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THE REPRODUCTIVE CYCLES OF THREE TROCHID GASTROPODS FROM THE TRANSKEI COAST, SOUTHERN AFRICA

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ABSTRACT

Changes in gonadal histology were used to determine the reproductive cycles of three trochid gastropods commonly found along the Transkei coast. They were dioecious, the sexes being evenly distributed both in terms of numbers and size. Despite some asynchrony, *Monodonta australis* had a distinct reproductive cycle with a short inactive period during the winter, gonadal development coincided with increasing sea temperatures and spawning took place from late summer to autumn. Both *Oxystele tabularis* and *O. variegata* exhibited asynchronous intermittent spawning throughout the study period. However, intensified spawning activity by *O. tabularis* was noted between April and September. The reproductive cycles and mechanisms of these trochids are compared with those elsewhere.

INTRODUCTION

Trochid gastropods are amongst the most conspicuous intertidal grazers in many parts of the world. Three species: *Monodonta australis* Lamarck, 1822, *Oxystele variegata* (Anton, 1839) and *Oxystele tabularis* (Krauss, 1848) are commonly found along the Transkei coast. The latter species is abundant throughout the intertidal zone, whereas *M. australis* and *O. variegata* are restricted in distribution to the upper littoral. Modern classifications of the family Trochidae treat *Oxystele* as a subgenus of *Diloma* Philippi, 1845, however, the name is so firmly entrenched in the South African literature that a change has been deemed injudicious (Kilburn & Rippey, 1982). This paper describes the reproductive cycles of the afore-mentioned trochids on the basis of changes in gonadal histology.

Little is known of the biology of trochid gastropods in southern Africa. The zonation, population dynamics and growth of *O. variegata* at Dalebrook on the Cape Peninsula have been described by Mcquaid (1982, 1983). The breeding cycle of this population was established by Joska & Branch (1983) from changes in the ratio of gonadal/somatic dry weight. The reproductive modes of other South African trochids have not been studied previously. Observations on the breeding cycle of trochids elsewhere have been made by Williams (1965), Desai (1966), Duch (1969). Underwood (1972a, 1974) and Grange (1976).

METHODS

At monthly intervals, between August 1982 and September 1983, specimens of *M. australis, O. tabularis* and *O. variegata* were collected from the shore at Hluleka (31 49′S, 29 19′E). All collections were made at spring low tides. Samples of 20 to 30 large specimens of each species were taken. It was not always possible to find this many *O. variegata.* Each individual was measured, either along the columellar axis in the case of *M. australis*, or across the maximum shell width in the case of the *Oxystele.*

Portions of the gonad and surrounding digestive gland were removed, fixed in either Bouin's or 10% formol-saline prior to routine preparation for histological examination. The embedded material was sectioned at 7 μm then 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). These maturity indices are based on those described by Orton, Southward & Dodd (1956) for the limpet *Patella vulgata.* Stage PS represents a gonad in which there was evidence of partial loss of gametes from the follicles. It could not be ascertained whether such follicles would continue to discharge until they emptied or whether they would produce more gametes and revert back to stage d_3 in preparation for further spawning. Quantitative analyses of some ovarian sections were also made by counting the numbers of pre- and post-vitellogenic oocytes in 5 to 10 microscopic fields at 400× magnification.

Table 1. Stages in the reproductive cycle of trochid gastropods.

Stage	Contents of follicles: Male	Contents of follicles: Female
Developing		
d_1	Some spermatogonia, mainly spermatocytes	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	Most oocytes now medium to large with vitellogenesis well advanced. Some small oocytes remain attached to trabeculae
d_3	Some spermatocytes, but spermatids and spermatozoa now predominant	Majority of oocytes large and of uniform size, surrounded by a basophilic jelly layer. Few small oocytes remain attached
Ripe	Follicle full of spermatozoa and spermatids. Few spermatocytes present	Uniform mass of large eggs with only traces of original trabeculae present
Spawned		
ps	Follicles show partial loss of spermatozoa	Less uniform in appearance. Mature oocytes still abundant but several gaps evident indicating partial spawning
sp	Most follicles empty a few with residual spermatozoa and spermatids	Pronounced gaps with a few residual mature oocytes. Small oocytes present on trabeculae

RESULTS

Monodonta australis

A total of 406 individuals were dissected, 205 of these were males and 201 females. There were no significant deviations from the expected 1:1 sex ratio nor could any difference in the size frequency distribution between sexes be detected. Specimens examined ranged in size from 13 to 30 mm. The ovary of *M. australis* retained a dark green pigmentation throughout the reproductive cycle. The testis underwent a colour change from grey-green (August 1982) through fawn (October 1982) to cream (January to March 1983) and then back to grey-green (June to September 1983).

The subjective staging of gonad development (Fig. 1) indicated little gametogenic synchrony, individuals in several developmental stages being present in most samples. From August 1982 to February 1983 the population showed a progressive increase in gonadal development. Ripe, pre-spawning female *M. australis* were evident between December 1982 and February 1983 and in August 1983. There was no evidence of cytolysis or resorption of unshed mature oocytes in spent females. Ripe males comprised a major proportion of the population in May and June 1983, but were also recorded in November 1982, February and August 1983. Relatively few *M. australis* were found in a spent or in an early phase of development which suggests that the resting stage between reproductive cycles is of short duration.

The percentage of mature oocytes increased gradually from August reaching a peak in January–February (Fig. 2a). Spawning took place between February and June, as indicated by the declining percentage of mature oocytes present in the ovaries. From August onwards the proportion of mature oocytes began to rise again.

Oxystele tabularis

A total of 398 specimens were examined, 186 of these were female and 212 male. There were no significant departures from the expected 1:1 sex ratio nor any differences in the size frequency

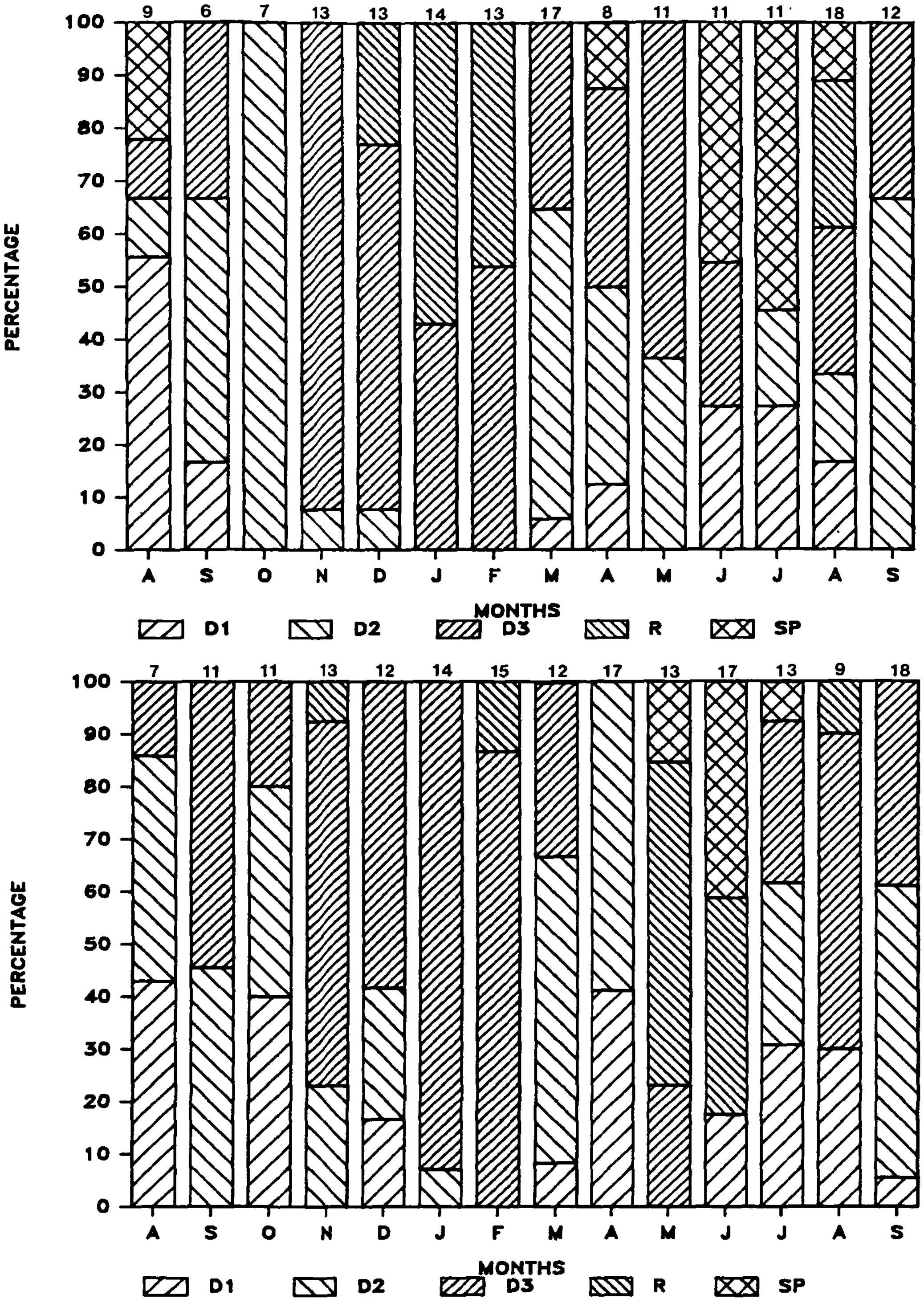
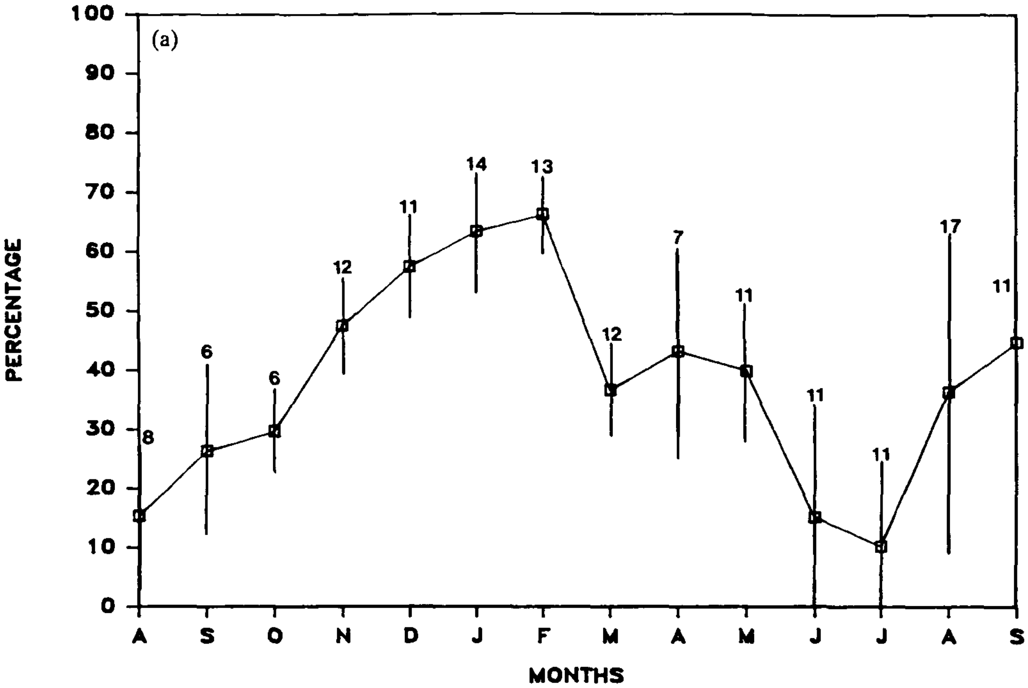


Fig. 1. The reproductive cycle of (a) female and (b) male *Monodonta australis* based on the proportion of the population at various maturity stages (d_1, d_2, d_3 developing; r, ripe; ps, partially spawned; sp, spawned). Numbers represent sample size.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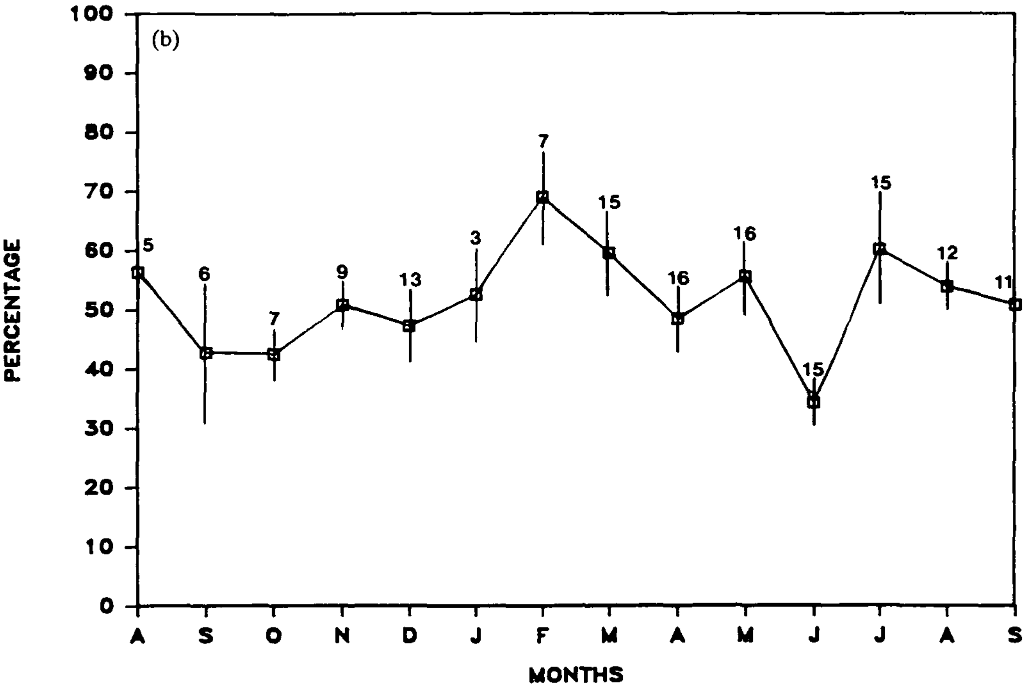
(b)
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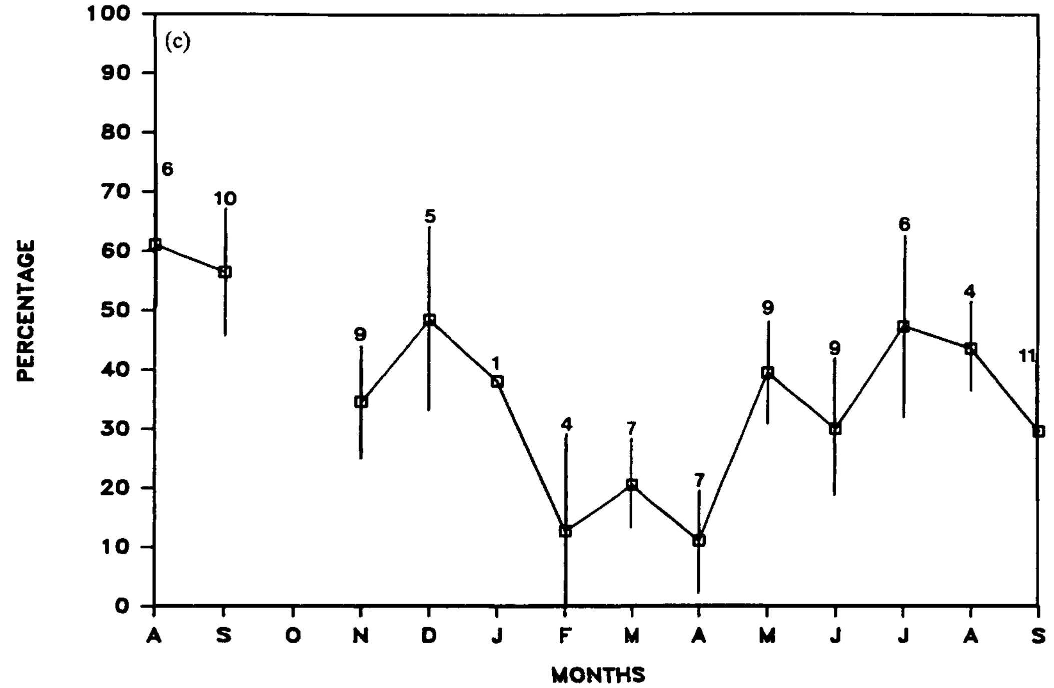

Fig. 2. Reproductive cycles of three trochid gastropods as indicated by the percentage of mature oocytes present in sectioned material (a) *Monodonta australis* (b) *Oxystele tabularis* and (c) *Oxystele variegata*. Vertical bars indicate standard deviations and numbers above the bar show the sample size.

distribution between sexes. Animals dissected ranged in width from 7 to 16 mm. As reproductive development progressed the testes changed colour from brown through green to orange or pink. The ovary retained a dark green pigmentation throughout the reproductive cycle.

The occurrence of individuals at various developmental stages in the monthly samples indicated that gametogenesis at the population level was asynchronous. From September 1982 to March 1983 *O. tabularis* underwent a gradual progression in gonadal development (Fig. 3). Ripe, pre-spawing females were found throughout the study period but were particularly common in August 1982 and from February to March 1983. Between April and September 1983 partially spawned females predominated. Spent females were observed between May and July. Progression of gonadal development took place at a slower rate in male *O. tabularis* with the majority of individuals being at stage d_2 between August and November 1982, and at stage d_3 from December 1982 to May 1983. Ripe males comprised a major proportion of the population in July to August 1983, but were also found in February and May. The percentage of ripe oocytes present in *O. tabularis* ovaries fluctuated between 34 and 69%, with no trends apparent (Fig. 2b).

Oxystele variegata

A total of 222 individuals were sectioned, ranging in width from 10 to 26 mm. There were no significant differences from the expected 1 : 1 sex ratio. No differences were found in the size frequency distributions of male and female specimens. Changes in the pigmentation of the gonads during the reproductive cycle were similar to those described in *O. tabularis*.

Gametogenesis was asynchronous, as indicated by the occurrence of individuals at various developmental stages in the monthly samples. No distinct trends in the reproductive cycle were detected (Fig. 4) possibly as a result of small sample size. Ripe females were found throughout the study period with some indication of an intensification of spawning activity in September 1983. This basically concurs with the findings of Joska & Branch (1983) on the reproduction of *O. variegata* in the Cape. They concluded that

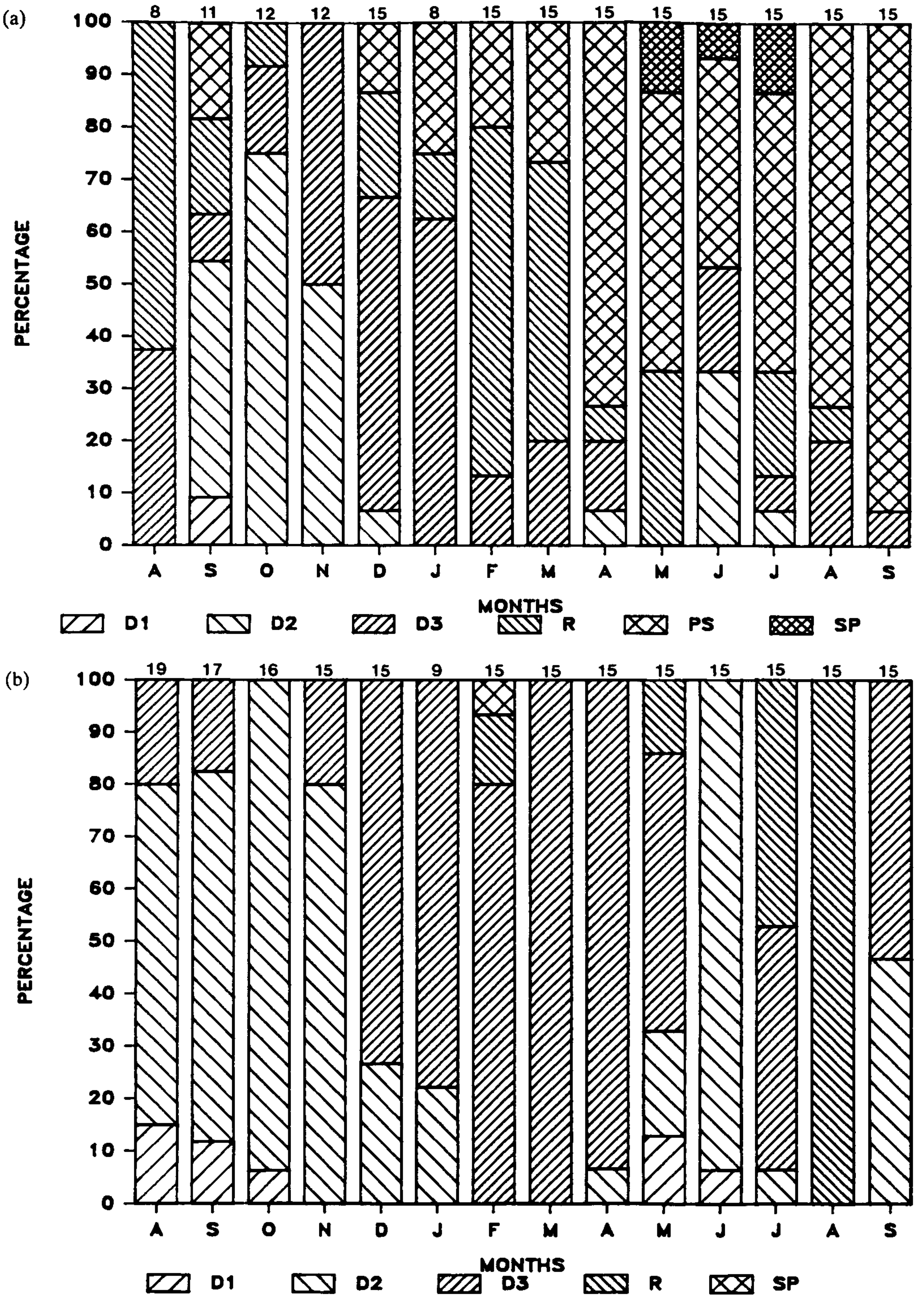

Fig. 3. The reproductive cycle of (a) female and (b) male *Oxystele tabularis* based on the proportion of the population at various maturity stages. (Abbreviations as in Fig. 1).

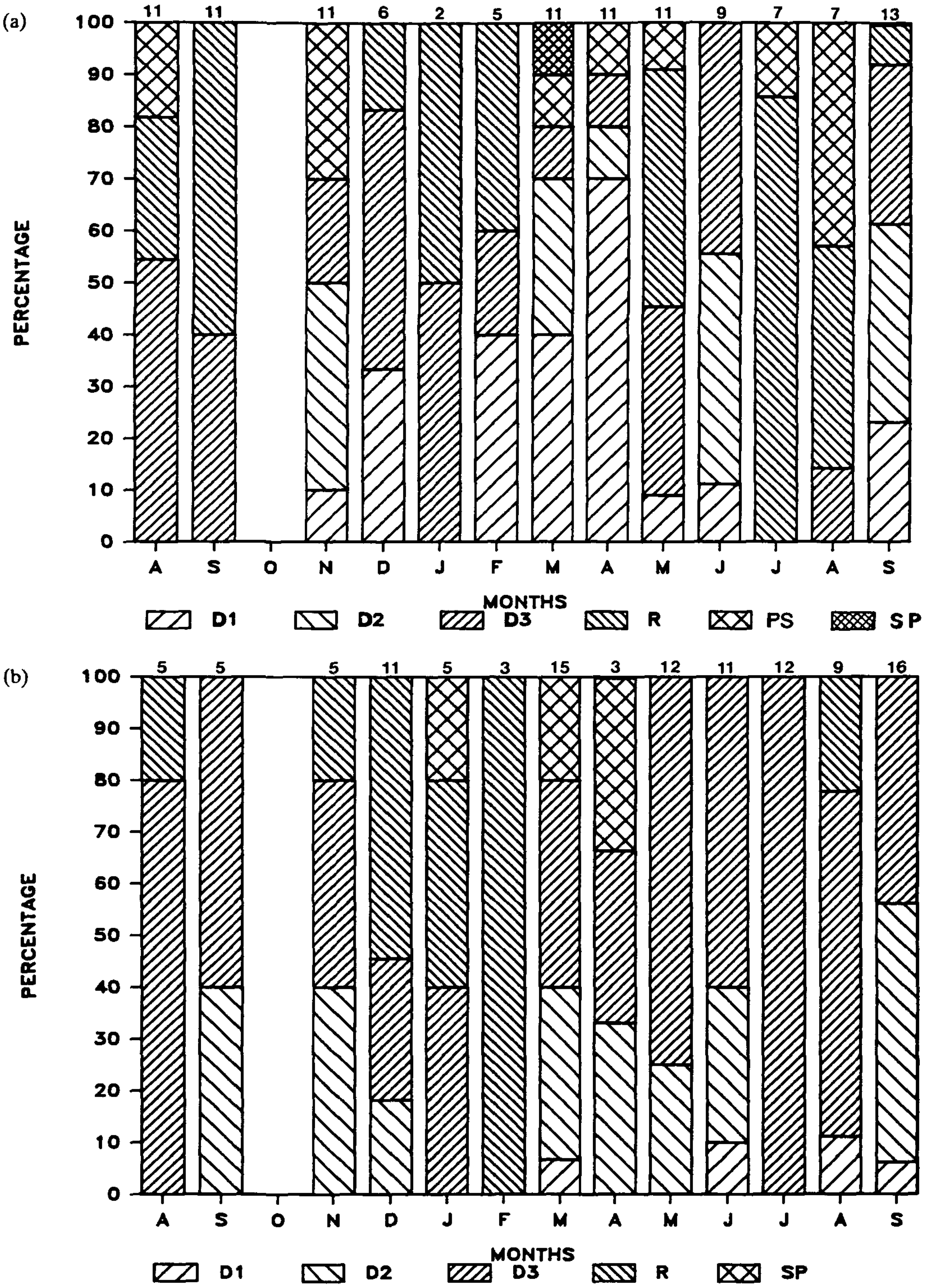

Fig. 4. The reproductive cycle of (a) female and (b) male *Oxystele variegata* based on the proportion of the population at various maturity stages. (Abbreviations as in Fig. 1).

this trochid was probably capable of spawning throughout the year, with increased activity in February and between September and October. On the Transkei coast males at an advanced stage of development were prevalent. Insufficient specimens were obtained to draw any conclusions from the analysis of percentage mature oocytes present in the ovaries (Fig. 2c). The occurrence of partially spawned females suggests that *O. variegata* may spawn piecemeal, as would also appear to be the case in *O. tabularis*.

DISCUSSION

Histological sections revealed that the mature oocytes of *M. australis, O. tabularis* and *O. variegata* were enclosed in a gelatinous coat. Simpson (1977) considered such a covering to be indicative of broadcast spawning and external fertilization. Several trochids have been identified as broadcast spawners, releasing their gametes freely into sea water, these include *Austrocochlea constricta* (Underwood, 1974); *Cantharidus coruscans* (Simpson, 1977); *Gibbula cineraria, Gibbula magus* and *Gibbula umbilicalis* (Robert, 1902); *Monodonta lineata* (Desai, 1966) and *Trochus niloticus* (Moorhouse, 1932). However, the mode of gamete release is not consistent amongst the Trochidae. Some species deposit their eggs in a jelly mass or ribbon: *Calliostoma papillosum* and *Calliostoma zizyphinum* (Lebour, 1936; and Crofts, 1955); *Cantharidus exasperatus* and *Cantharidus striata* (Robert, 1902); *Euchelus gemmatus* (Duch, 1969); *Gibbula tumida* (Gersch, 1936) and *Margarites helcinus* (Thorson, 1935). No brooding or laying of egg cases were observed in the Transkeian trochids.

There are no phylogenetic or geographic relationships amongst the Trochidae with respect to the pattern and timing of reproductive cycles. Both *O. tabularis* and *O. variegata* appear to breed continuously throughout the year, as do *Austrocochlea constricta* (Underwood, 1974), *Cantharidus coruscans* (Simpson, 1977) and *Gibbula cineraria* (Underwood, 1972a). Other species have well-defined reproductive cycles with distinct periods of inactivity, gametogenesis and spawning. Gametogenic development in *M. australis* coincided with increasing sea temperature (18° to 23°C) and spawning took place in late summer. Similar cycles have been reported in two British trochids, *Gibbula umbilicalis* and *Monodonta lineata* (Williams, 1965; Desai, 1966; Underwood, 1972a; and Garwood & Kendall, 1985). Grange (1976), however, has shown that the New Zealand trochid *Zediloma atrovirens* ripens as the sea temperature declines during autumn–early winter.

In broadcast spawners synchronization of gametogenesis within the population and the simultaneous release of gametes by males and females clearly enhances the likelihood of successful fertilization. Many broadcast spawners maximize their chance of reproductive success by having restricted, synchronized breeding periods (Giese, 1959). Synchronization of spawning activity is also thought to be important in continuous reproducers reliant on external fertilization (Creese & Ballantine, 1983). The three gastropods studied did not show the degree of synchrony expected of broadcast spawners. They all exhibited asychronous gametogenic development and spawning. Such reproductive cycles have been noted previously in broadcast spawning trochids (Williams, 1965; Desai, 1966; Simpson, 1977; Joska & Branch, 1983). The two continuous breeders, *O. tabularis* and *O. variegata*, appeared to spawn piecemeal. Such partial spawning activity, in which only a few ripe gametes are liberated at a time has been observed in trochids by Williams (1965) and Underwood (1972a).

Various other mechanisms have been proposed to enhance and maximize the chances of successful fertilization by broadcast spawners. Pair formation and/or aggregation in groups has been reported in several trochids (Desai, 1966; Duch, 1969; Simpson 1977). Both *O. tabularis* and *O. variegata* occur in clusters which ensures the close proximity of the sexes during spawning. Although development and spawning appeared to be asychronous within the population the possibility of group synchronism cannot be discounted. Several exogenous factors have been implicated in the co-ordination of spawning activity in trochid gastropods. Grange (1976) has shown that vigorous water movement during rough seas induced *Melagraphia aethiops* and *Z. atrovirens* to release gametes. This is unlikely to induce spawning in trochids on the Transkei coast since they are subjected to continuous heavy surf. Increasing temperature has been found to enhance spawning in some species (Gersch, 1936; Ducros, 1957; and Underwood, 1972b). Stimulatory substances released by the gonad have also been found to induce spawning by individuals of the opposite sex (Robert, 1902).

The reproductive strategies exhibited by the three species examined may constitute adaptive responses to the unpredictable temperature regime off the Transkei coast. The sea temperature ranges seasonally between 18° and 23°C, however, frequent incursions of cold water (10°C), resulting from upwelling, are experienced (Macnae, 1962). In the event of a sudden drop in sea temperature asychronous intermittent spawning would ensure that only a small proportion of potential recruits are lost at any one time. The prolonged recruitment from continuous dribble spawning may be an additional advantage in unpredictable environments (Newell, Hilbish, Koehn & Newell, 1982).

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