Abstract.–Fishery dependent and fishery independent distribution analyses together reveal that there are three discrete areas of *Argyrosomus inodorus* abundance between Cape Point and the Kei River: one in the southeastern Cape, one in the southern Cape, and one in the southwestern Cape. On the basis of migratory patterns determined from tagging and catch data, differences in growth rates, otolith-dimension and fish-length relationships, growth zone structure, sizes at maturity and sex ratios, and on the fact that each region has nursery and spawning areas, the conclusion has been drawn that these areas of abundance represent three separate stocks. Each stock apparently disperses offshore in winter (to ca. 100 m depth) and concentrates nearshore in summer (<60 m depth) in response to oceanographic patterns. Although there is evidence of spawning activity throughout the year, the main spawning season for silver kob is from August to December, with a peak in spring (Sep–Nov). Size at sexual maturity for silver kob was smaller in the southeastern Cape than in the southern Cape, and in both regions males matured before females. Median sizes at maturity (L_{50}) for females and males were 310 mm TL (1.3 yr) and 290 mm TL (1 yr) respectively in the southeastern Cape and 375 mm TL (2.4 yr) and 325 mm TL (1.5 yr) respectively in the southern Cape. East of Cape Agulhas, *A. inodorus* are found just beyond the surf zone to depths of 120 m. Adults occur predominantly on reefs (>20 m), whereas juveniles are found mainly over soft substrata of sand or mud (5–120 m depth). Young juveniles recruit to nurseries immediately seaward of the surf zone (5–10 m depth) but move deeper with growth. Because of lower water temperatures west of Cape Agulhas, the adults in this area are found from the surf zone to depths of only 20 m in summer.

Manuscript accepted 22 August 1996.
Fishery Bulletin 95:47–67 (1997).

The life history and stock separation of silver kob, *Argyrosomus inodorus*, in South African waters

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Silver kob, *Argyrosomus inodorus*, is an important commercial and recreational sciaenid fish (max. size 34 kg) that 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). It is not common between Cape Point and central Namibia; therefore it is likely that the Namibian populations are not continuous with those off the eastern seaboard of South Africa (Griffiths and Heemstra, 1995). Until recently *A. inodorus* was misidentified as *A. hololepidotus* throughout its distribution; off South Africa it was also confused with a sympatric species, *A. japonicus* (Griffiths and Heemstra, 1995).

The South African line fishery consists of about 2,900 commercial (Kroon[1]) and some 4,000 club-affiliated recreational (Ferreira, 1993) vessels. These vary from 5 to 15 m in length and operate on both east and west coasts. Silver kob is probably the most valuable species caught by the line fishery between Cape Point and East London if market value and annual catch are combined; *A. inodorus* is also landed as a bycatch of the sole- and hake-directed inshore trawl fishery between Cape Agulhas and Port Alfred (Japp et al., 1994) and is caught by rock and surf anglers and commercial beach-seine fishermen in the southwestern Cape. Although an important species, trawl and line catch per unit of effort for this species has declined substantially during the last three decades, and concern has been expressed over the large contribution of recruits to line catches in the southeastern Cape (Smale, 1985; Hecht and Tilney, 1989).

Knowledge of the life history of fishes "is an almost essential prerequisite to successful identification of stocks" (Pawson and Jennings, 1996) and is fundamental to stock assessment and to the formulation of effective management strategies for their sustainable use. Despite the importance of *A. inodorus* and evidence for declining catches, little has been published on its life history; wise management has therefore not been possible. Smale (1985) investigated the sex ratio and spawning seasonality of "*A. hololepidotus*" based on the catches of lineboat fishermen in Algoa Bay but inadvertently included both *A. inodorus* and *A. japonicus* in his study (established via voucher specimens and otoliths). Griffiths (in press, a) recently described the growth of *A. inodorus* from three geographical regions between Cape

[1] Kroon, W. 1995. Sea Fisheries, Permit Division, P. Bag X2, Roggebaai, 8012, Cape Town, South Africa. Personal commun.

Point and the Kei River. On the basis of grow rate, fish-length and otolith-dimension relationships, and the appearance of growth zones, he concluded that silver kob within this area comprise at least three separate stocks.

The objective of the present study was to provide information on 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. Because the identification of discrete stocks or "management units" is essential for effective management (Pawson and Jennings, 1996), the multiple stock concept is further developed with information on distribution and abundance, life history parameters, and mark-recapture data.

Materials and methods

The study area (from Cape Point to Kei River) was divided into three regions for sampling purposes (Fig. 1). These regions were identical to those used by Griffiths (in press, a); they were not divided according to political boundaries but rather generated 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 1) by the line fishery, 2) by the inshore trawl fishery, 3) by trawlers during South Coast Biomass Surveys conducted by the Sea Fisheries Research Institute, and 4) by research linefishing operations. Biological data were also obtained from silver kob caught by beach seines in False Bay (Oct 1991). Trawled fish were generally caught over sand or mud substrata, and line-caught fish over reef. Owing to the high relief rocky nature of the inshore habitat west of Cape Agulhas, this species is not trawled in the southwestern Cape.

Fish sampled for biological purposes were measured (to the nearest 1 mm [total length]), 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]), cut open, and sexed. Gonads were removed, assigned a visual index of maturity (see Table 1), and weighed to the nearest 0.1 g. Males were assigned an index of drumming muscle development (1=none, 2=partially developed, 3=fully developed). Owing to logistical constraints, monthly biological data were obtained only for the southeastern Cape; in the other two regions biological sampling was limited to the spawning season.

Areas of silver kob abundance were delineated by using returns from the commercial line fishery and data from South Coast Biomass Surveys (SCBS's). Line catches consisted predominantly of adult fish, whereas trawl catches from SCBS's comprised mostly juveniles and young adults (see below). Annual catch-per-unit-of-effort data (catch per outing) were plotted on a subregional basis for the commercial line fishery (an outing did not exceed one day), and the data from 14 SCBS's (Table 2) were used to calculate

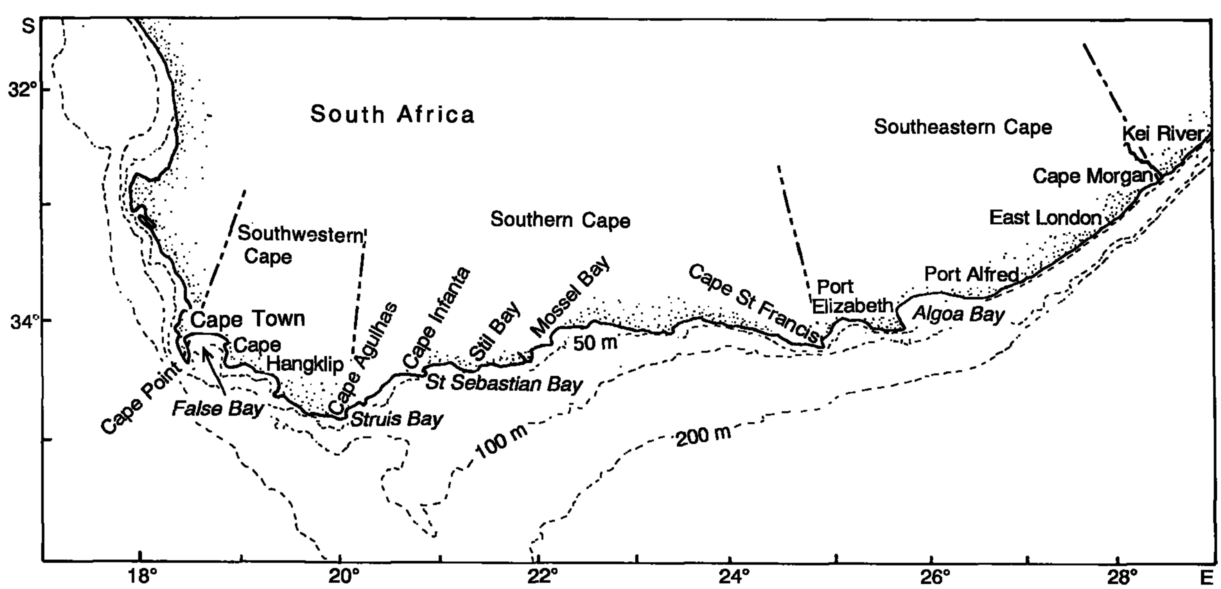

Figure 1

Map of the three coastal regions where silver kob were sampled, and localities mentioned in the text.

Table 1

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

Stage		Description
1	**Juvenile**	This stage is generally only found in fish < 200 mm TL. Testes are threadlike, and the ovaries appear as transparent pinkish flaccid sacs, about half the length of those at stage 2.
2	**Immature or resting**	Testes are extremely thin, flat, and pinkish white. Ovaries appear as translucent orange tubes. Eggs are not visible to the naked eye.
3	**Active**	Testes are wider, triangular in cross section and beige. Sperm are visible 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.
4	**Developing**	Testes become wider and deeper and are mottled and creamy beige. They are also softer in texture, rupturing when lightly pinched. Besides the obvious presence of sperm in the main sperm duct, some sperm are also present in the tissue. Ovaries become larger in diameter and opaque yellow in color. Clearly discernible eggs occupy the entire ovary.
5	**Ripe**	Testes still larger in cross section and softer in texture. They become creamier in color owing to considerable quantities of sperm. The ovaries are larger in diameter as a result of an increase in egg size.
6	**Ripe and running**	Testes even larger in cross section and uniformly cream in color. They are extremely delicate at this stage and rupture easily when handled. Sperm are freely extruded when pressure is applied to the abdomen of the whole fish. Ovaries amber in color and have a substantial proportion of hydrated eggs.
7	**Spent**	Testes are shrivelled and a mottled beige and cream. 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 those at stage 2 and have a few remaining yolked oocytes. These yolked oocytes are generally aspherical and appear to be undergoing resorption.

mean numbers of silver kob per 30-min trawl per grid block. The SCBS methods are fully described by Badenhorst and Smale (1991); therefore 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 5 × 5 nautical miles. The blocks trawled during each survey were determined semirandomly according to the ratio of blocks per stratum. Bobbins were not used; therefore trawling was limited to nonreef substrata. The shallowest depth over which the research vessel (*F.R.S. Africana*) could operate was 20 m. A 180-ft German trawler with a 25-mm-mesh (bar) liner attached to the trawl bag was used. Trawl duration was limited to 30 min, and the results of shorter trawls (owing to technical reasons or to hitting the reef) were standardized to that time. Bottom temperature was recorded immediately after most trawls with a Neil Brown MK III-B conductivity, temperature, and depth probe (CTD). Mean numbers of *A. inodorus* per trawl for each 1°C of bottom temperature were plotted to obtain the preferred temperature range of this species.

Table 2

Number of trawls in which juvenile *A. inodorus* were caught during South Coast Biomass Surveys between Cape Agulhas (20°E) and Port Alfred (27°E) during the period 1987–95.

Cruise	Total trawls	Trawls with silver kob
9 Sep–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	1,200	246

Migration of *A. inodorus* was studied by using tagging and catch data. A tagging program was initiated in February 1994. Silver kob captured with hook and line were tagged with plastic T-bar tags in False Bay (n=1,034), off Struis Bay (n=750), and off Stil Bay (n=291). The data for recaptured silver kob

(n=157), predominantly adults, were analyzed according to tagging locality, days free, and the minimum aquatic distance travelled.

Owners of commercial line boats 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 linefishermen in each of the three regions and the monthly catches made by the inshore trawl fishery in the southern Cape and the southeastern Cape for the period 1986–94 were expressed as percentages of the respective annual totals.

The median size at first maturity (L_{50}) for males and females was estimated by fitting a logistical function (LOGIT) to the fractions of mature fish (gonad stage 3+) per 50-mm length class (midpoint) that were sampled in the southern Cape and the southeastern 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. Because *A. inodorus* are not trawled in the southwestern Cape, few juveniles were sampled and L_{50} values could not be calculated for that region.

Reproductive seasonality was established in the southeastern Cape by calculating both gonadosomatic indices (GSI's) and the monthly percent frequency of each maturity stage for fish $>L_{50}$.

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

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 and Nov 1991) off East London, Port Alfred, Mossel Bay, St Sebastian Bay, and False Bay. Sex ratios were tested statistically for significant deviations from unity with a chi-square test ($P<0.05$).

Nursery areas were delineated by comparing the length-frequency distributions of silver kob caught 1) during South Coast Biomass Surveys (SCBS), 2) during experimental linefishing expeditions (no minimum size) and 3) by the line fishery (1990–94) as well as by analyzing the catch and effort distributions generated for silver kob during SCBS's (1987–95).

Results

Catch distribution and migration

Geographically related catch and CPUE trends for the line fishery consisted of three modal groups (Fig. 2), indicating that there are three areas of adult abundance between Cape Point and the Kei River (one in each region). Data from SCBS's showed that adult abundance trends were reflected in juvenile distribution, at least for the east coast (Fig. 3). Substantial differences in growth rates, otolith-dimension and fish-length relationships, and growth zone structure (Griffiths, in press, a) suggest that these areas of abundance represent three allopatric stocks. 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 (84%) did not move more than 50 km from their tagging locality (Fig. 4). Only one fish tagged in False Bay was recaptured outside of that bay. Of the silver kob tagged in the Struis Bay vicinity, five (5.3%) had migrated westwards to False Bay, and the rest were recaptured either within 50 km of the tagging locality (77.3%) or had moved eastwards (17%), but only as far as Mossel Bay. None of the tagged fish were recaptured in the southeastern Cape. Tagging data therefore support the three-stock concept but suggest that there is limited exchange between silver kob in the southern Cape and those in the southwestern Cape. Based on catch data, the foci of each stock are apparently False Bay, Stil Bay, and Port Alfred, which 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: therefore it is not surprising that of the recaptured silver kob that had moved substantial distances (>50 km) from this tagging locality, most had moved to the east.

Interviews with commercial linefishermen ([n=36]; also confirmed by author's personal experience) indicated that their silver kob catch was made on reefs 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 at depths of 50–120 m (Japp et al., 1994). Decreases in the line catches of all three stocks during winter (Fig. 5) and corresponding increases in the catches made by inshore trawlers (Fig. 6) suggest that silver kob move farther offshore at this time of the year. Because inshore trawlers fish over substrata that are different from those over which linefishermen fish and since they land mostly juvenile and young adult *A. inodorus* (Fig. 7), it could be argued that trawl catch data do not reflect the winter locality of the adult population. The offshore movement of adults is supported, however, by the recapture of four specimens (435–720 mm) 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, large adults

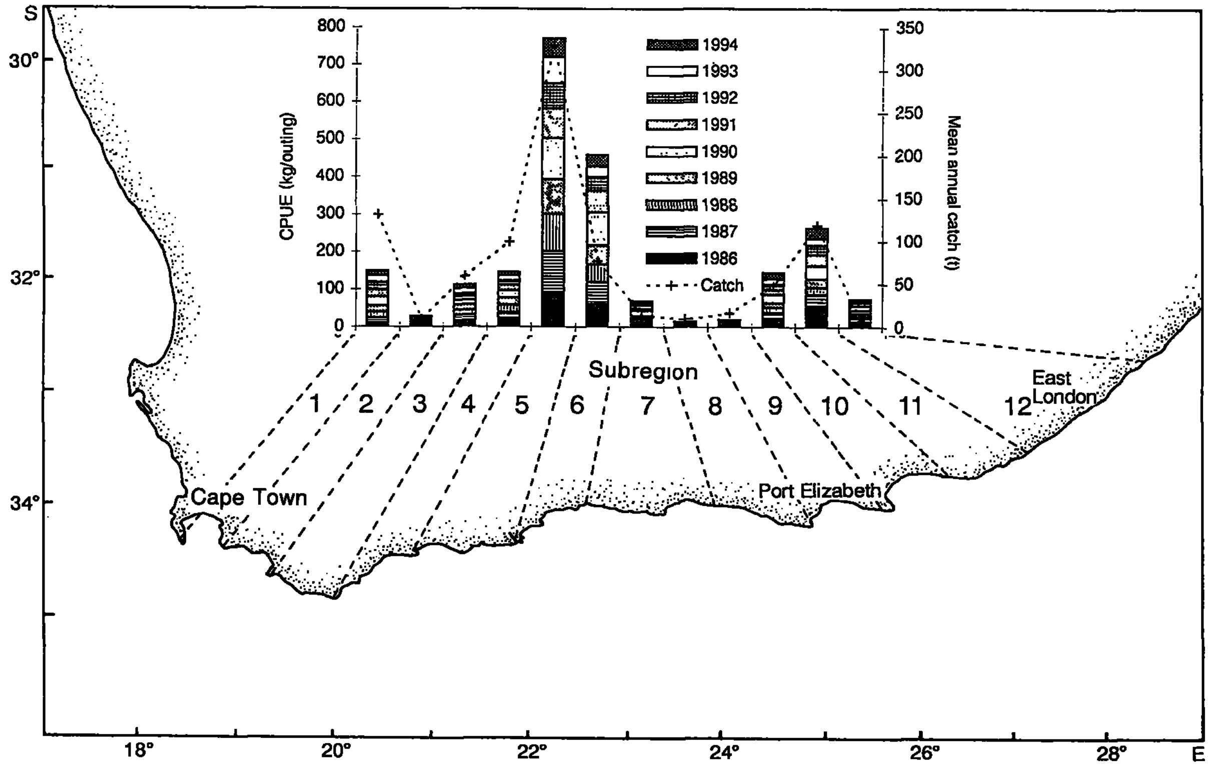

Figure 2

Annual catch per unit of effort and mean annual catch for commercial linefishermen operating in 12 subregions between Cape Point and the Kei River, 1986–94. See Figure 1 for localities.

are also found on predominantly untrawlable rocky substrata during their offshore winter distribution.

Size at maturity

Silver kob were found to mature at a smaller size in the southeastern Cape than in the southern Cape, and in both regions males matured at a smaller size than did 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 southeastern Cape than in the southern Cape (Fig. 8, A and B). Estimated median lengths at maturity (L_{50}) were 310 mm and 375 mm for the two regions respectively. All females in the southeastern Cape larger than 450 mm and all females in the southern Cape larger than 550 mm were mature (Fig. 8, A and B).

A comparison of the testes method with the drumming muscle method for estimating male maturity indicated that, within each region, the two methods produced similar estimates for 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 southeastern 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. 8, C and 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. 8, D and F).

Many of the smaller males (<300 mm) classified as mature (i.e. testes contained sperm), had disproportionately smaller gonads and also lacked drumming muscles. Because male drumming plays an important role in sciaenid spawning behavior (Takemura et al., 1978; Saucier and Baltz, 1993; Connaughton and Taylor, 1995; Connaughton, 1996), it is not known whether these fish would actually spawn. Even if the small males (without drumming muscles) managed to spawn with a communal spawn-

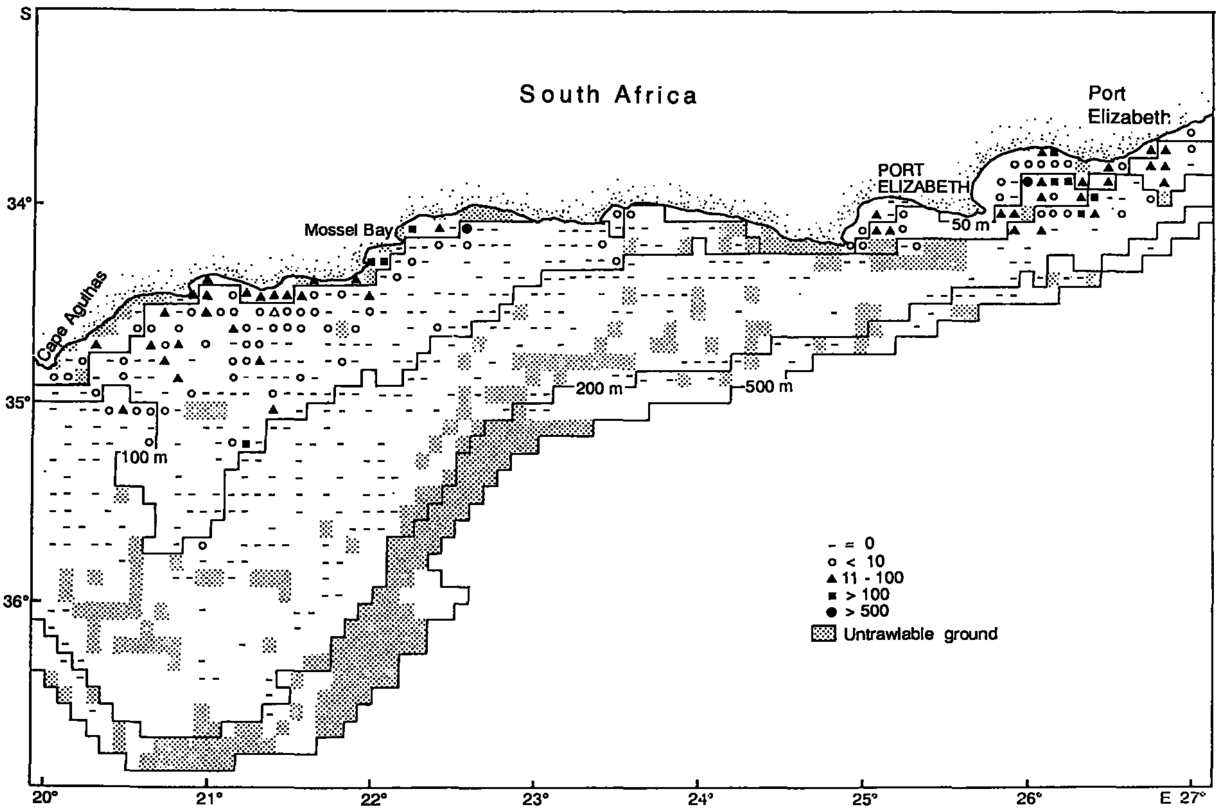

Figure 3

Mean number of juvenile *Argyrosomus inodorus* per trawl per grid block for 14 South Coast Biomass Surveys, 1987–95.

ing aggregation (doubtful as this may be), their contribution to the total reproductive output (of the aggregation), in relation to the small size of their testes, would likely be extremely low. Therefore, from a management view point, the L_{50} estimates based on drumming muscle development were regarded as more useful than those based on gonad staging.

According to Griffiths (in press, a), there was no difference between the growth rates of *A. inodorus* in the southeastern Cape and those in the southern Cape during 1990–91. The smaller sizes at maturity in the former region were therefore due to earlier maturity and not to slower growth. Female L_{50} and total maturity are attained at about 1.3 and 3.5 yr in the southeastern Cape and at about 2.4 and 4.7 yr in the southern Cape. Male L_{50}, based on testes staging and on drumming muscle development, was attained at <1 yr and at 1 yr for silver kob in the southeastern Cape, and at <1 yr (testes staging) and at 1.5 yr (drumming muscle development) in the southern Cape. Total male maturity was attained at about 2.8 yr in the southeastern Cape and at about 3.4 yr in the southern Cape.

Spawning

Gonadosomatic indices (Fig. 9) and gonad maturity indices (Fig. 10) for silver kob in the southeastern Cape showed that although some spawning occurred throughout the year, there was a clearly defined breeding season from August to December and that peak spawning occurred in spring (Sep–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 spawns from October to January (Griffiths, in press, b) in the southeastern Cape. The low proportion of ripe and running (stage-6) females sampled during the spawning season (Fig. 10; and Smale, 1985) suggests that females feed less and are therefore less prone to capture (with hook and line) after oocyte hydration. This inference is supported by a much higher proportion of stage-6 females in catches of silver kob caught by beach seines in False Bay than in catches made by using hook and line in four other localities

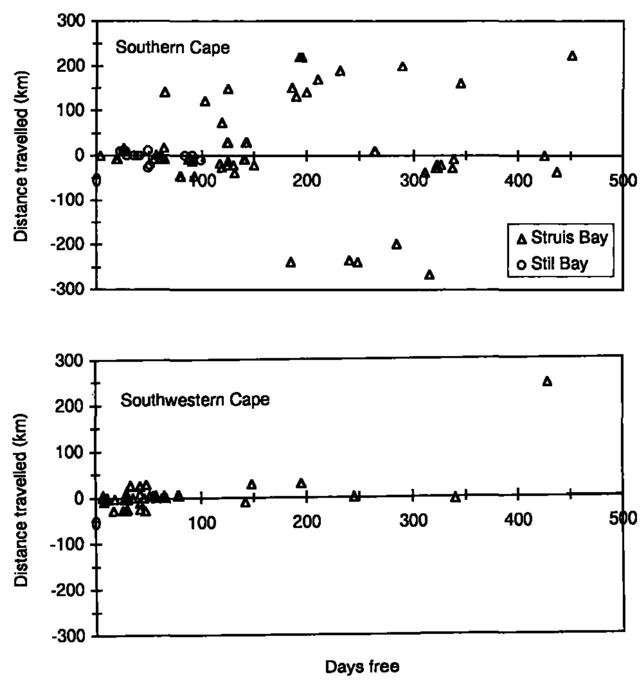

Figure 4

Minimum distance travelled versus days at liberty for recaptured *Argyrosomus inodorus* that were tagged in the southern Cape and in the southwestern Cape (False Bay), South Africa (1994–96). Positive values signify a coastwise migration to the east, and negative values a movement to the west.

(during similar months and times of day)(Fig. 11). Very low numbers of females with hydrated oocytes have also been reported in line catches of other sciaenids, e.g. *Sciaenops ocellatus* (Fitzhugh et al., 1988), *Micropogonias undulatus* (Barbieri et al., 1994), and *Atractoscion aequidens* (Griffiths and Hecht, 1995a); no hydrated oocytes were detected from line catches of *Argyrosomus japonicus* (Griffiths, in press, b). Most silver kob caught during SCBS's were juveniles. Nevertheless, none of the adult females that were trawled had hydrated oocytes, perhaps because these fish were captured on the nursery grounds and not on adult habitat where spawning is expected to occur (see below).

The large proportion of ripe and ripe and running (stages 5 and 6) males and females at each of the five sites between Cape Point and the Kei River (Fig. 11) during October–November suggests that spawning occurs throughout the study area and that peak spawning occurs during spring for all three stocks. The inshore distribution of the adults during spring and summer, the absence of *Argyrosomus* eggs and larvae in the Agulhas Current (ca. 200 m)(Beckley, 1993), and the occurrence of significant numbers of early stages of *A. inodorus* larvae (identified as "*A. hololepidotus*") in 5–7 m in Algoa Bay (Beckley, 1986) suggest that spawning occurs in less than 50 m depth of water. However, even though early life stages of 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 and the eggs and larvae are transported shorewards by currents.

Although spawning in other sciaenids, including *A. japonicus*, occurs at night (Fish and Cummings, 1972; Takemura et al., 1978; Holt et al., 1985; Saucier and Baltz, 1993; Connaughton and Taylor, 1995; Griffiths, in press, b), the fact that large proportions of ripe and running females caught in seine nets in False Bay (Fig. 11) were caught between 11:30 h and 14:30 h, suggests that spawning in *A. inodorus* may occur during the day. The water temperature in which ripe and running females were captured was 18–19°C, but as indicated for other sciaenids (Saucier

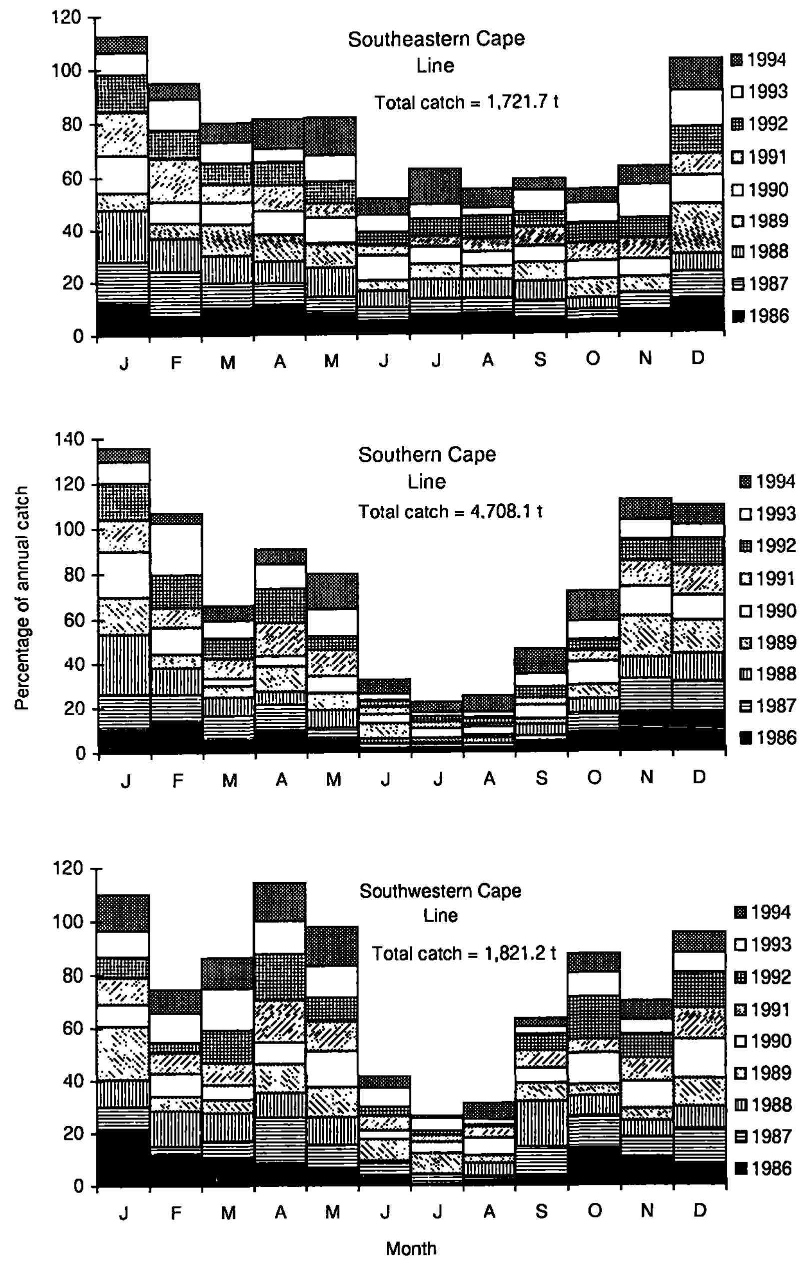

Figure 5

Cumulative monthly catches of *Argyrosomus inodorus* made by South African commercial linefishermen in each region, expressed as percentages of the respective annual catches, 1986–94.

and Baltz, 1993; Connaughton and Taylor, 1995), a range of spawning temperatures is expected. Hydrophonic monitoring of drumming levels (Takemura et al., 1978; Saucier and Baltz, 1993; Connaughton and Taylor, 1995) would provide better information on the times, sites, and oceanographic conditions necessary for spawning of 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. 10), as opposed to throughout the season, suggest that they are multiple spawners. Unfortunately partially spawned fish could not be identified macro-

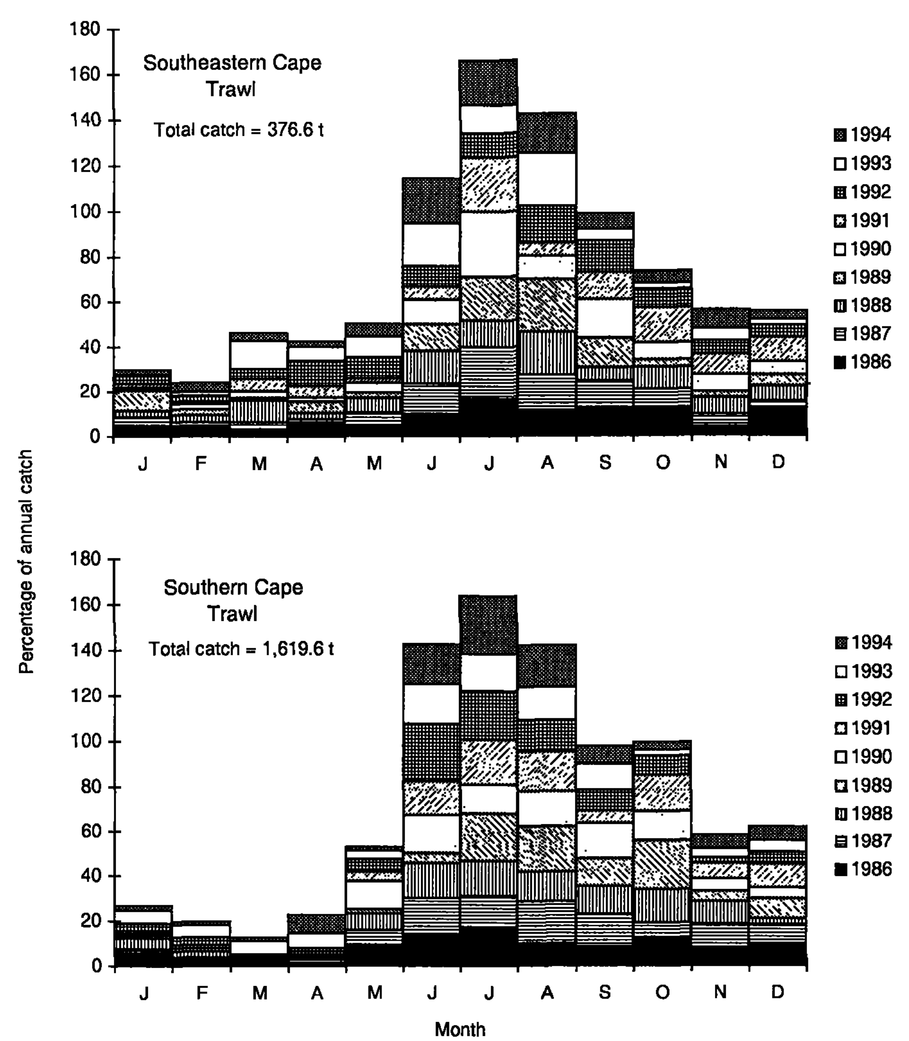

Figure 6

Cumulative monthly landings of *Argyrosomus inodorus* made by the inshore trawl fishery in the southeastern Cape and the southern Cape, expressed as percentages of the respective annual totals, 1986–94.

scopically. Multiple-batch spawning has been described for several other species of sciaenids, e.g. *Sciaenops ocellatus* (Fitzhugh et al., 1988), *Seriphus politus* (DeMartini and 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 and Wilson, 1993), and *Micropogonias undulatus* (Barbieri et al., 1994).

Sex ratios

From the total numbers of silver kob sampled, it was evident that there were significantly more females (1.6×) in the southeastern Cape, more males (1.2×) in the southern Cape, and more females (2.1×) in the southwestern Cape (Table 3). Except for the smallest size class sampled in the southeastern Cape (where males predominated), all other size classes sampled in the southeastern Cape and in the southwestern 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 southeastern Cape (1978–81). Although he included both *A. inodorus* and *A. japonicus* in his study, the latter species recruits to the line fishery only at about 1,000 mm TL (Griffiths, in press, b), therefore his speci-

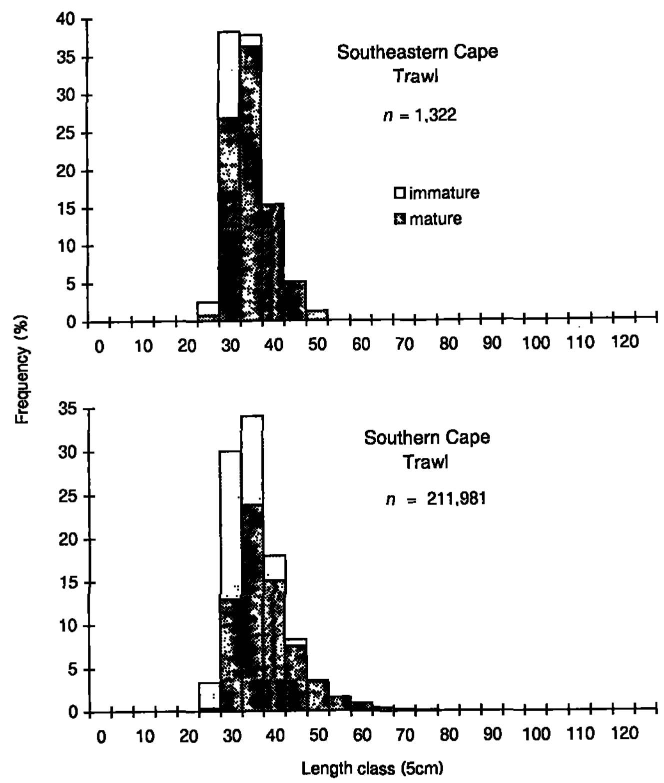

Figure 7

Total length distributions of *Argyrosomus inodorus* landed by the inshore trawl fishery in the southeastern Cape and in the southern Cape, 1990–94. The proportions of immature fish were based on regional averages of the values for males (drumming muscle method) and females presented in Figure 8.

Table 3

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

Total length (mm)	Southeastern Cape			Southern Cape			Southwestern Cape		
	M : F	*n*	χ^2	M : F	*n*	χ^2	M : F	*n*	χ^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	1,194	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	2,982	158.7*	1.2 : 1	1,764	20.1*	1 : 2.1	446	57.4*

mens 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 3). However, the ratios of only three of these size classes (each with more males) were significantly different from the expected 1:1. Because more males were sampled within most size classes in the southern Cape, it would appear 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. although a ratio of 1.2:1

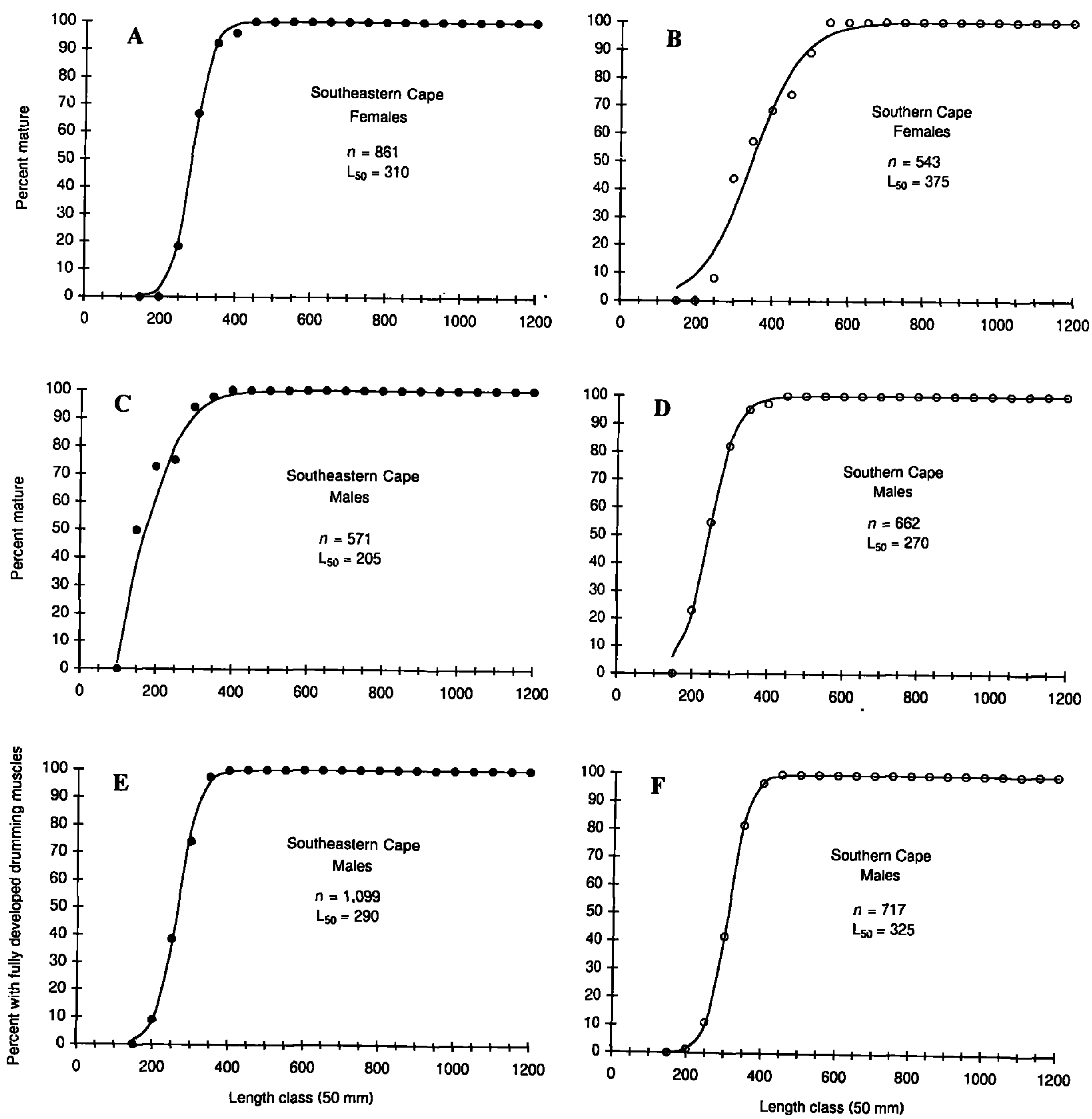

Figure 8

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 southeastern 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.

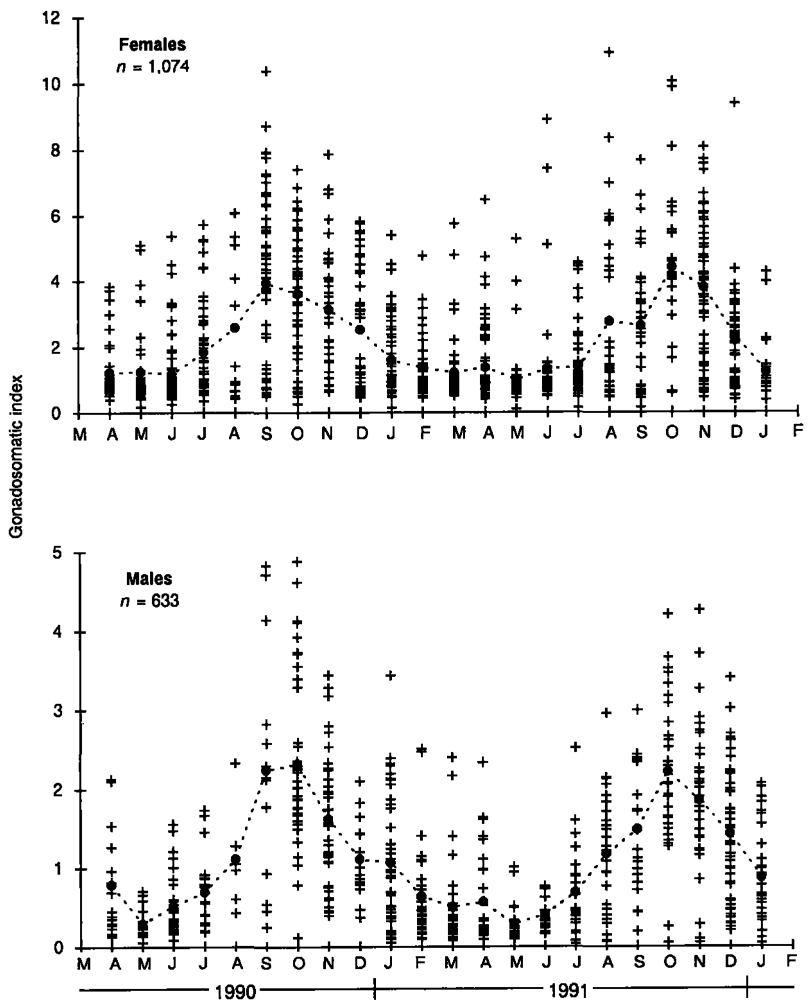

Figure 9

Mean monthly (circles) and monthly (crosses) gonadosomatic indices for mature female and male *Argyrosomus inodorus* sampled in the southeastern Cape, April 1990–January 1992. *n*=sample size.

(*n*=1,764) was significant (even at *P*<0.001), one of 1.3:1 (*n*=80) was not (Table 3). Thus 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.

Nursery areas

Argysomus inodorus landed by the line fishery were mostly adult fish between 40 and 120 cm TL (Fig. 12). Although fish <40 cm TL were not represented in the present study owing to the minimum size limit imposed on linefishermen, experimental linefishing indicated that silver kob on the linefishing grounds (reef substrata) were mostly >30 cm TL (Fig. 12) and that in the southeastern Cape and in the southern Cape they were generally larger than the female L_{50} estimates.

Argysomus inodorus trawled between Cape Agulhas and Port Alfred during SCBS's (nonreef substrata) ranged between 5 and 120 cm TL but were generally <45 cm TL, and largely immature (Fig. 13). The modal length class increased from 20–25 cm at depths of 25–50 m, to 25–30 cm at 50–100 m and 30–35 cm at 100–150 m; and the proportion of mature fish increased accordingly. Although depths <25 m were not sampled during SCBS's, silver kob (identified as "*A. hololepidotus*") trawled in <9 m during an earlier survey of the bays between Mossel Bay and Algoa Bay were mostly 9–18 cm TL (Smale, 1984). Beckley (1984) recorded *A. inodorus* (also iden-

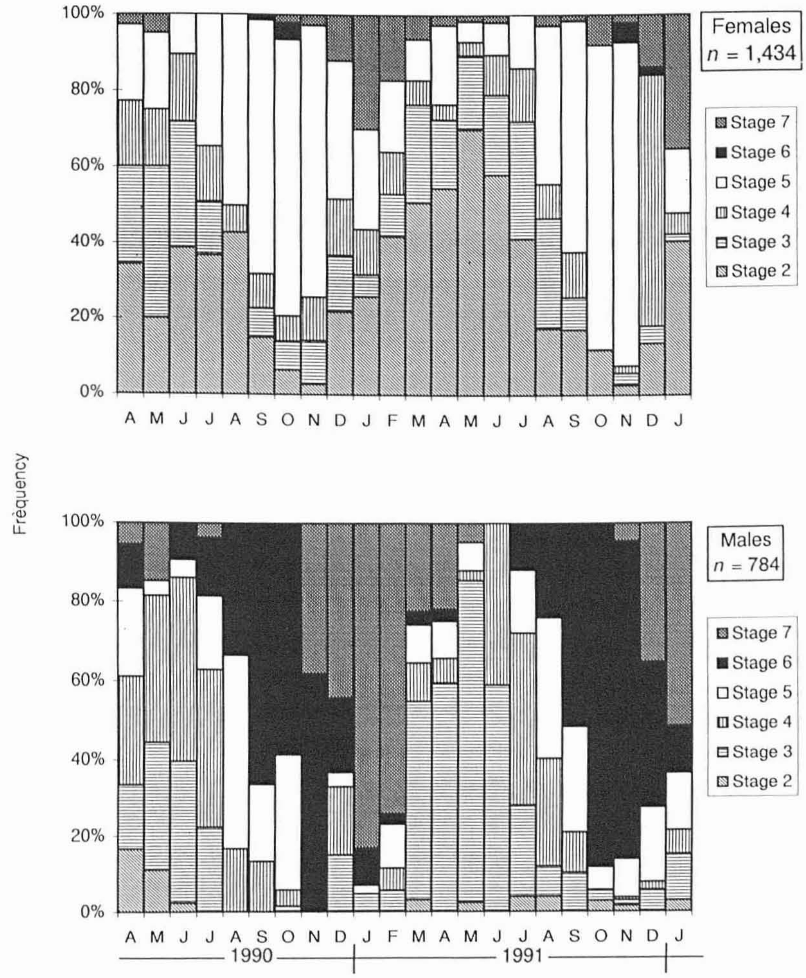

Figure 10

Monthly percentage of gonad stages for mature female and male *Argyrosomus inodorus* in the southeastern Cape, April 1990–January 1992. *n*=sample size.

tified as "*A. hololepidotus*") as small as 1.3 cm TL 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*. 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 finding suggests that juveniles are recruited to the nursery grounds just seaward of the surf zone and that they move farther 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). The 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. 3). Although the inshore areas of the southwestern Cape are not suitable for trawling, analysis of commercial beach-seine catches (Lamberth et al., 1994) revealed that juvenile *A. inodorus* (identified as "*A. hololepidotus*") are also found in False Bay.

Discussion

The results of this study strongly suggest that silver kob between Cape Point and the Kei River comprise three discrete stocks. The foci of each of these stocks are False Bay in the southwestern Cape, Stil Bay in the southern Cape, and Port Alfred in the southeastern Cape. Tagging evidence indicates that there is lim-

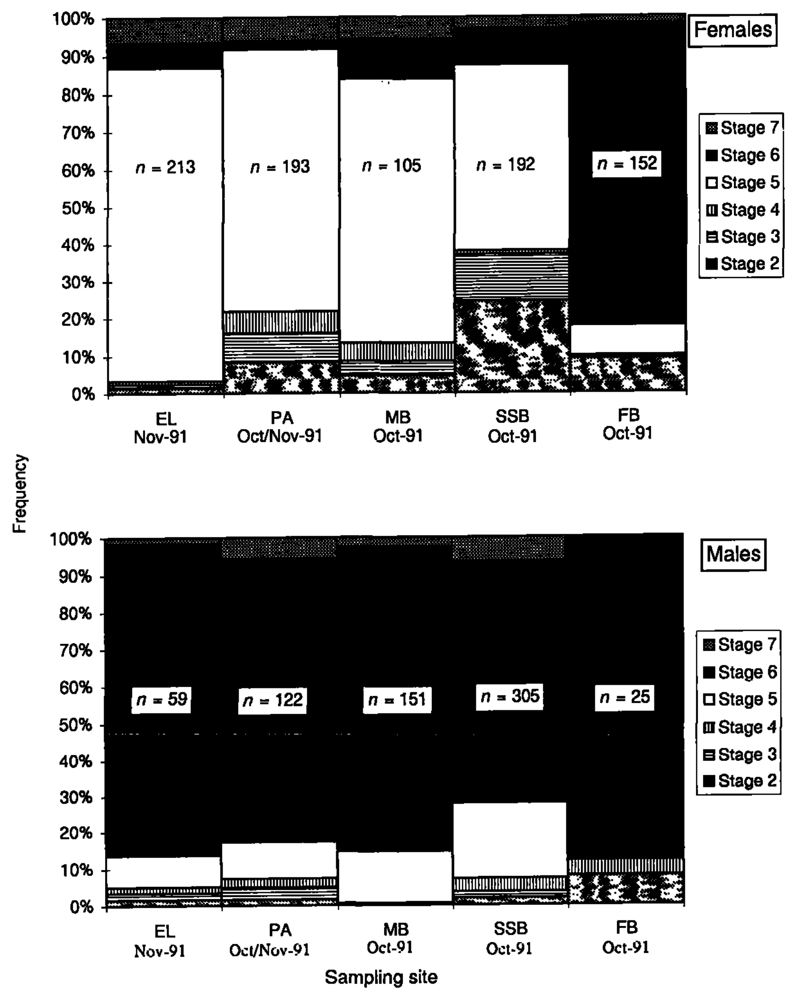

Figure 11

Percentage of gonad stages observed for male and female *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, whereas those in False Bay were caught with beach-seine nets.

ited exchange between the southwestern Cape and the southern Cape stocks but that there is no exchange between either of these two stocks and the one in the southeastern Cape. Analysis of catch and tagging data shows that each of the three stocks is concentrated inshore in summer but disperses seawards in winter.

The distribution of silver kob on the South African eastern seaboard, including the existence of the three stocks and their onshore–offshore movement, 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: 1) 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); 2) a zone of intermediate temperature (12–19°C) between 20 and 50 m; and 3) a bottom mixed layer of <12°C found below 50 m (Eagle and Orren, 1985; Swart and Largier, 1987; Goschen and Schumann, 1988; Boyd and Shillington, 1994; Greenwood and Taunton-Clark[2]). Silver kob prefer temperatures of 13–16°C (Fig. 14) and are therefore mainly confined to the

[2] Greenwood, C., and J. Taunton-Clark. 1992. An atlas of mean monthly and yearly average sea surface temperatures around the southern African coast. Sea Fisheries Research Institute, Private Bag X2, Roggebaai 8012, Cape Town, South Africa. Internal report 124, 112 p.

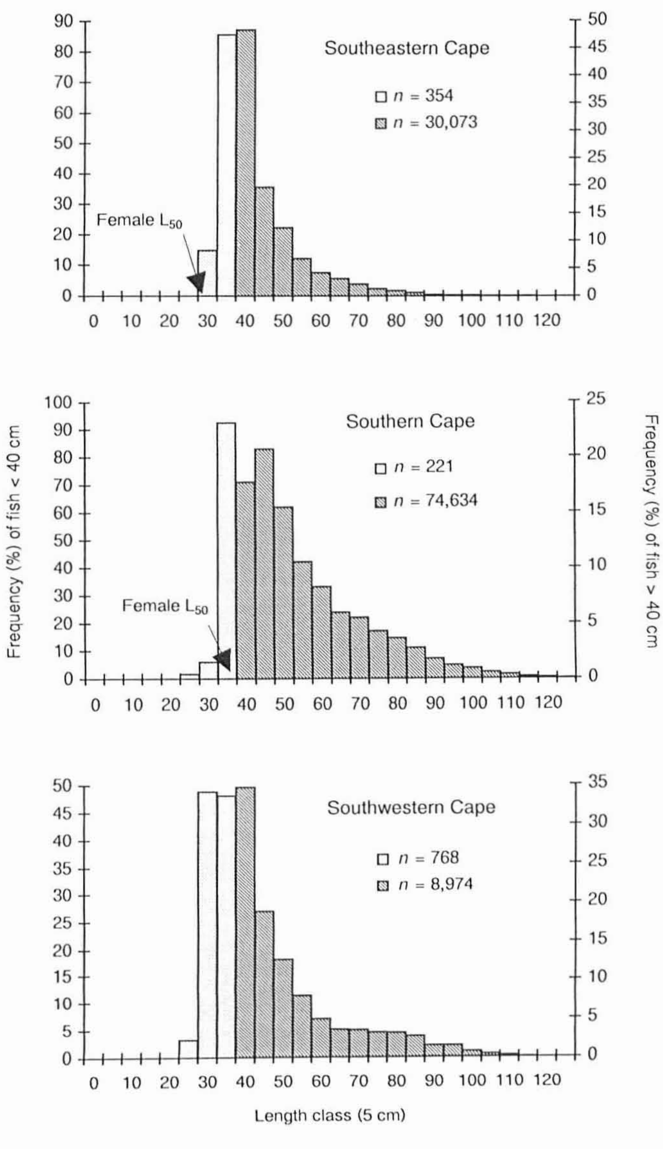

Figure 12

Regional total-length distributions of *Argyrosomus inodorus* 1) landed by the South African line fishery, 1990–94 (hatched lines) and 2) caught on linefish grounds during experimental fishing operations and which were below the minimum size limit (40 cm) (shaded area). Arrows indicate female median length at maturity (L_{50}). L_{50} was not estimated for the southwestern Cape.

intermediate zone. During spring, summer, and autumn, the intermediate zone is restricted to an area within a few kilometres of the coast and is within easy range of line boats (see 50-m isobath in Fig. 1). In winter the bottom mixed layer retreats down the shelf to about 100 m (Schumann and Beekman, 1984; Eagle and Orren, 1985; Swart and Largier, 1987). As the intermediate zone expands, I propose that *A. inodorus* stocks disperse seaward, moving beyond the grounds of the linefishery and onto the inshore trawling grounds. Because Agulhas Bank is much narrower in the southeastern Cape than in the southern Cape (Fig. 1), offshore movement would have been more constrained than in the latter region and hence would explain the higher winter line catches in the southeastern Cape (Fig. 5).

Owing to a higher degree of coastal upwelling off the southwestern Cape, the bottom mixed layer

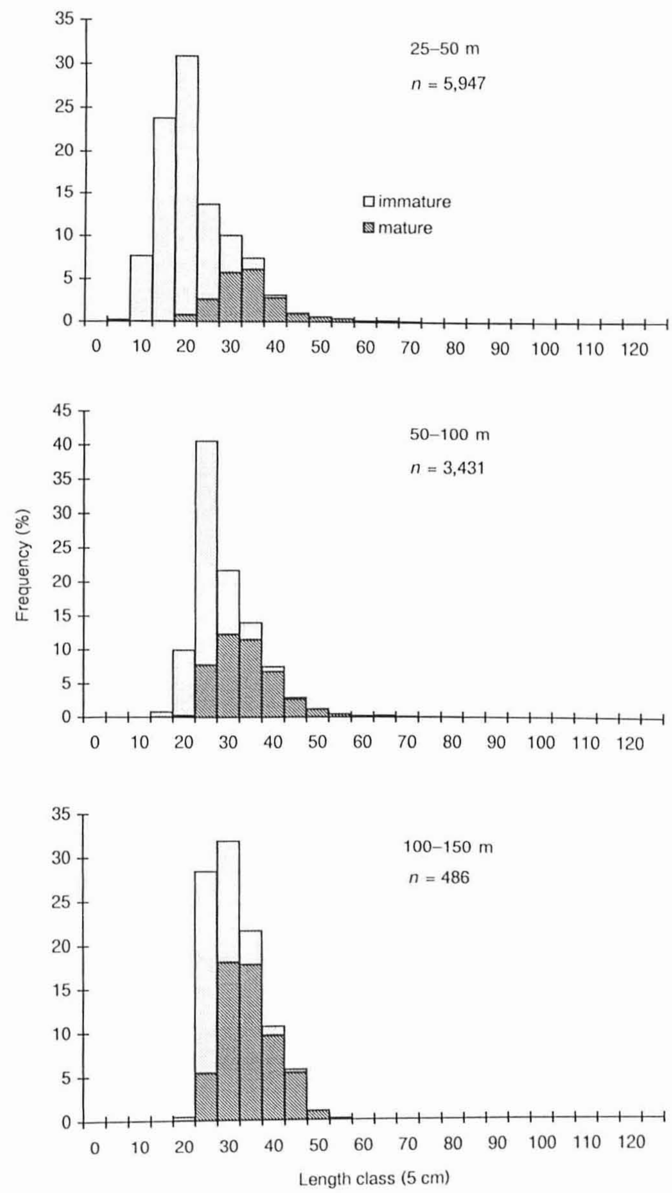

Figure 13

Total-length distributions per depth range for *Argyrosomus inodorus* trawled between Cape Agulhas and Port Alfred during South Coast Biomass Cruises, 1990–94. The proportion of immature fish in each length class is an average of the values presented for males (drumming muscle method) and females in the southeastern Cape and the southern Cape in Figure 8.

(<12°C) is shallower (20 vs. 50 m on the east coast) from spring to autumn, and the temperatures above 20 m are generally 13–19°C during this period (Atkins, 1970; Boyd et al., 1985; Largier et al., 1992; Greenwood and Taunton-Clark[2]). Because inshore temperatures are lower than those on the east coast, silver kob are caught by linefishermen from the surf zone to depths of 20 m. As along the east coast, the bottom mixed layer deepens to about 100 m in winter (Atkins, 1970; Boyd et al., 1985; Largier et al., 1992), and silver kob are expected to move offshore (as indicated by catch trends [Fig. 5]). Because the depth contours broaden east of Cape Hangklip, it is possible that there is also an easterly component to the offshore dispersal of silver kob. A seaward and eastward winter migration has also been postulated

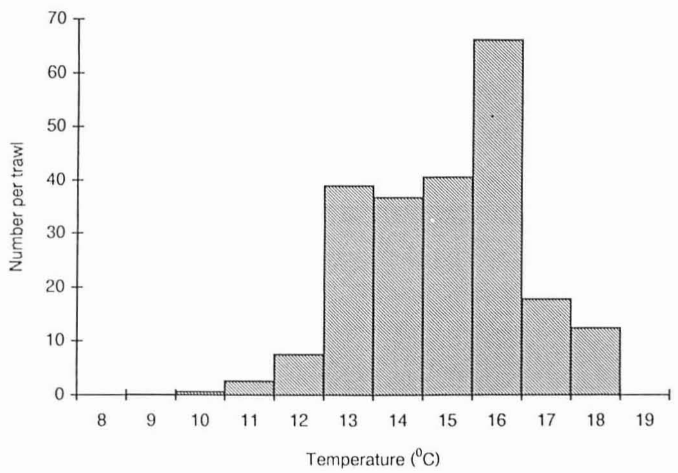

Figure 14

Mean number of *Argyrosomus inodorus* per trawl for each 1°C bottom temperature category during South Coast Biomass Surveys, 1987–95.

for subadult *Atractoscion aequidens* (Sciaenidae), occurring in the southwestern Cape (Griffiths and Hecht, 1995a).

Data from all 14 SCBS's revealed that the bottom mixed layer (<12°C) extends farther up the shelf (and is closer to the coast) in the area between Knysna and Cape St Francis (Fig. 15; see also Le Clus and Roberts, 1995), thus inhibiting exchange between the silver kob stock in the southern Cape and that in the southeastern Cape. Along the eastern and western sides of False Bay, the 20-m isobath is found <500 m from the shore (van Ballegooyen, 1991). Because suitable temperatures for silver kob are found at depths shallower than 20 m in the southwestern Cape during spring to autumn, the movement of silver kob into or out of False Bay (the focus of the southwestern 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 in False Bay and in the southern Cape.

Spawning occurred throughout the distributional ranges of all three stocks and peaked in spring (Sept–Nov) in all regions. Sizes and ages at maturity were, however, substantially smaller in the southeastern Cape than in the southern Cape. Female L_{50} was 310 mm TL (1.3 yr) in the former and 375 mm TL (2.4 yr) in the latter region. 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). Because fishing mortality is significantly higher in the southeastern Cape than in the southern Cape (F=0.67 vs. 0.42)(Griffiths, in press, c), the smaller sizes at maturity recorded for the southeastern Cape are possibly due to fishing pressure. The mechanisms accounting for the decreases in the size and age at maturity in the southeastern Cape, however, remain to be identified. One explanation is that the younger ages and smaller sizes at maturity for silver kob in the southeastern Cape could be the result of density-dependent effects; higher mortality results in more food for surviving fish, in additional energy for gonad growth, and consequently in earlier maturity. In several other species, ages or sizes (or both) at maturity have been correlated with the amount of accumulated surplus energy within a fish (Armstrong et al., 1989; Rowe et al., 1991; Berglund, 1992; Kerstan[3]). On the other hand, 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 ca. 2.8 yr in both the southeastern Cape and the southern Cape (Griffiths, in press, a). Approximately 95% of these

[3] Kerstan, M. 1995. Sex ratios and maturation patterns of horse mackerel (*Trachurus trachurus*) from the NE-and SE-Atlantic and the Indian Ocean—a comparison. ICES council meeting H:6, 20 p. (Mimeo.)

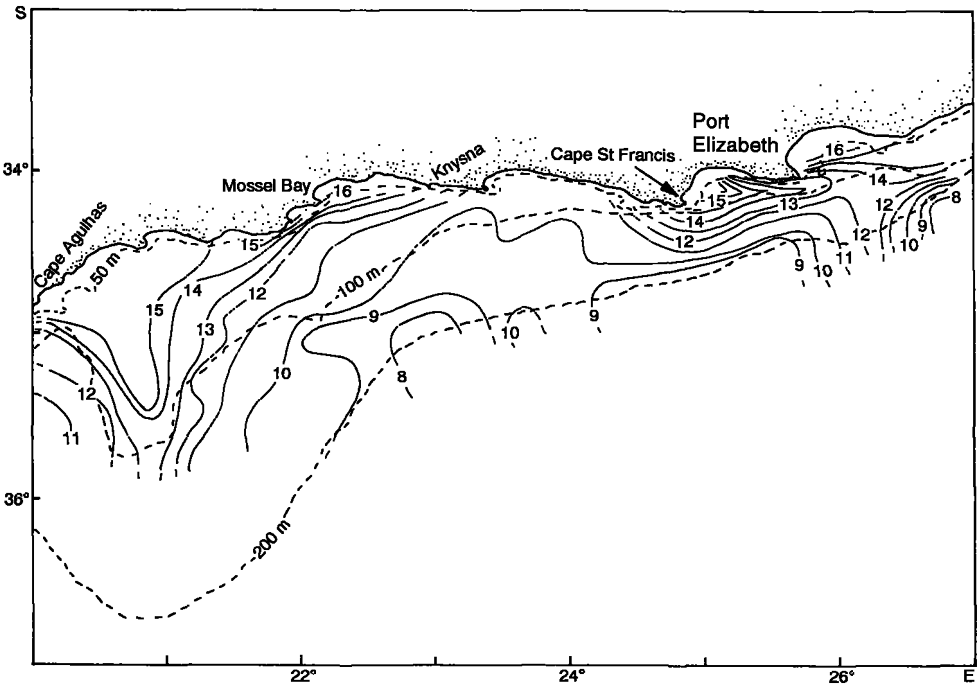

Figure 15

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) at shallower depths and closer to the coast between Knysna and Cape St Francis, was typical of SCBS's between 1987 and 1995. See Figure 1 for additional localities.

new recruits are mature in the southeastern Cape, but only 69% in the southern Cape. Assuming that size at maturity for silver kob in the southeastern 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 southeastern Cape line catch (ca. 50% by number)(Fig. 12), supports this hypothesis.

Investigation of sex ratios showed that there are substantially more females in the southeastern Cape (1.6×) and southwestern Cape (2.1×) stocks, but more males in the southern Cape (1.2×). Most natural populations tend to stabilize at sex ratios of 1:1 (Conover and Van Voorhees, 1990), including those of other sciaenids (Shepherd and Grimes, 1984; Murphy and Taylor, 1989; Wilson and Nieland, 1994; Ross et al., 1995; Griffiths and Hecht, 1995a). The deviations from this ratio observed for South African silver kob are not easily explained. Basically, the reasons for an observed sex ratio that deviates from unity may be grouped into three categories: 1) more individuals of either sex are produced (e.g. environmental sex determination); 2) equal numbers of both sexes are produced, but those of one sex are diminished through either emigration or mortality; and 3) sampling methods are biased towards one of the sexes. Although environmental sex determination can temporarily result in skewed sex ratios in some species (Conover and Heins, 1987), frequency-dependent selection is expected to return the ratios of such populations to equality through future generations (Conover and Van Voorhees, 1990). Higher proportions of either sex over most size classes (therefore spanning several age classes) in each region, with consistency over two periods (1978–81 and 1990–91) in the southeastern Cape, render environmental sex determination an unlikely cause of the observed sex ratios. Male emigration from the southeastern Cape and the southwestern Cape to the southern Cape is also unlikely. Because the smallest size class sampled in the southeastern Cape consisted of males without drumming muscles and also consisted of more males than females, it is tempting to suggest that male drumming during the protracted spawning season may have resulted in sex-selective predation in this region and in the southwestern Cape. However, there is no reason to believe that predation rates should be higher in the southeastern Cape and the southwestern Cape than in the southern Cape. Because capture methods were the same in all three regions, increased vulnerability of either sex to capture is not a plausible explanation either. Thus additional research is required before the regionally specific sex ratios observed for *A. inodorus* can be adequately explained.

Silver kob use inshore (<120 m depth) sand and mud substrata as nursery areas. They apparently recruit (ca.1.5 cm TL) just seawards of the surf zone (5–7 m depth) but move offshore with growth. Upon attaining maturity they recruit to adult populations that are found on reefs. Distributional analyses have revealed that juvenile *A. inodorus* between Cape Agulhas and the Kei River comprise two disjunct distributional ranges, one in the southern Cape and the other in the southeastern Cape. Although the inshore areas of the southwestern Cape are not suitable for trawling, analysis of commercial beach-seine catches (Lamberth et al., 1994) has revealed that juvenile *A. inodorus* (identified as "*A. hololepidotus*") are also found in False Bay. The existence of nursery areas and spawning grounds in each of the three sampling regions, and the differences in size at maturity and sex ratio, lend further credence to the separate stock concept.

Conclusion

Distributional analyses based on fishery dependant and fishery independent data revealed that there are three areas of silver kob abundance between Cape Point and the Kei River. The fact that each of these "populations" has its own spawning grounds and nursery areas and the fact that there are observed differences in growth rates, otolith-dimension and fish-length relationships, growth zone structure, sizes at maturity, and sex ratios, together indicate that these "populations" represent separate stocks. This three-stock concept is further supported by migratory patterns indicated from catch and tagging data and by the oceanography between Cape Point and the Kei River.

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 and Casselman, 1992; Pawson and Jennings, 1996), including those of sciaenids (Ramsey and Wakeman, 1987; Graves et al., 1992; King and Pate, 1992). Although none of the data used 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 indicates that each may respond differently to fishing and that the exploitation of one unit will not affect the size or composition of the other two, thereby supporting separate management of the three units and their stock status (Spangler et al., 1981; Brown and Darcy, 1987; Campana and Gagné, 1995; Edmonds et al., 1995; Pawson and Jennings, 1996).

Recent application of per-recruit models to South African silver kob (based on the results presented in this study) indicates that, owing to their different population parameters, each stock requires a different combination of fishing mortality and age at first capture for optimal exploitation (Griffiths, in press, c). Therefore *A. inodorus* should ideally be managed on a regional and not on a national basis. Studies of the life histories of two other South African sciaenids, *Atractoscion aequidens* (Griffiths and Hecht, 1995a) and *Argyrosomus japonicus* (Griffiths and Hecht, 1995b; Griffiths, in press, b), have revealed that they consist of single stocks with allopatric age or size-determined subpopulations, even though they occur from Cape Point to southern Mozambique and are therefore more widely distributed on the eastern seaboard than are *A. inodorus*. Inferences from stock structure, based on closely related taxa, are therefore not desirable because they could result in erroneous conclusions and consequently in poor management.

Acknowledgments

The author thanks Chris Wilke, Peter Sims, and John Prinsloo (Sea Fisheries Research Institute) for providing CPUE and length-frequency summaries for the line fishery, the inshore trawl fishery, and South Coast Biomass Surveys, respectively; M. Roberts, A. Boyd, and G. Nelson for oceanographic data and for helpful discussions on the oceanography of the study area; Malcolm Smale and Larry Hutchings for valuable comments on an earlier draft of the manuscript; and all those commercial and recreational fishermen who made their catches available for sampling. The project was partially funded by the Sea Fisheries Fund.

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