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

Manuscript submitted 22 September 2003 to the Scientific Editor's Office.

Manuscript approved for publication 30 August 2004 by the Scientific Editor.

Fish. Bull. 103:258–269 (2005).

Reproductive biology of carpenter seabream (*Argyrozona argyrozona*) (Pisces: Sparidae) in a marine protected area

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The carpenter seabream (*Argyrozona argyrozona*), known as "carpenter" regionally, is an endemic South African sparid found between St Helena Bay and KwaZulu-Natal (Fig.1) (Smith and Heemstra, 1986). Although the third most important species in the line-fishery in terms of landed mass, catch per unit of effort (CPUE) on traditional fishing grounds, declined by 95% during the twentieth century (Griffiths, 2000). Despite the importance of this resource, little research attention has been given to this species. The only previous study on the reproductive biology of carpenter was based on specimens collected towards the western extreme of the distribution range (west of Cape Agulhas), where most of the fish examined were reproductively inactive (Nepgen, 1977). As a result spawning seasonality was not accurately delineated and sizes at 50% maturity were not calculated. Assuming carpenter to be determinate spawners, Nepgen (1977) overestimated batch fecundity by counting immature oocytes.

The objective of the present study was to provide information on spawning seasonality, size at maturity, and annual fecundity of carpenter in the Tsitsikamma National Park (TNP), a 75-km no-take marine protected area (MPA) that has existed for 38 years (Fig. 1). It was envisaged that in conjunction with other studies on carpenter (Brouwer and Griffiths[1]) in exploited areas this information would assist in determining the affects of fishing on the life history of carpenter.

Materials and methods

Fish were caught from a research vessel at depths between 20 and 90 m by using handlines with baited hooks of 2/o–6/o in size. An attempt was made to sample 60 fish per month between March 1996 and June 1999, although weather conditions did not always allow this number. Sampling involved measuring total and fork length (FL) (mm), whole mass (g), gutted mass (g), determining the sex of fish, and removing the gonads. Gonads were staged macroscopically according to a seven-stage maturity index (Table 1) and weighed to the nearest 0.1 g. The whole gonads were preserved in 10% neutrally buffered formalin or alternatively fixed in Bouin's solution for 48 hours and then stored in 60% ethanol. Preserved samples were processed for histological analysis according to the techniques described by Osborne et al. (1999).

Length at maturity was modelled by using a 2-parameter logistic ogive of the form

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

where p_i = the proportion of mature fish in size class i, sampled during the spawning season (November to April);

[1] Brouwer, S. L., and M. H. Griffiths. In prep. Stock separation and life history of *Argyrozona argyrozona* (Pisces: Sparidae) on the South African east coast.

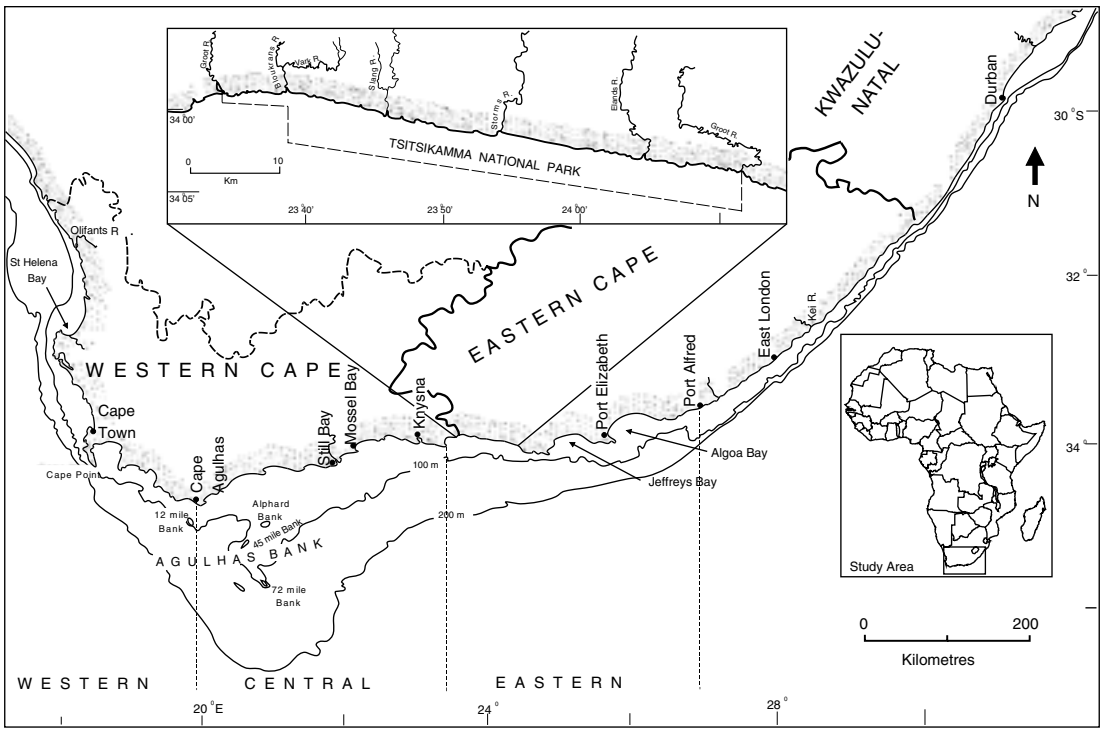

Figure 1

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

Table 1

Classification and descriptions of macroscopic and microscopic ovary and testis stages of carpenter (*Argyrozona argyrozona*) sampled in the Tsitsikamma National Park.

Stage		Macroscopic	Microscopic
1	Juvenile female	Ovotestis appears as a thin transparent vessel.	Both ovarian and testicular tissues are present in equal proportions; however in the later stages ovarian tissue becomes dominant.
1	Juvenile male	Ovotestis appears as a thin transparent vessel.	Both ovarian and testicular tissue present in equal proportions; however in the later stages ovarian tissue becomes dominant.
2	Immature, resting female	Translucent orange tubes, no eggs visible to naked eye.	Cells in the perinucleolus stage have a large nucleus containing 8–15 nucleoli located along the periphery of the nucleus. There may be remnants of the testes on the periphery of the ovary.
2	Immature, resting male	Testes thin white and flaccid but larger than those in stage 1, no sperm in tissue.	No sperm cells are noticeable and the seminiferous tubules appear to be empty. Remnants of ovarian tissue may be present in the centre of the testes.
3	Active female	Oocytes visible to naked eye as tiny granules in gelatinous orange matrix; little increase in diameter of ovary.	Vitellogenesis begins in the oocytes, which become more rounded and begin to accumulate yolk (yolk vesicles). Yolk appears as a narrow ring of small yolk vesicles in the periphery of the cytoplasm.

continued

L_i = length of size class i;
L_{50} = the length at which 50% of the fish are sexually mature (stage 4+); and
A = the width of the ogive.

The ogive was fitted by minimizing the negative log-likelihood. Differences in male and female L_{50} and a were tested by using a ratio test that minimizes the binomial log-likelihood of the form

$$-L = -\sum_{i=1}^{n}\left[m_i \times \ln\left(\frac{p_i}{1-p_i}\right) + n_i \times \ln(1-p_i) + \ln\binom{n_i}{m_i}\right],$$

where n = the number of samples in size class i; and
m_i = the number of mature fish in size class i.

Spawning frequency was estimated by using daily proportions of ovaries containing early postovulatory follicles (POFs), hereafter referred to as the spawn-

Table 1 (continued)

Stage	Macroscopic	Microscopic
3 Active male	Testes wider and triangular in cross section.	The seminal vesicles expand and become filled with spermatogonia.
4 Developing female	Ovary larger and orange-yellow in color. Eggs clearly discernible. Veins and arteries large and plentiful.	Yolk vesicles are common and primary yolk oocytes begin to appear, which are characterized by the formation of small spherical yolk granules.
4 Developing male	Testes wider and deeper, creamy white in colour, obvious presence of sperm in main sperm duct.	The seminiferous tubules of the testes are filled with spermatozoa, which are also present in the primary sperm duct.
5 Ripe female	Ovaries are large in diameter, may have a few hydrated eggs. Yellow oocytes take up all the space. Veins and arteries large and plentiful.	Tertiary yolk oocytes, characteriszed by large yolk plates, appear along with primary yolk and yolk vesicles. The nucleus becomes irregular in shape and smaller in size. The nucleus migrates to the animal pole of the cell after which hydration begins, resulting in increased transparency of the cells and an increase in cell size.
5 Ripe male	Sperm present in main sperm duct and in tissue. Gonad soft and breaks when lightly pinched.	The seminiferous tubules expand with copious amounts of spermatozoa that fill the lumen of the primary sperm duct.
6 Ripe, running female	Ovary amber in colour. Large with substantial proportion of gonad with hydrated eggs, which fill the lumen. Veins and arteries large and plentiful.	Filled with hydrated oocytes. Due to dehydration during the histological preparation, these oocytes appear as collapsed bags. Hydrated oocytes may squash and reshape the immature oocytes that surround them.
6 Ripe, running male	Free-flowing sperm extruded from fish when the abdomen is lightly squeezed. Testes very delicate and break easily when handled. Copious amounts of sperm present in main sperm duct and in tissue.	The seminiferous tubules of the testes appear distended and are filled with mature spermatozoa as is the lumen of the primary sperm duct.
7 Spent female	Ovary reduced in size similar to stage-2 flaccid ovary. Few yolked oocytes remaining. Ovary bloodshot.	Cells in various stages of atresia, and some hydrated and mature oocytes may be present in the tissue.
7 Spent male	Testes white in color, small shrivelled, and bloodshot.	The seminiferous tubules are no longer distended and have thicker walls than stage-6 tubules. They contain few spermatozoa, which are present in the lumen of the primary sperm duct. Large blood vessels are apparent in the tissue.

ing fraction (Hunter and Macewicz, 1985). POFs were aged by comparing them with known age POFs from spawning females under captive conditions. Female carpenter were held in a flow-through system at ambient sea temperature (mean 16°C, range 9.5–20°C) in 5000-liter circular tanks, were stimulated to ovulate with a commercially available GnRH-analogue (Davis, 1996). Three fish were sacrificed immediately after ovulation and then three fish every six hours over the following 48-hour period. Histological analysis of ovaries revealed three clearly defined POF stages (Fig. 2). The proportions of wild-caught fish with stage-1 POFs (the spawning fraction) were inverted to produce an estimate of spawning frequency (Wilson and Nieland, 1994).

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

Annual fecundity was calculated as follows:

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

where Af_t = the annual fecundity for fish t;
ls = the length of the spawning season (days) for fish of size class j;
sf = the spawning frequency (days) for fish of size class j (all months combined); and
fb_t = the batch fecundity of fish t.

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

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

where m_g = the gonad mass (g); and
m_s = the somatic mass (g) (minus gonad and stomach mass).

In order to investigate the relationship between spawning and temperature, temperature data were collected at the sampling site with a Seamon Mini (Hugrun, Iceland) recorder stationed at at a depth of 35 m on the reef from which the biological samples were collected. A thermistor array consisting of four underwater temperature recorders (UTRs) at depths of 12 m, 19 m, 27 m, and 35 m recorded the temperature every minute

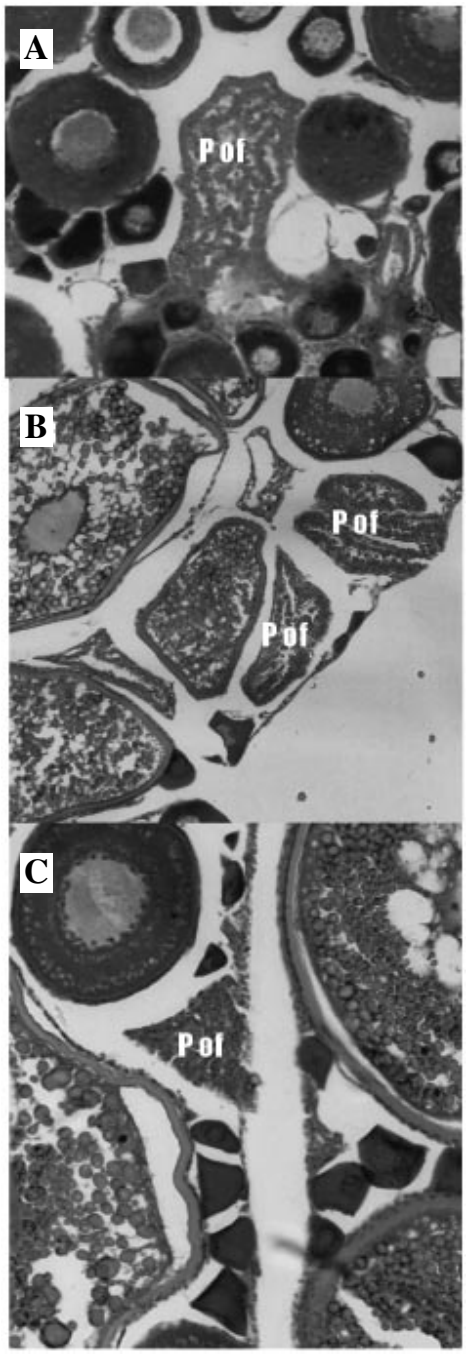

Figure 2

Postovulatory follicle (POF) stages determined from carpenter (*Argyrozona argyrozona*) chemically induced to spawn in an open circulating system housed at the Tsitsikamma National Park. (**A**) = stage 1 (0–6 hours), (**B**) = stage 2 (7–24) hours and (**C**) = stage 3 (25–48) hours.

and stored an hourly average (Roberts[2]). Photoperiod data were downloaded from the South African Astronomical Observatory database.[3] Pearson Rank correlation was used to measure the correlation between GSI and temperature, and GSI and photoperiod trends.

Results

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

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

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

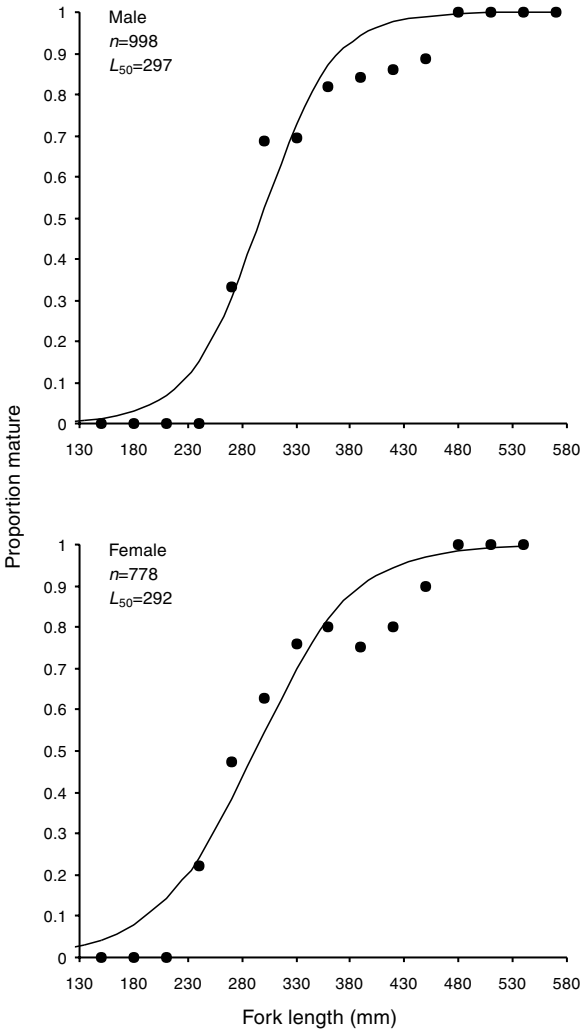

Figure 3

The proportion of mature carpenter (*Argyrozona argyrozona*) in length classes sampled in the Tsitsikamma National Park. The curves were fitted with a 2-parameter logistic ogive.

Batch fecundity was positively correlated with both fish mass (r=0.71) and fork length (r=0.71). No correlation was found between fish length and relative batch fecundity (eggs/fish somatic mass) (Fig. 6). The proportion of fish with stage-1 POFs revealed that spawning frequency and length of the spawning season increased with fish length (Table 3). Accounting for size-related patterns in spawning season (Fig. 7) and frequency, we found that annual fecundity increased allometrically with mass (Fig. 8) and age (Table 4). Hydrated egg size was significantly smaller and more variable (average 1.0 mm ±0.16) in fish below the length at 100% maturity (480 mm FL) than those above this length (1.1 mm ±0.09) (t-test, $P<0.005$).

[2] Roberts, M. J. 1999. CD-ROM, Tsitsikamma National Park oceanographic data, version 1.0. Marine and coastal management, Private Bag X2, Rogge Bay 8012, South Africa.

[3] http://www.saao.ac.za [Accessed August 2000].

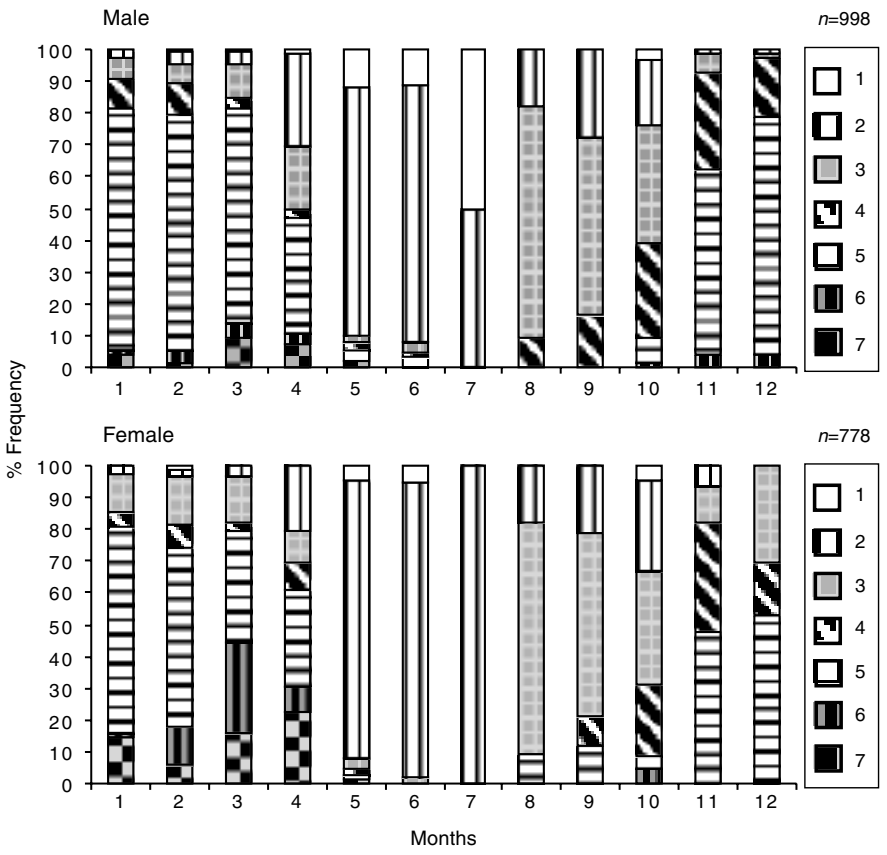

Figure 4

Monthly variation in the proportion of macroscopic gonad stages of carpenter (*Argyrozona argyrozona*) >L_{50} caught in the Tsitsikamma National Park (March 1996–July 1999). Numbers in the legend refer to the gonad stages in Table 1. 1 = juvenile, 2 = immature, 3 = active, 4 = developing, 5 = ripe, 6 = ripe, running, and 7 = spent.

Table 2

Spawning frequency determined for carpenter (*A. argyrozona*) from the proportion of ovaries with stage-1 POFs or macroscopically determined from hydrated oocytes.

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

A positive relationship between temperature at the time of spawning (back-calculated from stage-1 POFs, assuming a delay of 6 hours) and the proportion of ovaries with stage-1 POFs indicated that spawning events were positively correlated with temperature (r=0.93) over the range 9°C and 22°C (Fig. 9). GSI was how-

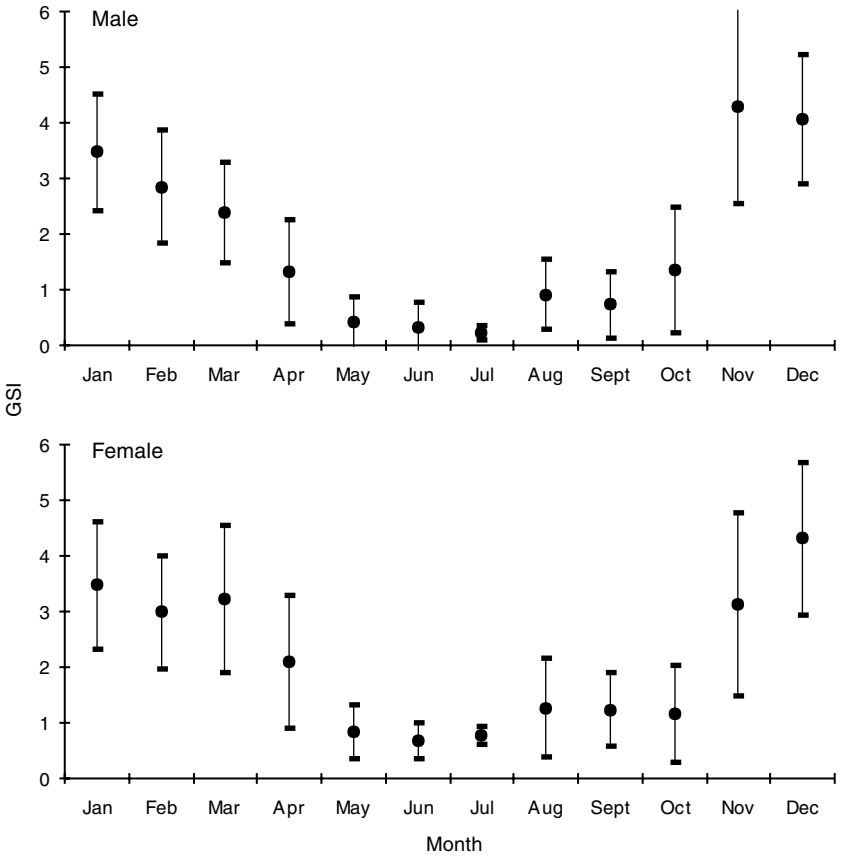

Figure 5

Seasonal variation of the standard deviation in the gonadosomatic index (GSI) and mean values (●) for male and female carpenter (*Argyrozona argyrozona*) sampled in the Tsitsikamma National Park.

ever strongly correlated (r=0.86) with photoperiod but exhibited a weak negatively relationship with seasonal temperature (Fig. 10).

Discussion

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

Upon reviewing 90 species of reef fish, Sadovy (1996) concluded that although GSIs reflect the gonad maturity patterns for a species, they are poor indicators of peak spawning times. By way of example, in red hind grouper (*Epinephelis guttatus*) yolked oocytes are present in the ovaries for four months of the year but actual spawning is limited to a period of 10 days (Sadovy, 1996). In the case of carpenter, however, the presence of POFs from November to April supports the six-month spawning season indicated by macroscopic methods (although in some larger individuals [>480 mm FL] hydrated

Table 3

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

Size class (mm)	Average spawning frequency (days)	Spawning season (months)
250–339	9	6
340–479	4	7
480+	3.9	9

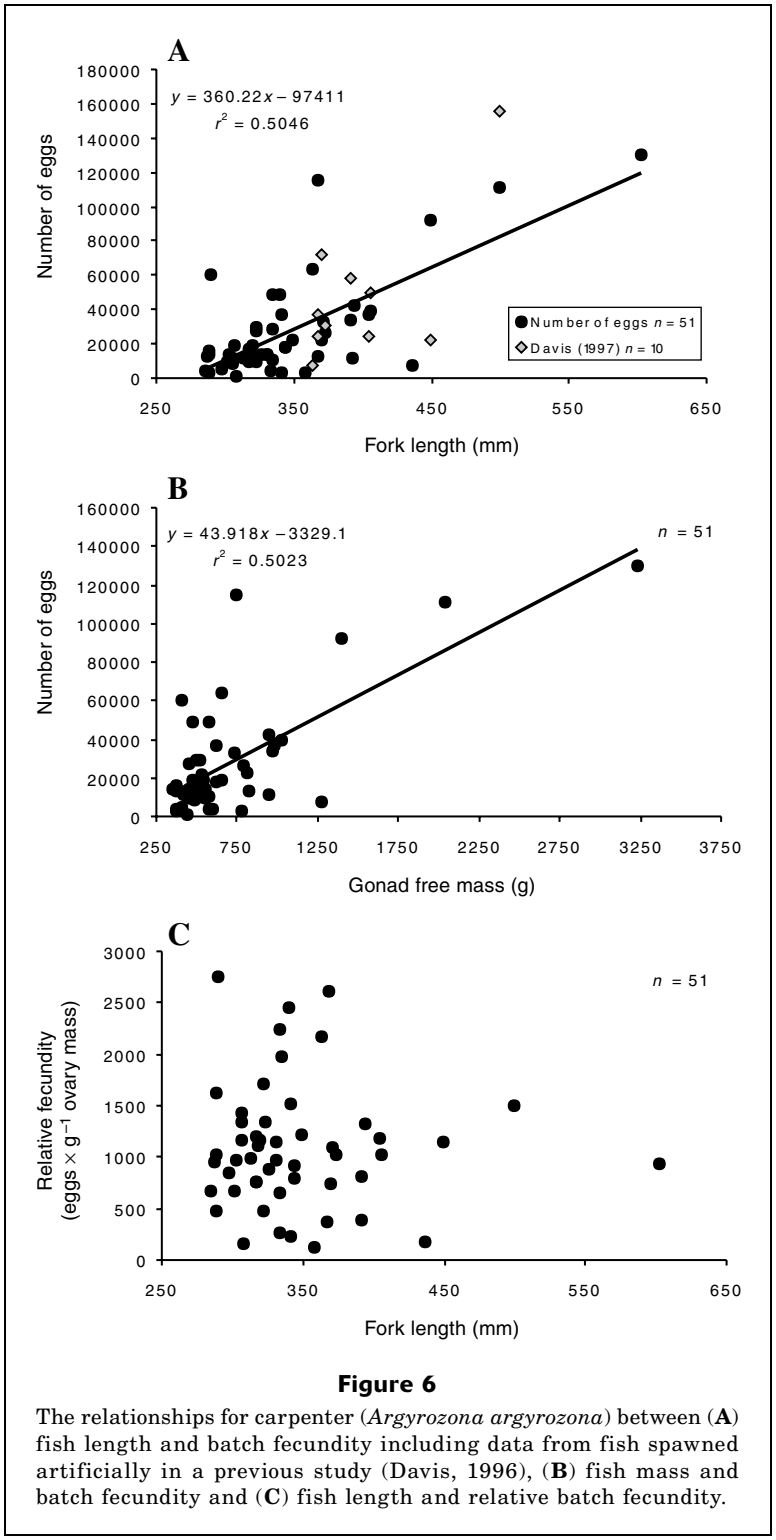

Figure 6

The relationships for carpenter (*Argyrozona argyrozona*) between (**A**) fish length and batch fecundity including data from fish spawned artificially in a previous study (Davis, 1996), (**B**) fish mass and batch fecundity and (**C**) fish length and relative batch fecundity.

oocytes and POFs were found from October to May). Monthly spawning fraction and percentage of ovaries with hydrated oocytes nevertheless reached a peak during January and February (Table 2); these trends were not detected in the monthly GSIs. But given that the macroscopic determinations of stage followed trends in the proportions of POFs that were present, we conclude that expensive and time-consuming histological analysis is not necessary for determining spawning peaks for this species.

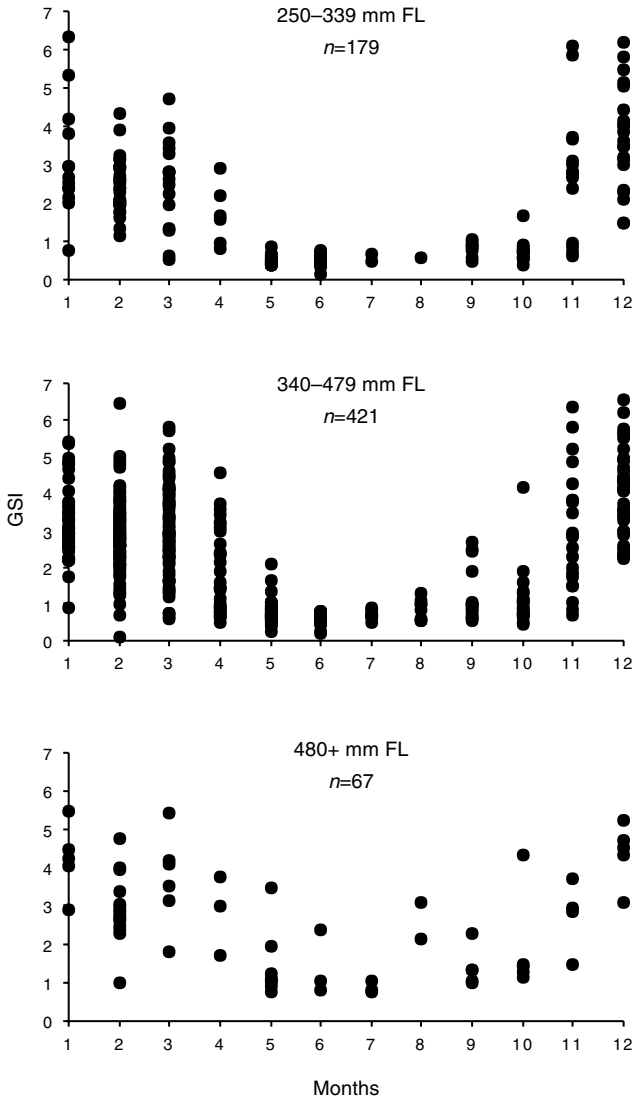

Figure 7

Seasonal variation in the gonadosomatic index (GSI) for female carpenter (*Argyrozona argyrozona*) from three size classes sampled in the Tsitsikamma National Park.

Apart from being indicators of spawning seasonality, GSI trends can provide insight into the mating patterns of a species (Sadovy, 1996). Pair-spawning sparids such as *Chrysoblephus laticeps* have low male GSI (±10% of female) during the spawning season (Buxton, 1990). Although the spawning behavior of carpenter has not been documented, the GSI of males (average 3.0 ±1.4) was similar to that of females (average 3.3 ±1.4) during the spawning season (Fig. 4). The large testes size suggests that carpenter are group spawners and that sperm competition is high (Sadovy, 1996). Further evidence for group spawning is the lack of sexual dimorphism in this species (Smale, 1988; Mann and Buxton, 1998; Griffiths et al., 2002).

Like many other South African sparids, carpenter are summer spawners (Buxton and Clarke, 1986; Buxton and Clarke, 1991; Buxton, 1993). Although various environmental cues have been suggested for this seasonal spawning, it is probably a combination of events that leads to gonad maturation and spawning. Smale (1988) and Garratt (1985) speculated that increases in gonad activity of *Petrus rupestris* and *Chrysoblephus puniceus* were attributed to an increase in photoperiod and water temperature respectively; Scott and Pankhurst (1992),

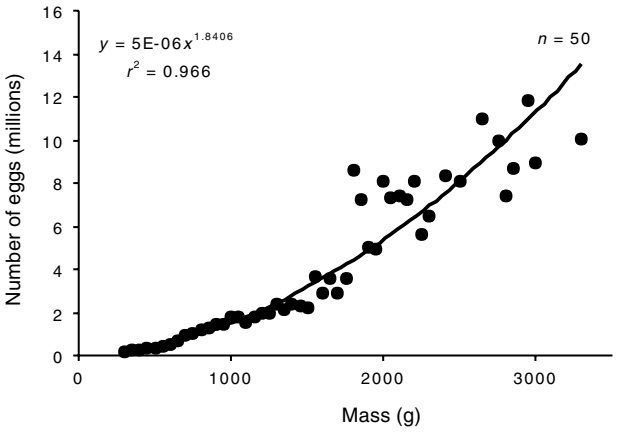

Figure 8

The relationship between annual fecundity and fish weight for carpenter (*Argyrozona argyrozona*) in the Tsitsikamma National Park.

Table 4

Age-based annual fecundity of carpenter (*Argyrozona argyrozona*) in the Tsitsikamma National Park.

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

however, showed that seasonal temperature regulated gonad development for *Pagrus aratus*. Based on the data collected during our study, photoperiod appears to be responsible for the onset of gonad maturation in carpenter; when day length increases (but water temperature is variable) in September and October, and their gonads begin to develop (Fig. 10). Photoperiod was also highly correlated with GSI (r=0.86), whereas temperature showed a weakly negative relationship (r=−0.16).

Nepgen (1977) calculated spawning frequency for this species with an oocyte-size-frequency analysis of inactive females. Finding only one peak in the oocyte-size-frequency distribution, he assumed that carpenter spawned only once a year. In our study POFs and various yolk stage oocytes were found to occur simultaneously, proving that carpenter are serial spawners. Accounting for monthly trends in spawning frequency and the length of the spawning season, carpenter in the Tsitsikamma National Park are estimated to spawn at least 30 times per year. This spawning frequency is similar to other predatory reef fishes, e.g., *Mycteroperca microlepis* (30–40 times per year) (Collins et al., 1998). Nevertheless, as with other species (Danilowicz, 1995), spawning fraction in carpenter during the spawning season was highly correlated with water temperature (r=0.931) (Fig. 9), indicating that short-term cold water upwellings, a common feature of the TNP during summer (Schumann et al., 1982), may negatively impact annual carpenter fecundity in this area.

Although fecundity in fishes is highly variable between individuals (Sadovy 1996), absolute fecundity increases with size (Hunter et al., 1985; Davis and West, 1993; Wilson and Nieland, 1994; Collins et al., 1998). In our study absolute annual fecundity increased markedly with fish size (Table 4) and spawning season was longer for large fish (Fig. 7) (Table 3). The positive correlation of batch fecundity and fish size (r=0.71), coupled with the increased length of the spawning season for the older fish, greatly increases the absolute annual fecundity of larger fishes (Fig. 8). Sadovy (1996) noted that for red snapper (*Lutjanus compechanus*) one large female (601 mm FL) will produce as many eggs as 212 small (420 mm FL) females. Similarly, one large female carpenter of 3.3 kg will produce as many eggs as 72 small ones of 0.3 kg. In addition to higher fecundity, the larger fish produce significantly larger eggs and presumably more viable larvae (Ojanguren et al., 1996; Pepin and Anderson, 1997).

Exploited populations were traditionally managed to maximize growth (Griffiths, 1997). However it is imperative to maintain sufficient numbers of reproduc-

tive adults to ensure egg production and avoid recruitment failure. To address proper management of line-caught fish in South Africa, spawner biomass per recruit models have been used (Griffiths, 1997). One assumption of this approach is that fecundity is linearly related to spawning biomass, regardless of individual size (Buxton, 1992). Because our study has shown that fecundity in carpenter is allometrically related to individual mass, egg-per-recruit models would be more appropriate for future stock assessment of this species.

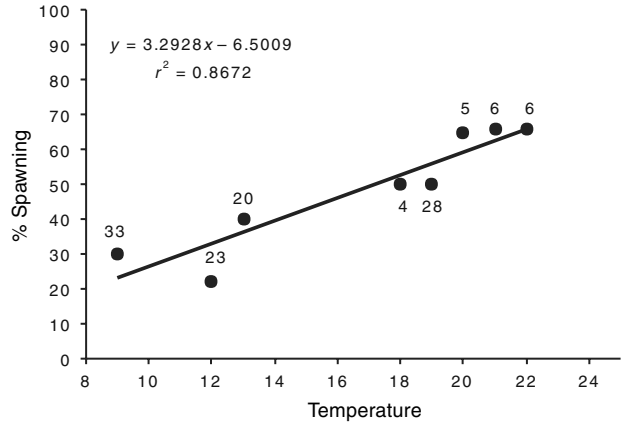

Figure 9

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

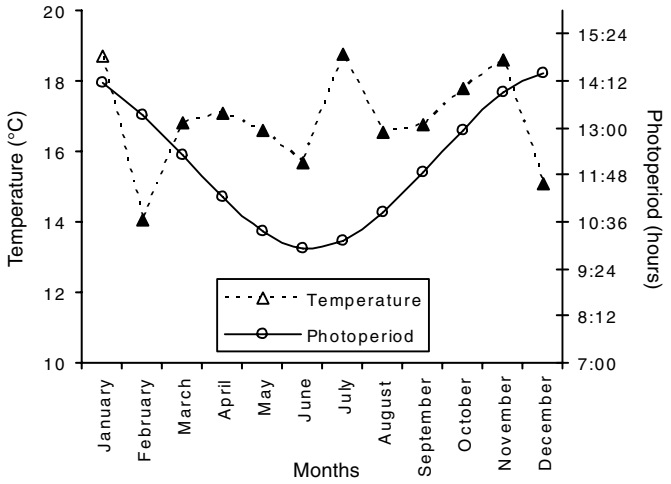

Figure 10

Monthly average temperature and photoperiod for the Tsitsikamma National Park.

Acknowledgments

We thank the staff at South African National Parks, for accommodation at the Tsitsikamma National Park and for use of their vessel. John Allen and Karoels Piterse are thanked for many hours at sea. Yolande Melo is thanked for her assistance with histological preparation and interpretation and Jeanine Van der Pol for assistance in laboratory and Tony Booth and two anonymous referees for constructive comments on this manuscript. This research was funded by the Marine Living Resources Fund.

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