Observations on the reproductive cycles of *Cellana capensis* (Gmelin, 1791) and *Patella concolor* Krauss, 1848 (Gastropoda : Prosobranchia : Patellidae)

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The reproductive periodicities of the patellid limpets *Cellana capensis* and *Patella concolor* were determined from changes in macro- and microscopic appearance of the gonads over a 14-month period. Both species appear to have protracted breeding periods with several peaks in spawning activity. Problems encountered with the application of standard sampling and analytical methods to species with such cycles are discussed.

Veranderinge in makro- en mikroskopiese voorkoms van die gonades van *Cellana capensis* en *Patella concolor* is gebruik om die reproduktiewe siklusse van hierdie diere oor 'n tydperk van 14 maande te bepaal. Beide spesies het klaarblyklik 'n verlengde broeiperiode met verskeie pieke van kuitskiet. Probleme met die toepassing van standaardmonsterneming en analitiese metodes by spesies met sulke siklusse word bespreek.

Most studies on the reproductive biology of intertidal molluscs which inhabit the rocky shores of southern Africa have been carried out in the cooler waters surrounding the Cape Peninsula (Newman 1967; Branch 1974 ; Griffiths 1977 ; Joska & Branch 1983). Little is known of the biology of subtropical east coast species. The present study forms part of an extensive survey of the reproductive cycles of intertidal molluscs commonly found on the Transkei coast (Lasiak 1986a, b, 1987, in press). In this paper data on the reproductive periodicity of two patellid limpets *Cellana capensis* and *Patella concolor* are presented.

A brief description of the ecology of these limpets is given in Branch (1975). They have similar geographical distributions, zonation and feeding habits. Both are generalized browsers and are found predominantly in the balanoid zone. *C. capensis* is found from Port Alfred up into East Africa, whereas, *P. concolor* occurs from Algoa Bay up to southern Mozambique.

Methods

At approximately monthly intervals, between August 1982 and September 1983, specimens of *C. capensis* and *P. concolor* were collected from intertidal sandstone platforms at Hluleka, Transkei (31°49'S / 29°19'E). Two subpopulations of *C. capensis* were sampled, one from the upper (HT) and the other from the mid-balanoid zone (MT). Spatially random collections of 20 to 30 of the larger individuals were made during spring low tide. Animals were preserved in 10% formol-seawater for a minimum period of two months to allow the gonad to harden into a compact mass.

The shell length of each individual was recorded prior to dissection. The gonad was exposed by cutting the foot away from the visceral mass and displacing it anteriorly. A subjective classification of gonadal development, based on the size of the gonad relative to the visceral mass, was made for each specimen. This technique followed the modification of Orton, Southward & Dodd (1956) classification scheme proposed by Ballantine (1961), under which six developmental stages are recognized. From this, the mean developmental stage of the population was estimated for each monthly sample.

To verify this classification scheme, each month subsamples of gonads at different developmental stages were routinely prepared for histological examination. The tissue was embedded in paraffin wax, sectioned at 7 μm, stained with Delafield's haematoxylin and counterstained with eosin. The sectioned material was allocated a subjective maturity index based on the differing proportions of various gametogenic cells present, as used for the gastropod *Turbo coronatus* (Lasiak 1986a). Quantitative analyses of some ovarian sections were made by counting the numbers of pre- and post-vitellogenic oocytes in 10 microscopic fields at 400× magnification.

Results

Changes in the mean monthly gonad indices (G.I.) of male and female *C. capensis* MT are shown in Figures 1a & b. Superimposed on these are box and whisker plots which indicate the central tendency of the data and the extreme values for each of the monthly samples. Although the male gonads tended to be larger than the female gonads the patterns of development were similar. Between September and November 1982 a sharp decline in G.I. was evident, indicating that spawning had taken place. There was no evidence of a distinct resting phase; redevelopment of the gonad appeared to take place immediately. Peak gonadal development was observed in February 1983. The subsequent gradual decline in G.I. suggested a protracted spawning period.

The subjective staging of histological sections showed that male *C. capensis* MT maintained a higher state of development than females. (Figures 2a & b). Although animals in breeding condition were found throughout most of the study period, ripe individuals were particularly prevalent in August/September 1982, January/February and September 1983. Sharp drops in the proportion of mature oocytes indicate that major spawnings took place between September and October 1982 and

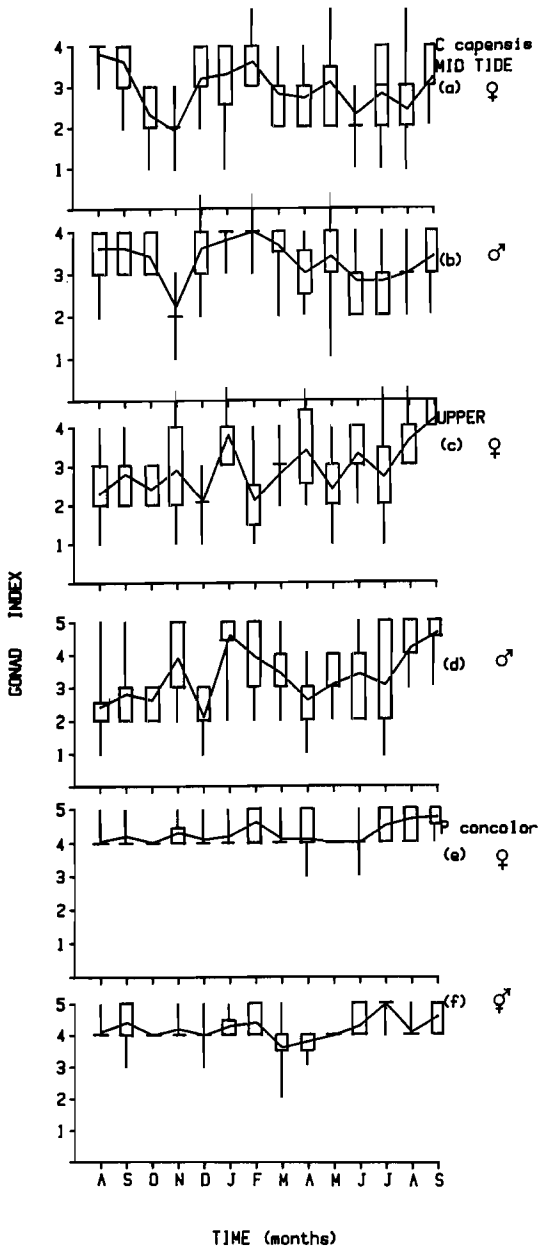

Figure 1 The reproductive cycles of (a) female MT *Cellana capensis*, (b) male MT *C. capensis*, (c) female HT *C. capensis*, (d) male HT *C. capensis*, (e) female *Patella concolor* and (f) male *P. concolor* determined on the basis of subjective visual grading of gonadal development. The mean monthly gonad index (G.I.) is shown superimposed on box and whisker plots which indicate central tendencies and extreme values each month.

from February to April 1983 (Figure 3a).

Comparison of box and whisker plots (Figures 1a–d) indicated that development in *C. capensis* HT was less synchronous than that exhibited by *C. capensis* MT. Spawning in male *C. capensis* HT took place between November and December 1982 and from January to April 1983. Greater variability was evident in the G.I. values of female *C. capensis* HT which suggests that spawning activity was poorly synchronized. Some spawning took place between November and December, January and February, and from April to May. Subjective staging of histological sections indicated two peaks in gonadal activity from August to October, and from January to May (Figures 2c & d). The latter was particularly evident in male *C. capensis* HT. Fluctuations in the percentage of mature oocytes suggest that spawning occurred between September and December and from April to June (Figure 3b).

Marked differences in the gonad condition of *P. concolor* were not observed. A high degree of development was maintained throughout the study period, as indicated by the G.I. (Figures 1e & f). Although the subsamples retained for histological analysis were small, distinct trends in the proportional representation of mature oocytes were apparent suggesting that spawning took place between September and November 1982 and from February to March 1983 (Figure 3c).

Discussion

Several methods have been used to determine reproductive periodicity in limpets. Extensive use has been made of subjective gradings based on the visual appearance of the gonad, in terms of size, shape, colour and texture (Orton *et al.* 1956 ; Fritchman 1961a, b & c ; Ward 1966 ; Blackmore 1969 ; Rao 1973 ; Picken 1980 ; Creese & Ballantine 1983). Widespread use of this technique reflects the fact that it requires virtually no equipment and relatively little skill, it is also quick and easy to apply. This technique, coupled with the estimation of gonad indices has, in the past, been used to accurately pinpoint the spawning periods of several South African patellid limpets (Branch 1974). However, no marked differences in the visual appearance of *P. concolor* gonads were observed during the present investigation. Although sharp drops in the G.I. value were evident in both MT and HT *C. capensis*, spawning periods could not be clearly defined solely from visual subjective gradings. The combination of G.I. and histological techniques used in the present study, however, indicated that both *C. capensis* and *P. concolor* have protracted breeding periods with several peaks in spawning activity. The afore-mentioned studies, employing subjective gradings, dealt with species exhibiting well-defined reproductive cycles with single annual spawning periods. However, the efficacy of this technique is clearly dependent not only on the length of the spawning season but also on the degree of gametogenic synchrony within the population.

Protracted breeding seasons have been reported more frequently in acmaeid and fissurellid limpets (Ward 1966; Underwood 1974; Creese 1980; Bretos, Tesorieri & Alvarez 1983) than in patellid limpets. The present study indicates that spawning in *C. capensis* MT took place between September and October and from February to April. However, spawning activity in *C. capensis* HT was not so well defined. This difference may reflect poorer developmental synchrony within the high shore population. Slight variations in the spawning activity of subpopulations of a related limpet *C. tramoserica* from different tidal levels have been noted by

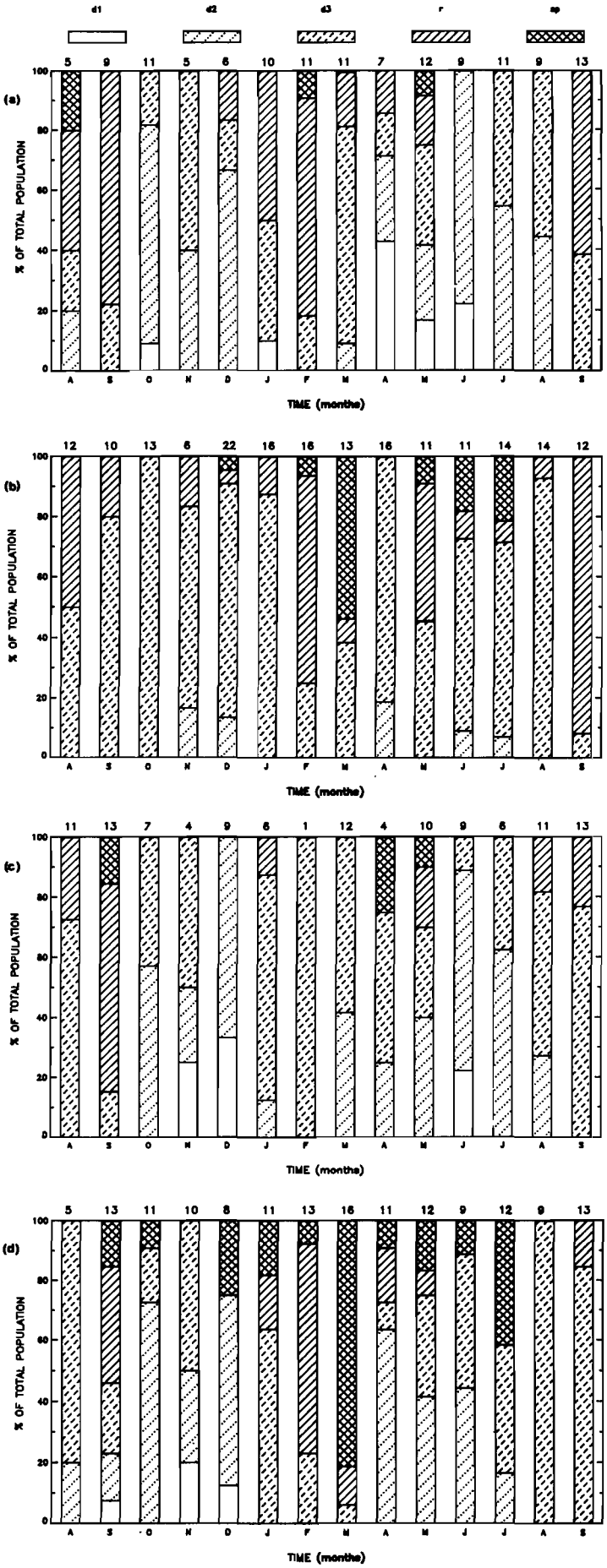

Figure 2 The reproductive cycle of (a) female MT *Cellana capensis*, (b) male MT *C. capensis*, (c) female HT *C. capensis* and (d) male HT *C. capensis* based on the proportion of the monthly sample at each maturity stage (d_1, d_2, d_3: developing; r: ripe; sp: spawned).

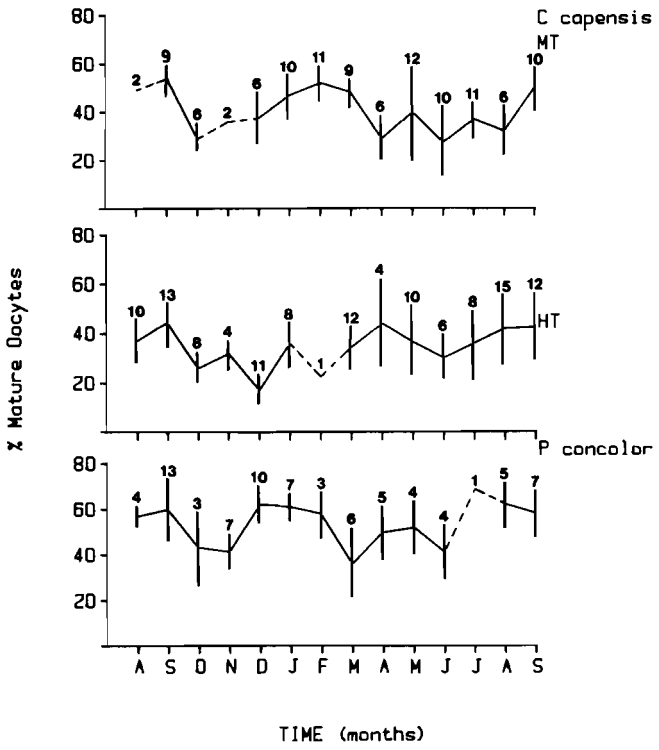

Figure 3 The reproductive cycles of (a) MT *Cellana capensis*, (b) HT *C. capensis* and (c) *Patella concolor* as indicated by the percentage of mature oocytes observed. Vertical bar indicates the standard deviation. Numbers above the bar indicate sample size.

Fletcher (1984). Most species of the genus *Cellana* exhibit protracted breeding periods with several peaks in spawning activity (Rao 1973 ; Underwood 1974 ; Creese & Ballantine 1983; Fletcher 1984). Unlike the majority of *Patella* species, which have marked annual cycles (Branch 1981), protracted breeding was evident in *P. concolor* with major spawnings occurring between September and November and from February to March. In the Western Cape, Branch (1974) noted that warm-water patellids tended to breed in spring–summer, whereas cold-water and ubiquitous species bred in autumn–winter. He also found spawning to be more protracted and less defined in populations from warmer waters. A recent study (Robson 1986) on the Natal coast has shown that *P. aphanes* also has a somewhat protracted breeding cycle involving two peaks in spawning activity between January and February and from April to June.

Further work is needed to establish whether the time spans identified reflect effective or potential spawning periods of *C. capensis* and *P. concolor*. Frequent sampling is needed to determine not only how synchronous, but also how often and when exactly spawning takes place (Creese & Ballantine 1983). It is also important that the techniques used to assess sexual development be capable of differentiating between partial and total spawnings. Both Rao (1973) and Underwood (1974) have suggested protracted breeding seasons in limpets to be associated with piecemeal spawning activity by individual limpets. However, Branch (1974) and Creese (1980) consider multiple spawnings to reflect the possibility that a variable proportion of the population may spawn throughout the breeding period. Recent studies on trochid gastropods (Garwood & Kendall 1985) have indicated that complete spawning does not always take place, it may be replaced by several partial spawnings. Histological studies involving the analysis of oocyte diameter frequencies and counts of mature oocytes per unit weight of gonad can fulfil this need. Precise knowledge of spawning extent and periodicity are needed prior to the assessment of gonadal output. Previous attempts (Branch 1975) to assess the effects of exploitation on gonadal output of *P. concolor* must be treated with caution as no information was then available on the gonadal cycle.

The relative expense, in terms of time, money and effort, involved in studies of invertebrate reproduction frequently necessitates compromises in either analytical methods and/or sampling frequency. Careful consideration needs to be given to both sampling and processing strategies. Methodology adequate for species with well-defined cycles involving a single spawning period may not be suitable for use in species exhibiting protracted spawning.

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