocytes are translucent). No spermatozoids are present.
3	Ripe	Ovary is swollen and amber in colour due to an increase in egg size. Large yellow eggs can clearly be seen with the naked eye. There is much vascularisation. Testes are swollen and pearly white. Considerable quantities of sperm are present throughout the organ. No vascularisation.	Ovaries contain all stages of tertiary yolk oocytes and post-ovulatory follicles as well. Testes include all stages of sperm development. Spermatozoa found in most lobules and the sperm duct.
4	Spent	Ovary is large, flattened reddish in colour with very few eggs visible. They have the appearance of a limp sac. Testes smaller than stage 3, no sperm is visible and they appear flaccid and haemorrhaged.	Ovary consists of vestigial oocytes. While spermatozoa may be present in some lobules of the testes, most lobules are small.
5	Both sexes	The spent/remnant ovaries are visible on the inside of the gonads and appear similar to those described for the spent stage whilst the male testes are developing on the outside of the gonads, are pinkish/whitish in colour.	Degenerating oocytes can be seen in amongst the male tissue.

Microscopic staging.

Microscopic gonad staging was conducted to substantiate the macroscopic gonad staging. Histological sub-samples of both male and female gonads at different stages of maturity, and gonads from those fish suspected of changing sex (Table 1), were examined under a microscope. The sub-samples (n = 20) were taken from gonads that had already been macroscopically staged and four samples were then randomly selected from each

stage. Preserved gonad samples were removed from the formalin solution after several weeks. Whole samples were washed in tap water and sections (+/- 5mm thick) were dissected from the anterior, middle and posterior of the left lobe (in order to determine whether development of gametes was uniform throughout the gonad). The remains of the gonads were returned to the formalin solution. The sections were placed in cassettes and dehydrated following the protocol in Table II. The samples were then embedded in wax for sectioning. It must be noted that the time factor is crucial when clearing with Toluene.

Table II: Sequence of steps in preparation of sectioning of gonads for histological study, showing the solutions used and the duration of each stage.

Step	Solution.	Time (hours).
1	Tap water	1
2	50% Alcohol	2
3	70% Alcohol	2
4	70% Alcohol	2
5	80% Alcohol	2
6	80% Alcohol	2
7	95% Alcohol	2
8	95% Alcohol	3
9	96.6% Alcohol	3
10	96.6% Alcohol	3
11	96.6% Alcohol	Overnight
12	Toluene	2
13	Toluene	2

The embedded gonads were sectioned at 5-7 μm thickness, and stained using Harris's haematoxylin and eosin (H&E) for microscopic examination.

The sex ratio (ratio of females to males) was determined on a monthly basis. The chi-squared test was used to compare sex ratios from each month. Expected values were taken as the mean over the whole period and these were compared to the observed sex ratios each month. Size at first maturity for females (FL_{50}) was determined from the population of mature fish in each size group using a maturity ogive (females were considered mature once attaining macroscopic stages 2, 3 and 4). The proportion of mature individuals within each size class was calculated and plotted against size. The data were fitted using an iterative least squares procedure (Microsoft EXCEL (Microsoft corp., 2000) SOLVER routine with Newton algorithm option) using the logistic formula:

$$\text{Proportion mature} = \frac{1}{1+e^{\frac{-size(mm)+L_{50}}{\sigma}}} \quad (1)$$

The parameters of the model were used to estimate the size when 50% of the individuals were mature.

Diet

The stomach and hindgut were removed from each fish and weighed (g). The fullness of the stomach was recorded for 284 fish using a nominal scale (Table III) and the contents were identified (but not counted) under a stereo dissecting microscope. Those contents that were immediately identifiable were recorded and discarded. Prey items that could not be identified immediately were stored in buffered 10% formalin unless they appeared too digested in which case they were discarded.

Table III: Nominal scale used to describe the fullness of the foregut of steentjies from Langebaan Lagoon.

Ranking	Description
0	The foregut is completely devoid of any food.
1	The foregut wall is not stretched at all and less than half of the space available contains food.
2	The foregut wall is not stretched and more than half of the space available contains food.
3	The foregut wall is not stretched but the food is taking up all available area.
4	The foregut wall is stretched almost to its limit but is not transparent.
5	The foregut wall is stretched to its limit and is completely transparent; the foregut is completely full of food.

Age estimation

South African sparids have generally been aged using otoliths. Alternate translucent and opaque zones are visible in otoliths and are assumed to reflect a seasonal cycle in the life history of the fish. A clearly defined, high contrast translucent zone is considered to mark the end of a year of growth and together with the opaque zone is usually referred to as an annulus. A count of the number of growth rings visible in an otolith is used to estimate the age of an individual. The most rapid and cost-effective technique is to read the otoliths whole. However, reading the growth rings of whole otoliths has proved to be

difficult in many cases because of the phenomenon of stacking of the zones, particularly in older fish (Radebe *et al.* 2002). This leads to underestimates of the age of old fish (Brouwer and Griffiths 2004). Sectioning of otoliths is therefore often necessary for estimating age of long-lived species accurately. The first step towards obtaining age information from otoliths is to establish the best method of otolith analysis. Both whole and sectioned methods were compared during this investigation. The effectiveness of each method was assessed using analyses of precision and bias. The rationale behind this approach was that if a given method did not permit clear identification of the relevant growth features in the otolith, this would be reflected in the reproducibility of the data generated using each method. Ideally, a validation study where known time periods are compared to the number of annual growth zones deposited during that period should be conducted to assess the accuracy of the age estimates obtained using a given method. Such a study was beyond the scope of the work described in this thesis, and analyses of precision and bias had to be used as an alternative. As pointed out by Campana (2001), however, a high level of precision does not imply that the age estimates are accurate, but rather indicates that the replicate age estimates are reproducible, implying that the interpretation criteria being employed by the reader(s) are stable over time.

Processing and reading of whole otoliths.

One otolith was selected per fish. Whole otoliths were immersed in water and observed against a black background with a dissecting microscope at 10.5X magnification using reflected light. Identification of growth zones was usually made on the posterior part of the otoliths. An initial test reading was conducted to set otolith interpretation criteria. Firstly, an annual growth zone was defined to be a prominent opaque zone followed by a definite, high contrast translucent zone. A second criterion was that a given annual growth zone can never be wider than the preceding annual growth zone. In relatively long-lived species (such as sparids), fish growth is generally rapid in the early life stages, slowing asymptotically with increasing age. It is extremely unusual for a fish to grow more rapidly later in its life than during the earlier stages. In view of the strong relationship between otolith size and fish size, these growth patterns are reflected in the otolith structure. To illustrate the second criterion, if the ring labelled "F" in Fig. 24 were interpreted to be the second annulus, "A2" would then be interpreted as the third. This would imply that the growth in year three were faster than that in year two as the width of the third growth zone is larger than that of the second. Because such an increase in growth rate is unlikely, the ring labeled "F" in Fig. 24 was interpreted to be a false ring, with rings "A1" and "A2" considered to be true growth rings.

The number of annual growth zones in each otolith was counted on four separate occasions (counting sessions) without any knowledge of the length or weight of the fish and with no reference to previous readings. The first of these was discarded as it was part of the learning process. A gap of at least two weeks between readings was implemented in order to avoid bias.

Sectioned otoliths.

One otolith from each fish was mounted in a rod of clear casting resin and sectioned transversely through the nucleus to a thickness of approximately 0.5 mm using two diamond coated circular saw blades. The otolith sections were mounted on labelled glass slides using DPX mountant and viewed under a dissecting microscope at 10.5X magnification with transmitted light. The most recent translucent margin was only counted as another year of growth if the entire otolith edge displayed the translucent characteristic. A partial ring was not counted as a year of growth. The first annulus was identified as the first translucent zone that displayed maximum clarity and contrast whilst fulfilling the growth zone width criterion.

A sub-sample of 35 whole otoliths was read by a second reader following the above procedure to assess the reproducibility of the results. An age for each fish was estimated as the mean of the replicate otolith readings. Residuals of each of the three replicate otolith counts were calculated as the difference between the age reading from each replicate and the mean of all replicates conducted on each otolith. The mean of the residuals from all otoliths was calculated for each replicate and plotted in order to depict any bias of repeated readings. The residuals were also used to calculate the Average Percentage Error (APE) (Campana 2001)

$$\mathrm{APE} = 100\% \times \frac{1}{R} \sum_{i=1}^{R} \frac{[X_{ij} - X_j]}{X_j} \qquad (2)$$

(where R is the number of times each fish is aged, X_{ij} is the ith age determination of the jth fish, and X_j is the mean estimate of the jth fish, when averaged across many fish, it becomes an index of average percent error) and the Coefficient of Variation (CV) (Campana 2001)

$$\mathrm{CV} = 100\% \times \frac{\sqrt{\sum_{i=1}^{R} \frac{(X_{ij} - X_j)^2}{R-1}}}{X_j} \qquad (3)$$

(where CV is the age precision estimate for the jth fish, it can be averaged across fish to produce and mean CV) for the two different reading techniques. The last three sets of the original age estimates were used in the precision and bias calculations as the first readings were 'test' readings. A single age estimate for each fish was derived from a rounded mean of the ages read (rounded up or down to the nearest year). The data collected using the sectioned otolith technique was used in analyses of growth and mortality.

Growth

The growth model used in this investigation was a Von Bertalanffy growth equation adapted to sex-specific growth curves (Garratt *et al.* 1993). The growth equations fitted to the steentjie length-at-age data were:

$$L_a^f = L_\infty^f (1 - e^{-K^f (a - t_0^f)}) \quad (4)$$

for females and

$$L_a^m = \sum_\alpha \beta_\alpha^a L_\infty^m (1 - e^{-K^m (a - t_0^{\alpha,m})}) \quad (5)$$

for males, where:

L_a^f and L_a^m are the mean lengths-at-age (mm) for females (f) and males (m) respectively, L_∞^f and L_∞^m are the asymptotic lengths (mm) for females and males, and K^f and K^m are growth rate parameters (y^{-1}) of females and males. The age at which females have zero length is t_0^f and β_α^a is the fraction of males at age a that changed sex at age α. For the growth equation of the age-α-cohort to be continuous during sex change $t_0^{\alpha,m}$ needs to be selected, and was set at 3, 4, 5, 6 or 7 yeas for these analyses. No males younger than 3 years or older than 7 years were found. First, the female growth curve was fixed using an iterative least squares procedure (Microsoft Excel solver routine with Newton algorithm option). Then the proportion of males which change sex at each age was calculated from the length-at-age data to give β_α^a values and that $t_0^{\alpha,m}$ was used to anchor each male curve such that there was continuity from female to male curves. Male curves were fitted separately for each α value using the solver routine.

Mortality

Total mortality was estimated using the equation for an exponential decay model based on the frequency of fish at each age based on Erzini *et al.* (2001):

$$N_t = N_0 e^{-Zt} \quad (5)$$

where N_t is the number of fish of age t, N_0 is the initial abundance and Z is the instantaneous mortality rate. This is a non-linear fit equivalent to standard catch-curve analyses. The non-linear fit was preferred as the data were homoscedastic. Fishing does not usually occur in the first year of life, so the data on which this estimation was based excluded fish younger than 2 years of age.

RESULTS

In total, 302 steentjies (136 – 312 mm FL) were sampled from Langebaan Lagoon during this investigation between depths of 3 and 11.5 meters, 243 of the sampled fish were females 55 were males and four individuals were found with hermaphroditic gonads. The sampling spanned six months: August (n = 7), September (n = 36), October (n = 39), November (n = 120), December (n = 68), and January (n = 32). There were difficulties when sampling small fish. This was originally thought to be due to gear selection but no small fish could be caught even when using gill nets.

Morphometrics and meristics

There was a small amount of variability in the counts of fin rays and spines are presented in Table IV. All fish larger than 269 mm FL (n = 25) were male (Fig. 3) and no males were found smaller than 234mm FL (Table V). On average, males were significantly larger than females ($t = 64.75$, $df = 301$, $p < 0{,}001$).

Table. IV: Counts of spines and fin rays for steentjies from Langebaan Lagoon (n=200). The numbers in parentheses indicate that rays are branched. Some of the rays examined had more than one branch.

		Spines	Rays
Dorsal	Mean	11	12 (+1)
	Min	10	11 (+1)
	Max	11	13 (+1)
Anal	Mean	3	10 (+1)
	Min	2	9 (+1)
	Max	4	11 (+1)
Pectoral	Mean		16
	Min		14
	Max		17

Table V: Descriptive statistics of steentjie length data sampled in Langebaan Lagoon during this study.

Parameter	Mean	SE*	Range	*n*
Combined sexes				
Total length *TL* (mm)	246.9	2.10	149 – 346	300
Fork length *FL* (mm)	222.7	1.90	136 – 312	302
Males				
Total length *TL* (mm)	295.1	2.61	259 – 346	59
Fork Length *FL* (mm)	266.8	2.41	234 – 312	59
Females				
Total length *TL* (mm)	235.2	1.86	149 – 302	241
Fork Length *FL* (mm)	212.1	1.67	136 – 269	243

* SE = standard error

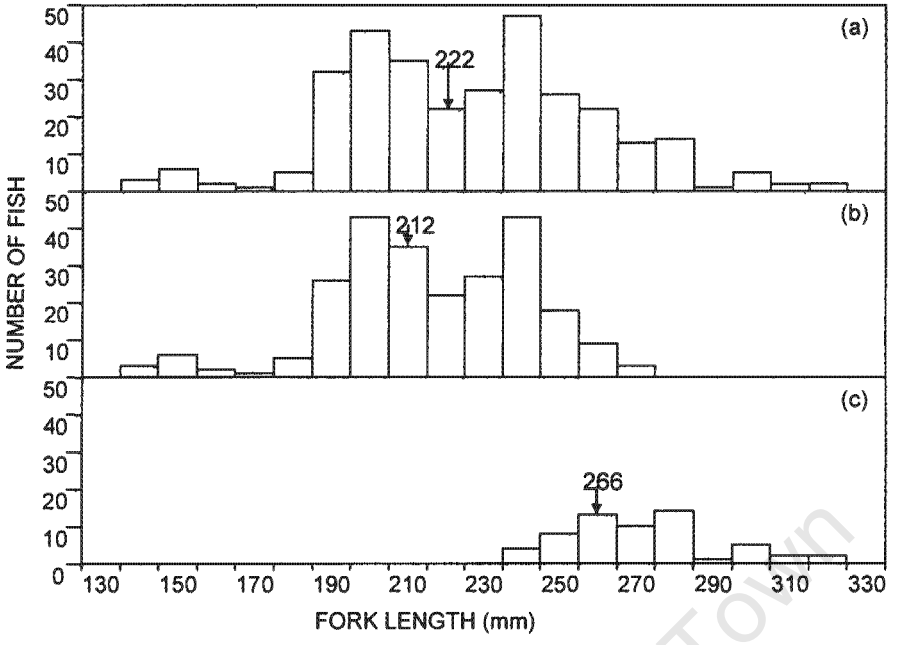

Fig. 3: Length frequency distributions of steentjies for Langebaan Lagoon for (a) combined sexes, (b) females and (c) males.

The relationships between the various morphometric variables measured during this study are illustrated in Figs. 4 to 7. Fork length (FL) showed a strong linear relationship to total length (TL), and was roughly 90% of TL (R^2 = 0.99). FL also showed a strong positive relationship with body depth (R^2 = 0.93) increasing by a factor of 2.2 with increasing body depth. Body weight increases exponentially with increasing body length (Fig. 6), while gutted mass displays a strong linear relationship with total mass (Fig. 7) with an R^2 value of 0.987.

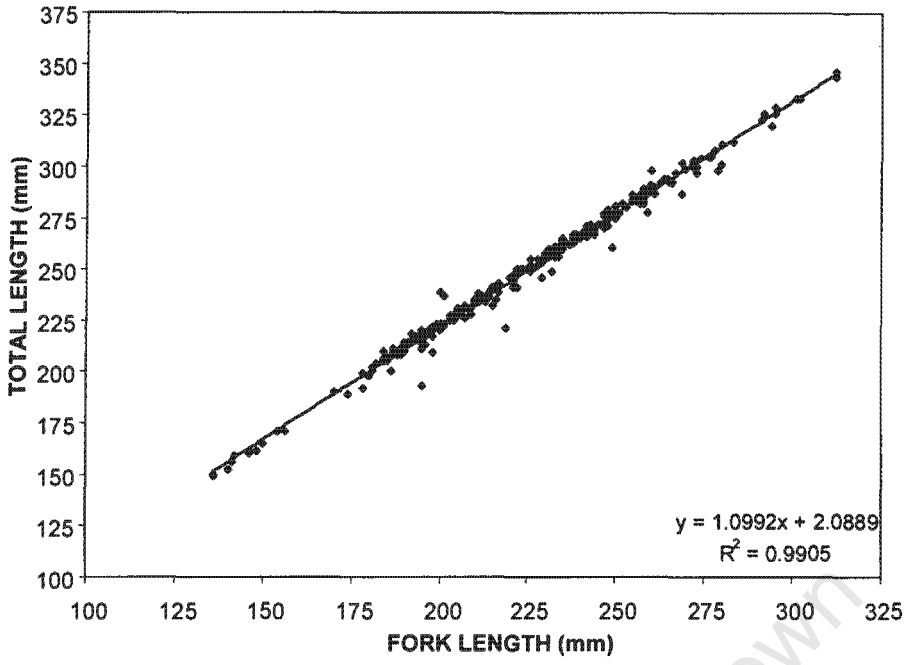

Fig. 4: Relationship between total length and fork length for 302 steentjies collected during this study.

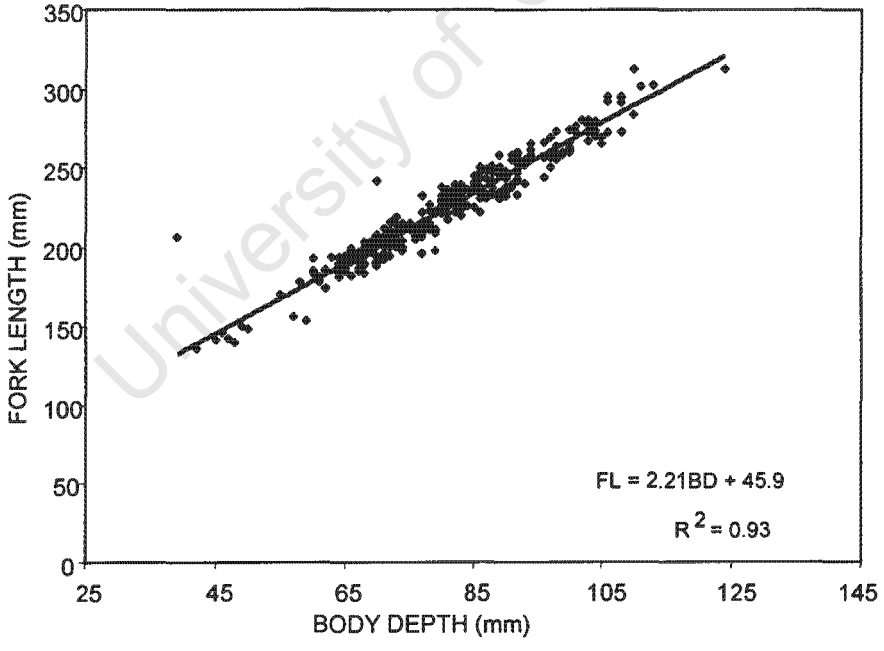

Fig. 5: Relationship between fork length and body depth (BD) for 302 steentjies from Langebaan Lagoon.

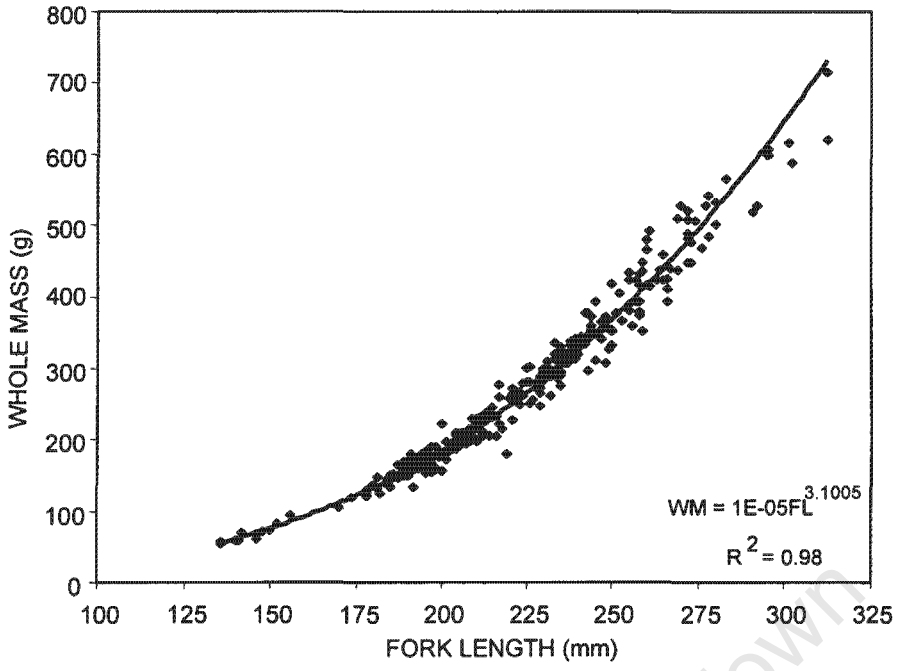

Fig. 6: Relationship between total mass and fork length for 302 steentjies from Langebaan Lagoon.

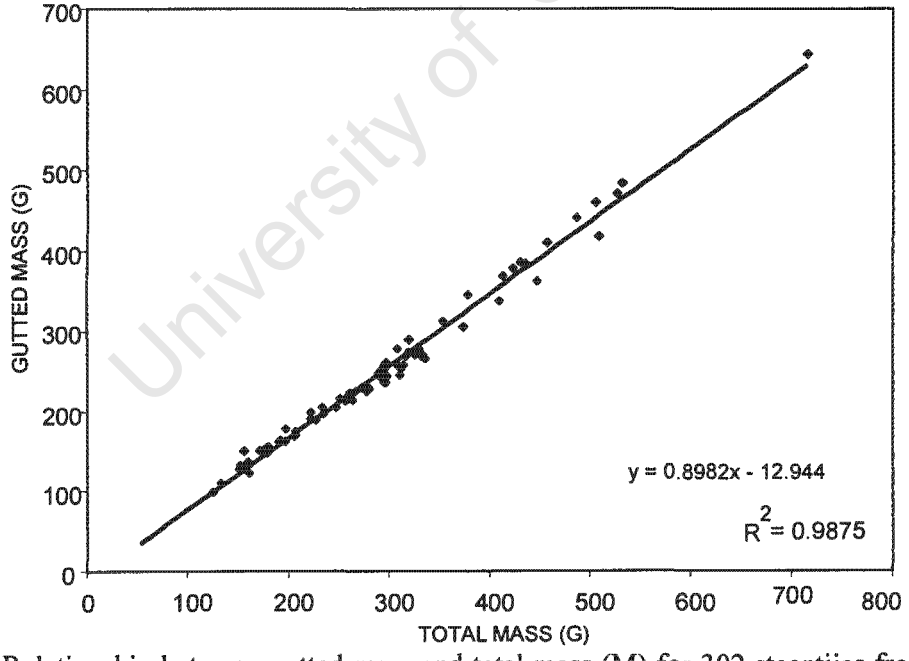

Fig. 7: Relationship between gutted mass and total mass (M) for 302 steentjies from Langebaan Lagoon.

Reproductive biology

Sexually active males are distinguishable from non-sexually active males and females by having the bright blue and yellow heads and blue markings on the flanks (Fig. 8). In frozen samples, all males appeared bluer and darker in colour than in fresh samples including those that did not display the mating colouration at the time of capture. All fish with the 'bluehead' phase were males with testes classified as either active or ripe (stages 2 and 3). None of the juvenile males exhibited the mating colouration and most spent males had lost their colouration (Table VI). Males without the mating colouration were found to have reduced gonad mass (Fig. 9) than similar sized males exhibiting mating colours. Although there were no significant differences in fork length between males with and without mating colouration ($U = 326$, $Z = -1.47$ and $p = 0.14$), there were significant differences between the gonad masses of the two groups ($U = 3.5$, $Z = 6.48$ and $p = <0.001$). The occurrence of mating colours became less frequent towards the end of the spawning season (Fig. 10).

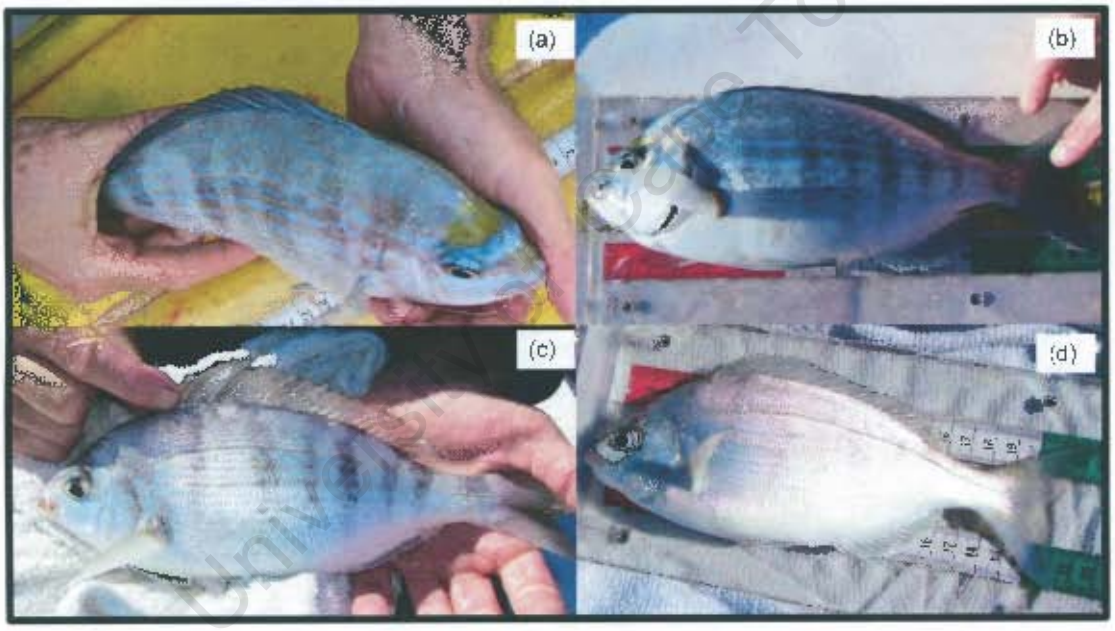

Fig. 8: Photographs of male (a, b) and female (c, d) steentjies in breeding season, illustrating sexual dichromatism.

Table VI: Macroscopic gonad stages of male steentjies with and without mating colours.

Gonad stage	With mating colours	Without mating colours	Total
1	0	7	7
2	13	4	17
3	12	4	16
4	4	15	19
Total	29	29	59

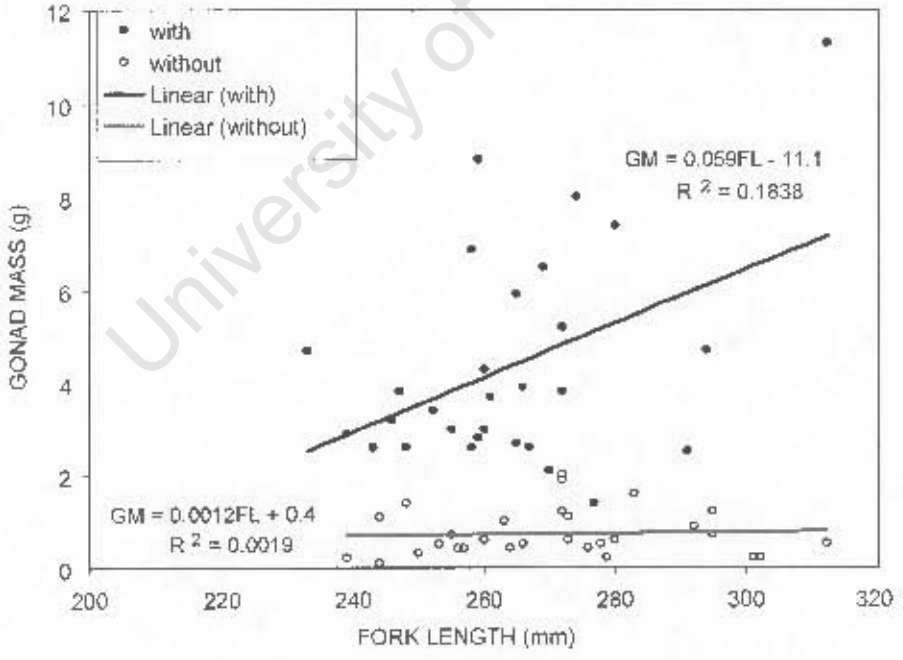

Fig. 9: Relationships between gonad mass and fork length of male steentjies with and without mating colouration from Langebaan Lagoon.

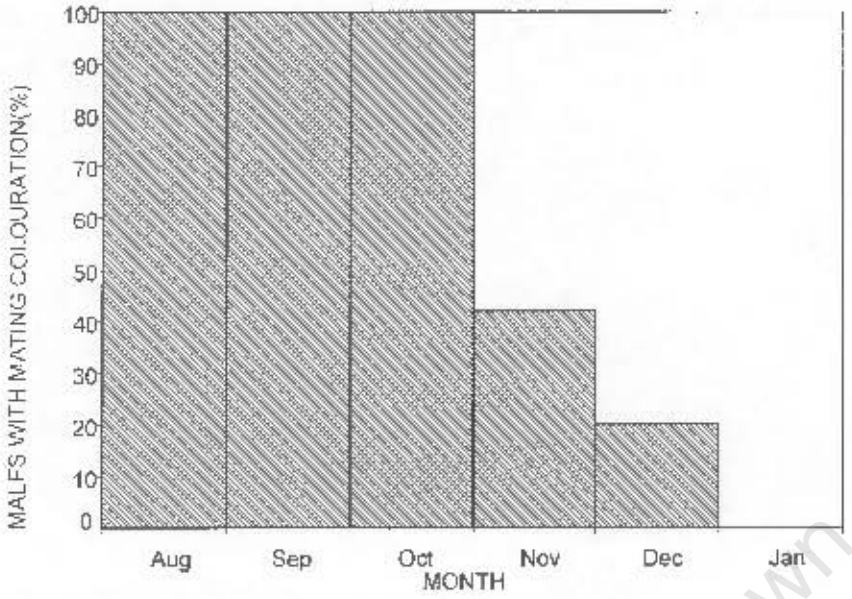

Fig. 10: Monthly percentage of males exhibiting mating colours.

In all samples collected during this investigation, the sex ratio was dominated by females (4.4 female: 1 male – all data) and there were no significant differences (χ^2 = 0.23, df = 5, $p < 0.99$) between the relative frequencies of males and females caught each month between August 2004 and January 2005 (Fig. 11).

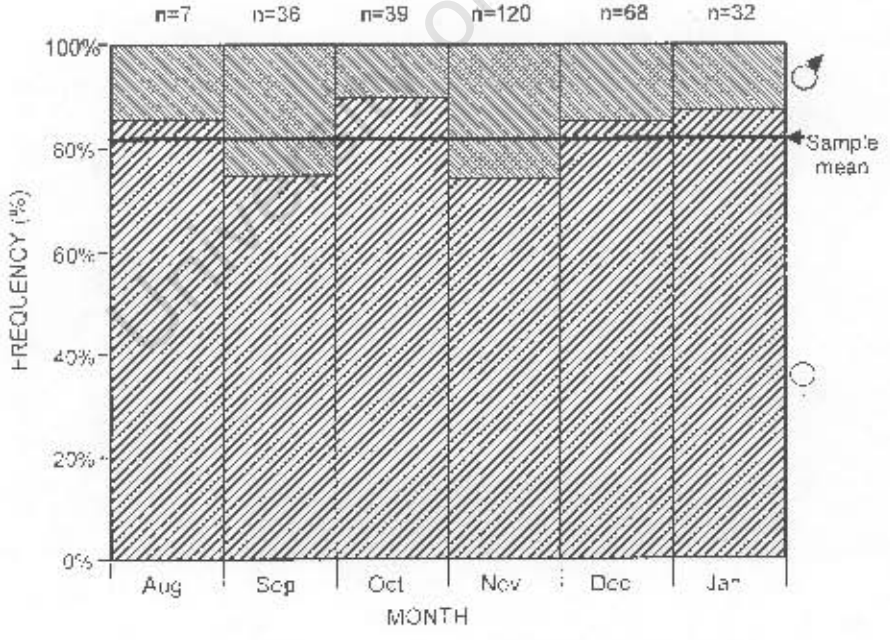

Fig. 11: Variations in the monthly sex ratios of steentjies from Langebaan Lagoon.

Macroscopic examination of gonads during the study period suggests a late winter-spring spawning season for steentjies in Langebaan Lagoon, with females and males displaying similar patterns in terms of the maturity (Fig. 12 and 13). In both sexes juvenile stages were only observed between November and January. Active females were present throughout the study period but active males were only found between September and November. For both sexes, an increasing number of spent individuals were observed between November and January, and Ripe females were present for a month longer (December) than ripe males. Monthly variations in the mean GSI (Fig. 14) further support a spring spawning season. The GSIs of both sexes show the same pattern with females having a much larger GSI in every month sampled; the GSI of both sexes had smallest values in January when the resting period would appear to start. The maturation process is slower for females, the GSI peaking one month after males.

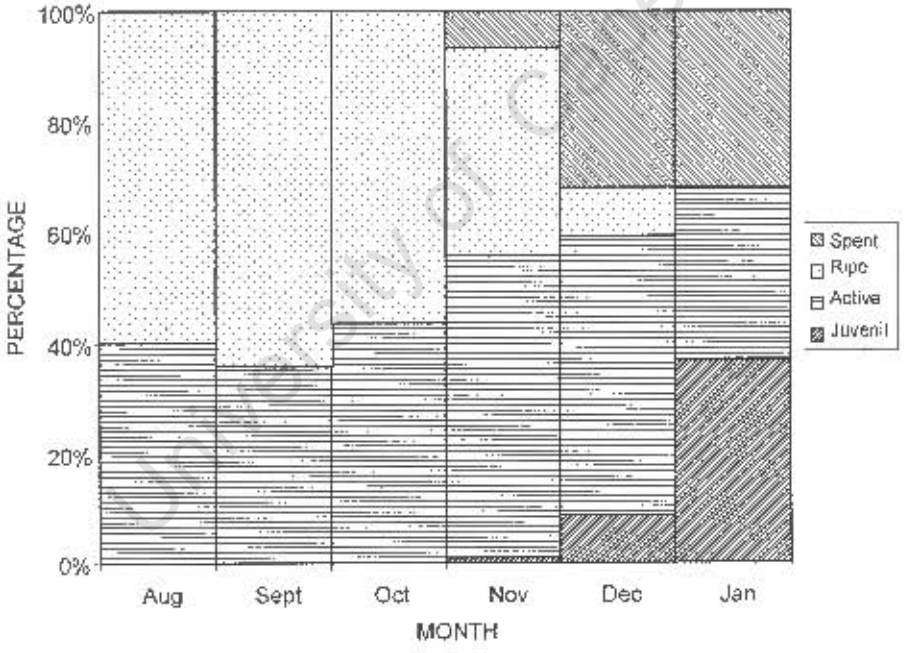

Fig. 12: Monthly percentage of macroscopic ovarian stages for steentjies caught during this study.

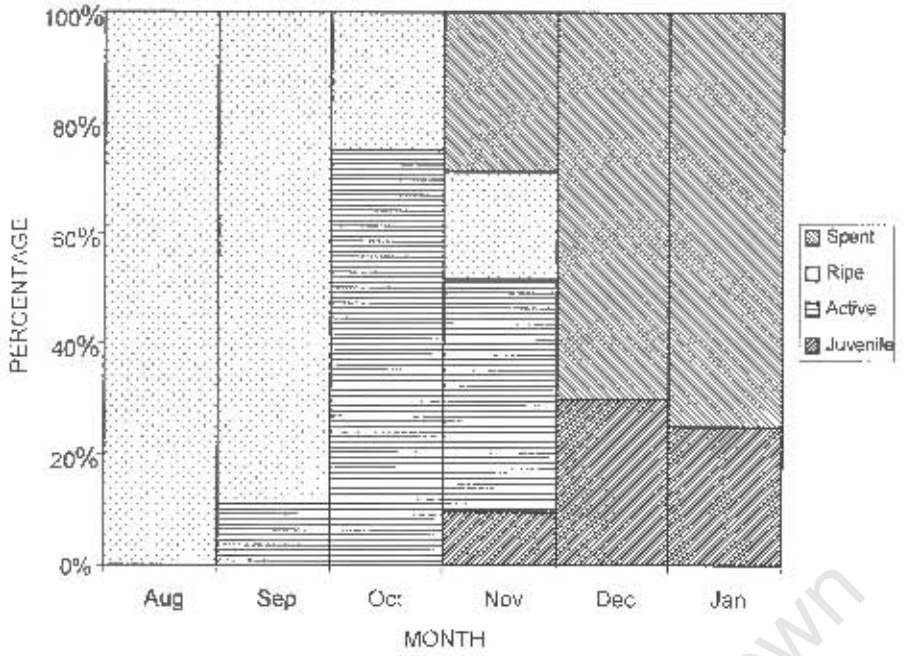

Fig. 13: Monthly percentage of macroscopic testicular stages for steentjies caught during this study.

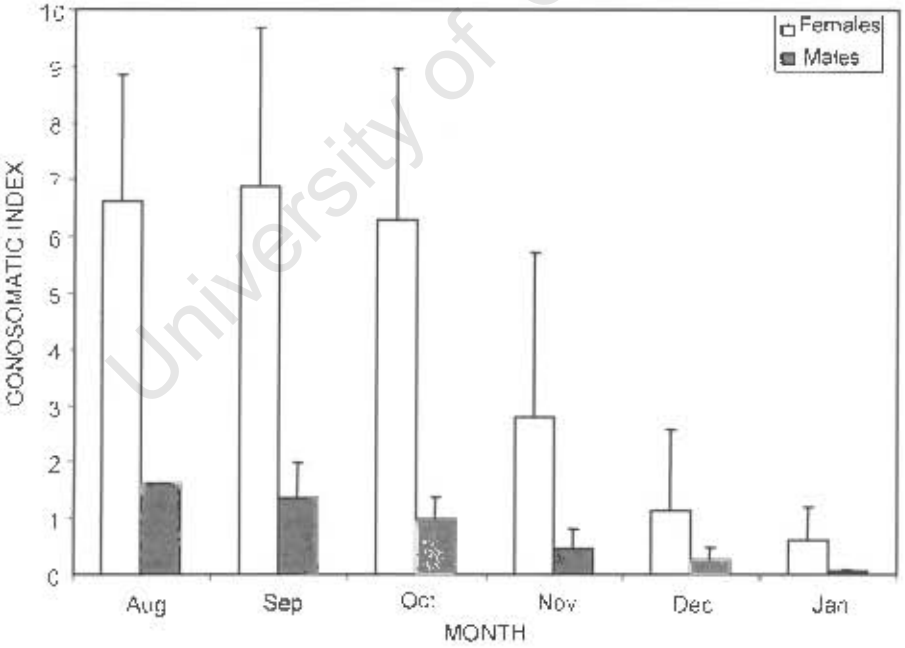

Fig. 14: Monthly variation in the gonadosomatic index (+ 1 S.E), calculated when there was more than one sample) in male and female steentjies sampled during this study.

All females < 150 mm FL were juvenile. There were no trends in FL and sexual staging for males as males of all size classes were present within each sexual stage. By relating macroscopic gonad stages to fork length (logistic ogive to proportion of mature fish per length class), the length-at-50%-maturity (FL) was estimated for females as 171 mm (FL). The smallest reproductively active female had an FL of 154 mm while the smallest reproductively active male was 239 mm (FL). The size at 50% sex change was determined from the whole sample of fish in each size group using a maturity ogive. The proportion of individuals that had changed sex was calculated and plotted against size. The data were then fitted using an iterative least squares procedure (Microsoft EXCEL (Microsoft corp., 2000) SOLVER routine with Newton algorithm option) using the logistic function (eq. 1), with the L_{50} representing the size at 50% sex change.

Four steentjies were found to have both ovaries and testes under macroscopic examination (Fig. 15). These individuals fell in the size range of overlap between the two sexes (243 – 279 mm FL). Microscopic examination of the histological sections indicated that there was some variation in the stages of ripeness along the length of the gonads. In most cases, the majority of the sections removed from the middle and posterior parts of the gonad were in agreement with the stage that had been allocated to that gonad macroscopically. Accordingly, the middle section was used when confirming the macroscopic staging (Figs. 16 to 18). Examinations of male gonad tissue containing atretic oocytes confirmed that steentjies are protogynous hermaphrodites (Fig. 19). Histological examination also indicated that some females classified as being ripe (macroscopically) had in fact already started developing male testes. However due to the relatively small sample size (n = 13) of the histological work it was not possible to make a statistically valid comparison between histological and macroscopic stages. The histological analyses performed during this investigation are preliminary due to time constraints.

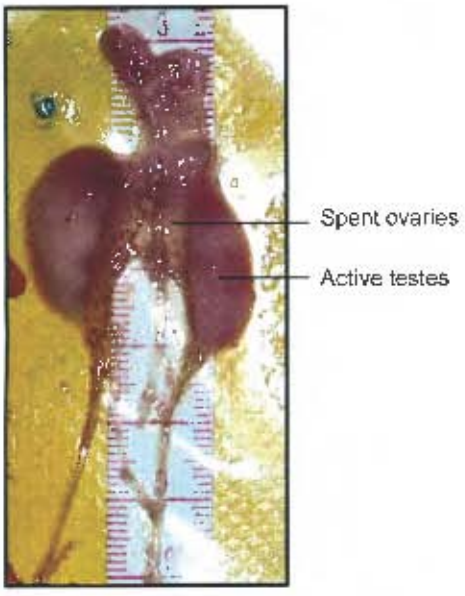

Fig. 15: Steentjie gonad depicting spent (remnant) ovaries and active testes.

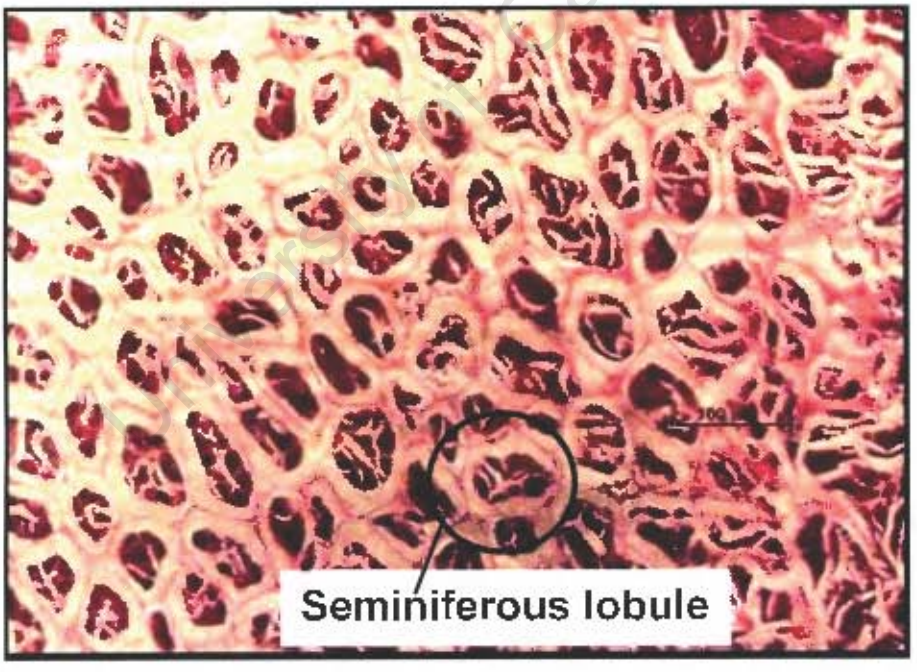

Fig. 16: Microscopic view of a juvenile male steentjie testes, removed from a fish frozen after capture from Langebaan Lagoon.

Fig. 17: Microscopic view of a ripe female steentjie ovary, removed from a fish frozen after capture from Langebaan Lagoon.

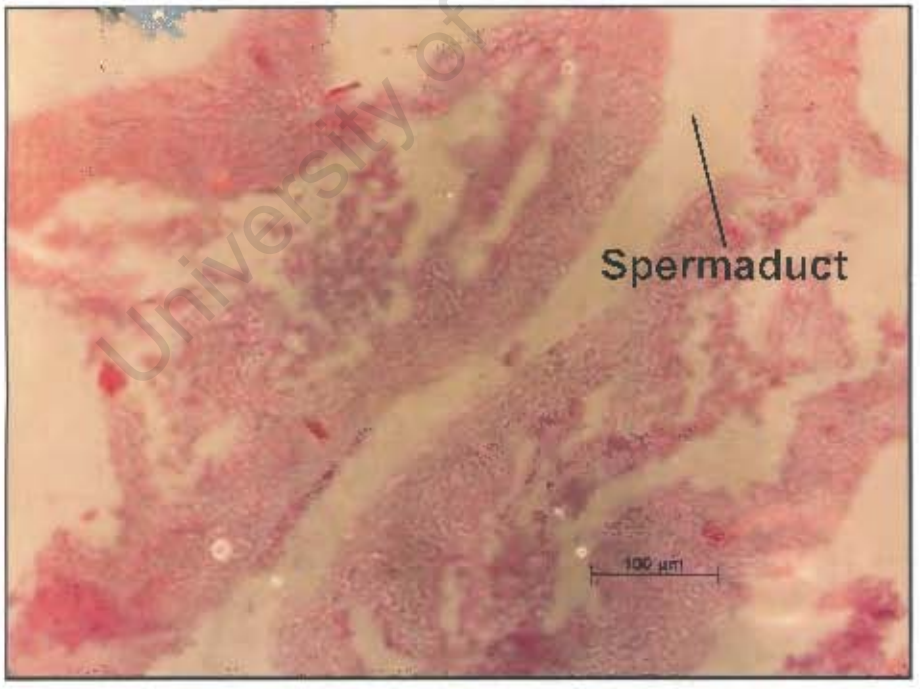

Fig. 18: Microscopic view of active male steentjie testis, removed from a fish frozen after capture from Langebaan Lagoon.

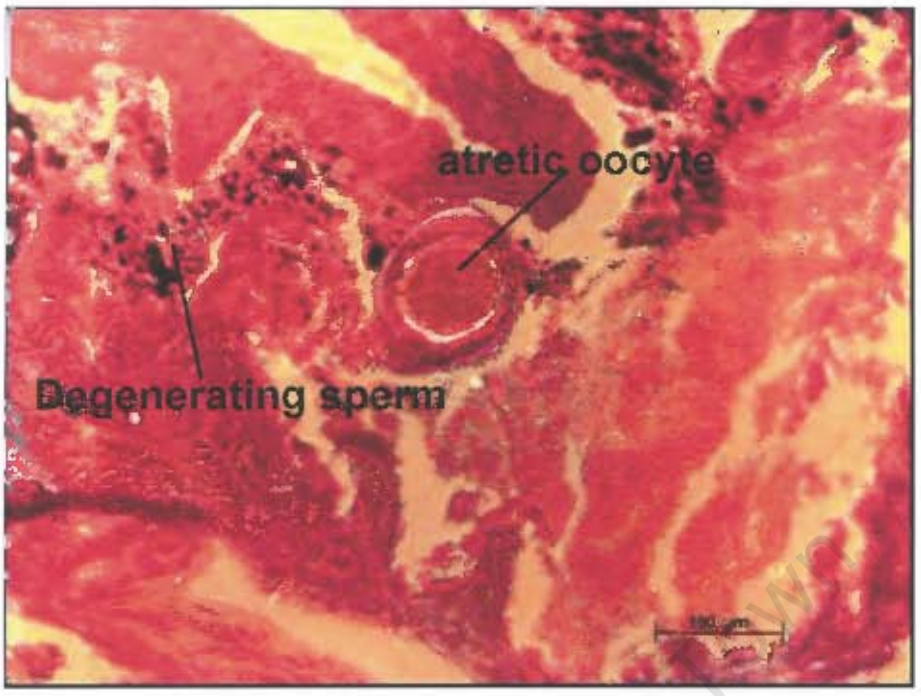

Fig. 19: Microscopic view of a mature male steentjie testis with a putative degenerating unyolked oocyte amongst the male tissue. The testis was removed from a fish frozen after capture from Langebaan Lagoon.

Diet

Of the 284 steentjies that had their foreguts examined, 255 (136 – 209 mm FL) contained food. The composition of foregut contents is shown as percentage occurrence in Fig. 20. It must be noted that in every foregut examined, there were unidentifiable elements (excluded from Fig. 20 to enable the identified elements to be depicted clearly) and several steentjies had up to three different food types present in the foregut at one time. Small individuals (< 178 mm FL) consumed only plant items. Larger fish consumed all food types but only steentjies 204 mm FL or larger consumed crab.

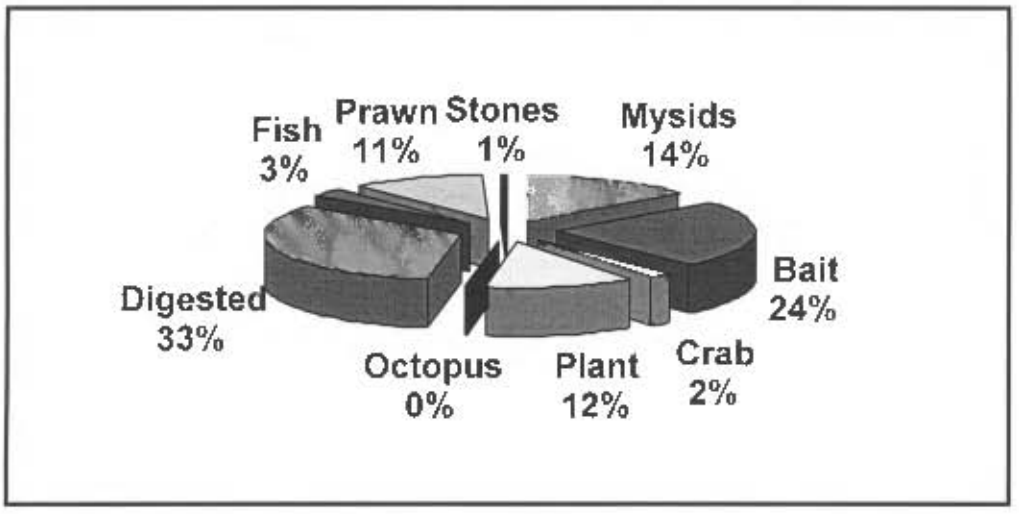

Fig. 20: Percentage occurrence of dietary items in 232 steentjies sampled from Langebaan Lagoon. Note: percentages add up to more than 100 because some fish had more than one item in their stomach.

The ranks for foregut fullness in each month are illustrated in Fig. 21 (males) and Fig. 22 (females) and indicate that males are at their fullest in November (where over 50% of the males were given the rank of 5), and January (all males were ranked either 4 or 5). In contrast, more females with a foregut fullness ranking of 5 were found in September than in other months (Fig. 22), but fewer females than males generally displayed rank 5 foregut fullness ($U = 3164.5$ and $p < 0.0001$).

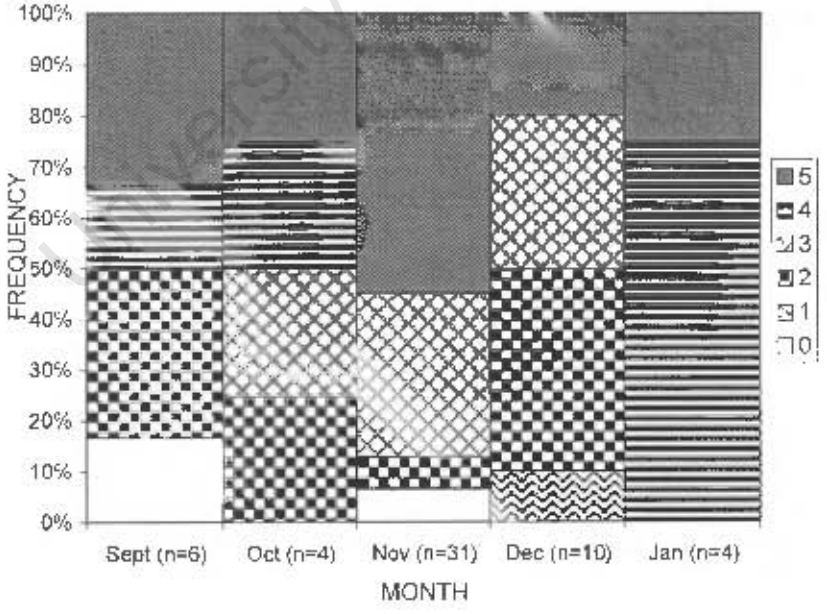

Fig. 21: Fullness of male steentjie foreguts during September to January in Langebaan lagoon.

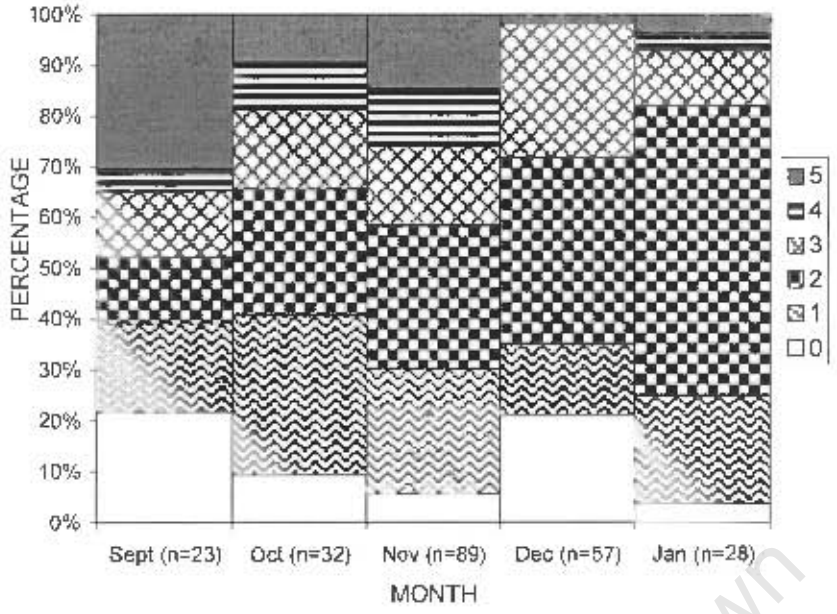

Fig. 22: Fullness of female steentjie foreguts during September to January in Langebaan Lagoon.

Age and growth

Otoliths from 302 fish were examined during this component of the study. Otolith weight displayed a strong linear relationship with fish length (Fig. 23) (R^2 = 0.88, p <0.0001). Of the 302 otoliths examined, data from 27 (8.9%) were discarded because of slides breaking during replicate readings. The remaining sample presented here is therefore based on a sample consisted of 275 otoliths from fish, of which 221 were female and 54 male. The smallest fish (136 – 146 mm FL) had otoliths with an opaque centre and either none, one or two translucent zones. The largest fish examined was 312 mm FL.

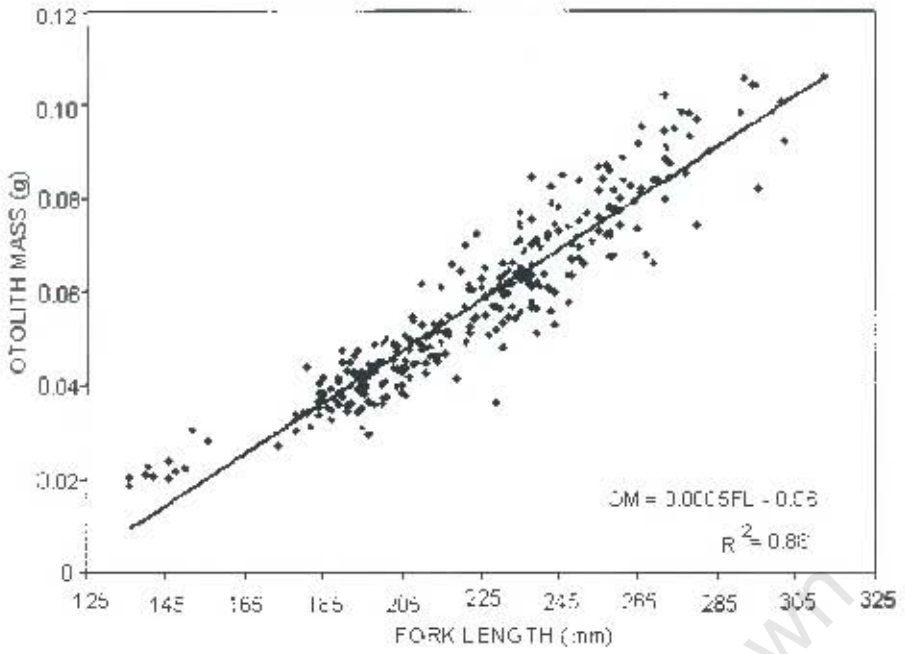

Fig. 23: Relationship between the otolith mass (OM) and fork length of 302 steentjies collected during this study.

In total, 101 otoliths were read whole (Fig. 24), and subsequent readings of these otoliths tended to yield fewer rings (increasingly negative residuals) than earlier readings (Fig. 25) indicating strong reader bias, and specifically a tendency to increasingly underestimate the age of the fish with successive readings. Because of this element of bias, the sectioned otolith method was subsequently adopted (Fig. 26). The mean residuals of each counting session using the sectioned otolith method (Fig. 27) showed no indication of bias; no directional trend in the mean of the residuals of each count is apparent.

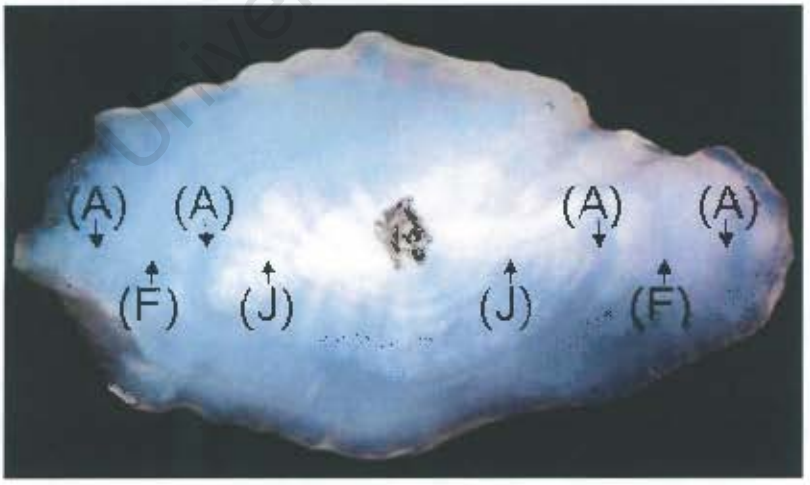

Fig. 24: Whole otolith of a 2-year-old steentjie showing a juvenile ring (J), false ring (F) and the true growth rings (A) under reflected light (X 10.5).

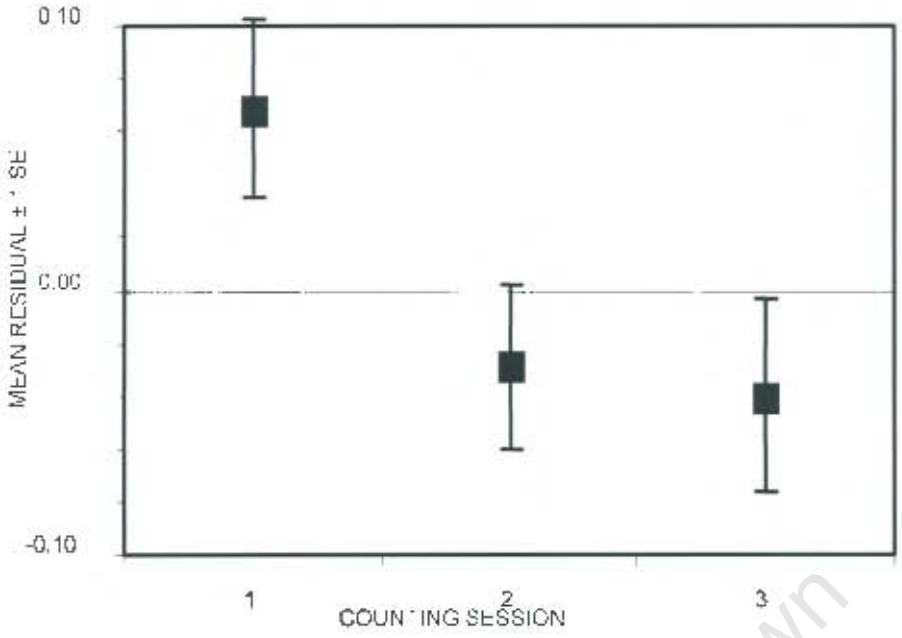

Fig. 25: Plot of mean residuals across all otoliths for each of the counting sessions for whole otoliths.

Fig. 26: Photomicrograph of a sectioned otolith from a 5-year-old steentjie (viewed under transmitted light at 14X magnification).

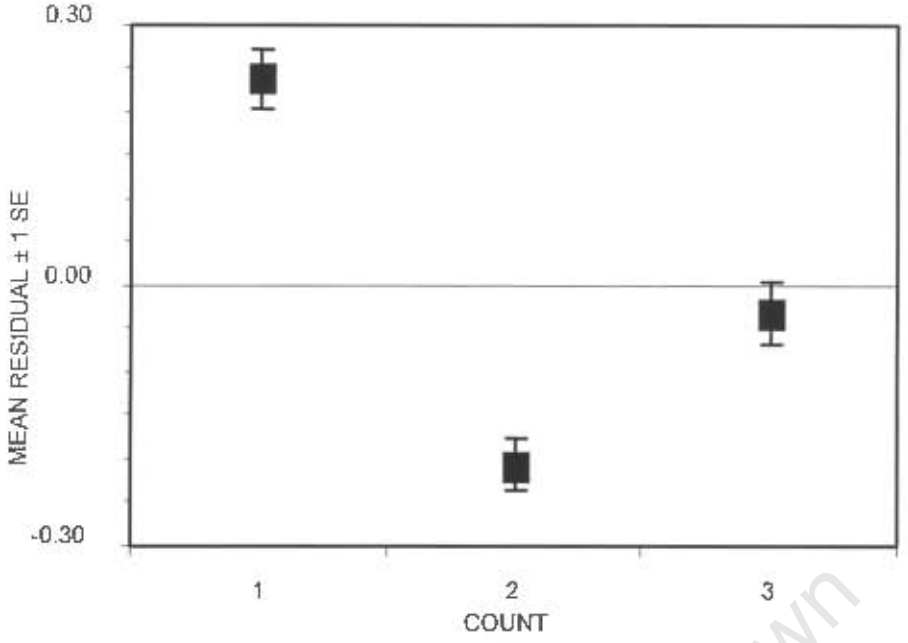

Fig. 27: Plot of mean residuals across all otoliths for each of the counting sessions for sectioned otoliths.

Indices of precision (APE, CV and D) were calculated from replicate age data obtained from the same fish using both techniques (Table VII). It should be noted that the first readings were excluded from these analyses as they were test readings aimed at clarifying otolith interpretation criteria. The whole otolith method appeared to be more suitable. The sectioned otolith method yields precision indices more than twice as high as those from the whole otolith data set. The data collected from the whole otoliths displays a strong element of bias (Fig. 25) with the reader tending to increasingly underestimate age with each successive reading. This element of bias was not apparent in the data collected using the sectioned otolith method. On the basis of the bias, it was decided to employ the sectioned otolith technique for the collection of further age data. In fact, the two methods gave similar age estimates, with the whole otoliths estimates being 0.4 years younger on average (Fig. 28).

Table VII: Indices of Precision calculated for whole and sectioned otolith readings of steentjies from Langebaan lagoon.

Precision indices	Values	
	Whole otoliths	Sectioned otoliths
APE	4.37 %	10.62
CV	6.75 %	15.32
D	3.9	8.84

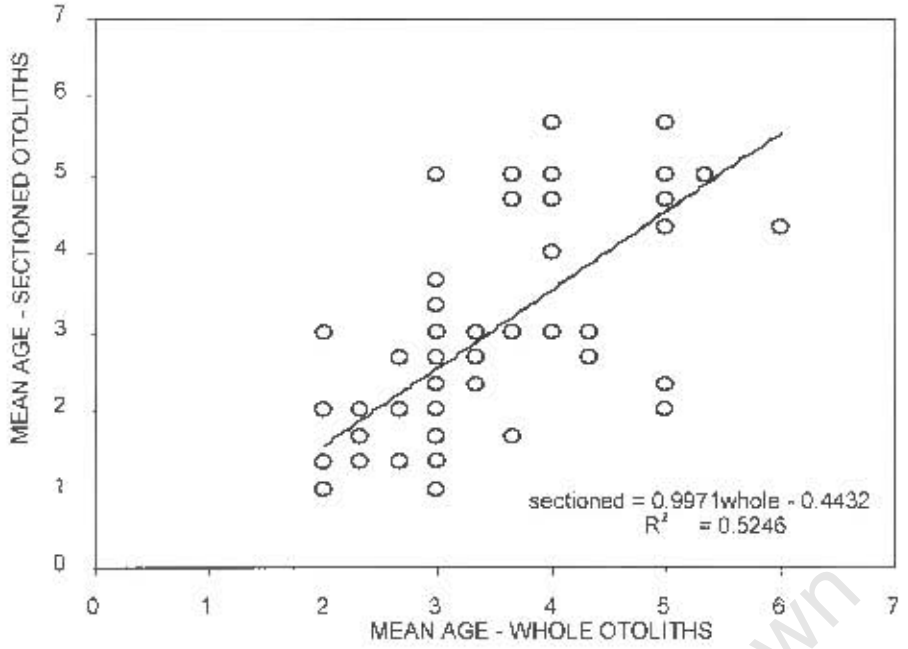

Fig. 28: Relationship between mean ages estimated from the sectioned and whole otolith readings.

The mean-length-at-age data for both sexes are displayed in Fig. 29. It is clear that males are larger than females of the same age. This difference is significant for each age class (when both sexes are present). An age-length-key for steentjies from this study by 1-cm FL classes is presented in Appendix A: Table A1.

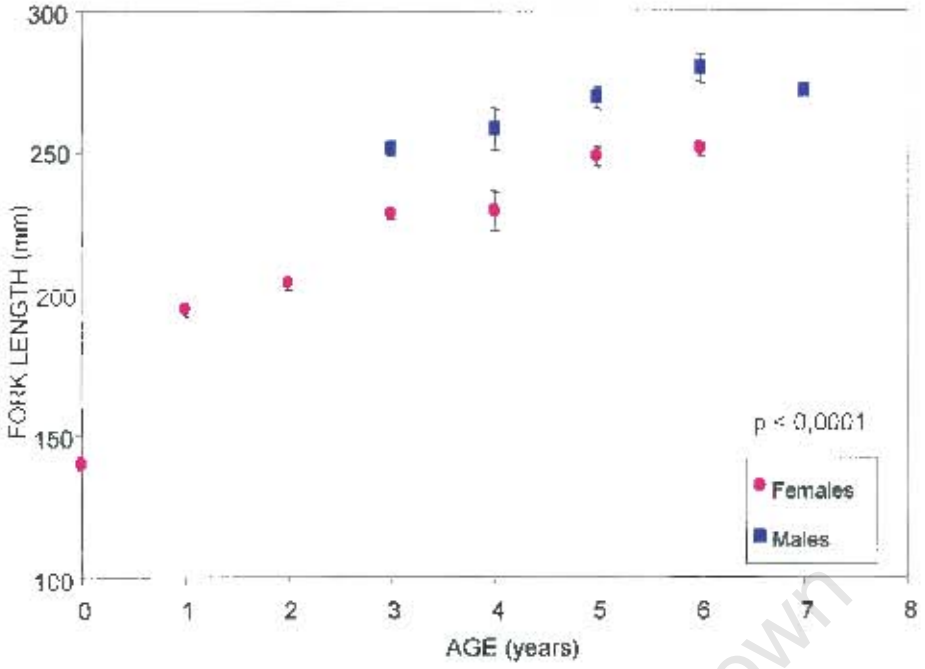

Fig. 29: Plot of mean-length-at-age (± SE) for steentjies caught in Langebaan Lagoon during this investigation.

Figure 30 shows the sex-disaggregated age-length relationships of male and female steentjies based on otolith ring counts. The Garratt *et al.* (1993) model allows for sex change from female to male over a range of ages (>3years), whereafter the males undergo a short period of accelerated growth (Fig. 30). The growth parameters associated with the model are provided in Table VIII.

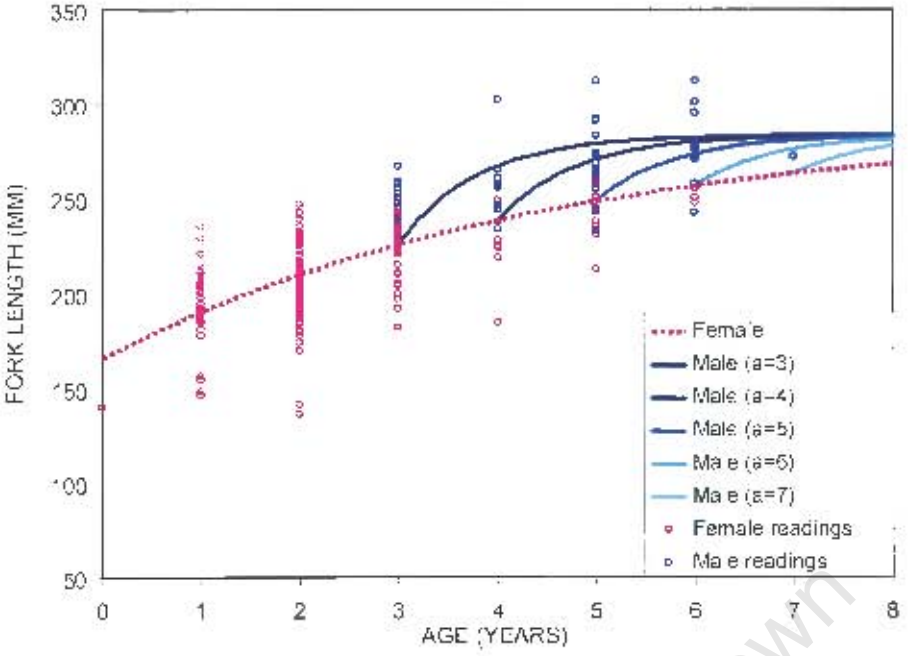

Fig. 30: Mean and observed length-at-age for males (in blue) and females (in dashed pink). The various shades of blue represent the mean length-at-age curves for different cohorts of males.

Table VIII: Growth parameters obtained from fitting the Garratt *et al.* (1993) growth model to the data collected on steentjies from Langebaan Lagoon. *SS* refers to the value of the sum of squares function corresponding to the parameter values given.

Parameter	Value
L_{∞}^{f}	289.15
L_{∞}^{m}	283.44
K^{f}	0.22
K^{m}	1.26
t_0^{f}	-3.82
SS	91476.76

Mortality

Instantaneous total mortality rate (Z) was estimated to be 0.7 y^{-1}, based on the data collected during this investigation (Fig. 31).

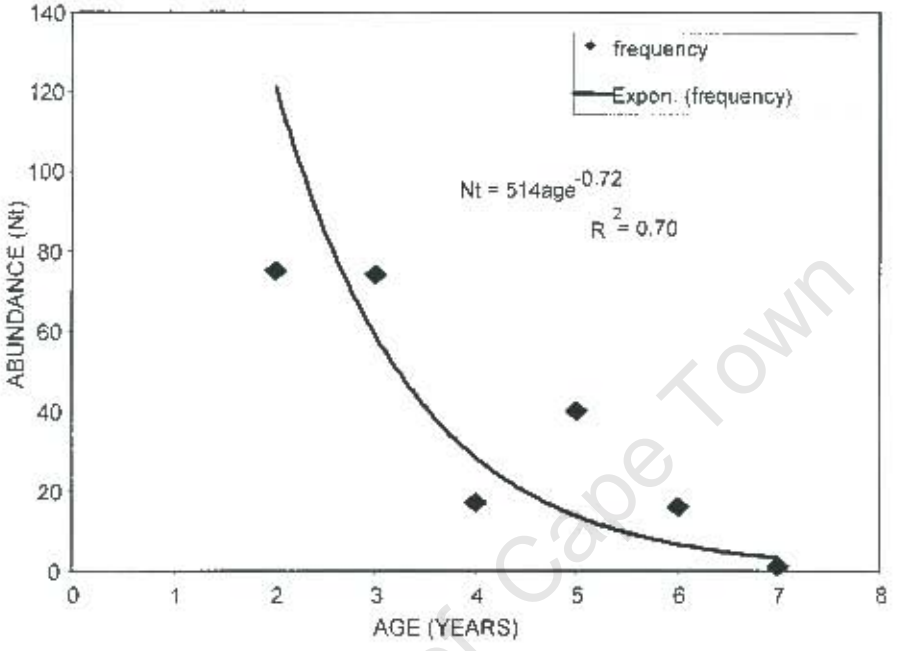

Fig. 31: Numbers at age of steentjies from Langebaan Lagoon caught from September 2004 to February 2005 (ages 0 and 1 have been excluded).

DISCUSSION

Morphometrics

Morphometric measurements are often used to aid identification of species of teleosts. Morphometric data can highlight differences between fish of different sub species and can be used in conjunction with genetics to indicate subspecies. External measurements and fin counts are rapid and inexpensive. Griffiths (1997) used morphometric data in conjunction with tagging and biological data to aid distinction between three stocks of the silver kob, *Argyrosomus inodorus*. As steentjies are thought to grow larger within the lagoon than on the south coast, fin count data were obtained in order to determine whether the isolated population at Langebaan is identical to those found on the south

coast. The fin counts made during this investigation (Table IV) were identical to those reported for the south coast (Smith and Heemstra 1986, van der Elst 1988). From these counts we cannot conclude that there are any taxonomic differences, but genetic testing would be required to verify this conclusion.

For future comparisons from other areas to be made with the data presented in this study, comparable data may need to be converted. At times, complete morphometric and mass data are not available. For example, in the commercial industry only the gutted mass might be available, and in some studies where only TL and not FL have been recorded. The relationships illustrated in Figs. 4 to 7 will facilitate conversion and thus enable effective comparisons.

Reproductive biology

The reproductive biology of South African sparid fish has been studied to a lesser extent by Coetzee (1978), Buxton and Garratt (1990), Booth and Buxton (1997), Griffiths *et al.* (2002) and others. Steentjies are sexually dichromatic, suggesting mate selection by females and paired spawning (Anderson 1994 and Griffiths *et al.* 2002). The sexual dichromatism observed during this investigation has been noted in a number of other sparids such as *Rhabdosargus globiceps* (Buxton and Garratt 1990), *Chrysoblephus puniceus* (Garratt 1993) and *Crysoblephus nufar* (Garratt 1991, Garratt 1993). Rudimentary hermaphrodites generally display random mating between pairs or group spawning (Buxton and Garratt 1990). In contrast, steentjies, which are sequential hermaphodites, display mate selection (P. A. Garratt, Two Oceans Aquarium, pers. comm.). Dichromatism is thought to be used as a method to attract and compete for ripe females in species such as *Crysoblephus nufar*, *Cheimerius puniceus* (Garratt 1991) and *Rhabdosargus globiceps* (Griffiths *et al.* 2002). It is also suggested that the brightness of the colouration may indicate the 'pecking order' (Garratt 1993) and that steentjie colouration appears to be directly related to gonad stage and mass (Table VI, Fig. 9). No significant difference was found between the lengths of those males that displayed the mating colouration and those that did not, indicating that the size of the fish was not directly related to mate selection.

The length frequency distributions (Fig. 3) are distinctly bimodal for all steentjies, and females displayed peaks at 200 and 240 mm FL. The second peak tails off more sharply in the female only length frequency distribution, corresponding to an increase in the number of males. Although steentjies are thought to be gonochoristic their reproductive biology has not been thoroughly researched (Smith and Heemstra 1986, van der Elst 1988). There were no small males or large females observed. All fish consequently

appear to pass through a female phase. There might be advantages for large males, given the reproductive behaviour observed by Beckley (1989), where large males might be expected to have greater success in defending their territory. The classic size advantage model was first dealt with by Ghiselin (1969) who suggested that protandry or protogyny could occur when an individual's reproductive success is related to size. This was discussed with regard to black sea bream by Gonçalves and Erzini (2000).

The bimodal distribution seen here is an indication that steentjies are protogynous hermaphrodites. A distinct bimodal size frequency distribution in *Rhabdosargus sarba* was reported by Yeung and Chan (1987) who provided conclusive evidence of protandry from the population structure, biopsy and gonadal histology. However, Sadovy and Shapiro (1987) cited by Garratt (1993) cautioned that bimodal size frequency distributions were inadequate indicators of sex change.

The sex ratio found during this investigation provides further evidence of steentjies being protogynous hermaphrodites. Griffiths *et al.* (2002) documented that sex ratios of protogynous hermaphrodites are typically skewed towards females (1:2–1:4 in unexploited populations and 1:2–1:19 in exploited ones). However, many problems have been associated with the use of sex ratios to diagnose sex change (Sadovy and Shapiro 1987 cited by Garratt 1993). The majority of steentjie samples collected for this study were collected during the steentjie spawning season, and given the suspected territorial mating behaviour of male steentjies, catchability of males could have been reduced with the gear used, thus biasing the sex ratios.

Garratt (1993) recommended that the strongest individual indicators of sex change in protandrous hermaphrodites are the transitional individuals whose gonads contain degenerating tissue from the previous sex and developing tissue of the future sex. Very little literature exists on protogynous sparids and transitional individuals have not been described macroscopically. The four transitional individuals found in this study contained degenerating ovarian tissue and developing testicular tissue and are therefore considered as good indicators of protogyny in steentjies (Fig. 15). This was further supported by histological analysis where females that were macroscopically identified as being ripe were found to have started developing testes but will be further substantiated in future analyses. However, it is important to note that the area of the gonad from which sections are taken can bias the results in several ways, because development of the future sex may be found in different parts of the gonad.

The macroscopic gonad stage data (Fig. 12 and Fig. 13) indicate the male and female stages mature at similar rates. The small GSIs of males (Fig. 14) could also be indicative of paired spawning; reduced sperm competition results in males having to produce much

less sperm, so the size of the testis (relative to body size) is reduced. This argument agrees with the nesting behaviour observed (Garratt 1991).

Mature males were present in the smallest male size classes. This may be a result of high fishing pressure, which favours earlier maturity (Griffiths *et al.* 2002), or it could be that males mature rapidly after sex change.

Diet

This study confirms previous observations of steentjies being omnivorous (Smith and Heemstra 1986, van der Elst 1988). Invertebrates provided 50% of the steentjie diet with 30% of the total diet composition consisting of mysids. Plants contributed the greatest amount to the diet (39%) but this may be biased by the smaller fish as all fish sampled between 136 and 178 mm FL were found to be eating only plants. Algae have been reported as a major dietary component for a number of other South African omnivorous sparids (Pulfrich and Griffiths 1988).

The diets of small and large fish have been reported to vary considerably for a number of fish species (Buxton 1984, Smale 1986, Pulfrich and Griffiths 1988). No juvenile steentjies were caught during this survey, but juveniles are thought to benefit from eating only zooplankton (Whitfield 1985 cited by Bennett 1986a). The diets of *Rhabdosargus globiceps*, *Rhabdosargus holubi*, and *Lithognathus lithognathus* change as the fish grow from eating zooplankton prey (fry/juvenile) to consuming larger invertebrates and plant material (full grown adults) (Bennett 1989a). This also appears to be the case with steentjies, as smaller fish feed exclusively on plant material, larger fish consume an increased variety of invertebrates in addition to plant material and the largest fish were able to consume crabs. This may be due to a change in their feeding behaviour and an increase in jaw strength enabling them to bite through the crabs exoskeleton. Berg (1979) suggested that the nature of the ingested food depends primarily on the morphology and feeding behaviour of the fish.

It was not possible to establish whether food is in any way limiting from the data presented in this study. To correctly establish the feeding chronology, food consumption and behavior of steentjies, a more extensive method of sampling must be undertaken than the one used during this study (Berg 1979, Buxton 1984, Pulfrich and Griffiths 1988). All fish sampled were caught by angling, which means that they were feeding (as opposed to guarding nests), which could bias the monthly trends. It was also not possible in this study to estimate the relative amounts of each food item present in the stomach. This

method could easily be improved by noting the proportions of food types within the stomach (Berg 1979). The fullness of the stomach may be related to the guarding of nests.

For both sexes food consumption varied over the months sampled. This could be due to prey availability or reproductive behaviour and related food requirements. Steentjies were least full in December which corresponds to the end of the reproductive season. This may be due to fish protecting fertilised eggs, thus restricting their feeding behaviour. An explanation for the males consistently having fuller stomachs than the females every month could be due to the males being considerably larger than the females and thus able to feed upon a greater variety of prey and larger individuals.

Age and growth

The relationship between fish growth and otolith size has been studied and allows the use of backcalculation for determining growth (Garrett *et al.* 1993). This investigation has shown a strong, significant relationship between otolith mass and fork length of steentjies (Fig. 23).

In order to compare the two methods of otolith analysis (whole versus sectioned), the precision and bias of replicate age estimates obtained by the two methods was evaluated. Precision was quantified by calculating the average percent error (Beamish and Fournier 1981), coefficient of variation (CV) and the D (index of precision) (Chang 1982). As pointed out by Campana (2001), a high level of precision does not imply that the age estimates are accurate, but rather indicates that the replicate age estimates are reproducible, implying that the interpretation criteria being employed by the reader(s) are stable over time. Bias, on the other hand, reflects a directional change in the interpretation criteria employed by a reader (or between different readers). A reader that ages the same fish consistently older (or younger) in successive replicate readings is considered to be biased. For example; a fish that is known to be 7 can be read as 6, 5, and then 4 in subsequent reading. A residual analysis approach provides a clear illustration of potential directional bias in replicate age data and was consequently adopted in this study.

Although random error cannot be avoided when reading otoliths, systematic or bias errors can lead to serious errors in population dynamics calculations (Lai and Gunderson 1987 cited by Campana 2001).It was therefore important to test which method of aging steentjies yielded the most reliable results. It was established that sectioned otolith readings had less bias than was the case of the whole otoliths. Once the otoliths were sectioned, the stacking phenomenon of growth zones towards the otolith margin was not apparent and the growth zones were clearer and easier to read. However, there were no

appreciable differences in the ages yielded. The slicing method tended, on average, to yield ages about 0.4 years lower than did the whole otolith method (Fig. 28), but this is not considered to represent a significant source of error in subsequent growth and mortality analyses.

The features interpreted to be growth rings in steentjie otoliths have not been validated (i.e. the assumed annual frequency of their deposition has not been confirmed). Validation studies conducted on other sparid species from various regions have confirmed that these features are deposited with an annual frequency (Booth and Buxton 1997, Radebe *et al.* 2002 and Brouwer and Griffiths 2004). It was consequently assumed that the growth zones identified in steentjie otoliths reflected an annual cycle in the growth of the otoliths. Validation of annulus deposition by steentjies would improve the readings made during this investigation and facilitate the development of accurate otolith interpretation criteria. Various chemical markers have been used to validate sparid aging techniques. Fluorochrome marking was generally held to be reliable, as discussed extensively by Lang and Buxton (1993). Sparid studies have shown that spawning season coincided with opaque zone deposition (Brouwer and Griffiths 2004). However, it has been suggested that tagging negatively affected growth in the sparid *Lithognathus lithognathus* (Attwood and Swart 2000) and *Argyrozona argyrozona* (Brouwer and Griffiths (2004). Although these methods are useful, if they affect the growth of the fish they will introduce an element of error into subsequent age estimates. It is worth noting that in some cases, back-calculation has proven to be a successful method for estimating age and growth, as in the case of *Diplodus sargus cadenati* (Sparidae) (Pajuelo and Lorenzo 2002).

There are three hypotheses regarding the sex-specific size-at-age differences in protogynous species: the 'transitional growth-spurt hypothesis', the 'juvenile growth hypothesis' and the 'larval growth hypothesis' (each of these has been described in detail by Walker and McCormick (2004)). The observed lengths varied widely within each age group (Fig. 30) and are equally scattered about the fitted growth model, demonstrating that the Garratt *et al.* (1993) model or the 'transitional growth-spurt hypothesis' adequately describes the growth of steentjies and their changing of sex in Langebaan Lagoon. Sex change can have a profound influence on growth rate of a fish species, as was shown by Garratt *et al.* (1993) for the sparid *Chrysoblephus puniceus*. This should be taken into account when undertaking a stock assessment using models such as yield per recruit. In the case of the steentjie, males reach a greater length than females at the same ages (Figs. 29 and 30), which was proposed as a characteristic of protogynous species by Garratt *et al.* (1993). It may be worth investigating whether this is also the case for other stocks of steentjies as environmental conditions may be a contributing factor.

Mortality

The total mortality rate estimated for steentjies during this investigation (0.72 y^{-1}) is much higher than natural mortality estimates of 0.47 y^{-1} calculated for the two banded bream by Gonçalves *et al.* (2003) but similar to the total mortality rate (0.625 y^{-1}). A review based on 10 species of Sparidae found that natural mortality rates ranged between 0.19 and 0.66 y^{-1} (Erzini *et al.* 2001 cited by Gonçalves *et al* 2003). The total mortality rate estimated in this investigation is substantially higher than these levels, indicating that fishing mortality is contributing to total mortality.

Conclusions and management

There is now a small length frequency data set where none existed before for west coast steentjies. These can be used as bench marks in future management. Outside the spawning season, males and females were practically indistinguishable, similar to findings discussed by Gonçalves and Erzini (2000). Samples studied throughout the year could allow the onset of the spawning season to also be linked to the mating colouration of the males. The spawning season that has been estimated from these data is the austral spring.

The age data collected during this investigation has allowed a growth model for protogynous hermaphrodites to be derived. However, more data is needed for male fish, to confirm the 'growth spurt' presented in the model.

Based on their presumed high residency (steentjies are not found anywhere else on the west coast of southern Africa), steentjies are predicted to be particularly vulnerable to over fishing. Larger reproductive males are likely to be targeted because of their size and because they are more aggressive. The current daily bag limit is 10 fish and there is no size limit on these fish at present, and means that both males and females are probably being caught. If this species of fish were to become commercially important, a maximum size limit of 260 mm (FL) could be imposed to reduce the numbers of males being caught, ensuring reproduction. It is assumed that it is the males that protect the eggs in the nests. Increased removal of breeding males could lead to a reduction in the number of eggs being produced and a reduction in the number of survivors. Based on their fast growth, steentjies could probably sustain increased fishing, but the presumed high residency (whilst guarding their nests) would indicate that steentjies could be vulnerable to overfishing. Further investigation into where and how predictably steentjies aggregate could also be useful, as this behaviour may also make them more vulnerable to exploitation as was reported by Bennett (1986b) for *Lithognathus lithognathus*.

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Age-length key of steentjies caught during this study.

	Age																				Size Class Total
	0		1		2		3			4			5			6			7		
Sex: / Size class	F	Tot	F	Tot	F	Tot	F	M	Tot	F	M	Tot	F	M	Tot	F	M	Tot	M	Tot	
13					1	1															1
14	1	1	2	2	1	1															4
15			2	2																	2
17			1	1	3	3															4
18			13	13	7	7	1		1	1		1									22
19			12	12	23	23	2		2												37
20			14	14	14	14	4		4												32
21			4	4	11	11	6		6	1		1	1		1						23
22			2	2	6	6	11		11	3		3									22
23			1	1	6	6	29	2	31	2	1	3	5	1	6						47
24					3	3	9	3	12	1	2	3	2	1	3	1	1	2			23
25							1	5	6	1	2	3	8	1	9	2	1	3			21
26								1	1		2	2	3	7	10						13
27														6	6		6	6	1	1	13
28														1	1		1	1			2
29														2	2		2	2			4
30											1	1					1	1			2
31														1	1		1	1			2
36														1	1						1
Age Total	1	1	51	51	75	75	63	11	74	9	8	17	19	21	40	3	13	16	1	1	275

APPENDIX A