ECOLOGY OF THE INVERTEBRATE PREDATORY FAUNA ACROSS CENTRE BANK, TAURANGA HARBOUR

A thesis
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by

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ABSTRACT

The distribution, abundance, population size structure and behaviour of three common invertebrate predators were studied on Centre Bank, the flood-tidal delta of Tauranga Harbour. The study assessed the role of the predators in controlling the distribution and abundance of bivalve shellfish and provided information concerning the biology of Centre Bank for Port of Tauranga Ltd.

Two broad-scale surveys were conducted to describe the broad-scale spatial patterns of *Patiriella regularis*, *Coscinasterias calamaria* and *Cominella adspersa*. Results found *P. regularis* was the numerically dominant species across Centre Bank and it maintained a widespread distribution over the sampling period. *C. calamaria* was of low abundance and typically exhibited a patchy distribution. *C. adspersa* was also found to be of low abundance and similarly distributed as *C. calamaria*. Size structures of all 3 species comprised mostly adults in both surveys.

Temporal monitoring at finer scales was undertaken, two-monthly, to describe small-scale spatial patterns. *P. regularis* was found at similar densities to that of the large-scale surveys and it was the most prevalent species across the grid. *C. calamaria* was present at higher abundances within a small patch of the grid and appeared stable over time. *C. adspersa* was initially absent from the grid, but became more abundant and widespead over the 9 month sampling period.

Investigations included monitoring the natural movement behaviour of *C. adspersa* in relation to tidal currents and the body condition. Results showed the directions moved and distances displaced by *C. adspersa* may be influenced by the rate and direction of current movement and therefore potentially influencing the dispersal ability of *C. adspersa*, in relation to available prey. An experiment to determine the body condition of *C. adspersa* in the field suggested that food deprivation may be less detrimental than first realised, or that *C. adspersa* is able to feed on a greater variety of food types than known of.

Little evidence was found that indicated predation was an important mechanism controlling bivalve populations across Centre Bank. However, predators may be potentially important as scavengers of decaying or dead organisms. Their predatory activities may also provide shell substrate for macroalgae, and this, in combination with dense aggregations of *C. calamaria*, appeared to provide habitat for small fishes.

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CHAPTER ONE
Introduction

1.1 Study Area

Tauranga Harbour is located in the Bay of Plenty on the north-east coast of the North Island, New Zealand (Figure 1.1). The harbour, a natural tidal estuary, occupies an area of 218 km^2 and is enclosed by a barrier system of two barrier tombolos, Mount Maunganui and Bowentown, and a barrier island (Matakana Island) (Park, 1991).

The harbour is a resource of high scenic, cultural and recreational importance. The area has received considerable public attention, as evidenced by the recently formed organisation "Friends of Tauranga Harbour". In addition, it is of significant shellfish resources of kaimoana.

A small area of Tauranga harbour was studied known as Centre Bank, (Figure 1.2), a flood tidal delta at the Tauranga Entrance to Tauranga Harbour, surrounded by naturally formed tidal channels (Western Channel and Otumoetai Channel) and dredged navigational channels (Cutter Channel and Maunganui Roads Channel). A flood tidal delta is a sand body located within a tidal inlet and comprises part of a larger dynamic equilibrium system of an entrance channel and ebb tidal delta. Flood tidal deltas protect the the inner estuary by dissipating wave energy, provide an important sand resource and regulate sediment exchange between the open coast and estuary (Hume *et al.*, 1992). They are dynamic areas subject to periods of erosion and deposition. Recent studies show Centre Bank to be relatively stable, although the Western Channel had undergone changes before 1990 (Mathew *et al.*, 1995) and following the 1992 major deepening of the adjacent shipping channels (Healy *et al.*, 1991). The area sampled, encompassing Centre Bank, covers an area of approximately 3.5 km^2 and depths range from less than 1 m to about 8 m below chart datum (Appendix 1).

1.2 Reasons for Study

Due to the natural changes occurring in the area and the dredging activities undertaken by Port of Tauranga Ltd., attention has focused toward Centre Bank, an area found to be sensitive to activities and whose biology is poorly understood.

Accordingly, Port of Tauranga Ltd. has recognised the need to undertake research for the type of planning it is engaged in (Bickers, 1992), and agreed to fund two projects to describe bivalve populations and the epibenthic invertebrate predators conspicuous across Centre Bank. This information will enhance the understanding of the subtidal biology of Tauranga Harbour and contribute to current biological databases being accumulated.

1.3 Study Objectives

The primary aim of this study was to describe the broad- and fine-scale patterns of distribution, abundance and population size structure of *Patiriella regularis* (Cushion starfish), *Coscinasterias calamaria* (11-armed starfish) and *Cominella adspersa* (Large Spotted Mud Whelk), the three conspicuous predatory species present across Centre Bank. A second aim was to undertake field and laboratory studies to investigate the behaviour and feeding biology of the three study species, to gain insight into what potential effects they may have on bivalve populations across Centre Bank.

1.4 Structure of Study

In order to achieve the objectives of this study, the thesis is structured as follows.

Chapter Two provides a review of predation by epibenthic invertebrates, background to the predatory species of this study and an outline of previous work undertaken in the area. Chapter Three describes the broad-scale spatial patterns of distribution, abundance and size structure of the predatory species across Centre Bank, based on surveying the area twice after undertaking a pilot study. Chapter Four describes the fine-scale spatial patterns of distribution, abundance and size structure of the predatory species over a small area of Centre Bank, based on regular surveying at 2-monthly intervals. Chapter Five details experimental investigations of the study species. Chapter 6 is a summary of results and conclusions, with suggestions for future research.

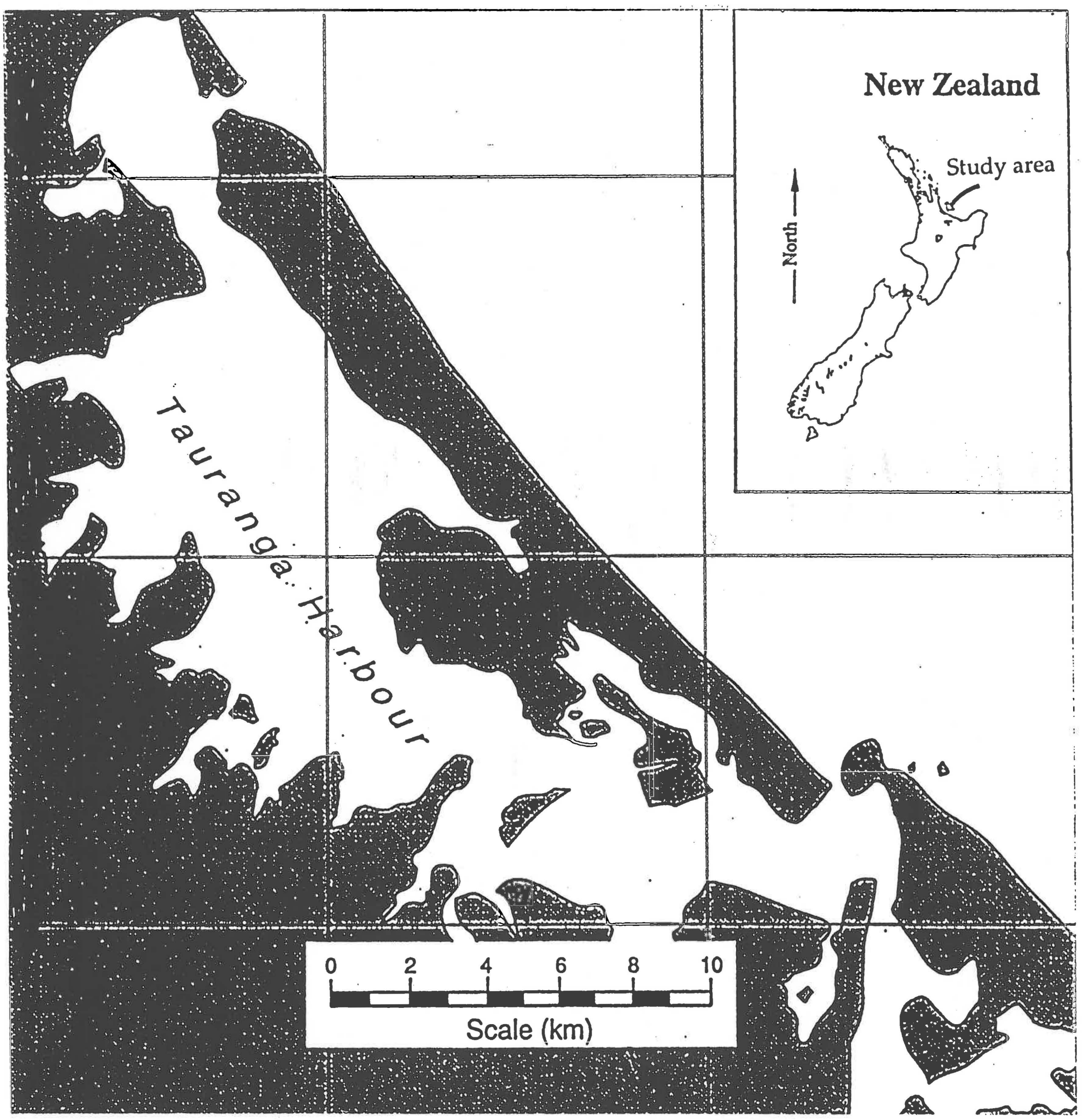

Figure 1.1: Location of Tauranga Harbour, North Island, New Zealand. (Adapted from Mathew *et al.*, 1995)

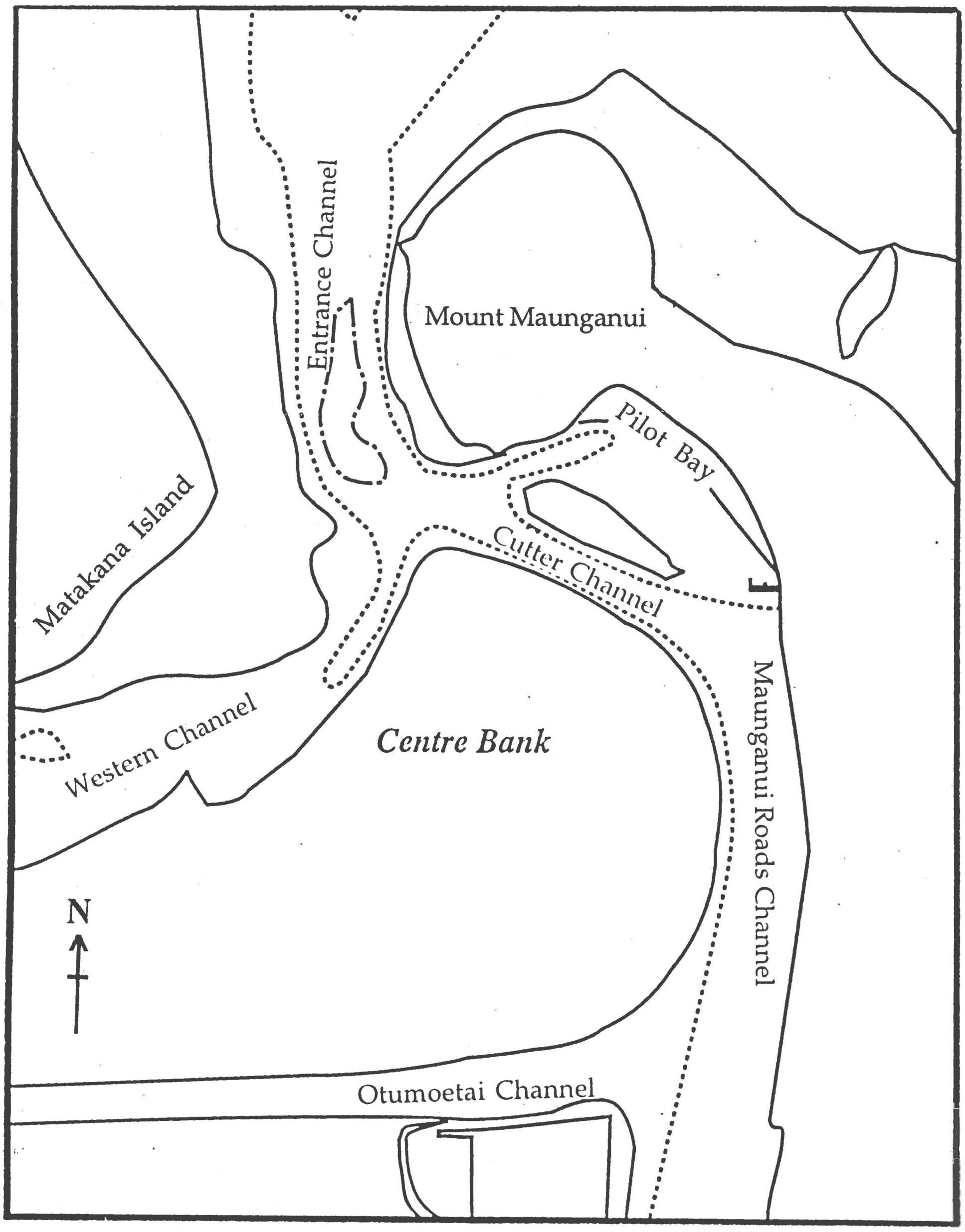

Figure 1.2: Location of Centre Bank, Tauranga Harbour. (Adapted from Mathew *et al.*, 1995)

CHAPTER TWO

Literature review and previous work

The purpose of this section is to (1) discuss the role and importance of predation by epibenthic invertebrates in shallow soft-sediment assemblages; (2) provide a description of the predators in this work and previous work conducted on them, and (3) review previous work conducted on and around Centre Bank.

2.1 Role and importance of predation by epibenthic invertebrates in shallow soft-sediment assemblages.

The structure of marine assemblages is a result of physical factors and biological interactions among organisms. It is described by the distribution, abundance, size structure, trophic relationships and diversity of species in the assemblage (Menge, 1982). The roles of physical factors (e.g., wave action, water movement, depth, substrate type, light, temperature, salinity, oxygen etc.), are relatively well known and can usually be measured and accounted for in the design of studies. However, the role of biological factors is more diverse and complex. It is one of the major goals of ecology to understand how the complex interactions among organisms affect the structure of assemblages (Wilson, 1991). The three major biological factors identified as having organising roles in marine assemblages are competition, predation and recruitment. Predation is broadly defined as "any ecological process in which energy and matter flow from one species to another" (Taylor, 1984). However, this includes all animals and some plants. The most common definition of predation is "when one organism kills another for food" (Taylor, 1984).

To test hypotheses of how marine assemblages are organised by biological factors, most work has been performed in rocky intertidal habitats (e.g., Connell, 1961; Paine, 1966, 1969, 1974; Menge, 1972; Osman, 1977; Peterson, 1979a; Fairweather, 1988a). To understand the role and importance of predation in soft-sediment assemblages, experimental research often is patterned after rocky intertidal paradigms, despite the habitats being distinct from one another. A common example of this is the employment of caging structures to include or exclude predators from an area. This method of experimental manipulation has become a powerful research tool in soft sediment habitats and has lead to the formulation of a number of theories concerning the roles of predatory invertebrates (Sih *et al.*, 1985; Wilson, 1991).

Some possible effects of predation disturbances by epibenthic invertebrates have been identified as: increase in prey abundance when predators are absent (e.g., Virnstein, 1977; Peterson, 1979b; Kneib, 1988); increase in species diversity when predators are absent (e.g., Virnstein, 1977; Peterson, 1979a); cause of patchy spatial distribution of prey (e.g., Duggins, 1983; Fairweather, 1988a; Hall *et al.*, 1991); and cause disturbance-related mortality (e.g., Palmer, 1988). These effects are most pronounced from the feeding of large vertebrate predators, such as grey whales (Oliver and Kvitek, 1984; Oliver and Slattery, 1985), walruses (Oliver *et al.*, 1983; Oliver *et al.*, 1985), sea otters (Estes *et al.*, 1978), bearded seals, dugongs, manatees (Oliver *et al.*, 1983) and rays (VanBlaricom, 1982; Thrush *et al.*, 1991). The effects of feeding excavations are dramatic and can be produced in short periods of time, reducing the abundance of the infaunal community, damaging the surrounding area and attracting opportunistic species which may feed on the particulate matter left behind. Predation may also affect the size structure and growth of prey (e.g., Virnstein, 1977; Palmer, 1984; Richardson and Brown, 1992; Underwood and Fairweather, 1992); affect prey morphology and evolution (e.g., Boulding, 1984; Appleton and Palmer, 1988; Palmer, 1990; Underwood and Fairweather, 1992); affect prey behaviour, such as avoidance and defensive responses (e.g., Feder, 1963; Phillips, 1976; Himmelman and Dutil, 1991; Legault and Himmelman, 1993) and foraging behaviour (Richardson and Brown, 1992); and prevent competitive exclusion by a dominant competitor (e.g., Virnstein, 1977; Peterson, 1979a; Dayton and Oliver, 1980; Wilson, 1991).

The intensity of any predatory effect will be modified by several characteristics of both predator and prey populations. Such factors may include: relative size of predators to prey; mobility of predators and prey; types of prey refugia; predatory feeding rates; whether the predator is specialised or a generalist (i.e., width and preference of diet); method of gaining access to prey tissue and efficiency (i.e., time and energy spent) of that method; current level of hunger of predator; learned behaviour of predator; sensory ability to locate prey from a distance (and for prey to detect predators) and to select prey; life stage or predator; predator and prey densities (see Underwood and Fairweather, 1992, for an excellent review; Seed, 1993). The behavioural characteristics of predators and prey are important in influencing the magnitude of the effects of predators on prey assemblages. These behaviours may differ among and within species and at different locations, and as the behaviours of predators in soft-sediments are less well known than those inhabiting rocky shores, establishing a paradigm for soft-sediment assemblages is difficult.

The importance of predatory interactions are often reported as significant, although this is a reflection of the interpretation by ecologists based on the design of their experiments. As on hard substrata, caging manipulations are an accepted and powerful method of investigating the role of predators on soft-sediment assemblages; however the interpretation of such manipulations must be approached with caution (Virnstein, 1978; Hulberg and Oliver, 1980; Hall *et al.*, 1990), as sediments create a range of problems (both direct and indirect) not encountered on rocky substrates. The best known of these is the influence of hydrodynamic changes in the presence of a cage causing sedimentation in and around the cage and smothering of infaunal organisms, or scouring of sediment from around the cage and exposure of infauna to predators (Hulberg and Oliver, 1980). Cages may become fouled by animals and plants attaching to the structure, reducing the supply of phytoplankton to filter-feeders, and the decomposition of accumulated seaweed can cause anoxic conditions in and around cages (Thrush, 1986). Enhanced recruitment of larval and juvenile predators and meiofauna may occur into cages, which act as a refuge from larger predators (Peterson, 1979a). Disturbance to sediment by cages can cause modification to the structure, composition and chemistry of the sediment, which most infaunal species are sensitive to (Kneib, 1991). Vegetation and animal (shell remains) refuges may act to camouflage prey, thus reducing predator-prey encounters (Kneib, 1991). Cage inclusions may alter the behaviour of predators when movement is restricted (Wilson, 1991), (this may be important for prey also, as little information is available on infaunal prey movement through the sediment, although some exists on movement through the water column (Hall *et al.*, 1990)). The influence of infaunal predators (such as polychaete worms) on community structure and their potential to obscure experimental studies when their effects are not taken into account, is becoming more widely recognised. Ambrose (1984, 1986, 1991) and Wilson (1986) review the predatory roles of infaunal predators in structuring soft-bottom assemblages. Kneib (1988) discussed methods of testing for indirect effects in soft-sediment assemblages, and Hulberg and Oliver (1980) investigated artifacts of different caging structures in experimental studies. Caging manipulations, although subject to artifacts, remain the only valid test for evaluating the effects of predation, thus the design and analyses must be rigorous especially when weak effects are claimed (Hall *et al.*, 1990). In addition to caging manipulations, observational data, gut content analysis or laboratory experiments should be conducted before acceptance of predation as the process causing experimental results (Virnstein, 1980).

Controversy has existed for some years over the relative role of predation compared to competition in organising the structure of marine assemblages. Before the early 1970's the role of competition was considered most important, but, during the 1970's and 1980's the role of predation had received more attention, and was considered to be more important, sometimes by reducing the effects of competition such as competitive exclusion. Sih *et al.* (1985) reviewed papers from 7 journals to assess the relative importance of these interactions and compared these between latitudes and systems. Results (see Table 10 of Sih *et al.*, 1985) of the study showed predation to be more important than competition in rocky intertidal systems, while competition was more important than predation in "other marine" (including soft-sediment) systems.

In summary, the role of epibenthic invertebrate predators in soft-sediment assemblages is becoming better understood, although it is still lagging behind hardshore systems. Caging manipulations have improved our knowledge of the roles predators may have in soft-sediment assemblages, but the significance of those roles has to be carefully interpreted, as soft-sediments are host to a range of artifacts caused by caging structures. Finally, establishing a paradigm concerning the roles of biological factors in structuring soft-sediment assemblages, is difficult, in part, because of the general lack of knowledge of predatory behaviour in soft-sediments, and the possibility that these behaviours differ among and within species and at different locations.

2.2 Study fauna review

The conspicuous species studied across Centre Bank are described, and an outline of previous work conducted on them, is given.

Patiriella regularis

P. regularis (Verril, 1867), the 'Cushion star' belongs to the Phylum Echinodermata, Class Asteroidea, Family Asterinidae (Plate 1). It is found up to 65 mm diameter, although Grace (1967) found some between 20-25 cm in diameter in Whangateau Harbour (New Zealand). It generally has 5 arms, although 4, 6, 7 or even 8 arms are not rare, and its colour varies widely, mostly green, but also mottled green and yellow, orange, blue black and red, and with cream coloured tube feet (Fell, 1962). It may be found inhabiting rocky or sandy substrates, intertidally and subtidally, and is the most common starfish of rocky shores in New Zealand (Morton and Miller, 1973).

Coscinasterias calamaria

C. calamaria (Gray, 1840) the 'eleven-armed' starfish belongs to the Phylum Echinodermata, Class Asteroidea, Family Asteriidae (Plate 2). Typically it has an arm spread of up to 350 mm and 11 arms, although, they may vary in size and number due to loss and regeneration. It is a brownish or reddish-brown colour with cream coloured tube feet (Fell, 1962). *C. calamaria* is the most common of the large many-armed starfishes in New Zealand, inhabiting subtidal and intertidal hard and soft substrates (Morton and Miller, 1973), although it is most common in harbours and wave sheltered shores (Barker, 1977). It is found in New Zealand (Feder and Christensen, 1966), and other countries around the Indo-Pacific (Menge, 1982; Bradstock, 1985; Britton and Morton, 1994).

Cominella adspersa

C. adspersa (Brugière, 1789), the 'Large Spotted Mud Whelk', belongs to the phylum Mollusca, class Gastropoda, family Buccinidae (Plate 3). The shell is large (up to 70 mm) and solid with a thickened aperture and conspicuous bright orange or yellow interior. Its outer shell is distinguished by spiral rows of reddish-brown spots on a buff to yellow-brown background (Powell, 1979). *C. adspersa* is one of the most common marine snails in New Zealand (Morton and Miller, 1973), found mainly in the North Island to northern part of the South Island (Powell, 1979). It is found intertidally and subtidally and mostly in muddy locations.

Many studies have been performed on the community role of asteroids in intertidal habitats, however less information is available on the distribution, abundance, feeding ecology and community role of subtidal asteroids, especially on southern hemisphere temperate shores, including New Zealand (Menge, 1982). This also applies to subtidal gastropods. Despite the common occurrence of these species on New Zealand shores, their role and impact in marine assemblages is little explored. They have been recorded in several faunal surveys (e.g., *P. regularis*, Lyttleton Harbour, (Poore, 1968; Knight, 1974), Banks Peninsula (Canterbury) (Davidson, 1989); *P. regularis* and *C. calamaria*, Otago Harbour and Blueskin Bay (Rainer, 1981), Whangateau Harbour, Auckland (Grace, 1966); *P. regularis*, *C. calamaria* and *C. adspersa*, Manukau Harbour (Grange, 1977, 1979); *C. adspersa*, Whangateau Harbour (Grace, 1967; Larcombe, 1968)). More comprehensive studies include, e.g. Grace (1967) studied the distribution and abundance of *P. regularis* and *C. calamaria* and their relationship to prey in Whangateau Harbour; Martin (1970) studied the feeding biology of *P. regularis* and *C. calamaria* and several other asteroid species (Whangateau Harbour); White (1971) studied the morphology of the anterior part of the alimentary canal and related this to feeding behaviour of *Cominella* species (Auckland); Barker (1977) studied the settling behaviour of juvenile *C. calamaria* at Maori Bay (Auckland) and in the laboratory; Burgett (1982) studied the ecology and behaviour of *P. regularis*. Cook (1989) studied the abundance, distribution and feeding biology of *C. calamaria* (Whangateau Harbour). It should be noted that Crump (1969), studied, in part, the biology of *P. regularis* and *C. calamaria*, but his work unfortunately was not viewed, thus is not made reference to.

2.3 Previous work on and around Centre Bank

The physical characteristics of Tauranga Harbour have been the most studied, such as the geomorphology, geology, sediment characteristics and dynamics, hydrodynamics, wave climate, bathymetry, and numerical modelling (see Davies-Colley, 1976; Davies-Colley and Healy, 1978a; Davies-Colley and Healy, 1978b; Dahm, 1983; de Lange, 1988; Hume *et al.*, 1992; Park, 1992; Bell, 1994; Mathew *et al.*, 1995). In addition, studies relating to the dredging of shipping channels and disposal of dredge spoil on the inner-shelf, environmental impacts and water quality assessment have been undertaken (e.g., W. D. Scott & Co. and Bruce Wallace & Partners, 1979;

Healy *et al.*, 1988, 1991; Roper, 1990; Foster, 1992; Warren, 1992; Burggraaf, 1993; Tian, 1993; Cole *et al.*, 1994).

In contrast, biological studies undertaken within Tauranga Harbour have been limited to few a studies. The first studies were conducted by Bioresearches Ltd. (1974, 1975a, 1975b, 1976) and later by Bay of Plenty Regional Council to provide a general description of the benthic intertidal ecology and to add to current regional databases.

During winter 1974 a preliminary assessment was conducted on some aspects of the ecology of the Welcome Bay region and Rereatukahia Estuary. The study briefly included the Mount Maunganui Town Beach and Wharf area, and found the ecology (including *C. adspersa* and *P. regularis*) of these areas to appear healthy and stable (Bioresearches Ltd., 1974). A second survey conducted during the summer of 1975 revisited Welcome Bay and Rereatukahia Estuary as part of a continuing monitoring programme to show seasonal fluctuations in the marine benthos. This survey showed the areas to have undergone very little change; populations of bivalves, gastropods, crustacea, polychaetes and coelenterates were relatively stable (Bioresearches Ltd., 1975).

The BOPRC initiated the Natural Environment-Regional Monitoring Network in July 1990. This programme included the Coastal and Ecology Monitoring Programme conducted during the summer months of each year. Fifteen monitoring sites were located within Tauranga Harbour, and samples taken were analysed to assess the diversity and abundance of macrofauna: gastropods, bivalves, crustacea, coelenterates and polychaetes. A separate study of the programme involved monitoring the sea lettuce *Ulva lactuca* at 3 sites, of which one was located near Sulphur Point Marina (Park, 1992).

The results of species diversity in all these surveys found that *P. regularis* and *C. adspersa* were present at most intertidal areas of Tauranga Harbour that were sampled.

However, none of the studies reported findings of *C. calamaria*, suggesting that its distribution is limited within Tauranga Harbour or that it is exclusively subtidal.

Plate 1: *Patiriella regularis*

Plate 2: *Coscinasterias calamaria*

Plate 3: *Cominella adpersa*

CHAPTER THREE

Centre Bank Survey

3.1 INTRODUCTION

It is well known that many marine assemblages exhibit patchy spatial distributions. Despite this, studies which attempt to describe the scales of distribution of fauna are scarce, particularly in soft sediments, and in addition, many are often poorly designed (Morrisey *et al.*, 1992). The assessment of variation at a range of spatial scales is necessary for adequate interpretation of the potential biotic and abiotic factors that may operate upon a marine assemblage (Legendre and Fortin, 1989; Thrush, 1991).

This part of the study sought to describe the broad-scale patterns of distribution, abundance and population size structure of *Patiriella regularis*, *Coscinasterias calamaria* and *Cominella adspersa* across Centre Bank. Fine-scale patterns were monitored by a grid sampling program discussed in Chapter Four. Two large-scale surveys were conducted across Centre Bank in May and November 1995, following a pilot study in December 1994.

3.2 PILOT STUDY

3.2.1 METHODOLOGY

Ideally to determine true population parameters such as abundance, one would count or measure every individual in the area being examined. However due to the inherent difficulties of doing this over a large area, and in fact in most biological studies, data are collected from samples of the population and inferences about the population are based on these sample data (Andrew and Mapstone, 1987). Centre Bank was divided into a grid of 54 sampling sites regularly spaced at 250 x 250 m apart. This method is known as stratified systematic sampling. It is the most efficient way of describing spatial pattern when the population is thought to be clumped or heterogeneous in space by providing a precise and unbiased estimate of the variable(s) under investigation (Ripley, 1981; McArdle and Blackwell, 1989).

The sampling sites were selected on map (NZMS 5412) and located in the field using 3 compass bearings on landmarks and harbour beacons and were recorded for later relocation. At each site 3 randomly-positioned replicate samples were collected by SCUBA within a 5 m x 5 m area using a 0.01 m^3 steel hand-held sampler. The samples were placed in separate plastic bags and labelled. These samples were passed through 1 mm mesh sieves back at shore, preserved in approximately 10% formalin and later sorted for numbers and sizes of each of the taxa collected.

3.2.2 RESULTS

Logistical constraints, such as time, people effort, equipment and cost, and safety considerations necessitated a reduction in sampling effort. The 54 sites were thus reduced to 27 sites approximately 250 m x 500 m apart - omitting every second transect (Figure 3.1). It was found that the sample unit size (0.01 m^3) used was inadequate to collect sufficient numbers of individuals, although this was a satisfactory size to collect bivalves for a companion study. The results of the pilot study are located in Appendix 2, but analyses of these results were not considered worthwhile because of the low numbers collected.

3.3 CENTRE BANK SURVEY

3.3.1 METHODOLOGY

3.3.1.1 Positioning of Survey Sites

Twenty-seven sites were chosen across Centre Bank (Figure 3.1) covering an area of 3.48 km^2, and ranging in depth between 0.5 m and 8 m (Appendix 1). The regularity of the site positions were not accurately achieved due to the positioning methods used in the pilot study. Site landmarks used in the pilot study were relocated on map (NZMS 5412) and their longitude and latitude coordinates found. These sites were then relocated in the field by use of a 'Navtrac 4000' differential Global Positioning System (GPS), enabling the original sites to be found to an accuracy of 1 m. The site and base station coordinates are located in Appendix 3.

3.3.1.2 Sampling Methods

At all sites, three randomly-allocated quadrats were sampled (by SCUBA) within a 5 m x 5 m area. The sample unit used was a 1 m^2 steel quadrat, which was found to collect a greater number of individuals and reduce sampling effort (i.e. time and cost). The number of individuals found within the quadrats was counted and recorded on underwater slates (including those only partially inside the quadrat) to provide density estimates per site. The top 5 cm of sediment was finger-ploughed for *C. adspersa*, which was often found below the sediment surface.

The size of *C. calamaria* was measured as the distance of its longest axis (to the nearest cm) along the oral ambulacral groove to avoid complications with missing and regenerating rays (Plate 4a). *P. regularis* was measured from ray tip

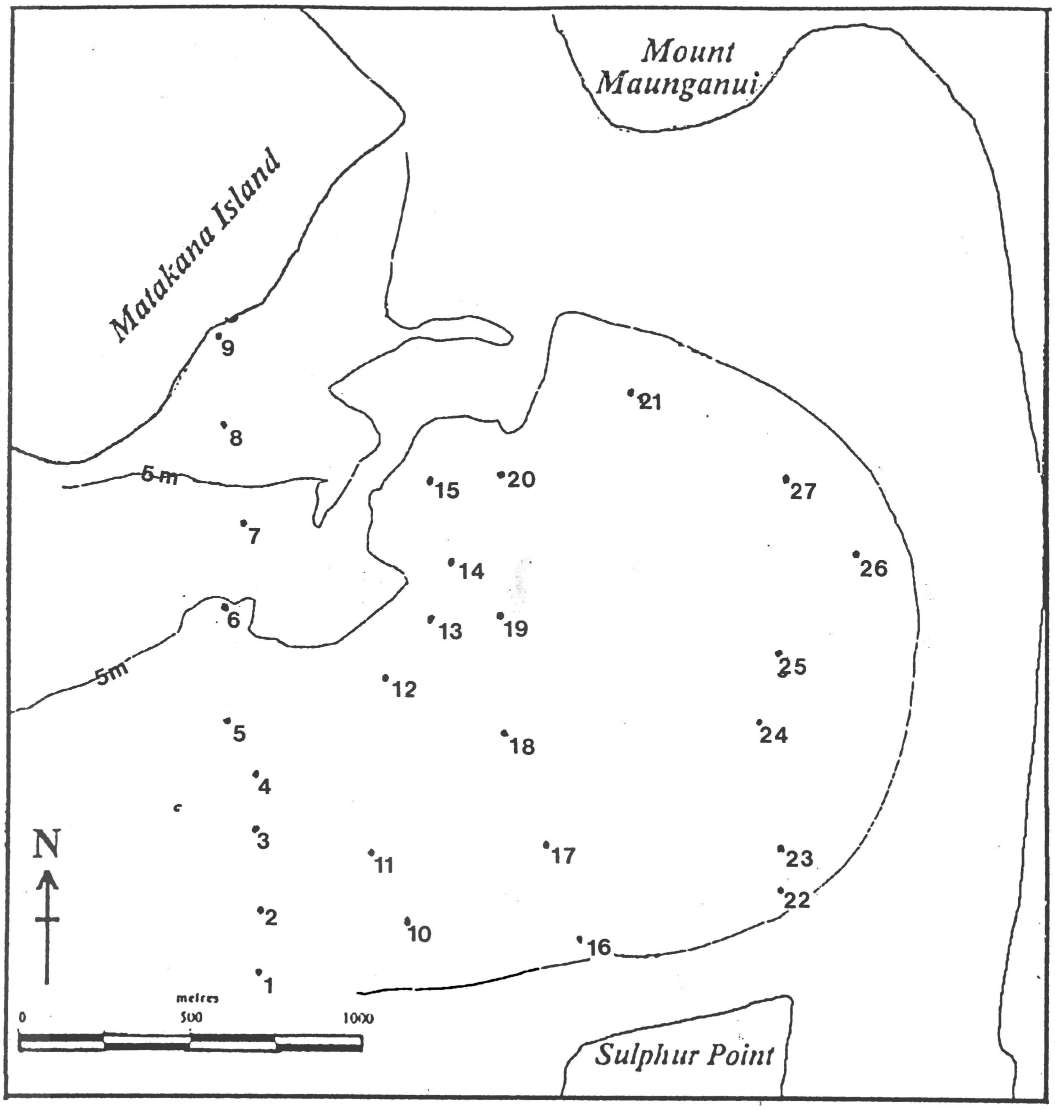

Figure 3.1: Centre Bank sampling sites.

to the opposite inter-ray (Plate 4b) to the nearest mm. In the unusual case of an even number of rays (typically 4) the size was measured along its longest axis. *C. adspersa* was measured from the tip of the aperture to the tip of the spire to the nearest mm using a ruler (Plate 4c).

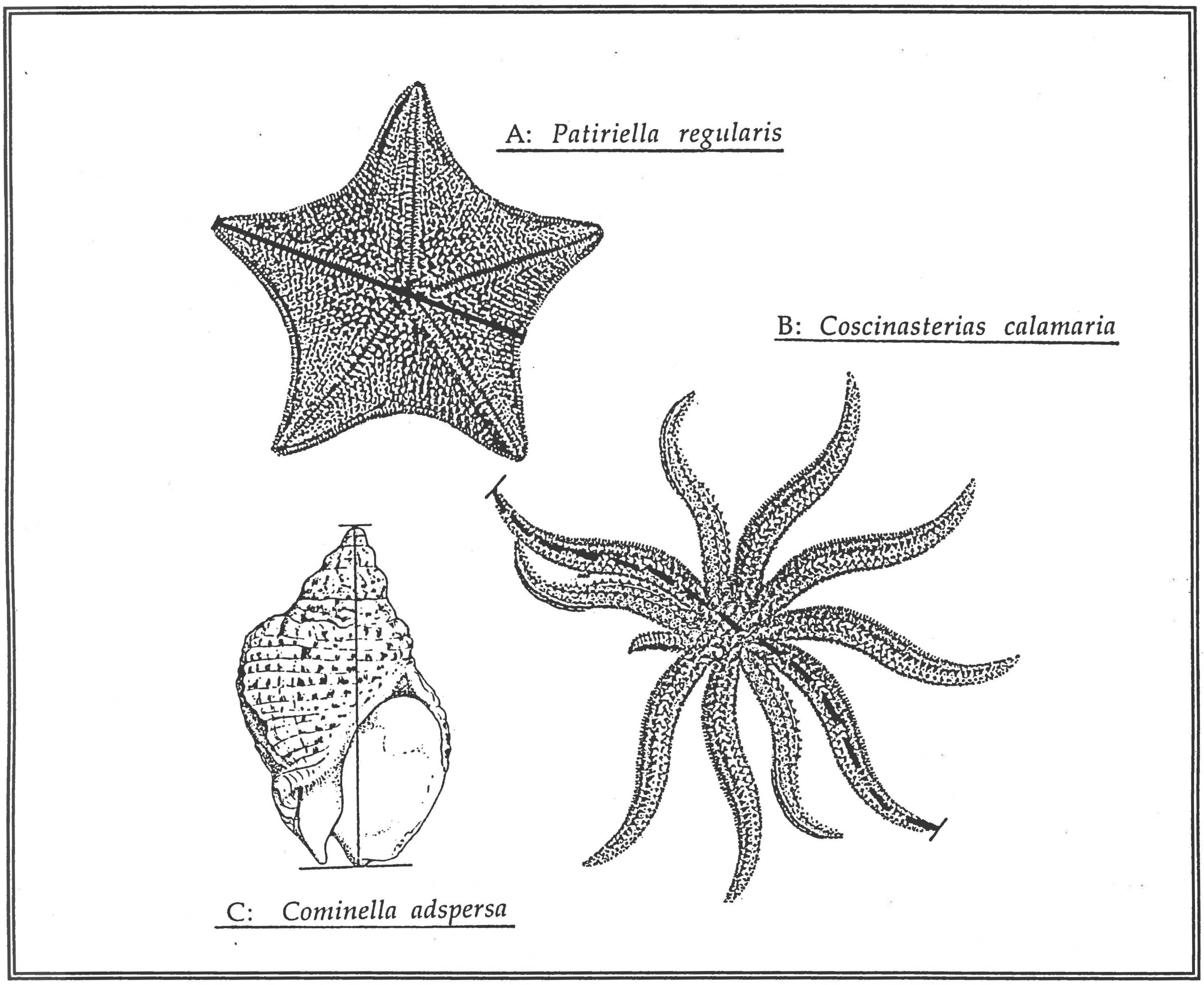

Plate 4: Line drawings showing methods used to measure (a) *P. regularis* (adapted from Fell (1962)), (b) *C. calamaria* (adapted from Fell (1962)) and (c) *C. adspersa* (by J. Gillespie). Measurements of *P. regularis* and *C. calamaria* taken on underside along oral ambulacral groove.

3.3.1.3 Data Analysis

Abundance

The mean density and standard error (SE) were calculated for each site per survey for each species. The SE is the estimated precision of the sample mean, used to estimate the true population mean density. The SE decreases with increasing precision, and is dependent on the size of the sample (i.e. number of individuals) and the number of replicate samples. Sample sizes of ≥ 30 individuals, give better estimates of the sample mean, than smaller (≤ 30) samples (which is related to the size of the sampling unit (e.g. quadrat)).

Spatial Distribution

The heterogeneous nature of the physical environment and the behaviour of species give rise to the spatial arrangement of individuals (Thrush *et al.*, 1989). Spatial distribution patterns exhibited by individuals are described by the intensity and form of pattern (Andrew and Mapstone, 1987; Thrush, 1991). *Intensity* of pattern is determined using methods such as the coefficient of variation and variance:mean ratio (given below) to describe the spatial pattern of abundance of taxa at an area as non-random (clumped), random or regular. The *form* of spatial pattern describes the arrangement of individuals in space and is based on measurements between sampling units, to identify distinct patches or density gradients running through an area.

(a) *Coefficient of Variation*

When populations differ markedly in their means the comparison of their variances or standard deviations would be risky as the variance is usually a function of the mean. Thus as a measure of the amount of variation in the population having different means, the coefficient of variation (CV) is calculated. It is the standard deviation (s) expressed as a percentage of the mean ($\bar{x}$).

The formula is:

$$CV = \frac{s \text{ x } 100}{\bar{x}} \tag{3.1}$$

(Sokal and Rohlf, 1973). The CV is used to compare the variation of populations independent of the magnitude of their means, and thus acts as a measure of the intensity of spatial pattern of a population. CV values less than 100% correspond to a relatively homogeneous population (i.e. little variation among mean values) and values greater than 100% are from populations which exhibit clumped or non-random distributions. The median CV of sites per survey was calculated as this was thought to provide a better estimate of variability than calculation of the mean, as the data did not exhibit normality within sites especially for *C. calamaria* and *C. adspersa*.

(b) *Variance:mean Ratio*

This is the simplest index of the intensity of spatial pattern and is commonly used (Andrew and Mapstone, 1987), perhaps due to its ease of computation. It is based on the characteristic that if the variance of a sample is equal to the mean density (a function of the Poisson distribution), individuals of a population are randomly distributed in space (provided the sample statistics, variance (s^2) and mean ($\bar{x}$) are derived from randomly allocated sampling units (Andrew and Mapstone, 1987)). The formula to calculate the variance:mean ratio (or coefficient of dispersion (CD)) is:

$$CD = \frac{s^2}{\bar{x}} \tag{3.2}$$

(Sokal and Rohlf, 1973). Values will be near 1 ('unity') in distributions that are essentially Poisson (random), be >1 in non-random/clumped samples and <1 in regular samples (Sokal and Rohlf, 1973), i.e. the CD has a minimum value when every quadrat contains the same number of individuals and has a maximum value when all individuals are found in one quadrat. This is a powerful test to detect non-randomness (however not as powerful for detecting regular patterns) when sample sizes are greater than 5 individuals (Andrew and Mapstone, 1987). Mean densities between 1 and 5 per unit produce conservative results and when mean densities are below 1 the results are considered invalid. It is a useful descriptive measure for detecting non-random pattern, but due to its strong dependence on sample unit size, number of replicate samples and number of individuals per sample unit, it is not considered a satisfactory comparative test when these variables differ among samples (Andrew and Mapstone, 1987). Hurlbert (1990) objects to the use of this method to detect departure from unity in a population, as the Poisson distribution is only one of many distributions for which the variance:mean would equal 1.0. Hurlbert found that although the populations exhibited variance:mean ratio of 1.0, they also deviated significantly from Poisson. Thus the measure of departure from Poisson does not admit all possibilities of the classification of pattern (i.e. random, regular and non-random).

(c) *Spatial Autocorrelation*

When a property of a population exhibits some degree of similarity in space it is said to be spatially autocorrelated (Sokal and Oden, 1978). Spatial autocorrelation can be measured by Moran's *I* spatial autocorrelation coefficient when data is quantitative, to visualise the variation in densities in all directions over space. It is similar to the Pearson's correlation coefficient since the numerator is the sum of cross-products of centered values and then the values of all pairs of points at given distance classes are compared (Legendre and Fortin, 1989). Positive autocorrelation indicates homogeneity or sameness; negative correlation, heterogeneity or dissimilarity (Sokal and Oden, 1978).

Moran's *I* is a simple and powerful test to detect spatial autocorrelation and it is commonly used to describe the spatial arrangement exhibited by soft-bottom fauna (Hall *et al.*, 1994). An omni-directional Moran's *I* was computed for densities of *P. regularis, C. calamaria* and *C. adspersa* in the two Centre Bank surveys_using Spatial Autocorrelation Analysis Program (SAAP) (Version 2.3, User's Guide, 1985) on an IBM PC.

Population Size Structure

The size structure of a population may be described by length (or size)-frequency distributions. Analysis of these distributions has been primarily done to determine the age classes within a population for management purposes and to monitor growth over time when tagging is impractical. The size-frequency distribution is a result of recent recruitment and mortality and the growth rates of individuals within a population (Hooker, 1995).

Due to the low numbers of *C. calamaria* and *C. adspersa*, and the non-normality of data per site, median sizes were computed - a non-parametric measure of central tendency. Sizes of each species from all sites were pooled to produce size-frequency histograms per survey, and corresponding summary statistics.

3.3.2 SURVEY RESULTS

3.3.2.1. Abundance

P. regularis was the numerically dominant species across Centre Bank. The ratio of *P. regularis* : *C. adspersa* : *C. calamaria*, based on total abundances, was 25.3 : 4.3 : 1 for May and 30.8 : 3.3 : 1 for November.

The abundance of each species was found to be lower in November compared to the previous survey in May (Table 3.1). *P. regularis* had the smallest decrease in abundance (only 5.4%), while the abundance of *C. calamaria* was 22.2% lower and that of *C. adspersa* was 39.1% lower. This was largely due to the overall low abundances of *C. calamaria* and *C. adspersa*, over Centre Bank; any small decline in abundance appeared large. For example, 6 less *C. calamaria* were counted in the November survey causing a 22.2% reduction in abundance, although 37 less *P. regularis* were counted (in November) resulting in only a 5.4% reduction, hence its decrease in abundance is of less consequence than for *C. calamaria* and *C. adspersa*.

Survey	*P. regularis*	*C. calamaria*	*C. adspersa*
May	684	27	115
November	647	21	70

Table 3.1: Total abundance of *P. regularis, C. calamaria* and *C. adspersa* in May and November 1995.

Patiriella regularis

P. regularis was found at 24 of the 27 sites (89% prevalence) across Centre Bank, for both May and November (Figure 3.2a). It was absent from sites 9 and 19 in both surveys and site 20 in May and site 15 in November. Its highest mean density was 25.67/m^2 in May, and 29.00/m^2 in November (both at site 21) (Table 3.2). The overall mean density across Centre Bank per survey was 8.42/m^2 (SE 1.75) for May and 7.99/m^2 (SE 2.07) for November.

Coscinasterias calamaria

C. calamaria was found at 11 of the 27 sites (41% prevalence) in May and 12/27 sites (44% prevalence) in November (Figure 3.2b). For both surveys, *C. calamaria* was present at sites 5, 6, 13, and 14 (Figure 3.1), but mean densities at these sites were lower in the November survey. The highest mean density in May was 2.00/m^2 and in November this was 1.67/m^2 (at sites 6 and 7, respectively). The overall mean density per survey was 0.33/m^2 (SE 0.21) in May and 0.26/m^2 (SE 0.23) in November (Table 3.2).

Cominella adspersa

C. adspersa was found at 10 of the 27 sites (37% prevalence) across Centre Bank in May and 11/27 sites (41% prevalence) in November (Figure 3.2c). It was present in both surveys at sites 5, 6, 14, 21, 22, and 23 (see Figure 3.1) where mean densities at these sites were generally greater in the May survey. Its

Site	*P. regularis*				*C. calamaria*				*C. adspersa*			
	May		November		May		November		May		November	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
1	4.33	2.33	6.67	1.33	0.00	0.00	0.33	0.33	0.00	0.00	0.00	0.00
2	15.67	2.96	3.67	0.33	0.00	0.00	1.00	1.00	0.00	0.00	0.00	0.00
3	7.67	0.88	2.67	1.45	0.00	0.00	0.00	0.00	0.00	0.00	0.67	0.67
4	16.67	1.76	4.67	1.67	0.00	0.00	0.33	0.33	0.00	0.00	2.00	1.00
5	16.67	0.33	8.33	0.33	0.67	0.67	0.33	0.33	5.67	0.33	4.00	4.00
6	9.67	2.60	9.67	2.67	2.00	0.58	0.33	0.33	2.67	1.45	0.33	0.33
7	8.00	3.79	5.00	1.15	0.00	0.00	1.67	1.20	0.33	0.33	0.00	0.00
8	8.67	3.38	1.67	1.20	1.33	0.88	0.00	0.00	1.00	0.58	0.00	0.00
9	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
10	14.67	2.19	8.33	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
11	6.67	2.19	9.67	5.36	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
12	6.67	2.33	18.00	12.01	0.00	0.00	0.00	0.00	0.33	0.33	0.00	0.00
13	2.00	1.15	5.00	2.08	0.33	0.33	0.33	0.33	0.00	0.00	11.67	6.69
14	3.00	1.00	3.33	2.40	0.67	0.33	0.33	0.33	1.33	0.88	1.00	0.58
15	2.33	1.33	0.00	0.00	1.33	0.67	0.00	0.00	0.00	0.00	0.00	0.00
16	8.33	1.86	5.33	1.20	1.00	0.58	0.00	0.00	0.00	0.00	0.00	0.00
17	8.00	1.15	24.67	2.73	0.33	0.33	0.67	0.67	0.00	0.00	0.00	0.00
18	13.00	1.73	17.00	4.04	0.33	0.33	0.33	0.33	0.00	0.00	0.00	0.00
19	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.67	0.88	0.00	0.00
20	0.00	0.00	0.33	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.33
21	25.67	3.76	29.00	2.52	0.33	0.33	0.33	0.33	19.33	8.25	1.00	0.58
22	5.33	2.40	4.67	1.86	0.00	0.00	0.00	0.00	1.00	0.58	1.00	1.00
23	13.67	1.20	9.33	3.84	0.00	0.00	0.00	0.00	1.00	0.00	1.00	0.58
24	3.00	1.73	8.00	2.08	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.33
25	10.67	2.91	8.00	1.00	0.00	0.00	1.00	0.58	0.00	0.00	0.00	0.00
26	3.33	0.88	7.33	1.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
27	13.67	1.33	15.33	2.60	0.67	0.67	0.00	0.00	0.00	0.00	0.00	0.00
Average	8.42	1.75	7.99	2.07	0.33	0.21	0.26	0.23	1.42	0.50	0.86	0.60

Table 3.2: Mean density ($1m^2$) and standard error (SE) for each species per site in May and November, 1995.

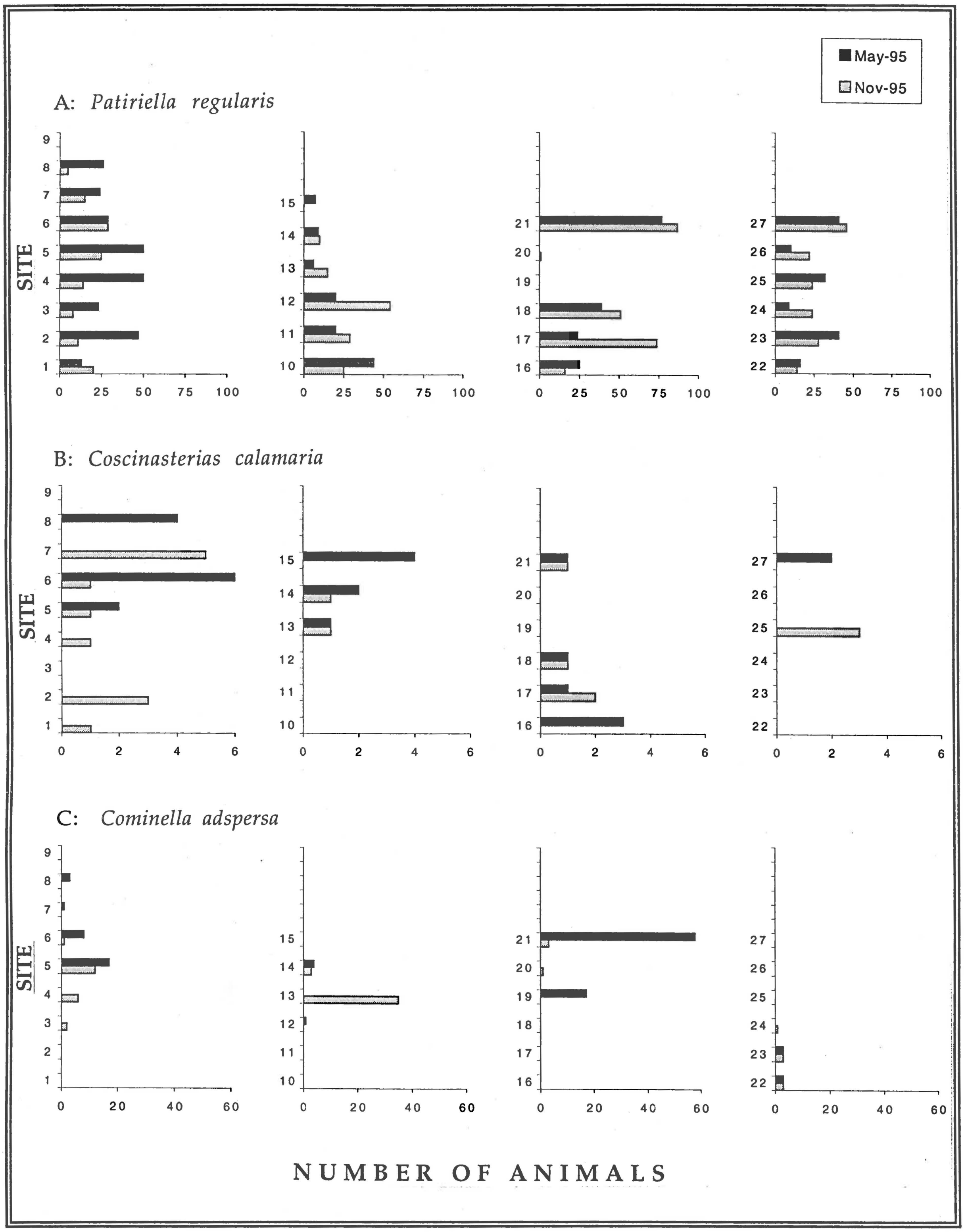

Figure 3.2: Map of total abundance per site for (a) *P. regularis*, (b) C. *calamaria* and (c) C. *adspersa*, in May and November 1995.

highest mean density in May was 19.33/m^2 at site 21, although densities at the remaining sites were 5.67/m^2 and less. The highest mean density in November was 11.67/m^2 at site 13, when densities at remaining sites were 4.00/m^2 or less. The overall mean density per survey was 1.42/m^2 (SE 0.5) in May and 0.87/m^2 (SE 0.6) in November (Table 3.2).

The precision of the estimates of the means were low. Standard errors (SE) for both surveys were between 20% and 88% (greatest for *C. calamaria* and *C. adspersa*) of the means, which indicated some degree of spatial heterogeneity of the three species over Centre Bank.

3.3.2.2. Spatial Distribution

The broad-scale spatial distribution patterns of the 3 species are described by the coefficient of variation, variance:mean ratio and Moran's *I* spatial autocorrelation.

(a) *Coefficient of Variation*

The median coefficient of variation (CV) for *P. regularis* was low (46.2% (May) and 43.1% (November)) compared to both *C. calamaria* and *C. adspersa* (Figure 3.3). CV values for *P. regularis* were less than 100% indicating a relatively homogenous distribution within sites across Centre Bank. *C. calamaria* exhibited a high median CV (173.2%) for May and November, where there was no variation of intensity in November (Figure 3.3). The CV of *C. adspersa* within sites increased from 97.2% in May to 173.2% in November, indicating greater variation within sites in November.

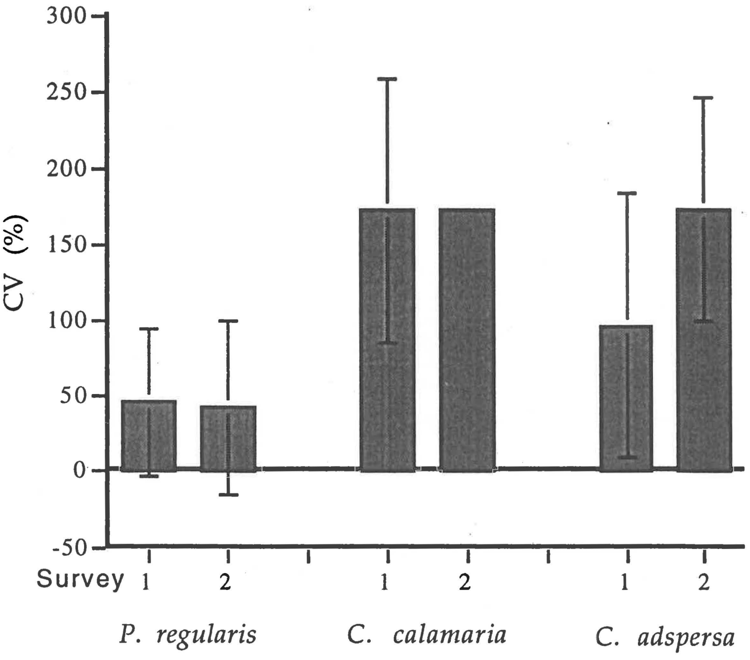

Figure 3.3: Plot of median CV (± Q3-Q1) for *P. regularis*, *C. calamaria* and *C. adspersa* per survey 1 (May) and 2 (November 1995).

(b) *Variance:mean Ratio*

Patiriella regularis

CD values derived from sites with mean densities >5 (marked by asterisk in Table 3.3) were approximately evenly divided into non-random (clumped) and regular patterns. Sites with mean densities between 1 and 5 provided conservative results, that tended toward values >1 or a non-random distribution also. The average CD value per site across Centre Bank was 1.78 in May and 2.85 in November, both indicating clumped distributions within sites, and a higher degree of heterogeneity in November.

	Patiriella regularis		*Coscinasterias calamaria*		*Cominella adspersa*	
Site	**May**	**November**	**May**	**November**	**May**	**November**
1	3.77	0.8*	.	1	.	.
2	1.68*	0.09	.	3	.	.
3	0.3*	2.38	.	.	.	2
4	0.56*	1.79	.	1	.	1.5
5	0.02*	0.04*	2	1	0.06*	12
6	2.1*	2.21*	0.5	1	2.38	1
7	5.38*	0.8	.	2.6	1	.
8	3.96*	2.6	1.75	.	1	.
9	.	.	.	.	.	.
10	0.98*	0.04*	.	.	.	.
11	2.15*	8.93*	.	.	.	.
12	2.45*	24.06*	.	.	1	.
13	2	2.6	1	1	.	11.51*
14	1	5.2	0.5	1	1.75	1
15	2.29	.	1	.	.	.
16	1.24*	0.81*	1	.	.	.
17	0.5*	0.91*	1	2	.	.
18	0.69*	2.88*	1	1	.	.
19	.	.	.	.	0.41	.
20	.	1	.	.	.	1
21	1.64*	0.14*	1	1	5.04*	1
22	3.25*	2.21	.	.	1	3
23	0.32*	4.75*	.	.	0	1
24	3	1.63*	.	.	.	1
25	2.38*	0.38*	.	1	.	.
26	0.7	0.73*	.	.	.	.
27	0.39*	1.33*	2	.	.	.
Average	1.78	2.85	1.16	1.38	1.36	3.27
SE	0.26	0.95	0.1	0.14	0.28	0.82

Table 3.3: Variance:mean ratio for *P. regularis*, *C. calamaria* and *C. adspersa* per site as an indication of the intensity of spatial pattern. Values >1 = non-random, 1 = random, <1 = regular distribution within sites. Values marked with asterisks were derived from sites with mean densities greater than five.

Coscinasterias calamaria

Most sites across Centre Bank had mean densities of *C. calamaria* less than 1 (Table 3.2) in May and November. Therefore, the results of this test for *C. calamaria* were not good indicators of the intensity of spatial pattern. Of the 27 sites in May, 4 sites (6, 8, 15, and 16) had mean densities between 1 and 5, which gave CD values approximately evenly distributed about 1 (a Poisson distribution), suggesting random pattern within sites in May. In November, 3 sites had mean densities between 1 and 5, which tended toward a clumped distribution of *C. calamaria* within those sites. The mean CD per site for all of Centre Bank was 1.16 in May and 1.38 in November; an increase of heterogeneity within sites in November.

Cominella adspersa

Most sites in May and November at which *C. adspersa* occurred, had mean densities less than 1, thus the CD results were not reliable. Three sites (5, 19 and 21) in May, had mean densities greater than 5 and the CD values were 0.06, 0.41 and 5.04, respectively (Table 3.3). In November, only 1 site (site 13) had a mean density greater than 5 and the CD indicated non-randomness within that site. Conservative CD results from sites with mean densities between 1 and 5 suggest regular, random and non-random distributions within sites across Centre Bank in May and random to non-random distributions within sites in November. The mean CD value of Centre Bank is 1.36 in May and 3.27 in November; a much larger degree of non-randomness within sites in November.

(c) *Spatial Autocorrelation*

Patiriella regularis

The spatial autocorrelogram for *P. regularis* in May (Figure 3.4), indicated that sites separated by up to 500 m (short distances) were positively correlated and those separated by 600 - 800 m were negatively correlated. The correlogram became positive again at 1600 m (long distances). The correlogram in November suggested a similar distribution pattern to May, although the secondary peak of positive autocorrelation was at slightly shorter distances and was stronger in November than in May.

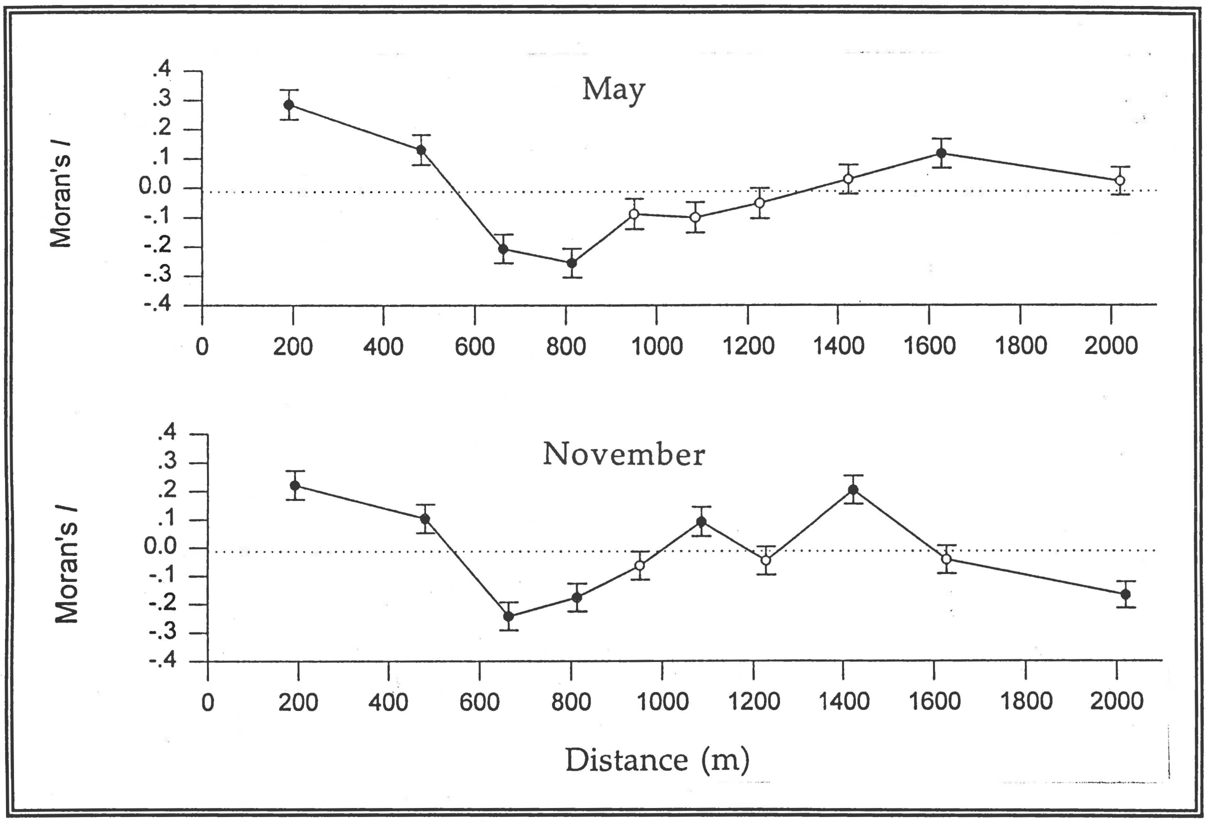

Figure 3.4: Correlograms of Moran's *I* versus distance for *P. regularis* in May and November 1995. Statistically significant autocorrelation coefficients ($p < 0.025$) are indicated by filled circles. Error bars = ± 1 SD.

Coscinasterias calamaria

In May, the correlogram displayed positive autocorrelation at distances up to 650 m apart (Figure 3.5), and negative autocorrelation between 800 and 1000 m. The November correlogram showed no similarity at short distances (up to 650 m apart), after which sites at greater distances apart were positively correlated up to 1200 m and again at 1600 m apart. Sites at greatest distance apart showed no spatial autocorrelation in both surveys; densities at those sites were most dissimilar. In addition, the autocorrelation coefficients of May were greater, indicating stronger spatial pattern than in November.

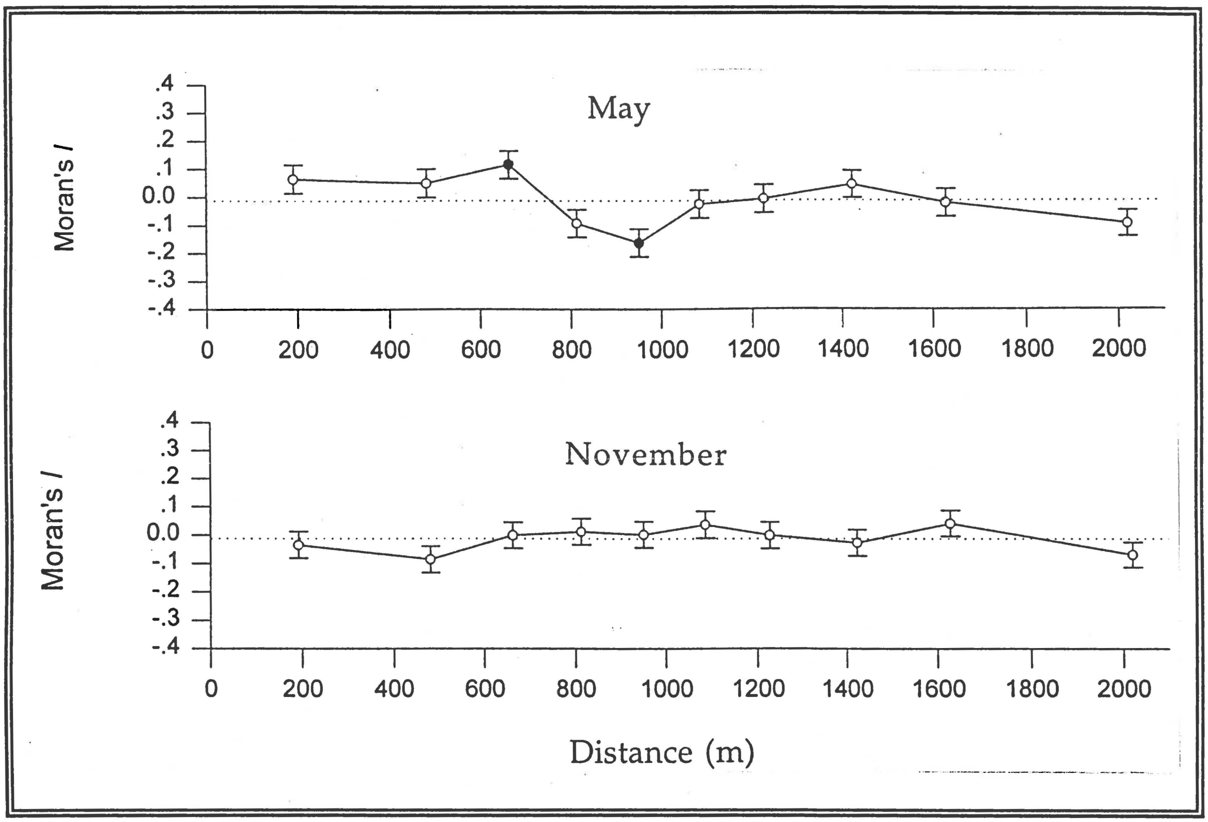

Figure 3.5: Correlograms of Moran's *I* versus distance for *C. calamaria* in May and November 1995. Statistically significant autocorrelation coefficients ($p < 0.025$) are indicated by filled circles. Error bars = ± 1 SD.

Cominella adspersa

In May, significant positive autocorrelation existed at sites up to 200 m, 650 m and about 1450 m apart (Figure 3.6). In November a similar pattern was evident where peaks of positive autocorrelation were at similar distances, although positive autocorrelation existed for sites at greater distances apart in November. The autocorrelation coefficient values were also higher in May, as for *C. calamaria,* indicating stronger spatial pattern.

The low autocorrelation values (between -0.3 and +0.3) for the 3 species, indicate little spatial pattern existed, and this was notably so for *C. calamaria* and *C. adspersa,* thus results of these correlograms are simply suggestive of the form of spatial pattern.

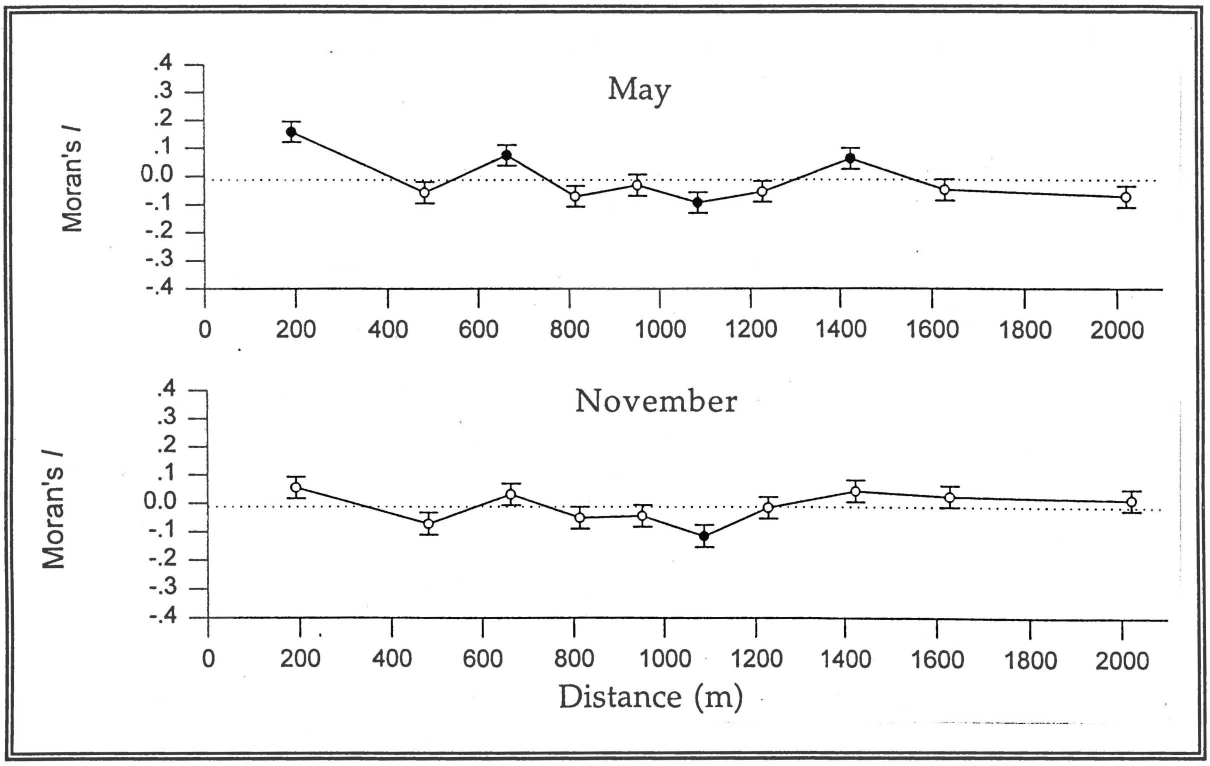

Figure 3.6: Correlograms of Moran's *I* versus distance for *C. adspersa* in May and November 1995. Statistically significant autocorrelation coefficients ($p < 0.025$) are indicated by filled circles. Error bars = ± 1 SD.

3.3.2.3. Population Size Structure

Patiriella regularis

Minimum and maximum sizes of *P. regularis* were 11 and 74 mm in May and 14 and 83 mm in November (Table 3.4). The smallest size was found at site 10 (May) and site 16 (November) and the largest size at site 12 for both surveys. Although the minimum and maximum sizes indicate larger individuals were found in the November survey, the median size over Centre Bank for November was 44 mm, while this was slightly higher (46 mm) in May. The November data are more negatively skewed indicating a tendency toward smaller sizes of *P. regularis* in this survey. For both surveys, the data remained unimodal with a common mode at 45 mm (Figure 3.7).

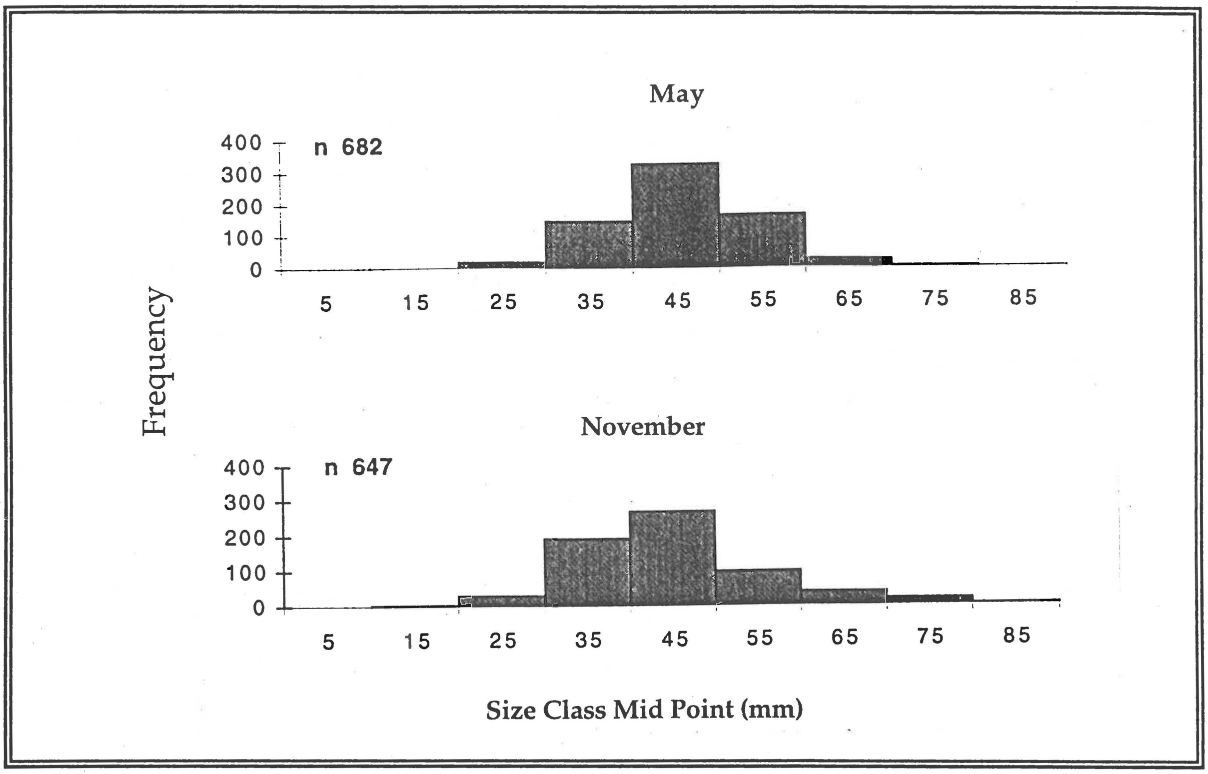

Figure 3.7: Size frequency distribution of *P. regularis* in May and November 1995.

Coscinasterias calamaria

A conspicuous shift in sizes of *C. calamaria* occurred between May and November (Figure 3.8), and this species had the most skewed distribution. However, the total abundance or sample size (27) was too small to make conclusive statements concerning size structure. The median size for May was 67 mm and 160 mm in November. The other measures of central tendency also indicate this. The minimum and maximum sizes for May were 28 mm (found at site 6) and 220 mm (site 5), and for the November survey these were 33 mm (site 13) and 280 mm (site 7).

Cominella adspersa

Minimum and maximum sizes across Centre Bank in May were 6 mm (site 19) and 68 mm (site 7), and in November were 12 mm (site 21 and 13) and 60 mm (site 5) (Table 3.4). The size-frequency distribution from the May survey is strongly unimodal, with a median size of 42 mm. The size-frequency

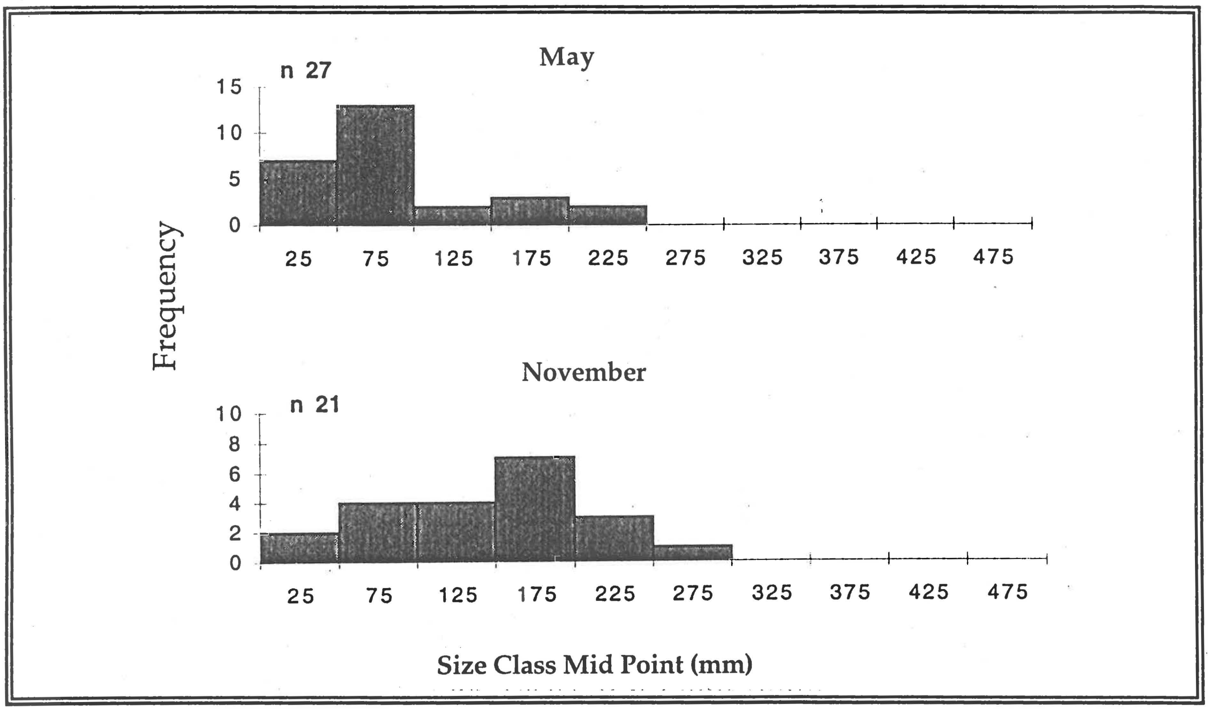

Figure 3.8: Size frequency distribution of *C. calamaria* in May and November 1995.

histogram from the November survey was bimodal, with the two common modes at 15 and 45 mm (Figure 3.9). A greater number of small (<20 mm) *C. adspersa* were found in November.

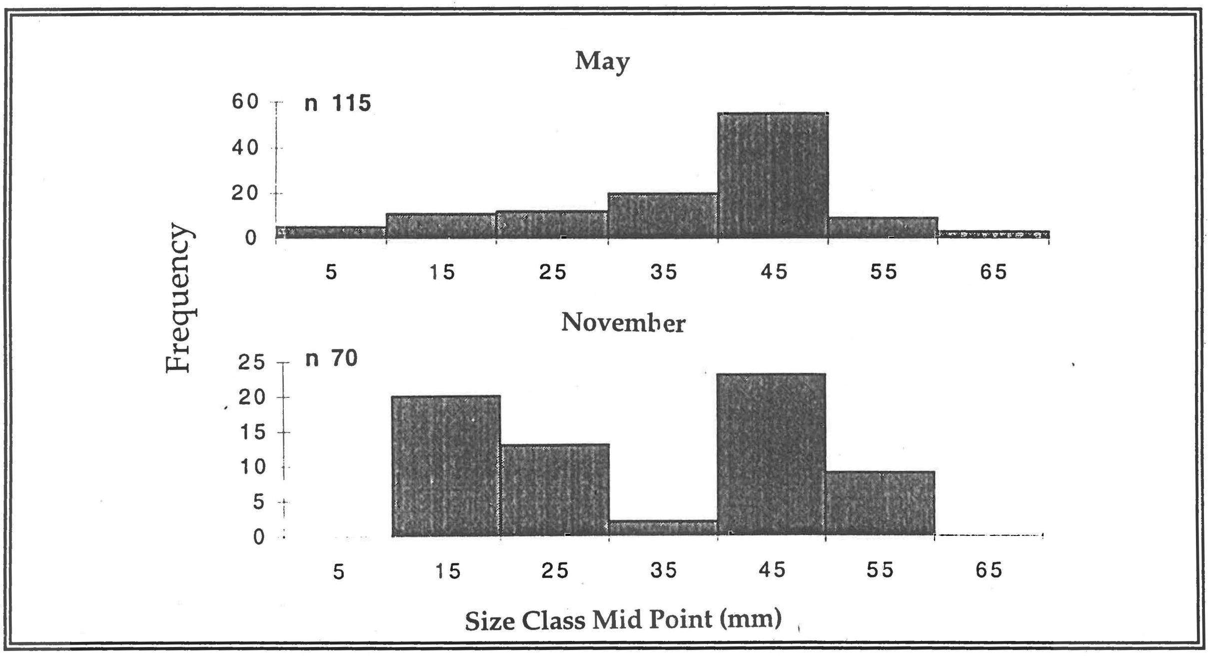

Figure 3.9: Size frequency distribution of *C. adspersa* in May and November 1995.

		Patiriella regularis **Size (mm)**			***Coscinasterias calamaria*** **Size (mm)**			***Cominella adspersa*** **Size (mm)**		
Site	Survey	Min	Max	Min	Min	Max	Med	Min	Max	Med
1	1	27	59	41						
	2	24	57	35	240	240	240			
2	1	26	58	43						
	2	35	54	43	170	205	185			
3	1	42	63	50						
	2	38	55	45.5				45	59	52
4	1	32	62	50						
	2	39	65	52	160	160	160	16	51	46.5
5	1	35	71	51	52	220	136	30	58	43
	2	39	74	52	190	190	190	42	60	46
6	1	22	62	50	28	190	48	19	59	33.5
	2	38	55	47	60	60	60	43	43	43
7	1	36	51	41.5				68	68	68
	2	35	66	45	90	280	130			
8	1	29	59	45	34	140	80	29	61	48
	2	32	50	41						
9	1									
	2									
10	1	11	60	44						
	2	30	50	36						
11	1	35	58	47						
	2	22	62	47						
12	1	45	74	58				46	46	46
	2	46	83	67.5						
13	1	41	65	50.5	62	62	62			
	2	44	67	50	33	33	33	12	53	20
14	1	33	60	52	87	165	126	18	52	25.5
	2	40	57	50	75	75	75	45	47	47
15	1	33	63	52	45	71	57.5			
	2									
16	1	34	52	45	67	233	71			
	2	14	58	44						
17	1	40	62	46	62	62	62			
	2	25	55	40	150	180	165			
18	1	26	60	42	133	133	133			
	2	29	62	42	54	54	54			
19	1							6	39	15
	2									
20	1									
	2	38	38	38				46	46	46
21	1	30	55	42	80	80	80	17	67	44.5
	2	23	80	41	205	205	205	12	46	45
22	1	44	61	51.5				29	49	45
	2	35	56	46.5				24	52	49
23	1	38	65	52				29	44	31
	2	36	60	46				33	41	35
24	1	36	51	39						
	2	27	50	42				30	30	30
25	1	31	51	43						
	2	23	62	40.5	46	200	140			
26	1	42	67	49.5						
	2	33	66	42.5						
27	1	28	59	45	31	48	39.5			
	2	33	60	48						

Table 3.4: Size data for *P. regularis, C. calamaria* and *C. adspersa* per site across Centre Bank in surveys 1 (May) and 2 (November 1995).

3.4 DISCUSSION

Abundance

Patiriella regularis was the most prevalent and numerically dominant species studied across Centre Bank. It was found to be up to 30 times more abundant than *C. calamaria* and up to 9 times more abundant than *C. adspersa*. Mean densities of *P. regularis* at sites were as high as $29/m^2$ although they displayed variable densities and had an overall lower mean density across Centre Bank of up to $8.42/m^2$. The highest density of *C. calamaria* at sites sampled was $2/m^2$, and its overall mean density across Centre Bank was up to $0.33/m^2$. Densities of *C. adspersa* were found up to $11.67/m^2$, although the mean density per site across Centre Bank was lower - up to $1.42/m^2$. The estimated precision of mean density calculated per site and survey was low. Numbers counted of each species, particularly *C. calamaria* and *C. adspersa*, were <30 individuals per sampling unit, causing data to be distinctly non-normal. Larger sampling units would have been more suitable for *C. calamaria* and *C. adspersa*, but less so for *P. regularis*. In addition, data of sparsely distributed species, as for *C. calamaria* and *C. adspersa*, contain a large number zeros and there may be no transformation capable of normalising the data (Hewitt *et al.*, 1993).

Densities of *P. regularis* and *C. calamaria* are comparable to other studies in Harbours. Grace (1967) reported mean densities of *P. regularis* of up to $8.88/\ m^2$ at shallow, sand/shell areas of Whangateau Harbour (NZ). He also found *C. calamaria* to reach densities of $0.55/m^2$ at areas where bivalves were most dense. Cook (1989) reported densities of *C. calamaria* of up to $1.98/m^2$, although these were variable, they were found at highest density in shallow subtidal areas characterised by shell debris also in Whangateau Harbour. Grange (1979) reported relatively high abundances of *C. calamaria* in areas of Manukau Harbour, also at stations with coarse shell debris. *P. regularis* was less common than *C. calamaria*, and found at fewer stations, while *C. adspersa* was relatively common and found at stations characterised by medium-fine sand with mud or shell grit. No quantitative data of mean densities were reported. Densities of each species found across Centre Bank, appear similar to other reports of densities, although these are limited and arise almost entirely from Whangateau Harbour.

Spatial Distribution Patterns

Most biological populations, including those of soft sediments, are typically characterised by neither random nor regular distributions, but rather clumped (or "patchy" or "aggregated") distributions in space and at a range of scales: <1 m to continental-wide (Legendre and Fortin, 1989; Thrush, 1991; Hall *et al.*, 1994). Spatial heterogeneity is fundamental in ecological theories, such as the assumption that individuals close together in space are influenced by the same generating processes such as epidemics, catastrophes, competition, predation, succession, evolution, adaptation, species diversity, etc. (Legendre and Fortin, 1989). It is also of practical importance in population sampling theory where spatial heterogeneity may impair the ability to use classic statistical techniques such as ANOVA, which assume data are drawn from independent and identically distributed random variables (Dutilleul, 1993). For example, positive autocorrelation at short distances and thus dependence among neighbouring samples bias tests such as ANOVA, correlation and regression by indicating significant results under the null hypothesis when this is an overestimation (Legendre and Fortin, 1989; Legendre, 1993). Spatial heterogeneity is also recognised as important in understanding population stability (Hassel and May, 1974; Levin, 1976).

Over Centre Bank, spatial heterogeneity was first indicated by the large variances and thus standard errors obtained and generally by the different mean densities among sites. The intensity of the spatial patterns using the coefficient of variation and the variance:mean ratio indicated clumped or heterogeneous distributions within sites (small scales) of *C. calamaria* and *C. adpsersa*. Conflicting results were obtained for *P. regularis*. The coefficient of variation suggested a homogenous distribution within sites while the average variance:mean ratio per site suggested a heterogenous distribution. The form of the correlogram of Moran's *I* for *P. regularis*, indicated that areas of similar (homogeneous) densities existed across Centre Bank at short and again at long distances separated by areas of dissimilar densities, thus a heterogeneous distribution. The correlograms of Moran's *I* for *C. calamaria* and *C. adspersa* also indicated a similar pattern of patchiness across Centre Bank, and are supported by the patterns of density.

However, the values obtained from Moran's *I* spatial autocorrelation coefficient were low - values ranged from -0.3 to +0.3, when values may be obtained greater than +1 and -1. Results of the autocorrelation were therefore only suggestive of spatial pattern across Centre Bank.

Factors causing spatial heterogeneity at large (100s of metres to km) scales.

Large-scale population variability is often considered to be the result of physical factors acting upon the population, while at small scales (10s of metres) interactions among individuals are considered to be the major influence causing heterogeneity. Thus physical factors may affect the distribution of individuals across Centre Bank, and these may include water depth, topography, sediment type, and water movement (Thrush, 1991; Morrisey *et al.*, 1992).

The distribution of individuals are tabulated (Table 3.5) according to the physical factors imposed upon them across Centre Bank. All species were found throughout the depth ranges and current velocities across Centre Bank. *C. calamaria* was not found or was of very low abundance at sites of coarse sand, but was found, and at greater abundance (although these were also low), at sites consisting of shell debris. Coarse sand of sandwaves and sites 22, 23, and 24 had low infaunal abundance and this may affect the distribution of *C. calamaria* at small scales across Centre Bank. Infaunal species and sediment are generally considered to be closely related (but see Snelgrove and Butman, 1994). The relationship between epibenthic fauna and sediment may be less strong than the relationship between epibenthic predators and infaunal prey. For example, *C. calamaria* is found at higher abundance in areas of high bivalve densities within the sediment, but has little interaction with the sediment itself.

P. regularis was prevalent across Centre Bank, being found at most sites. It was found at all water depths and currents, and at particularly high abundance (such as at site 21), compared to *C. calamaria* and *C. adspersa*.

C. adspersa was found at sites of different physical characteristics, but appeared to be most abundant in the shallow regions of Centre Bank, where current velocities were lower (see Appendix 4a and 4b). In the field, *C. adspersa* was observed to bury into the sediment during high current velocities, especially small (<20 mm shell length) individuals. The relationship between these physical factors is close (Jones *et al.*, 1990; Snelgrove and Butman, 1994). For

		P. regularis	***C. calamaria***	***C. adspersa***
Water depth:	0.5 - 3 m	√	√	√
	> 3m	√	√	√
Topography:	sandwaves	√	x	√
	flat	√	√	√
Sediment type:	coarse sand	√	x	√
	fine sand/shell	√	√	√
	coarse shell	√	√	√
Water current:	strong	√	√	√
	moderate	√	√	√

Table 3.5: Occurrence of *P. regularis, C.calamaria* and *C. adspersa* found across Centre Bank. √ = occurred and x = absent.

example, sediment type and topography are influenced by current velocities, where strong currents erode sediment and transport fine material, leaving behind a coarse well sorted sediment and shell lags (such as in Western Channel). Water depth influences current velocities, such that they are stronger in deeper areas, etc. For these reasons it is difficult to attribute the distribution of each of the study species to any one factor and any potential distributional factors should be assessed experimentally (Jones *et al.*, 1990). In addition, these physical features may not be causative factors affecting the distribution of the animals, but they may be correlated with other factors responsible for determining species distribution, such as water movement transporting food and planktonic larvae (Black and Moran, 1991; Morrisey *et al.*, 1992; Hooker, 1995). The spatial patterns exhibited by each species may, therefore, be most closely correlated to small-scale biogenic factors, as discussed in Chapter Four.

Population Size Structure

Juveniles of *P. regularis* (<3 mm, Burgett (1982)) and *C. calamaria* (<40 mm, Bradstock (1985)) were rarely found at sites across Centre Bank, although larger juveniles were; namely for *C. calamaria* in May. *C. adspersa* were found at a range of sizes - as small as 6 mm to sizes of up to 68 mm, and where the smallest sizes were found in May.

The size structure of a population is the result of recruitment, growth and mortality (Hooker, 1995). As a small area of Centre Bank was sampled over a greater time period and incorporated more sampling occasions, growth is discussed in Chapter Four.

Recruitment

Recruitment is an important biological process structuring marine assemblages. It facilitates the establishment and maintenance of a population and may determine the spatial and temporal abundance and distribution of the population (Santos and Simon, 1980; Prince *et al.*, 1987; Andrew, 1989). Many abalone fisheries have collapsed due to recruitment failure (McShane *et al.*, 1988) and yet, little is still known of recruitment processes for a number of species. The larval stage of marine invertebrates is the least understood of all marine life stages (Butman, 1987). Recruitment of juveniles to a population is influenced by a host of factors: larval availability, reproductive strategies and abundance of breeding stock, larval mortality, hydrodynamics and larval dispersal, larval behaviour, available substrata, etc. (Keough and Downs, 1982; Legendre and Demers, 1984; Scheltema, 1986; McShane *et al.*, 1988).

P. regularis and *C. calamaria* are broadcast spawners, releasing eggs and sperm into the water column during summer months (Burgett, 1982; Bradstock, 1985). This is common to intertidal and subtidal asteroids in temperate and tropical waters where water temperatures are not consistently low as in polar latitudes (Feder and Christensen, 1966). The success of fertilisation of eggs in the water column may be increased by the formation of breeding aggregations (Warner, 1979). This has been reported for *P. regularis* (Burgett, 1982) and a number of other asteroids (see Feder and Christensen, 1966). Given the abundance of adult *P. regularis*, as evidenced by size-frequency distributions, and their reproductive strategies, it may predicted that larval availability across Centre Bank would be high. However, water movement is a major determinant of the dispersal of planktonic larvae and may occur over various distances (cm to 1000's km) and time periods (minutes to a year) such that dispersal is either local or pelagic (Scheltema, 1986). The influence of regional hydrodynamic processes on larvae dispersal has been studied (Prince *et al.*, 1987; McShane *et al.*, 1988; Black and Moran, 1991) and localised dispersal due to reef retention was found to be an important process influencing the subsequent abundance of settling larvae.

dispersal has been studied (Prince *et al.*, 1987; McShane *et al.*, 1988; Black and Moran, 1991) and localised dispersal due to reef retention was found to be an important process influencing the subsequent abundance of settling larvae. Also fine-scale hydrodynamics have been found to be important in larval supply, where epibenthic structures enhance passive larval recruitment (Ekman, 1979, 1983). Whether retention or fine-scale local dispersion and subsequent settlement across Centre Bank occurs, requires study of the hydrodynamics, horizontal and vertical, and is unable to be determined here. Planktonic larvae have specific substratum requirements before they attach to and metamorphose to the juvenile form (Barker, 1977) and may include physical, chemical and biological features of the substratum (Barkai and Branch, 1988). This was described for *C. calamaria*, where the microtopography of the substratum appeared to have little influence on the selection of substratum, although the availability of a primary food source (microscopic algae, micro-organisms, diatoms etc.) did (Barker, 1977). This requirement for hard substrates has also been demonstrated for *P. regularis* whose planktonic larvae metamorphose on hard substratum after about 70 days (at 20°C) (Burgett, 1982). This fundamental requirement by larvae of *P. regularis* and *C. calamaria*, may contribute to their apparent absence at the sites sampled across Centre Bank. It could be inferred that the juvenile starfish are spending part of their early lives at inaccessible areas such as shell debris in channels and were not found due to their inconspicuous size, and recruitment to the population may not occur until late juvenile stage. These patterns have been observed for *Astropecten zebra* and *Astropecten velitaris* (Lemmens *et al.*, 1995) and *Asterias vulgaris* and *Leptasterias polaris* (Himmelman and Dutil, 1991) whose juveniles exhibited similar requirements resulting in differential habitat distribution to either deeper or shallower water where appropriate food sources were available. Recruitment did not occur until the late juvenile stage when juveniles were able to feed on similar food types as adults. Cannibalism by adult *P. regularis* and *C. calamaria* on their juvenile counterparts has been reported (Feder and Christensen, 1966; Martin, 1970) and could account for the regulation. However, it may be explained most simply as a consequence of unselective predation by adults (Jangoux, 1982).

Many species of gastropods have widespread dispersal of planktonic veliger larvae, while others have direct development of desmersal eggs (which may undergo pelagic dispersal) or viviparity (Underwood, 1979). The habitat of the breeding adults affects the reproductive strategy of gastropods. For example, viviparity and pelagic egg capsules are the most common among species inhabiting high intertidal areas, where harsh environmental conditions such as temperature and desiccation may prevent reproduction of demersal eggs (Underwood, 1979). In subtidal areas of the North Atlantic, the gastropod *Buccinum undatum*, reproduces by direct development of demersal eggs common to most neogastropods (Martel *et al.*, 1986a and b). The egg capsules either attach to some hard substrate or are laid in a mass of gelatinous material (Fretter, 1984). The latter may be common to species of soft-sediment areas where the tacky gelatinous material fastens to the sediment. This is a method apparently undertaken by *C. adspersa* (Bradstock, 1985).

Mortality

P. regularis and *C. calamaria* are reported as having life-spans of at least 10 years (Bradstock, 1985). Mortality is undoubtedly high for larvae during planktonic life and predation by e.g. fish, seabirds and crabs, may be an important mortality agent for young juveniles. Predation on settling larvae may also occur by suspension-feeding infaunal bivalves (André *et al.*, 1993).

Relationships have been found between reproductive cycles and longevity of gastropods. Castagna and Kraeuter (1994) reported the knobbed whelk *Busycon carica*, a long-lived predaceous gastropod, reaches reproductive maturity at the age of 9 years, and Powell and Cummings (1985) found that bivalves and gastropods of longer-than-average life spans coincide with long-term reproductive cycles of >1 year. Information concerning reproductive maturity and reproductive cycles of *C. adspersa* is lacking. Predation is likely to be more important for gastropods than for asteroids, due to asteroids being mostly composed of water and calcareous material, and in the case of *P. regularis*, a tough leathery outer epidermis (Bradstock, 1985).

Mortality may be the result of food deprivation. The ecological implications of food limitation in echinoderms are somewhat less detrimental than for gastropods, in that they are able to accommodate food limitation through variations in growth rate (Andrew, 1989), and are able to resorb skeletal material and shrink (Levitan, 1988). Therefore, the total biomass of echinoderms in a population may vary, rather than reductions in population size. Density variations or population size may, therefore, be more recruitment-driven for echinoderms than for gastropods (Andrew, 1989).

CHAPTER FOUR

Grid monitoring program

4.1 INTRODUCTION

The purpose of this program was to monitor the distribution, abundance, and population size structure of the three study species over a small area at regular intervals. Broad-scale sampling (as in Chapter Three) enables only broad trends to be identified, whereas fine-scale sampling provides an indication of the factors regulating the population and their distribution at small scales within relatively homogeneous physical environments (McArdle and Blackwell, 1989).

4.2 METHODOLOGY

4.2.1 Study Site

The selection of the monitoring site was largely based on the results of the Centre Bank pilot study in December 1994. In order to study all the animals of interest, a site was chosen between sites 11 and 12 of the Centre Bank survey, at position 176°09'78"E and 37°39'17"S. This site had a relatively high abundance of *Coscinasterias calamaria* and *Patiriella regularis* although *Cominella adspersa* was less common. Additional factors determining the selection of the monitoring site were practical considerations of regular surveying, such as the water depth and current strengths. Depths ranged from <1 m below chart datum to where some areas were exposed at low tide.

4.2.2 Sampling Design

A permanent grid was established over a 50 m x 15 m area. It was divided into 30 sites of 5 m x 5 m (Figure 4.1). This was achieved by a triangulation method (Underwood, 1977) where two pegs were hammered into the sediment 5 m apart to form a baseline. One 5 m length and one 7.07 m length of measuring tape were attached to both pegs and their ends brought together. The point of connection was the resultant location of a third peg, and so on (Figure 4.2). The pegs used were 0.6 m lengths of electrical conduit. The ends were painted with marine paint, and individually labelled with a plastic tag, etched with coordinates, to allow divers to easily locate themselves in the grid.

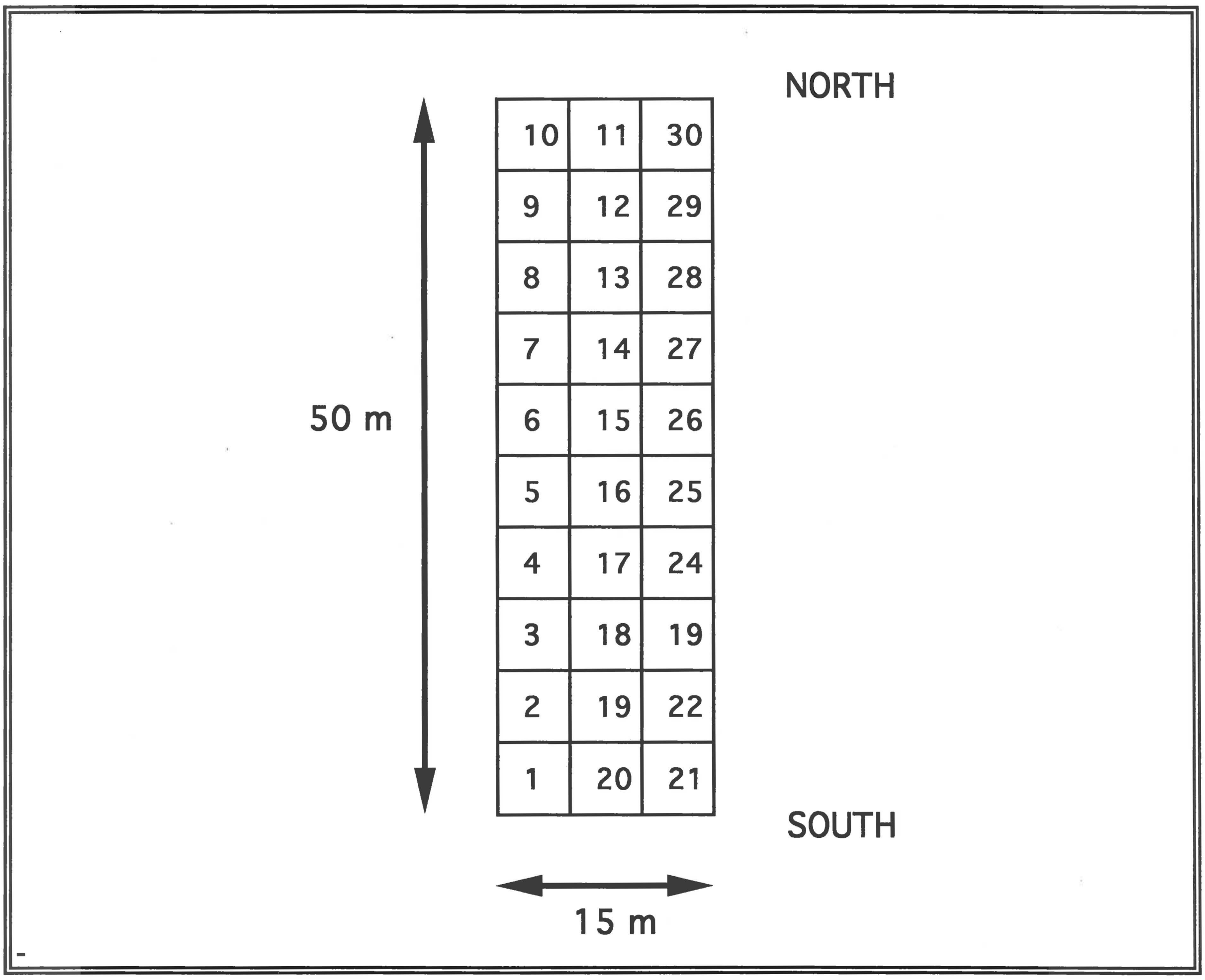

Figure 4.1: Layout of grid area, showing arrangement of sites 1 to 30.

At each site, 5 randomly-allocated replicates were sampled *in situ* using a 0.5 m^2 steel quadrat. Individuals within (and partially inside) quadrats were counted and measured. These data provided an estimate of the density per site of each species and the size structure of each species across the grid. Methods used to measure each species were described in section 3.3.1.2. The top 5 cm of sediment was finger-ploughed for C. *adspersa* which was often found below the sediment surface.

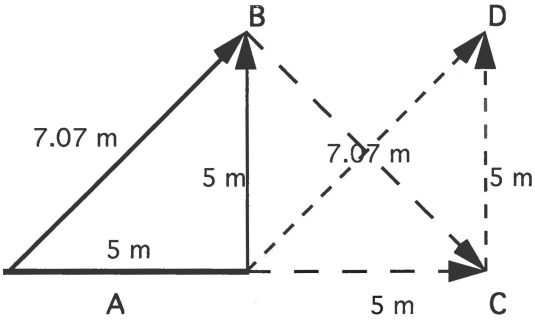

Figure 4.2: Triangulation method used to set up grid. Length A is the initial baseline. B, C and D are resultant locations of subsequent pegs.

4.2.3 Statistical Analysis Techniques

Mean densities and their standard errors per site and survey were calculated for each species. The intensity of spatial pattern of abundance was assessed using the coefficient of variation (CV) (Sokal and Rohlf, 1973) and variance:mean (Sokal and Rohlf, 1973) indices. The spatial arrangement of individuals were described using Moran's *I* spatial autocorrelation coefficient (Sokal and Oden, 1978). The population size structure was described by size-frequency histograms. See section 3.3.1.4 for description of these methods.

4.3 SURVEY RESULTS

4.3.1 Abundance

Densities of *P. regularis* in the grid were generally stable until November, when they declined. The total number of *P. regularis* counted in November was a 36% reduction from the September survey (Figure 4.1). Total numbers of *C. calamaria* were generally similar throughout the survey period, while *C. adspersa* experienced significant increase in abundance as its distribution over the grid became more prevalent (Table 4.1). The mean density and standard error per site for each survey and species are reported in Appendix 5.

Survey	*P. regularis*	*C. calamaria*	*C. adspersa*
March	684	71	0
May	601	96	10
July	717	92	6
September	755	84	46
November	480	84	124

Table 4.1: Total abundance of *P. regularis, C. calamaria* and *C. adspersa* for March to November 1995.

Patiriella regularis

This species was widespread over the grid area (Figure 4.3), where it was absent from only site 10 in November. Sites of markedly high abundance (>41, Figure 4.3) differed for each survey, but were generally found at the south end of the grid, at the base of a sandwave whose crest line lies west to east (see Figure 4.3).

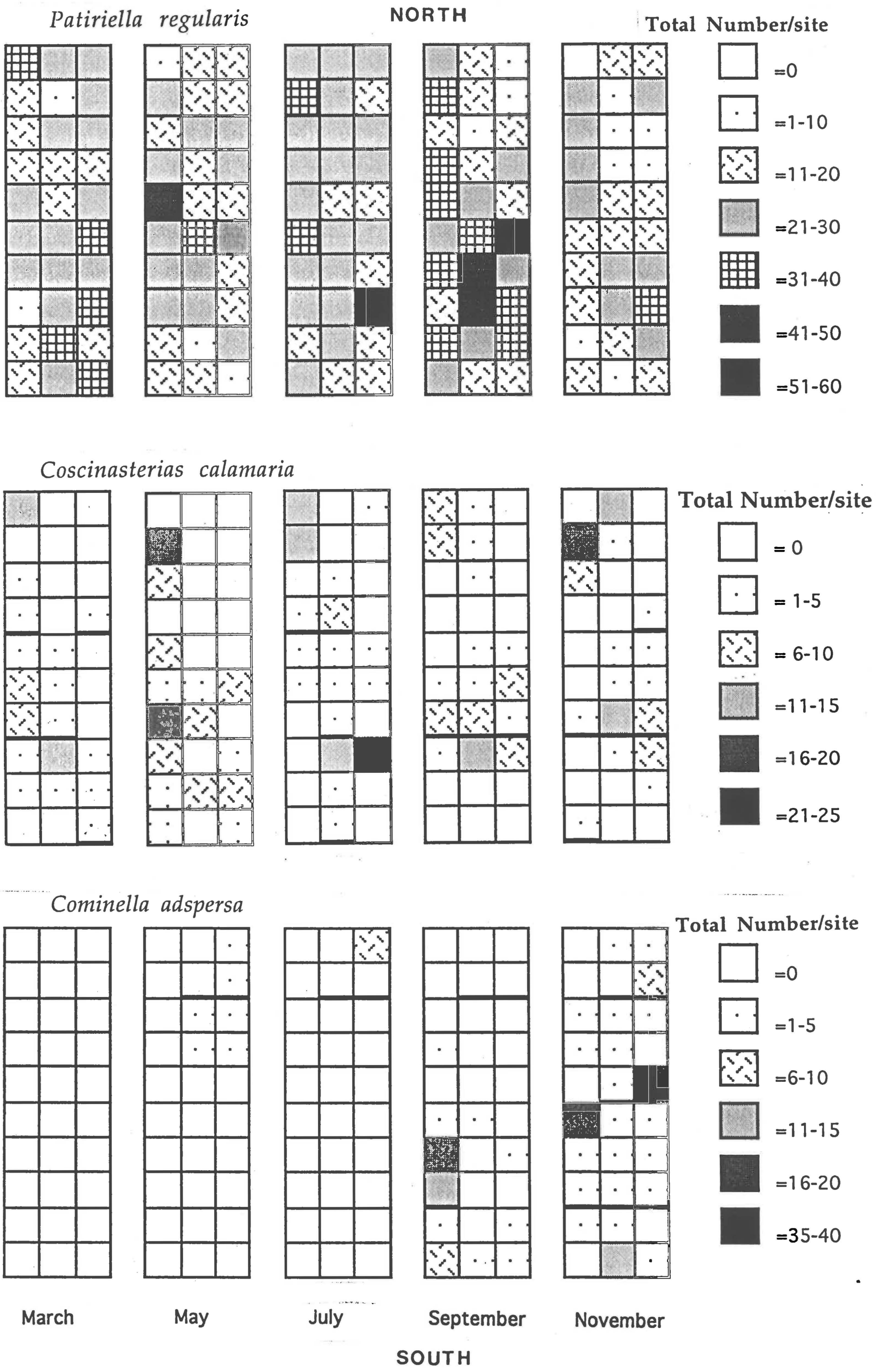

Figure 4.3: Densities of the three species in the grid, March to November 1995.

Coscinasterias calamaria

Sites of higher abundances were found at the southern end of the grid and the north-west area (sites 9, 10, 11 and 12), although it was absent from site 10 in November (Figure 4.3). The sites of higher density corresponded to areas at the base or foot of a sandwave, and where pipis (*Paphies australis*) appeared most abundant. The highest mean density obtained was 4.2/0.5 m^2 located at the base of a sandwave and overlying beds of pipis.

Cominella adspersa

The abundance of C. *adspersa* increased as the surveys continued (Figure 4.3). It initially occurred mainly in the northern half of the grid, but in September it occurred throughout the lower southern end with highest densities at sites 1, 3 and 4. In November it was more widely distributed, and sites 5, 20, 26 and 29 had greater densities than remaining sites. The highest density at site 26 (November) corresponded to an aggregation feeding on pipis.

4.3.2 Spatial Pattern Analysis

(a) *Coefficient of Variation*

The median coefficient of variation (CV) for *P. regularis* for each survey remained similar over time. All were below 100% (Figure 4.4), indicating a homogenous distribution of densities over the grid area. Greatest variation (interquartile range (Q3-Q1)) of CV values occurred in May and September where at some sites the CV was greater than 100% (heterogenous).

The CVs of C. *calamaria* were greater than 100% (Figure 4.4) for all surveys, indicating a heterogenous distribution within sites. Although the overall abundance of C. *calamaria* was the same for September and November (Table 4.1), the spatial intensity was greater in September (Figure 4.3).

C. *adspersa* also exhibited spatial heterogeneity within sites as the median CV for all surveys were greater than 100% (Figure 4.4). As C. *adspersa* became more prevalent across the grid, the CV decreased, although remained heterogeneous.

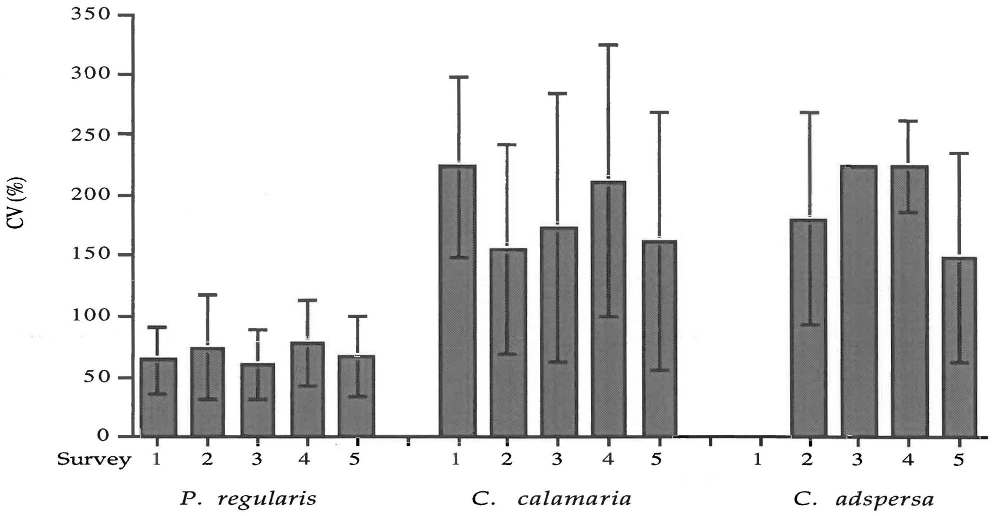

Figure 4.4: Plot of CV values (± Q3-Q1) per survey for each species. March (1), May (2), July (3), September (4) and November (5).

(b) *Variance:mean Ratio*

Patiriella regularis

Between March and November, most sites exhibited fluctuations in CD values, from regular (<1) to non-random (>1) (Table 4.2). Sites 1, 2, 11, 19 and 21 had CD values greater than 1 for all surveys, March to November. Most sites over the sampling period (March-November) with mean densities greater than 5 (indicated by an asterisk in Table 4.2), had CD values greater than 1 (mean 4.29, SD 2.71). Twenty-eight percent (42/150) of sites over the sampling period (March to November) had CD values less than 1 (mean 0.64, SD 0.22), of which, July and November had the highest frequency of regular/homogenous sites and this is reflected in the average CD value for the entire grid area of these surveys, where the CD are lower than the other 3 surveys (Table 4.2).

Coscinasterias calamaria

Between March and November no sites were found to have mean densities of *C. calamaria* greater than 5, thus the CD is based on sites with mean densities between 1 and 5, which provide only conservative results of the spatial intensity of patterns. Thirty-six of 81 sites (between March and November) which had calculable CD, had mean densities between 1 and 5, of which 35/36 sites had CD values greater than 1 (mean 4.10, SD 2.10) indicating a clumped distribution of *C. calamaria* within those sites. The overall mean CD value for each survey was greater than 1 (Table 4.2), indicating *C. calamaria* had a heterogeneous distribution over the grid area.

Cominella adspersa

One site (site 26, November) had a mean density greater than 5 and had a CD value of 37.56. This high value was due to 39/40 *C. adspersa* being found in 1 quadrat, thus the extremely aggregated distribution of *C. adspersa* within that site. In all surveys, sites which had mean densities between 1 and 5, had high CD values (mean 5.41, SD 3.47). Although these are conservative results they do suggest a heterogenous distribution of *C. adspersa* within those sites. The average CD value for each survey is above 1 (Table 4.2), indicating a heterogeneous distribution of *C. adspersa* over the grid area.

(c) *Spatial Autocorrelation*

Patiriella regularis

Spatial autocorrelation was initially low and increased in the final two surveys. In March, densities at separations up to 5 m showed no spatial autocorrelation, but were significantly positively correlated at separations about 7 m (Figure 4.5). Between May and November, significant positive autocorrelation existed at separations up to 5 m and generally become positively autocorrelated again at sites greater than 30 m apart, although this is only significant in May. The

Site	*Patiriella regularis*					*Coscinasterias calamaria*					*Cominella adspersa*			
	March	May	July	Sept	Nov	March	May	July	Sept	Nov	May	July	Sept	Nov
1	1.50	3.21	3.27	4.78*	1.46	.	2.00	.	.	1.00	.	.	4.86	.
2	2.88	1.33	4.71	3.02*	1.50	1.00	1.00	.	.	.	.	.	0.50	1.33
3	0.81	3.58	0.98	1.00	1.63	1.00	2.38	.	1.00	.	.	.	10.69	1.50
4	1.12	2.75*	2.25*	2.74*	0.84	2.71	5.75	.	6.00	1.00	.	.	7.41	1.00
5	1.12	1.80	1.05*	2.31	0.33	1.78	1.00	0.75	1.00	.	.	.	1.00	2.82
6	3.14	2.48*	2.00	6.20*	0.91*	1.33	2.00	1.00	.	.	.	.	.	.
7	3.50	0.41	2.00	1.13*	0.50	3.00	.	0.88	.	.	.	.	1.00	1.00
8	0.92	1.88	0.40	0.88	1.12	1.00	3.44	.	.	0.93	.	.	.	1.33
9	1.00	2.10	0.52*	8.56*	2.89	.	4.38	2.00	4.00	2.15	.	.	.	.
10	4.29	2.30	2.46	0.52*	.	6.38	.	3.46	4.00	.	.	.	.	.
11	2.91*	2.04	1.50	1.83	1.50	.	.	.	1.33	4.67	.	.	.	1.00
12	0.67*	0.31	0.20	3.77	1.44	.	.	.	3.00	1.00	.	.	.	.
13	0.40	0.70	0.89*	1.75	3.17	.	.	1.00	1.00	.	0.75	.	.	3.00
14	1.33	0.61	0.23*	2.09	1.50	.	.	7.00	.	.	2.00	.	.	0.75
15	1.16	0.61	1.16	1.29*	2.57	1.00	.	1.00	4.00	1.00	.	.	.	2.12
16	1.20	3.18*	1.44*	0.35*	1.63	3.00	2.00	1.00	1.00	0.50	.	.	1.00	5.00
17	2.45	7.83*	0.55*	3.83*	2.90	2.00	2.25	0.50	4.86	8.73	.	.	.	1.00
18	3.40*	0.62*	1.83	8.76*	0.63	4.92	.	5.12	8.73	3.00	.	.	.	1.00
19	6.92*	2.71	3.20*	2.78	1.06	2.00	3.92	3.00	.	.	.	.	.	1.00
20	1.60	4.53	3.95	2.00	0.67	.	.	1.00	.	.	.	.	1.00	9.71
21	11.49*	2.00	2.42	3.95	1.79	2.00	1.00	.	.	.	.	.	1.00	0.75
22	0.97	2.91	0.96	4.13*	1.89	0.75	7.00	.	.	1.00	.	.	1.00	.
23	6.46*	1.68	4.32*	1.84*	0.69*	1.00	1.00	6.83	2.61	1.64	.	.	.	0.75
24	1.89	4.18	1.75	4.52	0.76	.	.	.	2.13	2.25	.	.	1.00	0.75
25	3.74*	3.38	0.41*	9.27*	1.37	.	3.75	0.88	8.00	2.25	.	.	.	0.75
26	0.76	1.16	0.53	2.03	0.50	.	.	1.00	2.00	1.33	.	.	.	37.56*
27	1.85	1.59	0.88	4.60*	0.50	4.00	.	.	.	2.00	1.00	.	.	.
28	1.42*	0.98	1.91	0.45	1.42	.	.	.	.	.	0.75	.	.	0.50
29	1.55	2.38	1.17	0.75	2.90	.	.	.	.	.	0.75	.	.	0.21
30	0.33*	2.21	0.64	0.81	0.83	.	.	1.00	.	.	1.00	6.00	.	2.00
Average	2.43	2.25	1.65	3.05	1.41	2.29	2.86	2.20	3.42	1.64	1.04	6.00	2.77	3.34
SD	2.36	1.53	1.23	2.45	0.81	1.58	1.83	2.15	2.47	2.00	0.49	-	3.40	7.73

Table 4.2: Variance:mean ratio for *P. regularis, C. calamaria* and *C. adspersa* per site as an indication of the intensity of spatial pattern. Values >1 = non-random, 1 = random, <1 = regular distribution within sites. Values marked with an asterisks were derived from sites with mean densities greater than five.

correlograms of September and November were characterised by higher values of Moran's *I*, and a density gradient was able to be detected, where values gradually become negatively then positively autocorrelated as distances between sites increased.

Coscinasterias calamaria

Spatial autocorrelation was low throughout the sampling period, but became stronger after September. For all 5 surveys, densities at separations up to about 5 m were significantly autocorrelated (Fig. 4.6). In March, significant positive autocorrelation occurred again at distances about 43 m apart. In September and November, this occurred at sites about 25 m apart and remained positively autocorrelated up to 40 m apart. The correlograms of September and November provided a better indication of spatial pattern as Moran's *I* coefficients were larger. In addition, the correlograms showed a pattern that suggested 2 areas of high densities at 5m apart and again at about 25 m up to 40 m.

Cominella adspersa

The correlograms through time were variable in form. The May correlogram indicated densities at separations up to 10 m exhibited similar densities, while sites at greater separation showed no spatial autocorrelation; a density gradient running through the area (Figure 4.6). In July, the correlogram did not significantly deviate from E(*I*). In September, a similar pattern emerged, although sites up to 7 m apart showed most similarity among densities, and quadrats at greater distances showed negative spatial autocorrelation. The November correlogram showed different spatial form compared to previous surveys, but the low Moran's *I* coefficients and of which none were found to be significant, make interpretation of the correlogram unreliable.

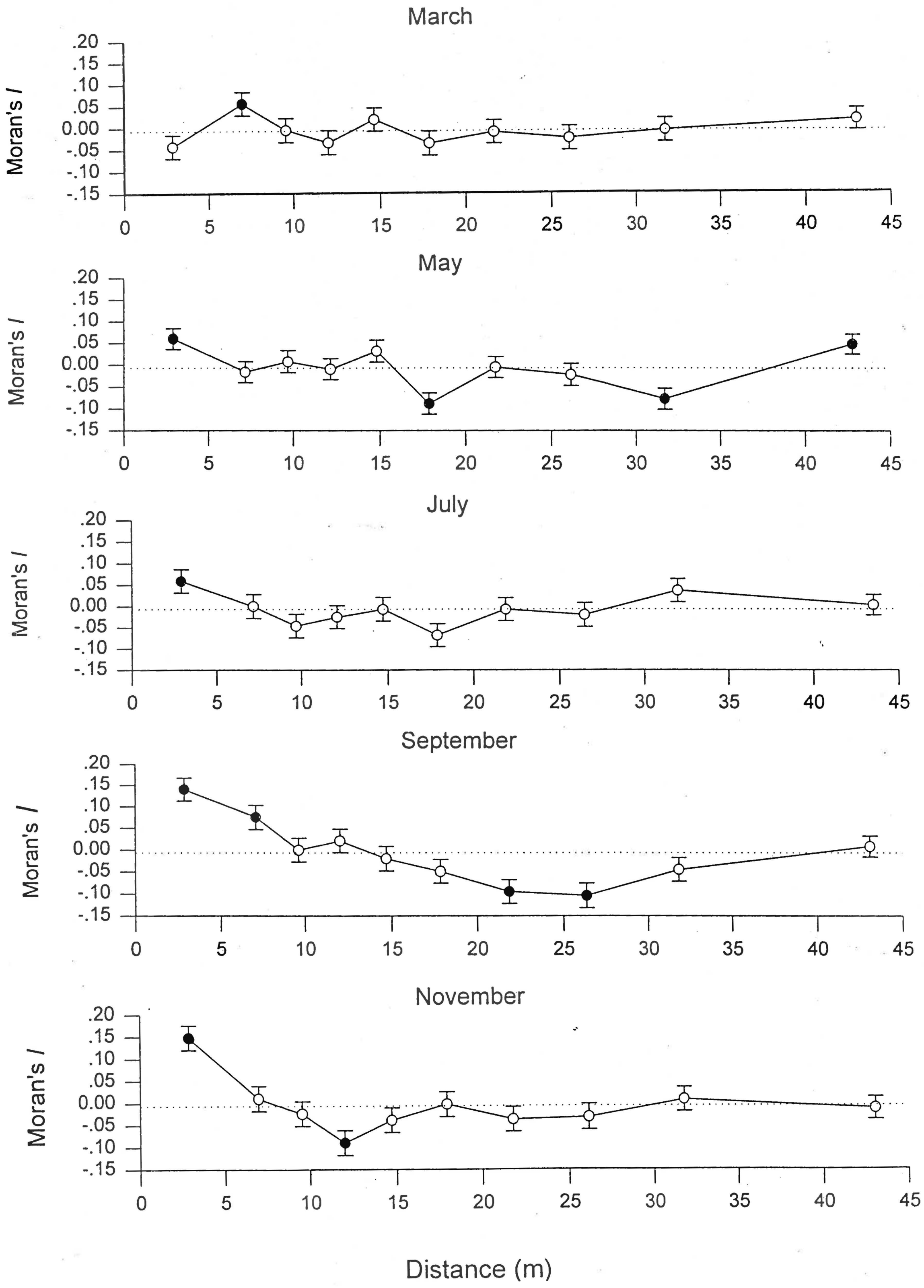

Figure 4.5: Correlograms of Moran's I versus distance for *P. regularis* between March and November 1995. Statistically significant autocorrelation coefficients ($p < 0.025$) are indicated by filled circles. Error bars = ± 1 SD.

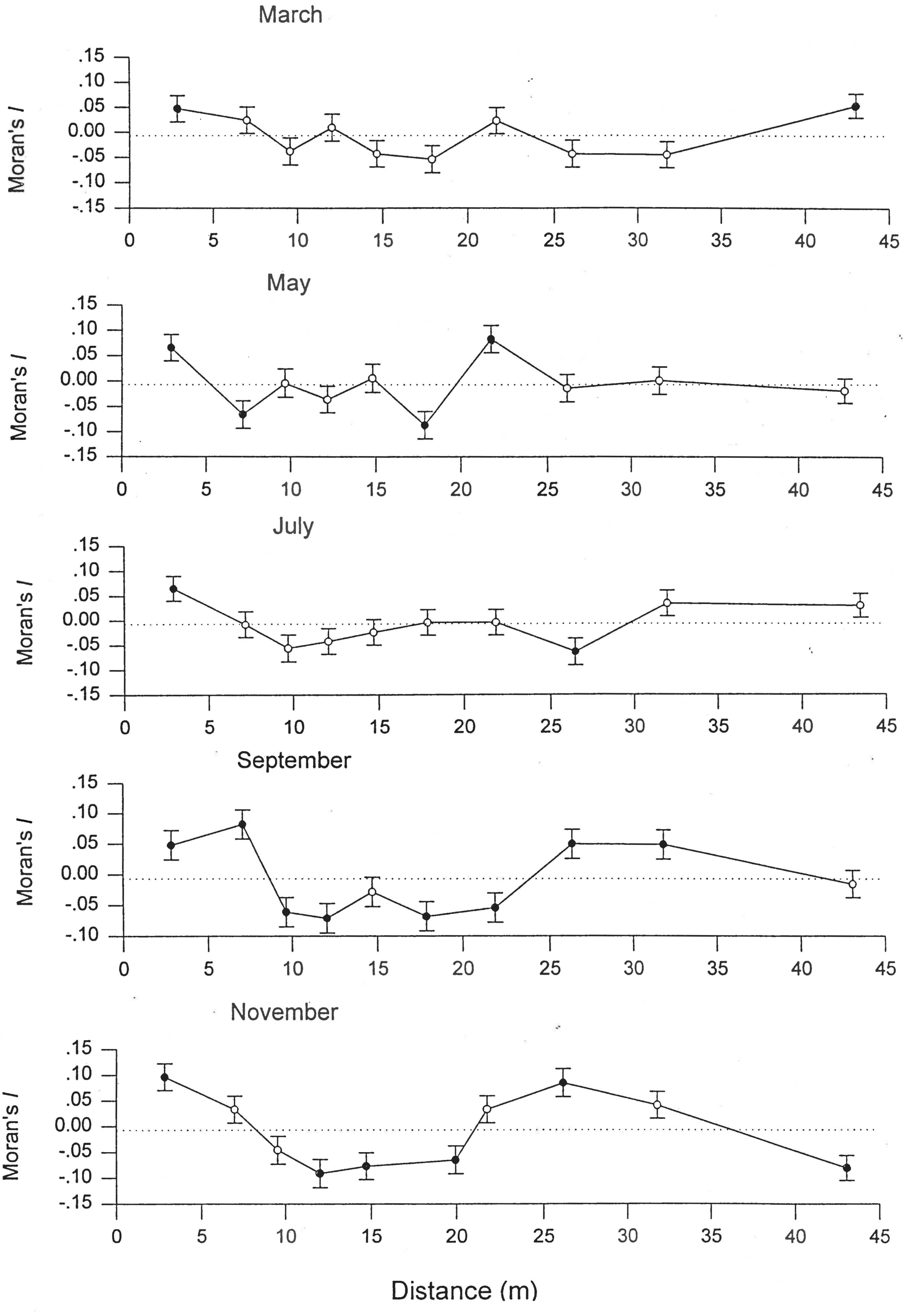

Figure 4.6: Correlograms of Moran's *I* versus distance for *C. calamaria* between March and November 1995. Statistically significant autocorrelation coefficients ($p < 0.025$) are indicated by filled circles. Error bars = ± 1 SD.

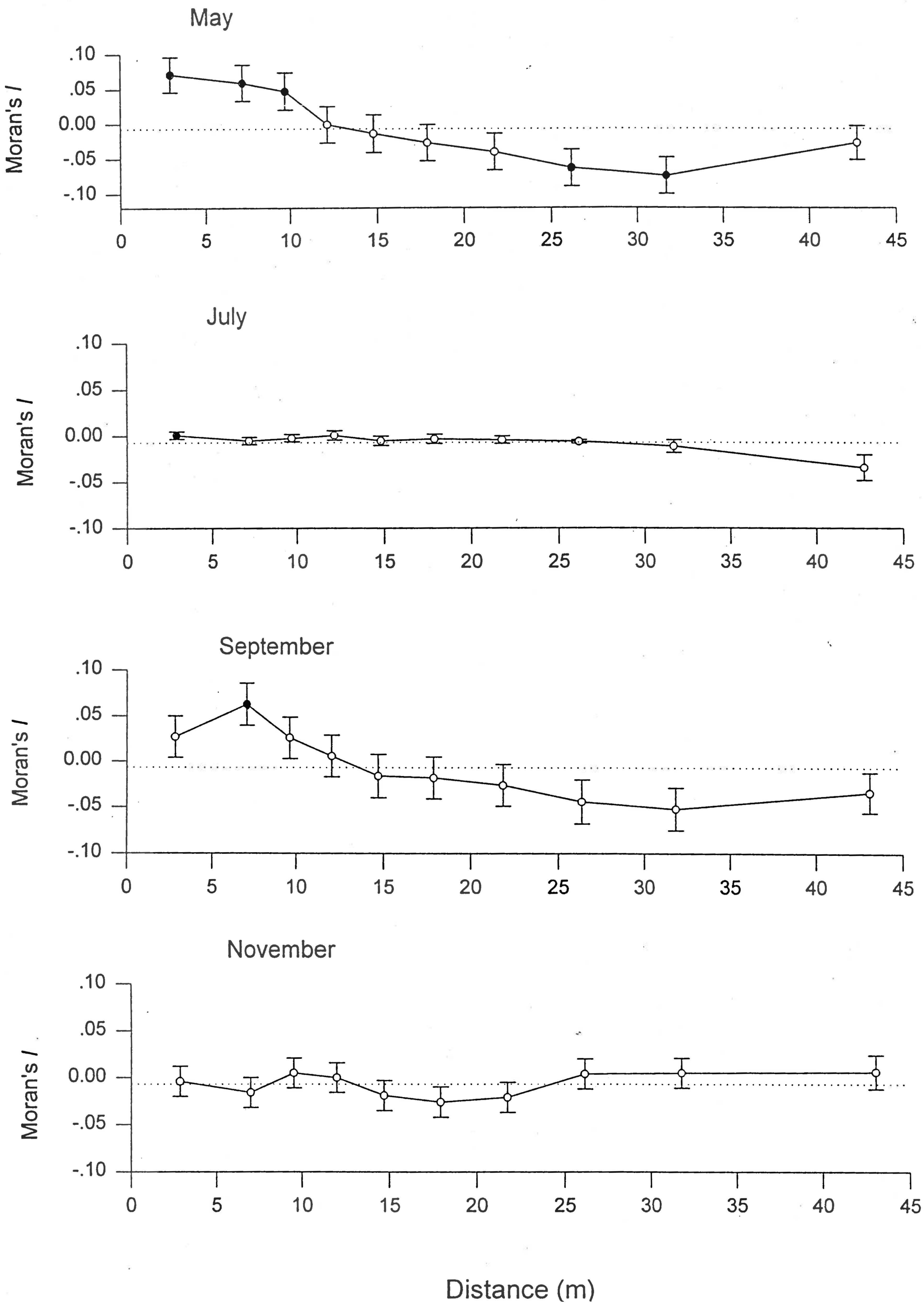

Figure 4.7: Correlograms of Moran's *I* versus distance for *C. adspersa* between May and November 1995. Statistically significant autocorrelation coefficients ($p < 0.025$) are indicated by filled circles. Error bars = ± 1 SD.

4.3.3 Population Size Structure

Patiriella regularis

The size frequency distribution of *P. regularis* remained relatively consistent over time (Figure 4.8). The modal size was at 55 mm for all surveys except in May, where a greater number of *P. regularis* were found within the 41-50 mm size class. Small (<20 mm) individuals were found, but were not common, in September and November.

Coscinasterias calamaria

Between March and May, *C. calamaria* exhibited a bimodal structure with common modes at 175 mm and 325 mm. From July to November *C. calamaria* at the 175 mm mode remained the most commonly found size class across the grid area, although large individuals up to 460 mm were present in September (Figure 4.9).

Cominella adspersa

In May and July, the numbers of *C. adspersa* found were too low to provide a reliable indication of size structure. More information is obtained from September and November plots, which distinctly show a modal size at 45 mm (Figure 4.10). The majority of the population of *C. adspersa* across the grid area, consist of smaller individuals, and were smaller than sizes found across the remainder of Centre Bank.

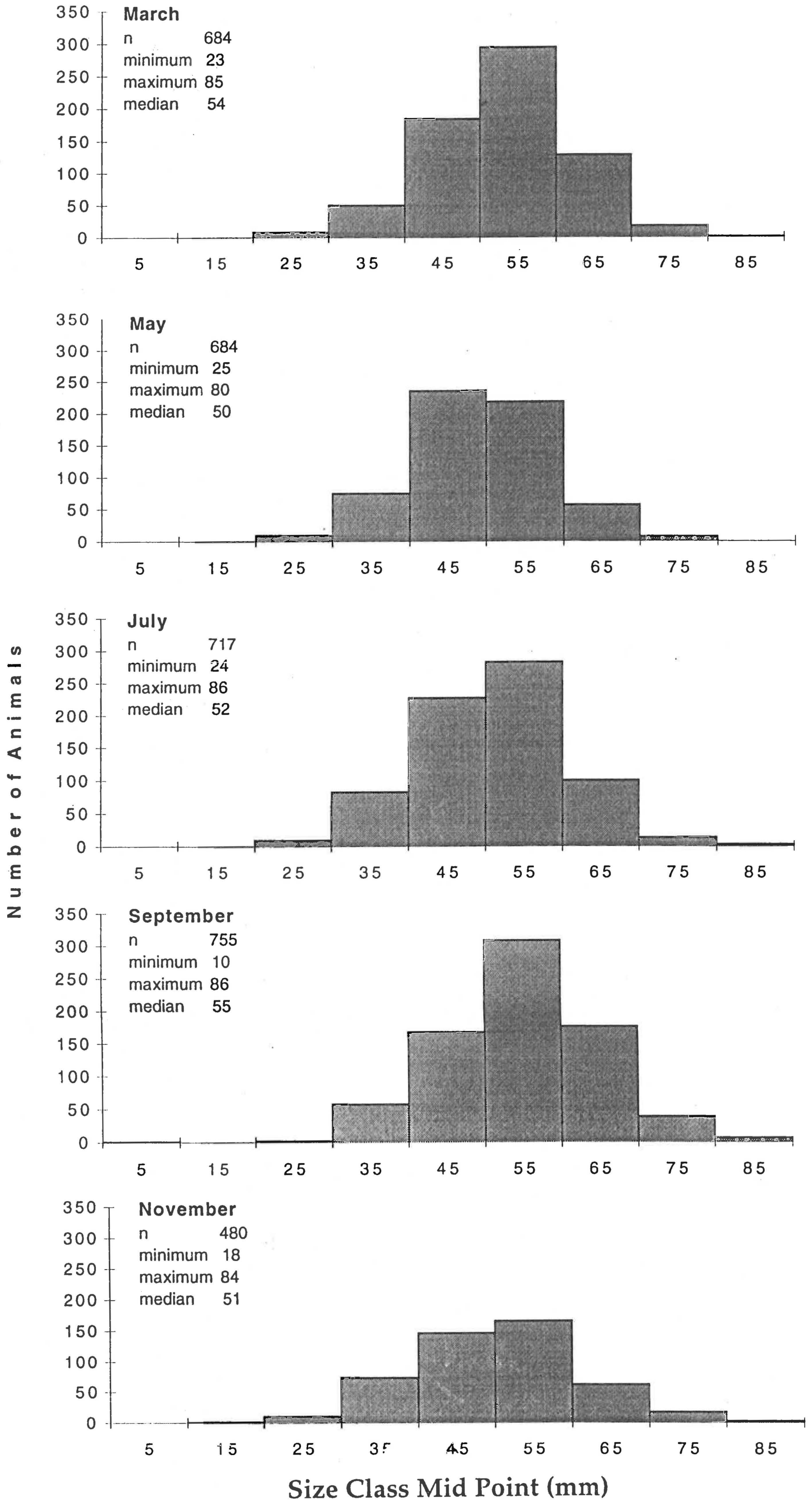

Figure 4.8: Size-frequency distribution of *P. regularis* between March and November 1995.

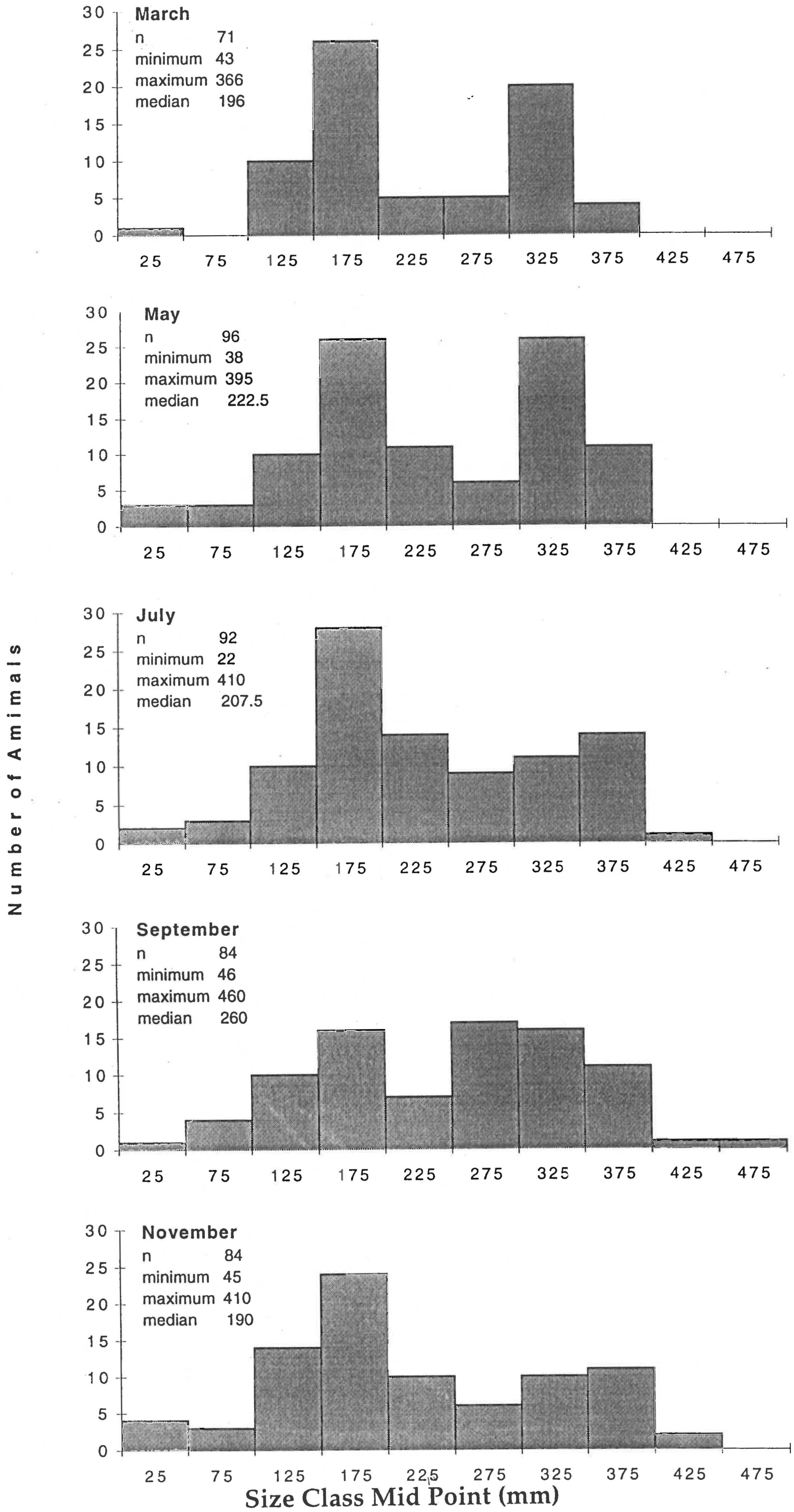

Figure 4.9: Size-frequency distribution of *C. calamaria* between March and November 1995.

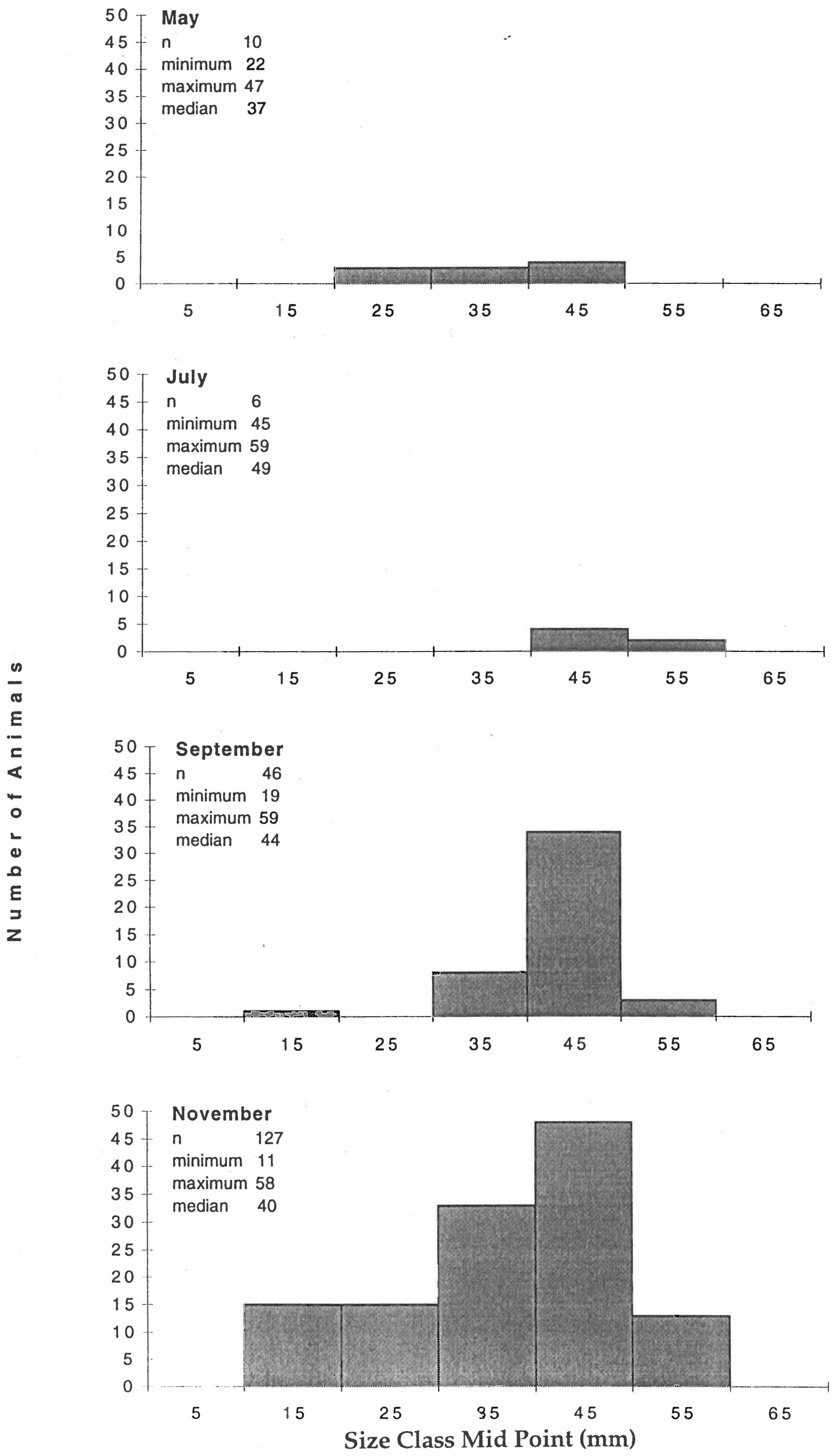

Figure 4.10: Size-frequency distribution of *C. adspersa* between May and November 1995.

4.5 DISCUSSION

Abundance

Patiriella regularis was the most abundant of the three study species during the grid surveys, as was also found across Centre Bank. Its density appeared to be relatively stable throughout the sampling period, but, its total abundance was unusually lower in November. This is speculated to be due to the occurrence of sea lettuce over most of the grid area during this time. Sea lettuce (a collective name given to 3 species of *Ulva* found in Tauranga Harbour (Gregor, 1995)), is a green alga found in shallow subtidal and intertidal waters of harbours and estuaries throughout New Zealand and world-wide (Park, 1992). It exhibits strong seasonal abundance trends, becoming most prevalent during summer months when water temperatures increase, and it may become particularly abundant when waters are nutrient enriched (Deely and McIntosh, 1994). High biomass of sea lettuce is reported as causing several problems to benthic fauna: physical interference, reduced water circulation (thus limiting food reaching suspension feeders and the recruitment of polychaete and bivalve larvae), sediments and water may become anoxic due to decomposition of the alga, and produce exudates which can have toxic effects on larvae (BOPRC and TDC, 1992). It has been documented as a cause of shellfish mortality within Tauranga Harbour (BOPRC and TDC, 1992). *P. regularis,* although found in areas of sea lettuce (pers. obs.) does not feed on the alga (Gregor, 1995), as it is unable to digest macropscopic algal tissue (Martin, 1970). Microscopic and encrusting algae are found on hard surfaces, such as shell debris across the grid. Thus sea lettuce may indirectly compete with *P. regularis* as it requires substratum to attach to, such as the shell debris. The presence of sea lettuce at localised areas of Centre Bank - those providing a suitable substratum such as shell debris - may effect *P. regularis* at small spatial scales. Abundances of *Coscinasterias calamaria* and *Cominella adspersa* appeared not to be affected by the presence of the alga. Mean densities of *C. calamaria* found across the grid were greater than those found across Centre Bank. This was due to the occurrence of a patch or aggregation characterised by high densities of up to 4.2/0.5 m^2 . *C. adspersa* became increasingly abundant across the grid and its distribution more prevalent through time. In November it was found throughout most of the grid, although typically at low density (<0.83/0.5 m^2). The dispersal ability of *C. adspersa* is examined in Chapter Five.

Densities of *P. regularis* and *C. calamaria* remained relatively stable (numerical constancy - Davis and VanBlaricom, 1978) throughout the sampling period, except in November when *P. regularis* may have been affected by the occurrence of sea lettuce. To estimate the stability of a population, monitoring periods of at least 2 years are recommended (McArdle and Blackwell, 1989) to assess seasonal fluctuations in abundance and the potential factors influencing the stability. Paine *et al.* (1985) and Davis and VanBlaricom (1978) further suggest that monitoring periods greater than that of the life-span of the species, provides a better indication of the stability of a population. The life-spans of *P. regularis* and *C. calamaria* are at least 10 years (Bradstock, 1985), and this sampling is therefore only able to assess the stability of populations in relation to movement. In addition, the stability of a population is best determined by the resistance, amplitude and elasticity of a population when subject to perturbations (Kikkawa, 1986).

Spatial Distribution Patterns

Both *C. calamaria* and *C. adspersa* were heterogeneously distributed throughout the grid area at small scales (within sites) and at larger scales (between sites). *P. regularis,* however obtained conflicting results (as in the Centre Bank surveys) where the coefficient of variation suggested a homogeneous distribution within sites across the grid area, and the variance:mean ratio indicated a heterogeneous distribution. Spatial autocorrelation showed that from March to

July, *P. regularis* exhibited similar densities at a range of distances, but in September and November a density gradient had emerged where sites closer in space showed greater similarity in density than sites at greater distances apart.

Two distinct patches of *C. calamaria* developed in the grid area in September and remained there in November. The map of abundance (Figure 4.3) also illustrated this pattern. Although the presence of a patch or aggregation was evident at areas of the grid (Plate 5), the density variability within sites was high, as shown by the tests for pattern intensity.

C. adspersa, due to its limited distribution in the early surveys generated plots of Moran's *I* which resembled density gradients; sites closest in space showed greatest similarity than sites at distances furthest apart. And as the abundance was low during these surveys, and not significantly different from zero, low values of Moran's *I* were obtained. In November as its abundance increased and was becoming more widespread through-out the grid, a spatial pattern became more evident where similar densities could be found at a range of distances, but were separated by distances of dissimilar densities.

Factors causing spatial heteogeneity at small (10s of metres) scales

Without experimental analysis, it is not possible to make clear and accurate statements about what important underlying processes are operating which affect the distribution of each species (Virnstein, 1977). As the grid was sampled within a small area (50 m x 15 m), biogenic processes (i.e. predator-prey interactions, competition, motility) are considered to be important processes causing spatial heterogeneity within relatively large homogeneous zones (Morrisey *et al.*, 1992).
C. calamaria is a carnivorous predator of a range of prey types (e.g., Arthropoda, Echinodermata, Mollusca (Martin, 1970)). Extra-oral ingestion enables it to feed on a range of prey sizes and its many arms allow it to manipulate a number of

prey at one time (Martin, 1970). The availability of food resources appeared to be of primary importance in determining the distribution of *C. calamaria*. The highest densities of *C. calamaria* were found overlying distinct beds of pipis, which were found in the vicinity of the base or foot of sandwaves located at both ends of the grid. The hydrodynamic patterns over those sandwaves may have uncovered pipis within the sediment, and hence increase exposure to predation. Cook (1989) speculated *C. calamaria* was unable to extend its tube tube to excavate deeply buried prey, as found in other asteroids (Birkland, 1974; VanVeldhuizen and Oakes, 1981), hence superficial prey may be potentially preyed upon by *C. calamaria*. Many bivalves bury deeply (i.e., to depths greater than the length of their own bodies) within the sediment (Barnes, 1980), facilitated by long siphons extending to the surface. However, pipis, have relatively short siphons and are found buried a few cms below the sediment surface (Bradstock, 1985). Small-scale changes in bank morphology influencing the availability of pipis, may facilitate predation by *C. calamaria* and thus may be a potential factor affecting its distribution. The stability of *C. calamaria* over beds of pipis suggest motility is minimal and that prey are not sufficiently depleted by *C. calamaria*, to cause migration from the area. Movement rates of echinoderms have been correlated with feeding activity (Harrold and Reed, 1985; Andrew and Stocker, 1986), where sated animals repeatedly exhibit lower movement rates than those in areas of low food abundance.

Movement and formation of aggregations due to perception of food by chemoreception has been shown to be an important mechanism for a number of asteroid species (see table 2, in Sloan and Campbell, 1982). Detection of food may be a combination of olfactory chemoreception, mechanical (e.g. vibration) and/or random encounter (Feder and Christensen, 1966; Binyon, 1972; Cook, 1989). Casual observations in the field showed that when pipis were broken open, a number of *P. regularis* migrated toward and located the pipis from about 1 to 2 m away, indicating an ability to chemosense prey at least at short distances. Cook (1989) attempted to determine if *C. calamaria* could detect prey items by olfaction using a Y-maze (a popular olfactometer). He could not conclusively determine whether *C. calamaria* was attracted to the stimulus due to problems with the experimental design. The detection of food by asteroids provides a possible mechanism of forming feeding aggregations in response to injured prey or by other attacking asteroids (Warner, 1979), and it is probably more important for subtidal marine asteroids than for wave-washed intertidal asteroids (Jangoux, 1982). Aggregations of *Acathaster planci* (crowns-of-thorns starfish) have been found to reach high densities and cover large areas of coral reefs in the Indo-Pacific, causing subsequent destruction of extensive areas during periods of infestation (Warner, 1979). *Asterias rubens* has been observed to reach mean densities of 97/m^2 and form aggregations several layers of starfish deep when feeding on Iceland scallops (Warner, 1979). Aggregations have also been thought to occur in response to breeding. *P. regularis* is reported to be a gregarious broadcast spawner (Martin, 1970) forming breeding aggregations during summer months. Aggregations of asteroids due to a social behaviour has been suggested, but generally is thought to be based upon reproductive behaviour (Warner, 1979). Aggregations of juvenile gastropods may increase their survival (Ray and Stoner, 1994), supporting the theory that aggregated individuals gain safety in numbers over ~~than~~ lone or randomly distributed individuals.

C. adspersa is a voracious carnivore of bivalves, crabs, other gastropods and dead or moribund animals (White, 1971), and particularly the common cockle (*Austrovenus stutchburyi*) (Powell, 1976) (where it is available). Across Centre Bank, feeding as aggregations on single prey items was commonly observed (Plate 6). Boring or drilling has been found to occur for other buccinid whelks (*Cominella eburnea* and *Cominella tasmanica*) in Australia (Peterson and Black, 1995) and Larcombe (1968) reported this for *C. adspersa*. Across Centre Bank bivalve shells were sometimes found to have fine bore holes over their surface; few were found with bore holes passing through the entire shell. Gastropods have a well-formed chemosensory ability (Lenhoff and Lendstedt, 1974), and some are able to locate prey up to 30 m away (Himmelman, 1988). The ability of whelks to perceive a food source in this manner has been exploited by fishers who use baited traps to fish for them (Himmelman, 1988). Their ability to disperse to areas of attraction may also be attributed to their increased abundance and prevalence across the grid area.

P. regularis is generally considered to be a generalist predator, commonly found to feed upon small bivalve molluscs, gastropods, coelenterates, arthropoda, chordata, echinoderms and dead or moribund animals, and microscopic and encrusting algae (Grace, 1977; Martin, 1970; Jangoux, 1982; Cook, 1989; Britton and Morton, 1994). *P. regularis* will attack prey that are able to be covered by the extended stomach (although digestion may not always follow; Martin, 1970) as they are unable to use force to gain access to prey tissue and do not adopt the humped position characteristic of *C. calamaria* (Plate 7) when pulling valves of the bivalve apart (Martin, 1970). They are able to prey upon small bivalves and this was observed in the grid. Their distribution may therefore be less influenced by pipi availability across the grid than the distributions of *C. calamaria* and *C. adspersa*. It may be that the hard surfaces such as shell debris are a source of microscopic alga and this may be an important food source for *P. regularis* in the grid.

Population Size Structure

The grid contained similar sized individuals of *P. regularis* and *C. adspersa* compared to those found across the remainder of Centre Bank, but *C. calamaria* was frequently found to be larger (up to 460 mm). The occurrence of a patch consisting of greater numbers of individuals may account for this, increasing the probability of finding a greater size range. Sizes of each species were found to be homogeneous within the grid area; there was no evidence of spatial pattern of sizes.

Temporal variations in size structure could not be clearly identified for *P. regularis* or *C. adspersa*. Median sizes of *C. calamaria*, however, generally showed an increase between March and September, with a slight decrease in size in November. This decline resulted from increased abundances of juvenile (< 60 mm, Barker, 1977) *C. calamaria*, although they were present throughout the sampling period.

To determine the growth and age of asteroids by size frequency distribution is problematic (Feder and Christensen, 1966). Growth of asteroids primarily depends on the quantity of available food. It was demonstrated for *Asterias forbesi*, that a well-fed individual may be several times the size of a poorly-fed one of the same age (in Swan, 1966). In the absence of food, asteroids may shrink and survive many months, thus obscuring size frequency distribution analysis as an estimate of growth. In addition, feeding may be seasonal and not continuous during periods of extreme high or low temperatures and during periods of spawning. In light of this, size frequency distributions may better reflect the trophic environment than the age of asteroid populations (Scheibling, 1980). Growth may be best estimated by measurement of weight and when are fed with a known amount of food.

Gastropods may give better indications of growth, as they lack a labile shell which may be resorbed in the absence of food. Therefore, growth may be better estimated by size frequency distributions. The numbers of *C. adspersa* collected during the sampling period were very low and not adequate to make estimates of growth. However, the size structure remained similar over time, suggesting little recruitment. Tagging studies are often the best measure of growth (Hooker, 1995), of individuals however the cryptic nature of *C. adspersa* would make this technically difficult.

Asteroids exhibit greater plasticity of growth than do gastropods (Andrew, 1989), such that asteroids are less vulnerable to food shortage, by being able to undergo adjustments in growth. Food was abundant in the grid, and it appeared that recruitment might be the dominant process controlling population dynamics.

Plate 5: Typical aggregation of *Coscinasterias calamaria* within grid.

Plate 6: Feeding aggregation of *Cominella adspersa* preying on a single *Paphies australis*.

Plate 7: Humped feeding posture of *Coscinasterias calamaria*.

CHAPTER FIVE
Experimental Studies

5.1 INTRODUCTION

The behaviour of predators and prey may modify any impact predation may have on prey populations. Examples of such behaviours were outlined in Chapter Two. Attempts were made to assess the impact *Patiriella regularis, Coscinasterias calamaria* and *Cominella adspersa* may have on bivalve populations on Centre Bank. Factors to be tested were prey type preference, sizes of prey able to be opened, feeding rates and predator motility.

Prey type preference is a learned behaviour of a predator to recognise and discriminate between different types and sizes of prey to gain maximum energy rewards and reduce handling time and energy spent gaining access to prey tissue. It has great advantages for predators as different prey types offer different caloric content and different morphology and sizes require different handling times (see review by Underwood and Fairweather, 1992). In return, the predator obtains greatest energy profitability, increased feeding rate, reduced risk of attracting other predators or scavengers to the area, and ensured survival. Such preference abilities, therefore, may determine predation risk and impact on prey populations.

Motile animals, unlike sessile animals, possess the ability to disperse to areas of more favourable conditions. There is a vast number of literature relating to the movement of intertidal gastropods, in particular the common periwinkle *Littorina littorea* (L.) in rocky intertidal habitats. Studies have found various environmental factors (such as light, gravity, wave action, temperature) are likely to be important in the movement and orientation of gastropods in establishing and maintaining their position on the shore. (see Underwood, 1979, for an excellent review).

It is well known that many marine gastropods have a well developed chemosensory ability (Lenhoff and Lindstedt, 1974) enabling them to detect and locate a food source by water-borne stimuli. The environmental factors experienced by intertidal gastropods are less likely to govern the movement of subtidal gastropods. The movement of water such as currents are important environmental factors, providing a mechanism by which gastropod predators may search and locate prey and thus ultimately affect its behaviour, diet and survival. Understanding the foraging behaviour of predatory gastropods in relation to these environmental factors can improve knowlege of their feeding biology and effects on prey species (Fairweather, 1988b).

5.2 Feeding biology of *P. regularis, C. calamaria* and *C. adspersa*

5.2.1 Methodology

Attempts were made to experimentally examine the feeding biology of the three study species by enclosure experiments in the field. The caging structures would have preferably been set up in the field on Centre Bank. However, the shallowness at low tide and frequency of small boats in the area rendered this unsuitable. An area adjacent Butters Wharf boat landing (Port of Tauranga) was chosen as the experimental site as it had easy access without use of a boat and a stable anchorage for experimental cages. Caging structures used were perforated plastic containers about 40 cm diameter and 15 cm deep, with plastic mesh lids. These were hammered to wooden planks and submerged by steel chain weights.

5.2.2 Results

The experimental site at low tide was subject to backwash from boats and sometimes exposure from the water. As a consequence, some accumulation of sediment within cages occurred and stresses involved did not mimic natural conditions. Cages with larger perforations would have been preferred, to facilitate drainage of sediment from the cages, however this would not have confined smaller bivalves (<15 mm shell length) particularly important for *P. regularis* experiments. As a consequence, all attempts failed to provide information on the feeding biology of each species, and time and cost contraints prohibited further experimentation.

5.3 *C. adspersa* Condition

5.3.1 Methodology

As experimental attempts in the field were unsuccessful, *C. adspersa* was brought back to the Salt Water Circulation Room (SWCR) at the University of Waikato to continue experimentation, as they were found to be more robust to handling than the starfish. Varying densities of *C. adspersa* were placed in aquaria with different sizes and types of bivalve (*Paphies australis* (pipi) and *Ruditapes largillarti*) which they were observed to feed upon in the field. In the two months of being kept in aquaria and supplied with prey items, *C. adspersa* was not found to attack or feed on any of the bivalves with which they were supplied.

Therefore, the effects of low food on the condition and survivorship of *C. adspersa* was of interest.

C. adspersa were collected from the field (20 October 1995) at a site known to be relatively abundant of them and at a range of sizes and were transported to the University of Waikato's SWCR in a damp sack. The maximum time spent out of water was 2 hours, and no *C. adspersa* had died as a result of this. At the SWCR they were immediately placed into an aquarium, with circulating saltwater (salinity 34 ppt, temperature 12°C) collected from the Harbour. Whelks were then individually removed and for measurement of their length and weight. Shell length (tip of aperture to spire, see section 3.3.1.2) was measured by a V-shaped pipi measurer (mean error 0.23 mm, SE 0.04, n 47). Weight was measured by electronic scales to 1 decimal place. *C. adspersa* were then divided into 4 groups of 2 x fed and 2 x starved, and placed in separate aquaria of approximately 40 animals. Fed *C. adspersa* were supplied with broken *R. largillarti,* as previous experimental study found they were not likely to attack the bivalves under laboratory conditions. *C. adspersa* were kept for 39 days, after which time they were reweighed and measured.

Due to the confounding problems and inherent difficulties of assessing the condition of an animal based on condition indices (a simplification of the length-weight relationship to a single parameter, e.g. Fulton's Condition Factor (K), Relative Condition Factor (K_n) and Relative Weight (W_r), Cone, 1989; Springer and Murphy, 1990), regression parameters were used to describe the relationship between length and weight of the three groups (wild, starved and fed) of *C. adspersa*.

As length-weight relationships are power functions, it is customary and appropriate to estimate regression parameters by transformation to a logrithmic scale (Gutreuter, 1990). The parameter *a* (y-intercept) and *b* (slope) are then easily estimared by linear regression:

$$\log_e(W) = \log_e(a) + b \log_e(L) \tag{5.1}$$

where W (weight) is a function of L (length) (Cone, 1989).

5.3.2 Results

Calculation of the regression coefficients found there was very little difference between the slope (*b*) and y-intercept (*a*) of *C. adspersa* from the field and after being deprived of and fed with bivalves after 39 days (Table 5.1).

	Wild	**Starved**	**Fed**
n	163	74	75
Y-intercept (SE)(mm)	-4.16 (0.04)	-4.22 (0.06)	-4.21 (0.07)
Slope (SE)	3.40 (0.03)	3.43 (0.04)	3.41 (0.04)
R^2	0.9894	0.9905	0.9880
CV	6.36	5.49	6.05

Table 5.1: Linear regression parameters for each group, wild, starved and fed.

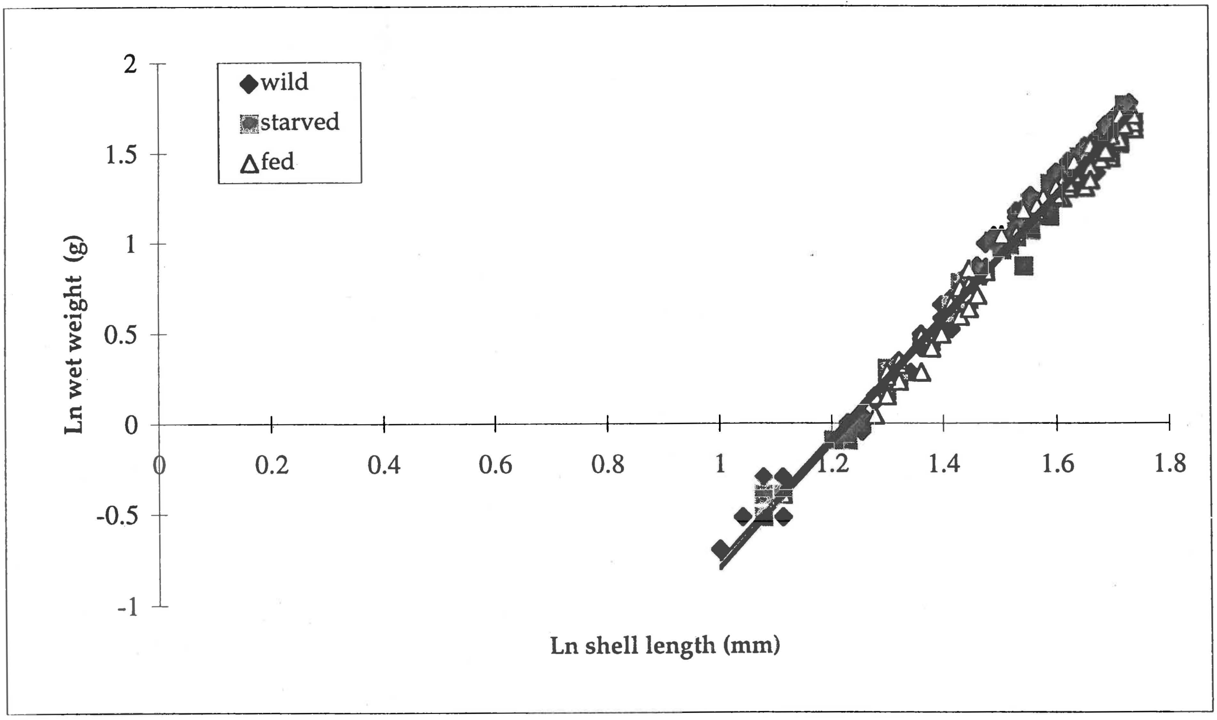

Figure 5.1: Length-weight relationships of wild, starved and fed groups. The fine regression line located above that of the others belongs to the "wild" group.

The two replicate samples of each starved and fed were pooled due to the small difference evident. According to the regression equations, starved *C. adspersa* were of greater weight per unit length than both wild and fed *C. adspersa* (Figure 5.1), although it was not a large difference; the standard errors around the y-intercept and slope for each group overlap, indicating no significant difference.

5.4 Movement Behaviour

5.4.1 Methodology

The objective of this work was to monitor rates of movement of *C. adspersa* and direction of movement to determine their dispersal ability and movement rate in relation to current direction, during ebb, flood and high (slack water) tidal cycles.

The experimental site was located on Centre Bank at position 176°09′8231″E 37°39′0000″S, approximately 100 metres north of the grid area. The site had a coarse sandy bottom with little topographical relief and was devoid of vegetation. This site was selected as it was relatively abundant with *Cominella adspersa*.

Movement direction and distance displaced were measured for each tidal cycle, ebb, flood and high. Three replicates samples of each tidal cycle, each comprising of 10 individuals, were conducted during 1/8/95, 18/8/95 and 17/10/95. Current directions and velocities are illustated in Appendix 4a (ebb) and 4b (flood) and were similar to those noted in the field.

Underwood and Chapman (1985) showed clumping of animals together at the start of an experiment increased directionality in their subsequent movement (i.e. trail following), therefore, *C. adspersa* were placed approximately 1.5 m to 2 m apart to avoid this (Figure 5.2). This also eliminated interaction at later stages of the experiment between adjacent animals, as the whelks were not tagged in attempt to minimise disturbance and ensure natural behaviour. The area, although relatively abundant in *C. adspersa*, was not difficult to keep cleared of additional whelks excluded from the experiment, by regular clearing when in the vicinity of each individual every 10 minutes. To further reduce possible confusion between whelks, notes were taken of each whelk's characteristics (i.e. size, shell colour and distinguishing features). It was also usually possible to follow their trails in the sediment.

Each individual was placed between pegs (1-10, in Figure 5.2), which typically involved handling for less than 5 seconds. The effect of this disturbance on movement was studied by observing the behaviour of 3 groups of whelks in different locations in the experimental area. In each group, 30 whelks were set apart approximately 10 cm from one another and handled equally to those in the experiment; only their shell was touched and for a short time while they were moved. Observations suggested that within 2 minutes, most had extended their proboscis, of which many were orientating on their foot. By the end of 10 minutes nearly all were moving, some of which became motionless or buried, while only very few never moved or buried from the start. This behaviour was also observed by the experimental whelks. The distances displaced by these whelks in a 10 minute period were up to 50 - 60 cm and movement direction

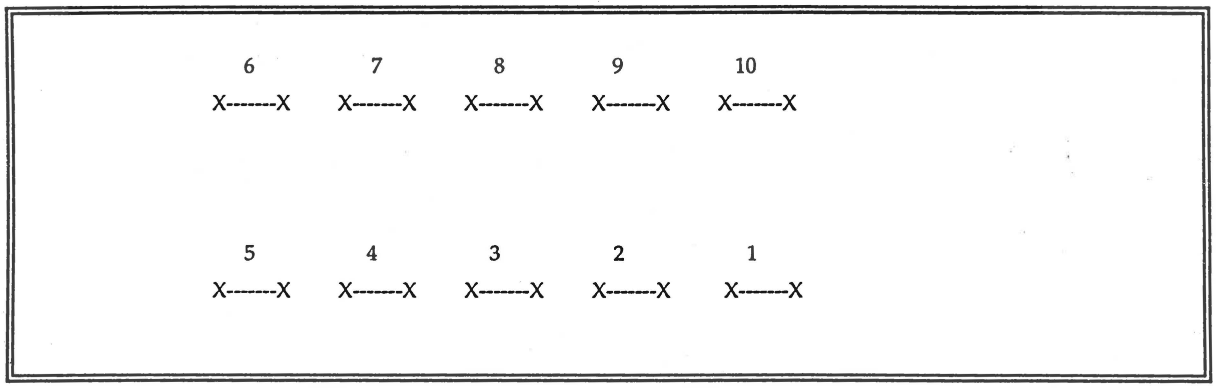

Figure 5.2: Arrangement of baseline pegs 1 - 10.

was random. Thus it was assumed the handling at the start of the experiment was insignificant and was overcome within a short period.

Movement was measured at 10 minute intervals over a period of 70 minutes (predetermined by the limit of one full SCUBA tank), thus 8 consecutive measurements were collected for each whelk.

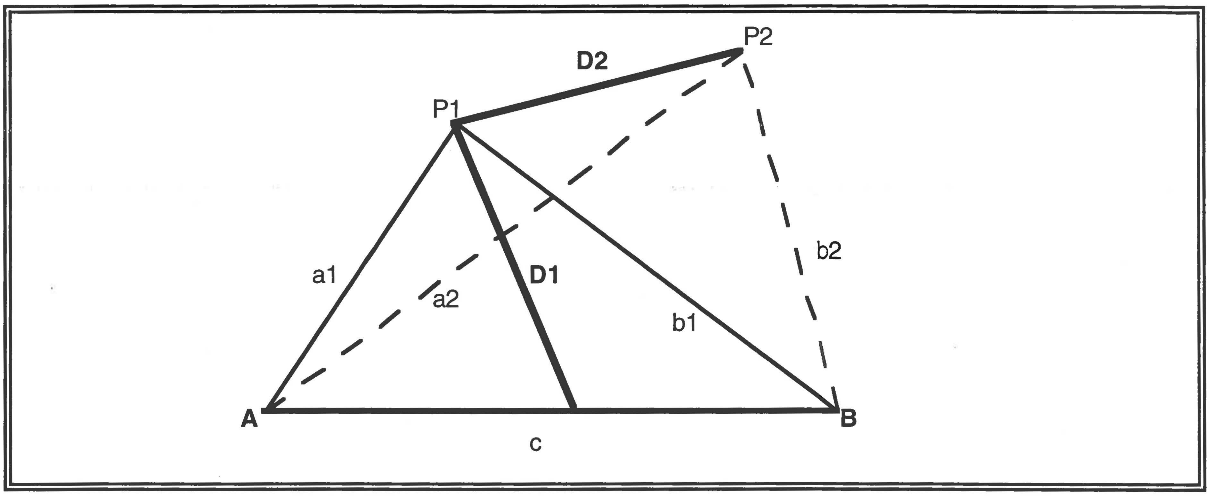

Figure 5.3: Diagram to illustrate the method of recording positions of C. *adspersa* in the field, from 2 baseline pegs A and B: D1 is the distance moved from the baseline to the first position (P1), and D2 is the second distance moved from P1 to P2. The distance and direction moved are calculated from a1, b1, a2, b2 and c (adapted from Underwood, 1977)

This method allowed their path of movement to be traced, thus their behaviour of movement more precisely, as opposed to daily measurements. Two pegs of known distance (A and B, Figure 5.3) apart were hammered into the sediment and the distance from each peg to the whelk was used to determine the individuals position as coordinates on a cartesian plane (Underwood, 1977). As there was little topographical relief in the area, movement on a plane was justified.

The distance and direction moved per 10 min period for each whelk were determined by the following formulae:

$$\text{distance} = \left\{x^2 + y^2\right\}^{1/2} \qquad \text{direction} = {}^{x}\!/_{y}\ \tan^{-1} \tag{5.2}$$

Coordinates x and y were calculated by coordinate geometry from data shown in Figure 5.3.

The mean direction moved per whelk and sample was then calculated, According to Mardia (1972), the mean direction $(\bar{\theta})$ of a set of data is calculated from the sine $\bar{S}/\bar{R}$ and cosine $\bar{C}/\bar{R}$, which are found by determining the mean resultant vector (R), and the mean resultant vector length $(\bar{R})$:

$$R = \left(S^2 + C^2\right)^{1/2} \tag{5.3}$$

where S is the sum of the sines and C is the sum of the cosines of all the angles in the sample. The mean resultant vector $(\bar{R})$ is equal to R/n or equation (5.4), $\bar{S}$ is equal to S/n and $\bar{C}$ is equal to C/n.

$$\bar{R} = \left(\bar{S}^2 + \bar{C}^2\right)^{1/2} \tag{5.4}$$

The value of $\bar{R}$ is between 0 and 1. It's value increases with decreasing variability among data points of a sample. A simpler and faster method presented in Upton and Fingleton (1989) for calculating the mean direction is:

$$\bar{\theta} = \tan^{-1}\left\{\left(\sum_i \sin\theta_i\right)/\left(\sum_i \cos\theta_i\right)\right\} = \tan^{-1}(X/Y) \tag{5.5}$$

where $\left(\sum_i \sin\theta_i\right)$ is the sum of the sines and $\left(\sum_i \cos\theta_i\right)$ is the sum of the cosines of all the angles in the sample and correspond to S and C in Mardia's (1972) above formulae. As angles were measured from the north and in a clockwise direction (*azimuthal* angles), a comprehensive definition to take into account the cyclic nature of the sine, cosine, and tangent functions is:

$$\bar{\theta} = \left\{ \begin{array}{ll} \tan^{-1}(X/Y) & \text{if } Y > 0, X > 0; \\ 180° + \tan^{-1}(X/Y) & \text{if } Y < 0; \\ 360° + \tan^{-1}(X/Y) & \text{if } Y > 0, X < 0. \end{array} \right\} \tag{5.6}$$

(Upton and Fingleton, 1989). Although $\bar{R}$ gives an indication of the concentration of data points about the mean direction, it is not interpretable in terms of degrees, hence the use of calculating the 95% confidence interval:

$$\bar{\theta} \pm \sin^{-1}\left\{u_\alpha\left(2\hat{W}\right)^{1/2}\right\} \tag{5.7}$$

where, $u_\alpha = 1.96$ (95% C.I.) and $\hat{W}$, the circular variance of $\bar{\theta}$ (Fisher and Lewis, 1983) is given by:

$$\hat{W} = n(1-\psi)/4R^2 \tag{5.8}$$

where,

$$\psi = \frac{1}{n}\left\{\cos 2\bar{\theta} \sum_i \cos 2\theta_i + \sin 2\bar{\theta} \sum_i \sin 2\theta_i\right\} \tag{5.9}$$

The 95% confidence intervals are calculated to compare mean directions when the data is determined, by an independant test, to be directional. Rayleigh's test was used to test for directionality in each of the replicate samples and combined treatments (Batschelet, 1981).

5.4.2 Results

Before comparisons among mean directions were made, Rayleigh's test was used to determine whether movement within each treatment (ebb, flood and high) and sampling occassions (1 Aug, 16 Aug and 17 Oct) was directional or random (Chapman, 1986).

Of the three treatments, whelks monitored during ebb and flood tides during the three sampling occasions, each moved in random directions (Rayleigh's Test, $P>0.05$), however whelks monitored during high tide showed directionality in their movement, and 95% confidence limits could subsequently be calculated (Table 5.2). The mean directions calculated for ebb and flood treatments are considered meaningless due to the random nature of the data, and therefore comparisons of 95% confidence limits among treatments was not possible (Underwood and Chapman, 1985; Chapman, 1986).

During high tide a period of about one hour was available to work within when currents were minimal. A slight current remained as flood tide subdued, which was of a SSW direction, and by the end of the monitoring period (70 min) a slight NW current was begining to become evident (Appendix 4a (ebb) and 4b (flood)). The movement of individual whelks showed little response to this slight shift in current directions. Of the the three sampling periods (1 Aug, 16 Aug and 17 Oct), during high tide, whelks during 16 Aug and 17 Oct tended to move in similar directions , thus the calculation of confidence limits for each sample. Whelks on 16 Aug were found to move between 279° and 25° (mean 332°) and whelks during 17 Oct generally moved between 316° and 16° (mean 346°), somewhat more directional than whelks during 16 Aug, but overlapping in directions moved. The combined mean direction moved for all three samples was 344° and a 95% confidence limit of 36° (308° to 20°), again suggesting an overall similar pattern; movement was NW during high tide.

	1 AUG	16 AUG	17 AUG	COMBINED
EBB TIDE				
n	**10**	**10**	**10**	**30**
Mean Direction (deg°)	**215**	**253**	**42**	**231**
R-bar	**0.63**	**0.38**	**0.29**	**0.22**
Rayleigh's *R*	0.015	0.24	0.44	0.24
P	<0.05	>0.05	>0.05	>0.05
95% C.L.	29	-	-	-
Mean Distance (cm/10 min)	13.69	6.15	3.40	7.75
S.E	3.99	0.76	0.99	0.98
FLOOD TIDE				
n	**10**	**10**	**10**	**30**
Mean Direction (deg°)	**169**	**313**	**262**	**283**
R-bar	**0.37**	**0.16**	**0.32**	**0.17**
Rayleigh's *R*	**0.26**	**0.78**	**0.37**	**0.43**
P	**>0.05**	**>0.05**	**>0.05**	**>0.05**
95% C.L.	**-**	**-**	**-**	**-**
Mean Distance (cm/10 min)	**5.94**	**8.51**	**14.97**	**9.81**
S.E	**1.83**	**2.35**	**3.95**	**0.86**
HIGH TIDE				
n	**10**	**10**	**10**	**30**
Mean Direction (deg°)	**229**	**332**	**346**	**344**
R-bar	**0.08**	**0.55**	**0.71**	**0.41**
Rayleigh's *R*	**>0.9**	**0.045**	**0.004**	**0.005**
P	**>0.05**	**<0.05**	**<0.05**	**<0.05**
95% C.L.	**-**	**51**	**36**	**36**
Mean Distance (cm/10 min)	**12.18**	**19.49**	**9.24**	**13.64**
S.E	**3.02**	**3.49**	**2.87**	**0.98**

Table 5.2: Summary of mean direction and distances displaced per sample and treatment.

Only whelks during ebb tide (NEE) on the 1 Aug were found to move in a common direction (215°± 29°), which was between almost parallel and perpendicular to the current direction, however movement was random within and between samples and treatments.

The greatest distance moved was 46.82 cm/10 min, during ebb tide, 1 Aug., when current velocity was not particularly strong. Mean distances moved per 10 mins per treatment (ebb, flood and high) were greater during high tide (mean 13.64, se 0.98) when current velocities were minimal. Mean dsitances measured for whelks during Ebb, 1 Aug and Flood, 17 Oct were higher than other measurements and of the combined samples and these occurred when current velocities were also low. It is expected movement rates are affected by current velocities and greater movements rates and dispersal during periods of slack water.

5.5 DISCUSSION

The unsuccessful experiments in the field and in the laboratory attempting to determine prey type preferences, prey size able to be manipulated, and feeding rates of the three study species, demonstrates the complexities of animal behaviour and importance of caging artifacts for the successful execution of exerimentalal studies (Virnstein, 1980). Unnatural and stressful conditions and sedimentation in the cages were attributed to the failure of these experimental attempts in the field. Laboratory experiments are moreso subject to artifacts by altering natural conditions such as temperature, sediment type, physio-chemical properties (Connell, 1974) and are usually unavoidable. Because of this, field experiments are preferred to laboratory studies, to minimise such factors and ensure natural behaviour of the animal under study (Connell, 1974).

In the laboratory, a particular artifact affecting the behaviour of C. *adspersa* was the availability of aquaria sides. C. *adspersa* were almost always found on the sides of aquaria and remained sitting at the air-water interface, hence detracted from feeding on available bivalves at the bottom of the aquaria.

Approximately 2 cm of sediment from the field was placed in each aquaria in attempt to enhance natural conditions. Bivalves were unable to completely bury within the sediment at this depth, thus were potentially available to the whelks. White (1971) noted that C. *adspersa* in the field, may climb and pass directly over*Austrovenous stutchburyi*. This sort of behaviour in the field may be due to not detecting or recognising the prey available, as it is also likely, a food source was detected elsewhere.

After 2 months of keeping C. *adspersa* in aquaria with live *Paphies australis* and *Ruditapes largillierti*, they were not found to attack or feed upon the supply, and remained alive after this period. The ability of asteroids to withstand long periods of food deprivation is related to their morphology and physiology (Andrew, 1989) and well documented (see Feder and Christensen, 1966). Plasticity of growth and subsequent survival in gastropods is less well-known. Thus the interest of C. *adspersa* survival in the absence of food and their body condition. This spurred the investigation of the condition of whelks in the field compared to those which were well fed and those deprived of food. According to the length-weight relationship by regression analysis, very little diffrence existed between weights of each treatment. The reasons of why this was so, are not clearly understood. Gastropods are unable to absorb nutrients from the water, unlike echinoderms; ingestion of food is necessary. Their ability to feed on primary surface films is not known. The starved whelks showed a greater weight per unit length (although this was not significant) than wild and fed whelks. It could be understood "fed" whelks were of poorer condition than wild whelks, as this would suggest, in part, that wild whelks were consuming a greater amount of food than were provided to "fed" whelks. The simplest explanation is for low metabolic rates and ingestion of material from surface films.

A posible explanation may be due to energetics of growth. Energy spent by feeding whelks may not be compensated for by the caloric content of *R. largillieti*. Quantitative data of this is not known. Edwards and Huebner (1977), found *Polinices duplicatus* (a naticid gastropod) were able to survive for about 9 months but not grow when fed various genera of polycheates, sipunculids, and holothuroids, butgrowth (measured as length and weight) was found to be greatest when fed with a supply of the clam *Mya arenaria*.

Negative social interactions among feeding whelks may reduce growth or weight, by interfering with ingestion rates and increasing respiration rates (Edwards and Huebner, 1977). For example, larger whelks could interfere with the feeding of smaller whelks and direct competition for food items. Thus this may account for the less weight gained by fed whelks when compared to those which were deprived of food. In addition, temperature may to influence feeding rates, where feeding may cease during periods of low water temperature. Water temperature in aquaria between 20 October and 29 November was 12°C, while in the field on 16 October this was 15°C. This was not considered to effect feeding rates of fed whelks as all supplied with food were fed upon. However, lower temperatures may reduce growth when ingested food does not exceed other physiological requirements (Edwards and Huebner 1977).

The movement of *C. adspersa* was found to be less directional in the presence of a current, than when very little current was present (i.e., during high tide). Data was considered directional if 95% confidence limits could be calculated for the set of data, after they were first shown to be directional by an independent test, such as Rayleigh's test (Chapman, 1986). Only on one occasion during ebb tide (1 Aug), was movement by whelks found to be directional, and 95% confidence limits were calculated. It was evident that distances displaced were greater during tides when current velocities were minimal, such as high tide and 1 Aug, ebb and 17 Oct, flood. Whelks used in the experiments were approximately 45-55 mm shell length, as during strong current velocities small

(<20 mm shell length) whelks would bury in the sediment or be washed around on the sediment surface.

The extent of hunger of whelks may increase movement rates and directionality when a food source is detected (Hughes and Dunkin, 1984). This may result in greater dispersal to areas governed by the direction of water movement. As observed in the field, this may be greatest when current velocities are lower during periods of slack water such as at high tide. The velocity of the current affects movement rate whereby strong currents reduce movement or cause whelks to bury in the sediment. In addition, current velocity may affect direction of movement. High current velocities could increase dilution of attracting substances and therefore reducing the area and distance over which a food source can be detected (Himmelman, 1988). For such reasons, the random nature of movement during flood and ebb tides may not be related to the absence of water-borne stimuli from upstream of the current, but may be that the direction from which the source is located, cannot be detected by whelks.

The environmental factors imposed on predatory gastropods, such as water movement in subtidal areas affect their ability to disperse to areas of attraction or by the prior feeding of other predators to the area. This may account for feeding aggregations and patchiness at scales of cms.

CHAPTER SIX

Summary and Conclusions

6.1 Introduction

Predation by epibenthic invertebrates has frequently been shown to be an important disturbance, affecting the abundance, distribution and size structure of prey populations (Wilson, 1991). The effect of such predation has been well documented on rocky intertidal habitats, although lesser studies have been conducted in subtidal soft sediments. A major determinant of the abundance, distribution and size structure of predator populations, is the quantity and quality of food. The behaviour of individuals within species and between species may vary, therefore modifying any impact the predators may have.

6.2 Summary of Distribution, Abundance and Size Structure Of the Three Study Species

The species studied were widespread across Centre Bank, being found at sites of different physical characteristics, and although not uniformly highly abundant, were occasionally present at high densities. Differences between species may be related to feeding mode; *P. regularis* was essentially independent of bivalves as it is apparently able to feed on detrital material. Large bivalves were not observed to be preyed upon by *P. regularis*, but smaller individuals may be a potential source of food. As *C. calamaria* is larger than *P. regularis* and *C. adspersa*, it may provide the most intense predation on bivalve populations. *C. adspersa* was observed to form feeding aggregations and this may decrease handling times of prey.

Little evidence exists that suggest predators of this study were limiting bivalve populations across Centre Bank. Experimental attempts to determine prey preferences, prey size able to be opened and feeding rates for each of the species were unsuccessful. As *C. adspersa* has received less attention in the literature than both the asteroid species, and as it was found to be robust to handling, it was used for experimental studies. The condition of *C. adspersa* was studied, and found food deprivation may not be as detrimental as initially thought and *C. adspersa* kept for 39 days without food, obtained greater weight per unit length than those fed. Their dispersal ability was found to be influenced by current direction and rate. Small *C. adspersa* typically buried in the sediment during periods of high current flow, and monitoring of movement rates and directions moved, suggested that hydrodynamic patterns may be a potential factor affecting the distribution at least at small-scales across Centre Bank.

Monitoring of a small grid area of Centre Bank at regular 2-monthly intervals, found predator densities to be largely unchanged over a 9 month period. Predation pressure exerted, especially by *C. calamaria*, was apparently insufficient to cause marked reductions of bivalves. The morphodynamic regime at small scales such as over sandwaves, is thought to be of greater importance in determining bivalve abundance.

6.3 Suggestions for future research

Future work should continue to monitor the long-term stability of biological populations which inhabitat a relatively unstable and unpredictable marine habitat. Although, Centre Bank is relativley stable at present, it has been subject to periods of natural deposition and erosion and has undergone morphodynamic changes as a result of dredging shipping channels. The stability or persistance of a marine assemblage subject to such a variable habitat is obviously of interest at the biological level, but also at the management level where planning and development of the area is likely. It is also of interest, because little work has been conducted on the biology of flood tidal deltas. It is suggested that monitoring continue at sites already surveyed during this work, by use of the GPS site coordinates given in Appendix 3. The large-scale surveying could be conducted more regularly than in this work, for example, at 3-monthly intervals to detect for seasonal trends and which may then also allow for differentiation between natural population fluctuations and arthropogenic fluctuations. The time, cost and effort involved sampling a large area of many sites, may be reduced by employing more divers at a time, and as data is collected in the field, the little time spent in the field could make such work feasilbe for further research.

Future research could also concentrate on determining the mechanisms giving rise to the observed patterns of distribution, abundance and size structure at broad- and fine-scales accross Centre Bank. Recruitment may be important to the biology of the asteroids studied, and warrants further investigation, such as types of substrata they may recruit to: fine shell debris, deep coarse shell debris or fine sand types. The paddle crab was commonly found across Centre Bank and may be an important predator. However, to study the animal would have necessitated another sampling design due to the cryptic nature of this species, and unfortunately this was out of the scope of this work. A separate study determining its predatory role would be of interest across Centre Bank.

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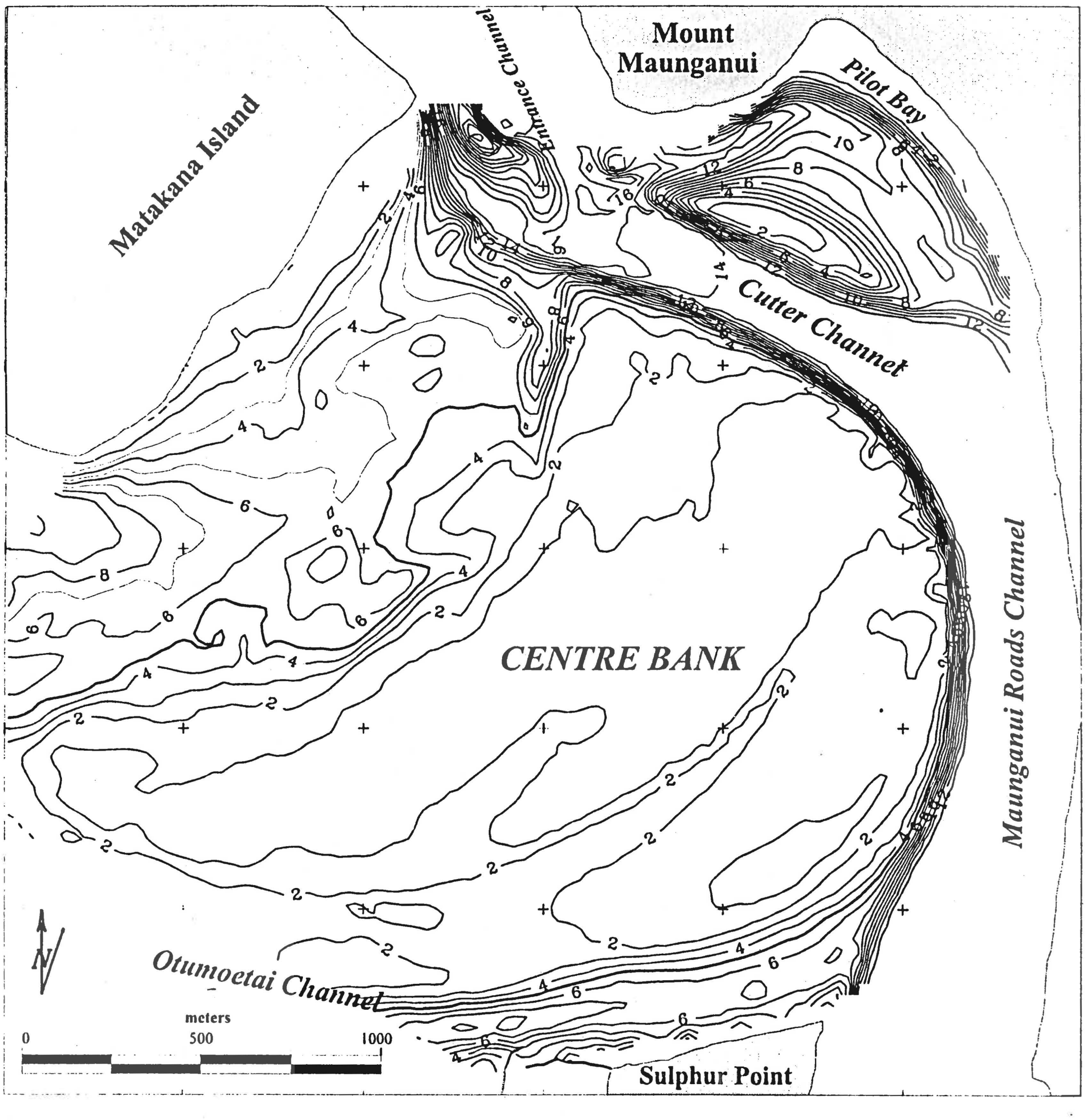
APPENDIX 1: Bathymetry across Centre Bank, August 1993
(depths (m) below chart datum)



APPENDIX 2: Centre Bank Pilot Study. Total numbers of each species found per site.

Site	***P. regularis***	***C. calamaria***	***C. adspersa***
1	1	0	0
2	2	0	0
3	2	0	0
4	0	0	0
5	0	0	9
6	0	0	2
7	1	0	1
8	2	0	2
9	0	0	0
10	1	0	0
11	0	0	1
12	2	2	0
13	4	0	3
14	1	1	0
15	0	0	0
16	8	0	0
17	1	0	0
18	4	0	1
19	1	10	3
20	0	0	0
21	2	0	2
22	0	0	0
23	0	0	0
24	1	0	0
25	5	0	0
26	0	0	0
27	2	0	3

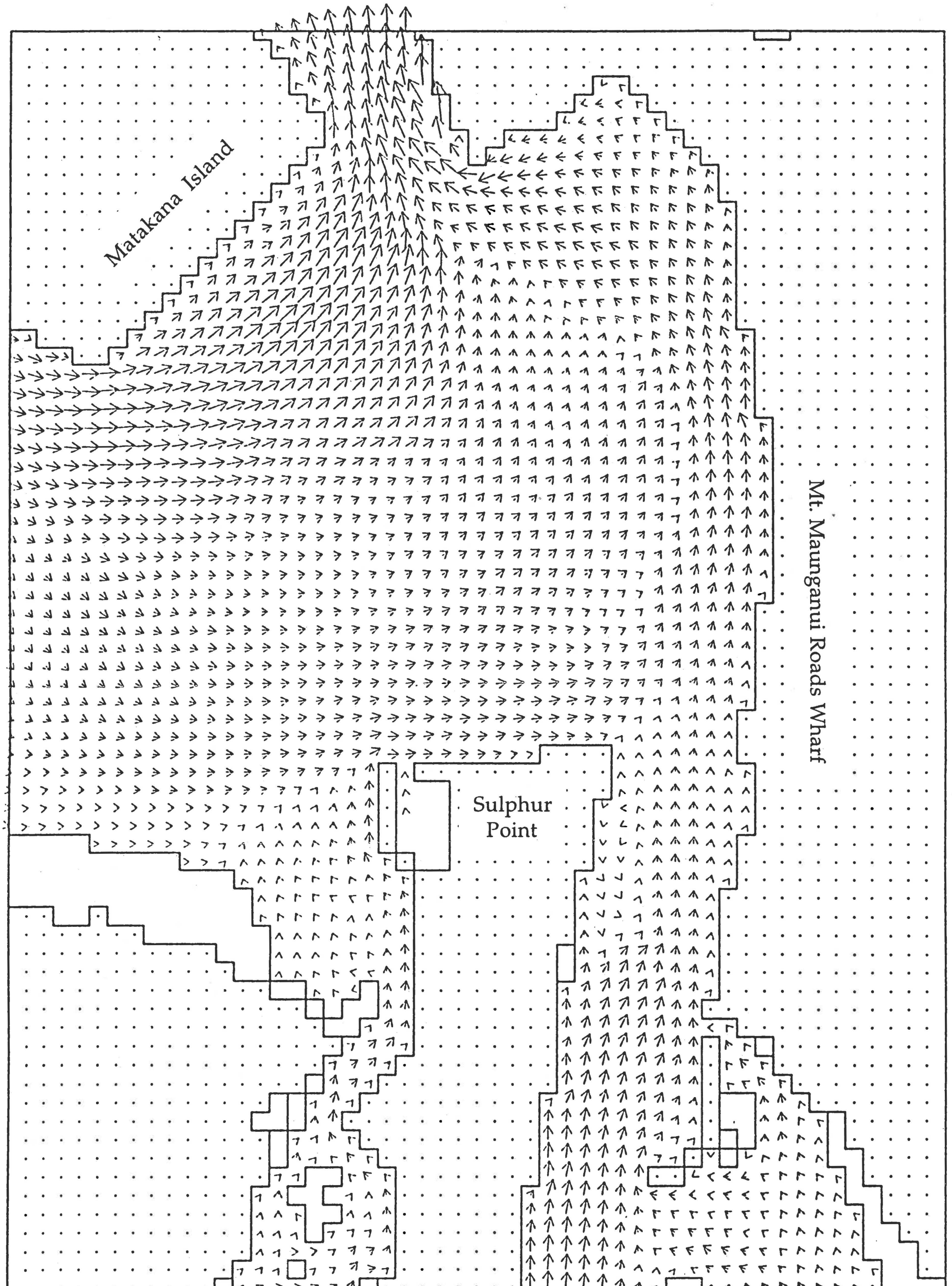
APPENDIX 3: GPS site and base station coordinates across Centre Bank.

SITE 1	37° 39’55″ S	176° 09’47″ E	**SITE 15**	37° 38’77 “S	176° 09’78 “E
SITE 2	37° 39’44 “S	176° 09’.45″ E	**SITE 16**	37° 38’47″ S	176° 10’09 “E
SITE 3	37° 39’32″ S	176° 09’.44″ E	**SITE 17**	37° 39’35 “S	176° 10’02 “E
SITE 4	37° 39’25″ S	176° 09’.42″ E	**SITE 18**	37° 39’19 “S	176° 09’97 “E
SITE 5	37° 39’17″S	176° 09’.37″ E	**SITE 19**	37° 38’97 “S	176° 09’96 “E
SITE 6	37° 38’97″ S	176° 09’36″ E	**SITE 20**	37° 38’76 “S	176° 09’95″ E
SITE 7	37° 38’84 “S	176° 09’39 “E	**SITE 21**	37° 38’64 “S	176° 10’16 “E
SITE 8	37° 38’70 “S	176° 09’37 “E	**SITE 22**	37° 39’42 “S	176° 10’49 “E
SITE 9	37° 38’53 “S	176° 09’35 “E	**SITE 23**	37° 39’35 “S	176° 10’49 “E
SITE 10	37° 39’45 “S	176° 09’74 “E	**SITE 24**	37° 39’16 “S	176° 10’43 “E
SITE 11	37° 39’36 S	176° 09’69″ E	**SITE 25**	37° 39’03 S	176° 10’45″ E
SITE 12	37° 39’09 S	176° 09’70 “E	**SITE 26**	37° 38’88 S	176° 10’62 “E
SITE 13	37° 38’99 S	176° 09’79 “E	**SITE 27**	37° 38’76 S	176° 10’48 “E
SITE 14	37° 38’91 S	176° 09’82 “E			

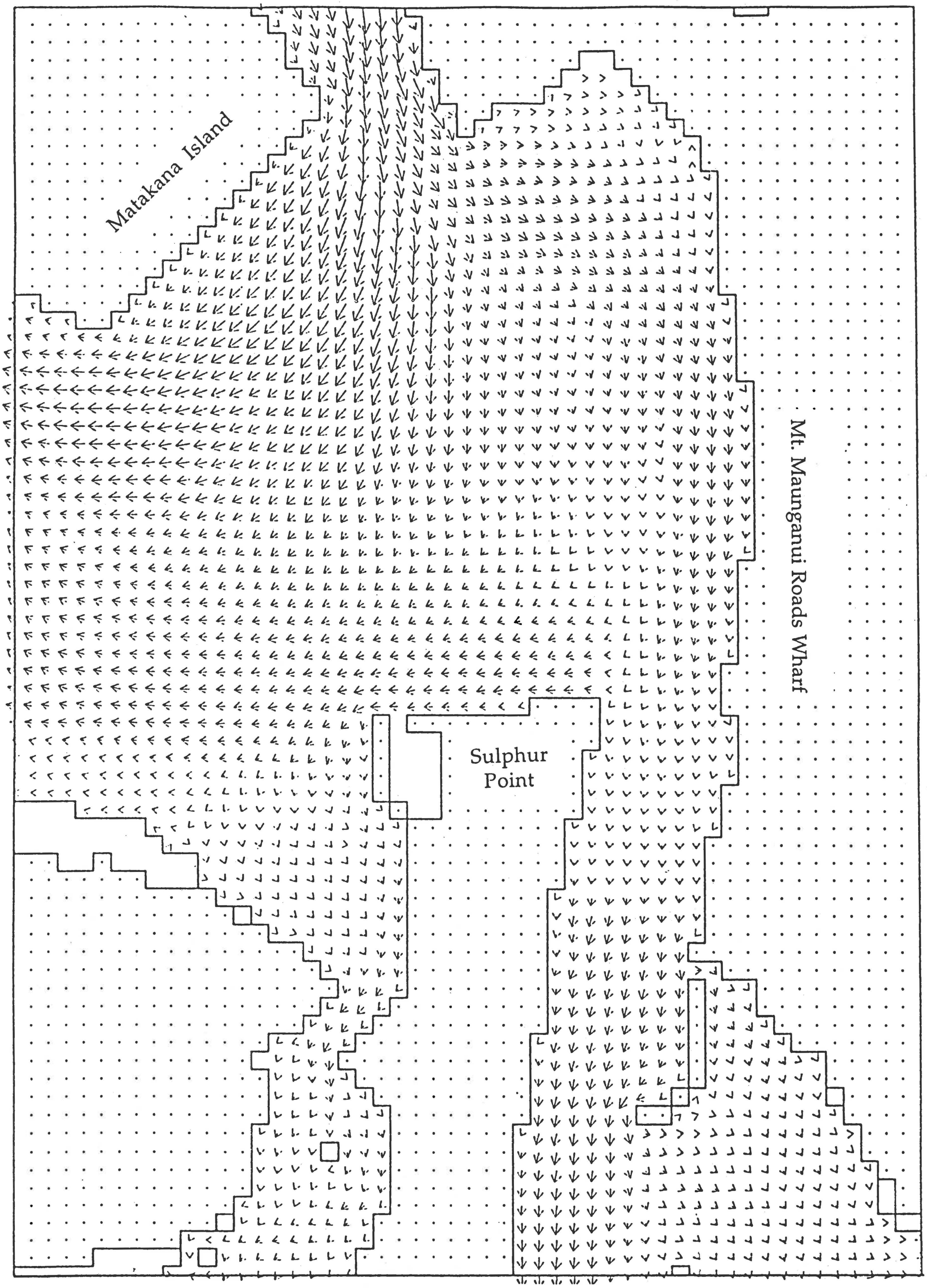
Base Station Coordinates

37° 40’39 “S   176° 10’45 “E (Butters Wharf Offices)

APPENDIX 4a: Mean tide velocity patterns at peak ebb tidal flows for 1994 bathymetry (velocity vector scale: 1 mm = 0.3 m/sec). (Adapted from Bell, 1994).



APPENDIX 4b: Mean tide velocity patterns at peak flood tidal flows for 1994 bathymetry (velocity vector scale: 1 mm = 0.3 m/sec). (Adapted from Bell, 1994).



APPENDIX 5: Grid Monitoring Programme: Mean density ($0.5m^2$) and standard error (SE) of *Patiriella regularis*, *Coscinasterias calamaria* and *Cominella adspersa* per site.

	March				**May**						**July**						**September**						**November**					
	P. regularis		*C. calamaria*		*P. regularis*		*C. calamaria*		*C. adspersa*		*P. regularis*		*C. calamaria*		*C. adspersa*		*P. regularis*		*C. calamaria*		*C. adspersa*		*P. regularis*		*C. calamaria*		*C. adspersa*	
Site	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
1	3.0	0.9	0.0	0.0	3.8	1.6	0.4	0.4	0.0	0.0	4.8	1.8	0.0	0.0	0.0	0.0	5.8	2.4	0.0	0.0	1.4	1.2	2.6	0.9	0.2	0.2	0.0	0.0
2	3.4	1.4	0.2	0.2	3.6	1.0	0.2	0.2	0.0	0.0	2.4	1.5	0.0	0.0	0.0	0.0	6.4	2.0	0.0	0.0	0.6	0.2	1.0	0.5	0.0	0.0	0.6	0.4
3	1.6	0.5	0.2	0.2	4.8	1.9	1.6	0.9	0.0	0.0	4.4	0.9	0.0	0.0	0.0	0.0	4.0	0.9	0.2	0.2	2.6	2.4	4.0	1.1	0.0	0.0	0.8	0.5
4	4.2	1.0	1.4	0.9	6.0	1.8	2.4	1.7	0.0	0.0	5.2	1.5	0.0	0.0	0.0	0.0	7.2	2.0	2.0	1.5	3.2	2.2	3.2	0.7	0.2	0.2	0.2	0.2
5	4.2	1.0	1.8	0.8	5.0	1.3	0.2	0.2	0.0	0.0	7.8	1.3	0.4	0.2	0.0	0.0	4.2	1.4	0.2	0.2	0.2	0.2	2.4	0.4	0.0	0.0	3.8	1.5
6	4.2	1.6	0.6	0.4	9.6	2.2	1.4	0.7	0.0	0.0	5.0	1.4	0.2	0.2	0.0	0.0	6.2	2.7	0.0	0.0	0.0	0.0	6.0	1.0	0.0	0.0	0.0	0.0
7	4.0	1.7	1.0	0.8	4.4	0.6	0.0	0.0	0.0	0.0	4.4	1.3	0.8	0.4	0.0	0.0	6.8	1.2	0.0	0.0	0.2	0.2	4.6	0.7	0.0	0.0	0.2	0.2
8	3.6	0.8	0.2	0.2	4.0	1.2	1.8	1.1	0.0	0.0	4.2	0.6	0.0	0.0	0.0	0.0	2.6	0.7	0.0	0.0	0.0	0.0	4.2	1.0	1.4	0.5	0.6	0.4
9	3.2	0.8	0.0	0.0	5.0	1.4	4.0	1.9	0.0	0.0	6.2	0.8	2.4	1.0	0.0	0.0	8.0	3.7	2.0	1.3	0.0	0.0	4.6	1.6	3.4	1.2	0.0	0.0
10	6.8	2.4	2.4	1.7	1.0	0.7	0.0	0.0	0.0	0.0	4.6	1.5	2.8	1.4	0.0	0.0	5.2	0.7	1.8	1.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
11	5.6	1.8	0.0	0.0	2.6	1.0	0.0	0.0	0.0	0.0	5.0	1.2	0.0	0.0	0.0	0.0	3.0	1.0	0.6	0.4	0.0	0.0	2.8	0.9	3.0	1.7	0.2	0.2
12	1.8	0.5	0.0	0.0	2.6	0.4	0.0	0.0	0.0	0.0	5.0	0.4	0.0	0.0	0.0	0.0	2.6	1.4	0.6	0.6	0.0	0.0	1.6	0.7	0.2	0.2	0.0	0.0
13	5.0	0.6	0.0	0.0	5.0	0.8	0.0	0.0	0.4	0.2	5.4	1.0	0.2	0.2	0.0	0.0	2.0	0.8	0.2	0.2	0.0	0.0	1.8	1.1	0.0	0.0	0.6	0.6
14	3.6	1.0	0.0	0.0	2.8	0.6	0.0	0.0	0.4	0.4	5.6	0.5	1.4	1.4	0.0	0.0	3.2	1.2	0.0	0.0	0.0	0.0	1.0	0.5	0.0	0.0	0.4	0.2
15	3.2	0.9	0.2	0.2	2.8	0.6	0.0	0.0	0.0	0.0	3.2	0.9	0.2	0.2	0.0	0.0	5.2	1.2	0.8	0.8	0.0	0.0	2.8	1.2	0.2	0.2	0.8	0.6
16	4.4	1.0	1.0	0.8	6.2	2.0	1.0	0.6	0.0	0.0	5.4	1.2	0.2	0.2	0.0	0.0	6.6	0.7	0.2	0.2	0.2	0.2	3.8	1.1	0.6	0.2	1.0	1.0
17	4.4	1.5	0.4	0.4	6.0	3.1	1.2	0.7	0.0	0.0	5.8	0.8	0.6	0.2	0.0	0.0	8.8	2.6	1.4	1.2	0.0	0.0	4.2	1.6	2.2	2.0	0.2	0.2
18	5.2	1.9	2.6	1.6	5.2	0.8	0.0	0.0	0.0	0.0	4.2	1.2	2.6	1.6	0.0	0.0	8.6	3.9	2.2	2.0	0.0	0.0	4.4	0.7	1.0	0.8	0.2	0.2
19	6.4	3.0	0.4	0.4	1.4	0.9	1.2	1.0	0.0	0.0	5.4	1.9	1.0	0.8	0.0	0.0	4.6	1.6	0.0	0.0	0.0	0.0	3.6	0.9	0.0	0.0	0.2	0.2
20	4.8	1.2	0.0	0.0	3.6	1.8	0.0	0.0	0.0	0.0	2.2	1.3	0.2	0.2	0.0	0.0	3.4	1.2	0.0	0.0	0.2	0.2	1.8	0.5	0.0	0.0	2.4	2.2
21	7.6	4.2	0.4	0.4	1.4	0.7	0.2	0.2	0.0	0.0	3.8	1.4	0.0	0.0	0.0	0.0	2.2	1.3	0.0	0.0	0.2	0.2	2.4	0.9	0.0	0.0	0.4	0.2
22	3.8	0.9	0.4	0.2	4.4	1.6	1.4	1.4	0.0	0.0	2.8	0.7	0.0	0.0	0.0	0.0	7.2	2.4	0.0	0.0	0.2	0.2	4.4	1.3	0.2	0.2	0.0	0.0
23	7.4	3.1	0.2	0.2	2.2	0.9	0.2	0.2	0.0	0.0	11.4	3.1	4.2	2.4	0.0	0.0	6.4	1.5	1.8	1.0	0.0	0.0	8.0	1.0	1.4	0.7	0.4	0.2
24	4.4	1.3	0.0	0.0	2.8	1.5	0.0	0.0	0.0	0.0	3.6	1.1	0.0	0.0	0.0	0.0	4.6	2.0	0.8	0.6	0.2	0.2	4.2	0.8	1.2	0.7	0.4	0.2
25	7.8	2.4	0.0	0.0	4.8	1.8	2.0	1.2	0.0	0.0	5.6	0.7	0.8	0.4	0.0	0.0	11.0	4.5	1.6	1.6	0.0	0.0	2.4	0.8	0.6	0.6	0.4	0.2
26	4.2	0.8	0.0	0.0	3.2	0.9	0.0	0.0	0.0	0.0	3.2	0.6	0.2	0.2	0.0	0.0	3.6	1.2	0.4	0.4	0.0	0.0	3.0	0.5	0.6	0.4	8.0	7.8
27	3.4	1.1	0.8	0.8	4.6	1.2	0.0	0.0	0.2	0.2	4.8	0.9	0.0	0.0	0.0	0.0	5.8	2.3	0.0	0.0	0.0	0.0	2.0	0.4	0.4	0.4	0.0	0.0
28	6.0	1.3	0.0	0.0	4.4	0.9	0.0	0.0	0.4	0.2	4.6	1.3	0.0	0.0	0.0	0.0	3.8	0.6	0.0	0.0	0.0	0.0	1.2	0.6	0.0	0.0	0.6	0.2
29	4.4	1.2	0.0	0.0	4.0	1.4	0.0	0.0	0.4	0.2	3.0	0.8	0.0	0.0	0.0	0.0	0.4	0.2	0.0	0.0	0.0	0.0	5.0	1.7	0.0	0.0	1.4	0.2
30	5.2	0.6	0.0	0.0	2.4	1.0	0.0	0.0	0.2	0.2	4.4	0.7	0.2	0.2	1.2	1.2	1.6	0.5	0.0	0.0	0.0	0.0	3.0	0.7	0.0	0.0	1.0	0.6
Mean	4.56	0.3	0.47	0.13	4.01	0.3	0.64	0.17	0.07	0.03	4.78	0.3	0.61	0.19	0.04	0.04	5.03	0.4	0.56	0.14	0.31	0.14	3.2	0.3	0.56	0.17	0.83	0.29