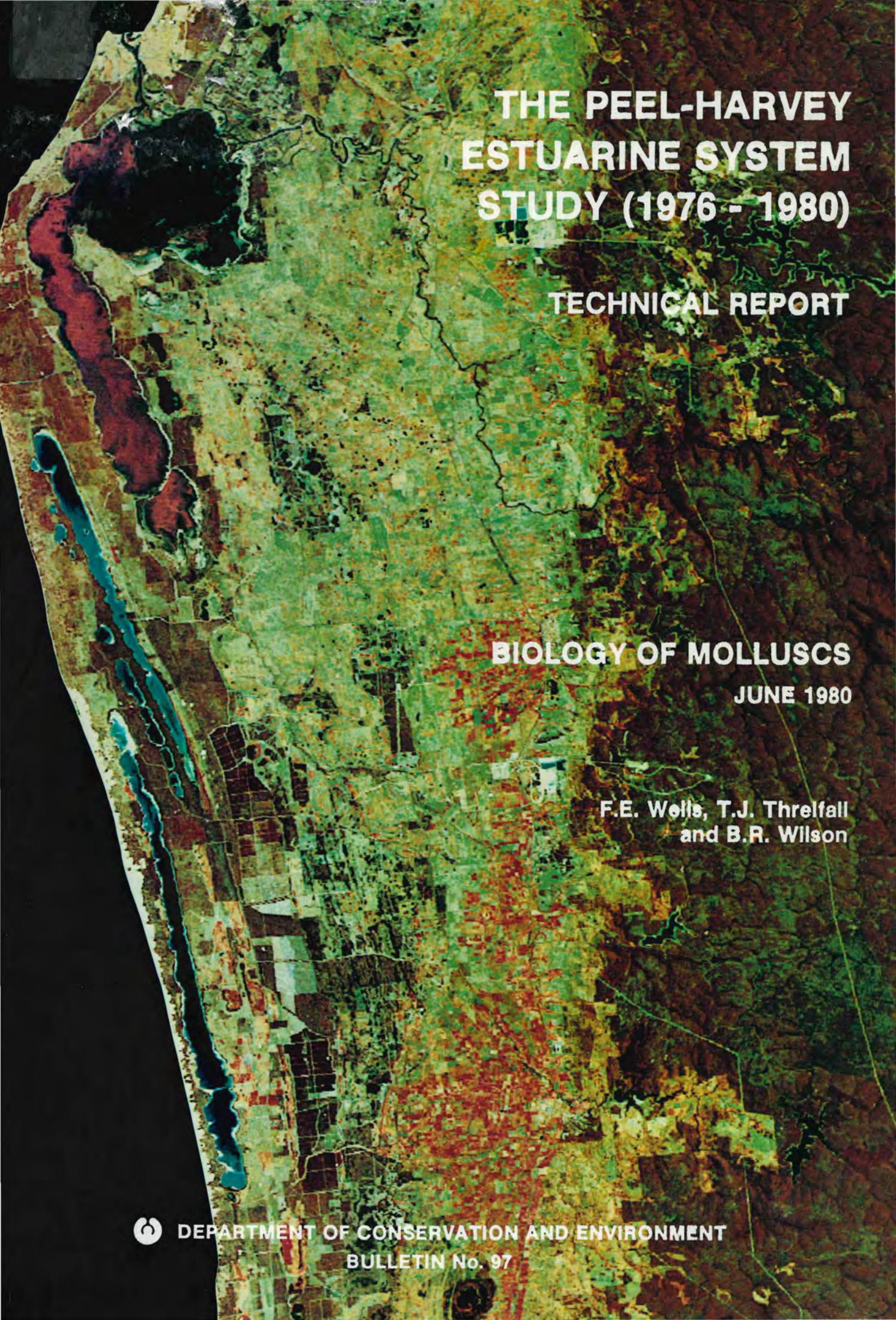

THE PEEL-HARVEY ESTUARINE SYSTEM STUDY (1976 - 1980)

TECHNICAL REPORT

BIOLOGY OF MOLLUSCS

JUNE 1980

F.E. Wells, T.J. Threlfall
and B.R. Wilson

DEPARTMENT OF CONSERVATION AND ENVIRONMENT
BULLETIN No. 97

A TECHNICAL REPORT to

THE PEEL-HARVEY ESTUARINE SYSTEM STUDY (1976-1980)

ASPECTS OF THE BIOLOGY OF MOLLUSCS IN THE PEEL-HARVEY ESTUARINE SYSTEM, WESTERN AUSTRALIA

by

F.E. Wells, T.J. Threlfall and B.R. Wilson

Western Australian Museum

June 1980

DEPARTMENT OF CONSERVATION & ENVIRONMENT

BULLETIN No. 97

PUBLICATIONS:
THE PEEL-HARVEY ESTUARINE SYSTEM STUDY (1976-1980)

This report is one of 14 technical reports that were presented to the Environmental Protection Authority's Estuarine and Marine Advisory Committee as part of the Peel-Harvey Estuarine System Study (1976-1980).

The publications arising from the study are listed below and are available from the Department of Conservation and Environment, 1 Mount Street, Perth WA 6000.

- The Peel-Harvey Estuarine System Study (1976-1980). A report to the Estuarine & Marine Advisory Committee December 1980. E.P. Hodgkin, P.B. Birch, R.E. Black, and R.B. Humphries, Department of Conservation and Environment, Report No. 9.

- The Peel-Harvey Estuarine System Study. A report by the Estuarine and Marine Advisory Committee to the Environmental Protection Authority, March 1981. Department of Conservation and Environment, Bulletin No. 88.

TECHNICAL REPORTS

BULLETIN No.

89 The Peel Inlet and Harvey Estuary System Hydrology and Meteorology. R.E. Black and J.E. Rosher. June 1980.

90 Sediments and Organic Detritus in the Peel-Harvey Estuarine System. R.G. Brown, J.M. Treloar and P.M. Clifton. August 1980.

91 The Ecology of *Cladophora* in the Peel-Harvey Estuarine System. D.M. Gordon, P.B. Birch and A.J. McComb. 1981.

92 The Decomposition of *Cladophora.* J.O. Gabrielson, P.B. Birch and K.S. Hamel. October 1980.

93 The Control of Phytoplankton Populations in the Peel-Harvey Estuarine System. R.J. Lukatelich and A.J. McComb. 1981.

94 Cyanobacteria and Nitrogen Fixation in the Peel-Harvey Estuarine System. A.L. Huber. October 1980.

95 Phosphatase Activities in the Peel-Harvey Estuarine System. A.L. Huber. October 1980.

96 The Sediment Contribution to Nutrient Cycling in the Peel-Harvey Estuarine System. J.O. Gabrielson. 1981.

97 Aspects of the Biology of Molluscs in the Peel-Harvey Estuarine System, Western Australia. F.E. Wells, T.J. Threlfall and B.R. Wilson. June 1980.

98 The Fish and Crab Fauna of the Peel-Harvey Estuarine System in Relation to the Presence of *Cladophora*. I.C. Potter, R.C.J. Lenanton, N. Loneragan, P. Chrystal, N. Caputi and C. Grant. 1981.

99 Phosphorus Export from Coastal Plain Catchments into the Peel-Harvey Estuarine System, Western Australia. P.B. Birch. October 1980.

100 Systems Analysis of an Estuary. R.B. Humphries, P.C. Young and T. Beer. 1981.

101 Peel-Harvey Nutrient Budget. R.B. Humphries and R.E. Black. October 1980.

102 Nutrient Relations of the Wetlands Fringing the Peel-Harvey Estuarine System. T.W. Rose and A.J. McComb. August 1980.

ABSTRACT

Thirty-four mollusc species were recorded from the Peel-Harvey estuarine system: 13 were marine, 9 of marine affinity, 9 estuarine, 1 freshwater, and 2 undetermined. The number of marine and marine affinity species is low compared to some of the other southwest estuaries. Factors limiting these species in Peel-Harvey are: habitat type, geographical location, and the temperature and salinity regime.

Hydrococcus graniformis and Arthritica semen were the dominant estuarine molluscs. Their biology was examined in detail to determine the mechanisms which allow them to survive in the estuary. Adaptations include continuous reproduction, protective mechanisms for developing young, lack of a planktonic stage, rapid growth rates and short maturation times, and wide temperature and salinity tolerances. Despite these adaptations densities of both species vary considerably from month to month. The two species play a key role in converting plant detritus into animal tissue available to the higher trophic levels.

A different strategy is pursued by the bivalve Anticorbula amara. Large numbers of gametes are expelled into the water column, where fertilization occurs. Heavy losses during the planktonic distributional phase are offset by the large number of larvae produced.

MANAGEMENT IMPLICATIONS

Hydrococcus graniformis and Arthritica semen are the dominant molluscs in the Peel - Harvey system, with populations usually measured in the thousands per square meter. Their lack of a planktonic distributional phase in the life cycle means that there is only limited reproductive exchange between the populations of the two species in Peel - Harvey and other southwestern estuaries. Both H. graniformis and A. semen are small species with maximum shell lengths of 3 to 4 mm. Their rapid growth rates and short maturation times combined with high population densities led to production estimates of 30 to 75 metric tons dry tissue weight for H. graniformis and 300 to 750 metric tons for A. semen. This is material converted from plant detritus to a form utilized by birds and fish.

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ACKNOWLEDGEMENTS

This report is a part of the general ecosystem study of the Peel - Harvey estuarine system conducted by the W.A. Department of Conservation and Environment. During our work we have frequently called on the other study groups for advice, comments and data; all of our requests have been promptly and effectively considered. The project coordinator, Dr E.P. Hodgkin, has been particularly helpful throughout our study. The Biochemistry, Botany and Zoology Departments of the University of Western Australia have all provided facilities at one time or another. Most important in this respect is the use of space at the Waterman marine laboratory arranged by Dr R. Black of the Department of Zoology. The Albany Residency Museum provided laboratory space and accommodation during our work in Albany. Assistance in the identification of problematic species was given by Dr W.F. Ponder, Mr R. Burn, Mr G.W. Kendrick, and Mrs S.M. Slack-Smith. Ms N. Gueho made the final sketches of the animal drawings. Mrs M. Konstantinu, Miss E. Ioannidis & Mrs W.G. Wallis typed the final manuscript. Drs P.F. Berry, E.P. Hodgkin and R.W. George critically read the full report and made a number of comments.

Particular thanks are due to two people who were employed in the early stages of the project and did much of the initial work on the routine sampling programme: Mr R. Buick and Mr N. Loneragan. Mrs W. MacGibbon did some of the early work on Hydrococcus reproduction as part of a student project at the W.A. Institute of Technology.

The study was funded by a grant from the W.A. Department of Conservation and Environment.

CHAPTER 1

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 predominately euryhaline marine forms which are able to adapt to the rigors 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).

Rochford (1951) divided Australian estuaries into 3 types characterized by their freshwater flow: (1) summer flood, winter drought; (2) winter flood, summer drought; and (3) estuaries with no well defined seasonal flood or drought. Southwestern Australian estuaries are in the second category. The dominant features of these estuaries are rainfall which is restricted to the winter months and poorly developed tidal oscillation (Spencer, 1956). Hodgkin (1976) emphasized the seasonality of salinity variations; animals are subjected to seasonal variations rather than diurnal ones. These are of the same timescale as the life-spans of the animals and mean that an animal cannot simply "close up" for a brief period during unfavourable conditions.

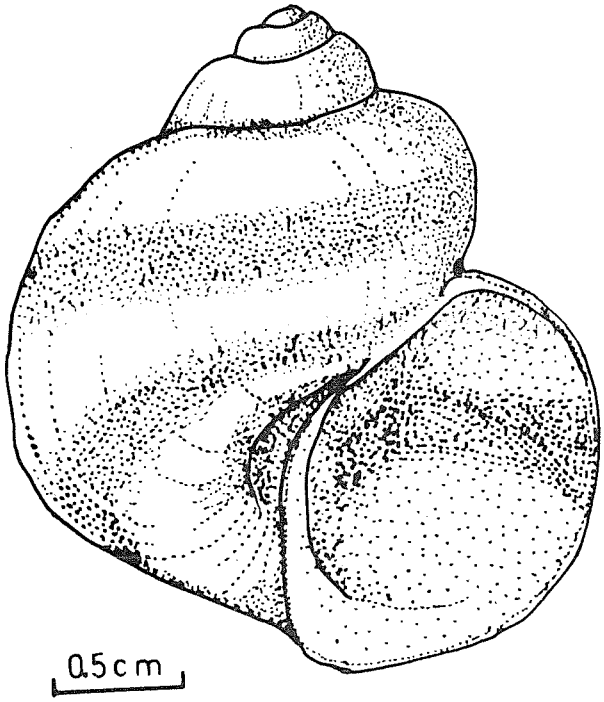
The strongly seasonal nature of southwest estuaries increases the stresses normally encountered by estuarine species.

Recently there have been a number of studies of particular animals in an attempt to understand the mechanisms by which animals are able to survive in and exploit these estuarine habitats (Wilson, 1968; 1969; Lucas and Hodgkin, 1970; Meagher, 1971; Smith, 1975; Bray, 1976). The most intensive investigation of a southwestern estuary was conducted in the Blackwood River. The results of the Blackwood work are summarized by Hodgkin (1976). The Blackwood study was followed by the examination of the Peel-Harvey estuarine system of which this report is a part.

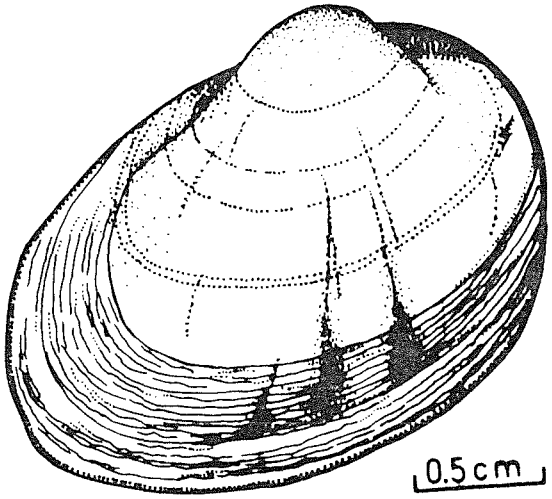
Little is known of the molluscs of southwestern Australian estuaries. There are available names for most of the large species but some taxonomic problems remain; many of the micro-molluscs are undescribed. Faunal lists have been prepared of the molluscs of the Blackwood estuary (Wallace, 1975a) and the Swan estuary (Chalmer, Hodgkin and Kendrick, 1976). In addition there are faunal lists for the marine embayments of Oyster Harbour and Princess Royal Harbour (Roberts and Wells, in press). Hodgkin (1977) drew on the available distributional data to compare the molluscs of southwest estauaries. 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. 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. The species selected were the snail Hydrococcus graniformis (Figure 1) and the bivalve A. semen (Figure 1). The two are the numerically dominant molluscs in the Peel-Harvey estuarine system and are widely distributed in other estuaries of the southwest.

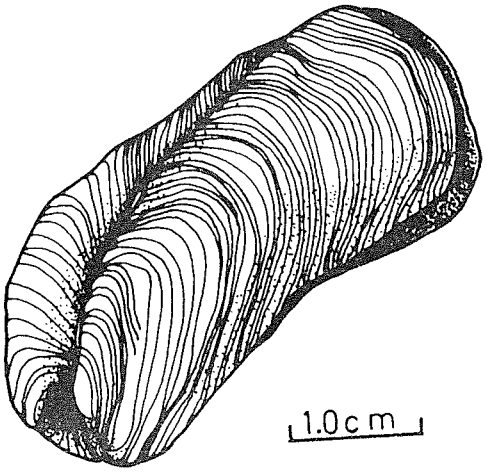
A subsidiary effort was made to determine the reproductive seasonality of the bivalve Anticorbula amara to provide a comparison between that species and the published information available on mytilid mussels (Wilson, 1968; 1969; Wilson and Hodgkin, 1967). Anticorbula amara superficially resembles a mussel (Figure 1) and the species has in fact been placed in the Mytilidae. It is currently placed in the family Lyonsiidae and the genus Anticorbula, but both placements are tentative and a detailed anatomical examination is required to determine the true affinities of the species.



H. graniformis



A. semen



A.amara

1. Drawings of the shells of Hydrococcus graniformis, Arthritica semen, and Anticorbula amara.

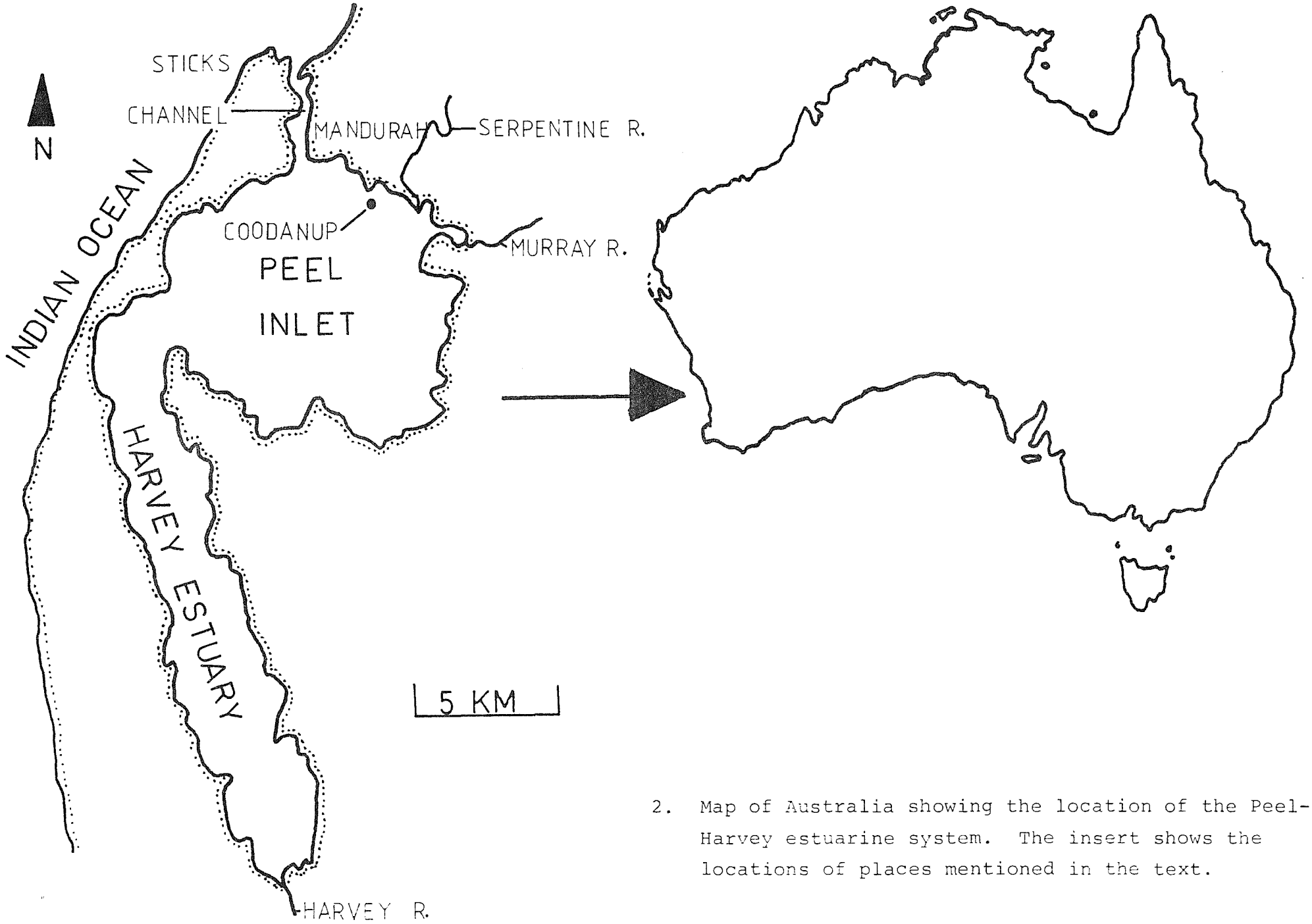
CHAPTER 2

HYDROGRAPHY OF THE PEEL - HARVEY ESTUARINE SYSTEM

The present report is one of a series of studies being undertaken in the Peel - Harvey estuarine system. Detailed examinations are being made of the hydrology of the system (Beer and Black, 1979) and an examination of the geology of the underlying sediments has recently been completed (Treloar, 1978). Preliminary information on the estuarine system is contained in Boulden (1970). Because of the detailed information that is already, or soon will be, published in the other studies no detailed account of the hydrology of the Peel - Harvey system will be presented here. Instead this section is intended merely to set the stage for subsequent chapters so that the work on molluscs may be considered in the perspective of their physical environment.

The Peel - Harvey estuarine system is a small body of water with an area of approximately 130 km^2. It is located 80 km south of Perth at $32^{o}36'S$ and $115^{o}42'E$. The largest body of water in the system is Peel Inlet (Figure 2) with an area of 70 km^2. The Inlet is shallow and circular with a maximum depth of 2 m. Shallow platforms less than 0.5 m in depth fringe the margins of Peel Inlet and account for over half of the total area. Harvey Estuary is a shallow coastal basin with an area of 60 km^2. There is an inlet channel, Mandurah Channel, leading from Peel Inlet to the sea at the town of Mandurah. The inlet channel has deltas at both ends.

Freshwater inflows into Peel Inlet occur from the 20 km long Serpentine River and the 24 km long Murray River. Both are tidal in their lower reaches, and both have deltas at



2. Map of Australia showing the location of the Peel-Harvey estuarine system. The insert shows the locations of places mentioned in the text.

their mouths in Peel Inlet. Harvey Estuary originally received water from all of the Harvey River, but the upper part of the river has been diverted and now flows directly into the sea. The total freshwater runoff into the Peel - Harvey estuarine system averages 430 x 10^6 m^3/year, with 364 x 10^6 m^3 coming from the Murray River. The freshwater inflow varies considerably from year to year, with the extremes for the Murray River being 60 to 1100 x 10^6 m^3/year. The river flow is strongly seasonal, with 95% occurring in the months of June to September. The amount of groundwater inflow into the system is unknown.

Seasonality of the freshwater inflow causes substantial changes in the salinity of the system during the year. The water of Harvey Estuary is nearly fresh during the winter and salinities in Peel Inlet briefly reach 5‰. With the lack of freshwater inflow and the increased evaporation in summer both Peel Inlet become hypersaline with salinities above 50‰ for several months.

Tides in southwestern Australia are usually 1 m or less and are often substantially altered by meteorological conditions (Hodgkin and DiLollo, 1958). In Peel Inlet tidal action is reduced and daily variations are less than 0.1 m. Meteorological conditions cause changes of up to 0.5 m over periods of 5 to 15 days.

CHAPTER 3

MOLLUSCS RECORDED IN THE PEEL - HARVEY ESTUARINE SYSTEM

The first step in examining the molluscs of the Peel - Harvey system was a preliminary survey to determine what species were present. Several visits were made to the system from December 1976 to March 1977; general collecting was done in all seasons on subsequent trips during the next 3 years as time permitted. Thirty-four species have been recorded (Table 1): 1 chiton, 21 gastropods and 12 bivalves. "Mandurah" on the table is broadly defined as the area between the bridge at Mandurah and the open sea.

Chalmer et al. (1976) developed the following classification for molluscs in the Swan estuary based on a subjective assessment of their distributional patterns and salinity tolerances. Marine species: those which occur in estuaries for only short periods or are present only at irregular intervals. Species of marine affinity: those with an essentially marine distribution but which also occur frequently in estuaries. Estuarine species: those that do not occur in marine or freshwater areas. Freshwater species: those that never occur in marine areas; they may be found in the upper reaches of estuaries. The categories are essentially those proposed by Day (1951) except for the absence of his fifth category of migratory species.

The determinations of Chalmer et al. (1976) and Roberts and Wells (in press) were applied to the species in the Peel - Harvey estuarine system (Table 2). There is a general progression from the large number of marine and marine affinity

Table 1. Mollusc species collected in the Peel-Harvey estuarine system.

Species	Habitat	Mandurah area	Peel Inlet	Harvey Estuary	Murray River	Serpentine River	Harvey River	Affinity
Class Amphineura								
Clavarizona hirtosa (Blainville, 1825)	On rocks	X	-	-	-	-	-	Marine
Class Gastropoda								
Notoacmea onychitis (Menke, 1843)	On rocks	X	-	-	-	-	-	Marine
Patella peronii (Blainville, 1825)	On rocks	X	-	-	-	-	-	Marine
Nerita atramentosa (Reeve, 1855)	On rocks	X	-	-	-	-	-	Marine
Littorina unifasciata Gray, 1826	On rocks	X	-	-	-	-	-	Marine
Hydrobia buccinoides (Quoy & Gaimard, 1834)	In sand	-	X	-	-	X	-	Estuarine
Hydrococcus graniformis Thiele, 1928	In sand	-	X	-	-	-	-	Estuarine
Potamopyrgus sp.	In sand	-	X	X	-	-	-	Estuarine
Tatea preissii (Philippi, 1846)	High intertidal Juncus	X	X	-	-	-	-	Estuarine
Batillariella estuarina (Tate, 1893)	In sand	-	X	-	-	-	-	Estuarine
Diala lauta A. Adams, 1862	In sand	-	X	-	-	-	-	Marine affinity
Hipponix conica (Schumacher, 1817)	On shells	X	-	-	-	-	-	Marine
Polinices conicus (Lamarck, 1822)	On sand	X	-	-	-	-	-	Marine
Bedeva paivae Cross, 1864	On rocks	X	-	-	-	-	-	Marine affinity

Table 1 (Contd.) Mollusc species collected in the Peel-Harvey estuarine system.

Species	Habitat	Mandurah area	Peel Inlet	Harvey Estuary	Murray River	Serpentine River	Harvey River	Affinity
Dicathais orbita (Gmelin, 1791)	On rocks	X	-	-	-	-	-	Marine
Nassarius burchardi (Philippi, 1851)	On sand	X	-	-	-	-	-	Marine affinity
Nassarius pauperatus (Lamarck, 1822)	On sand	X	-	-	-	-	-	Marine affinity
Toledonia sp.	On sand	-	X	X	-	-	-	Unknown
Liloa brevis (Quoy & Gaimard, 1833)	In sand	X	-	-	-	-	-	Marine
Dendrodoris nigra (Stimpson, 1855)	In sand	X	-	-	-	-	-	Marine
Salinator fragilis (Lamarck, 1822)	In sand	X	X	-	-	-	-	Estuarine
Siphonaria luzonica Reeve, 1855	On rocks	X	-	-	-	-	-	Marine
Class Bivalvia								
Brachidontes ustulatus (Lamarck, 1819)	On rocks	X	-	-	-	-	-	Marine
Mytilus edulis planulatus Lamarck, 1819	On rocks	X	X	-	-	-	-	Marine affinity
Xenostrobus securis (Lamarck, 1819)	On logs	-	X	-	X	-	-	Estuarine
Westralunio carteri Iredale, 1934	In mud	-	-	-	X	-	X	Freshwater
Arthritica semen (Menke, 1843)	In sand	X	X	X	X	X	-	Estuarine
Notospisula trigonella (Lamarck, 1818)	In sand	X	X	X	-	-	-	Marine affinity
Macomona mariae (Tenison Woods, 1875)	In sand	-	X	-	-	-	-	Marine

Table 1 (Contd.) Mollusc species collected in the Peel-Harvey estuarine system.

Species	Habitat	Mandurah area	Peel Inlet	Harvey Estuary	Murray River	Serpentine River	Harvey River	Affinity
Tellina deltoidalis Lamarck, 1818	In sand	X	X	-	-	-	-	Marine affinity
Tellina sp.	In sand	-	X	-	-	-	-	Unknown
Sanguinolaria biradiata (Wood, 1815)	Sand	X	X	-	-	-	-	Marine affinity
Irus crenata (Lamarck, 1818)	In rocks	X	X	-	-	-	-	Marine affinity
"*Anticorbula*" *amara* (Laseron, 1956)	On logs	-	X	X	X	X	-	Estuarine

Table 2. Affinity groupings of molluscs found in the Peel - Harvey estuarine system.

Grouping	Area				Total
	Mandurah	Peel	Harvey	Harvey R.	
Marine	12	1			13
Marine affinity	8	6	1		9
Estuarine	3	9	3		9
Freshwater				1	1
Undetermined		2	1		2
Total	23	18	5	1	34

species collected at Mandurah to the Harvey River, in which only a single freshwater species was found. All 9 of the estuarine species were recorded in Peel Inlet; 3 estuarine species were collected in Harvey Estuary and 3 at Mandurah.

The same classification scheme was used to categorize molluscs in other southwestern estuaries and marine embayments. The collections of the Western Australian Museum were utilized for this and additional material was collected in December 1979 (Table 3). The list is conservative; only those species which occur in estuaries and not in the open sea are recorded. Only limited distributional data are available for most species and nothing is known of their salinity tolerances. Because of this the classification of species is partly subjective and other authors might disagree. For example three cockles of the genus Katelysia occur on sandflats at the mouths of estuaries in the southwest. They are affected by lowered salinity for only brief periods during the year and we believe the species are better regarded as being of marine affinity; other authors might classify Katelysia as estuarine.

Table 3 shows there is a small suite of truly estuarine species in the southwest, most of which are widely distributed in the 12 estuaries and marine embayments surveyed. The Peel - Harvey system has the most estuarine species with 9 and several other estuaries have 7. The 9 species were recorded during a 3 year concentrated study during which several rare species were collected. Batillariella estuarina for example was recorded from a single live individual. Seven estuarine species were recorded from Broke Inlet in a single morning

Table 3. Distribution of "estuarine" species in southwestern Australian estuaries.

Species	Swan Estuary	Peel-Harvey estuarine system	Leschenault Inlet Estuary	Blackwood River estuary	Broke Inlet	Nornalup Inlet	Irwin Inlet	Parry Inlet	Wilson Inlet
Gastropods									
Batillariella estuarina		X		X				X	
Hydrobia buccinoides		X							
Hydrococcus graniformis	X	X	X	X	X	X	X		X
Potamopyrgus sp.	X	X	X	X	X	X	X	X	X
Salinator fragilis		X	X		X	X	X		X
Tatea preissi	X	X	X	X	X	X	X		X
Velacumantus australis	X								
Bivalves									
"*Anticorbula*" *amara*	X	X	X	X	X	X	X		X
Arthritica semen	X	X		X	X	X	X	X	X
Xenostrobus inconstans									
Xenostrobus securis	X	X	X	X	X	X	X		X

Table 3. Cont.

Species	Estuary Princess Royal Harbour	Oyster Harbour	Beaufort Inlet
Gastropods			
B. estuarina	X	X	
H. buccinoides		X	
H. graniformis	X	X	X
Potamopyrgus sp.			X
S. fragilis	X	X	
T. preissi			
V. australis			
Bivalves			
A. amara			
A. semen		X	
X. inconstans	X	X	
X. securis		X	

(Table 3). It is likely that concentrated collecting in Broke Inlet and several of the other estuaries would uncover more species, and the fact that Peel - Harvey has the highest recorded number of estuarine species should be considered with this in mind.

CHAPTER 4

DENSITY FLUCTUATIONS, GROWTH AND BIOMASS AT COODANUP

Introduction

During the initial survey of the Peel - Harvey estuarine system dense populations of Hydrococcus graniformis and Arthritica semen were found at Coodanup. A two year sampling programme was undertaken at Coodanup to establish such basic parameters of the two populations as fluctuations in densities, growth rates, and dry tissue biomass. With these data as a basis detailed studies could then be undertaken on the mechanisms which allow the populations of H. graniformis and A. semen to attain such high densities in the estuary.

Materials and Methods

Samples were collected monthly from March 1977 to February 1979 at Coodanup beach in Peel Inlet (Figure 2). 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. Salinities at the station varied from 2‰ to 53‰ and temperatures from 10^{o}C to 27^{o}C. 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. graniformis. Ten replicate samples were collected each month and were treated

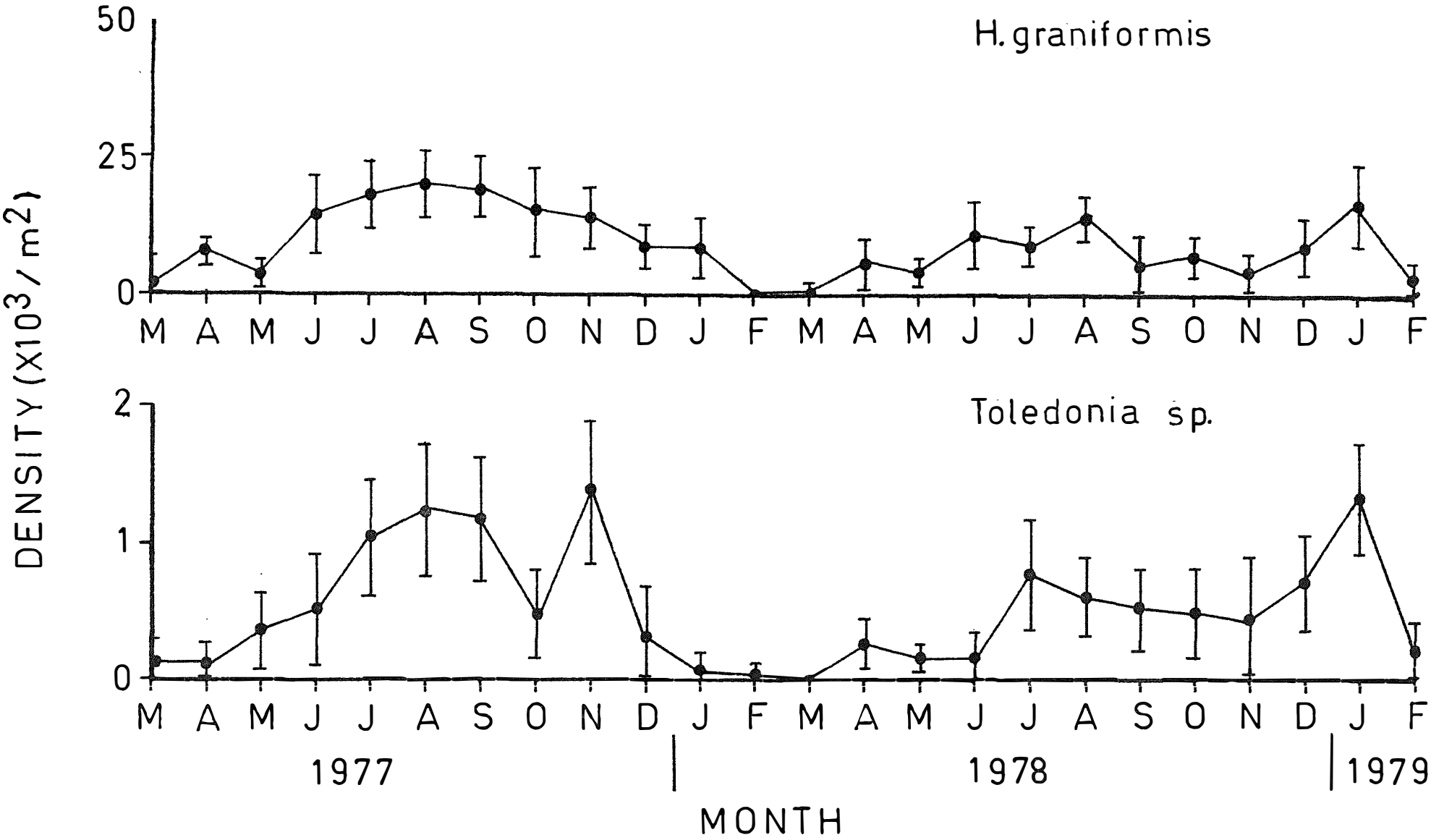
individually. All live molluscs were identified and counted. Three hundred individuals of H. graniformis, 200 of A. semen and as many individuals as possible of the other species were measured to the nearest 0.1 mm each month using a dissecting microscope equipped with an ocular micrometer. All H. graniformis egg capsules on the live molluscs were counted.

Results

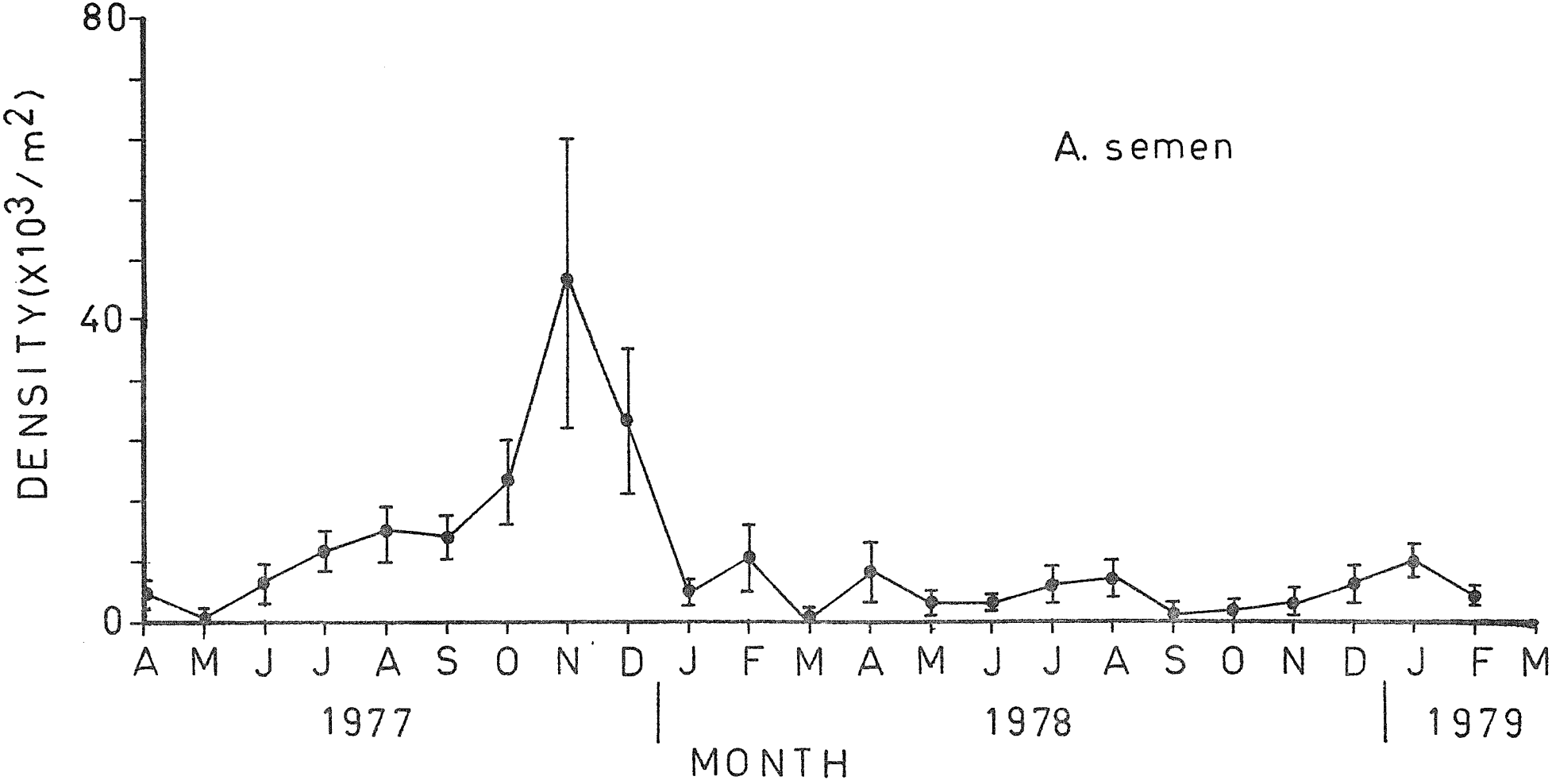
Population densities

Five species were collected in 6 or more months of the sampling programme at Coodanup: H. graniformis, A. semen, Tornatina sp., Potamopyrgus sp. and Toledonia sp. In addition 4 specimens of S. fragilis were collected in the routine samples. The intensive study reported later showed that low numbers of Macomona mariae and T. preissi are also present. The Coodanup samples collected from March 1977 to February 1979 were dominated by H. graniformis and A. semen, which constituted 48.3 and 41.2% respectively of the mean density of 19,650/m^2 (Table 4). Tornatina sp. (4.7%), Potamopyrgus sp. (3.1%) and Toledonia sp. together comprised only 10.4% of all molluscs collected.

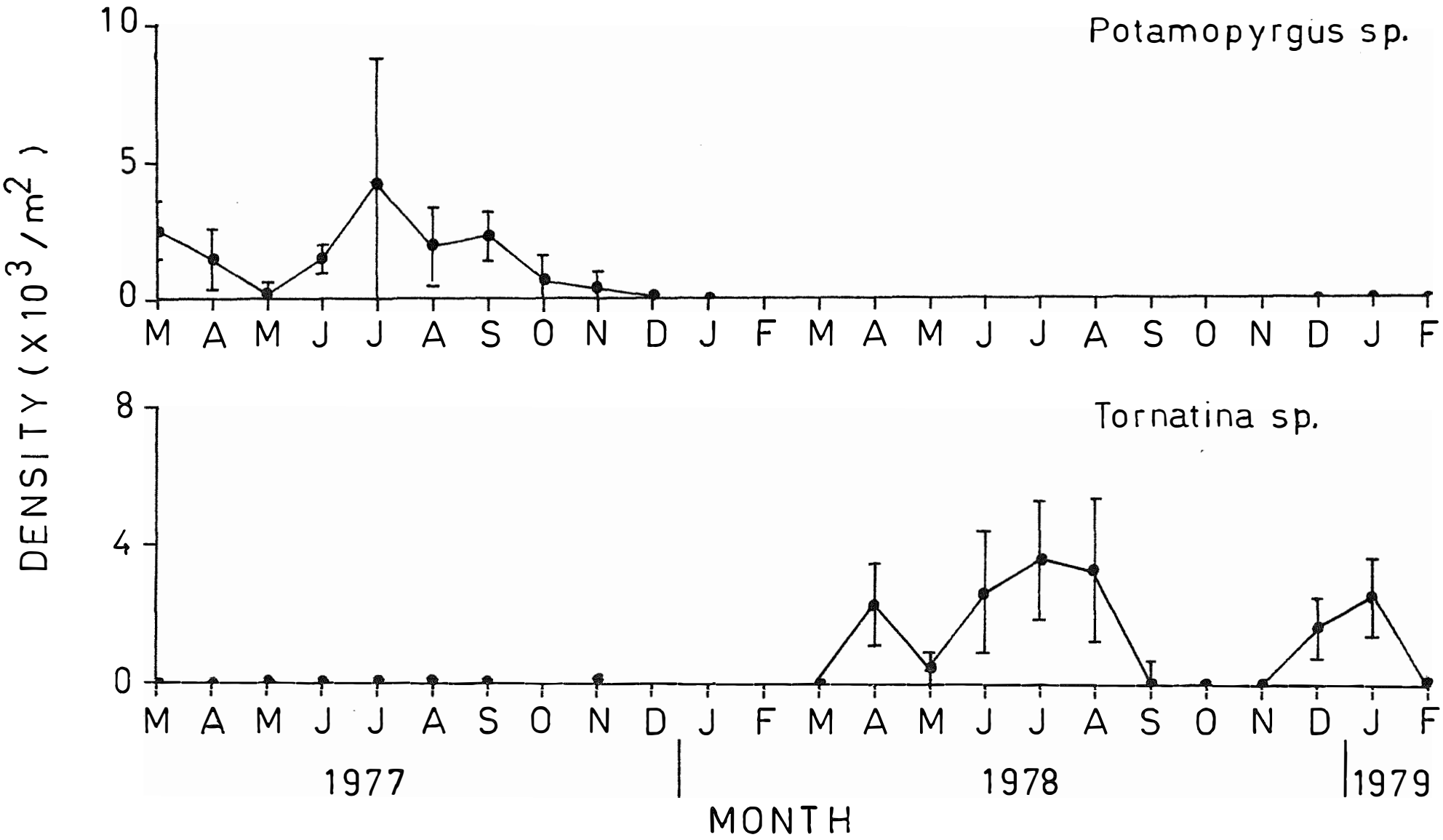
Density fluctuations of the five species regularly collected at Coodanup are shown on Figures 3, 4 and 5. All species showed considerable variation over the two years and many month to month changes were dramatic: the population of A. semen for example declined from 45,491/m^2 in November 1977 to 4,893/m^2 in January 1978. Three patterns are demonstrated on the figures. Hydrococcus graniformis and Toledonia sp. had similar population densities in the two years (Figure 3).



3. Densities of Hydrococcus graniformis and Toledonia sp. at Coodanup from March 1977 to February 1979. The mean and one standard deviation are shown.



4. Densities of Arthritica semen at Coodanup from March 1977 to February 1979. The mean and one standard deviation are shown



5. Densities of Potamopyrgus sp. and Tornatina sp. at Coodanup from March 1977 to February 1979. The mean and one standard deviation are shown.

Table 4. Population characteristics of species collected at Coodanup from March 1977 to February 1979.

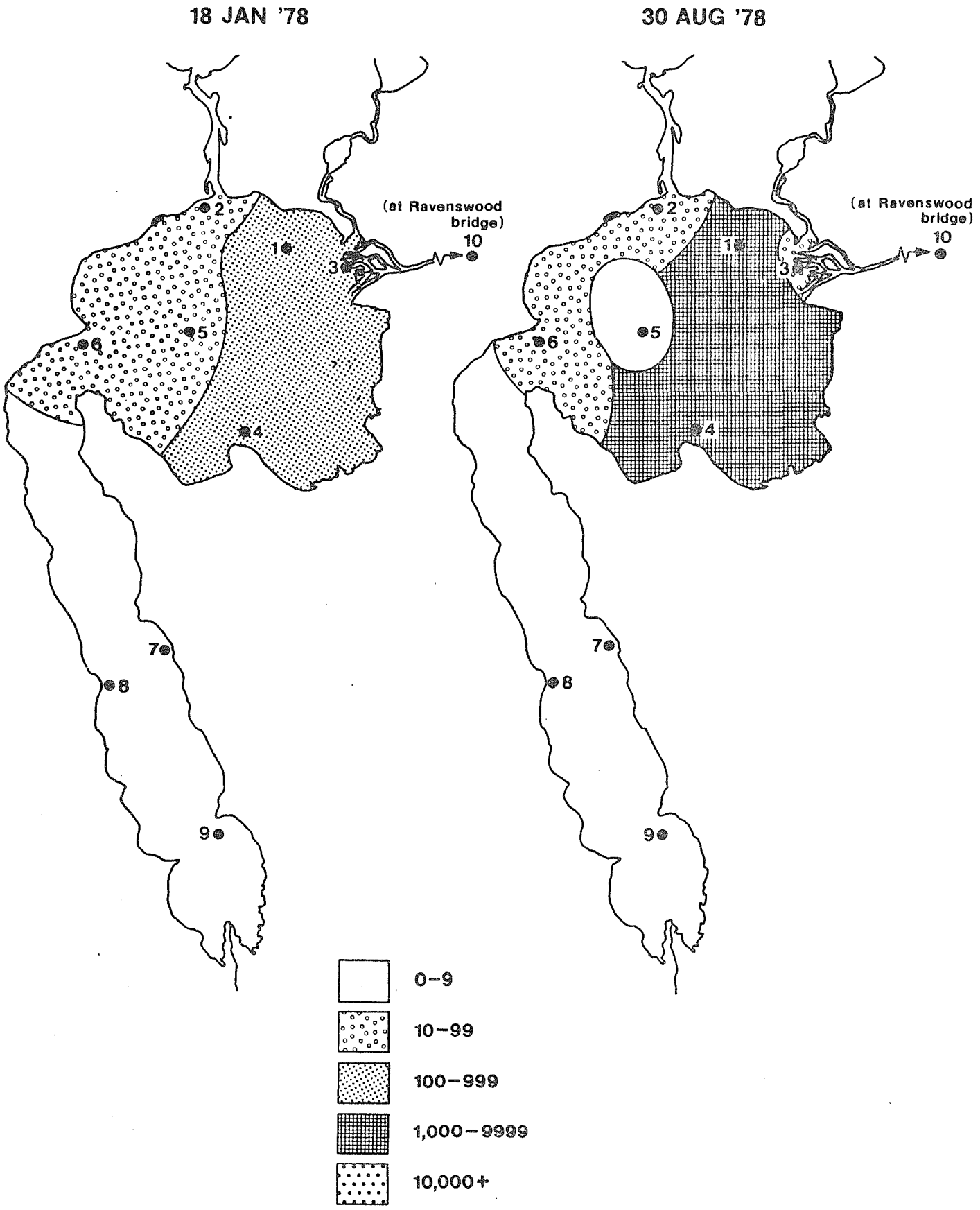
Species	Population density (no./m^2) Minimum	Maximum	Mean	Percent of total
Hydrococcus	700	19959	9487	48.3
Arthritica	0	27847	8105	41.2
Tornatina	0	4790	931	4.7
Potamopyrgus	0	4274	610	3.1
Toledonia	0	1391	517	2.6
TOTALS			19650	99.9

Arthritica semen (Figure 4) and Potamopyrgus sp. (Figure 5) had higher densities in the first year than in the second; only isolated individuals of Potamopyrgus sp. were collected after December 1977. Isolated individuals of Tornatina sp. were collected in the first year of sampling, but the species was consistently present in the second year.

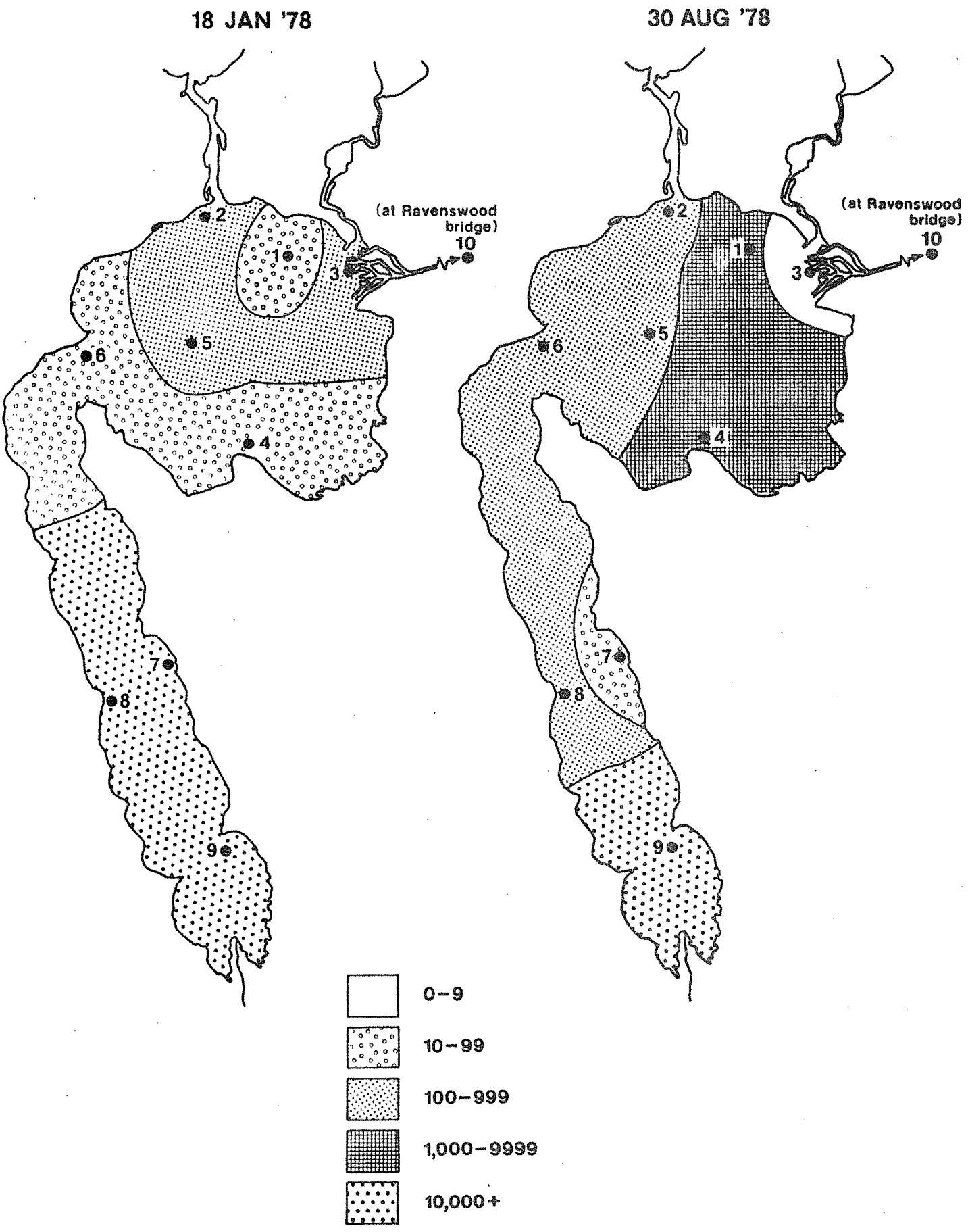
Densities in other areas

Because of the considerable time required to sort the monthly samples only one site could be monitored continuously. Samples were taken in other areas in January and August 1978, summer and winter respectively, to obtain estimates of the densities of H. graniformis and A. semen in other parts of the Peel-Harvey system. Ten sites were selected (Figures 6 and 7) to provide a coverage of the various habitats available to the two species in the estuary. Each site was sampled with the methods described for the Coodanup site.

The results of the survey are shown on Figures 6 and 7. In both seasons H. graniformis and A. semen were widespread in Peel Inlet, but H. graniformis was absent in Harvey Estuary and the Murray River. High densities of A. semen were encountered in Harvey Estuary and the species was present in the Murray River in January. Population density of H. graniformis in Peel Inlet increased from a mean of 196/m^2 in January to 1391/m^2 in August and A. semen went from 175/m^2 to 810/m^2. In Harvey Estuary A. semen had the reverse trend; the population declined from a mean of 23,281/m^2 in January to 4,836/m^2 in August.



6. Distribution of Hydrococcus graniformis in the Peel-Harvey estuarine system in January (summer) and August (winter) 1978.

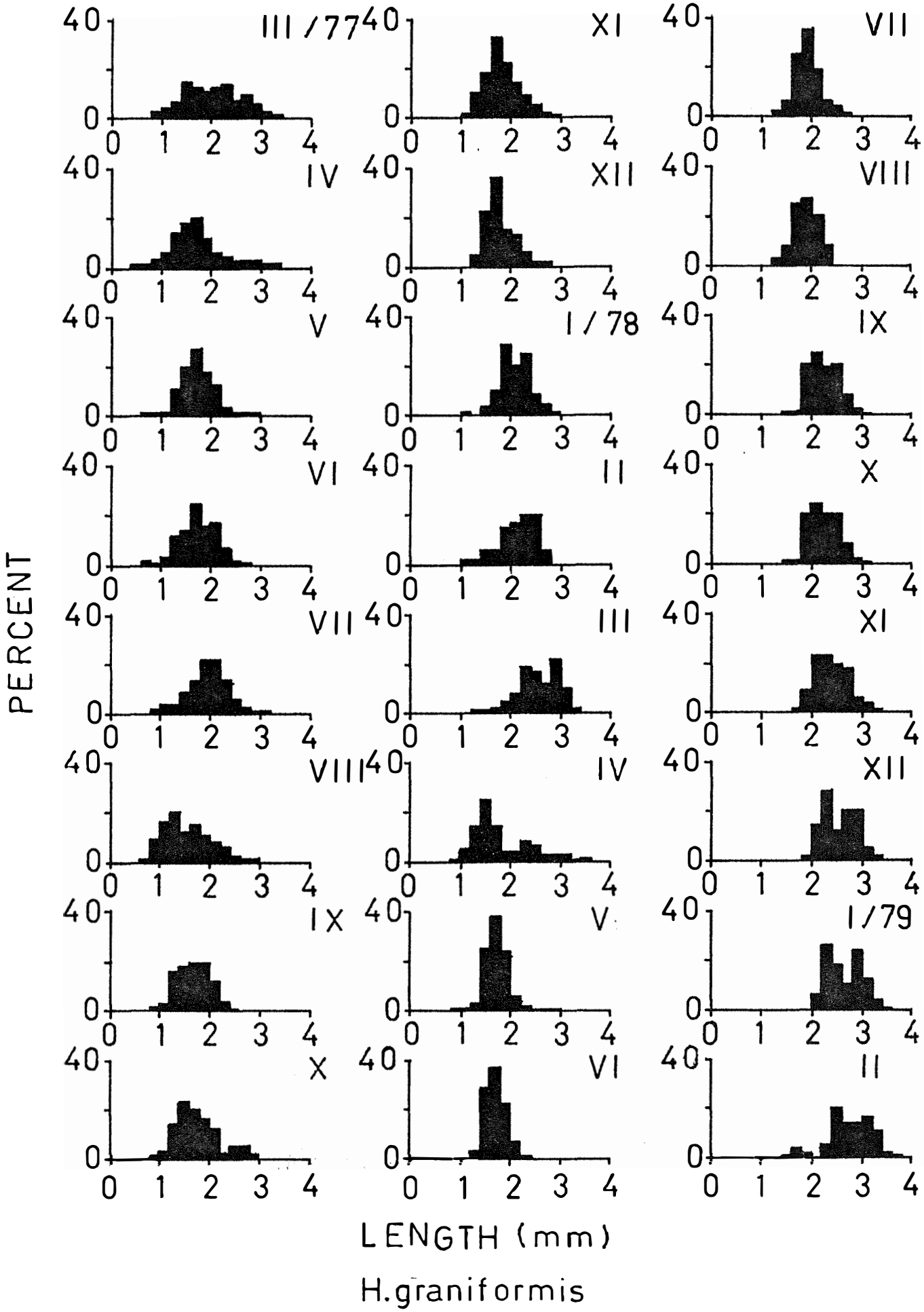


7. Distribution of Arthritica semen in the Peel-Harvey estuarine system in January (summer) and August (winter) 1978.

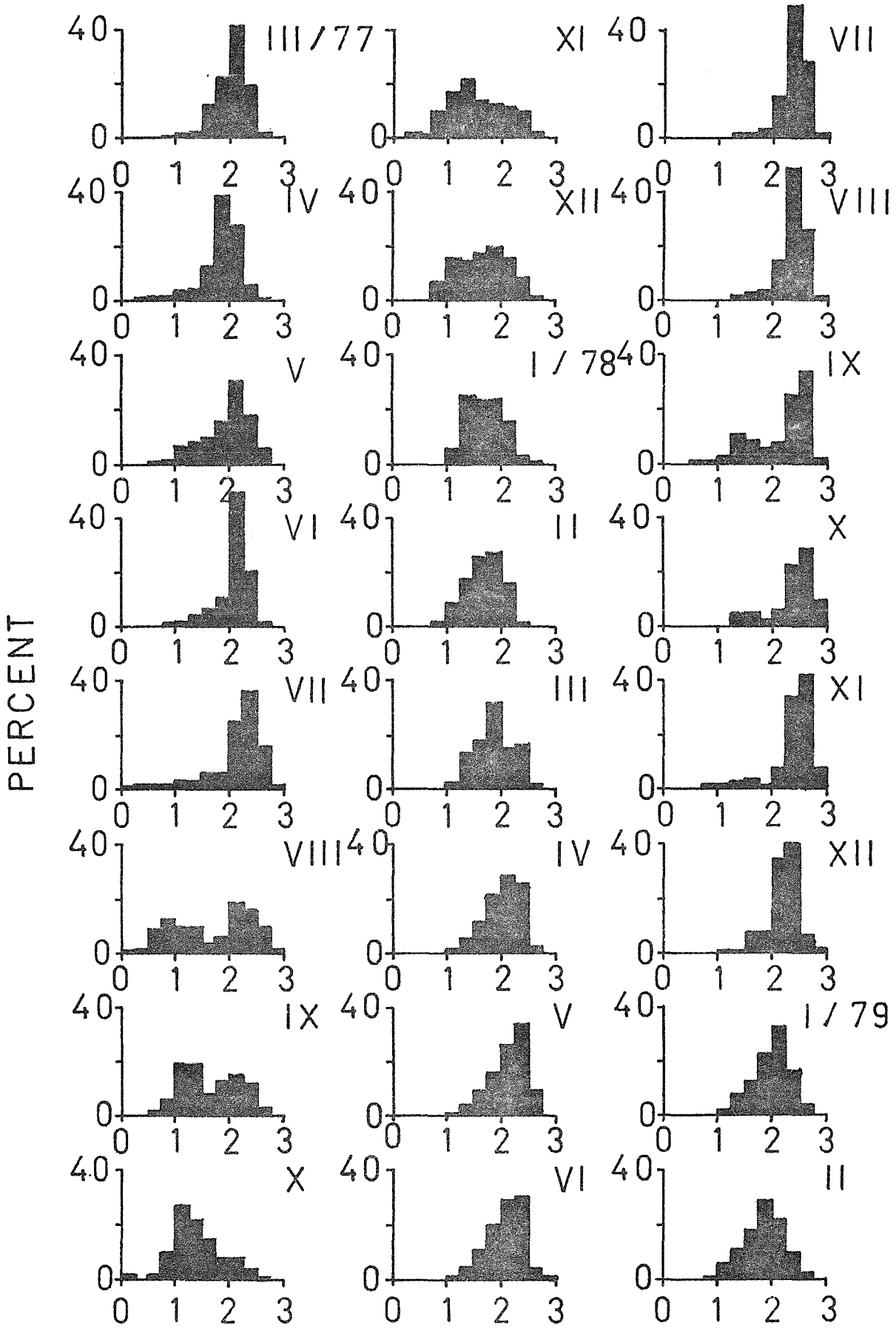
Growth

The size-frequency histograms of H. graniformis and A. semen collected at Coodanup during the two year sampling programme are shown on Figures 8 and 9. In examining the size-frequency histograms the mesh size of 1.0 mm used to collect the samples should be considered. Individuals smaller than 1.0 mm were in fact collected because they were trapped in the debris retained by the sieve, but it is doubtful that any size fraction smaller than 1.0 mm of the population of any of the three species was effectively sampled. The peak at 1.4 to 1.6 mm in the H. graniformis population in April 1978 was not apparent in the samples collected in March. This does not imply that the group of individuals in the 1.4 to 1.6 mm size class in April had grown to that size in a single month, but rather that they grew from a size of 1.0 mm or less.

All three species demonstrated steady recruitment throughout the study period. Because of the absence of discrete reproductive periods leading to recruitment in a restricted period the size-frequency histograms could not be used to directly estimate growth. However, Harding (1949) and Cassie (1954) described a method of estimating growth from such data using a probability paper method. The cumulative percentage of the population is plotted against size on probability paper. Inflection points, where the slope of the line changes, indicate the means of distinct groups of individuals. The growth of these groups can be examined sequentially in subsequent months. The probability paper method was applied to the data for H. graniformis and A. semen at Coodanup and resulted in an estimate of growth of 0.5 mm/month for H. graniformis and 0.3 mm/month for A. semen. These



8. Size-frequency histograms of Hydrococcus graniformis collected at Coodanup from March 1977 to February 1979.



A. semen

9. Size-frequency histograms of Arthritica semen collected at Coodanup from March 1977 to February 1979.

estimates are based on the young, rapidly growing portions of the populations with large numbers of individuals. Older individuals, which have begun to channel their available energy resources into sexual development and gamete production, probably have lower growth rates. Cassie (1954) presented a method for estimating mortality but the continuous reproduction shown by both H. graniformis and A. semen precluded its use for either species.

Growth rates of the two species have been used to provide a rough estimate of the lifespans and the times required to reach maturity (Table 5). Because only the small, rapidly growing individuals could be used in establishing an overall growth rate the times required to reach each developmental stage on Table 5 are underestimated. Hydrococcus graniformis matures in about 4 months and A. semen in 6 months. They can reach maximum size in 7 to 8 and 9 months respectively, but it is probable that a portion of the adults survive for a second year, though no annual rings were found on the shells.

Length-tissue weight relationship

Thirty-nine individuals of A. semen and 47 of H. graniformis were used to determine the length-tissue weight equations. The individuals selected were chosen to cover as much of the size range of each species as possible. Shells were measured with an ocular micrometer and were removed with a dilute solution of hydrochloric acid. The animals were then dried to a constant weight at 80^{o}C. The relationship between shell length and dry tissue weight was calculated from the equation $\ln Y = a + \ln X$ where X is shell length in mm and Y is dry tissue weight in mg. The equation for A. semen is $\ln Y = -1.13 + 2.14 \ln X$ and

Table 5. Times required to reach maturational stages for Hydrococcus graniformis and Arthritica semen at Coodanup in Peel Inlet.

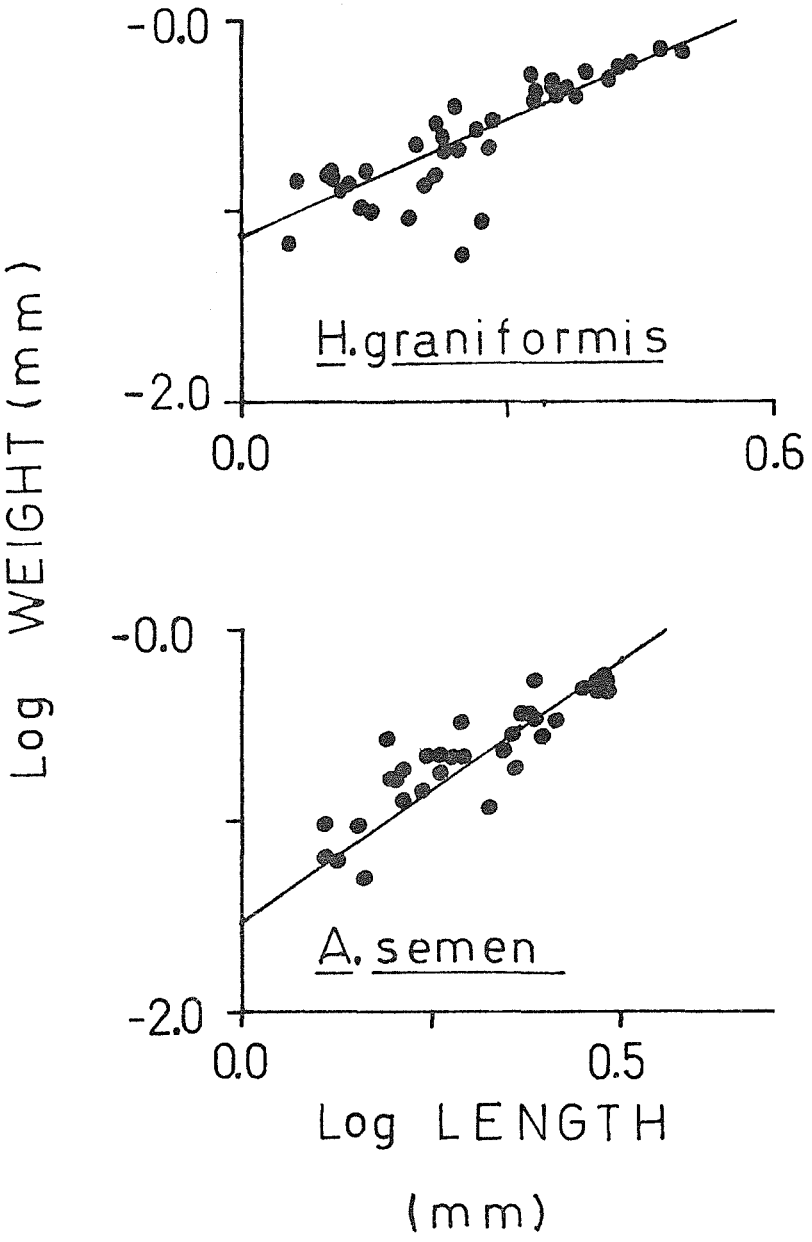
Stage	Species			
	Hydrococcus		Arthritica	
	Size (mm)	Months	Size (mm)	Months
Release	0.3	2/3	0.3 0.5	1-2
Maturity	2.0	4	2.0	6
Time to reach maximum size	3.8	7-8	3.0	9

for H. graniformis it is lnY = -1.51 + 2.58 lnX. The plots of the two equations and the data from which they are calculated are shown on Figure 10. The equation for A. semen explains 79.7% of the observed variation and that of H. graniformis explains 98.5%.

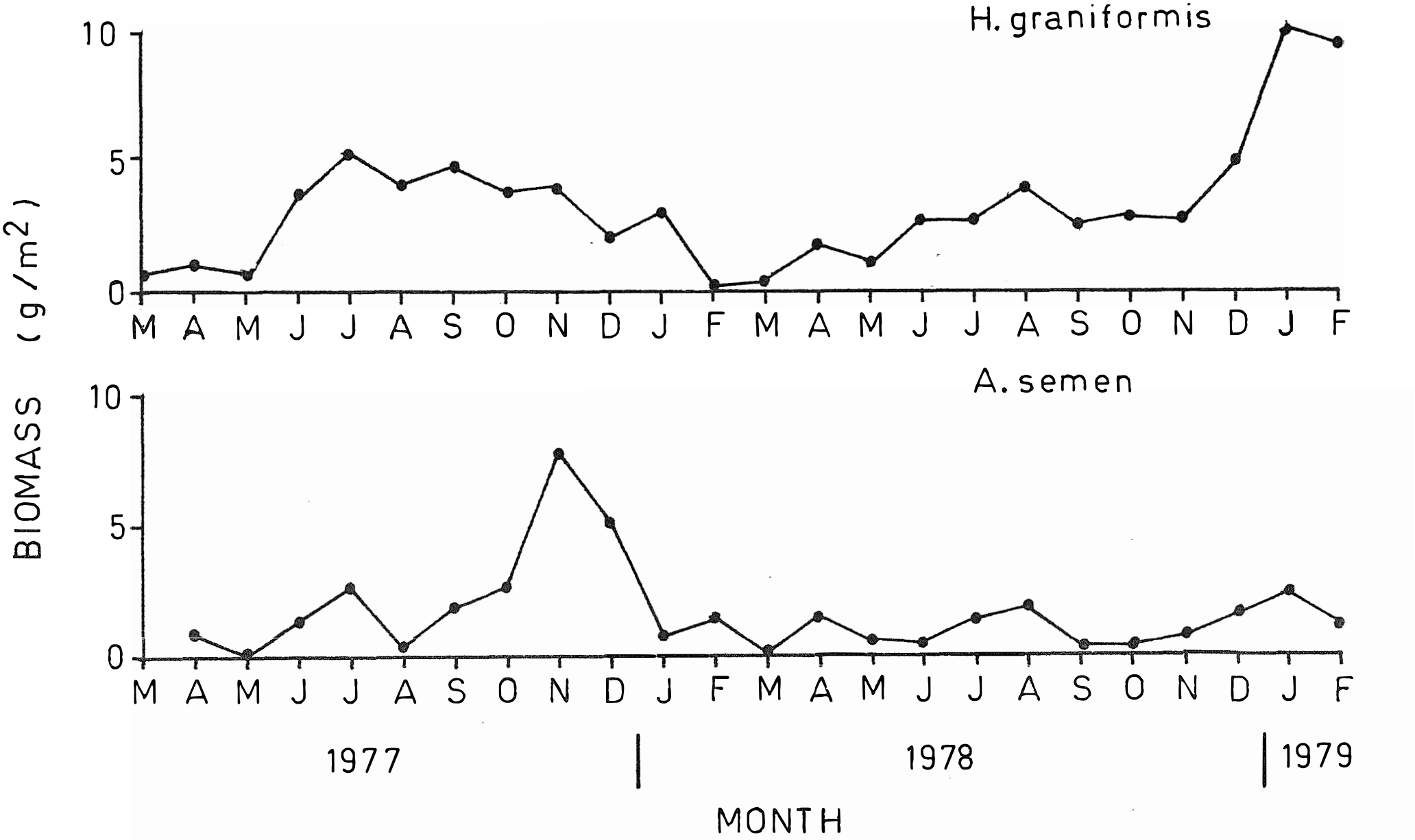
Biomass

The biomass of H. graniformis and A. semen fluctuated considerably during the two years (Figure 11). While the biomass figures are affected to some extent by changes in the size-frequency curves, most of the biomass fluctuations are caused by density variations.

Buchanan and Warwick (1974) provided production estimates for several small marine invertebrates in a temperate marine environment. The lifespans and weights of these animals are similar to H. graniformis and A. semen. All had production/biomass ratios of 1.9 to 2.5. Puttick (1977) found a P/B ratio of 5.0 for Assiminea globulus in South Africa. If it is assumed that the P/B ratios of H. graniformis and A. semen are similar an estimate of the production of the two species at Coodanup can be obtained. Mean biomass of H. graniformis was 3.4 g/m^2 and A. semen was 1.7 g/m^2; tissue production (dry weight) would then be 6.5 to 16.3 $g/m^2/yr$ for H. graniformis and 3.3 to 8.2 $g/m^2/yr$ for A. semen. If the estimates are extrapolated to the entire system, based on densities in Appendix 6, estimates of 0.3 to 0.8 $g/m^2/yr$ for H. graniformis and 2.4 to 6.0 $g/m^2/yr$ for A. semen are obtained. These figures are small, but when multiplied by the area of the system estimate the total dry tissue production of H. graniformis at 30 to 75 metric tons per year and A. semen at 300 to 750 metric tons per year.



10. Length-weight regressions for Hydrococcus graniformis and Arthritica semen collected at Coodanup in Peel Inlet.



11. Biomass of Hydrococcus graniformis and Arthritica semen at Coodanup from March 1977 to February 1979.

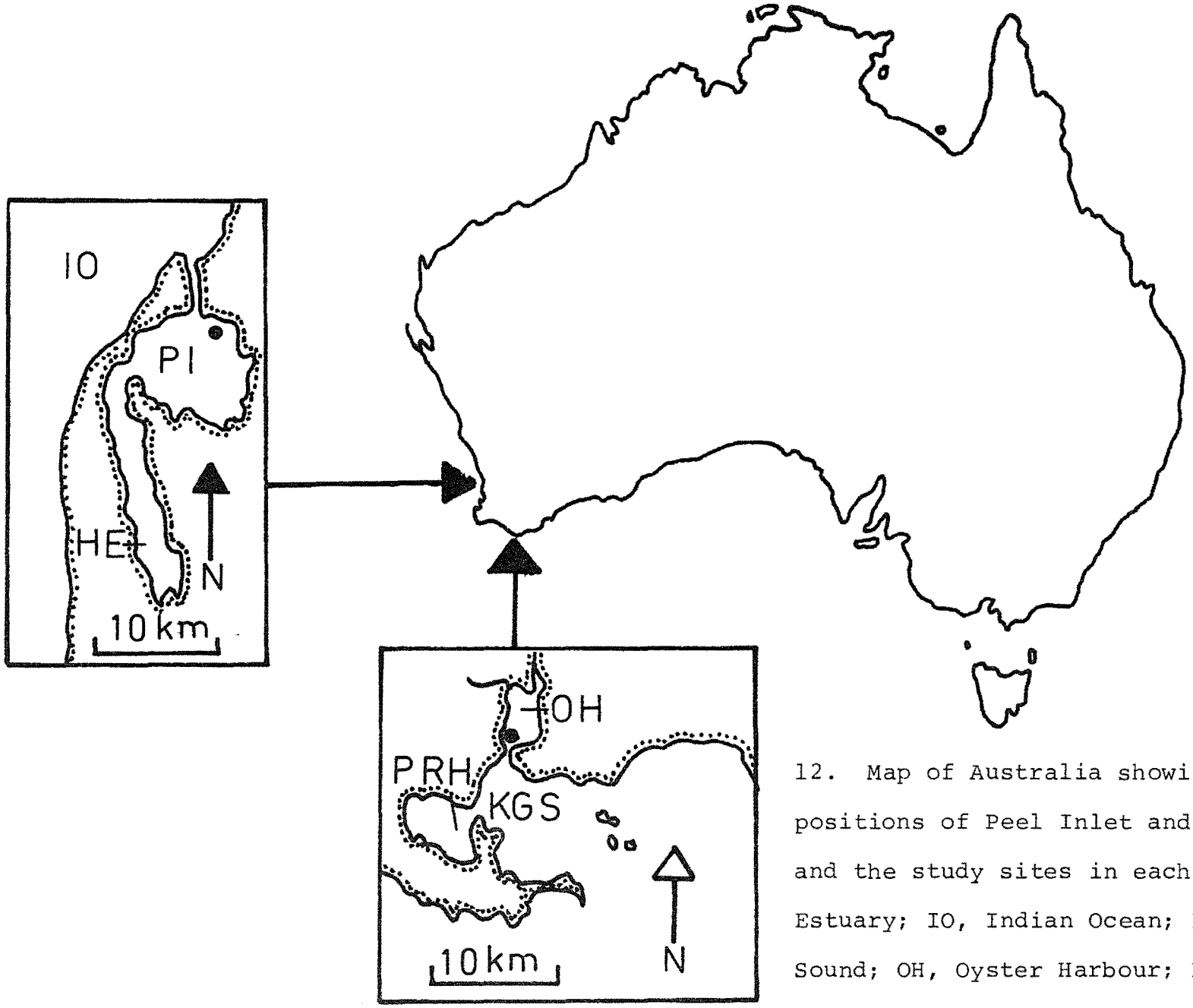
COMPARISON OF THE MOLLUSCS AT COODANUP WITH THOSE AT EMU POINT, OYSTER HARBOUR, ALBANY.

Introduction

During the general survey of the Peel-Harvey estuarine system it became obvious at an early stage that large benthic molluscs are almost entirely absent. However, large molluscs are present in other estuaries and marine embayments in southwestern Australia, such as the Swan River (Chalmer et al. (1976)) and Oyster Harbour (McKenzie, 1962). In an attempt to elicit hypotheses to explain the lack of large molluscs in Peel Inlet a comparison was made of the molluscs of the intertidal sandflat in Peel Inlet at Coodanup and a similar environment in another estuary. Oyster Harbour was chosen because it has the largest number of mollusc species of any estuary in southwestern Australia (Hodgkin, 1977; Roberts and Wells, in press). The two sandflats chosen were selected to be as comparable as possible in terms of shore height, sediment parameters, and location in their respective estuaries in terms of relation to freshwater inflows and the outlet channel.

Materials and Methods

Four transects 50 m apart were established at Coodanup on 16 and 20 November 1978 (Fig. 12) and at Emu Point in Oyster Harbour between 26 November and 8 December 1978. Each transect in Peel Inlet ran into the water from the hightide line for a distance of 100 m and was sampled at 10 m intervals.



12. Map of Australia showing the relative positions of Peel Inlet and Oyster Harbour and the study sites in each area. HE, Harvey Estuary; IO, Indian Ocean; KGS, King George Sound; OH, Oyster Harbour; PI, Peel Inlet; PRH, Princess Royal Harbour.

At each station a substrate sample $\frac{1}{4}m^2$ and 10 cm deep was collected and sieved through a steel mesh with apertures of 2 mm, in Oyster Harbour the transect was 200 m long with samples collected every 20 m. All live molluscs and all shells of Zeacumantus diemenensis and Batillariella estuarina collected were preserved in 10% formalin. In the laboratory all individuals were counted, excess water blotted off, and weighed to 0.1g on a Kahn microbalance. Subsamples of Z. diemenensis and B. estuarina were broken open to determine the ratio of live collected individuals to empty shells. Total number of individuals and total weights of both species were then adjusted accordingly. At each station a sample of $0.01\ m^2$ was removed and sieved through a 1 mm mesh. The remaining material was sorted under a dissecting microscope. All individuals of species not retained in the large mesh were identified, counted and weighed to 0.01g.

Depths of all stations were measured relative to each other as the tide rose. Depths relative to the tidal datum were calculated by comparing the level at high tide with the tidal predictions published for Bunbury and Albany (Anon, 1978).

A sediment sample of approximately 300 ml was collected and dried for 24 hours at approximately $80^{o}C$. All organic material was removed by adding hydrogen peroxide and heating the sediment to $60^{o}C$ for at least 24 hours. Subsequent addition of hydrogen peroxide produced no further reactions. Samples were then dried at $60^{o}C$ for 24 hours and sieved through a series of graded screens with mesh apertures of 1000, 500, 250, 125, and 63 µm. Each fraction was weighed separately to 0.1g. Phi values were calculated on the

Udder-Wentworth scale (Blatt, Middleton and Murray, 1972). The highest value of 5 was assigned to the fraction less than 63 μm and the lowest value of 1 was given to the fraction which was retained on the 500 μm sieve. Sediment characteristics were determined for each tidal level by methods described in Svedrup, Johnson & Fleming (1942) and Buchanan (1971).

Overlap between the molluscs collected at different depth levels was calculated using the modified Morisita (1959) index discussed by Horn (1966). The index has a value of 1 where the overlap is complete and 0 where there is no overlap. The dendrogram was calculated by the weighted pair group method using average linkage (Sokal and Sneath, 1963). The Simpson and the Shannon Wiener indices of species diversity were estimated for each tidal level using the equations cited by Krebs (1972).

Results

Features of the study areas

The beach at Coodanup has been described in the general description of Peel Inlet (Chapter 2).

Oyster Harbour is a shallow body of water 20 km^2 in area (Fig. 12) which was formed during the Pleistocene by the drowning of the King and Kalgan Rivers (McKenzie, 1962). Both rivers still flow into the harbour with the maximum flows occurring during the winter and little or no flow occurring during the summer. A channel leads from Oyster Harbour to the sea at Emu Point. The harbour is shallow with depths of 2 m or less except in the drowned river channels,

where the maximum depth can reach as much as 13 m. The tidal range at Albany is only 1.0 m throughout the year, and the mean tidal range is 0.4 m (Anon, 1978). Tides are variable: most are semidiurnal but at times are diurnal, or periods of several hours with the tidal level static at the midtide level occur. Predicted levels are substantially altered by atmospheric conditions (Hodgkin and DiLollo, 1958). The annual variation in water temperature at Emu Point is from 13 to 25^{o}C (McKenzie, 1962).

The shoreline at the study site is a gently sloping beach with muddy sand. The depth range between the hightide line and the end of the transects 200 m seaward is only 0.55 m; the entire area is exposed on exceptionally low tides. The lowest level examined is at about the extreme low water level. Considerable amounts of broken shell fragments occur on the beach. The characteristics of the sediment at the study site in Oyster Harbour are shown on Table 6. The striking feature of Table 6 is the uniformity of the measurements. The Ø value varied from 1.8 to 2.1 and the percentage of silts and clays in the sediment ranged from 0.10 to 0.24. The variations in the parameters measured at Coodanup were also small (Table 6). Sediments in both areas are well sorted, with those at Coodanup being coarser (median Ø values of 1.1 to 1.4) than those of Oyster Harbour (1.8 to 2.1).

Comparison of the molluscan faunas of the two areas

Table 7 shows the molluscs collected in Peel Inlet and Oyster Harbour during this quantitative study. Only 6 species were recorded in Peel Inlet while 24 were found in Oyster

Table 6. Characteristics of the sediments on intertidal sandflats in Peel Inlet and Oyster Harbour, Western Australia.

Shore height (m)	Median particle diameter (Ø)	Sorting coefficient (Ø)	Skewness (Ø)	Percentage silts & clays (by weight)
PEEL INLET				
-0.13	1.4	0.55	+0.10	0.60
-0.18	1.3	0.60	+0.05	0.65
-0.23	1.3	0.50	+0.10	0.80
-0.28	1.4	0.45	+0.05	0.50
-0.33	1.4	0.48	+0.03	0.70
-0.38	1.3	0.48	+0.05	0.54
-0.43	1.4	0.58	+0.03	0.80
-0.48	1.2	0.70	+0.05	1.10
-0.53	1.1	0.85	+0.03	0.50
OYSTER HARBOUR				
0.53	2.1	0.45	-0.08	0.24
0.48	2.1	0.52	-0.08	0.21
0.43	2.0	0.45	-0.07	0.12
0.38	2.0	0.46	-0.08	0.10
0.33	1.8	0.50	-0.03	0.10
0.28	2.0	0.43	-0.04	0.12
0.23	1.9	0.38	-0.01	0.13
0.18	2.0	0.41	-0.06	0.10
0.13	2.0	0.39	-0.01	0.10

TABLE 7. Densities and biomasses of the mollusc species collected on intertidal sandflats in Oyster Harbour and Peel Inlet, Western Australia.

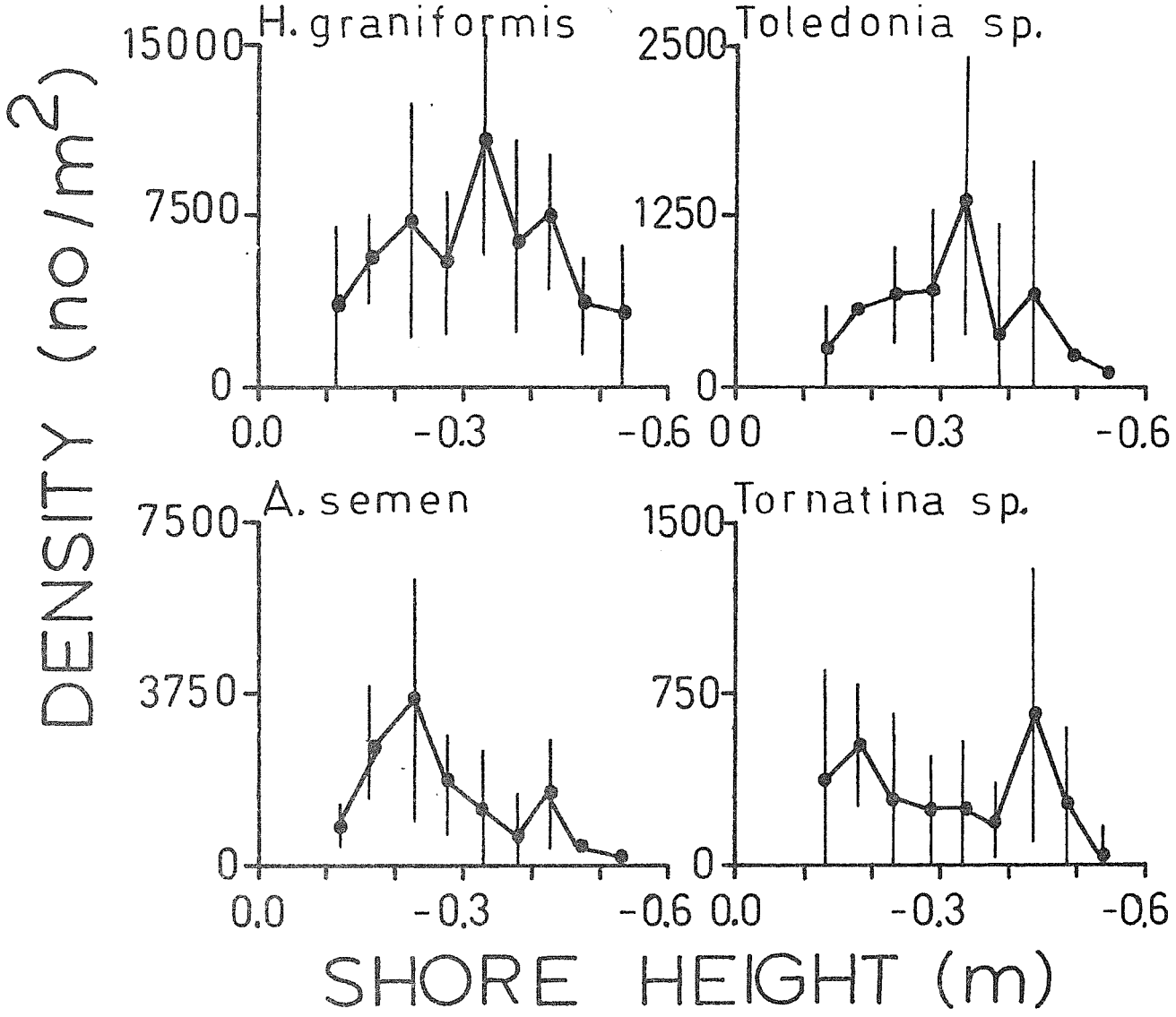
2mm MESH SAMPLES	No. individuals	Mean density (no./m^2)	Mean biomass (g/m^2)
PEEL INLET			
Macomona mariae (Tenison Woods, 1875)	1	0.02	0.01
OYSTER HARBOUR			
Salinator fragilis (Lamarck, 1822)	5672	128.91	30.92
Austrocochlea constricta (Lamarck, 1822)	1286	29.23	28.61
Katelysia scalarina (Lamarck, 1818)	707	16.07	48.19
Nassarius pauperatus (Lamarck, 1822)	382	8.68	8.50
Zeacumantus diemenensis (Quoy and Gaimard, 1834)	349	7.93	5.69
Xenostrobus inconstans (Dunker, 1856)	184	4.18	5.84
Sanguinolaria biradiata (Wood, 1815)	161	3.66	0.20
Bembicium auratum (Quoy and Gaimard, 1834)	80	1.82	1.26
Katelysia peroni (Lamarck, 1818)	32	0.73	1.35
Venerupis crenata Lamarck, 1818	30	0.68	0.50
Wallucina icterica Reeve, 1850	10	0.23	0.07
Nassarius burchardi (Philippi, 1851)	9	0.20	0.16
Brachidontes erosus (Lamarck, 1819)	2	0.05	0.29
Katelysia rhytiphora (Lamy, 1935)	1	0.02	0.67
Cominella eburnea (Reeve, 1846)	1	0.02	0.14
Dentimitrella lincolnensis (Reeve, 1859)	1	0.02	0.03
Bedeva paivae (Crosse, 1864)	1	0.02	0.01
Spisula trigonella (Lamarck, 1818)	1	0.02	0.01
TOTALS	8909	202.47	132.52

1mm MESH SAMPLES	OYSTER HARBOUR		PEEL INLET	
	Mean density (no./m^2)	Mean biomass (g/m^2)	Mean density (no./m^2)	Mean biomass (g/m^2)
Hydrococcus graniformis (Thiele,1928)	4674	18.05	5271	13.15
Arthritica semen (Reeve, 1846)	137	0.65	1322	3.78
Acteocina sp.	0	-----	487	0.83
Toledonia sp.	13	0.00	310	0.41
Tatea preissi (Philippi, 1846)	0	-----	6	0.03
Hydrobia buccinoides (Quoy and Gaimard, 1834)	191	0.35	6	0.01
Batillariella estuarina (Tate, 1893)	3338	51.00	0	-----
Mysella sp.	1512	0.91	0	-----
TOTALS - 1MM MESH	9865	70.96	7402	18.21
TOTALS - ALL SAMPLES	10067	203.48	7402	18.22

Harbour. Four species were common to the two areas, all of which were small species collected on the 1 mm mesh. Hydrococcus graniformis had a maximum density of 10,233/m^2 in Peel Inlet and 12,017/m^2 in Oyster Harbour. The maximum for A. semen in Peel Inlet was 3400/m^2 and the species reached only 483/m^3 in Oyster Harbour. Total densities of the small species at the different shore levels ranged from 2956/m^2 to 13,032/m^2 in Peel Inlet and from 1340/m^2 to 12,613/m^2 in Oyster Harbour. Thus there was a wide variation between different shore levels in each study area that equalled the level of difference encountered between Peel Inlet and Oyster Harbour.

The story is very different for the species retained on the 2 mm mesh. Only a single specimen was collected in the 2 mm mesh samples at Coodanup. This was a small individual of the bivalve species Macomona mariae. Eighteen species were collected on the large sieve in Oyster Harbour (Table 7). These species include a number of common forms which are found in most of the marine embayments and estuaries of the southwest: 3 species of Katelysia, 2 of Nassarius, S. fragilis, Z. diemenensis, B. estuarina, B. erosus, B. nanum and A. constricta. The species collected on the large mesh had an average density of 202.5/m^2 and a mean biomass of 132.5 g/m^2. All eighteen species collected on the 2 mm mesh in Oyster Harbour were completely absent in the Peel Inlet samples.

The mean number of individuals per square meter was ¼ lower in Peel Inlet than in Oyster Harbour: 7402/m^2 in Peel Inlet and 10,067/m^2 in Oyster Harbour. This was due to the numerical dominance of the small species. Biomass in Peel



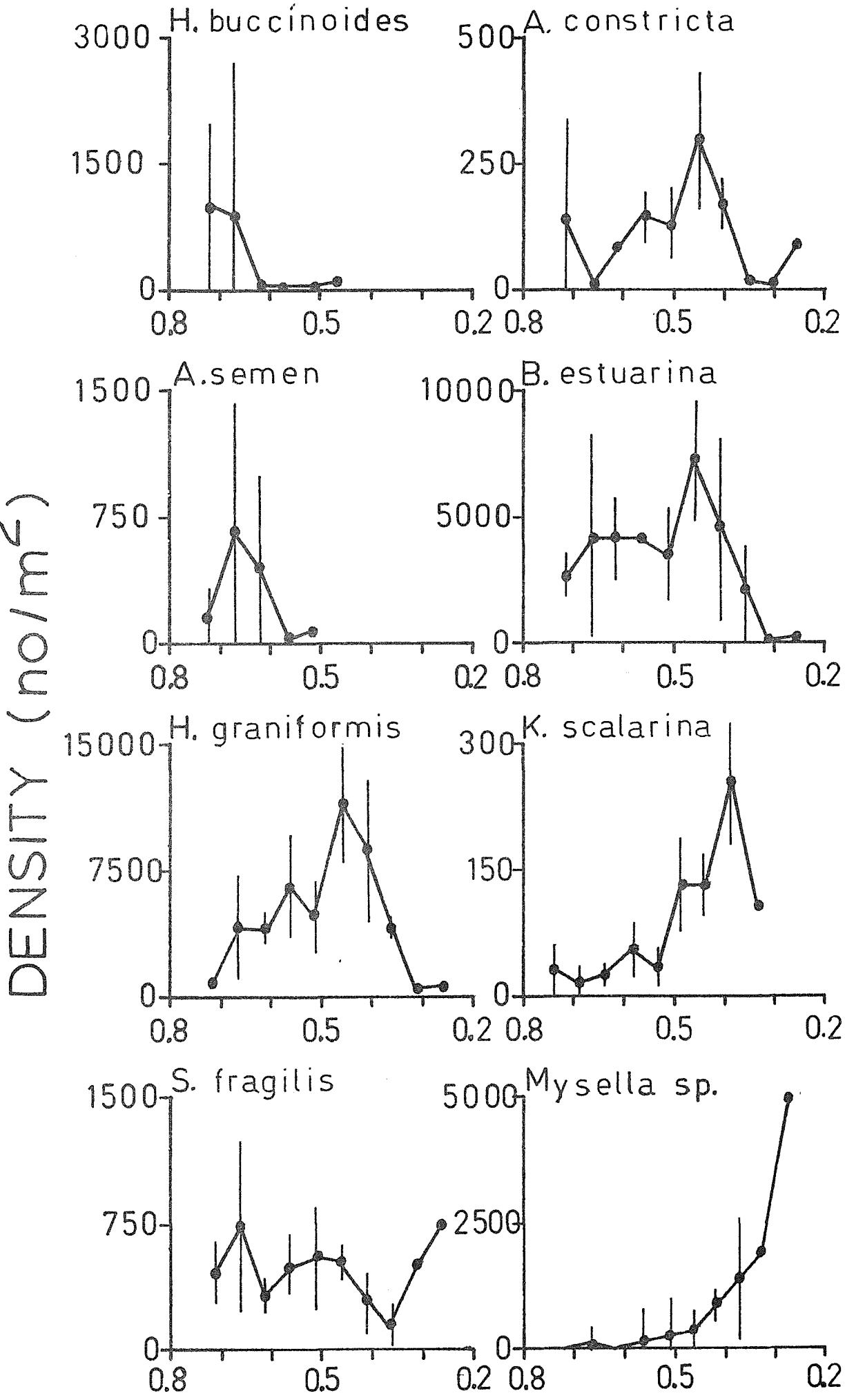
13. Zonation patterns of the numerically abundant species of molluscs on a sandflat in Peel Inlet. The mean and one standard deviation are shown.

Inlet (18.2 g/m^2) was only a tenth of that in Oyster Harbour (203.5 g/m^2). The greater biomass in Oyster Harbour was due to the large biomass of species retained on the 2 mm mesh.

Vertical distributions

The vertical distributions of molluscs in Peel Inlet (Figure 13) are diffuse. H. graniformis reached a peak density in the middle of the study area, as it did in Oyster Harbour. The population of A. semen is concentrated in the upper levels. The species still has high densities below the lowtide line. This is in contrast to Oyster Harbour where A. semen did not extend below the midtide region. Toledonia sp. and Tornatina sp. are widely distributed on the shoreline in Peel Inlet. Toledonia sp. reaches a maximum density in the middle of the survey area, at about the extreme lowtide level. Tornatina sp. occurred at relatively constant levels throughout the area surveyed.

The vertical distributions of eight of the common molluscs in Oyster Harbour are shown on Figure 14. Three patterns can be distinguished on the graphs. Hydrobia buccinoides and A. semen reach their maximum densities in the upper tide levels, above 0.65 m, and are less dense below that level. Potamopyrgus sp. was absent below 0.45 m and A. semen did not occur below 0.50 m. The next four species on Figure 14 (H. graniformis, S. fragilis, A. constricta, and B. estuarina) have their populations centered in the midtide region. H. graniformis and A. constricta reach definite peaks at 0.47 m. The populations of S. fragilis and B. estuarina are more evenly spaced throughout the tidal levels examined. The third pattern on Figure 14 is shown by K. scalarina and M. donaciformis which both attain their population maxima in the lower intertidal areas. The density of M. donaciformis was highest in the



14. Zonation patterns of the numerically abundant species of molluscs on a sandflat in Oyster Harbour. The mean and one standard deviation are shown.

lowest level examined on the shoreline and it is not known whether this species continues to increase in density subtidally.

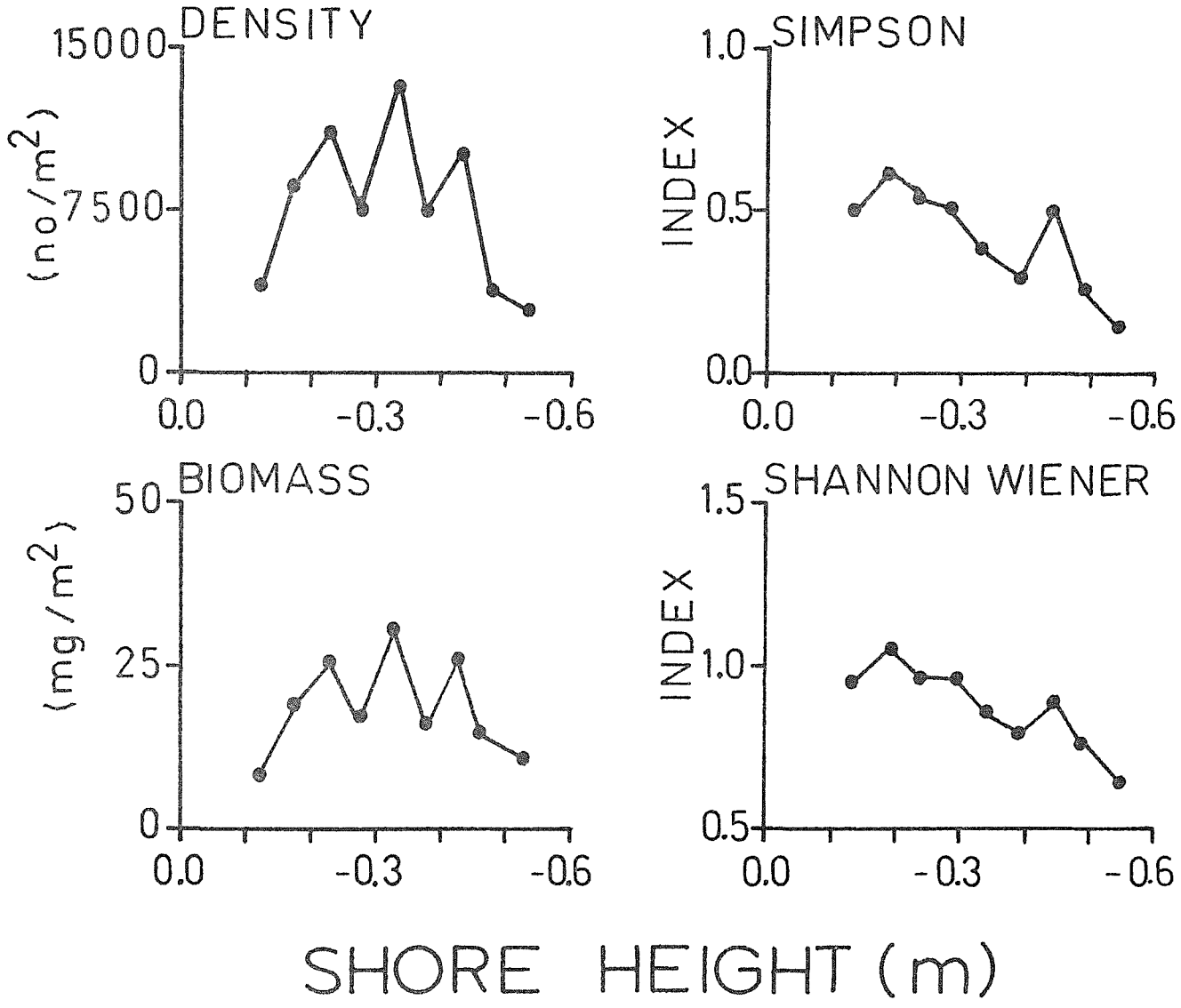
Densities and biomasses are higher in the middle levels examined at Coodanup and decline both above and below that area of the survey (Figure 15). There is a clear drop in the Simpson and Shannon-Wiener indices* with increasing depth in Peel Inlet (Figure 15). The diversity and evenness of species distributions decline on the lower shore levels because of the increasing relative importance of H. graniformis. In Oyster Harbour there is a marked drop in total mollusc density in the lower tidal levels (Figure 16), but biomass increases on the lower shoreline because of the large weights of individuals of the bivalve K. scalarina. The Simpson and Shannon-Wiener indices show no clear trends in Oyster Harbour.

Community structure

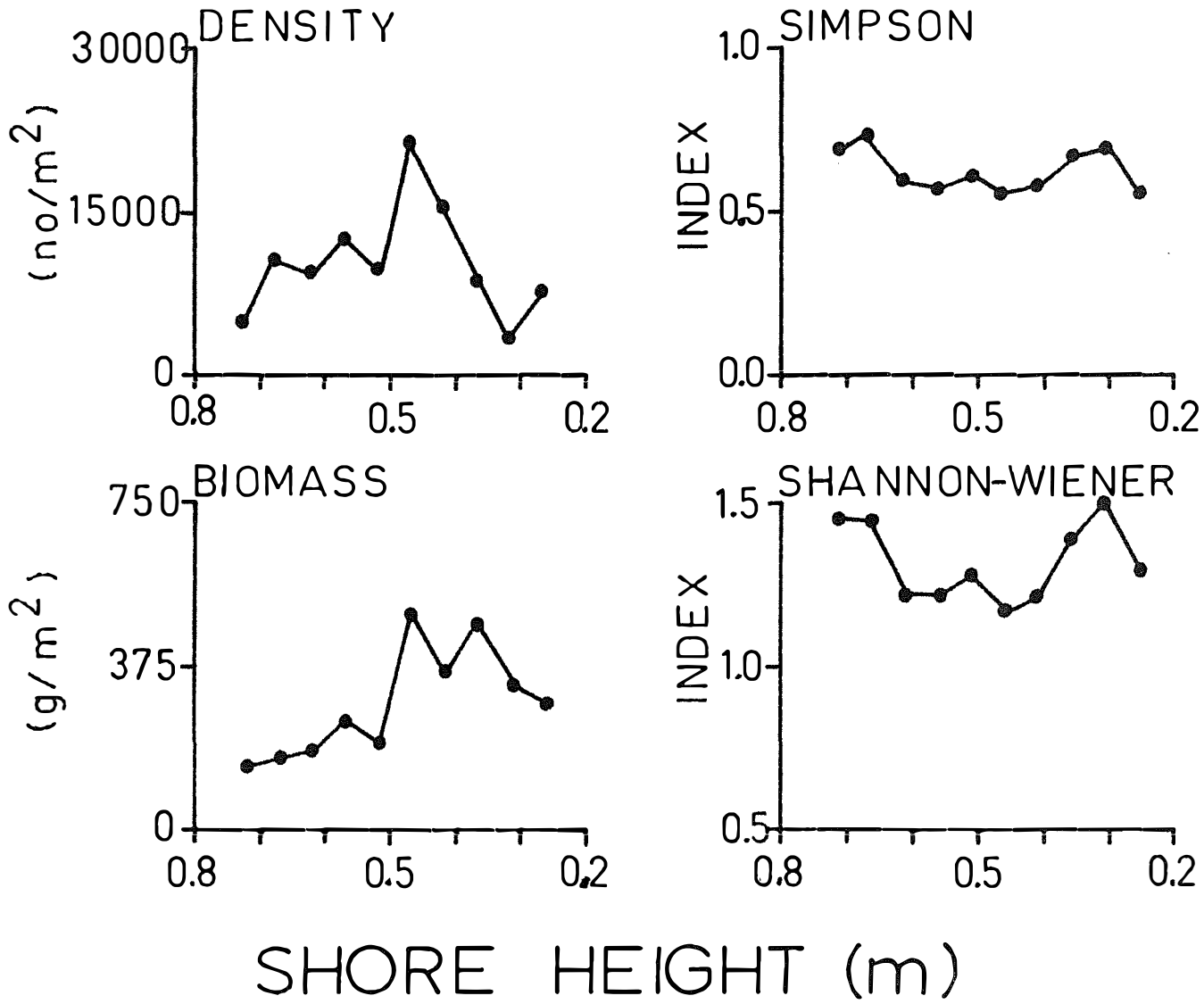
The dendrogram for Peel Inlet (Figure 17) seems on cursory examination to suggest two communities. The cluster on the left is composed of stations between - 0.33 and - 0.53 m. The cluster on the right is composed of stations between - 0.13 and - 0.28 m except for the station at - 0.43 m. Thus the two clusters do not reflect distinct vertical areas on the shoreline. The dendrogram indicates a single community with an association of 0.92. The species characteristic of this community are H. graniformis and A. semen.

The dendrogram showing the community structure of molluscs on the sand flat in Oyster Harbour is shown on Figure 17. Two groupings occur: a large cluster of stations on the right of the dendrogram and a smaller cluster of two stations on the

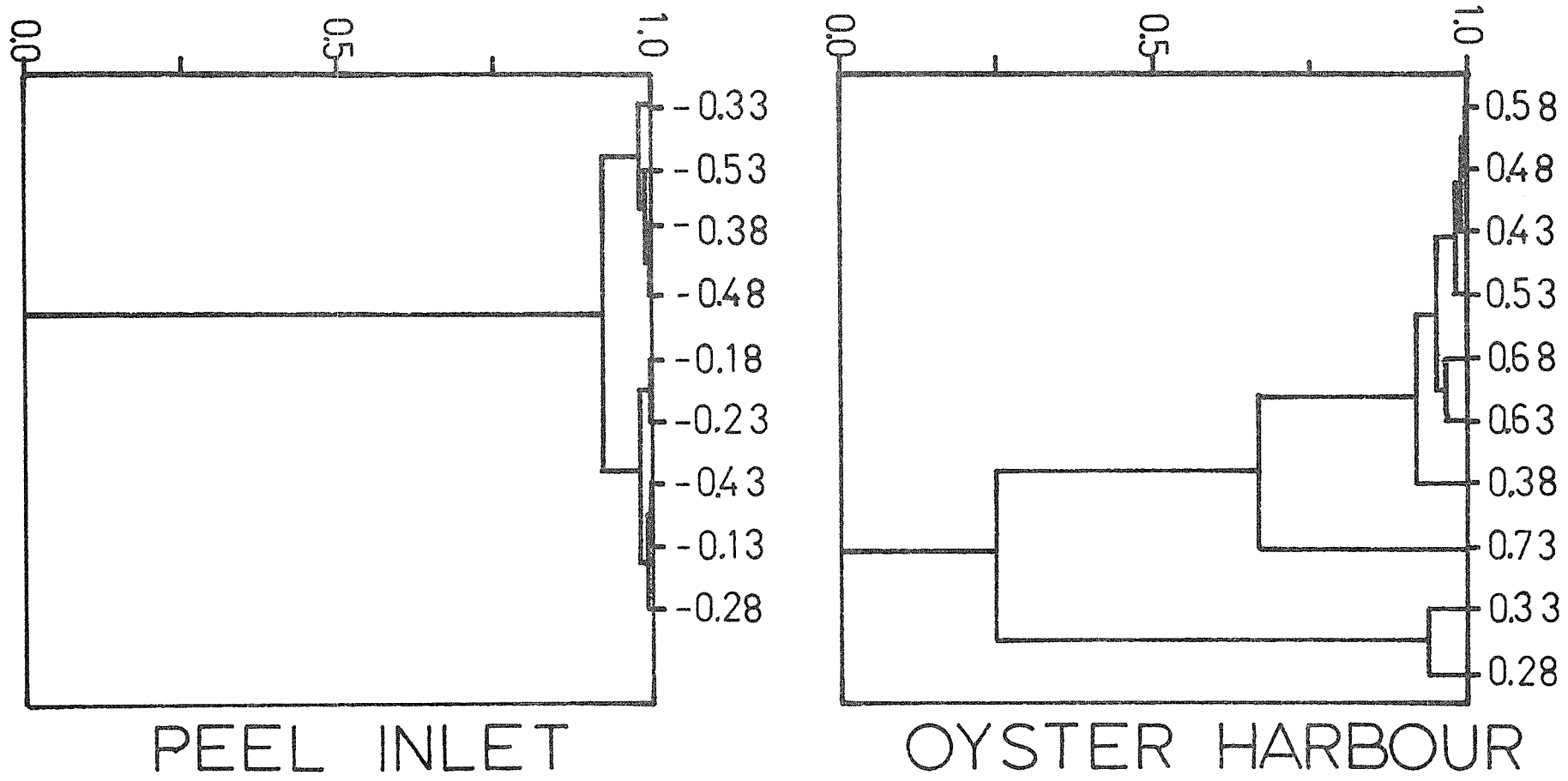
* See Appendix 6



15. Zonation patterns of total density and biomass of molluscs and the Simpson and Shannon-Wiener indices on a sandflat in Peel Inlet.



16. Zonation patterns of total density and biomass of molluscs and the Simpson and Shannon-Wiener indices on a sandflat in Oyster Harbour.



17. Dendrograms showing the faunal associations of molluscs on sandflats in Oyster Harbour and Peel Inlet.

left. The latter cluster is composed of the two lowest stations on the shoreline, and they have an association level of 0.95. The larger cluster, which includes eight stations, is divided into subclusters. The four stations at 0.43 to 0.58 m have an association level of 0.98. The two next higher stations on the shoreline, at 0.63 and 0.68 m, have an association level of 0.96 with the central stations. The next lowest station at 0.38 m has an association of 0.92. The basic pattern on the dendrogram then is of two communities on the shoreline. An upper community of molluscs is located between 0.38 and 0.68 m on the shoreline and has an association level of 0.92. The station at 0.73 m relates to this community at 0.67. This species used to characterize this community were selected according to the criteria outlined by Thorson (1957). They are B. estuarina and S. fragilis. The lower community associates with the upper community at only 0.26. The lower aggregation of molluscs is characterised by M. donaciformis and K. scalarina.

Discussion

The molluscan fauna of southwest estuaries can be divided into two groups: true estuarine species which are adapted specifically to the conditions found there and species entering the estuary from adjacent marine areas (marine or marine affinity). In the comparison of molluscs at Coodanup with those at Oyster Harbour the estuarine molluscs were recorded in about equal densities; these are largely the species collected on the 1 mm mesh. In both areas H. graniformis was the most abundant species; A. semen was second in Peel

Inlet and B. estuarina in Oyster Harbour. Total biomass of estuarine species was higher in Oyster Harbour because of the relatively large size of B. estuarina which was dense in Oyster Harbour but is rare in Peel Inlet. With the exception of X. inconstans species collected on the 2 mm mesh in Oyster Harbour were classified as marine or marine affinity (Roberts and Wells, in press). Only a single individual in these groupings was collected in the quantitative survey at Coodanup; marine and marine affinity species are uncommon in either Peel Inlet or Harvey Estuary though several species were collected at Mandurah. In the lack of marine and marine affinity species the Peel - Harvey system is similar to the Blackwood River (Table 8); the Swan estuary has large numbers of species of both categories.

In Peel Inlet several factors appear to limit the number of mollusc species that are marine or of marine affinity; habitat types, geographical location, temperature and salinity. The estuarine system is shallow, with a largely sandy bottom, and there is little variation in the available habitats. The geographical location of Peel Inlet is in an area where there are few tropical species and the pool of available temperate species is less than in areas further south (Wilson and Gillett, 1971; 1979; Wells, 1980). Many species which occur in the marine areas adjacent to the Peel-Harvey estuarine system are prevented from entering because of the variations in temperature and salinity in the estuary. Emery et al. (1957) have pointed out that the significant feature of these parameters is not the mean value, but rather the changes on a daily and seasonal basis and the rate at which they change. Salinity at Coodanup ranged from 2 to 53% and temperature from 10 to 27^{o}C.

Table 8. Affinity groups of molluscs in southwestern Australian estuaries. The sources of data are: Chalmer et al.(1976) - Swan River; Roberts and Wells, in prep. - Oyster Harbour and Princess Royal Harbour; Wallace (1975) - Blackwood River.

Species affinity	Swan	Peel-Harvey	Blackwood	Oyster Harbour	Princess Royal Harbour
Marine	64	13	3	69	35
Marine affinity	25	9	7	33	32
Estuarine	7	9	7	6	4
Freshwater	1	1	1	-	-
Total	97	32	18	108	71

Population densities at Coodanup appear high at first, up to 19,959/m^2 for H. graniformis and 45,491/m^2 for A. semen. The densities of minute bivalves have not been reported in detail from other areas, but hydrobiid gastropods are abundant in many estuarine areas. Densities of 40,000 to 50,000/m^2 have been recorded in a number of European estuaries (Hunter and Hunter, 1962; Newell, 1962; Muus, 1967; Anderson, 1971; Fenchel, 1975) and densities of Hydrobia totteni of 15,000 to 25,000/m^2 were reported in North America by Sanders et al. (1962) and Wells (1978). Biomass and production levels of these animals have not been reported, but Green (1968) and Fenchel et al. (1975) emphasized that despite their small size minute molluscs can play an important role in estuarine food webs because their high densities and relatively short life cycle provide a large total production.

The question is then two fold: what is the mollusc production based on, and what organisms in the foodweb utilize the mollusc production? Neither question has been examined directly in the Peel-Harvey study but information on related species can be used to suggest answers. Hydrobia ulvae is known to feed on algae and diatoms and bacteria attached to detritus (Newell, 1962; Green, 1968). Fenchel et al. (1975) examined the deposit-feeding role of H. ulvae in detail, particularly in relation to particle size selection. Leptonacean bivalves are suspension feeders (Morton, 1956; Purchon, 1968; McQuiston, 1969). Thus both of the abundant molluscs in Peel-Harvey probably depend heavily on detrital material or bacteria adhering to the detritus for their energy source. Much of the detritus would come from the breakdown of algae and other plants in the system. The mollusc production

is available to a variety of organisms including invertebrates, birds and fish. The prey preferences of few of these groups are known in Western Australia. Hydrobia totteni is known to be a major food source for wading birds, particularly sandpipers, in Nove Scotia (Mills, pers. comm.), and wading birds have been seen feeding on the sandflats in Peel Inlet where H. graniformis is abundant. Thomson (1957) examined the gut contents of 17 estuarine fish species in Western Australia and found that 7 fed on molluscs, though the species of molluscs involved were not listed. Whiting, bream and yellow-eye mullet fed most frequently on small mollusc species or the newly settled larvae of larger species. Up to 40% of the gut contents of these species were composed of molluscs. Wallace (1975b) investigated the food found in gut contents of the fish of the Blackwood River estuary. Several (Table 9) utilized molluscs for food, including H. graniformis and A. semen. The two species were encountered in high percentages of the guts of 8 species and were incidental food items in several other species. Thus H. graniformis and A. semen perform an important role in the ecosystem in coverting detrital material from plant breakdown into animal tissue available to the higher trophic levels of the foodweb.

Table 9. Percentage occurrence of *Hydrococcus graniformis*, *Arthritica semen* and *Anticorbula amara* in the guts of fish in the Blackwood River estuary (data from Wallace, 1975b).

	Aldrichetta forsteri (yellow eye mullet)	*Sillago schomburgkii* (Western yellow fin whiting)	*Cnidoglanis macrocephalus* (Cobbler)	*Mylio butcheri* (Black bream)	*Rhabdosargus sarba* (Silver bream)	*Atherinosoma* spp. (Hardyhead)	*Sphaeroides pleurogramma* (Banded toadfish)	*Contusus richei* (Prickly toadfish)
H. graniformis	14.4	3.3	14.3	5.0	31.4	6.1	68.8	45.4
Total gastropods	17.6	3.3	20.0	26.9	59.2	14.1	69.6	47.7
A. semen	36.3	-	2.8	22.4	33.5	24.8	16.0	29.5
A. amara	3.3	13.5	11.4	36.4	32.6	9.7	8.9	13.6
Total bivalves	37.5	22.0	40.0	56.7	54.7	32.4	29.5	43.2

CHAPTER 5

REPRODUCTION

Introduction

One of the key adaptations of species living in an estuarine environment lies in the method of reproduction. Many species have embryo retention mechanisms to protect the young during early developmental stages, and reproduction is timed to insure that the young have the greatest possible chance of encountering favourable conditions during development.

Materials and Methods

Specimens collected in the monthly sampling programme at Coodanup were used for the reproductive studies of H. graniformis and A. semen. In addition a sample of 235 H. graniformis 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.

The sampling station for Anticorbula amara was located on the Murray River 50 m upstream from the Ravenswood Bridge.

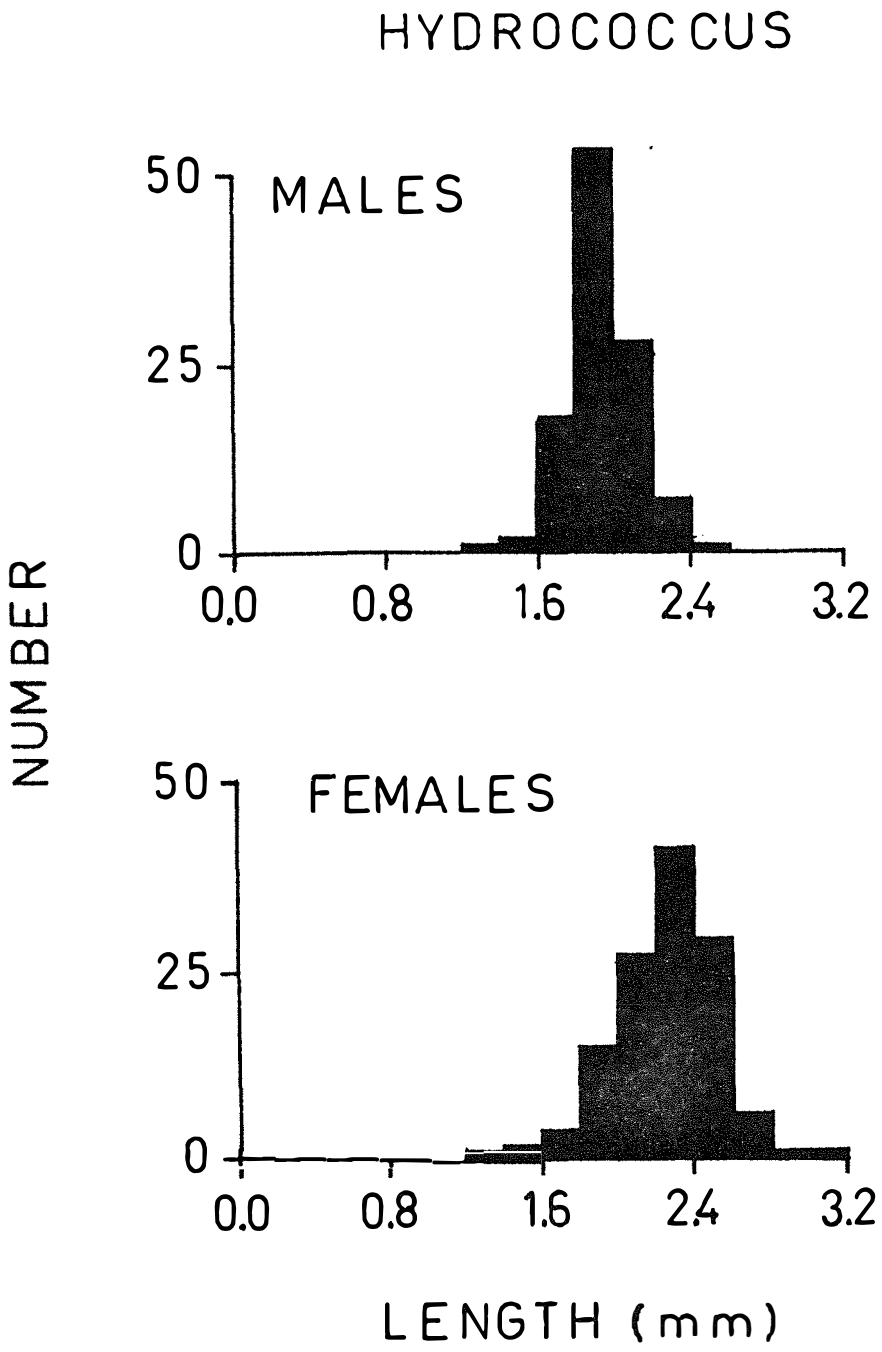
At least 100 individuals were collected every month from April 1977 to March 1979 from submerged logs at a depth of 0.5 m. The specimens were preserved in 10% formalin. Fifteen to 24 individuals greater than 2.0 mm in shell length were transferred to Bouin's fixative every month and treated histologically as described above.

Results

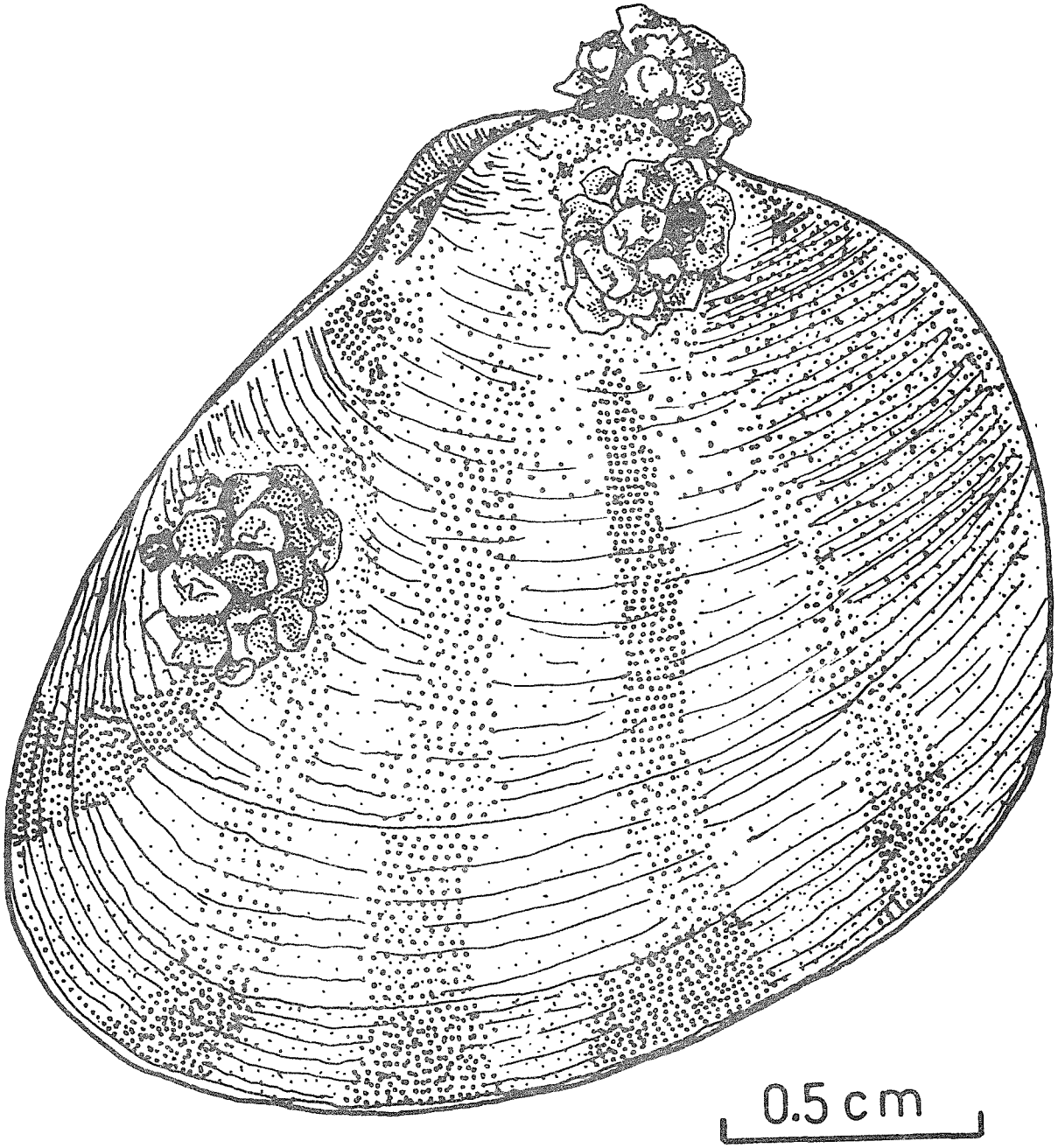
A. H. graniformis

Sexes are separate in H. graniformis, and there was no suggestion of hermaphroditism in the sectioned material. Of the 235 individuals sexed 108 were males and 127 were females (Figure 18). Deviation from the expected 50 : 50 ratio was not significant (t-test, 0.05 level). Mean size of females was significantly larger (2.22 $\pm$ 0.13 mm) than males (1.95 $\pm$ 0.13 mm) (t-test, 0.05 level). There is a considerable overlap in sizes of individuals of the two sexes (Figure 18) 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. graniformis attach egg capsules to any suitable hard substrate, most often shells of other H. graniformis or other live molluscs, but also dead shells and rocks. The transparent capsules are composed of sand cemented together with mucus (Figure 19). The capsules are lens shaped with a diameter of 0.5 mm (MacGibbon, 1978). A single embryo develops



18. Size-frequency characteristics of Hydrococcus graniformis males and females collected at Coodanup on 9 October 1978.



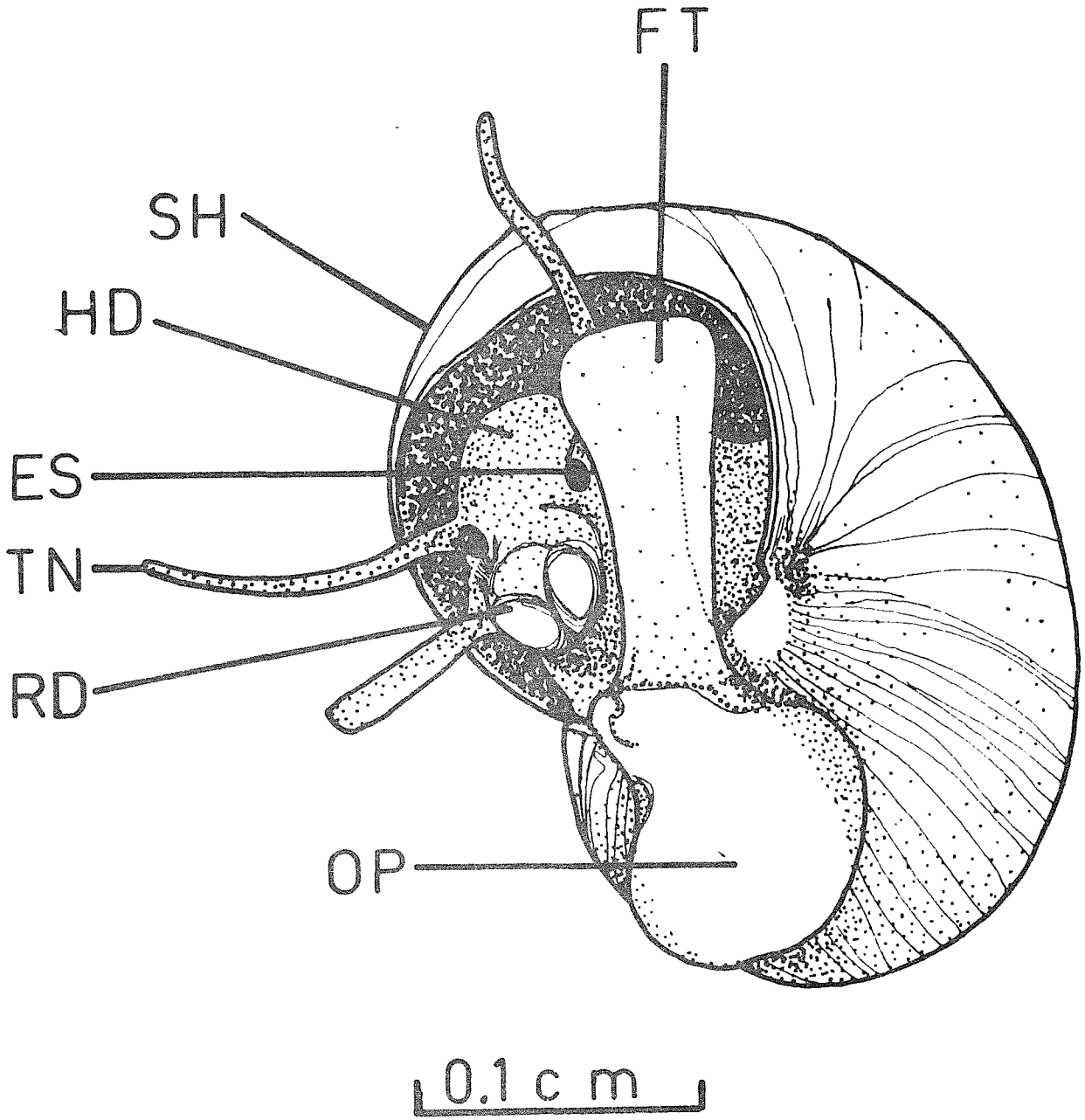
19. Egg capsules of Hydrococcus graniformis on a shell of Arthritica semen.

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 µm in diameter and the smallest embryo found in a capsule was a 4 cell stage 230 µm 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 20). 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 with a mean of 18. All oocytes in a female are in approximately the same stage of development. The accessory reproductive glands of females, particularly the mucous and albumen glands are enlarged to produce the capsules.

Female H. graniformis 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



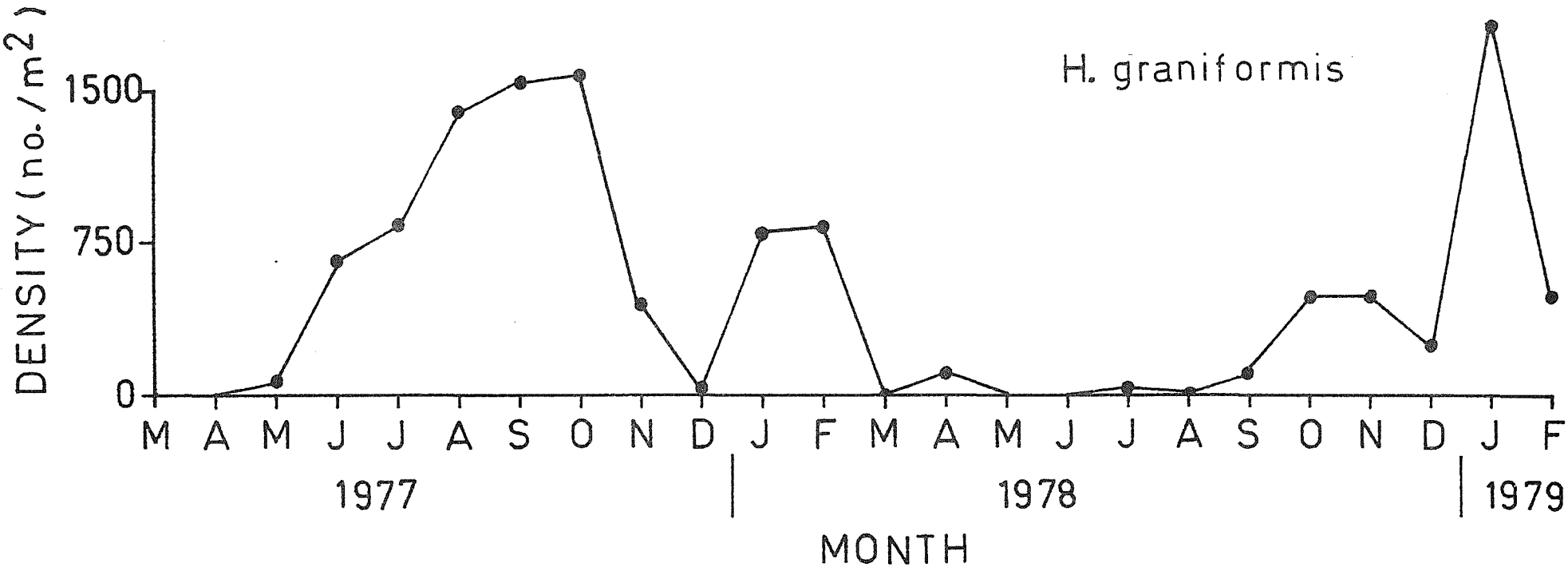
20. A crawling juvenile of Hydrococcus graniformis. ES, eye; FT, foot; HD, head; OP, operculum; RD, radula; SH, shell; TN, tentacle.

the field successfully hatched in the laboratory in about 12 days, though some required as long as 17 days (MacGibbon, 1978). 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.

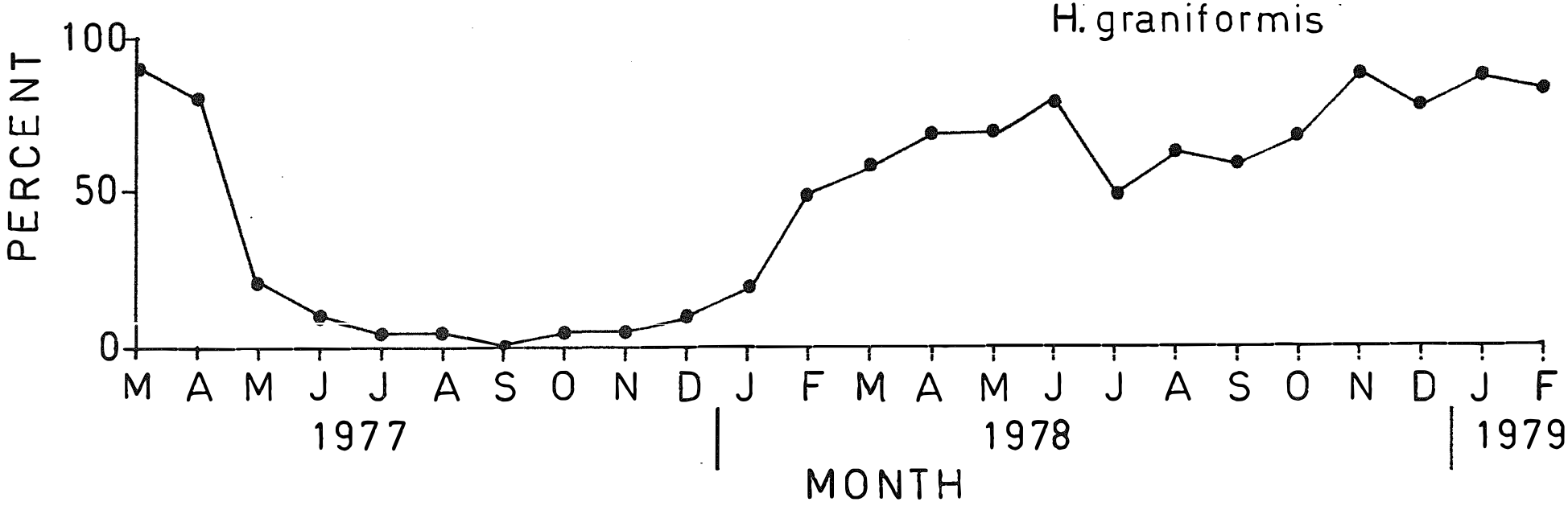
Reproduction in H. graniformis was almost continuous throughout the two years studied (Figure 21). Capsule density was generally less in the second year than in the first, but there is no obvious seasonal pattern of reproduction. Comparison of Figures 21 and 22 demonstrates an inverse relationship between capsule density and density of H. graniformis 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

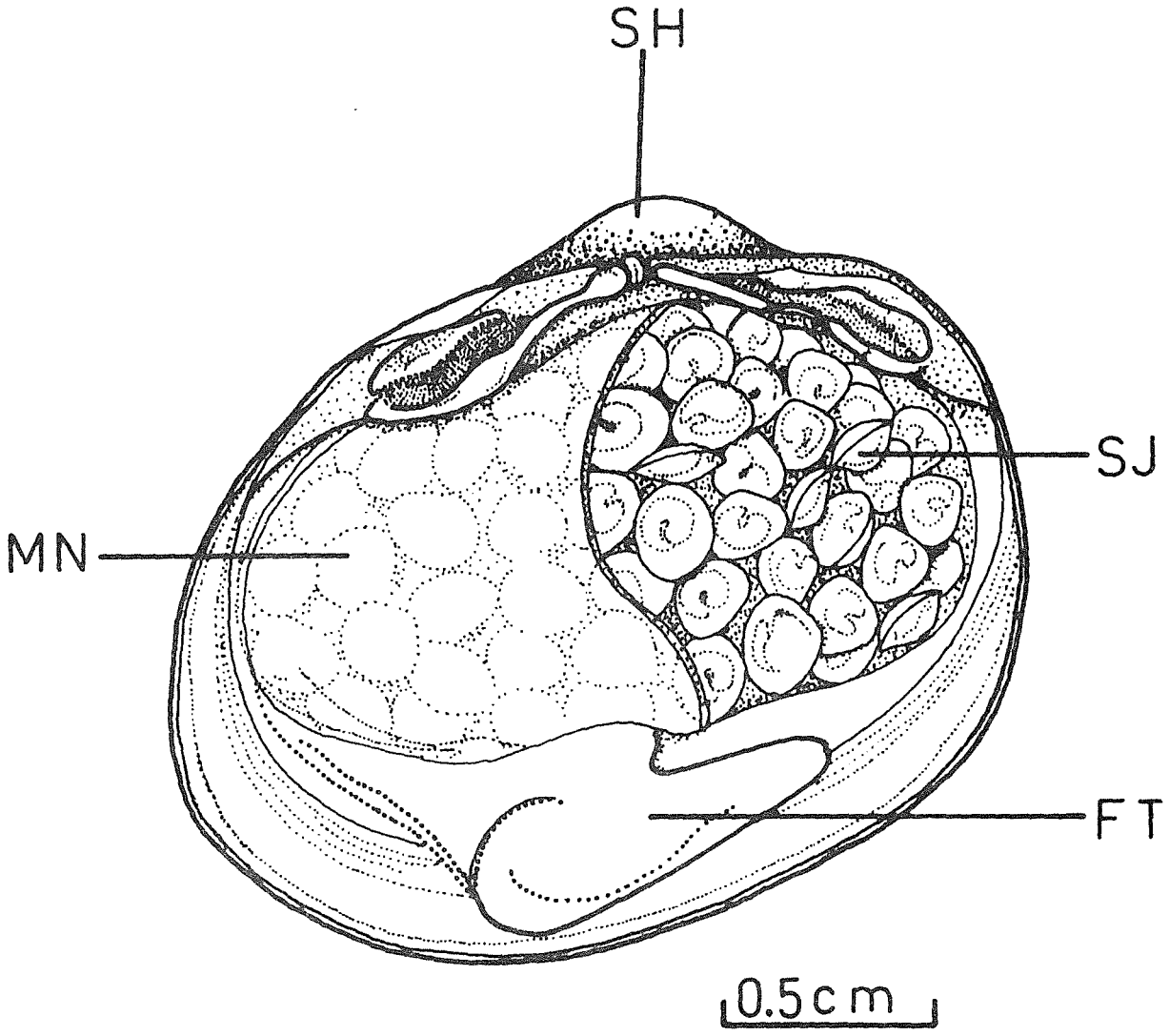
Arthritica semen is a protandric hermaphrodite, maturing first as males at a shell length of about 2.0 mm and after a brief male stage continuing development into a functional female stage. Larvae are retained by females and undergo development in a brood pouch located between the gills (Figure 23). Three embryonic stages were distinguished. In stage 1 the embryos are stuck together in a mass of developing eggs 0.03 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



21. Densities of egg capsules of Hydrococcus graniformis at Coodanup from March 1977 to February 1979.



22. Densities of adult Hydrococcus graniformis at Coodanup from March 1977 to February 1979.



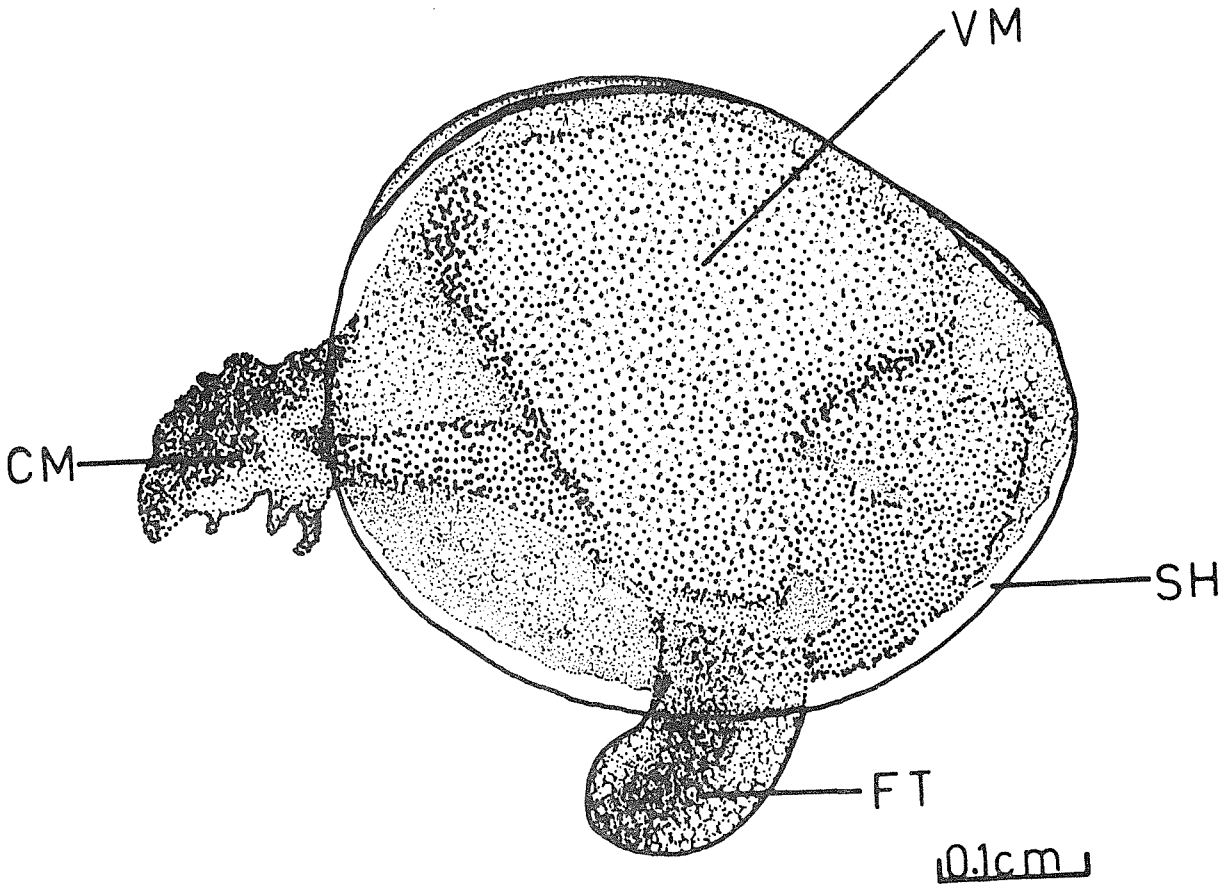
23. A female Arthritica semen with part of the mantle removed to show the shelled larvae.

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 24). 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.

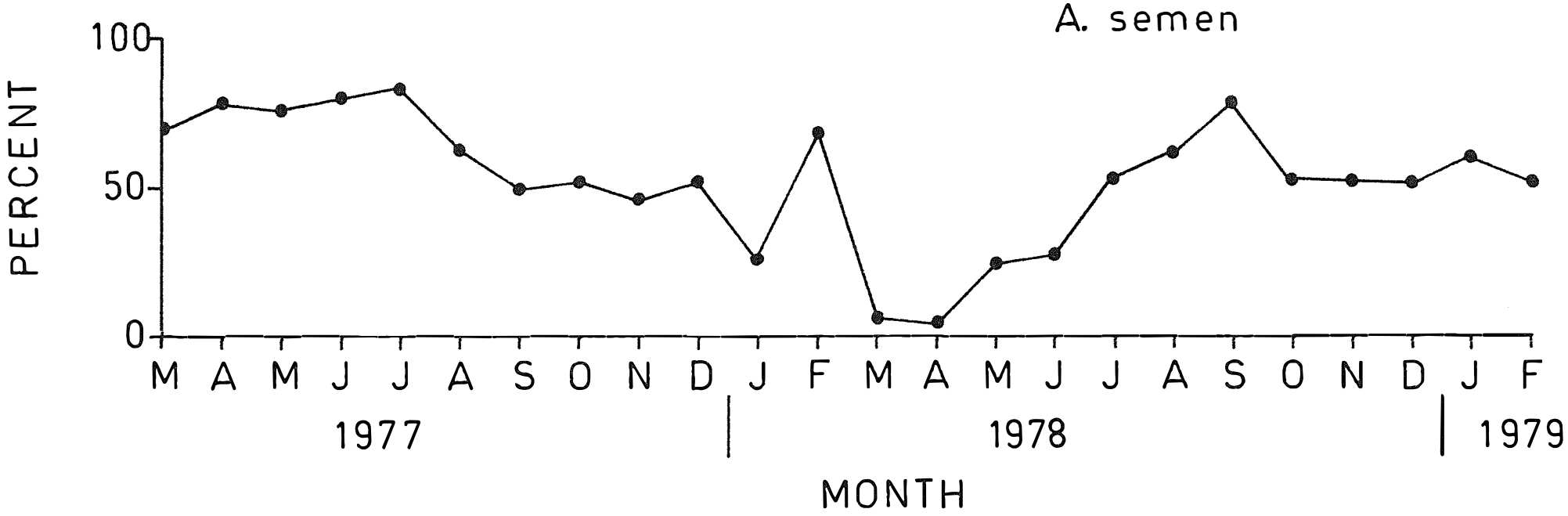
Each female of A. semen had embryos of only one stage of development; no females were found with two or more stages. All larvae develop at the same rate and are released at approximately the same time. There were no large females with a few shelled juveniles remaining and young embryos undergoing early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

The percentage of females brooding was variable, but reproduction was continuous throughout the two years examined (Figure 25). 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 26). Gaps in the graph in January, February and March 1978 are due to the low percentages of females in the population that were brooding. The mean number of embryos per female varied from a low of 30.8 in December 1977 to 63.3 in September 1977. There was no apparent seasonal trend in the mean number of embryos per female.

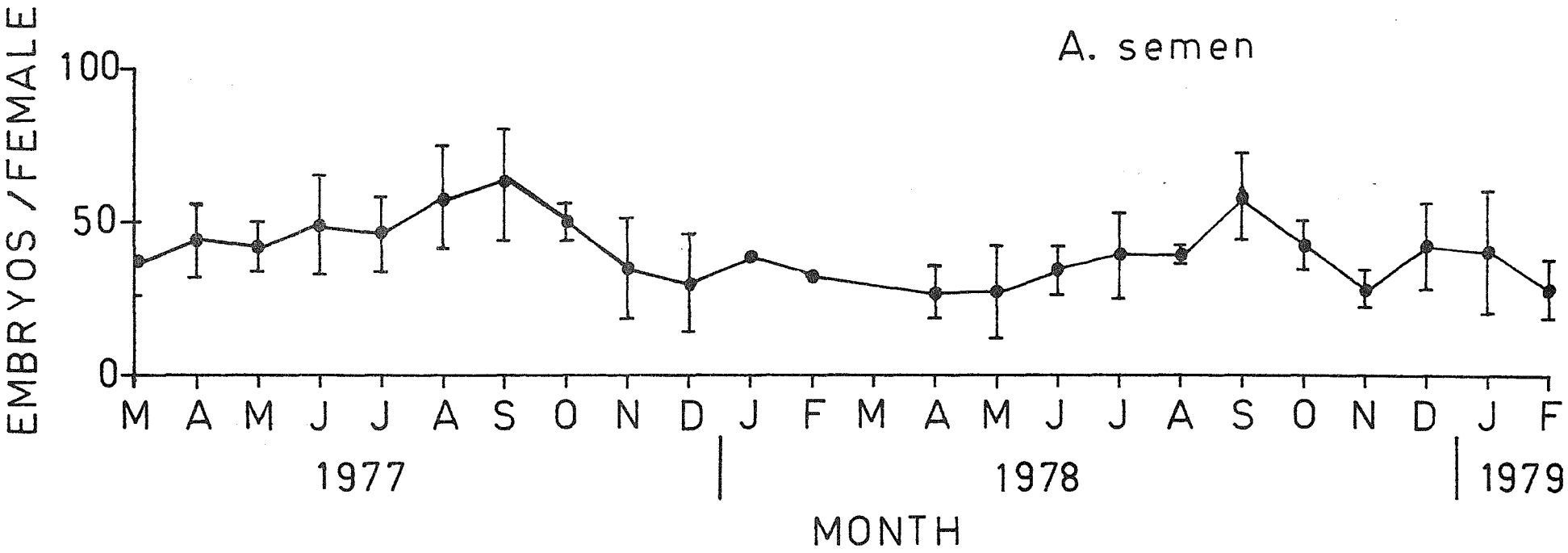
Figure 27 breaks the percentage of A. semen brooding into the 3 developmental stages. In all months stage 1 embryos



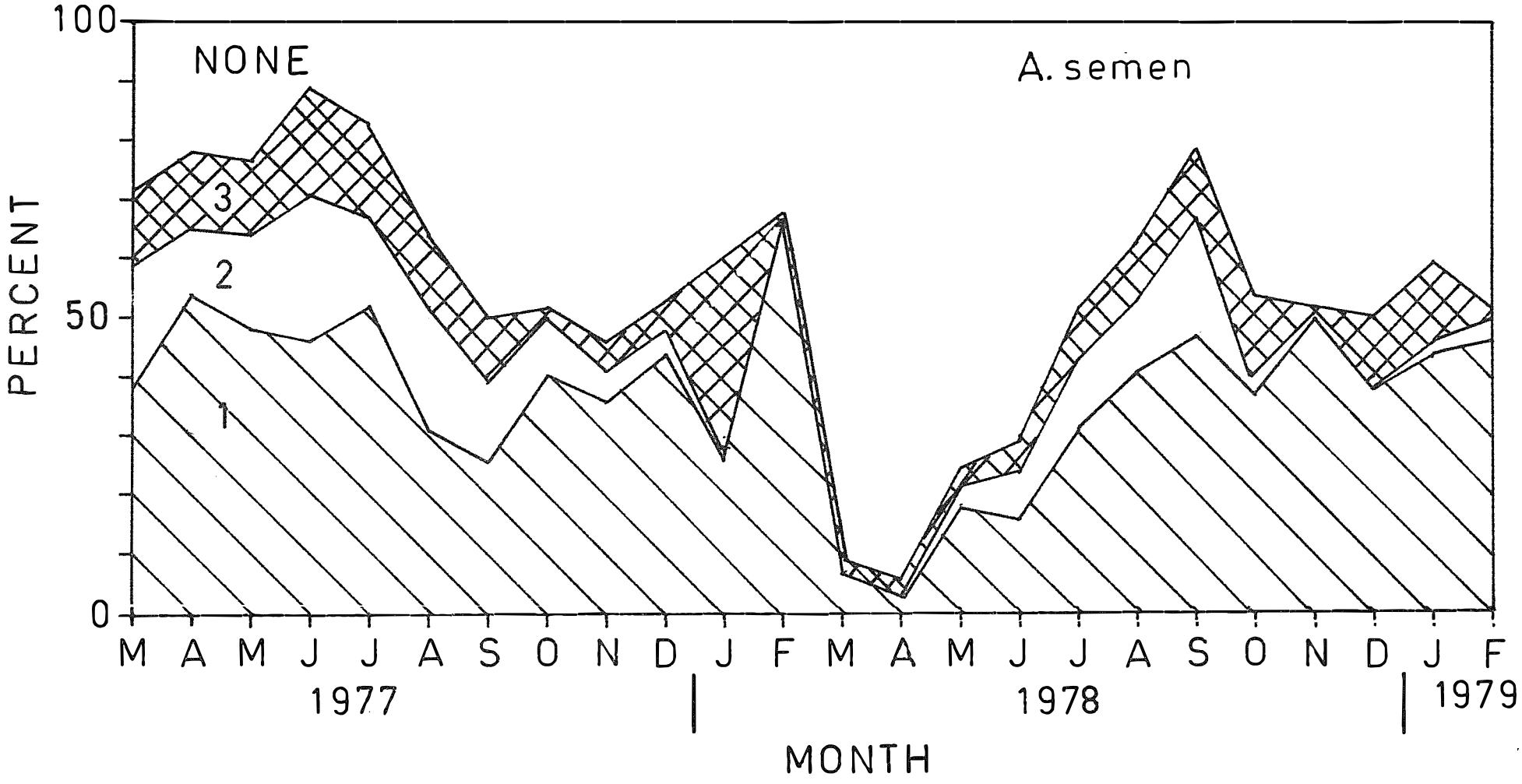
24. A larval Arthritica semen removed from an adult female.



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



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



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

were the majority of embryos being brooded. 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.

C. A. amara

Sexes are separate in A. amara. Gametes develop from primary germ cells enclosed in follicles in the gonad and go through several intermediate stages until they are discharged into the surrounding water where fertilization takes place. Fertilized young undergo a planktonic distributional phase of unknown duration before they settle to the bottom and metamorphose into the adult form.

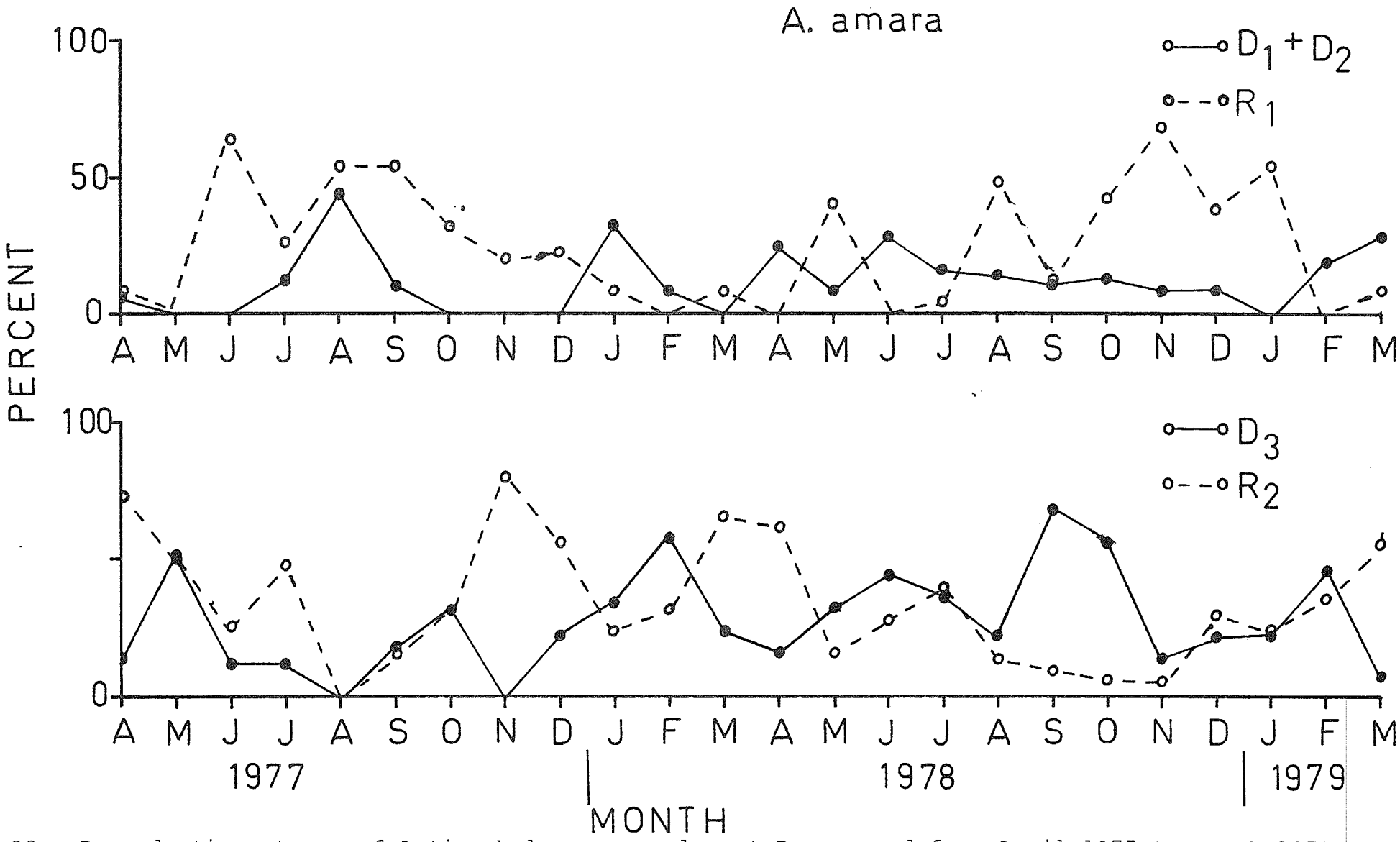
Each individual undergoes three basic stages in the reproductive cycle. Germ cells begin development in the gonad through three stages (D_1, D_2 and D_3). Development continues until the spermatocytes or oocytes are ripe and are spawned (R_1). After spawning a regression stage (R_2) occurs. In females this stage is marked by the presence of phagocytic cells in the gonad which are clustered around disintegrating oocytes. After the regression stage the gonad begins development for the next reproductive cycle. In mussels a resting stage occurs between the reproductive cycles (Wilson and Hodgkin, 1967). Three individuals of A. amara were found that were of indeterminate sex with tissues resembling empty gonad follicles. These may have been in

the resting stage, but if so the stage is brief in A. amara. Figures 28 and 29 show the percentages of male and female A. amara in the various reproductive stages at Ravenswood from April 1977 to March 1979. Percentages of individuals in each category varied from month to month, but spawning individuals (R_1) of both sexes were present in almost all months and were present in all seasons. There was a continuous reproduction with no clear seasonality.

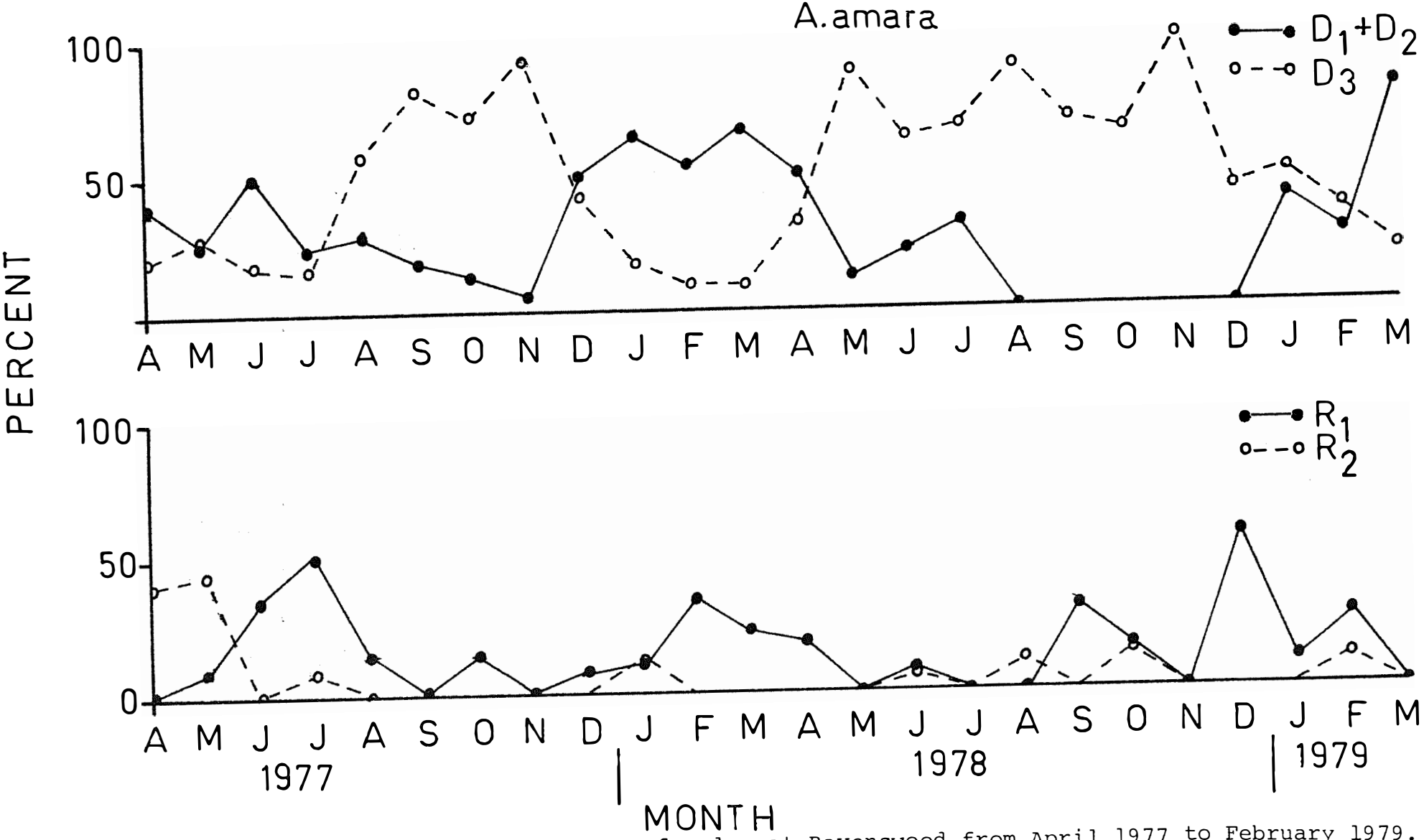
Discussion

The reproductive mechanisms of H. graniformis 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. graniformis 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. graniformis 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



28. Reproductive stages of Anticorbula amara males at Ravenswood from April 1977 to March 1979.



29. Reproductive stages of Anticorbula amara females at Ravenswood from April 1977 to February 1979.

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. graniformis and A. semen have developed mechanisms for solving the problem. A sufficient quantity of yolk and albumen is provided in the capsule of H. graniformis for the embryo to develop into the crawling stage. Nurse eggs are frequently found in gastropod egg capsules (Webber, 1977). These are eggs which do not undergo development and are consumed by the embryos developing in the same capsule. This mechanism is not employed by H. graniformis. 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. graniformis. 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. In the absence of a penis or spermatophores for sperm transfer 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 sperm are developed and released while the oocytes are still in the early developmental

In both H. graniformis and A. semen young emerge at a benthic crawling stage. This means that there is little risk of them 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. Hydrococcus graniformis 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. graniformis, 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.

The continuous reproduction found in H. graniformis and A. semen ensures that there is always a ready supply of developing young in the estuary to exploit favourable conditions. The rapid growth rate and short lifespan of the species means that the young can quickly mature and reproduce themselves while conditions are favourable.

The reproductive strategy of A. amara is completely different from those of H. graniformis and A. semen. In A. amara 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 A. amara 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. In its reproductive strategy A. amara is similar to the mussel Xenostrobus securis which lives in the same ecological setting, attached to logs in southwestern estuaries.

The extended spawning period of A. amara at Ravenswood is in sharp contrast with the findings of Chiffings (1971) for the species at two localities in the Swan-Avon system. Chiffings found discrete spawning seasons which occurred for short periods in May or June and October. The restricted spawning season of A. amara in this area could be due to the salinity regime. At Barker Bridge salinity varied from 1.5 to 18‰ and at Yalunga it was 3 to 8‰ (Chiffings, 1971). Our sampling station for A. amara was less than 2 km up the Murray River from its mouth in Peel Inlet. Salinities at the mouth during our sampling period were as high as 46‰, and were usually above 20‰ (Hodgkin, pers. comm.). This parallels the situation in X. securis in which the spawning season is salinity dependent (Wilson, 1968; 1969).

CHAPTER 6

TOLERANCES

Introduction

In examining the biology of H. graniformis and A. semen in the Peel - Harvey estuarine system one of the most important questions is: What physical parameters control the distribution of mollusc species in the system? Emery et al. (1957) considered temperature and salinity to be the most important determination for estuarine species. Salinity has been used to categorize estuarine animals into various tolerance groupings (Day, 1951; 1967; Chalmer, et al., 1976; Roberts and Wells, in press). Peel Inlet is located in an overlap zone between tropical and temperate faunas (Wilson and Gillett, 1971; 1979; Wells, 1980). Estuarine waters are more subject to temperature variations than the adjacent open sea (Emery et al., 1957). Because of this the temperature variations in Peel Inlet might be more important than in other estuaries. Day (1951) emphasized that the distribution of organisms in an estuary is not based on a single factor, but instead on a complex interaction between various parameters. In the case of Xenostrobus securis in the Swan River Wilson (1969) found the combination of temperature and salinity to be most important; of the two salinity was more important in controlling growth, reproduction and longevity in the species.

In the tolerance tests the animals were subjected to variations in temperature, salinity and oxygen which slightly exceeded the ranges found at Coodanup. In this way the results are relevant to the Peel Inlet situation.

Materials and Methods

In the salinity tolerance tests fresh, filtered seawater was diluted with distilled water to produce water with salinities varying from 5‰ to 30‰ in steps of 5‰. Fresh, filtered seawater was concentrated by boiling to produce salinities of 35‰ to 50‰. This water was poured from one container to another several times to insure that oxygen was available. For H. graniformis 30 individuals were placed in new 350 ml glass jars with plastic lids which were completely filled with water of the desired salinity. Four replicates were used for each step of 5‰; jars filled with estuarine water at the ambient salinity served as controls. The tests were conducted in July 1978 and February 1979 when the salinity in the estuary at Coodanup was 21‰ and 54‰ respectively. The jars were maintained at room temperature (approximately 25^{o}C). The numbers of animals active after 24 and 48 hours were counted.

Water was prepared in the same manner for Arthritica. Twenty specimens were placed in a 90 mm diameter, new petri dishes filled with water with 3 mm of washed sand of grain sizes ranging between 250 and 500 µm. Again four replicates were conducted at each of ten salinities ranging from 5‰ to 50‰. The animals were placed loosely on their

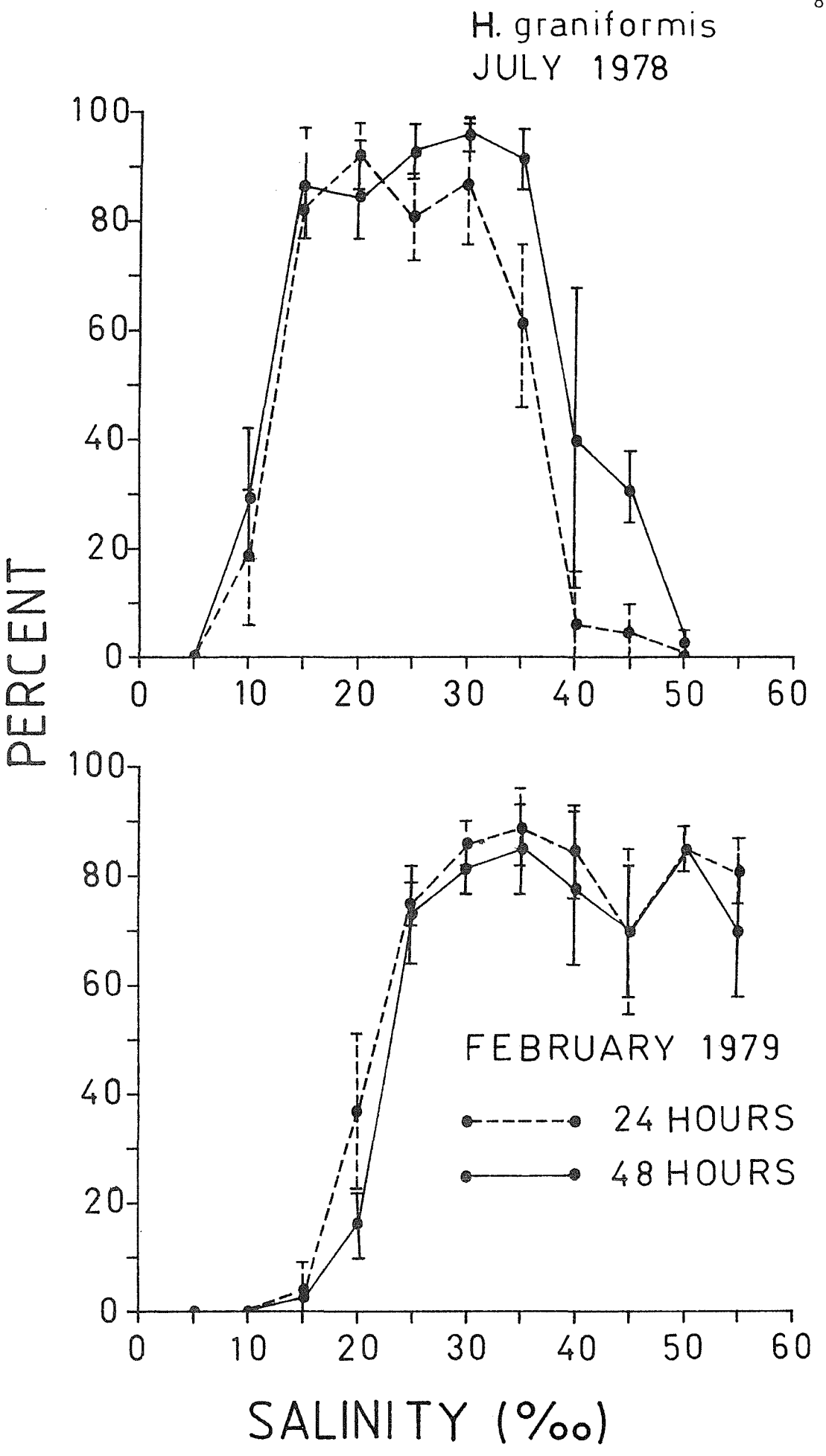
side on the sand surface. The number that had moved or burrowed into the sand after 24 hours was recorded. The animals were removed from the sand, placed again on the surface, and counted again after an additional 24 hours.

The tests to search for an interaction between the effects of temperature and salinity were conducted in the same manner as the salinity tolerance tests with the following differences. Because of the difficulty in obtaining sufficient numbers of animals only three replicates were used at each salinity level and only 20 animals were used in a jar. The tests were again conducted with salinities varying from 5‰ to 50‰ in steps of 5‰. Three sets of temperatures were used: 7^{o}, 17^{o} and 29^{o}C. The ambient salinity in the estuary when this experiment was conducted was 10‰ and the ambient temperature was 12^{o}C. Similar experiments were conducted on both H. graniformis and A. semen using a range of temperatures and salinities of 10, 27, and 45‰.

Results

A. H. graniformis

Hydrococcus graniformis had a wide salinity tolerance in both tests (Figure 30). In the July test, when the estuarine salinity was 21‰, the snails were most active at salinities of 15 to 35‰. In February, when the ambient salinity was 54‰, activity was high from 25‰ through all of the higher salinities tested. The tests did not reach the upper tolerance of H. graniformis in February. The



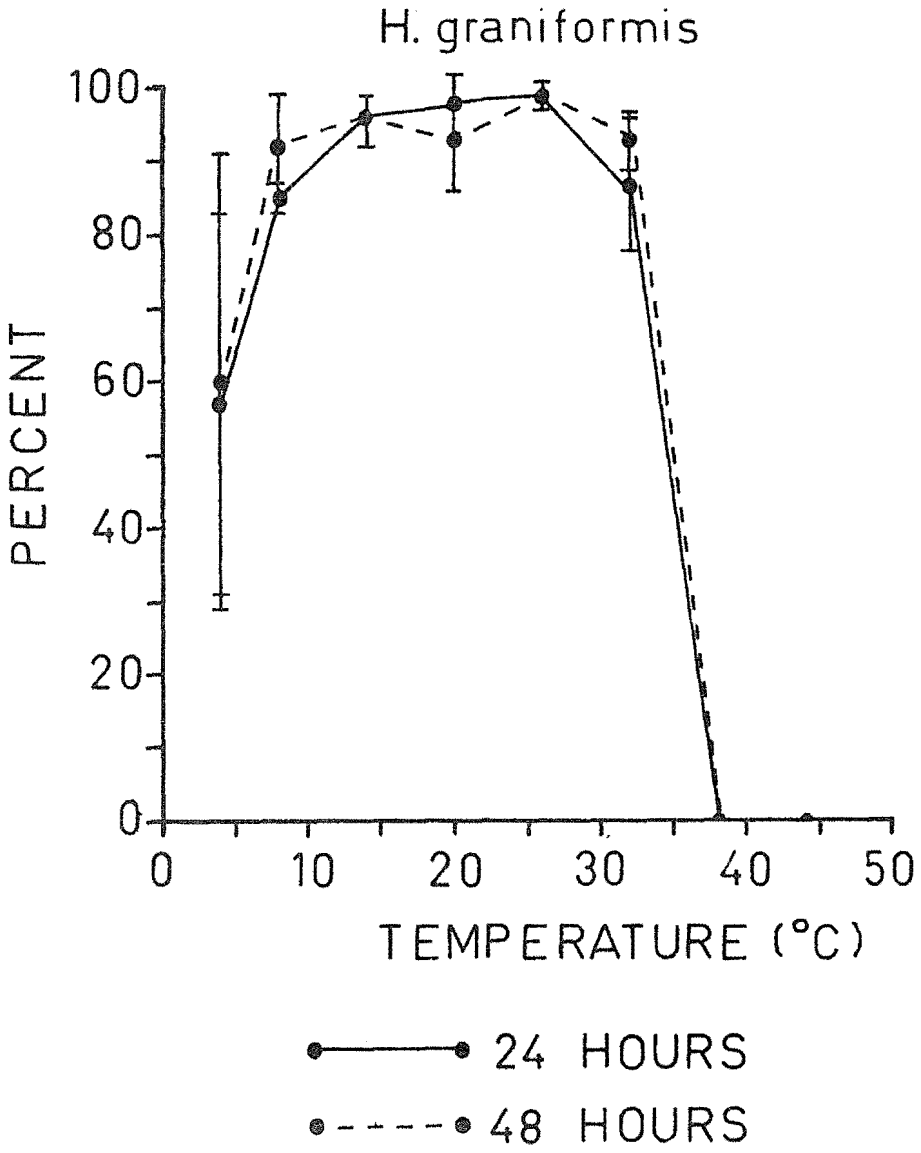
30. Salinity tolerance tests of Hydrococcus graniformis. The mean and one standard deviation are shown.

curve for February is shifted 10‰ to the right compared to the July graph, suggesting a partial adjustment of the higher ambient salinities. Hydrococcus graniformis also has a wide temperature tolerance (Figure 31), and was most active at temperatures of 8 through 32°C; no animals were active above 32°C.

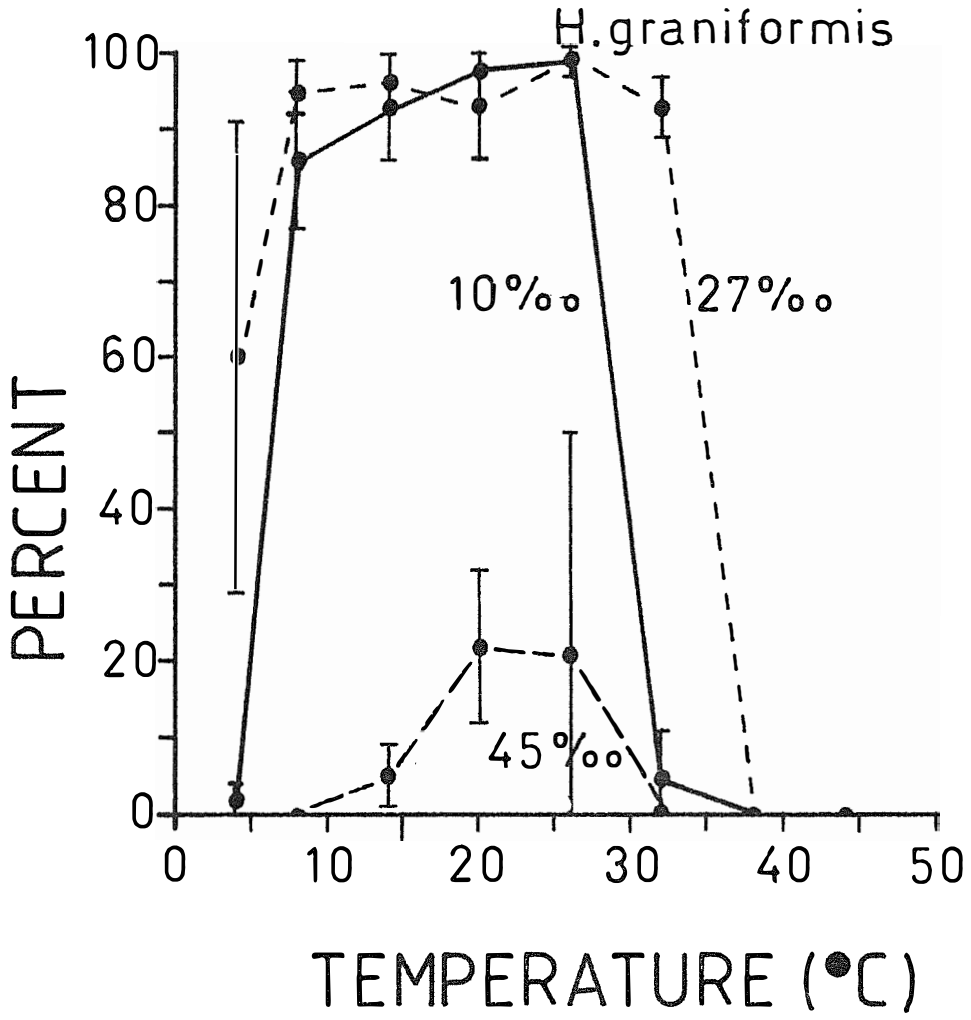
Two experiments were designed to search for an interaction between the effects of salinity and temperature on the activity of H. graniformis. In the first experiment animals were maintained in water of 3 salinities (10, 27 and 45‰) and were tested over a range of temperatures (Figure 32). Animals tested at 27‰ had the highest tolerances, between 8 and 32°C. At 10‰ the tolerances were reduced, with the greatest activity occurring between 8 and 26°C. Animals tested at 45‰ were most active at 20 and 26°C, but even at these temperatures activities were low compared to the results obtained at 10 and 27‰. The second test for an interaction used 3 temperatures (8, 16 and 29°C) and a range of salinities (Figure 33). Animals tested at 16°C were most active at salinities of 10 to 35‰. The pattern at 8°C was similar to 16°C but the rates were somewhat lower. At 29°C activities were highest in the salinity range of 20 to 40‰, somewhat higher than in 8 and 16°C.

B. A. semen

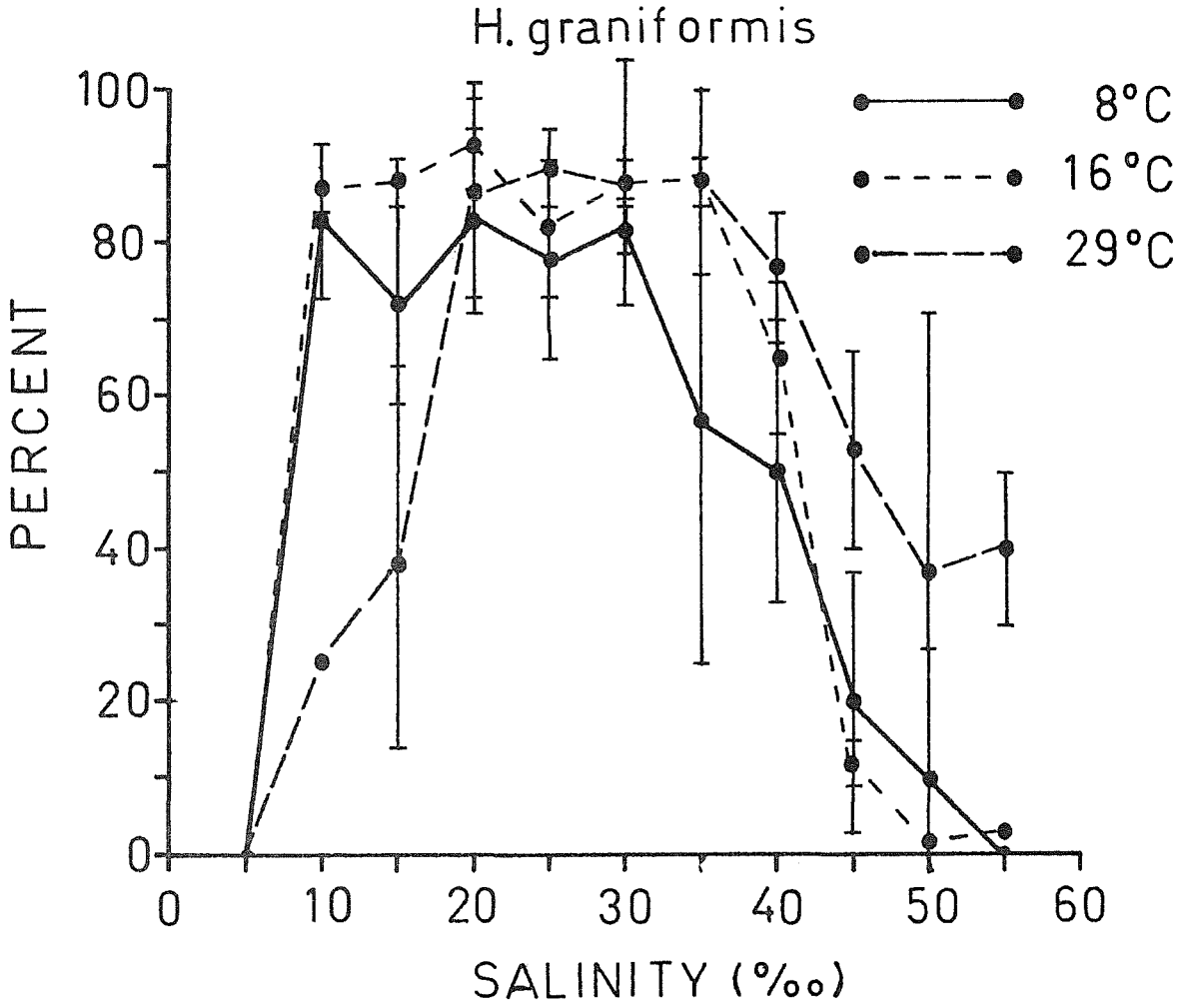
Activity of A. semen examined in July (ambient 21‰) was highest at salinities of 15 to 40‰ after 48 hours (Figure 34). In February (ambient 54‰) activity was high



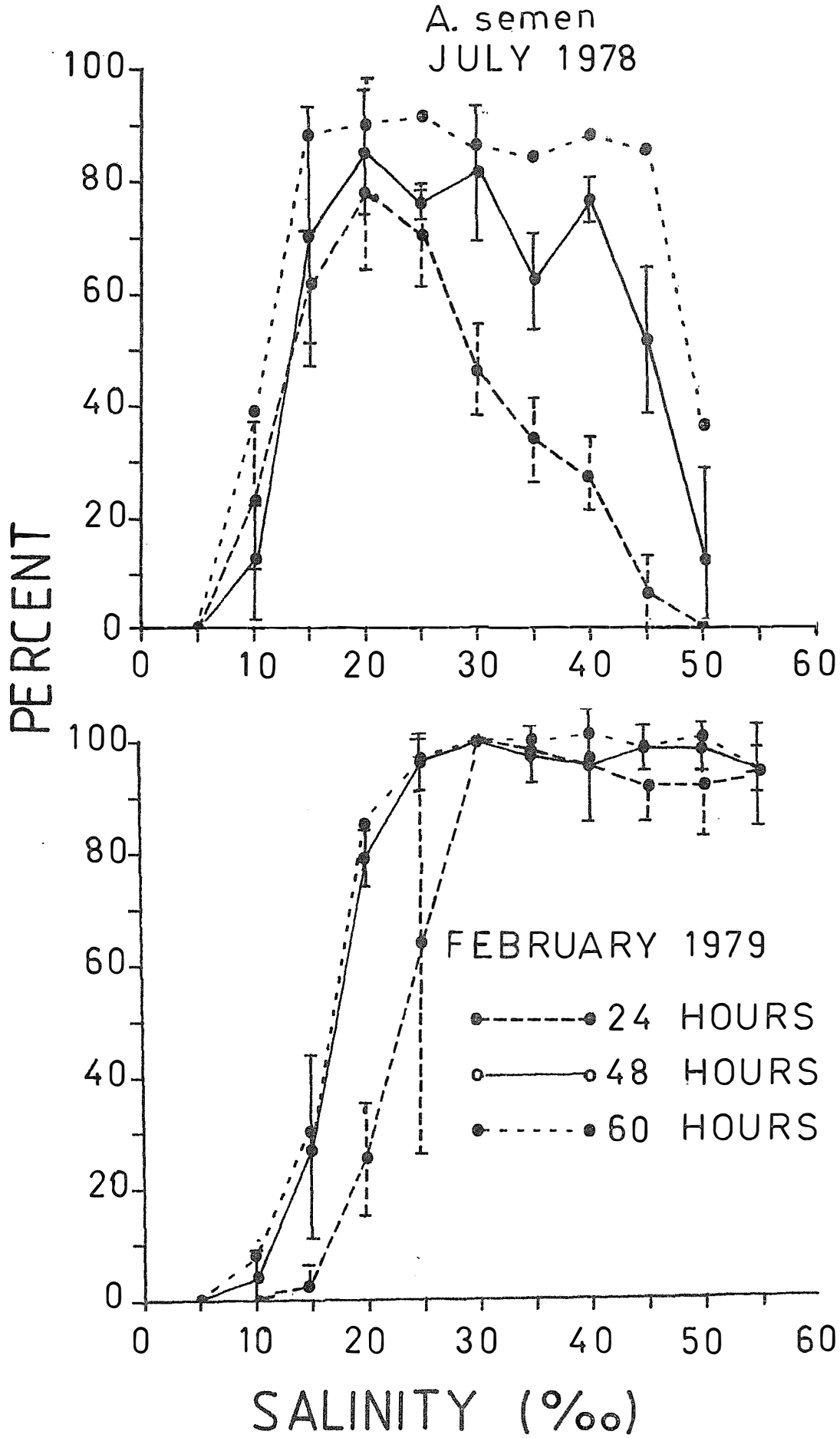
31. Temperature tolerance tests of Hydrococcus graniformis. The mean and one standard deviation are shown.



32. Temperature tolerance tests of Hydrococcus graniformis conducted at three salinities (10‰, 27‰ and 45‰). The mean and one standard deviation are shown.



33. Salinity tolerance tests of Hydrococcus graniformis conducted at three temperatures (8°C, 16°C and 29°C). The mean and one standard deviation are shown.



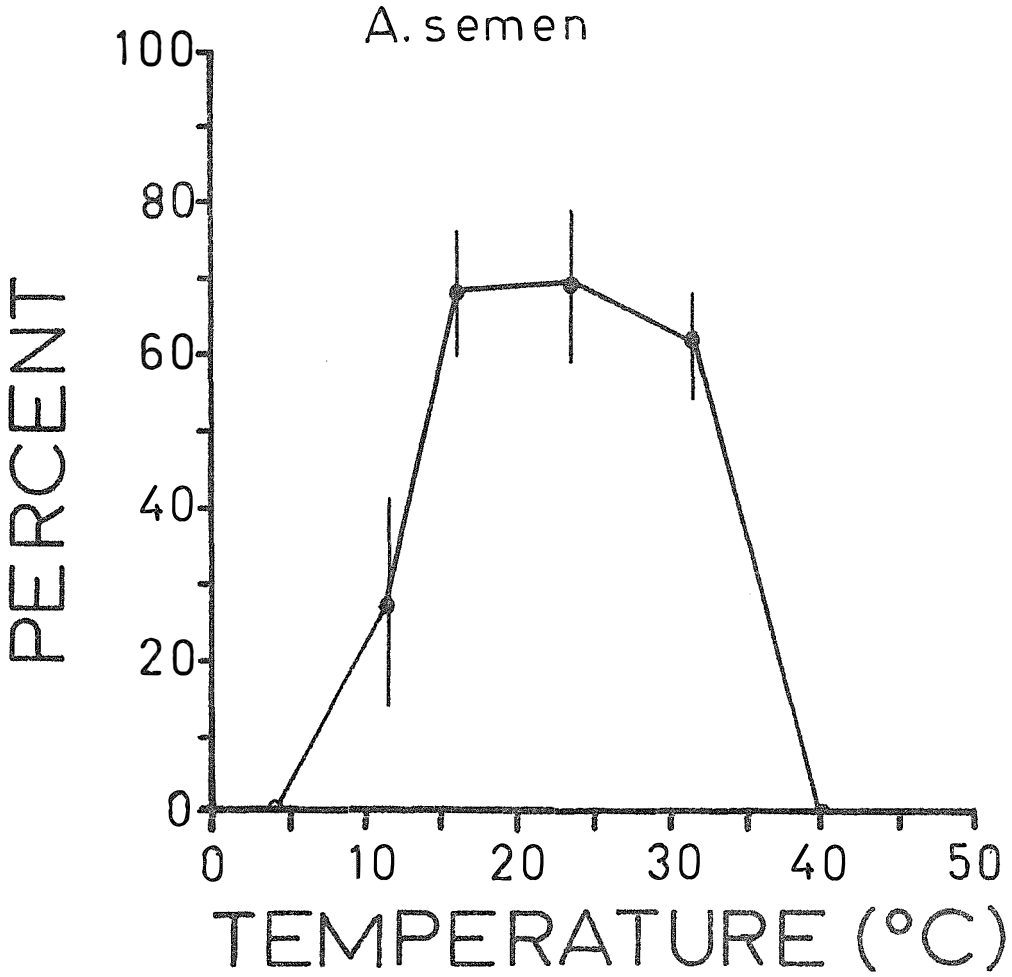
34. Salinity tolerance tests of Arthritica semen. The mean and one standard deviation are shown.

from 25‰ through the remaining salinities tested. The curve for February is shifted 5‰ to the right with respect to the July curve. In both tests higher activity rates were recorded after 48 hours than were found at 24 hours. Arthritica semen also had a wide temperature tolerance, with the animals being active at 18 to 32°C at a salinity of 27‰ (Figure 35).

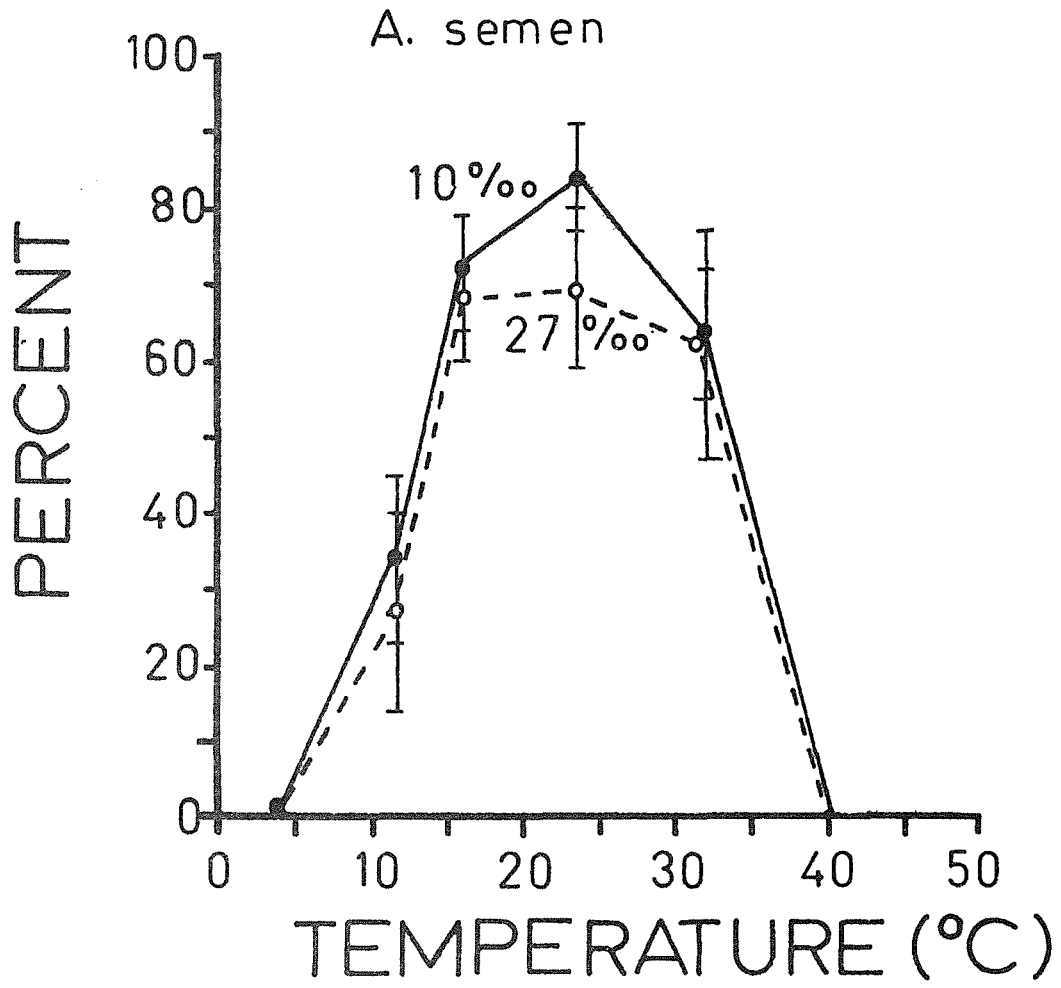
In the tests of A. semen at 3 salinities (10, 27 and 45‰) and a range of temperatures the results for 10 and 27‰ were similar (Figure 36) with the greatest activities being recorded at 18 to 32°C. No animals were active at 45‰.

Discussion

Both H. graniformis and A. semen have been shown to have wide salinity tolerances. H. graniformis was active from 15 to 35‰ in tests conducted when the ambient salinity was 21‰ and activity was greatest from 25 to 55‰ (the highest tested) when the ambient salinity was 54‰. A. semen had the same pattern of activity. Both species were inactive in the lowest salinities tested, 5‰, and had only moderate activities at 10‰. Salinities this low are reached briefly during the winter at Coodanup, and the animals could survive by closing their shells and waiting out the period of low salinity. This mechanism has been demonstrated for the bivalve Xenostrobus securis (Wilson, 1968; 1969) and two species of the gastropod genus Nassarius (Smith, 1975). The hypersaline conditions at Coodanup can persist for several



35. Temperature tolerance tests of Arthritica semen. The mean and one standard deviation are shown.



36. Temperature tolerance tests of Arthritica semen conducted at salinities of 10‰, 27‰ and 45‰. The mean and one standard deviation are shown.

months during the summer. Both species were active in the highest salinity recorded at Coodanup (54‰). Salinity tolerance curves of both H. graniformis and A. semen are shifted to the right in the February tests (summer) compared to the July tests (winter), suggesting that the animals become acclimatized to the increasing salinities in the estuary during summer.

H. graniformis was active in temperatures of 4 to 32°C and A. semen from 18 to 32°C. At 12°C about 40% of A. semen were active. Thus the two species were most active in temperatures similar to those recorded at Coodanup, 10 to 27°C. The temperature range in the shallow water at Coodanup might be greater than that measured because colder temperatures could be reached early on cold winter mornings and warmer temperatures could be attained on hot, still summer afternoons. However, the animals would be able to survive these brief periods of extreme conditions by closing up.

The temperature and salinity tests conducted were of only short duration. The tests were undertaken using the same techniques as those used for Hydrobia totteni (Wells, 1978), a species taxonomically related to H. graniformis. The tests of H. totteni were run for a period of 15 days with the activities checked every 3 days. There was no difference in the activities recorded after 3 days and the later periods of up to 15 days. At the end of the experiments the H. totteni were returned to ambient conditions. Animals that had been inactive at low temperatures became active, but those that had been inactive at high temperatures had died during the experiment.

Interactions between the effects of temperature and salinity have been shown in the gastropod Theodoxus fluviatilis by Kangas and Skoog (1978), which had a wider tolerance to salinity variations at 5°C than at 15°C. A similar examination was made for H. graniformis and A. semen. The test using 3 salinities and a variety of temperatures showed that each species had the same activity patterns in 10 and 27‰. At 45‰ the activity of H. graniformis had declined considerably and there were no A. semen active at all, suggesting that the combination of high temperature and salinity encountered at Coodanup during the summer could be lethal. This corresponds well with the population declines experienced by H. graniformis and A. semen shown earlier.

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APPENDICES

Appendix 1. Densities of molluscs collected at Coodanup during the period of March 1977 to February 1979. (In numbers per square metre ± 1 standard deviation).

MONTH	SPECIES				
	Hydrococcus	Arthritica	Toledonia	Potamopyrgus	Tornatina
12/iii/77	2502	---	141	2534	---
8/iv	8213 ± 4621	4135 ± 1758	132 ± 136	1401 ± 1010	10
10/v	3492 ± 2310	1000 ± 454	365 ± 288	233 ± 198	61
7/vi	14456 ± 2553	5117 ± 1929	518 ± 390	1543 ± 424	61
11/vii	18040 ± 6737	9817 ± 2142	1036 ± 419	4274 ± 4750	142
15/viii	19959 ± 6220	12629 ± 3043	1218 ± 483	2091 ± 1318	203
12/ix	19116 ± 5963	11502 ± 2632	1188 ± 437	1310 ± 711	---
11/x	15583 ± 7702	19025 ± 5324	467 ± 329	670 ± 854	41
7/xi	14618 ± 5479	45491 ±19472	1391 ± 531	487 ± 522	203
5/xii	9086 ± 4076	27847 ± 9534	335 ± 364	41 ± 70	---
5/i/78	8670 ± 4867	4893 ± 1819	91 ± 112	10 ± 32	---
6/ii	700 ± 500	8974 ± 3768	51 ± 72	--- ---	---
8/iii	822 ± 1340	751 ± 792	0 ± 0	--- ---	41 ± 78
10/iv	6081 ± 3951	6274 ± 3997	264 ± 181	--- ---	3046 ± 1479
8/v	4436 ± 2699	2274 ± 1191	162 ± 109	--- ---	741 ± 476
6/vi	11510 ± 6290	2170 ± 760	172 ± 180	--- ---	3431 ± 2142
10/vii	9300 ± 3732	4810 ± 2270	770 ± 410	--- ---	4770 ± 2280
7/viii	13956 ± 4001	5654 ± 2500	599 ± 285	--- ---	4324 ± 2618
6/ix	5766 ± 5608	1188 ± 871	528 ± 278	--- ---	91 ± 89
9/x	6883 ± 3516	1340 ± 576	477 ± 318	--- ---	112 ± 131
6/xi	5665 ± 3581	2355 ± 1443	426 ± 448	--- ---	223 ± 184
8/xii	8952 ± 5054	4872 ± 1806	704 ± 319	20 ± 43	2192 ± 1119
6/i/79	16659 ± 7210	7858 ± 2138	1299 ± 430	10 ± 32	2558 ± 1112
6/ii	3228 ± 2907	4548 ± 1271	203 ± 244	10 ± 32	101 ± 179
Aug 1st year	11203	12536	566	1216	60
Aug 2nd year	7772	3675	467	3	1803
2 year Aug	9487	8105	517	610	931

Appendix 2. Size-frequency data for Hydrococcus graniformis collected at Coodanup from March 1977 to February 1979.

	1977										1978	
Size class (mm)	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec	Jan	Feb
0.5-0.6		1.0										
0.6-0.7		0.5										
0.7-0.8		---	0.5	1.4		0.5	0.5					
0.8-0.9	0.6	1.0	---	---	1.0	2.0	---					
0.9-1.0	2.0	1.5	0.5	0.9	1.5	6.4	0.5	0.5				
1.0-1.1	1.2	3.0	0.5	2.0	2.5	7.3	2.0	1.0	1.0			1.4
1.1-1.2	2.6	3.0	0.5	0.9	2.0	8.4	1.4	2.0	0.5		1.0	---
1.2-1.3	3.1	4.5	2.9	5.6	2.0	8.4	6.9	5.0	3.9	0.5	---	1.5
1.3-1.4	2.8	13.5	8.1	6.6	4.0	11.3	8.9	8.9	5.3	4.5	---	---
1.4-1.5	6.9	5.5	9.2	6.0	4.5	5.4	8.9	12.4	7.8	7.0	2.6	---
1.5-1.6	8.2	13.5	10.5	8.0	2.5	6.4	11.3	10.5	10.8	15.0	0.5	5.8
1.6-1.7	8.8	13.5	15.9	14.0	10.5	8.9	11.3	12.9	19.5	26.5	5.0	4.3
1.7-1.8	5.0	5.5	12.0	11.2	8.5	5.9	5.4	7.0	12.6	9.5	5.6	1.5
1.8-1.9	6.3	5.5	7.2	7.4	13.0	5.0	8.4	9.9	9.8	5.5	12.7	2.9
1.9-2.0	6.3	6.5	11.1	8.4	14.5	5.0	9.8	6.5	8.8	9.5	14.7	11.6
2.0-2.1	6.3	3.0	9.2	8.9	8.0	5.0	7.9	4.5	4.4	11.0	10.7	11.6
2.1-2.2	8.1	2.5	3.8	8.6	9.0	3.5	3.5	6.9	4.9	2.5	9.1	5.8
2.2-2.3	5.7	2.0	2.4	3.3	5.5	4.4	7.9	1.0	3.9	5.0	11.7	7.2
2.3-2.4	5.0	3.0	1.9	4.2	5.0	2.0	2.9	1.5	2.4	0.5	13.2	16.0
2.4-2.5	1.9	1.5	0.5	0.5	0.5	1.0	1.0	3.0	2.4	1.0	5.6	17.4
2.5-2.6	3.2	1.5	1.0	0.9	1.5	0.9	0.5	2.0	0.5	0.5	3.0	7.2
2.6-2.7	6.3	0.5	0.5	0.5	2.0	0.5		2.5	1.0	0.5	3.1	4.4
2.7-2.8	3.1	2.0	---	0.5	1.0	0.5		1.5	0.5	1.0	1.0	1.4
2.8-2.9	2.5	1.5	1.0		---	0.5		0.5			0.5	
2.9-3.0	0.6	1.5			0.5	1.0						
3.0-3.1	1.8	1.5			0.5							
3.1-3.2	0.6	0.5										
3.2-3.3		0.5										
3.3-3.4		0.5										
3.4-3.5												
3.5-3.6												
3.6-3.7												
3.7-3.8												
Total	98.9	100.0	99.2	99.8	100.0	100.2	99.0	100.0	100.0	100.0	100.0	100.1
n	159	200	208	210	202	203	203	201	205	200	195	69

Appendix 2 (Cont.). Size-frequency data for Hydrococcus graniformis collected at Coodanup from March 1977 to February 1979.

Size class (mm)	1978 Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec	1979 Jan	Feb
0.5-0.6												
0.6-0.7												
0.7-0.8												
0.8-0.9		0.8										
0.9-1.0		0.4	0.4									
1.0-1.1		2.0	---									
1.1-1.2		2.8	0.4									
1.2-1.3	1.3	10.0	1.2		1.2	0.5						
1.3-1.4	---	14.0	2.0	2.9	0.8	1.5		0.4				
1.4-1.5	1.3	14.8	9.6	13.2	1.6	1.5		0.8				0.5
1.5-1.6	---	9.6	14.8	16.2	5.2	7.0	1.0	1.3				1.0
1.6-1.7	---	9.2	18.0	15.2	12.0	11.5	1.0	0.4				2.5
1.7-1.8	2.5	4.4	19.6	22.1	14.8	23.5	2.0	2.6	0.5			0.5
1.8-1.9	3.8	2.4	13.2	9.8	20.4	14.0	6.0	7.2	2.8	0.4		1.5
1.9-2.0	---	1.6	10.0	11.3	14.8	13.0	9.0	13.6	5.7	1.1		---
2.0-2.1	1.3	1.6	5.2	6.4	12.0	12.0	16.0	14.0	9.0	2.5	1.5	---
2.1-2.2	6.3	2.0	0.8	1.0	6.4	7.5	15.0	11.1	13.7	11.2	4.5	---
2.2-2.3	5.1	3.2	1.2	0.5	2.0	5.5	11.0	11.9	9.9	15.1	8.0	1.5
2.3-2.4	13.9	4.8	0.8	1.5	4.0	2.5	10.5	6.8	11.8	12.2	17.5	3.5
2.4-2.5	10.1	4.4	0.4		2.4		8.0	12.3	9.0	6.8	13.0	5.5
2.5-2.6	7.6	2.4	0.8		1.6		7.0	7.7	9.9	5.0	5.5	15.0
2.6-2.7	8.9	1.2	0.4		0.8		4.5	5.1	9.4	8.6	4.0	11.0
2.7-2.8	2.5	2.0	0.4				5.5	3.0	8.5	11.5	5.5	10.0
2.8-2.9	10.1	0.4	0.4				1.0	0.8	3.3	11.2	14.5	4.0
2.9-3.0	12.7	2.4	0.4				1.5	0.4	2.4	8.6	9.5	5.5
3.0-3.1	8.9	2.4					0.5	0.4	2.4	3.6	8.5	8.5
3.1-3.2	1.3	0.4					---		0.9	0.7	4.0	9.5
3.2-3.3	2.5	0.4					---		0.9	1.1	3.5	6.0
3.3-3.4		---					0.5			0.4	---	6.0
3.4-3.5		0.4									0.5	5.0
3.5-3.6												1.5
3.6-3.7												1.0
3.7-3.8												0.5
Total	100.0	100.0	100.0	100.1	100.0	100.0	100.0	99.8	100.1	100.4	100.0	100.0
n	79	250	250	204	250	200	200	235	212	278	200	200

Appendix 3. Size-frequency data for Arthritica semen collected at Coodanup from March 1977 to February 1979.

1977

Size class (m)	Mar	Apr	May	June	July	Aug	Sept	Oct
0.7 - 0.8						0.5		0.5
0.8 - 0.9					0.5	---		1.5
0.9 - 1.0					1.0	1.0		0.5
1.0 - 1.1		0.5			0.5	1.0		---
1.1 - 1.2		---	1.0		0.5	3.9	1.0	1.0
1.2 - 1.3		1.0	---		1.0	5.4	1.5	1.0
1.3 - 1.4		1.5	0.5		1.5	4.9	1.5	3.0
1.4 - 1.5	0.5	1.5	1.0	0.5	1.0	8.3	5.0	6.4
1.5 - 1.6	0.5	1.5	2.9	0.5	1.0	5.9	10.0	10.9
1.6 - 1.7	0.5	2.0	4.3	1.6	2.0	3.9	9.0	16.4
1.7 - 1.8	1.4	3.0	4.3	3.6	1.5	5.9	13.9	13.4
1.8 - 1.9	1.9	3.0	4.8	1.6	1.5	4.4	6.0	9.4
1.9 - 2.0	6.7	6.6	6.2	2.1	2.5	2.0	4.0	6.4
2.0 - 2.1	5.7	6.6	4.3	5.2	3.1	1.5	4.5	8.4
2.1 - 2.2	8.6	15.2	7.7	4.6	3.0	3.4	6.5	3.0
2.2 - 2.3	13.8	22.7	8.1	6.7	3.0	2.5	6.5	5.0
2.3 - 2.4	19.0	13.6	11.0	22.7	10.5	6.4	7.0	3.5
2.4 - 2.5	22.4	14.6	20.1	27.8	14.4	12.8	8.5	5.0
2.5 - 2.6	12.9	5.1	10.5	14.4	20.4	9.3	7.5	2.0
2.6 - 2.7	4.8	1.0	7.7	6.7	13.9	6.4	5.0	1.5
2.7 - 2.8	1.4	0.5	5.3	2.1	12.9	8.3	2.5	1.0
2.8 - 2.9			0.5		3.0	2.0	0.5	
2.9 - 3.0					---	0.5		
3.0 - 3.1					0.5			
Total	100.1	99.9	99.2	99.1	99.2	100.2	100.4	99.8
n	210	198	209	194	201	204	201	202

Appendix 3 (Cont.). Size-frequency data for Arthritica semen collected at Coodanup from March 1977 to February 1979.

	1977				1978			
Size class (mm)	Nov	Dec	Jan	Feb	Mar	Apr	May	June
0.7 - 0.8								
0.8 - 0.9								
0.9 - 1.0	0.5							
1.0 - 1.1	1.5							
1.1 - 1.2	0.5							
1.2 - 1.3	0.5							
1.3 - 1.4	3.0	1.9						
1.4 - 1.5	6.5	4.8		1.9				
1.5 - 1.6	8.5	5.7		1.9		0.8	0.5	
1.6 - 1.7	8.5	9.6	5.5	6.8	2.8	1.2	0.5	0.9
1.7 - 1.8	15.5	6.2	13.5	10.2	1.4	1.6	1.4	1.9
1.8 - 1.9	7.0	8.6	12.0	8.3	12.5	4.8	2.9	3.3
1.9 - 2.0	7.0	10.0	10.5	9.2	8.3	5.2	2.9	4.7
2.0 - 2.1	6.5	7.2	13.5	17.0	9.7	6.4	6.7	6.1
2.1 - 2.2	6.0	8.1	13.5	16.0	13.9	10.8	8.1	7.0
2.2 - 2.3	7.0	12.4	10.0	11.2	18.1	11.2	8.1	12.2
2.3 - 2.4	6.0	6.7	10.5	9.7	5.6	10.8	11.5	12.2
2.4 - 2.5	5.5	8.6	5.5	6.3	9.7	18.0	14.8	16.4
2.5 - 2.6	5.0	7.2	4.0	1.0	12.5	16.0	17.7	19.7
2.6 - 2.7	3.0	1.9	1.0	0.5	4.2	9.6	16.3	9.9
2.7 - 2.8	1.0	0.5	0.5		1.4	2.8	7.7	3.8
2.8 - 2.9	0.5	0.5				0.8	1.0	0.9
2.9 - 3.0	---							0.9
3.0 - 3.1	0.5							
Total	100.0	99.9	100.0	100.0	100.1	100.0	100.1	99.9
n	200	209	200	206	72	250	209	213

Appendix 3 (Cont.). Size-frequency data for Arthritica semen collected at Coodanup from March 1977 to February 1979.

	1978						1979	
Size class (mm)	July	Aug	Sept	Oct	Nov	Dec	Jan	Feb
0.7 - 0.8								
0.8 - 0.9								
0.9 - 1.0								
1.0 - 1.1								
1.1 - 1.2			0.9					
1.2 - 1.3			---					
1.3 - 1.4			---					
1.4 - 1.5			0.9		0.9			
1.5 - 1.6			1.7		0.9			
1.6 - 1.7			1.7		0.9			
1.7 - 1.8	0.8	0.8	3.5	2.0	0.9	0.5		
1.8 - 1.9	0.4	0.8	7.0	3.4	1.4	1.0		
1.9 - 2.0	0.4	2.8	6.1	2.0	2.3	0.5		
2.0 - 2.1	1.2	0.4	2.6	3.4	0.9	1.0		
2.1 - 2.2	0.4	1.6	4.3	1.0	0.5	3.5		
2.2 - 2.3	2.4	2.4	1.7	1.4	---	4.5		
2.3 - 2.4	7.2	3.2	6.1	2.5	2.3	3.0		
2.4 - 2.5	8.4	11.6	1.7	3.4	5.0	5.0		
2.5 - 2.6	20.8	21.9	12.2	9.8	6.8	16.0		
2.6 - 2.7	28.0	27.5	13.0	21.7	26.8	18.0		
2.7 - 2.8	21.6	21.5	19.1	25.1	28.6	24.5		
2.8 - 2.9	7.2	4.4	15.7	13.8	13.6	15.5		
2.9 - 3.0	2.0	1.2	1.7	8.4	6.4	5.0		
3.0 - 3.1				2.0	1.4	1.5		
					0.5	0.5		
Total	100.8	100.1	99.9	99.9	100.1	100.0		
n	252	251	115	203	220	200		

Appendix 4. Size-frequency data for Anticorbula amara collected at Ravenswood from October 1977 to February 1979.

	1977			1978						
Size class (mm)	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	June	July
0-1			4.8							
1-2			5.5							
2-3			3.4		0.9	1.5				
3-4		1.0	1.4		0.9	---	3.8	1.4		
4-5	0.9	---	0.7	2.2	2.8	9.1	5.8	---		1.8
5-6	---	---	2.8	7.4	0.9	8.3	15.4	1.1		4.6
6-7	---	1.0	2.8	9.6	1.9	15.2	6.7	2.2		10.8
7-8	---	1.9	8.3	20.6	5.6	18.9	18.3	14.4	14.3	13.0
8-9	0.9	2.9	4.1	19.1	12.4	14.4	10.6	16.7	11.9	18.9
9-10	3.6	4.9	2.1	15.4	16.8	12.1	13.5	18.9	21.4	20.7
10-11	3.6	9.7	6.9	8.8	22.3	4.5	4.8	20.0	16.7	14.8
11-12	5.4	20.4	6.2	3.7	16.8	3.8	3.8	8.9	7.1	9.5
12-13	7.2	6.8	9.7	2.9	7.5	3.8	4.8	6.7	14.3	5.3
13-14	18.9	15.5	16.6	2.2	8.4	3.8	5.8	4.4	7.1	0.6
14-15	30.6	10.7	13.9	2.2	1.9	1.5	2.9	2.2	4.8	
15-16	17.1	17.5	5.5	2.2		0.8	1.9	1.1	2.4	
16-17	5.4	5.8	3.4	2.9		2.3	1.0	2.2		
17-18	6.3	1.9	2.8				1.0			
18-19										
19-20										
20-21										
21-22				0.7						
Total	99.9	100.0	100.9	99.9	99.1	100.0	100.1	100.2	100.0	100.0
n	111	103	145	136	107	132	104	90	42	169

Appendix 4 (Cont.). Size-frequency data for Anticorbula amara collected at Ravenswood from October 1977 to February 1979.

	1978					1979		
Size class (mm)	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Mar
0-1								
1-2								
2-3		0.9	4.8			0.9	1.0	
3-4		0.9	9.6			6.2	4.0	2.0
4-5		3.6	21.2	3.0		8.8	13.0	2.0
5-6		5.4	9.6	11.0		4.5	16.0	5.0
6-7	1.5	5.4	12.5	16.0	1.2	10.6	30.0	12.0
7-8	---	8.1	8.7	17.0	15.1	14.2	12.0	16.0
8-9	1.5	18.9	2.9	3.0	19.8	6.2	8.0	18.0
9-10	7.5	13.5	6.7	4.0	19.8	8.8	5.0	14.0
10-11	24.2	16.2	14.4	13.0	18.6	11.5	3.0	14.0
11-12	21.2	17.1	4.8	11.0	12.8	6.2	4.0	6.0
12-13	15.2	8.1	1.9	12.0	11.6	10.6	2.0	5.0
13-14	19.7	1.8	1.0	6.0	1.2	3.5	2.0	5.0
14-15	6.1		1.0	3.0		0.9		1.0
15-16	3.0		1.0	---				
16-17				1.0				
17-18								
18-19								
19-20								
20-21								
21-22								
Total	99.9	99.9	100.1	100.0	101.0	99.9	100.0	100.0
n	66	111	104	100	86	113	100	100

Appendix 5. Survey of mollusc densities in the Peel - Harvey estuarine system in January and August 1978.

Station	Species					
	Hydrococcus		Arthritica		Toledonia	
	Jan (no/m^2)	Aug (no/m^2)	Jan (no/m^2)	Aug (no/m^2)	Jan (no/m^2)	Aug (no/m^2)
1	547	1743	42	1837	42	1186
2	42	23	295	116	0	367
3	210	23	463	0	42	0
4	295	6510	42	2511	126	23
5	42	0	168	163	0	0
6	42	47	42	233	0	116
7	0	0	18,103	47	589	465
8	0	0	14,229	558	0	70
9	0	0	37,511	13,903	0	0
10	0	0	758	0	0	0
Peel ($\bar{X}$)	196	1391	175	810	70	282
Harvey ($\bar{X}$)	0	0	23,281	4836	196	178

APPENDIX 6

Explanation of formulae used in the text

Shannon-Wiener index (summarized from Krebs, 1972).

This index is based on information analysis, and tries to measure the amount of order (or disorder) in a system. It basically attempts to answer the question: How difficult is it to predict what species the next individual collected will belong to? The formula is:

$$H = - \sum_{i=1}^{s} (p_i) (\log_2 p_i)$$

where H = the index

S = the number of species

p_i = the proportion of the total sample belonging to species i

The larger the value of H the more uncertainty there is in the system. Thus if all individuals are of the same species H will be 0. If there are two species, one with 99 individuals and one with 1 individual, H will be 1.00. Thus the index as used here measures the equality of distribution of individuals among the various species. The more even the distribution, the higher the value of H.

Simpson index (summarized from Krebs, 1972).

This index is based on probability theory, and measures the chance that 2 individuals picked randomly will be of the same species. The formula is:

$$D = 1 - \sum_{i=1}^{s} (p_i)^2$$

where D = the index

p_i = the proportion of individuals in species i

This index gives relatively little weight to rare species and emphasizes the more common ones. It varies from 0 where all individuals are of different species to 1 where all individuals are of the same species.

The dendrogram

The Morisita (1959) index as modified by Horn (1966) was used in calculating the dendrogram. The index is:

$$C\lambda = \frac{2 \Sigma x_i y_i}{\Sigma x_i^2 + \Sigma y_i^2}$$

where $C\lambda$ = the index

x_i = the proportion of individuals in species x

y_i = the proportion of individuals in species y

The index varies from 0 where there is no overlap to 1.00 where the overlap is total. This index was calculated for all possible combinations of shore height at stations sampled in Peel Inlet; similar calculations were made for Oyster Harbour. The data were then arranged in a dendrogram for each estuary using the weighted pair group method with average linkage (Sokal and Sneath, 1963). This technique groups stations together on a graph that have high (approaching 1) overlap with each other. As progressively lower overlaps are encountered more stations are included on the tree. Aggregations of stations with high overlaps suggest communities. Thus on Figure 17 the dendrogram shows 2 aggregations in Oyster Harbour: stations at shore levels of 0.38 to 0.73 m and stations at 0.28 to 0.33 m. There is only a low level of overlap between the two groupings, suggesting they are distinct associations.