Aspects of the reproductive biology of *Sarpa salpa* (Pisces: Sparidae) off the east coast of South Africa

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The reproductive biology of the sparid fish, *Sarpa salpa*, was investigated along the east coast of South Africa between January 1994 and March 1995. A protracted winter spawning season was identified, extending from April through to September, and it was evident that *S. salpa* migrate annually to KwaZulu-Natal from juvenile nursery areas in the Eastern and Western Cape. Size at 50% maturity for male *S. salpa* was attained at 145 mm fork length, while the adult sex ratio in the shore-based catch was 1:1.6 in favour of males. Frequency distribution by size indicated that males dominated the smaller size classes while females dominated the larger size classes. Histological examination of gonadal development revealed five types of gonads, namely undifferentiated, juvenile, male, intersex, and female gonads. Intersex gonads were characterised by degenerating testicular tissue separated from a dormant ovary by connective tissue. The population demography and the presence of intersexual individuals with degenerating testicular tissue was suggestive of protandrous sex change in *S. salpa*. This was confirmed during a captive study in which male *S. salpa* changed sex to female. Group spawning behaviour is postulated based on various morphological and indirect behavioural characteristics.

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Sarpa salpa is a widely distributed species, occurring in the Mediterranean, north-eastern and eastern Atlantic round South Africa to southern Mozambique (Smith & Heemstra 1986). It is an abundant inshore species, inhabiting subtidal gullies and shallow reefs (Smale & Buxton 1989; Verlaque 1990). The species is an important foodfish along the east coast of South Africa and is the second most abundant fish caught by shore-based anglers in this region (Joubert 1981a; Van der Walt & Govender 1996; Brouwer, Mann, Lamberth, Sauer & Erasmus 1997).

Sparid fishes exhibit a diverse sexuality (Atz 1964) which may be expressed as sequential hermaphroditism (protandry or protogyny) or late gonochorism (rudimentary hermaphroditism) (Buxton & Garratt 1990). The reproductive style exhibited by an exploited species is of considerable importance to fisheries management. This aspect becomes even more relevant in the case of sex changing fish (Punt, Garratt & Govender 1993). Confusion exists regarding the reproductive style expressed by *S. salpa*. Historically, *S. salpa* (*Boops salpa*) has been described as both protandrous (D'Ancona 1949) and as a rudimentary hermaphrodite (D'Ancona 1946; Reinboth 1962). More recent histological work in the Mediterranean has reported that the species exhibits a partial form of protandry (Michele & Lafaurie 1974; Febvre, Michele & Lafaurie 1975; Michele 1977), while Joubert (1981b) described the species as a rudimentary hermaphrodite, based on macroscopic evaluation of the gonads. By definition, protandrous hermaphrodites function first as males after which they change sex and function as females, with all females necessarily being derived from males (Buxton & Garratt 1990). Rudimentary hermaphrodites on the other hand, are where males and females develop from an immature bisexual gonad prior to sexual maturation and no sex change occurs in mature individuals.

In the present study, the gonadal anatomy and population demography of *S. salpa*, collected along the east coast of South Africa, was investigated in an attempt to clarify the sexual pattern and nature of hermaphroditism in *S. salpa*.

Materials and methods

Monthly samples of fish were obtained by sampling shore-based anglers' catches along the KwaZulu-Natal (KZN) south coast between the Tugela River (28° 13' S; 31° 30' E) and Port Edward (31° 03' S; 30° 14' E) from January 1994 to March 1995 (Figure 1). Small *S. Salpa* (< 150 mm TL) were poorly represented in KZN shore anglers' catches as fish of this size are primarily found in intertidal rockpools and estuaries in the Eastern and Western Cape (Christensen 1978; Lasiak 1983; Whitfield 1989; Whitfield & Kok 1992). In order to obtain a full size range of fish, a sample of small *S. salpa* were netted at Port Alfred (33° 36' S; 26° 54' E) in the Eastern Cape during October 1994 (Figure 1).

Each fish was measured (mm fork length), weighed (grams) and sexed macroscopically. Gonads were removed, weighed and visually assessed for their stage of maturation according to the criteria in Table 1. A monthly gonadosomatic index (GSI) (De Vlaming, Grossman & Chapman 1982), which involved calculating the mean proportion of gonad weight to body weight, was calculated:

$$GSI = \frac{Gonad\ mass(g)}{Body\ mass(g)} \times 100 \tag{1}$$

Size at sexual maturation was determined by expressing the proportion of reproductively active male fish (developing, ripe or spent) collected during the spawning season as a percentage of the total number of fish in each size class. Size at 50% maturity was estimated by fitting a logistic equation of the form:

$$Y = \frac{1}{1 + \exp(-(X_{mid} - X_{0.5})/\delta)} \tag{2}$$

where Y is the proportion of mature fish in length class X, X_{mid} is the midpoint of the class interval, $X_{0.5}$ is the length at 50% maturity and δ is the length of the maturity ogive
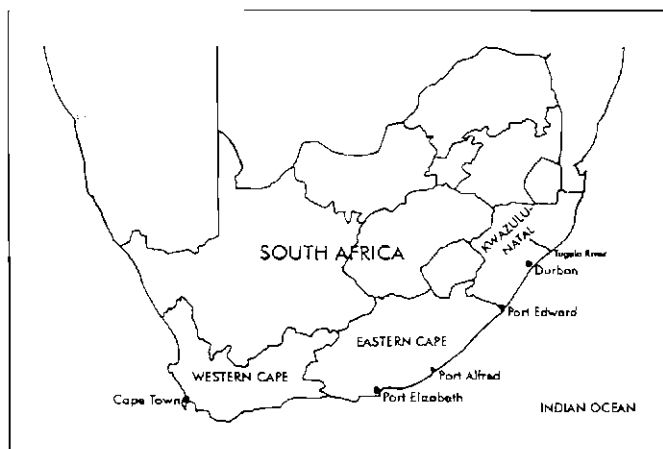
Figure 1 Map of South Africa showing areas mentioned in the text.

(Butterworth, Punt, Borchers, Pugh & Hughes 1989).

For histological examination, monthly sub-samples of gonads were fixed in Bouin's solution for three days and then transferred to 70% ethanol for storage. The tissues were embedded in paraffin wax, sectioned at 7 μm and stained with

Erlich's haematoxylin and eosin. Sections were taken from the area slightly posterior to the mid-region of the gonad as this region has been shown to be representative of the functional state of the gonads in a number of sparid species (Garratt 1993a).

To determine whether sex change occurred in *S. salpa*, a sample of seven ripe-running male fish (190–230 mm FL), caught by hook and line from the shore during August 1995, were placed in an aerated flow-through pool (6000 litres) located at SeaWorld, Durban. The fish were maintained at ambient light and temperature and fed twice daily on pilchard and lettuce. The experiment was terminated after eight months and all surviving fish were sacrificed and sex and stage of maturity was assessed visually.

Results

Reproductive seasonality

A total of 778 *S. salpa* was sampled during the period January 1994 to March 1995. Difficulties were experienced in macroscopic determination of the functional sex of inactive (stage 1) *S. salpa* gonads. The ovarian portion dominated the gonad in the majority of inactive gonads and was always larger than the testicular portion. Inactive gonads were histologically
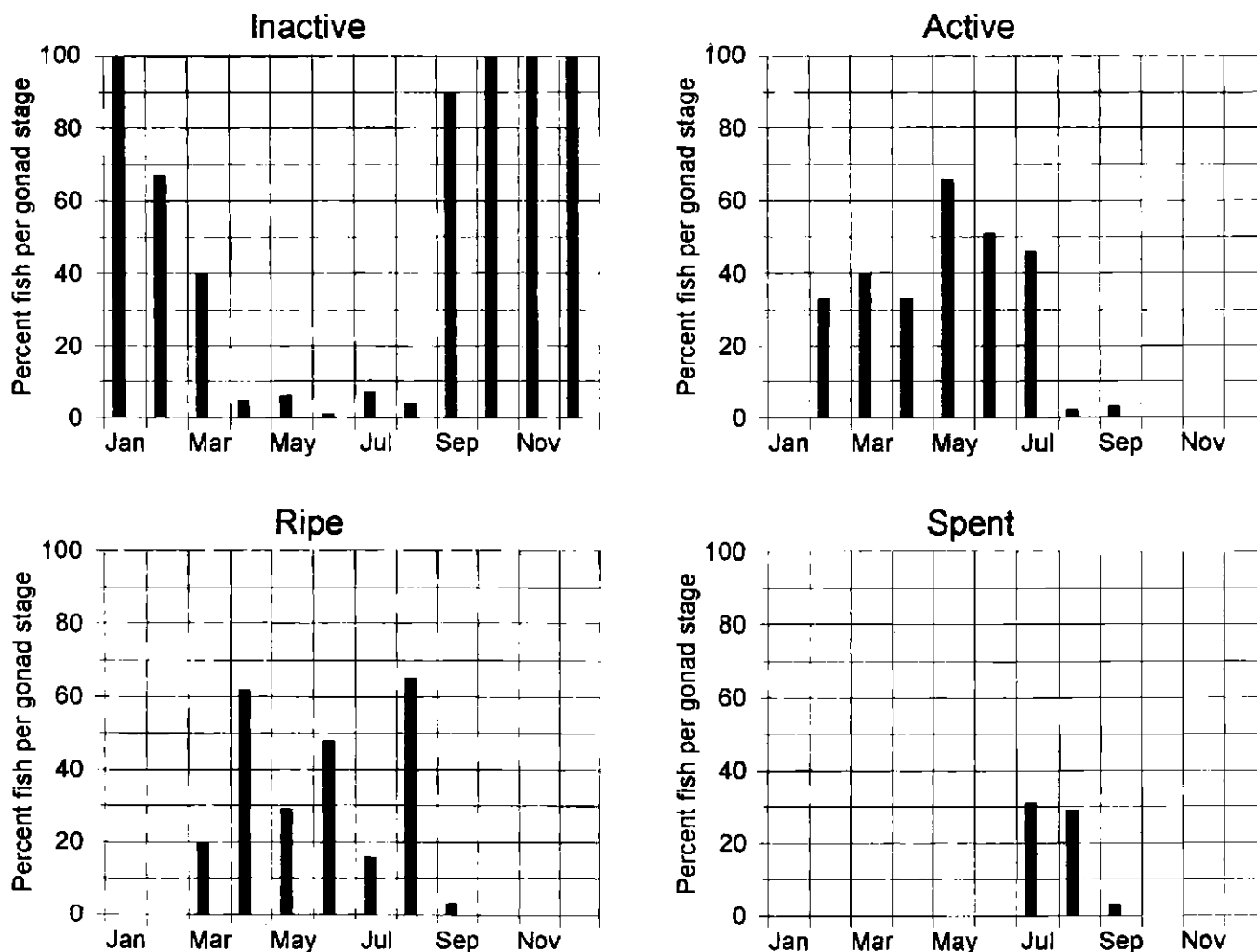

Figure 2 Monthly percentages of *Sarpa salpa* (males and females combined) in each maturity stage sampled from the shore-based catch in KwaZulu-Natal.
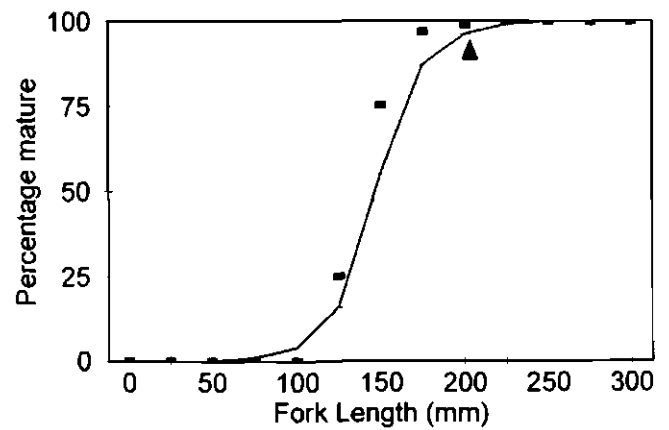
identified as functional males when they had a well-developed sperm duct. However, these gonads often had the macroscopic appearance of female gonads. Functional female gonads were histologically identified by having a degenerate testicular portion that was sometimes completely absent.

Monthly distributions of the various gonad maturity stages showed that the development of gonads began as early as February (Figure 2). The occurrence of ripe individuals from March to September indicated a protracted spawning season with reproductive activity peaking from April to August. The GSI values calculated for both males and females showed a similar protracted spawning season (Figure 3a & b).

Size at maturity, sex ratio and length frequency

Size at 50% maturity was attained at 145 mm FL (SE = 1.94) using the data for males (Figure 4), which is equivalent to an age of 1.5 years (Van der Walt & Beckley 1997). The calculation of size at maturity for females was not possible because of the low number of females in the smaller size classes. The logistic curve provided a good fit to the data set ($r^2 = 0.98$).

Because of the difficulties encountered in determining the functional sex of inactive *S. salpa* (stage 1), only fish that were reproductively active (stages 2, 3 or 4) were included in the determination of sex ratios. Of the reproductively active fish, 179 (38%) were females and 286 (62%) were males resulting in an adult sex ratio of 1:1.6 (F:M). Length frequency analysis showed that, after the attainment of sexual maturity, there was a distinct bimodal size distribution, with males
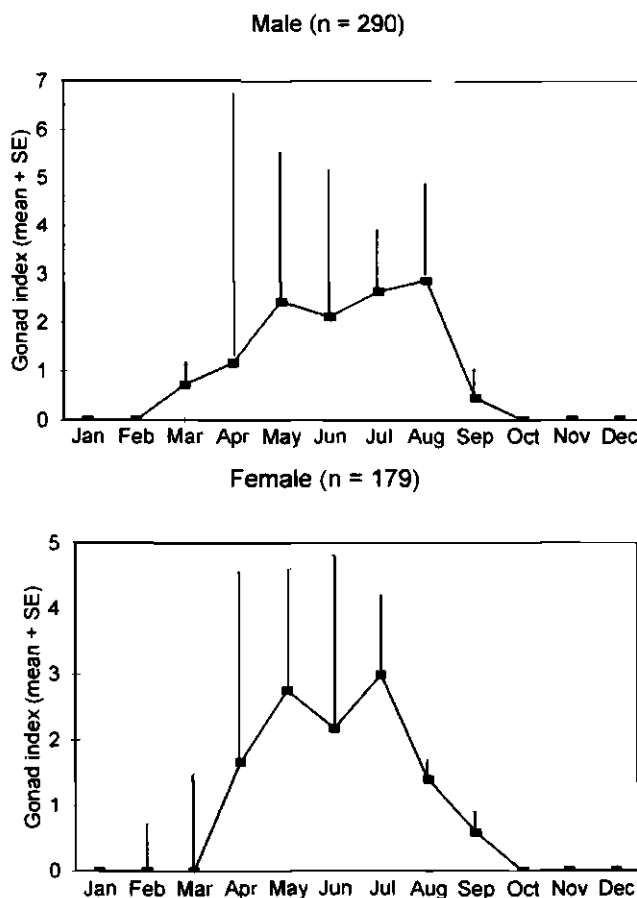
Male (n = 290)

Female (n = 179)

Figure 3a & b Seasonal variation in the gonado-somatic index of *Sarpa salpa* of both sexes from the shore-based catch in Kwa-Zulu-Natal.

Figure 4 Length at 50% maturity (male data only) of *Sarpa salpa* from the shore-based catch in KwaZulu-Natal. The arrow indicates the approximate size at which sex change occurs (n = 290).

dominating the smaller and females the larger size classes, respectively (Figure 5). The mean fork length of females (206 mm FL) was significantly larger than that of males (184 mm FL) ($t = 13.6, P = 0.05$).

Gonadal development

To determine the pattern of gonadal development occurring in *S. salpa*, gonads from 170 fish of successive size classes sampled throughout the year, were described on a basis of gross anatomical and histological observations. Five types of gonads were identified in *S. salpa*, namely undifferentiated, juvenile, male, intersexual and female gonads. The gonads of fish measuring less than 80 mm FL ranged from gonadal primordia with no sex cells evident, to gonads consisting of undifferentiated gonial tissue.

Differentiation of gonial cells occurred at approximately 100 mm FL and the juvenile gonad consisted of an ovotestis in which male and female tissue were clearly separated by connective tissue (Figure 6a). The female element dominated the ovotestis, with the male element only occupying a small part

Table 1 Description of the macroscopic maturity stages in *Sarpa salpa* (modified from Buxton 1990)

1. Inactive/resting	Gonads small. Ovaries long and thin, translucent orange in colour. Testes difficult to determine as ovarian tissue predominates.
2. Developing	Gonads increase in size. Ovaries become swollen and orange/yellow in colour, eggs visible to the naked eye. Testes clearly visible and are white in colour. Sperm is visible if the testes are cut and gently squeezed.
3. Ripe/ripe-running	Ovaries very large and swollen, hydrated eggs are visible in the ovarian tissue and in the lumen. In ripe-running females eggs were extruded from the uro-genital opening when pressure was applied to the abdomen. Testes large and swollen, white in colour but become pinkish as the spawning season progresses. Large quantities of sperm present in the sperm duct and is ex-truded from the urogenital opening in ripe-running males.
4. Spent	Ovaries are flaccid, bloodshot and reduced in size. Testes decreased in size and pinkish-grey in colour. Sperm may still be present in the sperm duct.
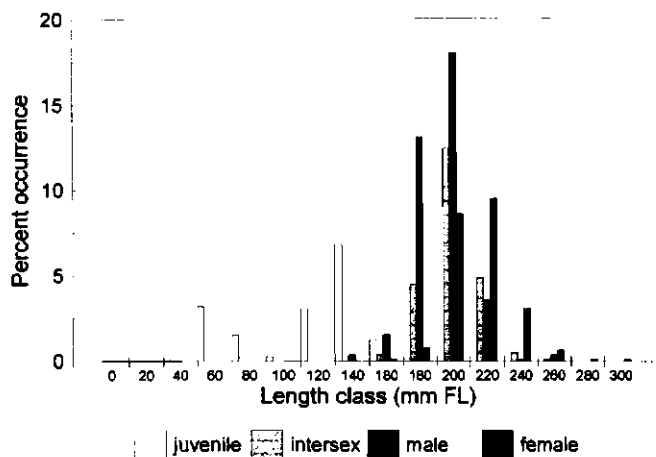
Figure 5 Length frequency distribution of *Sarpa salpa* from samples of the shore-based catch in KwaZulu-Natal with an indication of gonad type as determined by macroscopic determination (n = 778).

of the gonad. In the female portion, oogenesis had commenced but the oocytes were arrested in the previtellogenic stage. Spermatogenesis was not evident in the male element which consisted primarily of spermatogonia. At this stage, no sperm duct was evident.

The adult male testis consisted of elongated seminiferous tubules leading into secondary sperm ducts (Figure 6b). Posteriorly, these ducts combined to form the main sperm duct. In reproductively active males, the enlarged testicular portion was actively undergoing spermatogenesis similar to that described for other sparid species (Coetzee 1983; Buxton 1990; Micale & Perdichizzi 1994; Mann & Buxton in press) and the sperm duct was full of sperm. Even in ripe males, a portion of female tissue was present, although often partially enveloped by the sperm duct. This female element was always visible, even at the macroscopic level, and was retained throughout the spawning season. The testis of inactive males was considerably reduced in size and characterised by the presence of a well-developed sperm duct and proliferation of spermatogonia, although clusters of primary spermatocytes were also present. Unlike other South African sparids where sperm has been recorded throughout the year in the main sperm duct (Buxton 1990; Mann & Buxton in press), sperm was never found in the duct during the inactive male stage of *S. salpa*. During the inactive period, the overall appearance of the male gonad was dominated by ovarian tissue, consisting of dormant oocytes in the late perinuclear stage. Inactive male gonads were therefore classified as intersexual gonads.

Intersexual gonads were primarily observed in the 180–220 mm FL size classes (Figure 5) from September to March during the inactive phase of the gonad. Macroscopically, the ovarian portion dominated the volume of these gonads. Microscopically, this female tissue consisted of dormant oocytes at the perinuclear stage (Figure 6c). The male element comprised a well-developed sperm duct, which strongly suggested that these fish had functioned as males (P.A. Garratt, Two Oceans Aquarium, pers. comm.), and a testis, which appeared to be in the process of degeneration and atrophy. This regression was characterised by extensive vacuolation of the testis (Figure 6d). Intersexual gonads could only be identified

at a histological level and because it was not possible to examine the gonads from all inactive individuals histologically, it is likely that the proportion of intersexual gonads, relative to other gonad types, was higher.

The ovary of the adult female gonad was surrounded by the tunica albuginea, a connective tissue layer containing blood vessels and smooth muscle tissue (Figure 6e). Both ovaries fused posteriorly to form a short oviduct. Numerous ovigerous lamellae projected from the tunica albuginea into the ovocoele. The developing oocytes were found along the margins of these folds embedded in loose connective tissue. Oocyte development was asynchronous and similar to that described in other sparid species (Garratt 1985; Buxton 1990; Micale & Perdichizzi 1994; Mann & Buxton in press). A degenerate testis was apparent in most inactive female gonads and consisted of a lateral flap of vestigial testicular tissue containing a few spermatogonia. In ripe females this testicular element was often completely atrophied and no longer visible.

Captive fish

Four of the seven captive male fish died before the onset of the next spawning season and macroscopic assessment of their gonads revealed that they were inactive (stage 1) with ovarian tissue dominating the appearance of the gonad. However, the three surviving fish which were sacrificed in April 1996 at the onset of the spawning season, all had developing ovaries (stage 2) with eggs clearly visible to the naked eye (i.e. primary and secondary yolk vesicle oocytes). Only active female gonads will produce oocytes beyond the previtellogenic stage of development and this experiment therefore provided evidence of protandrous sex change in *S. salpa*.

Discussion

Reproductive seasonality

Gonadosomatic indices revealed that *S. salpa* off the KZN coast spawned during the winter months. This correlates well with the occurrence of *S. salpa* eggs recorded from April through to August off Rocky Bay (Dr A.D. Connell, CSIR, unpublished data) and with the recruitment of early juveniles into Cape nursery areas from May through to December (Christensen 1978; Lasiak 1983; Whitfield 1989; Whitfield & Kok 1992). The protracted spawning season of *S. salpa* recorded in this study is suggestive of serial spawning behaviour. Further evidence includes histological examination of ripe ovaries, which showed the occurrence of oocytes in all stages of development, as well as numerous clear spaces in the ovigerous lamellae where hydrated oocytes had collapsed during tissue preparation. This may be indicative of previous spawning activity (P.A. Garratt, Two Oceans Aquarium, pers. comm.). Furthermore, the low percentage of ripe-running females observed in this study is typical of that found for many serial spawners in which the final maturation of oocytes is believed to be a rapid process, and consequently, easily missed during sampling (Garratt 1985).

S. salpa is primarily exploited by shore-based anglers in KZN during the winter spawning season (Joubert 1981a; Van der Walt & Govender 1996) and catches consist predominantly of sexually mature individuals with a virtual absence of juveniles. This supports the proposal by Joubert (1981a; b) that adult *S. salpa* migrate from the temperate waters off the
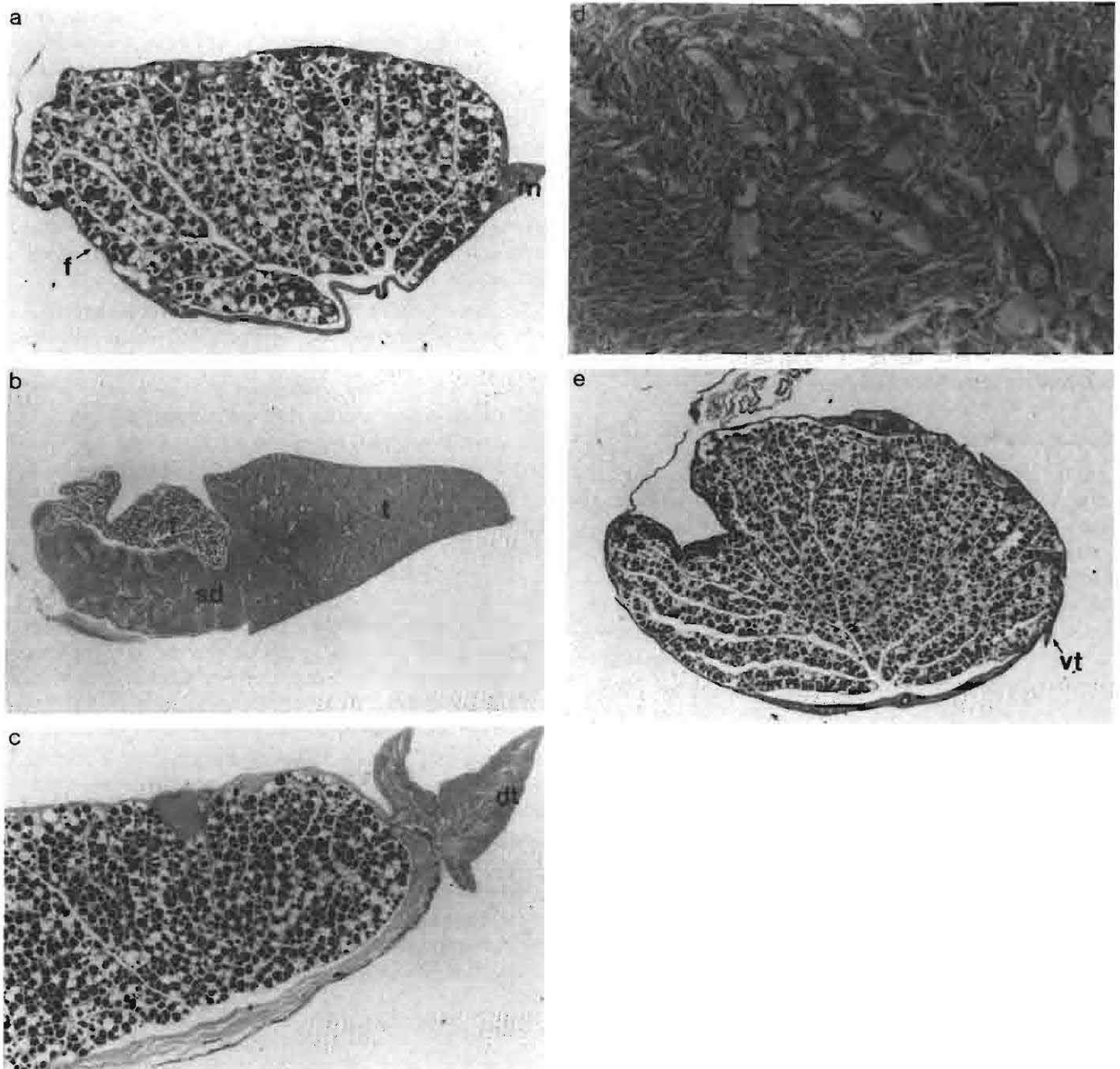
Figure 6 (a) Transverse section through an ovotestis of an immature individual (147 mm FL) showing the male (m) and female element (f) (× 64). (e) Transverse section through an inactive gonad of a mature female (205 mm FL) showing the vestigial testis (vt) (× 25). (b) Transverse section through a ripe gonad of a mature male (170 mm FL) showing the main sperm duct (sd), the testis (t) and inactive female element (f) (× 12). (c) Transverse section through an intersexual gonad of a mature individual (195 mm FL) showing a degenerating testis (dt) (× 40). (d) Transverse section through degenerating testicular tissue showing vacuolation (v) (× 400).

Western and Eastern Cape to the warmer waters off KZN. Similar northward migrations have been recorded for a number of other fish species found along the east coast of South Africa (Wallace 1975; Van der Elst 1976; Smale 1984; 1988; Garratt 1988; Bennett 1993). However, ripe *S. salpa* have also been observed in the Eastern Cape (Clarke 1988) and it would appear, therefore, that only part of the mature stock actually reaches KZN waters. It is also unlikely that there is a return migration, as populations of adult *S. salpa* appear to remain off the KZN coast throughout the year (Berry, Van der Elst & Smale 1982; Mann pers. obs.). The vulnerabil-

ity of *S. salpa* to capture appears to increase during the breeding season, a trend which has also been observed in the Mediterranean (Anato, Ktari & Kamoun 1983), and is probably because of increased feeding intensity by reproductively active fish. The marked decline in catch rates during the rest of the year may be related to cycles of algal productivity, algae being the principal dietary component of *S. salpa* (Joubert & Hanekom 1980). Biomass estimates, and hence food availability, can be expected to be higher during the summer months (Knoop 1987) and may, therefore, also explain the seasonal occurrence of *S. salpa* in shore-based catches.

The actual driving force behind the north-eastward movement of adult *S. salpa* from their nursery areas in the Eastern and Western Cape is unclear, but may be related to water temperature. This factor has been suggested to influence reproductive seasonality (De Vlaming 1972; Thresher 1984) and has been proposed for a number of other South African sparids (Garratt 1988; Smale 1988; Bennett 1993). Warmer water temperatures along the east coast could enhance growth and development of eggs and larvae (Bennett 1993). Other unrelated factors inducing migration could be decreased levels of predation on eggs and larvae (Bennett 1993) and the possible existence of a larval dispersal mechanism involving the Agulhas Current system. Oceanographic features associated with the shoreward edge of this southward flowing current appear to be involved in the dispersal of linefish larvae to nursery areas in the south (Beckley 1993).

Population structure

After the attainment of sexual maturity in *S. salpa*, the percentage frequency of gonad types in different size classes clearly showed that the ratio of males decreased with size, resulting in a distinct bimodal distribution (Figure 5). A similar distribution was recorded for this species by Joubert (1981b). Although bimodal size-frequency distributions and male-biased sex ratios have been used to diagnose the occurrence of sex change (Pollock 1985), it must be noted that these phenomena may also be produced by other biological mechanisms such as differential growth rates and maturation, differential mortality, differential migration, and selective capture (Sadovy & Shapiro 1987). Unfortunately, differences in growth could not be determined as sex specific growth estimates could not be obtained (Van der Walt & Beckley 1997). Later maturation in females may partly explain the distribution, although based on histological examination, it was apparent that many females may have functioned first as males and hence their later maturation. It is unlikely that differential mortality rates among males and females of different sizes exist in a shoaling fish like *S. salpa*, particularly as these shoals do not appear to be sex-specific (Van der Walt pers. obs.). Furthermore, selective capture and differential migration did not appear to be factors as *S. salpa* is an inshore species and the sample of fish from the KZN coast covered a wide area and range of sizes. These results are therefore, strongly suggestive of protandry in *S. salpa*.

Gonadal development

Based on the population structure and the histological examination of gonads of successive size classes, it was possible to hypothesize the pattern of gonadal development in *S. salpa*. Size at sexual differentiation in the family Sparidae varies considerably (Alekseev 1982) and in this study was recorded in sampled individuals between 100 and 149 mm FL. Relating this to age (Van der Walt & Beckley 1997), differentiation appears to occur towards the end of the first year or early in the second year of life. Histological examination revealed that the gonad differentiated into a juvenile ovotestis with male and female elements clearly separated by connective tissue (Figure 6a), a feature common to the Sparidae (Buxton & Garratt 1990). The ovarian portion of the juvenile ovotestis dominated the volume of the gonad and consisted of oocytes

arrested at the previtellogenic stage. At the onset of sexual maturation (L_{50} = 145 mm FL) during the second year of life, the juvenile ovotestes appeared to mature as a male in most individuals, although a few primary females were also observed between the 140 to 180 mm FL size classes (Figure 5). After functioning as a male during the first spawning season (April to August), the testicular portion of the gonad appeared to degenerate during the inactive stage (November to March) (Figure 6d). Most fish then appeared to mature as females during their third year of life between 180 and 220 mm FL, although some fish would retain the testis and continue to function as males.

This hypothesized sequence of development is suggestive of digynous protandrous hermaphroditism, where fish which mature as males from the juvenile ovotestis, function first as males and then either change sex to female or continue to function as males, whereas fish which mature as females from the juvenile ovotestis remain as functional females throughout their life cycle. A similar reproductive style has been reported in a number of sparid species including *Rhabdosargus sarba* (Yeung & Chan 1987), *Acanthopagrus australis* (Pollock 1985), *A. Berda* (Garratt 1993a), *Diplodus sargus* (Coetzee 1986, Abou-seedo, Wright & Clayton 1990; Micale & Perdichizzi 1994; Mann & Buxton in press) and *S. salpa* (as *Boops salpa*) in the Mediterranean (Michele 1977). However, Sadovy & Shapiro (1987) point out that the mere presence of non-functional gonadal tissue of one gender in individuals containing functional (or degenerating) tissue of the other gender, is not sufficient to label a species hermaphroditic. The strongest indicators of protandry are transitional individuals whose gonads contain degenerating testicular tissue and developing ovarian tissue (Shapiro 1987). Examples of such transitional gonads were not observed in this study but have recently been recorded in *D. sargus* (Micale & Perdichizzi 1994; Mann & Buxton in press). Nevertheless, the captive experiment in which three of the seven ripe male *S. salpa* changed sex to female provided conclusive evidence of protandrous sex change in this species.

Spawning behaviour

Evidence suggests that sex change in fish is initiated primarily by behavioural or demographic alterations within a fish's social system (Shapiro 1989). Of these alterations, the type of mating system employed appears to exert a major influence (Warner 1988a). No spawning behaviour was observed in *S. salpa* by the authors, however, various morphological and indirect behavioural characteristics were used to speculate on the type of mating system used. The most important of these characteristics included the overlap in size of functional males and females (although females dominated the larger size classes) and the large testis size in functional males. Similarity in the size of functional sexes suggests that reproductive success is not size related (Warner 1988b, Buxton & Garratt 1990). Large size of one sex is important to mating success in species where the ability to control territory or a group of smaller individuals is a major determinant in mating frequency (Shapiro 1987; Buxton & Garratt 1990). Large testis size is seen as an advantage in terms of sperm competition where males compete with each other to fertilize eggs (Choat & Robertson 1975; Buxton & Garratt 1990).

From these observations and the fact that *S. salpa* is a shoaling species consisting of similar sized individuals (Van der Walt pers. obs.) which lack sexual dimorphism, it is hypothesized that spawning takes place in a group spawning sequence. This has been unofficially confirmed off Durban Bluff where large shoals of *S. salpa* have been observed spawning (Dr A.D. Connell, CSIR, pers. comm.). In a spawning aggregation where male-male competition is strong, selective pressure may be placed on smaller males to change sex to female. However, if few males are present, selective pressure for males to change sex is reduced (Mann & Buxton in press). Similar group spawning behaviour has been described for *A. berda* (Garratt 1993b) and was postulated for *D. sargus capensis* (Mann & Buxton in press), both of which are protandrous hermaphrodites.

It is apparent therefore that partial protandrous hermaphroditism may be a more common reproductive style in South African sparids than was originally perceived (Buxton & Garratt 1990) and species such as *S. salpa, A. berda, D. s. capensis* and *R. sarba* may all fall into this category. Careful histological study is thus needed to distinguish between rudimentary (late gonochorists) and partially protandrous hermaphrodites as the general pattern of reproductive development is very similar (i.e. both reproductive styles show attributes such as large testis size and group spawning behaviour).

Acknowledgements

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