DISPERSAL, SETTLEMENT AND RECRUITMENT: THEIR INFLUENCE ON THE POPULATION DYNAMICS OF INTERTIDAL MUSSELS

THESIS

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ABSTRACT

Recruitment of planktonic larvae into sedentary benthic populations regulates the population dynamics of marine invertebrates. The processes controlling recruitment, however, are poorly understood, and recruitment remains largely unpredictable, which complicates management of exploited shellfish resources.

The mussels *Perna perna, Choromytilus meridionalis* and *Mytilus galloprovincialis*, found on the south coast of southern Africa, have planktonic larvae and sedentary adult stages. This thesis examines dispersal, settlement and early post-settlement growth and mortality, and their effect on recruitment and demography of intertidal mussel populations in the region of Algoa Bay on the south coast of southern Africa.

Temporal and spatial variation in the body mass, density and size structure of mussels, the distribution of bivalve larvae on plankton grids in the nearshore zone and the distribution of a recently introduced invasive mussel, *Mytilus galloprovincialis*, were examined between 1989 and 1992. Furthermore, data on hourly or daily changes in wind strength and direction, air and sea surface temperatures and low and high tide levels in the study region, were obtained.

There were 3-4 peaks in spawning (characterised by an abrupt decline in weight) and settlement activity annually. These peaks varied in exact timing, intensity and duration between sites and over time. However, at a site, spawning was followed by settlement 4-8 weeks later, and there was a significant ($P < 0.05$) direct correlation between spawning intensity prior to the appearance of a new cohort and the cohort density (settlement intensity).

The stochastic spatial and temporal variation in breeding activity was superimposed on a more general pattern of a higher intensity of spawning and settlement in Algoa Bay than on the open coast, and a higher settlement intensity on coastal sandstone shores than on dune rock shores. Spawning was more frequent in winter and spring, and the probability of spawning and settlement peaked around the spring and autumn equinox, if temperature and wind conditions were suitable.

Larval behaviour had little effect on their dispersal in the well-mixed nearshore region. Larvae were passively dispersed by currents, and their dispersal range and direction depended on prevailing winds and local topography. The sharp decline in density of recruit and adult *M. galloprovincialis* with increasing distance from the point of introduction, showed that some larvae were carried by wind generated currents over moderately long distances (~100 km). However, since most (76%) *M. galloprovincialis* recruited within 4 km of the parent population, it is possible that larvae become trapped in small gullies and crevices around rocky shores, and have a limited dispersal range. This could explain the link between local patterns of spawning and settlement.

The distribution and abundance of settlers on the shore was influenced by larval behaviour

and the availability of settlement substrata. Larvae "preferred" to settle primarily on foliose coralline algae and migrate to the adult mussel bed when they were larger (0.60-7 mm), but larvae also settled directly on adult mussels, possibly because the amount of coralline algae was limited. Both direct and secondary settlement were considered to be important in maintaining mussel populations since the rate of settlement was low (generally $< 60\ 000.\mathrm{m}^{-2}$).

Cohort analyses showed that prior to maturity post-settlement growth (~30 mm in 10 months) and mortality rates (60-100%) were high, but varied. When settlement intensity was low this variability uncoupled the relationship between spawning and recruitment intensity. Multiple regression analysis showed that together reproductive effort (gamete output), settlement intensity, growth and mortality prior to maturity, accounted for 76% of the variance in recruitment into mature adult populations.

The low settlement rate coupled with the short life span of mussels (<3 years), meant that populations underwent marked spatial and temporal variations in structure and abundance as settlement intensity varied, but there were consistent general differences between mussel populations on dune rock and sandstone shores in Algoa Bay and on the open coast.

It was concluded from these results that, spawning intensity and post-settlement growth and mortality, rather than dispersal, regulated recruitment and the structure and abundance of intertidal *P. perna* and *C. meridionalis* populations along the south coast of southern Africa.

On the basis of these results it is recommended that species with limited dispersal, variable recruitment and high natural mortality, such as *P. perna*, should be conserved by protecting a small part of the population in reserves, and controlling utilisation outside reserves to minimize disturbance to local brood stocks. Furthermore, since the potential for reseeding adjacent exploited areas is limited, several small reserves placed at regular intervals along the coast would be more effective than a single large reserve.

CONTENTS

This thesis is dedicated to a wonderful person and incredible woman, my mother, Elizabeth Gulle.

Declaration

This thesis documents original research, carried out in the Department of Zoology and Entomology, Rhodes University, between January 1989 and December 1994. None of it has been submitted in whole or in part for a degree at any other university.

I declare that the initial concepts, the collection and analysis of data, and the final synthesis were of my doing, and I accept responsibility for them. Wherever comparisons have been made with published literature or published data used, the sources have been referenced in the text. Any interpretations that are uncited are my own, and any assistance I have received is fully acknowledged

T.E. PHILLIPS

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INTRODUCTION

Eighty percent of the world's marine invertebrates have larvae which feed in the plankton for up to six weeks (Thorson 1950). The larvae recruit irregularly into benthic populations causing large fluctuations in their distribution and abundance (Roughgarden *et al.* 1984 & 1985, Connell 1985, Lewin 1986, Underwood & Fairweather 1989, Hughes 1990). Variable recruitment into adult populations has been attributed to random dispersal, settlement and post-settlement mortality occurring prior to maturity. However, no method exists for tracing the dispersal of larvae directly, and it is often logistically impossible to sample frequently enough to quantify actual settlement and early post-settlement mortality. This limits our understanding of these processes and their effect on recruitment and population dynamics.

Lamellibranch mussels belonging to the family Mytilidae are typical examples of marine invertebrates with this type of life history (Thorson 1961). Their reproductive cycle begins with gametogenesis and is followed by spawning and external fertilisation. The zygotes develop into veliger larvae that settle on the shore after 3-4 weeks and, after a period of time, the cycle ends with recruitment into the mature adult population (Thorson 1950, Seed 1969, 1975, & 1976, Bayne 1975 & 1976, Griffiths & Griffiths 1987). The mytilids *Perna perna, Choromytilus meridionalis, Aulacomya ater* and *Mytilus galloprovincialis* are common on intertidal wave beaten shores along the coast of South Africa (van Erkom Schurink & Griffiths 1990), where their recruitment patterns are known to be highly irregular (Berry 1978, Griffiths 1981, Crawford & Bower 1983, Lambert & Steinke 1986, Lasiak & Dye 1989). The reasons for this variability can only be speculated on, as little is known about their larval dispersal, settlement and early post-settlement growth and mortality. The purpose of this thesis was to: investigate these processes and their influence on the recruitment and population dynamics of intertidal mussels on the south coast of southern Africa; and to consider the practical implications of these results for the conservation and management of mussels which have been over-exploited by impoverished coastal communities on the east coast (Hockey & Bosman 1985, Siegfried *et al.* 1985, Lasiak & Dye 1989, van Erkom Schurink & Griffiths 1990).

Data were collected over a period of four years (1989-1992) mainly in the region of Algoa

Bay on the south coast (Fig. 1). The coast runs along a south west - north east axis, with Aston Bay forming the western limit and Haga Haga the eastern limit of the study region (Fig. 1). Algoa Bay is a crenulated bay, semi-enclosed by two prominent capes: Cape Recife (25°42 E,34°02 S) in the east and Cape Padrone (26°20 E, 33°45 S) in the west (Fig. 1).

The study region is characterized by long stretches of sandy beach (~82% of the shoreline) with isolated rocky outcrops distributed along 18% of the shoreline. The rock outcrops are either consolidated dune rock or sandstone (Figs. 2 & 3). The topography and intertidal zonation patterns of the characteristic biota occurring on the rocks, differ quite substantially between these two types of shore (Fig. 4, Dower 1990). In the lower littoral zone, the wide vertical faces and gently sloping wave-cut platforms on dune rock shores support extensive mussel beds, while the mussel zone is far narrower on the steep rocks of sandstone shores (Figs. 2 & 3, Freer 1983, Dower 1990).

Three species of mytilid (*Perna perna, Choromytilus meridionalis* and *Mytilus galloprovincialis*) are found within mussel assemblages on the south coast (van Erkom Schurink & Griffiths 1990). The descriptions of these mussels in Barnard (1964), Kilburn & Rippey (1982), Grant & Cherry (1985), Lasiak (1986), van Erkom Schurink (1991) and Branch *et al.* (1994), show that they have several distinguishing features. *P. perna* has a smooth, brown shell, while *M. galloprovincialis* generally has a blue shell that erodes to a white colour and *C. meridionalis* has a typically black shell that erodes to a blue colour (Fig. 5). The shell shape of *C. meridionalis* is narrow and high and is quite distinct from *P. perna* and *M. galloprovincialis* which have a similarly shaped broad, elongate shell. *P. perna* is slightly longer and more slender than *M. galloprovincialis* which is more squat with a broad base. Internally the mature gonad is not a discrete organ but is inextricably integrated with the visceral mass (Griffiths & Griffiths 1987). When mature, the male gonad in all species is an off-white or yellow colour that is easily confused with connective tissue which fills the mantle when no gametogenesis is occurring and the mussels are in a resting state (Lasiak 1986, van Erkom Schurink & Griffiths 1990). *P. perna* and *M. galloprovincialis* both have an orange female gonad, while that of *C. meridionalis* is chocolate brown (van Erkom Schurink 1991). The mussels can be distinguished from each other by the muscle scars on the interior of the shell and the resilial pitted ridge. *M. galloprovincialis* has both an anterior and posterior muscle, as well as a resilial pitted ridge. *P. perna* has a divided posterior muscle and a resilial pitted ridge, while *C. meridionalis* has no pitted ridge and an undivided posterior retractor muscle.

Various aspects of the distribution, reproductive cycle and population demography of these three species, were investigated during the course of this thesis.

Thesis structure

The thesis is divided into three sections. The first deals with larval dispersal. The aim was to examine the factors influencing the nearshore distribution and dispersal of bivalve larvae, and to estimate how far they settle from the parent population after 3-4 weeks in the plankton. Three methods were used to do this and these are covered in chapters 1, 2 and 3.

The second section (Chapter 4) examines settlement behaviour and the distribution and abundance of *P. perna* settlers on intertidal rocky shores.

Section 3 (Chapter 5) examines the influence of pre-settlement (reproductive effort, dispersal) and post-settlement factors (settlement intensity, growth, mortality) on recruitment and the structure and abundance of intertidal populations of *P. perna* and *C. meridionalis*.

The final chapter gives an overview of research in this field of ecology and presents the main conclusions of the research described in chapters 1-5. The practical implications of these results for the sustainable utilisation and conservation of shellfish resources are discussed briefly.

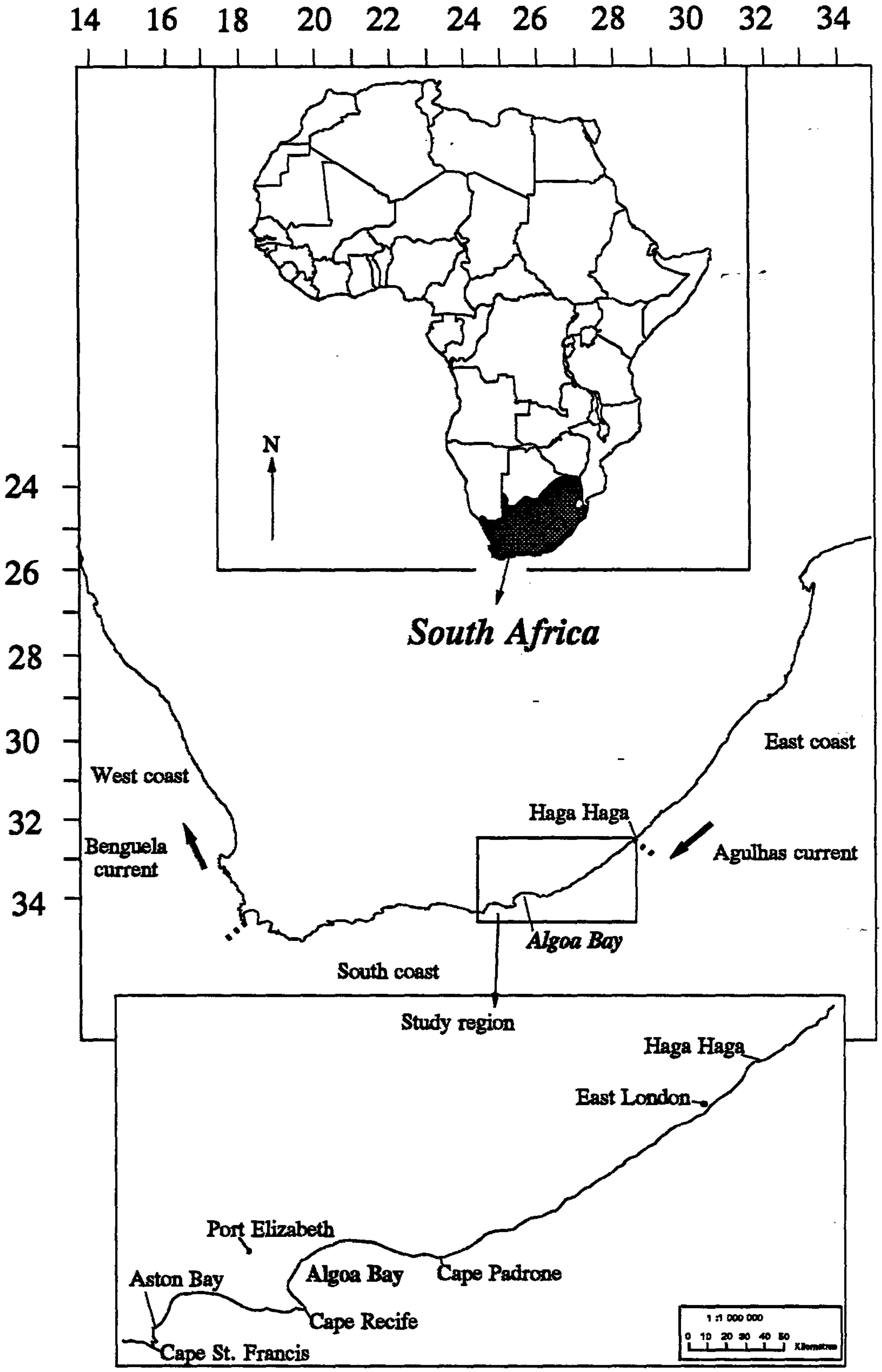


Figure 1: A map of South Africa and the study region on the south coast of southern Africa. The coastal climate and hydrography are largely determined by the Benguela and Agulhas currents and can be divided into three broad biogeographical zones, the cool temperate west coast, the warm temperate south coast and sub-tropical east coast.

A

B

C

Figure 2 (opposite page): A typical dune rock shore (A & B) showing an extensive bed of *Perna perna* (P) on the gentle slope and vertical rock face of a wave-cut platform (C).


A
B
C
m

Figure 3 (opposite page): Typical sandstone shores (A & B) showing the narrow mussel zone (m) on the pointed sandstone ridges (C).

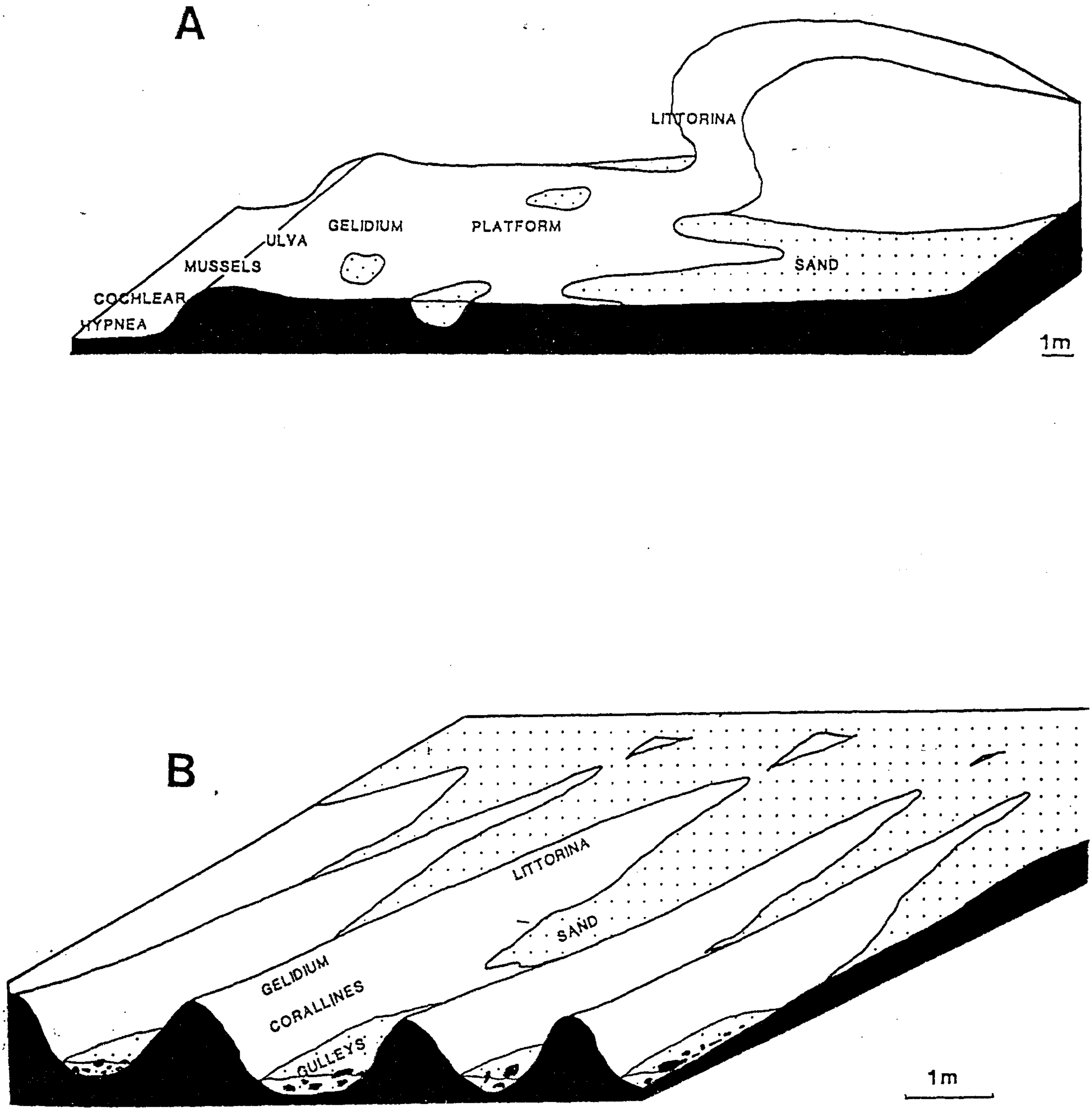


Figure 4: Stylised profiles of a dune rock shore (A) and a sandstone shore (B) indicating the characteristic species in the major zones on each rock type. *Ulva, Gelidium* and *Hypnea* are algae, corallines refer to foliose coralline algae, and cochlear to the limpet *Patella cochlear*. The profiles were reprinted from Dower (1990).


PP
MG


MG


CM

Figure 5 (opposite page): (A) *Perna perna* - PP, (B) *Mytilus galloprovincialis* - MG and (C) *Choromytilus meridionalis* - CM, in intertidal mussel beds on the South African coast.

SECTION ONE

DISPERSAL

CHAPTER 1

SYNCHRONOUS SPAWNING AND SETTLEMENT - IS THE DISPERSAL RANGE OF PLANKTONIC MUSSEL LARVAE LIMITED?

Introduction

Irregular mussel settlement along the coast of South Africa may be attributed to long range larval dispersal (Berry 1978, Griffiths 1981, Crawford & Bower 1983, Lambert & Steinke 1986). However, this has never been verified, because the movements of the microscopic planktonic larvae cannot be traced. In comparison to dispersal, spawning and settlement are relatively easy to quantify, and since dispersal forms a link between spawning and settlement, dispersal range can be inferred from the relationship between these two factors. However, very little is known about this relationship in South African mussels.

Widespread dispersal will uncouple the relationship between the intensity of spawning and settlement (Victor 1983 & 1986, McFarland *et al.* 1985, Robertson *et al.* 1988 & 1993, Robertson 1990, Hunte von Herbing & Hunte 1991, Meekan *et al.* 1993). However, recent evidence for haliotids (Shepherd *et al.* 1985, Shepherd & Turner 1985, McShane *et al.* 1988, Prince *et al.* 1987 & 1988), echinoderms (Hunte & Younglao 1988), scallops (Peterson & Summerson 1992), polychaetes and bivalves (Feller *et al.* 1992) show that local patterns of spawning (or any other measurement of reproductive effort) and settlement are linked, suggesting that the larval dispersal range may in fact be limited. In this case, factors controlling gametogenesis and spawning are more important determinants of settlement than dispersal.

It is commonly accepted that gametogenesis and spawning are controlled by a number of interacting environmental factors, for example: photoperiod (eg. Yoshioka 1989a, Martel & Chia 1991), food availability (eg. Chipperfield 1953, Kautsky 1982, Keats & Steele 1984, Hilbish & Zimmerman 1988, Harvey & Vincent 1989), tides (eg. Chipperfield 1953, Christy 1982 and literature therein, Berry 1986, Harvey & Vincent 1989, Yoshioka 1989a), and one of the most important factors - temperature (Chipperfield 1953, Wilson & Hodgkins 1967, Seed 1969 & 1976, Bayne 1975 & 1976, Bowman & Lewis 1977, Berry 1978, Barker 1979, Griffiths & Griffiths 1987, Harvey & Vincent 1989, Byrne 1990, Martel & Chia 1991).

The breeding pattern of intertidal mussels is likely to be affected by a combination of climatic and hydrological factors. On the South African coast, local air and sea temperatures, nutrient availability and thus phytoplankton production and food availability, as well as circulation patterns are largely controlled by wind but are modified by topography and tidal range (Griffiths 1977, Schumann *et al.* 1982, 1988 & 1991, Schumann 1987, Goschen & Schumann 1988, Roberts 1989, Schumann & Martin 1991). Thus temperature, wind and tidal range may be linked to spawning, and since they control circulation patterns, may influence larval dispersal and therefore the relationship between local patterns of spawning and settlement.

The purpose of this study was to deduce the dispersal range of mussel larvae from the relationship between local patterns of spawning and settlement and to examine the association between temporal fluctuations in spawning and settlement probability, wind, tidal range and temperature, along the south coast of southern Africa.

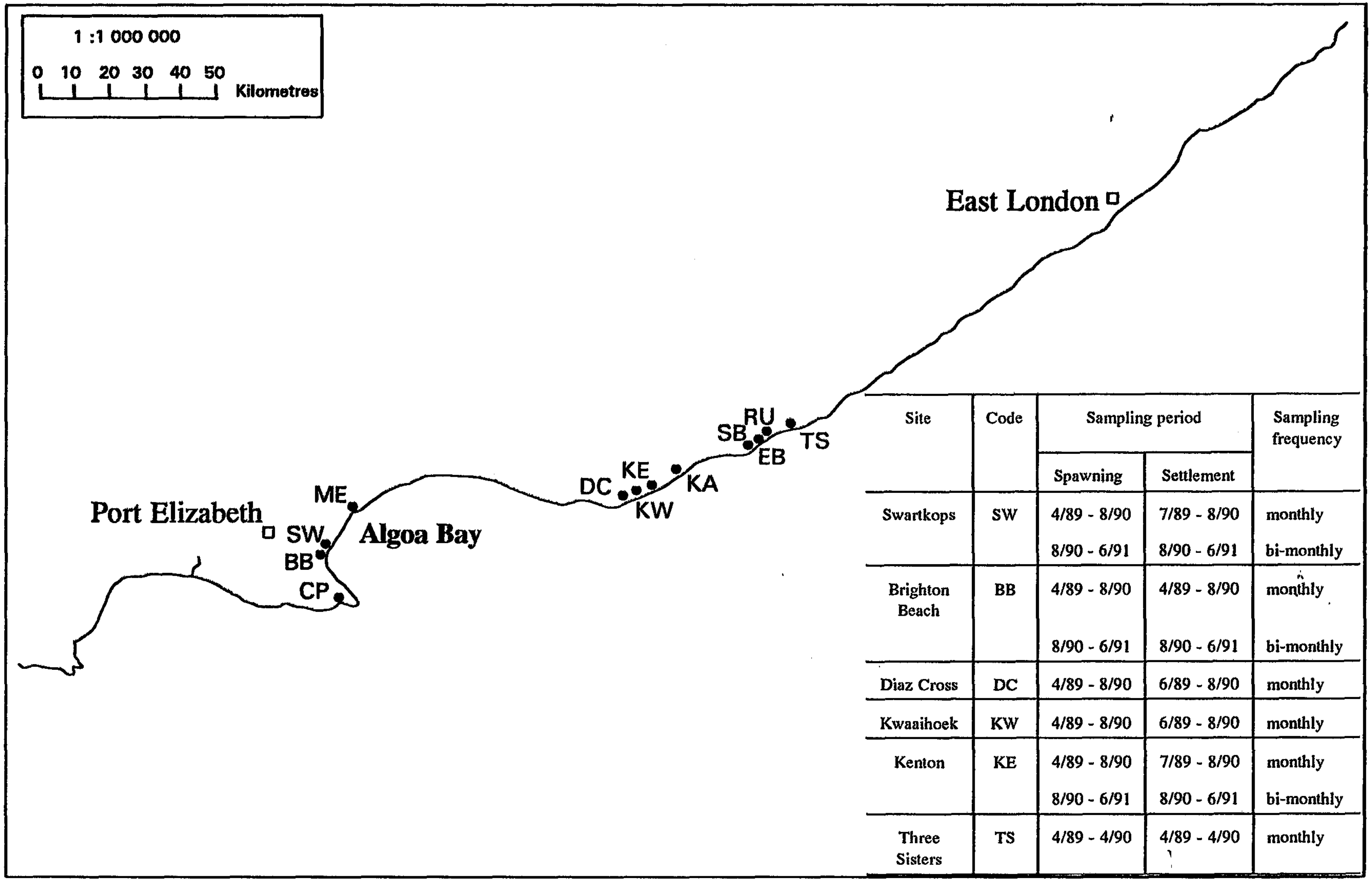
Methods

Study sites

The timing, intensity and duration of spawning and settlement in intertidal mussel populations, were studied at six sites in the Algoa Bay region on the south coast of South Africa, over one to two years (Fig. 1.1). The distribution of *Choromytilus meridionalis* in this region is extremely patchy and this mussel was sampled from only one site Swartkops inside Algoa Bay. *Perna perna* was sampled from Brighton Beach inside Algoa Bay and from four dune rock shores on the open coast, *viz*. Diaz Cross, Kwaaihoek, Kenton and Three Sisters.

Sampling periodicity

The sampling periodicity at each site is shown in Figure 1.1. Preliminary spawning samples were taken at Brighton Beach and Swartkops in March 1989 but actual sampling began in April 1989. Spawning samples were taken monthly at all sites from April 1989 up until August 1990, except for Three Sisters where sampling stopped in April 1990 because severe storms and rough conditions prevented sampling in June and July.



Site	Code	Sampling period		Sampling frequency
		Spawning	Settlement	
Swartkops	SW	4/89 - 8/90	7/89 - 8/90	monthly
		8/90 - 6/91	8/90 - 6/91	bi-monthly
Brighton Beach	BB	4/89 - 8/90	4/89 - 8/90	monthly
		8/90 - 6/91	8/90 - 6/91	bi-monthly
Diaz Cross	DC	4/89 - 8/90	6/89 - 8/90	monthly
Kwaaihoek	KW	4/89 - 8/90	6/89 - 8/90	monthly
Kenton	KE	4/89 - 8/90	7/89 - 8/90	monthly
		8/90 - 6/91	8/90 - 6/91	bi-monthly
Three Sisters	TS	4/89 - 4/90	4/89 - 4/90	monthly

Figure 1.1: The Algoa Bay region on the southern coast of South Africa showing the position of the study sites. *Choromytilus meridionalis* was studied at Swartkops (SW) and Melville (ME) and *Perna perna* at the rest of the sites. After August 1990, samples were taken every two months until June 1991 at Brighton Beach, Swartkops and Kenton.

Initially, attempts were made to estimate settlement by attaching a variety of artificial substrata, *viz.* asbestos plates, nylon pot scourers and ropes, to the rocks amongst the mussels at each site. To determine whether artificial substrata inhibited settlement, the mussel bed itself was sampled at Brighton Beach and Three Sisters. After two to three months it became apparent that no larvae or spat settled on the artificial substrata, although plantigrades of 1-5 mm settled in the mussel bed. Thus the mussel bed at all sites was sampled monthly from June/July 1989 until August 1990. Thereafter samples were taken every two months at Brighton Beach, Swartkops and Kenton until June 1991.

The settlement pattern was monitored at an additional six sites from June/July 1989 until August 1990. However, as the spawning pattern was not monitored at these sites the results are only presented in the chapter (5) on settlement and recruitment.

Spawning pattern

On the sub-temperate coast of South Africa simultaneous examination of histological sections of the mantle, gonad smears and changes in flesh weight indicated that *C. meridionalis* and *Aulacomya ater* did not build up any seasonal reserves in the tissues, and that changes in body weight were associated with gametogenesis and spawning, as the weight of other body parts, such as the adductor muscle, did not vary seasonally (Griffiths 1977 & 1981, Griffiths & King 1979). In this case sharp declines in body weight of standard sized individuals, calculated from length/weight regressions, indicated spawning, and the change in weight gave an approximate estimate of the magnitude of gamete output during spawning. It is likely that changes in weight of mussels on the sub-temperate south coast around Algoa Bay will also reflect gametogenic and spawning activity. Although this method may not be as accurate as directly examining the histological state of the gonad, it has the advantage of being less time consuming which allows the sample size to be increased. Small samples may give a biased indication of the reproductive condition of the population, as the reproductive state of individuals varies considerably (Seed 1969, Griffiths 1977, Berry 1978, Kautsky 1982). In this study, changes in the weight of a range of different sized mussels were measured, to establish the general reproductive condition of the population and estimate the gamete output during spawning.

Initially monthly samples of 30 individuals ranging in size from 30 mm to 80 mm were collected from the lower balanoid zone at each site. The sample size was later increased to 50 individuals because the sex of some of the smaller individuals was indeterminate when the mussels were in the initial stages of gametogenesis and could not be used in the analysis. When the mussels were ripe, several extra smaller individuals were included in the sample in order to obtain some idea of the reproductive condition of the population over a wider size range.

In the laboratory the mussels were heated until the shells gaped. This removed excess water from the flesh and facilitated removal of the flesh from the shell. The length of each mussel was measured to the nearest millimetre. The sex was noted from the colour of the gonad and the flesh was then removed from the shell and dried at 60°C for 48 hours and weighed.

Data analysis: Samples had a male to female ratio of 1:1. Data for males and females were combined in the analysis since examination of the gonads showed that they were in the same reproductive state, and there was no difference (Mann-Whitney, $P>0.05$) in the mean weight of similar sized males and females. Dry weight was regressed against shell length for each month. The weight of a standard sized individual, taken to be 65 mm for the purpose of comparison with similar estimates in the literature (van Erkom Schurink 1991), was calculated from these regression equations. The spawning periodicity was established by examining temporal changes in weight of the 65 mm individual, and the spawning intensity (gamete output) was estimated from the magnitude of the decline in weight during spawning.

The temporal spawning pattern of *P. perna* for the entire Algoa Bay region was analysed in terms of the probability of spawning each month. The percent probability of spawning in each month was defined as the number of sites at which spawning occurred out of the total number of sites which were sampled during that month. *C. meridionalis* was only sampled from one site so its spawning probability could not be established.

Settlement pattern

Sampling procedure: Settlement is known to vary on all spatial scales (Caffey 1985) and to minimize very small scale spatial variation, samples were taken from the same region in the lower balanoid zone of the mussel bed, at each of the six sites.

Each month samples were collected at spring low tides. All mussels within a quadrat placed on the mussel bed were collected for subsequent laboratory analysis. On all sampling occasions a quadrat of 0.125x0.125 m^2 was used, except in April 1989, March 1990 and February 1991, when sampling formed part of a survey for *Mytilus galloprovincialis* and a quadrat of 0.25x0.125 m^2 was used. Although these quadrats were small, continual destructive sampling in a small area can dramatically affect the mussel bed. Thus, only three samples were collected each month.

In the laboratory, different species were identified according to Kilburn & Rippey (1982) and von Erkom Schurink (1991). All mussels greater than 20 mm were measured to the nearest mm, the number in the size categories 0-4 mm, 5-9 mm, 10-14 mm and 15-19 mm, were recorded. For the purposes of this study mussels less than 20 mm were classified as recruits as they may move and resettle in other mussel populations. Mature adults (>25 mm) were sedentary and had traces of gonadial material.

In this study the periodicity of settlement was represented by temporal changes in density of recruits (0-19 mm). Settlement intensity was estimated as the maximum density of a newly settled cohort, calculated from size frequency histograms as described in chapter 5. The probability of settlement in the Algoa Bay region was calculated in the same manner as the spawning probability.

Environmental patterns

Environmental conditions were determined for the study period April 1989 to June 1991.

Wind: Hourly data on the velocity and direction of wind were obtained from a coastal station and from Hendrik Verwoerd airport at Port Elizabeth about 5 km from the coast (Fig. 1.1). Since the time series at the coastal station was incomplete and since the general patterns appeared to be similar, wind data from the airport were used in analyses. Mean monthly wind velocity ($m.s^{-1}$)

and the mean monthly frequency (hours) of winds blowing from the NE, NW, SE and SW were calculated.

Tidal range: The mean monthly low and high tide levels for the Port Elizabeth region, were calculated from the South African Navy Tide Books published in 1989, 1990 and 1991.

Temperature: The mean monthly air temperature was calculated from hourly air temperature measured at Hendrik Verwoerd airport.

The mean monthly water temperature was calculated from sea surface water temperature measured twice a day by the Humewood Beach Office in Port Elizabeth.

These data on the wind, tide and temperature conditions show general trends in the environmental conditions in the Algoa Bay region, but do not reflect specific local variations.

Statistical analysis

Following Zar (1984) and Sokal & Rolf (1981) all data analysed statistically in this thesis, were tested for normality (Kolmogorov-Smirnov test) and homoscedasticity (Bartletts & Cochrans tests), as these are the assumptions behind most parametric statistical tests. If these requirements were not met, parametric tests were performed on transformed data. If transformed data did not meet the requirements, the equivalent non-parametric test was performed on untransformed data.

Results

Spawning

Weight increased linearly over the range of sizes (generally 30-70 mm) collected each month. All monthly length/weight regressions were significant ($P<0.001$). The correlation coefficient generally ranged from 0.70 to 0.99, only dropping below this in 4 of the 97 regressions. Following Zar (1984) analysis of covariance (ANCOVA) showed that the slopes of monthly length/weight regressions differed significantly ($P<0.005$) at all sites (Table 1.1), and the body mass of a 65 mm

Table 1.1: Analysis of covariance (ANCOVA) comparing the slopes of monthly length/weight regressions at each of the sites.

Site	Source of variation	DF	Mean square	*F*	*P*
Swartkops	Common slope	1	29.022	1 382.000	<0.005
	Among slope	16	0.237	11.418	
	Error	592	0.021		
Brighton Beach	Common slope	1	37.194	977.803	<0.005
	Among slope	18	0.761	20.001	
	Error	613	0.038		
Diaz Cross	Common slope	1	39.651	1 468.556	<0.005
	Among slope	14	0.296	11.101	
	Error	497	0.027		
Kwaaihoek	Common slope	1	51.248	1 507.294	<0.005
	Among slope	15	0.510	15.021	
	Error	609	0.034		
Kenton	Common slope	1	41.885	2 094.250	<0.005
	Among slope	19	0.262	23.334	
	Error	798	0.020		
Three Sisters	Common slope	1	7.739	269.699	<0.005
	Among slope	13	2.591	90.291	
	Error	499	0.029		

mussel estimated from the regression equations fluctuated over time (Fig. 1.2). Monthly fluctuations in body mass were associated with changes in the state of the gonad, which varied considerably in size and colour from month to month. When the mass of a mussel was low the shells sounded almost hollow when tapped, and on examination appeared to be resting or in the initial stages of gametogenesis, as the gonad was small and concentrated around the digestive gland. In contrast, when a mussel was heavy it was mature as the gonad was large and occupied most of the mantle tissue. Mussels which had recently spawned were easily identified as the mantle cavity was empty, except for remnants of eggs or sperm which had not been released, and the mussels weighed considerably less than when mature. Subsequent to spawning, gametogenesis caused an increase in weight, with little indication of rest between repeated bouts of spawning, as was illustrated by the temporal variation in body mass of a 65 mm individual (Fig. 1.2).

Following Zar (1984) multiple range tests comparing slopes, and if these were equal, intercepts, of the length/weight regressions calculated for the month before and after a decline in weight of a 65 mm mussel, indicated that significant ($P<0.05$) declines in weight (spawning) occurred three or four times a year at each site (Table 1.2A & B). Although there was similarity between some sites, the exact timing, duration and intensity (gamete output) of each spawning event varied among sites. Seasonal decomposition (Dunstan 1993) was used to remove the general and seasonal components from the time series of changes in weight of a 65 mm individual, leaving the residual monthly fluctautions in body weight, which represented the exact timing and intensity of spawning. Following Dunstan (1993) cross correlation (with no lag) showed there was a significant, but weak correlation in the residual monthly fluctuation in body weight between Brighton Beach and Kenton ($r=0.3900$, $P<0.025$), and between Brighton Beach and Three Sisters ($r=0.5916$, $P<0.01$, Table 1.3). Although the strength of the correlation between Kenton and Kwaaihoek which were only four kilometres apart ($r=0.7416$, $P<0.0005$), suggested that sites close together have more similar patterns, these two sites each differed significantly ($P>0.05$) from that at Diaz Cross which was four kilometres west of Kwaaihoek (Table 1.3).

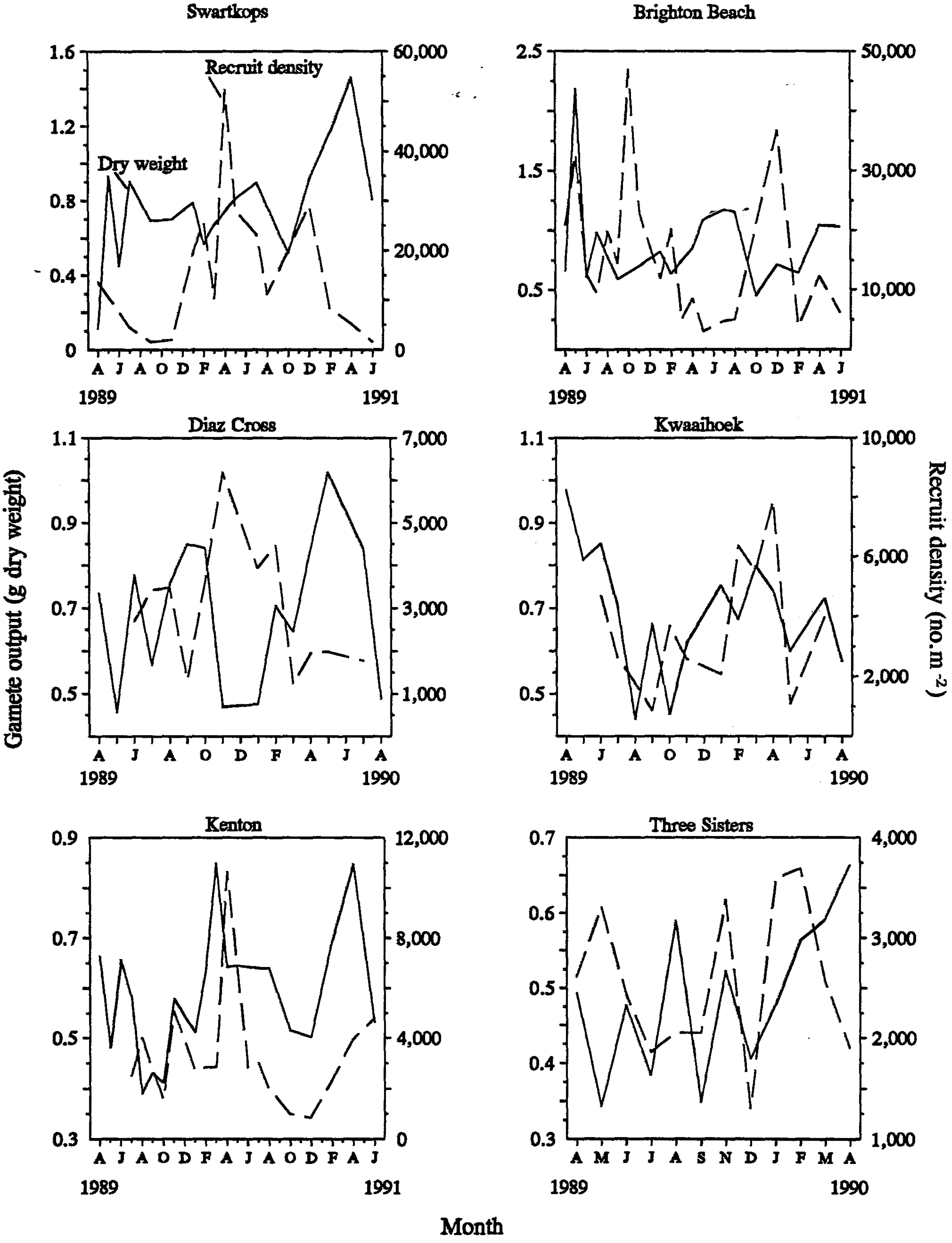


Figure 1.2: Temporal fluctuation in the recruit density (no.<20mm.m^{2}) and the dry weight (g) of a 65 mm individual, in the intertidal mussel population at the six study sites.

Table 1.2: Multiple comparison of the slopes (A) and, if the slopes were equal, the intercepts (B) of the length/weight regressions for the months before and after a decline in the dry weight of a 65 mm mussel, at each of the sites. The slopes of the two samples being compared are denoted as b_1 and b_2, and the intercepts as a_1 and a_b, q is the test statistic. Significant differences between the slopes, or if these were equal the intercepts, indicate a decline in weight and that spawning occurred between the two sampling dates. The DF for the critical value of q was calculated as N-$2k$, where N is the total number of mussels sampled at the site and k was the number of months during which sampling took place at that site.

(Table 1.2A)

Site	Dates (month/year)	b_1	b_2	*SE*	q	P
Swartkops	7/89 - 9/89	0.023	0.016	0.0006	12.6841	<0.01
$N = 642$	1/90 - 2/90	0.026	0.017	0.0005	19.6319	<0.01
$k = 17$	3/90 - 5/90	0.020	0.020	0	0	>0.05
	4/91 - 6/91	0.044	0.019	0.0004	64.0987	<0.01
Brighton Beach	5/89 - 6/89	0.074	0.002	0.0009	80.4641	<0.01
$N = 651$	7/89 - 9/89	0.027	0.014	0.0007	45.4908	<0.01
$k = 19$	1/90 - 2/90	0.013	0.016	0.0005	6.0000	0.05
	7/90 - 8/90	0.007	0.035	0.0012	23.8681	<0.01
	8/90 - 12/90	0.035	0.019	0.0007	24.3933	<0.01
	4/91 - 6/91	0.025	0.025	0	0	>0.05
Diaz Cross	6/89 - 7/89	0.022	0.013	0.0007	18.9917	<0.01
$N = 527$	10/89 - 11/89	0.026	0.002	0.0005	43.8020	<0.01
$k = 15$	2/90 - 3/90	0.020	0.020	0	0	>0.05
	5/90 - 7/90	0.026	0.024	0.0005	4.0009	>0.05
Kwaaihoek	6/89 - 8/89	0.026	0.015	0.0006	18.3333	<0.01
$N = 641$	9/89 - 10/89	0.032	0.022	0.0005	19.1864	<0.01
$k = 16$	1/90 - 2/90	0.019	0.023	0.0002	20.8530	<0.01
	3/90 - 4/90	0.023	0.029	0.0005	12.9235	<0.01
	4/90 - 5/90	0.029	0.015	0.0005	27.7634	<0.01

Table 1.2A continued

Site	Dates (month/year)	b_1	b_2	SE	q	P
Kenton	6/89 - 7/89	0.019	0.015	0.0005	7.9015	<0.01
$N = 838$	7/89 - 8/89	0.015	0.011	0.0005	8.5117	<0.01
$k = 20$	9/89 - 10/89	0.014	0.014	0	0	>0.05
	11/89 - 1/90	0.019	0.001	0.0004	44.6606	<0.01
	3/90 - 4/90	0.028	0.020	0.0004	21.1324	<0.01
	5/90 - 7/90	0.014	0.016	0.0004	5.0489	>0.05
	7/90 - 10/90	0.016	0.011	0.0004	17.3821	<0.01
	4/91 - 6/91	0.021	0.013	0.0003	24.3387	<0.01
Three Sisters	4/89 - 5/89	0.067	0.011	0.0006	93.6693	<0.01
$N = 513$	6/89 - 7/89	0.012	0.009	0.0006	5.1924	0.05
$k = 14$	8/89 - 9/89	0.019	0.015	0.0005	7.5290	<0.01
	10/89 - 11/89	0.022	0.014	0.0004	20.8473	<0.01

Table 1.2B

Site	Dates (month/year)	a_1	a_2	SE	q	P
Swartkops	3/90 - 5/90	-0.632	-0.491	0.9885	9.1034	<0.01
Brighton Beach	4/91 - 6/91	-0.582	-0.597	0.9799	1.0210	>0.05
Diaz Cross	2/90 - 3/90	-0.594	-0.655	1.0023	0.0435	>0.05
Diaz Cross	5/90 - 7/90	-0.671	-0.722	0.9282	0.0362	>0.05
Kenton	9/89 - 10/89	-0.479	-0.498	1.1918	0.0122	>0.05
Kenton	5/90 - 7/90	-0.265	-0.401	0.9867	0.0294	>0.05

Table 1.3: Cross correlation of the residual monthly fluctuations in body weight of a 65mm mussel, which reflects the spawning pattern of the mussel population, at each of the sites. The correlation coefficient (*r*) with no time lag between pairs of data sets is presented. Significant correlations are shown in italics. $P < 0.05$ is shown with one asterisk (*). The length of the time series varied between sites and where one time series was longer than another the shorter time series dictated the number of paired samples in the correlation, which is indicated in brackets.

Site	SW	BB	DC	KW	KE	TS
SW	X					
BB	-0.0515 (22)	X				
DC	-0.6118 (17)	-0.4372 (17)	X			
KW	-0.6077 (17)	-0.5825 (17)	0.2185 (17)	X		
KE	-0.0041 (22)	*0.39471** (22)	0.2779 (17)	*0.7416** (17)	X	
TS	0.4022 (13)	*0.5916** (13)	0.2709 (13)	-0.6581 (13)	-0.2400 (13)	X

The mean gamete output per spawning event was estimated as mean weight loss during the event. The mean value of 0.2025 ± 0.0341 g dry weight (range 0.0580 g - 0.7000 g) for a 65mm *P. perna* during spawning, did not differ significantly (ANOVA, P=0.7389) from the 0.2346 ± 0.0045 g (range 0.126 g - 0.6560 g) estimated for *C. meridionalis* (Table 1.4). ANOVA showed no significant differences (P=0.9536) in gamete output per spawning event among sites on the open coast or among sites in Algoa Bay (P=0.3401, Table 1.5), but average gamete output was significantly greater (P=0.005) in Algoa Bay (0.3225 ± 0.0617 g) than on the open coast (0.1516 ± 0.0248 g, Table 1.6). The annual gamete output of a 65 mm *P. perna* at each site ranged from 0.6622 g to 1.642 g, while the annual gamete output of a 65 mm *C. meridionalis* ranged from 0.9151 g to 1.0496 g.

Settlement

Temporal fluctuations in the density of recruits indicated that one or two new cohorts appeared in the mussel populations each year. Each cohort consisted of individuals settling during three to four peaks in settlement (see Chapter 5). Cross correlation of residual monthly fluctuations in recruit density showed the settlement pattern was similar at some sites (Table 1.7), but as with spawning, there was no relationship between the strength of the correlation and the distance between the sites (Fig. 1.3), due to small scale (<4 km) variation in the exact timing, intensity and duration of settlement peaks (Fig. 1.2). Settlement could occur at any time of year but the probability was greater in February and July and highest in October.

Spawning and settlement

Although spawning and settlement patterns appear chaotic at first, closer examination of the patterns at each site, showed that a protracted period of spawning was followed by an extended period of settlement, with several peaks in spawning and settlement activity during that time (Fig. 1.2). Furthermore, although the exact timing, intensity and duration of the peaks varied, each spawning peak was consistently followed by a peak in settlement activity 4-8 weeks later at the same

Table 1.4: One way ANOVA comparing the mean gamete output (g dry weight per spawning event) of *Perna perna* and *Choromytilus meridionalis* in the Algoa Bay region.

Source of variation	*SS*	*MS*	*DF*	*F*	*P*
Between groups	0.0027	0.0027	1	0.1170	0.7389
Within groups	0.5365	0.0233	23		
Total	0.5392				

Table 1.5: One way ANOVA comparing the mean gamete output (g dry weight per spawning event) of a 65 mm mussel among sites on the open coast (Diaz Cross, Kwaaihoek, Kenton, Three Sisters) and between sites within Algoa Bay (Swartkops and Brighton Beach).

Region	Source of variation	*SS*	*MS*	*DF*	*F*	*P*
Open coast	Between sites	0.0041	0.0013	3	0.1090	0.9536
	Within sites	0.1629	0.1253	13		
	Total	0.1670				
Algoa Bay	Between sites	0.0371	0.0371	1	1.2630	0.3401
	Within sites	0.1762	0.0294	6		
	Total	0.2133				

Table 1.6: One way ANOVA comparing the mean gamete output (g dry weight per spawning event) of a 65 mm mussel in Algoa Bay and on the open coast.

Source of variation	*SS*	*MS*	*DF*	*F*	*P*
Between groups	0.1589	0.1589	1	9.0609	0.0050
Within groups	0.3803	0.0165	23		
Total	0.5392				

Table 1.7: Cross correlation of the residual monthly variation in recruit density at each site. The correlation coefficient (r) with no time lag between pairs of data sets is presented, together with the number of data pairs in the correlation (n). The significant correlations are in italics. $P<0.05$ is denoted with an asterisk (*) and $P<0.001$ with two asterisks (**). There were too few pairs of data points to compare the settlement pattern at Three Sisters with the other sites, with the exception of Brighton Beach, where there were 13 data pairs and the settlement patterns were significantly correlated (r = *0.8686*, $P<0.001$).

	SW	BB	DC	KW	KE
SW	X				
BB	*0.6008** (19)	X			
DC	0.1182 (14)	*0.5185** (14)	X		
KW	0.1701 (14)	*0.7785*** (14)	*0.7374*** (14)	X	
KE	0.3675 (19)	-0.0934 (19)	-0.1128 (14)	-0.3950 (14)	X

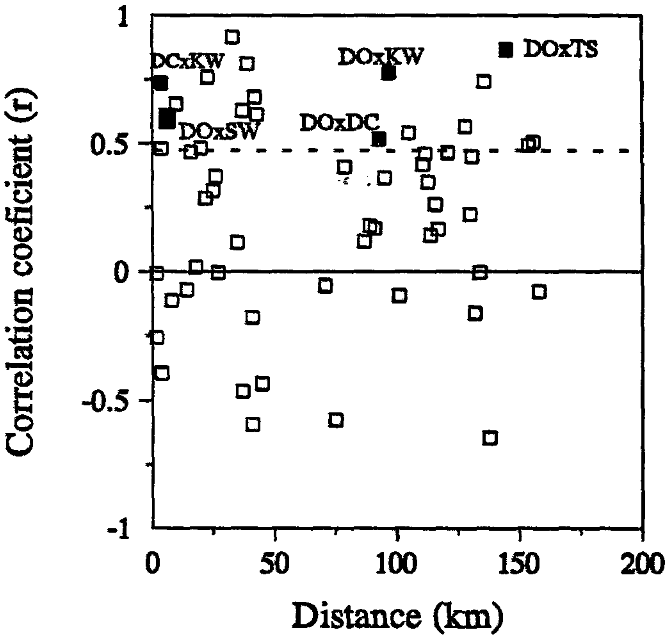


Figure 1.3: Variation in the strength of the correlation (*r*) between the residual monthly fluctuations in recruit density (no. <20 mm.m^{-2}) between sites with increasing distance (km) between the sites. The values above the dotted line are significant ($P<0.05$), and the solid squares refer to the cross correlations which have been labelled on the figure.

site. Cross correlation could not be used to verify this relationship because the time lag between spawning and settlement varied. However, there was a significant, positive linear correlation (regression, $P < 0.001$) between the intensity of spawning occurring prior to the appearance of a new cohort and the maximum density (settlement intensity) of the new cohort (Fig. 1.4).

Spawning, settlement and environmental patterns

Spawning and settlement can take place at any time of year in the Algoa Bay region (Fig. 1.2), but the probability of spawning and settlement was greater in some months than in others (Fig. 1.5a). Spawning was most likely in winter and spring (May-October) and peaks in spawning probability occurred immediately prior to, or shortly after, the autumn (March/April) and spring equinox (September/October). As expected, peaks in spawning probability were followed one to two months later by peaks in settlement probability, which therefore coincided with the autumn (April) and spring equinox (October) as well as the winter solstice (July).

Lagged cross correlation of spawning or settlement probability with wind, tide and temperature data showed that these general patterns were related to temporal fluctuations in environmental conditions. Spawning was inhibited by warm summer air (0 lag, $r=-0.6656$, $P<0.05$; Fig. 1.5b) and sea (0 lag, $r=-0.7199$, $P<0.05$; Fig. 1.5c) temperatures, and frequent south easterly winds (1 lag, $r=-0.7124$, $P<0.05$; Fig. 1.5d), but spawning peaks consistently occurred 2 months after peaks in the frequency of NW winds ($r=0.6014$, $P<0.05$; Fig. 1.5e). Spawning was not correlated ($P>0.05$) with NE winds (Fig. 1.5f), but settlement probability peaked 1-2 months after peaks in the frequency of NE (1 month lag, $r=0.5106$, $P<0.05$; Fig. 1.5f) and SE winds (2 month lag, $r=0.6513$, $p<0.05$; Fig. 1.5d). Unlike spawning, settlement was not correlated ($P>0.05$) with NW winds (Fig. 1.5e) or temperature (Fig. 1.5b & c). Neither spawning nor settlement were correlated with SW winds (Fig. 1.5g) or wind velocity (Fig. 1.5h).

There was little correlation between the fluctuation in spawning probability and the mean monthly high and low tide level (Fig. 1.5 i & j). Increasing high tide levels generally coincided

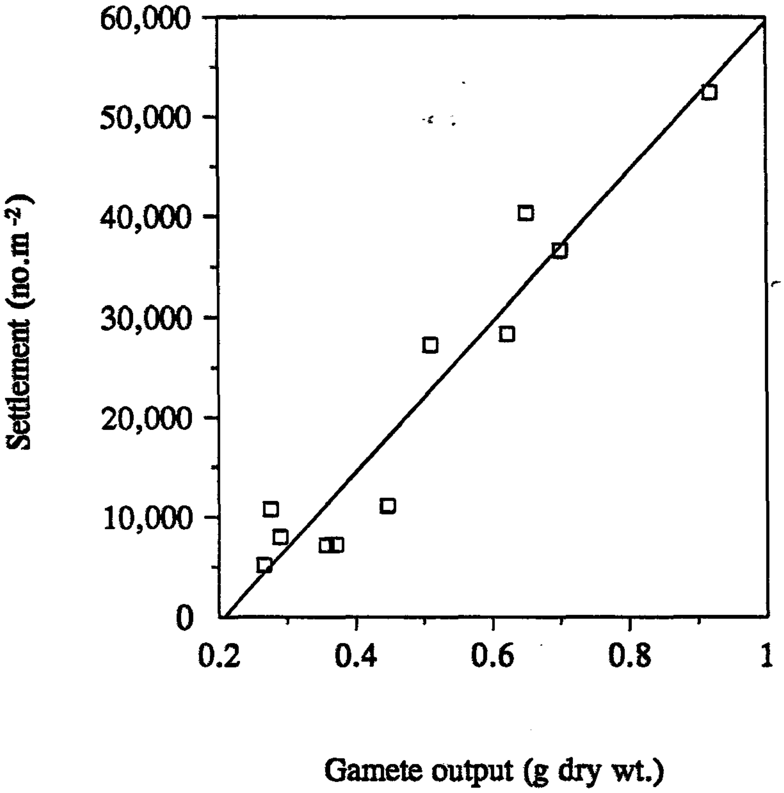


Figure 1.4: Regression ($y = a + bx$) of the gamete output (g dry weight) of a 65 mm individual during spawning occurring prior to the appearance of a new cohort against the maximum density of the new cohort (settlement intensity). The sample size was 11, the regression equation was $y = -15714 + 75\ 249x$, the r^2 value was 0.9245 and the probability $P < 0.001$.

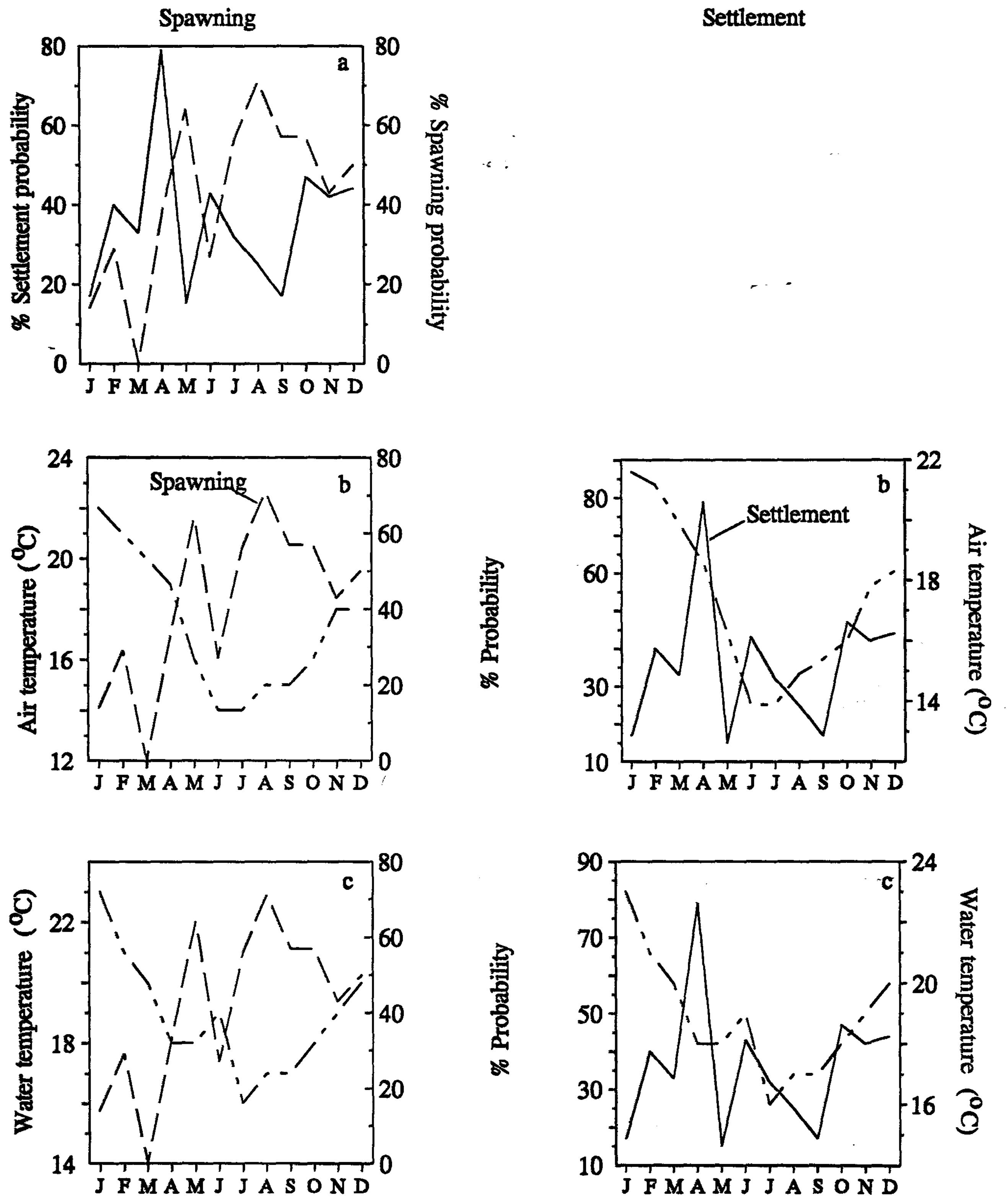


Figure 1.5: Temporal fluctuation in spawning and settlement probability of *Perna perna* (a), temperature (b & c), wind (d-h) and tide levels (i & j) in the Algoa Bay region.

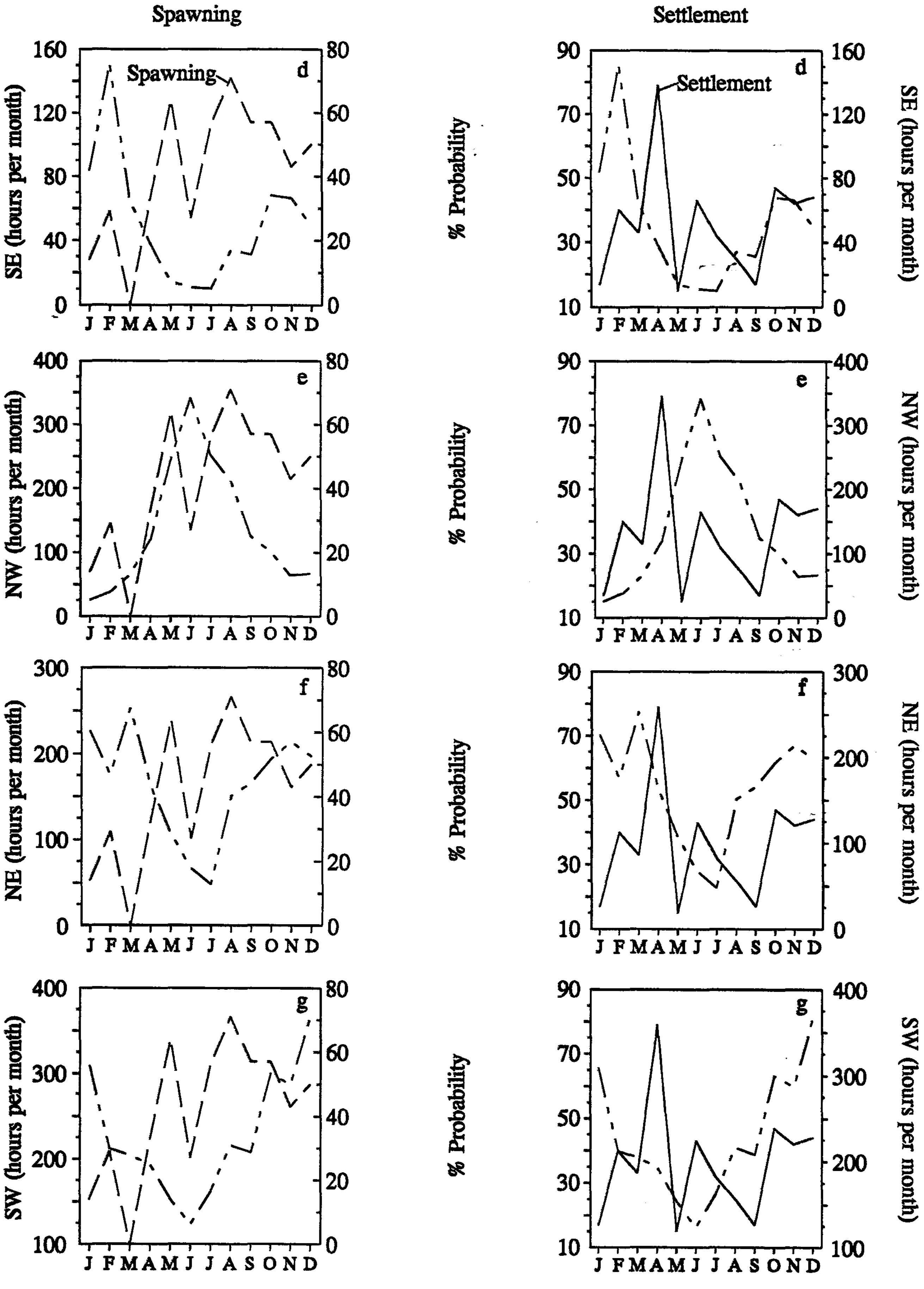


Figure 1.5 continued

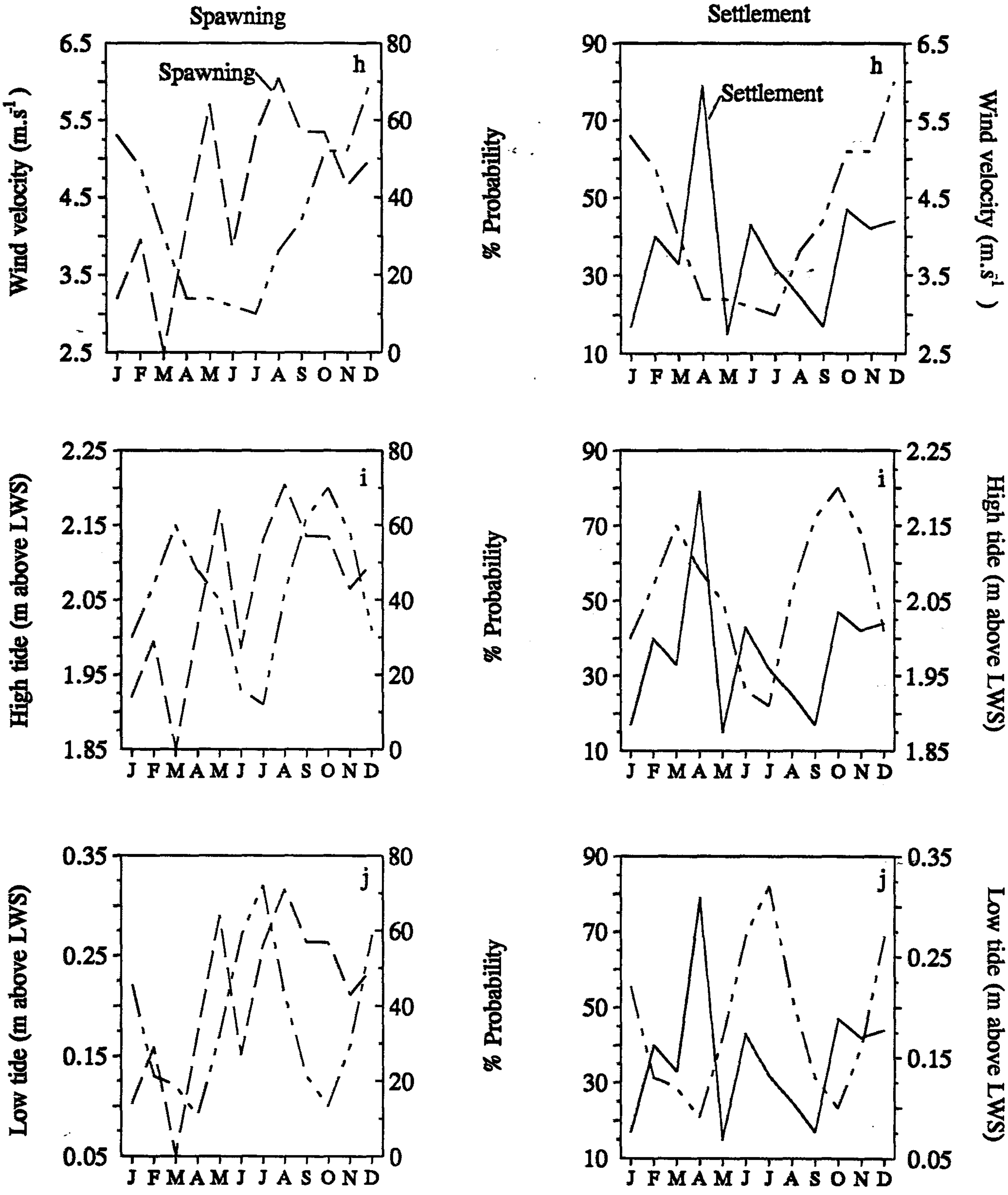


Figure 1.5 continued

with declining low tide levels and therefore with increasing tidal range. In contrast, declining high tide levels coincided with increasing low tide levels and therefore declining tidal range. Maximum tidal range during equinox spring tides, generally occurred every six months around spring (September/October) and autumn (March/April) alternating with minimum tidal range during neap tides in winter (June/July) and summer (December/January, Fig. 1.5i & j).

Spawning probability generally increased during periods of change in tidal range, after or prior to, equinox spring tides, while settlement probability increased when tidal range was at its maximum or minimum (Fig. 1.5i & j).

Discussion

The link between the timing and intensity of local patterns of spawning and settlement in intertidal mussel populations along the south coast of southern Africa, suggests that larval dispersal was limited (Fig. 1.4). The same thing can be said for: echinoderms, as there is a positive correlation between spawning and recruitment on an island and a good correlation between adult and recruit density on three islands (Hunte & Younglao 1988); for damsel fish, since larval production accounts for 50% of the variance in recruitment (Meekan *et al.* 1993); and for abalone and scallops, because of the positive stock-recruitment relationship (Prince *et al.* 1987 & 1988, McShane *et al.* 1988, Peterson & Summerson 1992).

As Hunte & Younglao (1988) point out, this evidence is purely circumstantial and must be viewed with caution, because results may be explained by selective settlement and/or reduced post-settlement mortality adjacent to adults. However, the primary determinant of settlement intensity is larval supply (Roughgarden *et al.* 1985, Bertness *et al.* 1992), and while selective settlement may modify local settlement patterns, it is unlikely to account for major differences in settlement intensity. Post-settlement mortality may be important, as most of these studies, including the present one, measure recruitment of juveniles shortly after settlement rather than settlement *per se*. Shortly after settlement, recruit density generally reflects settler density but density dependent post-settlement mortality may uncouple the relationship as time progresses (Caffey 1985, Connell 1985, Davis 1988, Fairweather 1988, Bertness 1989, McGuiness & Davis 1989, Holm 1990, Roegner 1991). Thus it is important to distinguish between the number of juveniles surviving the first few weeks after settlement (juvenile recruitment) and the number surviving to maturity (adult recruitment), but the terms settlement and juvenile recruitment can be used inter-changeably. Therefore, it seems feasible to attribute a link between the timing and intensity of spawning and recruitment of juveniles shortly after settlement, to limited larval dispersal.

One implication of the link between spawning and settlement, is that factors causing variation in the timing and intensity of spawning are the primary cause of variation in settlement. There is a definite association between spawning patterns and latitudinal gradients in factors such as temperature, photoperiod, phytoplankton production and thus food availability (eg. Wilson & Hodgkins 1967, Bayne 1975 & 1976, Lewis 1980, Griffiths & Griffiths 1987). Species which conform to the expected zoogeographical latitudinal pattern include: holothurians (Costelloe 1988), oysters (Braley 1982, Lasiak 1986), starfish (Barker 1979, Barker & Nichols 1983), barnacles (Lewis 1980 and literature therein, Kendall *et al.* 1985), limpets (Lewis 1980 and literature therein, Bowman & Lewis 1977), shrimps (Bauer 1989, Bauer & Rivera-Vega 1992), crabs (Dinnel *et al.* 1993) and amongst others mussels especially mytilids (Chipperfield 1953, Wilson & Hodgkins (1967), Seed 1976, Griffiths 1977, Lasiak 1986, Griffiths & Griffiths 1987, King *et al.* 1989, Shafee 1989, van Erkom Schurink 1991, Caceres - Martinez *et al.* 1993). In high latitude temperate and boreal climates, environmental conditions undergo extreme seasonal fluctuations, and are only suitable for breeding for a short period each year (Chipperfield 1953, Seed 1975, Lewis 1980, Kautsky 1982, King *et al.* 1989, Grehan 1991, Chen & Chen 1992). Therefore, breeding occurs at much the same time of year at different sites, but there are large interannual fluctuations in reproductive effort and recruitment (Lewis 1980). At the other extreme - breeding occurs throughout the year in tropical climates with constant environmental conditions (Thorson 1954, Brayley 1982, Bauer 1989, Bauer & Rivera-Vega 1992). The breeding pattern of mussels along the south coast of South Africa is what one would expect in moderate sub-temperate climates (Lasiak

1986). There were protracted periods (3-6 months) of spawning and settlement, with stochastic variation in the timing and intensity of peaks in activity between sites and over time (Fig. 1.1). Stochastic variation in spawning and settlement periodicity was superimposed on a more deterministic pattern of increased breeding activity at certain times of year (Fig. 1.5a). Unsurprisingly, these deterministic patterns were linked to variations in climatic and hydrological conditions. Warm summer temperatures inhibited spawning, and spawning probability was greatest in winter and spring when sea temperatures drop below 18°C (Fig. 1.5b & c). This is supported by van Erkom Schurink (1991) who recorded a correlation between the spawning activity of mussels and changes in temperature around the coast of South Africa. The coastal climate and hydrography along the coast of South Africa are largely determined by the Benguela and Agulhas currents, and can be divided into three broad biogeographical zones: the cool sub-temperate west coast, the warm sub-temperate south coast and sub-tropical east coast (Branch & Branch, 1981). *P. perna* is a warm-water species, and the reproductive output decreases from 0.7120 - 1.1642 g on the south coast in Algoa Bay (this study), to 0.52 - 0.82 g further south in False Bay at the tip of Africa (van Erkom Schurink 1991). In contrast, *C. meridionalis* is a cold-water species and the maximum annual gamete output decreases slightly from 0.78 - 1.23 g on the west coast (van Erkom Schurink 1991) to 0.9151 - 1.0496 g, on the south coast near the northern limit of its range (this study). This pattern suggests that temperature determines both the rate of gametogenesis and stimulates spawning. This is supported by Griffiths (1977) who linked gametogenesis and spawning to upwelling. She suggested that increased phytoplankton production and thus food availability following upwelling of cold, nutrient rich water, increased the rate of gametogenesis, and that once the gonad was mature, the sharp declines in temperature trigger spawning. Wind generates upwelling off the leeward side of prominent capes on the south coast (Schumann *et al.* 1982), and subsequent transport of this upwelled water results in small scale local variations in temperature and nutrient availability (Beckley 1988), which may account for the variation in the exact timing and intensity of spawning and settlement between sites only four kilometres apart.

Since winds influence circulation patterns, sea temperature and food availability (Griffiths

1977, Schumann *et al.* (1982), Shanks (1986a) was able to correlate daily settlement of barnacle cyprids with winds and tides causing onshore flow. He found a semilunar periodicity in daily settlement rate which suggests that they are carried onshore by tidally induced internal waves, and the distribution of these waves determine initial settlement patterns along the shore (Shanks 1983 & 1985, Shanks & Wright 1987). However, the evidence for correlation between wind generated currents and settlement is ambiguous. Variation in wind velocity accounted for a significant proportion of the short term variance in the abundance of drifting bivalves and gastropods (Armonies 1992), and maximum settlement rates have been recorded during periods of winds that create onshore flow (Hawkins & Hartnoll 1982), but they have also been recorded when winds are offshore (Bennell 1981). The most complete analyses of the relationship between environmental factors such as wind and temperature with settlement come from the long-term studies of a number of rocky shore species in the United Kingdom (Lewis 1980). Wind was successfully correlated with fluctuations in annual barnacle recruitment at several sites, and with differences in general recruit intensities between windward and downwind facing areas. In addition there was a more uniform recruitment pattern along straight coasts in comparison to the more irregular pattern on complex, convoluted coasts which affects the orientation of sites relative to the wind (Lewis 1980).

On the south coast of southern Africa frequent NW winds produce favourable conditions for gametogenesis and spawning in winter, while circulation patterns appear to be most favourable for settlement during the SE and NE winds which increase in frequency in spring through to early autumn (Fig. 1.5d, e & f). Tidal range, also influences the degree of cross-shelf flow (Romer 1986) and thus dispersal and settlement. Furthermore, it determines the period of immersion and emersion at high and low tide respectively, which could affect the rate of gametogenesis as it determines the length of time available for feeding (Keats & Steele 1984), as well as spat mortality which can be high after prolonged exposure to extremely high or low temperatures (Bowman & Lewis 1977, Lewis 1980). Peaks in spawning activity generally coincided with periods of change in tidal range immediately prior (February, August) and/or shortly after (May) the autumn (March/April) and spring (Septmeber/October) equinox (Fig. 1.5i & j). Since spawning followed settlement 4-8 weeks later, peaks in settlement activity coincided with periods of maximum tidal range during equinox spring tides (April, October), and with minimal tidal range during winter solstice neap tides (July) (Fig. 1.5 i & j).

Although periods of increased spawning and settlement activity can be predicted from easily measured wind, tide and temperature data, further research is required to assess whether this is also true for the intensity of spawning, especially since this study showed that spawning intensity is the primary determinant of juvenile recruitment.

In conclusion, links between local patterns of spawning and settlement suggest that larval dispersal is limited, and that settlement is primarily determined by wind, tidal range and temperature, as these factors affect gametogenic and spawning activity, circulation patterns determining larval dispersal, and probably spat survival.

CHAPTER 2

THE INFLUENCE OF LARVAL BEHAVIOUR AND CIRCULATION PATTERNS ON THE DISTRIBUTION AND DISPERSAL OF PLANKTONIC BIVALVE LARVAE

Introduction

Local patterns of spawning and settlement are linked in intertidal mussel populations along the south coast of southern Africa, suggesting that larval dispersal is limited (Chapter 1). However, larvae are only capable of weak swimming movements and should theoretically be transported hundreds of kilometres in the 3 to 4 weeks they spend in the plankton. Hydrographic processes acting on various scales influence larval distribution, dispersal and supply, and thus affect settlement patterns (Coe 1953, Bailey 1981, Frith 1981, Shanks 1983 & 1986a, Cowen 1985, Leis 1986, Frith & Mason 1986, Tanaka *et al.* 1986, Shanks & Wright 1987, Fechelm & Fissel 1988, Clancy & Epifanio 1989, Black & Moran 1991, Kingsford *et al.* 1991, Fowler *et al.* 1992, Graham *et al.* 1992). It is also known that passive dispersal of larvae by currents is modified by larval behaviour, which allows them to control their distribution to some extent, and may limit their dispersal (Crisp & Southward 1953, Thorson 1961, Banse 1968, Scheltema 1975, Levin 1983, Mileikovsky 1973, Gerrodette 1981, Leis 1986, Shanks 1986b, Palmer 1988, Davis & Butler 1989, Pillar *et al.* 1989). However, there is very little information on circulation patterns and larval behaviour around rocky shores which can be used to establish whether and how the dispersal range of bivalve larvae is limited.

Intertidal mussel populations on wave swept rocky shores in the Algoa Bay region, release their gametes into a high energy surf zone, where turbulence may disperse gametes and reduce fertilisation success to as little as 0.01 to 3% (Denny & Shibata 1989), but 80 to 100% of the eggs may be fertilised in small surge channels which act as containment vessels (Denny *et al.* 1992). Although these channels trap gametes for long enough (16 minutes) to ensure fertilisation, the retention time is far shorter than the average 3 to 4 weeks it takes mytilid larvae to complete development (Thorson 1950). Developing larvae swept out of these protected environments enter larger mainstream circulation cells in and adjacent to the surf zone (Denny *et al.* 1992), where their distribution and dispersal may be influenced by tides, wind, topography and possibly larval behaviour (Goschen & Schumann 1988, Talbot & Bate 1988a). In the Algoa Bay region, tides only have a limited capacity to transport larvae over distances greater than the tidal excursion, as there is little net tidal flux (Romer 1986). Dispersal is probably influenced mainly by wind generated currents. There are four predominant winds in this region (Roberts 1989, Schumann *et al.* 1991, Schumann & Martin 1991). Roberts (1989) used drogues with vanes suspended at different depths to measure current speed and direction generated by these winds in and immediately adjacent to the surf zone. He found that in Algoa Bay currents generally flow parallel to the coast in an easterly direction during calm periods or during south westerly, south easterly and north westerly winds, while wind from the north east produced a westward flowing current. The depth to which wind affects the current speed and direction depends largely on the strength of the wind. The current profile can be quite complex during light variable winds (Roberts 1989), and larvae at different depths may be transported in different directions. Consequently, if their weak swimming capabilities or adaptive behaviour allow them to control their vertical distribution, larvae may have some control over their dispersal, as has been documented for zooplankton in estuaries (Sandifer 1975, Cronin & Forward 1979, Mann 1988, Kaartvedt 1989, Laprise & Dodson 1989, Dauvin & Dodsin 1990), deeper coastal and oceanic waters (Scheltema 1975, Rimmer & Phillips 1979, Shanks 1986b, Epifanio *et al.* 1988 & 1989, Lipcius *et al.* 1990), and for the diatom *Anaulis birostratus* in the surf zone off sandy beaches (Talbot & Bate 1988a). In addition, irregular reef or shore topography modifies local flow patterns generated by winds, and minimal net water movement out of bays, small gullies or channels and eddies associated with reef edges, may have a marked effect on the distribution and dispersal of larvae in these areas (Black & Gay 1987, Black 1988, McShane *et al.* 1988, Sammarco & Andrews 1988, Denny *et al.* 1992).

Larval behaviour, reversals in current direction caused by changes in wind direction, as well as entrapment of larvae in areas of minimal water movement may affect the distance larvae are dispersed by currents. Direct *in situ* observations of large lecithotrophic larvae have shown that larval behaviour, swimming time, current speed and direction influence dispersal, and that two models can be used to estimate the dispersal distance. The first, assumes that distance dispersed (*d*) is equal to the product of swimming time (*t*) and the current speed (*s*) (Davis & Butler 1989). The second, $d=a\surd t$ ($\surd$ = square root), assumes that distance dispersed is proportional to the square root of swimming time, as larval movements are more random than linear (Gerrodette 1981). a is related to the diffusion constant used for describing Brownian or random motion (Gerrodette 1981). To calculate the dispersal range and direction of a larva it is necessary to take into account variations in the direction in which it drifts, as this may reduce the net distance the larva is transported if it drifts back and forth along the coast.

At present no means exist to follow the movements of microscopic larvae in the plankton in order to assess whether they are transported by wind generated currents and whether larval behaviour does influence their dispersal. However, larval dispersal can be simulated using dye, drift cards or tubes (Levin 1983, Tegner & Butler 1985) and drogues (Fortier & Legget 1985, Shanks & Wright 1987). Alternatively movements of larvae may be simulated by temporal changes in the distribution of phyto- or zoo-plankton at a series of stations arranged vertically or horizontally, often on a sampling grid (Heath *et al.* 1987, Talbot & Bate 1988 a,b & c, Pillar *et al.* 1989, Webb & Wooldridge 1990). These studies have mostly been undertaken on a large scale in deep water over the continental shelf or in the open ocean, and sampling periodicity varies from days to months and transects are generally kilometres long and located several kilometres apart. Few studies have examined larvae in the nearshore region but the present study redresses this imbalance. The purpose of the study was to follow the movement of larvae adjacent to the surf zone and to assess whether their movements were affected by wind-driven currents, and to examine changes in the vertical distribution of larvae and currents to assess whether vertical migration of larvae affects longshore dispersal. Finally, assuming that larvae are passively dispersed by wind-driven currents, the total distance travelled and the net direction and range of dispersal were estimated for planktonic larvae with an average life span of a month.

Methods

Larval distribution on plankton grids

Plankton sampling took place at Kenton, both in the surf zone and offshore of the breaker line 100 to 400 metres from intertidal wave cut platforms covered in dense beds of *Perna perna* (Fig. 2.1).

The position of sampling stations at Kenton was determined by observing the movements of rhodamine dye released from the shore shortly after high tide. Dye was released on three days in September 1990, each day from a different position on the kilometre-long shore line. On each occasion three sealed plastic bags each containing ~333 ml of rhodamine were thrown into the water at a rate of one every three minutes. Each bag burst open upon hitting the water, releasing the dye, so that three plumes of dye were clearly observed in the water. The movement of the dye was traced using photographs taken every 2-3 minutes for the 15 - 20 minutes the dye remained visible, from an aeroplane flying overhead at an altitude of 500 m. On one occasion the dye released into the surf did not move offshore and eventually accumulated in a shallow embayment (Fig. 2.2). However, at two other positions the dye was carried rapidly offshore in rip currents (Fig 2.3). Just beyond the surf, offshore movement of the dye ceased abruptly (Fig. 2.3) and it dispersed slowly along the back line of the surf in the direction of the wind, becoming more and more diffuse and eventually disappearing from sight 15 to 20 minutes after being released. The movement of larvae beyond the surf zone was simulated over a longer period by observing the movements of eight drogues which were released 20 m behind the surf zone from a boat on the 24 September 1990. The drogues consisted of bright yellow floats the tops of which protruded about 20 cm out of the water, from which orthogonal vanes (20 x 20 cm) were suspended on string at depths of one and three metres. Regardless of the depth of the vane most of the drogues drifted in a westerly direction but towards the shore, and were probably carried by a longshore current generated by the prevailing north easterly wind. Three of the drogues were trapped for over half an hour in a small eddy close to an exposed reef about 140 metres offshore, and one of these was washed onto the beach.

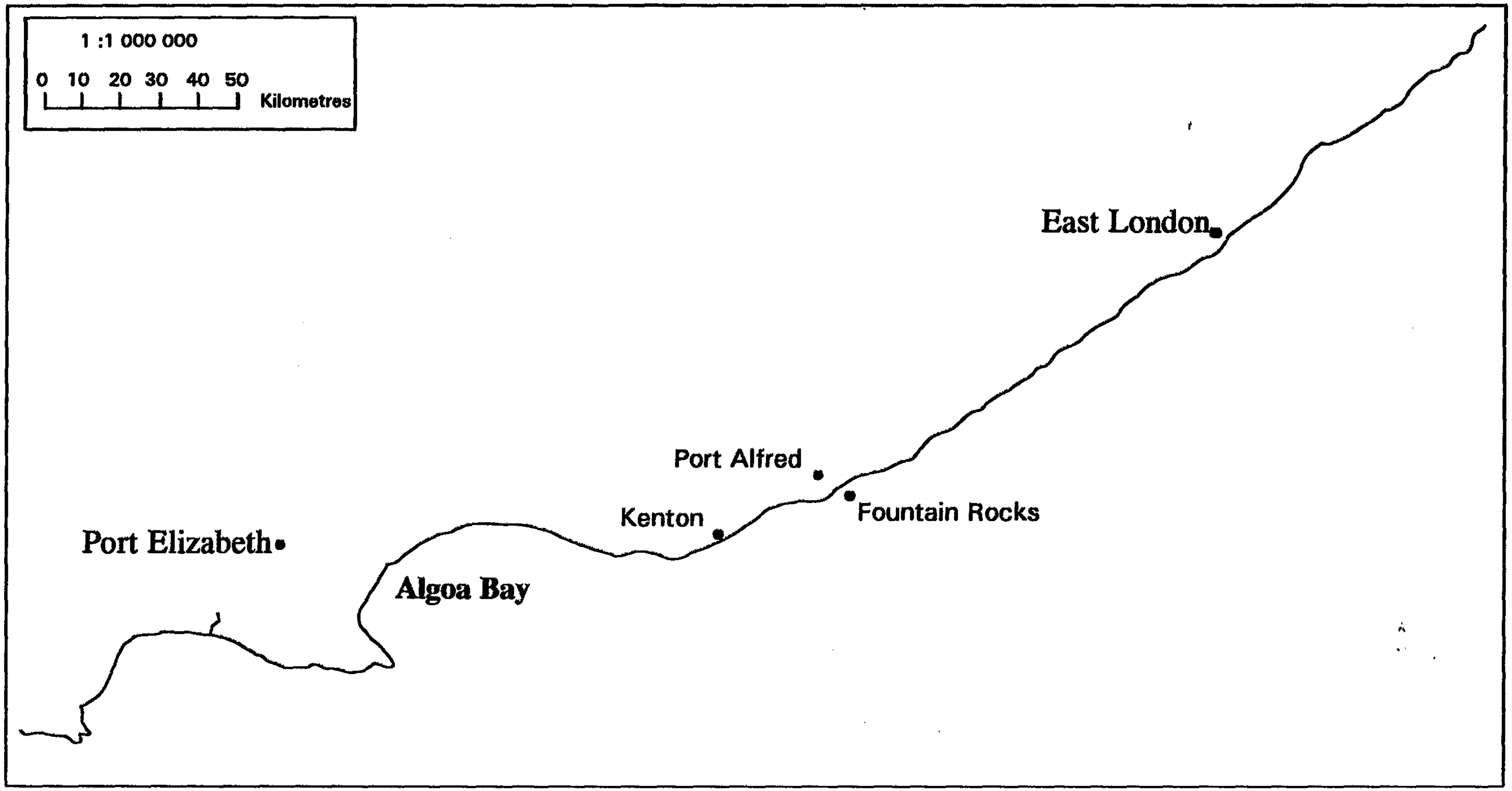


Figure 2.1: Map of the Algoa Bay region showing the study sites at Kenton and Fountain Rocks.

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Figure 2.2 (opposite page): Aerial photographs of the Kenon study site, showing how rhodamine dye released from the shore at one point, was washed back onshore, where it accumulated in gullies and surge channels. The time (minutes) elapsed since the dye was released is shown in the top left hand corner of the photographs.

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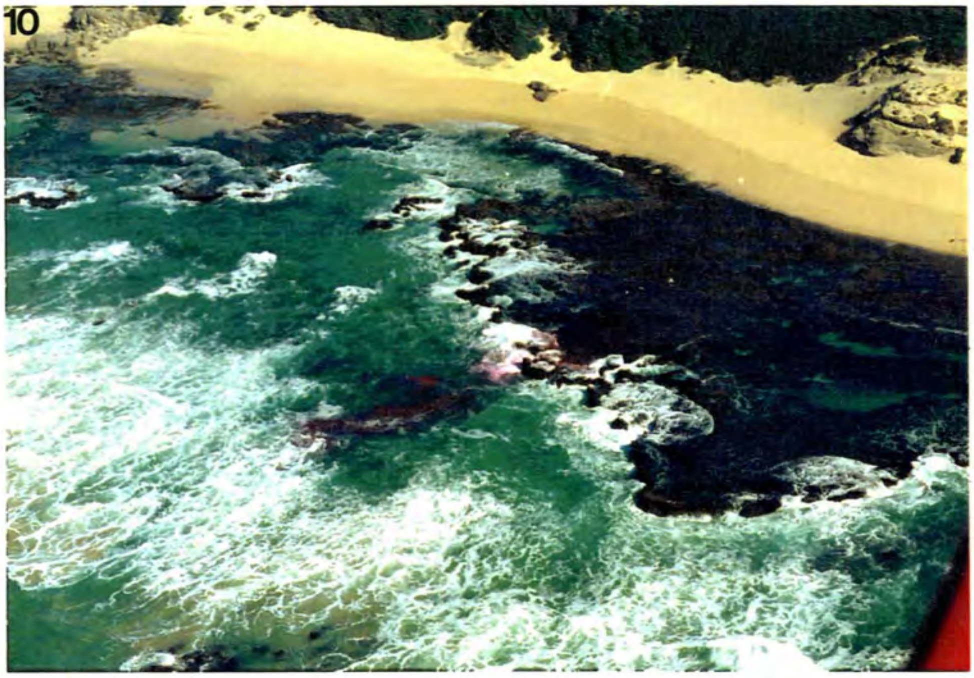

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Figure 2.3 (opposite page): Aerial photographs of Kenton, showing how rhodamine dye released from one point on the shore was rapidly transported offshore by a rip current, accumulating in the slack water immediately behind the surf zone. The sand in the water column immediately behind the surf zone is typically associated with rip current activity. The time (minutes) elapsed since the dye was released is shown in the top left hand corner of the photographs.

To assess whether larvae were found within the surf zone adjacent to the rocky shore, samples were taken from a gully into which the rhodamine dye released from the shore had been washed and trapped for 15 to 20 minutes. Two replicate vertical hauls of 3 to 6 metres, depending on the tide, were performed in the centre of the gully, every three hours over three 24 hour periods in September 1990. A 0.250 mm mesh plankton net 30 cm in diameter fitted with a cod end with a filtering mesh of 0.180 mm, was used to take the samples. The same plankton net was used for all plankton sampling in this study. The samples were preserved in phenoxytol and analysed later in the laboratory. In the laboratory plankton samples were examined under a dissecting microscope fitted with a micrometer. The total number of bivalve larvae in each sample was counted and a sample from each day was measured. All plankton samples taken during this study were processed in this manner.

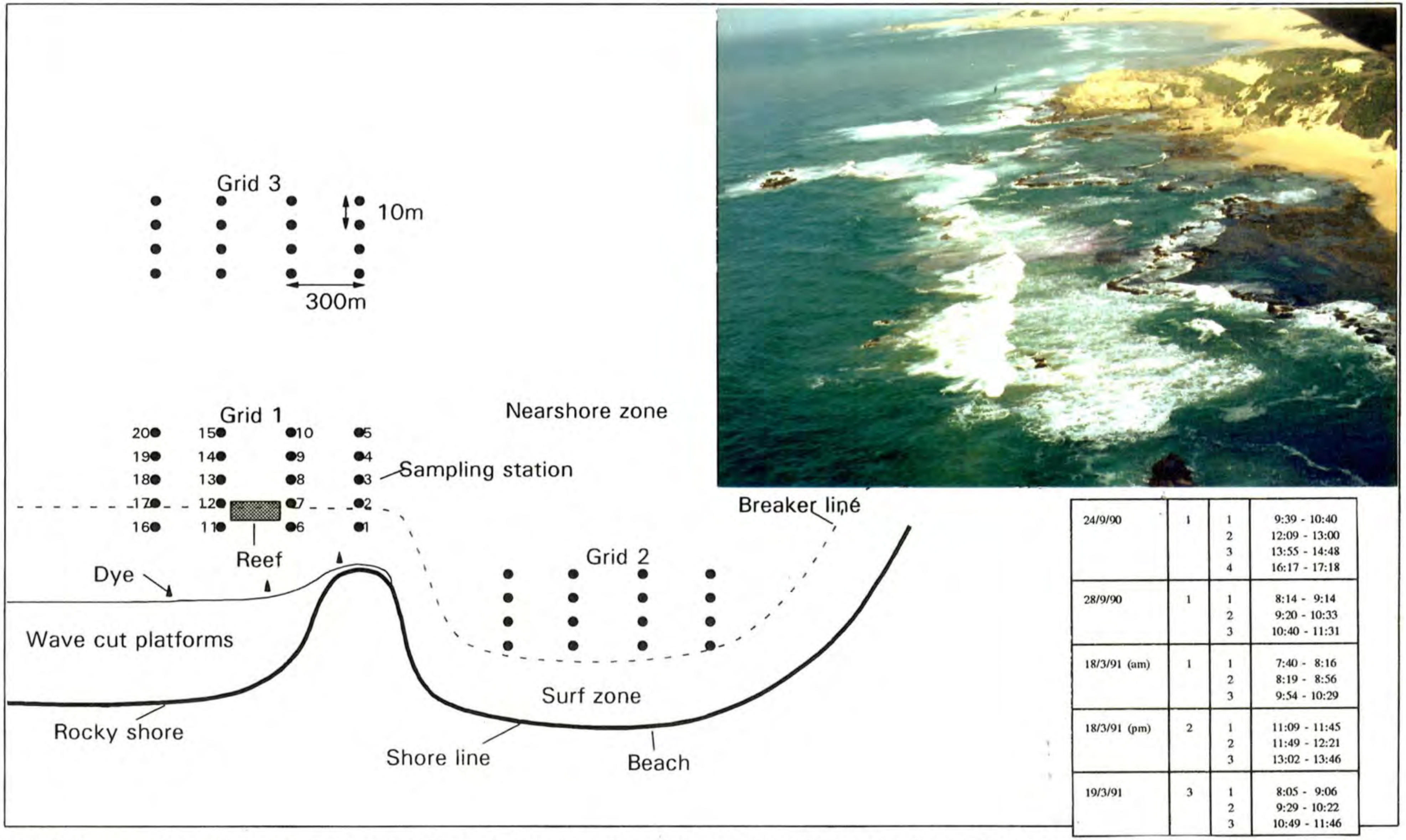
Small scale, short term changes in the distribution and abundance of bivalve larvae on a plankton grid located immediately offshore of the breaker line were examined at Kenton on the 24 and 28 September 1990 and the 18 and 19 March 1991. To establish the uniformity of the larval distribution in this region, sampling took place opposite a rocky shore (grid 1) and sandy beach (grid 2) in 10 m of water about 120 m offshore, and in 20 m of water about 400 m from the rocky shore (grid 3). The position of each grid, the date it was sampled, the dimensions and the arrangement of stations, are shown in Figure 2.4.

The aim of this experiment was to obtain an "instantaneous" picture of the distribution and abundance of larvae on the grid and to compare this to the distribution at a later time. In this respect the spatial and temporal aspects of the experimental design and the method of sampling were extremely important. One important consideration was to pinpoint the abundance of larvae at a station at one time, and another was to be able to sample all the stations on the grid before the larvae at one station could be carried to another station. This limited the size of the grid and meant that the sampling procedure at each station had to be quick and efficient. However, this had to be balanced by the fact that several samples are required to obtain a representative picture of the distribution and abundance of larvae, which are patchily distributed over a broad spectrum of scales

(Barnes & Hughes 1982). Working from a boat, the number of larvae at a station was established by hauling a plankton net vertically through the water column, from the bottom to the surface at a rate of approximately $0.33 m.s^{-1}$. The plankton net described above was light, easy to handle and fine enough to filter out veliger bivalve larvae of around 0.250 mm or more, which minimized the time (~3 minutes) spent at each station. Samples were preserved in phenoxytol. Each of the stations was numbered and the date, station number, time and depth of the haul were recorded. Stations were sampled in numerical order, beginning at station 1 nearest the shore and ending at station 25 furthest offshore (Fig. 2.4). A sampling session took an average of 50 minutes to complete (Fig. 2.4). The number of sampling sessions per day was limited by deterioration of weather conditions in the afternoon. There were four sampling sessions on the 24 September and three on the other days. The interval between sampling sessions had to be long enough to allow changes in the distribution of the larvae but short enough to avoid larvae being advected away from the grid between sessions. The interval between the start of each sampling session varied from 106 to 150 minutes on the 24 September but was shorter (39 to 85 minutes) on other sampling days (Fig. 2.4).

The spatial distribution of larvae within the grid during each sampling session was illustrated with a surface contour map using the computer software programme SURFER. The change in the distribution of larvae on a grid between sampling sessions was examined to follow the longshore movement of larvae.

To establish whether changes in larval distribution were due to dispersal by wind-driven currents, on each of the five sampling occasions the current speed and direction on the grid was recorded once or twice at one metre depth intervals down to 10 m. Variation in current speed on any one sampling occasion was small so further replication was considered unnecessary. A current meter equipped with a flow meter and a low velocity rotor, capable of measuring very low velocities, was used to measure current speed. The current meter was suspended overboard when the boat was anchored. A heavy arrow-shaped weight with a horizontal stabilising vane, ensured that the meter hung vertically down. The direction of currents at the different depths were



24/9/90	1	1	9:39 - 10:40
		2	12:09 - 13:00
		3	13:55 - 14:48
		4	16:17 - 17:18
28/9/90	1	1	8:14 - 9:14
		2	9:20 - 10:33
		3	10:40 - 11:31
18/3/91 (am)	1	1	7:40 - 8:16
		2	8:19 - 8:56
		3	9:54 - 10:29
18/3/91 (pm)	2	1	11:09 - 11:45
		2	11:49 - 12:21
		3	13:02 - 13:46
19/3/91	3	1	8:05 - 9:06
		2	9:29 - 10:22
		3	10:49 - 11:46

Figure 2.4: A photograph and stylised map of Kenton, showing where dye was released from the shore and the location of the sampling grids. The date and time each grid was sampled is shown in the table.

established by observing the direction in which the arrow of the stabilising weight pointed. This information was used to establish a vertical current profile and to calculate the mean current speed and direction on the grid for each sampling occasion. To assess whether current speed varied with depth, the current speed measured at various depths was regressed against depth. In addition, the wind direction and relative strength at the sampling site was noted at the start and finish of the sampling sessions. The direction of the wind, the general strength and direction of the currents, and the speed and direction in which larvae appeared to move were compared.

Horizontal stratification and vertical migration

To assess whether larval abundance was horizontally stratified at Kenton on the 24 and 28 September 1990, 1 and 10 m vertical hauls were performed at each sampling station. On the morning and afternoon of 18 March 1991, the vertical distribution of larvae on the grid was examined by doing ten vertical hauls starting at the surface and increasing in one metre intervals to 10 m. This procedure was repeated on the 19 March 1991 except the depth interval increased by 2 m. If larvae are distributed throughout the water column, the number of larvae captured would increase with the volume of water sampled. Consequently on the 24 and 28 September the abundance of larvae in the 1 and 10 m hauls were compared using Mann-Whitney test (Zar 1984), and on the 18 and 19 March 1991 the number of larvae in a sample was regressed against the vertical height of the sample.

To obtain an indication of whether or not larvae migrate vertically between dawn and dusk, sampling took place in October 1991 at Fountain Rocks, an exposed reef covered in dense beds of *P. perna* (Fig. 2.1). The reef is located at the mouth of the Kowie River about 150m offshore. The water depth around the reef ranged from 3 to 18 m, but was generally about 10 m. Although continuous sampling is ideal for observing changes in the vertical distribution of larvae, sea conditions in the vicinity of the surf zone made sampling too dangerous at night, and prevented continuous sampling from dawn to dusk. However, the most marked changes in the vertical distribution of many planktonic species occurs at dawn and dusk, and this horizontal stratification persists throughout the day (Barnes & Hughes 1982). Therefore, the vertical distribution of larvae was examined by taking 3-5 replicate samples from around the reef at dawn (5:30 - 7:10), during the day (9:36 - 11:00; 12:52 - 13:45) and at dusk (16:50 - 18:30), between the 16 and 18 October 1991. Sampling involved executing vertical hauls over discrete depth intervals of 1 to 2 m, from the surface to the bottom of the water column. The samples were collected with a 0.250 mm mesh strangle net, fitted with a cod end with a filtering mesh of 0.180 mm. The volume of water filtered was determined from the vertical height of the haul and from the diameter of the net. Samples were preserved in 90% alcohol. The concentration of larvae in each of the samples was calculated. A Kolmogorov-Smirnov test (Zar 1984) was used to compare the observed concentration at discrete depth intervals with those expected if the larvae were uniformly distributed.

On each sampling occasion the current direction was observed from the direction of motion of orthogonal vanes (20 x 20 cm) suspended at various depths. This was used to establish a vertical current profile that was compared with the vertical distribution of the larvae to test the hypothesis that larvae at different depths are carried in different directions. The direction and relative strength of the wind at the site during each sampling period was recorded and compared to the current direction.

The information on the vertical distribution of larvae at Kenton and at Fountain Rocks, together with the information on the vertical stratification of current direction and speed, was used to make a preliminary assessment of whether larvae close to shore could use vertical migration to control their longshore dispersal.

Larval dispersal range

If larvae are passively dispersed by wind driven currents, it can be assumed that larval dispersal rate and direction is the same as the prevailing current speed and direction. Roberts (1989) produced a model for the nearshore zone in Algoa Bay which allows current speed and direction to be estimated from the prevailing wind speed and direction (Table 2.1). Using this model the total distance travelled and the net range and direction of dispersal in a month, were estimated for larvae

Table 2.1: A summary of a conceptual model of the typical direction and speed of wind generated currents immediately behind the surf zone in Algoa Bay, recorded by Roberts (1989). The general direction in which these currents transport effluent released into or just behind the surf is also indicated. The *?* denotes a current speed and direction which was not recorded by Roberts (1989).

Wind		Current		Effluent
Direction	Speed	Speed and direction		Direction
	(m.s^{-1})	Surface (0.5 - 1 m)	Sub-surface (>1 - 5 m)	
SW	15	0.10 - 0.15 NE	0.15 - 0.02 NE	NE along coast
NE	15	0.03 - 0.06 SW	?	SW along coast
NW	<7	0.05 - 0.07 SE	0.03 E (1-2 m) N (>2 m)	SE offshore (<0.5m). NE longshore & sub-surface
SE	<7	<0.05 NW	<0.05 - 0.02 N	NE along coast
Calms	0	0 NE	<0.03 NE	NE along coast in residual sub-surface drift

produced each month between March 1989 and June 1991. Two estimates were made - the first using the relationship $d = st$ and the second $d = a\sqrt{t}$. d is the distance travelled, a is a proportionality constant estimated from s, the current speed, induced by wind blowing for time t, either from the NE, SW, SE or NW or the residual current velocity during calms. The frequency (hours.month $^{-1}$) and mean velocity of these winds each month and the duration of calm periods was calculated from hourly wind data recorded at Port Elizabeth Airport. The feasibility of using wind data collected 1-2 km inland rather than on the coast, was established by comparing the relative wind speed and direction recorded during each of the plankton sampling occasions at Kenton and Fountain Rocks, with that recorded over the same time period at Port Elizabeth Airport. Roberts (1989) showed that currents generally flow parallel to the coast in the direction of the wind. The total distance dispersed was calculated as the sum of the distance moved in each direction, while the net dispersal range and direction was calculated as the difference between the distance moved east during SW, SE, NW winds and calm periods and the distance moved west during NE winds.

Furthermore, these theoretical estimates were compared with those obtained when the mean larval dispersal rate (s'') and the square of the mean distance travelled by larvae per unit time (a''), estimated from the *in situ* experiments described above, were used to calculate the total distance travelled and the net range and direction of dispersal.

Results

Plankton samples taken 120 to 400 m offshore contained several species of bivalve larvae, but no larvae were found within the surf zone over three 24 hour periods. The bivalves fitted the description of mytilid veligers provided by Rees (1950) and Fuller & Lutz (1989), and ranged from 0.2 mm to 0.8 mm (Fig. 2.5 & Fig. 2.6).

Figure 2.5 (opposite page): The external morphology of various bivalve larvae, found in the water column adjacent to the intertidal mussel beds at Kenton. From the descriptions provided by Rees (1950) the larvae were identified as belonging to the families, Mytilacea (1,3,5 & 6), Anomiacea (2) and possibly Erynacea (4). The magnification varies but measurements showed the larvae were ~0.3 mm long.

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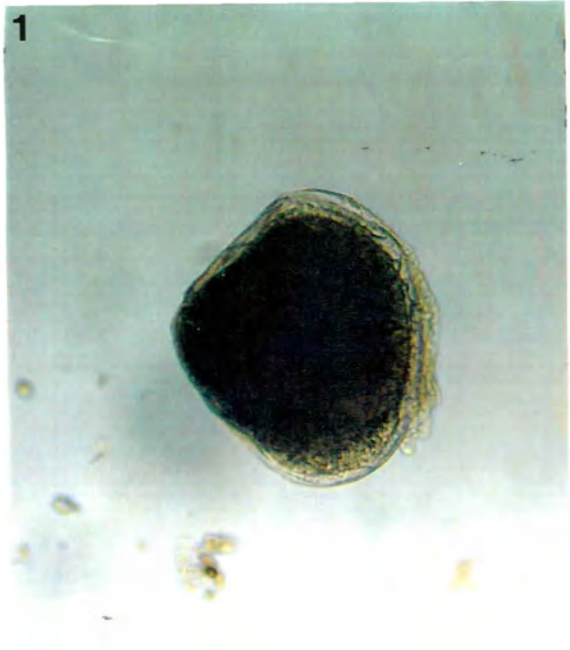

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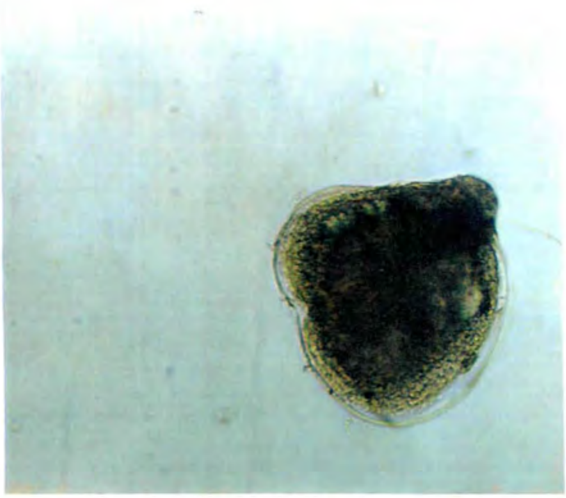

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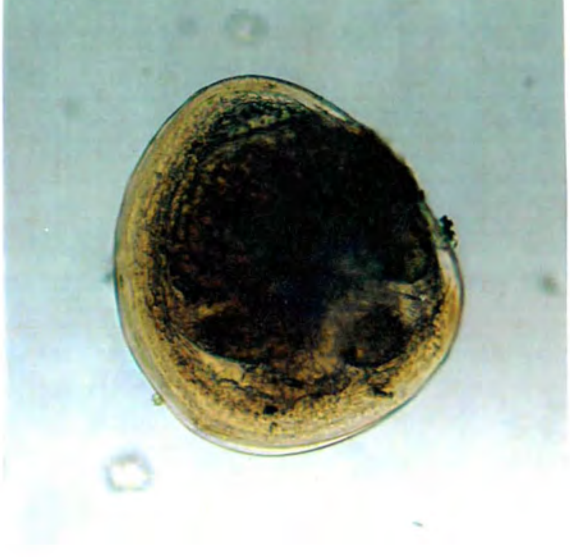

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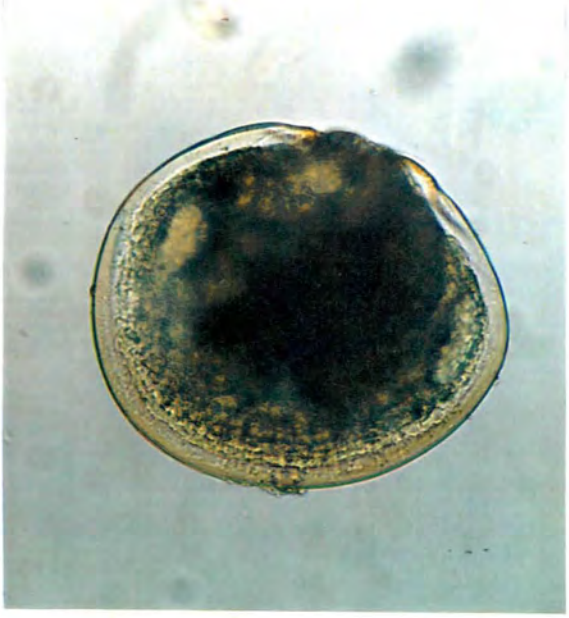

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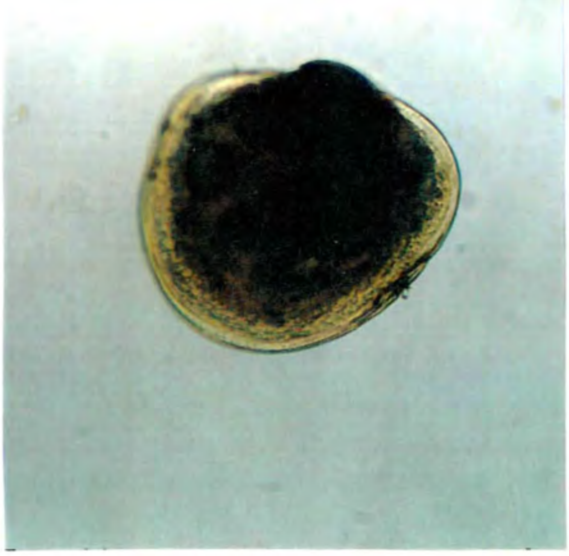

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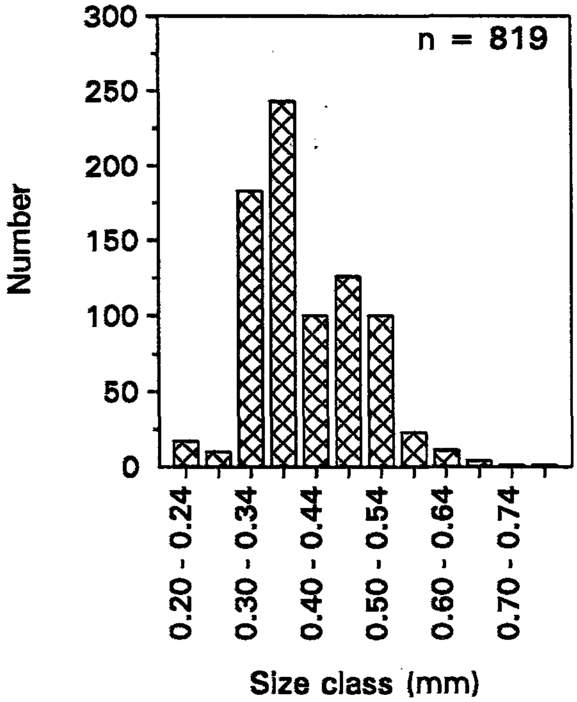


Figure 2.6: The size distribution of mytilid veliger larvae found in the nearshore region adjacent to the surf zone at Kenton.

Larval distribution on plankton grids

Surface contour plots indicate that the horizontal distribution of larvae on a grid was patchy (Fig. 2.7). The concentration of these patches varied on different sampling occasions. The size of these patches also varied, ranging from 10 to 30 m in width (offshore/onshore) to 100 to 600 m in length (longshore). During each of the sampling sessions on a grid, individual patches were classified according to their concentration and size, and the direction, distance and speed with which these patches moved between sampling sessions was determined. Although patches of larvae on a grid could be formed by the aggregation of scattered individuals, this was unlikely given the spatial and temporal design of the experiment. Changes in the position of patches were generally easy to follow on most of the grids sampled, as a sampling session began only ± 20 minutes after the previous one had finished (Fig. 2.4). On the 24 September 1990 the time lapse between sampling sessions was slightly too long (106-150 minutes), but a patch of larvae at the offshore edge (top) of the grid appeared to move along the shore in a westerly direction, with a slight onshore component, between the third and fourth sampling sessions (Fig. 2.7a). Analysis of the surface contour plots showed that larvae moved in opposite directions at different times, and in general, larvae 10 to 20 m or more behind the breaker line of the surf tended to drift parallel to but also towards the shore, while those closer to shore drifted parallel to the shore behind the surf zone (Figs. 2.7a-d).

These results indicate that it is possible to use this type of experimental design to trace indirectly the horizontal dispersal of larvae *in situ*, in the nearshore region. However, the experiment could be improved upon by increasing the dimensions of the grid to 5 or 6 transects, although this must be balanced by the speed with which one sampling session can be completed, and by increasing the number of sampling sessions to five or more if possible. On the 19 September 1990, sampling took place on a grid further offshore, in 20 metres of water, and it was difficult to identify any particular patch which could be followed (Fig. 2.7e). It is possible that the patches of larvae move across and off the grid far more quickly further offshore where the current speed was significantly greater (ANOVA, Tukey range test, $P<0.05$) than on the other grids close to shore (Table 2.2a & b). Alternatively because it was deeper further offshore and the larvae were

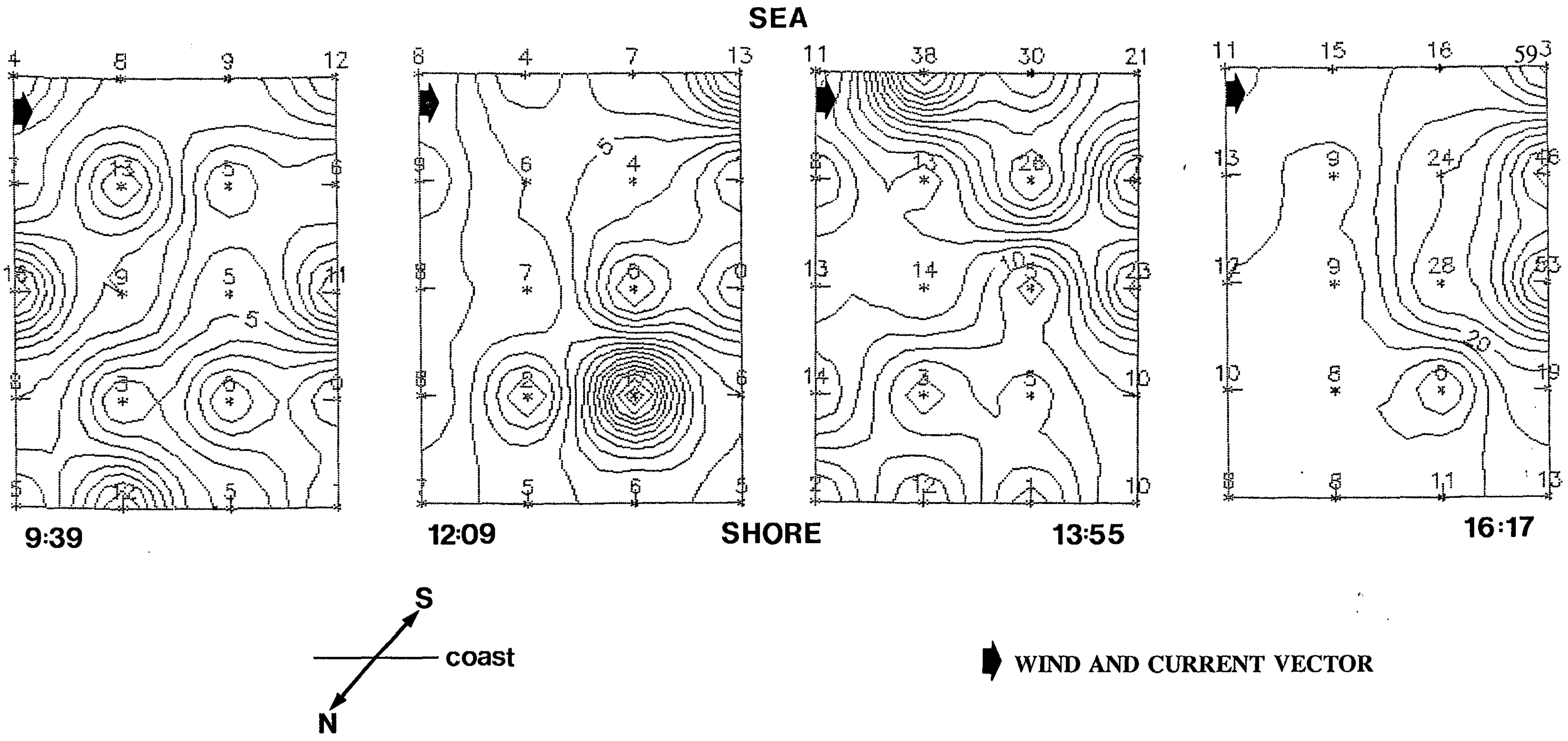
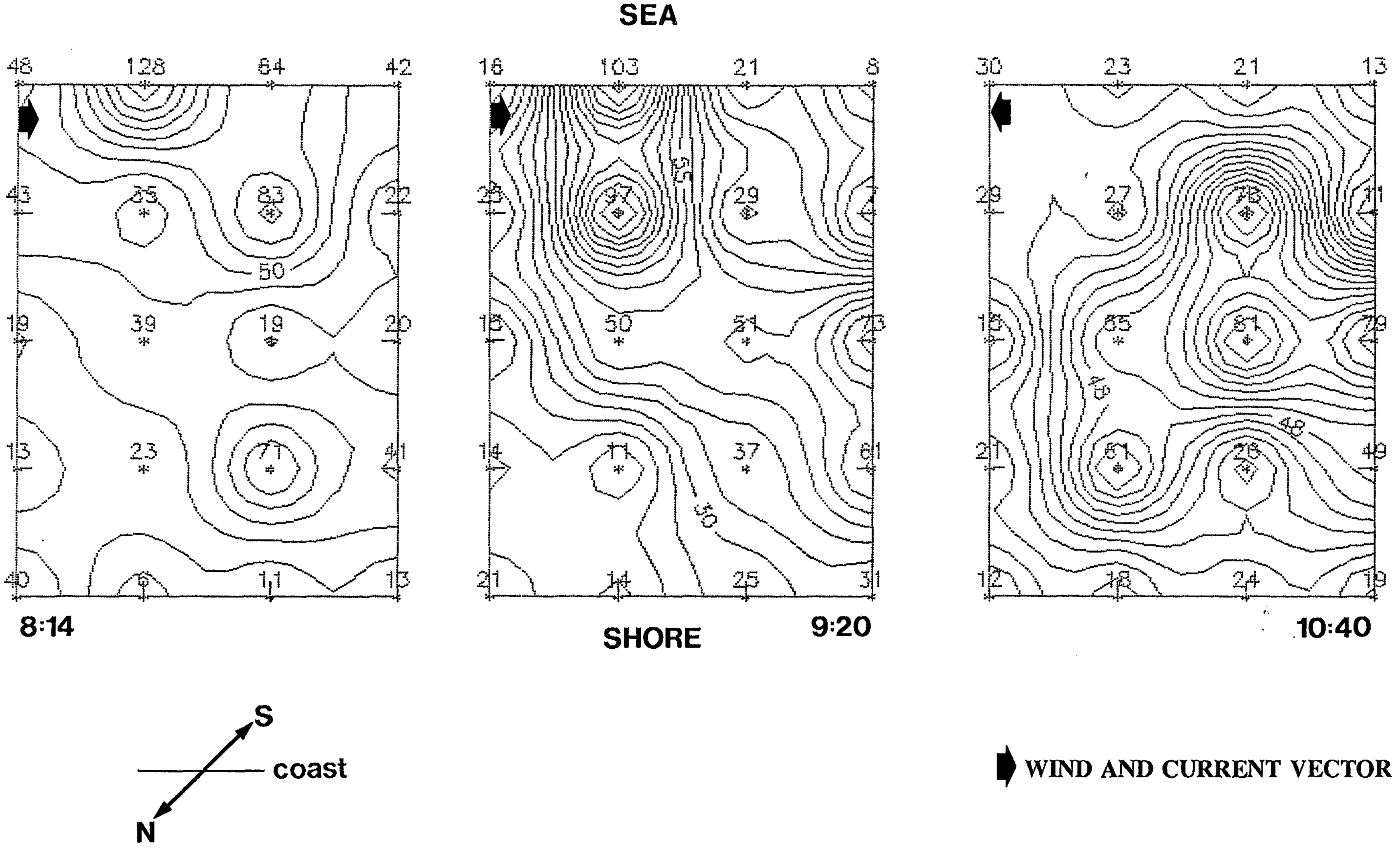


Figure 2.7a: Contour maps showing the temporal variation in the number of larvae in a sample (no.10 or 20 m^{-3}) at each station on the sampling grid at different times on the 24 (a) and 28 (b) September 1990; the morning (c) and afternoon (d) of the 18 March 1991; and on the 19 March 1991(e). The start times are shown below each map.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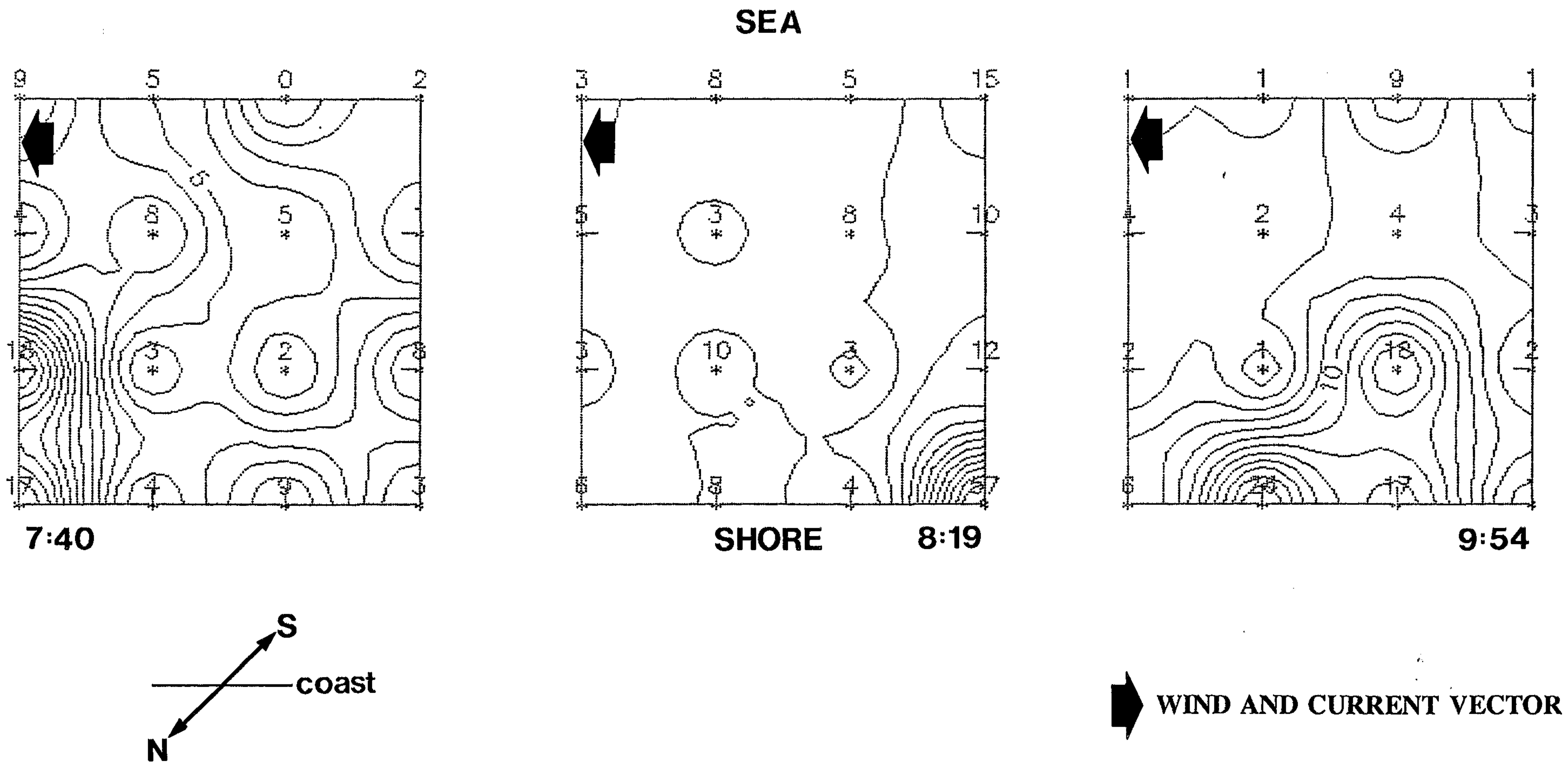
WIND AND CURRENT VECTOR

Figure 2.7b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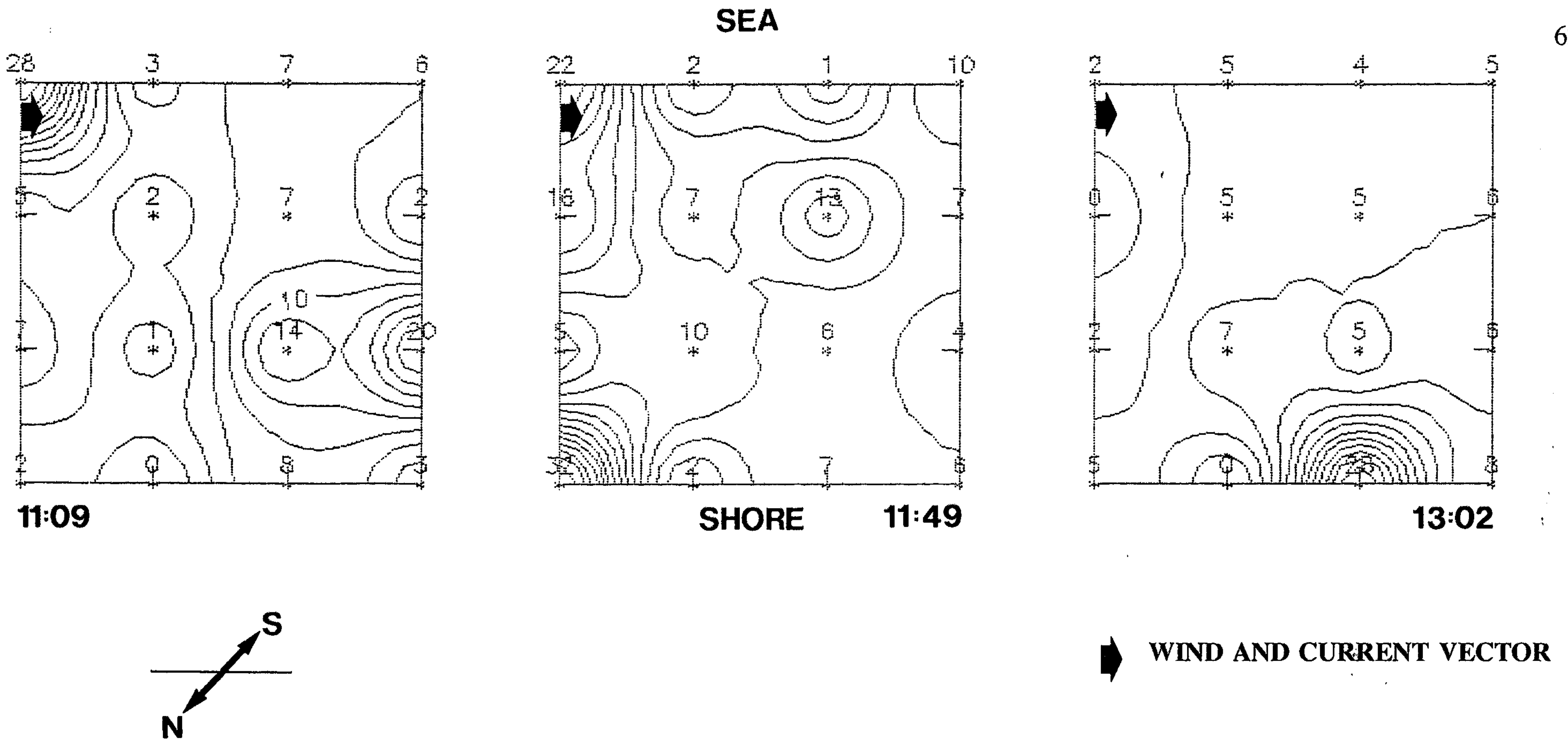
WIND AND CURRENT VECTOR

Figure 2.7c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16 7 13 7
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34 4 7 6
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WIND AND CURRENT VECTOR

Figure 2.7d

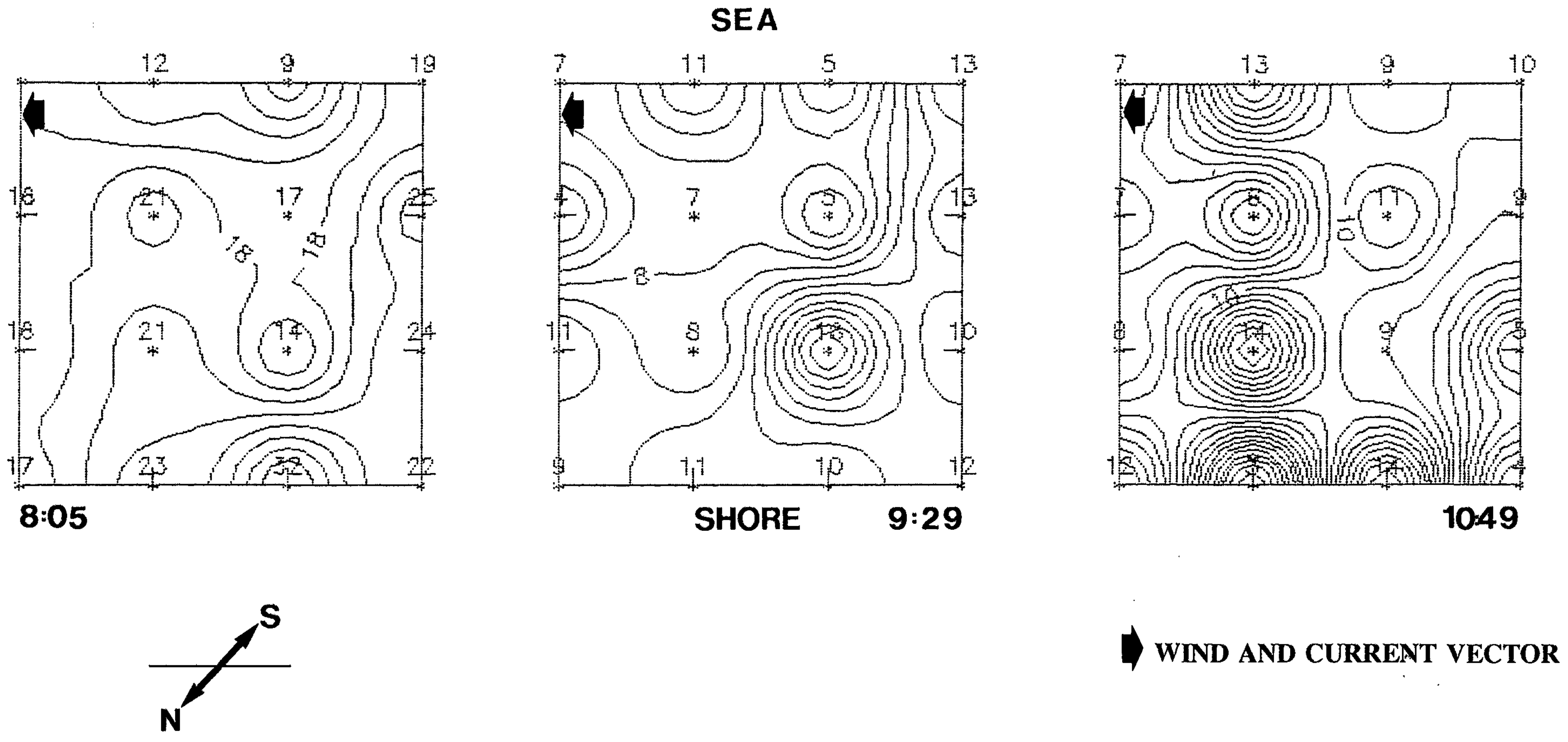
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Figure 2.7e

Table 2.2a: One way ANOVA comparing the mean current velocity (m.s^{-1}) measured on each of the grids sampled.

Source of variation	*SS*	*DF*	*MS*	*F*	*P*
Between groups	0.0391	4	0.0098	15.8830	<0.0001
Within Groups	0.0338	55	0.0006		
Total	0.0729	59			

Table 2.2b: Tukey multiple range test indicating the difference in the mean current velocity recorded on each of the five grids sampled. *HG* denotes homogenous groups. The mean abundance was the same on those dates with stars (*) in the same vertical line, but differed significantly from on those dates with stars in another vertical line. This interpretation of multiple range test results applies throughout this thesis.

Date	Grid	Count	Average (m.s^{-1})	*HG*	
24/9/90	1	20	0.1300	*	
28/9/90	1	10	0.1170	*	
18/3/91 (am)	1	13	0.1208	*	
18/3/91 (pm)	2	7	0.1329	*	
19/3/91	3	10	0.1780		*

distributed throughout a greater volume of water, these patches could have been missed because the resolution of the grid was too low. It is possible that high concentration patches of larvae could have been identified and followed had there been more sampling stations on the grid further offshore, as this would have counteracted the spatial effects of the increased volume of water.

The mean rate of larval patch movement (0.12 ± 0.09 $m.s^{-1}$) fell within the range of current speeds (0.03 to 0.21 $m.s^{-1}$), which were recorded on the grids during the sampling period (Fig. 2.8, Table 2.3). In addition, the direction in which the larvae moved generally coincided with the direction of wind driven currents (Fig. 2.7). On the 24 September a NE wind generated a SW current of 0.03 to 0.16 $m.s^{-1}$, and the larvae moved in a westerly direction along the shore at an average rate of 0.07 $m.s^{-1}$ (Fig. 2.7a, Fig. 2.8, Table 2.3). On the 28 September 1990 there was no wind during the sampling period but a strong NE wind which had previously been blowing had generated a SW current (0.09 to 0.14 $m.s^{-1}$), and the larvae drifted west at a rate of 0.06 to 0.08 $m.s^{-1}$ (Fig. 2.7b, Fig. 2.8, Table 2.3). A SW wind started blowing towards the end of the sampling period and resulted in a switch in the current direction in the afternoon, but this was unlikely to have affected the dispersal of larvae during the sampling period to any great extent (Fig. 2.7b). There was very little wind prior to the morning of the 18 March 1991 and it was calm during the sampling period, however, there was a strong residual NE flow of between 0.08 and 0.18 $m.s^{-1}$ (Fig.2.7c, Fig. 2.8), as commonly occurs on this coast during long calm periods (Roberts 1989, personal observation). By the time sampling began on a second grid on the afternoon of the 18 March 1991, a relatively strong NE wind had begun blowing and the current direction switched from NE to SW (Fig. 2.7c & d). This switch in the current direction was associated with a switch in the direction in which the larvae moved. In the morning the larvae moved in a NE direction at a rate of 0.13 $m.s^{-1}$ and were probably carried by the residual NE flow, while in the afternoon the larvae were carried in a SW direction at a rate of 0.30 $m.s^{-1}$, probably by a SW longshore current (Fig. 2.7c & d, Table 2.3). On the afternoon of the 18 March the current speed ranged between 0.12 and 0.16 $m.s^{-1}$ which was slower than the rate at which the larvae were observed to move. However, the current speed was measured 20 to 30 metres behind the surf zone whereas longshore currents in the

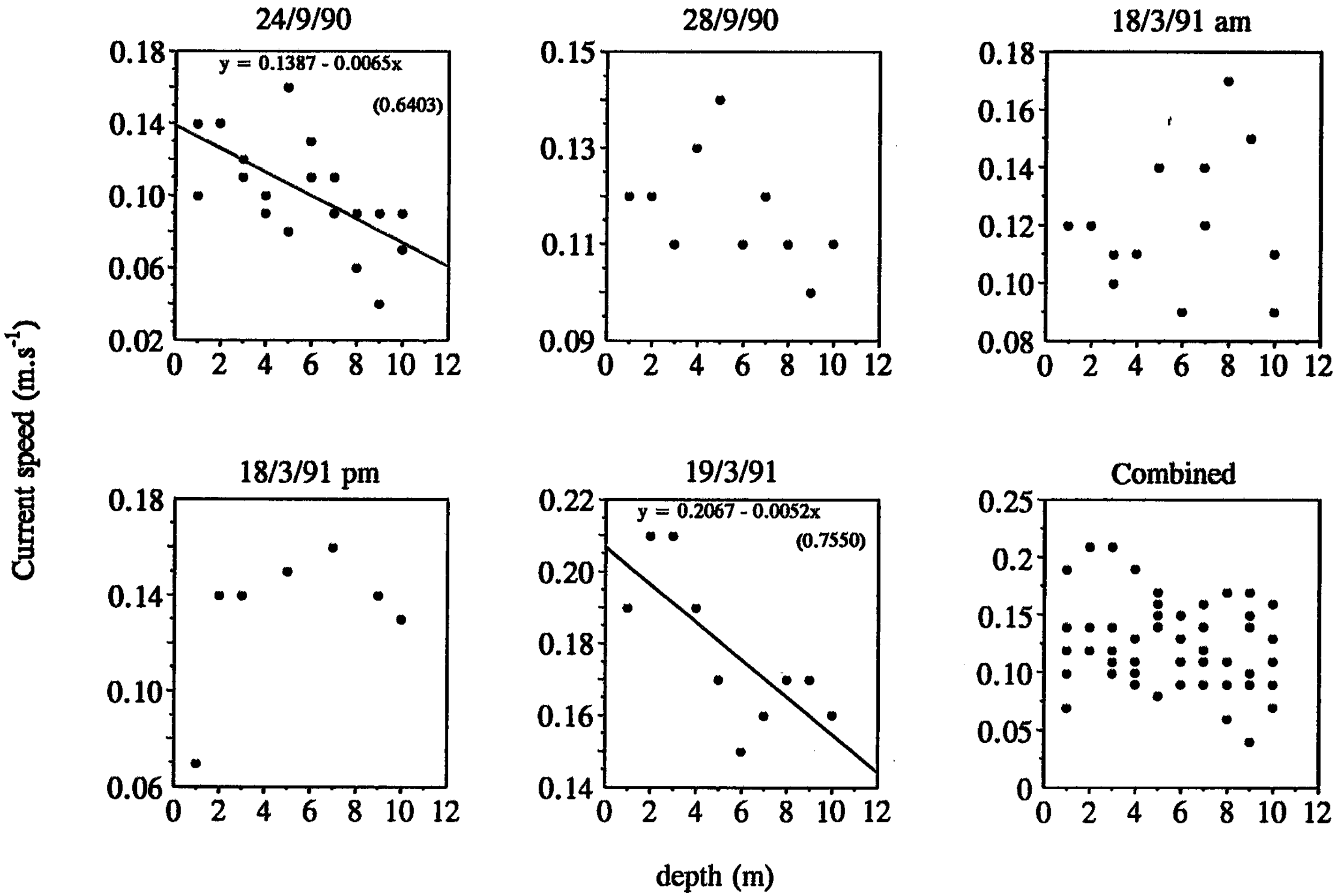


Figure 2.8: Regression of the current speed (dependent variable) against the depth at which the speed was measured (independent variable), during each of the sampling occasions at Kenton. Regression lines are only shown for the significant relationships. The regression equations are shown on the graphs, with the correlation coefficient (*r*) in brackets. This format is followed throughout this thesis.

Table 2.3: The direction and average longshore distance moved by high concentration patches of larvae, and the rate at which they travelled across the sampling grid.

Date	Longshore movement			Dispersal rate (*s*″)		Constant (*a*)
	Direction	Distance (m)	Time (minutes)	($m.s^{-1}$)	($km.h^{-1}$)	
24/9/90	SW	600	143	0.0699	0.2517	0.5496
	SW	600	147	0.0680	0.2449	0.5421
28/9/90	SW	300	79	0.0633	0.2278	0.3697
	SW	300	63	0.0794	0.2857	0.4140
18/3/91	NE	450	58	0.1293	0.4655	0.6473
	SW	600	33	0.3030	1.0909	1.1442
Mean ± SD				0.1188 ± 0.0934	0.4278 ± 0.3364	0.6112 ± 0.2797
a″						0.6050

Note: *a* = the square root of the mean square distance (km) travelled per unit time (hour)

: $a = \frac{2\sqrt{(x^2)}}{N_t}$ (Gerrodette 1981)

where in this case x is the change in position of a patch over a period of time (N_t)

: *a*″ = estimate of *a* using the mean current speed

eg. for current speed of 0.4278 $km.h^{-1}$ $a'' = \frac{2\sqrt{(0.4278km)^2}}{1h}$

surf zone or on the breaker line where the larval patch was situated, may flow far more rapidly (Roberts 1989). The larval dispersal rate was generally slower when patches were situated 20 to 30 metres behind the breaker line (Fig. 2.7, Table 2.3).

In general, the results indicate that short term changes in the distribution of larvae on fine scale plankton grids can be used to simulate larval dispersal in nearshore environments, and preliminary indications are that larvae are dispersed parallel to the shore by wind driven currents.

Horizontal stratification and vertical migration

Larvae were not concentrated at the surface of the water column, as ten metre vertical hauls retrieved significantly more larvae (Mann-Whitney, $P<0.0001$) than one metre hauls at the surface (Fig. 2.9, Table 2.4). On the 18 or 19/3/91, there was no linear relationship between the number of larvae and the depth sampled (height of vertical haul), so they were not evenly distributed throughout the water column (Fig. 2.10). In fact, larval abundance increased significantly with depth on the 18/3/91 (exponential regression, $r=0.50$, $P=0.01$), indicating that larvae were found throughout the water column but were concentrated below 7 m (Fig. 2.10). No such relationship was observed on the 19/3/91 when samples were taken further offshore (Fig. 2.10), but larval abundance was low, and it is not possible to comment on what would have been found had there been a concentrated patch of larvae in the vicinity. Samples of discrete depth intervals between the surface and bottom of the water column, also showed that larvae may be found at any depth in the water column (Fig. 2.11). Kolmogorov-Smirnov (K-S) comparisons showed that 9 of the 11 sampling occasions showed no significant difference (K-S, $P>0.05$) between the observed vertical distribution pattern and that expected for larvae with a uniform vertical distribution (Table 2.5). Only once did larvae accumulate near the bottom at dawn (K-S, $DN=0.67$, $P=0.0366$) and near the surface at dusk (K-S, $DN=0.875$, $P=0.0044$, Table 2.5). However, the significant change in abundance with depth on each occasion was based on only one datum point, and no such pattern was observed at other sites sampled at more or less the same time (Fig. 2.11), suggesting that vertical and horizontal patchiness rather than vertical migration explained these results. Interestingly on the

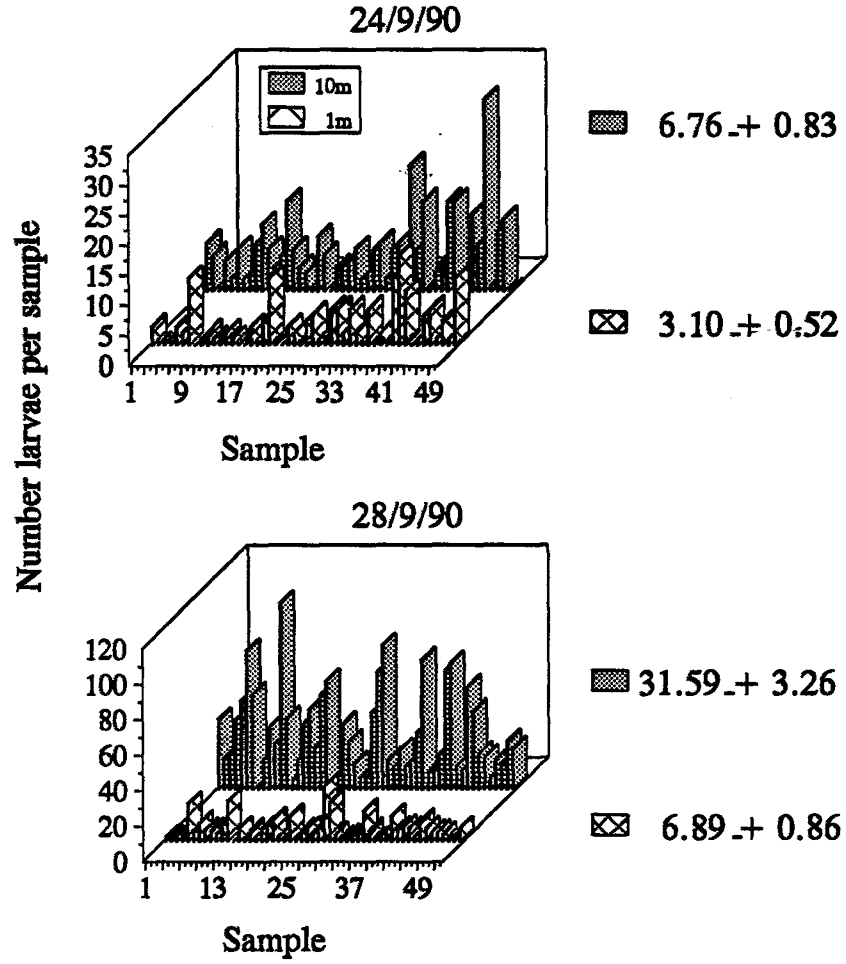


Figure 2.9: The number of larvae caught in vertical hauls of the uppermost metre of the water column and the entire ten metre depth of the water column, at each of the sampling stations on grid 1, on the 24 and 28 September 1990.

Table 2.4: Mann-Whitney tests comparing the mean number of larvae in the top metre of the water column and the mean number of larvae in ten metres of water. *Z* is the test statistic and *P* is the two-tailed probability of equalling or exceeding the critical value of *Z*.

Date	Group	*n*	Average rank	*Z*	*P*
24/9/90	1 metre	50	38.7100	4.0836	<0.0001
	10 metre	50	62.2900		
28/9/90	1 metre	53	32.3868	7.0775	<0.0001
	10 metre	53	74.6132		

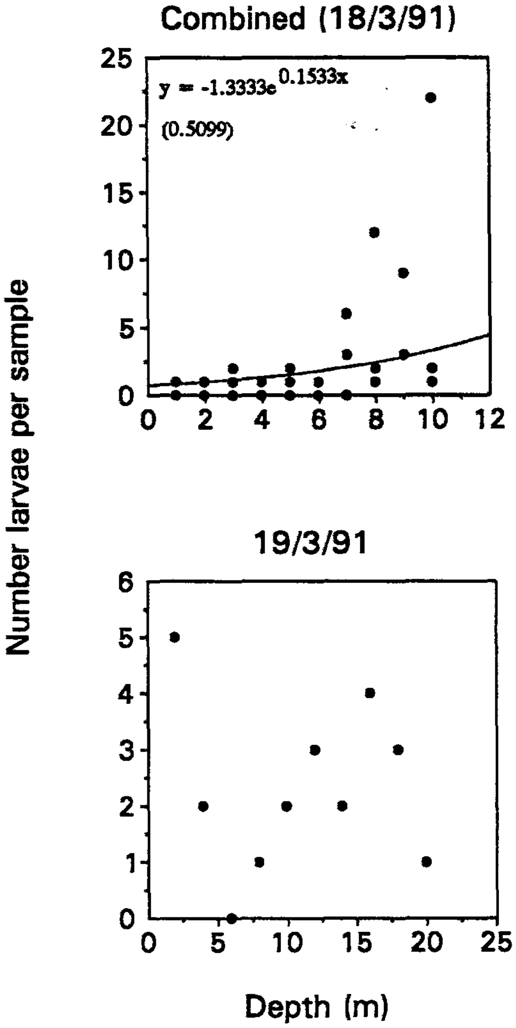


Figure 2.10: Regression of the number of larvae caught in a vertical haul (dependent variable) against the depth of the vertical haul (independent variable), on grid 1, 2 and 3, on the 18 and 19 March 1991. Regression lines are only indicated for relationships significant at the 0.05 level.

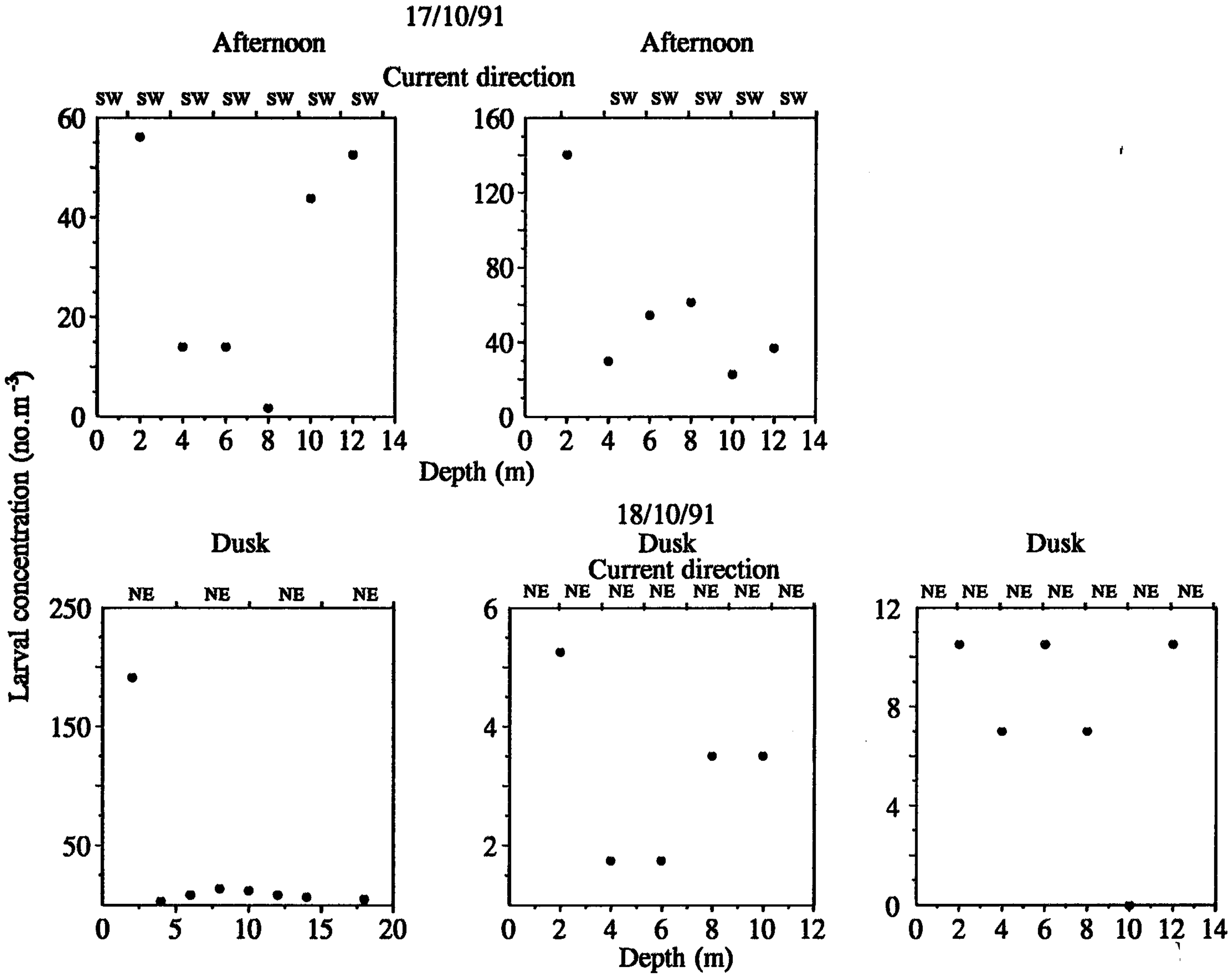


Figure 2.11: The concentration of larvae at discrete depth intervals at various times on the 16, 17 and 18 October 1991 at Fountain Rocks.

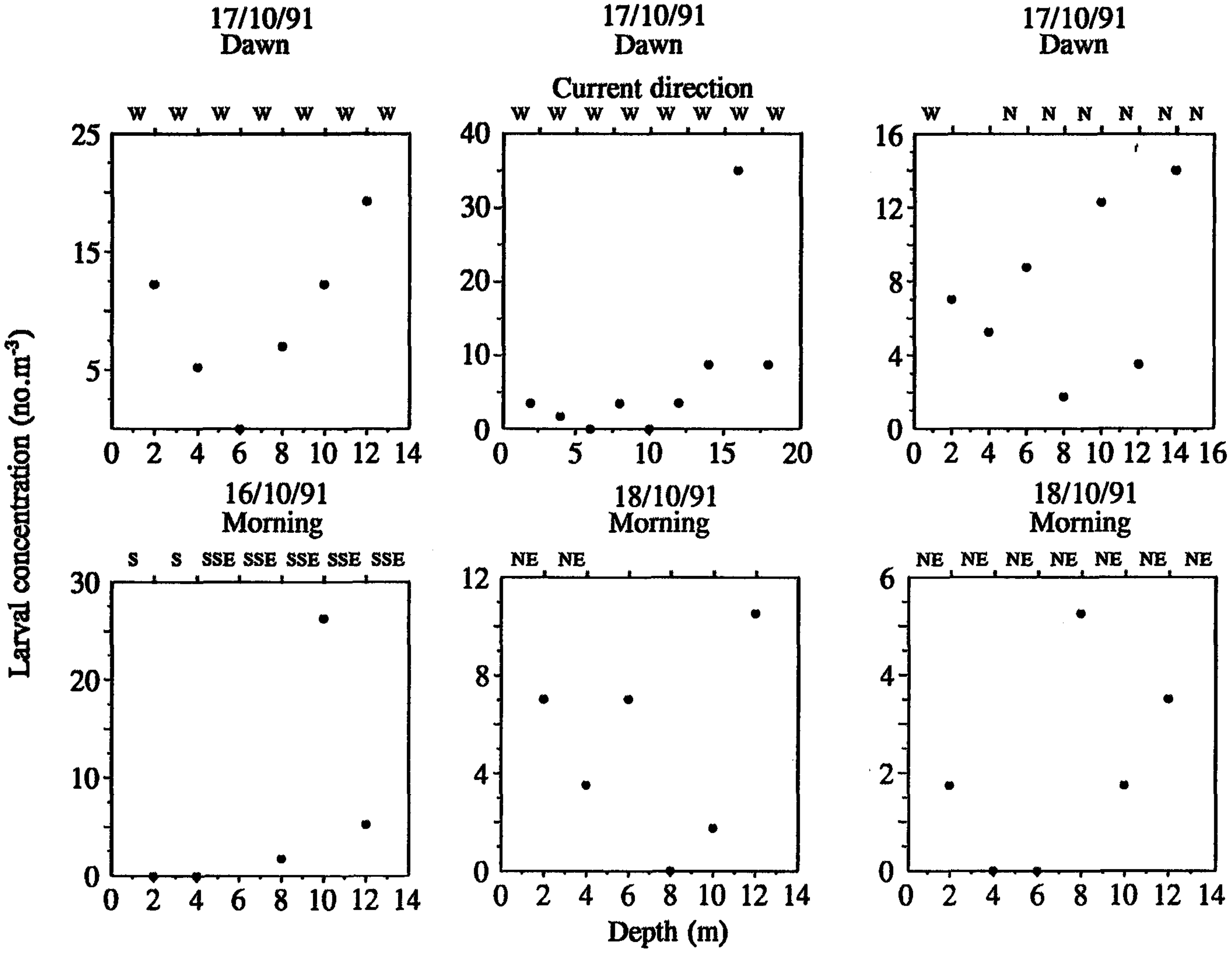


Figure 2.11 continued

Table 2.5: Results of Kolgomorov-Smirnov tests comparing the observed and expected concentrations at discrete depths on each sampling occasion.

Date	Time	Distance statistic (DN)	*P*
16/10/91	Morning	0.8	0.0815
17/10/91	Dawn	0.5	0.4413
17/10/91	Dawn	0.7	0.0366
17/10/91	Dawn	0.6	0.2032
17/10/91	Afternoon	0.5	0.4413
17/10/91	Afternoon	0.7	0.1389
18/10/91	Morning	0.5	0.4413
18/10/91	Morning	0.7	0.1389
18/10/91	Dusk	0.5	0.4413
18/10/91	Dusk	0.9	0.0044
18/10/91	Dusk	0.6	0.3291

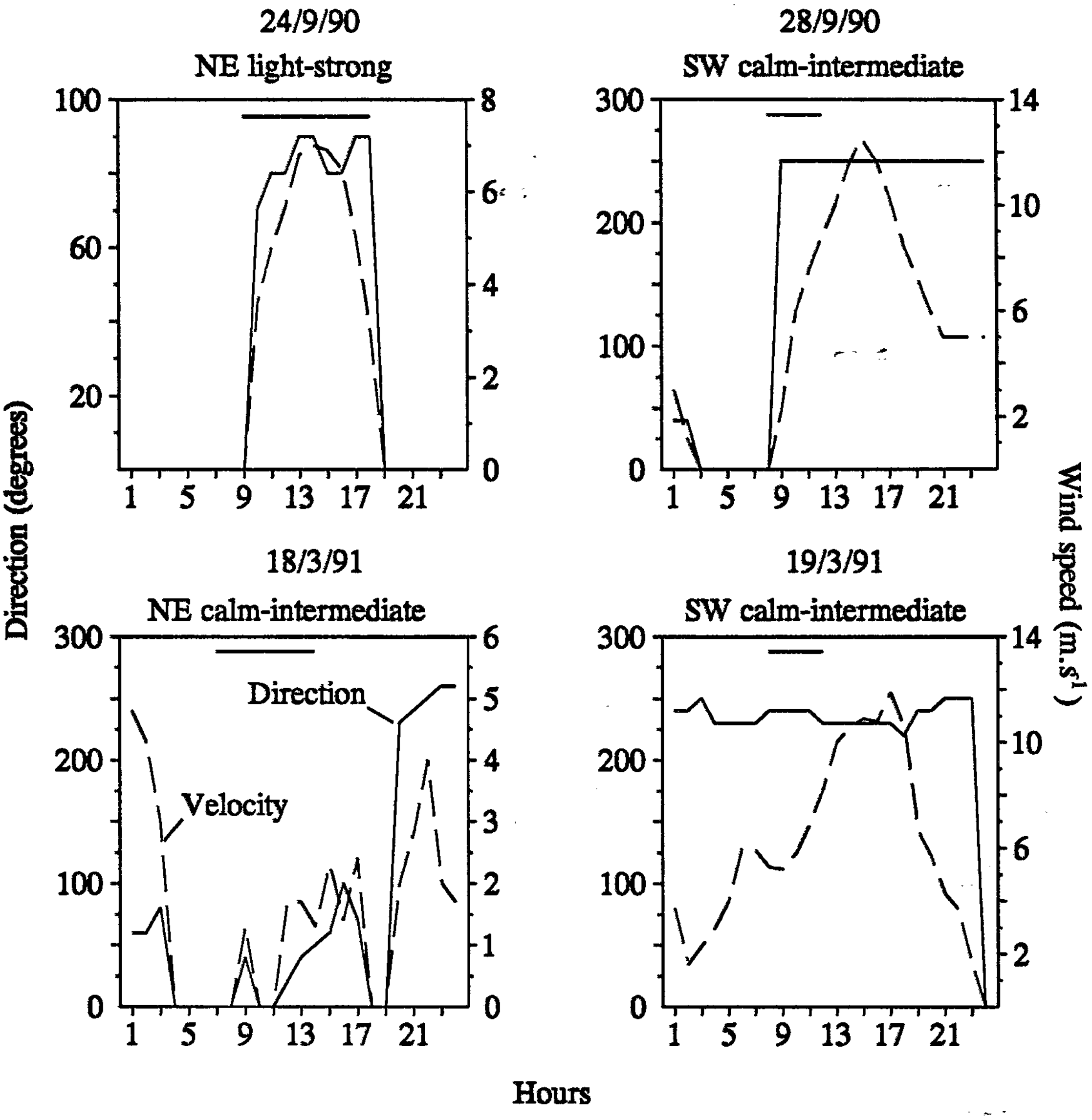
17 and 18 October larval concentrations recorded after noon were far higher than in the morning (Fig. 2.11). Although this may be related to offshore-onshore migration, this is unlikely since high larval concentrations were not recorded at all sites after noon (Fig. 2.11) and were recorded on plankton grids in the morning at Kenton (Fig. 2.7b). This again suggests that the observed larval distribution was determined by patchiness rather than active larval migration. In general, these results show that larvae may be found at any depth in the water column, and that although there may occasionally be a high concentration patch of larvae at the surface or bottom, there is little persistent horizontal stratification.

During the sampling events at Fountain Rocks the current flow in the top four metres of the water column was occasionally different from the subsurface flow, but on the whole, flow was largely barotropic moving in the same direction at different depths (Fig. 2.11). Flow was barotropic during the sampling events at Kenton, but highly statistically significant regressions ($r=0.64$, $P<0.0025$; $r=0.76$, $P=0.01$) indicated current speed decreased linearly with increasing depth, on two of the six occasions this relationship was examined (Fig. 2.8). These results show that larvae at the surface may be transported faster and in a different direction to those near the bottom, but that this occurs infrequently.

The lack of persistent horizontal stratification of larvae or currents suggests that larval behaviour has little influence over larval dispersal in nearshore waters. Given this, it is reasonable to assume that the larval dispersal rate and direction is determined by current speed and direction, and that these can be used to estimate the larval dispersal range.

Larval dispersal range

The direction and velocity of winds recorded hourly at Port Elizabeth on each of the sampling days are shown in Figure 2.12, together with the strength and direction of wind noted at the study site during sampling periods. The wind regime recorded at Port Elizabeth was similar to that observed at Kenton and Fountain Rocks during sampling, although there was a slight difference in the onset of different wind events or calm periods. For example on the 28 September 1990 a SW



24/9/90
NE light-strong

28/9/90
SW calm-intermediate

18/3/91
NE calm-intermediate

19/3/91
SW calm-intermediate

Figure 2.12: Hourly wind direction and speed recorded at Port Elizabeth on the 24 and 28 September 1990, and on the 18 and 19 March 1991. The duration of the sampling events at Kenton on each of these days are indicated by lines across the top of each of the graphs.

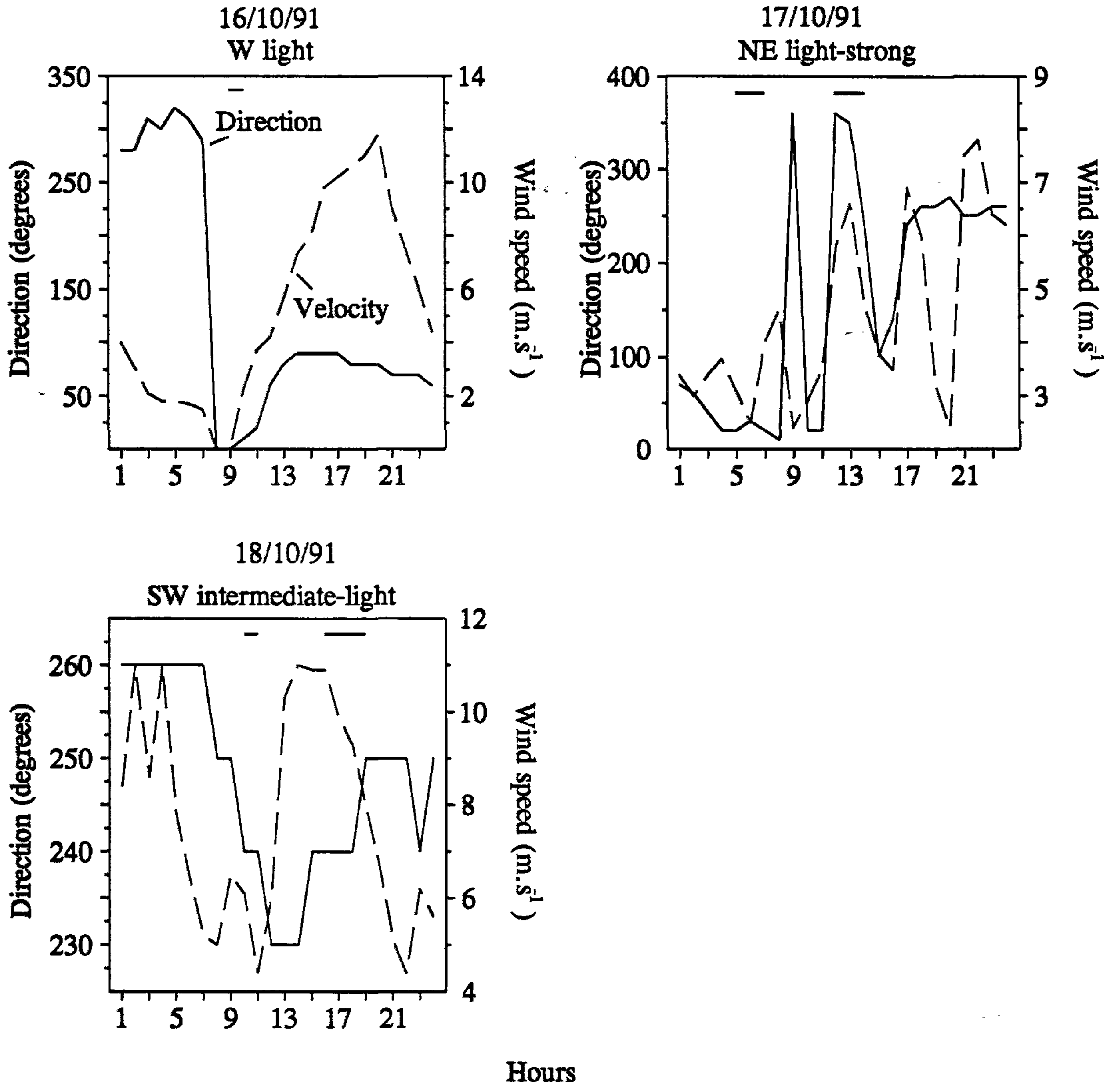


Figure 2.12 continued

wind of 4.9 km.h^{-1} was recorded during the study period at Port Elizabeth, whereas it was calm for most of this time at Kenton with the SW wind only starting to blow towards the end of the sampling period. Consequently, when the actual movements of larvae at a particular site are being monitored, it is best to record the wind and current conditions at that site, but the wind climate data recorded at Port Elizabeth are adequate when estimating the dispersal distance of larvae in the water over longer time periods, such as a month. A synopsis of the frequency of the winds in each month is presented in Table 2.6. The average speed (*s*) and direction of currents generated by these winds and the estimated dispersal proportionality constant (*a*) appear in Table 2.7-a. The distance travelled in each direction, calculated from the models $d=st$ (Table 2.8) and $d=a\surd t$ (Table 2.9), were used to estimate the total distance dispersed and the net range and direction of dispersal each month (Table 2.10-a). The first model generated estimates of the total distance travelled by larvae spawned during the months between March 1989 and June 1991, of 118 to 229 km (Table 2.10-a). However, variation in the frequency of winds which generated currents that caused the larvae to drift in opposite directions (E/W), resulted in marked variations in the net dispersal distance, which ranged from 54 to 180 km to the north of where they were originally spawned (Table 2.10-a). The dispersal range was greatest in winter (June - August) when north easterly winds were less frequent and current reversals less likely (Table 2.10-a). In addition, in winter, winds are light and variable (Schumann & Martin 1991) and north westerly winds may move larvae in the top half a metre of the water column offshore (Roberts 1989), although larvae below this are likely to move eastwards along the shore. Thus, in winter larvae are not only dispersed over longer distances but some may advect offshore into deeper waters and be dispersed by fast flowing coastal currents. The second model yielded estimates of the total distance dispersed which were considerably less (13 - 20 km; Table 2.10-a), as it accounts for various random effects, such as the entrapment of larvae in gullies or bays, which minimize the time larvae are carried linearly along the shore. In this instance, the net dispersal range of larvae dispersed passively by wind induced currents was only 8 to 14 km to the north, with an average of 12 km (Table 2.10-a).

These theoretical estimates, which assume that larval dispersal rate is equivalent to current

Table 2.6: The frequency (hours.month^{-1}) of winds blowing from the four principal wind directions in the Algoa Bay region, namely from the NE, SW, SE and NW, for the period 4/89 to 6/91.

Year	Month	Wind (hours.month^{-1})				
		NE	SW	SE	NW	Calms
1989	MAR.	199	317	35	98	95
	APR.	200	180	43	86	211
	MAY	122	195	13	151	263
	JUN.	61	150	18	239	252
	JUL.	43	156	18	327	200
	AUG.	167	169	30	246	132
	SEP.	163	201	33	235	88
	OCT.	213	229	85	144	73
	NOV.	248	227	93	54	98
	DEC.	153	396	33	84	78
1990	JAN.	280	263	89	35	77
	FEB.	196	79	244	63	90
	MAR.	283	176	73	30	182
	APR.	149	219	44	114	194
	MAY.	98	185	4	246	211
	JUN.	26	187	10	303	194
	JUL.	53	167	1	177	346
	AUG.	134	262	38	105	205
	SEP.	169	214	28	69	240
	OCT.	174	371	50	58	91
	NOV.	179	347	38	74	82
	DEC.	240	337	64	50	53
1991	JAN.	171	353	79	15	126
	FEB.	155	344	57	13	155
	MAR.	223	232	54	102	133
	APR.	140	184	26	157	213
	MAY	101	83	36	338	186
	JUN.	114	33	6	482	85

Table 2.7: The mean current speeds (s), dispersal rate (s'') and proportionality constants (a and a''), used in the calculations of the total distance dispersed and the net dispersal distance and direction of larvae in the water for 28 - 31 days.

			NE	SW	SE	SW	Calms
Roberts (1989)	s	$m.s^{-1}$	0.045	0.125	0.035	0.045	0.030
	s	$km.h^{-1}$	0.162	0.450	0.126	0.162	0.108
	a''		0.229	0.636	0.178	0.229	0.153
This study	s''	$m.s^{-1}$	0.119				
	s''	$km.h^{-1}$	0.428				
	a		0.611				

Table 2.8: The estimated distance ($d = st$) travelled by larvae in a westerly direction when the wind blows from the NE (W_{NE}) and in an easterly direction when the wind blows from the SW (E_{SW}), SE (E_{SE}) and NW (E_{NW}). The year and month in which spawning occurred between the 4/89 and 6/91 and the total distance moved east (T_E) and west (T_W) by the larvae for the month they remain in the plankton are shown.

Year	Month	Distance (km) moved E or W during each wind					Total distance (km)	
		W_{NE}	E_{SW}	E_{SE}	E_{SW}	E_{calms}	T_W	T_E
1989	MAR.	32	143	4	16	10	32	173
	APR.	32	81	5	14	23	32	123
	MAY	20	88	2	24	28	20	142
	JUN.	10	68	2	39	27	10	136
	JUL.	7	70	2	53	22	7	147
	AUG.	27	76	4	40	14	27	134
	SEP.	26	90	4	38	10	26	142
	OCT.	35	103	11	23	8	35	145
	NOV.	40	102	12	9	11	40	133
	DEC.	25	178	4	14	8	25	240
1990	JAN.	45	118	11	6	8	45	144
	FEB.	32	36	31	10	10	32	86
	MAR.	46	79	9	5	20	46	113
	APR.	24	99	6	18	21	24	144
	MAY	16	83	1	40	23	16	146
	JUN.	4	84	1	49	21	4	155
	JUL.	9	75	0	29	37	9	141
	AUG.	22	118	5	17	22	22	162
	SEP.	27	96	4	11	26	27	137
	OCT.	28	167	6	9	10	28	192
	NOV.	29	156	5	12	9	29	182
	DEC.	39	152	8	8	6	39	174
1991	JAN.	28	159	10	2	14	28	185
	FEB.	25	155	7	2	17	25	181
	MAR.	36	104	7	17	14	36	142
	APR.	23	83	3	25	23	23	135
	MAY	16	37	5	55	20	16	117
	JUN.	18	15	1	78	9	18	103

Table 2.9: The estimated distance ($d = a\surd t$) travelled by larvae in a westerly direction when the wind blows from the NE (W_{NE}) and in a easterly direction when the wind blows from the SW (E_{SW}), SE (E_{SE}) and NW (E_{NW}). The year and month in which spawning occurred between the 4/89 and 6/91 and the total distance moved east (T_E) and west (T_W) by the larvae for the month they remain in the plankton are shown.

Year	Month	Distance (km) moved E and W during each wind					Total distance (km)	
		W_{NE}	E_{SW}	E_{SE}	E_{SW}	E_{calms}	T_W	T_E
1989	MAR.	3	11	1	2	1	3	16
	APR.	3	9	1	2	2	3	14
	MAY	3	9	1	3	2	33	15
	JUN.	2	8	1	4	2	2	15
	JUL.	2	8	1	4	2	2	15
	AUG.	3	8	1	4	2	3	15
	SEP.	3	9	1	4	1	3	15
	OCT.	3	10	2	3	1	3	15
	NOV.	4	10	2	2	2	4	15
	DEC.	3	13	1	2	1	3	17
1990	JAN.	4	10	2	1	1	4	15
	FEB.	3	6	3	2	1	3	12
	MAR.	4	8	2	1	2	4	13
	APR.	3	9	1	2	2	3	15
	MAY	2	9	0	4	2	2	15
	JUN.	1	9	1	4	2	1	15
	JUL.	2	8	0	3	3	2	14
	AUG.	3	10	1	2	2	3	16
	SEP.	3	9	1	2	2	3	15
	OCT.	3	12	1	2	1	3	17
	NOV.	3	12	1	2	1	3	16
	DEC.	4	12	1	2	1	4	16
1991	JAN.	3	12	2	1	2	3	16
	FEB.	3	12	1	1	2	3	16
	MAR.	3	10	1	2	2	3	15
	APR.	3	9	1	3	2	3	15
	MAY	2	6	1	4	2	2	13
	JUN.	2	4	0	5	1	2	11

Table 2.10: The total distance dispersed ($T_E + T_W$) and the net dispersal range and direction ($T_E - T_W$) of larvae over a period of 28-31 days, estimated for each month in which spawning occurred between the 3/89 and the 6/91. The results of the simulations for $d = st$ and $d = a\sqrt{t}$ where (a) the current speed s and the proportionality constant a'' were estimated from Roberts (1989) for each wind direction, and (b) the mean dispersal rate s'' and proportionality constant a were calculated from longshore movement of high concentration patches of larvae (this study).

Year	Month	(a)				(b)			
		$d = st$		$d = a\sqrt{t}$		$d = st$		$d = a\sqrt{t}$	
		Total	Net	Total	Net	Total	Net	Total	Net
1989	MAR.	205	141 E	19	13 E	88	41 E	35	18 E
	APR.	156	91 E	17	11 E	86	38 E	35	18 E
	MAY	162	122 E	17	12 E	88	59 E	35	21 E
	JUN.	146	126 E	16	13 E	86	71 E	34	24 E
	JUL.	154	140 E	17	14 E	88	78 E	34	26 E
	AUG.	161	107 E	18	12 E	88	49 E	36	20 E
	SEP.	169	116 E	18	12 E	86	47 E	35	19 E
	OCT.	179	110 E	19	12 E	88	38 E	36	19 E
	NOV.	173	93 E	18	11 E	86	27 E	35	16 E
	DEC.	229	180 E	20	14 E	88	52 E	34	19 E
1990	JAN.	189	98 E	19	11 E	88	22 E	35	14 E
	FEB.	118	54 E	15	8 E	80	33 E	34	17 E
	MAR.	159	67 E	17	9 E	88	21 E	35	15 E
	APR.	168	119 E	18	12 E	86	50 E	36	21 E
	MAY	162	131 E	17	13 E	88	65 E	34	22 E
	JUN.	160	151 E	17	14 E	86	79 E	33	26 E
	JUL.	150	133 E	16	13 E	88	76 E	32	24 E
	AUG.	184	140 E	19	13 E	88	57 E	36	22 E
	SEP.	164	110 E	17	12 E	86	45 E	35	19 E
	OCT.	221	164 E	20	14 E	88	47 E	35	19 E
	NOV	211	153 E	19	13 E	86	43 E	34	18 E
	DEC.	212	135 E	19	12 E	88	31 E	34	15 E
1991	JAN.	213	157 E	19	13 E	88	48 E	34	18 E
	FEB.	206	156 E	19	13 E	86	49 E	33	18 E
	MAR.	178	106 E	18	12 E	88	35 E	36	18 E
	APR.	157	112 E	17	12 E	86	52 E	35	21 E
	MAY	133	100 E	15	11 E	88	64 E	35	23 E
	JUN.	121	84 E	13	8 E	86	58 E	31	18 E
Range		118 - 229	54 - 180 E	13 - 20	8 - 14 E	86 - 88	21 - 79 E	31 - 36	14 - 26 E
Mean		173	121 E	18	12 E	87	49 E	35	20 E

speed, were compared to those obtained using experimentally determined values of the mean rate of longshore larval dispersal (*s"*) and the square of the mean distance moved per unit time (*a"*) by high concentration patches of larvae (Table 2.7-b). The first model generated estimates of 86 - 88 km for the total distance dispersed, and 21 - 79 km to the north for the net dispersal range, which was shorter than the theoretical distance but fell within the lower part of this range (Table 2.10). The second model generated estimates of 30 to 36 km for the total distance dispersed and 16 to 28 km to the north for the net dispersal range, with an average of 21 km, which was slightly further than the theoretical estimate (Table 2.10).

In general although larvae may potentially travel up to 229 km in a month, the effect of wind reversals on currents, limits the net dispersal range considerably. In addition the dispersal range may be considerably reduced by topographical and hydrological features of the nearshore environment which trap larvae and restrict their movements.

Discussion

The microscopic size and dilution of planktonic larvae as they become dispersed in the plankton has complicated investigations of dispersal, but there have been major advances in this field during the last eight years.

Today it is known that larvae of coastal invertebrates are advected offshore into deeper waters over the continental shelf, but the abundance declines with distance offshore (Thorson 1950, Marliave 1986, Le Fevre & Bourget 1991), and most are probably found in the shallow nearshore zone inside the 30 m isobath. Larvae advected offshore, such as crab megalopae, barnacle cyprids as well as many other species of zooplankton and fish, accumulate in surface slicks associated with the convergence zones of internal waves, oceanic and tidal fronts, and they may well be transported shorewards by tidally forced internal waves (Shanks 1983, 1985 & 1986a, Shanks & Wright 1987, Kingsford & Choat 1986, Clancy & Epifanio 1989). Alternatively, in deep coastal and oceanic waters, diurnal and ontogenetic vertical migration may cause larvae to be carried offshore by surface currents and inshore by shoreward bottom currents (Rimmer & Phillips 1979, Scheltema 1975, Shanks 1986b, Epifanio *et al.* 1988 & 1989, Lipcius *et al.* 1990).

The present study shows that once larvae enter the nearshore waters in and adjacent to the surf zone, those at the surface may be transported faster and in a different direction to those on the bottom. However, this occurs infrequently, as there is no persistent horizontal stratification of larvae or currents, since turbulence created by wind and wave action mixes the water column (Beckley 1983, Goschen & Schumann 1988, Talbot & Bate 1988a&c, McShane *et al.* 1988, Denny & Shibata 1989, Denny *et al.* 1992). Thus, even if planktonic organisms are able to swim strongly enough, or have some sort of adaptive behavior which allows them to migrate vertically in the turbulent surf and nearshore zones (Talbot & Bate 1988a, Webb & Wooldridge 1990), this has little effect on the dispersal of larvae drifting in the water for long periods. Results also showed that in shallow areas (3-18 m) close to shore, concentrated patches of larvae were passively transported by wind generated currents (Fig. 2.7), which generally flow along isobaths parallel to the coast (De Wolf 1973, Black 1988, Goschen & Schumann 1988, McShane *et al.* 1988, Sammarco & Andrews 1988, Tanaka *et al.* 1986 and references therein, Roberts 1989, Hirota 1990, this study). Friction and wave action reduce nearshore current speeds (0 to 0.17 $m.s^{-1}$) and changes in wind direction result in current reversals, which reduces the dispersal range of larvae (McShane *et al.* 1988, Sammarco & Andrews 1988, Roberts 1989, Fig. 2.7 & 2.8). Furthermore, wind- and gradient-driven flow patterns are modified by irregular reef or shore topography which create localised oceanographic features such as jets, eddies and fronts which may retain pre-settlement fishes and zooplankton near reefs or within bays, thereby limiting their dispersal (Pearson 1970, Levin 1983, Ebert & Russel 1988, McShane *et al.* 1988, Sammarco & Andrews 1988, Kingsford *et al.* 1991). In the present study two models were used to generate estimates of the dispersal range of larvae passively dispersed by wind generated currents. Results showed that current reversals can reduce the dispersal distance of larvae in the open water column away from any topographical affects, by as much as 76% from 229 km to 54 km, and topographical effects can reduce this by a further 19% to 13 km. Therefore, it can be concluded from the results of this study that wind and topography are the primary determinants of the distribution and abundance of larvae close to shore, as larvae have little behavioural control over their passive dispersal by wind generated currents.

This conclusion agrees with the predictions of hydrodynamic models which use measurements of wind-, tide- and gradient-driven flows, to model the complex circulation patterns around shallow reefs, and to simulate dispersal of larvae in these environments (Black & Gay 1987, Black 1988, Black & Moran 1991, McShane *et al.* 1988, Sammarco & Andrews 1988). The models predict that areas with low flushing rates will have a greater abundance of larvae and settlers than areas with high flushing rates, and, at least in one instance, this has been verified with field data on the distribution and abundance of juveniles (Black & Moran 1991). For example, small scale topographical features such as surge channels or gullies (~10 to 12 m holding between 3.5 to 45 m^3 of water) are well mixed within themselves, but current speeds are low (~0.06 $m.s^{-1}$) and currents oscillate back and forth, thereby minimising net flow (McShane *et al.* 1988, Sammarco & Andrews 1988, Denny *et al.* 1992). McShane *et al.* (1988) predicted that haliotid larvae trapped in these channels would move no more than 500 m in their 3 to 7 day planktonic phase, and suggested that these larvae were able to resist advection away from the protection of the reef. Certainly high concentrations of planktonic organisms such as haliotid larvae and mysids have been found under rock crevices and overhangs, while comparatively few have been found in the open water column (Webb & Wooldridge 1990, McShane *et al.* 1988). McShane *et al.* (1988) also predicted that those larvae which were advected away from the protection of the reef by rip currents, would be passively dispersed by wind generated currents over distances of up to 12 km. Consequently hydrodynamic simulations of dispersal and the results of the present study, imply that in areas with irregular topography a larva may be dispersed over a short or long distance, depending on where it is produced or released. As discussed in Chapter 1, there is increasing evidence to suggest that the dispersal range of most planktonic larvae is limited, and this may be attributed to the type of topographical effects on circulation patterns described in this study. The following chapter examines the spread of an alien mussel after its introduction to the south coast, in order to test the hypothesis that topography limits the dispersal range of the majority of larvae while wind disperses a smaller proportion of larvae over considerably longer distances.

In conclusion, hydrodynamic models can be used to predict larval dispersal and settlement, and may therefore be useful for management of pest species (Black & Moran 1991) or resources with spatially variable settlement patterns. However, in contrast to shallow offshore reefs, very little is known of the circulation patterns or the distribution and abundance of larvae around rocky shores. In view of this, future studies should focus on generating hydrodynamic models simulating dispersal around rocky shores, and testing the predictions of these models with *in situ* measurements of the distribution and abundance of larvae, as was described in this study.

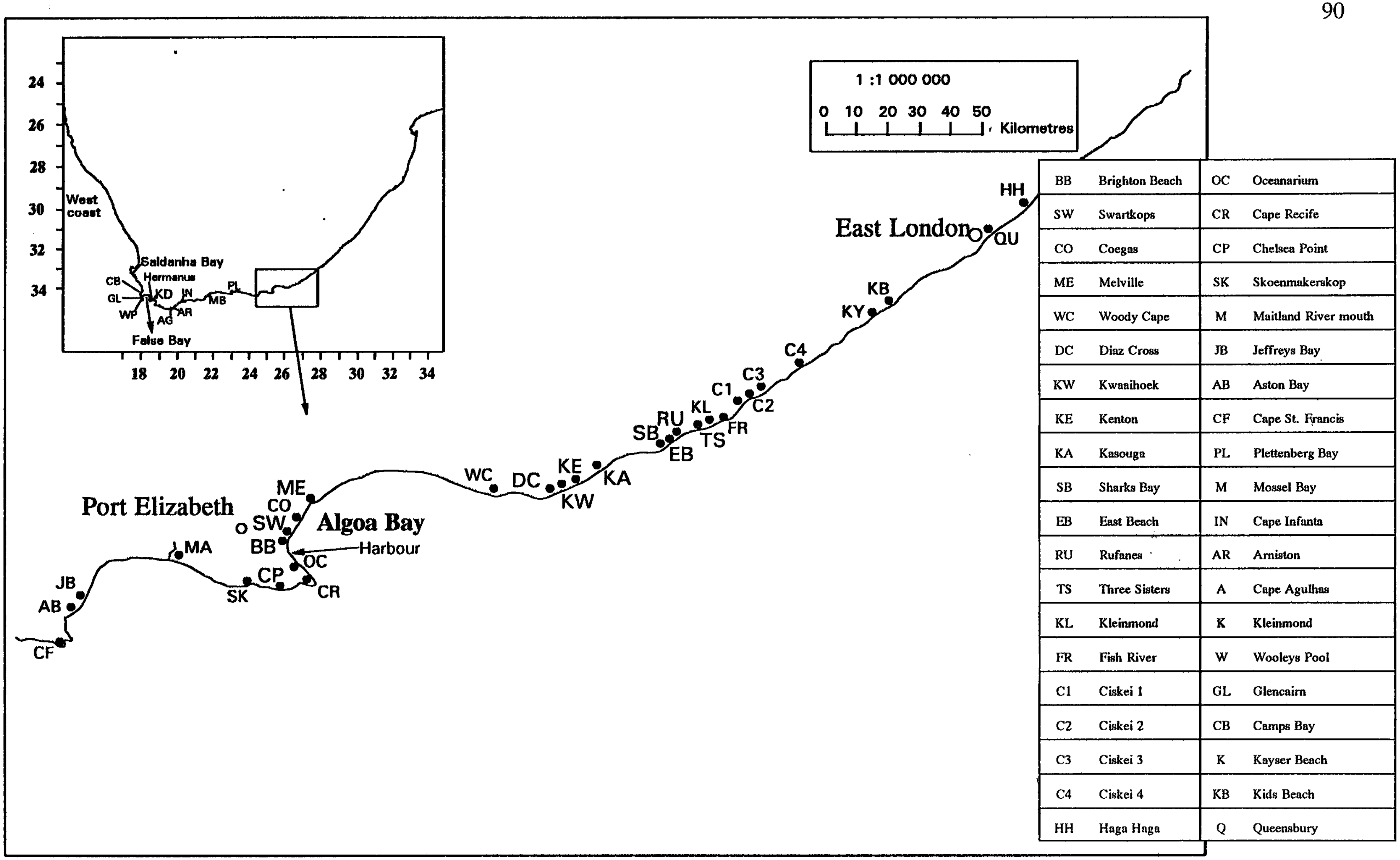
CHAPTER 3

THE INTRODUCTION, SPREAD AND DISTRIBUTION OF THE MEDITERRANEAN MUSSEL, MYTILUS GALLOPROVINCIALIS, ALONG SOUTH AFRICAN SHORES

Introduction

The exotic Mediterranean mussel, *Mytilus galloprovincialis*, was introduced to Port Elizabeth harbour in Algoa Bay (Fig. 3.1), for mariculture purposes in 1988 (van Erkom Schurink 1991). *M. galloprovincialis* is thought to be a recent derivative of the biologically similar European blue mussel *Mytilus edulis* (Barsotti & Meluzzi 1968). Today this highly invasive bivalve has successfully invaded many regions, and its distribution now ranges from the British Isles to the Atlantic coast of France and the Mediterranean Sea. It also occurs in several disjunct areas, including, Japan (Wilkins *et al.* 1983), Hong Kong (Lee & Morton 1985) and California (McDonald and Koehn 1988), where it was introduced as a result of human activity. *M. galloprovincialis* spread rapidly after being introduced to the west coast of South Africa, probably in the late seventies (Grant & Cherry 1985), and by 1990 was distributed between Luderitz on the west coast to Hermanus on the south coast (Fig. 3.1, van Erkom Schurink 1991). Since its introduction to the west coast, *M. galloprovincialis* has proven to be a highly invasive, dominant competitor capable of altering community structure and displacing the indigenous west coast ribbed mussel *Aulacomya ater* and the limpet *Patella granularis* (van Erkom Schurink 1991, Hockey & van Erkom Schurink 1992). Therefore, there was a possibility that *M. galloprovincialis* would spread in Algoa Bay, changing communities and displacing the indigenous South African mussels *Perna perna* and *Choromytilus meridionalis*.

On the west coast of South Africa *M. galloprovincialis* forms extensive multi-layered beds in the intertidal zone of exposed rocky shores. Part of the reason for its success is undoubtedly related to its high productivity, growth rate, reproductive output, and recruitment intensity (van Erkom Schurink 1991). Furthermore, *M. galloprovincialis* spreads via its planktonic larval phase which allows it to colonise new areas rapidly. It was shown in Chapters 1 and 2, that in the Algoa Bay region, larvae are passively transported along the coast by wind-driven nearshore currents, but it was suggested that nearshore topography may limit their dispersal considerably, resulting in a link



BB	Brighton Beach	OC	Oceanarium
SW	Swartkops	CR	Cape Recife
CO	Coegas	CP	Chelsea Point
ME	Melville	SK	Skoenmakerskop
WC	Woody Cape	M	Maitland River mouth
DC	Diaz Cross	JB	Jeffreys Bay
KW	Kwaaihoek	AB	Aston Bay
KE	Kenton	CF	Cape St. Francis
KA	Kasouga	PL	Plettenberg Bay
SB	Sharks Bay	M	Mossel Bay
EB	East Beach	IN	Cape Infanta
RU	Rufanes	AR	Arniston
TS	Three Sisters	A	Cape Agulhas
KL	Kleinmond	K	Kleinmond
FR	Fish River	W	Wooleys Pool
C1	Ciskei 1	GL	Glencairn
C2	Ciskei 2	CB	Camps Bay
C3	Ciskei 3	K	Kayser Beach
C4	Ciskei 4	KB	Kids Beach
HH	Haga Haga	Q	Queensbury

Figure 3.1: Map showing the sites along the South African coastline surveyed for *Mytilus galloprovincialis* between 1989 and 1992, together with other areas mentioned in the text.

between local patterns of spawning and settlement. If larvae which survive to recruit into the adult population are transported only short distances from where they are spawned, the density of *M. galloprovincialis* should decrease significantly with increasing distance from its point of introduction (Port Elizabeth harbour). However, while the majority of larvae may recruit locally, a small fraction may recruit further away, and the dispersal range of these larvae determines the rate at which *M. galloprovincialis* will invade the Algoa Bay region. Larvae carried offshore to the edge of the continental shelf will be transported rapidly south, by the Agulhas current. In contrast, those larvae remaining close to shore will be tranported more slowly along the coast by wind-driven currents, which flow predominantly eastwards but occasionally westwards.

The purpose of this study was to investigate the dispersal and spread of *M. galloprovincialis* in the Algoa Bay region, and to assess the possible impact of this invasion on indigenous mussel populations.

Methods

Study sites and sampling periodicity

Rocky outcrops to the east and west of Port Elizabeth harbour, between Cape St. Francis and East London, were examined annually for *M. galloprovincialis* from 1989 to 1992 (Fig. 3.1). The surveys included several sites beyond the eastern and western most points of the distribution of *M. galloprovincialis*. In 1992 the search for *M. galloprovincialis* was extended to cover the area between Camps Bay on the west coast and Haga Haga on the east coast of South Africa, including several of the original sampling sites in the Algoa Bay region (Fig. 3.1).

Sampling technique

Preliminary observations indicated that different mussel species dominated sand-covered rocks low on the shore (<0.68 m above mean low water spring tide level - MLWS) and rocks raised well above the sand level (>1.51 m above MLWS), while intermediate areas (0.66-1.51 m above MLWS) appeared to have a relatively mixed mussel fauna. Not all these habitats were necessarily found at a site. After searching visually for *M. galloprovincialis*, three quadrats of 12.5 x 25 cm were placed randomly in each habitat present, and cleared of all mussels.

The 1989 survey showed that the distribution of *M. galloprovincialis* was extremely patchy, and that it was not found on sand-covered rocks low on the shore (zone 1). Thus, in 1990 and 1991, the number of *M. galloprovincialis* in ten random quadrats (12.5 x 25 cm) on sand-free rocks was recorded. If the rocky outcrops stretched along the shore for more than 30 m, these samples were repeated three times, with a distance of at least 30 m between them.

In the 1992 survey, the vertical zonation pattern of *M. galloprovincialis* in intermediate and sand-free habitats was examined in greater detail. The mussel bed was divided into three basic zones, namely: a coralline or mixed algal - mussel zone (0.68-1.51 m above MLWS, zone 2), a pure mussel zone above this (1.51-1.73 m above MLWS, zone 3), and at the top of the mussel bed a barnacle - mussel zone (>1.73 m above MLWS, zone 4). The zones (2,3 and/or 4) present at each sampling site were identified, and the width and height of the zone above the low water mark were recorded. In each zone three quadrats of 12.5 x 12.5 cm were cleared of all mussels and the total percentage cover of mussels, the relative proportion of each species (%) and the number of *M. galloprovincialis* were recorded in 10 random quadrats of 25 x 25 cm. Samples were not removed from the shore at some sites, as there was a limited amount of time available in which to complete sampling.

All samples removed from the rocks were sorted into different mussel species, and the number of recruits (<20 mm) and adults (>20 mm) of each species recorded.

Each year the total density of *M. galloprovincialis* was regressed against the distance east and west of the point of introduction, and the dispersal range of larvae to the east and west was estimated from the regression curves fitted to the data. The rate of spread was calculated from the change in the distribution of *M. galloprovincialis* each year. The density and relative proportion of *M. galloprovincialis*, *Perna perna*, *Choromytilus meridionalis* and *Aulacomya ater* in zones 1, 2, 3 and

4 were calculated, to compare the habitat preferences and vertical distribution of the Mediterranean and indigenous South African mussels.

Results

Dispersal range and invasion rate

Regression analysis showed that the density of *Mytilus galloprovincialis* declined significantly ($P<0.01$) with increasing distance east of the point of introduction (Fig. 3.2a). Curves fitted to these data show that, during the four years of this study, about 76% were found within 4 or 5 km of the parent population, about 90% within 12 to 20 km, and none further than 166 km to the east of the harbour (Fig. 3.2a). In contrast, the maximum distance spread west of the harbour was only 29 km, and densities were low with little difference between sites (Fig. 3.2b).

The eastward limit of the distribution of *M.galloprovincialis* the first year after its introduction (1989), lay between Woody Cape and Diaz Cross, 70-97 km from the harbour. By 1990 this had increased by about 56 km and lay between Three Sisters and Kleinmond (KL). It increased by 13 km to Fish River by 1991, but *M. galloprovincialis* had spread no further by the time the 1992 survey took place (Fig. 3.3). Thus the rate of spread to the east declined steadily after the first year, giving an average rate of 42 $km.y^{-1}$ (Table 3.1). Both the intensity (density) and rate of spread were lower to the west of the harbour (Fig. 3.3, Table 3.1). The westward limit in 1989 was about 16 km from the harbour at Cape Recife, a further 12 km west at Chelsea Point in 1990 and a further 29 km west at Maitland River Mouth in 1991. It is possible that the long stretch of beach separating Maitland River Mouth and the next site, Aston Bay, prevented *M. galloprovincialis* from recruiting further west in 1991. Thus by 1991, three years after its introduction to Algoa Bay, *M. galloprovincialis* had spread along a total (east and west) of 223km of coastline.

By 1992 *M.galloprovincialis* encroaching eastwards from populations originally introduced

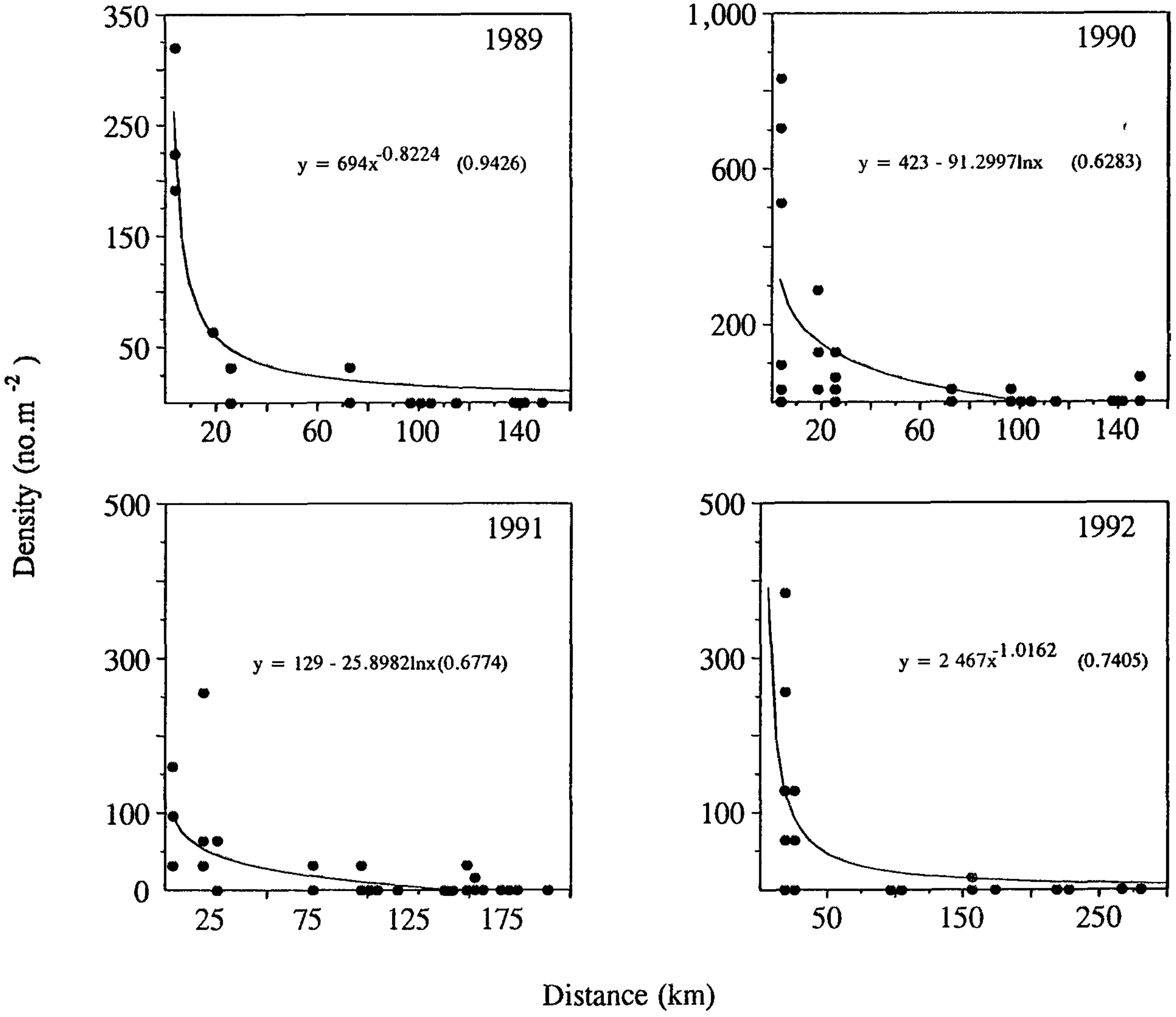


Figure 3.2a: Regressions of the density of *Mytilus galloprovincialis* against the distance east or of Port Elizabeth harbour in 1989, 1990, 1991 and 1992.

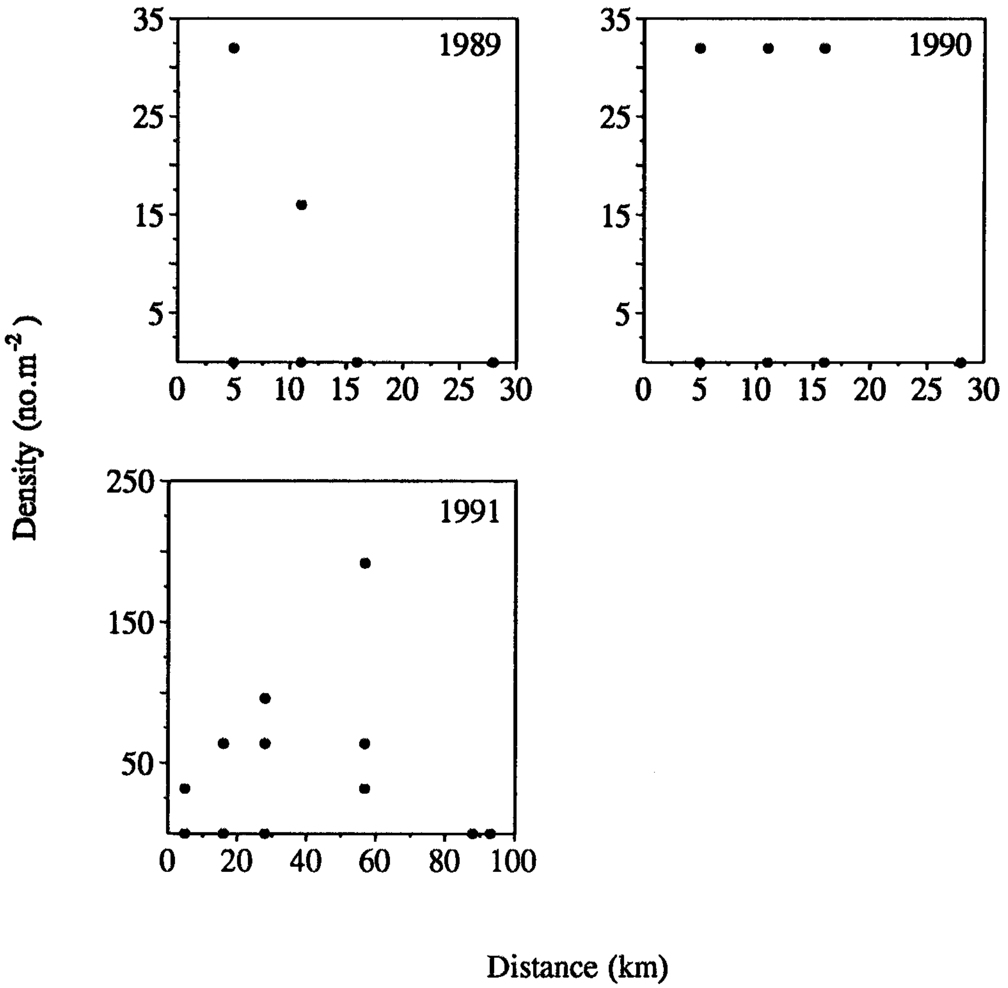


Figure 3.2b: The density of *Mytilus galloprovincialis* at sites west of Port Elizabeth harbour in 1989, 1990 and 1991.

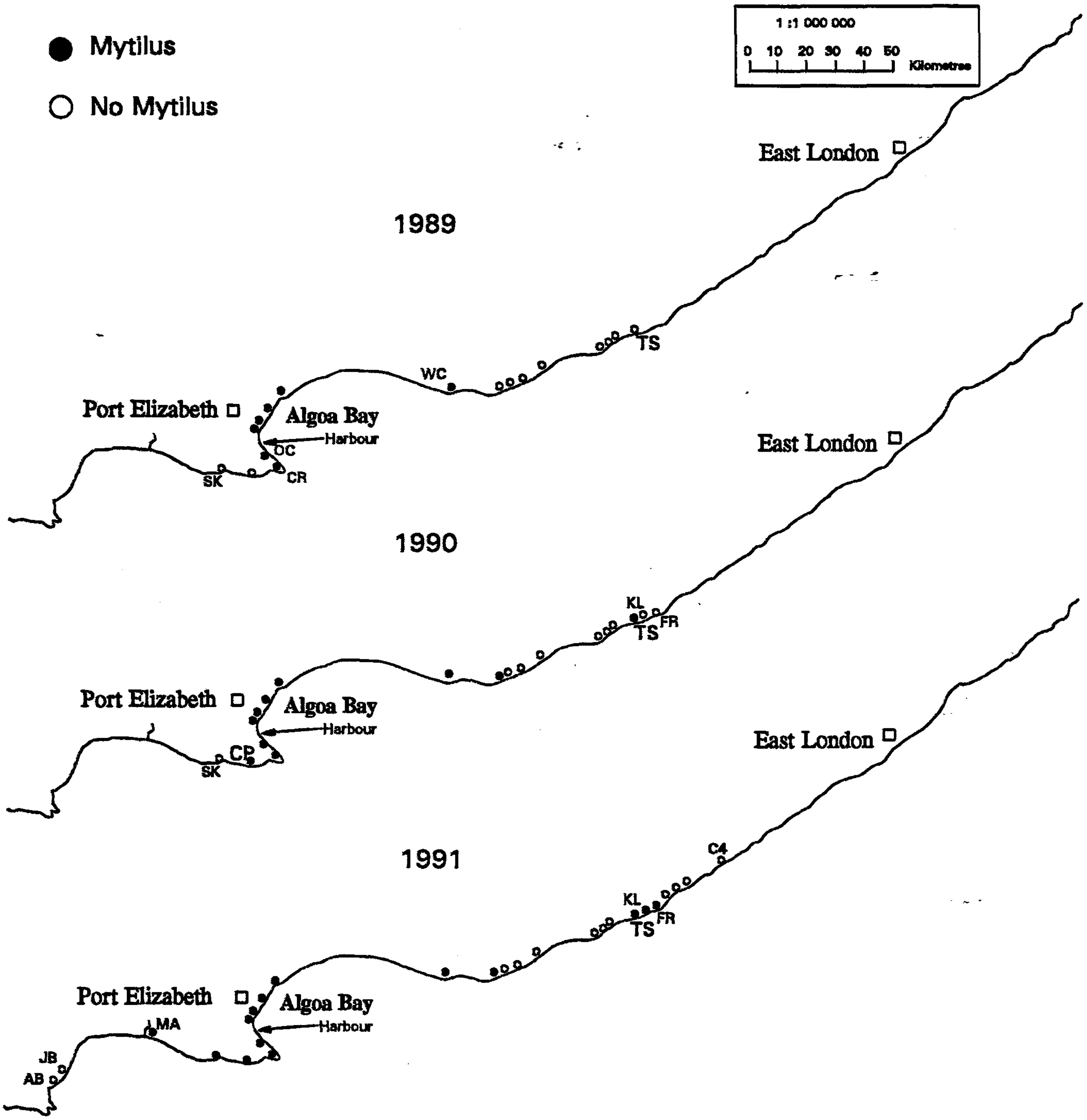


Figure 3.3: The distribution of *Mytilus galloprovincialis* in the region of Algoa Bay in 1989, 1990 and 1991.

Table 3.1: The yearly increase in the distribution range and the mean invasion rate of *Mytilus galloprovincialis* to the east (a) and west (b) of Port Elizabeth Harbour in Algoa Bay, where the alien was first introduced in 1988.

(a) East	1988	1989	1990	1991	1992
Distance increment (km)	0	97	56	13	0
Mean invasion rate (km.y^{-1})	Introduced	97	77	55	42
(b) West					
Distance increment (km)	0	16	12	29	-
Mean invasion rate (km.y^{-1})	Introduced	16	14	19	-

to the west coast of South Africa, had reached Cape St. Francis, a site just west of Algoa Bay, giving the Mediterranean mussel a more or less continuous distribution along the south coast from Cape Point to Fish River (Fig. 3.4). This continuous distribution made it difficult to determine the westward limit of larvae spawned from Algoa Bay populations in 1992. However, the absence of *M. galloprovincialis* between Maitland River Mouth and Cape St. Francis, suggests that those at Cape St. Francis and sites further west originally arose from west coast populations, while those at Maitland River Mouth and sites further east originally arose from Algoa Bay populations. Regression analysis of the 1992 survey data for sites between the harbour and Camps Bay on the west coast, indicated that the density of *M. galloprovincialis* increased significantly west of Kleinmond (KD), and was highest on the west coast, where it had been introduced about 15 years earlier (Fig. 3.5).

Distribution and zonation patterns

Four species of mussels were identified during the course of the four surveys, of these, *Choromytilus meridionalis* and *Mytilus galloprovincialis* were found on the west and south coast, *Aulacomya ater* was found on the west coast and in False Bay on the south coast, while *Perna perna* was only found on the south coast. Superimposed upon this geographical trend, was a variation in the species composition of mussel assemblages in different habitats. Surveys showed that, on the south coast at Maitland River Mouth and sites further to the east, rocks less than 0.68 m above MLWS permanently covered and scoured by sand, were dominated by *C. meridionalis*, with a small proportion of *P. perna* present, but no *M. galloprovincialis* (Fig. 3.6a). At the interface of beaches and rocky shores, or on beaches subject to marked seasonal fluctuations in sand level, low profile rocks (0.68m to 1.51 m above MLWS) were scoured and occasionally buried in sand. These rocks had a mixed mussel fauna consisting of varying proportions of *P. perna* and *C. meridionalis*, and a low percentage of *M. galloprovincialis* (Fig. 3.6b). Sand-free rocks (1.51 m above MLWS) were dominated by *P. perna* with a small proportion of *M. galloprovincialis* but no adult *C. meridionalis* (Fig. 3.6c). During the 1992 survey, the same pattern was observed on rocks 1.51 m above MLWS

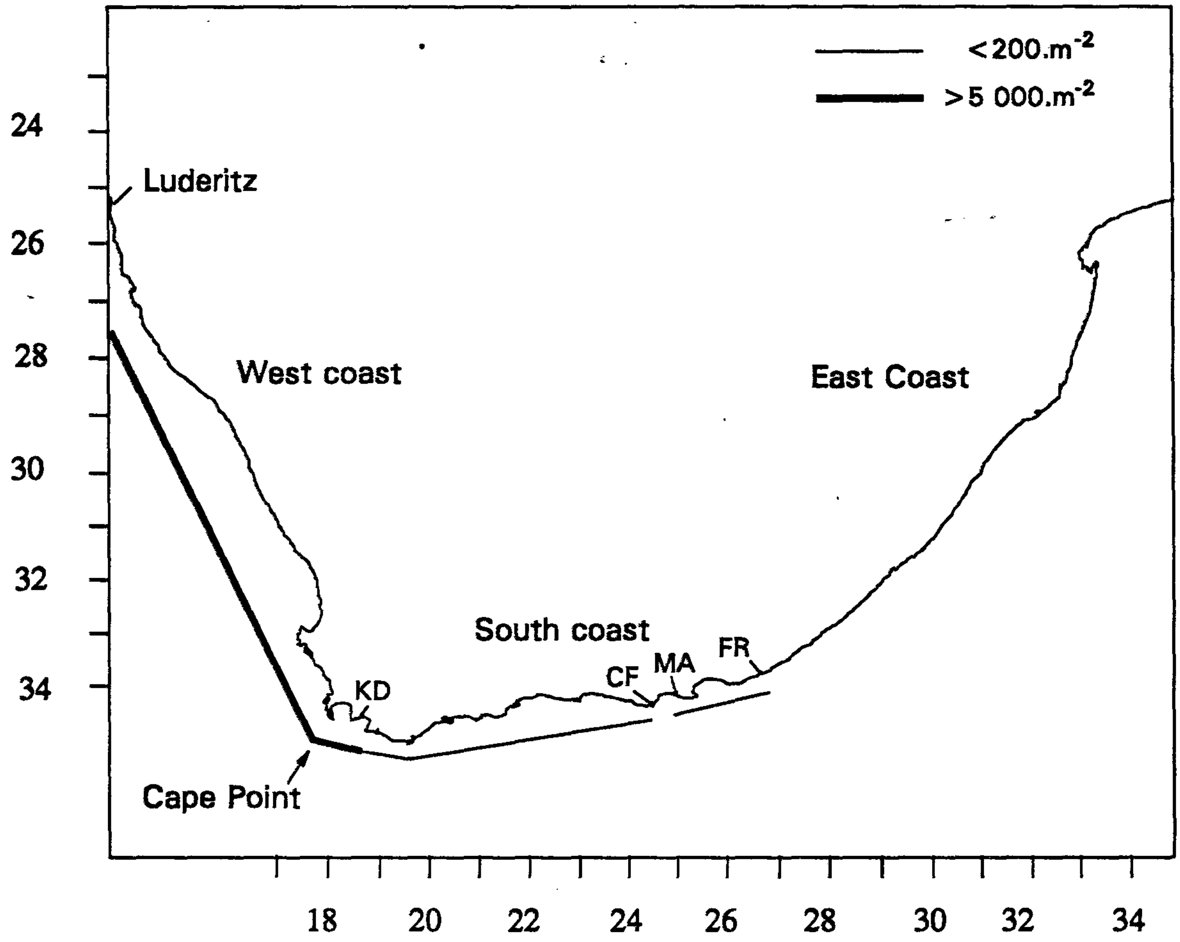


Figure 3.4: The distribution of *Mytilus galloprovincialis* along the coast of South Africa in 1992.

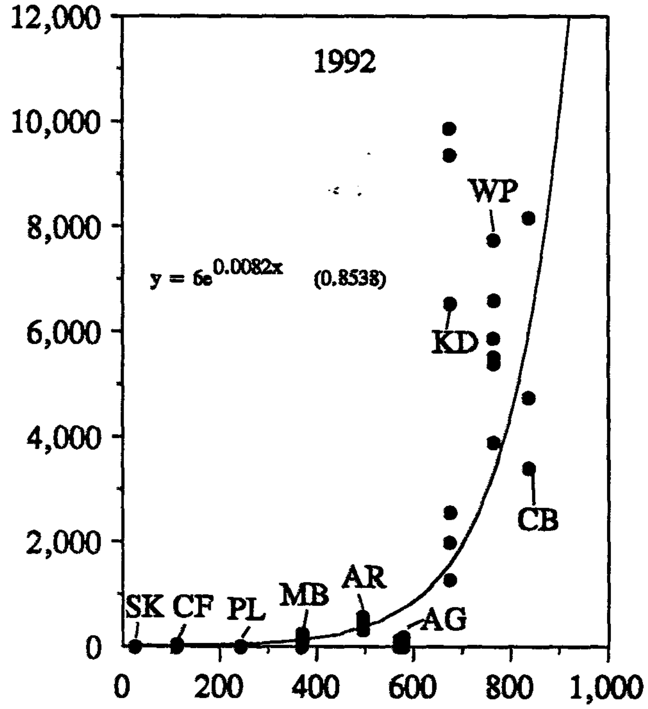


Figure 3.5: Regression of the density of *Mytlius galloprovincialis* against the distance west of Port Elizabeth harbour in 1992.

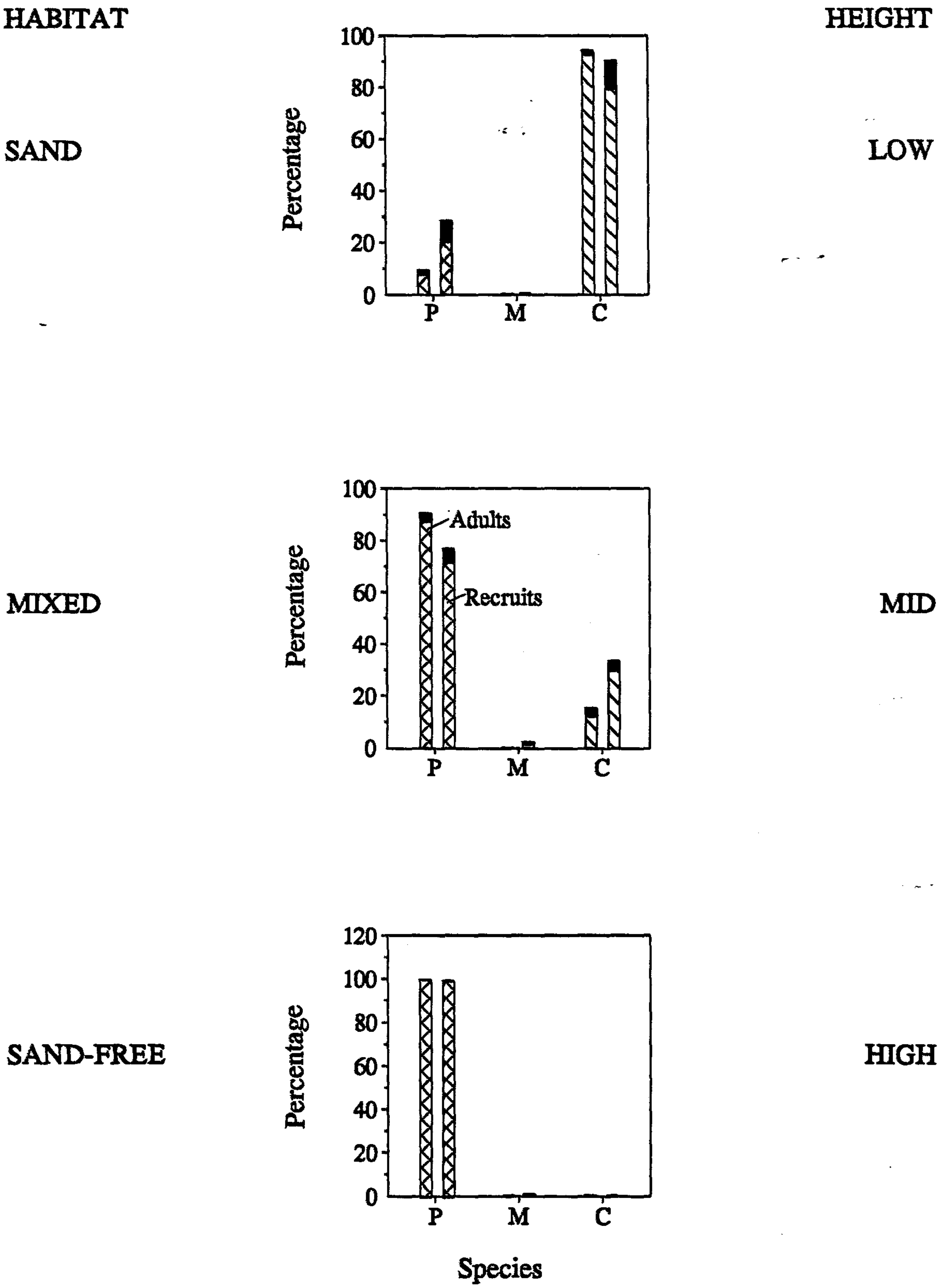


Figure 3.6: The species composition (mean percentage ± standard error) of mussel assemblages on low-shore (a), mid-shore (b) and high-shore (c) rocks, east of Maitland River Mouth. **P** stands for *Perna perna*, **M** for *Mytilus galloprovincialis* and **C** for *Choromytilus meridionalis*.

at sites on the south coast between Maitland River Mouth and Kleinmond (KD) (Fig. 3.7a). However, at Kleinmond (KD) and sites in False Bay these rocks were dominated by *M. galloprovincialis*, with a much smaller proportion of *P. perna, A. ater* and *C. meridionalis* recruits present (Fig. 3.7b). At Kleinmond (KD) mixed sand-rock habitats 0.68-1.51 m above MLWS had a simlar species composition, except that there were more *C. meridionalis* adults (38%) and fewer *M. galloprovincialis* adults (26%). The mussel fauna on the west coast 1.51 m above MLWS, consisted almost entirely of *M. galloprovincialis* with perhaps a few *A. ater* recruits (Fig. 3.7c). While surveys indicated that no *M. galloprovincialis* were found 0.68 m below MLWS (zone 1), above this, the density and relative proportion of *M. galloprovincialis* appeared to increase with increasing height on the shore, at some of the sites. Pooling the data from all four surveys, Kruskal-Wallis tests coupled with Mann-Whitney two-sample tests, confirmed this ($P < 0.05$) for recruit and adult *M. galloprovincialis*, at 40% of the sites where samples were taken from different heights on the shore. At these sites (eg. Cape Infanta) the abundance of *M. galloprovincialis*, was low in the algal-mussel zone (0.68-1.51 m above MLWS, zone 2), and was greatest above this in the pure mussel (1.51-1.73 m above MLWS, zone 3) and barnacle-mussel zones (>1.73 m above MLWS, zone 4) (Fig. 3.8).

It can be concluded from these results that the vertical distribution of *M. galloprovincialis* overlaps with *P. perna* and *A. ater*, but that *C. meridionalis* is found lower down on the shore. Furthermore, for each species the vertical zonation pattern of adults and recruits were similar, but *C. meridionalis* recruits had a slightly broader distribution than the adults, which were restricted to sand covered rocks low on the shore or damp sand-filled crevices.

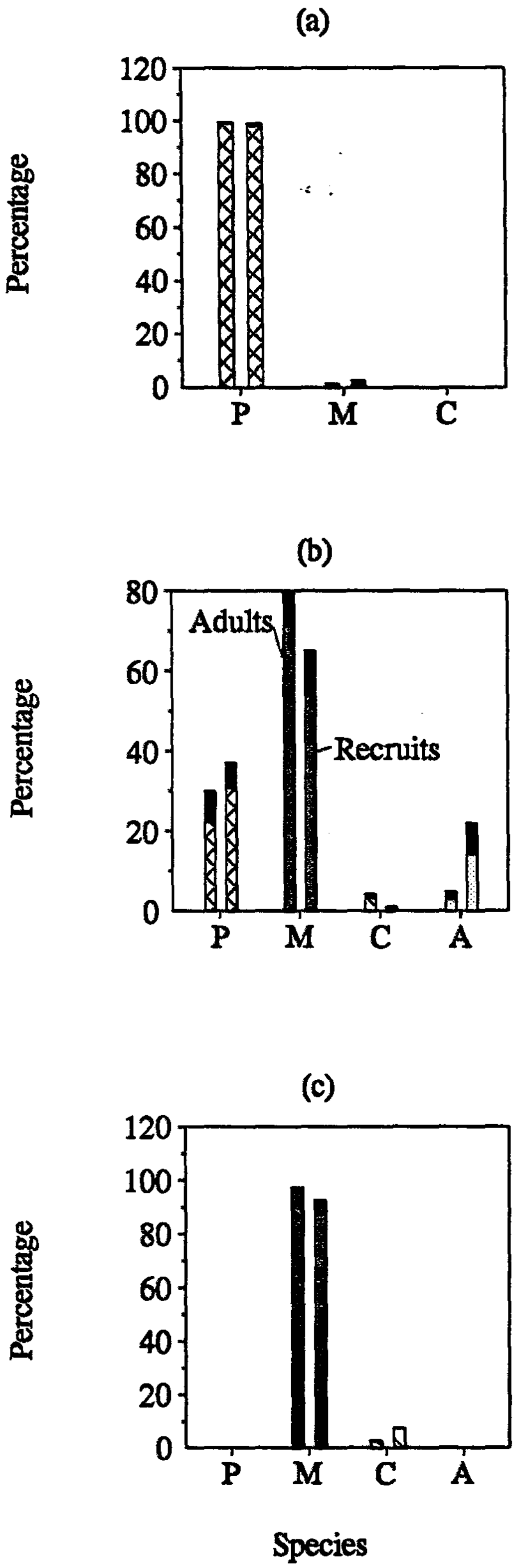


Figure 3.7: The species composition (mean ± standard error) of mussel assemblages 1.51 m above MLWS, between Kleinmond and Maitland River (a); 0.68 m above MLWS, at Kleinmond and in False Bay (b); and 1.51 m above MLWS on the west coast (c). **P** stands for *Perna perna*, **M** for *Mytilus galloprovincialis*, **C** for *Choromytilus meridionalis* and **A** for *Aulacomya ater*.

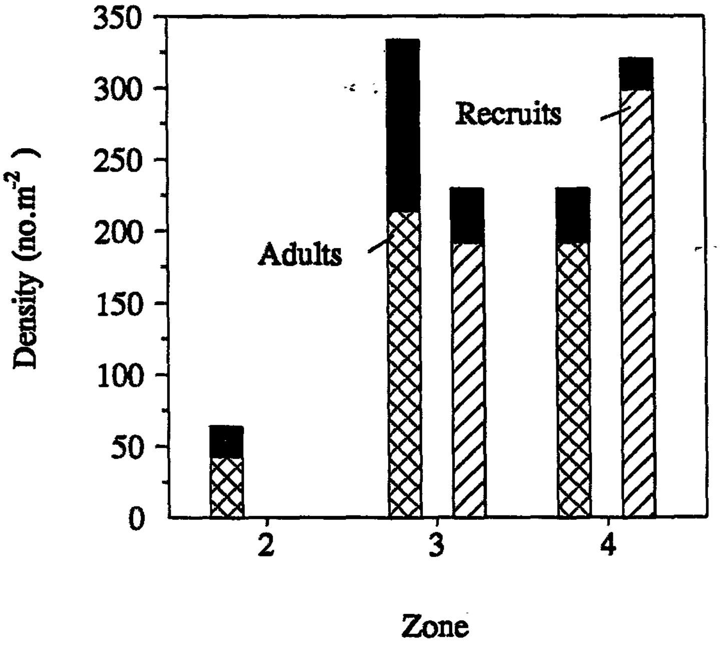


Figure 3.8: The density (mean ± standard error) of *Mytilus galloprovincialis* at Cape Infanta in zone 1 (0.68 - 1.51 m above MLWS), zone 3 (1.51 - 1.73 m above MLWS) and zone 4 (>1.73 m above MLWS).

Discussion

It was suggested in Chapter 1 that limited larval dispersal, was the primary reason for the link between local spawning and settlement patterns of mussels in the Algoa Bay region, as well as the positive correlation between the abundance of mature adults, larval or spore production and the abundance of recruits in local populations of other invertebrates and algae (Dayton 1972, Deysher & Norton 1982, Prince *et al.* 1987 & 1988, Hunte & Younglao 1988, McShane *et al.* 1988). Support for this hypothesis was obtained by following the introduction and subsequent spread of *Mytilus galloprovincialis*, in Algoa Bay.

The density of *M. galloprovincialis* decreased significantly with increasing distance from Port Elizabeth harbour, where it was introduced in 1988. About 76% were found within 5 km of the harbour and 90% within 20 km (Fig. 3.2a). The remaining 10% were found up to 73 km east of the harbour after a year and up to 166 km east after two years (Fig. 3.3). As this invasive mussel spreads via its planktonic larval phase, this suggests that the majority of the larvae which successfully recruited into benthic populations, had a limited dispersal range, but a small fraction were dispersed over longer distances. As discussed in Chapter 2, hydrodynamic models simulating larval dispersal show that larvae can be trapped in areas of minimal water movement near the parent population, which reduces their estimated dispersal range considerably. In support of this, the effective dispersal range (< 12-20 km) of about 90% of *M. galloprovincialis* larvae, coincided with the net dispersal distance (8-14 km) estimated from a model (see Chapter 2 for details) which takes topographical effects on circulation and dispersal into account ($d=a\sqrt{t}$, $\sqrt{}$ = square root, Table 3.2a). In contrast, hydrodynamic models simulating dispersal, predict that larvae advected into the open water column away from any topographical effects, will be passively dispersed by wind-generated currents, and this increases their estimated dispersal range considerably. Data presented in Chapter 2 provides evidence that in the Algoa Bay region, winds generally transport larvae parallel to the coastline in the direction of the wind, most often in an easterly direction but occasionally in a westerly direction.

Table 3.2: The predicted dispersal range of planktonic mussel larvae passively dispersed by wind generated nearshore currents (a) and those released into areas of minimal water movement or trapped by eddies (b). The values represent the predicted dispersal range of larvae occupying the plankton within the Algoa Bay region for a month, in 1989, 1990 and 1991, and were calculated from data presented in Chapter 2, which provides a detailed explanation of how these predictions were made. T_E is the total distance travelled east, T_W the total distance travelled west, T_{total} the total distance travelled and T_{net} the net dispersal range.

(a) $d = st$

	Year	T_E	T_W	T_{total}	T_{net}
Mean	1989	148	25	173	123E
Standard deviation		23	10	24	25E
Minimum		123	7	146	91E
Maximum		204	40	229	180E
Mean	1990	148	27	175	121E
Standard deviation		28	13	28	32E
Minimum		86	4	118	54E
Maximum		192	46	221	164E
Mean	1991	144	24	168	119E
Standard deviation		30	6	34	28E
Minimum		103	16	121	84E
Maximum		185	36	213	157E

(b) $d = a\sqrt{t}$

		T_E	T_W	T_{total}	T_{net}
Mean	1989	15	3	18	12E
Standard deviation		1	1	1	1E
Minimum		14	2	16	11E
Maximum		17	4	20	14E
Mean	1990	15	3	18	12E
Standard deviation		1	1	1	2E
Minimum		12	1	15	8E
Maximum		17	4	20	14E
Mean	1991	14	3	17	11E
Standard deviation		2	1	2	2E
Minimum		11	2	13	8E
Maximum		16	3	19	13E

In support of this, the intensity (density) and rate (distance spread each year) of invasion of *M. galloprovincialis* was far greater to the east than to the west (Fig. 3.2, Table 3.1). Furthermore, following the change in the distribution of *M. galloprovincialis* to the east in 1989 and 1990, it was apparent that the distance spread each year corresponded with the minimum net dispersal distance (T_{net}) predicted for larvae produced by newly established marginal populations, which were advected into the open water column and dispersed by nearshore wind generated currents (Table 3.1 & 3.2b). Similarly, following the change in distribution to the west from year to year, it was apparent that the distance spread each year coincided with the lower limit of the estimated mean dispersal range (eg. 25 - 10km = 15km west in 1989) of larvae only transported west of the harbour (T_W, Table 3.1 & 3.2b). It is possible that all recruits could have come from the original source population at the harbour as the maximum predicted dispersal range during this period was 36-40 km (T_W) to the west and 157-180 km (T_E) to the east (Table 3.2b), but this was unlikely, especially since the source population was removed towards the end of 1990 when the mussel was no longer being grown on ropes in the harbour. Despite the removal of the source population, *M. galloprovincialis* continued to appear on the coast in 1991 and 1992 (Fig. 3.2, Fig. 3.3), suggesting that reproductively viable populations had become established in the first two years it was introduced to Algoa Bay. The distance spread eastwards in 1990 was only 13 km and *M. galloprovincialis* did not spread any further in 1991 (Table 3.1). This suggests that recruits at the eastern limit of the distribution in 1991 and 1992 (157 km) came from a previously established marginal population around Woody Cape, 73 km east of the harbour (Fig. 3.1, 3.2 & 3.3), and that by 1992 no reproductive populations had been established further east.

In general, the decline in the density of recruits with increasing distance from isolated newly introduced adult populations (Fig. 3.2), coral reefs (Sammarco & Andrews 1988), deep sea hydrothermal vents, or from areas (reserves, offshore islands) which protect stocks of invertebrates heavily exploited in accessible regions (Hunte & Younglao 1988, Hockey unpublished data), as well as the simulation of larval dispersal using drift tubes (Levin 1983, Tegner & Butler 1985) and hydrodynamic models (Black & Gay 1987, Black 1988, McShane *et al.* 1988, Sammarco & Andrews

1988, Black & Moran 1991), all suggest that most larvae are trapped in areas of minimal water movement and settle within 300 m to 12 km of the parent population. A much smaller proportion of larvae advected into the open water column and passively dispersed by wind generated nearshore currents, settle up to 100-200 km away. This scale of dispersal is greater than the centimetres or metres observed *in situ* for large, short-lived planktonic (lecithotrophic) and demersal larvae (Olson 1985, Olson & McPherson 1987, Davis & Butler 1989), but shorter than the hundreds if not thousands of kilometres estimated for teleplanic larvae, which spend several months as opposed to several weeks (planktotrophic larvae) in the plankton (Scheltema 1966, 1968, 1971, 1972, 1977). It is also shorter than expected from the extensive geographic range (Buroker 1985) and widespread genetic homogeneity among populations of species with planktotrophic larvae (Scheltema 1975 & 1978, Koehn *et al.* 1976, Levitan & Suchanek 1978, Gosling & Wilkins 1981, Beaumont 1982, Janson 1987, Behrens Yamada 1989, Felvoden 1989, Watts *et al.* 1990, Grant & Lang 1991, Grant *et al.* 1992, Beaumont *et al.* 1993, Cochard & Devauchelle 1993, Mackie & Ansell 1993). One of the reasons for this may be that while recruitment is localised on an ecological time scale due to limited dispersal, on an evolutionary scale, repeated colonisation and dispersion of a small proportion of the larvae increases the biogeographic range considerably, and promotes gene flow between existing populations (Crisp 1958, Sammarco & Andrews 1988). Increased dispersal ability, and therefore gene flow, results in low rates of speciation and endemism (Scheltema 1975 & 1978, Hansen 1978, Jablonski & Lutz 1983, Buroker 1985, Kay & Palumbi 1987), but the rate of extinction is lower than for species with short-lived larvae, and several of the latter species have evolved alternative means of dispersal (Highsmith 1985, Jackson 1985, Johannesson 1988, Behrens Yamada 1989, O Foighil 1989). Consequently, the evolutionary advantages conferred by dispersal seem to outweigh the costs incurred through high larval and settler mortality, although there are probably several other biological and physical factors which contributed towards the evolution of planktonic larvae (Thorson 1950, Mileikovsky 1971, Grassle 1972, Strathmann 1974, Menge 1975, Scheltema 1977 & 1978, Jablonski & Lutz 1983, Buroker 1985, Highsmith 1985, Johannesson 1988, Motro 1991).

On a smaller scale several marine invertebrates, algae and fish, as well as terrestrial plants and animals (Cohen & Motro 1989) have some propagules which remain near the adults and some which disperse, suggesting there are ecological advantages to this. The advantages are clearly illustrated by the successful spread of *M. galloprovincialis* along South African shores. Although only a very small proportion (10%) of *M. galloprovincialis* larvae which successfully recruited into the adult population were dispersed over distances greater than 20 km, these larvae allowed *M. galloprovincialis* to "leap frog" along the coast, expanding its geographic distribution at an average rate of 42 km.y^{1} in the Algoa Bay region. There is convincing evidence that suggests *M. galloprovincialis* was introduced to Saldahna Bay on the west coast of South Africa around 1977. If this is the case the geographic distribution of *M. galloprovincialis* introduced to the west coast expanded by approximately 900km in about 10 years, ranging from Luderitz to Hermanus on the south coast in 1988 (Fig. 3.1). *M. galloprovincialis* originating from west coast populations, continued spreading eastwards along the south coast and by 1992 had reached Cape St. Francis, ~564 km east of Hermanus, and 621 km west of Maitland River, the westward distribution limit of the population originally introduced to Algoa Bay in 1988. Consequently, by 1992 *M. galloprovincialis* had a more or less continuous distribution from Luderitz on the west coast to the Great Fish River on the south coast of South Africa, a distance of some 1 859 km of coastline (Fig. 3.4). Furthermore, results show that *M. galloprovincialis* is found in extremely high densities (> 5 000 adults.m^{-2}) and is the dominant species (~96%) in mussel assemblages on the west coast, and on the south coast as far east as Kleinmond (KD) (Fig. 3.4, 3.5 & 3.9). The density declines sharply to <200 adults.m^{-2} to the east of Kleinmond (KD), where *M. galloprovincialis* has only recently been found, and the indigenous *Perna perna* still dominates (>90%) the mussel fauna (Fig. 3.4, 3.5, 3.7 & 3.8). However, in Algoa Bay the density of *M. galloprovincialis* at Brighton Beach (4km) and Coegas (19km), the two eastern sites closest to the harbour, more than doubled between 1989 and 1990, and continued to increase over the next two years at Coegas, although recruitment failure lead to a decline and virtual disappearance of the mussel bed (*P. perna* and *M.*

galloprovincialis) at Brighton Beach from 1990 to 1992 (Fig. 3.2). Therefore, it is likely that those larvae which recruit locally will rapidly build up populations in newly colonised areas east of Kleinmond (KD). Once this occurs, it is probably only a matter of time until *M. galloprovincialis* spreads into the Transkei on the east coast of South Africa, which may be advantageous, since *P. perna* forms an important part of the diet of Transkeins, and has been overexploited in unprotected areas (Siegfried *et al.* 1985, Lasiak & Dye 1989, van Erkom Schurink & Griffiths 1990). However, since the vertical distribution of *M. galloprovincialis* overlaps with that of *P. perna*, this is likely to be at the expense of *P.perna*, which unlike *M. galloprovincialis*, appears to be a weak competitor, slow to recover from disturbance (Lambert & Steinke 1986, Hockey & van Erkom Schurink 1992, Dye 1994).

With the introduction and subsequent spread of *M. galloprovincialis* there are now four species of mussel common along South African shores, including the indigenous *Choromytilus meridionalis*, *Aulacomya ater* and *P. perna*. The geographical distribution of these species described by van Erkom Schurink (1991) was confirmed in this study. The change in species composition of mussel assemblages with habitat and height on the shore was probably related to variation in the period of immersion and emersion, as well as sand burial and scouring. Since the psammophilic *C. meridionalis* is sensitive to dessication, it dominates low profile rocks covered in sand and only emersed for short periods at low tide. On the other hand, since the psammophobic *P. perna* and *M. galloprovincialis* are capable of withstanding prolonged periods of emersion at high tide, they dominate high shore sand-free rocks. Not unexpectedly, the species composition is mixed in intermediate mid-shore habitats. The similarity between the distribution of adults and recruits and the slightly broader distribution of *C. meridionalis* recruits, suggests that the zonation pattern of the various mussel species found on South African shores is determined by selective larval settlement and/or post settlement mortality, rather than factors affecting the adults. Several studies have shown that settlement patterns reflect the distribution of larvae and that selective settlement of larvae may reduce post-settlement mortality (Denley & Underwood 1979, Grosberg 1982, Hawkins & Hartnoll

1982, Petersen 1984, Davis 1987 & 1988, Bushek 1988, Young 1989a & b, Wilson 1990, Gunther 1991, Bertness *et al.* 1992, Hurlbut 1993, O Connor 1993), but others have shown that post-settlement mortality can still modify the distribution and abundance of juveniles on the shore (Buss 1981, Keough & Downes 1982, Wethey 1984 & 1986, McGuiness & Davis 1988, Osman *et al.* 1989 & 1992, Rowley 1989, Harvell *et al.* 1990, Grosberg 1991, Martel & Chia 1991, Feller *et al.* 1992). However, analysis of studies by Grosberg (1982), Dalby & Young (1992) and Fowler *et al.* (1992) showed that it is extremely difficult to distinguish between the effects of larval distribution, selective settlement and post-settlement mortality on settlement patterns.

In summary, viewed in isolation the results of the three independent studies described in this chapter and in Chapters 1 and 2 may be dismissed as being indirect and circumstantial. However, taken together they provide convincing evidence that approximately 76% of planktonic mussel larvae have a dispersal range of less than 5 km, 90% disperse less than 20 km, but about 10% are passively transported by wind-generated currents over distances of up to 100 km. One of the most important consequences of this is the positive correlation between reproductive effort and the intensity of settlement in local mussel populations. This relationship influences the management of shellfish resources with limited dispersal and spatially and temporally variable recruitment, an issue which will be addressed in Chapter 5 and the final synthesis of this thesis.

SECTION TWO

SETTLEMENT

CHAPTER 4

FACTORS INFLUENCING SETTLEMENT OF BIVALVE MYTILID LARVAE ON INTERTIDAL ROCKY SHORES.

Introduction

Larval dispersal, settlement and metamorphosis are critical stages in the life history of marine invertebrates, linking the reproductive efforts of adults to recruitment of offspring into local populations (Barker 1977). Dispersal of mussel larvae off the coast of South Africa was dicussed in the first three chapters, but little is known about the factors affecting settlement on South African shores.

It has been shown elsewhere, that after a period of development in the water, larvae become competent and metamorphose in response to various chemical or tactile environmental cues, which indicate the presence of a substratum or habitat suitable for juvenile life (Morse 1990). Substratum preferences and habitat selection by marine invertebrate larvae have been reviewed by many authors (Meadows & Campbell 1972, Scheltema 1974). Caffey (1982) pointed out that much of the very early work was based on single factor experiments done in the laboratory, and that while these experiments were useful in isolating each important factor, the experimental results may bear no relation to what happens under natural conditions where several factors interact to determine where larvae settle. To date there have been *in situ* observations of larval settlement on various artificial and natural substrata and in different habitats under varying physical (desiccation, wave action) and biological (predation, competition) conditions (Crisp & Barnes 1954, De Wolf 1973, Scheltema 1974, Denley & Underwood 1979, Sebens 1983, Benayahu & Loya 1984, Shepherd & Turner 1985, Davis 1987, Raimondi 1988, Dirnberger 1990, Tursi *et al.* 1990). In general larvae have been shown, in the laboratory and *in situ*, to prefer certain substrata and/or habitats over others and this selective settlement generally increases their post-settlement survival (Davis 1987). For example, gregarious settlers settle only on or near conspecifics (Crisp & Knight-Jones 1953, Bayne 1969, Sheltema *et al.* 1981, Young & Chia 1982, Jensen & Morse, 1984), while the larvae of weak competitors may settle away from stronger competitors (Petersen 1984). In areas where predation is intense, larvae tend to settle or survive in cryptic rather than exposed habitats (Costelloe 1988, Cameron & Fankboner 1989). Alternatively, larvae may settle on their food source (Sarver 1979) and in some cases the food source also provides protection from predators (Shepherd & Turner 1985). Turbulence and flow rate affect the rate of settlement in wave-exposed and sheltered areas. Intertidally, settlement is often concentrated in cracks and crevices which provide protection from wave action and as they retain water, perhaps decrease desiccation (Jensen & Morse 1984, Bergeron & Bourget 1986, Chabot & Bourget 1988). It has frequently been observed that more larvae settle on rough surfaces than on smooth surfaces and that larvae have a distinct preference for artificial substrata which simulate natural foliose algae and hydroids (Bayne 1964, King *et al.* 1990, Tursi *et al.* 1990).

The larvae of octocorals (Sebens 1983), abalone (Shepherd & Turner 1985) and mussels (De Blok & Geleen 1958, Bayne 1964, Seed 1969 & 1976, Bayne 1971, King *et al.* 1990) are commonly found *in situ* on various types of foliose algae. Maas Geesteranus (1942), Verwey (1952) and De Blok & Geleen (1958) noted that mytilid larvae settling on foliose substrata subsequently disappeared from the temporary sites of attachment and suggested that the plantigrades drifted around in the plankton before settling permanently onto adult mussels. Indirect support for this hypothesis was provided by the occurrence of metamorphosed mussel plantigrades in plankton samples (Bayne 1964, Sigurdsson *et al.* 1976) and by their appearance on spat collectors placed in the sea (Bayne 1964, Bohle 1971, Dare 1976, Blok & Tan-Maas 1977). Bayne (1964) first quantified this process of primary and secondary settlement. *Mytilus edulis* in North Wales have a clearly defined breeding period with distinct peaks in spawning, plankton availability and settlement. Bayne (1964) sampled the plankton, algae and mussels weekly during the breeding period and the resulting time series, indicated that *M. edulis* larvae settle from the plankton to foliose algae and, after a period of growth, the larger "late plantigrades" detach and undergo a period of bysso-pelagic dispersal, before settling permanently amongst adult mussels. This was supported by Seed (1969) and Dare (1976) working on *M. edulis* in northern Wales and northern England. However, other studies suggest or have shown that larvae do settle directly into adult beds (Cross and Southgate 1983 in McGrath *et al.* 1988, Fell & Balsamo 1985, Eyster & Pechenik 1987, McGrath & King 1991) or onto both foliose algae and adults (Petersen 1984, McGrath *et al.* 1988, King *et al.* 1989). There is little quantitative evidence that settlers on algae migrate to adult beds. Thus settlement on algae may in fact be "wasted settlement" rather than the primary source of recruits in adult mussel beds.

On the coast of southern Africa *Choromytilus meridionalis* and *Perna perna* settlers have been observed on a variety of foliose algae (du Plessis 1977, Berry 1978, Beckley 1979, Griffiths 1981, Lambert & Steinke 1986), but it is not known whether these settlers migrate to mussel beds or whether other larvae settle directly onto mussels.

The purpose of this study was to examine the influence of larval behaviour, substratum availability and wave action on the settlement pattern of mussels, and to assess how important direct, primary and secondary settlement are in maintaining mussel populations along the south coast of southern Africa.

Methods

Study sites

The intertidal distribution and abundance of planktonic larvae, settlers and late plantigrades were quantified simultaneously, at a wave-exposed and a wave-sheltered platform, situated about 30 m from each other at Kenton on the south coast (Fig. 4.1). These platforms are covered in *Perna perna* which forms a distinct mussel belt, extending from the lower to the upper balanoid, between 0.5 and 1.6 m above MLWS. The distribution of mussels within the mussel belt is irregular. Dense patches of mussels are surrounded by bare rock, and various algal and barnacle species growing on their shells and on the rocks. Algae such as *Cheilosporum cultratum, Gelidium pristoides, Gigartina paxillata, Hypnea spicifera, Jania sp., Laurencia spp., Plocamium corallorhiza* and *Pterosiphonia cloiophylla* occur intertidally at Kenton.

Sampling periodicity

Changes in the size and appearance of the gonad indicated that *Perna perna* spawned between


S
E

Figure 4.1 (opposite page): The wave-exposed (E) and sheltered-platforms (S) used as study sites at Kenton.

the 24 August and 2 September 1990 at Kenton. To quantify larval abundance and settlement, sampling took place as often as possible on a daily and weekly basis from the 6 to the 27 September 1990.

Sampling procedure

Larval abundance

The plankton present in the intertidal surf zone adjacent to the study sites was sampled daily on an incoming tide. A calibrated bucket was used to collect three water samples of 50 litres each, which were subsequently filtered through the 0.180 mm mesh of a cod end, attached to a 0.250 mm mesh plankton net, 30 cm in diameter. This method was abandoned after a week and instead, the same plankton net was used to collect three samples of approximately 320 litres each. Each sample was taken adjacent to the sheltered platform, by hauling the net vertically through water column ten times, since the water was only about 1 m deep. All plankton samples were emptied into separate labelled containers and preserved in phenoxytol.

A dissecting microscope fitted with a micrometer was used to count and measure the bivalve veligers present in the plankton samples.

Settlement

Settlement of larvae from the plankton onto mussels, bare rock, barnacles, encrusting and upright coralline algae as well as a mixture of other algae in the mussel belt, were examined on both the wave-exposed and the sheltered platforms. The availability of these substrata varied from the bottom to the top of the mussel belt and there were four clear vertical zones. The width and height of each zone was measured and the distribution and abundance of settlement substrata on the shore was assessed by estimating the percentage cover of the dominant space occupiers within two 50 x 50 cm quadrats in each zone.

The number and size frequency distribution of juvenile mussels (settlers and late plantigrades) on each substratum was quantified on a daily or weekly basis. Before the number of settlers and late plantigrades could be estimated it was necessary to define the size range of these propagules. Bivalve larvae collected in the plankton immediately behind the surf zone adjacent to the rocky platforms at Kenton in September 1990 consisted of two cohorts one with a mode at 0.35 to 0.39 mm and the other at 0.45 to 0.49 mm, but larvae ranged in size from 0.25 to 0.90 mm (Fig. 2.6, Chapter 2). Consequently, juvenile bivalves less than 1 mm long were considered to have recently settled on the shore, and increases in their density were regarded as being due to settlement of larvae. This would be verified by the presence of cohorts with modes of 0.35 to 0.39 mm and 0.45 to 0.49 mm on the shore. Juvenile mussels 1 to 19 mm in length were highly mobile and the sudden appearance of individuals of this size resulted in marked periodic increases in abundance at Kenton (Chapter 1) and several other sites along the coast of southern Africa (Berry 1978, Griffiths 1981, Lambert & Steinke 1986). Thus, juveniles less than 1 mm were classified as settlers, while individuals 1 to 19 mm were classified as late plantigrades.

Daily sampling: Where possible mussels and upright coralline algae on the shells or rocks around the mussels, were sampled daily between the 6 and 27 September 1990. Each day upright coralline algae and mussels with the byssus still attached were cleared from three 5x10 cm quadrats of each substratum. Samples were not taken from each zone as the settlement rate on a substratum was assumed to be equal at different heights above the low water level.

Weekly sampling: In addition to the daily samples a number of potential settlement substrata within the mussel bed were examined on the 6,11,18 and 26 September for juvenile mussels less than 20 mm in length. Bare rock, encrusting coralline algae and barnacles were examined *in situ* with a magnifying glass. Mussels with the byssus threads attached, upright coralline algae and a mixture of other algae consisting mainly of *Ulva sp.*, *Cladophora rugulosa*, *Plocamium corallorhiza* and *Gelidium pristoides*, were removed from ten 5x10 cm quadrats of each substratum.

All samples removed from the shore were preserved in phenoxytol. In the laboratory, samples were thoroughly rinsed and all juveniles less than 20 mm collected in a 0.180 mm sieve. Rinsed algae and mussel byssus threads were periodically checked under a dissecting microscope, to ensure that the rinsing procedure was effective in removing all the juveniles. A dissecting microscope fitted with a micrometer was used to count primary settlers less than 1 mm in length, and late plantigrades 1-19 mm long in the samples. To establish the size frequency distribution on each substratum on the 6, 11, 18 and 26 September, representative samples varying from approximately 50, but normally 150 to 1 300 individuals were measured.

Preliminary analysis of size frequency histograms indicated that there were four distinct cohorts of juveniles. Cohort 1 included mussels of 0.3 to 0.84 mm, cohort 2 mussels of 0.85 to 1.04 mm, cohort 3 mussels of 2 to 7 mm and cohort 4 mussels 8 to 19 mm in length. Four by four contingency tables and Chi-square tests comparing the expected and observed size distribution of juveniles, were used to examine the temporal variation in the relative proportion of individuals in cohorts one to four on coralline algae, other algae and mussel between the 6,11,18 and 26 September. If there was significant variation in the size distribution then the contingency tables were sub-divided by excluding various cohorts and days, and Chi-square tests were used to identify when and in which of the cohorts the change occurred.

Results

No bivalve larvae were found in the surf zone during the day (this study) or at night (Chapter 2), but bivalve juveniles were found on the shore at Kenton. Only bivalves belonging to the family Mytilidae were quantified. Settlers were not distinguished to species, but late plantigrades were *Perna perna*.

Settlement substrata

No settlers were observed on bare rock, encrusting coralline algae or barnacles in the mussel belt. Recently settled bivalves of 0.3-0.75 mm were found among the byssus threads of adult mussels, as well as on upright coralline algae and other types of foliose algae, where they occurred in small axils at the tips of finely branched fronds (Fig. 4.2).

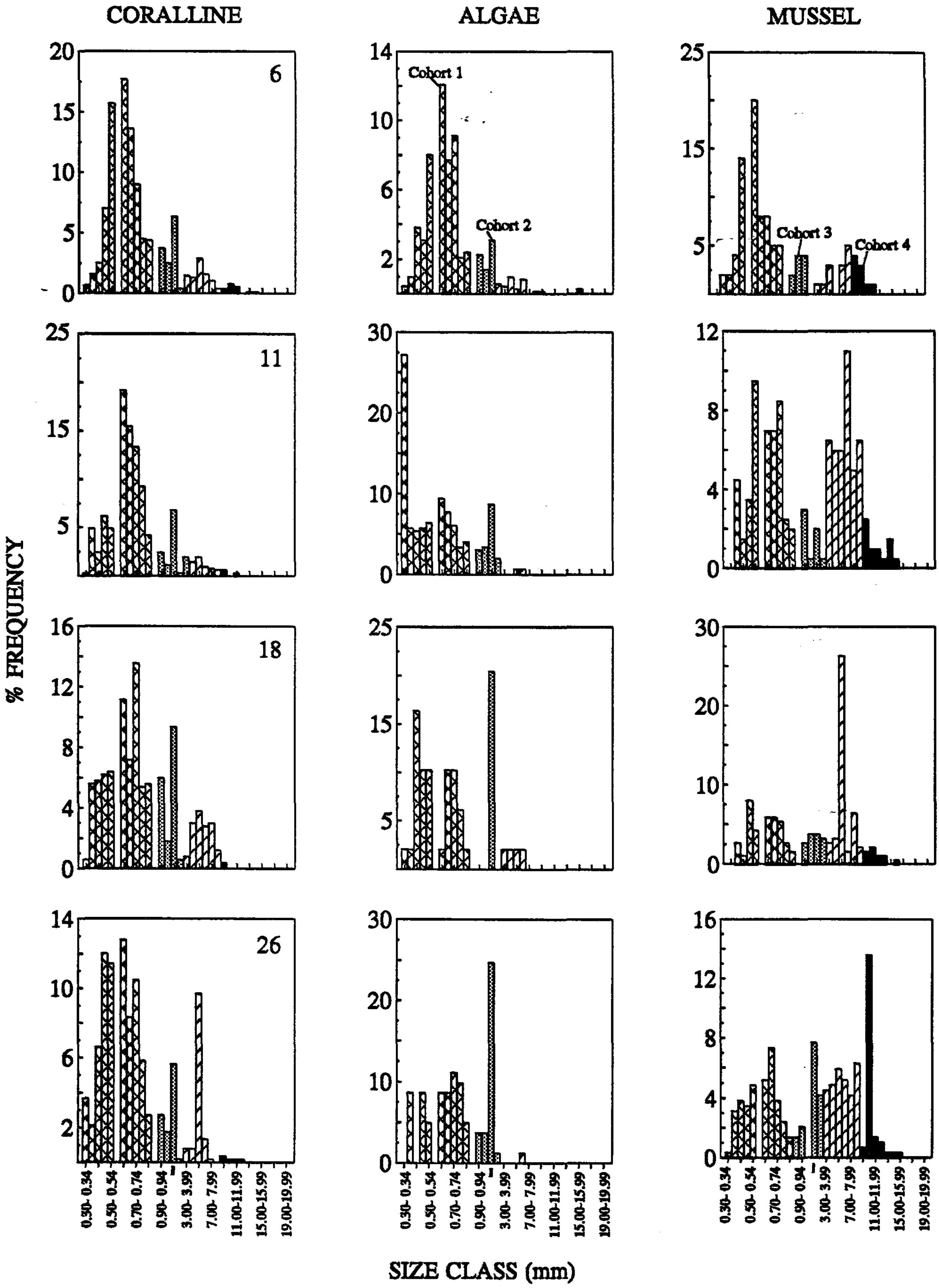


Figure 4.2a: The size frequency distribution of juvenile mussels (0.3-19 mm) on upright coralline algae, other algae and adult mussels on the 6,11 18 and 26 September 1990, at (a) the exposed and (b) the sheltered platform.

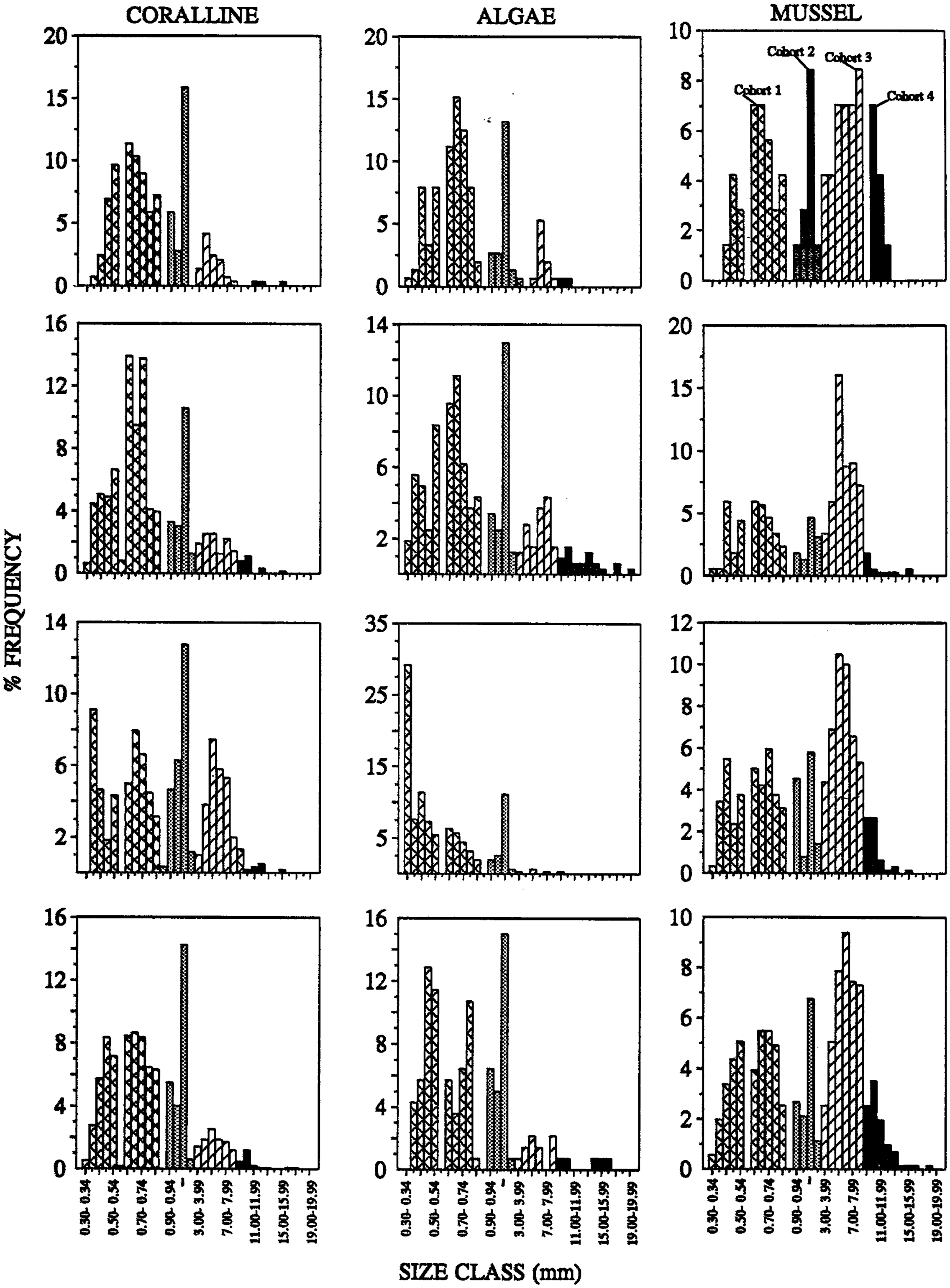

CORALLINE
ALGAE
MUSSEL
Cohort 1
Cohort 2
Cohort 3
Cohort 4
% FREQUENCY
0
5
10
15
20
0
4
8
12
16
2
6
10
14
25
35
0
2
4
6
8
10
12
0.30- 0.34
0.50- 0.54
0.70- 0.74
0.90- 0.94
3.00- 3.99
7.00- 7.99
11.00-11.99
15.00-15.99
19.00-19.99
SIZE CLASS (mm)

Figure 4.2b

The density of settlers (< 1 mm) on each of these substrata was highly variable resulting in high standard deviations around the mean density (Table 4.1). This was possibly due to patchy settlement, growth and/or mortality on the scale of a few metres. In addition, multiple range tests showed larvae did not settle with the same intensity on the different substrata, settler density was significantly higher (Kruskal-Wallis, $P < 0.00001$) on coralline algae than on mussels (Table 4.2). This was true on both the exposed and sheltered platforms. On the exposed platform density was similar on coralline and other types of algae, but on the sheltered platform it was significantly higher (Kruskal-Wallis, $P < 0.00001$) on coralline algae (Table 4.2). There was a slight difference in the density of settlers on a substratum if it was directly exposed or protected from wave action, but Mann-Whitney tests showed this was not significant (Fig. 4.3, Table 4.3) and as a result, the mean settlement intensity on the exposed and sheltered platform was the same (Mann-Whitney, $P = 0.4013$, Table 4.4).

The distribution and abundance of juveniles on the shore

The abundance and distribution of settlers and late plantigrades on the shore were determined by the "preference" of settling larvae for coralline algae over mussels, and the percentage cover and distribution of the settlement substrata.

Distribution of settlement substrata: The overall distribution pattern of coralline algae, other algae and mussels was similar at the exposed and sheltered sites, although there were slight differences in the absolute percentage cover of each substratum within each zone (Table 4.5). The most obvious difference between the exposed and sheltered sites was in the width of the zones, a factor probably related to differences in wave action, since the slope of the two platforms was similar. The combined width of zones 1 and 2 was reduced from 13 m on the exposed platform to about one metre on the sheltered platform (Table 4.5). Consequently, the mussel belt was much narrower (7.43 m) on the sheltered platform than on the exposed platform (19m). In Zone 1 (0.5 - 1.5 m above MLWS) at the bottom of the lower balanoid, the vertical face and top edge of the wave-cut platform were dominated by mussels and coralline algae growing on and amongst the

Table 4.1: Mean density ± standard deviation (s) of settlers on coralline algae, other algal species and on mussels, during September 1990. The sample size was 10 for each substratum. No settlers were recorded on bare rock, encrusting coralline algae or barncales.

Date	Corallines		Algae		Mussels	
	no.m^{-2}	s	no.m^{-2}	s	no.m^{-2}	s
(a) Exposed						
6	6370	2171	3880	3433	730	577
11	7320	6553	4182	2560	4000	2850
18	14840	8232	5460	3494	1200	706
26	1380	512	1600	989	1420	1640
(b) Sheltered						
6	4180	3339	1268	999	540	482
11	10820	8403	4040	2921	5160	5090
18	7100	3839	3680	1104	9980	8528
26	5780	1976	1980	1168	1360	1833

Table 4.2: Kruskal-Wallis and non-parametric multiple range tests (Sokal & Rohlf 1981) comparing the density (no.m^{-2}) of settlers (<1 mm) on different substrata, for the exposed and sheltered sites.

Platform	Substratum	Sample size	Average rank	Homogenous groups		Test Statistic	Probability
Exposed	Mussels	40	38.0750	*		29.898	<0.00001
	Algae	40	64.3049		*		
	Corallines	40	80.5375		*		
Sheltered	Mussels	40	48.0000	*		30.7957	<0.00001
	Algae	40	48.0875	*			
	Corallines	40	85.4125		*		

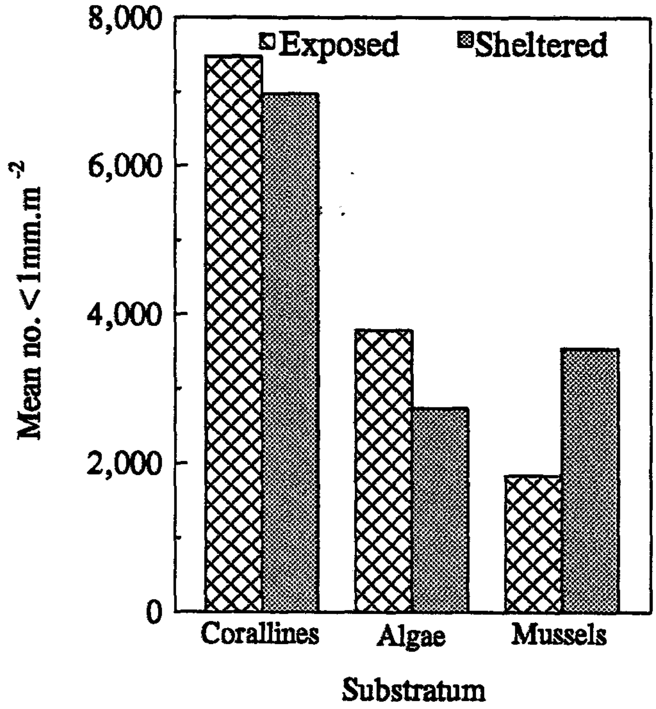


Figure 4.3: The mean density of settlers (no. < 1 mm.m^{-2}) on exposed and sheltered coralline algae, other algae and mussels.

Table 4.3: Non-parametric Mann-Whitney two sample tests comparing the density (no. < 1 $mm.m^{-2}$) of settlers on exposed and sheltered (a) coralline algae, (b) other algae and (c) mussels.

Site	Count	Average rank	Test statistic (Z)	Probability
(a) Coralline algae				
Exposed	40	37.4250	1.1790	0.2384
Sheltered	40	43.5750		
(b) Other algae				
Exposed	40	44.8250	-1.6607	0.0968
Sheltered	40	36.1750		
(c) Mussels				
Exposed	40	38.5250	0.7562	0.4495
Sheltered	40	42.4750		

Table 4.4: Non-parametric Mann-Whitney two sample tests comparing (a) the density of settlers (no. < 1 mm.m^{-2}) and (b) the abundance of settlers (no. < 1 mm.m^{-1}) on the exposed and sheltered platforms.

Site	Count	Average rank	Test statistic (Z)	Probability
(a) Density				
Exposed	120	117.244	0.8392	0.4013
Sheltered	120	124.787		
(b) Abundance				
Exposed	480	518.975	-4.0884	<0.0001
Sheltered	480	445.721		

Table 4.5: The percentage cover of coralline algae, other algae and mussels in the four zones constituting the mussel belt at the exposed (a) and sheltered (b) sites. The height on the shore above the mean low tide level at spring tides and the width of each zone are also recorded.

Height (m)	Zone	Corallines	Mussels	Algae	Total	Width (m)
(a) Exposed						
0.5 - 1.5	1	13	88	0	100	8
1.5 - 2.1	2	2	84	0	86	5
0.90 - 1.4 - 0.90	3	9	23	19	51	5
1.4 - 1.6	4	2	24	17	43	1
Mean		7	55	9	70	19
(b) Sheltered						
0.5 - 1.5	1	7	87	4	98	0.53
1.5 - 2.1	2	4	70	1	75	0.53
0.90 - 1.4	3	13	36	16	65	2.87
1.4 - 1.6	4	0	32	18	50	3.50
Mean		4	56	10	72	7.43

mussels (Table 4.5). In Zone 2 the rocky platform rises and drops sharply down again (1.5 m - 2.1 m - 0.9 m above MLWS), forming a rocky protrusion covered mainly with mussels, while above this the gently rising horizontal platform in zone 3 (0.90 - 1.4 m above MLWS) in the mid to upper balanoid, was covered by a mixture of mussels, coralline and other foliose algae growing in shallow depressions amongst the mussels (Table 4.5). The relatively flat rocky platform in Zone 4 (1.4 -1.6 m above MLWS) at the top of the mussel belt, was characterized by a sparse cover of mussels and the algae *Gelidium pristoides* (Table 4.5). Overall, mussel cover (~55%) was far greater than upright coralline algae (~6%) or other algal species (~10%). The percentage cover of mussels dropped with increasing height above the water (Table 4.5), consequently the total availability of these potential settlement substrata decreased from an average of 99% at the bottom of the mussel bed, to an average of 47% at the top of the mussel bed.

Distribution of settlers: The settlement intensity on a substratum was assumed to be equal in each of the zones. Consequently variations in the abundance of juveniles within and between zones (Table 4.6) was a reflection of the changes in the zone width and percentage cover of each substratum (Table 4.5), rather than changes in the settlement rate. Even though the density of settlers was greater on coralline algae than on mussels (Table 4.2), mussels covered a far greater area than coralline algae, and multiple range tests (Table 4.7) indicated there were significantly more (Kruskal-Wallis, $P < 0.00001$) settlers per metre of shore on mussels (59-60%) than on coralline (30-23%) or other algae (11-17%, Table 4.6). The preference of settling larvae for coralline algae was, however, clearly evident. For example, at the exposed site the mean percentage cover of coralline algae was only 13% of that of mussels (Table 4.5), but settlers prefer the former substratum and the total abundance of settlers on coralline algae (12 039.m^{-1}) was 52% of that on mussels (23 271. m^{-1}, Table 4.6). In zone 3 the percentage cover of coralline algae was 9% as opposed to 23% mussels (Table 4.5) and yet a multiple range test showed the mean abundance (Table 4.6) on the two substrata was no different (Table 4.8). A similar pattern occurred on the sheltered platform (Table 4.5, 4.6 & 4.8).

On the exposed platform the decrease in the percentage cover of mussels, and consequently

Table 4.6: The mean abundance of settlers per metre of shore on coralline algae, other algae and mussels in zones 1,2,3 and 4, for the exposed (a) and sheltered (b) sites. The percentage of the total number of settlers on the shore present in each zone and on each substratum is also recorded.

(a) Exposed

Zone	Corallines	Mussels	Algae	Total	Percentage
1	7777	12936	0	20713	52
2	748	7718	0	8466	22
3	3365	2176	3601	9142	23
4	149	441	644	1234	3
Total	12039	23271	4245	39555	
Percentage	30	59	11		

(b) Sheltered

Zone	Corallines	Mussels	Algae	Total	Percentage
1	340	1632	58	2030	11
2	194	1313	30	1537	9
3	3546	3658	1259	8463	48
4	0	3965	1727	5692	32
Total	4080	10568	3074	17222	
Percentage	23	60	17		

Table 4.7: Kruskal-Wallis and non-parametric multiple range tests comparing the abundance of settlers (no. < 1 mm.m^{-1}) on different substrata, for the exposed and sheltered sites.

Site	Substratum	Sample size	Average rank	Homogenous groups			Test statistic	Probability
Exposed	Algae	160	156.366	*			107.519	<0.00001
	Corallines	160	258.544		*			
	Mussels	160	314.744			*		
Sheltered	Algae	160	206.525	*			74.2442	<0.00001
	Corallines	160	197.527	*				
	Mussels	160	317.450		*			

Table 4.8: Non-parametric multiple range comparisons indicating the difference in the abundance of settlers (no. < 1 mm.m^{-1}) on coralline algae, other algae and mussels in each zone, for the exposed and sheltered sites. Data for each zone were tested separately.

Site	Zone	Substratum	Count	Average rank	Homogenous groups		
Exposed	1	Algae	40	0.0000	*		
		Corallines	40	76.1000		*	
		Mussels	40	86.9000		*	
	2	Algae	40	0.0000	*		
		Corallines	40	63.2000		*	
		Mussels	40	99.8000			*
	3	Mussels	40	48.6500	*		
		Corallines	40	63.1375	*	*	
		Algae	40	70.9634		*	
	4	Corallines	40	34.9500	*		
		Mussels	40	65.4750		*	
		Algae	40	82.0488		*	
Sheltered	1	Algae	40	25.3750	*		
		Corallines	40	68.7000		*	
		Mussels	40	87.4250			*
	2	Algae	40	24.5375	*		
		Corallines	40	65.7375		*	
		Mussels	40	91.2250			*
	3	Algae	40	43.5000	*		
		Mussels	40	60.7125	*	*	
		Corallines	40	77.2857		*	
	4	Corallines	40	20.5000	*		
		Algae	40	78.0250		*	
		Mussels	40	82.9750		*	

in the total availability of settlement substratum with increasing height on the shore (Table 4.5), resulted in a decrease in total settler abundance from 20 713. m^{-1} of shore at the bottom of the mussel bed to 1 234. m^{-1} at the top (Table 4.6). On the sheltered platform the reduction in the width of zones 1 and 2 where the availability of settlement substratum was highest, and the slightly higher percentage cover of mussels in zones 3 and 4 (Table 4.5), resulted in marked differences in the abundance and distribution of settlers across the mussel belt in comparison with the exposed site. On the exposed platform 74% of the settlers were concentrated in zones 1 and 2 at the bottom of the mussel bed while on the sheltered platform 80% were found in zones 3 and 4 at the top of the mussel bed (Table 4.6). Multiple range tests showed the mean abundance of settlers was significantly higher (Kruskal-Wallis, $P<0.00001$) in zones 3 and 4 than in zones 1 and 2 on the sheltered platform (Table 4.9). On the exposed platform mean abundance was greatest in zones 1 and 3 reflecting the presence of both algae and mussels, and significantly lower (Kruskal-Wallis, $P<0.00001$) in zones 2 and 4 where very few algae were available to settle on (Table 4.9). On both the exposed and sheltered platform the mean abundance was highest in zone 3 (Table 4.9) where all three types of settlement substrata were relatively abundant (Table 4.5). Although the rank mean density of settlers was equal (Mann-Whitney, $P=0.4013$) on the exposed and sheltered platforms (Table 4.3a), the rank mean abundance was significantly higher (Mann-Whitney, $P<0.0004$, Table 4.3b) in the exposed mussel bed than in the narrower sheltered mussel bed. The total abundance of settlers in the exposed mussel bed was 39 555. m^{-1} as opposed to the 17 222. m^{-1} in the sheltered mussel bed as a result of the greater area covered by the settlement substrata, particularly coralline algae (Table 4.5 & 4.6). Thus, although the settlement rate ($no.m^{-2}$) was equal on the exposed and sheltered platform, more larvae did not crowd into the narrower sheltered mussel belt. This suggests that there was a limit to the carrying capacity of a settlement substratum, that this was the same on both platforms and that larval availability equalled or exceeded this carrying capacity.

In general, although 59-60% of the total number of settlers on the shore on any particular day, settled directly onto mussels, a large proportion (40-41%) settled from the plankton onto foliose algae (Table 4.6).

Table 4.9: Kruskal-Wallis and non-parametric multiple range tests comparing the abundance of settlers (no. <1 mm.m^{-1}) in zones 1,2,3 and 4, for the exposed and sheltered sites.

Site	Zone	Sample size	Average rank	Homogenous group	Test statistic	Probability
Exposed	1	120	277.690	*	81.0297	<0.00001
	2	120	209.512	*		
	3	120	314.566	*		
	4	120	168.231	*		
Sheltered	1	120	203.342	*	105.9180	<0.00001
	2	120	175.458	* *		
	3	120	347.000	*		
	4	120	236.200	*		

Distribution of late plantigrades: Late plantigrades were observed among the byssus threads of adult mussels, as well as on foliose algae, although no individuals greater than 19mm were found on coralline or other algal species. The mean density of late plantigrades was highly variable on each substratum and standard deviations were high (Table 4.10). The mean density of late plantigrades on each substratum varied significantly (Kruskal-Wallis, $P < 0.05$, Table 4.11). Unlike settlers, the mean density of late plantigrades was higher on mussels than on coralline algae, and lowest on other algal species within the mussel belt (Table 4.11). Occasionally, late plantigrades accumulated in the holdfast of coralline algae attached to mussel shells in densities similar to those recorded on mussels, as was indicated by the multiple range test for the exposed site (Table 4.11). As with primary settlers, the availability of the settlement substrata influenced the abundance and distribution of the late plantigrades within the mussel bed, and this pattern (Table 4.12) was similar to that already described for settlers.

Settlement behaviour

The behaviour of settling larvae was examined using Kruskal-Wallis and multiple range tests to compare temporal variations in the density, and Chi-square tests to compare temporal variations in the size frequency distribution of juveniles on mussels and algae. In-depth analyses showed there were slight differences in the timing and frequency of events on sheltered and exposed shores but the general settlement patterns and behaviour of larvae (described below) were the same.

In general, increases in the density of settlers and the percentage of individuals 0.30 to 0.49mm in the population, indicate that direct settlement into the adult mussel bed and primary settlement on coralline algae occurred repeatedly, mainly between the 6 and 18 September (Fig. 4.2, Table 4.1, 4.13 & 4.14). The increase in density and the maintenance of constant levels of settlers from one week to the next showed that the pattern was the same on other types of algae, although the frequency and timing of peaks in settlement could not be determined (Table 4.1 & 4.15). The intensity of direct and primary settlement was low as the relative proportion of cohort 1 (0.30-0.84 mm) did not increase during settlement (Table 4.16, 4.17 & 4.18).

Table 4.10: Summary statistics for the mean density (no. m^{-2}) ± the standard deviation (s) of late plantigrades (1-19 mm) on coralline algae, other algae and mussels, during September 1990.

Date	Corallines		Algae		Mussels	
	no.m^{-2}	s	no.m^{-2}	s	no.m^{-2}	s
(a) Exposed						
6	1180	598	560	941	1040	1534
11	2040	1107	1620	656	2180	1089
18	2580	2273	900	981	1780	1615
26	180	148	420	175	1660	1831
(b) Sheltered						
6	1040	604	405	308	765	238
11	3860	3233	2460	2296	7680	10838
18	2320	1108	1000	618	7760	9111
26	1280	801	800	516	2880	2012

Table 4.11: Kruskal-Wallis and non-parametric multiple range tests comparing the density (no.m^{-2}) of late plantigrades (1-19mm) on different substrata.

Site	Substratum	Sample size	Average rank	Homogenous groups		Test statistic	Probability
Exposed	Algae	40	49.0854	*		7.4004	0.0247
	Corallines	40	65.3625	*	*		
	Mussels	40	68.8500		*		
Sheltered	Algae	40	42.4875	*		16.7043	0.0002
	Corallines	40	66.5875	*			
	Mussels	40	72.4250		*		

Table 4.12: The mean abundance per metre of shore of late plantigrades (1-19 mm) on coralline algae, other algae and mussels in zones 1,2,3 and 4, for (a) the exposed and (b) the sheltered site. The percentage of the total number of settlers on the shore present in each zone and on each substratum is also recorded.

Zone	Corallines	Mussels	Algae	Total	Percentage
(a) Exposed					
1	1555	11722	0	13277	55
2	150	6993	0	7143	30
3	673	1733	820	3226	13
4	30	342	147	519	2
Total	2408	20790	967	24165	
Percentage	10	86	4		
(b) Sheltered					
1	79	2465	25	2569	14
2	45	1983	6	2034	11
3	793	5523	536	6852	38
4	0	5987	735	6722	37
Total	917	15958	1302	18177	
Percentage	5	88	7		

Table 4.13: Kruskal-Wallis tests comparing the mean density of settlers (no. <1 mm.m^{-2}) on the 6, 11, 18 and 26 September on coralline algae and mussels.

Platform	Substratum	Date	Sample size	Average rank	Test statistic	Probability
Exposed	Corallines	6	10	21.4000	24.6889	<0.0001
		11	10	21.2500		
		18	10	32.6000		
		26	10	6.7500		
	Mussels	6	10	11.5500	20.0497	0.0002
		11	10	34.0000		
		18	10	18.6000		
		26	10	17.8500		
Sheltered	Corallines	6	10	20.5500	23.3492	<0.0001
		11	10	27.4500		
		18	10	28.0500		
		26	10	5.9500		
	Mussels	6	10	14.3000	5.7213	0.1260
		11	10	26.6500		
		18	10	21.4000		
		26	10	19.6500		

Table 4.14: Tukey multiple range test indicating the difference in the mean density of settlers (no. <1 mm.m^{-2}) on coralline algae and mussels, sampled during September 1990, from (a) the exposed and (b) the sheltered sites. The sample size was three except for the 6,11,18 and 26 September when it was ten.

(a) Exposed

Date	Corallines		Mussels	
	Average rank	Homogenous groups	Average rank	Homogenous groups
6	45.5000	***	25.5556	***
7	6.6667	*	4.5000	*
8	5.0000	*	4.5000	*
9	7.0000	*	21.1667	**
10	8.5000	*	32.6667	***
11	43.2000	****	59.4500	*
16	33.1667	**	42.1667	***
18	60.2000	*	35.1500	***
19	50.6667	**	57.1667	**
20	47.6667	**	31.3333	****
21	37.0000	**	43.0000	**
22	38.8333	***	48.5000	***
26	22.0000	*	33.9500	****
27	16.0000	*	23.8333	*****

Table 4.14 continued:

(b) Sheltered				
Date	Corallines		Mussels	
	Average rank	Homogenous groups	Average rank	Homogenous groups
6	29.5556	***	17.6667	****
7	24.3333	****	3.5000	*
8	10.6667	**	15.3330	*
10	7.0000	**	24.8333	***
11	54.5500	**	48.2000	***
15	24.5000	***	61.5000	***
16	14.0000	**	39.5000	*****
17	36.3333	***	63.6667	**
18	45.9500	***	64.0000	*
19	71.5000	*	56.3333	****
20	59.5000	**	41.5000	****
21	29.1660	****	42.6667	***
22	61.0000	*	52.0000	*****
23	18.8333	*****	36.1667	******
24	48.5000	**	43.5000	**
26	45.4000	****	27.9000	***
27	33.3333	***	26.5000	**

Table 4.15: The results of Kruskal-Wallis and non-parametric multiple range tests comparing the density of settlers (no. < 1 mm.m^{-2}) on algae other than corallines, on the 6, 11, 18 and 26 September 1990 at the exposed and sheltered platforms.

Platform	Date	Sample size	Average rank	Homogenous groups		Test statistic	Probability
Exposed	6	10	20.6000	*	*	11.2934	0.0102
	11	10	23.6818		*		
	18	10	28.4000		*		
	26	10	11.0500	*			
Sheltered	6	10	14.0000	*		12.5581	0.0057
	11	10	31.2727		*		
	18	10	20.2500	*			
	26	10	17.4500	*			

Table 4.16: The relative proportion (%) and number (n) of mussels in the mussel bed, within cohorts 1,2,3 and 4 on the 6,11,18 and 26 September 1990, at the exposed and sheltered sites. The results of Chi-square tests comparing the number within cohorts on different days are also recorded. If the number varied significantly the contingency tables were subdivided by excluding various days or cohorts and Chi-square tests used to determine on which day and in which cohort the change occurred. Of the latter tests only those which were not significant are shown here. A * indicates a cohort or date which has been excluded from that particular Chi-square test. DF denotes degrees of freedom.

Date	Exposed					Sheltered				
	1	2	3	4	n	1	2	3	4	n
6	35	13	31	21	71	68	10	8	14	100
11	31	8	49	12	374	46	5	35	13	201
18	38	11	39	12	637	43	13	34	10	157
26	36	11	35	17	732	44	14	29	14	273

CHI-SQUARE TESTS

Site	Test	DF	Test statistic	Probability
Exposed	6,11,18,26 x 1,2,3,4	9	38.4685	<0.0005
Sheltered	6,11,18,26 x 1,2,3,4	9	30.7198	<0.0005
	6,11,18,26 x 1,2,*,4	6	7.5499	>0.2000
	6,*,18,26 x 1,2,3,4	6	10.4057	0.1<p<0.2

Table 4.17: The relative proportion (%) and number (n) of mussels within each cohort 1,2,3,and 4 on coralline algae, on the 6,11,18 and 26 September 1990, at the exposed and sheltered sites. The results of Chi-square tests comparing the number of mussels within cohorts on different days, are also recorded. A * represents a date or a cohort which was excluded from that particular Chi-square test. DF denotes degrees of freedom.

Date	Exposed					Sheltered				
	1	2	3	4	n	1	2	3	4	n
6	76	13	9	2	760	63	25	11	1	290
11	80	10	8	2	615	68	17	12	4	634
18	66	17	15	2	510	46	24	25	5	593
26	80	11	8	1	487	64	23	10	3	1346

CHI-SQUARE TESTS

Site	Test	DF	Test statistic	Probability
Exposed	6,11,18,26 x 1,2,3,4	9	43.1106	<0.0005
	6,11,*,26 x 1,2,3,4	6	7.0052	0.1<p<0.2
Sheltered	6,11,18,26 x 1,2,3,4	9	122.4273	<0.0005
	6,11,*,26 x 1,2,3,4	6	15.5331	0.1<p<0.05
	6,11,*,26 x *,2,3,4	4	4.1791	>0.2000

Table 4.18: The relative proportion (%) and number (n) of mussels on algae other than corallines, in cohorts 1,2,3 and 4 on the 6,11,18,and 26 September 1990, at the exposed and sheltered sites. The Chi-square tests comparing the number within cohorts on different days are also recorded. A * represents a cohort which has not been included in that particular Chi-square test. DF denotes degrees of freedom. Cohorts 3 and 4 were merged as the number of mussels in these cohorts was occasionally below five, which is the minimum number required for a Chi-square test.

Date	Exposed				Sheltered			
	1	2	3+4	n	1	2	3+4	n
6	83	11	6	428	70	18	12	152
11	74	21	5	219	58	19	23	321
18	70	22	8	50	75	22	3	225
26	65	32	3	81	61	26	13	141

CHI-SQUARE TESTS

Site	Test	DF	Test statistic	Probability
Exposed	6,11,18,26 x 1,2,3+4	6	27.7945	<0.0005
	6,11,18,26 x 1,*,3+4	3	1.6096	>0.2000
Sheltered	6,11,18,26 x 1,2,3+4	6	49.7324	<0.0005
	6,11,18,26 x 1,2 *	3	3.5085	>0.2000

Except for settlers on exposed algae, the low settlement rate made it virtually impossible to estimate the growth rate of settled cohorts. However, shifts in the distribution of sizes within each cohort on the different substrata, and the significant increase (Chi-square, $P<0.0005$) in the proportion (10-11%) of cohort 2 relative to cohort 1 on exposed algae, suggest that growth of recently settled individuals was rapid (Fig. 4.2, Table 4.18). This was supported by the sharp decline in density of settlers between settlement events (Table 4.1 & 4.14), and the concomitant significant increase (Kruskal-Wallis, $P<0.0001$ & $P<0.0018$) in the density of late plantigrades between the 6 and 18 September (Table 4.10, 4.19). However, the magnitude of the decline (14-22%) in the number of juveniles (generally >0.60 mm - Fig. 4.2) on exposed and sheltered algae on the 11 and 18 September (Fig. 4.2, Table 4.17 & 4.18), and the magnitude of the increase (18-27%) of cohort 3 on mussels between the 6 and 11 September (Fig. 4.2, Table 4.16), exceeded that expected from normal levels of growth and/or mortality of larvae which settled on these substrata (10-11% exposed algae, Table 4.18).

In the absence of further settlement, rapid growth and mortality resulted in a marked decline in the density of both settlers and late plantigrades on algae and sheltered mussels between the 18 and 26 September (Table 4.1, 4.10, 4.14 & 4.19), although this did not exceed normal rates, since the relative proportion of cohorts did not vary significantly (Chi-square, $P>0.05$) from what was expected over this period (Table 4.17 & 4.18). Repeated settlement between the 18 and 26 September on exposed algae mitigated the decline in density on exposed mussels (Table 4.1, 4.10, 4.14 & 4.19).

The results thus indicate that larvae which settle primarily on algae occasionally disappear from this substratum, and that direct larval settlement on mussels is supplemented by occasional dense settlement of late plantigrades 2-7 mm in length in the adult bed. However, there was little temporal co-ordination between the disappearance of settlers greater than 0.60 mm from algae and the appearance of late plantigrades on mussels.

Table 4.19: Kruskal-Wallis and non-parametric multiple range tests comparing the mean density of late plantigrades on mussels, on the 6, 11, 18 and 26 September 1990 at the exposed and sheltered platforms.

Platform	Date	Sample size	Average rank	Homogenous groups	Test statistic	Probability
Exposed	6	10	8.6500	*	23.1491	<0.0001
	11	10	25.1000	* *		
	18	10	32.1000	* *		
	26	10	16.1500	* *		
Sheltered	6	10	8.7000	*	14.9718	0.0018
	11	10	23.1000	*		
	18	10	27.9000	*		
	26	10	22.3000	*		

Discussion

The size range of settling larvae varies with the rate of larval development and growth (Pechenik 1984 & 1990, Pechenik *et al.* 1990). Furthermore, once development is complete, larvae can delay settlement for short periods if settlement sites are unavailable (Bayne 1964, du Plessis 1977). Mytilid larvae generally settle when they are 0.25 to 0.5 mm long (McGrath *et al.* 1988).

The present study shows that mytilid (probably *Perna perna*) larvae of this size, settle simultaneously on algae and mussels, but settler density is greater on coralline algae than on mussels (Fig. 4.2, Table 4.1). Primary settlement on algae and direct settlement on mussels has also been recorded for *Mytilus edulis* in Ireland (McGrath *et al.* 1988, King *et al.* 1989), and *Mytilus californianus* and *M. edulis* on the east coast of North America (Petersen 1984). Furthermore, Petersen (1984) showed that, given a choice between algae and mussel byssus threads, larvae choose to settle on algae, which explains why he recorded a higher density of settlers on algae than on mussels. This "preference" for foliose algae is taken to the extremes in some areas around Britain and Ireland, where *M. edulis* larvae appear to avoid settling directly into the mussel bed (Bayne 1964, Dare 1976, McGrath & King 1991). Bayne (1964) recorded no mussels less than 0.75 mm on adult beds in the Menai Straits, North Wales. He estimated that *M. edulis* settlers grow at an avergae rate of 0.025 mm per day, and at this rate it would take approximately 17 days for an averaged sized settler (0.325 mm), and 28 days for the smallest sized settler (0.250 mm), to reach 0.75mm. Bayne (1964) sampled the mussel beds once every two weeks so it is unlikely that he would have missed direct settlement to the adult bed, and post-settlement mortality would have to have been extremely high to preclude the collection of any recently settled individuals from the mussel bed (McGrath *et al.* 1988). Dare (1976) recorded slightly smaller sized *M. edulis* (0.48-0.70 mm) in the mussel bed at Morecambe Bay in the Irish Sea. Since the sampling interval was two weeks and it would take only six days for recently settled mussels to reach this size, he may have missed direct settlement to the mussel bed. The same can be said for McGrath & King (1991) who sampled adult populations of *M. edulis* at 23 exposed sites around Ireland. The presence of a cohort with a modal size of 0.325 to 0.375 mm indicated that direct settlement had just occurred at 30% of these sites, while the presence of a cohort with a modal size of 0.40 to 0.50 mm indicated that direct settlement had occurred recently at another 35% of the sites. They found no or virtually no individuals less than 0.40mm at the remaining 8 sites, suggesting that direct settlement did not occur at 35% of the sites sampled. However, at these sites the fraction of individuals less than 1mm in the population was extremely low on the adult mussel bed and on algae, suggesting that there had been no settlement for quite some time. As they pointed out, if they had sampled these shores immediately after settlement they may have found that larvae did settle directly on the adult bed. Thus, while Bayne (1964) provided conclusive evidence that *M. edulis* larvae do not settle directly in the adult beds, the same cannot be said for Dare (1976) and McGrath & King (1991) as the sampling interval between settlement and sampling was too long. The present study on the closely related but faster growing brown mussel, *P. perna*, showed that, because of mortality and the rapid growth rate of settlers, if the sampling interval exceeds three to four days it is quite possible that peaks in settlement activity will be missed (Table 4.14).

The preceeding discussion shows that the settlement behaviour of mussel larvae is complex, and there are several questions which need to answered before it can be understood. Firstly, why do larvae prefer algae to mussels? Secondly, why settle on mussels at all if algae is the preferred settlement substratum i.e. why does direct settlement occur in some areas but not in others? Thirdly, what happens to settlers on algae - do they die or do they migrate to the adult bed?

There are several reasons why larvae settle from the plankton onto foliose algae and hydroids. Resident species are known to affect settlement and early post-settlement survival and growth by, for example, usurping available settlement space (Woodin 1976 & 1978, Woodin 1983, Osman *et al.* 1989), increasing settlement through gregarious responses (Crisp & Knight-Jones 1953, Scheltema *et al.* 1981, Jensen & Morse 1984, Osman *et al.* 1989) and altering current flow (Butman 1987, Eckman 1987, Eckman *et al.* 1989). Filter feeding communities like mussels may filter out larvae attempting to settle on them. Consequently, settlers will be concentrated on algae either because larvae avoid settling on the mussel bed or because mortality during settlement is higher on mussels than on algae. Early post-settlement predation and competition may also be important considerations. Shepherd & Turner (1985) suggested that larvae settled on coralline algae because the cryptic habitat provided a refuge from predators living in the adult matrix. Thorson (1957) and Bayne (1964) speculated that larvae settled on algae initially in order to avoid competition with adults. Petersen (1984) also showed that competition may be an important factor in that, *M. edulis* larvae settled on clumps of adult *M. edulis* but avoided clumps of the superior competitor *M. californianus*. However, selective settlement will concentrate larvae on algae, so while competition with adults decreases, the intensity of competition between settlers increases. Therefore, the larvae do not avoid competition they merely exchange one form for another. In addition, the intensity of predation and competition varies locally and primary settlement on algae is a biogeographically widespread phenomenon. This suggests that while predation and competition may modify local settlement patterns, they do not entirely explain the primary and secondary settlement behaviour of larvae. An alternative explanation is that initial settlement on algae may be a passive physical process. In 1886 Wilson (cited by Seed 1969) attributed the presence of small mussels, about 0.250 mm long, on zoophytes and seaweeds to a process of passive interception. De Blok & Geleen (1958) found that larvae settled on a variety of materials in the sea from twigs of birch and elm to artificial hydroids of soft plastic cotton to glass wool. They concluded that general morphology rather than chemical composition was important to settling larvae. Specifically, threadforms and little niches in the form of ramifications, which trap water and filter out particles from the water. The filiform nature of foliose algae, like the upright coralline algal species, may make it easier for larvae to settle and/or may passively filter out larvae from the water more efficiently than the monofilamentous byssus threads (Lane *et al.* 1985) of adult mussels. This will result in more settlers per unit area on algae than on mussels, as was shown in this study (Table 4.2) and by Petersen (1984). If settlement of mussel larvae is largely passive, then no matter where the site may be located a large proportion of larvae arriving at the site will settle naturally on algae.

It is more difficult to explain why larvae settle directly on the mussel bed at some sites but not at others, as McGrath *et al.* (1988) discounted the chance that genetic differences alone were responsible for contrasting settlement patterns. Bayne (1964) worked at a site sheltered from direct wave action while most other studies appear to have been located in relatively exposed areas. Even the platform sheltered from direct wave action in the present study was battered by waves at high tide, especially during rough seas. Consequently, as the morphology of the settlement substratum and the hydrodynamic field this creates immediately around the substratum influences the ability of larvae to settle, it is possible that variation in small scale hydrodynamic factors associated with the mussel bed, such as the time taken for water to percolate through the bed, will influence the ability of mussels to settle directly onto the adult bed at different sites. The slight differences in the frequency and timing of settlement on algae and mussels between a wave exposed and sheltered platform only 30 m apart (Table 4.14), also suggests that local hydrography plays an important role in determining small scale patterns of larval availability and settlement. Alternatively, as there appears to be a limit to the number of larvae that can settle on a substratum (this study), and as larvae choose to settle on algae rather than on mussels (Petersen 1984), if the availability of preferred algal settlement substrata exceeds requirements, then larvae need not settle directly on the mussel bed at all.

In the South African mussel population studied about 40% of the settlers on the shore were found on foliose algae (Table 4.6). If these primary settlers do not migrate to the adult bed a substantial proportion of the reproductive output would be lost, but in support of work by Bayne (1964) and Seed (1969), indirect evidence suggests that this does occur. *M. edulis* appear to migrate off algae and re-settle in the adult bed when they are 1-2 mm, possibly because their thigmotactical needs are no longer met by the temporary algal settlement site (Maas Geesteranus 1942, Bayne 1964, Seed 1969). The present study showed that *P.perna* of 0.60-7 mm periodically disappeared from the algae, resulting in a low proportion (<16%) of individuals greater than 2 mm (Table 4.20), and none larger than 19 mm on algae, just as Beckley (1979) found at a nearby site. Since there was no evidence of mass mortality, these disappearances probably occurred when plantigrades migrated off the algae. Furthermore, secondary settlement resulted in an increase in the density and relative

Table 4.20: The relative proportion (%) of juvenile mussels within each cohort (size category) on coralline algae (C), other algae (A) and mussels (M) at the exposed and sheltered sites. The data come from Figure 4.2.

Cohort	Size (mm)	Sheltered			Exposed		
		C	A	M	C	A	M
1	<0.80	61	65	36	76	77	48
2	0.80-1.00	22	21	11	12	17	11
3	2.00-7.00	13	9	40	10	5	29
4	8.00-19.00	3	5	14	2	1	13

proportion of plantigrades 2-7 mm long, which exceeded that expected from growth of larvae which settled directly in the mussel bed. These two results suggest that plantigrades which migrate off algae settle secondarily on mussels. The lack of temporal co-ordination between migration off temporary settlement sites and secondary settlement in the mussel bed, probably occured because the migrants undergo bysso-pelagic dispersal before settling, and may even settle elsewhere. Primary and secondary settlement behaviour may be common along the South African coastline since settlement of larvae onto algae and the sudden appearance of large numbers (4 600 - 210 000.m^{-2}, Berry 1978) of late plantigrades less than 10 mm long in the mussel bed, have been recorded in several places (du Plessis 1977, Berry 1978, Griffiths 1981, Crawford & Bower 1983, Lambert & Steinke 1986, Chapter 5).

Thus it appears that larvae passively and/or selectively settle on algae and later migrate to the mussel bed, unless algal settlement sites are saturated, in which case larvae settle directly on mussels. However, although larvae prefer algae and settle in low intensities on mussels, this study shows that the importance of direct settlement cannot be overlooked. Since mussels covered a far greater area on the shore than algae, 60% of the settlers on the shore at Kenton, were in fact found on mussels. It is difficult to assess the relative contributions of direct, primary and secondary settlement towards recruitment into mussel populations. Primary and secondary settlement behaviour is obviously crucial to the maintenance of mussel populations in areas where there is no direct settlement of larvae on mussels. For example, the populations of *Macoma balthica* in the North Sea probably arise entirely as a result of secondary settlement of larvae which settle six months before on high tidal flats in the Wadden Sea (Beaukema & de Vlas 1989). However, the settlement behaviour is less important in areas where the rate of direct settlement into the mussel bed is high enough to balance the losses from the population. In areas like Kenton where the rate of settlement is generally low (Chapter 5), and a large proportion of the settlers are found on both mussels (60%) and algae (40%), it is probable that direct and secondary settlement contribute equally towards recruitment into mussel populations.

SECTION THREE

SETTLEMENT, POST-SETTLEMENT GROWTH AND MORTALITY, RECRUITMENT AND POPULATION DYNAMICS

CHAPTER 5

PRE- AND POST-SETTLEMENT FACTORS DETERMINING RECRUITMENT AND POPULATION DEMOGRAPHY

Introduction

A combination of pre- and post-settlement factors result in variability in recruitment of mobile offspring into sedentary adult populations, and this variability affects the structure and abundance of the populations (Roughgarden *et al.* 1984 & 1985, Connell 1985, Lewin 1986, Menge & Sutherland 1987, Hughes 1990, Bertness *et al.* 1992, Milicich *et al.* 1992, Meekan *et al.* 1993). Along the south coast of southern Africa, fluctuations in spawning intensity are directly linked to fluctuations in settlement intensity (Chapter 1). However, it is not known whether spawning intensity is linked to the intensity of recruitment into the adult population, since little is known about the relationship between settlement and recruitment. Thus the relative importance of pre- and post-settlement factors determining recruitment, and the abundance and structure of intertidal mussel populations is unkown.

The relationship between settlement and recruitment of invertebrates and algae is determined by post-settlement factors which modify the distribution and abundance of settlers prior to maturity (Buss 1981, Keough & Downes 1982, Wethey 1984 & 1986, Caffey 1985, Sale & Farrell 1988, McGuiness & Davis 1989, Osman *et al.* 1989 & 1992, Rowley 1989, Harvell *et al* 1990, Grosberg 1991, Martel & Chia 1991, Feller *et al* 1992, O Connor 1993). These include factors such as canopy shading and sweeping, environmental stress and predation (Connell 1961a&b, Sutherland 1974, Hawkins 1983, Young & Chia 1984, Stoner 1990, Brawley & Johnson 1991, Michington & Scheibling 1991). Post-settlement growth and mortality are also influenced by settlement intensity. Therefore, the relationship between settlement and recruitment, is determined by settlement intensity (Connell 1985). When settlement intensity is low it has little effect on growth and mortality, and pre-settlement factors influencing settlement control recruitment (Buss 1981, Keough & Downes 1982, Connell 1985, Davis 1988, Fairweather 1988, Bertness 1989, Harvell *et al.* 1990, Reed 1990, Reed *et al.* 1991). However, high settlement intensity uncouples the relationship between settlement and recruitment by reducing growth and increasing mortality (Connell 1985, Davis 1988, Holm 1990, Hughes 1990, Karlson & Levitan 1990, Sutherland 1990, Robertson 1992).

Furthermore, due to the effect of settlement intensity on growth and mortality, the abundance and size structure of populations may be very different in areas receiving consistently different levels of settlement (Guillou & Hily 1983).

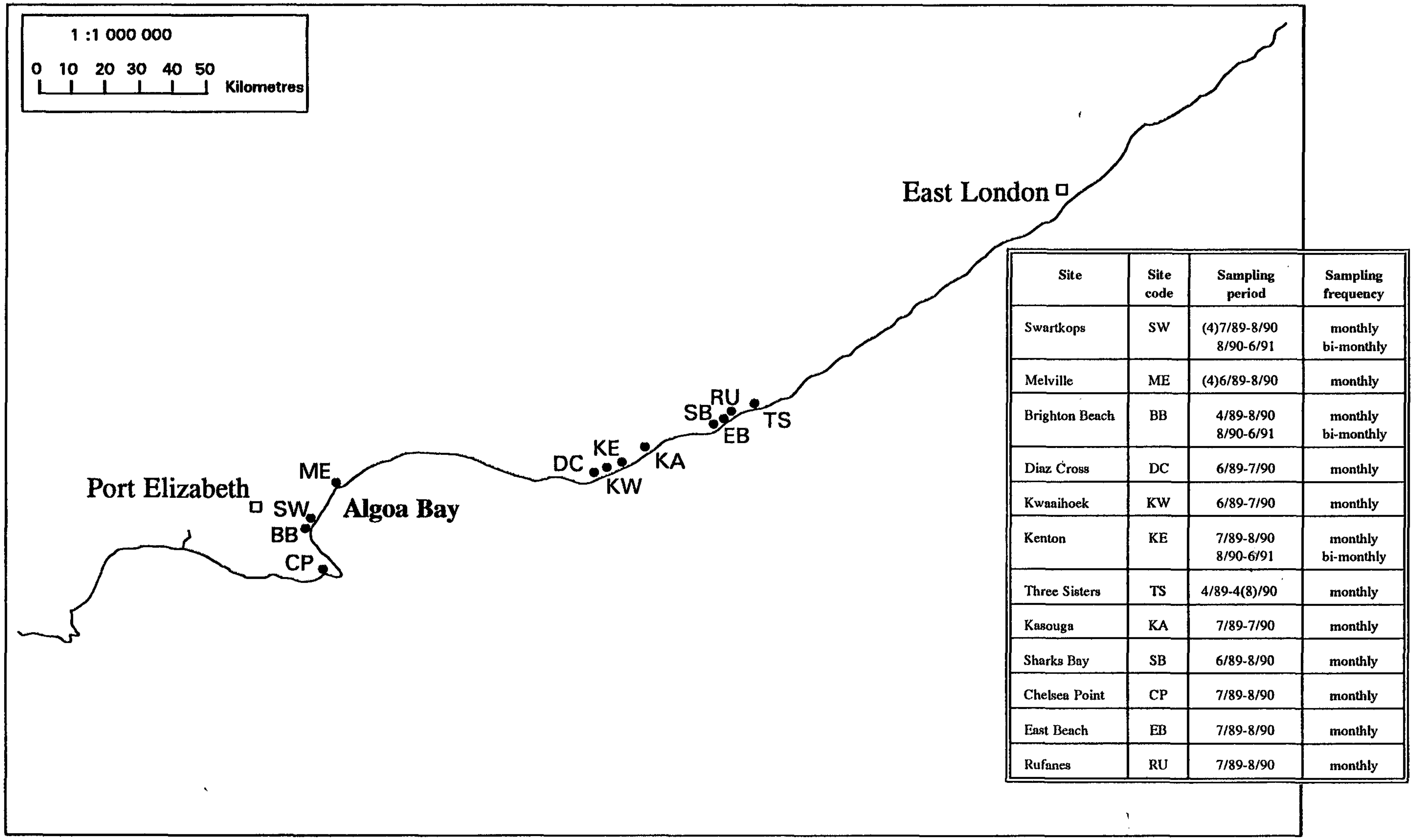
On the south coast spawning intensity was consistently greater in Algoa Bay than on the open coast (Chapter 1). This suggests that settlement intensity should be greater in the bay, and that the abundance and structure of mussel populations will vary between the bay and the coast.

This study examines patterns of settlement, post-settlement growth and mortality, and considers the relative importance of pre- (spawning intensity and dispersal) and post-settlement factors (settlement intensity, growth, mortality) to recruitment, the structure and density of intertidal mussel populations along the south coast of southern Africa.

Methods

Study sites

Study sites were chosen to represent the full range of regional (bays/open coast), local (sandstone/dune rock) and habitat (tidal elevation and the quantity of sand) conditions in the Algoa Bay region (Fig. 5.1). Sites on the open coast, were established at four dune rock shores (Diaz Cross, Kwaaihoek, Kenton, Three Sisters) and at five sandstone shores (Chelsea Point, Kasouga, Sharks Bay, East Beach, Rufanes). The three study sites (Brighton Beach, Swartkops, Melville) in the Bay were located on small platforms (~25 m^2) of consolidated dune rock. The mussel populations at Brighton Beach, Diaz Cross, Kwaaihoek, Kenton, Three Sisters, Kasouga and Sharks Bay, were free of sand as they were raised (>1.51m above MLWS) well above the seasonally fluctuating sand levels (Dower 1990). In contrast, sand was permanently found among mussels in the low shore (<0.68 m above MLWS) populations at Swartkops and Melville. Mussels found at intermediate heights (0.68-1.51 m above MLWS) on the shore at Chelsea Point, East Beach and Rufanes were scoured by sand at high tide and periodically buried, when the sand level rose in late



Site	Site code	Sampling period	Sampling frequency
Swartkops	SW	(4)7/89-8/90 8/90-6/91	monthly bi-monthly
Melville	ME	(4)6/89-8/90	monthly
Brighton Beach	BB	4/89-8/90 8/90-6/91	monthly bi-monthly
Diaz Cross	DC	6/89-7/90	monthly
Kwaaihoek	KW	6/89-7/90	monthly
Kenton	KE	7/89-8/90 8/90-6/91	monthly bi-monthly
Three Sisters	TS	4/89-4(8)/90	monthly
Kasouga	KA	7/89-7/90	monthly
Sharks Bay	SB	6/89-8/90	monthly
Chelsea Point	CP	7/89-8/90	monthly
East Beach	EB	7/89-8/90	monthly
Rufanes	RU	7/89-8/90	monthly

Figure 5.1: Map of the study region on the southern coast of South Africa indicating the position of the study sites. *Choromytilus meridionalis* was studied at Swartkops (SW) and Melville (ME) and *Perna perna* was studied at the rest of the sites.

summer between January and May (Dower 1990).

Sampling periodicity

The sampling periodicity at each site is summarised in Fig. 5.1 and explained in Chapter 1.

Sampling procedure

The technique used to sample mussel populations and process the samples, was described in Chapter 1.

Data were used to establish the monthly species composition, density, and size frequency distribution of mussels in the population at each site. The settlement pattern was established by examining temporal variations in the density of mussels <20 mm at each site. Cohort analysis of size frequency histograms was used to estimate post-settlement growth and mortality, settlement intensity and the intensity of recruitment into adult populations.

Cassie's (1954) method of probability analysis of cumulative frequencies obtained from size frequency histograms, was used to identify cohorts and estimate their mean size and density. This was complicated by repeated settlement occurring over extended periods and the difficulty in identifying discrete cohorts at sites where settlement intensity was low (eg. Three Sisters). Only those cohorts which could clearly be identified and followed until they disappeared or merged with other cohorts, were used in the following analyses. Regression of the change in mean size and density over time was used to estimate the growth and mortality rates of individual cohorts and all cohorts together. Settlement intensity was estimated as the density of a cohort at settlement, and recruitment intensity as the density of the cohort after 10 months on the shore, when it reached maturity.

Data on the spawning intensity (gamete output) prior to each settlement event were presented in Chapter 1.

Results

Species composition

Not unexpectedly (see Chapter 3) the species composition of mussel beds varied with height on the shore (Table 5.1). Populations low on the shore at Swartkops and Melville were dominated by *Choromytilus meridionalis* (90%) with a small proportion of *Perna perna* (10%). In contrast populations high on the shore were dominated by 94-99% *P. perna* with a trace (<1%) of *C. meridionalis* and *Mytilus galloprovincialis*. The species composition of populations at intermediate heights on the shore varied over time. For example, in April 1989 the mussel population at Chelsea Point consisted of 90% *P. perna* and 10% *C. meridionalis*, but when the mussel bed was next sampled in August 1989 the species composition had changed to 52% *P. perna* and 48% *C. meridionalis* (Table 5.2). Thereafter the proportion and density (Fig. 5.2, Table 5.2) of *C. meridionalis* declined steadily and by April 1990 the population was again dominated by 97% *P. perna* with only 3% *C. meridionalis* (Table 5.2). Similar temporal fluctuations in the abundance of *C. meridionalis* were recorded at East Beach and Rufanes, the other two intermediate sites (Fig. 5.2, Table 5.2).

Settlement, growth and mortality

The settlement patterns of different species were similar. Following Chapter 4 mussels <10 mm were classified as settlers, however, recruits of 10 -19 mm were highly mobile and capable of moving and re-settling elsewhere. Temporal variation in the density of settlers indicated that one or two new cohorts appeared in the population each year (Fig. 5.3). Each cohort settled over an extended period with 2-3 peaks in settlement activity during that time. The intensity, timing and duration of settlement peaks varied considerably between sites and over time (Fig. 5.3). Peaks in the density of recruits <20 mm (settlers <10 mm + juveniles 10-19 mm) were clearer than settlement peaks, at sites (eg. Three Sisters) where settlement intensity was low.

Cohort analysis showed that because of the extended settlement period, each cohort consisted of different aged mussels of varying size. To save space, examples of changes in the mean size, size range and density of each cohort in the population are given for Brighton Beach, Swartkops and

Table 5.1: The species composition of the mussel populations located less than 0.66-0.68 m (low), 0.66-1.73 m (mid or intermediate) and 1.51-2.15 m (high) above MLWS.

Site	Height	Percentage		
		Perna	*Choromytilus*	*Mytilus*
SW	Low	10	90	0
ME	Low	8	92	0
BB	High	94	4	2
DC	High	>99	<1	<1
KW	High	>99	<1	<1
KE	High	>99	<1	<1
TS	High	>99	<1	<1
KA	High	>99	<1	<1
SB	High	>99	<1	<1
CP	Mid	82	17	<1
EB	Mid	91	9	<1
RU	Mid	88	11	<1

Table 5.2: Temporal variation in the species composition (%) of populations at intermediate heights on the shore at (a) Chelsea Point, (b) East Beach and (c) Rufanes.

(a) Chelsea Point

Date	*Perna*	*Choromytilus*	*Mytilus*
04/89	90	10	0
07/89	75	23	2
08/89	52	47	1
09/89	76	24	0
10/89	64	33	3
11/89	74	25	1
01/90	72	27	1
02/90	79	20	1
03/90	62	38	0
04/90	96	2	2
05/90	96	4	0
07/90	97	3	0
08/90	88	11	1

(b) East Beach

Date	*Perna*	*Choromytilus*	*Mytilus*
07/89	86	13	0
08/89	90	10	0
09/89	93	6	0
10/89	95	5	0
11/89	93	7	1
01/90	93	6	0
02/90	97	3	0
03/90	98	2	0
04/90	88	11	0
05/90	82	18	0
07/90	93	7	0
08/90	86	14	1

Table 5.2 continued...

(c) Rufanes

Date	*Perna*	*Choromytilus*	*Mytilus*
07/89	94	5	1
08/89	90	10	0
09/89	86	14	0
10/89	93	5	2
11/89	72	28	0
01/90	71	29	0
02/90	87	4	0
03/90	86	14	0
04/90	97	3	0
05/90	93	6	1
07/90	79	20	2
08/90	86	12	2

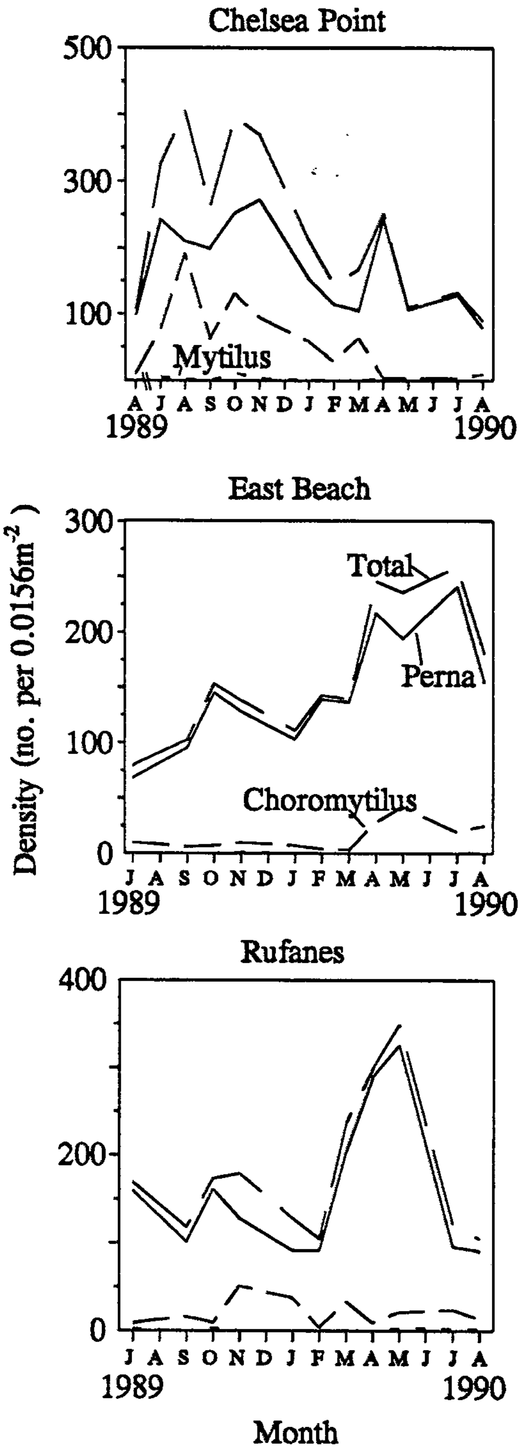


Figure 5.2: Temporal variation in the density of *Perna perna* and *Choromytilus meridionalis* at intermediate heights on the shore at Chelsea Point, East Beach and Rufanes.

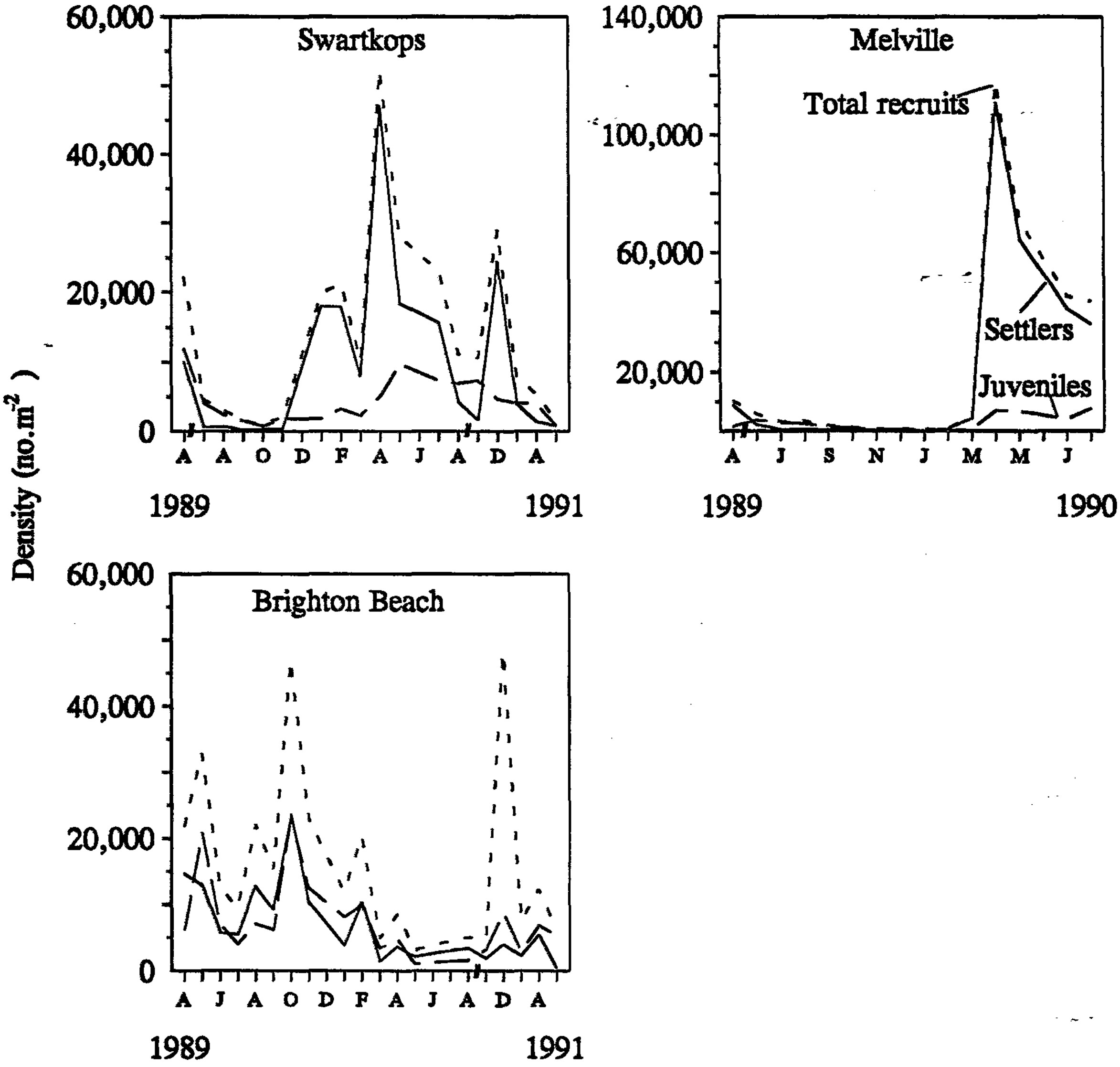


Figure 5.3a: Temporal fluctuation in the density of settlers (0-9 mm), juveniles (10-19 mm) and the total density of recruits (0-19 mm) at sites within Algoa Bay (a), and on dune rock (b) and sandstone (c) shores on the open coast.

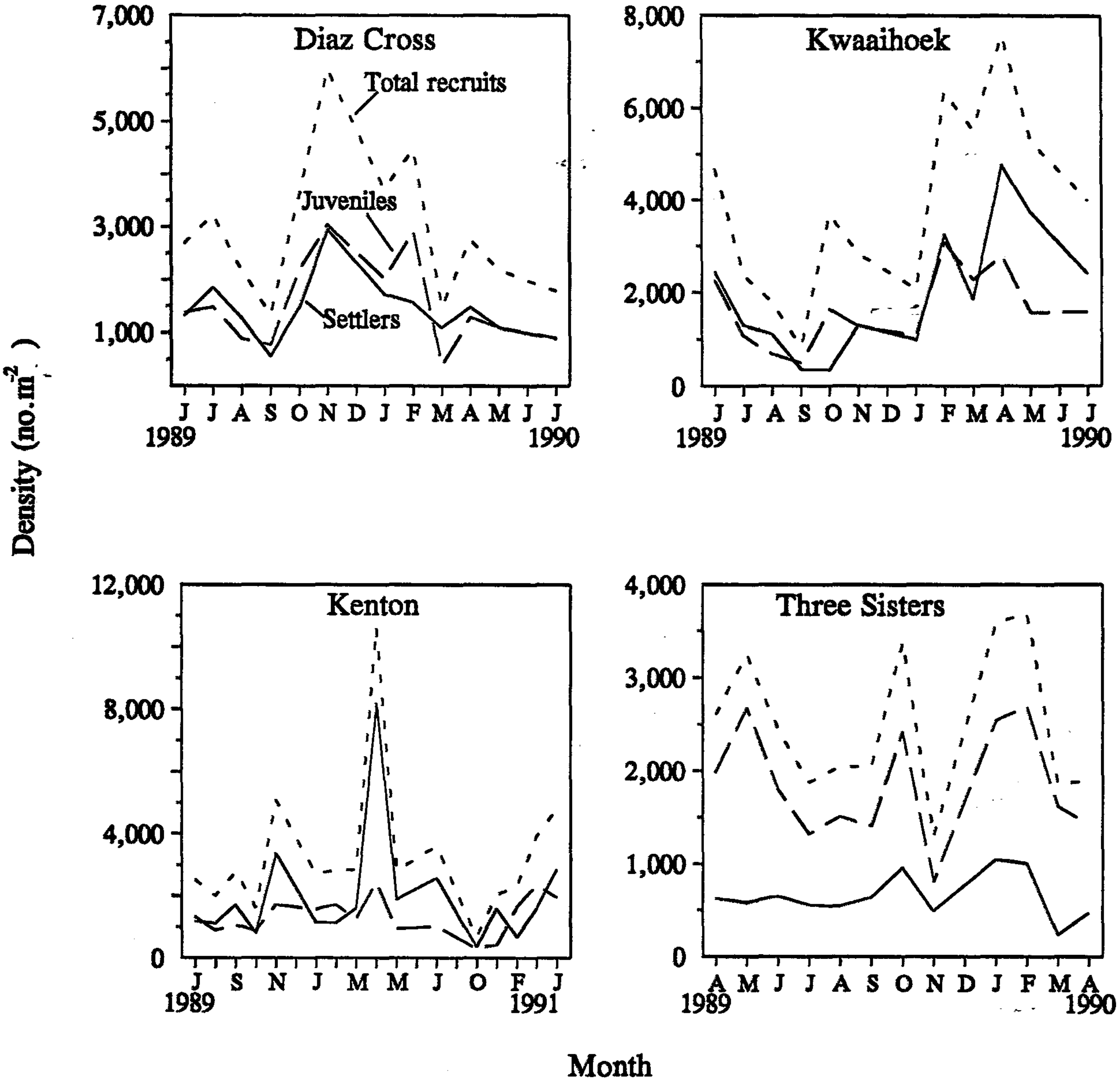

Diaz Cross
Total recruits
Juveniles
Settlers
7,000
5,000
3,000
1,000
J J A S O N D J F M A M J J
1989
1990
Kwaaihoek
8,000
6,000
4,000
2,000
0
J J A S O N D J F M A M J J
1989
1990
Kenton
12,000
8,000
4,000
0
J S N J M M J O F J
1989
1991
Three Sisters
4,000
3,000
2,000
1,000
0
A M J J A S O N D J F M A
1989
1990
Density (no.m^{-2})
Month

Figure 5.3b

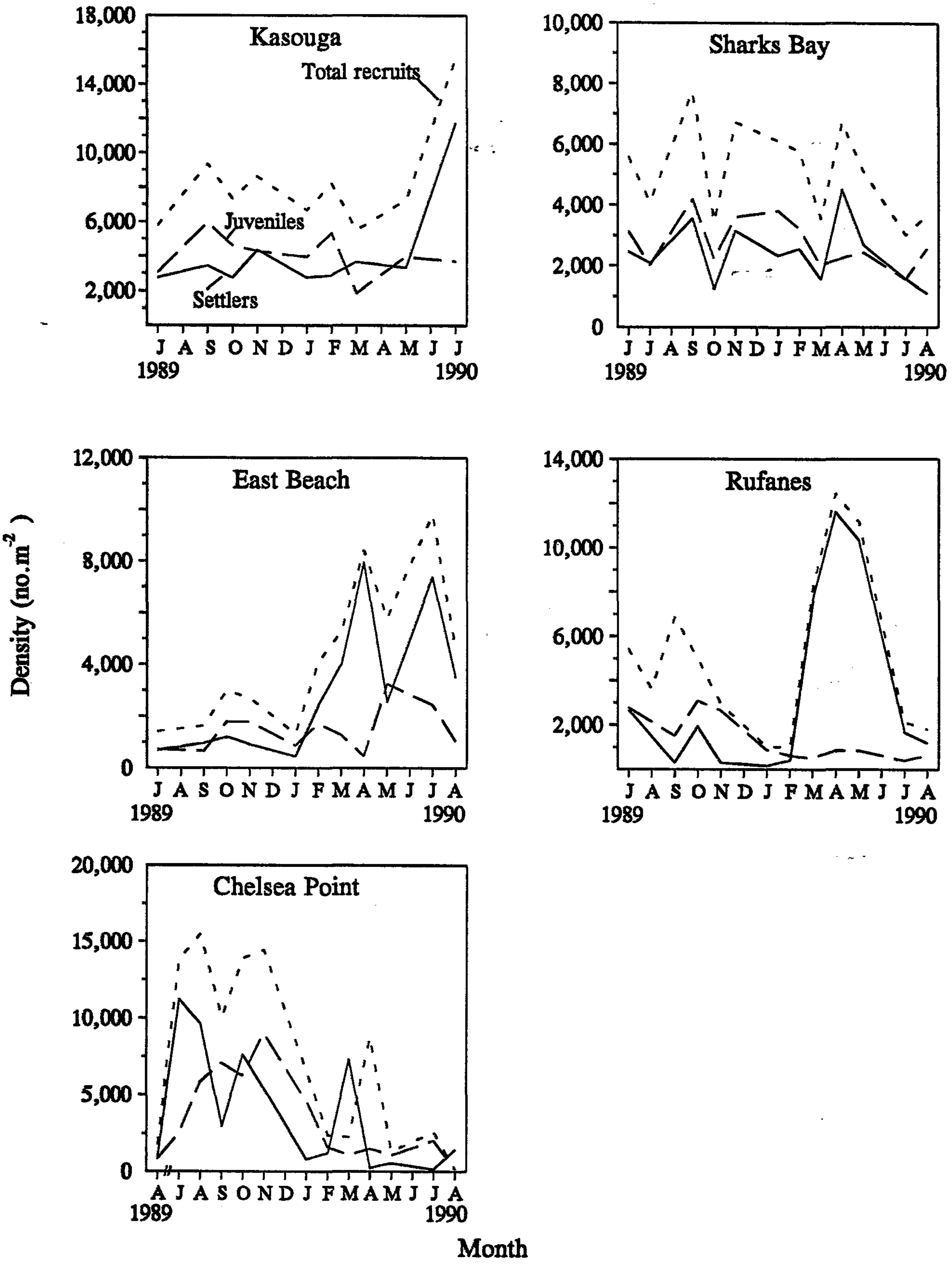

Kasouga
Total recruits
Juveniles
Settlers
18,000
14,000
10,000
6,000
2,000
J A S O N D J F M A M J J
1989
1990
Sharks Bay
10,000
8,000
6,000
4,000
2,000
0
J J A S O N D J F M A M J J A
1989
1990
East Beach
12,000
8,000
4,000
0
J A S O N D J F M A M J J A
1989
1990
Rufanes
14,000
10,000
6,000
2,000
J A S O N D J F M A M J J A
1989
1990
Chelsea Point
20,000
15,000
10,000
5,000
0
A J A S O N D J F M A M J J A
1989
1990
Density (no.m^{-2})
Month

Figure 5.3c

Melville only (Fig. 5.4). Unsurprisingly, regression analysis showed that the mean size and density of a cohort were usually significantly correlated ($P<0.05$, Table 5.3) with the period since settlement. The growth relationship varied for individual cohorts and regression curves which best fit the data were calculated, of which all, except one, were significant ($P<0.05$, Table 5.3). Not unexpectedly, density always declined exponentially. However, this relationship was not significant ($P>0.05$, Table 5.3) for some cohorts at open coast sites, probably because low settlement intensity and merging of cohorts made it difficult to estimate density accurately. Data for individual cohorts were pooled and a common growth and mortality curve calculated for mussels. Newly settled cohorts generally grew rapidly initially, and it was estimated from the common logarithmic growth curve, that they reach maturity (25-30 mm, Chapter 1) after 7 to 10 months (Fig. 5.5). However, because the growth of individual cohorts differed, there was some scatter about this, and the actual size of each cohort varied at maturity. Mortality was generally high during this time, and it was estimated from the common exponential decay curve, that only 17 to 29% of a cohort survived to maturity. It was also apparent that the mortality rate of individual cohorts varied quite substantially, and this resulted in a low correlation coefficient ($r=0.3718$, Fig. 5.6). Both mortality and growth slowed with time and age, adults only growing about 10 mm in their second year on the shore and even less in subsequent years (Fig. 5.5 & 5.6).

The density of *Perna perna* and *Choromytilus meridionalis* cohorts at settlement, ranged from approximately 5 000 - 60 000. m^{-2}, except on one occasion when the settlement intensity of *C. meridionalis* was 130 000. m^{-2}. Over the range of settlement intensities commonly recorded during this study, both growth and mortality of recruits were density independent, as regression analyses showed that there was no significant correlation between settlement intensity and the size or % mortality of individual cohorts after 10 months on the shore (Fig. 5.7 & 5.8). Thus, settlement intensity (5 000 - 130 000. m^{-2}) accounted for 73% of the variance in the intensity of recruitment into the mature adult population, and there was a positive linear relationship between these variables ($r=0.8554$, $P<0.001$, Fig. 5.9). However, analysis of this relationship indicated that it was not possible to predict recruitment into the adult population accurately when settlement densities were

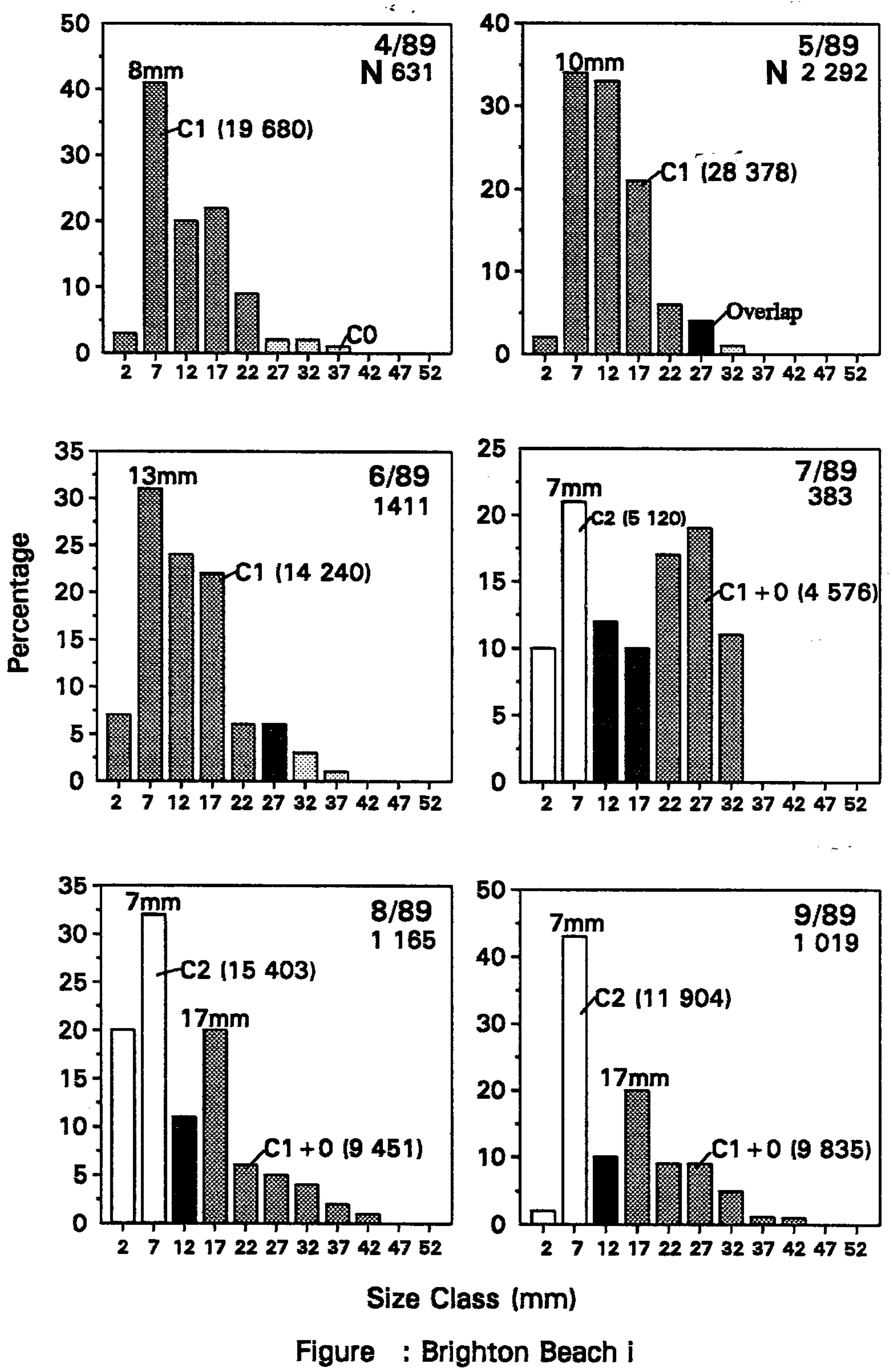


Figure 5.4: Temporal variation in the size frequency distribution at Brighton Beach, Swartkops and Melville. The modal size and density of each cohort in the population are indicated. The sample size (N) is shown in the top right hand corner, and the mid-point of each 4mm size class are shown on the X axis (eg. 0-4 mm size class denoted as 2 mm).

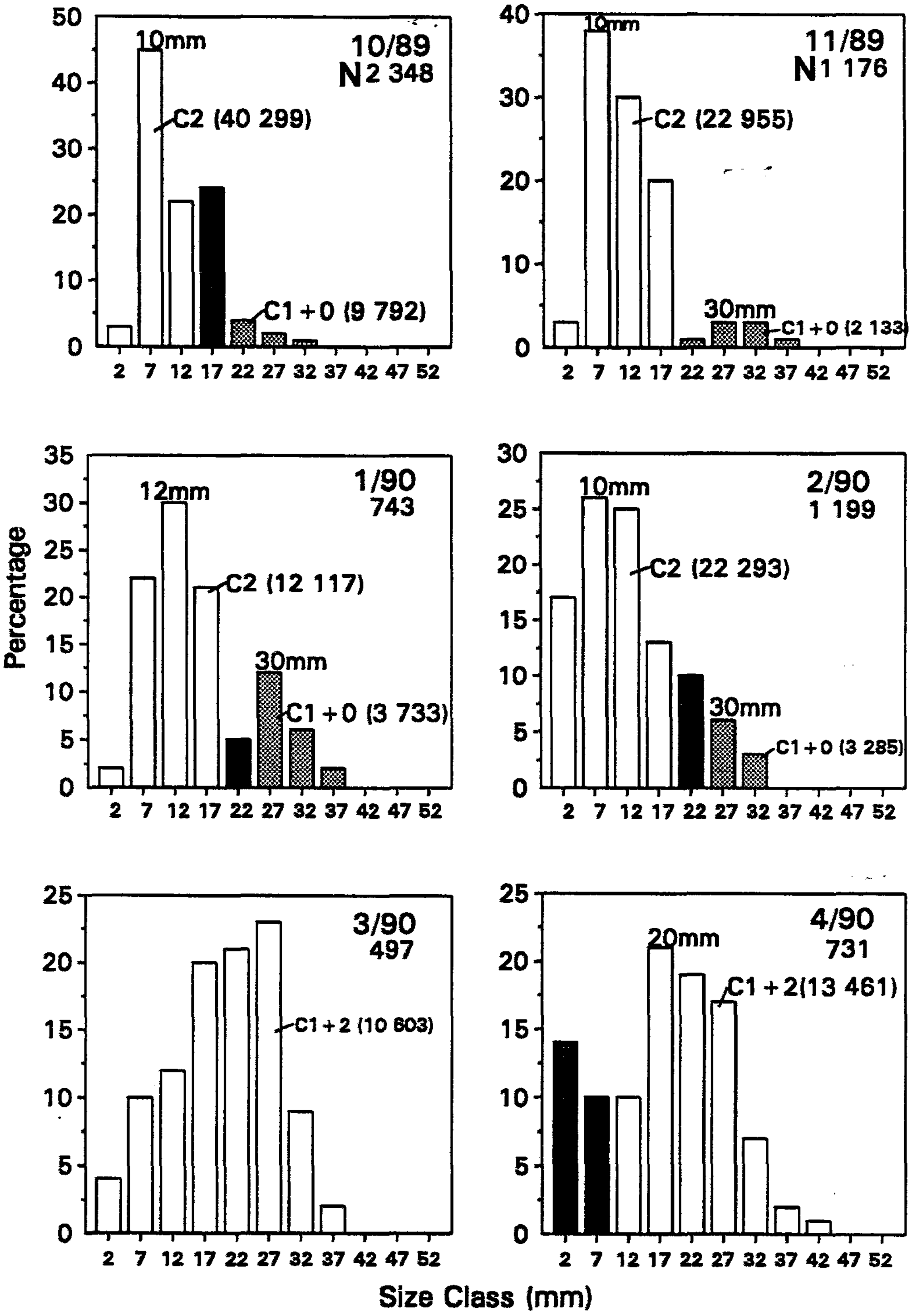


Figure : Brighton Beach ii

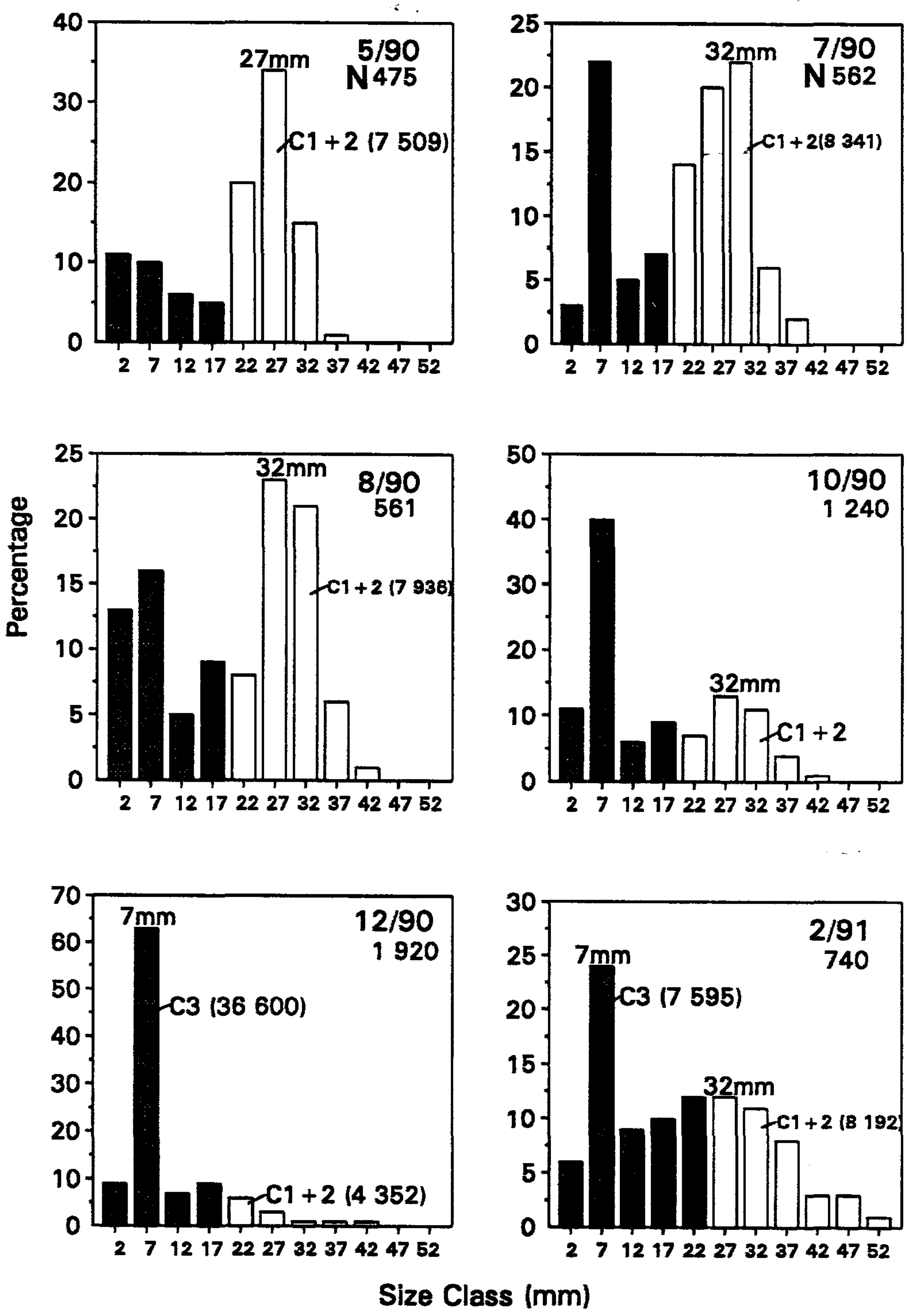


Figure : Brighton Beach iii

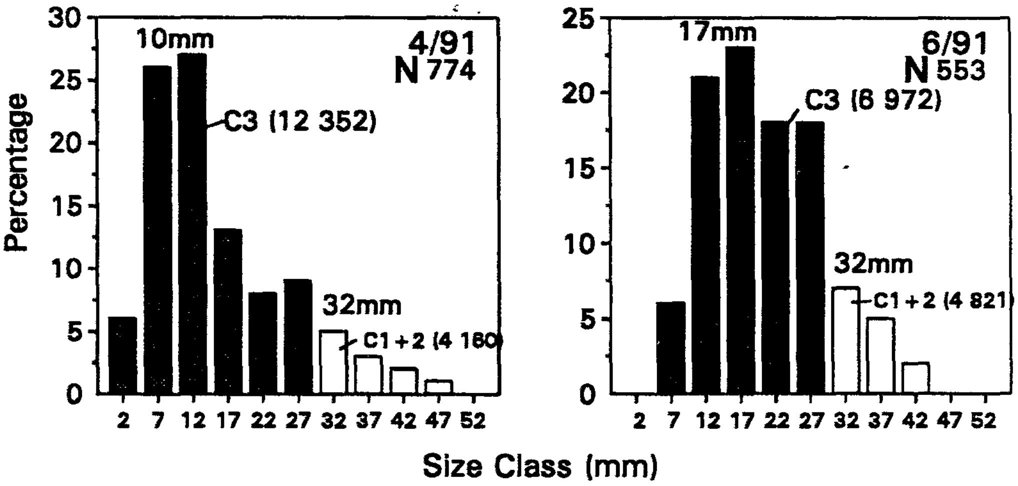


Figure : Brighton Beach iv

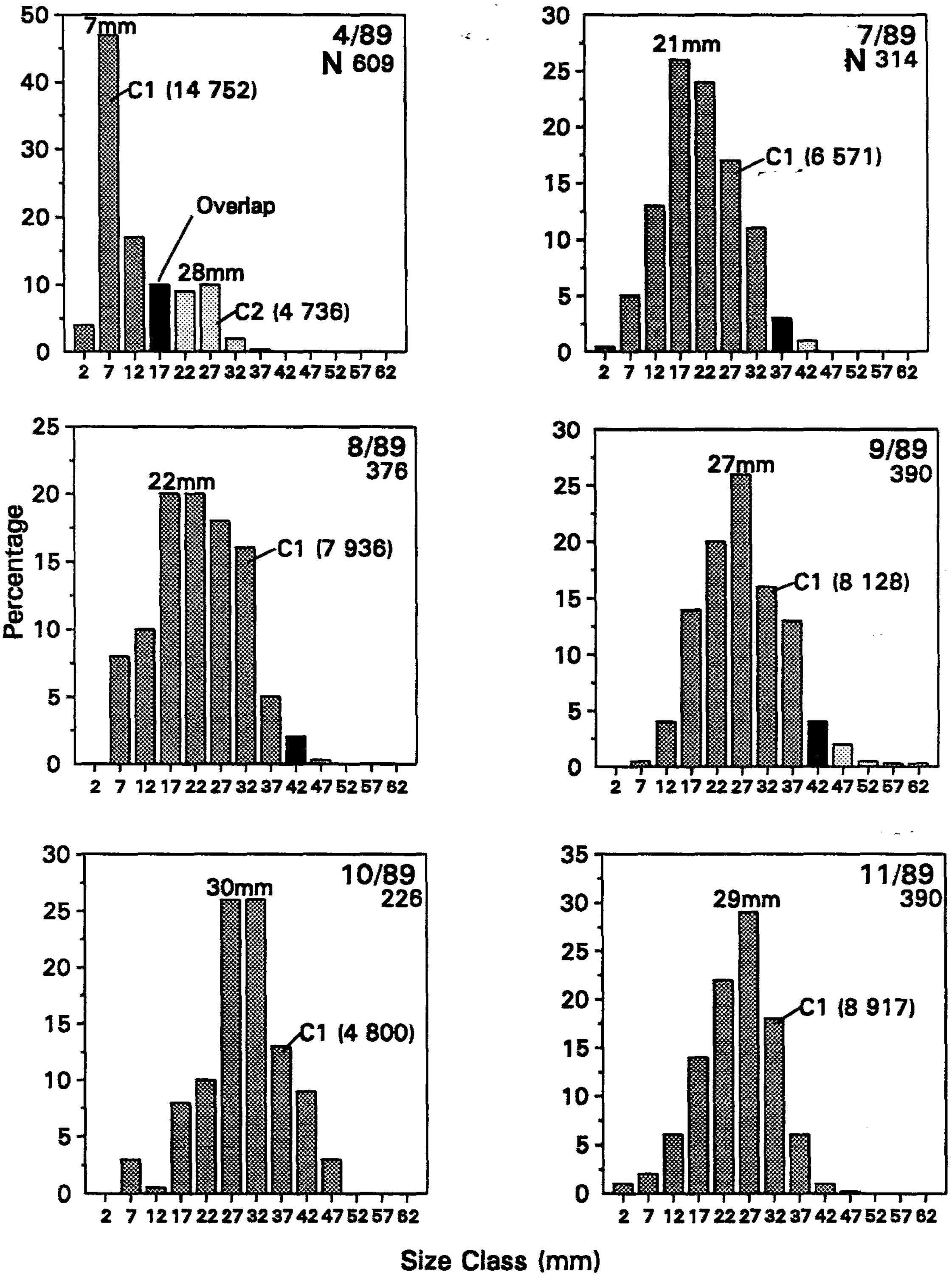


Figure : Swartkops i

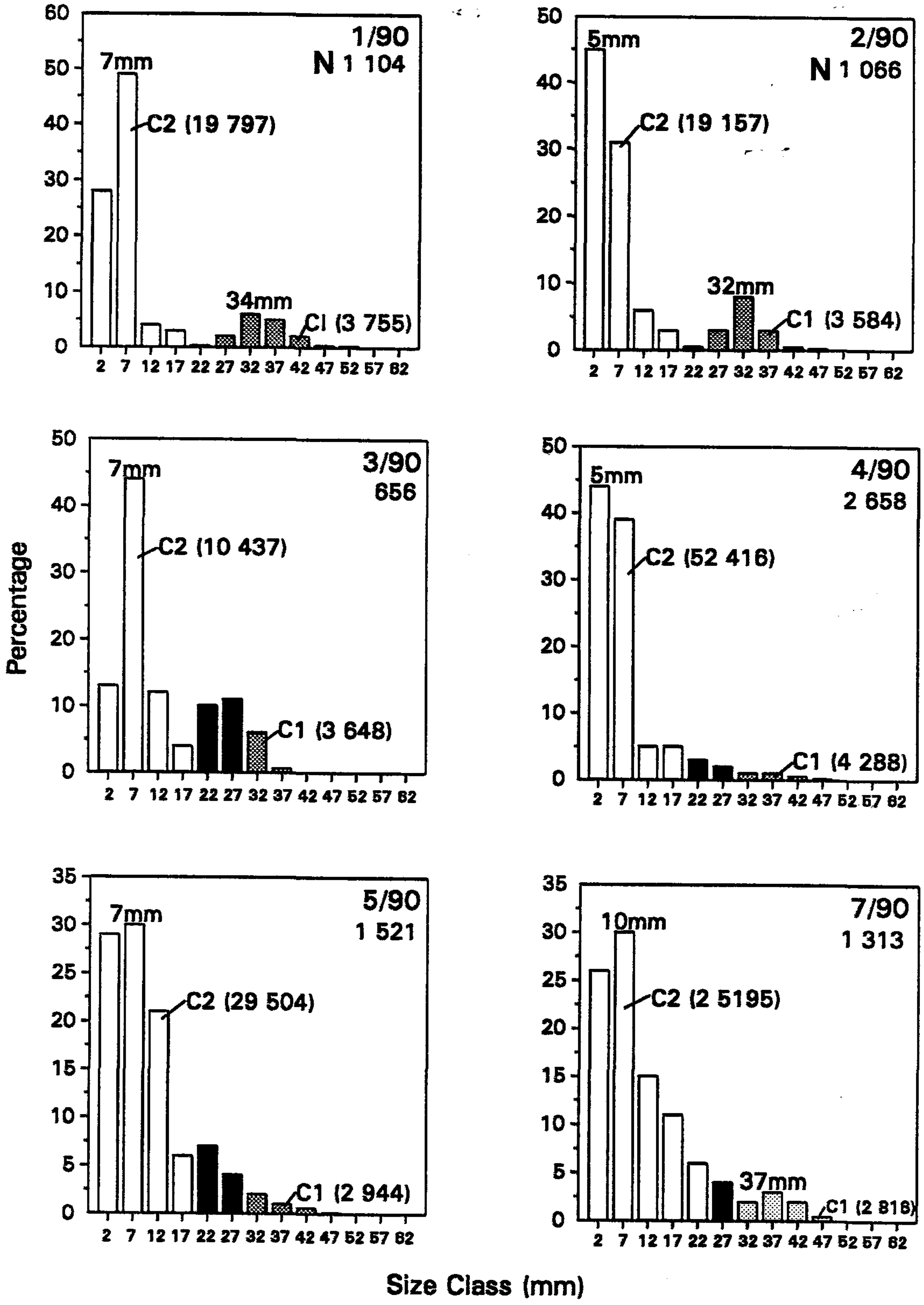


Figure : Swartkops ii

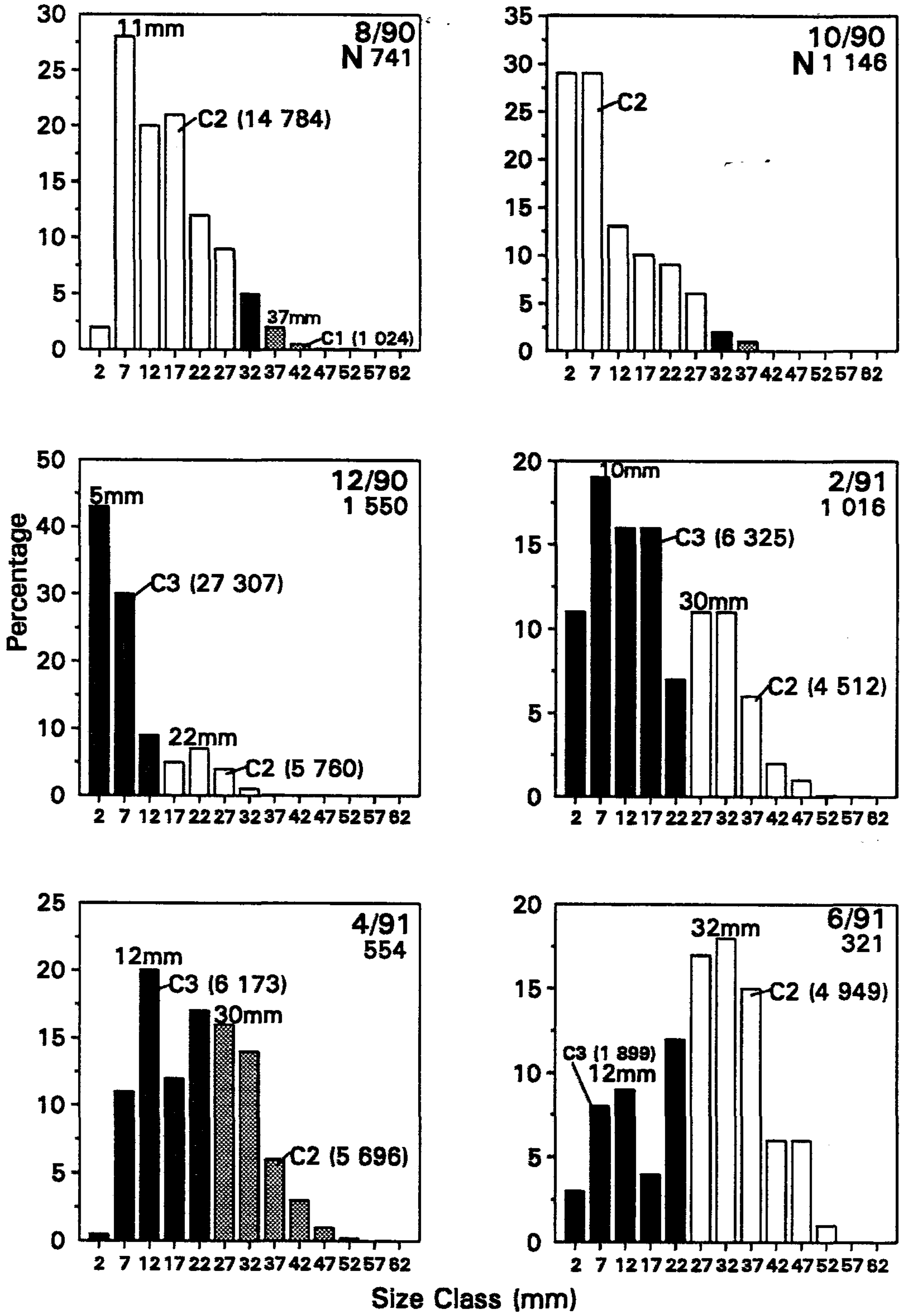


Figure : Swartkops iii

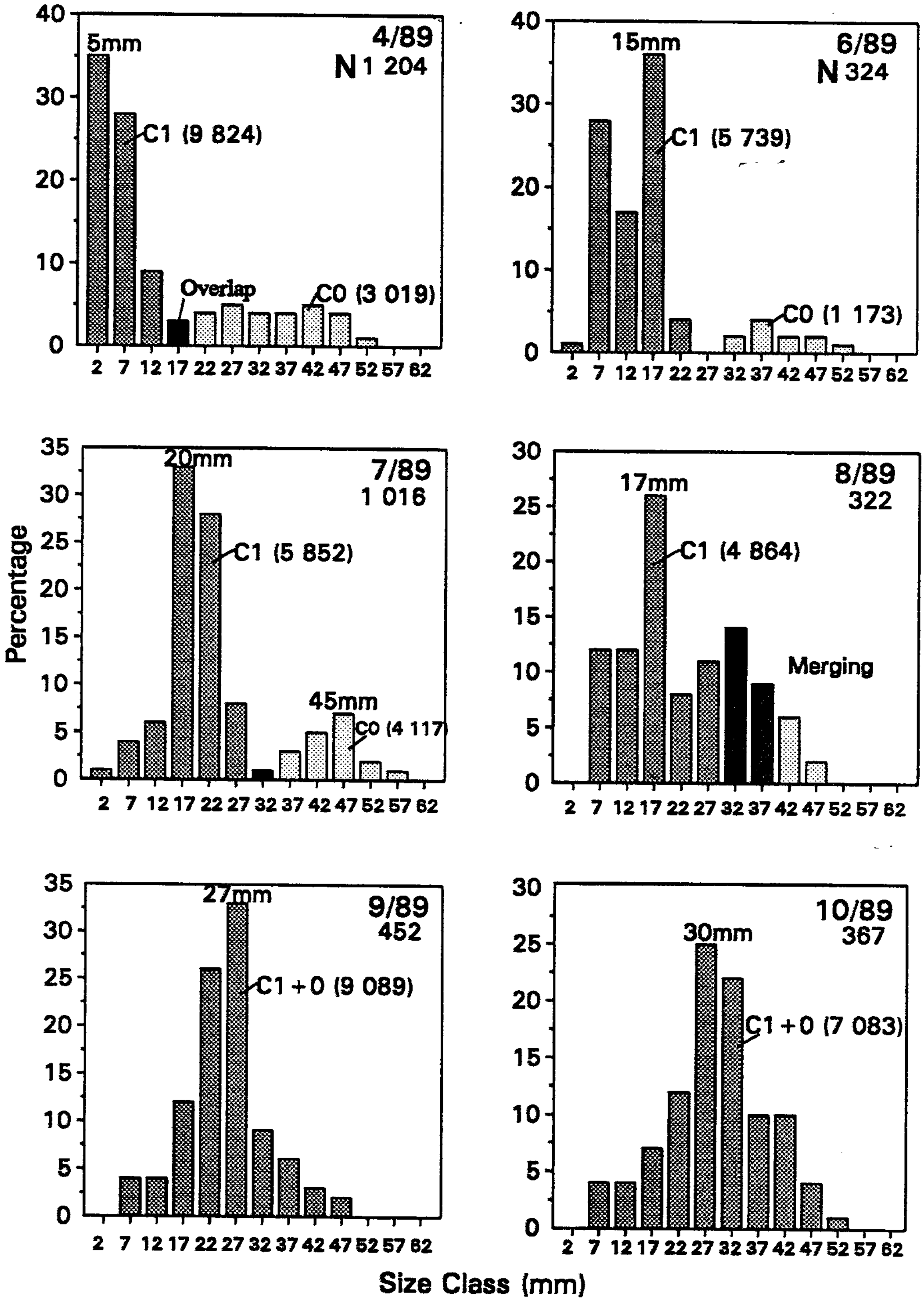


Figure : Melville i

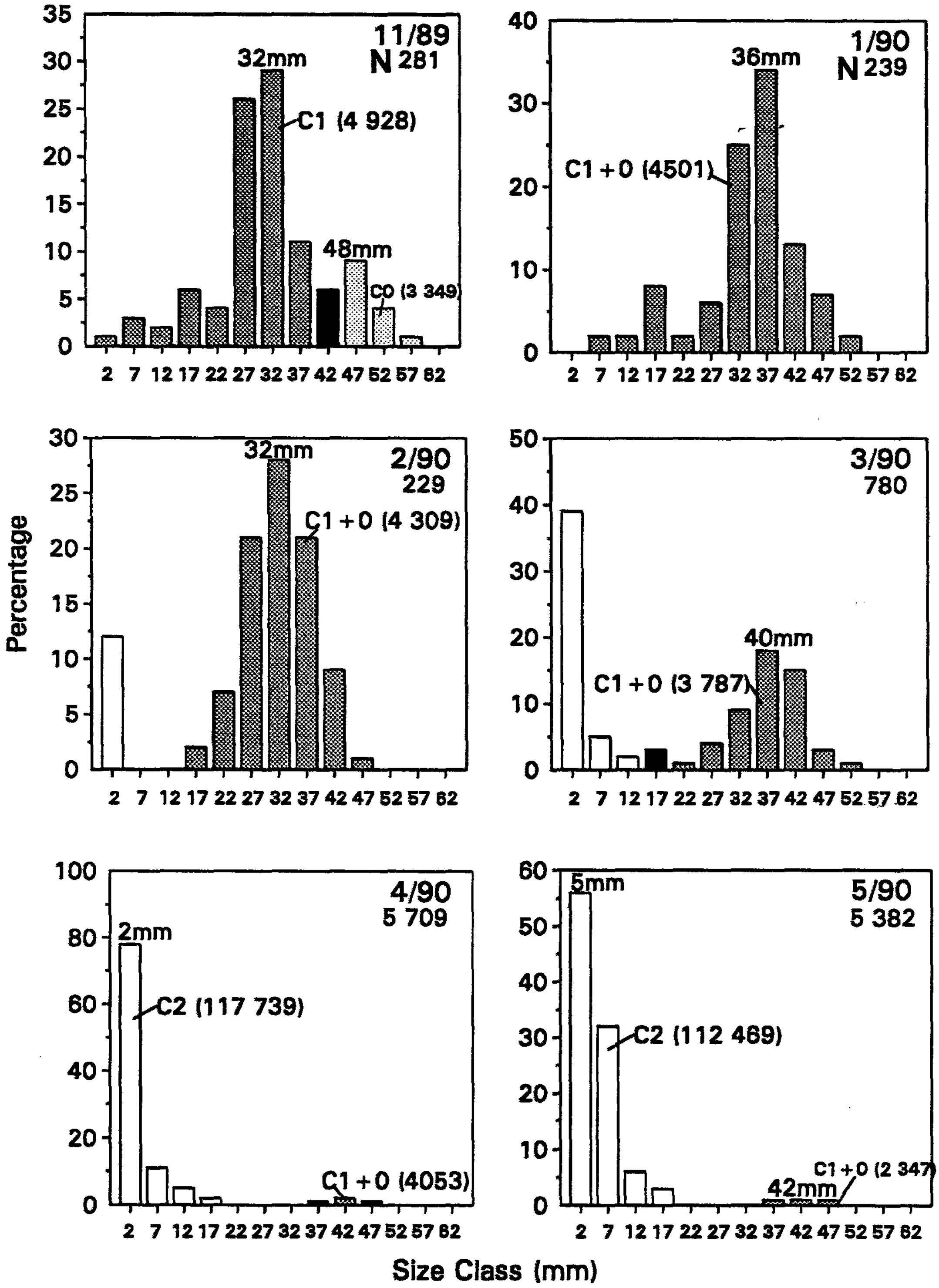


Figure : Melville ii

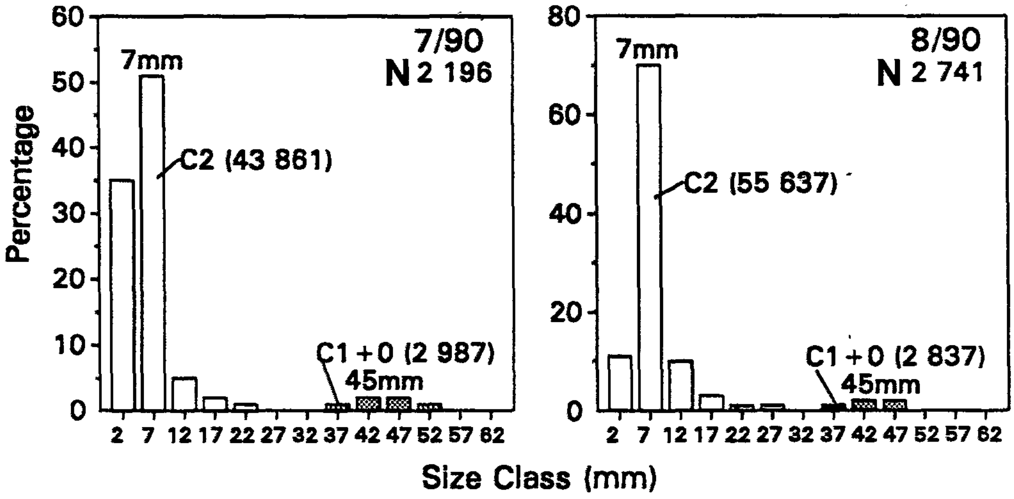


Figure : Melville iii

Table 5.3: Coefficients for regression (best fit) of the modal size (G=growth) and density (M=mortality) of a cohort (C) against the length of time since settlement (mode 2-7mm, maximum density). Data for regressions were obtained from Fig. 5.4, and the number of data pairs for regressions depended on the length of time cohorts could be clearly identified. No data are shown for Three Sisters, Kasouga or East Beach as either settlement intensity was too low to identify clear cohorts and/or the time series was not long enough to do a regression.

Site			Length	Type	*a*	*b*	r^2	*n*	*P*
BB	G	C1	4/89-10/89	Exponential	9.12	0.14	0.93	9	<0.05
	M	C1	5/89-7/89	Exponential	27 406.00	-0.60	1.00	3	<0.05
	G	C2	9/89-6/91	Logarithmic	4.06	9.82	0.80	14	<0.05
	M	C2	10/89-5/90	Exponential	33 076.00	-0.16	0.74	7	<0.05
	G	C3	12/90-6/91	Exponential	6.07	0.15	0.86	4	<0.05
	M	C3	12/90-6/91	Exponential	24 387.00	-0.22	0.58	4	>0.05
SW	G	C1	4/89-8/90	Power	15.10	0.33	0.89	10	<0.05
	M	C1	4/89-10/89	Exponential	13 748.00	-0.16	0.76	5	<0.05
	G	C2	4/90-6/91	Linear	1.85	2.18	0.83	8	<0.05
	M	C2	4/90-8/90	Exponential	47 773.00	-0.27	0.89	4	<0.05
	G	C3	12/90-6/91	Linear	6.30	1.15	0.90	4	<0.05
	M	C3	12/90-6/91	Exponential	22 326.00	-0.40	0.90	4	<0.05
ME	G	C1	4/89-8/90	Logarithmic	1.48	15.56	0.94	13	<0.05
	M	C1	4/89-8/89	Exponential	9 271.00	-0.17	0.90	4	<0.05
	G	C2	4/90-8/90	Linear	2.85	1.20	0.93	4	<0.05
	M	C2	4/90-8/90	Exponential	122 846.00	-0.24	0.80	4	<0.05

Table 5.3 continued...

Site			Length	Type	a	b	r^2	n	P
DC	G	C1	4/89-7/90	Power	5.60	0.76	0.98	9	<0.05
	M	C1	7/89-1/90	Exponential	11 126.00	-0.23	0.93	4	<0.05
	G	C2	3/90-7/90	Linear	3.20	2.03	0.88	4	<0.05
	M	C2	11/89-7/90	Exponential	6 400.00	-0.10	0.37	7	>0.05
KW	G	C1	6/89-3/90	Logarithmic	10.30	12.32	0.98	6	<0.05
	M	C1	6/89-10/89	Exponential	6 836.00	-0.37	0.99	4	<0.05
KE	G	C1	11/89-2/90	Exponential	2.18	0.01	0.91	3	>0.05
	M	C1	11/89-2/90	Exponential	4 764.00	-0.19	0.64	3	>0.05
	G	C2	4/90-2/91	Linear	3.28	1.08	0.82	5	<0.05
	M	C2	4/90-10/90	Exponential	7 782.00	-0.39	0.87	4	<0.05
SB	G	C1	11/89-3/90	Linear	7.43	2.14	0.97	4	<0.05
	M	C1	11/89-3/90	Exponential	6 991.00	-0.14	0.84	4	<0.05
	M	C2	4/90-7/90	Exponential	7 958.00	-0.34	0.89	3	>0.05
RU	G	C1	4/90-8/90	Power	2.07	0.97	0.96	4	>0.05
	M	C1	4/90-8/90	Exponential	12 256.00	-0.52	0.95	4	<0.05
CP	G	C1	7/89-1/90	Linear	9.58	1.30	0.87	7	<0.05
	M	C1	11/89-2/90	Exponential	15 778.00	-0.37	0.96	3	<0.05
	G	C2	4/90-8/90	Linear	7.45	3.40	0.89	4	<0.05
	M	C2	4/90-8/90	Exponential	5 013.00	-0.36	0.43	4	>0.05

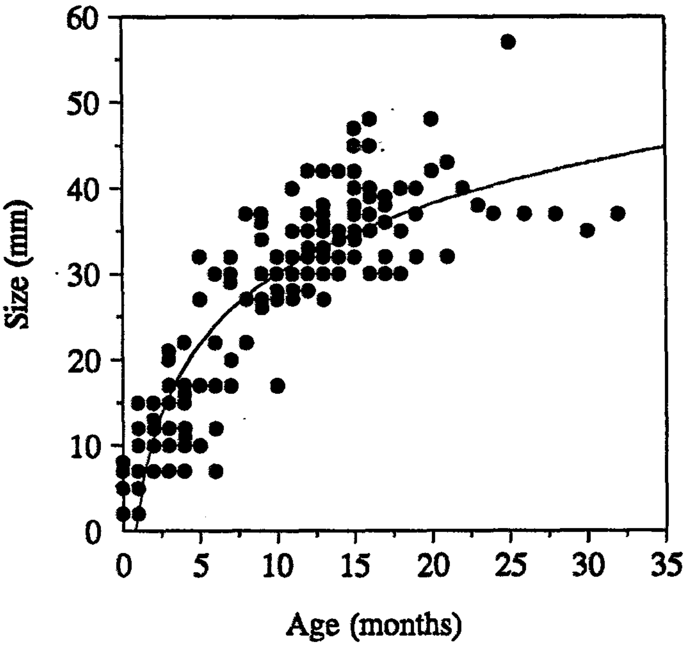


Figure 5.5: Regression of cohort age (independent variable) against the modal size (dependent variable) of a cohort. The data for different cohorts were pooled to establish a general growth curve for mussels. The coefficients of the logarithmic curve fitted to the data and the significance of the correlation are $a=2.8162$, $b=11.7961$, $r^2=0.7629$, $P<0.001$ and the sample size was 176.

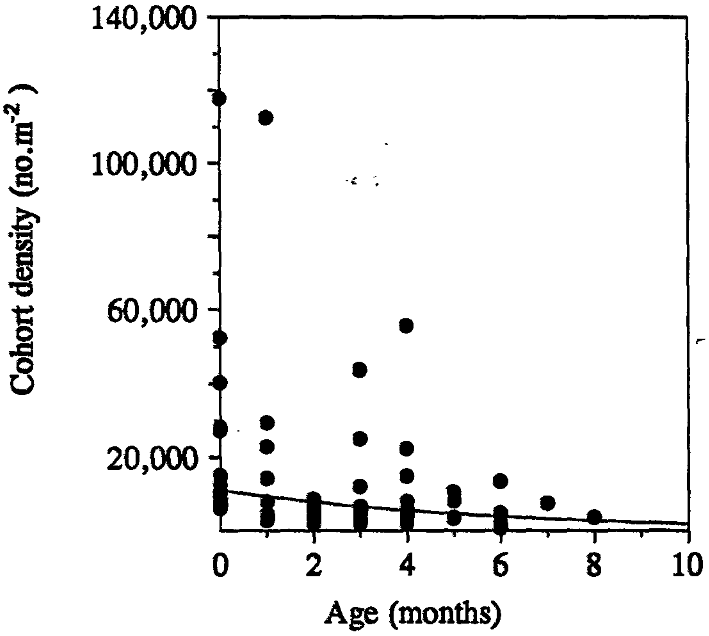


Figure 5.6: The change in density of settled cohorts over time. The data for the different cohorts were pooled to establish a general decay or mortality curve for mussels. The regression coefficients of the exponential curve fitted to the data and the significance of the correlation are $a=11\ 073$, $b=-0.1751$, $r^2=0.1382$, $P<0.001$ and the sample size was 75.

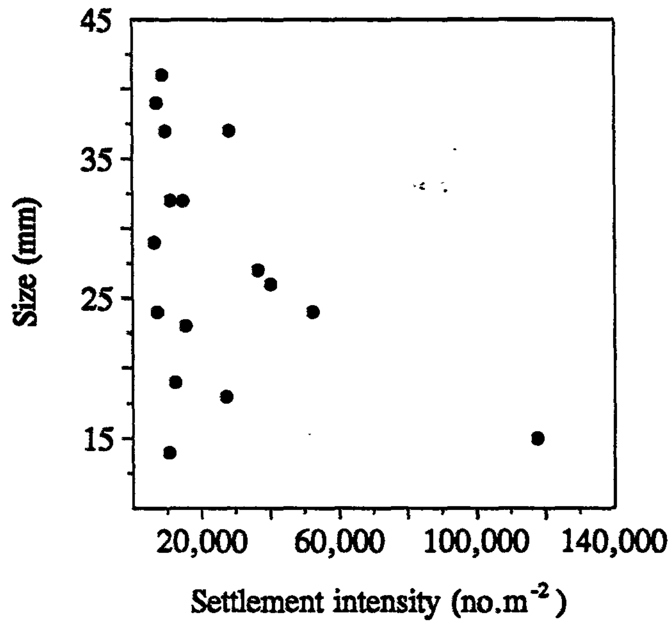


Figure 5.7: Regression of settlement intensity or density of a cohort at settlement (independent variable) against the modal size of a cohort after ten months on the shore (dependent variable). The modal size was calculated from the growth curve for each individual cohort.

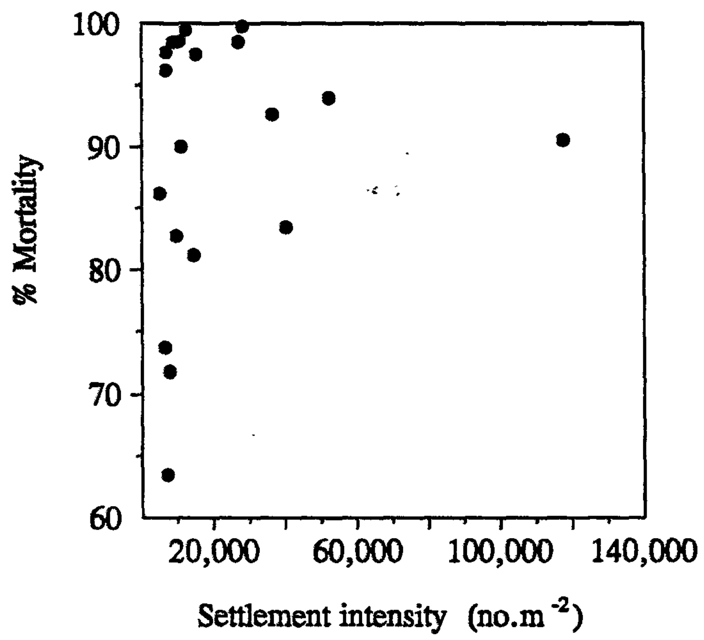


Figure 5.8: Regression of settlement intensity or density of a cohort at settlement (independent variable) against the mortality (%) suffered by a cohort during the 10 months prior to maturity (dependent variable). Mortality was calculated from the decline in density of each individual cohort. No curve was fitted to the data (sample size 19) as there was no significant relationship ($P > 0.05$) between these two variables.

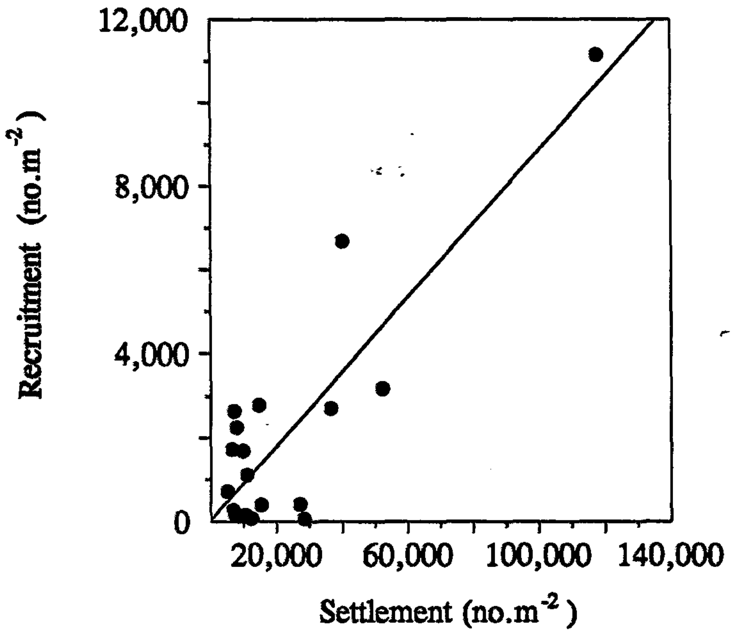


Figure 5.9: Regression of settlement intensity (density of newly settled cohort) against the intensity of recruitment into the mature adult population (density of cohort after 10 months). The recruitment intensity was calculated from the decline in density of each individual cohort. The coefficients of the linear curve fitted to the data and the significance of the correlation are $a=28.6745$, $b=0.0883$, $r^2=0.7317$, $P<0.001$ and the sample size was 19.

below 60 000. m^{-2}. Furthermore, when settlement intensities were below 60 000. m^{-2}, regression analysis showed there was a positive linear correlation between spawning intensity and settlement intensity (Chapter 1, Fig. 1.4), but not between spawning intensity and subsequent recruitment intensity (Fig. 5.10). Multiple regression analysis indicated that together spawning intensity, settlement intensity, growth and mortality prior to maturity accounted for 76% of the variance in recruitment into the adult population (Table 5.4).

Population size structure and abundance

Mean settlement intensity was significantly higher in Algoa Bay than on the open coast (ANOVA, $P<0.05$), and slightly, but not significantly, higher on coastal sandstone shores than on dune rock shores (Table 5.5). This was associated with differences in population size structure (Fig. 5.11) and abundance (Fig. 5.12) between the bay, coastal dune rock and sandstone shores. ANOVA and Tukey multiple range tests identified significant differences ($P<0.0001$) in the mean density of recruits <20 mm, immature adults 20-24 mm and mature adults >25 mm between Algoa Bay, coastal dune rock and sandstone shores.

Repeated high intensity settlement at sites in Algoa Bay (Fig. 5.3a), especially Brighton Beach, resulted in populations dominated by a high density of small individuals (2-30 mm) (Fig. 5.11a). The maximum mean cohort size of *P. perna* recorded at Brighton Beach was 30-32 mm, and it was estimated from the growth curves for individual cohorts at this site, that these individuals were less than a year old. The estimated longevity was slightly longer for *C. meridionalis* at Swartkops (1-2 years) and Melville (2-3 years) where maximum mean cohort sizes of 35mm and 47 mm respectively, were recorded (Fig. 5.4, Table 5.6). Populations underwent large temporal fluctuations in abundance (from ~5 000 to 130 000. m^{-2}) as recruit (16 471 ± 1 791. m^{-2}) and adult (3 441 ± 132. m^{-2}) densities varied greatly over time (Fig. 5.12a, Table 5.7 & 5.8).

In contrast populations on coastal dune rock shores (eg. Three Sisters, Fig. 5.3b) had a low density of large individuals, ~34-44% of which were >30 mm (Fig. 5.11b). The maximum mean cohort size ranged from 37 - 57 mm, and it was estimated that *P. perna* survived for 2-4 years on

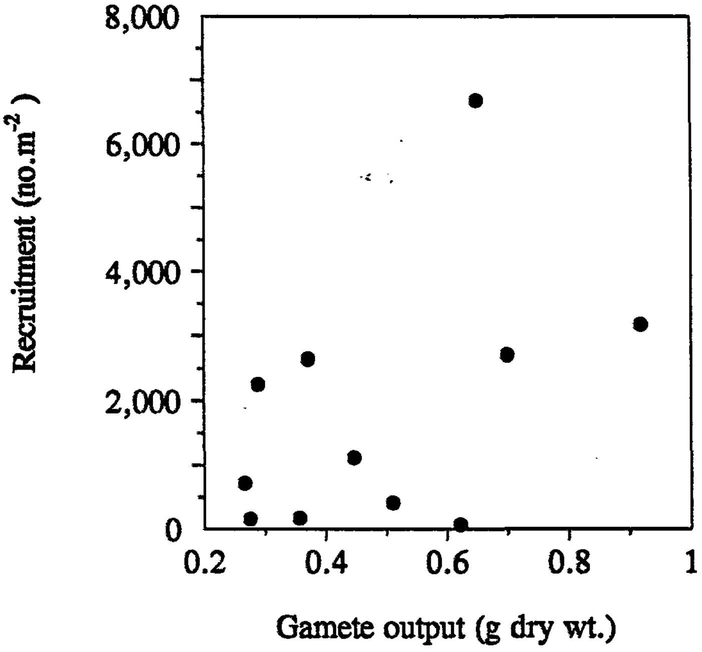


Figure 5.10: Regression of spawning intensity (gamete output in g dry weight) against the intensity of subsequent recruitment into the adult population. The regression equation, sample size and correlation coefficients were: $y = 1478x - 15\ 714$, $n = 11$, $r^2 = 0.2197$, $p>0.05$.

Table 5.4: Multiple regression model [$y = 15\,410 - 19\,980x_{(GO)} + 0.3380x_{(SI)} + 113x_{(G)} - 155x_{(M)}$] for gamete output (g) during spawning (from Chapter 1), settlement intensity, growth and mortality of settled cohorts in the 10 months prior to maturity (independent variables) against the intensity of recruitment into the mature adult population (dependent variable).

Independent variable	Coefficient	Standard error (SE)	t-value	*P*
Constant	15 410	3 809	4.0455	0.0155
Gamete output (GO)	-19 980	8 973	-2.2268	0.0899
Settlement intensity (SI)	0.3380	0.1	2.9956	0.0401
Growth (G)	113	67	1.6892	0.1664
Mortality (M)	-155	37	-4.2133	0.0135

$r^2 = 0.7551$, *SE* = *1 077, Durban Watt Statistic* = *2.7830*

Table 5.5: The range and mean (±standard error) settlement intensity (density of newly settled cohorts) at sites within Algoa Bay (AB) and on coastal dune rock (DR) and sandstone shores (SS).

Region	Site	*n*	Mean (no.m^{-2})	Standard error (no.m^{-2})	Range (no.m^{-2})
AB	BB	3	35 095	3 523	10 000 - 118 000
	SW	3	31 495	11 072	
	ME	2	63 782	53 598	
DR	DC	2	8 171	1 974	5 000 - 11 000
	KW	2	7 563	416	
	KE	2	7 968	2 806	
SS	CP	2	12 213	3 296	6 000 - 16 000
	KA	1	8 789	-	
	SB	3	6 521	259	
	EB	2	8 501	1 824	
	RU	1	12 501	-	

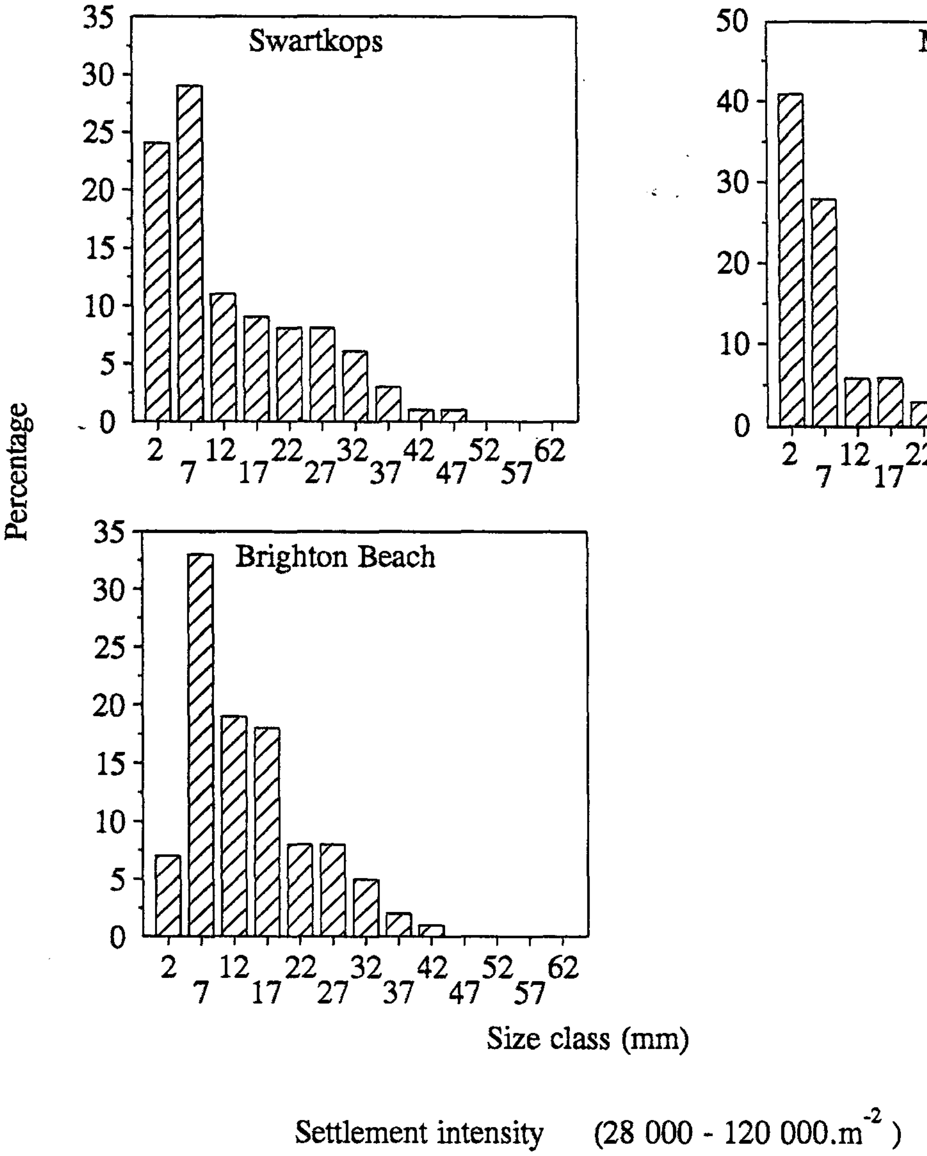


Figure 5.11a: The general size frequency distribution using pooled data from each month, of mussel populations within Algoa Bay (a), on dune rock (b) and sandstone (c) shores. The standard deviation for recruits (<20 mm) was 1-16% and for adults 1-9%. The sample size each month was approximately 1 000 in Algoa Bay, 600 on dune rock shores and 500 on sandstone shores. The mid-point of each 4 mm size class (eg. 0-4 mm size class is denoted as 2mm) are shown on the X axis.

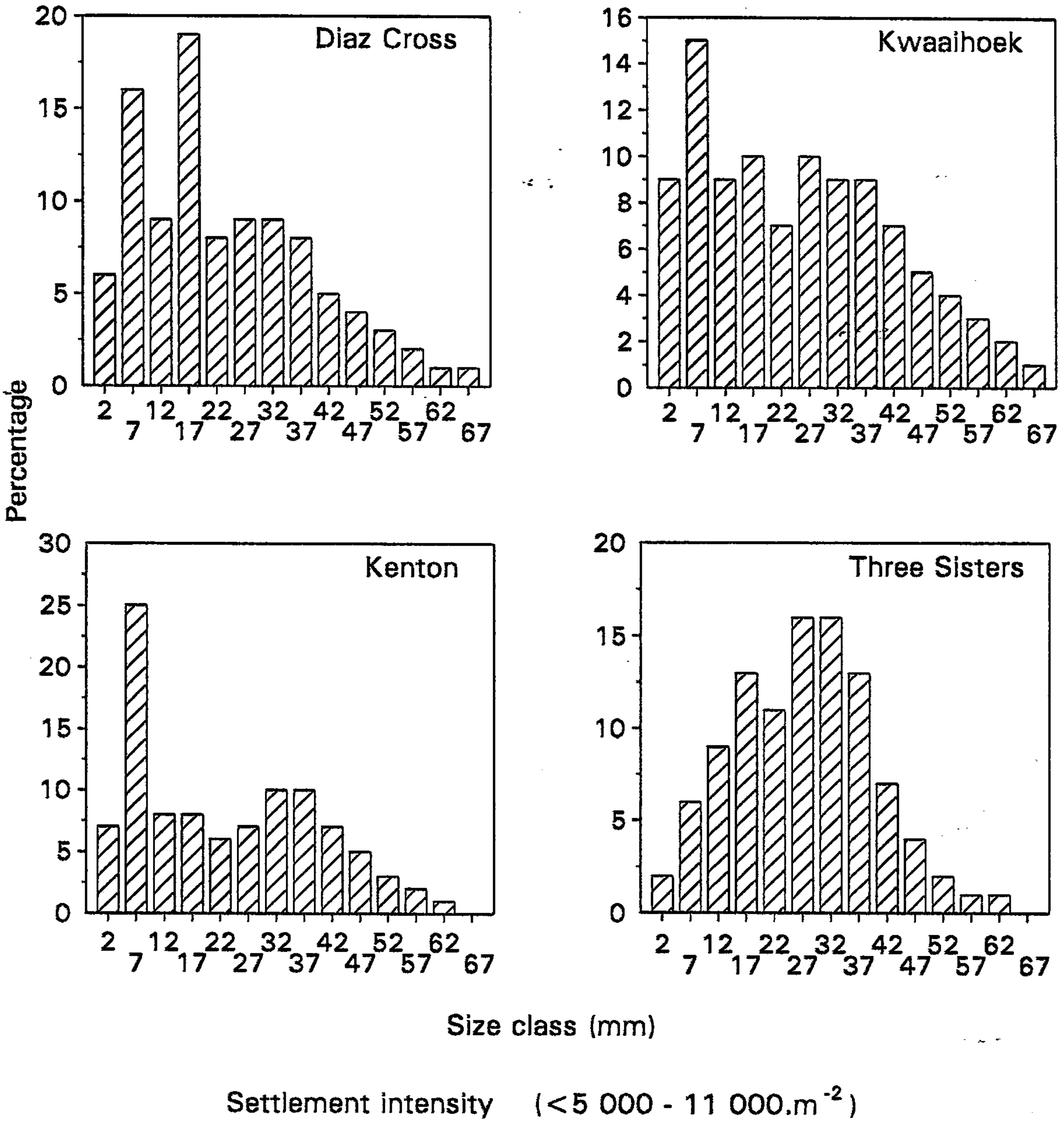
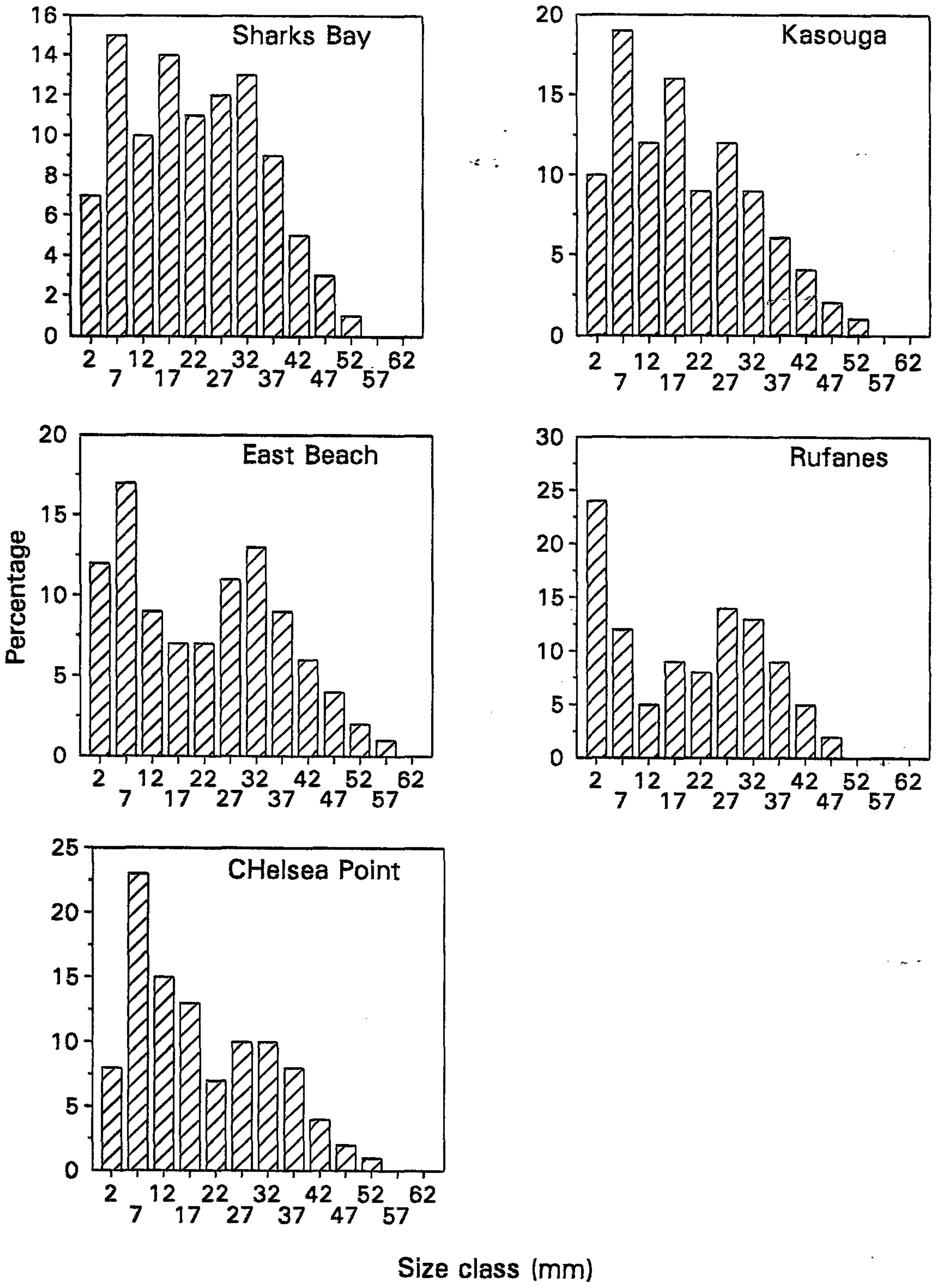

Diaz Cross
Kwaaihoek
Kenton
Three Sisters
Percentage
0
5
10
15
20
25
30
0
2
4
6
8
10
12
14
16
2
7
12
17
22
27
32
37
42
47
52
57
62
67
Size class (mm)
Settlement intensity (<5 000 - 11 000.m-2)

Figure 5.11b



Settlement intensity (6 000 - 16 000.m^{-2})

Figure 5.11c:

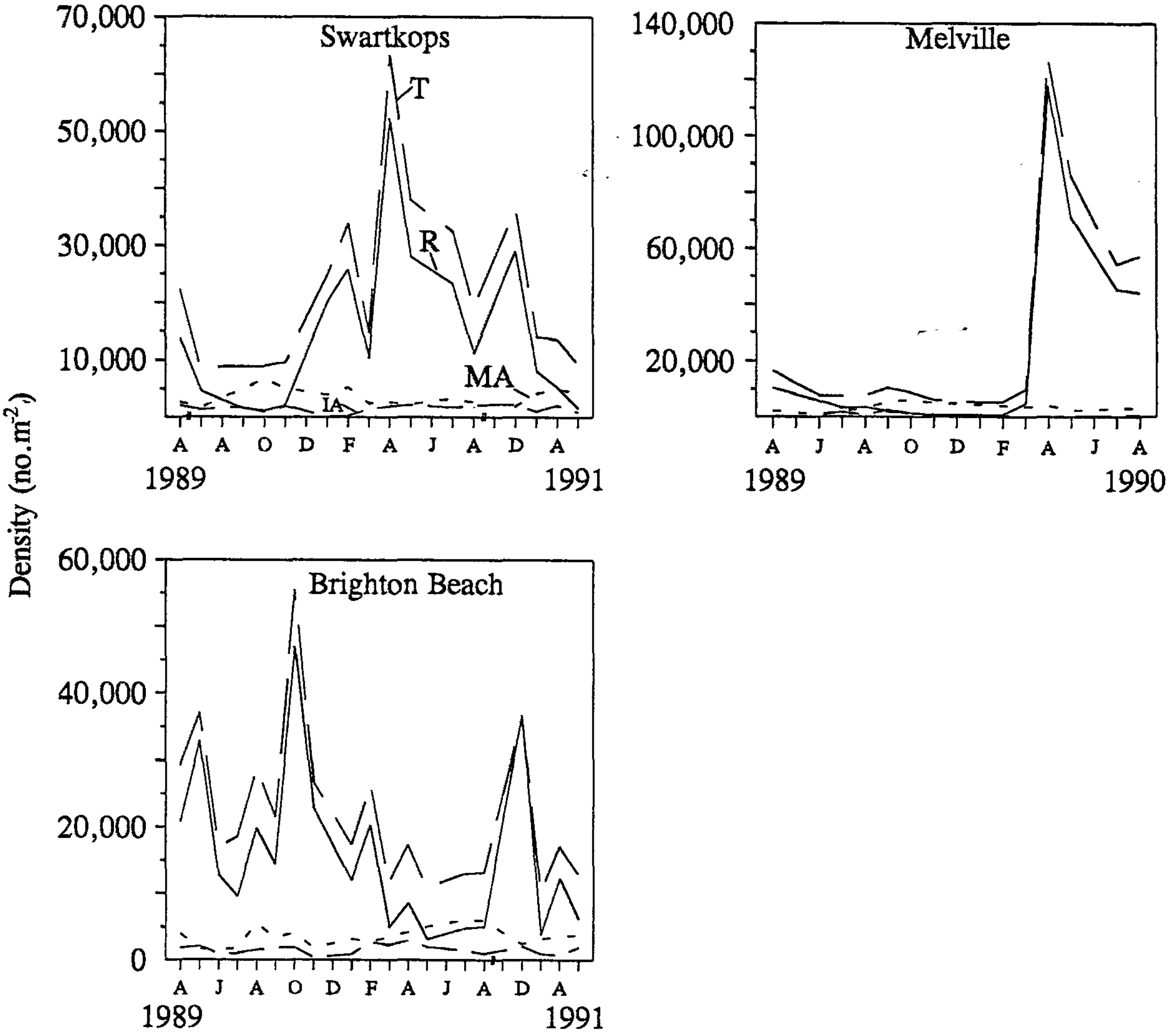


Figure 5.12a: Temporal variation in the total density of (R) recruits (0-19 mm), (IA) immature adults (20-24 mm), (MA) mature adults and in the (T) total density of mussels at sites within Algoa Bay (a), on dune rock (b) and sandstone (c) shores.

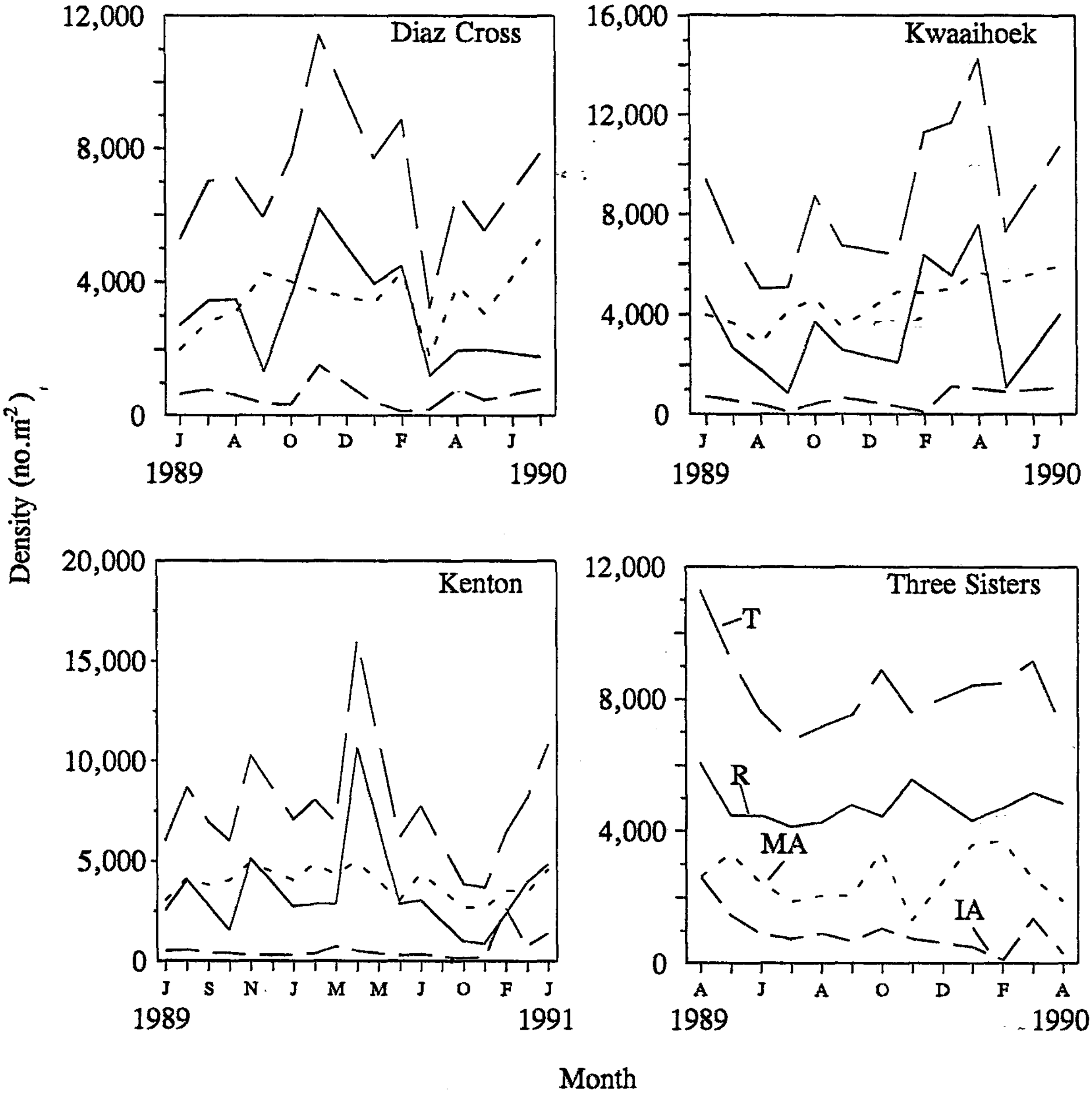

Diaz Cross
Kwaaihoek
Kenton
Three Sisters
T
R
MA
IA
Density (no.m^2)
Month
12,000
8,000
4,000
0
16,000
12,000
8,000
4,000
0
20,000
15,000
10,000
5,000
0
12,000
8,000
4,000
0
J A O D F A J
1989
1990
J S N J M M J O F J
1989
1991
A J A O D F A
1989
1990

Figure 5.12b:

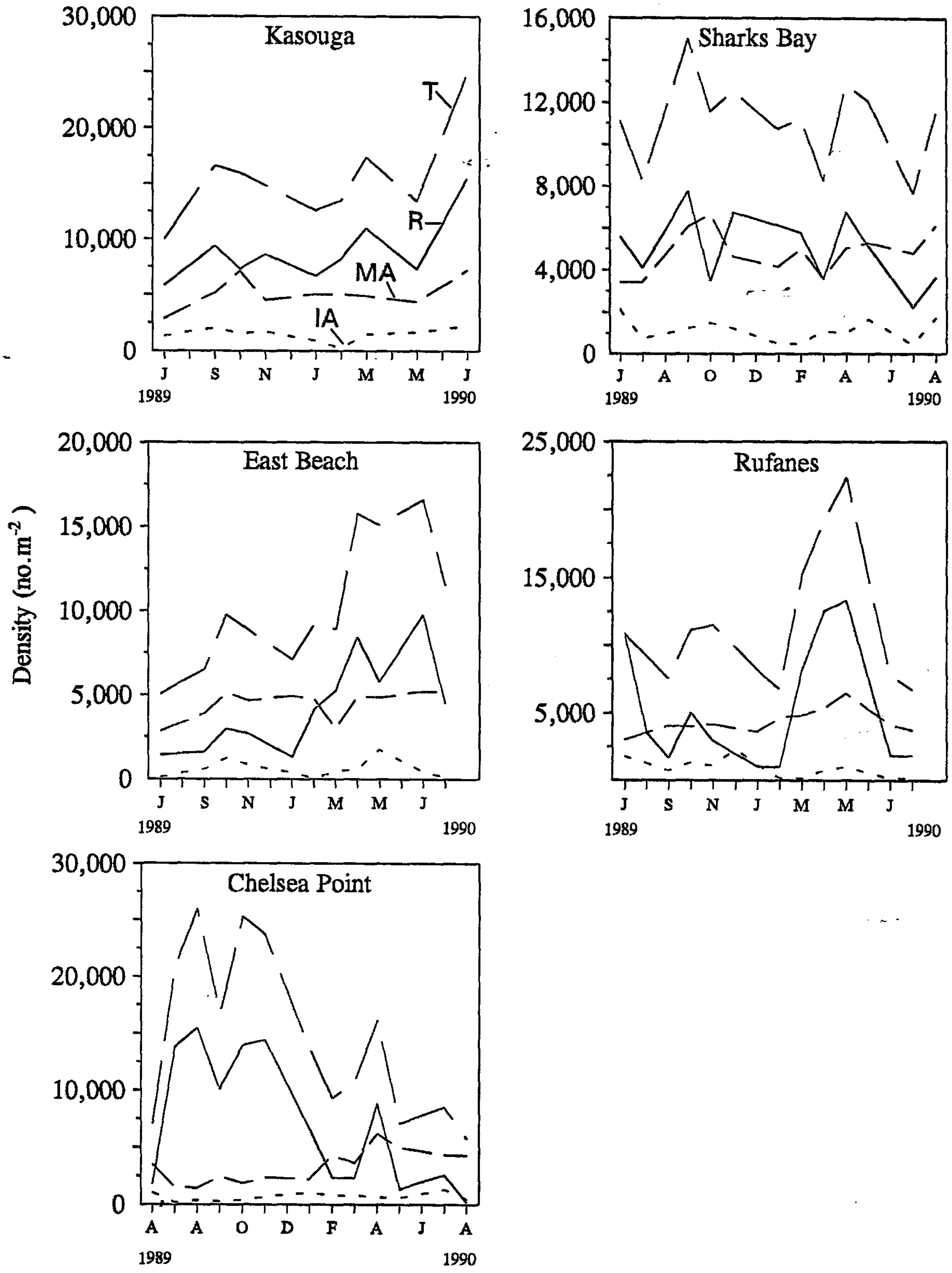

Density (no.m^{-2})
Kasouga
30,000
20,000
10,000
0
T
R
MA
IA
J S N J M M J
1989
1990
Sharks Bay
16,000
12,000
8,000
4,000
0
J A O D F A J A
1989
1990
East Beach
20,000
15,000
10,000
5,000
0
J S N J M M J
1989
1990
Rufanes
25,000
15,000
5,000
J S N J M M J
1989
1990
Chelsea Point
30,000
20,000
10,000
0
A A O D F A J A
1989
1990

Figure 5.12c:

Table 5.6: The maximum modal size of adult cohorts (from Fig. 5.4) and the age of these cohorts estimated from the growth curves for each newly settled cohort at a site. The age represents the longevity of most mussels at each site. The mean age ± standard error for each site is also shown. No estimates could be made for Kasouga, East Beach or Three Sisters.

Region	Site	Cohort	Maximum modal size (mm)	Estimated age or longevity (months)
AB	BB	C1	30	9
		C2		14
		C3		11
		mean		11 ± 3
	SW	C1	35	13
		C2		15
		C3		25
		mean		18 ± 6
	ME	C1	47	19
		C2		37
		mean		28 ± 13
DR	DC	C1	57	21
		C2		27
		mean		24 ± 4
	KW	C1	57	44
	KE	C2	40	34
	TS		37	-
SS	CP	C1	43	26
		C2		10
		mean		18 ± 11
	SB	C2	32	11
	RU	C1	34	18
	KA		30	-
	EB		35	-

Table 5.7: The mean density of recruits (0-19 mm), immature adults (20-24 mm), mature adults (>25 mm) and the range of total mean density for each site and group of sites in Algoa Bay (AB), on coastal dune rock (DR) and sandstone shores (SS). The density (no. m^{-2}) ± the standard error (beneath) is shown for each group and site.

Group	Site	Recruits		Immature adults		Mature adults		Total range
AB	SW	16 471 1 791	13 885 2 014	1 280 78	1 478 134	3 441 132	3 600 231	8 098 - 63 205
	ME		20 036 4 957		738 128		3 281 220	5 278 -127 607
	BB		15 704 1 780		1 563 116		3 438 237	10 897 - 55 385
DR	DC	3 089 139	3 109 251	690 49	586 58	3 976 86	3 150 147	3 205 - 11 432
	KW		3 588 348		559 68		4 227 193	5 000 - 14 274
	KE		3 296 324		636 126		3 987 143	3 814 - 16 111
	TS		2 483 179		957 111		4 680 149	6 738 - 11 282
SS	KA	5 727 360	8 699 759	905 53	1 477 121	4 360 118	5 308 348	9 979 - 24 915
	SB		5 716 548		829 67		3 999 184	7 628 - 15 021
	EB		4 084 680		655 117		4 517 173	5 043 - 16 603
	RU		4 824 833		848 131		4 268 207	6 731 - 22 340
	CP		6 380 959		550 64		1 459 215	4 359 - 25 962

Table 5.8: Summary table of results from Kruskal Wallis tests examining the monthly variation in the density of (a) recruits, (b) immature adults, (c) mature adults and the (d) total monthly density at each site. The test statistic (Three Sisters) and significance at the 0.05 level (*P*) are shown.

			Recruits		Immature adults		Mature adults		Total density	
Group	Site	Sample size	TS	*P*	TS	*P*	TS	*P*	TS	*P*
AB	SW	50	45	0.0002	26	0.0548	36	0.0028	45	0.0002
	ME	48	42	<0.0001	31	0.0040	37	0.0004	38	0.0003
	BB	60	44	0.0037	37	0.2650	40	0.0117	42	0.0055
DR	DC	67	28	0.0029	24	0.0127	1	0.4398	26	0.0067
	KW	51	30	0.0016	25	0.0102	20	0.0395	27	0.0041
	KE	49	27	0.0262	18	0.2426	30	0.0113	30	0.0118
	TS	61	14	0.3150	28	0.0051	18	0.1122	15	0.2288
SS	KA	30	9	0.3193	20	0.0119	18	0.0195	12	0.1348
	SB	39	20	0.0471	25	0.0078	26	0.0069	16	0.1443
	EB	35	14	0.1737	23	0.0114	19	0.0390	20	0.0309
	RU	33	21	0.0190	22	0.0148	14	0.1668	20	0.0315
	CP	46	34	0.0051	31	0.0096	37	0.0015	36	0.0019

the open coast (Fig. 5.4, Table 5.6). Recruit densities on dune rock shores (3 089 ± 139. m^{-2}) were lower and temporal fluctuations in density (~3 000 - 16 000. m^{-2}) smaller than in Algoa Bay, but the low intensity of continuous settlement maintained relatively stable and comparatively higher numbers of adults (3 976 ± 86. m^{-2}) in the population (Fig. 5.12b, Table 5.7, 5.8, 5.9 & 5.10). This reached an extreme at Three Sisters where settlement intensity was so low that recruit density did not fluctuate significantly over time, although settlement was high or frequent enough to replace lost mussels and maintain a constant density of adults in the population (Table 5.8).

Sites on sandstone shores receiving intermediate levels of settlement were generally bimodal with equal proportions and relatively high densities of recruits (5 727 ± 360. m^{-2}, 47%) and adults (4 360 ± 118. m^{-2}, 53%, Fig. 5.11c, Table 5.7). Recruit densities were intermediate between Algoa Bay and dune rock shores (Table 5.9 & 5.10) and populations underwent occasional marked temporal variations (~4 000 - 22 000. m^{-2}) in abundance (Fig. 5.12c, Table 5.7). Adults were smaller (maximum mean cohort size 30 - 37 mm), and survived for shorter periods (1-2 years), than on dune rock shores (Fig. 5.4, Table 5.6) but, although adult densities generally fluctuated over time (Fig. 5.12c, Table 5.8), adult density was equal to that on dune rock shores (Table 5.9 & 5.10).

Table 5.9: One-way ANOVA comparing mean recruit, adult and total population density in Algoa Bay, on dune rock shores and sandstone shores. The analysis was conducted on transformed data (ln density).

	Source of variation	Recruits	Adults	Total density
MS	Between groups	54.8137	3.0397	33.7129
	Within groups	1.5944	0.2134	0.3298
DF	Between groups	2	2	2
	Within groups	619	619	619
F		34.379	14.2410	102.2280
P		<0.0001	<0.0001	<0.0001

Table 5.10: Tukey multiple range test indicating the difference in mean recruit, adult and total population density (ln no.m^{-2}) between Algoa Bay, dune rock shores and sandstone shores. The analysis was conducted on transformed data. HG refers to homogenous groups.

	Recruits			Adults			Total		
Count	Group	Average	HG	Group	Average	HG	Group	Average	HG
234	DR	7.76	*	AB	8.00	*	DR	8.87	*
230	SS	8.12	*	SS	8.22	*	SS	9.29	*
158	AB	8.84	*	DR	8.24	*	AB	9.71	*

Discussion

Intertidal mussel populations along the south coast of southern Africa are a typical example of populations regulated by the supply of offspring: *Perna perna* and *Choromytilus meridionalis* grow rapidly (30-65 mm in the first year) and reach maturity at an early age (~10 months), but suffer high mortality (71-83% after ~10 months) and generally survive for less than 2-3 years (Berry 1978, Griffiths & Hockey 1987, Lasiak & Dye 1989, Fig. 5.5, 5.6, Table 5.6). Thus, populations consist of 1-2 juvenile and adult cohorts and undergo marked temporal and spatial variation in structure and abundance as settlement intensity varies (Fig. 5.4 & 5.12, Table 5.5 & 5.7). Other populations, such as the long-lived blue wrass (Warner & Hughes 1989, Hughes 1990) and echinoderm, *Amphiura chiajei* (Munday & Keegan 1992), have several adult year classes. This enables them to ride out periods of low settlement, unless settlement failure is prolonged, as Sutherland (1987) recorded for the barnacle, *Tetraclita panamaensis*. The settlement intensity of mussels along the south coast ranged from approximately 5 000 - 130 000.m^{-2} but was generally below 60 000. m^{-2} (Fig. 5.9). Furthermore, there were consistent differences in settlement intensity, and thus population structure and density, between Algoa Bay (10 000 - 118 000. m^{-2}), coastal dune rock (5 000 - 11 000. m^{-2}) and sandstone shores (6 000 - 16 000. m^{-2}; Table 5.5).

The supply of offspring is determined by a combination of pre- and post-settlement factors. Planktonic processes causing larval dispersal and survival, are more important determinants of recruitment than spawning intensity or post-settlement growth and mortality in populations of the barnacle, *Semibalanus balanoides* (Kendall *et al.* 1985), barnacle, *Chthamalus* (Kendall & Bedford 1987, Myares 1986) and bryozoan, *Membranipora* (Yoshioka 1989b). In contrast, the spawning intensity of mussels (this study) and the abundance of adult scallops (Peterson & Summerson 1992) together with post-settlement factors determine recruitment into the adult population, when larval dispersal is limited. The spawning intensity of mussels accounted for 92% of the variance in settlement intensity (Chapter 1), but since post-settlement mortality is high (71-83%) (Fig. 5.6), less than 30% of those settlers reach maturity, and spawning intensity accounts for a very low proportion of the variance in recruitment (Fig. 5.10). Therefore, estimates of post-settlement growth and mortality are required to make accurate predictions of recruitment. Together, spawning intensity, settlement intensity, growth and mortality of recruits prior to maturity, account for 76% of the variance in recruitment into the adult population (Table 5.4).

Thus, while environmental conditions controlling spawning are important determinants of settlement (Chapter 1), factors influencing post-settlement growth and mortality are important determinants of recruitment into adult populations. Variations in growth rate may be related to variations in reproductive effort (Gage 1990), since growth rates are high prior to maturity but decline with age, a pattern which has also been recorded for several other species (Duineveld & Van Noort 1986, Defeo *et al.* 1992, Munday & Keegan 1992, Ramon & Richardson 1992). It is unlikely that high post-settlement mortality was due to predation of juvenile mussels by small whelks found within the mussel bed, since their feeding rate is low (Griffiths & Hockey 1987). However, newly settled recruits are highly sensitive to extreme temperatures and food shortages, and variations in local environmental conditions may account for the variation in post-settlement mortality (Barnes 1956, Lewis 1980). Barnacles, like mussels, are filter-feeders forming dense aggregations on rocky shores, but when settlement intensity exceeds 250 000. m^{-2} competition among juveniles reduces growth and survivorship considerably (Barnes & Powell 1950, Connell 1985). Kautsky (1982) also suggested that the growth rate of *Mytilus edulis* recruits was stunted by very high settlement intensities. The settlement intensity of mussels on the south coast was considerably lower than 250 000. m^{-2} and did not affect growth or mortality of recruits prior to maturity (Fig. 5.7 & 5.8). However, *in situ* observations suggest that mortality of adults is high after intense settlement events, due to the same type of "biophysical" mortality as described by Griffiths (1981) for a population of *Choromytilus meridionalis*. Fairly intense settlement (>20 000. m^{-2}) occurred irregularly once every four to six years in the population studied by Griffiths (1981). After settlement, adult density declined markedly and adults suffered 100% mortality within a year of settlement. Sand and debris accumulating amongst the mussels, can have the same effect, as this weakens their attachment to the rocks and makes them more susceptible to wave action (Griffiths 1981). This "biophysical" mortality of adults explains why *P. perna* survived for less than a year in Algoa Bay (eg. Brighton Beach) where settlement frequently exceeded 20 000. m^{-2}, but for up to four years on coastal dune rock shores, where settlement intensity was below 11 000. m^{-2} (Table 5.5 & 5.6). Furthermore, very dense settlements or perodic sand burial may smother mussels resulting in mass mortality of adults and variations in species composition, as psammophilic species like *C. meridionalis* replace sand intolerant species like *P. perna* (Berry 1978, Fig. 5.2, Table 5.2). The predation rate of octopuses and oyster catchers feeding on larger adult mussels is high (Griffiths & Hockey 1987), and may also be partly responsible for the short life span of mussels.

The results of this study and those described in Chapters 1-4 all suggest that topography through its affect on local environmental conditions (temperature, food availability) and circulation patterns, plays a very important role in determining spawning, dispersal, settlement and spat survival. As a result, settlement, population structure and abundance vary predictably between different types of shore (Fig. 5.11 & 5.12, Table 5.7). In New South Wales in Australia, Caffey (1985) recorded significant variation in settlement of the barnacle, *Tesseropora rosea,* both within and between shores and at all temporal scales, even annual settlement. However, there appear to be consistent general differences between sites in the magnitude of annual recruitment. This was confirmed by Connell (1985) who ranked the sites according to the relative annual magnitude of recruitment and found that recruitment was consistently greater at some sites than at others. Lewis (1980) remarked on the same thing in his review of the long term studies (8-20 years) of annual recruitment of a number barnacle, limpet and other gastropod species at sites around Britain. Connell (1985) re-analysed the data from some of these studies and statistically confirmed that over a period of 5 years annual recruitment of *Semibalanus balanoides* (data from Kendall *et al.* 1982, and unpubl.) and *Patella vulgata* (data from Bowman & Lewis 1977) was consistently ranked higher at some sites than at others. Connell (1985) performed similar analyses and obtained the same result for the clam, *Tivela stultorum*, sampled over 20 years on three Californian beaches (data from Fitch 1952) and for the starfish, *Asterias forbesi*, sampled over 17 years at a number of sites on Long Island Sound. He suggested that local coastal morphology and geology are important in determining recruitment in that they produce a characteristic set of local physical conditions involving currents, wave action, substratum types, degree of desiccation etc., which would maintain that site at a particular level in a hierarchy of sites.

Thus, multi-scale studies have shown that recruitment is a combination of stochastic events, superimposed upon deterministic spatial and temporal patterns (Doherty & Williams 1988, Feller *et al.* 1992, Fowler *et al.* 1992). To predict the timing and intensity of recruitment, future studies need to focus on identifying the way in which easily measured climatic factors (wind, tides, temperature) affect spawning intensity and post-settlement mortality, during the "windows of time" when spawning and settlement are more likely to occur (Chapter 1), and in areas where breeding activity is likely to be greater than others.

SYNTHESIS

The aim of this thesis was to estimate the dispersal range of planktonic larvae and to establish the effect of larval dispersal, settlement and post-settlement mortality on the recruitment patterns and demography of intertidal mussel populations. This final synthesis gives an overview of research in this field of marine ecology, formulates the major conclusions of the research described in Chapters 1-5, and discusses their practical implications for management and conservation of over-exploited mussel populations.

The distribution and abundance of many plant and animal populations in a variety of terrestrial and marine habitats is known to be highly variable in space and time (Roughgarden *et al.* 1985, Henderson *et al.* 1988, DeSante 1990, Hughes 1990). Johnstone *et al.* (1924), Coe & Allan (1937), Hatton (1938), Burkenroad (1946), Thorson (1946 & 1950), Corlett (1948), Pyefinch (1948), Dickie (1955), Barnes (1956) and Southward & Crisp (1956), were amongst the first to suggest that variable recruitment may explain the large temporal variations in the distribution and abundance of "open" benthic marine invertebrate populations, maintained by an erratic supply of planktonic larvae.

Much research over the last 50 years has indicated that this is in fact the case. In the United Kingdom after the pioneering work of Burrows & Lodge (1949), Southward & Crisp (1954 & 1956), Southward (1956), Connell (1961a&b), Seed (1969), Feare (1970) and Lewis (1972), long term studies on the breeding and recruitment patterns of several rocky shore species were begun. These included the barnacles *Semibalanus balanoides* (Hawkins & Hartnoll 1982, Kendall *et al.* 1982 & 1985) and *Chthamalus spp* (Myares 1986, Kendall & Bedford 1987, Southward 1991), several patellid limpets (Bowman & Lewis 1977, Bowman 1985, Bowman & Lewis 1986, Guerra & Gaudencio 1986) and a few gastropods (Lewis 1986, Kendall & Lewis 1986, Kendall *et al.* 1987). Lewis (1980) summarizes the preliminary results of several of these long term studies on variation in spawning, recruitment and population abundance. Elsewhere much has been published about recruitment in coral reef fish populations (Sale *et al.* 1984, Shulman 1984 & 1985, McFarland *et al.* 1985, Victor 1986, Doherty & Williams 1988 & 1989, Doherty 1991, see Robertson 1992 for list), invertebrates such as corals (Gerrodette 1981, Sammarco 1983, Sammarco & Andrews 1988), abalone (Sheperd & Turner 1985, Prince *et al.* 1987 & 1988, McShane *et al.* 1988, McShane & Smith 1991, Shepherd *et al.* 1992), ascidians (Davis 1987 & 1988, Young 1989, Stoner 1990), sea urchins (Rowley 1989), holothurians (Young & Chia 1982), oysters (Dayton *et al.* 1989), bryozoans (Yoshioka 1982 & 1989b, Keough 1983 & 1986), barnacles (Caffey 1985), starfish (Barker & Nichols 1983) and polychaetes (Hannan 1984, Butman 1987, & 1989, Menard *et al.* 1989, Duggins *et al.* 1990, Dauvin & Gillet 1991). Another important source of information is that on the variability in recruitment, population abundance and demography of numerous exploited species (Cushing 1973 & 1975, Conan & Shafee 1978, Andrews 1979). Mussels are heavily exploited all over the world and extensive data have been published on their spawning, settlement and recruitment patterns (Chipperfield 1953, Bayne 1964, Seed 1969, Bayne 1976, Seed 1976, Kautsky 1982, Fell & Balsamo 1985, Tursi *et al.* 1990, King *et al.* 1989 & 1990, Petraitis 1990). Demographic models describing the dynamics of "open benthic marine populations" with planktonic larvae, provide the theoretical background for these empirical studies (Connell 1985, Roughgarden *et al.* 1984, 1985 & 1988, Menge & Sutherland 1987, Hughes 1990).

These studies encompass a variety of species, habitats, environmental conditions, methodologies and a range of temporal and spatial scales, but they all come to the same general conclusion - recruitment is highly variable and the effect of this variability on populations depends on the general intensity of recruitment. When recruitment intensity is generally high, variations in recruitment have little effect on populations (Connell 1985, Roughgarden *et al.* 1985, Southward 1991). If recruitment intensity is low, variation in recruitment has a marked impact on the distribution, abundance and demography of the populations (Woodin 1976, Dayton 1979, Peterson 1979, Underwood 1981, Keough 1983 & 1984, Underwood & Denley 1984, Watanabe 1984, Caffey 1985, Connell 1985, Roughgarden *et al.* 1985, Lewin 1986, Sutherland 1987, Underwood & Fairweather 1989, and see references in Peterson & Summerson 1992). For example, Menge (1991) showed that recruitment accounted for 11%, and predation and competition for 50 to 78% of the variation in abundance of sessile invertebrates in New England, where recruitment intensity was high. In Panama, where intensity was low, recruitment accounted for 39 to 87% and competition and predation for only 10% of the variation in abundance.

In recent years the emphasis has shifted away from quantifying variation in recruitment and it's effect on populations, towards identifying the factors responsible for this variation. Recruitment is the end point in a sequence of events and variation in recruitment could arise at any stage. Progress has been limited by the difficulty in monitoring dispersal, settlement and post-settlement mortality (Keough & Downes 1982, Martel & Chia 1991). Instead, links between patterns of spawning and settlement (Olson & McPherson 1987, Gaines & Roughgarden 1987), or settlement and recruitment (Sutherland 1974 & 1990, Buss 1981, Keough & Downes 1982, Whethey 1984 & 1986, Young & Chia 1984, Caffey 1985, Connell 1985, Davis 1987 & 1988, Fairweather 1988, Bertness 1989, McGuiness & Davis 1989, Osman *et al.* 1989 & 1992, Rowley 1989, Harvell *et al.* 1990, Holm 1990, Hughes 1990, Karlson & Levitan 1990, Reed 1990, Reed *et al.* 1991, Stoner 1990, Grosberg 1991, Feller *et al.* 1992, O Connor 1993) are established, but only a few studies (Yoshioka 1982, Bertness *et al.* 1992, Peterson & Summerson 1992) have been able to distinguish between pre- and post-settlement factors influencing recruitment.

The present study redressed this imbalance by examining dispersal, settlement and post-settlement mortality and their influences on the relationships between spawning, settlement and recruitment into the adult population; as well as the structure and abundance of intertidal mussel populations.

In agreement with the findings of more recent studies (Doherty & Williams 1988, Fowler *et al.* 1992), the supply of offspring to mussel populations along the south coast of southern Africa was regulated by the interactive effects of stochastic and deterministic processes acting over a variety of scales, at all stages of the reproductive cycle, *viz.* spawning, dispersal, settlement, post-settlement growth, mortality and recruitment. Stochastic variation in the exact timing and intensity of spawning and settlement at localities only 4 km apart, was superimposed on a more general pattern of increased breeding activity around the spring and autumn equinox, and a higher intensity of spawning and settlement in Algoa Bay than on the open coast (Chapters 1 & 5). These general patterns were linked to changes in wind, tide and temperature, which determine local environmental and hydrodynamic conditions.

The dispersal range of planktonic bivalve larvae was linked to wind and topography, through their effect on circulation patterns. Larvae in the open water column were dispersed back and forth along the coast by wind-driven currents and recruited up to 100 km from the parent population (Chapters 2 & 3). However, the number of larvae found in the open water column was very low in comparison to the number of settlers on the shore (Chapters 2, 4 & 5), suggesting that larvae must accumulate elsewhere. It is possible that the majority of larvae are trapped in small gullies or crevices around rocky shores and are not dispersed. In support of this, it was estimated that 76% of the larvae produced by an isolated population of the invasive *Mytilus galloprovincialis*, recruited within 5 km (Chapter 3). Limited larval dispersal could explain the link between local patterns of spawning and settlement observed for *Perna perna* and *Choromytilus meridionalis* (Chapter 1).

Spawning intensity was linked to settlement intensity, and when settlement intensity was very heavy (>100 000. m^{-2}) it could be linked to recruitment (Chapter 1 & 5). However, post-settlement mortality was highly variable and this uncoupled the relationship when settlement intensity was low (Chapter 5). Thus, since *P. perna* generally settles in low numbers (<60 000. m^{-2}), it's recruitment intensity cannot be predicted from spawning intensity unless mortality can be estimated.

In general, the research presented in Chapters 1-5 showed that the supply of offspring is one of the most important factors regulating intertidal mussel populations along the south coast of southern Africa. Variations in recruitment resulted in marked spatial and temporal variation in population structure and abundance, since settlement intensity was low and mussels were short-lived (Chapter 5). Furthermore, it can be concluded that, spawning intensity, dispersal, settlement and post-settlement mortality all influence the supply of recruits to benthic populations, but their relative importance depends on topography because of its effect on local environmental and hydrodynamic conditions.

Therefore, in order to predict the source and supply of offspring into benthic populations of marine invertebrates, future studies need to concentrate on modelling the hydrodynamic patterns around rocky shores, to simulate dispersal and settlement patterns. Furthermore, the effects of easily measured climatic factors such as wind, tides and temperature on spawning, post-settlement mortality need to be quantified.

One of the reasons for predicting recruitment is that it determines the ability of a population to recover from disturbance caused by prolonged exploitation pressure. Mussels are heavily exploited along the south and Transkei coasts of South Africa (Siegfried *et al.* 1985, Lasiak & Dye 1989, van Erkom Schurink & Griffiths 1990). As mentioned above, these populations are characterised by limited dispersal so the reproductive efforts of the adults are linked to settlement, and high levels of natural larval mortality which result in irregular recruitment. They are therefore, highly sensitive to the intense, concentrated harvesting practised by Transkeins, and the indigenous brown mussel, *Perna perna,* has been overexploited in many regions. It is recommended that management of shellfish resources with these characteristics should be approached by controlling utilisation to protect the local brood stock. Furthermore protecting a proportion of the population in several small reserves placed at regular intervals along the coast, may be effective in controlling the short-term effects of controlled harvesting. In the long-term, the small proportion of larvae produced by protected adult mussels that disperse over long distances, may allow recolonisation of exploited areas outside reserves, if concentrated harvesting is avoided.

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