# COMPARATIVE ECOLOGY AND PHYSIOLOGY OF FOUR SOUTH AFRICAN MUSSEL SPECIES, WITH NOTES ON CULTURE POTENTIAL

by

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# DECLARATION

I herby declare that this project was conceived and planned jointly by myself and Assoc. Prof. C.L. Griffiths, who was also responsible for the provision of funding. In Chapter 1, the mussel data were supplied by myself and the oystercatcher data by Dr. P.A.R. Hockey.

The experimental work, data collection and analysis, and initial write up of all the remaining chapters are my own work. If data collected by any other person were used in any part or form to help in the interpretation of my work, this is duly declared in the relevant section.

Assoc. Prof. C.L. Griffiths assisted in converting the "French-English" of my initial drafts into the "English-English" seen in this final version.

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## GENERAL ABSTRACT

The objective of this study was to compare the distribution patterns, reproductive cycles, growth rates and physiological processes in four species of South African marine mussels - Aulacomya ater, Choromytilus meridionalis, Mytilus galloprovincialis and Perna perna.

The first chapter is a preliminary account of the introduction of the invasive M.galloprovincialis, and its ecological effects. Its rate of invasion is estimated by monitoring changes in the diet of oystercatchers, as well as comparing its resistance to silt and dessication, and its reproductive and its growth strategies with those of other intertidal mussel species. It appears that although presently mainly confined to cool water of the west and south coasts, M. galloprovincialis will soon colonize in the near future the warmer waters of the east coasts.

The second chapter consists of a survey revealing the distribution patterns and standing stock of the four species around the South African coasts. The cool upwelled waters of the west coast support the major populations of A. ater, C. meridionalis and M. galloprovincialis, while the warm east coast is mainly colonized by the brown mussel P. perna. The Transkei and Natal coasts are intensively exploited by subsistence gatherers with an annual rate of removal approaching or even exceeding standing stock. The overall wild crop is ca > 1000 metric tons, while aquaculture output is estimated at 800 tons per annum.

The third chapter looks at the timing and the intensity of spawning of the four species. Gamete build up and release results in marked variation in flesh yield. The dry flesh weight of M. galloprovincialis can vary three-fold between ripe and spawned conditions at a length of 65mm. Equivalent figures for C. meridionalis, A. ater and P.perna are respectively 2.8, 2.3 and 2.2-fold. It appears that A. ater shows the greatest gamete output with three annual spawnings, followed by M. galloprovincialis and C. meridionalis with two protracted spawnings.

The fourth chapter deals with growth performance of the four species under different environmental conditions. A. ater consistently grows much slower than other species, is intolerant to aerial exposure or silt load and grows best in cold waters. C.meridionalis also likes cool water conditions, but is the most tolerant of silt load. M.galloprovincialis and P. perna are the least affected by tidal exposure and both grow faster in warm water conditions. In terms of aquaculture development, M.galloprovincialis is the most appropriate species to grow on the west and south coasts, while P. perna will be the candidate for the east coasts of South Africa.

The fifth chapter compares rates of filtration, respiration and ammonia excretion, as well as absorption efficiencies and subsequent scope for growth in the four mussel species. All species maintain a relatively steady scope for growth over the ration levels 1-7 mg $l^{-1}$. However, rates are the highest in M.galloprovincialis (254 J $h^{-1}$ at 7 mg $l^{-1}$ ration) followed by C.meridionalis and P. perna at 117 and 70 J $h^{-1}$ and finally A. ater, with only 23 J $h^{-1}$. Scope for growth in M. galloprovincialis is high at all temperatures (10-20°C) while that of A. ater is low and declines rapidly with temperature. The scope for growth of P. perna and C. meridionalis is intermediate, but while C. meridionalis becomes less efficient at higher temperatures P.perna show a rapid increase with increasing temperature. These physiological measures are correlated to the observed distribution pattern and growth rates in the field.

# INTRODUCTION

The original concept for this thesis arose from the recent discovery of the invasive introduced mussel Mytilus galloprovincialis on the west coast of South Africa. This raised a number of both theoretical and management issues. Amongst these were :

- To establish the current range and distribution pattern of the invasive species and the extent to which it has displaced existing endemic forms, or is likely to do so in the future.
- To compare the fitness of M. galloprovincialis relative to indigenous species in terms of the tolerance to temperature variation and ration level, and in terms of growth rate and reproductive output.
- To compare the species in terms of their suitability for aquaculture in different regions of the coastline subject to differing environmental regimes.

A great deal of existing data were available on the population dynamics and ecophysiology of the three indigenous South African mussel species, but because the conditions under which these studies were undertaken varied so greatly (especially with respect to temperature and feeding conditions) it was decided that comparable measurements could only be obtained by direct side-by-side observations of all four species.

The account to follow attempts to resolve some of these issues and is presented in the form of five independent papers. The format of each paper is designed to meet the requirements of the journal in which it has been published, or to which it is being submitted, hence the minor variations in layout between chapters.

Chapter 1 discusses the invasive biology of the mussel Mytilus galloprovincialis on the southern African coast, and is currently in press in *Transaction of the Royal Society of South Africa* . This paper was presented to the "Aquatic Invasive Symposium" held in Grahamstown, South Africa, in September 1988, at a very early stage of this thesis. It hence predates some of the information presented in subsequent chapters.

Chapter 2 covers the distribution, standing stocks, exploitation and culture of the four South African marine mussels, and has been published in the *Journal of Shellfish Research, Vol. 9, No. 1, pp 75-85* .

Chapter 3 compares the reproductive cycles and the reproductive outputs of the four species, and is currently in press in *Marine Ecology Progress Series* .

Chapter 4 discusses the factors affecting relative rates of growth in the four species, and is being submitted for publication in *Aquaculture* .

Chapter 5 compares physiological rate processes and Scope for Growth in the four species under differing conditions of food availability and temperature, and is being submitted to *Comparative Biochemistry and Physiology (A)* .

# CHAPTER 1

# THE INVASIVE BIOLOGY OF THE MUSSEL MYTILUS GALLOPROVINCIALIS ON THE SOUTHERN AFRICAN COAST

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## SUMMARY

The Palearctic mussel Mytilus galloprovincialis has recently invaded the southern African coast. Its present range extends from central Namibia to Hermanus, with a small outlying population at Port Elizabeth. It is most abundant on the southern Benguela coast, where it occurs intertidally. It grows vigorously on suspended mussel ropes, but is absent from subtidal benthic substrata where the silt-tolerant Choromytilus meridionalis predominates. Intertidally, it outcompetes the indigenous mussel Aulacomya ater, due to its superior reproductive output, faster growth rate and greater tolerance to desiccation. It is a superior competitor to the intertidal limpet Patella granularis for primary rock space, but is a favoured settlement and recruitment medium for this species. The rate of Mytilus invasion in the Saldanha region between 1979 and 1988 was rapid, as evidenced by major changes in the diets of African black oystercatchers Haematopus moquini. Although at present largely confined to the cold temperate coasts of southern Africa, Mytilus grows rapidly in warm water and its eventual colonization of the warm temperate and subtropical coasts seems inevitable, as does consequent competition with the indigenous brown mussel Perna perna. No control measures are in operation. This species must be considered as out of control and uncontrollable, and research into the potential for commercial exploitation is needed.

# INTRODUCTION

Mussels are dominant competitors for space on many shores (Suchanek 1985). Historically, the dominant indigenous mussels on the west coast of South Africa and southern Namibia were the black mussel *Choromytilus meridionalis* and the ribbed mussel *Aulacomya ater* (eg. Stephenson & Stephenson 1972, Volman 1978). The brown mussel *Perna perna* occurs rarely on the cold Benguela coast, but is common in warmer waters to the north and east (Berry 1978). In the early 1980s, the presence of a fourth species, superficially similar in appearance to *Choromytilus*, was detected (Grant *et al*. 1984). The initial identification of this species as *Mytilus galloprovincialis*, a Palearctic species, was subsequently confirmed (Grant and Cherry 1985, Grant 1987). It is not known precisely when or how *Mytilus* arrived in southern Africa, but it probably was within the past 30 years and was a man-mediated rather than a natural introduction (Grant 1987). The absence of *Mytilus* shells from Khoi-San middens and earlier raised beach deposits (120 000y b.p.) is evidence against the present population being a relict of a once more widely distributed population (Grant & Cherry 1985).

This study aims to 1) describe the distribution of *Mytilus* in southern Africa, 2) examine its habitat preference relative to indigenous mussel species, with special reference to desiccation, silt tolerance and water temperature, 3) quantify aspects of its life-history relevant to its invasive potential, specifically growth and reproductive rates, 4) assess its rate of invasion and competitive interactions with indigenous species, 5) provide a scenario for the future of *Mytilus* in southern Africa, and 6) discuss side-effects of the invasion and the practicality or desirability of control measures.

# METHODS

## 1. Distribution and habitat preference

Geographical distribution was determined during coastal surveys extending from Luderitz to the Transkei between 1984 and 1988. During these surveys, qualitative observations of habitat preferences of all four mussel species were made.

Zonation on the shore, and relative abundance of *Mytlius* and *Aulacomya* were determined at Marcus Island, Saldanha Bay (33°03'S, 17°58'E) in April 1988. Eight transects were laid out, extending from the mean low water mark at spring tides (MLWS) to the upper limit of occurrence of intertidal macroalgae. At 0.1 m intervals, the dominant space-occupying species or assemblage within a 0.1x0.1m quadrat was recorded. The vertical profile of each transect was drawn up in vertical intervals of 0.2 m and the upper limit of the occurrence of mussels was determined (= 1.2 m above MLWS). The mussel band was divided into three equal vertical zones (0-0.4 m, 0.4-0.8 m and 0.8-1.2 m above MLWS), referred to subsequently as the low, mid and high zones respectively. Within each zone, eight quadrats of 0.04 $m^2$ were cleared in areas of 100% mussel cover. The samples were sorted by mussel species, all mussels were measured (maximum length to the nearest mm) and total dry flesh weights (D) in grams were calculated for each species in each sample using the following regressions: *Aulacomya* $D = 1.3 \times 10^{-6} L^{3.276}$; *Mytilus* $D = 1.7 \times 10^{-6} L^{3.297}$. Comparable samples were collected in September 1979, when *Aulacomya* dominated the intertidal mussel comunity, and dry flesh biomass was determined in the same way. The percentage cover of mussels in each 0.4 m zone in April 1988 was calculated from the relative frequency with which mussels were recorded as dominant space occupiers within the three zones along the eight transects.

## 2. Survival, growth and reproduction

### Survival

Survival was determined in relation to desiccation and siltation stresses. Experiments were sited in a sea water dam at Saldanha with a damped tidal regime of ca one tidal cycle per week. Experimental procedure was identical for all four species. Mussels were placed in nylon bags and kept at constant tidal level within a metal frame. To test for desiccation tolerance, bags were placed at a high intertidal level where they were exposed for up to one week at a time. Survival was monitored at 8-10 week intervals for 42 weeks. In the second treatment, mussels were mantained on tiles a few cm above a silt substratum in a continually submerged location, and survival was monitored at the same intervals. After seven months in situ, major silt deposition occurred, allowing the impact of this on survival to be assessed.

### Growth

Approximately 1000 individuals of each species were collected, Perna from False Bay and the other species from Bloubergstrand (Fig.1). All individuals were approximately 30 mm in length at the time of collection, in November 1987. For each species, 50% of the mussels were settled on subtidal mussel ropes at Saldanha, and 50% on similar ropes in warmer water at Port Elizabeth. Subsequently, 30 individuals of each species were removed from the ropes at each site at roughly three-monthly intervals, and measured.

### Reproduction

Fifty individuals of each mussel species were collected monthly between January 1987 and December 1987 at False Bay (Perna perna) and Bloubergstrand (other species). Dry flesh biomass (somatic and gonadial combined) for each species in each month was regressed on length, and monthly dry flesh mass of a 65 mm individual was calculated. Differences in dry flesh mass between sequential months were assumed to reflect either a build-up or release of gametic material. Relative annual gamete release of the different species was obtained by summing all negative differences between dry flesh mass in sequential months, and was expressed as dry g of gametic material released per year.

## 3. Invasion rate and interspecific interactions

Invasion rates of Mytilus at Malgas (33°03'S, 17°56'E) and Jutten (33°05'S, 17°58'E) Islands were monitored through analysis of changes in the diets of African black oystercatchers Haematopus moquini. Within their prey spectrum, African black oystercatchers select prey in proportion to their relative abundance (Randall & Randall 1982). Therefore, changes in relative proportions of prey in the diet reflect changes in relative abundance of those species on the shore. When feeding chicks, oystercatchers form middens of emptied shells: these were collected at the two islands during the breeding seasons of 1979/80, 1980/81 and 1987/88. Collection details are presented in Table 1.

African black oystercatchers are territorial (Hockey 1984), hence the contents of any one midden reflect prey availability along only a small stretch of shore. Gross inter-annual differences in relative

| Season | Jutten Island |  | Malgas Island |  |
|---|---|---|---|---|
|  | No. middens | No. shells | No. middens | No. shells |
| 1979/80 | 25 | 13 995 | 9 | 4 586 |
| 1980/81 | 16 | 4 233 | 3 | 1 177 |
| 1987/88 | 18 | 7 363 | 6 | 2 088 |

Table 1. Mumbers of oystercatcher middens and shells collected at Jutten and Malgas Islands during three breeding seasons.

prey abundance were obtained from pooled samples (all prey items collected at one island in one year). Within-island and -year variability were analysed for Jutten Island using correspondence analysis (Greenacre 1984): only middens containing more than 50 prey items were included in analyses. Large samples of shells were measured in 1979/80 and 1987/88 to determine whether changes in prey abundance were paralleled by changes in prey size. All prey were identified to species level with one exception. Prior to 1987, all 'black' mussels were labelled as Choromytilus, because Mytilus was not recognized at that time. Hence 'black mussels' refer to an indeterminate mixture of these two species.

Interspecific competitive interactions were inferred from a) changes in species and prey size composition in oystercatcher middens, b) analysis of quadrats cleared in mussel beds (see distribution section) and c) experiments at Marcus Island designed to simulate possible strategies for commercial exploitation of the limpet Patella granularis. Sampling sites for the latter experiment were areas of open rock occupied by limpets but surrounded by beds of mussels, predominantly Mytilus. Five treatments, each with four replicates, involved manipulation of adult and/or juvenile limpet biomass. Control sites (n=4) were not subject to any manipulation. The areas of all patches (treatments and controls) were measured before manipulations (March 1987) and eight months later (November 1987).

Additional data concerning population biology of the limpet Patella granularis are included: these were collected during an extensive study on the roles of birds and nutrients in structuring intertidal communities (Bosman & Hockey 1986, 1988, in press, Bosman et al. 1987, Hockey & Bosman in press) - detailed methodology will be presented elsewhere.

Possible consequences of Mytilus invasion for the population dynamics of mussel predators were investigated by monitoring the reproductive output of oystercatchers. Oystercatcher chicks were caught and ringed annually at Marcus, Malgas, Jutten and Vondeling ($33^{o}09'$S, $17^{o}59'$E) Islands, between 1979 and 1988. African black oystercatchers lay either one or two eggs (rarely three) (Hockey 1983), and the proportion of pairs with two chicks was used as an index of annual productivity. To test for significant trends in productivity, a loglinear model with a logistic link function and a binomial error distribution was used (McCullagh & Nelder 1984).

## RESULTS

### 1. Distribution and habitat preference

Mytilus occurs on the southern African coast from at least Luderitz, Namibia to Hermanus, Cape Province (Fig. 1). Based on observations from the Orange River southwards, its distribution is probably continuous within this range altough the distribution is patchy to the east of Cape Point. A small outlying population was discovered at Port Elizabeth in March 1988.

Mytilus occurs on both sheltered and exposed rocky shores, but generally is absent from heavily silted or sanded areas, and does not extend its distribution on benthic substrata seaward of the infratidal fringe, although it flourishes on suspended mussel ropes. Both Aulacomya and Choromytilus occur predominantly subtidally. Intertidally, Choromytilus is confined to the low shore, and typically grows at a sand/rock interface, or in silted areas. Aulacomya extends its distribution to the mid shore, preferring exposed shores without silt or sand. Perna occurs both subtidally and intertidally, and is particularly abundant intertidally near the low water mark

A = Aulacomya ater
C = Choromytilus meridionalis
M = Mytilus galloprovincialis
P = Perna perna

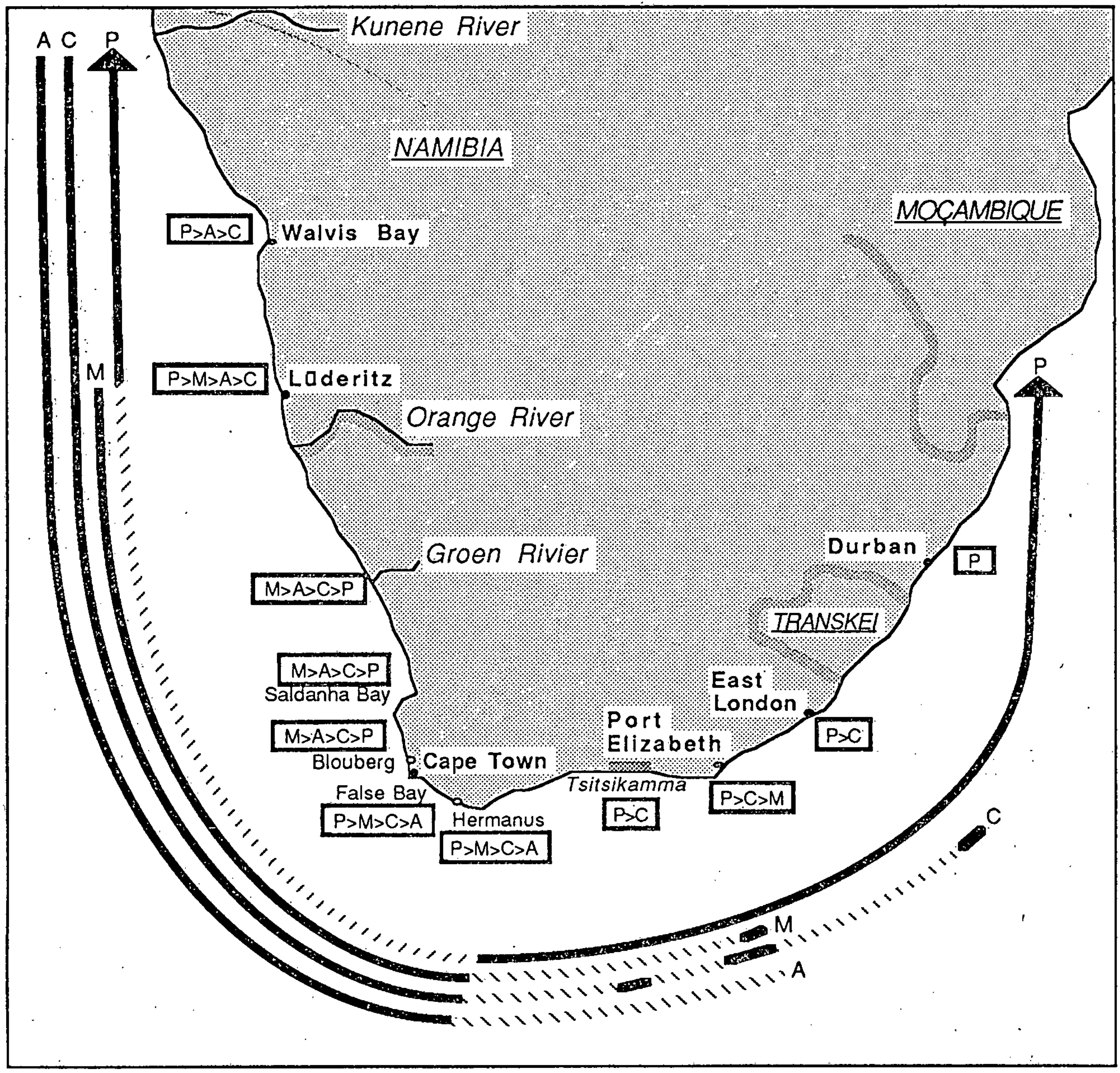

Figure 1. Distribution of three indigenous mussel species and Mytilus galloprovincialis in southern Africa. Relative abundances of the different species at selected localities appear in boxes.

imediately above the vertical faces of wave-cut platforms.

At Marcus island, both Aulacomya and Mytilus extended intertidally from MLWS to a vertical height of 1.2 m, 0.2 m above the mean high water neap tide level. The percentage cover of mussels decreased with increasing height above MLWS (Table 2). Biomass per unit area of 100% mussel cover showed opposite trends for the two species, with Mytilus biomass peaking in the high zone and Aulacomya peaking in the low zone (Table 2). Correcting for percentage cover in each zone, Mytilus biomass per unit area peaked in the mid zone and Aulacomya in the low zone (Table 2). In 1988, mid and low zone dry flesh biomasses of Aulacomya (4.32 and 8.36 g per 0.04 $m^2$ respectively) were appreciably lower than in 1979 (21.29 and 37.78g).

## 2. Survival, growth and reproduction

Tolerances to desiccation and siltation stress differed markedly between the four species. Mortality rates of mussels subjected to experimental desiccation showed that Mytilus was more desiccation-resistant than any of the indigenous species and that Aulacomya was the least tolerant of desiccation. Perna was more tolerant of desiccation than Choromytilus (Fig. 2). Choromytilus was more resistant to siltation than the other species: within 14 weeks of a major siltation event, mortality of all other species was 100% (Fig. 2).

At Saldanha, Mytilus and Choromytilus suspended on mussel ropes grew at comparable rates ( Fig. 3). Perna grew slightly less rapidly, and growth of Aulacomya was very slow relative to the other species. In warmer water at Port Elizabeth, Choromytilus and Aulacomya grew more slowly than in cold water at Saldanha, while Mytilus and Perna grow faster (Fig. 3).

| Shore zone | % mussel cover (mean ± S.D.) | dry flesh biomass per 0.04 $m^2$ of 100% cover | | mean dry flesh biomass per $m^2$ | |
|---|---|---|---|---|---|
| | | Mytilus | Aulacomya | Mytilus | Aulacomya |
| High (0.8-1.2m above MLWS) | 37.4 ± 33.6 | 47.4 ± 36.3 | 0.4 ± 0.5 | 444 | 4 |
| Mid (0.4-0.8m) | 63.0 ± 31.9 | 36.7 ± 19.6 | 4.3 ± 5.0 | 577 | 68 |
| Low (0.0-0.4m) | 70.1 ± 32.2 | 9.7 ± 13.6 | 8.4 ± 6.0 | 169 | 147 |

Table 2. Percentage cover, dry flesh biomass per 0.04 $m^2$ of 100% cover, and mean dry flesh biomass per $m^2$ of shore of Mytilus galloprovincialis and Aulacomya ater in three littoral zones at Marcus Island, April 1988.

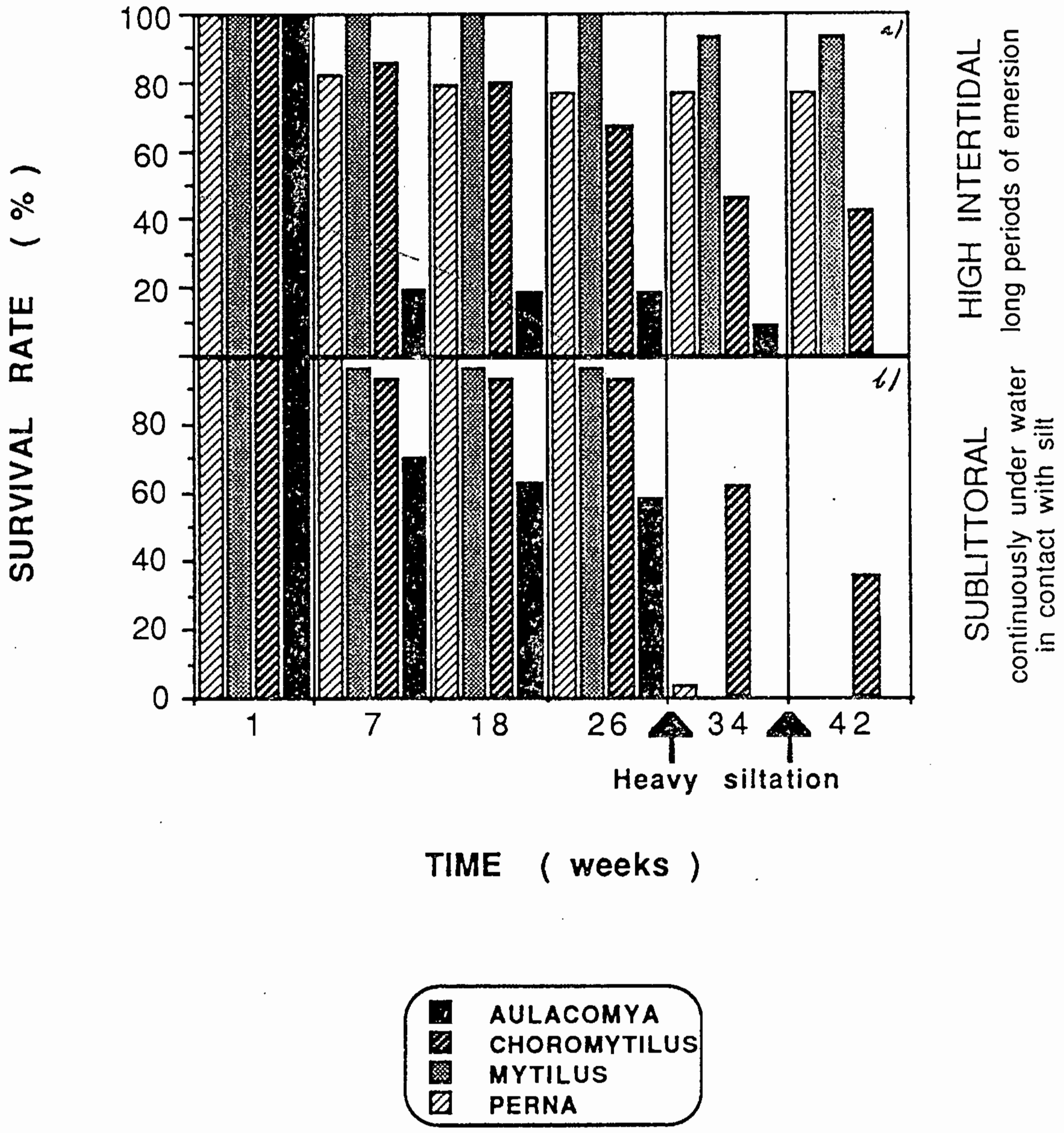

Figure 2. Survival rates of four mussel species a) exposed to desiccation stress and b) experiencing silt inundation.

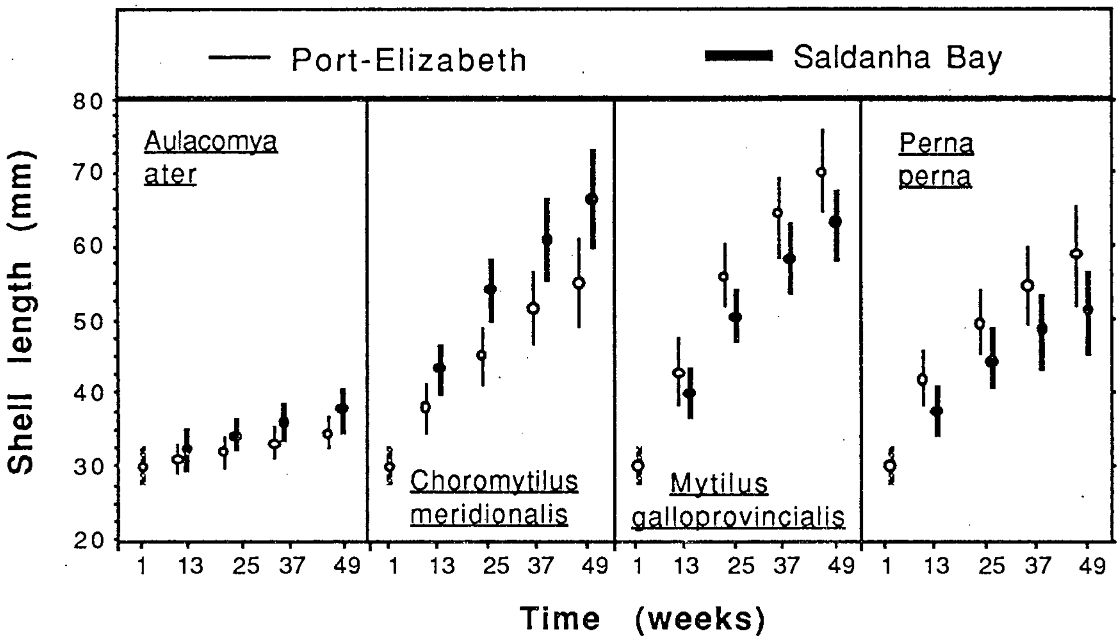

Figure 3. Comparative growth rates of mussels in cold (Saldanha) and warmer (Port-Elizabeth) waters.

For standard-sized mussels (65 mm), Aulacomya showed the greatest annual gamete release (2.20 g), followed by Mytilus (1.65 g). Annual gamete release of Choromytilus and Perna were, respectively, only 64% and 42% that of Mytilus (Fig. 4). It should be noted, however, that the Perna samples were collected from a population at the edge of its geographical range.

### 3. Invasion rate and interspecific interactions

Between 1979/80 and 1987/88 the numerical proportion of 'black' mussels in the diets of oystercatchers at Jutten and Malgas islands increased from 14% to 61% and from 30% to 95% respectively (Table 3). Correspondence analysis of individual midden contents from Jutten Island in the three years shows that these changes were widespread around the island, and not confined to a few pairs of birds (Fig.5). Seventy-eight percent of the variable (midden) points for 1987/88 fall outside the spread of variable points for 1979/80 and 1980/81 combined. Conversely, only 15% of the variable points for the two early breeding seasons fall within the spread of variable points for 1987/88. The principal distinguishing factor on axis 1 (x-axis) contrasts the high proportion of Aulacomya in middens in 1979/80 and 1980/81 with the high proportion of 'black' mussels in 1987/88. Factor 2 (y-axis) separates middens with a relatively high proportion of Patella granularis from those with high proportions of mussels (all species). Of importance here is that the distinction between Aulacomya and 'black' mussels explains a greater proportion of the inertia in the analysis (56%) than the distinction between mussels and limpets (30% of the inertia) (Fig. 5).

All species considered in Table 3 and Fig. 5 are primary space occupiers. The species showng the greatest, and most consistent,

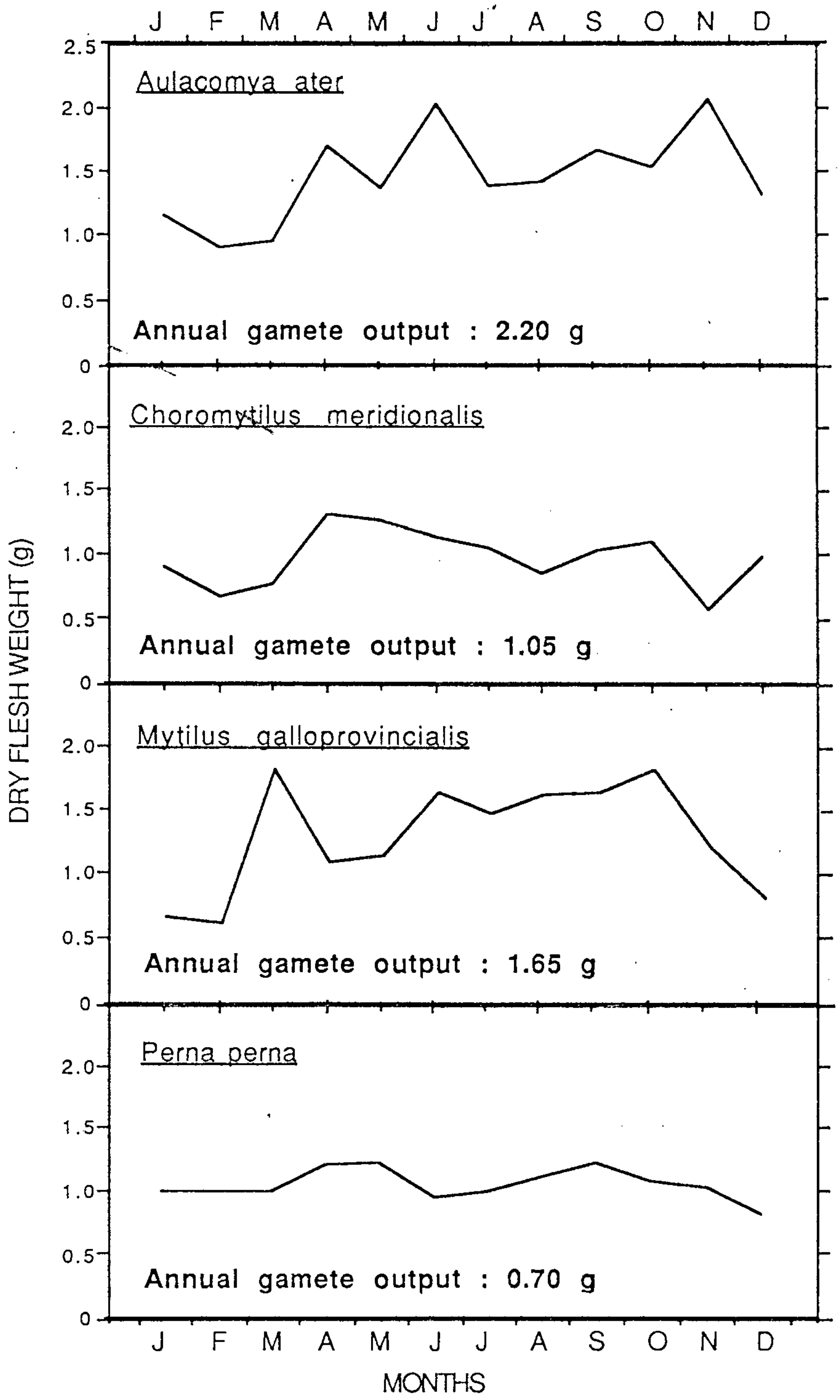

Figure 4. Monthly changes in dry flesh biomass and calculated annual gamete outputs of 65 mm mussels of four species.

| Prey Species | Jutten Island 1979/80 | Jutten Island 1980/81 | Jutten Island 1987/88 | Malgas Island 1979/80 | Malgas Island 1980/81 | Malgas Island 1987/88 |
|---|---|---|---|---|---|---|
| Aulacomya ater | 54.0 | 42.2 | 17.1 | 20.3 | 26.7 | 0.9 |
| Mytilus galloprovincialis | 13.6 | 21.7 | 42.2 | 30.4 | 40.4 | 91.8 |
| Choromytilus meridionalis | | | 18.8 | | | 3.5 |
| Limpets | | | | | | |
| Patella granularis | 28.2 | 31.0 | 12.9 | 40.3 | 26.0 | 3.3 |
| Patella argenvillei | 3.3 | 3.3 | 6.1 | 6.6 | 4.3 | 0.1 |
| Other species | 0.9 | 1.8 | 2.9 | 2.4 | 2.6 | 0.4 |

Table 3. Changes in percentage composition of African black oystercatcher diet at Jutten and Malgas Islands as determined from pooled midden collections.

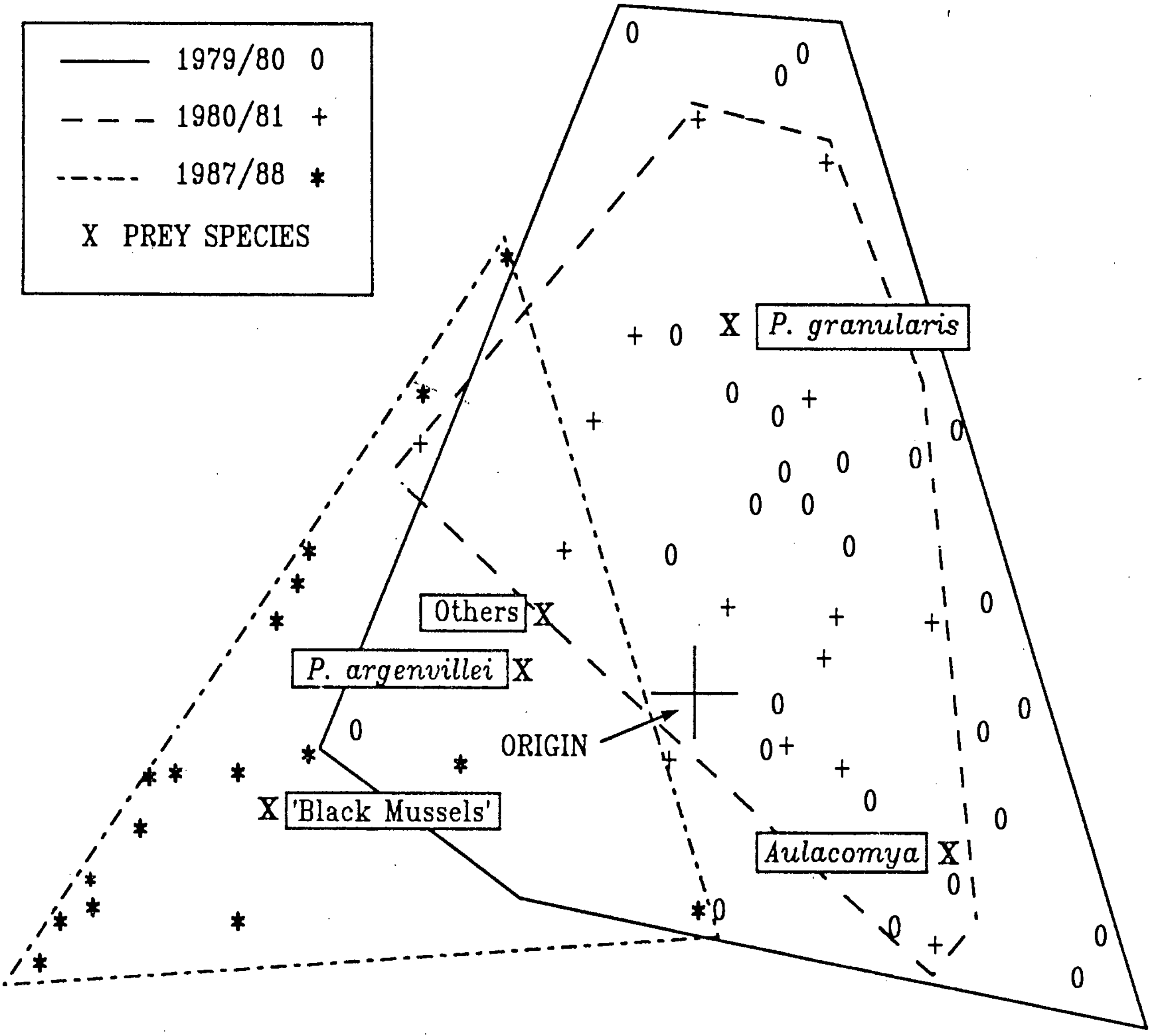

Figure 5. Correspondence analysis of contents of oystercatcher middens collected at Jutten Island in three breeding seasons.

decreases in relative abundance were Aulacomya and P. granularis. Aulacomya is slower-growing, less desiccation tolerant and slightly less fecund that Mytilus (Figs 2,4) and apparently is unable to compete for primary space with this species intertidally. Not only did Aulacomya become more scarce between 1979 and 1988, but individuals preyed on by oystercatchers became smaller (Jutten Island, $n = 8984$, $t_9 = 932.3$, $P<0.05$) (Fig. 6). This pattern of decreasing size of Aulacomya is also evident from samples of mussels collected in the mid and low zones at Marcus Island in 1979 and 1988. Modal size classes of Aulacomya >15 mm in the mid shore zone were 21-25 mm and 16-20 mm in 1979 and 1988 respectively. Corresponding values for the low zone were 31-35 mm and 21-25 mm.

Between 1979 and 1988 the proportions of P. granularis in oystercatcher middens decreased by 54% and 92% at Jutten and Malgas Islands respectively. Differences in the sample sizes between the two years at Malgas Island (1766 vs 74) precluded sound testing, but at Jutten Island, P. granularis preyed on in 1987/88 were larger than those taken in 1979/80 ( $n = 5101$, $t_{10} = 2.56$, $P<0.05$) (Fig. 7).

Following experimental reductions of P. granularis standing biomasses in patches surrounded by mussels, mean patch sizes eight months later were smaller on average for all treatments, ranging from 81% to 99% of pre-manipulation size. Control patches also decreased in size during the eight month period, by an average of 16%: these reductions were due to patch encroachment by Mytilus (Table 4). The effects of this encroachment into controls outweighed the predicted consequences of limpet biomass manipulation (Hockey, unpubl. data).

Although Mytilus apparently exerts some competitive dominance over P. granularis for primary rock space, it also provides a good settlement and recruitment site for P. granularis, from which recruits later move on to open rock faces. At five sites on the South

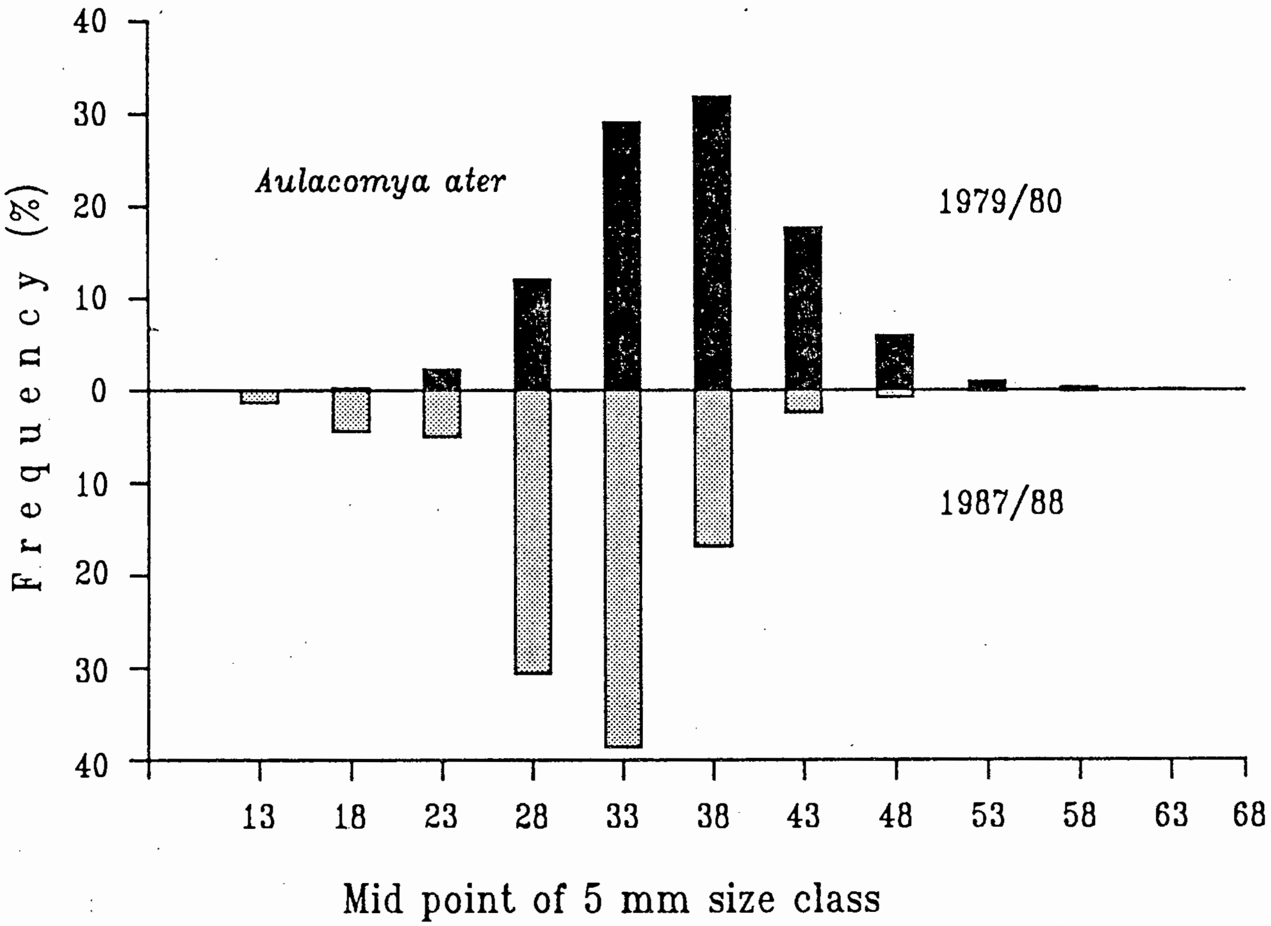

Figure 6. Size frequency distributions of Aulacomya ater in oystercatcher middens at Jutten Island in 1979/80 and 1987/88.

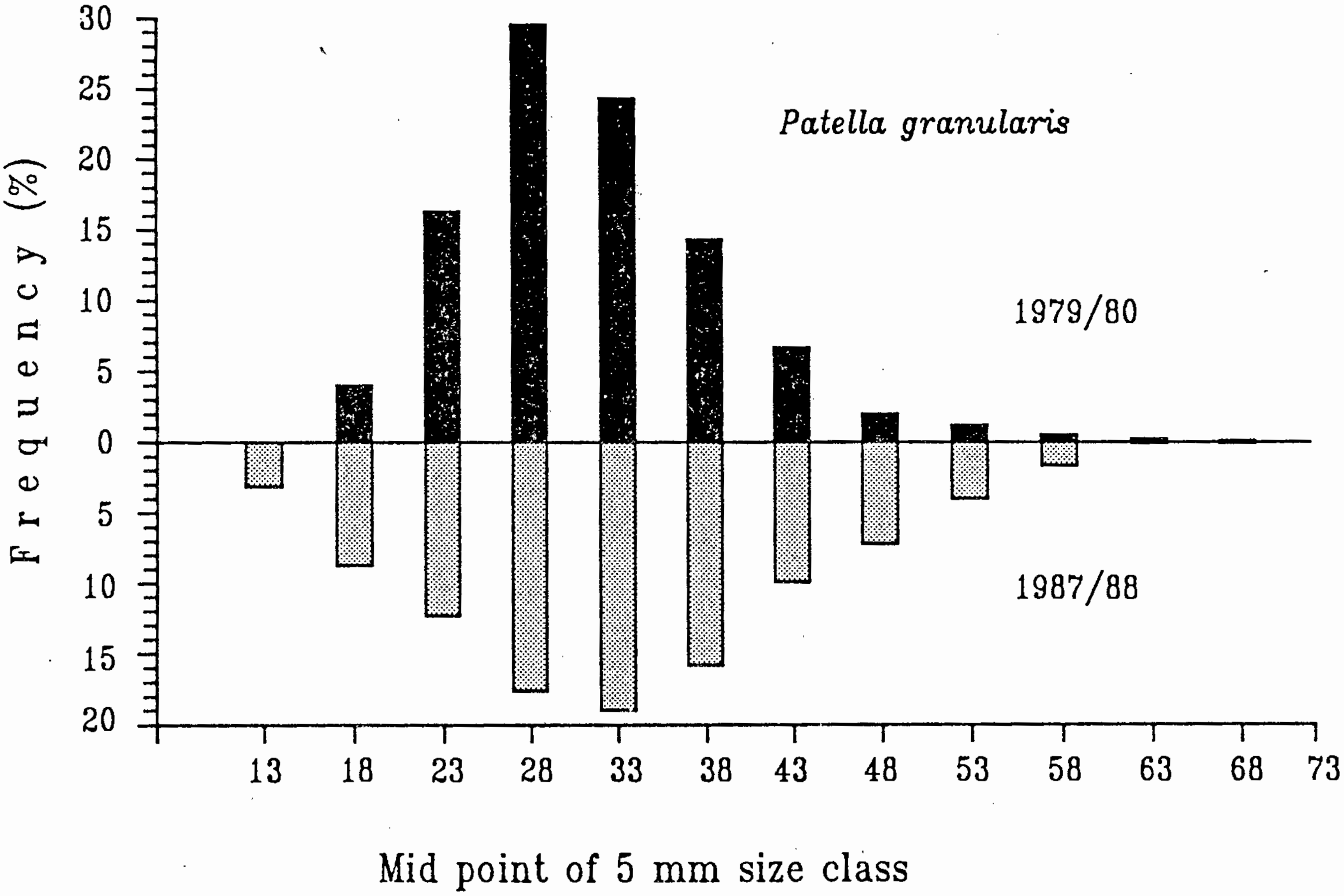

Figure 7. Size frequency distribution of Patella granularis in oystercatcher middens at Jutten Island in 1979/80 and 1987/88.

| | % Biomass removed in manipulation | | Mean (± S.D.) patch area as % of pre-manipulation patch area |
|---|---|---|---|
| Treatment | Adults | Recruits | |
| Control | 0 | 0 | 84 ± 2 |
| 1 | 0 | 100 | 88 ± 6 |
| 2 | 50 | 0 | 87 ± 9 |
| 3 | 50 | 100 | 99 ± 20 |
| 4 | 100 | 0 | 81 ± 13 |
| 5 | 100 | 100 | 91 ± 10 |

Table 4. Extent of encroachment by *Mytilus* into open rock areas dominated by *Patella granularis* in eight months following manipulations of limpet biomass (n=4 for all treatments and controls).

African west coast where intertidal mussels were absent, recruits (defined on the basis of growth rate as young of the previous settlement) ranged from 0 - 49% (mean 20 ±19%) of the limpet population. At six sites where mussels were present, recruits comprised 28.5 - 82.8% of the limpet population (mean 60 ± 22%). Mean adult density per m of shore was also greater at sites with mussels (317 vs 227) (Hockey, unpubl. data). These differences are probably recent and related to Mytilus encroachment. In surveys of mixed mussel beds (Mytilus and Aulacomya) at Marcus island (sample size =114 x 0.01 $m^2$), 397 P. granularis recruits were recorded on a total of 2769 Mytilus shells examined (1 : 6.97). On 1975 Aulacomya shells, only 106 P. granularis recruits were found (1:18.63) (Hockey, unpubl. data). No P. granularis recruits were found on shells of Choromytilus. Within Mytilus beds, length of an individual P. granularis (P) was closely correlated with the length of mussel (M) on which it sat ( $P = 7.63 + 0.23 M$, $P<0.001$). The maximum size attainable by limpets in a mussel bed is therefore limited by the size of individual mussels. Although limpets on mussels are smaller, on average, than limpets on open rock faces, they are an order of magnitude more abundant (mean = 623 per $m^2$ from 6 sites, cf. 96 per $m^2$ from 11 sites on open rock faces). Mean annual female gamete output, assuming parity in sex ratios (Bosman & Hockey 1988), on open rock faces at 11 sites in the southwestern Cape was calculated at 6.01 ± 2.73 wet g per $m^2$. Mean female gamete release of limpets on mussels at six sites was calculated at 8.44 wet g per $m^2$. Beds of barnacles, particularly Octomeris angulosus, are also favoured recruitment sites for P. granularis, but are relatively so scarce on the west coast as to be insignificant in the population dynamics of P. granularis.

Concomitant with increasing absolute and relative abundance of Mytilus at islands in and near Saldanha Bay, there has been a significant (P<0.05) trend of increasing productivity of African black oystercatchers (Fig. 8).

# DISCUSSION

The first confirmed record of M. galloprovincialis in southern Africa was of specimens dredged from 420 m off the coast of Natal (Grant & Cherry 1985). The species has not subsequently been recorded in Natal, and the extant population probably originated in the southwestern Cape. Grant et al. (1984) suggested that the large heterozygosity in Mytilus in South Africa argued against a recent dispersal from the Mediterranean via a small founder population, but was indicative of a relict population of a wider geographic distribution resulting from Pleistocene cooling. This theory was later rejected (Grant 1987) on the lack of evidence (middens and museum collections) for the historical occurrence of Mytilus in southern Africa. The dramatic colonization of west coast islands by Mytilus over the past 10 years, reflected in changing diets of oystercatchers, is further evidence for a recent invasion. Major harbour developments at Saldanha for the export of raw materials commenced in 1973, and in 1976 the first large tanker entered the Bay. In 1979 the sea water dam housing one of the Bay's mussel farms was completed, and was estimated to contain a standing stock of ca 100 t of Mytilus. Commercial production of Mytilus at this site was commenced in 1981, and the first year's production was approximately equal to the 1979 standing stock. Saldanha is considered to be the probable site of introduction.

Relative to indigenous mussel species, Mytilus exhibits several characteristics typical of an aggressive invasive species. Most important of these are its rapid growth rate at differing water

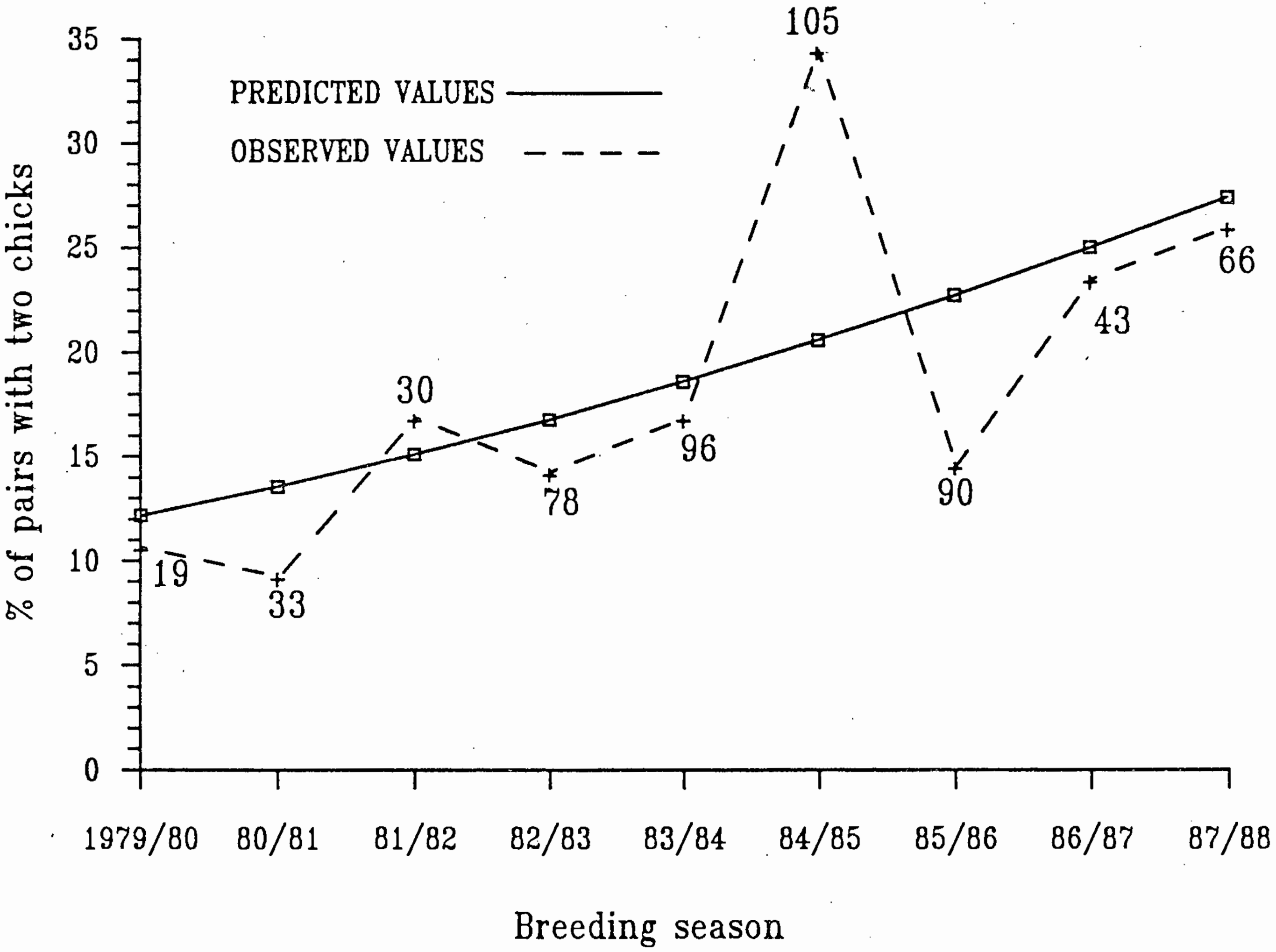

Figure 8. Observed and predicted (see methods) proportions of oystercatcher pairs at islands near Saldanha with two chicks, 1979/80 - 1987/88. Sample sizes (No. of pairs) entered adjacent to observed values.

temperatures, high fecundity and resistance to desiccation. Its failure to invade natural sublittoral substrata, despite its viability on suspended commercial mussel ropes, may reflect its intolerance of silt deposition and the competitive advantage that this affords the silt-tolerant Choromytilus (Barkai & Branch in press). However, it should be noted that Perna, which occurs subtidally, is also not silt-tolerant, and therefore that other factors are probably operating to prevent penetration of subtidal regions by Mytilus.

Mytilus clearly is a superior competitor for primary rock space to both the indigenous mussel Aulacomya and the dominant intertidal grazing herbivore, the limpet Patella granularis. Intertidally, Aulacomya has become much rarer, and individuals much smaller, in the past 10 years (e.g. Table 3, Fig. 5). It seems likely that invasion by Mytilus may drive Aulacomya close to local extinction intertidally.

Although the proportion of P. granularis in the diet of oystercatchers has decreased dramatically (Table 3), this is probably due more to a change in the distribution and size structure of the limpet population than to a change in abundance per se. Oystercatchers preferentially prey on medium-sized (25-45 mm) P. granularis (Hockey & Underhill 1984), which they remove from open rock faces (Hockey 1981). An increase in the ratio of mussel bed to open rock serves to increase absolute abundance and fecundity of P. granularis, but to decrease the abundance of animals >25mm in length, 25mm being close to the maximum size of P. granularis in mussel beds. Although fewer P. granularis were eaten in 1988 than in 1979, they were significantly larger (Fig. 7). Large limpets may be more resistant to patch encroachment by Mytilus than smaller limpets, but this is untested.

The implications of Mytilus invasion for macrofaunal diversity are unquantified. A high proportion of the macrofaunal diversity on rocky shores in southern Africa occurs within mussel beds. Both

Mytilus and Aulacomya grow in multi-layered and structurally heterogeneous matrices with abundant interstitial space. Physical attributes of beds of the two species are therefore similar and probably support similar interstitial communities. However, the high density of P. granularis on Mytilus beds relative to Aulacomya beds largely prevents the build-up of epiphytic macroalgae such as Gigartina and Pterosiphonia spp on Mytilus (Turpie 1986). Differences in limpet density are related to differences in morphology of the mussel shells (smooth vs ribbed), and may have implications for reduced diversity of associated macro- and meio-epifauna.

The continued spread of Mytilus along the southern African coast seems inevitable, as does an increased demand for its use in local myticulture. In 1986, the wholesale value of Mytilus was ca R 5000 per t. The introduction of Mytilus at Port Elizabeth almost certainly followed the transfer of mussel ropes from Saldanha. Establishment of other mussel-farming enterprises along the coast is likely to have the same consequence unless the transfer of ropes between farms is controlled. As a caveat to such a recommendation, the efficiency of mariculture as a source of protein production (Davies 1969, Winter et al. 1984) may, in concert with the problems of southern Africa's burgeoning population, place severe socio-economic pressure on the conservation ideal of preserving natural ecological processes.

Shellfish have been collected for subsistence purposes along the southern African coast for more than 60 000 years, and perhaps as long as 130 000 years (Volman 1978, Thackeray 1988). Subsistence exploitation is still widespread in some regions of the south and east coasts (e.g. Hockey et al. 1988, de Freitas & Martin in press), and shellfish populations are under additional pressure from bait collectors and commercial exploitation (Hockey & Buxton in press). In Transkei, shellfish provide up to 13.6% of the per capita annual protein requirement of coastal people (Hockey et al. 1988). Perna are favoured by collectors (Bigalke 1973, Siegfried *et al*. 1985), but intense exploitation pressure has reduced mussel stocks, leading to an increased preponderance of limpets in the diet and resulting in turn in fundamental changes in the structure of intertidal communities (Hockey & Bosman 1986).

*Perna* and *Mytilus* are similar in their tolerances to desiccation and siltation, and both grow rapidly. Any competitive interaction between them, at least intertidally, is likely to be more evenly balanced than that between *Mytilus* and *Aulacomya*. Invasion of the west coast by *Mytilus* appears to have increased food availability to oystercatchers, and invasion of the south coast may lead to increased standing stocks and production of edible shellfish for coastal subsistence communities. However, this increase is likely to be at the cost of diminished *Perna* stocks. *Perna* is not a competitive dominant ( Lambert & Steinke 1986) as is, for example, *Mytilus californianus* (Paine & Levin 1981). Exploitation of *Perna* beds typically leads to a community dominated by other sessile species such as coralline algae and barnacles (Hockey & Bosman 1986, Lambert & Steinke *op. cit*.), and the competitive dominance exhibited by *Mytilus* on the west coast suggests that it may provide a food source more resistant to exploitation than *Perna*.

Commercial exploitation of intertidal invertebrates, as distinct from mariculture, is in its infancy in southern Africa. A licence application for commercial exploitation of the limpets *P. argenvillei* and *P. granatina* on the Namaqualand coast is pending. Careful monitoring of the effects of limpet removal as they relate to potential encroachment and long-term establishment of *Mytilus* is required. The potential for commercial exploitation of *Mytilus* itself may prove to be a rewarding avenue of research.

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# CHAPTER 2

# MARINE MUSSELS IN SOUTHERN AFRICA - THEIR DISTRIBUTION PATTERNS, STANDING STOCKS, EXPLOITATION AND CULTURE

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## ABSTRACT

Four species of mussel are abundant in southern Africa. The cool, upwelled waters of the west coast support the major populations of three of these, the ribbed mussel *Aulacomya ater*, the black mussel *Choromytilus meridionalis* and the introduced Mediterranean species *Mytilus galloprovincialis*, which has recently become the dominant intertidal species in the area. The warmer south and east coasts are colonized mainly by the brown mussel *Perna perna*, although all of the other three species penetrate along the south coast and *Mytilus* appears to have the potential to dominate this region in the future, at the expense of *Perna* . The overall standing stock of intertidal mussels is estimated at 114 $\times 10^3$ metric tons whole wet mass. Of this 69% is found west of Cape Agulhas, 20% along the south coast, 4% in Transkei and 7% in Natal. *Mytilus galloprovincialis* comprises 44% of total standing stock, while *Perna perna* contributes 39%. Despite the abundance of mussels along both west and south coasts, exploitation is minimal in these regions. The reasons for this are that shellfish are not traditional food resources in these areas and, in the case of the west coast, because of low human population density and the perceived risk of paralytic shellfish poisoning. The much smaller resources along the Transkei and Natal coasts are heavily exploited, with annual rates of removal approaching or even exceeding standing stock in some areas. Overall crop is probably less than 2 000t, of which an estimated 316t is taken from the Transkei and 347t from Natal annually. Although mussel aquaculture is a recent development in southern Africa, the first farm having opened in 1984, current production of ca. 800t p.a. is already approaching the entire wild crop. Aquacultural output is, however, directed at the luxury market and is unlikely to play any role in reducing the pressure on wild stocks by subsistence gatherers .

# INTRODUCTION

South Africa has a long, wave-exposed coastline which extends for some 2 570km from the Namibian border (28°S 16°E) in the west to that with Mocambique (26°S 32°E) in the east (Fig. 1). Sea temperatures within this coastal strip are determined largely by the two major current systems. To the east the southerly-flowing Agulhas Current transports warm (21-26°C) water close inshore along the Natal coast, but south of East London this is deflected offshore by the progressively widening Agulhas Bank. The Benguela System of the west coast is characterized by frequent upwelling events, resulting in cooler conditions, with minimum temperatures of 9-10°C being experienced during summer, when offshore winds predominate, while maxima of 15-16°C occur in winter, when sun-warmed surface waters advect onshore (Branch & Griffiths 1988). Based on these current systems the southern African coastline can be divided into three major biogeographical provinces (Brown & Jarman 1978): a sub-tropical east coast region extending southwards to about East London; a warm-temperate south coast reaching from there to Cape Agulhas and a cold-temperate west coast region extending northwards into Namibia (Fig. 2).

Some 27 species of mytilid mussels have been recorded in southern African waters (Kilburn & Rippey 1982), four of which attain sufficient size and density to form extensive beds on rocky intertidal and subtidal reefs. Of these one, the brown mussel *Perna perna*, is found predominantly in the sub-tropical east and warm-temperate south coast regions. The other three, the indigenous black mussel *Choromytilus meridionalis*, the ribbed mussel *Aulacomya ater*, and the introduced European mussel *Mytilus galloprovincialis* (Grant *et al.* 1984; Grant & Cherry 1985), all attain their greatest densities in the cooler waters of the west coast (Fig. 2).

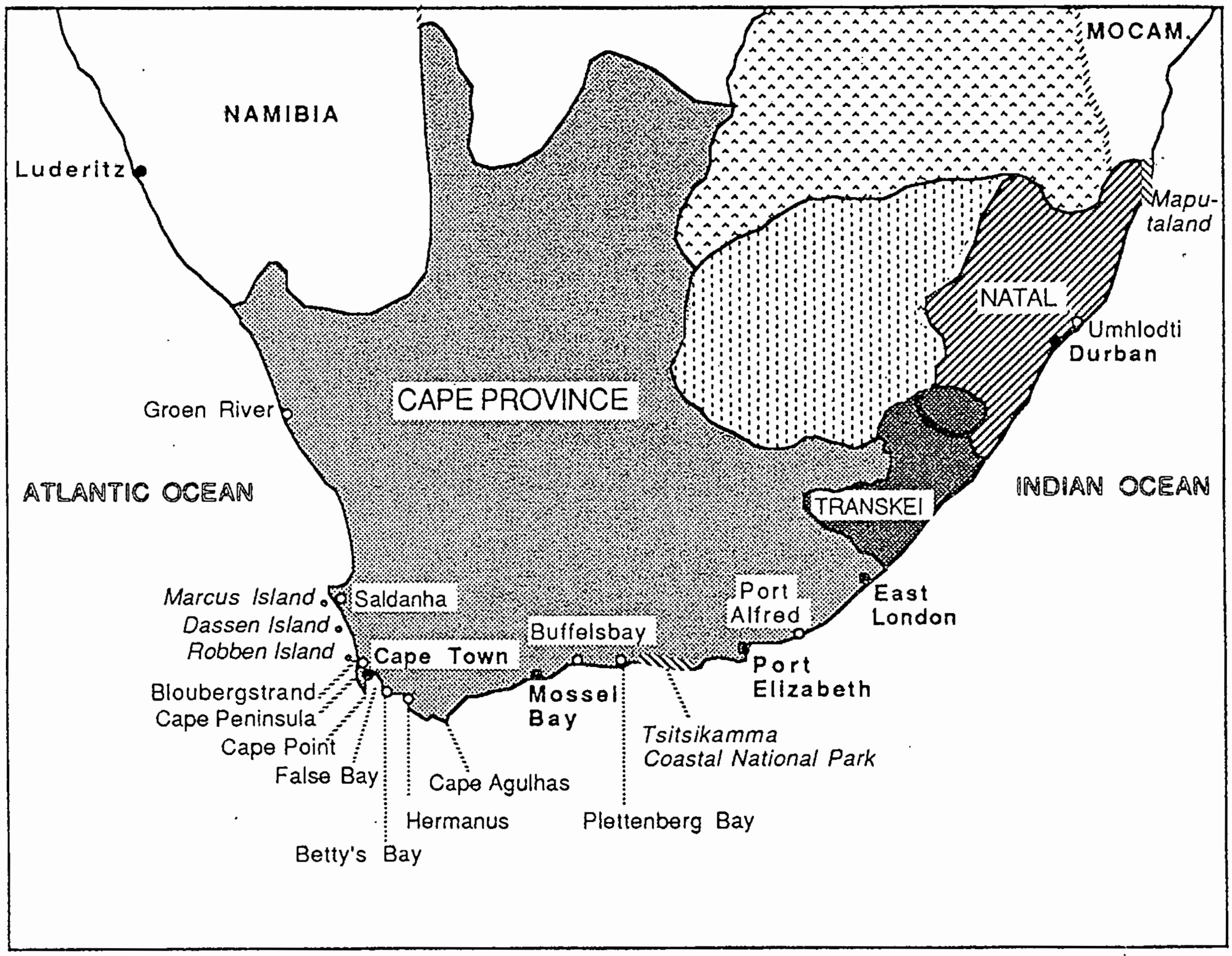


Figure 1. The southern African subregion showing sites referred to in the text.

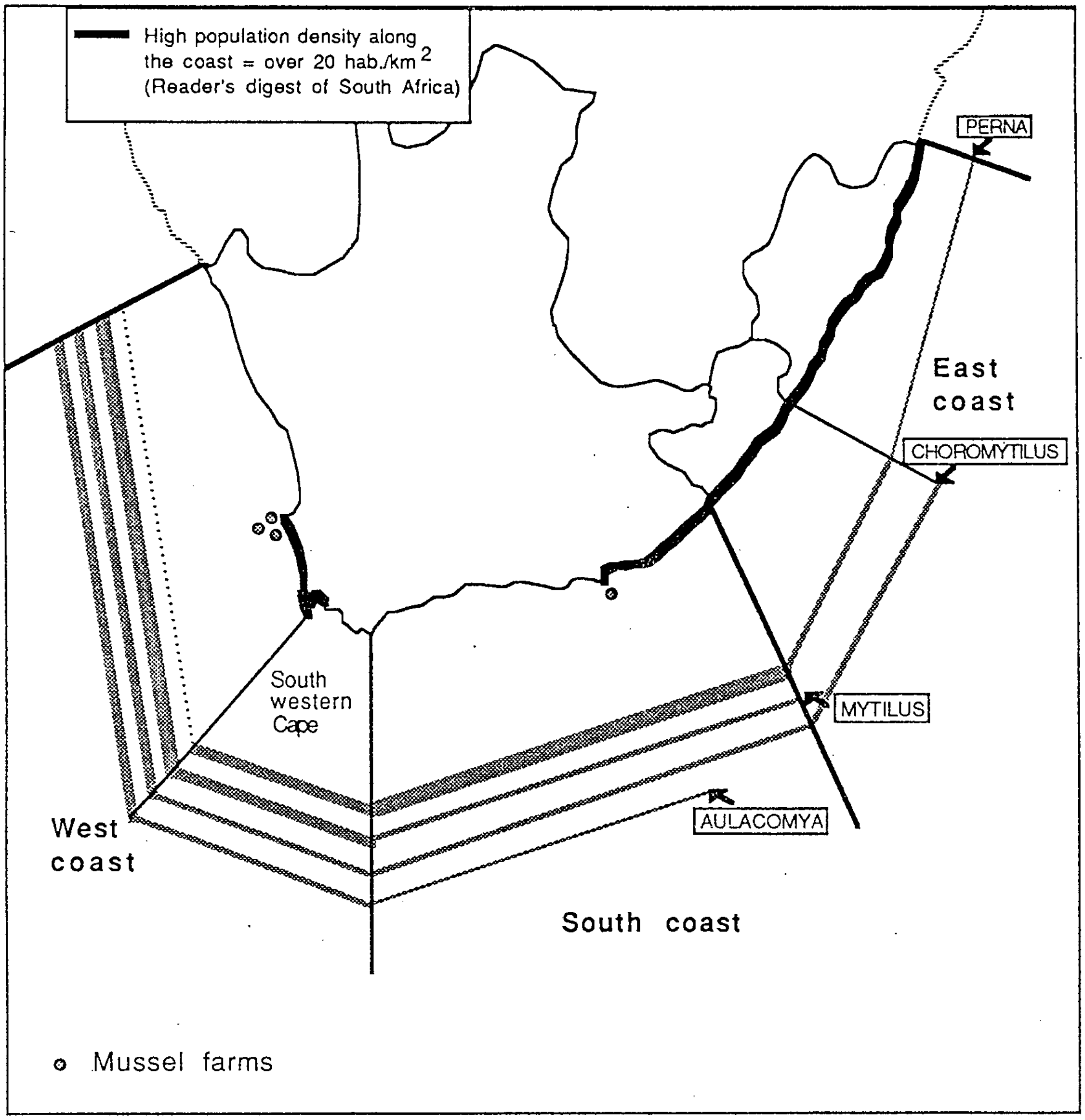


Figure 2. Distribution patterns of major mussel species around the southern African coastline - the thickness of lines indicates relative abundance. Locations of the four mussel farms currently in production are also shown.

In addition the smaller Semimytilus algosus has been recorded as abundant in northern Namibia. Penrith & Kensley (1970) give the southern limit of this species as Swakopmund ( 22°S), although recent data show it as occurring as far south as Elizabeth Bay ( 27°S) (C. Beyers, Sea Fisheries Research Institute, Swakopmund, pers. comm.).

Numerous publications have addressed aspects of the ecology or physiology of the various southern African mussel species. Most of these have been reviewed by Griffiths & Griffiths (1987) and Branch & Griffiths (1988). The rapidly increasing exploitation of Perna perna by indigenous peoples in the Transkei, and the effects of this on community structure have also received considerable attention (Bigalke 1973; Siegfried et al 1985; Hockey & Bosman 1986; Hockey et al. 1988; Lasiak & Dye, 1989).

In this paper we take a more comprehensive view of the mussel resources of the region by making a first estimate of the stocks of littoral mussel species and of their geographical distribution. This is then related to the exploitation pressure on such stocks and the recent development and rapid expansion of a mussel culture industry in the region.

## SPECIES CHARACTERISTICS

The features characterizing the four common mussel species found along the southern African coastline are summarized in Table 1. The ribbed mussel Aulacomya ater is the most easily recognized species, by virtue of the strong external radial sculpturing on its shell. Perna perna is most reliably distinguished by the divided posterior retractor muscle scar on the interior surface of the shell, but in the field the brown shell color provides a good identification feature, especially for specimens collected on the south and east coasts. On the west coast P. perna is uncommon and tends to occur singly amongst Mytilus galloprovincialis,

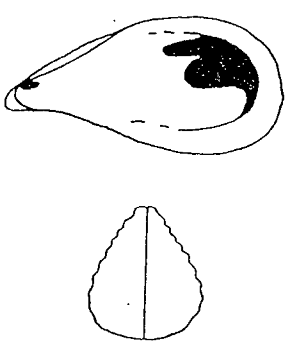
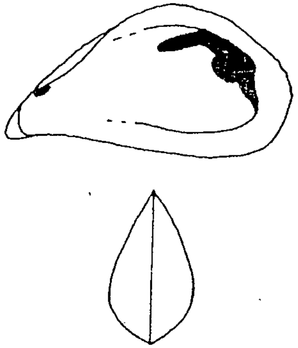
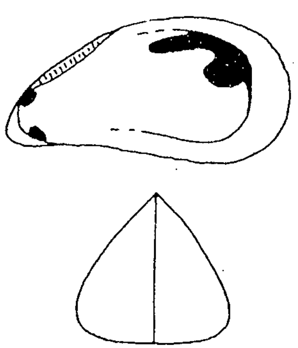
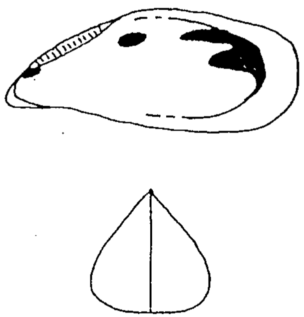
| | Aulacomya ater | Choromytilus meridionalis | Mytilus galloprovincialis | Perna perna |
|---|---|---|---|---|
| Internal view of shell (showing muscle scars in black)<br>& cross section profile |  |  |  |  |
| Resilial ridge | smooth | smooth | pitted | pitted |
| External shell colour & texture | BROWN to BLACK with marked wavy radial ribs | Usually BLACK occasionally dark brown, smooth | Typically BLACK shading to brown ventrally (rarely light brown throughout), smooth | BROWN sometimes tinged with GREEN especially on margins, smooth |
| Flesh colour | Brown ♀<br>Off-white to yellow ♂ | Dark choc. ♀<br>Off-white to yellow ♂ | Orange ♀<br>Off-white to yellow ♂ | Orange ♀<br>Off-white ♂ |
| Approximate maximum size | Intertidal 70 mm<br>Sublittoral 95 mm | Intertidal 90 mm<br>Sublittoral 150 mm | Intertidal 85 mm<br>Sublittoral 140 mm | Intertidal 90 mm<br>Sublittoral 125 mm |

Table 1. Features characterizing each of the four mussel species abundant along the southern African coastline.

which can also be brown. Confusion can thus occur, but after examination of the adductor scars of a few specimens identifications can usually still be made on the basis of color and shape, the shells of Perna tending to be more elongate and slender than those of Mytilus. Choromytilus meridionalis can be reliably distinguished from P. perna by shell color, but is easily confused with M. galloprovincialis, especially when small. The dark brown color of the female gonad in Choromytilus, the absence of pits in the resilial ridge and of an anterior adductor muscle are the best distinguishing features, but specimens can be also distinguished by shape in the field. Choromytilus is much thinner and more symmetrical in cross-section than Mytilus, large specimens of which can be so broad and ventrally flattened that they stand un-supported on the ventral shell surface.

## DISTRIBUTION PATTERNS

Distribution patterns were determined from museum collections, published distribution records and from direct field observations at sites in the Durban region and at 12 sampled, and numerous other visually examined, locations between East London and Groen River in the Cape Province, in addition to visual inspection of numerous other sites.

Detailed vertical zonation patterns were also examined at three locations in the south western Cape, where the ranges of all four mussel species overlap. These were carried out by removing a series of $0.0625m^2$ (25cm x 25cm) quadrats along a belt across the intertidal from high to low water of spring tides and counting the mussels of each species contained within each sample.

The ribbed mussel, Aulacomya ater, which is widespread on both Atlantic and Pacific coasts of South America (Suchanek 1986) has a southern African distribution extending from approximately Rocky Point

(18°S) in northern Namibia (Penrith & Kensley 1970), to Port Alfred (26°S) on the south-east coast (Fig. 2) (Day 1974; Kilburn & Rippey 1982). Aulacomya reaches its maximum abundance in the sublittoral and is the dominant species found in the kelp beds and sublittoral reefs along the Cape west coast (Pollock 1979; Field et al. 1980). Over the past decade there has been a marked decline in the numbers of Aulacomya in the intertidal, as they have become replaced by the invasive Mytilus, which is a superior competitor for intertidal space (Hockey & van Erkom Schurink, in press).

Choromytilus meridionalis is restricted to areas of cool upwelled water on the west and south coast of southern Africa. There is some doubt as to whether the species is taxonomically distinct from the South American C. chorus (Kilburn & Rippey 1982). The distribution ranges from about Walvis Bay (22°S) to northern Transkei (30°E), but there is a marked reduction in abundance east of Cape Agulhas. Extensive beds of C. meridionalis were long regarded as a characteristic feature of west coast rocky shores (e.g. Brown & Jarman 1978), but Mytilus galloprovincialis now dominates most intertidal wave-exposed sites in this region.

Observations by A. du Plessis (Sea Harvest Corporation, Saldanha Bay, unpublished) and Hockey & van Erkom Schurink (in press) suggest that this change has resulted from the recent introduction and rapid spread of Mytilus galloprovincialis at the expense of C. meridionalis, as postulated by Grant & Cherry (1985).

Intertidal populations of C. meridionalis are currently found on low-shore rock surfaces subject to sand cover or abrasion (Branch & Griffiths 1988). Extensive sublittoral beds still occur at selected sites throughout the region, as is evidenced by the abundance of large, fresh shells cast ashore following winter storms, and by direct diving observations, such as those at Marcus Island, Saldanha Bay, undertaken by Barkai & Branch (1988).

The brown mussel Perna perna is the dominant mussel species in northern Namibia, but is virtually absent on the central and southern parts of the west coast. It becomes dominant again along the south and east coasts of southern Africa into Mocambique (Fig. 2). Isolated individuals occur throughout the west coast, but do not form beds in the area between False Bay and central Namibia. Outside the southern African region P. perna is widely distributed in the tropical and subtropical regions of the Indian and Atlantic oceans (Berry 1978). Populations in the Mediterranean are considered by some recent authors to represent a distinct species, P. picta (Shafee 1989).

The Mediterranean mussel, Mytilus galloprovincialis, is widespread in the Mediterranean, along the Atlantic coast of Europe and in north west Africa, where it may hybridize with M. edulis (Beaumont et al 1989). It has also colonized Japan (Wilkins et al 1983; Hosomi 1984). The presence of this species along the west coast of South Africa was first reported by Grant et al (1984), although the identification was only confirmed the following year (Grant & Cherry 1985). M. galloprovincialis is currently the dominant intertidal mussel species over an extensive area stretching between Luderitz (26°S) and Cape Point (34°S), but also occurs in lower density on the east coast up to East London (27°E). This is despite the fact that it is thought to have been introduced very recently, perhaps only over the past 20 years (Grant & Cherry 1985).

M. galloprovincialis is a fast-growing species with a high reproductive output and a considerable tolerance for desiccation. It outcompetes the indigenous west coast species, at least in silt-free intertidal sites (Hockey & van Erkom Schurink, in press). For some unknown reason M. galloprovincialis is uncommon in the sublittoral, although it flourishes when permanently submerged in suspended rope culture (see below). Experimental studies ( chapter 4 ) have shown that M. galloprovincialis grows rapidly in the warmer conditions at Port

Elizabeth. This suggests that it has the potential to invade the south and east coasts in the future, in competition with Perna perna .

## VERTICAL ZONATION PATTERNS

Three mussel species coexist at sites on the west coast (Fig. 3a,b). Mytilus is usually the most abundant of these intertidally, occupying a distinct band in the mid intertidal that extends as much as 160cm above the low water spring tide level (LWS) (Fig. 3). Density tends to decline towards LWS and few specimens are found at or below this level. Choromytilus usually colonizes lower shore levels, and is the only species to survive in sandy pools or on flat rock platforms subject to sand scour (such as occur near LWS at Bloubergstrand) . As one moves downshore, Choromytilus density frequently increases abruptly at or near LWS and from there it extends in tightly-packed beds to at least 10m depth (e.g. at Marcus Island - Barkai & Branch 1988). Aulacomya reaches maximum intertidal concentrations at the lowest tidal levels and often monopolizes sediment-free sublittoral rocky reefs from this point down to at least 40m depth (Pollock 1979; Field et al. 1980). Small Aulacomya can nevertheless penetrate upshore to the mid-intertidal by living deep within the matrix of thick aggregations of Mytilus (or Choromytilus), which presumably protect them from desiccation.

Sites in the extreme south western Cape, such as False Bay (Fig. 3c), are the only areas in which sizeable populations of all four mussels coexist. Here both Perna and Mytilus are almost exclusively intertidal, with Mytilus occuring at higher elevations. Choromytilus and Aulacomya become more common at lower levels and predominate sublittorally. Distribution patterns in this overlap region are, however, highly variable, not only between adjacent sites ( perhaps subject to different

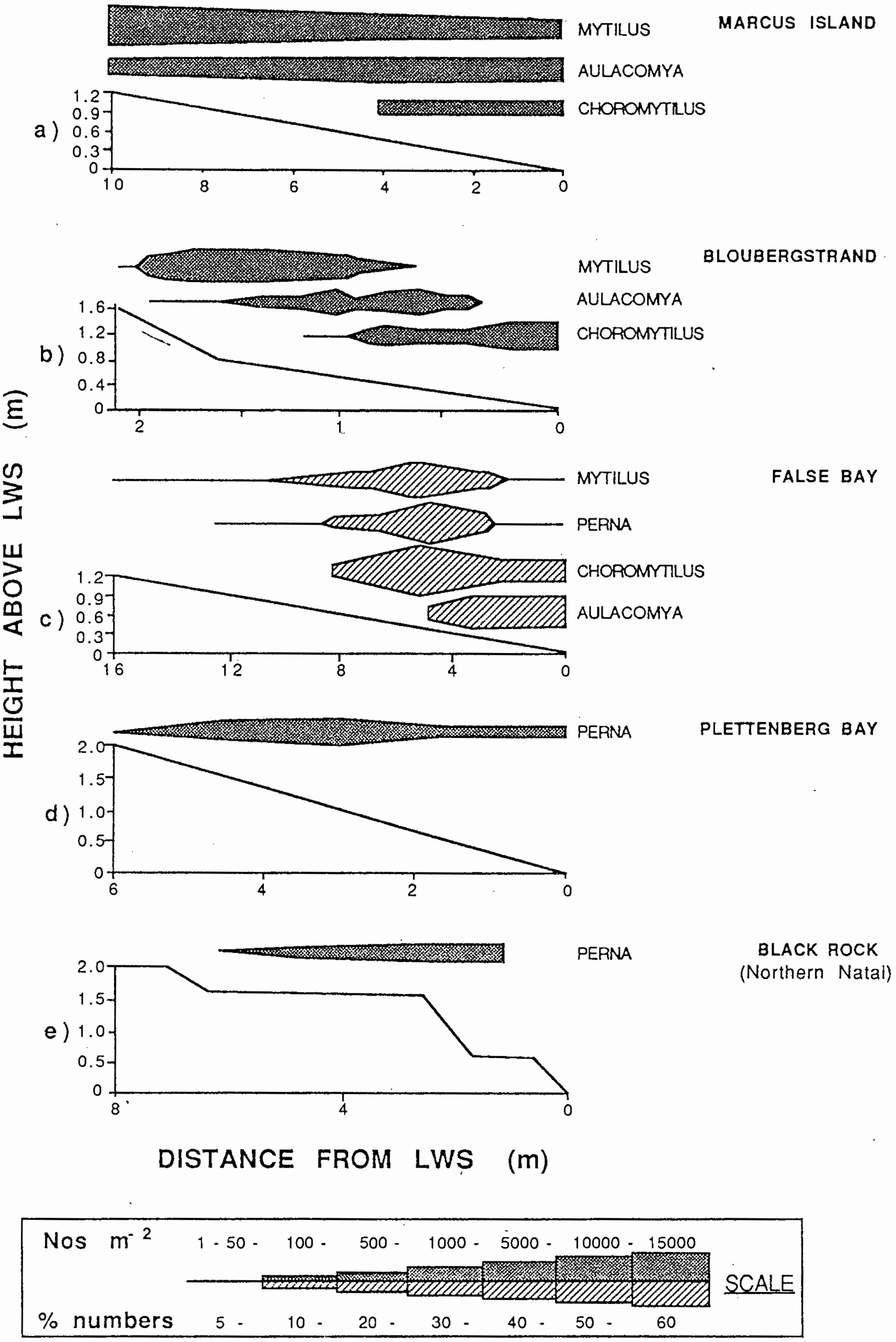


Figure 3. Intertidal distribution patterns of mussel species at a variety of sites around the southern African coastline. For site location see Fig1. Data for Plettenberg Bay after Wooldridge (1988) and for Black Rock after Jackson (1976).
The kite for False Bay is a composite of 8 different sites and his hence given in % by numbers.

temperatures or sediment loadings), but also over time, depending on the erratic recruitment of the various species (e.g. Griffiths 1981).

On the south and east coasts Perna perna is the only abundant mussel species. Populations at sites such as Plettenberg Bay (Fig. 3d) in the southern Cape reach their maximum abundance in the lower mid-intertidal, since they are largely excluded from the sublittoral fringe by characteristic dense bands of limpets, Patella cochlear, and large ascidians, Pyura stolonifera. In Natal and Transkei, where the cochlear zone is poorly developed or absent, P. perna reaches its maximum abundance in areas of heavy wave action from the mid intertidal to LWS and thereafter to depths of at least 5m (Jackson 1976; Berry 1978), although it is sometimes replaced in the lowest intertidal levels by dense beds of coralline algae (e.g. Fig. 3e). Unlike the situation on the west coast, deeper reefs are largely devoid of mussels (see for example Connell 1988).

## STANDING STOCKS

The standing stocks of mussels at each of our sampling sites around the Cape coast were estimated by measuring the vertical and horizontal extent, and hence the area, of intertidal mussel beds over 100m-long stretches of rocky shore. Mass of mussels per unit area was obtained by removing random 25x25cm ($0.0652m^2$) samples from various tidal elevations and measuring the whole wet mass of each species with a hand-held Salter balance.

Data for Natal and Transkei were extracted from unpublished reports and personal communications provided by R. Kyle (Bureau of Naturalresources, Kwangwanase ) and A. J. de Freitas ( Oceanographic

Research Institue, Durban). Approximate overall standing stocks for each region were extrapolated from these biomass figures (Table 2) using estimates of the length of rocky and mixed shore in each region, as provided by Bally et al. (1984). All the rocky shore and 25 % of the mixed shore was considered to be suitable mussel habitat.

While estimates obtained in this way are only first approximations of the stocks they are nevertheless sufficient to provide an index of relative abundance of the various species and of the geographic distribution of the mussel resources.

The west coast, from Cape Point northwards, is the area of maximal mussel standing stock, whether expressed in terms of biomass per km, or in total (Tables 2, 3). The intertidal mussel biomass averages 263 metric tons km$^{-1}$ and comprises 74% Mytilus, 16% Aulacomya and 10% Choromytilus. Based on a regional total of 245 km of suitable coastline, this represents an intertidal standing stock of ca 64 608 tons for the whole area.

Extensive sublittoral mussel resources also exist in this area. These comprise mainly Aulacomya ater, which can form dense beds that reach depths up to 40m and extend 1km or more offshore (Pollock 1979; Field et al 1980). Largely because Aulacomya forms the primary food resource for the commercially valuable rock lobster, Jasus lalandii, several authors have attempted to estimate the standing stocks of sublittoral mussels in the area. Based on such data, Wickens & Field (1988) have calculated the standing stocks of Aulacomya on three of the most important rock-lobster grounds, namely the Cape Peninsula, Dassen Island and Robben Island. These three areas support an estimated 51 858, 341 650 and 156 124 tons of whole wet mass respectively. Similar surveys by Field et al (1980) at two sites north of Cape Town (Kreeftebaai and Melkbos) estimated average mussel standing stocks of 2.35kg m$^{-2}$. Given a mean

| Region | Site | Mean wet biomass kg $m^{-2}$ |  |  |  | $m^2$ mussel bed $km^{-1}$ intertidal rocky shore |  |  |  | Regional standing stock tons $km^{-1}$ rocky shore |  |  |  | Total tons $km^{-1}$ for site | Source |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
|  |  | A | C | M | P | A | C | M | P | A | C | M | P |  |  |
| WEST COAST (Orange River to Cape Point) | Groen River | 18 | 7 | 31 | - | 3 200 | 1 700 | 5 000 | - | 58 | 12 | 155 | - | 225 | This study |
|  | Marcus Island | 9 | 5 | 30 | rare | 5 200 | 4 900 | 7 900 | - | 47 | 25 | 237 | <1 | 309 | This study |
|  | Bloubergstrand | 28 | 33 | 46 | rare | 900 | 1 300 | 4 100 | - | 25 | 43 | 189 | <1 | 257 | This study |
|  | MEAN | 18.3 | 15.0 | 35.7 | <0.1 |  |  |  |  | 43.3 | 26.7 | 193.7 | <1 | 263.7 |  |
|  | Total km of suitable mussel habitat = 245 km |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
|  | Total Biomass |  |  |  |  |  |  |  |  | 10 609 | 6 542 | 47 457 | ≤1 | 64 608 |  |
| S.W. CAPE (Cape Point to Cape Agulhas) | False Bay | 20 | 19 | 26 | 48 | 500 | 400 | 1 900 | 2 100 | 10 | 8 | 49 | 101 | 168 | This study |
|  | Hermanus | - | 9* | + | present | - | 600 | - | - | - | 5 | - | - | 5 | De Villiers 77 |
|  | Cape Agulhas | - | - | - | 43 | - | - | - | 1 900 | - | - | - | 82 | 82 | This study |
|  | MEAN | 6.7 | 9.3 | 8.7 | 30.3 |  |  |  |  | 3.3 | 4.3 | 16.3 | 61.0 | 85.0 |  |
|  | Total km suitable mussel habitat = 162 km |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
|  | Total Biomass |  |  |  |  |  |  |  |  | 535 | 679 | 2 641 | 9 882 | 13 770 |  |
| SOUTH COAST (Cape Agulhas to East London) | Mossel Bay |  |  | - | 39 |  |  | - | 1 770 |  |  | - | 69 | 69 | This study |
|  | Buffelsbay |  |  | - | 38 |  |  | - | 2 680 |  |  | - | 102 | 102 | This study |
|  | Plettenberg Bay |  |  | 3 | 35 |  |  | 350 | 2 800 |  |  | 1 | 98 | 99 | This study |
|  | Tsitsikamma |  |  | - | 13 |  |  | - | ? |  |  |  | - | - | Craw. & Bow.83 |
|  | Port Elizabeth |  |  | 5 | 32 |  |  | 820 | 1 560 |  |  | 4 | 50 | 54 | This study |
|  | Port Alfred |  |  | - | 52 |  |  | - | 2 090 |  |  | - | 109 | 109 | This study |
|  | East London |  |  | - | 38 |  |  | - | 1 470 |  |  | - | 56 | 56 | This study |
|  | MEAN |  |  | 1.1 | 35.2 |  |  |  |  |  |  | 0.7 | 69.1 | 69.8 |  |
|  | Total km suitable mussel habitat = 317km |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
|  | Total Biomass |  |  |  |  |  |  |  |  |  |  | 222 | 21 905 | 22 127 |  |

* based on density of 1.37$m^{-2}$ and mean length of 42mm  + survey pre-dates introduction of Mytilus

A = Aulacomya ater  C = Choromytilus meridionalis  M = Mytilus galloprovincialis  P = Perna perna

Table 2. Estimates of intertidal standing stocks and exploited mussel crop in metric tons for various regions around the southern African coast.

| Stock size (t) | West | S.West | South | Transkei | Natal | Total | % |
|---|---|---|---|---|---|---|---|
| Aulacomya | 10 609 | 535 | - | - | - | 11 242 | 9.8 |
| Choromytilus | 6 542 | 697 | - | - | - | 7 141 | 6.4 |
| Mytilus | 47 457 | 2 641 | 222 | - | - | 50 335 | 44.2 |
| Perna | <1 | 9 882 | 21 905 | <5 000 | 8 400 | ca.45 006 | 39.6 |
| Total | 64 608 | 13 770 | 22 127 | ≤5 000 | 8 400 | ca.113 905 | |
| Region as % total stock | 56.7 | 12.1 | 19.4 | ca.4.4 | 7.4 | | |
| Crop (ty$^{-1}$) | <100 | <<100 | ? | 316 | 347 | | |
| Crop as % standing stock | <1% | <1% | ? | ca.6.3 | 4.1 | | |

Table 3. Intertidal mussel stocks (in metric tons) and their rates of exploitation in each region. Sources of data see Table 2 and text.

reef width of 270m at these two sites, this is equivalent to 634 tons mussels km$^{-1}$ shore. Since there are about 200km of rocky shore on the west coast, exclusive of the three sites studied by Wickens & Field (1988), this would provide a further 126 800t. The sublittoral biomass for Aulacomya alone in the area is thus estimated at 676 000t, some 10 times the intertidal biomass. The extent of sublittoral Choromytilus beds has not been estimated, but in the limited areas in which these occur biomass can be as high as 35 kg m$^{-2}$ ( Barkai & Branch 1988).

The biomass of intertidal mussels in the south western Cape region averages 85 tons km$^{-1}$ (Table 2), considerably lower than on the west coast. Perna perna is the most important species in the south western Cape, making up 72% of the stock, although all four mussels are locally abundant in this overlap region. Sublittoral stocks have been poorly explored, although Aulacomya probably remains the most important species in the cooler sublittoral zone. A single survey by Field et al. (1980) in Betty's Bay revealed a mean standing stock of Aulacomya of only 7g m$^{-2}$ (whole wet weight) over a 1275m wide rocky reef. This is equivalent to a stock of 9t km$^{-1}$ coast or 1458t for the entire area, very much less than the intertidal stock. This may be realistic, since sublittoral reefs in this region are known to be dominated by sponges, echinoderms, ascidians and gastropods, rather than by mussels (Field et al. 1980).

Intertidal standing stocks of mussels along the South Coast (Table 2) are lower again than those in the S.W. Cape, with an average stock of 70 tons km$^{-1}$, consisting 99% of Perna perna. Although all three other species occur in this region, none forms extensive beds like those found farther to the west. Although P. perna beds undoubtedly penetrate below the low water mark onto shallow reefs, the few surveys that have been undertaken on the south coast indicate that they do not extend into deeper water. Studies such as those of Duvenage (1988) show that reefs below

10m depth are dominated by Porifera, Bryozoa and Cnidaria, with less than 1% of the biomass comprising Mollusca, most of which are gastropods.

Perna perna is the only abundant mussel in Transkei, but, as a result of intense exploitation pressure (see below) extensive intertidal beds are found only within nature reserves and on inacessible rock faces (Lasiak & Dye 1989). Elsewhere intertidal populations comprise either newly settled cohorts, or have been reduced to small groups of individuals scattered from the lower shore into the sublittoral fringe. Although Hockey & Bosman (1986) report P. perna densities ranging from 0 - 300 individuals $m^{-2}$ at four sites in the area, no biomass estimates are available for the Transkei. Some idea of overall standing stock can, however, be obtained from the rate of shellfish removal.

Hockey et al (1988) estimate that tribal peoples remove a total of 555 tons of shellfish from the Transkei coast per annum (see below). This rate of exploitation is severely depleting the resource (Siegfried et al 1985; Hockey & Bosman 1986; Lasiak & Dye 1988), despite the fact that P. perna has a high production to biomass (P/B) ratio of about 4 on the Natal coast (Berry 1978). At some sites, the annual rate of removal exceeds the standing stock (Siegfried et al 1985) indicating that overall stock is unlikely to substantially exceed the crop in these areas. Sections of the coast are, however, inaccessible and hence poorly exploited. These factors make it difficult to make a reliable estimate of standing stock, allthough it appears unlikely this could exceed 5 000t. Largely because of extreme exposure to wave action nothing is known of sublittoral mussel stocks in this area. These are protected from exploitation by virtue of their inaccessibility and are likely to exceed the intertidal stock.

In Natal, as in Transkei, P. perna is the only common mussel species. Some standing stock estimates have been published by Berry (1978), but the reef on which he worked has subsequently been covered by sand, eliminating the population. There are indications that population densities have declined throughout the region over the past decade, partly as a result of increased exploitation pressure (Martin & de Freitas 1987; de Freitas pers. comm.). Standing stock estimates are thus based on unpublished data provided by de Freitas (Oceanographic Research Institute, Durban, pers. comm.). Mussel standing stock within the mussel zone at two sites, Umhlodti and Cape Rock, are 2.1 kg $m^{-2}$ and 7.9 kg $m^{-2}$ (whole wet weight) respectively, giving an average of 5 kg $m^{-2}$. The average width of the mussel zone is estimated at 10m, and there are 168km of rocky shore in Natal. This gives a total potential area of mussel habitat of $1.68 \times 10^6$ $m^2$ and a standing stock estimate of 8 400 tons of mussels for the region as a whole.

## SIZE-FREQUENCY DISTRIBUTIONS

The size-frequency distribution of mussels were determined from a series of sites around the coast. Size-distributions are dependent upon recent settlement success, and hence vary with season and over time, even within a fixed site (e.g. Griffiths 1981).

Aulacomya ater is consistently smaller than other species. This can be attributed to the lower tolerance of this species to aerial exposure (Hockey & van Erkom Schurink, in press), its smaller terminal size in this area (Table 1) and its low rate of growth (Wickens & Field 1988).

Intertidal mussels of all species attain a much smaller terminal size than do sublittoral populations (Table 1), largely because of the reduced time available for feeding. For this reason few intertidal mussels exceed 75mm, even at sites which are unexploited because they are remote from centers of population (e.g. Groenrivier) or closed to the public (e.g. Marcus Island ). The largest mussels on west coast shores can either be

Choromytilus or Mytilus, depending on the topography of the site and the population age structure. Very large individuals of both species (>100mm) are sometimes encountered in the intertidal, but these are usually confined to lowshore gullies or have been displaced from sublittoral beds and become reattached in sheltered intertidal pools.

The size distributions of P. perna populations are extremely variable. This can be attributed to unpredictable settlement success in this species, combined with its rapid growth rate and short life span of only 2-3 years (Berry 1978). Intense human exploitation pressures nevertheless have had a marked impact on populations of P.perna, as is evidenced by the much higher proportion of larger (<50mm) individuals at unexploited, relative to exploited sites (Fig. 4 , see also Lasiak & Dye 1989 and Crawford & Bower 1983). The generally smaller average size of individuals in our more northerly samples is all the more notable given that P.perna grow more rapidly in the warmer waters of this region. Thus in Durban, intertidal populations attain 50-60mm in their first year (Berry 1978), whereas this declines to 30-40mm in Transkei (Lasiak & Dye 1989) and Tsitsikamma (Crawford & Bower 1983). Growth rates in the south western Cape are even slower (chapter 4).

## EXPLOITATION

The north western Cape coastal belt is a semi-desert region of poor agricultural potential which supports a sparce human population. This, combined with the restricted number of access points to the coast, has constrained exploitation of intertidal food resources. However, mussels are becoming more popular amongst urban residents, particularly immigrants from those European countries with a tradition of seafood consumption. This has led to some increase in consumption, particularly in the population centers around Cape Town. Many would-be collectors are,

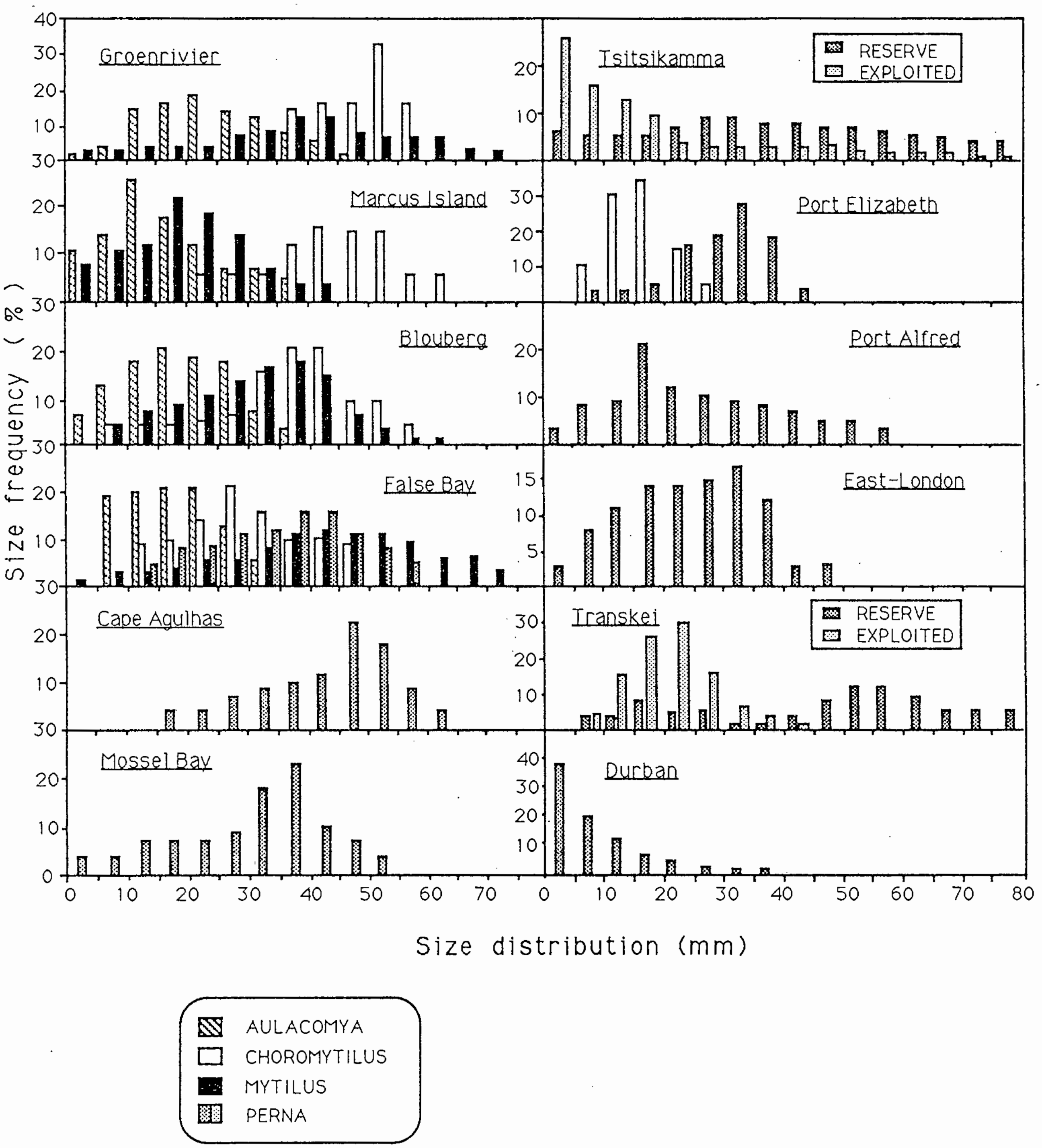


Figure 4. Size-frequency distributions of mussel species at a variety of sites arranged from west (top left) to east (bottom right) around the southern African coastline. Data for Tsitsikamma after Crawford & Bower (1983), for Transkei after Hockey (unpublished) and for Durban after Berry (1978).

however, discouraged from removing mussels by the risk of paralytic shellfish poisoning, which is a fairly common occurrence along the Cape west coast (Grindley & Nel 1970), caused by blooms of the dinoflagellates Gonyaulax grindleyi & G. catanella (Horstman 1981).

The net result of these factors is that, despite the abundance and ready availability of mussels in this region, they are subject to very low levels of human exploitation. While we are not in a position to quantify the amounts taken, these probably total <100t and are insignificant compared with the high rates of mortality resulting from intraspecific competition for space and consumption by natural predators (Griffiths & Hockey 1987).

A similar situation prevails in the south-western Cape region, although anglers in this area can inflict substantial damage to intertidal mussel beds while collecting mussel worms, Pseudonereis variegata, for bait (van Herwerden 1990). Here again the total biomass removed is probably less than 100t $y^{-1}$.

The southern Cape coast is a popular tourist area, and holidaymakers frequently collect mussels for food, particularly during the peak summer season. As a result, marked differences between the size-frequency distributions and biomass of Perna inside and outside of conservation areas may occur, as shown in Fig 4 (Crawford & Bower 1983). This effect is, however, probably confined to the vicinity of resorts or residential areas. More sustained and intense exploitation pressure occur to the east of this region, around East London, by virtue of increased densities of tribal peoples, who exploit the shore for their domestic needs. Unfortunately no quantification of the crop removal rate is available for this area.

Far better data are available for the Transkei, where Hockey et al. (1988) have estimated the annual rate of removal by rural shellfish collectors using aerial survey techniques. Exploitation pressure varies widely along the coast, depending upon human population density, rock type and geographical location. In general, subsistence exploitation is far more intensive in the southern sector (shown in Fig. 5), where it totals some 5 573 kg $km^{-1}$ of rocky shore $y^{-1}$, than in the more sparcely populated northern region (206 kg $km^{-1}$ $y^{-1}$).

Taking the relative lengths of coastline into consideration the total shellfish crop removed from the entire region has been estimated at 555t $y^{-1}$, of which 316t is P. perna (Hockey et al 1988).

While exploitation by rural peoples in the Transkei goes largely unregulated, the harvesting of intertidal and subtidal invertebrates in Natal is controlled by provincial ordinance, collectors being obliged to purchase a licence in order to collect from the shore. They are also required to submit catch returns, the analysis of which give an indication of total annual catch. The total number of mussel and general bait licenses (which also permit collection of mussels) increased from 1 012 in 1974 to 10 606 in 1986 and the mussel catch by licenced collectors rose from 105t $y^{-1}$ to 317t $y^{-1}$ over the same period (de Freitas & Martin 1988).

Since only those catches reported by license holders are incorporated into this figure, it clearly represents a minimum estimate. Not only are license holders likely to underestimate their take, but subsistence harvesting by tribal peoples is seldom included in catch returns. This can be significant in certain areas. Van der Elst & Tregoning (in press) have, for example, documented exploitation by rural people along the Maputoland coast, adjacent to the Mocambique border. Mussels are by far the most important marine crop in this area, each collector removing an average of 4-6kg shelled mussel flesh per collecting trip - this amount being determined simply by the maximum whole unshelled mussel weight the women can comfortably carry up from the shore in a single trip. The total whole wet mass of mussels removed during 1981 from this 83 km of shore - of which only 17 km are rocky - was estimated by van der Elst &

Figure 5. Intense exploitation of Perna perna in the southern Transkei by subsistence gatherers (photo: C.L. Griffiths)

Tregoning (in press) at 30t $y^{-1}$. This amount can be added to that for the rest of Natal, calculated above.

The total crop collected in Natal is thus at least 347t (1986 figures). The exploitation pressure on the shore both by rural peoples and license holders, continues to increase, as indicated by the demand for licenses in Natal, which is increasing at a rate of some 23% p.a (de Freitas & Martin 1988). Collected crops estimated above have thus probably already been considerably exceeded.

## CULTURE

Mussel culture is not a traditional activity in southern Africa. The first commercial culture facility, Seafarm, was established in 1984 and makes use of an enclosed "dam" cut off from Saldanha Bay by a causeway. Two additional operations, Atlas Sea Farms and Sea Harvest Corporation, began production in open water in the same area in 1987, while Atlas Sea Farms also operates a satellite facility at Port Elizabeth. All three companies use the Spanish method of rope culture, the ropes being suspended either from longlines or from rafts.

The three farms in Saldanha Bay primarily market the introduced _Mytilus galloprovincialis_. Wild seed, usually at a shell length of 20-40mm are collected either from caissons or other structures in the harbour, or settle naturally on the culture ropes. Mussels are marketed at a shell length of 55-90mm. Growth to this size is usually accomplished within 4-5 months, largely independent of time of year. Some _Choromytilus_ are found amongst the seed stock, but although these grow as fast and are as palatable as _Mytilus_, they are not favoured for marketing, largely because of the dark brown color of the female gonad.

The Atlas Sea Farms operation in Port Elizabeth grows mainly Perna perna, although some Mytilus have been translocated from Saldanha and grow well in the warmer water conditions at Port Elizabeth.

There has been a rapid increase in production of farmed mussels since 1984 (Fig. 6) . Output for 1989 is anticipated to be 800t whole wet mass. Most of this is sold live in the shell at a wholesale price of R 3 - 4 kg$^{-1}$ (about US$ 1 - 1.4 at current exchange rates) giving the industry as awhole a gross annual income of the order of R 3m (US$ 1m). Other processed products such as frozen seafood mixes, fresh and canned meats and smoked mussels under development are likely to absorb much of the future growth in output. Export potential is also being investigated.

## CONCLUSIONS

This paper presents a first attempt to quantify the marine mussel resources of the southern Africa region and to provide an overview of their distribution patterns, exploitation and management status.

Three indigenous and one introduced species of mussel occur in the region in sufficient densities to be considered exploitable. All four differ in their geographical ranges, vertical distribution patterns and in such biologically important parameters as growth rate and terminal size. These differences are reflected in the stock size, accessibility and vulnerability to exploitation, which show marked regional as well as species-specific variation.

The cooler west-coast region supports the major portions of the stocks of three of the four species. Of these the indigenous Aulacomya ater is primarily sublittoral and has a relatively slow growth rate and

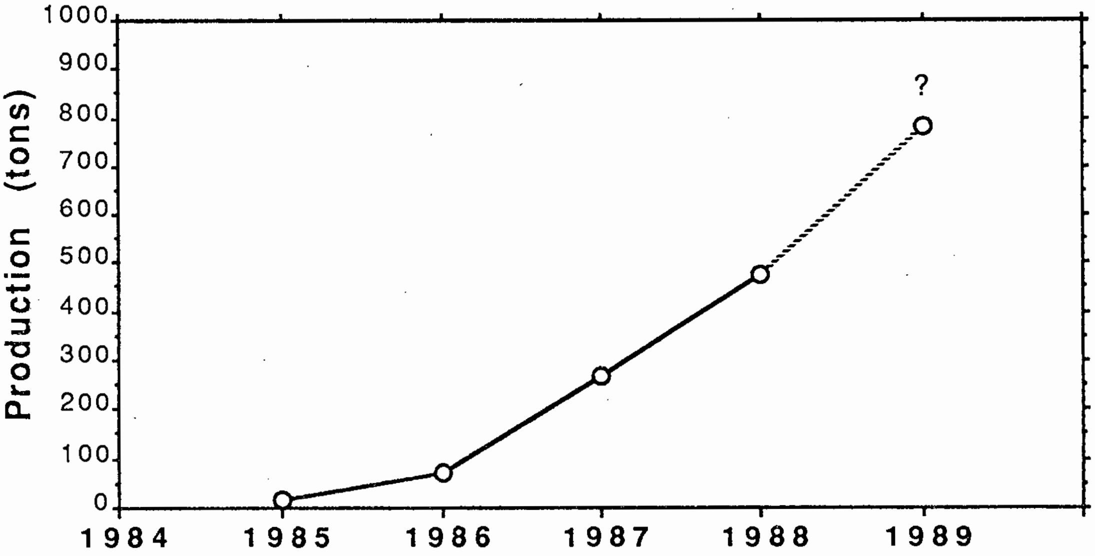


Figure 6. Annual production of cultured mussels in the southern African region 1984-1989.

small terminal size. Thus, although it attains a significant intertidal (and very large sublittoral) biomass, and is a crucial food source for some benthic predators, it is the least suitable of the species in terms of human exploitation and culture. Choromytilus meridionalis is a faster-growing, larger species and has hitherto been regarded as the major intertidal mussel species in this region. It has, however, recently been largely displaced by the introduced Mytilus galloprovincialis, although it remains abundant at some sites, notably those subject to sanding. Because of its high fecundity, rapid growth, considerable tolerance to aerial exposure and ability to grow in dense beds, M.galloprovincialis is now the dominant intertidal mussel along the coastline, comprising some 74% of the total littoral stock of 64 608 metric tons. The establishment of M. galloprovincialis has almost certainly increased total mussel biomass, since it both occupies a large vertical range and attains a higher biomass per $m^2$ than do the species it has displaced.

Moving from the west coast eastwards there is a progressive decline in the abundance of all three of the above species and they are replaced by a single, warm-water form, Perna perna. Mussel standing stock on the east coast is relatively low due in part to the narrower niche breadth of the single east coast species, relative to those of the three west coast forms combined. Other factors, such as human predation pressure and competition between space-occupying species on the shore in the different regions, also play some role, since there are few sites at which P. perna form the extensive beds typical of west coast shores, even in the absence of human exploitation pressure.

The more intense exploitation pressure on the east relative to the west coast makes it difficult to speculate as to the size of the original unexploited stock.

Paradoxically, the regions subject to most intense exploitation are those that probably always supported the smallest stocks, while the extensive resources along the west coast remain virtually pristine. In theory the annual removal of ca 1 000 tons could easily be sustained by the total stock of 114 000 tons without any adverse effects, were it to be evenly spread geographically. Indeed, under a properly managed regional management policy the resource could probably support a crop at least an order of magnitude larger than that taken at present. However, this is impractical since the demand originates from subsistence-gatherers who reside in areas distant from the centers of mussel abundance.

Within the commercial sector potential might exist for the exploitation of wild mussel stocks. This largely luxury market, however, demands a high quality product which is clean, free of sand and of regular size. Such a market is best supplied by mussels grown under controlled culture conditions. Such operations have shown an exponential growth in South Africa over the past few years. Indeed, the existing local market may already be approaching saturation and futher growth may depend upon either development of an export market or an increasing in shellfish consumption by the local population. Neither of these factors is likely to reduce pressure on wild resources by local people in the east coast, which, in the light of increasing population pressure, remains a serious management problem.

## ACKNOWLEDGEMENTS

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# CHAPTER 3

# A COMPARISON OF REPRODUCTIVE CYCLES AND REPRODUCTIVE OUTPUT IN FOUR SOUTHERN AFRICAN MUSSEL SPECIES.

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## ABSTRACT

The timing and intensity of spawning events in four southern African mussel species were deduced from fluctuations in the dry flesh weight of standard-sized individuals, as calculated from monthly length-weight regressions. The sex ratios in three of the four species (Aulacomya ater, Choromytilus meridionalis and Perna perna) were biased in favour of males, but this was not the case for Mytilus galloprovincialis. The calorific value of females was higher than that of males in all species. Aulacomya ater spawned three times a year, although these spawning events differed considerably in timing and intensity between years. Choromytilus meridionalis and M. galloprovincialis generally showed two protracted spawning seasons, one each during summer and winter. Perna perna from Natal spawned over an extended period from May/June - December, while those from the Cape and Transkei had a well marked winter spawning, accompanied by either one extended, or two discrete, spring or summer events. Gamete build up and release resulted in marked variations in flesh yield. This was greatest in M. galloprovincialis, where dry flesh weight can vary three fold between ripe and spawned conditions at a length of 65mm. Equivalent figures for A. ater, C. meridionalis and P. perna were 2.3-fold, 2.8-fold and 2.2-fold respectively. Total individual reproductive output was greatest in A. ater, because of its three annual spawnings, followed by M. galloprovincialis, C. meridionalis and P. perna. When extrapolated to a population level, beds of mussels were estimated to release 3.4 - 10.4 kg $m^{-2}$ $y^{-1}$ wet mass of gametes. This represents a large energy subsidy to adjacent benthic and pelagic communities.

# INTRODUCTION

The reproductive biology of marine mussels has been a subject of research for over 50 years and the subject has been reviewed several times, notably by Fretter & Graham (1964), Seed (1976), Sastry (1979), Suchanek (1985) and Griffiths & Griffiths (1987). A knowledge of the timing and intensity of spawning events is of particular importance to the mussel culture industry, since it can be used to predict subsequent spat settlement. Gamete release also has an immediate and important effect on the market value of the adult stock, since over half the total wet flesh mass can be lost in a single spawning event (see for example Griffiths 1977). On a wider ecological perspective mussel gametes can act as a significant energy subsidy into the pelagic and benthic filter-feeding communities adjacent to the beds. Griffiths (1981a) has, for example, estimated that Choromytilus meridionalis populations can release as much as 19.8 kg wet mass gametes $m^{-2} y^{-1}$ into the overlying water column, while Kautsky (1982) estimates reproductive output by Baltic Mytilus edulis as equivalent to half the total zooplankton production in the area. Since mussels are major space-occupiers, the frequency and intensity of spat settlement also has a profound influence on the communities colonizing both natural rocky shores and man-made structures. These effects include build-up of fouling layers, the displacement or facilitation of other sedentary species and the provision of food for a variety of predatory forms, including man (for review see Suchanek 1985).

The Southern African coastline is colonized by four abundant mussel species, the distribution patterns and diagnostic features of which are described by van Erkom Schurink & Griffiths (1990). One of the species, the brown mussel Perna perna, is a warm-water form which extends from Mocambique to the south-western Cape, but is rare along the Cape west coast, reappearing again in northern Namibia. The remaining forms, the ribbed mussel Aulacomya ater, the black mussel Choromytilus meridionalis and the introduced Mediterranean mussel Mytilus galloprovincialis, achieve their maximum biomass along the cooler west coast, although they all penetrate eastwards along the southern Cape coast at reduced densities.

Several earlier studies have addressed the reproductive biology of these species. In the case of P. perna reproductive cycles of populations from the Durban area (Berry 1978) and from Transkei (Lasiak 1986) have been documented, while some additional information is available on settlement patterns along the southern Cape coast (Crawford & Bower 1983). Reproductive cycles of A. ater from the Cape Town area are described by Griffiths (1977) and Griffiths & King (1979), the latter also providing quantitative estimates of gamete output. In the same area Griffiths (1977, 1981b) estimated reproductive output in several different populations of C. meridionalis. No previous studies have examined southern African M. galloprovincialis, although a number of authors have documented their spawning behaviour in the northern hemisphere, as reviewed by Seed (1976).

Our principal objective here is to compare the spawning cycles and reproductive output in southern African populations of these four mussel species. To do so we have elected to repeat the measurements for A. ater and C. meridionalis, while simultaneously measuring reproductive output for M. galloprovincialis and P. perna in the same geographical region (in the vicinity of Cape Town). This has been done not only to eliminate methodological differences between the various earlier studies, but also to minimize interannual variations that might be caused by temperature and other environmental conditions (such as food availability), which are well known to effect spawning intensity (see review by Seed 1976). Such variables probably account for at least some of the considerable interannual variations in gonad output noted by

Griffiths & King (1979), and Griffiths (1981b).

In addition to establishing the patterns of spawning over a two year period in this single geographic region, we incorporate other data and speculate as to the geographical and interannual variability in the reproductive cycles of southern African mussel species and estimate interspecific differences in reproductive output. The implications of reproductive activity for the flesh yield of collected mussels as well as for the biotic community as a whole are also considered.

## METHODS

The following analyses are based upon monthly samples of 50 mussels of each species collected during low water of spring tides between January 1987 and December 1988. Samples were structured to incorporate an even size spectrum of individuals over the length range 30mm and upwards and were removed from the lower portion of the intertidal range. Aulacomya ater, Choromytilus meridionalis and Mytilus galloprovincialis were collected at Bloubergstrand, in Table Bay, some 20km north of Cape Town (the same site used by Griffiths 1977). Perna perna, which is rare at this site, was collected from Diddo Valley in False Bay, some 50km to the south (Fig. 1).

In the laboratory, mussels were placed in a wire basket and briefly immersed in rapidly boiling water until the shell valves gaped. After rinsing in cold water the shell length of each individual was recorded, the byssus removed, the sex noted and the flesh transferred to an individually numbered aluminium dish to be dried for 48h at 55°C and then weighed.

Dry flesh weights were subsequently regressed against shell length for each sample and the predicted weight of a standard 65mm individual read from the regression equation. These data were subsequently plotted against time to provide an index of temporal cycles of gonad accumulation

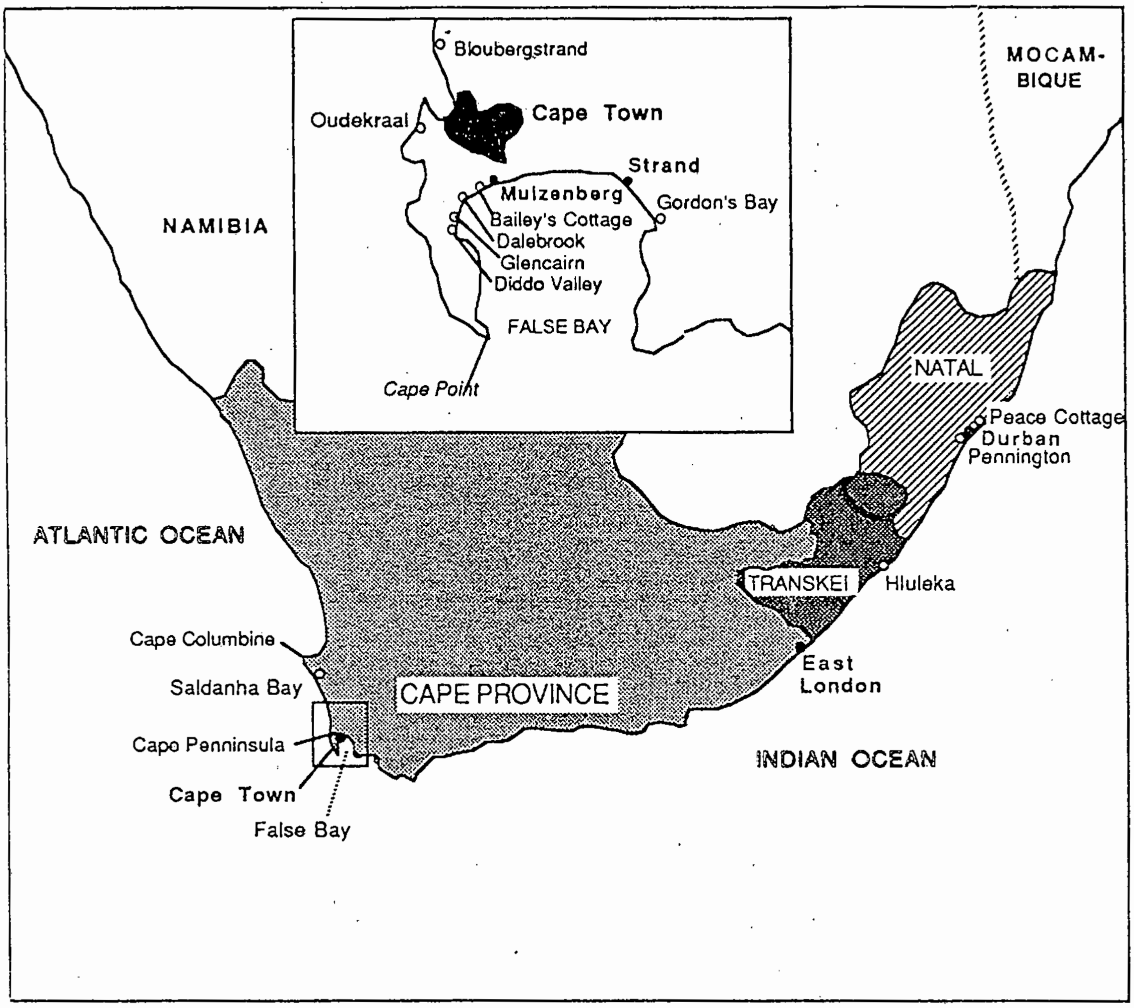


Figure 1. Map of South Africa, showing the locations of sites mentioned in the text.

and gamete release. This is essentially the same technique for obtaining gonad condition used by authors such as Berry (1978), Griffiths & King (1979), Bayne & Worrall (1980) and Kautsky (1982) and has previously been correlated with and shown to provide a realistic reflection of gonad release in A ater, C. meridionalis (Griffiths 1977), and P. perna (Berry 1978, Lasiak 1989). The uncoupling of shell and tissue growth (see Hilbish 1986) is not the problem here it is in Europe, where shell growth essentially ceases during winter. South African mussel grow fairly evenly throughout the year.

Calorific values for the flesh of males and females of each species were obtained by burning triplicate samples of each (derived from a pooled sample of 50 individuals of each sex) in a Digital Data Systems CP 500 Calorimeter.

## RESULTS AND DISCUSSION

### 1. Sex ratios and calorific values.

The mean ratios of males to females in the 24 monthly samples are depicted in the upper section of Fig. 2. The sex ratio in three of the species appears to be markedly skewed in favour of males, the disparity being greatest in A. ater (66M : 34F), followed by P. perna (64M : 36F) and finally C. meridionalis (60M : 40F). All three of these ratios differ significantly from equality (Chi-square tests, $p < 0.05$). Interestingly this tendency is not exhibited by M. galloprovincialis, where males were slightly outnumbered by females in the ratio of 48M : 52F . These proportions do not, however, significantly differ from equality ($p > 0.05$).

Although not all authors give sex ratios for their studies, populations showing similar, but less marked biases in sex ratios have been noted in

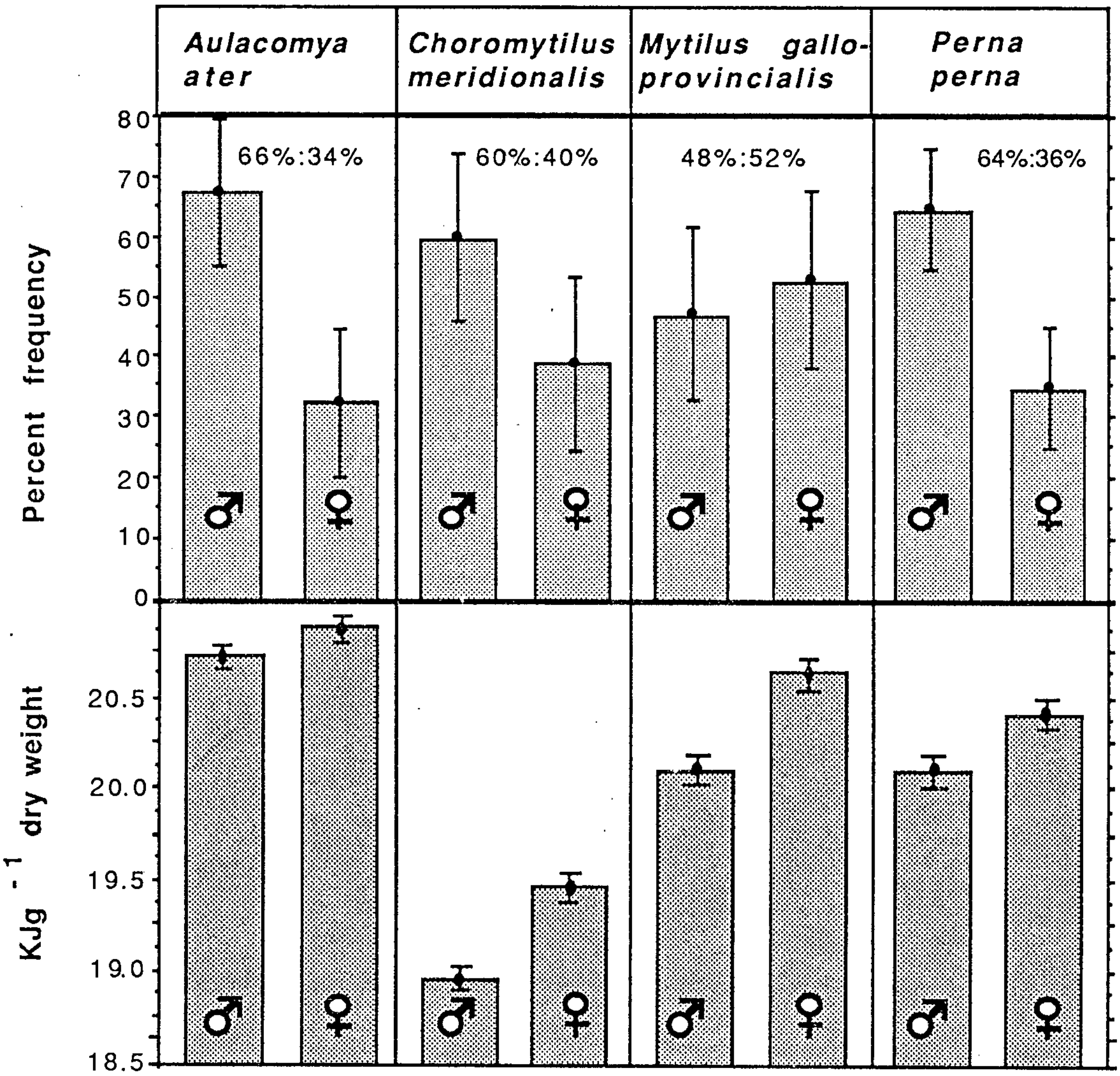


Figure 2. Sex ratios and comparative calorific values of males and females in four southern African mussel species.

the past. For example Griffiths (1977) gives a sex ratio of 57M : 43F for *C. meridionalis* and Lasiak (1986) one of 52M : 48F for *P. perna*. Griffiths & King (1979) did not state sex ratios for their population of *A. ater*, but reexamination of their data sheets shows that of 800 specimens sexed males comprised 53% and females 47%. There are no published records of sex ratios in *M. galloprovincialis* from southern Africa, but a predominance of females has been recorded in several northern hemisphere populations of the closely related *M. edulis* (e.g. Chipperfield 1953, Sugiura 1959, Kautsky 1982).

The ecological significance of these biased sex ratios can only be speculated upon. A male mussel produces approximately $10^4$ times more gametes per unit of reproductive output than a female and both tend to spawn similar amounts by weight (Thompson 1979). Given the presumed rapid dilution factor of sperm in the water column, it is not known whether the number of eggs fertilized is ultimately limited by the rate of egg or of sperm production. In any event this would probably be strongly influenced by such factors as packing density, spawning synchrony and water movement.

Flesh calorific values, shown in the lower panel of Fig. 2, were marginally, but significantly higher in females than in males for all four species (Student's t-test, $p < 0.05$). This is possibly a result of a high lipid content of the gonad material in the mantle of females, as noted for *M. galloprovincialis* by Lubet *et al* (1986). Mean values were highest in *A. ater* at 20.8 $KJg^{-1}$ dry flesh, followed by *M. galloprovincialis* at 20.4 $KJg^{-1}$ and *P. perna* at 20.3 $KJg^{-1}$, while *C. meridionalis* flesh had a considerably lower mean calorific value of 19.3 $KJg^{-1}$. These figures agree closely with the previously published values of 22.1 $KJg^{-1}$ for

A. ater (Griffiths & King 1979), 20.1KJg$^{-1}$ for M. galloprovincialis (Adachi 1972, Hosomi 1985), 20.3 KJg$^{-1}$ for P. perna (Berry 1978) and 19.5 KJg$^{-1}$ for C. meridionalis (Griffiths 1981a). The lower values in C. meridionalis may be a function of the frequent absence of interfollicular storage materials in the post-spawning gonad of this species, as discussed by Griffiths (1977).

## 2. Annual reproductive cycles.

Seasonal fluctuations in the dry flesh weights of standard 65mm shell length individuals of each species are illustrated in Fig. 3. The diagrams apply equally to males and females, since earlier workers have shown that condition factors of the two sexes cannot be distinguished (Griffiths 1977, Griffiths & King 1979). Spawning events appear on these plots as declines in dry flesh mass, the magnitude of which can be taken as indicative of the quantities of gametes released on each spawning. The relationships between these fluctuations in flesh weight and gamete maturation and release in both A. ater and C. meridionalis from the south western Cape have previously been demonstrated by Griffiths (1977) using gonad sectioning techniques.

In A. ater the diagram appears to show three spawning bouts in each year, although these differ considerably in timing and intensity between the two years of measurement. The remaining species show a fairly consistent pattern of two major spawnings each year, one in spring / early summer, between September and January, and the second in late autumn, usually between March and June . In C. meridionalis this second event may comprise a single protracted event, or a series of partial spawnings extending well into winter.

A number of other data sets, both published and unpublished, provide similar information as to the spawning cycles of these species and can be

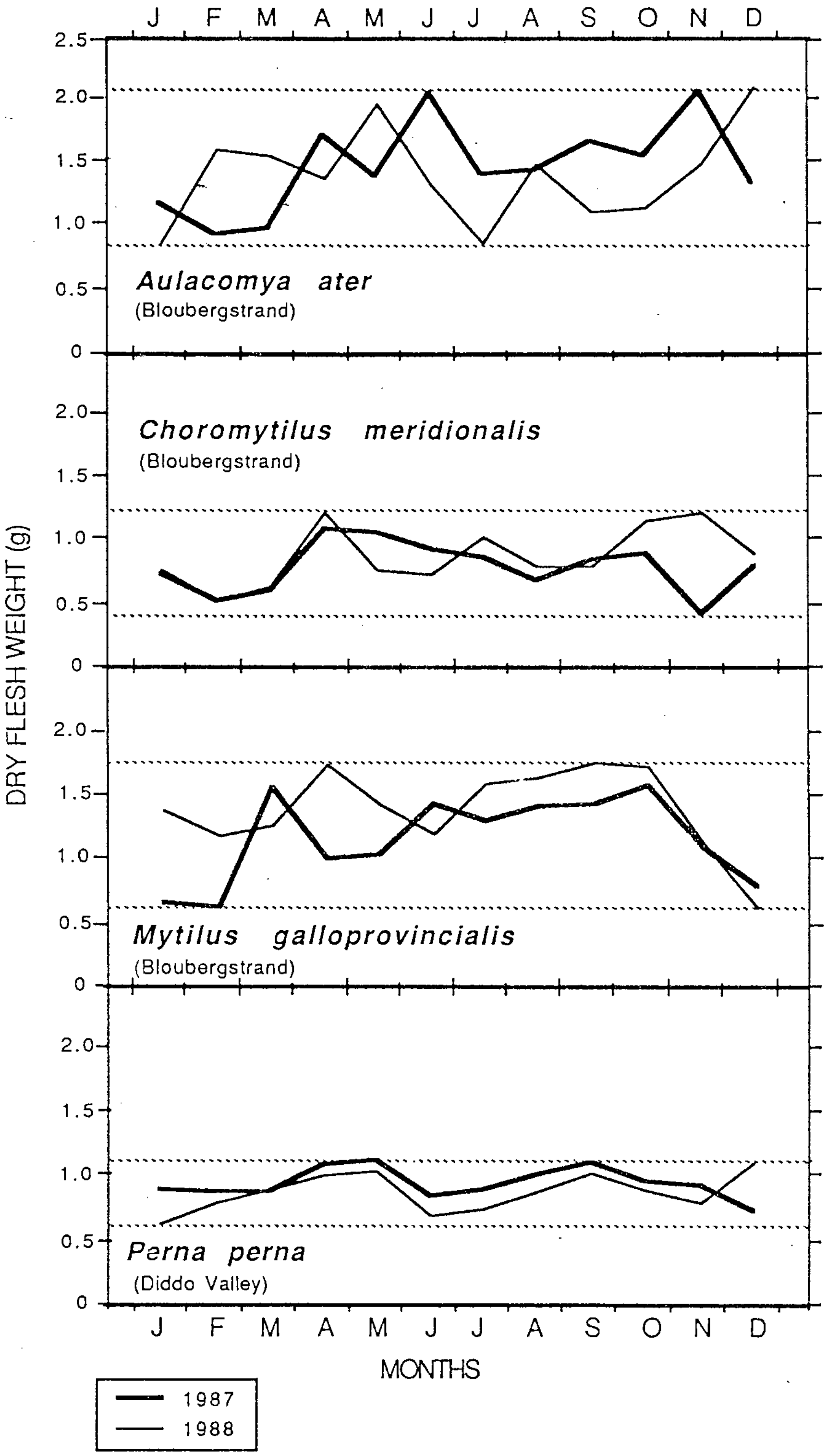


Figure 3. Seasonal fluctuations in dry flesh weight of standard individuals (65mm shell length) of each of four southern African mussel species over the years 1987-1988.

used to give an indication of interannual and geographical variations in reproductive behaviour. An attempt is made to interpret these patterns in Figs 4-7. Each horizontal block in these diagrams represents a year of observation in which recorded spawning are shown as black histogram bars. The height of each bar represents the intensity of the spawning, expressed as a percentage of total gonad output for that year. The shaded areas attempt to link these events into recognizable "spawning seasons".

Some manipulation of earlier data sets has been necessary to derive these diagrams (e.g. conversion of wet to dry weights from Griffiths & King 1979 and from adductor muscle weight to shell length from Griffiths 1977) and our interpretations of spawning events may slightly differ from those of the original authors. Adopting this technique should nevertheless result in an unbiased, standardised interpretation of condition indices from different sources.

Data sets for each species are arranged vertically from east to west in order to identify geographical gradients in reproductive seasonality. For the three essentially west coast species records are only available from sites in the south-western Cape, but for P. perna a far wider geographical range from Durban to Cape Town has been covered.

For A. ater six sets of observations are available, one from False Bay and the others from along the west coast, on or adjacent to the Cape Peninsula. The records from the west coast all show relatively similar patterns (Fig. 4) with three spawning each year, usually in December-February/March, April-July/August and September-October (December at the case of Bloubergstrand in 1974). These events show a high degree of variability in terms of relative intensity. The False Bay population (top) also spawned three times during the year, but these events appear more intense and isolated than in the west coast populations.

The reproductive cycles of C. meridionalis have been monitored five times in False Bay and over four years in Bloubergstrand on the Cape south west coast. With the one exception in the Strand, False Bay in 1988,

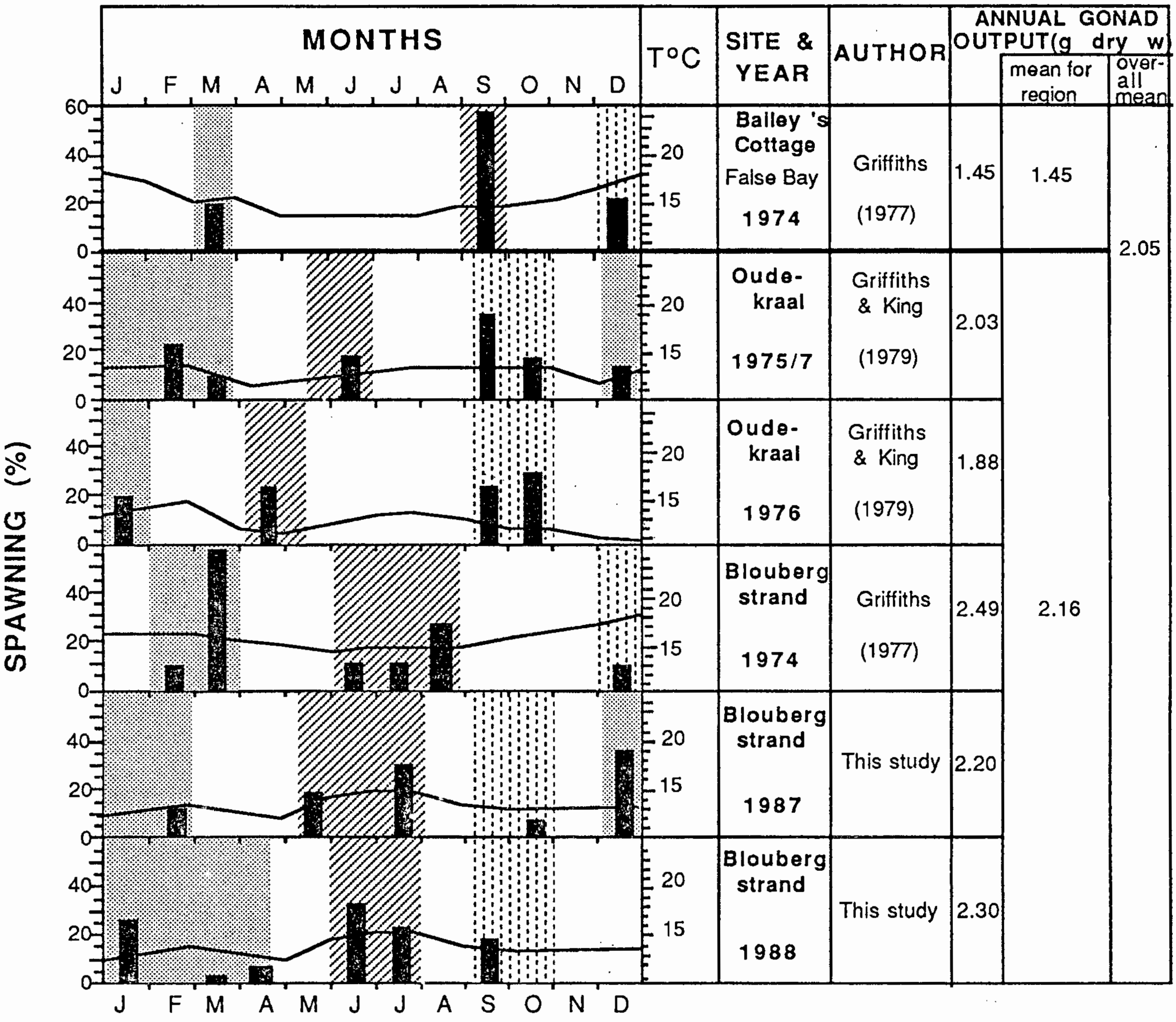
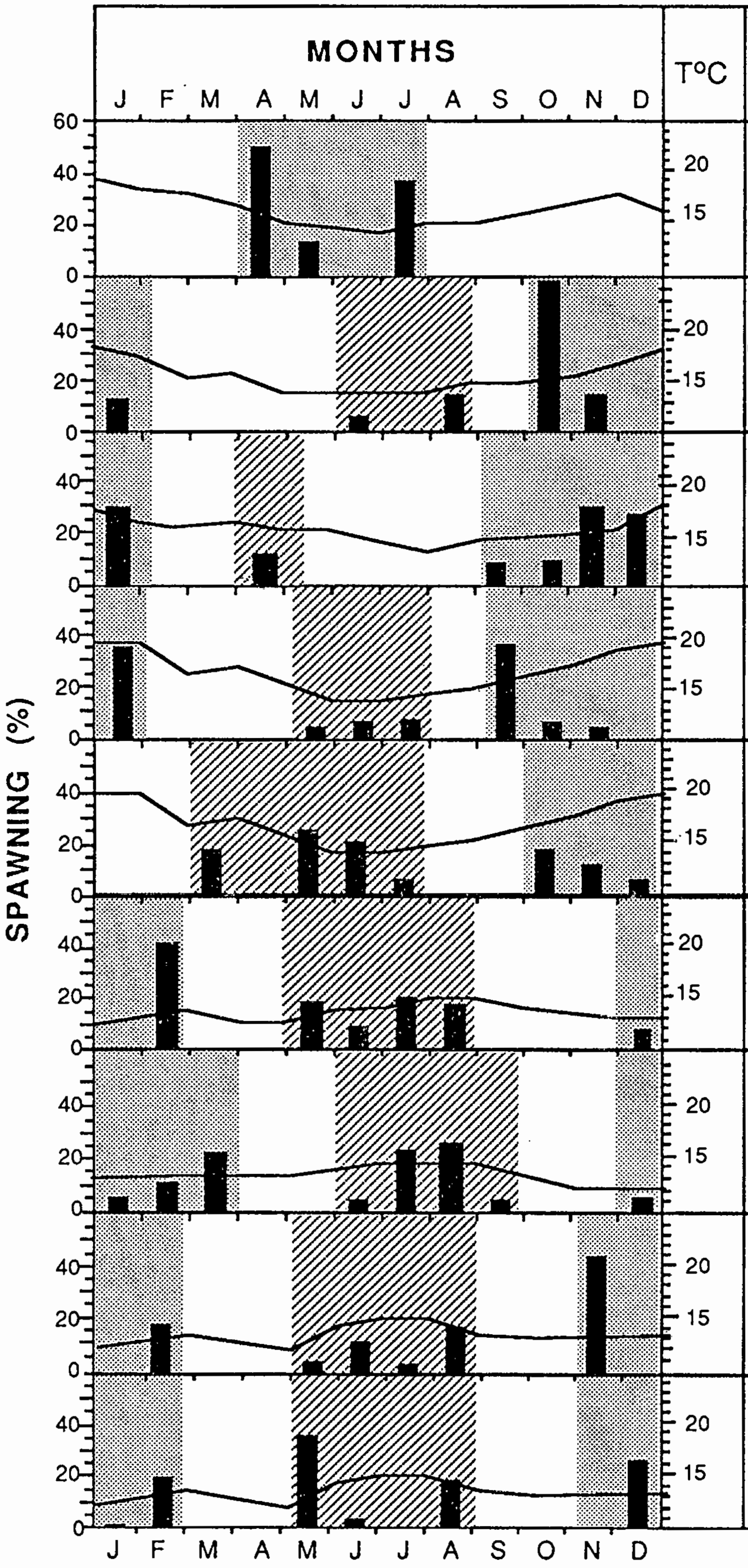


Figure 4. Synopsis of known records of reproductive seasonality and output in <u>A. ater</u>. Each horizontal block represents a year of observation. Weight loss as a result of spawning in each month is indicated by a histogram bar, scaled as a percentage of annual reproductive output. These bars are grouped into "spawning seasons" by shaded areas. A typical temperature curve for each site is overlaid. Total annual gonad output for a 65mm individual ( g dry mass $y^{-1}$) is shown on the right, both for that particular year and site, and as a regional and overall mean. Temperature data have been extracted either from the original papers of Griffiths (1977) and Griffiths & King (1979), or in the other cases obtained from Dr. J. Bolton (Botany Department, University of Cape Town, unpublished).



| SITE & YEAR | AUTHOR | ANNUAL GONAD OUTPUT(g dry w) | mean for region | over-all mean |
|---|---|---|---|---|
| Strand (False Bay) 1988 | Russel (pers.com.) | 0.78 | 0.91 | 1.02 |
| Bailey 's Cottage (False Bay) 1974 | Griffiths (1977) | 0.94 | | |
| Bailey 's Cottage (False Bay) 1975 | Griffiths (1977) | 0.97 | | |
| Bailey 's Cottage (False Bay) 1988 | Russel (pers.com.) | 1.03 | | |
| Glencairn (False Bay) 1988 | Russel (pers.com.) | 0.84 | | |
| Blouberg-strand 1974 | Griffiths (1977) | 1.23 | 1.16 | |
| Blouberg-strand 1975 | Griffiths (1977) | 1.19 | | |
| Blouberg-strand 1987 | This study | 1.05 | | |
| Blouberg-strand 1988 | This study | 1.15 | | |

Figure 5. Synopsis of known records of reproductive seasonality and output in C. meridionalis. (For interpretation see Fig. 4).

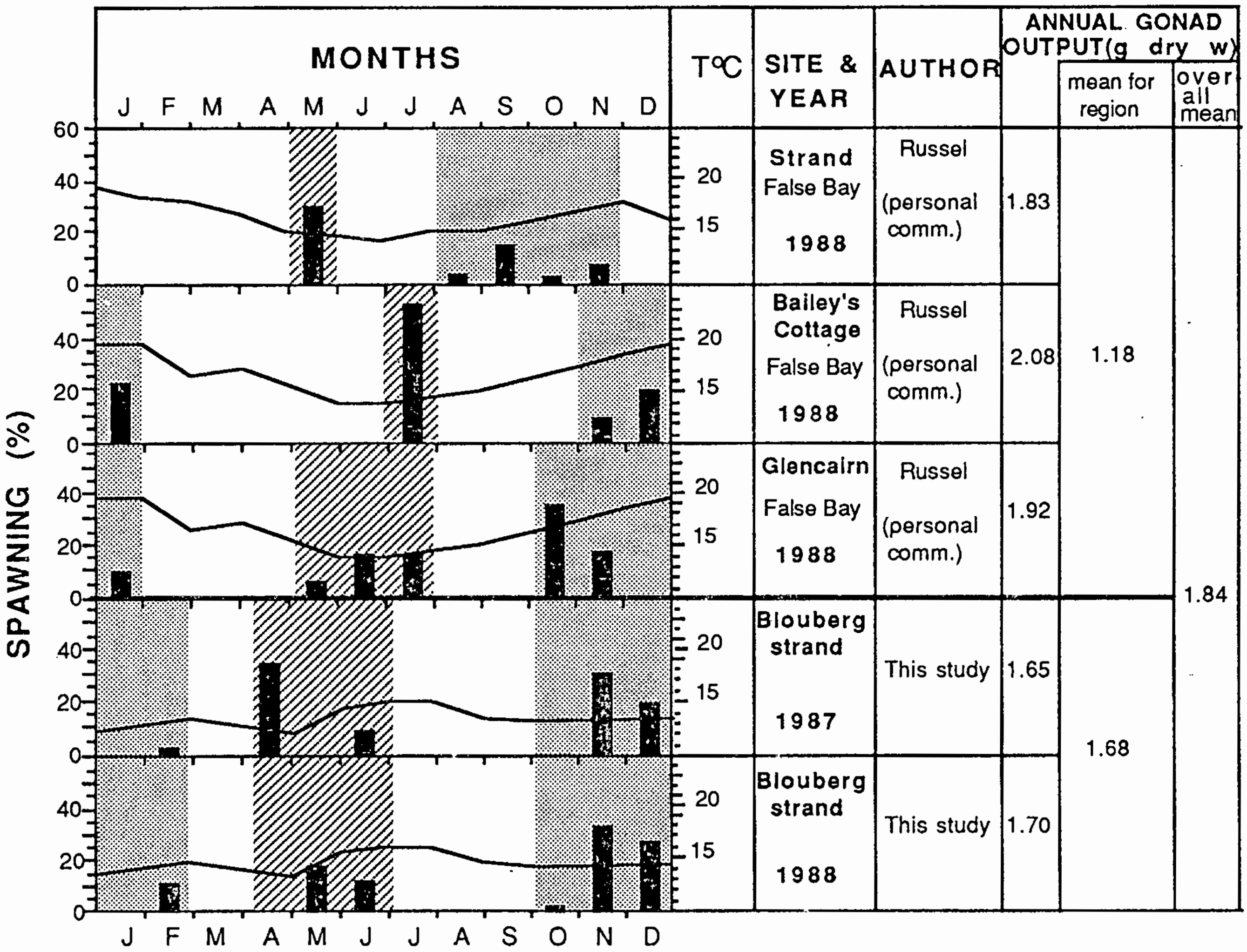


Figure 6. Synopsis of known records of reproductive seasonality and output in M. galloprovincialis. (For interpretation see Fig. 4).

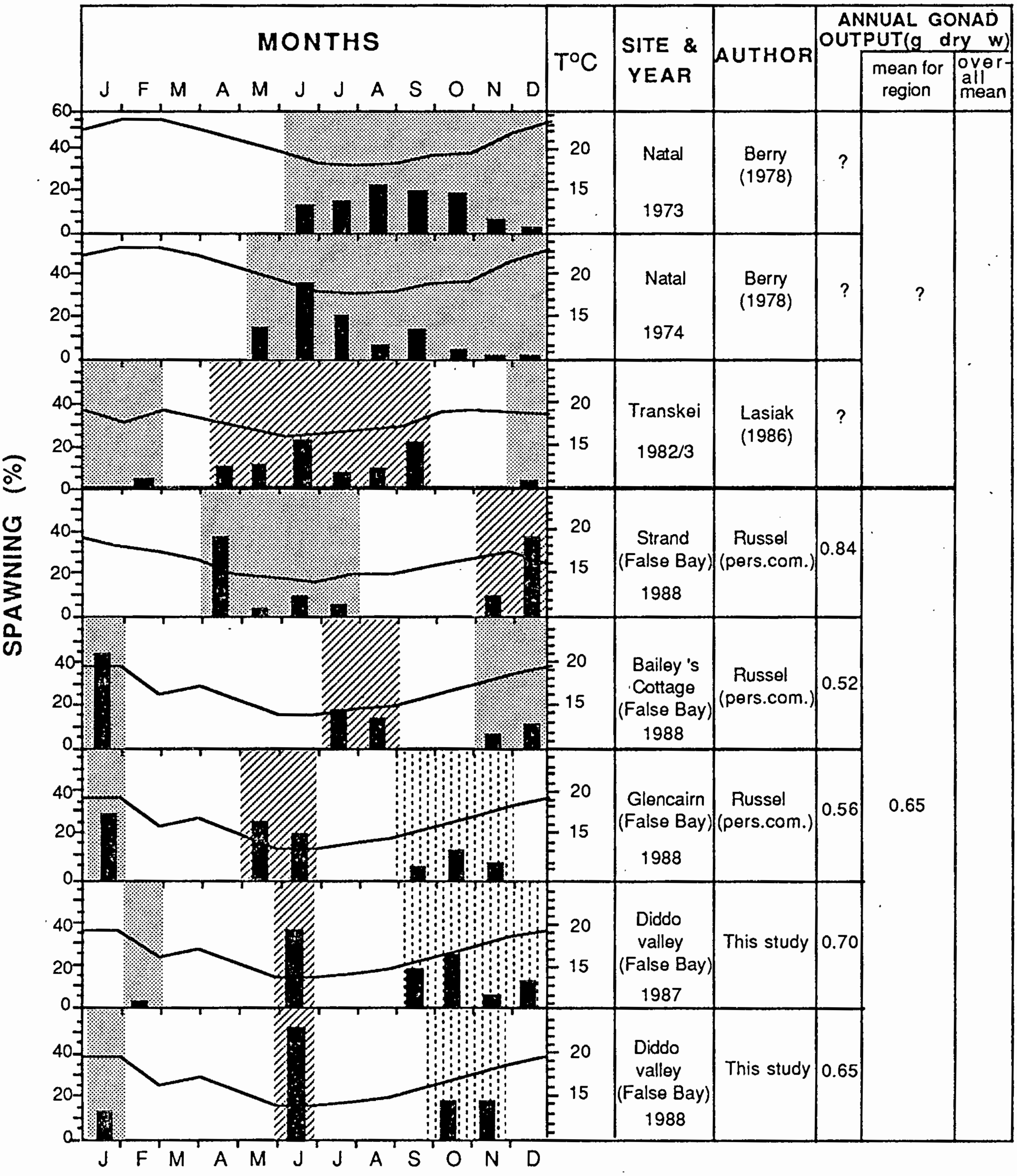


Figure 7. Synopsis of known records of reproductive seasonality and output in P. perna. (For interpretation see Fig. 4).

where a single spawning was observed, all the records show two protracted breeding seasons each year (Fig. 5). In False Bay these are very variable in their timing, but at Bloubergstrand a consistent pattern is evident, with one extended spawning occurring during summer (November - February/March) and the other in mid winter (May - August/ September).

For M. galloprovincialis three time-series are available from sites in False Bay and two from Bloubergstrand (Fig. 6). All the populations spawned over two usually extended periods, with four of the five populations doing so once in summer (October - February) and again in winter (April/May - July). Again the exception in the Strand site in False Bay, where the spawning seasons were displaced to May and August - November.

A large number of records of the breeding seasons of P. perna are available and are summarized in Fig. 7. In Natal Berry (1978) reported that most populations spawned in two conspicuous peaks between May and October (sometimes prolonged until December), the first event being the largest. However, since some activity occured in each month, we have interpreted this as a single prolonged spawning season (Fig. 7). In Transkei, Lasiak (1986) reports an extended breeding season from April to September, with minor events from December to February. In False Bay a rather variable pattern is evident with a brief but intense winter spawning that can occur between April - August, accompanied by either one extended or two discrete spring or summer events.

## 3. Settlement patterns.

A further index of reproductive activity can be obtained from seasonal records of spat settlement. These were not monitored during the present study, but are available from other southern African authors.

Several years of settlement data for P. perna are provided by Berry (1978). These suggest that major settlements usually occur over the period May - August, with a secondary peak in September - October. During 1976, however, this second settlement was the dominant one and resulted in a massive expansion of mussel cover over much of the Natal coast. Less detailed records for a site on the southern Cape coast are provided by Crawford & Bower (1983). These suggest that secondary settlements occur primarily over summer and early autumn (November - April).

For C. meridionalis from Saldanha Bay (some 100km north of Cape Town), du Plessis (1977) records a broad peak in settlement over the period October to early May, especially in October - December of each year. In some years this was supplemented by a further peak in March - April, or on one occasion in June - July. Similar findings are reported by Barkai & Branch (1988) working in the same area. They report settlement of C. meridionalis on sublittoral plates throughout the period September - June, but with highest recruitments in March - June. Griffiths (1981a) reports a much more irregular pattern for her study site in False Bay, which experienced a dense settlement in December 1974, which was not repeated until August 1978.

There are no published data on the recruitment patterns of A. ater or M. galloprovincialis in South Africa. Unpublished size-frequency analyses undertaken by Griffiths & King (1979), however, do show a strong settlement of A. ater occurring in September 1975 over a limited area. Similar patchy, intermittent settlement is noted by Pollock (1979), as might be expected from the irregular reproductive cycle of this species. In the case of M. galloprovincialis, in Saldanha Bay spat settle on mussel culture ropes mainly over the summer/autumn period, particularly in April (Atlas Sea Farms, pers. comm.). Only one author (du Plessis 1977) also measured the duration of larval life. For C. meridionalis this is reported to range from 31 - 60 days, with a peak of settlement between 35 - 50 days (mean temperature 15°C). These estimates are somewhat longer than most field measurements for other species. M. edulis larvae, for example, have an average lifespan of 3 - 5 weeks (Bayne 1976, Kautsky 1982). Duration of larval life is, however, very variable between species (see review by Sastry 1979) and is strongly influenced by a number of factors, particularly temperature and food ration (Bayne 1976). Moreover pediveliger larvae (at least in M. edulis) are known to be able to delay metamorphosis by as much as 40 days at 10°C or 2 days at 20°C if they are unable to find a suitable substratum on which to settle (Bayne 1975).

Given this larval duration there appears to be little correlation between the settlement patterns reported above and the presumed spawning events shown in Figs 4-7. This may be a reflection of large local and interannual variations in reproductive cycles, and even more so of high and variable dispersal and mortality during the larval stage. This is exemplified by the successive failures of C. meridionalis recruitment at specific sites in False Bay from 1974-1978, a period over much of which reproductive output was known to remain consistently high (Griffiths 1981a).

## 4. Fluctuations in flesh yield.

From the fluctuation in flesh mass plotted in Fig. 3 it will be apparent that the four mussel species all exhibit wide disparities both in the absolute dry flesh mass of standard size individuals and in the range over which these values fluctuate over time. These parameters are of particular importance to the mussel culture industry, since the value of the crop is determined largely by the flesh yield, especially when this is used for canning, or sold out of the shell in processed form.

The range over which flesh mass varies in each of the species is depicted more clearly in Fig. 8 . The upper curve in each diagram represents the dry flesh mass to shell length relationship in the month in which flesh mass or condition factor is maximal (averaged over the two years of measurement depicted in Fig. 3), while the lower curve represents the corresponding minimum. The shaded area thus indicates the range over which flesh mass fluctuates during a typical year. Values given in these diagrams may be converted to wet weights by multiplying by 7.1 for A. ater (Field et al 1980, Griffiths & King 1979), by 5.9 for C. meridionalis (Griffiths 1981a), by 3.7 for M. galloprovincialis (van Erkom Schurink & Griffiths, unpublished) and by 5.6 for P. perna (Berry 1978).

Two major features are evident from these plots. Firstly the relationships between shell length and both maximum and minimum dry flesh mass differ markedly between species. Indeed dry flesh mass can vary by almost two-fold between individuals of equivalent shell length but of different species. These variations are greatest when the mussels are in a ripe condition. At this point 65mm individuals can vary in dry flesh mass from maxima as high as 2.3 g in A. ater, through 2.1 g in M. galloprovincialis to as little as 1.4g and 1.3g in C. meridionalis and P. perna respectively. After spawning A. ater retains the highest body mass (1.0g at 65mm) followed by M. galloprovincialis (0.7g), P. perna (0.6g) and C. meridionalis (0.5g). To some extent these variations can be related to the geometry of the shells of the different species, the internal volume of the broader A. ater and M. galloprovincialis shells being considerably greater than those of the narrow, laterally-compressed C. meridionalis and often elongated, low-shelled P. perna (see diagrams in Berry 1978, van Erkom Schurink & Griffiths 1990).

Secondly, a comparison of the shaded areas in Fig. 8 gives a good indication of the variability in flesh mass and hence capacity of the various species to lay down and release gonad material within a single spawning cycle. Clearly this is greatest in M. galloprovincialis, where the accumulation of gonad material can result in an increase in weight of 3-fold over the spawned condition ( at 65mm ). Equivalent ratios for

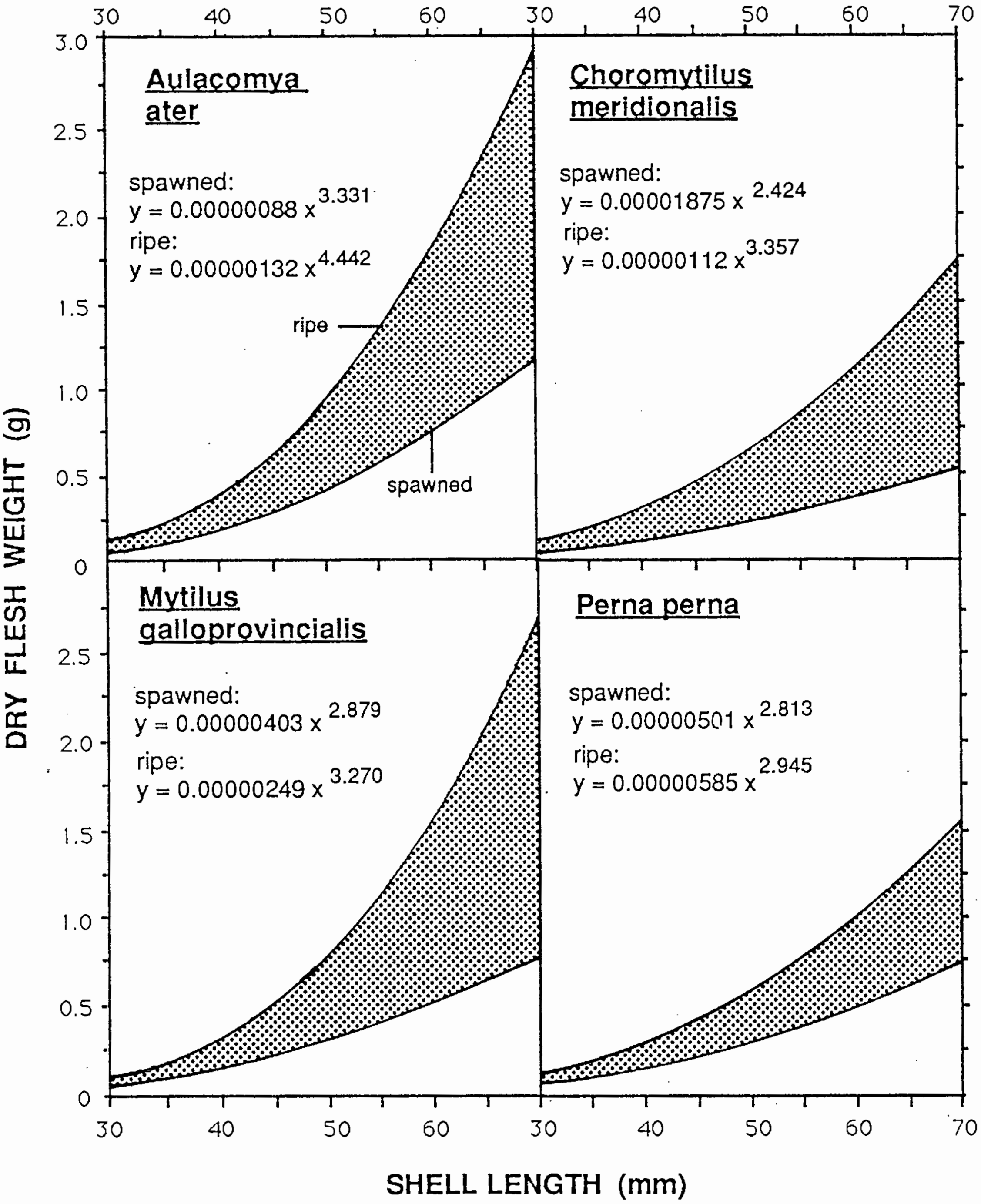


Figure 8. Ranges in variation in the length to weight relationships of southern African mussel species. The upper curve in each diagram represents the length to dry flesh mass relationship in the month of peak gonad condition (averaged over the two years of measurement shown in Fig. 3), while the lower curve represents the minimum relationship. The shaded area thus represents the range over which flesh weight values fluctuate during the reproductive cycle.

C. meridionalis would be 2.8-fold, for A. ater 2.3-fold, and for P. perna 2.2-fold. Put in another way, ripe 65mm individuals comprise 57%, 64%, 67% and 54% gonad material in A. ater, C. meridionalis, M. galloprovincialis and P. perna respectively.

Note that, impressive though these figures, they almost certainly represent underestimates of the true fluctuations in weight and hence gonad output, since they are based on averages derived from monthly length/weight regressions. Such infrequent samples would miss possible multiple cycles of spawning and gonad buildup with periodicities of less than one month and are also unlikely to capture either the immediate pre-spawning maximum, or the immediate post-spawning minimum conditions. Moreover, asynchrony between individuals is likely to have resulted in early spawners depressing the "pre-spawning" estimate and late ones elevating the "post-spawning" regression curves, thus contracting the true range of body weights experienced by individual mussels.

## 5. Reproductive output.

Annual gonad output is a function of both the weight loss on each individual spawning and the frequency of spawnings, which as discussed earlier, usually occur two or three times a year. For the 65mm mussels represented in Fig. 3, total annual gamete output may be estimated by summing the declines in dry flesh mass over the year. These total 2.3g for an individual 65mm A. ater, 1.7g for M. galloprovincialis, 1.1g for C. meridionalis and 0.7g for P. perna, averaged over the years1987 and 1988.

Clearly the larger figure for A. ater is a function of its three annual spawnings, whereas in the remaining forms, which each spawn twice a year, differences result from the volume on gonad material released at each spawning event. The approximate numbers of gametes involved may be guaged from figures given by Thompson (1979), who estimated that for M. edulis 1g dry gametes was equivalent to some $20\times10^6$ eggs or $20\times10^{10}$ sperm. Since packing densities of mussel beds can exceed 1000 individuals $m^{-2}$ at a length of 65mm (Griffiths & Hockey 1987), the total number of gametes released by mussel beds is clearly formidable - being of the order of $10^9$ eggs or $10^{13}$ sperm $m^{-2}$ $y^{-1}$.

In energetic terms releases of gametic material of this magnitude may have a profound effect on the entire economy of the shore. An attempt to assess this impact more accurately is made in Table I, in which we compare reproductive output in typical intertidal populations of our four study species. Mussel standing stocks at these sites were derived from field surveys (van Erkom Schurink & Griffiths 1990). Reproductive outputs were then calculated on the assumption that these populations consist of 65mm individuals, as follows. First the whole wet mass of a 65mm individual of each species was calculated, using the regression equations given in the legend to Table I. This figure was then divided into the standing stock to give an estimate of density. Population reproductive output was obtained by multiplying individual reproductive output, given above, by the density and the wet to dry conversion ratios (given above) to obtain wet equivalents of reproductive output per $m^{-2}$. The energy values of reproductive output is also given, based on the calorific values in Fig. 2, converted to wet weight equivalent and weighted accordingly to the sex ratios given in the same figure.

Clearly these figures are only approximations, since each population in fact consists of a size range of individuals, the larger of which will contribute greater reproductive output than assumed here, and the smaller ones less. It is nevertheless apparent that secondary production in the form of mussel gametes can be very significant, varying from 3.4 to 10.4 kg $m^{-2}$ $y^{-1}$ in the populations listed.

This secondary production can be compared to an estimated total

| Species | Site | Standing stock kg wet mass $m^{-2}$ | Reproductive output (Pr) kg (wet mass) $m^{-2}y^{-1}$ | KJ $m^{-2}y^{-1}$ | $Pr/B$ (kg) |
|---|---|---|---|---|---|
| **Aulacomya ater** | False Bay | 20 | 5.0 | 14 547 | 0.31 |
| | Bloubergstrand | 28 | 10.4 | 30 340 | |
| **Choromytilus meridionalis** | False Bay | 19 | 4.2 | 13 600 | 0.25 |
| | Bloubergstrand | 33 | 9.2 | 29 881 | |
| **Mytilus galloprovincialis** | False Bay | 26 | 3.4 | 18 753 | 0.16 |
| | Bloubergstrand | 46 | 8.7 | 47 903 | |
| **Perna perna** | False Bay | 48 | 6.2 | 22 421 | 0.13 |

Table I. Estimate reproductive output of representative population of each of four southern African species. Standing stocks were extracted from van Erkom Schurink & Griffiths (1990) and converted to an equivalent in 65mm mussels using the following total wet weight (y axis expressed in g) to shell length relationship (x axis expressed in mm):

A. ater : $y = 0.00005152\ x^{3.259}$

C. meridionalis : $y = 0.00020137\ x^{2.801}$

M. galloprovincialis : $y = 0.00012106\ x^{2.997}$

P. perna : $y = 0.00024210\ x^{2.796}$

seaweed production of ca 1100 g C $m^{-2}$ $y^{-1}$ (approx. 23 kg wet mass, according to the conversion given by Newell et al 1982) on an exposed South African rocky shore, as quoted by Branch & Griffiths (1988), or 17.5 kg wet mass $m^{-2}$ $y^{-1}$ total seaweed production for a productive kelp bed on the Cape Peninsula (Newell, et al 1982).

## ACKNOWLEDGEMENTS

We are indebted to Grant Russel of the Fishing Industry Research Institute for allowing us access to his unpublished data on annual variations in condition index in False Bay mussel populations, and to Diane Gianakouras for assistance with bomb calorimetry. Financial support was provided through an F.R.D. Core Programme Grant made to G.M. Branch, J.G. Field and C.L. Griffiths. Our thanks to Prof. G.M. Branch and Dr. V. Stuart for their constructive comments on earlier drafts of this manuscript.

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# CHAPTER 4

# FACTORS AFFECTING RELATIVE RATES OF GROWTH IN FOUR SOUTH AFRICAN MUSSEL SPECIES

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**Abstract** : The growth performances of four abundant South African mussel species are compared under a variety of environmental conditions. When maintained under suspended culture Choromytilus meridionalis and Aulacomya ater grew faster in Saldanha Bay, on the cooler Atlantic seaboard (15°C), than in Algoa Bay on the Indian Ocean coast (18°C). Mytilus galloprovincialis and Perna perna showed the reverse trend. The best growth performer in Saldanha Bay was C. meridionalis and in Algoa Bay M. galloprovincialis. A. ater consistently grew much slower than any other species. All species grew more rapidly at a high water circulation sitê than in one with restricted circulation. Similarly, increasing level of tidal exposure progressively retarded rates of growth in all species, although to different extents. A ater, which is predominently a subtidal species, was most severely effected, while P. perna and M.galloprovincialis were best able to maintain growth rates at increasing levels of aerial exposure. These findings were paralleled by mortality rates, which were greatest in A. ater and least in M. galloprovincialis. At low population densities increased crowding appeared to slightly accelerate growth, whereas high densities slowed growth in all species. High silt loads retarded growth 17-18% in A. ater and M. galloprovincialis, but accelerated it by 10% in C. meridionalis, which naturally dominate in sandy sites. Allometric relationships are used to demonstrate that equal increments in linear growth represent greater investments in shell or flesh weight in some species (notably A. ater and M. galloprovincialis) than in others (especially C. meridionalis). It is concluded that the best candidate for mariculture in both Saldanha Bay and Algoa bay, is M.galloprovincialis, although P. perna may become a suitable crop in subtropical sections of the coastline, should aquaculture ventures become developed in these areas.

**Key words** : Growth, mussels, aquaculture, tidal exposure, temperature, packing density, sediment load, water circulation.

# INTRODUCTION

There can be few aspects of molluscan biology that have received more attention than the growth rates of marine mussels and existing literature on the subject has been reviewed a number of times, notably by (Seed 1969, 1976 and Griffiths & Griffiths 1987). Rates of growth are influenced both by intrinsic, or genetic differences between species or populations (Gentilli & Beaumont 1988, Peterson & Beal 1989) and by extrinsic, or environmental conditions, including the nature and quality of food available, water temperature, rate of water exchange, packing density and duration of tidal exposure (Seed 1976, Griffiths & Griffiths 1987). Since the majority of publications document the growth of single populations under sometimes inadequatly specified conditions, they are of limited use in resolving the factors controlling growth, and have little predictive or comparative value. Some authors have attempted to compare growth rates within a single species monitored at different water depths (e.g. Kautsky 1982), tidal levels (Baird 1966, Griffiths 1981b) or temperatures (Thiesen 1973, Hickman 1979). Such studies often document remarkable plasticity in rates of growth. Mytilus edulis, for example, can attain 60-70 mm within 12-18 months under ideal conditions, but may take 15-20 years to reach 20-30 mm in the high littoral (Seed 1976). Interspecific comparisons between the growth rates of species held under comparable conditions are even more sparce, although a few paired sets of measurements are available, for example between Mytilus chilensis and Aulacomya ater (Davenport et al. 1984), Mytilus galloprovincialis and Perna perna (Abada-Boudjema et al. 1984) and Choromytilus meridionalis and Aulacomya ater (Barkai & Branch 1989).

An unusual opportunity to compare factors influencing the growth rates of mussel species can be found in the South Western Cape of South Africa, where four genera and species of mussel co-exist on the same shore (van Erkom Schurink & Griffiths 1990). At least some growth rate data are available for each of these species individually. In the case of *A.ater*, sublittoral populations have been monitored by Pollock (1979), Griffiths & King (1979) and Barkai & Branch (1989), but no data are available on growth of intertidal stocks. For *P. perna* sublittoral and intertidal growth rates are available from Durban (Berry 1978) and intertidal ones from Transkei (Lasiak & Dye 1989) and the southern Cape (Crawford & Bower 1983). These data indicate that the westward trend of declining water temperatures is paralleled by a pronounced reduction in growth rate. A good series of growth curves for *C. meridionalis* are available for sublittoral populations in Saldanha Bay (du Plessis 1977, Barkai & Branch 1989) and for a variety of intertidal exposure levels (Griffiths 1981b) at a site in False Bay in the south western Cape. No South African authors have measured growth in the recently introduced *M.galloprovincialis*, although a number of measurements have been made elsewhere (e.g. Abada-Boudjema *et al.* 1984, Ceccherelli & Rossi 1984).

Although the above studies might appear comprehensive, in reality many key questions remain unanswered. In particular little can be inferred about the relative rates of growth of the different species when maintained under comparable conditions, nor about the relative effects of water temperature, turbulence or tidal exposure on growth in the various species. Such parameters are not only of considerable academic interest, but would play an important role in the selection of optimal species for aquaculture. In the following account we attempt to resolve some of the factors controlling rates of growth in the four South African mussel species by means of directly comparable side-by-side growth measurements under a variety of environmental conditions.

# METHODS

Juvenile mussels used in the various growth experiments were collected near low water of spring tides from rocky shores at Bloubergstrand, Table Bay, some 20 km north of Cape Town (Aulacomya ater, Choromytilus meridionalis, Mytilus galloprovincialis) or from Dido Valley, False Bay, some 30 km south of Cape Town (Perna perna).

## 1. Variations between sites in submerged culture.

The objectives of this experiment were to compare the growth rates of the four mussel species when held in suspended culture at two existing culture sites subject to different temperature regimes. The sites were the Atlas Sea Farm facilities in Saldanha Bay, 110 km north of Cape Town along the Atlantic shoreline and in Algoa Bay, 700 km east of Cape Town on the Indian Ocean coast. These are the only two areas currently used for mussel culture in South Africa (van Erkom Schurink & Griffiths 1990). Samples of 300 - 400 mussels with an initial shell length of 30 mm (S.D. 2 mm) were bound onto culture ropes in the normal commercial way and suspended at depths of 0-3 m using the Spanish longline method. A random sample of 50 individuals was removed from each population before the ropes were bound and again at three month intervals over the next year, each individual was measured to 0.1 mm with vernier callipers and the mean length and standard deviation calculated. Temperature data for the two sites were obtained from the literature.

## 2. Effects of tidal exposure.

Experiments testing the effect of increasing aerial exposure on growth in the four mussel species were carried out in the calm semi-enclosed waters of the Seafarm culture facility in Saldanha Bay. Steel frames were constructed with horizontal bars placed below low water and at heights designed to provide approximately 10%, 30% and 50% exposure to air over a typical spring to neap tidal cycle. One frame was placed in 1m of water in a protected corner of the farm, subject to little water circulation, and a second at the same depth, but adjacent to the large inlet/outlet pipe connecting the farm to the open sea, where current speeds were high. Growth rates were monitored for samples of 50 mussels of each species at each level (i.e. 50 mussels X 4 levels X 2 sites for each species). The mussels were collected from the sites mentioned earlier and individually numbered with "Dymo" tape glued to the shell with Pratley's Quickset Clear Glue. Each group contained a size range of mussels, allowing a composite growth curve to be constructed over a relatively short period. The 50 mussels of each group were placed in 1 cm mesh monofilament netting bags which were stretched horizontally across the frames at the required levels. Changes in shell length of each individual were monitored at two monthly intervals for 24 months. Results were plotted using polynomial regression equations ( the early stages of the growth and $L_\infty$ measures required to fit van Bertalanffy or Gompetz growth equation not being available).

### 3. Packing density and sediment load.

Further factors thought to influence the growth rates of mussels include packing density and sediment load or turbidity. The effects of these factors were tested by binding groups of mussels on to plastic dinner plates and submerging these in the Seafarm facility in Saldanha Bay. In the packing experiment, groups of 12, 25, 50 or 100 mussels of initial size 35 mm (S.D. 2 mm) were bound on to 20 cm diameter plates. The plates were then attached horizontally to the metal frames referred to earlier and left for 6 months, after which the mussels were remeasured. In the sediment experiment sets of plates, each carrying 20 individuals of a particular species, were positioned just above the sediment surface, where each breaking wave stirred the sand into suspension. A second set was held ca. 50 cm above the sea floor, out of reach of most of the suspended material. Again mussels were remeasured after 6 months. Only the three mussels species found in Saldanha Bay, A. ater, C.meridionalis and M. galloprovincialis were used in these experiments.

### 4. Morphometrics.

All the above growth rate recordings were based on increments of shell length. Similar increases in shell length, however, represent different investments in shell material (or body mass) in different species, depending upon shell thickness and shape. Variations in shell volume associated with linear growth were estimated by plotting length related changes in height, width and hence volume for each species, using the IBM PC programme "SURFER". Plots for each species were based on a sample of 100 individuals covering the entire size range and collected from the sites given above.

## RESULTS AND DISCUSSION

### 1. Variations between sites.

Comparative growth rates of the four species in Saldanha Bay and in Algoa Bay are depicted in Fig. 1, together with representative temperature curves for the two sites, while growth curve parameters are shown in Table 1. Two features are immediatly evident from these plots. The first is that A. ater show extremely slow rates of growth relative to

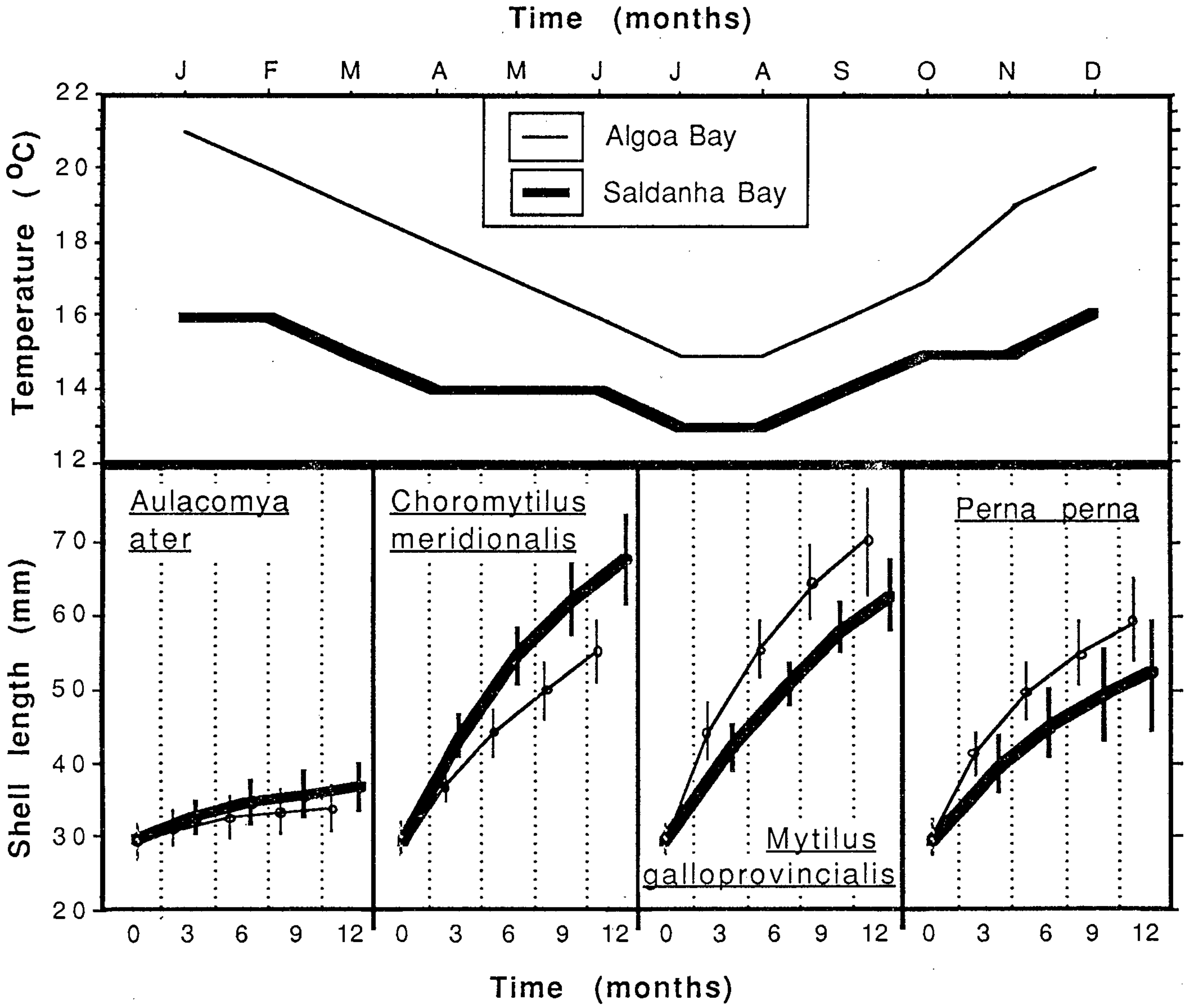

Figure 1. Comparative growth rates of the four mussel species in Algoa Bay and Saldanha Bay. Equations are given in Table 1. Temperature curves are derived from Beckley (1985) for Algoa Bay and from du Plessis (1977) for Saldanha Bay.

| Species | Site | a | b | c | $r^2$ |
|---|---|---|---|---|---|
| Aulacomya ater | Saldanha Bay | 29.929 | 1.014 | 0.032 | 0.97 |
| | Algoa Bay | 29.970 | 0.585 | 0.019 | 0.94 |
| Choromytilus meridionalis | Saldanha Bay | 29.929 | 4.848 | 0.143 | 0.96 |
| | Algoa Bay | 29.843 | 2.638 | 0.048 | 0.96 |
| Mytilus galloprovincialis | Saldanha Bay | 30.200 | 4.100 | 0.111 | 0.98 |
| | Algoa Bay | 29.943 | 5.238 | 0.159 | 0.95 |
| Perna perna | Saldanha Bay | 30.171 | 3.136 | 0.107 | 0.93 |
| | Algoa Bay | 30.314 | 3.924 | 0.127 | 0.99 |

Table 1. Polynomial regression equation, of the type $a+bx-cx^2$, describing the growth of the mussel populations as depicted in Fig. 1.

any of the remaining three species. The second is the marked, but inconsistent effects of culture site on relative rates of growth. In particular it should be noted that A. ater and C. meridionalis, which both have cool-temperate distribution patterns (van Erkom Schurink & Griffiths 1990) grow more rapidly in the cooler waters of Saldanha Bay than in Algoa Bay. Conversely, P. perna, the dominant mussel in the subtropical waters of the east coast of southern Africa, and M. galloprovincialis, both grow considerably faster in the warmer conditions of Algoa Bay. Overall the fastest growing species in Saldanha Bay was thus C. meridionalis, which showed a mean increase in shell length of 38 mm over the year, followed by M. galloprovincialis at 33 mm. In Algoa Bay M.galloprovincialis was the fastest growing species, showing an increment of 40 mm, well above those of P. perna (29 mm) and C. meridionalis (25 mm).

These temperature related trends appear to be supported by previously published data, although comparisons of this type must be treated with caution, since many other factors, apart from temperature, can influence rates of growth. Neverthelesss, it is significant to note that growth rates for A. ater recorded at temperatures as low as 5.8°C (Falkland Islands, Davenport et al. 1984) appear to exceed those on the west coast of South Africa (Griffiths & King 1979, Barkai & Branch 1989). In the case of C. meridionalis Griffiths (1981b) has noted that growth rates in Table Bay and Saldanha Bay can be as much as twice those in the warmer waters of False Bay during the first year following settlement. Physiological measurements by Clarke & Griffiths (1990) also indicate that metabolic energy balance in C. meridionalis deteriorates markedly as temperatures rise above 12°C. Conversely P. perna achieves growth rates even more rapid than those reported here in the subtropical waters of Natal, where they can attain 75 mm after one year and 104 mm after two years (Berry 1978).

The above results clearly indicate that the different mussel species vary considerably in their optimal temperature regimes and that increasing temperature above these optima can retard, rather than accelerate growth.

## 2. Effects of tidal exposure and water circulation.

Fig. 2 depicts composite growth curves for the four mussel species when held at various tidal elevations and at sites subject to both low and high rates of water exchange in Saldanha Bay. The parameters of these growth equations are listed in Table 2. A number of trends are evident from these plots. Perhaps most obvious are the extremely slow growth rates of A. ater under all conditions. These confirm the tendency discussed earlier. When the relative rates of growth of the remaining three species are compared, the fastest growth appears to be achieved by M. galloprovincialis, followed by P. perna and then C. meridionalis. At first glance this ranking would appear to contradict the earlier data for Saldanha Bay (Fig. 1), although closely resembling that for the warmer site in Algoa Bay. In fact the findings are complementary, since the Seafarm site at which these experiments were conducted is a semi-enclosed, shallow lagoonal area where temperatures are considerably higher (min. 12°C, max. 23°C, annual mean 18°C) than those in the outer bay, where the growth rates in Fig. 1 were obtained. The results provide strong evidence that temperature (rather than food availability) is the variable controlling relative rates of growth in these species.

Turning to the effect of water circulation it is clear that all four species show faster rates of growth at the high circulation site than in the low circulation one, these effects occurring irrespective of tidal elevation. This is a well documented phenomenon (e.g. Kerswill 1949) and

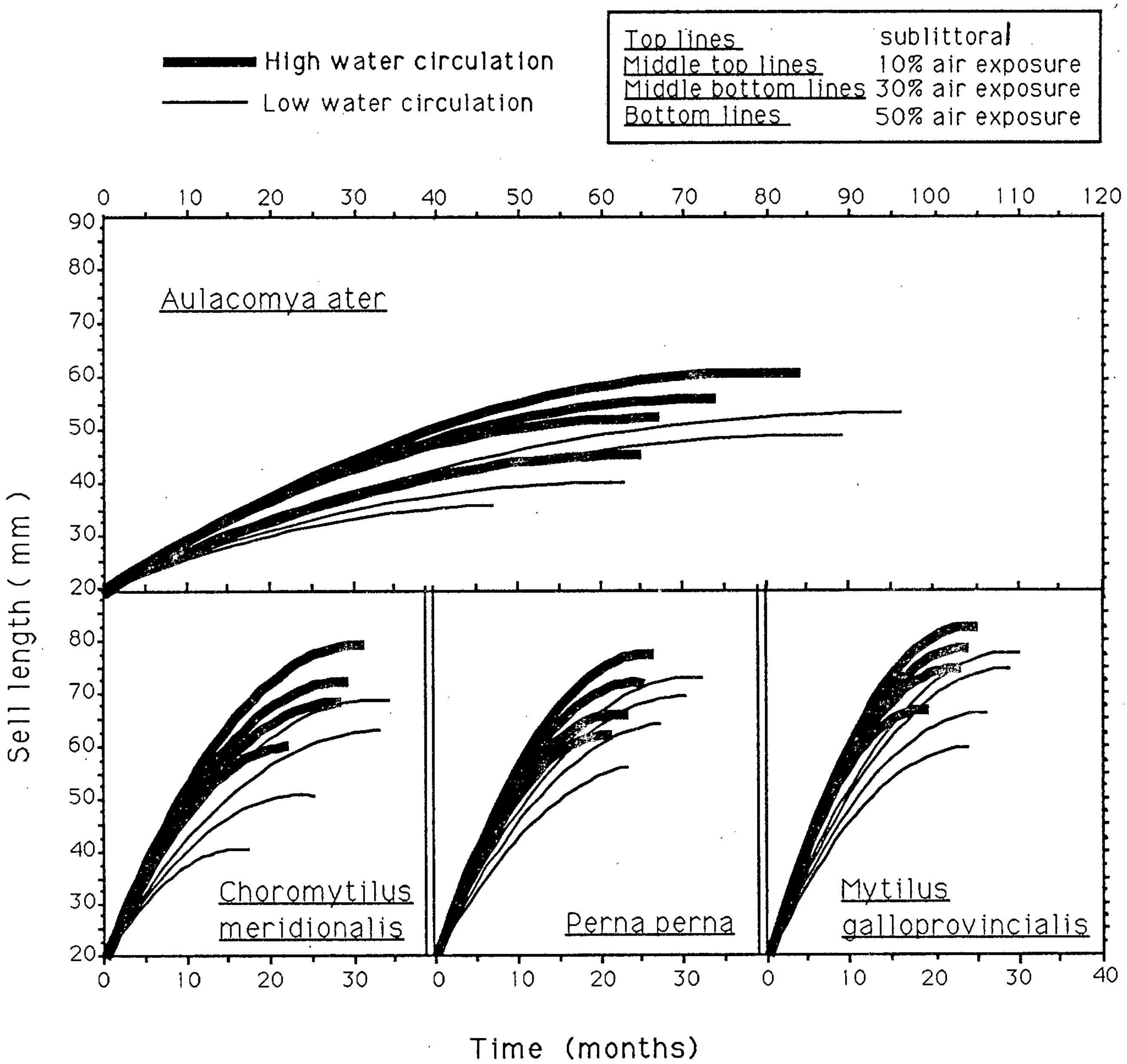

Figure 2. Growth curves for the four mussel species at different aerial exposure levels and at high and low water circulation sites in Saldanha Bay. Equations are shown in Table 2.

| Species | Water circulation | Aerial exposure | a | b | c | $r^2$ |
|---|---|---|---|---|---|---|
| Aulacomya ater | HIGH | sublittoral | 19.253 | 1.033 | 0.00645 | 0.96 |
| | " | 10% | 20.137 | 0.954 | 0.00638 | 0.95 |
| | " | 30% | 19.992 | 0.975 | 0.00742 | 0.97 |
| | " | 50% | 19.927 | 0.770 | 0.00587 | 0.99 |
| | LOW | sublittoral | 20.632 | 0.693 | 0.00372 | 0.98 |
| | " | 10% | 20.621 | 0.639 | 0.00362 | 0.94 |
| | " | 30% | 20.152 | 0.650 | 0.00535 | 0.92 |
| | " | 50% | 19.810 | 0.638 | 0.00642 | 0.91 |
| Choromytilus meridionalis | HIGH | sublittoral | 20.592 | 3.890 | 0.064 | 0.98 |
| | " | 10% | 20.319 | 3.666 | 0.064 | 0.96 |
| | " | 30% | 20.238 | 3.452 | 0.061 | 0.95 |
| | " | 50% | 19.932 | 3.672 | 0.084 | 0.96 |
| | LOW | sublittoral | 22.062 | 2.919 | 0.045 | 0.97 |
| | " | 10% | 21.406 | 2.567 | 0.039 | 0.97 |
| | " | 30% | 20.530 | 2.594 | 0.055 | 0.94 |
| | " | 50% | 20.044 | 2.570 | 0.079 | 0.92 |
| Mytilus galloprovincialis | HIGH | sublittoral | 20.250 | 5.197 | 0.108 | 0.97 |
| | " | 10% | 20.149 | 5.008 | 0.107 | 0.98 |
| | " | 30% | 20.129 | 4.952 | 0.112 | 0.99 |
| | " | 50% | 20.000 | 5.163 | 0.142 | 0.97 |
| | LOW | sublittoral | 20.321 | 3.978 | 0.069 | 0.99 |
| | " | 10% | 20.292 | 3.822 | 0.067 | 0.96 |
| | " | 30% | 20.240 | 3.569 | 0.069 | 0.95 |
| | " | 50% | 20.000 | 3.324 | 0.069 | 0.96 |
| Perna perna | HIGH | sublittoral | 20.303 | 4.431 | 0.087 | 0.98 |
| | " | 10% | 20.530 | 4.227 | 0.088 | 0.98 |
| | " | 30% | 20.314 | 4.172 | 0.097 | 0.95 |
| | " | 50% | 20.116 | 4.075 | 0.101 | 0.92 |
| | LOW | sublittoral | 21.253 | 3.308 | 0.054 | 0.96 |
| | " | 10% | 20.597 | 3.248 | 0.055 | 0.97 |
| | " | 30% | 20.264 | 3.026 | 0.053 | 0.93 |
| | " | 50% | 19.858 | 2.763 | 0.053 | 0.94 |

Table 2. Polynomial regression equation, of the type $a+bx-cx^2$, describing the growth rates of the mussel populations as shown in Fig. 2.

one of the main reason why mussels held in suspended culture usually grow considerably more rapidly than those held under comparable conditions on the shore. There appears to be a tendency for the effect of water circulation to differ between species. Thus at the sheltered site growth rates of C. meridionalis were retarded by an average of 29%, whereas those of A. ater slowed by 16%, M. galloprovincialis by 8% and P.perna by only 7%. While it is tempting to ascribe these variations to differential requirements for water movement it is equally probable that they are temperature effects, calmer embayments tending to become warmer by day than turbulent regions where solar heated surface layers become mixed into the water column. Comparison with the temperature related tendencies shown in Fig. 1 would tend to support this proposal.

Comparing rates of growth at the different tidal levels all species can be seen to show a marked and progressive decline in growth rate with increasing tidal elevation. This is a well documented phenomenon (Coulthard 1929, Dehnel 1956, Baird 1966, Griffiths 1981b, Della Via et al. 1987) and results from the reduced feeding time available to intertidal populations. Based on the progressive decline in growth rate found at increasing elevations, Baird (1966) estimated that a zero growth point for M. edulis would be reached at the 56% exposure level, while Seed (1969) estimated it at 75% and Gillmor (1982) at the 80% exposure level. In reality such estimates are speculative, since other factors, notably tolerance to extremes of temperature and desication, may become limiting well before scope for growth declines to zero. Thus although physiological experiments indicate that C. meridionalis is able to maintain a positive energy balance up to the 50% exposure level (Griffiths 1981a, Griffiths & Buffenstein 1981), partly by depressing respiration costs (Griffiths 1981c), populations in the field are often restricted to the 30% exposure level as a result of temperature induced mortalities (Griffiths & Hockey 1987).

What is perhaps of more interest is that the effects of increasing aerial exposure appear to be more severe in some of the species tested than in others. This differential reduction in growth performance is shown more clearly in Fig. 3. Also shown are the mortality rates of each population over the 24 month experimental period. It is clear from these diagrams that the four mussel species differ considerably in their ability to tolerate aerial exposure and that depression in growth rate is closely correlated with increasing mortality. The species best able to maintain growth in the intertidal are M. galloprovincialis and P. perna, which continue to grow at ca. 80% of the submerged rate even at the 50% exposure level, compared to 66% for C. meridionalis and only 54% for A.ater. Mortality rates show a parallel tendency, with M. galloprovincialis showing the best survivorship at high exposure levels, followed by P.perna, C. meridionalis and A. ater, less than 10% of which survived the 24 months at the 50% aerial exposure level.

These findings correlate with our observations in the field where in mixed beds the highest levels tended to be colonized by M.galloprovincialis, followed by P. perna and C. meridionalis. A. ater reaches maximum intertidal densities at the lowest tidal levels, becoming the dominant species on sediment-free sublittoral reefs. Although small individuals can penetrate upshore to the mid-intertidal, they do so by living deep within the matrix of thick aggregations of M. galloprovincialis, which presumably protect them from the rigours of desication and temperature (van Erkom Schurink & Griffiths 1990).

Because the data from Seafarm record growth increments of the same individuals over two month time intervals and are supported by in situ temperature recordings, they provide additional evidence for the relationships between increasing shell length and temperature.

Relationships between two-monthly increments in shell length and average water temperature for the sublittoral populations of all four species are shown in Fig. 4, the equations for these trends being given in and Table 3. These plots provide strong support for the contention that

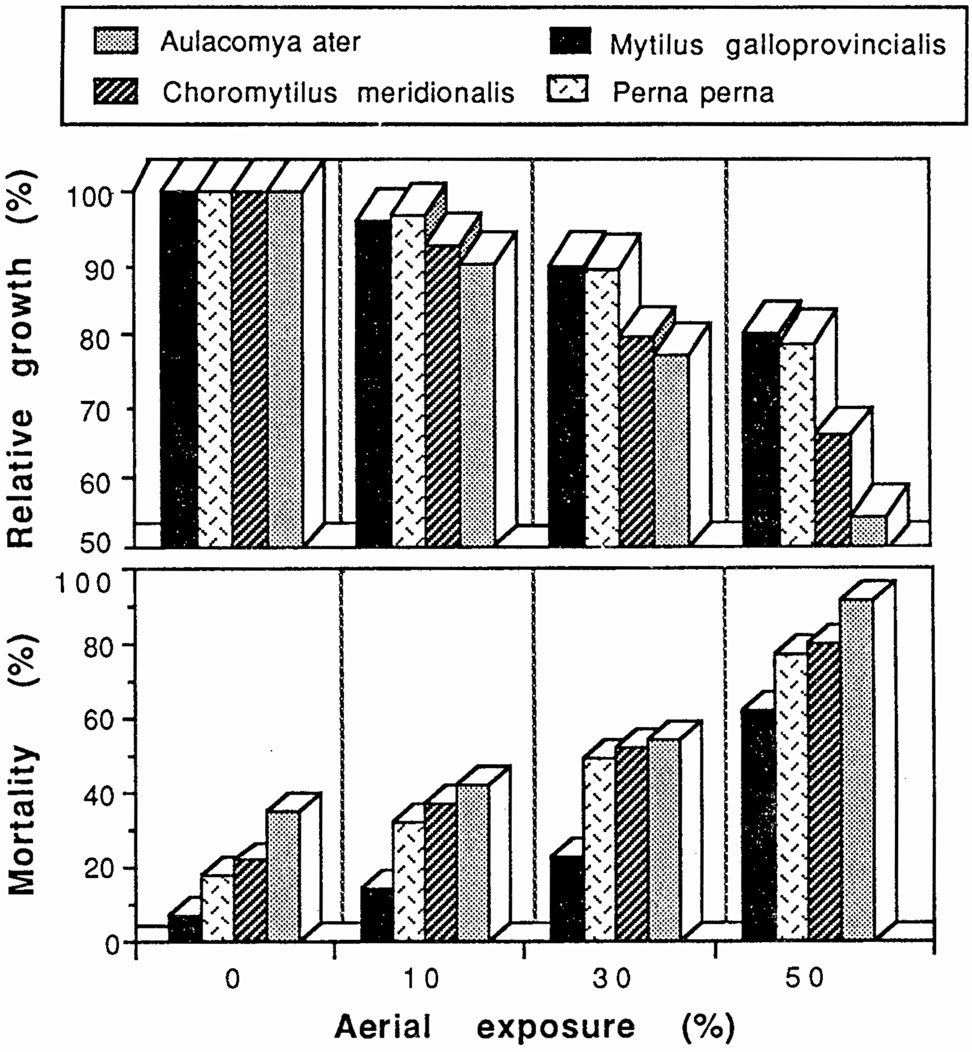

Figure 3. Tolerance to air exposure expressed as the decline in relative growth rate and the increase of mortality for the four mussel species.

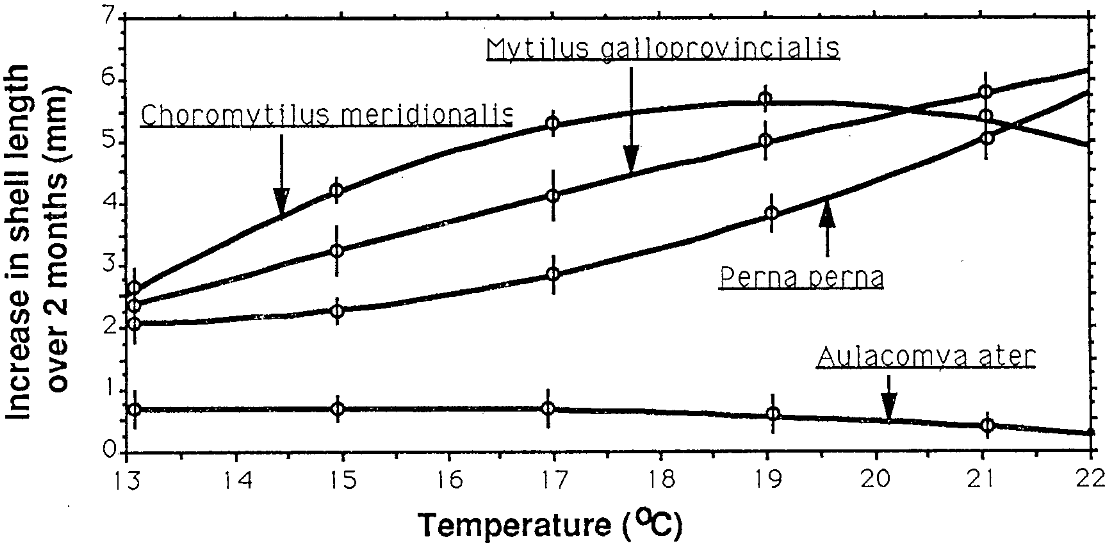

Figure 4. Growth rates of the four species at different seasonal temperatures occurring at Seafarm in Saldanha Bay. Equations are shown in Table 3.

| **Species** | **a** | **b** | **c** | **$r^2$** |
|---|---|---|---|---|
| Aulacomya ater | - 1.226 | 0.261 | 0.00878 | 0.98 |
| Choromytilus meridionalis | - 24.695 | 3.171 | 0.08300 | 0.96 |
| Mytilus galloprovincialis | - 4.718 | 0.614 | 0.00551 | 0.92 |
| Perna perna | 9.163 | - 1.111 | + 0.04300 | 0.95 |

Table 3. Polynomial regression equation, of the type $a+bx-cx^2$, describing temperature related changes in growth rate of the four mussel species, as depicted in Fig. 4.

growth rates in C. meridionalis and A. ater decline at high temperatures, at least above 18°C, whereas those of M. galloprovincialis and particularly P. perna accelerate with increasing water temperature up to the warmest temperatures attained at this site.

## 3. Packing density and sediment loading.

The results of the packing density experiments are shown in Fig. 5. Surprisingly these indicate that sparsely distributed mussels grow more slowly than those at intermediate concentrations, although growth rates decline again at high densities, presumably as a result of competition for resources, especially food. Most previous authors have found a negative correlation between growth rate and density (e.g. Seed 1969, Dare & Edwards 1976, Peterson & Beal 1989) although the densities reported by these workers tend to be high compared to those employed here. It would also appear that growth in C. meridionalis is more sensitive to density than is the case for A. ater or M. galloprovincialis. This would correlate with natural packing densities, C. meridionalis usually occurring in a monolayer, wheras both A. ater and M. galloprovincialis form dense multilayered beds (van Erkom Schurink & Griffiths 1990).

Effects of siltation on growth are summarized in Table 4 and indicate that while A. ater and M. galloprovincialis are adversely affected by suspended silt, growth rates of C. meridionalis increase under such conditions. The sensitivity of A. ater to siltation has previously been alluded to (Barkai & Branch 1989) while Ceccherelli & Baroni (1983) also report reduced growth rates in M. galloprovincialis in areas subject to high concentration of suspended silt. The positive influence of sand on growth in C. meridionalis is not unexpected, since this species is the dominant mussel in areas subjected to sand cover or abrasion (van Erkom Schurink & Griffiths 1990). Similar results have been reported for other silt-tolerent species, such as M. edulis. Both Winter (1976) and Kiorboe

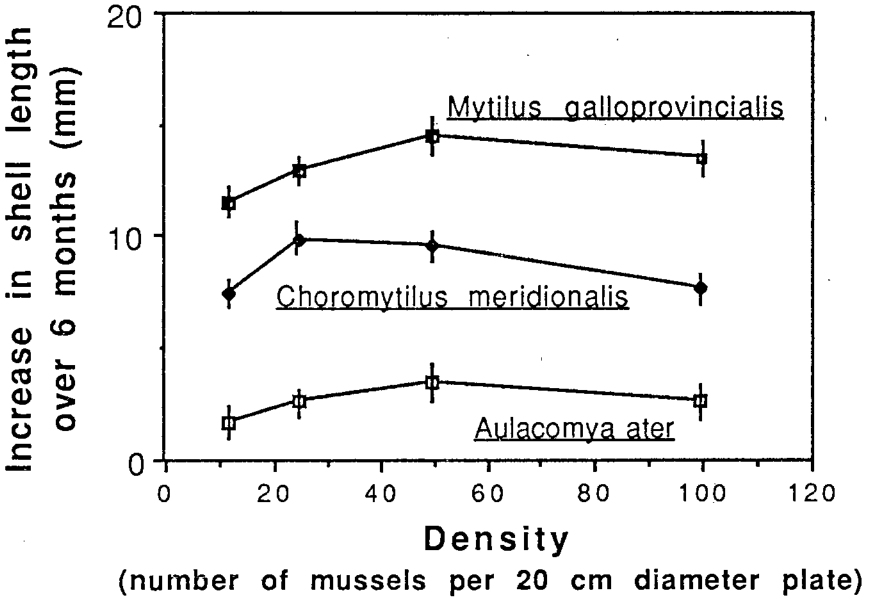

Figure 5. Six-monthly increments in shell growth of the four mussel species when held at four different packing densities.

| **Species** | **Six monthly growth increment (mm)**<br>No silt | Silt | % increase or decrease with silt |
|---|---|---|---|
| Aulacomya ater | 2.3 (0.2) | 1.9 (0.1) | - 17 % |
| Choromytilus meridionalis | 7.7 (0.5) | 8.5 (0.6) | +10 % |
| Mytilus galloprovincialis | 14.2 (1.7) | 11.7 (1.3) | - 18 % |

Table 4. Growth increments in the four mussel species after six months held under silt/no silt conditions. Standard deviation values are given in brackets.

et al. (1981) have found that adding silt to the food of this species can accelerate growth 30-70% above that for mussels fed the same ration, but without the silt.

## 4. Morphometrics.

All growth rates in this study have been recorded as length increments. While length is an extremely convenient and commonly used measure, equal length increments can represent very different investments in shell or body mass in different species or indeed populations, depending upon the allometry of growth. Regression equations relating shell length to height, width, thickness, internal volume and weight for the four South African mussel species studied here are presented in Table 5, while growth related changes in shell shape are depicted in Fig. 6. These indicate that A. ater has a particularly wide shell, while that of C. meridionalis is particularly narrow. The shell of M.galloprovincialis is both tall and moderately wide, while that of P. perna is very low but relatively wide. As a result an average sized individual of 50 mm shell length would have an internal shell volume of 10.1 $cm^3$ in A.ater relative to 8.9 $cm^3$ for M. galloprovincialis 8.3 $cm^3$ in C.meridionalis and only 7.1 $cm^3$ in P. perna. In term of shell thickness and weight A. ater has both the thickest and heaviest shell (1.5 mm and 8.5 g at 50 mm), while C. meridionalis has the thinnest and lightest (1.1 mm and 5.2 g at 50 mm). While we believe these relative proportions to hold true for populations maintained under comparable conditions, shell shape in bivalves is notoriously variable (Seed 1968 and 1973, Hosomi 1985, Vermeij 1990), depending upon population density and growth conditions (see review by Seed 1981). Such variations can occur even between closely adjacent populations, as demonstrated for M. galloprovincialis from our study site in Saldanha Bay (Raubenheimer & Cook 1990).

The most important allometric parameter for the culture industry,

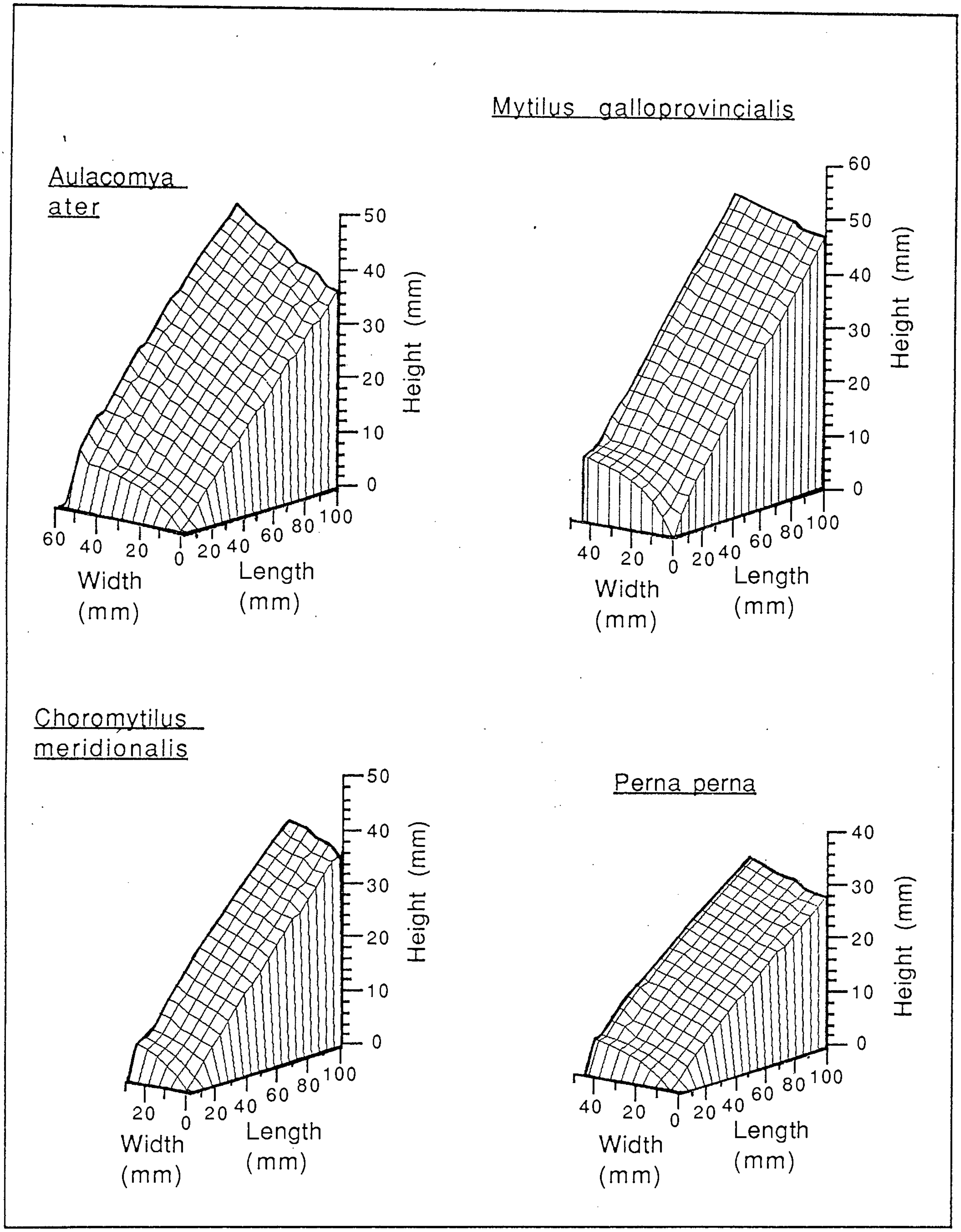

Figure 6. Three-dimensional figure showing the proportions of the shells of the four mussel species. Equations are shown in Table 5.

| Species | Shell | x = shell length (mm) | n = 100 |
|---|---|---|---|
| | | Regressions equations | |
| Aulacomya ater | height (mm) | $y = 0.613762 . x^{0.959}$ | $r^2 = 0.935$ |
| | width (mm) | $y = 0.200447 . x^{1.228}$ | $r^2 = 0.922$ |
| | thickness (mm) | $y = 0.028774 . x^{1.025}$ | $r^2 = 0.874$ |
| | volume ($cm^3$) | $y = 0.000052 . x^{3.112}$ | $r^2 = 0.980$ |
| | weight (g) | $y = 0.000023 . x^{3.276}$ | $r^2 = 0.959$ |
| Choromytilus meridionalis | height (mm) | $y = 0.710000. x^{0.928}$ | $r^2 = 0.975$ |
| | width (mm) | $y = 0.368129 . x^{0.955}$ | $r^2 = 0.951$ |
| | thickness (mm) | $y = 0.024322. x^{0.994}$ | $r^2 = 0.890$ |
| | volume ($cm^3$) | $y = 0.000214 . x^{2.702}$ | $r^2 = 0.986$ |
| | weight (g) | $y = 0.000158 . x^{2.657}$ | $r^2 = 0.976$ |
| Mytilus galloprovinc. | height (mm) | $y = 0.918333 . x^{0.857}$ | $r^2 = 0.965$ |
| | width (mm) | $y = 0.338800 . x^{1.044}$ | $r^2 = 0.964$ |
| | thickness (mm) | $y = 0.021727 . x^{1.028}$ | $r^2 = 0.919$ |
| | volume ($cm^3$) | $y = 0.000122 . x^{2.862}$ | $r^2 = 0.991$ |
| | weight (g) | $y = 0.000050 . x^{3.028}$ | $r^2 = 0.981$ |
| Perna perna | height (mm) | $y = 0.961612 . x^{0.787}$ | $r^2 = 0.958$ |
| | width (mm) | $y = 0.285102 . x^{1.092}$ | $r^2 = 0.959$ |
| | thickness (mm) | $y = 0.061235 . x^{0.779}$ | $r^2 = 0.914$ |
| | volume ($cm^3$) | $y = 0.000132 . x^{2.785}$ | $r^2 = 0.985$ |
| | weight (g) | $y = 0.000113 . x^{2.830}$ | $r^2 = 0.981$ |

Table 5. Regression equations describing the morphology of the shells of four South African mussel species.

that between flesh weight and shell length, has not been included in the above analysis. The reason for this is that while shell growth proceeds more-or-less regularly, at least in the temperature conditions of South African waters, flesh weight fluctuates wildly beyond the size at which the mussels attain maturity, as a result of cyclical periods of gamete build up and release. Typical seasonal fluctuations in shell growth and dry flesh weight for M. galloprovincialis from a subtidal site in Saldanha Bay are shown in Fig. 7. It is clear that while shell growth proceeds throughout the year, albeit at a slightly variable rate, flesh mass undergoes progressively larger oscillations and cannot be reflected by a single allometric equation.

A detailed analysis of the monthly fluctuations of dry flesh mass in standard sized individuals of all four of the species considered here have been presented in an earlier paper (van Erkom Schurink & Griffiths, in press). Although these indicate that dry flesh weight can vary by as much as 3-fold between ripe and spawned conditions some distinct interspecific trends can be seen. In particular it is evident that A. ater and M.galloprovincialis provide considerably higher average flesh yields than C.meridionalis and particularly P. perna of equivalent shell lengths. This is particularly the case when the mussels are in ripe condition, at which stage 65 mm length individuals can vary from a dry flesh mass of as much as 2.3 g in A. ater through 2.1 g in M. galloprovincialis to as little as 1.4 g and 1.3 g in C. meridionalis and P. perna respectively (van Erkom Schurink & Griffiths, in press).

Taking growth rates and flesh yield together it would thus appear that the introduced M. galloprovincialis presents the best candidate for mariculture in South Africa (see also Hockey & van Erkom Schurink, in press). Although C. meridionalis attained faster linear growth rates in Saldanha Bay (Fig. 1), these would not compensate for the increased flesh yield provided by M. galloprovincialis. The dark chocolate colour of the gonad in female C. meridionalis has, moreover, not gained acceptance in

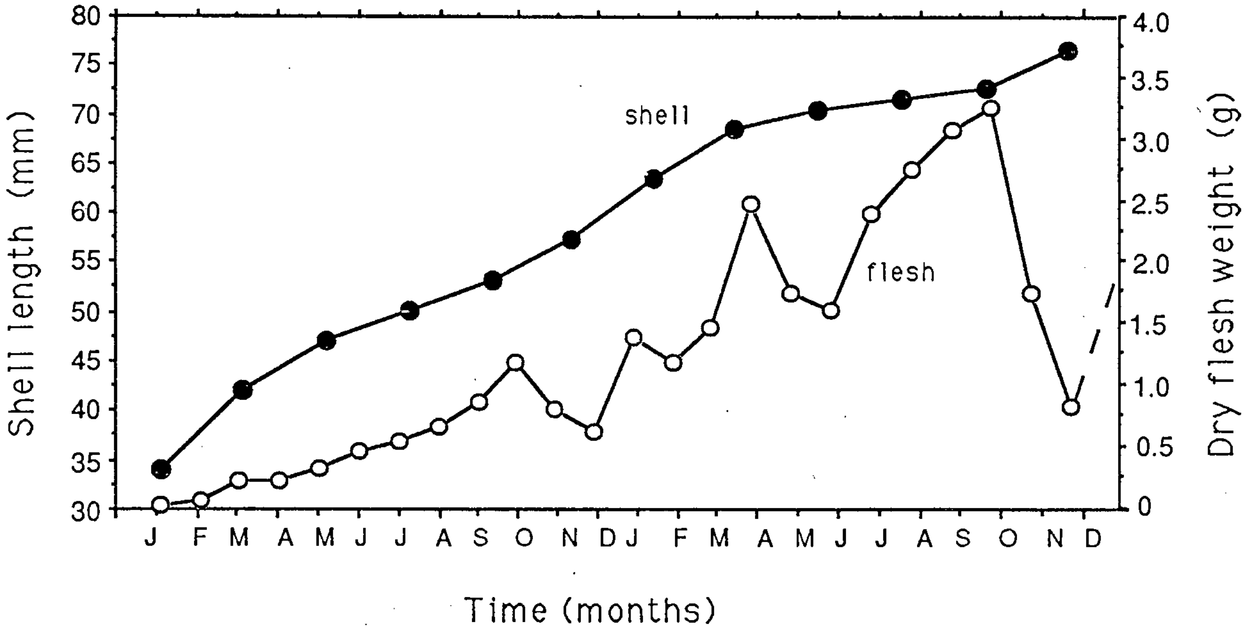

Figure 7. Growth of shell length and flesh weight in <u>Mytilus galloprovincialis</u> over two years, showing seasonal variations. Flesh dry weight was extracted from monthly regression equations derived by van Erkom Schurink & Griffiths (in press), while the shell length curve corresponds to the growth rate monitored sublittoraly at Seafarm in Saldanha Bay (this study).

the market place (van Erkom Schurink & Griffiths 1990). The extremely fast rates of growth attained by P. perna in Natal (Berry 1978) may make this species a valuable candidate for culture in the subtropical waters of this region. However, the viability and growth rates of M.galloprovincialis have not been tested under these conditions, neither has any culture operation been attempted in Natal to date.

## ACKNOWLEDGEMENTS

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# CHAPTER 5

# PHYSIOLOGICAL ENERGETICS OF FOUR SOUTH AFRICAN MUSSEL SPECIES IN RELATION TO BODY SIZE, RATION AND TEMPERATURE

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## ABSTRACT

Rates of filtration, respiration and ammonia excretion, as well as absorption efficiencies and subsequent scope for growth (or energy balance) are compared in four South African mussel species, Aulacomya ater, Choromytilus meridionalis, Mytilus galloprovincialis and Perna perna. Allometric relationships relating these parameters to body size suggest that M. galloprovincialis and C. meridionalis have the fastest feeding and metabolic rates, while A. ater combines very slow filtration with intermediate respiration and excretion rates. In response to increasing ration level all four species show increased filtration, respiration and excretion rates combined with declining absorption efficiencies. As a result all maintain relatively steady scope for growth over the ration levels 1-7 mg $l^{-1}$. Absolute rates are, however, highest in M.galloprovincialis (254 J $h^{-1}$ at 7 mg $l^{-1}$ ration) followed by C.meridionalis and P. perna at 117 and 70 J $h^{-1}$ and finally A. ater, with only 23 J $h^{-1}$. Increased temperature over the range 10-20°C results in an acceleration in filtration rate in M. galloprovincialis and especially P.perna, but declines in C. meridionalis and A. ater. Absorption efficiency is little affected by temperature while respiration and excretion rates rise. The overall result is that scope for growth in M. galloprovincialis is high at all temperatures while that of A. ater is low and declines rapidly with temperature. The scope for growth of P. perna and C. meridionalis is intermediate, but while C. meridionalis becomes less efficient at higher temperatures P.perna show a rapid increase with increasing temperature. The relationships between these physiological measures and the observed distribution pattern and growth rates in the field are discussed.

**Key words**: Mussels, filtration, absorption efficiency, respiration, excretion, energy balance.

# INTRODUCTION

For production to take place there must be a net increase in body energy - i.e. the energy content of the absorbed ration must exceed metabolic energy expenditure (R+U). Two techniques can be used to quantify production in marine bivalves. On the one hand actual rates of somatic growth and gonad output can be estimated in the field. These can then be correlated with environmental conditions. Alternatively short-term physiological estimates of net energy balance can be obtained by measuring the energy equivalent of the absorbed ration (ingestion x absorption efficiency) and subtracting from this both respiratory energy costs (R) and excretory losses (U). The resulting expression C x abs. eff.-(R+U) is termed the scope for growth (Warren & Davis, 1967; Bayne et al., 1976; Newell, 1979; Bayne & Newell, 1983; Griffiths & Griffiths, 1987). Although this technique does not differentiate between energy utilized for growth (Pg) and that used in reproductive output (Pr) it can be estimated relatively quickly under closely controlled conditions in the laboratory. It thus provides an excellent means of quantifying variations in energy balance of individual bivalves in relation to body size, or relative to such environmental parameters as food concentration or temperature.

An extremely large body of literature is available on both individual physiological rate processes and on factors influencing energy balance in marine mussels, and the topic has been reviewed many times, both with respect to individual variables such as filtration rate (Winter, 1977, 1978), or temperature (Newell & Branch, 1980), or in its entirety (Bayne, 1976; Griffiths & Griffiths, 1987). Although all these authors make exhaustive interspecific comparisons of various rates process the validity of such comparisons is confounded by the very often different experimental conditions ( especially food type and concentration, and temperature) under which the various measures were made. The objective of the present study is to attempt to compare physiological rate processes and scope for growth in the four mussel species which occur abundantly along the South African coast (van Erkom Schurink & Griffiths, 1990) under the same controlled conditions. In particular we intend to examine relationships between feeding rate, respiration rate and rate of ammonia excretion relative to body size, food concentration and temperature.

The four species in question are the ribbed mussel, Aulacomya ater, and the black mussel, Choromytilus meridionalis, which occur mainly along the west and south coasts of South Africa, the brown mussel Perna perna, which is most abundant on the east coast, and the recently introduced Mediterranean mussel Mytilus galloprovincialis, which is now the dominant intertidal species on the Atlantic seaboard. The distribution patterns, reproductive cycles and growth rates of these species have been compared in a recent series of publications by van Erkom Schurink & Griffiths (1990 and in press a, b). A good deal of physiological work has already been done on these species. Griffiths & King (1979) examined the effects of body size and suspension density on filtration rate, absorption efficiency, respiration rate and hence scope for growth in A. ater held at 12.5$^{o}$C and fed on cultured Dunaliella primolecta cells. A similar analysis has been undertaken on C. meridionalis by Griffiths (1980a), working at both 12$^{o}$C and 18$^{o}$C and also using D. primolecta as a food source. Some comparable data have been obtained by Berry & Schleyer (1983) for P. perna. However, the authors of that study worked at a higher temperature of 20$^{o}$C, calculated absorption efficiencies based on a natural detrital diet and measured respiration rates in unfed mussels, rather than relating respiration rate to increasing ration levels. The crucial importance of diet in scope for growth measurements has been emphasized in a further study of A. ater by Stuart (1982). Using aged kelp detritus as a diet she obtained much higher absorption efficiencies and hence enhanced scope for growth at high rations relative to those previously reported by Griffiths &

King (1979). In another South African study Clarke & Griffiths (1990) demonstrated dramatic deterioration in the energy balance of C.meridionalis as temperatures increase over the range 12.5 - 30°C, further emphasizing the pitfalls of comparisons made between data sets obtained at different temperatures.

## MATERIAL AND METHODS

Mussels for use in the physiological experiments described below were collected from near low water spring tide on rocky shores at either Bloubergstrand, some 20 km north of Cape Town (Aulacomya ater, Choromytilus meridionalis and Mytilus galloprovincialis), or from Dido Valley in False Bay, some 30 km south of Cape Town (Perna perna). On return to the laboratory the mussels were cleaned of fouling organisms, separated into size classes and held in mesh bags suspended in a closed-circuit aquarium system maintained at 15°C, where they were fed daily on cultured algae, Thalassiosira weissflogii. When experiments were conducted at temperatures other than 15°C mussels were transferred to sea water tanks maintained at the relevant temperatures 24h prior to the start of each run. After use, the dry flesh weight (48h at 60°C) of each animal, excluding byssus, was recorded together with its shell length measured to the nearest mm with vernier callipers.

### 1. Filtration rates.

Filtration, or clearance rates were estimated from the rates of decline in particle concentration in 1 liter experimental chambers, as measured with a Coulter Multisizer particle counter equipped with a 70 µm aperture tube. This aperture tube records particles over the size range 1.26 µm - 50.8 µm diameter, but only counts of particles above 2 µm diameter were used in our analyses, since counts of smaller particles were considered unreliable. In any event particles below 2 µm are inefficiently cleared by most mussel species (see review by Griffiths & Griffiths, 1987).

For each experimental run individuals, or small groups of similar-sized mussels were attached to Perspex grids placed in sealed 1l containers immersed in a constant temperature water bath. The water in each container was agitated from below by a magnetic stirrer. Inlet pipes connected each chamber to an upper reservoir containing 0.2 µm filtered seawater to which a known concentration of food particles was added. Outlet pipes drained each chamber into a lower reservoir. At the beginning of each run food suspension was run through the chambers for 5 mins. A 50 ml sample was then collected from the outlet pipe for particle analysis and clamps on both inlet and outlet pipes immediately closed. After 15 mins the clamps were opened again and the first 50 ml emerging from the outlet used as a second sample. The chambers were then flushed for a further 5 mins and the entire procedure repeated until 4 sets of samples had been collected from each chamber. Triplicate readings of particle concentration were taken from each of these water samples and filtration rates calculated from the standard formula :-

$$\text{Filtration rate} \quad \text{l h}^{-1} = \frac{(\log_e N_1 - \log_e N_2)\, V}{T\, N}$$

Where $N_1$ and $N_2$ = the initial and final particule counts, V = volume of the chamber in liters, T = time elapsed in hours, and N = number of animals in the chamber.

All feeding experiments were conducted using a mixed diet consisting one third of natural detritus backwashed from the filter on the seawater intake pipe of the Sea Fisheries Research Institute aquarium system in Sea Point, Cape Town, and two thirds of cultured Thalassiosira weissflogii cells, which have a cell diameter of 8-16 µm. The dry mass of the ration used in each run was determined by filtering a known volume of food suspension onto Whatman GF/F filter paper, rinsing with isotonic ammonium formate and drying for 48h at 60°C.

## 2. Respiration rates.

Respiration rates were measured at the same times as filtration rates, using YSI $O_2$ probes projecting through the lids of each chamber and connected via a switchgear to a chart recorder. Uniform oxygen saturation was maintained in the upper reservoir by aerating with air stones and mixing with a submerged circulation pump. Respiration rates are expressed in $\mu l\ O_2\ h^{-1}$ using the formula :

$$\text{Respiration rate } \mu l\ O_2\ h^{-1} = \frac{(\text{ppm}_1 - \text{ppm}_2)\ (700.8)\ V}{T\,N}$$

where $\text{ppm}_1$ and $\text{ppm}_2$ = initial and final $O_2$ concentration in parts per million, 700.8 = the conversion factor from ppm to $\mu l\ O_2\ h^{-1} l^{-1}$, V = volume of the chamber in liters, T = time elapsed in hours, and N = number of animals in the chamber.

## 3. Absorption efficiencies.

Absorption efficiencies were estimated by collecting all faeces and pseudofaeces produced over a 3h period following each set of filtration and respiration experiments, food concentration in the chambers being maintained at the relevant level over this period. Faecal samples were pipetted onto preashed and preweighed 25 mm diameter Whatman GF/F filter paper, rinsed with isotonic ammonium formate, dried for 24h at 60°C, weighed, ashed for 4h at 450°C and reweighed. The fraction of faeces lost on ashing was then compared with that for samples of food suspension treated in the same way. Absorption efficiency was calculated according to the method of Conover (1966) :

$$\text{Absorption efficiency \%} = \frac{E - F}{(1 - E)\,F} \times 100$$

where F = fraction of food lost on ashing, and E = fraction of faeces lost on ashing.

## 4. Excretion rates.

The principal excretory product in bivalve molluscs is ammonia (see review by Griffiths & Griffiths, 1987) and only this component was measured. Excretion rates were recorded at the same time as absorption efficiencies, that is over a 3h period following each filtration and respiration rate experiment. Water samples were removed from the chambers every 30 mins over this period and ammonia excretion rates estimated from the rate of increase in ammonia-N, as determined by the indophenol-blue spectrophotometric technique of Koroleff (1976), as adapted by Mostert (1983).

## 5. Scope for growth.

Short term estimates of energy balance, or Scope for Growth, were obtained by calculating the energy equivalent of the absorbed ration (Ab) from the feeding rate and absorption efficiency, and then substracting from this both respiratory energy expenditures and excretory losses.

The energy value of the food medium used was estimated by spinning down samples of food concentrate in a centrifuge, resuspending in isotonic ammonium formate and spinning down again. The resulting food pellets were dried for 48h at 60°C and then burned in a Digital Data System CP 500 Calorimeter. Respiratory oxygen consumption was converted to energy units using the standard oxycalorific equivalent 1 ml $O_2$ = 20.19 J (Griffiths, 1980b) and ammonia-N converted to energy units using the conversion 1 mg $NH_4$-N = 24.87 J (Elliot & Davison, 1975).

## RESULTS AND DISCUSSION

### 1. Allometric relationships.

Relationships between body size and metabolic rate processes are conventionally expressed in terms of the familiar allometric equation :

$$Y = a X^b$$

where Y represents the rate process in question, X the body size of the individual and a and b fitted parameters; a being the rate for an individual of unit body size and b the power by which that rate accelerates with increasing body size.

Amongst the Bivalvia body size is normally measured as either shell length (mm) or as dry flesh weight (g). Both measures have their shortcomings. Although simple to measure, shell length is not a consistent index of body size, since shell volume and hence body weight can vary considerably both within and between species (see for example Seed, 1973, 1981; van Erkom Schurink & Griffiths, in press b). Dry flesh weight that can only be ascertained after the completion of experimental procedures, requires the sacrifice of the specimen and is relatively time consuming. Moreover individual dry flesh mass can fluctuate by a factor of 2-3 over short time periods, as gonad material is rapidly accumulated and then released (van Erkom Schurink & Griffiths, in press a). For these reasons, and also to permit comparisons with the widest possible range of literature values we have elected to present equations relating metabolic rates to both shell length and dry flesh weight. The a and b values for such equations are listed in Table I, and the relationships between filtration rate, respiration rate and excretion rate of the four species as functions of shell length depicted comparatively in Figs 1-3 respectively.

In terms of filtration our results indicate that for individuals of equal shell length the fastest filtration rates would be attained by M.galloprovincialis, followed by C. meridionalis, then P. perna, with A. ater showing the slowest rate (Fig. 1). For example a 50mm A. ater would filter only 0.65 l $h^{-1}$, compared to 1.32 l $h^{-1}$ for a P. perna, 1.76 l $h^{-1}$ for a C. meridionalis and 2.27 l $h^{-1}$ for a M. galloprovincialis of equivalent length (a total range of 3.5 :1). A similar picture emerges when the rates are expressed per unit body weight. However, in such units the rates for the relatively fatter and heavier A. ater and M. galloprovincialis tend to decline relative to those of narrow shelled C. meridionalis and low shelled P. perna (van Erkom Schurink & Griffiths, in press b). This has the effect of reducing the disparity between M. galloprovincialis, C. meridionalis and P. perna, while accentuating the much lower rates of filtration exhibited by A. ater. Rates for a 1g dry flesh weight individual (given by the a values in Table I) would then range from a maximum of 4.1 l $h^{-1}$ in M.galloprovincialis to 3.5 l $h^{-1}$ in C. meridionalis, 2.6 l $h^{-1}$ in P. perna and only 0.89 l $h^{-1}$ in A. ater (a total range of 4.6 :1).

The weight specific filtration rate, or a values, reported above fall well within the wide range (of almost an order of magnitude from approximately 0.5 - 5.0 l $h^{-1}$) reported in previous reviews of bivalve feeding (Winter, 1976; Bayne et al., 1976; Bayne & Newell, 1983). The value of 0.89 for A. ater lies close to that of 0.94 reported for the same species by Griffiths & King (1979), but those for C. meridionalis and P.perna lie well below previously reported rates of 5.4 l $h^{-1}$ and 8.9 l $h^{-1}$ by Griffiths (1980b) and Berry & Schleyer (1983) respectively. In the case of P. perna this difference can readily be explained by variations in experimental temperature, Berry & Schleyer having conducted their

## LENGTH RELATIONSHIPS

| Parameter | | Species | | | |
|---|---|---|---|---|---|
| | | Aulacomya ater | Choromytilus meridionalis | Mytilus galloprovincialis | Perna perna |
| Filtration rate ($l_1 h^{-1}$) | *a* | 0.000084 | 0.000020 | 0.000017 | 0.000065 |
| | *b* | 2.29 | 2.93 | 3.02 | 2.54 |
| | r2 | 0.98 | 0.96 | 0.98 | 0.94 |
| Respiration rate ($\mu l$ $O_2$ $h^{-1}$) | *a* | 0.00030 | 0.0034 | 0.00047 | 0.00081 |
| | *b* | 3.38 | 2.92 | 3.35 | 3.17 |
| | r2 | 0.91 | 0.97 | 0.99 | 0.99 |
| Excretion rate ($\mu g$ $NH_4$-N $h^{-1}$) | *a* | 0.00072 | 0.000035 | 0.0015 | 0.0038 |
| | *b* | 2.59 | 3.52 | 2.30 | 2.10 |
| | r2 | 0.98 | 0.94 | 0.99 | 0.99 |

## WEIGHT RELATIONSHIPS

| Parameter | | Species | | | |
|---|---|---|---|---|---|
| | | Aulacomya ater | Choromytilus meridionalis | Mytilus galloprovincialis | Perna perna |
| Filtration rate ($l_1 h^{-1}$) | *a* | 0.89 | 3.49 | 4.08 | 2.55 |
| | *b* | 0.81 | 1.00 | 1.06 | 0.88 |
| | r2 | 0.99 | 0.98 | 0.99 | 0.98 |
| Respiration rate ($\mu l$ $O_2$ $h^{-1}$) | *a* | 295.8 | 575.4 | 435.5 | 411.2 |
| | *b* | 1.10 | 0.99 | 1.17 | 1.19 |
| | r2 | 0.97 | 0.98 | 0.99 | 0.99 |
| Excretion rate ($\mu g$ $NH_4$-N $h^{-1}$) | *a* | 26.61 | 72.95 | 18.66 | 24.38 |
| | *b* | 0.93 | 1.21 | 0.80 | 0.73 |
| | r2 | 0.99 | 0.96 | 0.98 | 0.97 |

Table I : Table showing the values of the intercepts (a) and slopes (b) of the regression lines relating filtration, respiration and ammonia-N excretion rates to both shell length and dry flesh weight in four South African mussel species.

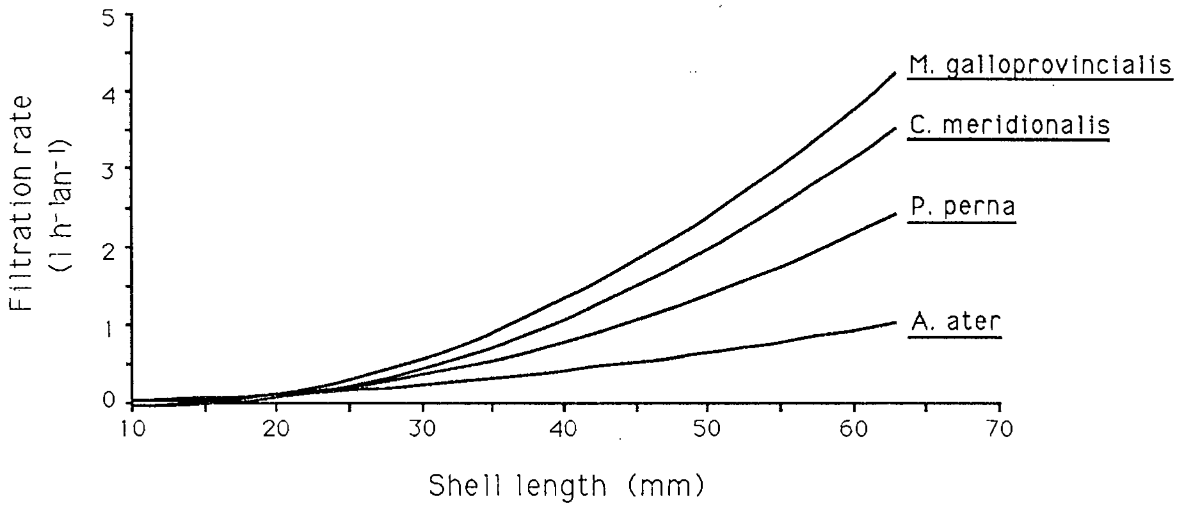

Figure 1 : Filtration rate related to shell length in the four mussel species maintained at 15°C and a ration equal to 3 mg $l^{-1}$. Because of the proximity of the curves standard deviations are omitted from this and subsequent figures.

experiments at a much higher temperature of 20°C.

The b values, or weight exponents given in Table I are generally higher than those reported in the literature, Bayne & Newell (1983), having for example calculated a mean value of 0.62 from a review of 19 studies of suspension feeding bivalves. These relatively high values could have resulted from the exclusion of large, senescent individuals from our study, studies incorporating larger-size individuals being known to produce lower b values than those derived from younger individuals ( Bayne et al., 1976; Griffiths & Griffiths, 1987). Relationships between body size and absorption efficiency were not tested, since the majority of authors (e.g. Thompson & Bayne, 1974; Griffiths & King, 1979; Stuart et al., 1982; Navarro & Winter, 1982) have shown absorption efficiency to be independent of body size.

Respiration rates, when expressed as function of shell length, are maximal in C. meridionalis (rather than M. galloprovincialis) at 302 µl $O_2h^{-1}$ at 50mm shell length (Fig. 2). The rate for M. galloprovincialis is considerably lower (226 µl $h^{-1}$) followed by that of A. ater (193 µl $h^{-1}$) and finally P. perna (163 µl $h^{-1}$). Conversion to weight units again has the effect of elevating the rates of C. meridionalis and P. perna, which have relatively low body mass to shell length relationships, as compared to those of the broader shelled and hence heavier M. galloprovincialis and A.ater. Thus in weight specific terms (given as the a values in Table I) the highest respiration rates occur in C. meridionalis (575 µl $O_2$ $h^{-1}$ $g^{-1}$), while P. perna and M. galloprovincialis have similar rates of 447 and 436 µl $O_2$ $h^{-1}$ $g^{-1}$ respectively and A. ater much lower ones of 262 µl $O_2$ $h^{-1}$ $g^{-1}$. All these values fall well within the wide ranges reported in earlier reviews. For example Bayne et al. (1976) list values of between 160 and 700 µl $O_2$ $h^{-1}$ $g^{-1}$ (mean 428) for 15 studies of marine mussels and Bayne & Newell (1983) 23 values of between 164 and 2 655 µl $O_2$ $h^{-1}$ $g^{-1}$ (mean 496)

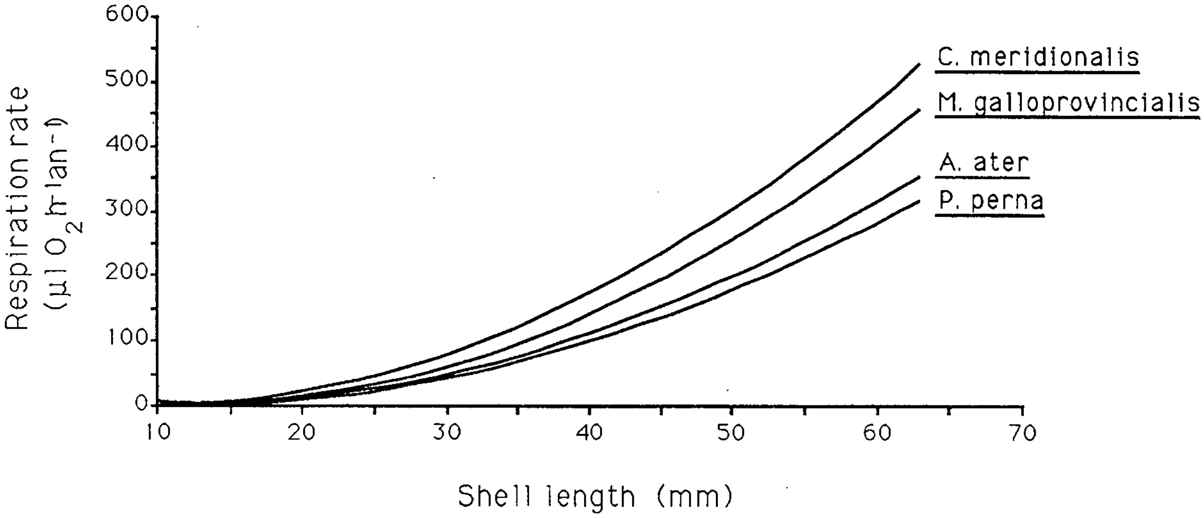

Figure 2 : Respiration rate related to shell length in the four mussel species maintained at 15$^{\circ}$C and a ration equal to 3 mg $l^{-1}$.

for suspension and deposit feeding bivalves tested under a wide range of conditions. Our rates for C. meridionalis are close to those recorded by Griffiths (1980b). Those for A. ater are somewhat higher than reported by Griffiths & King (1979), but were recorded at 15°C rather than 12.5°C used by these authors. Rates for P. perna are some 50% higher than those given in Berry & Schleyer (1983). Their readings were, however, made in the absence of suspended food material, the presence of which is known to result in an elevation of respiratory energy expenditure (see below).

Turning to rates of ammonia-N excretion (Fig. 3) it is evident that C.meridionalis has by far the fastest rate of excretion of the species tested, equivalent to 34 µg $NH_4$-N $h^{-1}$ at a length of 50mm. Despite its low feeding and respiration rates A. ater has the next highest excretion rate (18.0 µg $NH_4$-N $h^{-1}$) followed by P. perna (13.9 µg) and finally M.galloprovincialis at only 12.1 µg for a 50mm shell length individual.

The same order is maintained when rates are expressed per unit body mass, although the high figures obtained for C. meridionalis become even more pronounced at 73 µg $NH_4$-N $h^{-1}$ $g^{-1}$ for a 1g animal, more than double those for A. ater, P. perna and M. galloprovincialis at 27, 24 and 19 µg $NH_4$-N $h^{-1}$ $g^{-1}$ respectively. The rate for C. meridionalis is amongst the highest recorded to date, while the remaining figures are typical of those obtained in previous studies of bivalve excretion rates, as reviewed by Griffiths & Griffiths (1987). No previous measures of rates of ammonia-N excretion are available for A. ater, C. meridionalis or P. perna. Some data on excretion in M. galloprovincialis are given in Bayne & Scullard (1977a). Although the excretion rates reported therein are considerably lower than those estimated here, ammonia excretion rates are known to vary considerably with both reproductive and nutritional status ( Bayne & Scullard, 1977b).

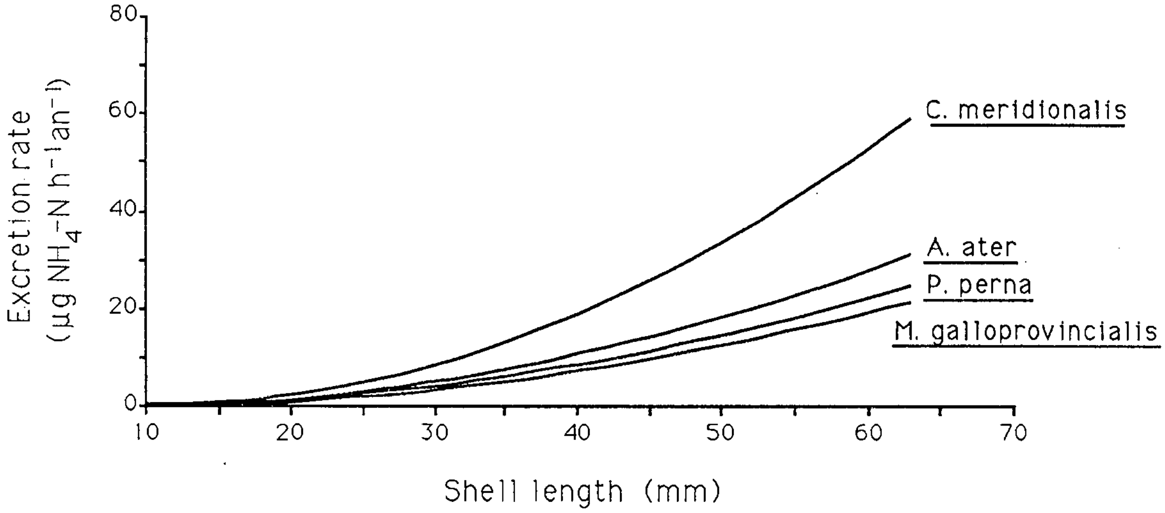

Figure 3 : Ammonia-N excretion related to shell length in the four mussel species maintained at 15$^{o}$C and a ration equal to 3 mg $l^{-1}$.

Taken overall, these allometric relationships indicate that maximum positive energy balance is likely to occur in M. galloprovincialis, which exhibit rapid rates of filtration in combination with relatively low rates of respiratory energy loss and especially excretion. Although C.meridionalis also show rapid rates of particle clearance, these are accompanied by extremely fast respiratory and excretory losses. A. ater filter and respire much more slowly than other species, but have comparable rates of excretion and so have low rates of energy aquisition. P. perna show intermediate rates for all parameters, but were tested at temperatures known to be below those at which they achieve maximum growth (van Erkom Schurink & Griffiths, in press b).

## 2. Physiological effects of changing ration level.

The results shown above give some indication of relative rates of energy aquisition and expenditure in the four mussel species at a single ration level of 3 mg $l^{-1}$. Actual metabolic balance is, however, determinated not only by the filtration or feeding rate, but also by the density of food particles in the water column, as well as the efficiency with which any ingested food is subsequently absorbed. Absorption efficiency, as well as filtration, respiration and excretion rates are all known to vary with food concentration (for reviews see Bayne & Newell, 1983; Griffiths & Griffiths, 1987). To integrate all these variations and calculate subsequent energy balance, or scope for growth, within feasible time limits we have confined the following analysis to mussels of a single size class of 50 mm ( ± 2 mm).

The results in term of filtration rate (Fig. 4) confirm the above observation that M. galloprovincialis shows the fastest filtration rates of the species tested, followed by C. meridionalis, P. perna and finally A. ater (Fig. 1). In addition it can be seen that all four species increase filtration activity by approximately 25-40% as ration level increases over

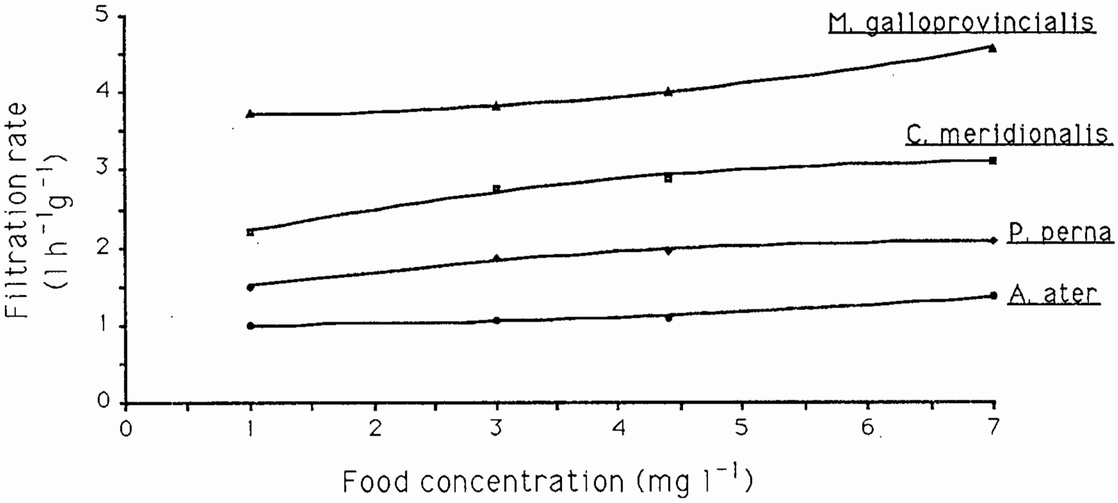

Figure 4 : Filtration rates of the four mussel species at different ration levels and at a temperature of 15$^{o}$C.

the fairly narrow range of 1-7 mg $l^{-1}$. In the case of A. ater very similar trends, both in term of absolute filtration rates and ration-induced accelerations of that rate have been reported by both Griffiths & King (1979) and Stuart (1982). Griffiths (1980b) found the filtration rate of C.meridionalis to be unaffected by ration level over the range tested here, although she reported an acceleration in rate at ration levels below 0.5 mg $l^{-1}$ (equivalent to concentrations below 4 x$10^6$ cells Dunaliella primolecta $l^{-1}$). No comparative data are available for either P. perna or M.galloprovincialis.

Turning to absorption efficiency all four species show similar and progressive declines in absorption efficiency from 70-80% at food concentrations of 1 mg $l^{-1}$ to between 15 and 45% at 7 mg $l^{-1}$ (Fig. 5). The highest absorption efficiencies were recorded for M. galloprovincialis, despite its rapid filtration rate, and the lowest for A. ater, despite its low rate of ingestion (see above).

Relationships of this type are well known in the bivalve literature (e.g. Thompson & Bayne, 1974; Widdows, 1978). At low ration levels it is thought that all the food ingested can be transported to, and processed by, the digestive gland. As ingestion ration increases, the capacity of the digestive gland is exceeded and more and more of the ingested material passes directly down the intestine to be passed out in the form of poorly digested socalled 'intestinal faeces', resulting in an overall decline in absorption efficiency (Widdows et al., 1979). Ultimately excess food may be rejected as pseudofaeces, after which ingestion ration and absorption efficiency stabilize.

Actual absorption efficiencies recorded for C. meridionalis herein are comparable with those given by Griffiths (1980b). In the case of A. ater efficiencies are intermediate between those recorded for specimens fed on cultured algae (Griffiths & King, 1979) and those fed on aged kelp bed detritus (Stuart et al., 1982). Such a result would be expected considering the mixed diet used in this study.

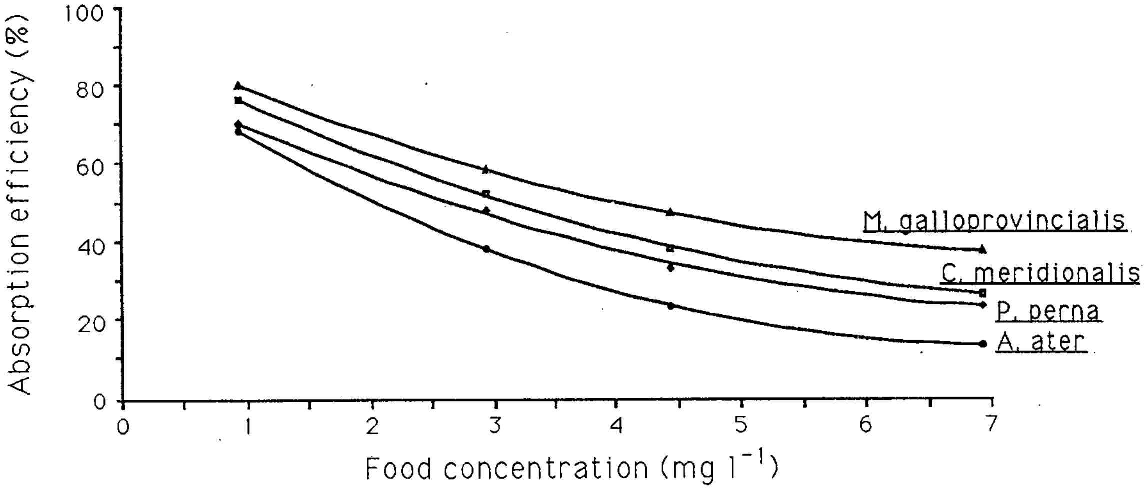

Figure 5 : Absorption efficiencies of the four mussel species at different ration levels when maintained at a temperature of 15$^{o}$C.

No measurable quantities of pseudofaeces were produced by any of the species over the range of food concentrations used in this study.

The effects of increasing ration level on respiratory activity are shown in Fig. 6. As might be expected, given the acceleration in filtration rate described above, and the increased metabolic costs associated with any increase in feeding activity (Bayne & Scullard, 1977b), all four species show increased rates of oxygen consumption at higher ration levels. Similar responses are widely reported in the literature (e.g. Thompson & Bayne, 1972; Bayne et al., 1976; Bayne & Scullard, 1977b; Navarro & Winter, 1982; Bayne et al., 1989). Ration induced accelerations in respiration rate similar to those shown in Fig. 6 have previously been reported in A. ater (Griffiths & King, 1979; Stuart, 1982), but no earlier data are available for M. galloprovincialis or P. perna. In contrast to our results Griffiths (1980b) reports that respiration rate is independent of ration level in C. meridionalis.

As is the case with filtration and respiration rates, rates of ammonia-N excretion also increase steadily with ration level (Fig. 7). No comparable data series have previously been obtained on the species considered here.

Changes in metabolic energy balance (or scope for growth) associated with increasing ration level may be calculated by converting the ingested rations calculated above into energy units, multiplying by absorption efficiency and then subtracting respiratory and excretory losses, also expressed in energy terms. Such plots are depicted in Fig. 8 and indicate that all four species achieve a strongly positive energy balance at food concentrations as low as 1 mg $l^{-1}$ (equivalent to only 1 ppm food). Increase in ration level from this point upwards to 7 mg $l^{-1}$ results in only marginal increases in scope for growth. This is because any increases in ingested ration (Fig. 4) are compensated for by declines in absorption efficiency (Fig. 3) and also by increased respiratory and excretory costs (Figs 6, 7). These results are in agreement with those obtained by other

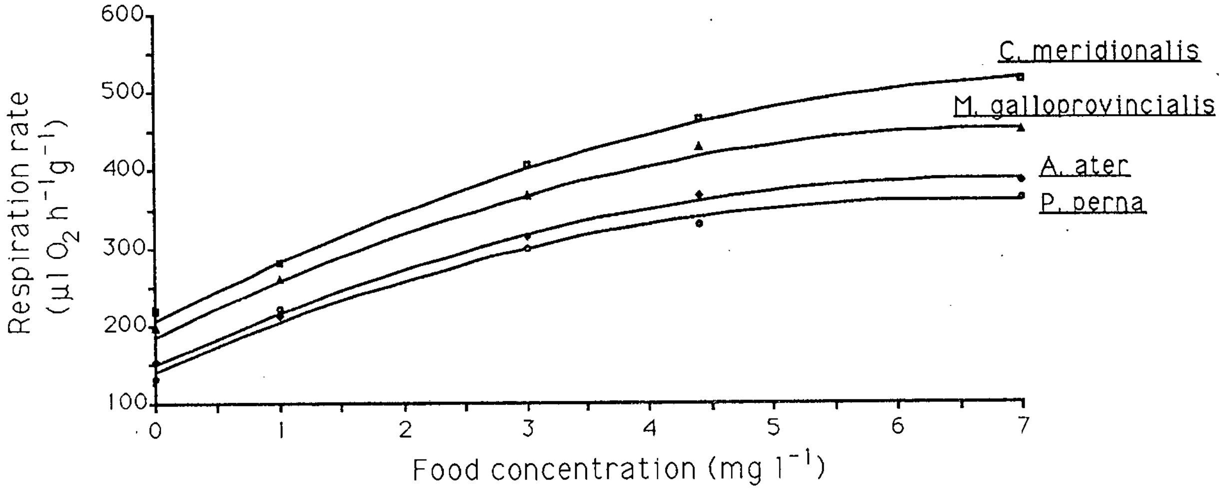

Figure 6 : Respiration rates of the four mussel species at different ration levels when held at 15°C.

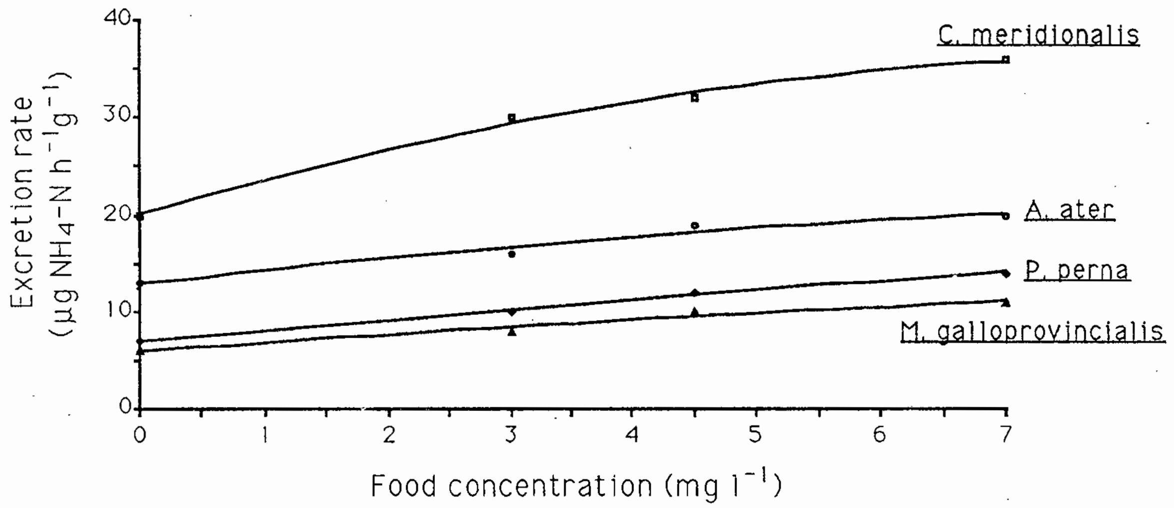

Figure 7 : Ammonia-N excretion rates of the four mussel species at different ration levels. Temperature is maintained at 15°C.

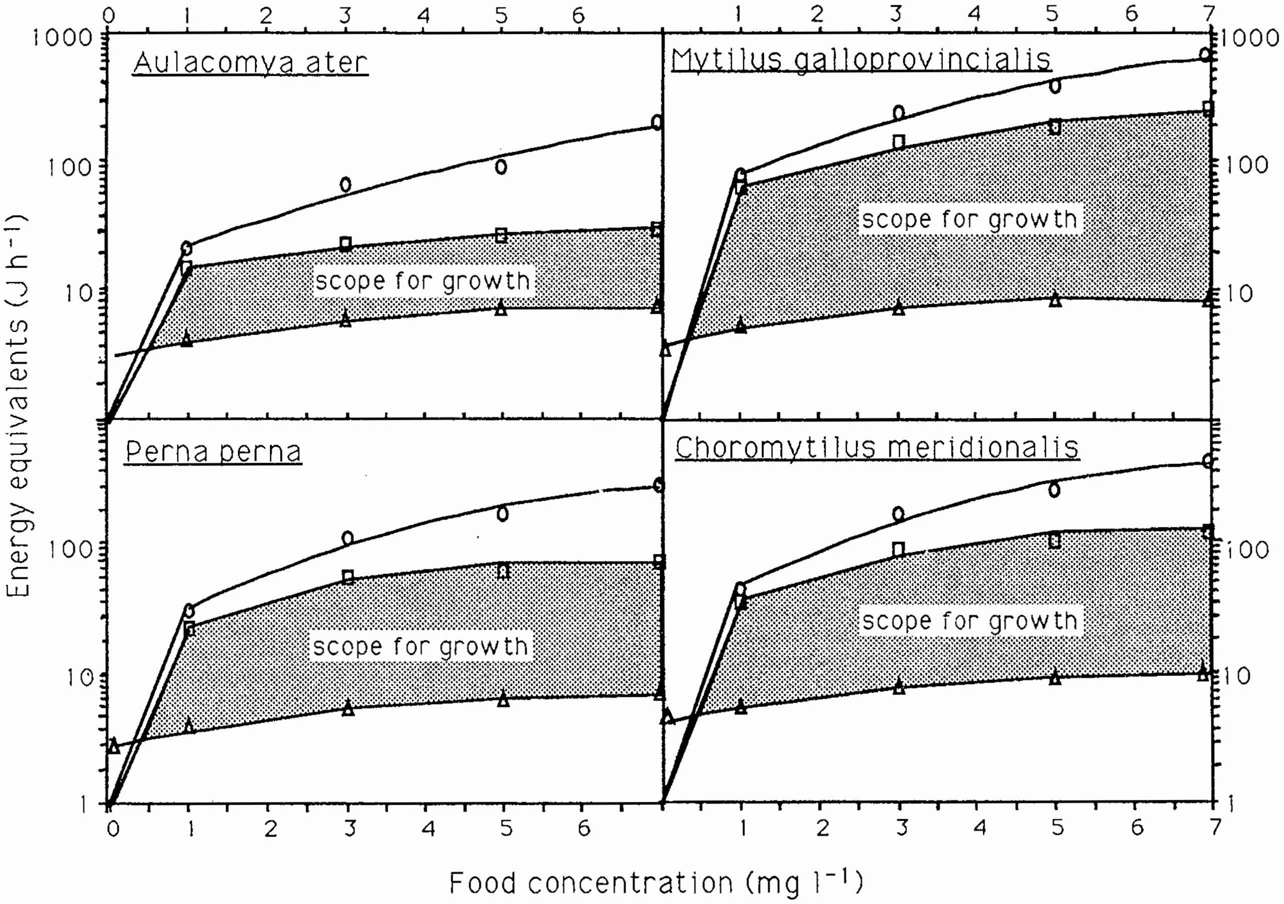

Figure 8 : Ingestion ration (0), absorbed ration (□), respiration rate (Δ) and subsequent scope for growth of the four mussel species at different ration levels. Temperature is maintained at 15°C.

workers who have used natural detritus as a food source, such as by Griffiths (1980a) for C. meridionalis, Stuart (1982) for A. ater and Bayne et al. (1989) for M. chilensis. Quite different results, in which optimal scope for growth occurs at low suspension densities of ca 1-4 mg $l^{-1}$ and declines at higher ration levels have been reported where cultured unicellular algae are used as food, such as by Griffiths & King (1979) for A.ater, Griffiths (1980b) for C. meridionalis and Navarro & Winter (1982) for M. chilensis.

Comparing absolute rates of energy gain by the four species minimal rates are clearly achieved by A. ater, which makes an optimal energetic profit of only 23 J $h^{-1}$ at a ration of 7 mg $l^{-1}$. By contrast M.galloprovincialis achieves maximal scope for growth of ca 254 J $h^{-1}$ and C. meridionalis and P. perna intermediate rates of 117 and 70 J $h^{-1}$.

These laboratory based physiological results correlate well with field data on growth and reproductive output (van Erkom Schurink & Griffiths, in press b) which indicate that A. ater is by far the slowest growing of the four species , while M. galloprovincialis is capable of maintaining rapid growth rates and simultaneously high reproductive output.

## 3. Influence of temperature on metabolic rates.

Variations in filtration rates of 50 mm shell length mussels held at 10, 15 and 20°C are depicted in Fig. 9. Two types of response are evident from these plots. On the one hand M. galloprovincialis and particularly P.perna show marked accelerations of filtration rate with increasing exposure temperature. This acceleration was very rapid in P. perna, in which filtration rates rose from only 0.8 l $h^{-1}$ at 10°C to 3.1 l $h^{-1}$ at 20°C, a $Q_{10}$ of 3.9 . By comparison the $Q_{10}$ for M. galloprovincialis is only 1.3 . Both these rates fall within the wide range reported by Winter (1977). In the reverse trend, C. meridionalis and A. ater both show maximal filtration rates at the lowest temperature tested and progressively slower ones at

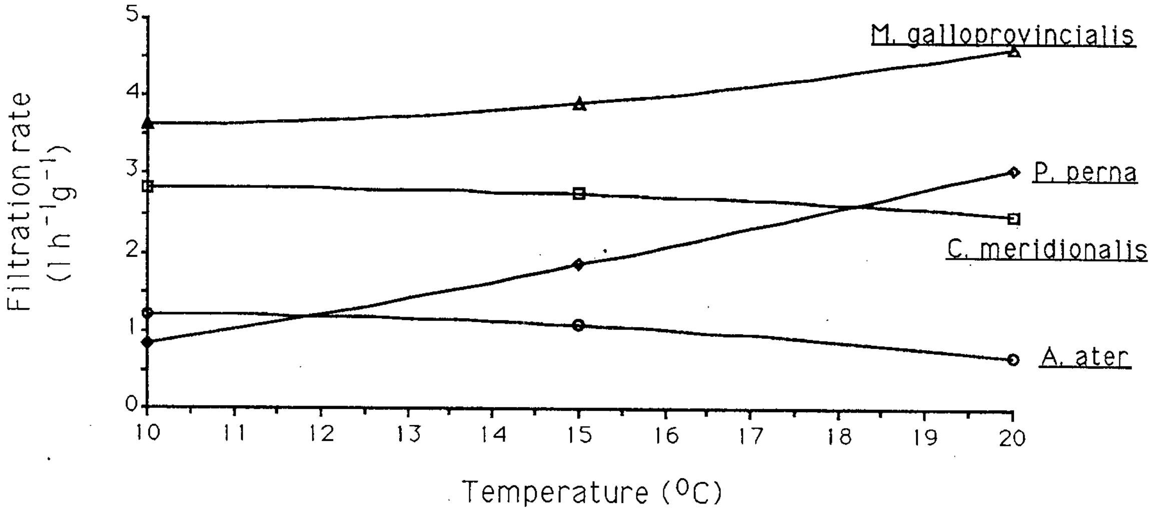

Figure 9 : Filtration rates of the four mussel species at different temperatures. Ration level is maintained at 3 mg $l^{-1}$.

higher temperatures. $Q_{10}$ values are thus negative in these species. In principle these results all correspond to the almost universal observation by earlier workers that filtration rates increase up to some optimumtemperature, but decline thereafter (for reviews see Winter, 1977; Newell & Branch, 1980). In particular the rapidly increasing trend observed in P.perna is not unexpected, since this species achieves its maximum abundance and growth rates in subtropical regions (van Erkom Schurink & Griffiths, 1990, in press b). What is suprising, however, is that rates should decline over the normal range of temperatures experienced by field populations, as is the case for C. meridionalis and A. ater, which are both fairly common along the southern Cape coast (van Erkom Schurink & Griffiths, 1990), where water temperatures average 15 -18°C (Bolton, 1986). Both species do, however, attain their maximum densities in the colder waters of the Cape west coast (van Erkom Schurink & Griffiths, 1990) where mean temperatures are only 12 -13°C (Bolton, 1986). The trends observed here also correlate with those of Clarke & Griffiths (1990) who report even more dramatic declines in filtration rates of C.meridionalis over the temperature range 12.5 to 21°C.

Absorption efficiencies (Fig. 10) were relatively unaffected by rising temperature, although a small but significant (Anova test) decline in efficiency occurs in the data for C. meridionalis and A.ater and an equally small increase in M. galloprovincialis and P. perna. Both tendencies have been reported by earlier workers. For example Widdows & Bayne (1971) report a decline in absorption efficiency in M. edulis over the temperature range 5 -15°C, while Winter (1969, 1977) records enhanced absorption efficiencies in Modiolus modiolus and Arctica islandica at 20°C relative to 4°C or 12°C. Temperature independent absorption efficiencies have also been reported (e.g. Wilbur & Hilbish 1989).

As expected respiration rates increased markedly with temperature in all four species (Fig. 11), $Q_{10}$ values ranging from 2.5 in A. ater to 1.7 in M.galloprovincialis. Relationships of this type have been widely reported

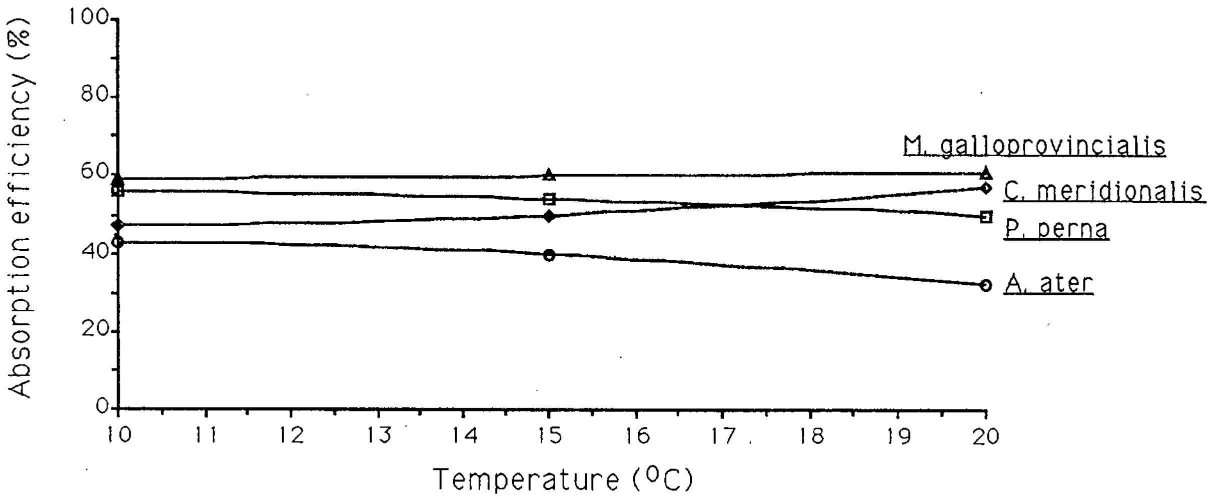

Figure 10 : Absorption efficiencies of the four mussel species at different temperatures. Ration level is maintained at 3 mg $l^{-1}$.

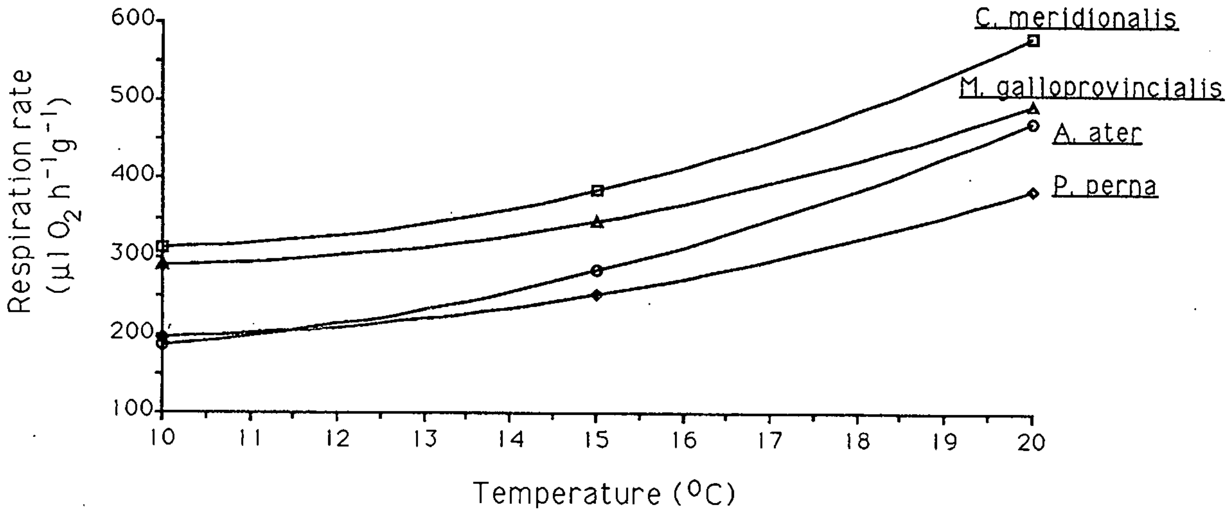

Figure 11 : Respiration rates of the four mussel species at different temperatures. Ration level is maintained at 3 mg $l^{-1}$.

by previous workers and the subject of temperature-related effects onmetabolism has been reviewed repeatedly (e.g. Bayne et al., 1976; Newell, 1979; Newell & Branch, 1980; Griffiths & Griffiths, 1987). All these authors report a variety of thermal responses, but with $Q_{10}$ values typically ranging about an average of 2, as indicated by our results.

Similar temperature-related increments occur in excretion rate (Fig. 12), presumably because protein catabolism is increased to meet elevated metabolic energy demands (Griffiths & Griffiths, 1987). $Q_{10}$ values range from 4.7 in P. perna to 2.1 in M. galloprovincialis with absolute rates being much higher in C. meridionalis than in the remaining species.

The combined acute effects of increasing temperature on ingestion ration, absorbed ration, respiration rate and subsequent scope for growth in 50mm mussels fed 3 mg $l^{-1}$ food suspension are plotted in Fig. 13. As shown in Fig. 12, excretion rates also very between species and with temperature. However, in energetic terms these losses are negligible, never exceeding 2 J $h^{-1}$, so they are omitted from the diagrams.

Examining each species individually it can be seen that, overall, M.galloprovincialis shows the fastest ingestion and absorption rates and that scope for growth in this species increases steadily with exposure temperature, from 129 J $h^{-1}$ at 10°C to 168 J $h^{-1}$ at 20°C, despite moderate increases in respiration rate. C. meridionalis shows a somewhat lower, but comparable absorbed ration and scope for growth of 94 J $h^{-1}$ at 10°c, but since filtration rates decline instead of rising with increasing temperature, while respiration rates increase relatively rapidly, scope for growth decreases to only 68 J $h^{-1}$ at 20°C.

Filtration rates and hence ingestion and absorption rations in P. perna are relatively low at 10°C resulting in a scope for growth of only 21 J $h^{-1}$, but because filtration rates and absorbed ration increase rapidly with temperature up to 20°C, scope for growth rises to 102 J $h^{-1}$. Because of its slow filtration rate and low absorption efficiency the absorbed ration in A. ater is low, so that despite a relatively slow respiration rate scope

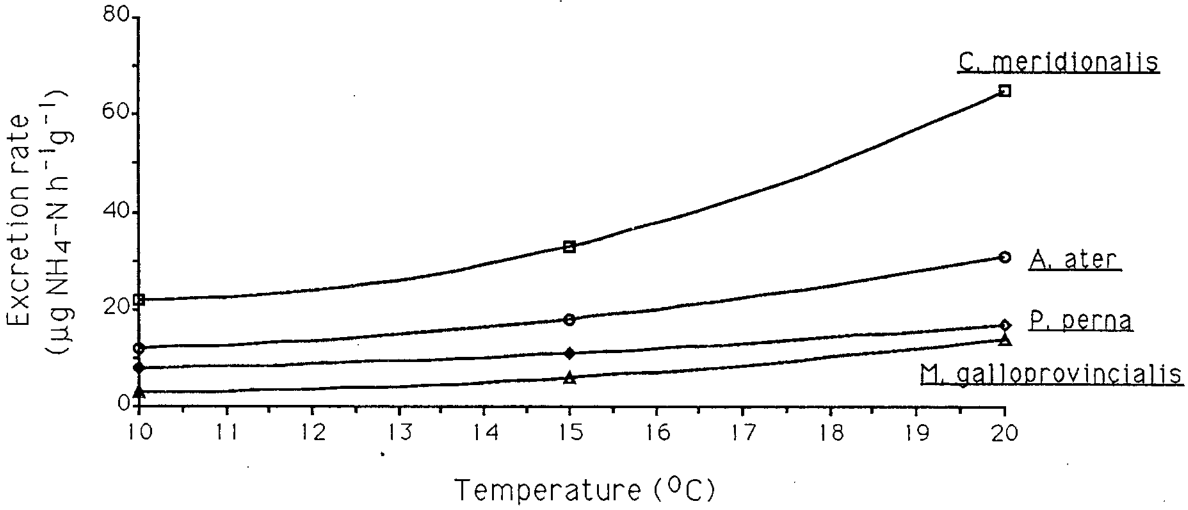

Figure 12 : Ammonia-N excretion rates of the four mussel species at different temperatures. Ration level is maintained at 3 mg $l^{-1}$.

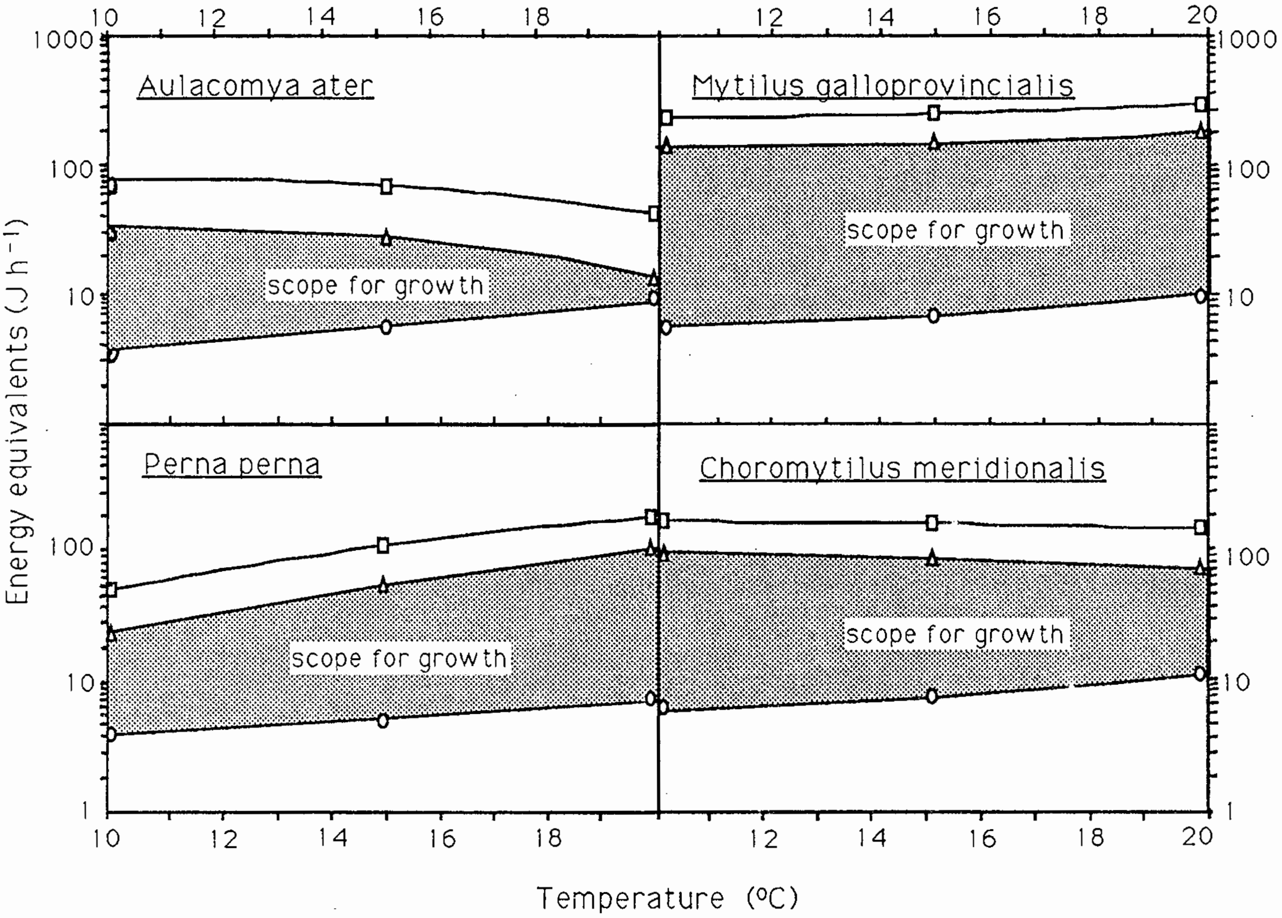

Figure 13 : Ingestion ration (□), absorbed ration (Δ), respiration rate (0) and subsequent scope for growth of the four mussel species at different temperatures. Ration level is maintained at 3 mg $l^{-1}$.

for growth is only 30 J $h^{-1}$ at 10°c. Moreover, ingestion rate and to a lesser extent absorption efficiency decline as temperature rises, while respiration rates increase relatively rapidly (Fig. 11). As a result scope for growth declines markedly as temperature rises, falling to only 4 J $h^{-1}$ at 20°C.

Taken overall, these results suggest that *A. ater* and *C. meridionalis* should be considered primarily as cold water forms, while *P. perna* clearly physiologically performs best at high temperatures. *M. galloprovincialis* is capable of rapid growth across a wide range of thermal conditions. Field observations support this senario, since *A. ater* and *C. meridionalis* attain maximum densities along the cool temperate west coast of South Africa, while *P. perna* is absent from this region, reaching maximum densities along the subtropical east coast.

Although *M. galloprovincialis* is currently most common along the cool west coast, where it was apparently quite recently introduced (Hockey & van Erkom Schurink, in press), it appears to be spreading rapidly into the warmer coastal regions along the Indian Ocean seaboard of South Africa (van Erkom Schurink & Griffiths, 1990). Growth rates studies by van Erkom Schurink & Griffiths (in press b) also show that *C. meridionalis* and *A. ater* both grow more rapidly at Saldanha Bay (15°C) than Algoa Bay (18°C), while *M. galloprovincialis* and *P. perna* show the reverse trend, as predicted from estimates of scope for growth. Our results would also predict that *M. galloprovincialis* is likely to continue to expand along the eastern Cape and Natal coastline, although it is likely to be outperformed by *P. perna* as temperatures increase beyond 20°C.

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