Reproductive strategies of *Hydrococcus brazieri* (Tenison Woods, 1876) and *Arthritica semen* (Menke, 1843) in Peel Inlet, Western Australia.

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ABSTRACT

Females of *Hydrococcus brazieri* deposit egg capsules on any suitable hard substrate within which a single embryo develops. Young of *Arthritica semen* develop in a brood pouch in the female. In both species the young emerge at a crawling juvenile stage. Adaptations of *H. brazieri* and *A. semen* for estuarine life include: continuous reproduction, lack of a planktonic stage, rapid growth rates and short maturation times. In these characteristics *H. brazieri* and *A. semen* are relatively r selected in comparison with the other group of dominant estuarine molluscs, the mussels.

INTRODUCTION

Estuaries have been defined by Pritchard (1967) as "semi-enclosed coastal bodies of water which have a free connection with the open sea and within which seawater is measurably diluted with freshwater from land drainage". The animals that inhabit this intermediate zone between the sea and freshwater are predominantly euryhaline marine forms which are able to adapt to the rigours of the estuarine environment. A few freshwater species inhabit upper estuarine areas if they can tolerate the increased salt concentration. In addition there are a few true estuarine species which are not found in other habitats (Day, 1967). The strongly seasonal nature of southwest estuaries increases the stresses normally encountered by estuarine species.

The biology of estuarine molluscs in the southwest was first examined by Wilson in a series of papers on the reproduction, growth and physical tolerances of mytilid bivalves (Wilson, 1968; 1969; Wilson and Hodgkin, 1967). Smith (1975) recently investigated two species of the snail genus *Nassarius* and Appleton (1980) is currently investigating the life cycle of *Velacumantus australis* in the Swan River.

All of the species studied to date reach an adult size of at least 10 mm. Only a single

account of the biology of smaller species has been completed, an unpublished BSc. thesis by Ashman (1969) on the bivalve *Arthritica semen;* this thesis had only a very preliminary examination of reproductive mechanisms. Small molluscs are known to reach very high densities in other parts of the world and to contribute substantially to secondary production (Green, 1968). This study was designed to examine the biology of 2 abundant species of small molluscs to determine their strategies for survival in the estuarine environment, based on work in the Peel-Harvey estuarine system.

The Peel-Harvey estuarine system is a small body of water with an area of approximately 130 km^2 on the west coast of Western Australia (32°36'S; 115°42'E). Peel Inlet and Harvey Estuary are the dominant features of the system. Both have extensive flats along their margins with depths of less than 0.5 m; maximum depths are about 2 m. The area is characterized by temperatures of up to 27°C and hypersaline conditions in summer. In winter temperatures reach as low as 10°C at Coodanup on Peel Inlet. Freshwater inflows from the Murray and Serpentine Rivers can depress salinities at Coodanup to as low as 5‰ for brief periods (Wells, Threlfall and Wilson, 1980).

A three year examination of the molluscs of the Peel-Harvey estuarine system has recently been completed (Wells, Threlfall and Wilson, 1980). A preliminary examination recorded 34 mollusc species in the system, 9 of which were regarded as being truly estuarine, ie. they occur in estuaries but not in adjacent marine or freshwater areas. A sample site was investigated at Coodanup for two years. During this time the gastropod *Hydrococcus brazieri* (Tenison Woods, 1876) and the bivalve *Arthritica semen* (Menke, 1843) were the dominant molluscs, together accounting for 89.5% of all individuals collected. The mean density of *H. brazieri* was 9487m^{-2} and *A. semen* averaged 8105m^{-2}. Both species are also abundant in a number of other southwestern Australian estuaries (Wells and Threlfall, 1981). Detailed studies were made of the two species to determine the mechanisms which allow them to be successful in the estuarine environment. Reactions to changes in the physical factors of temperature and salinity are reported elsewhere (Wells and Threlfall, 1982). The present paper examines the reproductive biology of *H. brazieri* and *A. semen.*

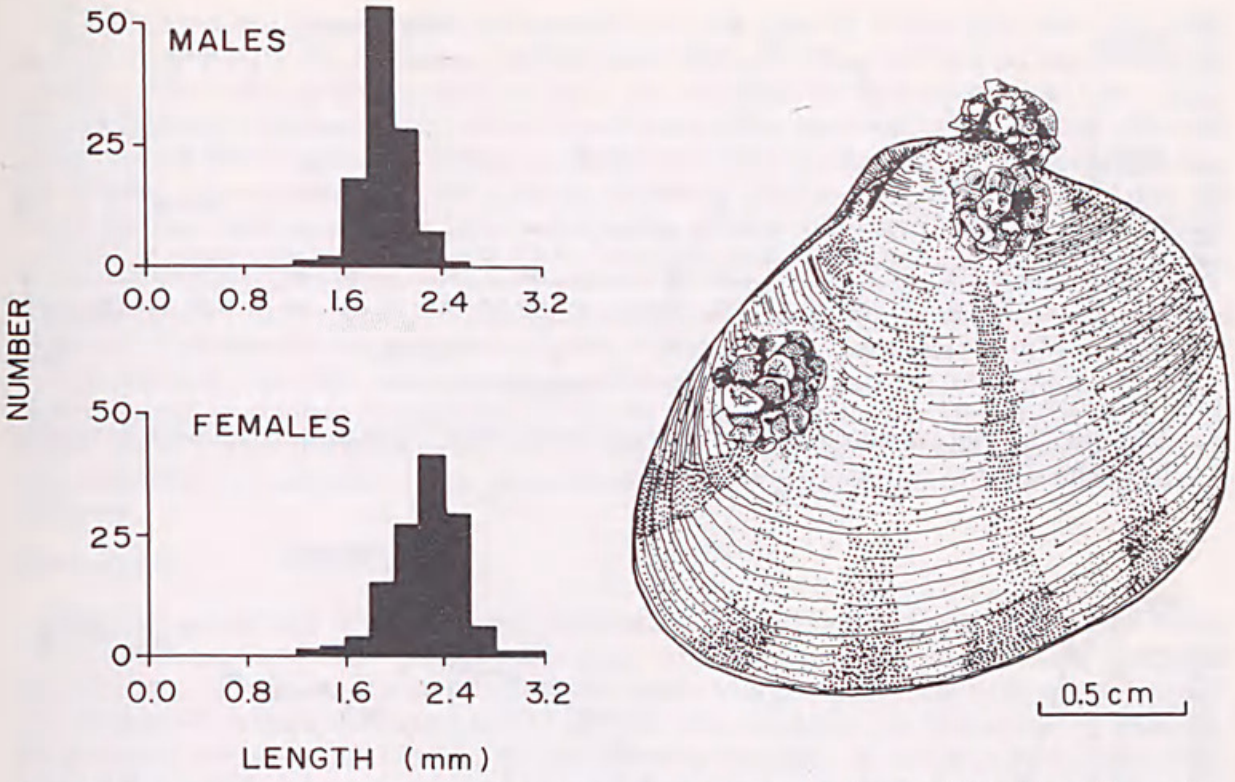
MATERIALS AND METHODS

Samples were collected monthly from March 1977 to February 1979 at Coodanup beach in Peel Inlet. The station was located 100 m offshore; water depth varied from 30 to 90 cm during the two years but the station was never exposed on our sample dates. It could conceivably have been exposed during the time between monthly samples. A corer with an area of 98.5 cm^2 was used to remove sediment to a depth of 2 cm. Samples were sieved through a 1 mm mesh in the field. The material obtained was searched with a dissecting microscope in the laboratory for live molluscs and capsules of *H. brazieri.* Ten replicate samples were collected each month and were treated individually. All live molluscs were identified and counted. Three hundred individuals of *H. brazieri,* 200 of *A. semen* and as many individuals as possible of the other species were measured to the nearest 0.1 mm each month using a dissecting microscope equipped with an ocular micrometer. All *H. brazieri* egg capsules on the live molluscs were counted. In addition a sample of 235 *H. brazieri* was obtained on 9 October 1978 using the same coring and sieving technique. All individuals were sexed using the presence of a penis as the distinguishing characteristic for males and its absence for females. To determine size at sexual maturity individuals of 1.5 mm or larger of both sexes were measured, the shell decalcified in Bouin's fixative, and the animals treated with standard histological techniques. They were embedded in paraffin, sectioned at 7 μm and stained with hematoxylin and eosin.

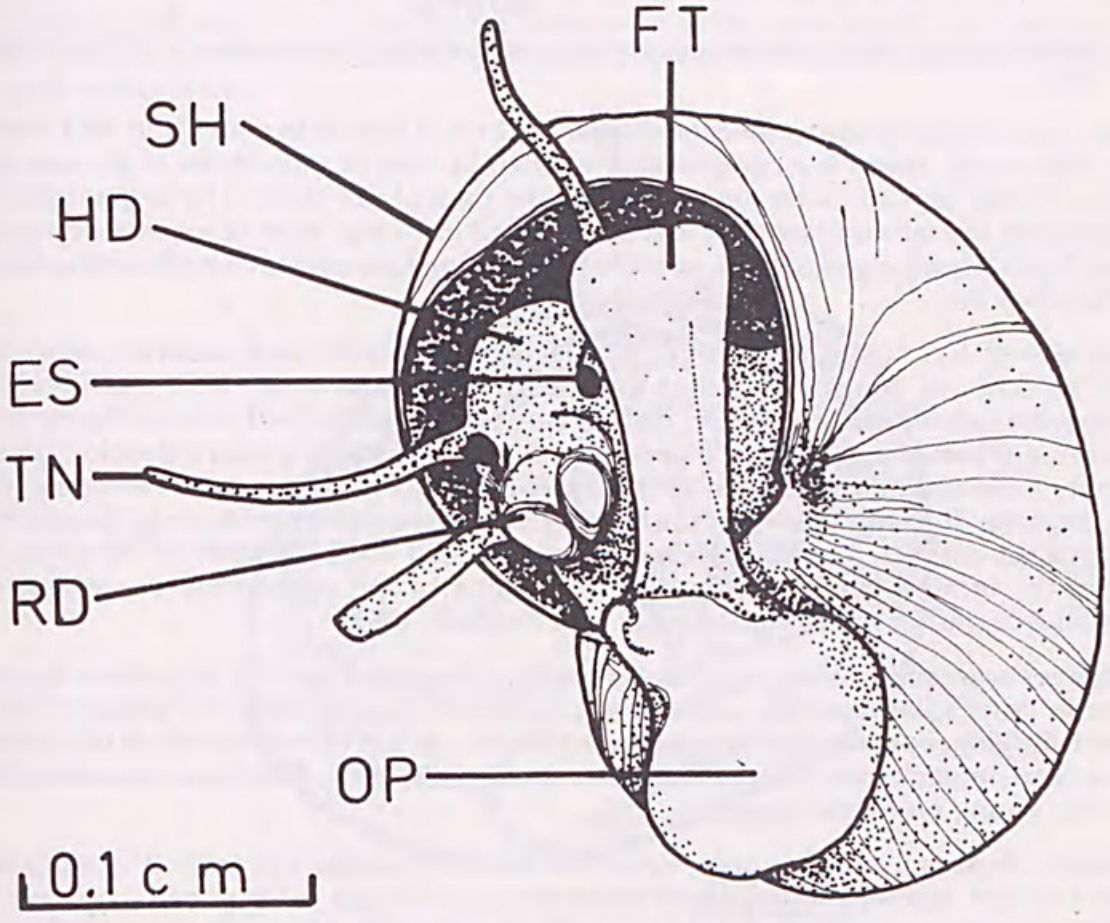
RESULTS

A. *H. brazieri*

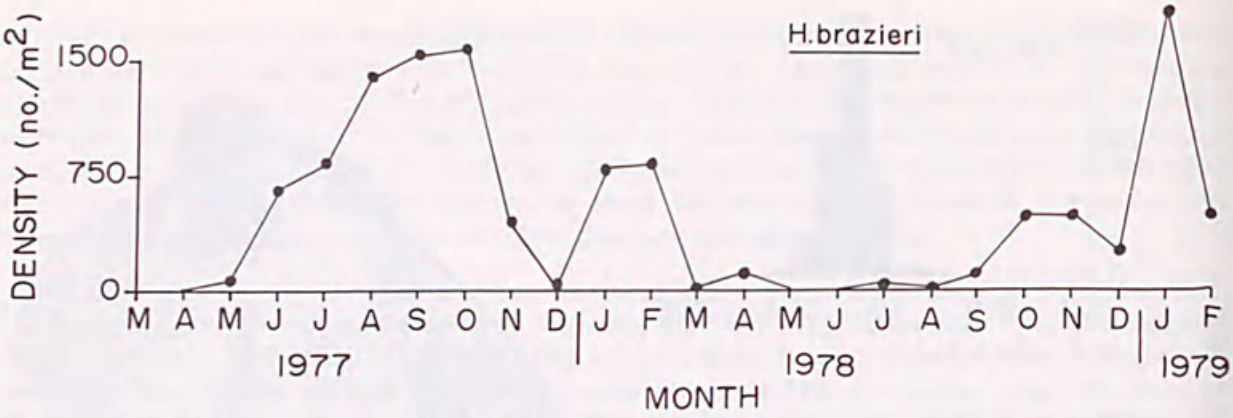
Sexes are separate in *H. brazieri,* and there was no suggestion of hermaphroditism in the sectioned material. Of the 235 individuals sexed 108 were males and 127 were females (Figure 1). Deviation from the expected 50 : 50 ratio was not significant (t-test, 0.05 level).



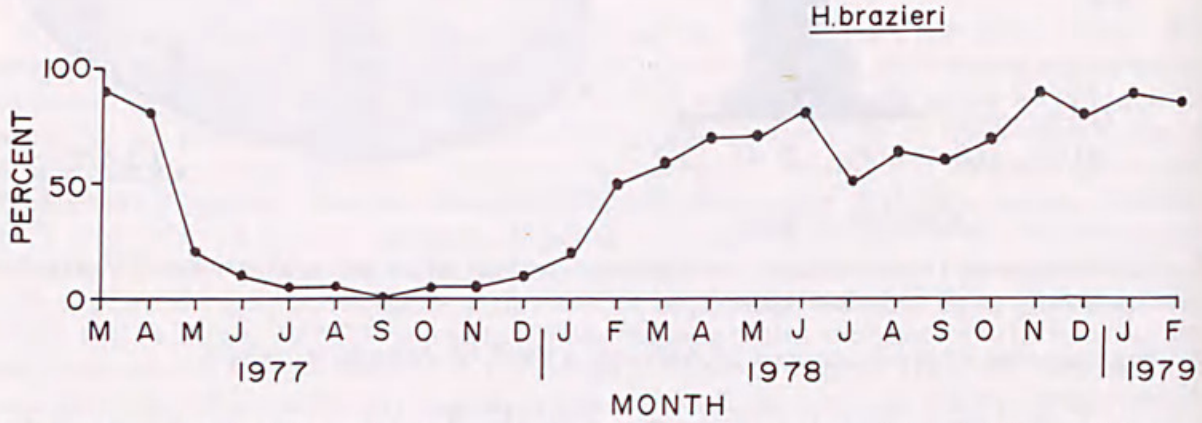
1. Size frequency characteristics of *Hydrococcus brazieri* males and females collected at Coodanup on 9 October 1978.
2. Egg capsules of *Hydrococcus brazieri* on a shell of *Arthritica semen*.



3. A crawling juvenile of *Hydrococcus brazieri*. ES, eye; FT, foot; HD, head; OP, operculum; RD, radula; SH, shell; TN, tentacle.



4. Densities of egg capsules of *Hydrococcus brazieri* at Coodanup from March 1977 to February 1979.



5. Percentage of adult *Hydrococcus brazieri* at Coodanup from March 1977 to February 1979.

Mean size of females was significantly larger (2.22 + 0.13 mm) than males (1.95 + 0.13 mm) (t-test, 0.05 level). There is a considerable overlap in sizes of individuals of the two sexes (Figure 1) and sex cannot be determined on the basis of size alone. The largest individual collected in the monthly samples was a female 3.8 mm long. Mature spermatocytes were found in sectioned males 2.0 mm or more long and mature oocytes were found in females of the same size.

Females of *H. brazieri* attach egg capsules to any suitable hard substrate, most often shells of other *H. brazieri* or other live molluscs, but also dead shells and rocks. The transparent capsules are composed of sand cemented together with mucus (Figure 2). The capsules are lens shaped with a diameter of 0.5 mm. A single embryo develops in each capsule; there are no nurse eggs. In rare cases two embryos were seen developing in the same capsule. The largest oocytes found in sectioned females were 90 μ m in diameter and the smallest embryo found in a capsule was a 4 cell stage 230 μ m in diameter. The differences in sizes are probably due to swelling of the egg during deposition as is frequently found in gastropods (Fretter and Graham, 1962).

Embryos emerge from the capsules as crawling juveniles (Figure 3). No veliger stage was found in developing embryos and there is no planktonic distributional phase in the life cycle. Emerging juveniles have a transparent shell 0.3 mm in diameter and are fully formed with a head, tentacles and operculum visible through the shell. There is no metamorphosis after the young leave the capsule.

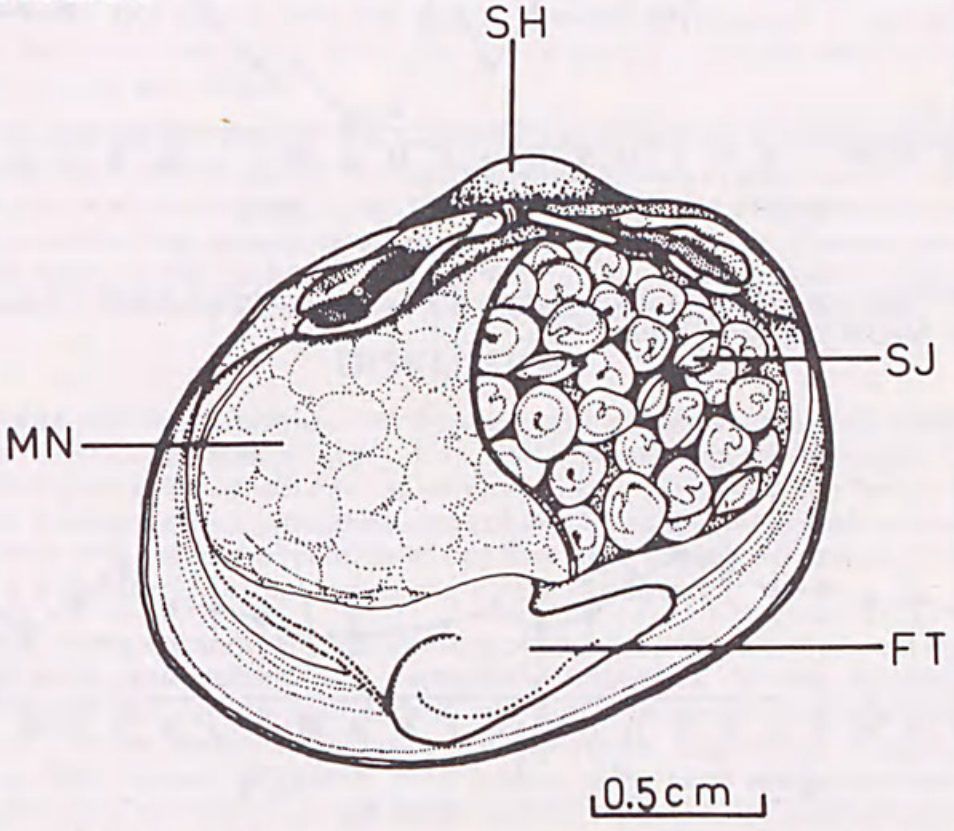
Females deposit more than one capsule but the total numbers deposited by individuals are not known. Eighteen females were dissected and the eggs in the gonads counted. The number of eggs ranged from 0 to 34 and with a mean of 18. All oocytes in a female are in approximately the same stage of development. Details of the anatomy of the reproductive system are given by Ponder (in press).

Female *H. brazieri* were placed in filtered estuarine water in 350 ml glass jars with a layer of sand on the bottom and were maintained at 25°C. Several individuals deposited egg capsules. The embryos began development and reached the shelled stage in 4 to 5 days. They continued to move about in the capsule but never hatched. After 42 days all of the juveniles had died without emerging. Capsules collected in the field successfully hatched in the laboratory in about 12 days, though some required as long as 17 days. Because the length of time these young had been developing before collection is unknown the figure of 12 to 17 days is only an estimate of the time required for intracapsular development.

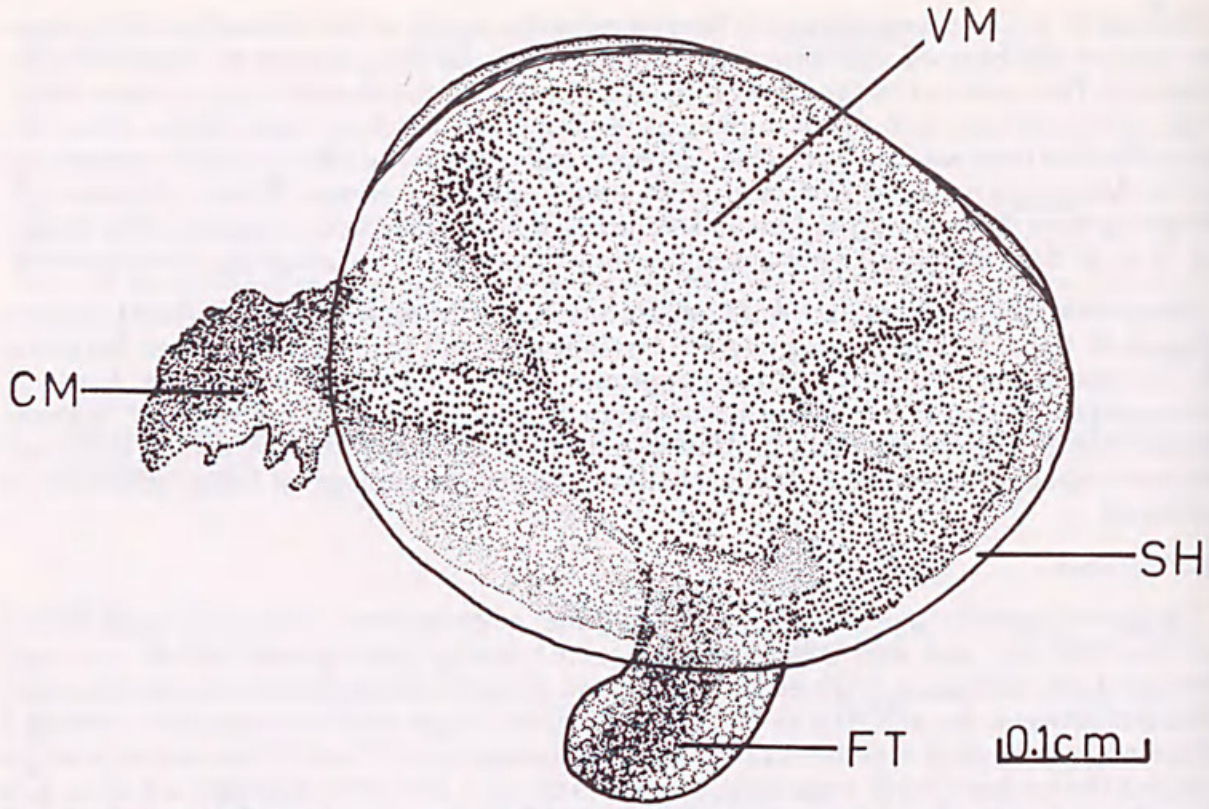
Reproduction in *H. brazieri* was almost continuous throughout the two years studied (Figure 4). Capsule density was generally less in the second year than in the first, but there is no obvious seasonal pattern of reproduction. Comparison of Figures 4 and 5 demonstrates an inverse relationship between capsule density and density of *H. brazieri* larger than 2.0 mm in shell length. During periods of high reproductive activity there are large numbers of juveniles in the population and the percentage of large individuals is reduced.

B. *A. semen*

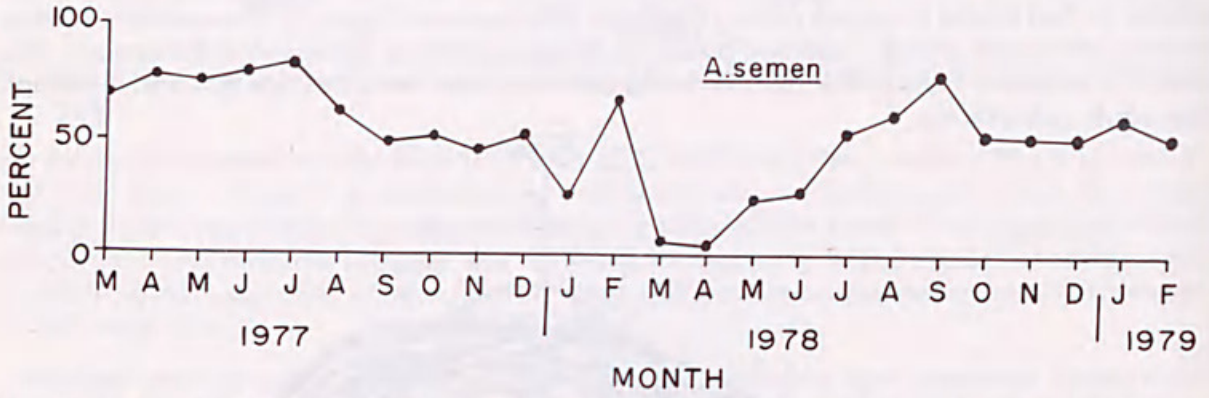
Arthritica semen is a protandric hermaphrodite, maturing first as males at a shell length of about 2.0 mm and after a brief male stage continuing development into a functional female stage. Larvae are retained by females and undergo development in a brood pouch located between the gills (Figure 6). Three embryonic stages were distinguished. In stage 1 the embryos are stuck together in a mass of developing eggs 0.33 to 0.37 mm in diameter. In stage 2 the embryos have separated, so each is distinct, and their diameter is 0.20 to 0.33 mm. Stage 3 embryos are juveniles with shells 0.20 to 0.50 mm in length. Some shell growth occurs while the juveniles are still in the female. Young are released as juveniles; we could find no trace of a velum in any individuals. During the embryonic stage a cephalic mass similar to that found in *Lasaea rubra* (Oldfield, 1964) occurs (Figure 7). The cephalic mass is composed of yolk which is utilized by the developing embryo while still in the female. The shell is transparent when the juvenile is released but later becomes opaque and develops the adult colouration.



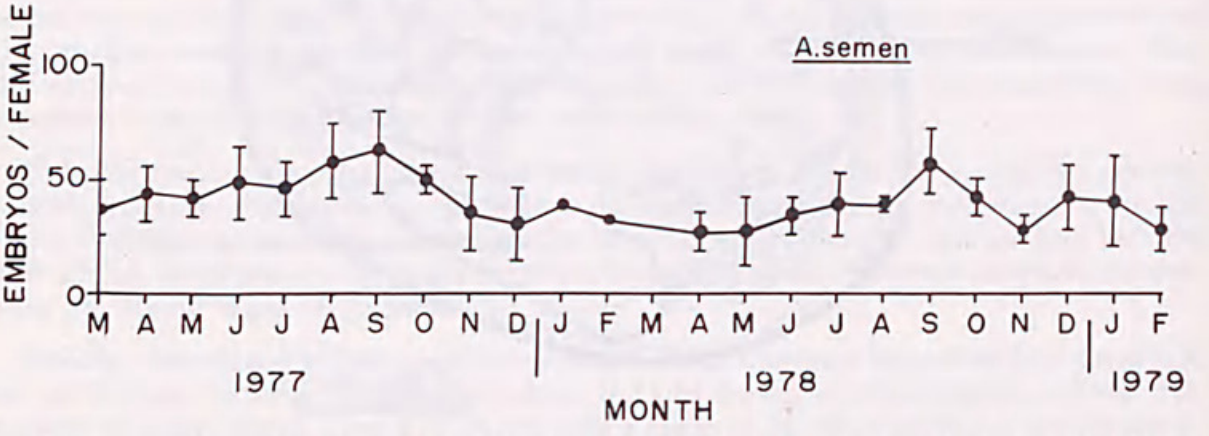
6. A female *Arthritica semen* with part of the mantle removed to show the shelled larvae. FT, foot; MN, mantle; SH, shell, SJ, shelled juvenile.



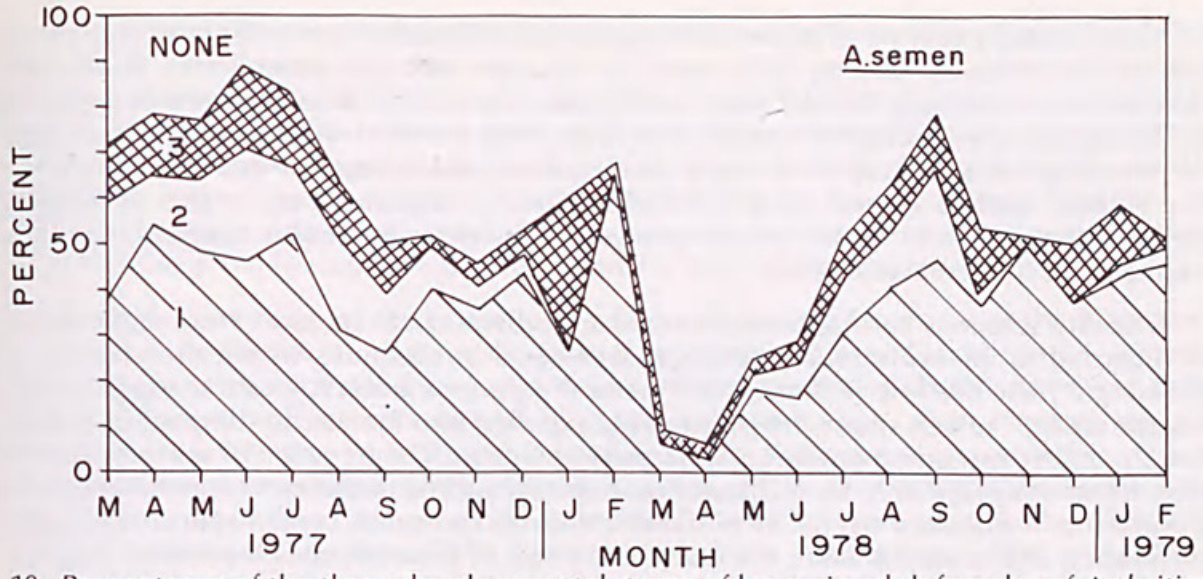
7. A larval *Arthritica semen* removed from an adult female. CM, cephalic mass; FT, foot; SH, shell, VM, visceral mass.



8. Percentages of *Arthritica semen* larger than 2.0 mm in shell length containing larvae from March 1977 to February 1979.



9. Mean number and one standard deviation of larvae in brooding females of *Arthritica semen* from March 1977 to February 1979.



10. Percentages of the three developmental stages of larvae in adult females of *Arthritica semen* at Coodanup from March 1977 to February 1979.

Each female of *A. semen* had embryos of only one stage of development; no females were found with two or more stages. All larvae develop at the same rate and are released at approximately the same time. There were no large females with a few shelled juveniles remaining and young embryos undergoing early development.

The percentage of females brooding was variable, but reproduction was continuous throughout the two years examined (Figure 8). The percentage of females brooding was at high levels in all months except March and April 1978, when only 4 and 5% had developing young. Not only does the percentage of females brooding larvae vary, but the number brooded per female varies also (Figure 9). The mean number of embryos per female varied from a low of 30.8 in December 1977 to 63.3 in September 1977. Gaps in the graph in January, February and March 1978 are due to the low percentages of females in the population that were brooding. There was no apparent seasonal trend in the mean number of embryos per female.

Figure 10 breaks the percentage of *A. semen* brooding into the 3 developmental stages. In all months stage 1 embryos were the majority. Stage 2 embryos were found in all months except February and March 1978. Stage 3 larvae were collected throughout the two year period. This verifies that reproduction is continuous in *A. semen*. There is no discrete period when stage 1 embryos begin development leading to a later period when release occurs. Instead embryos of all stages can be found at all seasons of the year.

DISCUSSION

The reproductive mechanisms of *H. brazieri* and *A. semen* are well suited to the estuarine environment in which they live. Both species employ strategies in which relatively few young are produced in comparison to species which broadcast their reproductive products directly into the water column (Webber, 1977). Both *H. brazieri* and *A. semen* have only moderate fecundities but they have developed several mechanisms for ensuring a high survivorship among the young produced.

Developing young are generally less tolerant of changes in the environment than adults are; temperature and salinity are particularly important. Young *H. brazieri* are encapsulated with the capsule wall providing a buffer between them and the external environment. This mechanism is similar to that reported in 4 species of *Hydrobia* (Fretter and Graham, 1962; Muus, 1967; Wells, 1978; Lassen, 1979), all of which are also estuarine species. Young are also protected in *A. semen* but the mechanism is quite different. In this species they are brooded in the female, as is common among other species of Leptonacea (Oldfield, 1964; Ponder, 1965). The developing young are protected from the external environment by the shell and tissues of the female.

A ready supply of food of the necessary quantity and quality is another critical problem for the developing young, and again *H. brazieri* and *A. semen* have developed mechanisms for solving the problem. A sufficient quantity of yolk and albumen is provided in the capsule of *H. brazieri* for the embryo to develop into the crawling stage. The strategy for ensuring the necessary food supply used by *A. semen* is the same as that employed by the related species *Lasaea rubra* (Oldfield, 1964). A cephalic mass in the developing embryo contains yolk. As the embryo grows and develops the yolk is consumed and the cephalic mass decreases in size.

Arthritica semen is hermaphroditic; sexes are separate in *H. brazieri*. Hermaphroditism is regarded as an evolutionary strategy developed in situations where the chances of meeting a mate are low (Beeman, 1977), and the phenomenon is found throughout the Leptonacea. *A. semen* sperm are presumably expelled into the surrounding water and are caught up in the incoming water of adjacent individuals. The question of self-fertilization was not investigated in *A. semen*, but most hermaphroditic molluscs have mechanisms to ensure that it does not occur. In protandric species such as *A. semen* sperm are usually developed and released while the oocytes are still in the early developmental stages.

In both *H. brazieri* and *A. semen* young emerge at a benthic crawling stage minimizing the risk of their being swept from the estuary by the general seaward drift of the water. It also ensures that the emerging young are in an area where conditions are favourable for further growth and development. One problem with this strategy is that it is more difficult to colonize new areas than would be the case if there was a planktonic distributional phase. *H. brazieri* actively crawls onto algae, which is readily moved about in the estuary by water currents. While *A. semen* is a less active crawler than *H. brazieri*, it does move about a bit and could also become entrapped in algae. Distribution between estuaries could occur in the same manner but is less likely. Transfer of small molluscs from one area to another on the feet of wading birds is well known and could occur in both species.

Several adaptations are shown by *H. brazieri* and *A. semen* which allow them to be successful in southwestern Australian estuaries. Both have wide temperature and salinity tolerances. *H. brazieri* is active in temperatures of 8 to 32°C and *A. semen* from 18 to 32°; about half of the *A. semen* tested were active at 8°C. *H. brazieri* is active in salinities of 15 to 35‰ in winter and 25 to at least 55‰ in summer. The salinity tolerances of *A. semen* are similar (Wells and Threlfall, 1982). This paper has shown several reproductive adaptations shared by the two species. Continuous reproduction ensures that there is always a ready supply of developing young in the estuary to exploit favourable conditions. The embryos are protected during early development and survivorship is higher than would be the case if there were no protection. The lack of a planktonic larval stage ensures that the young are not swept from the estuary by currents. Both species have rapid growth rates. *H. brazieri* grows at about 0.5 mm/month, at least in the early stages, and *A. semen* has a growth rate of 0.3 mm/month. *H. brazieri* reaches the minimum reproductive size in about 4 months and the maximum size in 7-8 months. *A semen* can reproduce in 6 months and reaches its largest size in 9 months. These are minimum figures; both species can survive for longer periods (Wells, Threlfall and Wilson, 1980). Thus even if large portions of the populations are decimated by unfavourable conditions the remaining individuals provide a core of mature adults and juveniles which will soon be mature which can re-establish the population.

Mytilid bivalves are the other major group of truly estuarine species in southwestern Australia. *Fluviolanatus amara*, also common, is a member of the Tapeziidae (Morton, 1982). While this species is not closely related to the Mytilidae it is ecologically similar. The reproductive strategy of *Xenostrobus securis* and other mytilids was examined by Wilson (1968; 1969) and Wilson and Hodgkin (1967). *F. amara* was investigated by Wells, Threlfall and Wilson (1980). The reproductive strategies of these species are completely different from those of *H. brazieri* and *A. semen*. In these mussels there is no provision for protecting young; the eggs and sperm are simply broadcast into the adjacent water column where fertilization occurs. Larvae undergo a planktonic distributional phase of unknown duration before settling and metamorphosing into the adult form. During the

planktonic stage larvae are distributed within and between estuaries, making it easier for the young to colonize logs than would be the case if there was no planktonic stage. However, they can also be swept out to sea or into a part of an estuary that is unsuitable for further development. In addition there are heavy losses from predation in the plankton and the food supply is uncertain. Few larvae from an individual female survive to the settlement stage. The low survivorship is overcome by production of large numbers of gametes by each adult individual. This is possible because there is no mechanism employed to provide nutrition or protection for the developing larvae.

Among the common species of molluscs which are restricted to estuaries there are then two basic strategies for survival: an r-type strategy exhibited by *H. brazieri* and *A. semen*. This strategy is characterized by rapid development, great population turnover, early reproduction, a high intrinsic rate of increase, small body size, short lifespan, density independent mortality, wide dispersal gradient, and poor completitive ability. The K selected species have opposite characteristics (Loya, 1976). This group is represented by the mussels. All of the common molluscs in Peel Inlet which were classified by Wells and Threlfall (1980) as "estuarine" fit into one of these two groups. The uncommon "estuarine" species (*Tatea preissi, Potamopyrgus* sp., *Batillariella estuarina,* and *Salinator fragilis*) have not been examined but may be more towards the centre of the r-k continuum.

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