SOME ASPECTS OF THE BIOLOGY OF NASSARIUS KRAUSSIANUS (DUNKER)(GASTROPODA : PROSOBRANCHIA : NASSARIIDAE), IN THE BUSHMANS RIVER ESTUARY, WITH PARTICULAR REFERENCE TO RECOLONISATION AFTER FLOODS.

by

CAROLYN GAY PALMER

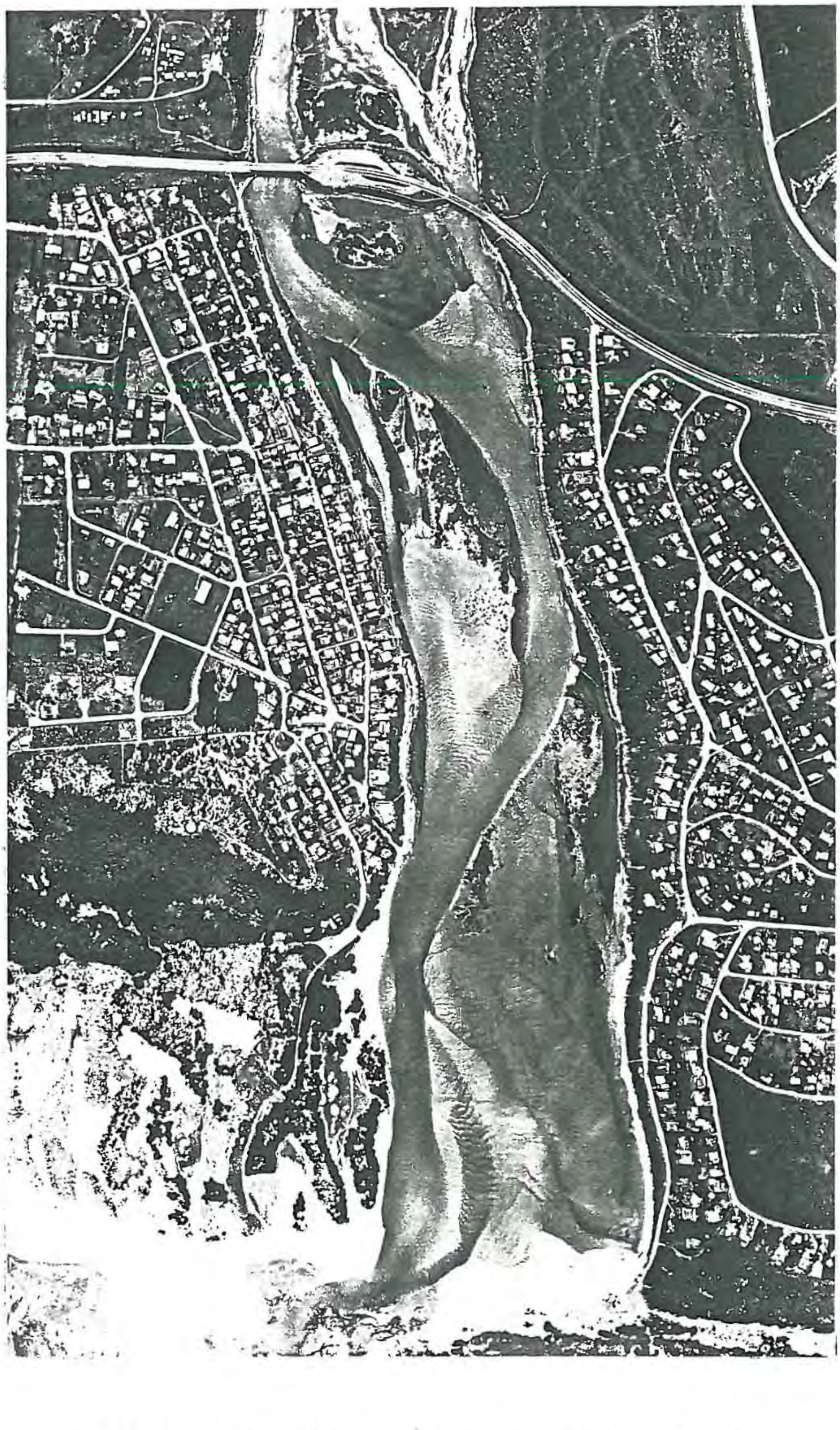
Thesis presented to Rhodes University for the degree of
Master of Science.

Department of Zoology and Entomology
Rhodes University
Grahamstown
Republic of South Africa

December, 1980.

CORRIGENDA

Page	
33	Line 7, 'von Bertalanaffy' should read 'von Bertalanffy'.
35	Table 2,'$0.1m^{-2}$, $0.06m^{-2}$, $0.25m^{-2}$' should read '$0.1m^2$, $0.06m^2$, $0.25m^2$'.
37	Facing legend to Fig. 9, line 11, 'June 1979' should read 'March 1980'.
42	Table 3,'Biomass g ash free shell free dry weight' should read 'Biomass g ash free shell free dry weight m^{-2}'.
46	Legend to Fig. 14, line 6, 'tp' should read 'to'
50	Legend to Fig. 15, Part c , should read 'The number of reproductively mature females recorded between April 1979 and June 1980. Not all the females shown in (a) above were reproductively mature, and only actively reproducing females were capable of spawning juveniles, shown in (b) above.'.
68	Lines 15-17 should read 'mud-flat (Fig. 13c), and, as already discussed, it seems unlikely that the large numbers of recolonising juveniles were spawned by the few surviving females.'.
72	Table 5, line 11, 'Cenastoderma' should read 'Cerastoderma'.
93	Facing legend to Fig. 27, line 7 'devloped' should read 'developed'.
99	Line 15, 'simliar' should read 'similar'.
120	Line 33, 'Table 7' should be 'Table 8'.
145	Cather, J.N. 1973. 'Ovoviviaprity' should read 'Ovoviviparity'.
148	Forbes, A.T. 1973a 'An unusual larval' should read 'An unusual abbreviated larval'.
163	Line 12, '16.7.80' should read '16.7.79'.



Frontispiece: An aerial photograph of the Bushmans River estuary taken in April 1979 by Professor D.A. Scogings.

CONTENTS

PART 2. POPULATION BIOLOGY

2.3 MATERIALS AND METHODS

2.4 RESULTS

PART 3. REPRODUCTIVE BIOLOGY

PART 1 : GENERAL INTRODUCTION

Early research into South African estuarine ecology took the form of extensive surveys (Day, 1951; 1956; 1959; Day, et al., 1952; Day, et al.,1953; Scott, et al., 1952; Millard & Harrison, 1953; Millard & Scott, 1953). Day (1951), in the first of a series of publications, reviewed estuarine conditions in general and provided the guidelines for this phase of research. He recognised five major faunal components: freshwater, stenohaline marine, euryhaline marine, estuarine and migratory. The first four of these emphasised the fundamental role of salinity in the distribution and composition of estuarine fauna. Substratum, in addition to salinity, was recognised as an important factor, and most estuaries were subsequently described in terms of the lower, middle and upper reaches, each with a particular gradient of salinity and substratum type. Although salinity and substratum were highlighted, the complexity of estuarine systems, and the significance of a wide range of limiting factors was recognised.

The surveys provided a record of the presence, abundance and distribution of estuarine fauna, identified the dominant estuarine species, and formed the foundation for further research. A comparison of the diverse faunal assemblages documented by these surveys enabled Day (1967) to list several reasons why the Knysna estuary was productive, possessing a rich estuarine fauna. Contributing factors were: the temperate climate, well distributed annual rainfall, wooded banks with little erosion, a variety of substrata and a permanently open mouth which allowed tidal exchange and energy input from the sea.

Surveys were followed by experimental research, with particular reference to the role of environmental factors in the distribution of estuarine fauna. Temperature and salinity were selected as relevant physical factors, however, a review of the results indicated that most estuarine organisms lived well within their temperature and salinity tolerance limits (Hill, in press). The wide tolerance limit of many species was demonstrated by the discovery of a relict estuarine fauna in an entirely freshwater environment, Lake Sibaya (Allanson, _et_ _al_., 1966). Recently, the concept of the way in which the distribution of organisms is controlled by physico-chemical and biological features of the environment has changed. It has become increasingly clear that most organisms live well within potentially lethal physical extremes, and that the occurrence of organisms in a particular environment is more directly controlled by factors such as resource partitioning, competition, and energy channelling into either growth or reproduction (Newell, 1979).

A review of the data for South African estuarine organisms certainly substantiates this view. Most of these organisms are able to osmoregulate (Hill, 1971; Forbes, 1974), some are able to tolerate wide fluctuations in body fluid osmolality (Skaer, 1974), whereas others cope with salinity extremes by behavioural avoidance (McLachlan & Erasmus, 1974). Adaptation to fluctuating and reduced salinities is essential, for without this, the survival of any organism as a permanent member of the estuarine community is impossible. The efficient osmoregulatory ability of many southern African estuarine organisms probably evolved in response to frequent floods which occurred along the east coast (Forbes, 1974; Hill, in press). Therefore, although the geographical distribution of estuarine organisms may be affected by salinity tolerance, animals living within their distribution range are seldom directly influenced by salinity extremes.

Similarly, most estuarine animals live within their temperature tolerance limits, and temperature extremes are seldom a direct cause of mortality (Hill, in press). Many benthic fauna are protected from elevated temperature by their burrowing habit (Hill & Allanson, 1971; McLachlan &

Erasmus, 1974). However temperature is not necessarily unimportant, and an fundamental effect of temperature may be to reduce fecundity (Hill, 1977).

The other environmental factor emphasised in the early survey work was substratum type, and one of the most significant suggestions arising from that era was Day's (1959) hypothesis that South African estuaries have a quiet water fauna similar to that of sheltered marine bays. Hill (in press) has observed that low salinities resulting from floods are of relatively short duration, and that deposition of silt has a much longer lasting effect. He suggested that the quiet water fauna of estuaries and sheltered bays comprised animals able to cope with and utilise fine sediments, rather than animals unable to live on wave-washed shores. The importance of sediments was demonstrated by McLachlan & Grindley (1974) when they found that the distribution of macrobenthos in the Swartkops River was determined primarily by substratum type.

Hill (in press) has suggested that the effects of silt deposition, and the relationship between estuarine animals and the substratum are areas in estuarine ecology requiring considerable attention. Studies of the population biology of dominant estuarine fauna have also been neglected, and the entire field of secondary production in estuaries is untouched, except for a study on the bivalve Musculus virgiliae Barnard, in Swartvlei, a coastal lake (Davies, 1979; 1980).

Thus, estuarine research in southern Africa "has reached the phase where it is worth standing back and assessing the results so far obtained, and then deciding in which direction we should now proceed" (Hill, in press). But before sophisticated analysis of resource partitioning, competition and energy transfer can be tackled, the basic biology of many organisms has still to be documented, as little is known about even some of the more abundant estuarine fauna.

Once a particular animal has been selected, investigation of its population biology, feeding and energetics should be followed by detailed study of its role within the community along the exciting guide-lines described by Newell (1979). This approach requires co-ordinated study of particular systems. Programmes of this type are scarce in southern Africa, but have been exemplified by work on the coastal lake systems of Lake Sibaya (Allanson, 1979) and Swartvlei (Howard-Williams & Allanson, 1978). A similar approach to estuaries would prove very fruitful.

In the present work, a previously unstudied prosobranch gastropod, *Nassarius kraussianus* (Dunker) (Appendix 1), was selected, and its population biology and reproductive strategy investigated in detail. At the same time, information on the feeding biology and general life style was gleaned by observation and simple experiment. This approach has resulted in a greater insight into the adaptations of *N. kraussianus* to an estuarine environment, and lays the foundation for further, more sophisticated study.

N. kraussianus is a small (1-9mm) prosobranch which is abundant between Still Bay and Mozambique on intertidal estuarine mudflats and in isolated rocky-shore pools (Kensley, 1973; Day, 1974; R.N. Kilburn, *pers.comm.*). In its estuarine habitat, *N. kraussianus* is an important member of the macrobenthos. A large intertidal mudflat in the Bushmans River estuary, easily accessible from the coastal road, provided an ideal study site, as it supported a richly diverse mudflat community of which *N. kraussianus* was a prominant member. The mudflat was surrounded by extensive intertidal and subtidal beds of *Zostera capensis* Setchell, which Liptrot (1978) described as an important primary producer in the Swartvlei estuary. In July and August 1979, the Bushmans River flooded and enormous silt loads were deposited over the study area. This provided a unique opportunity to monitor the recovery of an estuarine population after a major flood.

The present study was designed to assess the biomass of the N. kraussianus population and to elucidate the population structure. The life cycle of N. kraussianus was investigated so that recolonisation could be assessed in terms of reproductive strategy. Since estuarine invertebrates have evolved adaptive mechanisms to cope with low salinities in response to regular floods (Forbes, 1974); they have almost certainly evolved mechanisms for coping with siltation. It is difficult to imagine these as physiological adaptations, and the results of this study seem to indicate that reproductive strategy and recolonisation are vital adaptive mechanisms.

PART 2 : POPULATION BIOLOGY

2.1 INTRODUCTION

Accurate, quantitative sampling is the basis of any population biology study, and as the objects of the study will largely determine the methods used (Southwood, 1978), an outline of these would be valuable. In this study the aim was to quantify biomass, elucidate population structure and estimate growth. Later, it became necessary to include the concept of life cycle as an adaptation to environment. However, Mann (1971) has pointed out that there are several problems associated with quantifying benthic population data: first, distribution of the population is usually contagious, or patchy and the sampling error high; and second, benthic invertebrate populations are often subject to heavy predation and may have low standing stocks even though production is high. Despite these difficulties it is essential to estimate biomass, as all information on growth, mortality and production is based on biomass values. Annual biomass values enable comparison of different populations, and are especially useful if production can be estimated and the production to biomass ratio compared. The problems described by Mann (1971) were encountered in the field during this study, but because of the fundamental and comparative importance of biomass values, quantitative sampling of the *N. kraussianus* population was a major emphasis of the study.

Biomass data are often presented in the form of size-frequency histograms which differentiate the biomass contributions of animals of different sizes. Reproduction that occurs at discrete intervals is shown by the presence of cohorts in the size frequency distribution. If only one cohort is produced annually, the calculation of production is relatively simple (Winburg *et al.*, 1971). Frequently generations overlap, but if reproduction is discrete and not continuous, cohorts can still be distinguished and a polymodal size frequency distribution results. In this situation the probability paper method of Harding (1949) and Cassie (1950; 1954), is usually used to clearly identify the component cohorts. If reproduction is continuous, cohort analysis is impossible and an alternative sampling technique such as a mark-release-recapture programme would yield information about population growth and mortality (Appendix 2). In addition to size frequency distribution, other aspects of population structure, such as sex ratio and male/female size frequencies must be considered. These aspects of population biology have been widely documented in reports on a variety of molluscs, and *N. kraussianus* will be compared to other prosobranchs.

However, population biology need not result in a simple description of population parameters. For example an interesting ecological implication of sex ratio is resource partitioning. In a recent review, Newell (1979) has shown that many benthic detritivores have narrow feeding niches, which result in efficient resource partitioning. Browne (1978) noted that separate sexes in the prosobranch _Viviparous georgianus_ provided an opportunity for resource partitioning, and that differences in the sizes and growth rates of males and females were evidence that such partitioning probably occurred. This is an intrigueing idea, but one that needs rigorous investigation before it can be presented as fact. In the case of _N. kraussianus_ it must remain an interesting possiblity.

It is essential to view population biology as a dynamic process. This is clearly reflected by studies which have shown that the population parameters of a single species may vary considerably in different habitats. Two British populations of the isopod _Eurydice pulchra_ Leach, one estuarine (Fish, 1970), and one marine (Jones, 1970), were studied simultaneously but independently. The populations had different life cycles. Ovigerous females appeared earlier in the marine population, spawned, and juveniles grew to adult size in the same season with only a few broods overwintering as juveniles. In contrast, the estuarine population spawned later and most juveniles overwintered before growing to maturity. Similarly, the breeding of the amphipod Ampelisca brevicornis (da Costa) was restricted to between July and October in the North Sea (Klein, et al., 1975), whereas in the Mediterranean Sea it reproduced throughout the year (Kaim-Malka, 1969). In both these instances temperature played an important part, but very often factors such as food availability affect population parameters.

Thus, population parameters reflect adaptation to particular habitats, and while quantified measurements are important, it is essential to relate the results to the environment. This is well illustrated in a comparison of populations which inhabit both marine and estuarine environments, where the food availability, and patterns of energy flow, are totally different. These differences are inevitably reflected in a variety of reproductive and energy channelling strategies.

A comparison of two populations of the prosobranch Littorina littorea (L.), one estuarine and one from an exposed rocky shore, demonstrated the importance of food availability. Fish (1972) found that the estuarine population grew faster, matured earlier in the year, and that animals reproduced for the first time in their second winter, compared with the second or third winter in the open coast population. These differences were ascribed to the higher nutritional status of the estuary compared to the open coast. This phenomenon is not confined to populations in extremely disparate environments. Fish & Fish (1974) investigated the breeding cycle and growth of a single population of the prosobranch Hydrobia ulvae (Pennant) in the Dovey estuary and found that animals from muddier substrata, with higher silt-clay and organic carbon values, grew faster and attained larger sizes than animals in areas where the organic content of the substratum was lower.

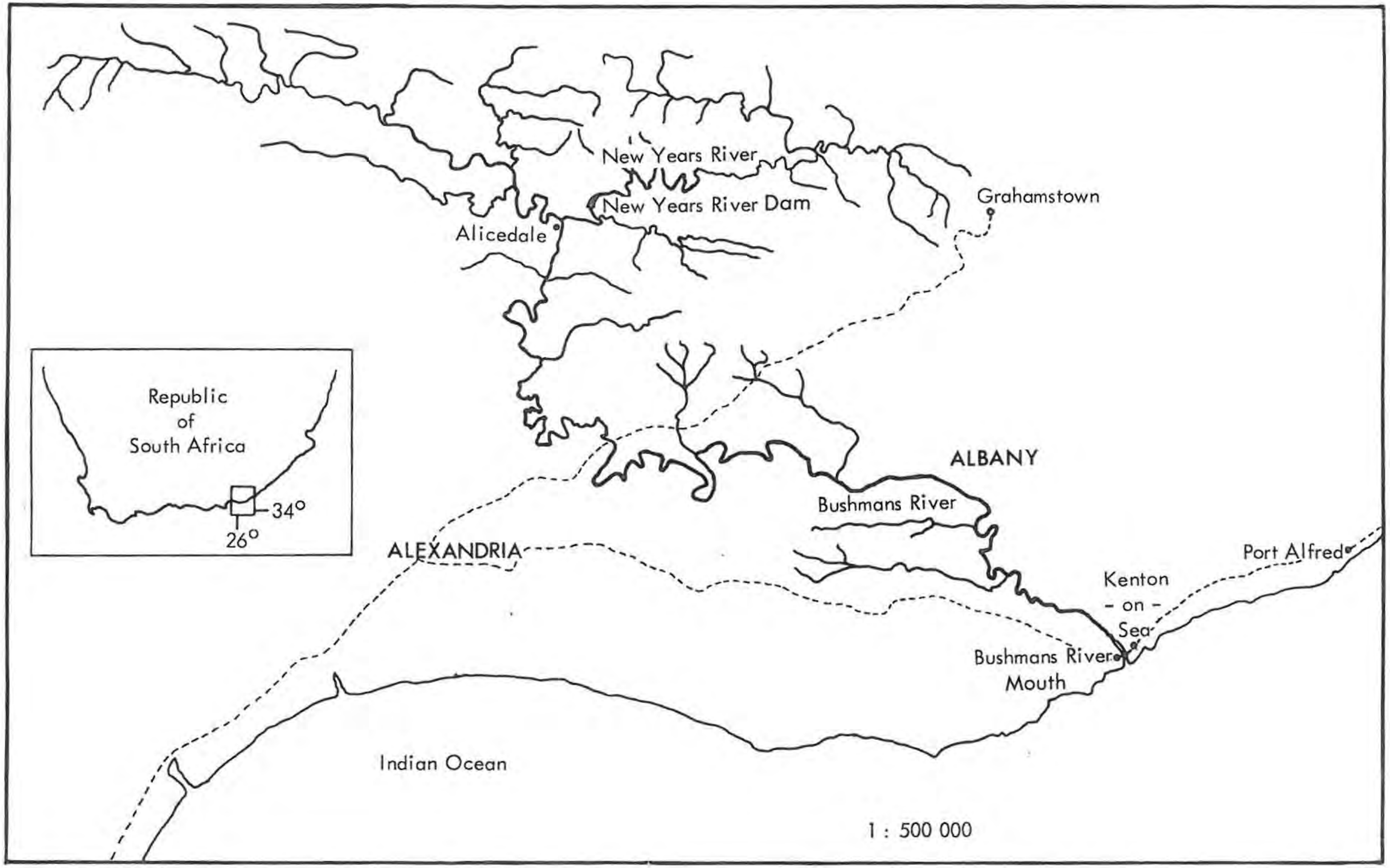
Clearly it is necessary to relate the population structure of a species to the environment in which it is studied, and to pay particular attention to factors such as temperature and food availability. If the population biology of a species is related to the environment in this way, future comparisons with other populations are easier and far more meaningful. This approach has been followed in the present study.

Finally, the results of quantitative population studies may also serve as valuable baseline information, facilitating the assessment of environmental impact on an area. Buchanan & Warwick (1974) emphasised the importance of this aspect in their investigation of the production of an offshore benthic community. A study of the Grevelingen estuary by Wolff & de Wolf (1977) was initiated for a similar reason. The estuary was to be dammed in the near future and the investigation was designed as a point of reference for future work describing changes after the closure of the estuary. Many estuaries on the east coast of South Afica evidence environmental degradation (Begg, 1978). A symptom of this problem is the high level of siltation in several of the estuaries, and one of the results is a reduction in the area covered by *Z. capensis*, an important primary producer. *Z. capensis* fronds also form an important substratum for organisms such as *N. kraussianus*, and the present study provides quantitative information on the current status of the *N. kraussianus* population and its associated habitat.

2.2 STUDY AREA

The Bushmans River estuary is situated in the eastern Cape Province of the Republic of South Africa and opens into the sea between the villages of Bushmans River Mouth and Kenton-on-Sea at 33^{o} 42'S; $26^{o}40$'E (Fig. 1). The river is the largest in the district; it is 170 km long, with its source 20 km west of Kommadagga, and has a catchment area of 2718 km^2 (Bushmans-Kariega Trust, 1975). The geological composition of the catchment area is grey and red mudstone and sandstone of the Middleton formation (Adelaide subgroup : Beaufort Group : Karoo Supergroup). Mudstone, which is unstable and extremely susceptible to erosion constitutes approximately 70% of this formation (Johnson & Keyser, 1976). The river flows through the districts of Alexandria and Albany which support extensive pastoral agriculture. Sheep, cattle and goats are the most important stock on the land and the stocking rate was calculated from data supplied by the Secretary of Statistics (1975) as one large animal unit to 5.62 ha.

The New Years River dam is the only major impoundment affecting the Bushmans River (Fig. 1). There is no sewage input into the system, though phosphorous and nitrogen may be washed into the river in run-off from fertilized agricultural lands.


New Years River
New Years River Dam
Grahamstown
Alicedale
Republic
of
South Africa
34°
26°
ALBANY
Bushmans River
ALEXANDRIA
Port Alfred
Kenton
- on -
Sea
Bushmans River
Mouth
Indian Ocean
1 : 500 000

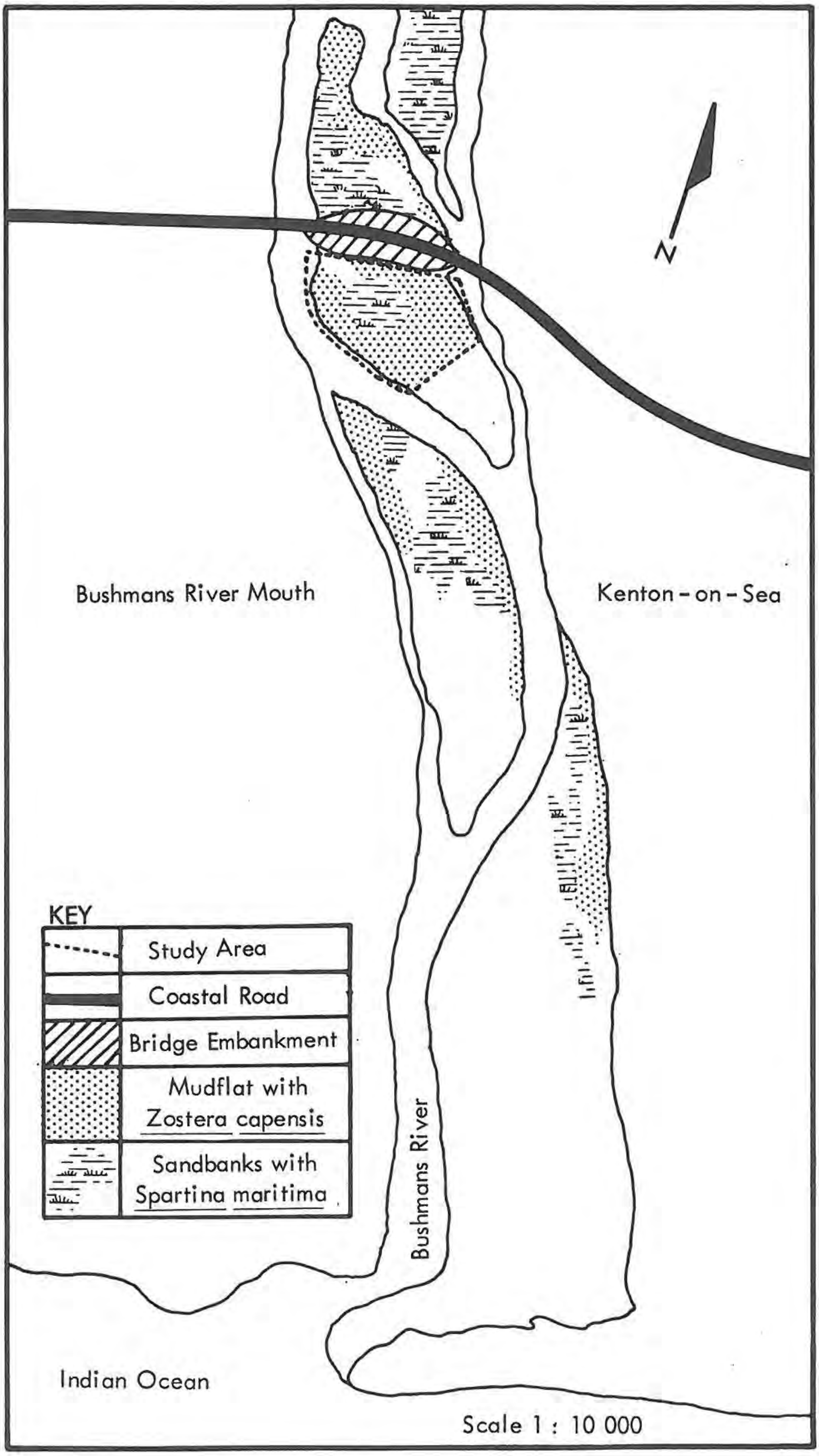
The estuary is tidal for 29 km inland and is crossed by a coastal road bridge 2 km from the mouth, at which point it is 381 m wide (Fig. 2). Water flows in two channels under the road bridge (east channel, 37 m; west, 56 m) and a rubble embankment (288 m) separates the two channels. On the seaward side, the embankment leads down to a 3.4 ha. mudflat which was selected as the study area.

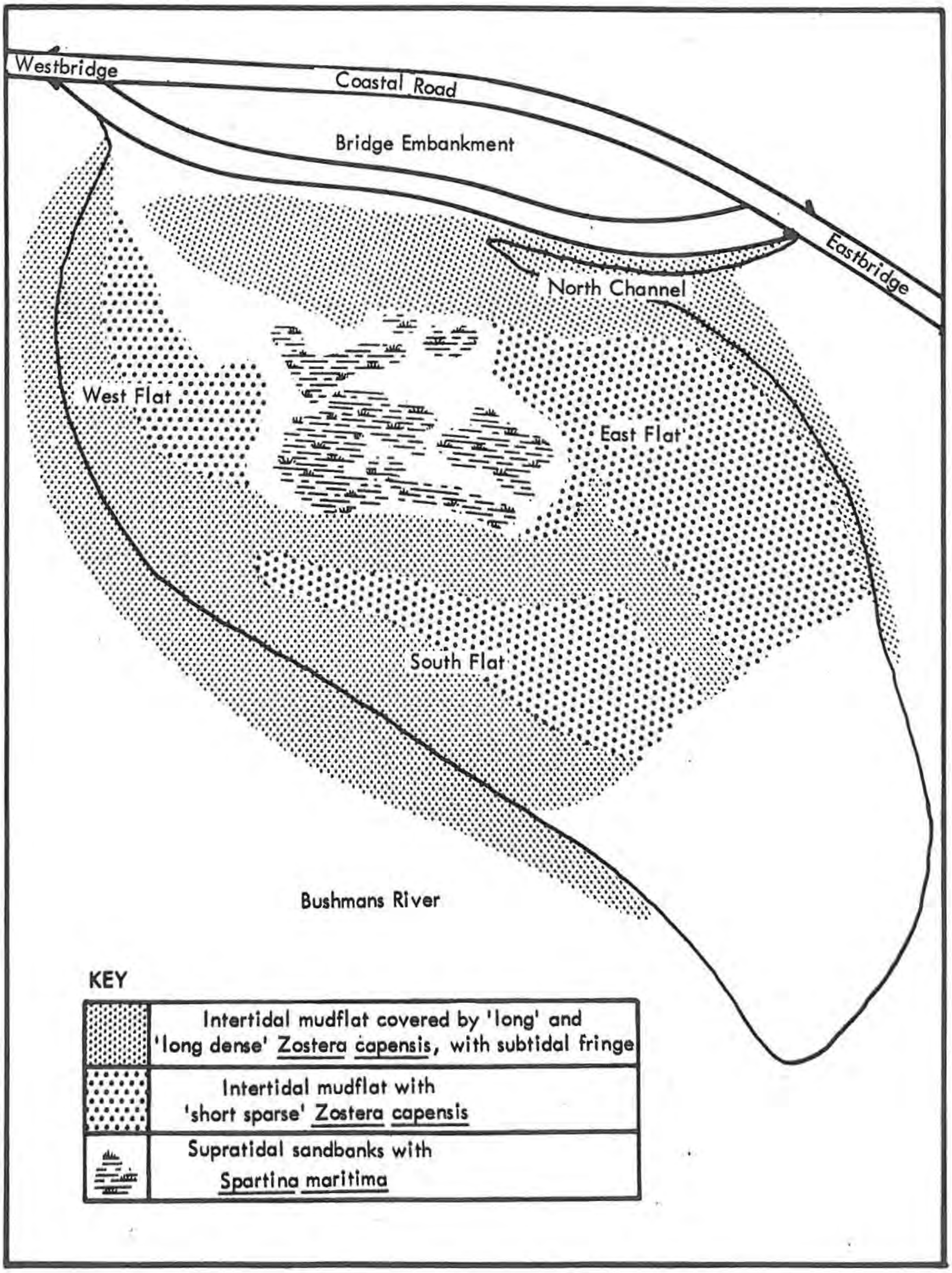
The mudflat is divisible into three regions (Figs. 3 & 4):

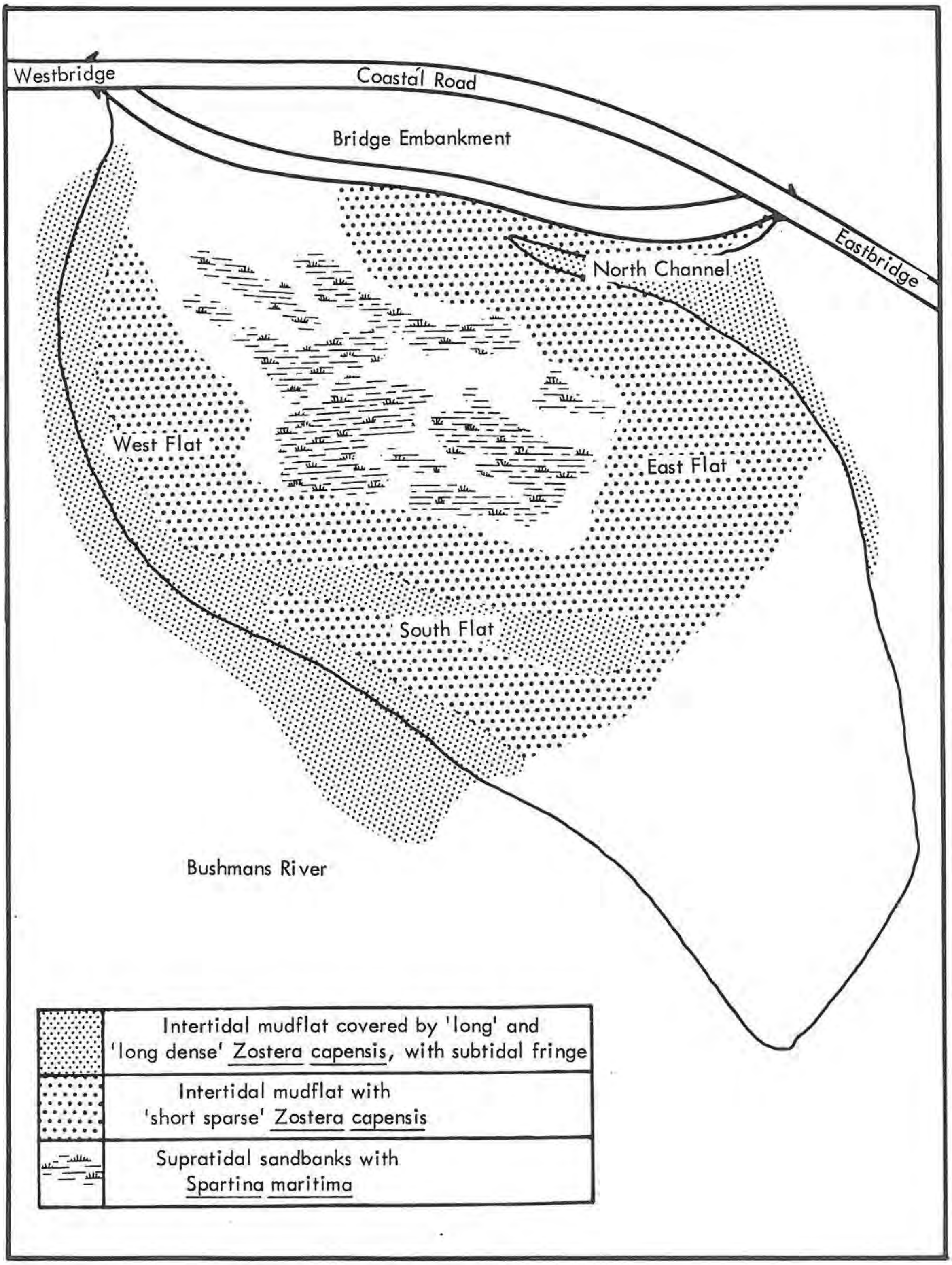
1. supratidal sandbanks with a sandy substratum, either exposed or covered by <u>Spartina maritima</u> (Curtis);
2. an intertidal fringe with a mud or sandy-mud substratum covered by <u>Zostera capensis</u> Setchell; and
3. a subtidal boundary with a sandy mud substratum and extensive dense <u>Z. capensis</u> beds giving way to deep clear water in channels.

The <u>Z. capensis</u> cover was not uniform and 4 categories were subjectively distinguished (Fig. 5):

1. 'short sparse' - fronds 15 cm or less in length, with rooted clumps separated by bare substratum,


N
Bushmans River Mouth
Kenton-on-Sea
KEY
Study Area
Coastal Road
Bridge Embankment
Mudflat with *Zostera capensis*
Sandbanks with *Spartina maritima*
Bushmans River
Indian Ocean
Scale 1 : 10 000


Westbridge
Coastal Road
Bridge Embankment
Eastbridge
North Channel
West Flat
East Flat
South Flat
Bushmans River
KEY
Intertidal mudflat covered by 'long' and 'long dense' Zostera capensis, with subtidal fringe
Intertidal mudflat with 'short sparse' Zostera capensis
Supratidal sandbanks with Spartina maritima


Westbridge
Coastal Road
Bridge Embankment
North Channel
Eastbridge
West Flat
East Flat
South Flat
Bushmans River
Intertidal mudflat covered by 'long' and 'long dense' Zostera capensis, with subtidal fringe
Intertidal mudflat with 'short sparse' Zostera capensis
Supratidal sandbanks with Spartina maritima

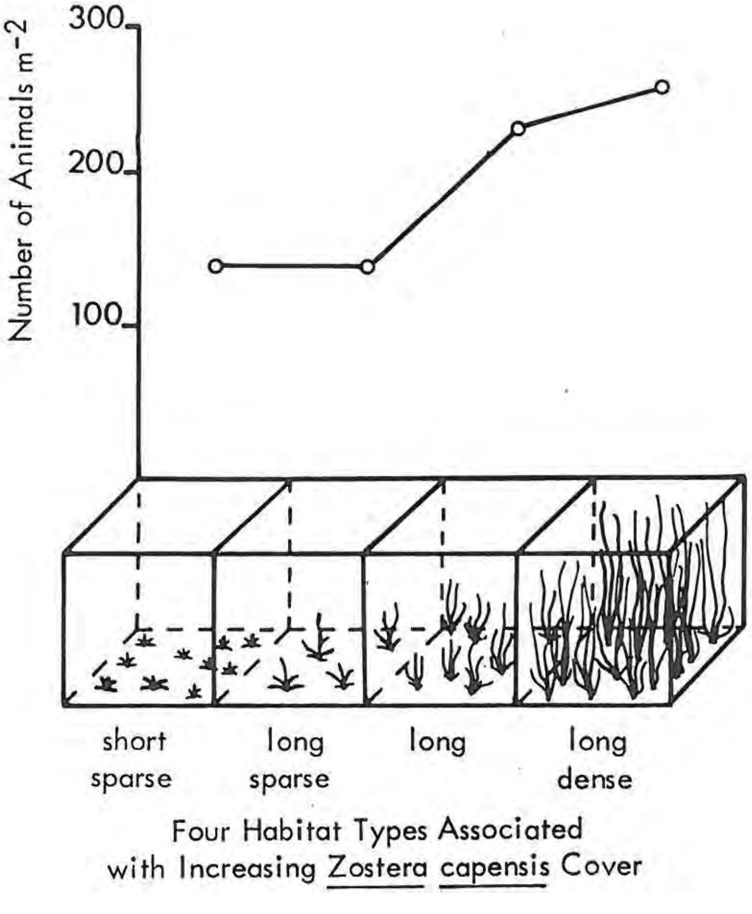


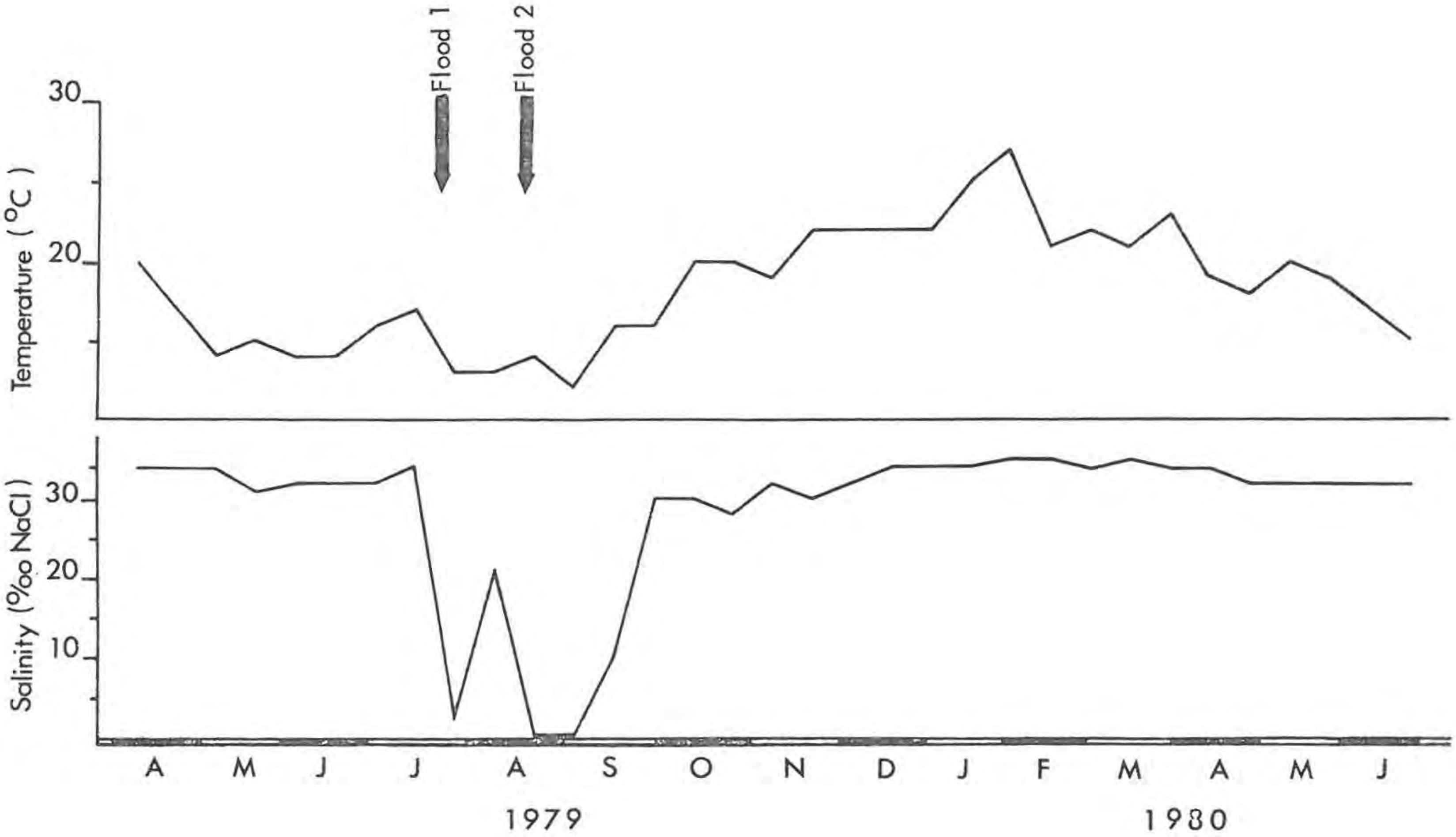
Fig. 5. Relationship between Zostera capensis habitat type and Nassarius kraussianus distribution during the pre-flood period (8.4.1979-14.7.1979).

2. 'long sparse' - fronds longer than 15 cm with rooted clumps separated by bare substratrum,
3. 'long' - fronds longer than 15 cm and individual fronds broader than 'long sparse' with rooted clumps close together in the substratum, and
4. 'long dense' - long (often greater than 1 m) broad fronds which formed a dense weed bed.

This classification was valuable because N. kraussianus was collected more frequently in 'long' and 'long dense' Z. capensis beds, than in other habitats (Fig. 5). All subtidal beds comprised 'long dense' Z. capensis, but intertidal Z. capensis cover varied (Fig. 4).

Water temperature and salinity were monitored fortnightly during the study (Fig. 6), using an American Optical Company Refractometer. The estuary mouth was open throughout the study period, and salinity showed a strong tidal influence; seldom falling below 30^{o}/oo NaCl in the western channel, except during the floods when salinities were very low (Fig. 6).

In July and August 1979 there were very heavy rains in the catchment area which caused severe unseasonal floods. Rainfall data for Grahamstown (Weather Bureau, 1979a;


Flood 1
Flood 2
30
20
Temperature (°C)
30
20
10
Salinity (‰ NaCl)
A
M
J
J
A
S
O
N
D
J
F
M
A
M
J
1979
1980

1979b), which is situated in the southern Cape coastal belt weather region, and is at the head of the New Years River catchment area (Fig. 1), indicate the severity of the floods. In July, 302 mm of rain fell in 8 days (normal 31.6 mm in 4 days). The maximum rainfall was recorded on 20.07.79, when 126 mm fell in 24 hours. This resulted in flood conditions in the Bushmans River, and the flood waters exceeded the maximum height that the gauging weir (P1M03) at Alicedale could record (3.2 m). Water height was estimated at 4.4 m. The flow rate at 2 m was $65m^3s^{-1}$ and the flow rate at the time of the flood was probably in the region of 100 m^3s^{-1} (Department of Water Affairs, Forestry & Environmental Conservation, pers.comm.). There was a second flood in August when, in Grahamstown, 272 mm fell in 9 days (normal, 36.8 mm in 5 days). The maximum rainfall recorded in a 24 hour period was on 20.08.79, when 175 mm fell. Flood waters again reached the 4 m mark but the volume of water may have been greater in the second flood, due to probable river bed scouring during the July flood (Department of Water Affairs, Forestry & Environmental Conservation, pers.comm.).

The geology of the catchment area and the high stocking rates probably contributed to the silt load carried by the flood waters. Generally the silt carrying capacity of water downstream of an impoundment is increased because silt is deposited in the impoundment (due to low velocity stream flow), and clearer water is discharged. In this way the presence of the New Years River dam may have resulted in increased silt loads in the Bushmans River. Silt laden flood waters flowed over the study area, and at the end of August 1979 a 20-50 cm layer of silt blanketed the entire area. Salinities dropped (Fig. 6), and except for a brief rise between floods, remained extremely low for 9 weeks. At the same time water temperatures were low (Fig. 6).

The effects of silt deposition were evident for the remainder of the study; that is until June 1980. Immediately after the floods the *Z. capensis* beds were smothered completely, and the emergence of recovering fronds was first noted some four months later, in January 1980. In July 1980, one year after the first floods, the *Z. capensis* beds had still not reached their preflood extent (compare Figs. 3 & 4), and 28% of the original cover had still to regenerate. Much of this area was covered by tidally carried seasand, and the barren sand banks which resulted were subsequently colonised by *Spartina maritima* (Curtis).

2.3 MATERIALS AND METHODS

2.3.1 PILOT STUDY

Many diverse collecting techniques are used to sample macrobenthic populations (Hairston, et al., 1958; Eberhardt, 1978). The quadrat is usually used in estuarine habitats, where the substratum is easily accessible, whereas the grab is used in deeper marine environments (Table 1). The estuarine mudflat chosen as the site for the present study was exposed at low tide and a quadrat technique was selected.

In March 1979 a pilot study was conducted to establish optimum quadrat size and number of samples. Quadrat areas of 0.25 m^2, 0.1 m^2 and 0.06 m^2 were used experimentally to establish which would yield a mean of approximately 30 animals $sample^{-1}$ (Cassie, 1971). A 0.1 m^2 quadrat was subsequently used (Fig. 7), and had the added advantage that if 10 samples were taken, a total area of 1.0 m^2 was sampled.

The optimum number of samples was difficult to assess. The mean and standard deviation for each set of samples were fitted into the equation given by Cassie (1971). The standard deviation was greater than the mean in several

STUDY AREA	AIM OF STUDY	OBJECT OF STUDY	SOURCE
Technique-Quadrat : area 0.05-0.25 m^2; substratum depth 1-25 cm; sieve mesh 1.0 mm			
East Canadian Estuary	Production	Mollusc community	Burke & Mann, 1974
Hamble Spit - estuarine mudflat	Production	Bivalve community	Hibbert, 1976
Lynher estuary mudflat	Production	Macrobenthic community	Warwick & Price, 1975
Thames estuary	Population dynamics	Polychaete-*Scoloplos armiger*	Gibbs, 1968
Hamble Spit - estuarine mudflat	Population dynamics	Bivalve-*Mercenaria mercenaria*	Hibbert, 1977
SUMMARY Estuarine mudflat	Production & population dynamics	Macrobenthic communities & populations	
Technique-Grab:volume 0.1 m^3; if sieved, sieve mesh 1.0 mm			
North Sea	Production & population dynamics	Amphipod-*Ampelisca brevicornis*	Klein *et al*, 1975
North east English coast	Production & population dynamics	Amphipod-*Ampelisca tenuicornis*	Sheader, 1977
Northumberland coast	Population dynamics	Macrobenthic community	Buchanan & Warwick, 1974
Greenland coast	Population dynamics	Bivalve community	Petersen, 1978
Greenland coast	Population dynamics	Polychaete community	Curtis, 1977
SUMMARY Deep marine	Production & population dynamics	Macrobenthic communities and populations	

Table 1. A summary of sampling techniques used in benthic invertebrate studies.

Fig. 7. A box-type quadrat ($0.1m^2$) was used to sample the *Nassarius kraussianus* population.

instances, indicating contagious distribution. The solutions of the equation indicated that approximately 741 samples per sampling occasion would be necessary to achieve a 10% error at a 95% confidence level. This was obviously not practically possible, and only ten samples could be easily collected in one low tidal cycle. The resultant error was calculated, using the coefficient of variation (Sokal & Rohlf, 1969), and ranged from 85 to 178%. A set of ten samples was collected fortnightly, using a box-type quadrat with an area of 0.1 m^2. The resultant error has been calculated and the results must be interpreted within those limits.

2.3.2 FIELD SAMPLING

The first set of samples was collected in April 1979, and collecting continued fortnightly until June 1980. The site of the first sample was chosen arbitrarily, usually near the north channel, or on the western flat (Fig. 3). The subsequent 9 samples were collected within the intertidal zone at random intervals, determined by pacing out distances generated from figures drawn from a table of random numbers. The substratum was removed to a depth of 5 - 10 cm, and sieved through a 0.5 mm sieve (B.S.410 Endecotts Ltd.). This was the most efficient mesh size as it retained small juveniles 1.0 mm in length, while eliminating the substratum. A finer mesh (0.3 mm) was used experimentally, but large sand grains retained in the sieve damaged the delicate shells of small juveniles. All vegetation was retained by the sieve, and with it many *N. kraussianus* attached to the *Z. capensis* fronds. The entire sieve contents were preserved in 4% formaldehyde and transported to the laboratory for processing .

2.3.3 LABORATORY PROCESSING

Samples were emptied into a shallow dish filled with water. The vegetation was carefully rinsed to dislodge snails, then discarded. The sorting dish was filled with water, and the fine organic detritus floated on the surface, while the snails and heavy sand grains sank to the bottom. In this way, all the vegetation was removed by successive periods of floatation. The remaining mixture of large sand grains and macrobenthic organisms was sorted under a Wild binocular microscope. *N. kraussianus* shells were removed, and whole animals and dead, empty shells were separated. Empty shells were counted, and the percentage bored through by the predatory gastropod *Natica tecta* was noted. Whole animals were measured across the base of the body whorl to an accuracy of 0.01 mm, using vernier calipers, and sorted into size classes: 1 mm (0.6 - 1.5); 2 mm (1.6 - 2.5); 3 mm (2.6 - 3.5); 4 mm (3.6 - 4.5); 5 mm (4.6 - 5.5); 6 mm (5.6 - 6.5); 7 mm (6.6 -7.5);

8 mm (7.6 - 8.5); and 9 mm (8.6 - 9.5) (Fig. 8). The number of animals in each size class was calculated using this technique, and size frequency histograms of the total number of animals in each size class were plotted.

Each snail was dissected in order to establish its sex and state of gonad development (see section 3.3.1). Snails in the 1, 2 and 3 mm size classes were classified as juveniles (no overt sex-distinguishing features were evident). The sex of animals in the 4, 5, and 6 mm size classes was determined on the basis of the presence or absence of a penis; the only overt characteristic. Adult males and females were easy to differentiate. Adult females (7, 8 and 9 mm) were characterised by the ovary, which was white when immature and a creamy-pink mottled colour when sexually mature; the oviduct; and the capsule gland, which changed from white to creamy-pink with maturity. Adult males (6, 7 and 8 mm) had a well developed penis; a coiled white Vas Deferens, and a testis which changed from pale to bright yellow with maturity. From this analysis sex ratios were calculated, and male and female size frequency distributions were plotted.

2.3.4 LENGTH-WEIGHT DETERMINATION

In March 1980, many animals were collected and transported alive to the laboratory, where they were

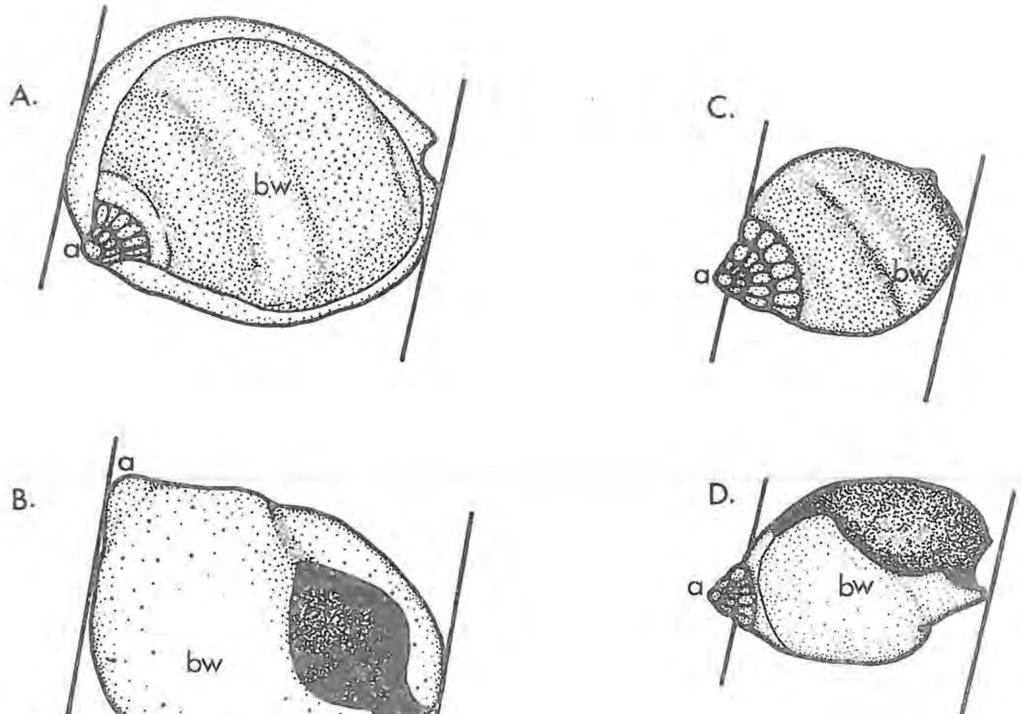


Fig. 8. Diagrams showing the shell length measurement of <u>Nassarius</u> <u>kraussianus</u>. In both adults (A & B) and juveniles (C & D) length was measured across the base of the body whorl (bw). The apex (a) was excluded from the measurement, because it is distinct in juveniles, but is often worn away in the adult, and may be exceeded in length by the callus.

measured and separated into size classes. Each size class was held in a glass tank filled with seawater, and when all the animals had been sorted they were killed with 4% formaldehyde and immediately placed in small aluminium dishes. Ten replicates of each size class were prepared, with the number of animals per dish varying according to size class: 2, 3, 4 and 5 mm - 10 per dish; 6, 7 and 8 mm - 5 per dish; and 9 mm - 3 per dish. A total of 580 animals was used. Total wet weight was recorded. The shells were removed, the bodies damp-dried on a paper tissue, and the shell free wet weight was recorded. Samples were dried to a constant weight at 70°C for 48 hours and shell free dry weight was recorded. Finally, samples were burned in a muffle furnace at 500°C for 4 hours, and ash free, shell free dry weight was recorded.

Ash free dry weight is the best measure of biomass as it renders comparable information about very different organisms; dry weight is also frequently recorded in the literature. Length-weight curves were drawn using the data generated from this procedure, and the ash free dry weight, or dry weight for a single animal of a particular size class could be read off these curves. By multiplying these values by the number of animals in each size class, numbers m^{-2} were converted to grams ash free, shell free dry weight, or grams shell free dry weight m^{-2}.

2.3.5 GROWTH DETERMINATION

Between 20.1.80 and 29.3.80 a cohort was distinguished, and its growth calculated. The mean length of the recolonising cohort was calculated for each sampling occasion using the method of Harding (1949) and Cassie (1950; 1954). These mean lengths were plotted against time, and a linear regression was fitted to the data points. A von Bertalanaffy growth curve did not fit the available data.

2.4 RESULTS

2.4.1 PILOT STUDY

The sampling method was based on the results of a pilot study. Using the number of animals sample^{-1}, the standard deviation, and the mean, the coefficient of variance was calculated (Sokal & Rohlf, 1969). This gave a measure of the error inherent in the sampling technique. These results are shown in Table 2.

On 25.3.79 three different quadrat sizes were used (Table 2). The smallest was 0.06m^2, and yielded a mean of 18 animals sample^{-1}, the standard error was ±5.0 and the calculated error was 113%. The 0.1m^2 quadrat enabled the collection of more animals, a mean of 34.1 sample^{-1}, and although the standard error was higher, ±9.41, calculated error was lower, 85%. Therefore the 0.1m^2 quadrat enabled the collection of statistically more reliable data. The 0.25m^2 quadrat resulted in a larger mean, 74.1, but the calculated error was 85%, no different from the samples collected with the 0.1 m^2 quadrat. In addition, these large samples took an excessive length of time to process, and 10 samples could only be collected during one tidal cycle if more than one person sampled. Therefore, as the larger sample size did not result in

DATE	NUMBER OF ANIMALS PER SAMPLE	TOTAL	MEAN	STD. DEVIATION	STD. ERROR	NUMBER OF ANIMALS M^{-2}	COEFFICIENT OF VARIATION
0.1 m^{-2} Quadrat							
25.3.79	50,5,5,32,17, 11,57,70,83,11	341	34.1	28.89	9.14	341	85%
1.4.79	164,30,29,5,1, 6,12,0,1,30	278	27.8	49.49	15.64	278	178%
0.06 m^{-2} Quadrat							
25.9.79	18,3,29,50,1, 11,16,12,36,4	180	18	15.9	5.0	288	113%
0.25 m^{-2} Quadrat							
25.3.79	75,126,30,47, 158,15,102,7	741	74.1	63.2	21.1	296	85%

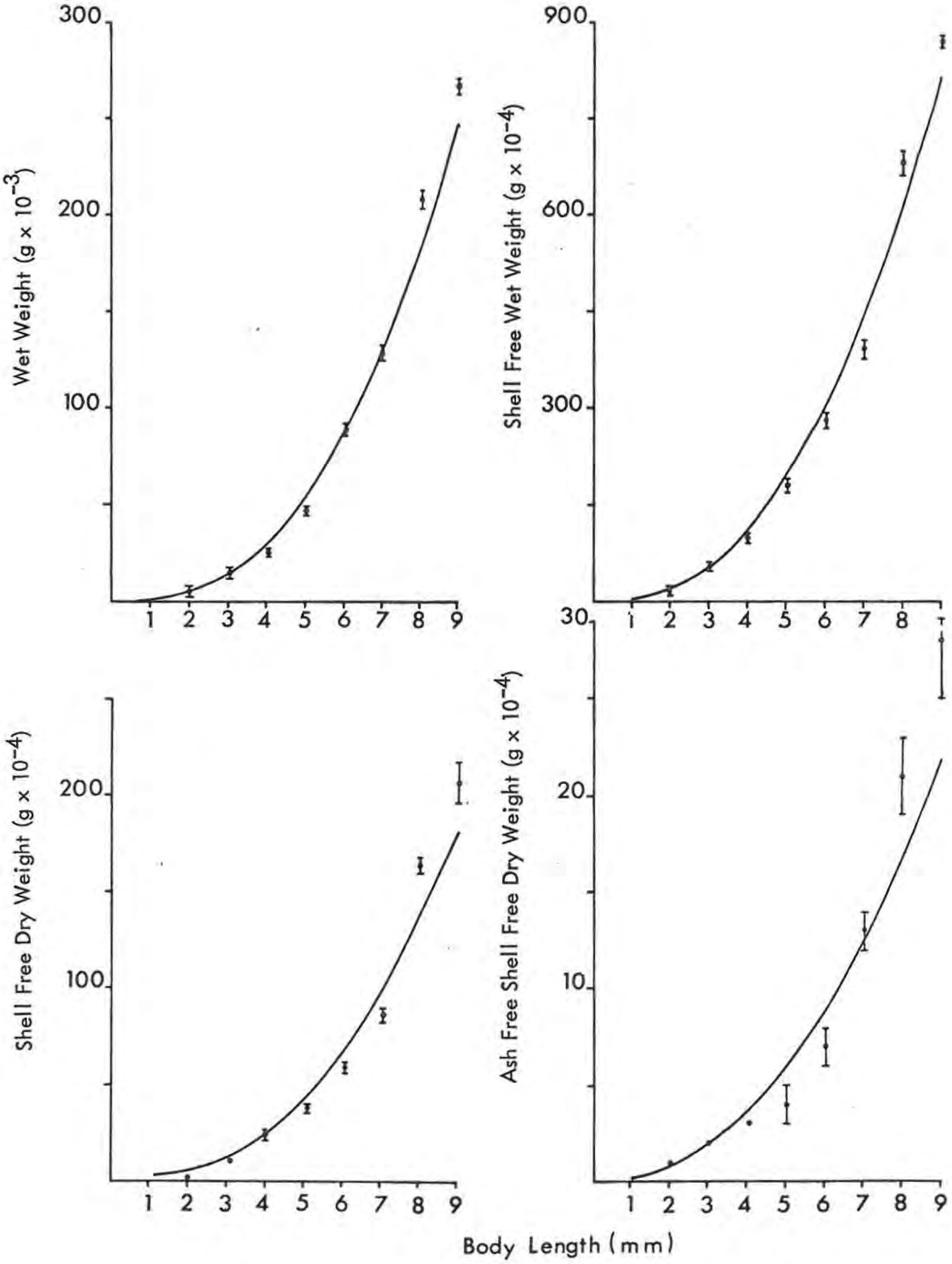
Table 2. Results of the pilot study conducted in the study area in March and April 1979.

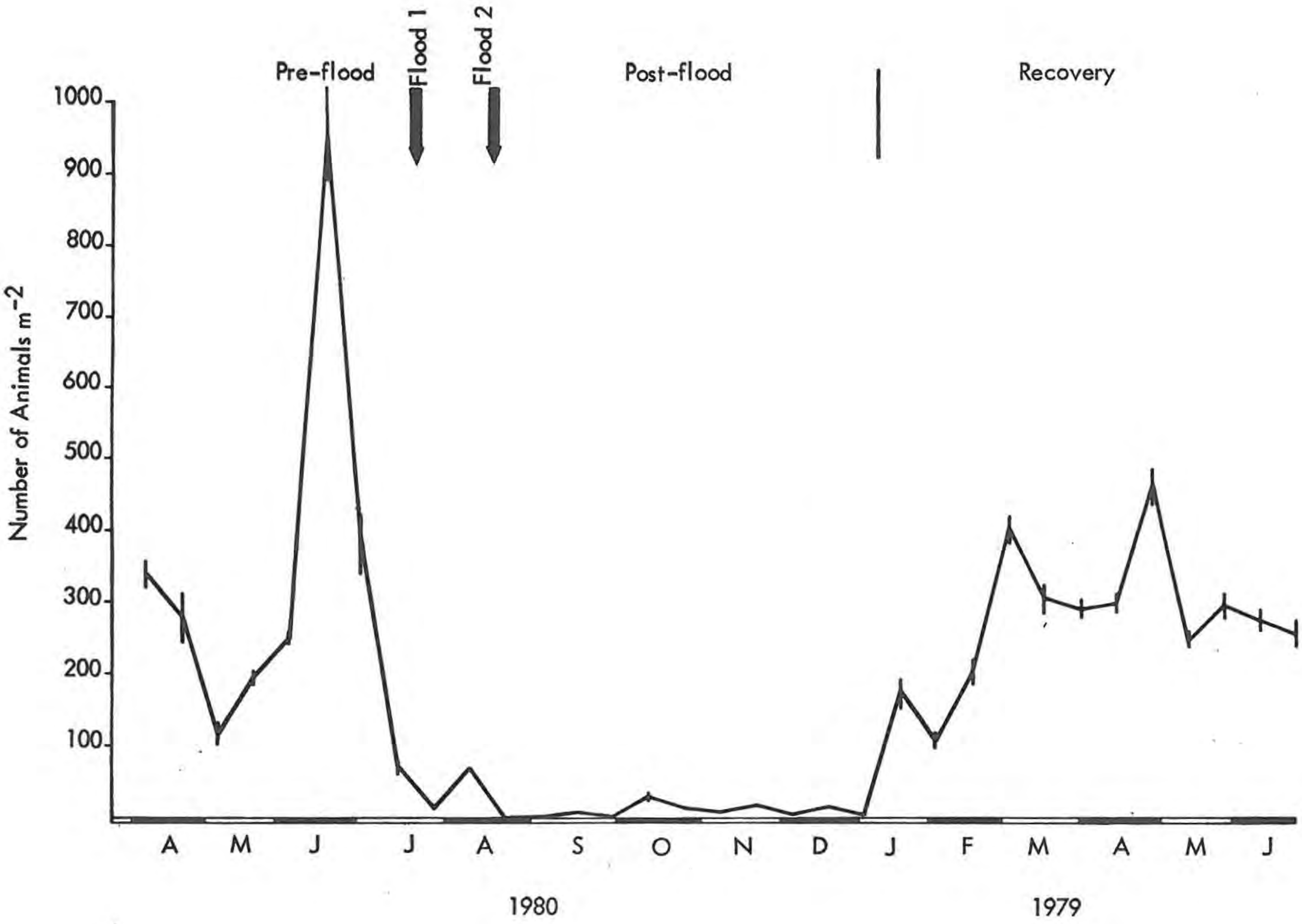
statistically more valuable data, the 0.1 m^2 was used a second time (1.4.79). The resultant standard deviation was greater than the mean, and the calculated error rose to 178% (Table 2). This was a direct result of the contagious pattern of distribution.

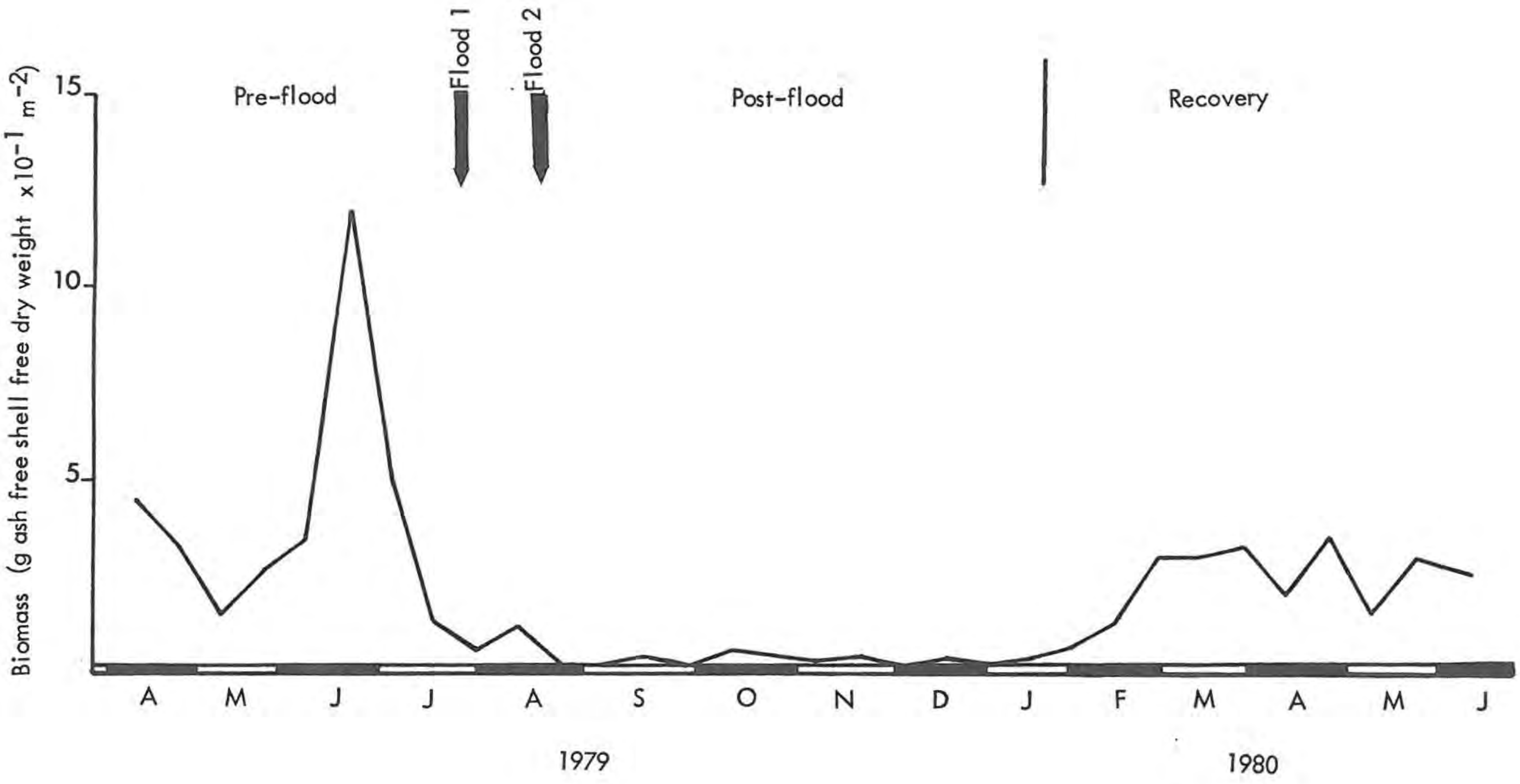
However, Cassie (1971) has noted that if patchy, or contagious distribution occurs, a larger number of samples is a better choice than an increase in sample size. The distribution of the N. kraussianus population was extremely patchy as indicated by the large standard error and standard deviation figures in Table 2. Thus, despite the exceptionally high percentage error, the 0.1m^2 quadrat enabled the collection of the largest number of samples in the available sampling time, and was used during the entire study. Finally, it is important to emphasise that all subsequent results must be viewed within the context of the high percentage error.

2.4.2 FIELD STUDY

The changes in population density are presented both as absolute numbers, and as biomass values. The latter were calculated using a set of length weight curves (Fig. 9). Population numbers throughout the study are shown in Fig. 10. Because of floods in July and August 1979 the study has been divided into three periods: pre-flood,


300
200
100
Wet Weight (g × 10⁻³)
900
600
300
Shell Free Wet Weight (g × 10⁻⁴)
1 2 3 4 5 6 7 8 9
200
100
Shell Free Dry Weight (g × 10⁻⁴)
30
20
10
Ash Free Shell Free Dry Weight (g × 10⁻⁴)
1 2 3 4 5 6 7 8 9
Body Length (mm)


Pre-flood
Flood 1
Flood 2
Post-flood
Recovery
Number of Animals m⁻²
1000
900
800
700
600
500
400
300
200
100
A
M
J
J
A
S
O
N
D
J
F
M
A
M
J
1980
1979


Biomass (g ash free shell free dry weight x10^{-1} m^{-2})
15
10
5
Pre-flood
Flood 1
Flood 2
Post-flood
Recovery
A
M
J
J
A
S
O
N
D
J
F
M
A
M
J
1979
1980

post-flood and recovery. In the pre-flood period the number of animals m^{-2} was extremely variable, ranging from 72 m^{-2} to 962 m^{-2}, with a mean of 324 m^{-2}. This resulted in a coefficient of variance which ranged from 61 to 212% (Sokal & Rohlf, 1969). For example, in mid-June, when 962 animals were collected, two samples each included more than 200 animals, and these biased the total. In contrast, a set of samples collected in mid-July, just before the first flood, contained only 72 animals, including 3 samples with no animals at all.

The population substantially declined in the post-flood period. The river first flooded in mid-July and the set of samples collected immediately afterwards contained only 13 animals. This increased to 71 on the following occasion, but in early August the river flooded a second time, and the 20 cm deep layer of silt deposited after the first flood increased to 50 cm after the second flood. (The depth of the silt layer was measured on each sampling occasion.) Population density dropped again after the second flood, and remained very low until January 1980.

The beginning of the recovery period was signalled by a dramatic increase in numbers in mid-January 1980, and densities remained high during the remainder of the study. These high densities were associated with variability, which resulted in a calculated coefficient of variance which ranged from 75 to 237%.

Density data were converted to biomass (g ash free, shell free dry weight), using a length:weight curve (Fig. 9), and plotted against time (Fig. 11). The pattern was similar to that shown in Fig. 10, and between April and mid-July 1979 biomass estimates were variable. The major difference between total numbers (Fig. 10) and total biomass (Fig. 11) was evident in January and February 1980 when the number of animals suddenly increased because of an influx of recolonising juveniles, whereas biomass increased slowly and steadily as these juveniles grew to adult size.

Figures 10 & 11 therefore clearly show the three periods during the study:

1. Pre-flood: April to mid-July 1979 (3.5 months),
2. Post-flood: mid-July 1979 to mid-January 1980 (6 months), and
3. Recovery: mid-January to June 1980 (5.5 months).

The mean number of animals m^{-2} and mean biomass for each of these periods, and for the whole study are shown in Table 3.

The total population can be viewed in a number of ways. For example, males and females, or animals in different size classes, can be analysed separately. Male

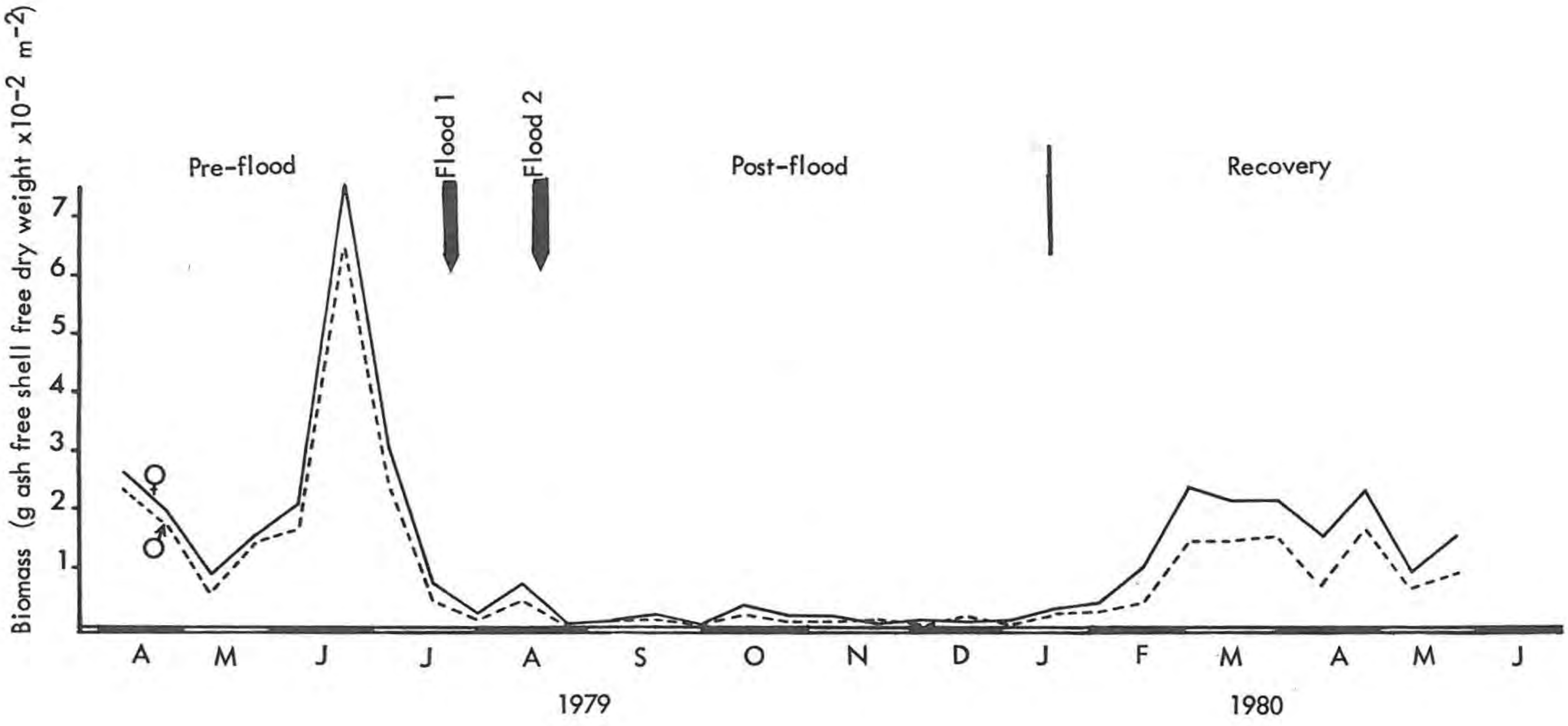
MEAN	TOTAL STUDY PERIOD	PRE-FLOOD PERIOD	POST-FLOOD PERIOD	RECOVERY PERIOD
Number of animals m^{-2}	184	325	14	251
Biomass, g ash free shell free dry weight	0.209	0.464	0.022	0.249

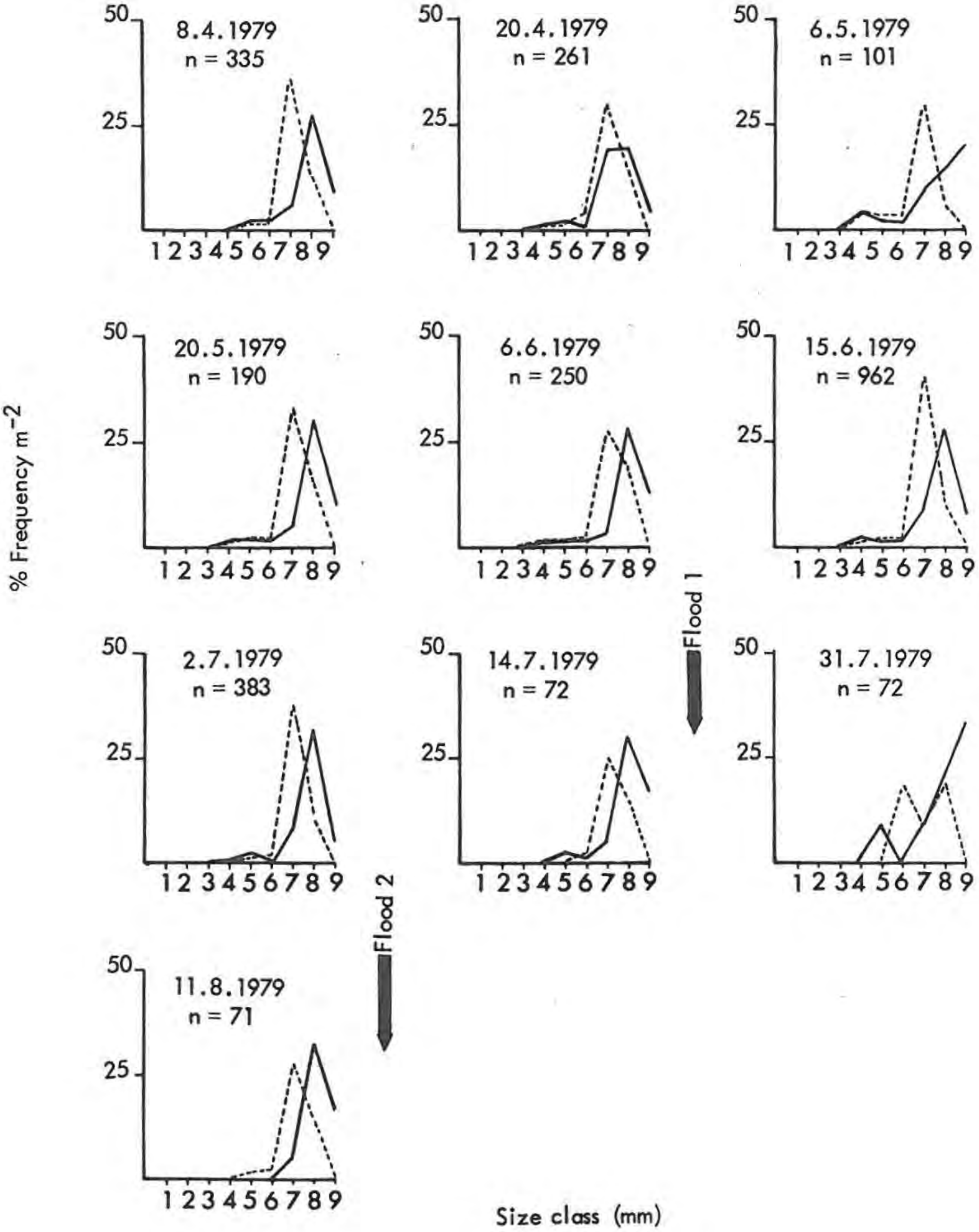
Table 3. A comparison of the population density and biomass values between the whole study period, and the pre-flood, post-flood, and recovery periods.

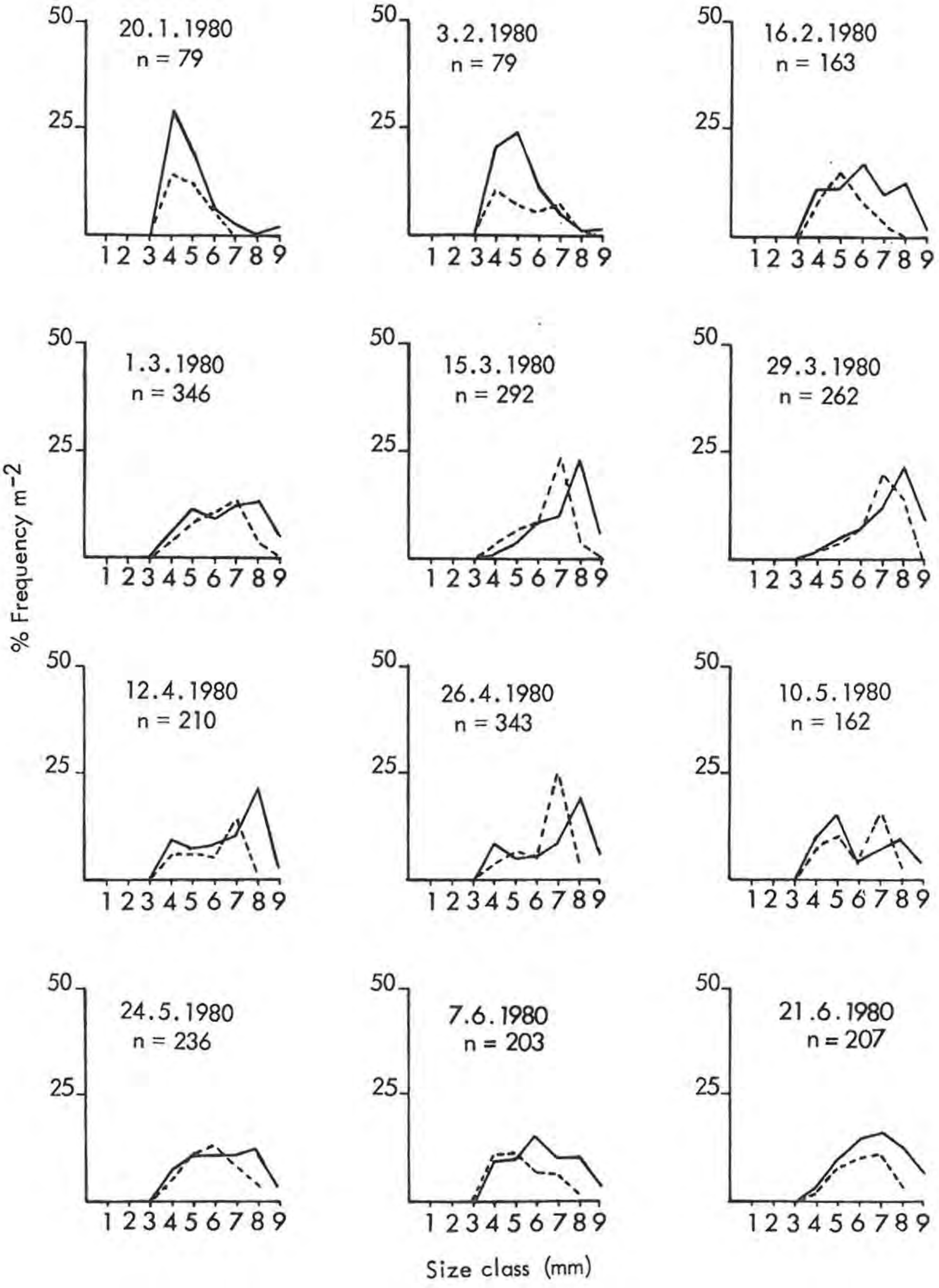
and female biomass values are shown in Fig. 12. Throughout the study the biomass values for males were lower than for females. The greatest difference was apparent in the recovery phase, but at no stage were the male and female biomass values significantly different (Chi-squared test - $p > 0.05$).

Figure 13 shows male and female size frequency distributions during the pre-flood period, together with the first two post-flood samples. The pattern was extremely consistent, and enabled a partial explanation of the higher female biomass values shown in Fig. 12. The male modal size class was 7 mm, whereas for females, it was 8 mm. Few males reached 8 mm shell length,and the 9 mm size class was exclusively female. Thus, most of the large animals were female.

So few animals survived the floods that male and female size frequencies were meaningless during the post-flood period. In January 1980, when the mudflat was recolonised, the male/female size frequency pattern was considerably different from the pre-flood period (Fig. 14). Females were more numerous, and the female modal peak appeared to move from 4 to 8 mm more rapidly than the male; indicating, for the first time, the possiblity of a faster female growth rate, with males growing more slowly and reaching a smaller size than females.

Biomass (g ash free shell free dry weight x10-2 m-2)
7
6
5
4
3
2
1
♀
♂
Pre-flood
Flood 1
Flood 2
Post-flood
Recovery
A
M
J
J
A
S
O
N
D
J
F
M
A
M
J
1979
1980


% Frequency m⁻²
8.4.1979
n = 335
20.4.1979
n = 261
6.5.1979
n = 101
20.5.1979
n = 190
6.6.1979
n = 250
15.6.1979
n = 962
2.7.1979
n = 383
14.7.1979
n = 72
31.7.1979
n = 72
11.8.1979
n = 71
Flood 1
Flood 2
50
25
1 2 3 4 5 6 7 8 9
Size class (mm)



20.1.1980
n = 79
3.2.1980
n = 79
16.2.1980
n = 163
1.3.1980
n = 346
15.3.1980
n = 292
29.3.1980
n = 262
12.4.1980
n = 210
26.4.1980
n = 343
10.5.1980
n = 162
24.5.1980
n = 236
7.6.1980
n = 203
21.6.1980
n = 207
50
25
1 2 3 4 5 6 7 8 9
% Frequency m-2
Size class (mm)

However, sex ratio, and the overall number of males and females would also affect the biomass values shown in Fig. 12. Sex ratios are listed in Table 4. In the pre-flood period, the sex ratio was 1:1, except for the sample collected on 14.7.79, when the male:female ratio dropped to 0.7. An unusually low number of animals was collected on that occasion and the sex ratio may not have been representative of the whole population. Thus, the 1:1 sex ratio indicates that the lower male and higher female biomass values in the pre-flood period were due to the different sizes attained, rather than to different numbers of the two sexes.

In the post-flood period the sex ratio changed, and a greater number of females seemed to have survived the flood. However, the sex ratio was extremely variable and it must be noted that very few animals at all were collected. If the relatively low number of animals collected on 14.7.79, just before the flood, failed to reflect the 1:1 pre-flood sex ratio, then the post-flood sex ratios, based on far fewer animals, must be viewed with caution.

In the recovery period females remained more numerous, but in contrast to the post-flood period the sample numbers were high, and the sex ratio values far less

DATE	NUMBER OF MALES	NUMBER OF FEMALES	MALE:FEMALE RATIO
Pre-flood			
8.4.79	173	162	1.06
20.4.79	131	130	1.0
6.5.79	48	53	0.9
20.5.79	100	91	1.1
6.6.79	121	120	1.0
15.6.79	503	452	1.1
2.7.79	188	189	1.0
14.7.79	29	41	0.7
Post-flood			
31.7.79	5	8	0.6
11.8.79	32	39	0.8
26.8.79	0	0	-
2.9.79	1	1	1.0
8.9.79	2	6	0.3
23.9.79	0	0	-
7.10.79	11	17	0.6
21.10.79	4	8	0.5
4.11.79	3	4	0.75
17.11.79	3	3	1.0
3.12.79	0	2	-
15.12.79	9	2	4.5
6.1.80	2	3	0.6
Recovery			
20.1.80	34	45	0.75
22.2.80	21	52	0.5
16.2.80	58	105	0.6
1.3.80	145	201	0.7
15.3.80	135	157	0.8
29.3.80	127	146	0.9
12.4.80	75	135	0.5
26.4.80	154	189	0.8
10.5.80	73	89	0.8
24.5.80	97	139	0.7
7.6.80	81	122	0.66
21.6.80	74	133	0.55

Table 4. The number of adult male and female animals collected between April 1979 and June 1980, and the resultant sex ratios.

variable. Females were consistently more abundant in the recovery period and this would have contributed to the greater difference in male and female biomass values over this period (Fig. 12).

The sex ratios in Table 4 are shown graphically in Fig. 15a, where the pre-flood, post-flood and recovery period characteristics can be compared quite easily. However, the male and female curves shown in Fig. 15a represent only part of the total population, because juveniles could not be sexed, and were excluded. Figure 15b shows the density changes in these juveniles. Note that few juveniles were collected in the pre-flood period, and that adult males and females comprised the bulk of the population. In the post-flood period, juveniles were completely absent until late November 1979, and then were present in very low numbers. Juveniles were abundant during the recovery period, increasing suddenly in January 1980. Juvenile numbers dropped between January and April 1980, but this simply reflects their growth to a size at which sexing is possible, and their inclusion in the male or female curves (Fig. 15a), rather than in the juvenile curve (Fig. 15b). In late April 1980, juvenile numbers increased as the recovering adult population began to reproduce once again.

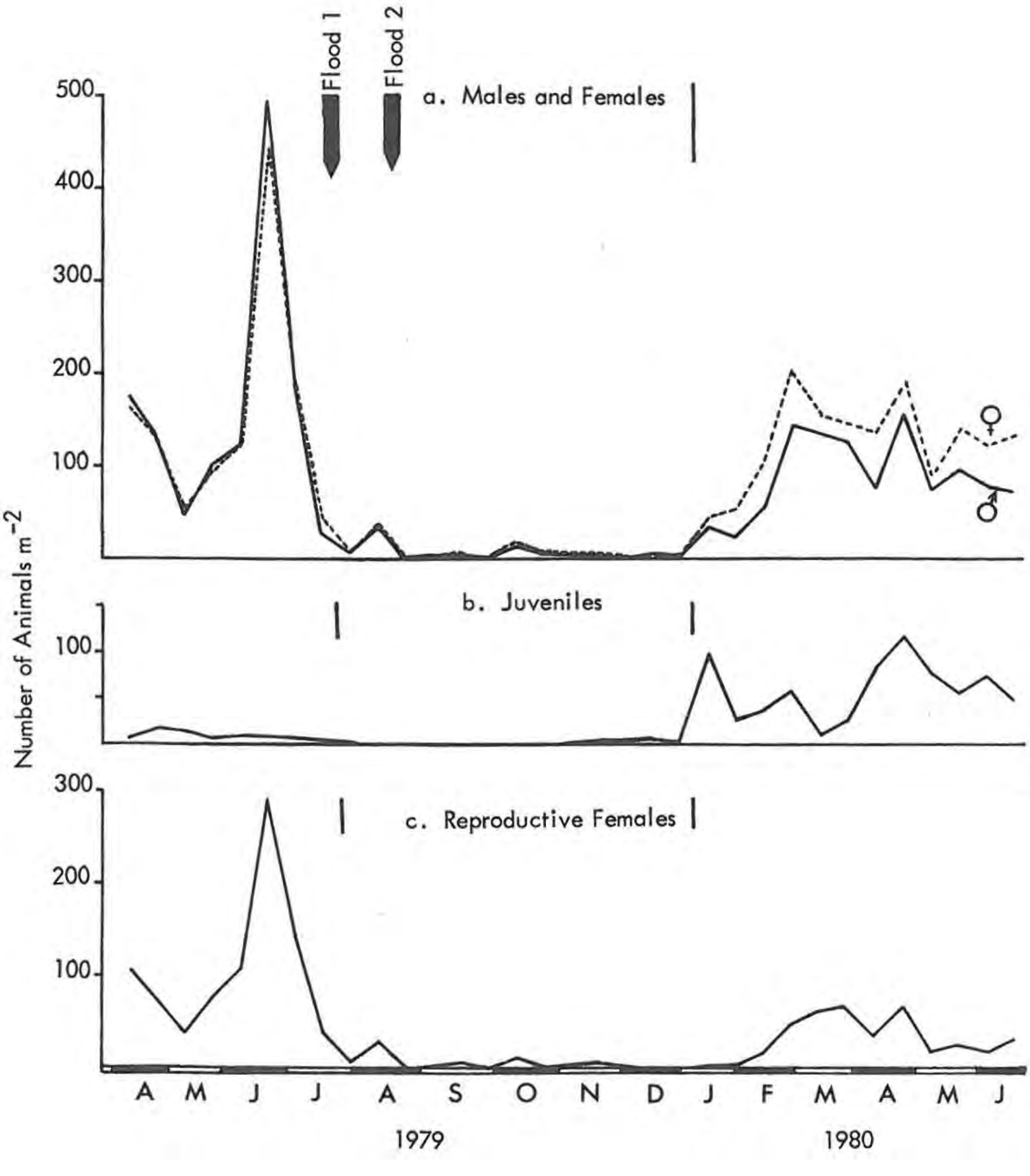
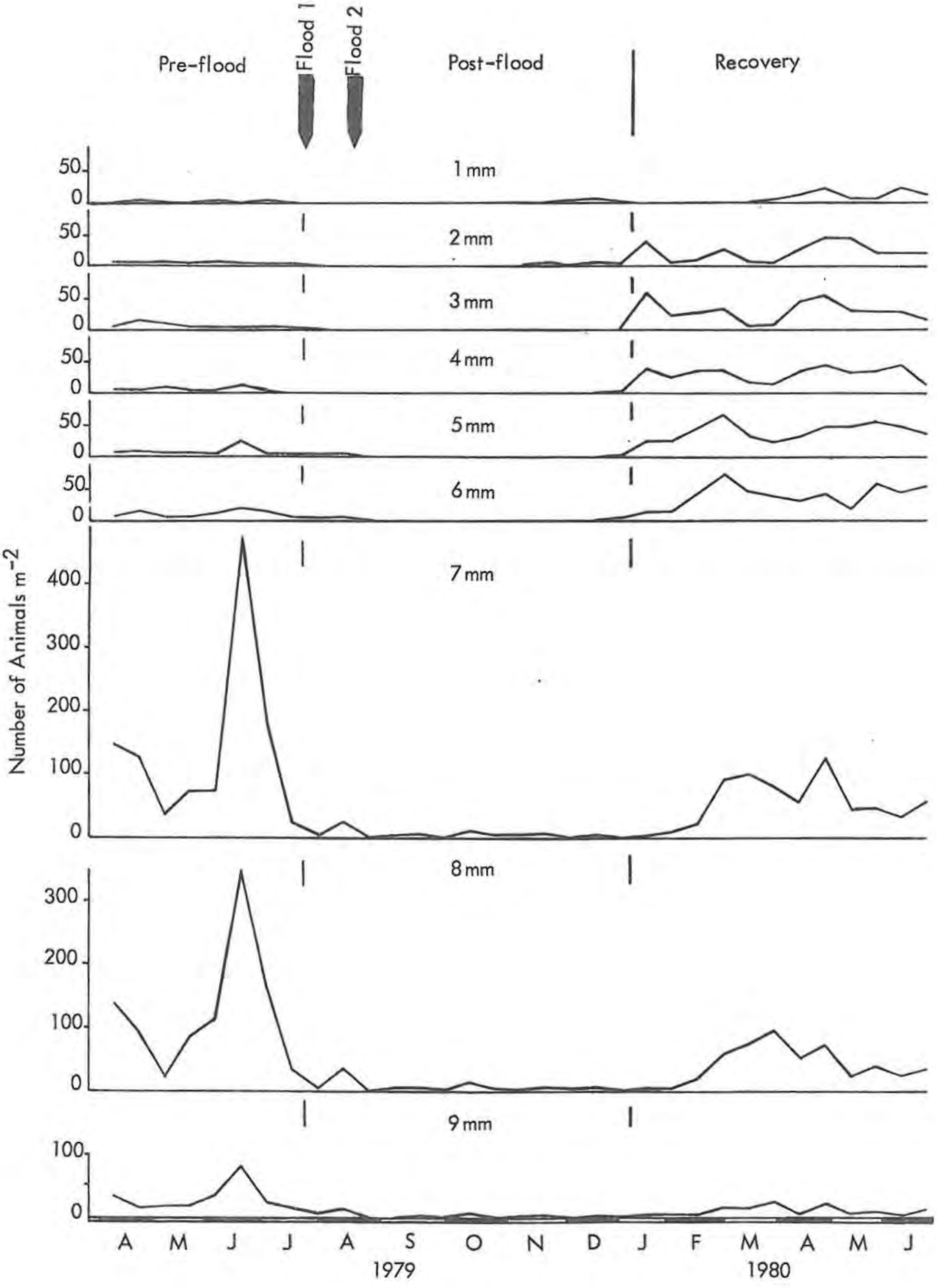

Flood 1
Flood 2
a. Males and Females
b. Juveniles
c. Reproductive Females
♀
♂
Number of Animals m^{-2}
500
400
300
200
100
100
300
200
100
A M J J A S O N D J F M A M J
1979
1980

Figure 15c shows the numbers of fully mature females in active breeding condition. Sex could be distinguished when the animals reached 4 mm in length, but they only reached reproductive maturity at approximately 7 mm in length. Thus, comparing Figs. 15a and 15c, many of the pre-flood females were actively reproductive, and most of the females which survived the flood remained in breeding condition. At the beginning of the recovery period very few females were in reproductive condition, and numbers increased slowly between January and April 1980. It is interesting to note that in January 1980, when the number of breeding females was very low, the number of juveniles suddenly increased. This indicated that the mudflat was probably recolonised by incoming juveniles, and that the increase in population density was a result of this recolonisation rather than the slow regeneration of the surviving post-flood population.

The whole pattern of population change over the study period is shown most clearly in an analysis of the different size classes (Fig. 16). Size classes 1, 2 and 3 mm were termed juveniles (sexes indistinguishable); classes 4, 5 and 6 mm were termed immature adults (pre-reproductive); and classes 7, 8 and 9 mm were termed adults (reproductive).


Pre-flood
Flood 1
Flood 2
Post-flood
Recovery
1 mm
2 mm
3 mm
4 mm
5 mm
6 mm
7 mm
8 mm
9 mm
50
0
400
300
200
100
Number of Animals m^{-2}
A
M
J
J
A
S
O
N
D
J
F
M
A
M
J
1979
1980

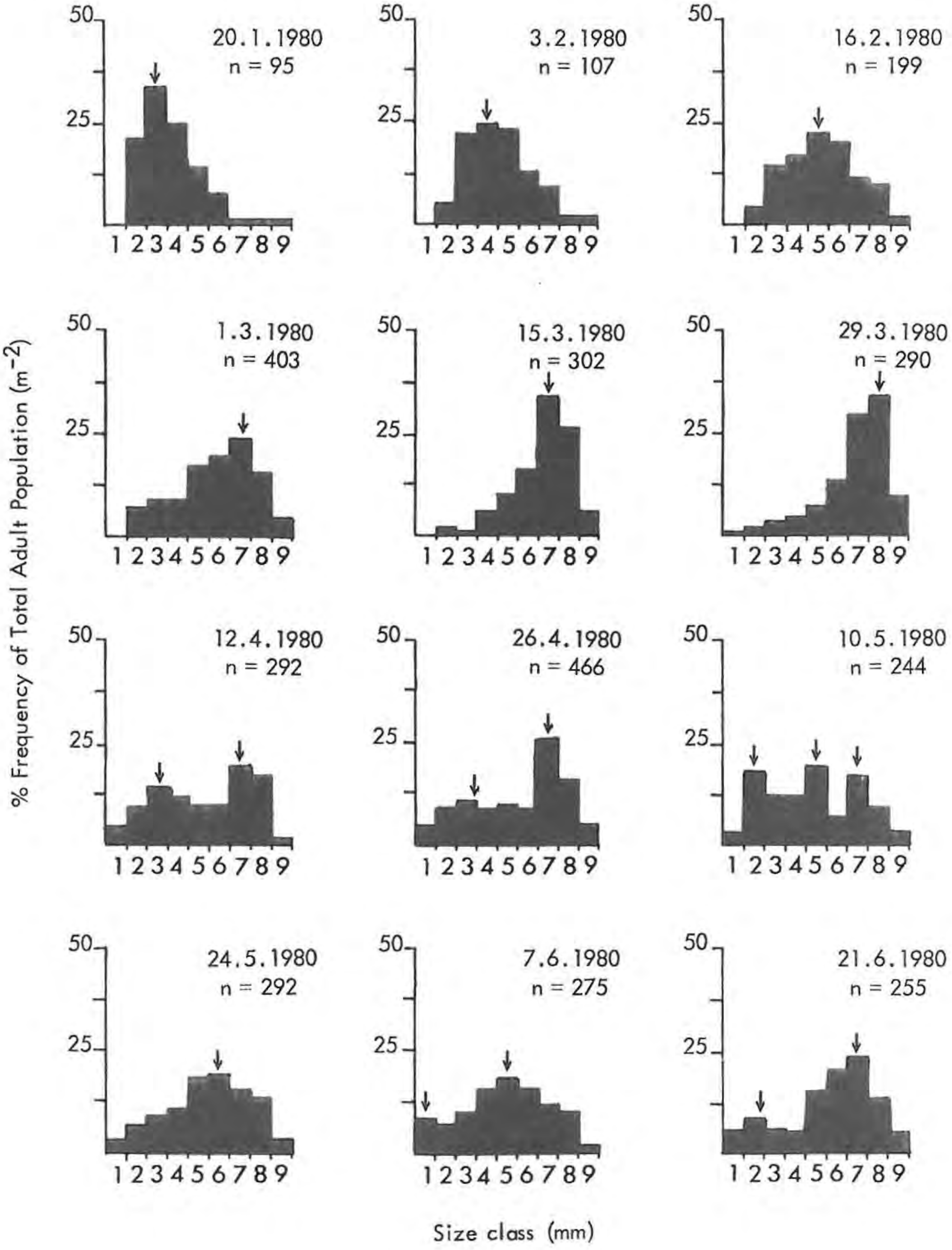
In the pre-flood period juveniles, and immature adults were present, but in low numbers. The paucity of 1 mm juveniles may have been exaggerated as these tiny animals were easily lost, over-looked or damaged, even when extreme care was exercised. At the same time adults were abundant, though 9 mm animals were less numerous than those in the 7 and 8 mm size classes. The pre-flood population therefore primarily consisted of mature, actively reproducing adults, and there were no discernable cohorts.

The whole population was drastically reduced after the floods. Immediately after the first flood, all animals less than 7 mm in length disappeared completely. A few 1 and 2 mm individuals were collected towards the end of the post-flood phase, but 3, 4, 5, and 6 mm snails were entirely absent (Fig. 16).

The first flood also reduced adult numbers considerably, but towards the end of July there were signs that a remnant of the population had survived. The second flood resulted in a long term reduction in adult numbers. These few remaining animals remained in breeding condition despite the environmental extremes. In the early post-flood phase low winter temperatures were combined with low salinities (Fig. 6) and a thick layer of silt. By 23.9.79 salinities had returned to the pre-flood level and the temperature was rising (Fig. 6), but the covering silt layer was still evident and population densities remained very low until January 1980. The 1 and 2 mm animals collected in November 1979, towards the end of the post-flood period, were probably the offspring of surviving adults and were termed the JI juveniles.

The recovery phase was characterised by a sudden influx of 2 and 3 mm juveniles (termed the JII juveniles). Animals in these size classes were abundant throughout the phase, but 1 mm juveniles were absent from the early stages of the recovery phase, and only reappeared in March 1980.

There was a lag before 5, 6, 7, 8 and 9 mm animals were collected, as it took some time for the recolonising juveniles to grow to these sizes. The influx of 2, 3, and 4 mm juveniles on 20.1.80 is shown in Fig. 17. This population of recolonising JII juveniles grew on the mudflat and the progress of the cohort was traced from 20.1.80 to 29.3.80. During this time the modal size class moved steadily from 3 to 8 mm, providing the only opportunity during the study to follow the history of a cohort. Juveniles in the 1 mm size class only appeared on 29.3.80, and this coincided with an increase in the number of reproductive females on the mudflat. This third group of juveniles was termed the JIII juveniles. As they grew

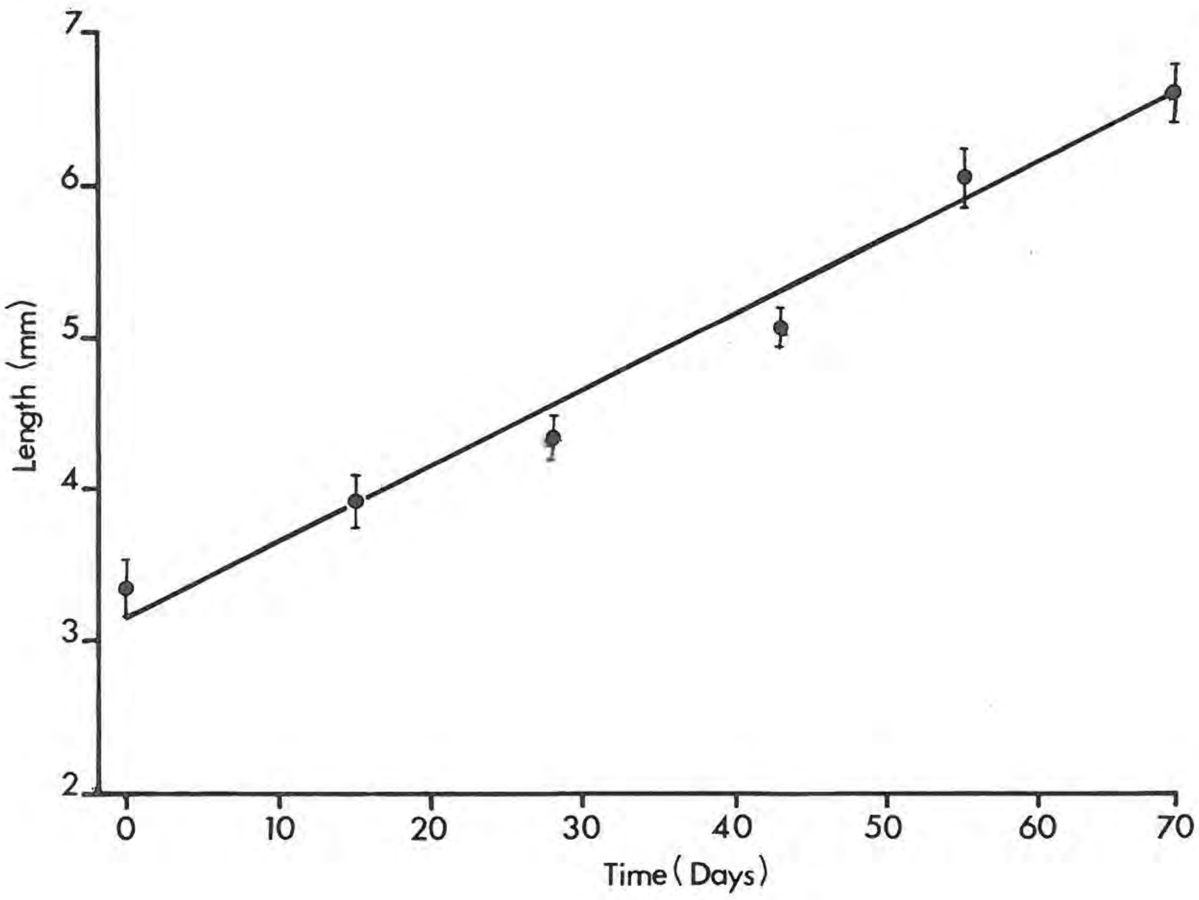

% Frequency of Total Adult Population (m^{-2})
50
25
20.1.1980
n = 95
3.2.1980
n = 107
16.2.1980
n = 199
1.3.1980
n = 403
15.3.1980
n = 302
29.3.1980
n = 290
12.4.1980
n = 292
26.4.1980
n = 466
10.5.1980
n = 244
24.5.1980
n = 292
7.6.1980
n = 275
21.6.1980
n = 255
1 2 3 4 5 6 7 8 9
Size class (mm)

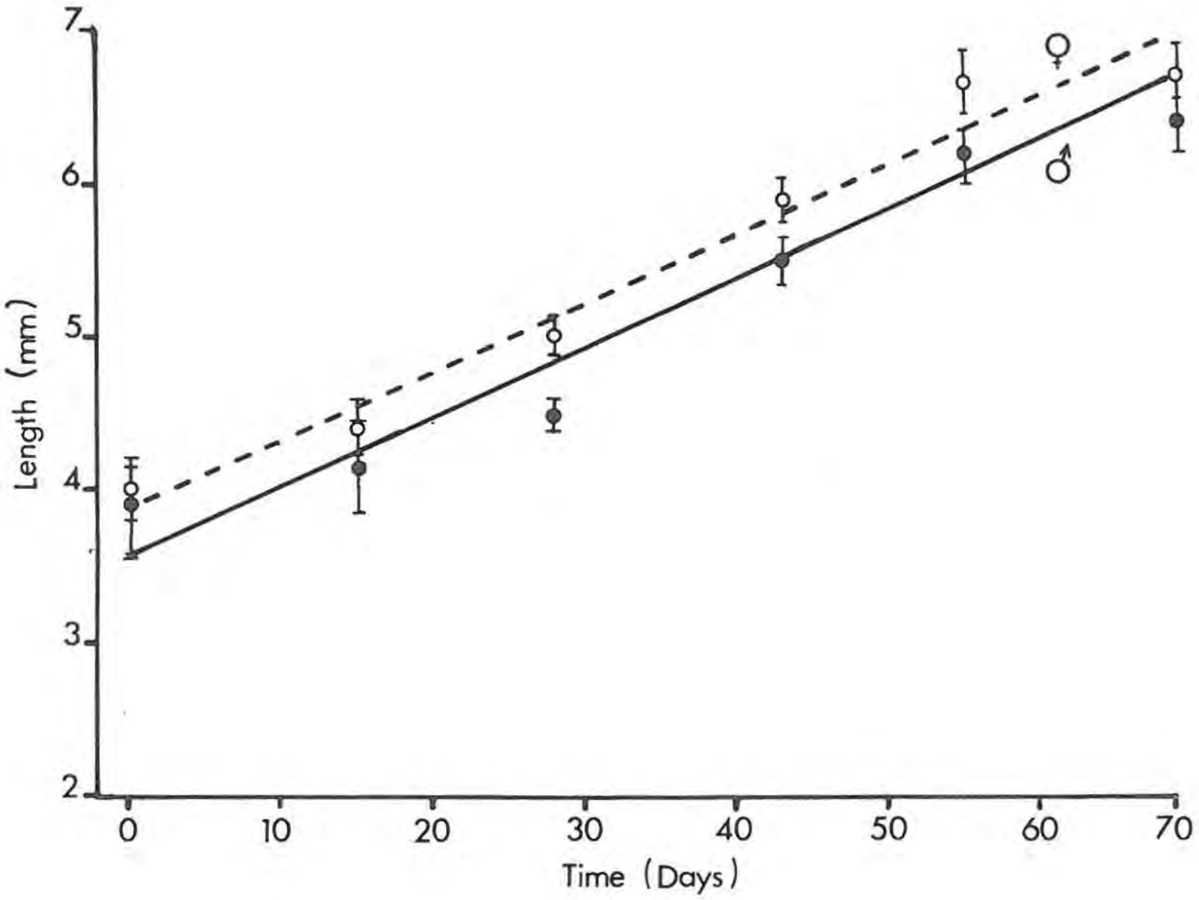
there was some evidence of a second cohort moving through the population, and in April 1980 the population structure was bimodal.

The growth of the whole cohort between 20.1.80 and 29.3.80 has been calculated. Figure 18 shows the mean length of the recolonising cohort plotted against time. The data points fit a linear regression (r=0.98), and growth over that time period, between mean lengths 3.35 and 6.6, was 0.05 mm day^{-1}.

Figure 19 shows the growth rate of both males and females between 20.1.80 and 29.3.80. Both sets of data fitted a linear regression (males - r=0.91, females - r=0.96). The growth rate, 0.05 mm day^{-1}, was identical for both sexes, and was the same as that calculated for the whole cohort. However, at any particular time females were consistently larger than males, indicating that they probably grew faster at an earlier stage in the life cycle.

In order to assess production of the N. kraussianus population an estimate of mortality as well as growth would have been necessary. This was not possible, but some evidence of quite considerable mortality was available. In the samples collected throughout the study, long-dead empty shells, as well as whole animals were sorted and


Length (mm)
2
3
4
5
6
7
0
10
20
30
40
50
60
70
Time (Days)


7
6
5
4
3
2
Length (mm)
0
10
20
30
40
50
60
70
Time (Days)
♀
♂

counted. In every sample, there were on average twice as many empty shells; though of course this represents an unspecified amount of accumulation. Of these, 95% had holes bored through the underside, indicating predation by the carnivorous gastropod *Natica tecta* which was abundant on the mudflat. A simple laboratory experiment indicated that one *N. tecta* (2 cm in length) consumed one adult *N. kraussianus* week^{-1} (Temperature 14°C±).

2.5 DISCUSSION

The high pre-flood and recovery densities of *N. kraussianus* in the study area (Fig. 10) give the first indication of its importance in the estuarine community. However, in both the pre-flood and recovery phases, there was considerable variation in the density estimates that was not associated with seasonal change. Contagious distribution is characteristic of benthic populations (Cassie, 1971; Southwood, 1978) and certainly, the distribution of *N. kraussianus* in the mudflat was extremely patchy. Three behavioural traits probably exaggerated this distribution pattern.

1. *N. kraussianus* has a sensitive chemosensory system; using the osphradium to rapidly locate carrion sources. Animals therefore congregate in large numbers in the vicinity of any such protein source.
2. The *Z. capensis* cover varies within the intertidal zone, and greater densities of *N. kraussianus* occur in areas of high *Z. capensis* cover (Fig. 5).
3. The intertidal *N. kraussianus* population extends subtidally. As the animals are extremely mobile, the dispersion of the population probably shifts

from time to time, with greater or fewer numbers remaining in the intertidal zone.

Two sets of samples illustrate the variability of N. kraussianus densities. On 15.6.79, 2 intertidal pools were sampled, and in each case over 200 animals were collected. In contrast, on 14.7.79, 3 samples from a similar habitat type were devoid of animals. The apparent decline in numbers before the flood is within the high sampling error and is simply a reflection of the contagious distribution pattern. Brown (1971) used a mark-recapture technique to estimate population density in Bullia rhodostoma Reeve, because of its intertidal-subtidal distribution, but found that incomplete mixing of the marked and unmarked individuals resulted in inaccuracies. A mark-recapture operation was attempted during the present study, but was interupted by the floods (Appendix 2).

Population densities and biomass were strikingly different in the pre-flood, post-flood and recovery phases (Figs. 10 & 11, Table 2). Immediately after the first flood, animals were buried under a 20 cm silt layer, and many must have been washed out to sea. The combined effect of low temperatures, low salinity and the smothering silt must have resulted in high mortality, but the samples collected on the 11.08.79 (Fig. 10 & 15) showed that a relatively large number of animals had survived. Certainly, silt covered animals were seen emerging from the substratum during field sampling trips. The second flood brought even greater silt loads, and the period of low salinity was extended, with the result that few animals survived the second catastrophe. Winter temperatures were at their lowest during the flood period, and remained below 15^{o}C until October 1979 (Fig. 6). Salinities followed a similar pattern (Fig. 6), and except for a brief period between the floods, the salinities were below 10 ^{o}/oo NaCl until October 1979, with a two week period at the end of August, when the system was fresh. Interestingly, salinities were again at high pre-flood levels for 3 months before the mudflat was recolonised, and at the same time high summer temperatures were recorded.

The longest lasting effect of both floods was the blanketing layer of silt. The _Z_. _capensis_ beds, where the highest pre-flood densities of _N_. _kraussianus_ had occurred, were completely smothered by the silt, and in fact, the entire study area became an expanse of barren unconsolidated soft mud. Stephenson, _et_ _al_.(1977) have stated that a severe flood of the Brisbane River resulted in "a blanketing of the surface by a layer of soft mud several cm thick" and that 14 months after the flood there was evidence of a "permanent change in the sediments of the area". This resulted in a reduction in faunal diveristy, followed by an "over-response" by a small number of species which recolonised the area in greater numbers than before the flood. Stephenson, *et al.*(1977) also noted that this "overshoot" could have been the combined effect of greater food supply in the deposit sediments, together with the elimination of predators and/or a reduction in the levels of predation. In the case of *N. kraussianus* there has been no evidence of an over-response, but interestingly, A. Bok (*pers.comm.*) has noted an increase in the density of the mud prawn *Upogebia africana* (Ortmann) in the study area since the 1979 floods.

The effect of silt deposition on both the vegetation, and the nature of the substratum seems to be a key factor in the recolonisation response of *N. kraussianus*. Population numbers were very low for 6 months after the floods, and during this time the habitat slowly began to show signs of recovery. The silt consolidated and the substratum began to regain its sand-mud texture, and many areas, where the pre-flood substratum had been mud, were covered by tidally carried sand and became barren sand banks. These were subsequently colonised by the salt marsh grass *S. maritima*. Once the mud substratum had compacted, *Z. capensis* fronds emerged in certain areas, notably the west and south flats, and by the beginning of January 1980 these areas were covered by "short sparse" regenerating *Z. capensis* (Fig. 4). Only then, in mid-January 1980, did the entire habitat; temperature, salinity, substratum, and vegetation, begin to resemble pre-flood conditions. As temperature and salinity had returned to pre-flood levels 3 months previously, substratum and vegetation seem to provide the characteristics necessary for recolonisation. In fact, the two should not be considered separately, as *Z. capensis* acts as an important substratum for *N. kraussianus*.

Scheltema (1961) has shown that *Nassarius obsoletus* (Say) larvae are able to delay metamorphosis until they encounter a favourable substratum. Scheltema proposed that the larvae detected organically rich substrata using sensitive chemoreception, without contact with the substratum. The stimulus to metamorphose and settle included this chemosensory response, followed by direct testing of the substratum. The organic content of the substratum was important, and possibly, in the case of *N. kraussianus* the post-flood silt layer only became attractive after *Z. capensis* regeneration and the accumulation of *Z. capensis*-based detritus.

N. kraussianus is dioecious, and sex ratio is, therefore, an important facet of the population structure. The pre-flood sex ratio was 1:1 (Table 4; Fig. 15a), which is unusual for a prosobranch. In most prosobranch populations, females are more numerous than males (Fretter

& Graham, 1962; Pelseneer, 1926; de Sacchi, 1967; Brown, 1971). There are exceptions, however, and in the most primitive prosobranch order, the Archaeogastropoda, there are several examples of male predominance (Newman, 1967; Ward, 1966; Glynn, 1970; Branch, 1974a). Two prosobranchs have been recorded with a juvenile 1:1 sex ratio, but a higher ratio of females:males occurred in the adult population (Moore, 1937; Turgeon & Fralick, 1973). A few prosobranchs do have an over-all sex ratio of 1:1 (Struhsaker, 1966; Edwards, 1968). One of these, *Olivella biplicata* (Sowerby) is also unusual in that the males are larger than the females (Edwards, 1968), whereas in most prosobranchs, including *N. kraussianus*, the females are larger (Webber, 1977). After the floods, the 1:1 sex ratio changed, and in the post-flood period, females became more common. Females appeared to have a higher post-flood survival rate, and even remained in an actively reproductive condition throughout the post-flood winter period (Fig. 15c). Winter breeding in the genus *Nassarius* has been recorded from other temperate waters. For example, *Nassarius trivittatus* Say, at Rhode Island, U.S.A., produces egg capsules in mid-December, in water temperatures as low as 3.3^{o}C (Pechenik, 1978).

There are several interesting theories about the adaptive advantages of a particular sex ratio (Hamilton, 1967; Maynard-Smith, 1978; Charnov, 1979), and the concept of a stable, outbreeding population having a 1:1 sex ratio seems applicable to the pre-flood population of *N. kraussianus*. However, it is difficult to speculate about a change in the sex ratio of a particular organism without detailed information on female longevity, age at first spawning, number of broods in a life time, and whether or not sex-biased mortality occurs. In the case of *N. kraussianus*, the most likely of these alternatives is differential mortality of males and females. Certainly, many survivors of the flood were females in reproductive condition (Fig. 15c), and possibly, juvenile females were more successful at recolonisation, or had a higher survival rate in the newly colonised area, because females were also more abundant in the recovery phase. This phenomenon may relate back to resource partitioning and energy channelling, with females growing larger (Fig. 19), and possibly having a greater survival potential than the smaller males.

A comparison of the number of reproductive females, and the number of juveniles in the population is particularly interesting (Figs. 15b & c). In the pre-flood phase, most of the adult females were in full reproductive condition, carrying embryos, but at the same time very few juveniles were collected.(Possible explanations of this are presented in Part 3). Reproductive females survived the flood in small numbers, but no juveniles at all were collected until December 1980, and then only a few individuals were found. Contrast this with mid-January 1980. The number of reproductive females was just as low, but there was a sudden influx of large numbers of juveniles. It is highly unlikely, therefore, that all these juveniles could have been spawned on the mudflat by the surviving females. The recovery of the population was, therefore, primarily effected by incoming juveniles. Catastrophes of the magnitude of the 1979 floods may occur only twice a century, but in terms of evolutionary time this is relatively frequent. This study seems to indicate that recolonisation may be an important adaptation to life in South African estuaries.

Not all size classes were affected to the same extent by the floods. Juveniles and immature adults were completely eliminated, and mature adults were the only survivors (Fig. 16). Considered in the context of life-cycle as an adaptation to estuarine conditions, this survival pattern makes sense, as the survival of reproductive adults after an environmental catastrophe would be advantageous to the population. Larval stages are particularly sensitive to environmental extremes (Forbes & Hill, 1969; Hill, 1974; Forbes, 1977). However, adaptations such as ovoviviparity (see Part 3), or the protection of larvae in a parental burrow (Forbes, 1973a; 1973b), would enhance their chances of larval survival, and dispersal would be more efficient if resilient post-larval juveniles were the dispersal stage, as is the case in *Callianassa kraussi* Stebbing (Forbes, 1973a; 1973b). Both Lockwood (1976) and Hill (in press) stress the importance of larval adaptations when considering adaptations of estuarine organisms, and obviously, maintenance of any population is dependent on its development pattern and reproductive strategy. This important concept will be developed in Part 3.

Fig. 17 shows the size frequency structure of the recovery phase. In the first set of samples (20.01.80), 1 mm animals were completely absent, the modal size class was 3 mm; and 2 and 4 mm animals were abundant. At the same time, there were very few reproductive females on the mud-flat (Fig. 13c), because, as already discussed, it seemed unlikely that the large numbers of recolonising juveniles were spawned by the few surviving females. In the late post-flood period (November and December 1979) a small number of 1, 2 and 3 mm animals was collected (Fig. 16). These JI juveniles could quite feasibly have been the off-spring of the surviving females. The recolonising JII cohort grew to adult size between January and March 1980, and provided the only opportunity for cohort analysis (Fig. 17). In addition to small juveniles, the recovery cohort also comprised 4, 5 and 6 mm animals which may have been early recolonisers, or JI juveniles, after 2 months growth. Small 1 mm animals appeared in late March 1980 (29.3.80), and were probably the off-spring of the JII cohort, which by then had reached adult size. The polymodal size frequency of the population after April 1980 (Fig. 17) is further evidence of continuous reproduction. The multiple modal peaks between April and June 1979 probably represent growth of successive broods of juveniles spawned by the newly established adult population.

Between 20.1.80 and 29.3.80 (Fig. 17), the modal peak of the recolonising cohort moved from 3 mm to 8 mm, providing a unique opportunity to quantify growth (Fig. 18). However, growth was only calculated over this 3 month period, when the mean length of the cohort increased from 3.35 mm to 6.6 mm. During this time growth was linear. The potential longevity of *N. kraussianus* is almost certainly at least 1 year, and animals have survived in the laboratory for 2 years. Therefore, energy is probably initially channelled into rapid growth to reproductive size, and thereafter, into reproduction. If the mark recapture study had been successful (Appendix 2) the total growth pattern would probably have been similar to those recorded by Branch (1974b) for a number of *Patella* species, except perhaps for growth rate. All the *Patella* species, and also the more closely related species, *Bullia rhodostoma* Reeve (McLachlan, *et al*., 1979), have a much slower growth rate than N. kraussianus, in that the linear phase of growth continues for much longer than three months. Interestingly, two faster growing Patella species, Patella granatina L. (Kommetjie) and Patella oculus Born (Kalk Bay), also have shorter life spans, and Branch (1974b) noted that generally long-lived animals grow more slowly than those with short life spans. B. rhodostoma and the Patella species live for several years (ranging from 4 -25). The longevity of N. kraussianus is unknown, but it appears to grow to maximum size in approximately 3 months.

The growth of males and females within the recolonising cohort has also been illustrated (Fig. 19). Measurements of male and female growth were limited to animals greater than 4 mm in length, simply because of the limitation of sexing smaller animals. Between 20.1.80 and 29.3.80 male and female growth rates were identical, but at any one time, the female size was greater. This seems to indicate that smaller females may grow faster than males. This would be extremely difficult to investigate as the sex of very small animals would have to be determined. The growth rates illustrated in Figs. 18 & 19 probably represent growth under optimal conditions, because the recolonising population was able to exploit an optimum habitat where food was abundant, at a time when temperatures were high.

As a general rule, population biology studies include an estimate of production, because biomass (B) and production (P) values, and the P:B ratio, are often used to compare populations. The biomass of N. kraussianus has been established but annual production is unknown, and the P:B ratio can only be estimated (Appendix 2). If turnover of the entire population was annual, the P:B ratio would be 1.0. N. kraussianus has a potential longevity of a least 2 years (from animals kept in laboratory tanks) but under natural conditions is probably heavily preyed upon (Blaber, 1973; Hill, 1976). A P:B ratio value of 1.0 or slightly less than 1.0 is the best estimate possible from the available information. This value falls well within the range shown in Table 5. Both dry weight and ash free dry weight values for N. kraussianus have been included. The dry weight values are comparable with 3 bivalves, but the ash free dry weight values are extremely low, and only one other mollusc, the bivalve Macoma balthica (L.), has a comparable value. A possible reason for the low value of N. kraussianus, is that the animal has a relatively massive shell, the body whorl of which has a heavily thickened callus (Fig. 8) which is probably an anti-predatory adaptation.

Several important questions which fall into two general groups, remain unanswered. The first group concerns feeding strategy and trophic position within the food web. For

SPECIES	B	P	P:B	SOURCE
Mya arenaria	*4.6	11.6	2.5	Burke & Mann, 1974
Macoma balthica	*1.3	1.9	1.5	Burke & Mann, 1974
Mytilus edulis	*3-15	4-20	1.3	Burke & Mann, 1974
Modilus demissus	* ?	?	0.2	Kuenzler, 1961
Nassarius kraussianus	*2-4			This study
Musculus virgiliae	75.56			Davies, 1979
Scrobularia plana	5-40	3-13		Hughes, 1970
Venerupis pullastra	135	20	0.15	Johannessen, 1973
Mytilus edulis	125-400	265		Milne & Dunnet, 1972
Cenastoderma edule	18-65	29-71	1-2.6	Hibbert, 1976
Mercenaria mercenaria	8-50	4-140	2-0.5	Hibbert, 1976
Scrobicularia plana	2.1	0.5	0.2	Warwick & Price, 1975
Macoma balthica	0.22	0.07	0.3	Wolff & de Wolf, 1977
Cardium edule	45.6	51.7	1.13	Wolff & de Wolf, 1977
Littorina littorea	9.81	6.13	0.61	Wolff & de Wolf, 1977
Hydrobia ulvae	9.37	12.79	1.36	Wolff & de Wolf, 1977
Bullia rhodostoma	?	?	0.9	McLachlan, *et al.*,1979
Nassarius kraussianus	0.23-0.54		1.0-	This study

Table 5. Mean annual biomass (B) and production (P) values for a range of molluscs from recent literature, expressed as g dry weight (*) and g ash free dry weight. Modified after Hibbert (1976).

example:

1. How was such a large population supported in the pre-flood phase?
2. What enabled the rapid growth shown by the recolonising cohort?
3. What is the feeding strategy of N. kraussianus?

No detailed study has been made of the feeding, but in Part 4, field and laboratory observations are recorded. These observations go some way in answering the above questions, and certainly provide direction for further research.

The second area with particular relevance to population biology, concerns the reproduction of N. kraussianus. The answers to several questions arising from this chapter hinge on an investigation of life cycle and reproductive strategy. "Fluctuations in abundance of a species are obviously related to its life history" (Boesch, *et al*., 1976). The following questions provided the stimulus, and research emphasis for the work presented in Part 3:

1. Why was the pre-flood population structure so consistently dominated by adults, with so few juveniles making up the population numbers?
2. How is N. kraussianus adapted to cope with intermittent physical extremes associated with an estuarine existance?
3. What are the mechanisms of recolonisation?
4. What is the significance of the recovery phase

population structure?

In answering these questions the theme of this section will be expanded, and the concept that recolonisation (and of course a life history enabling this) is a vital adaptation to life in southern African estuaries, will be discussed.

PART 3 : REPRODUCTIVE BIOLOGY

3.1 INTRODUCTION

Prosobranch reproduction is a widely documented subject (reviews : Fretter & Graham, 1962; Webber, 1977). Lebour (1934; 1935; 1936; 1937; 1945; 1947) was an important early contributor, whose research provided descriptive information on the patterns of development found in prosobranch families. As prosobranchs in various parts of the world were investigated, the descriptive literature proliferated (Natarajan, 1957; Anderson, 1966; Pilkington, 1974). Thorson (1935; 1946; 1950; 1961; 1966) provided a new research emphasis in his discussion of the ecological significance of larval development, particularly with regard to dispersal. Thorson's research provided the groundwork for the assessment of the evolutionary trends within the Prosobranchia (Mileikovsky, 1971; 1975; Radwin & Chamberlin, 1973; Shuto, 1974). Before these concepts can be discussed an overview of prosobranch reproduction is essential.

The anatomical differences which result in prosobranch classification into Archaeogastropoda, Mesogastropoda and Neogastropoda are accompanied by different reproductive strategies. Copulation and secondary sexual characteristics are rare in the most primitive prosobranch order, the Archaeogastropoda, although the Neritidae, the family most closely related to the mesogastropods, exhibit internal fertilisation. External broadcast fertilisation is usual, but some species embed fertilised eggs in mucus; and one Arctic species Acmeae rubella is ovoviviparous (Thorson, 1935). Generally archaeogastropods produce small eggs with little yolk (microlecithal) which develop into pelagic, planktotrophic larvae. The first free swimming stage is usually a trochophore which rapidly develops into a veliger. Planktotrophic veligers frequently remain in the plankton for several weeks (even months), and during this stage are dispersed by the ocean currents. After torsion, shell formation and metamorphosis, the veliger sinks to the bottom and assumes a benthic mode of life (Table 7). A few neritids and patellids produce yolky eggs, and in these cases the larvae are lecithotrophic with short pelagic lives.

Most mesogastropods exhibit internal fertilisation, and females deposit yolky eggs in a gelatinous mass or egg capsule. The trochophore is usually suppressed and larvae hatch as veligers, which may have either long planktotrophic or short lecithotrophic pelagic lives (Webber, 1977). Planktotrophic veligers hatch from small ova, and the protoconch, or larval shell, is therefore small, growing in a helical spiral during planktonic life.

In contrast, the lecithotropihc veligers develop from large ova, and the protoconch is large and bulbous. The veliger spends little time in the plankton, and the shell remains simple, showing little helical growth (Fretter & Pilkington, 1971; Shuto, 1974).

Neogastropods exhibit internal fertilisation, and many lay eggs in tough egg capsules. These eggs may be small and hatch as planktotrophic veligers with a long pelagic life, but usually they are large and yolky, and the planktonic life of the veliger is either short or absent. Nurse eggs are characteristic of certain neogastropod families, and most egg cases are filled with an albuminous nutritive fluid (Anderson, 1960).

Some of the evolutionary trends within the prosobranchs should already be obvious (Table 8). For example, protection during early development is progressively improved, from external fertilisation in archaeogastropods, to internal fertilisation and lecithotrophic development in most neogastropods.

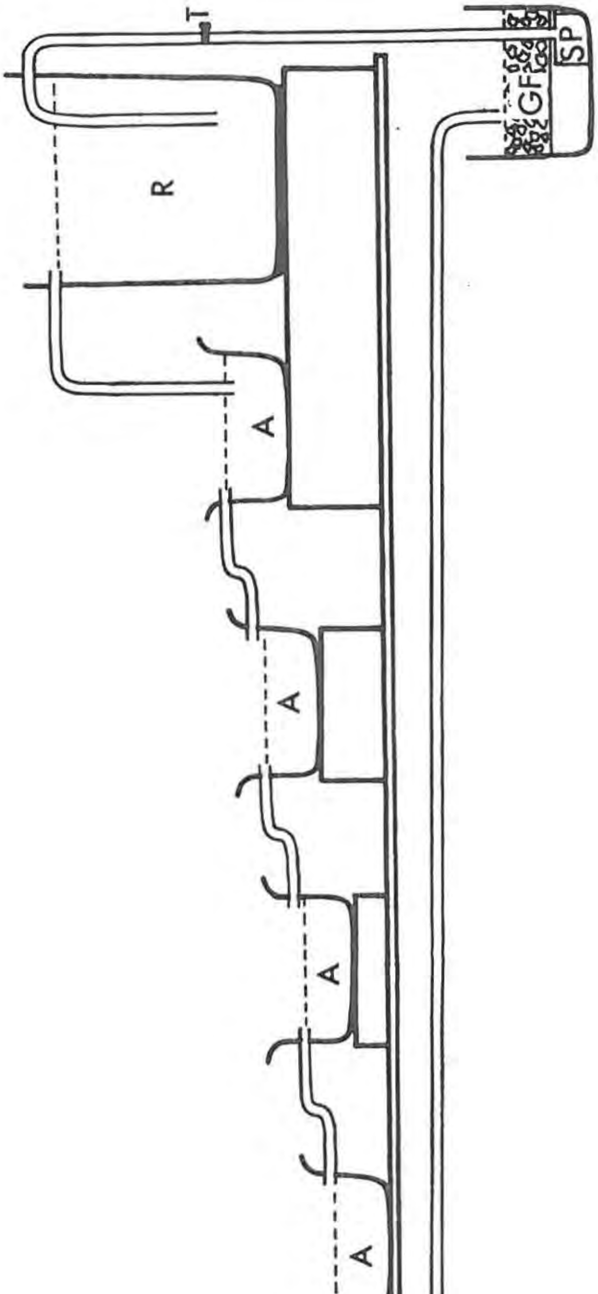
In South Africa there is very little descriptive information available on the development and reproduction of prosobranchs, although they abound along the coastline (Barnard, 1958; Kensley, 1973). As a result, there is even less information on larval ecology, and the patterns of dispersal and settlement. Brown (1971) briefly described the courtship and egg capsules of *Bullia rhodostoma* and *B. digitalis*. Branch (1974a) elucidated the reproductive cycles of 7 *Patella* species and subsequently discussed the effects of intraspecific competition on the recruitment, settlement and mortality of juvenile *P. cochlear* (Branch, 1975).

None of these studies deal with reproductive strategy in relation to dispersal. Dispersal is of particular interest in the context of the present study, and the reproductive biology and development of *N. kraussianus* were investigated in order to try and elucidate the mechanism of recolonisation; and to view the population structure in the light of the life history. In addition, the results contribute descriptive information about an important South African prosobranch, and enable a discussion relating the development and reproductive strategy to evolutionary trends within the Prosobranchia.

3.2 MATERIALS AND METHODS

Most animals used in the laboratory for development studies were collected in the field, and investigated almost immediately. However, an experimental population was maintained in a laboratory holding system, and fresh material was transferred to a separate part of the system as soon as possible after collection. The seawater holding system had a capacity of 150 litres, and water was circulated continuously over a gravel filter by an underwater pump (Fig. 20). The system was housed in a constant environment room ($26^{o}C \pm 2^{o}C$, 12 hour light/dark cycle).

More than 1000 animals were collected and kept in the holding system for 15 hours before they were separated into size classes, dissected, and the appearance of the reproductive system was noted. A descriptive gonad index for males and females was established on the basis of gross anatomical features. This index was based on a single collection of animals, and in order to investigate seasonal trends in gonad development, all animals collected during population estimate work, throughout the study period, were dissected and compared against the index. Ovaries and testes from animals in the mature stages were examined histologically in order to confirm the accuracy of the gonad index.


R
A
A
A
A
T
GF
SP

Gonads were fixed in a mercuric-chloride based fixative (Zenkers) (Humason, 1967) for 48 hours, then transferred to a Shandon Southern tissue processor for 12 hours, which dehydrated and infiltrated the material with paraffin wax. The wax impregnated gonads were manually embedded in wax blocks and left to cool. The blocks were sectioned (7µm) using a Leitz-Wetzlar microtome and finally stained. Most material was stained in conventional haemotoxylin and eosin, but clear detail of sperm packed in the Vas Deferens was achieved using Weigerts iron haemotoxylin and eosin Humason (1967). The descriptive gonad index was confirmed by the histological details of spermatogenesis and oogenesis.

Females carrying embryos were found throughout the study, and an in vitro investigation of development was undertaken. Large females (8 & 9 mm) were isolated in small glass aquaria filled with seawater. The shell of each female was cracked open using an adjustable hand-held vice to prevent damage to the body. The living body was removed and dissected in seawater. Egg cases were carefully removed from the uterus and placed in fresh seawater in an excavated glass block. The length of each female and the number of embryos in the uterus was recorded. The embryo was held in the constant environment room (conditions as above), the water was changed daily, and development was monitored using a Wild binocular dissecting microscope (X 500) and a _camera lucida_.

Several hundred embryos were removed from females; 75 were reared to 2 weeks; 52 to hatching, and 10 to metamorphosis. Young snails all died 2 weeks after metamorphosis.

3.3 RESULTS

3.3.1 GONAD INDEX

A gonad index based on size was applicable to the population throughout the study, indicating that the snails sexually matured with age, and did not reproduce seasonally. The index was initially described using the physical appearance of the gonad. The physical appearance did not vary seasonally, but only with increasing size and maturity. This descriptive index was subsequently confirmed by histological investigation. The gonad index comprised 5 stages for both males and females. Adult male and female anatomy is shown in Figures 21 & 22.

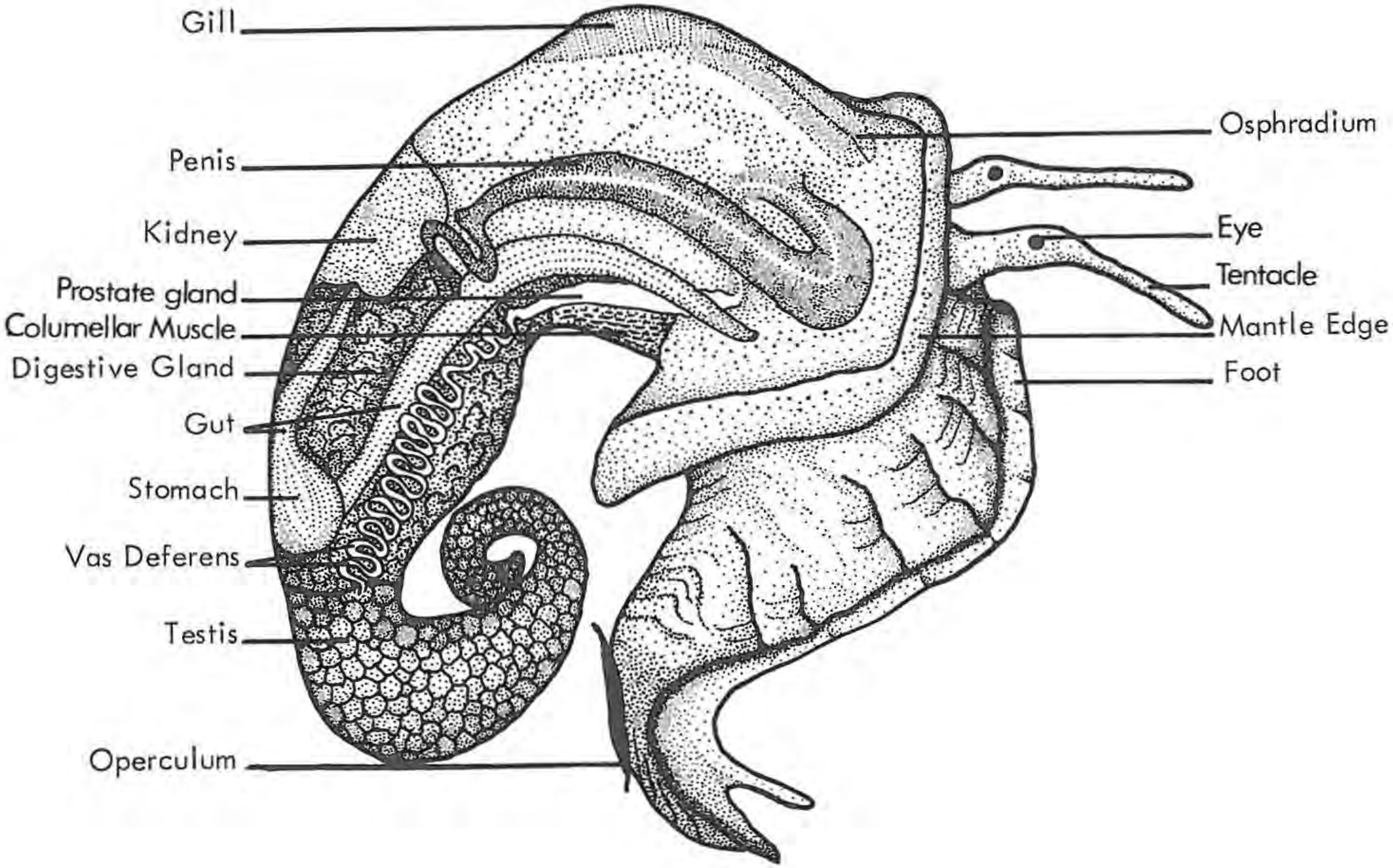
3.3.1.1 Physical Description

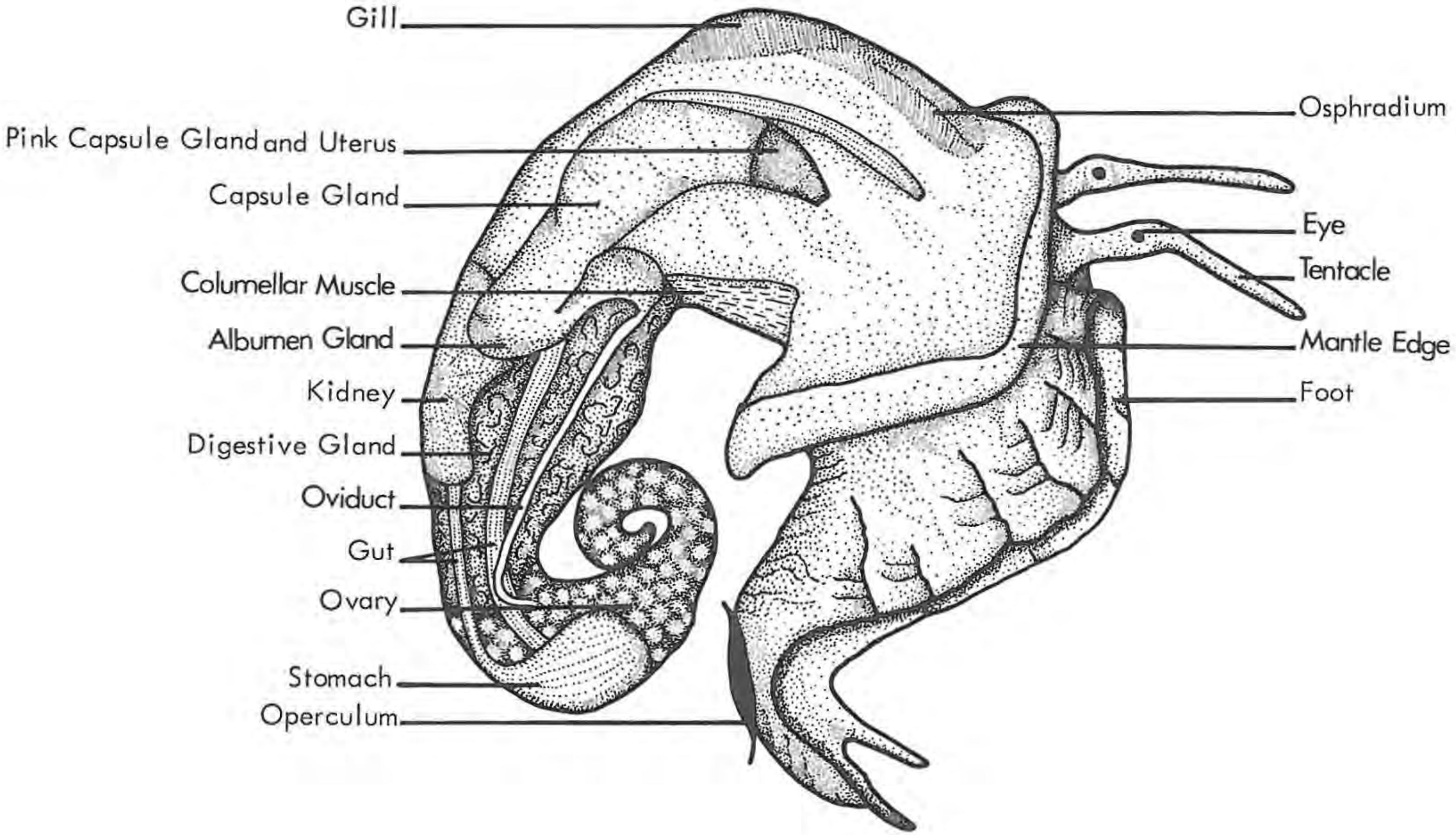
a. Males:

Stage I (4 mm). The first overt characteristic was the development of a penis, which in 4 mm males was an average of 1 mm in length.

Stage II (5 mm). The penis remained the only sex-linked characteristic in the 5 mm animal, but grew to approximately 2 mm in length.

Stage III (6 mm). In most 6 mm males the testis had developed and was pale yellow in colour. The Vas Deferens led from the testis to the penis. At


Gill
Penis
Kidney
Prostate gland
Columellar Muscle
Digestive Gland
Gut
Stomach
Vas Deferens
Testis
Operculum
Osphradium
Eye
Tentacle
Mantle Edge
Foot


Gill
Pink Capsule Gland and Uterus
Capsule Gland
Columellar Muscle
Albumen Gland
Kidney
Digestive Gland
Oviduct
Gut
Ovary
Stomach
Operculum
Osphradium
Eye
Tentacle
Mantle Edge
Foot

this stage the Vas Deferens was white, very thin, and coiled, and the penis was 3-4 mm in length.

Stage IV (7 & 8 mm). The adult, 7 and 8 mm, males were sexually mature. The increase in the length was accompanied by changes in shell shape. The underside of the body whorl thickened to form a callus, characteristic of mature adults. The penis was fully developed and up to 6 mm in length. The coiled duct of the Vas Deferens was much thicker than in Stage III, and led to the testis, which was bright yellow, and reproductively mature.

Stage V (some 7 & 8 mm). Most adult males were in Stage IV. A few appeared to be post-reproductive. The testis was dark orange-brown and the Vas Deferens was yellow.

b. Females:

Stage I (4-5 mm). No overt female characteristics were evident; thus 4 and 5 mm females were distinguished by the absence of a penis.

Stage II (6 mm). The first indication of ovary development was a concentration of vitelline granules at the distal end of the digestive gland.

Stage III (7 mm & a few 8 mm). The ovary was first apparent in 7 mm animals. Vitelline granules were present, giving the ovary a white appearance, but the ovary was not reproductively mature. The capsule gland had begun to develop and was a uniform white.

Stage IV (some 7 mm, most 8 mm, and all 9 mm). As with males, Stage IV indicated reproductive maturity, although mature females were usually larger than mature males. The ovary had swelled to fill the distal body coil, and was a mottled cream and pink. The ovary was linked to the capsule gland and uterus by a thick white oviduct. The capsule gland was turgid and cream coloured with a bright pink proximal tip. Most mature females had egg capsules in the uterus.

Stage V (very few 8 & 9 mm). A few females seemed to be post reproductive. The ovary had shrunk and was orange coloured, as was the capsule gland. The oviduct was dark brown.

3.3.1.2 Histological Description

a. Males:

Stages I (4 mm) and II (5 mm). No histological investigation of these stages was undertaken, as the testis had not yet developed.

Stage III (6 mm). Histological examination of the pale yellow testis showed that the animal was not sexually mature (Fig. 23). Spermatogonia lined the epithelia within the testis, and the cavities were filled with spermatocytes in a state of active meiosis. Spermatids were present in small numbers, but there were no mature sperm in either the testis, or the Vas Deferens.

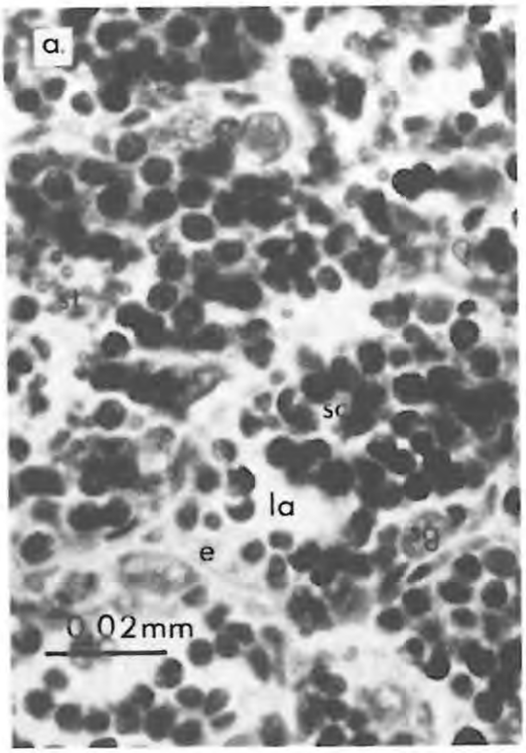
Stage IV (7 & 8 mm). The mature testis was histologically quite different (Fig. 24). Spermatogonia and spermatocytes lined the cavities within the testis, while these were filled with mature sperm. Spermatocytes were in a state of active meiosis, and spermatids were abundant. The Vas Deferens was packed with mature sperm (Fig. 25).

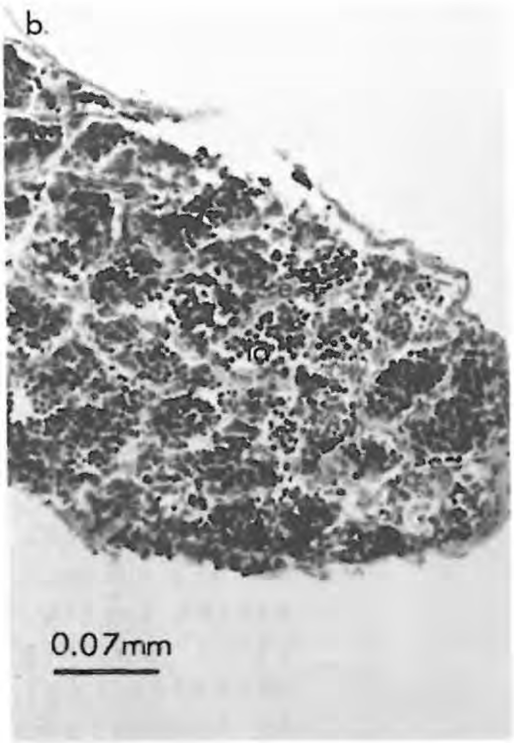
Stage V (some 7 & 8 mm). The testis was spent and contained only the remnants of the germinal epithelium (Fig. 26). Active spermatogenesis had ceased, and no spermatogonia or spermatocytes were evident.

b. Females:

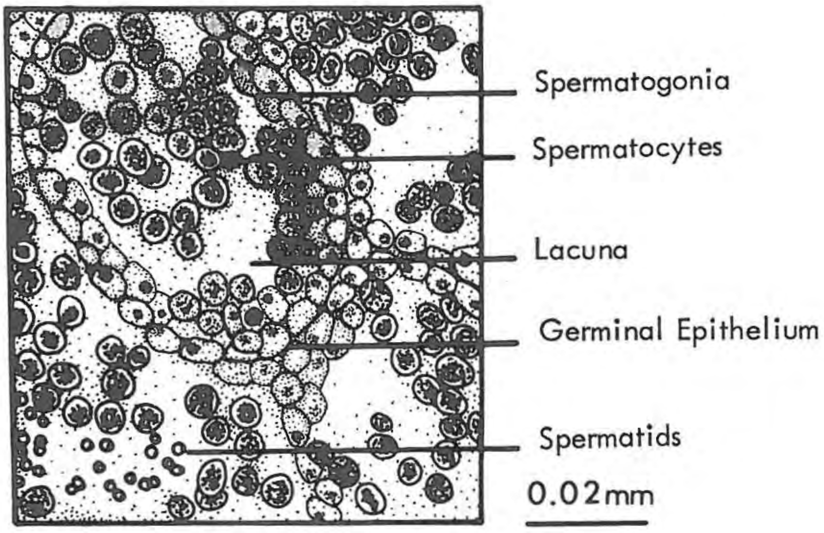
Stages I (4-5 mm) and II (6 mm). No histological investigation of these two stages was undertaken, as the ovary was undeveloped.

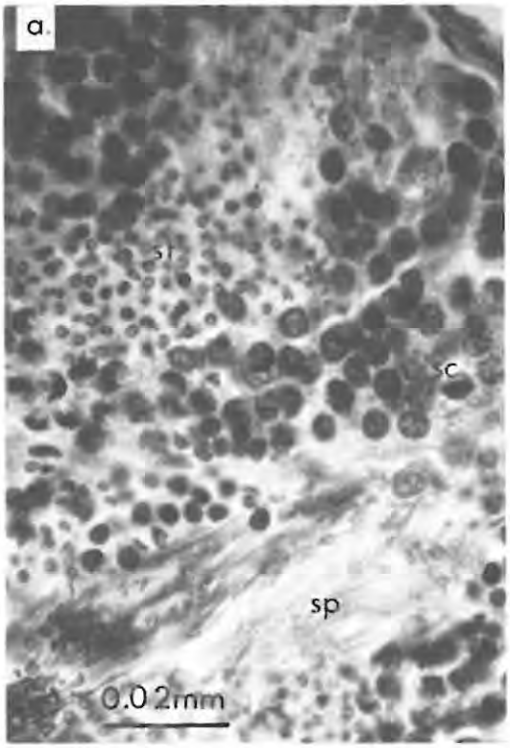
Stage III (7 mm and a few 8 mm). The maturing ovary was characterised primarily by the number of developing, but immature ova (Fig. 27). Epithelia within the ovary were lined with oogonia, giving rise to oocytes. These then matured and

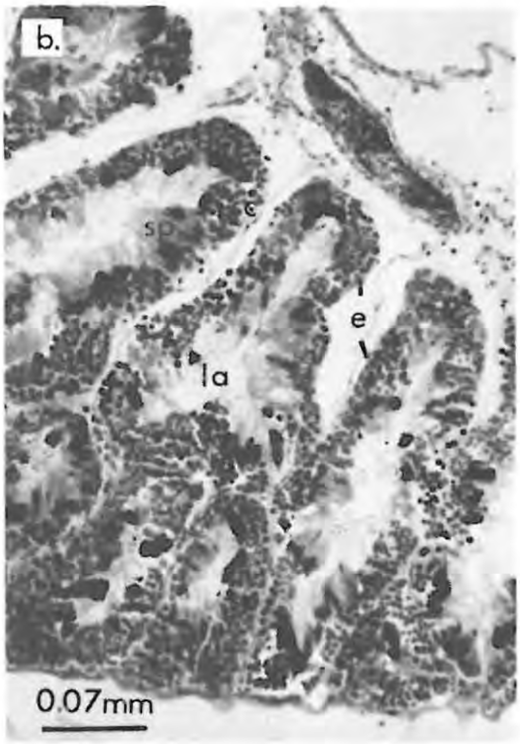

a.
st
sc
la
e
g
0.02mm


b.
la
0.07mm

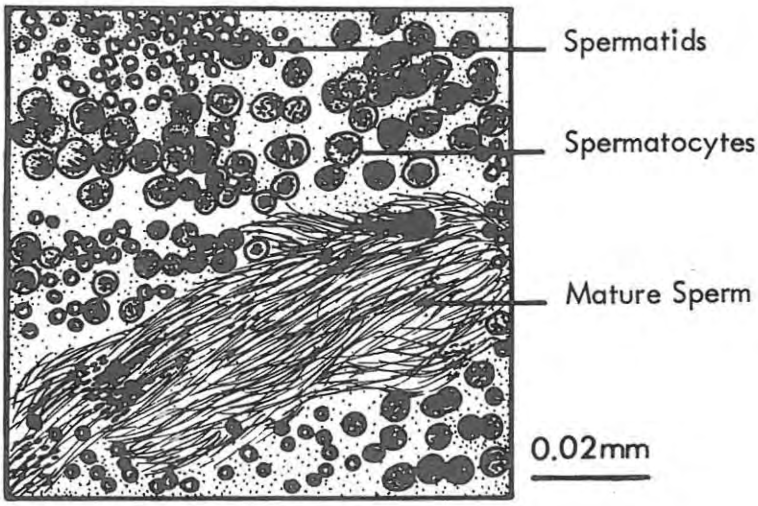
c.

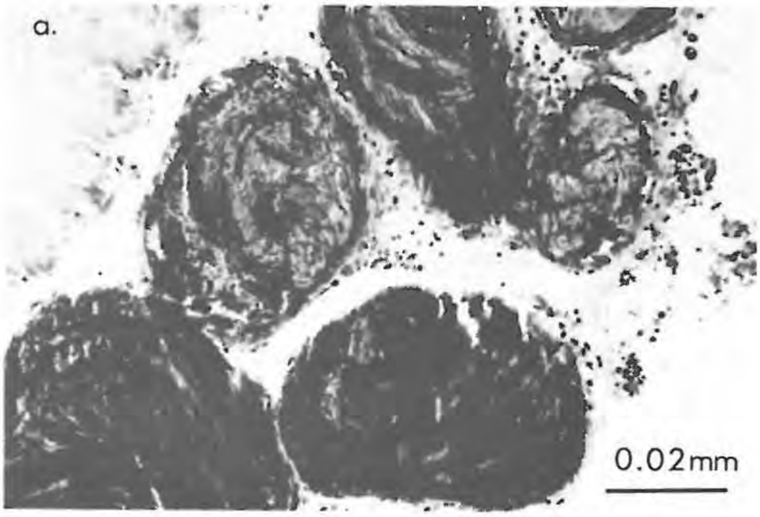

Spermatogonia
Spermatocytes
Lacuna
Germinal Epithelium
Spermatids
0.02mm


a.
st
c
sp
0.02mm

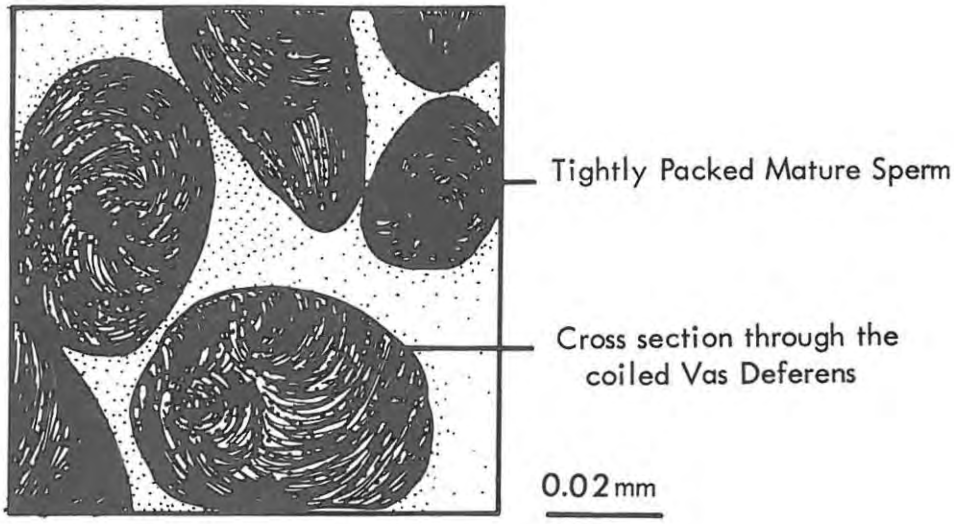

b.
sp
c
e
la
0.07mm

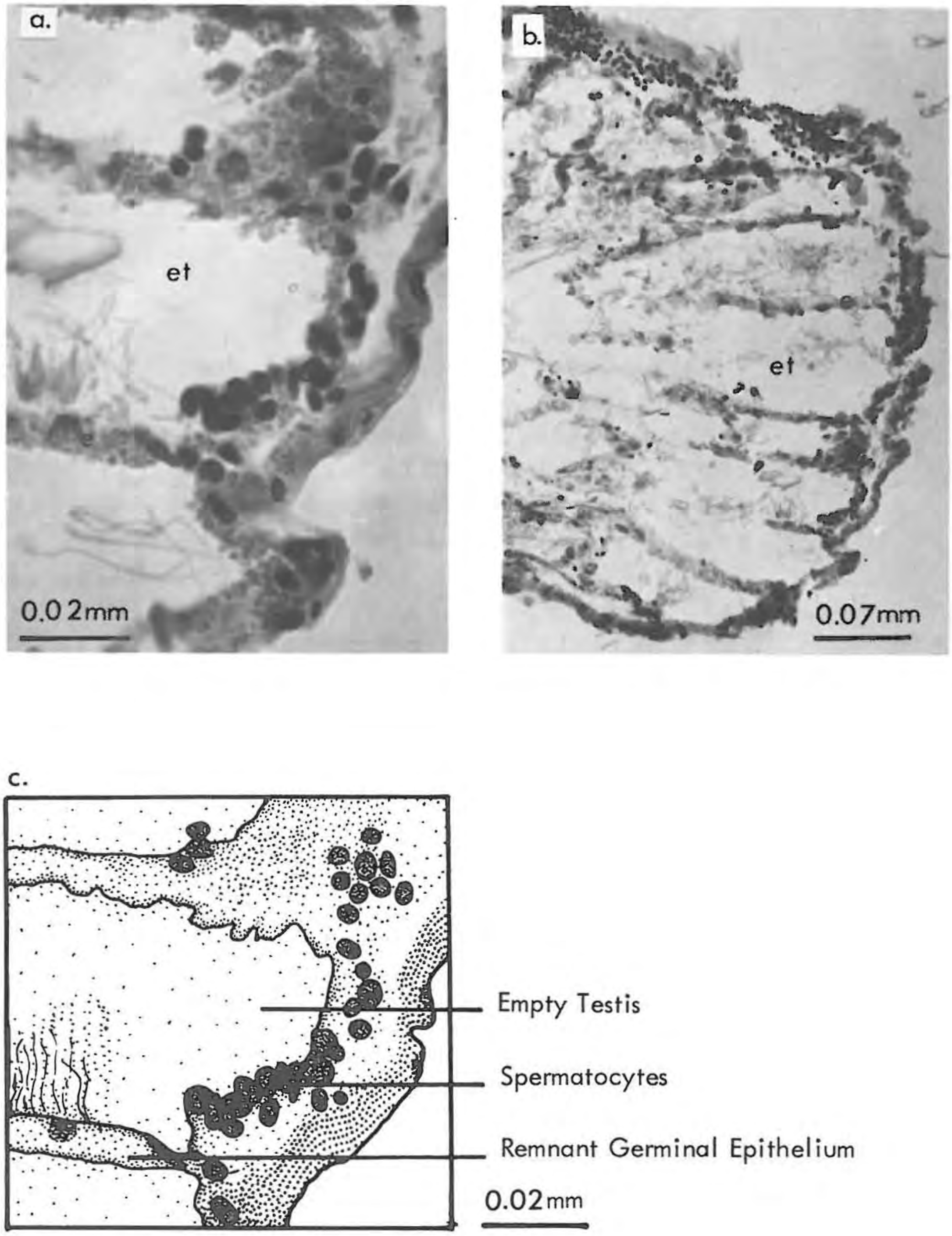
c.

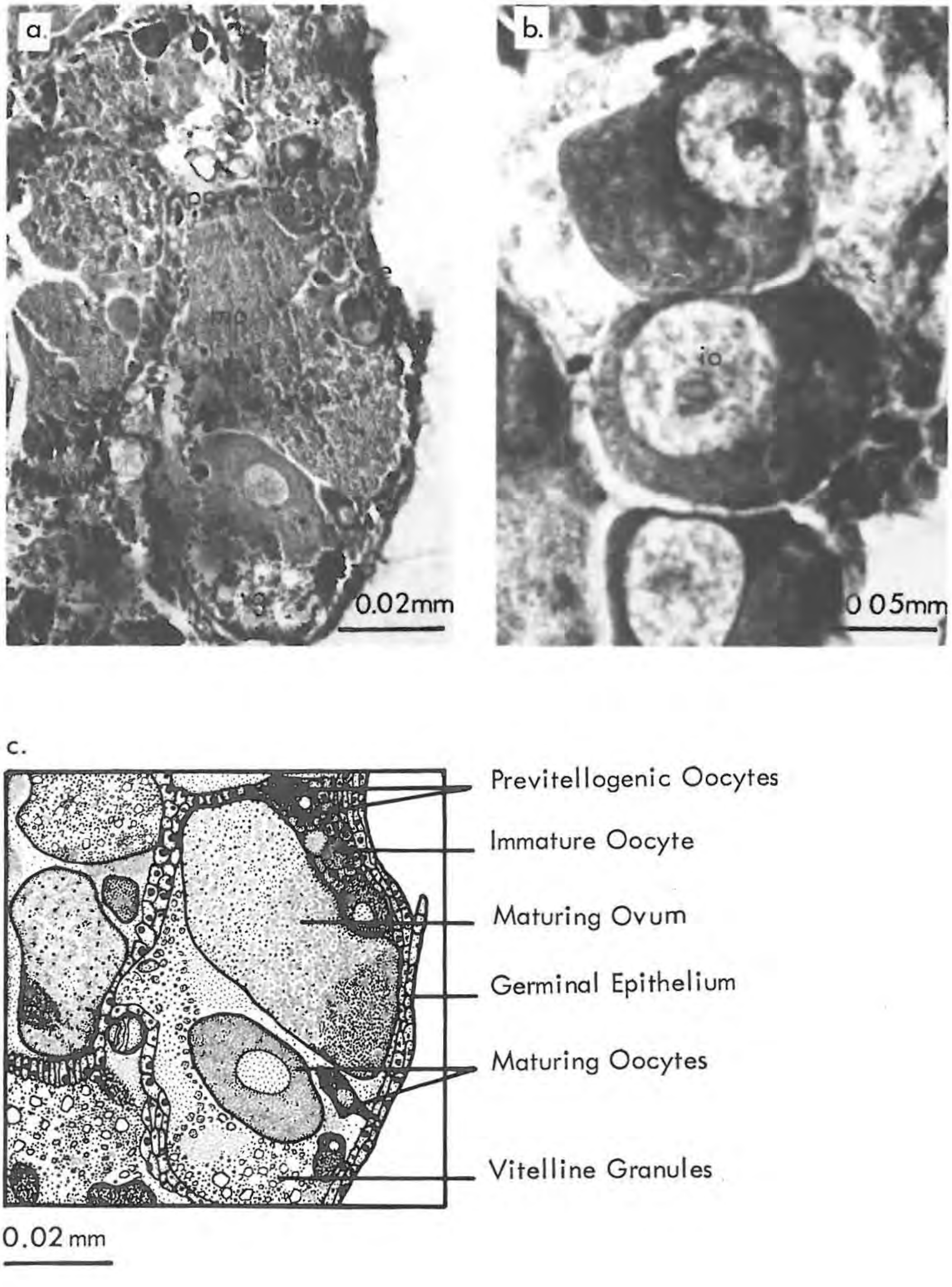

Spermatids
Spermatocytes
Mature Sperm
0.02mm


a.
0.02mm

b.


Tightly Packed Mature Sperm
Cross section through the coiled Vas Deferens
0.02mm


a.
et
0.02mm
b.
et
0.07mm
c.
Empty Testis
Spermatocytes
Remnant Germinal Epithelium
0.02 mm


a.
ps
mo
io
0.02mm
b.
io
0 05mm
c.
Previtellogenic Oocytes
Immature Oocyte
Maturing Ovum
Germinal Epithelium
Maturing Oocytes
Vitelline Granules
0.02 mm

developing ova were characterised by a large nucleus, and smooth, non-yolky texture.

Stage IV (8 mm). The mature ovary was filled with large, yolky ova, and pouches of vitelline granules (Fig. 28). Epithelial areas of active oogenesis were present, but were thinner than in Stage III. Oogonia, oocytes and early ova were present, and lined areas packed with large mature eggs. The material was extremely difficult to section, as the yolk crumbled away, leaving an empty outline, as in Fig. 28a.

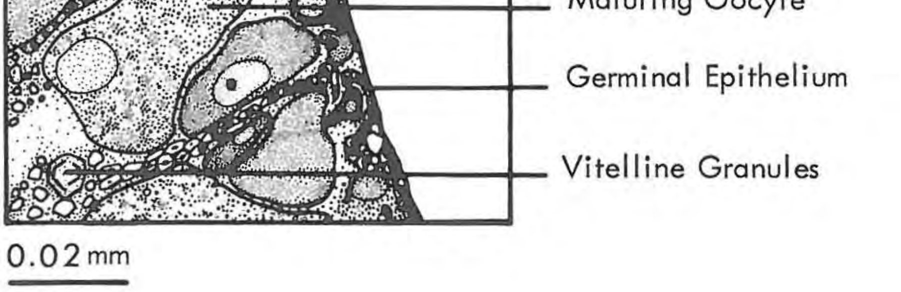
Stage V (very few 8 & 9 mm). No post reproductive females were investigated histologically. This stage was observed in a few females collected during sampling, and the animals had already been fixed in formaldehyde, which does not preserve cellular detail well enough for histological examination. No other post reproductive females were found, and therefore the histological status of the spent ovary is unknown.

A comparison of the physical and histological descriptions show that the two confirm one another, and therefore Stages I to V, for both males and females, were used to define the reproductive condition of the animals during the study.


a.
po
mo
ro
ov
vg
0.02mm


b.
vg
ov
e
0.07mm

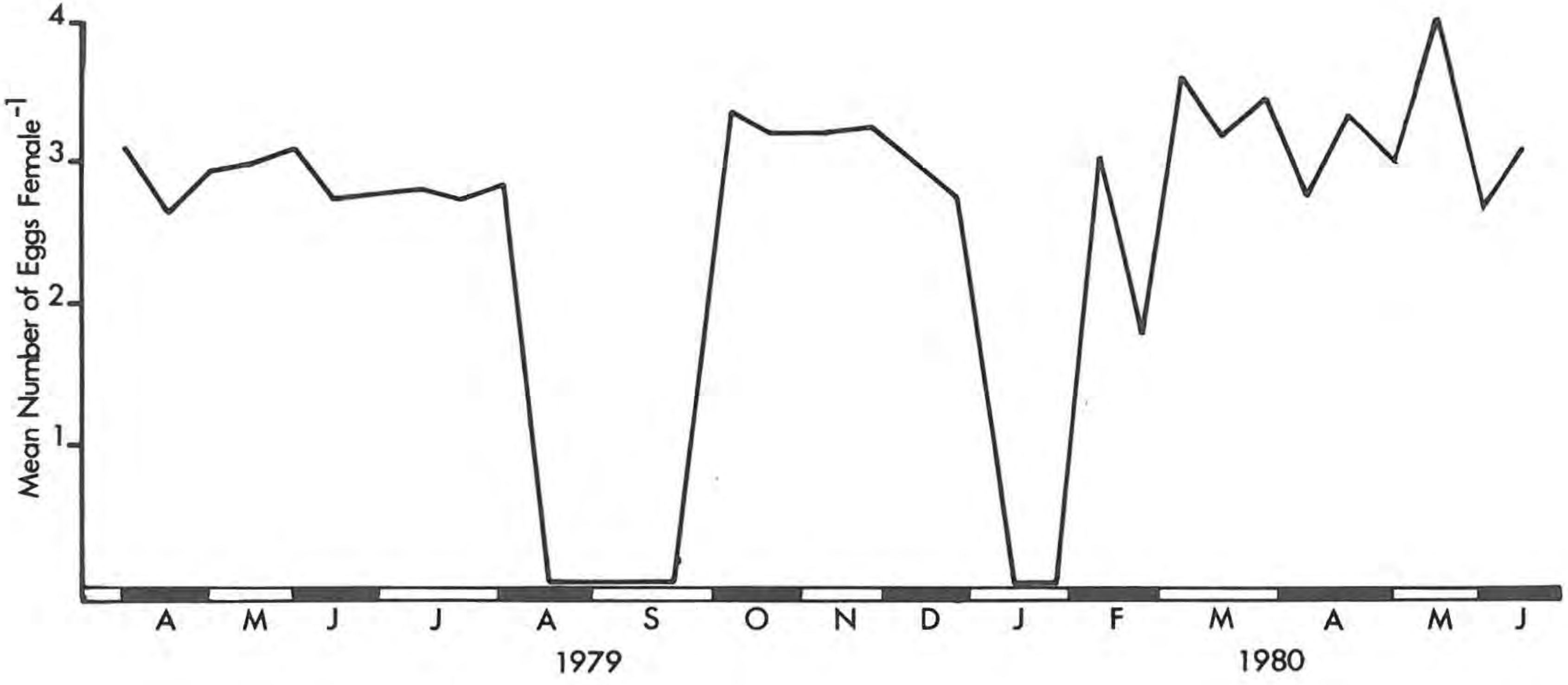
c.

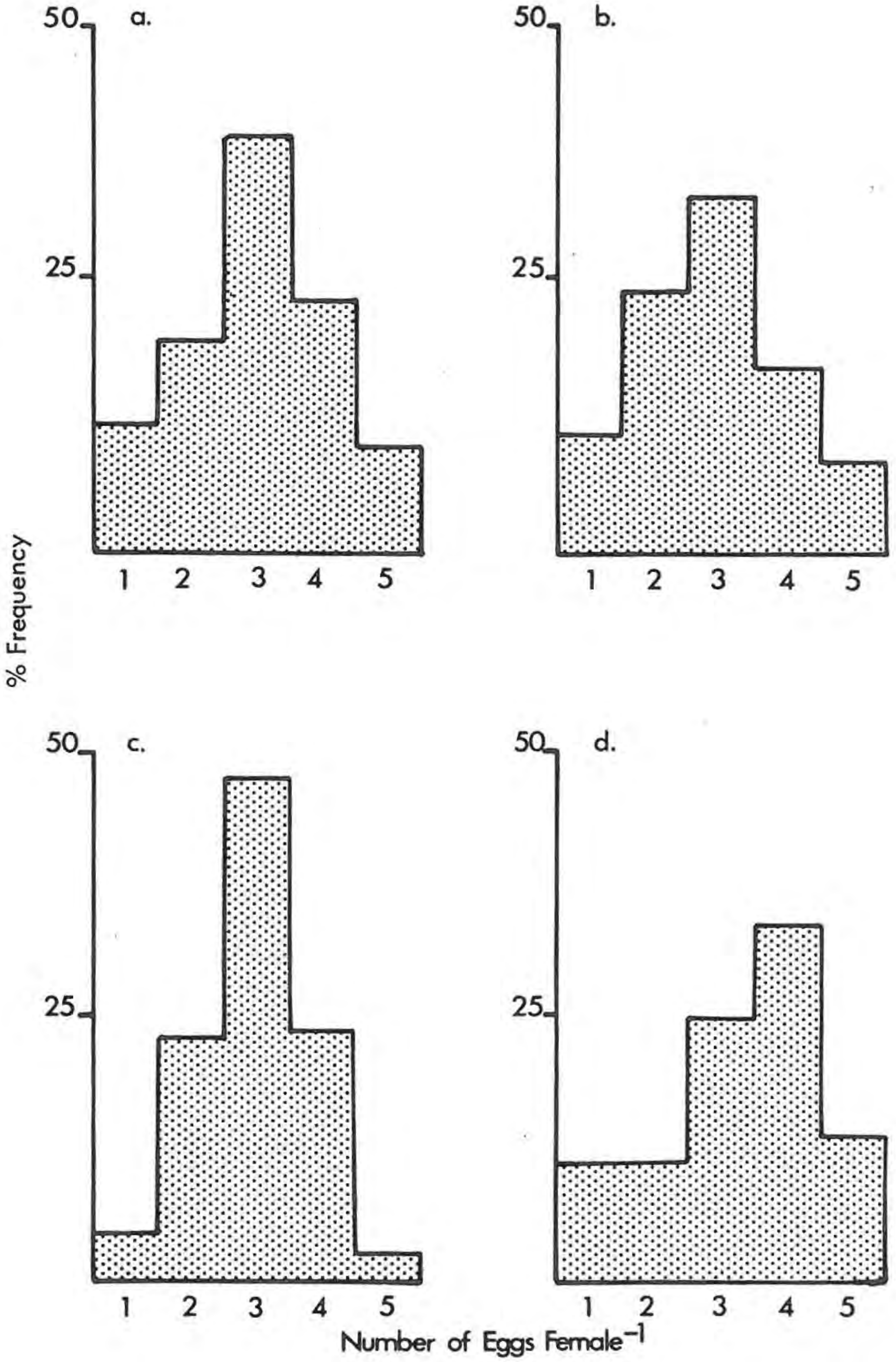

Previtellogenic Oocytes
Immature Oocytes
Maturing Oocyte
Germinal Epithelium
Vitelline Granules
0.02 mm

The gonad index was used to assess seasonal reproductive cycles. All dissected animals could be fitted into the gonad classification and there was no evidence of seasonal peaks in breeding (Fig. 29). This has already been discussed in Part 1. Reproductive females, carrying embryos, were found throughout the study, including the post-flood winter of 1979, when very few animals survived on the mud-flat.

The number of embryos per female varied from 1 - 5. In the pre-flood period the mean brood size was 2.89, with little variation about this mean. At the beginning and end of the post-flood period no reproductive females were collected, but in between, the brood size remained similar, with a mean of 2.92. In the post-flood period the variation was greater, and the mean brood size was 3.08. However, an analysis of variance showed that there was no significant difference in brood size between the three periods.

The percentage frequency of different brood sizes is shown in Fig. 30. Over the whole study, and in the pre-flood and post-flood periods, the modal brood size was 3, with an even distribution on either side. In the recovery period the modal brood size was 4, and the distribution was skewed towards 4 and 5.


Mean Number of Eggs Female^{-1}
4
3
2
1
A
M
J
J
A
S
O
N
D
J
F
M
A
M
J
1979
1980


% Frequency
50
25
a.
b.
c.
d.
1
2
3
4
5
Number of Eggs Female^{-1}

An interesting feature of the gonad index is that the correlation between size and a particular stage is more consistent in males than in females. For example, in males, Stage III included only 6 mm animals, whereas in females 7 & 8 mm animals were included. The index also enabled an analysis of the reproductive condition of the females in the pre-flood and recovery phases (Table 6). In the pre-flood phase 34% of all 7 mm females sampled were at Stage III and 66% had reached Stage IV, whereas in the recovery phase 70% of the 7 mm females sampled were at Stage III, and only 30% had reached Stage IV (full reproductive maturity). This seems to indicate that the 7 mm females sampled in the recovery phase were younger than those in the pre-flood population, and had not yet attained reproductive maturity. A simliar trend is evident in 8 mm females. In the pre-flood phase, 92% were at Stage IV and only 8% at Stage III, whereas in the recovery phase only 67% had reached Stage IV, and as many as 33% were still at Stage III. In both populations, all 9 mm animals were fully reproductively mature.

3.3.2 DEVELOPMENT

N. kraussianus is ovoviviparous, and carries up to 5 egg cases at one time within the uterus. Embryos hatch as advanced veligers, and not as benthic crawling juveniles.

SIZE CLASS	GONAD INDEX STAGE	%FEMALES FROM EACH SIZE CLASS IN EACH STAGE
PRE-FLOOD		
7	III	34
	IV	66
8	III	8
	IV	92
9	IV	100
RECOVERY		
7	III	70
	IV	30
8	III	33
	IV	67
9	IV	100

Table 6. In the pre-flood stage most of the adult females were sexually mature i.e. they could be classified as Stage IV for the gonad index. In the recovery phase few 7 mm females were sexually mature, and far fewer 8 mm females were sexually mature than in the pre-flood stage (67% as opposed to 92%). In both pre-flood and recovery phases all 9 mm females were mature.

However *in vitro* results have indicated that metamorphosis to a benthic juvenile occurs soon after hatching (Table 7).

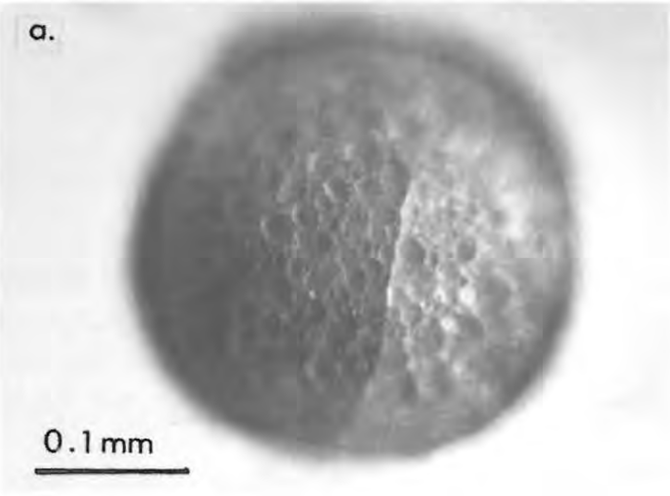
The development of *N. kraussianus* was investigated *in vitro* at 26°C ±2°C. Copulation and fertilisation were never observed; and as fertilisation is internal, an *in vitro* study of fertilisation could only have been attempted after extensive dissection. Egg cases were therefore removed from living females, and the fertilised eggs reared to metamorphosis. Each egg case was triangular in shape (Figs. 31 & 41), adhered to the uterus wall along the blunt apex of the triangle, and contained one spherical egg, bathed in a nutritive fluid (Fig. 31).

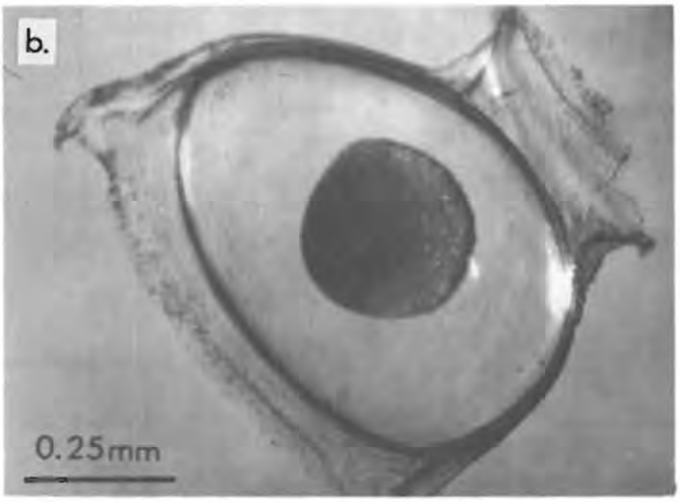
Although well over 300 eggs were removed from females, the earliest development stage observed was a 4-cell stage (Fig. 31). This was therefore taken as time zero, and all development times thereafter refer back to the starting point. Spiral cleavage was dextral, and the 8-cell stage was apparent 25 minutes later (Fig. 32). After one hour, the spherical blastula was composed of numerous large yolky megameres and smaller micromeres (Fig. 33). The blastula continued developing, and after 24 hours was pear shaped; megameres and micromeres were still distinguishable.

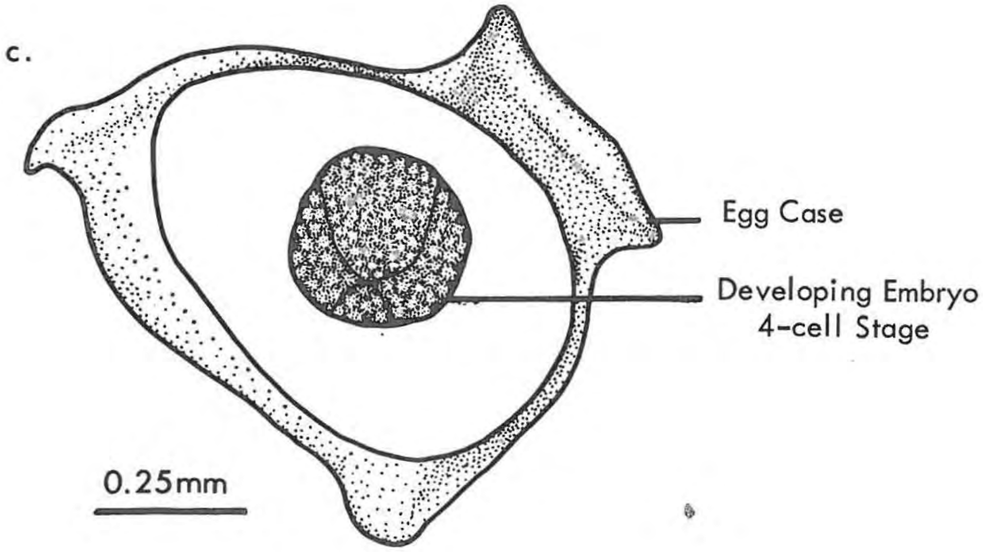
The onset of gastrulation was signified by an elongation of the embryo to an almost "dumbell" shape, 48-

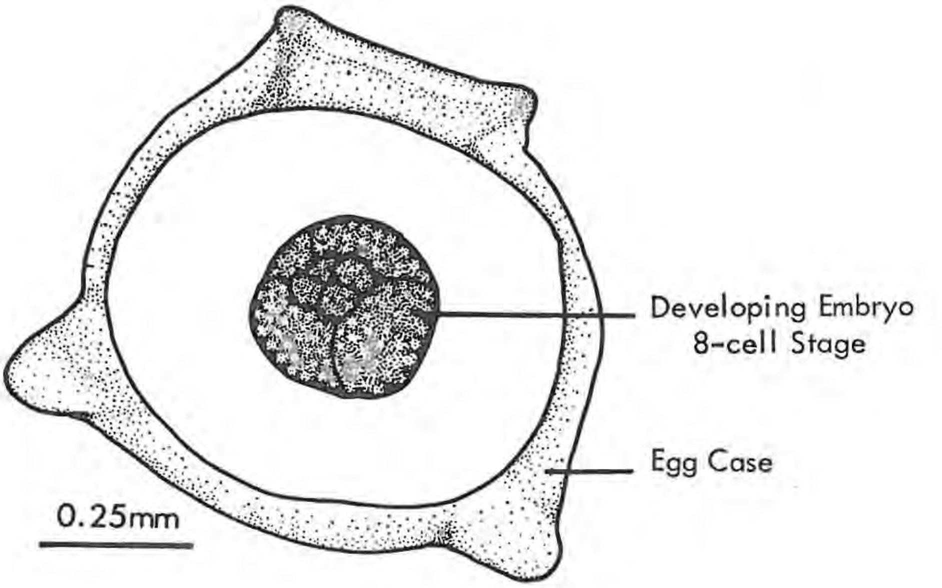
FIGURE	TIME FROM 4-CELL STAGE	STAGE OF DEVELOPMENT	EMBRYO OR SHELL LENGTH(um)	VELUM WIDTH (um)
Fig.31	0	4-cell	300	
Fig.32	25 minutes	8-cell	300	
Fig.33	1 hour	Spherical blastula	300	
	24-48 hours	Pear shaped blastula	350	
	48-72 hours	Gastrulation, embryo elongates, becomes "dumbell" shaped	400	
Fig.34	4 days	Velum ridge and foot rudiment appear		
Fig.35	5-6 days	Velum free and ciliated, mouth and anterior gut evident, larval heart beating, foot propodium develops, visceral mass curves over	425	
Fig.36	7 days	Shell formation begins	450	500
	8-9 days	Shell growth, and differentiation of the viscera	510	
	10-11 days	Shell growth	550	
Fig.37	12 days	Shell growth	600	820
Fig.38 Fig.39	13-18 days	Hatches as free swimming veliger	620	
	17-24 days	Settles and assumes a benthic mode of life	660	860
Fig.40	24-47 days	Metamorphosis complete	800	
	27-29 days	Crawling juvenile	900-1000	
	?	Juvenile with crenellated body whorl	1 mm	

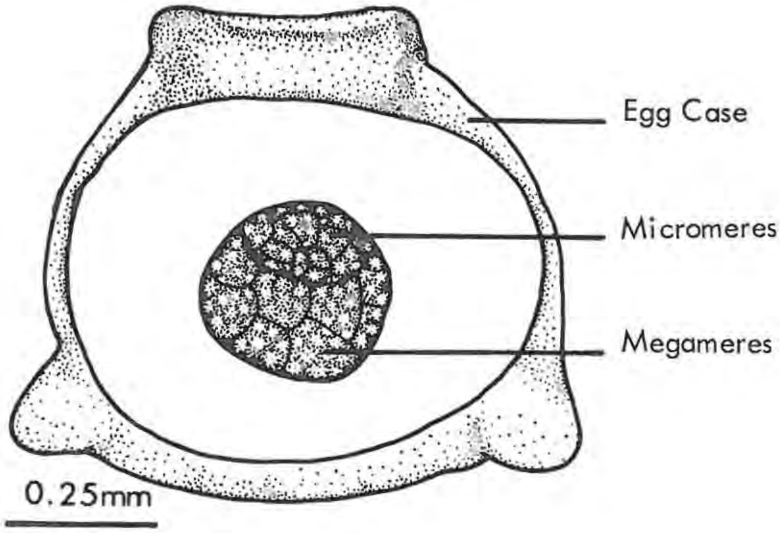
Table 7. A developmental timetable from the 4-cell stage to metamorphosis. Development was monitored *in vitro* at 26° C, ± 2° C, in February 1980.


a.
0.1 mm


b.
0.25mm

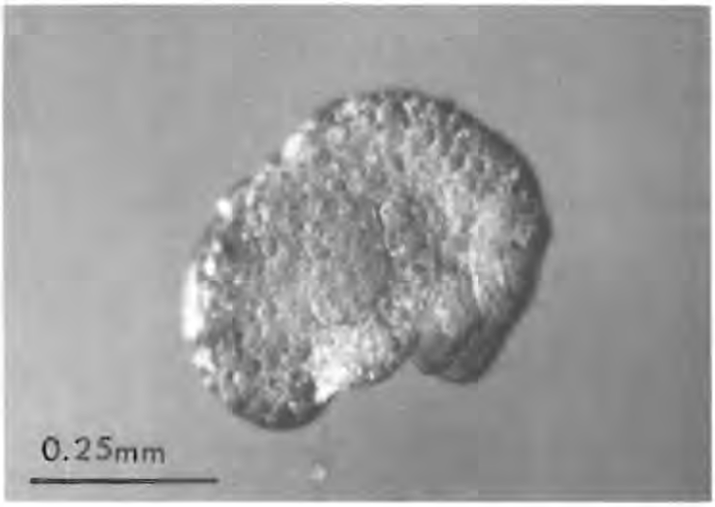

c.
Egg Case
Developing Embryo
4-cell Stage
0.25mm

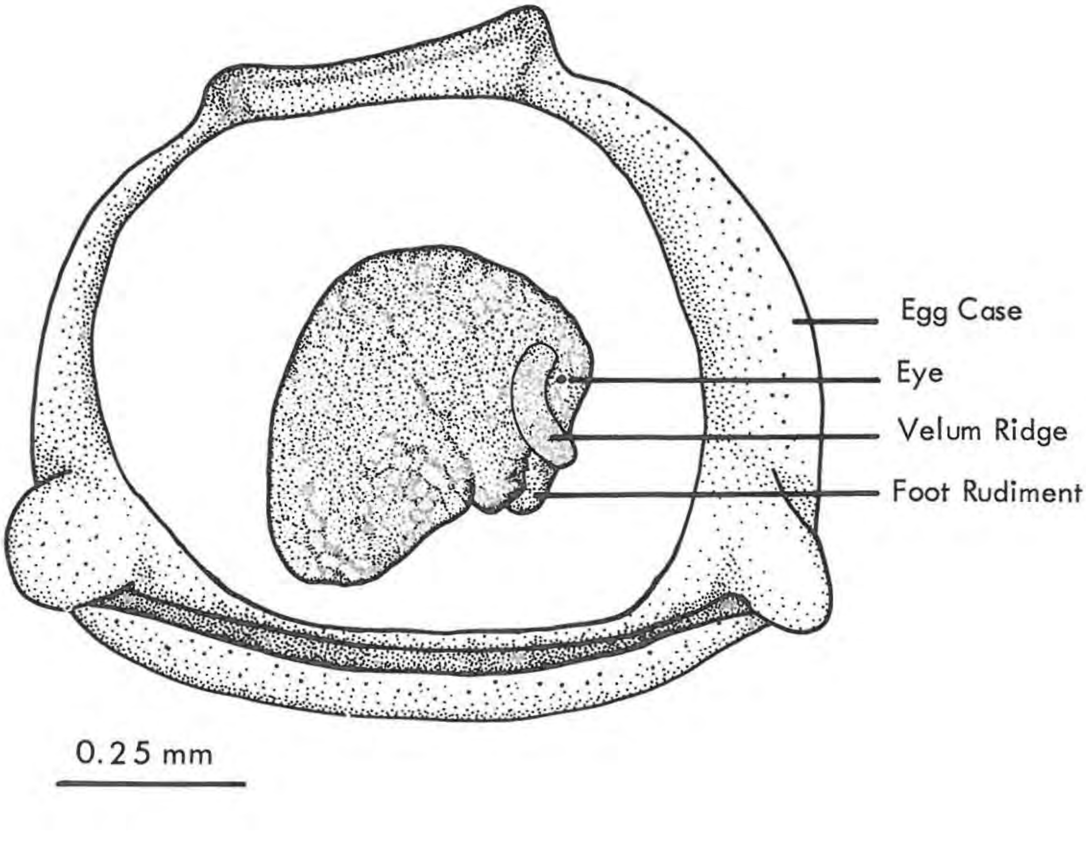

Developing Embryo
8-cell Stage
Egg Case
0.25mm

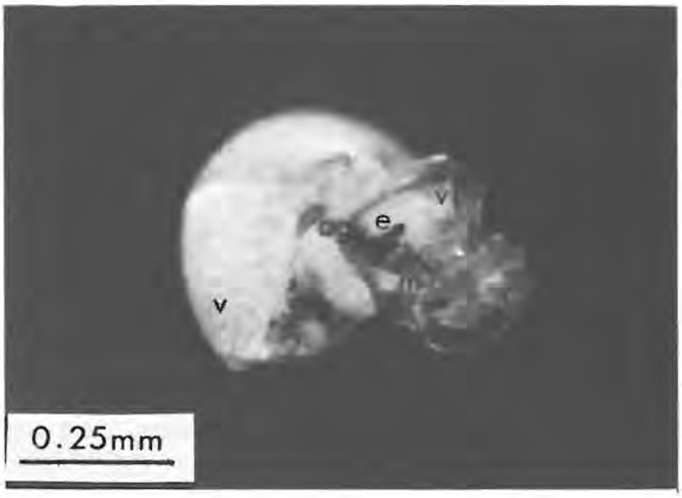

Egg Case
Micromeres
Megameres
0.25mm

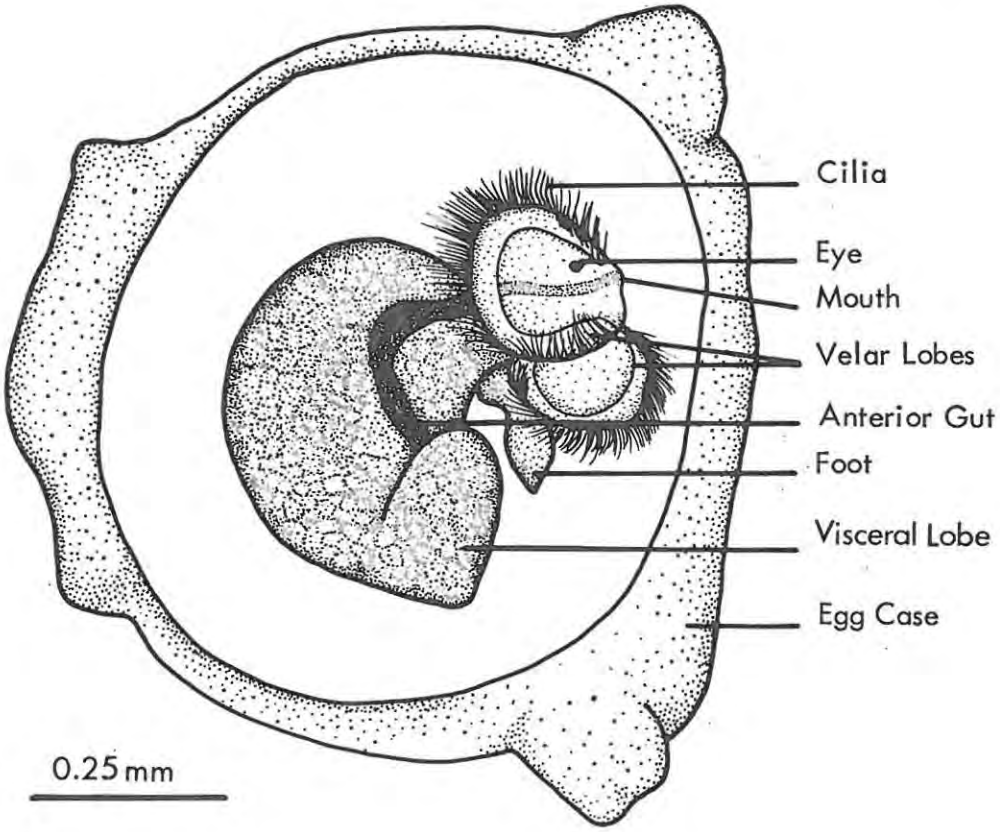
72 hours after the 4-cell stage (Fig.34). The first apparent features, characteristic of the "dumbell" stage, were the velum ridge and foot rudiment. The most rapid morphological change occurred during the subsequent 48 hours (5-6 days) (Table 7), as the embryo developed to the early veliger stage (Fig. 35). The ciliated velar lobes extended, and became free and mobile; the mouth appeared as an invagination between the velar lobes; and the larval heart beat was evident. At this stage the larva moved around for the first time, as undulations of the ciliated velum enabled it to rotate slowly within the egg case. The same stage (Fig. 35), was also characterised by further differentiation of the foot, which formed a heart-shaped, ciliated projection. In addition, the posterior end of the "dumbell" curved over, and comprised an undifferentiated visceral mass, or digestive lobe, with only the anterior gut apparent (Fig. 35).

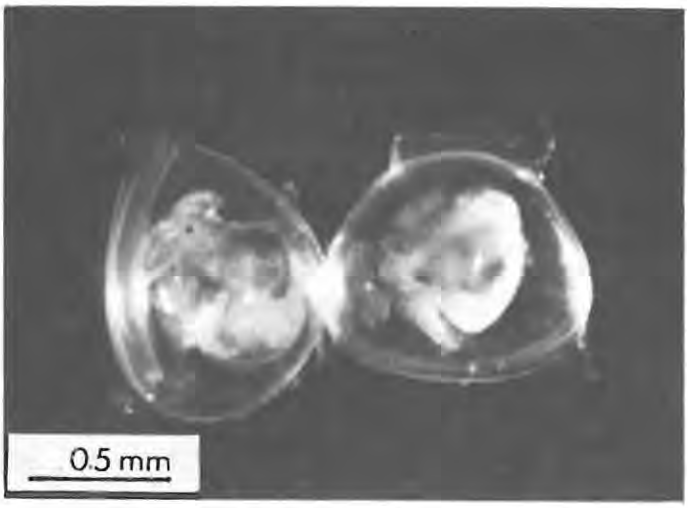
The next landmark in development was the onset of shell formation on day 7 (Fig. 36, Table 7), and once the shell completely covered the viscera, the larvae were termed advanced veligers (Fig. 37). By this stage the mobile velum was bordered by powerful cilia. These showed metachronal control, and enabled the veliger to rotate more rapidly within the egg case. Movement was limited to this rotation, and to retraction and extension of the velar lobes. When the veliger was stationary, the velum was withdrawn into


0.25mm

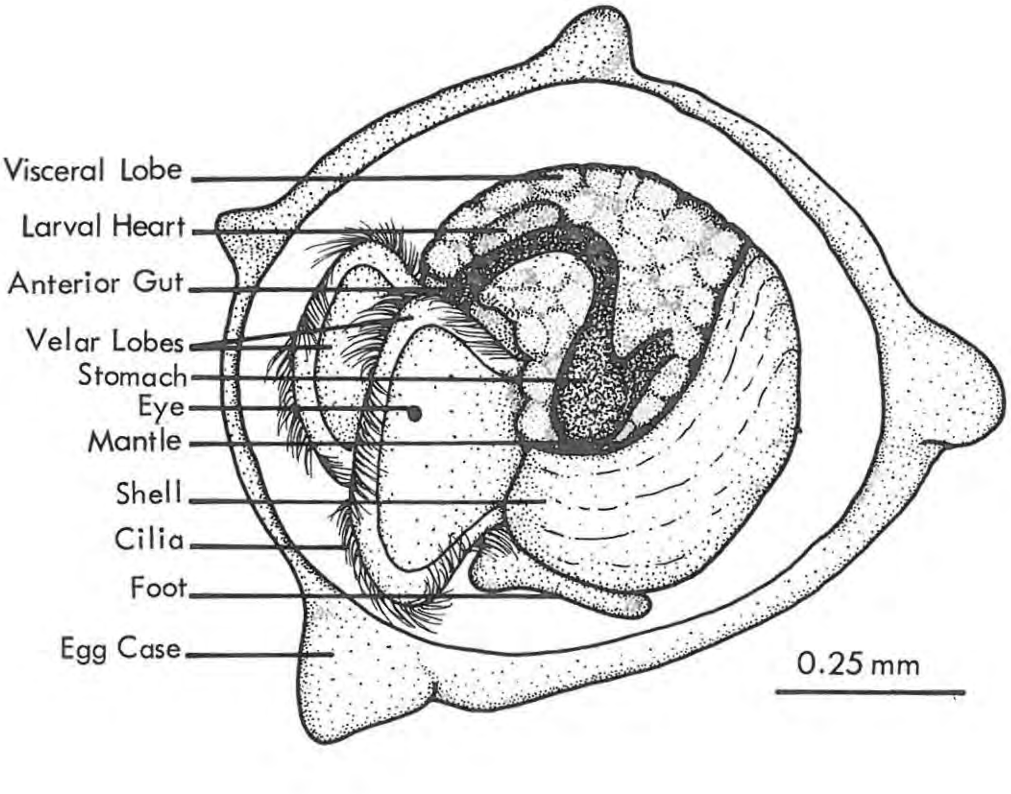

Egg Case
Eye
Velum Ridge
Foot Rudiment
0.25 mm


v
ag
e
v
0.25mm


Cilia
Eye
Mouth
Velar Lobes
Anterior Gut
Foot
Visceral Lobe
Egg Case
0.25mm

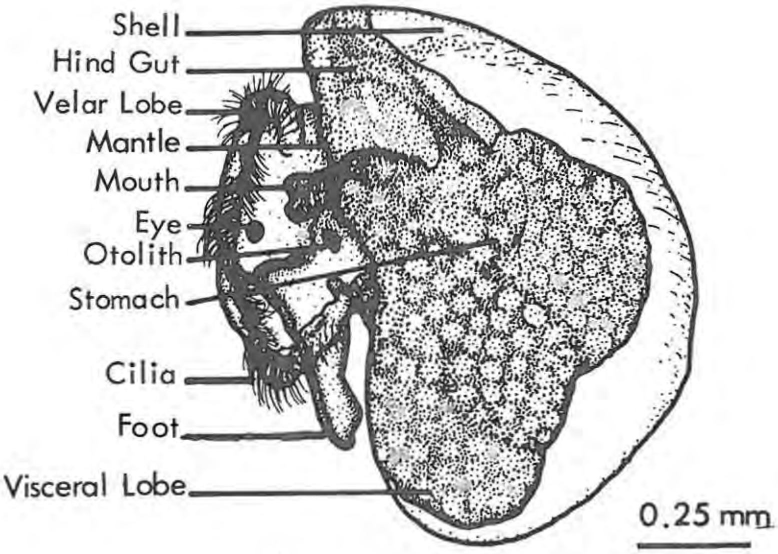


0.5 mm



Visceral Lobe
Larval Heart
Anterior Gut
Velar Lobes
Stomach
Eye
Mantle
Shell
Cilia
Foot
Egg Case
0.25 mm

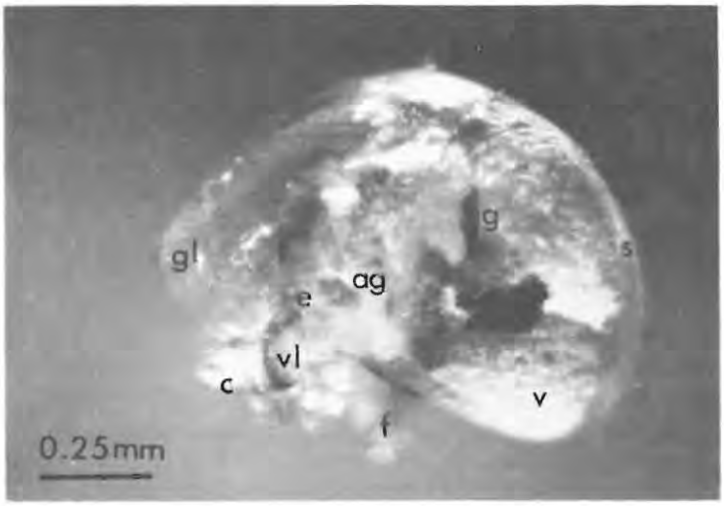

c
s
vl
0.25mm

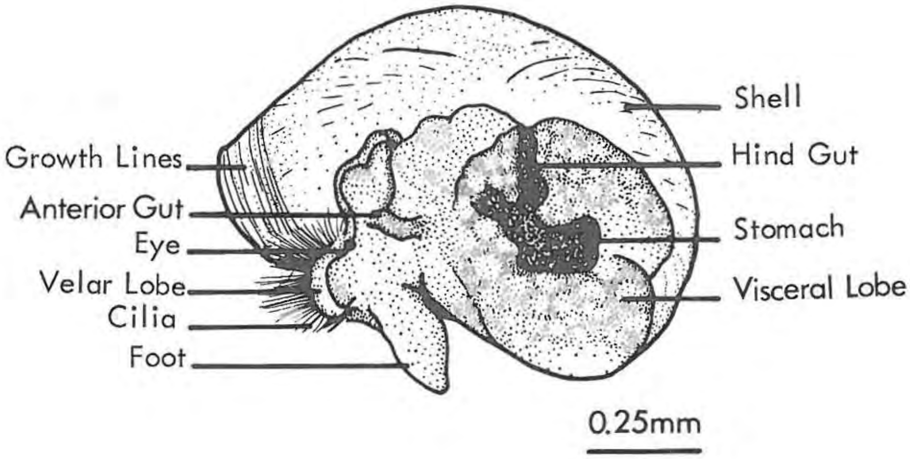

Shell
Hind Gut
Velar Lobe
Mantle
Mouth
Eye
Otolith
Stomach
Cilia
Foot
Visceral Lobe
0.25 mm

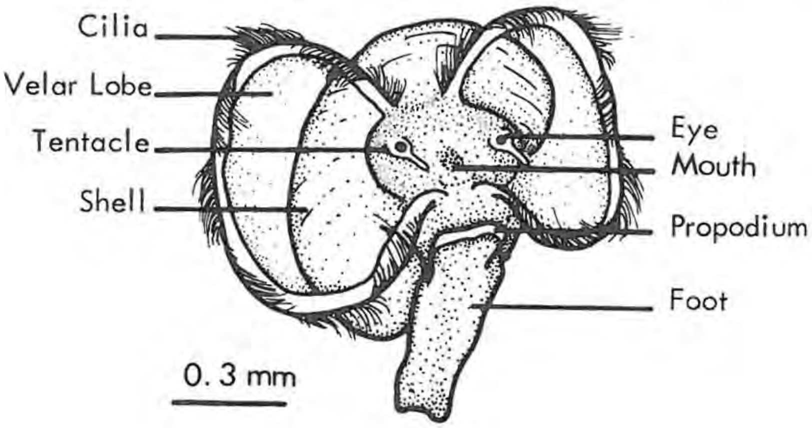
the shell. Just before hatching, movement was far more pronounced, and the foot, as well as the velum, was involved in locomotion. The foot was ciliated, with a prominent propodium, and was used to twist the veliger around within the egg case. Otoliths were clearly visible in the advanced veliger, and the digestive lobe had differentiated, so that the midgut and stomach were distinguishable (Fig. 37).

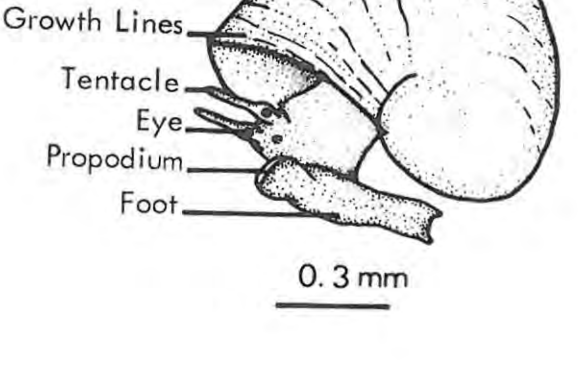
Hatching was never observed, but occurred between 13 and 18 days after the 4-cell stage (Table 7). Free-swimming veligers emerged, and were maintained in small excavated glass blocks, and fed on a culture of alga _Tetraselmis suecica_ (Kylin) Butcher. These veligers were capable of active swimming (Figs. 38 & 39), but remained on the bottom most of the time. Either the shell rested on the floor of the container and the velum was extended, with the cilia beating rapidly in the water column; or the veligers crawled round on the foot while "vaccuum-cleaning" the bottom with their velar cilia. In this way particulate matter was swept into a ciliated food groove around the edge of the velum, and then moved to the mouth. If disturbed while feeding in the water column, the veliger retracted into the shell and sank to the bottom (Fig. 38).

After 17 days, the veligers settled and assumed a benthic mode of life. Between 17 and 24 days, the velum was slowly resorbed until metamorphosis to an entirely benthic juvenile was complete (27 days)(Fig. 40).


g
gl
s
ag
e
vl
c
v
f
0.25mm


Shell
Growth Lines
Hind Gut
Anterior Gut
Stomach
Eye
Velar Lobe
Visceral Lobe
Cilia
Foot
0.25mm


Cilia
Velar Lobe
Tentacle
Shell
Eye
Mouth
Propodium
Foot
0. 3 mm


Shell
Growth Lines
Tentacle
Eye
Propodium
Foot
0. 3 mm

3.4 DISCUSSION

Thorson (1950) maintains that in order to understand the ecology of a species it is important to have a thorough knowledge of the most vulnerable stages of its life history; and in the case of benthic invertebrates these are the breeding and larval stages. In prosobranch molluscs, this has additional relevance because the larval stage, the veliger, is generally the stage during which dispersal occurs. Thorson (1950) defined three types of larval development:

1. pelagic development
   - i) planktotrophic (larvae have an extended planktonic existance and feed on phytoplankton),
   - ii) lecithotrophic (larvae have a short planktonic life and prior to entering the plankton, feed on the yolky egg for a considerable period),
2. direct development (larvae develop in egg capsules and emerge as fully developed juveniles), and
3. viviparous or ovoviviparous development

Pearse (1969) and Mileikovsky (1971) added a fourth type:

4. demersal development (larvae hatch as late veligers which have a short swimming-crawling existence near the substratum).

On the basis of numerous observations, Thorson (1950) formulated what came to be known as "Thorson's Rule", namely; that pelagic development is replaced by direct development along two gradients: from the equator to the poles; and from shallow shelf waters to abyssal waters.

The four strategies of larval development outlined above have several implications, the first of which is fecundity. Embryos that develop rapidly into planktonic larvae do not need a large egg with substantial food reserves, but are subject to high mortality, and are therefore produced in large numbers. Lecithotrophic development requires a higher energy input from the parent, as the egg is large and yolky. The larvae spend a shorter period as free swimming veligers in the plankton, and relatively fewer are spawned. Directly developing larvae derive all their nutrition from food within the egg case. Each egg requires a considerable energy input from the parent, which therefore has a low fecundity,but the developing embryos have a greater chance of survival as they are protected from the physico-chemical rigors and heavy predation of the pelagic environment.

The second important implication of life history strategy is dispersal. Pelagic larvae have the greatest potential for dispersal. This is enhanced by positive phototaxis in pelagic veligers which ensures that they remain in the surface waters and are transported in oceanic currents, circumventing the enormous barriers of abyssal depth which confine benthic organisms to restricted ranges (Thorson, 1950; Shuto, 1974). Yet, despite the advantages of efficient dispersal, such as an enhanced ability to exploit new environments and to recolonise depopulated areas, there is an evolutionary trend within the prosobranchs away from pelagic development (Shuto, 1974). The introductory comparison of the three prosobranch orders demonstrates this trend. The most primitive order, the archaeogastropods, generally have external fertilisation, high fecundity, pelagic planktotrophic larvae and a high dispersal potential. Mesogastropods are characterised by internal fertilisation and their eggs are laid in egg capsules. Their larvae may be lecithotrophic or planktotrophic, and direct development is not uncommon. N. kraussianus is a neogastropod, and this order will be dealt with in more detail.

Neogastropods exhibit the whole range of developmental strategies, from planktotrophic larvae to viviparity, and within the order there appears to be an evolutionary trend towards direct development (Radwin & Chamberlin, 1973). Of the 14 neogastropod families (Radwin & Chamberlin, 1973), only 4 have several species with direct development; the Muricidae, Volutidae, Columbellidae and Nassariidae; whereas in the other families, non-pelagic development is more common (Radwin & Chamberlin, 1973). These data should be viewed with care, because not all neogastropods have been investigated, and authors seldom have access to all the known information. For example Radwin & Chamberlin (1973) have recorded 14 pelagic species within the Nassariidae, and 5 non-pelagic species. I was only able to confirm 9 pelagic species from the literature, but found 13 non-pelagic species (Table 8). Nevertheless, there does seem to be a recurrent trend within the prosobranchs, as a group, towards non-pelagic development, and the evidence is worth pursueing in the present discussion.

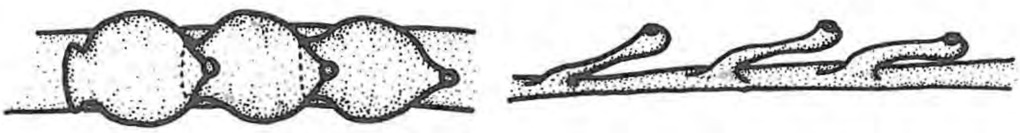
The Nassariidae belong to the most advanced neogastropod superfamily, the Buccinacea, which appears to comprise an approximately equal number of species with pelagic and non-pelagic development (Table 8). There seems to be an evolutionary relationship between capsule morphology, and development type, as has already been demonstrated in the Columbellidae (Bandel, 1974). Firstly there are species which produce tough vase- or flask-shaped egg capsules, usually with more than 30 eggs which hatch as pelagic, planktotrophic veligers (Fig. 41). Morphologically the vase shapes differ somewhat, from the spiny multi-faceted capsule of _N. obsoletus_ (Scheltema, 1962), to the four-sided vase of _Nassarius tiarula_ Kiener (Houston, 1978) and flattened vase of _N. reticulatus_ (Lebour, 1931) (Fig.41). A second major group of species has triangular egg capsules containing one egg which undergoes demersal, direct or ovoviviparous development (Fig. 41). Intermediate

NASSARIIDAE	EGG CAPSULE SHAPE	NUMBER OF EGGS PER CAPSULE	TYPE OF DEVELOPMENT	SOURCE
	Vase shaped		Pelagic	
Nassarius obseletus	multi-faceted,spiny	40-150	planktotrophic	Scheltema (1962, 1964a)
N. trivittatus	"	42-150	"	Scheltema (1964b)
N. tiarula	4-sided	50	"	Houston (1978)
N. jacksoniana	"	25-72	"	Natarajan (1957)
N. pygmaeus	flattened pouch	60-145	"	Vestergaard (1935) & Christiansen (1964)
N. vibex	"	12-30	"	Scheltema (1962)
N. incrassatus	"	50-100	"	Le Bour (1931)
N. reticulatus	"	100	"	Le Bour (1931)
Tritia festivus	"	40	"	Amio (1956)
T. acutidentata	"	2-4	Non-pelagic	Amio (1959)
T. dermestina	"	3-5	direct	Amio (1959)
	Triangular			
Nassarius costata	"	1	demersal	Natarajan (1957)
N. thersites	"	1	"	Natarajan (1957)
N. dorsata	"	1	"	Kasinathan *et al* (1974)
N. livescens	"	1	"	Amio (1956)
N. suturalis	"	1	"	Risbec (1932)
N. particeps	"	1	"	Anderson (1966)
N. kraussianus	"	1	Ovoviviparous	This study
N. albus	No capsule	1-5	"	Kaicher (1972)
N. muelleri	"	7-14	"	Knudsen (1956)
N. plicatellus	"	±50	"	Kilburn *pers. comm.*
Bullia digitalis	2 X 1.2 cm	1500-2000	direct	Brown (1971)
B. rhodostoma	"	1500-2000	"	Brown (1971)
B. tenuis	?	1	?	Brown (1971)

Table 8. A summary of the patterns of development in the family Nassariidae.

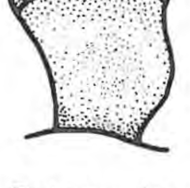
1. Multifaceted-spiny vase
Nassarius obsoletus
Scheltema, 1962

2. Four-sided vase
Nassarius tiarula
Houston, 1978



3. Flattened vase
Nassarius reticulatus
Lebour, 1931

4. Lens-shaped
Tritia festivus
Amio, 1956



5. Triangular
Nassarius costata
Natarajan, 1957

6. Triangular
Nassarius kraussianus
This study

between these two major groups are the three Tritia species described by Amio (1956; 1959). There, the egg cases were described as "lens" shaped, but these are in fact similar to the flattened vase type of N. reticulatus (Lebour, 1931) (Fig. 41). Tritia festivus (Powys) falls within the "pelagic" group (Table 8) on the basis of the number of eggs per capsule (40) and the type of development (pelagic). Tritia acutidentata (Smith) and Tritia dermestina (Gould) also have lens shaped capsules, but these contain a low number of eggs, and development is non-pelagic. In this regard, they are similar to the group with triangular egg cases (Table 8). There are also two species recorded in the literature as ovoviviparous: Nassarius albus Say (Kaicher, 1972; Cather, 1973), and Nassarius muelleri Von Maltzan (Knudsen, 1956). Both had embryos within the uterus, but no egg cases were present. Ovoviviparity has been recorded in one South African species, Nassarius plicatellus (A. Adams), from the Atlantic coast, which broods 10-12 young in the oviduct, releasing them either as late veligers, or at an early crawling stage (R.N.Kilburn, pers.comm.). Therefore, in a way similar to the Tritia species, N. kraussianus seems to occupy an intermediate position (Table 7). It has a triangular egg case, containing one embryo, and is also ovoviviparous; holding up to 5 egg cases within the uterus until the embryos hatch. N. kraussianus thus resembles both those species with a triangular egg case, and the ovoviviparous species which do not have an egg case.

Exceptions to the trend exhibited by the Nassariidae (Table 8) are three South African *Bullia* species. They have egg cases of "different" but unspecified shape, containing many eggs which undergo direct development (Brown, 1971).

As stated earlier, the dispersive advantage of pelagic development is obvious. Why then the trend to non-pelagic development? Radwin & Chamberlin (1973) and Shuto (1974) have suggested that certain neogastropods have become specialised, and specifically adapted to particular environments. If the adult of a species is highly specialised, then it would be advantageous for the larvae to settle in the parental habitat, and thus low fecundity, high larval survival and low dispersive ability would be advantageous. At this point, if the foregoing is correct, two important questions arise:

1. How is *N. kraussianus* specialised, and particularly adapted to its environment?
2. If non-pelagic development is such an advantage, how was the marsh so efficiently recolonised during the recovery phase?

The first question will be answered in the final section, when observations on the feeding biology of *N. kraussianus* are described. The second question is difficult, but there are at least two reasonable possibilities. The first is, that although the free swimming stage is short, it does exist (4-11 days), and the dispersal involved is not trans-oceanic, as it is in those species which produce pelagic larvae. Other estuarine and intertidal populations, such as the population near the mouth of the Kowie River, 25 km east of the Bushmans River, could have produced larvae that recolonised the study area. The larvae could have been transported by tidal exchange and shallow coastal currents. In addition, the possibility of post larval dispersal must not be ignored. In the laboratory, small juveniles (1-3 mm) readily float foot upwards, at the water surface. Larger animals also float, though more rarely. The floating behaviour of Hybrobia ulvae Pennant, a prosobranch which also occupies an intertidal habitat, is well documented (Newell, 1962; Anderson, 1971; Chatfield, 1972; Little & Nix, 1976), and has been cited as an efficient method of dispersal. In an earlier discussion of the population structure of the recovery phase (Fig. 17), it was noted that 2, 3 & 4 mm juveniles dominated the recovery cohort, and that 1 mm juveniles were only collected after the recovery cohort had grown to adult size. It is possible that recolonisation was primarily effected by the post larval juveniles floating upside down at the surface water film. These juveniles could conceivably have been carried from areas like the Kowie River estuary to the Bushmans River estuary by coastal currents and tidal exchange.

Thus, the efficiency of dispersal primarily depends on the larval type. The ability of benthic species to disperse geographically is quite different in the larval and post larval stages, as dispersal after settling is restricted by poor locomotory ability (Shuto, 1974). Thus, non-pelagic larvae have a greater chance of settling in the parental habitat, than pelagic larvae.

This concept leads back to Thorson's Rule. Although the "rule" that non-pelagic development occurs at the poles and in abyssal waters may be generally true, many exceptions have been recorded (Mileikovsky, 1971), and it would probably be better formulated in more general terms: that non-pelagic development is of advantage in extreme environments. Prosobranchs that inhabit extreme environments are probably, of necessity, specialised, and thus the larvae have the double advantage of parental protection from physical extremes during the most vulnerable period of their life history; and the possibility of settling in their parental habitat. In this context, R.N. Kilburn's (pers.comm.) statement is of value; "it was not surprising to learn that N. kraussianus was ovoviviparous, in view of the extreme conditions under which it thrives."

Estuaries are environments subject to physical extremes, as demonstrated by the severe floods during the present study, and the ovoviviparous development of N. kraussianus may be regarded as an adaptation to this environment, particularly, as Lockwood (1976) has pointed out, that one of the most important adaptations of estuarine organisms is a larval development pattern that enables retention within the estuary, rather than loss to the open ocean during tidal exchange.

The juveniles which colonised the mud-flat in January 1980 had grown to adult size three months later. However in June of the same year, the proportion of sexually mature females were still lower than that recorded during the pre-flood phase, but the 9 mm females of the recovery population were reproductively mature at all times. Once sexual maturity was attained, females reproduced continually. Although most prosobranchs seem to have seasonal reproductive peaks, there are species like N. kraussianus which reproduce all year round. These include two Hawaiian species of Littorina (Struhsaker, 1966) and N. trivittatus (Pechenik, 1978).

Finally, the life history data enable an estimate of population fecundity. In the laboratory it took a maximum of 18 days for the embryo to develop from the 4-cell stage to hatching (at 26°C ±2°C). If a three week cycle from fertilisation to hatching is postulated, and each female has an average of three embryos per brood, each female would produce 52 juveniles per year. This would probably be considerably lower at lower winter temperatures. In the pre-flood (summer) population there was an average of 109 reproductive females m^{-2} and thus a calculated fecundity of 5668 veligers hatching $m^{-2}year^{-1}$. In the recovery phase, the number of reproductive females m^{-2} was lower (33 m^{-2}), but the sex ratio was biased towards females, enhancing the reproductive potential of the population once the females reached reproductive maturity.

Although the study of reproduction and development has enabled a greater understanding of the population structure, many questions remain unanswered, and one is of particular interest:

> Why were so few juveniles found in the pre-flood population, when the large population of adult females was fully reproductive and the potential fecundity was so high?

Although this study has provided no factual answer, the question has provoked speculation in the final section of this report.

PART 4. ADAPTATIONS TO AN ESTUARINE ENVIRONMENT

One of the characteristics of estuaries is the importance of the detrital food web. Radwin & Chamberlin (1973) have suggested that neogastropods usually occupy high trophic levels in the food web, are seldom food limited, and therefore produce non-pelagic larvae with a high probability of remaining within the parental habitat. Food availability and feeding biology may affect the population biology and life cycles of organisms (Fish, 1972; Fish & Fish, 1974). Therefore, the feeding biology of *N. kraussianus* is probably very important in the present context. This aspect was not investigated, but as there were no other sources of information on *N. kraussianus*, it is worth describing some of the simple field and laboratory observations on feeding, and relating these to the pertinent literature.

N. kraussinaus belongs to the same family as the sandy beach scavenger *Bullia* spp., and like *Bullia* it has a well developed osphradium. Brown & Noble (1960) investigated *B. rhodostoma*, and showed that the osphradium was a chemosensory organ. *N. kraussianus* shows an acute chemosensory response and is rapidly attracted to decaying carrion. In the field large numbers were found congregated on dead fish, mud prawns, and on one snake carcass. In the laboratory, snails emerged from the sandy substratum and quickly converged on any introduced protein source. However, it seems unlikely that the high densities found on the mudflat could be supported entirely by carrion; especially as the habitat abounds in alternative, and more accessible food sources such as detritus.

One of the more interesting *Nassarius* species is the North American mud-snail *N. obseletus*. Its mode of life and morphological adaptations appear to be very similar to *N. kraussianus*. It occurs abundantly on intertidal mudflats and is primarily a deposit feeder, deriving most of its nutrition from the abundant microflora in the sediment (Scheltema, 1964a). In the field, *N. obseletus* was also found aggregated around carrion (Scheltema, 1964a). Recently Curtis & Hurd (1979) have shown that *N. obseletus* is an obligate omnivore, requiring both animal and plant food in its diet for growth and development.

Brown (1969) investigated the feeding of *N. obseletus* on the basis of functional morphology because of the unusual deposit feeding habit of the snail. Like *N. kraussianus*, *N. obseletus* is a member of the typically carnivorous rhachiglossan Gastropoda. Brown (1969) found that despite its deposit feeding habit, *N. obseletus* had most of the structural adaptations associated with a carnivorous mode of life:

1. development of the rhachiglossan radula, with three sharp cusped teeth per row, well adapted to tearing animal tissue;
2. size increase and elaboration of the proboscis which allows penetration of the feeding apparatus deep into animal tissue;
3. extension of the mantle into a long, movable siphon which allows a control of water flow into the mantle cavity;
4. a well developed osphradium over which inhalent water flows;
5. development of a valve in the oesophagus, the Gland of Leiblein, which allows protrusion and elongation of the proboscis without regurgitation of food;
6. conversion to extra cellular digestion;
7. specialisation of glands to produce extra-cellular enzymes, and
8. simplification of the stomach into a sac where enzymes and food are mixed and digestion occurs.

N. kraussianus has at least the first five of these adaptations, but like *N. obseletus* is not a carnivore at all. In the laboratory *N. kraussianus* grazes *Ulva* spp., *Chlorella* spp., and *Zostera capensis*, and has survived for up to 2 months without access to carrion. *Ulva* spp., *Chlorella* spp., filamentous algae and diatoms were found in the gut. *N. kraussianus* also displays deposit feeding behaviour. The hindgut of both laboratory and freshly collected animals was often packed with sand grains. Snails kept in clear water for several days also reingested faeces, suggesting that microflora may be another possible food source (Newell, 1965).

N. kraussianus appears to be a generalist feeder with a broad trophic niche. It is thus extremely well adapted to exploit the abundant detrital reserves on an estuarine mudflat. In addition to grazing and deposit feeding it can also take advantage of high energy food in the form of carrion and is able to locate this more limited food source very efficiently. This feeding strategy explains, in some measure, the way in which *N. kraussianus* is particularly well adapted to its environment, and indicates that it is unlikely to be food limited.

Ouite obviously, the feeding biology of *N. kraussianus* needs detailed investigation, but information in the preceeding discussion may provide an insight into the enigma outlined at the end of Part 3. That is, the surprising scarcity of juveniles in the pre-flood population comprising many reproductive females.

Of the food available to *N. kraussianus*, carrion was the least abundant. Curtis & Hurd (1979) have shown that *N. obseletus* (whose similarity to *N. kraussianus*) has been discussed), needs both vegetation and carrion to grow and reproduce successfully. The mean pre-flood population density of N. kraussianus was 324 m^{-2}, and possibly represented the maximum carrying capacity. Branch (1975), in a study of the intraspecific competition in Patella cochlear, noted that competition "reaches its highest intensity in intraspecific relationships where the requirements of individuals may be identical". N. kraussianus adults are behaviourally aggressive when feeding on carrion. Individuals physically dislodge one another, or cause one another to recoil from the food source by probing adjacent feet with the rasping proboscis. Perhaps it is adult-juvenile competition, and thus competitive exclusion of juveniles, which accounts for the low number of juveniles collected in pre-flood samples.

A second possibility is that population turnover was rapid, and that adult mortality enabled immediate replacement of dead adults with growing juveniles. This undoubtedly occurred to some extent, although the quantitative rates are unknown. Possibly both population turnover and competition contributed to the pre-flood population structure.

For the purpose of this discussion, I shall return to the concept of competitive exclusion of juveniles. It has been suggested that the ovoviviparity of N. kraussianus is advantageous because juveniles would probably settle in the adult habitat, a habitat to which the adult is particularly well adapted. Thus N. kraussianus embryos enjoy the protection of parental care until they hatch as weakly swimming veligers which settle rapidly. These juveniles settle in an environment where detritus and aquatic vegetation are abundant and they probably thrive. But suppose that at a certain stage they require high energy food, such as carrion, for further growth and development to sexual maturity. At this stage they may have to compete with adults. If these juveniles have grown to 1, 2 or 3 mm they are far less vulnerable than the free swimming veliger, and might be under pressure to emigrate from the parental habitat. These post larval juveniles would then become the primary recolonising agents. This could explain the influx of 2 and 3 mm animals from other areas during the recolonising phase. Recolonisation was delayed until January 1980, possibly because the substratum and habitat were not suitable before this, due to the blanketing silt layers and lack of Z. capensis cover.

Once the habitat was suitable for recolonisation, incoming juveniles did not have to contend with adult competition, and rapidly grew to adult size. Subsequently, juveniles were produced on the mudflat and 1 mm animals were collected during routine sampling. I predict, that as more animals reach reproductive maturity and the population of sexually mature adults reaches carrying capacity, that adult/juvenile competition will result in the stabilisation of the population, and that the population structure will return to the pre-flood pattern.

What, then, was the over all pattern of recolonisation? In July and August 1979 severe floods annihilated most of the N. kraussianus population, and rendered the environment nearly uninhabitable. For five and a half months only the few survivors remained in the area, but during this time environmental recovery; notably Z. capensis regeneration, was evident. In January 1980, the mudflat was recolonised by small juveniles, possibly from neighbouring estuaries. But are these observations sufficient to propose recolonisation as a major adaptation to estuarine conditions? Perhaps not in isolation, but there is some additional evidence in the literature.

Boltt (1975) first reported this sort of phenomenon. In January 1972, benthic populations of the St. Lucia, a coastal lake system, were drastically reduced by excessively high salinities, but by July of the same year, certain species had completely recovered. The species that recovered so dramatically were certain small polychaetes and the prosobranch gastropod Assiminia bifasciata (Nevill). These species were characterised by:

1. several consecutive spawning periods, and thus continuous reproduction throughout the year;

2. a short development time, and
3. large numbers of planktonic larvae

North and South Lakes are part of the large St.Lucia system. Salinities in South Lake were less extreme, and populations there, produced enough planktonic larvae to recolonise North Lake. Interestingly, the amphipod _Grandidierella lignorum_, which was abundant in North Lake before the high salinities, was not very successful at recolonising the area. This amphipod had a low fecundity, 6.5 eggs per female, and few of the larvae entered the plankton at all. Those that did, were planktonic for only a short time (Boltt, 1975). Thus, those animals with life cycles that included an efficient dispersal stage were more successful at recolonisation.

In St. Lucia, the larvae were the primary recolonising agents, and indeed planktonic larvae are an ideal dispersal stage, as they can be transported over vast distances by water currents. However, in an estuarine environment, it would be advantageous if dispersal could be effected by a post-larval stage, because larvae are usually physiologically more sensitive. Forbes (1973b) recorded a population of _Callianassa kraussi_ in the upper reaches of the Keurbooms River estuary at salinities below $5^{o}/oo$ NaCl. The females in the population were unable to reproduce, and the population was maintained entirely by recolonising post-larval juveniles which were spawned by down stream populations.

Recolonisation, then, seems to be an important adaptation to an estuarine existence; an existence to which *N. kraussianus* is extremely well fitted. It is probably a generalist feeder, and able to exploit both abundant detrital material, and high energy carrion. It has a remarkable life history. Eggs and early larvae are protected from environmental extremes and the danger of being swept out to sea, by the strategy of ovoviviparity. This non-pelagic development pattern also increases the probability of the short-lived, free swimming veligers settling in the parental habitat. In addition, both the brief larval stage, and the post-larval juvenile stage, are opportunities for dispersal, although of the two, the post-larval juveniles are probably more important in the context of recolonisation.

To conclude, estuarine organisms must have a wide range of adaptations; behavioural, physiological and biochemical, in order to cope with both the wide range of environmental extremes they encounter, and the rapid and irregular variation of these conditions. I suggest, that recolonisation, and life history strategy should be considered among the more important of these adaptations, and with Lockwood (1976) would like to misquote Pearse (1939)*, and reiterate "that 'heredity offered the means, and environment provided the necessity' for the plasticity of response that is the hallmark of an estuarine organism."

---

* "Heredity gave the ability and environment provided the opportunity" (Pearse, 1939).

SUMMARY

1. The development of estuarine research in South Africa has been reviewed, and the present state of knowledge assessed. Little is known about many abundant estuarine species, and a previously unstudied prosobranch *Nassarius kraussianus* (Dunker), was selected for investigation.

2. The study area, a mudflat on the Bushmans River estuary, was divided into three habitat types: supratidal, intertidal and subtidal, each with a particular substratum and pattern of vegetation cover. The distribution of *N. kraussianus* is associated with the nature of the substratum and the degree of *Zostera capensis* Setchell cover.

3. A brief review of pertinent literature indicated the necessity of relating population parameters to environmental conditions.

4. The population biology of *N. kraussianus* was investigated, and the size frequencies, sex ratios, and male/female size frequencies were recorded over three distinct periods: pre-flood, post-flood and recovery.

5. The Bushmans River flooded in July and August 1979, and the results of the flood have been described. The most immediate result was a period of low salinity, but the most persistant result was the deposition of silt, which had an important effect on the substratum and the *Z. capensis* beds.

6. The pre-flood population was characterised by patchy distribution, and by a large number of mature adults in relation to juveniles. Females were generally larger than males, and the sex ratio was 1:1. The presence of juveniles in consistantly low numbers indicated that reproduction may have been continuous, but that intraspecific adult/juvenile competition may have kept juvenile numbers low.

7. The post-flood period was characterised by extreme physical conditions, and the survival of a few adults. Juveniles were completely annihilated, and were absent until a few were spawned by the surviving adults towards the end of 1979 . Sex ratio was biased, and females predominated.

8. The recovery period began abruptly with the arrival of a large number of juveniles in the 2, 3 and 4 mm size classes. Recolonisation coincided with habitat recovery, and regeneration of the *Z. capensis* cover. Recolonising

juveniles grew quickly, reaching adult size in three months. After that, juveniles were spawned on the mudflat by the new population. During this period the sex ratio did not return to the pre-flood 1:1, but remained female biased. Males and females grew at the same rate over the period measured, but females were consistantly larger, indicating that at some stage female growth may be faster.

9. The recolonising juveniles arrived in a regenerated habitat, at a time when temperatures were high, and conditions for growth probably optimal. If intraspecific competition was a feature of the pre-flood population it would have been elimianted in the recovery phase, by the absence of adults.

10. N. kraussianus is apparently omnivorous and proabably not food limited. However, carrion, a limited resource, may be essential for growth to reproductive maturity. Adults and juveniles may compete for this resource, and any juveniles deprived of access to carrion may be stimulated to leave the parental habitat.

11. N. kraussianus is ovoviviparous, and carries up to 5 egg cases within the uterus. Each triangular egg case contains 1 egg which hatches after approximately 3 weeks, as a free swimming veliger. Veligers metamorphose, and settle after 4-7 days, assuming a benthic mode of life. Ovoviviparity

protects the developing embryo from the rigours of environmental extremes, and ensures that embryos are not swept out to sea. Additionally, veligers have a high probability of settling in the parental habitat.

12. This reproductive strategy has been compared with other prosobranchs, and the evolutionary trends within the Prosobranchia, and particularly the Nassariidae, have been related to their dispersal potential.

13. Developmental strategy is intimately related to recolonisation potential. Ovoviviparity, and the lack of pelagic larvae, did not limit the recolonisation potential of _N. kraussianus_, and recolonisation was probably effected by post-larval juveniles, which may disperse from neighbouring estuaries and coastal pools, by floating in coastal and tidal currents. Post-larval juveniles have two important advantages over larvae. They are less vulnerable to physical extremes, and they have a sturdy crennellated shell which probably affords them protection from predators.

14. Examples of larval recolonisation in estuarine populations have been reviewed, and the most fundamental conclusion of this work is that recolonisation is an important, and probably widespread, adaptation to estuarine conditions in South Africa.

ACKNOWLEDGEMENTS

I would like to extend sincere thanks to Dr. B.R. Davies for his constructive and enthusiastic supervision of this project. Thanks are also due to Professors B.R. Allanson, R.C. Newell, A.C. Brown, and G.M. Branch for their extremely helpful discussions, and particularly to Prof. J.G. Field for his invaluable criticism of Part 2.4.

Many people have assisted me in a variety of ways:

Mr. G.S. Butler spent many patient hours helping me with statistical procedures;

Mr. R. Cross and Mr. A. Bruton helped with all the photography;

Mrs. C.J. Eller typed the labels on the figures and maps;

Miss G.K. Eller sorted and catalogued many of the samples;

Dr. U. Fabris-Rotelli marked 2000 snails with a dentist's drill;

Mr. D. Forsyth built the holding system;

Mr. W. Holleman read and criticised two early drafts; and

Dr. R.N. Kilburn helped me to clarify nomenclature, and I found his correspondence particularly helpful.

My husband, Anthony, helped with every facet of the work. He encouraged me, assisted me with sampling, and typed all interim reports, several rough drafts and the final manuscript. For all his assistance and enthusiasm I extend my very grateful thanks.

In addition, I acknowledge with thanks all those who assisted me financially:

The Council for Scientific and Industrial Research;
Sasol;
The Wildlife Society of Southern Africa;
The Laura Starke Memorial Bursary; and
Rhodes University (Graduate Assistantship).

REFERENCES

ALLANSON, B.R., HILL, B.J., BOLTT, R.E. & SCHULZ, V. 1966. An estuarine fauna in a freshwater lake in South Africa. Nature, London 209: 532-533.

ALLANSON, B.R. (Ed.) 1979. Lake Sibaya Monographiae Biologicae 36 Junk, Den Hague. 364 pp.

AMIO, M. 1956. On the egg capsules and larvae of *Tritia festivus* (Powys) and *Nassarius livescens* (Philippi). Journal of the Shimonoseki College of Fisheries 6: 271-280.

AMIO, M. 1959. Studies on the eggs and larvae of marine gastropods II. Journal of the Shimonoseki College of Fisheries 8: 73-83.

ANDERSON, A. 1971. Intertidal activity, breeding and the floating habit of *Hydrobia ulvae* in the Ythan Estuary. Journal of the Marine Biological Association of the United Kingdom 51: 423-437.

ANDERSON, D.T 1960. The life histories of marine prosobranch gastropods. Journal of the Malacological Society of Australia 4: 16-29.

ANDERSON, D.T. 1966. Further observations of the life histories of littoral gastropods in New South Wales. Proceedings of the Linnean Society of New South Wales 90: 242-251.

BAILEY, N.T.J. 1951. On estimating the size of mobile populations from recapture data. Biometrika 38: 293-306.

BAILEY, N.T.J. 1952. Improvements in the interpretation of recapture data. Journal of Animal Ecology 21: 120-127.

BANDEL, K. 1974. Spawning and development of some Columbellidae from the Caribbean Sea of Columbia (South America). Veliger 16: 271-281.

BARNARD, K.H. 1958. Contributions to the knowledge of South African marine molluscs. Part II Gastropoda : Prosobranchiata : Rhachiglossa. Annals of the South African Museum 45: 1-237.

BEGG, G. 1978. The Estuaries of Natal. Natal Town and Regional Planning Report 41. 657 pp.

BLABER, S.J.M. 1973. The ecology of juvenile Rhabdosargus holubi (Steindachner) (Teleostei : Sparidae). Unpublished Ph.D. thesis, Rhodes University, Grahamstown.

BOESCH, D.F., WASS, M.L. & VIRNSTEIN, R.W. 1976. The Dynamics of Estuarine Benthic Communities. In: Estuarine Processes. 1. M. Wiley (Ed.). Academic Press, New York. 541 pp.

BOLTT, R.E. 1975. The benthos of some southern African lakes. Part V. The recovery of the benthic fauna of St. Lucia following a period of excessively high salinity. Transactions of the Royal Society of South Africa 41: 295-323.

BRANCH, G.M. 1974a. The ecology of Patella Linnaeus from the Cape Peninsula, South Africa, 2. Reproductive Cycle. Transactions of the Royal Society of South Africa 41: 111-160.

BRANCH, G.M. 1974b. The ecology of Patella Linnaeus from the Cape Peninsula, South Africa, 3. Growth-rates. Transactions of the Royal Society of South Africa 41: 161-193

BRANCH, G.M. 1975. Intraspecific competition in Patella cochlear Born. Journal of Animal Ecology 44: 263-282.

BROWN, A.C. 1971. The ecology of the sandy beaches of the Cape Penisula, South Africa. Part 2. The mode of life of Bullia (Gastropoda : Prosobranchia) Transactions of the Royal Society of South Africa 39: 281-319.

BROWN, A.C. & NOBLE, R.G. (1960) Function of the osphradium in Bullia (Gastropoda). Nature, London 188: 1045.

BROWN, S.C. 1969. The structure and function of the digestive system of the mud-snail Nassarius obseletus (Say). Malacologia 9: 447-500.

BROWNE, R.A. 1978. Growth, mortality, fecundity, biomass and productivity of four lake populations of the prosobranch snail, Viviparous georgianus. Ecology 59: 742-750.

BUCHANAN, J.B. & WARWICK, R.M. 1974. An estimate of benthic macrofaunal production in the offshore mud of the Northumberland coast. Journal of the Marine Biological Association of the United Kingdom 54: 197-222.

BURKE, M.V. & MANN, K.H. 1974. Productivity and production : biomass ratios of bivalve and gastropod populations an an Eastern Canandian Estuary. Journal of the Fisheries Research Board of Canada 31: 167-177.

BUSHMANS KARIEGA TRUST 1975. Report for the Department of Agricultural Technical Services. Unpublished.

CASSIE, R.M. 1950. The analysis of polymodal frequency distributions by the probability paper method. New Zealand Science Review 8: 89-91.

CASSIE, R.M. 1954. Some uses of probability paper in the analysis of size frequency distributions. Australian Journal of Marine and Freshwater Research 5: 513-522.

CASSIE, R.M. 1971. Sampling and statistics. pp 174-209. In: A Manual on Methods for the Assessment of Secondary Productivity in Fresh Waters. IPB Handbook No. 17. W.T.Edmonson & G.G.Winberg (Eds.).Blackwell Scientific Publications, Oxford. 358 pp.

CATHER, J.N. 1973. Ovoviviaprity in Nassarius albus. Journal of Conchology 110: 83-86, 88.

CHARNOV, E.L. 1979. The genetical evolution of patterns of sexuality : Darwinian fitness. American Naturalist 113: 465-480.

CHATFIELD, J.E. 1972. Studies on variation and life history in the prosobranch Hydrobia ulvae (Pennant). Journal of Conchology 27: 463-473.

CHRISTIANSEN, M.E. 1964. Some observations on the larval stages of *Nassarius pygmaeus* (Lamarck). *Pubblicazioni della Stazione zoologica di Napoli 34*: 1-8.

CURTIS, L.A. & HURD, L.E. 1979. On the broad nutritional requirements of the mud-snail *Ilynassa (Nassarius) obsoleta* (Say) and its polytrophic role in the food web. *Journal of Experimental Marine Biology and Ecology 41*: 289-297.

CURTIS, M.A. 1977. Life cycles and population dynamics of marine benthic polychaetes from the Disko Bay area of West Greenland. *Ophelia 16*: 9-58

DAVIES, B.R. 1979. *Secondary production studies on the bivalve Musculus virgiliae Barnard in the littoral Potamogeton pectinatus L. beds of a southern African coastal lake.* Abstract No. 14. *In*: *Societas Internationale Limnologiae* - United Nations Environmental Programmes Workshop on African Limnology, University of Nairobi, 16-23 December 1979. Abstracts of Poster Papers.

DAVIES, B.R. 1980. *The secondary production of the mytilid bivalve, Musculus virgiliae Barnard, in the littoral weed beds of a South Temperate, Coastal Lake (Swartvlei).* Final report to Inland Waters Ecosystems section of the Co-operative Scientific Programmes, National Environmental Research Programmes. Council for Scientific and Industrial Research, Pretoria. Manuscript.

DAY, J.H. 1951. The ecology of South African estuaries. Part 1. A review of estuarine conditions in general. *Transactions of the Royal Society of South Africa 33*: 53-91.

DAY, J.H. 1956. The ecology of South African estuaries. Part 7. The biology of Durban Bay. Annals of the Natal Museum 13: 259-312.

DAY, J.H. 1959. The biology of Langebaan lagoon : a study of the effect of shelter from wave action. Transactions of the Royal Society of South Africa 35: 475-547.

DAY, J.H. 1967. The biology of Knysna estuary, South Africa. In: Estuaries G.H. Lauff (Ed.). American Association for the Advancement of Science. pp 397-407.

DAY, J.H. 1974. A Guide to Marine Life on South African Shores. (2nd (revised) Edition). A.A.Balkema, Cape Town.

DAY, J.H., MILLARD, N.A.H. & HARRISON, A.D. 1952. The ecology of South African estuaries. Part III Knysna: A clear open estuary. Transactions of the Royal Society of South Africa 33: 367-413

DAY, J.H., MILLARD, N.A.H. & BROEKHUYSEN, G.J. 1953. The ecology of South African estuaries. Part IV The St. Lucia system. Transactions of the Royal Society of South Africa 34: 129-156.

DE SACCHI, F. 1967. On the variation in sexual rapport in the course of the year in Littorina obtusa (Gastropoda : Prosobranchia). Compte rendu hebdomadaire des seances de L'Academie des Sciences 264: 1504-1506.

EBERHARDT, L.L. 1978. Appraising variability in populations. Journal of Wildlife Management 42: 207-238.

EDWARDS, D.C. 1968. Reproduction in Olivella biplicata. Veliger 10: 297-304.

FISH, J.D. 1972. The breeding cycle and growth of open coast and estuarine populations of Littorina littorea. Journal of the Marine Biological Association of the United Kingdom 52: 1011-1019.

FISH, S. 1970. The biology of Eurydice pulchra (Crustacea:Isopoda). Journal of the Marine Biological Association of the United Kingdom 50: 753-768.

FISH, J.D. + FISH, S. 1974. The breeding cycle and growth of Hydrobia ulvae in the Dovey estuary. Journal of the Marine Biological Association of the United Kingdom 54: 685-697.

FORBES, A.T. 1973a. An unusual larval life in the estuarine burrowing prawn Callianassa kraussi Stebbing (Custacea : Decapoda : Thalassinidae). Marine Biology 22: 361-365.

FORBES, A.T. 1973b. A study of the burrowing sandprawn Callianassa kraussi Stebbing (Crustacea : Decapoda : Thalassinidea). Unpublished Ph.D. thesis, Rhodes University, Grahamstown.

FORBES, A.T. 1974. Osmotic and ionic regulation in Callianassa kraussi Stebbing (Crustacea : Decapoda : Thallassinidea). Journal of Experimental Marine Biology and Ecology 16: 201-311.

FORBES, A.T. 1977. Breeding and growth of the burrowing prawn *Callianassa kraussi* Stebbing (Crustacea : Decapoda : Thalassinidae). *Zoologica Africana* *12*: 149-161.

FORBES, A.T. & HILL, B.J. 1969. The physiological ability of a marine crab *Hymenosoma orbiculare* Desm. to live in a subtropical freshwater lake. *Transactions of the Royal Society of South Africa* *38*: 271-283.

FRETTER, V. & GRAHAM, A. 1962. *British Prosobranch Molluscs*. Printed for the Ray Society, London. pp 755.

FRETTER, V. & PILKINGTON, M. 1971. The larval shell of some prosobranch gastropods. *Journal of the Marine Biological Association of the United Kingdom* *51*: 49-62.

GLYNN, P.W. 1970. On the ecology fo the Caribbean Chitons *Acanthopleura granulata* Gmelin, and *Chiton tuberculatus* Linn. : Density, mortality, feeding, reproduction, growth. *Smithsonian Contributions to Zoology* *66*: 1-21.

GIBBS, P.E. 1968. Observations on the population of *Scoloplos armiger* at Whitstable. *Journal of the Marine Biological Association of the United Kingdom* *48*: 225-254.

HAIRSTON, N.G, HUBENDICK, B., WATSON, J.M. & OLIVER, L.J. 1958. An evaluation of techniques used in estimating snail populations. *Bulletin of the World Health Organisation, Geneva.* *19*: 661-672.

HAMILTON, W.D. 1967. Extraordinary sex ratios. *Science* *156*: 477-488.

HARDING, J.P. 1949. The use of probability paper for the graphical analysis of polymodal frequency distribution. *Journal of the Marine Biological Association of the United Kingdom* *28*: 141-153.

HIBBERT, C.J. 1976. Biomass and production of a bivalve community on an intertidal mud-flat. *Journal of Experimental Marine Biology and Ecology* *25*: 249-261.

HIBBERT, C.J. 1977. Growth and survivorship in a tidal-flat population of the bivalve *Mercenaria* *mercenaria* from Southampton Water. *Marine Biology* 44: 71-76.

HILL, B.J. 1971. Osmoregulation by an estuarine and marine species of *Upogebia* (Anomura : Crustacea). *Zoologica Africana* *6*: 229-236.

HILL, B.J. 1974. Salinity and temperature tolerance of zoeae of the Portunid crab *Scylla* *serrata*. *Marine Biology* *25*: 21-24.

HILL, B.J. 1976. Natural food, fore-gut clearance rate and activity of the crab *Scylla* *serrata*. *Marine Biology* *34*: 109-116.

HILL, B.J. 1977. The effect of heated effluent on egg production in the estuarine prawn *Upogebia* *africana* (Ortmann). *Journal of Experimental Marine Biology and Ecology* *29*: 291-307.

HILL, B.J. *in* *press*. Adapatations to life in southern African estuaries.

HILL, B.J. & ALLANSON, B.R. 1971. Temperature tolerance of the estuarine prawn *Upogebia africana*. *Marine Biology* *11*: 337-343.

HOUSTON, R.S. 1978. Notes on the spawning and egg capsules of two prosobranch gastropods : *Nassarius tiarula* (Kiener 1841) and *Solenospira macrospira* (Berry 1957). *Veliger* *20*: 367-368.

HOWARD-WILLIAMS, C. & ALLANSON, B.R. 1978. *Swartvlei Project Report. Part I. Introduction, research summary, management proposals for Swartvlei, and recommendations in the use of aquatic macrophytes as nutrient filters.* Institute for Freshwater Studies, Special Report No. 78/2.

HUGHES, R.N. 1970. An energy budget for a tidal-flat population of the bivalve *Scrobicularia plana* (Da Costa). *Journal of Animal Ecology* *39*: 357-381.

HUMASON, G.L. 1967. *Animal Tissue Techniques*. 2nd Edition. W.H.Freeman and Company, San Francisco.

JOHANNESSEN, O.H. 1973. Length and weight relationships and the potential production of the bivalve *Venerupis pullastra* (Montagu) on a sheltered beach in western Norway. *Sarsia* *53*: 41-48.

JOHNSON, M.R. & KEYSER, A.W. 1976. *Explanatory notes. 1:250 000 Geological Series 3226 King Williams Town.* Government Printer, Pretoria.

JONES, D.A. 1970. Population densities and breeding in *Eurydice pulchra* and *Eurydice affinis* in Britain. *Journal of the Marine Biological Association of the United Kingdom* *50*: 635-655

KAICHER, S.D. 1972. A second ovoviviparous *Nassarius*. *Nautilus* *85*: 126-128.

KAIM-MALKA, R.A. 1969. Biologie et ecologie de quelques *Ampelisca* de la region de Marseilles. *Tethys* *1*: 977-1022.

KASINATHAN, R., GOVIDAN, K. & NATARAJAN, R. 1974. Notes on the spawning and hatching of three species of marine gastropods. *Malacological Review* *1*: 133-138.

KENSLEY, B. 1973. *Sea Shells of Southern Africa : Gastropods.* Maskew Miller Ltd., Cape Town. 225 pp.

KLEIN, G., RACHOR, E. & GERLACH, S.A. 1975. Dynamics and productivity of two populations of the benthic tube dwelling amphipod *Ampelisca* *brevicornis* (Costa) in Helgoland Bight. *Ophelia* *14*: 139-159.

KNUDSEN, J. 1956. Marine Prosobranchs of Tropical West Africa (Stenoglossa). *Atlantide Report* *4*: 53-54.

KUENZLER, E.J. 1961. Structure and energy flow of a mussel population in a Georgia salt marsh. *Limnology and Oceanography* *6*: 191-204.

LEBOUR, M.V. 1931. The larval stages of *Nassarius reticulatus* and *Nassarius* *incrassatus*. *Journal of the Marine Biological Association of the United Kingdom* *17*: 797-818.

LEBOUR, M.V. 1934. Rissoid larvae as food of the young herring. The eggs and larvae of Plymouth Rissoidae. *Journal of the Marine Biological Association of the United Kingdom* *19*: 523-539.

LEBOUR, M.V. 1935. The breeding of *Littorina neritoides*. *Journal of the Marine Biological Association of the United Kingdom* *20*: 373-378.

LEBOUR, M.V. 1936. Notes on the eggs and larvae of some Plymouth prosobranchs. *Journal of the Marine Biological Association of the United Kingdom* *20*: 547-565.

LEBOUR, M.V. 1937. The eggs and larvae of the British prosobranchs with special reference to those living in the plankton. *Journal of the Marine Biological Association of the United Kingdom* *22*: 105-166.

LEBOUR, M.V. 1945. The eggs and larvae of some prosobranchs from Bermuda. *Proceedings of the Zoological Society of London* *114*: 462-489

LEBOUR, M.V. 1947. Notes on the inshore plankton of Plymouth. *Journal of the Marine Biological Association of the United Kingdom* *26*: 527-547.

LIPTROT, M.R.M. 1978. *Community metabolism and phosphorus dynamics in a seasonally closed South African estuary.* Unpublished M.Sc thesis, Rhodes University, Grahamstown. 130 pp.

LITTLE, C. + NIX, W. 1976. The burrowing and floating behaviour of the Gastropod *Hydrobia ulvae*. *Estuarine and Coastal Marine Science* *4*: 537-544.

LOCKWOOD, A.P.M. 1976. Physiological adaptation to life in estuaries. pp 315-392. *In*: *Adaptation to Environment*. R.C.Newell (Ed.). Butterworths, London 539 pp.

MANN, K.H. 1971. Use of the Allen curve method for calculating benthic production. pp 160-165. *In*: *A Manual in Methods for the Assessment of Secondary Prodcutivity in Fresh Waters*. *IPB Handbook No. 17* W.T. Edmondson & G.G. Winberg (Eds.). Blackwell Scientific Publications, Oxford. 358 pp.

MAYNARD-SMITH, J. 1978. *The Evolution of Sex*. Cambridge Univerisity Press, Cambridge. 222 pp.

MCLACHLAN, A. & ERASMUS, T. 1974. Temperature tolerances and osmoregulation in some estuarine bivalves. *Zoologica Africana* *9*: 1-13.

MCLACHLAN, A. & GRINDLEY, J.R. 1974. Distribution of macrobenthic fauna of soft substrata in Swartkops estuary. *Zoologica Africana* *9*: 211-233.

MCLACHLAN, A., COOPER, C. & VAN DER HORST, E. 1979. Growth and production of *Bullia rhodostoma* on an open sandy beach in Algoa Bay. *South African Journal of Zoology* *14*: 49-53.

MILEIKOVSKY, S.A. 1971. Types of larval development in marine bottom invertebrates, their distribution and ecological significance - a re-evaluation. *Marine Biology* *10*: 193-213.

MILEIKOVSKY, S.A. 1975. Types of larval development in Littorinidae (Gastropoda : Prosobranchia) of the World Ocean, and ecological patterns of their distribution. *Marine Biology* *30*: 125-135.

MILLARD, N.A.H. & HARRISON, A.D. 1953. The ecology of South African estuaries: Part V. Richards Bay. Transactions of the Royal Society of South Africa 34: 157-179.

MILLARD, N.A.H. & SCOTT, K.M.F. 1953. The ecology of South African estuaries : Part VI. Milnerton Estuary and the Diep River, Cape. Transactions of the Royal Society of South Africa 34: 279-324.

MILNE, H. & DUNNET, G.M. 1972. Standing crop, productivity and trophic relations of the fauna of Ythan estuary. In: The Estuarine Environment. R.S.K. Barnes & J. Green (Eds.). Applied Scientific Publishers, London.

MOORE, H.B. 1937. The biology of Littorina littorea. Part 1. Growth of the tissue, spawning, length of life and mortality. Journal of the Marine Biological Association of the United Kingdom 21: 721-742.

NATARAJAN, A.V. 1957. Studies on the egg masses and larval development of some prosobranchs from the Gulf of Mannar and Palk Bay. Proceedings of the Indian Academy of Science 46: 171-228.

NEWELL, R.C. 1962. Behavioural aspects of the ecology of Peringia (=Hydrobia) ulvae (Pennant)(Gastropoda : Prosobranchia). Proceedings of the Zoological Society of London 138: 49-75.

NEWELL, R.C. 1965. The role of detritus in the nutrition of two deposit feeders, the prosobranch Hydrobia ulvae and the bivalve Macoma balthica. Proceedings of the Zoological Society of London 144: 25-45.

NEWELL, R.C. 1979. Biology of Intertidal Animals. (3rd Edition (expanded)). Marine Ecological Surveys Ltd., Faversham, Kent. 781 pp.

NEWMAN, G.E. 1967. Reproduction of the South African Abalone Haliotis midae. Investigational Report of the Division of Sea Fisheries, South Africa 64: 1-24.

PEARSE, A.S. 1939. Animal Ecology. McGraw Hill Book Company, New York.

PEARSE, J.S. 1969. Slow development demersal embryos and larvae of the Antarctic sea star Odonaster validus. Marine Biology 3: 110-116.

PECHENIK, J.A. 1978. Winter reproduction in the gastropod Nassarius trivittatus. Veliger 21: 297-298.

PELSENEER, P. 1926. La proportion relative des sexes chez les animaux et particulierement chez les mollusques. Memoires de L'Academie r. de Belgique. Classe de Sciences. Collection in Serie II 8: 1-258.

PETERSEN, G.H. 1978. Life cycles and population dynamics of marine benthic bivalves from the Disko Bught area of West Greenland. Ophelia 17: 95-120.

PILKINGTON, M.C. 1974. The eggs and hatching stages of some New Zealand prosobranch molluscs. Journal of the Royal Society of New Zealand 4: 411-431.

RADWIN, G.E. AND CHAMBERLIN, J.L. 1973. Patterns of larval development in stenoglossan gastropods. Transactions of the Natural History Society of San Diego 17: 107-118.

RISBEC, J. 1932. Notes sur la ponte et al development de mollusques gasteropodes de Nouvelle-Caledonie. Bulletin de la Societe de zoologique de France 57: 358-374.

SCHELTEMA, R.S. 1961. Metamorphosis of the veliger larvae of Nassarius obsoletus in response to bottom sediment. Biological Bulletin (Woods Hole) 120: 92-109.

SCHELTEMA, R.S. 1962. Pelagic larvae of New England intertidal gastropods. 1. Nassarius obseletus Say, and Nassarius vibex Say. Transactions of the American Microscopical Society 80:1-11.

SCHELTEMA, R.S. 1964a. Feeding habits and growth in the mud-snail Nassarius obseletus. Chesepeake Science 5: 161-166.

SCHELTEMA, R.S. 1964b. Reproduction of Nassarius trivittatus off the coast of Georgia. Nautilus 78: 49-50.

SCOTT, K.M.F., HARRISON, A.D. & MCNAE, W. 1952. The ecology of South African estuaries : Part II. The Klein River estuary, Hermanus, Cape. Transactions of the Royal Society of South Africa 33: 282-331.

SECRETARY OF STATISTICS 1975. Report on Agricultural and Pastoral Production. Report No. 06-01-12. Agricultural Census No. 48. Government Printer, Pretoria.

SHEADER, M. 1977. Production and population dynamics of *Ampelisca tenuicornis* (Amphipoda) with notes on the biology of its parasite *Sphaeronella longipes* (Copepoda). *Journal of the Marine Biological Association of the United Kingdom* *57*: 955-968.

SHUTO, T. 1974. Larval ecology of prosobranch gastropods and its bearing on biogeography and paleontology. *Lethaia* *1*: 239-256.

SKAER, H.Le B. 1974. The water balance of a serpulid polychaete, *Mercierella egnimatica* (Fourel). 1. Osmotic concentration and volume regulation. *Journal of Experimental Biology* *60*: 321-330.

SOKAL, R.R. & ROHLF, F.J. 1969. *Biometry*. W.H. Freeman and Company, San Francisco.

SOUTHWOOD, T.R.E. 1978. *Ecological Methods* (2nd ed). Chapman and Hall, London. 524 pp.

STEPHENSON, W., COOK, S.D. & RAPHAEL, Y.I. 1977. The effect of a major flood on the macrobenthos of Bramble Bay, Queensland. *Memoirs of the Queensland Museum* *18*: 95-119.

STRUHSAKER, J.W. 1966. Breeding, spawning, spawning periodicity and early development in the Hawaiian *Littorina* : *L. pintado* (Wood), *L. picta* Phillipi and *L. scabra* (Linne). *Proceedings of the Malacological Society of London* *37*: 137-166.

THORSON, G. 1935. Studies on the egg capsules and the development of Artic marine gastropods. *Meddelelser om Gronland* *100*: 1-71.

THORSON, G. 1946. Reproduction and larval development of Danish marine bottom invertebrates. *Meddelelser fra Kommissionen fer Havundersogelser, Serie Plankton* *4*: 1-523.

THORSON, G. 1950. Reproductive and larval ecology of marine bottom invertebrates. *Biological Review* *25*: 1-45.

THORSON, G. 1961. Length of pelagic life in marine bottom invertebrates as related to larval transport by ocean currents. *In*: *Oceanography International Oceanographic Congress, New York* M. Sears (Ed.). American Association for the Advancement of Science, Washington.

THORSON, G. 1966. Some factors influencing the recruitment and establishment of marine benthic communities. *Netherlands Journal of Sea Research* *3*: 267-293.

TURGEON, K.W. & FRALICK, R.A. 1973. Size and sex ratio differences in *Urosalpinx* *cinerea* (Say) (Muricidae) from Great Bay, New Hampshire. *Nautilus* *87*: 112-113.

VESTERGAARD, K. 1935. Uber den Laich und die Larven von *Scarlia* *communis* (Lam.), *Nassarius* *pygmaeus* (Lam.) und *Bela* *turricola* (Mont.). *Zoologischer Anzeiger* *109* :219-222.

WARD, J. 1966. The breeding cycle of the Keyhole limpet *Fissurella* *barbadensis* Gmelin. *Bulletin of Marine Science of the Gulf and Caribbean* *16*: 685-695.

WARWICK, R.M. & PRICE, R. 1975. Macrofaunal production in an estuarine mudflat. Journal of the Marine Biological Association of the United Kingdom 55: 1-18.

WEATHER BUREAU 1979a. Monthly Weather Report. July. Government Printer, Pretoria.

WEATHER BUREAU 1979b. Monthly Weather Report. August. Government Printer, Pretoria.

WEBBER, H.H. 1977. Gastropoda : Prosobranchia. In: Reproduction of Marine Invertebrates Volume IV. A.C. Giese & J.S. Pearse (Eds.). Academic Press, New York.

WINBERG, G.G., PATALAS, K., WRIGHT, J.C., HILLBRIGHT-ILKOWSKA, A., COOPER, W.E. & MANN, K.H. 1971. Methods for calculating productivity. pp 296-317. In: A Manual for Assessment of Secondary Productivity in Fresh Waters. IPB Handbook No. 17. W.T. Edmondson & G.G. Winberg (Eds.). Blackwell Scientific Publications, Oxford. 358 pp.

WOLFF, W.J. & DE WOLF, L. 1977. Biomass and production of zoobenthos in the Grevelingen estuary, The Netherlands. Estuarine and Coastal Marine Science 5: 1-24.

APPENDIX 1

Barnard (1958), Kensley (1973) and Day (1974) have all used the name *Nassa kraussiana* rather than *Nassarius kraussianus*. Barnard (1958) first used the generic name *Nassa*: "Neither *Nassarius* Dumeril 1806 nor *Nassaria* Link 1807 (*Buccinidae*) are to be rejected on account of the similarity of their termination (Rules Zool. Nomencl. Art. 36. Rec.), though Iredale thought otherwise; but as they are very liable to confusion no apology is made for reverting to *Nassa*; Thiele accepted it several years after Iredale's proposed alteration; and everyone knows the distinctive facies of a '*Nassa*'."

However, R.N. Kilburn (*pers*.*comm*.) has pointed out that *Nassarius kraussianus* is the correct name, and writes: "the generic name *Nassa* Lamarck, 1799, once applied to the group, is preoccupied by an earlier *Nassa* Roding, 1798, founded for a certain species of Muricidae. The next available name is *Nassarius* Dumeril, 1806." In the light of Kilburn's statement I have adopted *Nassarius kraussianus* as the only acceptable name for the species, and have used this throughout the study. In addition, I have consistently assumed that the name *Nassa*, used in past literature, is equivalent to *Nassarius*.

APPENDIX 2

This study was initially designed as a detailed investigation of the population dynamics of N. kraussianus, and cohort analysis was developed to quantify growth and mortality. By June 1980 it was evident from the population structure, that reproduction was probably continuous (no cohorts were evident). A mark-recapture programme was, therefore, scheduled in order to measure growth and mortality, and in addition, to confirm the population estimates obtained by quadrat sampling.

The Bailey triple catch method was selected as the most suitable method (Bailey, 1951; 1952), with sampling on Days 1, 2, and 3, and a one week interval between samples. Animals marked on Days 1 and 2, would be recaptured on Days 2 and 3. This initial attempt at mark-recapture would also have given an indication of the feasibility of the method. The most important consideration when using this technique was the vast number of animals needed in order to have some chance of recapturing a marked animal.

On 15.7.80, 2000 snails were collected, and were marked that night using a high speed dentist's drill (Fig. 42). Four marking positions were chosen. Position 1 identified the date, and was notched once one Day 1 and twice on Day 2 (Fig. 42). Positions 2, 3 and 4 identfied the size of the marked animal at the time of marking:

5 mm - 1 notch at position 2,
6 mm - 1 notch at position 3,
7 mm - 1 notch at position 4,
8 mm - 2 notches at postion 2, and
9 mm - 2 notches at postion 3 (Fig. 42).

Thus, the growth of marked animals collected during routine sampling after the Bailey triple catch had been completed, could be assessed.

The animals were released at low tide on 16.7.80 (Day 1), and later that day it began to rain. By the following week, the projected Day 2, the Bushmans River had flooded, for the first time, and no marked animals were recovered.

In the subsequently altered study, it was confirmed that N. kraussianus does reproduce continuously. Thus, a mark-recapture study remains the only way in which growth and mortality could be accurately assessed. If such a programme is attempted in the future, road marking paint should be used to mark the animals. Snails marked in this way in the laboratory, in April 1979, still retained these marks in October 1980, despite constant burrowing into the substratum of the tank. A far more useful code could be designed using paint dots (Southwood, 1978).

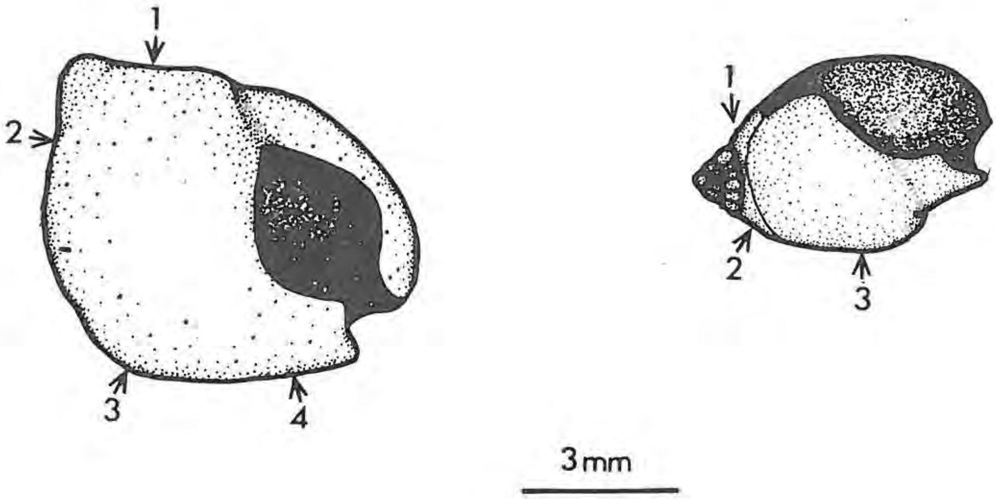


Fig. 42. Diagram showing the positions used to mark *N. kraussianus* shells. Arrows show the positions notched by the drill, and an explanation of the code appears in the text.