Reproductive biology of *Rhabdosargus sarba* (Sparidae) in Western Australian waters, in which it is a rudimentary hermaphrodite

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The reproductive biology of the tarwhine *Rhabdosargus sarba* has been studied in three very different environments in Western Australia, namely the lower reaches of the Swan River Estuary and marine waters at the same latitude, i.e. ~32°S, and a large subtropical marine embayment (Shark Bay) approximately 800 km further north. A macroscopic and histological examination of the gonads demonstrated that *R. sarba* is typically a rudimentary hermaphrodite in Western Australian waters, i.e. the juveniles develop into either a male or female in which the ovarian and testicular zones of the gonads, respectively, are macroscopically undetectable. This contrasts with the situation in the waters off Hong Kong and South Africa where *R. sarba* is reported to be a protandrous hermaphrodite. Although *R. sarba* spawns between mid-late winter and late spring in each water body, the onset of spawning in the estuary is delayed until salinities have risen well above their winter minima. Although males and females attain sexual maturity at very similar lengths in the Swan River Estuary and Shark Bay, i.e. each *L_{50}* for first maturity lies between 170 and 177 mm total length (TL), they typically reach maturity at an earlier age in the former environment, i.e. 2 vs 3 years old. During the spawning period, only 25 and 12% of the males and females, respectively, that were caught between 180 and 260 mm TL in nearshore marine waters were mature, whereas 94 and 92% of the males and females, respectively, that were collected in this length-range over reefs, were mature. This indicates that *R. sarba* tends to move offshore when it has become ‘physiologically’ ready to mature. The *L_{50}* at first maturity indicate that the minimum legal length in Western Australia (230 mm TL) is appropriate for managing this species.

INTRODUCTION

The tarwhine *Rhabdosargus sarba* is widely distributed throughout the Indo-Pacific, including on both the east and west coasts of Australia where it is frequently caught by commercial and recreational fishers (Kuiter, 1993; Kailola et al., 1995). Like other sparids, *R. sarba* possesses a unique gonad termed an ovotestis, which comprises paired bisexual gonads that each consist of a medio-dorsal ovarian zone and a latero-ventral testicular zone separated by a wall of connective tissue (Besseau & Bruslé-Sicard, 1995). However, while Kinoshita (1939) regarded *R. sarba*, which he referred to as *Sparus aries*, as exhibiting a protandric feature during early life, Yeung & Chan (1987) and Garratt (1993) considered this species to be a *bona fide* protandrous hermaphrodite.

*Rhabdosargus sarba* typically spawns in marine waters and sometimes near the mouths of large rivers (e.g. Wallace, 1975; Potter & Hyndes, 1999). The spawning season of *R. sarba* varies in its duration and timing in the Arabian Gulf, India and South Africa (Patnaik, 1973; Wallace, 1975; El-Agamy, 1989). Although there have been no reproductive studies aimed at determining the spawning season of *R. sarba* in Australian waters, the times when the post-larvae of this species are caught in eastern Australia indicate that the spawning period is protracted in that region (e.g. Miskiewicz, 1986; Smith & Suthers, 2000). The length at which *R. sarba* reaches maturity is greater in South African waters than in the Arabian Gulf and Chilka Lake in India (Patnaik, 1973; Wallace, 1975; El-Agamy, 1989). This difference may be related to the fact that *R. sarba* attains a far greater length in South African waters, i.e. 750 mm (van der Elst, 1988; Oceanographic Research Institute, 2000), than in the latter two regions, i.e. 300–390 mm (Patnaik, 1973; El-Agamy, 1989). Since the size at which *R. sarba* reaches maturity in Australia is not known, it is not possible to determine whether the minimum legal length (MLL) of 230 mm total length (TL), designated for *R. sarba* by the Western Australian Department of Fisheries, is appropriate for managing this species in this state.

The main aims of this study were as follows. (1) Determine the type of hermaphroditism exhibited by *R. sarba* in Western Australian waters and whether it is the same type in three very different environments, i.e. an estuary and marine waters in a temperate region and a large subtropical marine embayment (Shark Bay) ~800 km further north. (2) Ascertain if *R. sarba* spawns in both nearshore and offshore coastal waters and, if it spawns in estuaries, whether this depends on the presence of elevated salinities. (3) Determine whether the spawning season and size and age of *R. sarba* at first maturity in the three different environments differ and, in the light of the estimated sizes at maturity, whether the current MLL of...
Each fish was aged using the number of annuli on their scales and its gonads removed and weighed to the nearest 0.01 g. The TL and wet weight of each fish were recorded to the nearest 1 mm and 0.1 g, respectively, in the case of younger adults and less frequently in those of older adults. Fish with gonads at categories 3 and 4 were considered to be males and females, respectively.

Each gonad belonging to categories 3 and 4 was allocated, on the basis of its macroscopic appearance, to one of the following eight maturity stages, based on the scheme of Laevastu (1965), i.e. I, virgin; II, immature/resting; III, developing; IV, maturing; V, mature; VI, spawning; VII, spent; VIII, spent recovering.

Each month, the gonads of at least 20 individuals were removed from fish covering a range of lengths and gonad stages and placed in Bouin’s fixative for 48 h and dehydrated in a series of ethanols. The mid-region of each gonad, and in some cases also its anterior and posterior regions, were embedded in paraffin wax, cut into 6 μm thick transverse sections and stained with either Mallory’s trichrome or Ehrlich’s haematoxylin and eosin. The sections were used to determine which stages in spermatogenesis and oocyte development were present in the testicular and ovarian zones, respectively, and to validate that the predominant zone of each ovotestis had been assigned to the appropriate stage.

Figure 1. Locations of sites (●) at which Rhabdosargus sarba was sampled on the west coast of Australia.

230 mm TL is appropriate for managing this species of sparid throughout Western Australian waters.

MATERIALS AND METHODS

Sampling and measurements

Rhabdosargus sarba was collected from the following three localities in Western Australia (Figure 1). (1) Marine waters at ~32°S, including both nearshore waters (<1.5 m deep) and offshore waters over reefs (15–30 m deep). (2) The lower reaches of the Swan River Estuary, which is situated at a similar latitude, including both nearshore waters (<1.5 m) and a deep region of the entrance channel (~11 m). (3) Shark Bay, which is located at ~26°S, including both intertidal mangrove areas and waters over reefs (1–5 m deep). Nearshore and intertidal waters were sampled using a 21.5 m long seine net with a 3-mm mesh in the bunt. The waters over reefs were sampled by rod and line fishing. Water temperature and salinity at the bottom of the water column at each sampling site were measured on each sampling occasion. The TL and wet weight of each fish were recorded to the nearest 1 mm and 0.1 g, respectively, and its gonads removed and weighed to the nearest 0.01 g. Each fish was aged using the number of annuli on their otoliths, which had been validated as being formed once each year.

Each of the gonads of R. sarba could be assigned macroscopically to one of the following categories: (1) very thin, strand-like and sexually indeterminate; (2) ovotestes containing relatively substantial amounts of both immature testicular and ovarian material; (3) ovotestes in which only a testicular zone could be detected macroscopically; and (4) ovotestes in which only an ovarian zone could be seen macroscopically. A very small testicular and ovarian zone were usually observed in histological sections of ovotestes belonging to categories 3 and 4, respectively, in the case of younger adults and less frequently in those of older adults. Fish with gonads at categories 3 and 4 were considered to be males and females, respectively.

The percentage contributions made to each length-class by those males and females of R. sarba that were collected from marine waters at ~32°S and Shark Bay and possessed gonads at Stages III to VIII were subjected to logistic regression analysis, using bootstrapping of 1000 random samples, to determine the lengths at which 50% of this species first reached sexual maturity and their 95% confidence limits. The additional parameter P_max was incorporated into the traditional logistic equation for the data for the Swan River Estuary to allow for the fact that the prevalence of fish with gonads at Stages III to VIII in this water body never reached 100% in any size-class. The logistic regressions for males and females in each of the three environments were compared using a likelihood ratio test (e.g. Cerrato, 1990) and employing a Bonferroni correction.

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The reproductive variables

Water temperature and salinity

Mean monthly water temperatures in coastal marine waters at ~32°S and the lower Swan River Estuary were determined from the equation W1/(W2−W1)×100, where W1=wet weight of the gonad and W2=wet weight of the whole fish. The indices were calculated using data for fish ≥L_m at first maturity in Shark Bay and the lower Swan River Estuary, and for all fish caught over reefs in coastal marine waters at ~32°S since, during the spawning period, the vast majority of fish in these waters were mature (see results). The monthly proportions of mature and spawning fish, i.e. individuals possessing gonads at Stages V and VI, in sequential size-classes of fish from each of the three environments were also calculated.

RESULTS

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Reproductive variables

Water temperature and salinity

Mean monthly water temperatures in coastal marine waters at ~32°S and the lower Swan River Estuary...
declined markedly from their maxima of ~24–25°C in summer to their minima of ~15°C in winter and then rose sharply in spring. The mean temperatures for Shark Bay exceeded by up to ~3°C those in the more southern sampling localities in each month except August. The mean monthly salinities in marine waters at ~32°S were always close to full strength seawater, i.e. 35 psu, and between ~37 and 40 psu in Shark Bay. Although mean monthly salinities in the lower Swan River Estuary in late spring to early winter were similar to those in nearshore marine waters outside the estuary, they fell precipitously to a minimum of 23 psu in mid to late winter, and then rose sharply in early to mid-spring.

**Histology of gonads**

The gonads of *R. sarba* <80 mm in length contained predominantly connective tissue. Gonial cells were first found in a fish of ~80 mm in length, and oocytes were first observed in an individual with a length of 91 mm (Figure 2A). The gonad of the latter fish also contained clusters of the highly basophilic granulocytes that were...
often present in the gonads of fish with lengths of 80 to 100 mm.

The gonads of *R. sarba* with lengths of ~120 to 160 mm, i.e. <length at first maturity, were either small and strand-like and consisted almost exclusively of immature testicular tissue (Figure 2B) or were larger and consisted either of relatively substantial amounts of both immature testicular and ovarian tissue (Figure 2C) or of predominantly ovarian tissue (Figure 2D). In the first and second of these three categories of ovotestis, the testicular zone contained spermatogonia and spermatocytes and occasionally spermatids, whereas that of the third category contained only spermatogonia. All of the oocytes in the ovarian zone of each of the three categories were at a previtellogenic stage of development. Each of the above three categories of ovotestis could be clearly distinguished macroscopically by the time *R. sarba* had reached a length of 140 mm.

The ovotestes of a small proportion of larger (mature-sized) *R. sarba*, i.e. >180 mm, contained substantial proportions of both testicular and ovarian tissue (Figure 2E), and thus presumably corresponded to the second...
category of ovotestis described earlier for juveniles. During the spawning period, the ovarian zone of such ovotestes was always immature, whereas the testicular zone was mature, i.e. contained some spermatooocytes in addition to spermatocytes and spermatids (Figure 2F).

Just prior to and during the spawning period, many of the gonads of R. sarba of 180–220 mm consisted of developing or mature testicular tissue, i.e. contained predominantly spermatids and spermatozoa, and a very small amount of ovarian tissue in which the oocytes were at the chromatin nucleolar stage (Figure 3A) or occasionally the early yolk vesicle stage or cortical alveoli stage (Figure 3B). Chromatin nucleolar oocytes were occasionally undergoing atresia, while the cortical alveoli oocytes were almost invariably atretic. Comparisons of the gonads of larger fish throughout the year provided overwhelming evidence that, while the testicular zone of such ovotestes regressed to an immature state during the non-spawning period, that zone always remained dominant in terms of size. Fish with this type of ovotestis are clearly males.

In contrast to the above type of ovotestis, most of the other R. sarba, that were between 180 and 220 mm and caught either just prior to or during the spawning period, contained a large ovarian zone and a very small testicular zone. When the ovarian zone of these ovotestes were at Stages III and IV of maturity, they contained oocytes at various stages of maturation (Figure 3C), while the testicular zone in these ovotestes possessed only spermatogonia (Figure 3D). Later in its development, the ovarian zones of this type of ovotestis contained large numbers of yolk granule oocytes (Figure 3E) and, in the most advanced stages, also hydrated oocytes and/or post-ovulatory follicles. The associated testicular zone has become very small (Figure 3F) and cannot be detected macroscopically. Fish containing the above type of ovotestis are clearly females.

Sex ratios

The following quantitative account of the ways in which the prevalences of fish with different ‘types’ of gonads (including those fish that were destined to become or had clearly become either males or females) change with body size and age is based on a macroscopic examination of the gonads of R. sarba. Each of these ‘types’ can clearly be matched with a particular ‘type’ in histological sections. None of the gonads of individuals that were caught in coastal marine waters at ~32°S and measured <120 mm contained either testicular or ovarian tissue that could be identified macroscopically (Figure 4). Gonads in which both testicular and ovarian zones could be detected macroscopically, and thus corresponded to the gonads that were designated histologically as category 2 in juvenile fish (see previous section), were first found in the 120–139 mm length-class. The percentage contribution made by fish containing macroscopically identifiable testicular and ovarian tissue declined sequentially from 12% in this size-class to <5% in the 180–199 to 240–259 mm length-classes and remained at 0% in all subsequent length-classes. Juvenile fish with gonads in which only testicular tissue could be detected macroscopically were first recorded in the 120–139 mm length-class. At this stage, these gonads correspond to those designated histologically as category 1 in juveniles (see previous section). The contribution made by fish, in which only the testicular tissue in the gonads was macroscopically identifiable and which were thus males, remained at between 42 and 67% until the 280–299 mm length-class. Although the percentages of male R. sarba were as high as 79 and 70% in the two size-classes of largest fish, respectively, the numbers of fish collected in these size-classes were only 14 and 10, respectively. Fish with ovotestes in which only ovarian tissue could be detected macroscopically were also first recorded in the 120–139 mm length-class. At this stage, these gonads correspond to those designated histologically as category 3 in juveniles and were thus destined to become functional ovaries in adults (see previous section). The percentage of these females in each successive 20 mm length-class between 160–179 and 260–279 mm, each of which was particularly well represented and always contained <9% of fish possessing gonads with substantial amounts of testicular and ovarian tissue, lay between 33 and 57% (Figure 4).

The trends exhibited in Shark Bay by the percentage of fish with ovotestes containing both testicular and ovarian material and of the males and females were similar in the size-classes between 160 to 279 mm to those just described for the same and likewise well represented length-classes in marine waters (Figure 4). Although no R. sarba between 80 and 139 mm were caught in the Swan River Estuary, the data for the other size-classes are entirely consistent with those recorded for marine waters at ~32°S and Shark Bay (Figure 5).

The gonads of all 0+ fish were strand-like and did not contain clearly identifiable testicular or ovarian zones. The percentage of R. sarba with gonads containing macroscopically identifiable testicular and ovarian zones declined from 7% in the 1+ age-class to 2% in the 4+ age-class and 0% in all older age classes, while the percentage of males and females increased from 33 and 21%, respectively, in the 1+ age-class to reach, in the case of both sexes, between 40 and 60% in older age-classes. Similar trends were exhibited by R. sarba in the lower reaches of the Swan River Estuary and Shark Bay (Figure 5).

Length and age at maturity

The L50 of males at first maturity in coastal marine waters at ~32°S, derived from samples collected in both nearshore waters and offshore waters over reefs, was 206 mm, which was far greater than the 173 mm estimated for males in Shark Bay, and the 171 mm estimated for the Swan River Estuary (Figure 6). The L50 of 218 mm for females in marine waters at ~32°S was likewise greater than the 170 and 177 mm recorded for this sex Shark Bay and the Swan River Estuary, respectively. The L50 for the two sexes at first maturity were not significantly different \( P > 0.05 \) in any of the three water bodies. While the L50 for neither females nor males in the Swan River Estuary and Shark Bay were significantly different \( P > 0.05 \), they were each significantly different from those of the corresponding sex in marine waters at ~32°S \( P < 0.001 \).

Maturity was first attained at the end of their first year of life by very few males in marine coastal waters at ~32°S and by some males in the Swan River Estuary, and by some males at the end of their second year of life in Shark Bay (Figure 7). Some females had attained
Figure 4. Percentage of different categories of fish (based on macroscopic criteria) in sequential 20 mm length-classes of Rhabdosargus sarba caught in marine waters at ~32°S, the lower Swan River Estuary and Shark Bay. In this Figure and Figure 5, the categories are: fish with (1) indeterminate, i.e. small juveniles (dark grey); (2) ovotestes containing relatively substantial amounts of both immature testicular and ovarian tissue (white); (3) ovotestes in which only the testicular zone was macroscopically visible, i.e. definitive males (white and diagonal lines); and (4) ovotestes in which only the ovarian zone was macroscopically visible, i.e. definitive females (black). Sample sizes for each 20 mm length-class are shown.
maturity by the end of their second year of life in marine coastal waters and Shark Bay and by most females of that age in the Swan River Estuary.

During the spawning period of *R. sarba*, 12% of the females caught in nearshore shallow marine waters were mature, whereas 92% of that sex caught over reefs were mature (Figure 8). A comparable situation was found among males, with only 25% of those caught in nearshore, shallow marine waters during the spawning season being mature, whereas 94% of those caught in offshore marine waters during that period were mature (data not shown). This parallels the situation in Shark Bay where, during the spawning period, no mature male or female *R. sarba* were caught in shallow, mangrove areas, whereas 76 and 66%
Figure 6. Logistic regressions and their 95% confidence limits fitted to the percentage contributions made by mature individual male and female Rhabdosargus sarba at each length during the spawning season in marine waters at ~32°S, the lower Swan River Estuary and Shark Bay.
Figure 7. Percentage frequency of occurrence of gonads at Stages III–VIII in sequential ages of male and female *Rhabdosargus sarba* during the spawning season in marine waters at ~32°S, the lower Swan River Estuary and Shark Bay. Sample size for each age category is shown.
of the males and females, respectively, caught over reefs and in intertidal rocky areas were mature. Although the majority of female *R. sarba*, that were caught at lengths $<180$ mm in nearshore waters of the lower Swan River Estuary, were immature, the majority of females above this length were mature, as also were females in the deep waters of the channel of this estuary (Figure 8). The same trends were exhibited by males in the estuary (data not shown).

**Trends in reproductive variables**

The mean monthly gonadosomatic indices (GSIs) for the males and females of *R. sarba* peaked earlier in Shark Bay, i.e. middle to late winter, than in the Swan River Estuary, i.e. late winter to late spring (Figure 9). Although, due to inclement weather, no *R. sarba* were able to be caught in August and September in coastal marine waters at $\sim32^\circ$S, the trends exhibited by the GSIs in the preceding and following months clearly indicate that the mean monthly GSIs would have peaked in these waters at the same time or even slightly earlier than in Shark Bay.

The monthly percentages of male and female fish with gonads at Stages V/VI, i.e. mature/spawning, followed similar trends to those of the mean monthly GSIs, i.e. the months in which those percentages were low and high corresponded to those in which the GSIs were low and high, respectively (Figure 9).

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*Figure 8.* Percentage frequency of female *Rhabdosargus sarba* with gonads at Stages III–VIII in successive 20 mm length-class in shallow, nearshore and deeper, offshore marine waters over reefs at $\sim32^\circ$S and in shallow, nearshore and deep channel waters of the lower Swan River Estuary. Sample size for each length-class is shown.
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**Figure 9.** Mean monthly gonadosomatic indices ±SE and monthly prevalences (%) of gonad Stages V and VI collectively of *Rhabdosargus sarba* caught in marine waters over reefs, the lower Swan River Estuary and Shark Bay, using data for fish ≥L₅₀ at first maturity. Sample size for each month is shown.

The ovaries of many female *R. sarba* caught over reefs at ~32°S in June and July were in spawning condition, i.e. that in which both testicular and ovarian tissues are relatively abundant. Note that the term mature refers to the condition during the spawning period and that ovarian and testicular components of the ovotestes of mature males and females, respectively, could only be detected histologically and often only in the younger mature fish.

**DISCUSSION**

**Is Rhabdosargus sarba a protandrous hermaphrodite?**

Our results provide the following evidence that, in three very different environments in Western Australia, *Rhabdosargus sarba* is typically a rudimentary hermaphrodite (late gonochorist) *sensu* Buxton & Garratt (1990). Namely, it is a species in which their juveniles, which possess gonads with both testicular and ovarian tissue, eventually develop permanently into either males with prominent functional testes and rudimentary ovarian tissue or females with prominent functional ovaries and rudimentary testicular tissue (Figure 10). (1) Within each water body, the males and females of *R. sarba* attain maturity at a similar length and age. (2) The ratio of males to females was typically close to parity in all length- and age-classes above those at which maturity is typically first attained and which, in terms of numbers, were well represented in the samples. There was thus no tendency for the proportions of one sex to rise consistently with increasing length or age and for those of the other sex to exhibit the reverse trend. (3) Fish that contained gonads with testicular and ovarian zones that were both macroscopically conspicuous were relatively rare above the length and age at first maturity.

The overwhelming evidence that *R. sarba* is typically a rudimentary hermaphrodite in a range of Western Australian environments, contrasts with the conclusions drawn by Yeung & Chan (1987) and Garratt (1993) that this species is a protandrous hermaphrodite in the waters.
off Hong Kong and South Africa, respectively. The macroscopic and histological data provided by Yeung & Chan (1987) clearly demonstrated that the relative abundance of males in the assemblage they studied declined progressively with increasing body size, whereas that of females pursued the opposite trend, thus providing very strong evidence of protandry. The trends were not as clearly pronounced in Garratt’s study. Although our results are not consistent with the conclusion of Kinoshita (1939) that the testicular tissue develops first in juvenile *R. sarba* in a population in Japanese waters, it should be recognized that his results were based on a very small sample size and must thus be treated with caution (see also Garratt, 1993).

The contrast between our results and those produced by Yeung & Chan (1987) and Garratt (1993) suggests that whether or not *R. sarba* undergoes sex reversal might depend on environmental conditions. Certainly, the coexistence of male and female tissues in an individual gonad provides the structural basis for natural sex reversal (Yeung & Chan, 1987). However, our results have demonstrated that *R. sarba* is typically a rudimentary hermaphrodite in three very different environments in Western Australia, namely in both marine and estuarine temperate waters at ~32°S and in a subtropical embayment ~800 km to the north. Alternatively, the differences in the type of hermaphroditism exhibited in different regions by *R. sarba* could be due to, what are currently designated as that species, comprising either subspecies or even two or more species in those different regions (Kuiter, 1993). There is certainly a marked heterogeneity in size amongst populations, with *R. sarba* attaining a far greater length in the waters off South Africa (van der Elst, 1988; Garratt, 1993; Radebe et al., 2002) than in India (Patnaik, 1973), the Arabian Gulf (El-Agamy, 1989) and Australian waters (Kuiter, 1993).

**Scheme for gonadal changes in *Rhabdosargus sarba***

In Western Australian waters, the gonads of juvenile *R. sarba* develop from a thin strand-like structure, consisting predominantly of connective tissue, into gonads that contain gonial cells and then into ovotestes that possess either predominantly testicular tissue, into or larger structures that contain either relatively substantial amounts of both testicular and ovarian tissue or predominantly ovarian tissue (Figure 10). The change, in the majority of fish, from a gonad with just gonial cells into one in which the main component is almost exclusively testicular or ovarian tissue occurs over the relatively short period that it takes the fish to grow from ~90 to 120 mm. Since these differences in gonadal composition are already present in fish of 120–160 mm, they have developed prior to the length at which the first mature males and females were found. It is thus assumed that the juvenile fish in which the testicular zone predominates become functional males, whereas those in which the ovarian zone predominates become functional females. This conclusion is based on the fact, at any time of the year, the vast majority of fish caught well above the size at first maturity contained gonads in which only either testicular or ovarian tissue could be detected macroscopically. Thus, once a fish develops into either a definitive male or definitive female, it remains so for the rest of its life.

Fish with the least prevalent type of gonad, i.e. that in which both testicular and ovarian zones could be detected macroscopically, declined progressively as the lengths of *R. sarba* increased from 120 to 200 mm and were generally not found in the larger size-classes. While such fish must thus presumably develop into either definitive males or females during late juvenile or early adult life, it is not clear which is the predominant or exclusive direction of such change (Figure 10). Although, during the spawning period, the testicular zone of the ovotestes of these fish contains spermatozoa, it is relatively far smaller than that of definitive males, in which the testicular zone is very large and contains mature tissue and the adjacent ovarian zone cannot be detected macroscopically. Furthermore, whereas during the spawning period, the spermatogenic cells in the ovotestes of fish possessing conspicuous testicular and ovarian zones were at various stages of development and included substantial numbers of spermatocytes, those in the testicular zone of definitive males were almost invariably spermatids or spermatozoa. While the possibility cannot be excluded that the small number of mature-sized fish with the former characteristics could function as males, they are clearly not as functionally well adapted to do so as definitive males.

**Spawning period**

The sharp rise in the mean monthly GSIs and prevalence of Stage V/VI ovaries in the females of *R. sarba* in Shark Bay between June and July and their subsequent precipitous decline in September provide strong evidence that this species spawns in this subtropical embayment in July to September. Such a conclusion regarding the commencement date of spawning is consistent with hydrated oocytes first being recorded in the ovaries of fish in July. It is also broadly consistent with the trends exhibited by the mean monthly GSIs and prevalences of Stage V/VI testes among males. Although very unfavourable weather conditions prevented the collection of *R. sarba* in offshore coastal marine waters around reefs at ~32°S in August and September, the trends exhibited by the GSIs and prevalence of Stage V/VI ovaries in the preceding and subsequent months provide overwhelming evidence that, as in Shark Bay, spawning peaks in these temperate waters in mid- to late winter. However, in contrast with the situation in Shark Bay and in marine waters at ~32°S, the mean monthly GSIs did not peak in the Swan River Estuary until far later, i.e. mid-spring, and the prevalence of gonads at Stages V/VI remained high throughout spring. This implication that the spawning of the marine species *R. sarba* is delayed in the Swan River Estuary, compared with the other two water bodies, is almost certainly related to the fact that salinities are low in the estuary in winter and do not start rising markedly until early spring. The view that low salinities inhibit spawning in *R. sarba* is consistent with the fact that, in contrast to the situation in marine waters, many of the yolk granule oocytes present in Stage V ovaries of *R. sarba* in winter were atretic. Moreover, Mihelkakis & Kijima (1994) has shown that the production of live larvae of *R. sarba* with no abnormalities was far greater in salinities of 20 to 30 psu than in lower salinities.
Length and age at maturity

The lengths at which the males and females of *R. sarba* attain maturity in the Swan River Estuary, i.e. 171 and 177 mm, respectively, were very similar to the lengths which the corresponding sexes reach maturity in Shark Bay, i.e. 173 and 170 mm, respectively. However, *R. sarba* tended to reach maturity earlier in the Swan River Estuary than in Shark Bay, which implies that the attainment of maturity by this spadefish is related more to length and thus to growth rate than to age.

Few of the fish caught in nearshore marine waters at 32°S during the spawning period were mature, even at lengths well above the 170–177 mm at which 50% reached maturity in the Swan River Estuary and Shark Bay, whereas the vast majority of the fish of this size in offshore waters were mature. This implies that *R. sarba* tends to remain in nearshore marine waters until it is physiologically ‘ready’ to become mature. Since the number of fish caught in nearshore waters was greater than in offshore waters, and fish did not tend to become mature in those waters at the same age as in offshore waters, the logistic curves for the prevalence of mature male and female fish in nearshore and offshore waters collectively were shifted to the right. Thus, the $L_{50%}$ for male and female *R. sarba* at first maturity in coastal marine waters (i.e. 206 and 218 mm, respectively) were almost certainly anomalously high for the population in temperate marine waters as a whole.

The implications of the size at first maturity for management are far less severe for rudimentary hermaphrodites than for protandrous and protogynous hermaphrodites, where the direction of fishing effort towards large individuals can lead to a deleterious reduction in females and males, respectively (Buxton, 1992). Since *R. sarba* generally reaches first maturity at a length well below the current MLL for the retention of this species in Western Australia, i.e. 230 mm TL, the majority of the individuals of this species have the opportunity to spawn at least once before they are legally allowed to be fished.

Our gratitude is expressed to colleagues at the Murdoch University Centre for Fish and Fisheries Research and to R. Lopresti for help with sampling. G. Thomson for preparing the histological slides, N. Hall and S. de Lestang for providing statistical assistance and D. Fairdough for helpful criticisms of the paper. Financial support was provided by the Fisheries Research and Development Corporation, Fishcare, Western Australia and Murdoch University.

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Submitted 1 April 2003. Accepted 24 September 2003.