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Reproductive Biology of Snapper (*Pagrus auratus*) in Subtropical Areas of Its Range and Management Implications of Reproductive Differences with Temperate Populations

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Abstract

Snapper (*Pagrus auratus*) (Bloch and Schneider) sampled from the waters of the Queensland east coast (20° to 28°S) spawned from June to October, at least three months earlier than the New Zealand snapper (36° to 44°S) and snapper from other temperate latitudes. The size at which snapper reached sexual maturity (26 to 30 cm FL) was broadly similar to other more temperate areas. However, the apparent faster growth rate of tropical snapper enabled them to reach sexual maturity at less than 2 years of age, more than a year earlier than in more temperate latitudes. This suggests that the attainment of sexual maturity in snapper is more likely to be based on size than age. There were also fish as old as 5 years that had not yet matured. No specific snapper spawning grounds were sampled and snapper with ripe gonads were found throughout the species distribution in Queensland. Snapper mainly spawned in the evening and early morning. The timing of the spawning season relative to the timing of the winter growth check formation may be partially responsible for the difficulty in interpreting snapper otoliths in subtropical areas.

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Introduction

Knowledge of the reproductive biology of a fish species including size and age at maturity, spawning seasonality and distribution are important for understanding the life history of a species and for fisheries management. Size at maturity has often been used to determine an appropriate minimum legal size (Hill 1992), and the timing and spatial extent of spawning have been used in setting the parameters of fishing closures. The range of snapper (*Pagrus auratus*) that extends from temperate (40°S) to subtropical (20°S) Australian waters, suggests that there may be differences in reproductive chronology between sub-populations of this species in subtropical waters and cooler temperate waters, similar to what has been demonstrated in many other species (Abookire and Macewicz 2003; Kokita 2004). Much of the research on snapper reproductive biology has focussed on temperate waters, therefore the question of reproductive chronology throughout its range has not been adequately researched.

Despite an extensive literature dealing with reproductive biology of snapper in New Zealand (Cassie 1956b; Crossland 1977a; 1977b, Francis and Pankhurst 1988, Scott and Pankhurst 1992) and Japan (Matsuyama et al. 1987a, 1987b), little work has been published on the reproductive biology of snapper in Australia. The exception to this is the work of Battaglene and Talbot (1992), who noted that running-ripe wild snapper were found off Port Stephens (32° 40'S) in November. By comparison, New Zealand snapper spawn from October through February (Crossland 1977b; Scott and Pankhurst 1992) although year-to-year variation in the timing of spawning is related to water temperature (Scott and Pankhurst 1992). The presumed environmental trigger for spawning in New Zealand is an increase in water temperature between 15 and 18°C although snapper continue to spawn in 20°C (Francis and Pankhurst 1988). Battaglene and Talbot (1992) have also presented evidence for an 18°C spawning trigger on the southern east coast of Australia. The seasonal variation in sea surface temperature in Hauraki Gulf, the main snapper fishing area in the north island of New Zealand, is 14 to 22°C (Crossland 1977a). By comparison, sea surface temperatures at the northern limit of the species' range in Queensland (20°S) rarely fall below 20°C and can reach as high as 30°C. Even at a latitude of 27°S, oceanic sea surface temperatures during winter rarely fall below 19°C in coastal areas (Harris 1993a, 1993b). These differences suggest that other environmental influences may be involved in triggering the spawning of snapper in tropical/sub-tropical latitudes or that the temperature trigger is higher.

In this paper the reproductive characteristics of snapper at the northern extreme of their range in the Southern Hemisphere are described and compared with other areas. Implications of these differences for the management of the fishery are also discussed.

Materials and Methods

Snapper were collected mainly from commercial and recreational line fishers between July 1992 and October 1995, throughout their Queensland range from the Gold Coast (28°S) to the Swains Reefs (21°S) (Figure 1). These samples were augmented by collections from research line fishing cruises carried out east of Moreton Island during the months of June to September of 1994 and 1995. Sampling was most intense in 1993 and 1994 with up to four samples per week being collected from recreational and commercial fishers. Sampling at this intensity was only possible in the waters of southeast Queensland (25°S - 27°S).

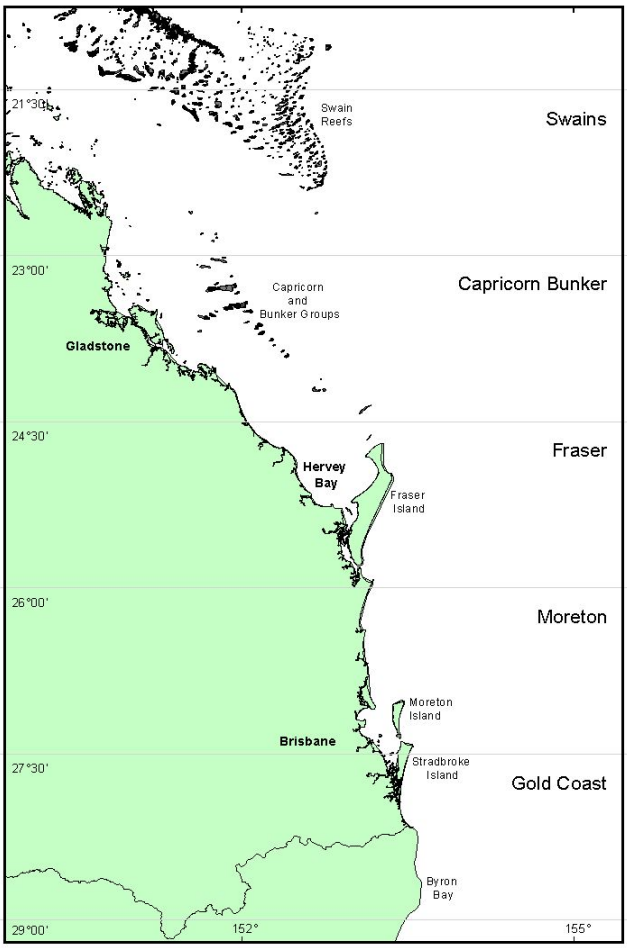

Fig. 1. Map of study area showing locations off the Queensland coastline, Australia.

Gonads for study were removed from freshly killed fish or fish that had been kept on ice after capture, but a proportion of gonads (< 20%) were from fish that had been frozen immediately after capture. Fish were measured (fork length, cm), weighed (wet weight, grams) and sagittal otoliths removed for ageing (Ferrell and Sumpton 1997). Gonads were removed, sexed, staged macroscopically (Tables 1 and 2) and placed in 10% neutral buffered formalin prior to histological processing or other analysis. Macroscopic and microscopic staging schemes were modified slightly from those of Matsuyama et al. (1987a, 1987b) and Scott and Pankhurst (1992) and were based on the most advanced oocyte stage observed in the section. Gonosomatic indices were calculated as the percentage gonad weight to the gonad-free wet body weight.

Specimens selected for histological preparation were removed from the fixative and a section was taken across one lobe unless there was an obvious difference between lobes or between regions of the lobe. If this was the case multiple sections were taken. Sections were cut at 6 microns and standard haematoxylin and eosin staining carried out. Spawning season was determined by the presence of females with hydrated oocytes based on macroscopic

staging or females with hydrated oocytes and postovulatory follicles (microscopic staging). Sexual maturity was determined by the presence of at least stage 2 gonads based on macroscopic and microscopic observation (Scott and Pankhurst 1992).

Table 1. Criteria used to classify female snapper, *Pagrus auratus* ovaries into macroscopic and microscopic histological reproductive stages (Table modified from Matsuyama 1987a and Scott and Pankhurst 1992).

Reproductive		Macroscopic Features	Histological Features
1	Immature	Ovary thin & firm Pale or translucent pink No oocytes visible	Tunica tightly encloses ovarian lamellae Oocytes without yolk globules densely staining basophilic No evidence of prior spawning
2	Resting	Ovary more rounded Pale, opaque pink or red No oocytes visible	Yolk globule stage oocytes predominate Tunica thick
3	Developing	Ovary enlarged Usually pale orange, sometimes pink Oocytes visible but small	Oocytes in yolk globule stage have developed without atresia or atresia of yolked oocytes is present, but <50% of oocytes are affected
4	Mature	Ovary enlarged Orange but not speckled in appearance Oocytes large and easily discernible	Yolk vesicles dominant Oocytes in the migratory nucleus stage, premature stage or mature stage.
5	Ripe	Ovary greatly enlarged translucent pale orange Hydrated, clear eggs giving a speckled appearance Eggs sometimes extruded by applying pressure to abdomen	Oocytes at all stages are present but yolk globule stage predominate Post ovulatory follicles present Some oocytes greatly enlarged and hydrated
6	Spent	Ovary dark red and bloodshot Thin and flaccid	Residual atretic oocytes Post ovulatory follicles Septa disorganised

During the spawning seasons of 1994 and 1995 the ovaries of fish (with stage 5 gonads) collected at various times of the day were examined for differences in oocyte size in order to better estimate time of spawning. A random sample of about 200 eggs from a sub-sample of these ovaries was measured using a binocular microscope interfaced to an image analysis system (OPTIMAS ^{TM}) to obtain size distributions of various oocyte types. The technique involved shaking the sample and pouring a sub-sample into a small petrie dish and then measuring all oocytes in the field of view. This procedure was repeated several times until approximately 200 oocytes had been measured. The resultant distributions were often multi modal reflecting the batches of oocytes at different stages of development. Eggs from these distributions were classified on the basis of their diameters into the following stages

(Scott et al. 1993): primary oocytes (0.05 to 0.19 mm), vitellogenic oocytes (0.2 to 0.49 mm), early final oocytes (0.5 to 0.69 mm) and hydrated oocytes (>0.7 mm). Analysis of variance was used to test seasonal variation in GSI and students t tests used to analyse size and age variations.

Table 2. Criteria used to classify male snapper, *Pagrus auratus* testes into macroscopic and microscopic histological reproductive stages (Table modified from Matsuyama 1987b and Scott and Pankhurst 1992).

Reproductive Stage	Macroscopic Features	Histological Features
1 Immature	Testis thin and flattened Translucent white threads	Testis composed predominantly of dense connective tissue Spermatogonia dominate
2 Developing	Testes enlarged Creamy white in colour	Lobules lined with spermatogonia crypts Spermatocytes proliferate Few spermatozoa
3 Mature	Opaque and white Viscous milt in sperm ducts	Spermatozoa predominate and crowd sperm ducts and sinuses Testis periphery contains crypts with cells of all developmental stages
4 Ripe	Testis firm, creamy white Free flowing milt in sperm duct	Spermatozoa predominate packing lobules and sperm ducts
5 Spent	Testis thin and flaccid Residual sperm visible as white areas in overall darker grey testes	Crypts beginning to form but empty Connective tissue dominates Residual spermatozoa present

Results

Over the range of latitudes (21° to 28°S) where samples of fish were collected, seasonal variation in gonosomatic indices (GSI's) did not differ between areas and in subsequent analyses these data have been grouped. Fish collected during the spawning season of 1992 were not included in the analysis, as these were mainly larger fish whose gonad weight was disproportionately large. For all other sampling months there were no significant differences in the size of fish used to estimate GSI ($P > 0.05$). Over the years when samples were collected the peak in female GSI (2% - 4.5%) occurred at the same time (during winter), although GSI's remained relatively high (>1%) until October (Figure 2). Female GSI's did not differ significantly in the peak spawning months of July ($F=1.74$, d.f.=2,63, $P>0.05$) and August ($F= 3.12$, d.f.=2,59, $P>0.05$) during 1993 to 1995. The pattern for male GSI was similar to that of the females, with GSI values (2% - 4.5%) also peaking during the winter (Figure 3). This study was primarily concerned with delineating female reproductive patterns and males were not as extensively sampled adequately to allow for a discussion of differences between years.

Figures 4 and 5 present the seasonal changes in microscopic staging of snapper that were assessed as sexually mature using macroscopic methods. Females with mature gonads began appearing as early as April. Spent females were only recorded from June to September with the latter month having the highest proportion of spent females, reflecting the end of the spawning season. Post spawning males were only present from August to November and there were also a high proportion of ripe males very early in the season (as early as April).

Microscopic observation of 0+ year old snapper gonads showed that they were all undifferentiated with no clearly discernible germinal tissue. Fish between 15 and 24 cm (between 1 and 2 years old) displayed a range of developmental patterns. Uniquely ovarian and testicular tissue was seen as well as a small number of ovo-testes (20% of samples). Ovo-testes were not seen in any fish older than 2 years. In the intensively sampled regions of Fraser and Moreton, the duration of the main spawning season varied between years from 67 to 130 days (Table 3).

Maturity was reached over a wide range of sizes with fifty percent sexual maturity occurring at approximately 23 cm fork length, although there were many larger individuals that had not yet spawned (Figure 6). There were some snapper in spawning condition as young as 1+ year old which had recruited to the fishery (Figure 7), but this only occurred very late in their first year when they were at least 22 months old. Whilst snapper appeared to mature at between two and three years of age there were fish as old as 5 that had apparently never spawned. However, all fish greater than five years of age and 33 cm in length were classified as sexually mature.

Oocyte development did not show strong small-scale temporal trends (Figure 8), possibly because there was insufficient resolution in the time of capture and the method of capture (i.e. line fishing) resulted in little control over the time of capture. The most obvious trend was for fish captured between 0700 and 1200 hr to have relatively poorly developed oocytes in comparison to those captured at other times. The strongest evidence for bimodality in oocyte size distributions can be seen in the samples collected between 0600 and 0700 hr.

Table 3. Times of earliest and latest spawning in the respective years of snapper, *Pagrus auratus* assessed by the presence of one or more "ripe", stage 5 females in samples (assessed either macroscopically or microscopically).

Region	Year	Earliest spawning	Latest spawning
Moreton	1993	Insufficient samples	8 November
Moreton	1994	19 June	31 October
Moreton	1995	30 July	7 October
Fraser	1993	24 June	10 November
Fraser	1994	19 June	29 October

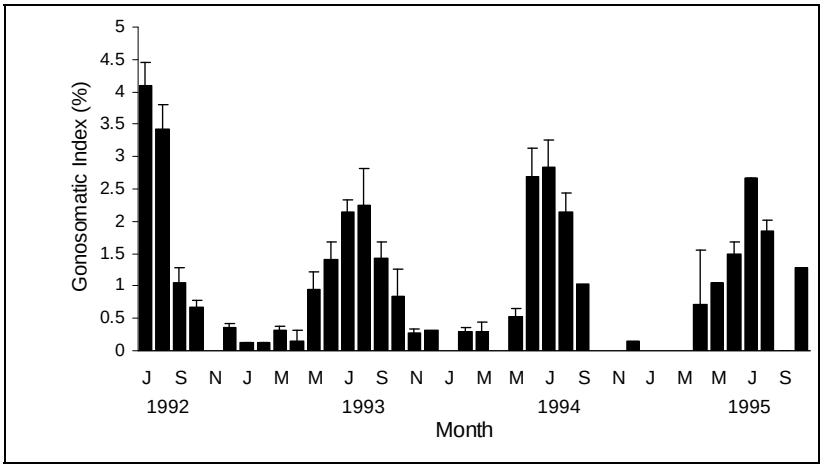

Fig. 2. Seasonal variation in gonosomatic indices of mature female snapper, *Pagrus auratus* sampled from 1992 to 1995 (Standard errors are shown as vertical bars. Points without errors represent a single sample).

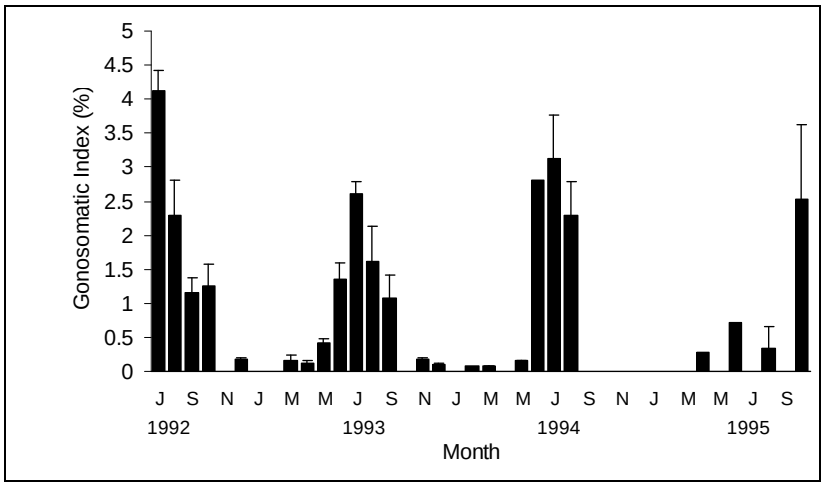

Fig. 3. Seasonal variation in gonosomatic indices of mature male snapper, *Pagrus auratus* sampled from 1992 to 1995. (Standard errors are shown as vertical bars. Points without errors represent a single sample).

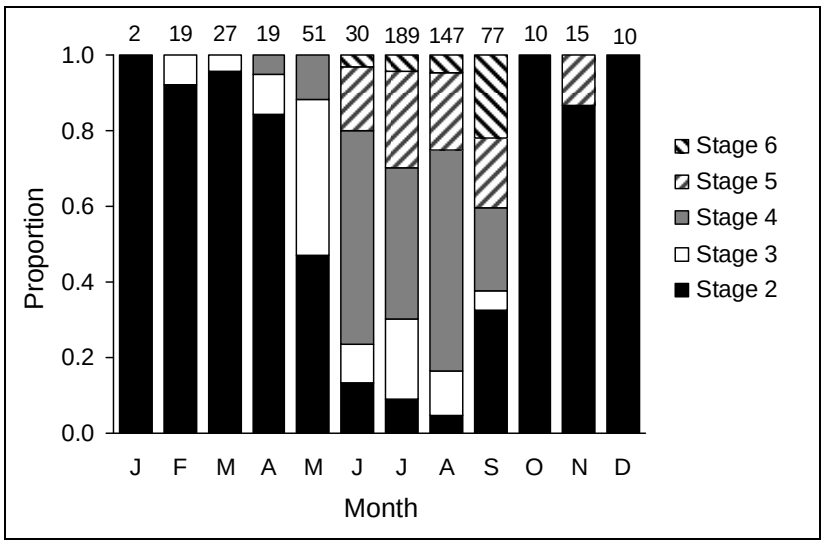

Fig. 4. Seasonal variation in the proportion of female snapper, *Pagrus auratus* of various histological reproductive stages (Table 2) during 1994 and 1995. Sample sizes are shown above each bar.

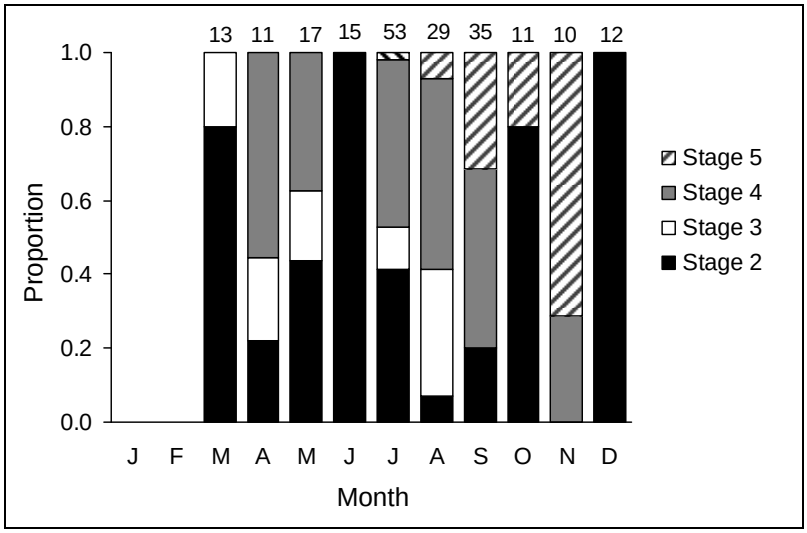

Fig. 5. Seasonal variation in the proportion of male snapper, *Pagrus auratus* of various histological reproductive stages (Table 2) during 1994 and 1995. Sample sizes are shown above each bar.

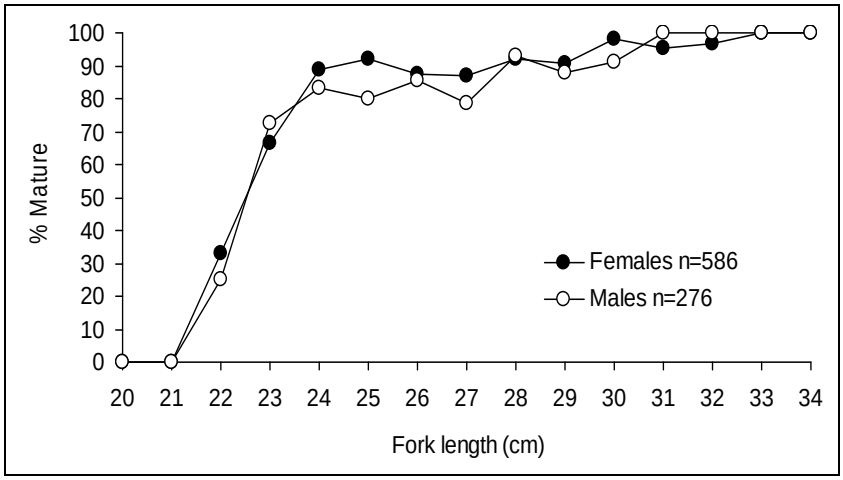

Fig. 6. Relationship between size and sexual maturity of male and female snapper, *Pagrus auratus* from southern Queensland waters.

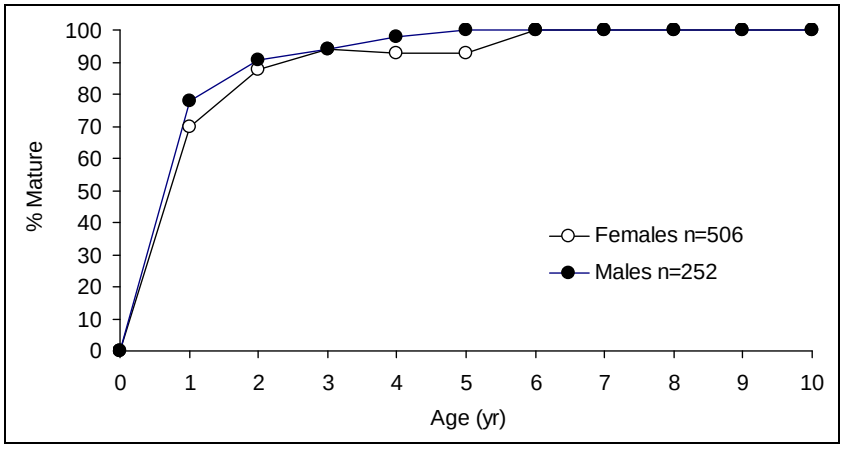

Fig. 7. Relationship between age and sexual maturity of male and female snapper, *Pagrus auratus* from southern Queensland waters.

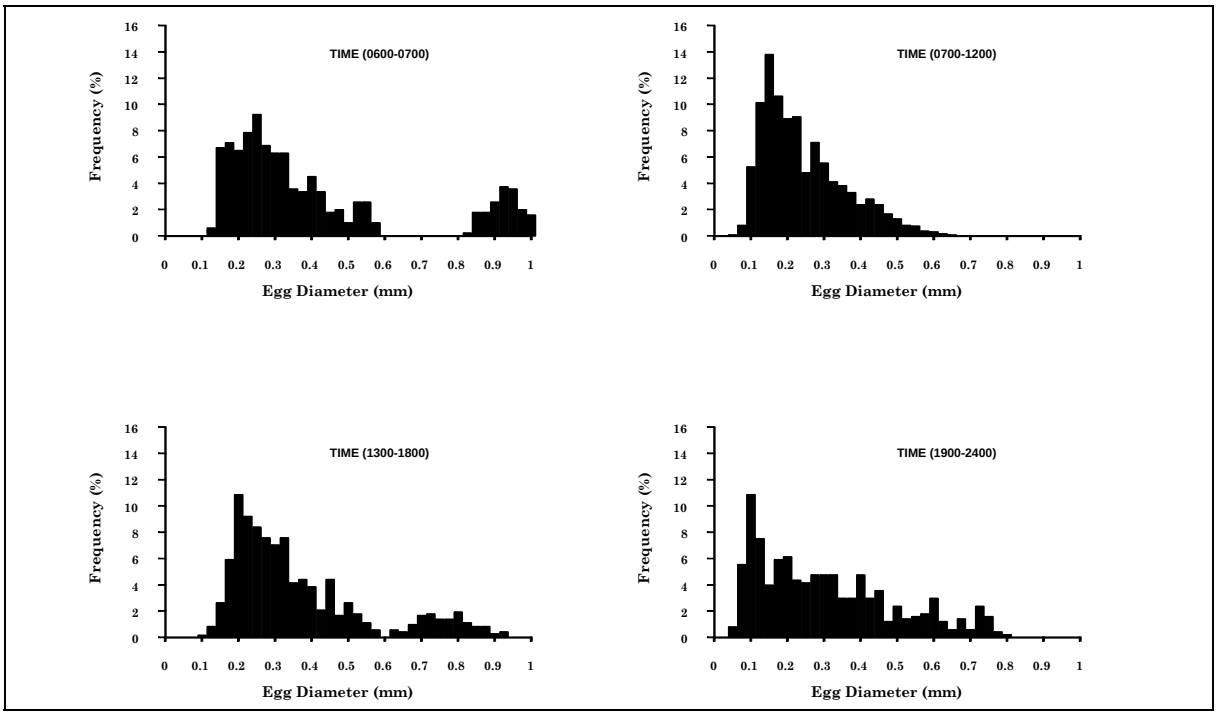

Fig. 8. Frequency distribution of oocyte diameters in the ovaries of ripe (Stage 5) female snapper, *Pagrus auratus* sampled during various times of the day. Each figure was obtained by measuring oocytes of 20 fish.

Discussion

The average length of the spawning period of snapper (approximately three months) did not differ markedly in duration from the spawning season of snapper in temperate areas, but the season began up to six months earlier than in some New Zealand populations where spawning occurs during October to February (see Cassie 1956a; Crossland 1977b). The much earlier spawning period in sub-tropical latitudes allows for at least another three months of early rapid growth during spring before growth slows during the first winter. In addition, juveniles produced from fish spawning earlier in the season would have an even longer growing season than snapper spawned later, and may provide for earlier recruitment into the fishery 18 months or more later.

Interpretation of growth checks on otoliths may also be complicated if spawning has an influence on otolith appearance. Snapper ageing validation studies have been carried out in areas where spawning occurs at the same time as the formation of growth checks in otoliths (Ferrell et al. 1992, Francis et al. 1992). If spawning occurs earlier in sub-tropical areas, formation of separate spawning and growth checks is likely to complicate the interpretation of otolith structure.

In subtropical waters snapper can reach maturity and are capable of spawning as early as the end of their second year of life, although a small proportion of fish as old as five years appear to never have spawned (or at least were not spawning during the particular spawning season in which they were sampled). Maturity was not closely related to either size or age since its onset occurred over a wide range of both sizes and ages. In general, snapper reached sexual maturity between 22 and 30 cm FL (50% maturity at 23 cm) and at an age between about 22 months and 5 years. The proportion of sexually mature snapper estimated for the lower limits of the size and age distributions cannot be considered precise because most of the fish that were sampled were from the commercial fishery (minimum legal size of approximately 25 cm FL) and thus not representative of the entire population. It is likely that the number of sexually mature age 2+ fish is considerably less than that estimated here because of only partial recruitment of this age class to the fishery. Regardless of this bias it is clear that by the end of their third year of life the majority of snapper are capable of spawning.

The size at which a fish reaches sexual maturity is an important reproductive parameter that is often a prime consideration by managers when setting minimum legal sizes. Hill (1992) stated that any minimum size restriction would increase the number of fish surviving to spawning age providing that the sizes protected would otherwise have formed part of the retained catch. Nevertheless, size at maturity is still a commonly required parameter by fisheries managers, conservation groups and fishers alike. The size and age at which snapper reach maturity is not known with great precision but the size range found in Queensland is in broad agreement with New Zealand snapper (Crossland 1977a) that mature at a length of 23-26 cm. However, the apparent faster growth experienced in more subtropical latitudes results in snapper reaching sexual maturity at a younger age than fish from temperate areas. Crossland (1981) noted that this was between 3 and 5 years in New Zealand. The conclusion to be drawn from this is that sexual maturity in snapper may be more closely related to size than to age.

Gonosomatic indices are typically poor predictors of reproductive stage because larger fish usually have disproportionately larger gonads than smaller individuals, with this trend increasing with advancing gonad development (West 1990). In the present study microscopic examination of snapper gonads showed that spawning was occurring earlier than the gonosomatic indices would indicate. Insufficient numbers of snapper were collected from all study regions to provide an accurate indication of small scale geographic variations in spawning season, but the fact that ripe and spent females were found throughout the study area confirms the absence of a specific spawning ground(s) along the sampled distribution range. This conclusion is consistent with the situation in New Zealand (Crossland 1981).

The conclusions drawn from this study assume that the catchability of snapper is the same before and after spawning. Since line fishing was the main method of sampling fish, any behavioural change that alters feeding patterns could impact on estimates of reproductive

parameters. This was particularly the case in the analysis of diurnal spawning time based on the size frequency of oocytes in the gonads of line caught fish. Scott et al. (1993) used trawl samples taken every 1.5 hours in their analysis of snapper spawning frequency in New Zealand. This is preferable to using line caught samples because fish that remain near the seabed are always catchable by trawl, while they may not always be catchable by line fishing techniques.

Intensive sampling conducted during this research showed that the length of the spawning season varied dramatically from year to year (i.e. between 67 and 130 days) although the peak of the season appears to be around half that figure. There are important management implications given that the spawning season for snapper in Queensland occurs during the winter. This is the time of the year when both weather and current conditions are more favourable to fishing. Winds are generally lighter in winter and tend to be offshore breezes (Australian Bureau of Meteorology). Likewise currents are generally not as strong (Harris 1993a, 1993b). These climatic features serve to focus the fishery on the spawning population.

Spawning closures have been used as a means of protecting spawning populations, for example barramundi (*Lates calcarifer*) in northern Queensland (Anon 1996), but they would not be recommended for the snapper fishery given the geographic and temporal range over which the species spawns. Defining area closures would also be difficult given the offshore nature of the fishery. The enforcement of area or temporal closures would prove difficult because of the remoteness of many of the fishing grounds. In addition, there are a number of other demersal and pelagic species that are taken from the same fishing grounds as snapper and it would be difficult to target these species without landing a considerable by-catch of snapper. Even though these fish could be released, there are survival problems since the fishery generally operates in relatively deep water (>30m) where barotrauma may cause mortality (Stewart 2008).

Alekseev (1982, 1983) reviewed the sexuality in the Sparidae and found a range of reproductive strategies including protandry and protogyny as well as simultaneous and rudimentary hermaphroditism. Juvenile sex inversion has previously been demonstrated in New Zealand snapper (Francis and Pankhurst 1988) and this was also evident in the population studied in Queensland. These data also confirm the conclusion that the attainment of sexual maturity may be size rather than age based, because no 3+ year individuals in the present study had ovo-testes whereas this condition was observed in 3+ year snapper sampled in New Zealand (Francis and Pankhurst 1988).

The juvenile sex inversion displayed by snapper may have no adaptive advantage for the species, since the benefits normally attributed to protogyny and protandry (increased population fecundity) are only relevant when the change occurs after the onset of sexual

maturity (Alekseev 1982). The same author also hypothesised that juvenile sex inversion was a secondary development from ancestral hermaphroditism towards gonochorism. Sadovy and Shapiro (1987) pointed out that the induction or modification of sex inversion could be caused by social or environmental factors. If this is the case, all populations may not exhibit sex inversion.

The environmental trigger for snapper spawning in New Zealand is believed to be rising water temperatures in spring (Scott and Pankhurst 1992). However, snapper in sub-tropical regions begin spawning when temperatures are falling, suggesting that it is not the change in temperature but possibly its absolute value or some other cue that initiates spawning activity in sub-tropical snapper. The fact that spawning is initiated at temperatures warmer than 18°C suggests that there is no universal temperature trigger that is applicable throughout the species distribution.

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