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Observations of the reproduction and population structure of the caenogastropod, *Gabbia vertiginosa* Frauenfeld, 1862 (Rissooidea : Bithyniidae)

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Abstract

Aspects of the reproduction and population structure of *Gabbia vertiginosa* (Bithyniidae) in the New England Tablelands, New South Wales, Australia, are described. The pattern of embryo growth from encapsulation in the pallial oviduct, deposition of fully formed embryonic snails in the habitat, to sexual maturity in the adult snail are examined. A three-year population study has shown the reproductive period of *G. vertiginosa* to commence in December and end in June/July with the possibility of three reproductive events per season.

Additional keywords: Bithynia, embryo.

Introduction

Gabbia vertiginosa Frauenfeld, 1862 (= *Gabbia australis* Tryon, 1865) is one of Australia's representatives of the family Bithyniidae (Caenogastropoda : Rissooidea) (see Ponder 2003). Other members of the family for which biological information is available are *Bithynia leachi* (Sheppard, 1823), *Bithynia tentaculata* (Linnaeus, 1758) and *Bithynia graeca* (Westerlund, 1879) (Lilly 1953; Graham 1971; Eleutheriadis and Lazaridou-Dimitriadou 1995). Most members of the family possess a calcareous operculum and prefer slow moving rivers, ponds and swampy backwaters where they live on and within vegetation in shallow, muddy substrates (Fretter and Graham 1962; McMichael 1967; Graham 1971; Ponder and De Keyzer 1998).

The shell colour of *G. vertiginosa* is a light horn, sometimes with a greenish tinge that is particularly evident on specimens collected from stagnant ponds (pers. obs.). Dark pigment contained within the epithelium of the animal is visible through the shell except in those snails that have passed through a rest period in adulthood (pers. obs.). The Bithyniidae filter feed and browse on the contents of ruptured plant cells, detritus and decaying weed (Lilly 1953). A freshwater plant common in aquatic habitats in eastern Australia, *Elatine gratioloides* (Elatinaceae), is used by *G. vertiginosa* in the New England Tablelands for food, shelter and deposition of egg capsules (pers. obs.). The distributional range of *G. vertiginosa* extends from the eastern areas of New South Wales from Sydney to southern Queensland (Ponder 2003).

Until Ponder's (2003) monograph of the Australian species, only a small amount of data on *G. vertiginosa* had been available. Simpson and Stanisic (1986) briefly discussed its ecology and distribution in the New England area and some information was provided by Ponder and De Keyzer (1998) in their overview of the family (see also Smith and Kershaw 1979). A series of observations and studies of *G. vertiginosa* were undertaken in this study to describe the reproduction and the population structure of the species. Larvae of

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trematode parasites found within snails examined during the study are described in Koch (2002, 2003, in press *a*, in press *b*).

Materials and methods

Snail collections

One particular site was chosen within the New England Tablelands for a medium-term study of *G. vertiginosa*. Within this habitat (Saumarez Road swamp, 5 km south south-west of Armidale, New South Wales, Australia: 31°50′S; 151°30′E) a large population of *G. vertiginosa* had been observed during 1999. Surveys of the snail population at this site were conducted in January, March, July and November of each year commencing July 2000 and ending in January 2003. The study area was 8 m in length and 0.5–1.5 m in width. This area was divided into 160 5-cm wide transects running from the shoreline out, with transect 0 at the northern end and transect 160 at the southern end of the habitat. Transects were chosen at random at each survey period using a table of random digits (Rohlf and Sokal 1969). The number of transects required for each survey was determined in a pilot study (March 2000) using the ratio estimation method for selecting sample units that are of irregular shape or length (Caughley and Sinclair 1994). Twelve transects were taken at each survey. Specially constructed wooden rectangles were used to mark out each transect during collection. All snails present in each transect were collected by careful and systematic sifting through the substrate and weed by hand with the intention of disturbing the habitat as little as possible. They were then placed in marked jars containing pond water for transportation to the laboratory. Sampling without replacement was the method of collection used for each survey (Sutherland 1996). During the study period, 4736 *G. vertiginosa* snails were collected. Voucher specimens are lodged in the Australian Museum (C.433803–C.433807).

Snails were dissected by carefully breaking away the shell and the tissue was examined in a cavity block under a stereomicroscope. Whole specimens were either placed immediately into absolute ethanol for future molecular studies, or in 10% neutral buffered formalin. All parasite larvae found during snail observations and dissections (another aspect of this study) were either preserved or used for infection experiments to obtain the adult worms for correct taxonomic placement of the species (see Koch 2002, 2003, in press *b*).

Water quality testing of pond water at surveys of the site was done using an Aquamerck 8024 kit produced by Merck KgaA Co. (Munich, Germany). Measurements are given in mm unless otherwise stated and, where ranges are shown, the mean is noted in parentheses.

Laboratory breeding

Larval capsules of *G. vertiginosa* (150 embryos in total) were found attached to snails and vegetation collected from Saumarez Road swamp. These capsules were retained in small glass bowls containing filtered pond water until hatching occurred and snail shell size had reached ≈ 3 mm. At this point, all snails were transferred to aerated aquaria where growth in their shell length was measured daily and recorded.

Aquaria were maintained in a laboratory open to natural light and ambient temperatures in order to closely simulate normal environmental conditions and photoperiods. Water temperatures in the aquaria ranged from 22°C between November 2000 and March 2001, to 5°C during the autumn/winter months April to June 2001 (≈ 4°C higher than average water temperatures during winter periods on the New England Tablelands (Bureau of Meteorology Australia 2002)). Snails were fed *Elatine gratioloides* collected from the habitat and commercial fish flakes and pellets. Flakes and pellets were only used when *E. gratioloides* was unavailable. At Day 220, the laboratory-bred snails were dissected and shell size and development of the reproductive organs were noted and compared against the data collected from *G. vertiginosa* harvested during surveys at the study site at Saumarez Road swamp.

Size and age measurements

Shell length (apex to the anterior tip of the aperture) was used as a guide to age and sexual maturity for both laboratory-bred snails and those taken from the natural habitat. Measurements were taken using Vernier calipers (Krist 2000). For the purposes of this study, embryos were defined as the developing snails contained within capsules, from the time of deposition on substrates to hatching from capsules (≈ 0.05–0.3 mm shell length). Juveniles were defined as those snails ranging from hatchlings (≈ 0.3 mm) to ≈ 4.5 mm shell length; snails greater than 4.5 mm shell length were classified as adults. Sexual maturity was defined as the presence of a fully formed seminal receptacle and an ovary in females and, in males, a mature seminal vesicle and testis, as studied under a light microscope.

Fig. 1. Preserved capsules of *Gabbia vertiginosa* collected from Saumarez Road swamp, Armidale, New South Wales. One capsule still contains an embryo at ~30 days after deposition; the others have hatched. Scale bar = 0.05 mm.

Results

Pre-deposition

As the embryos mature within the female, they travel along the ventral channel of the pallial oviduct towards the genital aperture. At this point in their development, the embryos had a basic snail-like appearance with the exception of the growth of the shell, which was just commencing. Once the genital aperture was reached, the embryos were encased in fully formed capsules in strings, ready for deposition on the substrate or the shell of other snails. The shell on embyros was translucent and the operculum present.

Deposition to hatching

Embryo casings consisted of two to six compartments in single strings, one embryo per compartment (Fig. 1). Embryos were translucent for about 25 days after deposition and then became opaque, although the shell remained translucent during encapsulation. Mean shell size at deposition was 0.05 mm. The deposition to hatching period was 30–34 (32) days at 22°C, during which embryonic movement could be observed when the capsules were touched.

Post hatching

Figure 2 shows the mean growth of the snails over 220 days from time of hatching. Shell size increased from 0.25–0.3 (0.275) mm to 0.3–0.4 (0.35) mm by Day 4. At Day 5,

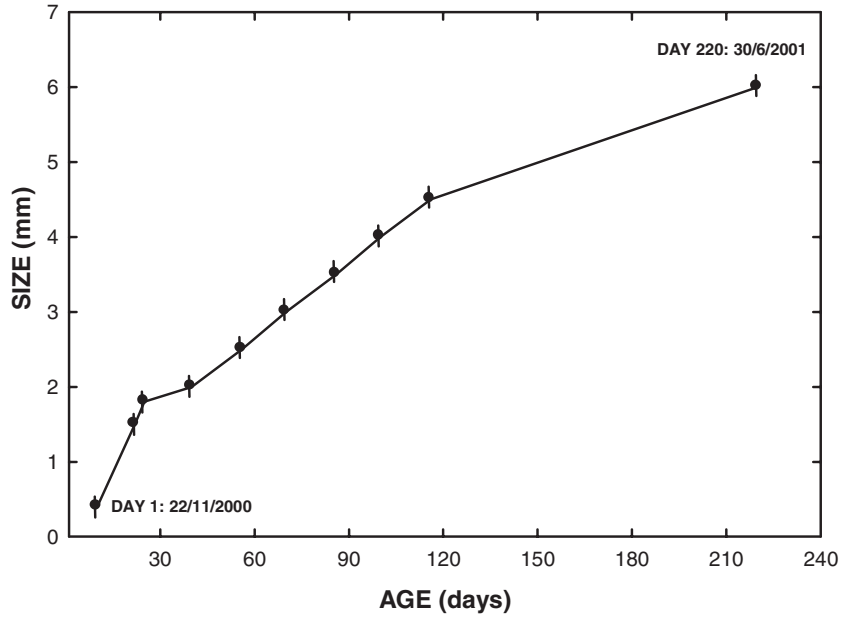

Fig. 2. Mean growth of 150 laboratory-bred *Gabbia vertiginosa* (size as shell length) over 220 days at 22°C (22 November 2000 to 30 June 2001) from newly hatched snails to sexual maturity. Error bars indicate standard deviations in snail shell lengths at each recorded day.

colouration of the shell had commenced from the apex of the whorl and down towards the outer lip of the aperture. Black pigment was also formed in the mantle and epithelial tissues. Sexual dimorphism became obvious at Day 19 (mean shell size 1.2 mm). The penis had differentiated and testicular tissue had acquired a pale orange colouration although neither the seminal vesicle nor seminal receptacle was developed. The mantle tissue was black and the rectum and faecal pellets within it were visible. By about Day 21, darkening of the shell had extended over the entire height of the spire (mean shell size 1.8 mm). Colouration of the shell was complete by about Day 35 (mean shell size 2.0 mm). Sexual maturity was complete in both sexes at about Day 135 (mean shell size 4.5 mm) with the largest shells reaching a mean of 6.0 mm by 220 days. Maximum life span of laboratory-bred snails was 20 months (mean 18 months).

Population structure over time

Analyses of quarterly snail collections and dissections between July 2000 and January 2003 showed the reproductive period of *G. vertiginosa* commenced in late December to early January and ended in late June to early July of each year. The appearance of embryos in January 2001 and the corresponding peak in the 0.3–2.0 mm size category in March 2001 paralleled the timeline (45–50 days) of laboratory-bred snails during the same growth phase from embryos to juveniles of mean shell length 2 mm (Figs 2, 3). A peak in the adult size class would be expected in July 2001 if development of field juveniles to sexual maturity (mean shell size 4.5 mm) continued to parallel laboratory growth timelines. The absence of this expected peak in the field suggests the species had high recruitment but low survival of juveniles leading into the winter of 2001. Declines in population densities are presumably part of the natural cycle of reproduction in a habitat with a diversity of climatic

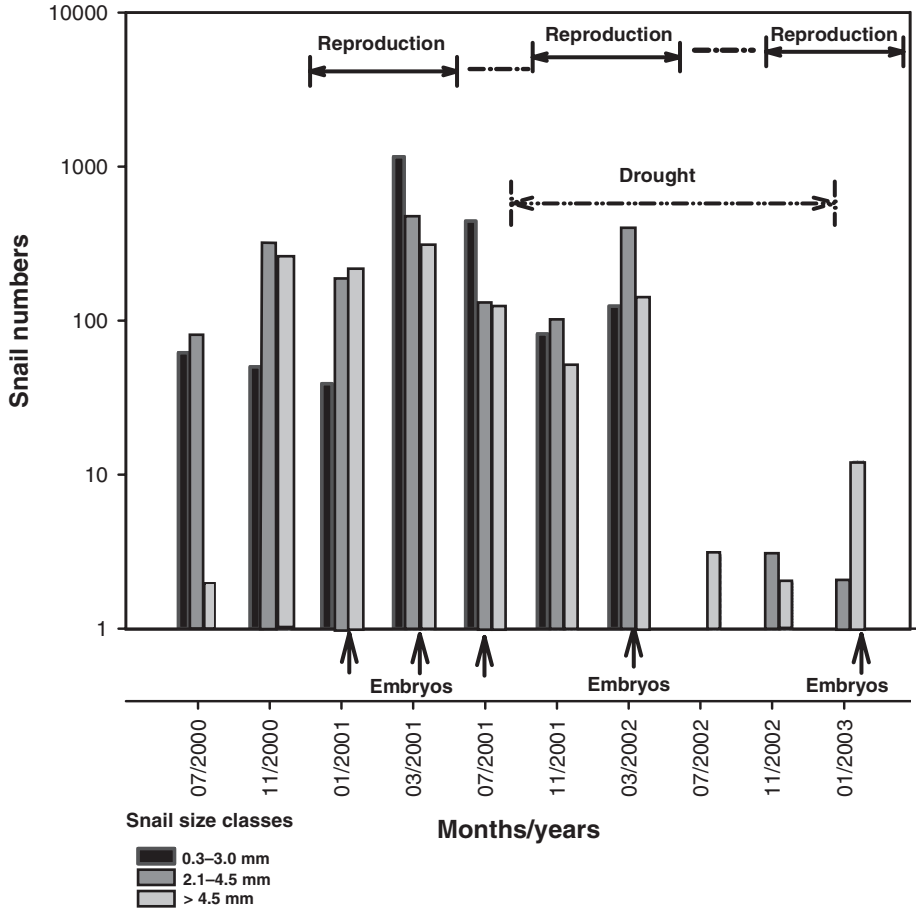

Fig. 3. Results of analyses of 4736 *Gabbia vertiginosa* collected from Saumarez Road swamp during quarterly surveys between July 2000 and January 2003 (*y*-axis log-transformed). Snails were divided into three shell-length classifications: 0.3–2.0 mm, 2.1–4.5 mm and >4.5 mm actual individual shell lengths. Approximate commencement of reproduction period was determined by date of first finding of freshly hatched snails in habitat (mean shell length at this stage: 0.25–0.3 mm) minus 30–34 days deposition to hatching period as determined in laboratory breeding trials. Approximate ending of reproduction period was determined by date of last finding of freshly hatched snails in habitat (mean shell length at this stage: 0.25–0.3 mm) minus 30–34 days.

conditions such as those that exist across the New England Tablelands (Bureau of Meteorology Australia 2001). The peak in size class 2.1–4.5 mm in March 2002 (a quarterly January 2002 survey was not done) suggests that embryos were deposited during the first weeks of January 2002 (72 days from deposition to mean shell size 3 mm; Fig. 2). The appearance of embryos in January, March and July of 2001 indicates that *G. vertiginosa* may be capable of reproducing more than once a year, if environmental conditions are favourable. Drought across the region caused a dramatic fall in snail densities from April 2002 onwards in response to reduced habitat, but some embryos were found in January 2003 indicating that reproductively viable adults still remained. Rainfall

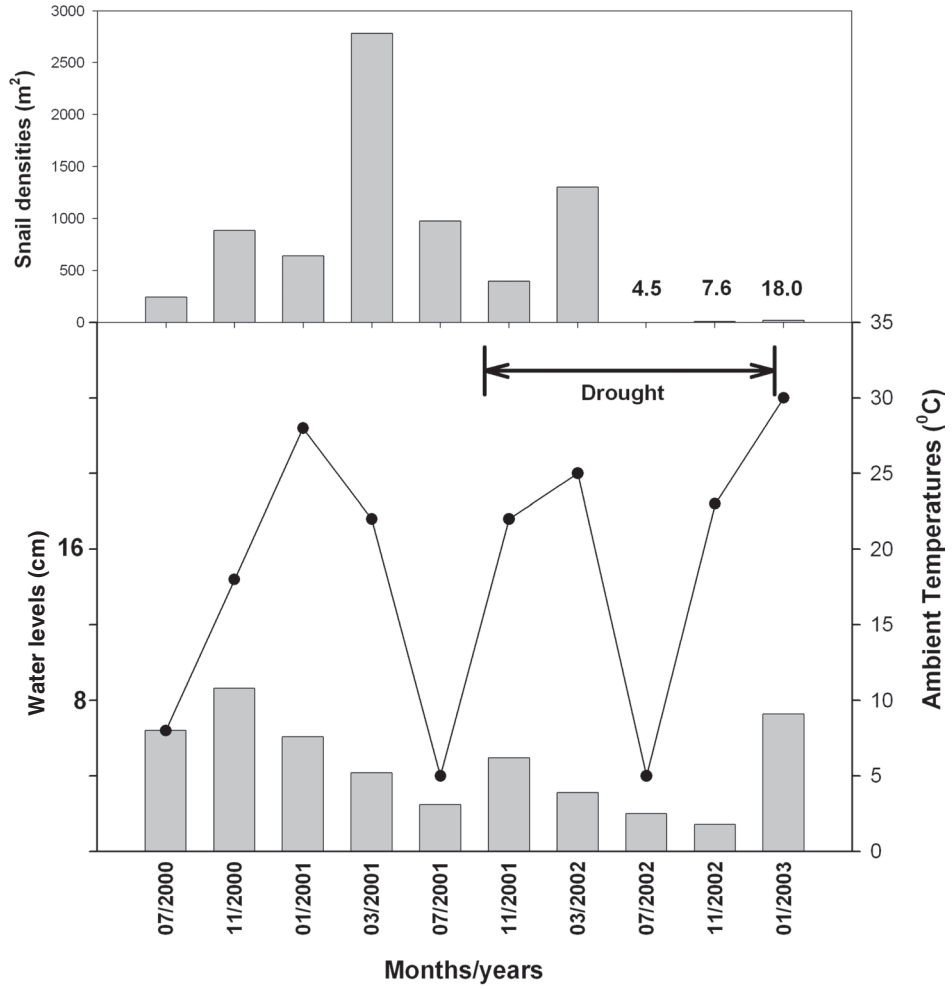

Fig. 4. Analyses of snail densities (upper panel) collected during each quarterly survey at Saumarez Road swamp between July 2000 and January 2003, in relation to habitat water levels (lower panel, bar graph) and ambient air temperatures at the site (lower panel, line graph).

across the New England Tablelands in January 2003 appears to have had a positive impact on snail reproduction leading to the small peak in juvenile numbers observed in March 2003.

Population densities for *G. vertiginosa* calculated at each quarterly survey at Saumarez Road swamp fluctuated with the changing of the seasons and dropped dramatically in the latter half of the drought period (Fig. 4). Densities were highest in March of each year, corresponding with the nearing of the end of summer. At this time, air and water temperatures averaged 23°C and habitat water levels were still high enough to support the growth of *E. gratioloides*, the latter apparently important to the survival, growth and reproduction of the snail. The severe drop in water levels in July and November 2002 reduced the coverage of *E. gratioloides* in the habitat from ≈ 2.5 m^2 to 0.2 m^2. Snail densities at these times were also at their lowest. Water quality tests conducted at the study

site gave consistent readings of about pH 8.0, calcium carbonate levels of 669 p.p.m. and dissolved oxygen at 5 p.p.m.

In the laboratory, snails were observed to graze upon the leaves of *E. gratioloides* leaving only the stalks of the plant untouched.

Discussion

This is the first medium-term study to provide a general picture of the reproduction and population structure of an Australian bithyniid. Its embryonic development has until now been known only from unpublished observations (W. Ponder, pers. comm. 2003) of embryos in the posterior sections of the pallial oviduct of a few specimens of *Gabbia vertiginosa.*

The pattern of growth and development of the hatchlings over time under laboratory conditions paralleled the Saumarez Road swamp collections. Eleutheriadis and Lazaridou-Dimitriadou (2001) found in *Bithynia graeca* that maturation of gonads corresponded to external morphometric changes in growth of the shell. A similar conclusion can be drawn for *G. vertiginosa*, as demonstrated by the size/time ratios described in Fig. 2. Further experiments on the relationship between sexual development and shell morphology are required.

Low snail densities at Saumarez Road swamp parallelled low water levels, greater extremes of temperature than usual and consequent low plant levels within the habitat between July 2002 and January 2003. Throughout the drought, birds such as wood ducks, which would normally graze across paddocks surrounding dams, resorted to feeding on weed in watercourses and dams for survival, thus further reducing the plant levels in those environments (pers. obs.). This significant behavioural adaptation in the wood ducks presumably caused a reduction in snail densities directly through consumption of snails associated with the water plants and indirectly through the loss of food resources and microhabitat for snail survival and reproduction. The population at Saumarez Road swamp was slowly rebuilding, with densities around 22 snails m^{-2} in March 2003.

From the present study, *G. vertiginosa* has been shown to be a hardy species with a high growth rate (88 days to 3.5 mm) compared with *Bithynia graeca*, an annual species that takes 210 days to grow to 3.5 mm (Eleutheriadis and Lazaridou-Dimitriadou 2001). The larger *B. tentaculata* can live up to 51 months but takes a full 2 years to reach sexual maturity (Vincent *et al*. 1981; Brendelberger 1995).

Gabbia vertiginosa is a fast-growing snail with a shorter life span than *B. tentaculata*. It reaches sexual maturity earlier and reproduces at least annually, although it is able to take advantage of favourable environmental cues to produce more than one recruitment cycle per annum.

Gabbia vertiginosa appears to be able to withstand harsh environmental conditions and has the ability to survive in habitats where the water is hard (669 p.p.m. calcium carbonate) and alkaline (pH 8.0) and with low dissolved oxygen levels (5 p.p.m.). In contrast, *Bithynia graeca* and *B. tentaculata* can tolerate only up to 110.3 p.p.m. carbonate and require ≈ 9.7 ppm dissolved oxygen for survival and reproduction (Lilly 1953; Eleutheriadis and Lazaridou-Dimitriadou 1995, 2001). Eleutheriadis and Lazaridou-Dimitriadou (2001) demonstrated that variation in pH, dissolved oxygen and carbonate hardness levels had detrimental effects on abundance, growth and reproduction of *B. gracea*. A similar controlled laboratory experiment with *G. vertiginosa* would benefit our present knowledge of the species' range of habitat parameters.

There is need for a more detailed and prolonged study of *G. vertiginosa*, both in natural habitats and under laboratory conditions, so that the biology and embryonic development of the species can be more fully understood under all conditions. Sampling with replacement of tagged snails would clearly define life span and reproductive patterns. A carefully planned laboratory breeding program is needed to describe the stages of embryonic development and provide information on the effects of environmental factors such as diet, pH, dissolved oxygen and temperature. Laboratory observations to date suggest that *G. vertiginosa* is not semelparous, in contrast to *B. graeca* and *B. tentaculata* (Calow 1978; Eleutheriadis and Lazaridou-Dimitriadou 2001), but further studies are required to build on the foundations of the profile of this species provided here.

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References

Brendelberger, H. (1995). Growth of juvenile *Bithynia tentaculata* (Prosobranchia, Bithyniidae) under different food regimes: a long-term laboratory study. *Journal of Molluscan Studies* **61**, 89–95.

Bureau of Meteorology Australia (2001). 'Climate activities in Australia 2001.' (Commonwealth Government Printery: Melbourne, Australia.)

Bureau of Meteorology Australia (2002). 'Weather of Australia.' Available online at http://www.bom.gov.au/ [accessed 10 October 2002].

Calow, P. (1978). The evolution of life-cycle strategies in freshwater gastropods. *Malacologia* **17**, 351–364.

Caughley, G., and Sinclair, A. (1994). 'Wildlife Ecology and Management.' (Blackwell Sciences: Cambridge, MA, USA.)

Eleutheriadis, N., and Lazaridou-Dimitriadou, M. (1995). Density and growth of freshwater prosobranch snails (*Bithynia graeca* and *Viviparus contectus*) in relation to water chemistry in Serres, Northern Greece. *Journal of Molluscan Studies* **61**, 347–352.

Eleutheriadis, N., and Lazaridou-Dimitriadou, M. (2001). The life cycle, population dynamics, growth and secondary production of *Bithynia graeca* (Westerlund, 1879) (Gastropoda) in Lake Kerkini, Northern Greece. *Journal of Molluscan Studies* **67**, 319–328. doi:10.1093/MOLLUS/67.3.319

Fretter, V., and Graham, A. (1962). 'British Prosobranch Molluscs. Their Functional Anatomy and Ecology.' (Adlard & Son Ltd: London, UK.)

Graham, A. (1971). 'British Prosobranch and other Operculate Gastropod Molluscs. Keys and Notes for the Identification of the Species.' (Academic Press: London, UK.)

Koch, M. (2002). First record and description of *Catatropis indicus* Srivastava, 1935 (Digenea : Notocotylidae), in Australia. *Memoirs of the Queensland Museum* **48**, 147–153.

Koch, M. (2003). 'Aquatic Snails and their Trematodes in the New England Tablelands (New South Wales, Australia): Low Diversity and Unstable Population Structure Explained by Unpredictable Environmental Fluctuations.' PhD Thesis. (University of New England: Armidale, NSW, Australia.)

Koch, M. (in press *a*). Faunal survey. I. The distribution of aquatic gastropods of the New England Tablelands. *Memoirs of the Queensland Museum.*

Koch, M. (in press *b*). Faunal survey. II. The distribution of digenetic trematodes within the New England Tablelands. *Memoirs of the Queensland Museum*.

Krist, A. (2000). Effect of the Digenean parasite *Proterometra macrostoma* on host morphology in the freshwater snail *Elima levescens*. *Journal of Parasitology* **86**, 262–267.

Lilly, M. M. (1953). The mode of life and the structure and functioning of the reproductive ducts of *Bithynia tentaculata* (L.). *Proceedings of the Malacological Society of London* **30**, 87–110.

McMichael, D. F. (1967). Australian freshwater mollusca and their probable evolutionary relationships – a summary of present knowledge. In 'Australian inland Waters and their fauna'. (Ed. A. H. Weatherley.) pp. 123–149. (Australian National University Press: Canberra, Australia.)

Ponder, W. (2003). Monograph of the Australian Bithyniidae (Caenogastropoda: Rissooidea). *Zootaxa* **230**, 1–126.

Ponder, W., and De Keyzer, R. (1998). Class Prosobranchia. In 'Mollusca: The Southern Synthesis. Fauna of Australia'. Vol. 5. (Eds P. Beesley, G. Ross and A. Wells.) pp. 759–761. (CSIRO Publishing: Melbourne, Australia.)

Rohlf, F., and Sokal, R. (1969). 'Statistical Tables.' (W.H. Freeman & Co.: New York, USA.)

Simpson, R., and Stanisic, J. (1986). Faunal survey of New England. II. The distribution of gastropod molluscs. *Memoirs of the Queensland Museum* **22**, 115–139.

Smith, B. J., and Kershaw, R. C. (1979). 'Field Guide to the Non-Marine Molluscs of South Eastern Australia.' (Australian National University Press: Canberra, Australia.)

Sutherland, W. (1996). 'Ecological census techniques – a Handbook.' (Cambridge University Press: London, UK.)

Tryon, G. W. (1865). Catalogue of Mollusca. *American Journal of Conchology* **1**, 68–70.

Vincent, B., Vaillancourt, G., and Harvey, M. (1981). Cycle de developpement, croissance, effectifs, biomasse et production de *Bithynia tentaculata* L. (Gastropoda : Prosobranchia) dans le Saint-Laurent (Quebec). *Canadian Journal of Zoology* **59**, 1237–1250.

Wright, C. A. (1971). 'Flukes and Snails.' (Allen & Unwin Ltd: London, UK.)