THE ECOLOGY OF BIVALVES ON CENTRE BANK, TAURANGA HARBOUR

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Penelope Jane Hull

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The Stars of Tauranga Harbour

ABSTRACT

An investigation into the ecology of bivalve molluscs on Centre Bank, the flood tidal delta of Tauranga Harbour was undertaken over the period December 1994 - March 1996. The primary purpose of which was to gather quantitative data on bivalve diversity, spatial patterns of distribution, abundance, and population size structure of bivalves present on Centre Bank. Experiments were conducted to assess the burrowing behaviour of the bivalve *Paphies australis*. It was intended that information obtained be such that it could be used as a base for future investigations into changes in the ecology of Centre Bank.

Two broad scale benthic surveys of 27 sites on Centre Bank, conducted 6 months apart resulted in a total of 31 bivalve taxa being identified. Temporal and spatial variation in abundance was prominent for all species. Three species *Paphies australis, Tawera spissa* and *Ruditapes largillierti* occurred in far greater abundances than any others. Distribution of bivalves in both surveys was patchy with some species showing strong associations with particular sites.

Small scale abundance patterns of *P. australis* was examined in detail by systematic sampling of a 50 m x 15 m grid. The grid was monitored at 2-monthly intervals from March 1995 to November 1995. Abundances at sites in the northern half of the grid were found to be very dense (up to 1400 m^2, mean shell length=55-65 mm), while densities at the southern end were noticeably lower. Through time densities across the grid appeared to decrease evenly in a constant north-west direction. The smothering effect of mobile sand ridges was speculated to be the cause of these density decreases.

Experiments examining the burrowing behaviour of the infaunal bivalve *Paphies australis* were conducted both in the field and in the laboratory. The ability of *P. australis* to bury into the sediment if left exposed on the sediment surface was examined in the field. It appeared that *P. australis* were able to bury relatively quickly with the majority of experimental animals reburying within 40 minutes. Laboratory experiments showed *P. australis* to be capable of burrowing to the sediment surface after being inundated with sediment to a depth of 10 cm.

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TABLE OF CONTENTS

CHAPTER ONE: INTRODUCTION

CHAPTER TWO:LITERATURE REVIEW

CHAPTER THREE: BROAD SCALE PATTERNS OF DISTRIBUTION AND ABUNDANCE OF BIVALVES ON CENTRE BANK

CHAPTER FOUR: FINE SCALE PATTERNS

CHAPTER FIVE: EXPERIMENTS

Experiment One: Burial

Experiment Two: Burrowing

CHAPTER SIX: SUMMARY AND RECOMMENDATIONS

APPENDICES

LIST OF FIGURES

LIST OF TABLES

LIST OF PLATES

Chapter One

CHAPTER ONE

INTRODUCTION

1.1 THE PROBLEM

Tauranga Harbour is a resource of great scenic, cultural and ecological importance with a high recreational use. It is extremely valuable economically to the Bay of Plenty area, due both to its commercial and recreational value. It is the country's largest external trade port by tonnage, and plays a vital role in ensuring New Zealand's continued economic development and welfare (Smith and Hughes, 1993). Extensive dredging and widening of the Port channels now positions the Port of Tauranga as one of the deepest general cargo ports in New Zealand (Smith and Hughes, 1993).

Recreational water activities undertaken within the harbour include swimming, SCUBA diving, sailing, water-skiing, windsurfing and others. Fishing is also a very popular activity and is widespread throughout the harbour. A large part of the recreational fishing which occurs within the harbour is undertaken by recreational shellfish gatherers. Shellfish species most commonly taken include *Paphies australis* (pipi), *Perna canaliculus* (green lipped mussel) and *Pecten novaezelandiae* (NZ scallop) (Park, 1991). The local Maori have a long association with Tauranga Harbour and the seafood resources it provides; the above-mentioned shellfish comprise an important part of kaimoana gathered from the area. Little is known about the ecology of recreationally gathered shellfish populations within Tauranga Harbour.

Sediment dynamics (Davies-Colley, 1976; Davies-Colley and Healy, 1978; Dahm, 1983) and hydrodynamics (Davies-Colley and Healy, 1978; Bell, 1991; Bell, 1994; Mathew *et al.*, 1995) of Tauranga Harbour have been well documented over time, particularly in relation to the impacts of port developments (de Lange and Healy, 1991). In contrast there is little ecological data recorded, subsequently knowledge of the harbour's ecology is largely based on qualitative data. General descriptions of benthic intertidal ecology within the Bay of Plenty region have been made by Bioresearches Limited (1974, 1975a, 1975b, 1976), and the benthos associated with an outfall pipe has been quantitatively described by Roper (1990). Parks' 1993/94 Coastal and Estuarine Ecology Monitoring Program completes four years of monitoring intertidal benthic community structure of rocky shore, open coast, estuary and harbour sites in the eastern Bay of Plenty (Park, 1994). Park's work has been carried out on intertidal sites, with minimal ecological information known about subtidal areas.

1.2 STUDY AREA

Tauranga Harbour is the southern of two estuarine lagoons enclosed by a barrier system of two tombolos and a barrier island, located on the north-east coast of New Zealand (Dahm, 1983) (Fig. 1.1). The harbour is nearly 40 km long, up to 10 km wide and covers an area of approximately 200 square kilometres. The Port of Tauranga is situated within the southern-most lagoon. The site of this study, the flood tidal delta, immediately inside the harbour, consists of the large shoal area known as Centre Bank (Davies-Colley, 1976). Water depth on Centre Bank is less than 1 m below chart datum over most of the area, and parts of the bank become exposed on an ebb tide. As yet bivalve molluscan populations of Centre Bank (Fig. 1.2) have not been comprehensively surveyed.

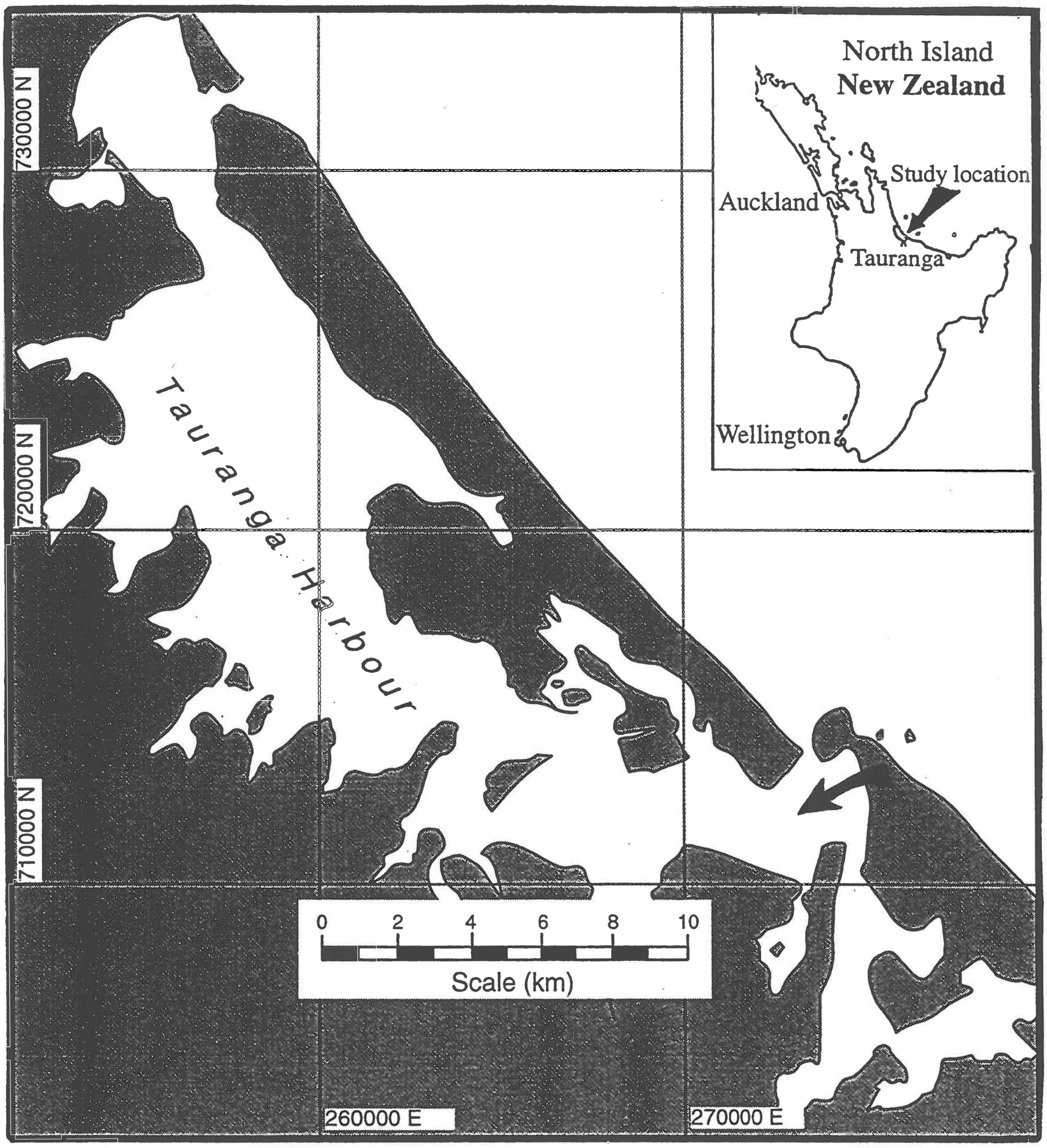


Figure 1.1 Location map of Tauranga Harbour

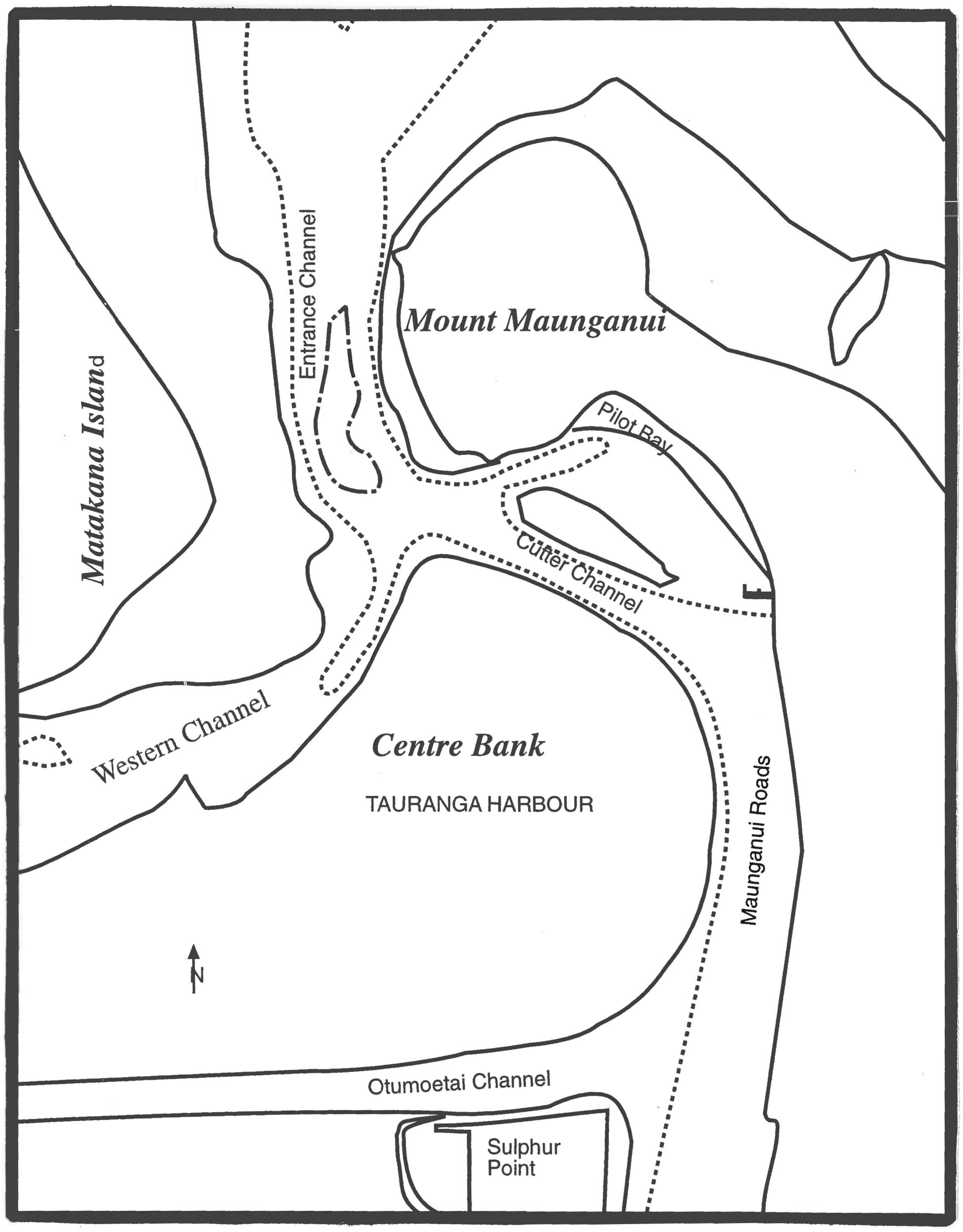


Figure 1.2 Location map of Centre Bank (flood tidal delta)

1.3 AIMS OF THE STUDY

Port of Tauranga Ltd. has recognized that its knowledge of ecology of the harbour was inadequate for the type of planning in which it was engaged (Bickers, 1992). The primary aim of this study was to describe the bivalve fauna of Centre Bank, thus obtaining information concerning spatial patterns of distribution, abundance and population size structure of bivalves present within the harbour. A second aim was to undertake field and laboratory experiments that investigate certain aspects of behaviour of the bivalve *Paphies australis*. This study aims to investigate a small but significant part of the harbour's bivalve population thus leading to a greater understanding of bivalve ecology within Tauranga Harbour, and to make a contribution to the biological database being accumulated by Port of Tauranga Ltd.

1.4 STRUCTURE OF THE STUDY

A literature review of previous studies of bivalve population ecology is presented in Chapter 2. Chapter 3 is concerned with a broad scale survey of Centre Bank. Chapter 4 details temporal change in bivalve density and population size structure over a 9 month period at a single site. Manipulative field and laboratory experiments are presented in Chapter 5. A summary of results, and suggestions for future research are given in Chapter 6.

Chapter Two

CHAPTER TWO

LITERATURE REVIEW

2.1 PROCESSES DETERMINING BIVALVE DISTRIBUTIONS, ABUNDANCE AND GROWTH

2.1.1 Bivalve Life Histories

Most marine bivalves have a planktonic larval phase (Barnes, 1980). The larvae have very different sensory modes, behaviour and morphology from adults (Barnes, 1980). This planktonic life phase has traditionally been viewed as the primary agent for larval dispersal to new or different areas. Substantial variation in recruitment of planktonic larvae can profoundly influence the dynamics of adult populations (e.g. Coe, 1953). The survival of a species over time, or in a given geographical area often depends upon its ability to disperse. Dispersal is especially important for sessile organisms, which may have limited mobility as juveniles or adults. The distance traveled by larvae can vary considerably, resulting in larvae settling within only a few metres of the adult population, or being transported across oceans via transoceanic currents (Scheltema, 1971).

Although larval dispersal has been considered to be the major mechanism controlling the distribution of many bivalves, there is increasing evidence that juveniles and less often adults can re-enter the water column after settlement (Martel and Chia, 1991; Armonies, 1992; Cummings *et al.*, 1993; Hooker, 1995b). Drifting can be accomplished by mucus threads, which increase the drag exerted on the bivalve, enabling it to be transported in relatively small currents (Sigurdsson *et al.*, 1976). Evidence of New Zealand bivalve species drifting is increasing. Grace (1972) observed approximately 12 *Paphies australis* (pipi), roughly 45 mm shell length, drifting in mid-water on the ebb tide at the entrance to the Whangateau Harbour. Hooker (1995b) observed adults and juveniles of *P. australis* drifting in mid-water inside the Whangateau Harbour, with mucus threads extended out through their siphons, (Hooker's (1995b) observations in the Whangateau Harbour confirming that Grace's (1972) report was not an isolated occurrence). Cummings *et al.* (1993) describe emergence and floating behaviours of *Macomona liliana* and document the presence of drifting threads. A further study undertaken in the Manukau Harbour by Cummings *et al.* (1995) documented the presence of post-metamorphic juveniles (and adults) of several benthic macroinvertebrate species in the water column.

2.1.2 Ecological Processes Affecting Bivalves: Competition and Predation

The mechanisms governing the structure of intertidal communities have been the subject of considerable manipulative experimentation, revealing competition and predation to be among the most important processes structuring the communities of rocky shores. Despite the fact that marine soft-sediments are the most common habitat on earth (Wilson, 1991), rigorous research is lacking on such communities. Hence the importance of biological processes in organizing soft-sediment communities is not as well understood as those of temperate rocky intertidal communities (Peterson, 1979; Wilson, 1991).

Competition

Competition involves the use of a limited resource by two or more species and results in some negative effects on each competing population (Mitchell *et al.*, 1988). There has been considerable investment of time, energy and ingenuity into the planning and carrying out of field experiments designed to eliminate alternative hypotheses, and thereby to support competition as an important process explaining present patterns of distribution and abundance of organisms (Underwood, 1986). Much has been written on the use of inadequate replication and controls in experiments designed to detect competition in the marine environment (Connell, 1974; Underwood, 1986; Hairston, 1989). Underwood (1986) states that competition is undoubtedly important as an organising force in the structure of intertidal communities, and that good field experiments adequately replicated and controlled for, will provide a powerful tool for unraveling complex biological communities.

In soft sediment environments, Peterson and co-workers (Peterson and Andre, 1980; Peterson, 1982a; Peterson and Black, 1987, 1991, 1993) have carried out many experimental studies examining competition as a means of determining distribution and abundance of bivalve species. The importance of density for bivalve growth and mortality has been investigated by Peterson and Beal (1989) and Peterson and Black (1988). The influence of density on resource depletion by suspension feeding bivalves was investigated by Peterson and Black (1987). Experimental manipulations of bivalve density have been carried out for the cockle *Austrovenus stutchburyi* in New Zealand. These involved the transplantation of cockles to different shore levels, and manipulation of densities, with the effect of competition for space on growth and survival being determined (Dobbinson *et al.*, 1989).

A series of experiments undertaken by Peterson (1982b) showed the positive effects of high prey density. His results suggested high densities of clams could act as a refuge against whelk predation. In another study Peterson and Black (1993) demonstrated that the addition of sufficient numbers of sham clams, (dead shells filled with sand and implanted in living position in the sediments), acted to prevent the enhancement of mortality at low density. This highlights the importance of a structural barrier and implies that the agent of mortality at low density is a predator.

Predation

The importance of predation as a factor determining species distribution and abundance has been investigated often. Predation has been shown to effect prey in several ways: the death of individuals, reduction in densities, mean sizes, or distribution of prey populations (Fairweather, 1988). Crabs, whelks, fish, asteroids and shore birds are specific epibenthic predators that have been identified as having a significant influence on infaunal abundance and biomass. A number of intertidal experiments involving the exclusion of these epibenthic predators have resulted in increases of infauna relative to unmanipulated controls (e.g. Peterson, 1982a, 1982b; Thrush *et al.*, 1994b). Yet other studies have found epibenthic predation to have a minimal impact on infaunal abundance and biomass (Raffaelli and Milne, 1987; Kneib, 1988).

There has been a limited number of investigations into predation in subtidal communities (Virnstein, 1977; Thrush, 1986). More recently Jones *et al.* (1992) has investigated the effect of fish predation on the demography of mollusc populations in the water of a tropical lagoon. Asteroids and whelks are common bivalve predators that are prominent across the soft-bottom community of Centre Bank, Tauranga Harbour. Fiona Putt, in a parallel study, has investigated the asteroids *Coscinasterias calamaria* and *Patiriella regularis* and the whelk *Cominella adspersa* ascertaining their distribution and abundance with a view to determining their effect on prey species.

Experimental analysis of the effects of predation in infaunal communities have generally involved the exclusion or enclosure of suspected predators. Comparisons allow the investigator to assess the strength of the predators' influence (Wilson, 1991). It is difficult to remove predators from soft-bottom habitats because they are either large and mobile or infaunal and cryptic. There may also be artifacts of caging; Hulberg and Oliver (1980) showed that in a high energy environment the shape of a cage has dramatic effects on the outcome of exclusion experiments. Virnstein (1980) urged that the results of caging experiments be augmented with observational data, gut content analysis, or laboratory experiments before acceptance of predation as the process producing any experimental differences. Aside from this Hall *et al.* (1990) believe that manipulative experiments still remain the only valid test of the predation hypothesis but that experimental design and analysis must be rigorous to be convincing.

When examining the processes of competition and predation in soft-bottom communities, thoughtfully conceived and carefully controlled field experiments offer the most satisfactory tests of hypotheses posed to clarify these mechanisms resulting in observed patterns of distribution and abundance (Dayton and Oliver, 1980). But field experiments are not always possible, and many experiments can only be performed in the laboratory. In the case of small infaunal organisms, laboratory observations and experimentation may provide a better insight into potentially important behavioral interactions, feeding mechanisms, mobility and searching patterns, than field experiments can. Dayton and Oliver (1980) believe that field experiments should be complemented by laboratory experiments and vice versa.

2.2 BIVALVE POPULATION ECOLOGY

2.2.1 Species Diversity

The idea that individuals or populations can provide an indication of the quality of their environment is widespread (Diaz, 1992). Species diversity is perhaps the best known community structure parameter. Other parameters include species composition, relative abundance, resemblance and spatial structure and pattern (Diaz, 1992). Measurements of diversity are frequently seen as indicators of the well-being of ecological systems (Magurran, 1988). Environmental monitoring makes use of the fact that polluted or stressed communities are characterized by a change in their species abundances.

The assumption is that the adverse effects of pollution etc. will be reflected in a reduction in diversity or by a change in the shape of the species abundance curve or distribution (Magurran, 1988). A huge number and variety of diversity indices are used, and a great deal of confusion exists over which diversity measure should be used for different circumstances. Magurran (1988) provides practical advice on the measurement of ecological diversity.

2.2.2 General Bivalve Population Ecology

Infaunal bivalves (or clams) can occur in very high abundances over extensive areas, and obtain the highest biomass of any infaunal animal (Mitchell *et al.*, 1988). As a result of the very high biomass, they are likely to be an ecologically important component of soft-sediment environments (Barnes, 1980). Numerous bivalve species are gathered recreationally and harvested commercially. If populations of such species are to be managed it is essential that the life history of the organism is understood. Population size structure, growth, movement and distribution provide part of the information required to understand bivalve life histories. Bivalves such as *Mercenaria mercenaria* (Peterson, 1986; Hunt *et al.*, 1987; Peterson and Beal, 1989; Walker and Heffernan, 1994) and *Mya arenaria* (Brousseau, 1978; Newell and Hindu, 1982; Brousseau and Baglivo, 1987; England and Heino, 1994) have been intensively studied on the east coast of the USA. Although bivalves of the intertidal zone have been studied in detail, much less is known of the macrofauna of the subtidal environment. One exception is bivalves of the genus *Donax* of wave swept beaches which have been extensively researched in South Africa and Florida (Mikkelsen, 1981; Leber, 1982; Donn, 1987; Stenton-Dozey and Brown, 1994).

2.2.3 New Zealand Intertidal Bivalve Ecology

The majority of research done on bivalve ecology within New Zealand has centered around intertidal populations. Studies on patterns of distribution and abundance of bivalve populations in New Zealand are not plentiful. The research that has been undertaken generally concentrates on either intertidal bivalves, or on one or two individual species. Manukau Harbour is a large shallow inlet where a number of studies of bivalve distribution have been conducted on the intertidal sandflats (Grange, 1977; Thrush *et al.*, 1989; Pridmore *et al.*, 1990; Roper *et al.*, 1992; Thrush *et al.*, 1992; Thrush *et al.*, 1994b). Similarly the distribution and abundance of bivalves at Ohiwa Harbour have been investigated (Paul, 1966).

Autecological research in New Zealand is dominated by investigations of the cockle *Austrovenus stutchburyi* (Stephenson, 1981; Blackwell, 1984; Belton, 1985; Dobbinson *et al.*, 1989; McArdle and Blackwell, 1989), an ecological equivalent to the northern hemisphere species *Mercenaria mercenaria* (Grace, 1972).

2.2.4 New Zealand Subtidal Bivalve Ecology

Investigations into bivalve ecology subtidally within New Zealand are sparse. Grange (1979) surveyed the macrobenthos at 42 stations in the channels and subtidal sandflats in the Manukau Harbour. Grant-Mackie (1987) described aspects of the biology of the subtidal horse mussel, *Atrina zelandica*. Surf clam distribution, biomass and yield estimates off New Zealand beaches have been obtained by Haddon *et al.* (in press), while a dredge survey of surf clams in Cloudy Bay, Marlborough was undertaken by Cranfield *et al.* (1994). Unpublished information has suggested that pipi may occur subtidally (Grace, 1972; Venus, 1984; Hooker, 1995a).

2.2.5 Family Mesodesmatidae

The Mesodesmatidae, probably the most-studied family of bivalves in New Zealand, is represented in New Zealand by 4 species: *Paphies australis* (pipi), *Paphies ventricosa* (toheroa), *Paphies subtriangulata* (tuatua), and *Paphies donacina* (deep water tuatua) (Hooker and Creese, 1995a). Due to the popularity of *P. ventricosa* (toheroa) with recreational and commercial harvesters, research projects were undertaken to further knowledge of the toheroa and ensure adequate protection for the beach stocks against over-exploitation (Redfearn, 1982). Drastic depletion of the toheroa in the late 1960s and early 1970s resulted in more intensive studies of the tuatua (Greenway, 1981; Richardson *et al.*, 1982; Redfearn, 1987; Grant, 1994), which was to become an accepted alternative shellfish.

The most familiar of the Mesodesmatidae, the pipi, has long been regarded as an intertidal species (Creese, 1988) but surveys of pipi distribution and abundance at Whangarei (Venus, 1984), Whitianga (Creese, 1988) and Whangateau Harbours (Grace, 1972; Hooker, 1995a) suggest that pipi also occur in subtidal habitats. Further subtidal studies of pipi have investigated reproductive biology (Hooker and Creese, 1995a, b) and post settlement movement (Hooker, 1995b).

To the best of my knowledge no study has investigated the distribution and abundance patterns of bivalve populations, in particular *P. australis*, on Centre Bank, Tauranga Harbour.

2.3 PREVIOUS INVESTIGATIONS OF ECOLOGY WITHIN TAURANGA HARBOUR

2.3.1 Ecological Monitoring Survey Report to Bay of Plenty Catchment Commission and Regional Water Board

Early ecological monitoring programs in the Bay of Plenty (B.O.P) were requested by the Bay of Plenty Catchment Commission and the Regional Water Board. In 1974 an Ecological Monitoring Survey of the reaches of the major B.O.P rivers, the Ohau Channel and parts of Tauranga Harbour was conducted (Bioresearches Ltd., 1974). Quantitative samples of macrofauna were obtained, animals identified and counted. Population size structure data were recorded for only two of the species found; *Amphibola crenata* and *Chione stutchburyi*. Subsequently, abundance data, but little population size structure information, was collected on the species present.

It was intended that the selected stations be monitored regularly so that patterns of ecological change could be determined. Reports based on the same sites as the 1974 Ecological Monitoring Survey were produced in both the winter and summer of 1975 (Bioresearches Ltd., 1975a, b). A final report (Bioresearches Ltd., 1976) attempted to collate information previously obtained. The report summary considered Tauranga Harbour to have exceptionally high ecological value, being generally in excellent ecological condition, with harbour habitats containing a high diversity of organisms.

2.3.2 Coastal and Estuarine Monitoring Program

A Regional Monitoring Network was initiated in 1990 by the Bay of Plenty Regional Council. As part of this Network an annual Coastal and Estuarine Ecology Regional Monitoring Program was scheduled to be undertaken over the summer period each year. Monitoring included 15 intertidal sites located within Tauranga Harbour. Two objectives of the Coastal and Estuarine Ecology Regional Monitoring Program were to (a) provide Council with reliable data regarding the ecological status of open coastal and enclosed estuarine benthic communities in the Bay of Plenty region and (b) to provide a basis for the reliable detection of long-term trends in benthic community structure of open coasts and estuaries (Park, 1992). The monitoring program has been undertaken every summer following the initial survey.

The majority of ecological studies carried out in Tauranga Harbour have been intertidal, and as yet studies of subtidal ecology of Tauranga Harbour have been extremely limited. Information that has been gathered on subtidal habitats within Tauranga Harbour has been descriptive. Quantitative descriptions of sediment type and bivalve taxa at several subtidal sites around the harbour were made by de Lange in 1983-1985, as part of the "Tauranga Harbour Study" (de Lange and Healy, 1985).

Chapter Three

CHAPTER THREE

BROAD SCALE PATTERNS OF DISTRIBUTION and ABUNDANCE OF BIVALVES ON CENTRE BANK

3.1 INTRODUCTION

The patchy nature of environments coupled with the behaviour of species determines the abundance and spatial arrangement of a population. A fundamental step in any ecological investigation is the description of spatial patterns of organisms (Andrew and Mapstone, 1987).

> "Spatial and temporal patterns of organisms in an ecosystem are important because they are the building blocks of the models from which we generate hypotheses, both about the patterns themselves and about processes that may govern them"
> (Andrew and Mapstone, 1987: pp. 39).

Identifying spatial patterns is essential for improving the design and interpretation of surveys and experimental studies by relating sampling programs to natural scales of variation (Livingston, 1987). Thrush (1991) points out that given the potential importance of spatial variation in density to ecology, it is important to quantify what sort of patterns actually occur. The analysis of spatial patterns in soft-bottom communities is inherently difficult, particularly because of the crypsis of many animals; many species are not apparent from the surface causing the need to disrupt the habitat to assess pattern (Thrush, 1991). Subsequently few studies have summarised the spatial patterns of marine organisms, especially those of cryptic soft sediment macrofauna (Thrush, 1991). Spatial patterns in soft-sediments are usually represented in the horizontal plane, since many benthic organisms use the sediment-water interface for feeding, movement and reproduction. Most studies analysing the intensity of pattern report random, clumped or regular spacing of individuals (Thrush, 1991).

3.2 METHODOLOGY

3.2.1 Sampling Design

A broad scale benthic survey was undertaken over a week in December 1994 (summer) to provide an assessment of bivalve diversity, spatial distribution, abundance and population size structure across Centre Bank. Sampling was repeated in May 1995 (winter). A systematic sampling design was used. The advantage of systematic sampling over simple random sampling is that it distributes the samples more evenly over the population and therefore often gives more accurate and precise results (Snedecor and Cochran, 1972). A grid of 54 sites at 250 m spacing was initially drawn up. However due to time constraints in the field the number of sites was reduced by removing alternate transects, leaving 27 sites on the remaining four transects 500 m apart (Fig. 3.1). Transects ran from the Otumoetai Channel north to the harbour entrance parallel to the Maunganui Roads wharf. Three of the remaining sites positioned close to the harbour entrance were not sampled as currents made sampling with SCUBA impossible.

Position Fixing

During the first survey site positions were determined by compass fixes on navigation markers in the harbour, similar to the method used by Roper (1990). Three bearings were recorded at each site, from which latitude and longitude were determined from Navigational chart N.Z. 5412 (Appendix I). The co-ordinates were then placed into the differential GPS (Navtrac 4000) which was used for site relocation during the second survey in May 1995. Navtrac position fixing gives an accuracy of +/- 5 m.

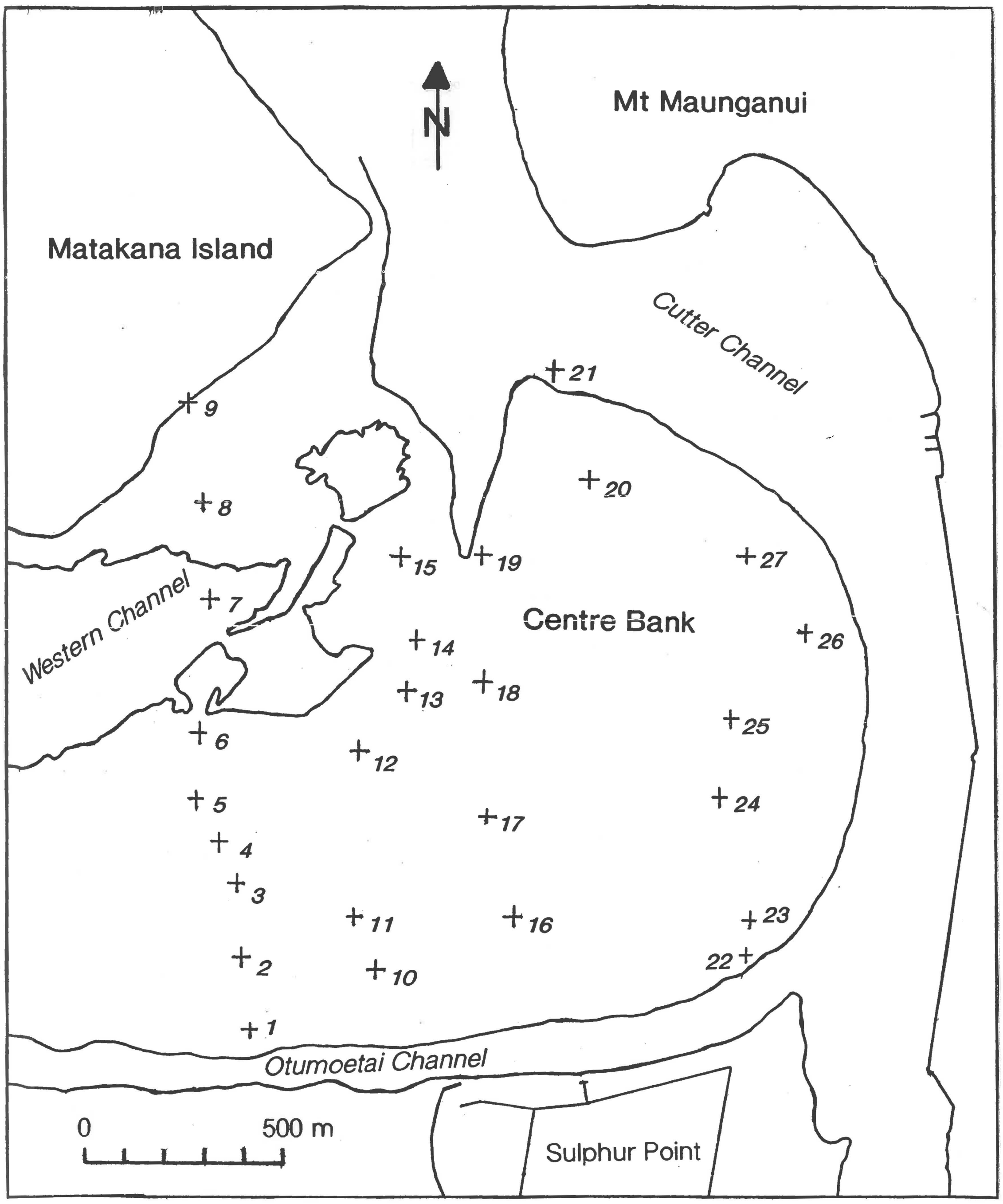


Figure 3.1 Location of sample sites across Centre Bank, for Survey 1 (December, 1994) and Survey 2 (May, 1995)

3.2.2 Field Collection

Samples were collected by SCUBA diving at water depths of 0-8 m. A metal hand sampler (Plate 3.1) was used to collect sediment to a depth of 9 cm, collecting a total volume of 0.01 m^3. A larger sized sampling unit is more likely to include a higher proportion of the total species pool present, but limits the number of samples which can be processed (Andrew and Mapstone, 1987). Replicate samples were positioned randomly (using randomly derived coordinates) within a 25 m^2 grid. The contents of the hand sampler were transferred to a plastic bag *in situ*. Three replicate samples were taken at each site. The number of replicates taken was determined by time constraints in the field and limited sample-sorting time. However Hartley and Dicks (1987) suggest that if each site is sampled at the same intensity and the samples are treated in the same way, then it is possible to make comparisons over the survey area.

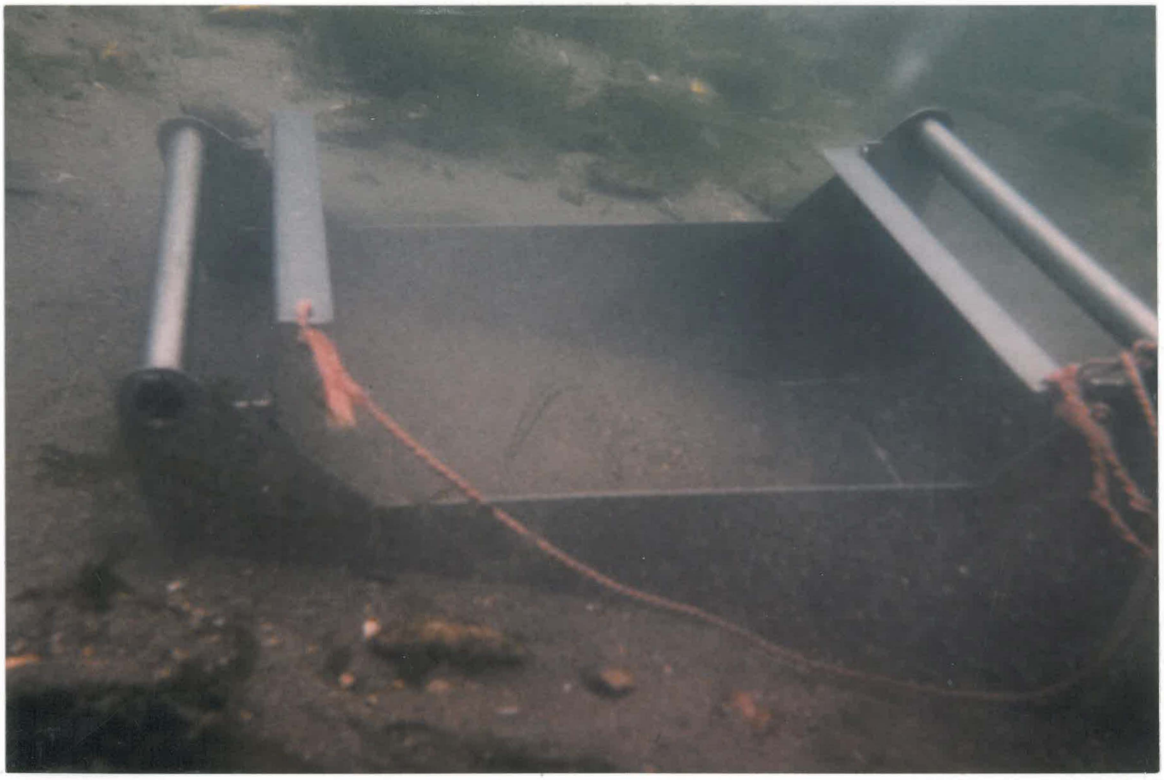


Plate 3.1 Hand sampler (0.01 m^3) used in Survey 1 (December, 1994) and Survey 2 (May, 1995)

Samples were sieved onshore. Study objectives determine the mesh size used in macrobenthic studies (Ferraro *et al.*, 1989). My sampling program was designed to obtain information on the size structure of both juvenile and adult bivalves. As sorting time with a 0.5 mm mesh sieve is much greater than for a 1 mm mesh (James *et al.*, 1995), I used 1.0 mm mesh. Hartley *et al.* (1987) cites a number of studies which show the use of the 1 mm mesh to be the most cost-effective compromise between ease of sorting and information gained. The samples were fixed in a 5% formalin solution (Holme and McIntyre, 1984), then stored until they could be sorted.

Sorting and Identification

Samples were re-sieved, thoroughly washed in freshwater to remove formalin and placed in a white plastic sorting tray covered with 2 cm of water. Each sample was sorted by eye with tweezers, all organisms being removed and placed in a labeled container containing 95% ethanol (Hureau and Rice, 1983). Samples were stored for subsequent identification.

All bivalves were identified to species level where possible using an Olympus S260 dissecting microscope at magnifications of 10-63x. All specimens were counted and measured (length along the anterior-posterior axis) to the nearest millimetre.

3.2.3 Statistical Analysis

Species Diversity Indices

Berger-Parker and Margalef's Indices

Diversity maybe divided into two distinct components: (1) the total number of species and (2) evenness (Magurran, 1988). Commonly both components are incorporated into a single numerical value; because of this there is much confusion regarding correct usage and interpretation of species diversity indices. Berger-Parker and Margalef's indices were chosen because they are straightforward measures of the abundance and dominance components of diversity, and are easily calculated and interpreted (Magurran, 1988). The Berger-Parker index is a simple dominance measure, both mathematically and conceptually (Southwood, 1978). This index expresses the proportional importance of the most abundant species

$$d=N_{max}/N$$

where N=total number of individuals, and N_{max}=number of individuals in the most abundant species. In order to ensure that the index increases with increasing diversity the reciprocal form of the measure is often adopted. Margalef's index is a historically well-known species richness index, based on the relationship between S (the number of species recorded) and N (the total number of individuals summed over all S species).

$$D_{mg}=(S-1)/\ln N$$

Multivariate Ordination Techniques

Canonical Discriminant Analysis (CDA)

Canonical discriminant analysis is a multivariate dimension-reduction technique (Williams, 1983). CDA reduces a data set to a set of dimensions that adequately describes the patterns in the data. Given two or more groups of observations with measurements on several quantitative variables, canonical discriminant analysis derives a linear combination of the variables that has the highest possible multiple correlation with the groups.

Multidimensional Scaling (MDS)

Multidimensional scaling (MDS) was another statistical method used for multivariate representation of community structure. An array of species counts arising in both field and experimental community studies do not always lend themselves to standard statistical tests based on multivariate normality. Instead a valid and more revealing approach uses informal display methods such as MDS (Clarke and Warwick, 1994). Non-metric MDS analysis preserves the rank order relations amongst similarities in the placing of samples in an ordination (Clarke and Ainsworth, 1993). Analysis followed the suggestions of Clarke (1993) and Clarke and Ainsworth (1993), data were reexpressed as Bray-Curtis similarities, then analysed using MDS. No data transformations were undertaken.

Spatial Analysis

Spatial autocorrelation analysis

Spatial density patterns were analysed using spatial autocorrelation. Spatial autocorrelation techniques utilise the information contained in the arrangement of samples across geographic space. Sokal and Oden (1978) outline the spatial autocorrelation process as testing whether the observed value of a variable at one locality is significantly dependent on values of the variable at neighbouring localities. In the case of quantitative variables, spatial autocorrelation can be measured by either Moran's I or Geary's C spatial autocorrelation coefficients (Sokal and Oden, 1978; Upton and Fingleton, 1985). Cliff and Ord (1973) suggest that Moran's I is generally more useful than Geary's C. Correlograms are the graphical summary of autocorrelation coefficients as a function of distance between pairs of localities. In order to more easily establish the concept of spatial autocorrelation, it is useful to entertain the idea of throwing a stick randomly around a field.

> "Imagine throwing a stick of specific length over an over again at a certain study area, while noting the values of a variate at the points at which the ends of the stick land. Affirming spatial autocorrelation is tantamount to saying that the values at the ends of the stick are usually like each other, or that they are usually different".
> (Upton and Fingleton, 1985: pp. 186)

Spatial autocorrelation techniques have been successfully applied in studies of infaunal intertidal bivalves (McArdle and Blackwell, 1989; Thrush *et al.*, 1989).

Correlograms were calculated using SAAP 2.3. Data were displayed as correlograms (plots of Moran's I statistic against distance), with replicate samples remaining separate from each other. Maps of taxa density (pooled across replicates at each site) across Centre Bank in Survey 1 and Survey 2 were constructed, to allow visual examination of changes in density and overall pattern across Centre Bank.

3.2.4 Population Size Structure

If an understanding of the dynamics of a species is to be obtained, some means of estimating the age composition is required (Krebs, 1978). Length-frequency analysis is a commonly used technique when determining the distribution of age classes within a population. A spread of size classes can indicate settlement, growth and aeging. The shape of a length-frequency histogram is used to indicate whether a population is young (with a predominance of smaller size classes), or old (with a predominance of larger size classes). Length-frequency analysis was conducted to document the population structure of several dominant bivalve species across Centre Bank.

Many bivalves are difficult to age directly from shell growth rings, as growth rings can be confused with disturbance rings caused by other factors such as predation attempts and fishing activity (Hooker, 1995a). Another method used to estimate age composition of a population is tagging or marking of individual animals and periodically measuring their sizes. The disadvantage of this method is that recapture rates of tagged or marked individuals, especially small individuals, can be very low (Kirkwood, 1983).

3.3 RESULTS

3.3.1 Taxa Abundance

A total of 25 bivalve taxa were identified to species level in the 80 samples taken in Survey 1 (December 1994) (Table 3.1; see Appendix II for details). The five most common taxa accounted for 84.9% of the 3,673 individual animals recorded. The most common was the morning star shell *Tawera spissa* (32.5%), then *Ruditapes largillierti* (22.1%) and *Paphies australis* (18.2%). A total of 20 taxa was identified from the same sites in Survey 2 (May 1995). In Survey 2 the five most common taxa accounted for 93.2% of the 6,532 individuals recorded. The most common taxon was *P. australis* (67%), then *T. spissa* (12%) and third most abundant *R. largillierti* (7%).

Table 3.1 Taxa recorded at Centre Bank, Tauranga Harbour

	Survey 1				Survey 2			
SPECIES CODE TAXA	**No. individuals**	**% Total**	**Maximum density**	**Size range (mm)**	**No. individuals**	**% Total**	**Maximum density**	**Size range (mm)**
1 *Paphies australis*	670	18.2	283	2-82	4369	67	3330	3-80
2 *Ruditapes largillierti*	813	22.1	423	2-80	453	6.9	197	1-59
3 *Tawera spissa*	1195	32.5	349	1-28	791	12.1	442	1-33
4 *Gari stangeri*	170	4.6	54	5-66	279	4.2	107	2-65
5 *Macomona liliana*	178	1.8	67	3-53	81	1.2	23	3-51
6 *Soletellina siliquens*	263	7.1	80	2-26	166	2.5	63	2-32
7 *Nucula nitidula*	52	1.4	19	2-9	199	3	97	2-9
8 *Nucula hartvigiana*	155	3.1	22	2-9	79	1.2	24	2-9
9 *Divaricella huttoniana*	60	1.6	18	1-16	35	0.5	6	2-9
10 *Perna canaliculus*	41	1.1	27	2-80	0	0	0	0
11 *Myadora striata*	10	1.0	9	5-39	47	0.7	18	4-50
12 *Scalpomactra scalpellum*	4	0.1	3	3-4	1	0.01	1	4-7
13 *Gari lineolata*	0	0	0	0	2	0.03	2	47-48
14 *Soletellina nitida*	6	0.1	5	5-9	17	0.2	5	4-16
15 *Dosinia subrosea*	2	0.05	1	11-50	3	0.04	1	35-46
16 *Gomphina maorum*	2	0.05	2	15-16	0	0	0	0
17 *Paphies subtriangulata*	9	0.2	3	2-6	0	0	0	0
18 *Modiolus areolatus*	9	0.2	5	3-5	0	0	0	0
19 *Arthritica bifurca*	15	0.4	4	3-4	0	0	0	0
20 *Notocallista multistriata*	1	0.02	1	13	0	0	0	0
21 *Zenatia acinaces*	3	0.08	1	8-12	0	0	0	0
22 *Hiatella arctica*	2	0.05	2	2-3	0	0	0	0
23 *Diplodonta striatula*	0	0	0	0	2	0.03	2	1-2
24 *Felaniella zelandica*	1	0.02	1	17	0	0	0	0
25 *Dosinia lambata*	0	0	0	0	1	0.01	1	1-3
26 *Tellina ?gaimardi*	0	0	0	0	3	0.04	1	0
27 Sp. 1	4	0.1	4	2-4	0	0	0	0
28 Sp. 2	4	0.1	4	1-3	0	0	0	0
29 Sp. 3	1	0.02	1	3	2	0.03	2	2
30 Sp. 4	0	0	0	0	1	0.01	1	4
31 Sp. 5	0	0	0	0	1	0.01	1	3
TOTAL NUMBER OF INDIVIDUALS FROM ALL SITES	**3,673**				**6,532**			

For Survey 1 (1994) the highest number of taxa was found at sites 2 and 6, with 11 species present. The lowest number of taxa (2) was recorded from site 23. All remaining sites recorded between 3 and 9 taxa. The number of taxa recorded was the same or lower in Survey 2 (1995) than in Survey 1 (1994) for all sites except three, (sites 18, 25 and 27) (Fig. 3.2). In 1995 site 27 recorded the highest number of taxa, 12. There were no bivalves at site 9. Several sites recorded a single taxon (e.g. 8, 12, 20 and 23). Remaining sites recorded between 2 and 9 taxa.

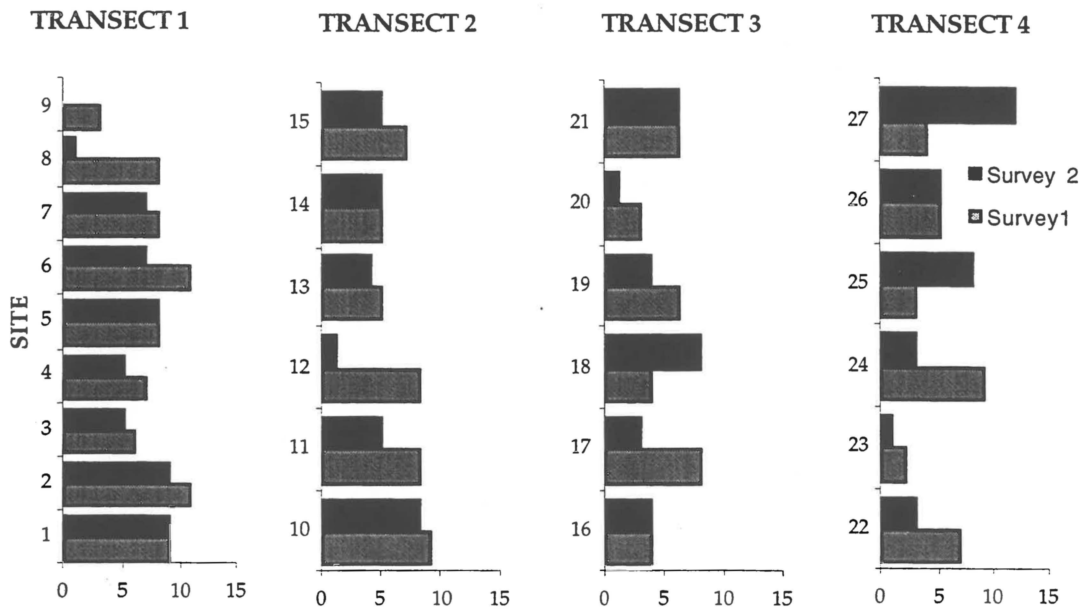


Figure 3.2 Number of taxa per site at Survey 1 (December, 1994) and Survey 2 (1995, May) of Centre Bank

3.3.2 Assemblage-level Patterns

Species Diversity Indices

Berger-Parker Index

Values of the Berger-Parker index varied in both space and time. In Survey 1 (1994) high values of evenness occurred at sites 2, 14, 15, 17, and 26, whereas high values occurred at sites 1, 21, 22 and 27 in Survey 2 (1995) (Fig. 3.3a). Of the two surveys, Survey 2 had lower Berger-Parker index values at more sites, suggesting that assemblages sampled in 1995 were dominated by individuals of one taxon. Site 4 had the lowest Berger-Parker index value for both surveys, hence greatest dominance by individuals of one taxon. A large decrease in the Berger-Parker index value through time was apparent at site 2 suggesting a change from evenness to dominance by individuals of one taxon. A value was not recorded for site 9 in Survey 2 as no bivalves were present.

Moderate increases in the Berger-Parker index occurred through time at sites 1, 22, and 27, indicating that individuals at these sites were more evenly distributed among a larger number of species in Survey 2 than in Survey 1. There was an increase in the number of species present but a decrease in the total number of individuals recorded. Sites 8, 12, 20, and 23 had the greatest dominance by individuals of one taxon for Survey 2, recording Berger-Parker index values of 1. Transect 3 appeared to be the most unchanged transect through time with sites showing a small drop in evenness. The exception was site 21, which showed an increase in evenness and recorded the highest Berger-Parker index value of all sites over both surveys.

Margalef's Index

High Margalef's index values occurred at sites 11 and 24 in 1994 and site 27 in Survey 2 (Fig. 3.3b). Moderate decreases in Margalef's index value from Survey 1 to Survey 2 occurred at sites 24 and 11 indicating a decrease in species richness, while at sites 8, 9, 12 and 23 Margalef's index decreased to zero in Survey 2. Large increases in Margalef's index value occurred at sites 25 and 27. Generally lower Margalef's index values occurred in Survey 2 compared to Survey 1, suggesting a small decrease in species richness through time.

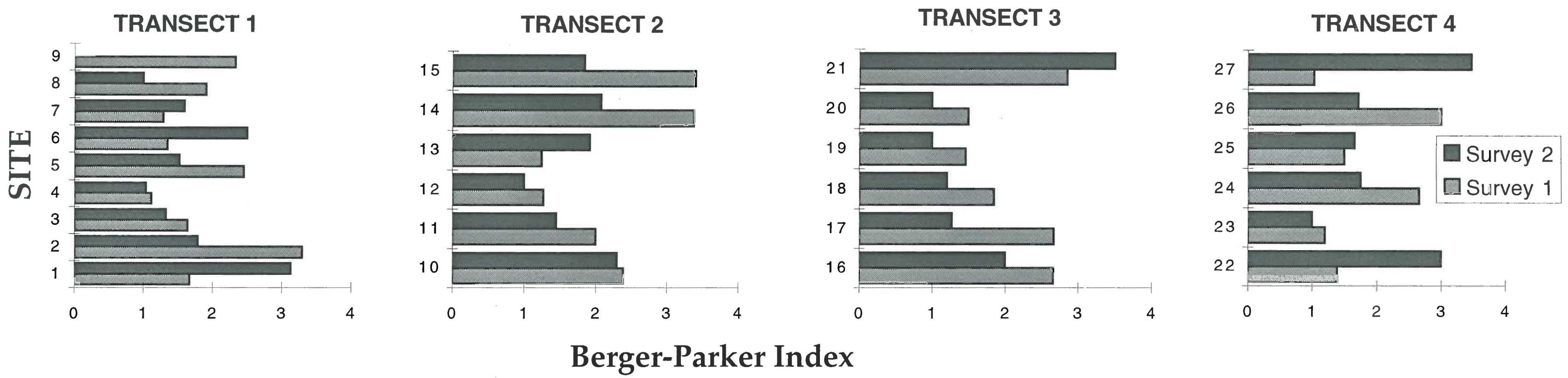


Figure 3.3a Berger-Parker Index for bivalve species at sites of Centre Bank Survey 1 (December, 1994) and Survey 2 (May, 1995)

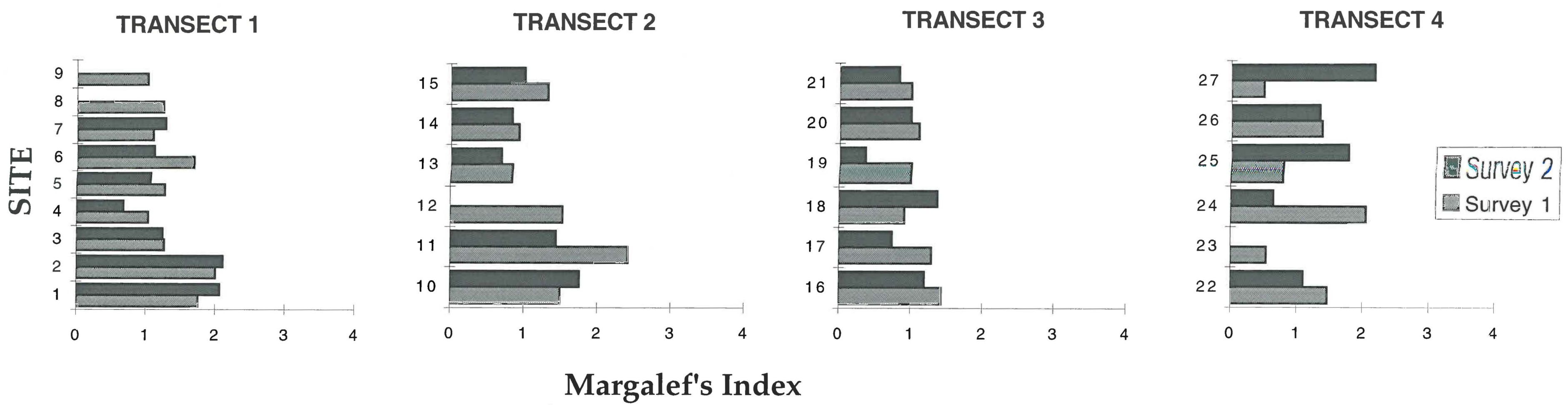


Figure 3.3b Margalef's Index for bivalve species at sites of Centre Bank Survey 1 (December, 1994) and Survey 2 (May, 1995)

Rank Sum Graphs

Rank sum graphs confirm patterns calculated by Berger-Parker and Margalef's indices. Rank sum graphs show species assemblage at site 4 to be unchanged, being dominated by *Paphies australis* in both surveys (Fig. 3.4). Rank sum graphs for sites 1, 22 and 27, correspond with Berger-Parker index values. Sites 1, 22 and 27 in Survey 2 display a decrease in the dominant bivalve recorded in Survey 1, while an increase in the number of species present is seen at site 27 (Fig. 3 5). In Survey 2, site 1 retained the same number of species as in Survey 1, though the species and their densities differed. Of the sites across Centre Bank site 8 showed most clearly a decrease in species richness (Fig. 3.6). *P. australis* was the only species recorded at site 8 in Survey 2, having a greater density than any other species recorded at site 8 in Survey 1.

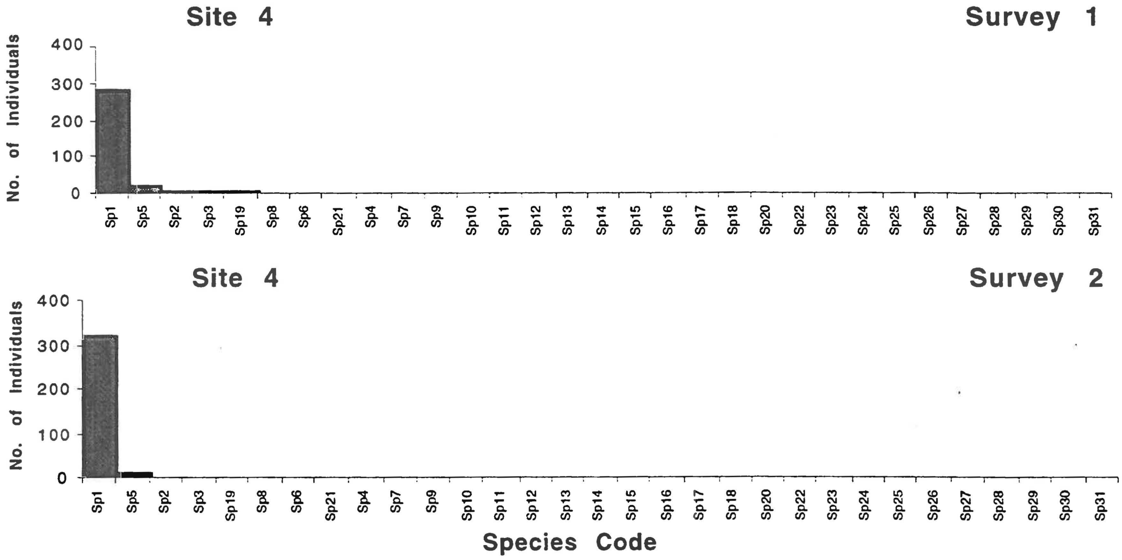


Figure 3.4 Rank sum graphs for individuals of species 1-31 at site 4. Site 4 had the lowest Berger-Parker Index value for both surveys, indicating a dominance by individuals of one taxon in Survey 1 (December, 1994) and 2 (May, 1995). Species codes given in Table 3.1

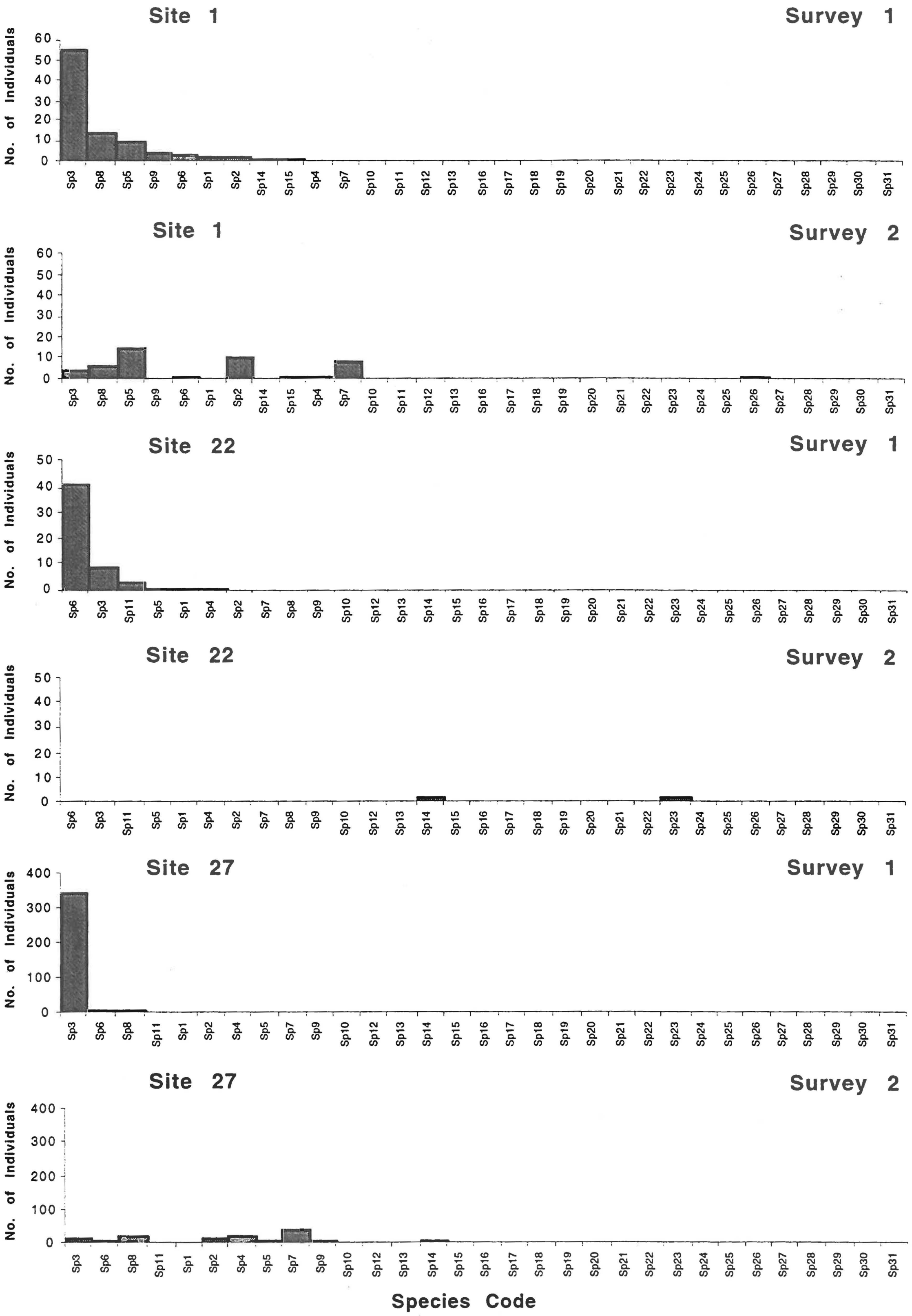


Figure 3.5 Rank sum graphs for individuals of species 1-31 at sites showing an increase in Berger-Parker Index values from Survey 1 (December, 1994) to Survey 2 (May, 1995), indicating greater evenness of species. Species codes given in Table 3.1

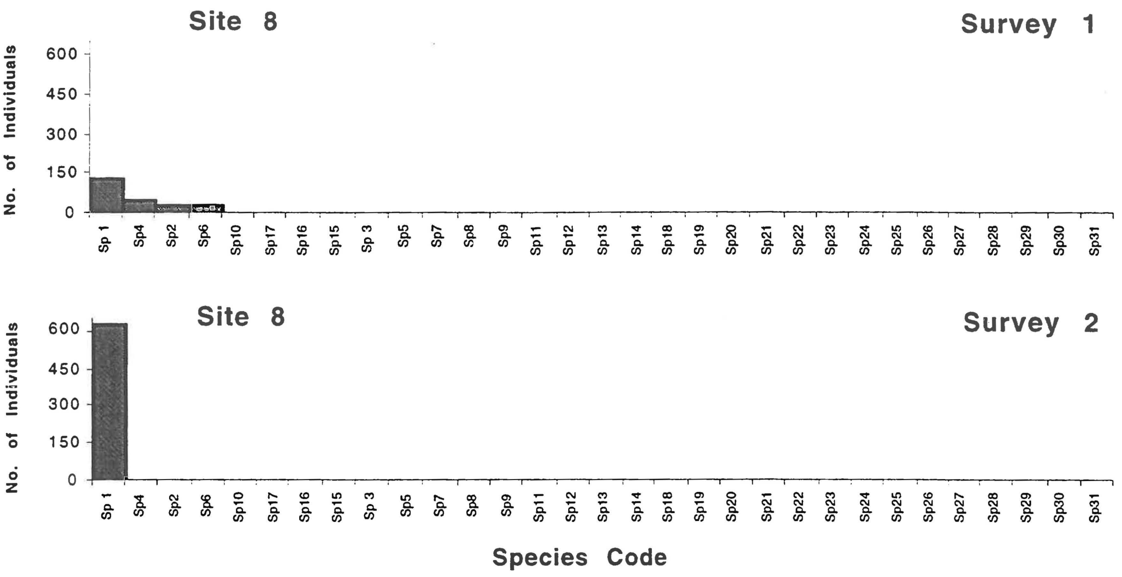


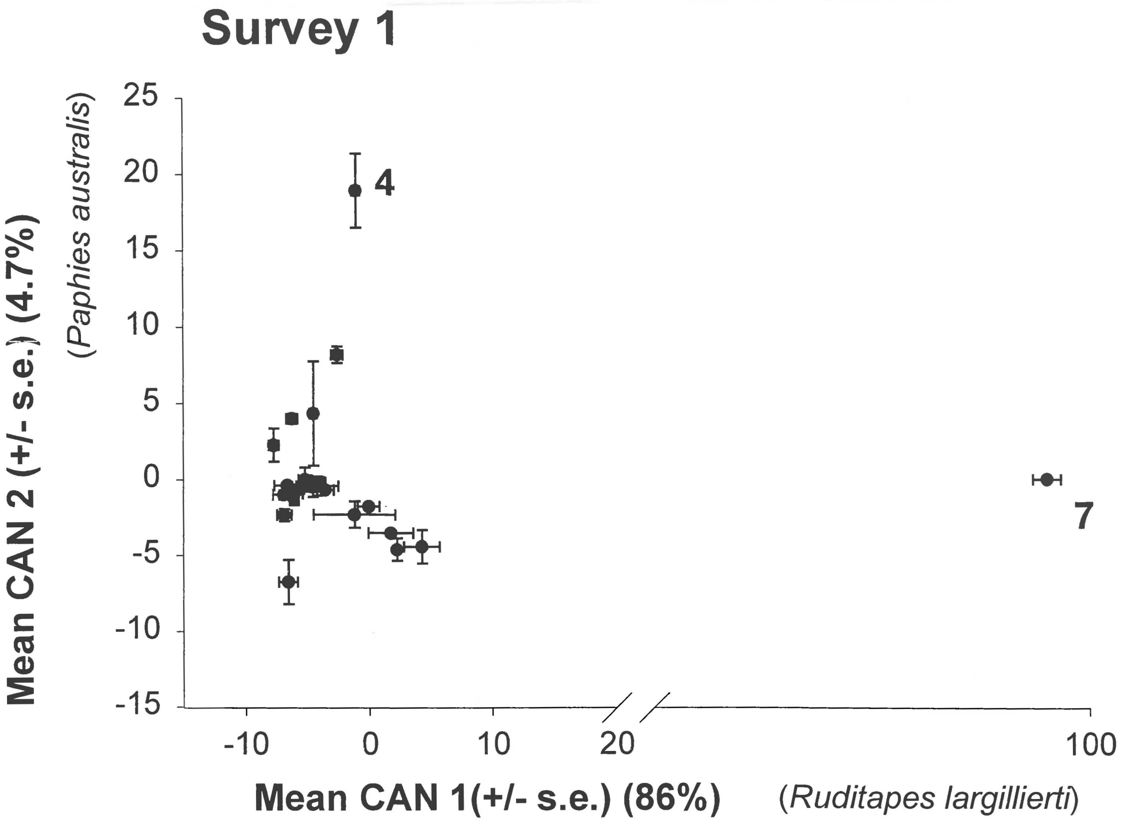
Figure 3.6 Rank sum graphs for individuals of species 1-31 at site 8, showing a large decrease in Margalef's Index from Survey 1 (December, 1994) to Survey 2 (May, 1995), indicating a decrease in species richness. Species codes given in Table 3.1

Multivariate Ordination Techniques

Principal Component Analysis was undertaken but showed no clear pattern and is therefore not presented.

Canonical Discriminant Analysis

The first 2 canonical variables accounted for approximately 90% of the variation in Survey 1 (1994) (Fig. 3.7). The species with the highest influence on CAN 1 was *Ruditapes largillierti*. *Paphies australis* and *Nucula hartvigiana* were the most important contributors to CAN 2. Sites 7 and 4 were distinct on CAN 1 and CAN 2 respectively. Both sites 7 and 4 were located on transect one, on the western side of Centre Bank. Site 7 was distinct from others being positioned in the Western Channel. In Survey 2 (1995) (Fig. 3.7) CAN 1 was dominated by *Gari stangeri*, with the next most important species in order being *Tawera spissa*, *Soletellina siliquens* and *R. largillierti*. *R. largillierti* was the most significant contributor to CAN 2, followed by *T. spissa* and *G. stangeri*. Site 5 was distinct, separating out from other sites along both CAN 1 and CAN 2. Similarly site 21 located slightly north of Centre Bank, separated out along both axes, negatively along the CAN 1 axis and positively along CAN 2.



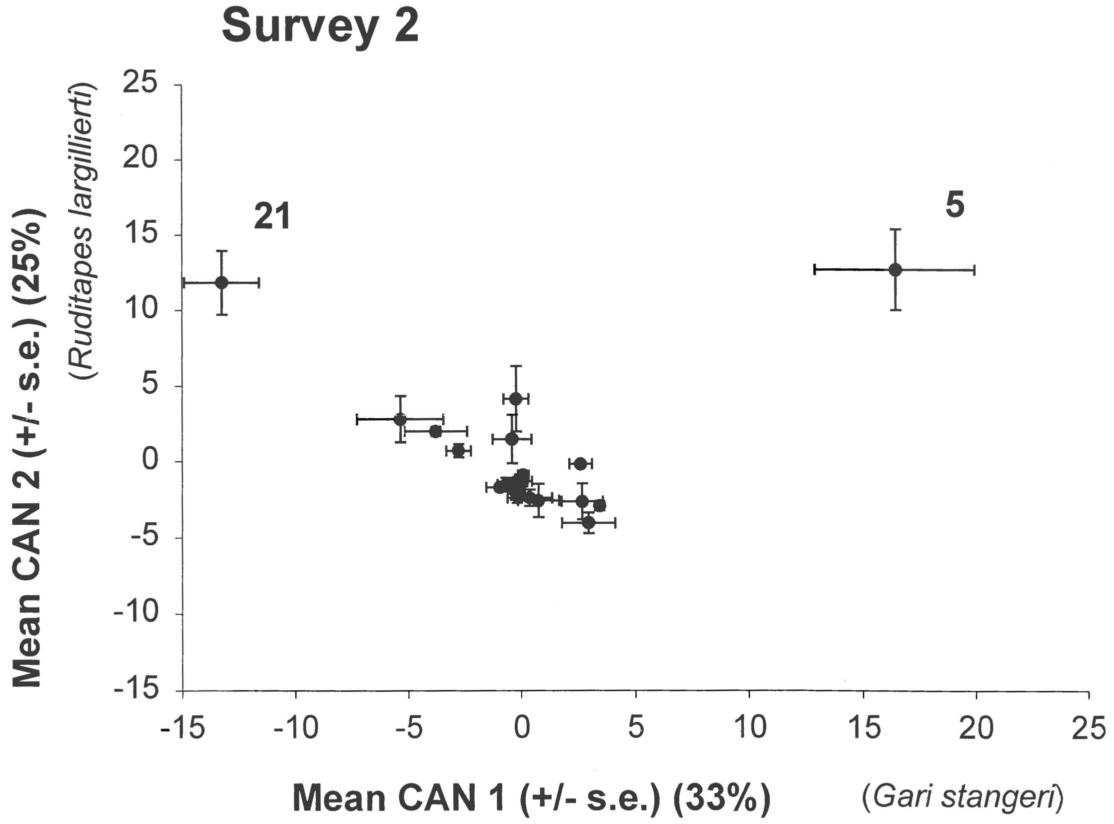


Figure 3.7 Canonical Discriminant Analysis of bivalve densities from Survey 1 (December, 1994) and Survey 2 (May, 1995) of Centre Bank. Labels indicate site numbers

Multidimensional Scaling

In Survey 1 sites 7 and 23 were the two most extreme sites on DIM 1, while sites 20 and 9 separate out along DIM 2 (Fig. 3.8a). The stress level is moderate at 0.14. In the 1995 survey site 23 remains separated out along DIM 1, while site 20 is still distinct on DIM 2 (Fig. 3.8b). Sites 22, 19 and 8 are also distinct from the remaining sites. A small group of seven sites appears distinct at the left of the 2-dimensional ordination. Stress is higher than in the first survey at 0.19, indicating a poor fit of the data to the model.

In Survey 1 both ordination techniques identified site 7 as being distinct from others, while there was little concordance between techniques for Survey 2 .

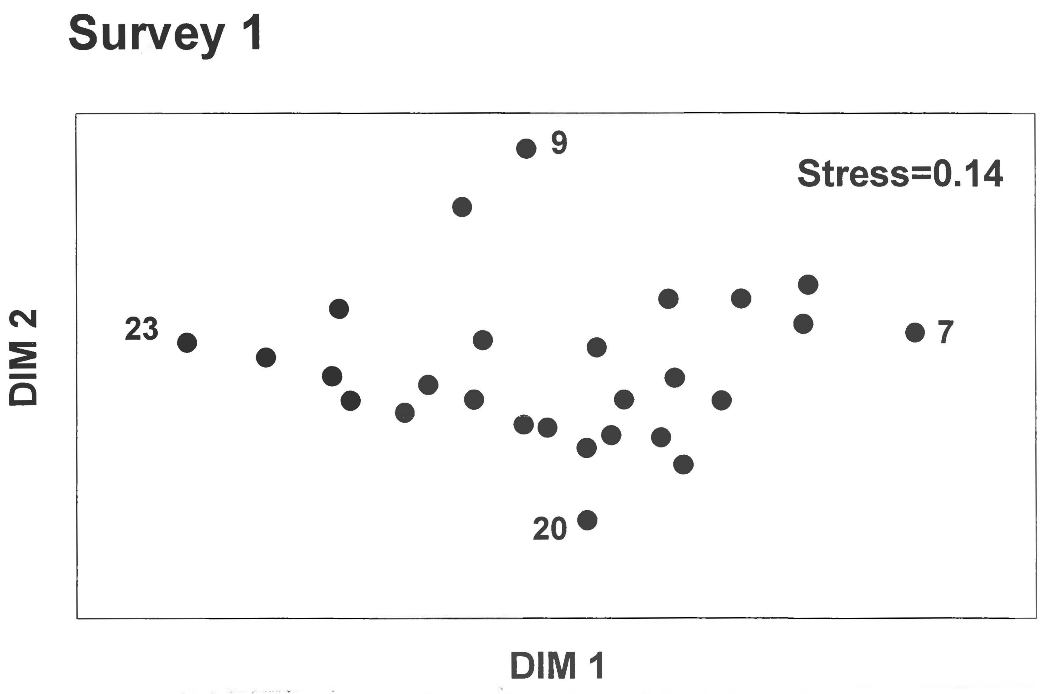


Figure 3.8a Multi-dimensional scaling (ordinations) of bivalve densities from Survey 1 (December, 1994) of Centre Bank. Labels indicate site numbers

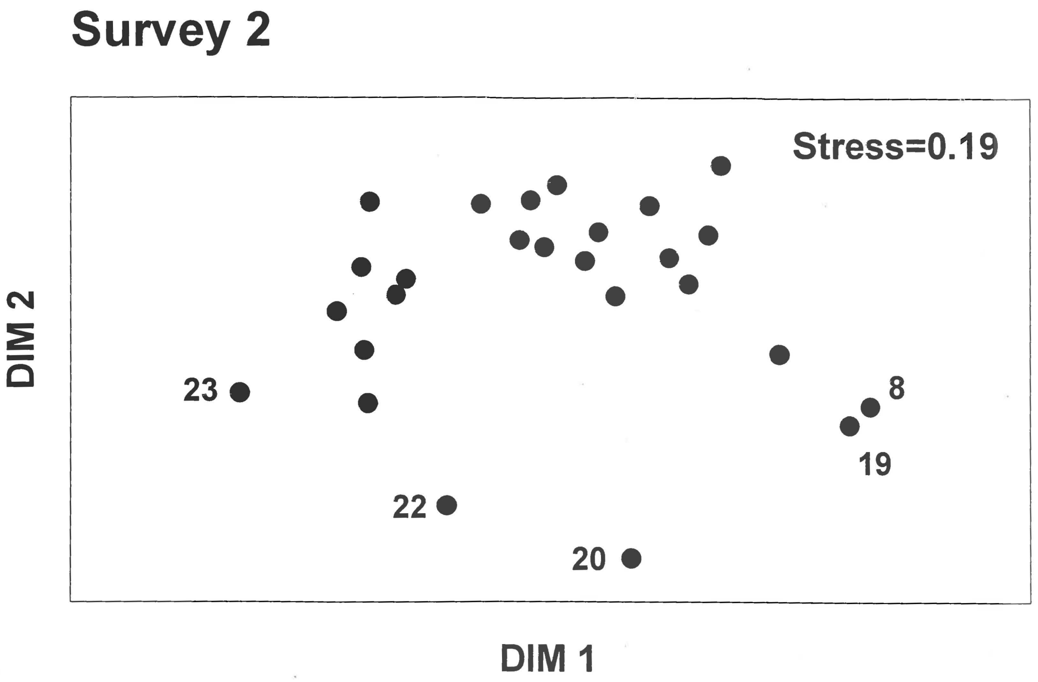


Figure 3.8b Multi-dimensional scaling (ordinations) of bivalve densities from Survey 2 (May, 1995) of Centre Bank. Labels indicate site numbers

3.3.3 Spatial Analysis

Spatial Patterns

Three abundant and widespread species were selected for analysis of their distribution across Centre Bank. Density of *Paphies australis* varied greatly among sites in both Survey 1 and Survey 2, with *P. australis* occurring at a number of sites in only one survey (Fig. 3.9a). *P. australis* was absent in both surveys at several sites (e.g. 5, 13, 17 and 24). At sites where *P. australis* was recorded in both surveys, densities were relatively similar. The exception was site 19, where density changed dramatically from a total of 93 individuals in Survey 1 to 3330 in Survey 2. Seven sites across Centre Bank, 4 on transect 1, recorded *P. australis* in Survey 1 and not Survey 2. *P. australis* appeared in Survey 2 at sites 6, 18, 21, 26 and 27 having been absent there in Survey 1. Correlograms of Moran's I for the density of *P. australis* in Survey 1 suggest positive autocorrelation at distances of up to 200 m (Fig. 3.9b, c). Significant negative autocorrelation occurred at approximately 500 m, with values becoming significantly positive again at approximately 1 km.

Significant negative autocorrelation occurred at distances of 1600 m and 2000 m in Survey 1. In contrast Moran's I values for distance classes in survey 2 did not deviate far from the expected values being significantly positive at 200 m and significantly negative at approximately 1 km.

Ruditapes largillierti showed two distinct areas of high density, one at sites 5, 6, 7, and 8 on transect 1, the other at sites 13, 14, and 15 on transect 2 (Fig. 3.10a). Site 17 was conspicuous recording a high density in Survey 1, then zero density in Survey 2. Similarly, individuals were recorded at sites 4, 10, and 12 in Survey 1, but did not appear in Survey 2. *R. largillierti* was not present in Survey 1 at sites 25 or 27, but appeared in moderate numbers there in Survey 2. Sites 18, 19 and 20 recorded consistent densities in Survey 1 and 2. The overall shape of the *R. largillierti* correlogram did not change from Survey 1 to Survey 2 (Fig. 3.10b, c). Correlograms of Moran's I for *R. largillierti* were significantly positive at a distance of 200 m for both surveys. Negative autocorrelation occurred at long distances of 1600 m and 2000 m in Survey 1 but was not present in Survey 2.

Tawera spissa was evenly distributed across the entire bank, with individuals being present at most sites in both surveys (Fig. 3.11a). *T. spissa* was absent from only 4 sites (8, 9, 20 and 23). Densities of *T. spissa* varied among sites and between the two surveys. At only 4 of the 14 sites (5, 18, 19 and 21) at which *T. spissa* occurred, did Survey 2 densities increase over densities recorded in Survey 1. In Survey 1 densities of *T. spissa* were found to be significantly positively autocorrelated at two extreme distances, 200 m and 2000 m (Fig. 3.11b). Distances between these two extremes were non-significantly negatively autocorrelated. The shape of the correlogram for *T. spissa* in Survey 2 was quite different, with densities being significantly positively autocorrelated at a short distance of 200 m then again at approximately 1 km (Fig. 3.11c). Densities of *T. spissa* were negatively autocorrelated at distances of 450-800 m.

All three abundant bivalves had similar scales of distribution of approximately 200 m. *Tawera spissa* differed from the other taxa in having a second positive peak of Moran's I at about 1 km.

Paphies australis

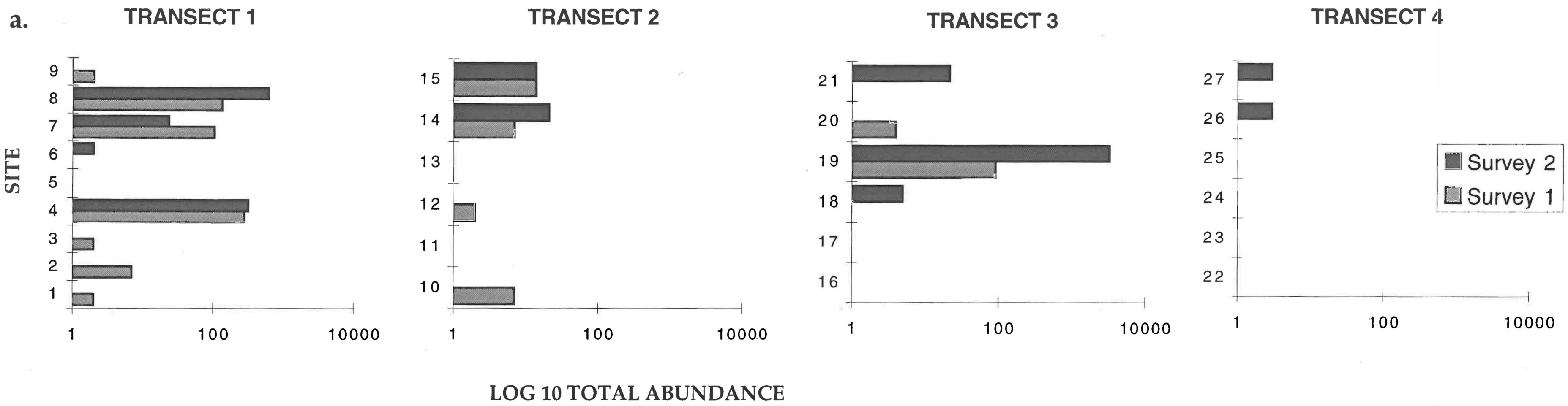


Figure 3.9a Total abundance of *Paphies australis,* Centre Bank, Survey 1 (December, 1994) and Survey 2 (May, 1995)

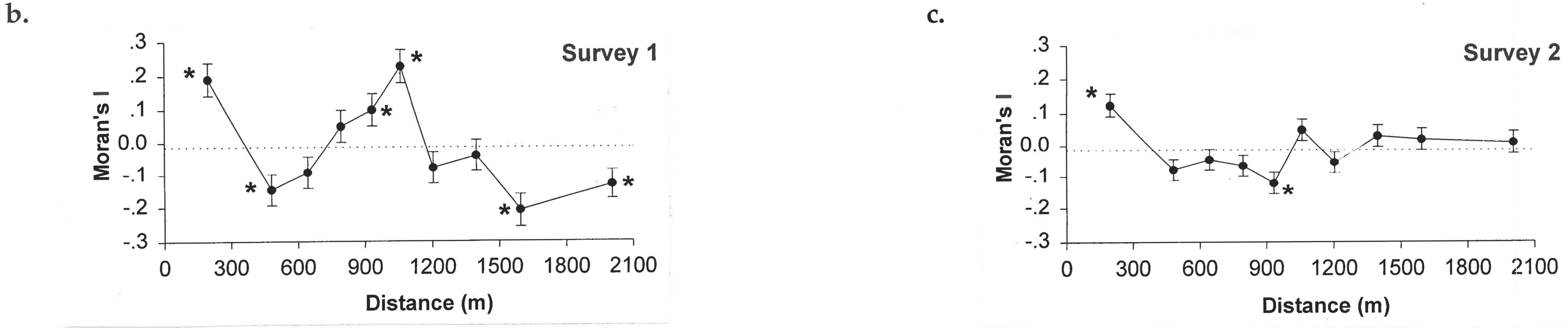


Figure 3.9b, c Spatial correlograms of Moran's I for *Paphies australis.* The dotted line represents the expected value of I. Starred I values are statistically significant (P< 0.05). Error bars represent +/- 1 s.d.

Ruditapes largillierti

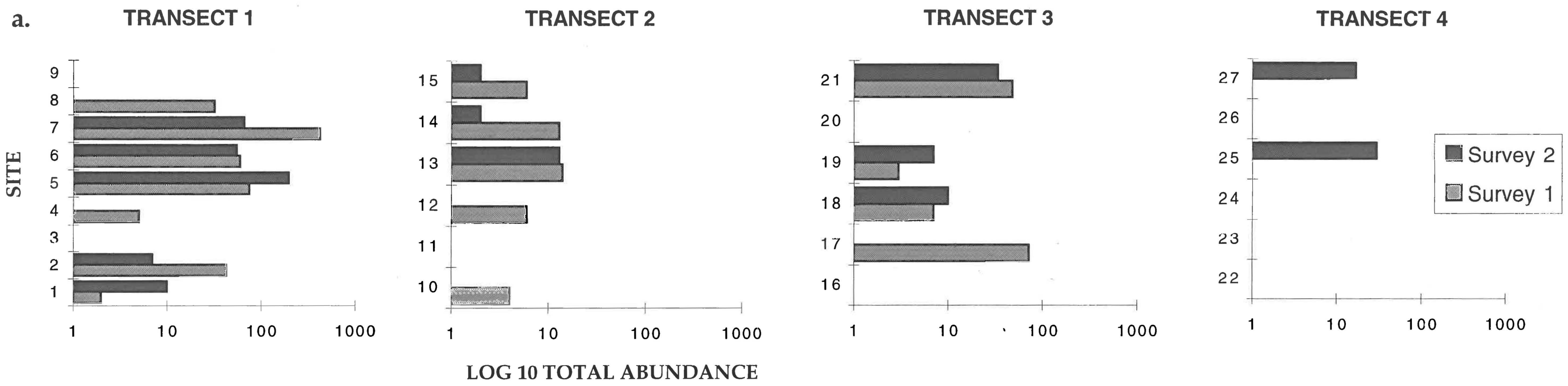


Figure 3.10a Total abundance of *Ruditapes largillierti,* Centre Bank, Survey 1 (December, 1994) and Survey 2 (May, 1995)

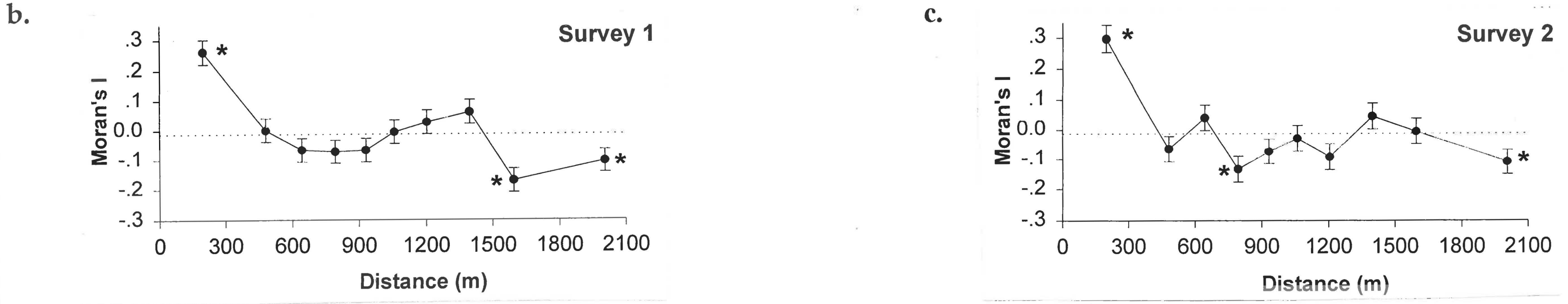


Figure 3.10b, c Spatial correlograms of Moran's I for *Ruditapes largillierti.* The dotted line represents the expected value of I. Starred I values are statistically significant (P< 0.05). Error bars represent +/- 1 s.d.

Tawera spissa

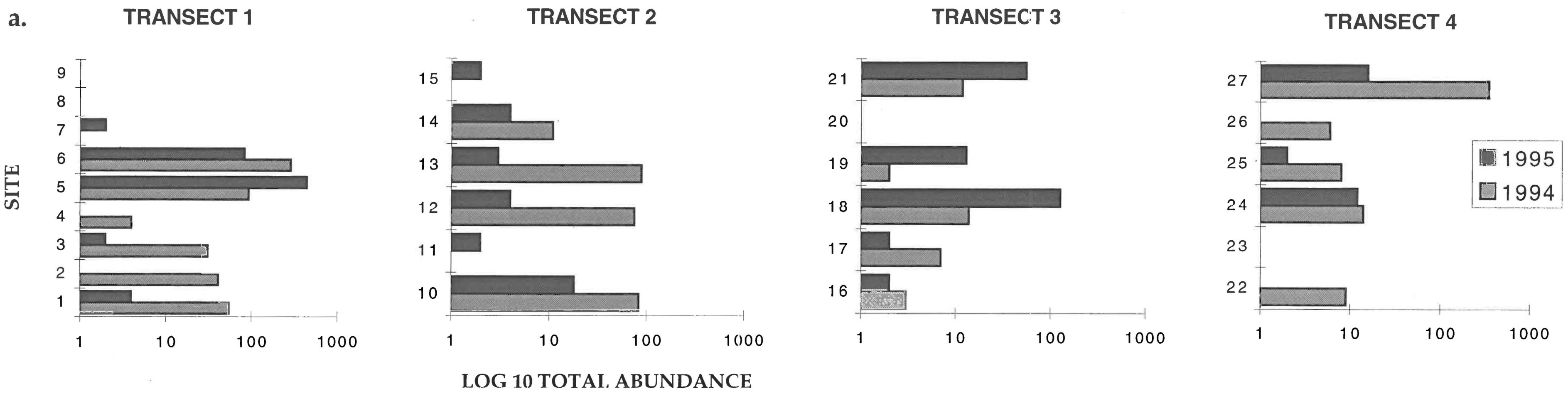


Figure 3.11a Total abundance of *Tawera spissa,* Centre Bank, Survey 1 (December, 1994) and Survey 2 (May, 1995)

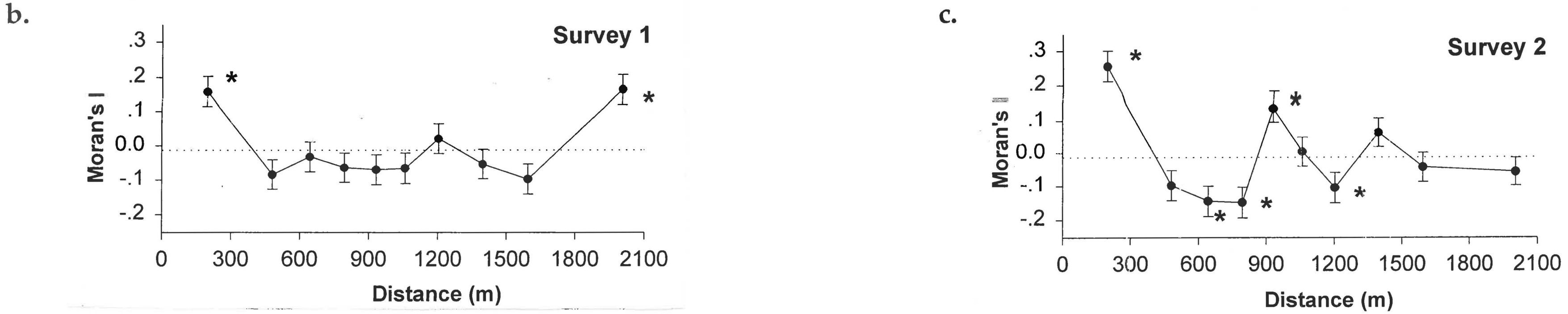


Figure 3.11b, c Spatial correlograms of Moran's I for *Tawera spissa.* The dotted line represents the expected value of I. Starred I values are statistically significant (P< 0.05). Error bars represent +/- 1 s.d.

3.3.4 Population Size Structure

Bivalve assemblages at sites across Centre Bank were dominated by *Paphies australis, Ruditapes largillierti* and *Tawera spissa.* In Survey 1 *P. australis* displayed an obvious bimodal size structure (Fig. 3.12a). There was a distinct group of juveniles centered around 5-10 mm, and a larger adult cohort, with the predominant size class being in the 55-65 mm range. The size structure of the *P. australis* population across Centre Bank changed dramatically from Survey 1 to Survey 2. The percentage of individuals in the 5-10 mm size class increased markedly between the two sampling occasions. The Survey 2 histogram indicates the two distinct size classes of pipi were still present. The 11.6% of the total comprising adults (55-65 mm) in Survey 2 is a marked decrease from 52.9% in 1994. Figure 3.12b indicates that the population size structure of *P. australis* in Survey 1 at site 19 is similar to that of the entire Centre Bank population. The increase in the 5-10 mm size class can be attributed to site 19 (Fig. 3.12b) where roughly 30 times (n=2899) more pipi were recorded in Survey 2 than in the December survey, with the majority (68%) being 5-10 mm.

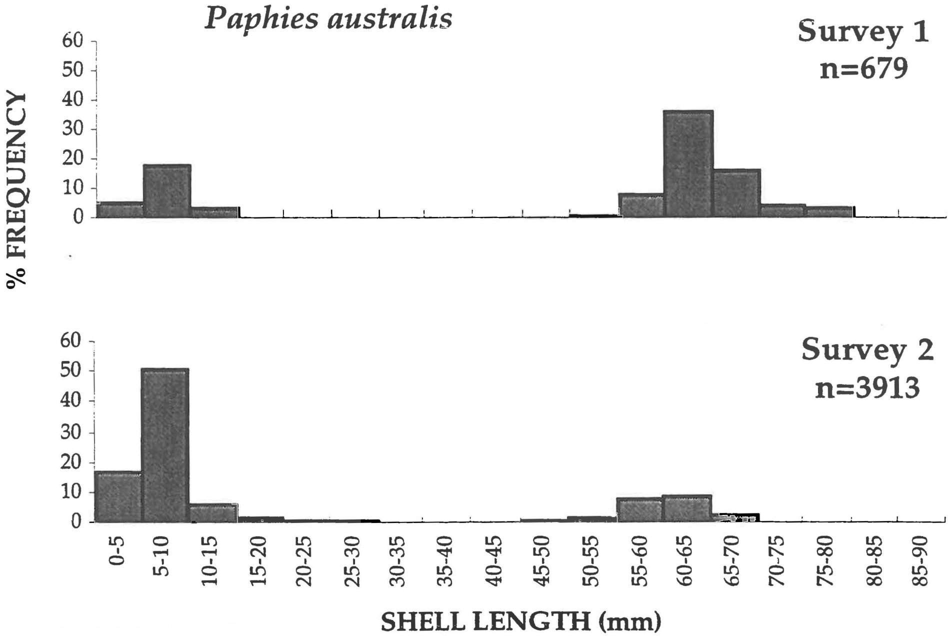


Figure 3.12a Length-frequency distributions for *Paphies australis* for Centre Bank, Survey 1 (December, 1994), Survey 2 (May, 1995)

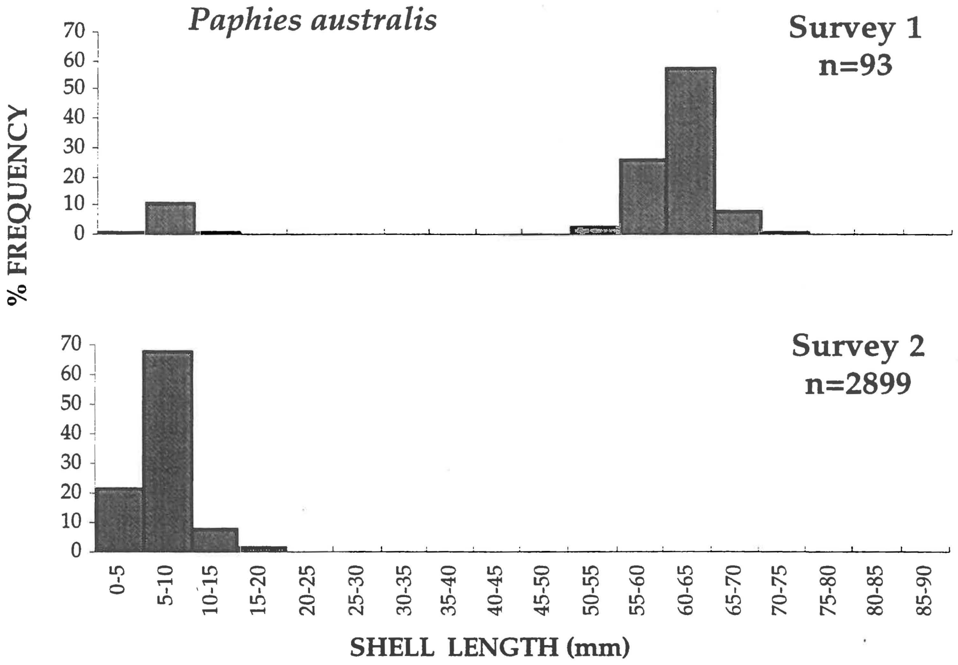


Figure 3.12b Length-frequency distributions for *Paphies australis* at site 19, Survey 1 (December, 1994), Survey 2 (May, 1995)

There were bimodal size frequency distributions for *Ruditapes largillierti* in both surveys. In Survey 1 the population was dominated by juveniles (0-15 mm) and an adult size class (45-60 mm) (Fig. 3.13a). Approximately half the juveniles recorded in Survey 1 occurred at site 7 (Fig. 3.13b). Distribution of size frequencies of *R. largillierti* were more evenly spread in the second survey. The juvenile cohort seen in Survey 1 was much less abundant in the second survey. Site 7 contributed far fewer individuals to the population size structure of *R. Largillierti* in Survey 2 than in Survey 1.

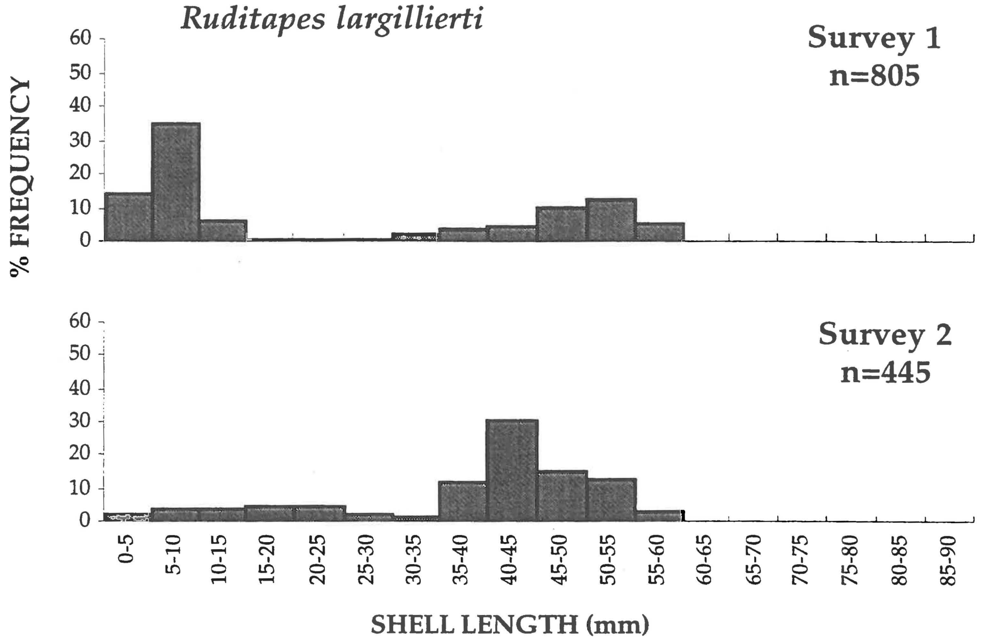


Figure 3.13a Length-frequency distributions for *Ruditapes largillierti* for Centre Bank, Survey 1 (December, 1994), Survey 2 (May, 1995)

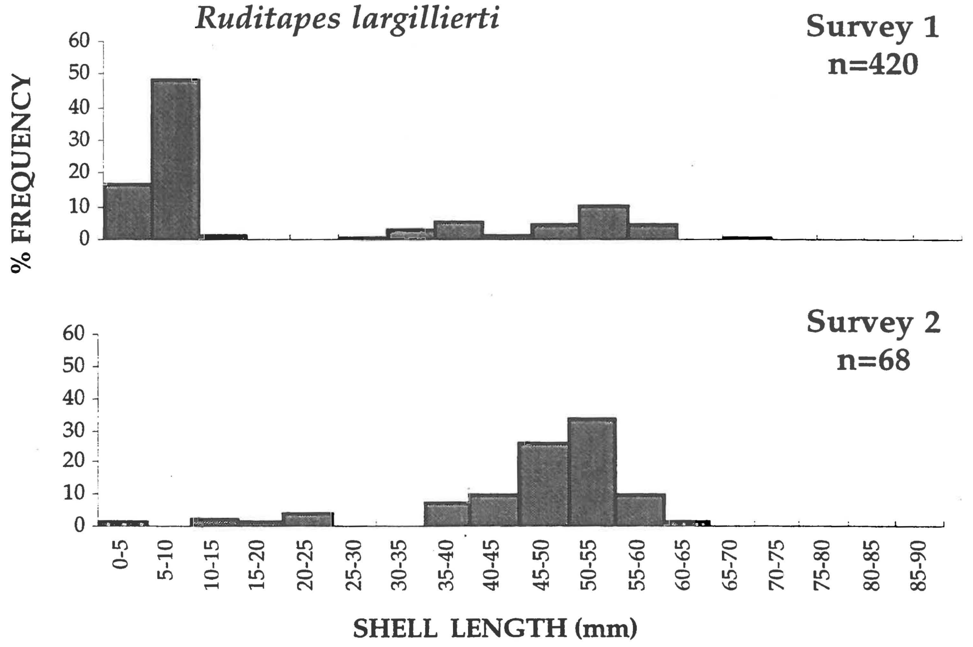


Figure 3.13b Length-frequency distributions for *Ruditapes largillerti* at site 7, Survey 1 (December, 1994), Survey (May, 1995)

Tawera spissa showed a bimodal structure in Survey 1 (Fig. 3.14a). There was a dominant cohort of very small animals 0-5 mm, with the remaining size classes combined accounting for less than 33% of individuals. Approximately one-third of all *T. spissa* recorded across Centre Bank in Survey 1 were found at site 54 (Fig. 3.14b). The length-frequency histogram for the *T. spissa* population in Survey 2 indicates that the cohort of small juveniles seen in Survey 1 decreased. The second larger cohort (20-25 mm) was still present in Survey 2, with all individuals being recorded from site 5 (Fig. 3.14c).

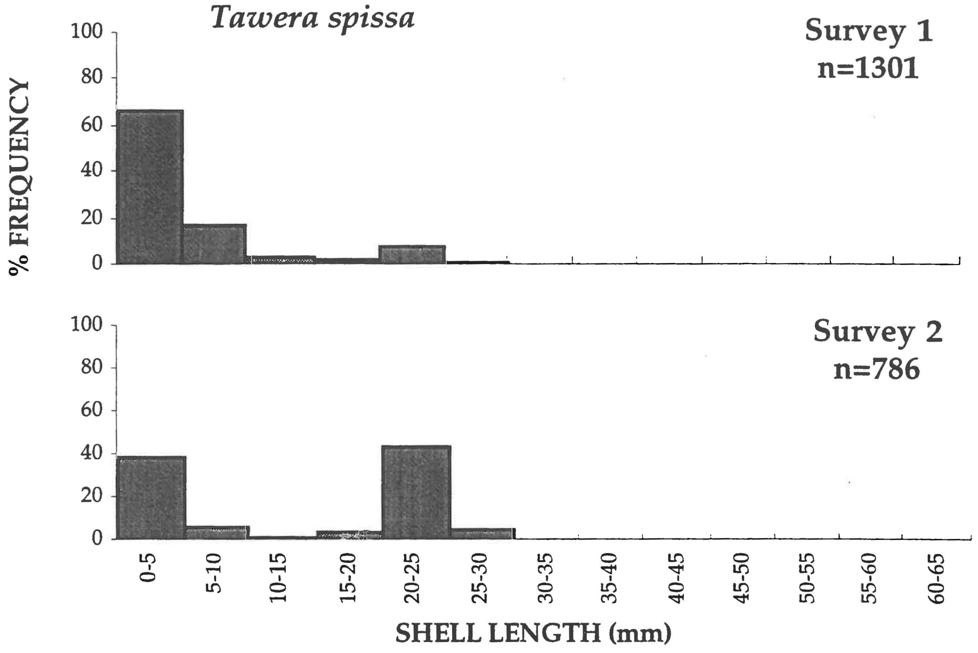


Figure 3.14a Length-frequency distributions for *Tawera spissa* for Centre Bank Survey 1 (December, 1994), Survey 2 (May, 1995)

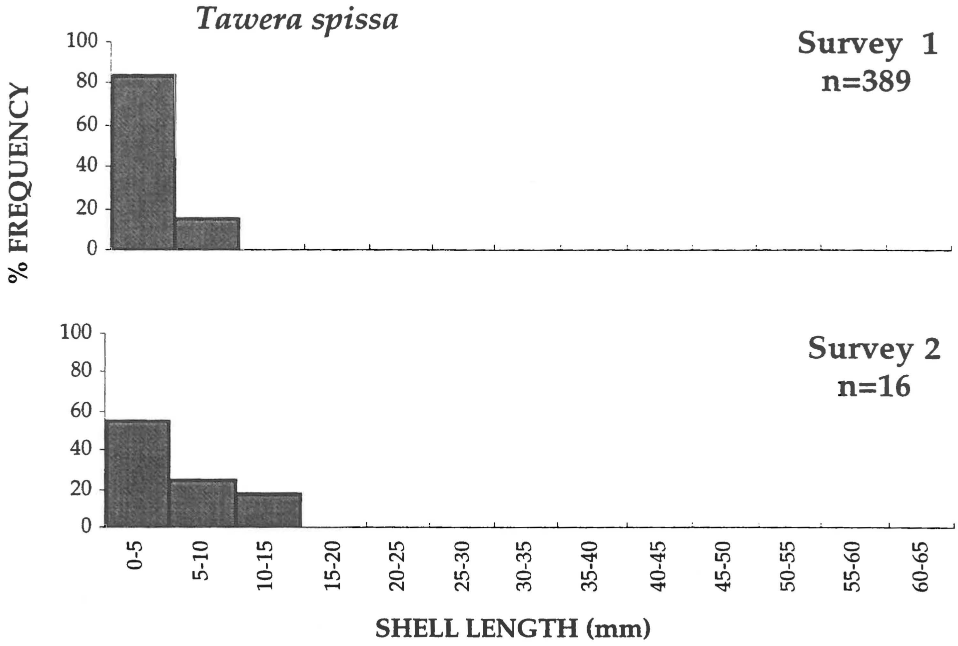


Figure 3.14b Length-frequency distributions for *Tawera spissa* at site 54 Survey 1 (December, 1994), Survey 2 (May, 1995)

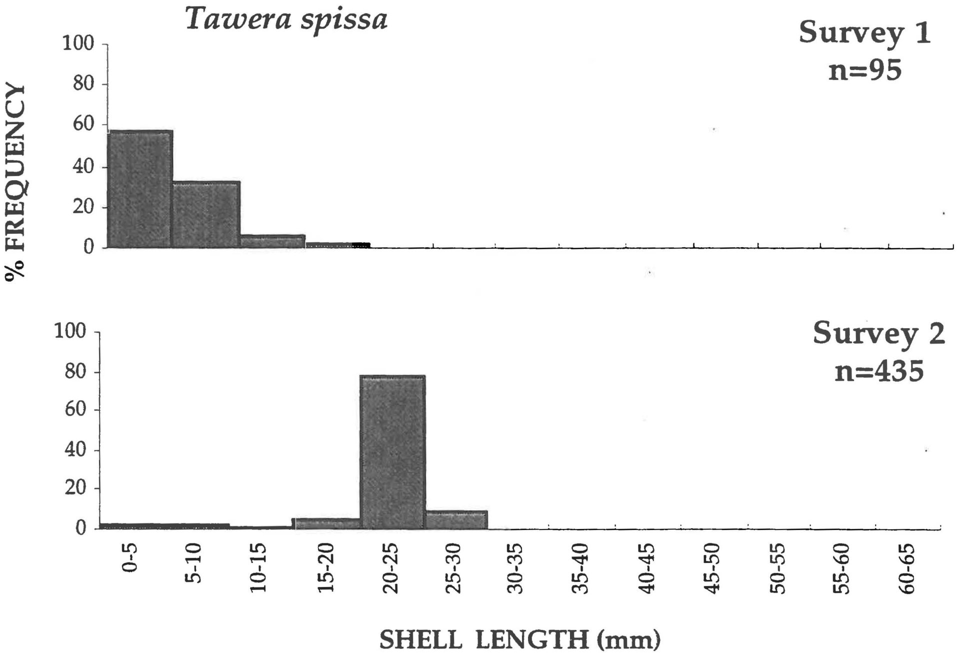


Figure 3.14c Length-frequency distributions for *Tawera spissa* at site 5 Survey 1 (December, 1994), Survey 2 (May, 1995)

3.4 DISCUSSION

Community Structure

A large number of individual bivalves (10,205) was recorded from sites across Centre Bank in Survey 1 (December, 1994) and Survey 2 (May, 1995). These individuals were derived from 31 species or taxonomic groups. Although the number of individual bivalves sorted increased from 3,673 individuals in 1994 to 6,532 in 1995, the number of taxa at the majority of sites decreased. The Berger-Parker index values for bivalve species at sites across Centre Bank, were on the whole lower in Survey 2 than in Survey 1. This suggests that assemblages at sites in the first survey were dominated by individuals of one taxon. Margalef's index values confirmed this with generally lower Margalef's values occurring in the second survey compared to the first, indicating a small decrease in species richness through time. It is difficult to explain or interpret the increase in bivalve density from Survey 1 to Survey 2, and the decrease in number of taxa, as sampling only occurred twice, 6 months apart. However, It appears that recruitment (e.g. pipi) and post-recruitment processes may both be important.

It is not possible from the data collected by this study to identify any single factor responsible for the grouping of sites indicated by the MDS ordination for the second survey (Fig. 3.8b), or for the outlying sites 4, 5, 7 and 21 shown by CDA (Fig. 3.7). Differences in environmental characteristics not addressed in this study may be important for explaining the weak grouping of sites seen in Survey 2. Turner *et al.* (1995) made use of multivariate ordination techniques (CANOCO and MDS) when studying community persistence at Manukau Harbour. They collected 36 cores from each of 6 sites, every 2 months for 5 and a half years. Samples were collected at 2 monthly intervals over 5 and a half years (between October 1987 and February 1993).

With the sampling done thus far there is no way of knowing if observed changes in species densities are smaller or larger than might normally be expected to occur given the natural temporal and spatial variability of bivalve populations. This study was not undertaken with the intention of sampling to detect and interpret changes in community structure, i.e. species diversity, distribution and abundance. To obtain data capable of detecting such changes, sampling would have to be done more frequently and for a greater length of time.

Density Distributions

Analysis of the densities of common bivalves demonstrated significant variations in abundance around the harbour. Some individual taxa showed marked affiliations with certain sites in both surveys e.g., *Ruditapes largillerti* at most sites along transect 1 (Fig. 3.10a), *Tawera spissa* at sites 5 and 6 (Fig. 3.11a) and *Paphies australis* at sites 4, 7, 8 and 19 (Fig 3.9a). Such affiliations might arise due to different physical characteristics (e.g. flow dynamics and sediment characteristics) and biological processes (e.g. recruitment, post-settlement movement and predation).

Physical characteristics

Water flow within the harbour is mainly tidal. Centre Bank (the flood tidal delta) causes the flood tide to diverge once through the entrance, resulting in extremely strong current flow through the Western Channel, but comparatively weak flow through the deeper Cutter Channel (Mathew *et al.*, 1995). The dominance of pipi at site 7 in both surveys may be associated with the physical characteristics of a harbour channel. Site 7 was located in the Western Channel with samples being taken at a depth of 6 m; no other sites were situated in channels. Similarly Grace (1972) and Hooker (1995a, b) found a large dense subtidal pipi population in the channels of the Whangateau Harbour.

Over the last few decades, many studies have correlated infaunal invertebrate distributions with sediment grain size (review of Snelgrove and Butman, 1994). Such studies have lead to the generalization of distinct associations between animals and specific sediment types. Snelgrove and Butman (1994) point out that the majority of studies have been descriptive and that there is actually little evidence that sediment grain size alone is the primary determinant of infaunal species distribution. Aspects of sediments that animals may respond to include grain size, organic content and stability. Sediment grain size within the channels of Tauranga Harbour and across Centre Bank is determined largely by the force of tidal currents within the harbour. Sediment grain size within the Western Channel is particularly coarse as all fine material is transported away by the strong tidal flow (Mathew *et al.*, 1995).

The organic content of bottom sediments may be a more likely causal factor than sediment grain size in determining infaunal distributions because organic matter in sediments is a dominant source of food for deposit-feeders and, indirectly (e.g. through resuspension), for suspension-feeders. Organic matter may limit distributions of organisms through differential settlement of larvae (or post-larvae) or differential post-larval survival (Snelgrove and Butman, 1994). There is evidence to suggest that some juvenile bivalves are able to actively avoid contaminated sediment (Pridmore *et al.*, 1991). There is minimal pollution apparent within Tauranga Harbour and it is therefore highly unlikely that the organic content of bottom sediments of Centre Bank are determining infaunal bivalve distributions.

Recruitment

Other affiliations of bivalves with particular sites could be attributed to biological processes, such as variations in recruitment. The main factor contributing to an increase in the total number of individuals recorded in Survey 2 is a disproportionate dominance by pipi at site 19 (Fig. 3.9a). Figure 3.12b indicates a very large recruitment of 0-10 mm juveniles to the site. This recruitment pulse at site 19 can be compared to a study by Hooker (1995a) where observed patterns indicated that pipi settle in discrete nursery areas and then move into adult beds at the harbour entrance.

Pulse recruitment of bivalve populations have been documented for many years (e.g. Coe, 1953). Coe (1953) reviewed the frequency of resurgent populations of the bean clam, *Donax gouldi,* at La Jolla California since 1894. He concluded that resurgent populations of marine littoral invertebrate in any locality depend upon a combination of the following circumstances: (a) a large spawning population; (b) suitable conditions during the period of pelagic larval life; (c) favourable currents which may bring the larvae to that locality at the exact time when they are ready for metamorphosis to the adult form and subsequent settlement in the substrate; and (d) adequate opportunities for continued growth. It would appear that these conditions were fulfilled for pipi at site 19.

Post-settlement movement

Post settlement dispersal must be taken into account when describing the spatial distribution/abundance patterns of soft-sediment macrofauna, as patterns observed on one occasion may alter markedly from one sampling date to the next (Cummings *et al.,* 1995). Post-settlement movement may be either passive or active. The boundary-layer flow regime may directly affect distributions through drag and lift forces on above ground features, such as tubes of animals themselves (Snelgrove and Butman, 1994). There is growing evidence that post-larval juveniles of a number of bivalve species are capable of active drifting (e.g. Beukema and de Vlas, 1989; Cummings *et al.,* 1993; Cummings *et al.,* 1995; Hooker, 1995b).

Explanations of why drifting occurs vary. Drifting by *Macomona liliana* may have been initiated by contaminants that triggered resident juveniles to leave an area (Pridmore *et al.,* 1991). Synchronous movement of post-settlement bivalves has been reported in *Macoma balthica,* where drifting was associated with a new moon (Armonies, 1992) as well as changes in water current and temperature (Sorlin, 1988). Hooker (1995b) hypothesized that high densities act as a trigger for pipi to drift in the water column.

Hooker (1995b) caught three common bivalve species, other than pipi, drifting in the entrance to Whangateau Harbour in 1993. The same three species (*Soletellina* sp., *Gari stangeri* and *Macomona liliana*), are also found across Centre Bank. Although a large recruitment occurred at site 19, pipi were not observed drifting when sampling during surveys 1 and 2. Hooker (1995b) also found that drifting was highly episodic; it is not surprising that drifting individuals were not observed given the short time spent in the field. The ability of post-settled pipi to actively migrate is likely to have important implications to their population dynamics (Hooker, 1995b) as well as their distribution across a harbour.

Predation

Predation is thought to play an important role in structuring soft-sediment invertebrate communities (reviewed by Wilson, 1991), but this conclusion is by no means universal. Thrush (1986) found evidence through caging experiments that the starfish *Luidia ciliaris* and crabs *Carcinus maenas* and *Liocarcinus depurator* reduced the total number of individuals of a soft-sediment community in an Irish sea-lough. In general, his results did not, however, indicate a major role of predation by large epibenthic organisms in organizing the assemblage. In a predator exclusion experiment conducted in the tropical coral reef system of the Great Barrier Reef, Jones *et al.* (1992) concluded that predation by fish is clearly intense, but does not have a significant effect on the demography of mollusc populations. Such studies cast doubt on the generality of the claim that predation is an important agent in structuring soft-sediment communities.

Vertebrate predators of bivalves such as eagle rays and wading birds, appear to be a prominent part of the ecology of Manukau Harbour (Thrush *et al.*, 1994b). In contrast wading birds would seldom have access to bivalve populations of a subtidal area such as Centre Bank. Fish, crabs and starfish in particular would have a greater potential to having an affect on prey densities in subtidal environments. Observations and data collected by Putt (personal communication) on three predators on bivalves present across Centre Bank, the asteroids *Coscinasterias calamaria* and *Patiriella regularis* and the whelk *Cominella adspersa* suggest that numbers of these predators are generally not high enough to effect the distribution of bivalve populations.

A predator found across both intertidal and subtidal environments is the paddle crab *Ovalipes catharus*. *O. catharus* was sighted numerous times in the field, but never when feeding. Wear and Haddon (1987) concluded from foregut content analysis of *O. catharus*, that a large component of the diet is bivalves, although in conclusion they thought it was probable that *O. catharus* has little direct impact on established beds of mature shellfish. I would assume this to be the case across Centre Bank also. *O. catharus* is an active and wide-ranging predator, the impact on bivalve density made by such a predator would be more patchy in space and time than the likes of whelks and starfish.

It is unlikely that any one factor alone can explain patterns of distribution and abundance of bivalves seen across Centre Bank. Physical characteristics such as harbour morphology and flow patterns, and biological processes such as recruitment and post-settlement movement seem most likely to ultimately determine the distribution or abundance of adult bivalves across Centre Bank.

Spatial Pattern

Spatial autocorrelation is probably the simplest technique for the detection of pattern and estimation of the scale on which influential processes operate (McArdle and Blackwell, 1989). Positive autocorrelation indicates homogeneity or sameness; negative heterogeneity or dissimilarity (Sokal and Oden, 1978). Correlograms showed a pattern that was variable through time with significant positive and negative autocorrelation occurring at all spatial distances greater than approximately 200 m. All three bivalves studied in detail were typically arranged in small-scale patches of homogeneous density in surveys 1 and 2.

Spatial patterns may be attributed to a variety of biotic and abiotic factors: e.g. the action of predators which evacuate sediment, larval settlement, competition, resource heterogeneity and differences in sediment characteristics (Thrush, 1991). Thrush *et al.* (1989) speculated that feeding pits generated by rays could play a role in influencing spatial pattern across the sandflats of Manukau Harbour. I observed ray pits on Centre Bank, but at much lower densities than in the study of Thrush *et al.* (1989). It is not possible to determine the effect of these predators without experiments. Manipulative field experiments are needed to test the proposed influences on spatial patterns.

It is difficult to compare spatial patterns identified in this study with other results as limited studies have been conducted in subtidal environments, Hooker (1995a) being one of the few. Hooker (1995a) found similar degrees of pipi density at 5 and 10 m scales, with variable patchiness at spatial distances of up to 50 m. Where patterns have been quantitatively assessed in soft-sediment environments, homogeneous density patches ranging from 0.01 m to 100 m radius have been described (review of Thrush, 1991).

Scale of Sampling

Many aspects of the ecology of bivalves including spatial pattern, can only be detected and accurately assessed when there are sufficient data to reveal long-term trends compared to short-term fluctuations (Thrush *et al.*, 1994a). Shallow-water coastal and estuarine habitats are considered to be rigorous and dynamic environments, characterised by predictable and unpredictable fluctuations in environmental variables and subject to continual disturbance (Turner *et al.*, 1995). The impact of such fluctuations and disturbances can only be determined if comprehensive data showing natural fluctuations are available. By sampling a subtidal macrobenthic community biweekly for 5 years, Service and Feller (1992) were able to detect seasonal variability related to physical and biological forcing functions. Such sampling intensity is not always logistically possible but desirable if community stability is to be determined. Without a long term perspective natural fluctuations of bivalve populations in Tauranga Harbour may not be identified. Interpretation of bivalve population fluctuations should be based on data collected over intervals of time greater than the life spans of the species investigated (Connell and Sousa, 1983).

The ability to predict ecological phenomena depends on both the spatial and temporal scales of variation (Thrush, 1991). It was not possible to apply temporal analysis to the data collected from Centre Bank, as sampling occurred too infrequently, a common logistical problem which often constrains subtidal sampling programs. Although there was no formal temporal analysis, the data from the two surveys conducted suggests that temporal change did occur. A change in bivalve density between surveys might be attributed to inaccuracies in positioning. Position fixing in Survey 1 being less accurate than GPS co-ordinates used in Survey 2, though bivalves were patchy at spatial scales of approximately 200 m or more. Patchy distribution of bivalves may account for the indicated temporal changes, with position accuracy having a smaller secondary influence.

With data collected from Survey 1 carried out in December 1994 and Survey 2 in May 1995, it has been possible to identify broad scale patterns of the distribution and abundance of particularly dominant bivalves. Through measurements of all bivalves sampled the population size structure of prominent bivalves has been established. Spatial analysis suggests that spatial patterns on the scale of 200 m dominated. Observed changes in distribution and abundance from Survey 1 to Survey 2 indicate that considerable change might occur at a given site over 6 months.. Therefore a smaller scale study was undertaken with greater temporal resolution in an attempt to investigate changes in bivalve ecology on a finer scale.

Chapter Four

CHAPTER FOUR

FINE SCALE PATTERNS

4.1 INTRODUCTION

The scale of sampling relative to the distribution patterns of the organisms to be sampled can influence both the precision and interpretation of the data. A unit that reflects species-specific time scales is therefore appropriate (McArdle *et al.*, 1990). Most theories on population distribution are based on broad scale sampling studies and such an approach can describe only broad trends. To gain insight into the proximal factors determining population regulation and distribution, any such study should consider the fine scale distribution patterns in survival, recruitment and growth (McArdle and Blackwell, 1989).

Fine-scale variability in population distribution patterns may be of greater importance than first realised. Several benthic studies of spatial pattern have focused on polychaete species, defining fine scale patterns (<10 cm) using multicell samplers (e.g. Rosenberg, 1974; Jumars, 1975; Volckaert, 1987). Larger scales of pattern have rarely been quantified for common infaunal bivalves. One such study demonstrated that common polychaetes and bivalves of Manukau Harbour exhibited large-scale patterns at scales of metres to tens of metres (Thrush *et al.*, 1989). The previous chapter described the distributions and spatial patterns of several bivalve taxa across Centre Bank. This chapter attempts to identify important features of the ecology of these taxa via repeated grid samples from a smaller scale sampling area.

4.2 METHODOLOGY

A sampling program was designed to monitor spatial and temporal change in densities and sizes of bivalves over a 9 month period. An area of 750 m^2 at 176° 09′ E, 37° 39′ S was marked out in a grid and regularly sampled (Fig. 4.1). This site was chosen because of the abundance of bivalves seen in Centre Bank Survey 1, and the accessibility of the area.

A grid 15 m x 50 m was marked at 5 m intervals with tagged and uniquely numbered 0.5 m lengths of plastic electrical conduit hammered into the sediment. This grid contained 30, 5 m x 5 m sites, which were each sampled every 2 months (Fig. 4.2). The grid was first sampled in March 1995, and subsequently in May, July, September and for a final time in November 1995. The time taken to sample the grid on each occasion varied from 2 days in summer to approximately 5 days during winter.

Data was collected by SCUBA diving. A 0.05 m^2 quadrat (Plate 4.1) was placed in the sediment at randomly determined co-ordinates within each site, and all bivalves within the quadrat were counted and measured to the nearest 1 mm *in situ*. The quadrat was carefully searched to depth of 100 mm. Measurements were recorded on underwater slates. After being measured each individual was replaced back into the sediment. Originally the intention was to take five random samples per 5 m x 5 m site, but due to time constraints and diver fatigue especially during winter months, the number of replicates per site was reduced to three; 90 quadrats were thus sampled on each occasion.

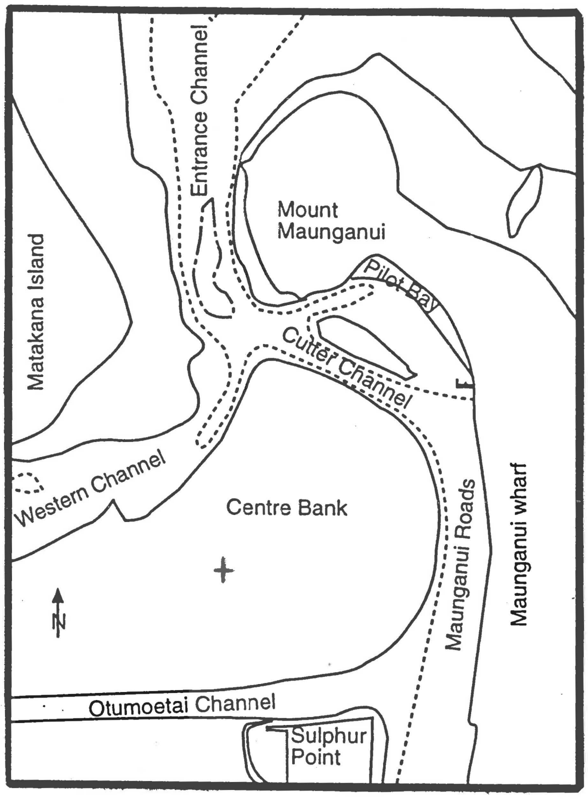


Figure 4.1 Location of the grid on Centre Bank

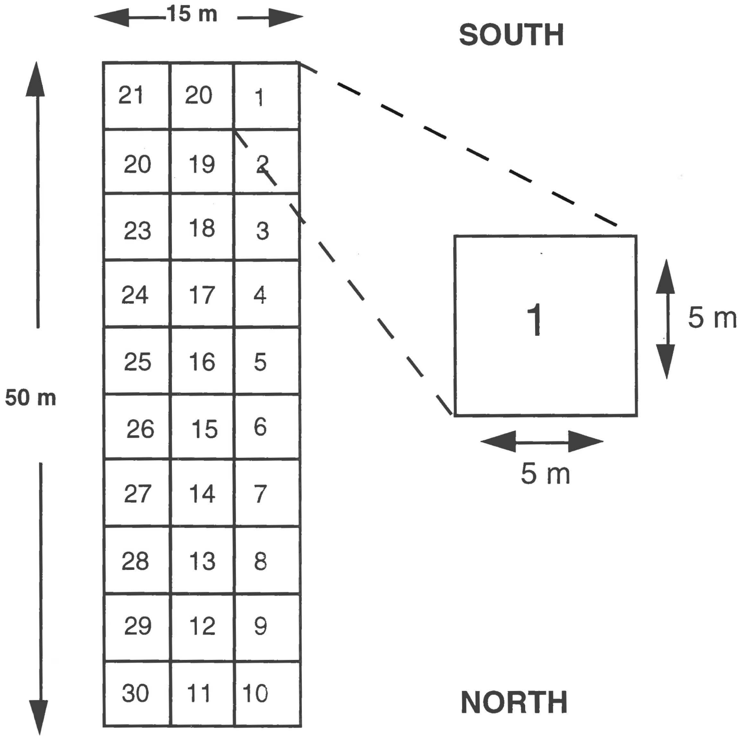


Figure 4.2 Arrangement of sites within the grid

Plate 4.1 Equipment used in sampling the grid, consisting of a hand sampler (0.05 m^2), a measuring board and underwater slates

4.2.1 Analysis

The coefficient of variation (sd/mean) was calculated and used to describe the amount of variation in bivalve densities among sites and sampling occasions. Spatial density patterns were analysed using Spatial Autocorrelation Analysis Program (SAAP, version 2.3). The results were displayed as correlograms (plots of Moran's I statistic against distance). To determine population parameters from a species that has no detectable growth bands/rings, and where tagging is not a feasible option, the alternative is to estimate the population parameters indirectly from population size structure (Pitcher and Hart, 1982). Length-frequency analysis is the most commonly used technique when determining the distribution of age classes within a bivalve population. Length-frequency data were displayed as length-frequency histograms.

4.3 RESULTS

4.3.1 Abundance

Paphies australis was the only bivalve species recorded from samples taken within the grid. The total number of individual pipi recorded for each month decreased from 4194 in March to 2454 in November. The total number of individuals in one replicate sample varied greatly both among sites and sampling occasions. A density of zero was recorded at one or more sites each month. Maximum density for one replicate (105 per 0.05 m^2) was recorded at site 9 in March (Plate 4.2). Mean density per site (the three replicate quadrats at each site averaged) ranged from 85 (representing a density of 1700 m^{-2}) to 0 , both recorded at site 18 in May and September respectively. Mean density across the grid decreased slightly from March to May, with July recording a similar density to May (Fig. 4.3). There was a further decline from September and November. September recorded the highest mean density (920 m^{-2}), followed by the lowest in November (540 m^2).

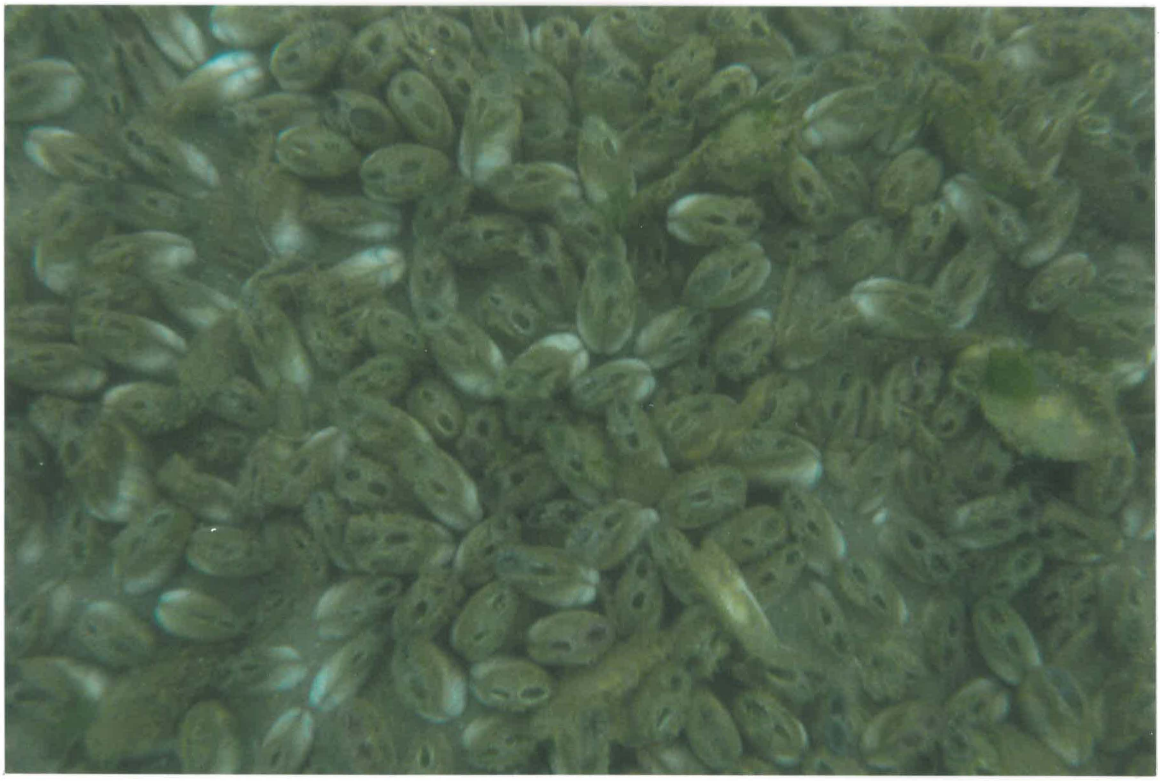


Plate 4.2 An area representative of high density grid sites

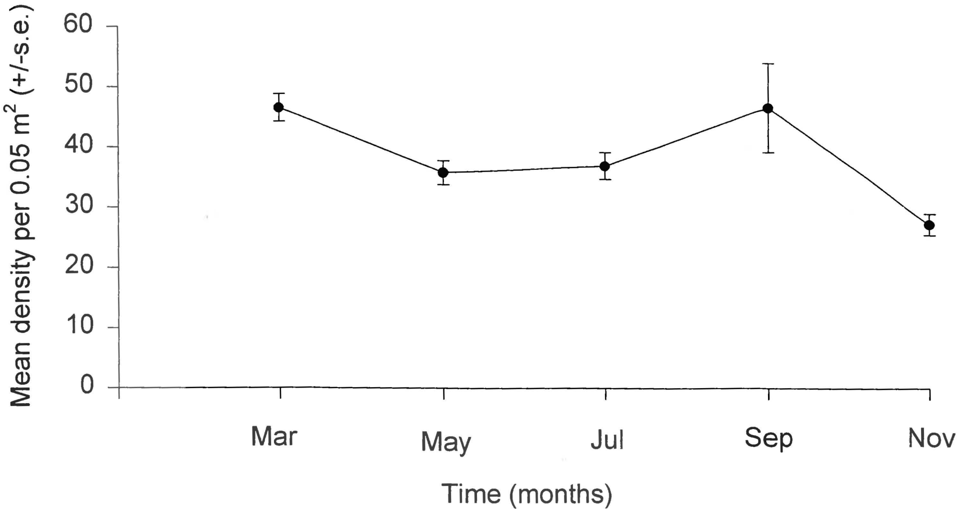


Figure 4.3 Mean density (+/- s.e.) per 0.05m^2 at the grid for each sampling occasion from March to November 1995

Mean densities of sites in the northern half of the grid were very high between May and September, with September having a greater number of particularly dense sites. Noticeably lower densities were seen in these sites in November (Fig. 4.4).

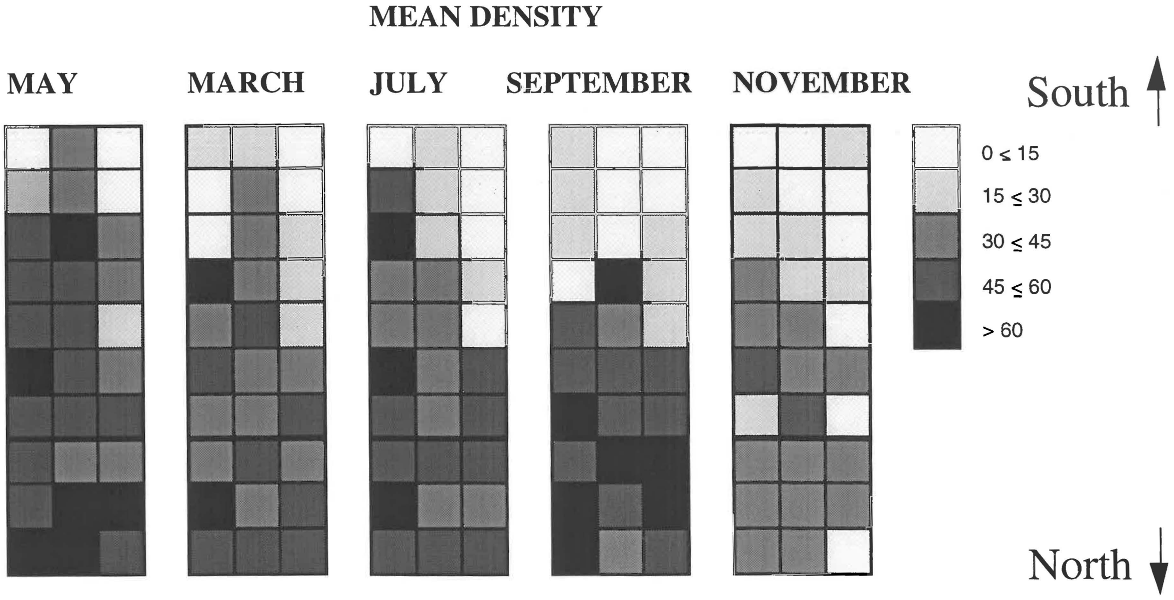


Figure 4.4 Mean density (0.05m^2) per site on each sampling occasion from March to November 1995, site numbers given in Fig. 4.2

4.3.2 Density Fluctuations Through Time

Coefficients of variation (CV) of mean density per site across all sites in the grid for March and May were approximately 41 (Table 4.1). The coefficient of variation increased in July to 47.2, followed by a decrease in September. November recorded the highest coefficient of variation for all five months.

Table 4.1 Mean coefficient of variation and interquartile range for site means in the grid, from March to November 1995 (n=30 sites)

Sample Date	Mean Coefficient of Variation	Interquartile Range
March 1995	41.3	29.2
May 1995	41.2	32.2
July 1995	47.2	41.4
September 1995	41.7	44.2
November 1995	48.5	66.2

Mean coefficients of variation for sites within the grid varied greatly over the 9 month sampling period. Maximum mean coefficient of variation occurred at site 2 (mean CV=120), sites 20 and 21 having slightly lower values 116 and 110 respectively (Table 4.2). Sites 1, 5, 19, 22, and 23 in the southern half of the grid recorded coefficients greater than 60. CVs at the remaining sites ranged from 10-53.

Table 4.2 Mean coefficient of variation of pipi density per site across all 5 sampling occasions. Table entries correspond to the layout of the grid in Fig. 4.4. Site numbers given in Fig. 4.2

Mean Coefficient of Variation

SOUTH

110	116	87
65	63	120
60	25	53
37	18	36
29	53	68
35	22	27
27	16	41
24	25	32
11	22	25
10	26	28

NORTH

Coefficients of variation in the 6 most southern sites (1, 2, 19, 20, 21, and 22) of the grid showed the greatest fluctuation (Fig. 4.5). A general trend could be seen where coefficients of variation increased in sites along the western border of the grid through time. Sites 5, 7, and 10 appeared to have relatively stable coefficients of variation for sample occasions March through to September, but values in November increased sharply.

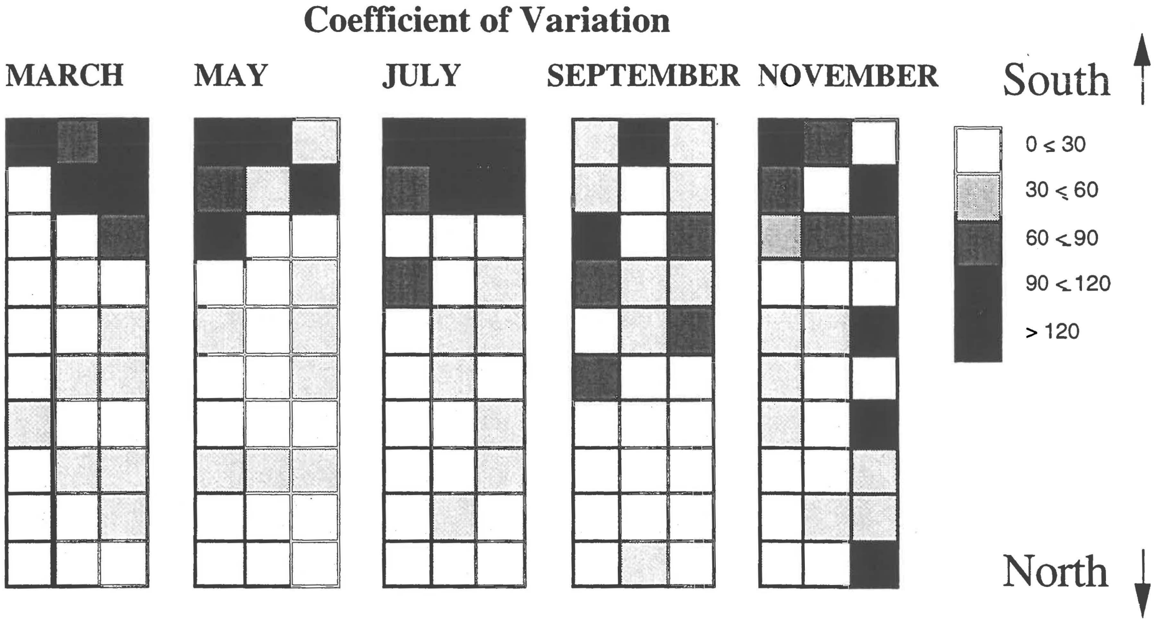


Figure 4.5 Coefficient of variation for sites on each sampling occasion from March to November 1995. Site numbers given in Fig. 4.2

Mean density at sites 22 and 23 on the eastern side of the grid fluctuated through time (Fig. 4.6). At those two sites, initial densities in March were moderate with a mean density of between 30-45 individuals per replicate. Densities on the May sampling occasion decreased to between 0-15 individuals, then increased in July. The next two sampling occasions saw densities reduced to lower than 30 pipi per replicate. Likewise sites 18 and 19 initially recorded high mean densities, which gradually decreased with time, although there was a slight increase in November. Mean densities at sites 1 and 2 were low in March and remained so at each of the following sampling occasions; mean density never exceeding 25 pipi. A mean density of zero was recorded at site 1 in March, but increased slightly in the November sampling occasion.

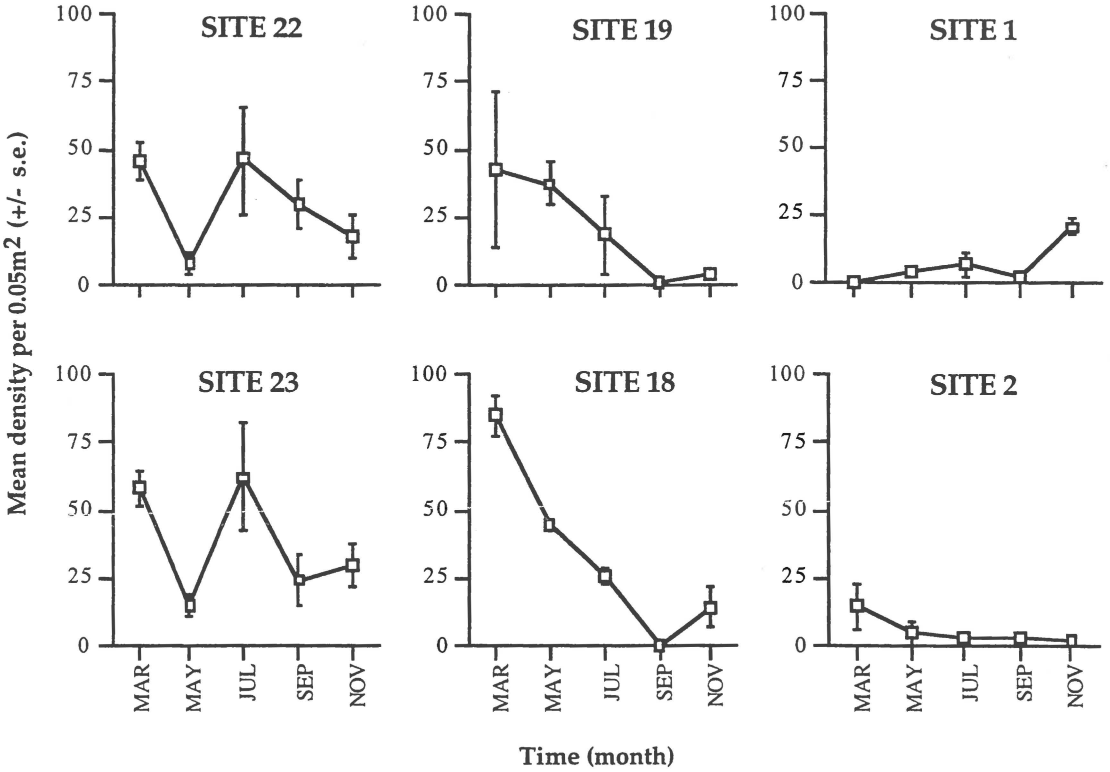


Figure 4.6 Mean density per 0.05 m^2 (+/- s.e.) at the 6 most southern sites of the grid

4.3.3 Spatial Analysis

Spatial patterns

The overall shape of the correlograms of Moran's I for *Paphies australis* density did not change remarkably among months (Fig. 4.7). The overall trend was for correlograms to become stronger with time. Up until September significantly negative Moran's I values increased, deviating away from the expected Moran's I values. In November these values decreased, moving back towards the expected Moran's I values. The March correlogram suggested significant positive autocorrelation at short (up to 7 m) and long (approximately 30-35 m) distances. Significant negative autocorrelation occurred at approximately 43 m. Distances between these two extremes were non-significantly positively autocorrelated, lying close to the expected Moran's I values. Correlograms for July and September appeared very similar with densities of *P. australis* being significantly positively correlated at the first 4 distance classes, and negatively correlated at distances greater than 25 m. Values between these distances did not deviate far from the expected Moran's I values. The September correlogram changed slightly, with only the sixth distances class being non-significant. The correlogram of Moran's I for November showed a similar trend to previous months being significantly positively autocorrelated at short distances, with significant negative autocorrelation appearing at distances of approximately 17 m and greater.

4.3.4 Population Size Structure

No significant change in population size structure occurred during the 9 month sampling period. The dominant size class remained at 60-65 m m throughout the study, accounting for a maximum of 61% of individuals sampled in September and a minimum of 52% in May (Fig 4.8). A very small number of pipi greater than 70 mm were recorded each month with the exception of May, when none were found. Juvenile pipi of 10-20 m m appeared only in May and in low numbers.

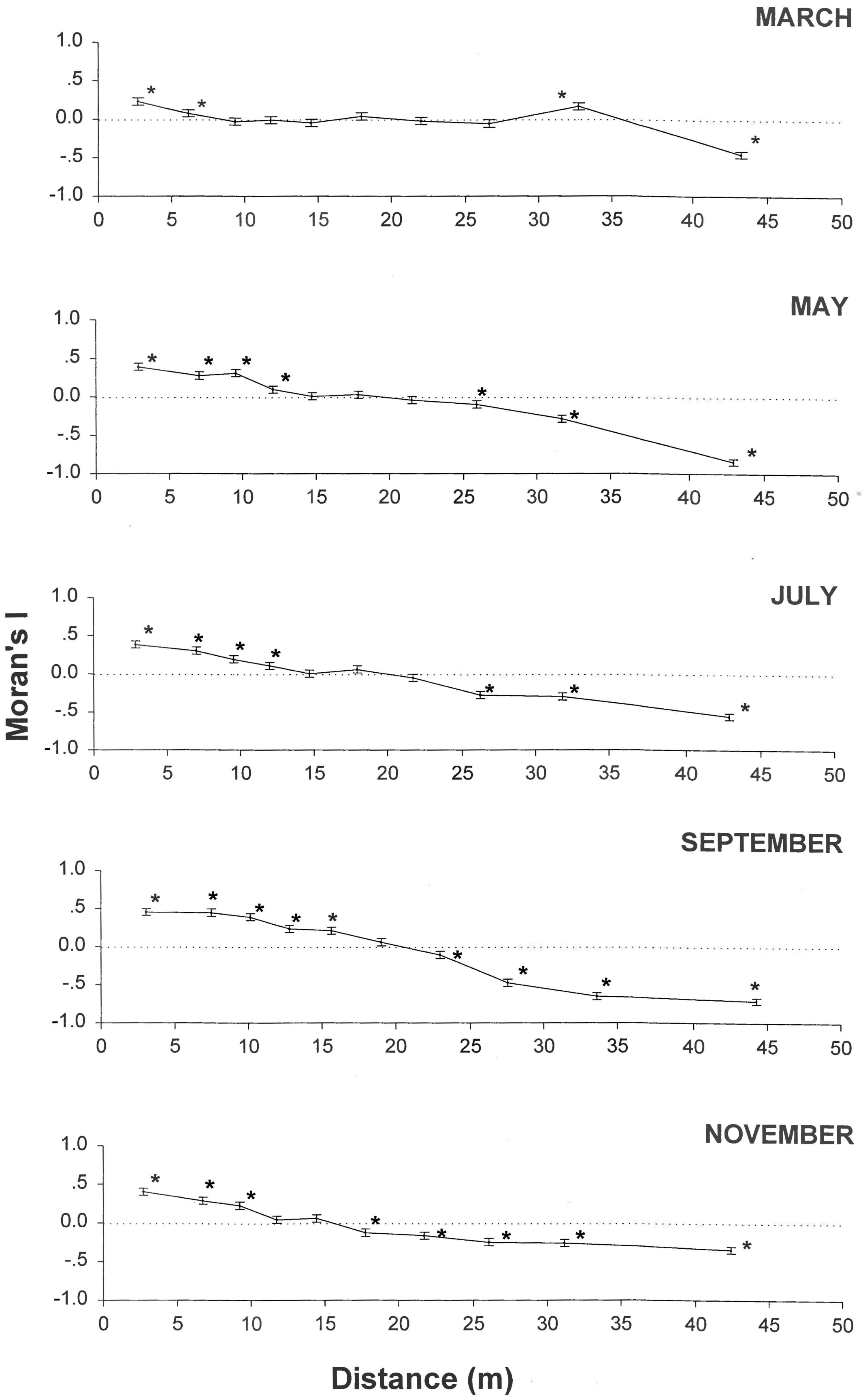


Figure 4.7 Spatial correlograms of Moran's I for sampling occasions March through to November. The dotted line represents the expected value of I. Starred values are statistically significant ($P<0.05$). Error bars represent +/- 1 s.d.

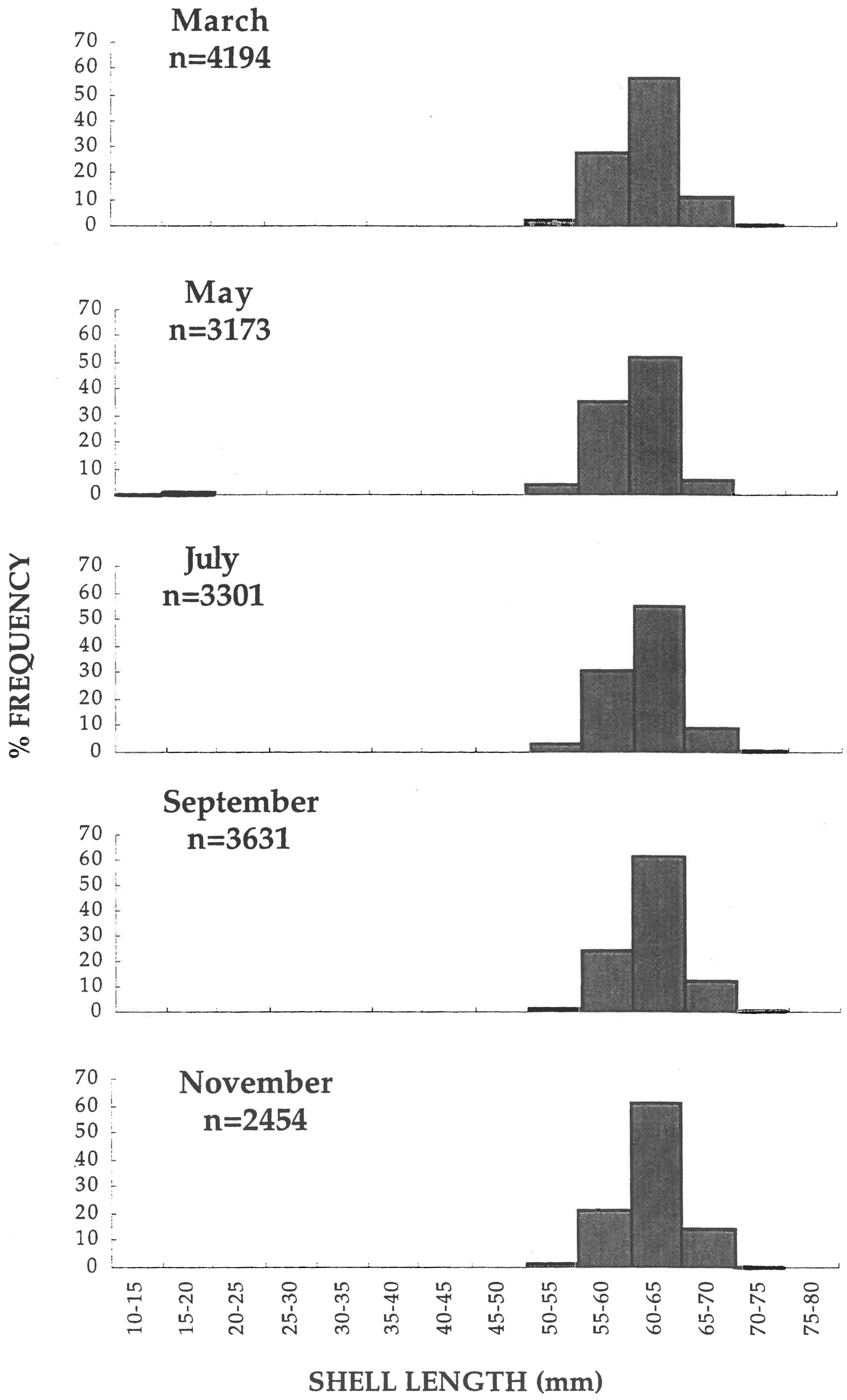


Figure 4.8 Length-frequency distributions for *Paphies australis* on the five sampling occasions

4.4 DISCUSSION

Pipi have been considered a predominantly intertidal species (e.g. Morton and Miller, 1973) but several studies have found evidence of large subtidal populations (Creese, 1988; Hooker, 1995a). The grid in this study was positioned over a dense subtidal pipi population on the flood tidal delta. A systematic sampling design was used to sample the area marked out. In studies such as this where the aim is to investigate spatial pattern in a measured variable the use of random sampling is particularly limiting (McArdle and Blackwell, 1989). The statistical advantages of systematic sampling are that it can be considerably more powerful and convenient (McArdle and Blackwell, 1989). The logistics of subtidal sampling were made much easier by systematic sampling, once the grid was set up it was just a matter of repeated sampling through time.

The technique used to sample bivalves across the grid was the same as that used in a study by James and Fairweather (1995), that compared two rapid methods for sampling pipi that did not involve sieving; finger-dredging and a knife technique. Results show that the finger-dredging technique provided the same information as the traditional method of digging and sieving volumes of sand (as in Chapter Three), but was quicker and less laborious than sieving whole samples of a similar volume. James and Fairweather (1995) remark that finger-dredging would be less useful for sampling pipi smaller than 5 mm in length. Although an effort was made not to miss juveniles when sampling the grid, no pipi 5 mm or less in length was recorded. Juveniles were sighted only rarely within the grid. The finger-dredging technique was very efficient allowing data to be collected quickly without the inconvenience of transporting and sieving large volumes of sediment.

The population of pipi in the grid was dominated by adults (>50 mm shell length), with smaller juvenile pipi recorded very rarely. Similar population dynamics were found by Hooker (1995a) in a subtidal channel of Whangateau Harbour, Northland and by Venus (1984) at a single subtidal site in the Whangaeri Harbour. Recruitment into the population sampled did not appear to occur in the 9 months that the grid was sampled. In May 1995 a large recruitment of pipi was recorded approximately 700 m towards the harbour entrance from the site of the grid (Section 3.3.4). Recruitment into the grid may be through secondary settlement of post-metamorphic juveniles. Pipi entering the water column at site 19 may be transported via incoming tides to the vicinity of the grid site. The population studied by Hooker (1995a) did not show regular recruitment. Hooker (1995a) thought that it unlikely that irregular recruitment would lead to major declines in the population in the short-term. It may however, have major consequences for populations that are heavily harvested.

Density distributions

High densities of pipi (>700 m^{-2}) were a feature of the grid on the first four sampling occasions, although density fell slightly in November to 500 m^{-2}. The densities of pipi in the grid compare closely to those reported for Mair Bank, the flood tidal delta of Whangarei Harbour (Venus, 1984). Densities found within the grid are comparable to subtidal channels in the Whangateau Harbour, (Hooker, 1995a). Pipi density in the main channel of Whangateau Harbour was discretely arranged often exhibiting densities of >500 m^{-2} (Hooker, 1995a). When sampling of a pipi bed that extended a considerable distance offshore from Whitianga Beach, Creese (1988) found densities of up to 200 m^{-2} .

Densities of pipi across the grid through time appeared to decrease evenly in a constant direction (NW) (Fig. 4.4). A large sand ridge was located across the southern end of the grid. In March the ridge was positioned across sites 1 and 2. Although the dimensions of the ridge was not measured its position in relation to the grid were noted on each sampling occasion. From these observations it appears that the sand ridge was mobile, and over the 9 months the grid was sampled, it moved in a northern direction. The low densities seen at the southern end of the grid can thus be explained by the smothering effect of the sand ridge (see below).

The decrease in density from September to November at site 10 may also be explained by a sand ridge, which was not present in September but covered the whole of site 10 by November. Sand ridges were up to 1 m high, several metres wide and were easily seen at low tide when the tops of the ridges became exposed. Sand ridges appeared to be migrating over a defined area in the middle of Centre Bank. With the ability to migrate over and subsequently smother pipi, (dead pipi were dug out from below the ridges) sand ridges emerge as an important factor in the distribution and abundance of pipi in a localized area of Centre Bank.

An understanding of how predators react to variations in habitat and prey characteristics is often a key to explaining local patterns of animal distribution and abundance observed in nature (Peterson, 1982b). Predators within the grid did not appear to occur in high enough numbers to dramatically affect the distribution or abundance of pipi (Putt, personal communication). Prey characteristics which successfully inhibit the efficiency of bottom-feeding predators include an ability to reach sizes large enough to escape the predators' handling capacities. The majority of pipi in the grid were 55-65 mm in length, a single whelk (*Cominella adspersa*) or asteroid (*Patiriella regularis*) was never seen feeding on a pipi of this size. These predators were usually seen feeding in groups of 5 or more on a single pipi (pers. obs.). A single whelk or starfish may be able to open a pipi, with the smell attracting other predators which then converge on the prey. A alternative explanation is that a single predator is unable to open a pipi and a number of predators are required to open the prey.

Peterson and Black (1993) concluded from studies of two coexisting cockles occurring at high densities in Western Australia, that access to the cockles is reduced at higher densities and that this is a mechanism whereby density operates to protect cockles from predation. The same predatory asteroid present in the experimental tests conducted by Peterson and Black (1993) *Coscinasterias calamaria* is present on Centre Bank. Peterson and Black (1993) hypothesized that foraging by *C. calamaria* may be inhibited by tight packing of cockle shells. Similarly the very dense populations of pipi in parts of the grid on Centre Bank, may inhibit the foraging behaviour of *C. calamaria*.

Effects of high density

The population size structure of pipi within the grid changed very little over the time the grid was sampled. Only a very limited number of juvenile pipi was recorded, on one sampling occasion. Larval cannibalism by adults may be occurring in the densely populated grid sites. The interactions between established adults and settling larvae have long been considered important in structuring marine soft-sediment communities (Woodin, 1976). In the presence of dense adult assemblages, successful larval recruitment may be rare (Woodin, 1976). Suspension feeders filter particles out of the water column. Settling larvae are small enough to be ingested and it has been suggested that much of the mortality of settling larvae is due to such filtration (Peterson 1982a). If not ingested by adult suspension feeders larvae settle on the sediment surface where they are susceptible to being ingested by deposit feeders or disturbed by burrowing and siphon activity (Ambrose, 1984). In areas where successful larval recruitment is rare assemblages of perennial forms should frequently be dominated by single age classes. Hooker (1995a) found such a population of pipi and the population at the grid studied here also fit this description.

Hooker (1995a) described recruitment of pipi to an intertidal site on Omaha Spit in his study of populations in Whangateau Harbour. Primary settlement of larvae is likely to be at specific settlement sites or discrete nursery areas where adults are absent, such as the sandy shores of Matakana Island on the north side of the Western Channel. Currents are the most likely mechanism for transporting juveniles to settlement sites and therefore determine the location of such sites. Once pipi actively enter the water column for a second time, currents probably play a dominant role in determining where they will settle. Drifting juvenile pipi are too large to be ingested by adults and currents appear the most likely explanation for patchy recruitment.

Spatial pattern

High order (long distance) negative spatial autocorrelation of pipi density become more prominent through time. Distances approximately 33 m and greater were significantly negatively correlated in the first sampling occasion in March, and by November high order negative spatial autocorrelation was occurring at distances of approximately 17 m and greater (Fig. 4.7). Negative spatial autocorrelation is found when the most different localities are furthest apart. This implies that for high densities at one point a given distance away there will be a corresponding low density area or vice versa. This is consistent with mean density plotted for each sampling occasion (Fig. 4.4), where the number of low density sites increases with time, and those low density sites were clustered at the south of the grid. A common correlogram profile observed in natural populations studied over large distances is the combination of short distance positive autocorrelation with long distance negative autocorrelation (Sokal and Oden, 1978), as found in this study.

In summation repetitive grid sampling allowed fine scale pattern of an area of Centre Bank to be described. Population size structure remained practically unchanged during the 9 month sampling period. Density stayed consistently high at several sites across the grid, while other sites showed a sudden decrease in density from one sampling to the next. Sand ridges are speculated to be the cause of these density decreases. Predation appeared to have little affect on the density of grid sites.

Chapter Five

CHAPTER FIVE

EXPERIMENTS

Experiment One: Investigation into the ability of *Paphies australis* to bury into sediment.

5.1 INTRODUCTION

Since the introduction of experimental methods to the study of marine soft-sediment communities, the depth of understanding and the strength of inferences have increased greatly (Wilson, 1991). Experiments allow a greater insight into environment-infauna interactions. Coupled with a knowledge of a species' spatial distribution and abundance, behavioural experiments will extend the understanding of the species' ecology. Behavioural experiments may provide an explanation, or mechanism for the observed distribution and abundance of a particular species. Behavioural experiments were conducted with the intention of adding to the data on population aspects of *Paphies australis* outlined in the previous two chapters.

Infaunal bivalve species have siphons with which they consume oxygen and food from the surface or overlying water and then expel wastes through (Barnes, 1980). Bivalves are normally burrowed in the substrate, with the tips of the two siphons exposed at the substrate surface, during feeding. The length of siphon determines the maximal depth to which a bivalve will bury (Trueman *et al.*, 1966). Predation risk is maximal for infauna living near the surface, because most predators do not dig for prey (Zwarts and Wanink, 1989). Therefore the deeper a bivalve can bury the less likely it is to be preyed on by surface predators.

Once disturbed and exposed individuals become susceptible to predation. Two asteroids, *Coscinasterias calamaria* and *Patiriella regularis* present on Centre Bank have been observed preying on exposed bivalves including *Paphies australis* (pipi) (Plate 5.1). Field observations suggest that *P. australis* are able to rebury into the sediment after being exposed by a disturbance. At present Centre Bank remains relatively undisturbed by anthropogenic activity. If Centre Bank was required for port construction, transplantation of bivalves to alternative locations may be a feasible option to avoid the destruction of an established bed. It is not known if pipi are likely to rebury after being dug up and displaced elsewhere.

Laboratory experiments conducted by Creese (1988) confirm that *P. australis* can rebury. The field experiment that follows aimed to determine how long it took *P. australis* to rebury once placed exposed on the sediment surface of Centre Bank. Pipi were chosen for experimental manipulation because they are prolific across Centre Bank and are valued as a recreational shellfish species.

Plate 5.1 *Coscinasterias calamaria* feeding on *Paphies australis*, Centre Bank

5.2 STUDY SITE

The study area for this experiment was located 10 m off the northeast corner of the permanently marked grid on Centre Bank (176° 09′E, 37° 39′S) as described in Chapter 4. Pipi were extremely abundant in this area and were easily collected.

5.3 METHODS

Collecting, arranging and subsequent observations of the pipi was done by SCUBA diving. All animals used were from one naturally occurring size cohort (60-65 mm) (see section 4.3.3). Three treatments with 10 pipi per treatment were used in this experiment. In the first treatment pipi were pushed halfway into the sediment with the anterior end uppermost (after Creese, 1988); in the second treatment pipi were placed laterally on top of the sediment, and in the final treatment they were pushed upside down into the sediment with the posterior end uppermost (Plate 5.2).

Plate 5.2 Arrangement of pipi used in the burial experiment, Centre Bank

Each individual pipi was carefully extracted from the sediment and positioned on the surface. At 5 minute intervals the activity of each pipi was noted and the extent to which each had buried was recorded and classified as one of the following five burial behaviours.

Behavioural categories

(a) I= Inactive

(b) P= Probing with foot (Protrusion of the foot into the sediment)

(c) L= Lifting

(d) BU= Burial underway (More than half the animal is buried)

(e) BA= Buried (Shell no longer visible)

Observations were limited to the initial stages of the burrowing processes before the animal was lost from sight. Each of the three treatments were replicated four times per trial. Each trial of the experiment lasted 40 minutes and was completed twice at high tide and four times at mid tide, the time half way between high and low tide. Mid tide included both incoming and outgoing tides. Low tide was excluded from this experiment as it occurred at inaccessible times.

5.4 RESULTS

5.4.1 Number and Position of Pipi Puried

Trials clearly showed that pipi placed upright with anterior end uppermost and pipi placed laterally could rebury into sediment. Pipi placed upside down (posterior end uppermost) in the sediment were unable to rebury into the sediment at either high or mid tide, in the 40 minutes they were observed (Fig. 5.1). At high tide a greater mean number of pipi placed laterally were left at the surface after 40 minutes than pipi initially placed upright in the sediment (Fig. 5.1).

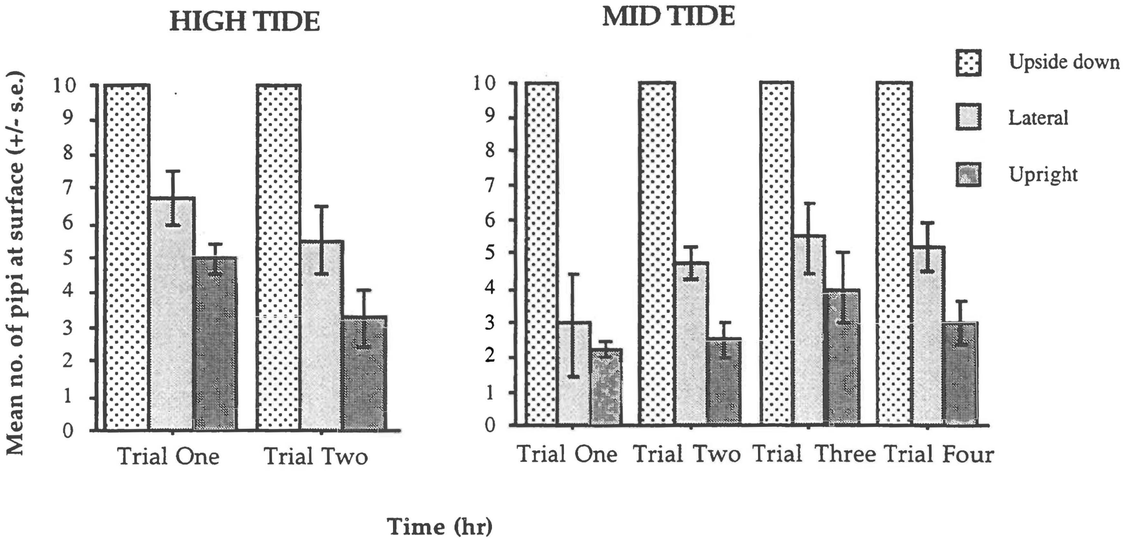


Figure 5.1 Mean number of pipi at the sediment surface after 40 minutes, high and mid tide

Trials conducted at mid tide showed a similar pattern to the results of the high tide trial. Although a number of pipi placed laterally buried, a greater number of pipi placed upright in the sediment were able to bury (Fig. 5.1). This pattern occurred each time the trial was conducted. Overall with pipi of all three orientations combined, there appears no significant difference between the percentage of pipi buried at mid tide than at high tide (Table 5.1). Forty-one percent achieved complete burial during trials conducted at mid tide and slightly less, 33%, buried during high tide trials. Of the 41% of pipi that buried at mid tide, 24% were pipi placed upright in the sediment and 17% had originally been placed laterally. At high tide the percentage of pipi buried was smaller than at mid tide, with 20% of all individuals that were placed upright in the sediment burying and 13% of those placed laterally.

Table 5.1 Percentage of pipi buried after 40 minutes, at high and mid tide

	Percentage of pipi buried	
Orientation	High Tide	Mid Tide
Upside down	0%	0%
Lateral	13%	17%
Upright	20%	24%
Total %	**33%**	**41%**

5.4.2 Rate of Burial

Excluding pipi placed upside down, pipi at high tide buried regardless of their initial position (Fig. 5.2). Pipi in either position showed a much slower rate of burial in trial one compared with the rate of burial displayed in trial two. In trial one the number of upright and laterally positioned pipi at the surface decreased gradually through time. This pattern occurred in trial two for pipi positioned laterally only. The rate at which upright pipi at the surface decreased was initially (first 10 minutes) rapid in trial two but then declined (Fig. 5.2).

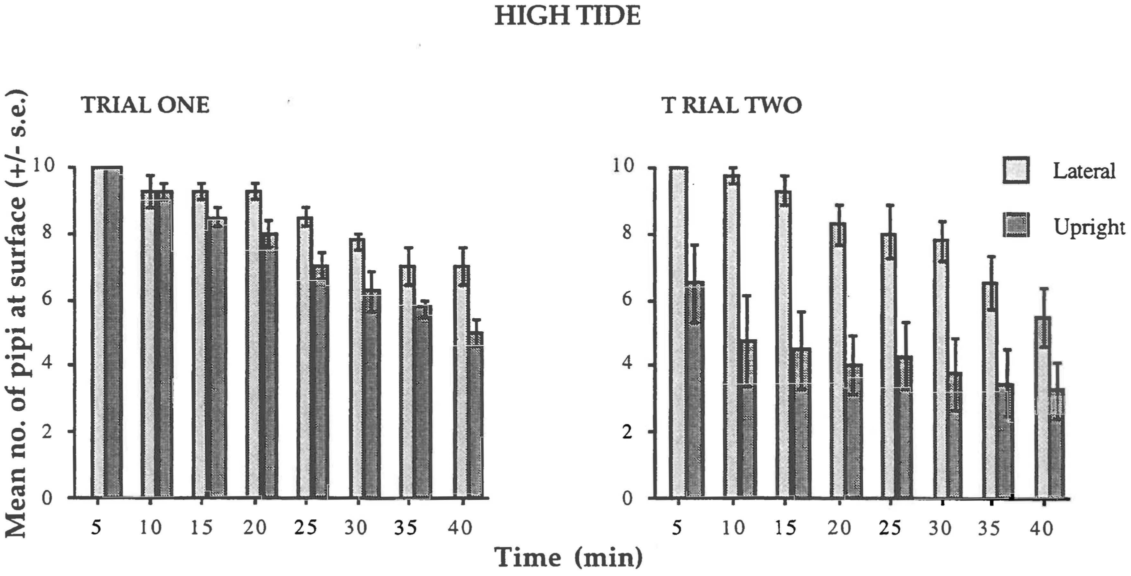


Figure 5.2 Mean number of pipi at the surface through time at high tide. Note all pipi placed upside down remained at the surface and were not plotted

At mid tide pipi placed upright buried at a greater rate than those placed laterally (Fig. 5.3). Only a small number of pipi completely buried themselves in less than 5 minutes; the majority of these had initially been placed upright in the sediment. The majority of upright pipi had buried within the first 20 minutes of each trial, whereas the number of pipi placed laterally at the surface appeared to decrease more evenly through time.

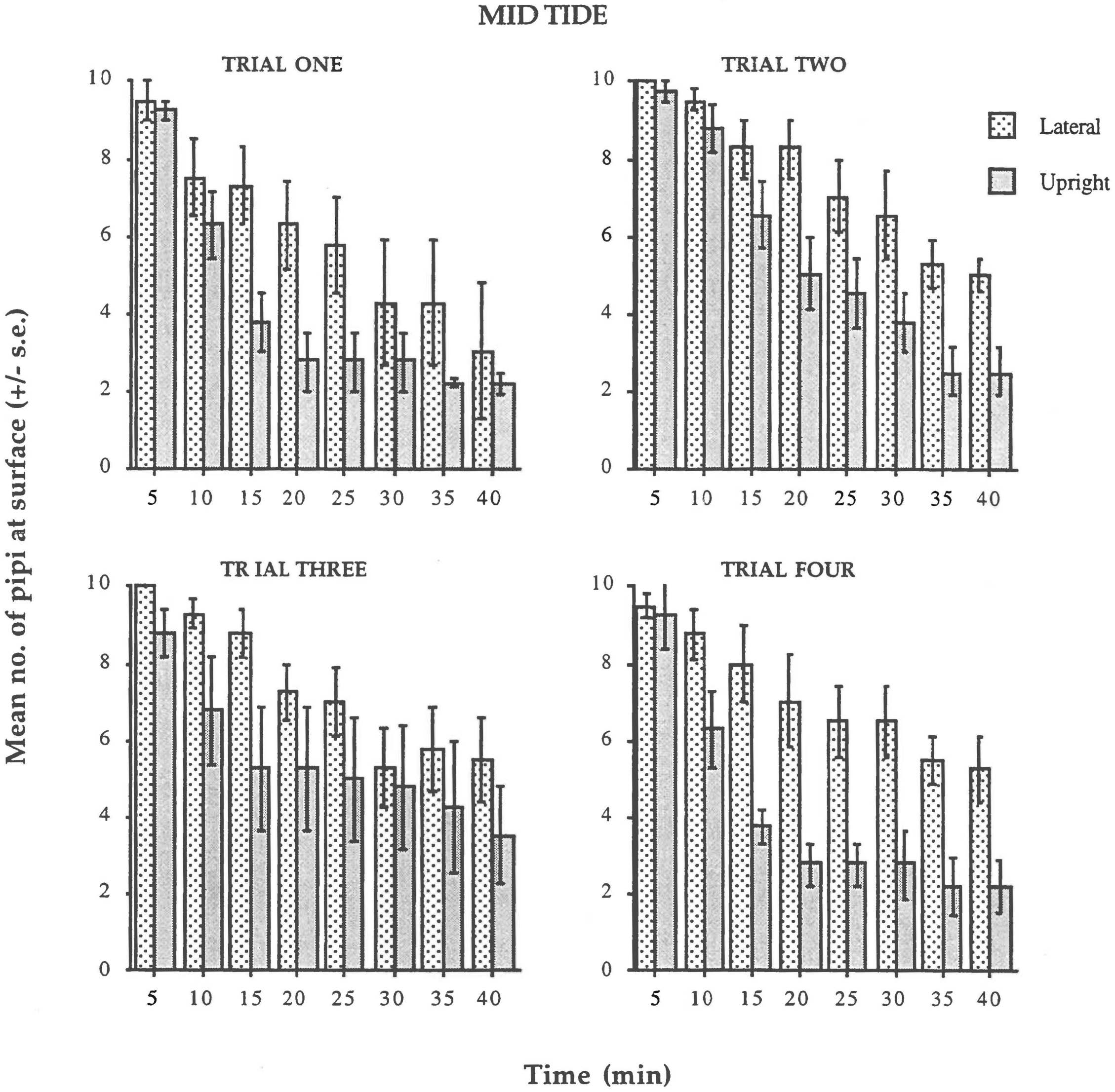


Figure 5.3 Mean number of pipi in two positions at the sediment surface through time at mid tide. Note all pipi placed upside down remained at the surface and were not plotted

5.5 DISCUSSION

The majority of investigations into the burrowing behaviour of bivalves have occurred under laboratory conditions (Trueman, 1971; McLachlan and Young, 1982). Laboratory experiments are limited to a certain extent in their usefulness, in that a large number of variables are often unavoidably changed. These may include sediments, temperature and physico-chemical parameters of water, causing the experimental organisms to become stressed, altering their behaviour (Connell, 1974). It is for this reason that field experiments are often preferred over laboratory experiments. For an investigation into the burrowing activity of *Paphies australis* on Centre Bank it was thought that a field experiment would best give an accurate estimate of burrowing ability and burial rate.

Pipi of the size used in this experiment appear capable of burying back into the sediment, with the exception of when they were placed upside down in the sediment. All marine animals that burrow have a digging period consisting of two parts. The first involves the initial stages of penetration and the second locomotion through the substrate (Trueman and Ansell, 1969). In the first phase, the foot is extended sideways and downwards probing into the sand. Placed upside down pipi were unable to use their foot to gain sufficient purchase on the sediment. Therefore digging and subsequent burial could not occur. In contrast pipi placed upright in the sediment started burial at the second phase needing only to dig to a greater depth to be buried. Placed laterally, pipi undertook all stages comprising the digging cycle as described for a variety of representative bivalve genera by Trueman and Ansell (1969).

Placing pipi laterally appeared to inhibit the rate of burial but not actual burial itself. Once probing had commenced lifting and subsequent burial almost always followed. A very small number of pipi probed sideways and downward into the sediment only to become inactive again. Following probing a static upright position is secured by the foot making a major probe downwards tending to raise the shell if penetration is not easily obtained

(Plate 5.3). Not all pipi were successful in their first attempt to acquire a static upright position. This could be because pipi in the area where the experiment was executed are particularly dense.

Plate 5.3 Pipi in foreground "Lifting", behavioural category (c)

Morphology, temperature and sediment particle size all influence burrowing rate in bivalves (McLachlan *et al.*, 1995). It is well known that shell shape and ornamentation affect burrowing ability in bivalves, with streamlined shape and thin shells without ornamentation aiding rapid burial (Trueman *et al.*, 1966). Unlike some bivalves that possess spherical shells sculptured with radial ribs and concentric rings, the shape of the pipi is suited for burial into sediment. The shell of the pipi is laterally elongate-ovate, equilateral and much longer than high, unsculptured and lacking rings (Powell, 1979), therefore providing little resistance to movement through sediment.

Low temperatures have been shown to have a retarding effect on burial rates of bivalves of the genus *Donax* (Donn and Els, 1990; McLachlan and Young, 1982). This experiment was carried out over three weeks in winter (August), when water temperature stayed relatively constant at 12°C. Faster rates of burial could well be seen for the same experiment if conducted during a summer month.

In summary, in areas of high density, pipi disturbed and left exposed on the sediment surface might be (depending on the predators present) susceptible to predation during winter months. Such conditions make reburial slower and more difficult due to low temperatures and lack of space for the foot to gain purchase on the sediment. It would appear that the transplantation of pipi is biologically feasible. Pipi left in an upside down position in this experiment did not bury, though this experiment was conducted over a short time period, and observations of a longer duration would give a better indication as to whether they could eventually bury. Of the three positions, pipi placed upside down would appear to be the most susceptible to predation and/or eventual starvation.

Experiment Two: **Investigation into the ability of *Paphies australis* to burrow up through sediment.**

5.6 INTRODUCTION

Sediment can accumulate on top of benthic fauna due to anthropogenic activities or by the nature of the environment. Tauranga Harbour is naturally a dynamic environment, with shifting channels and sand bars. Sediment movement can be expected at many areas. The flood tidal delta of Tauranga Harbour, Centre Bank, is an area of very active sediment movement (de Lange, 1988; Mathew *et al.*, 1995). With strong currents present within the harbour, sediment is continually being transported by natural processes and may accumulate on top of benthic infauna.

Morphological changes of the flood tidal delta system due to a major dredging program involving deepening and widening of the main shipping channels have been examined by Mathew *et al.* (1995). Volumetric calculations showed a large proportion of Centre Bank and the Western Channel underwent either erosion or accretion during 1990-1994; the magnitude of these changes were at least 20-30 cm, and in some places much more, up to 7 m. However it was found that volumes of deposition and erosion were not significant after allowing for the error in measurements and calculations (Mathew *et al.*, 1995). With such accretion and erosion occurring across the flood tidal delta system pipi are likely to be either inundated and buried by sediment or scoured out and left exposed on the sediment surface. Observations from the grid (Section 4.4) suggested that changes to sediments could be substantial and occur over a relatively short time.

Direct disposal of dredge spoil can be of major concern as dumping of dredge spoil can smother benthic organisms having a detrimental effect on their survival (Maurer *et al.*, 1980). Routine dredging of the port channels is necessary, has occurred in the past and is planned for the future (Healy *et al.*, 1991). The dumping of dredged sediment from channels at present does not interfere with bivalve populations of Centre Bank, but through lack of possible alternatives, areas within Centre Bank may in the future be required for dredge spoil dumping. If dredge spoil dumping on a bivalve bed occurred, whether organisms could survive such treatment, and successfully re-establish themselves would be of concern (Maurer *et al.*, 1980).

The previous experiment aimed to examine the ability of *Paphies australis* to rebury if they became scoured out by sediment movement. Complementary to Experiment One, this experiment aimed to investigate the ability of *P. australis* to survive being inundated by sediment. The experiment was designed to determine if the initial orientation of pipi affected the rate at which they were able to burrow.

5.7 METHODS

Ideally experiments would have been carried out in the field, where the bivalves could respond to their natural surroundings. Due to time and practical constraints this was not possible and experiments were conducted in the saltwater circulation room at the University of Waikato. Water temperature within the circulation system was constant at 12°C, with water salinity 34 ppt.

In August 1995 *Paphies australis* from the dominant size cohort, sediment and water were collected from Tauranga Harbour and transported back to the salt water circulation room. *P. australis* were placed in a single aquarium containing approximately 5 cm of sediment and left for 72 hr before being used in experiments. The sediment collected was evenly distributed among the remaining aquaria. All aquaria were continually supplied with recirculated sea water collected from the harbour (Plate 5.4).

Plate 5.4 The arrangement of experimental aquaria in the tankroom at the University of Waikato salt water circulation room

All aquaria initially contained 5 cm of sediment, and pipi over which the 2 treatment sediment depths (5 and 10 cm) were added. This resulted in two treatments, with three replicate aquaria of each treatment. Within each aquarium 5 pipi were placed in an upright position (anterior end uppermost) and another 5 were laid on their sides on top of the sediment.

a) *P. australis* covered with 5 cm of sediment
b) *P. australis* covered with 10 cm of sediment

It was established in the previous experiment that pipi placed upside down (posterior end uppermost) in the sediment were unable to bury, and thus the position was not used in this experiment. Each pipi was tagged using individually numbered plastic mollusc tags (Hallprint Pty Ltd, South Australia) to determine whether the original position of the pipi had been upright or lateral. The tagging method followed that used by Hooker (1995a). Pipi were arranged haphazardly in the container. The number of pipi with siphons showing at the surface was recorded every hour for the first 6 hr of the experiment. Each aquarium was checked again after 12 hr and a final observation was taken after 24 hr. The experiment was conducted three times and each is referred to as a trial.

5.8 RESULTS

Immediately upon dumping of additional sediment, the siphons of all pipi were closed and withdrawn, and no activity was observed while sediment was added. After 24 hr the majority of pipi had migrated up to the surface and were feeding normally (Fig. 5.4). A greater number of pipi initially placed in an upright position reached the surface than those placed laterally. This was evident in treatment (a) where pipi were covered with 5 cm of sediment. Pipi buried under 10 cm of sediment (treatment b) did not show this pattern as strongly. The same number of pipi placed laterally reached the surface as those pipi placed upright in trials two and three of treatment (b).

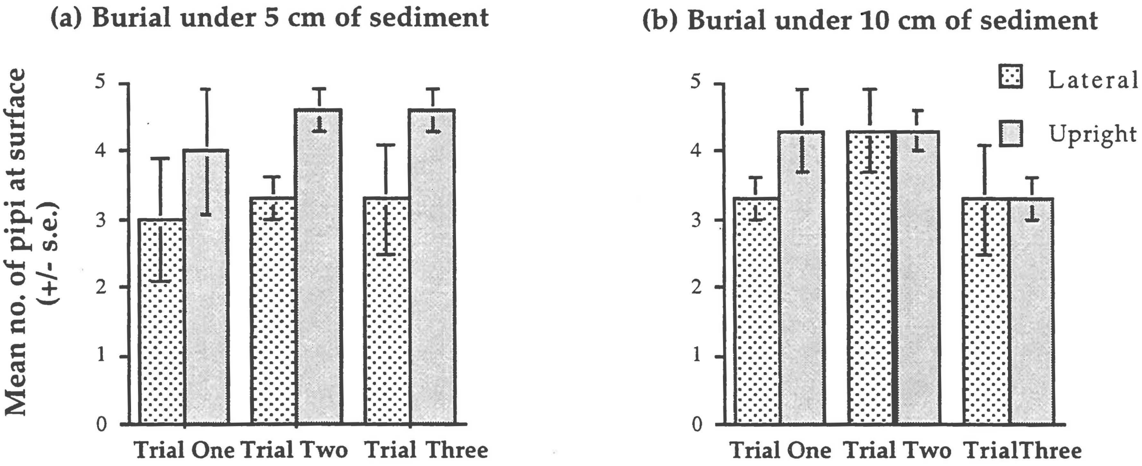
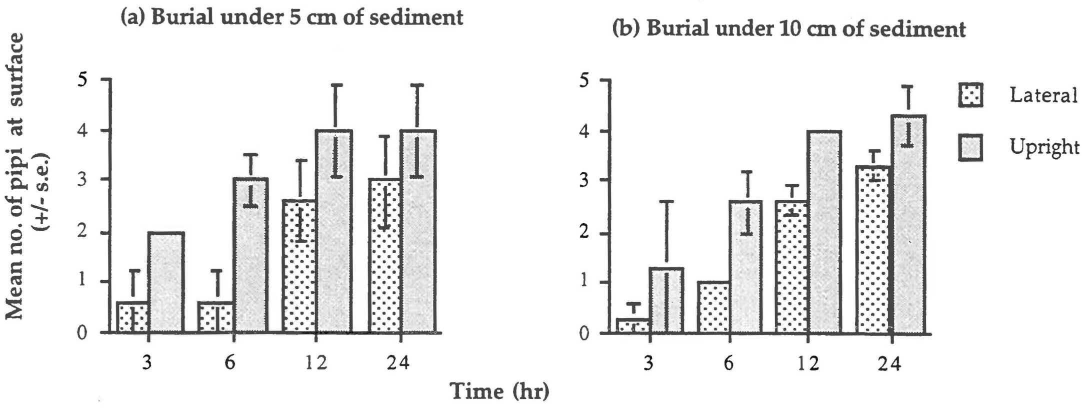


Figure 5.4 Mean number of pipi with siphons showing at the surface after 24 hr, burial under two different sediment depths, and with pipi in two different orientations. N=3 replicates

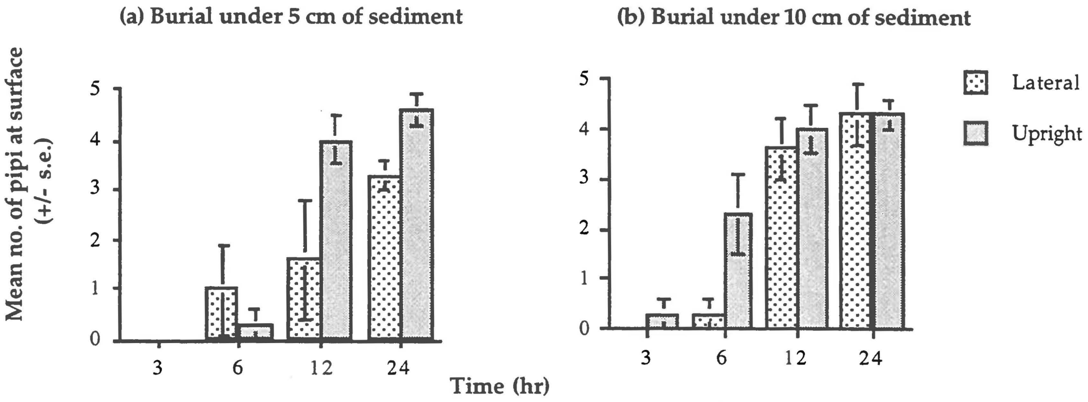
There was considerable variability in the ascension rates of individual pipi. In general fewer pipi placed laterally were able to reach the surface compared to those placed upright in the sediment (Fig. 5.5). A very small percentage

(13%) of pipi resumed normal feeding at the surface after 3 hr, of which the majority (9%) had originally been placed upright in the sediment. Overall few pipi placed in either position migrated up through the sediment to the surface in less than 6 hr; this was clearly seen in both treatments of trial two, and treatment (b) in trial three. Most pipi which reached the sediment surface to resume normal feeding from an initially upright position had done so after 12 hr.

Trial One



Trial Two



Trial Three

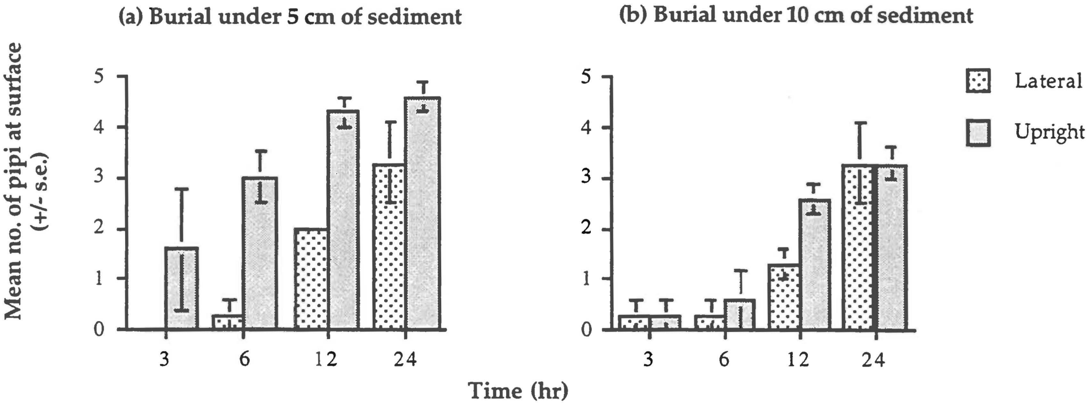


Figure 5.5 Mean number of pipi with siphons showing at the surface through time, burial under two different sediment depths, and with pipi in two different orientations. N=3 replicates

5.9 DISCUSSION

Pipi live in a dynamic environment in which currents and wave action can continually disturb the seabed. It is therefore not suprising to find that pipi can withstand burial under a certain amount of sediment. Pipi of the size used in this experiment (60-65 mm) appear quite robust surviving inundation of up to 10 cm of sediment. Results show that regardless of the initial position, pipi in this experiment were able to burrow up through sediment to resume normal feeding at the surface. Although pipi placed in either orientation could burrow up to the surface, pipi with an initial upright orientation in the sediment burrowed at a greater rate than those placed laterally. This is predictable as an upright orientation, anterior end uppermost, is the natural resting position of the pipi.

Those pipi orientated sideways on the sediment, an unnatural position, at the start of the experiment would experience a large initial resistance to movement, with resistance decreasing once an upright position was reached. Similar resistance to vertical movement occurs in the cockle when buried under sediment (Chang and Levings, 1978). This is due not to the orientation of the cockle but to the general shell configuration. Cockle shells are generally solid, spherical and can be sculptured with numerous strong rounded radial ribs, and concentric ridges. These features increase the friction and resistance to movement. In a laboratory study which compared the effects of burial by different depths of dredge sand on two benthic animals, it was found that the broad shell of the relatively sedentary heart cockle *Clinocardium nuttallii* resulted in severe resistance to upward movement, especially in stable substrates such as sand (Chang and Levings, 1978).

As discussed in the previous experiment (see section 5.4.1) pipi placed upside down were unable, in the time observed, to use their foot to gain sufficient purchase on the sediment, which drastically reduces any chance of subsequent burial. Pipi placed upside down and buried by sediment may be able to gain sufficient purchase on the sediment above them, unlike pipi in the previous experiment where the foot was totally surrounded by water. A time frame greater than this experiment (24 hr) may be required before pipi are recorded at the sediment surface after being buried by sediment.

Creese's (1988) laboratory experiments found similar results to the experiment reported here. He buried pipi of three different size classes under 1 cm, 5 cm, and 10 cm of sediment. The same three orientations were used. A further experiment were pipi were inundated with 40 cm of sediment was also carried out. The experiments where conducted over a longer time frame of one month. Ascension rates were slower, with the first siphons showing at the surface after 2 days, and pipi still reaching the surface after 5 days. The slower rates of ascension seen in Creese's experiments compared to the experiment reported here, may be due the increased stress induced by handling and removal from natural surroundings. Creese found that smaller pipi (<45 mm) always recovered faster and more fully than larger ones (>55 mm). Small pipi placed upside down and buried showed an ability to survive such treatment. He also found that medium-sized pipi can even cope quite well with burial under 40 cm of sand, or with continual reburial under 15 cm of sand per day (resulting in a total inundation of 60 cm in 4 days). Practical constraints, namely the size of aquaria, prevented investigations with greater sediment depths.

Several trials of the experiment in this study showed that pipi buried under 10 cm of sediment reached the surface at the same time as pipi buried under 5 cm of sediment. Such results implies that pipi buried under 10 cm of sediment burrowed to the surface at a greater rate than pipi buried under half this depth. In a core burial experiment (where animals' movements were channeled to the vertical axis) using the bivalve *Mercenaria mercenaria*, Maurer *et al.* (1980), found there was an increase in the mean vertical distance that *Mercenaria mercenaria* migrated with increasing depth. The vertical migration distance, when covered with 1-2 cm of sediment was 0.8-1.6 cm, when covered with 14-16 cm of sediment mean vertical migration was a distance of 3.6-4.2 cm (Maurer *et al.*, 1980). The mean vertical distance of migration was highest in the deepest sediment. It was concluded that *M. mercenaria* was able to migrate at least through 16 cm of sand within 24 hr.

Assuming that laboratory experimental conditions are more restrictive and deleterious than field conditions it is encouraging to see how hardy *Paphies australis* is. This experiment, in conjunction with others (Maurer *et al.*, 1980; Creese, 1988) suggests that it is possible to estimate the survivorship of *P. australis* under various dredge spoil disposal depths. If pipi were to become buried as a result of dredge spoil disposal results of this experiment imply that if the rate of inundation of sediment was no greater than 10 cm per day, the majority of pipi would survive such treatment, and successfully re-establish themselves.

Chapter Six

CHAPTER SIX

SUMMARY AND RECOMMENDATIONS

6.1 INTRODUCTION

The aim of this investigation has been undertaken to provide Port of Tauranga Ltd. with quantitative information concerning the ecology of bivalves on Centre Bank. The investigation was in the form of two baseline surveys conducted six months apart, regular 2 monthly sampling of a smaller scale grid and experiments on aspects of bivalve behaviour.

6.2 SUMMARY OF THE ECOLOGY OF BIVALVES ON CENTRE BANK

Two broad scale surveys documented the bivalve species present on Centre Bank. Three bivalves species *Paphies australis, Ruditapes largillierti* and *Tawera spissa* occurred in far greater abundances than any other bivalves. Spatial analysis showed these three species to be widely distributed across Centre Bank, with similar scales of distribution of approximately 200 m. A number of sites in each survey were dominated by individuals of one taxon. Such associations may be due to physical characteristics such as flow dynamics and sediment characteristics, or biological processes i.e. recruitment and post-settlement movement.

Repetitive grid sampling allowed fine scale patterns of a smaller area of Centre Bank to be described. At this finer scale the densities of *Paphies australis* on Centre Bank, Tauranga Harbour compare closely to those reported for pipi elsewhere in New Zealand (Venus, 1984; Creese, 1988; Hooker, 1995a). Within the grid site the population size structure of pipi remained practically unchanged during the 9 month sampling period.

Density stayed consistently high at several sites, while other sites showed a sudden decrease in density from one sampling to the next. Sand ridges are speculated to be the cause of these density decreases.

Experiments showed that *P. australis* is capable of burying into sediment as well as burrowing up to the sediment surface after being inundated with sediment. Burial rates were relatively quick compared to other similar laboratory experiments. Pipi buried under 10 cm of sediment burrowed to the sediment surface at a greater rate than pipi buried under half this depth. If pipi were disturbed and subsequently buried by sediment or exposed on the sediment surface, the experiments conducted imply that the majority of pipi could survive and successfully re-establish themselves.

6.3 RECOMMENDATIONS AND SUGGESTIONS FOR FURTHER RESEARCH

More frequent sampling (approximately 3 month intervals), of survey sites on Centre Bank would allow bivalve distribution and abundance to be described more usefully. The increased sampling intensity would permit a more accurate insight into short term temporal change. The logistic problems involved with regular subtidal sampling are numerous. Coupled with the sorting and identification of samples from an area the size of Centre Bank, conducting surveys at regular intervals becomes extremely time consuming.

Sampling survey sites across Centre Bank using the *in situ* finger-dredging technique described by James and Fairweather (1995), and used to sample the grid, would considerably reduce the energy required to transport large volumes of sediment to shore. The very time-consuming processes of sorting and identifying samples would be eliminated altogether. Dive bottom times would increase but could be counteracted by using a team of divers competent in biological sampling. The volume of information gained when using the finger-dredging technique may be reduced if the intention of sampling is to record all bivalves present on Centre Bank.

Because of the dominance of *Paphies australis*, *Ruditapes largillierti* and *Tawera spissa* on bivalve assemblages of Centre Bank, I would recommend that future broad scale sampling surveys concentrate on one of these species. Continued use of GPS co-ordinates for site location would be essential to ensuring accurate positioning

A more complete knowledge of the sand ridges identified in the vicinity of the grid would lead to a greater understanding of their role in determining bivalve distribution and abundance. Pilot measurements of a set of sand ridges in close proximity to the grid was initiated, with the presence of benthic fauna on top and to either side of the ridge at set distances being recorded, but fell outside the scope of this study. Continued sampling of selected sand ridges would help to determine whether or not bivalves are capable of living in or beneath these features, and the subsequent role played by sand ridges in bivalve distribution and abundance. Video footage of sites within the grid would have enabled the migration of sand ridges and changes in benthic fauna assemblage to be more clearly seen and subsequently described.

Experiments conducted as part of this study reinforced the idea that *Paphies australis* is able to actively burrow. A greater knowledge could be gained if more than one cohort was investigated, i.e. juveniles (10-15 mm) a second cohort (30-40 mm), and adults (55-65 mm) as used in this study. The experiments conducted in this study would have benefited from increased replication in time. Investigations into the rates of burrowing would advance on the information gained in this study. Temperature and sediment grain size have been documented as factors effecting bivalve burrowing rates. Bivalve density below the surface and the presence of predators may also bring about a change in burrowing rates and are worthy of investigation particularly via manipulative experiments.

There is wide scope for further investigation into the ecology of Centre bank. Through my study it has emerged that certain taxa show marked affiliations for particular sites. I believe that further work carried out on Centre Bank should concentrate on the processes giving rise to these associations between sites and taxa. Physical characteristics (e.g. flow dynamics and sediment characteristics) and biological processes (e.g. recruitment and post-settlement movement) appear to be the dominant factors contributing to bivalve distribution patterns seen on Centre Bank. Further research looking at recruitment and post-settlement in conjunction with physical characteristics of the harbour would be extremely useful.

Parr (1993) used cylindrical tube traps (modified from Yund *et al.*, 1991) to passively monitor the delivery of larvae to recruitment sites, such traps provide a method for obtaining information on recruitment dynamics. With the use of a "pipi catcher" Hooker (1995a) was able to gather quantitative information on drifting behaviour of pipi in the entrance to Whangateau Harbour. Setting similar devices at different sites on and around Centre Bank would provide a further insight into the movement and distribution mechanisms of bivalves on Centre Bank. Tagging and recapture of bivalves is another technique that could be used on Centre Bank to obtain information on movement as well as growth and population structure. Such information is important if the ecology of subtidal bivalve populations are to be understood.

Animal /sediment relationships are recommended as a basis for further research (Snelgrove and Butman, 1994). If the influence of sediment factors such as sediment grain size, organic content and sediment stability on the distribution of bivalves on Centre Bank can be determined, predictions of changes to bivalve distribution caused by alteration of sediment characteristics might be made.

References

REFERENCES

Ambrose Jr., W. G. 1984. Influence of residents on the development of a marine soft-bottom community. *Journal of Marine Research.* 42: 633-654.

Andrew, N. L. and Mapstone, B. D. 1987. Sampling and the description of spatial patterns in marine ecology. *Oceanography and Marine Biology Annual Review.* 25: 39-90.

Armonies, W. 1992. Migratory rhythms of drifting juvenile molluscs in tidal waters of the Wadden Sea. *Marine Ecology Progress Series.* 83: 197-206.

Barnes, R. D. 1980. *Invertebrate Zoology* (Fourth Edition). Holt-Saunders International Editions, Saunders College, Philadelphia. 1089 pp.

Bell, R. G. 1991. Port of Tauranga Model Study (Deepened Shipping Channel Proposal). Consultancy Report No. 6127/1. 22 pp.

Bell, R. G. 1994. Port of Tauranga Model Study: Sulphur Point Wharf Extensions. Consultancy Report No. POT 002/1. 23 pp.

Belton, R. J. 1985. The New Zealand clam *Chione* (Austrovenus) *stutchburyi.* Unpublished report to the Winston Churchhill Memorial Trust Fellow. 51 pp. (Copy held by University of Waikato Library).

Beukema, J. J. and de Vlas, J. 1989. Tidal-current transport of thread-drifting postlarval juveniles of the bivalve *Macoma balthica* from the Wadden Sea to the North Sea. *Marine Ecology Progress Series.* 52: 193-200.

Bickers, A. 1992. "The Engineer and scientist in sustainable management of coastal and marine resources". *New Zealand Engineering* 2 pp.

Bioresearches Limited. 1974. A preliminary assessment of some aspects of the ecology of the Tauranga Harbour. Unpublished report to the BOP Catchment Commission. 39 pp.

Bioresearches Limited. 1975a. Ecological monitoring survey of the lower reach of the major Bay of Plenty rivers, the Ohau Channel, and parts of the Tauranga Harbour. (Winter 1975). Unpublished report prepared for the BOPCC.

Bioresearches Limited. 1975b. Ecological monitoring survey of the lower reach of the major Bay of Plenty rivers, the Ohau Channel, and parts of the Tauranga Harbour. (Summer 1975). Unpublished report prepared for the BOPCC.

Bioresearches Limited. 1976. Aspects of the ecology of Tauranga Harbour. Vol 1. Report. Unpublished report to the B.O.P Catchment Commission and Regional Water Board.

Blackwell, R. 1984. Aspects of the population biology of *Chione stutchburyi* in Ohiwa Harbour, Bay of Plenty. Unpubl. PhD Thesis, University of Auckland, New Zealand.

Brousseau, D. J. 1978. Population dynamics of the soft-shell clam *Mya arenaria*. *Marine Biology*. 50: 63-71.

Brousseau, D. J. and Baglivo, J. A. 1987. A comparative study of age and growth in *Mya arenaria* (soft shelled clam) from three populations in Long Island sound. *Journal of Shellfish Research*. 6: 17-21.

Chang, B. D. and Levings, C. D. 1978. Effects of burial on the heart cockle *Clinocardium nuttallii* and the Dungeness crab *Cancer magister*. *Estuarine, and Coastal Shelf Science*. 7: 49-412.

Clarke, K. R. 1993. Non-parametric multivariate analysis of changes in community structure. *Australian Journal of Ecology*. 18: 117-143.

Clarke, K. R. and Ainsworth, M. 1993. A method of linking multivariate community structure to environmental variables. *Marine Ecology Progress Series*. 92: 205-219.

Clarke, K. R. and Warwick, R. M. 1994. Similarity-based testing for community pattern: The two-way layout with no replication. *Marine Biology*. 118: 167-176.

Cliff, A. D. and Ord, J. K. 1973. *Spatial autocorrelation: Monographs in spatial and environmental systems analysis*. Pion Limited, London. 266 pp.

Coe, W. R. 1953. Resurgent populations of littoral marine invertebrates and their dependence on ocean currents and tidal currents. *Ecology*. 34: 225-229.

Connell, J. H. 1974. Ecology: Field experiments in marine ecology. Pp 21-54. *In* Experimental marine biology, R. Mariscal (ed.). Acedemic Press, New York.

Connell, J. H. and Sousa, W. P. 1983. On the evidence needed to judge ecological stability or persistence. *American Naturalist*. 121: 789-824.

Cranfield, H. J., Doonan, I. J. and Micheal, K. P. 1994. Dredge survey of surf clams in Cloudy Bay, Marlborough. N.Z. Fisheries Technical Report No. 39. 18 pp.

Creese, R. G. 1988. Aspects of the ecology of pipi at Whitianga. Unpublished Finial Report to Wilkins and Davies Marinas Ltd. 23 pp .

Cummings, V. J., Pridmore, R. D., Thrush, S. F. and Hewitt, J. E. 1993. Emergence and floating behaviours of post-settlement juveniles of *Macomona liliana* (Bivalvia: Tellinacea). *Marine and Freshwater Behaviour and Physiology*. 24: 25-32.

Cummings, V. J., Pridmore, R. D., Thrush, S. F. and Hewitt, J. E. 1995. Post- settlement movement by intertidal benthic macroinvertebrates: Do common New Zealand species drift in the water column? *New Zealand Journal of Marine and Freshwater Research*. 29: 59-67.

Dahm, J. 1983. The geomorphic development, bathymetric stability and sediment dynamics of Tauranga Harbour. Unpubl. MSc Thesis, University of Waikato, New Zealand.

Davies-Colley, R. J . 1976. Sediment dynamics of Tauranga Harbour. Unpubl. MSc Thesis, University of Waikato, New Zealand.

Davies-Colley, R. J. and Healy, T. R. 1978. Sediment and hydrodynamics of the Tauranga Harbour. *New Zealand Journal of Marine and Freshwater Research*. 12: 225-236.

Dayton, P. K. and Oliver, J. S. 1980. An evolution of experimental analyses of population and community patterns in benthic marine environments. Pp 93-119. *In* Marine benthic dynamics. K. R. Tenor and B. C. Coull (eds.), University of South Carolina Press, Columbia.

de Lange, W. P. 1988. Wave climate and sediment transport within Tauranga Harbour, in the vicinity of Pilot bay. Unpubl. PhD Thesis, University of Waikato, New Zealand.

de Lange, W. P. and Healy, T. R. 1985. Beach nourishment of Pilot Bay Beach, Tauranga Harbour, New Zealand. *Proceedings of the 7th Australasian Conference on Coastal and Ocean Engineering*. Christchurch, New Zealand. Vol 1, 501-508 pp.

de Lange, W. P. and Healy, T. R. 1991. Hydrodynamics and sediment transport in a mesotidal estuarine lagoon: A comparison of analytical approaches. *Proceedings of 10th Australasian Conference on Coastal and Ocean Engineering*. Auckland, New Zealand. 97-102 pp.

Diaz, R. J. 1992. Ecosystem assessment using estuarine and marine benthic community structure. Pp 67-81. *In* Sediment toxicity assessment. G. A. Burton Jr. (ed.), Lewis Publishers Inc., Boca Raton, USA.

Dobbinson, S. J., Barker, M. F. and Jillett, J. B. 1989. Experimental shore level transplantation of the New Zealand cockle *Chione stutchburyi*. *Journal of Shellfish Research*. 8: 197-212.

Donn, T. E. 1987. Longshore distribution of *Donax serra* in two log-spiral bays in the eastern Cape, South Africa. *Marine Ecology Progress Series*. 35: 217- 222.

Donn, T. E. and Els, S. 1990. Burrowing times of *Donax serra* from the south and west coasts of South Africa. *Veliger*. 33: 355-358.

England, V. P. M. and Heino, M. P. 1994. *In situ* measurement of seasonal variation in burial depth of *Mya arenaria* Linne. *Journal of Molluscan Study*. 60: 465-467.

Fairweather, P. G. 1988. Predation can increase variability in the abundance of prey on seashores. *Oikos*. 53: 87-92.

Ferraro, S. P., Cole, F. A., De Ben, W. A. and Swartz R. C. 1989. Power-cost efficiency of eight macrobenthic sampling schemes in Puget Sound, Washington USA. *Canadian Journal of Fish and Aqutic Sci*ence. 46: 2157-2176.

Grace, R. 1972. The benthic ecology of the entrance to the Whangateau Harbour, Northland, New Zealand. Unpubl. PhD Thesis, University of Auckland, New Zealand.

Grange, K. R. 1977. Littoral benthos-sediment relationships in Manukau Harbour, New Zealand. *New Zealand Journal of Marine and Freshwater Research*. 11: 111-123.

Grange, K. R. 1979. Soft-bottom macrobenthic communities of Manukau Harbour, New Zealand. *New Zealand Journal of Marine and Freshwater Research*. 13: 315-329.

Grant, C. M. 1994. Demographic and reproduction of the tuatua *Paphies subtriangulata*. Unpubl. MSc Thesis, University of Auckland, New Zealand.

Grant-Mackie, E . 1987. Aspects of the biology of the horse mussel *Atrina zelandica*. Unpubl. MSc Thesis, University of Auckland, New Zealand.

Greenway, J. 1981. Dargiville tuatua. *Catch* June: 14-15.

Haddon, M., Willis, T. J. Wear, R. G. and Anderlini, V. C. (in press). Biomass and biology of five species of surf clam off an exposed west coast North Island beach, New Zealand. *Journal of Shellfish Research.*

Hall, S. J., Raffaelli, D. and Turrell, W. R. 1990. Predator-caging experiments in marine systems: A reexamination of their value. *American Naturalist.* 136: 657-672.

Hairston, N. G. 1989. *Ecological experiments: Purpose, design, and execution.* Cambridge University Press, Cambridge. 370 pp.

Hartley, J. P. and Dicks, B. 1987. Macrofauna of subtidal sediments using remote sampling. Pp 106-127. *In* Biological surveys of estuaries and coasts. Estuarine and Brackish-water science association handbook. J. M. Baker and W. J. Wolff (eds.), Cambridge University Press, Cambridge.

Hartley, J. P., Dicks, B. and Wolff, W. J. 1987. Processing sediment macrofauna samples Pp 131-138. *In* Biological surveys of estuaries and coasts. Estuarine and Brackish-water science association handbook. J. M. Baker and W. J. Wolff, Cambridge University Press, Cambridge.

Healy, T. R., McCabe, B. and Thompson, G. 1991. Port of Tauranga Ltd. Environmental Impact Assessment: Channel deepening and widening dredging programme 1991 to 1992. Report to the Port of Tauranga Limited. 122 pp.

Hooker, S. 1995a. Life history and demography of the pipi *Paphies australis* (Bivalvia: Mesodesmatidae) in northeastern New Zealand. Unpubl. PhD Thesis, University of Auckland, New Zealand.

Hooker, S. 1995b. Preliminary evidence for post-settlement movement of juvenile and adult pipi, *Paphies australis* (Gmelin, 1790) (Bivalvia: Mesodesmatidae). *Marine and Freshwater Behaviour and Physiology.* 27: 37-47.

Hooker, S. and Creese, B. G. 1995a. The reproductive biology of pipi, *Paphies australis* (Gmelin, 1790) (Bivalvia: Mesodesmatidae). I Temporal patterns of the reproductive cycle. *Journal of Shellfish Research.* 14: 7- 15.

Hooker, S. and Creese, B. G. 1995b. The reproductive biology of pipi, *Paphies australis* (Gmelin, 1790) (Bivalvia: Mesodesmatidae). II Spatial patterns of the reproductive cycle. *Journal of Shellfish Research.* 14: 17-24.

Holme, N. A. and McIntyre, A. D. 1984. *Methods for the study of marine benthos.* Blackwell Scientific Publications, Oxford. 387 pp.

Hulberg, L W. and Oliver, J. S. 1980. Caging manipulations in marine soft- bottom communities: importance of animal interactions or sedimentary habitat modifications. *Canadian Journal of Fish and Aquatic Science.* 37: 1130- 1139.

Hunt, J. H., Ambrose, Jr. and Peterson, C. H. 1987. Effects of the gastropod, *Ilyanassa obsoleta* (Say), and the bivalve *Mercenaria mercenaria* (L.), on larval settlement and juvenile recruitment of fauna. *Journal of Experimental Marine Biology and Ecology.* 108: 229-240.

Hureau, J. C. and Rice, A. L. 1983. Guidelines for marine reference collections. Unesco Reports in Marine Sciences. Vol 22. 19 pp.

James, R. J. and Fairweather, P. G. 1995. Comparison of methods for sampling the pipi, *Donax deltoides* (Bivalvia: Donacidae), on sandy ocean beaches. *Marine and Freshwater Research.* 46: 1093-1099.

James, R. J., Lincoln Smith, M. P. and Fairweather, P. G. 1995. Sieve mesh-size and taxonomic resolution needed to describe natural spatial variation of marine macrofauna. *Marine Ecology Progress Series.* 118: 187-198.

Jones, G. P., Ferrell, D. J. and Sale, P. F. 1992. Fish feeding and dynamics of soft-sediment mollusc populations in a coral reef lagoon. *Marine Ecology Progress Series.* 80: 175-190.

Jumars, P. A. 1975. Environmental grain and polychaete species diversity in a bathyal community. *Marine Biology.* 30:253-266.

Kirkwood, G. P. 1983. Estimation of von Bertalanffy growth curve parameters using both length incremants and age/length data. *Canadian Journal of Fish and Aqutic Sci*ence. 40: 1405-1411.

Kneib, R. T. 1988. Testing for effects of predation in an intertidal soft-bottom community. *Ecology.* 69: 1795-1805.

Krebs, C. J. 1978. *Ecology: The experimental analysis of distribution and abundance.* Harper International Edition. 678 pp.

Leber, K. M. 1982. Bivalves (Tellinacea: Donacidae) on a North Carolina beach: Contrasting population size structures and tidal migrations. *Marine Ecology Progress Series.* 7: 297-301.

Livingston, R. J. 1987. Field sampling in estuaries: The relationship of scale to variability. *Estuaries.* 10: 194-207.

McArdle, B. H. and Blackwell, R. G. 1989. Measurement of density variability in the bivalve *Chione stutchburyi* using spatial autocorrelation. *Marine Ecology Progress Series*. 52: 245-252.

McArdle, B. H., Gaston, K. J. and Lawton, J. H. 1990. Variations in the size of animal populations: Patterns problems and artifacts. *Journal of Animal Ecology*. 59: 439-454.

McLachlan, A. and Young, N. 1982. Effects of low temperature on the burrowing rates of four sandy beach molluscs. *Journal of Experimental Marine Biology and Ecology*. 65: 275-284.

McLachlan, A., Jaramillo, E., Defeo, O., Dungan, J., Ruyck, A. and Coetzee, P. 1995. Adaptations of bivalves to different beach types. *Journal of Experimental Marine Biology and Ecology*. 187: 147-160.

Magurran, A. E. 1988. *Ecological diversity and its measurement*. Cambridge University Press, Cambridge. 167 pp.

Martel, A. and Chia, F. 1991. Drifting and dispersal of small bivalves and gastropods with direct development. *Journal of Experimental Marine Biology and Ecology*. 150: 131-147.

Mathew, J., Healy, T. R. and de Lange, W. P. 1995. Changes to a large flood tidal delta system following major channel dredging, Tauranga Harbour, New Zealand. *4th International Conference on Coastal and Port Engineering in Developing Countries*, Rio de Janeiro, Brazil. 1464-1471 pp.

Maurer, D., Keck, R. T., Tinsman, J. C. and Leathem, W. A. 1980. Vertical migration and mortality of benthos in dredged material: Part 1 Mollusca. *Marine Environmental Research*. 4: 229-319.

Mikkelsen, P. S. 1981. A comparison of two Florida populations of the Coquina Clam *Donax variabilis* Say, 1822 (Bivalvia : Donacidae) I. Intertidal Density, Distribution and Migration. *Veliger*. 23: 230- 239.

Mitchell, L. G., Mutchmor, J. A. and Dolphin, W. D. 1988. *Zoology*. The Benjamin Cummings Publishing Company Inc. 862 pp.

Morton, J. E. and Miller, M. 1973. *The New Zealand seashore*. Second edition. Collins, London. 673 pp.

Newell, C. R. and Hindu, H. 1982. The effect of sediment type on growth rate and shell allometry in the soft shelled clam *Mya arenaria* L. *Journal of Experimental Marine Biology and Ecology*. 65: 285-289.

Park, S. 1991. Bay of Plenty Regional Council, Coastal Overview Report 1991. BOPRC Technical Publication Number 3. 92 pp.

Park, S. 1992. Bay of Plenty Regional Council, Regional Monitoring Network, Coastal and Estuarine Ecology Program 1990/1991. Technical Report Number 13. 50 pp.

Park, S. 1994. Environment B.O.P Natural Environment Regional Monitoring Network, Coastal and Estuarine Ecology Program 1993/1994. Environmental Report Number 94/20. 93 pp.

Parr, S. W. 1993. Bivalve larvae in the Whangateau Harbour. Unpubl. MSc Thesis, University of Auckland, New Zealand.

Paul, L. J. 1966. Observations on past and present distribution of mollusc beds in Ohiwa Harbour, Bay of Plenty. *New Zealand Journal of Science*. 9: 30-40.

Peterson, C. H. 1979. Predation, competitive exclusion, and diversity in the soft-sediment benthic communities of estuaries and lagoons. Pp 233-264. *In* Ecological processes in coastal and marine systems. R. J. Livingston (ed.), Plenum Press, New York.

Peterson, C. H. 1982a. The importance of predation and intra- and interspecific competition in the population biology of two intertidal suspension feeding bivalves. *Protothaca staminea* and *Chione undatella*. *Ecological Monographs*. 52: 437-475.

Peterson, C. H. 1982b. Clam predation by whelks (*Busycon* sp.): Experimental tests of the importance of prey size, prey density, and seagrass cover. *Marine Biology*. 66: 159-170.

Peterson, C. H. 1986. Quantitative allometry of gamete production by *Mercenaria mercenaria* into old age. *Marine Ecology Progress Series*. 29: 93-97.

Peterson, C. H. and Andre, S. V. 1980. An experimental analysis of interspecific competition among marine filter feeders in a soft sediment environment. *Ecology*. 61: 129-139.

Peterson, C. H. and Beal, F. B. 1989. Bivalve growth and higher order interactions: Importance of density, site, and time. *Ecology*. 70: 1390-1404.

Peterson, C. H. and Black, R. 1987. Resource depletion by active suspension feeders on tidal flats: Influence of local density and tidal elevation. *Limnology and Oceanography*. 32: 143-166.

Peterson, C. H. and Black, R. 1988. Density-dependent mortality caused by physical stress interacting with biotic history. *American Naturalist.* 131: 257-270.

Peterson, C. H. and Black, R. 1991. Preliminary evidence for progressive sestonic food depletion in incoming tide over a broad tidal sandflat. *Estuarine, Coastal and Shelf Science.* 32: 4.5-413.

Peterson, C. H. and Black, R. 1993. Experimental tests of the advantages and disadvantages of high density for two coexisting cockles in a Southern Ocean lagoon. *Journal of Animal. Ecology.* 62: 614-633.

Pitcher, T. J. and Hart, P J. 1982. *Fisheries ecology.* Croom Helm, London. 414 pp.

Powell, A. W. P. 1979. *New Zealand Mollusca.* William Collins Publishers Ltd., Auckland. 500 pp.

Pridmore, R. D., Thrush, S. F., Hewitt, J. E. and Roper, D. S. 1990. Macrobenthic community composition of six intertidal sandflats in Manukau Harbour, New Zealand. *New Zealand Journal of Marine and Freshwater Research.* 24: 81-96.

Pridmore, R. D. Thrush, S. F. Wilcock, R. J., Hewitt, J. E. and Cummings, V. J. 1991. Effects of the organochlorine pesticide technical chlordane on the population structure of suspension and deposit feeding bivalves. *Marine Ecology Progress Series.* 76: 261-271.

Raffaelli, D. And Milne, H. 1987. An experiment investigation of the effects of shorebird and flatfish predation on estuarine invertebrates. *Estuarine, Coastal and Shelf* Science. 24: 1-13.

Redfearn, P. 1982. Larval shell development of the toheroa, *Paphies ventricosa* (Gary, 1843) (Mactracea: Mesodesmatidae). *New Zealand Journal of Marine and Freshwater Science.* 16: 241-252.

Redfearn, P. 1987. Larval shell development of the northern tuatua, *Paphies subtriangulata* (Bivalvia, Mesodesmatidae). *New Zealand Journal of Marine and Freshwater Science.* 21: 65-70.

Richardson, J. R. Aldridge, A. E. and Smith, P. J. 1982. Analyses of tuatua populations- *Paphies subtriangulata* and *P. donacina. New Zealand Journal of Zoology.* 9: 231-238.

Roper, D. S. 1990. Benthos associated with an estuarine outfall, Tauranga Harbour. *New Zealand Journal of Marine and Freshwater Research.* 24: 487-498.

Roper, D. S., Pridmore, R. D. and Thrush, S. F. 1992. Recruitment to the macrobenthos of *Macomona liliana* (Bivalvia: Tellinidae) in Manukau Harbour, New Zealand. *New Zealand Journal of Marine and Freshwater Research*. 26: 385-392.

Rosenberg, R. 1974. Spatial dispersion of an estuarine benthic faunal community. *Journal of Experimental Marine Biology and Ecology*. 15: 69-80.

Scheltema, R. S. 1971. Larval dispersal as a means of genetic exchange between geographically separated populations of shallow water benthic marine gastropods. *Biology Bulletin*. 140: 284-322.

Service, S. K. and Feller, R. J. 1992. Long-term trends of subtidal macrobenthos in North Inlet, South Carolina. *Hydrobiologia*. 231: 13-40.

Sigurdsson, J. B., Titman, C. W. and Davies, P. A. 1976. The dispersal of post-larval bivalve molluscs by byssus threads. *Nature*. 262: 386-387.

Smith, I. A. and Hughes, W. R. 1993. Port of Tauranga 1993 Economic Impact Study. Report to the Port of Tauranga Limited. 67 pp.

Snedecor, G. W., and Cochran, W. G. 1972. *Statistical methods*. The Iowa State University Press. USA. 593 pp.

Snelgrove, P. V. R. and Butman, C. A. 1994. Animal-sediment relationships revisited: Cause versus effect. *Oceanography and Marine Biology Annual Review*. 32: 111-177.

Sokal, R. R. and Oden, N. L. 1978. Spatial autocorrelation in biology 2. Some biological implications and four applications of evolutionary and ecological interest. *Biological Journal Linnean Society*. 10: 229-249.

Sorlin, T. 1988. Floating behaviour in the tellinid bivalve *Macoma balthica*. *Oecologia*. 77: 273-277.

Southwood, T. R. E. 1978. *Ecological methods*. Chapman and Hall, London. 254 pp.

Stenton-Dozey, J. M. E. and Brown, A. C. 1994. Exposure of the sandy-beach bivalve *Donax serra* Roding to a heated and chlorinated effluent 1. Effects of temperature on burrowing and survival. *Journal of Shellfish Research*. 13: 443-339.

Stephenson, R. L. 1981. Aspects of the energetics of the cockle *Chione* (Austrovenus) *stutchburyi* in the Avon-Heathcote estuary, Christchurch, New Zealand. Unpubl. PhD Thesis, University of Canterbury, New Zealand.

Thrush, S. F. 1986. Community structure on the floor of a sea-lough: Are large epibenthic predators important? *Journal of Experimental Marine Biology and Ecology*. 104: 171-183.

Thrush, S. F. 1991. Spatial patterns in soft-bottom communities. *Trends in Ecology and Evolution*. 6: 75-79.

Thrush, S. F., Hewitt, J. E. and Pridmore, R. D. 1989. Patterns in the spatial arrangements of polychaetes and bivalves in intertidal sandflats. *Marine Biology*. 102: 529-535.

Thrush, S. F., Pridmore, R. D. and Hewitt, J. E. 1994a. Impacts on soft- sediment macrofauna: The effects of spatial variation on temporal trends. *Ecological Applications*. 4: 31-41.

Thrush, S. F., Pridmore, R. D., Hewitt, J. E., Cummings, V. J. 1994b. The importance of predators on a sandflat: interplay between seasonal changes in prey densities and predator effects. *Marine Ecology Progress Series*. 107: 211-222.

Thrush, S. F., Pridmore, R. D., Hewitt, J. E., Cummings, V. J. and Latimer, G. J. 1992. Ecological monitoring program for the Manukau Harbour: presentation of data collected up to February 1992. Water Quality Centre Consultancy Report 6120/2, prepared for the Auckland Regional Council.

Trueman, E. R. 1971. The control of burrowing and the migratory behaviour of *Donax denticulatus* (Bivalvia: Tellinacea). *Journal of Zoology. London*. 165: 453-469.

Trueman, E. R. and Ansell, A. D. 1969. The mechanisms of burrowing into soft substrata by marine animals. *Oceanography and Marine Biology Annual Review*. 7: 315-366.

Trueman, E. R., Brand, A. R. and Davis, P. 1966. The effect of substrate and shell shape on the burrowing of some common bivalves. *Proceedings of the Malacological Society of London*. 37: 97-109.

Turner, S. J., Thrush, S. F., Pridmore, R. D., Hewitt, J. E., Cummings, V. J. and Maskery, M. 1995. Are soft-sediment communities stable? An example from a windy harbour. *Marine Ecology Progress Series*. 120: 219-230.

Underwood, A. 1986. The analysis of competition by field experiments. Pp 240-268. *In* Community ecology, pattern and process. J. Kikkawa and D. J. Anderson (eds.), Blackwell Scientific Publications.

Upton, J. G. J., and Fingleton, B. 1985. *Spatial data analysis by example*. Vol 1. Point pattern and quantitative data. John Wiley & Sons, Chichester. 409 pp.

Venus, G. C. 1984. *Paphies australis* (pipi) in the Whangarei Harbour. Whangarei Harbour Study Technical Report No. 6. Unpublished report to the Northland Harbour Board, New Zealand. 59 pp.

Virnstein, R. W. 1977. The importance of predation by crabs and fishes on benthic infauna in Chesapeake Bay. *Ecology*. 58: 1199-1217.

Virnstein, R. W. 1980. Measuring effects on benthic communities in soft sediments. Pp 281-290. *In* Estuarine perspectives. V. S. Kenndey (ed.), Acedemic Press, New York.

Volckaert, F. 1987. Spatial pattern of soft-bottom Polychaeta of Nova Scotia, Canada. *Marine Biology*. 93:627-639.

Walker, R. L. and Heffernan, P. B. 1994. Temporal and spatial effects of tidal exposure on the gametogenic cycle of the northern quahog *Mercenaria mercenaria* (Linnaeus, 1758), in coastal Georgia. *Journal of Shellfish Research*. 13: 479-486.

Wear, R. G., and Haddon, M. 1987. Natural diet of the crab *Ovalipes catharus* (Crustacea, Portunidae) around central and northern New Zealand. *Marine Ecology Progress Series*. 35: 39-49.

Williams, B. K. 1983. Some observations on the use of discriminant analysis in ecology. *Ecology*. 64: 1283-1291.

Wilson, W. H. 1991. Competition and predation in marine soft-sediment communities. *Annual Review of Ecology Systematics*. 21: 221-241.

Woodin, S. A. 1976. Adult-larval interactions in dense infaunal assemblages: Patterns of abundance. *Journal of Marine Research*. 34: 25-41.

Yund, P. O., Gaines, S. D. and Bertness, M. D. 1991. Cylindrical tube traps for larval sampling . *Limnology and Oceanography*. 63: 1167-1177.

Zwarts, L. and Wanink, J. 1989. Siphon size and burying deposit- and suspension-feeding benthic bivalves. *Marine Biology*. 100: 227-240.

Appendices

APPENDICES

APPENDIX I

Location of sample sites, Centre Bank, Survey 1 and 2

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

APPENDIX II

SPECIES CODE	TAXON	SITE 1		SITE 2		SITE 3	
		NO. OF INDIVIDUALS		NO. OF INDIVIDUALS		NO. OF INDIVIDUALS	
		Survey 1	Survey 2	Survey 1	Survey 2	Survey 1	Survey 2
1	*Paphies australis*	2	0	7	1	2	0
2	*Ruditapes largillierti*	2	0	43	0	0	0
3	*Tawera spissa*	55	10	41	7	31	1
4	*Gari stangeri*	0	4	5	1	0	2
5	*Macomona liliana*	10	1	7	5	2	0
6	*Soletellina siliquens*	3	15	9	1	5	2
7	*Nucula nitidula*	0	1	1	1	0	1
8	*Nucula hartvigiana*	14	6	22	24	0	0
9	*Divaricella huttoniana*	4	0	2	0	10	0
10	*Perna canaliculus*	0	0	1	0	0	0
11	*Myadora striata*	0	0	0	0	1	0
12	*Scalpomactra scalpellum*	0	0	0	0	0	18
13	*Gari lineolata*	0	0	0	0	0	0
14	*Soletellina nitida*	1	0	5	0	0	0
15	*Dosinia subrosea*	1	0	0	0	0	0
16	*Gomphina maorum*	0	0	0	0	0	0
17	*Paphies subtriangulata*	0	0	0	0	0	0
18	*Modiolus areolatus*	0	0	0	0	0	0
19	*Arthritica bifurca*	0	0	0	0	0	0
20	*Notocallista multistriata*	0	0	0	0	0	0
21	*Zenatia acinaces*	0	0	0	0	0	0
22	*Hiatella arctica*	0	0	0	0	0	0
23	*Diplodonta striatula*	0	0	0	0	0	0
24	*Felaniella zelandica*	0	0	0	0	0	0
25	*Dosinia lambata*	0	0	0	0	0	0
26	*Tellina ?gaimardi*	0	1	0	1	0	0
27	Sp. 1	0	0	0	0	0	0
28	Sp. 2	0	0	0	0	0	0
29	Sp. 3	0	0	0	0	0	0
30	Sp. 4	0	0	0	0	0	0
31	Sp. 5	0	0	0	0	0	0
TOTAL NUMBER AT SITE		**92**	**47**	**142**	**42**	**41**	**24**

APPENDIX II contd.

SPECIES CODE	TAXON	SITE 4		SITE 5		SITE 6	
		NO. OF INDIVIDUALS		NO. OF INDIVIDUALS		NO. OF INDIVIDUALS	
		Survey 1	Survey 2	Survey 1	Survey 2	Survey 1	Survey 2
1	*Paphies australis*	283	323	0	1	1	2
2	*Ruditapes largillierti*	5	1	75	197	60	55
3	*Tawera spissa*	4	1	93	442	283	83
4	*Gari stangeri*	0	0	10	0	3	13
5	*Macomona liliana*	19	11	5	8	9	0
6	*Soletellina siliquens*	1	0	7	2	8	12
7	*Nucula nitidula*	0	0	18	3	4	39
8	*Nucula hartvigiana*	2	0	18	13	9	0
9	*Divaricella huttoniana*	0	0	2	0	1	0
10	*Perna canaliculus*	0	0	0	0	0	0
11	*Myadora striata*	0	0	0	0	0	0
12	*Scalpomactra scalpellum*	0	0	0	0	10	0
13	*Gari lineolata*	0	0	0	0	0	0
14	*Soletellina nitida*	0	0	0	1	0	0
15	*Dosinia subrosea*	0	0	0	0	0	0
16	*Gomphina maorum*	0	0	0	0	0	0
17	*Paphies subtriangulata*	0	0	0	0	0	0
18	*Modiolus areolatus*	0	0	0	0	0	0
19	*Arthritica bifurca*	0	0	0	0	0	0
20	*Notocallista multistriata*	0	0	0	0	0	0
21	*Zenatia acinaces*	0	0	0	0	0	0
22	*Hiatella arctica*	0	0	0	0	0	0
23	*Diplodonta striatula*	0	0	0	0	0	0
24	*Felaniella zelandica*	0	0	0	0	0	0
25	*Dosinia lambata*	0	0	0	0	0	0
26	*Tellina ?gaimardi*	0	0	0	0	0	0
27	Sp. 1	0	0	0	0	0	0
28	Sp. 2	0	0	0	0	1	0
29	Sp. 3	0	0	0	0	0	0
30	Sp. 4	0	0	0	0	0	0
31	Sp. 5	0	0	0	0	0	0
TOTAL NUMBER AT SITE		**319**	**337**	**228**	**667**	**383**	**208**

APPENDIX II contd.

	SITE 7		**SITE 8**		**SITE 9**	
SPECIES CODE TAXON	**NO. OF INDIVIDUALS**		**NO. OF INDIVIDUALS**		**NO. OF INDIVIDUALS**	
	Survey 1	**Survey 2**	**Survey 1**	**Survey 2**	**Survey 1**	**Survey 2**
1 *Paphies australis*	106	24	136	625	2	0
2 *Ruditapes largillierti*	423	66	32	0	0	0
3 *Tawera spissa*	0	2	0	0	0	0
4 *Gari stangeri*	1	7	54	0	0	0
5 *Macomona liliana*	0	0	0	0	0	0
6 *Soletellina siliquens*	0	2	25	0	0	0
7 *Nucula nitidula*	3	2	0	0	0	0
8 *Nucula hartvigiana*	0	2	0	0	0	0
9 *Divaricella huttoniana*	0	0	0	0	0	0
10 *Perna canaliculus*	6	0	8	0	0	0
11 *Myadora striata*	0	0	0	0	0	0
12 *Scalpomactra scalpellum*	0	0	0	0	3	0
13 *Gari lineolata*	0	0	0	0	0	0
14 *Soletellina nitida*	0	0	0	0	0	0
15 *Dosinia subrosea*	0	0	1	0	0	0
16 *Gomphina maorum*	0	0	2	0	0	0
17 *Paphies subtriangulata*	3	0	3	0	2	0
18 *Modiolus areolatus*	5	0	0	0	0	0
19 *Arthritica bifurca*	0	0	0	0	0	0
20 *Notocallista multistriata*	0	0	0	0	0	0
21 *Zenatia acinaces*	0	0	0	0	0	0
22 *Hiatella arctica*	2	0	0	0	0	0
23 *Diplodonta striatula*	0	0	0	0	0	0
24 *Felaniella zelandica*	0	0	0	0	0	0
25 *Dosinia lambata*	0	0	0	0	0	0
26 *Tellina ?gaimardi*	0	0	0	0	0	0
27 Sp. 1	0	0	0	0	0	0
28 Sp. 2	0	0	0	0	0	0
29 Sp. 3	0	0	0	0	0	0
30 Sp. 4	0	0	0	0	0	0
31 Sp. 5	0	0	0	0	0	0
TOTAL NUMBER AT SITE	**549**	**105**	**261**	**625**	**7**	**0**

APPENDIX II contd.

SPECIES CODE	TAXON	SITE 10 NO. OF INDIVIDUALS Survey 1	SITE 10 NO. OF INDIVIDUALS Survey 2	SITE 11 NO. OF INDIVIDUALS Survey 1	SITE 11 NO. OF INDIVIDUALS Survey 2	SITE 12 NO. OF INDIVIDUALS Survey 1	SITE 12 NO. OF INDIVIDUALS Survey 2
1	*Paphies australis*	7	0	1	0		
2	*Ruditapes largillierti*	4	1	0	0	2	0
3	*Tawera spissa*	84	18	1	2	6	0
4	*Gari stangeri*	0	0	0	0	76	4
5	*Macomona liliana*	67	23	1	0	0	0
6	*Soletellina siliquens*	8	0	1	0	2	0
7	*Nucula nitidula*	2	0	1	0	4	0
8	*Nucula hartvigiana*	22	6	0	0	0	0
9	*Divaricella huttoniana*	3	0	2	1	1	0
10	*Perna canaliculus*	0	0	0	0	0	0
11	*Myadora striata*	0	0	9	1	0	0
12	*Scalpomactra scalpellum*	0	0	0	0	3	0
13	*Gari lineolata*	0	2	0	0	0	0
14	*Soletellina nitida*	0	1	0	1	0	0
15	*Dosinia subrosea*	0	0	0	0	0	0
16	*Gomphina maorum*	0	0	0	0	0	0
17	*Paphies subtriangulata*	0	0	0	0	0	0
18	*Modiolus areolatus*	0	0	0	0	0	0
19	*Arthritica bifurca*	4	0	2	0	3	0
20	*Notocallista multistriata*	0	0	0	0	0	0
21	*Zenatia acinaces*	0	0	0	0	0	0
22	*Hiatella arctica*	0	0	0	0	0	0
23	*Diplodonta striatula*	0	0	0	0	0	0
24	*Felaniella zelandica*	0	0	0	0	0	0
25	*Dosinia lambata*	0	1	0	0	0	0
26	*Tellina ?gaimardi*	0	0	0	0	0	0
27	Sp. 1	0	0	0	0	0	0
28	Sp. 2	0	0	0	0	0	0
29	Sp. 3	0	0	0	0	0	0
30	Sp. 4	0	1	0	0	0	0
31	Sp. 5	0	0	0	0	0	0
TOTAL NUMBER AT SITE		**201**	**53**	**16**	**5**	**97**	**4**

APPENDIX II contd.

SPECIES CODE TAXON	SITE 13		SITE 14		SITE 15	
	NO. OF INDIVIDUALS		NO. OF INDIVIDUALS		NO. OF INDIVIDUALS	
	Survey 1	**Survey 2**	**Survey 1**	**Survey 2**	**Survey 1**	**Survey 2**
1 *Paphies australis*	1	0	7	21	14	14
2 *Ruditapes largillierti*	14	13	13	2	6	2
3 *Tawera spissa*	89	3	11	4	1	2
4 *Gari stangeri*	5	40	19	57	27	28
5 *Macomona liliana*	0	0	0	0	0	0
6 *Soletellina siliquens*	3	21	21	35	13	6
7 *Nucula nitidula*	0	0	0	0	0	0
8 *Nucula hartvigiana*	0	0	0	0	0	0
9 *Divaricella huttoniana*	0	0	0	0	0	0
10 *Perna canaliculus*	0	0	0	0	27	0
11 *Myadora striata*	0	0	0	0	0	0
12 *Scalpomactra scalpellum*	0	0	0	0	0	0
13 *Gari lineolata*	0	0	0	0	0	0
14 *Soletellina nitida*	0	0	0	0	0	0
15 *Dosinia subrosea*	0	0	0	0	0	0
16 *Gomphina maorum*	0	0	0	0	0	0
17 *Paphies subtriangulata*	0	0	0	0	0	0
18 *Modiolus areolatus*	0	0	0	0	4	4
19 *Arthritica bifurca*	0	0	0	0	0	0
20 *Notocallista multistriata*	0	0	0	0	0	0
21 *Zenatia acinaces*	0	0	0	0	0	0
22 *Hiatella arctica*	0	0	0	0	0	0
23 *Diplodonta striatula*	0	0	0	0	0	0
24 *Felaniella zelandica*	0	0	0	0	0	0
25 *Dosinia lambata*	0	0	0	0	0	0
26 *Tellina ?gaimardi*	0	0	0	0	0	0
27 Sp. 1	0	0	0	0	0	0
28 Sp. 2	0	0	0	0	0	0
29 Sp. 3	0	0	0	0	0	0
30 Sp. 4	0	0	0	0	0	0
31 Sp. 5	0	0	0	0	0	0
TOTAL NUMBER AT SITE	**112**	**77**	**71**	**119**	**92**	**52**

APPENDIX II contd.

SPECIES CODE	TAXON	SITE 16		SITE 17		SITE 18	
		NO. OF INDIVIDUALS		NO. OF INDIVIDUALS		NO. OF INDIVIDUALS	
		Survey 1	Survey 2	Survey 1	Survey 2	Survey 1	Survey 2
1	*Paphies australis*	0	0	0	1	0	2
2	*Ruditapes largillierti*	0	0	72	0	7	10
3	*Tawera spissa*	3	2	7	2	14	128
4	*Gari stangeri*	0	0	5	0	0	0
5	*Macomona liliana*	0	3	21	0	1	5
6	*Soletellina siliquens*	0	0	80	0	0	0
7	*Nucula nitidula*	0	0	3	0	0	0
8	*Nucula hartvigiana*	1	0	21	0	0	0
9	*Divaricella huttoniana*	1	6	5	0	0	0
10	*Perna canaliculus*	0	0	0	0	0	0
11	*Myadora striata*	3	1	0	11	4	1
12	*Scalpomactra scalpellum*	0	0	0	0	0	0
13	*Gari lineolata*	0	0	0	0	0	0
14	*Soletellina nitida*	0	0	0	0	0	2
15	*Dosinia subrosea*	0	0	0	0	0	2
16	*Gomphina maorum*	0	0	0	0	0	0
17	*Paphies subtriangulata*	0	0	0	0	0	0
18	*Modiolus areolatus*	0	0	0	0	0	0
19	*Arthritica bifurca*	0	0	0	0	0	0
20	*Notocallista multistriata*	0	0	0	0	0	0
21	*Zenatia acinaces*	0	0	0	0	1	0
22	*Hiatella arctica*	0	0	0	0	0	0
23	*Diplodonta striatula*	0	0	0	0	0	0
24	*Felaniella zelandica*	0	0	0	0	0	0
25	*Dosinia lambata*	0	0	0	0	0	0
26	*Tellina ?gaimardi*	0	0	0	0	0	0
27	Sp. 1	0	0	4	0	0	0
28	Sp. 2	0	0	0	0	0	0
29	Sp. 3	0	0	0	0	1	2
30	Sp. 4	0	0	0	0	0	0
31	Sp. 5	0	0	0	0	0	0
TOTAL NUMBER AT SITE		**8**	**12**	**218**	**13**	**28**	**155**

APPENDIX II contd.

SPECIES CODE TAXON	SITE 19		SITE 20		SITE 21	
	NO. OF INDIVIDUALS		NO. OF INDIVIDUALS		NO. OF INDIVIDUALS	
	Survey 1	Survey 2	Survey 1	Survey 2	Survey 1	Survey 2
1 *Paphies australis*	93	3330	4	0	1	22
2 *Ruditapes largillierti*	3	7	0	0	48	34
3 *Tawera spissa*	2	13	1	0	12	56
4 *Gari stangeri*	0	0	0	0	41	107
5 *Macomona liliana*	32	0	0	0	0	0
6 *Soletellina siliquens*	5	1	0	0	16	63
7 *Nucula nitidula*	0	0	0	0	19	97
8 *Nucula hartvigiana*	0	0	0	0	0	0
9 *Divaricella huttoniana*	0	0	0	0	0	0
10 *Perna canaliculus*	0	0	0	0	0	0
11 *Myadora striata*	0	0	0	0	0	0
12 *Scalpomactra scalpellum*	0	0	0	0	0	0
13 *Gari lineolata*	0	0	0	0	0	0
14 *Soletellina nitida*	0	0	0	0	0	0
15 *Dosinia subrosea*	0	0	0	0	0	0
16 *Gomphina maorum*	0	0	0	0	0	0
17 *Paphies subtriangulata*	0	0	1	0	0	0
18 *Modiolus areolatus*	0	0	0	0	0	0
19 *Arthritica bifurca*	1	0	0	0	0	0
20 *Notocallista multistriata*	0	0	0	0	0	0
21 *Zenatia acinaces*	1	0	0	0	0	0
22 *Hiatella arctica*	0	0	0	0	0	0
23 *Diplodonta striatula*	0	0	0	0	0	0
24 *Felaniella zelandica*	0	0	0	0	0	0
25 *Dosinia lambata*	0	0	0	0	0	0
26 *Tellina ?gaimardi*	0	0	0	0	0	0
27 Sp. 1	0	0	0	0	0	0
28 Sp. 2	0	0	0	0	0	0
29 Sp. 3	0	0	0	0	0	0
30 Sp. 4	0	0	0	0	0	0
31 Sp. 5	0	0	0	1	0	0
TOTAL NUMBER AT SITE	**137**	**3351**	**6**	**1**	**137**	**379**

APPENDIX II contd.

SPECIES CODE TAXON	SITE 22		SITE 23		SITE 24	
	NO. OF INDIVIDUALS		NO. OF INDIVIDUALS		NO. OF INDIVIDUALS	
	Survey 1	**Survey 2**	**Survey 1**	**Survey 2**	**Survey 1**	**Survey 2**
1 *Paphies australis*	1	0	0	0	0	1
2 *Ruditapes largillierti*	0	0	0	0	0	0
3 *Tawera spissa*	9	0	0	0	14	12
4 *Gari stangeri*	0	0	0	0	0	0
5 *Macomona liliana*	1	0	0	0	0	0
6 *Soletellina siliquens*	41	0	1	0	3	0
7 *Nucula nitidula*	1	0	0	0	0	0
8 *Nucula hartvigiana*	0	0	0	0	3	0
9 *Divaricella huttoniana*	0	0	0	0	18	0
10 *Perna canaliculus*	0	0	0	0	0	0
11 *Myadora striata*	3	0	5	4	6	8
12 *Scalpomactra scalpellum*	0	0	0	0	0	0
13 *Gari lineolata*	0	0	0	0	0	0
14 *Soletellina nitida*	0	2	0	0	0	0
15 *Dosinia subrosea*	0	0	0	0	0	0
16 *Gomphina maorum*	0	0	0	0	0	0
17 *Paphies subtriangulata*	0	0	0	0	0	0
18 *Modiolus areolatus*	0	0	0	0	0	0
19 *Arthritica bifurca*	0	0	0	0	1	0
20 *Notocallista multistriata*	0	0	0	0	0	0
21 *Zenatia acinaces*	0	0	0	0	0	0
22 *Hiatella arctica*	0	0	0	0	0	0
23 *Diplodonta striatula*	0	2	0	0	1	0
24 *Felaniella zelandica*	0	0	0	0	0	0
25 *Dosinia lambata*	0	0	0	0	0	0
26 *Tellina ?gaimardi*	0	0	0	0	0	0
27 Sp. 1	0	0	0	0	0	0
28 Sp. 2	0	0	0	0	0	0
29 Sp. 3	0	0	0	0	0	0
30 Sp. 4	0	0	0	0	0	0
31 Sp. 5	0	0	0	0	0	0
						0
TOTAL NUMBER AT SITE	55	4	6	4	47	21

APPENDIX II contd.

SPECIES CODE TAXON	SITE 25		SITE 26		SITE 27	
	NO. OF INDIVIDUALS		NO. OF INDIVIDUALS		NO. OF INDIVIDUALS	
	Survey 1	Survey 2	Survey 1	Survey 2	Survey 1	Survey 2
1 *Paphies australis*	0	0	0	1	0	3
2 *Ruditapes largillierti*	0	30	0	0	0	17
3 *Tawera spissa*	8	2	6	0	349	16
4 *Gari stangeri*	0	1	0	0	0	24
5 *Macomona liliana*	0	2	1	0	0	7
6 *Soletellina siliquens*	1	3	1	0	7	9
7 *Nucula nitidula*	0	6	0	0	3	44
8 *Nucula hartvigiana*	0	0	0	0	0	23
9 *Divaricella huttoniana*	3	1	5	3	0	4
10 *Perna canaliculus*	0	0	0	0	0	0
11 *Myadora striata*	0	0	5	3	1	0
12 *Scalpomactra scalpellum*	0	5	0	0	0	1
13 *Gari lineolata*	0	0	0	0	0	0
14 *Soletellina nitida*	0	0	0	0	0	4
15 *Dosinia subrosea*	0	0	0	0	0	0
16 *Gomphina maorum*	0	0	0	0	0	0
17 *Paphies subtriangulata*	0	0	0	0	0	0
18 *Modiolus areolatus*	0	0	0	0	0	0
19 *Arthritica bifurca*	0	0	0	0	0	0
20 *Notocallista multistriata*	0	0	0	0	0	0
21 *Zenatia acinaces*	0	0	0	0	0	0
22 *Hiatella arctica*	0	0	0	0	0	0
23 *Diplodonta striatula*	0	0	0	0	0	0
24 *Felaniella zelandica*	0	0	0	0	0	0
25 *Dosinia lambata*	0	0	0	0	0	0
26 *Tellina ?gaimardi*	0	0	0	0	0	1
27 Sp. 1	0	0	0	0	0	0
28 Sp. 2	0	0	0	0	0	0
29 Sp. 3	0	0	0	0	0	0
30 Sp. 4	0	0	0	0	0	0
31 Sp. 5	0	0	0	0	0	0
TOTAL NUMBER AT SITE	**12**	**50**	**19**	**7**	**360**	**153**