THE TAXONOMY AND LIFE-HISTORY OF *ARGYROSOMUS JAPONICUS* AND *A. INODORUS*, TWO IMPORTANT SCIAENIDS OFF THE SOUTH AFRICAN COAST.

THESIS

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by

MARC HASTINGS GRIFFITHS

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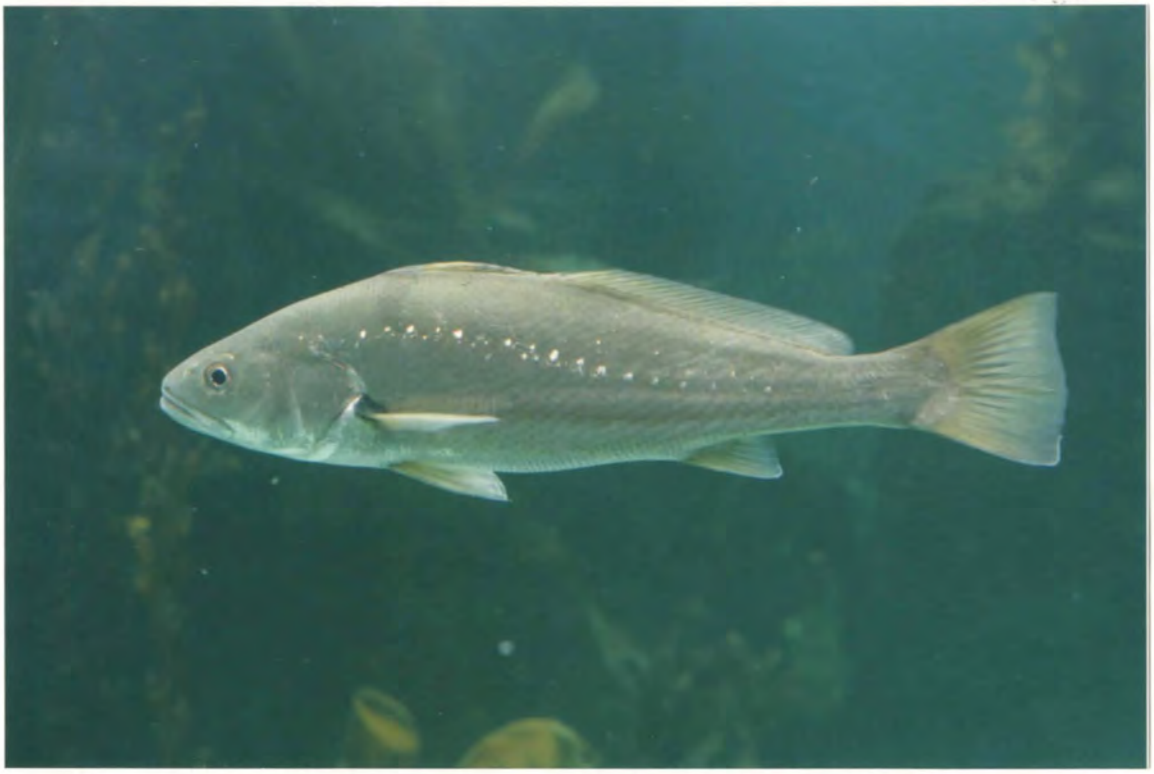
Argyrosomus japonicus (Temminck & Schlegel 1843)



Argyosomus inodorus (Griffiths & Heemstra 1995)

Then God said, " Let us
make man in our image, in
our likeness, and let them
rule over the **fish of the sea**
and the birds of the air......."

(Ge 1: 26, NIV)

This thesis is dedicated to: the Alpha and the Omega
who created a world captured in time
delicately balanced
yet designed to change,
with the seasons
and with the years;
producing beauty beyond description,
creatures, wondrous in form
and fascinating in function,
adaptable yet dependant
their lives intricately woven
into the fabric of life.

To discover secrets of nature,
and to but touch such truths
that we may never firmly grasp,
is to glimpse His infinite wisdom
and the awesome power
of His hand.

PREFACE

This thesis is submitted as a collection of five 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) to each of the papers was unavoidable. Where dual authorships are concerned (see appendix A), the senior author was responsible for all data collection, data analyses, concepts, hypotheses and conclusions.

ACKNOWLEDGEMENTS

Many people contributed to the success of this project and I would like to thank the following:

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Specimens were loaned by the British Museum (Dr Nigel Merret), Muséum National d'Histoire Naturelle, Paris (Dr Marie-Louise Bauchot, Guy Duhamel & Bernard Séret), Institut Royale des Sciences Naturales de Belgique (Dr J.-P. Gosse), the Australian Museum (Mr Mark McGrouther), and the Hebrew University of Jerusalem (Dr D. Golani).

This work was funded by the Sea Fisheries Fund.

GENERAL ABSTRACT

A study of the biology, anatomy and taxonomy of the sciaenid fishes of the genus *Argyrosomus* from South Africa and Namibia revealed that three species were confused under the name "*Argyrosomus hololepidotus* (Lacepède 1801)". Comparison of morphometric and meristic data, otoliths, swim-bladders, drumming muscles, and other morphological features of specimens from southern Africa, Madagascar, the Mediterranean, the eastern Atlantic Ocean, Japan and Australia, revealed that "*A. hololepidotus*" is a complex of four species: *A. japonicus* (Temminck & Schlegel 1843), which occurs off southern Africa, Japan and Australia; *A. inodorus* sp. nov., which is known from Namibia to the Kei River ($32^0 40$'S) on the east coast of South Africa; *A. coronus* sp. nov., which is known from central and northern Namibia and Angola, and *A. hololepidotus*, which appears to be endemic to Madagascar.

Both *A. japonicus* and *A. inodorus* are important recreational and commercial linefish species in South Africa. Although *A. inodorus* occurs on the east and west coasts of South Africa, and *A. japonicus* is found between Cape Point and Mozambique, the former species is abundant only between Cape Point and the Kei River, and the latter species from Cape Agulhas to northern KwaZulu/Natal. The life-histories of *Argyrosomus japonicus* and *A. inodorus*, within these respective ranges, were elucidated using length-at-age, reproductive, catch and effort, size composition, otolith dimension/fish length and tagging data.

Median sizes at maturity (L_{50}) for *A. japonicus* were 920 mm TL (5 years) for males and 1070 mm TL (6 years) for females. All males >1100 mm TL (7 years) and all females >1200 mm TL (8 years) were mature. Females grew faster than males, but in both sexes growth slowed dramatically after maturity. Maximum age recorded was 42 years, but fish older than 27 years were rare. Adult *A. japonicus* were predominantly found in the nearshore marine environment, but also occurred in estuaries and in the surf zone. Spawning takes place in the nearshore environment, from August to November in Natal, and from October to January in the Southern and South-Eastern Cape regions. A large proportion of the adult population migrate to Natal to spawn, although spawning may continue once they return to the Cape. Early juveniles of 20-30 mm TL recruit into turbid estuaries along the entire east coast, possibly aided by olfactory cues. They appear to remain in the upper reaches of the estuaries where they find suitable food and refuge from predators until they grow to about 150 mm TL. Juveniles larger than this size were found in the middle and lower reaches of estuaries and also in the surf zone. Juvenile *A. japonicus* (< 1000 mm TL) generally did not migrate long distances, but remained as separate sub-stocks until they reached maturity.

A. inodorus grows more slowly than *A. japonicus*, and attains a lower maximum age (25 years) and a smaller maximum size (34 vs 75 kg). There was no significant difference between the growth rates of male and female *A. inodorus*. Those in the South-Western Cape initially grew faster than those on the east coast, but growth slowed sooner in the former region with the result that these fish attained a smaller maximum size. Although ripe *A. inodorus* were sampled throughout the year, there was a distinct spawning season from August to December, with a peak in spring (Sept-Nov). Spawning occurred throughout the study area for this species, in <50 m depth. Size at sexual maturity for *A. inodorus* was smaller in the South-Eastern Cape than in the Southern Cape. Median size at maturity for females was attained at 310 mm TL (1.3 years) in the former and at 375 mm TL (2.4 years) in the latter region, and the length at which all females were mature was 400 mm (3.5 years) and 550 mm (4.7 years) respectively. For males the estimates of L_{50} and total maturity were 200 mm (1 year) and 400 mm (2.8 years) for the South-Eastern Cape and 250 mm (1.5 years) and 450 mm (3.4 years) in the Southern Cape. East of Cape Agulhas, *A. inodorus* was found from just beyond the surf zone to depths of 120 m. Adults occurred predominantly on reef (>20 m) while juveniles were found mainly over soft substrata of sand/mud (5-120 m depth). Early juveniles do not enter estuaries, but apparently recruit to nursery areas immediately beyond the backline of breakers (5-10 m depth), and then move seawards with growth. No juveniles were obtained from the area west of Cape Agulhas as substrates <200 m depth were unsuitable for trawling. Due to lower water temperatures, the adults in this area were found from within the surf zone to depths of only 20 m. East and west of Cape Agulhas there was evidence of offshore dispersal in winter, in response to oceanographic changes. Based upon otolith morphology, juvenile and adult distribution patterns, sizes at sexual maturity and on tagging data, *A. inodorus* between Cape Point and the Kei River apparently exist as three separate stocks, one in the South-Eastern Cape, one in the Southern Cape and one in the South-Western Cape, with limited exchange.

The life-histories of *A. japonicus* and *A. inodorus* are discussed in terms of their management. The large size at maturity of *A. japonicus* together with evidence for considerable human impact on the early juvenile, juvenile, and the adult phases of the life-cycle indicate that estuarine nursery habitats need to be conserved, that the minimum size limit should be increased, and that current bag limits for this species should be reviewed. Although the current minimum size limit provides protection for *A. inodorus* until maturity, evidence is presented which indicates that at least one and possibly all of the stocks of this species are currently over-exploited. Stock assessment of the South African *A. japonicus* and *A. inodorus* resources, and the implementation of effective management strategies, are therefore a matter of urgency.

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CHAPTER 1

GENERAL INTRODUCTION

GENERAL INTRODUCTION

The Sciaenidae is one of the largest perciform families, consisting of approximately 70 genera and over 270 extant species (Chao 1986a). They are commonly referred to as croakers or drums, in reference to the sounds that the males of most species produce using specialized muscles which attach to the wall of the swimbladder (Chu et al. 1963, Trewavas 1977, Johnson 1978). Sciaenids occur in temperate and tropical coastal waters throughout the world; they are particularly abundant around the mouths of large rivers, but poorly represented in oceanic island groups e.g. Hawaii (Sasaki 1989). Diverse morphological variation has facilitated adaptation to a wide range of habitats, including benthic and pelagic environments (Sasaki op cit.). The family is noted for its tolerance of brackish conditions, and five of its genera consist of freshwater species (Schwarzhans 1993). Due to combinations of flesh quality, individual size and abundance, sciaenids support many important fisheries in both hemispheres (Fischer & Whitehead 1974, Chao & Trewavas 1981, Mohan 1984, Chao 1986a&b). Maximum sizes within the family may vary from about 18 cm TL, e.g. *Larimus fasciatus* (Standard & Chittenden 1984), to more than 180 cm TL, e.g. *Argyrosomus japonicus* (Griffiths & Heemstra 1995), and maximum ages range from 1.5 years in *Cynoscion nothus* (DeVries & Chittenden 1982) to more than 50 years in *Sciaenops ocellatus* (Ross et al. 1995) and *Pogonias cromis* (Murphy & Taylor 1989). They are gonochoristic multiple spawners which spawn in coastal waters or large estuaries. In all cases the eggs are small and pelagic, and the juveniles generally utilize estuaries or shallow (< 100 m depth) coastal areas as nurseries (Johnson 1978, Holt et al. 1985, Wilson & Nieland 1994, Griffiths & Heemstra 1995).

The kob, *Argyrosomus hololepidotus*, belongs to a genus which is restricted to the eastern Atlantic and Indo-West Pacific regions. It currently consists of 10 medium to large species, and probably includes the largest representatives of the family (Griffiths & Heemstra 1995). Prior to this study "*A. hololepidotus*" was regarded as an important sport and food fish species, recorded on the west coast of Africa (south of the equator) and on the east coast as far north as Maputo, off the east coast of Madagascar, off Mauritius, off India, and along the southern and south-eastern seaboards of Australia (Trewavas 1977, Heemstra 1986, Kailola et al. 1993). Along the South African coastline "*A. hololepidotus*" was considered to be a premier linefish species, caught by estuarine and surf anglers and by commercial and recreational lineboat fishers to depths of 100 m. It has also been an important by-catch of inshore trawlers operating in depths of between 50 and 100 m (van der Elst 1981, Heemstra 1984, Penney et al. 1989, Branch et al 1993, Japp et al. 1994).

Considering its importance, surprisingly little work has been undertaken on the life-history of "*A. hololepidotus*" in South African waters, and as a result wise management has not been possible. Biological knowledge prior to the initiation of this project included: feeding in several South African estuaries (Whitfield & Blaber 1978, Marais 1984, Coetzee & Pool 1991), and in the marine environments of the Cape Provinces (Nepgen 1982, Smale 1984, Smale & Bruton 1985); reproductive seasonality in Algoa Bay (eastern Cape)(Smale 1985); age and growth in KwaZulu/Natal (Wallace & Schleyer 1979); and the identification of estuaries (Whitfield & Blaber 1978, Marais & Baird 1980, Marais 1981, 1983a&b, Ratte 1982, Coetzee & Pool 1991, Whitfield et al. 1994) and shallow marine mud/sand substrata (Wallace et al. 1984, Smale 1984, Smale & Badenhorst 1991) as important nursery areas. Due to the paucity of fish < 350 mm TL in the Algoa Bay linefishery, Smale (1985) was unable to estimate sizes at 50% and 100% maturity for "*A. hololepidotus*", although he did suggest that maturity was attained below 250 mm TL. Sizes-at-maturity, the extent of the spawning grounds, stock separation, migration or stock assessment had therefore not been addressed. A review of the literature revealed that nothing was known of the biology of this "species" on the west coast of Africa. In Australia this "species" is also widely targeted by recreational and commercial fishers, using a variety of catch methods (Kailola et al. 1993), yet very little is known about its life-history off that continent (Hall 1984, 1986, Anon 1993, Gray & McDonall 1993). As in South Africa, Australian research has concentrated on the occurrence and feeding of "*A. hololepidotus*" (mulloway) in estuaries (Potter et al. 1983, Hall 1984, 1986, Loneragan et al. 1987, Gray & McDonall 1993). Based on observations of ripe fish from the mouth of the Murray River, Hall (1984) suggested that Australian mulloway mature at about 700 mm TL, and spawn from October to December. He did not, however, calculate lengths at 50% or 100% maturity, nor did he accurately delineate the spawning season.

Knowledge of the life-history of an animal is fundamental to the formulation of effective management strategies. Information on growth rate, the existence of discrete stocks and the sizes/ages at maturity is essential for accurate stock assessments (Gulland 1983, Butterworth et al. 1989, Clark 1991, Punt 1993, Campana & Gayné 1995). Sizes at maturity are often used as a basis for minimum size limits (Penney et al. 1989). The identification of spawning aggregations and nursery areas can be used for the implementation of closed seasons or closed areas, or to motivate for the reversal of habitat degradation. The current South African catch restrictions, including a 400 mm TL minimum size limit for commercial and recreational linefishers (in existence since 1940) (Notice No. 1696, Government Gazette Vol. 122 of 25 October 1940) and a bag limit of 10 fish/man/day for recreationals (Government Gazette No. 9543 of 31 December 1984), were determined arbitrarily and were not based on life-history parameters or the results of stock assessments. Although long term catch data are not available for the recreational or the commercial linefisheries, circumstantial evidence indicated that kob stock(s) were declining. Hecht and Tilney (1989) reported a substantial decline in "*A. hololepidotus*" CPUE in the Port Alfred linefishery from 1982-1987, and also expressed concern over the large contribution of recruits to the total catch. Smale (1985) demonstrated a steady downward trend in the national trawled catch of this "species" (1968-1981), and also provided evidence suggesting that trawl catches in the eastern Cape had crashed between 1967 and 1972 .

Motivated by evidence for declining catches, a project was initiated in 1990 to study the stock separation and biology of "*A. hololepidotus*" throughout its distribution in South African waters, with a view to providing information which could be used for stock assessments and for formulating an effective conservation strategy. It soon became obvious, however, that there were two species, with vastly different life-histories, confused under the scientific name *A. hololepidotus*. The objectives of the project therefore had to change to establish the proper identity and distribution patterns of the two species, to elucidate their life-histories, and to provide information relevant to the management of both.

Theoretically, to establish the identity of the South African species, one would only have needed to compared specimens with descriptions of the known congeneric species. However, the original descriptions and figures of *A. hololepidotus* (Lacepéde 1801) and *A. japonicus* (Temmink & Schlegal 1843) are poor, and in fact contain insufficient detail to distinguish between most *Argyrosomus* species. In addition a review of the literature showed that specimens of "*A. hololepidotus*" from South Africa and Australia had never been directly compared with specimens of *A. hololepidotus* from Madagascar (type-locality), or with specimens of *A. japonicus* from Japan (type-locality). It therefore became necessary to designate neotypes for *A. hololepidotus* and *A. japonicus* (to promote taxonomic stability), and to compare specimens of the two South African species with specimens of all closely related *Argyrosomus* species. Although Trewavas

(1977) revised the sciaenid fishes of the Indo-West Pacific regions, she was unable to obtain specimens of *A. hololepidotus* and *A. japonicus* from their type-localities (Madagascar and Japan respectively), and as a result her description of *A. hololepidotus* was unwittingly based on specimens of *A. japonicus* from South Africa and Australia.

The second chapter of this thesis consists of a taxonomic comparison of the two South African species with *Argyrosomus* specimens from southern Africa, Madagascar, the Mediterranean Sea, the eastern Atlantic Ocean, Japan and Australia. It is shown that the "*A. hololepidotus*" of recent authors is a complex of four species, and that the true *A. hololepidotus* is endemic to Madagascar. The two South African species were identified as *A. japonicus* and *A. inodorus* sp. nov., and the Australian "*A. hololepidotus*" was found also to be *A. japonicus*. Off South Africa, *A. japonicus* was most abundant between Cape Agulhas and northern KwaZulu/Natal, and *A. inodorus* was most abundant between Cape Point and the Kei River. The life-histories of *A. japonicus* and *A. inodorus* were studied throughout these respective ranges. Age and growth studies are presented in chapters three and five. Information on the life-histories of *A. japonicus* and *A. inodorus* is presented in chapters four and six respectively, including spawning seasonality, size at maturity, juvenile and adult distribution, and migration.

Information relevant to stock separation is presented in both the age and growth and the life-history papers of each species. A stock may ideally be defined as "an intraspecific group of randomly mating individuals with temporal or spatial integrity" (Ihssen et al. 1981), and ideally each stock should have its own genetic identity (Campana & Casselman 1993). However, management units of fish differentiated on the basis of phenotypic characters are generally accepted as stocks (particulary if exploitation in one area has negligible effects on other such units), even though the degree to which the conditions of random mating and temporal and spatial genetic integrity are satisfied, is usually unknown (Ihssen et al. 1981, Saila & Martin 1987, Campana & Casselman 1993, Edmonds et al 1995). Spangler et al. (1981) concluded that "it is not necessary to agree on a single definition of a 'stock' to communicate the implications of the concept for fisheries management".

In the final chapter, the life-histories of *A. japonicus* and *A. inodorus* are summarized, compared with other sciaenids and then discussed in terms of the management of these two important species.

CHAPTER 2

A CONTRIBUTION TO THE TAXONOMY OF THE MARINE FISH GENUS *ARGYROSOMUS* (PERCIFORMES: SCIAENIDAE), WITH DESCRIPTIONS OF TWO NEW SPECIES FROM SOUTHERN AFRICA

ABSTRACT

Griffiths, Marc H. and Phillip C. Heemstra. 1995. A contribution to the taxonomy of the marine fish genus *Argyrosomus* (Perciformes: Sciaenidae), with descriptions of two new species from southern Africa. *Ichthyological Bulletin of the J.L.B. Smith Institute of Ichthyology*, No. 65, 40 pages.

Study of the biology, anatomy and taxonomy of the sciaenid fishes of the genus *Argyrosomus* from South Africa and Namibia revealed that three species were confused under the name "*Argyrosomus hololepidotus* (Lacepède, 1801)". Comparison of morphometric and meristic data, otoliths, swim-bladders, drumming muscles, and other morphological features, of specimens from southern Africa, Madagascar, the Mediterranean Sea, the eastern Atlantic Ocean, Japan and Australia, established that the "*A. hololepidotus*" of recent authors is a complex of four species: *A. japonicus* (Temminck & Schlegel, 1843), which occurs off southern Africa, Japan and Australia; *A. inodorus* sp. nov., which is known from Namibia to the Kei River (32°40'S) on the east coast of South Africa; *A. coronus* sp. nov., which is known from central and northern Namibia and Angola, and *A. hololepidotus*, which appears to be endemic to Madagascar. These four species are compared with *A. regius* (Asso, 1801) of the Mediterranean and eastern Atlantic, *A. thorpei* Smith, 1977 from South Africa, Mozambique and the west coast of Madagascar, and *A. beccus* Sasaki, 1994 known only from Durban harbour. To promote stability in the nomenclature and to resolve the confusion in the taxonomy of *Argyrosomus* species, neotypes are selected for *A. hololepidotus* and *A. japonicus*. The biology, distributions and fisheries of six species are reviewed. Distribution patterns for the southern African species and a key to the seven species known from Africa and Madagascar (*A. regius, A. japonicus, A. inodorus, A. coronus, A. thorpei, A. beccus*, and *A. hololepidotus*) are provided. The composition and distinction of the genus *Argyrosomus* are briefly discussed.

A CONTRIBUTION TO THE TAXONOMY OF THE MARINE FISH GENUS *ARGYROSOMUS* (PERCIFORMES: SCIAENIDAE), WITH DESCRIPTIONS OF TWO NEW SPECIES FROM SOUTHERN AFRICA.

by

Marc H. Griffiths[1] and Phillip C. Heemstra[2]

INTRODUCTION

Sciaenid fishes of the genus *Argyrosomus* occur in the eastern Atlantic and Indo-West Pacific regions, and are important food species wherever they are found. Close similarity in the external appearance of these species has resulted in a difficult and sometimes confused taxonomy. Correct identification of *Argyrosomus* species is essential from a management perspective, as different species often exhibit different life history traits, and therefore require separate conservation strategies.

Since 1977 two species of *Argyrosomus*, "*A. hololepidotus*" and *A. thorpei*, were recognised as important recreational and commercial fishes off South Africa. In 1990, a project initiated by the first author (MHG) to study the biology of "*Argyrosomus hololepidotus*", revealed that two species were confused under this name. In order to establish their identity, these two species were compared with other species of *Argyrosomus*. The results are presented in this paper, together with descriptions of *A. hololepidotus*, *A. regius*, *A. japonicus* and *A. thorpei*. Neotypes are designated for *A. hololepidotus* and *A. japonicus*. Two new species, *A. inodorus* and *A. coronus* are also described from southern Africa, bringing the total number of *Argyrosomus* species to ten.

Taxonomic differences between *A. inodorus* and *A. japonicus* were studied in detail, as both species are important in recreational and commercial fisheries in South Africa. The habitats and distributions of the Southern African *Argyrosomus* species are discussed, and the biology and fisheries of the six African species are reviewed.

MATERIALS AND METHODS

The specimens examined are listed after each description. Institutional abbreviations follow Leviton et al. (1985). Sex is indicated by the letters M (male) and F (female); juveniles, too small to be sexed, are indicated by "J". In cases where additional fresh specimens were examined but not preserved, the total sample number (n) includes these fresh specimens. Except as indicated below, measurements and counts used in this study were based on the methods of Hubbs and Lagler (1964). Counts of gill-rakers and swim-bladder appendages exclude rudiments (structures wider than long). Swim-bladder appendages were counted on the left side of the swim-bladder. Orientation of swim-bladder appendages may vary depending on the amount of fat in which they are embedded. Our descriptions of appendage orientation for the species treated here are based (when possible) on specimens with little or no fat.

Vertebral counts were made on skeletons (see below) or on radiographs. Caudal vertebrae were taken as those with fused transverse processes or distinct haemal spines. Body depth was measured between the origins of the first dorsal and the pelvic fins. Caudal peduncle length was measured obliquely from the end of the second dorsal fin base to the lateral line at the base of the caudal fin. Pre-pelvic length was taken from the tip of the lower jaw to the origin of the pelvic fin. The least fleshy interorbital width was measured. As specimen treatment causing shrinkage of the eye (e.g. storage in alcohol or freezing), generally also caused shrinkage in this measurement, data for fresh specimens is provided in the key where relevant. Pectoral fin length was measured from the origin of the most dorsal ray to the tip of the longest ray. Anal and pelvic fin lengths were taken from the fin origin to the distal tip of the fin. The first lower-limb gill-raker (next to the raker at the angle), and the longest gill filament of the first gill arch were measured. The heights and lengths of scales on the body at the tip of the adpressed left pectoral fin were measured. The length of the longest urinary bladder (left or right, Fig. 1) of

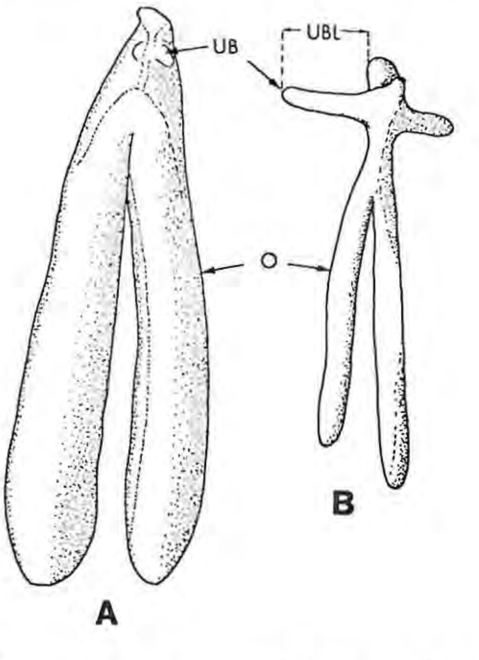

Figure 1. Ovaries (O) and urinary bladders (UB) of South African: A) *Argyrosomus inodorus*, 825 mm TL; B) *Argyrosomus japonicus*, 860 mm TL, illustrating differences in size of bladders and the bladder length measurement (UBL).

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A. japonicus and *A. inodorus* was measured to the nearest millimetre. The size of the bladder was influenced by the degree of fullness at the time of death. In order to compensate for bladder fullness, measurements were taken from fresh material after the bladders were emptied and straightened. The shape of the caudal fin varies with species, specimen size and expansion. To compensate for variable expansion, the fin was fully splayed (while still wet) on a smooth surface, and then allowed to contract to the "natural" position. Variation in caudal fin shapes and terminology are illustrated in Figure 2. Notes on life colour were taken from fresh specimens. The examination of more than five hundred live *A. inodorus* and *A. japonicus* suggest that both species darken after death.

Sonific (drumming) muscles run in a narrow longitudinal band (one on each side) along the inside of the ventrolateral wall of the posterior part of the body cavity. The muscle fibres run transversely to the long axis of the muscle and are attached to the medial surface of the peritoneum. They are not connected to the swimbladder.

Morphometric ratios are expressed as percentages of head length (HL) (measurements on head only) and standard length (SL). Unless indicated as "TL", all fish lengths are of SL. For statistical analyses, measurements were expressed as fractions of SL and then arcsine-transformed. Meristic data and morphometric ratios (except *A. hololepidotus* with n = 2 or 3) were compared using ANOVAs and Tukey studentized range tests. Morphometric ratios for *A. inodorus* and *A. japonicus* were also analyzed according to 100 mm SL size classes to compare characters that show allometric growth (e.g. eye diameter) or those which grow at different rates in the two species (e.g. pectoral fin length).

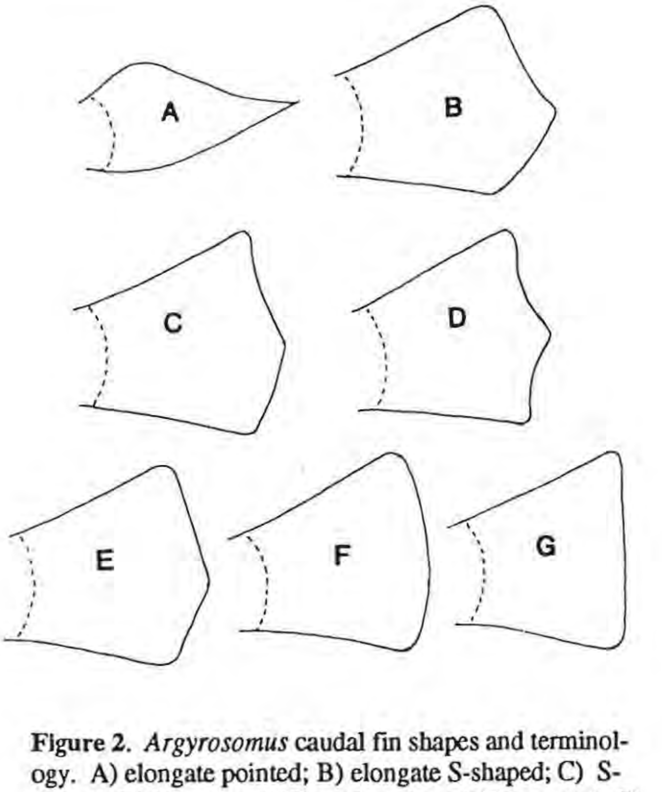


Figure 2. *Argyrosomus* caudal fin shapes and terminology. A) elongate pointed; B) elongate S-shaped; C) S-shaped; D) bi-concave; E) wedge-shaped; F) rounded; G) truncate.

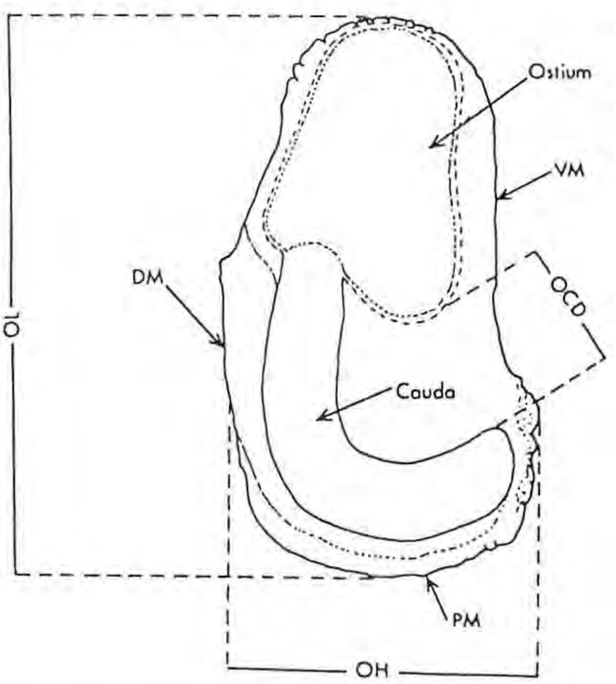


Figure 3. Otolith terminology and measurements: DM = Dorsal Margin, OL = Otolith Length, OH = Otolith Height, OCD = Ostium to Cauda Distance, PM = Posterior Margin, VM = Ventral Margin.

In addition to comparing the general morphology of the sagittae of five *Argyrosomus* species, the relationships between sagittal measurements (and weight) and TL for *A. inodorus* and *A. japonicus* were compared using regression analysis. Total length (TL) was used instead of SL, because it could be measured more rapidly when recording data from commercial catches. Otoliths were taken from all sizes (*A. inodorus*, 60 - 1378 mm TL; *A. japonicus*, 36 - 1750 mm TL) represented in the catch. Otolith weight (to the nearest milligramme) and measurements (to the nearest 0.01 mm, see Fig. 3) were taken from the left sagitta. Fish lengths and otolith measurements (including weight) were log-transformed and straight line regressions were calculated. The corresponding regression lines for *A. inodorus* and *A. japonicus* were tested for differences in slope and intercept (Myers, 1990).

Twelve skeletons of *A. inodorus*, 7 of *A. japonicus*, 2 of *A. thorpei* and 1 of *A. coronus* were compared. Measurements of cranial features (Figs 4 & 5) were taken as follows: pre-supraoccipital crest length (PSOCCRL) was measured point-to-point along the median axis from dorsoanterior tip of mesethmoid to dorsal end of frontal/supraoccipital suture; supraoccipital crest length (SOCCRL) was measured similarly to PSOCCRL from frontal/supraoccipital suture to the posterior edge of supraoccipital crest, immediately below the dorso-posterior angle; neurocranial length (NCL) was taken from the anterior tip of the vomer to the posterior tip of the basioccipital; neurocranial width (NCW) is the distance between the anterior ends of the sphenotic bones. The left dentary was measured from the anterior tip to the posterior tip of the ventral processes (Fig. 6). The length of the left premaxilla was measured as the maximum straight line distance between anterior and posterior tips.

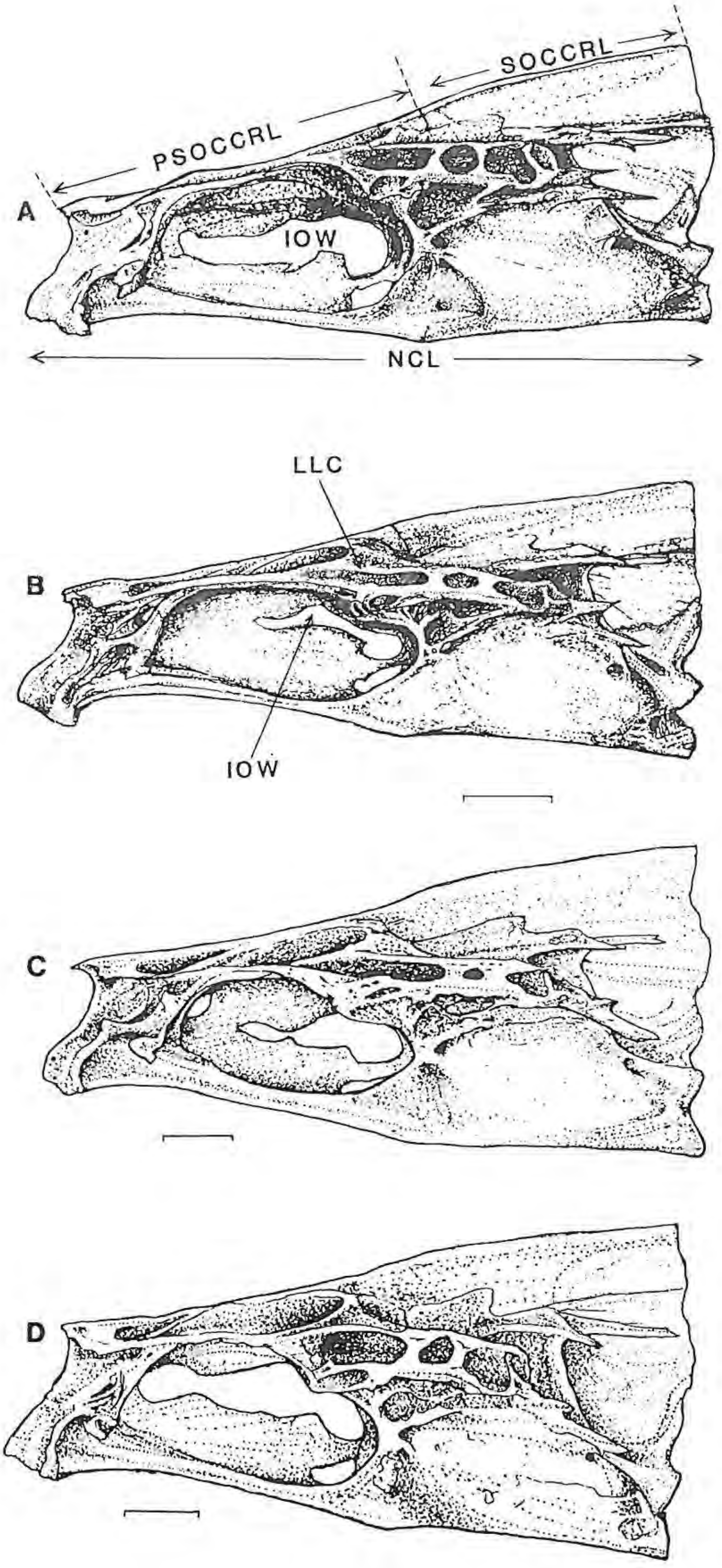


Figure 4. Neurocrania (lateral view): A) *Argyrosomus inodorus*, 365 mm SL; B) *A. japonicus*, 365 mm SL; C) *A. coronus*, 495 mm SL; D) *A. thorpei*, 452 mm SL. IOW = Interorbital Window; LLC = Lateral Line Canal; NCL = Neurocranial Length; PSOCCRL = Pre-Supraoccipital Crest Length; SOCCRL = Supraoccipital Crest Length. Scale bar = 10 mm.

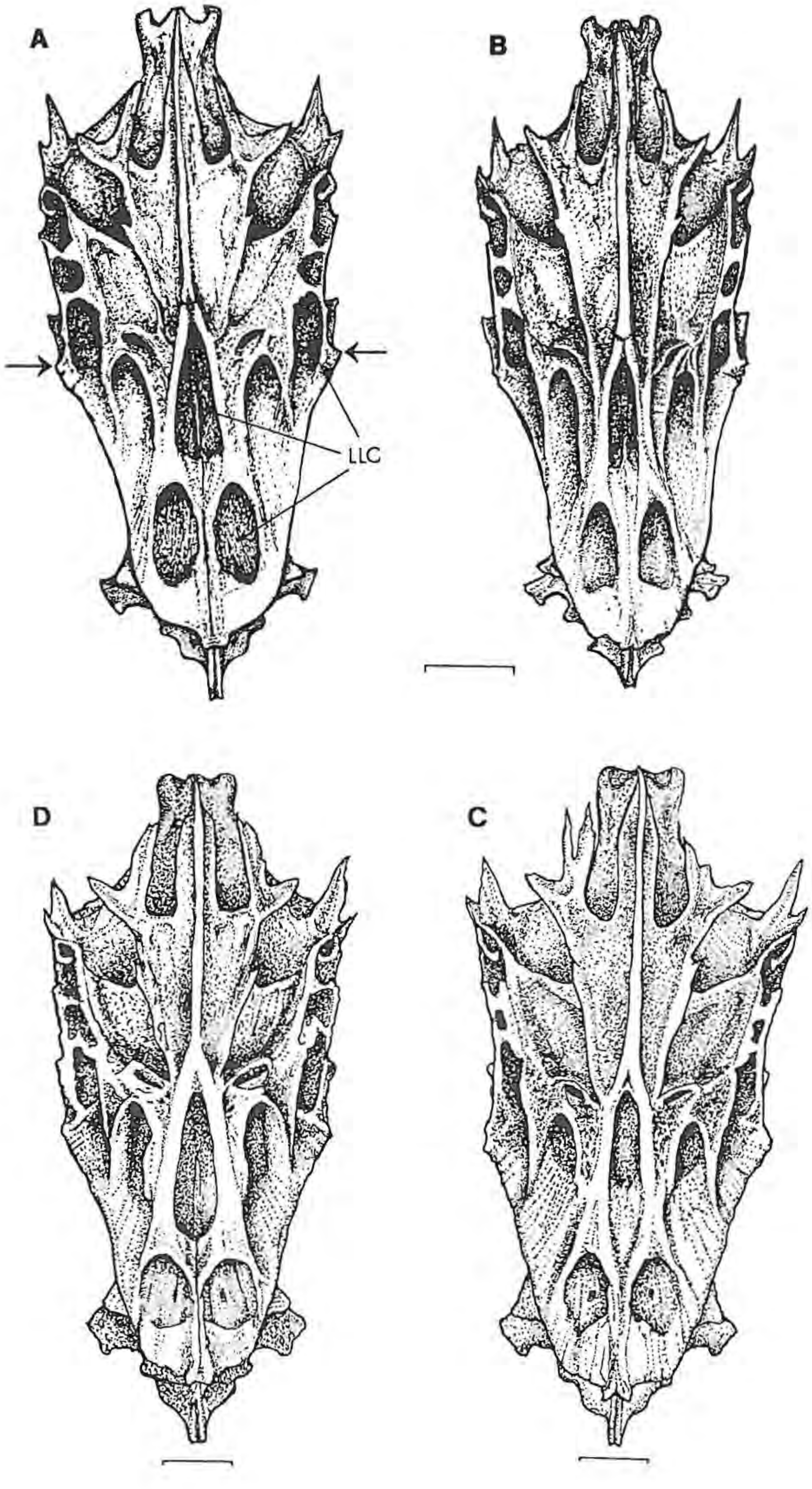


Figure 5. Dorsal view of neurocrania: A) *Argyrosomus inodorus*, 365 mm; B) *A. japonicus*, 365 mm; C) *A. coronus*, 495 mm; D) *A. thorpei*, 461 mm. Neurocranial width is the distance between the anterior ends of the sphenotic bones (arrows); LLC = Lateral Line Canal. Scale bar = 10 mm.

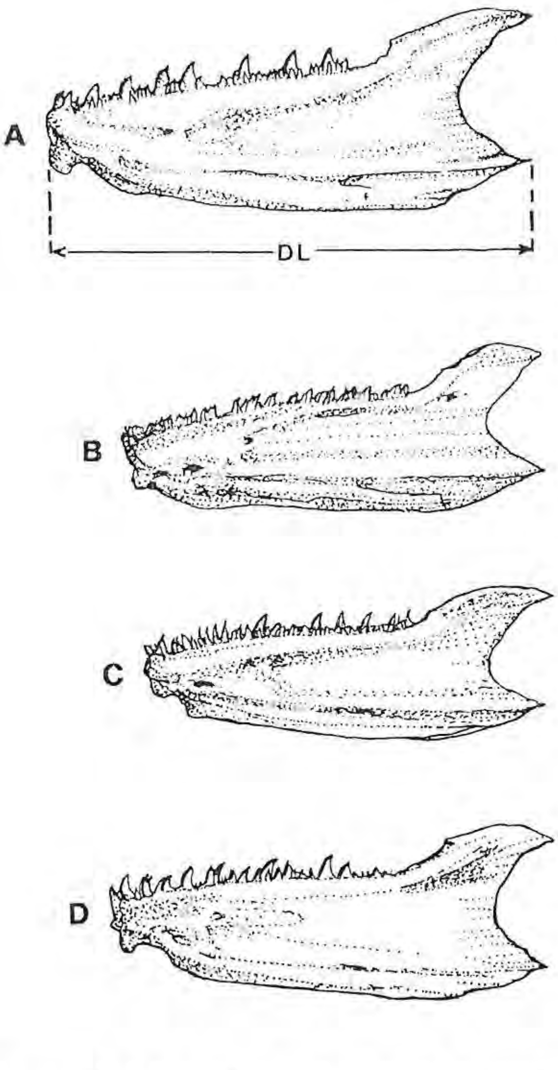


Figure 6. Left dentaries (lateral view): A) *Argyrosomus japonicus*, 525 mm; B) *A. thorpei*, 461 mm; C) *A. inodorus*, 433 mm; D) *A. coronus*, 495 mm. DL = Dentary Length

In order to establish the habitat and distribution patterns of *A. inodorus*, *A. japonicus* and *A. thorpei*, the southern African coastline was divided into ten regions (Fig. 7). Regional boundaries within each country do not necessarily coincide with political boundaries. Whole specimens (or otoliths of specimens) from four habitats (estuary, surf zone, nearshore hard bottom and nearshore soft bottom) within each region were examined. The "nearshore habitat" is defined as the marine coastal waters between depths of 10 and 100 m. *Argyrosomus* species are infrequently caught deeper than 100 m in South African waters. Catch methods included gill netting (estuaries), seine netting (estuary and surf zone), line fishing (estuary, surf zone and nearshore hard bottom) and trawling (nearshore soft bottom). The percentage contributions (by number) of each species to the total *Argyrosomus* catch in each regional habitat were calculated. For Natal nearshore hard bottom (reef) catches, numerical contributions were calculated by dividing the total catch of each relevant species (over the period 1988-1992) by the average individual weight of the respective species in the catch. This was possible as the commercial fishermen who provided the catch data differentiate between *A. thorpei* and *A. japonicus*, and examination of 3852 specimens of *Argyrosomus* from Natal revealed that *A. inodorus* does not occur there.

Biological and fishery notes are based on a three year (1990-92) sampling programme during which over 10 000 fish were examined from localities along the entire South African seaboard. Catch statistics (where not referenced) are from the databases of the Sea Fisheries Research Institute in Cape Town.

Argyrosomus Pylaie, 1835

Argyrosomus Pylaie, 1835: 532. Type species *Argyrosomus procerus* Pylaie, 1835 (substitute name for "*Sciaena aquila* Cuvier" = *Cheilodipterus aquila* Lacepède, 1803, = *Perca regia* Asso, 1801 = *Argyrosomus regius*) by monotypy. See Trewavas (1977) for details of synonymy.

DESCRIPTION: Body fairly elongate and moderately compressed; dorsal profile more convex than ventral profile. Mouth terminal, slightly oblique; jaws equal anteriorly, or lower jaw protrudes slightly. Chin without barbel but with three pairs of mental pores: the median pair rounded, the second oval or elongate, and third pair narrow slits, each pair progressively further apart. No large canines; teeth differentiated in size; upper jaw with outer row of enlarged teeth and narrow inner band of smaller teeth; lower jaw with single inner row of enlarged teeth and outer row of smaller teeth; smaller teeth in both jaws less visible in larger specimens. Anterior nostril round to oval, the posterior one slightly larger and oval to slit-like. Preopercle serrated; operculum ending in two weak, flattened spines (often hidden by skin).

Pectoral fins relatively short (15-23% SL), with a dark fleshy axillary fold at upper end of fin base. Caudal fin pointed (in small juveniles) to S-shaped, rhomboid, rounded or even truncate (in young and adults). Lateral-line scales 47-53 (usually 51) to base of caudal fin; lateral-line tubules arborescent; lateral-line scales extend to end of caudal fin.

Sagitta moderately elongate, with prominent postcentral umbo on outer surface; inner (medial) surface convex, with enlarged, spoon-shaped ostium and strongly curved, J-shaped cauda with bluntly rounded tip; otoliths of adults generally deepest within posterior third, close to tip of cauda. The sagitta of the type species (*A. regius*) is indistinguishable from that of *A. hololepidotus* or *A. japonicus* (Figs 11, 14 & 15). Since *A. regius* is the type-species of the genus, this general otolith morphology is referred to as the *Argyrosomus* form.

Swim-bladder typically carrot-shaped (tapering posteriorly) with 21-45 short appendages that may or may not (individual variation) be embedded in a wedge of fatty tissue; no appendages enter the head (i.e. pierce the transverse septum); most appendages arborescent, divided initially into two distinct limbs which are often orientated dorso-posteriorly and ventro-anteriorly, respectively; last 2-6 appendages reduced in size and bud-like or weakly

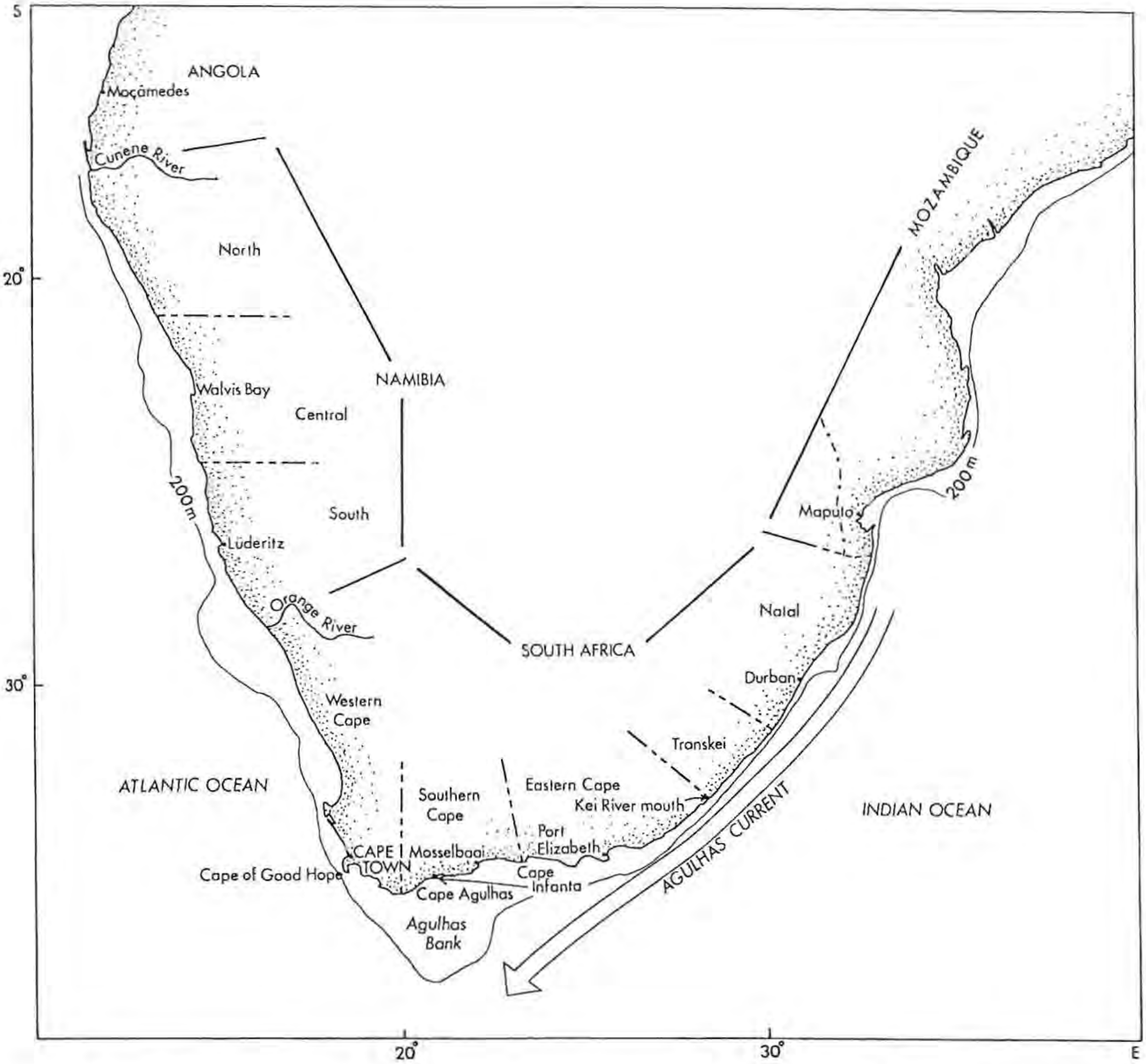


Figure 7. Map illustrating localities and the 10 southern African regions used in the distribution analysis of *Argyrosomus* species.

branched (last appendage not tubular). Drumming muscles of *Argyrosomus* species may be present in both sexes or in males only. Generally 11 abdominal and 14 caudal vertebrae.

REMARKS: In her excellent revision of the Indo-West Pacific sciaenids, Trewavas (1977) recognized five species of *Argyrosomus*: *A. regius, hololepidotus, japonicus, miiuy* and *amoyensis*. Mohan (1984) added *Sciaena heinii* Steinachner, 1902 to the genus (Trewavas [1977: 451] treated *S. heinii* as a "doubtful species", because she had not examined any specimens and was unsure of its generic assignment). Mohan's (1984) description of the swim-bladder, otolith, dentition and external morphology of this species agrees with those of *Argyrosomus* (as described above).

A comprehensive revision of the genus *Argyrosomus* was beyond the scope of our present work, but some comments (we hope constructive) on the currently accepted limits and definition of this genus are in order. Sasaki (1989) recognized the genus *Miichthys* Lin, 1983 for *Sciaena miiuy* Basilewsky, 1855 and put this species in a new monotypic tribe, Miichthyini, "distinguished by the combination of well curved sulcus tail [cauda of the sagitta], absence of enlarged swim-bladder appendages, absence of cephalic swim-bladder appendages, scaly dorsal fin.". As discussed by Sasaki (1989: 81, 90-92), the otolith and swim-bladder features that distinguish *Sciaena miiuy* from *A. japonicus* and other members of his tribe Argyrosomini are relatively primitive (plesiomorphic) character states. The presence of enlarged anterior swim-bladder appendages is a dubious synapomorphy for the tribe Argyrosomini, because it appears only in larger specimens. Enlarged appendages are known in *A. regius, A. japonicus*, and *A. inodorus*, but they were not present in 46 cm SL specimens of *A. thorpei*. They are not known for *A. hololepidotus, A. coronus* or *A. amoyensis*, but this may be because the swim-bladders of larger individuals of these three species have not been examined.

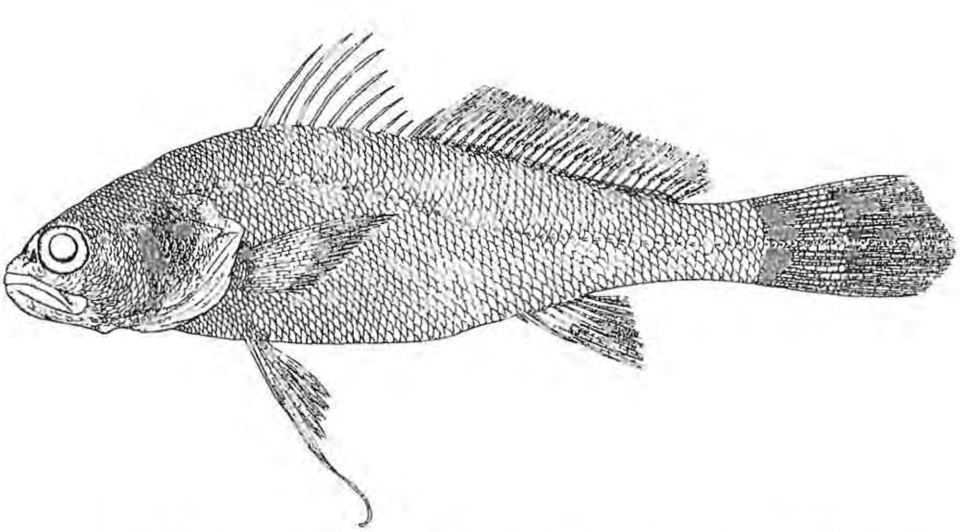


Figure 8. *Argyrosomus beccus* Sasaki, holotype, 175 mm SL, USNM 325504, Durban; after Sasaki, 1994.

The two autapomorphies: ("frontal projecting downward" and "caudal fin being truncate to lunate in adults") cited by Sasaki (1989: 118) for *A. japonicus* are also dubious as defining character states for the genus *Argyrosomus*. The "frontal projecting downward" refers to the increased ossification of the interorbital septum in *A. japonicus* (Fig. 4B), in which the frontals are fused ventrally into a median lamina that extends ventrally and fuses with similar lamina arising from the median ethmoid and parasphenoid bones. In *A. coronus* (Fig. 4C) the frontal and parasphenoid bones are also fused, but in *A. inodorus* (Fig. 4A) and *A. thorpei* (Fig. 4D), the interorbital septum is not so well ossified, and the median frontal lamina does not contact the parasphenoid bone. The state of the interorbital septum in *A. hololepidotus*, *A. amoyensis*, and the type-species (*A. regius*) are unknown. The value of this character state (increased ossification of interorbital septum) as an indication of a monophyletic genus is further diminished by its homoplastic development in more distantly related genera (e.g., *Johnius* and *Kathala*, Sasaki, 1989).

Judging from several thousand South African specimens and eight specimens from Japan (including the photograph of Masuda et al., 1988: Pl. 147, Fig. E), it is not quite accurate to describe the caudal fin of *A. japonicus* as "truncate to lunate in adults". The caudal fin of adults is most commonly S-shaped (Fig. 2C, with the rear margin of the upper half of the fin concave and the lower half convex), less frequently bi-concave (Fig. 2D) and seldom wedge shaped (Fig. 2E) or truncate (Fig. 2G). In view of the ontogenetic variation in caudal fin shape, and the fact that other (distantly related) sciaenids also have s-shaped or truncate caudal fins, the value of the caudal fin shape as a defining character state for the genus *Argyrosomus* is also questionable.

Although Sasaki's (1989) evidence for recognition of *Miichthys* and the tribes Miichthyini and Argyrosomini is not convincing, we do not have sufficient information to contest or support these taxa.

Sasaki (1994) described *Argyrosomus beccus* as a new species from South Africa based on three specimens (175, 191 & 230 mm SL) collected from Durban Harbour in 1969. No further specimens of this anomalous species have been collected in South African waters. Anatomically, it differs strikingly from other species of *Argyrosomus* in having an unusually short beak-like snout, with a slight concavity in the dorsal head profile just before the eye (Fig. 8). The snout length (6.1-6.3% SL, 20-21% HL) is shorter than the eye diameter (7.3-8.3% SL, 24-27% HL); whereas, in the six species that we measured, the snout lengths (7.4-9.6% SL, 24-31% HL) are always longer than the eye diameters (4.7-7.9% SL, 14-24% HL). The interorbital width of *A. beccus* is also much narrower (4.7% SL, 15.2-15.6% HL) than in the other five species (6.0-8.5% SL, 19-29% HL).

KEY TO SPECIES OF *ARGYROSOMUS* FROM AFRICA AND MADAGASCAR

1a. Snout length 20-21% HL, shorter than eye diameter (24-27% HL) . . . . *A. beccus*

1b. Snout 24-31% HL and longer than eye diameter (14-24% HL) 2

2a. Axillary skin fold above pectoral fin base scaly; anterior part of lateral line strongly curved; peritoneum pigmented with fine black dots; fins orange brown or dusky yellow in life; otolith (sagitta) with tip of cauda expanded and truncate . . . . *A. thorpei*
(Algoa Bay to southern Mozambique)

2b. Axillary skin fold of pectoral fin without scales; anterior part of lateral line slightly curved; peritoneum unpigmented; otolith cauda J-shaped, the tip rounded and not expanded . . . 3

3a. Caudal peduncle depth 58-74% peduncle length; ostium to cauda distance 37-63% otolith height; drumming muscles absent in females; length of body scales at tip of pectoral fin 1.8-2.5% SL; interorbital width 20-25% HL (23-26% in fresh specimens); swim-bladder appendages 31-42 . . . . *A. inodorus* sp. nov.
(Namibia to Kei River)

3b. Caudal peduncle depth 68-94% peduncle length; ostium to cauda distance 23-34% otolith height; drumming muscles present in both sexes of adults (> 27 cm SL) 4

4a. Interorbital width 24-29% HL (27-30% in fresh specimens) 5

4b. Interorbital width 20-24% HL (22-25% in fresh specimens) 6

5a. Swim-bladder appendages 36-45; caudal peduncle depth 68-82% peduncle length; length of midlateral body scales 1.8-2.3% SL, lower jaw 44-48% HL . . . *A. regius* (Mediterranean, eastern Atlantic, and Red Sea)

5b. Swim-bladder appendages 28-38; caudal peduncle depth 76-94% peduncle length; length of midlateral body scales 2.2-2.7% SL, lower jaw 46-50% HL . . . . . *A. coronus* sp. nov. (Namibia and Angola)

6a. Suborbital width 10.5-12%HL; swim-bladder appendages 34-36 . . . . *A. hololepidotus* (Madagascar)

6b. Suborbital width 8.4-10.5%HL; swim-bladder appendages 21-31 . . . . *A. japonicus* (Indo-West Pacific to False Bay, South Africa)

Argyrosomus regius (Asso, 1801)

(Fig. 9)

Sciaena umbra var. Brünnich, 1786: 99.

Perca regia Asso, 1801: 42 (coasts of Spain).

Cheilodipterus aquila Lacepède, 1803: 685, Pl. 21, Fig. 3 (French Atlantic).

Sciaena umbra (non Linnaeus): Cuvier, 1814: 13, Pl.

Sciaena aquila: Cuvier, 1816: 298; Risso, 1826: 411 (Mediterranean); Cuvier, in Cuvier & Valenciennes, 1830: 28, Pl. 139; Day, 1880-1884: 150, Pl. L (Great Britain); Smitt, 1892: 50, Fig. 13.

Pseudosciaena aquila: Bleeker, 1863: 142; Bleeker, 1876: 329.

Perca vanloo Risso, 1810: 298, Pl. 9, Fig. 30 (Western Meditteranean).

Argyrosomus procerus Pylaie, 1835: 532 (substitute name for *Sciaena aquila* Cuvier).

Johnius hololepidotus (non Lacepède): Fowler, 1936: 884 (described from Mediterranean specimens).

Argyrosomus regius: Trewavas, 1966: 4; 1973: 397; 1977: 324, Fig. 8; Seret, 1981: 266.

For additional references see Trewavas, 1973.

Neotype: MNHN 7511, La Rochelle, French Atlantic; designated by Trewavas (1966) quoting a description by P.J.P. Whitehead (MS).

DIAGNOSIS: A species of *Argyrosomus* with the following combination of characters: dorsal fin rays 26-30; gillrakers 3-5 + 8-10; swim-bladder carrot shaped, with 36-45 arborescent appendages; caudal peduncle length 11-13% SL; peduncle depth 68-82% peduncle length; interorbital width 7.3-8.5% SL (24-29% HL); suborbital width 8.4-11% HL; lower jaw length 45-48% HL; midlateral body scale length 1.8-2.3% SL; drumming muscles present in both sexes; urinary bladders large; sagitta typically *Argyrosomus* (Fig. 10), OCD 26-32% OH; pectoral fins 18-21% SL, not reaching past vertical at tip of pelvic fins; pectoral fin axillary fold scaleless; peritoneum unpigmented; anterior part of lateral line slightly curved.

DESCRIPTION: Based on 19 whole specimens (173-433 mm) plus otoliths, swim-bladders, interorbital widths, head lengths and SL of 7 others collected for us by Bernard Séret. Due to the poor condition of five specimens (MNHN 7511, MNHN 7533, MNHN 7945, MNHN 1524, and the neotype), only the interorbital width and SL measurements of these fish were included in the following description. Trewavas' (1977) data (10 specimens 135-965 mm SL) are given in parentheses.

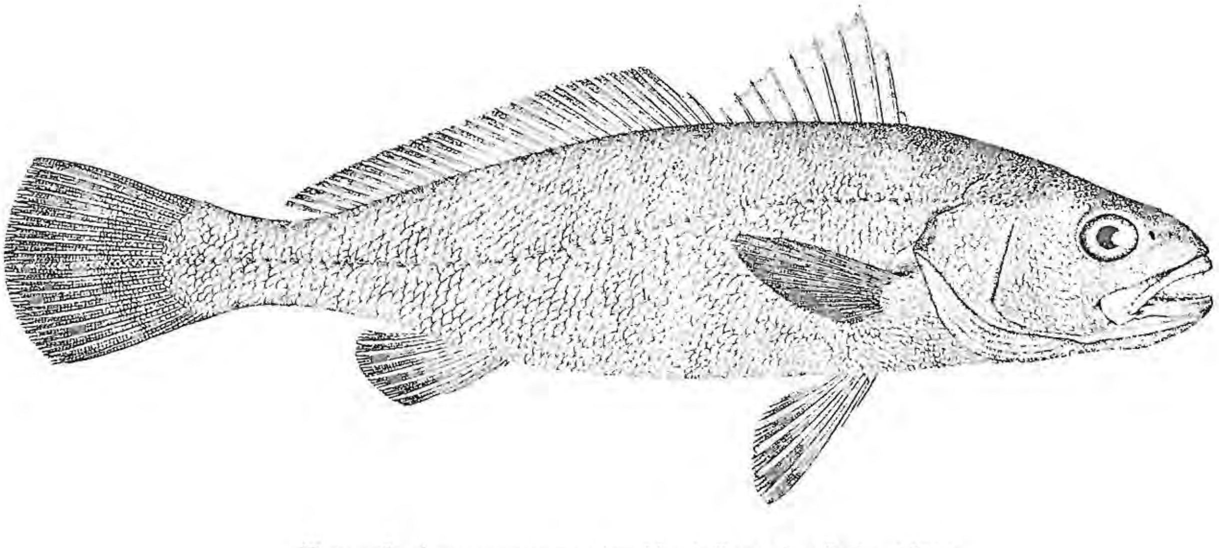


Figure 9. *Argyrosomus regius*, North Sea (after Smitt, 1892)

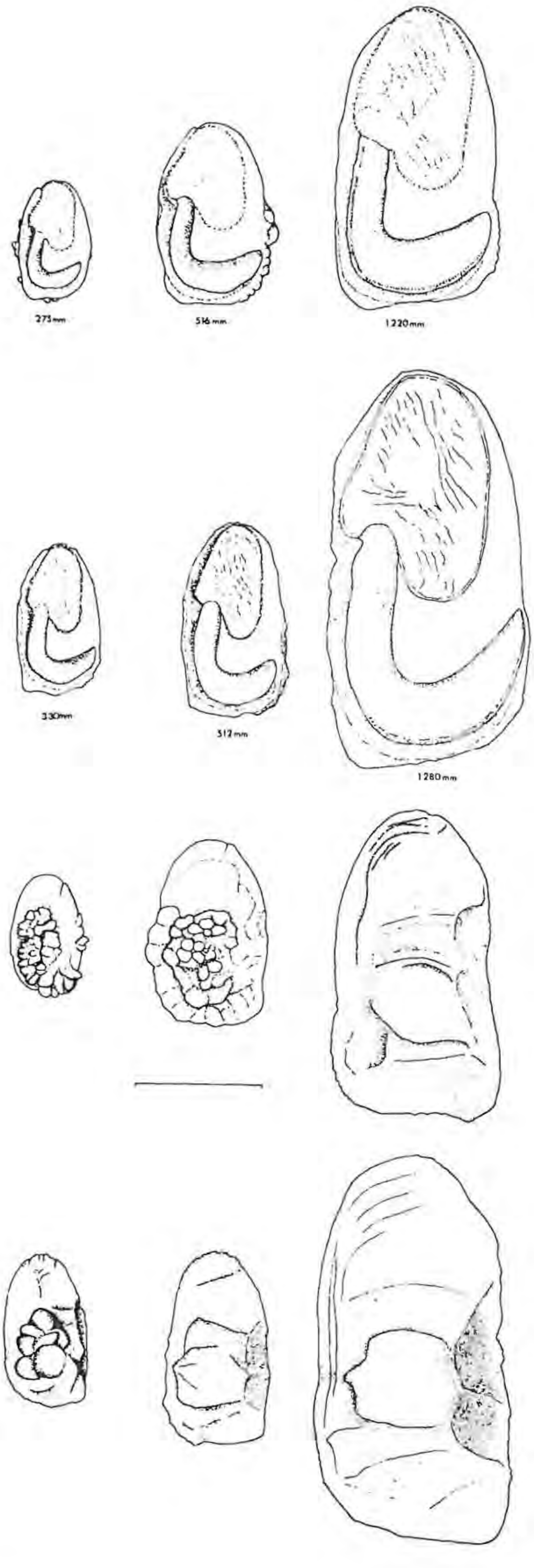


Figure 10. Medial (above) and lateral (below) views of sagittae of *Argyrosomus regius* (top and third rows) and *A. coronus* (second and bottom rows). The largest specimen for *A. regius*, was redrawn from Chaine (1938). Scale bar = 10 mm.

Dorsal fin X+I,26-30 (IX-X+I,26-29); anal fin II,7; pectoral-fin rays 16-18; lateral-line scales 49-53(47-51); gill-rakers 3-5 + 8-10 (2-5 + 9); swim-bladder appendages 36-45 (40-42); vertebrae 11 + 14.

Proportions as %SL: head length 28-34 (27-35); predorsal length 33-37; pre-pelvic length 29-39, usually 30-34; body depth 24-34 (25-36); caudal peduncle length 11-13; peduncle depth 7.9-10.8; snout 8.1-9.6; eye diameter 5.5-6.5 at 173-222 mm, 4.1-5.1 at 261-339 mm and 4.3 at 433 mm SL; interorbital width 7.3-8.5; suborbital width 2.7-3.5; upper jaw 12-14; lower jaw 14-16; pectoral fin 18-21 (18-23); pelvic fin 19-21 at 173-198 mm, 17-19 at 261-342 mm and 17 at SL 433; anal fin 14-18; third dorsal spine 11-16; second anal spine 7.0-8.9 (6-9); gill-raker 1.6-2.4; gill-filament 2.8-3.3.

Proportions as % HL: snout 26-29 (26-31); eye diameter 17-19 at 173-222 mm, 12-16 at SL 261-342 mm and 14 at 433 mm SL (15-19 at SL 193-494 mm and 10-11 at SL 950-965 mm); interorbital width 24-29 (21-26); suborbital width 8.5-11; upper jaw 38-42 (39-44); lower jaw 45-48 (42-49); gill-raker 5.0-7.2; gill-filament 9.1-11.

Proportions as % eye diameter: gill-raker 32-45; gill-filament 49-56 at 173-198 mm, 63-69 at 261-342 mm and 76 at 433 mm SL.

Scales cycloid on snout and below eye, otherwise finely ctenoid. Lateral line evenly curved. Caudal fin elongate pointed in small specimens, S-shaped in those of medium size, and according to Trewavas (1977), bi-concave ("symmetrically concave") in very large individuals. Drumming muscles well developed in both sexes. Urinary bladders large, as in *A. japonicus*.

Swim-bladder appendages proximally divided into two limbs (Fig. 11) that are orientated dorsoposteriorly and ventroanteriorly along entire length of bladder. Branches arising from both limbs project posteriorly and lie against the bladder (throughout length); but in specimens where large quantities of fat are present the branches project laterally (Fig. 11). Disproportionate appendage enlargement was not observed in any *A. regius* (173-480 mm) examined by us, but it was illustrated by Cuvier (1814).

Otoliths (Fig. 10): Description as for *A. japonicus*; OCD 24-34% OH.

COMPARISONS: Specific differences between *A. regius* and the congeners described in this paper are dealt with

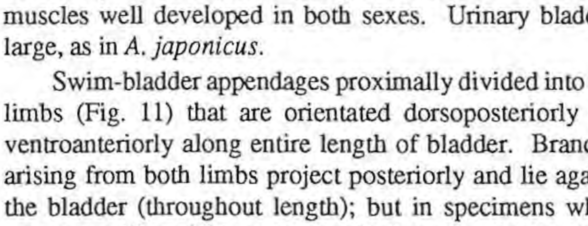


Figure 11. Swim-bladder appendages (anterior view) from mid-way along left side of swim-bladder:
A) *Argyrosomus hololepidotus*, 465 mm SL, neotype;
B) *A. regius*, 430 mm SL; C) *A. coronus*, 471 mm SL.
Scale bar = 10 mm.

under the "comparisons" sections of the respective species (below) and in Tables 2-6.

DISTRIBUTION: *A. regius* occurs throughout the Mediterranean and Black Sea, northwards along the Atlantic coasts of Europe to the British Isles, southern Norway and Sweden; it has been recorded along the west coast of Africa to the Gulf of Guinea (Trewavas, 1977; Chao & Trewavas, 1981; Séret, 1981; Chao, 1986). *A. regius* has entered the Red Sea through the Suez canal (Steinitz, 1967; Mohan, 1984). The species occurs in inshore and shelf waters, close to the bottom or near the surface (depth range 15-200 m); it also enters estuaries and coastal lagoons (Chao, 1986).

FISHERIES: *A. regius* is an important food fish in the Bay of Biscay (French Atlantic) and along the coasts of Senegal and Mauritania (Moal, 1957; Balguerias, 1985; Quéro & Vayne, 1987). It is caught with hook and line, trawl nets, gillnets, circular nets and seines. The flesh is sold fresh, salted or dried.

BIOLOGY: Although sexual maturity is attained by some individuals at 80 cm TL, most adults off the west coast of Africa are larger than 110 cm TL (Moal, 1957). Spawning occurs during May to July in the Bay of Biscay, from April to July in the southern Mediterranean (Chao, 1986) and from January to May off west Africa (Mauritania, Moal, 1957; Tixerant, 1974 in Champagnat & Domain, 1978). Both adults and juveniles are migratory, moving longshore or offshore/onshore in response to change in water temperature (Moal 1957; Champagnat & Domain, 1978; Oliver & Lafon, 1981; Quéro & Vayne, 1987; Quéro, 1989). The largest size recorded is 182 cm TL and 103 kg (Quéro & Vayne, 1987).

MATERIAL EXAMINED:

MEDITERRANEAN SEA: Israel: HUJ 6906 (F 325 mm); HUJ 14451 (J 173 mm); HUJ 16342 (F 198 mm); RUSI 30254 (M 261 mm); RUSI 30255 (M 269 mm); RUSI 30256 (F 227 mm). Egypt: HUJ 5182 (M 255mm & 300 mm); MNHN 4978 (F 222 mm); MNHN 7495 (J 189 mm); MNHN 7533 (M 264mm, 286 mm [gonads missing]); MNHN 1524 (286 mm [gonads missing]). ATLANTIC OCEAN: France: MNHN 7511 (Neotype, no gonads, 425 mm, La Rochelle); RUSI 40772 (M 433 mm); RUSI 40776 (M 430 mm); RUSI 40777 (F 325 mm including otoliths); RUSI 40972 (355 mm, otoliths & swim-bladder only); RUSI 40973 (455 mm, otoliths & swim-bladder only); RUSI 40974 (430 mm, otoliths & swim-bladder only); RUSI 40975 (465 mm, otoliths & swim-bladder only); RUSI 40976 (460 mm, otoliths & swim-bladder only); RUSI 40977 (480 mm, otoliths & swim-bladder only); RUSI 40978 (430 mm, otoliths & swim-bladder only). Mauritania: MNHN 1987-1617 (M 322 mm); RUSI 40971 (M 342 mm, F 319 mm, including otoliths).

Argyrosomus japonicus (Temminck & Schlegel, 1843)

(Fig. 12)

Sciaena japonica Temminck & Schlegel, 1843: 58, Pl. 24, Fig. 1 (vicinity of Nagasaki, Japan; based on description and plate in unpublished manuscript of D.W. Burger; specimen not preserved).

Sciaena antarctica Castelnau, 1872: 100, Pl. 1 (Melbourne market); Macleay, 1881: 520; Tenison-Woods, 1883: 53, Pl. 16; Stead, 1906: 113, Fig. 42; Ogilby, 1908: 66, Pl. 37; Roughley, 1916: 112, Pl. 35, 1951: 70, Pl. 28; McCullock, 1922: 58, Pl. 58; Waite, 1923: 129. (Australia).

Sciaena margaritifera Haly, 1875: 269 (off Natal, South Africa).

Sciaena aquila (non Lacepède): Castelnau, 1878: 381.

Corvina axillaris (non Cuvier): De Vis, 1884: 538 (Brisbane River; so synonymized by Ogilby, 1918).

Sciaena neglecta Ramsey & Ogilby, 1886: 941 (coast of New South Wales; so synonymized by Ogilby, 1918).

Sciaena hololepidota antarctica: (*non* Lacepède); Ogilby, 1918: 70, Pl. 21 (Queensland).

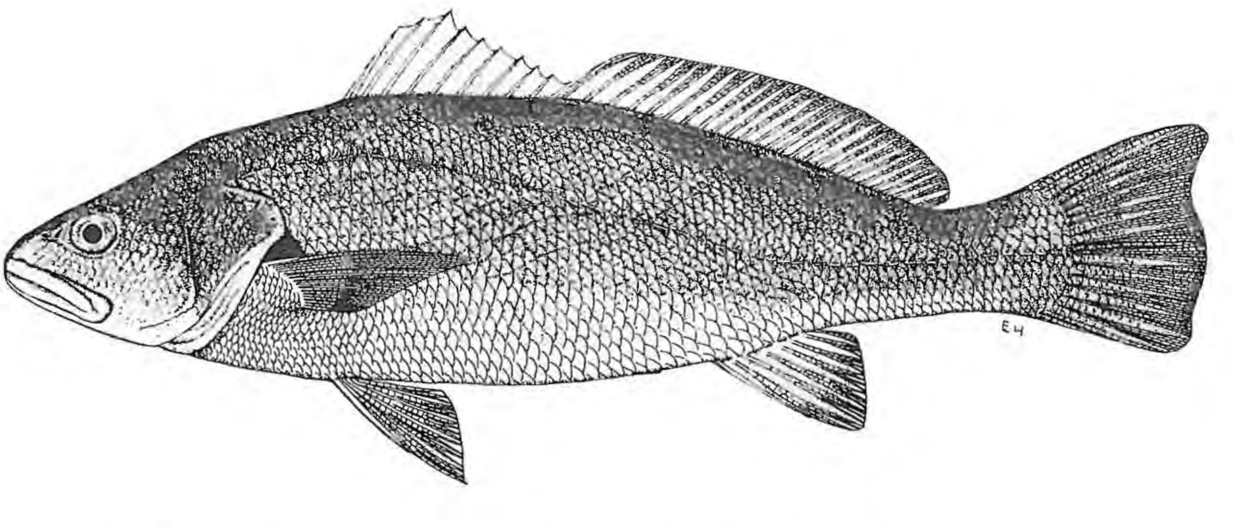


Figure 12. *Argyrosomus japonicus*, 454 mm SL, RUSI 38457; Eastern Cape Province.

Nibea japonica: Matsubara, 1937: 41, Figs 9 & 10 (near Tokyo); Chu, Lo & Wu, 1963: 55, Figs 31, 57, 83; Taniguchi, 1969: Figs 4 A & B; Masuda et al. 1988: Pl. 147 E.

Argyrosomus japonicus: Lin, 1938: 170; Lin, 1940: 244, Fig. 1 (Hong Kong); Matsubara, 1955: 645, Pl. 67, Fig. 229 (Japan); Chu, 1956: 25, Pl. 2, Fig. 3 (Taiwan); Kamohara, 1964: 50 (Japan); Fischer & Whitehead, 1974: SCIAEN Argyr 4; Sasaki, 1994.

Johnius hololepidotus (non Lacepède): Smith, 1949: 226, Fig. 552; Smith & Smith, 1966: 43.

Pseudosciaena antarctica: Ogilby & Marshall, 1954: 70, Fig. 85 (Queensland).

Argyrosomus hololepidotus (*non* Lacepède): Smith & Smith, 1966: 43; Fischer & Whitehead, 1974: SCIAEN Argyr 3; Trewavas, 1977: 326, Figs. 9, 12, 47 & 54 (Australia & South Africa); van der Elst, 1981: 261; Mohan, 1984: SCIAEN Argyr 3; Heemstra, 1986: 616, Pl. 71; Grant, 1987: 221, Fig. 493; Kailola et al. 1993: 318; Kuiter 1993: 199; Gomon, 1994; Branch et al. 1994: 250.

Johnius antarctica: Grant, 1978: 474, Pl. 201 (Australia).

Argyrosomus sp.: Sainsbury et al., 1984: 230, fig.

Neotype: RUSI 44704, 499 mm SL, Meitsu, Nango-Cho, Miyazaki Prefecture, southeast coast of Kyushu, Japan, depth 50 m; 21st October 1993. Collected by Yukio Iwatsuki.

DIAGNOSIS: A species of *Argyrosomus* with the following combination of characters: dorsal fin rays 25-30; gill-rakers 4-5 + 10-12; swim-bladder carrot shaped, with 21-31 arborescent appendages; caudal peduncle length 11-13% SL; peduncle depth 70-92% peduncle length; interorbital width 6.4-7.4% SL (21-24% HL); suborbital width 8.4-10.5% HL; lower jaw length 48-52% HL; midlateral body scale length 2.4-3.1% SL; drumming muscles present in both sexes; urinary bladder length 2.0-9.6% SL; otolith shape like *A. regius* (Figs 13-15; see description below), OCD 23-41% OH; pectoral fins 17-21% SL, usually not reaching vertical at tips of pelvic fins; pectoral axillary fold scaleless; peritoneum unpigmented; anterior part of lateral line slightly curved.

DESCRIPTION: Based on 66 preserved specimens (119-638 mm), seven skeletons (318-590 mm) and the otoliths of 543 fish that were not preserved. Data from the neotype are in parenthesis. Dorsal fin X+I,25-30 (X,29); anal fin II,7; pectoral-fin rays 15-17 (17); lateral-line scales 50-53 (51); gill-rakers 4-5 + 9-12 (4 + 9); swim-bladder appendages 21-31 (30); vertebrae 11 + 14.

Proportions as % SL: head length 28-33 (28.5); pre-dorsal length 32-36 (33); pre-pelvic length 31-36 (31); body depth 25-30 (25); caudal peduncle length 11-13 (13); peduncle depth 8.8-10.6 (9.0); snout length 7.7-9.0 (8.3); eye diameter 5.2-7.0 at 119-298 mm, 4.4-5.2 at 301-387 mm and 3.9-5.0 (3.9) at 403-638 mm SL; interorbital width 6.4-7.4 (6.8); suborbital width 2.6-3.2 (2.6); upper jaw 12-13.5 (12); lower jaw 13.5-16 (14.0); pectoral fin 17-21 (17); pelvic fin 17-22 at 119-298 mm, 17-20 at 301-387 mm and 15-18 (16) at 403-634 mm SL; anal fin 15-19 at 119-298 mm, 15-17 at 301-387 mm and 12-15 (14) at 403-638 mm SL; third dorsal spine 11-15 (12); second anal spine 7.5-12 at 119-298 mm and 5.7-7.9 at 301-638 mm SL; gill-raker 1.8-2.8 at 119-298 mm, 1.8-2.2 at 301-387 mm and 1.6-2.1 (2.0) at 403-638 mm SL; gill-filament 2.6-3.4 (2.9).

Proportions as % HL: snout 26-30 (29); eye diameter 16-23 at 119-298 mm, 15-18 at 301-387 mm and 13-16 (13.6) at 403-638 mm SL; interorbital width 21-24 (24); suborbital width 8.5-10.4 (9.2); upper jaw 40-45 (42.5); lower jaw length 48-52 (49); gill-raker 6.2-8.9 at 119-298 mm, 6.3-7.1 at 301-387 mm and 5.3-9.0 (6.9) at 407-664 mm SL; gill-filament 8.5-11.4 (10.1).

Proportions as % eye diameter: gill-raker 32-57 (51); gill-filament 45-63 at 130-298 mm, 55-68 at 301-387 mm and 57-80 (74) at 407-664 mm SL.

Dorsal profile generally has a hump or "shoulder" behind the head. Axillary fold at base of pectoral fin scaleless. Scales weakly ctenoid on body (including belly and chest), nape, interorbital region, preoperculum and below eye; those on body not easily lost; length of midlateral body scales 2.4-3.1% SL. Lateral line evenly curved. Pectoral fin of most fish less than 100 cm not reaching vertical at tip of pelvic fins, but on some fish the pectoral and pelvic tips are equal. Caudal fin typically pointed (Fig. 2A) in fish less than 10 cm, becoming elongate S-shaped (Fig. 2B) in fish 15-35 cm SL and S-shaped (Fig. 2C) in fish larger than 40 cm SL; the caudal fin of large adults is occasionally bi-concave, wedge shaped or slightly rounded (Fig. 2F). Drumming muscles well developed in males and females but thicker in mature males than in mature females; although poorly developed in small individuals, drumming muscles were observed in all specimens greater than 27 cm. Peritoneum not pigmented. Urinary bladders large (Fig. 1). Pyloric caeca 7-10 (n = 64).

Swim-bladder (Figs 13B, D & 14B) appendages 21-31, those along anterior half of bladder divided basally into dorsoposterior and lateroanterior limbs, but along posterior half of bladder, the lateroanterior limbs become ventroanteriorly orientated, and the branches arising from them are orientated posteriorly, lying against the bladder (Fig. 14B). As a result, the arborescent appendages of the posterior half of the swim-bladder are not clearly visible in ventral view (Figs 13B & D). Disproportionate enlargement of 1-6 appendages (Figs 13D & 14B) occurs with increased size (16 of 61 specimens); the smallest specimen with enlarged appendages was 360 mm SL. The enlargement begins as a swelling at the base of the appendage, proceeding through the branches to the distal ends. Ventral surface of swim-bladder covered with small black/grey dots (more obvious in smaller individuals) which apparently disperse, becoming less concentrated with growth.

Otoliths: Sagitta (Figs 15-17) typically *Argyrosomus* (like that of *A. regius*): moderately elongate and roughly triangular; ventral margin evenly rounded in smaller otoliths, becoming straighter with growth, with a bulge in the posterior third; margin of ventral bulge often denticulate; dorsal margin slightly convex and, in specimens 15 - 33 cm TL, commonly with a mediodorsal denticle (Fig. 17, first row); posterior margin generally straight and posterodorsal angle 90° or less; posteroventral angle becomes more acute with size; ostium to cauda distance (OCD) 23-41% OH. The

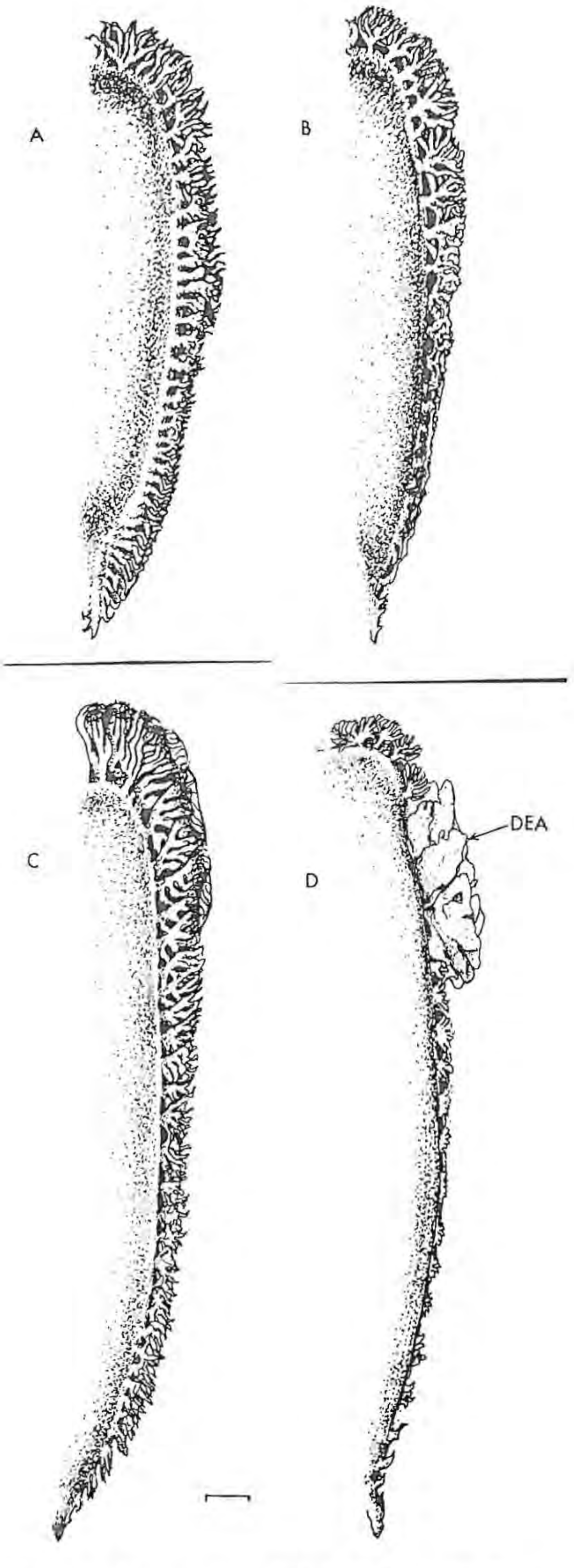


Figure 13. Ventral view of left half of swim-bladders: *Argyrosomus inodorus:* A) 355 mm, RUSI 38480; C) 640 mm, RUSI 42240. *A. japonicus*: B) 325 mm, RUSI 38450; D) 638 mm, RUSI 38452. DEA = Disproportionately Enlarged Appendage. Scale bar = 10 mm.

otolith dimension/fish length relationships are given in Table 1; statistically there is no difference between the sexes. Intraspecific variation in otolith morphology is illustrated in Fig. 17.

Neurocranium (Figs 4 & 5): Length of neurocranium (NCL) 20-22% SL. Pre-supraoccipital length 10-11% SL and 49-53% NCL. Supraoccipital crest length 9.2-10.2% SL and 43-49% NCL (318-560 mm). Neurocranial width 7.3-8.4% SL and 34-39% NCL. Premaxilla 8.1-8.9% SL and 39-42% NCL. Dentary 9.5-10.1% SL and 44-48% NCL. Third and fourth neural spines 7.5-8.3 and 8.9-9.9% SL respectively.

Colour: In life, silvery grey becoming darker above and lighter below; dorsal surface with a bluish bronze sheen that may become coppery on head. Larger fish (>80 cm) are golden brown; dorsal and caudal fins grey/brown, becoming darker with age, often with a reddish hue - due to vascular distension or haemorrhaging (possibly during capture). Pectoral and anal fins white in fish less than 10 cm, changing to yellow and finally to grey or grey/brown in fish greater than 35 cm, also becoming darker with size. Mouth lining of juveniles white, becoming yellow and finally yellowish grey in large adults. Axillary fold of pectoral fin grey to black, generally with an irregular coppery-bronze patch.

Preserved specimens vary in colour according to treatment; usually grey but sometimes brown; darker above and lighter below. Dark patches on scales may give appearance of oblique stripes. Fins grey, sometimes with one or two longitudinal stripes on dorsal fin; the pelvic and pectoral fins usually pale.

COMPARISONS (see Tables 2-6): *A. japonicus* differs from *A. regius* in having a lower modal number of pectoral-fin rays; longer midlateral scales; longer lower jaw; narrower interorbital width (Fig. 18); fewer and smaller arborescent swim-bladder appendages that, on the anterior half have ventral limbs that are orientated anterolaterally (vs anteroventrally), and branches arising from these project laterally (vs posteriorly and against the bladder); and a higher modal number of gill-rakers. Our comparison of otoliths from *A. regius* (Fig. 10) and *A. japonicus* (Figs 15-17) using our material and the illustrations of Chaine (1938) and Schwarzhans (1993) for both smaller and larger *A. regius* specimens, revealed no differences in the sagittae of these two species.

REMARKS: The original description of Temminck and Schlegel (1843: 58, Pl. 24, Fig. 1) was based on the description and plate in Burger's unpublished manuscript. According to Boeseman (1947: 62) "there never was a specimen in Burger's or Von Siebold's collection,". Boeseman (1947: 62) also pointed out "that Burger's descriptions without exception proved to be rather inexact. Temminck and Schlegel generally corrected and completed Burger's data with characters from the specimen(s) [from Burger's collection] ... Burger's plates too often show inaccuracies, but these also sometimes have been corrected by the authors [Temminck & Schlegel]...In this case, however, there was no way to verify Burger's data and plate. On account of this, it is very difficult, if not impossible, to make a final statement as to the identity and synonymy of Temminck &

Schlegel's species." In view of the uncertainty of the identity of *Sciaena japonica* from Temminck & Schlegel's original description and illustration, the absence of a type specimen, and the presently confused taxonomy of *Argyrosomus* species, we believe that designation of a neotype for *Sciaena japonica* will promote stability of nomenclature and help to resolve the taxonomic confusion associated with these species.

Trewavas (1977: 330) commented: " As Lin (1940) pointed out, the resemblence [of *A. japonicus*] to *A. hololepidotus* is striking. The apparent differences are mostly correlated with size and are due to allometry." Trewavas' concept of "*A. hololepidotus*" was based on South African and Australian specimens of *A. japonicus*, as she did not examine any specimens from Madagascar. Her account of *A. japonicus* was compiled from published descriptions of specimens from Japan and China, and she went on (1977: 331) to observe that "there is no inherent improbability in Lin's suggestion (1940) that the relationship between *A. japonicus* and *A. hololepidotus* may be that of races of one species".

Our comparison of specimens from South Africa, Japan and Australia confirms that these populations are conspecific. Previous recognition of "*A. hololepidotus*" and *A. japonicus* as separate species was due to taxonomic inertia and the fact that none of the previous authors had directly compared specimens from Japan with those from South Africa or Australia.

Although the South African, Japanese and Australian populations of *A. japonicus* seem to be well isolated geographically (see below), and the smaller size of Australian specimens (see below) implies some genetic differences between South African and Australian populations, the absence of any significant morphological (including branching patterns in the swimbladder appendages) or meristic differences in the specimens that we have examined from these populations requires that we recognize them as single species. Examination of molecular characters (proteins, DNA, etc) or some morphological features that we may have overlooked may show significant differences between these allopatric populations; but until such evidence is discovered, we accept the null hypothesis of conspecific identity of these populations by default (i.e., the burden of proof for recognition of separate species requires some tangible evidence other than apparent allopatry).

DISTRIBUTION: *A. japonicus* is found on the African southeast coast from the Cape of Good Hope to southern Mozambique; in Australia it is known along the entire southern seaboard from North West Cape (north of Shark Bay) in Western Australia to the Burnett River (north of Brisbane) in Queensland (Trewavas, 1977; Grant, 1978; Sainsbury et al., 1984; Kailola et al., 1993; Starling, 1993); in the northern Indian Ocean, it occurs off Pakistan and the northwest coast of India (Mohan, 1984) (as "*A hololepidotus*"); and in the Northern Pacific it has been reported from Hong Kong northwards along the Chinese coast to southern Korea and Japan (Trewavas, 1977).

Along the South African coast *A. japonicus* occurs abundantly from Cape Agulhas to northern Natal (Table 7). It is found in estuaries (preferring those that are turbid), in the surf zone, and in the nearshore zone to depths of about 50 metres. In the nearshore environment, the species rarely

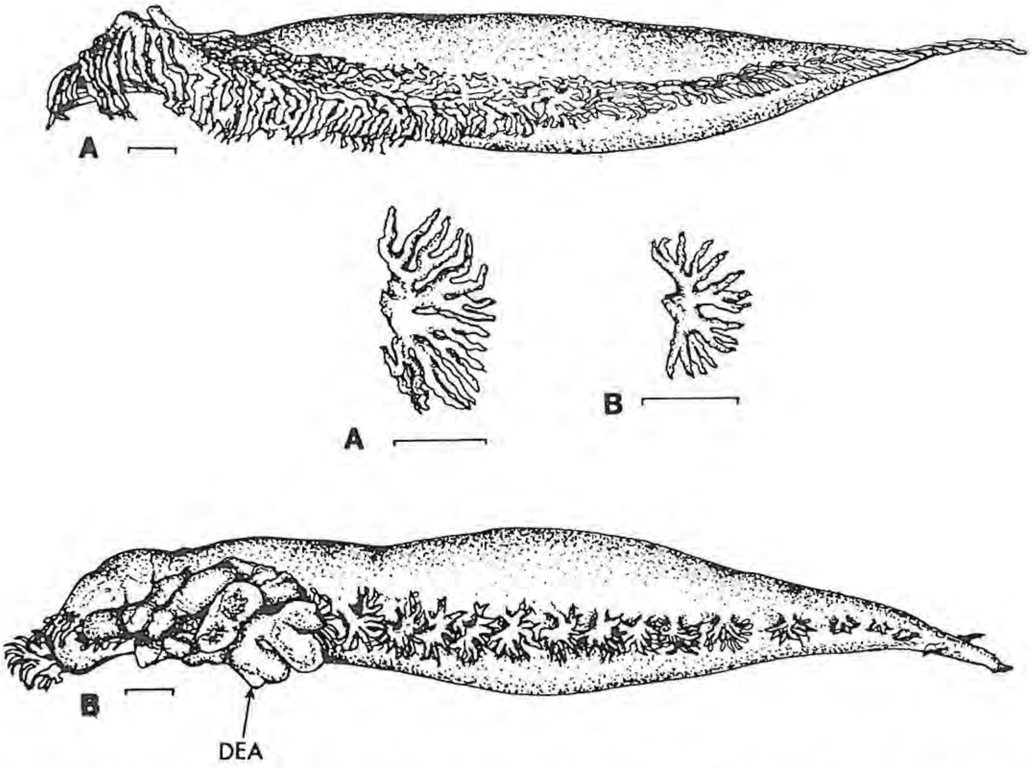


Figure 14. Lateral view of swim-bladders and anterior view of middle appendage: A) *Argyrosomus inodorus*, 640 mm, RUSI 38480; B) *A. japonicus*, 638 mm, RUSI 38452. DEA = Disproportionately Enlarged Appendage. Scale bars = 10 mm.

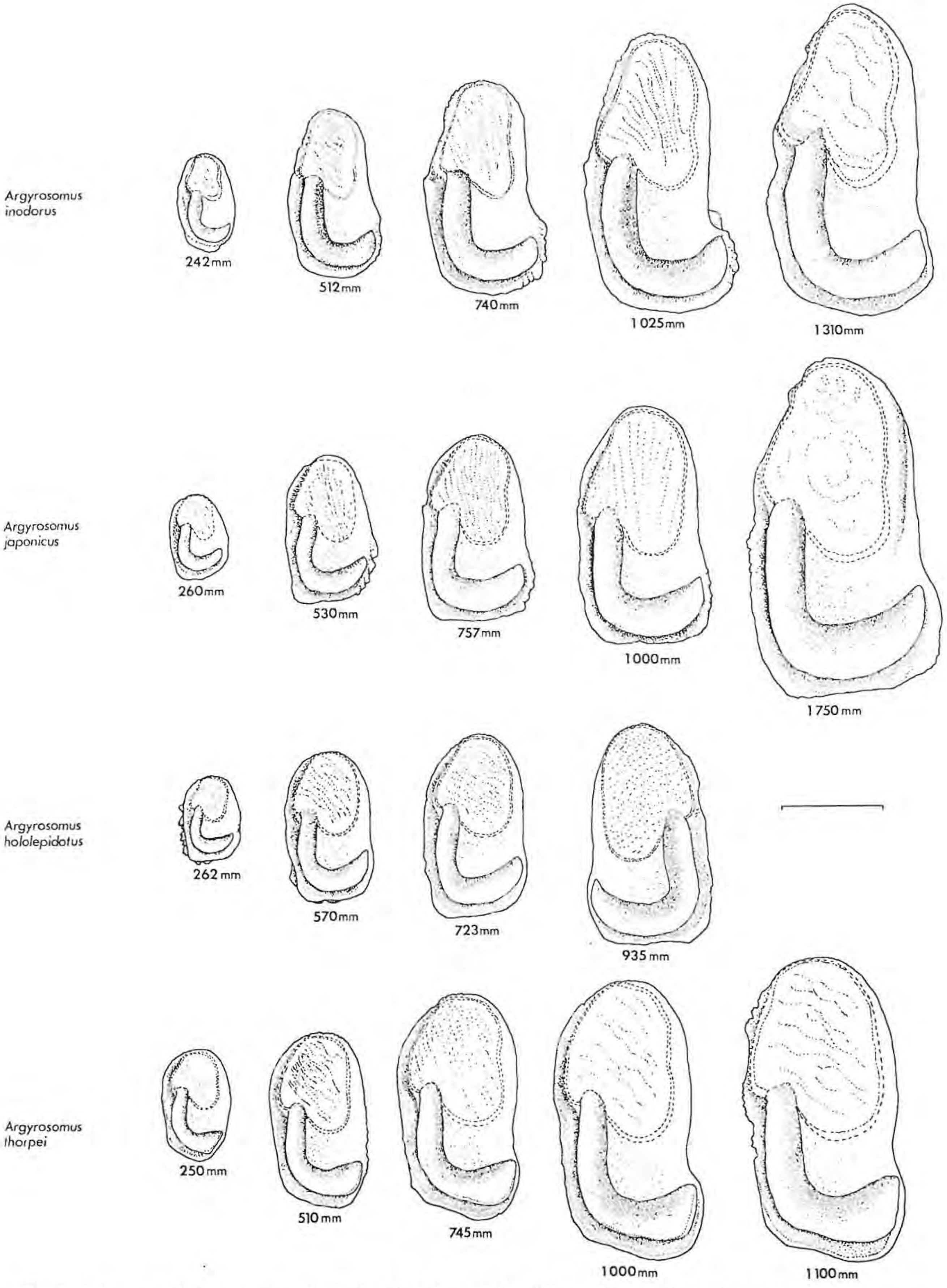


Figure 15. Medial view of *Argyrosomus* sagittae, showing inter-specific differences and morphological changes with growth. Those for *A. inodorus* and *A. japonicus* were chosen as typical of the size classes represented. Fish sizes given are of TL. Scale bar = 10 mm.

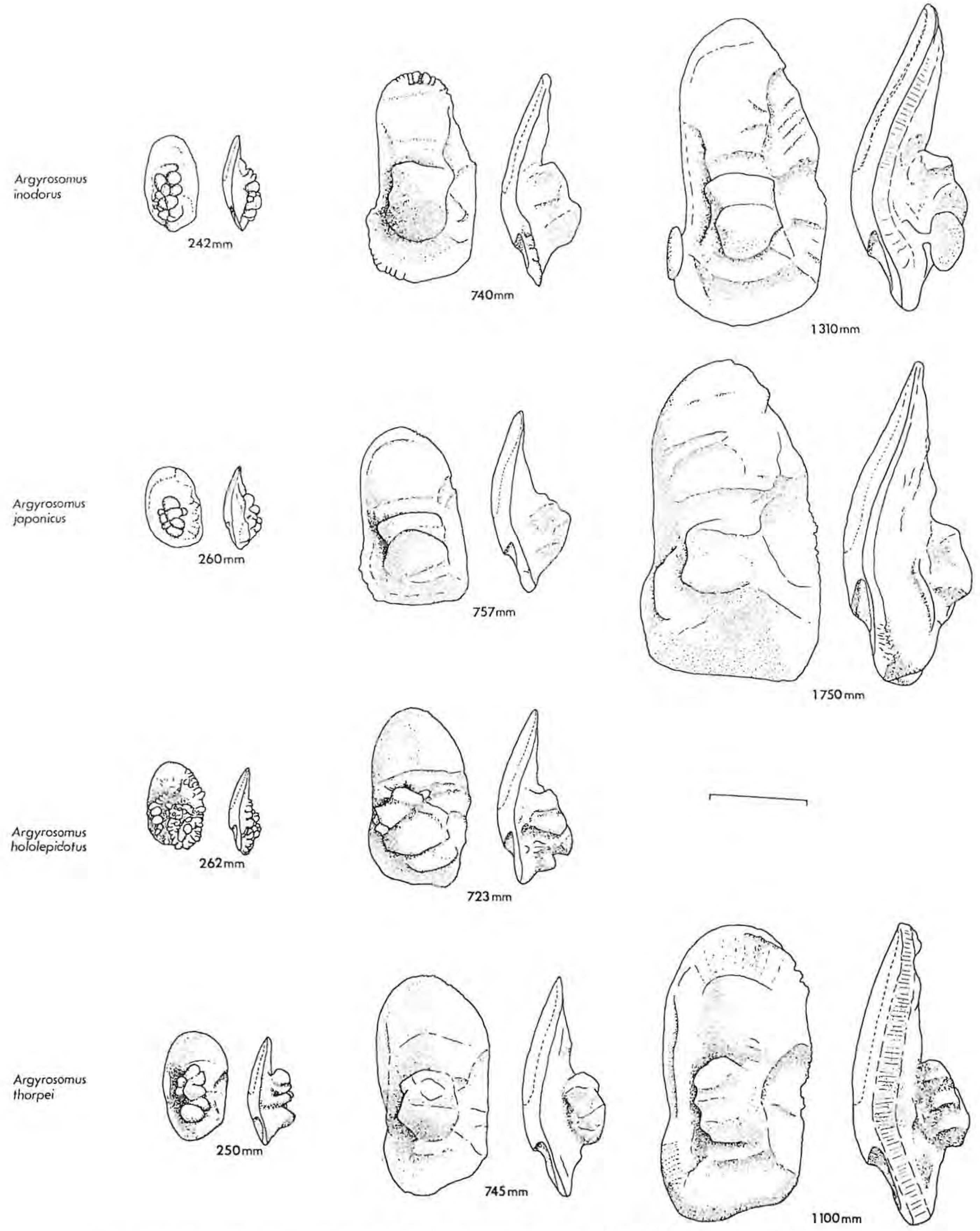


Figure 16. Lateral and ventral views of some sagittae illustrated in Figure 15. Scale bar = 10 mm.

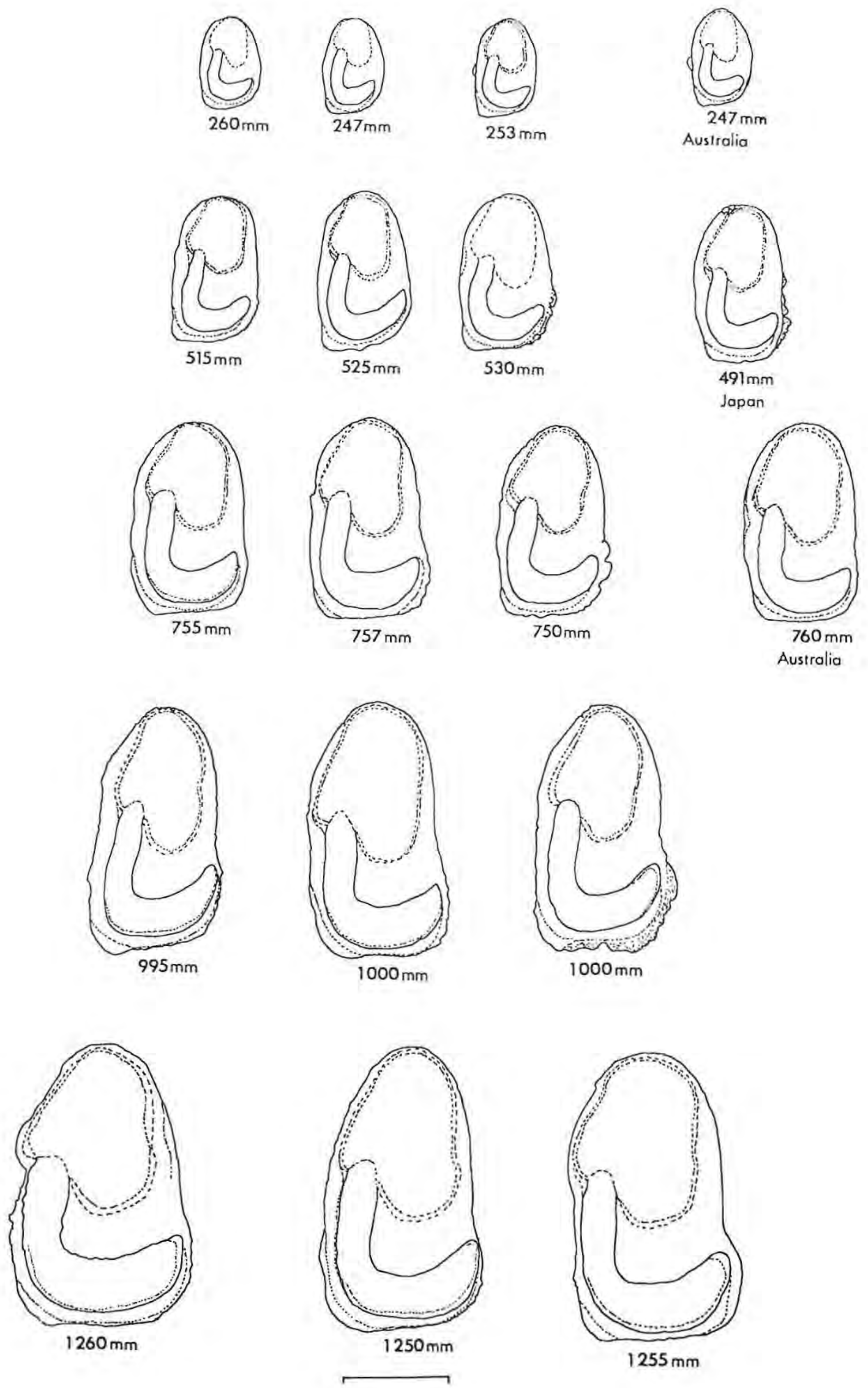


Figure 17. Intraspecific variation of sagittae from South African *Argyrosomus japonicus* and similar-sized specimens from Japan and Australia.

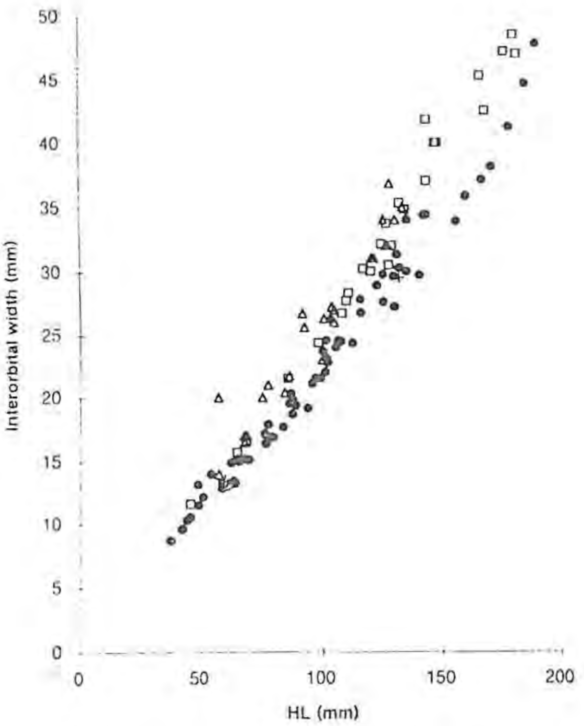


Figure 18. Relationship between interorbital width and head length (HL) for *Argyrosomus regius* (squares), *A. japonicus* (circles), *A. hololepidotus* (crosses) and *A. coronus* (triangles).

ventures onto the "soft" (flat) substrates exploited by trawlers, but prefers "linefish grounds" (especially wrecks or high profile reefs that are associated with sand). West of Cape Agulhas, the relative proportion of *A. japonicus* found in *Argyrosomus* catches declines markedly, and the species is not known in the cold waters from the Cape of Good Hope to Namibia north of Lüderitz (Table 7).

FISHERIES: Due to its large size, palatability and abundance, *A. japonicus* is perhaps the premier angling species of the inshore environment (estuaries and surf zone) along the South African east coast (Cape Agulhas to Natal). Commercial line boat fishermen operating in the nearshore environment catch an average of 197 tons per annum (1988-1992). Recreational boat-fishermen often target this species and are believed to catch at least as much, and possibly more than the commercial fishermen. The flesh is generally sold fresh, but sometimes frozen.

In Australia *A. japonicus* (previously identified as *Sciaena antarctica, Johnius antarctica*, or more recently as "*Argyromosus hololepidotus*") is an important commercial and recreational angling species known as the "mulloway". It is caught in estuaries, in the surf and offshore, using hook and line, gill nets, seine nets and trawl nets (Roughley, 1951; Ogilby, 1954; Grant, 1978; Hall, 1985; Jones, 1991; Kailola et al., 1993; Starling, 1993). From 1964 to 1990, the annual Australian catch has fluctuated between 175 and 575 tons (Kailola et al., 1993).

BIOLOGY: In South African waters, 50% sexual maturity for *A. japonicus* is attained at 110 cm TL for females and at 95 cm TL for males (Griffiths & Hecht, 1993 [species A]). Although there is strong evidence for a spawning migration of adult fish to Natal in spring, reproductive activity is also observed in the Cape Province (as far west as Cape Infanta). Adult fish are found mainly in the nearshore environment (beyond the surf zone) but at times visit inshore habitats. Juvenile fish (<100 cm TL) remain exclusively in the inshore habitats (surf and estuaries) with small juveniles (<15 cm TL) found only in estuaries. Juvenile recruitment to estuaries occurs at about 30 mm TL. The maximum size recorded is 75 kg (181 cm TL). Fish of 45 kg are common, and those between 50-60 kg are not unusual.

In Australia, *A. japonicus* attains sexual maturity at 75 cm TL, and spawning apparently occurs in the summer months (Hall, 1986). According to Kailola et al. (1993), the maximum size in Australia is 43 kg, but Gomon (1994) states that the mulloway attains a length of over 2 metres and a weight of nearly 60 kg.

MATERIAL EXAMINED:

JAPAN: BMNH 1987.5.7.1 (M 297 mm); BMNH 1987.5.7.2 (M 339 mm); BMNH 1987.5.7.3 (F 268 mm). MIYAZAKI: RUSI 44704 (F 499 mm, neotype); RUSI 43674 (F 491 mm); RUSI 40776 (M 267 mm, F 275 mm). Otoliths from four fish 325 - 610 mm TL. AUSTRALIA: AMS I 4453 (347 mm); AMS I 7658 (M 301 mm); AMS I 25605-002 (360 mm); AMS I 27322-007 (J 190 mm); AMS I 17178039 (J 168 mm) RUSI JB1 (J 195 mm). Otoliths from 75 fish 53 mm-880 mm TL). SOUTH AFRICA: Natal: BMNH 1862.11.9.13-14 (230 & 237 mm, Syntypes of *S. margaritifera*, Haly, 1875); RUSI 37391 (J 194 mm & 195 mm). Eastern Cape Province: BMNH 1994.11.30:4 (F 285 mm); MNHN 1994-0570 (F 270 mm); RUSI 11924 (447 mm); RUSI 30147 (F 635); RUSI 32506 (M 370 mm & F 363 mm); RUSI 32507 (F 360 mm); RUSI 32508 (M 387 mm); RUSI 33459 (M 403 mm); RUSI 35450 (F 447 mm); RUSI 37049 (F 436 mm); RUSI 37053 (F 344 mm); RUSI 37055 (F 526 mm); RUSI 37321 (M 382 mm); RUSI 37322 (M 231 mm, F 368 mm); RUSI 38050 (M 338 mm, F 298mm & J 250 mm); RUSI 38064 (Js 134mm & 120 mm); RUSI 38064 (J 168mm & 192 mm); RUSI 38065 (J 148, 202 & 216 mm); RUSI 38066 (J 218 mm & 143 mm); RUSI 38081 (J 158 mm); RUSI 38448 (F 416 mm); RUSI 38449 (F 471 mm); RUSI 38450 (M 355 mm); RUSI 38451 (M 484 mm); RUSI 38452 (F 638 mm); RUSI 38453 (M 424 mm); RUSI 38454 (F 430 mm); RUSI 38455 (F 415 mm); RUSI 38456 (F 574 mm); RUSI 38457 (M 454 mm); RUSI 38458 (F 537 mm); RUSI 38460 (F 612 mm); RUSI 38461 (M 571 mm); RUSI 41130 (298 mm); RUSI 42165 (J 218 mm, 221 mm & 189 mm and one F 245 mm). Southern Cape Province: RUSI 39136 (M 320 mm); RUSI 39138 (F 304 mm); RUSI 39140 (F 340 mm); SAM 33472 (M 330 mm); USNM 332447 (M 290 mm). Otoliths from 543 fish (37-1750 mm TL) collected from various localities along the South African east coast.

***Argyrosomus hololepidotus* (Lacepède, 1801)**

(Fig. 19)

Labrus hololepidotus Lacepède, 1801 (3): 517, Pl. 21, Fig. 2 (based on the unpublished figure of Philibert Commerson, who [according to Cuvier & Valenciennes, 1830] obtained the specimen from Fort Dauphin, Madagascar).

Sciaena aquila (non Lacepède): Pellegrin 1914: 225 (Madagascar).

Argyrosomus hololepidotus: Bauchot & Bianchi, 1984: 88; Mohan, 1984, SCIAEN Argyr 3 (in part).

Holotype: none

Iconotype: Lacepède, 1801, Pl. 21, Fig. 2 (from Philibert Commerson's drawing).

Neotype: RUSI 41433, female 465 mm, Fort Dauphin, Madagascar; collected by Marc H. Griffiths, 3rd April 1993. According to Cuvier and Valenciennes (1830),

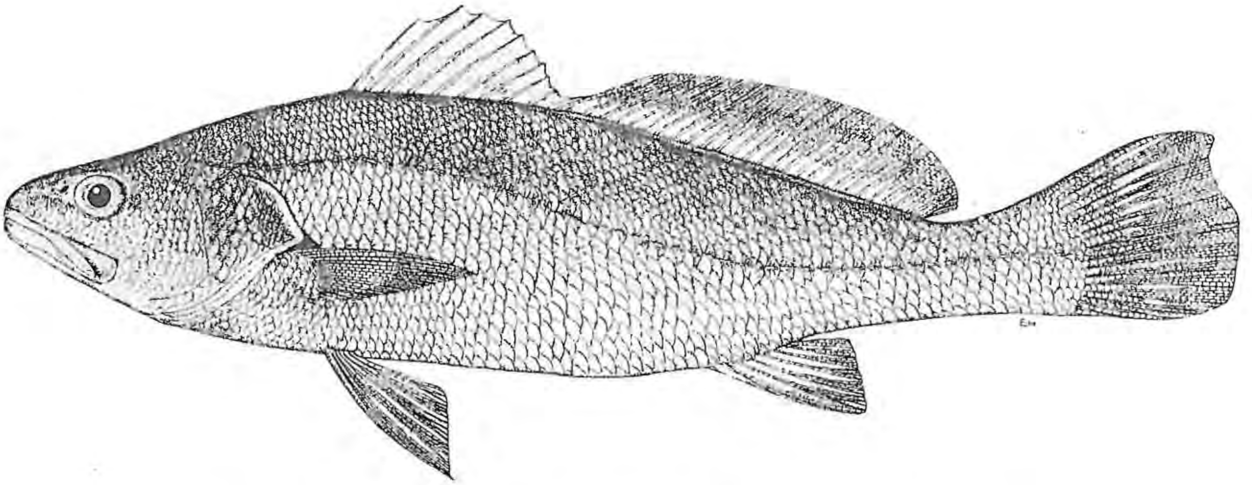


Figure 19. *Argyrosomus hololepidotus*, neotype, 465 mm SL, RUSI 41433; Madagascar.

Commerson's original specimen from Fort Dauphin, Madagascar and his description of the species were lost. Because sciaenid taxonomy depends heavily on internal anatomy (Trewavas, 1977), the iconotype (an engraving of Commerson's figure) contains too little detail to differentiate between *Argyrosomus* species. It is therefore necessary to designate a neotype to resolve the taxomomic confusion that besets this name.

ADDITIONAL MATERIAL: RUSI 41432, J 204 mm, and a fresh specimen (M 615 mm) examined at the Fort Dauphin fish market. Meristic data from the third specimen were recorded, and the otoliths were collected; otoliths of four larger specimens were also collected.

DIAGNOSIS: A species of *Argyrosomus* with the following combination of characters: dorsal fin rays 27-28; gill-rakers 4-5 + 9; swim-bladder carrot shaped, with 34-36 arborescent appendages with lateroanterior limbs throughout length of bladder; caudal peduncle length 12-13% SL; peduncle depth 75-77% peduncle length; interorbital width 6.3-7.3% SL (22% HL); suborbital width 11-12% HL; lower jaw length 50% HL; midlateral body scale length 2.5-2.8% SL; drumming muscles present in both sexes; sagitta similar to that of *A. regius*, OCD 28-34% OH; pectoral fins 17-18% SL, not reaching vertical at tip of adpressed pelvic fins; pectoral fin axillary fold scaleless; peritoneum unpigmented; anterior part of lateral line moderately curved.

DESCRIPTION: Data for the neotype in parentheses. Dorsal fin X+I,27-(28); anal fin II,7; pectoral fin rays 16-(17); lateral-line scales 50 - (51); gill-rakers 4-(5) + 9; swim-bladder appendages (34)-36; vertebrae 11 + 14.

Proportions as % SL: head length (29)-30; pre-dorsal length 34; pre-pelvic length 32; body depth (26)-27; caudal peduncle length (12)-13; peduncle depth (9.0)-9.7; snout length (7.4)-7.8; eye diameter (4.7)-5.5; interorbital width (6.3)-6.7; suborbital width (3.0)-3.4; upper jaw (12)-12.5; lower jaw (14)-15; pectoral fin (17)-18; pelvic fin (18)-20; anal fin (14)-16; third dorsal spine (13); second anal spine (6.7)-8.5; gill-raker (1.8)-1.9; gill-filament 2.9-(3.2); scale length (2.5)-2.8.

Proportions as % HL: snout (26)-27; eye diameter (16.5)-18; interorbital width (22)-23; suborbital width (10.5)-12; upper jaw 42-(43.5); lower jaw 50; gill-raker (4.2)-6.3; gill-filament 10-(11).

Proportions as % eye diameter: gill-raker 34-(39); gill-filament 54-(68).

Dorsal profile of *A. hololepidotus* includes a hump or "shoulder" behind the head. Pectoral fins not reaching vertical at tip of pelvic fins (for fish 204-615 mm). Scales ctenoid on body, belly, nape, interorbital region, operculum and below eye. Caudal fin elongate S-shaped (Fig. 2B) in smallest fish and S-shaped (Fig. 2C) in two larger specimens examined; it is probable (as in *A. japonicus)* that the caudal fins of fish less than 10 cm SL are pointed. Gill-raker at angle shorter than outer gill-filaments (at angle) in larger fish, and equal to gill-filaments in 204 mm specimen. Drumming muscles present in both sexes. Urinary bladders large, as in *A. japonicus*. Pyloric caeca 8 or 9.

Swim-bladder carrot shaped (Fig. 20) with 34-36 appendages. Proximal two limbs of arborescent appendages orientated dorsoposteriorly and lateroanteriorly throughout length of bladder. Branches arising from anterior limb project at 90° to the bladder, and those from the dorsal limb project posteriorly and lie against the bladder. In specimens with significant quantities of appendage fat, the lateroanterior limb becomes orientated ventroanteriorly and the branches of both limbs project laterally at 90° to the bladder (with only slight posterior orientation at their tips) (Fig. 20). Last two appendages on each side of the bladder bud-like, and the four preceding these, weakly branched.

Otoliths: Comparisons of sagittae from *A. hololepidotus, A. japonicus* (Figs 15 & 16) and *A. regius* (Fig. 11 and the illustrations of Chaine, 1938 and Schwarzhans, 1993) revealed no significant differences. The denticles observed along the dorsal margin of the smallest otolith figured for *A. hololepidotus* (Figs 15 & 16) are also sometimes found in small specimens of *A. japonicus* and *A. regius*. The OCD is 28-34% OH for *A. hololepidotus*.

Colour: Fresh colour of neotype silvery grey becoming darker and bluish above and white below; flanks and dorsal surface with a distinctly bronze sheen. Pectoral, dorsal and

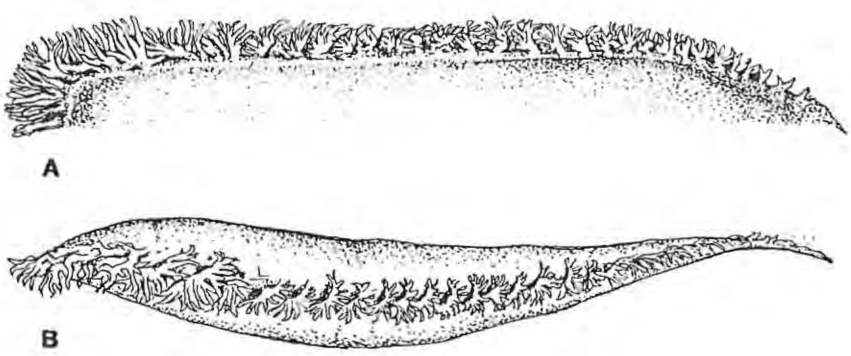


Figure 20. Swim-bladder of *Argyrosomus hololepidotus* 465 mm, Neotype, RUSI 41433: A) lateral and B) ventral (left half) views. The orientation of the swim-bladder appendages of this specimen was modified by the large quantity of fat that was removed from between the appendages (see description).

caudal fins brownish grey; pelvic and anal fins almost white with streaks of grey. Fleshy fold at axil of pectoral fin black and scaleless. After fixation the neotype darkened, becoming distinctly brown; this dark brown colour is possibly due to the use of paraformaldehyde (to prepare the formalin solution). Mouth lining pale grey; inner aspect of operculum dark grey. Peritoneum unpigmented.

COMPARISONS (Tables 2 - 4): *A. hololepidotus* differs from *A. japonicus* by having a wider suborbital, more swim-bladder appendages and fewer lower gill-rakers. Furthermore, the branches arising from the ventral limbs along the posterior half of the swim-bladder (Fig. 20), project laterally from the bladder and do not lie against it as in *A. japonicus* (Figs 13 & 14), and in specimens with little or no appendage fat, the ventral limb is orientated lateroanteriorly (vs ventroanteriorly) in the posterior half of the bladder.

A. hololepidotus differs from *A. regius* by having fewer and smaller swim-bladder appendages (Fig. 11), which have ventral limbs (in specimens with little or no appendate fat) that are orientated anterolaterally (vs anteroventrally) and branches arising from these which project at 90° from the bladder (vs posteriorly and lying against the bladder); wider suborbital; shorter pectoral fin; longer scales; narrower interorbital; and longer lower jaw.

A. hololepidotus was also compared with data and illustrations of *A. amoyensis* from Trewavas (1977), Mohan (1984) and the original description of *Nibea miichthioides* Chu et al. 1963. *A. hololepidotus* differs in having 9 (vs 8) lower gill-rakers, interorbital width 22-23% HL (vs 19% HL), and suborbital width 11-12% HL (vs 9% HL). The swim-bladder of *A. amoyensis* is spindle shaped (tapering anteriorly and posteriorly), there are only 22-29 appendages, and they are not obviously divided into dorsal and ventral limbs. The sagitta of *A. hololepidotus* (Figs 15 & 16) is similar to that of *A. amoyensis* (Trewavas, 1977: Fig. 9b; Chu et al., 1963: Fig. 82), but it lacks the protuberance found on the posterodorsal corner in *A. amoyensis*.

DISTRIBUTION: *A. hololepidotus* is known only from Madagascar. The neotype, Commerson's original specimen (Cuvier & Valenciennes, 1830) and the specimens listed by Pellegrin (1914) were all collected from Fort Dauphin on the southeast coast of Madagascar. Although Mohan (1984) indicated that *A. hololepidotus* is found along the entire east coast and northern parts of the island, fisheries personnel in Madagascar report that it is common only on the southeast coast.

FISHERY: *A. hololepidotus* or the "fyandava" (Malagasy name) is generally caught by artisanal fishermen using dugout canoes and handlines in 20 - 40 m of water.

BIOLOGY: All three specimens (204-615 mm) examined in this study were immature, suggesting a large size at sexual maturity (similar to *A. japonicus* and *A. regius*). The maximum size, as measured from marks on the oars and gaffs of fishermen, was 135 cm TL.

***Argyrosomus thorpei* Smith, 1977**

Argyrosomus thorpei Smith 1977: 561, Pls. I & II; van der Elst, 1981: 262; Mohan, 1984: SCIAEN Argyr 7; Heemstra, 1986: 617, Pl. 71.

Afroscion thorpei: Trewavas, 1977: 337; Schwarzhans, 1993: 134, Figs. 244-245.

Holotype: RUSI 674 (320 mm SL from Natal)

Paratypes: RUSI nos 675-680, 2651A & B, BMNH 1976.10.18.1

DIAGNOSIS: A species of *Argyrosomus* with the following combination of characters: dorsal fin rays 26-28; gill-rakers 4-6 + 10-12; swim-bladder carrot shaped, with 25-33 arborescent appendages; caudal peduncle length 12-14% SL; peduncle depth 65-79% peduncle length; interorbital width 6.0-7.9% SL (19-26% HL); suborbital width 10-12% HL; lower jaw length 47-52% HL; midlateral body scale length 2.6-3.3% SL; drumming muscles present in both sexes; urinary bladders large; sagitta with anterior two-thirds expanded, posterodorsal angle >90°, posterior margin straight, cauda with distal portion expanded and tip truncate, OCD 34-44% OH; pectoral fins 20-23% SL, reaching past vertical at tip of pelvic fins; pectoral fin axillary fold scaly; peritoneum pigmented; anterior half of lateral line strongly curved.

DESCRIPTION: Based on 16 preserved specimens (166-474 mm), two fresh specimens, two skeletons (452 & 461 mm) and otoliths of 53 other fish. Dorsal fin X+I,26-30; anal fin II,7; pectoral-fin rays 15-17; lateral-line scales 49-52; vertebrae 11 + 14.

Proportions as % SL: HL 29-32; pre-dorsal length 33-37; pre-pelvic length 32-34; body depth 24-30; caudal peduncle length 12-14; peduncle depth 8.4-10.2; snout 8.1-8.9; eye diameter 6.8-7.9 at 166-238 mm, 4.8-5.4 at 315-390 mm and 4.0-4.2 at 441-474 mm SL; interorbital width 6.0-7.9; suborbital width 3.0-3.7; upper jaw 12-14; lower jaw 14-16; pectoral fin 20-23; pelvic fin 16-21 at 166-238 mm, 17-18 at 315-390 mm and 16-17 at 403-634 mm SL; anal fin 15-17 at 166-238 mm, 14 at 315-390 mm and 13 at 460 mm SL; third dorsal spine 10-15; second anal spine 4.4-7.9 at 166-238 mm and 6.7-7.7 at 315-474 mm SL; gill-raker 2.7-3.0 at 166-238 mm, 2.4-3.0 at 315-390 mm and 2.3-2.5 at 441-474 mm SL; gill-filament 2.6-3.4.

Proportions as % HL: snout 26-29; eye diameter 19-21 at 166-238 mm, 17-19 at 315-390 mm and 15-17 at 403-474 mm SL; interorbital width 19-26; suborbital width 10-12; upper jaw 39-44; lower jaw 47-52; gill-raker 9.0-9.8 at 166-238 mm, 8.1-10.0 at 315-390 mm and 8.1-8.5 at 441-474 mm SL; gill-filament 9.1-11.6.

Proportions as % eye diameter: gill-raker 42-56; gill filament 51-55 at 166-238 mm, 53-68 at 315-390 mm and 66-74 at 441-474 mm.

Scales cycloid on snout, below eye, on interorbital region and on extreme anterior part of chest; ctenoid on rest of body. Anterior half of lateral line strongly curved. Caudal fin elongate S-shaped in juveniles, becoming slightly S-shaped and occasionally truncate in adults (Fig. 2). The correction made to the caudal fin in the photograph of the holotype (Smith, 1977) is probably erroneous. Gill-raker at angle of first arch at least equal to outer (shorter) gill-filaments in fish less than 46 cm, but gill-raker shorter than gill-filaments in larger fish. Smith (1977) reported no sonific muscles for *A. thorpei*, but we found drumming muscles in both sexes (n = 48) in specimens larger than 23 cm (including the paratypes listed). Urinary bladders large (as in *A. japonicus*).

Swim-bladder carrot shaped, with 25-33 appendages (for illustration see Smith 1977, Pl. 2); the ventral limb is orientated lateroanteriorly, rather than venteroanteriorly and the branches arising from it project laterally and at no stage lie against the bladder. The dorsal limb is orientated dorsoposteriorly, but along the posterior three quarters of the bladder it curves through 150° so that the tip points anteriorly. The branches on this limb project posteriorly to dorsally; and lie against the swim-bladder; last 1-3 appendages are bud-like and the 1-3 preceding appendages weakly branched. Disproportionate swim-bladder enlargement not observed in any *A. thorpei* that we examined.

Otoliths: Sagittae of *A. thorpei* (Figs 15 & 16) very distinctive, moderately elongate, the anterior two-thirds expanded, resulting in a broadly rounded apex; dorsal and posterior margins relatively straight; posterodorsal angle >90°; ventral margin convex in smaller fish, becoming concave with growth; cauda strongly curved with distal portion expanded and tip truncate.

Neurocranium (Figs 4 & 5) and skeleton: Length of neurocranium (NCL) 20-21% SL; pre-supraoccipital crest length 10-11% SL and 49-51% NCL; supraoccipital crest length 8.5-8.9% SL and 41-44% NCL (452-461 mm SL); neurocranial width 8.1-8.4% SL and 40-41% NCL. Premaxilla 8.6-8.7% SL and 42-43% NCL; dentary 9.8-10% SL and 48% NCL; interorbital septum relatively unossified. Third and fourth neural spines 8.9% and 8.5-8.7% respectively.

Colour: Silvery grey becoming darker and blue (with a coppery sheen) above and lighter below; fins yellow grey to orange brown, occasionally reddish (particularly caudal) as a result of vascular distension and haemorrhaging; mouth lining pale yellow; inside of operculum grey/black with yellow tinge; peritoneum pigmented with grey/black dots. After preservation the colour depends on treatment, and may vary from dark brown to grey, or even silver. A dark spot on each dorsal body scale may give the appearance of oblique stripes; fins greyish or brown; peritoneum and ventral surface of swim-bladder with fine black/grey dots.

COMPARISONS (Tables 2-6): The body of *Argyrosomus thorpei* is slightly more compressed than the other species described in this paper. Teeth of lower jaw with *Argyrosomus* pattern of differentiation, but smaller than in equal-sized specimens of the other species (Fig. 6).

Differences between *A. thorpei* and *A. japonicus* include: a wider suborbital, scaly pectoral fin axillary fold, anterior half of lateral line more strongly curved, longer caudal peduncle, longer gill-rakers; sagitta with a more obtuse posterodorsal corner, anterior two-thirds of otolith and distal portion of the cauda expanded (Fig. 15); neurocranium wider, with wider lateral line canals (Fig. 5) and larger inter-orbital window (Fig. 4).

A. thorpei differs from *A. hololepidotus* in having fewer swim-bladder appendages, more lower gill-rakers, longer pectoral fin, anterior half of lateral line more strongly curved, scaly pectoral fin axillary fold, pigmented peritoneum; sagitta with a more obtuse posterodorsal corner and anterior two-thirds of otolith and distal portion of the cauda expanded (Fig. 15).

REMARKS: Based on otolith shape, Trewavas (1977) established the monotypic genus, *Afroscion*, for *Argyrosomus thorpei* Smith, 1977. This genus was not recognized by Mohan (1984), Heemstra (1986) or Sasaki & Kailola (1988). The recent discovery of *Afroscion trewavasae* Schwarzhans 1993, based on otoliths from the Lower Pliocene of Morocco, led Schwarzhans to reinstate the genus *Afroscion*, arguing that it represents a lineage separated from *Argyrosomus* for a considerable period of time. According to him, "the shape of the dorsal rim and the absence of a concavity at the ventral rim (of the otolith) are the most obvious diagnostic differences" for the genus. Schwarzhans (1993), however, described the dorsal margins ("rims") of both genera as being flat, and we found that the ventral margin of *Argyrosomus* sagittae becomes concave with growth (Fig. 15). Although *A. thorpei* differs from other species of *Argyrosomus* by its scaly pectoral axillary fold, pigmented peritoneum, strongly curved lateral line, and distinctive otolith morphology, we believe these differences are insufficient to justify a separate generic status.

DISTRIBUTION: *A. thorpei* is known from the southeast African coast from Port Elizabeth to Mozambique and also from the west coast of Madagascar. In South Africa it is mostly caught beyond the surf zone (to depths of 80 m) and seldom found south of Natal (Table 7).

FISHERIES: Natal commercial lineboat fishermen catch an average of 107.1 tons and the recreational line-boat sector land an estimated 23 tons (ORI unpublished data) per annum (1988-1992). Shore anglers occasionally catch this species at selected sites on the Natal north coast. *A. thorpei* is also caught in large numbers by line-boat fishermen operating in Mozambique.

BIOLOGY: The size at 50% sexual maturity is 33 cm TL, and spawning occurs during winter (van der Elst et al., 1990). Juveniles are found on sand or mud substrata and the adults predominantly on reef (Fennessy, 1994). Maximum size recorded is 12.0 kg.

MATERIAL EXAMINED:

SOUTH AFRICA: Natal: RUSI 675 (M 365 mm); RUSI 676 (F 365 mm); RUSI 677 (M 474 mm); RUSI 678 (M 375 mm); RUSI 680 (F 315 mm); RUSI 2651 (M 390 mm); RUSI 10264 (F 385 mm); RUSI 10694 (J, 166 mm and 2 F, 171 & 185 mm); RUSI 11613 (F, 238 mm); RUSI 13065 (1 M 460 mm and 2 F, 379 mm & 441 mm); RUSI 28382 (M 231 mm). Plus otoliths from 30 fish (14 - 110 cm TL). Eastern Cape Province: Algoa Bay: RUSI 10264 (M 385 mm). MOZAMBIQUE: RUSI 39881 (M 203 mm); RUSI 48480 (F 452 mm, skeleton); RUSI 48481 (F 461 mm, skeleton); the meristic counts of the two fish from which the skeletons were prepared, were also recorded.

Argyrosomus inodorus sp. nov.

(Fig. 21)

Sciaena hololepidota (non Lacepède): Cuvier & Valenciennes, 1830: 38 (in part); Smith, 1849 Pl. 15 (in part); Pappe, 1853: 15; Barnard, 1927: 569 (in part) Pl. 23, Fig. 3; Biden, 1930: 108 (in part) Pl. 13.

Johnius hololepidotus (non Lacepède): Smith, 1949: 226 (in part, not Fig. 552, which is *A. japonicus*).

Argyrosomus hololepidotus (non Lacepède): Trewavas, 1977: 327 (in part, not figs); Heemstra, 1986: 616 (in part, not figs); Bianchi et al., 1993: 164; Schwarzhans, 1993: 138, Fig. 255.

Holotype: RUSI 44705, male, 447 mm SL, South Africa, False Bay, depth 10 m; collected by M. H. Griffiths, 5 June 1994.

Paratypes: 78 specimens (131-860 mm). NAMIBIA: Walvis Bay: RUSI 15257 (M 605 mm). Swakopmund: RUSI NP (M 392 mm); RUSI 48475 (F 415 mm); RUSI 48476 (F 424 mm); RUSI 48477 (M 338 mm); RUSI 48478 (F 332 mm); RUSI 48479 (M 315 mm). SOUTH AFRICA: Eastern Cape Province: AMS I. 34965-001 (F 462 mm, M 308 mm); BMNH 1994.11.30:2 (M 305 mm); BMNH 1994.11.30:3 (F 266 mm); MNHN 1994-0568 (M 558 mm); MNHN 1994-0569 (F 307 mm); NSMT-P 46548 (M 348 mm); NSMT-P 46549 (F 521 mm); RUSI 11924 (F 470 mm); RUSI 38464 (F 306 mm); RUSI 38466 (F 274 mm); RUSI 38467 (F 330 mm); RUSI 38469 (F 283 mm); RUSI 38471 (F 304 mm); RUSI 38474 (F 374 mm); RUSI 38476 (F 258 mm); RUSI 38478 (F 289); RUSI 38479 (M 299 mm); RUSI 38480 (F 325 mm); RUSI 38481 (F 265 mm); RUSI 41138 (F 368 mm); RUSI 41141 (F 293 mm); SAM 33473 (F 276 mm); SAM 33474 (M 381 mm); USNM 331636 (F 357 mm, M 296 mm). Western Cape Province: RUSI 37390 (J 131-157 mm); RUSI 38475 (F 275 mm); RUSI 39836 (5 M 211-287 mm & 3 F 212-227 mm); RUSI 41129 (F 301 mm); RUSI 41132 (M 308 mm); RUSI 41133 (F 362 mm); RUSI 41134 (M 240 mm); RUSI 41136 (F 369); RUSI 41139 (J 154 mm); RUSI 41140 (M 366 mm); RUSI 41143 (M 306 mm); RUSI 41145 (M 364 mm); RUSI 41147 (F 267 mm); RUSI 41148 (F 219 mm); RUSI 41149 (F 267 mm); RUSI 41150 (F 202 mm); RUSI 41151 (F 235 mm); RUSI 41153 (F 234 mm); RUSI 41154 (J 167 mm); RUSI 41156 (F 407 mm); RUSI 41160 (J 179 mm); RUSI 41161 (M 595 mm); RUSI 41162 (J 161 mm); RUSI 41163 (F 227 mm); RUSI 41167 (F 234 mm); RUSI 41435 (J 141 mm); RUSI 42241 (M 660 mm); RUSI 42242 (F 510 mm); RUSI 42246 (M 664 mm); RUSI 42240 (F 640 mm); RUSI 42243 (F 527 mm); RUSI 42244 (M 387 mm); RUSI 42245 (M 383 mm); RUSI 42247 (F 650 mm); RUSI 42248 (F 860 mm); RUSI 44706 (453 mm); RUSI 44707 (435 mm).

DIAGNOSIS: A species of *Argyrosomus* with the following combination of characters: dorsal fin rays 25-29; gill-rakers 4-6 + 10-12; swim-bladder carrot shaped with 31-42 arborescent appendages, the latero-anterior limb of appendages present throughout length of bladder; caudal peduncle length 12-15% SL; peduncle depth 58-74% peduncle length; interorbital width 6.3-7.8% SL (20-25% HL); suborbital width 8.6-10.9% HL; lower jaw length 47-51% HL; midlateral body scale length 1.8-2.5% SL; drumming muscles present only in males; urinary bladders rudimentary, length 0.1-3.3% SL; sagitta (Figs 15, 16 & 22) elongate, with pronounced bulge in posterior third of ventral margin; OCD 37-63% OH; pectoral fins 19-23% SL, reaching to or beyond vertical at tip of adpressed pelvic fins of fish 25-90 cm SL (in South African specimens); pectoral fin axillary

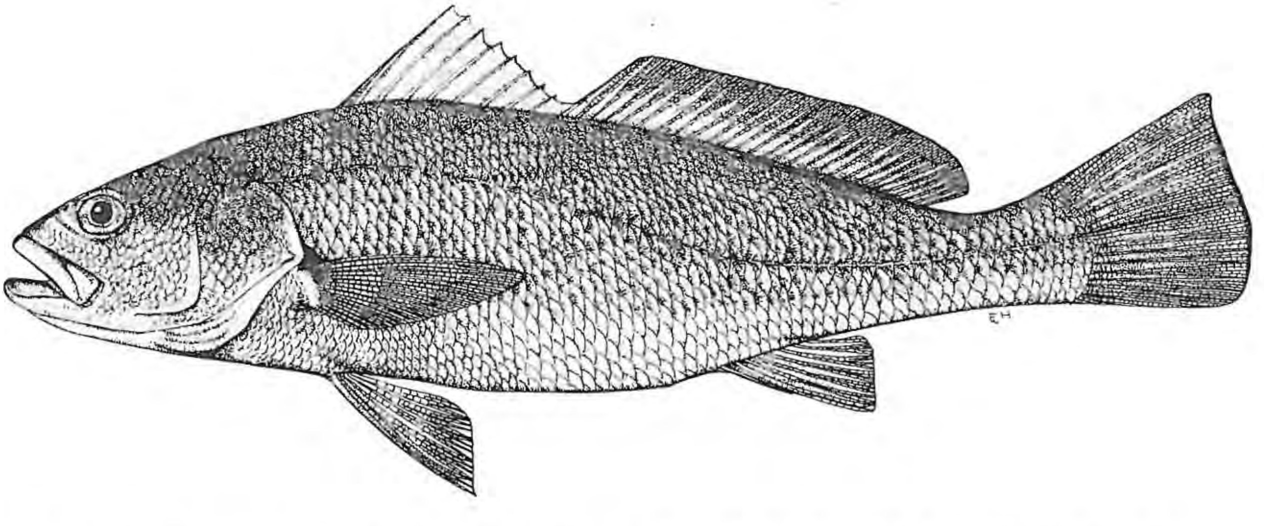


Figure 21. *Argyrosomus inodorus* sp. nov., holotype, 447 mm SL, RUSI 44705; South Africa: False Bay.

fold naked; peritoneum unpigmented; anterior part of lateral line slightly curved.

DESCRIPTION: Based on 79 preserved specimens (131-860 mm), 12 skeletons (300-517 mm) and otoliths and total lengths of 623 fish from South Africa, and 85 from Namibia, that were not preserved. Counts and measurements for the holotype are in parentheses. Dorsal fin X+I,25-29 (27); anal fin II,7 [one specimen from Walvis Bay with 8 rays]; pectoral fin rays 16-17 (17); lateral-line scales 50-53 (51); gill-rakers 4-6 + 10-12; swim-bladder appendages 31-41; vertebrae 11 abdominal and 14 caudal.

Proportions as %SL: HL 28-33 (30); pre-dorsal length 32-36 (33); pre-pelvic length 30-36 (34); body depth 24-28 (25.5); caudal peduncle length 12-15 (13.5); peduncle depth 7.7-9.6 (9.2); snout 7.1-9 (8.5); eye diameter 5.8-7.3 at 131-299 mm, 4.9-6.2 at 301-387 mm, 4.0-5.0 (5.0) at 404-664 mm, and 3.3 at 860 mm SL; interorbital width 6.3-7.8 (7.2); suborbital width 2.6-3.3 (3.0); upper jaw 12-14 (12); lower jaw 14-18 (14.5); pectoral fin 19-23 (21.6); pelvic fin 16-20 at 131-387 mm, 15-17 (17) at 407-664 mm, and 14 at 860 mm SL; anal fin 14-18 at 131-299 mm, 13-15 at 301-387 mm, 12-14 (13.9) at 407-664 mm and 12 at 860 mm SL; third dorsal spine 11-15 (12); second anal spine 5.1-11.7 (7.2); gill-raker 2.0-2.9 at 131-299 mm, 1.8-2.6 at 301-387 mm, 1.6-2.1 at 407-664 mm and 1.2 at 860 mm SL; gill-filament 2.6-3.6.

Proportions as % of HL: snout 24-30 (28.5); eye diameter 18-24 at 131-299 mm, 16-20 at 301-387 mm, 13-17 (17) at 407-664 mm SL, and 11 at 860 mm SL; interorbital width 20-25 (24); suborbital width 8.6-10.9 (10.1); upper jaw 39-44 (40); lower jaw 47-51 (49); gill-raker 6.7-9.1 at 131-299 mm, 6.0-8.8 at 301-387 mm, 5.3-7.0 at 407-664 mm and 3.9 at 860 mm SL; gill- filament 8.9-13.3.

Proportions as % eye diameter: gill-raker 32-46; gill-filament 37-53 at 131-299 mm, 46-77 at 301-387 mm, 55-88 at 407-664 mm and 107 at 860 mm SL.

Dorsal profile evenly rounded. Eye obliquely egg shaped. Nostrils as for *A. japonicus*. Scales deciduous, weakly ctenoid on body (including belly and chest), nape of neck, interorbital region, operculum and below eye. Skin fold at base of pectoral fin scaleless. Pectoral fins reach to or beyond vertical at tip of adpressed pelvic fins for South African specimens 25-90 cm SL, but on smaller fish the pelvic fins extend past tip of pectorals. Caudal fin shape changes with growth; it may be pointed (<10 cm SL, Fig. 2A), elongate and S-shaped (10-22 cm SL, Fig. 2B), or strongly to slightly S-shaped (>30 cm, Fig. 2C). Caudal fin of larger specimens occasionally wedge-shaped to slightly rounded or truncate (Figs 2 E, F & G). Gill-raker at angle of first arch equal to or longer than outer gill-filaments at angle for specimens less than 55 cm, but gill-filaments longer than gill-raker at angle in larger individuals. Drumming muscles present only in larger males, and are poorly developed (or even absent) in most males less than 25 cm SL (n = 8350). Urinary bladders (Fig. 1) rudimentary or sometimes absent in South African specimens, but possibly larger in those from Namibia. Pyloric caeca 7-10 (n = 335).

Swim-bladder (Figs 13A & C & 14A) carrot-shaped, tapering posteriorly, with 31-42 appendages. Most appendages arborescent, basally divided into dorsoposterior and lateroanterior (rather than ventroanterior) limbs, none of which significantly overlap the bladder. Branches arising from anterior limb project at 90° to bladder throughout its length and at no stage lie against it. The last 1-3 pairs of appendages are bud-like and the 1-3 pairs preceding these, weakly branched. Disproportionate appendage enlargement (see *A. japonicus*) was observed only in the 860 mm specimen, which was the largest of 86 *A. inodorus* examined. Ventral surface of swim-bladder with a sparse pattern

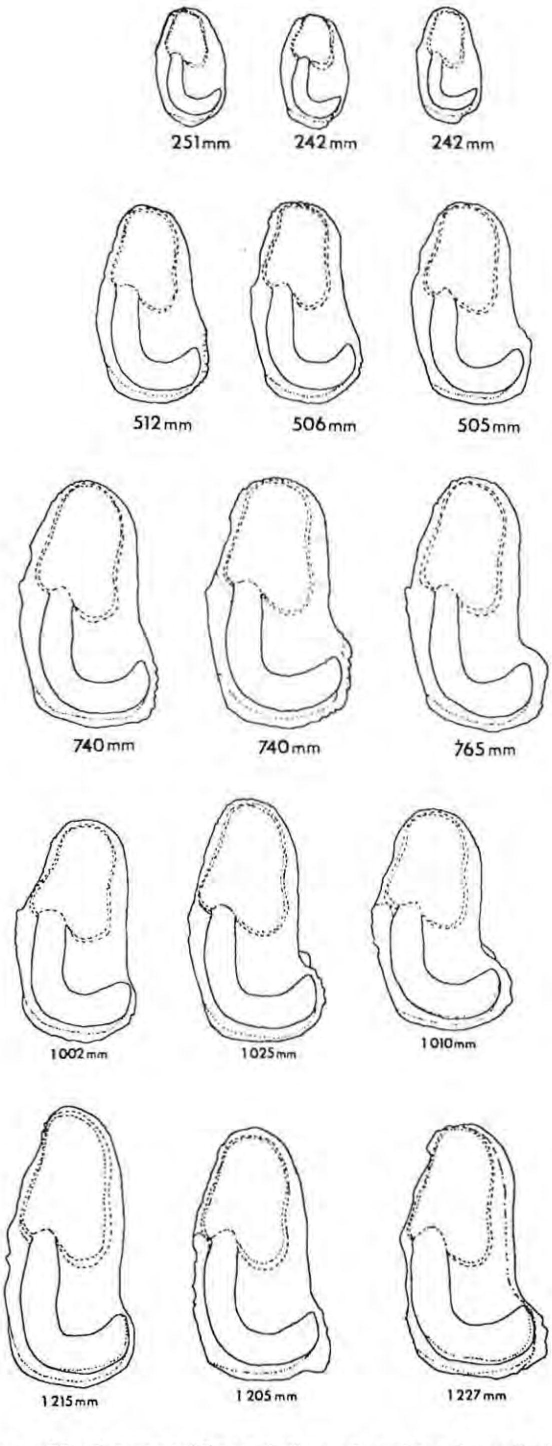


Figure 22. Intraspecific variation of sagittae from 5 size classes of South African *Argyrosomus inodorus*; sizes are total lengths. Lower two rows of drawings (otoliths from fish 1002 - 1227 mm) have been reduced (x 0.75) for purposes of reproduction.

of small black/grey dots that do not appear to increase in size or number, but disperse, with growth.

Otoliths: Sagitta (Figs 15, 16 & 22) elongate; posterior margin rounded, posterodorsal angle usually greater than 90°; ventral margin evenly curved in juveniles, but with a prominent, often denticulate, bulge in posterior third of otoliths of adults; OCD large (37-63% OH). A lateral process (Fig. 16, top row) often occurs just below umbo in larger specimens. Otolith dimension/TL relationships are given in Table 1; statistically, there were no differences between the sexes.

Neurocranium (Figs 4 & 5) and skeleton: Length of neurocranium (NCL) 20-22% SL; pre-supraoccipital crest length 10-12% SL and 51-56% NCL; supraoccipital crest length 8.0-8.8% SL and 39-43% NCL (300-546 mm SL); neurocranial width 8.1-9.2% SL and 39-45% NCL. Premaxilla 8.1-9.1% SL and 40-42 % NCL; dentary 9.3-10.3% SL and 46-49% NCL; interorbital septum relatively unossified. Third and fourth neural spines 6.9-8.0 and 8.2-9.3% SL respectively.

Colour: In life, body silvery becoming green/brown above and white below. Dorsal surface with a copper to bronze sheen which may be very pronounced on head; dorsal and caudal fins pale yellow grey to pale grey/brown; anal, pelvic and pectoral fins from almost white to brown/grey; fins (particularly caudal) occasionally reddish as a result of vascular distension and haemorrhaging. Pectoral fin axillary fold black with a copper/bronze patch. Mouth lining varies from pale yellow to yellow/grey; inner aspect of operculum grey to black, sometimes with a yellow tinge.

In alcohol, body silvery to grey, with a dark spot on each dorsal body scale, sometimes giving rise to oblique stripes; fins pale to dark grey. One or two longitudinal stripes may be visible on dorsal fins.

COMPARISONS (Tables 1-6 & 8): *A. inodorus* differs from *A. japonicus* in having a more even dorsal profile, larger eye (Fig. 23, Table 8) longer pectoral fins (Fig. 24; significant for fish >30 cm SL, Table 8), which reach to or beyond vertical at tip of pelvic fins in fish 25-90 cm SL, shorter scales (Fig. 25), which are more easily lost; a longer and shallower caudal peduncle (Figs 26-28); no drumming muscles in females; rudimentry urinary bladders (Figs 1 & 29); and a higher modal number of lower gill-rakers (Tables 4 & 5). *A. inodorus* also has more swim-bladder appendages (Tables 2 & 3), the appendages are larger (particularly along anterior part of bladder), with the lower limbs orientated anterolaterally (vs anteroventrally) throughout length of bladder (Figs 13 & 14), and the branches arising from the dorsal and ventral limbs of the appendages along the posterior half of the swim-bladder project at right angles from the bladder (in *A. japonicus* these branches extend posteriorly and lie against the bladder, Figs 13 & 14).

The sagitta of *A. inodorus* (Figs 15, 16 & 22) is longer than that of *A. japonicus* (Fig. 30, Table 1), it has a more obtuse posterodorsal angle, rounded (vs straight) posterior margin, pronounced bulge on ventral margin, a greater OCD (Fig. 31, Table 1), and lower OCD:OH ratio (Fig. 32, Table 2).

The neurocranium is wider than that of *A. japonicus* (Fig. 33), it also has an enlarged lateral-line canal system (Figs 4 & 5), a larger interorbital window with frontal and parasphenoid bones not connected (Fig. 4), and shorter supraoccipital crest (Fig. 34, Table 2).

The fish weight/TL and otolith weight/TL relationships for *A. inodorus* and *A. japonicus* are also significantly different ($P < 0.0001$, Table 1). The OCD:OH ratio was not

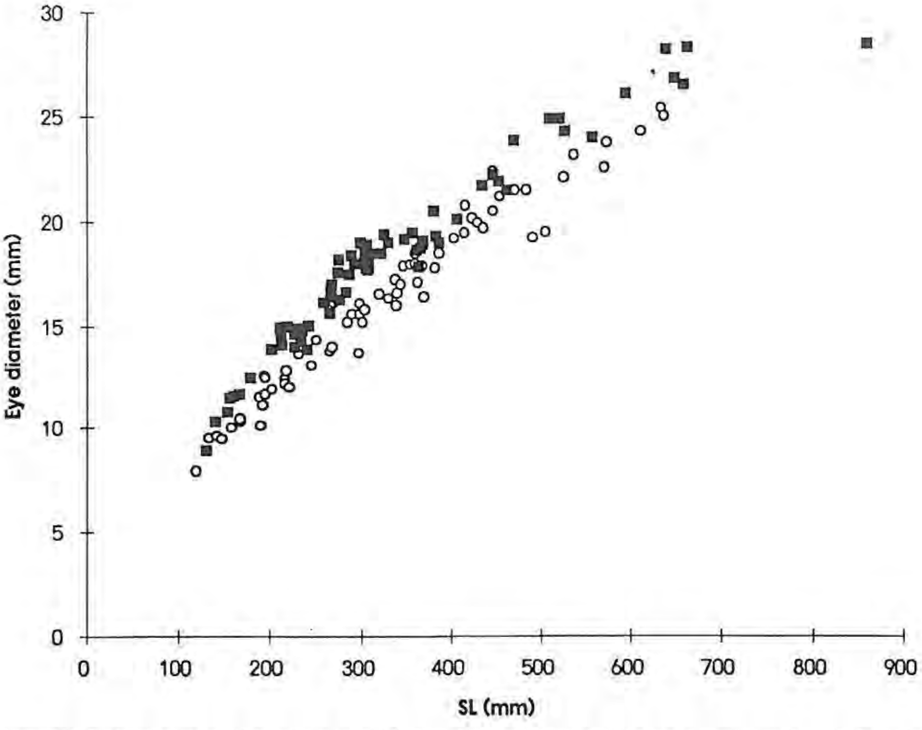


Figure 23. Relationship between eye diameter and SL for *Argyrosomus inodorus* (squares) and *A. japonicus* (circles).

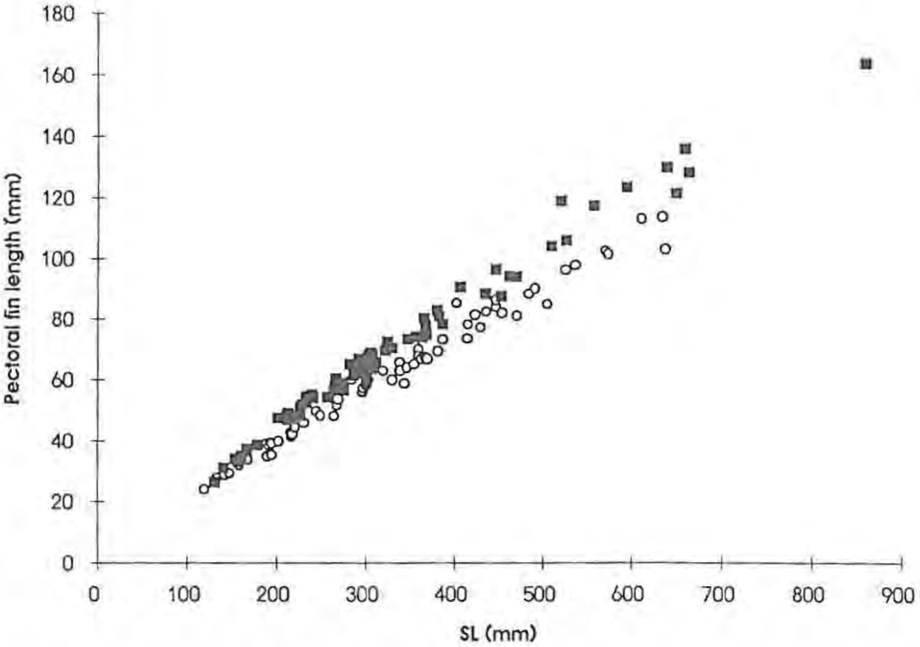


Figure 24. Relationship between pectoral fin length and SL for *Argyrosomus inodorus* (squares) and *A. japonicus* (circles).

allometric for either *A. inodorus* or *A. japonicus* (see Fig. 32) and consequently should assist in the identification of these two species when only otoliths are available (e.g. studies on the feeding of *Argyrosomus* predators or on the middens of ancient southern African man).

Differences between *A. inodorus* and *A. hololepidotus* (Tables 2-4) include: more lower gill-rakers; narrower suborbital width; longer pectoral fin and caudal peduncle; shorter scales; reduced urinary bladders; and drumming muscles in males only. The sagitta of *A. inodorus* (Figs 15, 16 & 22) has a more obtuse posterodorsal angle, rounded (vs straight) posterior margin, pronounced bulge in posterior portion of ventral margin, greater OCD (Fig. 15), and a lower OCD:OH ratio (Table 2).

A. inodorus differs from *A. regius* (Tables 2 & 3-6) in having more lower-limb gill-rakers, narrower interorbital, longer pectoral fin, caudal peduncle and lower jaw, smaller urinary bladders, drumming muscles in males only, and lower limb of arborescent swim-bladder appendages orientated anterolaterally (vs ventroanteriorly), with branches projecting at 90° to the bladder (vs projecting posteriorly and against the bladder). The sagitta of *A. inodorus* (Figs 15, 16 & 22) has a more obtuse posterodorsal angle, rounded (vs straight) posterior margin, pronounced bulge in posterior

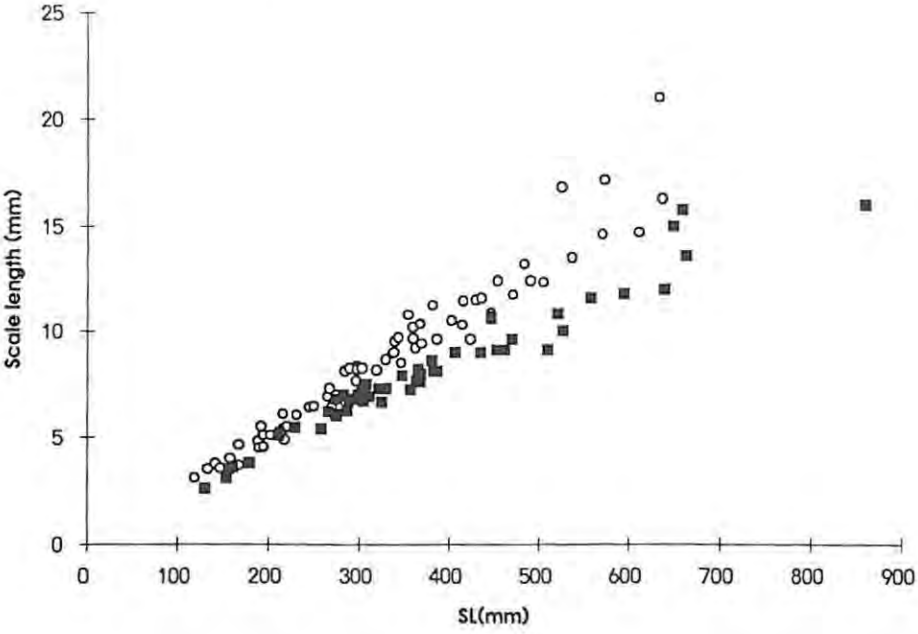


Figure 25. Relationship between midlateral body scale length and SL for *Argyrosomus inodorus* (squares) and *A. japonicus* (circles).

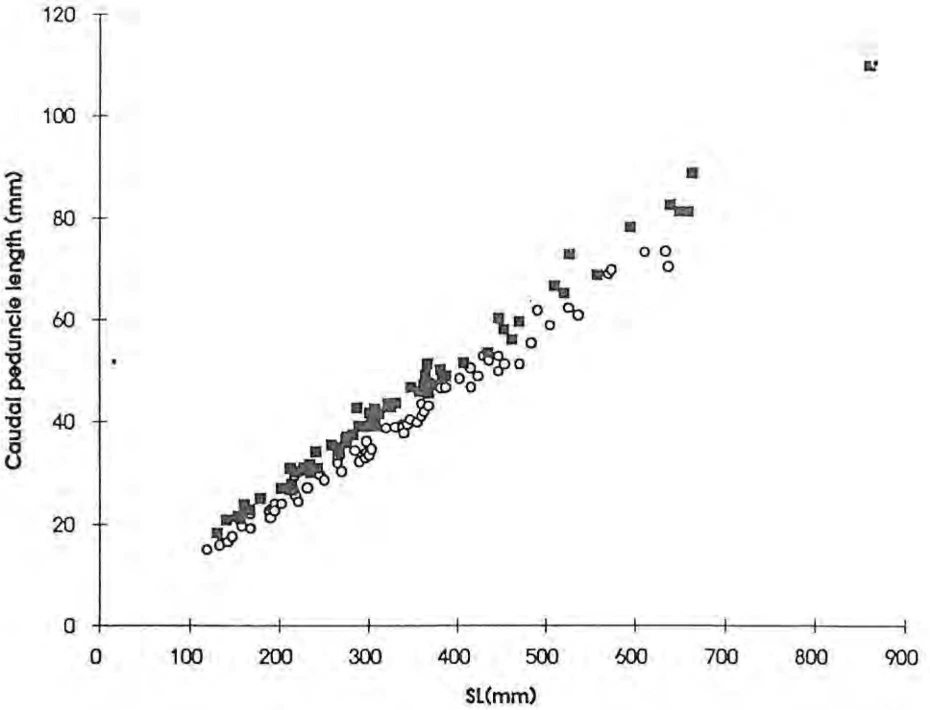


Figure 26. Relationship between caudal peduncle length and SL for *Argyrosomus inodorus* (squares) and *A. japonicus* (circles).

portion of ventral margin, greater OCD (Fig. 15), and lower OCD:OH ratio (Table 2).

A. inodorus differs from *A. thorpei* (Tables 2-6) in having a slightly curved lateral line, shorter midlateral body scales, narrower suborbital width, more swim-bladder appendages, reduced urinary bladders, drumming muscles in males only, and naked pectoral axillary fold. The sagitta has a rounded posterior margin, anterior two-thirds of otolith tapering to form a sharply rounded apex, tip of cauda not expanded and OCD greater (Fig. 15).

A. inodorus was compared with data and illustrations of *A. amoyensis* from Trewavas (1977), Mohan (1984) and the original description of *Nibea miichthioides* Chu et al. (1963). *A. inodorus* has more lower gill-rakers (10-12 vs 8); a carrot-shaped (vs spindle-shaped) swim-bladder with more appendages (31-41 vs 22-29); wider interorbital (width 20-25% vs 19% HL); and longer pectoral fin (19-23% vs 17% SL). The sagitta of *A. inodorus* (Figs 15, 16 & 22) is also distinct from that of *A. amoyensis* (Trewavas, 1977: Fig. 9b; Chu et al., 1963: Fig. 82); it is more elongate,

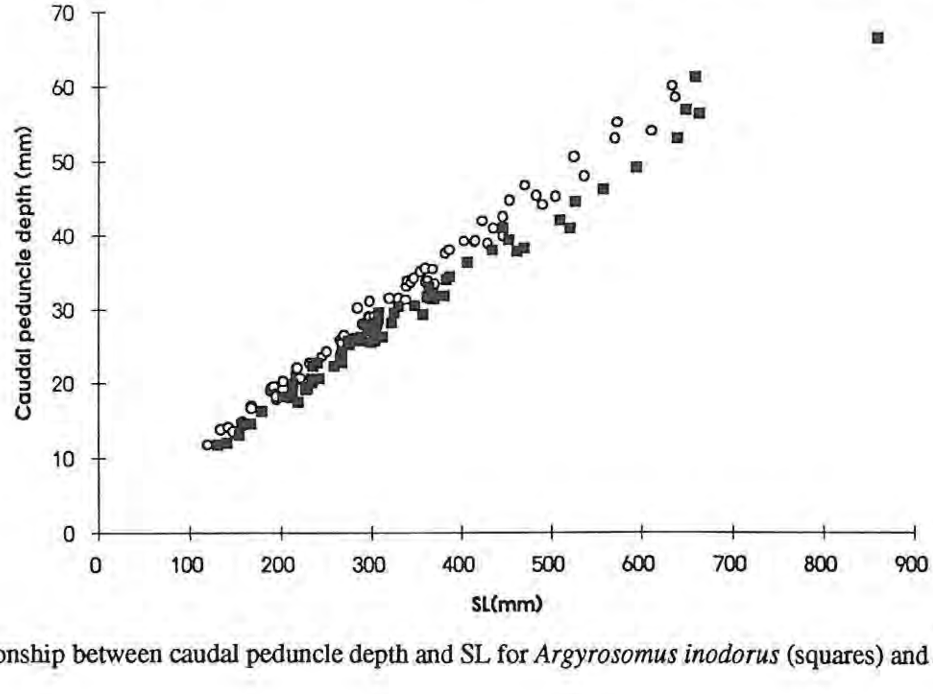


Figure 27. Relationship between caudal peduncle depth and SL for *Argyrosomus inodorus* (squares) and *A. japonicus* (circles).

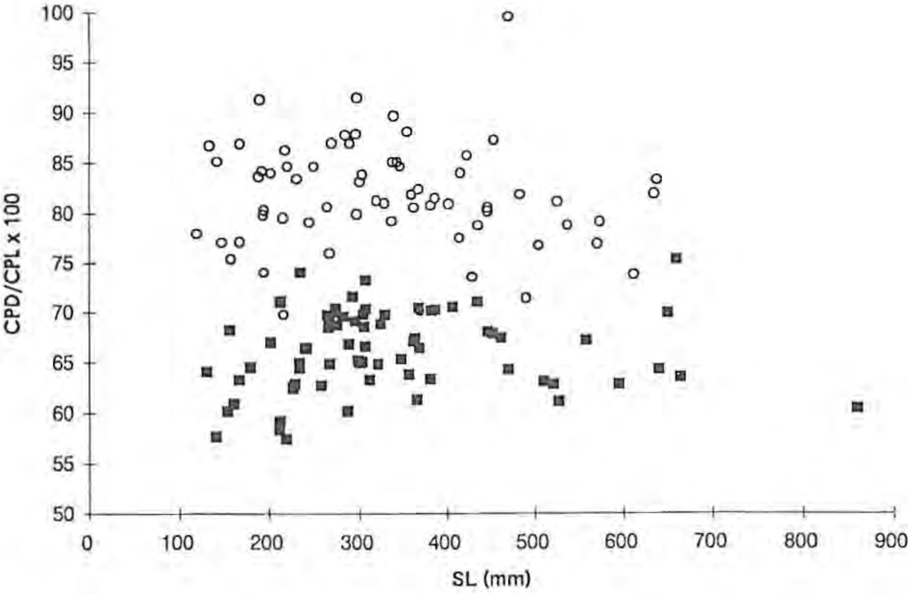


Figure 28. Relationship between CPD (caudal peduncle depth) as % CPL (caudal peduncle length) and SL for *Argyrosomus inodorus* (squares) and *A. japonicus* (circles).

with a prominent bulge on posterior sector of ventral margin, rounded (vs straight) posterior margin, greater OCD, more elongate ostium with concave ventral and dorsal margins, and it lacks the protuberance on the posterodorsal corner in *A. amoyensis*.

A. inodorus differs from *A. beccus* Sasaki (1994) in having 10-12 lower gill-rakers (vs 8-9); swim-bladder appendages 31-41 (vs 23); longer snout (8-9% SL (vs 6.1-6.3% SL), snout convex (concave in *A. beccus*); eye diameter 5.8-7.3% SL (vs 7.3-8.3% SL, for fish of comparable size); wider interorbital 6.3-7.8% SL (vs 4.7% SL), and pelvic fin length 16-20% SL (vs 22-23% SL, for fish of comparable length). The sagitta of *A. inodorus* (Figs 15, 16 & 22) is easily distinguished from that of *A. beccus* (Sasaki, 1994: Fig. 2B); it is more elongate, with concave (vs convex) dorsal and ventral margins, a longer ostium, pronounced bulge in posterior third of ventral margin, angle of posterodorsal corner > 90° (vs 80-90°), posterior margin rounded (vs straight in *A. beccus*), OCD distinctly greater, and postcentral umbo on lateral surface of sagitta less than 50% of otolith length (about 75% in *A. beccus*).

Based on descriptions of *A. heinii* by Steindachner (1907) and Mohan, (1984), *A. inodorus* can be distinguished by lower limb gill-rakers 10-12 (vs 9); dorsal-fin rays 25-29 (vs 32-33) and an S-shaped (vs emarginate) caudal fin in adults.

Based on the description of *A. miiuy* by Trewavas (1977), *A. inodorus* has lower limb gill-rakers 10-12 (vs

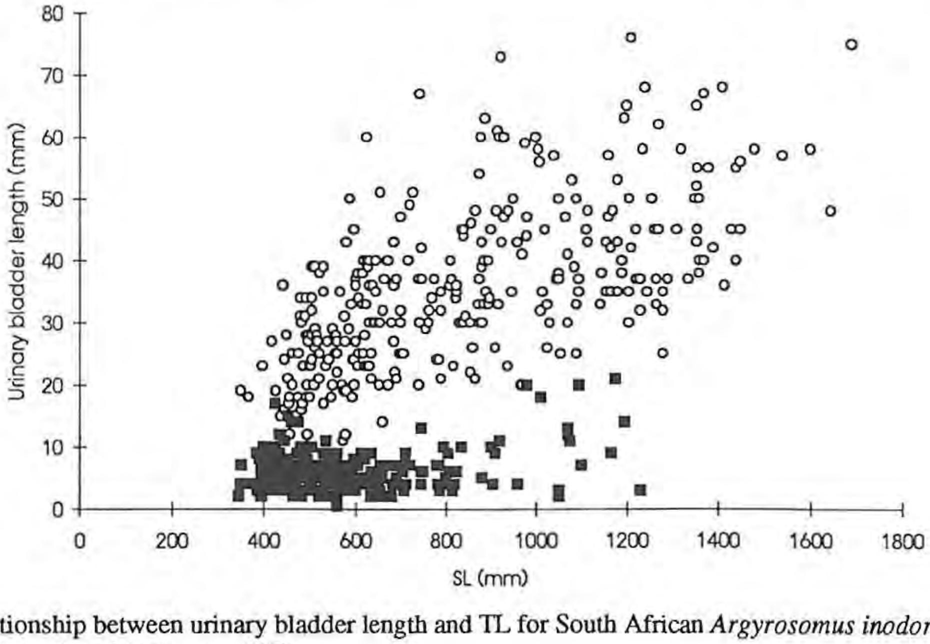


Figure 29. Relationship between urinary bladder length and TL for South African *Argyrosomus inodorus* (squares; n = 265) and *A. japonicus* (circles; n = 312).

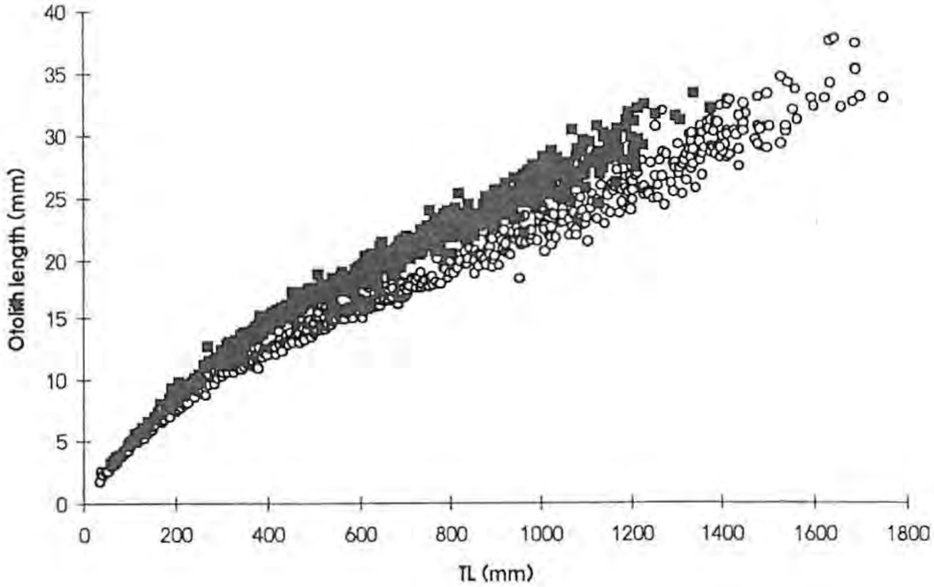


Figure 30. Relationship between otolith length and TL for *Argyrosomus inodorus* (squares) and *A. japonicus* (circles).

9-10), snout length 24-30% HL (vs 22-24% HL), interorbital width 20-25% HL (vs 19-21% HL), upper jaw length 39-44% HL (vs 44-46% HL) and lower jaw length 47-51% HL (vs 53-55% HL). The swim-bladder appendages are much longer in *A. miiuy*, and at about 27 cm SL, almost completely enwrap the bladder (Trewavas, 1977). The caudal fin is also more elongate in *A. miiuy* than in *A. inodorus*, and at 305 mm SL is pointed (Chu et al., 1963) as opposed to S-shaped. Comparisons of the sagitta of *A. inodorus* (Figs 15, 16 & 22) and *A. miiuy* (Chu et al., 1963: Fig. 90; Schwarzhans 1993: Figs 239-240) reveal that the otolith of *A. miiuy* is more slender, with concave to straight (vs straight or convex) dorsal margin, posterodorsal corner more obtuse, posterior margin sharply rounded to pointed (vs rounded), the cauda is less curved, and the postcentral umbo on the lateral surface of the otolith is about 65% of the otolith length (less than 50% in *A. inodorus*).

ETYMOLOGY: *Inodorus*, Latin for "without smell". *A. inodorus* was first suspected of being a different species because it lacked the strong brassy/metallic smell that is typical of *A. japonicus* found in South African waters.

REMARKS: For many years *A. inodorus* has been confused with *A. japonicus* (as "*A. hololepidotus*"). However, based on the distribution patterns of the two species (this study), the catch localities, the sizes of the specimens examined and the descriptions of the caudal fin, it is almost certain that all of the authors mentioned in the synonymy (above)

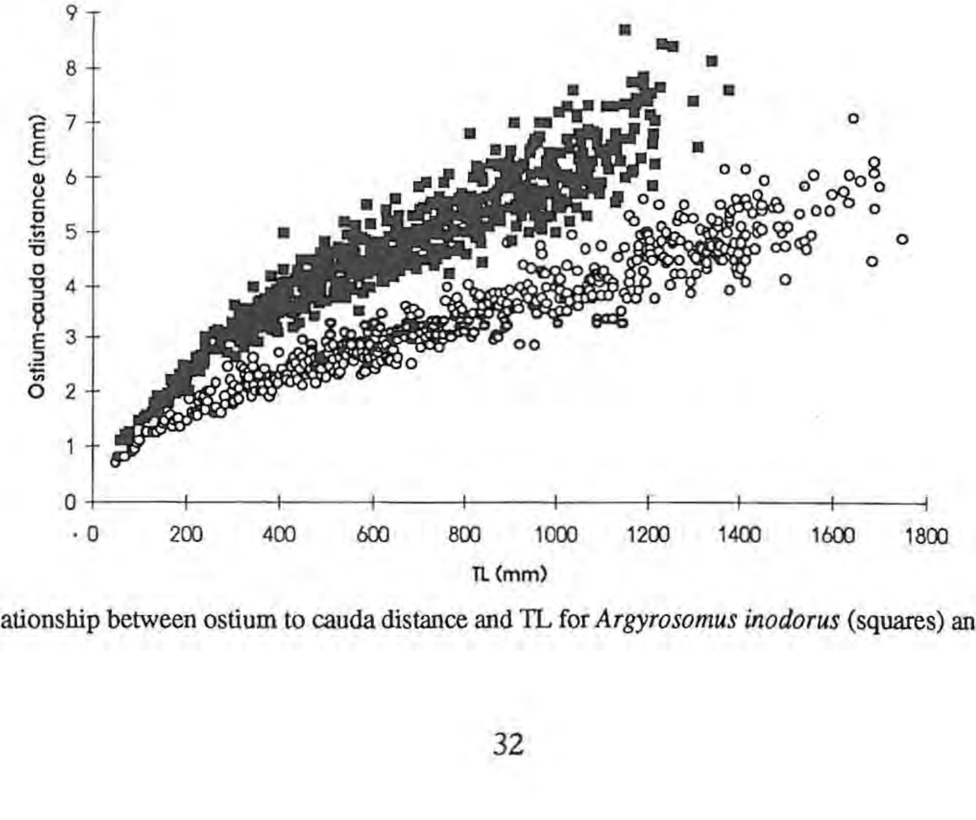


Figure 31. Relationship between ostium to cauda distance and TL for *Argyrosomus inodorus* (squares) and *A. japonicus* (circles).

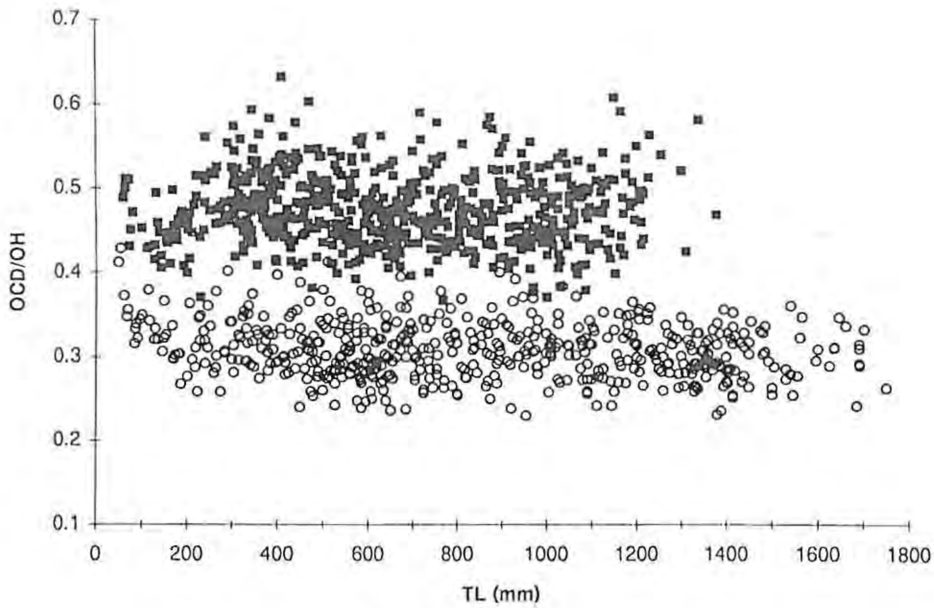


Figure 32. Relationship between OCD (ostium to cauda distance) as a ratio of OH (otolith height) and TL for *Argyrosomus inodorus* (squares) and *A. japonicus* (circles).

were inadvertently referring to *A. inodorus* (in part or in full).

DISTRIBUTION: *A. inodorus* occurs from Namibia southwards around the Cape of Good Hope and northwards at least as far as the Kei River (Fig. 7). In the area between the Kei River and Cape Agulhas, *A. inodorus* rarely enters estuaries or the surf zone, and is caught mostly by skiboat fishermen and trawlers at depths of 10-100 metres (Table 7). However, as one rounds Cape Agulhas and enters the cooler waters of the west coast, the species becomes more abundant in the surf zone. The proportion of *A. inodorus* in *Argyrosomus* catches declines in northern Namibia, where water temperatures are higher, and the species is not known in Angola.

FISHERIES: *A. inodorus* is highly regarded as a table fish (mostly sold fresh, but sometimes frozen) and it is an important commercial and recreational species wherever it is found. The majority of the South African catch is made between the Cape of Good Hope and the Kei River. Commercial line-fishermen operating from vessels of between 5 and 15 m in length, catch an average of 835 tons per annum (1988-1992). Although no statistics are available for recreational boat fishermen, their catches are expected to be of a similar magnitude. The South African trawl fishery is responsible for an average by-catch of 217 tons per annum, and Western Cape shore angling and beach seine catches are estimated at 26 and 4 tons respectively (Lamberth et al. 1994).

In Namibia *A. inodorus* is most abundant north of Meob (200 km south of Walvis Bay). Line-boat fishermen catch an average (1989/93) of 413 tons per annum (unpublished data, Namibian Ministry of Sea Fisheries), and shore anglers land in excess of 40 000 fish (approx. 130 tons) a year (Lenssen et al. 1991). Namibian *A. inodorus* are restricted to a narrow coastal band of 1-20 m, apparently as a result of an anoxic zone which extends beyond this depth (Hart & Curry, 1960; Boyd, 1983; Bailey et al., 1985).

BIOLOGY: In South Africa *A. inodorus* attains 50% sexual maturity at 31 cm TL (males) and 34 cm TL (females), with spawning activity observed throughout its distribution, from the Cape of Good Hope to the Kei River Mouth, during spring/summer (Griffiths & Hecht, 1993 [species B]). Nursery grounds consist of soft-bottom bay areas at depths less than 50 m (Wallace et al., 1984; Smale & Badenhorst, 1991; as "*A. hololepidotus*"). Maximum size recorded was 145 cm TL (36.3 kg). Common to 115 cm TL (15 kg).

Argyrosomus coronus sp. nov.

(Fig. 35)

Sciaena aquila (*non* Lacepède): Poll, 1954: 234 Fig. 71, Pl. II, Figs 2, 6 & 7 (Atlantic Ocean off Angola).

Argyrosomus hololepidotus (*non* Lacepède): Trewavas, 1977: 327 (in part not figs); Chao & Trewavas, 1981: SCIAEN Argyr 3. Bianchi et al. 1993: 164 (in part).

Holotype: RUSI 48468, female, 430 mm SL, northern Namibia, 4 km south of Hoarusib River, surf zone, collected by M.H. Griffiths, 15 March 1995.

Paratypes: 18 specimens (147-595 mm). ANGOLA. IISNB 9723 (J 202 mm, J 220 mm); IISNB 9724 (F 523 mm); IISNB 9725(J 147 mm). NORTHERN NAMIBIA. RUSI 48458 (F 408 mm); RUSI 48459 (F 385 mm); RUSI 48460 (F 440 mm); RUSI 48461 (M 408 mm); RUSI 48462 (F 408 mm); RUSI 48463 (M 424 mm); RUSI 48464 (M 361 mm); RUSI 48465 (F 365 mm); RUSI 48466 (M 595 mm); RUSI 48467 (M 471 mm); RUSI 48469 (F 355 mm); RUSI 48470 (M 281 mm); RUSI 48471 (M 312 mm); RUSI 48472 (M 370 mm); RUSI 48473 (M 495 mm, skeleton).

DIAGNOSIS: A species of *Argyrosomus* with the following combination of characters: dorsal fin rays 26-30; gillrakers 4-5 + 8-10; swim-bladder carrot shaped, with 28-38 arborescent appendages; caudal peduncle length 10-12% SL; peduncle depth 76-94% peduncle length; interorbital width 7.5-8.3% SL (24-27% HL); suborbital width 8.2-10.2% HL; lower jaw length 46-50% HL; midlateral body scale length 2.2-2.7% SL; drumming muscles present in both sexes; urinary bladders large; sagitta typically *Argyrosomus* (Fig. 11), OCD 26-34% OH; pectoral fins 18-21% SL, not reaching past vertical at tip of pelvic fins; pectoral fin axillary fold scaleless; peritoneum unpigmented; anterior part of lateral line slightly curved.

DESCRIPTION: Based on 19 preserved (147-595 mm), 7 fresh specimens (486-598 mm), one skeleton (495 mm) and 107 otolith pairs (281-1110 mm). Counts and measurements for the holotype are in parentheses.

Dorsal fin X+I,26-30 (27); anal fin II,7; pectoral-fin rays 16-18 (18); lateral-line scales 50-53 (51); gill-rakers 4-5 + 8-10; swim-bladder appendages 28-38; vertebrae 11 + 14.

Proportions as % SL: head length 31-32 (31); pre-dorsal length 33-36 (35); pre-pelvic length 33-36 (34); body depth 25-28 (27); caudal peduncle length 10-12 (12); peduncle depth 8.6-10 (10); snout 8.4-9.3 (9.2); eye diameter 6.7 at 147 mm, 5.2-6.0 at 202-281 mm, 4.7-5.0 at 312-385 mm, 4.2-4.7 (4.5) at 408-471 mm and 3.8-4.4 at 523-595 mm SL; interorbital width 7.5-8.3 (8.2); suborbital width 2.6-3.2 (2.9); upper jaw 12-14 (13); lower jaw 15-16 (15); pectoral fin 18-21 (20); pelvic fin 21 at 147 mm, 19-20 at 202-281 mm, 17-18 at 312-385 mm, 16-18 (17) at 408-471 mm and 15-18 at 523-595 mm SL; anal fin length 18 at 147 mm, 15-17 at 202-281 mm, 15-16 at 312-385 mm, 14-15 (15) at 408-471 mm and 13-14 at 523-595 mm SL; third dorsal spine 13-15 at 202-281 mm, 11-13 at 312-385 mm, 11-13 (13) at 408-471 mm and 11 at 595 mm SL; second anal spine 9.7 at 147 mm, 7.5-8.7 at 202-281 mm, 6.4-8.3 at 312-385 mm, 6.8-8.3 (7.2) at 408-471 mm and 5 at 595 mm SL; gill-raker 1.6-2.3; gill-filament 3.0-3.8.

Proportions as % HL: snout 27-31 (30); eye diameter 22 at 147 mm, 17-19 at 202-281 mm, 15-16 at 312-385 mm, 14-15 (14) at 408-471 mm and 14 at 523-595 mm SL; interorbital width 24-27 (27); suborbital width 8.2-10.4 (9.2); upper jaw 38-43 (43); lower jaw 46-50 (49); gill-raker 5.0-7.4; gill-filament 9.9-12.1.

Proportions as % eye diameter: gill-raker 31-53; gill-filament 56 at 147 mm, 60-62 at 202-281 mm, 65-73 at 312-385 mm, 67-78 at 408-471 mm and 83 at 523-595 mm SL.

Dorsal profile of *A. coronus* includes a hump or "shoulder" behind the head. Pectoral fins not reaching past vertical at tip of pelvic fins (for fish 147-595 mm). Nostrils as for *A. japonicus*. Caudal fin mostly S-shaped (281-595 mm), but sometimes wedge shaped, bi-concave or rounded. Lateral line evenly curved, axillary skin fold at base of pectoral fin scaleless.

Scales cycloid below eye, but ctenoid on body (including belly and chest), nape of neck, interorbital region, and operculum. Gill-rakers at angle shorter than outer gill-filaments at angle (281-593 mm). Drumming muscles well developed in both sexes. Pyloric caeca 8-10. Urinary bladders large, as in *A. japonicus*.

Swim-bladder (Fig. 36) carrot shaped with 28-38 appendages, each proximally divided into two limbs. The

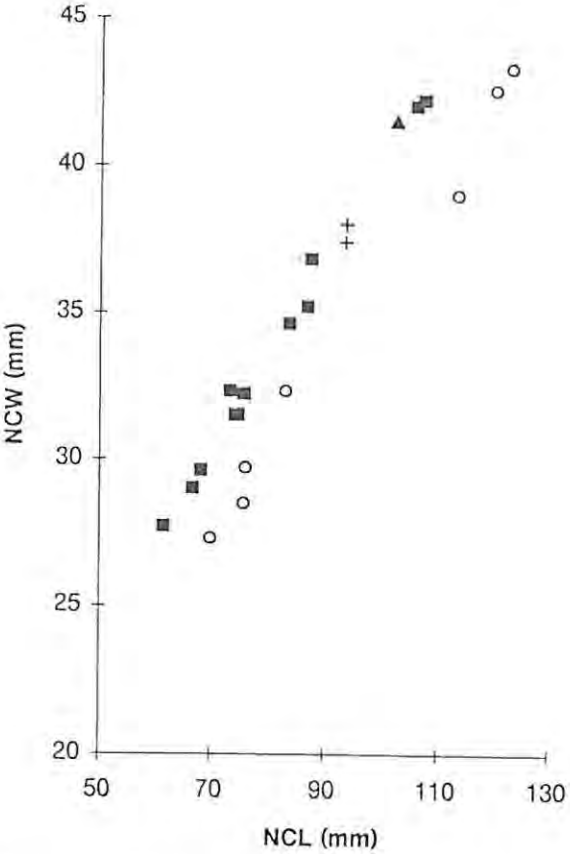


Figure 33. Relationship between NCW (neurocranial width) and NCL (neurocranial length) for *Argyrosomus inodorus* (squares), *A. japonicus* (circles), *A. coronus* (triangles) and *A. thorpei* (crosses).

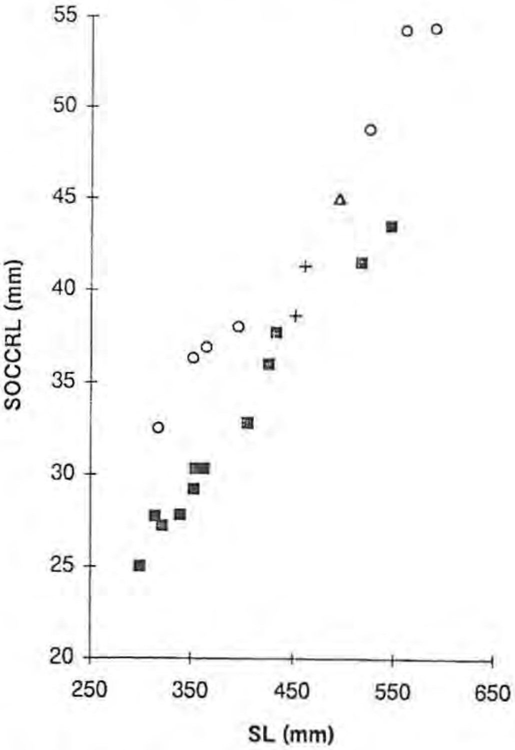


Figure 34. Relationship between SOCCRL (supraoccipital crest length) and SL for *Argyrosomus inodorus* (squares), *A. japonicus* (circles), *A. coronus* (triangles) and *A. thorpei* (crosses).

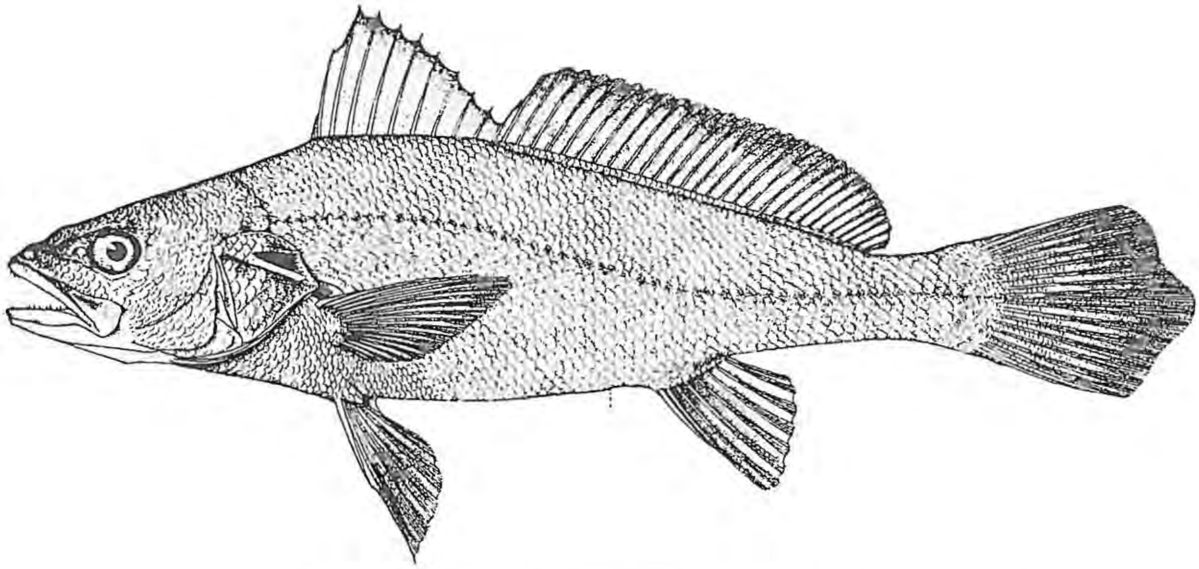


Figure 35. *Argyrosomus coronus* sp. nov., 368 mm TL, Angola (after Poll, 1954).

ventral limb is orientated lateroanteriorly, rather than ventroanteriorly and the branches arising from it project laterally and at no stage lie against the bladder. The dorsal limb is orientated dorsoposteriorly, but along the posterior three quarters of the bladder it curves through 150° so that the tip points anteriorly. The branches on this limb project posteriorly to dorsally and lie against the swim-bladder. In specimens with large quantities of appendage fat, the lateroanterior limb is orientated more ventroanteriorly and the branches arising from both limbs project at 90° to the bladder. The last 0-3 appendages bud-like and the 1-3 proceeding these weakly branched. Disproportionately enlarged appendages were not observed in any *A. coronus* (147-595 mm) examined by us.

Otoliths (Fig. 10): Description as for *A. japonicus*, but cauda more strongly curved (less angular) and posterior margin of cauda more rounded; OCD 26-34% OH.

Neurocranium (Figs 4 & 5) and skeleton: Length of neurocranium (NCL) 21% SL; pre-supraoccipital crest length 11% SL and 52% NCL; supraoccipital crest length 9.1% SL and 44% NCL (495 mm); neurocranial width 8.4% SL and 41% NCL. Interorbital septum relatively well ossified with frontal fused with medial ethmoid and parasphenoid bones. Premaxilla 7.7% SL and 37% NCL; dentary 9.2% SL and 44% NCL. Third and fourth neural spines 8.9 and 8.3% SL.

Colour: In life, silvery grey/brown becoming darker above and lighter below; dorsal surface with a bluish bronze sheen that may become coppery on head. Some individuals darker brown than others; fins dark grey/brown; mouth lining yellow, some with a touch of grey; inside of operculum yellow and dark grey. Axillary fold of pectoral fin grey to black, generally with an irregular coppery-bronze patch.

Preserved specimens vary, usually grey, darker above and lighter below. Dark patches on scales may give appearance of oblique stripes. Fins grey, sometimes with one or two longitudinal stripes on dorsal fin.

COMPARISONS (Tables 2-6): *A. coronus* generally has a more pointed head (resulting from a less convex snout, Fig.

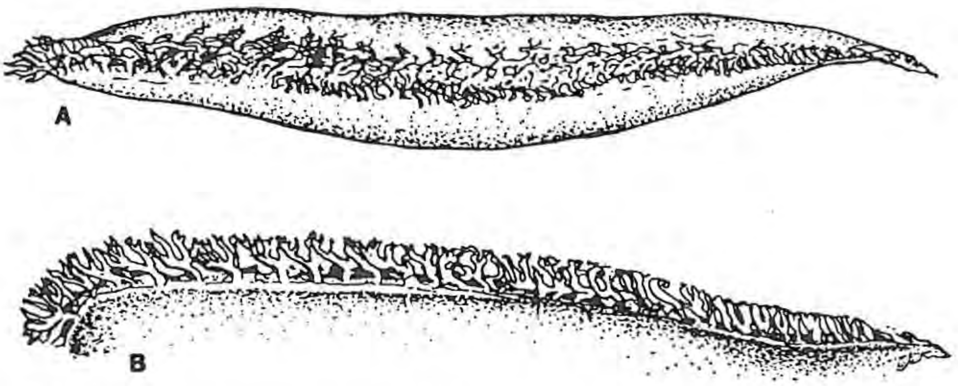


Figure 36. Swim-bladder of *Argyrosomus coronus*, 360 mm SL: A) lateral view and B) ventral (left half) views.

35) than the other species described in this paper, including *A. regius* (Figs 9, 12, 19 & 21).

A. coronus differs from *A. regius* in having a higher modal number of lower limb gill-rakers; a slightly longer lower jaw; longer midlateral scales (Fig. 37); a shorter and deeper caudal peduncle (Fig. 38); fewer arborescent swim-bladder appendages, in which the lower limb is orientated latero-anteriorly (vs ventro-anteriorly) with branches that project at 90° to the bladder (vs project posteriorly and lie against the bladder). The otoliths of *A. coronus* are more elongate (Figs 10 & 39) than those of *A. regius*; the cauda is more curved, with a more rounded posterior margin (Fig. 40); and the curvature of the posterior margin of the ostium is more acute.

Differences between *A. coronus* and *A. japonicus* include a lower modal number of upper gill-rakers, a higher modal number of pectoral fin rays, a wider interorbital (Fig. 18), shorter lower jaw; a wider neurocranium (Fig. 33), with wider lateral line canals on the dorsal surface (Fig. 5); and a shorter pre-maxilla (7.7% vs 8.1-8.8% SL) and dentary (9.2% vs 9.3-10.1% SL). *A. coronus* also has more arborescent swim-bladder appendages, and in the posterior half of the bladder the lower limbs are orientated anterolaterally (vs anteroventrally) with branches projecting at 90° to the bladder (vs projecting posteriorly and lying against the bladder, Figs 13, 14 & 36). The saggitta of *A. coronus* has a more strongly curved cauda, which is less angular, and has a more acutely rounded posterior margin (Figs 10 & 15). Fresh specimens of *A. coronus* also lack the strong metallic odour of South African *A. japonicus*.

A. coronus differs from *A. hololepidotus* in having a wider interorbital (Fig. 18), a narrower suborbital, and a shorter and deeper caudal peduncle. The saggitta of *A. coronus* (Fig. 10) has a more strongly curved cauda, which is less angular, and has a more rounded posterior margin than that of *A. hololepidotus* (Fig. 15).

Differences between *A. coronus* and *A. thorpei* include fewer lower limb gill-rakers, a higher modal number of pectoral fin rays and swim-bladder appendages, a wider interorbital, a narrower suborbital, a naked (vs scaled) pectoral axillary fold, a shorter caudal peduncle, shorter midlateral body scales, and a slight (vs strong) anterior curve of the lateral line. The sagitta of *A. coronus* is not expanded in the anterior two-thirds, it has a more acute posterodorsal angle, a cauda which is neither expanded in the distal portion nor truncated at the tip, and a shorter OCD (Figs 11 & 15).

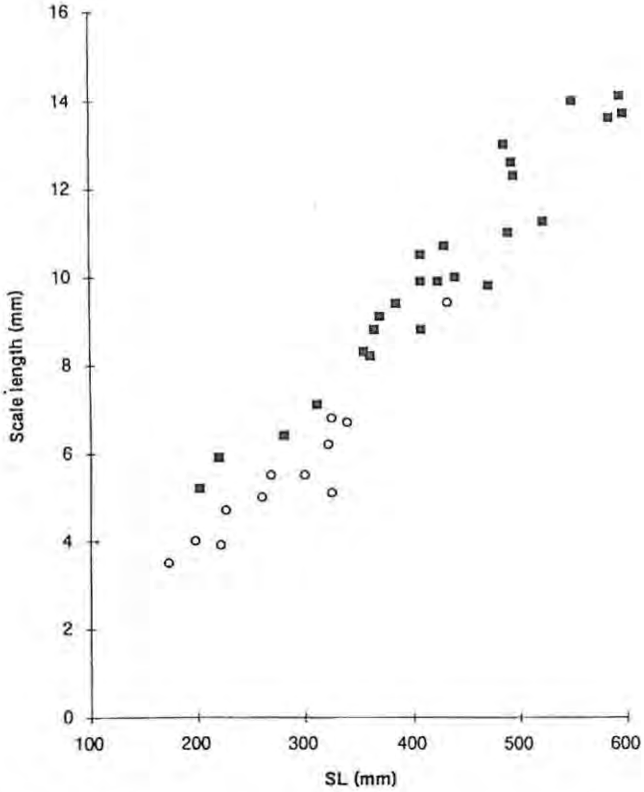


Figure 37. Relationship between scale length and SL for *Argyrosomus regius* (circles) and *A. coronus* (squares).

A. coronus differs from *A. inodorus* in having lower modal numbers of upper and lower gill-rakers, a lower modal number of swim-bladder appendages, a wider interorbital (Fig. 41 and Table 2), a shorter and deeper caudal peduncle (Fig. 42 and Table 2), a smaller orbital diameter

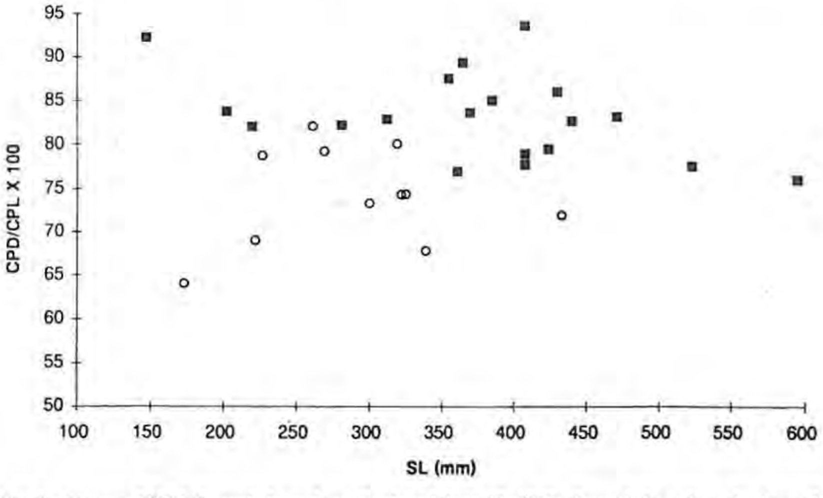


Figure 38. Relationship between CPD (caudal peduncle depth) as % CPL (caudal peduncle length) and SL for *Argyrosomus regius* (circles) and *A. coronus* (squares).

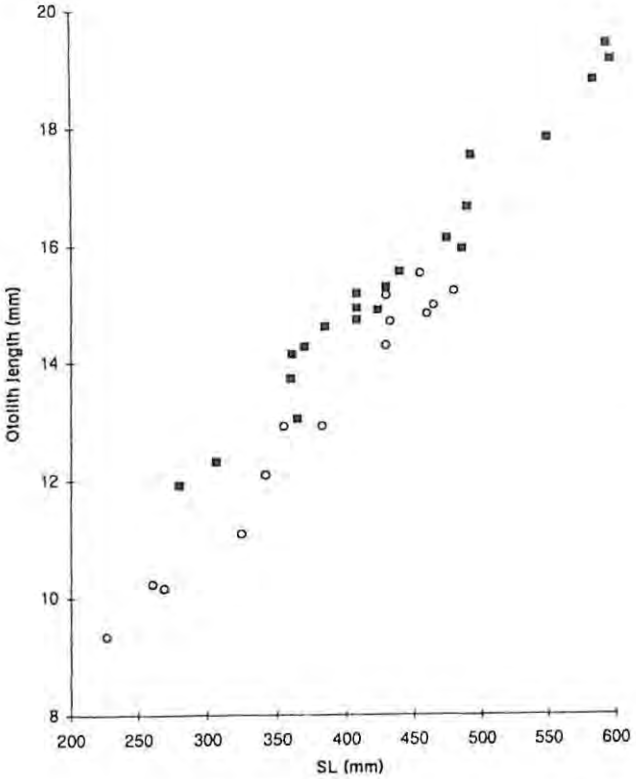


Figure 39. Relationship between otolith length and SL for *Argyrosomus regius* (circles) and *A. coronus* (squares).

(Fig. 43), larger urinary bladders, drumming muscles in both sexes (vs in males only), a longer supraoccipital crest (Fig. 34 and Table 2), a smaller interorbital window (frontal and parasphenoid bones connected, Fig. 4) and shorter premaxilla (7.7 vs 8.1-9.1% SL) and dentary (9.2 vs 9.3-10.2% SL). The sagitta of *A. coronus* (Fig. 10) has a more acute posterodorsal angle, a smaller OCD (Fig. 44), a lower OCD:OH ratio (Fig. 45), a straight (vs rounded) posterior margin, and it lacks the prominent bulge found on the ventral margin in *A. inodorus* (Fig. 15). *A. coronus* is generally darker and more brown in colour (body) than *A. inodorus*, and the fins are dark grey/brown (vs yellow/grey).

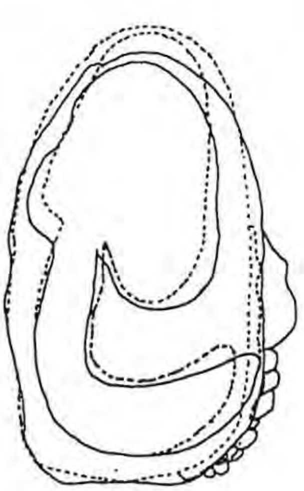


Figure 40. Superimposed sagittae of *Argyrosomus regius*, 516 mm TL (solid line) and *A. coronus*, 512 mm TL, (broken line).

A. coronus was also compared with data and illustrations of *A. amoyensis* (from Trewavas, 1977; Mohan, 1984 and the original description of *Nibea miichthioides* Chu et al., 1963). *A. coronus* differs in having 8-11 (vs 8) lower gill-rakers, interorbital width 24-27% HL (vs 19% HL). The swim-bladder of *A. amoyensis* is spindle shaped (tapering anteriorly and posteriorly), there are only 22-29 appendages (vs 28-38), and they are not obviously divided into dorsal and ventral limbs. The sagitta of *A. coronus* (Fig. 10) is similar to that of *A. amoyensis* (Trewavas, 1977: Fig. 9b; Chu et al., 1963: Fig. 82), but it is slightly more elongate, has a more strongly curved (less angular) cauda, and lacks the protuberance found on the posterodorsal corner in *A. amoyensis*.

A. coronus differs from *A. beccus* Sasaki (1994) in having swim-bladder appendages 28-38 (vs 23); longer snout (8.4-9.3% vs 6.1-6.3% SL), snout convex (concave in *A. beccus*); eye diameter 5.2-6.7% SL (vs 7.3-8.3% SL, for fish of comparable size); wider interorbital 7.5-8.3% SL (vs 4.7% SL), and pelvic fin length 19-21% SL (vs 22-23% SL, for fish of comparable length). The sagitta of *A. coronus* (Fig. 10) is distinguished from that of *A. beccus* (Sasaki, 1994: Fig. 2B); in that it is more elongate, with a longer ostium, a more strongly curved cauda, and the postcentral umbo on the lateral surface of the otolith is less than 50% of the otolith length (about 75% in *A. beccus*).

Based on descriptions of *A. heinii* by Steindachner (1907) and Mohan (1984), *A. coronus* can be distinguished by dorsal-fin rays 26-30 (vs 32-33) and an S-shaped (vs emarginate) caudal fin in medium sized fish.

Based on the description of *A. miiuy* by Trewavas (1977), *A. coronus* has snout length 27-31% HL (vs 22-24% HL), interorbital width 24-27% HL (vs 19-21% HL), upper jaw length 38-43% HL (vs 44-46% HL) and lower jaw length 46-50% HL (vs 53-55% HL). The swim-bladder appendages are much longer in *A. miiuy*, and at about 27 cm SL, almost completely enwrap the bladder (Trewavas, 1977). The caudal fin is also more elongate in *A. miiuy* than in *A. coronus*, and at 305 mm SL is pointed (Chu et al., 1963) as opposed to S-shaped. Comparisons of the sagitta of *A. coronus* (Fig. 10) and *A. miiuy* (Chu et al., 1963: Fig. 90; Schwarzhans, 1993: Figs 239-240) reveal that the otolith of *A. miiuy* is more slender, with concave or straight (vs straight or convex) dorsal margin, sharply rounded or pointed (vs straight) posterior margin, posterodorsal corner more obtuse, cauda less curved, and the postcentral umbo on the lateral surface of the otolith about 65% of the otolith length (less than 50% in *A. coronus*).

ETYMOLOGY: This species is named *Argyrosomus coronus* in honour of Corona Griffiths, wife of the first author, in appreciation of her contributions to the illustrations of this paper and her help with field work. The specific name is treated as a noun in apposition.

REMARKS: Although morphometric differences between *A. coronus* and *A. regius* are subtle, and possibly would not justify species recognition, we have placed much weight on swim-bladder appendage counts, and on differences in otolith morphology for the following reasons: Swim-bladders of *A. regius* specimens from the Mediterranean, French

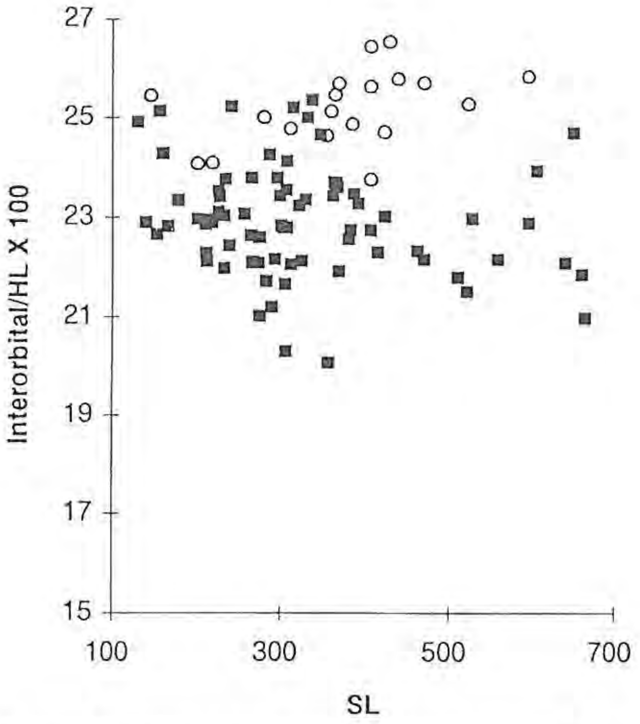


Figure 41. Relationship between interorbital width as % HL and SL for *Argyrosomus coronus* (circles) and *A. inodorus* (squares).

Atlantic and north Africa provided no evidence for a cline in appendage counts. Counts of *A. coronus* specimens from Namibia and Angola were also similar. In addition the numbers of appendages of other *Argyrosomus* species were found to be consistent over wide distributional ranges e.g. *A. japonicus* from South Africa, Australia and Japan; and *A. inodorus* from the eastern seaboard of South Africa and from central Namibia. Differences in the morphology of the otoliths of specimens from the northern and southern hemispheres were also regarded as important because these structures often do not differ between recognized *Argyrosomus* species e.g. *A. regius*, *A. japonicus* and *A. hololepidotus*.

The recognition of *A. coronus* as a separate species also assists with species identification in Namibia. This species has a shorter and deeper caudal peduncle and a lower number of swim-bladder appendages than *A. regius*, and together with interorbital width is therefore more easily separated from *A. inodorus*.

DISTRIBUTION: Known from Namibia and Angola. It becomes more abundant in *Argyrosomus* catches as one moves northwards (Table 7) indicating that it prefers warmer waters. Found in estuaries, the surf zone and further offshore. Reports of "*A. hololepidotus*" from the west coast of Africa, south of the equator (Trewavas, 1977; Mohan, 1984; Heemstra, 1986), are probably based on specimens of *A. coronus*.

FISHERIES: In Namibia *A. coronus* is caught by commercial and recreational fishermen in fairly low numbers. Areas further north are closed to the public. In southern Angola it is caught with hand lines, gillnets, trapnets and occasionally purse seines; mostly in depths of 20-40 m, but also in the surf zone and in depths to 100 m (B.Bennett pers comm).

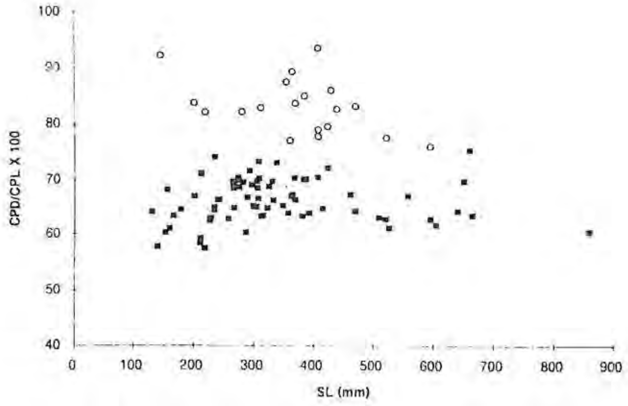


Figure 42. Relationship between CPD (caudal peduncle depth) as % CPL (caudal peduncle length) and SL for *Argyrosomus coronus* (circles) and *A. inodorus* (squares).

BIOLOGY: The biology of this species has not been studied. Personnel of the Namibian Ministry of Sea Fisheries found fish up to 13 kg to be immature, suggesting a large size at maturity, similar to that of *A. japonicus* and *A. regius*. Adults are rarely found in Namibia but according to Bruce Bennett (pers comm) are abundant in southern Angola (common to 50 kg). Maximum size 77 kg. The lack of permanent estuaries in southern Angola suggests that this habitat type does not play an important role in the life history of *A. coronus*.

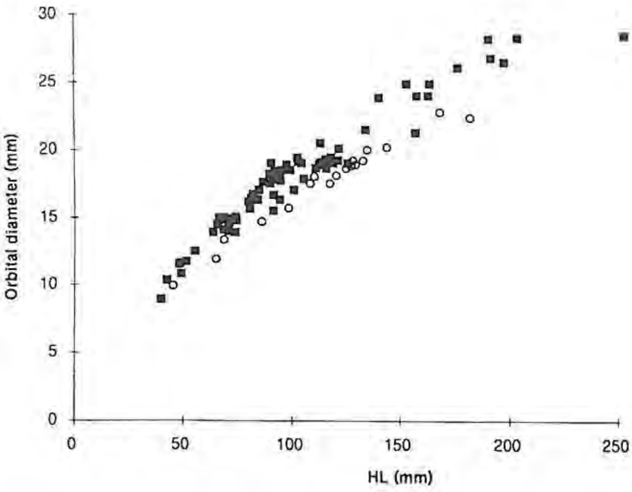


Figure 43. Relationship between orbital diameter and HL for *Argyrosomus coronus* (circles) and *A. inodorus* (squares).

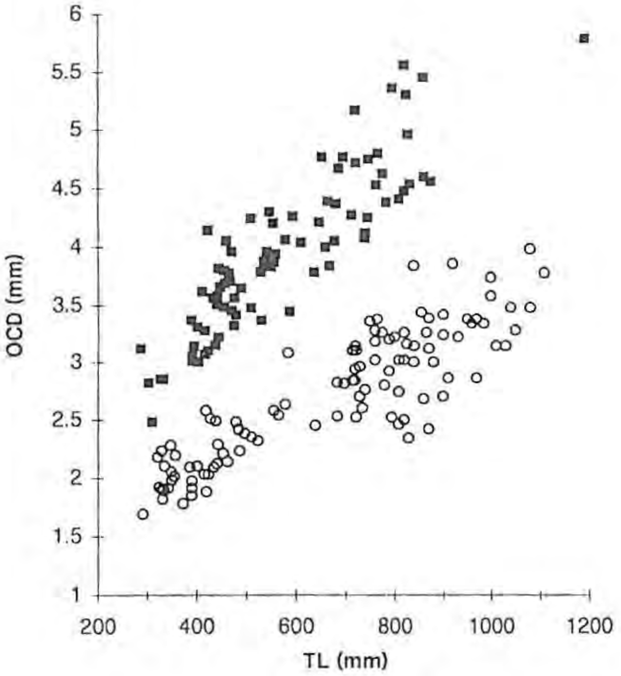


Figure 44. Relationship between OCD (ostium to cauda distance) and TL for *Argyrosomus coronus* (circles) and Namibian *A. inodorus* (squares)

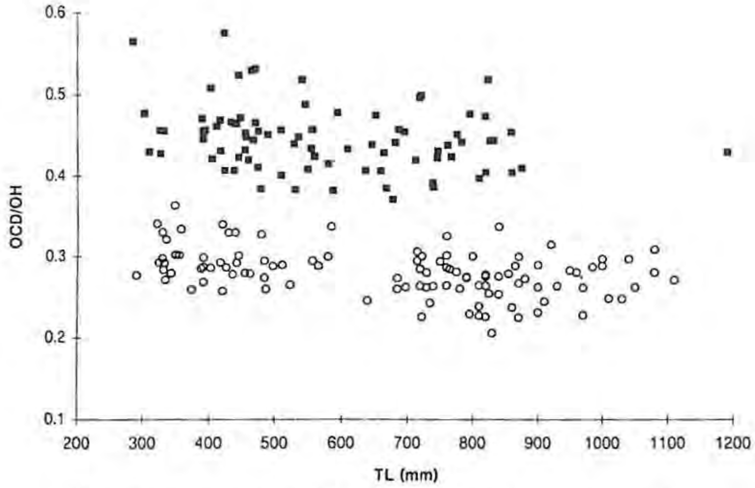


Figure 45. Relationship between OCD (ostium to cauda distance) as a ratio of OH (otolith height) and TL for *Argyrosomus coronus* (circles) and Namibian *A. inodorus* (squares).

Table 1. Regression equations for data from *Argyrosomus japonicus* (J) and *A. inodorus* (I) from South African waters for weight/total length (W/TL), otolith dimension/TL, and standard length/total length (SL/TL) relationships. OL = otolith length, OH = otolith height, OC = ostium to cauda distance and OW = otolith weight. The asterisk (*) denotes a significant difference ($P < 0.01$) between the slopes and/or intercepts of the corresponding relationships, after log - transformation.

	Relationship	r	n	Range (TL)	F-ratio	P
J	$W(g) = 8.391X10^{-6}TL(mm)^{3.025}$	0.999	1215	37-1750 mm	29.6	<0.0001*
I	$W(g) = 6.832X10^{-6}TL(mm)^{3.055}$	0.997	3146	60-1378 mm		
J	$OL(mm) = TL(mm)^{0.706}/5.678$	0.995	543	37-1750 mm	1238.3	<0.0001*
I	$OL(mm) = TL(mm)^{0.699}/4.691$	0.993	623	60-1310 mm		
J	$OH(mm) = TL(mm)^{0.630}/5.931$	0.989	542	37-1750 mm	19.0	<0.0001*
I	$OH(mm) = TL(mm)^{0.603}/4.932$	0.990	623	60-1310 mm		
J	$OC(mm) = TL(mm)^{0.589}/14.821$	0.969	539	50-1750 mm	3251.2	<0.0001*
I	$OC(mm) = TL(mm)^{0.607}/10.717$	0.972	616	60-1310 mm		
J	$OW(g) = TL(mm)^{2.008}/479004$	0.989	542	37-1750 mm	138.6	<0.0001*
I	$OW(g) = TL(mm)^{1.896}/195344$	0.989	623	60-1310 mm		
J	$SL = 0.877\ TL - 10.882$	0.999	167	35-1790 mm	-	-
I	$SL = 0.886\ TL - 14.882$	0.999	408	140-970 mm	-	-

Table 2. Diagnostic characters of *Argyrosomus* species. CPD = caudal peduncle depth, CPL = caudal peduncle length, F = female, M = male, OCD = ostium-cauda distance, OH = otolith height, *Argyr.* = as for *A. regius*.

	hololepidotus	*inodorus*	*japonicus*	*regius*	*coronus*	*thorpei*
Gill-rakers (lower limb)	9	10-12	9-11	8-10	8-10	10-11
Swim-bladder appendages	34-36	32-41	21-31	36-45	28-38	25-33
Interorbital width (%HL)	22-23	20-25	21-24	24-29	24-27	20-21
Suborbital width (%HL)	10.5-12	8.6-10.9	8.4-10.5	8.5-11	8.2-10.2	10-11.5
Lower jaw length (%HL)	50	46-51	48-52	44-48	46-50	49-53
CPD as %CPL	75-77	58-74	70-92	68-82	76-94	65-79
CPL as %SL	12-13	12-15	11-13	11-13	11-12	12-14
Pectoral fin length (%SL)	17-18	19-23	17-21	18-21	17-21	20-23
Midlateral body scale length (%SL)	2.5-2.8	1.8-2.5	2.4-3.1	1.8-2.3	2.2-2.7	2.6-3.3
Supraoccipital crest length (%SL)	-	8.0-8.8	9.2-10.2	-	9.1	-
Urinary bladder length (%TL)	large	0.1-3.3	2.0-9.6	large	large	large
OCD as %OH	28-34	37-63	23-41	26-32		34-44
Otolith morphology	*Argyr.*	distinct	*Argyr.*	*Argyr.*	*Argyr.*	distinct
Anterior curve of lateral line	slight	slight	slight	slight	slight	strong
Pectoral fin axillary fold	scaleless	scaleless	scaleless	scaleless	scaleless	scaly
Drumming muscles	M & F	M only	M & F	M & F	M & F	M & F

Table 3. Frequency distributions for swim-bladder appendage counts in *Argyrosomus hololepidotus* (H), *A. inodorus* (I), *A. japonicus* (J), *A. coronus* (C), *A. regius* (R), and *A. thorpei* (T).

			Swim-bladder appendages																								
	n	x	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45
H	3	35														1	1	1									
I	77	35.8											1	3	9	9	15	8	10	7	7	4	3	2			
J	63	26.3	1	2	6	6	12	5	15	5	4	6	1														
C	24	31.9								3	4	2	1	4	4	2	1	1	1	1							
R	23	39.3																3	4	2	1	5	3	2	1	1	1
T	18	29.4					1	1		3	3	4	4	2													

Table 4. Frequency distributions for meristic characters in *Argyrosomus hololepidotus* (H), *A. inodorus* (I), *A. japonicus* (J), *A. coronus* (C), *A. regius* (R) and *A. thorpei* (T)..

	Upper Gill-rakers					
	n	x	3	4	5	6
H	3	4.7		1	2	
I	76	5.2		1	59	16
J	66	4.6		24	42	
C	25	4.1		23	2	
R	17	4.3	1	10	6	
T	18	5.1		1	15	2

	Lower Gill-rakers						
	n	x	8	9	10	11	12
H	3	9		3			
I	76	11			17	48	11
J	66	9.9		11	51	13	
C	25	9.5	1	11	12	1	
R	19	9.1	1	16	2		
T	18	11.1			1	15	2

	Pectoral fin-rays					
	n	x	15	16	17	18
H	2	16.5		1	1	
I	393	16.5	11	193	185	4
J	68	16.1	3	50	12	
C	23	16.7	1	5	16	1
R	19	16.9		5	11	3
T	18	16	3	12	3	

	Dorsal fin-rays							
	n	x	25	26	27	28	29	30
H	3	27.3			2	1		
I	381	27.1	10	85	160	99	26	1
J	61	26.7	4	28	23	12	2	
C	24	27.2		5	12	5	1	1
R	18	27.6	1	1	6	6	3	1
T	18	27.1		3	11	3	1	

Table 5. ANOVA: Multiple range tests of meristic characters that show significant differences (P < 0.0001). Mean values increase from left to right; * indicates a significant difference at the 1% level and # a difference at the 5% level. *Argyrosomus inodorus* (I), *A. japonicus* (J), *A. regius* (R), and *A. thorpei* (T).

Character	Species
Pectoral fin-rays	T J * I # R
Gill-rakers (upper)	R * J * T I
Gill-rakers (lower)	R * J * I T
Swim-bladder appendages	J * T * I * R

Table 6. ANOVA: Multiple range tests of arc-sine transformed morphometric ratios that show significant differences (P < 0.0001). Mean values increase from left to right; * signifies a difference significant at the 1% level and # a difference at the 5% level. *Argyrosomus inodorus* (I), *A. japonicus* (J), *A. regius* (R), and *A. thorpei* (T).

Character	Species
Suborbital width	J * I R * T
Interorbital width	J T I * R
Pre-dorsal length	I * T J R
Body depth	I R * J # T
Caudal peduncle length	J # R * T I
Caudal peduncle depth	I R * T J
Scale height	R * I * J * T
Scale length	R I * J T
Gill-raker length	R J I * T

Table 7. The distribution of South African *Argyrosomus* species, based on relative contributions (% by number) to catches made in four habitat types of 10 regions (see Fig. 7 for regional boundaries). *A. inodorus* (I), *A. japonicus* (J), *A. coronus* (C), *A. thorpei* (T).

	Estuary	Surf zone	Nearshore reef	Nearshore sand/mud
S. Mozambique	-	-	99.8%T:0.2%J (n=1021)	-
N. Natal	100%J (n=45)	35%T:65%J (n=32)	95%T:5%J (n=557955)	100%T (n=832)
S. Natal	100%J (n=13)	100%J (n=36)	85%T:15%J (n=87456)	-
Transkei	100%J (n=410)	100%J (n=16)	-	-
E. Cape	100%J (n=670)	98%J:2%I (n=590)	1.3%J:98.7%I (n=2629)	100%I (n=1050)
S. Cape	100%J (n=168)	100%J (n=58)	1.5%J:98.5%I (n=22128)	100%I (n=1473)
S.W. Cape	Rare	3.3%J:96.7%I (n=333)	100%I (n=558)	100%I (n=33)
W.Cape	Rare	100%I (n=9)	100%I (n=42)	Rare
S. Namibia	no estuaries	100%I (n=229)	-	-
C. Namibia	no estuaries	93%I:7%C (n=740)	100%I (n=225)	100%I (n=52)
N. Namibia	no estuaries	50%I:50%C (n=408)	100%I (n=220)	-
S. Angola	-	100%C (n=30)	100%C (n=10)	100%C (n=6)

Table 8. Arcsine-transformed morphometric ratios for *A. inodorus* and *A. japonicus* that showed significant difference (ANOVA) only when analysed according to size class. 1 = 100-199 (n = 7+10), 2 = 200-299 (n = 28+13), 3 = 300-399 (n = 21+13), 4 = 400-499 (n = 6+11), 5 = 500-599 (n = 4+5) * = 5% level ($p<0.05$), ** = 1% level ($p<0.01$). Size class ranges are of mm SL.

Character	Size classes (100mm)				
	1	2	3	4	5
Eye diameter	*	**	**	*	*
Pectoral fin length			**	*	*
Anal fin length		**	**	*	

CHAPTER 3

AGE AND GROWTH OF DUSKY KOB, *ARGYROSOMUS JAPONICUS*, WITH COMMENTS ON STOCK SEPARATION IN SOUTH AFRICAN WATERS

AGE AND GROWTH OF DUSKY KOB *ARGYROSOMUS JAPONICUS*, WITH COMMENTS ON STOCK SEPARATION IN SOUTH AFRICAN WATERS

ABSTRACT

The ages of dusky kob *Argyrosomus japonicus*, sampled from three regions along the South African eastern seaboard during 1991 and 1992, were determined from longitudinal sections of otoliths. The otoliths were selected from fish 35 - 1750 mm total length. Ages from 0 to 42 years were recorded, but fish older than 27 were rare. Analysis of otolith margins indicated that a single opaque and a single translucent zone were being deposited annually. The first annulus was validated by analysis of daily increments. Observed lengths-at-age were highly variable. The fitted generalized von Bertalanffy growth equations were:

$$L_t = 1\,473[1-e^{-0{,}228(t+2{,}620)}]^{2{,}468} \text{ for females,}$$
$$L_t = 1\,372[1-e^{-0{,}260(t+4{,}282)}]^{4{,}619} \text{ for males.}$$

Growth was faster in females, but in both sexes it slowed down after an age of 8 years. The relationships between otolith dimensions (length, height, mass and ostium to cauda distance) and fish length, in each of three regions, suggested that South African juvenile *A. japonicus* exist as three or more allopatric populations.

INTRODUCTION

The dusky kob *Argyrosomus japonicus* has a wide distribution, occurring in both northern and southern hemispheres. It is found on the east coast of southern Africa from Cape Point to Mozambique (Griffiths & Heemstra 1995), along the southern seaboard of Australia from North West Cape to the Burnette River (Kailola et al. 1993, Starling 1993), and from Hong Kong northwards along the Chinese coast to southern Korea and Japan (Trewavas 1977). Until recently it was misidentified as *A. hololepidotus* in both southern Africa and Australia, and in South Africa was also confused with a sympatric congeneric species, *A. inodorus* (Griffiths & Heemstra 1995).

In South Africa *A. japonicus* is an important commercial and recreational linefish, which is abundant from Cape Agulhas to northern KwaZulu/Natal (Griffiths & Heemstra 1995). Information on its growth rate and the existence of discrete stocks is essential to understanding its life history, for stock assessment and also for improved management advice. Wallace & Schleyer (1979) modelled the growth of *A. japonicus* from the otoliths of 148 specimens gill-netted in the estuaries of KwaZulu/Natal. Based predominantly on young fish (only seven fish older than 7 years), their derived growth function incompletely described the growth of the species. In this paper the growth of *A. japonicus* is described on the basis of data from fish ranging in age from 1 to 42 years. Samples were obtained from localities throughout its range of distribution in South African waters.

Otolith shape has proved to be a useful indicator of stock identity in fish. The otoliths of fish from different areas are generally compared on the basis of linear measurements of definable structures (Messieh 1972, Rojo 1977, King 1985, Payne 1985, Grygiel 1987, Japp 1990, Dawson 1991, Smith 1992), or on the basis of mathematical descriptions of shape, particularly Fourier series (Bird et al. 1986, Castonguay et al. 1991, Smith 1992, Campana & Casselman 1993). The possibility of more than one stock of dusky kob existing along the South African east coast was investigated by comparing the relationships between fish length and four otolith measurements, for fish obtained from three different regions.

MATERIAL AND METHODS

The South African east coast was subdivided into four regions for sampling purposes (Fig. 3.1). Saggital otoliths were collected, and total fish length (nearest mm) and fish mass were recorded from male and female dusky kob caught by recreational and commercial linefishers operating in estuaries, in the surf zone and nearshore (beyond the surf to 100 m deep) in KwaZulu/Natal, the South-Eastern Cape and the Southern Cape during 1991 and 1992. No fish were sampled in the Transkei. Fish <350 mm TL were collected from estuaries using seine-nets. Mass was measured to the nearest gramme (< 500 g), to the nearest 20 g (500 g - 5 kg), to the nearest 100 g (5 - 25 kg), or to the nearest 200 g (>25 kg). The otoliths were removed ventrally by first removing the gillrakers and then cutting away a portion of bone in the pro-otic/exoccipital region. They were lifted out of the skull with forceps, cleaned and stored dry in envelopes.

Age determination

A total of 572 otolith pairs were used for age determination. These were selected so that, where possible, every 10 mm length class within the range of fish sampled (35-1750 mm TL) was represented by two pairs (one male and one female) from each region (Fig. 3.2). To avoid errors resulting from an insufficient number of older specimens (Hirschhorn 1974), the otoliths from

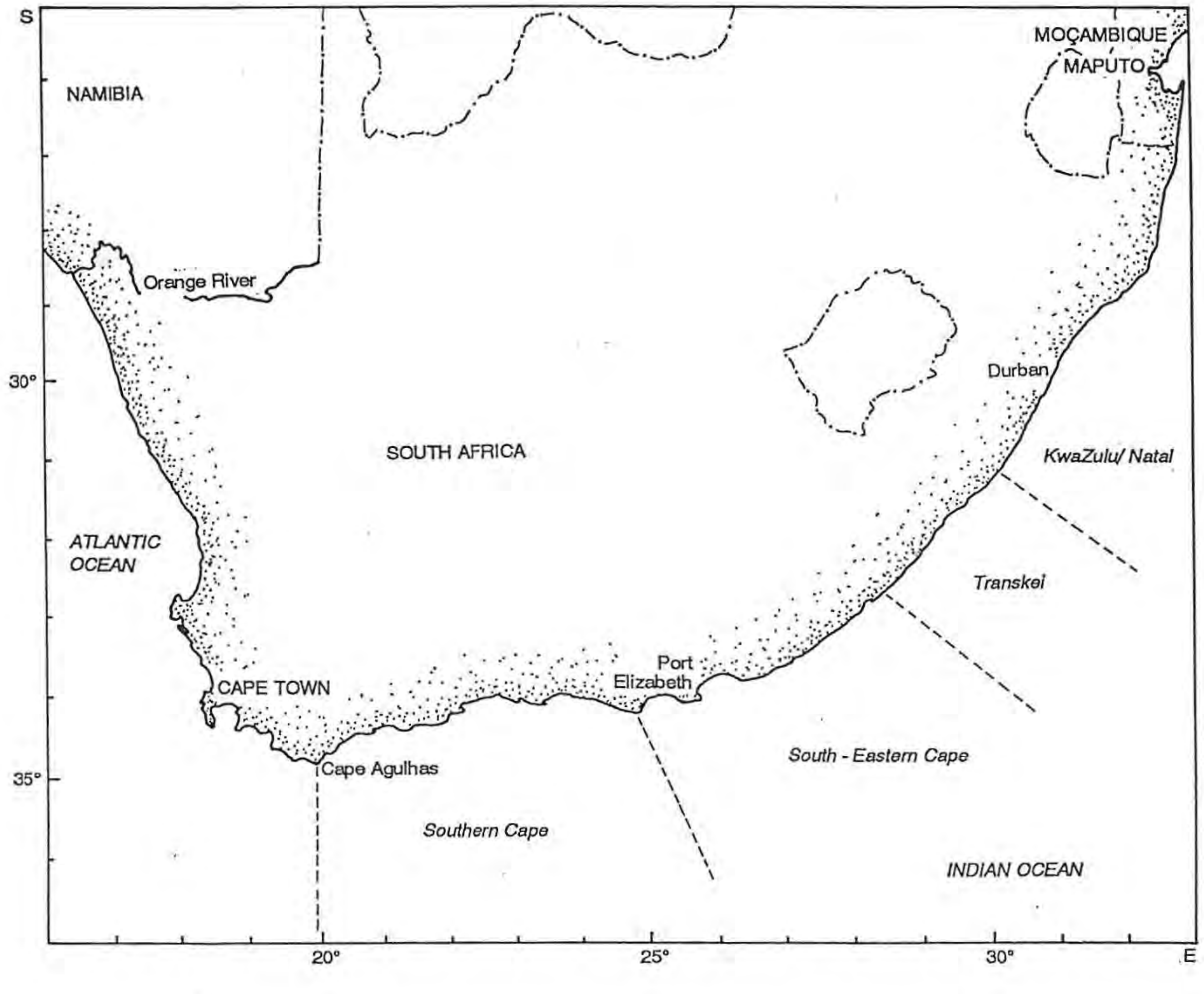


Fig. 3.1: Map of South Africa showing the three sampling regions.

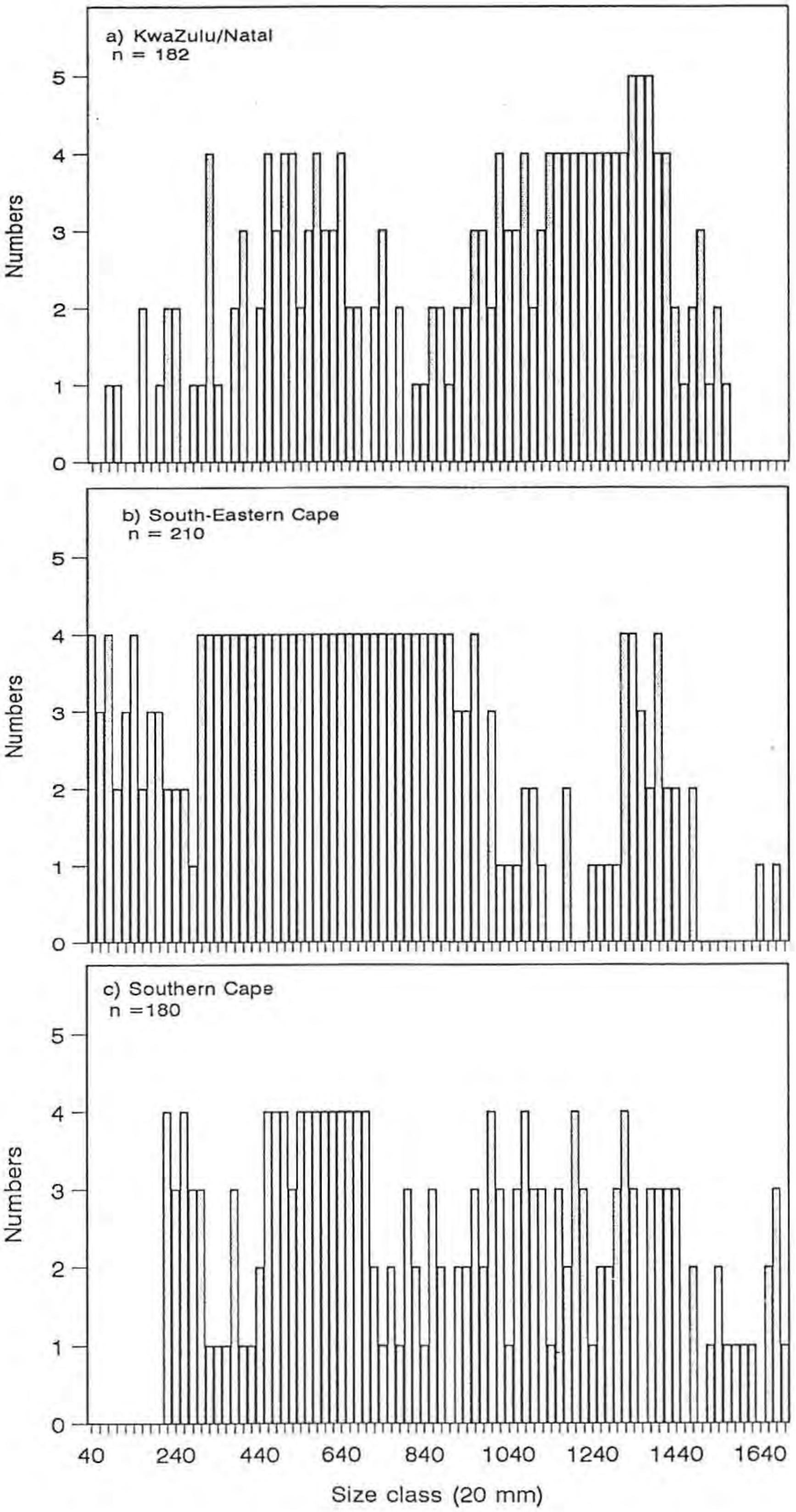


Fig. 3.2: Length frequency histograms of *A. japonicus* used for the growth analysis and the otolith dimension/fish length comparisons from a) KwaZulu/Natal, b) the South-Eastern Cape, c) the Southern Cape.

all fish >1300 mm TL were included in the analysis. Owing to the thickness and the overall opacity of dusky kob otoliths, they were all sectioned. Wallace and Schleyer (1979) showed that longitudinal sections of *A. japonicus* sagittae consisted of distinct opaque and translucent zones. Depending on otolith size, between two and six longitudinal sections (0,5-0,7 mm) were cut from each right otolith to ensure that the core was included. A single diamond-wafering blade was used, with a saw similar to that described by Rauck (1976). Each section was then mounted on a glass slide using DPX mountant and examined on a black background under a dissecting microscope (6×) with reflected light.

The number of opaque (white) zones (Fig. 3.3) was enumerated three times, each on a different day, without any reference to fish size. If no readings coincided the otolith was rejected. The periodicity of growth zone deposition was determined by plotting the monthly percentages of otoliths with opaque margins. Due to the clarity of the growth zones of *A. japonicus* marginal increment analysis (see Capter 5) was not regarded as necessary. The first annulus was validated on the basis of daily increment counts. Seven otolith sections, each with one opaque zone, were mounted on SEM statives with colloidal silver. These were then polished with 0,05 μm alumina paste, etched for 5 minutes with 0,1% HCl, rinsed with water and cleaned using ultrasound. Finally, they were coated with gold-palladium (20 nm) and viewed under a scanning electron microscope at 4 500× magnification. The number of daily growth increments (Fig. 3.4a) between the primordium (Fig. 3.4b) and the medial margin (Fig. 3.3) of each otolith was counted.

Growth in length

The von Bertalanffy (1957), the generalized von Bertalanffy, the Richards and the Schnute growth models (Schnute 1981) were fitted to the length-at-age data (excluding 0-year-old fish) for males, females and sexes combined, using an iterative, non-linear minimization procedure (Butterworth et al. 1989, Punt & Hughes 1989). Minimization of the sum of squared absolute (as opposed to relative) differences was used, because the residuals for this method were homoscedastic for most models fitted. One-sample run tests (Draper & Smith 1966) showed that the residuals were not randomly distributed about the three-parameter von Bertalanffy (1957) function, using either the absolute or the relative error models. Likelihood ratio tests (Draper & Smith 1966) revealed that the four-parameter Schnute and generalized von Bertalanffy models best fitted the data.

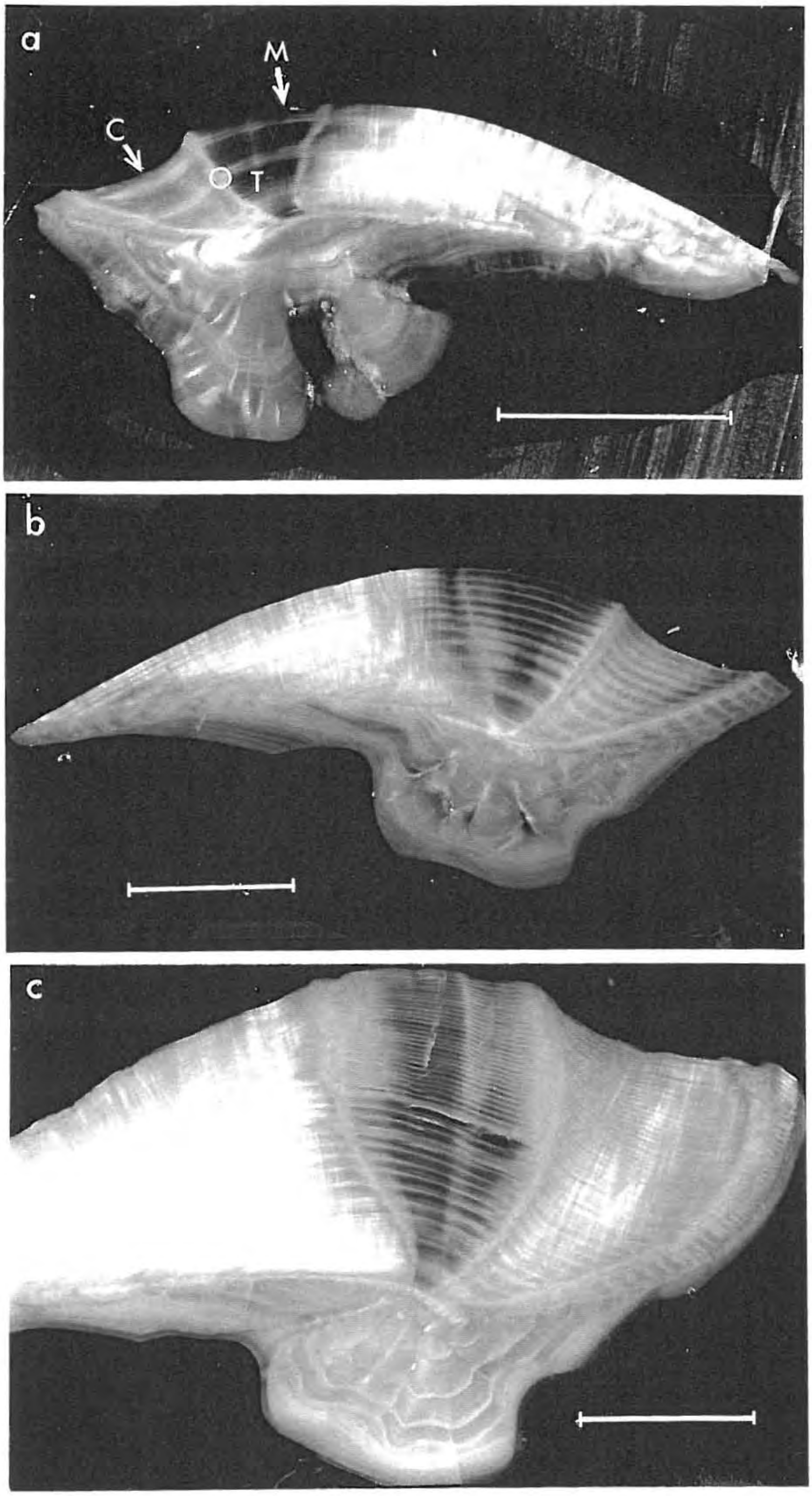


Fig. 3.3: Longitudinal otolith sections of a) 3-year-old, b) 11-year-old, c) 42-year-old *A. japonicus* from South Africa. O = opaque, T = translucent, M = medial margin, C = cauda (the tri-angular structure below the cauda is referred to as the window). Scale bar = 5 mm.

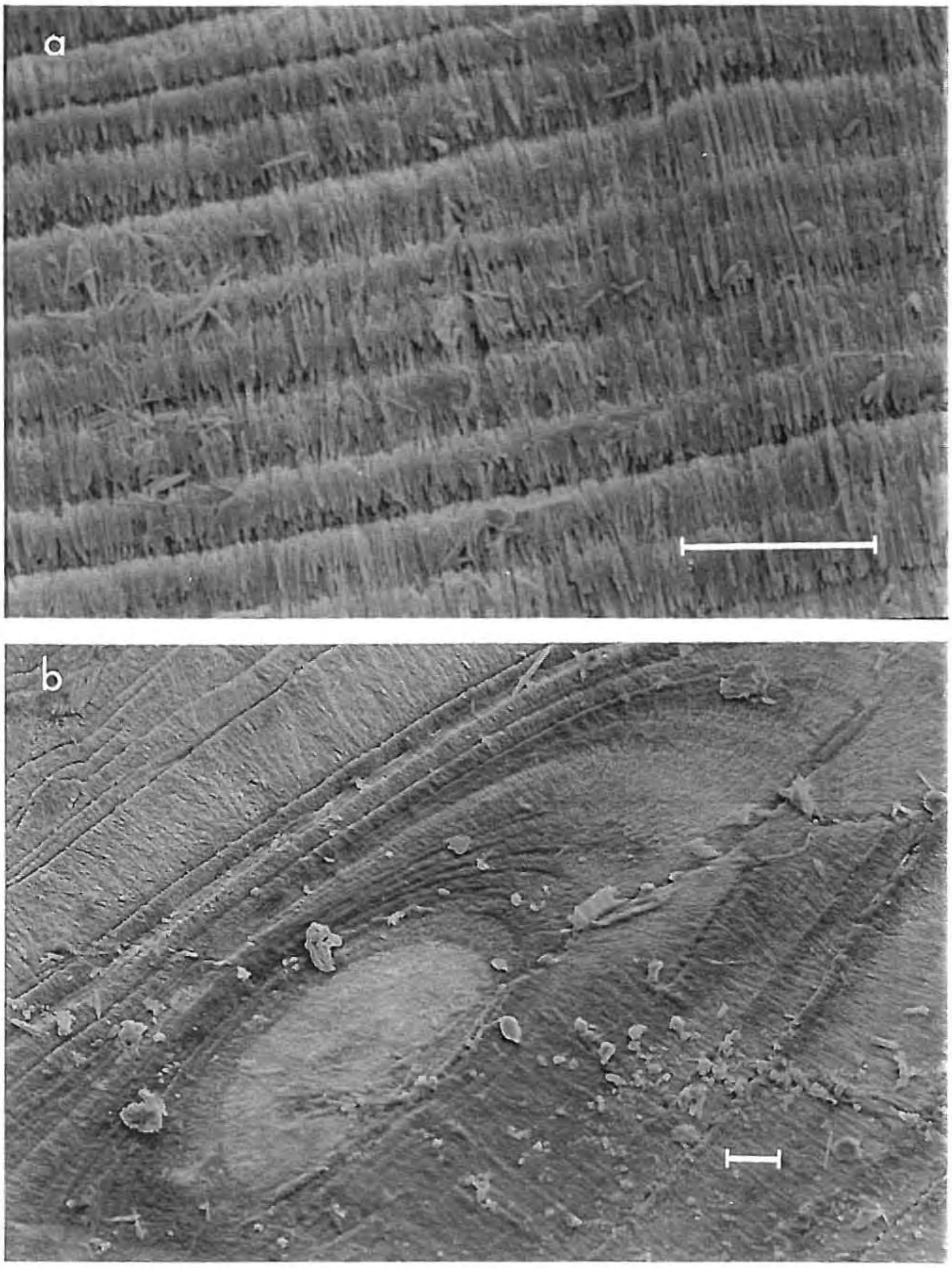


Fig. 3.4: Electronmicrograph of a) Daily growth increments and b) the primordium of a 490 day old *A. japonicus* otolith. Scale bar = 10 μm.

As there was little difference between the models, and because von Bertalanffy growth parameters can be directly incorporated into stock assessment models (Ricker 1975, Vaughan & Kanciruck 1982), for estimating natural mortality (Pauly 1980) and often used in comparing life history styles of fish (Beverton 1992), the data for the generalized form

$$L_t = L_\infty[1 - e^{-k(t-t0)}]^p$$

are presented in this paper. Standard errors and the 95% confidence intervals for each parameter of the model were calculated using a non-parametric bootstrap technique (Efron 1981) and the percentile method (500 bootstraps), respectively.

To allow for the conversion of total length-at-age to mass-at-age and standard length-at-age, the relationships between total fish length and both mass and standard length were also derived.

Fish length/otolith dimension relationships

The left otolith from every pair used for the growth analysis (Fig. 3.2) was measured for length (OL), height (OH), ostium-cauda distance (OCD, ±0,01 mm) and mass (OM, ± 0,0001 g) according to the methods of Griffiths & Heemstra (1995). The otolith dimensions and fish length (TL) data were log-transformed, the relationships modelled by means of linear regression, and the results compared between areas by testing for differences in slope and intercept using the F statistic (Draper & Smith 1966).

RESULTS AND DISCUSSION

Age and growth

Longitudinal sections of the saggital otoliths of *A. japonicus*, of all ages, show distinct opaque and translucent bands which can be used for age determination (Fig. 3.3). These were most visible in and around the "window" (beneath the cauda, Fig. 3.3). Only 13 otoliths (2,4%) were rejected on the basis of non-matching counts. One opaque zone is deposited annually in spring (Fig. 3.5), which is in agreement with the findings of Wallace & Schleyer (1979), and which

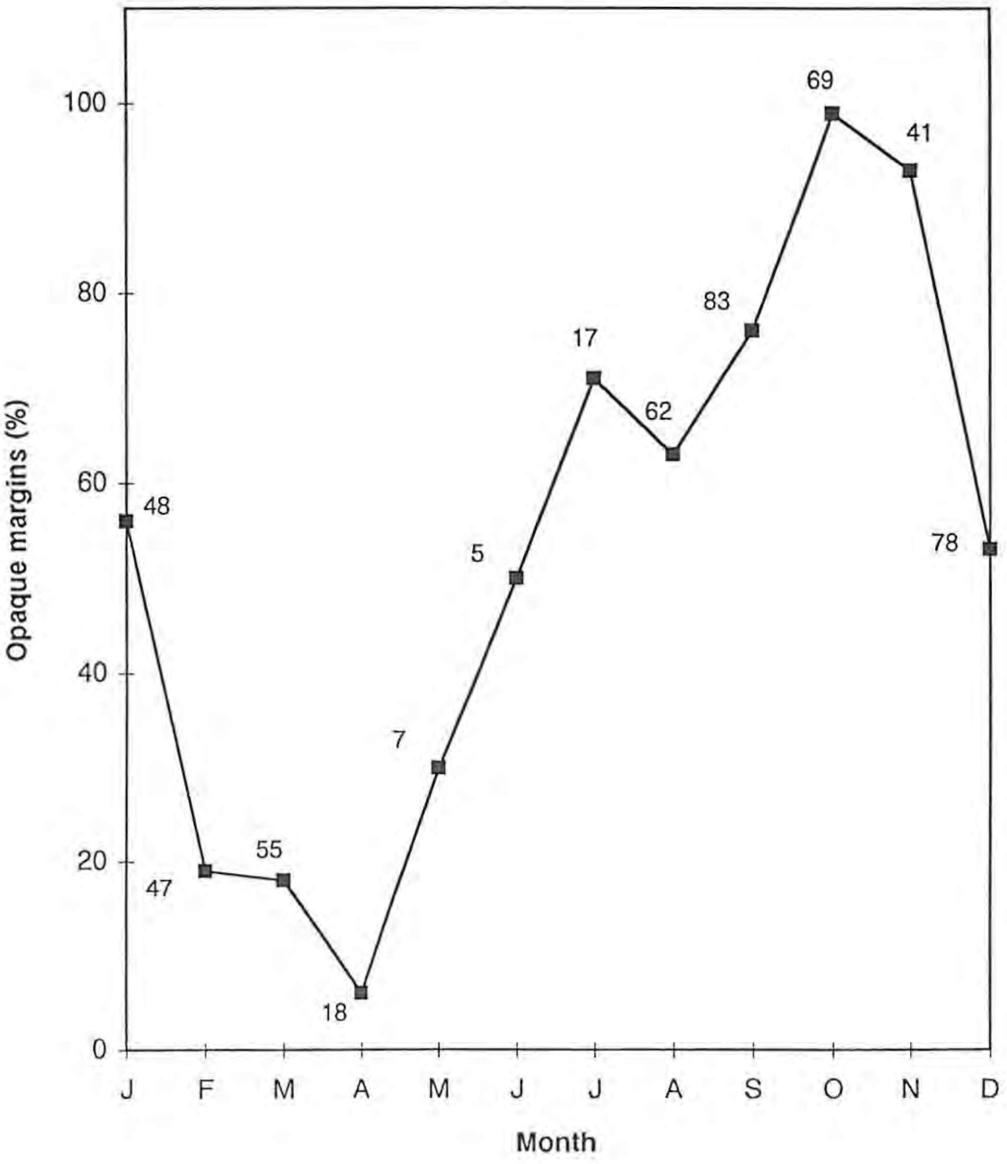


Fig. 3.5: Monthly frequency of *A. japonicus* otoliths (>0 years) with opaque margins. The numbers indicate the size of the sample.

coincides with the spawning season (see Chapter 4).

Between 380 and 540 daily growth increments were observed for otoliths with one opaque zone (i.e. >360 but substantially <720), confirming that this was the first annulus (Morales-Nin & Ralston 1990, Buxton & Lang 1993, Mug-Villanueva et al. 1994). Daily counts of > 360 can be attributed to the fact that some of the otoliths examined had hyaline margins (therefore slightly older than one year) and also to the fact that specimens may have been spawned early in the protracted (Chapter 4) spawning season. Since the initial discovery of daily growth increments in fish otoliths (Pannella 1971), they have been observed in at least 50 families (including the Sciaenidae) and in over 300 species (see Secor et al. 1992). Although periodicity of microincrement (Fig. 3.4) formation in *A. japonicus* was not validated, it was assumed to be daily because of the close similarity of these structures to the daily increments of other species (Morales-Nin & Ralston 1990, Lang & Buxton 1993, Mug-Villanueva et al. 1994), viewed using similar methods. The fact that dusky kob with one complete opaque zone (i.e. 1+ years) were aged from 1-1.5 years using microincrements, also supports this assumption (Geffen 1992).

Observed lengths varied greatly within age-groups (Fig. 3.6, Table 3.1), which is common for sciaenids, e.g. *Sciaenops ocellatus* (Beckman et al. 1989, Ross et al. 1995), *Micropogonias undulatus* (Barbieri et al. 1994a), *Pogonias cromis* (Beckman et al. 1990), *Cynoscion nebulosus* (Murphy & Taylor 1994) and *Cynoscion regalis* (Lowerre-Barbieri 1995). The dispersion of size at age in organisms with indeterminate growth is, theoretically, the result of the variability of growth parameters between individuals (Bowker 1995). Individual variation in growth parameters may be a result of genetic differences and/or the effects of the environment over the life-span of the individual (Kirkpatrick 1984). Increased dispersion of lengths at age after age 2, suggests that the high variation in lengths at age in *A. japonicus* is not a result of a protracted spawning season (generally resulting in higher dispersion in lower age groups)(Bowker 1995), but that it is due to differences in individual growth rate. Variation in length was reasonably constant over most ages for females. This dispersal pattern is common for long lived species and indicates individual differences in L_∞ (Bowker op cit.). It may therefore be assumed that female *A. japonicus* will grow to the maximum size that genetic and environmental constraints will allow. Male dusky kob, on the other hand, showed a decline in the dispersion of length with age (Fig. 3.6), suggesting growth compensation, i.e. the catching up in length of slow-growing or late-born individuals with fast-growing of early-born individuals towards the end of the lifespan (Ricker

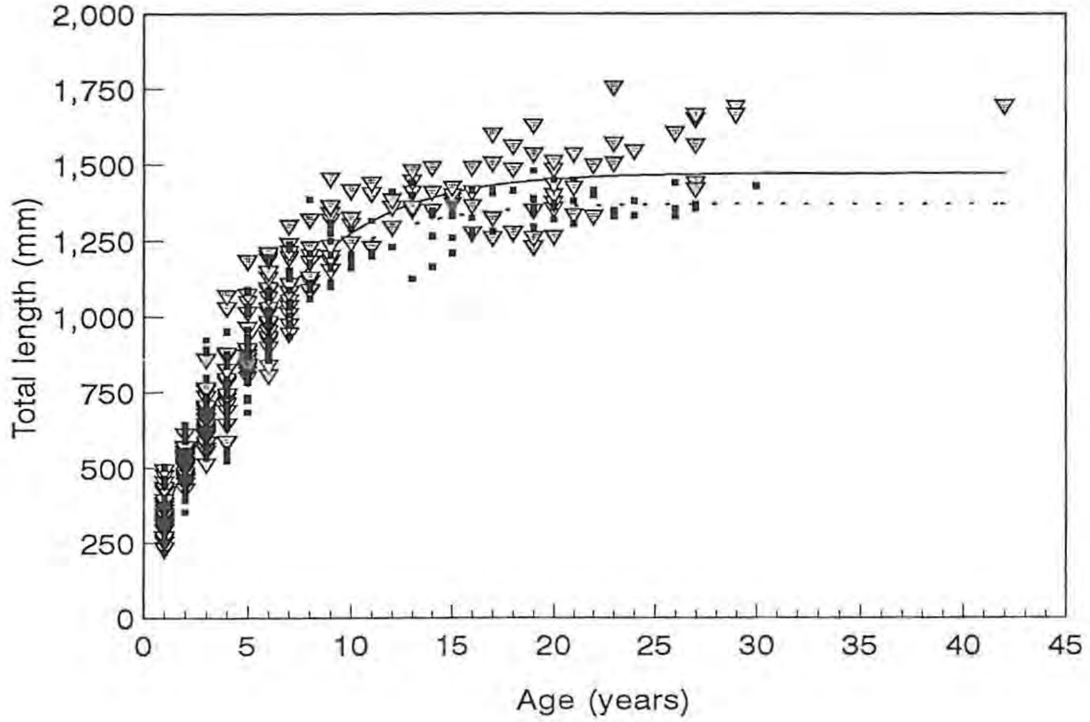


Fig. 3.6: Calculated von Bertalanffy (four-parameter) growth curves and observed lengths-at-age for male (squares and dotted line) and female (triangles and solid line) *A. japonicus* off South Africa.

Table 3.1: Age - length key for *A. japonicus* from South African waters (1991/2) in 50-mm intervals

Size class	Number of fish at age (yrs)																														
(mm)	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	36	42
200-249	5																															
250-299	13																															
300-349	20																															
350-399	14	1																														
400-449	9	6																														
450-499	6	15	4	1																												
500-549	2	18	6	3																												
550-599		7	17	4																												
600-649		5	23	4																												
650-699			17	4	1																											
700-749			6	11	2																											
750-799			2	12	2																											
800-849			1	5	8	2																										
850-899			3	5	7	5																										
900-949			1		3	8	2																									
950-999			1	3	2	8	5																									
1000-1049					4	8	7																									
1050-1099					3	7	7	5																								
1100-1149						3	6	3	3				1																			
1150-1199						2	3	3	5	3				2				1	1													
1200-1249						2	4	4	3	2	3	2			1				1													
1250-1299							1		2	1		1		1	1	3	2	2	2	1												
1300-1349								1	4	2	1		1	2	3	1	1		2	1	3	1	2	1		1						
1350-1399								1	2			2	1	1	3	1			3	5	1		1	1		1	2	1				
1400-1449										1	2	1	4	1	1	2	2	1		1	1	2				1	2			1		
1450-1499									1				1	1		1		1	1	2	1	1				1						
1500-1549											1						1		1	1	1		1	1			1					
1550-1599																	1	1					1				1					
1600-1649																			1							1	1					
1650-1699																											1		2		1	1
1700-1749																																
1750-1799																							1									

1979). Although phenomena such as von Bertalanffy buffering, sperm competition and size selective mortality ensure that the sizes of males remain similar to those of females in communal spawning fishes, there is a greater selective advantage for slightly larger females (fecundity allometrically related to fish length) than slightly larger males (Parker 1992, Roff 1992). It is therefore not surprising that female *A. japonicus* tended to be larger than males, and that individual L_∞ appeared to be more variable in females.

The four parameters of the generalized von Bertalanffy model are given in Table 3.2, with standard errors and the 95% confidence intervals for each parameter. A likelihood ratio test (Draper & Smith 1966) showed that the differences between male and female growth were highly significant ($F = 407,7$; $df = 4$ and 510; $p = 0,05$). Growth in both sexes was rapid for the first eight years, after which it slowed dramatically, but more so in males than in females (Fig. 3.6). Due to the large variation in lengths-at-age, the data sets of this study were regarded as being too small to test for differences in growth rate between regions; particularly if differences in growth rates between the sexes, and the wide range of ages over which the length data were distributed, are taken into account.

According to Roff (1983), faster female growth is a life history strategy in fish for increasing reproductive potential through increased egg production (discussed in terms of the life-history of *A. japonicus* in Chapter 7). Faster female growth has also been observed for the red drum, *Sciaenops ocellatus* (Beckman et al. 1989). The transition from fast to slow growth in *A. japonicus* apparently takes place when the fish attain sexual maturity. Maturity of all fish is attained at about 1100 mm TL in males and at 1200 mm TL in females (see Chapter 4). These lengths correspond to ages of 8 and 9 years respectively. Female *A. japonicus* did not appear to live longer than males. Excluding one female of 42 years and one male of 30, the remaining ages (up to 29) were evenly distributed among the sexes (Fig. 3.6). Although the oldest dusky kob aged in this study was 42 years, the paucity of fish >27 years in the sample may be the result of exploitation. According to Ricker (1963), populations which include appreciable numbers of fish older than 12 years prior to exploitation will be extremely sensitive to fishing. The growth of *A. japonicus* is discussed in terms of its general life-history in subsequent chapters.

The rate of growth modelled in this study was compared with that modelled by Wallace & Schleyer (1979). The fact that Wallace & Schleyer aged *A. japonicus* was confirmed by the examination of unsectioned otoliths. Owing to a truncated data range (only five fish >7 years and a maximum age of 12 years), the model of Wallace & Schleyer (1979) incompletely describes the growth of the dusky kob (Fig. 3.7). Nevertheless, the calculated lengths of fish from two to seven years of age are comparable. The substantially lower length at one year (220 mm TL) in the Wallace & Schleyer (1979) study (357 mm TL was the estimate in this study) can be attributed to the fact that, in the earlier study, t was 0,2 years (vs 1 year) and fish of 1.2-1.8 years were therefore not regarded as one year old. The smaller one-year-olds of the present study were also about 220 mm TL (Fig. 3.6, Table 3.1).

Table 3.2: Parameter estimates, Standard errors (*SE*) and the 95% confidence intervals (*CI*) for the generalized von Bertalanffy growth model fitted to length-at-age data for *A. japonicus* (0-year-olds omitted)

Parameter	Value			
	K	L_∞	t_0	p
Males (n = 262)				
Model	0,260	1 372,297	-4,282	4,619
SE	0,028	18,767	9,860	2 108,380
Left 95% *CI*	0,199	1 343,574	-30,572	1,251
Right 95% *CI*	0,30	1 403,604	-0,920	8 673,815
Females (n = 257)				
Model	0,228	1 472,865	-2,620	2,468
SE	0,049	39,909	7,510	1 312,944
Left 95% *CI*	0,112	1 435,260	-30,006	0,605
Right 95% *CI*	0,280	1 585,783	0,280	4 912,945
Both sexes (n = 519)				
Model	0,241	1 427,3	-3,194	3,067
SE	0,032	19,874	6,046	1 094,626
Left 95% *CI*	0,155	1 403,574	-26,651	0,806
Right 95% *CI*	0,276	1 486,934	-0,145	2 872,233

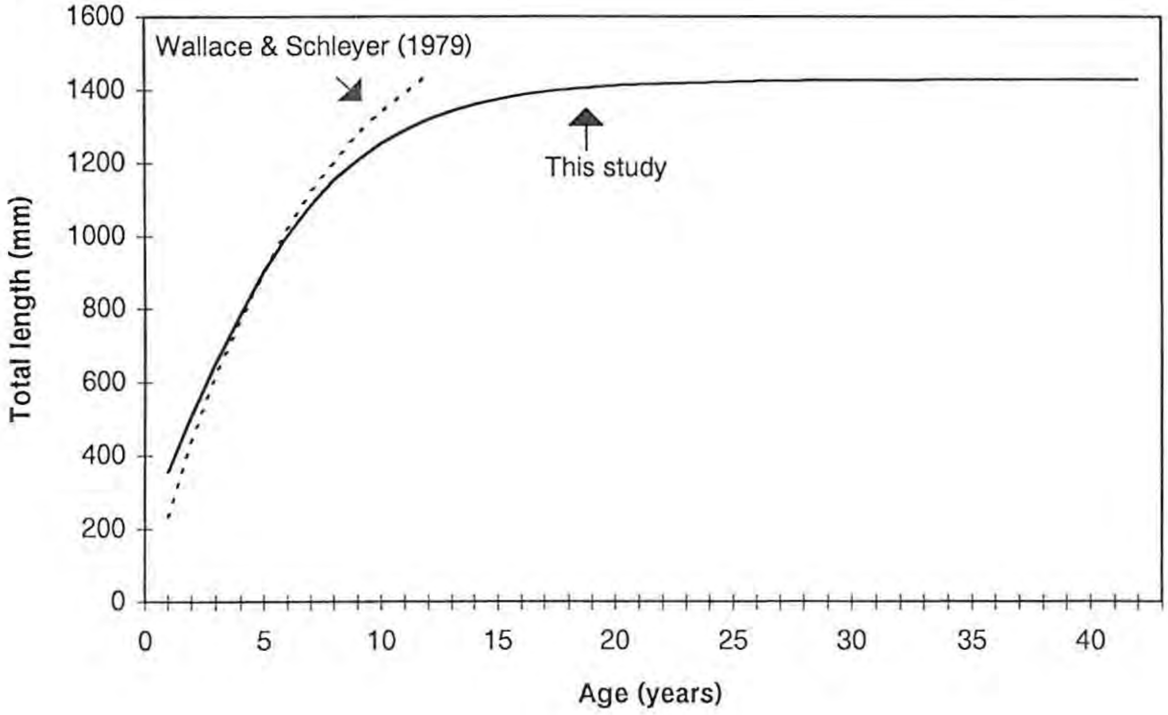


Fig. 3.7: Comparison of the growth curve calculated for *A. japonicus* in this study with that of Wallace and Schleyer (1979).

Morphometric relationships

The length/mass and total length/standard length relationships for South African *A. japonicus* are described in Figure 8. The power curve and straight line models respectively provided good fits to the observed data. Tests for difference in slope and intercept, after log-transformation (Draper & Smith 1966), showed that the length/mass relationships for males and females did not differ significantly.

Fish length/otolith dimension relationships

The relationships between otolith dimension and total length were significantly different between regions (Table 3.3), but not between sexes within regions ($p > 0,05$). The relationships between TL and both otolith length and otolith mass for each of the three regions are illustrated in Figure 9. As otolith shape is strongly influenced by environmental conditions (Campana & Casselman 1993), these results may not reflect genetic differences between regions. Analysis of commercial catch returns and tagging data indicates that juvenile dusky kob (<1100 mm TL) are fairly resident, remaining close to the estuaries into which they recruited as early juveniles (<150 mm TL), but that a large proportion of the adult population migrate from the Cape to KwaZulu/Natal to spawn (see Chapter 4). The otolith dimension/total length relationships and migratory information therefore collectively indicate that South African *A. japonicus* exist as a single stock consisting of one adult and several allopatric juvenile populations. Therefore while juvenile exploitation in one area would not affect catches in another, juvenile exploitation in all areas would impact on the adult population. Similarly, excessive exploitation of adults, particularly in KwaZulu/Natal, where they form easily targeted spawning aggregations (see Chapter 4), could reduce recruitment levels in all regions. It would therefore be wise for *A. japonicus* to be managed on a national basis as opposed to regionally.

In this chapter, the growth of South African *A. japonicus* is comprehensively described, and stock discrimination for this species is attempted for the first time. In later chapters the growth of dusky kob is discussed in terms of its life-history, as are the implications of its stock structure to management in the South African context.

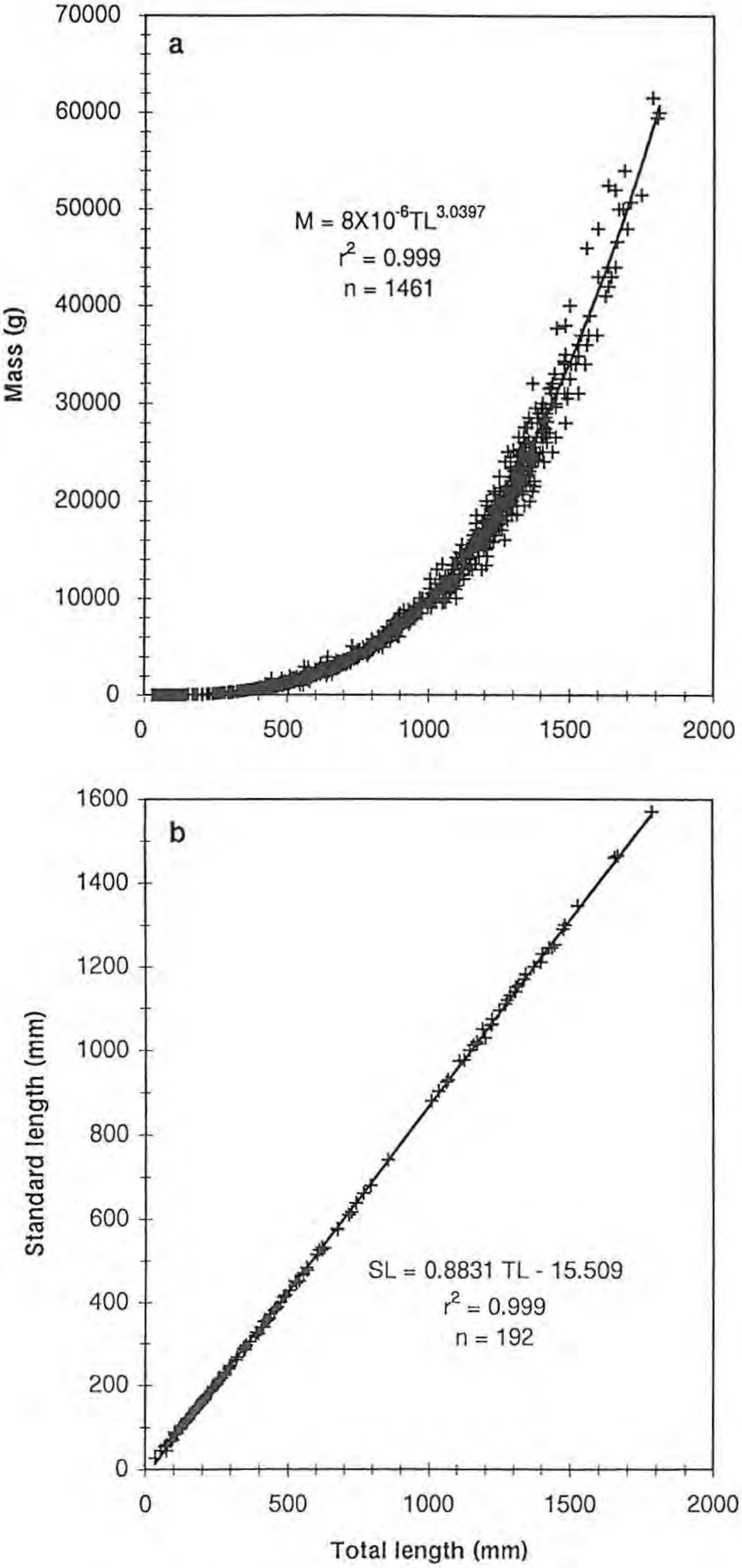


Fig. 3.8: Relationships between total length and a) mass, b) standard length for *A. japonicus* off South Africa.

Table 3.3: The relationships between otolith dimensions and total fish length (TL) for *A. japonicus* from KwaZulu/Natal (KN), the South-Eastern Cape (SEC) and the Southern Cape (SC). The relationships for each region were statistically compared (differences in slope and intercept) after straight line regressions were fitted to the log-transformed data

Region	Relationship†	*n*	*r*	Comparison		
KwaZulu/Natal	$OL(mm) = TL(mm)^{0,674}/4,607$	176	0,991		KN	SEC
South-Eastern Cape	$OL(mm) = TL(mm)^{0,723}/6,374$	208	0,996	SEC	**	
Southern Cape	$OL(mm) = TL(mm)^{0,687}/4,960$	159	0,993	SC	**	**
All areas	$OL(mm) = TL(mm)^{0,723}/6,374$	543	0,995			
KwaZulu/Natal	$OH(mm) = TL(mm)^{0,604}/4,984$	176	0,980		KN	SEC
South-Eastern Cape	$OH(mm) = TL(mm)^{0,635}/6,180$	208	0,992	SEC	**	
Southern Cape	$OH(mm) = TL(mm)^{0,634}/6,022$	159	0,985	SC	*	*
All areas	$OH(mm) = TL(mm)^{0,630}/5,931$	543	0,989			
KwaZulu/Natal	$OC(mm) = TL(mm)^{0,595}/15,619$	176	0,949		KN	SEC
South-Eastern Cape	$OC(mm) = TL(mm)^{0,588}/14,299$	208	0,984	SEC	**	
Southern Cape	$OC(mm) = TL(mm)^{0,629}/19,915$	159	0,966	SC		**
All areas	$OC(mm) = TL(mm)^{0,589}/14,821$	543	0,969			
KwaZulu/Natal	$OM(mm) = TL(mm)^{1,888}/212\ 701,23$	176	0,982		KN	SEC
South-Eastern Cape	$OM(mm) = TL(mm)^{2,088}/831\ 782,92$	208	0,993	SEC	**	
Southern Cape	$OM(mm) = TL(mm)^{1,837}/145\ 124,25$	159	0,987	SC	*	**
All areas	$OM(mm) = TL(mm)^{2,008}/479\ 004,00$	543	0,989			

OL = otolith length, OH = otolith height, OC = ostium to cauda distance, OM = otolith mass
* = $p < 0,05$
** = $p < 0,01$

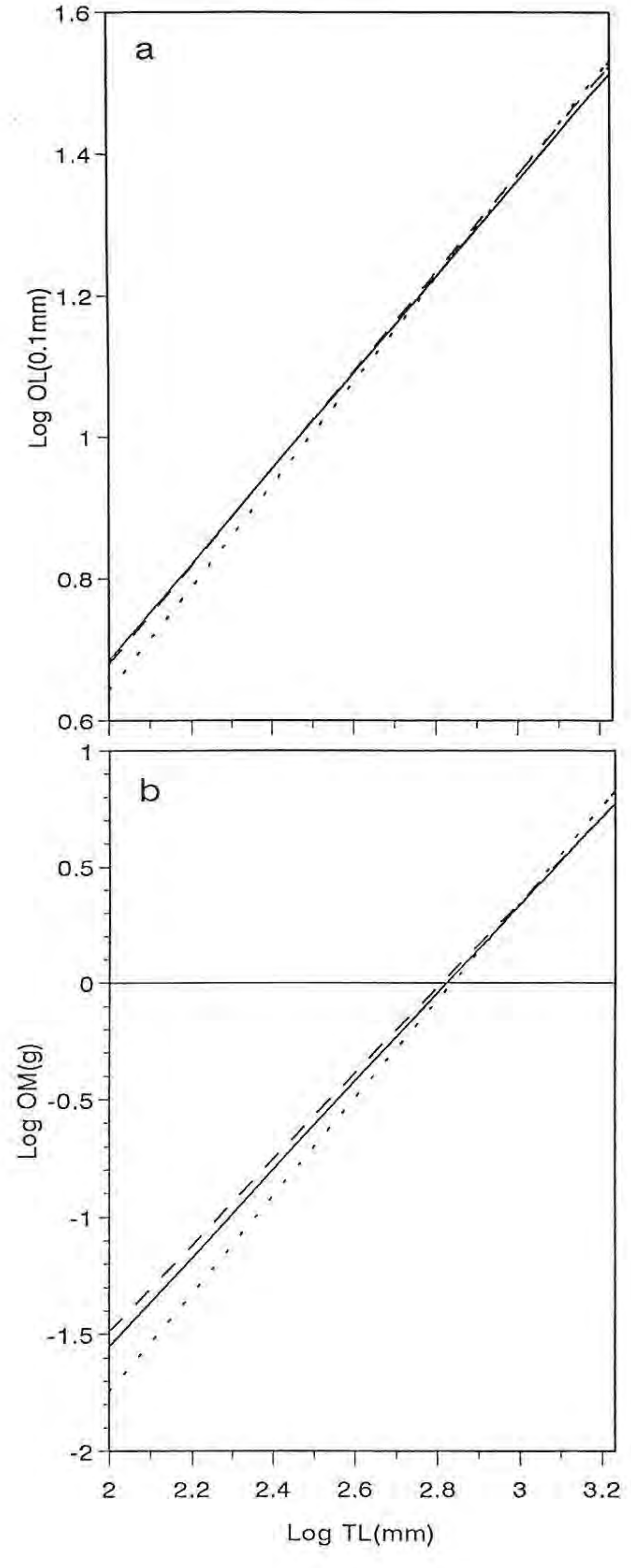


Fig. 3.9: Relationships between total length (TL) and a) otolith length (OL) b) otolith mass (OM) for *A. japonicus* from KwaZulu/Natal (solid line), South-Eastern Cape (dotted line) and the Southern Cape (dashed line).

CHAPTER 4

THE LIFE HISTORY OF *ARGYROSOMUS JAPONICUS* OFF THE EAST COAST OF SOUTH AFRICA

THE LIFE HISTORY OF *ARGYROSOMUS JAPONICUS* OFF THE EAST COAST OF SOUTH AFRICA

ABSTRACT

The life history of *Argyrosomus japonicus* occurring off the east coast of South Africa was studied and elucidated using biological, size composition and tagging data from fish caught in the estuaries, surf zone and nearshore marine environment (surf zone to 100 m depth) of three coastal regions. Capture methods included hook and line (all habitats), seine netting (estuaries and surf zone) and trawling (estuaries only). Median sizes at maturity were 920 mm TL for males and 1070 mm TL for females. All males >1100 mm TL and all females >1200 mm TL were mature. Adult fish are found predominantly in the nearshore marine environment, but also frequent estuaries and the surf zone. Spawning takes place in the nearshore environment, from August to November in KwaZulu/Natal, and from October to January in the Southern and South-Eastern Cape regions. A large proportion of the adult population migrate to KwaZulu/Natal to spawn, although spawning may continue once they return to the Cape. Early juveniles of 20-30 mm TL are recruited into turbid estuaries along the entire east coast, possibly with the aid of olfactory cues. They appear to remain in the upper reaches of the estuaries where they find suitable food and refuge from predators until they grow to about 150 mm TL. Juveniles larger than this size are found in the middle and lower reaches of estuaries and also in the surf zone. Juvenile *A. japonicus* (< 1000 mm TL) generally do not migrate long distances, but remain as separate allopatric populations until they reach maturity. In the Great Fish River estuary juvenile *A. japonicus* (< 70 mm TL) fed initially on mysids and copepods. Copepods were replaced by swimming prawns and teleosts with an increase in predator size, but mysids remained a significant dietary component of all juveniles (20-800 mm TL). It is postulated that the protection from predation afforded by estuarine and surf zone nursery areas has allowed *A. japonicus* to evolve a life-history with a large size at maturity, thereby 'preadapting' it to a migratory life-style.

INTRODUCTION

The dusky kob, *Argyrosomus japonicus*, is a large sciaenid fish (maximum size 75 kg, Griffiths & Heemstra 1995) which occurs in both the northern and the southern hemispheres. It is found on the eastern seaboard of southern Africa from the Cape of Good Hope to Mozambique (Griffiths & Heemstra 1995), along the entire southern seaboard of Australia (North West Cape to the Burnette River)(Kailola et al. 1993, Starling 1993), and from Hong Kong northwards along the Chinese coast to southern Korea and Japan (Trewavas 1977). Until recently it was misidentified as *A. hololepidotus* in both southern Africa and Australia; and in South Africa it was also confused with a new species, *A. inodorus* (Griffiths & Heemstra 1995).

Valued as a food fish throughout its distribution, *A. japonicus* is particularly important to commercial and recreational fisheries off Australia and South Africa. Despite this, very little has been published on the life-history of the dusky kob. Based on the distribution patterns of *A.*

japonicus and *A. inodorus* (Griffiths & Heemstra 1995) and on voucher specimens, several of the South African publications on *"A. hololepidotus"*, including feeding (Nepgen 1982, Smale & Bruton 1985), reproduction (Smale 1985), juvenile distribution (Wallace et al. 1984, Smale 1984, Smale & Badenhorst 1991) and description of the early life history stages (Beckley 1990), deal exclusively or predominantly with *A. inodorus*.

In South Africa *A. japonicus* is abundant only along the east coast (Cape Agulhas to northern KwaZulu/Natal) (Griffiths & Heemstra 1995). This paper describes aspects of the life history of *A. japonicus* occurring in this area, including its reproductive biology, juvenile and adult distribution, and migration.

MATERIALS AND METHODS

The South African east coast was divided into four regions for sampling purposes (see Fig. 4.1 for details). Regional boundaries do not necessarily coincide with political provinces, but were created to increase analytical resolution. During a 48 month period from January 1990 to December 1993, biological and length frequency data were collected from dusky kob caught by recreational and commercial linefishers, fishing in estuaries, the surf zone and the nearshore marine environment (the coastal waters beyond the surf zone to 100 m depth) off KwaZulu/Natal, the South-Eastern Cape and the Southern Cape. The localities sampled in each region are listed in appendix 1. No fish were sampled in the Transkei (see Fig. 4.1). Five seine-netting operations were undertaken to the Great Fish River estuary, in the South-Eastern Cape, between December 1991 and February 1993. A 30 m x 1.5 m net with a 5 mm mesh (bar) bag was employed at several sites (10 to 15 sites per trip) between the head and mouth of the estuary. Bottom salinities were recorded at every station in order to explain the distribution of early juvenile *A. japonicus* in the Great Fish River estuary.

Fish sampled for biological purposes were measured to the nearest 1 mm (total length) and weighed, to nearest gram (fish < 500 g), the nearest 20 g (500 g - 5 kg), the nearest 100 g (5 kg - 25 kg) and to the nearest 200 g (>25 kg). They were then cut open and sexed. The gonads were removed, assigned a visual index of maturity (modified from Griffiths and Hecht 1995, see Table 4.1) and weighed to the nearest 0.1 g.

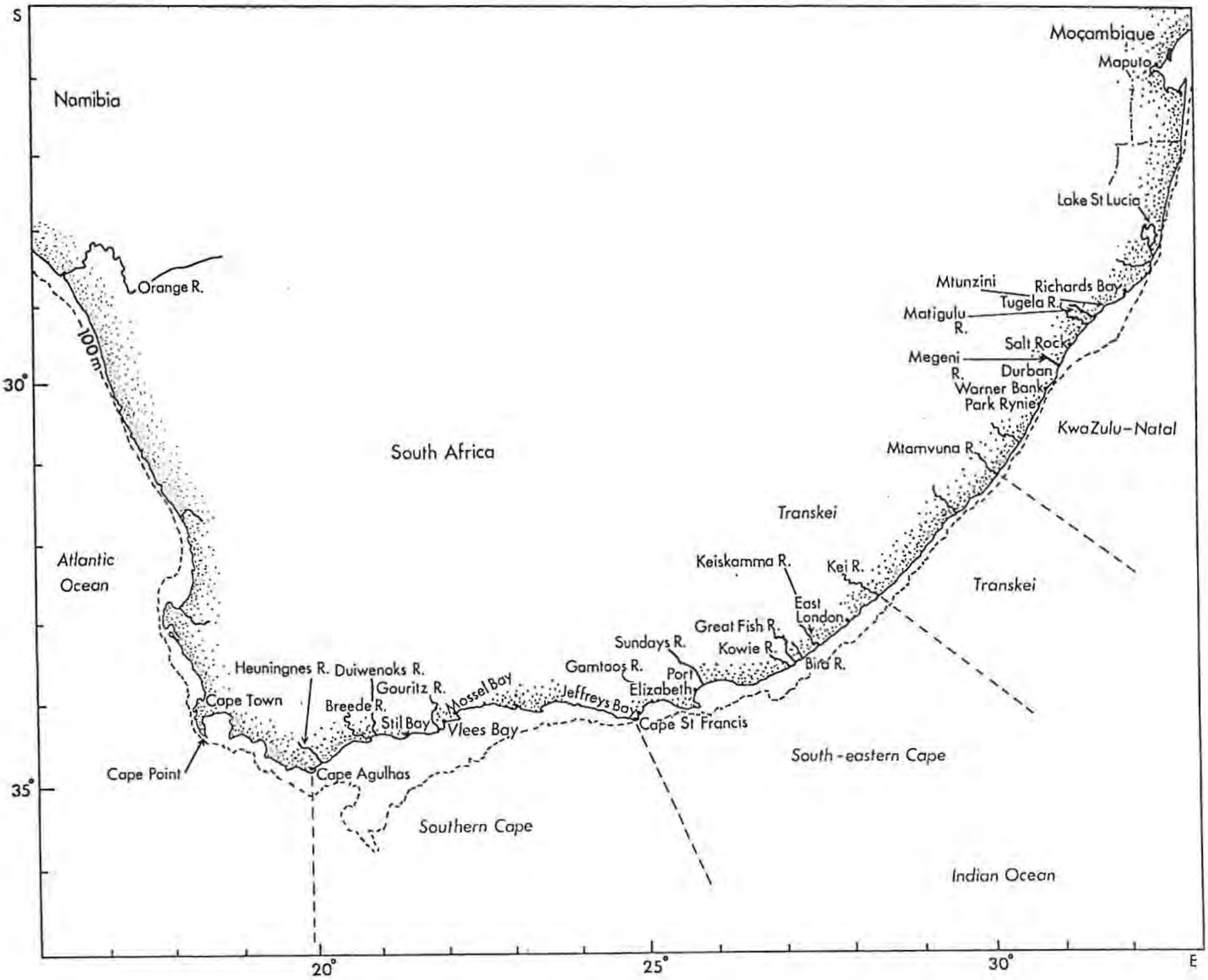


Fig. 4.1: The division of the South African east coast into four coastal regions, the sampling sites, and localities mentioned in the text.

Table 4.1: Classification and description of the macroscopic gonad maturity stages of *Argyrosomus japonicus*.

STAGE I. Juvenile
This stage is generally only found in fish < 600 mm TL. Testes are thread-like, and the ovaries appear as transparent/pinkish flaccid sacs, about half the length of those in Stage II.

STAGE II. Immature or Resting
Testes are extremely thin, flat and pinkish white in colour. Ovaries appear as translucent orange tubes. Eggs are not visible to the naked eye.

STAGE III. Active
Testes are wider, triangular in cross-section and beige in colour. Sperm is present if the gonad is cut and gently squeezed. Eggs become visible to the naked eye as tiny yellow granules in a gelatinous orange matrix. There is very little increase in the diameter of the ovary.

STAGE IV. Developing
Testes become wider, deeper and are mottled and creamy beige in colour. They are also softer in texture, rupturing when lightly pinched. Besides the obvious presence of sperm in the main sperm duct, some sperm is also present in the tissue. Ovaries become larger in diameter and opaque yellow in colour. Clearly discernible eggs occupy the entire ovary.

STAGE V. Ripe
Testes still larger in cross-section and softer in texture. They become creamier in colour due to considerable quantities of sperm. The ovaries are larger in diameter as a result of an increase in egg size.

STAGE VI. Ripe/Running
Testes even larger in cross-section, and uniformly cream in colour. They are extremely delicate at this stage and easily rupture when handled. Sperm is freely extruded when pressure is applied to the abdomen of the whole fish. Although no stage VI ovaries were observed for *A. japonicus*, this stage would have been characterized by hydrated eggs and, based on other sciaenids, amber colouration.

STAGE VII. Spent
Testes are shrivelled in appearance and a mottled beige and cream in colour. A little viscous semen may still ooze from the genital pore when pressure is applied to the abdomen. Ovaries are reduced in size, similar in appearance to Stage II, with a few yolked oocytes remaining. These yolked oocytes are generally aspherical and appear to be undergoing resorption.

Additional length (TL) data were obtained for: (i) the KwaZulu/Natal region, from fish sampled with a small otter trawl in the Mgeni, Matigulu and Mtamvuna estuaries (T. Harrison, Council for Scientific and Industrial Research, Durban), and from fish seined in the Durban surf zone (S. Chater, Oceanographic Research Institute, Durban); (ii) for the South-Eastern Cape region, from fish seined in the Algoa Bay surf zone (T. Lasiak, University of Port Elizabeth), and in the Keiskamma and Kei river estuaries (H. Kok, Port Elizabeth Museum); (iii) and for the Southern Cape, from fish seined in the Breede River estuary (H. Kok, Port Elizabeth Museum). All netted fish (trawled or seined) were caught with nets which had a bag mesh of 5 mm (bar), except those from the Durban surf zone where the mesh size was 12 mm. The weights of fish caught during fishing competitions (measured to the nearest 100 g using asized balances) were also obtained from angling clubs in the above three regions. These weights were converted to total lengths using the length/weight relationship derived by Griffiths & Hecht (in press). All length measurements were analyzed according to region, habitat and catch method using length frequency histograms.

Migration was studied using tagging and catch data. The Oceanographic Research Institute in Durban initiated a national tagging programme in 1984, which provides anglers with equipment to tag their catch (van der Elst 1990). The data for recaptured dusky kob (n = 263), predominantly juvenile fish, were analyzed according to region. Adult migration was also inferred from the catch returns of commercial lineboats in KwaZulu/Natal. The catch returns from the South-Eastern Cape and the Southern Cape could not be used as fishers do not distinguish between *A. japonicus* and *A. inodorus* (Griffiths & Heemstra 1995), a closely related species which also occurs in these regions. The monthly catches of *A. japonicus* made in KwaZulu/Natal for the period 1987-1993 were expressed as percentages of the respective annual totals. *A. japonicus* is highly prized by the KwaZulu/Natal commercial linefishers, and as confirmed by personal experience, the observed catch trends reflect abundance in the region rather than shifts in targetted effort.

Reproductive seasonality was established by calculating both gonadosomatic indices (GSIs) and the monthly percent frequency of each maturity stage, for fish larger than the median size at sexual maturity (L_{50}) (see below).

$$\text{GSI} = (\text{gonad weight}/\text{fish weight}) \times 100.$$

L_{50} for males and females was estimated by fitting a logistical function to the fractions of the mature fish (gonad stage III+) per 50 mm length class, sampled during the breeding season (Beacham 1983, Barbieri et al. 1994b). Due to the migratory nature of the adults, data from all regions were combined. Sex ratios were tested for significant deviations from unity with a chi-square test ($\propto = 0.05$).

The diet of *A. japonicus* in the Great Fish River was studied in an attempt to explain the size related distribution patterns of juveniles in estuaries. Stomach contents were examined fresh. Each prey item was identified to the lowest possible taxon and then analyzed according to broad taxonomic groupings, using percent frequency of occurrence (%F) (Hynes 1950).

RESULTS AND DISCUSSION

Reproductive biology

The relationships between fish length and sexual maturity for male and female *A. japonicus* are illustrated in Figure 4.2. L_{50} for males was calculated at 920 mm and 1070 mm for females. All males larger than 1100 mm and all females larger than 1200 mm were sexually mature.

Using the growth models presented in Chapter 3, L_{50} and total maturity are attained at ages of 5 and 7 years for males, and at 6 and 8 years for females. Growth rate was found to decline after maturity in both sexes (Chapter 3), suggesting that a large proportion of adult surplus energy is channelled into reproduction.

Adult fish were found to be most abundant in the nearshore marine environment, but did frequent estuaries and surf zones in all three regions (Fig. 4.3). Substantial increases in the catches of commercial line-boats in late winter and spring (Fig. 4.4), together with the advanced condition of the gonads of these fish (Figures 4.5a & 4.6b), suggests that a large proportion of the adult population in the Cape regions migrate to KwaZulu/Natal to spawn (*A. japonicus* is not abundant in Mozambique, Griffiths & Heemstra 1995). The absence of fish with spent gonads (stage VII) in KwaZulu/Natal and their presence in the Cape regions (Figures 4.5 & 4.6) implies a return migration once spawning has been completed in KwaZulu/Natal. The occurrence of ripe and ripe/running gonads (stages V & VI) in the South-Eastern Cape and the Southern Cape indicates that some spawning also occurs in these regions. Although ripe running males (stage VI) were found in all regions, this gonad stage was never observed for females. Since a large proportion of the adults sampled during the spawning season were captured at night (when they are thought to spawn, see below), and because sciaenid oocytes generally hydrate for at least 3-9 hours prior to spawning (Fitzhugh et al. 1988, 1993), the absence of stage VI female *A. japonicus* in the catches can only be attributed to a loss in appetite after oocyte hydration, with the result that they are temporarily not vulnerable to the hook and line fishing method. Higher proportions of ripe running females in net as opposed to line caught catches of *Sciaenops ocellatus* (Fitzhugh et al. 1988, Wilson & Nieland 1994), and *Argyrosomus inodorus* (Chapter 6), confirm that the

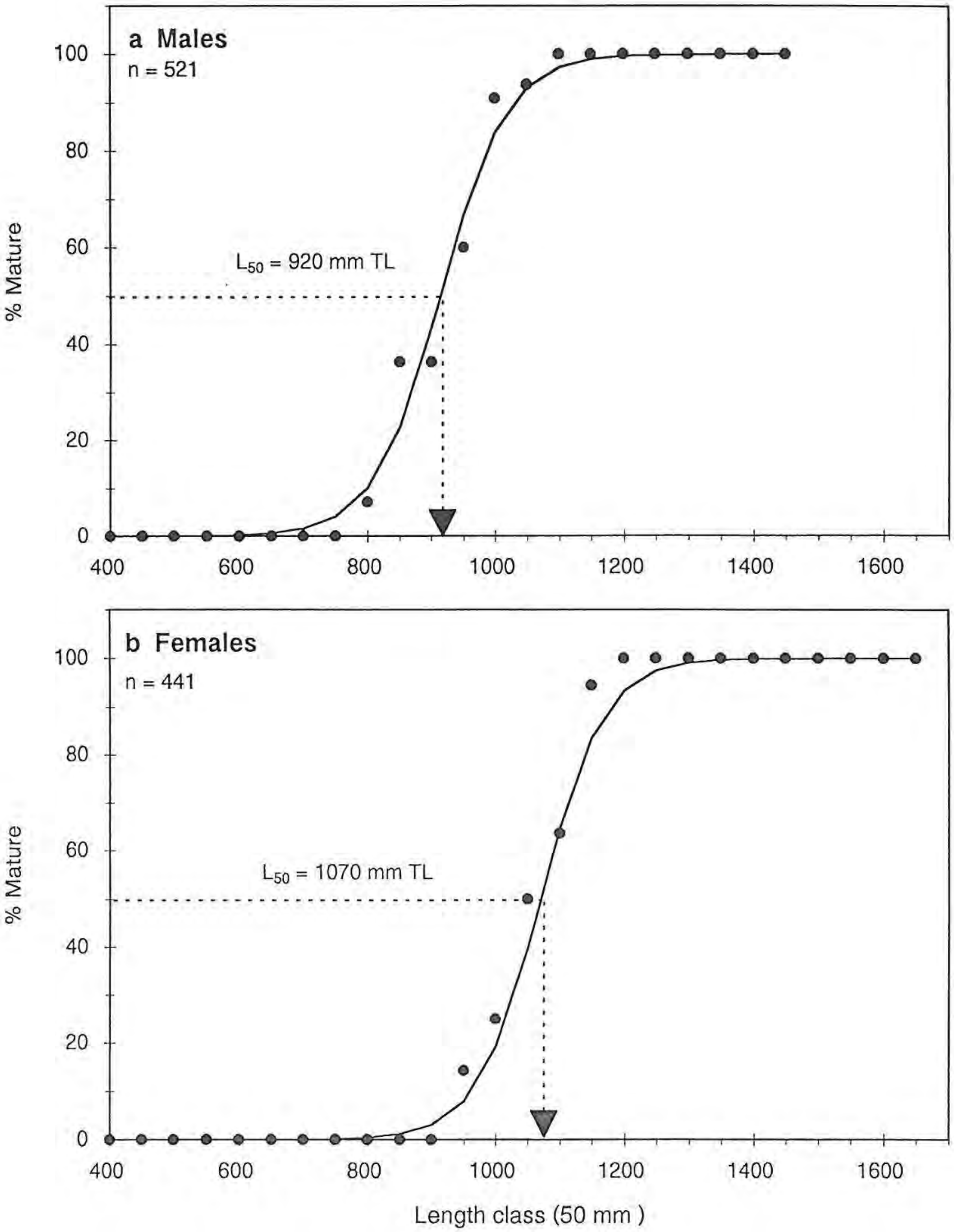


Fig. 4.2: Percentage of mature male (a) and female (b) *A. japonicus,* by 50 mm total length intervals, sampled during the spawning period. The solid line describes the fitted logistical function. Arrows indicate median length at first maturity (L_{50}). n = sample size.

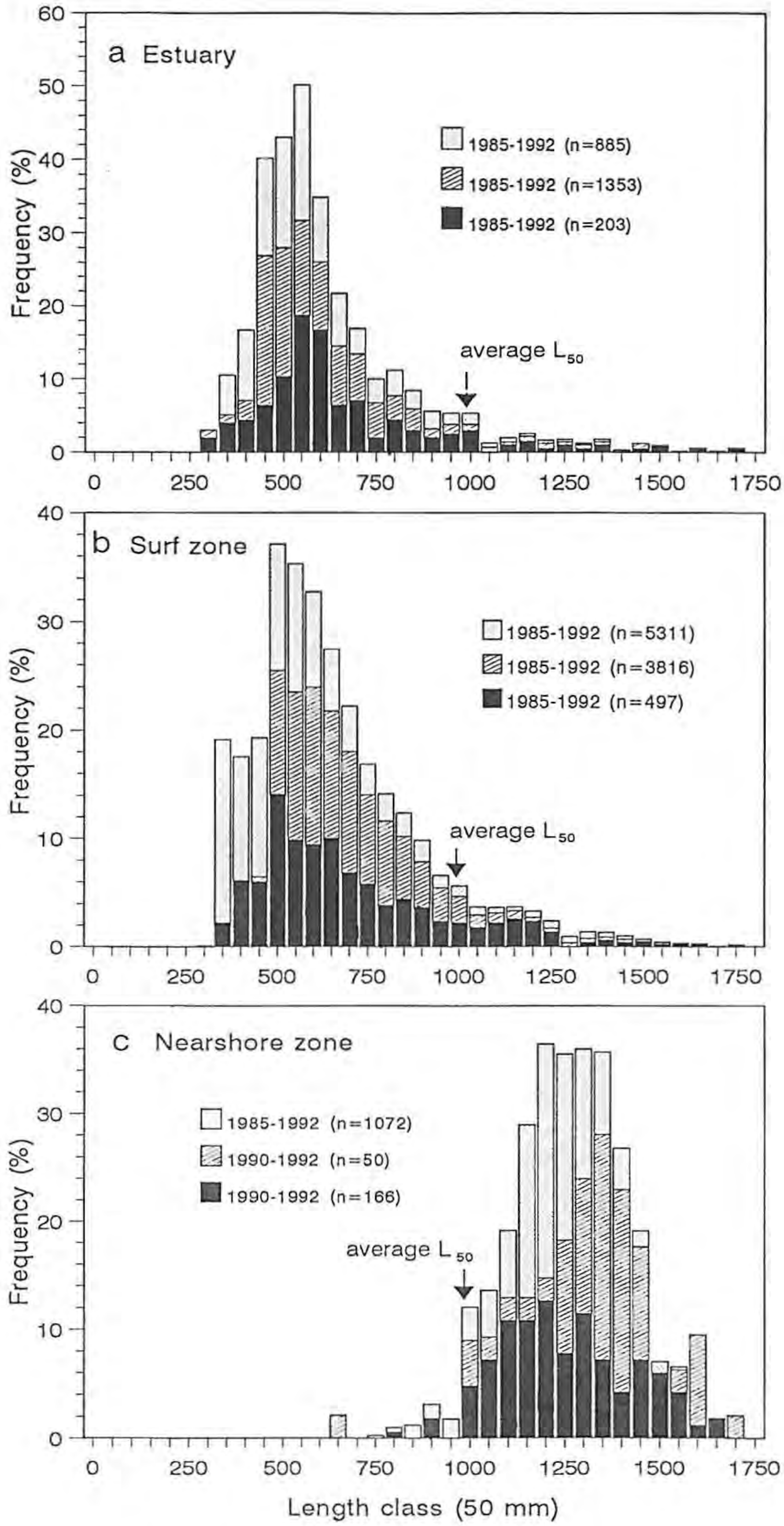


Fig. 4.3: Total length distributions of South African *A. japonicus* caught by hook and line from estuaries (a), the surf zone (b) and the nearshore marine environment (c) of KwaZulu/Natal (shaded bars), the South-Eastern Cape (hatched bars) and the Southern Cape (solid bars). Arrows indicate the average median length at maturity (L_{50}) for males and females (i.e. 995 mm TL).

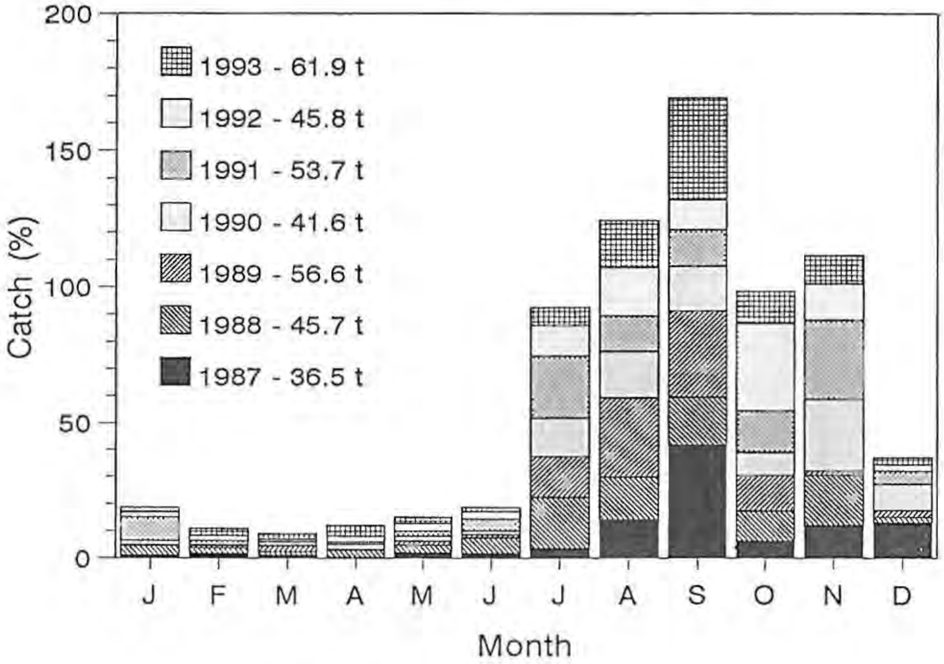


Fig. 4.4: Monthly catches of adult *A. japonicus* caught by nearshore commercial linefishers in Kwazulu/Natal, expressed as percentages of the respective annual catches

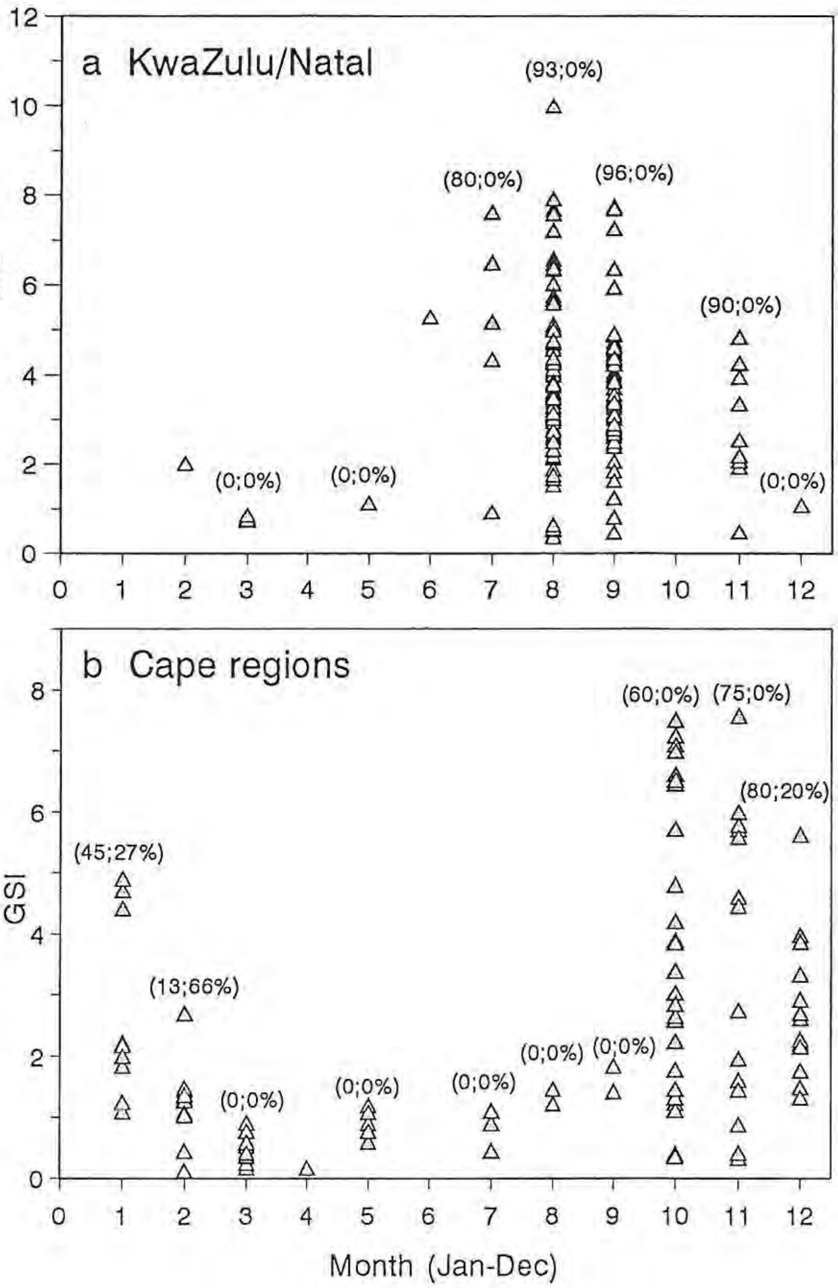


Fig. 4.5: Monthly gonadosomatic indices (GSI) for female *A. japonicus* (> 1070 mm TL) sampled in KwaZulu/Natal (a) (n = 158) and the Cape regions (b) (n = 103), during the period 1990-1993. The numbers in parentheses give the monthly percentages of ovaries in the ripe (V) and spent (VII) macroscopic stages. No ripe/running (VI) ovaries were observed.

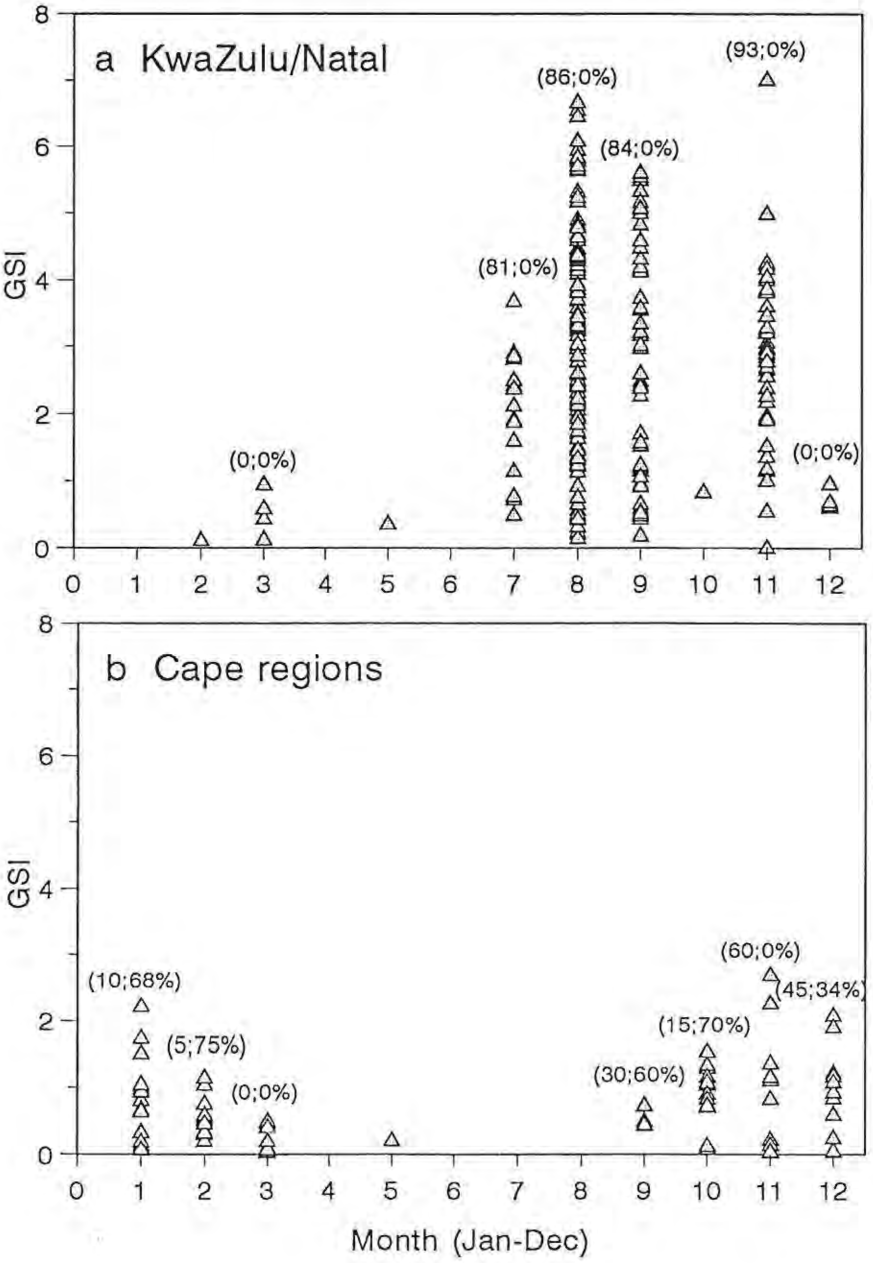


Fig. 4.6: Monthly gonadosomatic indices (GSI) for male *A. japonicus* (> 920 mm TL) sampled in KwaZulu/Natal (a) (n = 241) and the Cape regions (b) (n = 83), during the period 1990-1993. The numbers in parentheses give the monthly percentages of testes in the ripe to ripe/running (V & VI) and spent (VII) macroscopic stages.

females of some sciaenids feed less when their ovaries mature to stage VI. The collection of eggs and larvae (see below) substantiate that spawning occurs within the area exploited by linefishers. The sex ratio, based on all *A. japonicus* sampled, did not deviate from unity ($x^2 = 1.52$, $n = 1588$). There were, however, statistically ($x^2 = 8.49$) more males sampled from the landings of KwaZulu/Natal lineboat fishers during the spawning season (242 males : 182 females). This lends credence to the hypothesis that females lose their appetite during the egg hydration period.

Spawning occurs over protracted periods, from July to November in KwaZulu/Natal and from October to January in the two Cape regions (Figures 4.5 & 4.6). Earlier spawning at lower latitudes has been observed for several sciaenid species including *Argyrosomus regius* (Moal 1957, Tixerant 1974 in Champagnat & Domain 1978, Chao 1986b), *Pogonias cromis* (Peters & McMichael 1990), *Sciaenops ocellatus* (Ross et al. 1995) and *Cynoscion regalis* (Shepherd & Grimes 1984).

Since the onset of spawning has been correlated with water temperature in many fishes (see Conover 1992), including sciaenids (Brown-Peterson & Thomas 1988, Peters & McMichael 1990, Saucier & Baltz 1993, Wilson & Nieland 1994), the warmer waters of KwaZulu/Natal (Greenwood & Taunton-Clark 1992) are presumably more conducive to earlier spawning of *A. japonicus* in this region. The absence of spent fish in KwaZulu/Natal and the later spawning season in the Cape regions, suggests that spawning, at least in some fish, may continue once they return to the latter regions.

Spawning apparently occurs in the nearshore environment. Connell (CSIR, Durban, personal communication 1994) has repeatedly collected large numbers of *A. japonicus* eggs (hatched and reared to 300 mm TL for identification) within 1 m of the surface, in 30-40 m of water off the KwaZulu/Natal coast during spring (1990-1994). Furthermore *Argyrosomus* eggs and larvae have not been recorded further offshore in the Agulhas Current (Beckley 1993). When found in South African estuaries, *Argyrosomus* eggs and larvae generally occur in low numbers in the mouth regions (Melville-Smith & Baird 1980, Melville-Smith 1981, Beckley 1984a, Harrison & Whitfield 1990, Whitfield 1994a, Whitfield et al. 1994), indicating that they are incidentally transported into and out of the estuaries via tidal action. Although Whitfield (1989) recorded more *Argyrosomus* larvae entering the Swartvlei estuary (incoming tide) than those leaving (outgoing tide), early juveniles (< 150 mm TL) of *A. japonicus* were absent from that system

(Whitfield & Kok 1992). Beckley (1986) recorded significant numbers of *Argyrosomus* larvae from the nearshore region in Algoa Bay (South-Eastern Cape) which she described as "*A. hololepidotus*". Based on pigment patterns (compared with Connell's larvae), she now believes that these larvae were those of *A. inodorus* (personal communication 1995). According to the ontogenetic development of *A. japonicus* eggs collected in KwaZulu/Natal, and the time of sampling; spawning appears to occur at night (Connell, CSIR, Durban, personal communication 1995). Studies on nine other sciaenids show that spawning after dark appears to be common in this family (Fish & Cummings 1972, Takemura et al. 1978, Holt et al. 1985, Saucier & Baltz 1993, Connaughton & Taylor 1995). Holt et al. (1985) suggest that this is an adaptation which reduces egg loss, since zooplanktivores are less active at night.

Nursery areas

Wallace et al. (1984), Smale (1984) and Smale & Badenhorst (1991) reported that the sandy and muddy substrates of the nearshore marine environment in the Cape regions were important nursery areas for "*A. hololepidotus*". However, a recent study on the taxonomy and distribution of South African *Argyrosomus* species (Griffiths & Heemstra 1995) has shown that the species inhabiting this environment is *A. inodorus* and not *A. japonicus*. Similarly the juvenile "*A. hololepidotus*" trawled from the nearshore marine environment in KwaZulu/Natal (Tugela Banks)(Wallace 1975) have since been identified as *A. thorpei* (Fennessy 1994).

Length frequency analyses of line caught fish reveal that immature *A. japonicus* (< 1000 mm TL) are found in all three regions, exclusively in the estuarine and surf zone habitats (Fig. 4.3). The absence of juveniles from the nearshore marine environment is not believed to be a function of gear selectivity as large numbers of *A. inodorus* (Chapter 6) and *A. thorpei* (Fennessy 1994) between 300 mm and 1000 mm TL are caught by South African linefishers. Furthermore, juvenile *A. japonicus* have never been recorded from trawl grounds in the nearshore zone (Griffiths & Heemstra 1995).

Although there is strong evidence for the longshore migration of adult *A. japonicus*; tagging data indicate that juvenile fish generally do not move great distances (Figures 4.7 & 4.8). Despite liberty periods of up to 1713 days, 83% of the 253 fish recaptured were found less than 10 km from the site where they were tagged, and only 5% had moved more than 30 km. This suggests

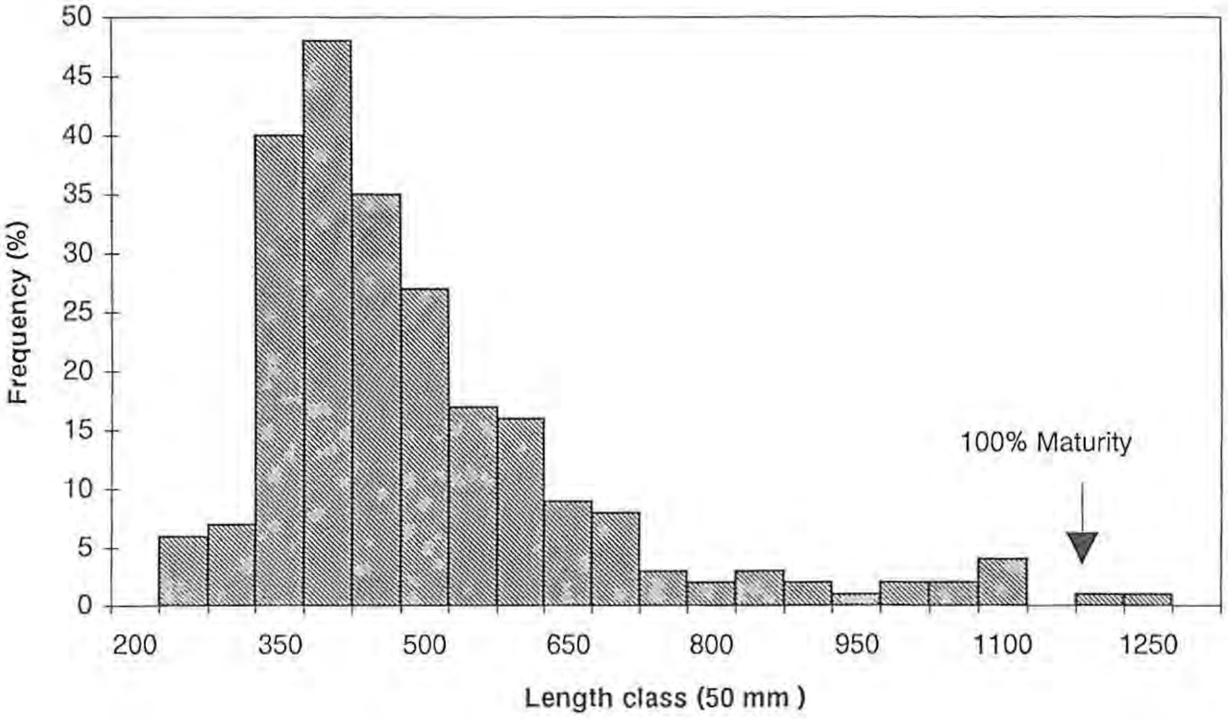


Fig. 4.7: The total length distribution of recaptured *A. japonicus* tagged along the South African east coast (n = 263). The size at 100% maturity, for males and females combined, is indicated with an arrow.

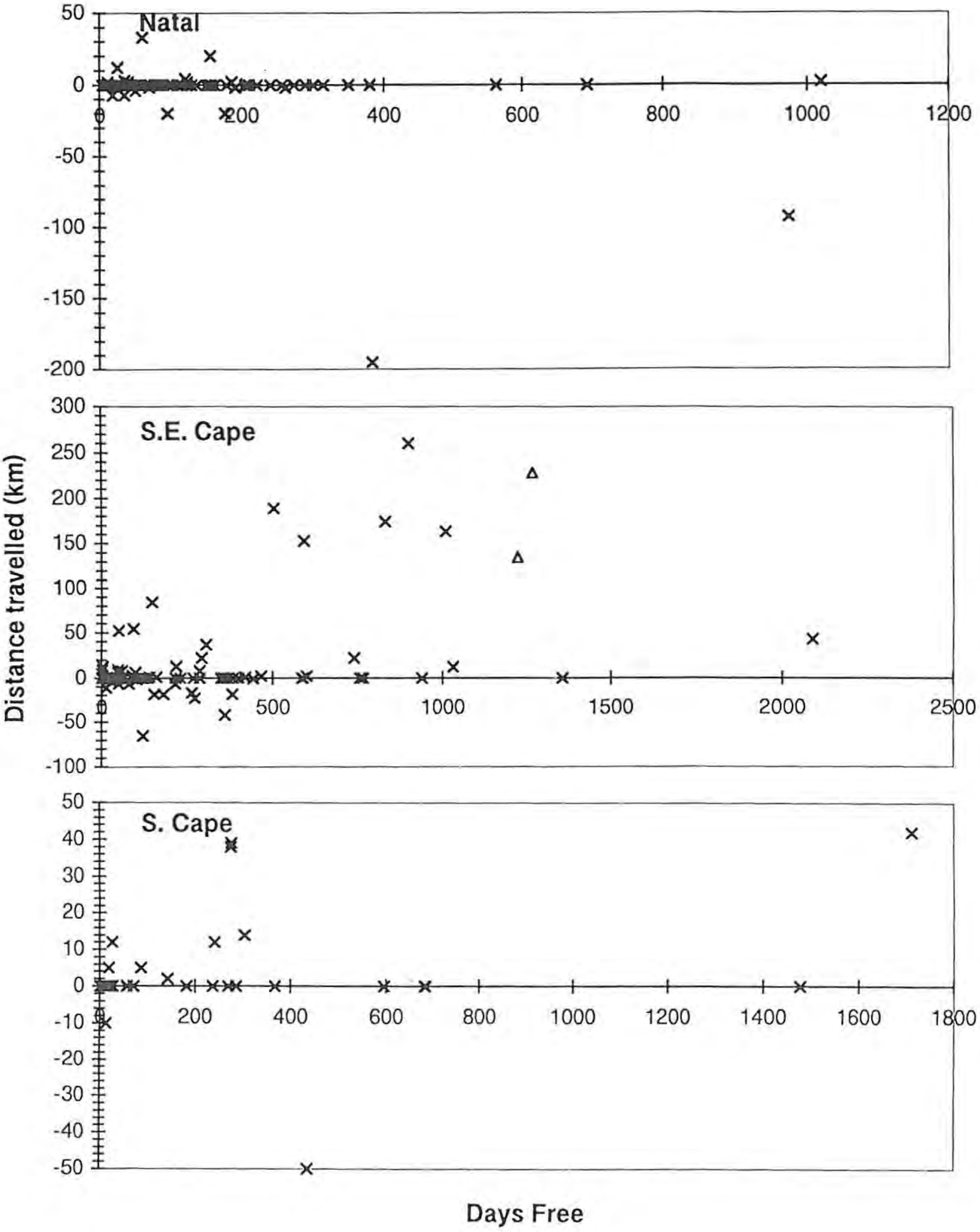


Fig. 4.8: Minimum distance travelled versus time at large for tagged *A. japonicus* recaptured in KwaZulu/Natal (n = 109), the South-Eastern Cape (n = 115) and the Southern Cape (n = 39). Positive values indicate northward and negative values southward movement. Tri-angles = fish larger than the size at 100% maturity for males and females (1200 mm TL).

that juvenile fish exist largely as separate populations along the South African east coast, mixing only after they attain maturity. Differences in the otolith dimension/fish length relationships of *A. japonicus*, from the three different regions (Chapter 3), support this conclusion. Based on the very short distances travelled by juvenile dusky kob, and the fact that early juveniles are found only in estuaries (see below), it is likely that populations of juvenile *A. japonicus* focus around their natal estuaries. Juvenile *A. japonicus* tagged in Australia (as *A. hololepidotus*) (Anon 1993) also showed low rates of migration.

The 400 mm TL minimum legal size limit for *A. japonicus* in South Africa and the minimum weights eligible for competition points (translating to 367 mm TL for KwaZulu/Natal and 462 mm TL for the Cape regions), have precluded any distribution analyses based on line caught data of fish smaller than these lengths. While several gillnetting studies (Whitfield & Blaber 1978, Marais & Baird 1980, Marais 1981, 1983a&b, Ratte 1982, Coetzee & Pool 1991, Whitfield et al. 1994) confirm that dusky kob <400 mm are abundant in estuaries along the east coast, this method does not effectively capture *A. japonicus* <150 mm and thus these studies provide no information on early life history. The length frequency distributions of trawled and seined *A. japonicus*, however, show that dusky kob of 150-400 mm TL do occur in the surf zone (Fig. 4.9), but that those between 20 and 150 mm are found exclusively in estuaries (Fig. 4.10). Early juveniles (<150 mm) were recorded from the Matigulu estuary in northern KwaZulu/Natal through to the Breede estuary in the Southern Cape (Fig. 4.10). They appear to recruit into estuaries at 20-30 mm TL (Fig. 4.10), which according to the growth rates of captive fish (reared from wild eggs) are about four weeks old (Connell, CSIR, Durban, personal communication 1995).

The absence of early juveniles from the non-turbid Swartvlei and Knysna estuaries, including the upper reaches (Whitfield & Kok 1992), suggests that turbid systems are more important as nursery areas for this species. Unfortunately little research has been done in the upper reaches (see below) of South African estuaries using equipment suitable for capturing early juvenile kob (e.g. seine nets or otter trawls), and, as a result, quantitative comparisons are not possible. Early juvenile *A. japonicus* have, however, also been recorded (as *A. hololepidotus*) from three other (relatively turbid) systems, including Lake St Lucia (50-240 mm TL) and Richards Bay (60-120 mm TL) in northern KwaZulu/Natal (Wallace & van der Elst 1975), and the Sundays River estuary (27-232 mm TL) in the South-Eastern Cape (Beckley 1984a). In a review of fishes gill-

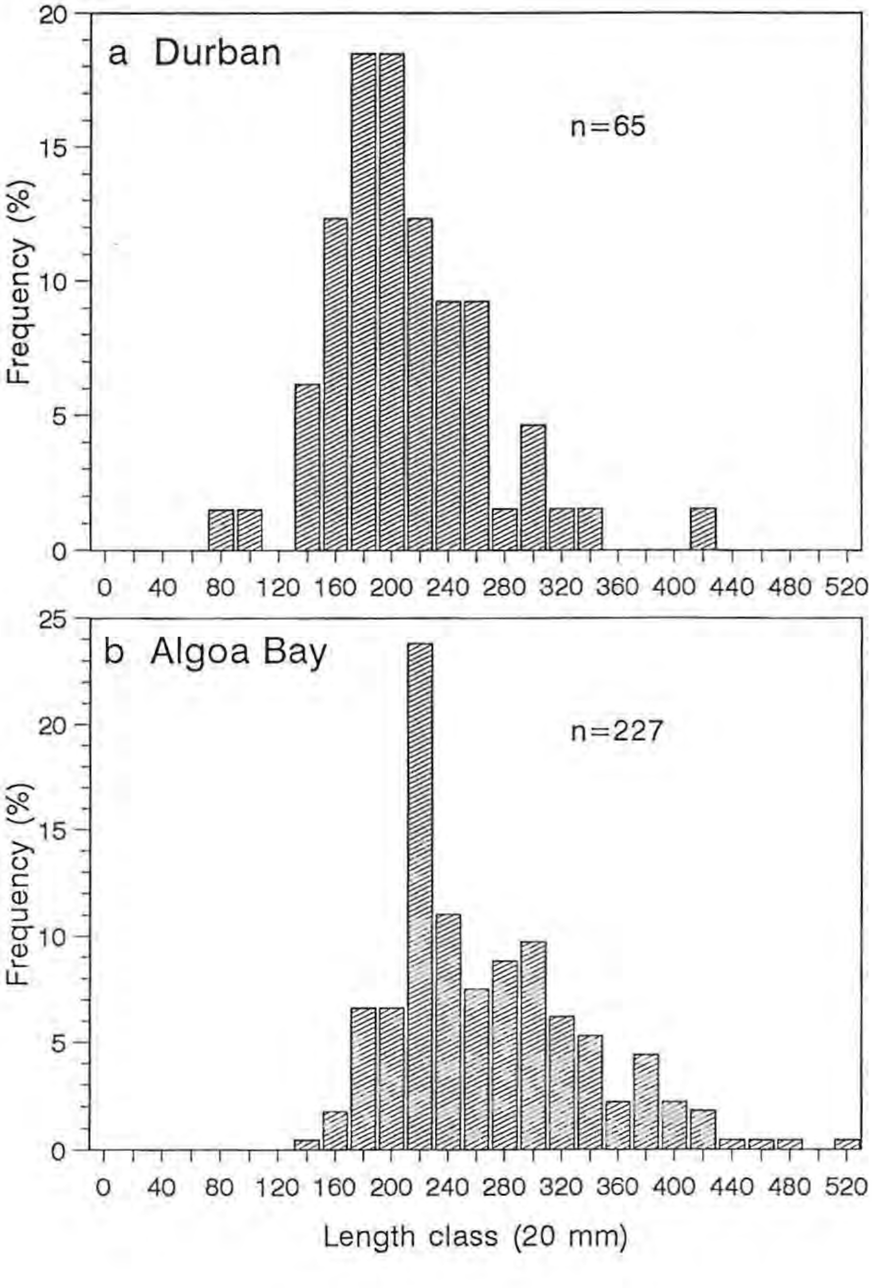


Fig. 4.9: Total length distributions of *A. japonicus* seined in the surf zones of Durban (KwaZulu/Natal) (a) and Algoa Bay (South-Eastern Cape) (b).

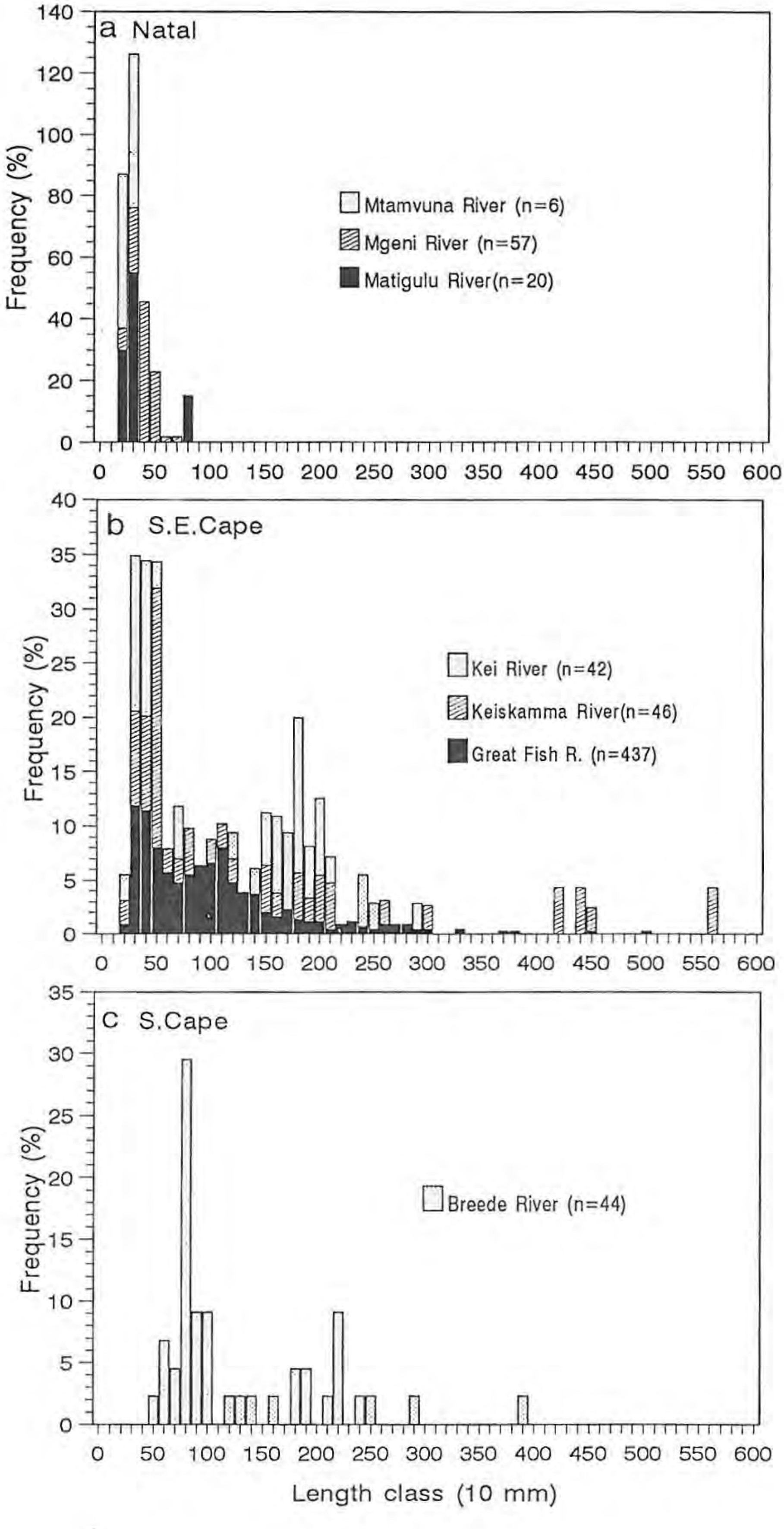


Fig. 4.10: Total length distributions of *A. japonicus* otter trawled in three KwaZulu/Natal estuaries (a), beach seined in three South-Eastern Cape estuaries (b), and beach seined in one Southern Cape estuary (c). The names of the estuaries sampled and the numbers of fish measured are given.

netted and beach-seined in Western Australian and South African estuaries, Potter et al. (1990) concluded that "The juveniles of this species (*'A. hololepidotus'*) are not abundant in the estuaries of either region until they attain a length of at least 150 mm". This is in contrast to the findings of this study and the study of Gray & McDonall (1993) in Australia, which show that early juveniles of < 100 mm TL occur abundantly in estuaries of both countries. The erroneous conclusion reached by Potter et al. (1990), can probably be attributed to the fact that seine nets were used to sample the early juvenile component in all studies they reviewed. Although seine nets were successfully used in the Great Fish River estuary in the present study, they are not suited to the upper reaches of many South African estuaries (early juvenile habitat, see below) as the water is often too deep and the banks steeply sloped and covered with dense macrophytic growth.

Whitfield (1994b) developed a classification of southern African estuarine fishes based on their utilization of estuaries. He classified *A. japonicus* (as *A. hololepidotus*) as a species whose "juveniles occur mainly in estuaries, but are also found at sea" (category IIb of Whitfield). In lieu of the estuarine dependency of the early juveniles, it is suggested that this species be moved to category IIa, which consists of species whose juveniles are dependent on estuaries as nursery areas. Several teleost species which migrate to KwaZulu/Natal to spawn, have their eggs and larvae passively transported, by the peripheral inshore waters of the Agulhas Current, to nursery areas in the South-Eastern Cape and in the Southern Cape e.g. *Pomatomus saltatrix* (van der Elst 1981), *Lichia amia* (van der Elst 1981), *Atractoscion aequidens* (Griffiths & Hecht 1995). Unlike these three species, the juveniles of *A. japonicus* occur abundantly in KwaZulu/Natal as well as in the two Cape regions. Since *A. japonicus* is not abundant in Mozambique (Griffiths & Heemstra 1995), this suggests that dusky kob early juveniles may recruit directly into estuaries in the vicinity of the spawning area; or that the eggs and larvae may be dispersed to the south west by the peripheral inshore waters of the Agulhas Current. The degree of dispersion would presumably be affected by the offshore distance of the spawning site, the further offshore, the greater the rate of southward drift.

After recruitment the distribution of early juveniles (<150 mm TL) within estuaries is poorly understood. In the Hawksbury River (Australia) they were most abundant in the middle reaches where salinities were about 12 p.p.t. (Gray & McDonall 1993). In the Great Fish River estuary (South Africa) >90 % of the early juveniles were seined only in the upper reaches where salinities were 0-5 p.p.t., and none were caught at salinities above 16 p.p.t. (Fig. 4.11). This is supported by the work of Whitfield et al. (1994) who found no early juvenile dusky kob in the middle to lower reaches of the Great Fish River estuary using similar sampling methods. The upper regions of the Kei, Keiskamma and Breede estuaries were not effectively sampled, for reasons mentioned above. Interviews with competition anglers (n = 12) suggests that fish larger than 400 mm TL occurred predominantly in the middle and lower reaches of the Great Fish estuary and not in the upper regions. Results of the dietary analysis (Fig. 4.12) showed that the smallest early juveniles (20-70 mm TL) in the Great Fish River estuary fed predominantly on calanoid copepods (exclusively *Pseudodiaptomus hessei*) and mysids (predominantly *Mesopodopsis slabberi*). As the fish increased in size, copepods disappeared from the diet and the proportion of teleosts and swimming prawns (Penaeidae) increased. Mysids, however, remained an important dietary component of all size classes of *A. japonicus* examined in the estuary (up to 800 mm TL). A study on the zooplankton of the Great Fish River estuary (Grange 1992) showed that *P. hessei* was most abundant in the upper reaches (salinities < 8 p.p.t.) and that *M. slabberi* was most abundant in the middle and lower reaches (salinities 10-35 p.p.t). These findings explain the confinement of the smallest (20-70 mm TL) but not the larger (70-220 mm TL) early juveniles to the upper reaches of this estuary. Studies on cost-benefit analysis predict that predator avoidance will also influence the response of fish to spatial heterogeneity in their environments (Huntingford 1993). Empirically, fish have been shown to select areas of lower food abundance when those of increased food availability are associated with a higher risk of predation (Ehlinger 1989, Gotceitas & Colgan 1990, Croy & Hughes 1991). Since *A. japonicus* are cannibalistic (personal observation, Great Fish and Keiskamma estuaries, 1991/92), it is suggested that both predator avoidance and food availability play effective roles in the distribution of the early juveniles in estuaries. Research on the distribution and abundance of early juveniles in other estuaries (with different environmental conditions) would, however, improve understanding of the nursery function of estuaries for *A. japonicus*.

It is generally accepted that spawning is timed to maximize the probability of offspring survival (Cushing 1990, Wootton 1990, Conover 1992). Most of the South African east coast has a spring/summer rainfall pattern. This coincides with the spawning activity of *A. japonicus*, and theoretically increases the nursery potential of the east coast (i) by opening many small estuarine systems which close during autumn and winter (many of which contain kob), (ii) by producing higher mysid and copepod biomasses (Grange 1992), and (iii) by establishing salinity gradients

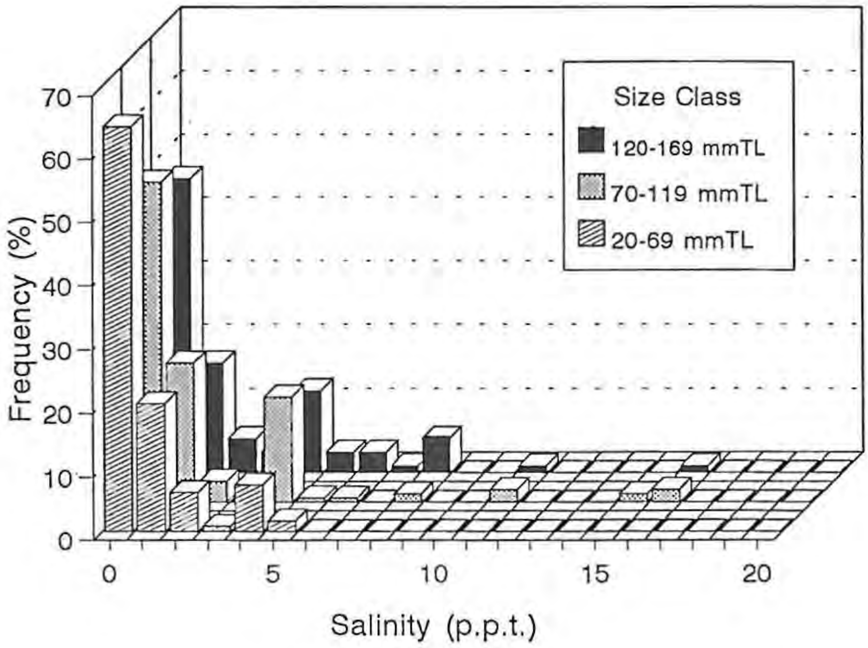


Fig. 4.11: The distribution of catch (by number) vs. salinity for three size classes of early juvenile *A. japonicus* seined in the Great Fish River estuary during 1991/92 (n = 373).

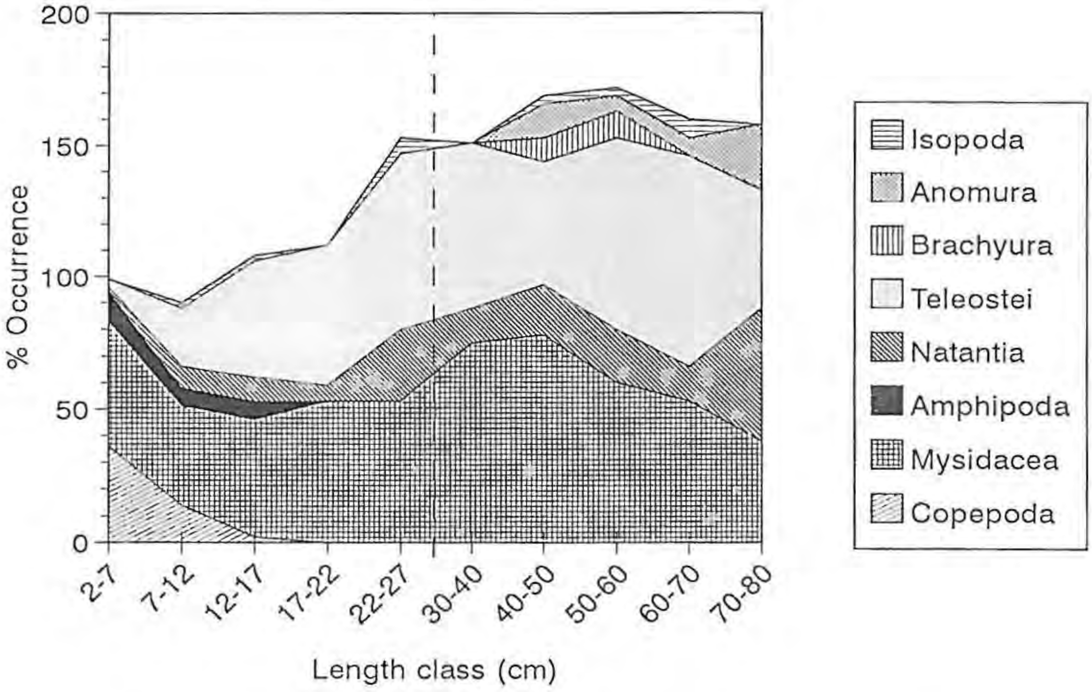


Fig. 4.12: Changes in diet with size for 365 *A. japonicus* from the Great Fish River estuary. Fish were grouped into 5 cm (<30 cm TL) and 10 cm (>30 cm TL) length classes.

which may provide protection for early juveniles. Given the affinity of early juvenile *A. japonicus* for the regions of estuaries which are turbid and have low salinity (this study), and the preference of the juveniles for turbid estuaries with relatively high fresh water input (Marais 1981, 1988, Plumstead et al. 1985), fresh water flowing into the marine environment may also assist dusky kob in locating estuaries. After studying salinity and turbidity gradients in conjunction with juvenile fish abundance in three South-Eastern Cape estuaries (including the Great Fish), Whitfield (1994) concluded that olfactory cues entering the adjacent marine environment are probably the most important factors influencing the immigration of estuarine-dependent species. The introduction of adequate fresh water during the spawning season could, therefore, be crucial to early juvenile survival and to the life history of *A. japonicus*. In Australia, juvenile recruitment in the Coorong Lagoon has also been correlated with the rate of fresh water inflow (Hall 1984, Anon 1988).

Life-history comparisons

The life-history of *A. japonicus* (Subfamily Otolithinae) is remarkably similar to those of *Sciaenops ocellatus* and *Pogonias cromis* (Subfamily Sciaeninae), two long lived species from North America. All three of these species live in excess of 40 years; maturity occurs at a relatively large size (58-91% L_∞), after which growth slows dramatically; the adults are found predominately in the nearshore zone (10-100 m depth), and spawn mainly in this environment; and finally the early juveniles (< 80 mm TL) actively recruit to the upper reaches of estuaries (salinities low to moderate), but later move to the lower reaches and into shallow coastal waters (Peters & McMichael 1987, 1990, Murphy & Taylor 1989, 1990, Nieland & Wilson 1993, Wilson & Nieland 1994, Ross et al. 1995).

Compared to *A. inodorus* (♀ L_{50} = 340 mm @ 2 years, max. age = 25 years, Chapters 5 & 6) and *A. thorpei* (♀ L_{50} = 329 mm @ 3 years, max. age = 12 years, van der Elst et al. 1990), both of which have marine nursery areas (Chapter 6, Fennessy 1994), *A. japonicus* (♀ L_{50} = 1070 mm @ 6 years, max. age = 42 years, Chapter 3) has a large size at sexual maturity and a long life-span. Female L_{50} occurs at 60 % of maximum length for *A. japonicus* (L_{max}= 1810) (Griffiths & Heemstra 1995), at 30 % of L_{max} for *A. thorpei* (L_{max} = 1100 mm TL, Fennessy, ORI, Durban, personal communication 1995), and at 23 % of L_{max} for *A. inodorus* (L_{max} = 1450 mm TL, Griffiths & Heemstra 1995). Sexual maturity in *A. japonicus* is therefore delayed with the result that it has a larger size at first maturity than sympatric *Argyrosomus* species, even when expressed as a dimensionless ratio. Considering that fecundity in fishes is generally a power curve function of length (Roff 1988, Wootton 1990), the reproductive strategy of *A. japonicus* appears to be one of maximized individual fecundity. Faster growth (Chapter 3) and later maturity in females than in males, are possibly adaptations which increase individual fecundity even further.

It is generally accepted that life time fecundity is an appropriate measure of fitness for marine fishes (Roff 1988, 1991, 1992). Therefore if there were no costs associated with reproduction, fish would attain maturity within their first year and at the smallest possible size (Wootton 1990, Roff 1992). Roff (1984, 1991) showed (theoretically and empirically) that the optimal size (and age) at maturity is determined by trade-offs between fecundity (which increases with age/size), growth rate and natural mortality. In other words, reproductive losses due to delayed maturity may be offset by future gains through increased individual fecundity, particularly if the pre-maturity growth rate is high (as in *A. japonicus*, Chapter 3) and the chances of surviving to, and/or for several years after, maturity are good. This would imply that *A. japonicus* experiences lower rates of natural mortality than *A. inodorus*. Juvenile dusky kob are found in estuaries and in the surf zone, where they avoid numerous nearshore marine predators which feed on small sciaenids, including *A. inodorus* and *A. thorpei* (Cliff et al. 1989, 1990, Cliff & Dudley 1991a&b, 1993, Ebert 1991, Smale 1991). Since natural mortality (except in very old individuals) is inversely related to fish size (Wootton 1990, Roff 1992), the large size of the adult dusky kob implies a low rate of predation in the marine environment. It is therefore postulated that *A. japonicus* evolved its life history strategy, including delayed reproduction, a large size at first maturity, and long life-span, as a result of lower rates of natural mortality.

It is logical that species which live long lives must have evolved mechanisms for decreasing natural mortality, including predator avoidance. Such mechanisms include cryptic behaviour and the use of refuges in reef fishes e.g. the Serranidae, and high swimming speeds and shoaling in pelagic species e.g. the Scombridae (Wooton 1990, Pitcher & Parrish 1993). The Sciaenidae are believed to have evolved from a common New World (eastern Pacific and western Atlantic) marine ancestor (Sasaki 1989). Since the life-history of *A. japonicus* bears closer similarity to long lived species from a different hemisphere and Subfamily, than it does to those of shorter lived sympatric *Argyrosomus* species, with marine nursery areas, it is possible that estuarine utilization (including adaptation to low salinity) has facilitated the evolution of longevity within the Sciaenidae. This does not imply that all sciaenids which utilize estuaries should have long life-spans, but suggests that in this family, the adaptation to low salinities may have provided the option for some species to evolve life-histories based on longer lifespans. In terms of the trade-off concept, reduced juvenile mortality would have facilitated later maturity. Due to the costs of reproduction, later maturity would have increased longevity. It also would have allowed a longer period of fast prematurity growth, which in turn would have reduced natural mortality further, not only for now faster growing juveniles, but also for the larger adults that were consequently produced, therefore increasing potential life span even further.

Roff (1988) predicted mechanistically and showed empirically, that migratory fishes are larger and have larger sizes at maturity, than closely related non-migratory taxa. He also postulated that "Large species may be 'preadapted' to migration by virtue of their larger size, or large size may evolve in concert with the evolution of migration: both processes are a priori reasonable and neither can be discounted." Since a portion of the adult dusky kob population do not partake in the spawning migration to KwaZulu/Natal (± 1000 km), but spawn in the Cape regions, the former scenario is probably more applicable to this species i.e reduced mortality having paved the way for delayed maturity and therefore preadapting *A. japonicus* for migration. *A. inodorus* on the South African east coast exist as two allopatric stocks, and hence do not undergo substantial long-shore migration (Chapter 6).

Impact of man

The life cycle of *A. japonicus* may be divided into four phases: (i) eggs and larvae, which occur pelagically in the nearshore marine environment; (ii) early juveniles, which are found in the upper reaches of estuaries; (iii) juveniles, which inhabit the middle to lower reaches of estuaries and the surf zone; and (iv) adults, which occur predominantly in the nearshore marine environment, but frequent estuaries and the surf zone. The last three phases are particularly vulnerable to the activities of man.

The adult population form dense aggregations during the spawning season (particularly in Kwazulu/Natal), and are heavily targeted by recreational and commercial lineboat fishers. Juvenile *A. japonicus* effectively inhabit a narrow coastal band consisting of estuaries and the surf zone. Although these environments are not exploited commercially at present, they are readily accessible to recreational anglers, whose numbers, according to van der Elst (1989), are increasing exponentially. Intense exploitation of the juvenile and adult populations of a species which has evolved a life-history strategy based on low natural mortality, is likely to severely reduce the average lifetime fecundity of recruits, which may ultimately lead to recruitment overfishing.

Although the early juveniles are not directly exploited, they are estuarine dependant and rely on the timeous inflow of sufficient freshwater to locate estuaries, for the opening of the mouths of closed systems, for increasing the production of important food items, and to create salinity gradients and turbid conditions for their protection from predators. Any factor that impedes river flow (e.g. droughts, construction of dams or excessive irrigation) or results in the pollution, siltation, or closing of estuaries (e.g. industrial effluent or poor agricultural practices), would theoretically increase the rate of early juvenile mortality, thus affecting recruitment. Most of South Africa's estuaries have already been degraded to some degree as a result of human activity, and reduced freshwater inflow (resulting from catchment degradation and the construction of reservoirs) is a major problem facing these systems (Heydorn 1986, Whitfield & Bruton 1989).

If *A. japonicus* is to be successfully managed as an important commercial and recreational species in South Africa, a holistic approach is required in order to address all phases of the life cycle.

Appendix 1. The localities in each region from which biological and length data were obtained from South African line-caught *Argyrosomus japonicus* (1990-1993). In the case of the surf zone and nearshore environments, catches were made up to 30 km on either side (coastwise) of the listed locality.

REGION	HABITAT		
	Estuary	Surf Zone	Nearshore (10-100 m depth)
KwaZulu/Natal	Lake St Lucia Richards Bay Tugela River Durban Bay	Numerous localities between Lake St Lucia mouth and the Mtamvuna River	Lake St Lucia mouth Mtinzini Richards Bay Salt Rock Durban Warner Beach Park Rynie
South-Eastern Cape	Kei River Keiskamma River Great Fish River Sundays River Swartkops River Gamtoos River	Keiskamma mouth Bira mouth Kowie mouth Sundays mouth Gamtoos mouth Jeffries Bay	Port Elizabeth
Southern Cape	Gouritz River Duiwenoks River Breede River Heuningsnes River	Klein Brak mouth Mossel Bay Vlees Bay Stil Bay Breede mouth	Mossel Bay Stil Bay Breede River

CHAPTER 5

AGE AND GROWTH OF SILVER KOB, *ARGYROSOMUS INODORUS*, WITH COMMENTS ON STOCK SEPARATION IN SOUTH AFRICAN WATERS

AGE AND GROWTH OF SILVER KOB, *ARGYROSOMUS INODORUS*, WITH COMMENTS ON STOCK SEPARATION IN SOUTH AFRICAN WATERS

ABSTRACT

Silver kob, *Argyrosomus inodorus*, sampled from three regions along the South African eastern seaboard during 1991/1992, were aged using longitudinal otolith sections. Otoliths (n=750) were selected from fish covering a wide size range (60-1310 mm TL). Ages 0-25 years were recorded but fish older than 13 years were not common. Marginal increment analysis indicated that for fish of 2-11 years, one opaque and one translucent zone were deposited annually. The first annulus was validated using daily increments. Observed lengths-at-age were highly variable. Statistically there was no difference between growth in the Southern Cape and South-Eastern Cape, or between the sexes. Fish in the South-Western Cape initially grew faster than those in the other two regions, but growth declined earlier and a smaller maximum size was attained. The growth models which best fitted the observed length-at-age data were the Richards for the east coast (S.E. Cape & S. Cape combined) and the Logistic for the South-Western Cape. The derived parameters were as follows:

$$L_t = 1141.8[1 + 1/0.261 \times e^{-0.646(t-6.928)}]^{-0.261} \quad \text{East Coast}$$
$$L_t = 1087[1 + e^{-0.409(t-3.339)}]^{-1} \quad \text{South-Western Cape}$$

The relationships between otolith dimensions (length, height, mass and ostium to cauda distance) and fish length, in each of three regions, suggested that South African *A. inodorus* exist as at least three stocks. The nature of growth zones in the sectioned otoliths confirmed this conclusion.

INTRODUCTION

The silver kob, *Argyrosomus inodorus* (Griffiths & Heemstra 1995), is an important commercial and recreational species off the coasts of Namibia and South Africa. It occurs from northern Namibia to the Kei River on the east coast of South Africa; but is only abundant off central and northern Namibia, and off the South African eastern seaboard from Cape Point to East London. Until recently *A. inodorus* was misidentified as *A. hololepidotus*, and on the east coast of South Africa was also confused with a sympatric congeneric species, *A. japonicus* (Griffiths & Heemstra op cit.).

Information on the growth rate of silver kob and on the existence of separate stocks, is essential to understanding it's life history, for stock assessment and also for improved management advice. Studies on North American sciaenids indicate that saggital otoliths provide the most accurate estimates of age for this family as a whole (Theiling & Loyacano 1976, Goeman et al. 1984, Barger 1985, Maceina et al. 1987, Lowerre-Barbieri et al. 1994). In this study the otoliths of *A.*

inodorus, from three regions along the South African eastern seaboard, were aged, and the growth of this species described for the first time. The study of Wallace and Schleyer (1979) on "*A. hololepidotus*" was based on *A. japonicus* (Griffiths & Hecht in press).

Otolith shape has proved to be a useful indicator of stock identity in fishes (Campana & Casselman 1993). The otoliths of fish from different areas are generally compared using linear measurements of definable structures (Messieh 1972, Rojo 1977, King 1985, Payne 1985, Grygiel 1987, Japp 1990, Dawson 1991, Smith 1992), or by using mathematical descriptions of shape, particularly Fourier series (Bird et al. 1986, Castonguay et al. 1991, Smith 1992, Campana & Casselman 1993, Colura & King 1995). The possibility of more than one silver kob stock existing along the South African eastern seaboard was investigated by comparing the relationships between fish length and four otolith measurements, and also by comparing the growth zones of sectioned otoliths, from the three coastal regions.

MATERIALS AND METHODS

The South African eastern seaboard from Cape Point to the Kei River was divided into three regions for sampling purposes (Fig. 5.1). Regional boundaries did not necessarily coincide with political boundaries. During a two year period (1990/91) saggital otoliths, total fish length (nearest mm) and fish mass were collected from male and female silver kob, caught by recreational and commercial line-fishers and by trawlers. Landing sites included: Port Alfred and Port Elizabeth in the South-Eastern Cape; Mossel Bay, Stil Bay and the Breede River in the Southern Cape; and False Bay in the South-Western Cape. Temporal trends in the availability of specific size classes were not observed for any of the fisheries. Fish mass was measured to the nearest gram (< 500g), to the nearest 20g (500g - 5kg) and to the nearest 100g (5 - 25kg). The otoliths were removed ventrally by first removing the gill rakers and then cutting away a portion of bone in the prootic/exoccipital region. They were lifted out of the skull with forceps, cleaned and stored dry in envelopes.

Ageing

A total of 212 otolith pairs from the South-Western Cape, 247 from the Southern Cape and 203 from the South-Eastern Cape were used for ageing. These were selected for each region so that,

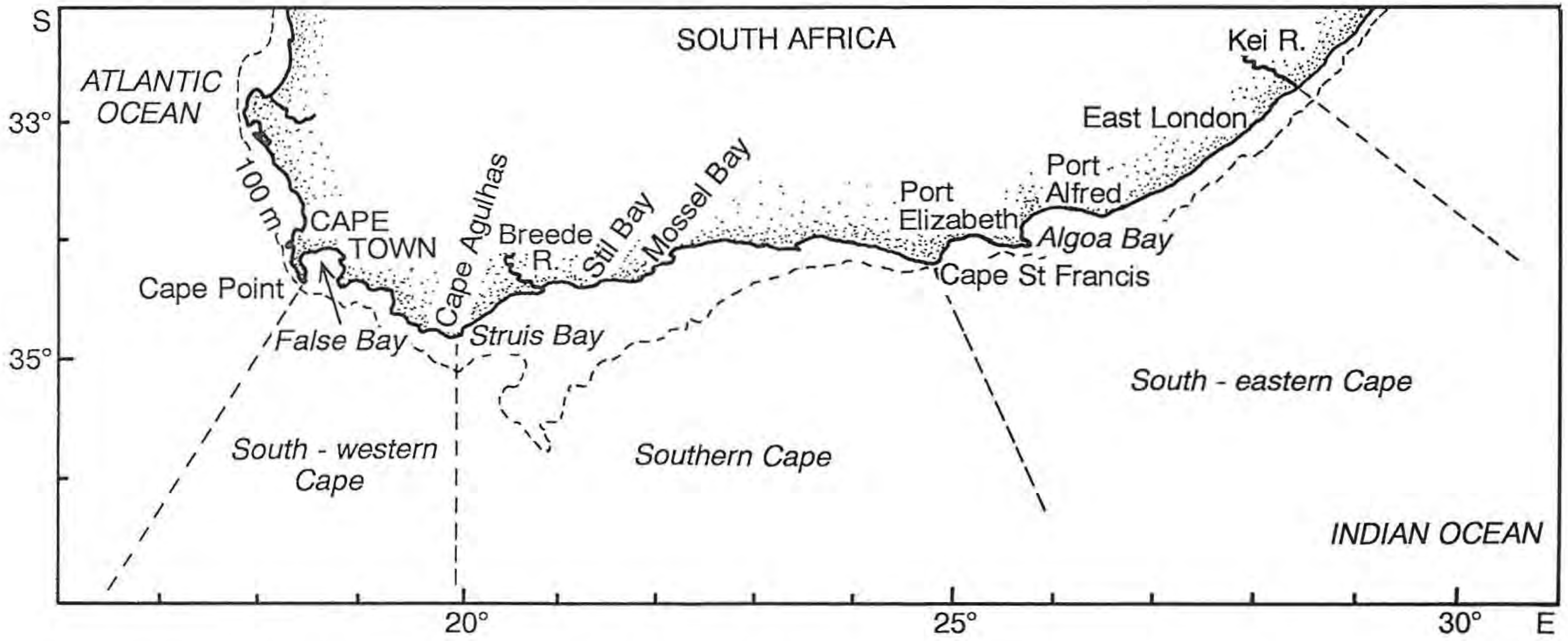


Fig. 5.1: Map of South Africa showing the three sampling regions.

where possible, every 10-mm size class, within the range of fish sampled (63 - 1310 mm TL), was represented by two pairs (one male and one female) from each region (Fig. 5.2). Due to the thickness and overall opacity of silver kob otoliths, those of all sizes were sectioned. Longitudinal sagittal sections have proved to be good indicators of age for South African sciaenids i.e. *Atractoscion aequidens* (Griffiths & Hecht 1995) and *A. japonicus* (Griffiths & Hecht in press). Depending on otolith size, between two and four longitudinal sections (0.5-0.7 mm) were cut from each right otolith to ensure that the core was included. A single diamond wafering blade was used, with a saw similar to that described by Rauck (1976). Each section was then mounted on a glass slide using DPX mountant and examined on a black background using a dissecting microscope (6X) and reflected light. The number of opaque (white) zones (Fig. 5.3) were counted four times, at least one week apart, without any reference to fish size. If less than three readings coincided the otolith was rejected. The periodicity of growth zone deposition (for ages 2-11 yrs) was determined using marginal increment analysis (Bagenal & Tesch 1978). Because growth zones became narrower with age, the marginal increments were analysed according to two age groups i.e. 2-7 and 8-11 years. Marginal increments of South-Eastern Cape fish were not analysed as the growth zones in this region were not as clear as those in the Southern Cape and the South-Western Cape. An additional 88 otoliths from the South-Western Cape and the Southern Cape were sectioned to increase sample numbers for months which were not adequately represented by the otoliths selected for ageing. The first annulus was validated using daily growth increments. Seven otolith sections, each with one opaque zone, were mounted on SEM statives with colloidal silver. These were then polished using 0.1 μm alumina paste, etched for 2.5 mins with 0.1% HCl, rinsed with water and cleaned using ultrasound. Finally they were coated with gold-palladium (20 nm) and viewed with a Leica S-440 SEM at 2500 X. The structure of the daily growth increments were similar to those of *A. japonicus* (Griffiths & Hecht in press), and were counted between the primordium and the proximal margin, along an axis just anterior to the "window" (below the cauda, see Fig. 5.3).

Growth in length

Several growth models were fitted to the length-at-age data for each of the three regions, including the Schnute, special von Bertalanffy, generalized von Bertalanffy, Richards, Gompertz and the Logistic (Schnute 1981). Zero-year-old fish were excluded from the curve fitting procedure because the sampling gear used selected only the larger individuals of this age

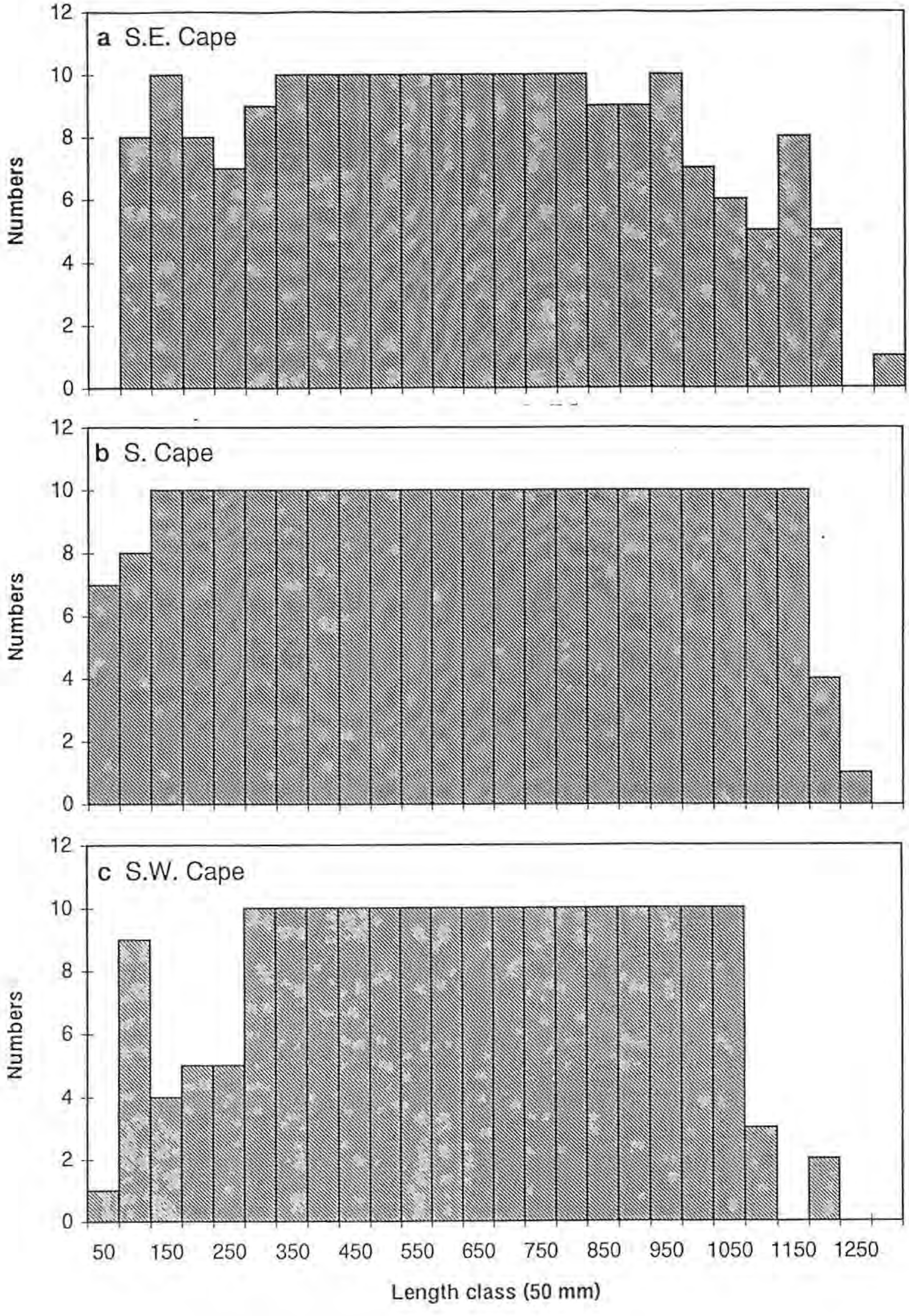


Fig. 5.2: Length frequency histograms of *A. inodorus* used for the growth and the stock separation analyses from a) the South-Eastern Cape, b) the Southern Cape, and c) the South-Western Cape.

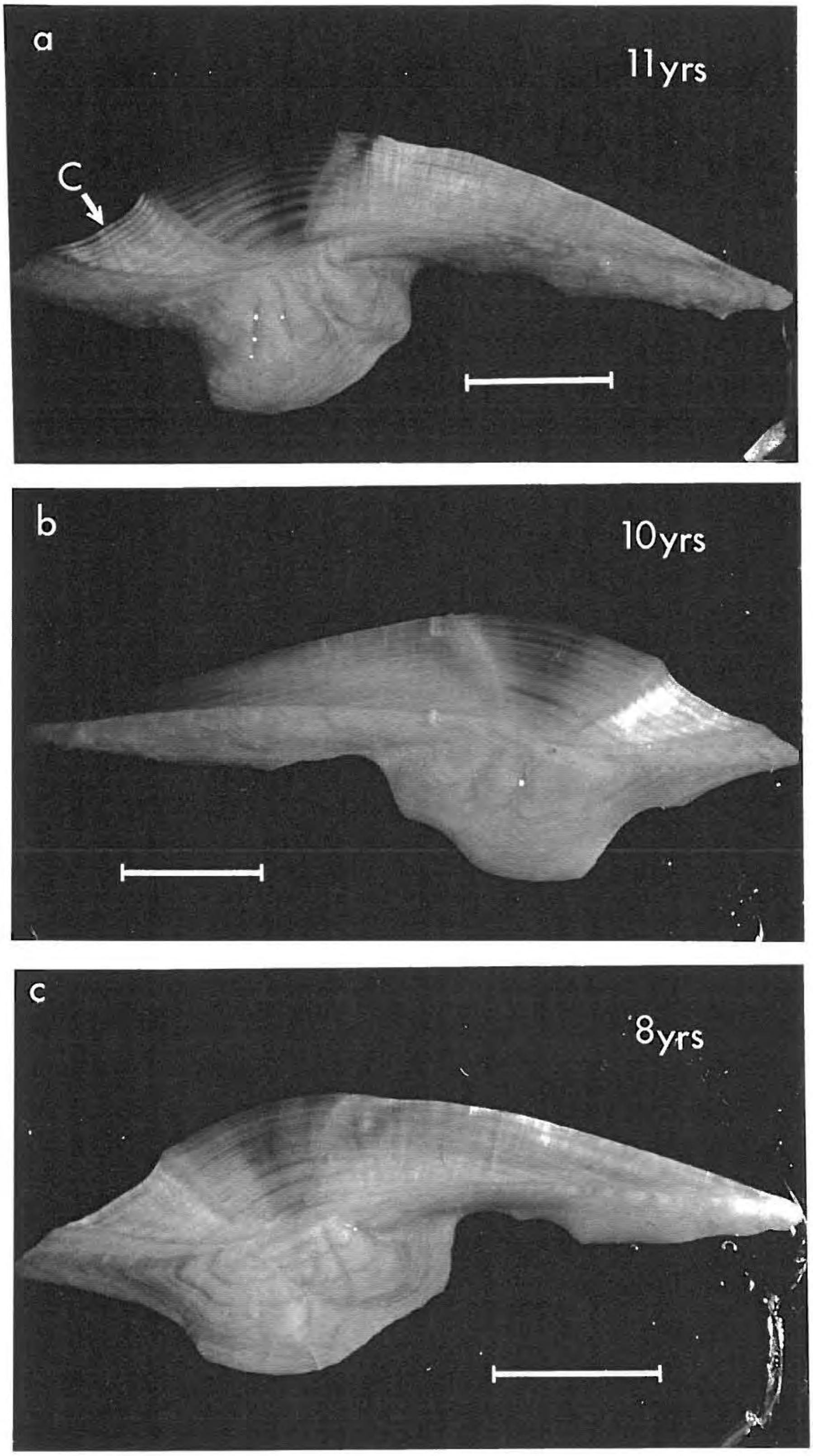


Fig. 5.3: Longitudinal otolith sections of *Argyrosomus inodorus* from: a) the South-Western Cape, Type 1; b) the Southern Cape, Type 2; and c) the South-Eastern Cape, Type 3 . See Table 5.1 for otolith Type descriptions. C = Cauda (the triangular structure below the cauda is referred to as the window). Scale bar = 5 mm.

category. Using an iterative, non-linear minimization procedure, each model was fitted twice to each data set, once minimizing the sum of the squared absolute differences, and once minimizing the sum of the squared relative differences (Butterworth et al. 1989, Punt 1992). The models were then tested for goodness of fit against the following criteria:

a) randomness of residuals (one-sample runs test; Draper & Smith 1966).
b) trends in residuals (residual plot).
c) credible L_∞ values.
d) lowest sum of squared residuals.

L_∞ is the calculated asymptotic length to which the average uncaptured fish in a population would grow and is not intended to represent those of record size (Ricker 1975). Casselman (1983) pointed out the L_∞ value should be credible when compared to observed measures, if a derived curve is to be accepted as a good model of growth. Derived curves with L_∞ values substantially larger than record sizes were regarded as inadequate.

Standard errors and 95% confidence intervals were calculated for each parameter of the models which best fitted the data, using the non-parametric bootstrap technique (Efron 1981) and the percentile method (500 bootstraps) respectively.

Growth rates between regions and between sexes were compared by performing likelihood ratio tests (Draper & Smith 1966) on curve fitting data for combined and separate data sets ($p = 0.05$). Analysis of variance (ANOVA) and studentized Tukey's range test were also used to determine the significance of differences in the average observed lengths-at-age between regions and between sexes.

To allow for the conversion of total length-at-age to mass-at-age or standard length-at-age, the relationships between total fish length and mass, and total fish length and standard length were also derived.

Fish length/otolith dimension relationships

The left otolith from every pair used for the growth analysis (Fig. 5.2) was measured for length (OL), height (OH), ostium-cauda distance (OC)(to the nearest 0.01mm) and mass (OM)(to the nearest 0.0001g), according to the methods of Griffiths & Heemstra (1995). Theotolith dimension and fish length (TL) data were log-transformed, the relationships were modelled using linear regressions, and compared between areas by testing for differences in slopeand intercept using the F statistic (Draper & Smith 1966). Sectioned otoliths were also assigned to one of four types, based on the structure of the growth zones (Table 5.1). The sectioned otoliths from the three regions were then compared using frequency distributions of the four types.

Table 5.1: Four otolith types of South African *Argyrosomus inodorus*, based on longitudinal sections.

Type	Description
1	Growth zones appear as distinct opaque (wide) and translucent (narrow) bands in and around the window (below the cauda). See Fig. 5.3a.
2	Growth zones less distinct, with translucent zone narrower than type 1, and opaque zones slightly more diffuse. See Fig. 5.3b.
3	Translucent zones still narrower, opaque zones fairly diffuse with translucent checks. Type 3 sections were difficult to read. See Fig. 5.3c.
4	Section consisting of numerous opaque and translucent checks, which are irregular in size and do not comprise identifiable growth zones.

RESULTS

Ageing

Longitudinal sections of the saggital otoliths of *A. inodorus*, from the South-Western Cape, showed distinct opaque (wide) and translucent (narrow) bands which can be used for ageing (Fig. 5.3). These were most visible in and around the "window" (beneath the cauda, Fig. 5.3). Moving eastwards to the Southern Cape and the South-Eastern Cape, the growth zones of sectioned otoliths became progressively less distinct, with the translucent band narrowing and the opaque band becoming more diffuse (Fig. 5.3). As a result, the predominant otolith type in the South-Western Cape was 1, in the Southern Cape was 2, and in the South-Eastern Cape was 3 (Fig. 5.4). One otolith (0.4%) from the South-Western Cape, three otoliths (0.9%) from the

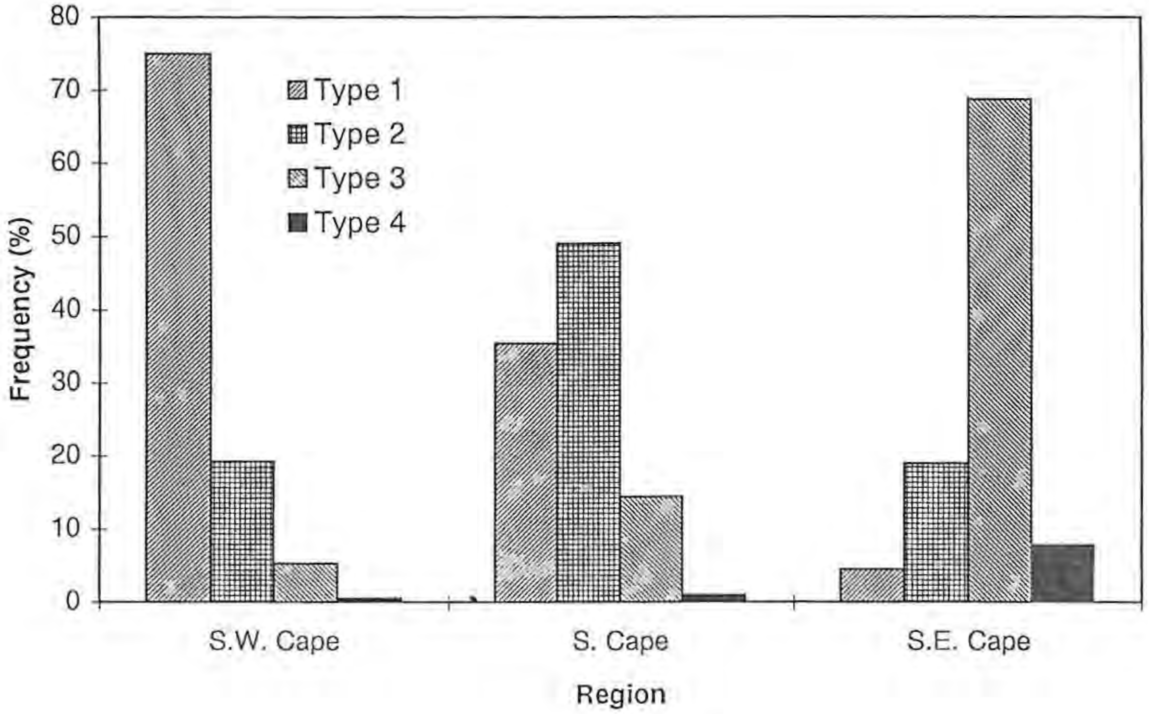


Fig. 5.4: Frequency distributions of the four otolith Types for *Argyrosomus inodorus* from the South-Western Cape, the Southern Cape and the South-Eastern Cape.

Southern Cape and 14 (6.9%) from the South-Eastern Cape were rejected because at least three (of the four) counts did not agree.

Between 373 and 574 daily growth increments were counted for otoliths with one opaque zone (i.e. >360 but substantially <720)(including 2 with juvenile rings), confirming that this was the first annulus (Morales-Nin & Ralston 1990, Buxton & Lang 1993, Mug-Villanueva et al. 1994). Daily counts of > 360 can be attributed to the fact that some of the otoliths examined had hyaline margins (therefore slightly older than one year) and also to the fact that specimens may have been spawned early in the protracted (Chapter 6) spawning season. Marginal increment analysis (Fig. 5.5) revealed that one translucent and one opaque zone is deposited annually in the otoliths of silver kob from 2-11 years old. The exceptionally large standard deviations associated with the months of February and March (Fig. 5.5a&b) can be attributed to the fact that marginal increments at this time of the year are based on either completely formed or recently initiated annuli. The wide opaque zone was formed from August to February, which coincided with the spawning season (see Chapter 6). A juvenile check (confirmed by daily growth analysis) was sometimes present in silver kob otoliths. It was narrower than the first annulus, and was probably formed in those specimens which were spawned early in the five month (see Chapter 6) spawning season. Although only the first eleven annuli were validated, it was assumed that each opaque band also represented an annulus in older specimens. Observed lengths varied greatly within age-groups (Fig. 5.6). The oldest silver kob aged was 25 years, but there were few fish older than 13 years (Fig. 5.6) .

Growth

Based on the criteria for goodness of fit used in this study, the models which best fitted the length-at-age data were the logistic (with absolute error structure) for the South-Western Cape and the Richards (with absolute error structure) for the South-Eastern Cape and for the Southern Cape. The length-at-age data for the South-Eastern Cape and the Southern Cape fish were very similar (Fig. 5.6), ANOVAs revealed no significant differences in mean lengths-at-age (1-11 yrs), and a likelihood ratio test (F = -1.07; Df = 4 & 447) indicated that there was no significant difference between the fitted curves. The data for the South-Eastern Cape and the Southern Cape were therefore pooled to provide an east coast data set. ANOVAs and likelihood ratio tests also revealed that growth between the sexes did not differ significantly on the east coast (p = 0.35-

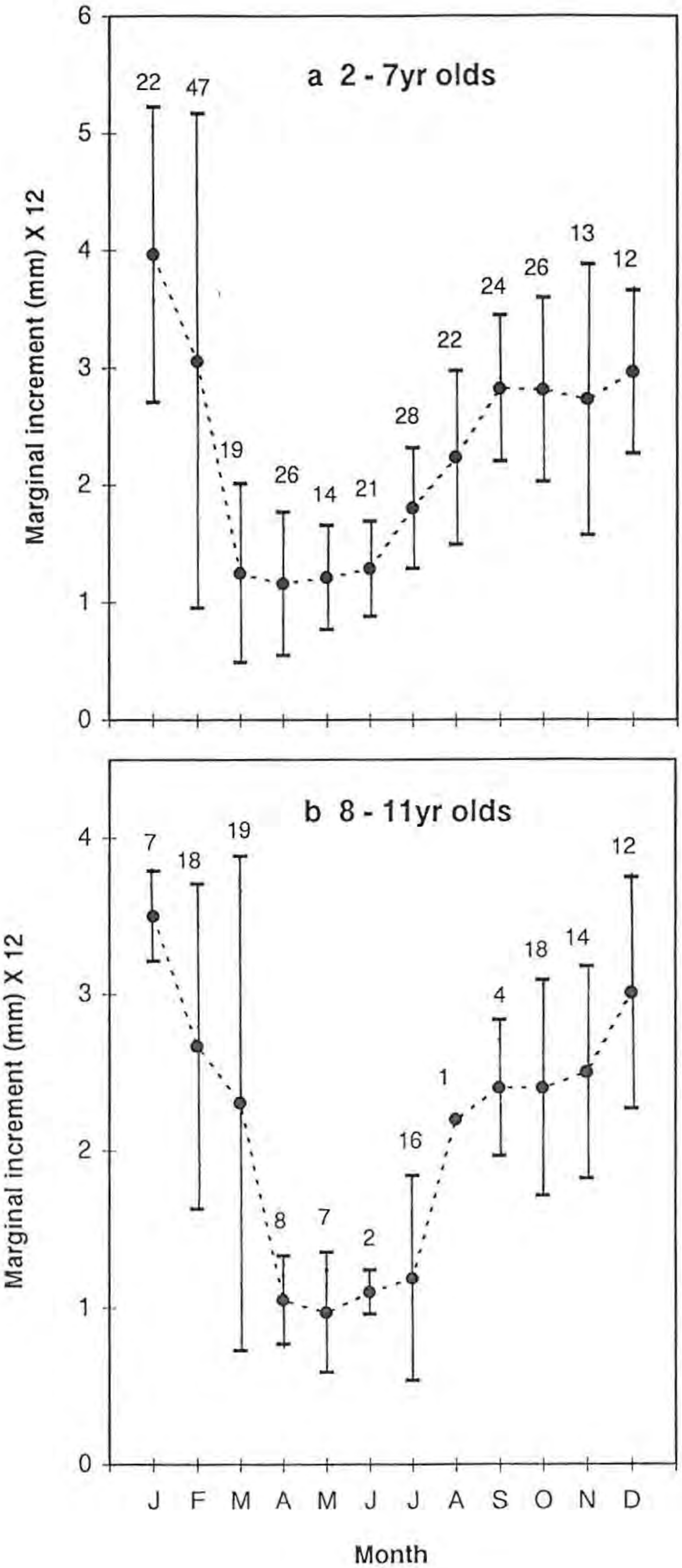


Fig. 5.5: Mean monthly marginal increments (at 12X magnification) of a) 2-7 year and b) 8-11 year *Argyrosomus inodorus* from the South-Western Cape and the Southern Cape. Vertical bars are 1 standard deviation. Numbers of otoliths are indicated above bars.

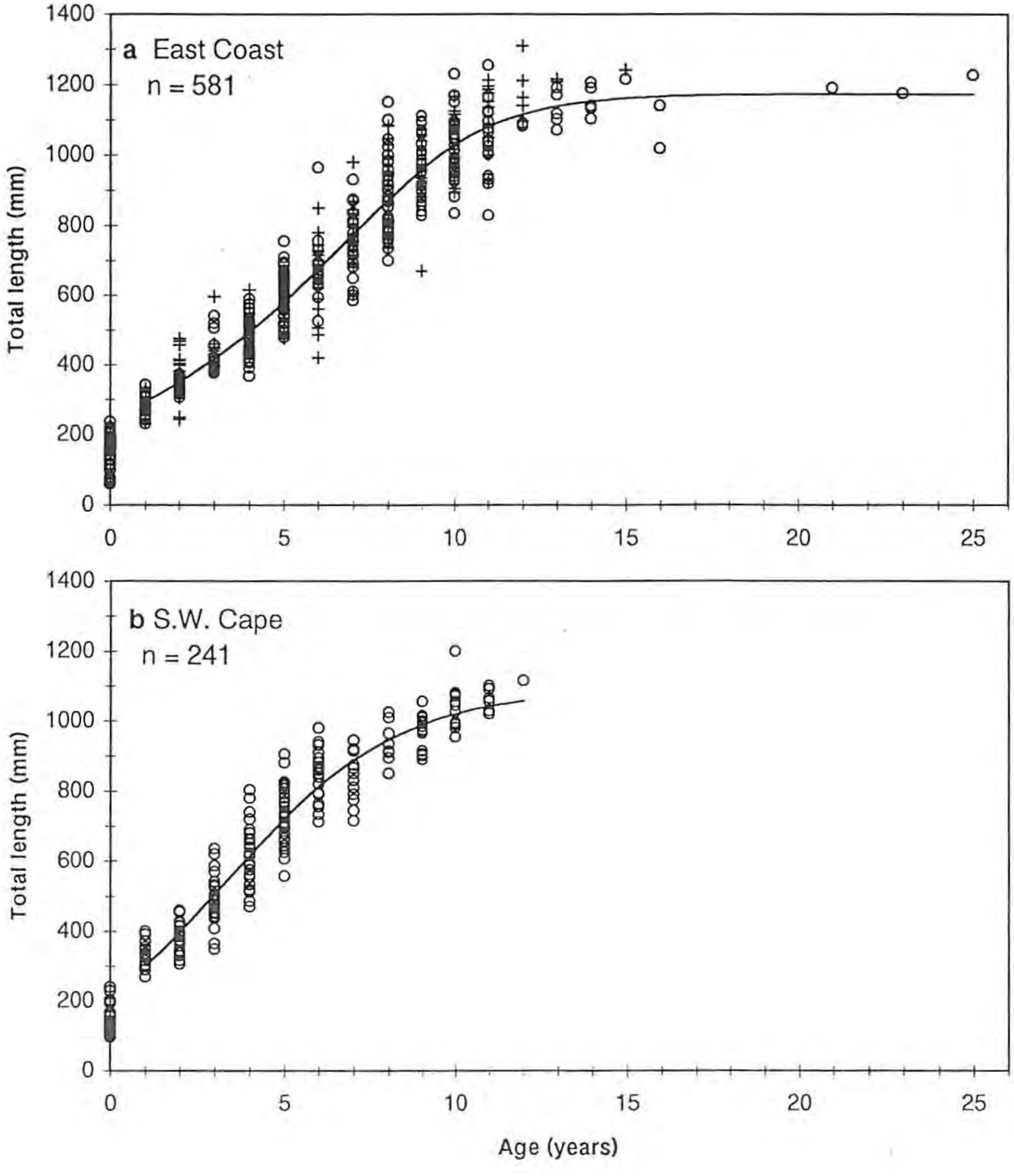


Fig. 5.6: a) The Richards growth model fitted to combined observed data for *Argyrosomus inodorus* from the Southern Cape (circles) and the South-Eastern Cape (crosses) and b) the Logistic model fitted to observed data from the South-Western Cape.

0.84; F = 2.0, df = 4 & 447), but that differences between growth rate off the east coast and off the South-Western Cape, were highly significant (Logistic: F = 58.67, df = 651 & 3; Richards: F = 67.56, df = 649 & 4). Due to the large variation in lengths-at-age observed for silver kob, the South-Western Cape observed data set was considered too small to test for differences between the sexes. The derived parameters of the models are given in Table 5.2, with standard errors and the 95% confidence intervals for each parameter. The observed data and fitted curves are illustrated in Figure 5.6. Although the special (three parameter) von Bertalanffy growth model has a long history in age and growth studies, it did not adequately fit the observed data for silver kob. Residuals were not random, residual plots revealed strong trends, L_∞ values were unrealistically high (125% and 190% of recorded maximum lengths), and the sums of squared residuals were not as low as for other models.

Table 5.2: Parameter estimates, standard errors and the 95% confidence intervals (CI) for the Logistic and Richards growth models, fitted to *A. inodorus* age data from the South-Western Cape and the east coast (S. Cape + S.E. Cape) respectively.

Region (n)	Parameters			
	K	L_∞	t_*	p
S.W.Cape(n=202)				
Logistic Model	0.409	1086.84	3.339	-
Standard error	0.021	20.881	0.119	-
left 95% CI	0.368	1029.719	3.131	-
right 95% CI	0.451	1084.672	3.59	-
East Coast (n=453)				
Richards Model	0.548	1172.29	6.67	0.325
Standard error	0.108	33.633	0.450	0.154
left 95% CI	0.343	1138.41	5.645	0.25
right 95% CI	0.670	1259.14	7.107	0.716

The growth of silver kob in the South-Western Cape and on the east coast had a similar pattern. It was rapid in the first year, slowed down for one (South-Western Cape) or two (east coast) years, whereafter it increased, and remained fairly constant for several years and then finally approached an asymptote (Fig. 5.6). Despite similar growth patterns, growth in the South-Western Cape was initially faster (1-7 years) than on the east coast, but it slowed sooner (8 vs 11 yrs) with the result that *A. inodorus* in the former region attained a smaller maximum size (Fig. 5.7).

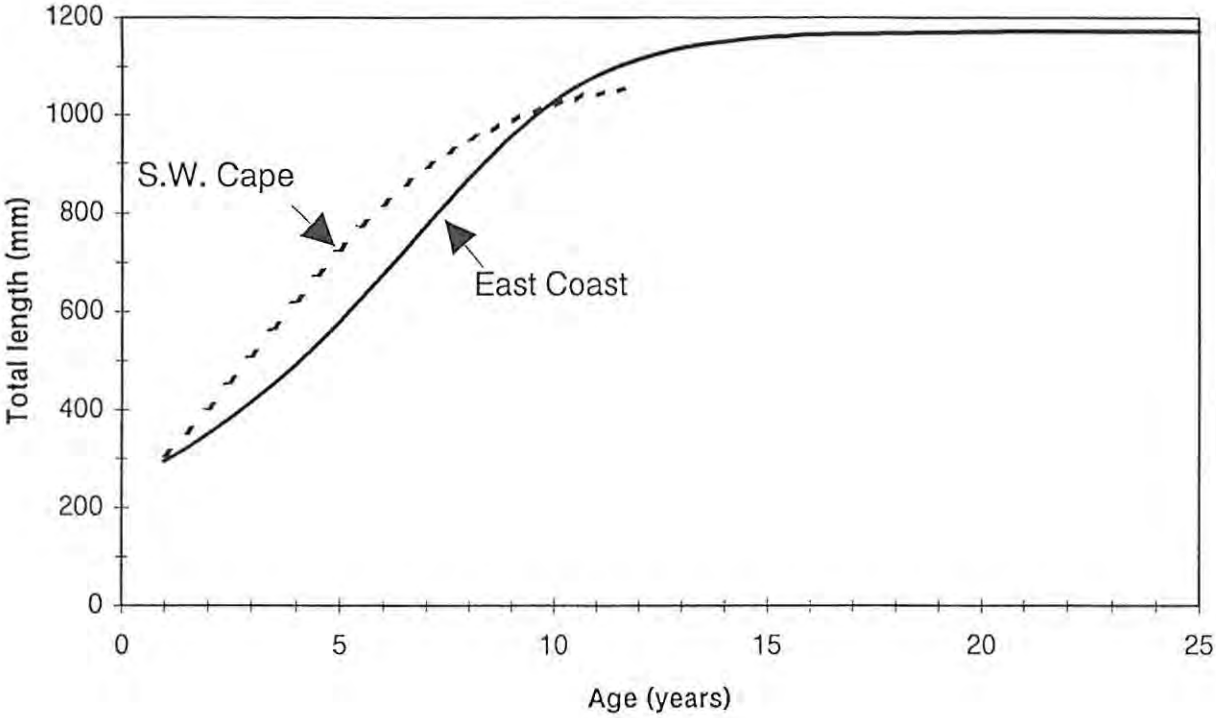


Fig. 5.7: Comparison of growth curves for *Argyrosomus inodorus* from the South-Western Cape and the east coast (Southern Cape + South-Eastern Cape).

Morphometric relationships

The total length/mass and total length/standard length relationships for South African *A. inodorus* are described in Table 5.3. The relationships between otolith dimension and total length were significantly different between regions (Table 5.4) but not between sexes within regions (p>0,05). Based on the degree of significance, and on the number of characters for which differences were found (Table 5.4), there was a closer similarity between the otolith dimension fish length relationships of the South-Western Cape and the Southern Cape, than between either of these regions and those of the South-Eastern Cape (see also Fig. 5.8a-d).

DISCUSSION

This study shows that longitudinal sections of *A. inodorus* otoliths have clear growth zones, particularly in the South-Western Cape and the Southern Cape, which can be used for ageing. The high variability of observed lengths within age groups is not unusual for sciaenids e.g. *Sciaenops ocellatus* (Beckman et al. 1989, Ross et al. 1995), *Micropogonias undulatus* (Barbieri et al. 1994a), *Pogonias cromis* (Beckman et al. 1990), *Cynoscion nebulosus* (Murphy & Taylor 1994), *Atractoscion aequidens* (Griffiths & Hecht 1995), *Cynoscion regalis* (Lowerre-Barbieri et al. 1995) and *Argyrosomus japonicus* (Griffiths & Hecht in press). Since variation in observed lengths progressively increased after age one (Fig. 5.6a&b), the high variance observed for *A. inodorus* is not likely to be due to its protracted (see Chapter 6) spawning season, but is probably a result of variation in individual growth (Bowker 1995). Declining variance in older silver kob (Fig. 5.6a&b) could theoretically be attributed to growth compensation (Ricker 1979), or to size selective mortality i.e. fast growing individuals die before slow growing individuals thus reducing the variance of length in the oldest age groups (Ricker 1969, 1979). The low number of silver kob older than 13 years, even though the maximum age was 25 years, is possibly a result of exploitation. According to Ricker (1963), populations which include appreciable numbers of fish older than 12 yrs, prior to exploitation, will be extremely sensitive to fishing. South African *A. inodorus* have been exploited for at least 150 years (Smith 1849, Pappe 1866).

Table 5.3: Total length (TL)/ mass(M) and total length/ standard length (SL) relationships for South African *Argyrosomus inodorus*.

Relationship	r	n	range
$M(g) = 6x10^{-6}TL(mm)^{3.0657}$	0.997	3150	60 - 1340 mm TL
$SL(mm) = 0.8999TL(mm) - 20.958$	0.999	454	100 - 1210 mm TL

Table 5.4: The relationships between otolith dimensions and total fish length (TL) for *A. inodorus* from the South-Eastern Cape (SEC), the Southern Cape (SC) and the South-Western Cape (SWC). OL = Otolith length, OH = otolith height, OC = Ostium to cauda distance and OM = Otolith mass. The relationships for each region were compared statistically (differences in slope and intercept) after straight line regressions were fitted to the Log-transformed data. ** = $p<0.01$, * = $p<0.05$.

Region	Relationship	n	r	Comparison		
S.E. Cape	$OL(mm) = TL(mm)^{0.6358}/3.115$	212	0.991		SEC	SC
S. Cape	$OL(mm) = TL(mm)^{0.713}/5.116$	247	0.994	SC	**	
S.W. Cape	$OL(mm) = TL(mm)^{0.704}/4.831$	203	0.995	SWC	**	
All	$OL(mm) = TL(mm)^{0.699}/4.691$	662	0.993			
S.E. Cape	$OH(mm) = TL(mm)^{0.593}/4.562$	212	0.981		SEC	SC
S. Cape	$OH(mm) = TL(mm)^{0.6107}/5.216$	247	0.993	SC	**	
S.W. Cape	$OH(mm) = TL(mm)^{0.586}/4.430$	203	0.990	SWC	**	**
All	$OH(mm) = TL(mm)^{0.603}/4.932$	662	0.990			
S.E. Cape	$OC(mm) = TL(mm)^{0.558}/7.938$	212	0.956		SEC	SC
S. Cape	$OC(mm) = TL(mm)^{0.628}/12.001$	247	0.979	SC	**	
S.W. Cape	$OC(mm) = TL(mm)^{0.602}/10.434$	203	0.965	SWC	**	*
All	$OC(mm) = TL(mm)^{0.607}/10.717$	662	0.972			
S.E. Cape	$OM(mm) = TL(mm)^{1.618}/31417.38$	212	0.989		SEC	SC
S. Cape	$OM(mm) = TL(mm)^{1.943}/265858.16$	247	0.991	SC	**	
S.W. Cape	$OM(mm) = TL(mm)^{1.925}/240054.58$	203	0.990	SWC	**	
All	$OM(mm) = TL(mm)^{1.896}/195344.0$	662	0.989			

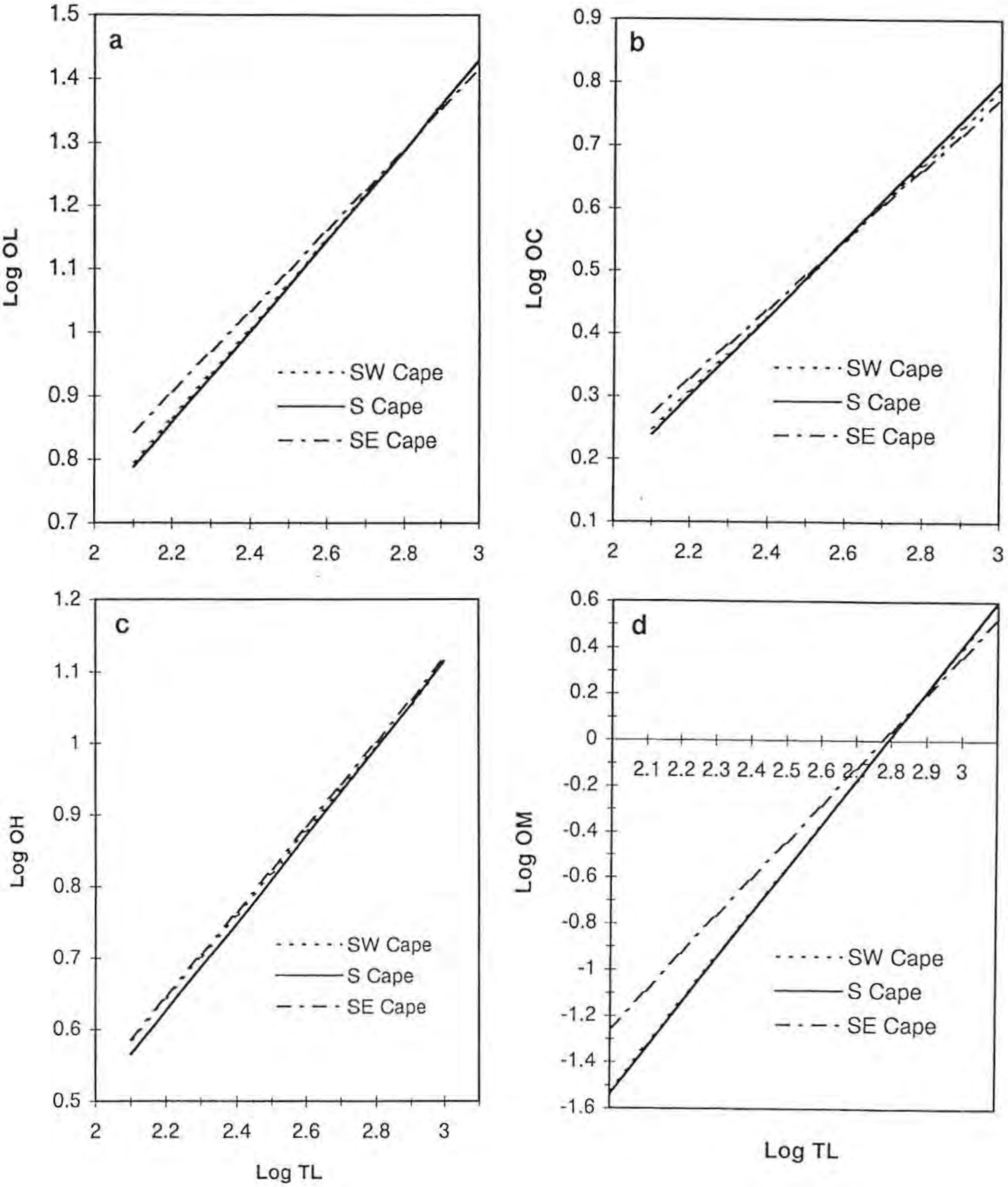


Fig. 5.8: Regional relationships of total fish length (TL) and a) otolith length (OL), b) ostium to cauda distance (OC), c) otolith height (OH) and d) otolith mass (OM). The mathematical descriptions of these relationships and the significance of the observed differences are given in Table 5.4.

The poor fit of the special von Bertalanffy model to the observed data for *A. inodorus* and other sciaenids, e.g. *Pogonias cromis* (Beckman et al. 1990), *Cynoscion nebulosus* (Murphy & Taylor 1994), *Sciaenops ocellatus* (Ross et al. 1995), *Atractoscion aequidens* (Griffiths & Hecht 1995) and *Argyrosomus japonicus* (Griffiths & Hecht in press), emphasizes the importance of fitting a variety of models to observed data and assessing the goodness of fit. The parameters of derived von Bertalanffy functions (e.g. L_∞ and K) are often used for mortality estimates (Pauly 1980), stock assessment (Butterworth et al. 1989, Punt 1993), or for comparing the life history strategies of fishes (e.g. Roff 1984, 1988, 1991, Beverton 1992). The parameters of von Bertalanffy functions which do not adequately fit observed data, are likely to produce erroneous results when used in subsequent analyses and should therefore be used with caution.

The decline in growth rate between the ages of one and two years, can probably be attributed to sexual maturity. Females attain 50% maturity at 310 mm TL in the South-Eastern Cape and at 375 mm TL in the Southern Cape (see Chapter 6), which is at ages 1.3 years and 2.4 years respectively. This implies that young adults allocate a larger percentage of available energy to reproduction (and less to growth) than do older fish. Maturity is also associated with emigration from the mud/sand bottomed nursery grounds to the reef substrates inhabited by adults (see Chapter 6). On the east coast this emigration requires a dietary switch from mysids and juvenile fish (Smale 1984) to larger teleosts and squid (Smale & Bruton 1985).

Silver kob in the South-Western Cape initially grew faster than those on the east coast, but growth slowed sooner with the result that they attained a smaller maximum size. Shepherd & Grimes (1983) found that initial growth rates of *Cynoscion regalis* from three regions in the middle Atlantic Bight, were also inversely correlated with maximum size. They attributed this to the size of available prey. Jones and Johnston (1977, in Shepherd & Grimes 1983) predict that fishes pass through a series of food niches during a lifetime, and that the upper limits of growth are determined in part by the optimal size for exploiting the final food niche available in the given environment. In the South-Western Cape adult *A. inodorus* feed mainly on pelagic fish, particularly *Engraulis japonicus* (Nepgen 1982), but in the South-Eastern Cape, although pelagic bait fish are consumed, they feed predominantly on larger demersal teleosts and squid (Smale & Bruton 1985). It is therefore plausible that anchovies provide for optimal growth for silver kob of 400 - 800 mm TL, but that for fish larger than this length prey size becomes limiting in terms of growth. Similarly, the size of the prey on the east coast adult habitat may be larger than is optimal for growth of young adults; and in conjunction with the allocation of energy to developing gonads, may also contribute to the decline in growth after maturity. The shorter post-maturity period of depressed growth observed in the South-Western Cape as opposed to the east coast, is presumably due to the smaller size of adult prey in the former region.

Catch per unit effort data indicate that there are three areas in which *A. inodorus* is particularly abundant along the South African eastern seaboard, one each in the South-Eastern Cape, the Southern Cape, and the South-Western Cape (see Chapter 6). Results presented in this study showed that there were significant differences between the otolith dimension/fish length relationships of all three regions, but that the relationships of the South-Western Cape and the Southern Cape, were more similar than those of the South-Eastern Cape. Fish growth on the other hand was similar in the South-Eastern Cape and Southern Cape, but significantly different to growth in the South-Western Cape. Although relative otolith size may be influenced by somatic growth rate (Templeman & Squires 1956, Reznick et al. 1989, Dawson 1991), greater differences in otolith demension/fish length realationships between regions with similar growth, than between those with disimilar growth, indicates that the observed differences in otolith dimension/fish length relationship were not a function of growth rate. Since otolith shape (Campana & Casselman 1993, Colura & King 1995) and fish growth (Wootton 1990, Jørgensen 1992, Brander 1995) are strongly influenced by environmental conditions, the observed regional differences in this study may not have a genetic basis. They do, however, suggest that South African *A. inodorus* exist as three allopatric stocks (management units). The concept of separate silver kob stocks is further supported by the regional differences in annulus structure (this study), low rates of exchange between regions (as determined from tagging data), differences in the sizes at maturity in the Southern Cape and in the South-Eastern Cape, and discontinuity in the distribution of juvenile *A. inodorus* trawled between Cape Agulhas and Port Alfred (see Chapter 6). It is therefore recommended that silver kob in the South-Eastern Cape, the Southern Cape and the South-Western Cape be treated as separate stocks for management purposes.

CHAPTER 6

THE LIFE HISTORY OF *ARGYROSOMUS INODORUS* IN SOUTH AFRICAN WATERS

THE LIFE-HISTORY OF *ARGYROSOMUS INODORUS* IN SOUTH AFRICAN WATERS

ABSTRACT

The life-history of *A. inodorus* occurring between Cape Point and the Kei River was studied using biological, length frequency, catch and tagging data. These data were obtained from fish that were caught by trawlers, by recreational and commercial lineboat fishers, during biomass surveys and during scientific linefishing operations. Although there was evidence for spawning activity throughout the year, the main spawning season lasted from August to December, with a peak in spring (Sept-Nov). Spawning appeared to occur throughout the study area, in <50 m depth. Size at sexual maturity was smaller in the South-Eastern Cape than in the Southern Cape. Mean size at maturity (L_{50}) for females was attained at 310 mm TL (1.3 years) in the former and at 375 mm TL (2.4 years) in the latter region, and the lengths at total female maturity were 400 mm TL (3.5 years) and 550 mm (4.7 years) respectively. For males the estimates of L_{50} and total maturity were 200 mm (1 year) and 400 mm TL (2.8 years) for the South-Eastern Cape and 250 mm TL (1.5 yrs) and 450 mm (3.4 years) in the Southern Cape. East of Cape Agulhas, *A. inodorus* was found from just beyond the surf zone to depths of 120 m. Adults occur predominantly on reef (>20 m), while juveniles are found mainly over soft substrata of sand/mud (5-120 m depth). Early juveniles use areas immediately seaward of the surf zone (5-10 m depth) as nurseries, but move deeper (<100 m depth) with growth. No juveniles were collected from the area west of Cape Agulhas because substrata <200 m depth were not suitable for trawling. Responding to the lower water temperatures west of Cape Agulhas, adults in this area were found from within the surf zone to depths of only 20 m during summer. *A. inodorus* occurring throughout the study area apparently disperse offshore in winter (to to 120 m depth), in response to oceanographic changes. Evidence is also presented which suggests that *A. inodorus* between Cape Point and the Kei River exist as three allopatric stocks, with limited exchange.

INTRODUCTION

The silver kob, *Argyrosomus inodorus* (Griffiths & Heemstra), is a medium sized sciaenid (max. size 34 kg) which is known from northern Namibia on the west coast of southern Africa to the Kei River on the east coast of South Africa (Griffiths and Heemstra 1995). Until recently it was misidentified as *A. hololepidotus* throughout its distribution, and off South Africa it was also confused with a sympatric species, *A. japonicus* (Griffiths & Heemstra 1995).

The South African linefishery consists of about 2900 commercial (W. Kroon, Sea Fisheries, personal communication) and at least 4000 club affiliated recreational (Ferreira 1993) vessels. These boats vary from 5-15 m in length and operate in the marine environment on both east and west coasts. Combining market value and annual catch, the silver kob is probably the most valuable species caught by the linefishery between Cape Point and East London. It is not common between Cape Point and central Namibia, and on the east coast does not occur north of the Kei River (Griffiths & Heemstra 1995). *A. inodorus* is also landed as a by-catch of the sole and hake directed inshore trawlfishery, between Cape Agulhas and Port Alfred (Japp et al. 1994), and is caught by rock and surf anglers and commercial beach seine fishers in the South-Western Cape.

Knowledge of the life-history of an animal is fundamental to the formulation of effective management strategies for its conservation. Despite its importance, very little has been published on the life-history of *A. inodorus*, and as a result, wise management has not been possible. Smale (1985) investigated the sex ratio and spawning seasonality of "*A. hololepidotus*" based on the catches of lineboat fishers in Algoa Bay, but inadvertently included both *A. inodorus* and *A. japonicus* in his study (established via voucher specimens and otoliths).

This paper describes aspects of the life-history of *A. inodorus* occurring between Cape Point and the Kei River, including reproductive seasonality, spawning grounds, size at maturity, juvenile and adult distribution and migration. The existence of discrete stocks is inferred from spatial patterns of abundance, from life-history information and from mortality estimates.

MATERIALS AND METHODS

The study area (Cape Point to Kei River) was divided into three regions for sampling purposes (Fig. 6.1). Regional boundaries did not necessarily coincide with political boundaries, but were chosen to increase analytical resolution. Biological (March 1990 - January 1992) and length frequency (January 1990 - December 1994) data were collected in each region from fish caught by (i) the linefishery, (ii) the inshore trawlfishery, (iii) during South Coast Biomass Surveys conducted by the Sea Fisheries Research Institute (trawled), and (iv) on research linefishing operations. Biological data were also obtained from silver kob beach-seined in False Bay (Oct. 1991). Trawled fish were generally caught over sand/mud substrata and line-caught fish over reef. Due to the high relief rocky nature of the inshore habitat west of Cape Agulhas, this species is not trawled in the South-Western Cape. In the case of the fishery based length frequency data, vessels were randomly selected (throughout the year) and their entire silver kob

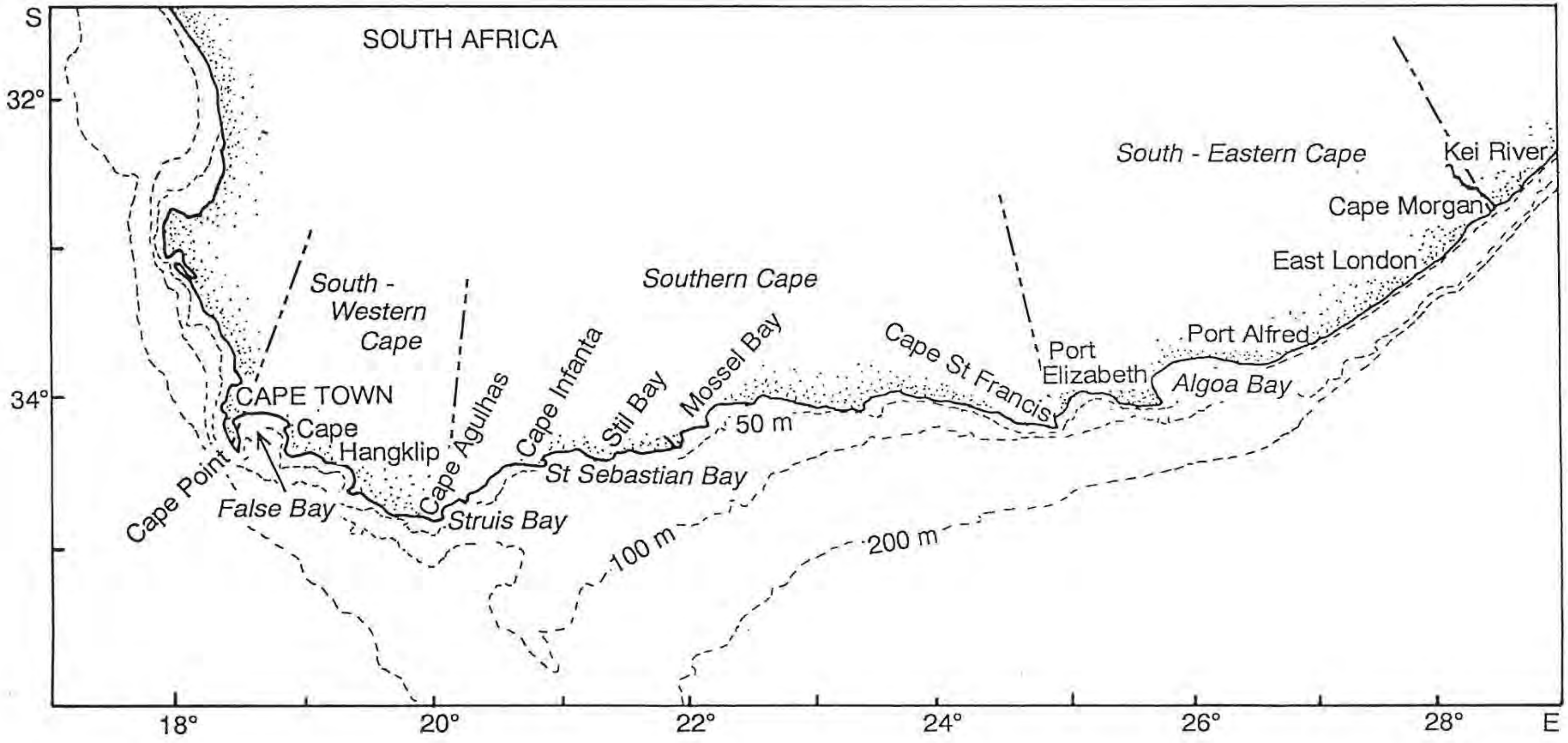


Fig. 6.1: The division of the study area into four coastal regions and the localities mentioned in the text.

catch measured for total length (to the nearest mm). The equipment and methods used by the linefishers in each of the three regions was similar. Research linefishing entailed using similar equipment, but with no minimum size limit.

Table 6.1: Classification and description of the macroscopic gonad maturity stages of *Argyrosomus inodorus*.

STAGE 1. Juvenile
This stage is generally only found in fish < 200 mm TL. Testes are thread-like, and the ovaries appear as transparent/pinkish flaccid sacs, about half the length of those in Stage II.

STAGE 2. Immature or Resting
Testes are extremely thin, flat and pinkish white in colour. Ovaries appear as translucent orange tubes. Eggs are not visible to the naked eye.

STAGE 3. Active
Testes are wider, triangular in cross-section and beige in colour. Sperm is present if the gonad is cut and gently squeezed. Eggs become visible to the naked eye as tiny yellow granules in a gelatinous orange matrix. There is very little increase in the diameter of the ovary.

STAGE 4. Developing
Testes become wider, deeper and are mottled and creamy beige in colour. They are also softer in texture, rupturing when lightly pinched. Besides the obvious presence of sperm in the main sperm duct, some sperm is also present in the tissue. Ovaries become larger in diameter and opaque yellow in colour. Clearly discernible eggs occupy the entire ovary.

STAGE 5. Ripe
Testes still larger in cross-section and softer in texture. They become creamier in colour due to considerable quantities of sperm. The ovaries are larger in diameter as a result of an increase in egg size.

STAGE 6. Ripe/Running
Testes even larger in cross-section, and uniformly cream in colour. They are extremely delicate at this stage and easily rupture when handled. Sperm is freely extruded when pressure is applied to the abdomen of the whole fish. Ovaries amber in colour with a substantial proportion of hydrated eggs.

STAGE 7. Spent
Testes are shrivelled in appearance and a mottled beige and cream in colour. A little viscous semen may still ooze from the genital pore when pressure is applied to the abdomen. Ovaries are reduced in size, similar in appearance to Stage II, with a few yolked oocytes remaining. These yolked oocytes are generally aspherical and appear to be undergoing resorption.

Fish sampled for biological purposes were measured to the nearest 1 mm (total length) and weighed, to the nearest gram (fish < 500 g), the nearest 20 g (fish 500 g - 5 kg), or the nearest 100 g (fish 5 kg - 25 kg). They were then cut open and sexed. The gonads were removed, assigned a visual index of maturity (modified from Griffiths and Hecht 1995, see Table 6.1) and weighed to the nearest 0.1 g. In addition, males were assigned an index of drumming muscle development (1-none, 2-partially developed, 3-fully developed). Due to logistical constraints, monthly biological data were only obtained for the South-Eastern Cape.

Reproductive seasonality was established in the South-Eastern Cape by calculating both gonadosomatic indices (GSIs) and the monthly percent frequency of each maturity stage, for fish larger than the median size at first maturity (L_{50}) (see below).

$$GSI = \text{gonad weight}/(\text{fish weight} - \text{gonad weight}) \times 100.$$

The extent of the spawning area was determined by computing the percent frequency of each maturity stage for fish ($>L_{50}$) that were sampled during peak spawning (Oct/Nov 1991) off East London, Port Alfred, Mossel Bay, St Sebastian Bay and False Bay.

The median size at first maturity (L_{50}) for males and females was estimated by fitting a logistical function (LOGIT) to the fractions of the mature fish (gonad stage III+) per 50 mm length class (mid-point), sampled in the Southern Cape and the South-Eastern Cape during the breeding season. Many of the smaller males with active testes lacked drumming muscles. Logistical functions were therefore also fitted to the fractions of males (per 50 mm length class) with fully developed drumming muscles. Since *A. inodorus* are not trawled in the South-Western Cape, few juveniles were sampled and L_{50} values could not be calculated for this region. Sex ratios were tested statistically for significant deviations from unity with a chi-square test ($p<0.05$).

Total annual mortality was estimated for *A. inodorus* in each of the three study regions using catch curve analyses. Age-length keys, constructed from length-at-age data presented in Chapter 5, were used to transform length frequency distributions to age frequency distributions (Butterworth et al. 1989). Instantaneous total mortality (Z) was then estimated from the slope of a straight line fitted to points greater than the age of full recruitment to the fishery (Ricker 1975).

Nursery areas were delineated by comparing the length frequency distributions of silver kob caught during South Coast Biomass Surveys (SCBS), during experimental linefishing expeditions (no minimum size) and by the linefishery (1990-1994); and by analysing the catch and effort distributions generated for silver kob during SCBSs (1987-1995). SCBS methods are fully described by Badenhorst & Smale (1991), so only a summary is given here. The survey area extended from Cape Agulhas to Port Alfred, and seawards to a depth of 500 m. This area was divided into four depth zones (0-50 m, 51-100 m, 101-200 m and 200-500 m) which were in turn subdivided into blocks of 5x5 nautical miles. The blocks trawled each survey were determined semi-randomly according to the ratio of blocks per stratum. Bobbins were not used so trawling was limited to non-reef substrata. The shallowest that the research vessel (*F.R.S. Africana*) could operate was 20 m. A 180 foot German trawl was used with 25 mm mesh (bar) liner attached to the bag. Trawl duration was limited to 30 mins, and the results of shorter trawls (due to technical reasons or to hitting reef) were standardized to that time. Bottom temperature was recorded immediately after most trawls using a Neil Brown MK III-B CTD. Data from 14 SCBSs (Table 6.2) were used to calculate mean numbers of silver kob per 30 min trawl, per block. Total numbers of *A. inodorus* trawled per bottom temperature category (1^0C), were plotted to obtain an indication of the preferred temperature range of this species.

Table 6.2: Number of trawls in which juvenile *A. inodorus* were caught during South Coast Biomass Surveys between Cape Agulhas (20^0E) and Port Alfred (27^0E) during the period 1987-1995.

Cruise	Total trawls	Trawls with silver kob
9 Sept. - 4 Oct. 1987	88	24
11 May - 2 Jun. 1988	93	8
11 May - 28 May 1989	62	12
24 May - 12 Jun. 1990	58	12
8 Sep. - 26 Sep. 1990	73	21
8 Jun. - 1 Jul. 1991	91	24
14 Sep. - 2 Oct. 1991	75	30
1 Apr. - 20 Apr. 1992	82	6
3 Sep. - 20 Sep. 1992	87	32
19 Apr. - 10 May 1993	109	9
2 Sep. - 28 Sep. 1993	106	30
8 Jun. - 3 Jul. 1994	89	11
22 Sep. - 16 Oct. 1994	92	18
23 Apr. - 15 May 1995	95	9
All Cruises	1200	246

Migration of *A. inodorus* was studied using tagging and catch data. A tagging programme, employing plastic T-bar tags, was initiated in February 1994. Silver kob, captured with hook and line, were tagged in False Bay (n = 888) and off Struis Bay (n = 750). The data for recaptured silver kob (n = 79), predominantly adults, were analyzed according to tagging locality, days free and the minimum aquatic distance travelled. Owners of commercial lineboats and inshore trawlers are required to submit daily catch returns to the Sea Fisheries Research Institute. The monthly catches of *A. inodorus* made by commercial linefishers in each of the three regions, and the monthly catches made by the inshore trawlfishery in the Southern Cape and the South-Eastern Cape, for the period 1986-1994, were expressed as percentages of the respective annual totals. The silver kob is highly prized by commercial linefishers in the three Cape regions and so the observed catch trends are more likely to reflect abundance on the fishing grounds rather than shifts in targetted effort (also confirmed by personal experience). Annual catch per unit effort data (catch/outing) was plotted on a sub-regional basis for the commercial linefishery in order to establish areas of abundance. The duration of an outing did not exceed one day.

RESULTS AND DISCUSSION

Spawning

GSIs (Fig. 6.2) and gonad maturity indices (Fig. 6.3) for the South-Eastern Cape showed that while some spawning occurred throughout the year, there was a clearly defined breeding season from August to December, and that peak spawning occurred in spring (Sept-Nov). These results are in general agreement with those of Smale (1985) for Algoa Bay, but his spawning season appears to have been "extended" by about one month, through the inclusion of *A. japonicus*, which spawn from October-January (Chapter 4) in the South-Eastern Cape. The low proportion of ripe/running (stage 6) females sampled during the spawning season (Fig. 6.3, and Smale, 1985) suggests that females feed less and are therefore less prone to capture (with hook and line) after oocyte hydration. This is supported by a much higher proportion of stage 6 females in catches of silver kob beach-seined in False Bay, than in catches made using hook and line in four other localities (during similar months and times of day)(Fig. 6.4). Very low numbers of females with hydrated oocytes have also been reported for the line catches of other sciaenids e.g. *Sciaenops ocellatus* (Fitzhugh et al. 1988), *Micropogonias undulatus* (Barbieri et al. 1994b) and *Atractoscion aequidens* (Griffiths & Hecht 1995); and in *Argyrosomus japonicus* (Chapter 4) were totally absent. Most of the silver kob caught during SCBSs were juveniles (see below). Nevertheless none of the adult females that were trawled had hydrated oocytes. This is attributed to the fact that these fish were captured on the nursery grounds and not on the adult habitat,

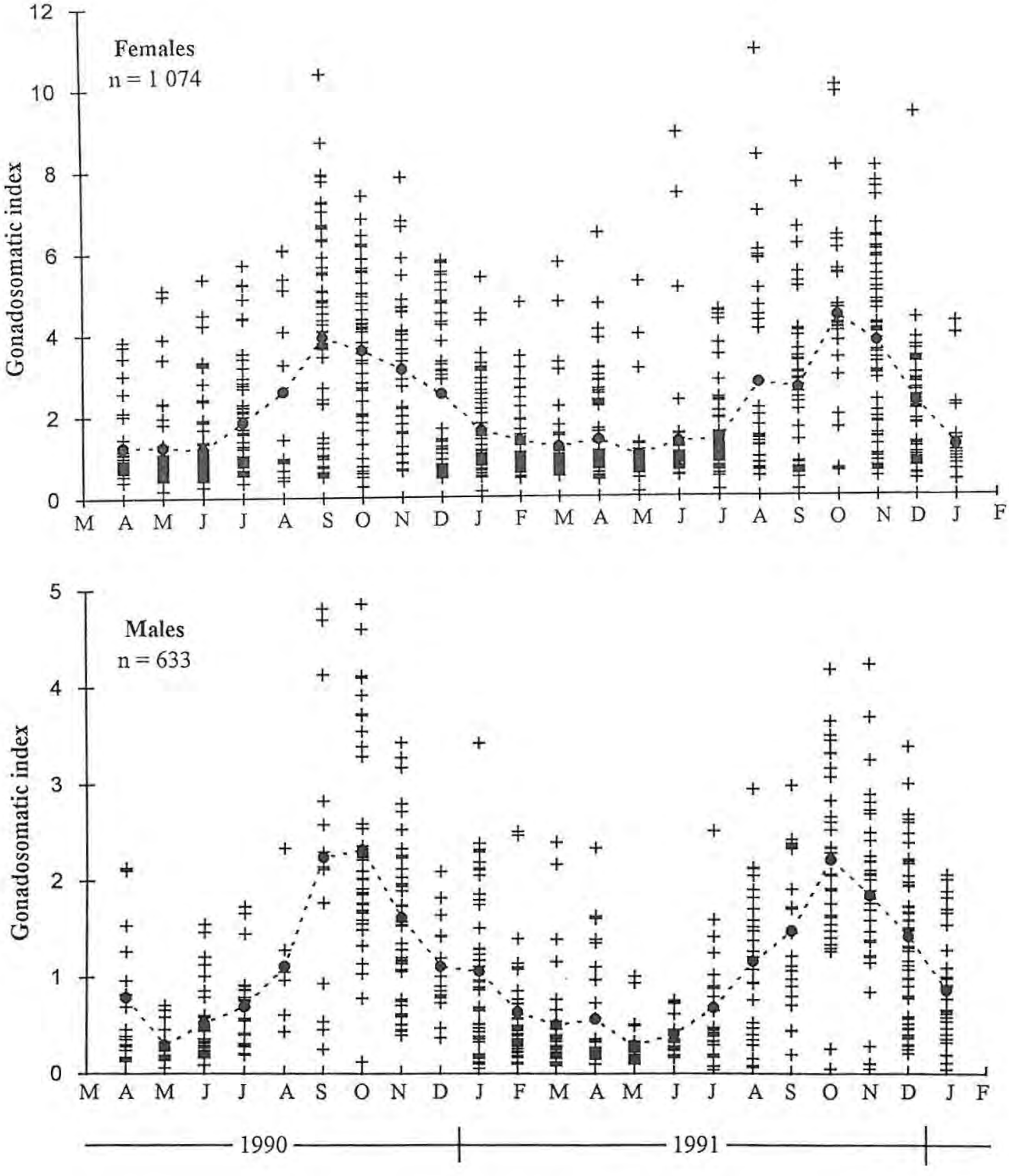


Fig. 6.2: Mean monthly (circles) and monthly (crosses) Gonadosomatic Indices for mature female and male *Argyrosomus inodorus* sampled in the South-Eastern Cape, April 1990 - January 1991. n=sample size.

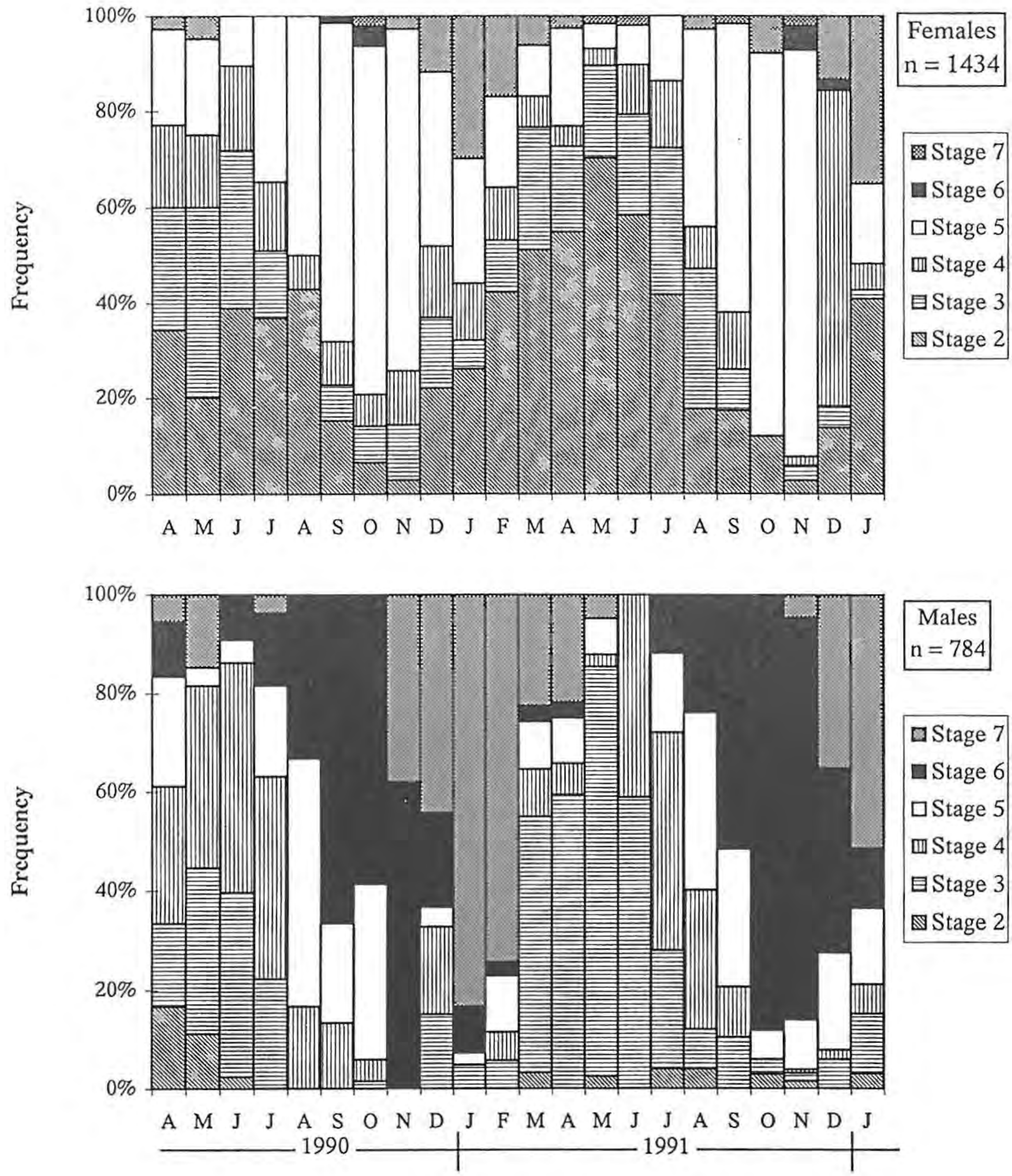


Fig. 6.3: Monthly percentage of gonad stages for mature female and male *Argyrosomus inodorus* in the South-Eastern Cape, April 1990 - January 1992. n=sample size.

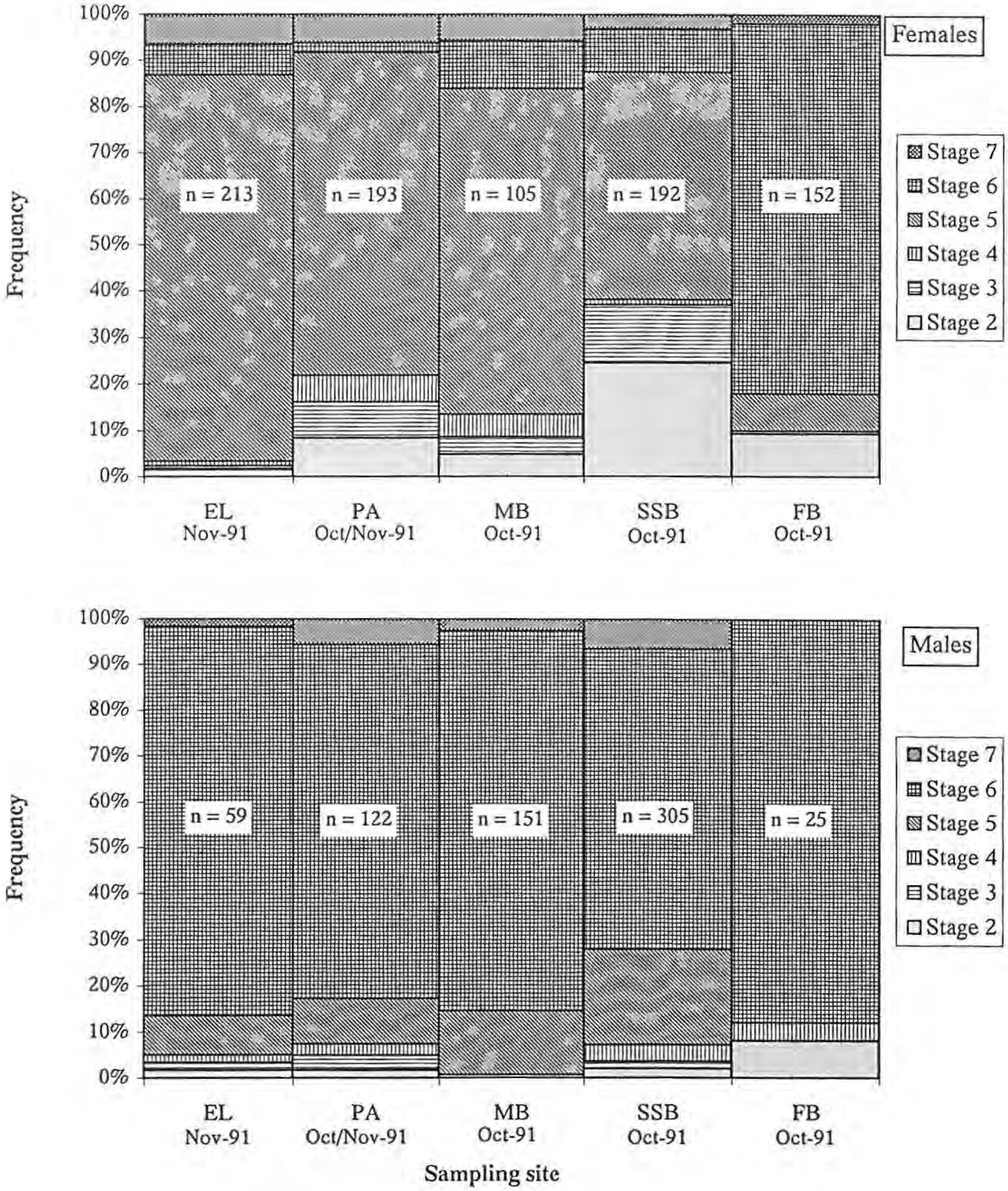


Fig. 6.4: Percentage of gonad stages for female and male *Argyrosomus inodorus* at five localities, during the peak spawning season in 1991. EL=East London, PA=Port Alfred, MB=Mossel Bay, SSB= St Sebastian Bay, FB=False Bay and n=sample size. Fish sampled at the first four localities were caught by hook and line, while those in False Bay were caught using seine-nets.

where spawning is expected to occur (see below).

The large proportion of ripe and ripe/running males and females at each of the five sites between Cape Point and the Kei River (Fig. 6.4), during October/November, suggests that spawning occurs throughout the study area, and that peak spawning occurs during spring in all areas. The inshore distribution of the adults during spring/summer and the correlation between juvenile size and depth (see below) suggests that spawning occurs in less than 50 m depth of water. Additional evidence which supports shallow water spawning includes: the absence of *Argyrosomus* eggs and larvae in the Agulhas Current (± 200 m) (Beckley 1993); the occurrence of significant numbers of *Argyrosomus* early larvae in 5-7 m in Algoa Bay (Beckley 1986); and the tidal transport of *Argyrosomus* eggs and larvae, albeit in low numbers, into and out of the mouth regions of Southern Cape and South-Eastern Cape estuaries (Melville-Smith & Baird 1980, Melville-Smith 1981, Beckley 1985, Harrison & Whitfield 1990, Whitfield 1994a, Whitfield et al. 1994). Although the *Argyrosomus* eggs and larvae described in the above studies (all as "*A. hololepidotus*") could have belonged to either *A. japonicus* or *A. inodorus*, the greater abundance of adult *A. inodorus* (66x > *A. japonicus*) on the east coast between Cape Agulhas and the Kei River (Griffiths & Heemstra 1995), suggests that they were more likely to have been those of silver kob. Furthermore, after recently examining the larvae of *A. japonicus* in Natal, Beckley is now convinced, on the basis of pigment patterns, that the larvae she collected in Algoa Bay (Beckley 1986) were those of *A. inodorus* (personal communication 1995).

Even though eggs and larvae, and juvenile recruits (see "nursery areas", below) are found just seaward of the surf zone (5-7 m), it is not certain whether spawning occurs in this area, or whether it occurs in slightly deeper water, with the eggs/larvae transported shorewards by currents. Although spawning in other sciaenids, including *A. japonicus*, occurs at night (Fish & Cummings 1972, Takemura et al. 1978, Holt et al. 1985, Saucier & Baltz 1993, Connaughton & Taylor 1995, Chapter 4), the fact that the large proportions of ripe/running females caught in the seine-nets in False Bay (Fig. 6.4) were caught between 11hr30 and 14hr30, suggests that spawning in *A. inodorus* may occur during the day. The water temperature in which the ripe/running females were captured was 18-19°C, but as indicated for other sciaenids (Saucier & Baltz 1993, Connaughton & Taylor 1995), a range of spawning temperatures is expected. Hydrophonic monitoring of drumming levels (Takemura et al. 1978, Saucier & Baltz 1993, Connaughton & Taylor 1995) would provide better information on times, sites, and oceanographic conditions for spawning in silver kob.

Although the ovaries of *A. inodorus* were not examined microscopically, substantial increases in the number of spent gonads towards the end of, and immediately after the five month spawning season (Fig. 6.3), as opposed to throughout the season, suggests that they are multiple spawners. Unfortunately partially spawned fish could not be identified macroscopically. Multiple/batch spawning has been described for several other species of sciaenid, e.g. *Sciaenops ocellatus* (Fitzhugh et al. 1988), *Seriphus politus* (DeMartini & Fountain 1981), *Cheilotrema saturnum* (Goldberg 1981), *Genyonemus lineatus* (Love et al. 1984), *Cynoscion nebulosis* (Brown-Peterson et al. 1988), *Pogonias cromis* (Fitzhugh et al. 1993, Nieland & Wilson 1993) and *Micropogonias undulatus* (Barbieri et al. 1994b).

Size at maturity

Silver kob were found to mature at a smaller size in the South-Eastern Cape than in the Southern Cape, and in both regions males matured at a smaller size than females. Females began to mature at about 250 mm in both regions, but the percentages of mature fish in consecutive size classes increased more rapidly in the South-Eastern Cape than in the Southern Cape (Fig. 6.5a&b). Estimated median lengths at maturity (L_{50}) were 310 mm and 375 mm respectively. All females in the South-Eastern Cape larger than 450 mm, and all females in the Southern Cape larger than 550 mm, were mature (Fig. 6.5a&b).

A comparison of the testes and drumming muscle methods for estimating male maturity indicated that, within each region, the two methods produced similar estimates for the length at total maturity, but that the testes method produced higher estimates for the proportions of mature fish in size classes below this length. In the South-Eastern Cape males began to mature at 150 mm (testes method) and at 200 mm (drumming muscle method), L_{50} was calculated at 205 mm (testes method) and 290 mm (drumming muscle method) and total maturity was attained at 400 mm (both methods)(Fig. 6.5c&e). In the Southern Cape males began to mature at 200 mm (testes method) and at 250 mm (drumming muscle method), L_{50} was calculated at 270 mm (testes method) and 325 mm (drumming muscle method) and total maturity was attained at 450 mm (both methods)(Fig. 6.5d&f).

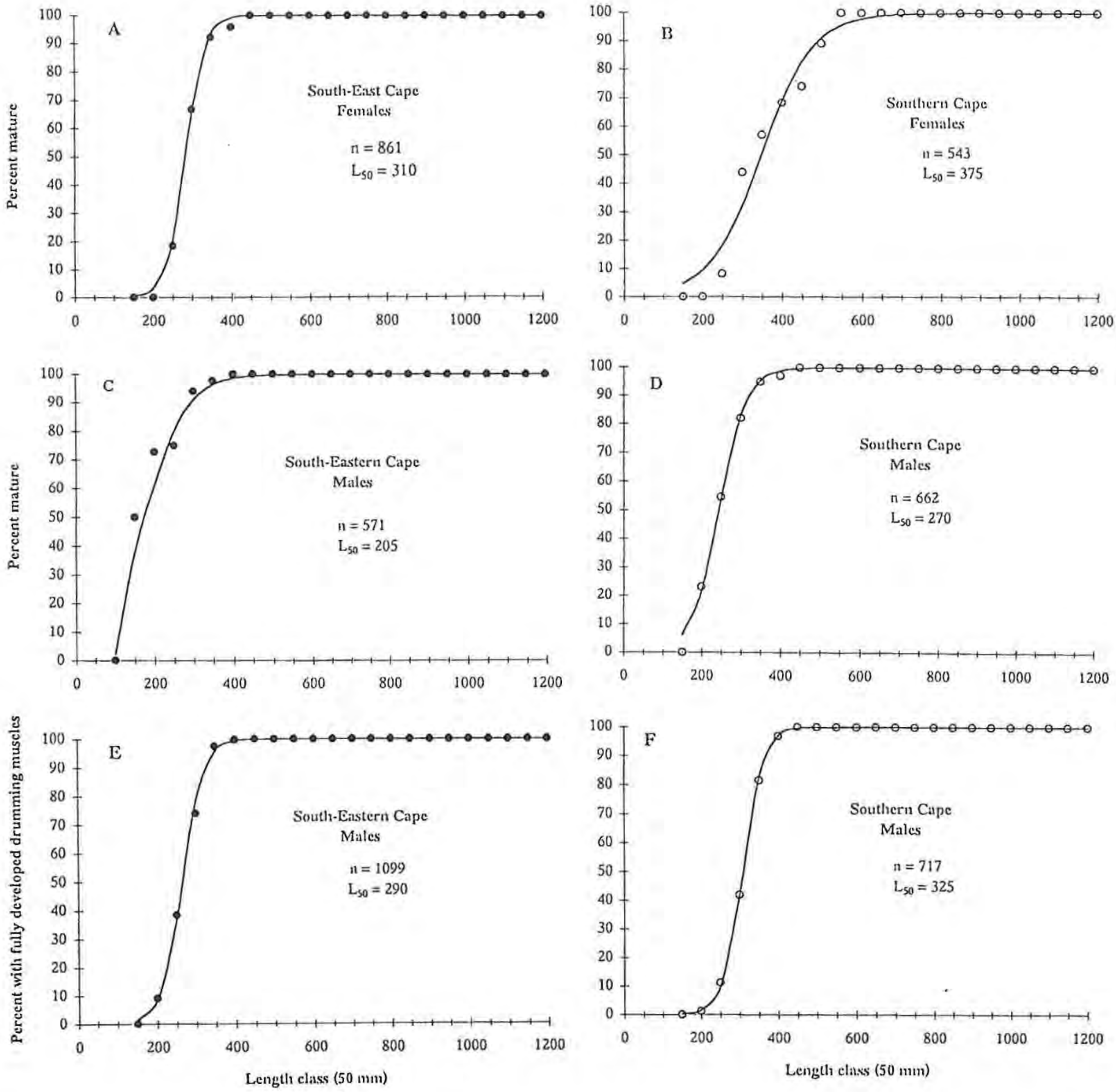


Fig. 6.5: Percentage of mature female (gonad stage 3+) and male (gonad stage 3+ and drumming muscle stage 3) *Argyrosomus inodorus*, by 50 mm total length intervals, sampled during the spawning period in the South-Eastern Cape and in the Southern Cape. The solid line describes the fitted logistical function. L_{50}= median length at first maturity (mm total length), n = sample size.

Many of the smaller males (<300 mm) classified as mature (testes contained sperm), had disproportionately smaller gonads, and also lacked drumming muscles. Since male drumming plays an important role in sciaenid spawning behaviour (Takemura et al. 1978, Saucier & Baltz 1993, Connaughton & Taylor 1995), it is not certain whether these fish would actually spawn. Sciaenids generally form large spawning aggregations (Saucier & Baltz 1993, Connaughton & Taylor 1995, Griffiths & Hecht 1995, Chapter 4) which is indicative of communal spawning.

Lack of sexual dimorphism in *A. inodorus* and the large size of the ripe testes (c. 50% of ripe ovaries, Fig. 6.2) also suggest that this species is a communal spawner and that paired mating behaviour does not occur (Balon 1975, Parker 1992). Since sneak mating behaviour is practised by species which exhibit mate selection and paired spawning (Magurran 1993, Turner 1993), this alternative male reproductive tactic is considered unlikely in *A. inodorus*. Assuming the small males (without drumming muscles) manage to spawn with a communal spawning aggregation (doubtful as this may be), based on the small size of their testes, their contribution to the total reproductive output (of the aggregation) is likely to be extremely low. Therefore, from a management view point, the L_{50} estimates based on drumming muscle development are perhaps more useful than those based on gonad staging.

There was no difference between the growth rates of *A. inodorus* in the South-Eastern Cape and the Southern Cape during 1990/91 (Chapter 5). The smaller sizes at maturity in the former region were therefore due to earlier maturity and not slower growth. Female L_{50} and total maturity are attained at about 1.3 and 3.5 years in the South-Eastern Cape and at about 2.4 and 4.7 years in the Southern Cape. Male L_{50} based on testes staging and on drumming muscle development was attained at <1 year and at 1 year for the South-Eastern Cape, and at <1 year and about 1.5 years in the Southern Cape. Total male maturity was attained at about 2.8 years in the South-Eastern Cape and at about 3.4 years in the Southern Cape.

Estimated total mortality was similar in the South-Western Cape and the Southern Cape ($Z = 0.57$ and 0.65 respectively) but was substantially higher in the South-Eastern Cape ($Z = 0.84$)(Fig. 6.6). Since changes in ages and sizes at maturity have been correlated with exploitation rate for several fish species (Healey 1975, Borisov 1978, Ricker 1981, Beacham 1983, Wysokinski 1984, Armstrong et al. 1989), it is possible that the smaller sizes at maturity recorded for the South-Eastern Cape are due to the higher mortality rates in this region.

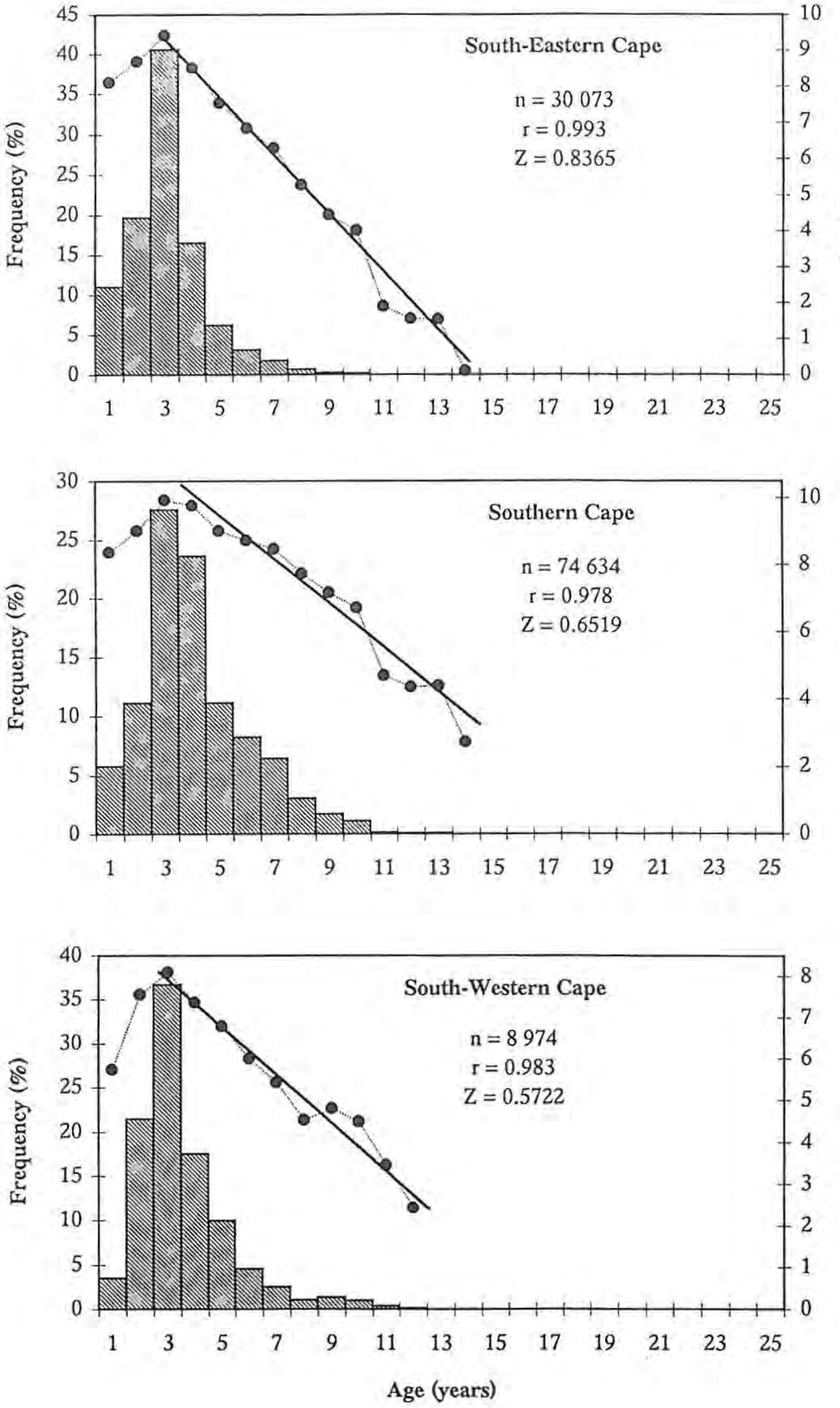


Fig. 6.6: Regional age distributions (bars) and catch curves (circles) for *Argyrosomus inodorus* landed by the South African linefishery, 1990-1994. The slope of the descending limb of the catch curve being the estimate of total mortality (Z).

The mechanism by which exploitation may have decreased the size and age at maturity in the South-Eastern Cape, remains to be identified. One explanation is that the smaller ages and sizes at maturity in the South-Eastern Cape could be the result of density-dependent effects; with higher mortality resulting in more food for surviving fish, additional energy available for gonad growth, and consequently earlier maturity. Ages and/ or sizes at maturity have been correlated with the amount of accumulated surplus energy in several other species (Armstrong et al. 1989, Rowe et al. 1991, Berglund 1992, Kerstan 1995). Alternatively, Ricker (1981) stated that " If a fish matures before it is large enough to be vulnerable to fishing, its expectation of contributing to future generations will be greater than that of a sibling of the same size that does not mature until a year later. The result can be a gradual decrease in the mean size at maturity". Female silver kob attain the minimum size limit for the line-fishery (400 mm TL) at c. 2.8 years in both the South-Eastern Cape and the Southern Cape (Chapter 5). Approximately 95% of these new recruits are mature in the South-Eastern Cape, but only 69% in the Southern Cape. Assuming that size at maturity for silver kob in the South-Eastern Cape was at one time similar to that in the Southern Cape, the removal of late maturing fish before they had spawned for the first time, could have reduced the sizes and ages at maturity to those recorded in this study. The large contribution of recruits (400-450 mm TL) to the South-Eastern Cape line-catch (c. 50% by number)(Fig. 6.7), support this hypothesis .

Sex ratios

Based on the total numbers of silver kob sampled, there were significantly more females (1.6x) in the South-Eastern Cape, more males (1.2x) in the Southern Cape and more females (2.1x) in the South-Western Cape (Table 6.3). Except for the smallest size class sampled in the South-Eastern Cape (where males predominated), all other size classes sampled in the South-Eastern Cape and in the South-Western Cape contained significantly more females. Smale (1985) also recorded consistently higher proportions of female "*A. hololepidotus*" per 100 mm length class, for fish sampled in the South-Eastern Cape (1978-1981). Although he included both *A. inodorus* and *A. japonicus* in his study, the latter species only recruits to the linefishery at about 1000 mm TL (Chapter 4), so his specimens below this length were mostly *A. inodorus*. Of the 11 size classes sampled in the Southern Cape, eight contained more males and three contained more females (Table 6.3). However, the ratios of only three of these size classes (each with more males) were significantly different from the expected 1:1. Consistently more males within most

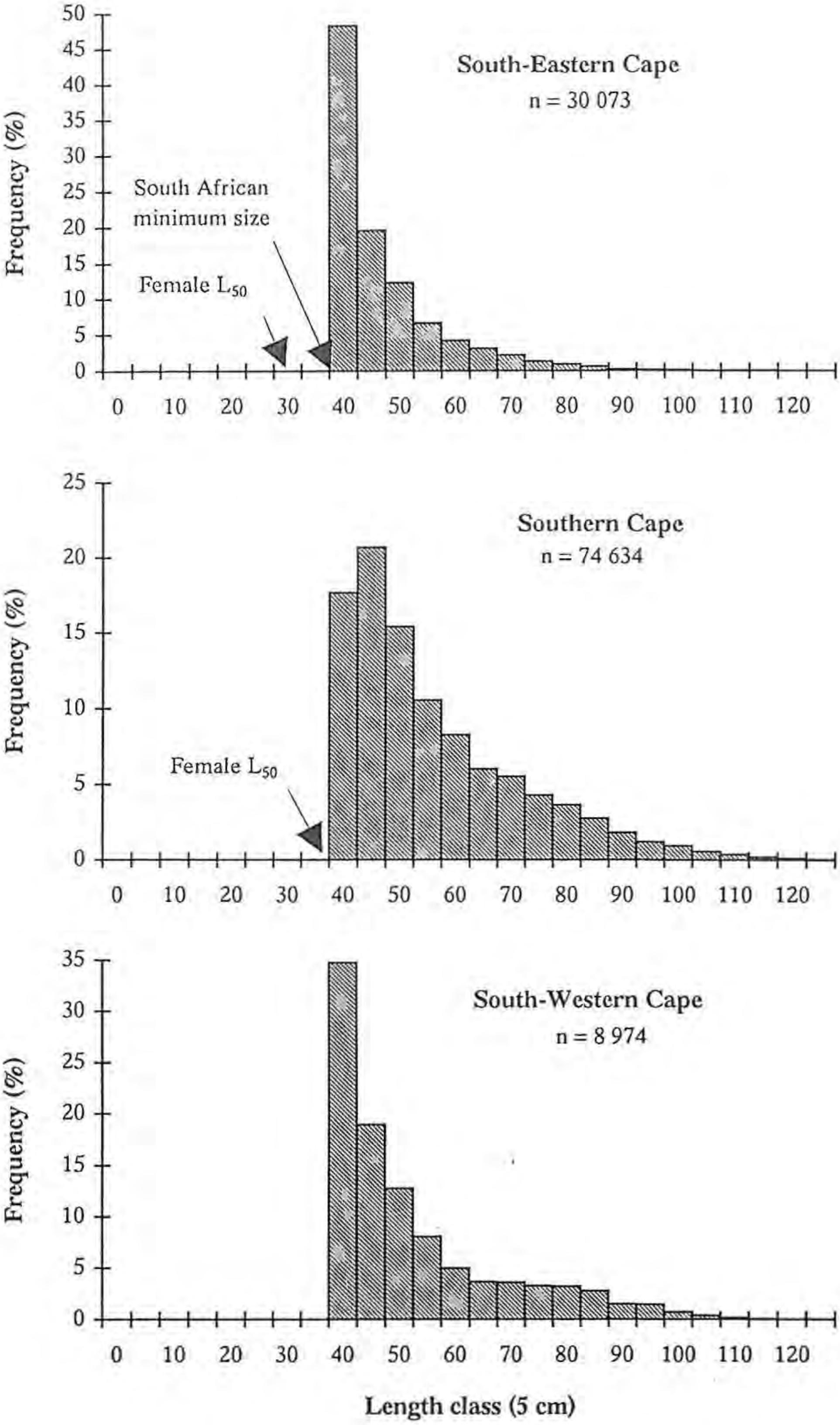


Fig. 6.7: Regional total length distributions of *Argyrosomus inodorus* landed by the South African linefishery, 1990-1994. Arrows indicate female median length at maturity (L_{50}) and the minimum legal size limit (400 mm). n=sample size.

of the size classes sampled in the Southern Cape indicates that there are more males than females in this region, and that the lack of significance for several of the size classes could be due to limitations of the statistical test. The chi-square test is based on absolute differences (between observed and expected) and does not take into account sample size e.g. while a ratio of 1.2:1 (n = 1764) was significant (even at $p<0.001$), one of 1.3:1 (n = 80) was not (Table 6.3). This suggests that researchers studying sex ratios should make every effort to obtain large samples, particularly if the chi-square method is to be used as a test for significant difference.

Table 6.3: Sex ratios of *Argyrosomus inodorus* from three regions along the South African eastern seaboard. * = significant difference at $p<0.05$.

Total Length (mm)	South-Eastern Cape			Southern Cape			South-Western Cape		
	M : F	n	x^2	M : F	n	x^2	M : F	n	x^2
100-199	1.4 : 1	188	4.2*	1.2 : 1	114	0.9			
200-299	1 : 1.2	562	4.4*	1.1 : 1	320	1.3			
300-399	1 : 1.7	1194	72.4*	1.2 : 1	289	2.5	1 : 1.3	72	0.9
400-499	1 : 2.0	541	61.9*	1.3 : 1	544	10.6*	1 : 3.1	49	12.8*
500-599	1 : 2.9	212	49.1*	1.5 : 1	212	9.1*	1 : 1.7	57	4.0*
600-699	1 : 2.0	119	7.1*	1 : 1.2	76	0.8	1 : 2.6	36	7.1*
700-799	1 : 1.8	58	4.4*	1 : 1.2	30	0.1	1 : 1.8	61	13.8*
800-899	1 : 1.5	56	2.6*	1.1 : 1	25	0.0	1 : 2.0	77	8.1*
900-999	1 : 3.2	25	6.8*	1.9 : 1	43	3.9*	1 : 2.8	57	12.8*
1000-1099	1 : 6.3	21	11.6*	1.3 : 1	80	1.0	1 : 2.6	29	5.8*
1100-1199	1 : 1.5	5	0.2	1 : 1.1	30	0.1			
All Sizes	1 : 1.6	2982	158.7*	1.2 : 1	1764	20.1*	1 : 2.1	446	57.4*

Most natural populations tend to stabilize at sex ratios of 1:1 (Conover & Van Voorhees 1990), including those of other sciaenids (Shepherd & Grimes 1984, Murphy & Taylor 1989, Wilson & Nieland 1994, Ross et al. 1995, Griffiths & Hecht 1995). The deviations from this ratio observed for South African silver kob are not easily explained. Fundamentally the reasons for an observed sex ratio which deviates from unity may be grouped into three categories, (i) more individuals of either sex are produced e.g. environmental sex determination, (ii) equal numbers of both sexes are produced, but those of one sex are diminished through either emigration or mortality, and (iii) sampling methods are biased towards one of the sexes. Although environmental sex determination can temporarily result in skewed sex ratios in some species (Conover & Heins 1987), frequency-dependent selection is expected to return the ratios of such populations to equality, through future generations (Conover & Van Voorhees 1990). Regionally higher proportions of either sex within most size classes, with consistency over two periods (1978-1981 and 1990-1991) in the South-Eastern Cape, render environmental sex determination an unlikely cause of the observed sex ratios. The results of this study do not indicate significant migration between regions (see "migration" and "stock differentiation" below). Male emigration from the South-Eastern Cape and the South-Western Cape to the Southern Cape is therefore unlikely. Since the smallest size class sampled in the South-Eastern Cape consisted of males without drumming muscles, and also of more males than females, it is tempting to suggest that male drumming during the protracted spawning season could have resulted in sex selective predation in this region, and in the South-Western Cape. However, there is no reason to believe that predation rates should be higher in the South-Eastern Cape and the South-Western Cape than in the Southern Cape. As capture methods were the same in all three regions, increased vulnerability of either sex to capture is not plausible either. It is therefore concluded that additional research is required before the regionally specific sex ratios observed for *A. inodorus* can be adequately explained.

Nursery areas

A. inodorus landed by the linefishery were mostly adult fish between 400 and 1200 mm (Fig. 6.7). Although fish <400 mm were not represented due to the minimum size limit imposed on linefishers, experimental linefishing indicated that silver kob on the linefishing grounds (reef substrata) were mostly >310 mm (Fig. 6.8), and that in the South-Eastern Cape and in the Southern Cape they were generally larger than the female L_{50} estimates.

A. inodorus trawled between Cape Agulhas and Port Alfred during SCBSs (non-reef substrata) ranged between 50 and 1200 mm, but were generally <450 mm, with the majority of the fish smaller than the Southern Cape female L_{50} (375 mm) (Fig. 6.9). The modal length class increased from 200-250 mm at depths of 25-50 m, to 250-300 mm at 50-100 m and 300-350 mm at 100-150 m. Although depths <25 m were not sampled during SCBSs, silver kob (as "*A. hololepidotus*") trawled in <9 m during an earlier survey of the bays between Mossel Bay and Algoa Bay, were mostly 90-180 mm (Smale 1984). Beckley (1984b) recorded *A. inodorus* (also as "*A. hololepidotus*") as small as 13 mm just behind the breakers (5-7 m depth) in Algoa Bay. Voucher specimens (including otoliths) from both of these studies were identified as *A. inodorus*.

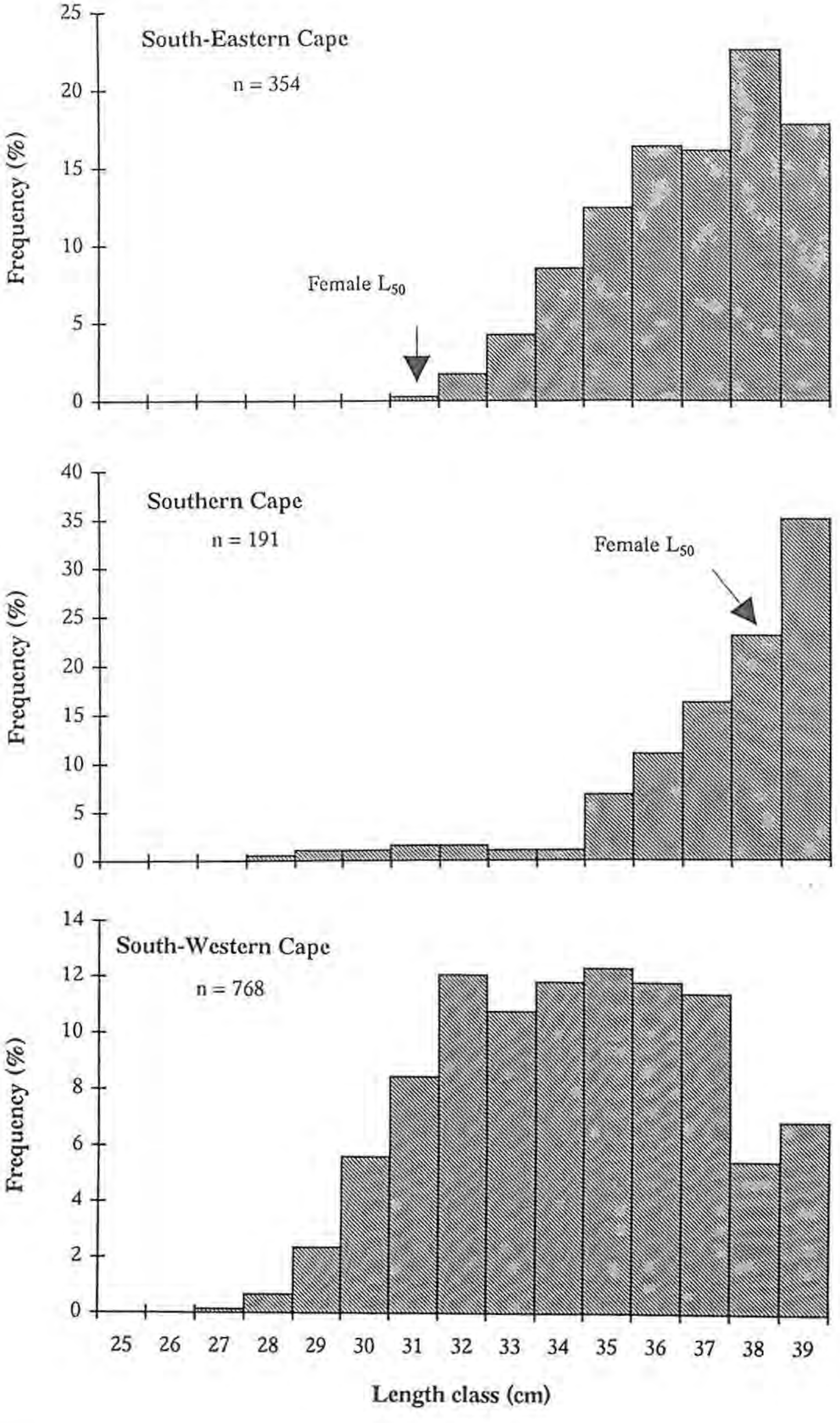


Fig. 6.8: Regional total length distributions of *Argyrosomus inodorus* below the minimum size limit, caught on linefish grounds during experimental fishing operations. Arrows indicate female median length at maturity (L_{50}). L_{50} was not estimated for the South-Western Cape.

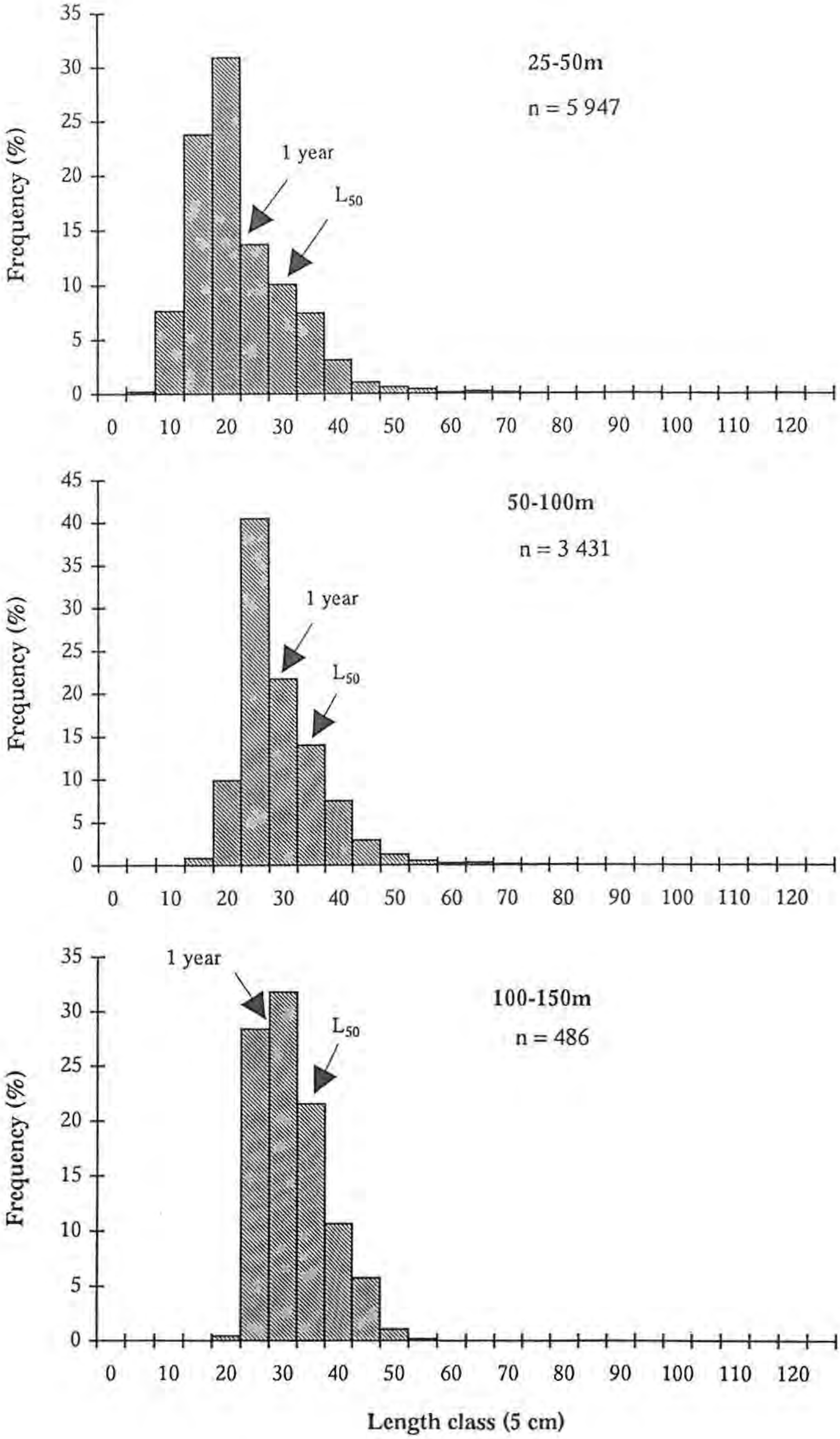


Fig. 6.9: Total length distributions, per depth range for *Argyrosomus inodorus* trawled between Cape Agulhas and Port Alfred during South Coast Biomass Cruises, 1990-1994. Total length at 1 year and L_{50} are indicated with arrows.

There is therefore a trend of increasing length with increasing depth and distance from the shore, for juvenile silver kob occurring between Cape Agulhas and Port Alfred. This suggests that the juveniles are recruited to the nursery grounds just seaward of the surf zone and that they move further offshore as they grow. Silver kob do not enter estuaries, and between Cape Agulhas and the Kei River, they do not occur in the surf zone (Griffiths and Heemstra 1995). SCBS CPUE-analyses revealed that juvenile *A. inodorus* were not homogenously distributed over the survey area, but were found mostly in <120 m depth, and comprised two disjunct distributional ranges i.e. Cape Agulhas to Mossel Bay and Cape St Francis to Port Alfred (Fig. 6.10).

It is generally accepted that reproductive strategies in fishes are geared towards placing offspring in environments that will ensure survival (Cushing 1990, Wootton 1990, Conover 1992). Growth in fishes is temperature dependent, and natural mortality generally decreases with size (Wootton 1990, Tsukamato et al. 1989, Ross et al. 1995). Therefore, since bottom temperatures are generally higher in water <20 m depth on the east coast (see below), the occurrence of early juveniles in shallow water, where they would grow faster, could be a strategy aimed at reducing natural mortality. Because *A. inodorus* are cannibalistic (Smale 1984, Smale & Bruton 1985), the spatial separation of adults (reef) and juveniles (sand/mud), and the separation of juveniles by size (according to depth), may be further strategies aimed at reducing mortality. The juveniles and adults of congeneric species also occupy different habitats. Juvenile *A. thorpei*, in northern Kwazulu-Natal (South Africa), are found on muddy marine substrata, while the adults occur over reef (Fennessy 1994). Juvenile *A. japonicus* are found in turbid estuaries and surf zone environments, and the adults, while entering these habitats, occur mainly over marine reef (Chapter 4). The juveniles of *A. japonicus* are also separated by size, with early juveniles inhabiting upper reaches of South African estuaries, and the larger juveniles in the middle to lower reaches (Chapter 4).

Migration

Interviews with commercial linefishers (n = 36) (also confirmed by personal experience) indicated that their silver kob catch is made on reef at depths of 20-60 m to the east, and 5-20 m to the west of Cape Agulhas. Inshore trawling between Cape Agulhas and Port Alfred occurs on soft ground, in depths of 50-120 m (Japp et al. 1994). Decreases in the line catches in all three regions during winter (Fig. 6.11), and corresponding increases in the catches made by inshore

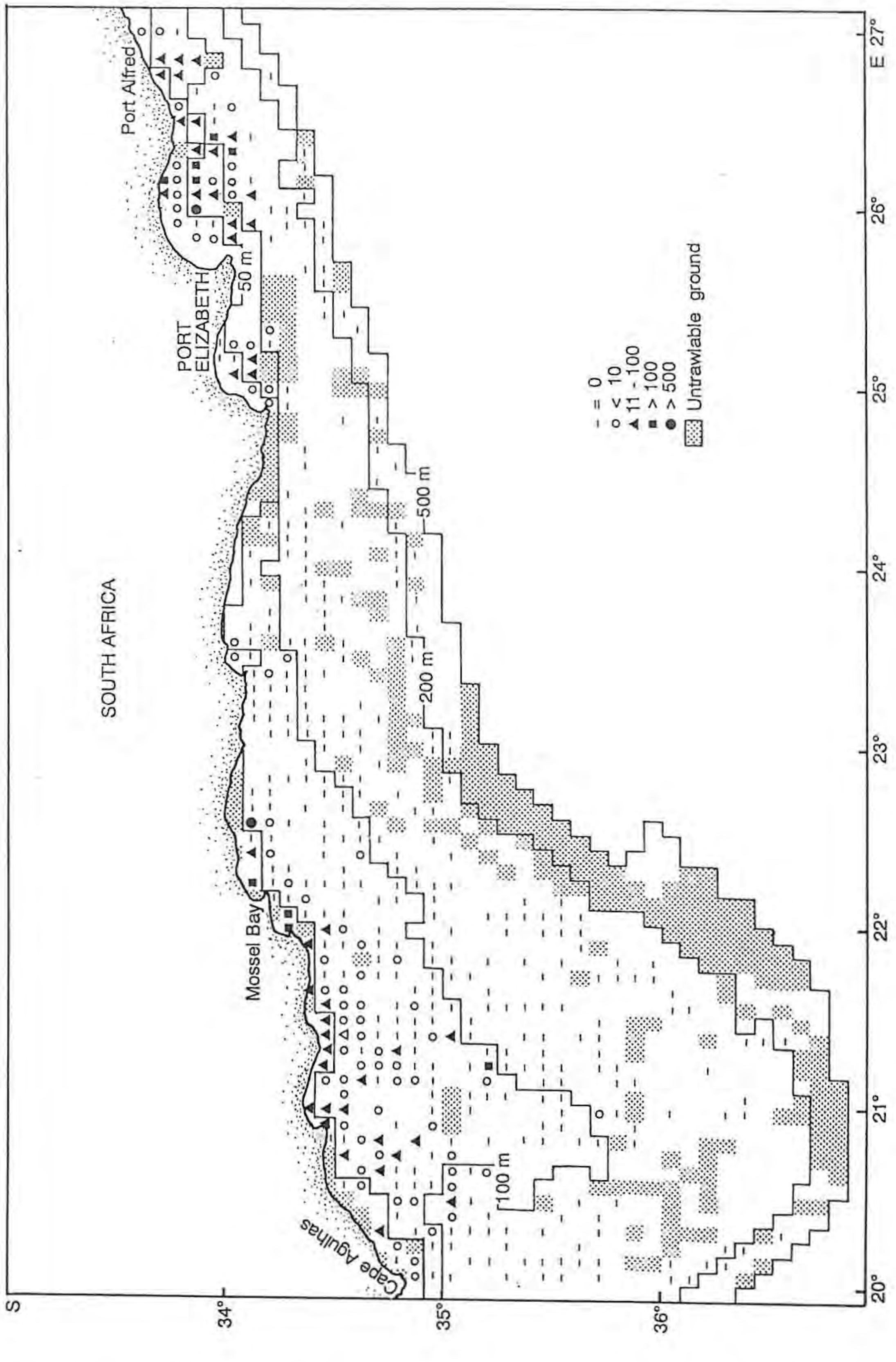
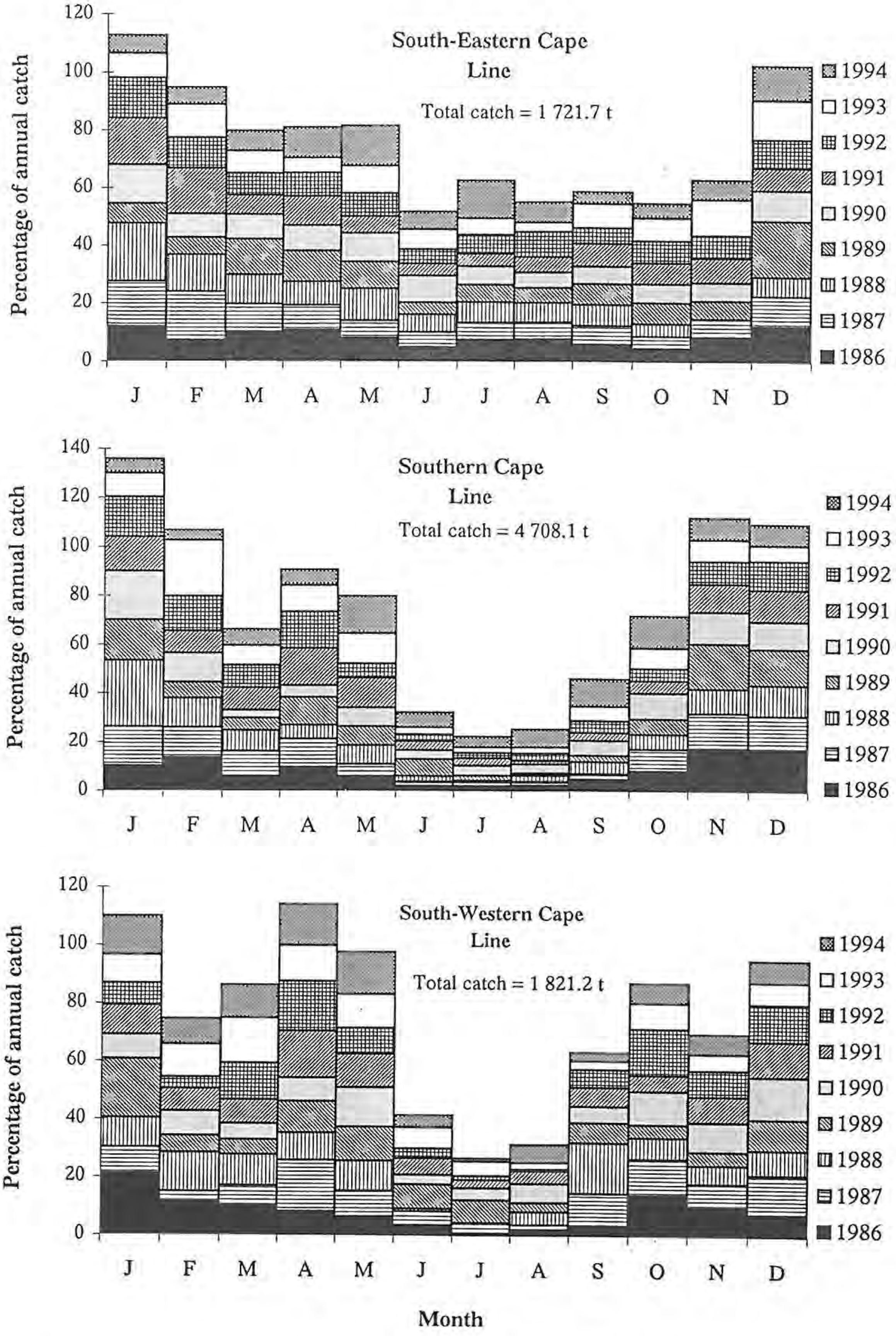


Fig. 6.10: Mean number of juvenile *Argyrosomus inodorus* per trawl per grid block for 14 South Coast Biomass Surveys, 1987-1995.


South-Eastern Cape
Line
Total catch = 1 721.7 t

Southern Cape
Line
Total catch = 4 708.1 t

South-Western Cape
Line
Total catch = 1 821.2 t

Fig. 6.11: Monthly catches of *Argyrosomus inodorus* made by South African commercial linefishers in each region, expressed as percentages of the respective annual catches, 1986-1994.

trawlers (Fig. 6.12), suggests that silver kob move further offshore at this time of the year. Because inshore trawlers fish over different substrata (to lineboats), and land mostly juvenile and young adult *A. inodorus* (Fig. 6.13), it could be argued that trawl catch data do not reflect the winter locality of the adult population. However the offshore movement of adults is supported by the recapture of four specimens (435-720 mm TL), tagged in 30 m of water off Struis Bay in summer 1995, by inshore trawlers operating in 80 m off Stil Bay and off Cape Infanta, in the winter and early spring of that year. Presumably the large adults are also found on untrawlable rocky strata during their offshore winter distribution.

Seasonal onshore/offshore movement of *A. inodorus* is also supported by regional oceanographic patterns. During spring, summer and autumn, the east coast between Cape Agulhas and the Kei River, is characterized by three zones: (i) a warm inshore band (0-20 m) with an average temperature of 21°C, although in certain areas temperatures can drop to <12°C for brief periods following coastal upwelling; (ii) a zone of intermediate temperature (12-19°C) between 20 and 50 m, and (iii) a bottom mixed layer of <12°C found below 50 m (Eagle & Orren 1985, Swart & Largier 1987, Goschen & Schumann 1988, Greenwood & Taunton-Clark 1992, Boyd & Shillington 1994). Silver kob prefer temperatures of 13-16°C (Fig. 6.14), and are therefore mainly confined to the intermediate zone. During spring, summer and autumn the intermediate zone is restricted to within a few kilometres of the coast and is within easy range of line-boats (see 50 m isobath in Fig. 6.1). In winter the bottom mixed layer retreats down the shelf to about 100 m (Schumann & Beekman 1984, Eagle & Orren 1985, Swart & Largier 1987). As the intermediate zone expands, it is proposed that *A. inodorus* stocks disperse seawards, moving beyond the grounds of the linefishery and onto the inshore-trawling grounds. Since the Agulhas Bank is much narrower in the South-Eastern Cape than in the Southern Cape (Fig. 6.1), offshore movement would be more constrained than in the latter region, and hence the less pronounced trend in the South-Eastern Cape line-catches (Fig. 6.11).

Due to a higher degree of coastal upwelling off the South-Western Cape, the bottom mixed layer (<12 °C) is shallower (20 vs 50 m on the east coast) during spring to autumn, and the temperatures above 20 m are generally 13-19 °C during this period (Atkins 1970, Boyd et al., 1985, Greenwood & Taunton-Clark 1992, Largier et al. 1992). Because the inshore temperatures are lower than on the east coast, silver kob are caught by linefishers from within the surf zone to depths of 20 m. As along the east coast, the bottom mixed layer deepens to about 100 m in

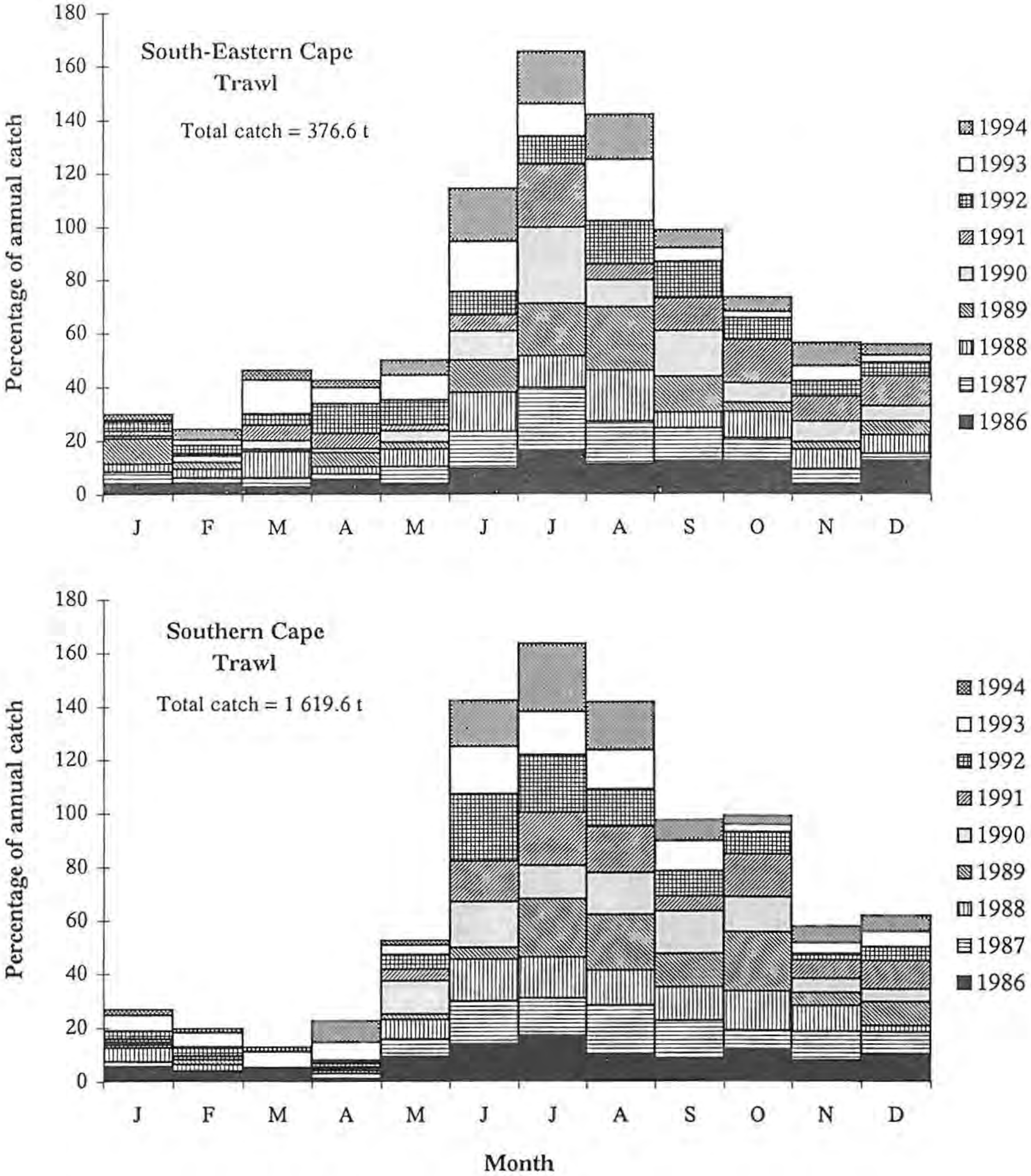


Fig. 6.12: Monthly landings of *Argyrosomus inodorus* made by the inshore trawlfishery in the South-Eastern Cape and the Southern Cape, expressed as percentages of the respective annual totals, 1986-1994.

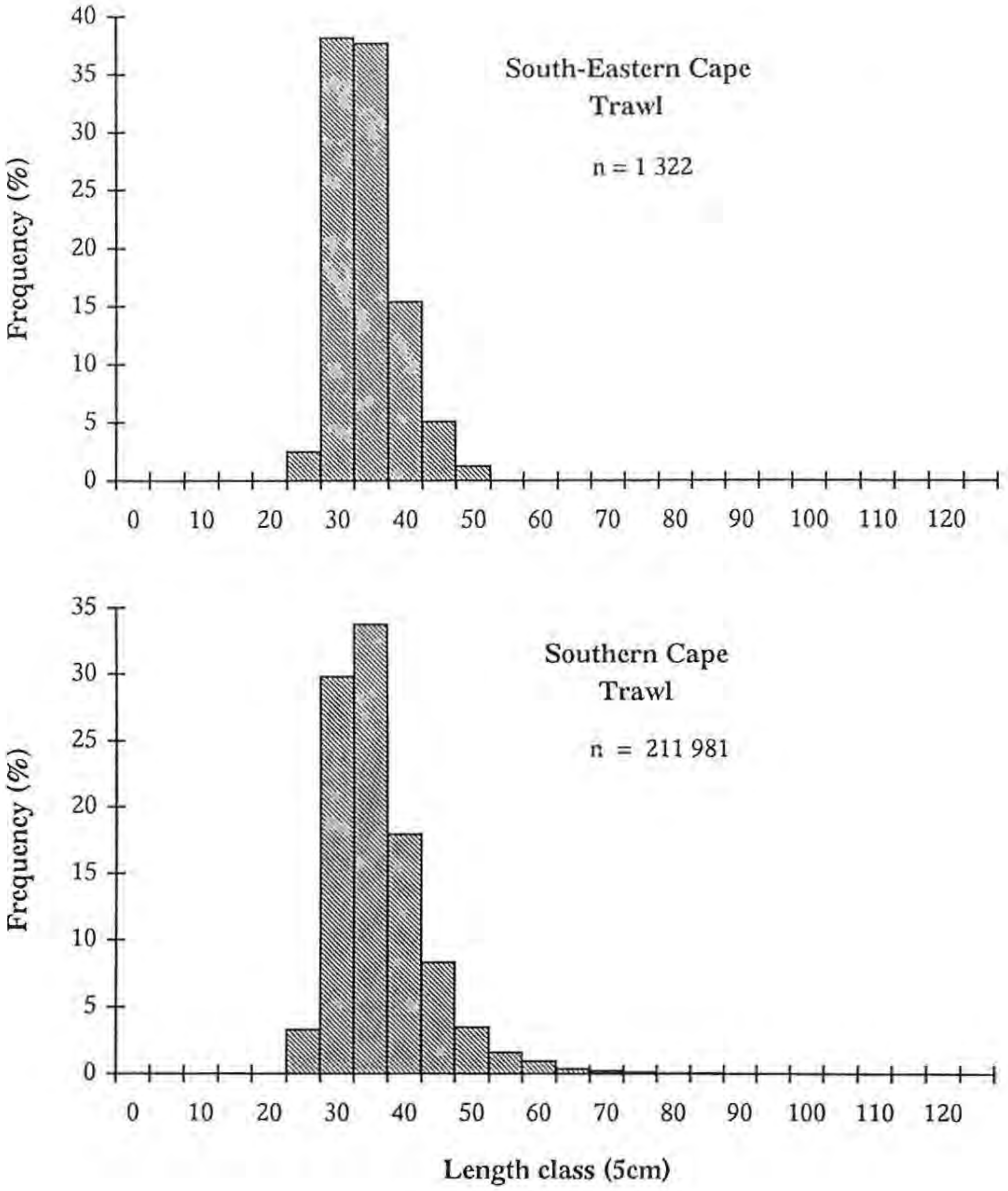


Fig. 6.13: Total length distributions of *Argyrosomus inodorus* landed by the inshore trawlfishery in the South-Eastern Cape and in the Southern Cape, 1990-1994.

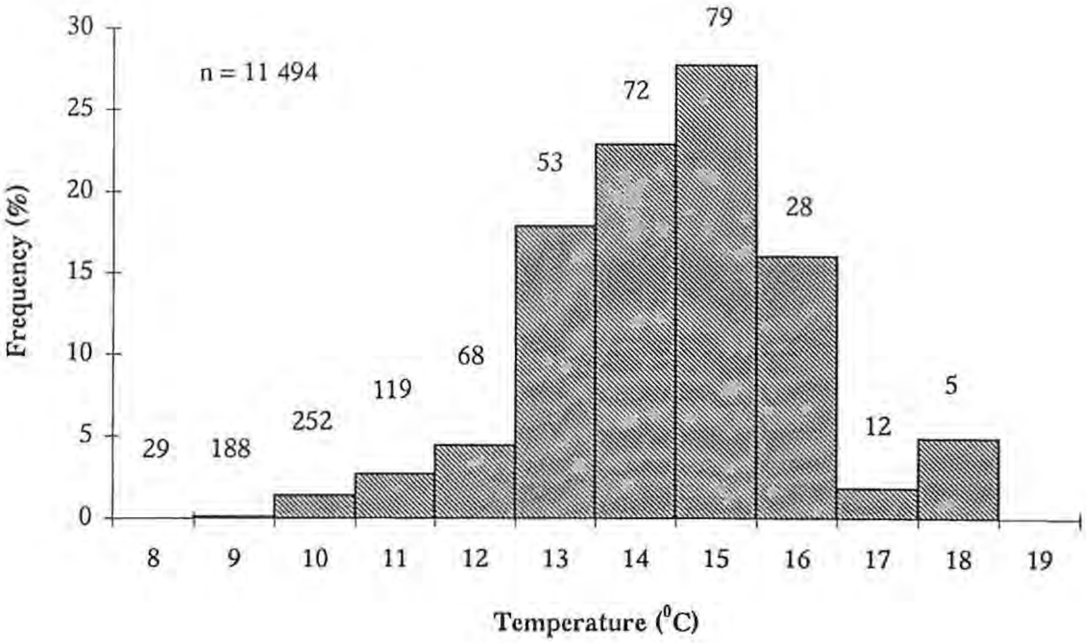


Fig. 6.14: Total number of *Argyrosomus inodorus* trawled per 1^{0}C bottom temperature category during South Coast Biomass Surveys, 1987-1995. The numbers above the bars indicate the number of trawls per 1^{0}C.

winter (Atkins 1970, Boyd et al. 1985, Largier et al. 1992), and the silver kob are expected to move offshore. This is supported by catch trends (Fig. 6.11). Since the bathymetry broadens eastwards of Cape Hangklip, it is possible that there is also an easterly component to the offshore dispersal. A seaward and eastward winter migration has also been postulated for sub-adult *Atractoscion aequidens* (Sciaenidae), occurring in the South-Western Cape (Griffiths and Hecht, 1995).

Stock differentiation

Geographically related catch and CPUE trends for the linefishery consisted of three modal groups (Fig. 6.15). This suggests that there are three areas of adult abundance between Cape Point and the Kei River (one in each region). Data from SCBSs showed that adult abundance trends were reflected in juvenile distributions, at least for the east coast (Fig. 6.10). Comparisons of the growth rates, the otolith dimension/fish length relationships, and the growth zone structure of fish from the three areas, strongly suggest that they represent three allopatric stocks (Chapter 5). Tag returns from the present study revealed that South African silver kob are capable of migrations of 240 km in six months, but that most fish (>80%) did not move more than 50 km from their tagging locality (Fig. 6.16). None of the fish tagged in False Bay were recaptured outside of that bay. Of the silver kob tagged in the Struis Bay vicinity, two (5.4%) had migrated westwards to False Bay, but the rest were recaptured either within 50 km of the tagging locality (72%), or had moved eastwards (28%), but only as far as Mossel Bay. None of the tagged fish were recaptured in the South-Eastern Cape. Tagging data therefore supports the three stock hypothesis but suggests that there might be limited exchange, particularly between the Southern Cape and the South-Western Cape. Based on catch data, the foci of each stock are apparently False Bay, Stil Bay and Port Alfred, and are separated by distances of 396 and 630 km respectively. Struis Bay is situated towards the westerly extreme of the area occupied by the Southern Cape stock, and it is therefore not surprising that of the recaptured silver kob which had moved substantial distances (>50 km) from this tagging locality, most had moved to the east. Further evidence for separate stocks is provided by differences in the sizes at sexual maturity between the Southern Cape and the South-Eastern Cape, no indication of seasonal movement between regions from line or trawl fishery catch trends, and indications of different mortality rates in the three regions.

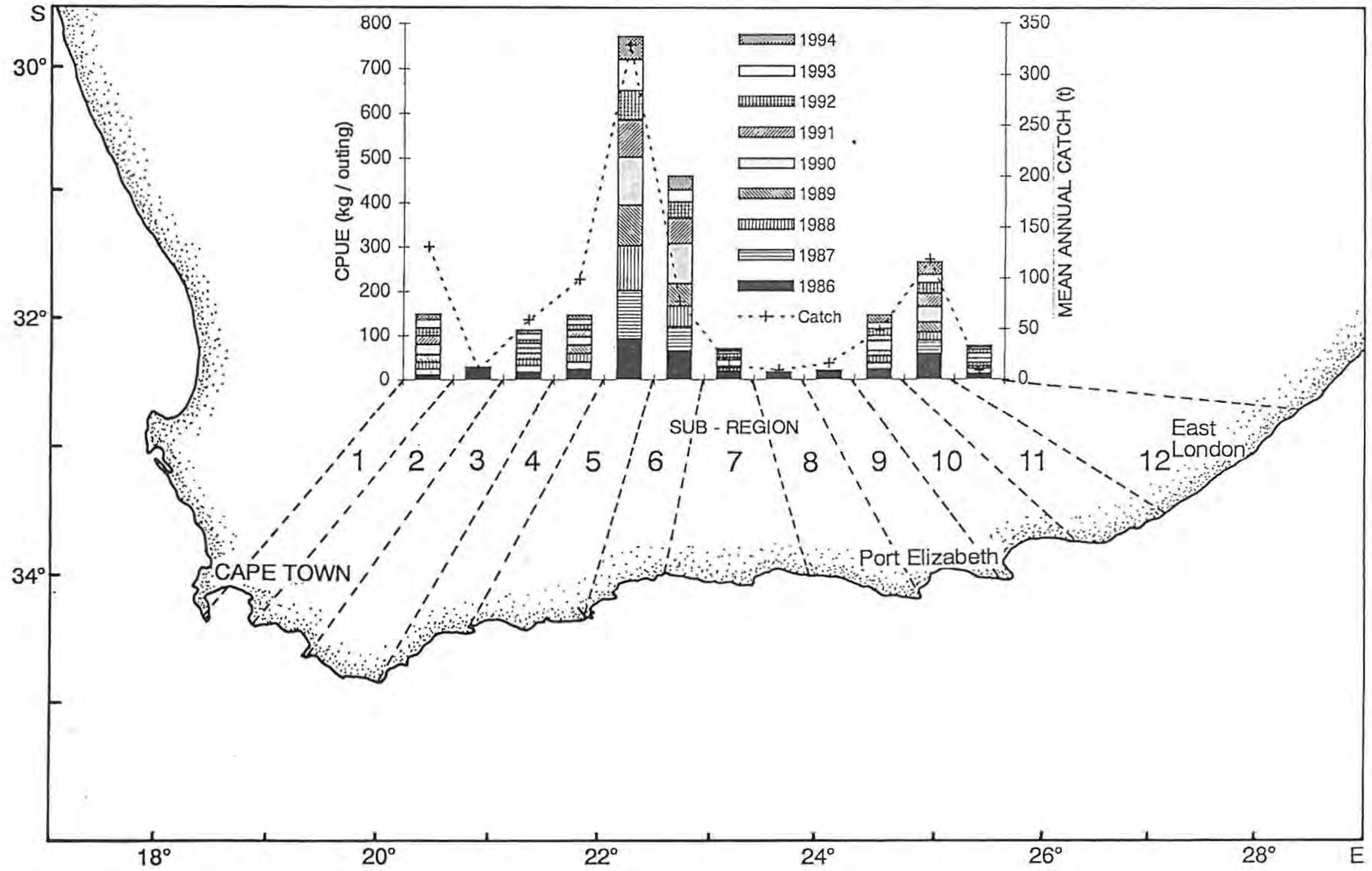


Fig. 6.15: Annual catch per unit effort and mean annual catch for commercial linefishers operating in 12 sub-regions between Cape Point and the Kei River, 1986-1994. See Fig. 1 for localities.

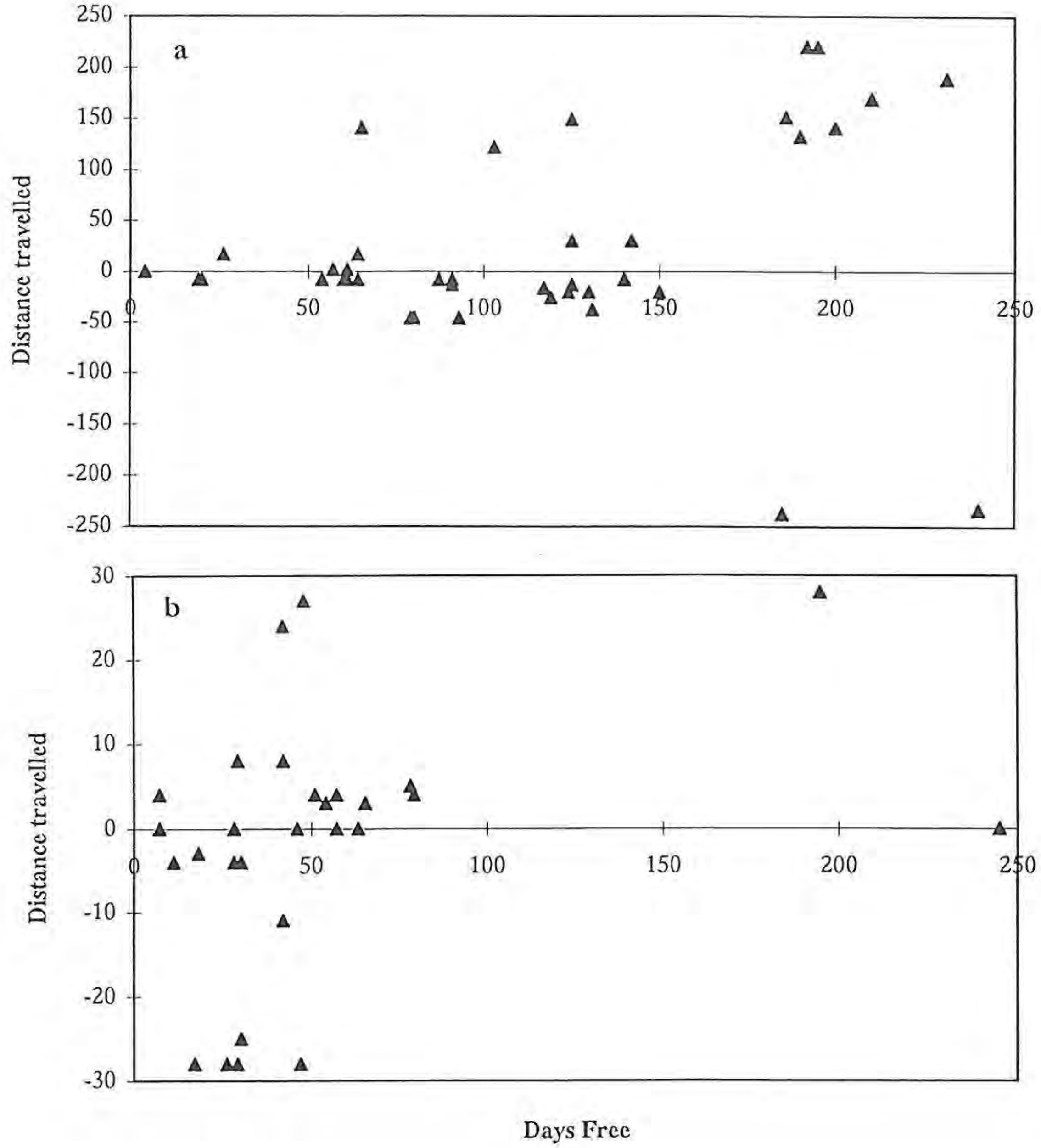


Fig. 6.16: Minimum distance travelled versus days at liberty for recaptured *Argyrosomus inodorus* that were tagged a) off Struis Bay and b) in False Bay, South Africa (1994/95). Positive values signify a coastwise migration to the west, and negative values a movement to the east.

Although genetic differentiation should ideally form the basis of inferences concerning stock distinction, analyses based on protein electrophoresis and mitochondrial DNA have generally been unsuccessful in differentiating between marine stocks (see Campana & Casselman 1992), including those of sciaenids (Ramsey & Wakeman 1987, King & Pate 1992, Graves et al. 1992). While none of the data used in this study to infer separate silver kob stocks, necessarily reflect genetic differences (Ihssen et al. 1981), the identification of three allopatric units of fish with different population parameters (e.g. mortality, growth and size at maturity) indicates that each may respond differently to fishing, and that the exploitation of one unit should not affect the size or composition of the other two; thus supporting separate management of the three units, and their recognition as stocks (Spangler et al. 1981, Brown & Darcy 1987, Campana & Gagné 1995, Edmonds et al. 1995).

It would appear that physical oceanography plays an important role in separating the three silver kob stocks occurring between Cape Point and the Kei River. Data from all 14 SCBSs revealed that the bottom mixed layer (<12^0C) extends further up the shelf (and is closer to the coast) in the area between Knysna and Cape St Francis (Fig. 6.17, see also Le Clus and Roberts in press), thus inhibiting exchange between the Southern Cape and the South-Eastern Cape silver kob stocks. Along the eastern and western sides of False Bay, the 20 m isobath is found <500 m from the shore (van Ballegooyen 1991). Since suitable temperatures for silver kob are found shallower than 20 m in the South-Western Cape during spring to autumn, the movement of silver kob into or out of False Bay (the focus of the South-Western Cape stock) during this period, is therefore restricted. In addition, the upwelled bottom mixed layer frequently extends to the shore between Cape Hangklip and Cape Agulhas, particularly from December to April (Boyd et al. 1985, Largier et al. 1992), thus further limiting exchange between False Bay and the Southern Cape.

Life-history comparison and fishery implications

The life-history strategies of *A. japonicus* and *A. inodorus* are compared in figure 18. *A. inodorus* does not live as long as *A. japonicus*, it has a smaller age and size at maturity, and does not grow as large. In addition female L_{50} is attained at 28% of L_∞ in *A. inodorus* and at 74% L_∞ in *A. japonicus*. Life-history studies indicate that the optimal size/age at maturity in marine fishes is that which will maximize life time fecundity, and that delayed maturity is advantageous only

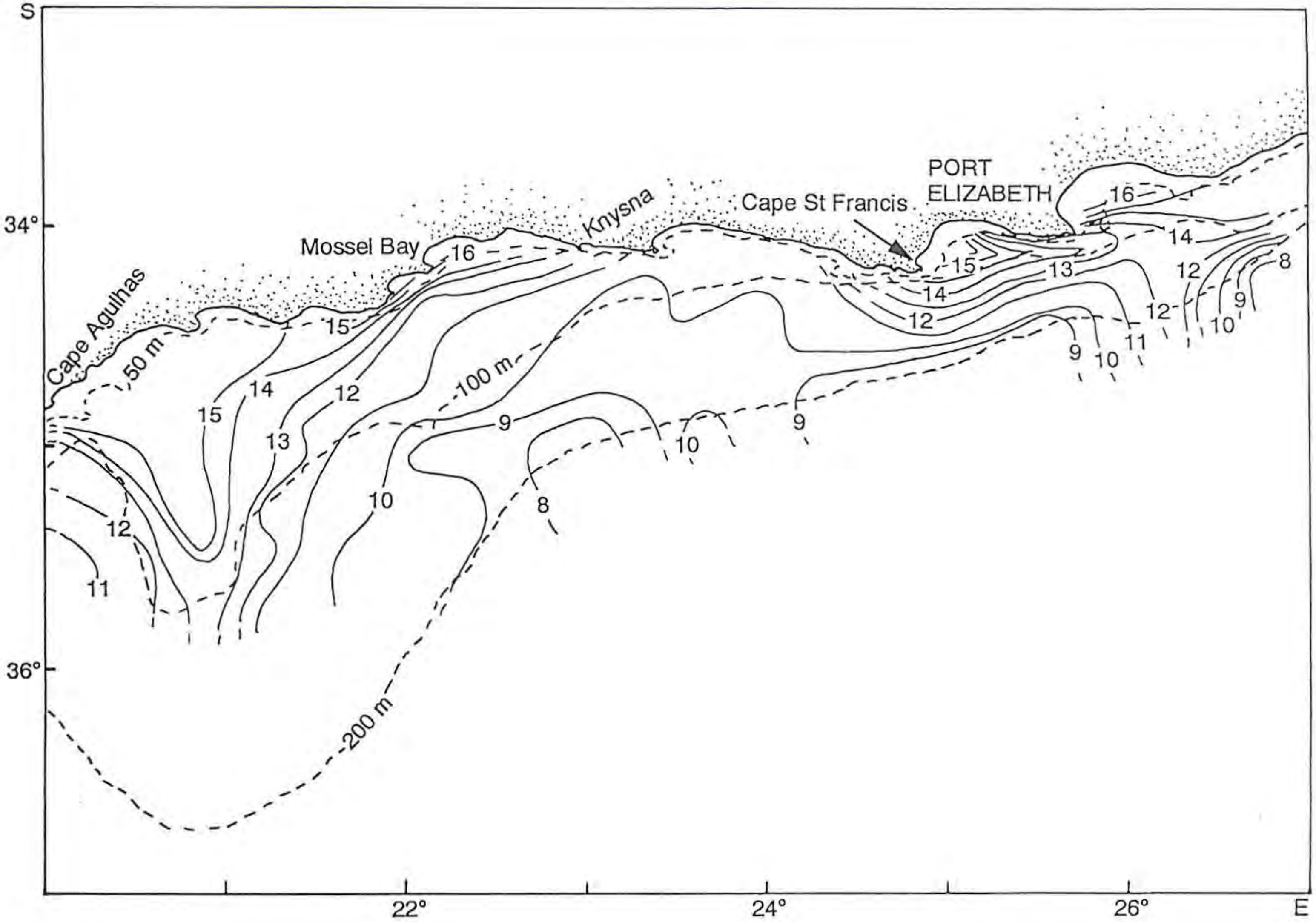


Fig. 6.17: Bottom temperature structure on the central and eastern Agulhas Bank during the October 1987 South Coast Biomass Survey. This temperature pattern, with cold water (<12 °C) shallower and closer to the coast between Knysna and Cape St Francis, was typical of SCBSs between 1987 and 1995. See Fig. 1 for additional localities.

if there is a good chance of surviving to maturity, or several years thereafter (Roff, 1984, 1988, 1991). It therefore follows that later maturity in *A. japonicus* is indicative of lower natural mortality. This is attributed to their utilizing estuarine and surf zone environments as nurseries, which have fewer predators than the marine environment beyond the surf zone (Chapter 4). Additional support for lower mortality rates in *A. japonicus* includes (i) their higher maximum age (Hoenig, 1983), (ii) their higher age at maturity (Rikhter and Efanov, 1977), and (iii) since natural mortality in fishes (excluding very old specimens) is inversely correlated with individual size (Peterson & Wrobleski 1984, Tsukamoto et al. 1989, Ross et al. 1995), their larger lengths-at-age.

Having a higher rate of natural mortality, one may expect *A. inodorus* to have a life-history strategy that is more resilient to fishing pressure than *A. japonicus* (Clark 1991). Silver kob have, however, been exploited for about one and a half centuries (Smith 1849, Pappe 1866), and although long term catch data are not available for the linefishery, circumstantial evidence indicates a downward trend. Over the last 10 years the national commercial catch has decreased from 959 t to 646 t despite slight increases in effort (National Marine Linefish System, Sea Fisheries Research Institute, Cape Town). Hecht & Tilney (1989) reported a substantial decline in silver kob CPUE in the South-Eastern Cape from 1982-1987, and Smale (1985) demonstrated a steady downward trend in the national trawled catch of this species (1968-1981). The large contribution of the first size class (400-450 mm) available to the linefishery, to the total silver kob catch in the South-Eastern Cape between 1990-1994 (Fig. 6.7), and the paucity of fish >13 years, (even though the maximum age recorded in this region was 25 years, Chapter 5), also implies heavy exploitation. Comparison of the length frequencies of this study, with those from earlier studies in the South-Eastern Cape (Smale 1985, Hecht & Tilney 1989), indicate that even though large *A. inodorus* (450-1000 mm) were poorly represented in line catches (of this region) as early as 1978 (information on length frequencies prior to this date do not exist), their proportion in the catch has declined further since then. Because fecundity is typically a power curve function of length, even small decreases in size structure could result in large decreases in egg production (Buxton 1992). Although the relationship between stock size and recruitment level is difficult to model, it is generally accepted that below a certain spawner biomass, recruitment will be detrimentally affected (Pitcher & Hart 1982, Clark 1991). Since trawlers catch mostly juvenile and young adult silver kob, the steady decline of national trawl landings and the sharp decline in South-Eastern Cape trawl landings (Smale 1985), suggest that the adult

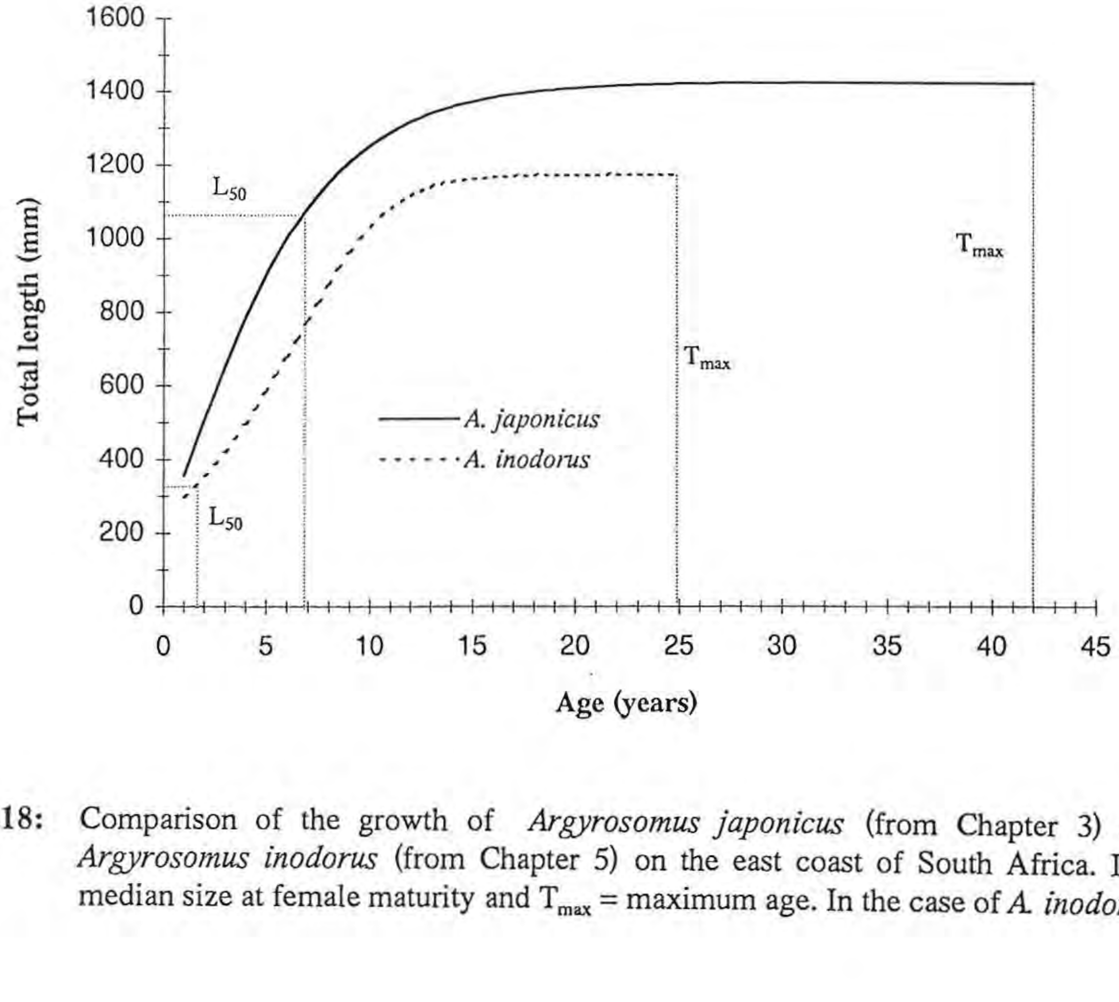


Fig. 6.18: Comparison of the growth of *Argyrosomus japonicus* (from Chapter 3) and *Argyrosomus inodorus* (from Chapter 5) on the east coast of South Africa. L_{50}= median size at female maturity and T_{max} = maximum age. In the case of *A. inodorus*,

biomass has been reduced sufficiently to affect recruitment, and that recruitment overfishing may already have occurred. Such information highlights the urgent need for assessment of the stocks of this valuable species, and for the implementation of appropriate management measures. In the absence of long term catch data, and information on the spawner biomass recruit relationship, yield per recruit and spawner biomass per recruit models represent the most appropriate assessment methods available (Butterworth et al. 1989, Punt 1993). Implications of recruitment overfishing suggest that the spawner biomass per recruit model is especially appropriate for silver kob. Life-history information provided in this paper will facilitate spawner biomass per recruit analyses and will also assist with the formulation of effective conservation measures to facilitate its sustained utilization. Future research should concentrate on the identification of spawning sites (and whether they need protection), and on the impact of the inshore trawlfishery on *A. inodorus* stocks. Estimates of batch fecundity and spawning frequency are also required for *A. inodorus*, and so are L_{50} values for the South-Western Cape.

CHAPTER 7

GENERAL DISCUSSION

GENERAL DISCUSSION

From Chapter 2, it is clear that until very recently there were two kob species in South African waters confused under the scientific name *"Argyrosomus hololepidotus"*, i.e. *A. japonicus* and *A. inodorus*; and in Australia *A. japonicus* had also been misidentified as *A. hololepidotus*. This discovery obviously has greater ecological and management significance in South Africa than in Australia. However, given the extent of the distribution of kob in Australia, it would not be surprising if more than one species of *Argyrosomus* exist there too.

Life-history comparisons

The life-histories of South African *A. japonicus* and *A. inodorus* are summarized in Table 7.1. *A. japonicus* occurs from Cape Point to Mozambique. Juveniles are found in estuaries and in the surf zone and the adults, while entering these environments, occur mainly on reefs in the inshore zone (10-100 m). *A. inodorus* prefers cooler water and is found along the South African west coast and on the east coast as far as the Kei River. As a result of oceanographic conditions they occur mainly from the surf zone to depths of about 20 m west of Cape Agulhas and from 20-120 m east of this point. Juveniles are found over sand/mud substrata and the adults over reef. *A. japonicus* has a larger median size at maturity for females (1070 mm vs 340 mm) than *A. inodorus*, it lives longer (42 years vs 25 yrs) and also has a larger maximum size (1800 mm vs 1450 mm).

Dimensionless ratios provide a useful means for comparing the life-histories of animals that grow to different sizes (see Beverton 1992 for review). In order to gain a general perspective on the life-histories of *A. inodorus* and *A. japonicus*, the relationships between median length at maturity (L_{50}) and asymptotic length (L_∞) and between age at L_{50} (T_{50}) and maximum observed age (T_{max}) of these two species were compared with those of 12 other sciaenids using dimensionless ratios (Table 7.2.). L_∞ was accepted as the maximum size to which the average fish in a population would grow in the absence of exploitation. In the case of studies where L_∞ values were not credible (e.g. substantially greater than record size), the maximum size sampled, was used instead. Beverton (1992) calculated fairly narrow ranges of L_{50}/L_∞ and

T_{50}/T_{max} for the Pleuronectiformes (40-62% and 17-63%), the Gadiformes (45-78% and 24-38%), the Clupeiformes (70-88% and 19-31%) and the genus *Sebastes* (64-82% and 12-30%), indicating possible phylogenetic constraints within these taxa. The wide range of L_{50}/L_{∞}(27-92%) and T_{50}/T_{max} (5-67%) observed in Table 7.2, not only expands the ranges of these parameters known for fish (both lower and upper limits), but also suggests a large degree of genetic variation within the family Sciaenidae. This is perhaps also reflected in their diverse morphology and adaptation to a wide range of habitats (Sasaki 1989).

Table 7.1: A summary of the life history parameters of Argyrosomus japonicus and A. inodorus found in South African waters. T_{max} = maximum age, L_{50}= median length at maturity and $L\infty$ = the theoretical maximum size. The L_{50} value presented for *A. inodorus* is an average of values estimated for the Southern Cape and the South-Eastern Cape regions.

	A. japonicus	*A. inodorus*
Maximum size	75kg (1810 mm TL)	34kg (1450 mm TL)
Distribution in South Africa	Cape Point - Mozambique, abundant from Cape Agulhas to northern Natal	Orange River - Kei River, abundant from Cape Point to East London
Female L_{50}	1070 mm TL	340 mm TL
Adult Habitat	Reef, but enters estuaries & surf zone	Reef 0-20m west of Cape Agulhas 20-120m east of " "
Juvenile Habitat	30-150 mm TL upper reaches of estuaries, 150-1000 mm TL estuaries & surf zone	Marine mud/sand substrata, size increases with depth.
Spawning season	Natal - August to November Cape - October to January	Cape - August to January
T_{max}	42 years	25 years
Female L_{∞}	1473 mm	1172 mm

Comparisons with other sciaenids revealed that *A. japonicus* matures at a relatively large size in relation to its L_{∞} and at an intermediate proportion of its maximum age (Table 7.2). The fact that *A. japonicus* matures at as much as 73% of its L_{∞} but at only 14% of its T_{max} is a result of the fast prematurity growth and the long life-span observed for this species (Chapter 3). This also indicates that after maturity a large percentage of surplus energy is channelled into reproduction. In contrast to *A. japonicus*, *A. inodorus* matures at a relatively small proportion of its L_{∞} (27-32%) and at a low percentage of its T_{max} (5-10%). Early maturity at a small size (relative to its L_∞) indicates that part of the reproductive strategy of *A. inodorus* is to maximize the number of breeding individuals (as opposed to individual adult size in *A. japonicus*).

Table 7.2: Life-history parameters and dimensionless ratios for the females of 3 southern African and 11 North American sciaenids. L_{50} = median length (mm) at maturity, L_∞ = theoretical asymptotic length (mm), T_{50} = age (years) at L_{50}, and T_{max} = maximum age (years) recorded. TL = Total Length and FL = Fork length. In the case of short lived species which matured within their first year, L_{50} was taken as the mean length at which the ripe (stage 5) gonad stage was attained. In situations where L_∞ values were unrealistically high (#), the maximum size sampled (not record size) was used as a substitute.

Species	L_{50}	L_∞	T_{50}	T_{max}	L_{50}/L_∞	T_{50}/T_{max}
Pogonias cromis						
north-east Florida	675 FL^{1}	1172 FL^{1}	5.5^{1}	55^{1}	57.6%	10.0%
Gulf of Mexico	645 FL^{2}	1100 FL^{3}	5^{2}	43^{3}	58.6%	11.6%
Sciaenops ocellatus						
Florida (Gulf coast)	825 TL^{4}	934 TL^{4}	5^{4}	24^{4}	88.6%	20.8%
Florida (Atlantic coast)	900 TL^{4}	980 TL^{4}	5^{4}	33^{4}	91.8%	15.1%
North Carolina	810 TL^{5}	1163 TL^{5}	3^{5}	56^{5}	69.6%	5.3%
northern Gulf of Mexico	733 TL^{6}	1078 TL^{7}	4^{6}	36^{7}	68.0%	11.1%
Aryrosomus japonicus	1070 TL*	1473 TL*	6*	42*	72.6%	14.3%
Argyrosomus inodorus						
South-Eastern Cape	310*	1172 TL*	1.3*	25*	26.5%	5.2%
Southern Cape	375*	1172 TL*	2.4*	25*	32.0%	9.6%
Cynoscion nothus	190 TL^{8}	230 TL^{8}	1^{8}	1.5^{8}	82.6%	66.6%
Cynoscion regalis	256 TL^{9}	826 TL^{10}	1^{9}	11^{10}	31.0%	9.0%
Cynoscion nebulosus	344 TL^{11}	687 TL^{12}	1.5	12^{12}	50.1%	12.5%
Cynoscion arenarius	160 TL^{21}	574 TL$^{21\#}$	0.8^{21}	3^{21}	27.9%	26.6%
Larimus fasciatus	146 TL^{22}	180 TL$^{22\#}$	1^{22}	2.5^{22}	81.1%	40.0%
Genyonemus lineatus	150 TL^{13}	414 TL$^{13\#}$	1^{13}	12^{13}	36.2%	8.3%
Micropogonias undulatus	182 TL^{14}	312 TL^{15}	1^{14}	8^{15}	58.3%	12.5%
Micropogonias furnieri	310 TL^{16}	829 TL^{16}	2^{16}	7^{16}	37.3%	28.6%
Atractoscion aequidens	969 TL^{17}	1190 TL^{17}	5^{17}	9^{17}	81.1%	55.5%
Atractoscion nobilis	680 TL^{18}	1465 TL^{19}	4^{19}	25^{20}	46.7%	16.0%

[1]Murphy & Taylor 1989, [2]Nieland & Wilson 1993, [3]Beckman et al. 1990, [4]Murphy & Taylor 1990, [5]Ross et al. 1995, [6]Wilson & Nieland 1994, [7]Beckman et al. 1988, [*]This study, [8]De Vries & Chittenden 1982, [9]Shepherd & Grimes 1984, [10]Shepherd & Grimes 1983, [11]Brown-Peterson et al. 1988, [12]Maciena et al. 1987, [13]Love at al. 1982, [14]Barbieri et al. 1994a, [15]Barbieri et al. 1994b, [16]Manickchand-Heileman & Kenny 1990, [17]Griffiths & Hecht 1995, [18]Clark 1930, [19]Thomas 1968, [20]Fitch & Lavenberg 1971, [21]Shlossman & Chittenden (1981), [22]Standard & Chittenden 1984.

Studies based on mechanistic modelling and supported by empirical evidence, show that size at maturity in marine fishes is generally that which will maximize life time fecundity based on the trade-off between growth, reproductive effort and natural mortality (Roff 1984, 1988, 1991, Beverton 1992). Since fecundity in fishes increases allometrically with length, initial losses incurred by delayed maturity may be offset by gains through increased individual fecundity, particularly if the chances of surviving to adulthood (or a number of years thereafter) are good. This would imply that *A. japonicus* has a lower rate of natural mortality than *A. inodorus*. Additional evidence supporting this conclusion includes (i) higher maximum age (Hoenig 1983); (ii) larger sizes at age (Chapter 6, Fig. 6.17), because natural mortality in fishes (excluding very old specimens) is inversely correlated with individual size (Peterson & Wrobleski 1984, Tsukamoto et al. 1989, Ross et al. 1995); (iii) the relatively predator free nursery area (estuaries and surf zone); and (iv) the large individual size of *A. japonicus* (adults) which enter the nearshore environment. Lower rates of natural mortality may therefore have facilitated delayed maturity in *A. japonicus*, which in turn would have allowed for a longer period of fast growth prior to the onset of maturity. Both of these factors contributing to large adult size and individual fecundity. Delayed maturity and low natural mortality both serve to increase life span (Roff 1992). Faster growth in female *A. japonicus* than in males can be regarded as an adaptation to increase individual fecundity (Roff 1983), and is therefore consistent with the general life-history strategy of this species. It is postulated that *A. inodorus*, because of higher rates of natural mortality, has "opted" for early maturity in order to maximize its life-time fecundity. The biological consequences of this strategy are slower somatic growth, shorter life-span and smaller maximum size. To conclude, *A. japonicus* and *A. inodorus* are believed to have evolved alternate life-history strategies in response to different environmental conditions, particularly natural mortality. Evidence presented in Chapter 4 suggests that adaptation to low salinity and the utilization of estuaries as nurseries has resulted in lower natural mortalities and has been central to the evolution of the *A. japonicus* type life-history in the Sciaenidae as a whole. Unfortunately it was not possible to compare life-time or relative reproductive effort of *A. japonicus* and *A. inodorus* because information on batch fecundity and spawning frequency of these two species is not available.

The females of both *A. japonicus* and *A. inodorus* matured at larger sizes and later ages than the males. Larger female size at maturity is common in sciaenids (Table 7.3), and is probably an adaptation to increase life-time fecundity within the confines of the mortality-growth trade-off.

Table 7.3: Male median length at maturity (L_{50}) as a percentage of female L_{50} for ten sciaenid species.

Species	♂ L_{50}/♀ L_{50}	Data Source
Argyrosomus japonicus	86%	Chapter 4
A. inodorus	86%	Chapter 6
A. inodorus	94%	Chapter 6
Cynoscion regalis	96%	Shepherd and Grimes, 1984
Cynoscion regalis	84%	Merriner, 1976
Sciaenops ocellatus	78%	Ross et al., 1995
Sciaenops ocellatus	96%	Wilson and Nieland, 1994
Pogonias cromis	91%	Murphy and Taylor, 1989
Pseudotolithus typus	81%	Zuyev and Giragosov 1990
P. senegalensis	71%	Zuyev and Giragosov 1990
Genyonemus lineatus	93%	Love et al. 1984
Micropogonias furnieri	88%	Manickchand-Heileman and Kenney 1990
Micropogonias undulatus	105%	Barbieri et al., 1994

Management implications

Background

The South African linefishery is a multi-user, multi-species fishery consisting of approximately 205 species (van der Elst 1989). The user groups may be broadly divided into recreational and commercial components. The commercial component consists of 2900 boats (W. Kroon, Sea Fisheries, personal communication, 1995) of between 5 and 15 m. On average they have a crew of 7 fishers, and operate in the marine environment in depths of 5 to 100 m, using fishing rods or handlines. The recreational component may be further divided into estuarine anglers, who fish from boats (±50 000, van der Elst 1989) or river banks (numbers unknown); rock and surf anglers (± 300 000, van der Elst 1989); and a recreational lineboat sector (> 4000 boats & ± 12 800 anglers, van der Elst 1989, Ferriera 1993) which operates in a similar environment to the commercial component. Distribution analysis of dusky and silver kobs (Griffiths & Heemstra 1995), revealed that rock and surf and estuarine anglers catch *A. japonicus* (mostly juveniles) along the east coast of South Africa (Cape Agulhas to northern KwaZulu/Natal), and that lineboaters in this area catch the adults of both *A. japonicus* and *A. inodorus* as far as the Kei

River, but only *A. japonicus* to the north of this locality. Due to the cooler conditions found west of Cape Agulhas all sectors on the west coast catch *A. inodorus*.

Minimum size and bag limits constitute the two most effective methods of effort control for the multi-species, multi-user South African linefishery, particularly where migratory species are concerned. Closed seasons, e.g. during the spawning period, invariably prevent one or more regions/fishing sectors from exploiting a migratory resource, and marine reserves provide only partial protection. Commercial and recreational lineboat fishers often argue against size and bag limits on the grounds that due to the multispecies nature of the fishery, fish are accidentally caught in excess of species specific quotas, and because of the effects of barotrauma, these and undersized fish often die when returned to the water. However *A. japonicus* and *A. inodorus* generally form shoals of equal sized fish which are mostly targeted for on specific grounds. It is therefore possible for lineboat fishers to move away from such areas once bag limits are reached or if the captured fish do not satisfy the minimum legal size limit.

Historically minimum size limits for the South African linefishery were first introduced in 1940 (Notice No. 1696, Government Gazette Vol. 122 of 25 October 1940). These, including a 400 mm TL limit for "*Johnius hololepidotus*", were determined arbitrarily since biological data were not available, and stock assessments had not been undertaken. Biological studies on linefish species were only initiated in the mid 1970s (van der Elst & Atkins 1991). Daily bag limits for the linefishery were not introduced until 1984 (Government Gazette No. 9543 of 31 December 1984), and were only implemented for recreational anglers. At this time it also became general policy to set minimum size limits for linefish species at the sizes at 50% maturity (or L_{50}) (if biological information was available), in order to allow the individuals of a species at least one opportunity to spawn before being caught (Penney et al. 1989). Due to a lack of biological information, the "*A. hololepidotus*" size limit has remained unchanged since 1940. The suite of bag limits for the South African linefishery is currently structured to constrain recreational effort on all species, and also to divert effort from vulnerable reef dwelling sparids, to more "resilient" shoaling fishes (Penney et al. 1989). Perceived as a resilient species, a bag limit was not introduced for "*A. hololepidotus*" in 1984. A generous daily limit of 10 fish/man (the maximum allowed) was legislated in 1992 (Government Gazette No. 14353 of 23 October 1992), but only to curtail the illegal sale of fish by recreationals. In the absence of the taxonomic and biological findings presented in this thesis, it is not difficult to understand why "*A. hololepidotus*" was perceived as being a resilient species. It was found along the entire South African coast, occurring in estuaries, the surf zone and the nearshore marine environment. In addition Smale (1985) suggested that it had a small size at first maturity (c. 250 mm) and a protracted spawning season, and Wallace & Schleyer (1979) indicated that it grew reasonably fast. However, when considered as two separate species, with different life-history strategies and stock structures, the "*A. hololepidotus*" resource is perhaps not as resilient as previously believed.

Argyrosomus japonicus

Species such as *A. japonicus*, which have evolved life history strategies based on low rates of natural mortality, are expected to be extremely sensitive to fishing pressure. The South African *Atractoscion aequidens* resource, another shoaling sciaenid with late maturity (Griffiths & Hecht 1995), declined dramatically over the last century due to inadequate protection (Griffiths 1988, Penney et al. 1989). Although there are no long term catch data available for *A. japonicus*, the facts that: (i) juveniles are restricted to estuaries and the surf zone where they are easily accessible to rapidly expanding recreational sectors; (ii) adults form heavily targeted spawning aggregations; (iii) declining fresh water input into South African estuaries is probably already affecting early juvenile recruitment; (iv) the current 400 mm TL size limit does not provide protection until maturity; and (v) the paucity of fish older than 27 years, even though the maximum age was 42 years, are all reasons for concern. It is therefore recommended that management strategies be introduced which will afford better protection for this valuable species. It is of interest to note that in response to declining catches of *A. japonicus* in Southern Australia (Hall 1984, 1986), a recreational daily bag limit of three per angler was introduced, and the minimum size limit was increased for marine waters from 460 to 750 mm TL (Jones 1991), which is the length at which they are thought to reach maturity in this region (Hall 1984). The South African situation of a 400 mm TL minimum legal size limit for a species which has a female L_{50} of 1070 mm TL, and is believed to be under pressure, is clearly unacceptable. Rock and surf and estuarine anglers catch predominantly juvenile fish, and a minimum size limit of 1070 mm TL would effectively and exclusively reserve *A. japonicus* for lineboat fishers. Since *A. japonicus* grow fastest until ± 900 mm TL or an age of 5 years (see Chapter 5) and because natural mortality (particularly for larger fish) is expected to be low, it could be argued that production would be increased by a minimum size limit of this magnitude. However dusky kob leave the nursery area at about seven or eight years (age at total maturity for males and females), so a minimum size limit of 900 mm TL would essentially limit the period of a cohorts life-span for which it was available to rock and surf and estuarine anglers to only two or three years (vs 20-30 years for lineboaters). Because of these complex management issues size limits based strictly on biological (L_{50}) or production (e.g. yield per recruit models) criteria are inappropriate for South African *A. japonicus*. It is recommended that the size limit be increased from 400 (1.3 years) to 600 mm TL (2.6 years). This minimum size should theoretically result in increased production (due to fast growth and low mortality), larger fish in the recreational fishery, and provide adequate exposure of each cohort to the recreational fishery. Where possible minimum size limits for the South African linefishery are standardized to improve management efficiency (Penney et al. 1989). A 600 mm TL minimum size limit for *A. japonicus* would also conform to an existing size limit category e.g. for *Lithognathus lithognathus* (Sparidae), *Sparodon durbanensis* (Sparidae) and *Atractoscion aequidens* (Sciaenidae). To ensure that some fish survive to maturity, to protect the spawner stock and to guard against recruitment overfishing, it is suggested that the recreational fishers be permitted only one fish larger than 1100 mm TL per day, that the bag limit for recreational fishers be reduced, and that a bag limit be introduced for commercial fishers. Club records and observations made throughout the sampling phase of this project, indicated that recreational fishers rarely catch even half of the current bag limit for kob, in terms of *A. japonicus*. As a result, halving the current daily limit would have little effect on the recreational effort expended on this species. If bag limits for *A. japonicus* are to reduce effort, it is therefore imperative that they be realistic. Since a target for effort reduction has not been identified (stock assessment not yet completed), and because current effort levels are unknown, it is recommended that new bag limits be the South African Marine Linefish Management Association, which consists of scientists and representatives of all fishing sectors.

Although juvenile *A. japonicus* along the South African east coast seem to exist as separate populations, focused around the estuaries to which they were recruited as early juveniles, the adults apparently comprise a single population (of which a large proportion migrate to Natal to spawn). Therefore, since catches of juveniles or adults in any region will impact on the national adult population, it is suggested that catch restrictions for this species be uniform throughout the country. Although it may be difficult at this stage for the layman to distinguish between *A. inodorus* and *A. japonicus*, habitat/fishing-sector specific size limits would achieve the desired effect. Since lineboat fishers do not catch juvenile dusky kob, the 400 mm limit (appropriate for *A. inodorus*) could be applied to this sector without increasing pressure on juvenile *A. japonicus*. Because rock and surf and estuarine anglers between Cape Agulhas and the Kei River rarely, and in KwaZulu/Natal never catch *A. inodorus*, the minimum size for kob caught in these two environments (surf zone and estuaries) could therefore be increased to 600 mm, without depriving anglers of "legitimate" catches of *A. inodorus*. Kob caught by rock and surf anglers along the South African west coast, are predominantly *A. inodorus*, so the size limit appropriate for this species (400 mm TL) could be applied to all fishing sectors or habitats west of Cape Agulhas.

The recently proposed introduction of commercial gillnet and beach-seine fisheries to the estuarine and surf zone environments of the east coast of South Africa, will potentially increase pressure on juvenile *A. japonicus*, and also on other important linefish species e.g. *Lichia amia*, *Lithognathus lithognathus* and *Pomadasys commersonnii*. Unless gear limitations can be enforced to protect linefish, such fisheries are considered to be highly undesirable. Estuaries identified as important nursery areas for dusky kob should be protected from further degradation (including river catchments), and if possible rehabilitated. In the case of systems that are dammed, water should ideally be released during spring/summer, the period of early juvenile recruitment and dependence.

Argyrosomus inodorus

Growth rates, otolith dimension/fish length relationships, growth zone structure, juvenile and adult distribution patterns (based on CPUE data), sizes at sexual maturity, tagging data and mortality estimates, collectively suggest that *A. inodorus* between Cape Point and the Kei River, exist as three separate stocks. Each of these stocks apparently move onshore in summer and offshore in winter, in response to oceanographic conditions. Since the silver kob stocks are spatially separated, with one in the South-Eastern Cape, one in the Southern Cape and one in the South-Western Cape; and because each stock has specific life-history parameters, it is clear that catches in one region would not affect those in another and that this species requires regional management. In other words, separate stock assessments are required, and minimum size and bag limits in each region should be based on the dynamics of each respective stock. The life-history of *A. inodorus* suggests that it should be more resilient to fishing pressure than *A. japonicus*. Although the current size limit, by co-incidence, has provided protection from linefishers until maturity since 1940, catch data from the last decade, length frequencies from the last two decades, and the paucity of fish older than 13 years (although the maximum age was 25 years), suggests heavy exploitation, particularly in the South-Eastern Cape. Dramatic declines in the annual landings by the inshore trawling industry, which mainly catch juveniles and young adults, indicate that the adult stocks have been reduced to the point that recruitment is affected, suggesting recruitment overfishing. Assessment of the South African *A. inodorus* stocks is therefore a matter of urgency. In the absence of long term catch data, and information on the spawner biomass recruit relationship, yield per recruit and spawner biomass per recruit models represent the most appropriate assessment methods available (Butterworth et al. 1989; Punt 1993). Life-history information provided in this thesis is therefore essential for the assessment of this valuable resource, and will assist with the formulation of effective conservation measures (bag and minimum size limits) for each stock. The size composition, growth rates and sizes at maturity also constitute useful base-line data against which future responses to fishing and the effects of management strategies can be gauged.

Evidence presented in Chapter 6 indicated that the Southern Cape stock of *A. inodorus* experiences lower rates of total mortality than the South-Eastern Cape stock, despite much larger annual catches, therefore suggesting a larger stock size in the former region. This is probably because the Agulhas Bank is wider in the Southern Cape (100 m isobath further offshore), thus providing this region with a larger carrying capacity for *A. inodorus*. As evinced by catch trends, winter catches constitute a larger percentage of the annual catch in the South-Eastern Cape than in the Southern Cape, therefore indicating that a larger proportion of the stock in the former region do not move beyond the range of the lineboats in winter. The narrower shelf in the South-Eastern Cape is believed to constrain seaward movement in winter, and in all probability is a contributing factor to the high mortality rates apparent for this region.

Although exploitation with most methods causes a decline in the relative abundances of larger fish (being older they are exposed to fishing for longer), this phenomenon is more prevalent in linefisheries because larger fish generally outcompete smaller conspecifics when feeding. The removal of larger fish can have profound implications (excluding those associated with species exhibiting sex change) for the management of a stock. Evidence presented in Chapter 6 indicates that the size and age at sexual maturity has declined in the South-Eastern Cape as a result of fishing pressure. Due to the costs of reproduction, earlier maturity is predicted to result in higher natural mortality (Borisov 1978, Roff 1992). In *A. inodorus*, maturity is associated with the emigration from the nursery environment, which presumably has some survival value for juveniles, to the adult habitat. Maturity has also been associated with a decrease in growth in young adult silver kob, and since mortality is size dependent, this may serve to increase the rate of natural mortality experienced in the first few years of life. Removal of larger fish also reduces the average age and size of individuals in the spawner stock. Since reproductive effort in fishes increases with size (Roff 1992), not only is the spawner stock diminished by exploitation, but the reproductive effort per unit mass of spawner stock is also reduced. Parrish et al. (1986) and Alheit (1989) emphasized that old individuals contribute a relatively greater proportion of a population's total annual egg production, and pointed out that the selective removal of larger fish could well increase the danger of recruitment overfishing. Although the largest *A. inodorus* observed in the South-Eastern Cape was 1310 mm TL, c. 50% of the fish landed by lineboats in this region were between 400-449 mm TL. Considering the paucity of fish between 450 and 1300 mm, it is not surprising that trawl catches have indicated a massive decline in recruitment. Unfortunately information on size composition and sizes at maturity is not available for unexploited stocks of *A. inodorus*, and it is therefore not possible to ascertain the degree to which fishing pressure has altered the South African stocks. Since the South African linefishery is more than 100 years old (Penney et al. 1989) and the silver kob is a relatively long lived species, it is possible that sizes at maturity in Southern Cape were also larger, and it is expected that the proportion of larger fish in all regions was substantially higher, prior to exploitation. A maximum size limit should therefore be considered as a management option for this species, in order to increase recruitment levels.

The by-catch of linefish species by the hake and sole directed inshore trawlfishery (operating between Cape Agulhas and Port Alfred) has been a point of contention for several decades, and it is the perception of many linefishers that the trawlers are responsible for declining kob catches. Of further concern to linefishers is the fact that the trawlers catch kob below the legal minimum size for the linefishery (400 mm TL). Results of this study show that the kob species occurring on the inshore trawlgrounds is strictly *A. inodorus*, indicating that trawlers cannot be implicated in catch reductions experienced by rock and surf or estuarine anglers on the east coast (they catch *A. japonicus*). While 68% of the landed inshore trawl silver kob catch is below 400 mm TL, only 25% is below the average L_{50} (340 mm TL) for female *A. inodorus* in the South-Eastern and Southern Cape regions (see Chapter 6). Silver kob are not trawled in the South-Western Cape, due to the rocky nature of the inshore substrata, and the line-caught fish in that region appear to represent a separate stock. The line and trawl catches of *A. inodorus* made in the South-Eastern Cape and Southern Cape were therefore compared in order to obtain some indication of the impact of the inshore trawl fishery on the stocks of these two regions (Table 7.4). In terms of landed weight, the inshore trawl catch constituted only 18-37% of the commercial line-catch in the South-Eastern Cape and 25-40% of commercial line-catch in the Southern Cape, over the last nine years (Table 7.4). It should also be noted that silver kob are heavily targeted by recreational lineboat fishers (Smale 1985, Hecht & Tilney 1989, Griffiths & Heemstra 1995). Hardly any catch statistics are available for the recreational sector, so the figures for the total linefish catch would therefore be substantially higher than the commercial figures shown in Table 7.4. The legal closure of all bays between Cape Point and Port Alfred to trawling (in order to reduce conflict with linefishers), together with the rocky nature of inshore substrata on the east coast, has essentially limited inshore trawling to depths of >50 m. Since sand/mud substrata of <50 m (particularly bays) are important nursery grounds for *A. inodorus* (Chapter 6), the banning of trawling in bays can be regarded as an important management strategy for the protection of juvenile fish. Superficially, therefore, inshore trawling does not appear to have a large impact on the two east coast silver kob stocks. However, allegations by lineboaters that inshore trawlers discard large quantities of silver kob, too small to be utilized (<250 mm TL), are currently being investigated by means of an onboard observer programme. The possibility of reducing user conflict by seasonally closing limited areas to trawling (e.g. over winter when trawl catches of silver kob are highest) is also being studied through this programme.

Table 7.4: The annual weight (kg) of *Argyrosomus inodorus* landed by inshore trawlers and commercial linefishers in the South-Eastern Cape and in the Southern Cape regions. The trawl catch is expressed as a percentage of the line catches.

YEAR	LINE CATCH		TRAWL CATCH		TRAWL CATCH AS % OF LINECATCH	
	S.E. Cape	S. Cape	S.E. Cape	S. Cape	S.E. Cape	S. Cape
1986	292664	522998	53249	248887	18.2	47.6
1987	181059	529444	45924	259493	25.4	49.0
1988	121659	486383	36791	203223	30.2	41.8
1989	151514	595029	56144	201719	37.0	33.9
1990	225853	759036	37940	219836	16.8	28.9
1991	213508	560410	33110	146484	15.5	26.1
1992	168503	484478	31056	121105	18.4	25.0
1993	162271	473127	38033	128787	23.4	27.2
1994	205255	326414	44303	90107	21.6	27.6

Conclusion

To conclude, the research presented in this thesis has clearly demonstrated that there are two South African species that were previously described as "*A. hololepidotus*", and it has provided information, relevant to management, on the life-histories of both. Furthermore it has revealed the urgent need for stock assessment of South African *A. inodorus* and *A. japonicus*, and for the implementation of conservation strategies appropriate for each species. Topics identified for future research include: confirmation of multiple spawning and measures of batch fecundity and spawning frequency in both species, the physical requirements (e.g. depth, temperature, substratum type, locality, time of day) for spawning in both species, the size and age at maturity for *A. inodorus* in False Bay, and the identification of estuaries (other than the Great Fish River) and the physical parameters which are important for the recruitment of early juveniles of *A. japonicus*.

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APPENDIX A

PAPERS EMANATING FROM THIS THESIS

GRIFFITHS, M.H. in prep a. On the life history of *Argyrosomus japonicus* (Sciaenidae) off the east coast of South Africa. (Submitted to *Env. Biol. of Fish.*)

GRIFFITHS, M.H. in prep b. Age and growth of South African silver kob, *Argyrosomus inodorus* (sciaenidae), with evidence for separate stocks, based on otoliths. (Submitted to *S. Afr. J. mar. Sci.*)

GRIFFITHS, M.H. in prep c. On the life-history of the silver kob, *Argyrosomus inodorus* (Griffiths & Heemstra) (Sciaenidae), in South African waters. (Submitted to *Fish. Bull., Wash.)*

GRIFFITHS, M.H. & T. HECHT. in press. Age and growth of the dusky kob, *Argyrosomus japonicus*, in South African waters. *S. Afr. J. mar. Sci.* **16**:

GRIFFITHS, M. H. & P.C. HEEMSTRA. 1995. A contribution to the taxonomy of the marine fish genus *Argyrosomus* (Perciformes: Sciaenidae) with descriptions of two new species from southern Africa. *Ichthyol. Bull., J.L.B. Smith. Inst. Ichthyol.* **65**: 40 pp.