The reproductive cycle of the intertidal gastropod *Turbo coronatus* Gmelin 1791, on the Transkei coast

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Histological methods were used to determine the reproductive cycle of *Turbo coronatus*. Ovarian development was assessed from the relative proportions of mature and immature oocytes in sectioned material. Testicular tissues were subjectively given a maturity index based on the relative proportions of the various spermatogenic cells present. *Turbo coronatus* has a protracted breeding period with peak spawning taking place from December to February.

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Die broeisiklus van *Turbo coronatus* is deur histologiese metodes bestudeer. Die relatiewe getalle van ryp en ontwikkelende oösiete in die snitte is gebruik om die ontwikkelingstadium van die ovarium te bepaal. Die relatiewe verhoudings van verskillende spermatogenetiese selle is gebruik om 'n ontwikkelingsindeks vir die manlike geslagsklier op te stel. *Turbo coronatus* het 'n verlengde broeiperiode waarin piek kuitskiet tussen Desember en Februarie plaasvind.

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Little is known of the biology of the genus *Turbo* in southern Africa. Lombard (1977) studied growth, reproduction, respiration and feeding of, and energy flow through *Turbo sarmaticus* in the Eastern Cape. Seasonal variations in energy and biochemical composition of *T. sarmaticus* have also been described (McLachlan & Lombard 1980). *Turbo coronatus* is a common tropical Indo-Pacific species which extends south to East London (Kilburn & Rippey 1982). On the Transkei coast this gastropod is found in mid-tidal pools usually under rocks, in crevices or buried under sand.

This paper describes the reproductive cycles of both male and female *T. coronatus*, as determined from histological studies.

Methods

Random samples of 25 to 30 specimens of *T. coronatus* were collected from tidal pools within Hluleka nature reserve, at monthly intervals, between August 1982 and September 1983. All collections were made at spring low tides. Individuals were measured along the columellar axis to the nearest 0,1 mm before cracking open the shell and removing the soft parts.

Portions of the gonad and underlying digestive gland were fixed in Bouin's solution or 10% formal-saline and routinely prepared for histological examination. The embedded material was sectioned at 7 µm and stained with Delafield's haematoxylin and eosin. The sectioned material was subjectively allocated a maturity index based on the differing proportions of the various gametogenic cells present (Table 1). Quantitative analyses of some ovarian sections were also made by counting the numbers of previtellogenic (immature) and post-vitellogenic (mature) oocytes in 5 to 10 microscopic fields at 400 × magnification.

Results

The sex of *T. coronatus* could not be determined from external features. Examination of the soft tissues indicated that *T. coronatus* was dioecious; no evidence of hermaphroditism was found. The ovary was green whilst the testis was creamy-white in colour. Juveniles showed only the dark brown colour characteristic of the digestive gland. Specimens dissected were within the 14,5 to 38,5 mm size range, the shell height of the smallest individuals with mature gonads being 16 mm. The sex ratios found in the monthly samples and the total collection were compared with 1:1 ratio using the χ^2 test. In eight out of 14 samples males outnumbered females. However, only the August 1982 and overall collection differed significantly from the expected 1:1 ratio. There was no difference in the size distribution between sexes. Of the total sample of

Table 1 Stages in the reproductive cycle of *Turbo coronatus* (based on the scheme used by Orton, Southward & Dodd 1956)

	Contents of follicles	
Stage	Male	Female
Developing d_1	Some spermatogonia, mainly spermatocytes.	Mainly small immature oocytes interspersed with groups of undifferentiated germ cells attached to trabeculae.
d_2	Number of spermatocytes approximately equal to that of spermatids and spermatozoa.	Vitellogenesis well advanced in most oocytes, which are now medium to large in size. Some small oocytes remain attached to trabeculae.
d_3	Some spermatocytes, but spermatids and spermatozoa now predominant.	Majority of oocytes are large and of uniform size, surrounded by a basophilic jelly layer. Few small oocytes remain attached.
Ripe r	Follicle full of spermatozoa and spermatids. Few spermatocytes present.	Uniform mass of large eggs with only traces of original trabeculae present.
Spawned sp	Follicles mostly empty, some with residual spermatozoa and spermatids.	Pronounced gaps with some residual mature oocytes. Small oocytes present on trabeculae.

393 *T. coronatus* examined, 219 were male and 174 female.

The gonad lies along the length of the digestive gland and overlaps it laterally. The internal arrangement of the gonads conforms to those of *Turbo intercostalis* and *Turbo torquatus* described by Joll (1980). Previtellogenic oocytes remain attached to the ovarian trabeculae for much of their development. At a later stage they are attached to the trabecular surface, merely by a stalk. These developing oocytes have clear nuclei with a deeply stained nucleolus. As vitellogenesis commences the oocytes detach from the trabeculae. The cytoplasm of these oocytes takes on a granular appearance owing to the deposition of yolk granules. Post-vitellogenic oocytes are surrounded by a basophilic jelly layer. With the exception of resting males, all stages of spermatogenesis were apparent in the testes. The spermatogenic cells were arranged in overlapping layers spreading out from the trabeculae into the lumen.

The mean percentage of mature oocytes increased steadily from September reaching a peak in January, when the eight females examined contained only mature oocytes (Figure 1). Thereafter, the percentage mature oocytes declined (indicating spawning activity) reaching its lowest level in May. The proportion of vitellogenic oocytes began to climb again from June onwards. Females with mature oocytes accounting for over 70% of the oocytes counted were recorded from November to March and from June to July.

The subjective staging (Figure 2) indicates little gametogenic synchrony; *T. coronatus* individuals at several developmental stages were present in most samples. Between August and December 1982 the population exhibited a progressive increase in gonadal development. Ripe, pre-spawning individuals comprised a major proportion of the population in December and January. However, low levels of breeding activity, indicated by the presence of ripe or spent *T. coronatus* were apparent throughout the study period. No *T. coronatus* were observed in a resting condition.

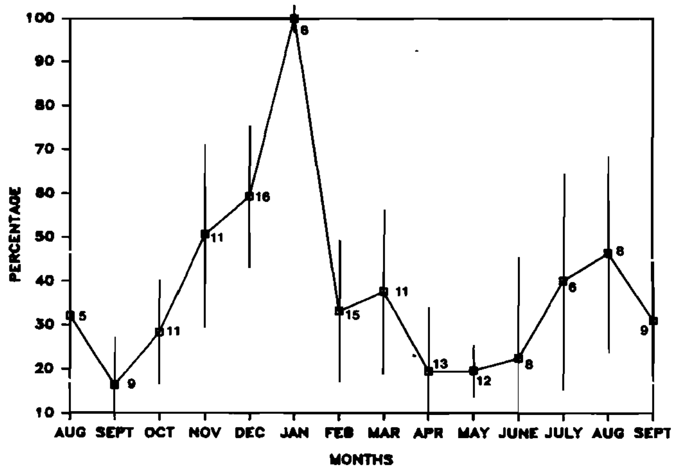

Figure 1 The reproductive cycle of female *Turbo coronatus* as indicated by the percentage of mature oocytes present in samples. Vertical bar indicates standard deviation. Numbers above the bar indicate sample size.

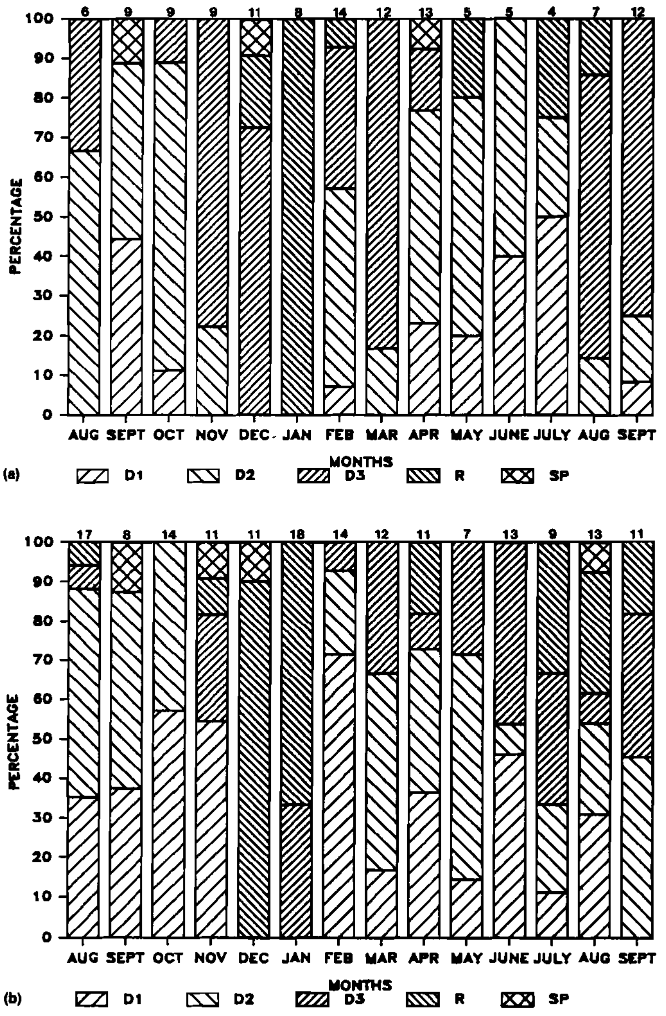

Figure 2 The reproductive cycle of (a) female and (b) male *Turbo coronatus* based on the proportion of the population at each maturity stage (d_1, d_2, d_3: developing; r: ripe; sp: spawned).

Discussion

A distinct peak in the spawning activity of *T. coronatus* was evident between December and February. In Port Elizabeth the congeneric *T. sarmaticus* has been found to spawn during the summer – autumn period (December – April) (Lombard 1977; McLachlan & Lombard 1980). Prolonged breeding seasons have been reported in three Australian turbinids, *Subninella undulata* (Underwood 1974), *T. intercostalis* and *T. torquatus* (Joll 1980). However, the cold temperate New Zealand turbinid *Lunella smargada* has a short spawning period of only two months (Grange 1976). The presence of individual *T. coronatus* at various developmental stages in the monthly samples coupled with low levels of breeding activity throughout the year suggests that this species may have an extended breeding season with multiple spawnings. Alternatively, *T. coronatus* may exhibit group synchronism. From the present study it is not possible to draw any conclusions on how synchronous spawning is amongst individual *T. coronatus* within the population. Neither is it possible to define how often or exactly when spawning takes place. As Creese & Ballantine (1983) have pointed out monthly samples are not frequent enough to establish how synchronous spawning is.

It is not possible to ascertain whether an animal spawns partially or completely from histological studies. Circumstantial evidence, in the form of large variations in the proportion of mature oocytes present during spawning plus the fact that mature oocytes were present throughout the year, suggests that *T. coronatus* may be a partial spawner. Joll (1980) suggested that turbinids might spawn partially at the beginning and completely towards the end of the breeding cycle. Partial spawning throughout the breeding period may well maximize the potential reproductive success. Completely spawned *T. intercostalis* and *T. torquatus* were observed by Joll (1980) but neither *T. coronatus* (this study) or *S. undulata* (Underwood 1974) were shown to spawn totally.

The exogenous and endogenous factors important in regulating reproductive activity in prosobranchs are poorly understood (Webber 1977). Most attention has been directed at determining the key environmental factors that synchronize the reproductive cycle of marine gastropods to prevailing environmental conditions. Several workers have reported correlations between environmental parameters and reproductive cycles (Webber & Giese 1969; Sutherland 1970; Pearse 1978), however few have demonstrated causal relationships. Underwood (1974) suggested that only the first phase of the reproductive cycle, gametogenesis, is likely to depend on simple environmental triggers. Vitellogenesis is dependent on the availability of nutrients, either in the form of a nutrient reserve or food ingested. Spawning itself, is dependent on the completion of vitellogenesis.

No information is available on temporal fluctuations in food availability or environmental conditions along the Transkei coast during the course of this study. However, the reproductive cycle of *T. coronatus* can be considered relative to general trends in sea surface temperature described by Christensen (1980). The gametogenic progression, observed between August and December, coincides with increasing sea temperature and the peak in spawning activity occurred during the period of maximum sea temperature. However, the fact that low levels of breeding activity occurred throughout the year suggests that some other external stimulus stimulates spawning. Studies on turbinids elsewhere have shown that spawning can be induced by temperature change (Ai 1965) and by rough water (Grange 1976). The latter is unlikely to influence spawning in *T. coronatus* which inhabits an area characterized by vigorous wave action.

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