

## Short Communications

### Reproductive cycle of the supralittoral gastropod *Littorina kraussi* (Rosewater, 1970)

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The reproductive cycle of *Littorina kraussi* was determined on the basis of changes in gonadal histology over a 14-month period. This animal is dioecious, the sexes being evenly distributed both in terms of numbers and size. Despite some asynchrony within the population, *L. kraussi* showed a well defined reproductive cycle. Gonadal proliferation took place from August to January with peak spawning taking place from December to March.

Die reprodktiewe siklus van *Littorina kraussi* is bepaal op die basis van verandering in gonadiëse histologie oor 'n tydperk van 14 maande. Die dier is eenslagtig en die geslagte is eweredig versprei, beide in terme van getalle en grootte. Ten spyte van asinkronie binne die bevolking, het *L. kraussi* nogtans 'n goed gedefinieerde reprodktiewe siklus. Gonadiëse proliferasie het plaasgevind tussen Augustus en Januarie, met die piek kuitskietperiode vanaf Desember tot Maart.

Several criteria have been used to define the reproductive cycles of littorinid gastropods. Temporal changes in the incidence of copulation and spawning have frequently been described (Linke 1933; Lenderking 1954; Fretter & Graham 1962; Struhsaker 1966; Borkowski 1971; Pilkington 1971; Berry & Chew 1973; Gallagher & Reid 1974). Seasonal changes in the morphology and histology of the reproductive tract have also been outlined (Williams 1964; Palant & Fishelson 1968; Bergerard 1971; Fish 1972; Underwood 1974; Jordan & Ramorino 1975; Goodwin 1978). Spawning periods have also been inferred from data on the recruitment of juveniles (Underwood 1974; Potter 1984). This paper describes the reproductive cycle of the common supralittoral gastropod *Littorina kraussi* solely on the basis of changes in gonadal histology observed during a 14-month study.

Specimens of *L. kraussi* were collected monthly, between August 1982 and September 1983, from rocky shores within Hluleka Nature Reserve, Transkei (31°49'S/29°19'E). All samples, varying in size from 10 to 25 animals, were taken at spring low tide. The shell height of each individual was recorded prior to dissection. Portions of the gonad and interdigitating digestive gland were removed, fixed in either Bouin's fluid or 10% formal-saline, embedded in paraffin wax and sectioned at 7 µm. The sections were stained with Delafield's haematoxylin and counterstained with eosin. Sections were allocated a maturity index based on the criteria given in Table 1. Although some cognizance of follicle contents is used, the arbitrary stages are also based on the relative size and apposition of gonadal follicles within the connective tissue surrounding the digestive gland.

A total of 255 sexually mature individuals, ranging in size from 7 to 24 mm shell height, were examined. The sex ratios found in the monthly collections were compared using the

$\chi^2$  test, and only three samples (August, September and November 1982) showed significant departures from a 1:1 ratio ( $p < 0,005$ ). There were no differences in the size distribution of male and female *L. kraussi*.

Detailed descriptions of the morphology and histology of the genital systems of littorinids are given in Linke (1933), Fretter & Graham (1962) and Bedford (1965). The gonad is situated in the visceral apex overlying the digestive gland. The gonoducts are found along the columellar surface of the visceral coil. In males the duct dilates to form the seminal vesicle whilst in females it becomes convoluted before linking up with the receptaculum seminis. Examination of sectioned material revealed six distinct developmental stages in the gonads of *L. kraussi*: inactive (in), early ( $d_1$ ), mid ( $d_2$ ), and late developing ( $d_3$ ), ripe (r) and partially spent (ps) (Table 1).

All the ovarian sections inspected contained both immature and mature oocytes. These were easily distinguished on the basis of size and staining properties, as described by Underwood (1974). Cytolysis of unshed mature oocytes was evident in partially spent animals. There was considerable variation in the extent of cytolysis, in some instances it appeared to be restricted to a few follicles, whereas in others extensive cytolysis was evident throughout the gonad. There was no relationship between the extent of cytolysis and size of individual.

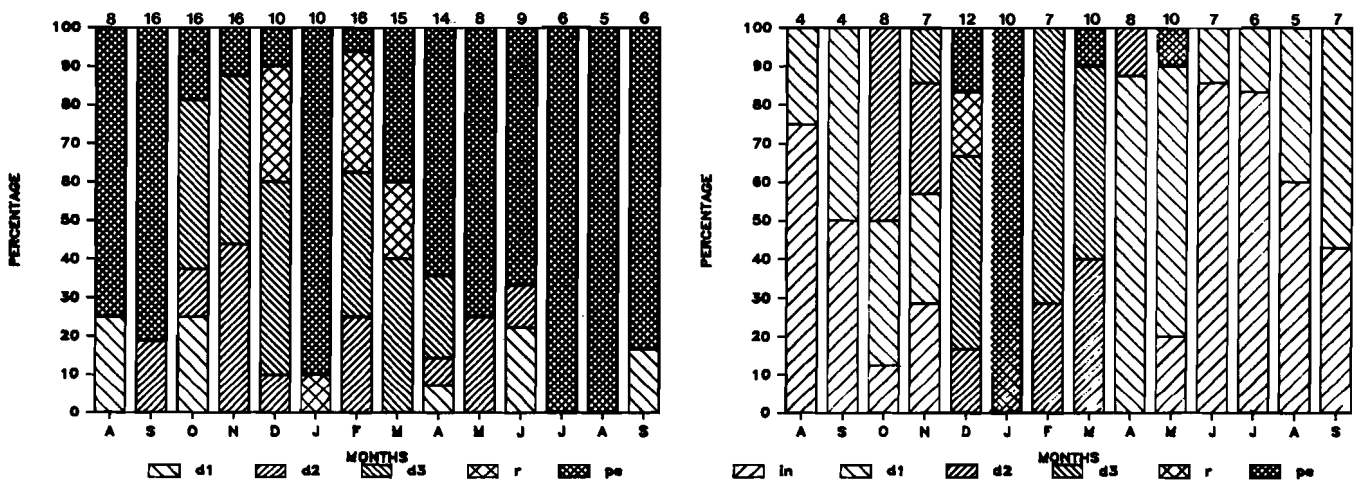
Within the gonadal follicles of all male *L. kraussi* the various stages of spermatogenesis were observed simultaneously. In addition to the gametogenic cells several larger bodies, characterized by a finely vacuolated cytoplasm, were found lying alongside spermatozoa in the lumen of the follicles. The term nurse-cells has been given to these bodies, as they are thought to aid in the transfer of sperm to females (Fretter & Graham 1962). Spermatozoa, apparently attached to these nurse-cells, were frequently observed in an unorientated mass within the seminal vesicle. Phagocytosis of ripe spermatozoa and nurse-cells, by amoebocytes, was evident within gonadal follicles and ducts. Degeneration of ripe eggs and phagocytosis of male sexual products have been noted in other littorinids (Linke 1933; Palant & Fishelson 1968; Underwood 1974). No attempts have been made to assess the energetic cost of these processes.

The subjective staging of gonadal development indicated little gametogenic synchrony within the population (Figure 1), individuals in several developmental stages being present in each of the samples. From August to January *L. kraussi* showed a progressive increase in gonadal development. Ripe, pre-spawning animals were found from December to March. In female *L. kraussi* development appeared to be a continual process, there being no well-defined period of inactivity. Partially spent individuals, in which cytolysis of unspawned mature oocytes was evident, also showed signs of continued gametic proliferation. These animals may be capable of spawning again later in the reproductive cycle. Totally spent individuals were not observed in female *L. kraussi* making it difficult therefore to separate late spent from early developing littorinids. Inactive males, with rudimentary follicles devoid of gametic activity, were prevalent from June to September.

Little is known of the reproductive biology of South African littorinids. Histological studies indicate that *L. kraussi* spawns during summer (December to March) on both the Transkei (this study) and Natal coasts (Potter 1984). From monthly counts of juveniles and copulating pairs at Chaka's Rock, Natal, Potter (1984) has established that *Nodolittorina natalensis* spawns in summer, whereas *L. africana africana*,

**Table 1** Arbitrary stages in the reproductive development of *Littorina kraussi*

Stage	Relative size of follicles	Male follicle contents	Female follicle contents
Inactive	Rudimentary follicles visible within the connective tissue matrix surrounding the digestive gland.	Lumina packed with undifferentiated tissue, no spermatogenic cells seen.	
Developing d <sub>1</sub>	Follicles still small.	All stages of spermatogenesis now apparent, also a few nurse-cells evident. Large quantities of undifferentiated tissue still present.	Much intrafollicular material. Some immature oocytes at the edge of the follicles and a few mature oocytes in the lumina.
d <sub>2</sub>	Follicles enlarged, occupying more space within the connective tissue matrix.	Quantity of undifferentiated tissue clearly reduced, contents otherwise as in d <sub>1</sub> .	Numerous immature oocytes at the edge of the follicles, similar number of mature oocytes lying free in the lumina. Little intrafollicular material present.
d <sub>3</sub>	Follicles large, occupying most space within the connective tissue matrix.	No undifferentiated tissue. Follicles packed with all stages of spermatogenesis plus the occasional amoebocyte. Vesicula seminalis densely packed with spermatozoa and nurse-cells.	Densely packed with mature oocytes, some immature oocytes also present.
Ripe r	Follicles closely apposed to each other and the digestive gland.	Contents as above, some evidence of dispersion of spermatozoa and nurse-cells. Vesicula seminalis densely packed as above.	Follicles partially empty, numerous mature oocytes and a few immature oocytes still evident.
Post-spawning ps	Follicles reduced in size, connective tissue evident in the interstices.	All stages of spermatogenesis still evident, but clearly reduced in numbers. Numerous amoebocytes evident within follicles. Vesicula seminalis invaded by numerous amoebocytes, dispersal of contents also seen.	Some mature and immature oocytes present. Degeneration of mature eggs evident, their contents having been released into the lumina.



**Figure 1** The reproductive cycle of (a) female and (b) male *Littorina kraussi* based on the proportion of the population at various maturity stages (in, inactive; d<sub>1</sub>, d<sub>2</sub>, d<sub>3</sub> developing; r, ripe; ps partially spawned). Numbers represent sample size.

despite evidence of a summer peak in spawning activity, breeds throughout the year. In the Western Cape, McQuaid (1981) found *L. africana knysnaensis* to recruit throughout the year with peak settlements in winter (May to June) and summer (December to January). These differences in spawning periodicity may reflect variations in geographical distribution of the species. The temperature regime may be suitable for continuous reproduction in the warm temperate *L. africana*, whereas spawning in the two tropical species *L. kraussi* and *N. natalensis* may be restricted to the warmer months towards their southern limit of distribution (Potter 1984).

Detailed comparison of the present study with that of Potter (1984) revealed considerable differences in the reproductive

cycles of animals at Hluleka and Chaka's Rock. At the latter site, Potter (1984) found that males maintained a high level of gametogenic activity throughout the year whereas females were virtually inactive between April and November. The present study, however, indicated a definite period of inactivity in male *L. kraussi* (June to September) and although cytolysis was evident in females, gametic production appeared to be continuous. Reasons for these differences remain obscure.

Many supralittoral littorinids, including *L. kraussi* (Lasiak & Dye, pers. obs.) exhibit pelagic development involving the release of planktonic egg capsules and planktotrophic larvae (see Mileikovsky 1975, for review). These animals are dependent on some means of facilitating the delivery of egg capsules

to water. This problem has been overcome by downshore migrations during the breeding season (Lysaght 1941; Lebour 1945; Kojima 1959; Pilkington 1971) and by rhythmic spawning activity concomitant with spring tides (Lysaght 1941; Lenderking 1954; Struhsaker 1966; Borkowski 1971; Berry & Chew 1973; Gallagher & Reid 1974; Grahame 1975). In other gastropods it has been shown that spawning activity is stimulated by rough seas (Rao 1973; Grange 1976). A further possibility is the release of eggs into littoral fringe tide pools. Downshore migration of mature female *L. kraussi* prior to spawning has been observed on the Natal coast (Potter 1984). Whether this species has other adaptations promoting the successful delivery of eggs has yet to be established.

Histological studies on the reproductive systems of littorinids have met with varying success. Goodwin (1978) found that the gonads of *L. obtusata* maintained a high level of development throughout the year. He found no significant variations in the relative proportions of different spermatogenic stages, nor did his visual examination of ovarian sections produce any clear trends. Similarly, Jordan & Ramorino (1975) observed that most of the *L. peruviana* they examined had ripe gonads throughout the year. However, clear annual rhythms of development and degeneration have been demonstrated in the gonads of *L. kraussi* (this study), *L. punctata* and *L. neritoides* (Palant & Fishelson 1968) and *L. unifasciata*, *N. pyramidalis* and *Bembicium nanum* (Underwood 1974). To provide a complete picture of reproductive periodicity histological studies should be combined with field observations on the incidence of copulation and the settlement of juveniles.

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