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ECOPHYSIOLOGY

OF

THE BLACK MUSSEL

CHOROMYTILUS MERIDIONALIS

(KRAUSS)

BY

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Thesis submitted in the Faculty of Science for the degree

Doctor of Philosophy

February 1980

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Adult and juvenile Choromytilus meridionalis (Kr.)
at Bailey's Cottage, False Bay.

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ABSTRACT

The thesis describes the reproduction, population dynamics and production, filtration, respiration and assimilation of the black mussel Choromytilus meridionalis (Kr.) at Bailey's Cottage, False Bay, South Africa. The reproductive season and gonad development is described from monthly measurements made over a period of 4 years. Spawning usually extends from July to February and is characterised by peaks of gamete release interspersed with regeneration of the gonad. Individual fecundity varies from year to year and increases with increasing body size, representing 61-97% of production. Although large volumes of gamete material are emitted annually, spat settlement at the study site is only successful at 4 to 6 year intervals. The population dynamics at different shore levels is described in detail. Adult mussels are physically displaced by the settlement of a new cohort which migrates up the shore. Mussels show a decline in growth with increasing shore height. Population structure is mainly affected by wave action, intertidal height and intraspecific competition and except for Natica (Tectonatica) tecta, the population in False Bay is not predator controlled. N. tecta at Bailey's Cottage are confined to sandy pools and prey on mussels up to 55 mm shell length. They are capable of eliminating a dense mussel population within 1.5 years of spat settlement. Prey size selection, consumption rates and the method of boring in N. tecta are described.

The filtration and respiration rates and assimilation efficiencies of mussels fed on different rations of Dunaliella primolecta have been measured. The filtration and respiration rates remain unaffected by ration level and assimilation efficiency averaged 80% between $0.4 - 10 \times 10^6$ cells l^{-1} . Above 10×10^6 cells l^{-1} ($3 \text{ mg } l^{-1}$ dry wt.) the assimilation efficiency fell to zero. Rising sea temperatures during summer did not affect the filtration rate, while respiration rate increased with increasing temperature and showed no seasonal acclimation to temperature change. Following starvation in the laboratory, the filtration rate and assimilation efficiency changes and a positive energy balance is maintained at lower food concentrations.

Examination of the food ration available in seawater throughout the year at Bailey's Cottage shows an average ration of $8.3 \text{ mg } l^{-1}$ dry weight of which $2.65 \text{ mg } l^{-1}$ ($16.2 \text{ J } l^{-1}$) represents organic material. A large quantity of sand is present in the diet. Phytoplankton seldom contribute a significant proportion of the food. Assimilation efficiency averaged 40% in the field and was measured at ration levels considerably above the maximum ration for positive assimilation efficiency using algal culture. Laboratory feeding experiments employing pure algal cultures do not reflect natural conditions.

The effects of aerial exposure on growth, feeding and

respiratory rates are examined. Littoral mussels are unable to enhance energy gain during the limited feeding periods. However, quiescence and aerobic respiration during exposure reduce metabolic expenditure enabling the maintenance of a positive energy balance and a slow growth rate.

Annual production and energy flow are calculated at 4 shore levels over a 3 year period. Production varies with shore level, population structure and age of the different cohorts. Reproductive effort may measure 80% of population production. Production values measured in C. meridionalis are amongst the highest found in bivalve species. Associated with the high productivity is a high energy flow to other consumers. Up to 90% of the food energy filtered from the seawater annually is released in gamete output, faeces, pseudofaeces and mortality of the mussels.

ACKNOWLEDGEMENTS

This work was funded as part of the Kelp Bed Research Programme by the South African Committee for Oceanographic Research. I wish to thank Prof. J.G. Field for his encouragement and supervision of this project, and for constructive criticism of the final manuscripts. Thanks are also due to Dr. C.L. Griffiths for helpful discussion and forbearance at playing second fiddle to numerous filter feeding bivalves. Prof. R.C. Newell is thanked for reading some of the manuscripts and suggesting the separation of data on aerial exposure into two manuscripts. Prof. G.M. Branch offered constructive criticism of the paper on population production.

My thanks are also due to various student assistants, in particular Miss F.J. Stratton. She offered invaluable assistance in routine data gathering and analyses. Messers K. Achleitner, T. Longman, J. Frantz and J. Williams are thanked for technical assistance.

I wish to express my gratitude to Miss M. Taswell, Mrs. L. Freeland and especially Mrs. S. Hardman for assistance in typing the manuscripts.

STATEMENT

This study was conceived by the candidate and executed with the help of Miss R. Buffenstein and various student assistants. Part-time student help in routine analyses was used for:- measuring, weighing, muffle furnace operations, bomb calorimetry and data analyses. Miss R. Buffenstein completed some of the work as a Zoology Honours degree candidate. She determined the effects of state of tide and aerial exposure on the filtration rate of mussels as part of one of her honours projects. This was done under my supervision and she has been made co-author of the relevant manuscript. Experimental design for investigation of physiological responses was by the candidate. Respirometers and a flow-through feeding apparatus were constructed (see appendix 1 & 2) with the aid of technicians in the Zoology Department.

INTRODUCTION

The interest which has centred on bivalve species in recent years has been aptly summarised by Bayne (1976).

He states:-

"Mussels have been the subject of a considerable amount of research effort, reflecting both their ecological and economic importance. Their geographical distribution is worldwide and they are the dominant organisms in many littoral and shallow sublittoral ecosystems, including rocky and sediment shores on open coasts and in estuaries and marsh. Mussels therefore aroused interest not only in the factors controlling their own population ecology, but also in their role in the structure and function of the communities of which they are a characteristic and important component." Much of the overseas work has concerned the blue mussel Mytilus edulis L. and following its selection for study by the International Biological Programme in 1968, and extensive literature has become available on this species. Research has covered many aspects, from ecophysiology to pollution monitoring and larval biology and aquaculture. These topics have been reviewed by various authors and edited by Bayne (1976). However, most of the data pertains to the Northern Hemisphere. Little information is available on Southern Hemisphere bivalves and, in particular, on the dominant bivalves on the South African coast.

The high densities and biomass exhibited by the mytilid species Choromytilus meridionalis (Kr.), Perna perna (L.) and Aulacomya ater (Molina) on rocky substrates in the littoral and sublittoral, indicates that they are dominant and important species in the South African marine environment. Unfortunately the detailed surveys on the sublittoral distribution of marine organisms on the West coast (Pollock, 1978; Currie & Cook, 1975; Field et al., 1980) have not been duplicated on the South and East coasts. Thus, whereas considerable information is available on the density and distribution of A. ater, dominant on the West coast, little information is as yet available on the sublittoral distribution of C. meridionalis on the South coast and P. perna on the East coast. The three species show considerable overlap in distributional range and C. meridionalis may be found in mixed populations with both P. perna and A. ater (own observation; Currie & Cook, 1975).

The importance of the local mussel species is not only reflected in their dominance and distribution, but in the fact that they are important prey items in the diet of commercially exploited rock-lobsters; each is a potential-prey species for aquaculture; and they are potential indicator species for pollution monitoring. Adults of the spiny lobster Panulirus homarus (L.) feed predominantly on P. perna (Berry, 1971; Smale, 1978) and the rock-lobster Jasus lalandii (Milne Edwards) preys upon A. ater and C. meridion-

alis (Pollock, 1978; Griffiths & Seiderer, 1980). Commercial exploitation of large stocks of J. lalandii on the South African west coast forms an important source of revenue. Although A. ater appears to be the dominant bivalve species in this area, large beds of C. meridionalis are also found (Pollock, 1978; Currie & Cook, 1975). Furthermore Griffiths & Seiderer (1980) have shown preferential selection of C. meridionalis by J. lalandii.

All three mussel species have been the subject of investigation for aquaculture purposes. A. ater is harvested in Chile (Hancock, 1969) and cultivation of P. perna occurs in Venezuela, Brazil and Angola (Berry, 1978). Preliminary studies on C. meridionalis were undertaken by De Villiers (1977) and Du Plessis (1977). However, the latter investigations were inconclusive and a paucity of information remains regarding the biology and physiology of C. meridionalis.

Mussels, in particular M. edulis, have been the subject of research into their potential as pollution monitoring indicators and fouling organisms. This is reviewed by Roberts (1976). The use of chlorine as an antifouling agent, with particular reference to C. meridionalis, has been examined by Currie & Cook (1975). Stuart (1978) continued this work by investigating the responses of the heart beat and valve adduction to low level chlorination.

Currie et al. (1974) examined the effects of ammonium nitrate on fertilisation and early development of C. meridionalis. These studies are hampered by the usual problems experienced in such work on bivalves (Roberts, 1976) and by the variability displayed within and between individual mussels. Considerably more background information is required before meaningful interpretation of the physiological responses of C. meridionalis to pollutants may be made.

From the above discussion it is clear that C. meridionalis may be of considerable ecological importance. In order to remedy the paucity of information regarding this species the following study was undertaken. The aim was to obtain detailed information regarding the reproduction, growth, population dynamics, metabolic rates and energy flow and to present this in a form which could be used for comparison with data from other bivalve species. Such data are essential to further detailed studies on the importance of this species in marine communities, commercial cultivation, pollution monitoring etc.. This study was undertaken in collaboration with C.L. Griffiths and P.F. Berry, who simultaneously conducted similar, but less extensive studies on A. ater and P. perna respectively. Although future publications will involve ecophysiological comparisons between the species, this was not the aim of the present work.

The main study was conducted at Bailey's Cottage, False Bay as this was the closest population which remained relatively unexploited by man, and allowed regular intensive sampling. The closest suitable site on the West coast was Ou Skip Rocks, 34 Km north of Cape Town. The distance precluded the frequent visits and facility with which animals could be returned to the laboratory for immediate physiological experiment, offered by Bailey's Cottage.

The work was divided into several phases, many of them running concurrently, and is presented as follows:-

Paper 1 deals with the reproductive season, gonad development and an assessment of gonad output by C. meridionalis. The project originated in a study of the reproductive cycles of several littoral invertebrate species on rocky shores and A. ater and C. meridionalis were amongst those studied. The variability in fecundity and spat settlement noticed during this investigation led to the examination of the population dynamics.

Paper 2 presents an investigation of the population dynamics. This was conducted over a 4 year period in order to allow for natural long-term fluctuations in the population. Despite the rigours of aerial exposure, C. meridionalis appear to survive successfully in the littoral zone and measurements were conducted at 4 different shore levels to

examine the effects of increasing aerial exposure on population structure.

Paper 3 examines the predation rate and population structure of the boring gastropod Natica (Tectonatica) tecta which preys on C. meridionalis at Bailey's Cottage. This was found to be the only significant predator of mussels in False Bay.

Paper 4 deals with the feeding, respiration and assimilation of C. meridionalis. Standard techniques were used in this investigation. Experiments employed the use of the unicellular alga Dunaliella primolecta which was cultured for this purpose. Feeding experiments were generally done in 2 l containers, but a constant flow apparatus was designed and constructed to check the data obtained using a static system. This apparatus is illustrated in appendix 1. Part of the apparatus used for measurement of respiration rates involved the use of YSI pO_2 probes. Respirometer chambers were constructed to house the probes and a constant-flow system designed and constructed. This is illustrated in appendix 2.

Paper 5 presents an analysis of the food available to mussels in the field. Data obtained with the aid of algal cultures is frequently extrapolated to field conditions. However, recent evidence indicates that detritus rather than algae, forms the major component of the mussel diet in the field

(Fox & Coe, 1943; Jørgensen, 1955; Widdows et al., 1979). The latter authors have also indicated the importance of silt in the mussel diet. Analysis of the available ration and organic material as a food source in the water at Bailey's Cottage was undertaken for the period of one year. The assimilation efficiency of mussels feeding on natural detritus in the laboratory and the field is compared with results obtained with the aid of D. primolecta culture.

Papers 6 & 7 examine the effects of aerial exposure on energy gain and expenditure in littoral mussels. The rigours of exposure and reduced feeding time may be expected to affect the energy balance of organisms occupying the littoral habitat. This problem is investigated by examining the length/weight relationships, filtration rates, assimilation efficiencies and respiration rates of mussels at different shore levels.

Paper 8 Information given in the above papers is combined in an examination of production and energy flow at 4 shore levels over a 3 year period. The influences of mussel age and increasing shore height on production are examined.

Concurrent with population dynamics studies, several attempts were made at culturing the larval stages of C. meridionalis to settlement. Unfortunately, fertilised ova could not be maintained beyond the straight-hinge (D-shape)

stage and died after 14 days. Experiments were therefore, not conducted on the larval stages. However, C. meridionalis has been cultured to settlement at the Oyster Research Unit, Knysna (Du Plessis, 1977; A. Genade pers. comm.).

The data in this thesis have been presented as above, and in the form of separate manuscripts ready for submission for publication. Although the topics are handled separately, they form a unit by presenting a logical sequence, successively complementing existing knowledge. Paper 8 is followed by a discussion of general conclusions, more detailed discussions being given in the relevant papers. Because the data are presented as separate manuscripts, each has a slight variation in format according to the requirements of the journals to which they will be submitted. Presentation of the thesis in this form necessitates each section having its own reference list, introduction and conclusions inclusive, rather than a single reference list at the end of the thesis, the more usual practice.

The first paper on reproductive cycles has already been published, while the second, on population dynamics, has been accepted for publication in *Estuarine and Coastal Marine Science*.

The presentation of individual papers and the general conclusion are followed by an appendix, referred to above and in the text. Finally, a supporting paper on the

larval development of the barnacle Tetraclita serrata Darwin, referred to in paper 2, has been included. Barnacle nauplii generally feed on phytoplankton, however during attempts to rear this species it was found that the nauplii are carnivorous and select Choromytilus ova from a variety of organisms offered in the plankton. T. serrata was reared to cyprid stage on this diet and the larval stages described. Although no further evidence is available, the nauplii may be important predators of the early mussel developmental stages.

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PAPER 1. REPRODUCTIVE CYCLES IN LITTORAL POPULATIONS OF

CHOROMYTILUS MERIDIONALIS (KR.) AND AULACOMYA ATER

(MOLINA) WITH A QUANTITATIVE ASSESSMENT OF GAMETE

PRODUCTION IN THE FORMER.

J. exp. mar. Biol. Ecol., 1977, Vol. 30, pp. 53-71
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REPRODUCTIVE CYCLES IN LITTORAL POPULATIONS OF
CHOROMYTILUS MERIDIONALIS (Kr.) AND *AULACOMYA ATER* (Molina)
WITH A QUANTITATIVE ASSESSMENT OF GAMETE PRODUCTION IN
THE FORMER

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Abstract: Changes in ovary weight and ovary smears of *Choromytilus meridionalis* (Kr.) and *Aulacomya ater* (Molina) showed the breeding season to extend throughout the spring and summer months (Aug.-Feb.). Release of gametes was intermittent with regeneration of the gonad after peak spawning periods. Populations spawned synchronously or asynchronously with an average of 50% of individuals spawning at any one time. The end of the breeding season was marked by gonad depletion and resorption of gametes. Gametogenesis followed rapidly and large quantities of reserve material were not deposited in the mantle during the winter months as in *Mytilus edulis*.

The False Bay population of *Choromytilus meridionalis* has predominantly synchronous spawning and gamete production for two breeding seasons was calculated. The quantity of gametes released varied annually and was not significantly different in males and females. Mean gamete production was calculated as $1.17 \times$ standing crop expressed as dry flesh weight, or $1.33 \times$ energy value of the standing crop per annum.

INTRODUCTION

Although there is considerable information on the distribution patterns and zonation of South African marine invertebrates little is known of their reproductive cycles and larval development. Data have now been collected to establish their general reproductive patterns and spawning periods. Information on the reproductive cycles of South African marine mollusca is restricted to description of the spawning seasons of the abalone (Newman, 1970), the sand mussel (De Villiers, 1973), and seven species of *Patella* (Branch, 1974). No data are available on the dominant bivalve species of South African rocky shores.

MATERIALS AND METHODS

Samples were collected at monthly intervals at low water spring tide from Bailey's Cottage, False Bay (Indian Ocean), and Bloubergstrand, Table Bay (Atlantic Ocean). *Choromytilus meridionalis* (Kr.), the principle subject of the study, was collected over a 2½-year period and *Aulacomya ater* Molina for 20 months for comparative purposes. Sampling at each collecting site was done within a limited area to reduce possible

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variation in reproductive pattern due to difference in habitat or environmental conditions.

ANALYSIS BY WEIGHT

A rapid and quantitative method of gonad analysis was required and a weighing technique was used in preference to histological sectioning as used by Chipperfield (1953) and Wilson & Hodgkin (1967). This method provided a quantitative estimate of gonad production which may be used in comparing reproduction in populations from different areas. Such analyses have been used by Branch (1974) for limpets, Baissac (unpubl.) for the oyster *Crassostrea cucullata*, and for the bivalve *Scrobicularia plana* by Hughes (1970). This technique should be supported by some form of histological analysis to detect changes in gonad structure which may affect weight, e.g., accumulation of reserve material and the presence of parasites. Weight analysis of bivalves is complicated by the fact that the gonad cannot be separated from the rest of the body and must be weighed together with the visceral mass. It is, therefore, necessary to assume minimal seasonal variation in body parts other than the gonad. Reserve material (glycogen and fat), when present in bivalves, is deposited in the mantle, e.g., *Mytilus edulis* (Chipperfield, 1953) and oysters (Loosanoff, 1962) where its presence may be easily observed by histological sectioning and gonad smears. It is usually deposited during winter months when the animals remain in a sexless condition and is used in gamete formation in the spring. Provided the presence of such reserve material is noted it does not affect the analysis.

Monthly samples of ≈ 20 –25 mussels (selected to cover the size range of adults present) were placed in a deep-freeze for two days prior to preservation in 5% formalin. Freezing causes the shells to open and facilitates preservation and later removal of the body from the shell. All samples were preserved for a minimum of three weeks prior to gonad analysis. The small and insignificant change in weight on preservation with formalin (Branch, 1974) stabilizes within three weeks.

Shell length was not used as a criterion of size of individual because of the possibility of this varying with habitat, density, and age – particularly when comparing populations from two different coasts (Dehnel, 1956; Lubinsky, 1958; Seed, 1968). The weight of the posterior adductor muscle was considered to give the best estimate of body size. When plotted against body minus adductor weight (i.e., with shell, byssus, and posterior adductor removed, hereafter referred to as body weight) a linear relationship is found for samples in which the individuals are in a similar state of gonad development. Baissac (unpubl.) has found a similar linear relationship in the oyster *Crassostrea cucullata*.

The mussels from each monthly sample were removed from their shells, drained, and the byssus discarded. The posterior adductor muscle was removed and the wet weight of this and the body without the adductor determined. The appropriate regression equation allowed the body weight of standard animals of 3 or 4 selected

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adductor weights to be calculated. The standard individuals were chosen to represent the normal size range of the population sampled and this allows a comparison of mussels from the two collection sites to be made. A plot of the estimated body weight of standard animals from each monthly sample gives the change in gonad weight during the sampling period (see Fig. 5). Male and female *Choromytilus meridionalis* were analysed separately. In *Aulacomya ater* there was little difference in the results from males and females and so those from the two sexes were combined.

During months of spawning a plot of body against adductor weight showed considerable scatter. From subjective grading of the external appearance of the gonad and smears of the ovary, spawned and unspawned animals could be distinguished, and separate regression lines fitted to each category. In this way, for each standard sized animal, two values of body weight were obtained, the area between these values representing the difference in gonad weight due to spawning (shaded areas in Fig. 5). In all cases the correlation coefficient was > 0.9 . In a few samples one or two individuals were found in which the weight did not agree with the bulk of the sample and these were omitted from the calculations so as to obtain a more representative estimate of the majority of the population.

All calculations were done using a FORTRAN V programme on a Univac 1106 computer.

GONAD SMEARS

A gonad smear of a part of the ovary of each female was made and the number of previtellogenic, immature, and mature ova in one microscope field ($\times 100$ magnification, $100 +$ ova) was counted. These were reduced to percentages and the mean value of each category for each monthly sample was examined (Fig. 5). This method was used by Branch (1974) for limpets. Both samples from different areas, and histological sections, showed no observable difference in structure or state of development within the gonad of an individual mussel.

SUBJECTIVE GRADING AND ARTIFICIAL FERTILISATION

Several adults were opened each month and the gonad stripped for artificial fertilization of the oocytes, either in the field or in the laboratory within a few hours of collection. The motility of the spermatozoa was noted; when mature they become motile within a few minutes after addition to sea water. Ova to which a small quantity of semen was added (at least two males and two females were used) were maintained in the laboratory for 24 h and examined for cleavage stages. This technique allowed an assessment of maturity of ova in *Choromytilus meridionalis*. Successful fertilization was not obtained in *Aulacomya ater*; several methods of artificial induction of

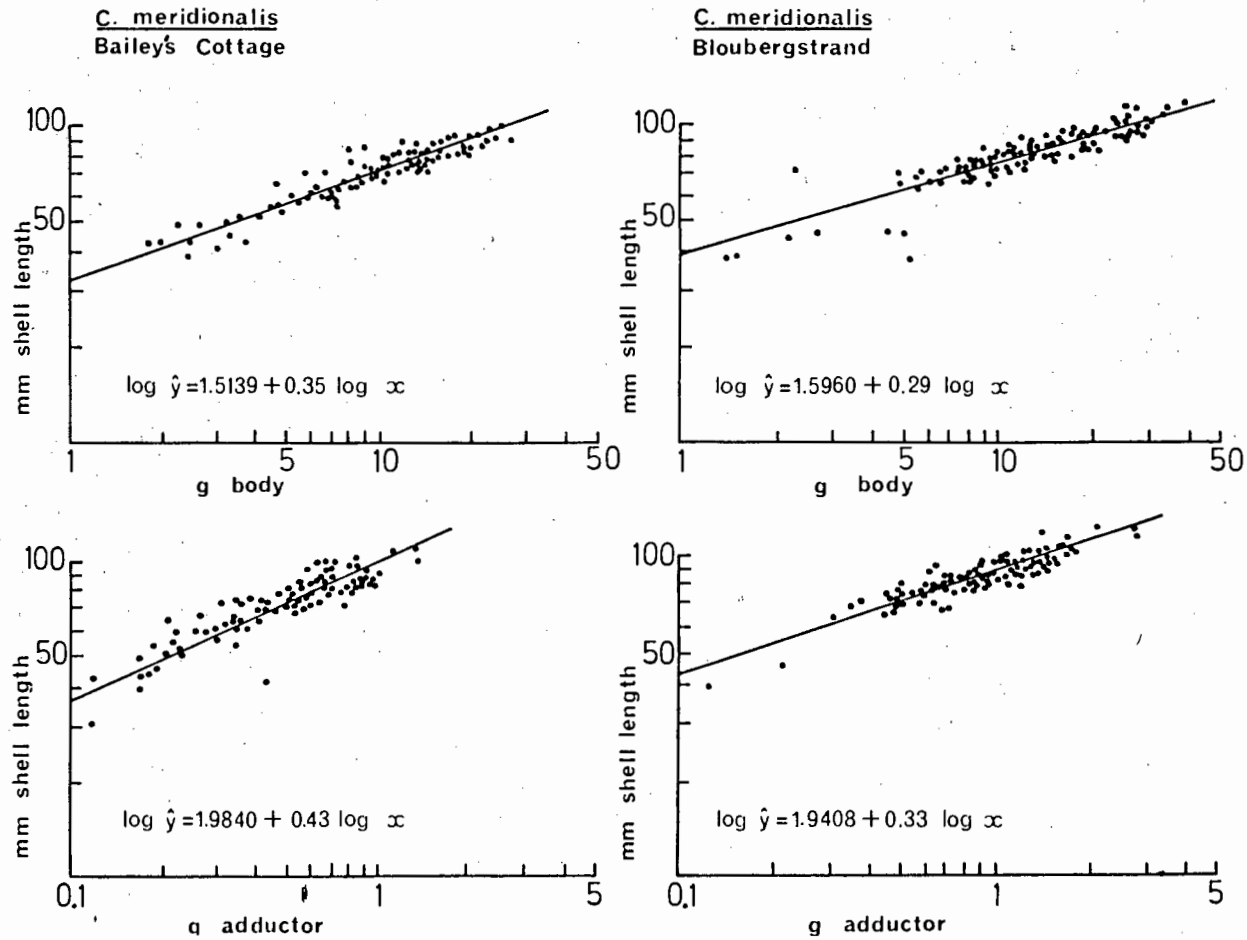


Fig. 1. Relation between weight of posterior adductor muscle and shell length for *Choromytilus meridionalis* collected during 1974 from Bailey's Cottage and Bloubergstrand.

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maturation division in ova, and of spawning (Kume & Dan, 1968) were attempted without success.

Each mussel used for weight analysis was subjectively graded as regards the external appearance of the gonad (thick, thin) and smears were assessed for the appearance and density of mature ova and the presence of interfollicular material (spawned, mature, developing). This was useful in interpreting weight data and egg counts.

HISTOLOGY

Portions of the gonad cut from the mantle were embedded in paraffin wax, sectioned at 8 μm and stained in Haematoxylin-Eosin. Sections were used to determine the gonad structure and quantity of interfollicular reserve material present and to confirm the analysis of egg smears.

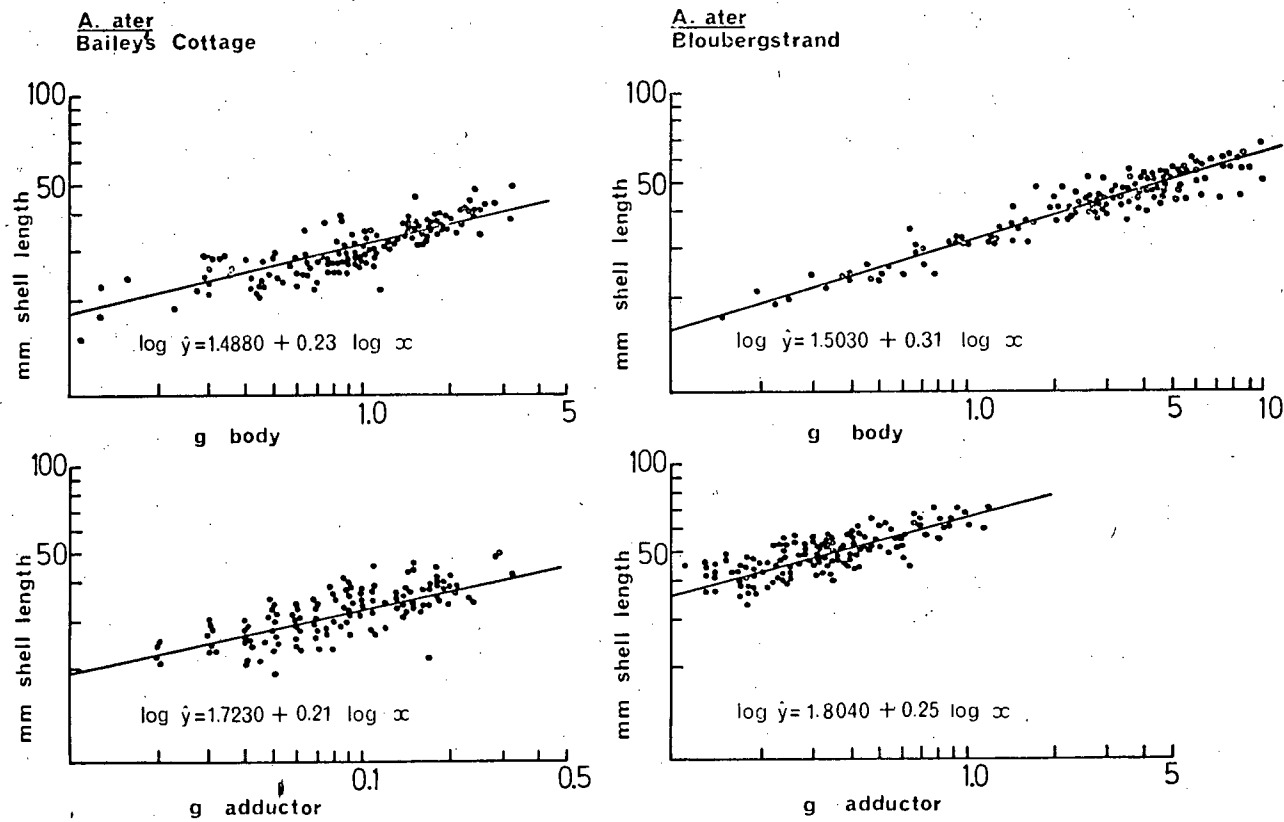
RESULTS

Choromytilus meridionalis has a 'patchy' distribution on the west and south coasts of southern Africa, occurring in dense beds or not at all. It extends from the sublittoral (20–30 m depth, rocky substrata) into the balanid zone, frequently in areas of considerable water turbulence and sand movement on gently sloping rocky platforms. *Aulacomya ater* extends deeper than *Choromytilus meridionalis* and forms extensive beds on rocky substrata and in kelp holdfasts. It is the dominant mussel and frequently the dominant animal on sublittoral rocks (Velimirov *et al.*, 1977). *Aulacomya ater* extends into the littoral zone but there the animals are smaller. Littoral *A. ater* in False Bay are stunted in growth, less common, and are restricted to habitats which compared with those in Table Bay (see Fig. 3), must be considered protected.

LENGTH-WEIGHT RELATIONSHIPS

Figs 1 and 2 show the relation between adductor and body weights and shell length in *Choromytilus meridionalis* and *Aulacomya ater* collected over a 12-month period at Bailey's Cottage and Bloubergstrand. There was no significant difference between the slopes and intercepts of the regression lines from the two collecting sites nor differences between males and females. The scatter in body weights is due to the presence of individuals in different stages of spawning. Variability in posterior adductor weight for any shell length may be due to differences in shell width, particularly in *A. ater* where this is pronounced, or adductor size may vary according to degree of exposure to wave action (not tested). No seasonal changes in adductor weight were found.

The size-frequency distribution of mussels collected during a 12-month sampling



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Fig. 2. Relation between weight of adductor muscle and body and shell length of *Aulacomya ater* collected from Bailey's Cottage and Bloubergstrand.

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period is shown in Fig. 3. There was no detectable size difference between the sexes. In both species, larger individuals were found on the west coast, particularly in the sublittoral zone where they attain a considerably larger size than littoral animals (120–150 mm shell length in *Choromytilus meridionalis*, 70–80 mm in *Aulacomya ater* is not uncommon). Littoral *A. ater* in False Bay are particularly stunted and restricted to rock crevices and overhangs.

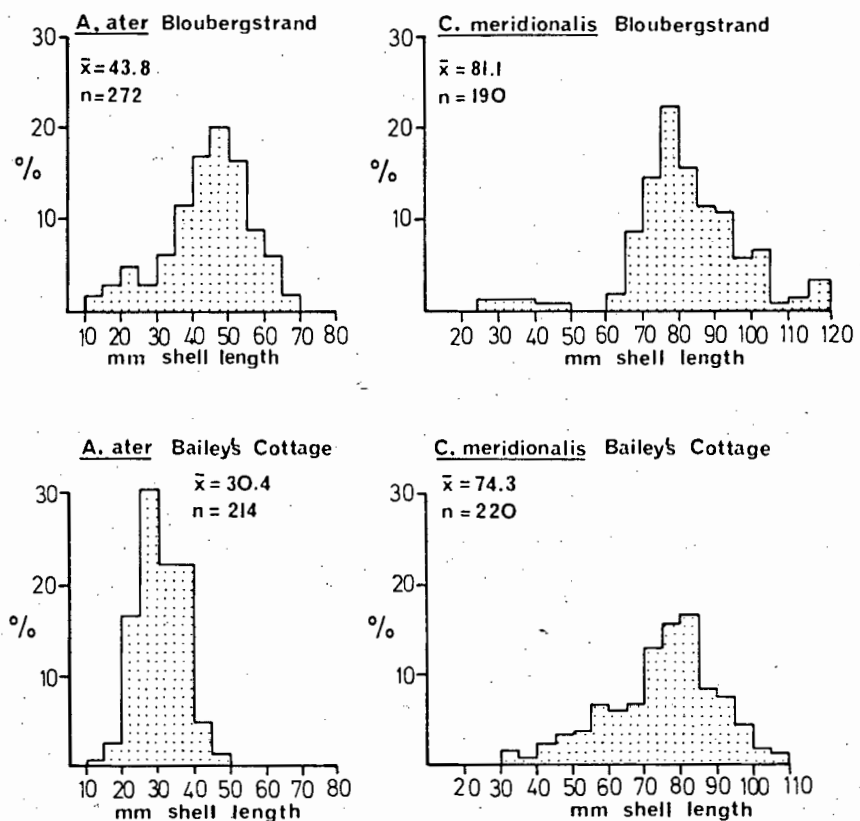


Fig. 3. Size-frequency distribution of *Choromytilus meridionalis* and *Aulacomya ater* collected from Bailey's Cottage and Bloubergstrand during 1974. --

CHOROMYTILUS MERIDIONALIS GONAD STRUCTURE

The sexes are separate and females may be distinguished by the chocolate-brown colour of the ovary, while the testis is yellow to white, depending on its state of development. No hermaphrodites were found. The gonad in *C. meridionalis* (and *Aulacomya ater*) ramifies over, and into, the visceral mass and extends into the mantle as described by White (1937) for *Mytilus edulis*. In mature animals the gonad extends as a thickened lobe in the midline between the gills, posterior to the foot.

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Gonad development is similar to that described by Wilson & Hodgkin (1967) except that fewer phases of development can be distinguished because of the rapid and continual gametogenesis throughout the breeding season and the frequent absence of a post-spawning resting phase with its associated proliferation of interfollicular material common in other species. In *M. edulis* this material has been shown to serve as a nutrient reserve which is utilized during oogenesis and vitellogenesis (reviewed by Gabbott, 1976). In *Choromytilus meridionalis* the spawned gonad is thin and transparent so that the remaining follicles can easily be distinguished. Resorption of mature gametes by phagocytic cells occurs. Females at Bailey's Cottage may lose all trace of gonad, although this condition is not common and in three years of observation occurred only in samples collected in the first few months of 1976. Females were distinguished by the presence of patches of yellowish-brown vitelline material in the mantle. Males do not show complete regression of the gonad; testis is always present, although the spermatozoa may not be mature. Gametogenesis in both sexes usually occurs soon after spawning and smears show previtellogenic, immature, and resorptive ova. Proliferation of interfollicular material takes place at this time, but is small and forms only a thin layer between the follicles. Gonad smears may be ambiguous, and throughout most of the year show mature sized ova and spermatozoan development but this does not indicate maturity and readiness to spawn. The gonad may appear 'ripe' for several months prior to spawning but during this period the results of artificial fertilization are poor with a high percentage of abnormally developing embryos. This is not the case once spawning begins. During the winter months the gonad may show regression with a decline in the body weight of the animal, and this may represent periods of poor food availability and utilization of the gonad as an energy source.

Mature ova may be rounded (60–70 μm diameter), or elongate with one end attached to the germinal epithelium. When placed in sea water they assume a rounded shape within 30 min and may be successfully fertilized before or after rounding. Spermatozoa usually show motility 5 min after addition to sea water. Fig. 4 shows typical ovary smears and sections of the gonad.

CHOROMYTILUS MERIDIONALIS REPRODUCTIVE CYCLE

The results of the weight analysis and egg smears are shown in Fig. 5. Intermittent gamete release took place over several months with peak periods which varied annually in timing and intensity. There was a rapid regeneration of the gonad between spawning peaks. The end of the breeding season was marked by the poor condition of the gonad. Small individuals had a limited synchronous spawning period preceded by a short conditioning period. The spawning season of mussels at Bailey's Cottage lasted for 7 months (Aug.–Feb.). There were 2 or 3 peak periods of gamete release during this time. Gamete release in males was more gradual and extended over a slightly longer period than that of females. In 1974 synchronous release of ova took

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place in January/February (end of previous season), August, October/November and January 1975. Gametogenesis during spawning was extremely rapid and mature ova were always present in gonad smears. During 1975 the gonad remained thin

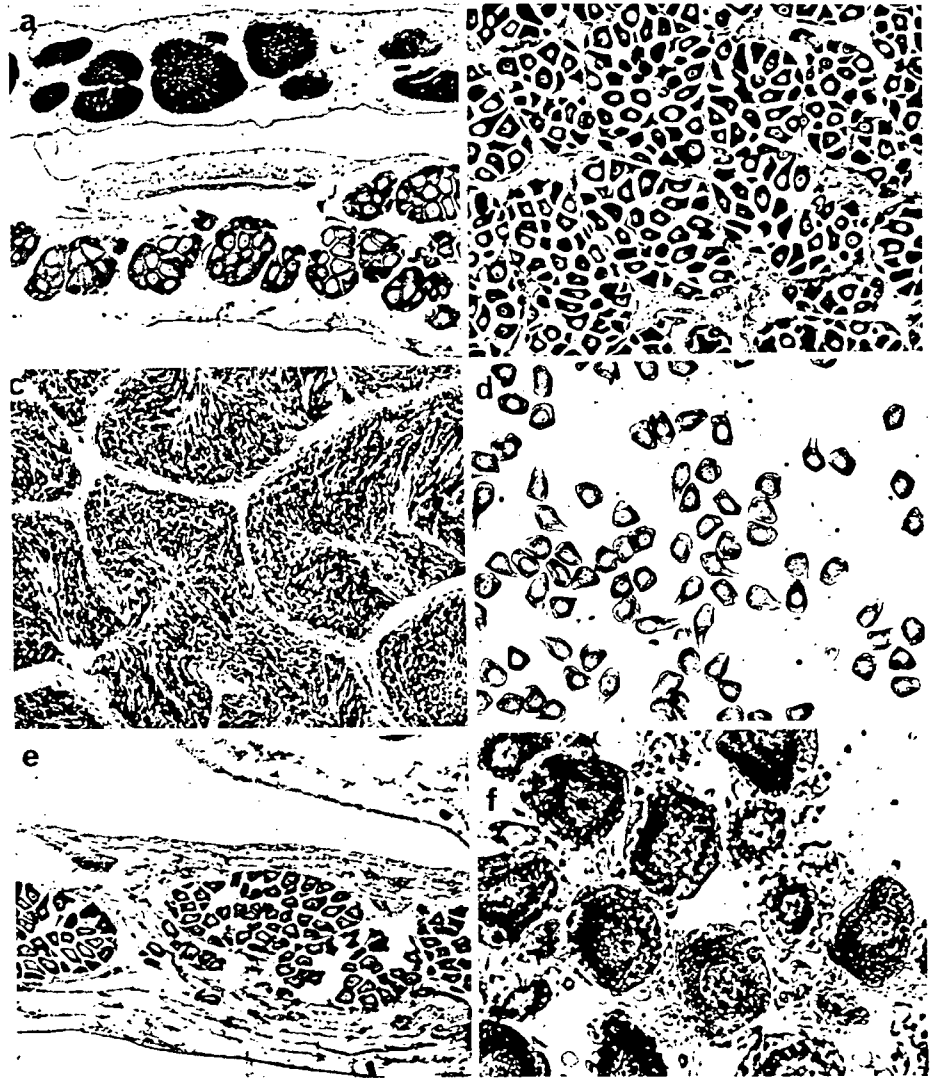


Fig. 4. *Choromytilus meridionalis*: a. T.S. of developing gonad in juvenile male and female; b. T.S. of mature spawning female showing continuous oogenesis; c. T.S. of mature male; d. gonad smear of 'ripe' female with predominantly mature oocytes; e. T.S. of spawned female at end of breeding season with characteristic incomplete spawning; f. gonad smear after end of breeding season showing resorption of oocytes.

with little regeneration prior to the September spawning. Rapid development took place in November, and in December there was an unusually synchronous and rapid spawning (over 2 weeks) with complete loss of gametes in 80% of the female popu-

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lation. This was accompanied by slight proliferation of interfollicular material, but this was insufficient to thicken the mantle which remained thin and gelatinous in appearance until May 1976 when regeneration of the follicles began. Males retained

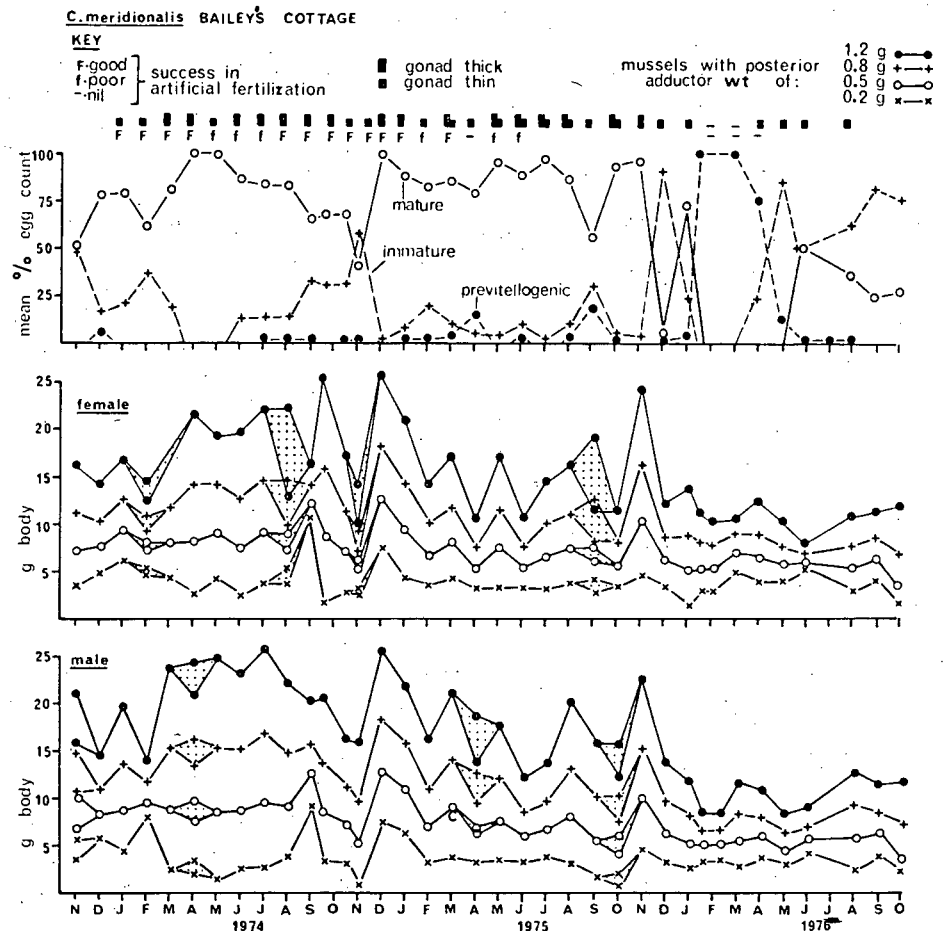


Fig. 5. Results of gonad analysis of *Choromytilus meridionalis* from Bailey's Cottage: change in body weight of standard sized animals of adductor muscle weight 0.2–1.2 g; mean percentage of previtellogenic, immature, and mature oocytes present in ovarian smears of monthly samples; variation in success of artificial fertilization, and visual assessment of gonad development in samples collected 1973–76.

a small number of follicles throughout this time. Normally gametogenesis took place within one month of the end of the spawning period.

The reproductive cycle of mussels at Bloubergstrand was similar to that given above (Fig. 6). The major spawning was in August or September and then from late December to February/March. There was continual regeneration of the gonad during

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spawning and sudden total release of all gametes was not observed, so that the gonad usually appeared in good 'condition' with a high percentage of mature ova. It is probable that there is continuous spawning throughout the year in a small percentage of mussels from both localities.

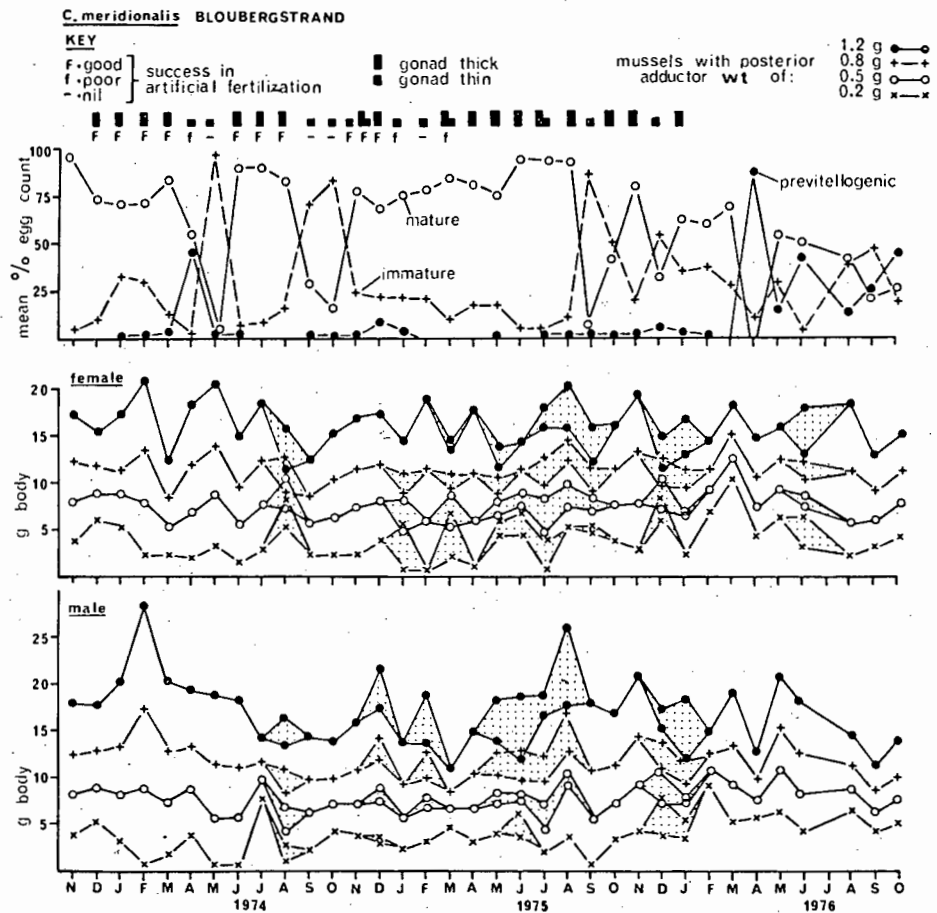


Fig. 6. Results of gonad analysis of *Choromytilus meridionalis* from Bloubergstrand: change in body weight of standard sized animals of adductor muscle weight 0.2–1.2 g; mean percentage of previtellogenic, immature, and mature oocytes present in ovarian smears of monthly samples; variation in success of artificial fertilization and visual assessment of gonad development in samples collected 1973–76.

There was an equal distribution of the sexes at Bloubergstrand but in False Bay of the 700 adults sampled 43% were female. A χ^2 test showed that this differs significantly from an expected 50% ($P < 0.001$). This cannot be attributed to size selection during sampling since males and females are not significantly different in shell length or body weight.

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AULACOMYA ATER GONAD STRUCTURE

The structure and seasonal development of the gonad is similar to that of *Choromytilus meridionalis* and differs only in the presence of interfollicular material during the non-breeding period (Fig. 7).

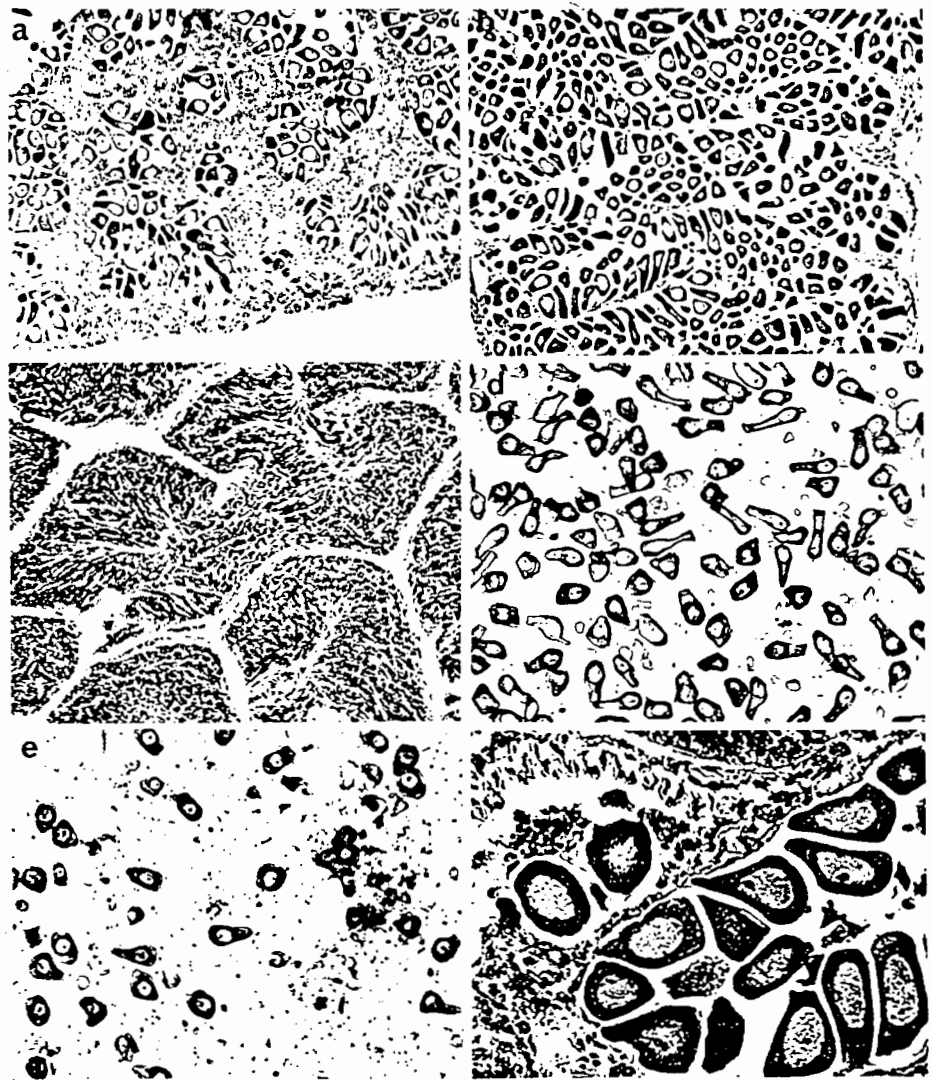


Fig. 7. *Aulacomya ater*: a. T.S. of developing ovary in juvenile mussel; b. T.S. of mature ovary; c. T.S. of mature testis; d. gonad smear of mature spawning female with continuous oogenesis; e. gonad smear of female at end of spawning season with increase in interfollicular material; f. T.S. of spawned ovary showing start of resorption.

Separate analysis of weight data from males and females showed no significant difference and so the results were pooled. C. L. Griffiths (unpubl.) working on sub-

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littoral *Aulacomya ater* has also found no significant difference in the amount of gamete material released between the sexes during spawning.

AULACOMYA ATER REPRODUCTIVE CYCLE

The breeding season at Bailey's Cottage was similar to that of *Choromytilus meridionalis* and extended from August/September to January or March (Fig. 8)

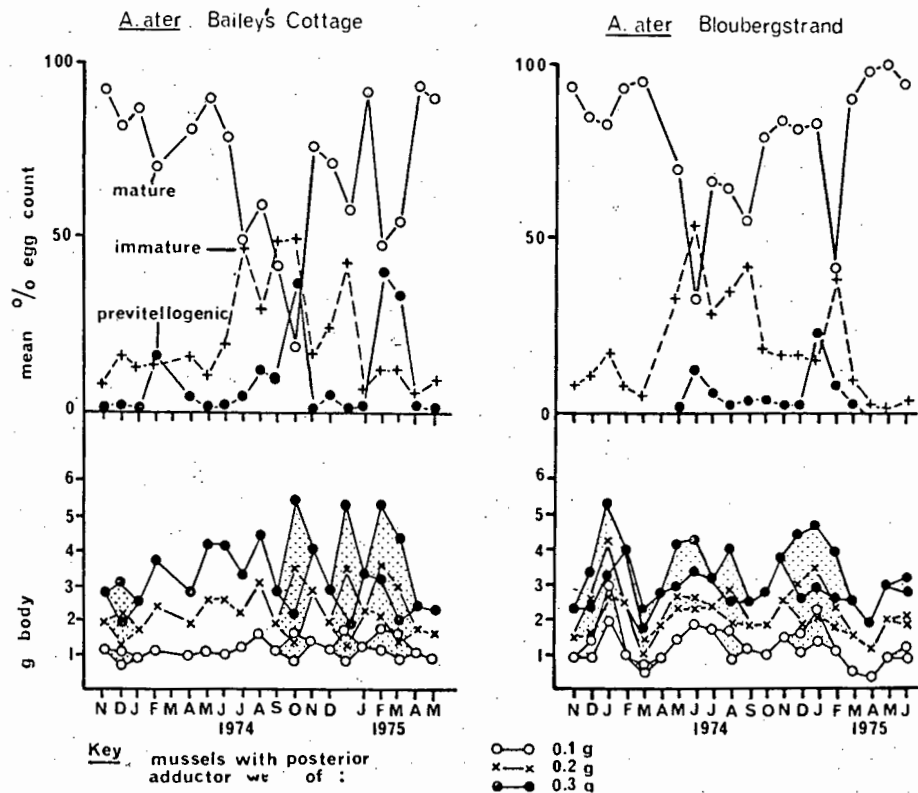


Fig. 8. Change in body weight of standard sized (adductor wts 0.1, 0.2 and 0.3 g) *Aulacomya ater* and mean percentage of previtellogenic, immature and mature oocytes present in gonad smears of monthly samples.

In 1974/75 there were three peak periods of gamete release (Oct., Dec., and Feb./March). Spawning individuals showed the development of interfollicular material but this did not thicken the gonad to the extent found in *Mytilus edulis* and it was utilized during gametogenesis which took place soon after spawning. The mature gonad showed only small quantities (if any) of nutrient reserve between the follicles.

Mussels at Bloubergstrand had two major annual spawning periods, December/January–March and June–August. There was a marked change in body weight with rapid development of the gonad prior to spawning. Interfollicular material was small

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and did not thicken the mantle to any extent. C. L. Griffiths (unpubl.) has determined the spawning season of sublittoral *Aulacomya ater* and found synchronous release of gametes from September to December, 1975 and in April, 1976. There were thus two peak periods annually but these were slightly in advance of the littoral population.

It is probable that a small percentage of the population on the west coast spawn continuously throughout the year as in *Choromytilus meridionalis*. Continual settlement of spat has been found, although this is very small compared with the peak period settlement, and in adult populations of *Aulacomya ater* it is normally difficult to distinguish cohorts on the basis of size classes.

DISCUSSION

The time of spawning in bivalves may vary with habitat (Young, 1945; Wilson & Hodgkin, 1967) and shore level (Dehnel, 1956; Seed, 1969), and attempts to determine the factors which induce spawning are still inconclusive (reviewed by Chipperfield, 1953; Seed, 1976). Young (1945) found variability in the behaviour of *Mytilus californianus* when subject to the same spawning stimulus and also a difference in the reaction of any single mussel to the same stimulus applied at different times. It is now generally accepted that spawning is induced by a combination of environmental factors and that their interaction may vary seasonally, so that there are annual variations in onset and intensity of spawning.

In asynchronous, intermittent spawning, as in *Choromytilus meridionalis* and *Aulacomya ater*, stimuli which initiate maturation and spawning must recur over several months. Elevated sea temperatures, temperature, shock *etc.*, have been found to induce spawning of many mussel species in the laboratory (reviewed by Walne, 1964) and in *Choromytilus meridionalis* 'ripe' individuals may occasionally be induced to spawn by heating and shaking vigorously enough to bang the shells against each other.

The major factors affecting local field populations are sea temperature, food availability and wave action, all of which are directly related to prevailing weather conditions. In mussels which do not store large reserves in the mantle and which have intermittent gonad regeneration, immediate food availability must be of prime importance in maturation of the gonad. The maturation period and the time of year at which animals become receptive to spawning stimuli will vary according to conditions which result in upwelling and its associated phytoplankton blooms (west coast), or merely rough sea conditions producing mixing of the inshore waters and suspension of organic debris (False Bay). During winter months (April-Aug.) a N.W. wind predominates which produces storms and strong wave action on the west coast. Thereafter, the wind slowly changes to S.E. which results in periodic upwelling of cold clear water which is nutrient-rich and which gives rise to large phytoplankton and zooplankton blooms. This has been shown to take place mainly in September and from November to February (Hutchings, Sea Fisheries Branch,

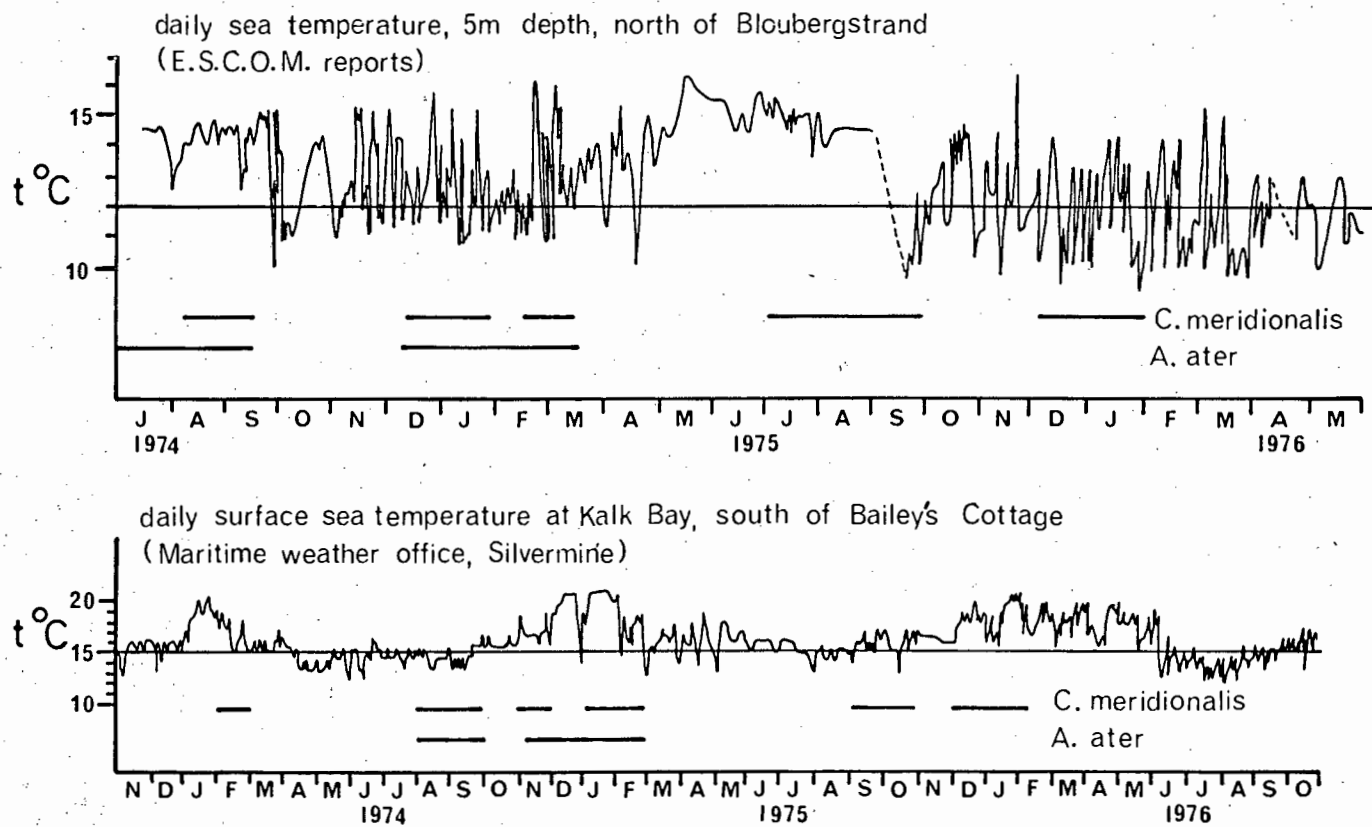


Fig. 9. Daily sea temperature in vicinity of the collecting sites and the spawning seasons of *Choromytilus meridionalis* and *Aulacomya ater* as determined by gonad analysis: sampling of *A. ater* discontinued after June, 1975.

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unpubl.). Fig. 9 shows daily sea temperatures north of Bloubergstrand and south of Bailey's Cottage, reflecting temperatures at the collecting sites. Upwelling at Bloubergstrand is indicated by the rapid decline and fluctuation in temperature between August and February. In False Bay the S.E. wind causes intermittently rough conditions and there is a gradual rise in sea temperature through the summer, with an occasional rapid decline in temperature due to upwelling (see Fig. 9, Dec. and Feb.). Thus, food availability may be of greater importance in maturation of the gonad than temperature which differs considerably on the two coasts. Once maturation is complete some stimulus must be required to initiate spawning since gamete release does not necessarily immediately follow maturation. Temperature may at this time become an influencing factor, particularly the rate of change of temperature since it is an indicator of upwelling, an advantageous time for larvae to feed in the plankton. Supporting evidence for this is the spawning noted at Bailey's Cottage which was synchronous with a period of upwelling in Jan.-Feb. 1974 and the rapid and complete spawning over a two week period in late December 1975.

Measurement of fecundity in mytilids has previously been based on egg counts, a method which has produced highly variable results (Bayne, 1976). Weight analysis on pre- and post-spawning field populations gives a better estimate of fecundity. This method is, however, based on the assumption that major changes in body weight are due to gonad development and that the remainder of the body does not undergo cyclical change.

The results of weight analysis of *C. meridionalis* over a year are given in Fig. 10. Assuming that all individuals attain the same degree of gonadal development and then spawn completely, the loss in weight of gametes is 50-60% of the body weight of an unspawned animal of any size. This species shows gonadal regeneration and consecutive spawning during the breeding season and so the total amount spawned is considerably greater. A direct assessment of fecundity may be obtained from Fig. 5 where synchronous weight changes predominated and the end of the breeding season was marked by gonad depletion. The loss in weight after March was due to resorption of the remaining gonad. The fecundity of standard sized animals was calculated for two breeding seasons, 1974-75 and 1975-76 (Fig. 11) by summation of the loss in body weight at each spawning during a breeding season (July-Feb.). Total loss due to gametes was greater in 1974-75 and there was a slight difference between the sexes. Mussels < 20 mm shell length are immature. Fecundity does not increase linearly with size expressed as adductor weight and this may be due to differential regeneration of the gonad, particularly in females where large mussels show three major periods of gamete release compared with two in young individuals.

From Fig. 11 the mean fecundity of mussels in different shell-length size classes may be calculated to give the gamete production of the midshore population of *C. meridionalis* at Bailey's Cottage during the 1975-76 breeding season (Fig. 12). The biomass (mean of 3 samples) was 790 g/m² dry flesh weight + 505 g/m² organic content of shell = 1295 g/m² (organic content of shell of mature adults = 7.4% of

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dry shell weight and 64 % of dry flesh weight). This amounts to a total biomass energy value of 25668 kJ/m². The calculated gamete production of the population was 1516 g/m²/yr or 34144 kJ/m²/yr. Calorific values, determined using a Ballistic

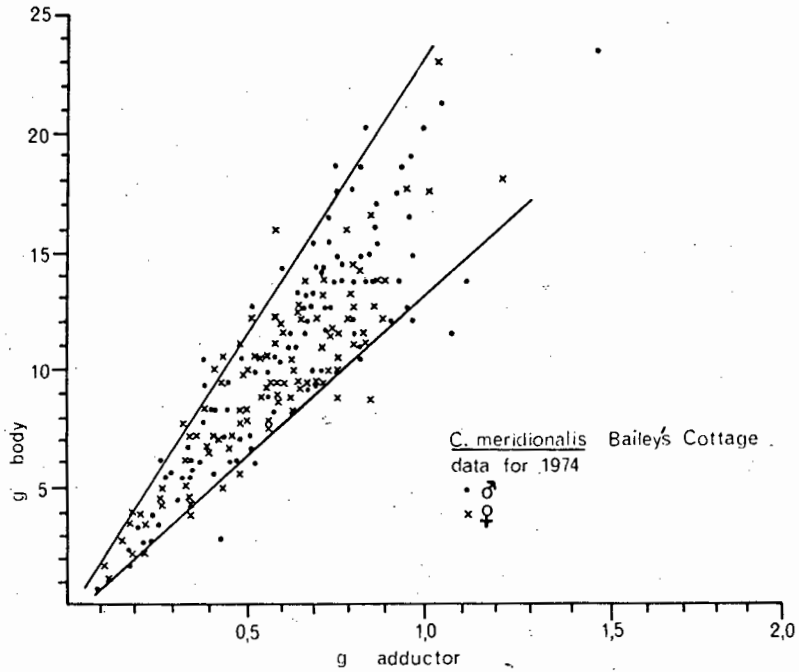


Fig. 10. Relation between body and posterior adductor muscle weights for all *Choromytilus meridionalis* collected during 1974: area between lines indicates variation in body mass due to spawning.

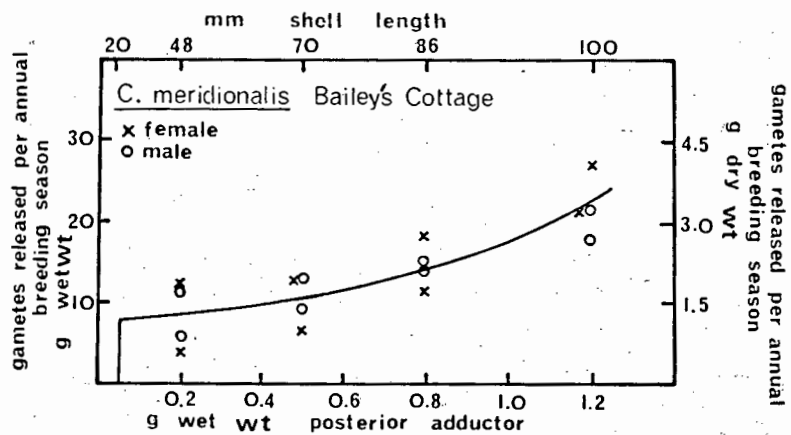


Fig. 11. Calculated total gamete loss in 4 sizes of male and female *Choromytilus meridionalis* at Bailey's Cottage during 1974-75 and 1975-76 breeding seasons.

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Bomb Calorimeter, were as follows: dried whole mussel minus shell and byssus 19.5, shell organic content 20.3, ovary 23.8 and testis 21.2 kJ/g (mean of several samples).

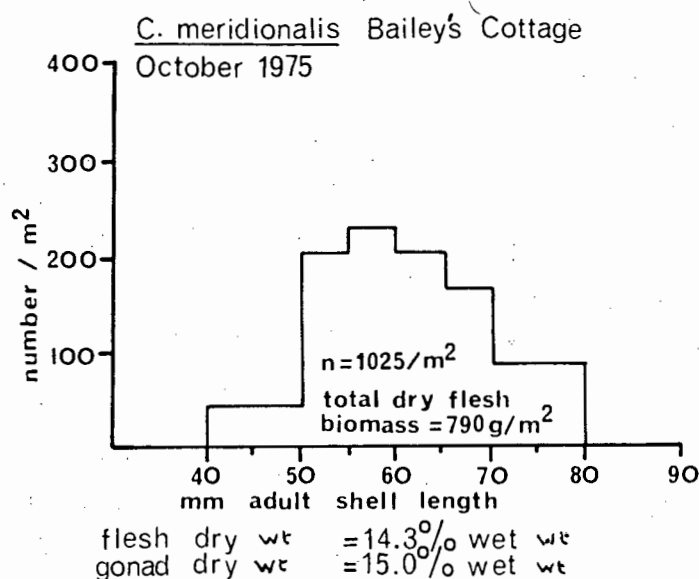


Fig. 12. Size-frequency distribution of the mid-shore population of *Choromytilus meridionalis* sampled in October 1975 (mean of 3 samples. 1/40 m²).

The mean reproductive output is $1.17 \times$ biomass, or $1.33 \times$ energy value of the standing crop per year. This value may be considerably higher in a 'good' year (max. values in Fig. 11). This compares favourably with data on *Mytilus edulis* (*Choromytilus meridionalis* closely resembles this species) by Dare (1975, quoted by Seed, 1976 where the standing crop was 1.2 kg/m^2 or 27588 kJ/m^2 . The production:biomass ratio was 2.5 to 3, about twice that given above; however, for *Mytilus edulis*, the total production and not merely gonad production was calculated. It is interesting to note the similarity in biomass of the two species and that Dare has suggested that this is the 'carrying capacity' of the area at Morecambe Bay, U.K. This also appears to be the case in False Bay where a solid mussel bed of maximum density is formed over the rock substrata. Total gamete production may be expected to vary with size (Fig. 11) and density of adults, and possibly with shore level. The annual energy export from a mussel bed in terms of gametes is thus extremely high.

ACKNOWLEDGEMENTS

My thanks are due to Miss F. Stratton for assistance in gonad analyses and computer card punching. This work was supported as part of the Kelp Bed Research Programme by the South African National Committee for Oceanographic Research.

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PAPER 2. POPULATION DYNAMICS AND GROWTH OF THE BIVALVE

CHOROMYTILUS MERIDIONALIS (KR.) AT DIFFERENT TIDAL LEVELS.

Population Dynamics and Growth of the Bivalve
Choromytilus meridionalis (Kr.) at Different
Tidal Levels

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Keywords: Bivalves, population dynamics,
growth rates, reproduction,
littoral.

Settlement, growth, and reproductive output of a population of Choromytilus meridionalis have been monitored at different shore levels at Bailey's Cottage, False Bay, South Africa. Settlement was irregular, occurring at 4 to 6 year intervals, and confined to the sublittoral and lower littoral of rocky areas. Spat settled on the existing mussel bed and adjacent clean rock surfaces. Continual migration of young mussels up the shore took place during the first 1 to 1.5 years of growth until an even distribution up to 0.5 m above L.W.S. was achieved. Juveniles displaced older individuals by moving between them and

forcing them off the rocks so that the majority of the adult population were eliminated from the bed within the first year after spat settlement. Mortality in individual cohorts was largely caused by strong wave action and competition for space. The density of individuals within the mussel bed was closely related to mean shell length.

Growth rates varied with habitat and declined markedly with increasing height above L.W.S..

Sexual maturity was attained at approximately 20 mm and reproductive output rose from 5 kJ y^{-1} at this length to 80 kJ y^{-1} at 100 mm shell length. Since packing densities were much higher in smaller individuals the annual gamete output assessed on an area basis, remained fairly constant as the mussels grew, and averaged $1392 \text{ g m}^{-2} \text{ y}^{-1}$ dry weight ($31320 \text{ kJ m}^{-2} \text{ y}^{-1}$). Energy expended as gonad output exceeded that due to mortality by a factor of ten.

Introduction

A considerable literature has recently become available on the population structure, breeding biology and physiology of bivalves, in particular Mytilus edulis. Much of this work has been reviewed by Seed (1976) and Bayne et al. (1976). On the South African coast, 3 dominant mytilid species inhabit the rocky littoral and sublittoral zones: the black mussel, Choromytilus meridionalis (Kr.) and the ribbed mussel, Aulacomya ater (Molina) are the dominant bivalves on the west and south coasts of southern Africa, whilst in the east these give way to the brown mussel Perna perna (L.). Berry (1978) has described the population dynamics and production of P. perna. This mussel grows rapidly; it may breed 6 months after settlement, and the average population survives 3 years. Preliminary observations indicate that C. meridionalis and A. ater have slower growth rates and longer population turnover times. Griffiths and King (1979a & b) describe the filtration and respiration rates and the very slow growth rate of A. ater. Although C. meridionalis appears to be more successful at colonising the littoral zone, particularly in sand abraded areas, (littoral A. ater are markedly stunted in growth

(Griffiths, 1977)). Field et al. (1980) have shown that A. ater is the dominant species in the rocky sublittoral of the west and south-west coast of southern Africa.

In order to investigate the variable spawning and spat settlement patterns demonstrated in C. meridionalis by Griffiths (1977) and du Plessis (1977) and to obtain data comparable to that available for P. perna, A. ater and M. edulis, the reproductive output, population dynamics and growth of this species were studied.

Materials and Methods

(a) Study sites

Dense populations of Choromytilus meridionalis are found in the rocky littoral and sublittoral between Dalebrook and Muizenberg in False Bay, and on the west coast, particularly at Bloubergstrand and northwards (Fig. 1). In False Bay, areas are subject to considerable wave action and sand abrasion, particularly in summer (Sept. - Feb.), when a strong south-easterly wind predominates. Aulacomya ater and Perna perna are not common in False Bay although occasional P. perna are found amongst C. meridionalis

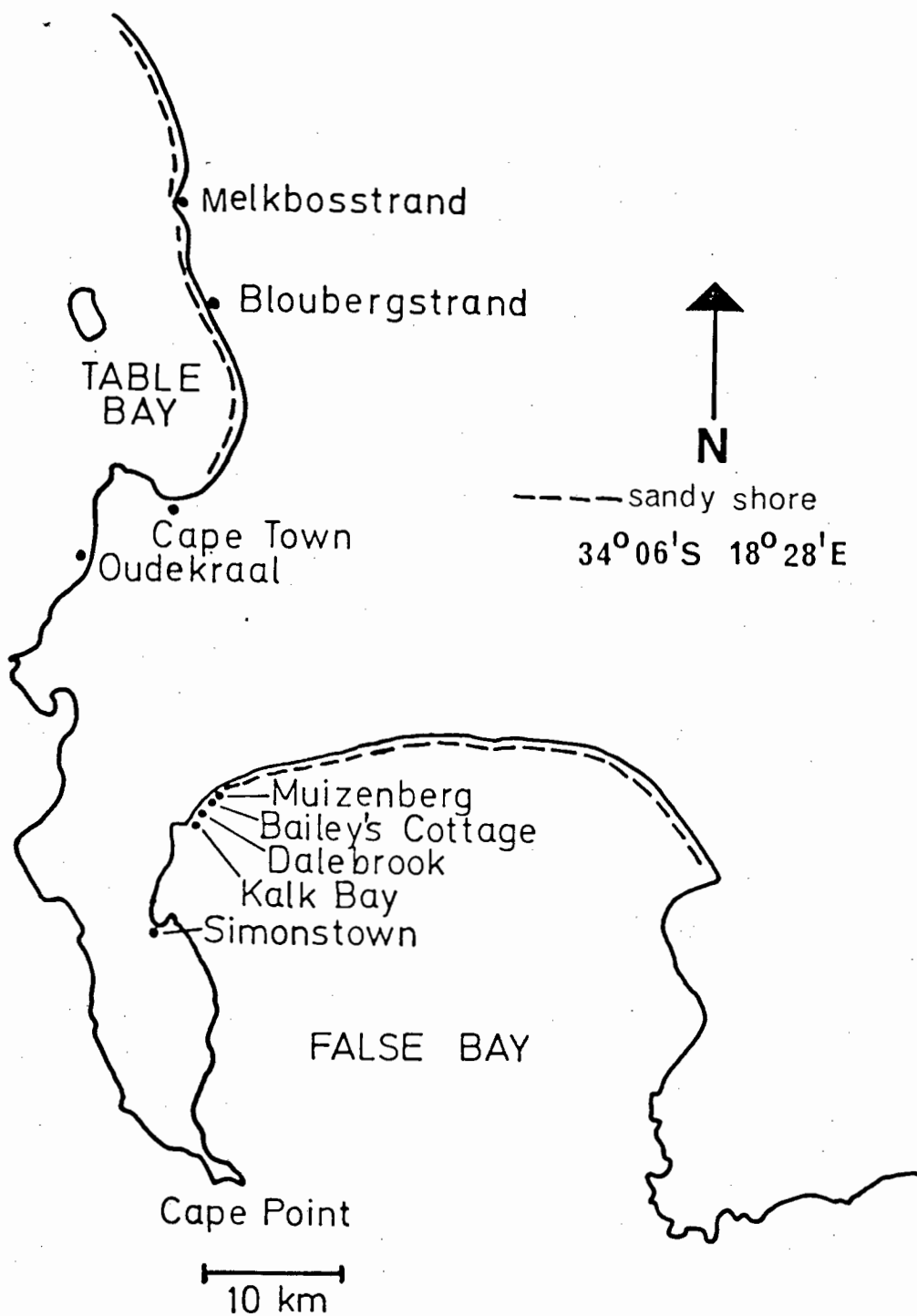


Fig. 1. Map of south western Cape Province showing collecting sites mentioned in the text.

on rocky platforms in the lower littoral. Both A. ater and P. perna occur amongst barnacles in the balanoid zone, where they appear to be severely stunted in growth.

C. meridionalis at Bailey's Cottage, the principle study site, form a dense continuous covering over the rocky substrate and sand filled gullies, from 3-4 m depth in the sublittoral, to approximately one metre above L.W.S. Because of the shallow offshore sandy substrate, the coastal area is subject to considerable sand movement (deposition and scouring) during strong wave action and changing water current patterns. The collecting sites at Bailey's Cottage were situated on a transect normal to the coastline, across the densely packed mussel bed. Mussels were sampled at different shore heights as follows:

BLWS - 0.5 m below L.W.S. where mussels were never exposed by the tide.

LWS - at or immediately above (0.16 m) L.W.S. where mussels were exposed for short periods only.

Midshore - 0.38 m above L.W.S. An area covered with numerous boulders and densely colonized by the alga Ulva sp. during summer.

Topshore - The highest point on the transect line at which C. meridionalis occurred, 0.5 m above L.W.S. (Adjacent to the transect line mussels occurred in damp crevices up to 0.85 m above L.W.S.).

At Dalebrook an isolated, densely packed population of C. meridionalis occupied approximately 4 m² of horizontal rocky surface immediately below L.W.S.. This area was first colonized in December 1974 and contained a single cohort throughout the study period. This was sampled in order to investigate the variability in population structure and growth which may occur in different habitats.

(b) Population studies

Choromytilus meridionalis, like some populations of Mytilus edulis (Seed, 1969), appears to favour gently sloping rocky platforms which are slow draining, and avoids steeper, fast-draining surfaces. Thus, mussels generally occupy horizontal surfaces. Samples of 1/40 m² were considered sufficient in size to reflect population density. These were removed from the mussel bed at 3-monthly intervals for growth and biomass analysis. At Bailey's Cottage 2 samples were taken at BLWS and Topshore

and 3 at LWS and Midshore. At Dalebrook a sublittoral sample was collected every 3 months for density, biomass and growth measurements. Only those mussels which had the anterior apex of the shell within the grid area were collected. Sample size and number were restricted for the following reasons. Densities were very high and appeared to be extremely uniform at any shore level. However, the area of substrate covered was limited. Removal of large samples, particularly in areas where sand had been deposited between the mussels, so that the byssus extended through several centimetres of sand to a rocky substrate, resulted in instability of the population around the edges of the cleared area.

All mussel shells were cleaned of epibiotic growth and the byssus was cleaned of adhesive shell and sand particles. The size-frequency distribution was plotted and the total dry weight (shell and byssus included) of each sample was measured. Because successive spat settlements were separated by several years, cohorts at Bailey's Cottage could be clearly separated on a shell length basis. If a sample contained more than one cohort, each was treated separately.

Large samples of mussels were collected adjacent to the transect line for length/weight analysis. The relationship between shell length and flesh, shell and byssus dry weight and ash free dry weight (450°C for 3h) was measured. The organic remains of shell and byssus were obtained by removal of CaCO_3 with dilute HCl. The energy equivalents of the different body components (Gallenkamp ballistic bomb and Phillipson microbomb calorimeters) were determined as described by Crisp (1971). Table 1 lists the regression equations obtained and other parameters necessary for comparison of C. meridionalis with other bivalves.

(c) Growth

Data obtained from measurements of length increments of mussels following an extensive spat settlement in December 1974 were fitted by computer to Gompertz, Sigmoid and von Bertalanffy growth curves using the method of least squares. The maximum shell length was not specified as this varied with sampling area. Field sampling did not give a reliable estimate of L_{max} (the maximum length attained (Thiesen, 1973)) because of the continuous process of elimination of larger mussels from the bed by competition and storm action.

Table 1. Length-weight, percentage composition and energy values for Choromytilus meridionalis from Bailey's Cottage. Extra conversions are included to facilitate comparison with published data. Equations in the form of $y = ax^b$ where x = shell length in mm.

y (grams)	a	b	r ²
Total dry weight	6.911×10^{-4}	2.291	.99
Dry flesh weight	1.251×10^{-5}	2.646	.98
Ash free dry flesh	1.2397×10^{-5}	2.626	.85
dry shell weight	7.934×10^{-4}	2.23	.99
dry byssus weight	2.5939×10^{-6}	2.524	.27
Mean annual gamete production (wet)	7.9×10^{-3}	1.615	.86
Mean annual gamete production (dry)	1.334×10^{-3}	1.615	.86

Composition of dry whole mussel	8.39 % flesh
	91.44 % shell
	0.17 % byssus
Composition of dry shell	95.58 % calcium carbonate
	1.002 % ash
	3.418 % organic matter
Composition of wet somatic flesh	82.12% water, 16.88% dry flesh
Composition of dry somatic flesh	11.61% inorganic material
	88.39% organic material
Energy values dry whole mussel (+ shell)	2.55 kJ g ⁻¹
dry flesh	19.5 kJ g ⁻¹
dry whole shell	0.957 kJ g ⁻¹
dry whole byssus	17.23 kJ g ⁻¹
dry gonad	22.5 kJ g ⁻¹

(d) Reproduction

Monthly samples of 20 to 25 mussels of different shell lengths were removed from the lower littoral at Bailey's Cottage adjacent to the transect line. Specimens were frozen and processed as outlined by Griffiths (1977), although the parameters used for monthly regression analyses were shell length and wet flesh mass. (In a previous paper, wet adductor mass was plotted against wet flesh mass, however regression analysis has shown the former to be linearly correlated to shell length, an easier parameter to measure). From the power curves generated for each monthly sample the weights of selected sizes of individuals were derived and plotted against time. Declines in body weight during the spawning season were calculated by subtraction to obtain estimates of gamete production. Changes in the body weight reflect spawning seasons, and possibly changes in food supply, and are independent of shell length. The spawning season was confirmed by examining gonad smears of all female individuals sampled, as described by Griffiths (1977). In C. meridionalis gametogenesis occurs continuously throughout the year and there is no evidence of a post-spawning resting phase or deposit of nutrient reserve as found in M. edulis (Seed, 1976).

Investigation of the organic material available as food in seawater has shown that this does not vary seasonally (unpublished data). Thus, decline in body weight is unlikely to reflect starvation.

Results

Bailey's Cottage

(1) Spat settlement

During 1974 the reproductive state of an adult mussel population (Cohort 1 mean length 61 mm) was examined at Bailey's Cottage. On 1.12.74 a dense settlement of young mussels (cohort 2) averaging 1.8 mm shell length was detected principally on the algae Ulva sp. and Polysiphonia incompta Harvey on rock surfaces, and around the base of the adult mussels. Settlement took place within 1 to 2 weeks and did not recur until August 1978 when there was an extensive settlement of cohort 3. Similar patterns of spat settlement have been observed in Mytilus edulis (Bayne, 1976; Suchanek, 1978) which closely resembles C. meridionalis in many respects.

The spat settled on the adult mussels near the posterior end extending 1/3 towards the anterior region. Where the adults were partially buried in

sand, they settled mainly at the shell/sand interface approximately 1/3 from the posterior end. The adults of cohort 1 were thus densely ringed by spat.

Settlement was restricted to the sublittoral and lower littoral zones and, except in the case of cohort 3, did not initially extend to the midshore level. Maximum densities in the sublittoral zone reached 21000 m^{-2} in cohort 2 and 46000 m^{-2} in cohort 3, three months after settlement (Fig. 2). The initial increase in density results from migration of spat up the shore due to overcrowding in the sublittoral. Density in the upper shore levels remained low during this period with $2500 \text{ mussels m}^{-2}$ colonising the Topshore area. Peak density in this zone did not occur until one year after settlement - again due to migration of young mussels into the area (Fig. 2). Cohort 3 was not only a considerably heavier spat settlement but extended higher up the shore than did cohort 2. Densities at the Topshore level attained $10\ 000 \text{ m}^{-2}$ and peak settlement was simultaneous at all shore levels. This cohort resulted from an abnormally late spawning season. The spat settled earlier in the life cycle of cohort 2 (42 mm shell length, $3\frac{1}{2}$ -4 years of age) than had been the case when cohort 2 settled on cohort 1 (61 mm shell length, 5-6 years of age).

Cohort 2:

(mm) shell length	12.9	16.4	18.4	21.3	23.7	28.5	32.6	34.0	37.3	38.3	42.0	44.5	46.9	50.1	50.3
age (months)	5.2	8.0	11.2	13.5	17.0	20.9	23.9	27.3	29.7	33.2	36.2	39.1	42.6	45.1	47.9

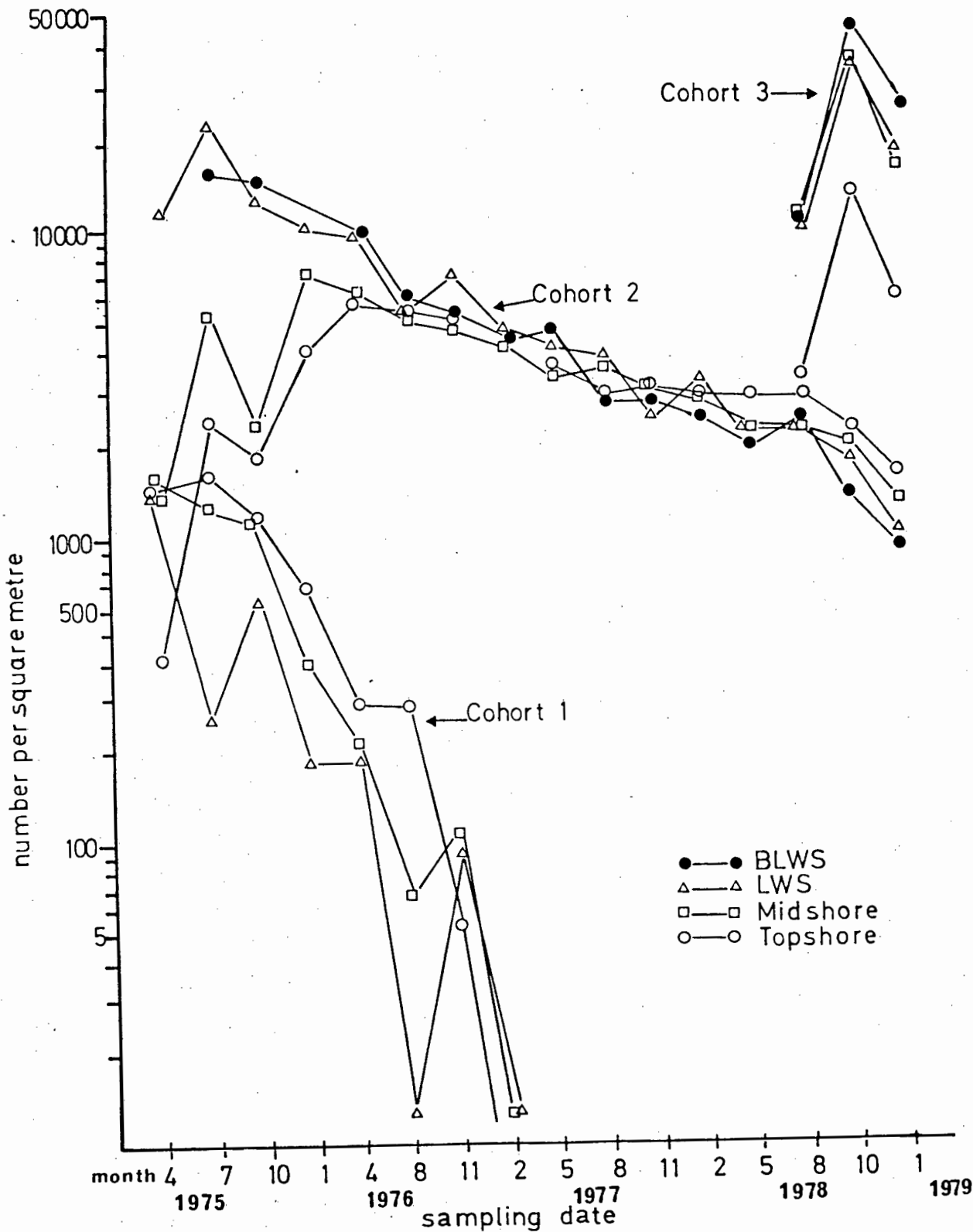


Fig. 2. Density of 3 cohorts of mussels at 4 shore levels at Bailey's Cottage, together with the average shell length of cohort 2 mussels on each sampling date.

(2) Density and biomass changes

Quantitative sampling for population density and growth rates at Bailey's Cottage commenced in April 1975, at which time the population consisted of a dense cover of cohort 1 mussels averaging 61 mm shell length and the spat (cohort 2) with a mean shell length of 11 mm. Figures 2 to 5 show the changes in numbers and biomass of three cohorts monitored at different shore levels at 3-monthly intervals.

At low shore levels cohort 2 declined from 21 000 after peak settlement to 6 000 m⁻² in August 1976. Following this there was a steady decline in mortality. At higher shore levels, the numbers continued to increase after spat settlement during the first 1 to 1½ years of growth, until in August 1976 there was a relatively uniform population of 5 500 to 6 000 m⁻² (mean shell length 23-28 mm) at all shore levels. Severe competition for space at lower levels and the limited ability of young mussels to survive the rigours of aerial exposure are probably responsible for the observed settlement and migration pattern in C. meridionalis. Upward migration occurs when mussels are washed out of the lower portion of the bed, transported shorewards, and re-attach in pools and gullies during calm conditions. Similar

migration patterns of mussels into higher shore areas have been observed in Mytilus californianus (Suchanek, 1978) and Mytilus edulis (Dare, 1976). Examination of size-frequency histograms of mussels at different shore levels during October 1975 and January 1976 (Fig. 3) shows that the increased density at higher shore levels is not due to spat settlement, but to invasion of similar sized mussels.

Changes in biomass expressed as grams total dry weight m^{-2} are shown in Fig. 4. Cohort 2 mussels at the higher shore levels show a lower biomass, although densities at the different shore levels are relatively uniform. This is explained by the slower growth rate observed at this level so that all individuals contributing to the top-shore samples were smaller in size and weight. The fluctuations in biomass may be attributed to sampling variability, spawning loss - this may be considerable, and environmental factors influencing feeding and mortality.

Fig. 5 shows the total mean standing crop (all cohorts combined) of mussels in the sublittoral and littoral zones. The mean standing crop (whole animal) of 7500 to 8500 $g m^{-2}$ (19125 - 21675 $kJ m^{-2}$)

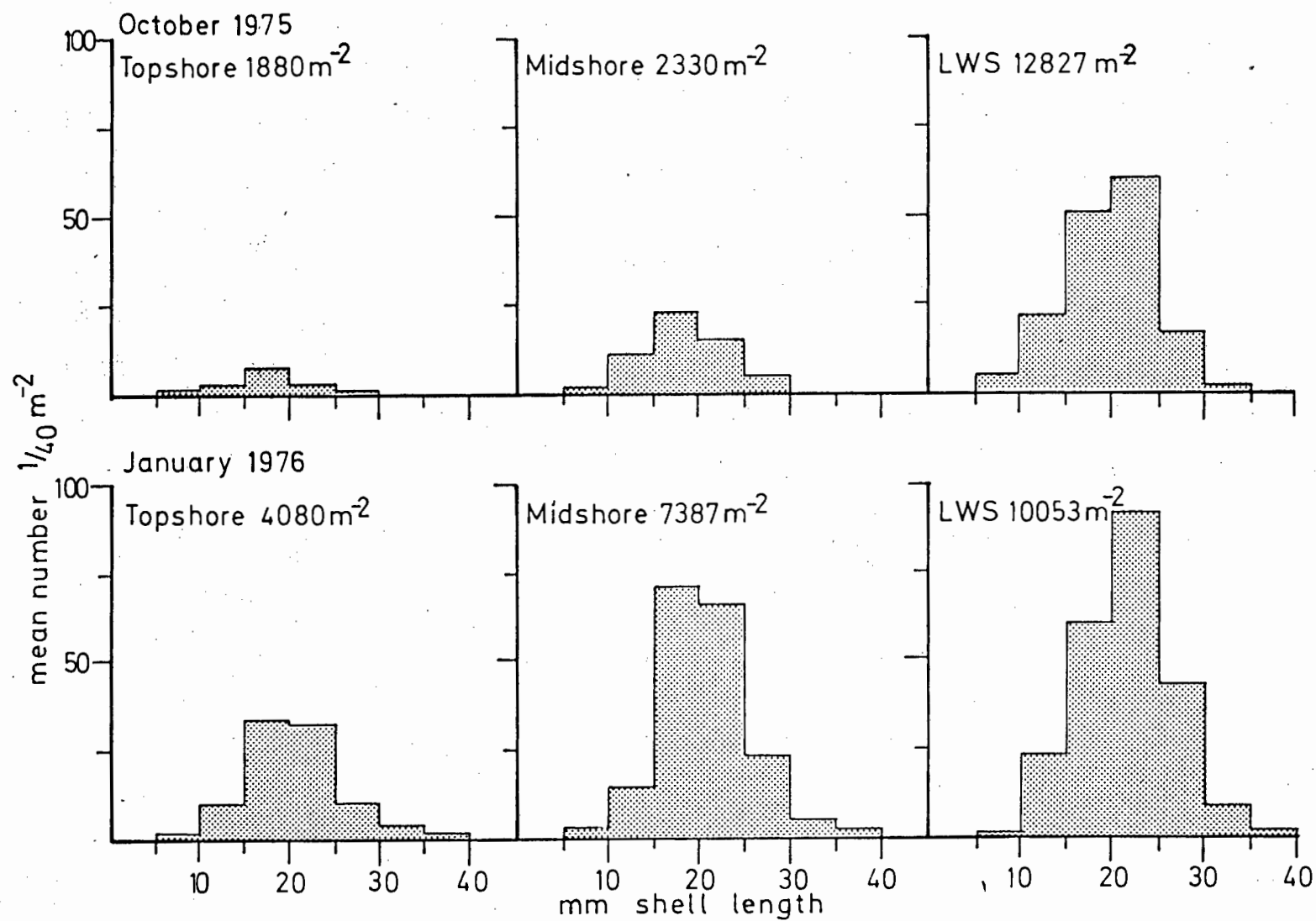


Fig. 3. Size-frequency histogram of *C. meridionalis* at 3 shore levels during October 1975 and January 1976, to show migration into the upper shore levels.

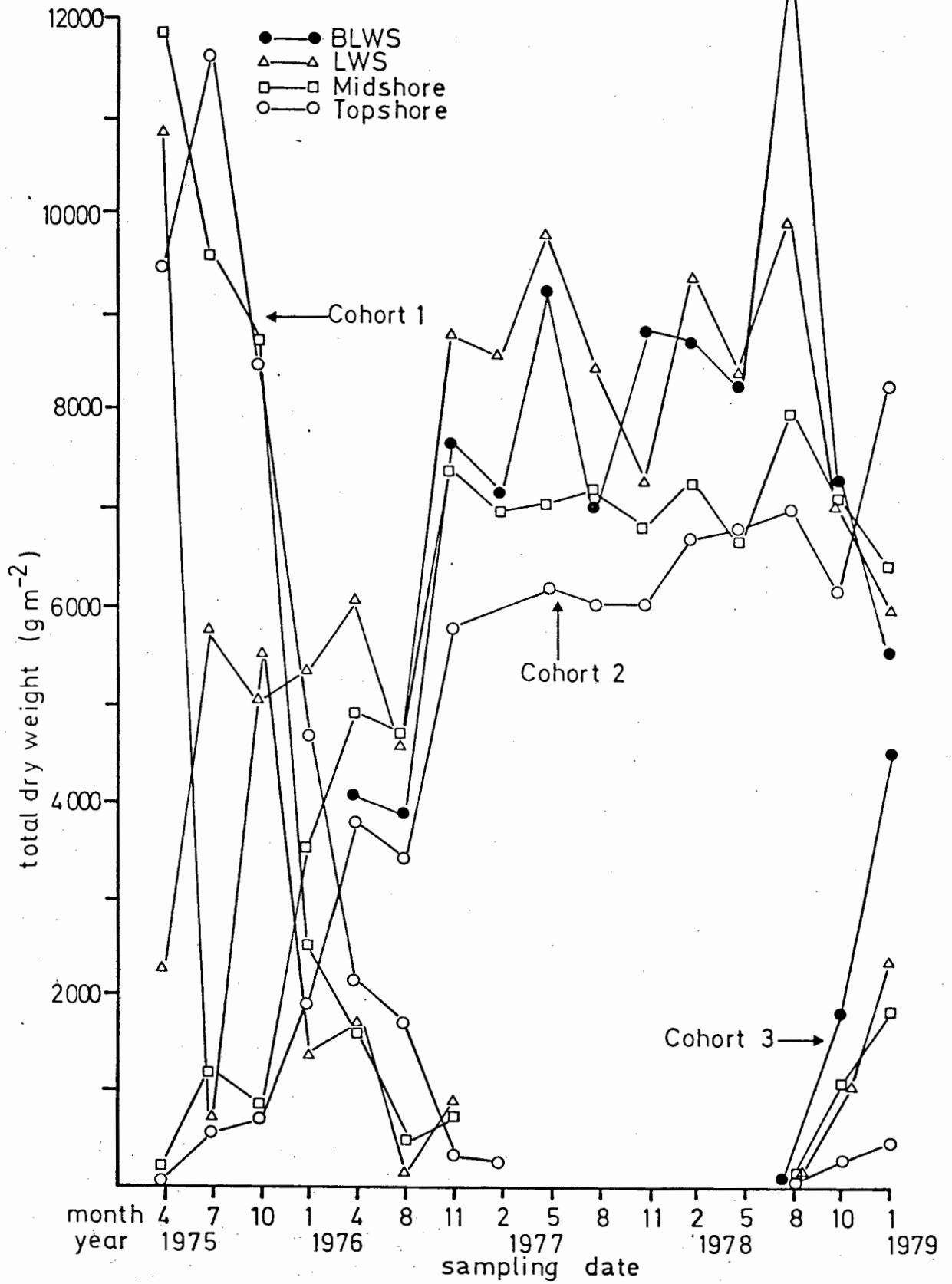


Fig. 4. Standing crop of 3 cohorts of *C. meridionalis* over 4 years at 4 shore levels at Bailey's Cottage, False Bay.

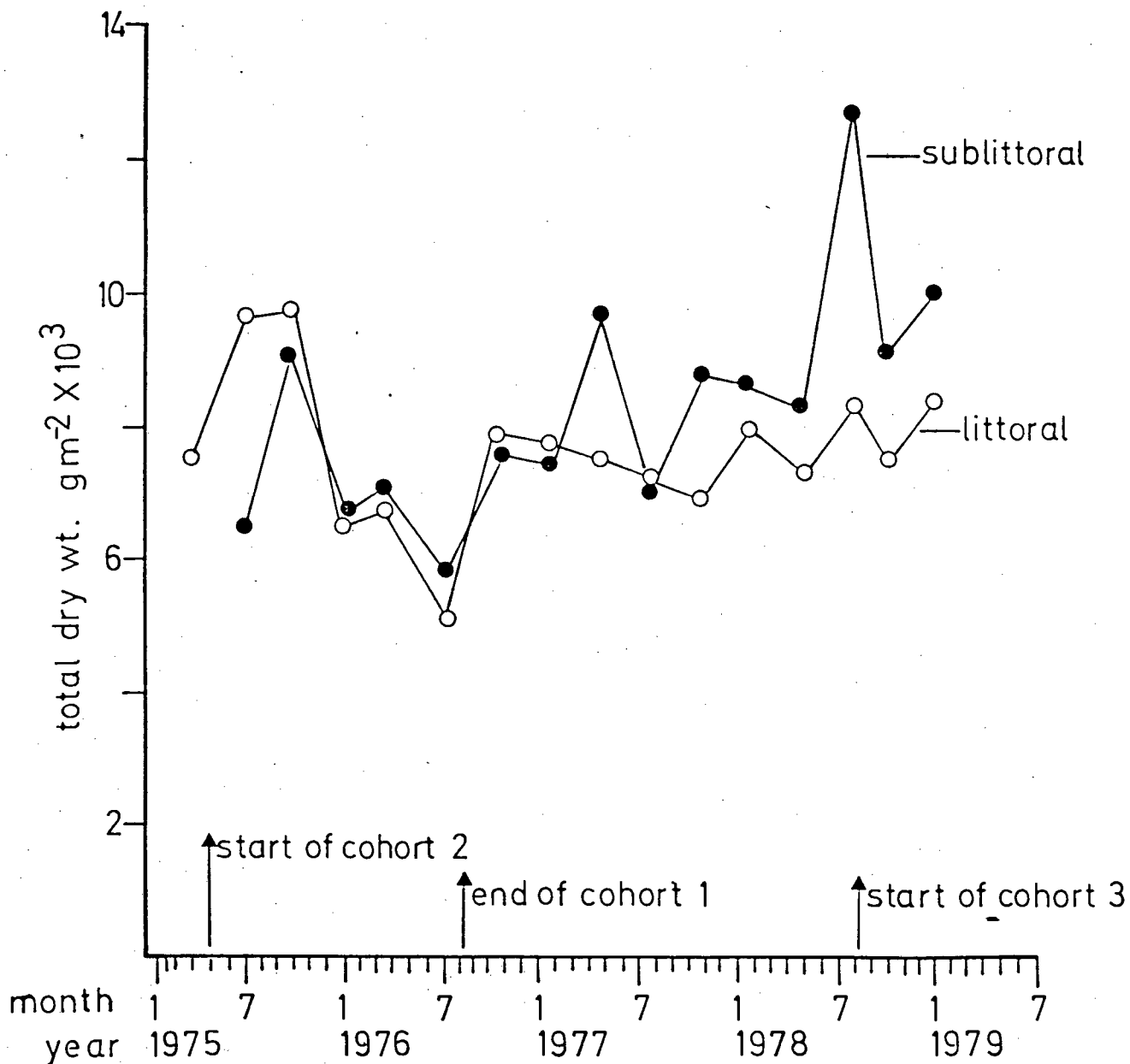


Fig. 5. Total standing crop dry weight (flesh + shell) of *C. meridionalis* in the sublittoral and littoral zone (mean of 3 shore levels) at Bailey's Cottage.

is considerably greater than that of Crassostrea virginica (6501 - 10554 kJ m⁻²) considered by Dare (1976) to be high for a macroinvertebrate population.

Dalebrook

Data obtained from a single cohort population, the same spat settlement as cohort 2 at Bailey's Cottage, may be compared with the BLWS population at Bailey's Cottage (Fig. 6). The mussels formed a densely packed, clearly delimited bed on the sublittoral rocky platform (no sand) at Dalebrook. Population densities were lower during the first years of growth because there were no substrate irregularities to produce a greater effective surface area as at Bailey's Cottage. Biomass figures were comparable initially, but significantly lower by late 1977 considering that the density and mean length from the two localities was the same. This phenomenon cannot be explained.

Factors Affecting Density

- (1) Intra- and inter-specific competition
for space

Intraspecific competition is an important factor in the population dynamics of M. edulis (Newcombe 1935). Other than catastrophic mortality due to

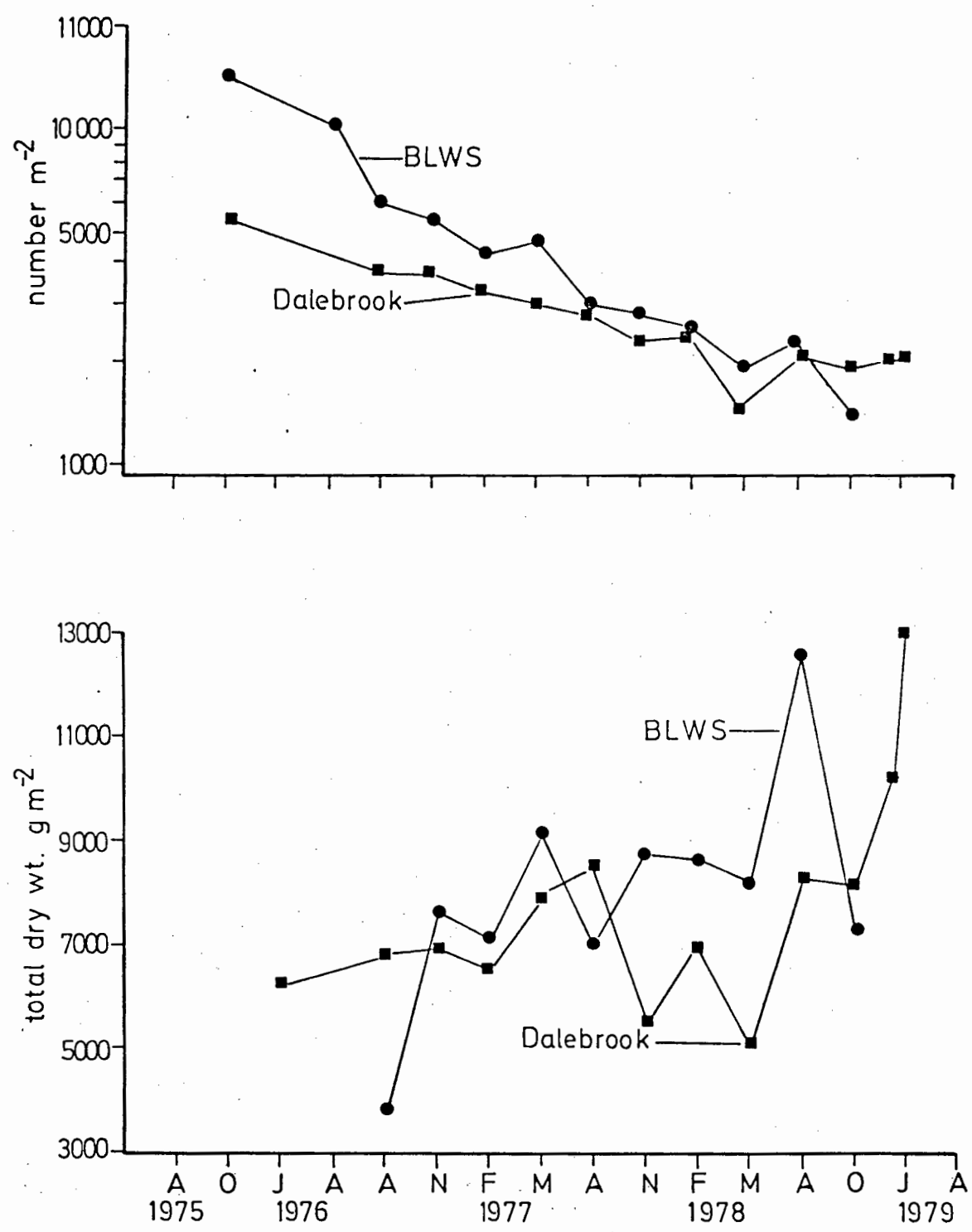


Fig. 6. The numbers and standing crop of a sublittoral population of *C. meridionalis* at Dalebrook compared with a similar population (BLWS) at Bailey's Cottage.

environmental causes, intraspecific competition in C. meridionalis is considered a major cause of mortality in the mussel bed. Settlement of spat produces a high mortality in the adult population through competition for space and possibly food. Savage (1956) found a similar occurrence in M. edulis while Dare (1976) observed that spat, rather than adults, died during new settlements. Competition and elimination of adults is less evident where a mosaic pattern of alternating but adjacent areas of small and large mussels constitute the mussel bed. In this case the spat colonise denuded areas within the mussel bed, a common phenomenon on the west coast of South Africa. As the spat grow to 15 mm they move from the adults' shells onto the substrate. There they form a solid bed beneath the adults, pushing them to the surface where they are removed by wave action. Mussels thus removed may be washed into the Topshore area where some reattach to the substrate. This causes an increase in the upper shore population (Jan. 1979 in Figs 2 and 4). In Perna perna the spat do not migrate to the substrate, resulting in adult mortality and detachment of both adults and juveniles (Berry, 1978).

Mortality of C. meridionalis in False Bay appears to be governed more by space availability than by predators (see below). Thiesen (1973) has demonstrated a similar situation in M. edulis growing on Fucus. The substrate has a limited carrying capacity in terms of space and during the logarithmic growth phase of the mussels, mortality must continue in order to maintain an even substrate coverage. During this phase the faster growing mussels tend to protrude above the bed and may frequently be squeezed to the surface by smaller adjacent mussels. Alternatively, groups of larger mussels may cause 'humping' of the mussel bed, producing more tenuous byssal attachments until they are dislodged by wave action. Thus density may be expected to decline with increasing shell length. Data of mean shell length and density of all samples of cohort 2 (Dalebrook included) have been plotted in Fig. 7. Density declines rapidly with growth until 40 to 50 mm shell length. This graph gives the best estimate of substrate carrying capacity for different sizes of mussel.

Fig. 2 showed that mortality is uniform throughout the population. This indicates the absence of a controlling factor eg. predation or environmental factors, at any particular shore level. A similar sequence of events has been shown by Hibbert (1977) in Mercenaria mercenaria.

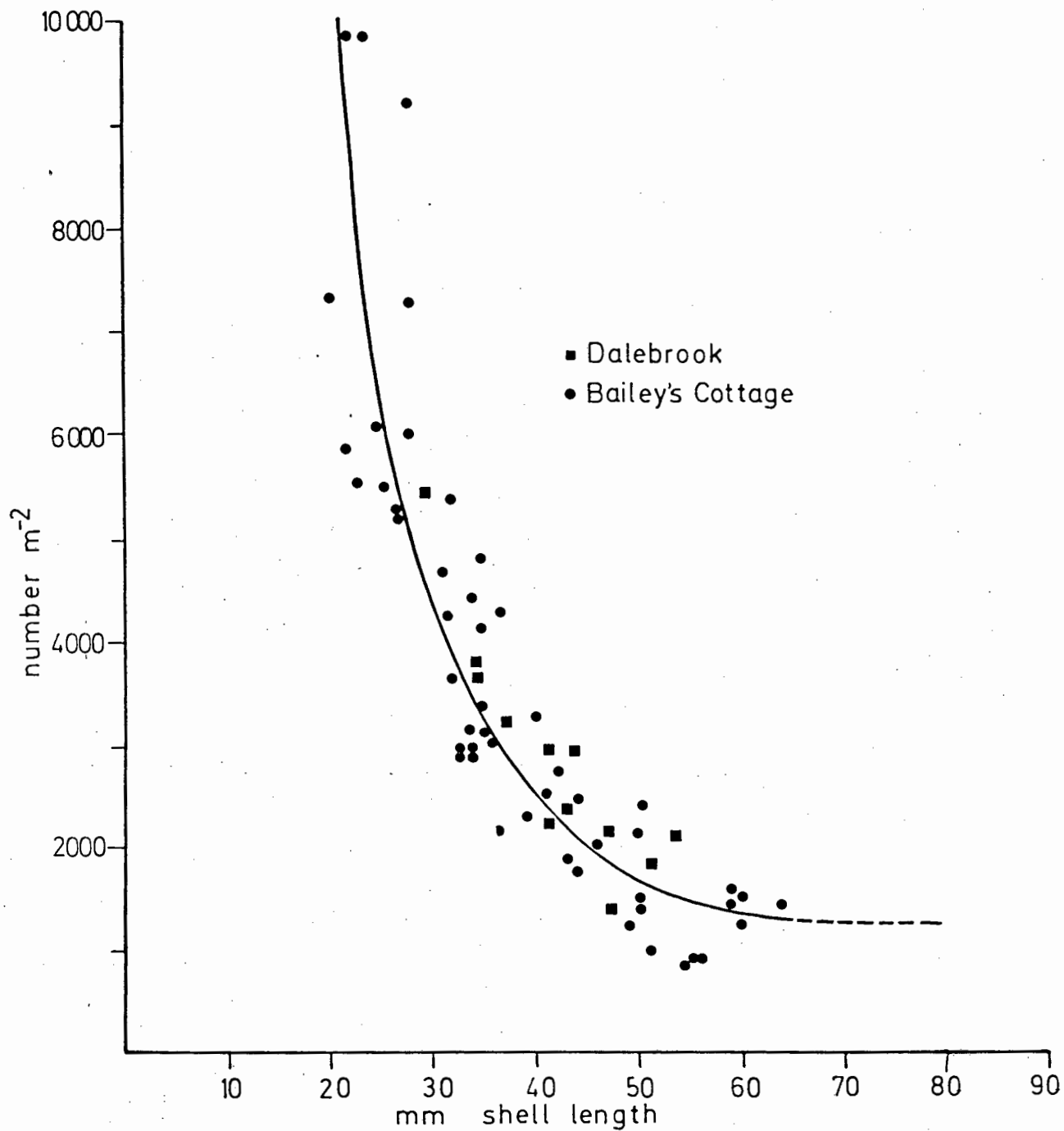


Fig. 7. Substrate carrying capacity of different sized cohort 2 *C. meridionalis* obtained by plotting density at known shell lengths (data from Fig. 2).

Fig 8 shows mortality of cohort 2 at different shore levels in terms of total dry weight and energy equivalents. Examination of data for the lower shore levels shows that whereas mortality in terms of numbers was initially high and declined with time (Fig. 2) in terms of biomass or energy, the loss was surprisingly constant, averaging 3000 kJm^{-2} over a three year period. Data for higher shore levels was influenced by delayed settlement or migration during 1976, but thereafter attained similar mortality levels.

On the west coast there is considerable competition for space. Aulacomya ater dominates the sublittoral rocky substrate in this region (Field et al. 1980). Several years of SCUBA observations at Oudekraal on the west coast indicates that whereas C. meridionalis larvae are present in the water column for most of the time and will readily settle on ropes or buoys suspended in the water, they seldom settle on the rocky substrate. Sublittoral settlement has only once been observed in this area. Strong wave action denuded an area of rock and this was rapidly colonised by A. ater and C. meridionalis spat with very little mixing of the two populations.

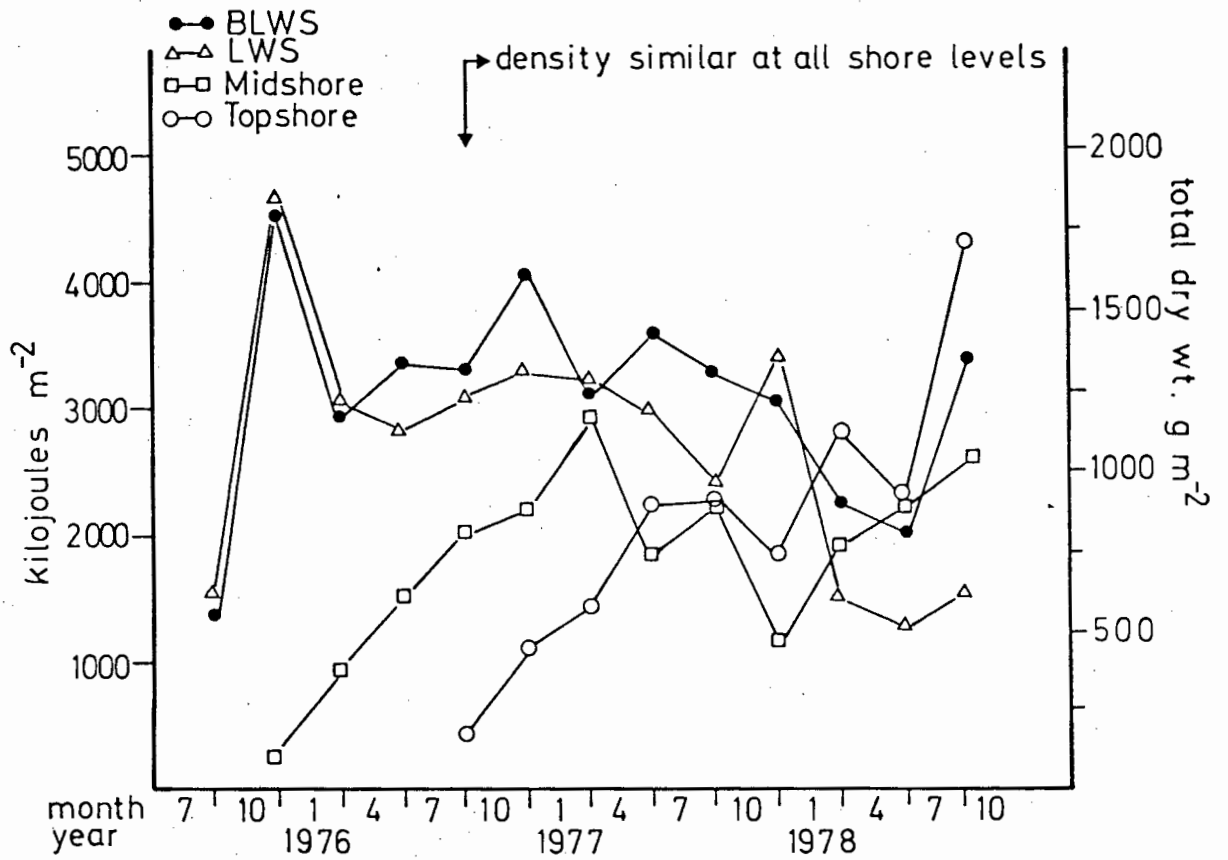


Fig. 8. Mortality (loss) of cohort 2 at different shore levels in terms of kJ m^{-2} from a densely packed *C. meridionalis* bed at Bailey's Cottage. After July 1976 the density was the same at all shore levels.

C. meridionalis grew rapidly but disappeared together with most of the A. ater population within one year. This is believed to be due to predation by the rock-lobster Jasus lalandii which is common in the area. Griffiths and Seiderer (1980) have shown that J. lalandii selects C. meridionalis preferentially to A. ater.

(2) Environmental factors

Settlement of a new cohort enhances sand retention in the interstices between individuals. A sand layer gradually builds up between the substrate and the mussels. The deepening sand layers beneath the mussels causes them to lengthen the byssus and form new attachments to surface debris. Byssal attachment then becomes tenuous and wave action may finally rip the mussels from the bed rather like rolling up a blanket.

Silting may also produce instability in the juvenile population. They may either be completely covered (a condition they can tolerate for several days) or form raised clumps ('humping') with tenuous attachment to the underlying substrate. These clumps tend to be removed by wave action exposing

the underlying sand layers of adjacent populations, which may in turn be washed away. Where sand is not present, as at Dalebrook, silting does not cause mortality in the population.

Another cause of density changes arises from the summer settlement of algae: Ulva sp., Gigartina hystrix (Ag.) Setch et Gard., Caulacanthus ustulatus Papenf. and Gelidium pristoides (Turn.) Kütz on the shells of the mussels. This also promotes siltation causing 'humping' of the mussel bed and large areas may suffer catastrophic mortality due to storm damage. Up to 50% of the mussel bed at the mid-shore level has been observed to be eliminated due to siltation.

Mortality due to overheating and desiccation has twice been observed, particularly in mussels lying exposed on the surface of the bed instead of embedded in it. At the upper shore level 10% or more of mussels may die during a heatwave coincident with L.W.S. about midday. This has been reported in M. edulis by Suchanek (1978) and is regarded as the controlling mechanism delimiting extension into the upper shore areas.

(3) Predation

In False Bay possible predators include the rock-lobster Jasus lalandii (Milne Edwards), rare in the collecting areas; the musselcrackers Sparodon durbanensis (Castlenau) and Cymatops nasutus (Castlenau), also rare due to overfishing; man; the kelp gull Larus dominicanus Lichtenstein (Siegfried, 1977); the oystercatcher Haematopus moquini Bonaparte; the starfish Marthasterias glacialis (Linn.) which may be found in the lower reaches of the mussel bed, and the gastropod Natica (Tectonatica) tecta Anton, in sandy rock pools. All predators except birds and man are restricted to the lower littoral and sublittoral areas, as they are unable to survive and feed out of water. Branch (1978) has shown that M. glacialis feeds mainly on mussels. However, they do not occur at Bailey's Cottage or Dalebrook in sufficient numbers to significantly affect the mussel population. This supposition is supported by examining the mortality of cohort 2 mussels at different shore levels (Fig. 8). Bearing in mind that mortality at the upper shore levels began later because of migration, the net loss varies from 2000 - 3000 kJm^{-2} or 700-1250 g total dry weight. Mortality is slightly higher in the lower shore areas but this may be explained by migration and physical

factors alone, the higher shore levels being subject to considerably less wave action, sand deposition and seaweed settlement, all of which remove mussels from the bed. If the lower limits of extension of the bed were predator limited as described by Lubchenco and Menge (1978), one would expect the standing crop in the sublittoral and littoral to differ significantly. A survey of the mussel bed below L.W.S. has shown that the mussels extend in apparently equal density to the rock-sand interface approximately 60 m from L.W.S. The average biomass of sublittoral mussels was 8605 g m^{-2} or 21943 kJ m^{-2} while the average biomass of the littoral population was 7664 g m^{-2} or 19556 kJ m^{-2} (calculated from Fig. 5).

Growth rates

The spat of cohort 2 was first noticed on seaweed at Bailey's Cottage on 1.12.74 and it was estimated that spatfall had occurred within 3 weeks of this date (for derivation of the growth curves the spat were assumed to be 1 week old on the above date). Growth curves for mussels are generally calculated from time of settlement and the larval stage is not taken into account. It was found that the von

Bertalanffy growth equation gave the best fit to the data and that the sampling intervals during the first year were not sufficiently close together to allow a Gompertz fit to the early phase (Thiesen, 1973).

Fig. 9 shows growth curves generated for mussels belonging to cohort 2 at different shore levels at Bailey's Cottage and for the sublittoral population at Dalebrook. These were compared with a growth curve obtained from similar data (B. Currie, unpublished) for a sublittoral mussel population growing on an offshore wave recording tower at Melkbosstrand, Table Bay (Fig. 1). The growth equations are given in Table 2. Seed and Brown (1975) have found that growth rates in M. edulis may be extremely variable within and between habitats. In C. meridionalis growth rates varied with shore level, the slowest rates occurring at higher shore levels, as is the case in Mytilus edulis (see Newcombe, 1935 and Suchanek, 1978). Differences in growth rates only became markedly apparent after two years because prior to this there was continual migration from low to high shore levels.

Growth of C. meridionalis during the first year was considerably faster than the 5-7 mm recorded for M. edulis by Seed (1969) but was comparable to other

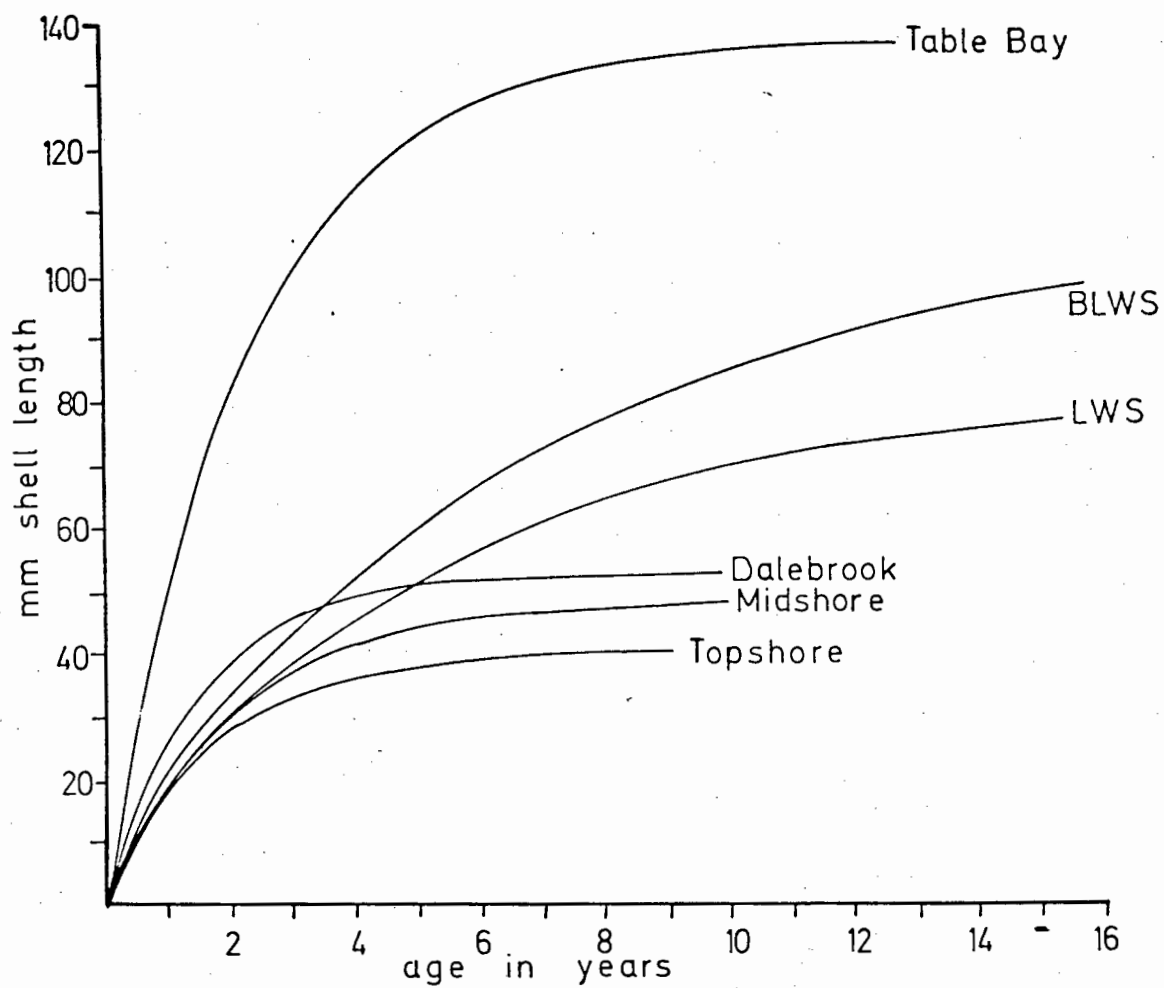


Fig. 9. Growth curves for *C. meridionalis* at Bailey's Cottage and Dalebrook in False Bay, and in Table Bay.

Table 2 Von Bertalanffy growth equations ($L_t = L_\infty(1 - e^{-k(t-t_0)})$) obtained for Choromytilus meridionalis in different habitats and at different shore levels. Length in mm.

	L_∞	K	t_0
<u>Table Bay:</u>			
Melkbosstrand	135,97	0,447727	+0,049096
<u>False Bay:</u>			
Dalebrook	53,09	0,620488	-0,102357
Baileys Cottage			
Top	41,01	0,558843	-0,036408
Mid	48,41	0,491615	-0,036173
LWS	81,87	0,179794	-0,538461
BLWS	106,26	0,153188	-0,309774

growth curves for M. edulis and M. californianus reviewed by Seed (1976). Comparison of C. meridionalis data with those of Griffiths and King (1979b) shows that although Aulacomya ater is initially very slow growing (the Gompertz model best fits data) both species attain lengths of 55 mm in approximately the same time span (5-6 years for sublittoral population). The other common southern African mytilid, Perna perna has been found by Berry (1978) to attain growth rates equivalent to that of West coast C. meridionalis (60 mm in the first year). The rate of growth of C. meridionalis in Table Bay and Saldanha Bay (du Plessis 1977) is approximately twice that of False Bay individuals during the first year of settlement. Water temperatures on the west coast are colder, averaging 12°C over most of the year, a factor that might be expected to result in a slower growth rate (Dehnel, 1956). However, the area is characterised by intermittent dense plankton blooms resulting from upwelling of nutrient-rich water, and food levels may be considerably higher than those in False Bay, enhancing the growth rate.

The growth curves in Fig. 9 reflect the mean of widely differing individual growth rates. Mussels are renown for the varying growth rates found within a single cohort. Larger individuals at Bailey's Cottage appear to be selected against in that they are frequently forced to the surface of the bed by their neighbours, and then dislodged by wave action. Thus the growth curves underestimate the potential growth rate.

Reproduction

Fig. 10 shows the wet flesh weight of standard sized males and females of 20, 60 and 100 mm shell length, derived from monthly length-weight regression analyses over a 4 year period. The spawning season differs in duration in males and females, in different sized individuals and in successive years. The reproductive cycle has been described in greater detail by Griffiths (1977). During the first 3 years gamete release took place principally between July and February. The end of the spawning season was usually marked by resorption of ova within the follicles resulting in a weight loss during March. During 1974/75 and 1975/76 the amount spawned was similar. However, 1976/77 was atypical in that smaller mussels of both sexes (cohort 2 in their first full year of breeding) spawned more than usual. Large males also spawned slightly more than usual, while females showed considerably reduced gamete loss. The reproductive season in 1977/78 extended over a longer period with considerable gamete release occurring between March and May. The reason for this is unknown, but the late spawning correlated with a spat settlement (cohort 3) first found in August 1978.

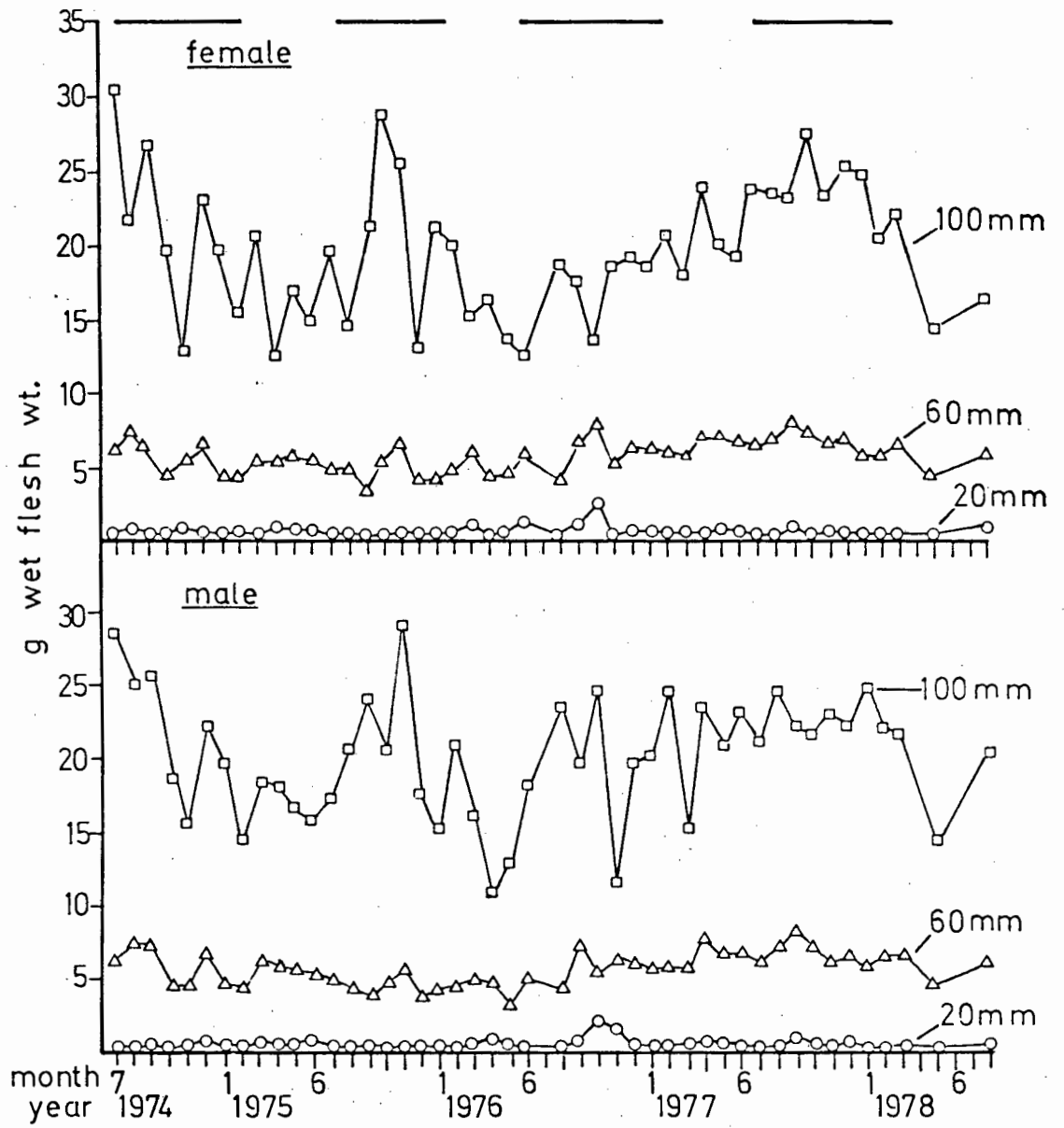


Fig. 10. Variation in the wet flesh weight of male and female *C. meridionalis* of 20, 60 and 100 mm shell length over 4 years. The duration of the breeding seasons are shown as horizontal lines at the top of the graph.

Mean annual gamete production in relation to shell length is given in Table 3. No difference was detected between males and females so the data were pooled. The relative amounts of reproductive material released by mussels of different sizes varies from approximately 5 times the flesh mass at 20 mm to 0.8 times at 100 mm. Similarly, Griffiths and King (1979b) found that annual reproductive output (P_r , see Crisp 1971) in 15 and 80 mm Aulacomya ater was 3 times and 0.5 times the mean flesh weights respectively. This is contrary to the findings of Browne and Russell-Hunter (1978) for iteroparous (multiple breeding) molluscs. Choromytilus meridionalis is not a particularly short lived species and the C_r to C_{AF} ratio (carbon used in reproduction: carbon contained in an average female) changes from 5.5; 2.6; 1.7; 0.8 in 20; 40; 60; 80 mm individuals respectively, although total energy expelled as gametes is highest in large mussels because of their size.

Total annual gamete production per unit area by different age cohorts can be calculated from regressions of carrying capacity and gonad output against shell length (Fig. 7, Table 3). Table 4 gives the predicted values. Whereas density declines,

Table 3 Calculated annual gamete output in male and female *Choromytilus meridionalis* of initial lengths 20, 40, 60, 80 and 100 mm. Growth of mussels in each size range is taken into account by determining the length during the midpoint of each spawning season and calculating gamete loss for this sized individual.

Shell length (mm)	Breeding seasons:- Gamete production in grams wet wt.					
	July 1974 - Feb 1975	July 1975 - Feb 1976	July 1976 - Feb 1977	July 1977 - May 1978	Mean Annual Production	Total kJ
<u>Female</u>						
20	0,999	0,882	3,262	0,949	1,523	5,785
40	2,691	3,143	5,594	2,849	3,569	13,554
60	4,954	4,657	4,744	5,083	4,860	18,459
80	11,617	7,660	2,357	9,146	7,695	29,225
100	31,189	23,730	8,540	17,085	20,136	76,478
<u>Male</u>						
20	0,649	0,671	1,992	0,947	1,065	4,045
40	2,583	2,158	4,272	3,009	3,006	11,416
60	5,284	3,403	3,470	5,269	4,357	16,549
80	10,414	6,766	7,487	7,783	8,113	30,814
100	21,451	22,531	26,673	16,561	21,804	82,811

Regression equations from the above data: $y = \text{gamete production wet wt. (g)}$, $x = \text{shell length (mm)}$

Female $y = 0,0150x^{1,4596}$ $r^2 = 0,73$ $n = 20$

Male $y = 0,0042x^{1,7711}$ $r^2 = 0,88$ $n = 20$

Male + Female $Y = 0,0079x^{1,6154}$ $r^2 = 0,86$ $n = 40$

Dry flesh = 16.88 % wet flesh wt. Gametes = 22.5 kJ g⁻¹ dry wt.

Table 4. Substrate carrying capacity of a Choromytilus meridionalis single cohort population at Bailey's Cottage in terms of numbers and biomass derived from Fig. 7, and calculated annual gamete production by the population of different shell lengths (growth taken into account). Dry flesh weight = 16.88% of wet flesh wt. Energy equivalents: dry flesh = 19.5 kJ g⁻¹, dry gonad = 22.5 kJ g⁻¹

Shell length (mm)	Average number m ⁻²	Total dry biomass g m ⁻²	Dry flesh biomass g m ⁻²	Calculated gamete production (dry wt.) g m ⁻² y ⁻¹
25	6325	7006,8	395,6	1530
30	4400	7321,6	444,4	1429
35	3300	7811,0	502,8	1386
40	2550	8129,4	553,4	1326
45	2000	8346,5	592,5	1260
50	1700	8976,0	666,4	1258
55	1500	9845,1	755,7	1290
60	1350	10767,6	855,9	1336
65	1300	12439,8	1019,0	1469
70	1280	14470,8	1220,7	1634
				$\bar{X} = 1392$
				$= 31320 \text{ kJ m}^{-2} \text{ y}^{-1}$

and biomass increases with increasing shell length, the mean annual gamete production by the population remains at a constant level (mean $1392 \text{ g m}^{-2} \text{ y}^{-1}$ dry wt., $31320 \text{ kJ m}^{-2} \text{ y}^{-1}$).

While the number per metre² of an individual growing from 25 to 70 mm declines as shown in Fig. 7, the biomass doubles (Table 4) and the dry flesh weight trebles. The calculated annual gamete output (growth taken into account) for one year by a mussel starting the year at the shell length recorded in the left hand column, remains fairly constant at $1392 \text{ g m}^{-2} \text{ y}^{-1}$. Although cohort 2 at Bailey's Cottage reached breeding age in January 1976 and spawned equivalent amounts of gametes annually thereafter, none of these spawnings produced successful recruitment until August 1978. It would appear that environmental or biological factors affect spat settlement rather than variation in gonad output from a growing population.

Discussion

Although the ecology of Choromytilus meridionalis is in many respects similar to that of M. edulis (reviewed by Seed, 1976) there are also considerable

sea conditions. The nauplii of the barnacle Tetraclita serrata Darwin, common on the South African coast, have been shown to survive and grow on a diet of Choromytilus ova in the laboratory (Griffiths, 1979).

The calculated average annual export of weight and energy from the sublittoral population (= lower littoral as well) is as follows:-

Annual total dry flesh weight 835 g or $3129 \text{ kJ m}^{-2} \text{ y}^{-1}$

Annual total gamete loss 1392 g or 31320 kJ m⁻² y⁻¹

Total 2227 g or $34449 \text{ kJ m}^{-2} \text{ y}^{-1}$

Where all this energy goes to remains speculative at this stage. However, data indicate that the mussel bed zone in a coastal area is a region of high animal density and high energy turnover.

Acknowledgements

My thanks are due to various student assistants, in particular Miss F. Stratton, who assisted with sample collection and analysis. Dr. C.L. Griffiths and Prof. J.G. Field for helpful criticism of the manuscript and Mrs. S. Hardman for typing the manuscript. This work was supported as part of the Kelp Bed Research Programme by the South African National Committee for Oceanographic Research.

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PAPER 3. PREDATION ON THE BIVALVE CHROMYTIUS
MERIDIONALIS (KR.) BY THE GASTROPOD NATICA
(TECTONATICA) TECTA.

PREDATION ON THE BIVALVE CHOROMYTILUS MERIDIONALIS (KR.)BY THE GASTROPOD NATICA (TECTONATICA) TECTA ANTON

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Abstract: The effects of a population of the boring gastropod Natica tecta on the bivalve Choromytilus meridionalis were investigated at Bailey's Cottage, False Bay, South Africa. In July 1979 the N. tecta density on the mussel bed averaged 69 m^{-2} and the population consisted mainly of reproductively mature individuals between 20 - 33 mm shell width.

Laboratory experiments on N. tecta showed that prey size selection is an increasing function of predator size. The prey size range taken by large N. tecta is also greater than that taken by small individuals. The position of the borehole on the mussel shell is a function of the way in which the shell is held by the foot during the boring process. Consumption rates measured in the laboratory showed an increase from approximately 1 kJ per week in 18 mm N. tecta to 4.5 kJ per week in 28 mm individuals. Population consumption in the field was calculated as $663 \text{ kJ m}^{-2} \text{ month}^{-1}$. It was estimated that at this rate the

standing crop of mussels in the pool would be eliminated within 10 months. Field measurements showed significant depletion after 6 months.

New spat settlements of mussels occur every 4 to 6 years. The growth curve shows that after one year the population mean size exceeds 30 mm shell length, which is beyond the prey selection size range of small N. tecta. It was concluded that at the time of a new mussel settlement a niche is provided for the simultaneous settlement and growth of juvenile N. tecta in high densities. However, within one year the increase in prey size, together with depletion due to over-exploitation, limits population growth and density in N. tecta.

INTRODUCTION

During a long term study on the population dynamics of Choromytilus meridionalis (Kr.) at Bailey's Cottage, False Bay, South Africa (Griffiths, 1980) a considerable number of mussel shells on the drift-line were found to have been bored. This was caused by a population of Natica (Tectonatica) tecta Anton (for synonymy see Kilburn, 1976) confined to a large rock pool at the site. The N. tecta had been noted in low numbers for several years, but following a spat settlement of mussels, had increased in density and appeared to be rapidly depleting the mussels in the pool.

In order to assess the effects of the gastropods upon the mussel bed, the population structure of both species was measured and the predation rate of N. tecta examined in the laboratory.

MATERIALS AND METHODS

(1) Field measurements

The population density and size structure of N. tecta and C. meridionalis were measured in July 1979 and January 1980 at Bailey's Cottage ($34^{\circ}06'S$ $18^{\circ}28'E$).

The gastropods were assessed by sampling all individuals in three 0.25 m^2 quadrats from each of the following substrates:- clean sand one metre from the edge of the mussel bed, mussels partially embedded in sand, and mussels on rock without sand. The sizes of N. tecta were recorded as the maximum width of the basal whorl (Fig. 1), which was found to be linearly correlated with operculum width.

The growth rate of mussels in the pool following a spat settlement in 1975 was determined by calculating the mean shell length of samples of approximately 60 mussels collected periodically for the following 3.5 years. In July 1979 the mussel bed was uniform in density and the standing crop per m^2 was calculated from measurements of the size-frequency distribution of mussels in three samples of 0.025 m^2 . The

energy value of the mussel flesh available as food to N. tecta was calculated from the following equation and conversion value

(Griffiths, 1980):-

$$[\text{g dry flesh wt.}] = 1.252 \times 10^{-5} \cdot [\text{shell length (mm)}]^{2.646}$$

energy value of mussel dry flesh = 19.5 kJ g⁻¹.

In January 1980, the density of remaining mussels was assessed from 9 samples measuring 0.25 m² taken at random over the area where the mussel bed had previously extended.

(2) Laboratory studies

Natica tecta from the study site were maintained at 14°C in 22 x 41 x 14 cm tanks in a large recirculating aquarium system. A layer of sand was provided in each tank to simulate the natural habitat. Paired N. tecta of 8 different size classes were placed in separate tanks together with approximately 45 mussels ranging from 10 - 60 mm shell length in increments of 2 - 3 mm. The gastropods were allowed to feed for 7 days after which time all drilled mussel shells were removed and replaced with live mussels of the same length. This procedure was repeated weekly for 6 weeks.

The relationship between borehole width and shell length was plotted from the drilled shells. The site of the borehole drilled in each shell, measured as a percentage of shell length and shell width respectively, was plotted for shells drilled in the laboratory and in

the field.

Summation of the data on weekly consumption rates by each N. tecta pair gave the number and size distribution of prey taken relative to predator size. The energy consumed during the 6 week period, and the average weekly consumption were calculated using the regression equation and conversion value above.

RESULTS AND DISCUSSION

(1) Field measurements

A survey of the False Bay coast in the region of Bailey's Cottage showed that N. tecta occurred only in the pool at Bailey's Cottage. Within the pool a mean of 12 N. tecta m^{-2} was found on sand where no mussels were present. Densities of 56, 60 and 72 m^{-2} (\bar{x} 69 m^{-2}) were found on the mussel bed partially covered in sand, while no gastropods were found on mussels attached to rock without sand. N. tecta thus prefers sandy areas containing partially buried C. meridionalis. In these areas they may be found on the surface or partially to completely buried in sand. They do not require to be buried in order to feed as reported by Fretter & Graham (1962).

Fig. 1 shows the size-frequency distribution of the gastropods on the mussel bed in July 1979. No small individuals were found. The large number of egg strands produced in the field and the laboratory

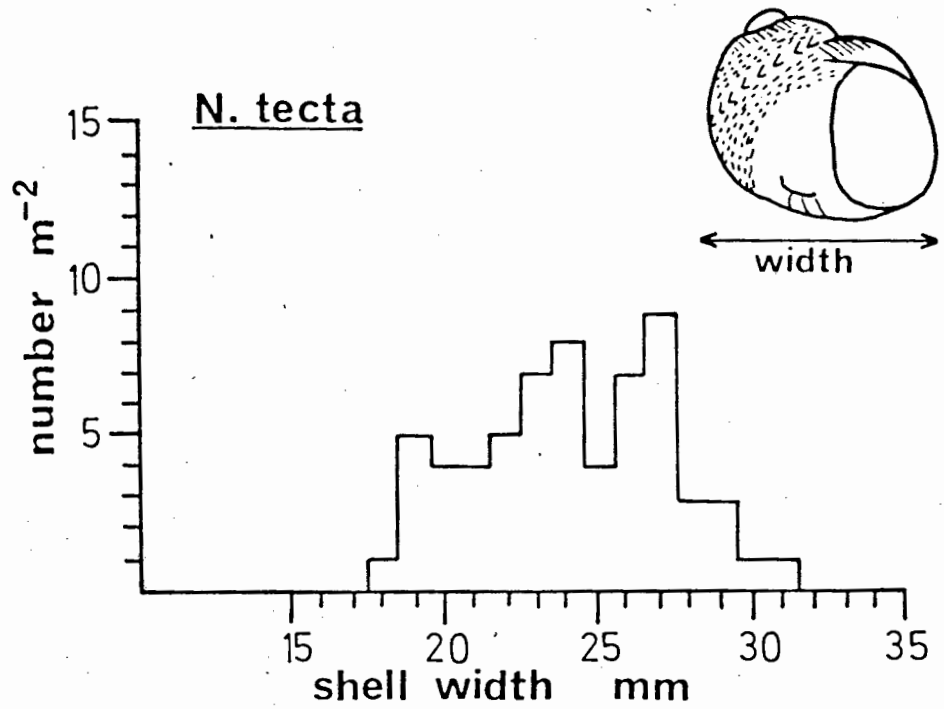


Fig. 1. Size-frequency distribution of N. tecta at Bailey's Cottage, July 1979 (mean of three $0.25\ m^2$ quadrats). Inset shows plane of shell width measurement.

indicated that the population consisted predominantly of breeding individuals. By January 1980 the N. tecta population on the mussel bed had declined to an average of 12 m^{-2} .

The area of the pool covered by mussel bed was 62 m^2 . The density of mussels declined from a uniform coverage of 5653 m^{-2} in July 1979 to 100 m^{-2} in January 1980 when only isolated clumps remained. Fig. 2 shows the population size-frequency distribution in July 1979. Two cohorts can be distinguished on the basis of shell length. The dominant cohort resulted from a blanket settlement of mussels in August 1978, and at the time of sampling were 12 - 45 mm long with a mean of 23 mm. Mussels between 46 - 72 mm represented an older cohort aged 3.7 years.

The growth rate of C. meridionalis in the pool is shown in Fig. 3. They grow to a mean size of 30 mm within the first year, and growth begins to slow after 3 years, at a length of 50 mm.

(2) Laboratory studies

Natica tecta survived well in the laboratory and were maintained for up to 3 months without mortality. Observations on feeding in the field and laboratory showed no observable differences other than the fact that prey in the aquarium was less densely packed and may have been more accessible for drilling.

Plate 1 shows N. tecta and an example of a bored mussel shell.

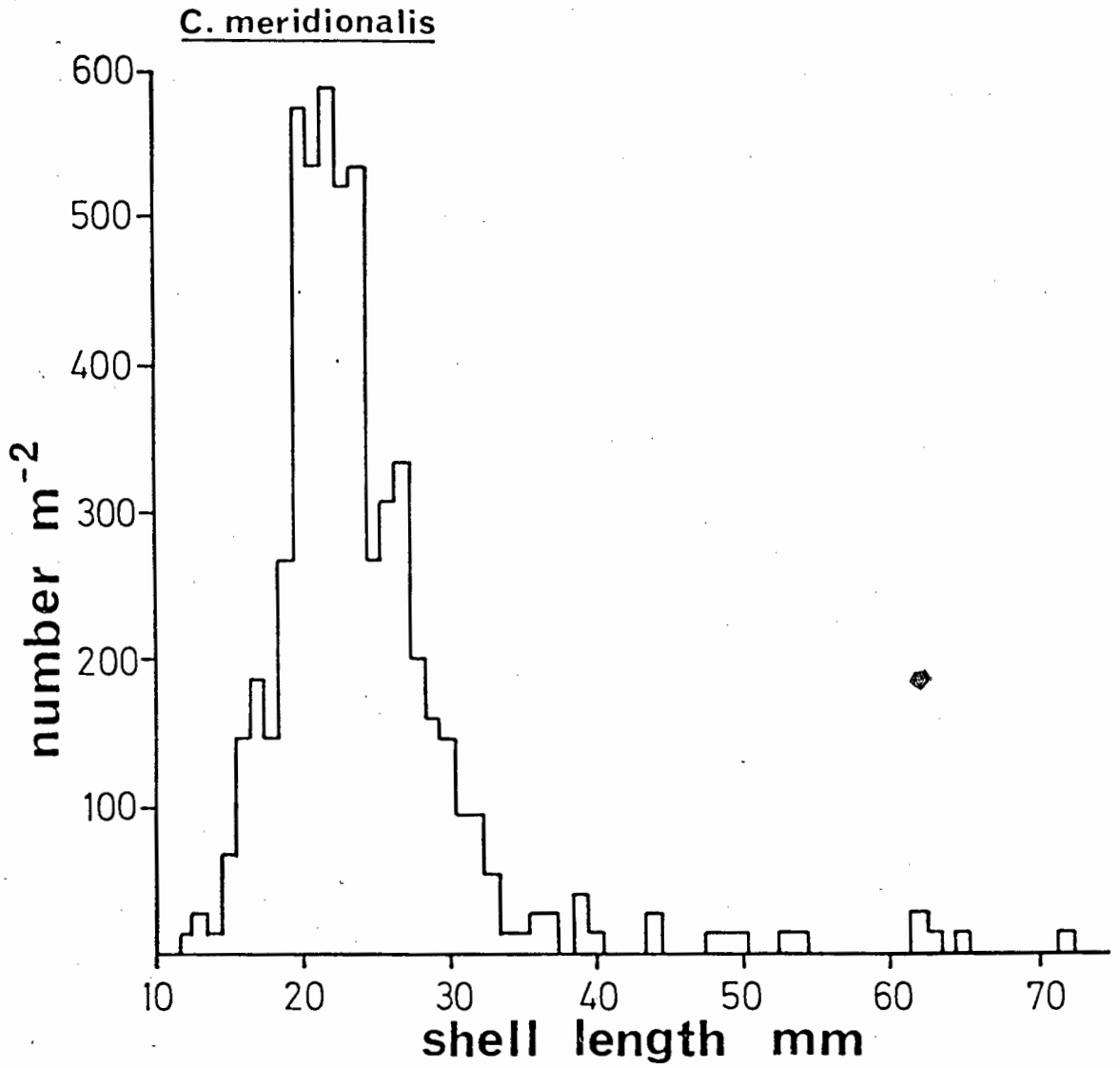


Fig. 2. Size-frequency distribution of C. meridionalis at Bailey's Cottage, July 1979 (mean of three 0.025 m² quadrats).

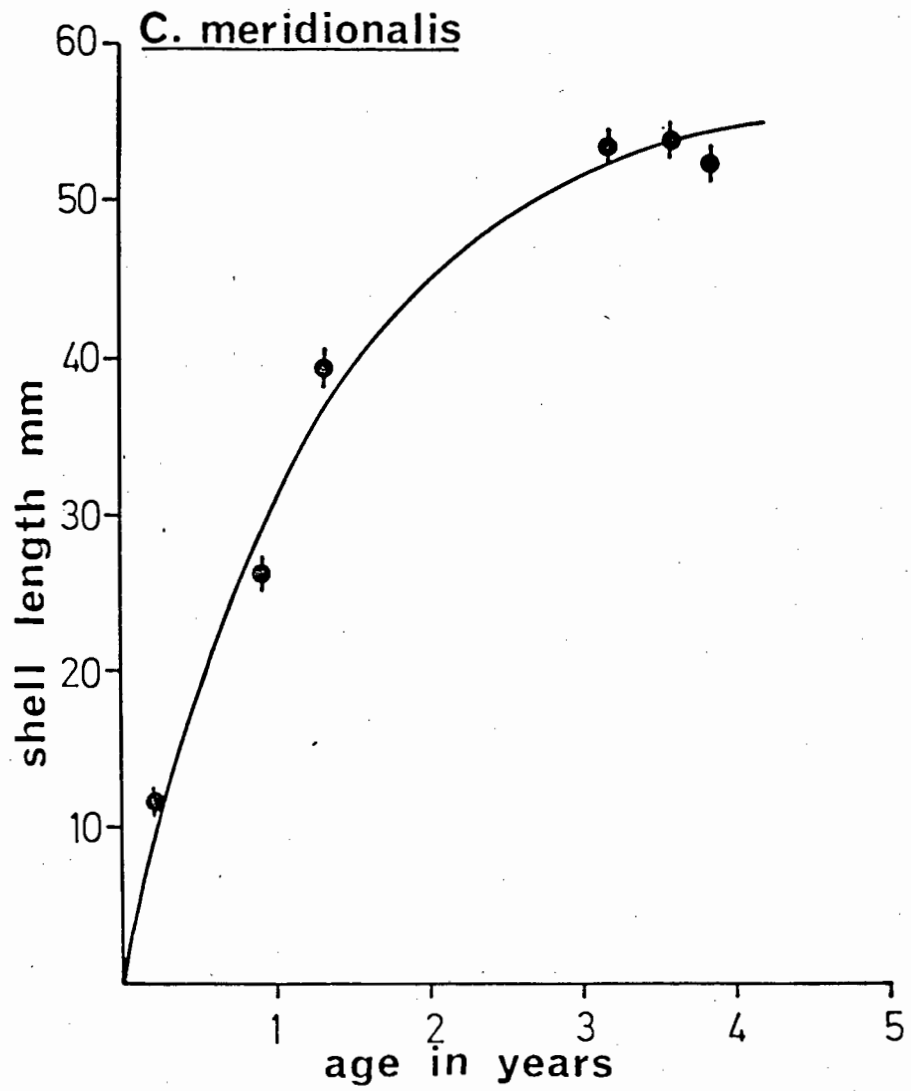


Fig. 3. Growth rate of C. meridionalis in the pool at Bailey's Cottage. Line fitted by eye. Vertical bars indicate standard error.

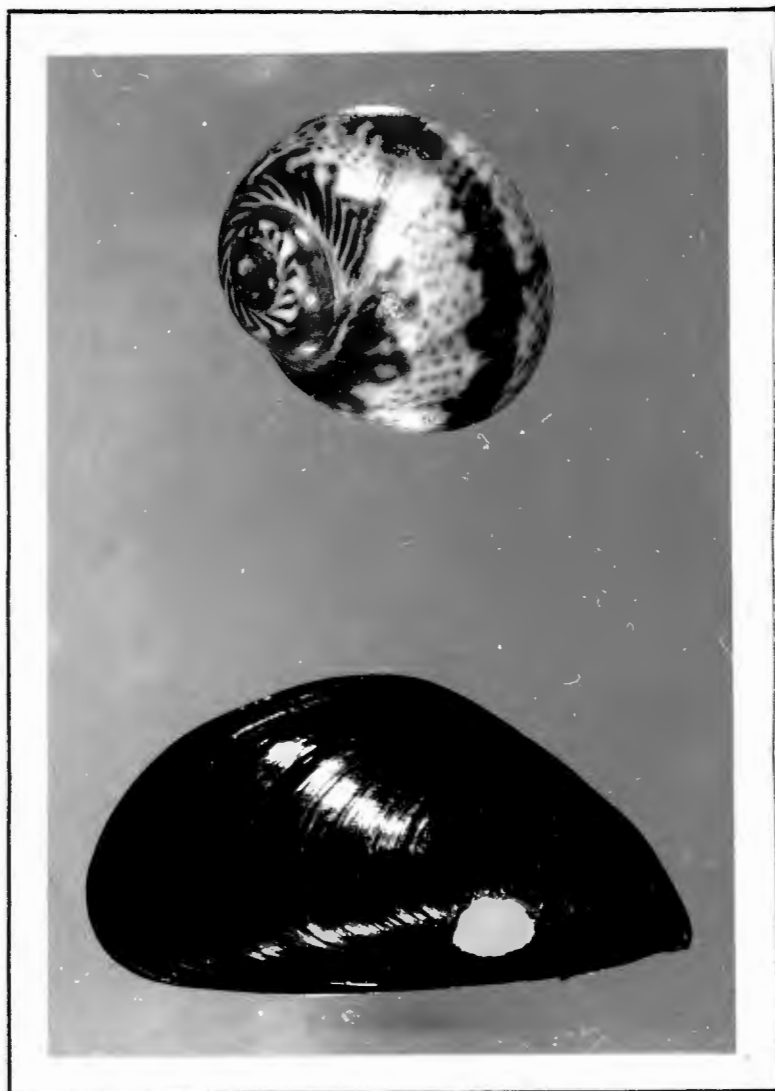


Plate 1. N. tecta and a C. meridionalis shell showing the position and nature of the borehole.

Considerable controversy has surrounded the mechanism of boring in the Naticidae and is reviewed by Fretter & Graham (1962) and Orton (1966). Natica species drill characteristically tapered holes by alternative rasping of the radula and application of an accessory boring organ (on the proboscis ventral lip) to the boring site. The accessory boring organ is considered to secrete an enzyme, rather than an acid as in boring Muricacea, which assists in shell penetration (Fretter & Graham, 1962).

Fig. 4 shows the positions of the holes drilled in mussel valves in the laboratory and field. In the laboratory where mussels were easily accessible to manipulation by the foot, the holes were concentrated in an area slightly anterior and ventral to the centre of the shell. In this position the proboscis penetrates the mantle cavity in the region of the mussel foot. Holes drilled in the field occur in a similar region to those drilled in the laboratory but show slightly wider dispersion.

The site of the holes drilled by gastropods into bivalve prey varies with different predator/prey species combinations (Ansell, 1960), but frequently occurs in the dorsal region overlying the bivalve gonad. It has been suggested that in these cases alimentary conditioning occurs in selection of the borehole site (Verlaine, 1936, quoted by Negus, 1975). However, Ansell (1960) and Negus (1975) suggest that the position of the holes drilled by N. alderi (Forbes) and N. catena Da Costa) respectively, is related to the way in which the prey is held by the foot. Data on N. tecta confirm this view. The foot firmly envelopes most of the

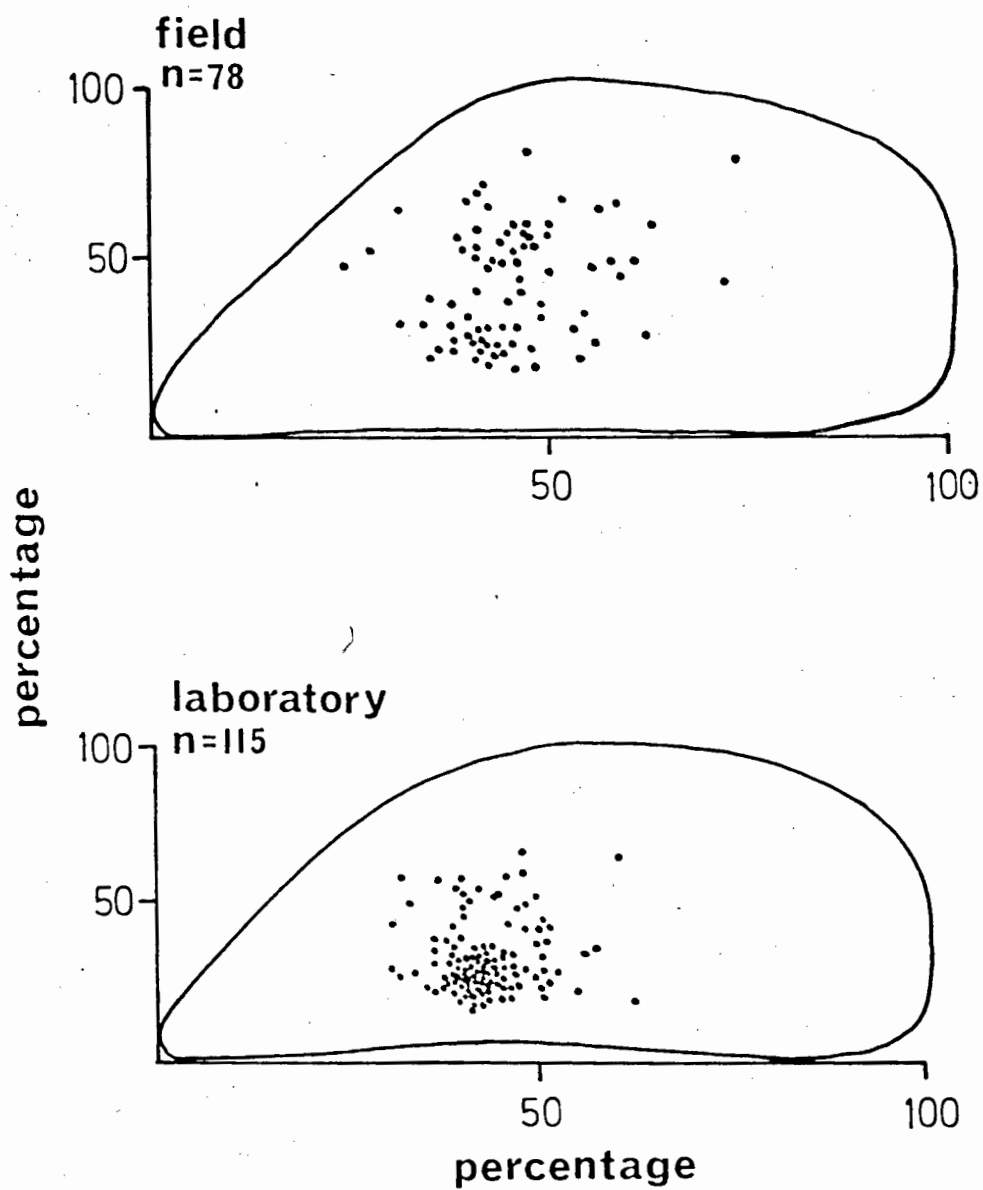


Fig. 4. The site of boreholes in *C. meridionalis* valves drilled by *N. tecta* in the field and the laboratory. Position plotted as percentage of shell height and shell length.

mussel which is held with the anterior and posterior ends projecting laterally on either side of the gastropod. Because of the byssal attachment, the dorsal surface of the mussel is always anterior to the radula. The area of the shell thus exposed for boring is limited. This explains the constancy of positioning of the boreholes. Except for the occasional remaining strands of posterior adductor muscle, all tissue is removed from the shell.

Of a total of 231 shells drilled in the laboratory, 55.8% were bored through the right valve. A χ^2 test showed no significant difference in the number of left and right valves bored ($0.1 > p > .05$).

Borehole width is probably an indication of predator size. A plot of hole width versus shell length is shown in Fig. 5. There was considerable scatter in the data, but size selection is indicated. A similar relationship was found by Ansell (1960) for holes drilled by N. alderi in Venus striatula (Da Costa).

Prey size selection was confirmed by laboratory feeding experiments. Fig. 6a shows the number and size distribution of prey consumed by different sized N. tecta. Each histogram represents all mussels consumed by two individuals during a six week period. The histograms show that small N. tecta consume smaller sized mussels and take prey over a more limited size range than do larger individuals. The number of prey taken in each size range is a poor reflection of the size of prey from which most energy is gained. Fig. 6b shows the energy value of the flesh consumed from the different prey size classes. Because

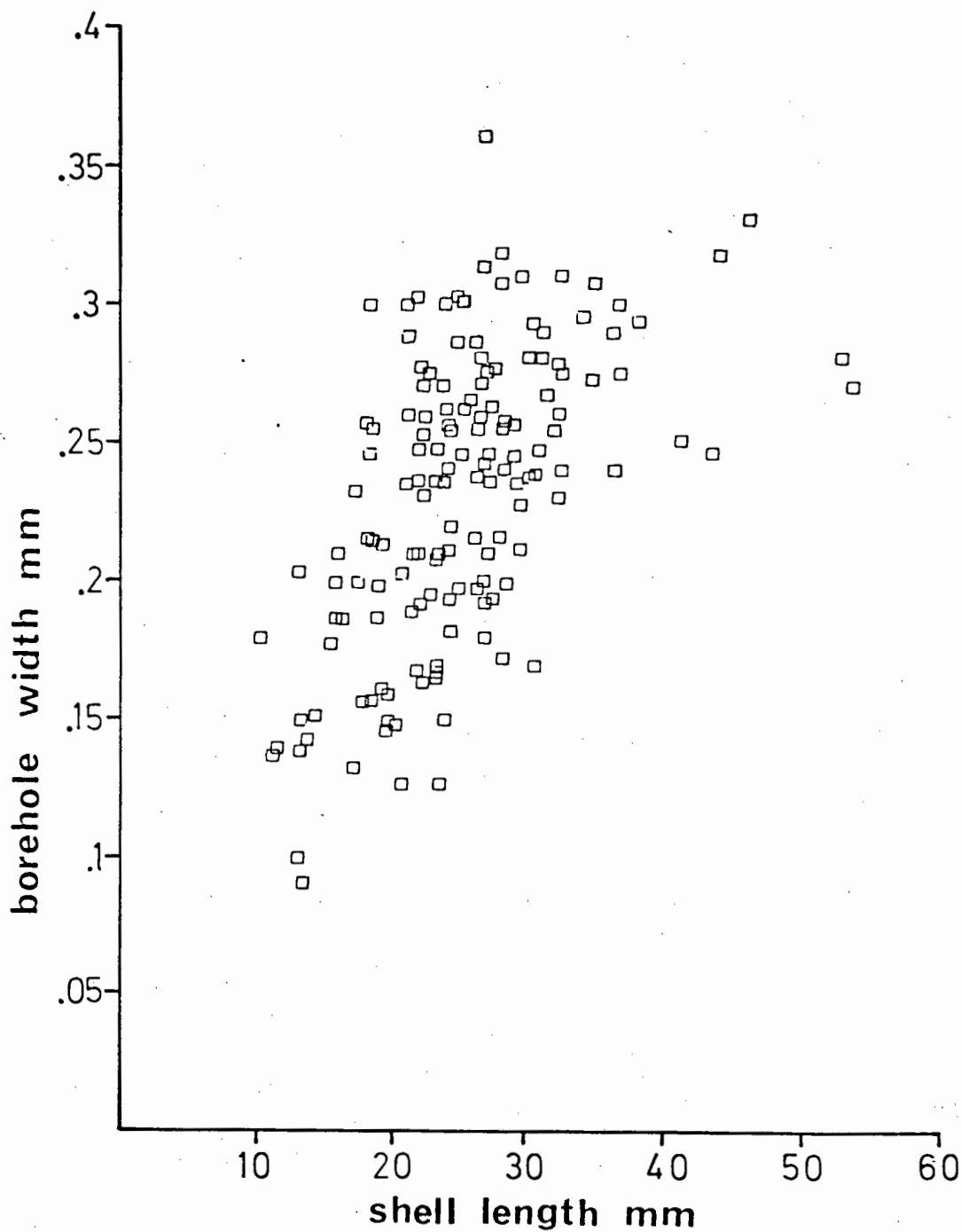
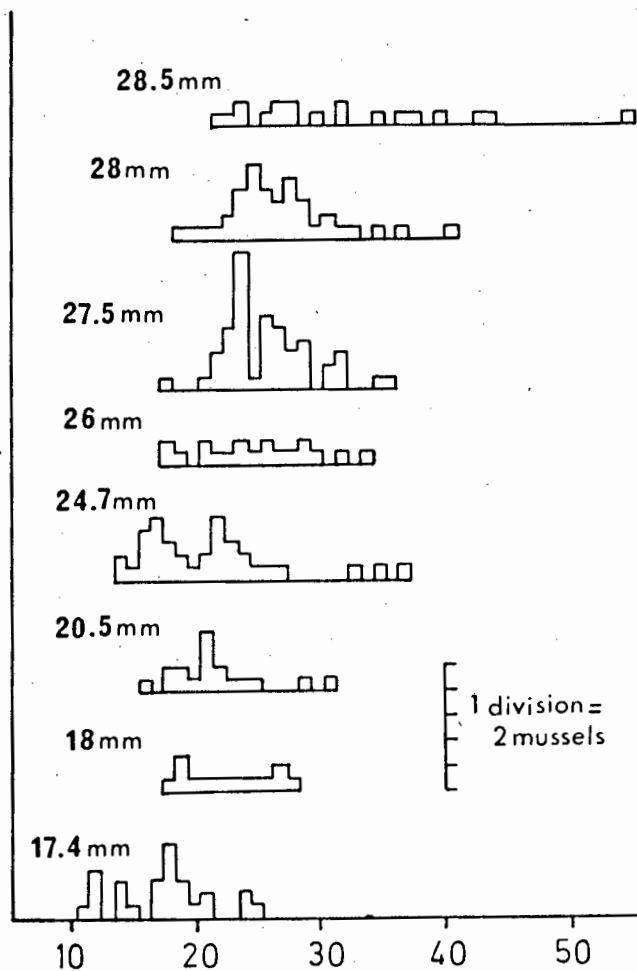


Fig. 5. Width of borehole plotted against mussel shell length in mm.

(a) number



(b) energy

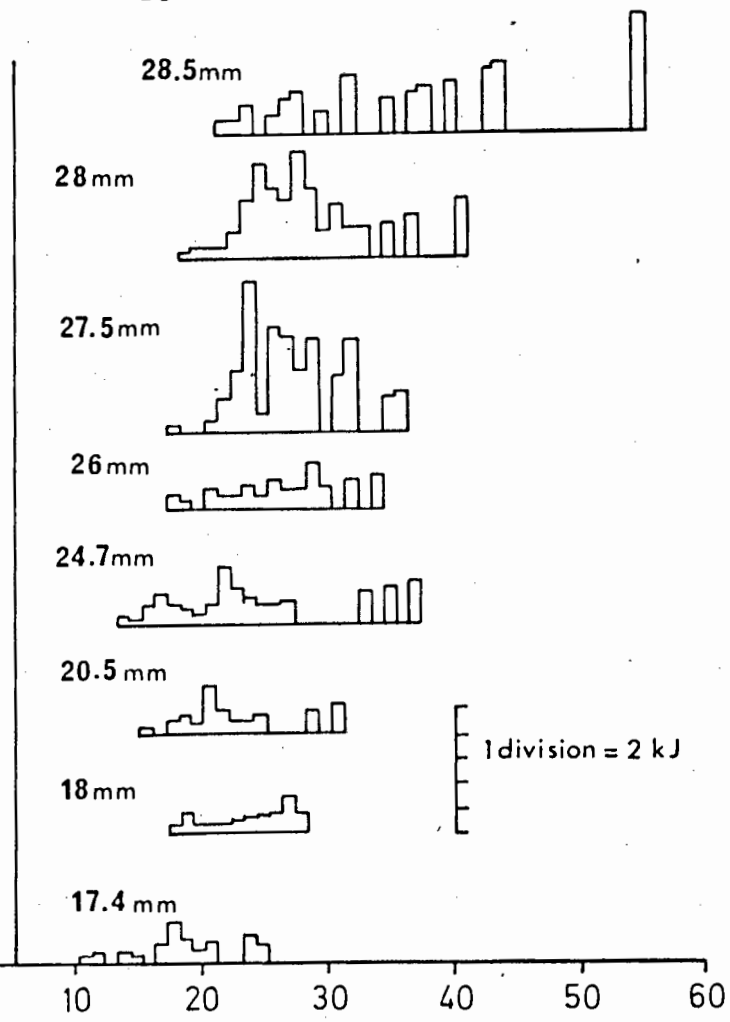


Fig. 6. The consumption rates of 8 different sized *N. tecta* fed on a size range of *C. meridionalis*. Each histogram represents consumption by 2 individuals over a 6 week period. (a) Number of mussels consumed, (b) energy consumed in kJ.

larger prey represent a greater energy source, more energy was obtained by drilling few large mussels than many small ones. However, the energy expended on drilling different sized mussels is not known. Thus the optimal prey size giving maximum energy gain for effort expended has not been estimated.

Fig. 7 shows the mean energy consumption per week of N. tecta of different sizes. Consumption increases rapidly in individuals larger than 20 mm width. Although further investigation is required, laboratory observation indicates that this may represent the size at which individuals attain sexual maturity. A power curve was fitted to the data:-

$$\left[\text{consumption (kJ week}^{-1}) \right] = 2.39 \times 10^{-4} \cdot \left[\text{shell length (mm)} \right]^{2.9132}$$

$$r^2 = 0.88, \quad n = 8.$$

Population consumption, calculated using the above regression equation and the size-frequency distribution of N. tecta at Bailey's Cottage (Fig. 1), averaged 663 kJ m^{-2} per month.

Both laboratory and field data indicate that C. meridionalis larger than 55 mm are not preyed upon by N. tecta. Thus mussels larger than this size may be free from predation pressure. The energy available to N. tecta as mussel flesh in July 1979 in the size range 10 - 55 mm shell length was calculated from Fig. 2 and represented 6765 kJ m^{-2} . At the above consumption rate the gastropods would exhaust this food supply within 10 months. However, in addition to exploitation by N. tecta, continuous natural mortality of the mussel population would

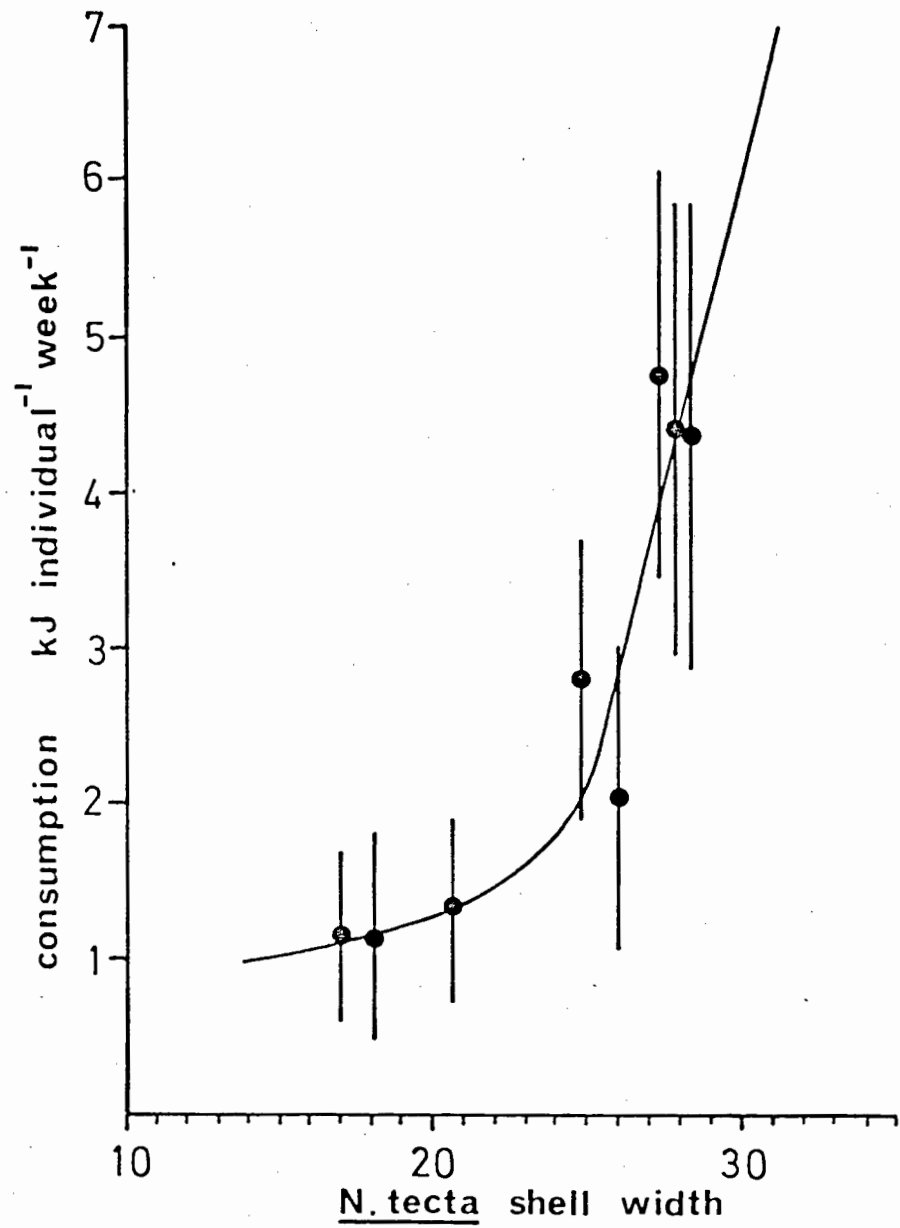


Fig. 7. Average weekly energy intake by different sized N. tecta. Vertical bars indicate one standard deviation.

enhance depletion of the standing crop. This was confirmed by field measurements in January 1980 which showed a marked decline in both mussel and gastropod densities, only 6 months after the initial sampling date. The mussel population was thus severely depleted within 1.5 years of settlement in the pool.

The noticeable increase in N. tecta densities at a time when large numbers of suitable prey are present parallels the observation by Ansell (1960) for N. alderi. This species appeared in an area where it had not previously been recorded, in association with increased densities of Venus striatula. Studies conducted over a longer time period may well show cyclical changes in N. tecta densities at Bailey's Cottage in association with changes in the population structure of C. meridionalis. The mussel population consists of predominantly one cohort which is displaced by spat settlement at 4 to 6 year intervals (Griffiths, 1980). A new spat settlement appears to offer a niche for the settlement and growth of N. tecta. However, because of a rapid growth rate, the mussels exceed the prey size selection range of small N. tecta (<20mm shell width) within one year. This may be expected to limit recruitment of gastropod population. No alternative food source for small N. tecta has been found in the pool, and it is interesting to note that despite the high rate of egg laying, no juvenile gastropods were found during the sampling period. After the first year of mussel growth only large N. tecta may be expected to survive on the mussel bed until the next spat settlement occurs.

Laboratory predation rates and field measurements on the population

decline of both species indicates that N. tecta exploits its food source to the maximum and that predator and prey population densities and size-frequency distributions are interdependent.

SUMMARY

(1) In July 1979 the N. tecta population on a mussel bed in a pool at Bailey's Cottage, False Bay, South Africa averaged 69 m^{-2} and consisted of individuals between 20 to 30 mm shell width. By January 1980 the density declined to 12 m^{-2} . No juveniles were found.

(2) C. meridionalis, the prey species, averaged $5\ 653 \text{ m}^{-2}$ and consisted predominantly of mussels between 12 - 45 mm. By January 1980 the mussel density declined to 100 m^{-3} (1.5 years after settlement).

(3) N. tecta drill the shells of C. meridionalis, the position of the borehole being related to the way in which prey is held during boring.

(4) Prey size selection occurs, the size of prey taken being an increasing function of predator size.

(5) At densities of 69 m^{-2} the N. tecta population consume 663 kJ m^{-2} per month from a standing crop of mussels averaging $6\ 765 \text{ kJ m}^{-2}$.

(6) Depletion of the mussel bed was attributed to exploitation by N. tecta.

(7) It is concluded that predator and prey population densities and size-frequency distributions are interdependent.

ACKNOWLEDGEMENTS

This work was supported as part of the Kelp Bed Research Programme by the South African National Committee for Oceanographic Research. Mr J. Williams is thanked for the photograph.

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PAPER 4. FILTRATION, RESPIRATION AND ASSIMILATION IN

THE BLACK MUSSEL CHOROMYTILUS MERIDIONALIS (KR.) .

Filtration, Respiration and assimilation
in the black mussel Choromytilus meridionalis (Kr.)

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Abstract

Filtration rates, respiration rates and assimilation efficiencies of Choromytilus meridionalis (Kr.) fed on Dunaliella primolecta were examined. No seasonal or tidal changes in filtration rate were recorded. Filtration rates were variable within and between individuals but were independent of algal concentration over the range $0.4 - 50 \times 10^6$ cells l^{-1} . Below 0.4×10^6 cells l^{-1} the filtration rate increased with declining ration. Respiration rate was not affected by ration level but increased with rising temperature.

Assimilation efficiencies were high, averaging 80% between $0.5 - 8 \times 10^6$ cells l^{-1} , but declined to zero at 30×10^6 cells l^{-1} .

The effects of starvation on the filtration rate, respiration rate and assimilation efficiency were also studied. Following starvation filtration rates increased at all cell concentrations while the curve for assimilation efficiency showed translation to the left so that efficiency declined

to zero at 20×10^6 cells l^{-1} instead of 30×10^6 cells l^{-1} . The net result was a shift of the zone of positive scope for growth into a region of lower cell concentrations.

C. meridionalis may co-exist with the bivalve Aulacomya ater in the field. Assimilation efficiency and scope for growth were compared in the two species. The scope for growth in C. meridionalis may be related to its higher filtration rate and was more than twice that of A. ater. However A. ater obtained a positive scope for growth over a wider range of algal ration levels.

INTRODUCTION

The use of cultured algal species as a food source has proved valuable in obtaining data on the filtration rates, respiration rates and assimilation efficiencies of filter feeders. The use of monocultures has the further advantage of facilitating comparison between data from different species fed on the same or similar diets. This technique has been applied to the study of bivalves in particular, and a considerable body of information is presently available. Much of this has been summarised by Bayne et al. (1976) with special reference to the European mussel Mytilus edulis.

Griffiths and King (1979a) have obtained data on the filtration and respiration rates of the South African bivalve Aulacomya ater when fed on Dunaliella primolecta. However, due to a paucity of information on local or southern hemisphere species, their data could only be compared with that of northern hemisphere bivalves. In order to obtain further data on local species and permit future comparison of the eco-physiology of the different bivalve species, the filtration rates, respiration rates and assimilation efficiency of Choromytilus meridionalis are investigated. Dunaliella primolecta monoculture was used as a food source to obtain data comparable with that on A. ater.

Of the three common rocky littoral and sublittoral mytilid bivalves found on the coast of South Africa, A. ater and C. meridionalis have similar distributions around the southwestern Cape Province, while Perna perna is dominant in the warmer waters of the east coast. Comparative data on the reproductive cycles, growth and population dynamics of C. meridionalis (Griffiths, 1977; Griffiths, 1980) and P. perna (Berry, 1978) show that these species have considerably faster maturation times and growth rates than A. ater (Griffiths & King, 1979b) and hence would be more suitable to commercial cultivation. However, little is known of the metabolic requirements for maintenance of a positive energy balance in the laboratory or field.

MATERIALS AND METHODS

Mussels were collected at low water spring tide (L.W.S.) level from the shore at Bailey's Cottage, False Bay, South Africa (34°06'S 18°28'E). They were housed in a recirculating aquarium (3500 l capacity) at ambient sea temperature (12°C in winter, 18°C in summer). Except for experiments on the effect of laboratory storage, when animals were maintained for 3 weeks, all individuals were used within 3 days of collection, usually on the same day. Mussels were cleaned of epibiotic growth and the byssus threads remained intact unless discarded by the animal.

(1) Filtration rate

Filtration rates were determined by measuring the rate of decline of a suspension of Dunaliella primolecta with a model TA II Coulter Counter with a 70 µm aperture. Each mussel was attached to a fine mesh-covered grid with a rubber band so that it was maintained in a natural upright position. The grid was suspended in a glass beaker containing a magnetic stirrer bar and 2 l of 0.45 µm filtered seawater. Faecal strands eliminated during the experiment became trapped on the mesh and were removed immediately with a pipette. Algal concentrate was added to give the desired concentration and the decline in algal numbers measured at 10 or 15 min intervals. Further algal concentrate was added at intervals to maintain the concentration. Unavoidable fluctuation in cell concentration occurred in this system but efforts were made to contain this within 20% of the desired concentration by frequent addition of culture.

Filtration rate was calculated according to the standard formula:

$$\text{Filtration rate (lh}^{-1}\text{)} = \left(\frac{\log_e N_1 - \log_e N_2}{T} \right) \times V$$

where N_1 = cell concentration at time t_1 , N_2 = cell concentration at time t_2 , T = time elapsed between readings in h, V = volume of solution in litres. Six readings were obtained from each individual tested.

Bayne et al. (1976) and Winter (1969) have reviewed the numerous methods employed by authors to measure the filtration rates of bivalves. The disadvantage of the above method is the constant fluctuation in cell count experienced by the animal and the short duration of the experiments. This may obscure changes in filtration rate with cell concentration and give a slight overestimate of filtration rate until the animal has adjusted to the experimental conditions. However comparison of this method with results obtained from a recirculating constant flow apparatus[†] using 20 l of water containing algal cells, showed that reliable results may be obtained with C. meridionalis.

(2) Respiration

The respiration rate of mussels feeding at different concentrations of algal culture was measured using a Gilson Differential respirometer and constant pressure respirometers (Davies, 1966). Mussels were placed in 0.45 μm filtered seawater and respiration measured at 10 min

[†] see appendix 1

intervals for 1 h. The oxygen consumption was then measured for a further 10 min interval following injection of known concentrations of algal culture into the water. The flasks were then opened and a suitable time interval allowed for utilisation of the remaining algae before more concentrate was injected and another reading taken. In this manner 6 continuous readings of respiration rate before feeding, and 6 intermittent readings during feeding, were obtained.

Respiration rates at different temperatures were measured using the Gilson respirometer for mussels 10-44 mm shell length. For mussels 30-110 mm, 6 YSI pO_2 probes connected via a switch gear mechanism to a multichannel chart recorder were used. The switchgear maintained constant potential across all electrodes while monitoring each probe for 5 sec every 1.25 min. Mussels were attached to perspex grids with the aid of rubber bands and inserted into 500 ml perspex containers which were sealed with oxygen probes placed centrally in the lids. Water was maintained in rapid circulation with a magnetic stirrer. Each chamber lid contained inlet and outlet pipes (clamped shut when not in use) enabling replenishment of the water at intervals⁺. The volume of oxygen in the water at the start of each experiment was determined by replicate Winkler analysis (Strickland and Parsons, 1968).

(3) Assimilation efficiency

Assimilation efficiencies were determined according to the method of Conover (1966).

⁺ see appendix 2

Assimilation of Dunaliella primolecta cells was measured simultaneously with filtration studies. Mussels were maintained in the laboratory for 24 h prior to use, allowing evacuation of sand from the gut. Preliminary studies showed that approximately 1 h elapsed between onset of feeding and the appearance of algal cells in the faeces. Faeces produced within the first 1.5 h were thus discarded and all subsequent faeces over a 4-5 h period collected for analysis. Faecal strands and replicate 10 ml volumes of algal concentration of known cell concentration, were filtered onto pre-ashed, weighed 25 mm diameter GFC filters. Each sample on the filter was flushed with ammonium formate isotonic with seawater. Filters were dried, weighed and ashed at 450°C for 3 h, and weighed again. The ratio of the ashfree dry weight to dry weight of food and faeces were used in the Conover ratio. An electronic microbalance was used for weighing filters (readability 1 µg).

(3) Length-weight relationships

Data on length-weight relationships of different body components and their calorific values are taken from Griffiths (1980).

RESULTS AND DISCUSSION

Filtration rates

Preliminary experiments showed no difference in filtration rates in mussels whose byssal threads were attached to the substrate, detached or absent, although such differences

have been noted in M. edulis (Theede, 1963 quoted by Winter, 1969). In C. meridionalis byssal production appears to occur regularly throughout life, particularly in areas where continuous deposition and erosion of sand occurs. Individuals in the laboratory show considerable mobility and facility of byssal production.

Age of D. primolecta culture was found to affect filtration and assimilation. Filtration rates were higher and assimilation efficiency lower on young culture in the exponential growth phase than on culture which has passed the peak growth phase by several days. Consequently only cultures in the latter stage of the exponential growth phase and immediately about the peak were used in experiments.

No pseudofaeces were produced in the experiments. A minimum concentration of 50 to 60 x 10⁶ cells l⁻¹ being required before this occurred. Once pseudofaeces production is initiated the filtration rate no longer equals ingestion rate. Foster-Smith (1975) quantified pseudofaeces production in M. edulis. The amount of food rejected rose rapidly with increasing concentration from 50-100 x 10⁶ cells l⁻¹. An interesting and inexplicable feature in C. meridionalis was that pseudofaeces production was initiated at a concentration well above that at which the assimilation efficiency on algal cells fell to zero (see below).

Variability in filtration rate is a common feature in bivalves (Winter, 1969; Schulte, 1975). C. Meridionalis was no exception and Fig. 1 demonstrates the fluctuation in high and low filtration rates which may occur with some regularity. This may reflect digestive gland activity eg. saturation and reduction of the filtration rate until this has cleared. However digestive gland phasic activity has hitherto been reported over a longer time cycle, usually associated with tidal exposure (Owen, 1974; Morton, 1977).

The controversy of tide induced rhythms in filtration rate has been reviewed by Winter (1969) who found existing data inconclusive. There was no evidence of tidal rhythmicity in M. edulis. The filtration rates of C. meridionalis (40 mm, ambient sea temperature 12°C) was measured during 2 h periods corresponding to high and low water spring tide in the field. Mussels were collected at the appropriate state of tide from the sublittoral and 0.85 m above L.W.S. (high-shore) immediately prior to measurement in the laboratory. Fig. 2 and Table 1 show that there was no significant difference in filtration rate at times corresponding with high or low tide. However, the rate of filtration was slightly higher in highshore mussels compared with sublittoral individuals. This may be a consequence of aerial exposure.

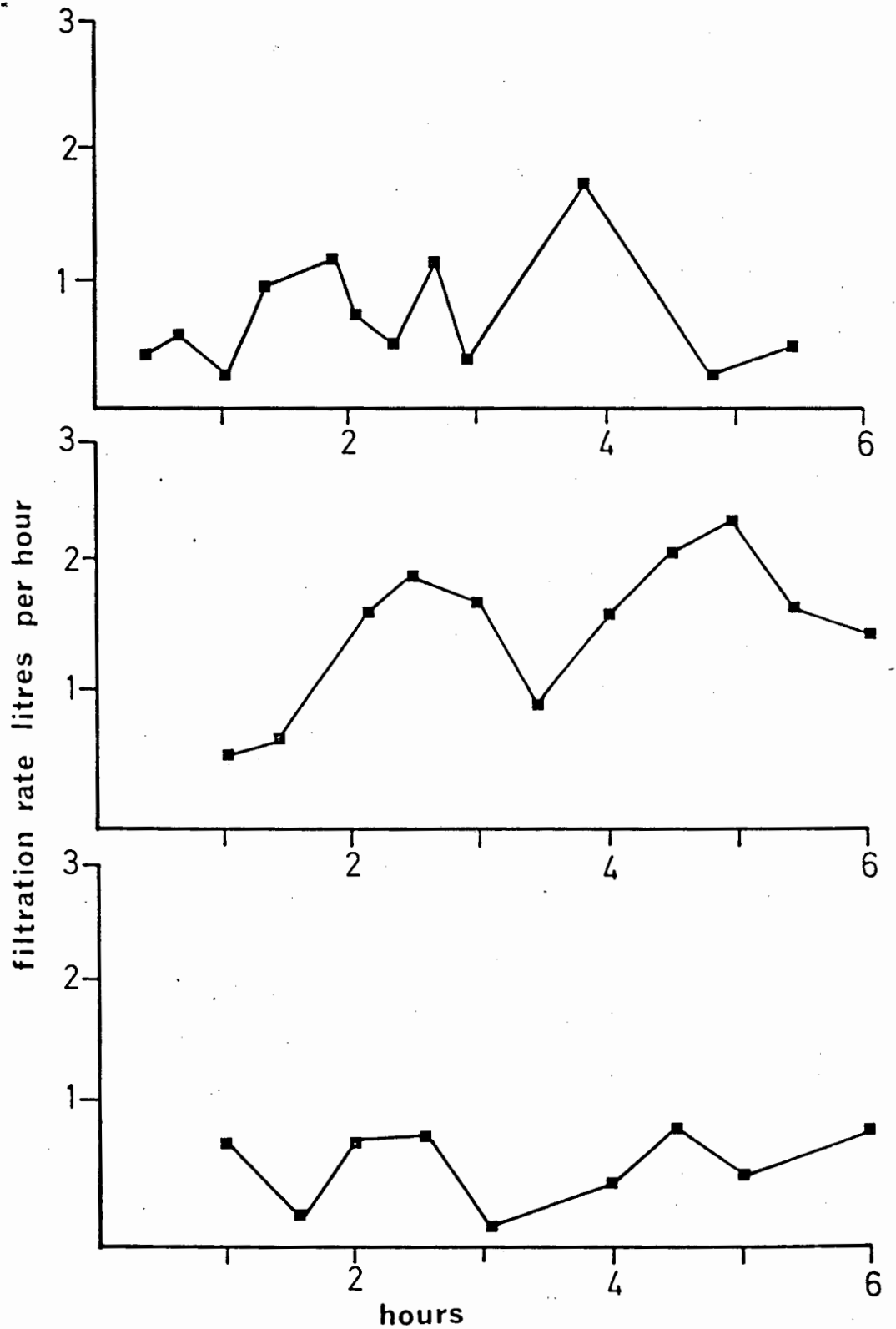


Fig. 1. Changes in filtration rate over time in three 40 mm *C. meridionalis* fed on 10×10^6 cells *D. primolecta* l^{-1} at $12^\circ C$. (Filtration rates slightly depressed due to use of aged algal culture).

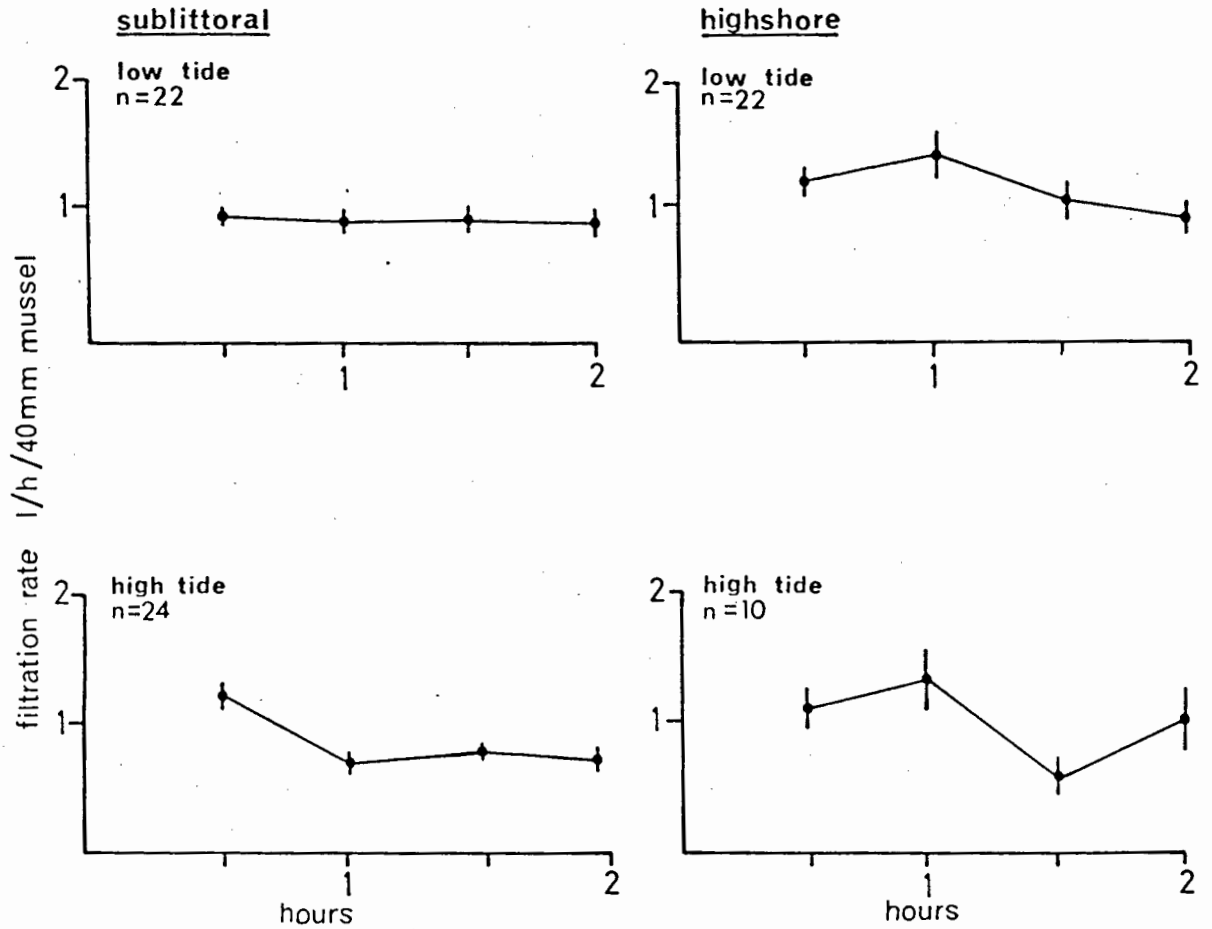


Fig. 2. Mean filtration rate and one standard error of 40 mm mussels over a 2 h period during low and high tide at L.W.S.. Mussels collected from the sublittoral and 0.85 m above L.W.S. and fed 10×10^6 cells l^{-1} at $12^\circ C$. (Filtration rate slightly depressed due to use of aged algal culture).

Table I. The effect of state of tide on filtration rate of 40 mm C. meridionalis collected from the sublittoral and 0.85 m above L.W.S. (high-shore)

Mean filtration rate and standard error				
	n	low tide	high tide	n
Sublittoral	22	0.94 \pm 0.05	0.87 \pm 0.06	24
High-shore	22	1.16 \pm 0.06	1.10 \pm 0.11	10

Fig. 3 shows the filtration rates of 20-100 mm length mussels at 10×10^6 cells l^{-1} during summer (ambient sea temperature $18^{\circ}C$) at $18^{\circ}C$ and $12^{\circ}C$ and during winter at ambient sea temperature of $12^{\circ}C$. The regression equations for these data and the pooled data (no significant difference between slopes and intercepts) are given in Table 2. There was no change in filtration rate with ambient temperature change. Schulte (1975) and Widdows (1978) have shown that acclimation of the filtration rate to temperature change may be expected within the normal environmental range.

Bayne et al. (1976) have summarised the weight exponents found in relating filtration rate to size in different bivalve species. These vary from negative values to 0.76. The significance of this is difficult to interpret, particularly where filtration rate may vary with experimental technique and ration level. Comparison between published data is further complicated because the weight exponent has been found to vary with the size of individuals sampled. It is generally higher in experiments including small individuals and low (e.g. 0.38 in Widdows, 1978) when mostly large specimens are used. The equation for C. meridionalis was:

$$lh^{-1} = 5.3676 \times [g \text{ dry flesh weight}]^{0.5959}$$

and included a large size range of 15-110 mm specimens (0.02 - 3.2 g dry flesh wt.).

Measurements from C. meridionalis and A. ater (Griffiths and King, 1979a & b) were obtained under similar experimental

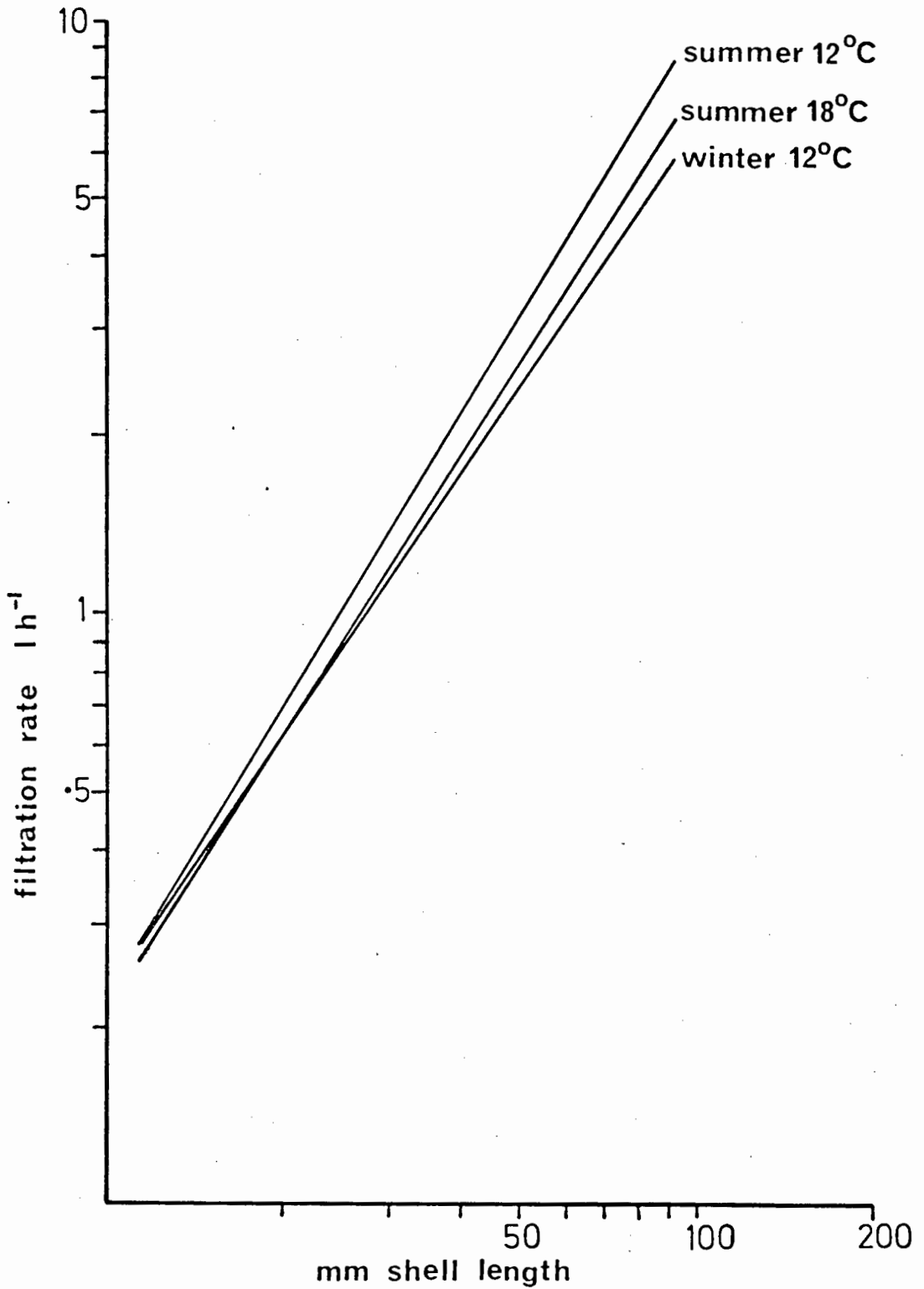


Fig. 3. Filtration rates of different sized mussels fed on 10×10^6 cells l^{-1} measured in summer at 18°C (ambient sea temperature) and at 12°C , and in winter at 12°C (ambient sea temperature). Regression equations given in Table II.

Table II. The filtration and respiration rate of C. meridionalis at different seasonal sea temperatures and the respiration rate at different algal concentrations. Equations in the form $y = ax^b$ where y = filtration rate in lh^{-1} , or respiration rate in μlh^{-1} , or dry flesh weight in g, and x = mm shell length.

<u>Filtration rate</u>	a	b	r^2	n
Summer 12°C	0.00478	1.66	.89	27
Summer 18°C	0.00565	1.57	.86	18
Winter 12°C	0.00755	1.47	.76	19
Pooled data	0.00644	1.58	.85	64
<u>Respiration rate</u>				
Summer 18°C	0.2900	1.78	.89	69
Summer 25°C	0.6516	1.74	.86	22
Winter 12°C	0.1751	1.83	.91	12
18°C : no food	0.2900	1.78	.89	69
250 cells. ml^{-1}	0.6138	1.60	.74	35
1000 " "	0.1778	1.94	.76	44
10000 " "	0.1306	2.03	.71	33
20000 " "	0.2742	1.81	.88	28
40000 " "	0.2483	1.81	.89	21
<u>Dry flesh wt.</u>	1.251×10^{-5}	2.65	.98	116

conditions and the filtration rate of 50 mm individuals at 10×10^6 cell l^{-1} at $12^{\circ}C$ may be compared. Measurement of the gill area of a size range of live specimens (unpublished data[†]) has shown no difference in filtration area in the two species. A 50 mm C. meridionalis (dry flesh mass 0.39 g) filtered at 3.1 lh^{-1} compared with 1.26 lh^{-1} in the same sized A. ater (dry flesh mass 0.54 g). The filtration rate in A. ater increases with ration level, however the maximum rate measured in a 50 mm mussel was 1.6 lh^{-1} at 32×10^6 cells l^{-1} . Thus a 50 mm A. ater, which is nearly twice the weight of C. meridionalis, filters, and grows, at a considerably slower rate.

The effect of increasing cell concentration on filtration rate has been examined in several bivalve species. Experiments on M. edulis show conflicting results. Widdows (1978), Foster-Smith (1975) and Thompson and Bayne (1974) have shown no effect of concentration on the feeding rate of M. edulis while Winter (1969) and Schulte (1975) demonstrated declining filtration rates with high cell concentrations. The filtration rate of 45 mm C. meridionalis was measured at different concentrations of D. primolecta (Fig 4a). No threshold concentration for the onset of filtration was recorded as occurs in M. edulis (Thompson and Bayne, 1972) and A. ater (Griffiths and King, 1979a). The

[†] see appendix 3

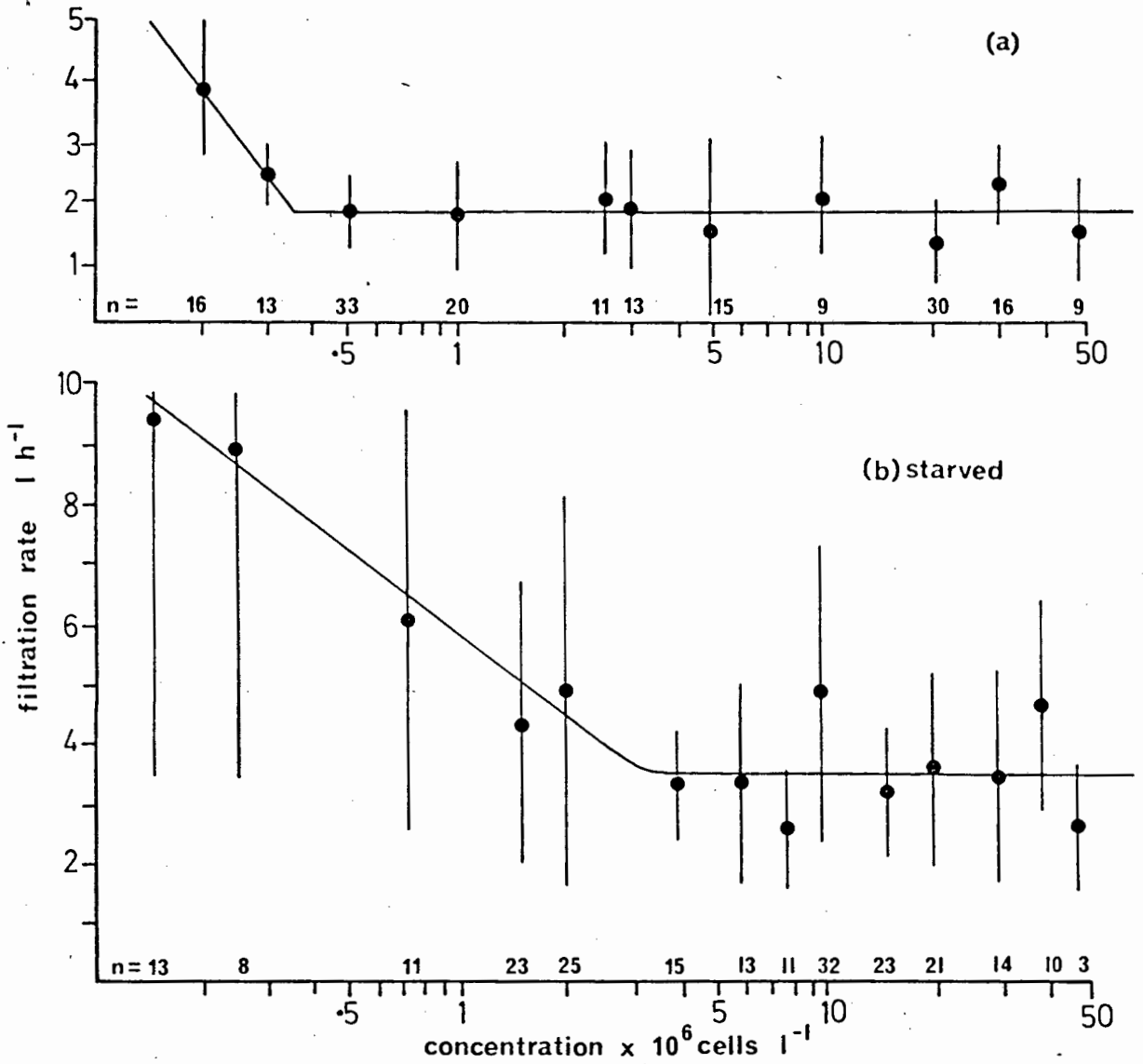


Fig. 4. Filtration rate of 45 mm *C. meridionalis* at different cell concentrations at 18°C. (a) unstarved animals (b) starved for 3 weeks. n = number of individuals used for each data point, vertical bars indicate one standard deviation.

filtration rate remained constant at 1.82 lh^{-1} between $0.4 - 50 \times 10^6$ cells l^{-1} and increased with declining ration below 0.4×10^6 cells l^{-1} . These data were compared with those obtained from starved (45 mm) mussels maintained in the laboratory for 3 weeks. During this time the organic material in the water was approximately half that recorded in the field ($1.07 \text{ mg AFDW l}^{-1}$ in aquarium, $2.65 \text{ mg AFDW l}^{-1}$ in natural seawater). Reduced ration resulted in a marked rise in filtration rate (Fig. 4b), particularly at low cell concentrations. The variation in rate displayed by individuals increased as indicated by the standard deviations in Fig. 4b. This data indicates that although compensation to lower ration levels does not occur in the short term, C. meridionalis may adjust the filtration rate when subject to limited food availability over 2 to 3 weeks. However, under conditions of prolonged starvation it may be expected that a marked decline in filtration rate would occur. Starvation usually results in a decline in the metabolic rate to a basal level (Bayne, 1973; Bayne et al., 1976).

Respiration

Preliminary experiments showed that the rate of oxygen consumption was not influenced by detachment or removal of byssal threads or state of tide.

The respiration rate of a size range of mussels was measured at ambient sea temperature during summer (18°C) and winter (12°C) and is shown in Fig. 5 and Table II. Oxygen consumption was also measured at 25°C in summer. Although C. meridionalis in False Bay seldom experience sea conditions in excess of 20°C, specimens on the south-east coast of the Cape Province are subject to warmer sea temperatures. The respiration rate showed no seasonal acclimation to temperature change and increased with rising temperature. Q_{10} values for a 45 mm mussel between 12-18°C and 18-25°C were 1.69 and 2.55 respectively. This is equivalent to the routine rate of oxygen consumption and is similar to the response measured in other mytilids (Bayne et al., 1976). The routine rate may not only be affected by temperature but by state of gametogenesis. Bayne and Thompson (1970) and Bayne (1973) found that the respiratory rate in M. edulis was higher in late winter during active gametogenesis and lower during the gonad resting stage in late summer. In C. meridionalis however, gametogenesis is almost continuous with extended spawning peaks in summer and winter (Griffiths, 1977) and unlikely to produce seasonal change in respiratory rate.

For comparison of respiration with that of other species, oxygen consumption in C. meridionalis may be expressed as a function of dry flesh weight in g. At 18°C, 'a' = 0.576 ml O₂ h⁻¹ and 'b' = 0.673, and at 12°C 'a' = 0.430 ml O₂ h⁻¹ and 'b' = 0.692. Both the intercepts and weight exponents compare

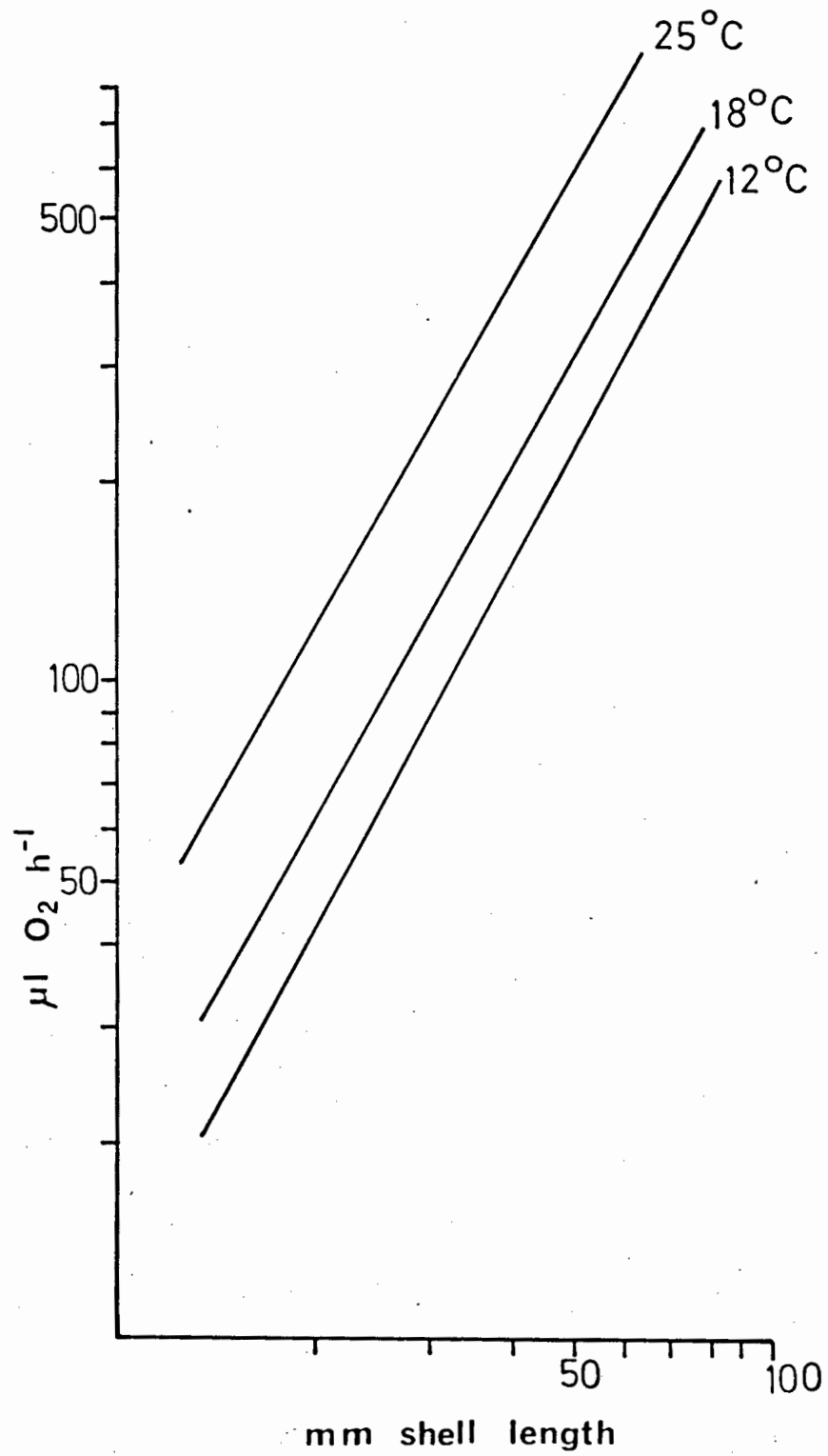


Fig. 5. Respiration rate of *C. meridionalis* measured during summer at 18°C and 25°C and in winter at 12°C.

favourably with those obtained for routine rates of oxygen consumption in other bivalve species (summarised by Bayne et al., 1976). However the respiratory rate in Aulacomya ater is considerably lower than that in C. meridionalis and Griffiths & King (1979a) report that 'a' = $0.17 \text{ ml O}_2 \text{ h}^{-1}$.

Thompson and Bayne (1974) working on M. edulis and Griffiths and King (1979a) on A. ater have demonstrated increasing oxygen consumption with increasing ingestion ration. The respiration rates of a size range of C. meridionalis (10-100 mm) was measured at 18°C at 250, 1000, 10000, 20000 and 40000 cells ml^{-1} , and compared with the rate measured in the absence of food. Table II presents the regression equations for this data. There was no significant difference between the slopes and intercepts. Oxygen consumption in C. meridionalis is not influenced by ration level.

Although the filtration rate increased, the respiration rate of mussels starved in the aquarium for 3 weeks did not differ from that of unstarved mussels, indicating that the level of stress was not severe. Starvation in M. edulis and M. californianus is usually accompanied by a decline in filtration and respiration rate, the time taken for this to occur varying with gametogenic state (Bayne, 1973; Bayne et al., 1976).

Assimilation Efficiency

The assimilation efficiencies of 45 mm mussels fed on various concentrations of D. primolecta are shown in Fig. 6a.

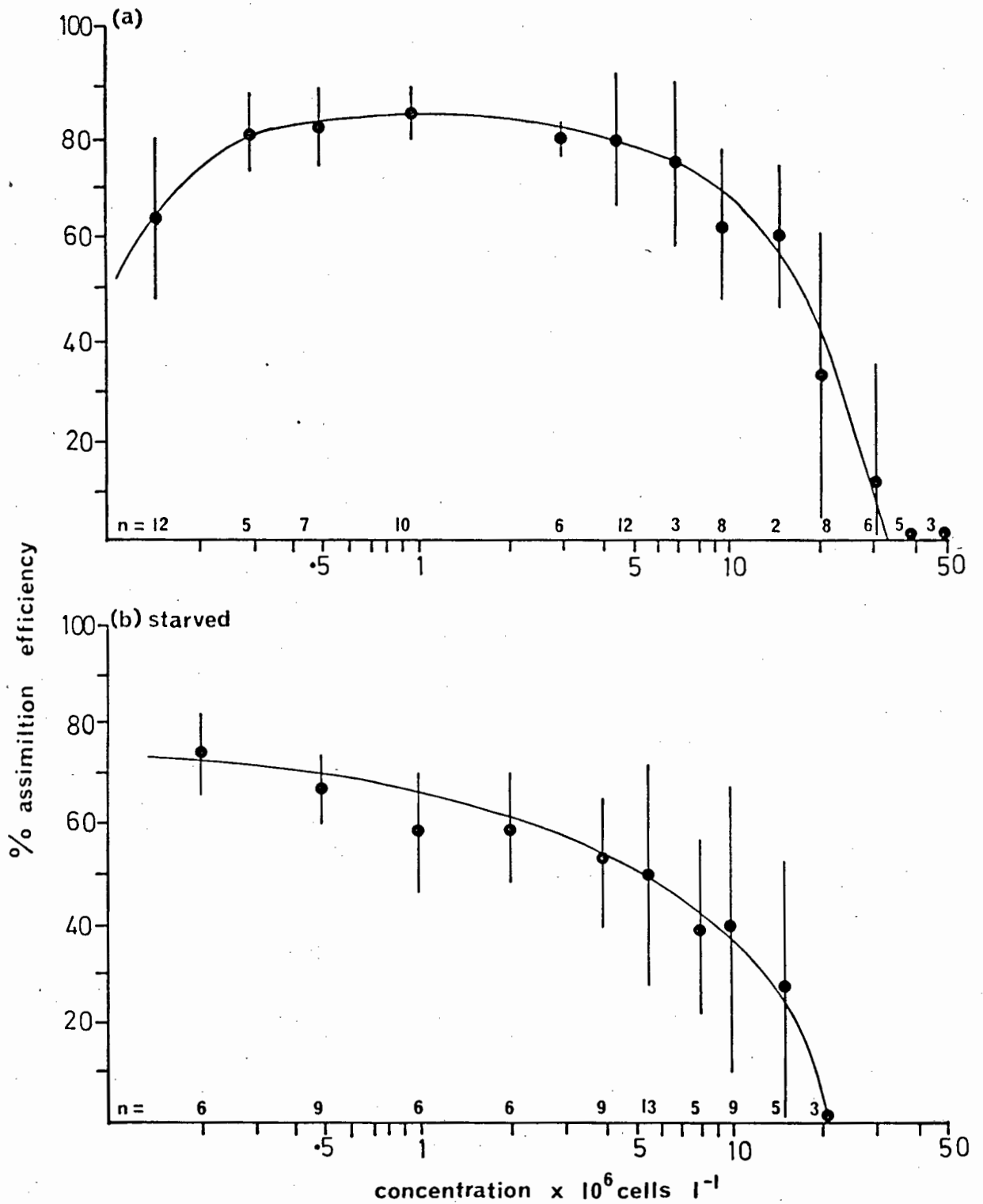


Fig. 6. Assimilation efficiency of 45 mm *C. meridionalis* when fed different algal rations. Vertical bars indicate one standard deviation, n=number of individuals used for each data point. (a) unstarved mussels (b) starved for 3 weeks.

Efficiency was slightly reduced at low cell concentrations but maintained 80% between 0.5×10^6 to 8×10^6 cells l^{-1} before declining to zero between $30-40 \times 10^6$ cells l^{-1} . No pseudofaeces were produced over this range. High assimilation efficiencies have also been found in M. edulis (Thompson & Bayne, 1972) and A. ater (Griffiths and King 1979a) and in both these species there is a decline to zero between $20-30 \times 10^6$ cells l^{-1} .

Starvation for 3 weeks (see filtration section) resulted in a lateral shift of the assimilation efficiency curve to the left so that efficiency declined to zero at about 20×10^6 cells l^{-1} (Fig. 6b). The effect of increased filtration rate and lateral shift of the assimilation efficiency curve on the assimilated ration and scope for growth is presented in Fig. 7. The calculated values are shown in Table III. The assimilated ration and scope for growth curves are displaced to the left when compared with unstarved mussels. It would appear that metabolic effort was concentrated on obtaining a positive energy balance from a lower ration level, the optimum being reduced from 20×10^6 cells l^{-1} to 10×10^6 cells l^{-1} .

The assimilation efficiency and scope for growth of C. meridionalis have been compared with that of A. ater (from Griffiths and King, 1979a) in Fig. 8. The assimilation efficiencies in A. ater are similar to those in C. meridionalis but remain positive at considerably higher ration levels.

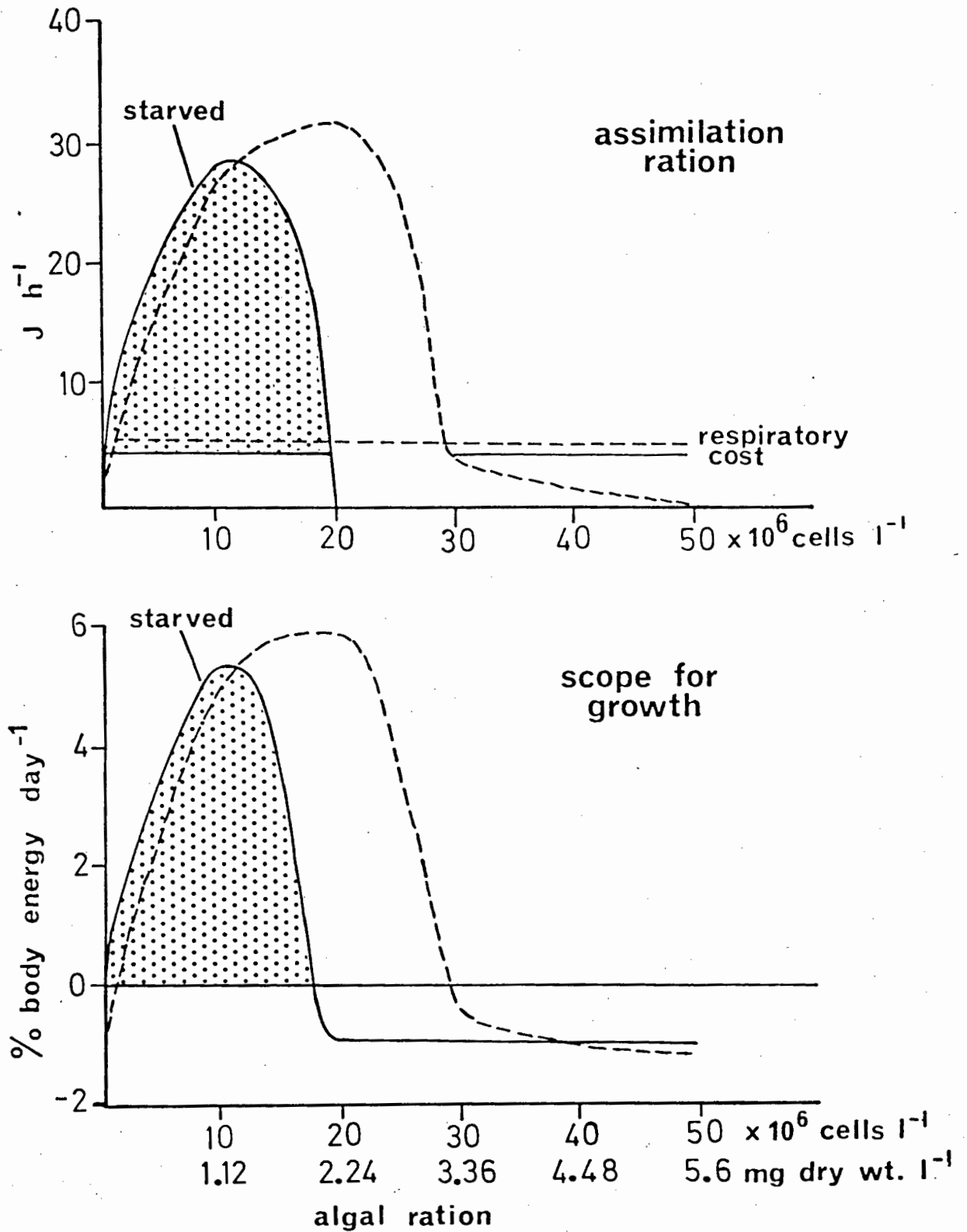


Fig. 7. Assimilation ration and scope for growth of starved and unstarved 45 mm *C. meridionalis* at different algal concentrations.

Table III. Choromytilus meridionalis. Calculation of assimilation ration and scope for growth in starved and unstarved 45 mm mussels.

Starved:	Ration $\times 10^6$ cells l^{-1}	Ration $J l^{-1}$	Filtration rate lh^{-1}	Ingestion ration Jh^{-1}	Assimilation efficiency %	Assimilation ration Jh^{-1}	Respiratory cost Jh^{-1}	Scope for growth Jh^{-1} % body $kJ day^{-1}$	
		0.2	0.4359	8.7	3.792	72	2.731	215.5 ml O_2 = 4.351J	- 1.620
	0.5	1.0898	7.3	7.955	68	5.410	+ 1.059		+0.24
	1.0	2.1795	5.9	12.859	65	8.358	+ 4.007		+0.89
	5.0	10.8976	3.6	39.449	49	19.330	+14.979		+3.33
	10.0	21.7952	3.6	78.899	36	28.403	+24.052		+5.34
	20.0	43.5904	3.6	157.797	0	0	- 4.351		-0.97
	30.0	65.3856	3.6	236.695	0	0	- 4.351		-0.97
	50.0	108.9760	3.6	394.490	0	0	- 4.351		-0.97
Unstarved:	0.2	0.4359	3.8	1.656	72	1.193	254 ml O_2 = 5.128J	- 3.935	-0.87
	0.5	1.0898	1.8	1.983	79	1.567		- 3.561	-0.79
	1.0	2.1795	1.8	3.967	84	3.332		- 1.796	-0.40
	5.0	10.8976	1.8	19.834	77	15.272		+10.144	+2.25
	10.0	21.7952	1.8	39.667	68	26.974		+21.846	+4.85
	20.0	43.5904	1.8	79.334	40	31.734		+26.606	+5.91
	30.0	65.3856	1.8	119.002	3	3.570		- 1.558	-0.35
	50.0	108.9760	1.8	198.336	0	0		- 5.128	-1.14

Conversions: 10^6 cells D. primolecta = 0.112 mg dry wt.; 1 mg D. primolecta = 19.46J;
 1 ml O_2 = 4.83 cal = 20.19J. 45 mm C. meridionalis = 10804.2J

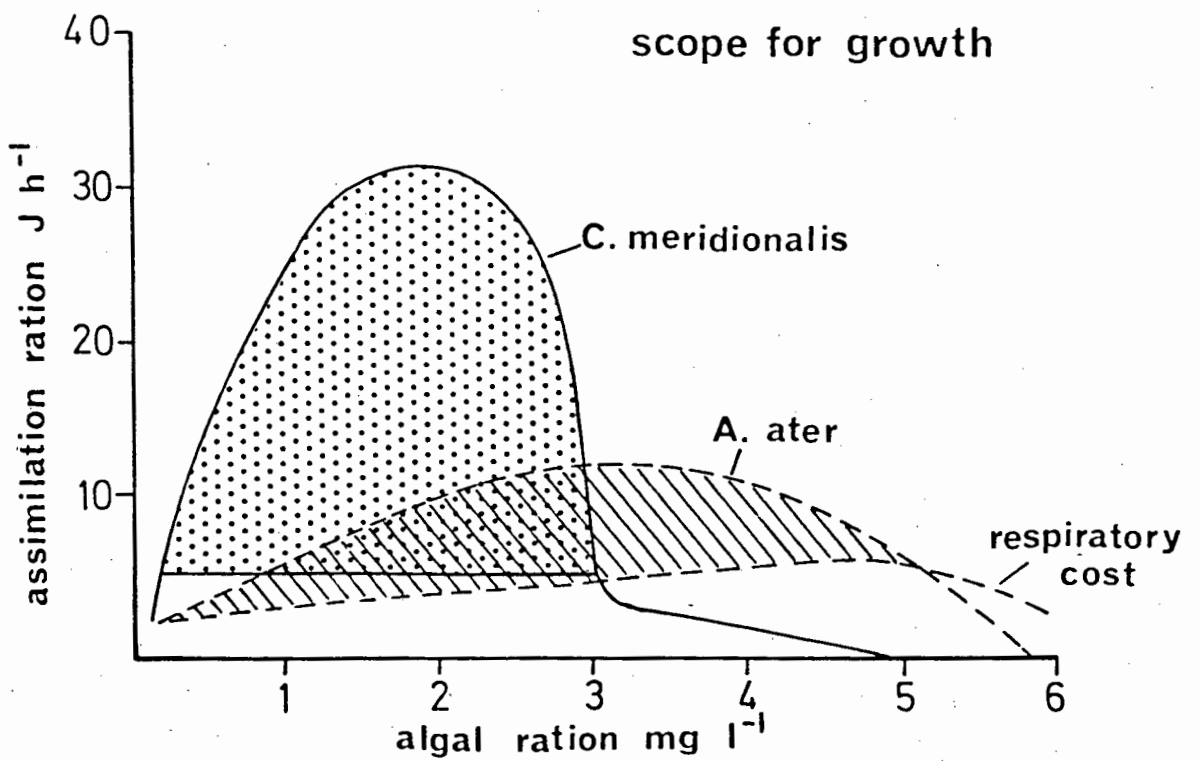
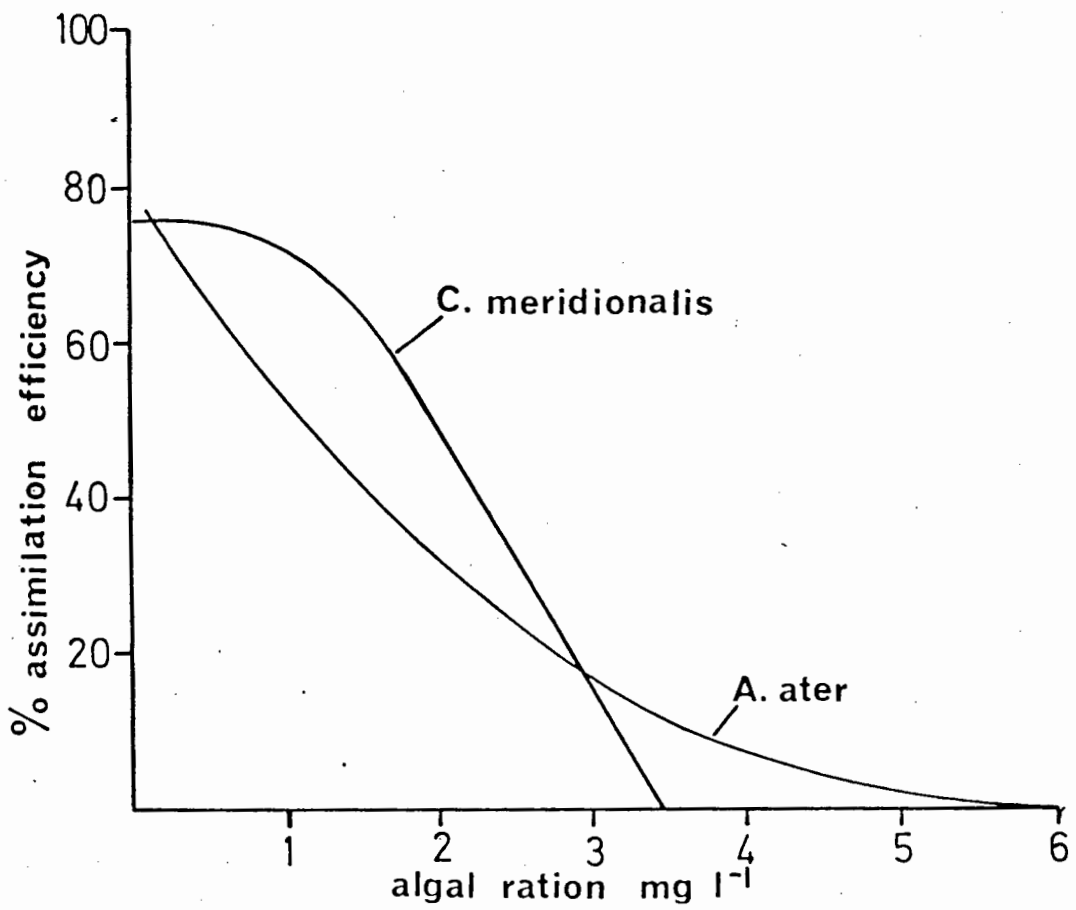


Fig. 8. Comparison of the assimilation efficiencies and scope for growth of *C. meridionalis* and *A. ater* (Griffiths & King, 1979a) fed on *D. primolecta*.

However, because of the lower filtration rate the maximum assimilated ration in A. ater is less than half that of C. meridionalis and the scope for growth considerably reduced. Data from Griffiths & King (1979b) show that A. ater has a slower growth rate and heavier flesh mass than comparable sized C. meridionalis. A. ater reaches breeding condition at 15 mm in the third year of growth, while C. meridionalis reaches the reproductive size of 20 mm within the first year (Griffiths, 1980). Comparison of data in Fig. 8 also shows that the optimum scope for growth occurs at different ration levels in the different species. Positive scope for growth in C. meridionalis feeding on D. primolecta varies from 0.2 - 3 mg l⁻¹ with a peak at 2 mg l⁻¹, compared with a range of 0.2 - 5 mg l⁻¹ in A. ater with peak at 3 mg l⁻¹. The different physiological responses and growth strategies in C. meridionalis and A. ater are interesting in view of the fact that these species frequently occur as adjacent populations, and occasionally may be completely intermingled, in both the littoral and sublittoral zones.

ACKNOWLEDGEMENTS

Miss F. Stratton is thanked for technical assistance and Dr. C.L. Griffiths and Professor R.C. Newell for reading the manuscript. This work was supported as part of the Kelp Bed Research Programme by the South African National Committee for Oceanographic Research.

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PAPER 5. NATURAL FOOD AVAILABILITY AND ASSIMILATION
IN THE BIVALVE CHOROMYTILUS MERIDIONALIS (KR.) .

Natural food availability and assimilation in the bivalve
Choromytilus meridionalis (Kr.).

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ABSTRACT

Samples of seawater overlying a bed of the mussel Choromytilus meridionalis (Kr.) at Bailey's Cottage, False Bay, South Africa, were analysed for organic and inorganic content in the particle size ranges 2-100 μm and 100-200 μm diameter. Organic matter comprised 10-30% of total sample weight, the remainder being predominantly sand. Changes in weight of particulate matter in samples taken throughout the year showed no clear seasonal pattern. Particulate organic material considered available as food to the mussels averaged 2.65 mg l^{-1} . Particulate inorganic matter averaged twice this amount. The energy value of the organic material averaged 6.1 kJ g^{-1} . Phytoplankton was present in 34% of the samples and is not considered an important constituent in the diet of mussels.

The assimilation efficiency of mussels feeding on natural detritus averaged 40% over the ration levels 3-18 mg l^{-1} dry weight of particulate matter. However, assimilation efficiency on pure Dunaliella primolecta culture

declined to zero at a ration of 3 mg l^{-1} while pseudofaeces production was initiated at 6 mg l^{-1} . It was concluded that the presence of particulate inorganic matter may be an important dietary requirement, 'diluting' the food and enabling assimilation to continue at the high ration levels experienced in the field.

INTRODUCTION

The employment of algal monocultures has greatly facilitated investigation of the feeding processes of bivalves. Much of this work has centred upon the effects of different ration levels on filtration rates and assimilation efficiencies in Mytilus edulis, and has been reviewed by Bayne et al. (1976). However, investigation of food availability in natural seawater has shown that phytoplankton cells are seldom present in sufficient numbers to contribute significantly to the mussels' diet. Authors such as Fox & Coe (1943), Jørgensen (1955) and Widdows et al. (1979) have shown that particulate organic matter is the major food source of many filter feeding bivalves. Recently, work by Winter (1976) and Widdows et al. (1979) has centred attention on the fact that seawater in the vicinity of mussel beds frequently contains large quantities of particulate inorganic detritus. They have shown that suspended silt influences feeding and growth in M. edulis, and Widdows et al. caution on the extrapolation of laboratory experiments employing dense algal cultures to field conditions.

The filtration rates and assimilation efficiencies of

Choromytilus meridionalis (Kr.) fed different rations of Dunaliella primolecta have been described by Griffiths (1980). In order to test the applicability of these data to field conditions, the levels of naturally available food were examined at the study site. The assimilation efficiencies of mussels feeding on organic detritus in the laboratory and field were then examined and compared with data obtained with the aid of algal cultures.

MATERIALS AND METHODS

Mussels (45 mm shell length) and seawater were sampled at Bailey's Cottage, False Bay, South Africa (34°06'S 18°28'E). A large densely packed mussel bed extends from the surf zone in the sublittoral to an average of 0.5 m above L.W.S.. Water for analysis and experiments was collected in seawater 0.5 m deep immediately above the mussel bed. Data on the assimilation efficiencies of 45 mm C. meridionalis feeding on D. primolecta culture were obtained from Griffiths (1980). Widdows (1978) has shown a slight increase in assimilation efficiency of M. edulis with increasing body size when fed at high algal rations. However, other authors (eg. Griffiths & King, 1979) have found assimilation efficiency to be independent of size. Although preliminary data on C. meridionalis shows no marked affect of body size on assimilation, for comparative purposes only 45 mm mussels were used in experiments presented here.

Seawater analysis

Water was sampled between Feb. 1978 and Feb. 1979. The samples included two 21 day series of daily records during summer and winter, and 5 continuous days out of each of the remaining months. On each day 500 ml of seawater was filtered through 200 μm and 100 μm mesh sieves and the fraction caught on the 100 μm sieve, and the filtrate, were filtered through separate preashed, weighed GFC filters (25 mm diam.). Filtered seawater (0.45 μm) was used to wash the particulate matter in the sieve onto the filter. Each filter was flushed with ammonium formate isotonic with seawater, and the dry weight and ash free dry weight (450°C for 3 h) obtained. An additional 50 ml sample was filtered onto 1 μm Nucleopore filter paper and the residue gently scraped off and concentrated on a glass slide for microscopic examination. An estimate of the presence of phytoplankton in the sample was obtained by subjective assessment of the percentage of the sample volume represented by algal species.

The calorific value of seawater was obtained by filtering the 100 μm fraction of 20 litres of seawater collected over the mussel bed, onto a 0.45 μm Millipore filter (142 mm diam.). The residue on the filter was flushed with distilled water to remove salts, gently scraped from the paper with a blunt instrument, washed into a crucible with distilled water and dried at 60°C for 2 days. The energy value of the particulate matter thus concentrated was measured with a Phillipson microbomb calorimeter. The ash remaining after firing (predominantly sand) was weighed and the energy

value of the ash free dry weight of the sample calculated. Grinding the sample to obtain a homogeneous distribution of particulate matter reduced variability in consecutive readings of the same sample. All weighings were done on an electronic microbalance (readability 1 μg).

Assimilation of detritus in the field

Samples of 500 ml of seawater collected at Bailey's Cottage were passed through a 100 μm sieve. The particulate matter in the 2-100 μm particle range was then concentrated onto preashed weighed GFC filters and treated as above. Simultaneous with water collection, 6 mussels were removed from the mussel bed and placed in seawater. All faeces produced within 2 hours were concentrated onto weighed GFC filters (preashed) and washed with ammonium formate. Filters were dried at 60°C, weighed and ashed at 450°C for 3 hours and weighed again. The ratio of the ash free dry weight to dry weight of the water sample ie. food, and the faeces were used to determine the assimilation efficiency according to the method described by Conover (1966).

Assimilation of detritus in the laboratory

Mussels were allowed to feed in the laboratory on the detritus in freshly collected seawater to assess whether data comparable with that in the field (above) could be obtained. Large quantities of seawater were collected over the mussel bed each day and filtered through a 100 μm sieve to eliminate large sand particles and debris. Mussels

collected the previous day were placed in a recirculating constant flow system[†] which fed water to 4 animal chambers, each of 500 ml capacity. The flow rate exceeded 2 l h^{-1} . Tests using algal culture showed that this rate was sufficiently fast to prevent depletion of food within the animal chambers. The importance of this has been discussed by Hildreth & Crisp (1976). The 20 litres of seawater contained within the system was changed at 0.5 h intervals to maintain the food concentration for the 3-4 h duration of the experiment. Replicate 500 ml samples of the water prior to use, and faeces collected immediately they were produced, were filtered onto separate preashed and weighed GFC filters and analysed as above. Faeces produced during the first hour of the experiment were discarded.

RESULTS

Seawater analysis

The quantities of particulate organic and inorganic matter in the particle size ranges 2-100 μm and 100-200 μm , measured during one year, are shown in Fig. 1. Organic material comprised 10-30% of the total sample weight, the remainder being predominantly sand. Widdows et al. (1979) found that organic material represented 6-25% of the particulate matter available to M. edulis in the Lynher estuary, and Verwey (1952) an average of 12% in the Waddensea. The organic material in the 2-100 μm range varied from 5-25% of the total sample weight. Peaks in the amount of inorganic particulate matter generally coincided with rough

[†] see appendix 1

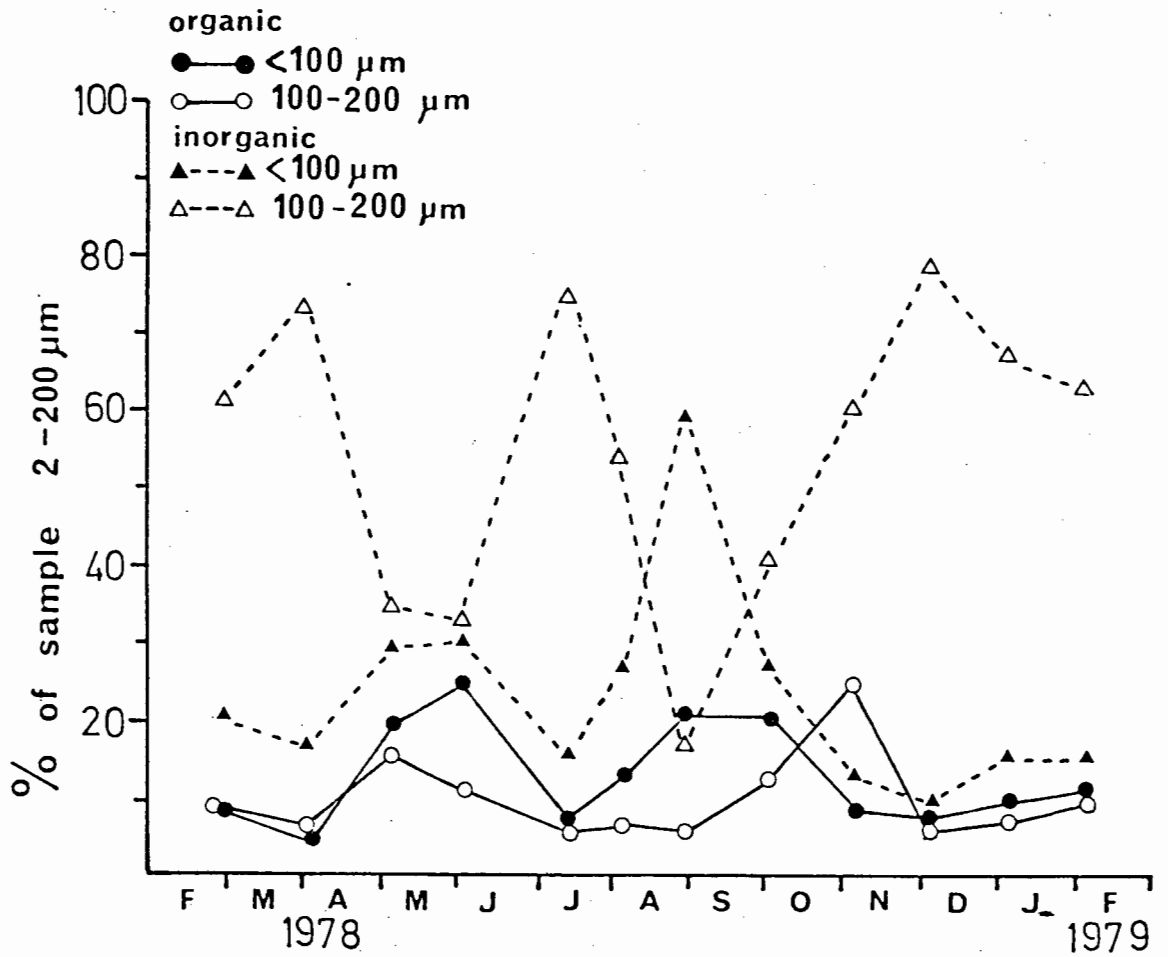


Fig. 1. The distribution of organic and inorganic matter in seawater in the particle size ranges 2-100 μm and 100-200 μm diameter. Measured as mg dry weight l^{-1} and expressed as a percentage of the total sample weight.

sea conditions.

Fig. 2 shows the variation in the dry weight of particulate organic material in the 2-100 μm and 100-200 μm range during the year. There was no clear seasonal pattern and the data were surprisingly constant at an average of 2.65 mg l^{-1} and 2.13 mg l^{-1} respectively. Table 1 summarises the data on the distribution of particulate organic and inorganic material. Whereas the 2-100 μm particulate organic material was represented predominantly by free or aggregated particles in the water column, those in the 100-200 μm range were more difficult to assess. During filtering very few free particulates were seen. It was concluded that the greater portion of the organic matter in this size range was attached to the sand grains. This would be rejected in the pseudofaeces.

The origin of the detrital matter at Bailey's Cottage could not be determined. It consisted of brown irregularly shaped particles without cellular structure. From Sept. 1978 to Feb. 1979 the detritus was dominated by uniform particles having the appearance of faecal pellets averaging 20 x 140 μm . Their origin is unknown.

A rough estimate of the presence of phytoplankton is shown in Table 2. The phytoplankton present were predominantly Nitzschia and Rhizosolenia species. The latter was particularly abundant in May 1978 when it formed more than 90% of the sample. However, phytoplankton was recorded on only 34% of the days sampled and cannot be considered a major constituent in the diet of filter feeders at Bailey's Cottage.

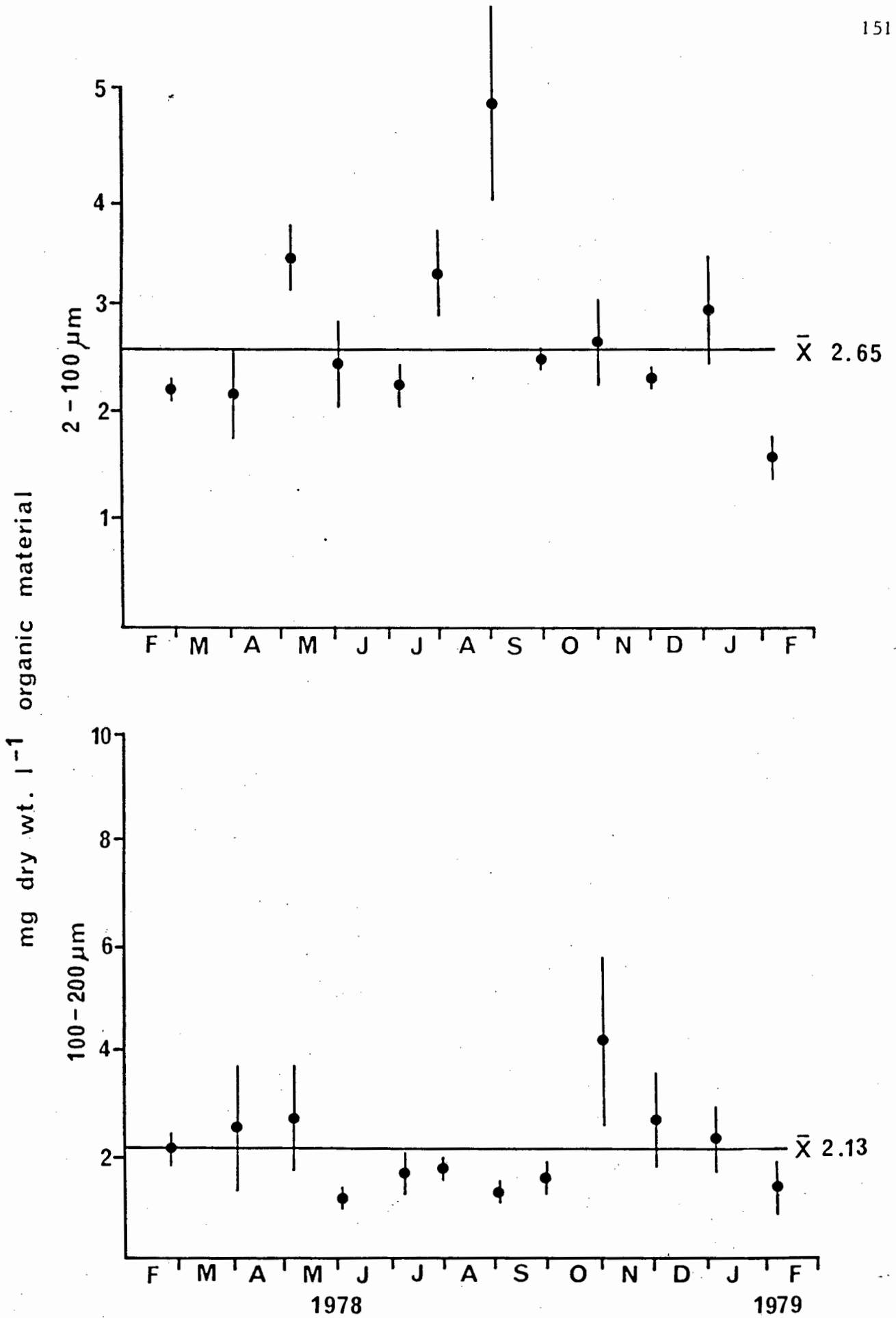


Fig. 2. Changes in weight of particulate organic matter in the size ranges 2-100 μm and 100-200 μm diameter in seawater at Bailey's Cottage during one year. Vertical bars represent one standard error.

Table 1. Proportion of organic and inorganic particles in size ranges $<100\mu\text{m}$ and $100 - 200\mu\text{m}$ in seawater over a mussel bed at Bailey's Cottage, February 1978 to February 1979. (n = 97).

	Organic		Inorganic	
	$<100\mu\text{m}$	$100-200\mu\text{m}$	$<100\mu\text{m}$	$100-200\mu\text{m}$
Average mg l^{-1}	2.65	2.13	5.69	15.21
One standard deviation	1.14	1.49	4.47	21.49
Maximum mg l^{-1}	6.95	10.29	25.76	109.12
Minimum mg l^{-1}	1.11	0.39	0.42	0.06
Mean % of sample	13.0	9.3	23.3	54.4

Table 2. The number of days on which phytoplankton were recorded during the sampling period and an estimate of its abundance (2-100 μm particle size range).

month	days sampled	days algae recorded	phytoplankton as percentage of sample volume	
			range	mean
Feb./March	21	5	10-60	24
April	5	5	6-30	15
May	5	5	90-98	95
June	5	0	-	-
July	5	1	-	50
July/Aug.	21	8	5-80	28
August	5	0	-	-
September	5	0	-	-
October	5	0	-	-
November	5	0	-	-
December	5	1	-	5
January	5	5	5-50	18
February	5	1	-	2

The energy value of organic material (2-100 μm) in seawater over the mussel bed is shown in Table 3. Each value represents the mean of 2 or 3 readings on one sample. Twenty-five samples were taken on different days, under varying sea conditions, and different states of tide. There was considerable variability in readings on the same sample and between samples. The energy available in seawater averaged 5.74 kJ g^{-1} AFDW (ash free dry weight) and inorganic material constituted 53% of the samples. Paine (1966) has shown that endothermy may occur in samples containing CaCO_3 and a correction factor of $0.6 \text{ J mg}^{-1} \text{ CaCO}_3$ may be applied. Assuming that 50% of the inorganic matter in Table 3 may represent CaCO_3 from exoskeletons or shells of marine organisms, the mean energy value may be increased by 6% to 6.1 kJ g^{-1} AFDW.

Assimilation of natural detritus

The average ration available as food in seawater falls above the range of positive assimilation efficiency in C. meridionalis when feeding on algal culture. Griffiths (1980) found that the assimilation efficiency fell to zero at a ration of 3 mg l^{-1} Dunaliella primolecta and pseudofaeces production was initiated at 6 mg l^{-1} dry weight. The average ration in seawater (<100 μm particle size range, organic + inorganic) was 8.3 mg l^{-1} .

Fig. 3 shows the assimilation efficiency of mussels feeding on natural detritus in the field and in the laboratory. No pseudofaeces production occurred in laboratory

Table 3. Energy values of organic matter (< 100 μ m particle size) in seawater at Bailey's Cottage.

kJ g^{-1} dry weight	kJ g^{-1} AFDW	% inorganic	
3.81	7.71 *	52.0	
1.70	6.28	73.0	
2.75	10.10 *	70.5	
4.00	10.90	53.0	
0.69	1.97	64.2	
2.38	5.74	58.6	
2.48	4.71	52.5	
0.34	1.59	78.4	
0.39	1.71	77.5	
0.79	2.37	66.8	
4.80	10.69	55.1	
2.06	5.21	61.1	
2.34	5.27 *	55.5	
1.47	3.27	55.1	
0.37	1.14	67.7	
3.59	4.87	26.0	
4.00	6.27	34.7	
1.79	3.82	53.2	
2.83	3.97	25.9	
3.76	6.72	44.0	
3.61	7.83	54.0	
6.01	10.34	41.9	
2.74	4.64	40.9	
4.63	7.39	37.3	
5.70	9.08 *	33.8	
<u>mean</u>	<u>2.76</u>	<u>5.74</u>	<u>53.3</u>

* Sampled during phytoplankton bloom

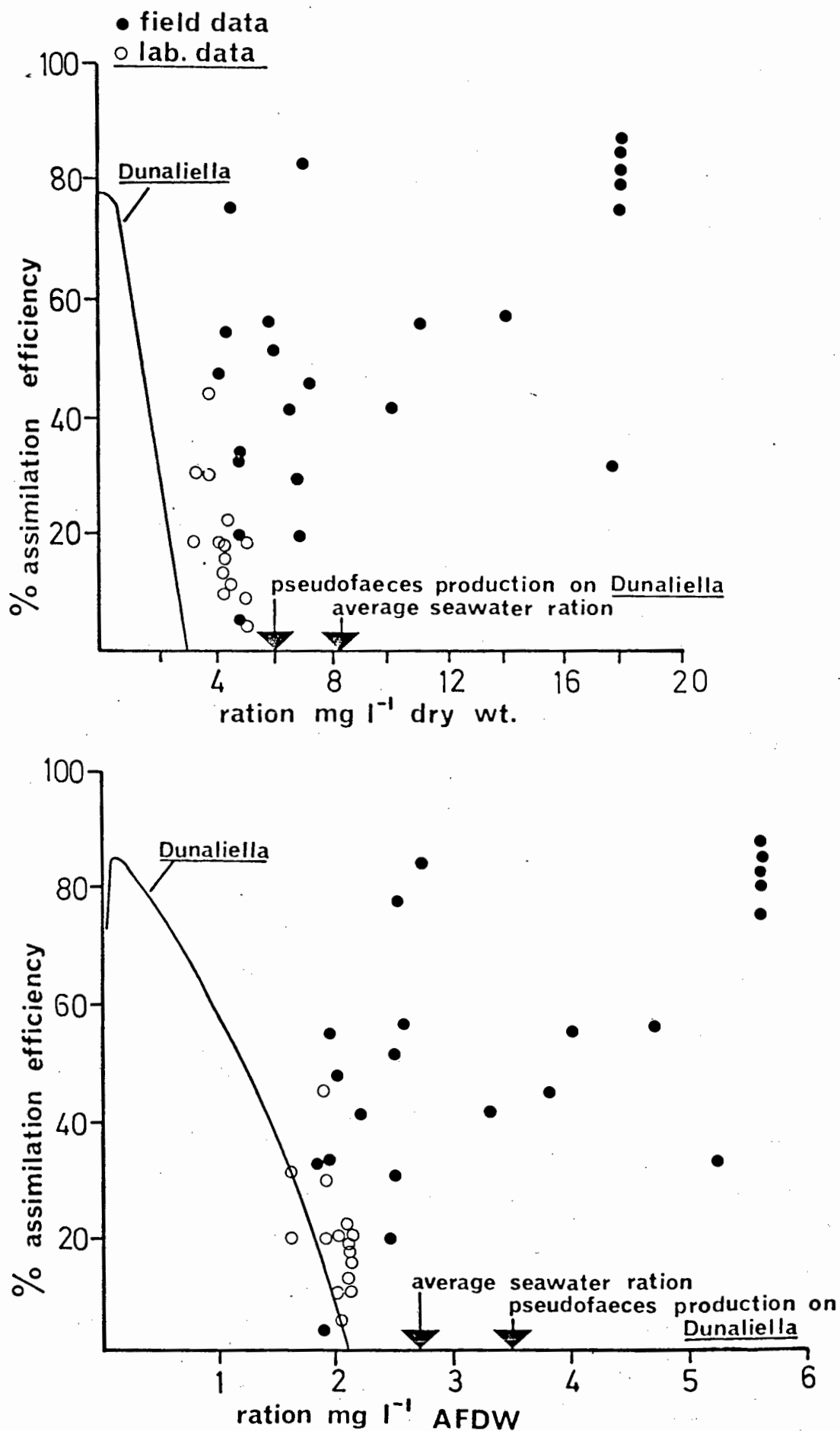


Fig. 3. The assimilation efficiency of *C. meridionalis* when feeding on natural detritus in the field and the laboratory. Curve of assimilation efficiency when feeding on pure *D. primolecta* culture given for comparison. Ration levels expressed as particulate dry weight (includes sand) and AFDW (2-100 μ m particle size range).

experiments. The curve for assimilation efficiency on D. primolecta is given for comparison. The data were plotted in terms of ration dry weight and AFDW. Laboratory measurements showed no detectable difference in the filtration rate of 45 mm mussels when feeding on detritus or algal culture. An average assimilation efficiency of 40% (S.E.=4.1%, n = 37) was obtained over a wide range of ration levels. Variability in the data (maximum efficiency 87%, minimum 4.5%) may be a function of experimental technique. Water sampled at any one instant in the field may not reflect that which has been filtered by the mussel during the hour prior to removal from the bed. Furthermore, Foster-Smith (1975) has shown that some retention of ingested material may occur in M. edulis and that this may be mixed with material ingested later and subsequently defaecated. Although the passage of algal cells through the gut of C. meridionalis may take place within 1 hour, sand particles may be egested up to 12 h after removal of mussels from the natural habitat.

DISCUSSION

Microscopic examination of the faeces collected from 45 mm C. meridionalis in the field showed that they contained large quantities of sand mixed with detritus. The particulate matter in faeces averaged 50 μm , with particles seldom exceeding 100 μm diameter. Examination of the distribution of particulate matter in seawater showed that

13% of the organic particulate matter occurred in the 2-100 μm size range. However, more than 50% of the sample consisted of sand particles in the 100-200 μm size range. Most of the organic material in this range was attached to the sand grains. Mussels filtering on the shore were observed to continuously eject large quantities of sand in the form of pseudofaeces. On the basis of these observations it was concluded that the bulk of food available to the mussels is represented by particles measuring 2-100 μm diameter, and that particles exceeding this size are rejected as pseudofaeces.

Several authors have examined particle size selection in mussels and Bayne et al. (1976) conclude that selective removal does not occur in mussels feeding on natural seawater (2-100 μm particle size range). Although authors such as Vahl (1972, see also review by Bayne et al., 1976) have shown retention of particles below 2 μm by the mussel gill, this size range could not be measured in the present study. In view of the large quantities of organic detritus measured in the 2-100 μm size range, particles below 2 μm are unlikely to form a significant proportion of the diet.

Total organic particulate matter at Bailey's Cottage averaged 5 mg l^{-1} , while an average of 2.65 mg l^{-1} was considered available to the mussels. Armstrong & Atkins (1951) report 1.6-1.8 mg l^{-1} particulate organic material in the English channel, Widdows et al. (1979) 1.5-1.9 mg l^{-1} in the Lynher estuary, and Verwey 3 mg l^{-1} available to mussels in the Waddensea. Other values measured

generally average less than 1 mg l^{-1} (Jørgensen, 1955). However, it is doubtful that samples taken in the relative calm of deeper waters may be compared with those from the surf zone. Wave action and continual resuspension of the sandy substrate will enhance degradation of organisms and faeces and maintain high levels of organic detritus in the water column.

The energy value of organic detritus at Bailey's Cottage averaged 6.1 J mg^{-1} . Widdows et al. (1979) obtained a value of 23.5 J mg^{-1} of food available to M. edulis by analysing the proportions of carbohydrates, lipids and proteins in seawater. At food suspensions of $1.5\text{-}1.9 \text{ mg l}^{-1}$ (Widdows et al., 1979) the energy available to M. edulis in the Lynher estuary is $35.2\text{-}44.7 \text{ J l}^{-1}$ of seawater. By comparison, the ration available to C. meridionalis at Bailey's Cottage averages 16.2 J l^{-1} .

The assimilation efficiency on natural detritus proved variable but averaged 40%. Although the method used may over- or under-estimate the true assimilation efficiency in the field, it is clear that C. meridionalis must be able to maintain a positive energy balance over the normal range of particulate material present in seawater. Experiments using D. primolecta are thus not directly applicable to natural conditions in the field.

The presence of large quantities of inorganic matter in the bivalve diet appears to be a common phenomenon and Winter (1976) has shown that silt has a beneficial effect

on growth in M. edulis. However, this is not merely a result of the presence of silt, but an interaction between total particulate concentration and the ratio of food to silt in the water. Widdows et al. (1979) found that increasing particle concentration results in increasing pseudofaeces production in M. edulis, and the ingestion ration remains at a constant level. This limits the amount of food entering the gut, enabling digestion to continue at high particulate concentrations. However, the presence of inorganic particles 'dilutes' the available food ration, and increasing inorganic particulate matter in the diet results in a decline in the energy assimilated. The ratio of organic to inorganic matter is thus important in influencing the energy balance.

In C. meridionalis a constant filtration rate is maintained over a wide range of ration levels (Griffiths, 1980) and pseudofaecal production must be important in limiting the ingestion ration at high food levels. When feeding on a concentrated food source such as algal culture, with little particulate inorganic material present, pseudofaecal production is not initiated sufficiently early to limit the ingestion ration before assimilation efficiency falls to zero. Such a concentrated food source would not be experienced in the field. The presence of particulate inorganic matter may prove an important dietary requirement in C. meridionalis in 'diluting' the high organic levels in the sea and allowing a positive assimilation efficiency over a wide range of ration levels.

ACKNOWLEDGEMENTS

This work was supported as part of the Kelp Bed Research Programme by the South African National Committee for Oceanographic Research.

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PAPER 6. AERIAL EXPOSURE AND ENERGY INPUT IN THE

BIVALVE CHOROMYTILUS MERIDIONALIS (KR.) ,

Aerial exposure and energy input in the bivalve
Choromytilus meridionalis (Kr.).

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ABSTRACT

The effects of aerial exposure on growth, filtration and assimilation were examined in Choromytilus meridionalis (Kr.) from Bailey's Cottage, False Bay, South Africa. The maximum height at which these mussels occur on the shore corresponds to 50% aerial exposure. Growth rates declined with increasing shore height. The relationships between flesh and shell dry weight and shell length were not significantly different in littoral and sublittoral mussels. Littoral mussels did not show enhanced filtration rates or assimilation efficiencies relative to continually submerged individuals. Thus littoral mussels experience a decline in ingestion ration which is directly correlated with increasing shore height. Under conditions of limited food availability littoral organisms frequently employ conservative mechanisms to limit energy expenditure. In C. meridionalis this is evidenced by limitation of the growth rate. Energy conservation may also be facilitated by quiescence and reduced respiratory cost during exposure. This requires investigation.

INTRODUCTION

Although bivalves are predominantly sublittoral organisms, some species extend into the littoral zone and have been shown to display limited 'adaptation' to aerial exposure (Bayne et al., 1976). While the shell may offer some protection against desiccation, littoral mussels are subject to raised body temperatures, reduced feeding time and limited oxygen exchange. These factors may be expected to influence the energy balance relative to that of continually submerged individuals. However, as evidenced by the large areas of the shore which are covered by high densities of Choromytilus meridionalis (Kr.), this species is able to successfully survive such conditions and must experience a positive energy balance.

While there is an extensive literature on the physiological responses of mussels under sublittoral conditions, limited information is available on the effects of aerial exposure on those species extending into the littoral. The growth of littoral mussels has been shown to decline with increasing shore height and this has been regarded as a function of the decreased feeding time during exposure. Baird (1966) and Coulthard (1929 quoted by Seed, 1976) found that the level of zero growth corresponded to a shore height where mussels were exposed to air for 50 - 56% of the time. Reduced feeding time has been considered to affect tissue weight and Baird & Drinnan (1956) and Seed (1973) have reported declining tissue weight with increasing shore heights in Mytilus edulis. Air

exposure may also affect metabolism and highshore individuals tend to show reduced metabolic rates (reviewed by Anderson, 1978). However, conflicting evidence exists. Segal et al. (1953) found reduced filtration rates in upper-shore M. californianus and suggested that low shore level mussels were 'cold-adapted'. Pamatmat (1969) reached a similar conclusion, although Anderson (1978) and Moon & Pritchard (1970) found the reverse condition in Mya arenaria and M. californianus respectively.

In view of the above findings, littoral and sublittoral C. meridionalis were examined to determine the effect of aerial exposure on the growth rates and allometric relationships of this species. Survival under conditions of limited food availability, such as experienced by littoral mussels, is dependent on the balance between energy intake and metabolic expenditure. Various conservation strategies in the form of increased consumption rates or decreased metabolic rates may be employed by littoral organisms in order to maintain a positive energy balance (Newell, 1980). C. meridionalis were examined in order to establish whether reduced feeding time may be compensated by increasing the filtration rate or assimilation efficiency.

MATERIALS AND METHODS

Mussels were collected from a dense mussel bed at Bailey's Cottage, False Bay, South Africa (34°06'S 18°28'E). The population extended from the sublittoral (3 - 4 m depth) to 0.5 m above L.W.S. (low water spring tide) while a small

segment of the population extended to 0.85 m above L.W.S. For comparative studies mussels were collected from immediately below, and 0.5 m or 0.85 m above L.W.S. Mussels were cleaned of epibiotic growth, the byssal threads retained intact, and placed directly into chambers for measurement of filtration rates.

The proportion of time highshore mussels were exposed over a 14 day tidal cycle was calculated by measuring the height above L.W.S. and observing the length of time the individuals were exposed during several neap and spring tides. These values were compared with tables of predicted hourly tidal heights in False Bay. Having established that field measurements gave good agreement with the tide tables, the number of hours during which mussels at 0.5 m and 0.85 m above L.W.S. were exposed over 4 randomly selected 14 day tidal cycles was calculated from the tables.

(1) Weight analysis and growth

The growth rates of mussels collected from different shore levels at Bailey's Cottage over 4 years are given by Griffiths (1980a).

Population structure in the sublittoral and highshore zone (0.5m) was determined by removal of replicate samples of 0.025m^2 on 22.5.78 and size-frequency histograms constructed. Three samples of mussels, 60 individuals from each shore level (L.W.S. and 0.5 and 0.85 m above L.W.S.), were analysed to determine the effect of increasing shore height on flesh and shell dry weight. The flesh was removed from the shells and

both were dried at 60°C for 3 days.

(2) Filtration rates

Filtration rates were measured by recording the rate of depletion of Dunaliella primolecta cells by mussels placed in 2 l of 0.45 µm filtered seawater containing 10×10^6 cells l^{-1} . Water in the vessels was stirred with a magnetic stirrer and cell concentrations were measured at 10 min intervals using a model TA II Coulter Counter fitted with a 70 µm aperture. Although preliminary experiments showed no change in filtration rate with decline in cell concentration to 5×10^5 cells l^{-1} , the cell concentration in experimental vessels was maintained within 20% of the initial value by regular addition of algal concentrate.

(3) Assimilation efficiency

Assimilation efficiencies were measured during filtration rate experiments. Faeces produced during the first 1.5 h of an experiment were discarded to allow clearance of sand etc. from the gut. Algal cells took approximately 1 h to appear in the faeces after the onset of feeding. The ratio of ash free dry weight to dry weight of food and faeces produced after this time was calculated, and the assimilation efficiency determined by the method of Conover (1966). Replicate samples of algal culture of known concentration and of faeces, were filtered onto pre-ashed and weighed GFC filters (25 mm diam.). Filters were flushed with ammonium formate isotonic

with seawater before drying. An electronic microbalance was used for all weight determinations (readability 1 μ g).

RESULTS AND DISCUSSION

Weight analysis and growth

The calculated percentage time during which mussels were exposed to air during a 14 day tidal cycle was as follows:-

Below L.W.S. (BLWS) - 0%

0.5 m above L.W.S. (Topshore) - 28.5%

0.85 m above L.W.S. - 50%.

Data on growth during the first 4 years of life at BLWS and topshore have been fitted to von Bertalanffy growth equations (Table I) and the resulting curves are shown in Fig. 1. The growth rate declined with increasing shore height as found by Dehnel (1956) and Baird (1966). However, during the first year following settlement, the growth rates at the two shore levels were the same, and divergence only appeared after 1.5 years. This anomaly results from the constant migration of mussels up the shore, increasing the apparent growth rate of topshore mussels (Griffiths, 1980a).

Fig. 2 shows size-frequency histograms typical of the sublittoral and topshore zones after 3.5 years mussel growth. Topshore mussels showed a smaller mean size due to the slower growth rate. The lower density in sublittoral mussels was related to their greater average length, intraspecific competition for space results in a decline in density with increasing length (Griffiths, 1980a). Although the mean

Table I. Regression equations ($y = ax^b$) of dry flesh and shell weight in grams, to shell length in mm, in C. meridionalis collected at L.W.S. and 0.5 m and 0.85 m above L.W.S., and growth equations for sublittoral and littoral (0.5 m above L.W.S.) mussels at Bailey's Cottage, False Bay.

	a	b	r^2	n
<u>Dry flesh weight</u>				
L.W.S.	2.311×10^{-5}	2.4624	0.94	60
0.5 m above L.W.S.	8.208×10^{-5}	2.1269	0.91	60
0.85 m above L.W.S.	1.173×10^{-4}	1.9532	0.86	60
<u>Dry shell weight</u>				
L.W.S.	3.000×10^{-4}	2.4458	0.97	60
0.5 m above L.W.S.	2.360×10^{-4}	2.5394	0.97	60
0.85 m above L.W.S.	2.686×10^{-4}	2.5120	0.96	60

Von Bertalanffy growth equation $L_t = L_\infty (1 - e^{-k(t - t_0)})$

Sublittoral (BLWS)

$$L_\infty = 106.26 \text{ mm}$$

$$k = 0.153188$$

$$t_0 = -0.309774$$

0.5 m above L.W.S.

$$L_\infty = 41.01 \text{ mm}$$

$$k = 0.558843$$

$$t_0 = -0.086408$$

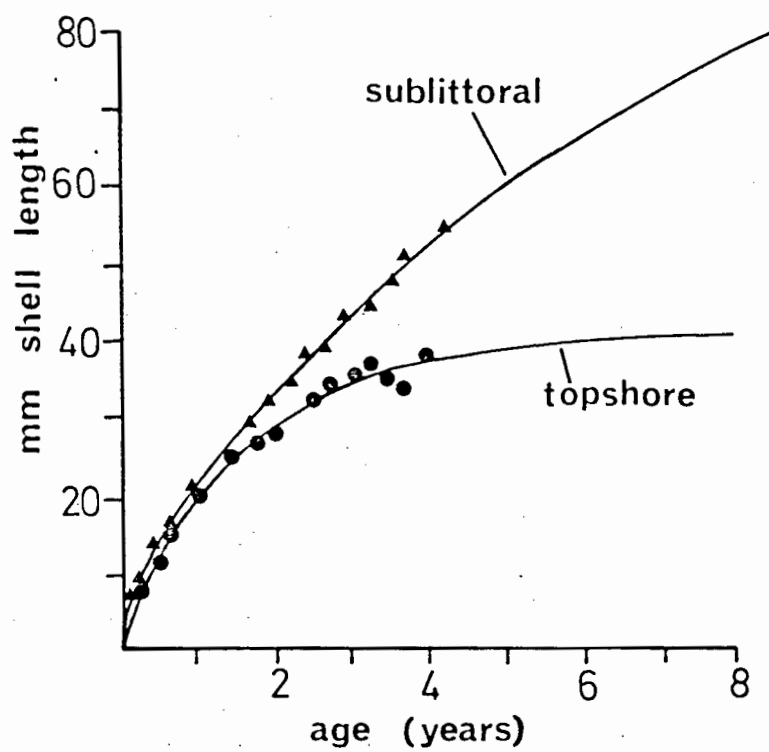


Fig. 1. Growth curves of *C. meridionalis* growing in the sublittoral and 0.5 m above L.W.S. (topshore) at Bailey's Cottage.

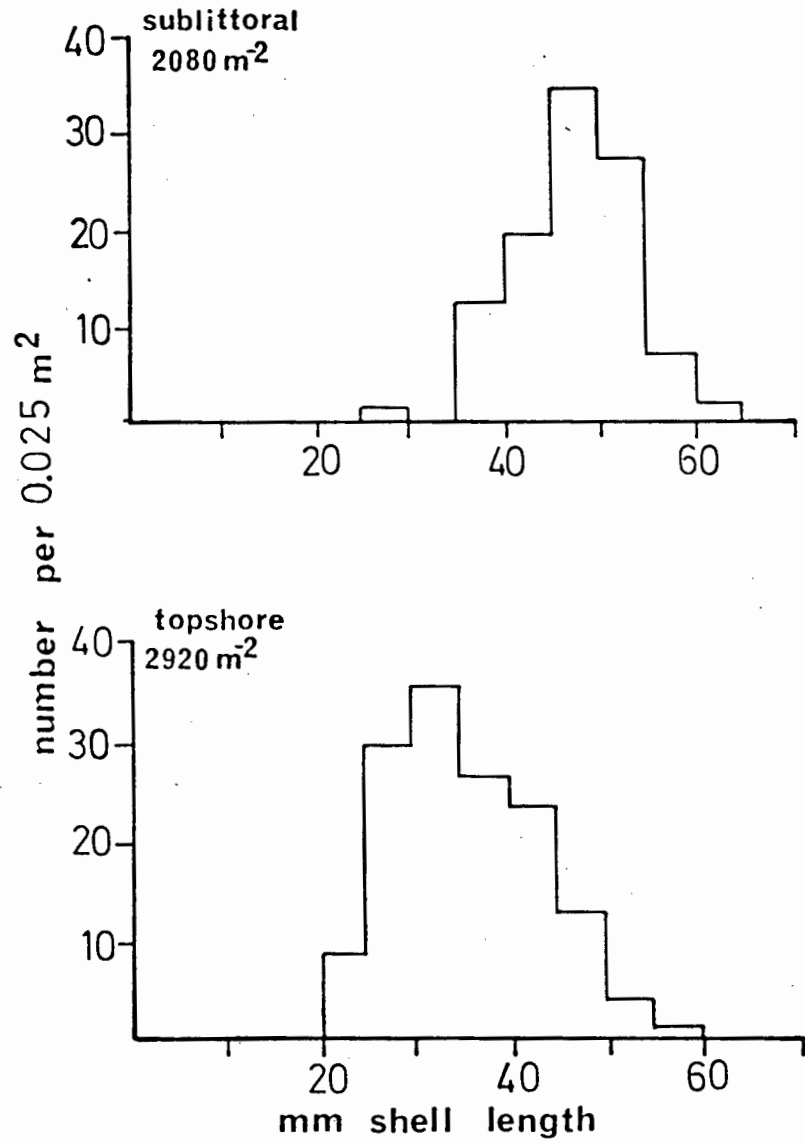


Fig. 2. Size-frequency distribution of sublittoral and topshore (0.5 m above L.W.S.) *C. meridionalis* at 3.5 years age.

population length was smaller at the topshore level, a few individuals in the larger size range found in the sublittoral (45 - 60 mm), were always present. While the larger mussels may reflect a more rapid growth rate by a few individuals, it is considered that they represent mussels which have migrated into the upper shore levels due to detachment by strong wave action lower down the shore.

The effects of increasing shore height on flesh and shell weight have been investigated by several authors. Baird & Drinnan (1956) and Seed (1973) found a declining flesh weight with increasing shore height in M. edulis. This was considered an influence of decreased feeding time. Comparison of the dry flesh and dry shell weight of C. meridionalis of different shell lengths, collected at 3 shore levels, is shown in Fig. 3. The regression equations fitted to the data are given in Table I. There was considerable scatter in the dry flesh weight to shell length, a reflection of the variability in spawning state. Individuals within the population spawn at different times and thus may contain varying amounts of gametogenic material (Griffiths, 1977). The latter may account for a considerable proportion of the somatic weight. The relationship between flesh weight and shell length for littoral and sublittoral C. meridionalis was similar to that found by Dame (1972) in Crassostrea virginica. The growth relationships in the different samples varied with size and the fitted lines were not parallel. Because of this, and

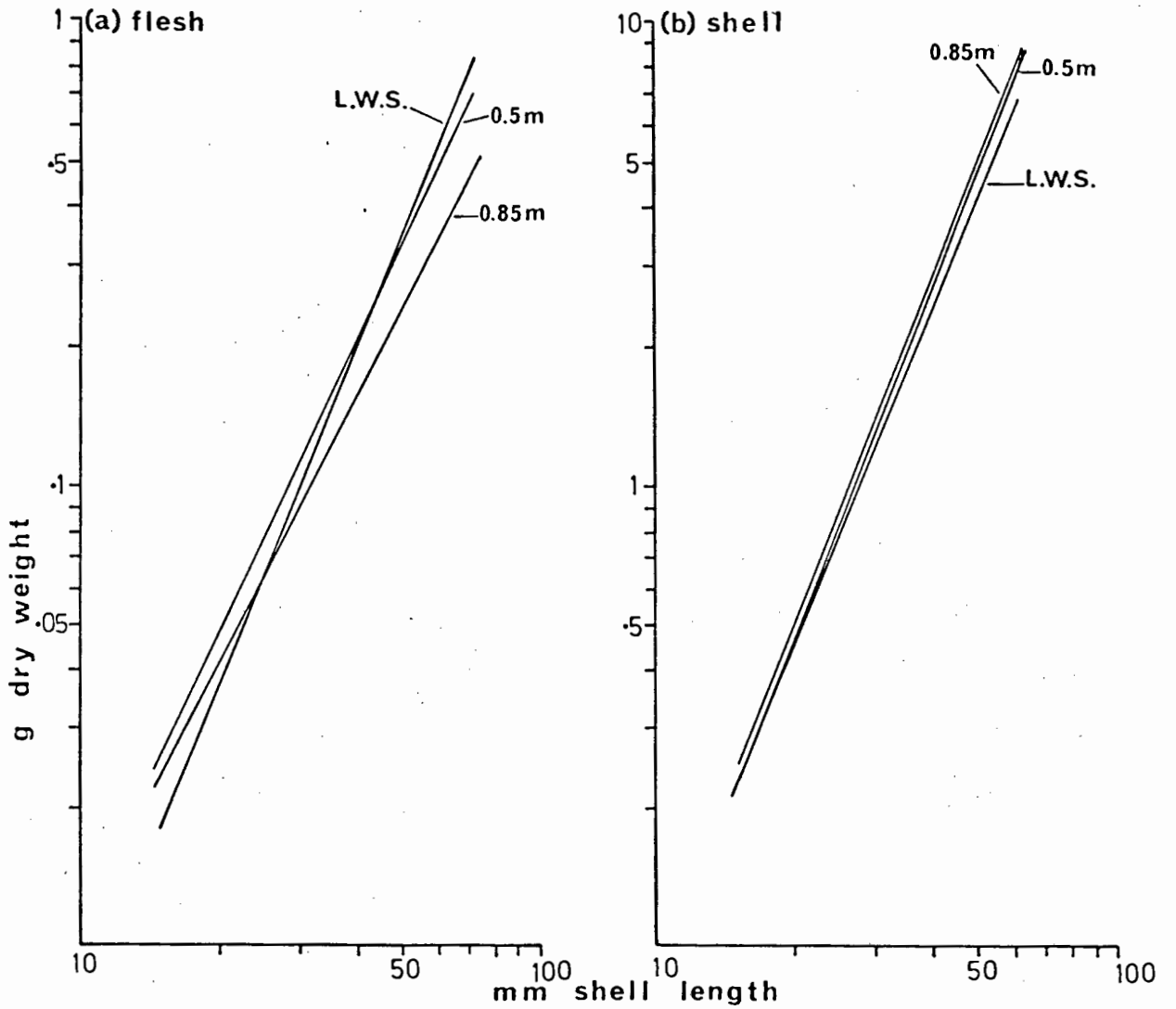


Fig. 3. Dry flesh and dry shell weight plotted against shell length for mussels collected in the sublittoral and 0.5 m and 0.85 m above L.W.S. at Bailey's Cottage.

the scatter in the data, analysis showed no significant difference between the slopes or the intercepts. Littoral mussels, although smaller in size, therefore have a somatic and gonad weight comparable with that of similar sized sublittoral mussels.

Analysis of shell weight to shell length (Table I, Fig. 3) showed a trend towards lighter shells with increasing air exposure although the slopes and intercepts were not significantly different. Although conclusive evidence is not available, it has been suggested that the trend towards lighter shells with increasing air exposure is due to chemical erosion of the shell during anaerobic metabolism (Dame, 1972). Alternatively, low shore mussels have a longer submergence time in which shell deposition may occur. Both an increase and a decrease in the ratio of shell weight to dry body weight have been recorded in other species (reviewed by Dame, 1972). An interesting exception is found in Modiolus demissus where no change in shell weight with increasing shore height was found (Lent, 1969). Lent attributed this to air-gaping, which enables aerobic metabolism during exposure to air, and adaptation to survival in the littoral zone.

Filtration rates

A detailed study of the factors influencing filtration rate in C. meridionalis when fed Dunaliella primolecta culture, has been made by Griffiths (1980b). The rate remained unaffected by state of tide, seasonal sea temperature change and a wide range of ration levels. However, filtration rates were found to increase with starvation,

and littoral mussels were investigated to determine whether aerial exposure, and consequent limitation of feeding for periods of up to 6 h, produced starvation and thus an increase in filtration rate. The feeding rate of mussels collected 0.85 m above L.W.S. after 6 h exposure in the field was compared with that of sublittoral mussels which had remained submerged. To exclude the effect of size on filtration rate, only 40 mm mussels were tested. Fig. 4 shows the filtration rates of mussels fed on 10×10^6 cells l^{-1} D. primolecta for a period of 5 h following collection in the field. The filtration rate did not differ in the two groups and littoral mussels did not show the initial increased rate or 'overshoot' characteristic of some bivalve species (Bayne et al., 1976). The ingestion rate during the 5 h of feeding averaged 86×10^6 cells in both samples. A further experiment was conducted where mussels were collected after exposure in the field, divided into two groups, and tested after an exposure period of 6 and 9 hours respectively. Fig. 5 shows that increased exposure resulted in a rise in the filtration rate during the first 30 minutes after immersion to 5.2 lh^{-1} , compared with 2.7 lh^{-1} after 6 h. This increased the ingestion rate by 12×10^6 cells, or 14%. However, this has been interpreted as a stress induced response and would be insufficient to significantly increase the energy gain and make good the loss in feeding time.

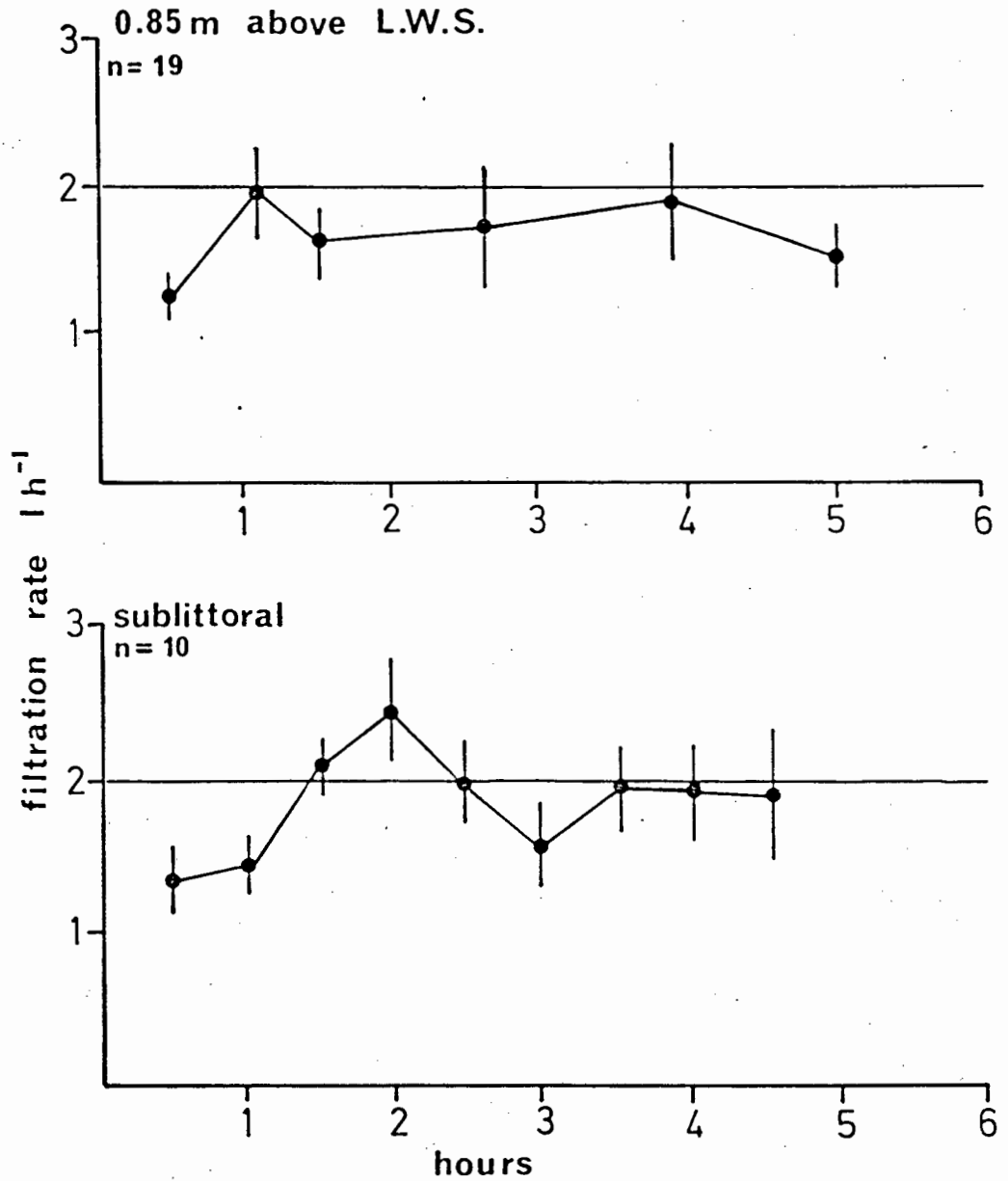


Fig. 4. Filtration rates of 40 mm *C. meridionalis* over a 5 h period at 12°C. (a) mussels collected 0.85 m above L.W.S. after aerial exposure in the field (b) sublittoral mussels continually submerged. Vertical bars indicate one standard error.

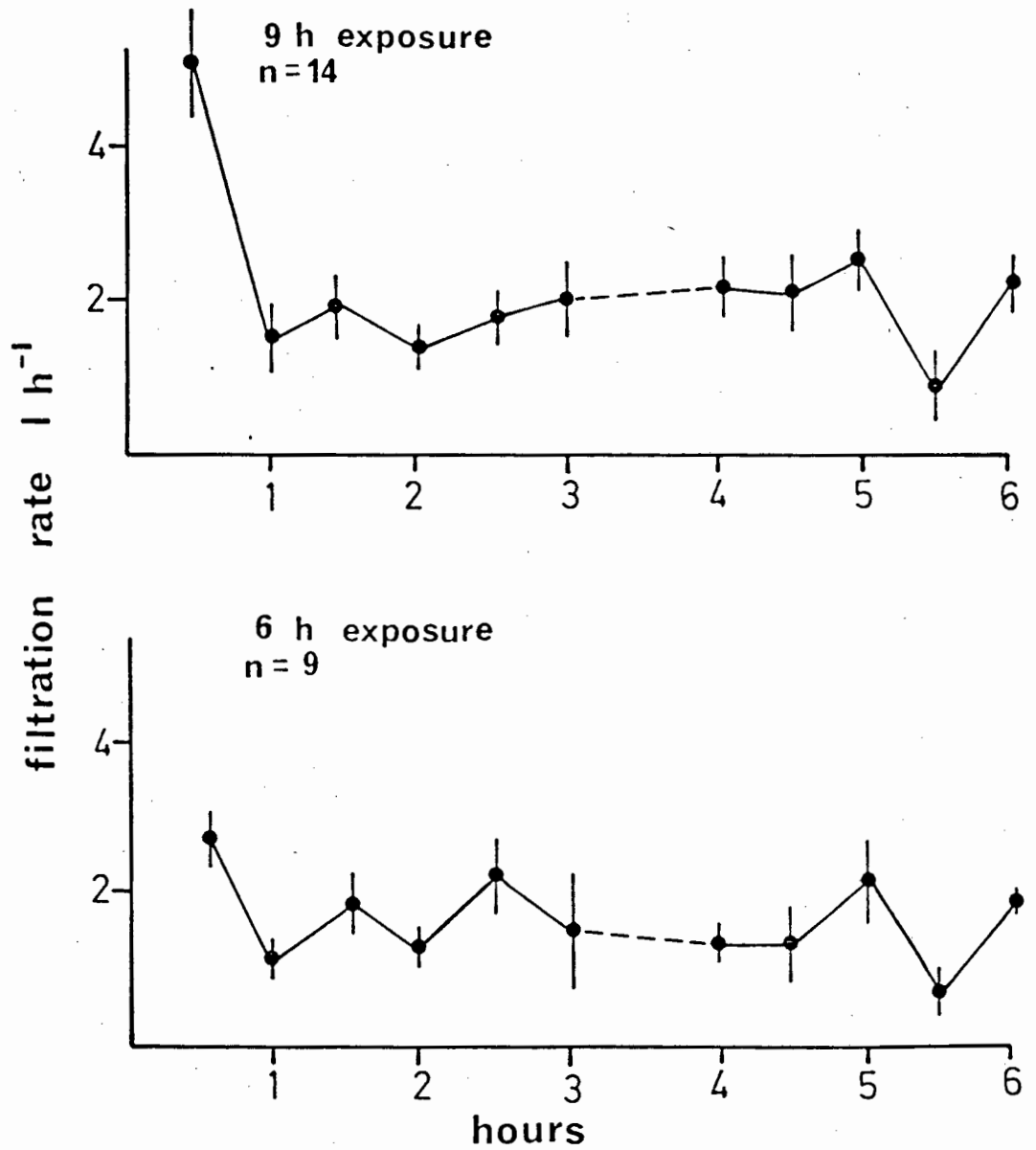


Fig. 5. Filtration rate of 40 mm *C. meridionalis* (0.85 m above L.W.S.) at 12°C after 6 and 9 h aerial exposure. Vertical bars indicate one standard error.

Assimilation efficiency

The assimilation efficiency of sublittoral C. meridionalis when fed a range of algal rations has been examined by Griffiths (1980b). A ration level of 10×10^6 cells l^{-1} gave an assimilation efficiency averaging 60% in 45 mm mussels. Although size has been shown to have little or no effect on assimilation efficiency in bivalves (Griffiths & King, 1979; Bayne et al., 1976), the following experiment employed only 40 mm mussels. Table II shows the assimilation efficiencies of C. meridionalis when fed 10×10^6 cells l^{-1} following collection at 0.85 m above L.W.S. after a period of 6 h aerial exposure in the field. Sublittoral mussels, which were not subject to aerial exposure, were measured simultaneously. The assimilation efficiency averaged 60% and did not differ in the two groups. Littoral mussels, therefore, do not enhance their energy gain by increased assimilation efficiency during the limited feeding period.

CONCLUSIONS

The growth rate of C. meridionalis has been shown to decline with increasing aerial exposure. The population does not extend above the predicted level for zero growth (Baird, 1966). The absence of significant weight difference between similar sized mussels in the sublittoral and upper shore zones, indicates that reduced feeding time affects growth rate but not flesh or gonad weight.

Table II. Assimilation efficiencies of sublittoral mussels while continually submerged, and upper shore mussels (0.85 m above L.W.S.) during submergence after a period of 6 hours exposure in the field. Both fed on 10×10^6 cells l^{-1} D. primolecta at 12°C .

Sublittoral	0.85 m above L.W.S.
51.9	47.7
49.1	48.1
64.0	66.5
69.4	62.5
63.5	65.8
73.9	60.3
68.7	66.0
<u>67.4</u>	<u>62.0</u>
\bar{x} 63.4	\bar{x} 59.8

Newell (1980) has discussed the mechanisms whereby species living under conditions of limited food resources may adjust various components of the energy budget to maintain positive energy balance or scope for growth. Theoretically mussels living in the littoral zone may increase consumption rates or absorption efficiencies to enhance energy intake during immersion, or they may suppress metabolic expenditure and limit energy input into growth and reproduction to conserve limited resources. A combination of these mechanisms may also be employed. Studies on C. meridionalis have shown no increase in filtration rate or absorption efficiency in responses to aerial exposure, and energy intake is thus directly influenced by duration of exposure. Whether enhanced assimilation efficiency of the food which is present in the gut during exposure takes place, is not known. Elwin & Gonor (1979) have shown enhanced assimilation efficiency with increasing exposure in Mytilus californianus fed on algal culture. During exposure littoral species may be subject to temperatures well above those experienced by submerged individuals, however there is conflicting evidence as to the effect of temperature upon assimilation efficiency and ingestion rate. Widdows & Bayne (1971) found a decrease, and Winter (1969) an increase, in absorption efficiency with rising temperature in M. edulis, and Seiderer & Newell (1979) showed increased α -amylase activity in the crystalline style of C. meridionalis acclimated to higher temperatures.

However, present data indicate that the assimilation efficiency of C. meridionalis does not change following field aerial exposure. During the above experiments the air temperatures averaged 6°C or more above ambient sea temperature.

It is thus concluded that littoral C. meridionalis do not enhance energy gain during immersion and that they experience a progressive decline in food resources with increasing shore height. This becomes a limiting factor at the level of 50% exposure. Although experiencing reduced food availability, they nonetheless have a positive energy balance and are able to survive, grow and reproduce. Under these conditions conservation of metabolic energy expenditure must be important in maintenance of energetic gain. In C. meridionalis reduction in growth rate would reduce energy expenditure. A further mechanism which may be employed is that of lowering the energetic cost of metabolism. Quiescence during aerial exposure may prove a significant energy conservation strategy.

ACKNOWLEDGEMENTS

Miss F.J. Stratton is thanked for technical assistance and Professor R.C. Newell for constructive criticism of the manuscript. This work was supported as part of the Kelp Bed Research Programme by the South African National Committee for Oceanographic Research.

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PAPER 7. AERIAL EXPOSURE AND ENERGY BALANCE IN LITTORAL
AND SUBLITTORAL CHOROMYTILUS MERIDIONALIS (KR.)
(BIVALVIA) .

Aerial exposure and energy balance in littoral and sublittoral
Choromytilus meridionalis (Kr.) (Bivalvia).

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ABSTRACT

The routine rate of oxygen consumption of sublittoral Choromytilus meridionalis (Kr.) is known to increase with rising temperature. The respiration rate of littoral mussels in water following aerial exposure in the field was compared with that of continually submerged individuals. During winter the rate was lower, and during summer, higher than that of sublittoral mussels. This phenomenon is probably a result of the reversed temperature differential between air and sea temperatures in summer and winter. The respiration rate of littoral mussels in air was temperature independent and averaged 11% of that measured in water.

The energy utilised in growth, reproduction and respiration in littoral and sublittoral mussels was calculated for the first 5 years of growth. Upper shore mussels show a reduced growth rate and their smaller

individual size, coupled with reduced respiratory energy demand during aerial exposure, results in an energy requirement of less than half that of sublittoral mussels after 5 years. Assimilation as a percentage of consumption averaged 16% in sublittoral and 18.5% in upper shore areas. It is concluded that quiescence and reduced metabolism during aerial exposure, coupled with reduced energy allocation to growth, permit the mussels to maintain a large reproductive output in the littoral zone.

INTRODUCTION

Littoral organisms display varying degrees of adaptation to aerial exposure. These have been reviewed by Newell (1979), and for mussels in particular, by Bayne et al. (1976). The black mussel Choromytilus meridionalis (Kr.) is a predominantly sublittoral species which may densely cover rocky shores to a height of 0.5 - 0.85 m above low water spring tide (L.W.S.). The limit of upward extension corresponds to 50% aerial exposure during a 14 day tidal cycle (Griffiths & Buffenstein, 1980). Examinations of population structure, growth rates and allometric relationships have shown that littoral mussels, other than displaying a slower growth rate, do not appear to be adversely affected by aerial exposure (Griffiths & Buffenstein, 1980; Griffiths, 1980a). Nonetheless, as in all littoral species they must be subject to reduced

feeding times, raised body temperatures and desiccation when exposed. Although littoral organisms generally show sufficiently wide physiological tolerance limits to survive normal environmental conditions (Newell, 1979), it may be expected that factors such as limited food resources would affect energy balance. Different conservative strategies may be employed by organisms living under such conditions, in order to maintain a positive energy balance (reviewed by Newell, 1978, 1980). In littoral mussels these could take the form of enhanced feeding rates or assimilation efficiencies to compensate for reduced feeding time, or conservation of metabolic expenditure.

Energy gain in C. meridionalis has been examined by Griffiths & Buffenstein (1980). Littoral mussels were found to maintain the same filtration rate and assimilation efficiency after aerial exposure as sublittoral individuals not subject to such conditions. They are thus unable to enhance energy input during the limited feeding period. In the present paper the metabolic expenditure of littoral and sublittoral mussels is compared. Data from these studies are then used to contrast the energy requirements for growth, reproduction and respiration with that available as food in seawater.

MATERIALS AND METHODS

Mussels were collected from a dense bed extending from the sublittoral into the littoral at Bailey's Cottage, False Bay, South Africa ($34^{\circ}06'S$ $18^{\circ}28'E$). For comparative studies, mussels were collected immediately below L.W.S. and 0.5 m or 0.85 m above L.W.S.. The tidal range averaged 1.5 m and littoral mussels at the above shore levels were exposed for 28.5% and 50% of a 14 day tidal cycle respectively.

Respiration studies

Mussels were collected from the field, cleaned of epibiotic growth, and placed directly into respirometer chambers. Littoral mussels were collected immediately before or after tidal exposure to air. Sublittoral mussels were collected at low water and maintained submerged. A size range of 10 - 100+ mm shell length C. meridionalis was used for each experiment when possible. However, littoral mussels seldom exceeded 70 mm.

The oxygen consumption of mussels in water was measured using 6 YSI pO_2 probes connected to a multichannel chart recorder via a switchgear mechanism. The latter maintained a constant potential across the electrodes and allowed successive monitoring of each probe for 5 sec every 1.25 min. Oxygen content of the water was measured at the start of each experiment by replicate Winkler analysis (Strickland & Parsons, 1968). When oxygen

levels fell to 85% of the starting value eg. during experiments lasting 5 h, the water in each respirometer was flushed and replaced with fresh oxygenated water.

Respiration in air was measured using a Gilson Differential respirometer for mussels 10 - 45 mm shell length and constant pressure respirometers (Davies, 1966) for mussels 40 - 110 mm shell length. In all cases 6 readings were obtained from each mussel at each temperature.

Energy flow

The energy required for growth, reproduction and respiration in sublittoral and Topshore (0.5 m above L.W.S.) mussels was calculated as follows. Using von Bertalanffy growth equations for mussels at the two shore levels (Griffiths, 1980a), the shell length at yearly intervals was calculated for the first 5 years of growth. The flesh weight at these shell lengths was derived from the equation given by Griffiths (1980a):

$$[\text{dry flesh wt. (g)}] = 1.251 \times 10^{-5} \cdot [\text{shell length (mm)}]^{2.646}$$

Regression equations of dry flesh weight to shell length at different shore levels did not differ significantly (Griffiths & Buffenstein, 1980) and the above equation applied to all shore levels. Flesh weight was converted to energy equivalents (19.5 kJ g^{-1}) and the growth

increment for each year calculated. Gonad production and respiratory cost were determined for mussels of the mean shell length during each year. On the basis of there being no significant difference in flesh weight, the quantity of gonad produced in similar sized individuals was assumed to be the same for all shore levels. Gamete output was calculated from the equation given by Griffiths (1980a):

$$[\text{dry wt. gamete output (g)}] = 1.334 \times 10^{-3} \cdot [\text{shell length (mm)}]^{1.615}$$

Energy values of ovary and testis averaged 22.5 kJ g^{-1} dry weight. The annual respiratory cost in sublittoral mussels was calculated from equations in Table 1 (see results), assuming 6 months at summer (18°C) and winter (12°C) sea temperatures and an energy conversion of $1 \text{ ml O}_2 = 4.83 \text{ cal} = 20.19 \text{ J}$ (Hughes, 1970). Calculation of Topshore respiration incorporated respiration in air for 28.5% of the time.

The annual filtered ration or consumption, was calculated by multiplying the filtration rate by the energy value of the available ration in seawater (Griffiths, 1980b, 1980c).

$$[\text{filtration rate l h}^{-1}] = 6.44 \times 10^{-3} \cdot [\text{shell length (mm)}]^{1.5764}$$

The average ration available in seawater at Bailey's

Cottage between Feb. 1978 - Feb. 1979 was 16.2 J l^{-1} .

There was no seasonal pattern in food availability (Griffiths, 1980c).

RESULTS

The routine rate of oxygen consumption in C. meridionalis remains unaffected by state of tide and ration level (Griffiths, 1980b). The relationships between respiration rate and shell length of mussels in air and water are shown in Fig. 1 and the regression equations listed in Table 1. Respiration in air was measured in mussels collected in the field immediately after exposure by the receding tide. Recordings were made during summer and winter at 18°C and 12°C respectively, and during summer at 25°C . The latter approximates air temperature during summer. The data showed considerable scatter and analysis showed no significant difference between the slopes and the intercepts of the equations. Scatter in the data may be dependent on the degree of valve closure, although the valves of C. meridionalis do not gape noticeably as in Modiolus species (Coleman & Trueman, 1971).

The routine rate of sublittoral mussels in water increases with temperature and there is no evidence of acclimation to seasonal changes in sea temperature. The Q_{10} value between 12°C and 18°C is 1.69. Bayne et al. (1976) have summarised data on Q_{10} values of routine oxygen consump-

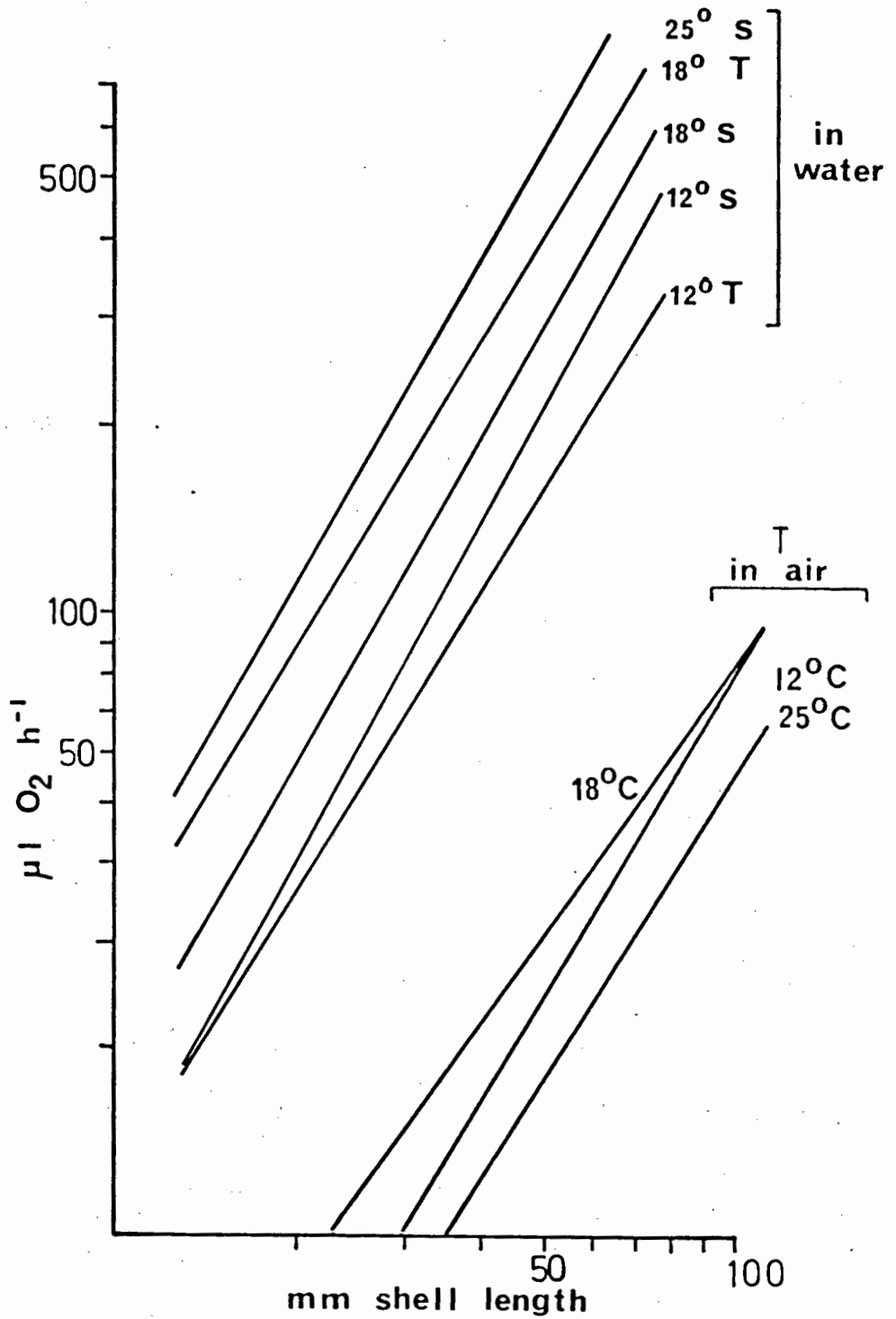


Fig. 1. Respiration rates of *C. meridionalis* in summer at 18°C and 25°C and in winter at 12°C. Data shows oxygen consumption in water and in air. S=sublittoral mussels, T=topshore mussels.

Table 1. Regression equations relating C. meridionalis oxygen consumption in air and water at different seasonal temperatures to shell length. Equations in the form $y=ax^b$ where $y=\mu l O_2 h^{-1}$ and x =shell length in mm.

	a	b	n	r^2
BLWS in water:				
summer 18°C	0.2900	1.78	69	.89
summer 25°C	0.6516	1.74	22	.96
winter 12°C	0.1751	1.83	12	.91
0.85 m above L.W.S. in water:				
summer 18°C	0.6569	1.66	23	.74
winter 12°C	0.2631	1.66	13	.88
0.85 m above L.W.S. in air:				
summer 18°C	0.1429	1.38	48	.68
summer 25°C	0.0380	1.58	15	.65
winter 12°C	0.0349	1.69	13	.76
pooled data in air	0.0441	1.64	76	.73

tion in bivalves and values of 2 or more are common over the normal environmental temperature range.

The respiration rate of littoral mussels in water was measured following aerial exposure during L.W.S. in the field. During winter the respiration rate was slightly lower than that of sublittoral mussels. The lines were not parallel, possibly indicating a size related response. During summer the oxygen consumption of littoral mussels was 45% higher than that of sublittoral individuals at ambient sea temperature of 18°C. In this case the response measured in small and large mussels was the same. Raised respiratory rates may result from an overshoot in the rate at the onset of feeding and respiration following aerial exposure (Bayne et al., 1976). Examination of data obtained from individual littoral C. meridionalis during summer showed no overshoot in the respiratory rate upon submergence. Fig. 2 gives examples of the oxygen consumption of individual mussels, recorded from the initiation of filtering activity upon immersion. The respiration rate remained high throughout the 5 h period of measurement.

Fig. 3 contrasts the oxygen consumption by littoral and sublittoral mussels over a 14 day tidal cycle in

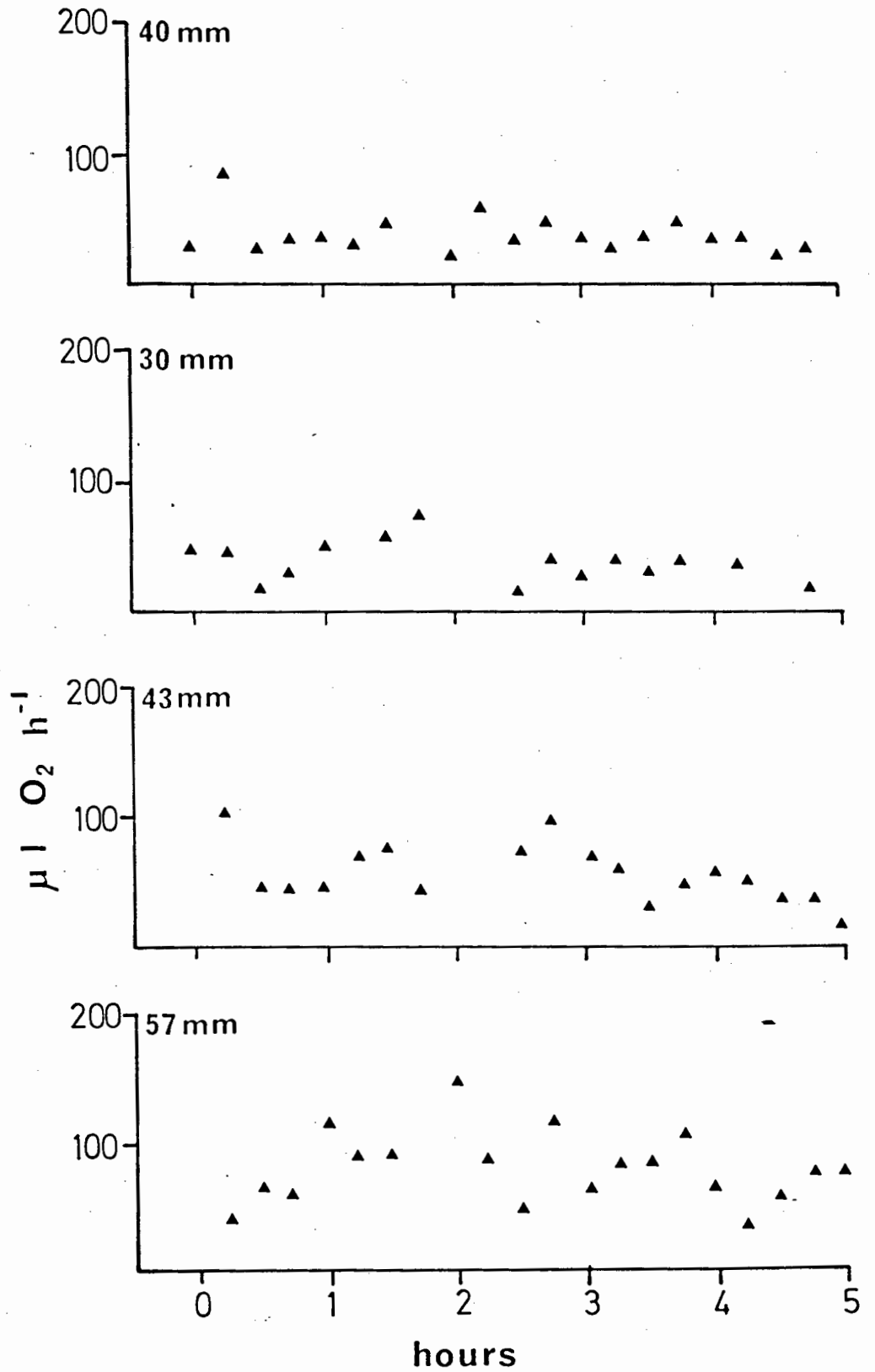


Fig. 2. Respiration rate in water of individual mussels collected 0.85 m above L.W.S. after 6 h aerial exposure in the field.

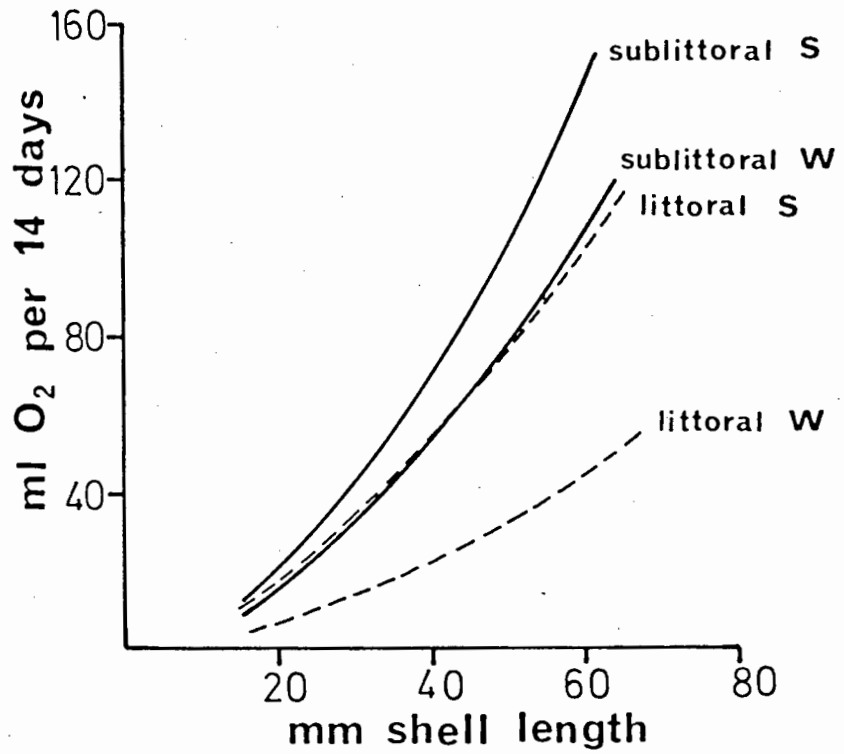


Fig. 3. Oxygen consumption expressed as ml O₂ per 14 day tidal cycle in sublittoral and littoral mussels during summer (S) and winter (W). Littoral respiration includes that in air and water based on 50% exposure time.

summer and winter. Littoral mussels were assumed to occur at 0.85 m above L.W.S. which is subject to 50% aerial exposure. During summer and winter the oxygen consumed by littoral C. meridionalis averaged 79% and 47% of that of sublittoral individuals respectively. Although respiration in littoral mussels during immersion in summer is higher than that in the sublittoral, respiration in air offsets this and provides an overall saving in metabolic expenditure.

Energy balance

The energy utilised in growth, reproduction and respiration in sublittoral and Topshore (0.5 m above L.W.S.) mussels during the first 5 years after settlement are shown in Fig. 4 and Table 2. Topshore mussels show reduced growth and this, coupled with reduced respiratory demand due to aerial exposure, results in an energy requirement less than half that of sublittoral mussels after 5 years. Growth at this shore level during the first year is overestimated as a result of migration of mussels into the area from lower shore levels.

Fig. 4 demonstrates that the greatest proportion of the assimilated energy is spent on respiration, the least on growth, and an average of 27% on reproduction in the 5th year. In bivalves, gamete production frequently represents the major proportion of production. In C. meridionalis calculated gamete production is 78% and

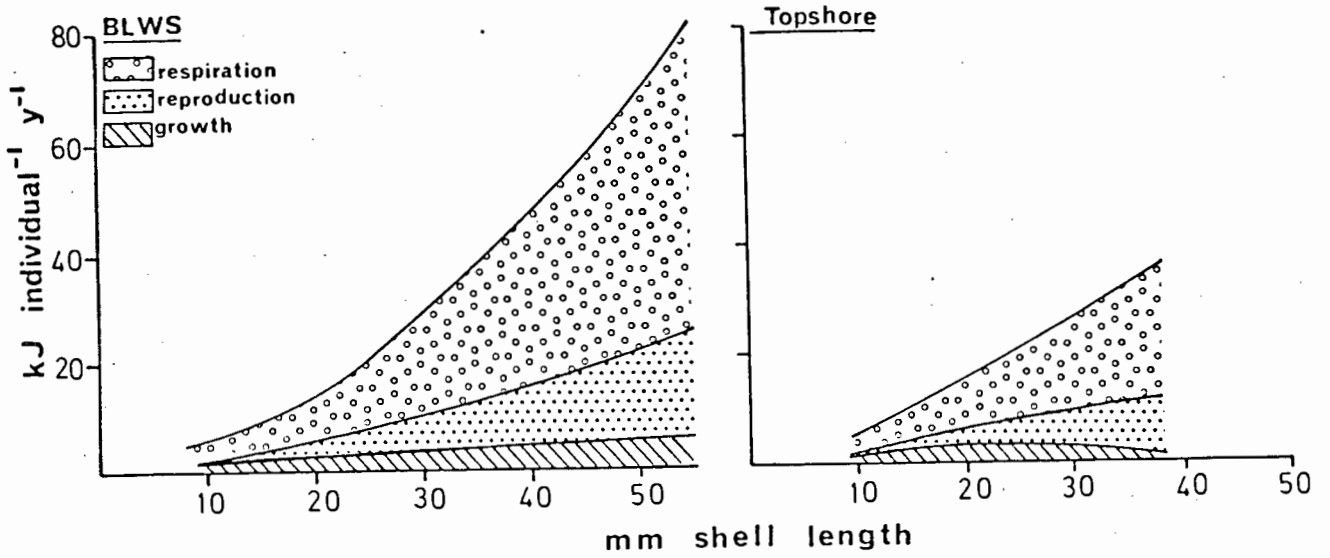


Fig. 4. Calculated energy requirements for growth, reproduction and respiration in sublittoral and Topshore (0.5 m above L.W.S.) *C. meridionalis* during the first 5 years of growth. Consumption (=filtered ration) expressed as $\text{kJ individual}^{-1} \text{y}^{-1}$ is also shown.

Table 2. Calculation of energy requirements and filtered ration for individual C. meridionalis in the sublittoral and 0.5 m above L.W.S. (Topshore) during the first 5 years of growth.

age y	length mm at end of year	total energy kJ individual ⁻¹	growth increment kJ y ⁻¹	gonad production kJ y ⁻¹	respiration kJ y ⁻¹ individual ⁻¹	assimilation kJ y ⁻¹ individual ⁻¹	filtered ration kJ y ⁻¹ individual ⁻¹
<u>sublittoral:</u>							
1	19.32	1.558	1.558	-	4.242	5.799	32.6
2	31.67	4.831	3.273	5.609	13.985	22.867	150.4
3	42.26	9.356	4.525	10.219	27.299	42.043	271.1
4	51.35	14.619	5.263	14.960	41.759	61.982	393.1
5	59.15	20.213	5.594	19.553	56.289	81.436	509.5
<u>Topshore:</u>							
1	18.66	1.438	1.438	-	3.855	5.292	22.3
2	28.23	3.712	2.274	4.897	11.260	18.431	94.4
3	33.70	5.570	1.858	7.675	17.867	27.400	146.2
4	36.83	6.827	1.257	9.479	22.170	32.896	179.6
5	38.62	7.611	0.784	10.558	24.795	36.137	200.0

93% of production in the sublittoral and littoral zones respectively in the 5 th year. P_r in littoral mussels forms a higher percentage of P because of the declining growth rate.

Table 2 shows the calculated filtration ration available from seawater. In order to maintain the necessary energy gain for survival and reproduction, C. meridionalis requires to assimilate an average of 16% of the filtered ration in the sublittoral and 18.5% in the littoral zone. Data for the first year of growth at Topshore were excluded from this calculation as P_g was overestimated. The low assimilation values calculated above, reflect the fact that bivalves feeding at high ration levels reject a considerable proportion of the filtered ration in the pseudofaeces and faeces (Widdows et al., 1979).

Calculations of reproductive effort were based on the assumption that gamete output by similar sized mussels does not change with increasing shore height. The similarity in the calculated assimilation requirements in littoral and sublittoral mussels indicates that estimates of reproductive effort in littoral mussels are reasonable. An overestimate of littoral reproduction would have resulted in a considerably higher value.

DISCUSSION

Temperature dependence of the routine rate of oxygen consumption is a common phenomenon in bivalves. This was confirmed in C. meridionalis. The differences

measured in the oxygen consumption of littoral mussels while submerged in seawater has been attributed to the temperature regime during aerial exposure. During winter shore air temperatures may be similar or lower than ambient sea temperature and oxygen consumption was reduced. However, during summer respiration in highshore mussels in water exceeded that of sublittoral individuals by 45%. This is considered a consequence of high tissue temperatures resulting from insolation during exposure on hot summer days. Adjustment of the respiration rate following aerial exposure has also been reported in Transennella tantilla (Pamatmat, 1969). However in this case acclimation occurred. The respiration rate showed cold acclimation during autumn when air temperatures were lower than sea temperatures.

Aerial respiration has been equated to the standard rate (Newell & Northcroft, 1967) of oxygen consumption of bivalves in water and is characterised by temperature independence over the normal environmental temperature range. This has been demonstrated in M. edulis (Coleman, 1973a), Cardium edule (Boyden, 1972) and Modiolus demissus (Kuenzler, 1961). However, in C. meridionalis, although aerial respiration is characterised by temperature independence, the rate is 15% at 12°C and 6% at 18°C of the routine rate during immersion. This is considerably lower than the 65%, 63% and 73% reduction measured in C. edule, M. demissus and Mytilus californianus respectively (Bayne et al., 1976).

Whether aerial respiration reflects the total energy demand during exposure is questionable. Livingstone & Bayne (1974), De Zwaan & De Bont (1975) and De Zwaan & Wijsman (1976) have suggested that anaerobic and aerobic metabolism may operate together during aerial exposure. In this case the total energy demand will not be reflected by oxygen consumption alone. The 'overshoot' in respiration rate commonly recorded after aerial exposure has been considered to be due to oxygen debt and flushing of the metabolites of anaerobic respiration. C. meridionalis does not display an 'overshoot' and aerobic metabolism may be sufficient to meet the reduced metabolic demands during quiescence. Further evidence such as the monitoring of the end products of anaerobiosis is required. However, it is doubtful that anaerobic metabolism would significantly increase energy expenditure. De Zwaan & Wijsman (1976) have calculated that a 20 fold reduction in respiratory energy demand occurs during anaerobic metabolism in M. edulis. Reduction in the respiratory rate during exposure in littoral C. meridionalis lowered the total respiratory cost (in air and water) to 65% of that of sublittoral mussels.

Choromytilus meridionalis shows controlled shell gape and a continued, but slower, heart rhythm recorded with an impedance pneumograph during air exposure (V. Stuart pers. comm), factors which indicate that it is relatively well adapted to aerial respiration (Bayne et al., 1976). Modiolus modiolus, which is less well

adapted, displays bradycardia and uncontrolled shell gape (Coleman, 1973b).

The slowing growth rate in highshore mussels (Fig. 4) indicates that reduction in respiratory cost is insufficient to match the energy lost in reduced feeding time. Consideration of the energy apportionment has shown that the greater percentage (67% in sublittoral mussels) of energy expenditure goes into respiration, with the least into growth. Mussels have long been considered 'r' strategists (Bayne, 1976) and even in littoral specimens a considerable portion of the energy budget may be expected to be channelled into reproduction. The assimilation ration necessary for continued reproduction in highshore C. meridionalis is only slightly higher than that of sublittoral individuals. Reproduction may thus continue at the expense of growth in the littoral environment. The reduced gamete production of smaller, relative to larger mussels (purely a function of size), need not cause a lower reproductive output by the littoral population as a whole. Previous calculations have shown that due to the higher packing density of smaller mussels, the reproductive output by a single cohort is approximately the same at 25 mm or 70 mm shell length (Griffiths, 1980a). Littoral mussels may therefore continue to make a significant contribution to population spawning, although they decline in size with increasing shore height.

Limitation of the energy input into growth, and the

reduced metabolic demand due to quiescence and aerial respiration during exposure, may thus be advantageous to survival of healthy, reproductively active individuals in the littoral zone.

ACKNOWLEDGEMENTS

This work was supported as part of the Kelp Bed Research Project by the South African National Committee for Oceanographic Research. Miss F. Stratton is thanked for assistance and Prof. J.G. Field for constructive criticism of the manuscript.

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PAPER 8. PRODUCTION AND ENERGY FLOW IN RELATION TO AGE
AND SHORE LEVEL IN THE BIVALVE CHOROMYTILUS MERIDIONALIS

(KR.)

Production and energy flow in relation to age and shore level in the bivalve Choromytilus meridionalis (Kr.).

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Keywords: Bivalve, production, energy flow, littoral sublittoral.

Annual production (P) in terms of growth (P_g) and reproduction (P_r) was calculated for individual Choromytilus meridionalis of various shell lengths. Peak growth production occurred at approximately 60 mm ($P_g = 5.6 \text{ kJ individual}^{-1} \text{ y}^{-1}$). Reproductive output increased with increasing size once sexual maturity was attained and rose from 5.2 kJ y^{-1} in a 20 mm mussel to 51.4 kJ y^{-1} in a 100 mm individual, representing 61 - 97% of total production.

Population production was calculated for each of three successive years ($Y_0 - Y_2$) at four shore levels (sublittoral, LWS, Midshore and Topshore) following spat settlement in the lower shore areas. Production was greatest in the sublittoral and at LWS and declined with increasing shore height. Maximum production took place in Y_1 , when the mussels were fully

mature and P_r represented 80% of production. Production in Y_2 decreased as a result of slowing growth rates, particularly at higher shore levels, and a decline in density throughout the population. Maximum population production was $100 \times 10^3 \text{ kJ m}^{-2} \text{ y}^{-1}$ (sublittoral in Y_1), when the mussels grew from 26 to 38 mm and the P/\bar{B} ratio was 5.1.

Population respiration at the various shore levels was calculated taking into account aerial respiration during exposure at low tide. Respiration averaged 66% of assimilation, where $A = P_g + P_r + R$. Population energy flow was highest in the lower sampling stations, the maximum recorded at LWS being $211 \times 10^3 \text{ kJ m}^{-2} \text{ y}^{-1}$.

Energy budgets were calculated for mussels in the sublittoral and Topshore areas. Approximately 90% of the energy filtered from seawater per annum was released to other consumers in the form of gamete output, faeces and pseudofaeces production and through mortality of mussels.

Introduction

Although several studies of production in bivalves have been made, few have incorporated reproductive output by the population. This is because of the difficulty of quantifying gamete production where the gonad is an

integral part of the somatic tissue and cannot be separated as a discrete organ. However, recent data have shown that the contribution made to production by reproductive output may be as high as 80% or more in bivalves (Bayne, 1976; Rodhouse, 1978; Thompson, 1979). Reproductive effort has also been shown to increase with size, ranging from 10 - 20% of production in small bivalves to 60 - 90% in large individuals (Bayne, 1976; Griffiths & King, 1979; Thompson, 1979). Studies which do not incorporate reproductive effort would thus considerably underestimate total production ($P_g + P_r$) and the turnover ratio (P/\bar{B}). Even in populations comprising mostly young individuals, high density and a rapid growth rate may result in a large gamete production per unit area.

Variability in fecundity from year to year may also affect estimates of reproductive effort, particularly in short term studies. Gamete output varies annually in Choromytilus meridionalis (Griffiths, 1977) Mya arenaria (Brousseau, 1978) and Mytilus edulis (Thompson, 1979). It is thus clear that comparisons of production among species should be made with caution. In many cases more information is needed before meaningful interpretations may be made. For example, Dame (1976) found that 30% or more of the standing crop energy of Crassostrea virginica may be contained in the shell organic matrix. In many production studies this component has not been

taken into account. Furthermore, production by a species in one area may not necessarily be equated with that in another area because of differing growth rates and food supply. Finally, Hughes (1970) and Green (1973) have demonstrated that productivity within a single species extending over the littoral zone may vary with intertidal height.

In order to investigate the effects of increasing age and position on the shore on production and reproductive effort, a population of C. meridionalis was studied at different shore levels over a period of 4 years. Because the population consisted of only 2 cohorts, adults and a new spat settlement, the data enabled comparison between cohorts of different ages and densities. Population respiration was also calculated and combined with production estimates to give energy flow through the population.

Materials and Methods

Data presented here were obtained during a 4 year study of a mussel population extending from the sublittoral into the littoral zone at Bailey's Cottage, False Bay, South Africa (34°06'S 18°28'E). Every three months two or three samples of 0.025 m² were collected at 4 different shore levels on the shore. The sampling stations are given below. Exposure at these levels was calculated

as the percentage of a 14 day tidal cycle during which the mussels were exposed to air.

BLWS - 0.5 m below L.W.S., exposure time 0%

LWS - 0.16 m above L.W.S., exposure time 4.2%

Midshore - 0.38 m above L.W.S., exposure time 17%

Topshore - 0.5 m above L.W.S., exposure time 28.5%.

The samples during the first two years contained two cohorts, easily separated on the basis of shell length. The cohorts were treated separately and the size-frequency distribution, mean shell length and total weight obtained for each sample. From these data, the mean shell length and mean weight per individual at each shore level on successive sampling dates were obtained.

Individual production and energy flow

a. Growth

Annual growth production by individual sublittoral C. meridionalis of different shell lengths was calculated for mussels between 10 - 100 mm initial shell length.

The von Bertalanffy growth equation for sublittoral mussels at Bailey's Cottage was as follows (Griffiths, 1980a):-

$$\text{Length (mm)} = 106.259483 (1 - e^{-0.153188(t - (-0.309774))})$$

Growth was continuous throughout the year.

The shell lengths at time 't' (initial length) and time 't + 1' (length one year later) were converted to total dry weight of mussel using the length/weight equation below (Griffiths, 1980a), and the growth increment found by subtraction.

$$[\text{Total dry weight (g)}] = 6.911 \times 10^{-4} \cdot [\text{shell length (mm)}]^{2.291}$$

The energy equivalent of the total mussel (shell and byssus organic material inclusive) was 2.55 kJ g^{-1} .

b. Reproduction

Reproductive effort was calculated from the equation relating mean gamete output per year to shell length (Griffiths, 1980a).

$$[\text{Dry wt. gamete output (g y}^{-1}\text{)}] = 1.334 \times 10^{-3} \cdot [\text{shell length (mm)}]^{1.6154}$$

During a 4 year study the annual spawning season extended over several months. It can generally be divided into two sectors, July - October and October - February (Griffiths, 1977, 1980a). The growth interval of one year was assumed to extend from July to June of the following year. Because of the continuous growth of the mussels and the fact that an individual would be larger in the second half of the breeding season than in the first, the shell

length at the midpoint of each sector of the spawning season (31st Aug. and 31st Dec.) was derived from the growth curve given above. Gamete output for the appropriate sector was then calculated for individuals of these lengths. Summation of gamete output for the two sectors of the breeding season gives the annual reproductive effort. The energy equivalent of gamete material was 22.5 kJ g^{-1} .

c. Respiration and assimilation

Annual respiration of individual sublittoral mussels when at different shell lengths was calculated from the equations relating oxygen consumption to shell length given by Griffiths (1980b). These were obtained from measurements of mussels from Bailey's Cottage and are given in Table 2 (see results section). Mean annual shell length was used for each size class interval and it was assumed that the mussel spent half the year at each of the ambient sea temperatures (winter 12°C , summer 18°C). Assimilation was calculated by summation of $P_g + P_r + R$.

Population production

a. Growth

Population production was calculated over 3 years from the time of peak settlement of cohort 2 at BLWS and LWS (July 1975, when the mussels were 7 - 8 months old). Thus $Y_0 =$ July 1975 - June 1976, $Y_1 =$ July 1976 - June 1977 and $Y_2 =$ July 1977 - June 1978. During this time cohort 1 consti-

tuted a declining population which showed no growth increments. Thus in cohort 1, P_g was zero.

Calculation of growth production in cohort 2 followed the method outlined by Crisp (1971). Survivorship curves and Allen curves were constructed for the three year period, and the area under the Allen curves representing growth production, was divided into Y_0 , Y_1 and Y_2 . A smoothed curve was fitted to the data on mussel density to reduce sampling variation. However, the mean weight of an individual within each sample was regarded as reflecting the weight of individual mussels at that time and a smoothed curve was not fitted to growth data. This allowed for fluctuations in body weight due to spawning.

b. Reproduction

Comparison between tissue weight and shell length in BLWS and upper shore mussels has shown no significant differences between similar sized mussels at the two shore levels (Griffiths & Buffenstein, 1980). It was thus assumed that the quantity of gonad formed within the mantle and body tissues did not change with increasing shore height. Unless the frequency of spawning differs, the gamete output of similar sized individuals at different shore levels may be assumed to be the same.

Gamete production by cohort 2 was calculated as follows.

The breeding season extending from July to February was divided into two sectors as above, and the mean shell length of the population at the midpoint of each sector calculated from von Bertalanffy growth equations relating to each shore level (Griffiths, 1980a). Due to the prolonged spawning season found in 1977 - 1978, an extra period of 3 months (March - May, midpoint 15th April) was added to this season. Having established the mean population length for each breeding sector, the flesh weight of individuals at these shell lengths was derived from shell length to flesh weight regressions obtained for each month of each spawning season (Griffiths, 1977, 1980a).

Summation of any decline in somatic weight between successive months gives the amount spawned by an individual for each breeding sector. Gamete output was calculated separately for males and females and an average figure obtained assuming a 1:1 ratio of the sexes in the field. From population density figures the mean number m^{-2} at each shore level was calculated for each sector of the breeding season. This was multiplied by the calculated gamete output to give an estimation of population gamete production. Summation of production within the sectors for each year gave the annual production.

Gamete production in cohort 1 was calculated in a similar manner. Reproductive effort, initially calculated as wet weight was converted to dry weight and energy

equivalents using the conversions:- dry weight = 16.88% of wet weight, gamete material = 22,5 kJ g⁻¹ dry weight (Griffiths, 1980a).

c. Respiration and assimilation

The respiratory rate of C. meridionalis in air and water has been described by Griffiths (1980c). The average shell length of mussels in each cohort at each shore level was plotted against sampling date and this was used to derive the size of the mussels during each month of the year. Knowing the percentage of time during which mussels at the different shore levels are exposed to air, and the seasonal sea temperature, the oxygen consumption in air and water was calculated for each month from equations relating respiratory rate to shell length. To simplify calculations the months were allocated to only two seasons and the average summer or winter sea temperatures (18°C and 12°C) assumed to apply for six months each. Population respiration was derived by multiplying the individual oxygen consumption appropriate to each month by the population density, and summing the values for the year. Oxygen consumption was converted to energy equivalents assuming 1 ml O₂ = 4.83 cal = 20.19 J (Hughes, 1970).

Assimilation or energy flow was calculated by summation of population growth and reproduction and respiration ($P_g + P_r + R$) expressed as energy equivalents for each shore level and each year.

d. Energy budget

The standard energy budget equation where $C = P_g + P_r + R + F + U$ is described by Crisp (1971). Values for different terms of the equation were calculated for mussels in the Topshore and BLWS samples only, data for the remaining shore levels being intermediate between the two.

Annual population consumption was determined as follows. The average length of a mussel at the two shore levels for each month of the year was derived from plots of mean shell length of each cohort against sampling date. The amount of water filtered by these individuals during each month was then calculated from the equation below and multiplied by the population density for that month. Cessation of feeding during aerial exposure in the topshore sample was taken into account.

$$[\text{Filtration rate l.h}^{-1}] = 6.44 \times 10^{-3} \cdot [\text{shell length (mm)}]^{1.5764}$$

Filtration rate has been shown to remain unaffected by temperature change or ration level (Griffiths, 1980b). Summation of the water filtered for each month of the year gave the annual amount filtered by the population. This was then multiplied by the energy value of organic matter available as food to the mussels in seawater at Bailey's Cottage. Measurement of the available ration over a period of one year showed that an average of 2.65 mg l^{-1}

was available to the mussels. This had an energy value of 6.1 kJ g^{-1} dry weight (Griffiths, 1980d).

The energy flow into faeces and pseudofaeces (F) and urine (U) was not determined and was obtained by subtraction of assimilation from consumption. Values for growth, reproduction and respiration (= assimilation) were obtained as described in the sections above.

The energy loss to other consumers was calculated in a similar manner to that of Hibbert (1977) for Mercenaria mercenaria. Energy loss is represented by mortality (M) calculated from the equation $P_g = \Delta B + M$ (Crisp, 1971); gamete loss to predators, which has been assumed to be 99% (Hibbert, 1977); and that lost as faeces, pseudofaeces and urine (calculated above). Energy loss was calculated as the average value for the three years ($Y_0 - Y_2$) in the Topshore and BLWS samples only.

Results

Individual production

Production in terms of growth and reproduction for individual sublittoral mussels of different shell lengths is shown in Table 1. The turnover ratio (P/\bar{w}) was highest in young mussels between 20 - 30 mm when growth was rapid and reproductive maturity had been reached. C. meridionalis becomes reproductively mature at an age of approximately

Table 1. Annual production, respiration and assimilation in individual C. meridionalis of different shell lengths expressed as total dry weight and energy equivalents..

length at t (mm)	length at t+1 (mm)	dry wt. at t (g)	dry wt. at t+1 (g)	\bar{w} (g)	P_g (kJ)	P_r (kJ)	R (kJ)	A (kJ)	P/\bar{w}	$\frac{P_r}{P} \times 100$
10	23.67	0.14	0.97	0.55	2.13	-	8.80	10.93	1.51	-
20	32.25	0.66	1.98	1.32	3.35	5.22	18.30	26.87	2.55	61
30	40.83	1.67	3.39	2.53	4.38	8.88	30.35	43.61	2.05	67
40	49.41	3.24	5.25	4.24	5.14	13.22	44.70	63.06	1.70	72
50	57.99	5.39	7.58	6.49	5.56	18.21	61.17	84.94	1.44	77
60	66.57	8.19	10.39	9.29	5.61	23.78	79.64	109.03	1.24	81
70	75.15	11.66	13.72	12.69	5.25	29.91	99.99	244.18	1.09	85
80	83.73	15.83	15.57	14.70	4.45	36.56	122.14	163.15	0.96	89
90	92.31	20.74	21.97	21.36	3.16	43.71	146.01	192.88	0.86	93
100	100.89	26.40	26.94	26.67	1.38	51.40	171.27	224.05	0.78	97

1 year or 20 mm shell length. As expected, growth declines with age and an increasing proportion of production is represented by gamete output. At 20 mm, 61% of production comprises reproductive effort and this reaches 97% in 100 mm mussels. The annual energy contributions towards P_g and P_r for C. meridionalis of different sizes are illustrated in Fig. 1.

Assimilation (Table 1) varies from 11 kJ individual⁻¹ y⁻¹ in 10 mm mussels to 224 kJ y⁻¹ in 100 mm individuals. An average of 74% of the energy intake is spent on respiration.

Population production

At the beginning of the sampling period, cohort 1 averaged 58 mm shell length. Mortality of cohort 1 proceeded from the lower shore upwards, adults being absent from BLWS at the onset of sampling. The maximum density of this cohort occurred at the Topshore station. Mortality of cohort 1 resulted from competition with the blanket settlement of cohort 2 in the lower shore areas. As the young mussels grew, they migrated up the shore and displaced the adult population (Griffiths, 1980a). There was thus delayed settlement of cohort 2 at the Midshore and Topshore levels and peak density did not occur there until several months after settlement at BLWS and LWS.

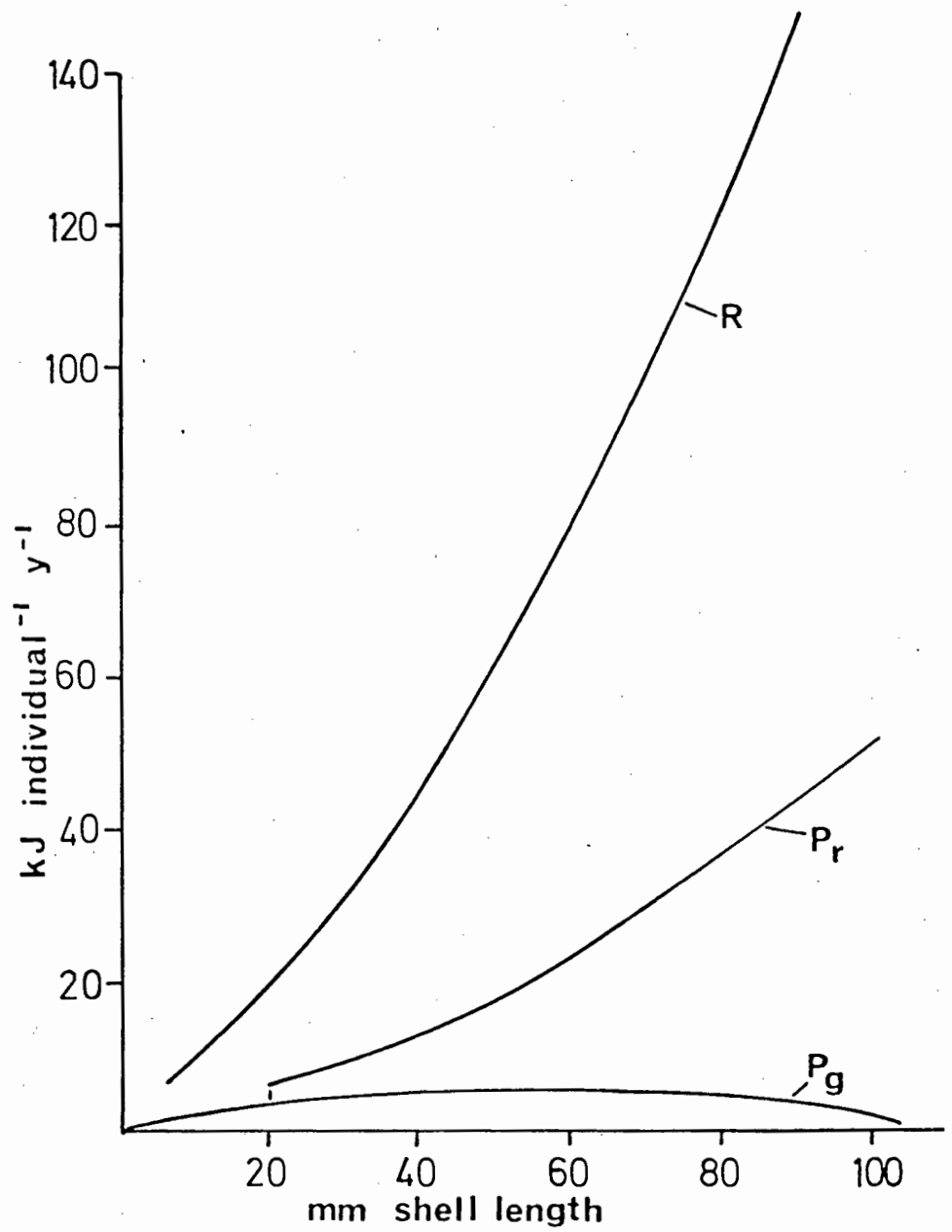


Fig. 1. Energy used in growth and reproduction and respiration by individual sublittoral C. meridionalis when at different shell lengths.

Survivorship curves for cohort 1 are shown in Fig. 2. The population declined from approximately 1500 mussels m^{-2} to zero within 1.5 years. There was no individual weight (\bar{w}) increment during the sampling period and no specimens of cohort 1 occurred at BLWS. The apparent lack of growth resulted from the high mortality of the largest mussels giving a declining mean shell length in successive samples. Allen curves could therefore, not be constructed for cohort 1 and P_g could not be estimated from field measurements. Since this study is concerned with production of the living mussel population, it is not appropriate to apply other methods of calculating growth production as elimination (Crisp, 1971).

Survivorship and Allen curves for calculating growth production in cohort 2 are shown in Fig. 3. The greatest density of spat settlement took place in the lowest shore area, with peak density at the higher shore levels being considerably delayed. Population growth production was divided into three one year intervals and Fig. 3 shows the changes in production with shore height and age. Growth in terms of total dry weight and energy equivalents is shown in Table 2.

Growth production in cohort 2 was highest in the sublittoral during all years and attained a maximum of 7.8 $kg\ m^{-2}$ or 20102 $kJ\ m^{-2}$ in Y_1 when the mussels were 1.6 to 2.6 years old. Maximum growth production occurred at all shore levels in Y_1 and declined in Y_2 . High values

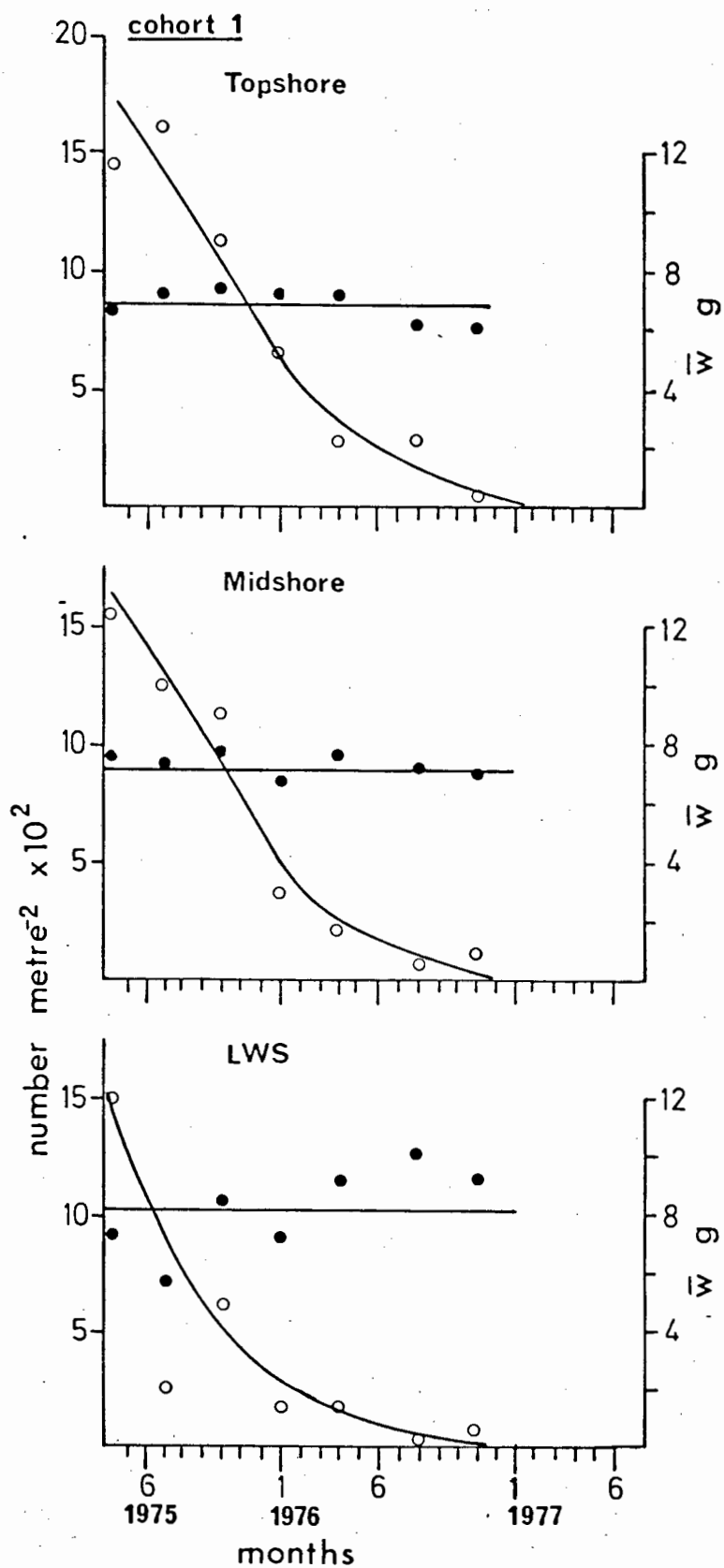


Fig. 2. Survivorship curves for cohort 1 C. meridionalis at different shore levels at Bailey's Cottage. Open circles-numbers, closed circles-mean weight per individual.

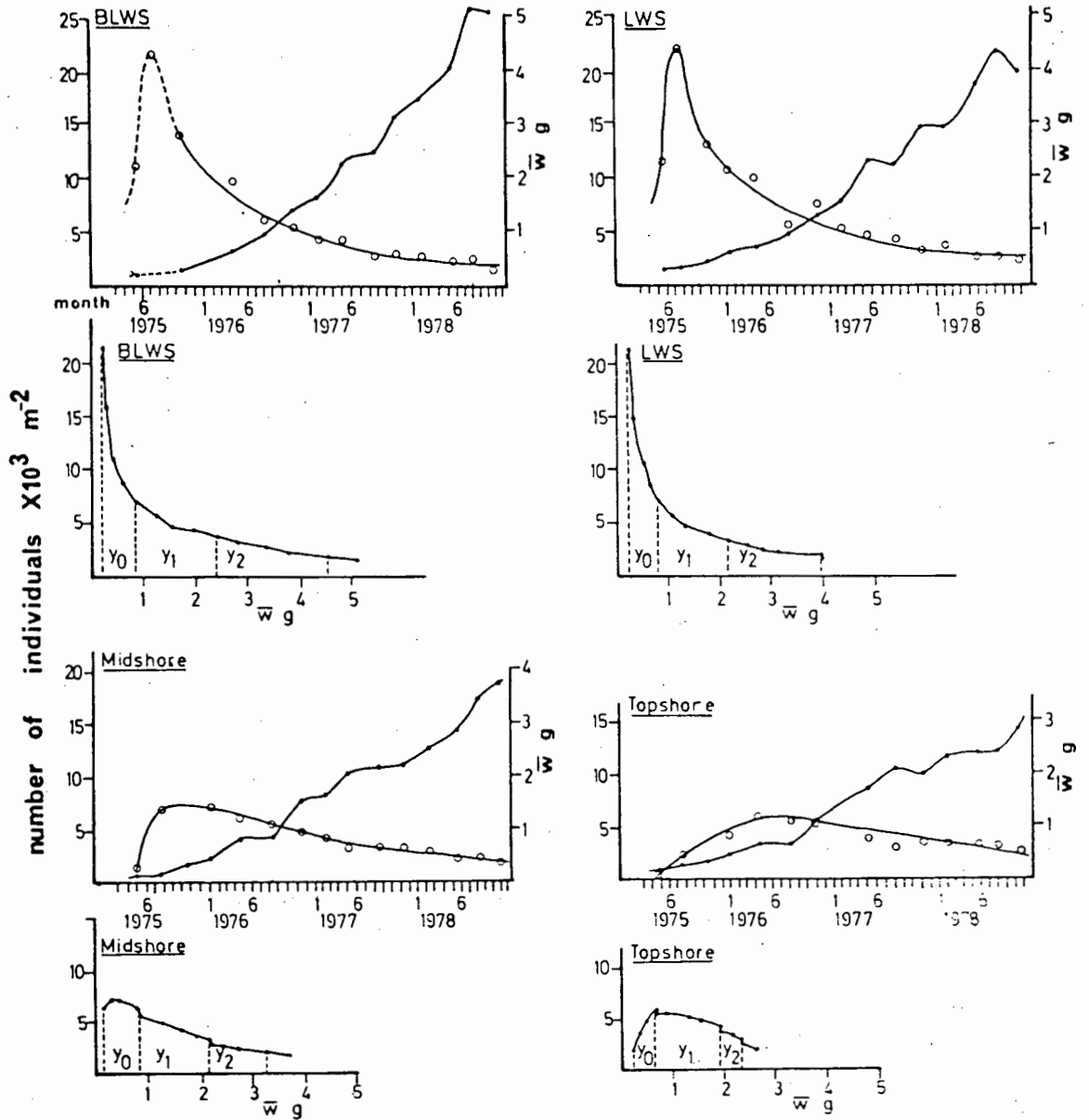


Fig. 3. Survivorship and Allen curves for cohort 2 *C. meridionalis* at different shore levels at Bailey's Cottage. Allen curves subdivided to give production for three years, Y_0 - Y_2 . Open circles-numbers, closed circles-mean weight per individual.

Table 2. Mean annual biomass, production, respiration and energy flow in a *C. meridionalis* population at Bailey's Cottage. Data expressed as dry weight and energy equivalents (\bar{B} and P_g include shell and byssus weight).

	length mm	\bar{B} Kg m ⁻²	P_g g	P_r g	kJ x 10 ³ m ⁻² y ⁻¹				
					\bar{B}	P_g	P_r	R	A
<u>Topshore</u>									
Y ₀ cohort 1	58	5.8	-	571.7	14.8	-	12.9	43.3	56.2
cohort 2	12-23	2.1	1737.9	167.1	5.5	4.4	3.8	30.9	39.1
Y ₁ cohort 1	57	2.3	-	116.2	5.8	-	2.6	8.7	11.3
cohort 2	23-33	5.1	6675.3	3344.0	12.9	17.0	75.2	72.4	164.7
Y ₂ cohort 1	-	-	-	-	-	-	-	-	-
cohort 2	33-34	6.5	1464.9	1297.9	16.5	3.7	29.2	66.9	99.9
<u>Midshore</u>									
Y ₀ cohort 1	59	4.6	-	484.4	11.8	-	10.9	37.2	48.1
cohort 2	15-26	3.0	5730.3	298.9	7.7	12.1	6.7	68.9	87.7
Y ₁ cohort 1	56.5	0.8	-	36.0	1.9	-	0.8	1.5	2.3
cohort 2	26-35	6.3	5960.4	3201.4	16.2	15.2	72.0	95.0	182.2
Y ₂ cohort 1	-	-	-	-	-	-	-	-	-
cohort 2	35-40	7.0	2726.7	1234.7	17.9	7.0	27.8	78.4	113.1
<u>LWS</u>									
Y ₀ cohort 1	60	2.2	-	275.7	5.6	-	6.2	22.5	28.7
cohort 2	17-25	5.4	6614.6	460.4	13.8	16.9	10.4	133.4	160.6
Y ₁ cohort 1	66	0.7	-	15.8	1.7	-	0.4	2.4	2.8
cohort 2	25-35	7.4	6595.7	3619.1	18.8	16.8	81.4	110.2	208.5
Y ₂ cohort 1	-	-	-	-	-	-	-	-	-
cohort 2	35-42	8.6	4834.3	1246.8	22.0	12.4	28.1	96.2	136.6
<u>BLWS</u>									
Y ₀ cohort 2	17-26	5.7	6970.1	462.0	14.6	17.8	10.4	110.4	138.6
Y ₁ cohort 2	26-38	7.7	7883.5	3558.6	19.7	20.1	80.1	101.5	201.7
Y ₂ cohort 2	38-49	8.6	5964.2	1272.4	22.0	15.2	28.6	85.8	129.6

in Y_1 may be attributed to the fact that the mussels were still in the exponential growth phase with \bar{w} (mean individual weight) increasing rapidly while densities remained relatively high at all shore levels. Production in Y_2 declined as a result of the lower mussel densities measured at all shore levels. Projection of P_g beyond Y_2 would have shown a further decline in growth production due to increased mortality in cohort 2 resulting from a new settlement, a third cohort, upon the existing population.

The method used for calculating population reproductive output is illustrated in Table 3 and the results for the different shore levels are shown in Table 2. Reproductive effort in cohort 1 was a significant proportion of production during Y_0 in the upper shore levels. This reflects the higher density of large mussels near the upper limits of the mussel bed during that year. P_r in cohort 2 during Y_0 was low because sexual maturity was only attained in the last few months of the breeding season of that year. During Y_1 (1976 - 1977) gamete production was unusually high in the smaller sized mussels (Griffiths, 1980a). As in growth production, maximum reproductive effort occurred at LWS and BLWS with $P_r = 3.6 \text{ kg m}^{-2}$ or 81430 kJ m^{-2} .

A maximum total population production ($P_g + P_r$) of $100 \times 10^3 \text{ kJ m}^{-2}$ was found at BLWS in Y_1 . Table 4 shows reproductive effort as a percentage of production, and the

Table 3. Calculation of population gamete production for Y_1 in Topshore mussels (July 1976-June 1977). Breeding season divided into sectors, 1= July-Oct., 2=Nov.-Feb.. Regression equations $y=ax^b$ where y =wet flesh wt. in grams, x =shell length in mm.

	female			male		
	a	b	r^2	a	b	r^2
July	1.463×10^{-2}	1.466	.83	1.857×10^{-4}	2.494	.88
August	1.886×10^{-5}	2.999	.79	6.899×10^{-6}	3.268	.88
September	3.628×10^{-3}	1.842	.89	2.867×10^{-3}	1.916	.85
October	9.563×10^{-2}	1.076	.29	2.855×10^{-5}	2.969	.42
November	1.966×10^{-4}	2.488	.94	4.292×10^{-2}	1.219	.66
December	6.673×10^{-4}	2.232	.90	4.585×10^{-4}	2.310	.96
January	9.106×10^{-4}	2.157	.90	2.452×10^{-4}	2.459	.96
February	2.936×10^{-4}	2.423	.94	7.334×10^{-5}	2.765	.90
		female	male	mean gamete loss	density m^{-2}	population gamete output (g)
<u>Sector 1</u>						
mean shell length (mm)		26.56	26.56			
flesh wt. (g) in:						
July		1.794	0.661			
Aug.		0.352	0.176			
Sept.		1.526	1.538			
Oct.		<u>3.263</u>	<u>0.483</u>	1.494	5680	8468.9
Σ weight decline between months		1.442	1.540			
<u>Sector 2</u>						
mean shell length (mm)		28.99	28.99			
flesh wt. (g) in:						
Oct.		3.263	0.483			
Nov.		0.856	2.603			
Dec.		1.224	1.142			
Jan.		1.300	0.968			
Feb.		<u>1.026</u>	<u>0.810</u>	2.237	5070	11341.6
Σ weight declines		2.681	1.793			
g total wet wt. gametes released m^{-2} in $Y_1 = 19810.5$						

Table 4. Population production and assimilation in cohort 2
C. meridionalis

	$\frac{P_r}{P} \times 100$	$\frac{P_g}{A} \times 100$	$\frac{P_r}{A} \times 100$	$\frac{P}{A} \times 100$	$\frac{R}{A} \times 100$	$\frac{P}{B}$
Topshore:						
Y ₀	45.9	11.3	9.6	20.9	79.1	1.50
Y ₁	81.5	10.3	45.7	56.0	44.0	7.15
Y ₂	88.6	3.7	29.2	32.9	67.1	1.99
Midshore:						
Y ₀	35.8	13.7	7.7	21.4	78.6	2.44
Y ₁	82.6	8.3	39.5	47.8	52.2	5.40
Y ₂	79.9	6.1	24.5	30.6	69.4	1.94
LWS:						
Y ₀	38.0	10.5	6.4	16.9	83.1	1.97
Y ₁	82.9	8.1	39.1	47.2	52.8	5.22
Y ₂	69.5	9.0	20.5	29.5	70.5	1.84
BLWS:						
Y ₀	36.9	12.8	7.5	20.3	79.7	1.93
Y ₁	79.9	9.9	39.7	49.6	50.4	5.14
Y ₂	65.3	11.7	22.1	33.8	66.2	1.99

turnover ratio, in cohort 2. Reproductive effort averaged 38% in Y_0 and 79% in Y_1 and Y_2 . The highest turnover ratio was found in the topshore sample at 7.2 in Y_1 , but was also high at other shore levels during that year (≈ 5.2). During Y_0 and Y_2 the turnover ratio averaged 2.0.

Respiration and Assimilation

The method used to calculate population respiration is shown in Table 5 and the results are given in Table 2. Population respiration was influenced by density and was greatest at LWS during Y_0 , when respiration of cohort 1 and cohort 2 was 155800 kJ m^{-2} . The energetic cost of respiration was generally high throughout the sampling period. Aerial respiration in littoral *C. meridionalis* has been found to reduce the respiratory cost below that of sublittoral mussels (Griffiths, 1980c). During Y_2 when mussel densities were much the same at all sampling stations, the declining size and longer periods of aerial respiration with increasing shore height, combined to produce the trend towards a lower respiratory cost in the upper littoral.

Respiration accounts for a considerable proportion of energy flow. In cohort 1 it contributed 77% of energy flow in Y_0 , and in cohort 2, approximately 80% in Y_0 , 50% in Y_1 and 68% in Y_2 . Whereas P_g in cohort 2 averaged 10% of assimilation throughout the sampling period, P_r varied

Table 5. Population respiration calculations for *C. meridionalis* cohort 2 at Topshore during Y_0 = July 1975 - June 1976. Exposure time in air 28.5%.

Regression equations $y = ax^b$ where $y = \mu\text{l O}_2$ consumed h^{-1} , $x = \text{mm shell length}$.

				a	b	r^2	n
Aerial respiration at 12°C and 18°C				0.0441	1.64	0.73	76
Winter sea temperature 12°C				0.2631	1.66	0.88	13
Summer sea temperature 18°C				0.6569	1.66	0.74	23
month	sea temperature °C	mean length mm	mean density no m^{-2}	mls O_2 mussel $^{-1}$ month $^{-1}$ in water	mls O_2 mussel $^{-1}$ month $^{-1}$ in air	total mls O_2 mussel $^{-1}$ month $^{-1}$	population respiration mls O_2 month $^{-1}$
J	12	12.5	2400	9.58	0.57	10.15	24360
A	12	14.0	2200	11.44	0.69	12.13	26686
S	18	15.8	2000	32.96	0.84	33.80	67600
O	18	17.1	1880	38.30	0.95	39.25	73790
N	18	18.4	2680	43.26	1.03	44.29	118697
D	18	19.5	3380	47.88	1.19	49.07	165857
J	18	20.4	4080	51.07	1.27	52.34	213547
F	18	21.2	4700	49.49	1.19	50.68	238196
M	12	21.8	5300	23.98	1.36	25.30	134090
A	12	22.7	5840	24.98	1.46	26.44	154410
M	12	22.9	5780	26.07	1.53	27.60	159528
J	12	23.1	5720	25.75	1.49	27.24	155813
Total ml O_2 y^{-1} =						1532574	
Total kJ y^{-1} =						30943	

from 6 - 40%. In fully mature mussels during Y_1 and Y_2 it averaged 32% of assimilation. Energy flow or assimilation was maximal at the lower sampling stations during Y_1 when $A = 211100 \text{ kJ m}^{-2} \text{ y}^{-1}$. Average figures for the 4 sampling sites in each year were $Y_0 = 140000$, $Y_1 = 193000$ and $Y_2 = 120000 \text{ kJ m}^{-2} \text{ y}^{-1}$.

Energy budget

Energy budgets for the C. meridionalis population (cohort 1 + cohort 2) for the 3 year sampling period at the Topshore and BLWS shore levels are shown in Table 6. In the present study, consumption is regarded equal to filtered ration and is not the same as ingestion ration. A considerable proportion of the filtered ration may be rejected as pseudo-faeces before entering the mouth. Widdows et al. (1976) have also shown that a considerable proportion of the ingested ration may be rejected as undigested faeces. Thus a large quantity of the energy available as food in the water column is concentrated by the mussels and released as faeces and pseudofaeces. Table 6 shows that this represents an annual average of 80% of consumption in the upper littoral zone and 85% in the sublittoral. It is probable that some of this is recycled to the mussel population through degradation by wave action and sand abrasion. Of the remaining food filtered, an average of 1%, 7% and 12% is used for growth, reproduction and respiration respectively at Topshore and 2%, 4% and 9% in the sub-

Table 6. Energy budget for *C. meridionalis* population at BLWS and Topshore.

C=filtered ration, P_g =growth production, P_r =reproductive output, (F+U)= faeces, pseudofaeces and urine. Values given as $\text{kJ m}^{-2} \text{y}^{-1}$.

	C	=	P_g	+	P_r	+	R	+	(F+U)
<u>BLWS:</u>									
Y_0	1296569	=	17773	+	10395	+	110403	+	1157998
Y_1	1049747	=	20102	+	80069	+	101492	+	848084
Y_2	846794	=	15208	+	28629	+	85797	+	719860
average	1064370	=	17694	+	39698	+	99231	+	908647
<u>Topshore:</u>									
Y_0	616153	=	4431	+	16623	+	74253	+	520850
Y_1	648006	=	17022	+	77855	+	81066	+	472063
Y_2	534070	=	3735	+	29203	+	66936	+	434196
average	599410	=	8396	+	41227	+	74085	+	475703

littoral.

The energy loss in mortality, gametes and faeces, pseudofaeces and urine is shown in Table 7. The greater percentage of this is represented by F + U. Mortality is compared with the other categories. Calculations of mortality were based on the energy value of the whole mussel of which 1% represents the energy content of byssus and 34.4% the shell organic matrix. These will not be available as an energy source to most scavengers, predators and decomposers. The energy available to other trophic levels in the form of flesh only is $3540 \text{ kJ m}^{-2} \text{ y}^{-1}$ and $10033 \text{ kJ m}^{-2} \text{ y}^{-1}$ at Topshore and BLWS respectively. An average of 87% at topshore and 91% at BLWS of the annual energy consumption is lost to other consumers.

Discussion

Production calculations for different sized individuals are useful in eco-physiological comparisons between species and in the assessment of rates of energy flow for commercial cultivation studies. Although absolute production figures in similar sized C. meridionalis will vary with habitat and food availability, the turnover ratio and percentage of production represented by reproductive effort are likely to vary less in sublittoral than littoral populations.

Comparison of production by individual C. meridionalis

Table 7. Mean annual ($Y_0 - Y_2$) loss from the C. meridionalis population (cohort 1 + cohort 2) at Bailey's Cottage as kJ m^{-2} released to other consumers.

	Mortality	Gametes	F + U
BLWS	15531	45128	908647
Topshore	5479	40815	475703

with that of Aulacomya ater (Griffiths & King, 1979) the dominant bivalve species on rocky substrates on the west coast of South Africa, shows that A. ater has higher absolute values for P_g . The turnover ratios in small mussels are also very high, being 29 in 5 mm and 9 in 15 mm mussels, declining to 0.8 in 85 mm individuals. In both species maximal growth production occurs at ~ 60 mm, which would probably be the harvesting size for commercial exploitation. Although C. meridionalis attains this size within 1 year on the west coast (Griffiths, 1980a), A. ater takes 6 years, making it a less commercially viable species.

In C. meridionalis P_r is a significantly high proportion of total production. This is consistent with the high fecundity and energetic cost of reproduction common in planktotrophic species. Reproductive effort accounts for 61 - 97% of production in C. meridionalis, and 25 - 80% in A. ater (Griffiths & King, 1979). The percentage contributed by reproductive effort increases with increasing size and the declining growth rate. Bayne (1976) has summarised reproductive effort as a percentage of production in several bivalve species. The values for gamete production are high and vary with age from 8 - 94%.

Population production, respiration and assimilation have been summarised in Fig. 4. Although cohort 1 contributed significantly towards energy flow in the upper

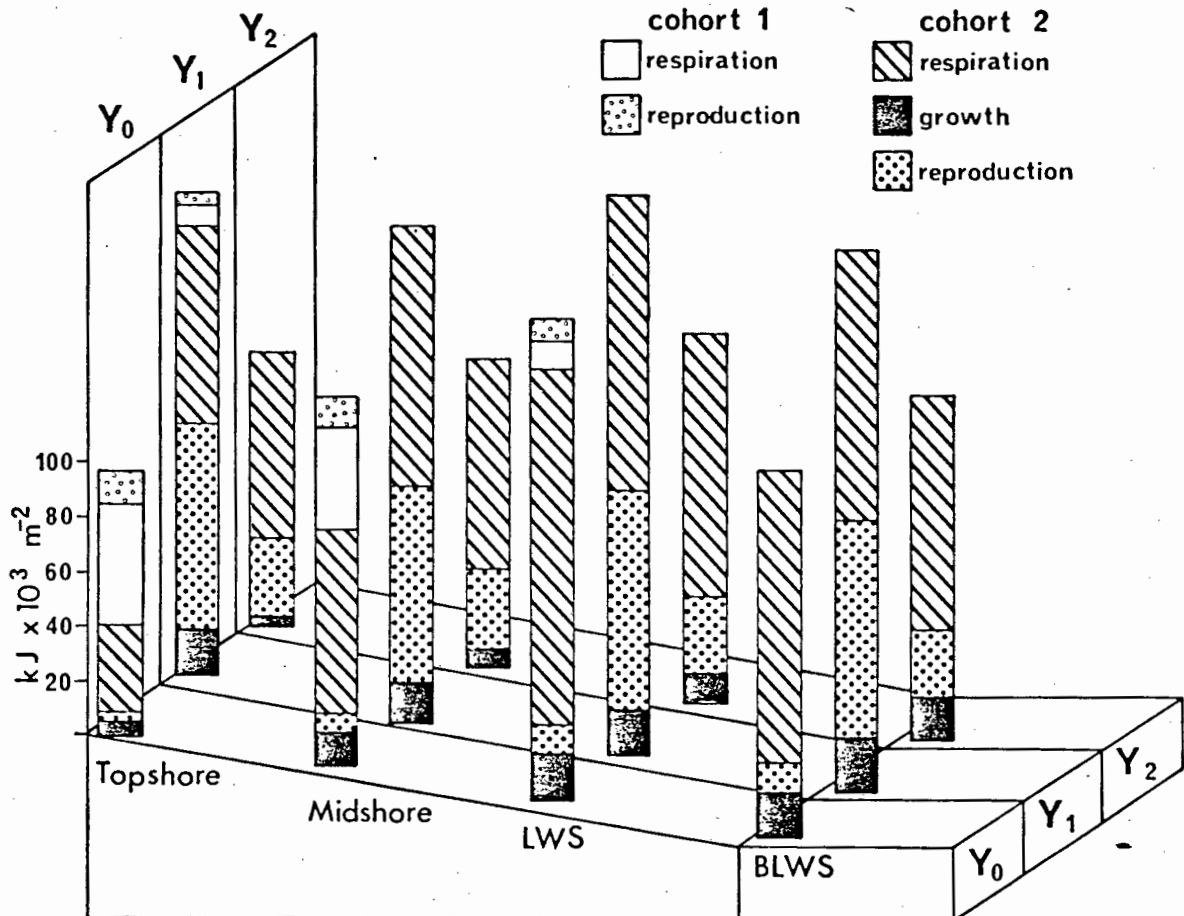


Fig. 4. Production and assimilation at different shore levels in a *C. meridionalis* population over a period of three years.

shore levels in Y_0 and Y_1 , maximal energy flow took place in the sublittoral and LWS in Y_1 and cohort 2 contributed most of this. Mussels in Y_2 showed a marked increase in size in all except the Topshore samples, however the decline in density (Fig. 3) produced a lower energy flow at all shore levels. Both P_g and P_r are consistently higher in the lower shore areas, a result of faster growth rates and higher densities. Maximum growth and reproductive effort occurred in Y_1 when cohort 2 was 25 - 35 mm shell length. However, the trend towards higher productivity in lower shore areas changes in an adult population once a new cohort settles upon it. With the resultant gradual elimination of the older cohort from the sublittoral upwards, production in this cohort increases with increasing shore height (cohort 1 in Fig. 4). This would not apply to areas where mosaic populations occur and discrete groups of adult and juvenile mussels form the mussel bed. Such population structures are common in some areas on the west coast of South Africa. Although data are lacking, this type of population structure in C. meridionalis appears to be common of areas where more frequent, but less dense, settlement occurs.

Estimation of gamete output in bivalves is difficult and data presented for C. meridionalis may be biased by such factors as possible variation in somatic or adductor weight during the year, or less frequent spawning in higher shore mussels. However, the volume of the gonad is suffic-

iently great compared with the remaining somatic tissue to make variations in the latter insignificant compared with the large volume of gametes produced in a single spawning. M. edulis may lose up to 80% or more of the gonad weight in one spawning and the gonad may form 50% or more of the body weight (Thompson, 1979). C. meridionalis is similar in this respect and unpublished laboratory observations show that up to 1/3 of the body weight may be lost during a single spawning. However, in the field even larger quantities may be lost through repetitive spawning interspersed with gonad regeneration (Griffiths, 1977). Even if fecundity has been overestimated by 50% in higher littoral mussels, P_r still forms a major component of production.

Table 8 shows comparative data for several bivalve species where, in addition to P_g , values for P_r and A are available. Actual values for production and energy flow have been converted to $\text{kJ m}^{-2} \text{y}^{-1}$ and percentages. The data vary according to population age structure, growth rates and densities and reflect conditions pertinent to each species in the habitat in which it was measured. Both P. perna and C. meridionalis occur in greater densities with a larger mean biomass and faster growth rates than the remaining species listed. Thus higher values for production and energy flow may be expected. Maximum production was measured in a P. perna population consisting of several rapidly growing newly settled cohorts and one or two older cohorts averaging 77 - 116 mm shell length.

Table 8. Comparison of production and energy flow in some bivalve populations. Units expressed in $\text{kJ m}^{-2} \text{y}^{-1}$.

*energy in shell and byssus included, + based on flesh weight only

P_r	P_g	P	\bar{B}	P/\bar{B}	$\frac{P_r}{P} \times 100$	A	$\frac{P}{A} \times 100$	Species and source of reference
11.7	58.1*	69.8	89.9	0.8*	16.8	234.1	29.0	<u>Modiolus demissus</u> Kuenzler 1961
17.6	55.6*	73.1	28.0	2.6*	24	301.4	24.3	<u>Scrobicularia plana</u> upper shore, Hughes 1970
267.5	250.8*	518.3	167.2	3.1*	52	3206.9	20.7	" " lower " " "
26.6	29.3*	55.9	-	-	48	134.2	29.5	<u>Ostrea edulis</u> beds 2 & 3, Rodhouse 1979
255.0	300.0*	555.0	767.3	0.7*	46.0	1563.3	35.5	<u>Mercenaria mercenaria</u> 8 cohorts, Hibbert 1977
2098.0	42.0	2140.0	4891.0	0.4	45.5	4242.0	50.0	<u>Crassostrea gigas</u> mature, Bernard 1974
2804.8	14466.9 ⁺	17271.8	8573.2	2.1 ⁺	16.2	40913.8	42.0	<u>Crassostrea virginica</u> , Dame 1976
15757.0	107216.0*	122973.0	17263.0	4.3 ⁺	12.8	-	-	<u>Perna perna</u> 9-71 mm cohort 2, Berry 1978
12396.0	14993.0*	27389.0	10385.0	0.8 ⁺	45.3	-	-	" " 85-112, cohort 1, Berry 1978
28153.0	130795.0*	158948.0	63248.0	2.5*	18.0	-	-	" " Y_1 , Berry, 1978
24166.0	152512.0*	176678.0	27431.0	6.4*	13.7	-	-	" " Y_2 , Berry, 1978
10395.0	17773.0*	28168.0	14601.0	1.9*	37.0	13857.0	20.3	<u>C. meridionalis</u> BLWS 17-26 mm Y_0 , this study
80069.0	20102.0*	100171.0	19503	5.1*	80.0	201660.0	49.6	" " " 26-38 mm Y_1 , " "
28629.0	15208.0*	34837.0	22006.0	2.0*	65.0	129630.0	33.8	" " " 38-49 mm Y_2 , " "

Production measured $158948 \text{ kJ m}^{-2} \text{ y}^{-1}$ in Y_1 and $176678 \text{ kJ m}^{-2} \text{ y}^{-1}$ in Y_2 . Values for P_r in P. perna are high, but the percentage reproductive effort is low because of the rapid growth rate in this species. P_r as a percentage of P varies among the species, but it should be borne in mind that this will alter according to the age structure of the population at the time of sampling.

Assimilation or energy flow and net growth efficiency ($\frac{P}{A} \times 100$) are high in Crassostrea virginica and C. meridionalis, and would probably be greatest in P. perna if data were available. These bivalves form very dense populations and represent maximum energy flow measured in bivalve species. In comparison of net growth efficiency among species, considerable variation may be expected due to the fact that P includes an estimate of gamete production. Many authors have failed to measure P_r and thus an underestimate of growth efficiency would result. Values of P_r may vary considerably according to the reproductive activity of the species measured. Spawning in the South African mytilids C. meridionalis, P. perna and A. ater extends over several months (average 7, 8 and 5 months respectively) with successive peaks of spawning and gonad regeneration (Griffiths, 1977; Berry, 1978; Griffiths & King, 1979). Thus the energy utilised in reproductive effort and hence net growth efficiency is considerably greater than of northern hemisphere bivalves where P_r is based upon a

single spawning lasting 1 to 2 months (remaining species listed in Table 8). Annual population energy flow in C. meridionalis is in some years 5 fold greater than that previously measured in a bivalve species.

Data presented here for C. meridionalis illustrate how production and energy flow may vary with shore height. Variability in annual fecundity, and increasing fecundity with increasing age coupled with a declining growth rate, are all factors which influence production and net growth efficiency. Thus data obtained over an annual cycle for species where a stable multicohort population covering all size classes exists at the time of sampling, may be expected to give a reasonable estimate of average production values. However, data obtained over only one year should be approached with caution. This is of particular importance in measuring an unstable, rapidly growing population containing few cohorts. Data for C. meridionalis illustrate the variability which may be obtained and the fact that measurements for more than one year are required for a reasonable estimate of production and energy flow.

Values obtained in energy flow studies may be compared with the energy available as a food source to the population in the natural environment. Few studies have involved such comparisons. However, Bernard (1974) and Widdows et al. (1979) have demonstrated that only a

small fraction of the energy available is actually assimilated. A large proportion of the food processed in filter feeders is concentrated and rejected as pseudo-faeces and undigested faeces (Haven & Morales-Alamo, 1966). In sublittoral C. meridionalis assimilation requirements represent 15% of the energy content of the food which may be filtered from seawater, the rest being eliminated. The average value of energy released by sublittoral C. meridionalis in the form of population mortality, reproductive output and faeces and pseudofaeces represented 91% of that consumed per metre² per year. In Mercenaria mercenaria Hibbert (1977) found an energy transfer of 73% of consumption to other consumers. Thus although C. meridionalis may have high energy demands in the form of growth, reproduction and metabolism, a major portion of the energy in suspension is concentrated and released to filter and deposit feeders.

Acknowledgements

My thanks are due to various student assistants, in particular Miss F. Stratton. Prof. G.M. Branch and Prof. J.G. Field provided constructive criticism of the manuscript. This work was supported as part of the Kelp Bed Research Programme by the South African National Committee for Oceanographic Research.

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CONCLUSIONS

CONCLUSIONS

In addition to the detailed discussions in the preceding papers, several general conclusions may be drawn from this study. The data presented form a comprehensive background to knowledge of the ecology of C. meridionalis and may be useful in several respects.

Experiments involving measurement of the physiological responses and energy balance of C. meridionalis have application not only to an understanding of the ecophysiology of this species, but to future research involving laboratory maintenance, aquaculture and pollution monitoring. Choromytilus meridionalis maintains a positive scope for growth over a wide range of algal ration levels ($2-30 \times 10^6$ cells l^{-1} ; up to $3.4 \text{ mg } l^{-1}$ dry wt.). However, because the filtration rate remains unaffected by temperature while the respiration rate increases markedly, the positive scope for growth declines with rising temperature. Unless some form of compensation occurs, sea temperature may be a limiting factor in distribution. Seiderer & Newell (1979) have shown adjustment in the α -amylase activity of the crystalline style in response to increase in temperature. This may affect assimilation efficiency, but requires more detailed investigation.

As shown by several authors for other bivalve species, phytoplankton do not appear to form a major part of the diet

of C. meridionalis in the field. Furthermore a positive assimilation efficiency is maintained at ration levels considerably above those at which it falls to zero on a pure algal diet. It is not known whether this results from a different method of mechanical handling of the food in the field and the presence of large quantities of inorganic particles, a combination of 'dilution' of the organic matter with inorganic material and the onset of pseudofaeces production, or is a function of the nature and digestibility of the particulate matter. The experiments presented here indicate that a more detailed study of the nature of the food source in the field and of the feeding processes is required.

Choromytilus meridionalis shows maximal growth in the sublittoral. Aerial exposure limits the feeding time and hence energy input, and growth declines with increasing shore height. Respiration in air is 11% of that in water and has been shown to afford considerable saving in metabolic expenditure during exposure at low water. This leaves scope for growth and reproduction in littoral mussels, although at a reduced rate. The energy flow through the littoral population is, however, considerably lower than that in the sublittoral.

Comparison of data obtained from C. meridionalis with that of A. ater (Griffiths & King, 1979a & b) shows that whereas C. meridionalis grows considerably faster in length

it does not do so on a weight basis. A. ater are wider and consequently similar sized individuals are considerably heavier than C. meridionalis. The growth curves, and thus the rates of growth based on shell length, differ in the two species. However, the growth rate of C. meridionalis on the West coast approximates that of P. perna on the East coast (Berry, 1978). The filtration and respiration rates of A. ater are slower than those of C. meridionalis. However, when fed an algal diet, A. ater maintains a positive scope for growth over a considerably wider range of ration levels. The importance of these data related to the individual species in the field, is as yet uncertain, however they illustrate considerable physiological differences.

The high biomass and productivity of C. meridionalis make it an ecologically important, and in certain habitats, the dominant species in the marine sublittoral and littoral environment. Although confirmatory evidence is required, observations on this species, particularly on the West coast, indicate that it is an opportunistic species. It occurs predominantly in sand abraded rocky areas subject to denudation by storm action. The mussels are able to survive considerable sand deposition, and the larvae, which may be present in the water column throughout most of the year on the West coast (Du Plessis, 1977) rapidly recolonise denuded areas. The importance of C. meridionalis as a prey item in the diet of the commercially exploited rock-

lobster Jasus lalandii, has not been fully investigated. Although A. ater dominates the lobster feeding grounds, C. meridionalis forms extensive beds in some areas (Pollock, 1978) and is preferentially selected by J. lalandii (Griffiths & Seiderer, 1980). The latter authors have shown that predatory pressure is concentrated towards the smaller size classes of mussels and that these are usually overexploited. Compared with A. ater, C. meridionalis is more easily cracked and has a more rapid growth rate and population turnover time and this may be advantageous to the feeding of young lobsters. Griffiths & Seiderer (1980) suggest that predatory pressure may limit C. meridionalis distribution in areas of high lobster density.

The unpredictability and variation in intensity of spat settlement precludes the regular harvesting of C. meridionalis natural populations on a commercial basis (A. Du Plessis pers. comm.). Aquaculture may well require laboratory cultivation of larvae to settlement. The rapid growth rates and attainment of a marketable size within one year under optimal conditions, make both C. meridionalis and P. perna (Berry, 1978) viable species for cultivation. At present C. meridionalis are not heavily exploited as a food source. However, the infrequent spat settlements observed on the False Bay coast and at Hermanus make them vulnerable to overexploitation by man. The sublittoral stocks are at present probably sufficient to afford recruitment, although the littoral zone may be denuded

between spat settlements.

The reproductive season in South African mytilids extends over many months and in C. meridionalis on the West coast, appears to continue throughout most of the year (Du Plessis, 1977; Griffiths, 1977). Reproductive output is thus considerably higher than found in Northern Hemisphere bivalves. Although fecundity in C. meridionalis is variable from year to year, large quantities of gametes are nonetheless released each year. At Bailey's Cottage recruitment is not an annual event and gametes represent a vast energy resource, averaging $45 \times 10^3 \text{ kJ m}^{-2} \text{ y}^{-1}$ which is lost from the population. While spawning may produce recruitment in adjacent areas through transport of the larvae by currents, it has been estimated that 99% of gametes spawned do not reach settlement (Bayne, 1976). The extended spawning season and large volumes of gametes released, may thus be expected to afford an exploitable energy-rich food source for other trophic levels. Calculations of population production, assimilation and consumption has shown that a considerable proportion of the energy available in seawater in the form of particulate organic matter is concentrated by C. meridionalis and released in the form of faeces and pseudofaeces. While some of this may well be re-utilised by the mussels, it must also form a large potential food source for other consumers. Whereas production as growth and reproduction averaged $58 \times 10^3 \text{ kJ m}^{-2} \text{ y}^{-1}$ in the sublittoral at Bailey's Cottage, the average

annual loss of energy from the mussel bed was 970×10^3 kJ m⁻². The importance of this large energy flow through the mussel bed to other members of the marine community deserves further investigation.

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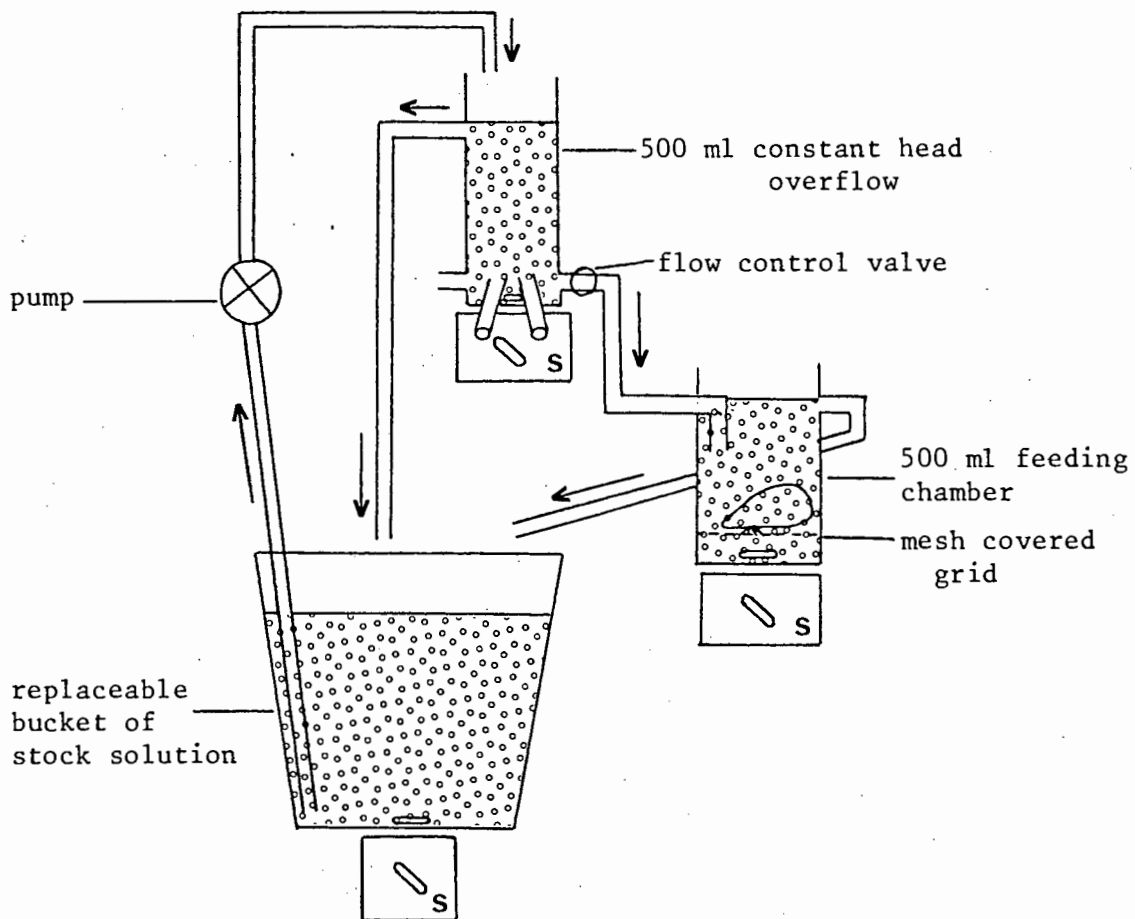
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APPENDIX 1.

DESIGN OF CONSTANT FLOW FEEDING APPARATUS

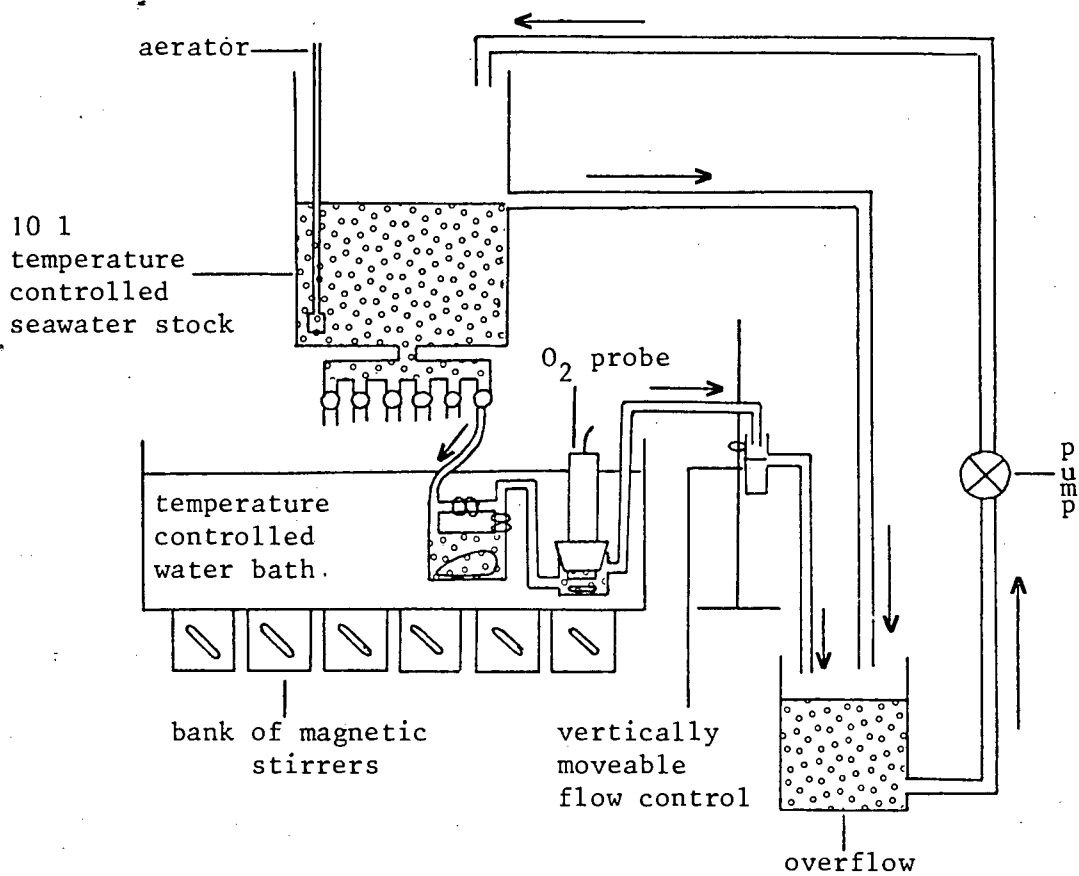
CONSTANT FLOW FEEDING APPARATUS



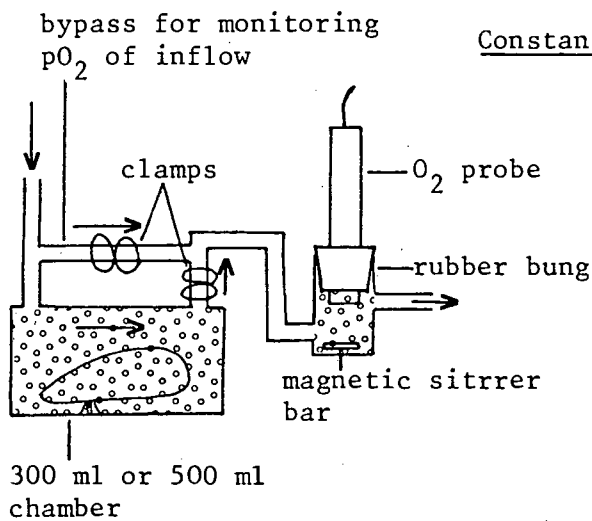
S = magnetic stirrer

APPENDIX 2.

RESPIROMETER DESIGN

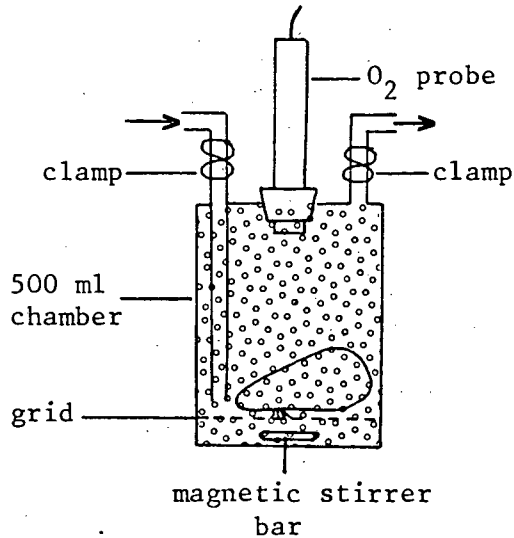


ALTERNATIVE RESPIROMETER CHAMBERS



Constant flow

Closed system but allowing flushing and replenishment with fresh oxygenated seawater



APPENDIX 3.

MEASUREMENT OF GILL AREAS

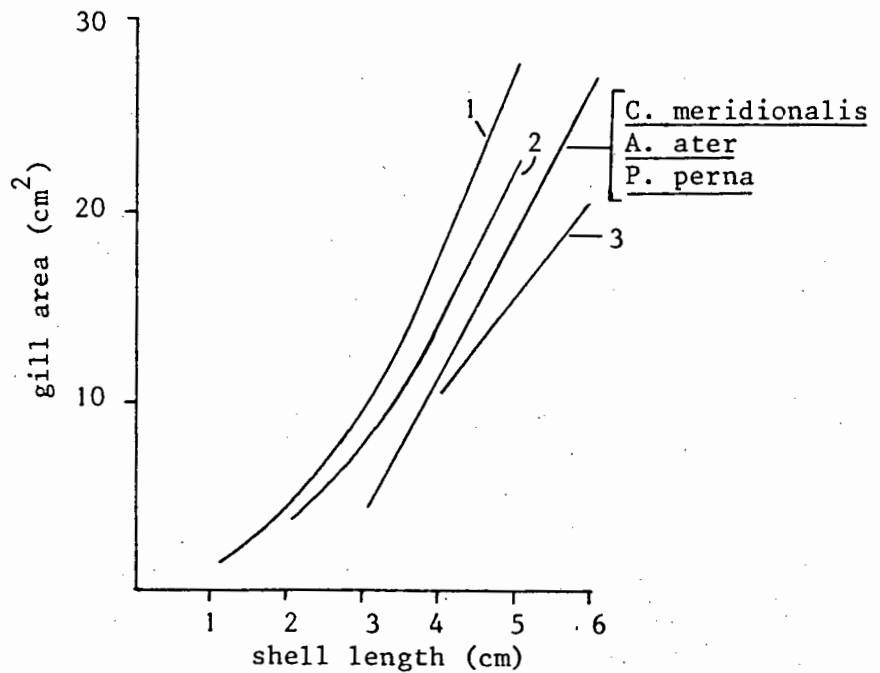
Measurement of the gill area of *C. meridionalis*, *A. ater*
and *P. perna*.

The gill area of different sized mussels of each of the above species was measured as follows. Individual mussels were submerged in fresh seawater and one valve of the shell and the mantle edge beneath this were removed. This exposed the surface of the outer demibranch and this was photographed together with a mm rule placed alongside. The shell length of the mussel was noted and the outer demibranch dissected away to expose the inner demibranch which was also photographed as above. Negatives obtained in this manner were placed in a photographic enlarger and the image projected onto graph paper. The outline of each gill was traced and the magnification of the mm rule noted and used to calculate the gill area from the graph paper. The inner and outer demibranchs differed in size and the areas obtained for each were summed and multiplied by four (this allowed for ascending and descending lamellae of each gill) to give the total gill area. Total gill area of each species was plotted against shell length and a regression equation (see overleaf) fitted to the data. Mussels less than 30 mm were not measured and a linear regression gave the best fit.

There was no significant difference in the data obtained from the three species and the relationship between area and shell length proved similar to that found in *M. edulis* (see overleaf).

Equations ($y=mx + c$) relating gill area in mm^2 to shell length in mm in C. meridionalis, A. ater and P. perna.

	m	c	r^2	n
<u>C. meridionalis</u>	90.89	-2562	0.98	20
<u>A. ater</u>	84.76	-2308	0.88	11
<u>P. perna</u>	79.0	-1968	0.95	14



Comparison of the relationship between gill area and shell length in Mytilus edulis and three South African mytilids. (1, Hughes, 1969; 2, Foster-Smith, 1975; 3, Dral, 1967 copied from Bayne et al. 1976)

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SUPPORTING PAPER - THE REPRODUCTIVE SEASON AND LARVAL

DEVELOPMENT OF THE BARNACLE TETRACLITA SERRATA

DARWIN.

THE REPRODUCTIVE SEASON AND LARVAL DEVELOPMENT OF THE BARNACLE *TETRACLITA SERRATA* DARWIN

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SUMMARY

The presence of embryos in the mantle cavity of *Tetraclita serrata* Darwin, and in *Octomeris angulosa* Sowerby and *Balanus maxillaris* Gronovius for comparison, has been monitored. In all species breeding extended over five to eight months, depending on the species. Breeding seasons showed slight variation annually. *T. serrata* nauplii were cultured on a diet of mussel eggs in the laboratory and the anatomical features of the different nauplius stages are described.

INTRODUCTION

The principal reference on breeding cycles and larval development of South African barnacles remains that of Sandison (1954), which followed Millard's (1952) description of barnacle settlement and fouling in Table Bay. No work has since been published on reproduction or larval development of local species. There remains a paucity of information regarding reproductive seasons of barnacles on different regions of the South African coast. Except for the cosmopolitan species *Balanus amphitrite* var. *denticulata* (Costlow & Bookhout 1958) no South African barnacle has been raised successfully beyond the third nauplius.

To augment the above data and to determine the times at which mature embryos could be obtained for experimental culture, the breeding seasons of *Balanus maxillaris* Gronovius, *Octomeris angulosa* Sowerby and *Tetraclita serrata* Darwin were examined. In addition the nauplius larvae of *T. serrata* were cultured to the cyprid stage. The descriptions given here augment those of the first two naupliar stages described by Sandison (1954). The only other species of *Tetraclita* in which larval development has been described is *T. purpurascens* from New Zealand (Barker 1976).

MATERIALS AND METHODS

(a) *Breeding cycles*

Barnacles were collected from Bloubergstrand, Table Bay on the west coast, and Dalebrook, False Bay, on the eastern side of the Cape Peninsula. The west coast is influenced by the Benguela upwelling system with summer temperatures of 10–12 °C and warmer winter temperatures of about 15 °C, while False Bay is influenced by the Agulhas current, with summer and winter sea temperatures of 18–20 °C and 13–15 °C respectively. *T. serrata* and *O. angulosa* are the dominant intertidal barnacles and are restricted to the balanoid zone of exposed rocky shores. These species were sampled in the mid-balanoid zone, 12–15 individuals being found sufficient to reflect the state of development of the majority of the population. Samples were collected at monthly intervals. Due to scarcity of

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specimens, *B. maxillaris* were sampled only at Dalebrook and 6–9 individuals were examined per month. This gave a rough estimate of the duration of the breeding season. *B. maxillaris* is the largest of the South African barnacles, predominantly sub-littoral but extending into the cochlear zone where it is usually solitary and averages 3 cm in height (Day 1969). Under favourable conditions in the sub-littoral zone this barnacle may form large clusters in which individuals average 10 cm or more in height.

After collection all individuals were opened and the mantle cavity examined for the presence of embryos, which were examined microscopically. Individuals were assigned to one of the categories recognized by Sandison (1954):

- Stage I. No embryos present in the mantle cavity
- Stage II. Embryos present in the mantle cavity, 2–16 celled stage
- Stage III. Embryos many celled with beginning of appendage buds
- Stage IV. Visible eye spot and distinct appendages with setae
- Stage V. Fully developed with gut giving a purplish black colour to the lamellae

The percentage of individuals assigned to each category was plotted for each monthly sample.

Settlement of *T. serrata* and *O. angulosa* in the field was monitored by clearing two adjoining areas, each 25 cm² (1/16 m²) in the mid-balanoid zone at Dalebrook. Newly settled barnacles of each species were counted at monthly intervals and the rock surfaces again cleared of all animals. Surveillance of adjacent densely populated rock surfaces showed that when barnacle settlement occurred in these areas simultaneous settlement took place in the cleared areas.

(b) *Larval development*

All sea water was filtered through Watmans No. 1 filter paper immediately prior to use. Finer filtration and sterilization were found unnecessary provided water was changed on alternate days. Lamellae with stage V embryos were placed in sea water with continuous aeration until stage I nauplii hatched—usually overnight. Larvae were then pipetted into 1 litre glass beakers so that each contained 600–800 nauplii. Cultures were maintained on various diets and water and food supply changed every one to three days depending on diet. Where necessary food was maintained in suspension by slow emission of large air bubbles (diam. 1 cm, 1–2/second) from the base of the vessel. This prevented collection of larvae on the light side of the vessel which would result in crowding and depletion of food in that area.

Several authors, including Moyse (1960, 1963), Tighe-Ford *et al.* (1970) and Barker (1976) have successfully cultured barnacle nauplii on high algal concentrations, and supplementary foods such as invertebrate eggs have been used by Costlow & Bookhout (1958). Preliminary experiments in rearing *T. serrata* on different concentrations of the flagellate *Dunaliella* and the diatom *Phaeodactylum* were unsuccessful and development beyond the third nauplius stage did

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not occur. Ova which were taken from a selection of intertidal invertebrates were then offered as food and nauplii were observed to grasp, pierce and ingest the contents of the eggs of the mussel *Choromytilus meridionalis* (Kr.). Nauplii were subsequently fed on a mixture of *Phaeodactylum* (50 000 cells/ml) and *Choromytilus* ova sieved to a size range of 45–70 μm (100 to 250 ova/ml). Stages III to VI nauplii could also survive on a pure egg diet.

Larvae were handled with a large bore pipette or a plastic siphon tube in preference to sieving, which may damage nauplii. Microscopic examination of nauplii was performed daily and when 50% had metamorphosed to the next naupliar stage a sample of healthy individuals was preserved in formalin for dissection. Drawings were done with the aid of camera lucida and phase contrast illumination.

RESULTS AND DISCUSSION

(a) Breeding season

Studies presented here and subsequent data indicate that the breeding season is variable annually. A similar phenomenon has been found in littoral mussels (Griffiths 1977) and limpets (Branch 1974), and is probably dependent on natural variation of environmental factors. Examination of lamellae in the mantle cavity occasionally showed the presence of two broods (stage II or III, and stage V embryos). Nauplii of the older brood were considerably fewer, and were frequently shrivelled and deformed, so that it is doubted that such individuals would hatch.

The presence of embryos in different stages of development in the mantle cavities of *T. serrata*, *O. angulosa* and *B. maxillaris* is shown in Figures 1 and 2. In *B. maxillaris* from False Bay, embryos were present from May to October but only in July and August were all sampled individuals brooding. Thus the peak reproductive period is probably confined to three or four months in late winter (July–September). Sandison (1954) found gonad activity in individuals from Table Bay in September and data from miscellaneous collections by colleagues confirm the absence of reproductive activity in summer and early winter (November–April). Little is known about this barnacle and the larval stages remain undocumented.

At Dalebrook in False Bay, *O. angulosa* stage V embryos were found from July 1974 to February 1975 when sampling ceased (Fig. 1). However, during the 1973/4 breeding season embryos were present until May. *Tetraclita serrata* showed a similar breeding pattern at Dalebrook. In July/August 1975 all individuals contained stage II embryos and from November to February 1975 stage V embryos were present with a peak of over 50% of individuals in stage V during January of both years (Fig. 1).

Octomeris and *Tetraclita* from the west coast were found to contain stages IV and V embryos between August and December 1974 (Fig. 2). However, in 1973 the breeding season ended later and extended into January. It is not known

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DALEBROOK

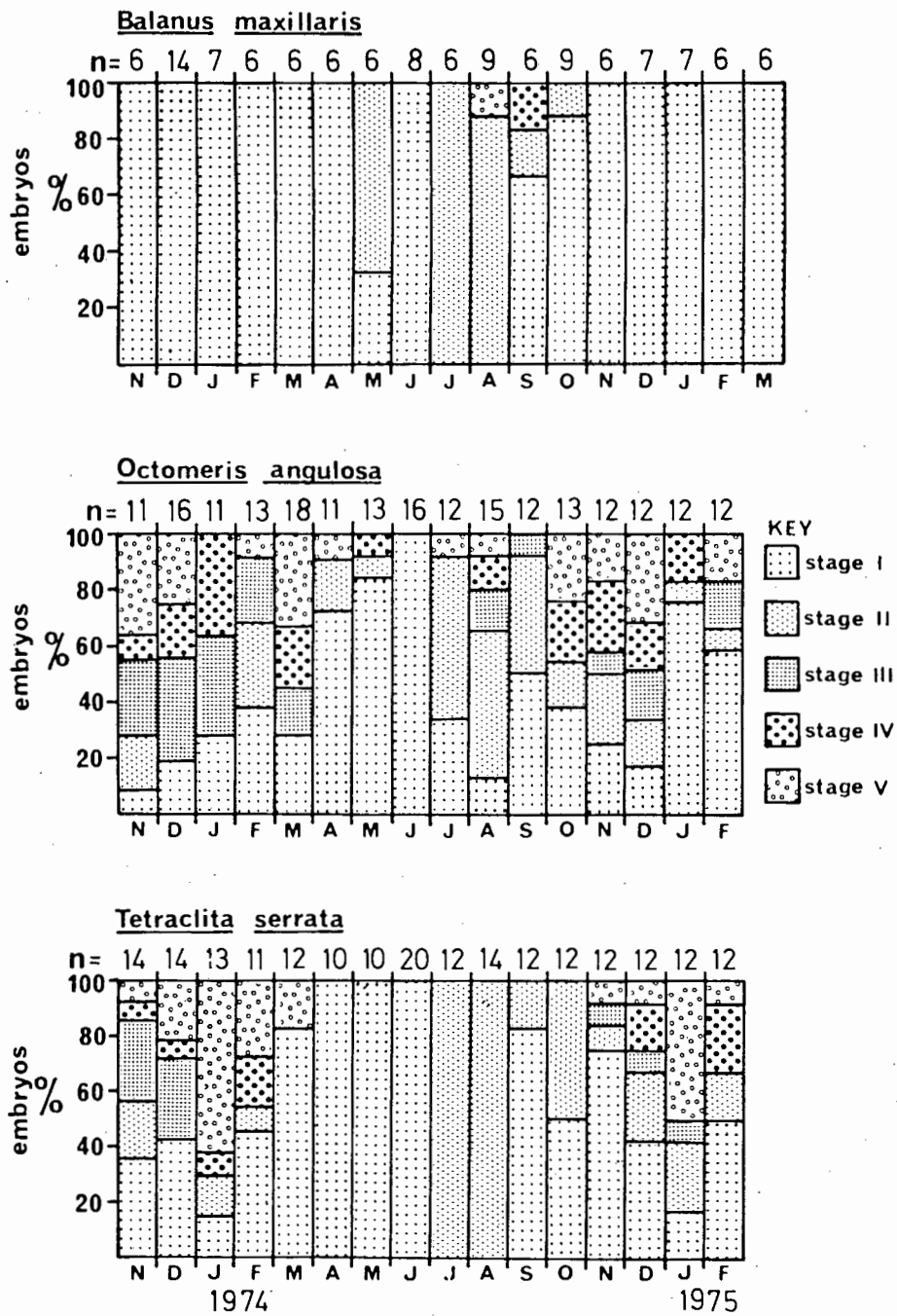


Fig. 1. The percentage of different developmental stages of embryos present in monthly samples of *B. maxillaris*, *O. angulosa* and *T. serrata* collected from Dalebrook, False Bay.

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sea temperature at commencement of the breeding season at both collection sites averaged 14 °C, conditions towards the end of the season differed markedly. At Bloubergstrand and Dalebrook sea temperatures were lowered and elevated respectively. The breeding season of *B. maxillaris* was restricted to a period of relatively stable sea temperatures. Conclusions regarding the factors influencing onset of breeding cannot be drawn until data such as the seasonal availability of food and the effect of air temperatures during tidal exposure are obtained.

Table 1.
Settlement of barnacles at Dalebrook. Mean number /m² from 2 cleared areas.

Year	1974								1975					
Month	M	J	J	A	S	O	N	D	J	F	M	A	M	J
<i>O. angulosa</i>	576	112	64	272	320	64	16	0	256	640	384	352	112	112
<i>T. serrata</i>	320	32	16	16	0	0	16	0	112	240	192	96	32	16

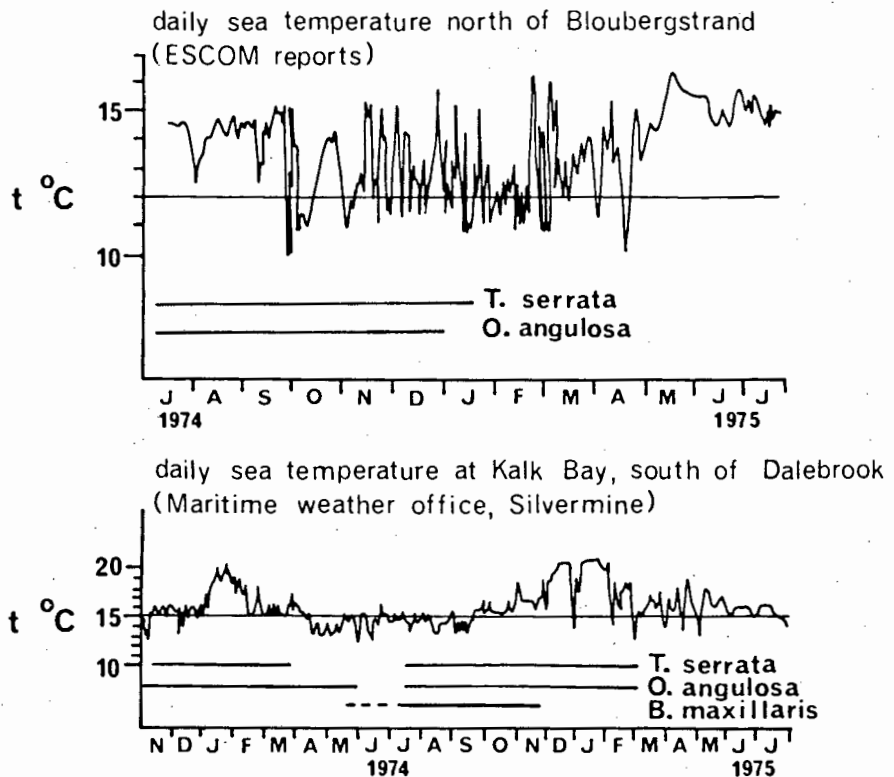


Fig. 3. Daily sea temperatures near the two collection sites and the duration of the breeding season of *B. maxillaris*, *O. angulosa* and *T. serrata*.

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(b) Larval development of T. serrata

Whereas characters such as shape and size of the carapace and the anteriorly directed fronto-lateral horns may be of value in distinguishing some of the naupliar stages of *T. serrata* from those of other South African species described by Sandison (1954), these characters are not distinctive in all cases. Due to the anatomical similarity of balanid nauplii there is no ready means of identifying species from a mixed plankton haul. The setation formulae of many species are similar (Knight-Jones & Waugh 1949; Costlow & Bookhout 1958) and the validity of this character in species identification has been questioned. None the less, when used in conjunction with carapace size and structure, shape of the labrum and spination of the abdominal process, it remains the only means of identifying species. Several methods of setal formulation have been developed, some being more informative of setal types (Bassindale 1936, Jones & Crisp 1954, Newman 1965), but until a standardized formula and, more important, the anatomical function of the different setal types, are recognized, detailed illustrations of limbs should not be replaced by formulae. There remains little information on the functions of the naupliar limbs in swimming and feeding. While the antennal and mandibular exopodites may not show intraspecific differences because they are primarily used in locomotion (Lockhead 1936), more detailed investigation of the setal types of the endopodites may reveal differences linked with diet. In *T. serrata* the endopodites show an unusual variety of stout setae bearing strong spines and serrated edges which may be used in piercing ova.

Norris & Crisp (1953) and Jones & Crisp (1954) recognized the usefulness of spination and relative lengths of the abdominal and caudal processes in distinguishing the six naupliar stages of most species. These features, together with the dimensions (Table 2) and shape of the carapace (Fig. 4) and the abdominal process (Fig. 5) enable separation of the naupliar stages of *T. serrata*. These may be summarized as follows:

Stage I. Fronto-lateral horns directed latero-posteriorly. Slightly elongate tapering body terminating in abdominal and caudal processes bearing minute

Table 2.
Mean carapace dimensions of laboratory cultured *T. serrata* compared with those of *T. purpurascens* (Barker, 1976).

Stage	<i>Tetraclita serrata</i> Mean Carapace length × width	<i>Tetraclita purpurascens</i> Carapace length × width
I	274 × 154	290-310 × 130-140
II	408 × 235	450-470 × 190-200
III	465 × 280	530-550 × 220-246
IV	360 × 350	330-350 × 240-260
V	420 × 378	430 × 330-340
VI	540 × 506	500-520 × 400-430
Cyprid	580.	550-580 × 240-260

(Length not inclusive of posterior spines in stages IV-VI)

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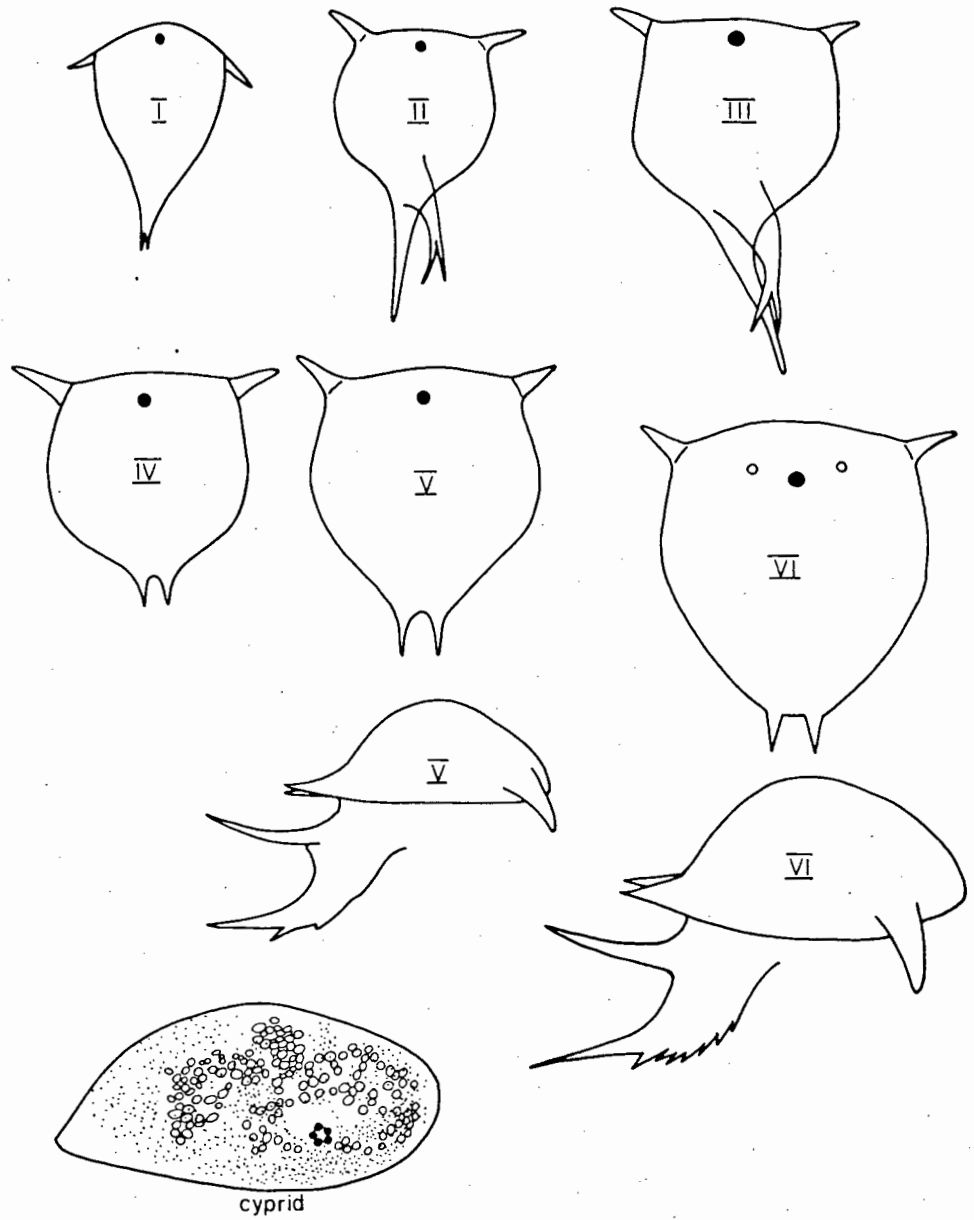


Fig. 4. Carapace outlines of *T. serrata* nauplius and cyprid stages.

TETRACLITA SERRATA - REPRODUCTIVE SEASON AND LARVAL DEVELOPMENT

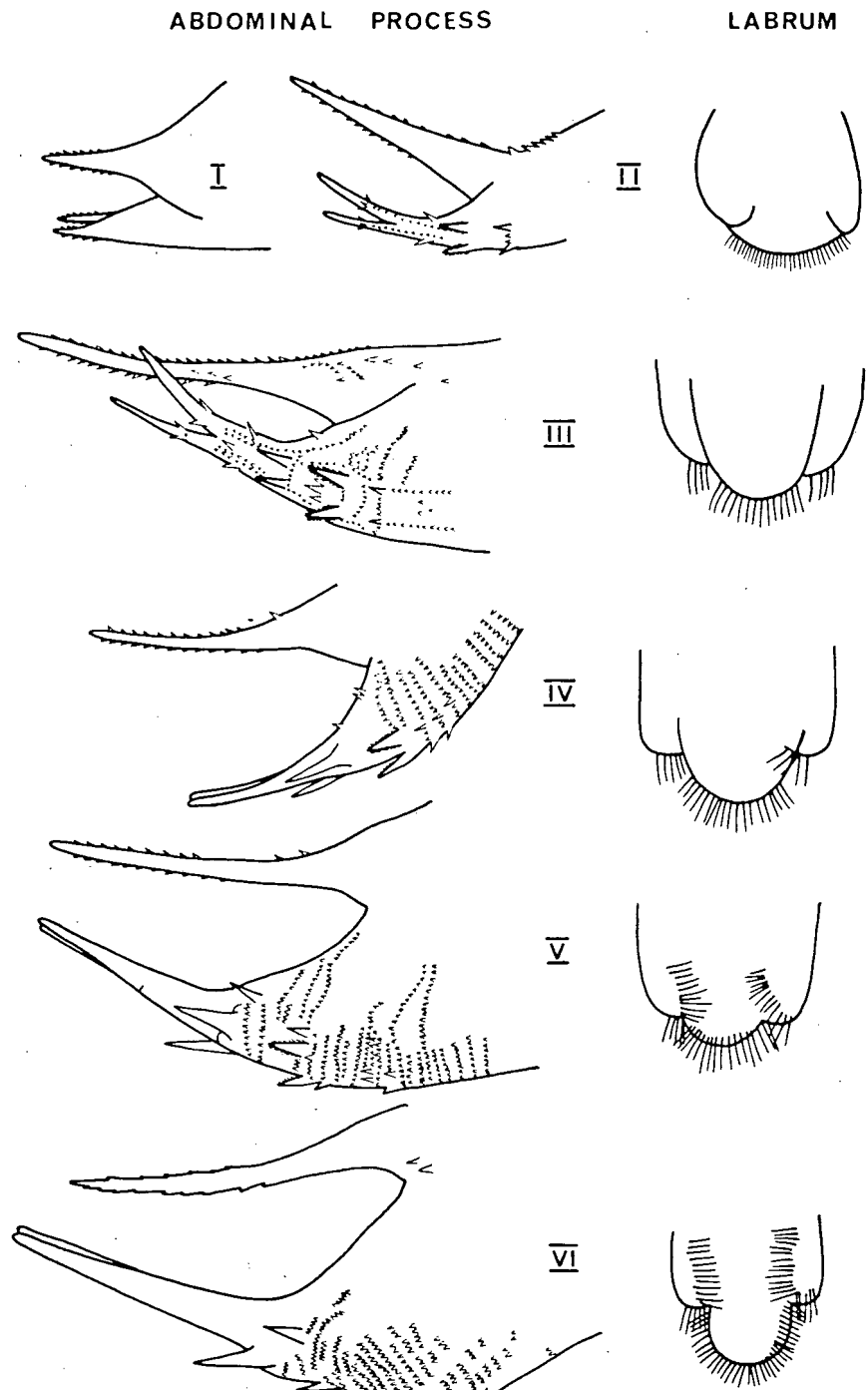


Fig. 5. The abdominal and caudal process and labrum of *T. serrata* nauplius stages I-VI.

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marginal spinules. With the exception of *Balanus trigonus* (250 μm) and *B. amphitrite* (210 μm) other described South African stage I nauplii are considerably smaller than those of *T. serrata* (274 μm) and differ in shape.

Stage II. Carapace rounded with fronto-lateral horns projecting anteriorly (characteristic of stages II–VI). Abdominal process with one prominent pair of finely setulose ventral spines (Fig. 5).

Stage III. Carapace more quadrangular than rounded. Abdominal process with two prominent pairs of ventral spines, the anterior pair larger and setulose (Fig. 5).

Stage IV. Posterior border of the carapace extended into two spines and abdominal process with a large pair of smooth spines on the stem (characteristic of stages IV–VI). In addition the abdominal process bears a pair of prominent lateral setulose spines (Fig. 5). The abdominal process is shorter than the caudal process.

Stage V. Carapace large, rounded with a notably convex dorsal surface. Abdominal spination similar to stage IV but with two additional pairs of smooth lateral spines. Abdominal process as long as the caudal process.

Stage VI. Penultimate segment of antennule swollen (Fig. 6). Carapace very large and markedly convex with stout posterior spines. Abdominal process longer than caudal, bearing 6 ventral pairs of spines, a larger seventh pair on the stem and one dorso-lateral pair (Fig. 5).

Cyprid. No distinctive features. Anteriorly rounded with a brown pigmented carapace. The distribution of oil droplets has been indicated in Fig. 4, although this may not be representative of natural conditions as it may be dependent to some extent on the nature and availability of food.

The structure of the antennules, antennae and mandibles of each of the six nauplius stages is illustrated in Figures 6, 7 and 8. The carapace dimensions (Table 2) and the setation formula (after Bassindale 1936) (Table 3) have been compared with those of *T. purpurascens* (Barker 1976), the only other species in the genus in which larvae have been described. The diagnostic features of both species of *Tetraclita* agree with those listed by Crisp (1962) for the Balanidae, except that the numbers of ventral and lateral spines on the abdominal process differ in some stages. Furthermore stage I nauplii of *T. serrata* may be seen to possess minute spinules on the abdominal and caudal processes and on the setae of the appendages when examined at magnification $\times 500$ (Fig. 5), a feature not previously recorded in stage I nauplii. Similar spinules were not observed on stage II appendage setae but were consistently found in later nauplius developmental stages. The presence of spinules did not indicate that setules would appear on these setae after the next moult, e.g. distal setae of the mandibular endopodite of stages III, IV and V. However, normal progressive development of setules on the setae occurred with each successive moult in stages II to VI, as noted by Crisp (1962). The setation formula of the antenna of stage II differed from that of Sandison (1954) who described it as 025.03222G. This may have been precocious development of the setae as it is common in some species (Norris *et al.*, 1951).

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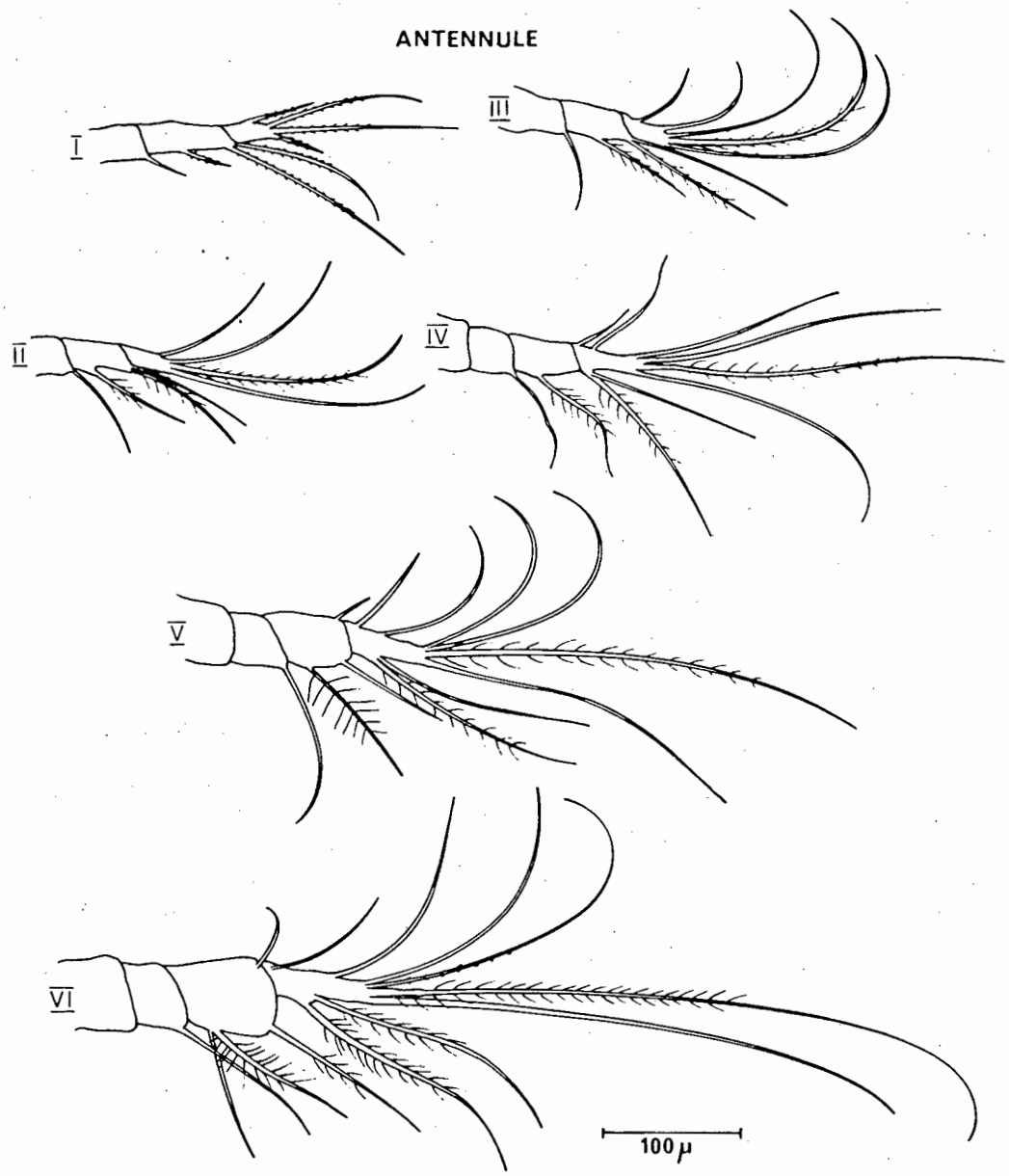


Fig. 6. The structure of the antennule of the six nauplius stages of *T. serrata*.

TRANSACTIONS OF THE ROYAL SOCIETY OF SOUTH AFRICA

ANTENNA

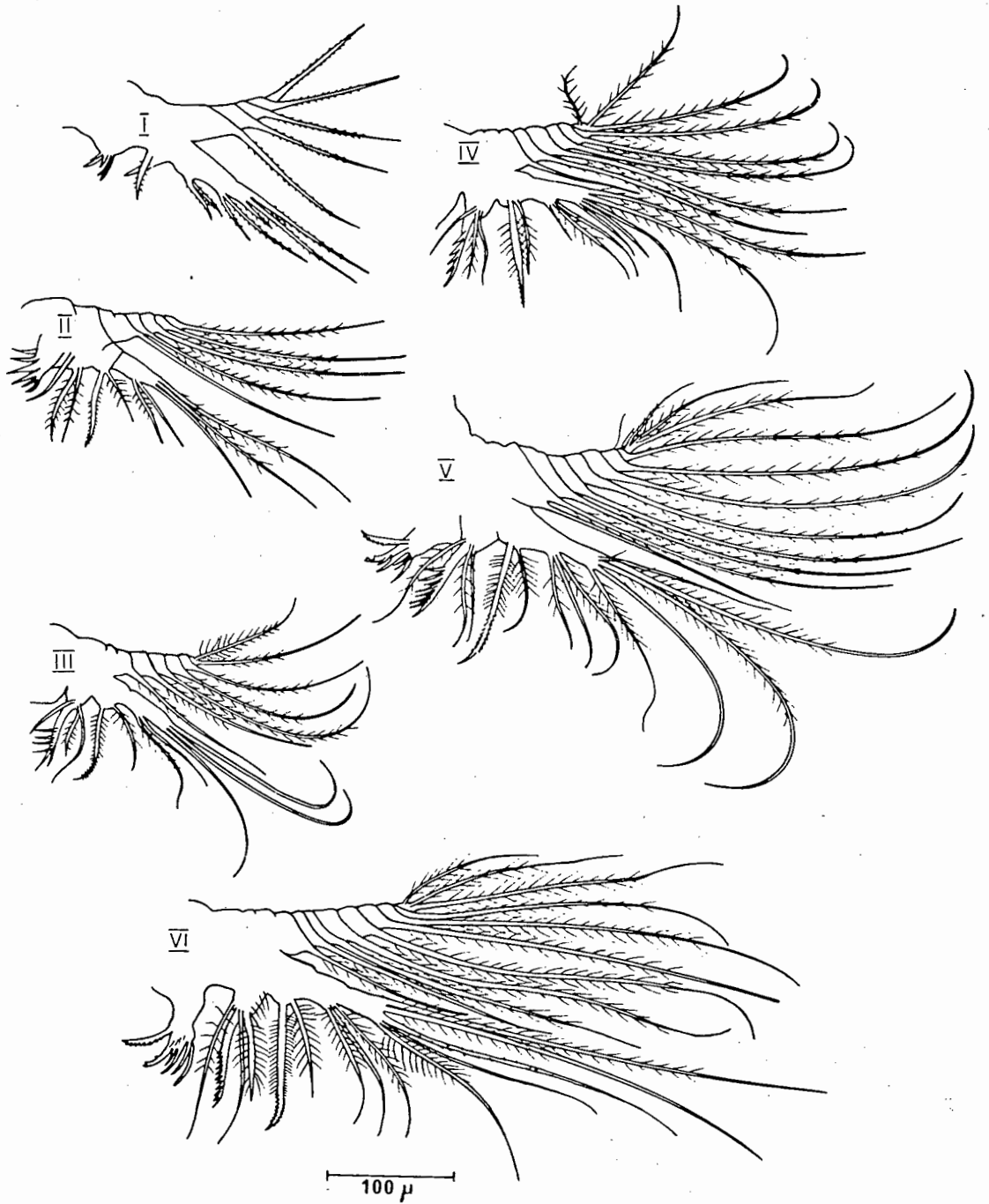


Fig. 7. The structure of the antenna of the six nauplius stages of *T. serrata*.

TETRACLITA SERRATA - REPRODUCTIVE SEASON AND LARVAL DEVELOPMENT

MANDIBLE

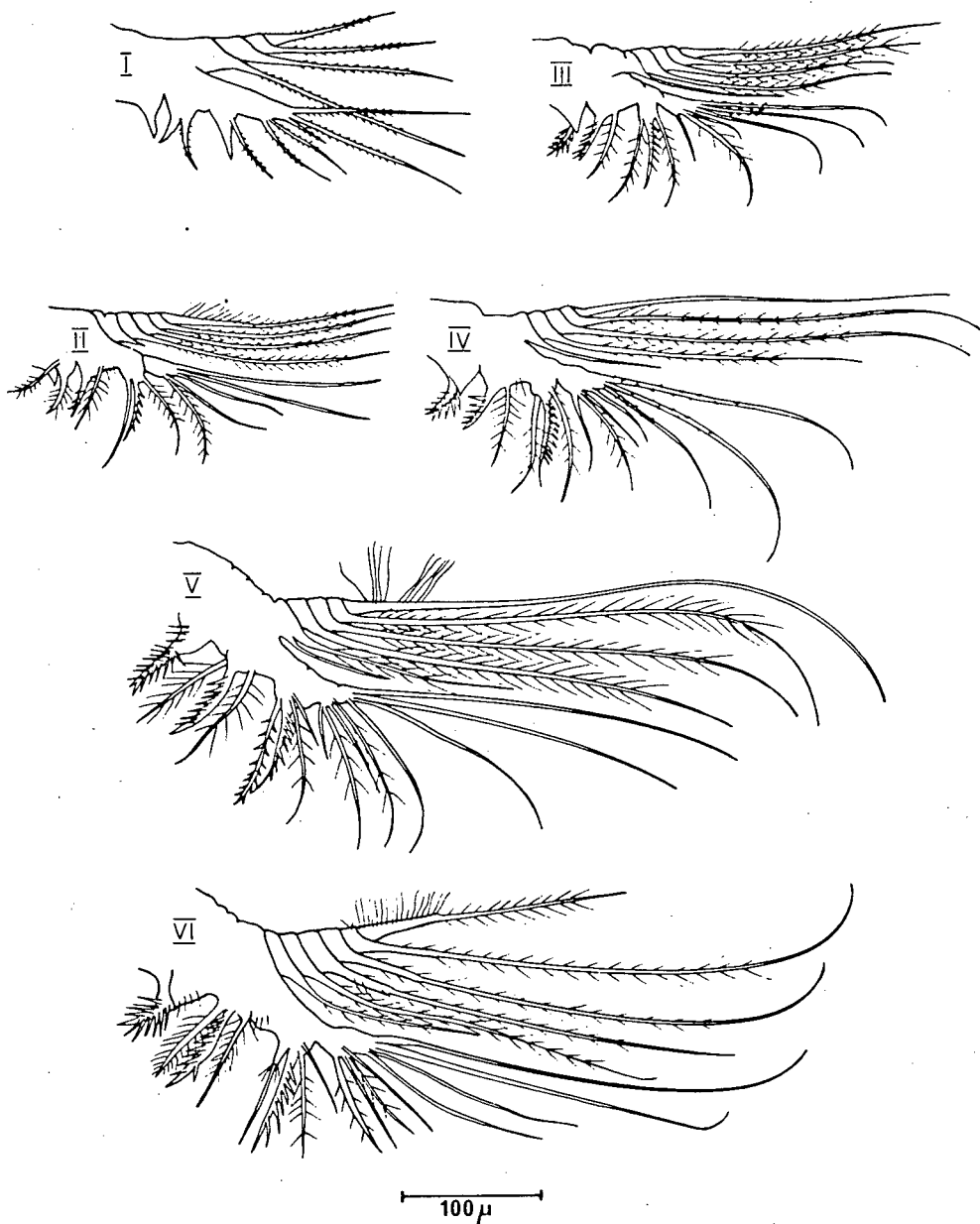


Fig. 8. The structure of the mandible of the six nauplius stages of *T. serrata*.

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Table 3.
Setal formula of *T. serrata* and *T. purpurascens* (Barker, 1976).

<i>Tetraclita serrata</i>			
Stage	Antennule	Antenna	Mandible
I	04211	014.03222G	013.03222G
II	04211	014.03222G	014.03232G
III	14211	025.03224G	014.03332G
IV	114211	036.05324G	014.04332G
V	11142111	038.05324G	015.04443G
VI	11142121	038.05324G	015.04443G
<i>Tetraclita purpurascens</i>			
I	04211	014.03222G	013.03222G
II	04211	025.03223G	014.03232G
III	14211	025.03224G	014.03333G
IV	114211	036.05324G	014.04343G
V	11142111	037.05324G	015.04443G
VI	11142121	037.05324G	015.04443G

Comparison of *T. serrata* with *T. purpurascens* nauplii showed that they were markedly similar in size and shape although the latter species possessed a slightly more elongate carapace. The setation of stage I appendages was similar but differences were present in either the antenna or mandible of later stages. There are no distinctive features which enable easy separation of *Tetraclita* nauplii from those of other balanid genera.

ACKNOWLEDGEMENTS

This work was supported as part of the Kelp Bed Research Programme by the South African National Committee for Oceanographic Research. Thanks are due to Dr G. M. Branch for constructive criticism of the manuscript.

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