The ecology of the benthos in Liverpool Docks.

Thesis submitted in accordance with the requirements of the University of Liverpool for the degree of Doctor in Philosophy.

by

Stephen Brian Wilkinson

April 1995

Port Erin Marine Laboratory
Department of Environmental and Evolutionary Biology
University of Liverpool
Port Erin
Isle of Man

"In science as in life men are governed
more by words than by clear concept"

Shelling (cited by Birch 1957)

ACKNOWLEDGEMENTS

I would like to thank both my supervisors Prof S.J.Hawkins and Dr G.R.Russell for their advice and guidance throughout this project and for enduring an often awkward student. Thanks also to Dr J.R.Allen (aka 'Boss') for useful discussions on many aspects of this study and encouragement when it was most needed.

I have been ably assisted in both the laboratory and field a number of people. Thanks must go first and foremost to Jimmy McGill for assistance on many cold and boring dives and other services rendered. I was also assisted at various times, both in the field and the laboratory, by Gill Haynes, Tony Tollitt, Nick Cole and Ron Dyson. Thanks also to the Merseyside Development Corporation and in particular Bill Broadbent for allowing access to the docks, often at very short notice.

During the last three years I have benefitted from the friendship of numerous friends both in Liverpool and the Isle of Man. In particular I would like to thank all those at LUSAC especially JJJimmy 'the tongue' McGill, Little Al, Eeny, Feisty and Bob for excellent holidays, beer, curries and many happy memories. Life at Liverpool would not have been the same without them. Thanks also to all members of the 'Freshwater Posse' and more recently the 'Brackish Babes' who had the misfortune to share a lab with me. Frequent visits to the Isle of Man were made possible by free accommodation provided by my supervisor at 'Thie Na Grumpy' and once on the Island sanity was preserved particularly by Timmy and Rich.

Finally, thanks must go to my parents for kindling the spark of interest in all things marine, many years ago. Perhaps those cold wet mornings crawling about on the shore were not in vain!

ABSTRACT

A broadscale survey of the benthos was carried out in the docks around Liverpool and the results indicated that the walls of the majority of the South Docks were dominated by *Mytilus edulis*. This species tended to be less abundant in docks close to the intake from the Mersey while *Molgula manmattensis* tended to be more abundant at these sites. These differences may be due to a combination of either increased suspended solids or decreased phytoplankton. The walls of Albert, Queens and Princes Docks were surveyed over a three year period. The results indicated that the abundance of *Mytilus* was relatively constant between years. Other more ephemeral species, such as *Ciona*, showed considerable variation both within and between years.

Closer examination of the *Mytilus* population structure has indicated that it was dominated by one or two cohorts which had settled in 1988 - 1989. Much less recruitment has occurred subsequently. Reasons for this lack of recruitment are examined, however, the most likely explanations are increased predation from *Carcinus* and/or intraspecific interactions from the adult bed, either filtering out *Mytilus* larvae or reducing food supply to new settlers.

Monitoring of the zooplankton indicated considerable temporal and spatial variation, despite the fact that the docks are effectively a closed ecosystem. The observed variations are attributed to either adult or larval behaviour or changes in primary production affecting secondary production.

Tiles have been used to follow the pattern of annual succession and the effect of timing of available space on this pattern of succession. Results were integrated with changes observed in the wall benthos and variations in larval supply. Considerable differences were observed in the community that developed on suspended tiles, tiles fixed to the dock wall and cleared areas of the dock wall. One of the primary factors affecting this was thought to be reduced food supply on the wall due to the dense filter feeding assemblage there. No evidence was found of any strong interspecific interactions in the successional sequence. Rather, the community composition was typical for the time of year. The community development is described with regard to the life-history strategies of the species in the fouling assemblage.

Tiles were also used to look at the annual pattern of algal settlement. This indicated that diatoms were the principal settlers early in the year, brown ephemerals such as *Giffordia* and *Punctaria* during spring and green ephemerals such as *Enteromorpha* and *Cladophora* over the summer period. Amphipods were the dominant grazers of this assemblage. Tiles left in place for two to three months initially developed dense algal growth but this was subsequently replaced by a cover of *Botryllus*. This change was thought to be accelerated by the grazing amphipods. No perennial algae were recorded in the docks; reasons for this are proposed.

Finally, an assessment is made of the overall stability of the benthic ecosystem found in the docks around Liverpool and a number of possible management options, which could be used to improve the stability, are suggested.

CONTENTS

ACKNOWLEDGEMENTS 3

ABSTRACT 4

CHAPTER 1 - GENERAL INTRODUCTION 9

CHAPTER 2 - LIVERPOOL DOCKS - A REVIEW

2.1 Introduction 15
2.2 History and redevelopment plans 17
    2.2.1 The South Docks 17
    2.2.2 The Wirral Docks 17
    2.2.3 The Central Docks 21
2.3 Research on Liverpool Docks 22
2.4 Water impoundment regime 24
    2.4.1 South Docks 24
    2.4.2 Wirral Docks 28
    2.4.3 Central Docks 28
2.5 The Physico-Chemical environment of Liverpool Docks 29
    2.5.1 Salinity 29
    2.5.2 Oxygen / Temperature 29
    2.5.3 Water clarity 31
    2.5.4 pH 31
    2.5.5 Nutrients 33
2.6 The Mersey Ecosystem 34

CHAPTER 3 - GENERAL METHODS

Introduction 40
3.1 Development of methods for non-destructive sampling of the dock wall community 40
    3.1.1 Introduction 40
    3.1.2 Methods 41
    3.1.3 Results 43
    3.1.4 Discussion 43
3.2 Introduction to multivariate statistics 47
    3.2.1 Introduction 47
    3.2.2 Which technique? 48
    3.2.3 Correspondence Analysis 49
    3.2.4 Principal Component Analysis 51
3.3 Nomenclature 52

CHAPTER 4 - SPATIAL COMPARISON OF DOCKS IN THE LIVERPOOL AREA

4.1 Introduction 54
4.2 Materials and Methods 57
    4.2.1 Study site 57
    4.2.2 Environmental parameters 57
    4.2.3 Sediment fauna 60

4.2.4 Photographic sampling of the walls 60
4.2.5 Destructive sampling of the wall benthos 60
4.2.6 Timed search 61
4.2.7 *Mytilus* population 61
4.2.8 Multivariate analysis 62
4.3 Results 63
4.3.1 Physico-chemical parameters 63
4.3.2 Sediments 63
4.3.3 Mud fauna 63
4.3.4 Vertical distribution of species on dock wall 66
4.3.5 Multivariate analysis of dock wall communities 76
4.3.6 Destructive samples 78
4.3.7 Mytilus population structures 85
4.3.8 Species present 85
4.4 Discussion 91

CHAPTER 5 - TEMPORAL CHANGES IN THE WALL COMMUNITIES IN THE LIVERPOOL DOCKS

5.1 Introduction 103
5.2 Methods 107
5.2.1 Study sites 107
5.2.2 Sampling 107
5.2.3 Multivariate analysis 107
5.3 Results 109
5.3.1 Albert and Queens Docks 109
5.3.2 Princes Dock 120
5.3.3 Multivariate analysis 121
5.4 Discussion 126

CHAPTER 6 - MYTILUS POPULATION DYNAMICS AND GROWTH

6.1 Introduction 135
6.2 Materials and methods 142
6.2.1 Spatial distribution 142
6.2.2 Population structure and absolute growth 142
6.2.3 Biometric growth 144
6.3 Results 147
6.3.1 Spatial distribution 147
6.3.2 Mytilus population structure and dynamics 147
6.2.3 Relative growth 158
6.4 Discussion 162
6.4.1 Spatial distribution 162
6.4.2 Mytilus population dynamics 165
6.4.3 Relative growth 174
6.4.4 Future research 177

CHAPTER 7 - SPATIAL AND TEMPORAL VARIATION IN THE ZOOPLANKTON

7.1 Introduction 181
7.2 Methods 184
7.2.1 Temporal monitoring 184
7.2.2 Spatial survey 184

7.3 Results 186
    7.3.1 Temporal changes 186
    7.3.2 Spatial comparison 201
7.4 Discussion 203
    7.4.1 Vertical distribution 203
    7.4.2 Temporal variations 204
    7.4.3 Spatial distribution 210
    7.4.4 'Supply-side ecology' - implications 211
    7.4.5 Future research 212

CHAPTER 8 - COMMUNITY DEVELOPMENT ON TILES IN ALBERT DOCK

8.1 Introduction 215
8.2 Materials and methods 219
    8.2.1 The relationship between larval supply and settlement density 219
    8.2.2 The pattern of community development 219
    8.2.3 The effect that time of deployment has on community development 220
    8.2.4 Comparison of community development on suspended tiles, tiles fixed to the wall and cleared areas of the dock wall 223
    8.2.5 Effect of predation on the pattern of community development 223
8.3 Results 225
    8.3.1 Larval supply 225
    8.3.2 General pattern of community development 225
    8.3.3 Effect of time of deployment on pattern of succession 232
    8.3.4 Comparison of community development on tiles and on the dock wall 239
    8.3.5 Effect of caging 239
8.4 Discussion 243
    8.4.1 Effect of substrate and position 243
    8.4.2 The successional sequence 246
    8.4.3 The persistence of species in the docks 250
    8.4.4 Summary 251

CHAPTER 9 - PRELIMINARY OBSERVATIONS ON ALGAL SETTLEMENT AND DYNAMICS IN AN ENCLOSED DOCK BASIN

9.1 Introduction 253
9.2 Methods 257
    9.2.1 Assessment of dock flora 257
    9.2.2 Experimental design 257
    9.2.3 Community analysis 257
    9.2.4 Diatom preparations 259
    9.2.5 Physico-chemical environment 260
    9.2.6 Multivariate analysis 260
9.3 Results 263
9.4 Discussion 273

CHAPTER 10 - GENERAL DISCUSSION

10.1 Introduction 287
10.2 Spatial variation of the benthos 287
10.3 Benthic algae 289
10.4 The stability of the benthic community in the South Docks in relation to management 289
10.5 Summary 293

REFERENCES 294

APPENDIX 1 328

APPENDIX 2 330

CHAPTER 1

GENERAL INTRODUCTION

GENERAL INTRODUCTION

There has been a trend in recent years to redevelop deteriorated inner city sites into areas of greater aesthetic appeal as part of urban renewal schemes (Hindle 1993). Some of the most successful projects have been those involving the redevelopment of disused dock basins (Pidwill 1993, Ridding & Gardner 1993). These redevelopments have included schemes to create shopping centres, office space and housing (e.g. Liverpool South Docks complex, London Docklands, Salford Quays). Some sites, including Liverpool, have also promoted tourism and established other recreational facilities such as water sports centres, marinas, museums and art galleries. The Albert Dock Complex in Liverpool has been one of the most successful dockside redevelopments and now rates as one of the top tourist attractions in Britain, as well as supporting a variety of business and recreational ventures. The ecology of the benthos of these basins are the subject of my thesis.

At most of these sites the dock basin has been retained full of water to enhance the appeal of the site. Unfortunately, the estuarine water source for such sites is often heavily polluted from industrial, agricultural and domestic sources from the whole catchment basin. Not surprisingly this often causes water quality problems in the dock basins (Hendry *et al*. 1988a, Allen *et al*. 1992, Walker *et al*. 1993, White *et al*. 1993). In particular, the high nutrient loading and enclosed nature encourage dense algal blooms. As well as being visually unattractive these blooms, coupled with high organic loading of the sediments, can lead to problems of bottom anoxia when the blooms begin to decay (Allen *et al*. 1993, Walker *et al*. 1993). If the bottom water is disturbed under these conditions bad smells in the surrounding area may result. Clearly, maintaining good water quality is of great importance in redeveloped dockland areas and affects the likely return of the large sums of money invested in redevelopment.

Docks are an unusual habitat sharing features in common with both marine and freshwater ecosystems (see comments in Hawkins *et al*. 1992a). They are closed systems, akin to freshwater lakes, and yet are also saline, which allows them to support many benthic filter feeders, more typical of marine systems. There are a number of other natural habitats with which docks share much in common. These include lagoonal systems, estuaries and bays with restricted entrances and saline lakes (Allen 1992). The relative rarity of lagoons around Britain and Europe as a whole, has led to suggestions that artificial lagoons, such as docks, could be used to conserve specialist lagoonal species (Barnes 1991, Allen *et al*. in sub.). Habitats, such as lagoons and saline lakes, also share many of the water quality problems found in docks. They are often highly eutrophic resulting in dense phytoplankton blooms. The relatively enclosed nature also often leads to thermal and salinity stratification. These factors may combine to reduce the concentration of dissolved oxygen in the bottom water (Dorey *et al*. 1973, Crawford *et al*. 1979, Grizzle 1984)

A nationwide survey of ten docks was made by Hendry *et al*. (1988a). They suggested that problems caused by high nutrient concentrations, algal blooms, anoxic water and low species diversity were a typical feature of these habitats and attributed the problems to the poor quality source water used to fill the basins. More detailed studies have been made of individual dock systems. Changes in the water quality and invertebrate and fish communities as a result of the isolation and artificial mixing of the freshwater basins at Salford Quays have been described (Hendry *et al*. 1989, Bellinger *et al*. 1993, Walker *et al*. 1993, White *et al*. 1993). The problems associated with the hydrography at

Preston Docks, particularly with regard to the low salinity, have also been examined (Conlan *et al.* 1988,1992, Conlan 1989). At Salford Quays, some of the basins have been developed as a recreational fishery (White *et al.* 1993) and the potential for other docks to support populations of fish has also been considered (Conlan *et al.* 1988, Hendry *et al.* 1988b).

Some of the earliest research was carried out on Sandon Dock in the Liverpool area (Russell *et al.* 1983, Cunningham *et al.* 1984, Hawkins *et al.* 1992a,b, Hawkins *et al.* 1993). Results from Sandon Dock suggested that a dense natural settlement of the filter feeder *Mytilus edulis* (henceforth referred to as *Mytilus*) on the dock walls and suspended culture ropes considerably reduced phytoplankton blooms improving water quality. Following the redevelopment of the area surrounding the South Docks improvements were also observed following a similar natural settlement of *Mytilus* and experimental introduction (Allen 1992, Allen *et al.* 1992, Allen & Hawkins 1993a&b). There was concern, however, over the long term sustainability of this system. Much of this thesis is concerned with addressing this question. I concentrated on the benthic filter feeding communities which play a key role in ecosystem function.

In addition to the applied aspect of this study however, docks are of interest from a purely ecological point of view. As mentioned above they are an unusual habitat, having features in common with marine and freshwater systems. They are also well suited for testing ecological ideas and are very amenable to manipulation. This is aided by their relatively discrete nature, simple shape with flat walls and ease of access in all weather conditions. Therefore this study also aims to use the dock ecosystems as a model system in which ecological ideas could be tested. It is also hoped to eludicate any particularly unusual aspects of the ecosystem worthy of further investigation.

The following chapter provides a brief introduction to the previous work that has been carried out on the docks around Liverpool, including the history and redevelopment plans of these areas. Chapter 3 describes the methodology used to describe the community on the dock walls and also provides an introduction to some of the multivariate methods used and the interpretation of these. The sediment and wall communities of nine docks in the Liverpool area are described in chapter 4 and this is followed by a description of the temporal changes in three of these sites over the course of this study (Chapter 5). Chapter 6 focuses on the growth and population dynamics of *Mytilus* in the docks. Both temporal and spatial variation in the zooplankton is described in chapter 7, particularly with regard to larval forms. This chapter also explores the decrease in zooplankton observed by Allen (1992), also seen in Sandon Dock (Cunningham *et al.* 1984). Some of the results from this chapter are integrated with chapter 8 which looks at community development on tiles suspended in Albert Dock. Chapter 9 provides some preliminary observations on the algal community in the docks, again using tiles but attached to the dock wall. Finally chapter 10 integrates the results from chapters 4 to 9 to assess the overall sustainablity of the dock ecosystem, particularly with regard to the South Docks. This chapter also includes possible management options available and suggested areas for further research.

CHAPTER 2

LIVERPOOL'S DOCKS - A REVIEW

2.1 INTRODUCTION

Quite a considerable amount of research (see Allen 1992, Hawkins *et al.* 1992 for reviews) has been carried out on docks in the Liverpool area over the last 15 years and much of this is pertinent to the findings of the present study. This chapter first summarises the history of docks in the area (based on Ritchie-Noakes 1984, McCarron & Jarvis 1992) and future redevelopment plans. It then goes on to describe what is known about the Mersey ecosystem before reviewing the research that has been carried out on the docks themselves.

The role of Liverpool as a port began early in the 17th century, long before the building of any dock. At this time ships used the slight shelter provided by a small tidal inlet, known as the 'Pool'. The large tidal range (as much as ten metres) strong currents and shifting mud banks made access for ships difficult and often hazardous on the Mersey. By the late 17th century substantial numbers of ships were sailing into Liverpool and increasingly finding facilities inadequate. This became particularly true as ships got larger and more liable to damage when grounded and therefore had to be kept afloat.

By 1700 Liverpool's population had grown to 6000 and imports of tobacco and sugar and exports of salt were growing rapidly (Ritchie-Noakes 1984). Accommodating any further expansion in trade was getting difficult. At the instigation of the Corporation in 1709, Liverpool saw the beginning of the construction of the first commercial dock in the world. The 'Old Dock' as it came to be known, permitted the loading and unloading of ships at all states of the tide without forcing them to be left stranded. Docks had been known elsewhere, for instance the Navy had built one at Deptford early as the 16th century, but Liverpool's was the first to be designed specifically for trade (Ritchie-Noakes 1984). The development of the so-called 'three-cornered trade' was particularly important to the success of Liverpool as a port. This involved taking salt to Africa, slaves to America and returning to England with sugar and tobacco (Ritchie-Noakes 1984). The expansion of trade in Liverpool was facilitated by improved canal and river links during the first half of the 16th century and later by a better road network. During the 19th century the industrial revolution resulted in a considerable increase in the population of Liverpool, while the growth of the British Empire at this time also led to an increase in trade (Ritchie-Noakes 1984). By 1900 trade inwards had risen to 12.4 million tons and the Mersey Docks and Harbour Company (MDHC) had approximately fifty working docks under their control (McCarron & Jarvis 1992).

The pattern of decline seen in other major ports during the second half of the 20th century was particularly obvious in Liverpool. The older, inner city docks had neither the size nor the surrounding space to allow their continued use as ship size and cargo volumes rapidly expanded. This led to a number of sites falling into disuse and dereliction, particularly during the 1970s. During the early 1980s some of these areas came under the control of the Merseyside Development Corporation (MDC) for redevelopment. The MDC has also been heavily involved in the planning and development of other sites that have remained under MDHC control.

The docks around Liverpool can be divided into four main chains, namely : the Wirral Docks, the South Docks (the chain including Albert Dock), the Central Docks (from Princes north to Bramley Moore) and the North Docks (those north of Bramley Moore). Redevelopment is now planned for at least part of all of these chains, except the North

Docks which remain commercially active and under the control of the MDHC.

2.2 HISTORY AND REDEVELOPMENT PLANS

2.2.1 The South Docks

The South Docks date back to the mid 18th century (McCarron & Jarvis 1992), however their small size led to the rather premature decline of this chain. Albert Dock (Fig 2.1) was last used properly during the Second World War and was finally closed in 1972. Brunswick remained active, serving a granary, until it too was finally closed in 1975. After this the gates were left open, allowing the docks to fill rapidly with silt. When the chain came under MDC control in 1981, the silt was 10m deep and only covered at high tide, while the warehouses had been allowed to fall into ruin. The MDC installed new gates to isolate the docks from the Mersey and they were then dredged to a depth of between three and six metres (see Table 2.1). One dock, Queens Graving, was dredged to a depth of 10m and isolated from the rest of the chain. The dredging commenced in 1981 beginning in Canning Dock and working south to Brunswick. The operation was finally completed in 1985 when new gates were installed at the Brunswick entrance and water was returned to the docks. Since then considerable development has taken place around the chain and the area now supports a marina, a shopping centre, a water sports centre, a museum, an art gallery, the new Customs and Excise building as well numerous flats.

2.2.2 The Wirral Docks

While much of this chain still remains commercially active, three docks have been targeted for redevelopment, namely Wallasey, Morpeth and Egerton (Fig 2.2). Wallasey was

Table 2.1 Approximate areas, maximum depths and volumes of main docks in the Liverpool area planned for redevelopment.

DOCK	SURFACE AREA (m^2)	DEPTH (m)	VOLUME (m^3)
<u>South</u>			
Canning HT	10341	5.5	56876
Canning	17873	5.0	89365
Albert	31290	6.1	190869
Salthouse	25969	3.9	101279
Wapping Basin	6681	3.5	23384
Dukes	6500	4.0	26000
Wapping	20081	4.5	90365
Queens	47296	4.2	201008
Queens Branch 1	19853	4.1	81397
Queens Graving	4712	10.0	47120
Coburg	30700	3.7	113590
Brunswick	64505	4.0	258020
Brunswick Lock	808	4.0	3232
<u>Central</u>			
Princes	35430	7.0	248010
<u>Wirral</u>			
Morpeth	67200	8.5	571200
Egerton	27500	6.0	165000
Wallasey	50000	0.5	25000

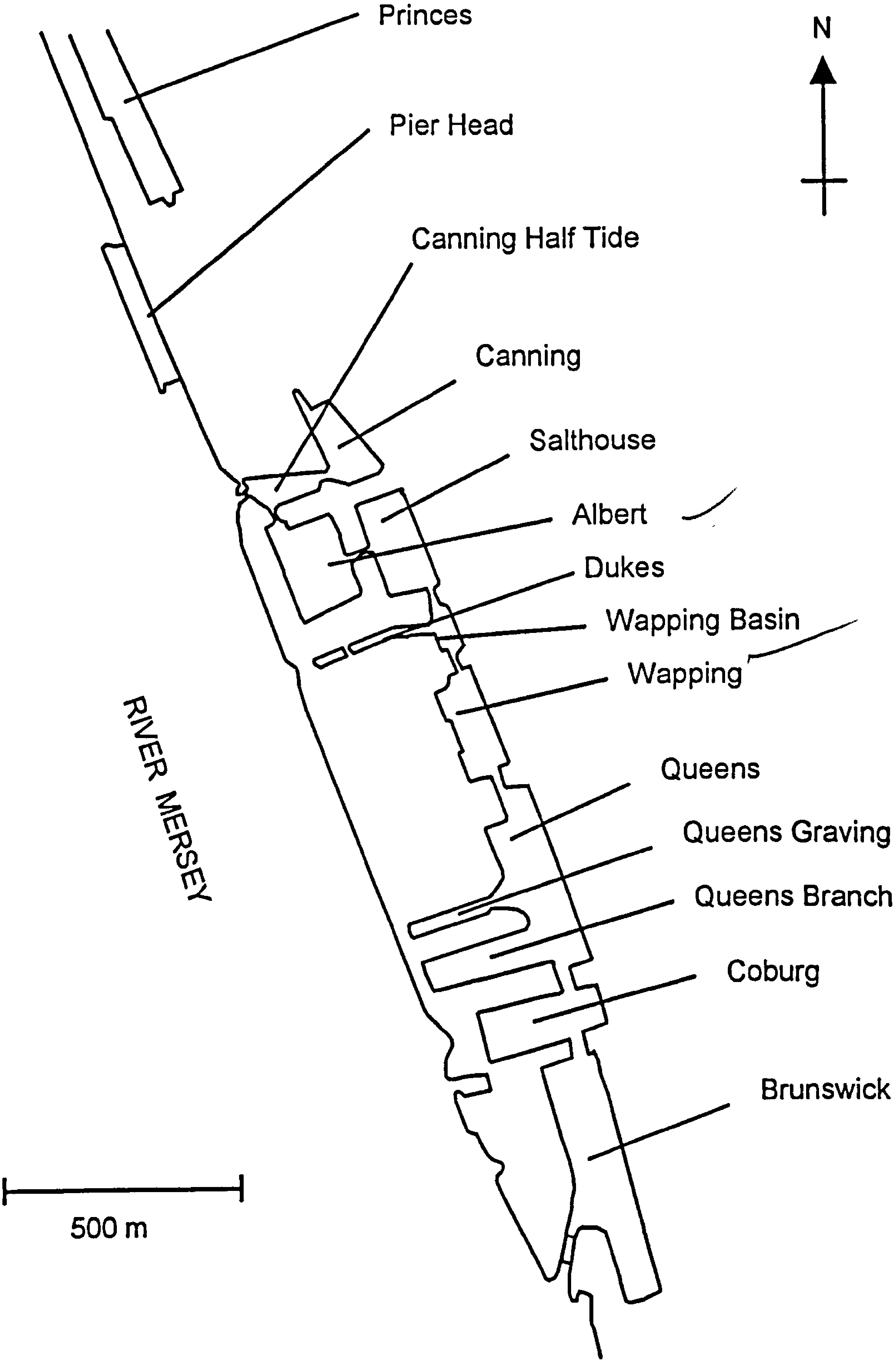

Fig 2.1 The layout of the South Docks, Liverpool, with the relative position of Princes Dock also shown.

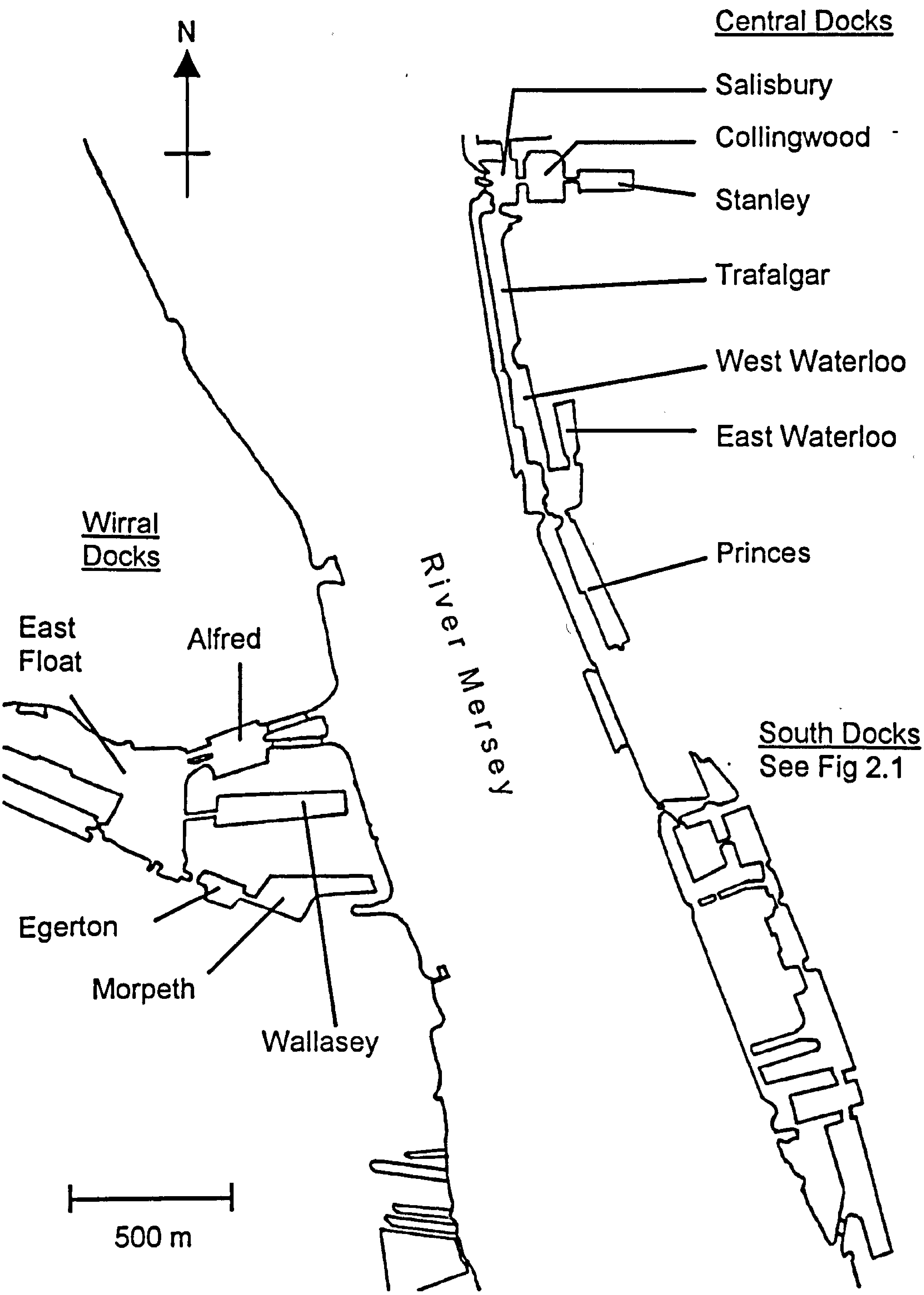

Fig 2.2 The layout of Wirral and Central Docks, Liverpool. (See Fig 2.1 for more detail of South Docks)

opened in 1877, originally designed as a low water basin, but later remodelled into a normal dock. The construction of a pumping station on this site in 1890, to move water into the Wirral Dock system resulted in a heavy deposition of silt in the basin. It finally became useless during the 1960s and now stands almost completely full of silt. Morpeth and Egerton were opened in 1847. In 1990 these docks were partially in-filled leaving them completely isolated from the Mersey, except for an impoundment system where water can be pumped in from the East Float when required. Impoundment is relatively infrequent however, as the dock level remains reasonably constant. A project known as 'Twelve Quays', is planned for this area. This would create up to 500 new houses and 46000 m^2 of business/office space.

2.2.3 The Central Docks

The Central Docks are situated at the end of a chain that is still commercially active and some, particularly the northernmost members of this group, are still in use. These docks remain in MDHC control. Princes Dock (Fig 2.2), opened in 1821, is one of the oldest extant docks in Liverpool, although docks have stood on the site of the South Docks for much longer. Princes Dock is situated at the southernmost end of the Central Docks chain. Its last major traffic was the P&O Belfast passenger service which finally ceased operation in 1981. There are now plans to develop the area into a new commercial centre, overlooking the river. Waterloo followed Princes into disuse in 1988. Since then the large grain warehouse on this site has been converted into flats and more are now planned. Trafalgar Dock was originally opened in 1836 but underwent considerable remodelling in 1929. It is now used only for temporarily berthing vessels and there are plans for conversion to a business park, once the old power station on the site has been demolished. Stanley Dock was constructed to allow vessels access to the Leeds-Liverpool canal via a series of locks. Presently it has temporary uses, such as housing a Sunday market, but it is practically redundant awaiting development into a combined residential and commercial centre. Bramley Moore and Nelson Docks were both opened in 1848. Nelson's last regular trade was in bulk rum while Bramley Moore was used mostly as a coal export and bunkering service. Both of these docks are still used occasionally, particularly by coastal container vessels and there are no plans at present to redevelop them. Similarly, Collingwood Dock which also opened in 1848 is to remain in use as an area for the berthing and repair of small boats.

2.3 RESEARCH ON LIVERPOOL DOCKS

The uniform and relatively enclosed nature of dock basins makes them a very amenable environment for biological observation or manipulation. However, whilst in use access to the docks for research was limited. Some of the early reports on the Mersey Estuary do include reference to the species present in the surrounding docks. Corlett (1948) compared settlement patterns on tiles suspended in Princes Dock and the estuary itself. However, it is only since the docks began to fall into disuse that there has been much research into their ecology. Particularly in the last 15 years there has been a rise in interest in this area of research, spurred on by the increased use of docks for redevelopment purposes and the importance of water quality. While a considerable amount of work has been done on the ecology of docks elsewhere around Britain (eg. Conlan *et al.* 1988, Hendry *et al.* 1988a, Boyd 1989, Conlan 1989, Ridling & Gardener 1993, Walker *et al.* 1993) the relatively high salinity of those in the Liverpool area, and the considerable redevelopment that is going on here, has helped make these some of the most interesting and best studied.

James and Gibson (1980) carried out a study of the fauna and heavy metals present in the mud in Collingwood Dock. They found very high levels of lead and zinc with *Capitella capitata* the dominant infaunal species. Pollution of this kind is a problem experienced in all docks in the Liverpool area.

In 1977 Sandon Dock was isolated in the hope of using it for the aquaculture of salmonids and oysters by the Fisheries Unit of Zoology, University of Liverpool. Shortly after this however a natural settlement of *Mytilus* led to the development of the dock for the exploitation of this species. Work began monitoring changes in both the water quality and the benthos (Naylor 1983, Russell *et al.* 1983, Cunningham *et al.* 1984, Hawkins *et al.* 1992a,b). The greatly improved water clarity here was attributed to filter feeding by the large *Mytilus edulis* population that settled in this dock, combined with an air-mixer that was employed to prevent stratification. By 1983 however, *Mytilus* was suffering from poor recruitment, and sea squirts such as *Ciona* and *Ascidiella* were rising in abundance (Naylor 1983). In 1983 the project was abandoned and the dock infilled and turned into a sewage treatment works (see Hawkins *et al.* 1992b, 1993 for reviews).

The redevelopment of the South Docks in 1985 gave further opportunity for study of the ecology of this unusual habitat. Since 1988 a programme of routine monitoring of changes in the physical environment, nutrient concentrations, plankton densities and benthic development has been maintained (Heaps 1988, Mincher 1988, Lonsdale 1990, Allen 1992, Allen *et al.* 1992, Hawkins *et al.* 1992b, Allen & Hawkins 1993, Hawkins *et al.* 1993, Zheng 1995, Hunt 1993, 1994). In 1991 this monitoring programme was extended to include Princes Dock (Zheng 1995). Some preliminary data have also been gathered on changes in the physico-chemical environment of the Wirral Docks, Morpeth and Egerton (Hunt

1993).

The redevelopment of the South Docks allowed further experiments to be carried out on the roles of artificial mixing and filter feeding by *Mytilus* in grazing phytoplankton blooms and improving overall water quality (Allen 1992, Allen *et al.* 1992, Allen & Hawkins 1993a&b). Some preliminary investigations were also made on the importance of macroalgae present in the system (Head 1990). There have been a number of studies of the fish community present and an assessment made of the potential for recreational angling in the system (Heaps 1988, Mincher 1988, Lonsdale 1990, Burton & Allen 1993). While significant populations of fish have been found, the problem with heavy metals and other contaminants outlined above present risks for human consumption (Burton & Allen 1993). The main species present are whiting (*Merlangius merlangus*), plaice (*Pleuronectes platessa*), flounder (*Pleuronectes flesus*) and sprat (*Sprattus sprattus*), although a sea trout was recently caught in Salthouse (W. Zheng pers. com., Liverpool University).

2.4 WATER IMPOUNDMENT REGIME

2.4.1 South Docks

Water is constantly lost from the South Docks, mainly through leakage and docking operations at both Canning and Brunswick Docks. A small amount is also lost through evaporation (see Parkman Consulting Engineers 1991 for exact figures). While a certain amount is also gained through dock/lock levelling and rainfall there is considerable net loss which must be constantly replaced. Considerable work has been put into small engineering works to restrict leakage.

Originally the docks were topped up approximately every 2-4 weeks, generally when the level was about 0.5m below the normal 8.5m ACD (Above Chart Datum). Water was replaced in a single operation by opening both inner and outer penstocks at Brunswick Lock (see Fig 2.3). This strategy resulted in considerable disturbance of the water in Brunswick. In the summer of 1991, a more frequent top-up regime, impounding lower volumes with each operation, was recommended (J.Allen, Liverpool University, pers. comm.). Then in May 1992 impounding pumps were brought into operation which worked on an automatic basis. When the water level in the docks was below 8.5m ACD and the river level was between 6.5m and 8.5m ACD on a flood tide water was automatically impounded into the docks. While water can be impounded under manual control on the ebb tide, studies have shown that levels of sewage-derived micro-organisms are much higher in water impounded at this time (Hunt 1993, 1994). Only impounding when the river is between 6.5 and 8.5m ACD and the relatively high level intake of the impounding pumps, ensures quite a low silt loading in the water impounded in this fashion.

Disturbance of the water column while the old impounding system was in operation could be seen as far north as the marina but probably extended below water level beyond this point. This was particularly the case when the difference in level between the river and docks was large (Allen 1991). Since the impounding pumps came into operation any obvious disturbance is confined to a small area just inside the lock gates into Brunswick Dock. The constant impounding system has also led to a much more constant water level within the docks (see Fig 2.4), particularly over the summer period when much greater fluctuations were caused through increased boat traffic to and from the river. In addition it is likely that this impounding strategy has reduced the amount of silt brought into the docks. As well as gradually filling the basin this silt is also likely to bring large amounts of nutrients adsorbed onto the surface

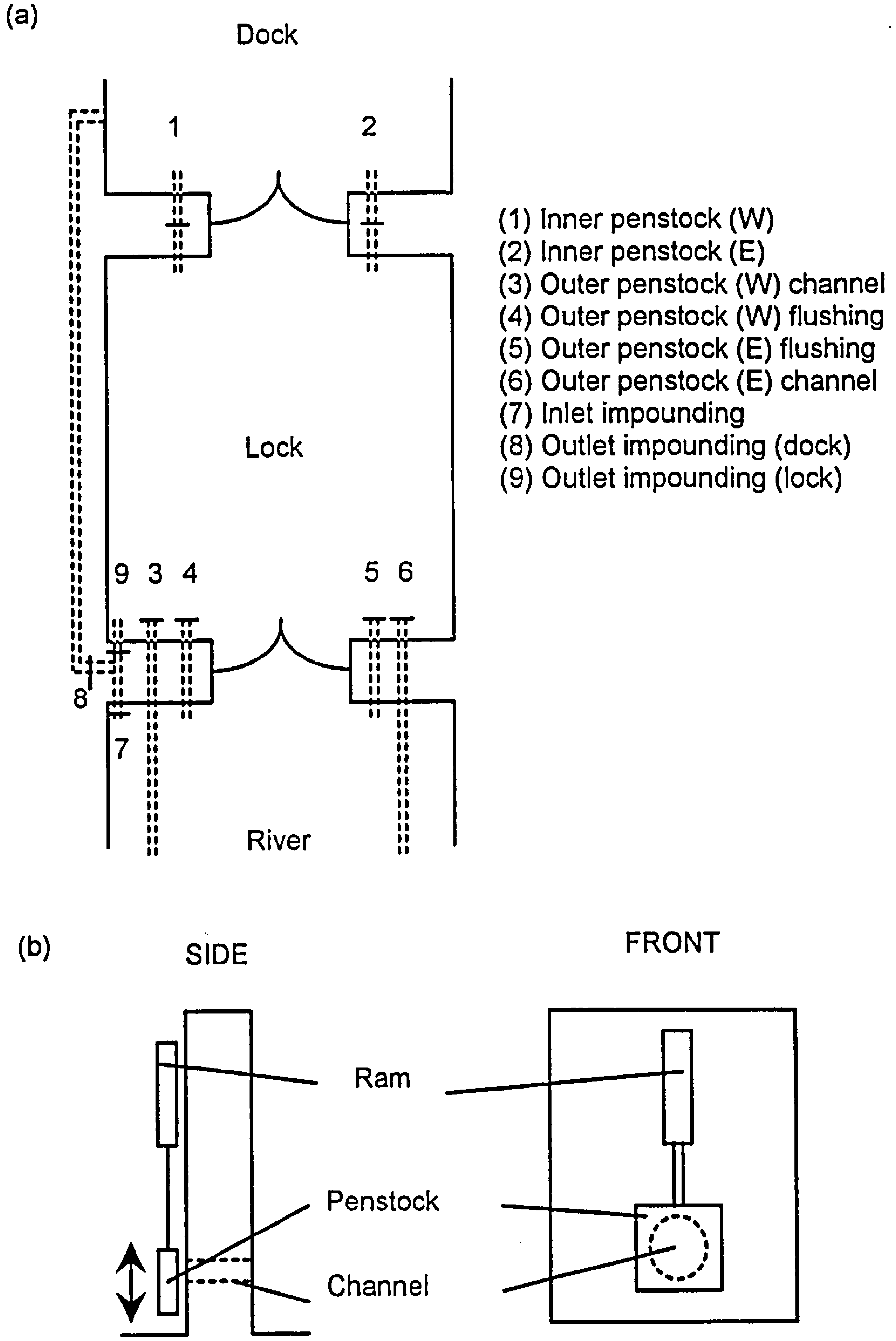

Fig 2.3 (a) Channels used to move water between the Mersey, the lock and dock basin and (b) diagram of penstock mechanism.

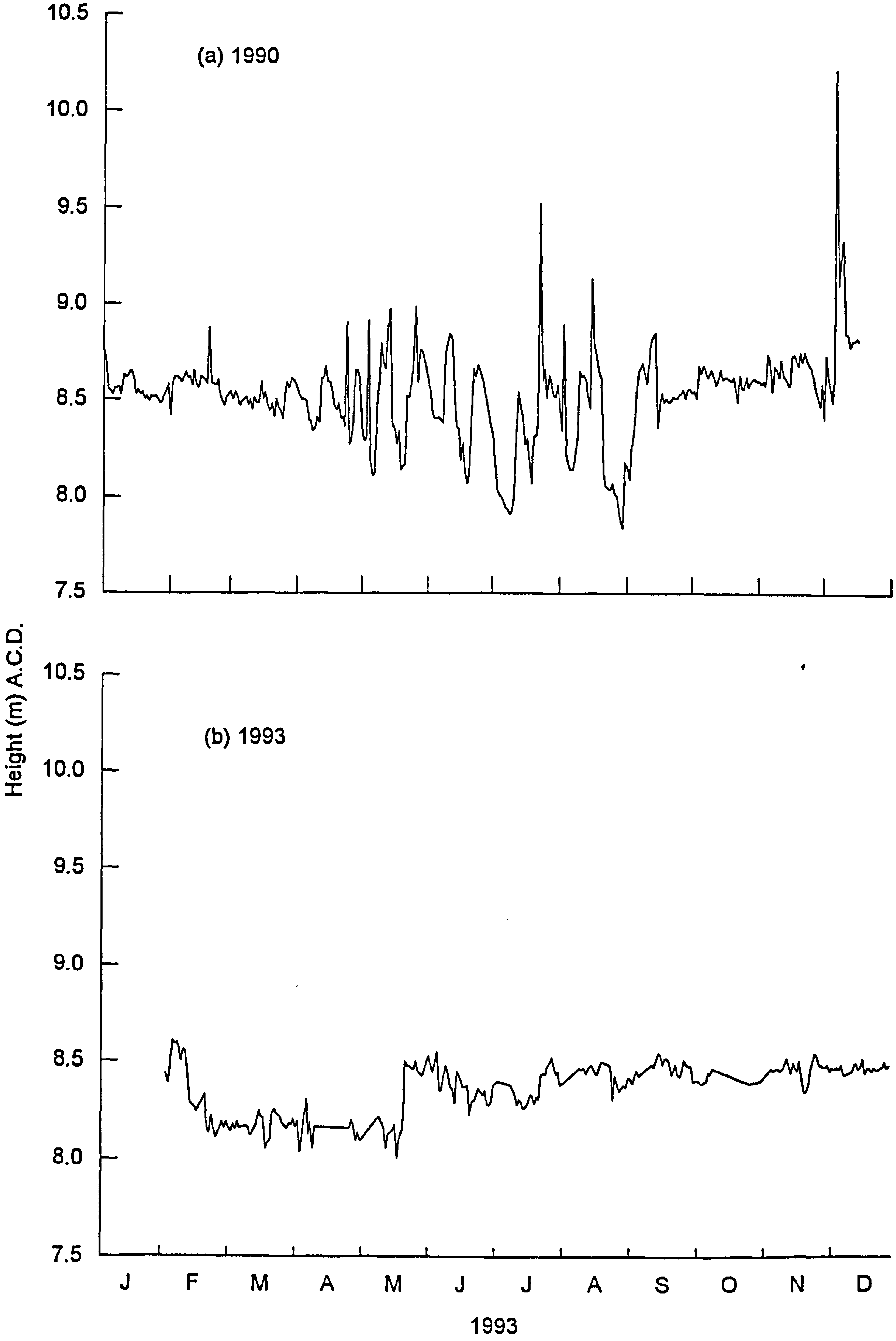

Fig 2.4 Variation in water level in the South docks during 1990 before the continuous top-up regime was introduced and during 1993 after its introduction(Data courtesy of the Merseyside Development Corporation)

of the particles.

One other point that is worth mentioning concerns the build up of silt at the river entrance to Brunswick Lock. Spray bars have been introduced on the wall just outside the dock complex which have been quite successful at reducing the build-up. However, periodically, approximately once per month on spring tides, a considerable volume of water is released from the docks by opening both inner and outer gates to further clear the channel. During these operations the dock level is reduced by about 0.1m, giving a total volume released of nearly 30 000 litres.

2.4.2 Wirral Docks

Despite the completely enclosed nature of Morpeth and Egerton Docks a certain amount of leakage through the dock wall does occur. At first a strategy of constantly topping up the level was employed, buying water from the MDHC, which was pumped in from East Float. This proved quite expensive, however, and ceased in 1992, when the water level was stabilised at 9.3m ACD. Since then there has only been one major input of water into these docks (in October 1993) when the level was raised by 1.22m. Work is under way to find and plug the leaks in these docks. The pumping house beside Wallasey Dock is still used to move water through Wallasey into the East Float. Plans regarding the future of this have not been finalised, but it seems likely that a channel will be created along one side of the dock to allow this procedure to continue after redevelopment of the dock.

2.4.3 Central Docks

Relatively little information is available on water losses and gains from these docks. Two pumping houses are in operation, one at Langton river entrance which moves water into Canada basin and the second at Seaforth. The water level in these docks is constantly topped up.

Salinity - determines species assemblage

Preston dock - 1-5‰ - no filter feeders established
Sandon dock - 24-28‰
Princes - 26-30‰
Morpeth - 18%
Wirral - less saline

2.5 THE PHYSICO-CHEMICAL ENVIRONMENT OF LIVERPOOL DOCKS

2.5.1 Salinity

The salinity (measured as conductivity) of the docks under investigation is of prime importance because it is this that ultimately determines the species assemblage that can be supported. This is particularly pertinent from a biomanipulation perspective as it can limit the presence of certain species of filter-feeders. For example, Preston Docks generally have a salinity of 1-5‰, and so far no species of filter feeder has been found that will flourish in this environment (Conlan 1989, Conlan *et al.* 1992, Hawkins *et al.* 1992b, 1993).

The salinity of Sandon Dock was in the range of 25-31‰(Russell *et al.* 1983). The South Docks have a slightly lower salinity, ranging from 24‰ - 28‰ (Allen 1992, Allen & Hawkins 1993b, Zheng 1995). Haloclines are very rare though Allen (1992) did record a 3‰ difference between surface and bottom of Queens Graving Dock on one occasion which she attributed to surface run-off. The salinity in Princes is generally a little higher than that found in the South Docks and fluctuates between 26‰ and 30‰ (Zheng 1995). As yet little information is available as regards the long term variations in the salinity of the Wirral Docks. Certainly they are less saline than those around Liverpool and presently Morpeth is about 18‰. The information that is available seems to indicate that the fluctuations in salinity are quite large (Hunt 1993, pers. obs.) which may be at least partly due to the completely enclosed nature of these docks.

2.5.2 Oxygen / Temperature

Both Princes and the South Docks system show a similar pattern of temperature variation, with a summer maximum of 20°C and winter minimum of about 5°C (Zheng 1995). It has

O_2/ temp

Princes and South - 20°c → 5°c

Thermal strat - 5°c difference in deeper docks (Albert, Graving)

Morpeth similar to South docks

South docks - Instances of supersaturation vs anoxia (top + bottom)

artificial mixing

been suggested that the extreme temperatures experienced in the docks may limit the survival of some species here (Russell *et al*. 1983). Thermal stratification of up to a 5°C (surface to bottom) difference do periodically occur in deeper docks (eg. Albert, Graving) and are generally less apparent in the shallower docks such as Queens (Allen 1992, Zheng 1995). From the results available from Morpeth, it seems this dock shows similar temperature profile to that observed in the South Docks (Hunt 1993, 1994).

Instances of oxygen supersaturated surface water and hypoxic bottom waters have been recorded in the South Docks (Allen 1992, Zheng 1995). The periods of hypoxia resulting from high biological oxygen demands of the sediments and bottom waters were confined to 1988 and 1989 when dense phytoplankton blooms were more prevalent (Allen 1992). Allen (1992) recorded polychaete mortality and flatfish with respiratory problems during hypoxic conditions. Fish kills and a build up of hydrogen sulphide were also recorded in the South Docks at this time. In Albert Dock oxygen concentrations of less than 20% were recorded for a maximum duration in any one period of more than two months in 1988, two to three weeks in 1989 and not at all in 1990 and subsequently. In 1991 a low cost mixing device (designed by Allen, Liverpool University), consisting of a perforated tube connected to a compressor, was installed in Albert Dock. This has been switched on in the summer months when thermal stratification or low bottom oxygen concentrations were detected. Data available for Princes are comparable with the South Docks, prior to the installation of the mixer, with an oxygen minimum of 15% and instances of supersaturation during the summer months. High surface oxygen levels are present in Morpeth (greater than 80%) throughout the water column during the whole year most of the time. However there have been periodic problems with serious anoxic events in this dock (Hunt 1994), including a major kill of eels due to anoxia in 1994.

Water clarity - due to variations in plankton concentrations.

Albert + Queens - clear in winter, turbid in summer.

Princes - high clarity

pH

pH is generally a reflection of the severity of algal blooms

2.5.3 Water Clarity

Water clarity has been assessed in the docks by means of a Secchi Disc. As the muddy bottom is relatively undisturbed any changes in water clarity are largely due to variations in plankton concentrations. The general pattern observed since 1988 in Albert and Queens Docks is one of clear water over the winter period followed by more turbid conditions during the summer (Fig 2.5). The minimum value recorded in these docks is about 1m, and generally the Secchi Disc can be seen on the bottom of the docks over the winter. In general, since 1988 there has been an improvement in the water clarity (particularly during 1989-1990) with longer periods of very clear water in the winter and shorter periods of lower turbidity in the summer (Fig 2.5). Studies on Princes Dock so far indicate that water clarity is very high, with a Secchi Disc minimum recorded to date of 2m in spring 1992 (Fig 2.5). The opposite situation has been found in Morpeth which until recently suffered from constant blooms of the dinoflagellate *Prorocentrum minimum* even in the winter months. Here the Secchi extinction depth was generally less than 0.5m for most of the summer with a winter maximum of 2.4m in 1993 and 1.8m in 1994 (Hunt 1993, 1994).

2.5.4 pH

The range of pH experienced in a dock is generally a reflection of the severity of algal blooms in that area. Since isolation from the Mersey, in the South Docks there has been a decrease in the range of pH from 1.6 units (7.4-9.0) in 1988 to 1.0 unit (7.3-8.3) in 1990 (Allen 1992). A very high range has been recorded in Morpeth (6.9-9.1 in 1993 and 7.6-9.5 in 1994; Hunt 1993,1994). At present no data are available on diurnal changes of the pH in the docks.

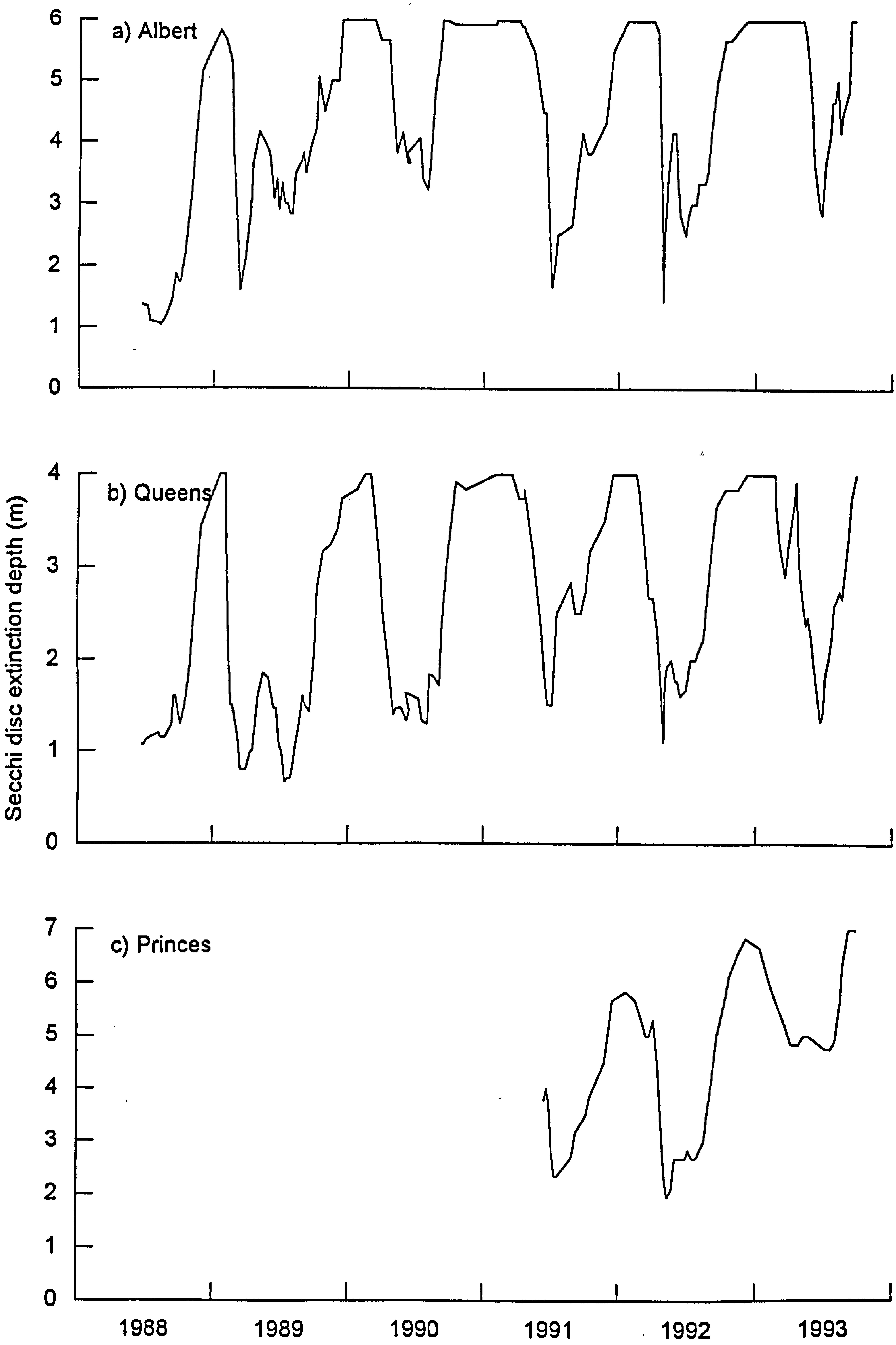

Fig 2.5 Variation in water clarity in Albert, Queens and Princes Docks over time (note difference in y-axis reflecting the maximum depth of each dock). Data 1988-1990 courtesy Allen 1992; 1990-1992 courtesy Zheng 1995.

Nutrients

Nutrients → phytoplankton densities

vertical stratification of nutrients

Ammonia high at bottom - anaerobic conditions where denitrification cannot take place

oligotrophication?

2.5.5 Nutrients

Fluctuations of total inorganic nitrogen and silica in the South Docks are closely related to changes in phytoplankton densities, with nutrient concentrations highest at times of low phytoplankton biomass (Allen 1992, Zheng 1995). The depletion of silica only limits the growth of diatoms, with flagellates remaining unaffected by the concentration of this nutrient. Ammonia tends to reach its winter peak earlier than nitrate and then tails off (Allen 1992). This is probably as a result of the time it takes for the ammonia being released from decaying phytoplankton to be oxidized to nitrate by nitrifying bacteria (Webb 1981). Vertical stratification of nutrient concentrations has been observed when dense stands of phytoplankton close to the surface cause greater depletion of nutrients than occurs in the bottom waters. Ammonia concentrations are often greater towards the dock bottom, particularly in anaerobic conditions when denitrification cannot take place.

Orthophosphate concentrations do not follow the changes in phytoplankton density and differ from the pattern in the open coastal waters of the Irish Sea(Slinn 1974, Slinn & Eastham 1984). Levels are low in spring and then gradually rise over the summer before peaking in early autumn and then gradually declining over the winter. This pattern is most likely caused by phosphate flux from the sediment to the water, with varying oxygen concentrations (Allen 1992). Phosphate release from sediments is known to be greater when oxygen concentration is low (Mortimer 1971). These results seem to suggest that phytoplankton growth in the South Docks may be limited by low dissolved nitrogen and silica concentrations, but not by dissolved phosphate (Allen 1992). Further research is required to verify this hypothesis.

Nutrient analysis of Princes Dock reveals a number of

Meso Eutrophic – problem for enclosed basins, which stratify in the summer.

→ algal blooms

differences from the pattern observed in the South Docks (Zheng 1995, Table 2.2). Concentrations of dissolved silicate and ammonium are generally lower in Princes and the peak observed in the phosphate concentrations in the South Docks during the summer is absent from Princes. There is little difference in the winter maxima of dissolved nitrate concentrations, however, nitrate tends to fall lower in the South Docks than Princes. Reasons for these differences are unclear at present. They may reflect chemical differences in the sediment in the two systems. In particular if Princes Dock has been relatively undisturbed for a long time the sediments may have low nutrient concentrations in the surface layers. The South Docks were dredged quite recently and may have had no time to form a sealing crust. Another possibility which may account for the absence of the phosphate peak in Princes, is that the large *Mytilus* population in the South Docks is actually releasing significant amounts of nutrients into the water column (Asmus & Asmus 1991, Zheng 1995).

Nutrient data for the Wirral Docks are scarce with surveys just starting. From what is available, it appears that there is no fixed annual pattern; the dissolved concentrations of nitrate, ammonium and phosphate all show large and erratic changes (Hunt 1993, 1994). Very high concentrations of ammonium have been periodically recorded in Morpeth and Egerton (Hunt 1993, 1994).

2.6 THE MERSEY ECOSYSTEM

The Mersey Estuary is the source of water for the docks described above. The Mersey is usually considered one of the most polluted rivers in Europe (Clarke 1989). During the late 19th and 20th centuries the area surrounding the Mersey saw a large increase in both population density and industrial activity. The catchment area now supports over five million people and this leads to high quantities of

Table 2.2 - Maximum and minimum recorded concentrations of nutrients in Albert, Queens, Princes and Morpeth Docks compared with the River Mersey. Data, except that for Morpeth, are courtesy of Zheng and relates to period 1991-1993. Morpeth data from Hunt (1993) are from Nov 1992 - June 1993.

	Nitrate (N mg/l)	Reactive Silicate (Si mg/l)	Ortho-Phosphate (P mg/l)	Ammonium (N mg/l)
Albert	0.01-1.15	<0.01-1.35	0.03-0.93	0.01-0.33
Queens	0.01-1.42	0.01-1.21	0.03-0.96	0.01-0.38
Princes	0.20-1.31	0.04-0.86	0.04-0.32	0.01-0.17
Morpeth	<0.01-1.11	N.A.	0.03-0.40	0.01-3.29
Mersey	0.40-1.79	0.01-1.65	0.02-0.48	0.10-0.68

sewage and other domestic waste. Much of this has been discharged directly into rivers or coastal waters. As part of the Mersey Basin Campaign a primary treatment facility has been set up at Liverpool. This has led to a large increase in the quantity of sludge being dumped at sea. The sewage input leads to high biological oxygen demands and associated oxygen depletion. Improvements are beginning to be seen, however, following the introduction of primary treatment. In particular the degree of anoxia found in the estuary is decreasing. The high nutrient loading in the river is enhanced by agricultural run-off, making the Mersey extremely eutrophic. This particularly presents problems in the enclosed dock basins which heat up relatively quickly and stratify during the summer, encouraging algal blooms.

Large quantities of industrial waste are also released into the Mersey. Particular problems have been experienced with heavy metals which become elevated in concentration in sediments (Rae & Aston 1981, Riley & Towner 1984, Leah *et al.* 1992). There are also high concentrations of persistent organics, such as hexachlorocyclohexane (HCH), dichlordiphenyltrichlorethane (DDT), and polychlorinated biphenyls (PCBs) (Irish Sea Study Group 1990).

The estuary itself is quite a harsh environment having a large tidal range, an often unstable bottom and high quantities of fine silt. These factors combine with the pollution problems mentioned above to contribute to the relative paucity of species in Liverpool Bay. While historically the area did support important fisheries for shrimp and flounder, the industrial revolution and associated pollution increase has taken its toll (Wilson *et al.* 1988). By the early 20th century the Mersey was considered very polluted especially with regard to sewage (Fraser 1938) leading to frequent periods of anoxia.

The Liverpool Marine Biology Committee carried out a certain amount of research on the Mersey Estuary and Liverpool Bay towards the end of the 19th century (Liverpool Marine Biology Committee reports series). This was particularly concerned with compiling species lists for the area. Since that time however, relatively little work has been carried out on the estuary and much of what has been done remains unpublished in the so-called 'grey literature'. There have been some studies on the phytoplankton (Fraser 1931, Sharples 1969, 1972). Johnstone *et al.* (1934) recorded a higher standing crop of phytoplankton in the areas of Liverpool Bay where outflow from the Mersey raised nutrient concentrations. Foster *et al.* (1984, 1985) also looked at the effect of the physical and chemical conditions on phytoplankton distribution in Liverpool Bay. Zooplankton has also been looked at by relatively few workers. Scott (1905, 1906, 1907) compared the Mersey with other offshore stations. One of the most important early studies looked at changes in the zooplankton composition at Pier Head during 1930-31 (Fraser 1931). Pierce (1941) looked at the chaetognatha at the same site. A more detailed review of what has been done, including much unpublished work can be found in Williamson (1975). More information is available on the benthic invertebrates. In the 1930s the area was comprehensively described by Fraser(1931, 1935, 1938), Bassindale (1938) and Corlett (1948). The fouling community found on buoys, lightships and other hard substrates has been briefly studied. Both Fraser (1938) and Corlett (1948) described quite similar communities dominated by *Mytilus*. Amongst the *Mytilus* a number of smaller species were found including *Balanus* spp, hydroids, *Tubularia* and *Polydora ciliata*. Corlett (1948) also carried out some work using tiles placed in the Mersey. The physical instability of the sediment has been implicated as an important factor in reducing the number of species (Fraser 1935). Bassindale (1938) studied the distribution of intertidal infauna within the Mersey. More recently Holland (1989) found a decreasing gradient of species diversity in an inland direction. This was attributed to both falling salinity and the impact of sewage pollution. The instability of the sediment leads to continual readjustment of the community distribution (Moore 1978). Carter (1985) recorded a more diverse infauna in the mud of the upper estuary than previous studies. However, Bamber (1988) recorded a more impoverished fauna and attributed the changes to pollution or the occurrence of a very cold winter. Wilson *et al.* (1988) recorded improvements in water quality, as measured by reduced anoxia and also an increase in the variety of fish caught.

As mentioned above there is a considerable amount of additional information available on the Mersey in unpublished reports. In particular, a study was recently carried out with reference to the possible construction of the Mersey barrage. This includes two years of results on changes in phytoplankton, zooplankton, invertebrates and fish (Environmental Resources Limited 1993a,b,c).

CHAPTER 3

GENERAL METHODS

INTRODUCTION

This chapter is divided into two sections. The first describes the development of the method used to record the composition of the dock wall community, using underwater photography. The second section provides a general introduction to the multivariate statistical methods that will be utilised extensively in this thesis. In particular it includes details of how to interpret the output produced, presented here in the form of biplots.

3.1 DEVELOPMENT OF METHODS FOR NON-DESTRUCTIVE SAMPLING OF THE DOCK WALL COMMUNITY

3.1.1 INTRODUCTION

Methods for sampling benthos can be broadly partitioned into two groups, namely destructive and non-destructive. When sampling a relatively small ecosystem such as the docks the use of destructive sampling techniques could have quite large effects on the community. Describing the spatial and temporal variation in the wall community in the docks was a major part of this study. There was therefore a need to develop a non-destructive technique to describe the wall community in the docks.

Underwater photography has a number of advantages over other non-destructive methods, such as estimating percentage cover of species using point quadrats actually in the water. First, photography means that the actual field work is relatively fast, allowing a large number of sites to be sampled in a short period of time. In addition a permanent record is kept on film which can be reanalysed to study different aspects of the community at some time in the future. The technique is also relatively cheap, once the initial equipment outlay has been met. A review of some of the methods that have been used and problems encountered with underwater photography can be found in Holme & McIntyre (1984).

This chapter aims to assess the use of a Nikonos V underwater camera to photographically record the wall community found in the docks. It includes determination of the sample size required, and the best techniques for analysing the photographs obtained. It also aims to verify that the description of the community obtained using underwater photography matches that obtained using the more traditional method of a point quadrat used underwater.

3.1.2 METHODS

a) Sampling technique

The dock wall benthos was photographically recorded using a Nikonos V underwater camera, equipped with a 28mm lens, SB103 strobe flash and Nikonos close-up kit. This gave a total photographable area of 240mm by 170mm. All photographs were taken onto Fujichrome slide film, 400asa. The slides were projected onto a screen with a uniform arrangement of points. The biota present at each point when the slide was projected was recorded. An effort was made to focus on the primary cover species at each point. The total number of each large solitary species in each slide was also counted. Points where the biota could not be identified with certainty were excluded from the analysis.

b) Assessment of method

A pilot study was run in order to determine the number of photographic quadrats required to give a good estimate of community composition (essentially accuracy) and the number of points required to estimate percentage cover on each slide (essentially precision). Twenty photographs were taken at 2m depth in Albert Dock on 15 January 1992. Each slide was analysed as above using first 50 and then 25 points to estimate the percentage cover of each species present. As the two estimates were made from each slide, a paired t-test was applied, after arcsin transforming the data, to test whether the number of points analysed affected the estimated percentage cover. The results were also plotted as a scatter graph. To assess the affect of the number of slides used on the overall estimate of cover, the results were plotted as number of slides analysed against mean cumulative estimate of percentage cover of each species (see Fig 3.1). A similar graph was produced for the cumulative estimate of the variance of the mean (see Fig 3.2).

A second exploratory study was carried out in Salthouse Dock in July 1992 in order to assess the accuracy of using photography to estimate percentage cover. The percentage cover of each species was estimated using point quadrats underwater. A 0.5 X 0.5m quadrat was divided into one hundred squares, and the top left corner of each square was regarded as a point. The quadrat was haphazardly positioned on the dock wall and the biota present at each point recorded onto a slate. As with the analysis of the slides, the primary cover of species at each point was recorded. Five replicate quadrats were assessed in this manner. On the same occasion twenty-four photographic quadrats were taken and analysed as above. The percentage covers from each method were transformed using an arcsin transformation (Zar 1984) and compared using a two-tailed t-test.

3.1.3 RESULTS

The estimate of the mean percentage cover for the three major classes stabilized quite quickly, after analysing about ten photographs (Fig 3.1). The variance of the estimate took longer to stabilise but certainly fifteen to twenty photographs appears to be a sufficient sample size to get a reasonably accurate estimate of this parameter (Fig 3.2). No significant difference was found between the mean percentage cover estimated using 25 points or 50 points (Table 3.1). Similarly no significant difference was observed in the percentage covers estimated using photography or in-water quadrats (Table 3.2). It should be noted however that the estimates of percentage cover of the less obvious species such as *Botryllus* and sponge were higher using photography. Although these differences were not significant this may be partly due to the low number of in-water quadrats used. However, it seems likely that photography is the best way of assessing such species as each point can be examined more carefully.

3.1.4 DISCUSSION

Photography was adopted as the method used to study variation in the wall community both spatially and temporally. Between twelve and eighteen photographs were taken at each site on each date. The distribution of space occupied on each slide was estimated using 25 points as there was little difference in estimates made using more than this number of points.

Table 3.1 Assessment of effect of number of points used on the estimate obtained for percentage cover. Data were arcsin transformed before analysis. ('Var' means variance, 'N.S.' indicates no significant difference at 5% level).

	25 points		50 points			
Class	Mean	Var	Mean	Var	pair t	Result
Bare	0.5452	0.0435	0.5311	0.0304	0.3007	N.S.
Sponge	0.6104	0.0161	0.6061	0.0319	0.8222	N.S.
Mytilus	0.6005	0.0211	0.5847	0.0581	0.9356	N.S.

Table 3.2 Comparison of photography and in-water point quadrats as methods for estimating percentage cover. Data were arcsin transformed before analysis. ('Var' means variance, 'N.S.' indicates no significant difference at 5% level).

	Slides (n=24)		Point quadrat (n=5)			
Class	Mean	Var	Mean	Var	t	Result
Bare	0.4577	0.0150	0.5011	0.0088	-0.2990	N.S.
Botryllus	0.3832	0.0207	0.2603	0.0098	1.0544	N.S.
Mytilus	0.8849	0.0321	0.9558	0.0024	-0.3509	N.S.
Sponge	0.1926	0.0161	0.0929	0.0202	1.2238	N.S.

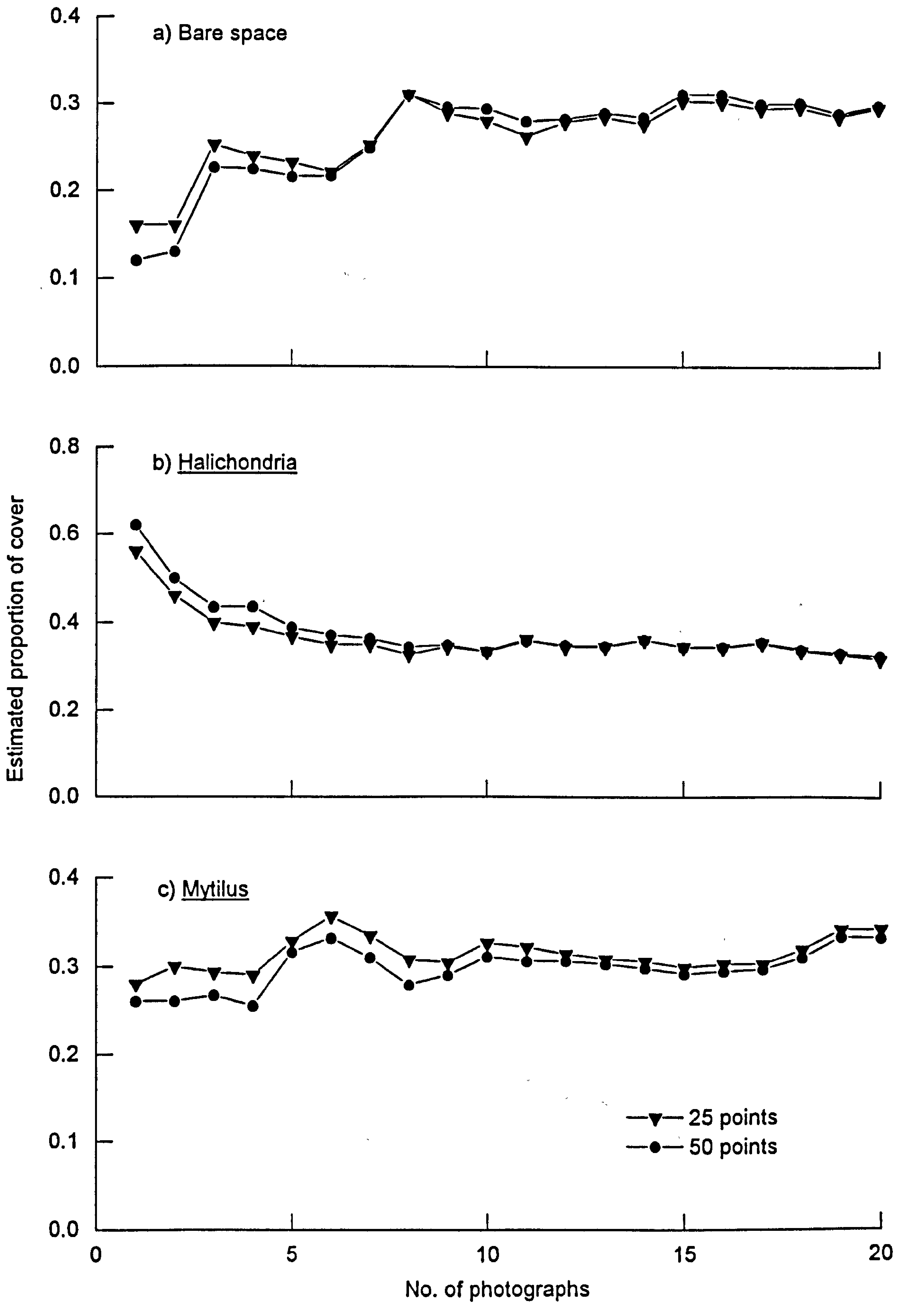

Fig 3.1 Effect of increasing sample size and number of points on estimate of mean proportion occupied. Data from Albert Dock January 1992.

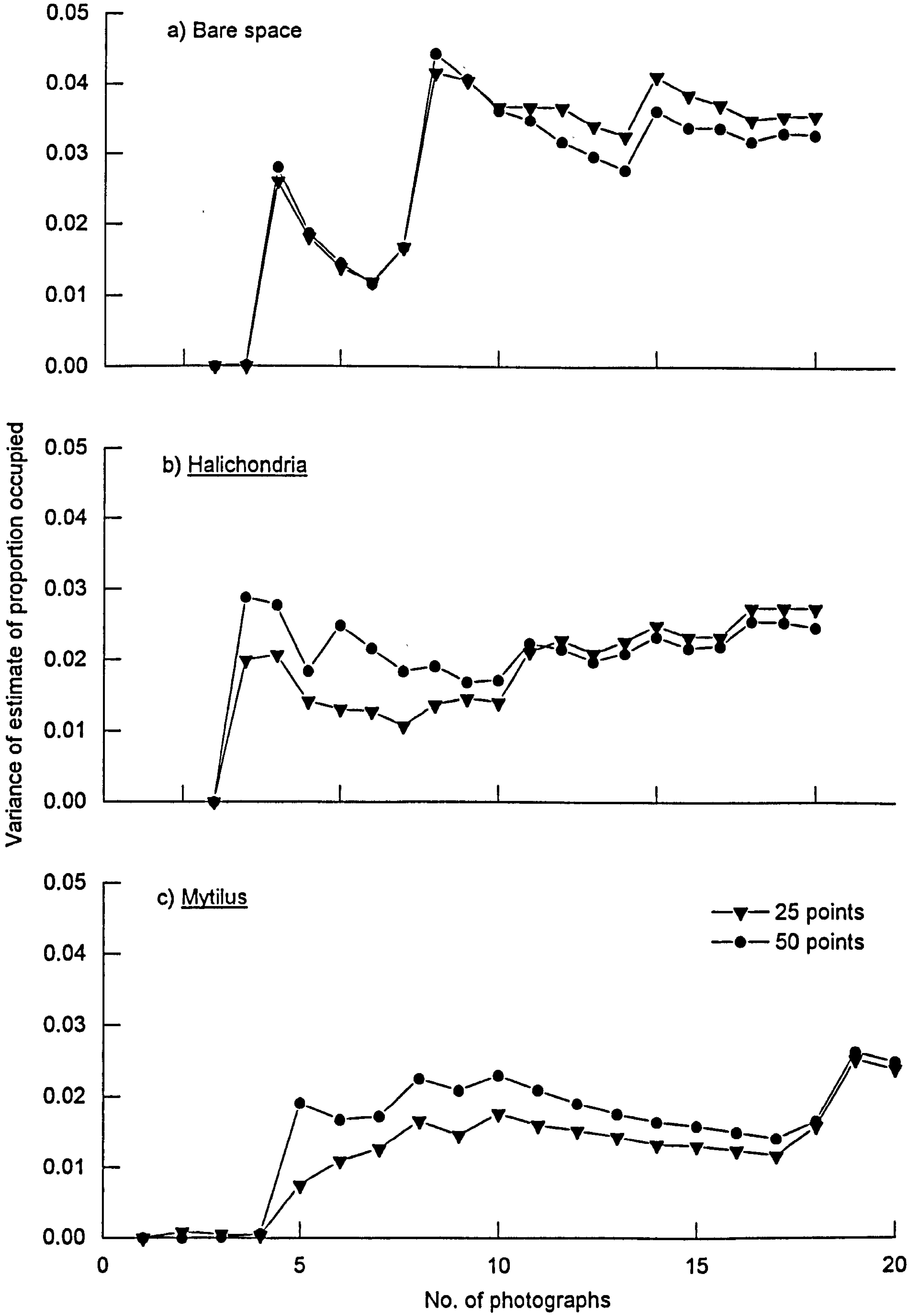

Fig 3.2 Effect of increasing sample size and number of points used to estimate cover on variance of estimates. Data from Albert Dock, January 1992.

3.2 INTRODUCTION TO MULTIVARIATE STATISTICS

3.2.1 Introduction

The rapid development of personal computers in recent years has led to an increase in accessibility of multivariate statistical methods. Some of these techniques allow the visual representation of large amounts of information on community structure in relatively simple two or three dimensional plots. This can be very useful, particularly for targeting areas to concentrate further analysis. However the interpretation of the biplots produced using these methods requires the use of a different set of rules than when interpreting normal bivariate plots.

The application of multivariate analysis to ecological communities is still in its infancy and there remains much dispute over which techniques are theoretically the best to use. Multidimensional scaling (MDS) has gained popularity, particularly in marine ecology (Warwick & Clarke 1991). However, this analysis involves an extra step once sites have been grouped, in order to determine which species are most important in the separation of the sites. Principal Components Analysis (PCA) and Correspondence Analysis (CA) present both sites and species simultaneously. Theoretically MDS is probably a better technique to apply, though it is much more computer intensive. However, there is likely to be relatively little difference in the results produced by the different methods, particularly when the environmental gradient is short. For longer gradients MDS is almost certainly the best procedure to employ. In this study all the gradients considered were relatively short and therefore PCA and CA were adopted as the techniques employed, due to their ease of use. The following sections briefly describe the main underlying principle of these two techniques (i.e. PCA and CA) and how to interpret the output produced. The first section explains the selection of which technique to apply before going on to describe the basic principles on which these techniques work. The rules used to interpret the output produced are also described here.

3.2.2 Which technique?

Species abundance tends to rise and fall over an environmental gradient and is generally accepted to follow a bell-shaped curve (Whittaker 1967). Multivariate techniques such as Principal Component Analysis (PCA) and Correspondence Analysis (CA) seek to construct theoretical environmental variables that maximise the dispersion of species, while assuming that each species abundance will rise and fall in the form of a bell shaped curve along this environmental gradient. The difference between the above two methods (i.e. PCA and CA) is that PCA assumes a linear fit. This procedure is used when the environmental gradient lengths being considered are relatively short and the change in species abundance can therefore be likened to a straight line (see fig 3.3). Species abundance rises and falls over a distance of approximately four standard deviation units. If the length of the gradient being considered is less than 2.5 standard deviation units then linear techniques are adopted. Therefore before beginning the analysis it is necessary to establish the length of the gradient being considered. Detrended Correspondence Analysis (DCA) is a useful procedure for doing this as it plots the axes in terms of standard deviation units. Therefore a preliminary analysis of the data is carried out using DCA to assess the spread of the data. When the gradient lengths are short a linear model is adopted (PCA), otherwise the data are fitted to a bell shaped curve (CA).

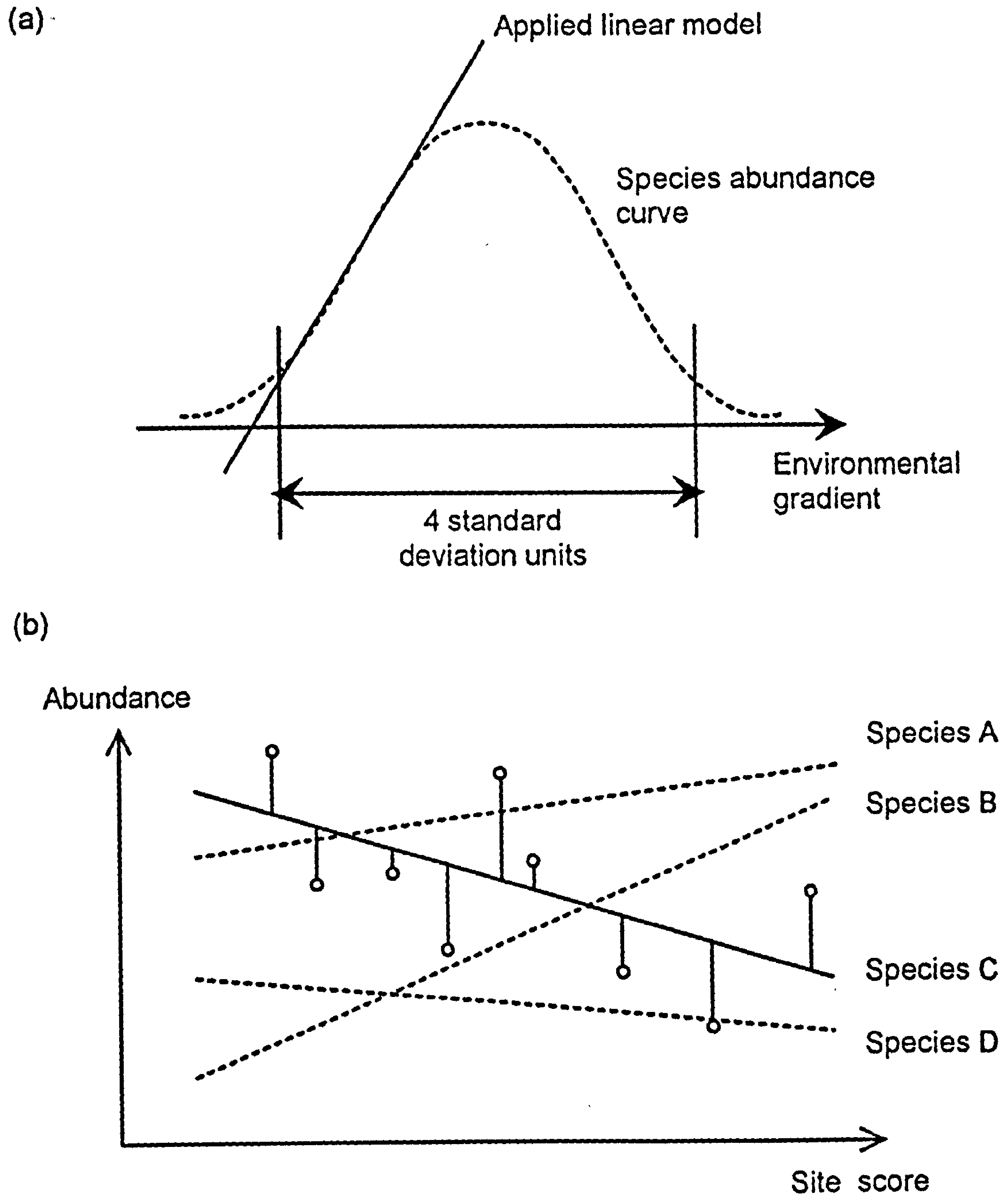

Fig 3.3 Principal Components Analysis (a) demonstration of how a linear model can be applied to changes in species abundance when gradient lengths are relatively short. (b) hypothetical example of how PCA minimises residuals.Note, abundance points for one species only are shown.

3.2.3 Correspondence Analysis

Weighted averaging is a useful technique for estimating the optima of a species on an environmental gradient. For abundance data the weighted average is calculated as :-

$$u = (y_1x_1 + y_2x_2 + y_3x_3 \ldots\ldots y_nx_n) / (y_1 + y_2 + y_3 \ldots\ldots y_n)$$

where 'u' is the weighted average, 'y' is the species abundance and 'x' is the value of the environmental variable being considered. This technique is used as an approximation to fitting a unimodal or Gaussian-like curve to the data using regression (see ter Braak & Looman 1986).

As mentioned above, CA aims to construct the theoretical variable that best explains the species data (ie. that maximises the dispersion). The first axis represents the first theoretical variable. Further axes can be constructed with the proviso that they are uncorrelated with any previous axis. A full explanation of the algorithms used to derive these axes can be found in Jongman *et al.* (1987); only a brief description is provided here. Essentially the procedure begins with arbitrary site scores. Then two-way weighted averaging is applied to first calculate new species scores as weighted averages of the site scores and then new site scores as weighted averages of these species scores. The new site scores are standardized and the process repeated until the values for the site scores converge. There is an associated eigenvalue (λ) for each axis which gives a measure of the dispersion of the species scores on that axis. It is therefore a measure of the importance of that axis, or how much of the variation in the species scores that axis explains.

Following a CA, the species and site data can be summarised in a joint plot. Site scores are weighted averages of the species scores and site points therefore lie at the centroid of the species that occur in them. Therefore sites that lie close to a species point have a high abundance of that species. The species points are close to the optima of the bell shaped response surface for that species.

3.2.4 Principal Component Analysis

PCA can be considered as 'the ordination technique that constructs the theoretical variable that minimises the total residual sum of squares after fitting straight lines to the species data' (Jongman *et al.* 1987). Fig 3.3 shows a hypothetical example of the construction of the first principal component (here the horizontal axis) with the residual distances displayed for one species. Similar points and residuals exist for each of the other species. As with CA, the first axis explains the species data best. The second and higher axes also explain the species data best with the constraint of being uncorrelated with previous axes. The algorithm used to calculate PCA is very similar to that for CA. Again full details can be found in Jongman *et al.* (1987). Essentially PCA can be considered an extension of straight line (or least squares regression). As with CA, there is an eigenvalue associated with each principal component which gives a measure of the variance explained by that axis. With PCA the eigenvalue is also equivalent to the maximised regression sum of squares.

When a given variable is known to have a strong influence, PCA will probably only show what is already known. To examine unknown variation, each set of species data can first be regressed on this variable and PCA performed on the residuals of this regression. This is known as a partial PCA and can be carried out through the program CANOCO (ter Braak 1987-1992) by specifying so-called 'covariables'. This can be particularly useful if groups of sites (or replicates) are recognised before sampling. The group means can then be analysed rather than the deviations from the overall mean.

Following a PCA, species and site data can be plotted in the form of a biplot. Often species and site values have different orders of magnitude and therefore each of these is usually plotted on separate scales. Species are plotted as vectors, calculated by plotting the gradient of the fitted species line for each principal component against one another. The vector therefore represents the direction in which the abundance of a species increases most sharply. Lines drawn perpendicular to these vectors therefore represent constant abundance of that species. Therefore extrapolation of hypothetical lines from sites to a meet a given species vector at right angles allows the sites to be ranked according to the abundance of that species. Similarly, the angle between two vectors gives an indication of the correlation between two species. Two vectors at almost the same angle show high positive correlation, opposite directions negative correlation while two at right angles indicates no correlation between the two species.

Only a very brief description of these techniques has been provided here. For further details the reader is referred to Jongman *et al.* (1987).

3.3 Nomenclature

Throughout this thesis nomenclature follows Howson (1987) for fauna and South & Titley (1986) for macroflora unless otherwise stated. A number of the more abundant species are refered to by their generic names only (ie. *Ciona* = *Ciona intestinalis*, *Ascidiella* = *Ascidiella aspersa*, *Molgula* = *Molgula manhattensis*, *Botryllus* = *Botryllus schlosseri*, *Styela* = *Styela clava*, *Aurelia* = *Aurelia aurita*, *Obelia* = *Obelia dichotoma*, *Halichondria* = *Halichondria bowerbankii* and *Mytilus* = *Mytilus edulis*).

CHAPTER 4

SPATIAL COMPARISON OF THE BENTHOS OF DOCKS IN THE LIVERPOOL AREA

4.1 INTRODUCTION

As indicated by chapter 2, a relatively large amount of research has now been carried out on the South Docks, particularly with reference to factors affecting water quality (Allen 1992, Zheng 1995). Work has tended to concentrate on a relatively small number of docks, particularly Albert, Queens and Queens Graving. However, little effort has been made to characterise just how typical these docks are of the system as a whole. The planned redevelopment of other docks in the Liverpool area will necessitate the application of what has been learned from the South Docks to these other locations. With this in mind the programme of water quality monitoring has now been extended to encompass Brunswick, Princes and Morpeth Docks (Wanstall & Fielding unpublished). The potential importance of the benthos, and particularly *Mytilus* and other filter feeders in the case of the South Docks, in controlling phytoplankton has been clearly demonstrated (Allen 1992, Allen *et al.* 1992, Allen & Hawkins 1993a,b). The manipulation of benthic filter-feeders remains one of the major potential management options open as regards the improvement of water quality in disused dock basins. In light of this it is clearly important to gain a more detailed description of the broadscale spatial variation in physical factors and benthic communities in a variety of the docks in Merseyside.

A general description of the development of the wall benthos of Albert and Queens Docks following the isolation of the South Docks can be found in Allen (1992), Hawkins *et al.* (1992) and Allen *et al.* (in submission). These studies indicated relatively little difference between the two docks studied, both being dominated by a dense *Mytilus* population. Wilkinson *et al.* (1990) carried out a broader survey of seven docks, including sites from both the South, the Central and the Wirral Dock chains. This preliminary survey relied solely on settlement ropes and wall scrapes taken without diving. Similarly Hunt (1994) used settlement ropes to compare Albert, Queens, Brunswick and Morpeth Docks. In both of these latter studies differences were observed between the docks. However, as they relied on samples taken without diving, it was hard to relate to detailed descriptions of the benthos.

The soft mud bottom of the docks represents an extensive and therefore very important habitat, which remains relatively poorly studied. This is despite its potential as a substrate for another benthic filter feeding assemblage in the form of burrowing bivalves. The benthic community will also reflect the occurrence of stressful conditions such as anoxic events. Again Allen (1992) and Allen *et al.* (in submission) described changes in the fauna of Albert and Queens Docks. These studies indicated a community dominated by small short lived species, with little evidence of the development of a more permanent community. Similar results were recorded by Hunt (1993) following a survey of the mud fauna of Salthouse, Brunswick and Morpeth docks. All of these studies relied on the use of grab samples taken from the surface. Experience has shown these to be unreliable and difficult to quantify as the grab often encounters hard objects on the dock bottom and fails to close properly. There has been no attempt to describe either the physical or chemical characteristics of the mud in any of the Liverpool docks.

The present study aims to compare both the wall and mud benthos of seven of the South Docks and two others in the Liverpool area which are scheduled for redevelopment in the near future. Certain physical parameters were also measured at each site, including some preliminary observations on the physical structure of the mud present in the docks. It was hoped that the survey would provide an insight into how widely applicable are the results gained from those South Docks that have been studied in some detail. This chapter also places in a broader context the observations on the temporal variation in the dock wall communities in three docks (chapter 5). In addition it provides some information on the benthic algae which will be considered further in chapter 9. The variation of major species with depth in each dock was compared. The potential importance that the large population of *Mytilus* in the South Docks has in reducing phytoplankton blooms is well recognised (Allen & Hawkins 1993a&b). Particular attention was therefore paid to quantifying the biomass and population structure of this species and the results integrated with chapter 6. Extensive use was made of multivariate analysis in an attempt to characterise the communities found in the docks studied.

4.2 MATERIALS AND METHODS

4.2.1 Study Site

The survey was carried out between the 26th August and the 10th September 1993. A total of nine docks were chosen for inclusion in the study. These included seven of the South Docks, namely Canning, Albert, Salthouse, Wapping, Queens, Coburg and Brunswick. Princes Dock, at the southern end of the Central Docks and Morpeth on the Wirral were also included. Only one area of each dock was examined. The positions of these are shown in Fig 4.1.

4.2.2 Environmental parameters

For each site studied a number of physical characteristics of the dock were recorded, including maximum depth, surface area and perimeter. The latter two parameters were measured from large scale ordnance survey maps of the area. Water clarity was measured using a Secchi Disc 0.30m in diameter. Oxygen concentration, temperature and conductivity were also recorded at 1m depth intervals (using 'pHOX 52E' meter to measure conductivity and 'WTW Microprocessor Oximeter OXI 169' for temperature and oxygen measurement).

A sample of the sediment from each dock was retained for particle size analysis. The full details of the methods used can be found in Holme and McIntyre (1984). Approximately 20g of dried sediment was placed in a beaker and 200ml of 6% hydrogen peroxide added. This was left to stand overnight and then heated gently in a water bath. The aim of this was to remove all organic matter, but despite using twice the amount of hydrogen peroxide recommended by Holme and McIntyre (1984) some bubbling was still observed, indicating a very high organic loading in the sediment. The sample was filtered in a Buchner funnel, using Whatman no. 50 filter paper and distilled water to remove any electrolytes. It was then washed into a beaker with about

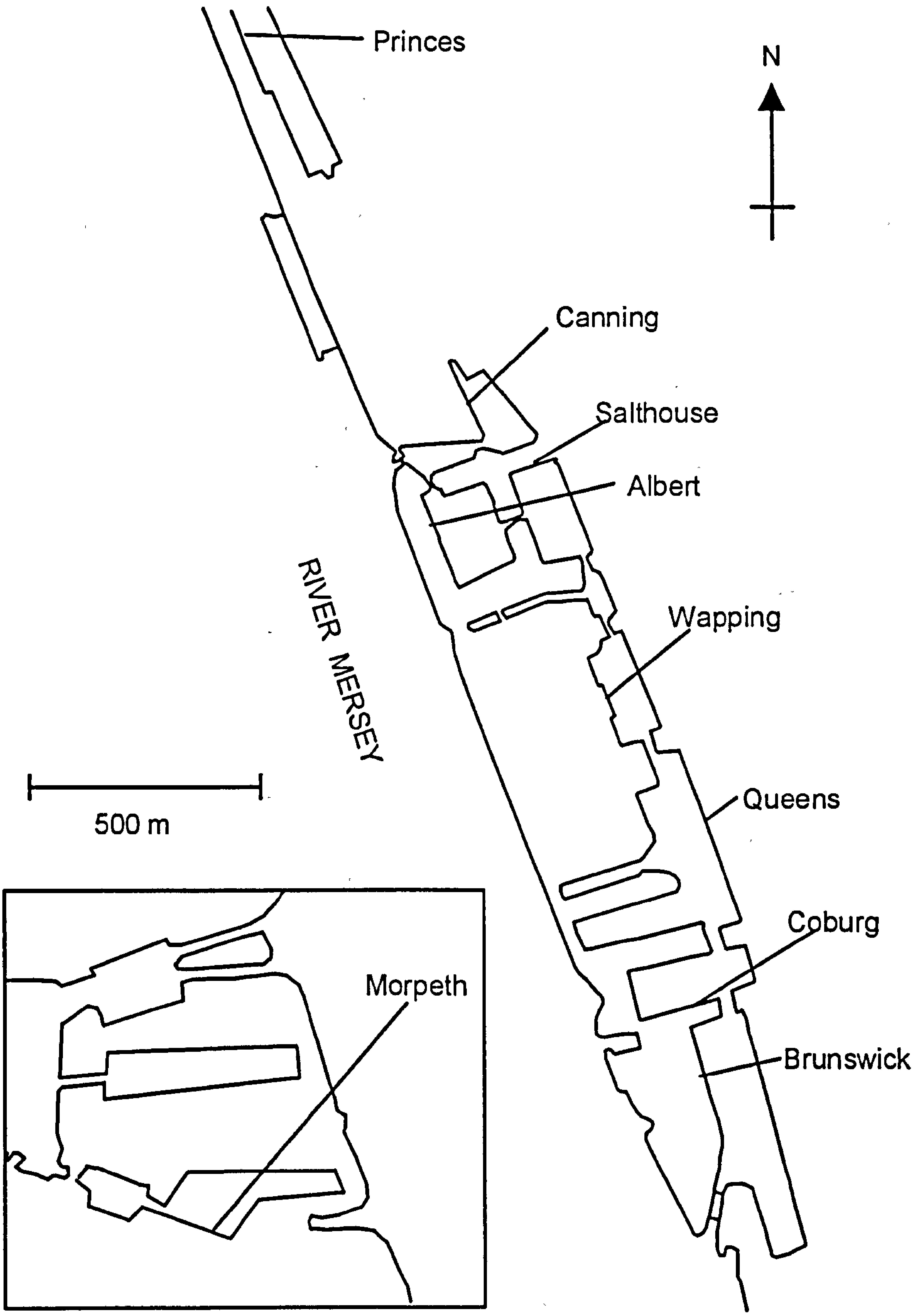

Fig 4.1 Map showing area of each of the docks sampled during the spatial survey.

200ml of distilled water and 10ml of sodium hexametaphosphate solution (6.2g/l) was added. This was stirred and left to stand overnight.

The sediment was resuspended and transferred to a 62μm sieve placed in a white basin. Approximately 300ml of distilled water was added and the sediment wet sieved by agitating and 'puddling' until most of the fine fraction had passed through. The sieve and its contents were transferred to the oven and dried at 70°C. Once dry the sieve was again agitated over a large sheet of white paper to remove any remaining material of <62μm. The residue remaining in the sieve after this was transferred to a graded column of sieves and manually rocked and tapped. The weight of material in each fraction was then determined.

The fine material that remained in the basin was transferred to a measuring cylinder and the total volume made up to one litre. This was shaken to evenly suspend the mud throughout the water column. The cylinder was placed upright and a 20ml pipette sample was immediately withdrawn from a depth of 10cm. This was transferred to a pre-weighed crystallizing basin and dried at 70°C. After 7min 44sec a second 20 ml pipette sample was removed and transferred to another basin. A third sample was taken after 2h 3min. The weight of suspended solids in the first sample represented the total amount less than 62μm. The second sample corresponded the amount less than 15.6μm and the third to less than 3.9μm (ie. the clay content). Full details of the theory behind this method can be found in Holme and McIntyre (1984).

Results from the analysis of the fine and coarse fractions were combined and cumulative frequency curves constructed for weight/particle size at each site. Further statistical analysis was not possible due to the large portion of the samples that was less than 3.9μm.

4.2.3 Sediment fauna

The sediment at each site was sampled using a 0.09m^2 Van Veen type grab operated by a diver to avoid problems of closure failure. Three replicate samples were taken from each site and analysed separately. The mud was wet sieved over a 500μm mesh and any fauna retained was identified and enumerated. The extremely thixotropic nature of the dock mud meant that sieving had to be assisted by constant washing of the sample to assist the breakup of the sediment. The large amount of material retained from some samples meant that subsampling by weight was occasionally necessary. Subsamples were always at least a quarter of the mass of the total sample. Numbers of organisms were scaled up to mean densities per square metre.

4.2.4 Photographic sampling of dock walls

The methods used to photographically record the dock wall benthos follow the description given in chapter 3. Twelve photographs were taken at each 1m vertical intervals beginning at the water surface and working to the dock bottom. This was carried out on one broad transect, approximately 50m long in each dock. The slides were analysed as described in chapter 3.

4.2.5 Destructive sampling of wall benthos

The wall benthos was also sampled destructively. Quadrats (0.25mX0.25m) were haphazardly positioned on the wall at a depth of approximately 1m and all material within these areas was removed and transferred to a bag for later analysis. Five replicate samples were taken from each dock and analysed separately. In the laboratory, each of these samples was washed over a 1mm sieve and all the larger organisms and algae were separated, identified and enumerated before being transferred to preweighed foil boats for dry weight determination. *Mytilus* were removed and analysed separately. The residue retained in the sieve was subsampled by weight and examined microscopically under a magnification of X25. All infauna present in each subsample were removed, identified and enumerated. In all cases the subsample comprised at least 20% of the total weight of each sample.

4.2.6 Timed search

A five minute timed underwater search was carried out at each site to roughly estimate the abundance of rarer or more mobile species which would have been missed by the sampling strategies employed above. Abundances were recorded on a scale of 0 to 3, '0' being absent, '1' indicating one or two individuals, '2' representing between two and ten specimens and '3' if more than ten were recorded. It should be noted that as more docks were surveyed, the species list increased and the new species were recorded as absent in previously surveyed docks. This was justified as the diver was previously familiar with all the species likely to be encountered and the failure to record a given species was therefore more likely to be due to low numbers of that species rather than operator error.

4.2.7 *Mytilus* population

Given the relatively large size of adult *Mytilus*, compared to the area being photographed as described above, it was felt that estimation of the density of this species would have been inaccurately estimated using photography alone. Therefore an attempt was made to estimate densities using a board 0.15m across. This was held against, and moved down the wall and the number of *Mytilus* encountered in the vertical strips so formed was recorded by the operator. The wall was sampled in contiguous 1m vertical sections, beginning at the surface and working to the dock bottom. The number of *Mytilus* in each 1m section was recorded. This was repeated three times, giving replicate estimates of the density of *Mytilus* for each 1m depth interval.

The lengths of all *Mytilus* collected in the destructive samples of the wall were measured to the nearest 1mm using Vernier callipers. A sample of fifty, of as great a size range as possible were selected and analysed biometrically. The length of each was recorded as above before the soft parts of each were removed and transferred to individual preweighed foil boats, which were dried at 70°C for 48hrs. These boats were then reweighed to the nearest 0.1mg thus allowing the estimation of the dry weight of the soft parts of each animal. The shells were air dried and weighed to 0.01g. The results from this are considered in chapter 6.

4.2.8 Multivariate analysis

Results from both the photographs and the scrapes of the dock wall were analysed using multivariate techniques, through the program CANOCO (ter Braak 1987-1992). Preliminary examination of the data using Detrended Correspondence Analysis (DCA), detrending by segments as recommended by ter Braak (1987-1990), indicated minor nonlinearity (gradient lengths of less than 2.6 standard deviation units in all cases). Therefore linear techniques were used for all subsequent analyses.

Species counts were transformed using a log(x+1) transformation while a square root transformation was used for percentage covers. Both these data sets were analysed after centring the data by species, in other words PCA on a covariance matrix. No attempt was made to relate the measured environmental variables to the community composition for two reasons. First the number of measured variables was high, relative to the number of sample sites which tends to lead to multicolinearity when canonical techniques are applied. Secondly, it was felt that as these variables were measured at only one point in time they may not be truly representative of the dock over the time scale required to act on the organisms present. Results were presented as correlation biplots, produced using CALIBRATE (Juggins 1994).

4.3 RESULTS

4.3.1 Physico-chemical parameters

A summary of the measured physico-chemical parameters is provided in Table 4.1. There was no evidence of temperature stratification in any of the docks studied. Low bottom oxygen was only recorded in Morpeth Dock. Morpeth showed a number of other anomalies having a lower salinity and lower water clarity than any other dock included in the survey. The water clarity was generally in the range of two to four metres, though it was considerably clearer in Princes. Princes also had a slightly higher salinity than the South Docks.

4.3.2 Sediments

The mud present in the docks is extremely fine with a considerable portion usually finer than the smallest clay fraction analysed (<3.9μm). This prevented further analysis of the data. From the phi diagrams, plotted for each site (Fig 4.2) differences between the docks are slight, except for Wapping. Albert, Princes and Morpeth had a slightly higher proportion of coarser material than was found elsewhere, having a median particle size in the class of phi 6-7. Apart from these four docks, the remainder all had a median particle size in the range 7-8 phi units. Wapping shows a more classical S-shaped curve. This is mostly due to a relatively high proportion of fine sand in the sediment in this dock. This is as a result of building work carried out during the redevelopment of the system when a large amount of sand appears to have been dumped into the dock basin.

4.3.3 Mud fauna

Results from analysis of the mud fauna were extremely variable, with most means having very large variances (see Table 4.2). The community was dominated by small short

Table 4.1 Main physical parameters measured for the docks included in the spatial survey. ('S' indicates surface; 'B' indicates bottom; salinity readings were the same at both surface and bottom)

	Canning	Albert	Salthouse	Wapping	Queens	Coburg	Brunswick	Morpeth	Princes
Depth (m)	5.0	4.5	5.0	4.5	4.2	3.7	4.0	8.5	7.0
Area (m^2)	17800	20000	25900	20000	67000	30700	64500	67200	35400
Perimeter (m)	610	550	640	550	1390	590	1240	N.A.	1030
Salinity (‰)	28	28	28	28	28	28	28	18	29
Secchi (m)	3.25	3.25	3.9	3.25	2.75	3.00	2.50	1.00	6.00
Oxygen (%) S	75	71	76	71	69	64	64	87	73
B	75	71	78	74	67	65	66	6	60
Temperature S	16.2	16.0	16.0	16.0	16.0	15.9	15.9	15.6	16.3
(°C) B	16.2	16.0	16.0	15.9	15.9	15.9	15.9	15.3	16.3

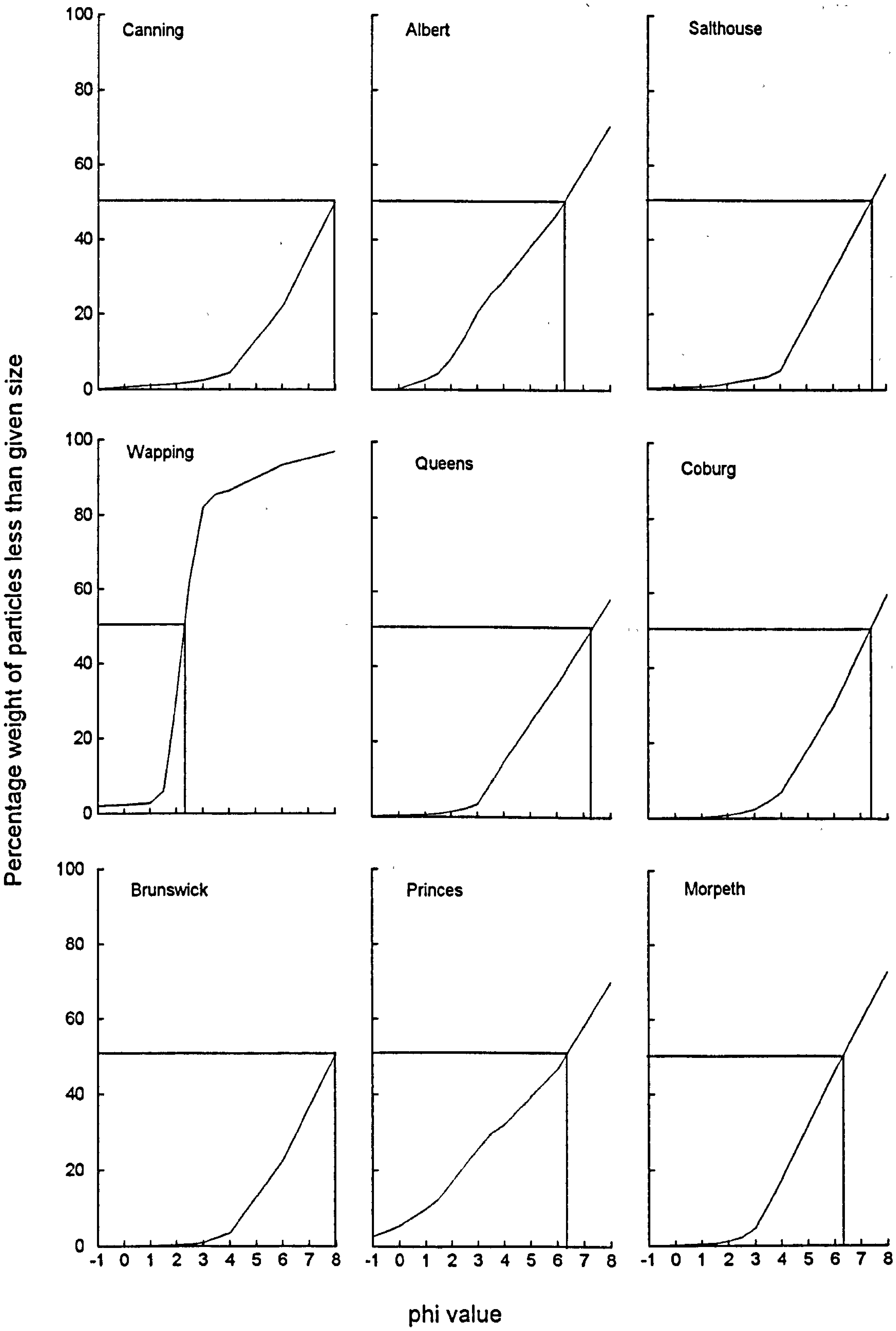

Fig 4.2 Graphs showing particle size distribution of mud sample taken from docks included in spatial survey. Medians are indicated.

lived species of polychaetes and amphipods. Many of the smaller polychaetes were damaged and impossible to identify to species. They were grouped together as spionids, probably being a mixture of *Strablispio martinensis* and *Polydora ciliata*. Great variation in both species present and densities was also found between docks.

In general Salthouse, Wapping and Queens showed the greatest faunal densities, with polychaete densities greatest in Queens and amphipods most abundant in Wapping (see Table 4.2). Princes also showed quite high densities of both polychaetes and amphipods. Morpeth lacked amphipods but quite high densities of polychaetes were recorded. The mud from Brunswick, Coburg and Canning was relatively devoid of life compared with the other sites studied (Table 4.2).

4.3.4 Vertical distribution of species on dock wall

A number of species showed differential abundance with depth. The most obvious of these were the algal species which tended to be most abundant close to the surface. Green algae were absent from Coburg, Brunswick and Princes (Fig 4.8a, 4.9a, 4.10a) and were found only in the sample taken just below the surface in Wapping, Queens and Canning Docks (Fig 4.3a, 4.6a, 4.7a). Green algae did penetrate to a depth of 1m in Salthouse (Fig 4.5a) and to 2m in Albert Dock (Fig 4.4a). Red algae were less abundant than greens. They were recorded at the surface in Salthouse (Fig 4.5b), at a depth of 1m in Canning (Fig 4.3b) and to 2m depth in Albert Dock (Fig 4.4b). No red algae were recorded from any of the other sites. As mentioned above, *Mytilus* tended to be most abundant around the mid-depths of all of the South Docks studied, except Brunswick where it was absent (Fig 4.9e). In Princes Dock, the highest densities were recorded in the surface sample (Fig 4.10e). In general the more common solitary ascidians (*Ciona* and *Ascidiella*) increased in abundance towards the dock bottom (Fig 4.4f, 4.5f,g).

Table 4.2 Average densities per square metre of benthos found in benthic grabs of the mud. Values in brackets are standard errors of the estimates (n=3 in all cases).

	Canning	Albert	Salthouse	Wapping	Queens	Coburg	Brunswick	Princes	Morpeth
Corophium insidiosum	-	-	89 (32.3)	3911 (2184.1)	105 (64.1)	-	-	222 (57.7)	-
Microdeutopus gryllotalpa	4 (3.5)	4 (3.5)	726 (364.9)	1670 (731.5)	7 (7.5)	-	-	89 (46.2)	-
Jassa marmorata	-	-	-	-	-	-	41 (20.8)	11 (11.0)	-
Gammarus salinus	-	-	4 (3.5)	44 (25.4)	-	-	-	-	-
Tubificoides	7 (3.5)	33 (27.7)	893 (341.8)	-	7615 (3790.3)	-	4 (3.5)	567 (342.4)	170 (170.3)
Spionids (unid.)	-	337 (233.2)	-	996 (457.3)	9085 (8477.2)	67 (35.8)	-	100 (23.1)	167 (117.8)
Tubificids	-	-	-	-	3185 (3102.1)	-	-	4 (3.5)	78 (77.9)
Molgula manhattensis	-	-	-	-	-	-	15 (9.8)	-	-

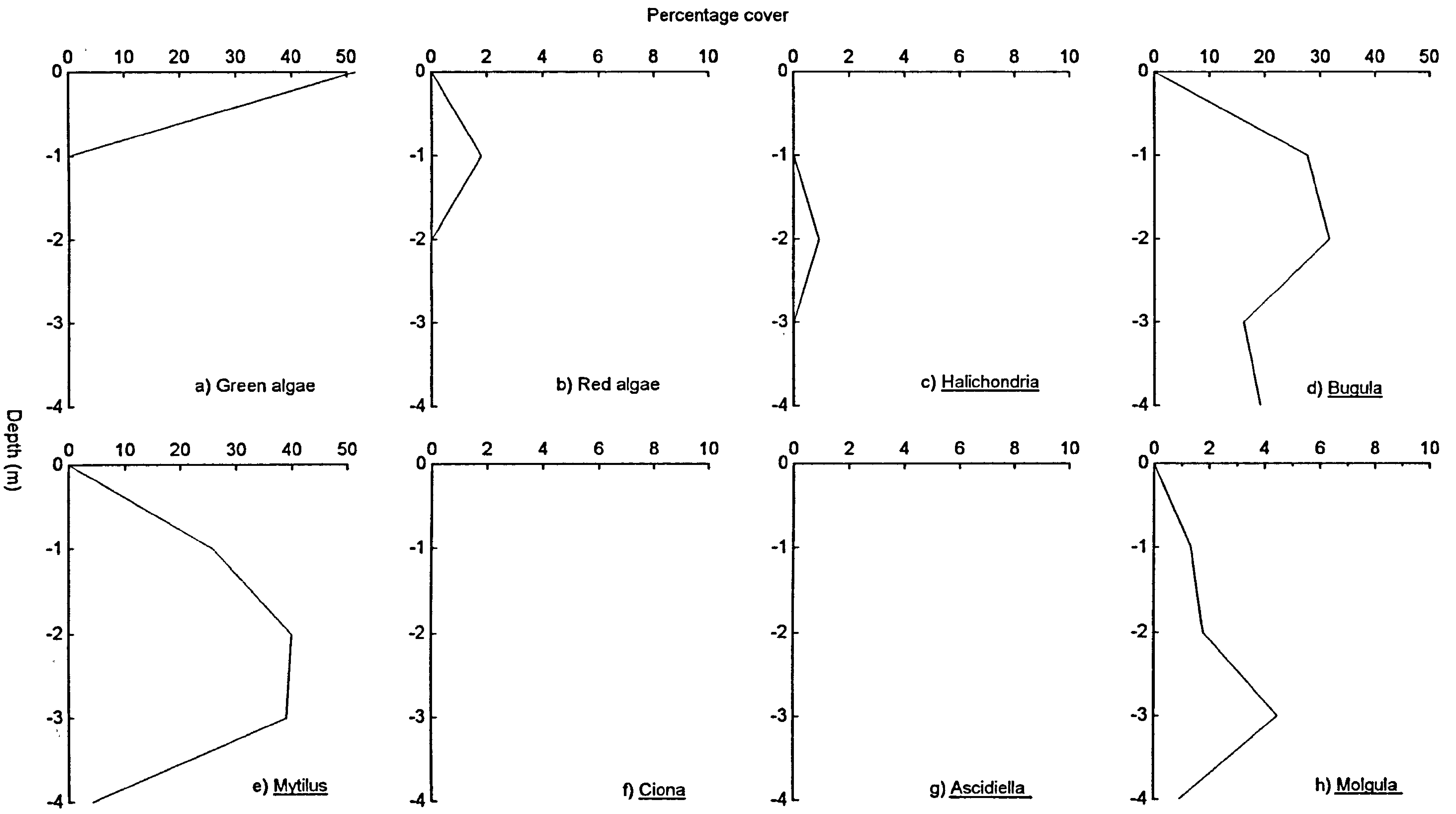

Fig 4.3 Changes in vertical zonation of green algae, red algae, Halichondria, Bugula, Mytilus, Ciona, Ascidiella and Molgula in Canning Dock. Estimates are mean percentage cover calculated from twelve photographs taken at each 1m depth interval. Note changes in abundance scale.

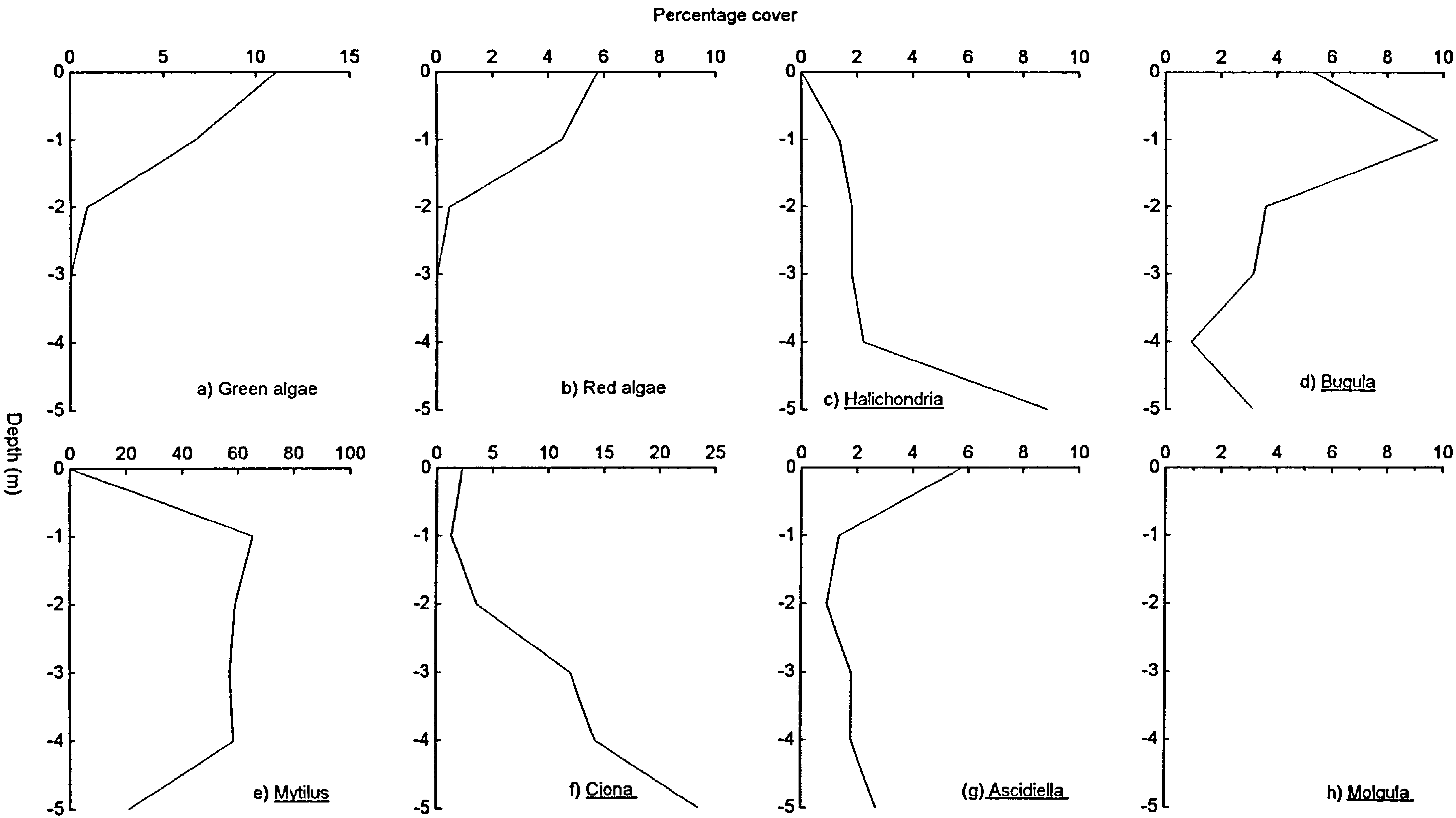

Fig 4.4 Changes in vertical zonation of green algae, red algae, Halichondria, Bugula, Mytilus, Ciona, Ascidiella and Molgula in Albert Dock. Estimates are mean percentage cover calculated from twelve photographs taken at each 1m depth interval. Note changes of abundance scale.

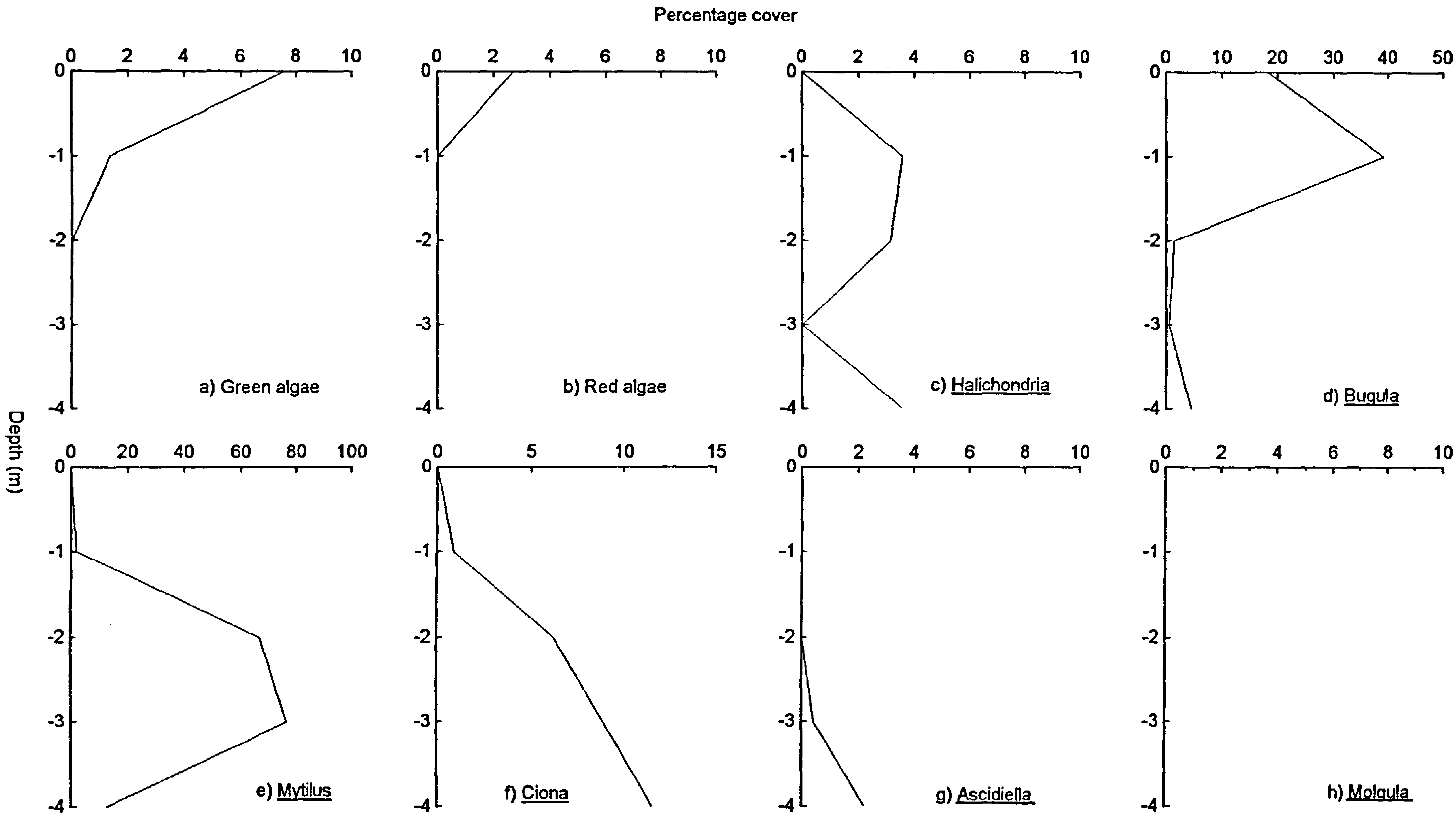

Fig 4.5 Changes in vertical zonation of green algae, red algae, Halichondria, Bugula, Mytilus, Ciona, Ascidiella and Molgula in Salthouse Dock. Estimates are mean percentage cover calculated from twelve photographs taken at each 1m depth interval. Note differences in abundance scale.

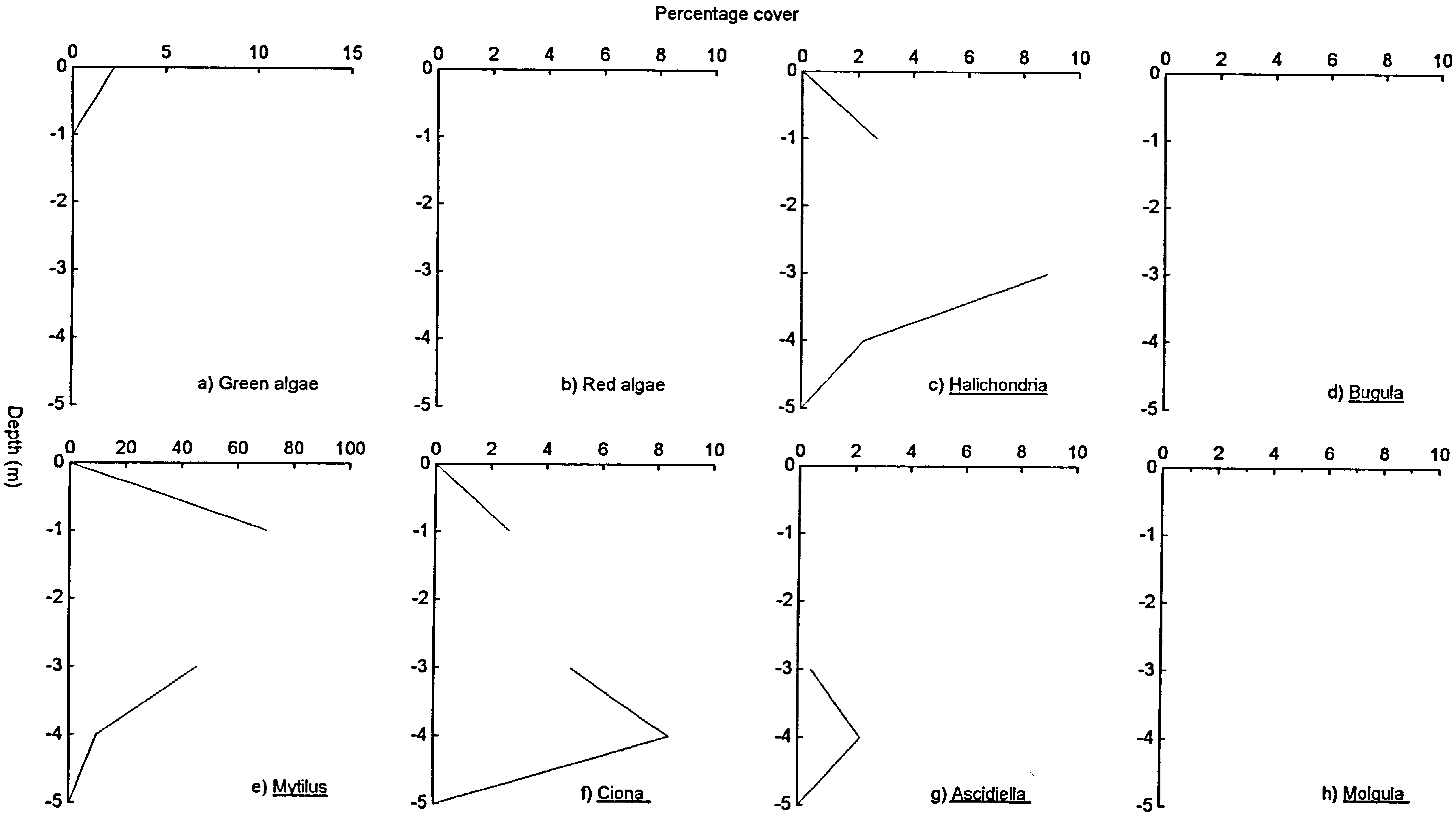

Fig 4.6 Changes in vertical zonation of green algae, red algae, Halichondria, Bugula, Mytilus, Ciona, Ascidiella and Molgula in Wapping Dock. Estimates are mean percentage cover calculated from twelve photographs taken at each 1m depth interval. No data available from 2m depth. Note differences in abundance scale.

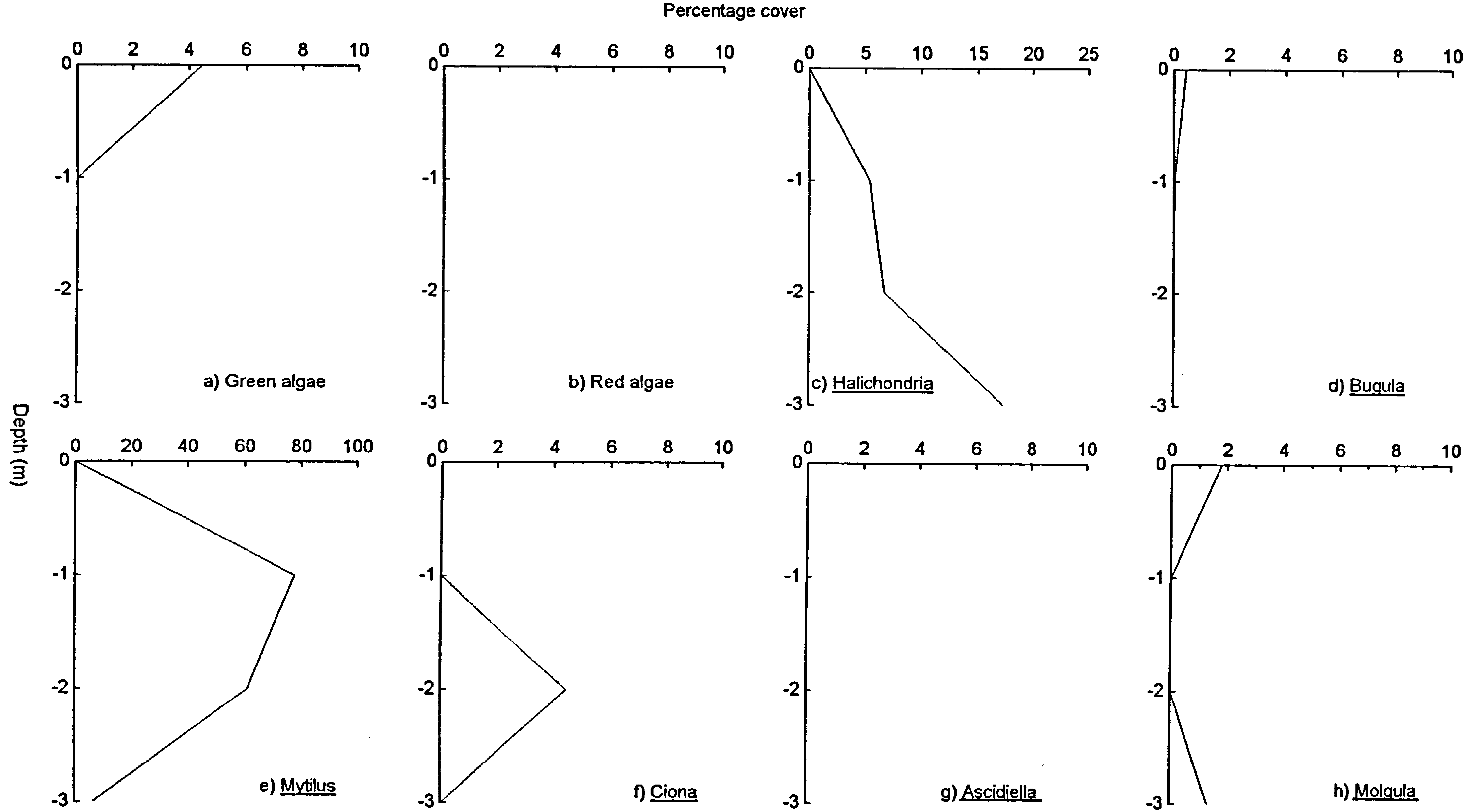

Fig 4.7 Changes in vertical zonation of green algae, red algae, Halichondria, Bugula, Mytilus, Ciona, Ascidiella and Molgula in Queens Dock. Estimates are mean percentage cover calculated from twelve photographs taken at each 1m depth interval. Note differences in abundance scales.

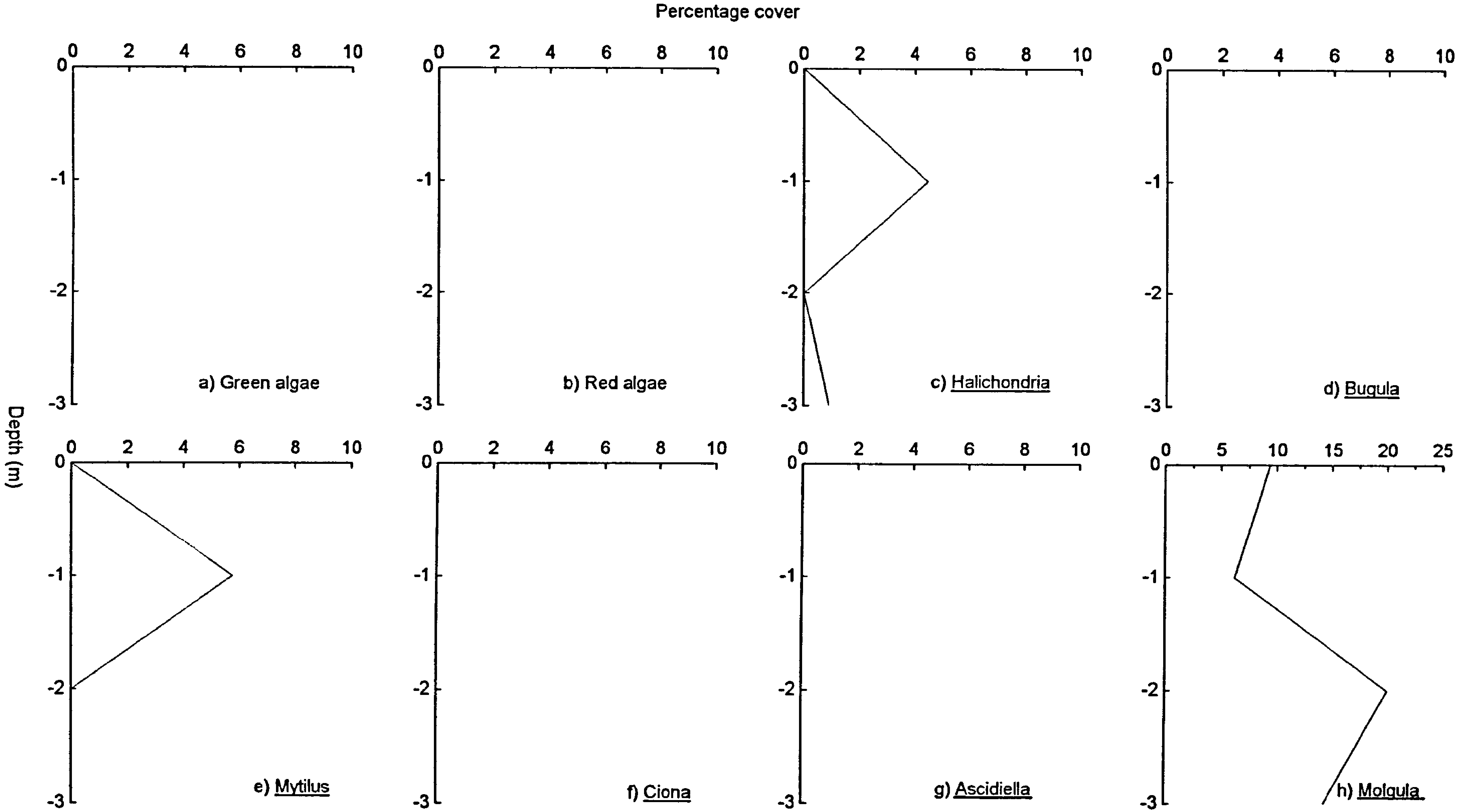

Fig 4.8 Changes in vertical zonation of green algae, red algae, Halichondria, Bugula, Mytilus, Ciona, Ascidiella and Molgula in Coburg Dock. Estimates are mean percentage cover calculated from twelve photographs taken at each 1m depth interval. Note differences in abundance scale.

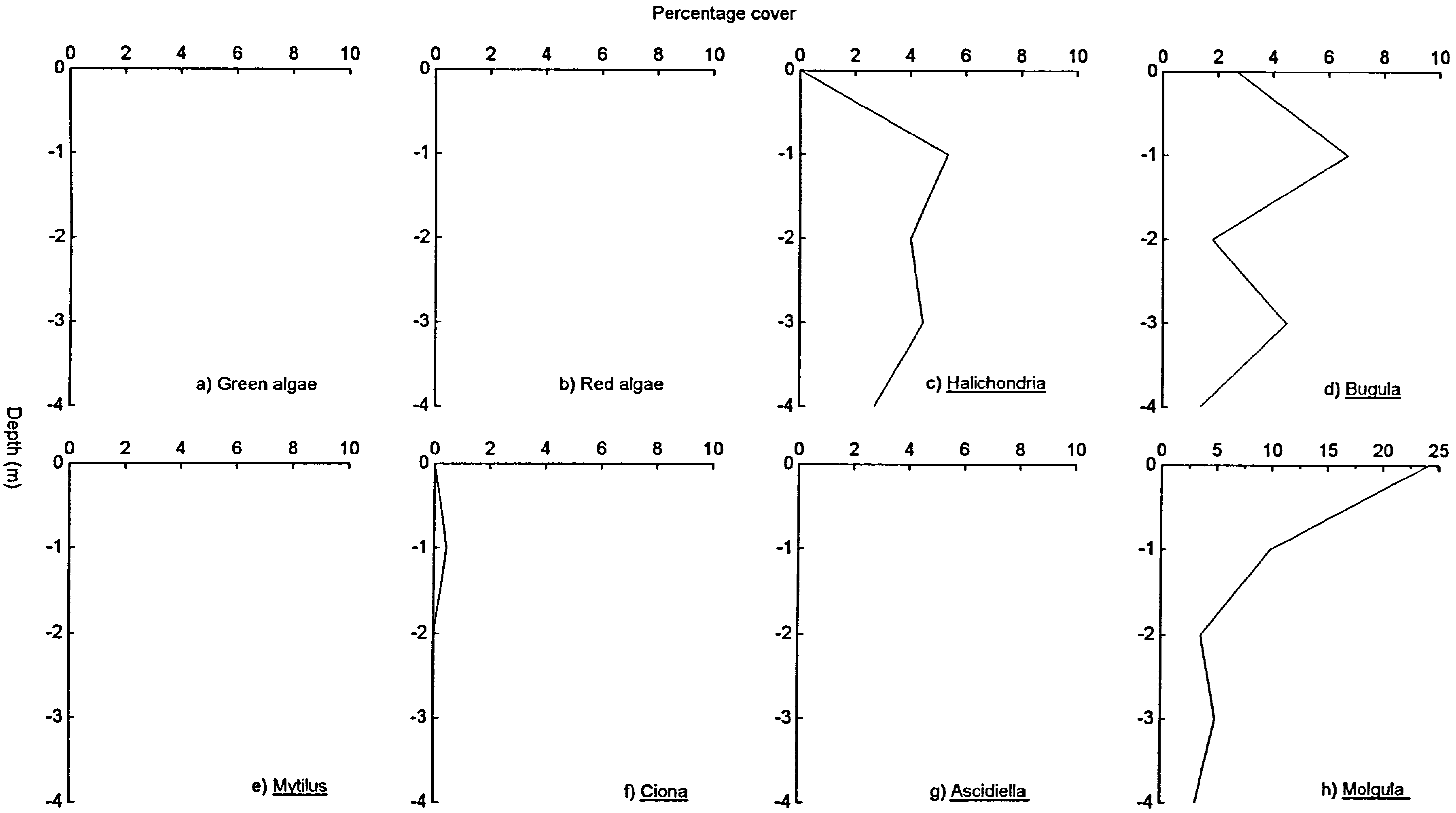

Fig 4.9 Changes in vertical zonation of green algae, red algae, Halichondria, Bugula, Mytilus, Ciona, Ascidiella and Molgula in Brunswick Dock. Estimates are mean percentage cover calculated from twelve photographs taken at each 1m depth interval. Note changes in abundance scale.

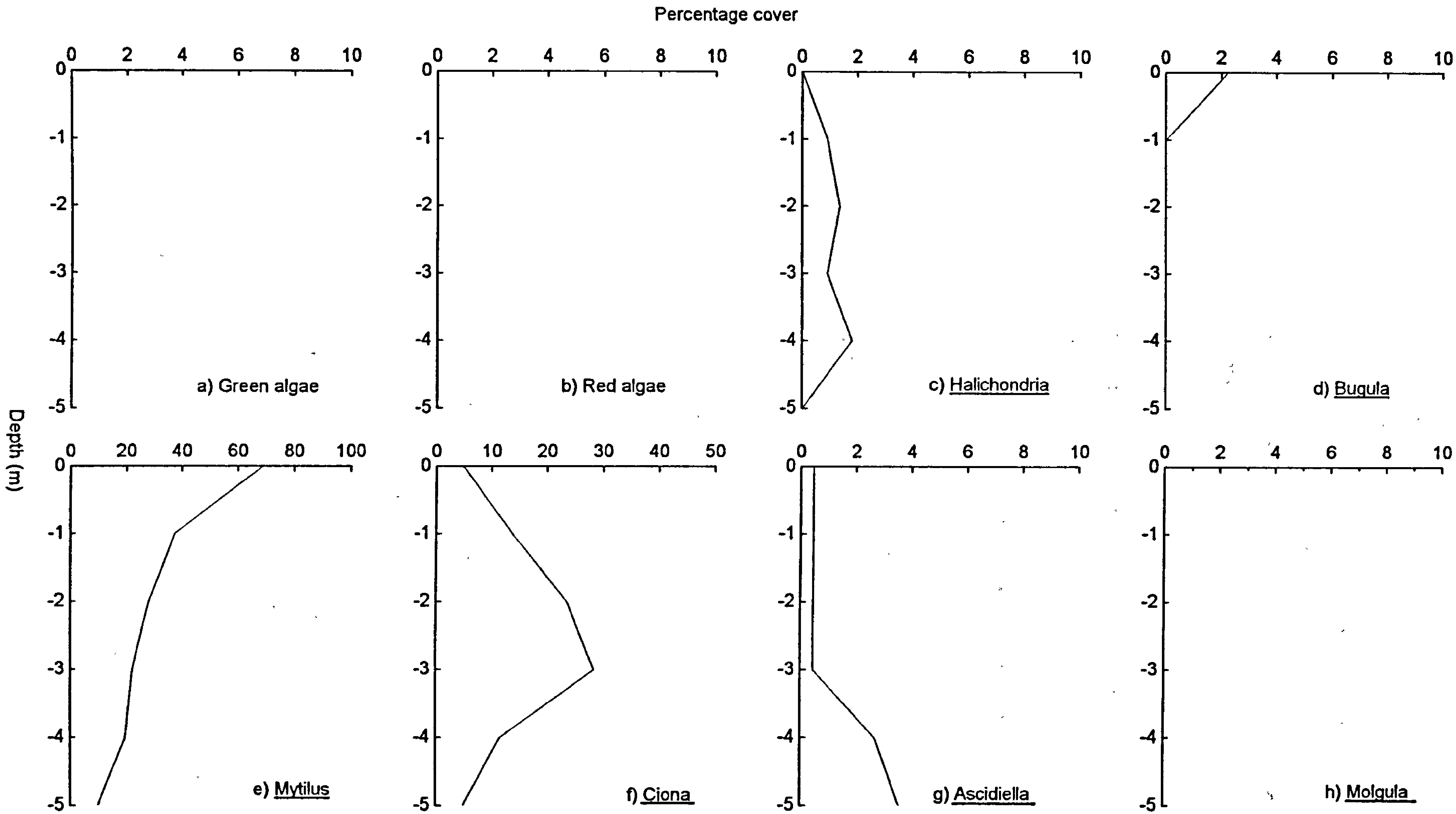

Fig 4.10 Changes in vertical zonation of green algae, red algae, Halichondria, Bugula, Mytilus, Ciona, Ascidiella and Molgula in Princes Dock. Estimates are mean percentage cover calculated from twelve photographs taken at each 1m depth interval. Note differences in abundance scale.

Some also (particularly *Molgula*) tended to increase towards the surface (Fig 4.7h, 4.4g, 4.9h). Interestingly, in Princes Dock, *Ciona* was most abundant around the middle of the wall (Fig 4.10f), where the cover of *Mytilus* was relatively low compared to many of the other docks (Fig 4.10e). *Ciona* and *Ascidiella* were most abundant in Albert, Salthouse, Wapping and Princes Docks (Fig 4.4f, 4.5f, 4.6f, 4.10f). The erect bryozoan, *Bugula simplex* was most abundant in Canning and Salthouse Docks (Fig 4.3d, 4.5d) but was also frequently recorded in Albert and Brunswick (Fig 4.4d, 4.9d). Generally this species was most abundant around a depth of 1m.

4.3.5 Multivariate analysis of dock wall communities

a) Counts

Principal components analysis of counts of species in photographs of the dock wall accounted for 88% of the variation in the first two axes. The ordination diagram indicates that the dominant species separating the sites are *Molgula*, *Ciona*, *Ascidiella* and *Mytilus*, as indicated by the longer vectors for these species (see Fig 4.11). The species vector for *Molgula* is almost in the opposite direction to those for the other three species, indicating an inverse correlation in the abundance of these two groups. *Styela* is closely correlated with *Ciona* and *Mytilus*. The ordination roughly groups Brunswick, Coburg and Canning (Fig 4.11a), the docks close to intake points from the Mersey, with lower numbers of *Mytilus*, *Ciona* and *Ascidiella* but higher densities of *Molgula*. Princes displayed highest densities of *Mytilus* and *Ciona*. The spread of the points for a given site gives a rough indication of the diversity at that site. In order to show this more clearly a 'hull' has been drawn around the points for each site. This suggests that the diversity in Brunswick and Coburg Docks is relatively low, Princes is higher but the highest diversity is found in Albert, Salthouse, Wapping, Queens and Canning Docks.

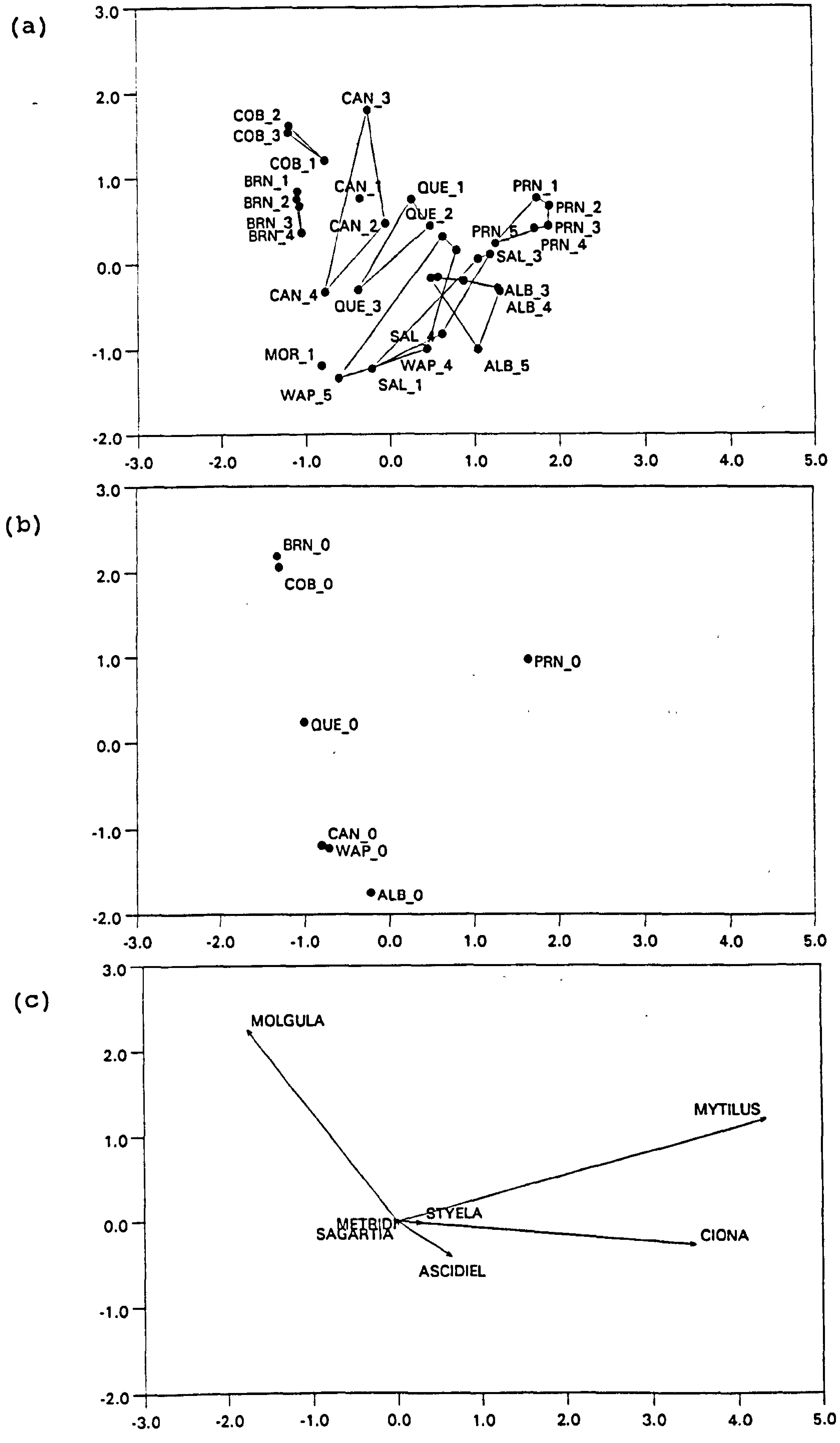

Fig 4.11 Principal Components Analysis of counts of solitary species in photographs taken at 1m depth intervals in each dock sampled. Analysis after log transforming and centring data. ordination accounts for 88% of the variation. (BRN = Brunswick, COB = Coburg, CANN = Canning, QUE = Queens, WAP = Wapping, SAL = Salthouse, ALB = ALbert, PRN = Princes, MOR = Morpeth; prefixes indicate depth e.g. _1 = 1m depth).

b) Percentage cover data

The ordination patterns of species and sites obtained from analysis of the percentage cover data of the photographs of the wall show similar patterns to analysis of the count data (Fig 4.12). The ordination explained 71% of the total variance in the first two axes. Using species counts alone obviously excludes some potentially important species from the analysis, including the bryozoan *Bugula*, *Halichondria* and *Botryllus*. From the ordination diagram it can be seen that bryozoan and *Halichondria* are particularly useful in separating sites (Fig 4.12). Again, *Ciona*, *Ascidiella* and *Mytilus* were well correlated. *Halichondria* is also quite closely correlated with this group. *Bugula* shows no correlation with *Mytilus*. Canning appears to be quite different, particularly on the basis of bryozoan abundance. Brunswick and Coburg are also quite well separated, mostly due to the lower *Mytilus* densities at these sites. The rest of the docks appear to be quite similar in species composition. Ordination of the surface samples for these sites shows the species composition to be more similar to Brunswick and Coburg, indicating that this area is relatively devoid of species.

4.3.6 Destructive samples

It should be borne in mind with the results obtained from scrapes of the dock wall that the degree of replication is much less than was possible with photographs and also that samples were taken from one depth only. However the results do include small species which would have been missed if photography alone had been used, particularly amphipods.

a) Infauna

Fig 4.13 shows how the composition of infauna varies between the docks. Low densities of amphipods were recorded in Brunswick, Coburg, Princes and Morpeth Docks. The highest densities of all four species (i.e. *C. insidiosum*, *M. gryllotalpa*, *J. marmorata*, *G. salinus*) were found in

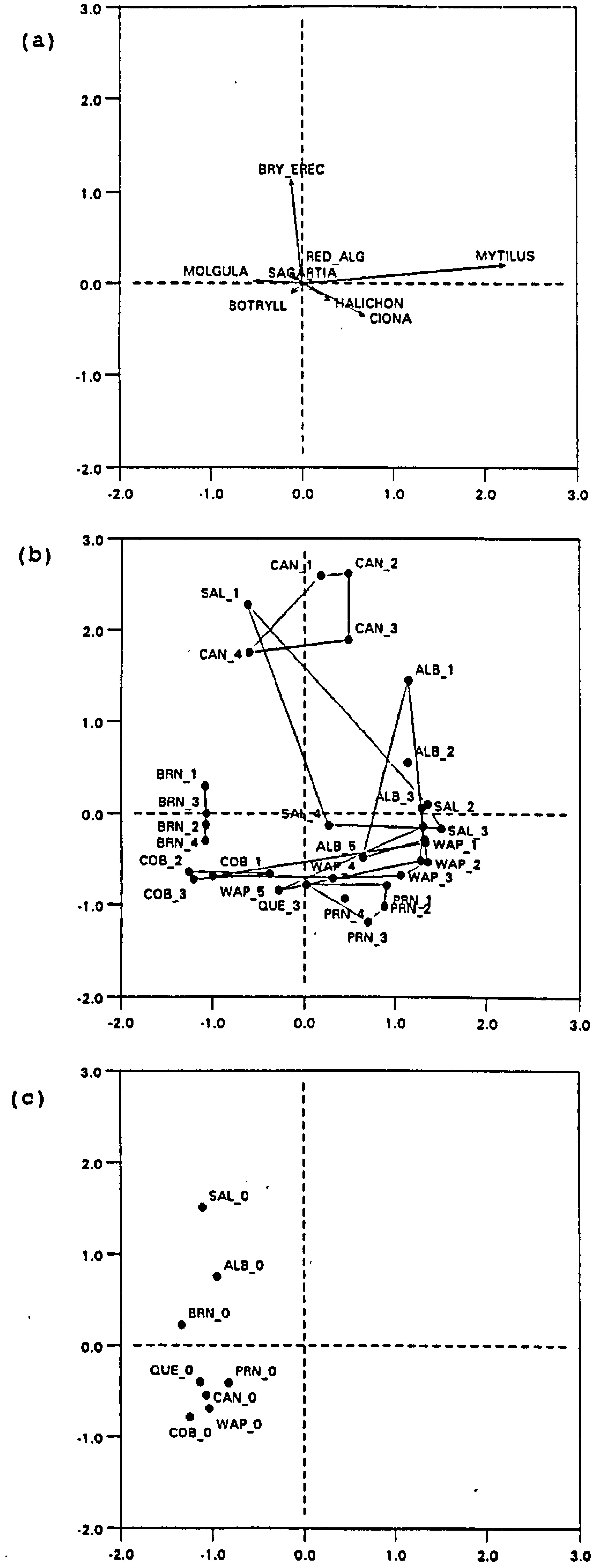

Fig 4.12 Principal Components Analysis of percentage cover data of species in photographs taken at 1m depth intervals in each dock sampled. Analysis after root transforming and centring data. ordination accounts for 71% of the variation. (BRN = Brunswick, COB = Coburg, CANN = Canning, QUE = Queens, WAP = Wapping, SAL = Salthouse, ALB = ALbert, PRN = Princes, MOR = Morpeth; prefixes indicate depth e.g. _1 = 1m depth).

Queens Dock, with lower numbers in Wapping, Salthouse, Albert and Canning Docks. In addition, *Jaera praehirsuta* was recorded in low numbers from Canning and Princes Docks. This is the first isopod recorded from the docks.

b) Macrofauna

The destructive samples were largely dominated, in terms of mass, by *Mytilus* (Fig 4.15). Both the mass of *Mytilus* and total biomass per unit area were highest in Salthouse, Wapping and Queens Docks (Fig 4.15g,h). The biomass in Brunswick, Coburg and Princes Docks was relatively low, due to the absence of a dense *Mytilus* population in these docks. As found from the photographic survey of the dock wall above, *Molgula* was most abundant in Brunswick, Coburg, Queens and Canning Docks (Fig 4.14d, 4.15f). *Styela* was only found in low densities, tending to be more abundant where *Molgula* was low or absent (Fig 4.14b,d, Fig 4.15 d,f). *Halichondria* showed a similar pattern of distribution to *Mytilus*, being more abundant in Salthouse, Wapping and Queens Docks (Fig 4.15b). The erect bryozoan, *Bugula*, was most abundant in Canning Dock (Fig 4.15a). The mass of *Ciona* was generally low, except in Princes Dock (Fig 4.15c). Similarly, *Ascidiella* was only present in low biomass being most abundant in Albert Dock (Fig 4.15e).

c) Community ordination

The pattern of species distributions obtained from ordinating the data from the destructive samples was quite similar to that obtained from the photographic sampling (Fig 4.16). Queens, Wapping, Salthouse, Albert and Princes Docks had similar numbers of *Mytilus*. Queens and Wapping Docks had a greater density of amphipods. Again *Ascidiella*, *Ciona*, *Styela* and *Mytilus* showed quite high positive correlation with one another and were negatively correlated with *Molgula*. No species included in this analysis appeared to be positively correlated with *Molgula*. Canning appeared to have a species composition intermediate between that of

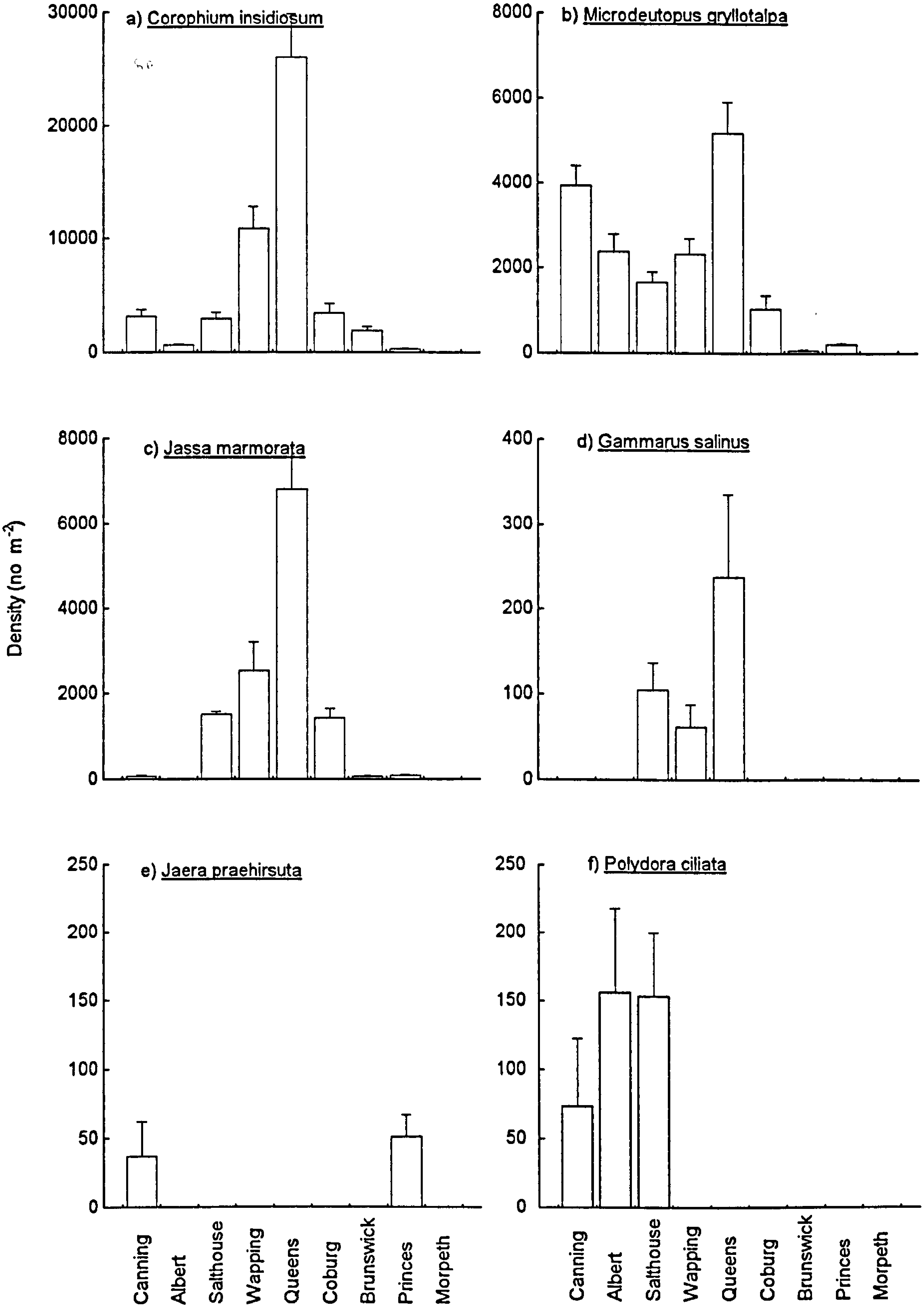

Fig 4.13 Variation in density of associated fauna in destructive samples taken from a depth of 1m. Error bars represent standard error of estimate. Note differences in scale. (n = 5 in all cases)

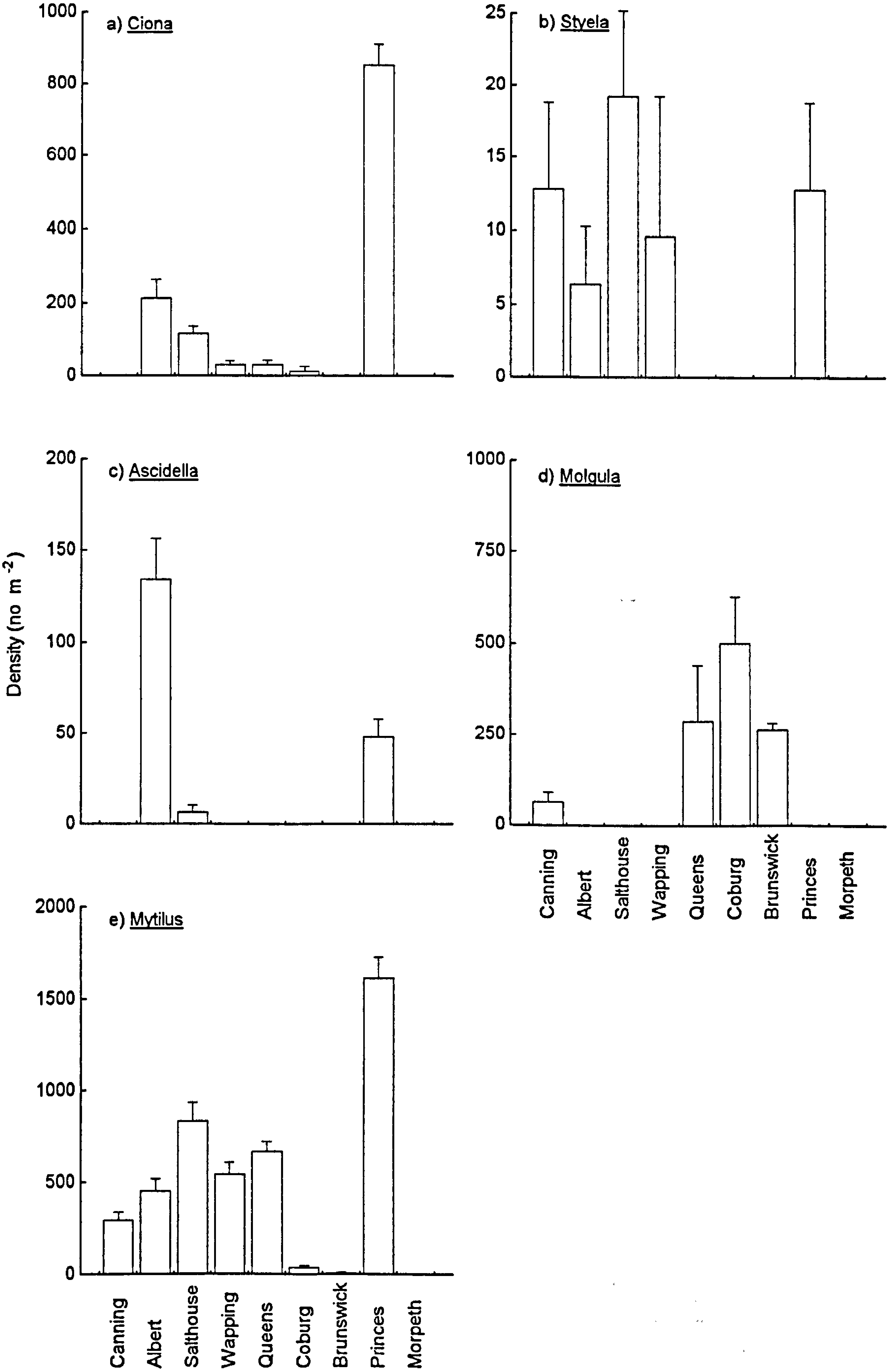

Fig 4.14 Variation in density of Ciona, Styela, Ascidiella, Molgula and Mytilus in destructive samples taken at a depth of 1m. Error bars represent standard errors of estimate (n=5 in each case). Note differences in scale.

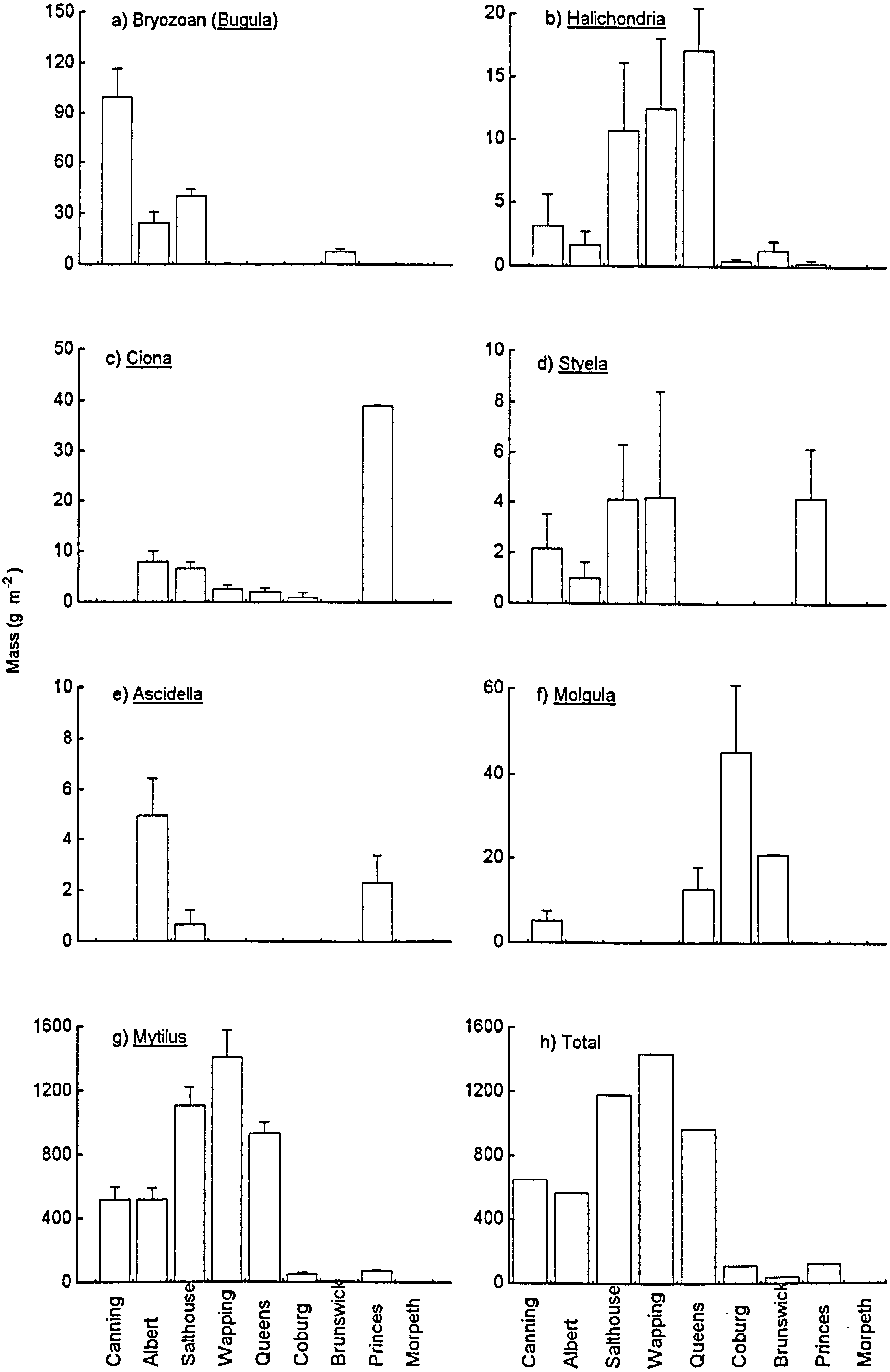

Fig 4.15 Variation in mass of different species on dock wall at 1m depth for docks included in spatial survey (Error bars represent standard errors)

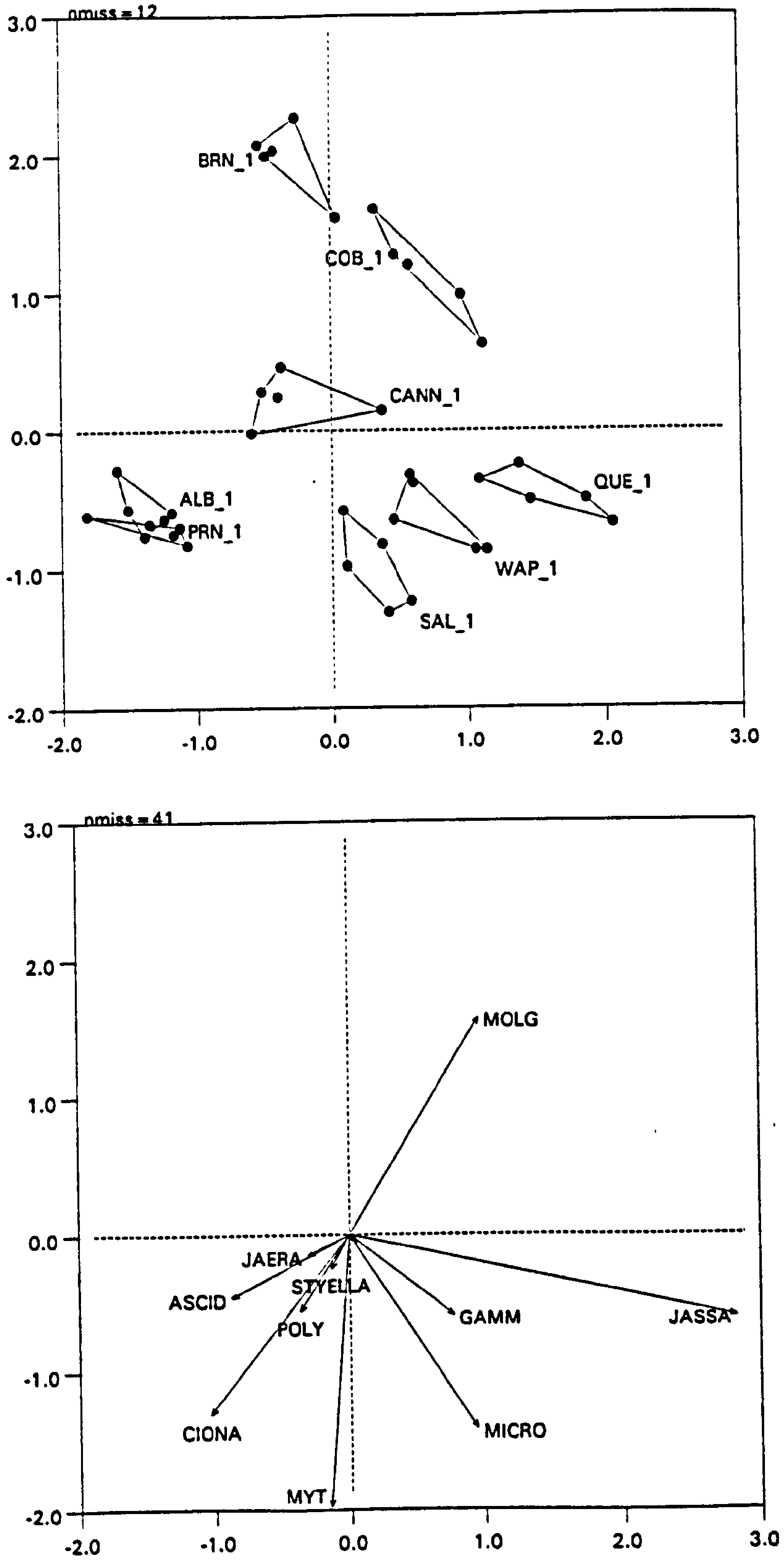

Fig 4.16 Principal Components Analysis of counts of solitary species found in destructive samples of the dock wall benthos. Each sample is shown as a separate point. Analysis after log transformation and centring data. Ordination diagram accounts for 69% of the variation (BRN = Brunswick, COB = Coburg, CANN = Canning, QUE = Queens, WAP = Wapping, SAL = Salthouse, ALB = ALbert, PRN = Princes).

Brunswick/Coburg Docks and the rest of the South Docks.

4.3.7 *Mytilus* population structures

The density of *Mytilus* was assessed using three different methods. Estimates made from scrapes taken from the dock wall were considerably higher than densities calculated either from photographs of the wall or using a board as described in 4.2.7 above (see Table 4.3). This may indicate that these latter two methods fail to take the three dimensional nature of the *Mytilus* population into consideration. *Mytilus* densities appear to be greatest and reasonably constant from 1 to 3 metres depth, with very low densities both close to the dock bottom and near the surface. Densities were high in most of the docks examined, particularly Albert through to Queens. Coburg and Brunswick had very low densities, and none at all were recorded from Morpeth. The *Mytilus* population in Princes was dominated by high densities of juvenile specimens. Their relatively small size meant that densities here could be accurately estimated using photography.

Very similar *Mytilus* population structures were found in all the South Docks studied, where a sufficient number of *Mytilus* were collected. The modal length was relatively large, around 60-65mm, with most of the population clustered quite closely around this size (see Fig 4.17). Low densities of smaller juvenile mussels were recorded in all docks where an adult population was present. Princes lacked the large numbers of adult mussels, being completely dominated by juvenile individuals, with a modal length frequency class of 20-25mm.

4.3.8 Species present

Data from the timed searches are presented in Table 4.4. This method did detect a few species which would have been missed in the methods above, in particular *Carcinus maenas* and *Anguilla anguilla*. Table 4.5 presents a complete list

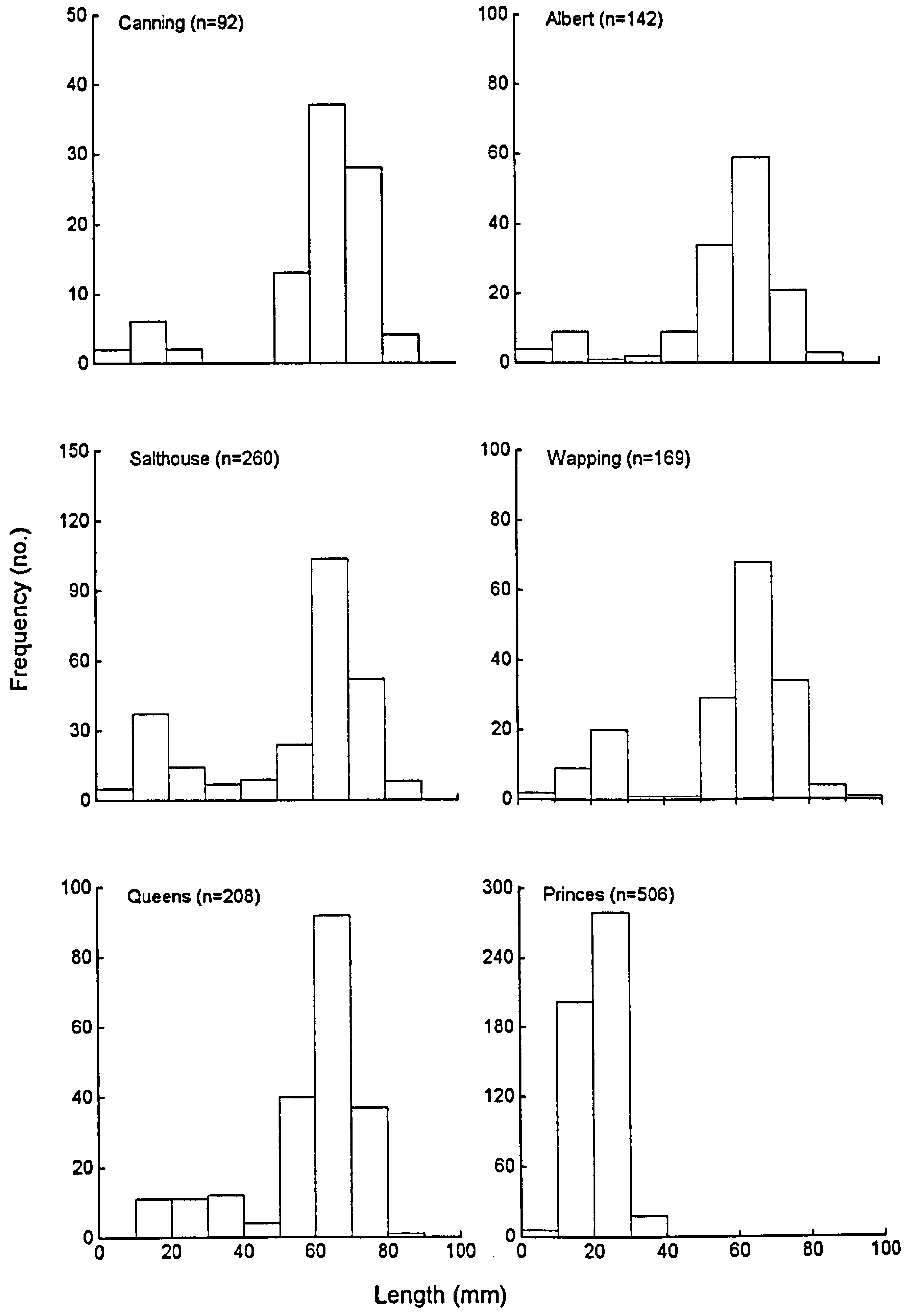

Fig 4.17 Length frequency histograms of Mytilus collected in destructive samples of the dock wall at a depth of 1m in August to September 1993

Table 4.3 Results from five minute timed underwater search in each dock studied. (Scale : 0 - absent; 1 - 1 or 2 found; 2 - between 2 and 10 found; 3 more than 10)

	Canning	Albert	Salthouse	Wapping	Queens	Coburg	Brunswick	Princes	Morpeth
Sagartia troglodytes	2	2	0	3	3	2	1		0
Metridium senile	1	2	3	3	3	3	2	2	0
Ciona intestinalis	2						2	3	0
Styela clava	3		3	3	2		2	3	0
Anguilla anguilla	2	0	1	1	1	0	0	0	0
Carcinus maenas	1			1		2	1	2	0
Crangon crangon	0	0	0	0	0	0	1	0	0

Table 4.4 Average number of *Mytilus* per square metre calculated by running a board down the dock wall and recording the number of individuals encountered. Values in brackets are standard errors of estimates (n=3). Densities calculated from photographs (n=12) and scrapes (n=5) from 1m depth are also included for comparison.

	Canning	Albert	Salthouse	Wapping	Queens	Coburg	Brunswick	Morpeth
0-1m	120 (21.4)	213 (58.1)	207 (19.2)	247 (26.9)	244 (27.0)	71 (2.2)	0	0
1-2m	587 (81.9)	331 (81.0)	558 (53.9)	580 (52.9)	576 (47.5)	11 (8.0)	2 (2.2)	0
2-3m	422 (34.9)	500 (17.6)	558 (82.6)	511 (45.9)	378 (11.8)	9 (2.2)	2 (2.2)	0
3-4m	67 (11.5)	569 (43.3)	291 (76.4)	256 (61.4)	29 (8.0)	0	0	0
4-5m	0	180 (47.3)		76 (2.2)				0
5-6m				0				0
Photographs from 1m	215 (27.1)	341 (46.0)	474 (47.9)	446 (32.7)	333 (28.9)	0	0	0
Scrapes from 1m	1472 (44.0)	2272 (65.5)	4160 (106.1)	2704 (67.0)	3328 (51.5)	176 (10.6)	32 (3.9)	0

of the species found at each site during this study. Only three benthic species were recorded from Morpeth Dock. Of the rest of the docks studied, the highest number of species was recorded in Queens Dock, and the lowest in Coburg and Brunswick Docks. Almost identical numbers of species were recorded from the other South Docks studied.

Table 4.5 Summary of total species found in each dock included in spatial comparison. (Can = Canning, Alb = Albert, Slt = Salthouse, Wap = Wapping, Que = Queens, Cob = Coburg, Brn = Brunswick, Mrp = Morpeth, Prn = Princes)

	Can	Alb	Slt	Wap	Que	Cob	Brn	Mrp	Prn
Tubificoides (unid)	+	+	+		+		+	+	+
Spionid (unid)		+		+	+	+		+	+
Tubificids (unid)					+			+	+
Polydora ciliata	+	+	+						
Bugula simplex	+	+	+		+		+		+
Conopeum reticulum	+	+	+	+	+	+	+	+	+
Carcinus maenas	+			+		+	+		+
Corophium insidiosum	+	+	+	+	+	+	+		+
Crangon crangon							+		
Gammarus salinus			+	+	+				
Jassa marmorata			+	+	+	+	+		+
Microdeutopus gryllotalpa	+	+	+	+	+	+			+
Jaera praehirsuta	+								+
Ascidiella aspersa		+	+	+	+				+
Botryllus schlosseri		+	+	+	+	+	+		
Ciona intestinalis	+	+	+	+	+		+		+
Molgula manhattensis	+				+	+	+		
Styela clava	+	+	+	+	+		+		+
Obelia dichotoma		+	+		+				
Metridium senile	+	+	+	+	+	+	+		+
Sagartia troglodytes	+	+		+	+	+	+		
Mytilus edulis	+	+	+	+	+	+			+
Halichondria bowerbankii	+	+	+	+	+	+	+		+
Anguilla anguilla	+		+	+	+				
Total no. species	16	16	17	16	20	12	14	4	16

4.4 DISCUSSION

The biological communities found in any area are ultimately, either directly or indirectly, governed by the physical environment of that area (Wethey 1984, Connell 1985, Hawkins & Hartnoll 1985, Stoner 1990). Indirect effects are those mediated through other species which are themselves affected by the physical environment (Hruby 1976).

Saline enclosed dock basins are unusual marine habitats in many ways (Allen 1992, Hawkins *et al.* 1992a). Their isolated or semi-isolated nature results in a number of physical and chemical conditions that are not normally experienced in other marine systems, which are generally much more open. The exceptions to this are lagoons and some sealochs with which docks share some features (Allen 1992). The limited exchange of water will limit the supply of larvae or propagules. The history of an area can also have an unusually large affect on the community structure as it will be heavily dependent on exactly which larvae have arrived and at what stage this occurs in the recovery of the system. Isolation may be beneficial in that the levels of certain parameters may also be reduced compared to the estuary outside, such as suspended solids or dissolved nutrient concentrations. However, enclosure and the shelter created by surrounding buildings can lead to stratifiction of the water column.

The physico-chemical measurements made of the docks in this study are of little use without a much longer set of data taken over the annual cycle. Many of these variables show considerable fluctuations in time (Allen 1992, Zheng 1995) and the readings taken on a single occasion in this study are not necessarily typical of the dock as a whole. On the basis of the measurements made, Morpeth is the only dock which stands out as being considerably different from the rest. This dock had lower salinity, lower dissolved bottom oxygen and lower water clarity than the other docks included in this comparison. No evidence of either oxygen or temperature stratification were observed in any of the other docks surveyed. However, the measurements of the physical parameters were made at the end of the summer, a time when stratification would have been expected to be less strong. Other work indicates major problems with water clarity and hypoxia in Morpeth Dock (V.Wanstall & N.Fielding, Liverpool University, pers. comm.). In the South Docks chain, low water clarity is generally more typical of Brunswick and Coburg Docks and to a lesser extent Queens. However, there have been no major problems with bottom hypoxia in recent years in any of these docks (Zheng 1995, V.Wanstall & N.Fielding, Liverpool University, pers. comm.). Water clarity is generally high in Albert and Princes Docks (Zheng 1995, V.Wanstall & N.Fielding, Liverpool University, pers. comm.).

All docks have fine sediment reflecting their shelter and lack of currents. Sediment enters the system in the form of a suspension carried in any water that is exchanged while vessels are entering or leaving, or whilst topping up levels. If there is a large exchange of water and the suspended sediment loading of the source is high, as is the case with the Mersey, then the dock may experience problems with silting up. Hence water exchange in active docks should be kept to a minimum. This strategy is also useful in the docks being redeveloped for alternative uses as it cuts down the cost of future dredging as well as minimising nutrient inputs and hence bloom stimulation (as recommended by Allen 1992). The material that is deposited is generally very fine, as most coarser material will probably not be carried far, except in relatively high energy environments. Two other factors may alter the sediment structure in enclosed docks. The first of these is the dumping, either accidental or deliberate, of sediment by man. Secondly the remains of organisms such as barnacles or *Mytilus* may have quite a strong influence on the particle size in certain instances, particularly near the dock wall.

The results of the particle size analysis of the dock mud, showed Wapping to be considerably different from the other sites. It has a much higher proportion of relatively coarse material, particularly fine sand. However this is most likely as a result of building works here, when a relatively large amount of sand was deposited in the dock. While the rest of the docks show minor variations the sediment has essentially the same structure in all of them, being dominated by the fine clay fraction and smaller. The small variations that were observed may be due to small sample sizes.

The physical properties, particularly particle size, of sediment will obviously have a strong influence on the species it supports (Buhl-Mortensen & Holisaeter 1993, Diaz & Erseus 1994). Fine sediment will tend to be a harsher environment than coarser sediment, being less physically stable and having a lower oxygen concentration (Pearson & Rosenberg 1978, Weston 1990, Buhl-Mortensen & Holisaeter 1993). No attempt was made to assess the organic content of the mud in this study, although this parameter should definitely be included in future studies.

It is now ten years since the completion of dredging of the South Docks in 1985. Since that time large fluctuations have been observed both in the species and density present in the sediment (Allen *et al*. (in submission)), with no real evidence of community development. Longer-lived species, such as *Macoma*, have been recorded but have failed to establish in large numbers. The absence of such species may primarily be due to three causes. Firstly they may be limited by some aspect of the physical environment (Rachor 1977, Jorgensen 1980). Secondly insufficient larvae may be reaching the docks (Josefson 1985) or finally they may limited by biological factors such as predation (Reise 1979, Commito 1982, but see Berge & Valderhaug 1983).

The fact that *Macoma* has been recorded indicates that while larval supply may still be important other factors are certainly having an effect. In relatively benign environments predation is normally held to have greater importance in structuring communities (Menge & Sutherland 1987, Menge & Farrell 1989). A number of bottom feeding fish species such as flounder (*Pleuronectes flesus*) and cod (*Gadus morhua*) have now been recorded from the docks and it is possible that these may have a strong influence on the development of the bottom community. Little work has been done, either on the diet of these species or the size of the population in the docks, making further speculation on the importance of this factor difficult. The unusual physical structure of the sediment seems to be the most likely factor limiting community development here. Its very fine nature makes it physically quite unstable. In addition, particularly during the summer, problems are often experienced with hypoxia, caused by the decomposition of phytoplankton on the dock bottom (Tangen 1977, Pearson & Rosenberg 1978, Boulch 1984, Weston 1990, Rosenburg *et al*. 1991, Buhl-Mortensen & Holisaeter 1993, Diaz & Erseus 1994). This, combined with the apparent high organic loading of the mud itself and the possible presence of other chemical pollutants, combine to make this a harsh environment (James & Gibson 1980, Walker *et al*. 1993). Rachor (1977, 1980) recorded a decline in the benthic fauna in the German Bight, as a result of increased input of sewage and other organic material. Similarly, Pearson and Rosenburg (1978) described a community such as that found in the South Docks as being typical of sediment following organic enrichment. Jorgensen (1980) recorded depletion of benthic fauna due to anoxic bottom water leading to a rise in hydrogen sulphide. The erratic nature of changes in the mud community may simply be a reflection of this severity, with perhaps many individuals being killed during times of extreme conditions. This has led to a community dominated by so-called 'r'-strategy species (MacArthur & Wilson 1969); high numbers of small short lived individuals (see Levin 1984). These probably colonise during benign periods of the year (winter, spring and autumn) and die during occasional anoxic events in the summer (Allen *et al.* 1992).

The greatest abundance of small polychaetes was found in Queens Dock, while amphipods were most abundant in Wapping Dock. The abundance of the sediment infauna may relate to the productivity of the dock concerned. Results showing changes in the water clarity of the docks studied during 1994 are presented in appendix 1. These suggest relatively poor water quality in Brunswick Dock, generally improving towards Albert. Preliminary microscopic examinations of the water in Brunswick indicate relatively low densities of phytoplankton, the poor water clarity being primarily as a result of suspended solids in this dock. Phytoplankton density also tends to be lower in clearer docks such as Albert. It is possible that the higher densities of sediment infauna found in Wapping and Queens Docks indicate a greater availability of phytoplankton in these docks. It should be remembered, however, that the error bars of the density estimates are quite large and further results, particularly on a temporal basis are required to verify the ideas suggested here. Attention should focus on the amount of organic material available within the sediment as many of the species present in the mud are deposit feeders.

In summary the mud remains relatively devoid of life, particularly species of larger burrowing bivalves. In the Baltic, low oxygen conditions appear to limit the survival of organisms, particularly in the central basin (Andersin *et al.* 1977, 1978, Hallfors *et al.* 1981). In areas of higher oxygen concentrations, a variety of species of polychaetes and bivalves are found (Elmgren 1975, 1978). More critical oxygen conditions lead to a dominance of polychaetes such as *Capitella capitata*, *Scoloplos armiger* and *Harmothoe sarsi*, (Andersin *et al*. 1978) similar to the community found in the docks. Mattsson and Linden (1983) also found a similar community below mussel ropes which was attributed to increased organic content and hydrogen sulphide in the sediment. Such a community appears typical of areas where the conditions within the sediment are quite harsh.

The very fine particle size of the sediment is probably one of the primary factors limiting the survival of organisms within the mud. Therefore, manipulating the particle size of the sediment is a potential management strategy which could increase the filtration power available in any given dock. In Wapping Dock, where the sediment is coarser, casts similar to those of *Arenicola* were observed, although this species was not actually detected during the survey, probably due to an insufficiently large sample size. This may indicate that conditions in such sediment are more suitable for this species. Sediment manipulations have been successfully applied to some freshwater systems (Brookes 1988). The possibility of the application of this technique to the docks is currently an active area of research (N.Fielding, Liverpool University, pers. comm.). The possibility will be considered further in chapter 10.

The vertical distribution of algae in the docks will primarily be limited by available light. The deepest penetration of green algae was observed in the docks which tended to have the clearest water such as Albert and Salthouse (Fig 4.4a, 4.5a) with little or no algae recorded in the murkier docks such as Brunswick (Fig 4.9a,b). Red algae were less abundant than green algae and were only found in Canning, Albert and Salthouse Docks, being most abundant in Albert (Fig 4.4b). The increased abundance of red algae in Albert Dock is almost certainly a reflection of greater light penetration in this dock. Russell *et al.* (1983) also attributed the depth of penetration of algae in Sandon Dock to water clarity (see also Hawkins *et al.* 1992b). *Mytilus* tended to be most abundant at the mid-depths of the walls in all docks except Princes where the highest densities were recorded just below the surface (Fig 4.10e). The decrease observed in *Mytilus* abundance towards the surface in the South Docks is most likely due to fluctuations in the water level, leaving mussels exposed for long periods. Alternatively, it may be that the often quite high densities of algae close to the surface are reducing the supply of phytoplankton to mussels in this area through overgrowing the mussels and hence reducing water exchange. In Princes Dock, where the *Mytilus* densities are highest just below the surface, there was no benthic algal growth on the walls due to shading from a pontoon. In addition, the water level in this dock is maintained at a very constant level. The decline in *Mytilus* density towards the bottom may be due to periodic low oxygen supplies, greater silt or lower densities of phytoplankton here. Russell *et al.* (1983) also recorded a decrease in the density of *Mytilus* towards the dock bottom. *Ciona* and *Ascidiella* tended to be most abundant in the clearer docks, namely Albert, Salthouse, Wapping and Princes. It is difficult to suggest reasons for this pattern without further information on gradients in the physico-chemical environment. However, increased amounts of suspended solids in other docks are a strong possibility. It appears that solitary tunicates are more abundant where densities of *Mytilus* are lower, such as towards the dock bottom (Fig 4.4f, 4.5f,g) or the surface (Fig 4.4g). This is likely to be as a result of interspecific competition with *Mytilus*. Again Russell *et al.* (1983) recorded similar results with increased densities of *Ascidiella* in Brocklebank Dock where *Mytilus* was rare. The erect bryozoan *Bugula* was most abundant at around a depth of 1m. This may be purely a behavioural settlement reaction of this group, or it may be that it is taking advantage of being able to overgrow *Mytilus*. The importance of larval behaviour in determining species distributions is well known (Denley & Underwood 1979, Connell 1985, Stone 1990)

The community observed in the docks is strongly characterised by *Mytilus* and the tunicates *Ciona*, *Ascidiella* and *Molgula*. The abundance of *Molgula* tends to be greatest when the abundance of the other three is low. It is interesting that the PCA analysis tended to group Brunswick, Coburg and Canning Docks as having similar community composition. These three sites are closest to the two sets of lock gates (Fig 4.11, 4.16) which may indicate the importance of water exchange on what grows in the surrounding area. In particular, the water brought in tends to be highly loaded with suspended solids and nutrients. Suspended solids may interfere with the filter feeding mechanisms of some of the species, while higher nutrient levels will almost certainly increase productivity in these areas. Decreased rates of filtration have been observed in both mussels (Winter 1973, Navarro & Winter 1982) and ascidians (Robbins 1983) with increased suspended particle loading, however this has not resulted in a decrease in ingestion rates. A number of workers, however, have shown that increased amounts of suspended sediment can limit the survival of both larvae and adults of some filter feeders, including *Mytilus* (Peddicord 1980, Nelson *et al*. 1987, Seaman *et al*. 1991). It seems likely that increased levels of suspended sediments as a result of intake of water from the Mersey may be responsible for the change in community composition observed in Brunswick Dock and others (Coburg and Canning) close to the point of intake. This appears to result in a switch from a *Mytilus* dominated community to one with a greater proportion of ephemeral species, particularly *Molgula*.

The variation in the densities of amphipods on the dock walls appears to be related to a combination of dock water clarity and *Mytilus* density. Amphipod densities were very low in Brunswick, Coburg, Princes and Morpeth Docks probably due to the absence of an adult mussel matrix at these sites. Most of the amphipod species found in the docks are either filter or detrital feeders. The *Mytilus* matrix probably provides space amongst the shells and byssus threads; they also provide food, in the form of faeces or pseudofaeces. The highest numbers of amphipods were observed in Queens Dock, declining in Wapping and Salthouse Docks. This correlates with the water clarity in these docks, which partially relates to the standing crop of phytoplankton. Water clarity tended to be worst in Queens, improving towards Salthouse (see Appendix 1). Amphipod densities were also lower in Canning Dock, perhaps due to the lower density of *Mytilus* here.

Mytilus is the main species dominating the wall community in terms of biomass in most of the docks studied, although it has only recently arrived in Princes Dock. It was, however, only found in low numbers in Coburg and Brunswick Docks and was completely absent from Morpeth. Reasons for the spatial distribution of *Mytilus* are discussed fully in chapter 6. The *Mytilus* length frequencies from the Canning, Albert, Salthouse, Wapping and Queens Docks show a very similar size distribution, dominated by larger individuals. This will also be considered in more detail in chapter 6. It is probably a reflection of the very high initial settlement of *Mytilus* throughout the South Docks in the autumn of 1988 (Allen 1992). Since this time there has been relatively little recruitment to the population. Princes Dock had very few adult *Mytilus* but large numbers of juvenile individuals. This was the result of a heavy settlement of *Mytilus* in this dock in 1993 (see chapter 5). The analysis and discussion of the biometric data on the mussels are presented in Chapter 6.

The walls of the majority of the docks studied were dominated by an often very dense population of *Mytilus*. Examination of the size distribution of this species using length frequency histograms, revealed essentially three population structures. The first was very low densities, or complete absence of the species, as was observed in Morpeth and Brunswick Docks. The second, as represented by the majority of the South Docks was a population dominated by quite large individuals (60 to 80mm) with relatively low numbers of juveniles. A third type was observed in Princes Dock were the population was made up entirely of small mussels, between 10 and 30mm in length. The reason for these different structures will be addressed in Chapter 6.

Fouling communities similar to that observed on the subtidal walls of docks around Liverpool have been recorded in a number of other studies. Fraser (1932, 1935, 1938) and Corlett (1948) documented *Mytilus* dominated communities, with *Balanus*, hydroids and polychaetes on buoys and other floating structures in the Mersey Estuary. A number of other studies using tiles in harbours or estuaries have also recorded similar communities (Scheer 1945, Dean & Hurd 1980, Harms & Anger 1983). Hendry *et al*. (1988a) carried out a survey of nine other docks around Britain, which included a description of the benthos. They recorded a relatively sparse community in most of the docks studied, though this was mainly a result of low salinities. However, even some of the higher salinity docks examined, such as Portway Marina, Penarth, appeared to have very little community development (Hendry *et al*. 1988a).

The Baltic is another environment which shares much in common with that found in the docks. As in the docks, the water level remains relatively constant and any change is primarily as a result of weather, rather than tides. The area supports a mixture of marine and freshwater species, depending on the salinity and degree of shelter. The shallower areas are dominated by a belt of *Cladophora glomerata* with *Fucus vesiculosus* found below this in more saline areas. There are large areas of the subtidal which are dominated by *Mytilus* (Kautsky 1981). Low oxygen conditions, particularly in the central basin may limit the survival of organisms, particularly in the mud. In such areas, the sediment fauna is dominated by species such as *Capitella capitata*, *Scoloplos armiger* and *Harmothoe sarsi*, similar to the species observed in the docks.

The benthic community found in the docks around Liverpool is unusual in two respects. Firstly, *Mytilus* is not normally found in the subtidal and secondly there is a complete absence of perennial algae in any of the docks studied. Reasons for these two anomalies will be considered further in chapter 6 and chapter 9 respectively.

SUMMARY

While some broad similarities were observed in the communities found in the docks studied, they were far from identical. The mud appeared to be a relatively impoverished environment, probably due to the very fine particle structure. An apparent gradient was found, in the wall communities with a *Molgula* dominated community being present near the gates to the Mersey to a *Mytilus* dominated community with higher diversity further from the gates. Reasons for this are unclear but may be due to increased levels of suspended solids in docks close to the gates, due to increased intake of water from the Mersey. There also appears to be evidence of vertical zonation of organisms on the dock walls. The community found on the dock walls around Liverpool shares much in common with other fouling communities and the communities found in lagoonal areas such as the Baltic. The two most unusual aspects of the dock community are the presence of *Mytilus* in the subtidal and absence of perennial macroalgae. Reasons for these will be considered in subsequent chapters.

CHAPTER 5

TEMPORAL CHANGES IN THE WALL COMMUNITIES IN THE LIVERPOOL DOCKS

5.1 INTRODUCTION

The docks around Liverpool have experienced a variety of different histories since the decline of shipping (see chapter 2). Their past has led to an apparent mosaic of different recolonisation states (see chapter 4), generated from essentially the same propagule source, the Mersey Estuary and Liverpool Bay. Patterns of distribution and community structure are also modified by the degree of interchange with the Mersey and the characteristics of the dock basins themselves. Moreover, the range of recolonisation states allows some speculation on the community development of a wider range of temporal scales than the time actually available for the study. It should also allow some degree of prediction on what changes can be expected in the communities found in the different docks.

Most studies of succession or re-colonisation are carried out on relatively small scale patches. These areas may be either artificial or natural. There is a large body of literature on the use of artificial substrates, usually tiles or plates of some description (Scheer 1945, Sutherland 1974, 1981, Sutherland & Karlson 1977, Anger 1978, Dean & Hurd 1980, Kay & Keough 1981, Chalmer 1982, Harms & Anger 1983, Keough 1983, 1984a). One of the shortfalls of these studies is the lack of integration of results with changes that are actually occurring in the resident community. Studies on natural substrates have either involved simply monitoring changes in a community through time which incorporates natural disturbance events (Sousa 1979b, Cross & Southgate 1983, Hawkins & Hartnoll 1983, Svane 1984, Terry & Sell 1986, Vance 1988, McCook & Chapman 1993)or, more commonly, experimental disturbances of an area are made and then the pattern of community development observed (Lubchenco & Menge 1978, Farrell 1989, Sousa 1979, Hawkins 1981, Lubchenco 1983, Turner 1983b, Vance 1988, Svane 1988, Janke 1990). Larger scale studies on recolonisation are rare. Those that have been carried out have usually followed community development on some new structure such as breakwaters (Hawkins et al. 1983), artificial reefs (Carter *et al.* 1985, Woodhead & Jacobson 1985, Terry & Sell 1986) or islands such as Surtsey (Fridriksson 1975). Serious pollution incidents and particularly oil spills often leave large areas of substrate totally devoid of life. Various studies have followed the recolonisation of these areas (Southward & Southward 1978, Ibanez & Dauvin 1988).

The term 'stability' has been much misused in the field of ecology. Holling (1973) attempted to separate the *stability* and *resilience* of a system. He defined stability as the ability of a system to return to equilibrium after a perturbation and the resilience as the ability to resist perturbations. The most widely used measure of stability is the fluctuation of abundances of populations around an equilibrium density (Gray 1977). The relative abundance patterns of species and the stability of species composition have also been used (Gray 1977). Sutherland (1974) looking at community development on tiles described a situation of 'multiple stable states', where there was more than one type of community structure that could persist through time. Problems arise, however, in determining the temporal and spatial scales at which a community should be viewed when considering how stable it is. If these scales are large enough any community can be considered stable, but at a finer scale, few are. Connell and Sousa (1983) considered that the spatial scales used by Sutherland and Karlson (1977) were too fine and that while multiple stable states were theoretically possible no workers had provided sufficient evidence to prove the existence of such phenomena. Sutherland and Karlson (1977) concluded that rather than asking 'Is a community stable?'

we should be looking at what effects given perturbations will have on the community. A lot of information can still be gained from studying changes in a community through time, particularly with a view to identifying the kind of perturbations that are occurring and how frequently. Such information is essential when assessing the stability of a system and this indeed is an area were many studies are flawed in their assessment of stability (Connell & Sousa 1983).

Multivariate methods can be a useful means of graphically displaying differences in communities in time (Ibanez & Dauvin 1988, Gravina *et al.* 1989) and space (van Tongeren ??). They can also give an indication of the species diversity at a site (ter Braak 1983). Little use has been made, however, of these methods for simultaneously assessing both temporal and spatial differences in communities. A multivariate approach, however, should ease the separation of the data into community types over the temporal and spatial scales being considered and is a useful means of providing a general overview of differences in the communities.

The spatial survey carried out in 1993 gave an indication of the range of communities present in the docks around Liverpool. For this temporal study it was impossible to follow changes in all of these docks and two were therefore selected, namely Albert and Queens, these being considered typical of the South Docks. Pevious information was also available for these (Allen 1992). A preliminary examination of the walls in Princes Dock indicated the absence of a dense population of *Mytilus* in this dock. Therefore at the start of 1993 this dock was added to the temporal monitoring programme in order to compare and contrast changes there with those in the South Docks.

The primary aim of this study was to describe the natural seasonal and longer-term variation that occurs in the wall benthos of the selected docks. The results were integrated with those from the spatial survey described in chapter 3 in attempt to classify the docks into broadly similar community states and suggest causes for these states. The study concentrated on changes in the abundance of the most common species. Extensive use will be made of multivariate statistical techniques as a means of viewing temporal and spatial differences in communities.

5.2 METHODS

5.2.1 Study site

The south facing wall of Albert Dock and the west facing wall of Queens Dock were selected for temporal monitoring from January 1992 until July 1994. In addition the east facing wall of Princes Dock was added to the study in January 1993. Quite large variation was found in community structure with depth (see chapter 4). Therefore in this study work focused on the community present at a depth of 2m in these docks. This depth always remains below any fluctuations in water level due to the impoundment regime.

5.2.2 Sampling

The communities were sampled non-destructively, approximately every two months, using underwater photography. Abundance was assessed by projecting the slides taken on a screen. Counts were made of solitary species and percentage cover of primary space occupiers was calculated using a series of twenty five points drawn on the screen. Full details of the methods and required sample size can be found in chapter 3. For this study eighteen photographs were normally taken in each dock on each visit. The communities in Albert and Queens Docks were dominated by *Mytilus* which itself provided a secondary substrate onto which other organisms could settle and grow. Therefore, in addition to assessing the primary space occupiers (eg. *Mytilus* and *Ciona*), as described in chapter 3, the abundance of secondary cover species (eg. *Botryllus*, *Obelia* and benthic algae) was also assessed using the same methods.

5.2.3 Multivariate analysis

Preliminary examination of the community data using detrended correspondence analysis (DCA) indicated relatively short gradient length with less than 2.5

standard deviation units. Therefore the linear technique of principal components analysis (PCA) was adopted for studying community structure. Both species counts and percentage cover data were analysed after centring the data by species in other words PCA on a covariance matrix. Species counts were transformed using a log(x+1) transformation while a square root transformation was used for percentage cover data. The temporal data available from Queens, Albert and Princes Dock were simultaneously analysed with the data from 2m depth in the other docks studied in the spatial comparison described in chapter 4. The analysis was carried out using 'CANOCO' (ter Braak 1987-1992) and results presented graphically using 'CALIBRATE' (Juggins 1994). This allowed sites to be presented individually on a biplot while the model used between the biplots remained the same. Therefore the different biplots are directly comparable.

5.3 RESULTS

5.3.1 Albert and Queens Docks

Considerable changes were observed over time in the biota on the walls of both the docks studied (see Fig 5.1 - 5.4 and 5.8 - 5.9). *Mytilus*, the dominant species in Albert and Queens Docks, was the only species which really persisted from year to year. Most of the other species were seasonal or ephemeral in nature. It is also interesting that bare space remained almost constant.

The abundance of *Mytilus* in Albert Dock, as estimated either from numbers or percentage cover, apparently remained reasonably constant over the period of study. This species occupied between forty and fifty percent of the space on the wall. It should be noted that photography did not allow accurate determination of the density of this species (see Chapter 4). The relatively large size of the individuals compared to the area photographed and the stacking of individuals on top of one another meant that densities of this species were probably underestimates. Problems were also experienced in assessing the true percentage cover of *Mytilus*, as it was frequently obscured by secondary cover species. The results from Queens Dock again show *Mytilus* as the dominant species, though densities appear about half that observed in Albert Dock.

Apart from *Mytilus*, the major space occupiers on the dock wall were *Ciona intestinalis*, *Ascidiella aspersa*, *Botryllus schlosseri* and *Halichondria bowerbankii*. Some of these species tended to show annual peaks in abundance. For example, *Botryllus schlosseri* in Albert Dock had a particularly obvious seasonal pattern, with peaks of almost identical amplitude being observed each June / July during the three years of study (Fig 5.1c). These peaks were also observed in Queens Docks but were more variable in size

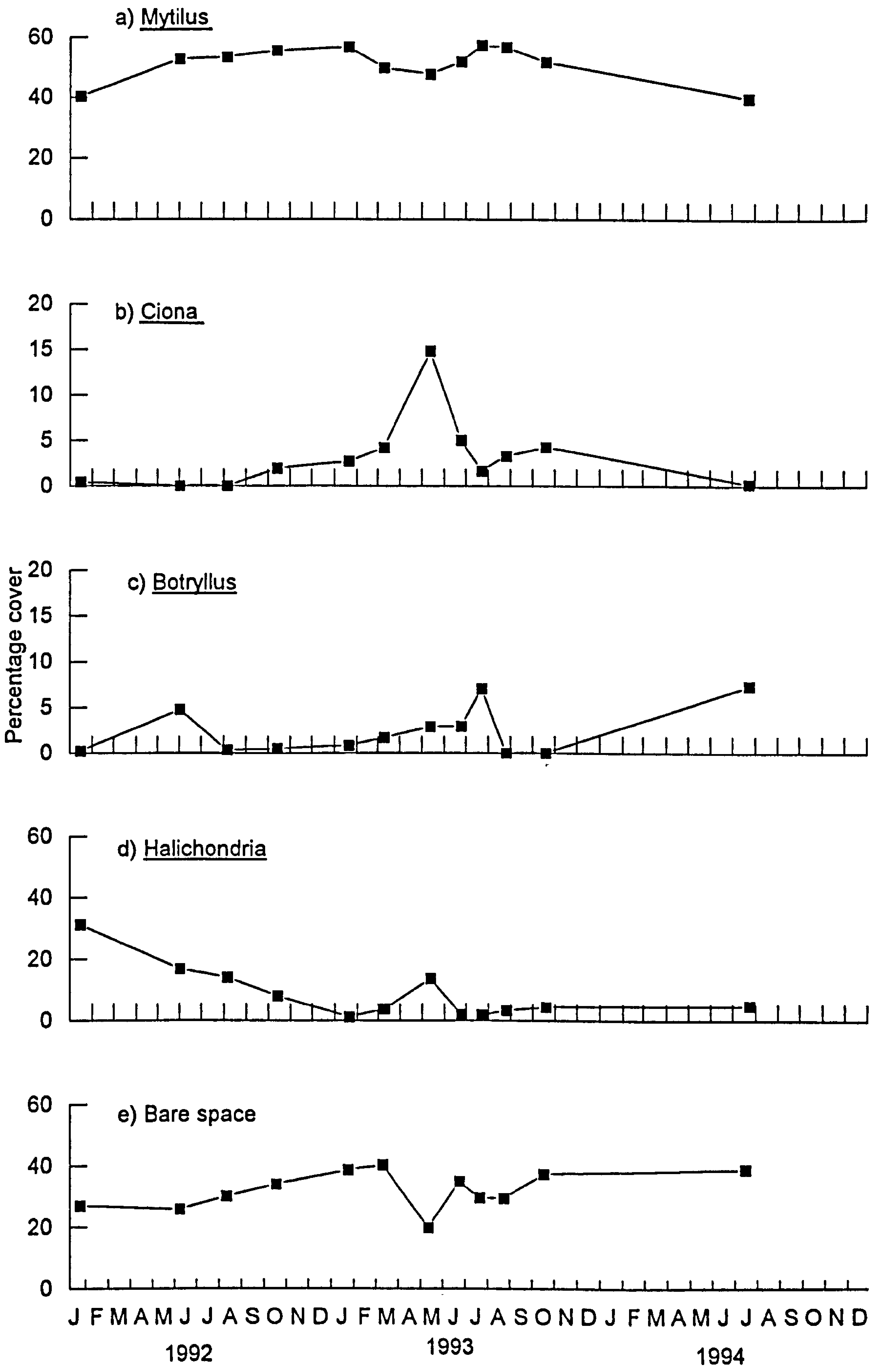

Fig 5.1 Variation in percentage cover of dominant species and bare space with time at a depth of 2m in Albert Dock. Note changes in scale. (n = 18 in all cases)

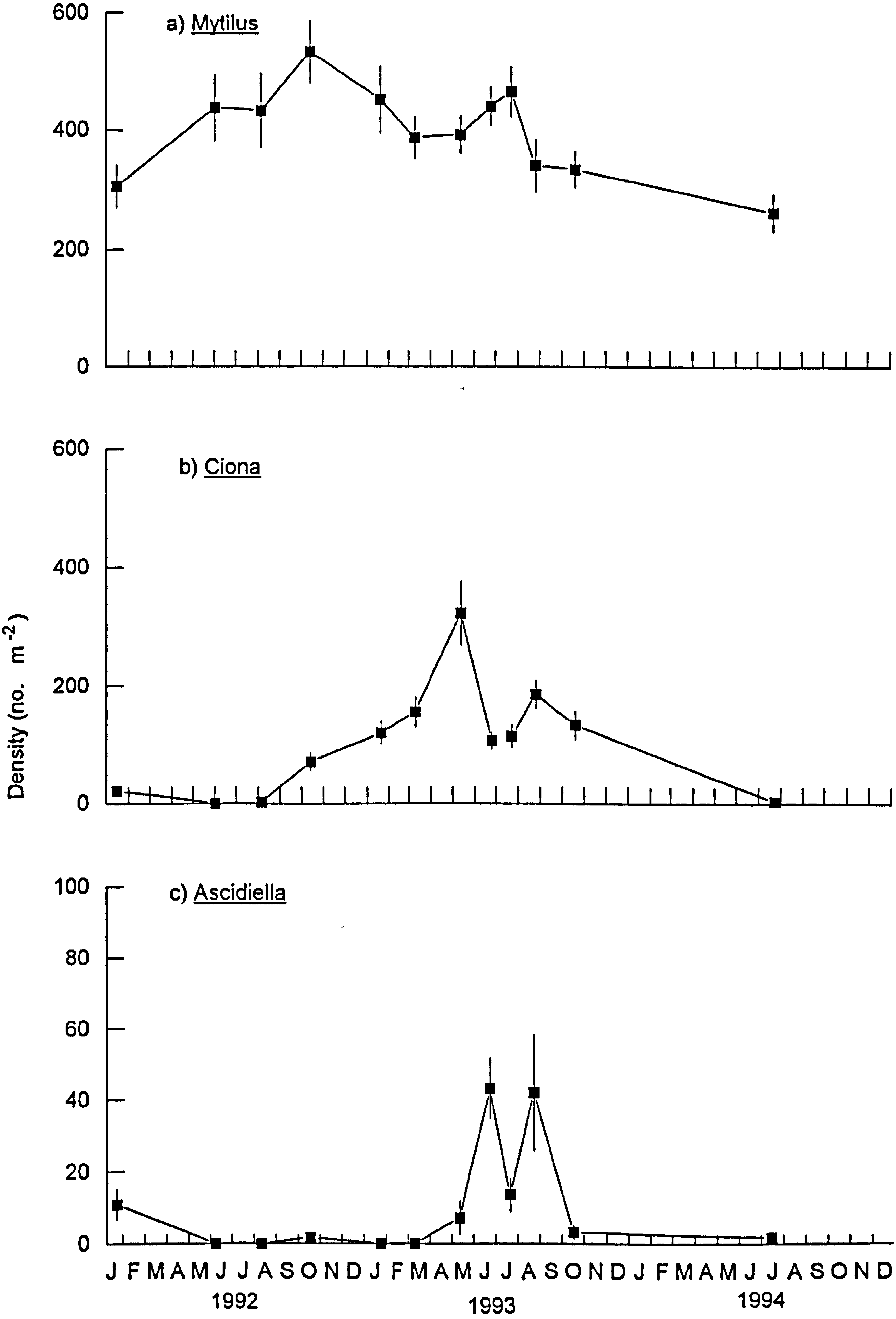

Fig 5.2 Variation in density of major species at 2m depth on Albert Dock wall with time. Note change in scale (Error bars = Standard Error; n = 18 in all cases)

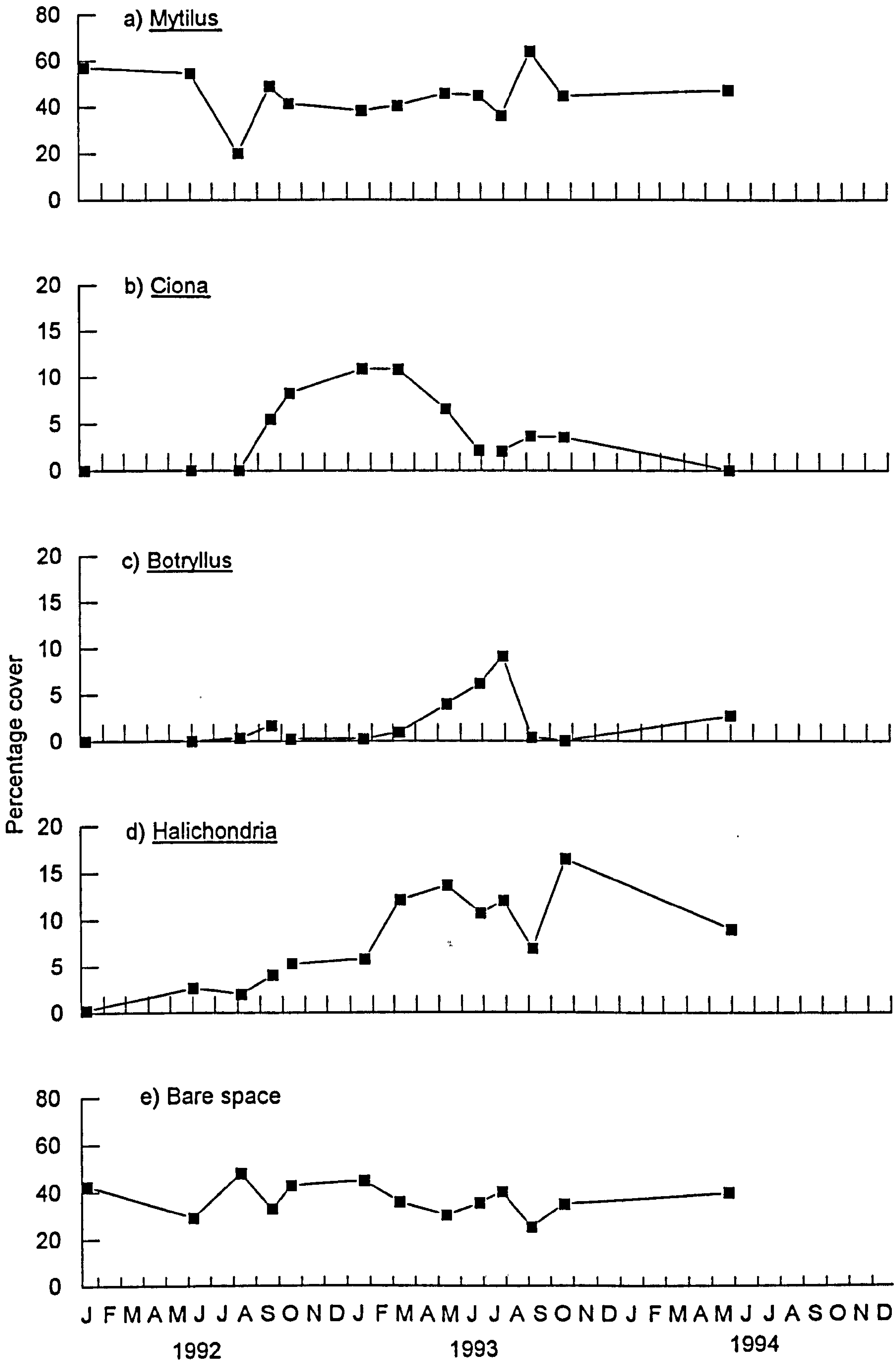

Fig 5.3 Variation in percentage cover of dominant species and bare space with time at a depth of 2m in Queens Dock. Note changes in scale. (n = 18 in all cases)

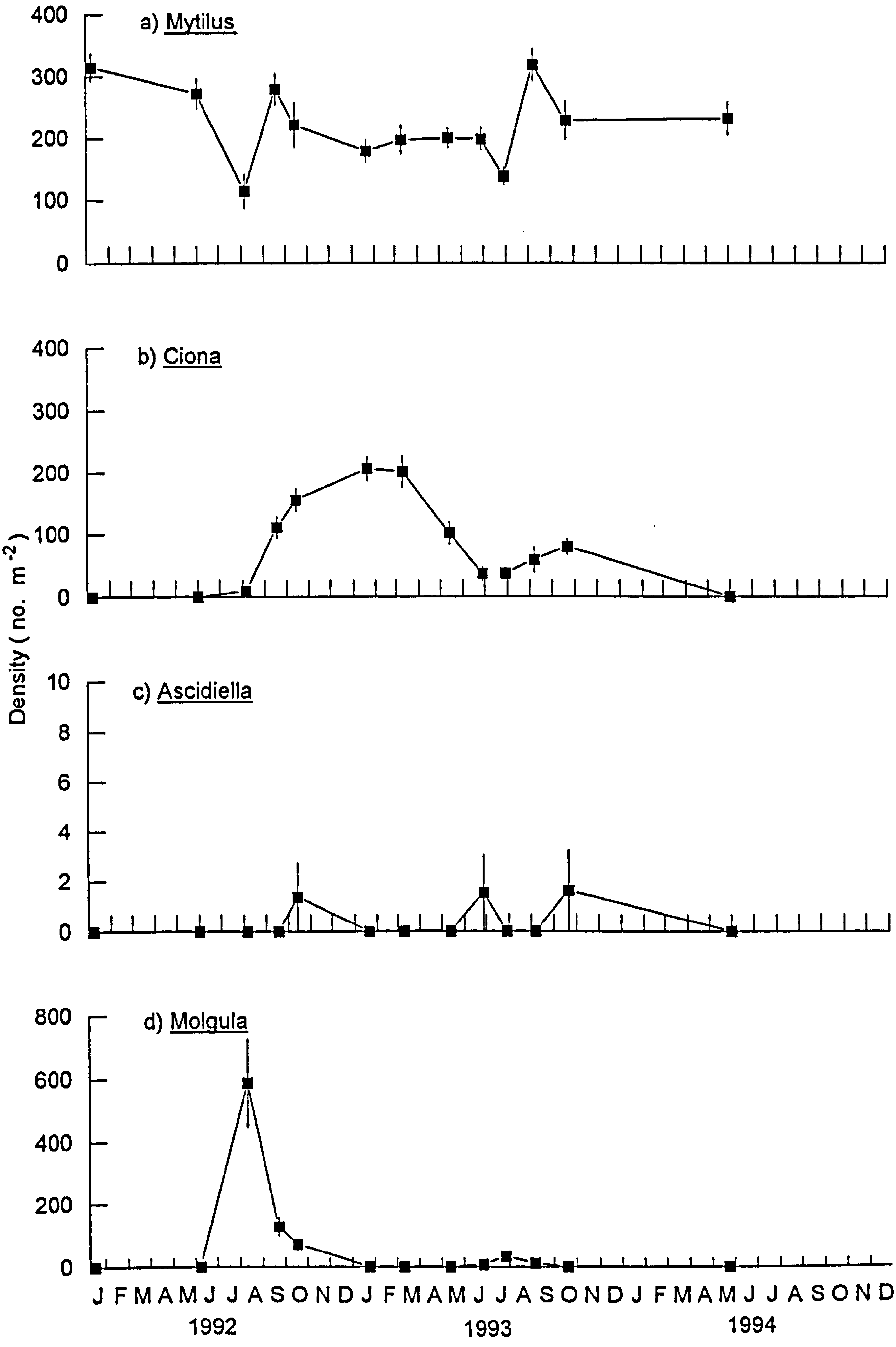

Fig 5.4 Variation in density of major species with time at a depth of 2m on Queens Dock wall Note changes in scale (Error bars = Standard Error; n = 18 in all cases)

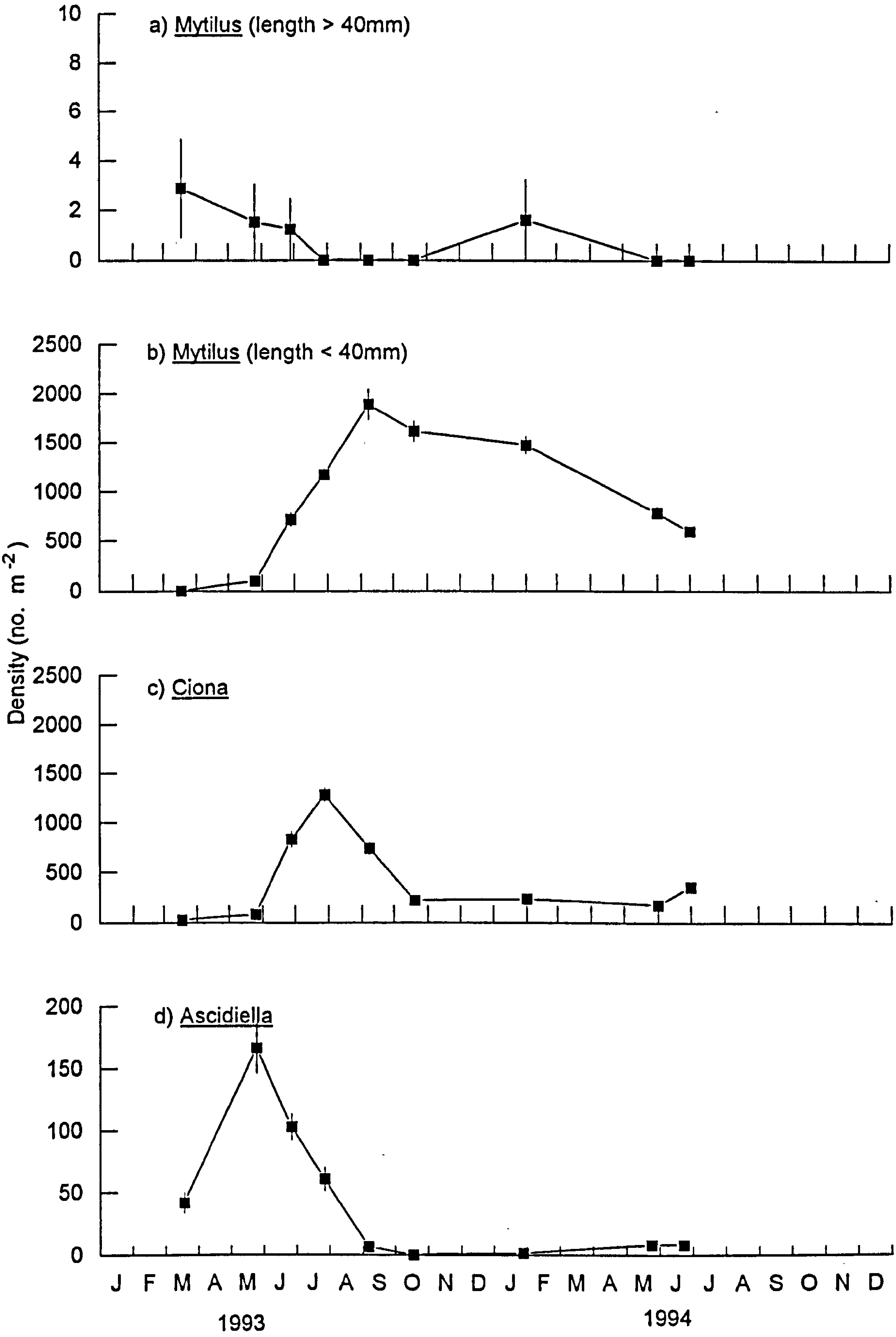

Fig 5.5 Variation of density of dominant species with time at a depth of 2m in Princes Dock. Note differences in scale. (Error bars = Standard Error; no error bar indicates that the range of error falls within the symbol; n=18 in all cases).

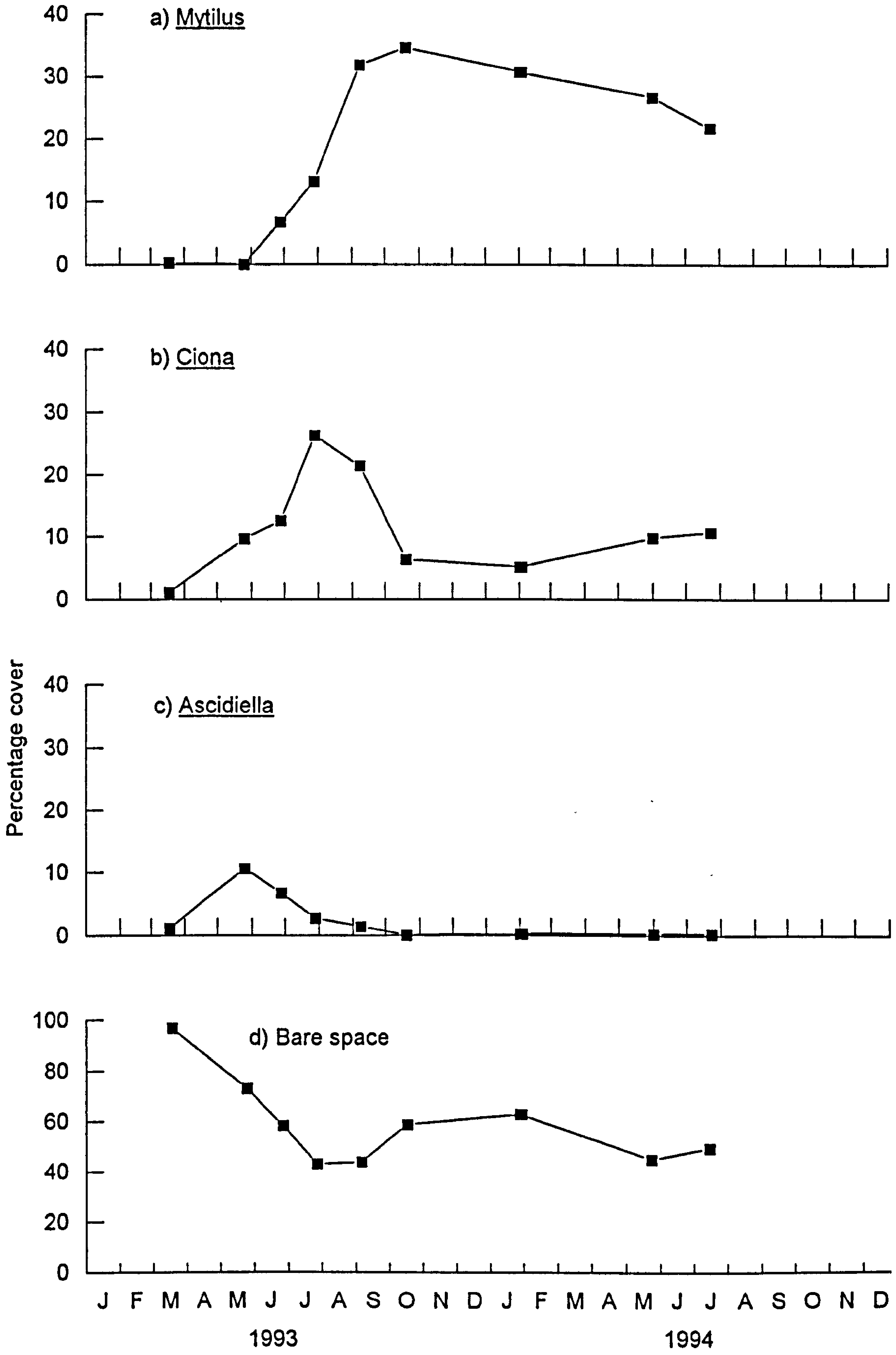

Fig 5.6 Variation in percentage cover with time of major occupiers and bare space at a depth of 2m in Princes Dock. Note changes in scale. (n = 18 in all cases)

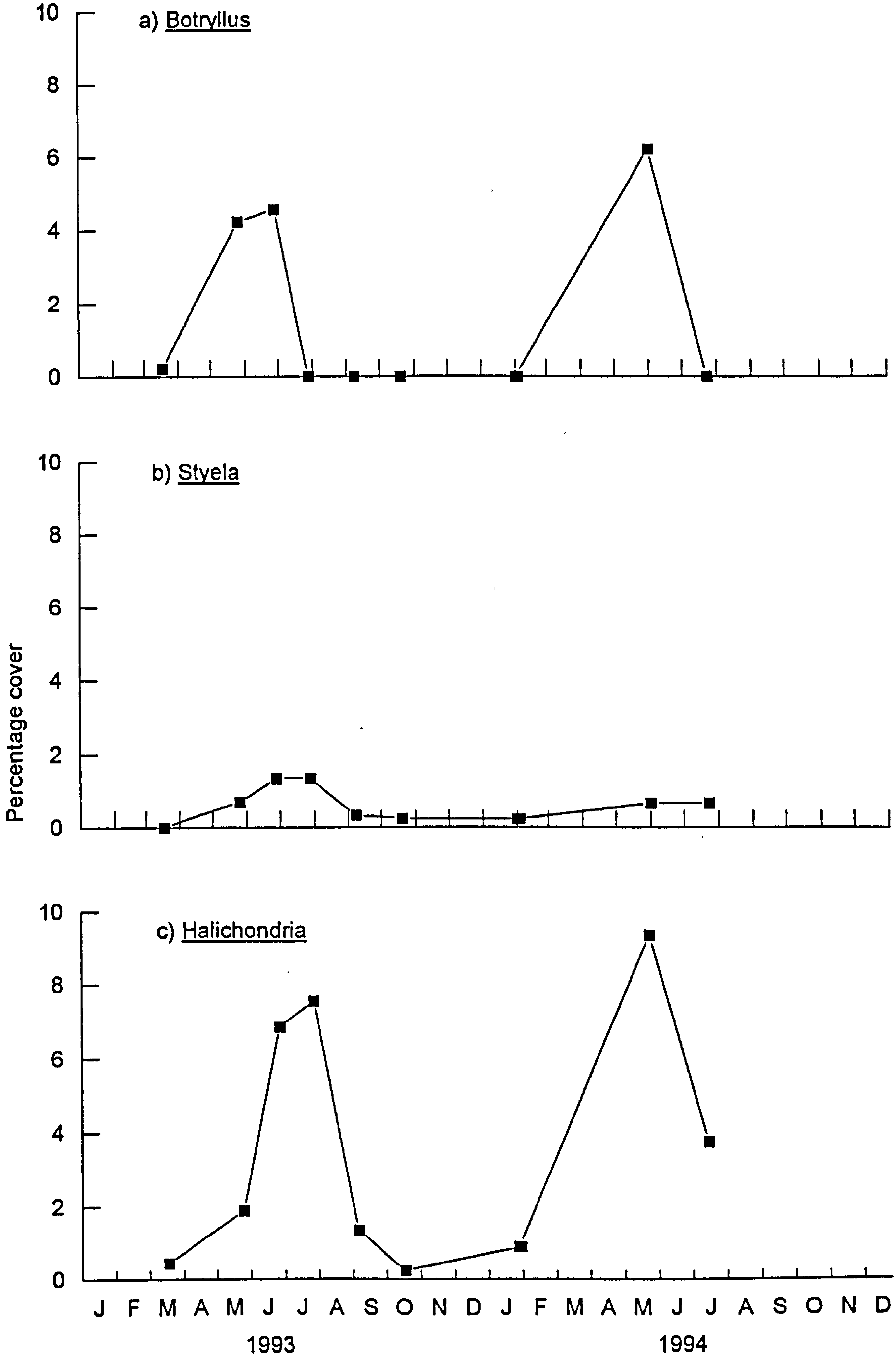

Fig 5.7 Variation in percentage cover with time of minor occupiers at a depth of 2m in Princes Dock. (n = 18 in all cases)

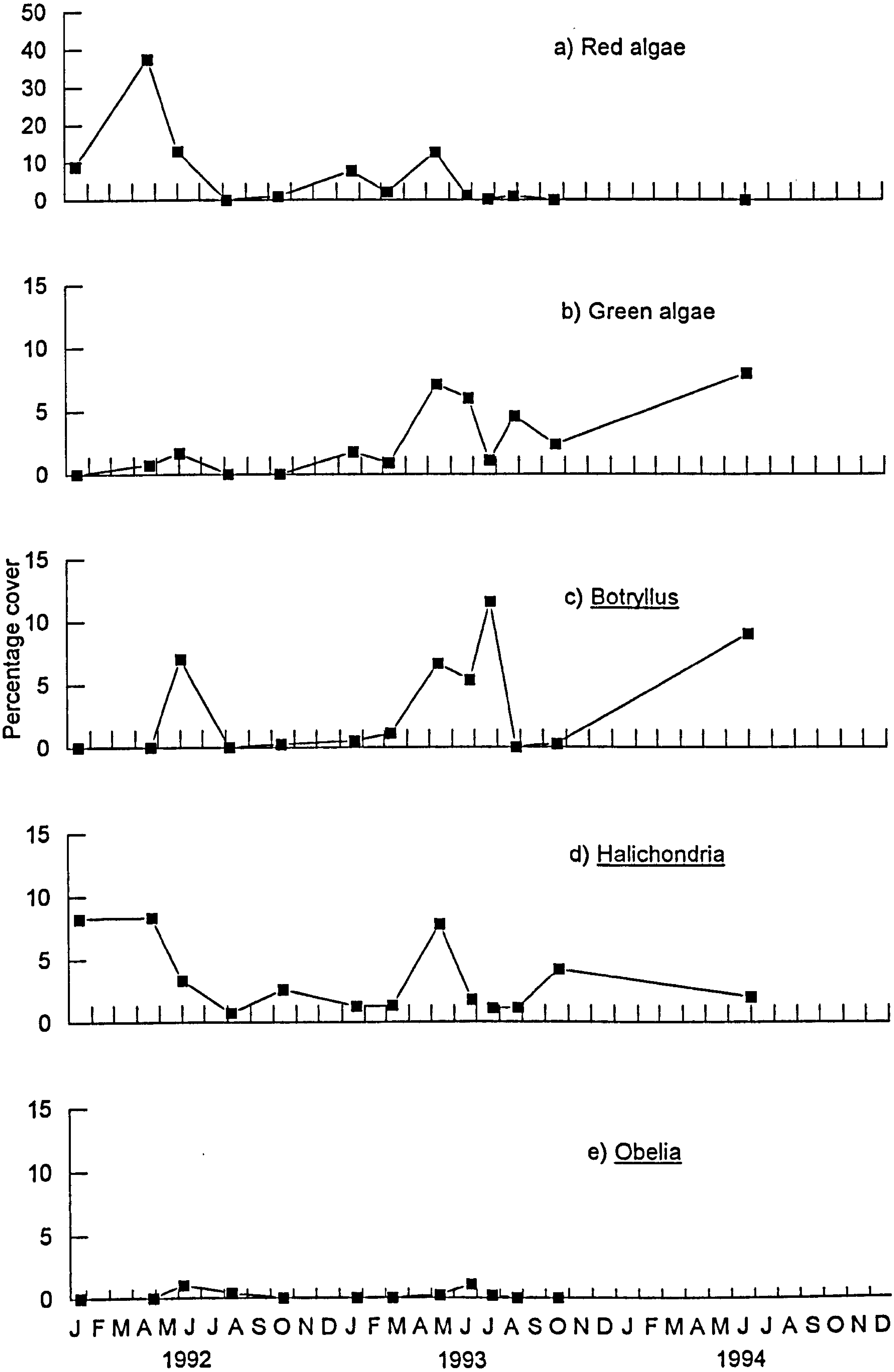

Fig 5.8 Variation in percentage cover of secondary cover species at a depth of 2m in Albert Dock. Note change in scale. (n = 18 in all cases)

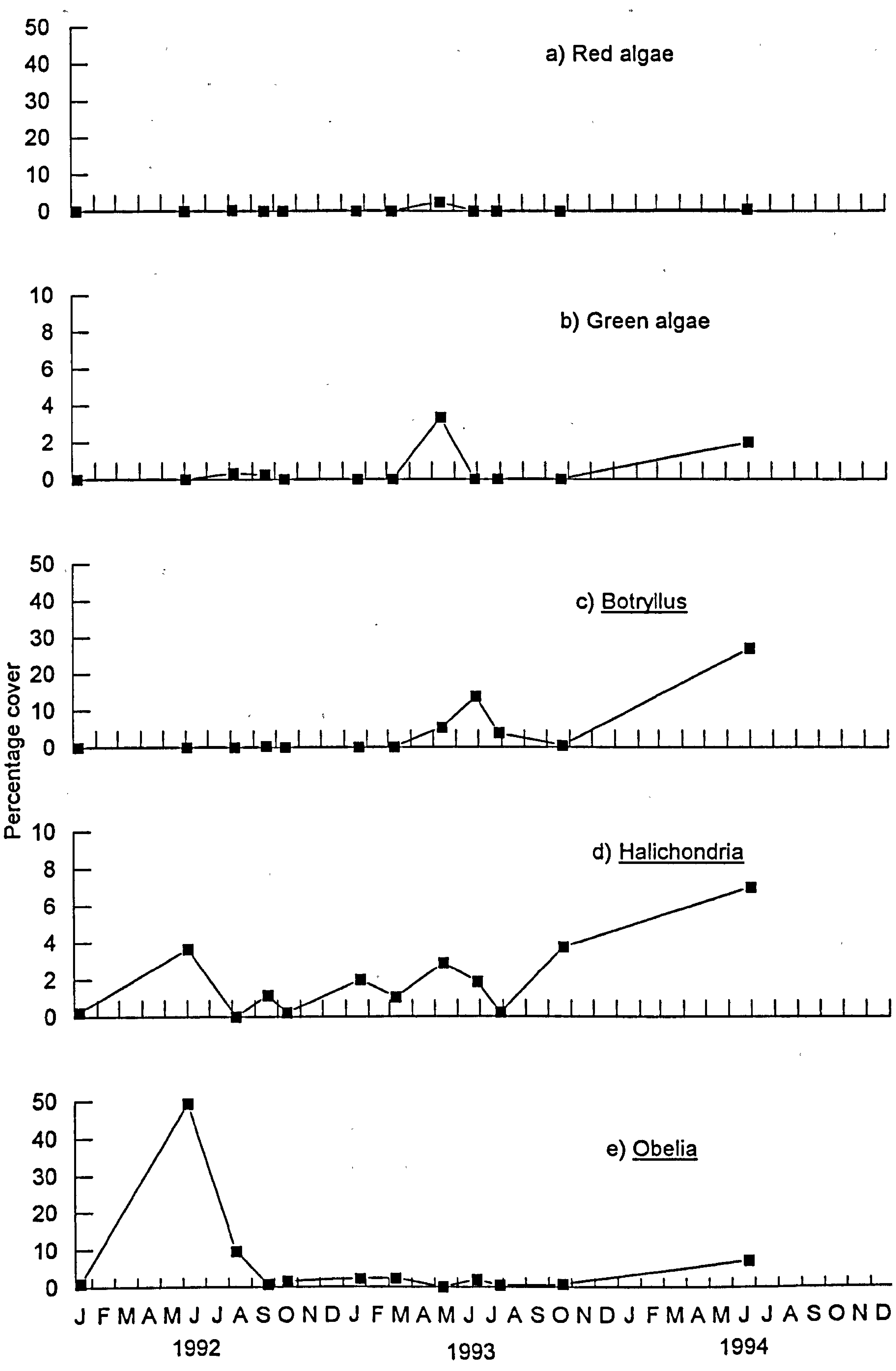

Fig 5.9 Variation in percentage cover of secondary cover species at a depth of 2m in Queens Dock. Note differences in scale. (n = 18 in all cases)

here (Fig 5.3c). While a large peak was observed in 1993, those in 1992 and 1994 were very small. *Ascidiella*, *Halichondria* and red and green algae also tended to have seasonal patterns, being more abundant in the summer (Figs 5.2c, 5.8-5.9). However, these patterns were not found in all docks in all years.

Ciona was most abundant in both Albert and Queens Docks during 1993 (Fig 5.1b, 5.3b). It was relatively unimportant as a space occupier in 1992 and 1994. *Halichondria* showed a similarly irregular pattern of abundance. At the initiation of the study in 1992 this species occupied almost as much space as *Mytilus* in Albert Dock (Fig 5.1d). However an almost linear decline was observed after this time, apart from a small increase in May 1993. *Halichondria* has increased in Queens and by 1994 occupied about ten percent of the available space (Fig 5.3d). *Ascidiella aspersa* was quite abundant in Albert Dock in 1993 (Fig 5.2c) but not during either of the other two years of study. This species was never abundant in Queens Dock (Fig 5.4c). Similarly *Molgula* showed only one peak in abundance in Queens Dock in 1992 (Fig 5.4d). Between thirty and forty percent of wall in both docks remained bare through-out the study. No definite pattern was observed in the variation in the proportion of bare space (Fig 5.1e, 5.3e).

A greater abundance of both red and green algae was found in Albert Dock compared with Queens (Fig 5.8a,b, 5.9a,b). Again these groups tend to be annual, being most abundant in May and June. It was not possible to identify the algae to species from the photographs but the red algae was probably mostly *Ceramium* species, while greens included *Ulva lactuca* and various *Enteromorpha* species. Hydroids (probably *Obelia dichotoma*) were frequently observed in Queens Dock, but this species was never rarely recorded in Albert Dock. In Queens Dock, hydroids peaked in the summer of 1992 (Fig 5.9e).

The shells of *Mytilus* provided a secondary substrate for some other species, most notably *Botryllus* and *Halichondria* (Fig 5.8c,d, 5.9c,d). The change in abundance of these species tends to follow that observed on the wall. In Albert Dock *Halichondria* was initially quite abundant on *Mytilus* shells in 1992 (Fig 5.8d). It then declined and peaked again in May 1993. In Queens Dock this species remained relatively constant covering around two percent of the area of *Mytilus* shells (Fig 5.9d). The patterns of abundance of *Botryllus* on *Mytilus* shells mimicked those observed on the walls, peaking during June - July each year in Albert Dock and in 1993 in Queens Dock (Fig 5.8c, 5.9c). It was impossible to assess the number of barnacles (*Balanus crenatus*, *Balanus improvisus* and *Elminius modestus*) using the methods outlined above, due to insufficient resolution on the slides. However, these remained important space occupiers, both on the dock wall and on *Mytilus* shells, throughout the study.

5.3.2 Princes Dock

The changes observed in Princes Dock were very different from those observed in the South Docks. Initially, during a pilot study of this dock in 1992, the walls were largely bare, with only low densities of *Ascidiella* and a cover of barnacles. Detailed observations of changes in the community began in 1993. This year saw a rise in abundance of first *Ascidiella* (Fig 5.5d) then this species declined and *Ciona* became the dominant species, reaching densities of over 1000 m^{-2} (Fig 5.5c). During the summer of 1993 there was a very heavy spatfall of *Mytilus*. Prior to this, *Mytilus* numbers had been very low, never more than 4 m^{-2}(Fig 5.5a). However by the end of the summer of 1993, densities were over 1500 m^{-2} (Fig 5.5b). A considerable decline followed and by July 1994 densities had dropped to about 500 m^{-2} (Fig 5.5b). Percentage cover remained quite high, at around twenty percent, as the *Mytilus* grew (Fig 5.6a). *Ascidiella* did not show the same peak in abundance in 1994, displayed in 1993 (Fig 5.5d). The peak in *Ciona* abundance was also not as marked (Fig 5.5c). Both *Botryllus* and *Halichondria* showed marked peaks in both 1993 and 1994 around June to July (Fig 5.7a,c). As in the South Docks barnacles were important occupiers of space in Princes Dock. Again, however, using the methods outlined above it was often impossible to discern if space was definitely occupied by this group. In addition, silt and other species made it impossible to separate live and dead casts and barnacles were therefore grouped with bare space. This is a problem which should be addressed in future surveys, and would necessitate the application of a destructive sampling programme.

5.3.3 Multivariate analysis

The PCA analysis of densities of solitary species described 76% of the variance in the first two axes (Fig 5.10). *Mytilus* and *Ciona* were the principal species separating the community compositions found, as indicated by the longer vectors of these species. Fig 5.10a includes the community composition from the spatial analysis, to give an indication of the variation between docks. Brunswick, Coburg and Morpeth docks tended to have lower densities of *Mytilus* and *Ciona*, while Princes had higher densities. The ordination of the temporal changes (Fig 5.10b-d) shows the amount of variation found within docks. Consistent changes were observed in the communities between years, particularly Albert Dock, as indicated by the lack of overlap of points from each year on the ordination diagram (Fig 5.10b). Both Albert and Queens showed similar degrees of variation. The points plotted showing the temporal variation in the community observed in Albert Dock encompass the points from the spatial survey of Salthouse, Wapping, Queens and Canning Docks (Chapter 4) indicating that the communities observed in these docks are relatively similar (Fig 5.10a,b). The points showing the temporal changes in Queens Dock (Fig 5.10c) tend to be slightly to

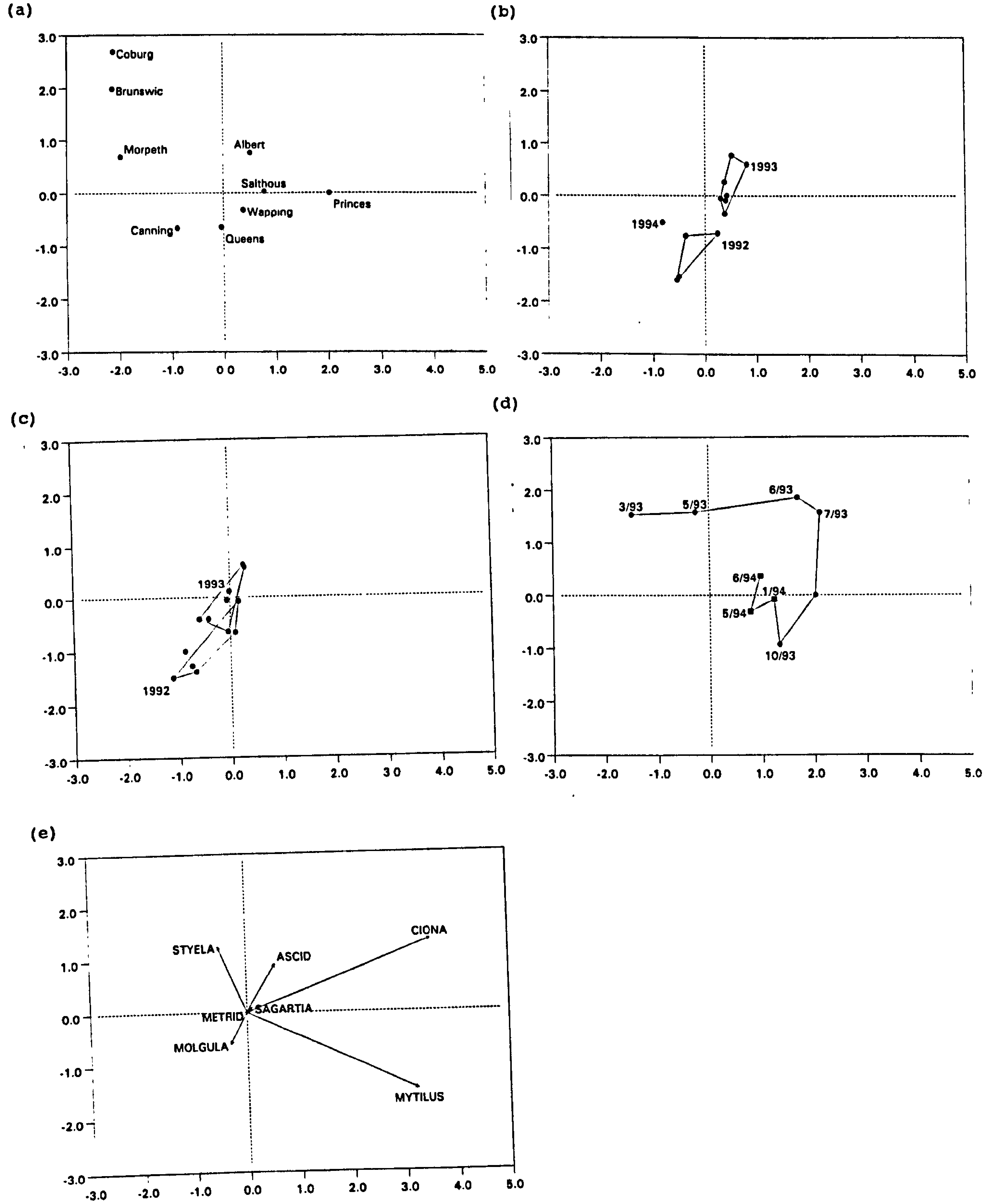

Fig 5.10 Principal Components Analysis of temporal changes on the dock walls in Albert, Queens and Princes Docks, at 2m depth. Analysis of counts of solitary species only, after log transformation and centring data. Ordination diagram accounts for 76% of the variation. a) Data from spatial survey, included for comparison (Aug 1993) b) Changes in Albert Dock c) Changes in Queens Dock d) Changes in Princes Dock e) Species vectors for ordination.

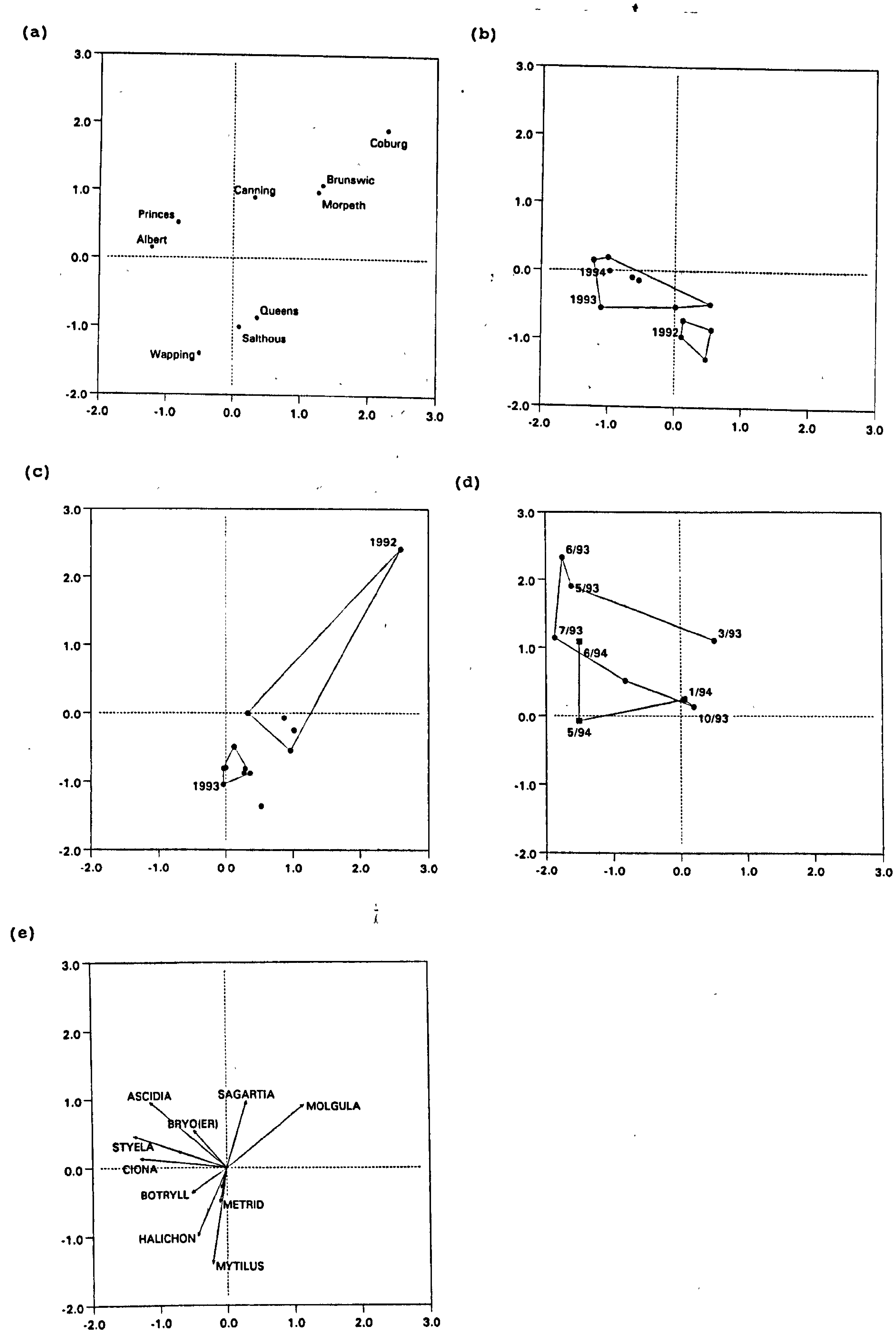

Fig 5.11 Principal Components Analysis of temporal changes on the dock walls in Albert, Queens and Princes Docks, at 2m depth. Analysis of percentage cover occupied. PCA carried out after root transforming data, centring and standardising. Ordination diagrams account for 36% of the variation. a) Data from spatial survey, included for comparison (Aug 1993). b) Changes in Albert Dock c) Changes in Queens Dock d) Changes in Princes Dock e) Species vectors for ordination.

the left of the ordination indicating fewer *Mytilus* and *Ciona* than observed in Albert, Salthouse and Wapping Docks. Princes Dock was considerably different (Fig 5.10d). The ordination shows the development of the community from essentially a bare wall to a community very similar to that found in the South Docks. However, on the final sampling date (June 1994) the community still had higher densities of *Mytilus* and *Ciona*, as indicated by the position of this point to the right of Albert and Queens Docks on the ordination diagram.

Similar analysis of percentage cover data of all species described 36% in the first two axes (see Fig 5.11). From this ordination three groups of species can be tentatively identified. First there is *Molgula*, increasing to the top and right of the ordination; secondly there is *Ascidiella*, *Styela* and *Ciona* to the top and left; finally there is *Mytilus* and *Halichondria* to the bottom of the ordination. From the results from the spatial survey reproduced in Fig 5.11a, the sites can be roughly grouped. The first group includes Coburg, Brunswick and Canning which tend to have higher *Molgula*. Morpeth also comes out close to these three sites on the ordination, despite the absence of *Molgula* in this dock, due to the low total percentage cover at this site. Secondly, Albert and Princes can be grouped together, tending to have higher numbers of *Ciona*, *Styela* and *Ascidiella*. Finally, the third group includes Wapping, Salthouse and Queens towards the bottom of the ordination. The diagrams showing the change in communities through time indicates quite large variation within docks. In particular, one point for Queens in 1992 encompasses Brunswick and Coburg due to high numbers of *Molgula* in Queens at this time (Fig 5.11c). This analysis indicates that the communities found in different docks were not discrete but show considerable overlap. The results from Princes stress how quickly the communities can change. Within one year, the community at this site changed from one very similar to that found in Brunswick, to one very close to that found in Albert Dock.

5.4 DISCUSSION

The results presented in this chapter, and particularly the ordinations from the multivariate analysis, suggest that a number of benthic communities exist in the docks around Liverpool. However, these are not discrete and show considerable temporal variation. It is important when studying the dynamics of these communities to consider the differing life-history strategies of the species found (Huston & Smith 1987, McCook 1994), as well as the physical and biotic processes normally invoked to explain changes in communities. These include predation (Connell 1961b, Paine 1966, Russ 1980, Sih *et al*. 1985), grazing (Sousa 1979b, Lubchenco 1982, 1983, Farrell 1991), competition (Lubchenco 1982, 1983, Wethey 1984, Hawkins & Hartnoll 1985, Farrell 1991), physical disturbance (Sousa 1979a,b, Menge & Sutherland 1987, Petraitis *et al*. 1989) and larval supply (Connell 1985, Roughgarden *et al*. 1987, Underwood & Fairweather 1989, Bingham 1992). In this discussion I will first consider the different communities found with reference to the physical and ecological forces structuring them. Then the causes and reasons for the seasonality observed in the benthic communities are considered. Finally, I will discuss the sustainability of these communities on the basis of current knowledge.

The results from chapter 4 suggested three community structures. First there was the *Molgula* dominated community found in Brunswick and Coburg Docks. The second community is that dominated by *Mytilus* and is found through-out the remainder of the South Docks. There was also indications of a third community, similar to that found in Princes Dock, dominated by tunicates such as *Ciona* and *Ascidiella*. The results from the temporal observations presented in this chapter indicate the considerable variation found in single docks within and between years. This suggested that rather than being discrete communities they are actually a continuum, with the exact composition probably being affected by the exact history of the site. One species which is of particular importance is *Mytilus*, and there is now strong evidence that this species experiences quite large variation in the amount of settlement between years in the docks as happens elsewhere (Seed 1974). Allen (1992) recorded a very heavy spatfall in the South Docks in September 1988. Similarly, the temporal study of Princes Dock wall described above, recorded quite a heavy settlement in the summer of 1993. The importance of larval supply and recruitment in structuring communities is now well recognised (Osman 1977, Sutherland & Karlson 1977, Connell 1985, Roughgarden *et al.* 1987, Underwood & Fairweather 1989, Raimondi 1990, Bertness *et al.* 1992, Bingham 1992). This has important implications when considering the stability of a system (see below). The very low densities of *Mytilus* in Brunswick and Coburg Docks and an increased density of *Molgula* in these docks was one of the strongest gradients observed in the community structure. Reasons for this are unclear but it seems likely that proximity of these basins to the main entrance to the Mersey could be an important factor. Certainly, Secchi disc readings in Brunswick are generally lower than other docks in the chain. This indicates either higher densities of phytoplankton or suspended solids at this site. Preliminary examination of the water in this dock suggests that it is mainly due to suspended solids resulting from the high sediment loading of water brought in from the Mersey (N.Fielding, Liverpool University, pers. comm.). It is possible that *Mytilus* may not be able to tolerate such increased levels. In addition, preliminary results indicated an increase in the abundance of *Botryllus schlosseri* and *Obelia dichotoma* on ropes suspended in Brunswick Dock compared with those suspended in Albert and Queens Docks. Such species may smother newly settled *Mytilus* making survival of this species impossible here.

However, Lesser *et al.* (1992) concluded that where food was not a limiting factor, interspecific competition for food by the fouling community would not significantly affect the growth of *Mytilus*.

There appears to be a switch in the dominant tunicate species found with *Molgula* dominating in Brunswick, Coburg and Queens Docks with *Ciona* and *Ascidiella* more abundant in Albert and Princes. This again may be due to the possibly increased suspended sediment loading in docks closer to the entrance to the Mersey causing a switch in the relative competitive abilities between these species. The high densities of tunicates recorded in Princes Dock suggest that in the absence of a dense population of *Mytilus* this group could become more important to the ecosystem functioning.

The importance of consumers in structuring communities has been shown for a number of ecosystems (Connell 1961, Paine 1966, Russ 1980, Lubchenco 1982, 1983, Sih *et al.* 1985, Farrell 1991). Generally predation is held to have a relatively stronger influence in benign environments, such as the docks (Menge & Sutherland 1987, Menge & Farrell 1989). In the South Docks the main benthic predators are *Carcinus maenas*, *Pleuronectes flesus* (flounder) and *Gadus morhua* (cod). *Asterias rubens* was recorded in Sandon Dock (Russell *et al.* 1983) and also in Princes Dock (pers. obs.). While this species has also been recorded occasionally from the South Docks it has not proliferated here. The absence of such a powerful predator from the South Docks undoubtedly has a strong influence on the community structure. Reasons for this are unclear. Kautsky (1981) attributed the presence of *Mytilus* in the sub-tidal of the Baltic to the absence of predators, as a result of low salinity here. However, the salinities found in the Baltic were very low (eg. 6‰) and seems unlikely that the conductivity found in the South Docks could limit the presence of *Asterias*. As yet, little data are available on the effect of predation on the benthic community found in the docks.

It is interesting that no large molluscan grazers such as littorinids or *Patella* have colonised the dock walls. This contrasts with the importance of these groups in open coastal systems (Hawkins & Hartnoll 1983). *Patella* may be excluded by low salinity and the absence of a large adjacent seed population for larvae, the nearest large populations being on the north Wales coast. *Littorina littorea* are common, however, in the outer Mersey and Dee and their absence is puzzling.

A variety of classifications have been suggested to describe the life-history strategies of organisms, most notably the r and K models (MacArthur & Wilson 1967) and the S, C and R strategies (Grime 1979). Rather than discrete categories, these should be viewed as continua. Here I briefly discuss the life-histories of the more abundant species in the docks, with particular reference to the r and K strategies of MacArthur and Wilson (1967)(see also Stearns 1976). The vast majority of the species found in the docks tend to be short lived annuals. The colonial tunicate, *Botryllus* was most abundant early in the year, peaking in abundance around June, and over winters by simply slowing down all physiological activities. Eggs develop within the adult before being liberated as tadpole larvae which swim for 1 to 2 days before settling and metamorphosing (Herdman 1924). This species devotes a lot of energy to reproduction and could be classed as a typical 'r' selected species. The other tunicates (namely *Ciona*, *Ascidiella*, *Styela* and *Molgula*) are solitary species. *Ciona*, *Ascidiella* and *Styela* all have external fertilization and the larva then develops from the fertilised egg (Herdman 1899, Millar 1953). Two of these species are annuals, namely *Ciona* (Dybern 1965) and *Molgula* (pers. obs.). *Ascidiella* also tends to be an annual species but may live for up to two years (pers. obs.). *Styela* tends to be longer lived than *Ciona* and probably living for around two years. Grave (1944), working on *Styela partita,* recorded that the larvae of this species remain in the water column for up to four days. *Ciona* larvae remain in the water column for up to 36 hours (Berrill 1935) and *Ascidiella* for up to 1 day (Herdman 1899).

Halichondria bowerbankii also tends to be an annual species reaching maximum size in July / August when it reproduces (Barthel 1986). However, this species has not really persisted in the docks from year to year. Hummel *et al.* (1988) recorded that *Halichondria panicea* suffered from increased bacterial growth, leading to mortality, in conditions of reduced flow rate. The reduced water movement found in the docks may also cause problems with ventilation and removal of excretory products (Hummel *et al.* 1988).

The hydroid *Obelia* produces planktonic medusae which remain free swimming for about two months (Russell 1953), before maturing and sexually reproducing. The fertilised egg develops into a planula before settling and maturing into a colony (Barnes *et al.* 1988). There may be more than one successive generation per year (Russell 1953). The planktonic medusae are most abundant from spring to late autumn (Russell 1953), though the hydroid colonies die back over the winter (pers. obs.). The balanoid barnacles (*Balanus improvisus* and *B. crenatus*) and *Elminius modestus* common in the docks and Mersey will spend three to four weeks in the plankton as a nauplius before settling. *Semibalanus balanoides* lives for an average of three years total (Moore 1934).

Mytilus is by far the longest lived benthic species found in the docks and can live for up to twenty years (Seed & Suchanek 1992). This species has two main spawning periods each year, one in spring and the second in early summer (Seed & Suchanek 1992). Fertilisation is external and the larval development is complicated, typically lasting one to four weeks, though may be considerably longer. The larvae feed during planktonic development. *Mytilus*, although at the 'r' end of the spectrum is probably the most 'K'-like of the species in the docks because of its longevity.

It therefore appears that the benthic community found in a number of the South Docks is persistent, over the timescale of this study, due to the presence of the long lived species *Mytilus*. The remaining species are all relatively short lived, less than two years, and very typical 'r' selected species. The seasonal nature of the physical environment in the docks, with harsh winter and favourable summer conditions, favours the existance of fast growing annual species.

Numbers of the annual species vary considerably between as well as within years, though the reasons for this interannual variation are unclear. The nature of their life-history means that they must find a means to overwinter and this is likely to be a susceptible stage of growth, both because conditions are harsh at this time and the total biomass of the population will be low. Small fluctuations in this biomass may have a disproportionately large effect on the population size the following year. Although the dock environment remains relatively constant between years, it may be that small interannual fluctuations may affect the competitive ability of a species or mean that the cues to spawn are not supplied. In addition, annual species are heavily dependent on larval recruitment which in itself is responsible for much of the stochastic variation observed in natural communities (Osman 1977, Roughgarden *et al.* 1987, Underwood & Fairweather 1989, Raimondi 1990, Bertness *et al.* 1992).

Ecological stability is a very difficult concept to assess (Connell & Sousa 1983). Assessment of the appropriate scale of observation, both temporal and spatial has rarely been attempted and this has led to the definition of so-called stable states or multiple stable states with insufficient data (see Connell & Sousa 1983). Allen (1992) considered that the switch from poor water quality to clear water quality was an example of multiple stable states (sensu Lewontin 1969). However, Connell and Sousa (1983) questioned whether instances such as this did indeed represent multiple states. Firstly the time period observed was relatively short and certainly not equal to the lifespan of *Mytilus*, the longest lived species in the docks. Connell and Sousa (1983) considered this a prerequisite for establishing the stability of a community. Indeed, the observations on the benthos are still not sufficient to assess the overall stability of the benthic community found in the docks, but from the results available *Mytilus* does appear to be a persistent species. There has been little change in the cover of this species over the period of this study. In addition the results from Princes Dock suggest that this species will recolonise, provided that there is sufficient larval supply. There is also strong evidence that the *Molgula* dominated community found in Brunswick and Coburg Docks is the result of different environmental conditions rather than an alternative state under identical environmental conditions. It is worth mentioning that the existence of multiple stable states in the docks could not be proved without evidence of identical larval recruitment into the different basins, and such data would be difficult to obtain. The potential importance of variations in larval recruitment between years also means that quite a long period of observation is required to assess the stability of the annual species present in the system.

Future research into temporal changes in the community should concentrate on a more detailed description of changes in Brunswick and Coburg Docks. In addition to simply describing changes on the wall through time it would be useful to actually deploy tiles in these and other docks. Such tiles could firstly be used as a means of studying differences in community development in a more controlled way. They would also allow transplant experiments to be carried out, enabling the testing of some of the hypotheses suggested above. In particular it would be interesting to follow the survival of some species such as *Mytilus* in Brunswick Dock where it is not very common.

The *Mytilus* dominated community found in many of the South Docks appears to be quite persistent, at least over the time scale of this study. In the event of a crash in this *Mytilus* population it seems likely that there would be a switch to an ephemeral community dominated by ascidians. The development of the community in Princes Dock highlights the importance that an episodic larval recruitment from outside the docks can have. This occurred in ALbert and Queens in 1988 and in Princes in 1993. The reduced exchange of water between the Mersey and the South docks will obviously limit the occurrence of such events. This may be an important factor in the long term composition of the communities in the South Docks.

CHAPTER 6

MYTILUS POPULATION DYNAMICS AND GROWTH

6.1 INTRODUCTION

The previous two chapters have shown the dominance of *Mytilus* in the community structure of many of the docks under investigation. Biofiltration by *Mytilus* has also been proposed as a likely mechanism controlling water quality in the docks (Allen 1992, Allen & Hawkins 1993; see below). Its disproportionate influence is at least partly due to the longevity of *Mytilus* relative to many other species in the docks, most of which tend to be short-lived ephemerals (eg. *Botryllus*) or annuals (e.g. *Ciona*). This chapter focuses on the ecology of mussels in the docks, but starts with a general review of the biology of *Mytilus* to set the scene.

Mytilus is a common species which is also important commercially. It is also amenable to experimental manipulation. These factors have resulted in an enormous amount of literature on all aspects of its biology, including physiology, growth and population biology (see Bayne 1976, Gosling 1992 for reviews). *Mytilus* is a very strong competitor, often dominating areas where it can survive (Dayton 1971, Menge 1976, Dean & Hurd 1980, Harms & Anger 1983). The dense stands of *Mytilus* that result often lead to intense intraspecific competition (Kautsky 1982). Death from intraspecific competition is an important source of mortality in rapidly growing populations and can result in the entire mussel matrix becoming unstable (Richardson & Seed 1990). Newly settled spat may also suffer from food limitation if they settle within the adult matrix, although those settling on top of the matrix may actually out-compete the adults leading to destabilisation of the matrix (Seed 1969b). Total space domination by *Mytilus* is generally prevented through physical disturbance (Dayton 1971) or predation (Paine 1966, 1974, Dayton 1971).

Mytilus is generally an intertidal species (Seed & Suchanek 1992) but is occasionally found subtidally (Newcombe 1935, Paine 1976b, Seed & Suchanek 1992). As well as occurring on natural substrata, it has been recorded on offshore oil platforms (Page & Hubbard 1987, Richardson & Seed 1990) and dock pilings (Suchanek 1978). The upper limit of *Mytilus* is set by the physical extremes of the environment, most notably high temperatures and desiccation (Suchanek 1978, 1985, Tsuchiya 1983). It is very tolerant to low temperatures and has been known to withstand partial freezing of its tissues (Williams 1970). Physical conditions may also be important in limiting the lower limits of *Mytilus*, for example sand movement smothering the population (Littler *et al*. 1983). However, increased predation pressure lower on the shore is more normally accepted as the factor setting the lower limit of this species. Removal of predators has been shown to allow the downward extension of *Mytilus* (Paine 1966, 1974, 1976a). Similarly, Kautsky (1981) attributed the presence of *Mytilus* in the subtidal of the Baltic Sea to an absence of predators here caused by the extreme physico-chemical conditions. The removal or exclusion of predators has been shown to allow the growth of *Mytilus* where it is not normally found (Ebling *et al*. 1964, Paine 1976a, Davies *et al*. 1980, Seed 1986). There is a refuge in extremely wave exposed sublittoral fringes (Hiscock 1983).

The abundance and high energetic value of *Mytilus* make it very attractive as a prey species. Important predators include asterians (Kitching *et al*. 1959, Ebling *et al*. 1964, Kitching and Ebling 1967, Paine 1974, Menge 1983), dogwhelks (Seed 1969a), crabs (Kitching & Ebling 1967, Menge 1983), fish (Dare 1976) as well as shore birds (Dit-Durell & Goss-Custard 1984, Ens & Goss-Custard 1984, McGrorty *et al*. 1990). Optimal foraging by a predator represents the combination of factors associated with maximising an organisms energy intake relative to the time and effort involved in acquiring food. With *Mytilus*, the strength of the shell is the major factor determining the handling time for potential predators(Elner & Hughes 1978, Seed 1980, 1986). This ensures that predators tend to concentrate on smaller *Mytilus*. Experiments in the laboratory and field have demonstrated that *Carcinus maenas* is capable of taking animals up to 45mm in length (Ebling *et al*. 1964, Dare *et al*. 1983) but the actual size taken depends heavily on what else is available, shell thickness and time since the predator last fed.

Relative to many other species in the marine environment, *Mytilus* often exhibits quite a protracted spawning period in both natural (Wilson & Seed 1974, Seed & Brown 1977, Fell & Balsamo 1985, McKenzie 1986, King *et al*. 1989) and cultured populations(Lutz *et al*. 1980, Wilson 1987). For some populations, low levels of larval release have been recorded throughout the year (Seed 1975). The normal pattern involves the redevelopment of the resting gonad from October to November. By early spring the gonads are ripe and this is followed by a period of partial spawning. By early summer the gonads are again ripe, particularly in animals living in more favourable conditions, and less intensive spawnings may occur throughout the summer. During August and September the gonads enter a resting phase (Seed & Suchanek 1992). Some doubt remains over factors affecting gametogenesis though temperature and food abundance are certainly very important (Chipperfield 1953, Kautsky 1982a, Seed & Suchanek 1992). *Mytilus* reaches sexual maturity in the first year of life.

A number of factors are known to cause the stimulation of spawning. These include temperature changes (Chipperfield 1953, Wilson & Seed 1974, Kautsky 1982a, Wilson 1987), physical stimuli such as scraping or jarring (Suchanek 1978, Wilson 1987) as well as phases of the moon, tidal fluctuations and salinity changes. The relative contribution of these remains uncertain (Seed & Suchanek 1992). Some endogenous rhythm may also be involved (Seed 1975).

The larva develops into a trochophore and then a veliger before secretion of a shell occurs, around twelve days after fertilization (Bayne 1976). It remains in the water column for a total of around three weeks (Bayne 1976) before primary settlement occurs. This is generally on filiform structures or materials such as algae or hydroids, when the plantigrade is between 250μm and 400μm long. The larva may then detach and drift again in the water column, using long fine byssus threads to remain suspended (Board 1983, Lane *et al.* 1985). The plantigrade can retain the ability to drift up to a size of 2-2.5mm before secondary settlement occurs on the adult mussel bed. The initial primary settlement is believed to reduce intraspecific competition and the danger of being accidentally swallowed by the adults. There is a growing body of evidence that two stage settlement may not always occur and that the larvae may settle directly on the adult bed (McGrath *et al.* 1988, King *et al.* 1990).

Measurement of absolute growth in *Mytilus* is hindered by the problem of ageing individuals. This is made difficult by the extended settlement season and often very variable growth rate found between individuals. The simplest method of ageing relies on length frequency distributions but this is of limited use with *Mytilus* (see Seed 1976). External growth check lines caused by reduced growth over the winter have been used with varying degrees of success (see Seed & Richardson 1990 for review). Annual growth lines laid down in the nacreous layer have proved most reliable, particularly where the external growth checks are not obvious (Lutz 1976, Richardson *et al.* 1990). Growth rate is ultimately determined by the harshness of the environment with rates of up to 50mm in 6-8 months having being recorded from the relatively favourable subtidal (Page & Hubbard 1987). While individuals on upper or exposed shores live longer they are generally much smaller than those from lower on the shore (Seed 1969b).

Various condition indices have been derived for assessing the relative growth of *Mytilus*, particularly with a view to assessing the optimum time for harvesting cultured populations (Mason 1976). These generally reflect the reproductive condition of the population (Kautsky 1982). Relative growth has also been quantified using allometry (see Seed 1980b for review). While a considerable amount of work has been done on the relative growth in intertidal populations, few data exist for the subtidal except in culture (but see Mason 1976, Lutz *et al*. 1980, Kautsky 1982b). The ratio of shell weight to dry weight of soft tissues seems to relate to the degree of stress the animals are under. Kautsky (1982b) showed that low salinity could cause stress resulting in an increase in the ratio of shell weight to dry tissue weight. Similarly, mussels on the high shore have heavier shells and lower tissue weight than those from lower down (Baird & Drinnan 1957, Seed 1973). Under favourable conditions increase in tissue weight can more than keep pace with increase in shell weight resulting in a drop in the shell to tissue weight ratios. More exposed or turbulent conditions prevent efficient filtration and accumulation of organic matter but shell deposition still proceeds relatively rapidly (Seed 1973).

The control of phytoplankton by filter feeders has been shown in a number of both marine (Smaal *et al*. 1986, Loo & Rosenburg 1989, Hily 1991) and freshwater ecosystems (Reeders *et al*. 1989, Dorazio *et al*. 1987). Particular interest has centred upon the possibility of manipulating the biota to improve water quality (Reeders *et al*. 1989, Shapiro 1990). Studies on Sandon Dock suggested that *Mytilus* could control phytoplankton levels in isolated dock basins (Russell *et al.* 1983). Therefore, following the redevelopment of the South Docks an attempt was made to test the hypothesis that *Mytilus* could be used to improve water quality. An experiment was set up using an isolated dock to which *Mytilus* were added and a control which was left without added mussels. Unfortunately a heavy natural settlement of *Mytilus* throughout the South Docks made definitive testing impossible (Allen 1992) as no spatial control was possible - although before and after comparisons could be made. Large improvements in water clarity and reductions in chlorophyll 'a' were recorded during this time and these were attributed to control of the phytoplankton through biological filtration by *Mytilus* (Allen 1992, Allen & Hawkins 1993). The possibility that *Mytilus* may also filter out pathogens indicated by *Escherichia coli* (Birbeck & McHendry 1982) adds further to its importance in an area where water suitable for contact water sports is desirable.

Zooplankton has also been shown to have an effect on reducing phytoplankton in freshwater systems (Dorazio *et al.* 1987). However, it is difficult from a management point of view, to increase the density of zooplankton artificially. In freshwater systems this has been achieved through the removal of planktivorous fish which has resulted in an increase in grazing zooplankton species and an associated improvement in water clarity (Shapiro & Wright 1984). Relatively large filter feeders such as *Mytilus* are easier to manipulate. In addition, the perennial nature of *Mytilus* ensures that this species begins grazing plankton before it reaches bloom proportions.

Some data have already been gathered on the *Mytilus* populations in the dock basins in the Liverpool area (Hawkins *et al.* 1992a,b). A natural settlement occurred in Sandon Dock and there were attempts to exploit it commercially. Signs of food shortage were observed here as indicated by higher shell to meat ratios than were found at an intertidal site (Naylor 1983). A very low spat settlement on ropes and the dock wall was also recorded (Naylor 1983, Hawkins *et al.* 1992). Some preliminary observations were made on the size structure and condition of *Mytilus* in the South Docks following the heavy settlement of this species here (Allen 1992). This chapter builds on the data set recorded by Allen (1992). It aims to describe changes that have occurred in the age/size structure of the *Mytilus* population found in the South Docks. The absolute growth of *Mytilus* in this environment will be measured. The relative growth of *Mytilus* in the docks will be described in relation to shell length, width, height, weight and dry tissue weight. The variation of relative growth with regard to time and position in the dock will also be assessed. The future of the *Mytilus* population in the South Docks is discussed.

6.2 MATERIALS AND METHODS

6.2.1 Spatial Distribution

The vertical distribution of *Mytilus* on the dock walls was determined through destructive sampling of quadrats. The quadrats (0.25m X 0.25m) were haphazardly positioned on the dock wall and the *Mytilus* present in each removed and returned to the laboratory. Five quadrats were cleared at each 1m depth interval in Albert (in October 1992) and Queens Docks (in January 1993). In the laboratory the density at each depth interval was calculated. All animals were measured to the nearest 1mm to examine the population size stucture with depth. A sample of the animals from each depth was kept for later biometric analysis.

6.2.2 Population Structure and Absolute Growth

The *Mytilus* populations of Albert and Queens Docks were sampled destructively at a depth of 2m by SCUBA divers. Note that this differed from Allen (1992) who sampled at a depth of 1m. The reason for the change was partly due to large fluctuations in water level that were anticipated during the course of this study. Quadrats were positioned haphazardly on the wall and the contents of these scraped into fine mesh bags. The size of the quadrats varied from 0.25m X 0.25m to 0.50m X 0.50m depending on the density of the population being sampled, and 3 - 5 quadrats were cleared on each visit. Generally a sample size of about 200 individuals was considered desirable to adequately describe the population structure. However it was felt, particularly in the latter stages of the study that frequent removal of such large samples could be quite detrimental to the population. Some of the later sample sizes were therefore smaller. Animals were taken to the laboratory where the length of each was measured to the nearest 1mm using Vernier callipers. From each sample approximately fifty animals of as great a size range as possible were selected and frozen for later biometric analysis.

Changes in the population structure were assessed by examination of length frequency histograms. Results obtained from these were backed up by aging a sample from each dock. In the present study a combination of methods were used. In order to assess the reliability of the external growth checks, twelve individuals were examined using the acetate peel technique described below. The results from this indicated that the external checks were a good indicator of the age of individuals. A sample of approximately 100 from each site was measured and aged using these external checks, combined with historical length frequency histograms.

The use of acetate peel techniques to age *Mytilus* has been previously described by Lutz (1976) and Richardson *et al.* (1990). The methods used here follow those used by these workers. Specimens were first sectioned by grinding on a belt-sander and then mounted in resin (Metaserv s.w. resin). The mounts were then ground flat on wetted (P120D and P400C grade) silicon carbide paper and polished using a cloth soaked in 'Brasso'. The sectioned valve surfaces were etched by submersion in 0.01M HCl for 30 minutes, rinsed with distilled water and allowed to dry. Acetate peel replicas of the etched surfaces were obtained by allowing a small piece of replicating material to become almost molten after 30 seconds in ethyl acetate. The strips were applied to the etched shell surface and left for five minutes for the ethyl acetate to evaporate, before being removed and mounted on a glass slide for microscopical examination (Richardson *et al.* 1979).

A dense natural spatfall of *Mytilus* occurred in Princes Dock during the summer of 1993. This population was sampled destructively on three occasions, August 1993, February 1994 and July 1994. A dense *Mytilus* settlement also occurred on a set of tiles, deployed in Albert Dock in January 1992. Samples of this population were taken in July 1993 and July 1994. All of these samples were analysed as above.

Measurements of the absolute growth of Mytilus were used to calculate a von Bertalanffy growth curve :-

$$L_t = L\infty\ [1-\exp(-k\ (t-t_0))]$$

where Lt is the length at time t, $L\infty$ is the asymptotic length, t_0 is the hypothetical length at time zero and k is a rate constant. The equation was solved using the program FISHPARM (Saila *et al.* 1988).

6.2.3 Biometric relationships

The length, width and height (see Fig 5.1) of each of the fifty individuals kept for biometric analysis, were measured to the nearest 1mm using Vernier callipers. The soft tissues of each were then removed and transferred to individual pre-weighed foil boats. These were dried to constant mass at 70°C for 48 hours before being reweighed to the nearest 0.0001g. The shells were dried at 70°C for 1 hour and then weighed to the nearest 0.01g. At the start of the study this biometric analysis was primarily to gain an idea of the actual filtering power available in the docks and the sampling occasions were somewhat erratic. In order to study the annual pattern of biometry in this habitat, the *Mytilus* population at 2m depth in Albert Dock was sampled at approximately monthly intervals over a one year period beginning in July 1993.

The relative growth of a species describes how different aspects of an individuals size change in relation to one another as the organism grows. In this study relative growth was analysed by fitting pairs of variables to the allometric growth equation

$$y = A.x^b$$

rewritten as

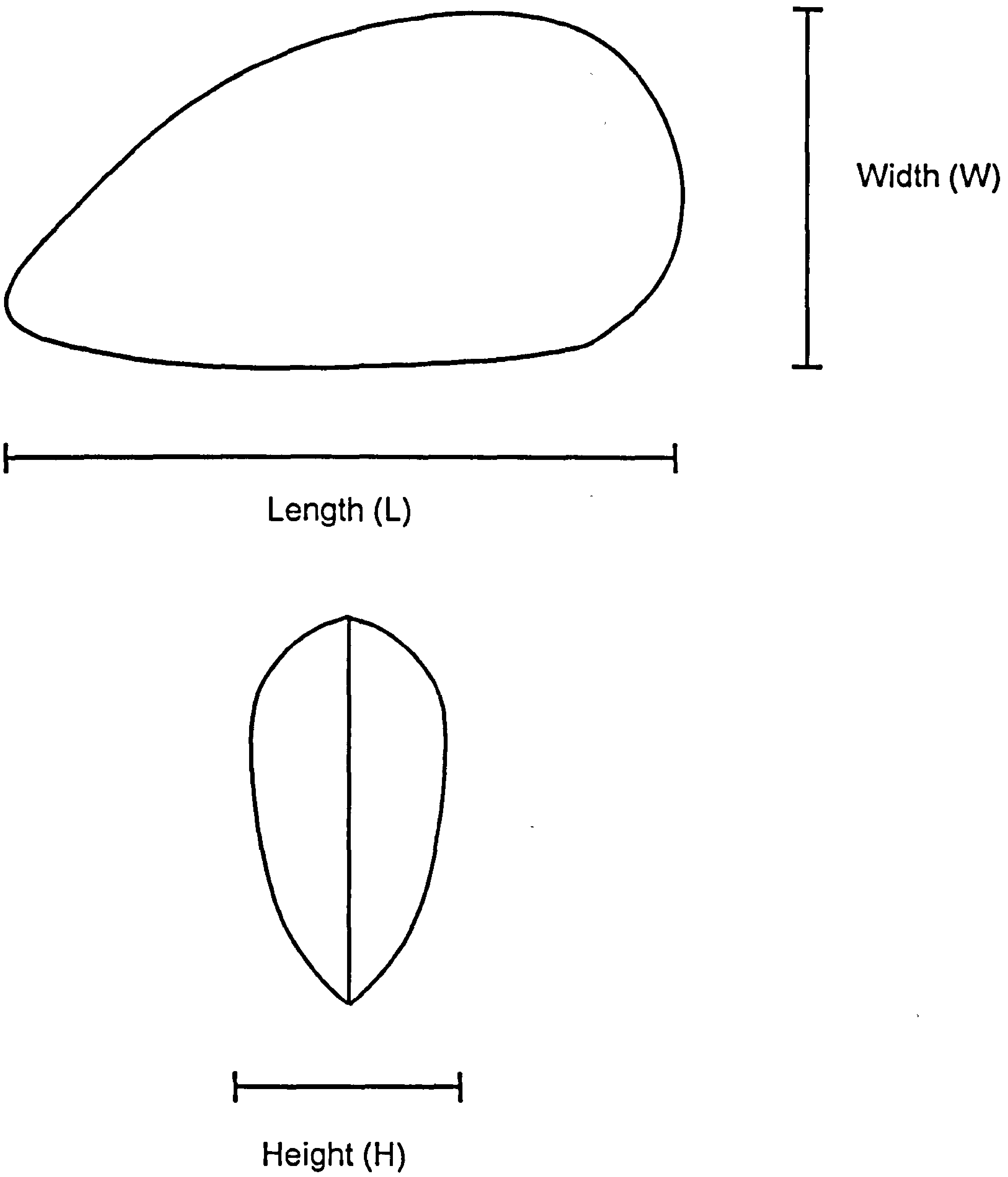

Fig 6.1 Diagram showing dimensions measured and terminology used for biometric study of *Mytilus*

$$\log y = \log A + b \log x$$

The constants A and b were estimated by least squares regression using SAS. Length was used as the dependent variable (ie. 'x') in all comparisons. The exponent 'b' is the growth coefficient and represents the relative growth of the variables under consideration. Where both variables are measured in the same units, values of 'b' less than 1 indicate negative allometry (ie. that y is increasing more slowly than x). Values greater than 1 indicate the reverse (positive allometry). A value of unity describes isometric growth, where both variables are increasing at the same relative rate. Where 'y' represents a weight and 'x' is length, an isometric relationship is indicated by a 'b' value of 3 (ie. x^3). Values of 'b' were statistically compared to the isometric value using two tailed t-tests.

Two surveys were carried out to document the variation in the biometric indices over small spatial scales. The first was carried out in July 1993 and compared the size frequency and biometrics of animals beneath pontoons in Albert Dock and those on an unshaded wall. The second study, carried out in January 1993, looked at variation of these parameters in animals collected from different depths in Albert and Queens Docks (see 6.2.1). These were analysed separately as described above.

6.3 RESULTS

6.3.1 Spatial distribution

The density of *Mytilus* tends to be greatest around the mid depths of the dock wall, decreasing both towards the dock bottom and the water surface (Fig 6.2). The results presented here do not show the decline towards the dock bottom to the extent actually observed, particularly in Albert Dock (Fig 6.2). This is due to the fact that the population was only sampled at 1m depth intervals and the decrease towards the bottom occurred over a relatively short distance. Further information on the spatial distribution of *Mytilus* can be found in Chapter 4.

6.3.2 *Mytilus* population structure and dynamics

Inspection of the length frequency histograms for the period of study suggests that there has been relatively little recruitment to the population at either site since 1990 (Fig 6.4 - 6.5). Settlement of juveniles has been recorded (see for example Queens Dock in August 1992 Fig 6.5), but numbers have generally been very low. The populations are apparently dominated by older individuals which have been gradually increasing in size, since they first settled in 1988 or 1989. As densities decline, the younger cohorts have increased in importance, particularly in Queens Dock (Fig 6.5 - July 1994).

While mean length has steadily increased and stabilised since the settlement of the populations, the density, particularly in Albert Dock, has shown a considerable decline (Fig 6.6b). Initially, in 1988 and the start of 1989, the population density in Queens Dock was relatively low but by the end of 1990 the density was about 1000 /m^2. Densities in Albert have, until quite recently been higher than those found in Queens. Between 1990 and 1992 both

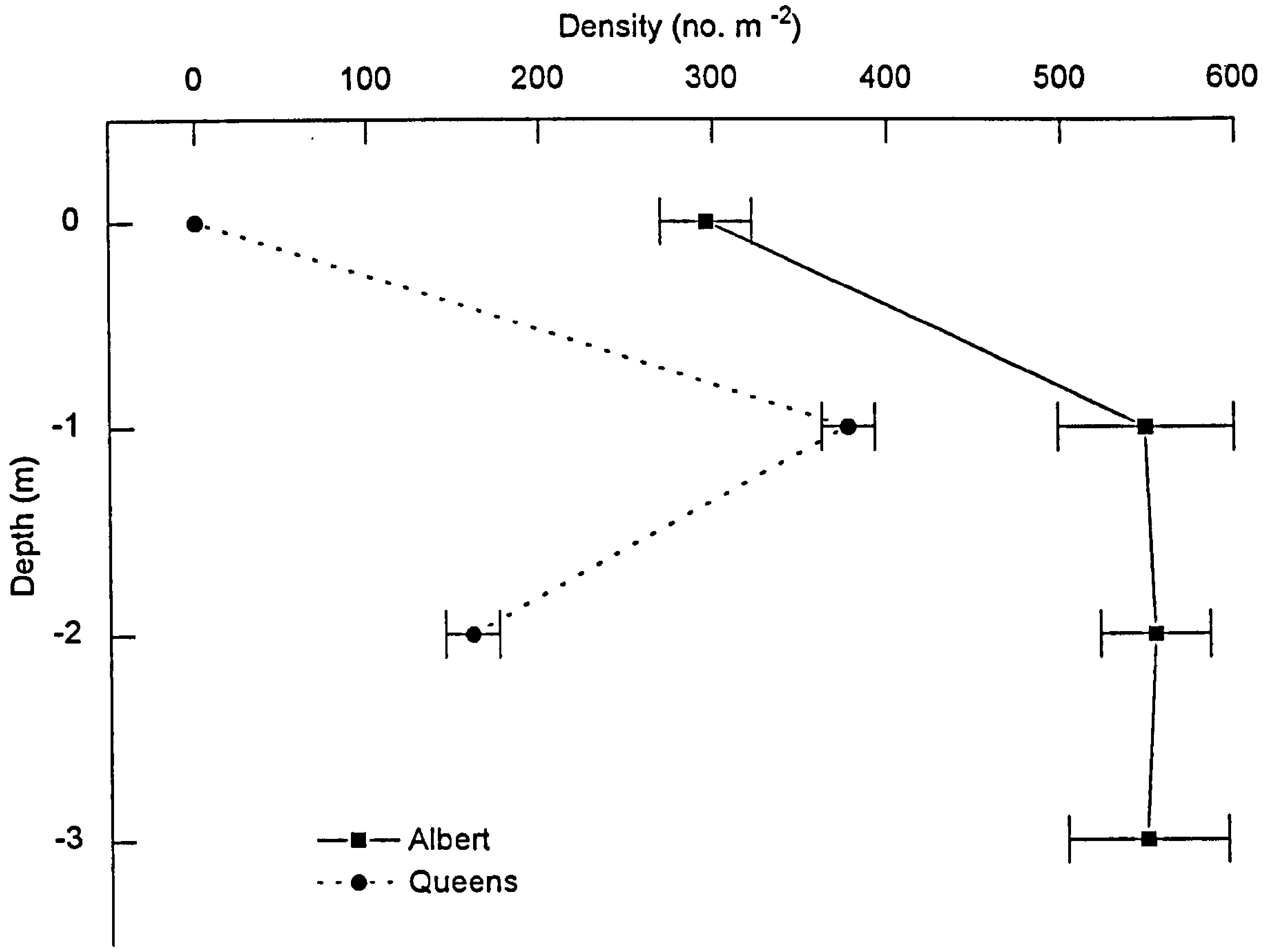

Fig 6.2 Variation in density with depth of Mytilus in Albert (14/10/92) and Queens (21/1/93) Docks. Standard errors of estimates also plotted.

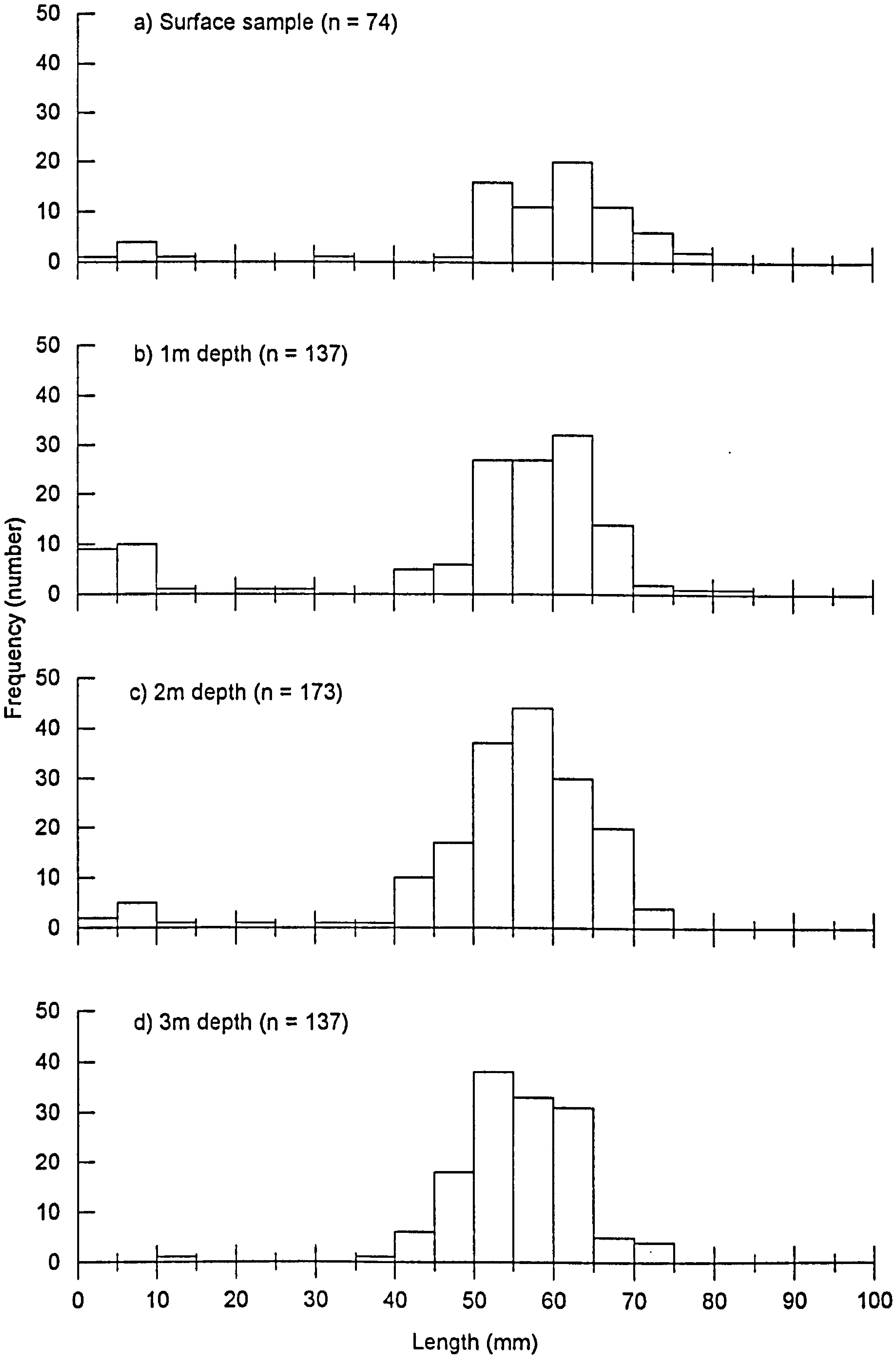

Fig 6.3 Variation of length frequency distribution of <u>Mytilus</u> with depth in Albert Dock. Population sampled 14 October 1992.

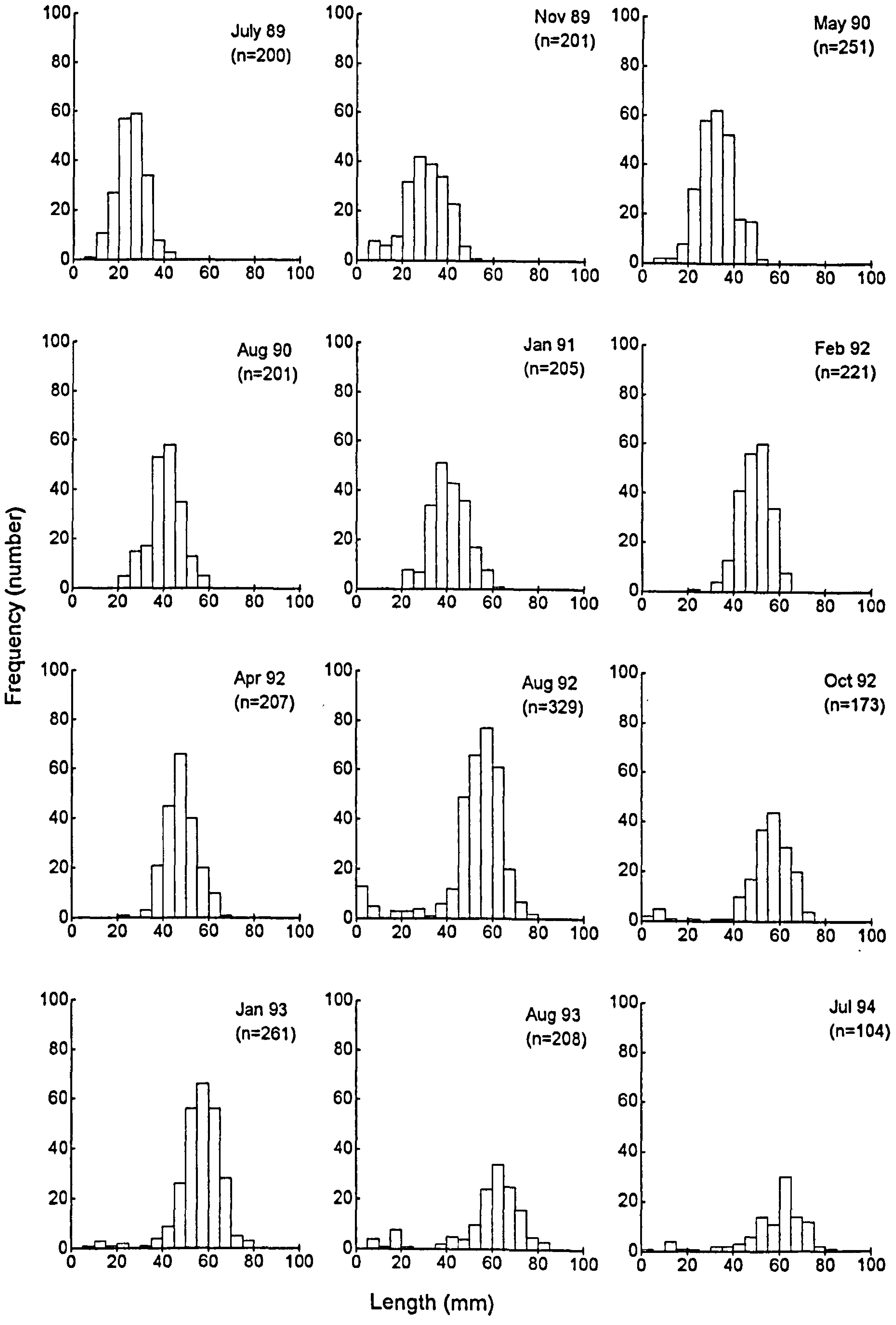

Fig 6.4 Length frequency histograms of Mytilus collected from Albert Dock (1 - 2m depth). Data for 1989-1991 courtesy Allen 1992. Class intervals of 5mm.

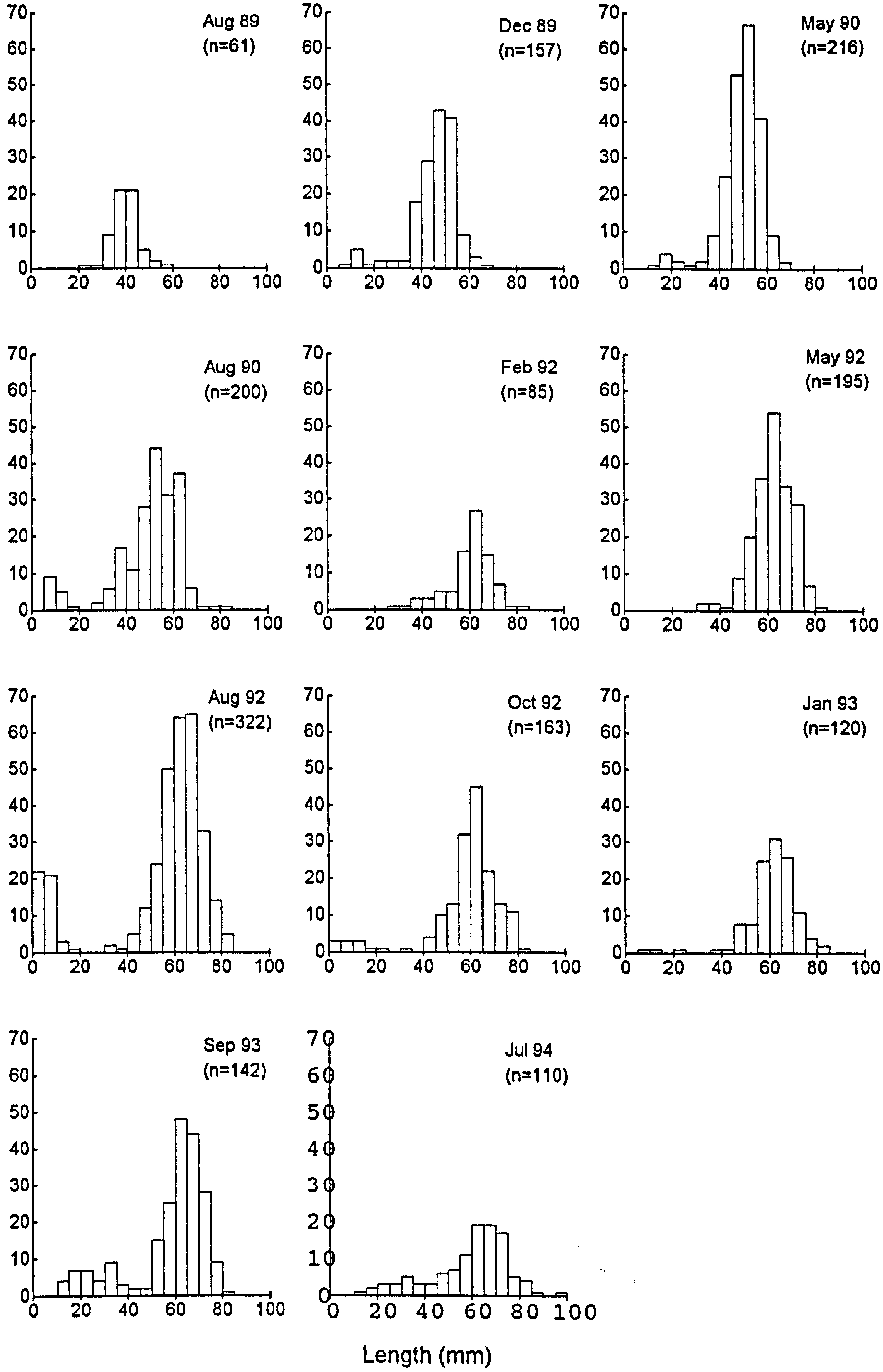

Fig 6.5 Length frequency histograms of Mytilus collected from Queens Dock (1 - 2m depth). Data for 1989-1990 courtesy of Allen 1992. Class intervals of 5mm.

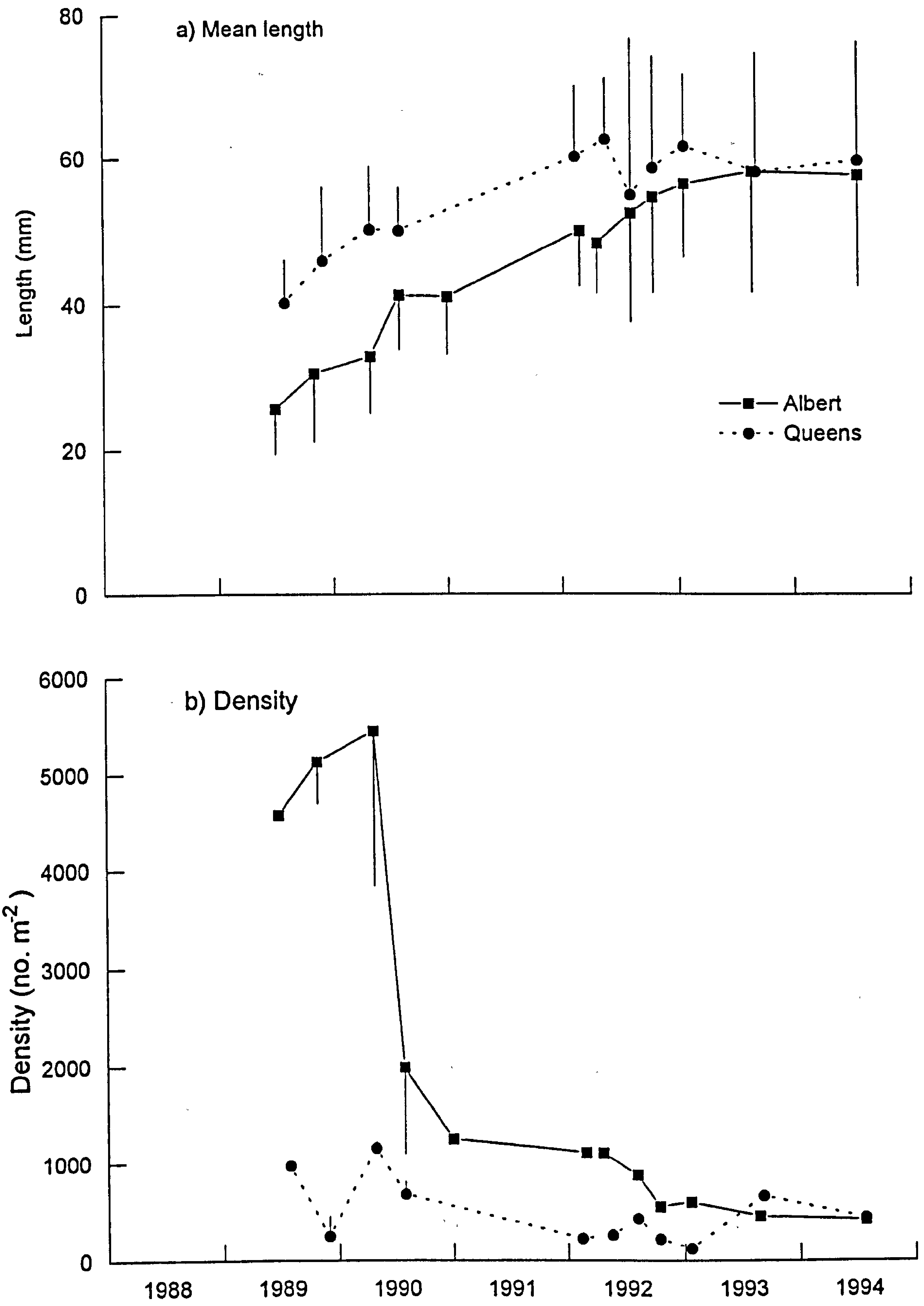

Fig 6.6 Change in mean length (a) and density (b) of Mytilus on the walls at a depth of 1-2m in Albert and Queens Docks. (Data 1989-1991 courtesey Allen 1992) Error bars represent standard deviation.

sites showed a noticeable decline in the density of *Mytilus*. Part of this decline is probably due to the fact that prior to 1992 the *Mytilus* population was sampled at a depth of 1m while after this date the sampling was carried out at two metres depth. Densities at 2m are generally lower than at 1m (Fig 6.2, see also Allen 1992). This does not account for the entire drop in density. In particular there is relatively little difference in the density in Albert Dock between 1 and 2m. In addition, there appears to be reltively little difference in the population size structure with depth (Fig 6.3). The density at 2m at both sites is now almost identical, at around 400 /m^2 (Fig 6.6b).

The *Mytilus* population in Queens Dock had, until quite recently, a noticeably higher mean length than its Albert Dock counterpart. However during 1993 and 1994 the difference declined and by 1994 both populations had almost exactly the same mean length (Fig 6.6e). From 1988 until the end of 1992 there had been a steady increase in the average lengths of both populations and it was only since 1993 that it has levelled off, at around 55-60mm (Fig 6.6a).

The total biomass of *Mytilus* per square metre was estimated where sufficient data are available (Fig 6.7). These figures undoubtedly include large errors having been calculated simply from the mean density multiplied by the mean weight. The mean weight itself was estimated from the average length and the fitted length-weight regression. Despite the errors, however, there has been a gradual increase in the total weight which appears to have levelled off in the last two years at around 4kg/m^2 (Fig 6.7). The pattern for Queens is much more erratic, probably as a result of a more patchy distribution of *Mytilus* on the wall of this dock. Again however, the total biomass seems to fluctuate around 4kg/m^2 (Fig 6.7).

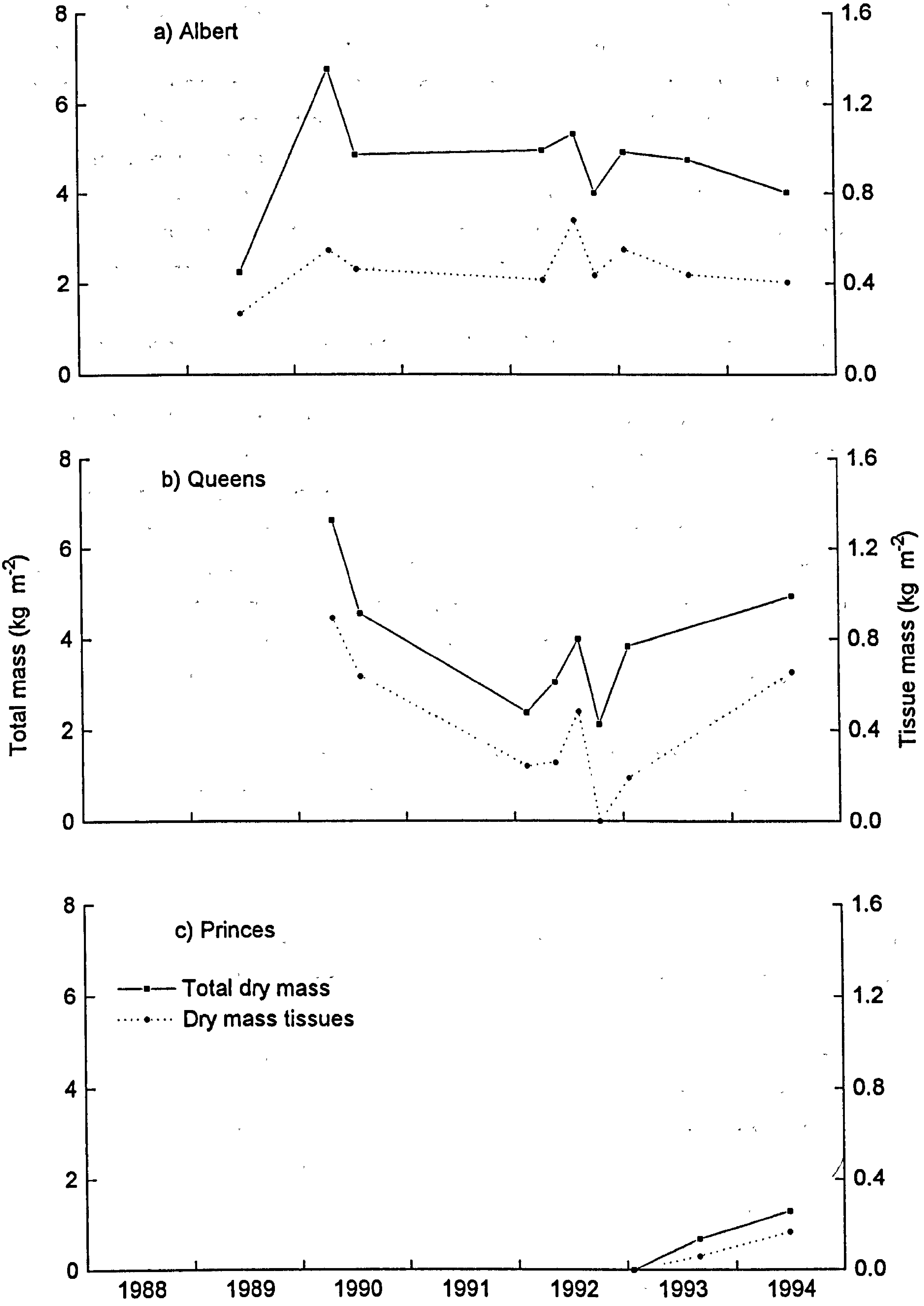

Fig 6.7 Changes in the total and tissue mass of <u>Mytilus</u> on the walls of (a) Albert, (b) Queens and (c) Princes dock at a depth of 1-2m (Figures for 1989-1990 courtesy of Allen 1992)

The population age structure at both sites is summarised in Fig 6.8. Difficulties were sometimes experienced separating the older year classes as the growth checks were often very close together and hard to distinguish. However there is little doubt that the populations in both Albert and Queens docks are dominated by animals that settled during 1988 and 1989. Only five percent of the population in Albert and eight percent of that in Queens was less than three years old when sampled in January 1993 (Fig 6.8).

A very heavy settlement of *Mytilus* occurred on a set of tiles deployed in Albert Dock in January 1992. This is despite the fact that little settlement was recorded on the dock wall at this time (Fig 6.4). The complex shape of the frame used to suspend the tiles made the estimation of densities difficult. Analysis of the age structure of the population showed there was a dominance of the original cohort settling, with subsequent cohorts comprising quite a low percentage of the whole population (Fig 6.9). The recruitment rates observed were higher than observed on the wall. In July 1993 the number of new settlers comprised thirty percent of the population, while the following year this figure had fallen slightly to seventeen percent. At least some of the individuals that settled in 1993 survived to the following year (Fig 6.9).

The walls of Princes Dock were virtually completely bare at the start of this study. During the summer of 1993 a heavy settlement of *Mytilus* occurred at this site (see Chapter 5). Densities were initially very high, around 1600 m^{-2} but one year later they had dropped to about 800 m^{-2}. This compares quite well with the density of about 1000 m^{-2} found in Queens Dock one year after initial settlement but is considerably lower than the 5000 m^{-2} found in Albert Dock. The mean length for the population one year after settlement was 33.4mm, which is also quite similar to that found in the South Docks at a comparable time. When the

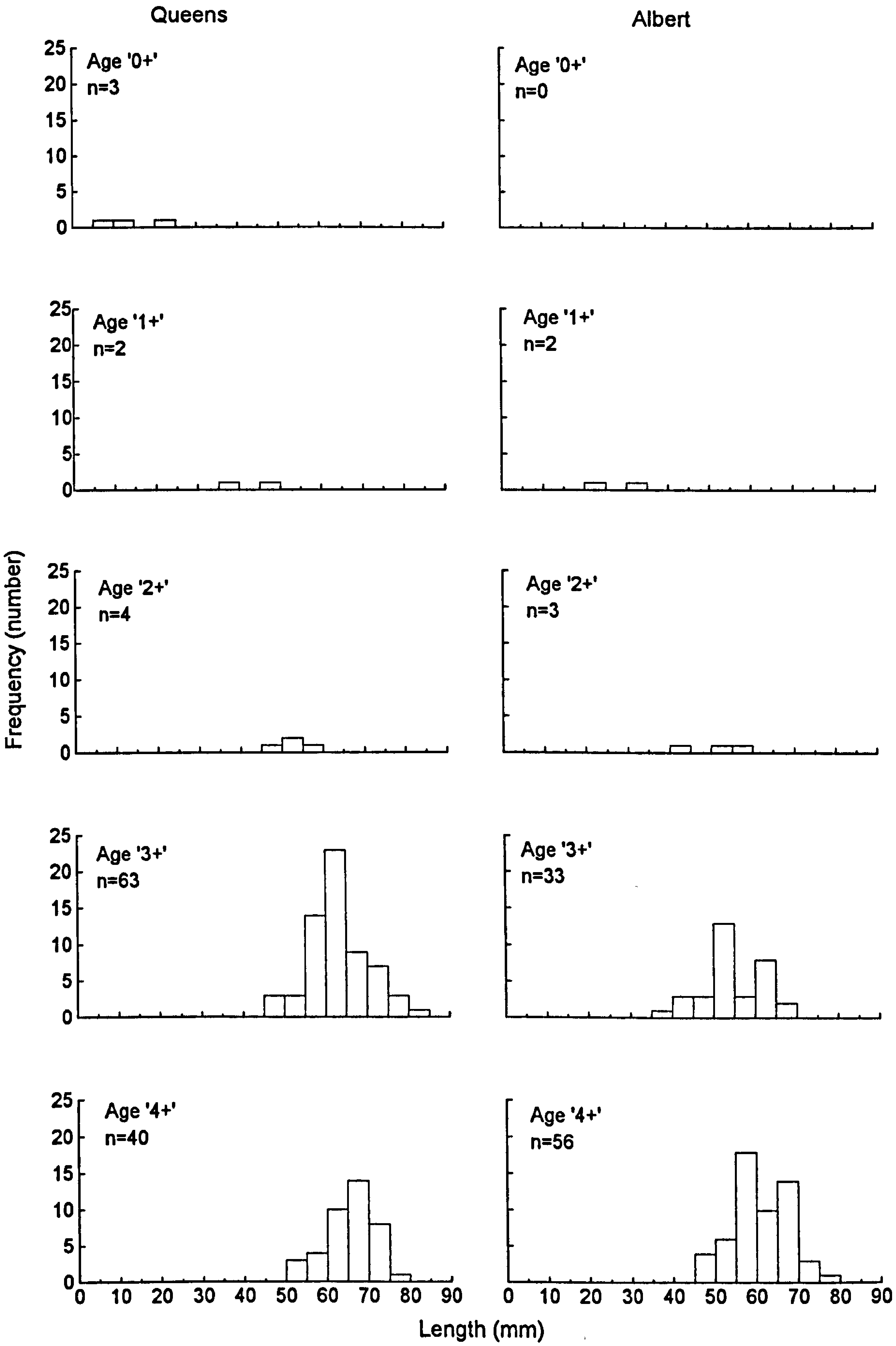

Fig 6.8 Length frequencies of different age classes of Mytilus populations at 2m depth in Albert and Queens Docks. Sample taken in January 1993. Animals aged using external growth checks

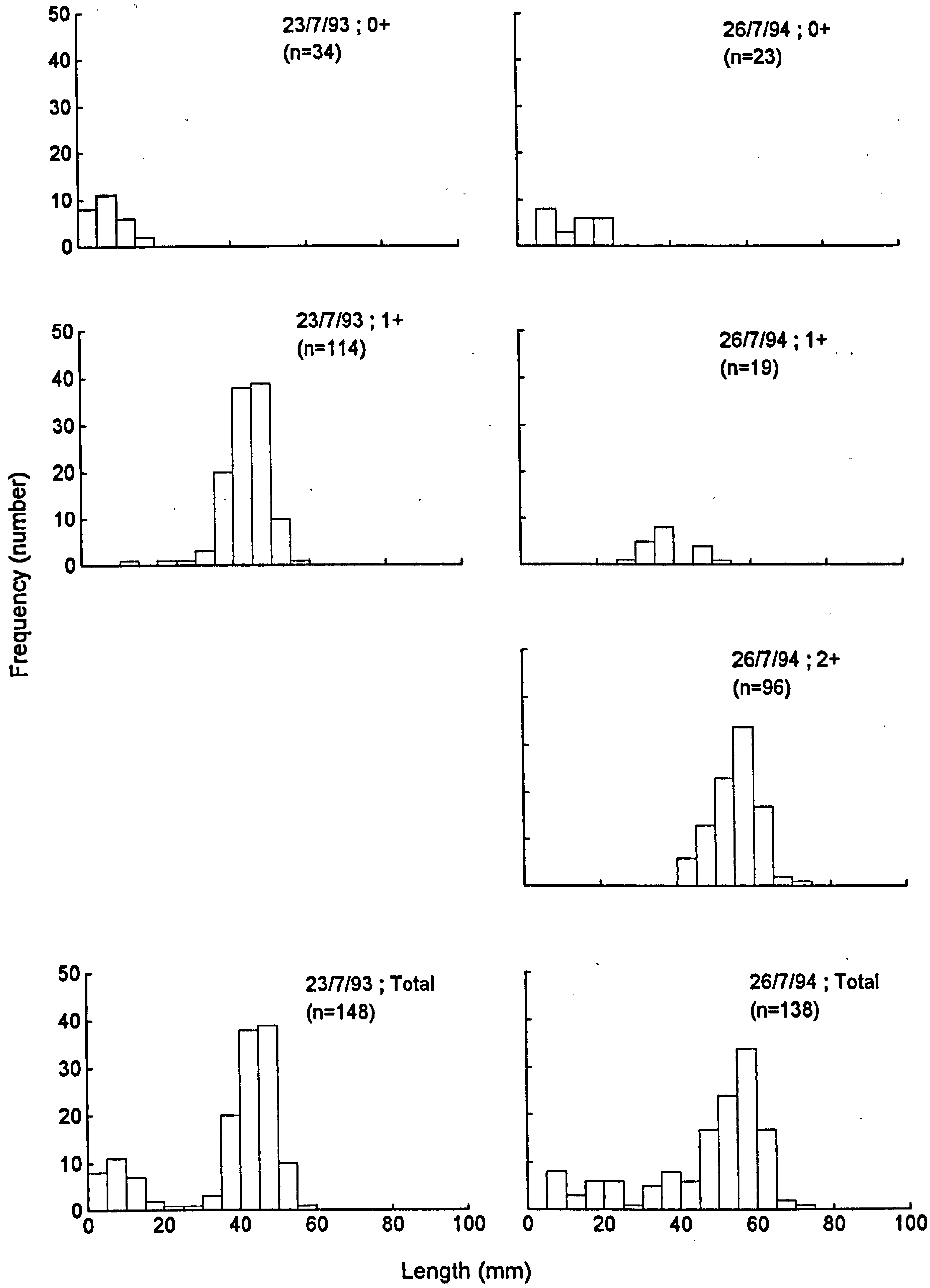

Fig 6.9 Changes in the population age/size structure of Mytilus settling on tiles suspended below a pontoon in Albert Dock in January 1992. (0+ indicates animals which have newly settled that year)

population in Princes was sampled in July 1994 very little evidence of further recruitment was observed (Fig 6.10).

The calculated von Bertalanffy growth curve is fitted to the mean length figures for each age class in Fig 6.11. The value for L_∞ of 67.7mm is considerably smaller than maximum recorded length for *Mytilus* from the docks of nearly 100mm.

6.3.3 Relative Growth

The results from allometric analysis of growth are summarised in Appendix 2. Shell width was negatively allometric relative to shell length, the slope 'b' differing significantly from the isometric value of '1' in almost all cases (Table A2.1). Shell height also showed a tendency to negative allometry but was not significantly different in most cases (Table A2.2). Similarly both shell weight and dry weight of the soft parts generally displayed negative allometry relative to the shell length (Table A2.3 - A2.4). However while shell weight differed significantly from the isometric value of '3' in almost all cases, the difference was generally not significant for dry weight. Standard errors for the slopes for the relationship between shell length and dry weight were generally quite large (Table A2.4).

The ratio between shell weight and dry weight of the body has been widely used as an index of the condition of *Mytilus*. Low values indicate relatively healthy or unstressed animals. Table A2.5 summarises the results from the South Docks, including figures obtained from the spatial survey carried out in the summer of 1993 (see Chapter 4). The figures are all between 0.6 and 1.3. The spatial comparison showed Brunswick and Queens to have the animals with the lowest ratios, with the highest ratios in Albert and Salthouse Docks (Table A2.5d).

Statistical analysis of the relative growth data for

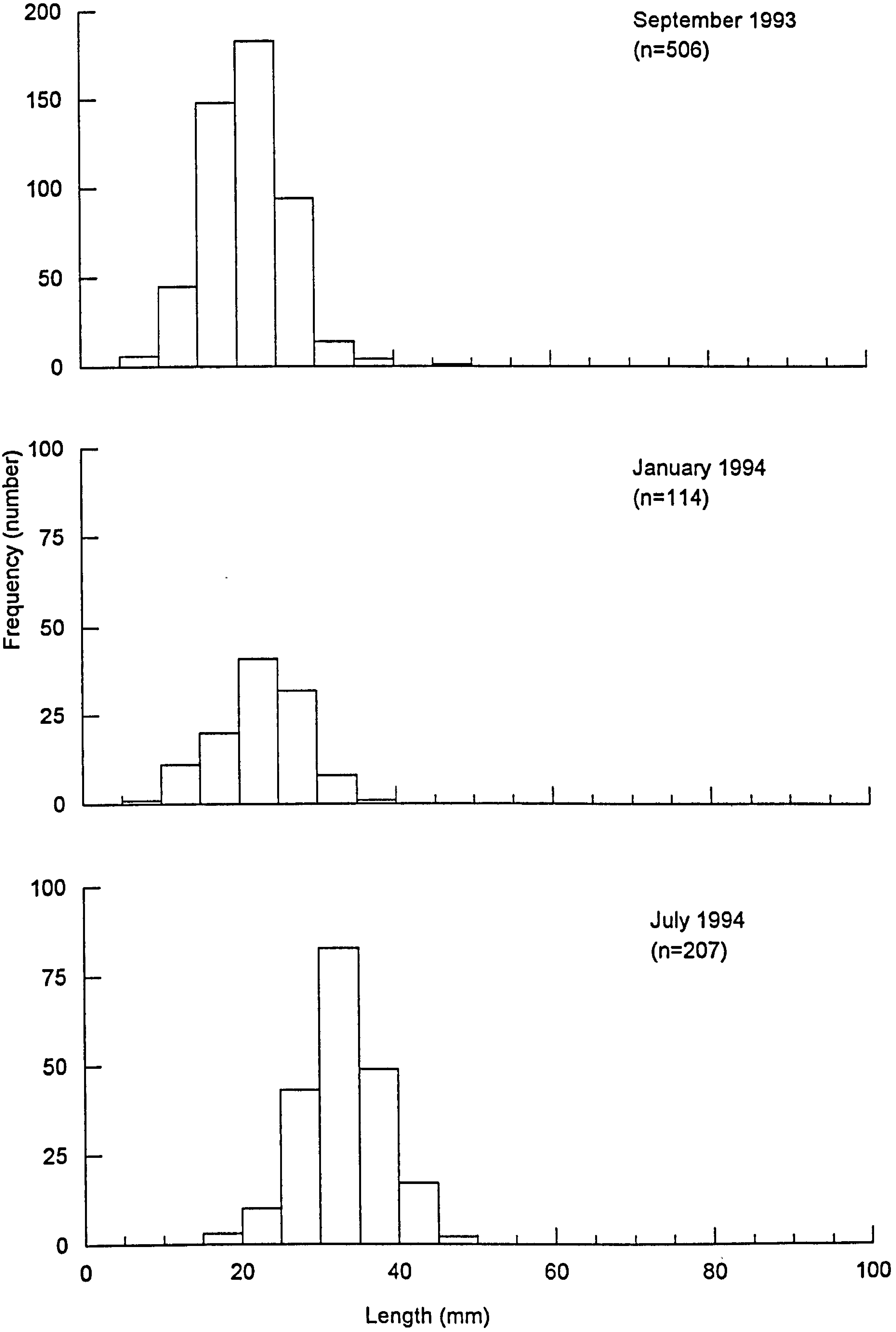

Fig 6.10 Changes in the Mytilus length frequency for the population at 1m depth in Princes Dock. (Note differences in scale)

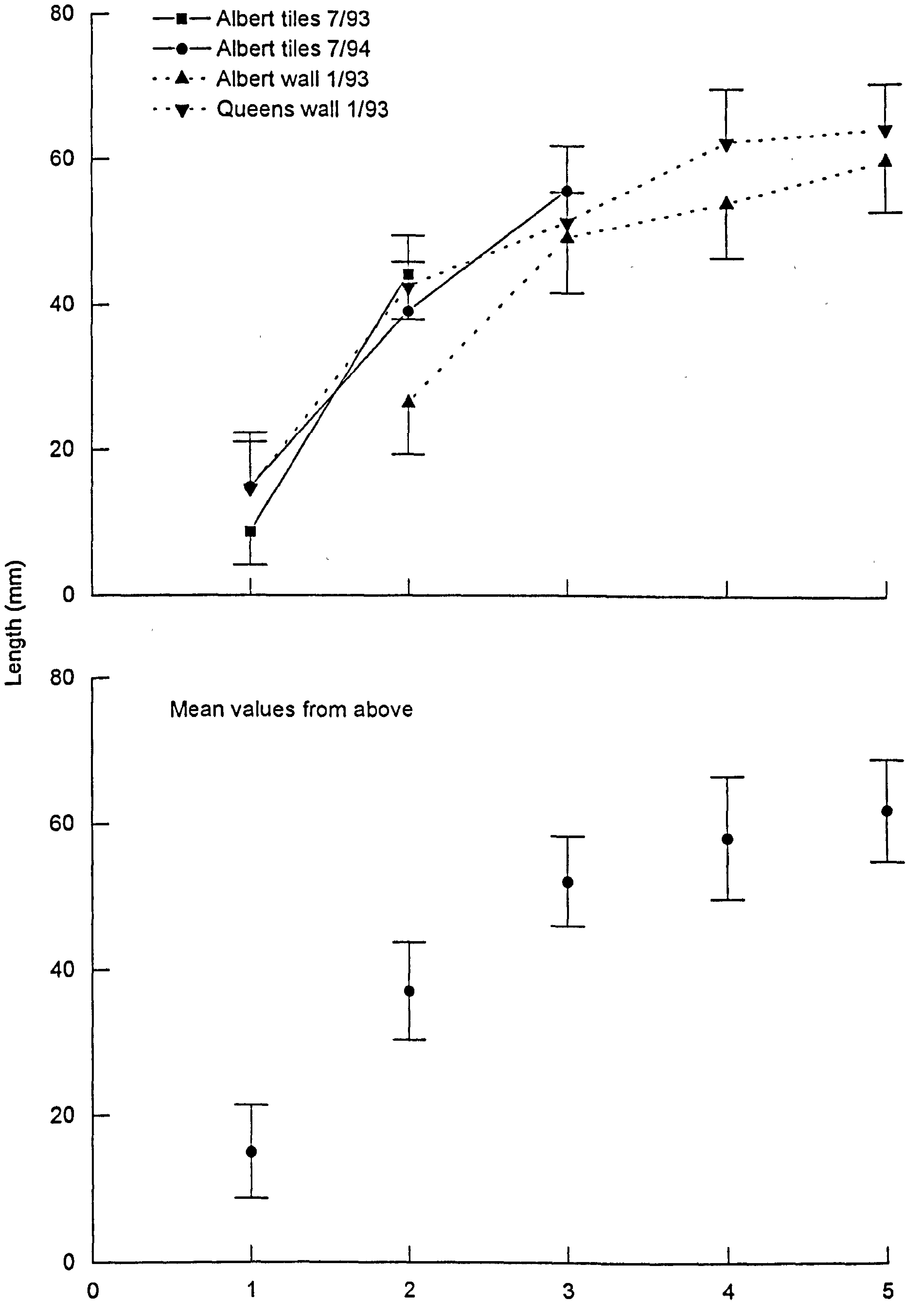

Fig 6.11 Estimates of absolute growth of Mytilus made using growth check lines on the shell. Error bars represent + / - one standard deviation of the estimate.

Mytilus in different docks revealed a significant difference in the slopes of the length - shell weight relationship (Table A2.6). No significant difference was observed in the corresponding slopes for length - dry weight but the intercepts were significantly different. The lowest values for the intercepts were recorded for Brunswick, Canning and Salthouse Docks.

Table A2.7 compares the biometric relationships with depth for Albert Dock. No significant difference was observed in the slopes of any of the relationships examined. Only the intercept for the relationship between length-dry weight showed any significant difference, with lower intercept values recorded for animals from 2 and 3m depth compared with those from nearer the surface.

Table A2.8 summarises the data comparing relative growth of *Mytilus* growing on areas of the wall which are covered and not covered by pontoons. Again no significant difference was observed in the slopes of the relationships examined. Significant differences were observed, however, in the intercepts between length-height, length-shell weight and length-dry weight. Animals growing below the pontoon had lighter shells but greater dry weight of tissues than animals growing on uncovered wall. This resulted in a lower condition index (shell weight / dry weight soft parts) for animals growing below the pontoon; 0.74 compared with 1.24 for animals on uncovered wall (calculated for a standard animal of 45mm length).

6.4 DISCUSSION

Mytilus edulis is a very important species in the docks; both numerically and as the major space occupier. Thus it strongly influences benthic community structure whilst functionally it is the major phytoplankton grazer. Chapter 5 indicated that little change was occurring in the cover of the *Mytilus* population and that the population was therefore reasonably stable. Assessment of the population structure, however, suggests that this is not the case, although the total biomass has remained constant. This is potentially worrying from a management point of view. Therefore it is important to gain some understanding of the major factors affecting the population before any serious deterioration in water quality occurs. In this discussion I will first examine the spatial distribution of *Mytilus* and then consider the population structure and suggest reasons for the observed pattern. Comparison will be made with other subtidal populations of *Mytilus* and also *Modiolus modiolus*. Next the growth of *Mytilus* in the docks will be discussed and finally suggestions will be made for areas requiring further research.

6.4.1 Spatial Distribution

In the South docks, *Mytilus* tends to be most abundant around the mid-depths of the wall, decreasing in density both towards the surface and dock bottom (Fig 6.2). A similar pattern of distribution was observed in Sandon Dock (Russell *et al.* 1983). The reduction in density towards the surface is due primarily to fluctuations in the water level. The level frequently drops by as much as half a metre and the section of wall exposed may remain emersed for days at a time. *Mytilus* cannot tolerate such extended periods of emersion, particularly if the physical conditions are harsh, for example during hot, dry spells. There is also likely to be an adverse effect of benthic macroalgae on *Mytilus* growing near the surface. Dittman & Robles (1991) found that mussels overgrown with epiphytes had lower rates of growth and reproduction than naturally clear mussels. Conditions towards the dock bottom may also be quite harsh at certain times of year, when the oxygen concentration may drop considerably as a result of the decay of phytoplankton. This may be at least partly responsible for the decline in density of *Mytilus* towards the dock bottom. In addition there is also likely to be a higher suspended silt loading towards the dock bottom which may influence the ability of *Mytilus* to settle or survive. A number of workers have suggested that suspended silt may have a detrimental affect on filter feeders (Peddicord 1980, Nelson *et al*. 1987, Seaman *et al*. 1991).

Phytoplankton densities generally tend to be highest close to the dock surface, where there is greatest available light (Allen 1992 Hawkins *et al*. 1993). Comparison of the relationship between length and dry weight of mussels from different depths in Albert Dock revealed a significant difference in the intercept with depth (Table A2.7). Lower values for the intercept were recorded for animals from two and three metres depth compared with those from nearer the surface. This indicates that animals of a given length from greater depths tend to have a lower mass of dry tissue than those from nearer the surface. This may well be due to lower phytoplankton densities at these depths. However the animals were still in quite good condition and it seems unlikely that low food levels have a very strong effect on vertical distribution, but may limit the density at any given depth.

Chapter 4 showed very low densities of *Mytilus* on the walls of Brunswick and Coburg Docks compared with other South Docks studied. It is possible that settlement and survival of *Mytilus* in these two docks is being limited by similar factors as are now limiting the recruitment in Albert and

Queens Docks. However, there is obviously no intraspecific competition with adults here and food supply is definitely not limiting. In addition, predators are not noticeably more abundant. This seems to suggest that some other factor may be limiting the recruitment of *Mytilus* at these sites. One possibility is that in the past, when water was taken into the docks it was done by simply opening the lock gates and allowing water to flow in from the Mersey. This caused quite a lot of disturbance, and in particular there was a considerable increase in suspended solids. This may have been a cause of mortality in *Mytilus* at this time. A more constant top-up regime is now in operation which has reduced the levels of suspended solids, however, there is evidence that levels are still higher in docks close to the intake from the Mersey. This has been confirmed from studies on settlement ropes (pers. obs.). Ropes that had been deployed in Brunswick gathered a much greater amount of sediment than similar ropes placed in Albert Dock. There are plans to set up sediment traps to examine this more carefully. Silt on the dock wall surface may also prevent the settlement of *Mytilus*. It may simply be that there has not been a sufficiently heavy settlement of *Mytilus* here to overcome the demands of predators that are present.

In summary, the *Mytilus* distribution tends to be concentrated around mid-depths on the dock wall. The upper limit is probably set by a combination of the physical extremes experienced during periods of prolonged emersion and competition from benthic macroalgae. The decrease in density observed towards the dock bottom is probably a result of low phytoplankton densities here, combined with periodic reduced oxygen concentrations and possibly a higher suspended silt loading. Larval behaviour may also be important. *Mytilus* is most abundant in the South Docks chain from Albert to Queens Dock. The much lower densities which were observed in Coburg and Brunswick may indicate that conditions in Albert to Queens Docks were more suitable for the settlement and survival of *Mytilus* at the time of the heavy spatfall.

6.4.2 *Mytilus* Population Dynamics

There is little doubt that the *Mytilus* populations now present in Albert and Queens Docks settled over quite a short time, probably one or two years. Since 1989 there has been little recruitment to either population (Fig 6.4, 6.5). This has resulted in an almost continuous increase in the mean length of the population which has only now started to level off, at a mean length of 55-60mm (Fig 6.6). The calculated von Bertalanffy growth curve gave an $L\infty$ of 67.7mm. This compares well with the mean length of the population. It is considerably smaller than the largest individual recorded from the docks which was nearly 100mm long (pers. obs.). This discrepancy is an artifact of fitting a von Bertalanffy growth curve as this is based on the population; individual growth rates may vary considerably. The biomass figures for Albert Dock initially increased and then levelled off at around 4 kg/m^2 total and 0.4 kg/m^2 dry tissue mass (Fig 6.7a). Figures for Queens display considerable fluctuations. This is due in part to the patchiness of the mussel population on the dock wall. However, the most recent figures compare quite well with those for Albert Dock (Fig 6.7a,b). The biomass of *Mytilus* in Princes Dock is still quite low by comparison but has been increasing since the large settlement in 1993(Fig 6.7c). The figures here are comparable to those from Albert Dock in 1989, a similar time after initial settlement. These results seem to suggest that the *Mytilus* population presently on the walls of the South Docks is around the carrying capacity for this area. The reductions in density that have been observed may simply be due to intraspecific competition causing self-thinning of the population (Fig 6.6b). The area close to the wall frequently suffers from reduced densities of phytoplankton. This leads to a considerable increase in secchi-disc extinction depth beside the wall, compared with as little as 1m out from it (pers. obs.). Frechette and Bourget (1985) recorded similar food depletion above a mussel bed. Similarly Beatty and Aldrich (1989) recorded improvements in the condition of *Mytilus* when they were suspended off the bottom. They attributed this either to a decrease in the proportion of silt or an increase in the density of phytoplankton. In the often calm environment of the docks, however, the problem of low phytoplankton levels is likely to be exacerbated due to limited mixing of the water. Intraspecific competition has been implicated as the most important source of mortality in rapidly growing populations (Richardson & Seed 1990). Mortality is likely to be highest when the animals are under greatest metabolic stress, such as during reproduction (Emmett *et al.* 1987). Other factors which could be important sources of mortality in the docks include excess silt or detritus (Ceccherelli & Rossi 1984), biodeposits (Dare 1976, Tsuchiya 1980) or overgrowth by fouling organisms (Dittman & Robles 1991). However, studies on the fouling community of mussel ropes indicated that *Mytilus* was the superior competitor and that if food was limiting it was more likely to have an adverse affect on other species such as *Ciona*, rather than *Mytilus* (Lesser *et al.* 1992).

Predation is very unlikely to be a significant cause of mortality in the South Docks population now as the animals have reached sufficient size that they cannot really be taken by the predators present (crabs, fish) in the docks. There is evidence that crabs preferentially feed on small *Mytilus* which can be crushed rather than larger individuals with longer handling times and hence lower net energetic gain (Elner & Hughes 1978). *Asterias* is the only predator which could potentially consume the size of *Mytilus* found in the docks. This species is absent from the South Docks, despite having been recorded from Sandon and Princes. It is difficult to say what natural life span can be expected for

Mytilus in this environment. Low shore animals generally survive for two to three years but predation is the major cause of mortality here (Seed 1969b). On the upper shore, where growth is slow and predation pressure low, *Mytilus* can live for in excess of twenty years (Seed 1969b, Thiesen 1973). Seed (1969b) and Ceccherelli & Rossi (1984) considered that faster growing individuals probably would not be so long-lived because they would reach a size limit imposed by the environment more rapidly. This was based on the assumption that every habitat probably has an upper growth limit set by both physical and biotic conditions and animals dying as a result of 'outgrowing' this. *Mytilus* has the ability to respire up to eighty percent of its tissue mass before death (Kautsky 1981). This means that even if a large portion of the population were to die at the same time there would probably be few problems with increased biological oxygen demands through decay.

The lack of recruitment to these populations could be due to a number of factors (see Fig 6.12 for summary). Firstly, gametogenesis may not be occurring as normal, perhaps because certain environmental cues are missing. This is a very unlikely explanation however, and sexually mature male and female individuals are definitely present here (pers obs). It is worth mentioning that the salinity range for *Mytilus* fertilization is 15-40‰ (Bayne 1976). While this does not present a problem in the South Docks, it could become a limiting factor in some of the lower salinity docks such as Morpeth. A more likely cause of the low recruitment is that spawning cues are missing so that animals are not spawning at all or do not do so in co-ordinated manner (see Fig 6.12). The spawning stimuli are poorly understood but certainly there is evidence that temperature changes, mechanical stimuli scraping or jarring and waves, tidal fluctuations, salinity changes or phases of the moon may all be important (Chipperfield 1953, Wilson & Seed 1974, Suchanek 1978, Kautsky 1982a, Wilson 1987). In

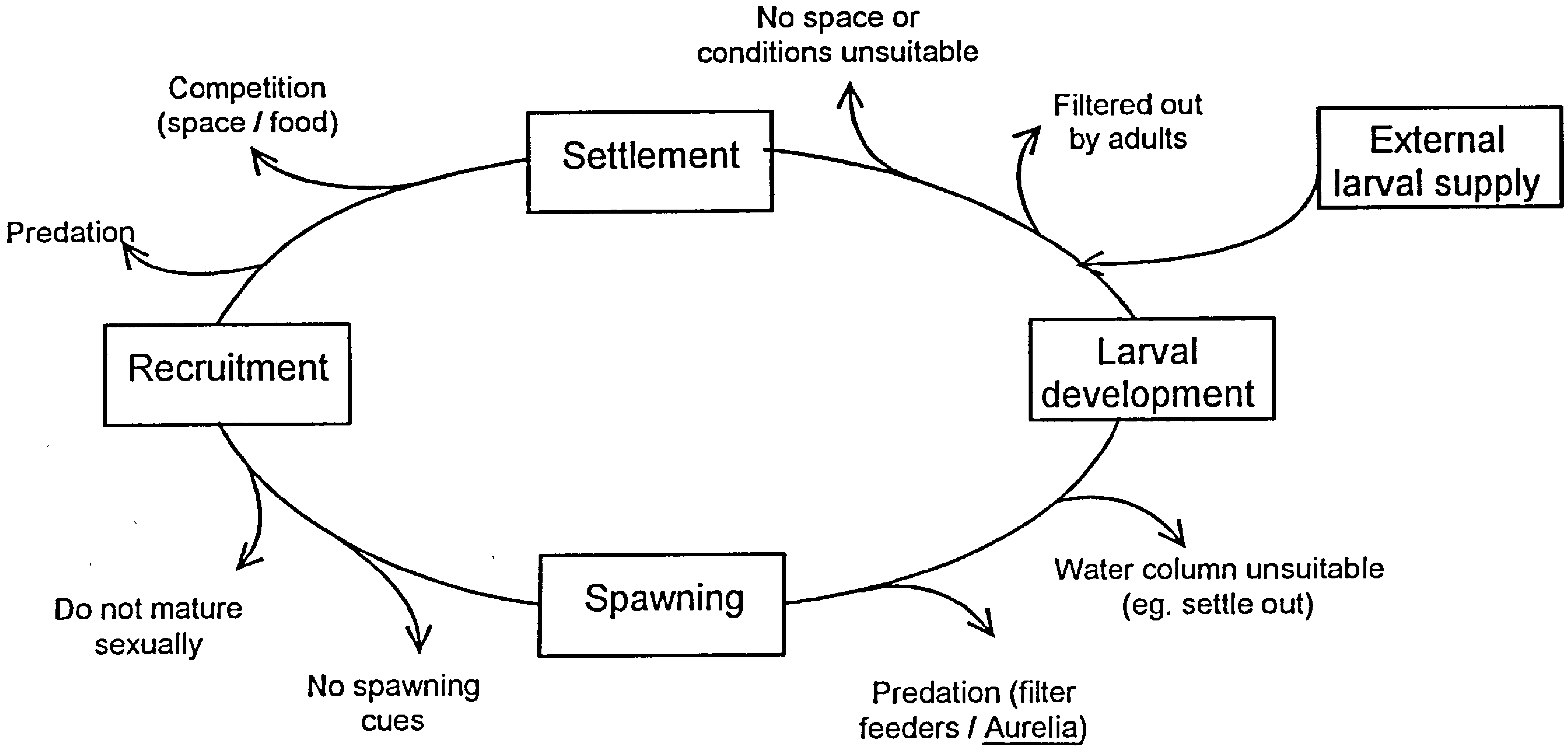

Fig 6.10 Schematic drawing showing summary of the possible factors which may be limiting <u>Mytilus</u> recruitment in the South Docks

the relatively static environment of the docks many of these possible cues could be missing making the coordination of spawning difficult. The release of sperm following disturbance of the water column by boats in the vicinity of male mussels has been observed in August 1992 (pers obs). This adds weight to the theory that spawning cues may be limiting recruitment in this system. No attempt was made to study changes in gonadal development of the dock populations; this is certainly an area worthy of further study. *Mytilus* sperm has been recorded in settled phytoplankton samples (Wanstall pers. comm.) indicating that at least some gamete release is occurring naturally.

There is considerable evidence that benthic filter feeders may limit larval recruitment by filtering out larvae (Cowden *et al.* 1984, Young 1988, see Young & Chia 1987 for review). The relatively long larval life of *Mytilus* means that planktonic larvae will be susceptible to this form of predation for a considerable period of time. In the docks, given the size of the adult *Mytilus* stand it is easy to see how filtration could considerably deplete either numbers of gametes or larvae of *Mytilus* or indeed other species (Fig 6.12). The long larval life of *Mytilus* combined with the relatively calm conditions found in the docks, means there is also a danger that the larvae may simply settle out onto the mud bottom (see Fig 6.12). This may be particularly a problem during the post-larval stage. Lane *et al.* (1985) calculated a settling rate of 1 mm / sec for a 2mm post-larval *Mytilus*. In the relatively shallow water of the docks, if we assume no mixing at all, this means that larvae would settle from the surface to the dock bottom in as little as one and a half hours. In reality there is likely to be at least some upward mixing but the probability of settling out during the three weeks spent in the plankton (Bayne 1976) must still be quite high.

Some settlement of *Mytilus* is still definitely occurring in the docks. A heavy settlement was observed on tiles deployed in Albert Dock in January 1993 and also on ropes suspended below the pontoons (Allen 1992). This suggests that the mussels are reaching sexual maturity, spawning successfully and that fertilization and settlement are possible here. Interestingly though no such settlement was recorded on further sets of tiles deployed the following year (see Chapter 8). This may have been due in part to the use of polypropylene tiles rather than the original stone floor tiles. Alternatively this observation may indicate considerable annual variation, due to the presence or absence of some of the cues outlined above. In 1992, when heavy settlement was recorded on the tiles, settlement on the wall was also high relative to other years (see Fig 6.4). Considerable recruitment variation was also found between years in Sandon Dock (Naylor 1983, Hawkins *et al.* 1992b). Variation in the supply of *Mytilus* larvae between years was suggested by Paine (1974) as the reason for the failure of Dayton (1971) to replicate the results of Paine (1966), to extend the lower limit of *Mytilus* through predator removal. Similar annual variation as been recorded for many other species (see Chapter 7).

The heavy settlement of *Mytilus* on the tiles seems to indicate that conditions on the dock wall are in some way unsuitable for recruitment (see Fig 6.12). There are three possible reasons for this. First certain necessary settlement cues may be missing. Second the survival of larvae settling on the wall may be limited by competition from the adults or other species. Space is unlikely to be limiting as indicated by the availability of this throughout the year (see Chapter 5). Finally the settled larvae may be consumed by benthic predators before they have a chance to recruit into the population.

A large body of information exists on how important cues can be for the settlement of larvae (see Chapter 7). The absence of such cues around the dock walls could be causing reduced settlement in these areas, assuming conditions here are different in some way than when the initial settlement occurred in 1988. Normally *Mytilus* has a period of primary settlement, before detaching and subsequently resettling onto the adult bed. The primary settlement is normally on filiform structures in an area away from the adult bed and this behaviour is believed to reduce competition from the adults while the larvae are still at quite a delicate stage (Seed & Suchanek 1992). In Albert and Queens Docks there are few areas where adult *Mytilus* are not present, and cues for primary settlement may be missing. This could lead to the larvae having to settle directly into the adult bed where competition will be strong or alternatively not settle at all and eventually sink out on the soft mud bottom. Direct settlement on the adult bed is known in other populations (McGrath *et al.* 1988, King *et al.* 1990) and this may well be occurring out of necessity in the docks.

Predation is widely held to be the major factor limiting the extension of *Mytilus* into the subtidal (Ebling *et al.* 1964, Paine 1976b, Kautsky 1981, Seed 1986). In the docks *Carcinus maenas* is probably the most important predator on *Mytilus*, although there are others such as flounder and plaice. *Asterias* is absent from the South Docks, despite having been recorded from Sandon and Princes Docks. It is possible that the initial settlement of *Mytilus* occurred before the arrival of predators in the docks, and the *Mytilus* were therefore able to reach a size too large to be consumed before predators arrived in significant numbers (Paine 1976). Since then the number of predators has increased and newly settling spat may be consumed before they have a chance to recruit into the main population. This idea would seem to be backed up by evidence from the tiles. As these were suspended below the pontoon it was not possible for *Carcinus* to gain access to them and thus a predation refuge from *Carcinus* at least was formed. However, when the tiles were re-examined in 1994, the size structure of the population was very similar to that observed on the wall, dominated by older, larger individuals. Some settlement had occurred in both the years following the settlement of the initial cohort but this was a relatively small proportion of the whole population (Fig 6.9). Although small, the proportion of recent year classes recruiting to the population on the tiles is certainly higher than observed on the wall. The size structure on the tiles, while still dominated by larger older individuals definitely appears more sustainable than that observed on the wall.

The tiles remained suspended below the pontoon and no *Carcinus* was ever recorded on them. This would seem to implicate intraspecific competition for either space or food as being one of the major factors limiting the recruitment of juvenile *Mytilus*, though the filtration of larvae by adults remains a possibility. Space, however, seems unlikely to be limiting, as considerable amounts of space have been opening up on the wall recently with the declining density of *Mytilus* (Fig 6.6b; see also chapter 5). As mentioned above, it seems likely that the current mass of *Mytilus* on the walls is close to the carrying capacity of the system. If this is the case then the recruitment of further individuals to the population will be limited simply by food supply. If this is indeed limiting recruitment then it is only when the total mass of *Mytilus* begins to decline that new recruits will be able to settle and grow. In addition, the intense competition that is probably experienced here if not actually causing mortality in the juvenile *Mytilus* will certainly cause reduced growth rates. This would mean that they are exposed to the threat of predation for longer.

Further evidence comes from studies on Princes Dock. When the walls of this dock were first examined in 1992 they were almost completely bare, except for barnacles and low densities of *Ascidiella*. A few quite old specimens of *Mytilus* were recorded. During the summer of 1993 a heavy spatfall occurred, with densities of 1600 / m^2. The number of adults in the dock at this time was very low and it seems likely that the majority of the larvae came from outside the dock. Large mortalities were recorded within the first year after settlement and density was reduced to 800/m^2 by July 1994. However, despite the fact that *Carcinus* is definitely present in this dock, it seems that the largest source of mortality was from starvation of the mussels over the winter when food supplies were low (see Table A2.5.c). There was little opportunity for the newly settled juveniles to build up reserves to cope with the winter period. Again further studies of this population seem to indicate that a similar structure as observed in the South Docks is beginning to emerge, with little recruitment occurring and the population becoming dominated by an older cohort (Fig 6.10). These observations from Princes Dock serve to emphasise how important a single large recruitment event can be in structuring the population. It is interesting that this is essentially the same way as the population in the South Docks began, probably with a large input of larvae from the Mersey in 1988 (Allen 1992). A similar event was also observed in Sando Dock (Hawkins *et al*. 1992b) It is possible that in order for some or a number of settling larvae to survive, they must settle in sufficiently high densities as to completely swamp any predators that are present (Paine 1974). It is also noteworthy that prior to this large settlement in Princes dock no problems with poor water quality were experienced.

While *Mytilus* is typically an intertidal species, a number of subtidal populations have been studied. Richardson *et al*. (1990) recorded a similar population structure to that observed in the South Docks, with a high proportion of relatively large individuals. Similarly, a markedly bimodal size distribution has been recorded for a number of populations of the horse mussel, *Modiolus modiolus* (Comely 1978, Anwar *et al*. 1990). Comely (1978) considered some of the populations he studied to be quite unstable, unless a large recruitment event occurred in time the population would die out altogether. He attributed the lack of recruitment to heavy predation pressure at the sites studied. Unlike *Mytilus*, which reaches sexual maturity after one year, *Modiolus* does not become sexually mature until it is two to three years old (Jasim & Brand 1989). By this time it has attained a length of between 40 and 50mm. This delay of sexual development is believed to allow extra energy to be devoted to somatic growth and hence reach a size escape from predation more quickly (Seed & Brown 1977, Brown 1984). The early sexual development of *Mytilus* may be another factor limiting its extension into the subtidal, as this will reduce the early growth rate and hence the length of time an individual is vulnerable to predation.

In summary, the *Mytilus* population in the South Docks is dominated by one or two older cohorts. The exact reasons for the lack of recruitment to the population are unclear, but it seems likely that a combination of factors are responsible. In particular, the high biomass of *Mytilus* now present on the walls leads to very intense intraspecific competition which has an adverse effect on newly settled individuals. This competition, as well as possibly causing mortality directly also slows growth of the juveniles and means they are susceptible to predation for longer.

6.4.3 Relative Growth

The growth and condition of *Mytilus* have been reported by numerous authors using a variety of approaches. The range of methods used makes it difficult to compare the results presented here with many of those available in the literature. The following discussion is concerned mainly with comparison with the results presented by Seed (1968, 1973) and Richardson & Seed (1990).

The results presented here (see Tables A2.1 - A2.4) indicate that the growth of *Mytilus* is not uniform. Shell width appears to be negatively allometric to length (Table A2.1). Shell height is more or less isometric compared with length, with a tendency to negative allometry (Table A2.2). These results compare well with those presented by Seed (1973) and Richardson & Seed (1990), except that these authors suggested that the length - height relationship had more of a tendency to be positively allometric, indicating height is increasing relatively faster than length.

In the past there has been controversy over changes in the condition of *Mytilus* growing in the intertidal compared with those growing in the subtidal. Rao (1953) found that subtidal populations had heavier shells than animals of similar size growing in the subtidal. He attributed this to the fact that the rate of calcium deposition was probably dependent on the length of time the animal remained submerged. He also suggested that the ratio of shell weight to dry weight of soft parts was an index of the number of hours the animals were submerged per day, so that animals that spent longer submerged had higher ratios. Baird & Drinnan (1957) presented contrasting results, however. They found that mussels periodically exposed to the air had higher shell to tissue ratio than those constantly submerged. They attributed this to energy demands of basal metabolism during shell closure which reduced meat faster than internal corrosion reduced the shell. This conclusion was supported by further results from Coleman & Trueman (1971) and Seed (1973).

The results presented here also agree with the figures produced by Seed (1973). Animals growing in the docks had very low shell to dry weight of tissues ratios, between 0.62 and 1.26 (Table A2.5). The lowest ratios were recorded from Brunswick and Queens Docks. This may be due in part at least to the greater densities of phytoplankton in these docks during the summer and also perhaps the lower densities of *Mytilus*. These factors combine to reduce intraspecific competition for food and therefore there is more phytoplankton available to each individual for conversion into tissue.

It is interesting that the relationships between both shell weight and dry weight with shell length are negatively allometric (Table A2.3 - A2.4). Richardson & Seed (1990) working on a *Mytilus* population growing on an oil platform recorded isometric growth between length and shell weight and very positive allometric growth between length and dry weight of tissues. The differences may again be due to the high levels of competition for food that are likely to be experienced in the docks. The greater degree of water movement and therefore food availability that is likely to be found on offshore oil platforms may result in greater accumulation of dry mass in larger animals.

Quite large standard errors were associated with the estimates of slope between length and dry weight (Table 5.4). Again this may simply indicate high intraspecific competition for food. However another possibility is that the animals are at a range of sexual maturity. This would add weight to the hypothesis suggested above, regarding spawning stimuli which may be missing in the dock environment. The population may therefore display a tendency to release gametes over a wide time scale. Such reproductive activity has been observed for *Modiolus modiolus* (Seed & Brown 1977, Brown 1984). However, further research is required to test this hypothesis, looking at the actual sexual condition of individuals over the year, as well as the total weight of internal tissue.

In summary, the *Mytilus* present in the docks do not show uniform growth. Shell width, height, weight and dry tissue weight all tend to show negative allometry relative to shell length, indicating shell length tends to increase relatively faster than these other parameters. While these results are comparable to literature values, the relationship between tissue weight and shell length has been previously found to be positively allometric for animals growing in the subtidal. This, combined with the high degree of variation in this relationship, suggests that *Mytilus* in the docks are experiencing high levels of intraspecific competition.

6.4.4 Future Research

There is no doubt that the *Mytilus* population in the South docks is now suffering seriously from low recruitment. Clearly it is important at this stage to ascertain the major reasons for this before the population starts to decline. From the results presented in this study, it seems likely that larval supply, competition and predation are the major factors limiting recruitment and the next step is to discern which of these is the most important. One way of approaching this problem, though drastic, is to clear a large area of wall, in an effort to eliminate as far as possible competition from the adults. It should be remembered that the boundary layer of reduced phytoplankton densities through *Mytilus* grazing is quite large and so any area scraped would have to be sized accordingly. Preliminary investigations cleared areas 0.5m X 0.5m but no recruitment was observed in these. This probably indicates that this area is insufficiently large. While the boundary layer of reduced phytoplankton densities has been qualitatively observed it has yet to be quantified; this is another area requiring attention. In 1991 an artificial mixer was installed in Albert Dock. Little work has been done in assessing the effect this has. One potential beneficial effect it could have would be the break down of the layer of phytoplankton depleted water close to the wall. This is certainly an area in need of testing, for it could potentially increase the filtration power in the dock, if the ideas above regarding high intraspecific competition limiting biomass are correct. It is suggested that monitoring the density and structure of the *Mytilus* population continue, but that sampling be reduced to once annually.

The absence of *Mytilus* from Brunswick and Coburg Docks is another question which should be addressed. This is particularly important in case the factors limiting recruitment here also apply to the system as a whole. Tiles could be used, both to test if *Mytilus* are settling and as a means of transplanting newly settled *Mytilus* into the dock to assess their survival. In a similar way, the transplant of *Mytilus* to Morpeth Dock could be used to assess whether biological filtration from *Mytilus* could be used to improve water quality. Preliminary investigations here seem to indicate that *Mytilus* will not survive in this dock under current water quality conditions.

Finally, it appears from the above study that recruitment of *Mytilus* to the docks tends to be quite intermittent. The reasons for this may become clear from the investigations already suggested. However, a more detailed study of the reproductive cycle would eliminate the possibility that *Mytilus* recruitment here is being significantly affected by the absence of the correct cues. Some indication of the potential larval supply direct from the Mersey is also required.

The water quality management of the South Docks has been greatly eased by a fortuitous natural spatfall of *Mytilus edulis*. Our understanding of the effect of this species and its population dynamics has greatly increased over the last six years. However, in order to ensure its survival here, it is important to assess what the main physical and biological influences are on this species in the unusual environment found in the docks.

CHAPTER 7

SPATIAL AND TEMPORAL VARIATION IN THE ZOOPLANKTON

7.1 INTRODUCTION

Historically, most of the work that has been carried out in benthic marine community ecology has tended to concentrate on post recruitment processes (Paine 1966, Dayton 1971, Connell 1975, 1983, Lubchenco 1978). Recently, more attention has been focused on recruitment processes and in particular the importance of larval supply (Sutherland 1974, Denley & Underwood 1979, Keough 1983, Underwood & Denley 1984, Gaines & Roughgarden 1985, Underwood & Fairweather 1989, Minchinton & Scheibling 1991, Watanabe & Harrold 1991, Bertness *et al.* 1992, Grosberg & Levitan 1992, Hurlbut 1992). Recruitment to an adult population can be broadly divided into three stages. First, a propagule must be produced, grow, survive and reach an area; second it must settle and finally the individual must survive for some arbitrary period of time (see comments in Keough & Downes 1982, Davies 1987, Richmond & Seed 1991).

The supply of propagules to a site is dependent on a number of factors. First, the propagule must actually be produced. This will depend on a sufficient supply of energy being made available to the adults to produce gametes. Glynn (1988), Bertness *et al.* (1991) and Richardson (1991) suggested that variations in primary and therefore secondary production resulted in variations in larval production. The gametes must then be released in synchrony before subsequent fertilisation may occur (see comments in Giese & Pearse 1974). Competent larvae then remain in the water column for some predetermined period of time, which varies according to species (see Grave 1944 for tunicate larvae, Bayne 1976 for *Mytilus*). During this time large and small scale hydrographic forces can have a substantial effect on the larval distribution (Foster 1975b, Grosberg 1982, Keough & Chernoff 1987, Minchinton & Scheibling 1991). Ecological systems can be broadly divided into two classes, namely open and closed, which will have consequences for how the larvae will be distributed (Minchinton & Scheibling 1991). In closed systems the propagules tend to be dispersed within the geographical boundaries of the adult population. In these systems, the prediction of demography is possible, given the reproductive output of the adults. However, most marine systems tend to be much more open. Here, real prediction becomes intractable and reliance must be placed on the number of competent propagules that reach a potential settlement site (Keough 1983). This technique has been adopted by most workers on fouling assemblages in the marine environment (eg. Sutherland & Karlson 1977, Chalmer 1982, Keough 1983). As well as arriving in an area, larvae often require quite specific cues before they will settle (Scheltema 1974, Young & Braithwaite 1980, Keough & Downes 1982, Peterson 1984, Svane 1988, Stone 1990, Roberts *et al.* 1991, Minchinton & Scheibling 1993).

Given the importance of larval supply in determining the community structure of a region, there has been surprisingly little work on relating the two. Work has tended to concentrate more on post-settlement processes, such as disturbance (Dayton 1971, Sousa 1979a,b, 1984, Keough & Connell 1984, Petraitis *et al.* 1989), competition (Connell 1975, 1983, Lubchenco 1982, 1983, Schoener 1983, Wethey 1984) and the role of consumers (Paine 1966, Russ 1980, Lubchenco 1982, 1983, Sih *et al.* 1985, Farrell 1991). The studies that have, however, looked at larval supply have stressed the over-riding importance this process can have (Sutherland 1974, Connell 1985, Gaines & Roughgarden 1985, Menge 1992), accounting for as much as 79% of the observed variation (Minchinton & Scheibling 1991).

The docks in Liverpool represent one of the few marine systems that can be regarded as largely closed. While some larval input does come from outside the system through locking operations, most is likely to be internally generated. However, the heavy initial settlement of *Mytilus* in the South Docks in 1989 emphasises how important the external source of supply can be. A similar episodic recruitment event of *Mytilus* was observed in 1993 in Princes Dock (see Chapter 5). Chapter 6 indicated that recruitment of *Mytilus* in the South Docks was being limited in some way and larval supply was one area suggested for further study.

This study examines zooplankton in two contexts: its main emphasis is larval supply to the benthic communities studied; holoplankton are also described as they are essential to the functioning of the whole ecosystem and give insights into interactions between the benthos and the plankton. The temporal changes in the zooplankton in Albert, Queens and Princes Docks over a two year period are described. The data for Albert Dock will also be integrated with that presented by Allen (1992) and Zheng (1995) in order to gain an insight into the longer term changes that have occurred over the last seven years, particularly with regard to the holoplanktonic species. As far as possible, changes in the larval composition will be related to the community descriptions (see Chapter 5).

7.2 METHODS

7.2.1 Temporal monitoring

The zooplankton in Albert, Queens and Princes Docks was sampled at approximately biweekly intervals, throughout 1992 and 1993. Each sample consisted of three replicate 20m horizontal tows taken just below the water surface using a 250μm mesh plankton net with 0.3m diameter mouth. During 1993, in addition to taking horizontal hauls in Albert Dock, vertical hauls were also taken. The zooplankton net was lowered to the dock bottom and slowly pulled to the surface. Three replicates were taken on each occasion and analysed as below. Material was immediately preserved in 5% formalin/seawater solution. Samples containing adult *Aurelia* were discarded and retaken. Material was sorted and counted in a Bogorov tray under a binocular microscope, using a magnification of X25. Holoplankton were only identified to sub-class (i.e. copepods and cladocerans). During 1993 copepods were further classed as either harpacticoid or calanoid species. Larvae were identified as far as possible, usually to species level. Problems were experienced with some groups, particularly tunicates, due to the lack of larval identification keys. This made it impossible to separate with certainty the larvae of *Ciona* and *Ascidiella*. Tenuous identifications of these species were made based on the relative abundances of the adults and larval species encountered in different docks and the information available from keys. These results should be interpreted with caution. Where possible the samples were analysed to completion though very high numbers sometimes made this impossible and volumetric subsampling was carried out.

7.2.2 Spatial survey

A spatial comparison of the zooplankton in Albert Dock was carried out on 8th April 1993. Three vertical hauls were taken at each of three stations in Albert Dock. The

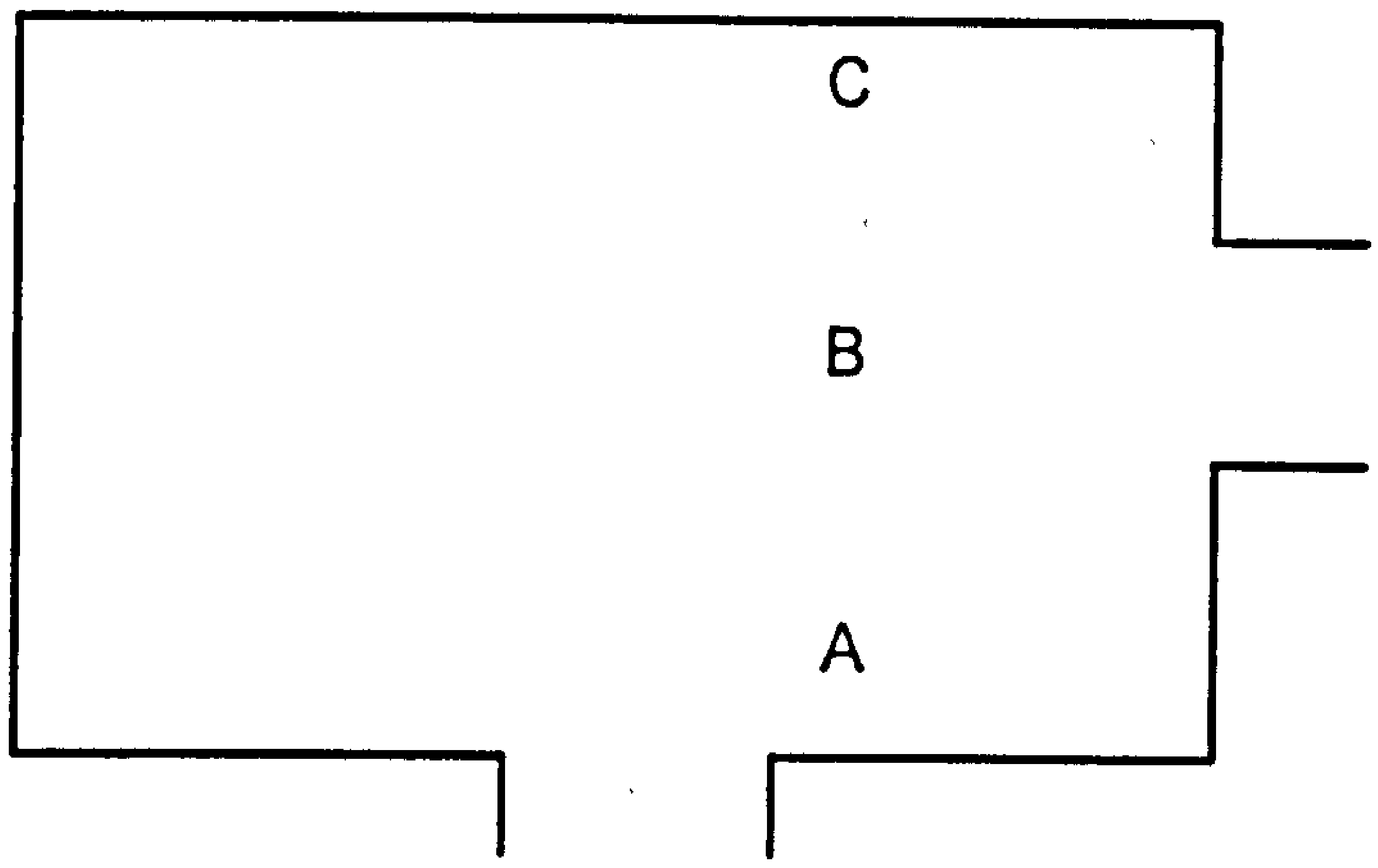

Fig 7.1 Schematic plan of Albert Dock showing the approximate positions of the sites used for studying the spatial variation of zooplankton

stations were situated beside the east and west walls of the dock and one in the centre of the dock (see Fig 7.1). In order to increase sample size a zooplankton net with a mouth diameter of 0.50m was used, rather than the normal 0.3m diameter used for horizontal tows. As before, the net had a mesh size of 250μm and three replicate hauls were taken.

7.3 RESULTS

The general trend in the densities of zooplankton found in all three docks studied was one of much greater abundance in 1992 than in 1993. This was particularly true for the obligate planktonic grazers such as *Acartia* and *Eurytemora* and the more common larval species, such as barnacle nauplii (see Fig 7.5, 7.8a-c). Princes Dock did show a number of differences from the pattern observed in the two South Docks under investigation.

The comparison between species composition in vertical and horizontal zooplankton tows in Albert Dock during 1993 showed that broadly similar patterns of abundance were found with both methods (Figs 7.2 - 7.4). Some discrepancies were found however. In some samples numbers of cladocerans (Fig 7.2a), *Carcinus* zoea (Fig 7.3a) and *Botryllus* larvae (Fig 7.4c) were greater in horizontal than in vertical tows. Similarly numbers of copepods were greater in vertical tows in May 1993 (Fig 7.2b). Numbers of what was probably *Ciona* larvae were also generally higher in vertical tows (Fig 7.4b).

7.3.1 Temporal Changes

a) Zooplankton Grazers

The copepods found in the samples were predominantly the calanoid species *Eurytemora affinis*, although considerable numbers of the harpacticoid species *Tigriopus brevicornis*

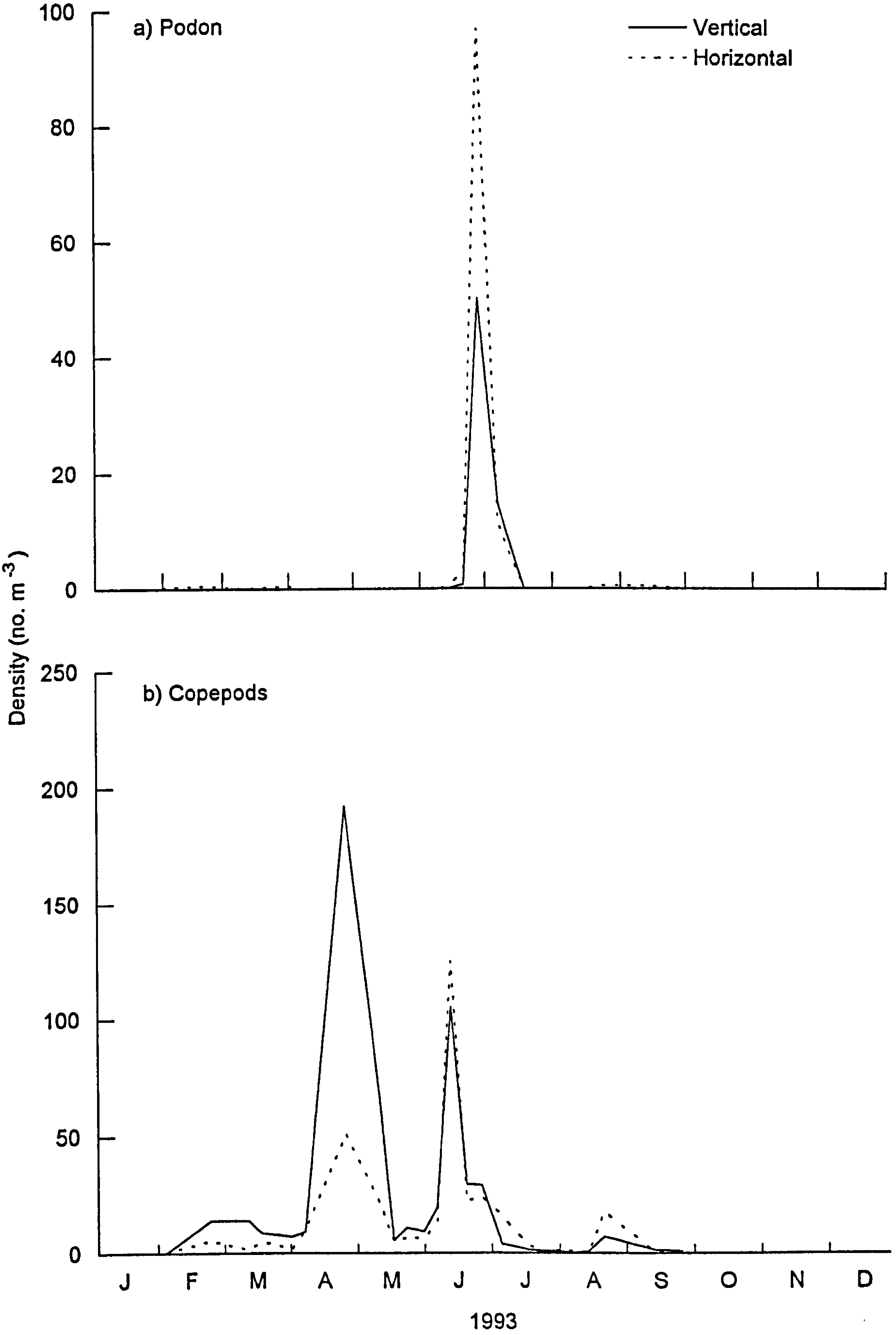

Fig 7.2 Comparison of zooplankton caught in horizontal and vertical hauls in Albert Dock during 1993

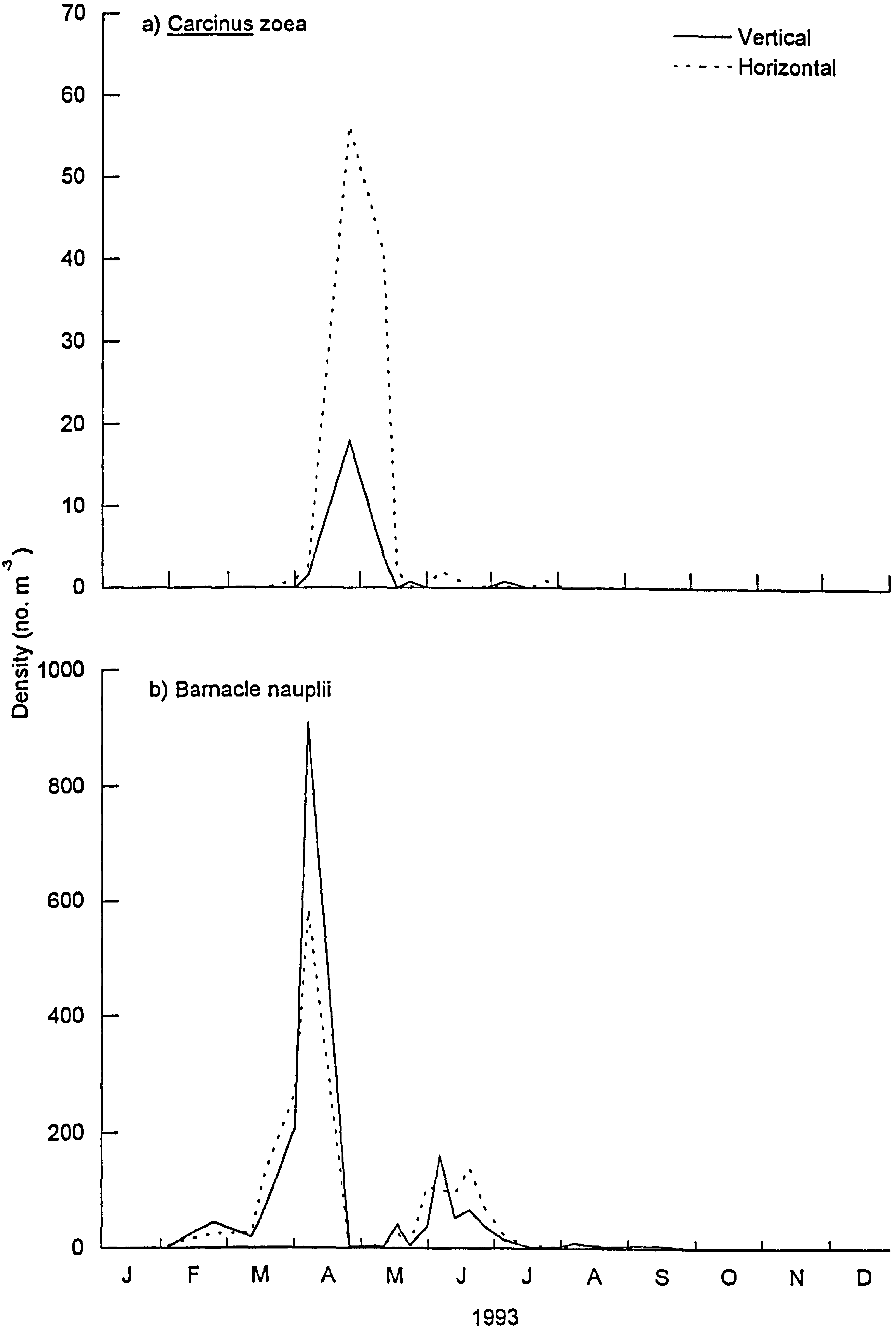

Fig 7.3 Comparison of zooplankton caught in horizontal and vertical hauls in Albert Dock during 1993

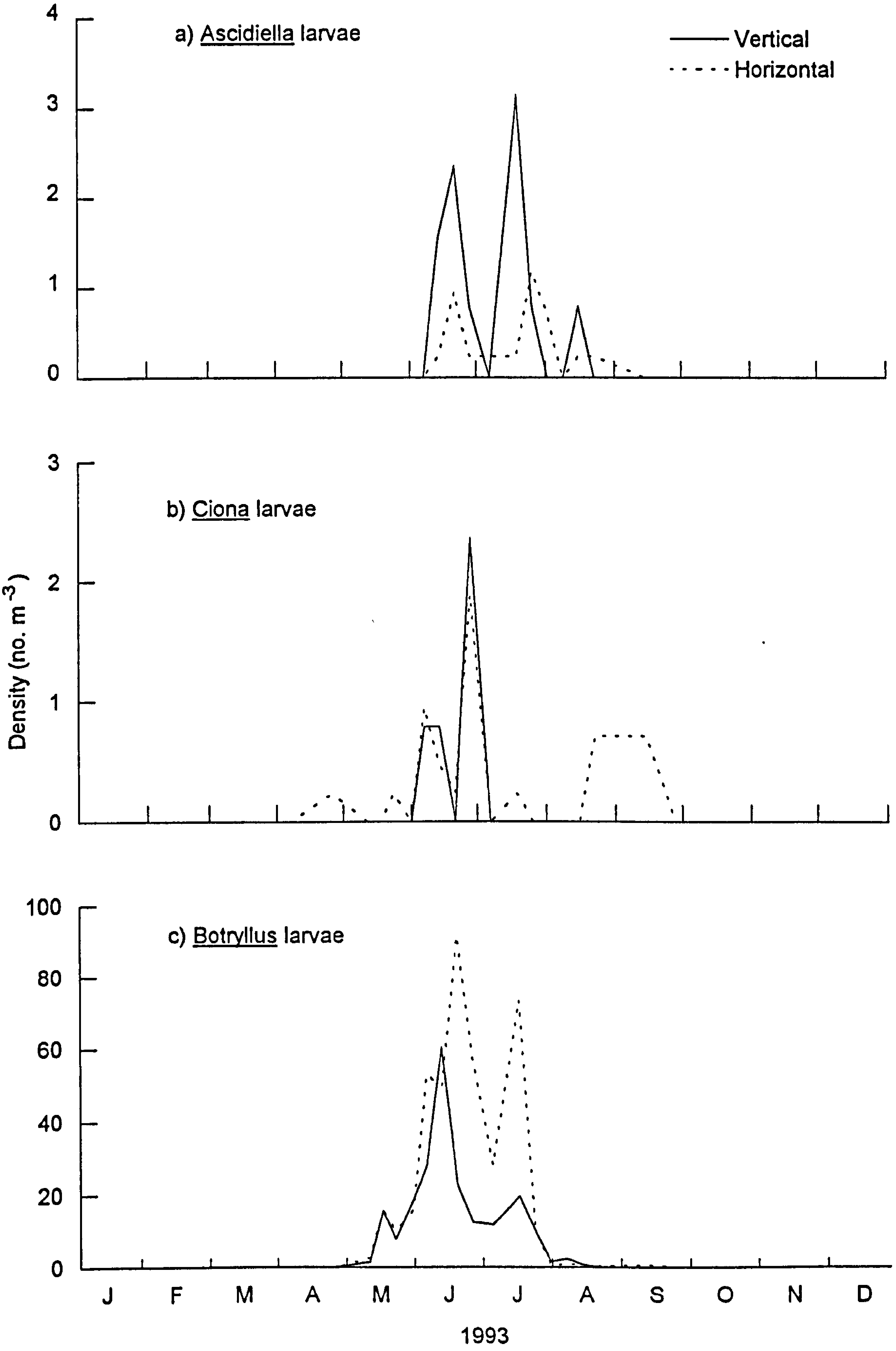

Fig 7.4 Comparison of zooplankton caught in horizontal and vertical hauls in Albert Dock during 1993

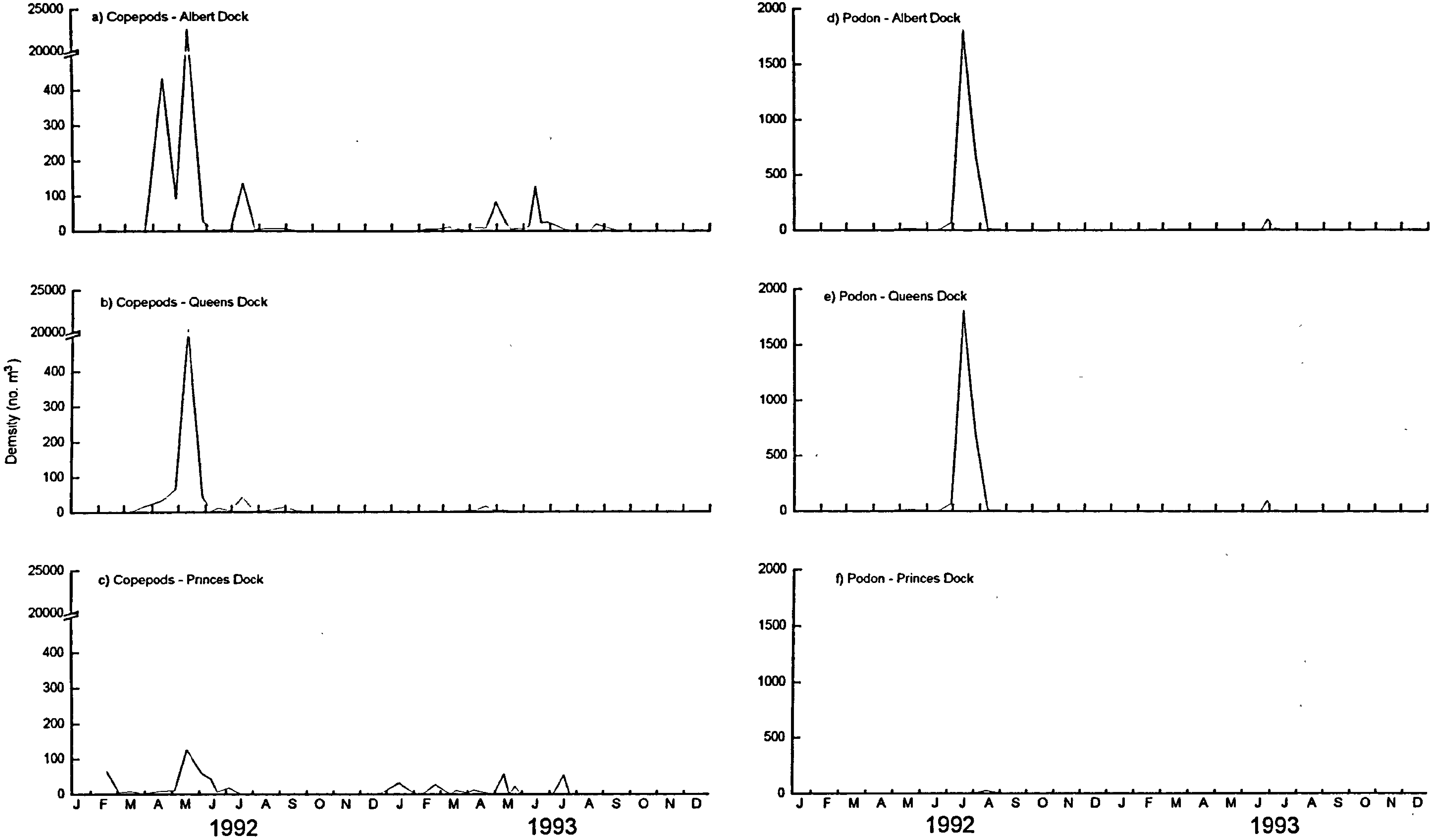

Fig 7.5 Variation in number of total copepods and podon in horizontal zooplankton hauls taken just below the water surface during 1992 and 1993

were also found on some occasions. One very large peak was found in numbers of copepods in both Albert and Queens Docks in May 1992 (Fig 7.5a,b). Princes also showed slightly higher levels at this time (Fig 7.5c). Generally, however, copepod densities remained less than 100 m^{-3}. A similar pattern was observed for *Podon* (Fig 7.5d-f). Again this species showed one very large peak in July 1992 in Albert and Queens Docks. Apart from this one occasion, however, numbers remained low and did not show any increase in Princes Dock at any time.

Figure 7.6 shows how the copepods were split between harpacticoid and calanoid species during 1993. No clear pattern emerges, except that calanoid species tended to be more abundant later in the year in Albert and Princes Docks. Densities of both groups of copepods in Queens Dock tended to be very low during 1993 (Fig 7.6b).

No attempt was made to assess the density of adult *Aurelia* in this study, as the net used was small and not really appropriate for the study of such a large species. However, juvenile *Aurelia* medusi were enumerated and this probably gives an index of the abundance of adult *Aurelia*. Numbers were generally much higher in Princes Dock, peaking in April in both the years studied (Fig 7.13d-f). Abundances peaked at a similar time in Albert and Queens Docks but numbers here were generally lower, except for those found in Queens Dock in 1993.

Shortly after the initial isolation of the South Docks the density of copepods and total zooplankton were very high (Fig 7.7a; data from Allen 1992). Densities during 1989 were much lower and have remained reasonably low since that time. There is a possible trend of increasing densities of copepods since 1992 (Fig 7.7b).

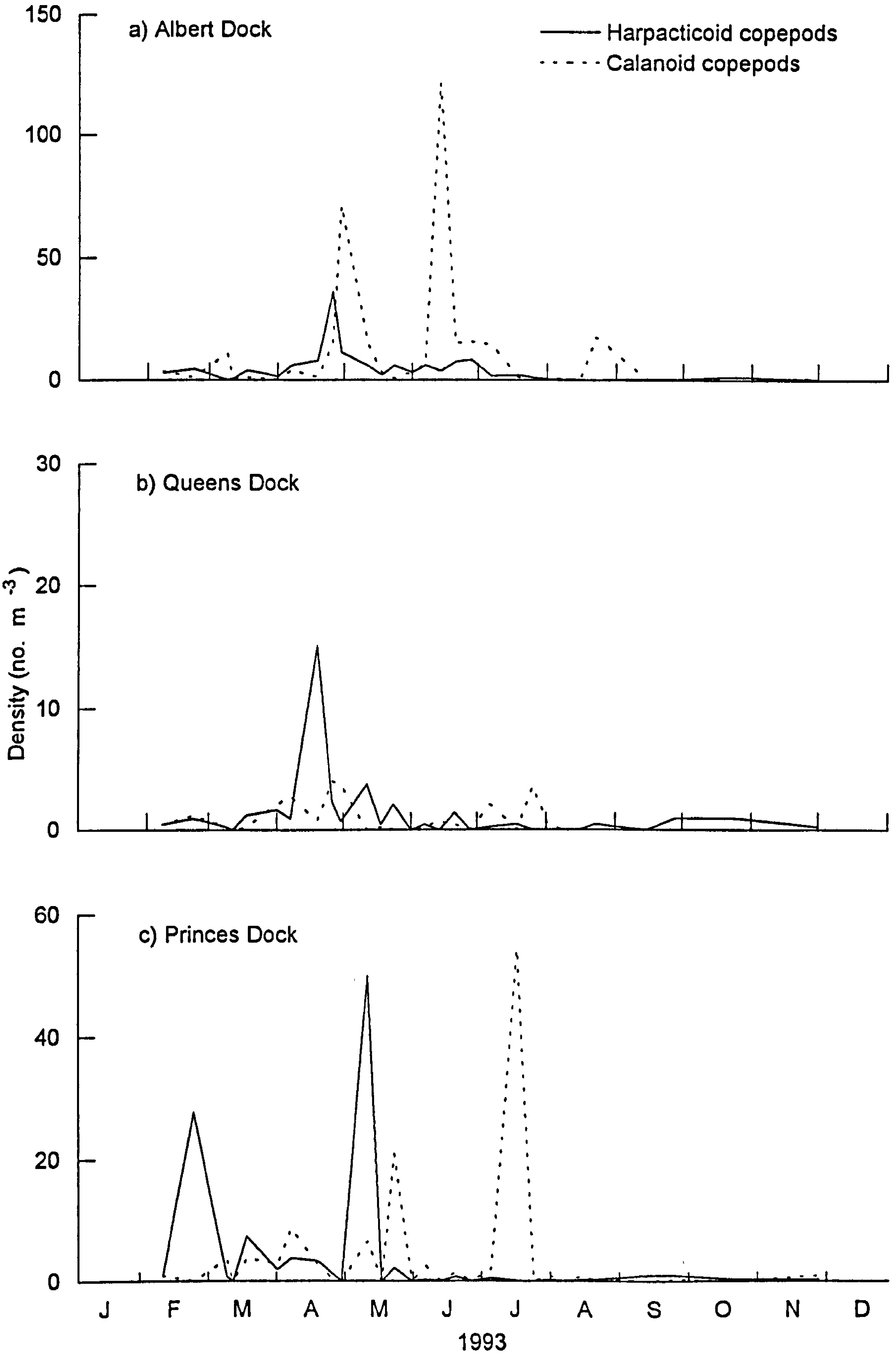

Fig 7.6 Graphs showing how the densities of copepods were split between harpacticoid and calanoid species during 1993. All results from horizontal tows taken just below the surface.

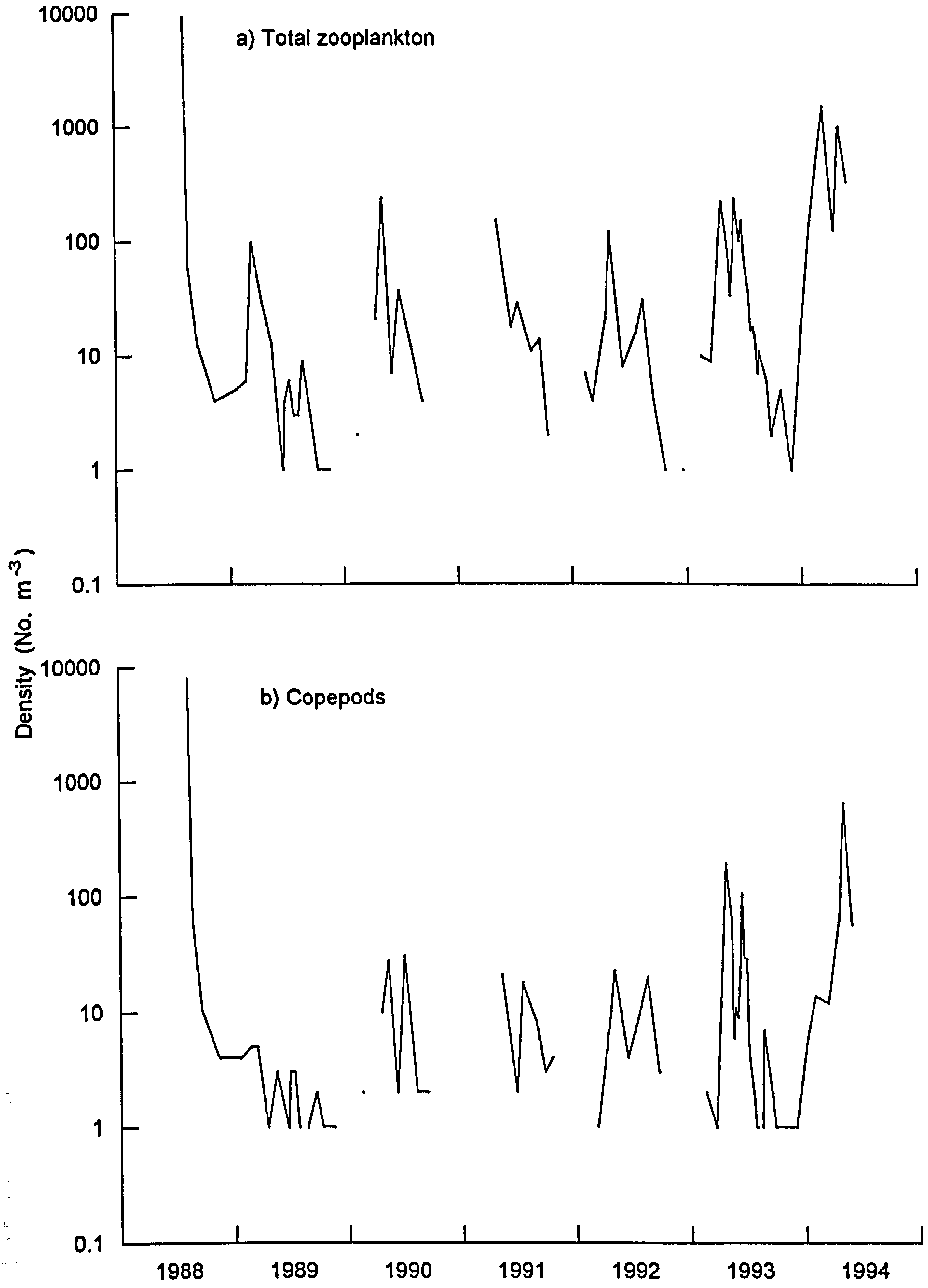

Fig 7.7 Changes in density of total zooplankton and copepods in vertical hauls taken in Albert Dock since 1988. Note log scale. Data 1988-1990 Allen (1992), 1991-1992 Zheng (1995), 1994 Fielding (unpubl.)

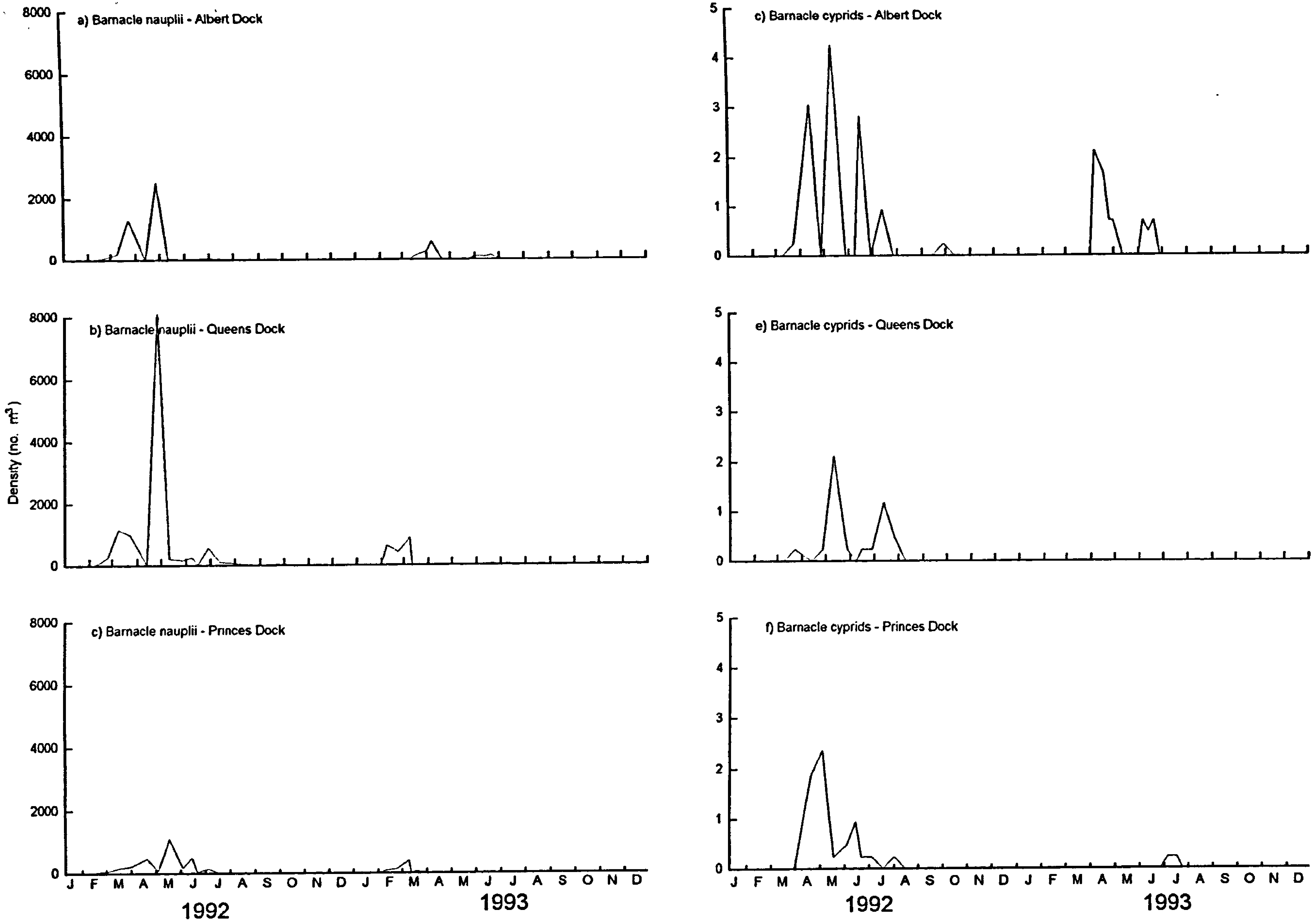

Fig 7.8 Variation in number of barnacle nauplii and cyprids in horizontal zooplankton hauls during 1992 and 1993.

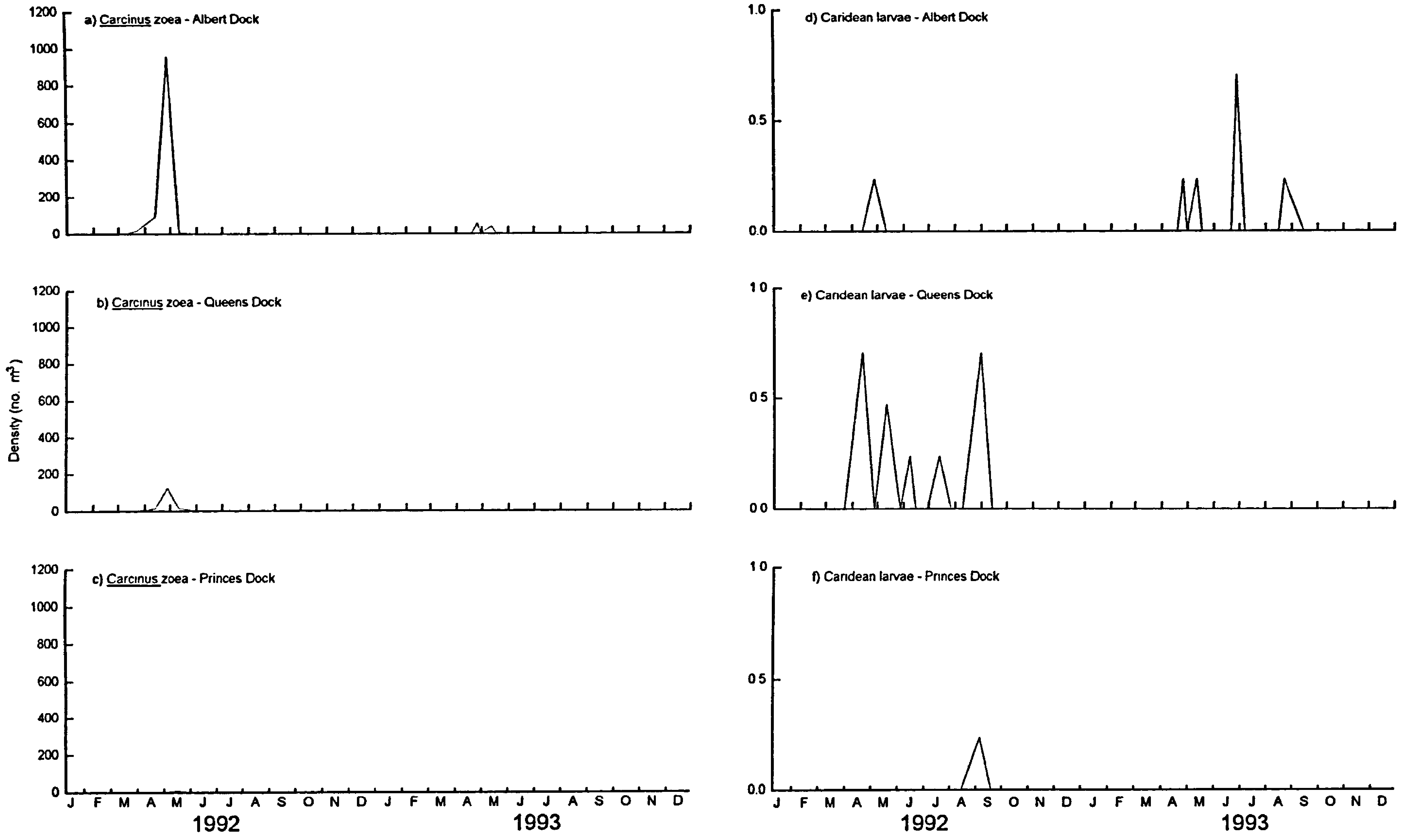

Fig 7.9 Variation in number of Carcinus zoea and caridean larvae in horizontal zooplankton hauls during 1992 and 1993.

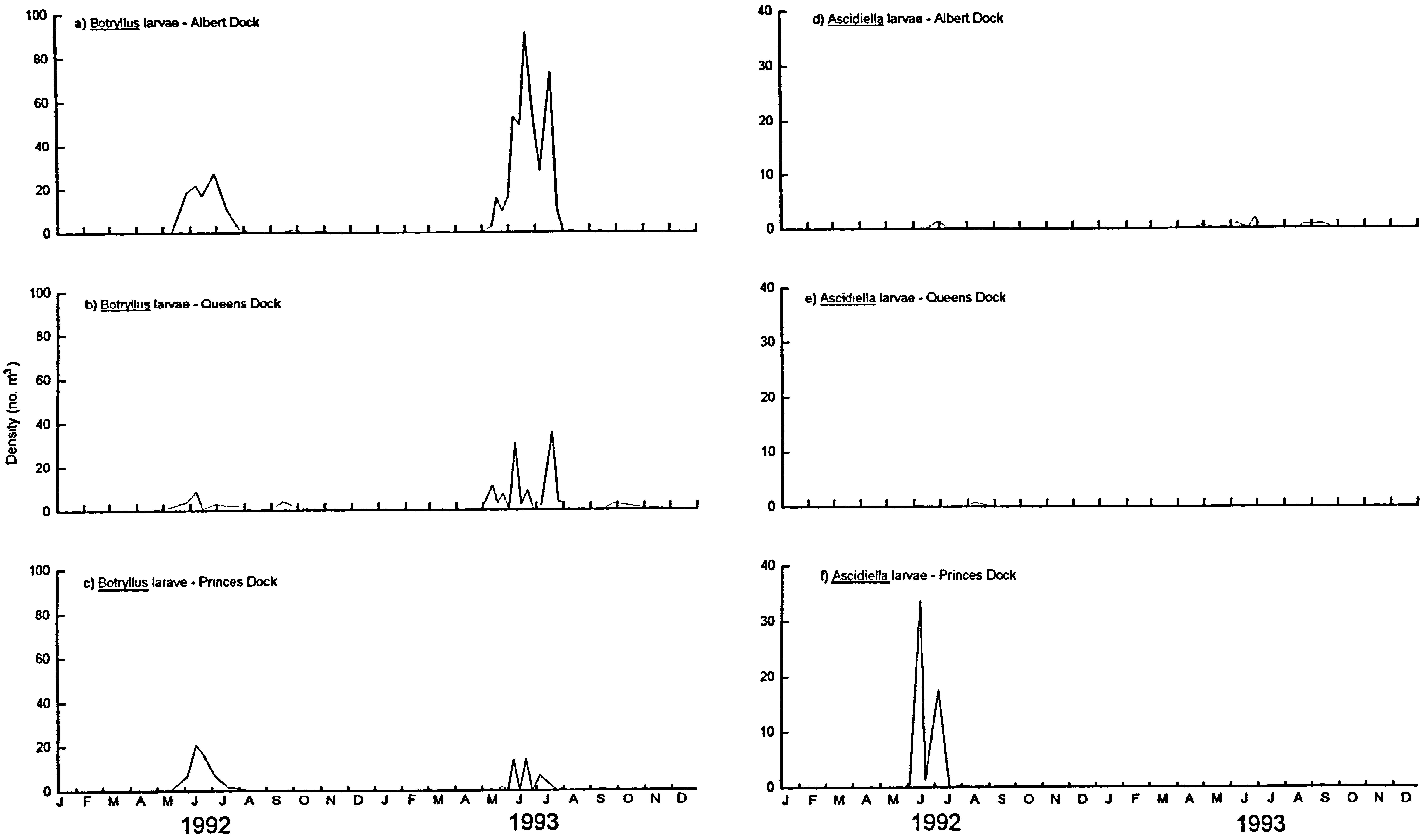

Fig 7.10 Variation in number of Botryllus and Ascidiella larvae in horizontal zooplankton hauls taken just below water surface during 1992 and 1993.

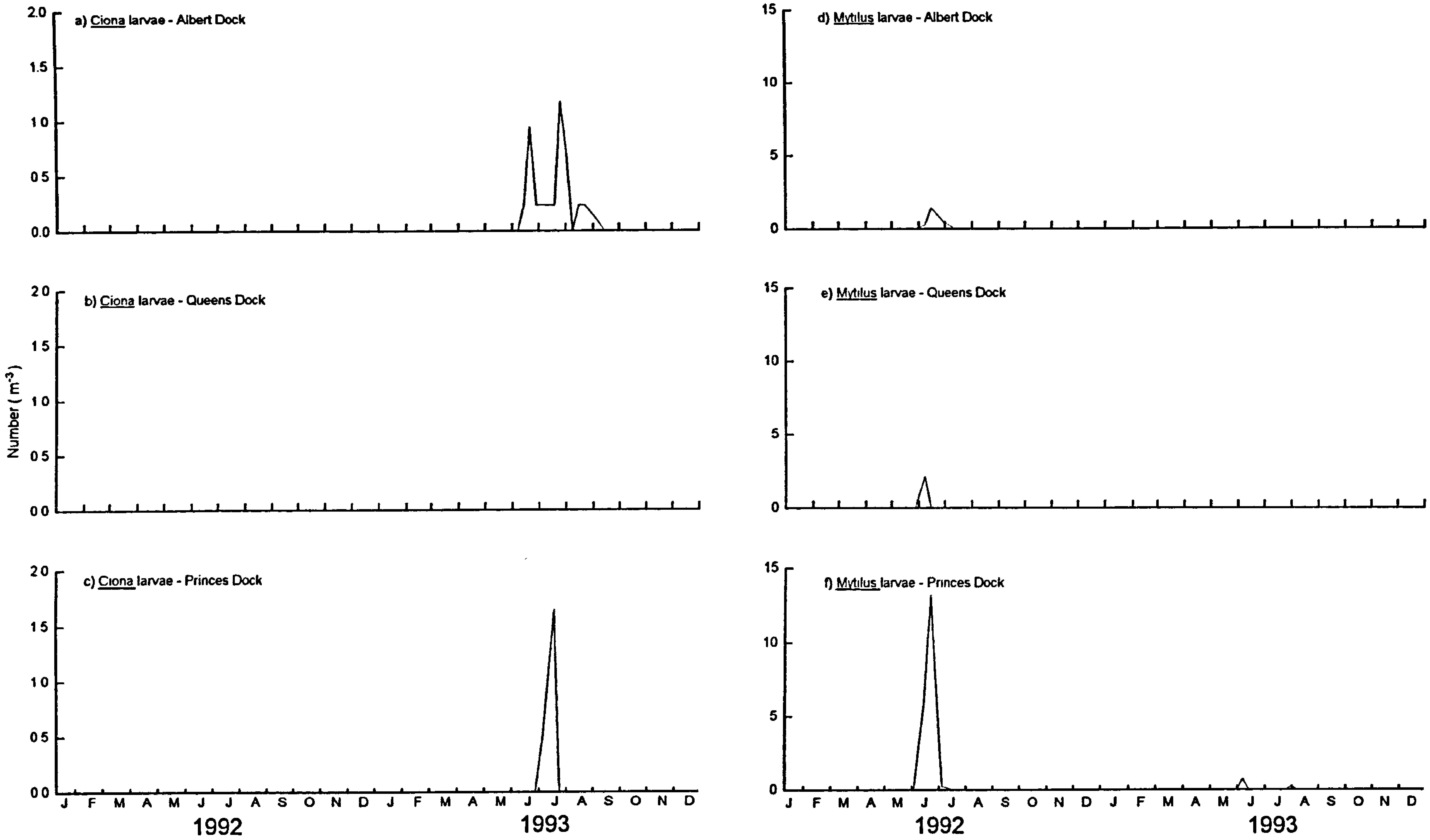

Fig 7.11 Variation in number of Ciona larvae and Mytilus larvae in horizontal zooplankton hauls during 1992 and 1993.

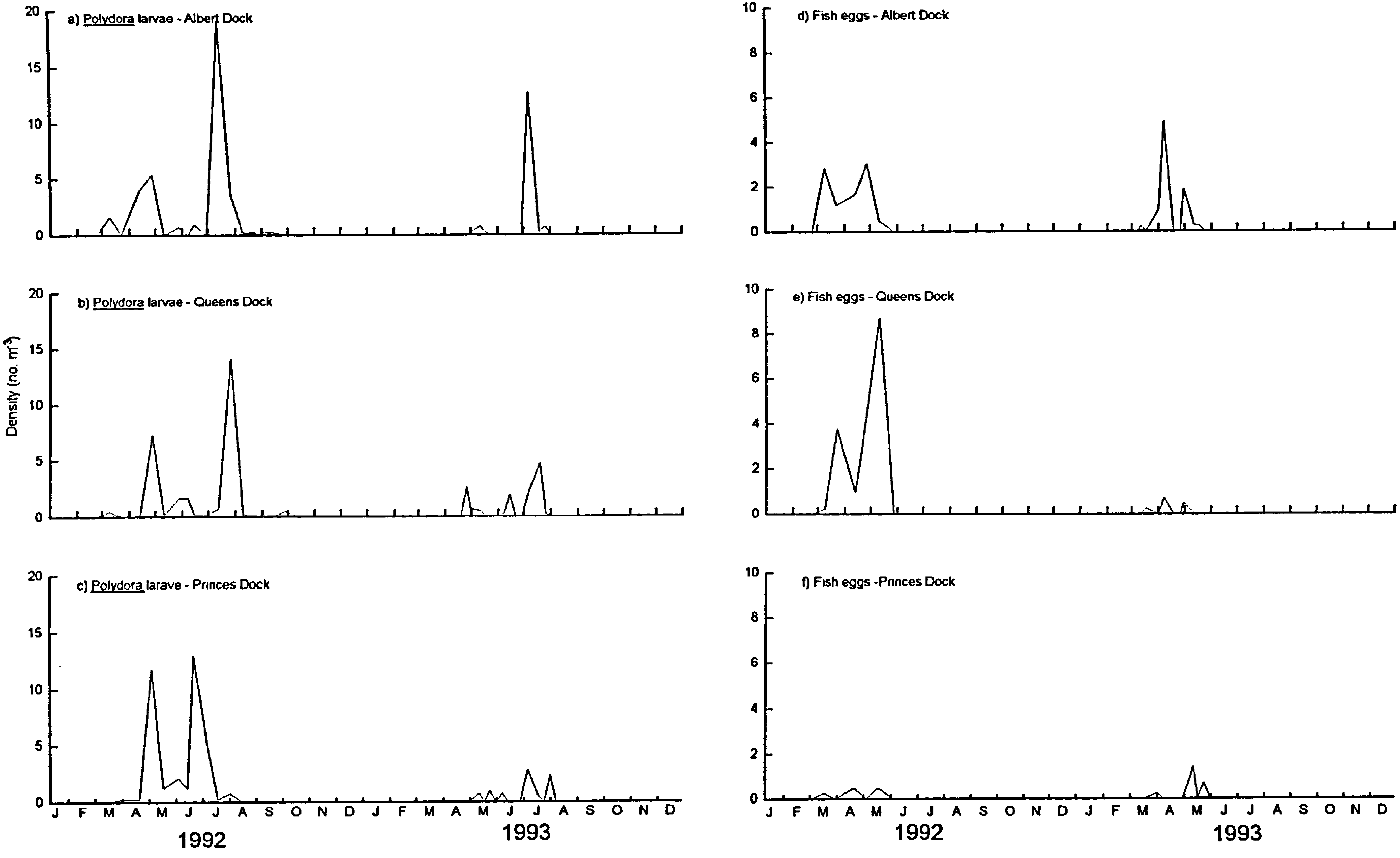

Fig 7.12 Variation in number of Polydora larvae and fish eggs in horizontal zooplankton hauls taken during 1992 and 1993.

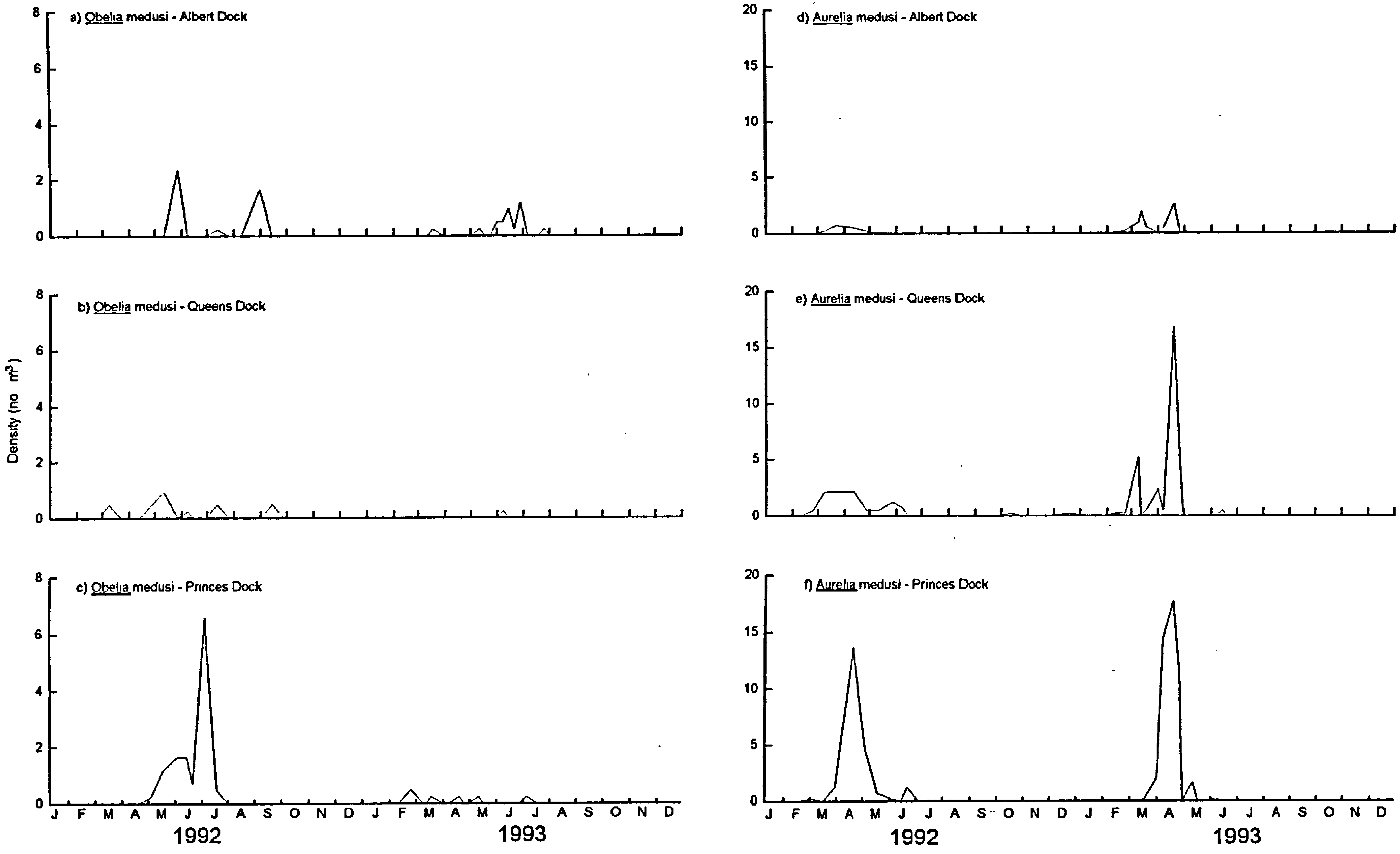

Fig 7.13 Variation in number of Obelia medusi and Aurelia medusi in horizontal zooplankton hauls taken during 1992 and 1993.

b) Larval Species

Barnacle nauplii dominated the meroplankton (Fig 7.8a-c). As mentioned above this group was much more abundant in 1992 than in 1993 in all three docks studied, with densities as high as 8000 m^{-3} recorded in Queens Dock in May 1992. It also appears that this group shows a number of peaks in abundance during the year and to a large extent these peaks occur at similar times in different docks (Fig 7.8a-c). A similar pattern of greater abundance in 1992 than 1993 was observed for barnacle cyprids (Fig 7.8d-f). Densities of this group were much lower however, and the relationship between barnacle nauplii and barnacle cyprids looks weak. In particular, despite relatively low numbers of nauplii in Albert Dock in 1993, quite high numbers of cyprids were recorded. The number of cyprids was only a very small proportion of the number of nauplii recorded.

Carcinus zoea showed one very large peak in Albert Dock in April 1992 and much smaller peaks in Queens and Princes Docks at the same time (Fig 7.9a-c). Densities in 1993 were much lower. The density of Caridean larvae was generally low though-out the study (Fig 7.9d-f), with numbers being generally higher in the South Docks than in Princes Dock, peaking in 1992 in Queens Dock and 1993 in Albert Dock.

Botryllus larvae, which could be identified with certainty, were the most abundant larvae of the tunicate species encountered (Fig 7.10a-c). Numbers of this group were greatest from May to July and were most abundant in Albert Dock, particularly in 1993. Numbers of what were thought to be *Ascidiella* larvae showed one large peak in Princes Dock in 1992 and very low densities in Albert Dock in 1993 (Fig 7.10d-f). *Ciona* larvae densities were highest during 1993 in Albert and Princes Docks (Fig 7.11a-c). Larval numbers of this species peaked in June-July at both sites. *Mytilus* larvae were infrequently recorded in zooplankton hauls during this study (Fig 7.11d-f). The highest number was recorded in Princes Dock during June 1992, with much lower numbers in Albert and Queens Docks at the same time. No *Mytilus* larvae were recorded in Albert and Queens Docks during 1993 and the numbers in Princes Dock during this year were much lower.

Polydora larvae also showed peaks in abundance during a single year and the timing of the peaks was broadly comparable between sites (Fig 7.12a-c). Numbers of this species were again greater in 1992 than in 1993 at all three sites. The abundance of fish eggs (unid.), was generally higher in the South Docks and particularly Albert Dock (Fig 7.12d-f). Again quite large variation was found between years, particularly in Queens Dock.

A number of relatively rare larval species showed no fixed pattern of abundance. Numbers of the medusal stage of *Obelia* remained low and unpredictable (Fig 7.13a-c). One large peak was observed in Princes Dock in July 1992 (Fig 7.13c).

7.3.2 Spatial Comparison

The spatial study of zooplankton in Albert Dock showed some quite marked patterns of abundance (Fig 7.14). A number of larval species, including barnacle nauplii and cyprids, *Carcinus* zoea and juvenile *Aurelia* medusae were more abundant in the middle of the dock than closer to the dock walls (Fig 7.14a,b,c,g). Copepods on the other hand, particularly the benthic harpacticoid species, showed the opposite distribution, being more abundant close to the walls. There is also evidence that some species, particularly *Polydora* larvae and fish eggs, were more abundant at site 'C' (Fig 7.14d,h).

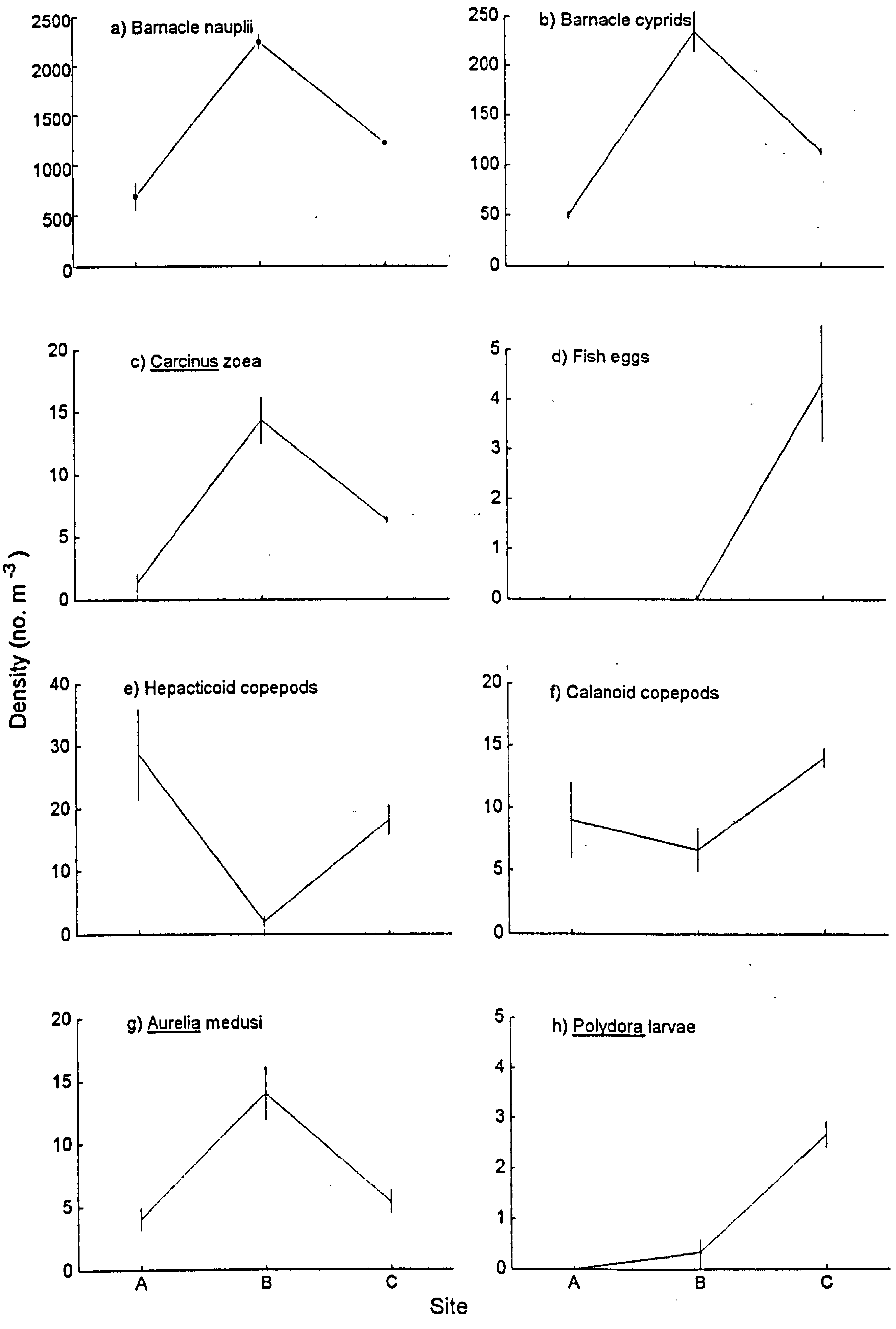

Fig 7.14 Differences in densities of zooplankton species at three sites in Albert Dock sampled in April 1993. See fig 7.1 for positions of sites. Error bars are standard errors of estimate, from three vertical hauls. Note differences in scale.

7.4 DISCUSSION

The results of this study really highlight the problems of predicting larval supply and show just how variable zooplankton densities can be. The docks are essentially a closed system with a relatively constant community structure. Despite this, however, differences were found in the density of almost all the species studied, over the range of spatial and temporal scales examined.

7.4.1 Vertical Distribution

There is evidence of vertical zonation of a number of the zooplankton species recorded (Fig 7.2 - 7.4). In the temporal section of this study (see below), horizontal tows were adopted as the main method used. This was because larval species were the primary interest and it was felt that vertical hauls would provide too small a sample to detect many of the rarer species. Vertical zonation of larvae in the water column has been recorded in a number of other studies (eg. Hurlbut 1991, Thiebaut *et al.* 1992, Gray 1993, Ropke 1993, Batty 1994, Raby *et al.* 1994, Marsden 1994). These studies have attributed the vertical distribution to variations in food supply (Raby *et al.* 1994), temperature (Thiebaut *et al.* 1992, Ropke 1993, Batty 1994) or hydrostatic pressure (Marsden 1994). The reason for the existence of vertical zonation patterns of larvae may reflect reduced competition for food or reduced predation levels (Gliwicz 1986, Foster & Harris 1989, Raby *et al.* 1993). Hurlbut (1991) considered the vertical distribution of larvae of the ascidian *Didemnum candidum* with regard to depth of settlement. While the distribution of the larvae did reflect the vertical distribution of settlement there was no evidence that the larvae were more likely to settle at any particular depth.

The reasons for the vertical distribution of larvae in this study are unclear. *Ascidiella* is known to have strong photonegative settlement tendancies and this may be reflected in the apparently greater abundance of the larvae of this species at depth (Fig 7.4a). A number of species tended to be more abundant in the horizontal tows than in the vertical ones such as Podon (Fig 7.2a), *Carcinus* zoea (Fig 7.3a) and *Botryllus* larvae (Fig 7.4c). It seems unlikely that predation pressure would be significantly reduced in the docks through vertical zonation of larvae though such behavioural responses may reflect conditions in the 'normal' environment of these species. It seems likely, however, that phytoplankton densities will be greatest close to the surface and larvae, such as *Carcinus* zoea, may simply be taking advantage of this. Further tests would be needed to confirm this. However, the fact that there is vertical zonation of zooplankton means that the results from the horizontal tows are of limited value for comparison with previous work which used vertical hauls (Allen 1992, Zheng 1995).

7.4.2 Temporal Variations

a) Water clarity

Unfortunately full details of the phytoplankton composition are not available for the entire period of this observation. Secchi extinction depths, however, give a rough indication of phytoplankton densities. A comparison of the Secchi Disc readings in 1992 and 1993 is displayed in Fig 7.14 for Albert, Queens and Princes Docks. The water in all three sites was much clearer in 1993 than in 1992, the difference being particularly obvious around April. The fact that this was observed at all three sites independently, provides strong evidence that weather conditions in 1992 were very favourable for the growth of phytoplankton.

b) Holoplankton

In the period just after the isolation of the South Docks

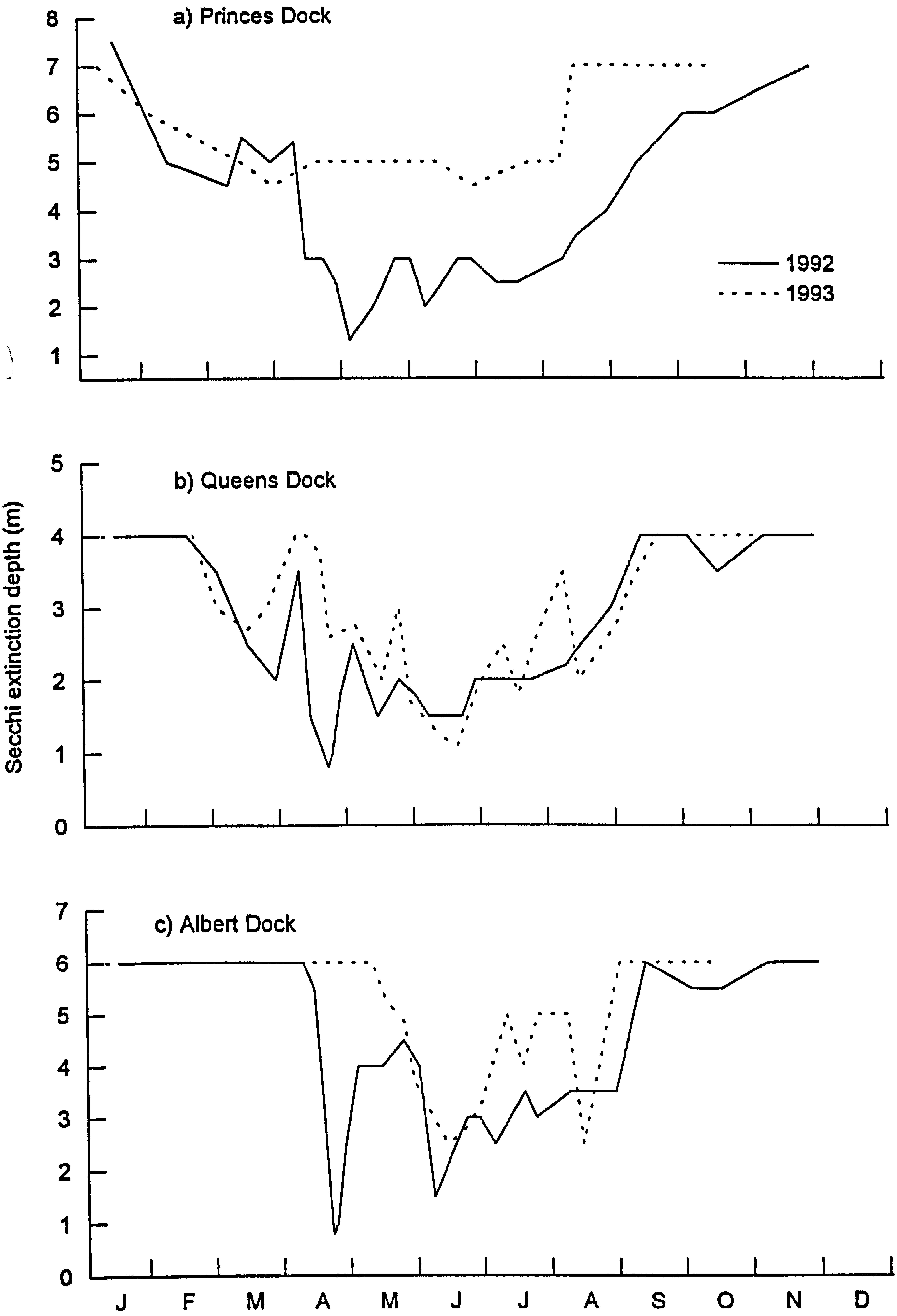

Fig 7.15 Comparison of secchi extinction depths in 1992 and 1993 in Princes, Queens and Albert Docks. Data for 1992 courtesy of Zheng (1995)

there were very dense blooms of phytoplankton and accompanying this a large zooplankton community. The changes that have been observed in total zooplankton densities since this time are summarised in Fig 7.7. Following the general improvement in water quality during 1989 there was a considerable decline in zooplankton density and since this time it has remained fairly constant. This decline may be a result of changes in the physical environment, increased competition for food or increased levels of predation.

Allen (1992) considered that changes in the physical environment were unlikely to be responsible. The increase in water clarity as a result of decreased phytoplankton abundance has been attributed to the dense filter feeding assemblage on the dock walls (Allen 1992, Allen *et al.* 1992, Allen & Hawkins 1993a&b). The reduced levels of phytoplankton may have resulted in the decrease in zooplankton, reflecting a switch from a pelagic to a benthic dominated system. Direct filtration of zooplankton by mussels may also have been partly responsible for the observed decline in zooplankton densities.

Grazing by copepods has been suggested as a means of controlling phytoplankton density (Shapiro & Wright 1984, Dorazio *et al.* 1987, Shapiro 1990). However, Olsson *et al.* (1992) showed that grazing effects were relatively small in their experimental marine system. The removal of predators of zooplankton has been shown to indirectly reduce phytoplankton abundance. Shapiro & Wright (1984) and Shapiro (1990) were able to achieve an improvement in water quality through the removal of planktivorous fish in freshwater systems. Similarly, in marine systems, increased densities of *Aurelia* which feeds on zooplankton, has been attributed to increases in algal abundance (Olsson *et al.* 1992, Lindahl & Hernroth 1983).

The higher densities of holoplanktonic species in 1992 compared with 1993 is almost certainly a result of higher phytoplankton levels in 1992. Juvenile *Aurelia* medusae did not follow this pattern. However the life cycle of *Aurelia* is more complicated than that of copepods or cladocerans as it involves both a pelagic and a benthic phase (see Barnes 1988). The adult *Aurelia* is pelagic and towards the end of the summer reproduces. The larvae settle in the form of a scyphistoma. The following year these produce pelagic medusae which develop into adults (Moller 1980). Therefore, densities of *Aurelia* are probably strongly dependent on how favourable conditions were the previous year, as well as present conditions. It is possible that the increased numbers in Queens Dock in 1993 were a result of the favourable conditions the previous year.

c) Larvae

Variation in larval supply has been attributed to a variety of factors including primary production (Glynn 1988, Bertness *et al.* 1991), larval behaviour (Hurlbut 1991, Thiebaut *et al.* 1992, Ropke 1993, Raby *et al.* 1994) and hydrodynamic forces (Foster 1975b, Grosberg 1982, Minchinton & Scheibling 1991). Variations in adult abundance and behaviour with regard to cues to spawn may also be important (Giese & Pearse 1974).

Considerable differences in a number of species of larvae were observed within docks between years (see Fig 7.8a,b, 7.9a, 7.10a,b,f). Such differences are unlikely to be caused by hydrodynamic forces or larval behaviour (but see spatial comparison below). It seems likely therefore that these changes are primarily a result of changes in the larval production. This may be mediated through either variation in the size of the adult population, changes in primary and therefore secondary production or the absence of the correct cues to induce spawning.

The higher levels of phytoplankton in 1992 probably also contributed to the higher densities of many larval species in this year. In particular barnacle nauplii, *Obelia* medusae, and *Polydora* larvae numbers were higher in 1992 than in 1993. For longer-lived species such as *Balanus* the increase in larval numbers was probably simply a result of higher food supply for the adults leading to the production of more gametes. Shorter lived species such as *Polydora* may have shown increases in population size.

Mytilus is an important species in the docks. Chapter 6 showed that recruitment of this species is limited and suggested a number of possible limiting factors (see Fig 6.10). Adequate supply of larvae was implicated as one of the more likely reasons for the lack of recruitment. This study of zooplankton revealed very low numbers of *Mytilus* larvae in any of the docks studied, despite very large *Mytilus* populations in Albert and Queens Docks. This adds weight to the idea that for some reason the production or survival of *Mytilus* larvae in the docks is limited in some way. It is also interesting that although a very heavy settlement of *Mytilus* occurred in Princes Dock in 1993, the number of *Mytilus* larvae detected in this year was actually lower than in 1992 when there was apparently little settlement. Therefore it seems likely that the external supply of larvae is very important, and that these individuals settle relatively quickly after arriving in the dock. Another possibility is that the net used is simply not suitable for the collection of *Mytilus* larvae. However, it is hard to equate this hypothesis with the presence of some larvae in the samples.

Number of *Botryllus* larvae showed the opposite pattern from most other species, generally being more abundant in 1993 than in 1992. This pattern is also reflected in the abundance of *Botryllus* on the dock walls. Abundance was generally greater in Albert Dock in 1993, compared with

1992, particularly as a secondary cover species growing on *Mytilus* (Fig 5.8). Similarly abundance was greater in Queens Dock in 1993 (see Fig 5.3, 5.9). No data are available for the abundance of *Botryllus* in Princes Dock during 1992.

The absence of a good identification key for solitary tunicate larvae was unfortunate, particularly because it is relatively easy to assess the density of the adult populations of these species. The other problem with sampling this group is that the larvae tend to have short lives, generally around one to two days (Herdman 1899, Berrill 1935). Some species also show diurnal patterns of release (Yamaguchi 1975, Svane & Young 1989, Hurlbut 1992). Variation on such fine temporal scales was not examined in this study although it may have been important. However, quite marked differences were found both within and between docks. In particular, the larvae thought to be of *Ascidiella* were most abundant in Princes Dock in 1992, while densities remained low in the other docks studied. Densities of the other unidentified tunicate larvae, probably *Ciona*, were much lower, despite quite a large population of this species. This may have been a reflection of the short larval life, so that large numbers of larvae are produced but densities remain low. Despite this, however, the densities of the larvae of *Ciona* were more abundant in 1993 than in 1992 in Albert Dock (Fig 7.11a), which is also the pattern observed in the population on the dock wall (Fig 5.1b). Further information is definitely required, both on the actual identity of the larvae concerned and on the time of release and length of life of larvae of these species. This information is probably most easily obtained from laboratory investigations.

It is unfortunate that for many of the larvae encountered there are little data on variation in the size of the respective adult population. This was due to problems of actually assessing numbers of species such as *Balanus* or *Polydora* from photographs. Many species were either too small or too cryptic to estimate densities. In addition, while the population size of *Mytilus* was easily assessed, larvae of this species were rare and it is therefore impossible to relate larval density to the size of the adult population. The problems of identifying the tunicate larvae also prevents any assessment of how important the size of the adult population is in controlling larval densities. *Obelia* colonies were most abundant in Queens Dock in 1992, but larval densities of this species did not show a considerably higher abundance in this dock at this time. In conclusion, the results of this study suggest a poor relationship between adult and larval densities. This may be a result of monitoring the larval densities at inappropriate scales.

It is worth bearing in mind that although this study seems to emphasise the importance of productivity on the supply of larvae other factors may also be important. In particular, before the successful production of larvae certain spawning cues must be present, if the release of gametes is to be coordinated. In the marine environment larval release is often correlated with tides (Paula 1989, Zimmerman & Felder 1991), though a causal relationship has been hard to prove (Giese & Pearse 1974). Tides are absent from the docks and this may present problems to some species trying to reproduce here. As mentioned in chapter 6 the relatively still nature of the water column in the docks may present problems to larger larvae with a prolonged pelagic phase. In these conditions such larvae may be susceptible to settling out.

7.4.3 Spatial Distribution

The comparison of the composition of the zooplankton at three sites in Albert Dock yielded results that have important implications for interpreting the temporal results. Copepods were more abundant close to the dock wall, while most of the larval species were found in greater abundance towards the centre of the dock. It is probable that copepods, particularly the benthic species tend stay close to the wall because they require some aspect of the wall habitat. Copepods have a varied diet, and can consume either phytoplankton, detritus, or in some cases benthic algae (Rieper-Kirchner *et al.* 1991, Milliou & Moraitou-Apostolopoulou 1991, Kleppel 1993). While phytoplankton densities are likely to be lower close to the wall, the latter two food sources are probably much more abundant. In addition, the *Mytilus* matrix may offer protection from predatory fish, though the risk of being consumed by benthic filter-feeders is obviously higher close to the wall. The larval species may have moved away from the wall, either to avoid the dense filter feeding assemblage or to benefit from the greater phytoplankton densities to be found in the centre of the dock. A number of studies have shown the potential importance of filter-feeders removing larvae from the water column (Young & Gotelli 1988, Young & Chia 1987, Young 1990). With such a density of filter feeders on the dock walls, the reduction of larvae through predation may be an important source of mortality.

It is possible that currents could also be important in determining zooplankton distributions in the dock environment. In particular wind has been observed to have quite a strong influence on the distribution of *Aurelia*. This species is frequently observed in very high numbers in leeward areas of the docks following strong winds (pers. obs.). In the spatial comparison of Albert Dock, two groups, *Polydora* larvae and fish eggs, were found in greater numbers at site 'C'. This pattern may well have been the result of wind driven mixing.

7.4.4 Implications to 'supply-side ecology'

The main contribution of this study to the more general field of 'supply-side ecology' is that it stresses that the large fluctuations observed in larval numbers may be due to more than simply transport processes. Transport processes have been implicated as one of the major causes of interregional variation in the supply of larvae (Grosburg 1982, Roughgarden *et al.* 1987). While this study does not prove the importance of production it certainly looks very likely to be an important factor, at least within the environment of the docks. It is also important that the whole ecology of the ecosystem is taken into consideration. In particular the lifecycle of a species will have a strong influence on when increases in production will be reflected in increased larval densities. In summary it is not really enough to look at the effect of variations in the supply of larvae on a community. Rather we must now begin to assess which factors are most strongly influencing these variations in supply. Such studies must encompass all stages in the lifecycle, including population density, gamete production, fertilization as well as the fate of the larvae themselves. In normal marine systems such studies are further complicated by the problem of separating local supply and that from further afield. The docks provide an ideal habitat for exploring this area further.

7.4.5 Further research

The results presented here provide some tentative hypotheses on what the major influences are on the supply of larvae in the docks. The study has helped highlight a number of areas which should be considered in future studies of larval supply here. In particular it is recommended that zooplankton is sampled using vertical hauls, though using a net with 0.5m diameter mouth to keep the sample size large. In addition it is important to assess how much is being missed using a 250μm mesh net; it is possible that some of the smaller tunicate larvae may be passing through this mesh. More attention should also be concentrated on the spatial distribution of larvae in the docks and reasons for the patterns observed. However, the main advantage of the docks is that it is relatively easy to quantify the adult assemblage producing the larvae. Future studies should devote more attention to assessing the adult abundance of more cryptic species such as barnacles and polychaetes. In addition it would be very useful if the sexual condition of these species could be assessed at a number of points during the year.

CHAPTER 8

COMMUNITY DEVELOPMENT ON TILES IN ALBERT DOCK

8.1 INTRODUCTION

The concept of succession was first put forward by Clements (1916, in Clements 1928). He regarded it as a unidirectional process to, in the absence of disturbance, a fixed climax, where early species modified the environment making it less suitable for themselves but possibly more suitable for later colonists. This idea of so called 'classical succession' was also developed by Odum (1969). It is noteworthy that early studies (Clements 1928, Eglar 1954) concentrated on terrestrial forests and fields, where organisms have a longer term effect on the environment.

Marine fouling communities display some fundamental differences in that the organisms do not alter the substrate they occupy and there is no possibility of storing dormant seeds as in terrestrial systems (Sutherland & Karlson 1977). The concept of classical succession is flawed in that recurrent disturbance is an integral part of any ecosystem and this often prevents the local establishment of a climax community (Dayton 1971, Sousa 1979a,b, Pickett & White 1985, Petraitis *et al*. 1989). This has led to the redefinition of the concept of succession and this in turn has often led to confusion about exactly what is meant by the term. For the purpose of this chapter, succession is defined as the '(directed) changes in community composition in time in response to external changes or disturbance' (McCook 1994, see also Horn 1974, Connell & Slatyer 1977, Chalmer 1982).

Connell & Slatyer (1977) proposed three mechanisms by which succession can proceed. They suggested that early colonists may either encourage later arrivals (facilitation), discourage them (inhibition) or have no effect (tolerance). A great deal of work has been concentrated on testing for these possibilities and there is now ample evidence for their existence (Sousa 1979, Lubchenco 1982, 1983, Turner 1983a, Walker & Chapin 1986, Farrell 1991). Some workers have also examined the effect of consumers on succession with reference to these models (Lubchenco 1982, 1983, Janke 1990, Farrell 1991) There is now widespread acceptance that rather than discrete mechanisms these models represent extremes of a continuum (Connell *et al*. 1987, McCook 1994). More recently their use as an all encompassing model of succession has been questioned (Walker & Chapin 1987, McCook 1994). In effect, the models simply document the net competitive interactions and evolved adaptions between two species. While these may be important in the successional process they are not necessarily the ultimate mechanism (Walker & Chapin 1987, McCook 1994).

A number of other models have been suggested as explanations of succession (see McCook 1994 for review). In particular there is a growing body of evidence that life-histories may be the principal driving force (Noble & Slatyer 1980, Botkin 1981, Huston & Smith 1987, Walker & Chapin 1987, Underwood & Anderson 1994). The importance of life-histories was been recognised by earlier workers (eg. Odum 1969) but has only recently been invoked as the principal mechanism. This is despite the fact that species are often classified by successional timing according to life history traits (eg. Odum 1971). Some of the strongest evidence for the importance of life histories comes from the simulation models of Huston and Smith (1987) who were able to account for a variety of patterns of forest succession by simply altering relative growth rates, size and sapling establishment rates. These models have yet to be integrated into the community development observed in marine systems.

The majority of studies on succession in the marine environment have used tiles or other artificial substrates often deployed at different times of year (Scheer 1945, Sutherland 1974, 1978, 1981, Sutherland & Karlson 1977, Anger 1978, Keough 1983, 1984a, Turner & Todd 1993, Underwood & Anderson 1994). A number of others have followed changes on cleared areas of natural substrate (Dayton 1971, Osman 1977, Sousa 1979a, Vance 1988, Farrell 1989, 1991). Very few have attempted to corroborate results obtained by making clearances on the actual substrate (but see Svane 1988). This is despite the growing body of evidence that the type of substrate can have a strong affect on the community that develops (Svane 1988, McGuinness 1989, Richmond & Seed 1991). In addition few studies have even considered the composition of the resident community at all. Without such observations, an experiment with tiles becomes little more than a 'stamp collecting' exercise since what is observed on the tiles may bare no resemblance at all to what is happening within the community.

There is now a considerable amount of evidence that both larval supply and settlement play important roles in structuring benthic communities (Sutherland & Karlson 1977, Connell 1985, Roughgarden *et al.* 1987, Underwood & Fairweather 1989, Bertness *et al.* 1992). However, while a number of studies using tiles have recorded settlement rates none have documented the actual supply of larvae at the study site.

This chapter describes the pattern of community development on tiles placed in Albert Dock at different times of year. Rather than attempting to test the models proposed by Connell & Slatyer (1977), interest centres on whether the observed patterns can be explained through differing life-history strategies of the resident species. The results are integrated with data on larval availability from chapter 7. The comparability of the community development on the tiles with that on cleared areas of the dock wall is assessed.

Finally, an attempt is also made to test the effect of predators on the community that develops through the use of cages.

8.2 MATERIALS AND METHODS

The study was carried out along the north facing wall of Albert Dock, beginning in March 1993. Six frames were suspended at a depth of 2m under the pontoons along this wall. Each frame held thirty tiles in five rows of six. Tiles were made from black polypropylene plastic, cut into 0.12m X 0.12m squares, the surface of which was roughened with sandpaper grade 1.5. They were attached to the frames by a single brass bolt through the centre of the tile.

8.2.1 The relationship between larval supply and settlement density

In order to document variation in settlement density through the year, six temporary tiles, one attached to each frame, were deployed every two weeks. These were left in position for two weeks before being returned to the laboratory and replaced with fresh tiles. The tiles were examined using a dissecting microscope under a magnification of X20. Any settlers were identified and counted. The results were integrated with larval densities obtained from the vertical zooplankton hauls presented in chapter 7. The results were presented as time series graphs showing larval and settler densities.

8.2.2 The pattern of community development

A total of thirty tiles per frame were deployed in March 1993 in order to document the pattern of community development. Beginning in May one of the tiles from each frame was removed and returned to the laboratory every two weeks (see Table 8.1). No growth was observed on the tiles before this time. The percentage cover of each species was determined using a grid of 100 points placed over each tile and recorded the species present at each point. All material was then removed from the tile and sorted according to species. Solitary species were enumerated and all material was dried, keeping species separate, to constant mass at 70°C for 48 hours.

The results were presented as time series graphs showing the average mass of each species per tile. For solitary species the average number per tile and the mean weight of an individual were also calculated.

8.2.3 The effect that time of deployment has on community development

Due to limited space on the frames it was not possible to study the effect of time of deployment using the destructive sampling method described above. Six tiles, one per frame, were deployed roughly every two weeks between May and August 1993 (see Fig 8.1 and Table 8.1). These were photographed at intervals (see Fig 8.1 and Table 8.1) and the photographic slides produced were projected onto a screen and analysed as described in chapter 3. In April 1994 all these tiles were removed and returned to the laboratory where they were analysed as described in section 8.2.2.

Results were plotted both as mean mass of each species per tile, mean number per tile and mean mass of an individual of each species on tiles deployed at different times of year. The changes in percentage cover data, obtained from the photographic slides were also presented in a multivariate ordination diagram. Preliminary examination of the community data using detrended correspondence analysis (DCA) indicated relatively short gradient lengths of less than 2.5 standard deviation units. Therefore the linear technique of principal components analysis (PCA) was adopted. Percentage cover data were first root transformed and then analysed after centring by species, in other words PCA was undertaken on a covariance matrix. The analysis and production of biplots was carried out using the program 'CALIBRATE' (Juggins & ter Braak 1994).

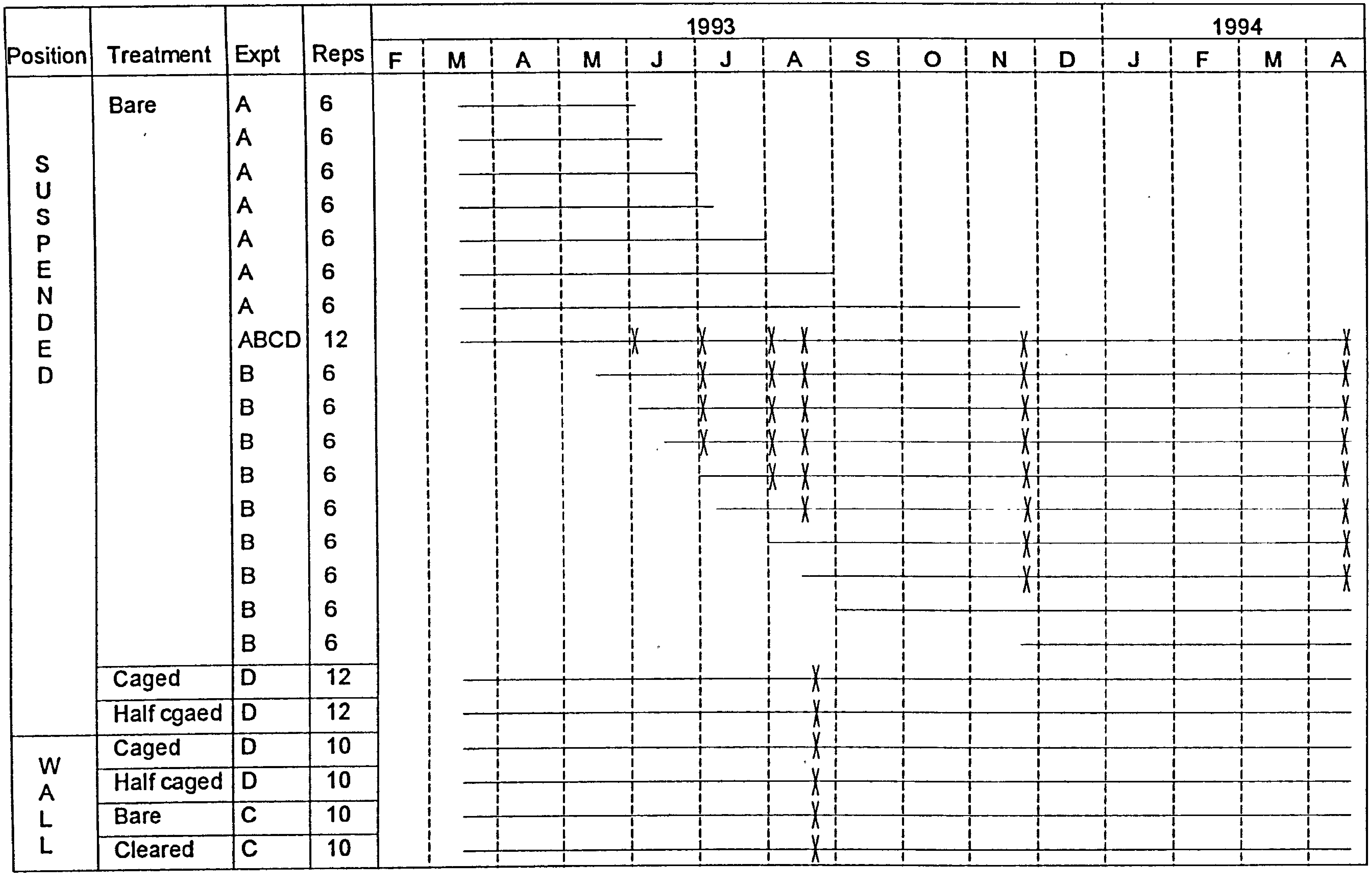

Fig 8.1 Summary of experiments carried out using tiles in Albert Dock during 1993 / 1994. The horizontal line indicates the period when the tiles were submerged. A cross on the line indicates when the treatment was photographed. See table 8.1 for further details of the experiments A to D.

Table 8.1 Summary of experiments being carried out using tiles in Albert Dock during 1993. Key to experiments listed in Fig 8.1.

Expt	Aim	Method
A	Describe pattern of succession	Tiles deployed in March and periodically 'harvested' during year
B	Effect of time of deployment on community that develops	Tiles deployed at various stages of the year and harvested the following March. Look at larval availability. Use temporary tiles to assess what is settling.
C	Comparison of community development on tiles with dock wall	Compare community development on suspended tiles, tiles attached to the wall and cleared areas of the wall.
D	Test effect of caging	Compare community that develops after 1 year on bare tiles, tiles in half cages and tiles completely caged.

8.2.4 Comparison of community development on suspended tiles, tiles fixed to the dock wall and cleared areas of the dock wall

In order to assess how typical results gained from tiles suspended in Albert Dock were of those that occur on the dock wall itself, a series of clearances were made on the dock wall. Ten areas, approximately 0.3m X 0.3m were cleared of *Mytilus* and an area at the centre of this patch, approximately the size of a tile was scrubbed bare using a wire brush. A further ten areas were also cleared and a tile fixed in the centre of each by a single brass screw through the centre, screwed into a hole that had previously been drilled in the dock wall.

The three treatments were sampled photographically on 2 August 1993 and the slides analysed as described in chapter 3. The percentage cover of each species was analysed across treatments using a one way ANOVA, following arcsin transformation (Zar 1984), using the program 'SAS'.

8.2.5 Effect of predation on the pattern of community development

Cages were used to exclude predators from tiles deployed in March 1993. Two randomly selected tiles on each frame were surrounded by a wire mesh cage 0.25m X 0.25m X 0.10m, with a $1cm^2$ mesh size. In order to test for any effects the cage itself had on community development two control cages, with two sides removed, were also fixed to the random positions on the frame. A similar experiment was set-up on the dock wall. For each tile, a small area of the wall, approximately 0.3m X 0.3m was cleared of *Mytilus*, as described above. A tile was then attached to the centre of this area. In addition to the ten bare tiles fixed to wall, ten completely caged and ten half caged (with two sides removed) were also attached. The three treatments were haphazardly arranged along the dock wall.

The treatments were photographically sampled on 2 August 1993 and the results analysed as described in section 8.2.4.

8.3 RESULTS

8.3.1 Larval supply

A relatively poor relationship was observed between barnacle cyprids and the number of settled barnacles on the temporary tiles (Fig 8.2). There were two main peaks in abundance of barnacle cyprids but settlement was only recorded following the second, smaller peak in June. No settlement on the tiles was recorded following the larger peak in cyprid densities in April, although settlement was definitely recorded on the wall at this time (pers. obs.). Quite good correspondence was also observed between the peaks in density of *Botryllus* and *Ciona* larvae and the heaviest settlement of these species (Fig 8.3). The relationship was not as good for *Ascidiella* (Fig 8.4a) but the higher density of larvae and settlers of this species was still during the same period of time. Similar results were obtained for *Obelia* (Fig 8.5). No bryozoan larvae were detected (Fig 8.4) and no effort was made to separate *Elminius* nauplii and cyprids from those of *Balanus*.

8.3.2 General pattern of community development

The tiles were initially deployed in February 1993 although they were disturbed a number of times during that month. By mid May a covering of diatoms and algae had developed. *Botryllus* was the first obvious faunal settler, settling in large numbers during June (Fig 8.7a). The abundance of this species was greatest towards the end of June when other larger solitary species, particularly *Ciona* and *Ascidiella* began to replace it (Fig 8.7c,e). Of these two species, *Ciona* was the more abundant both in terms of mass (Fig 8.7c) and number (Fig 8.6a). The density of *Mytilus* on the tiles remained low throughout the study (Fig 8.6c), but despite this, this species made a considerable contribution to the total mass present on the tiles by August (Fig 8.7g). *Ciona* and *Ascidiella* both peaked in abundance in mid

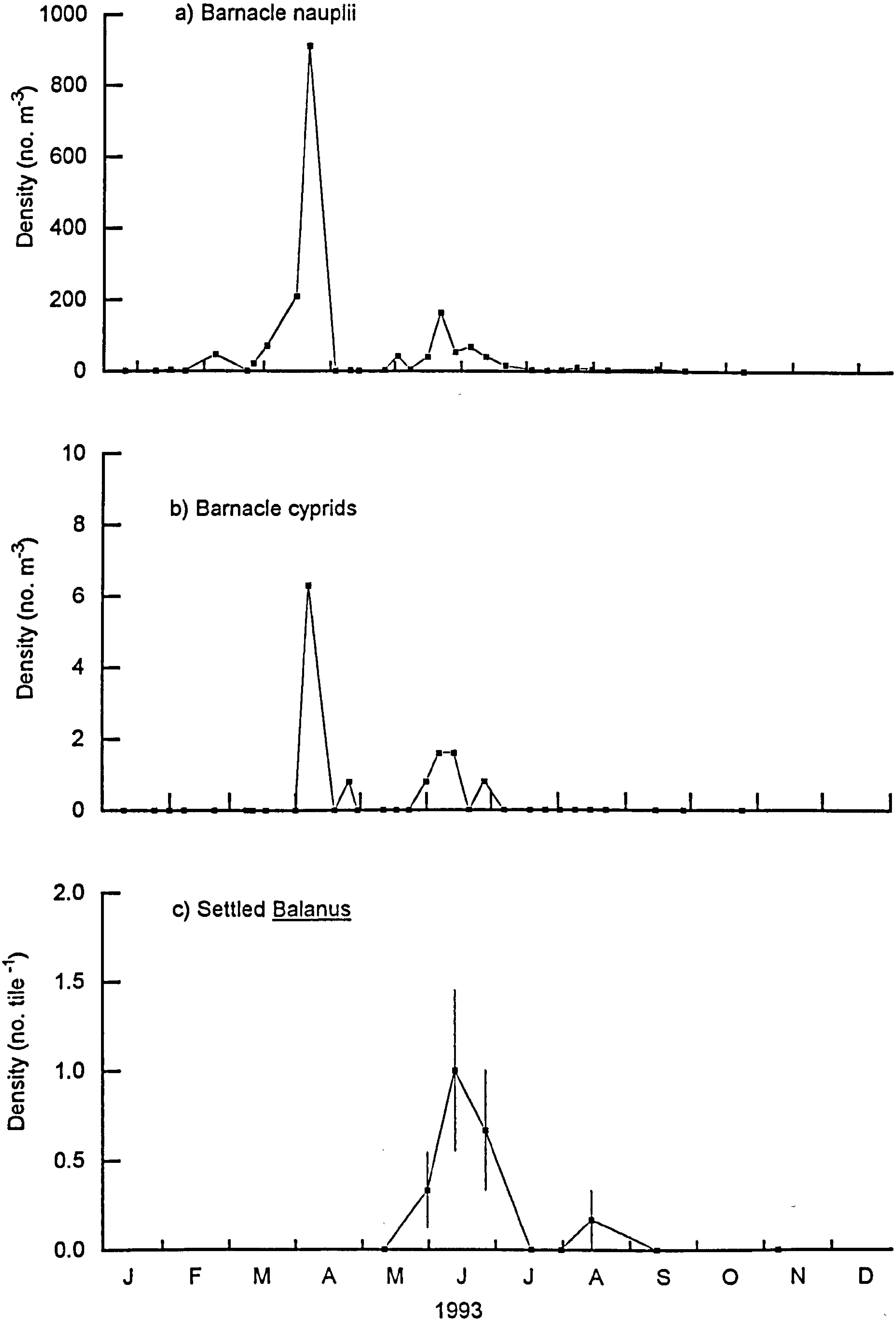

Fig 8.2 Variation in density of barnacle nauplii and cyprids in vertical zooplankton hauls and number of settled Balanus per tile in Albert Dock during 1993. Counts of settlers are from temporary tiles deployed for two week periods.

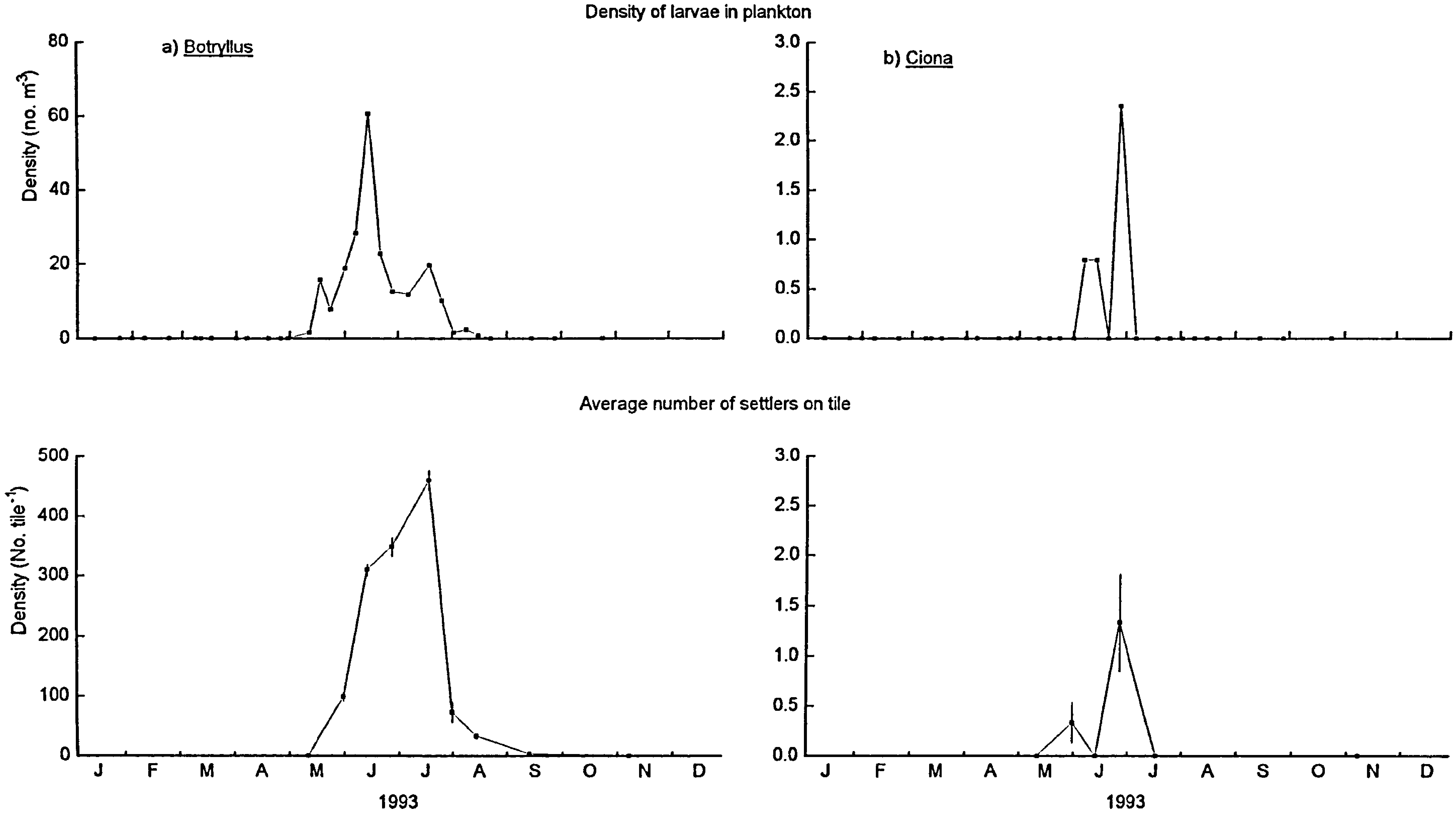

Fig 8.3 Variation in density of Botryllus and Ciona larvae and the density of settlers of these species on temporay tiles (deployed for two week periods) suspended in Albert Dock during 1993. Error bars represent standard errors.

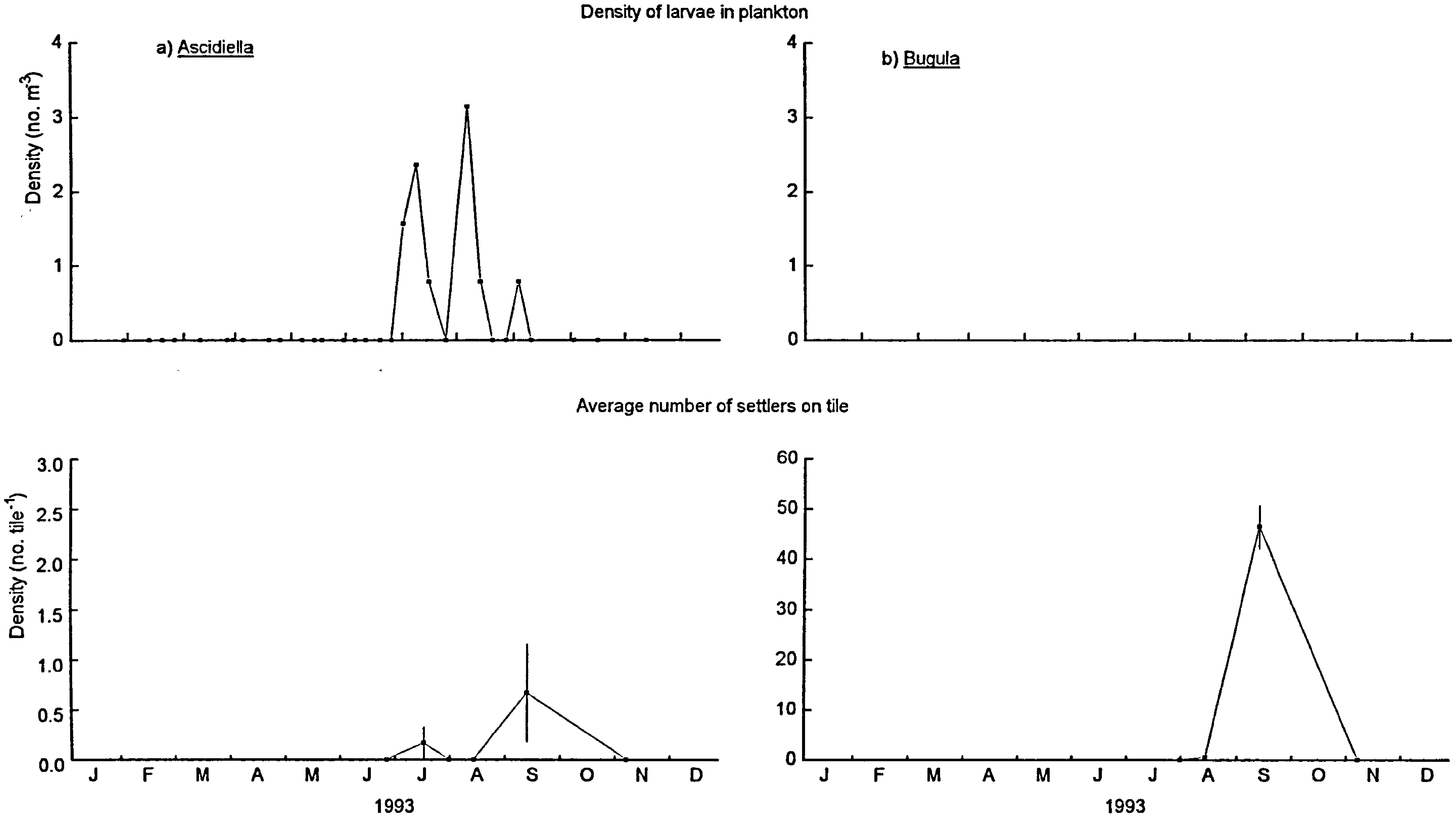

Fig 8.4 Variation in larval density and number of settlers of Ascidiella and Bugula on tiles deployed in Albert Dock. Tiles were deployed for two week periods. No bryozoan larvae were detected during this time. Error bars represent standard errors.

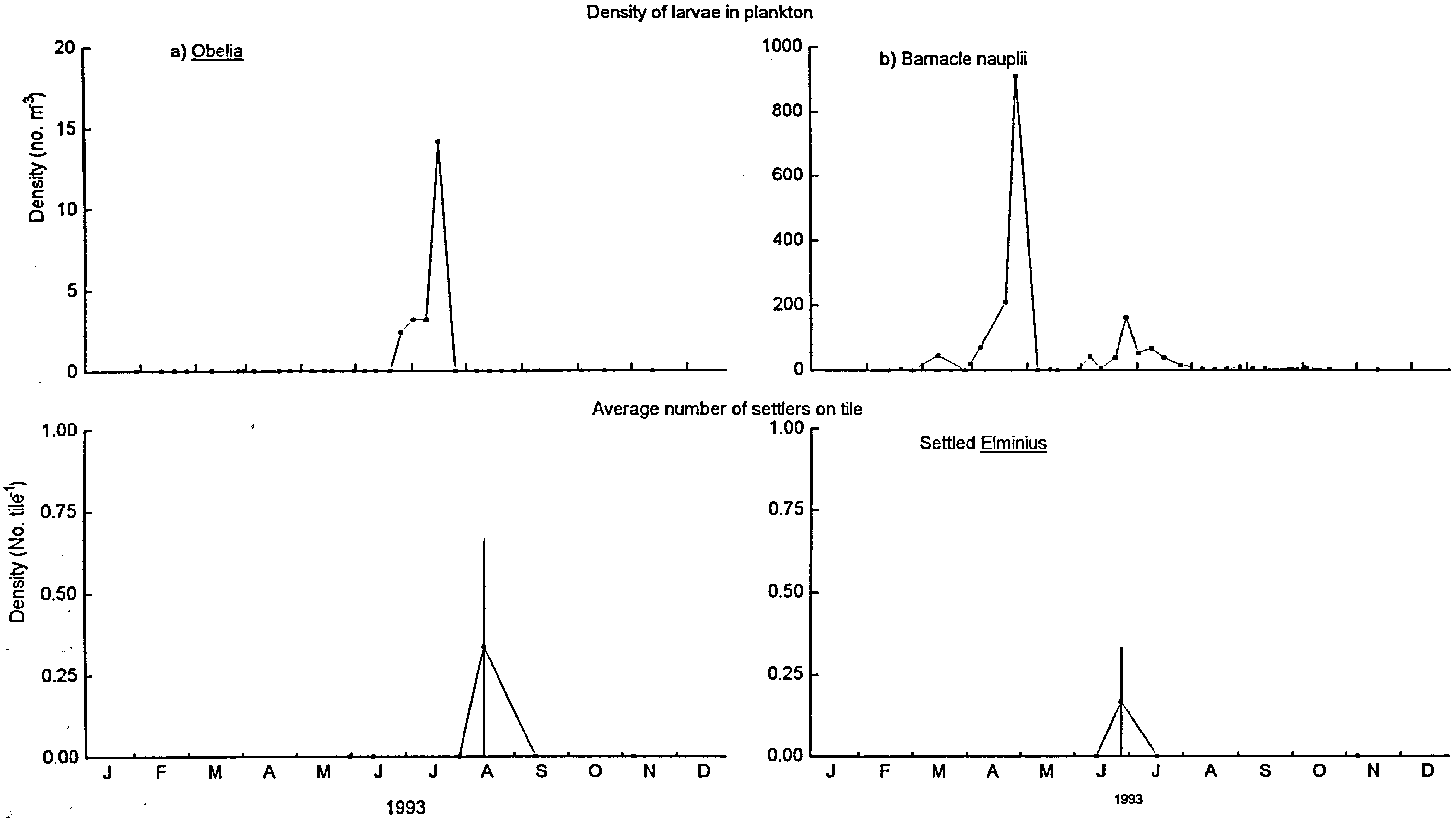

Fig 8.5 Variation of density of larvae in vertical zooplankton hauls and number of settlers on temporary tiles (deployed for two weeks) in Albert Dock during 1993. The numbers of barnacle nauplii include both Balanus and Elminius nauplii. Error bars represent standard errors.

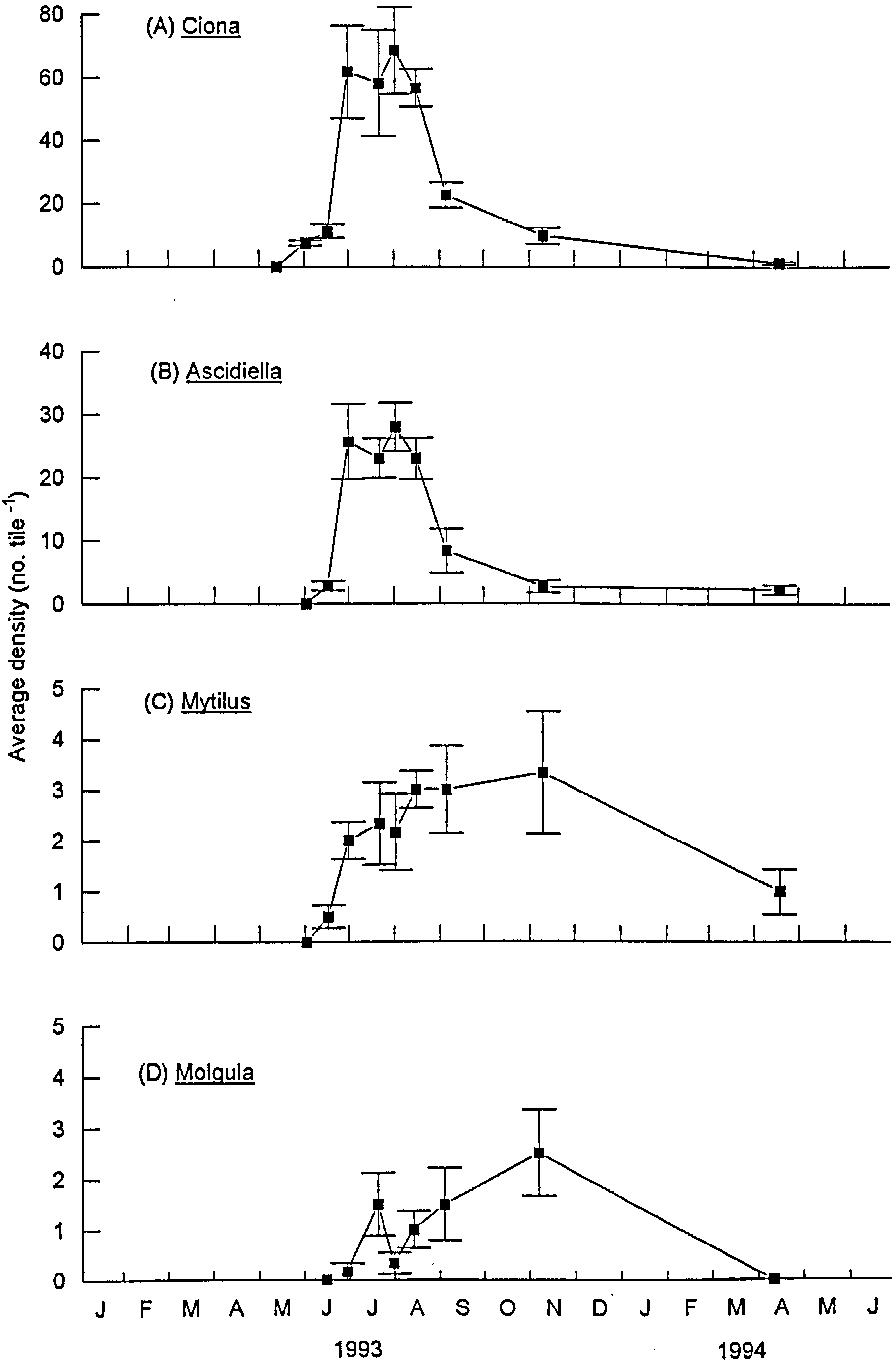

Fig 8.6 Variation in average number of most abundant solitary species on tiles placed at 2m depth in Albert Dock February 1993. All tiles deployed in February and six removed for analysis on each sampling occasion. Error bars represent standard errors.

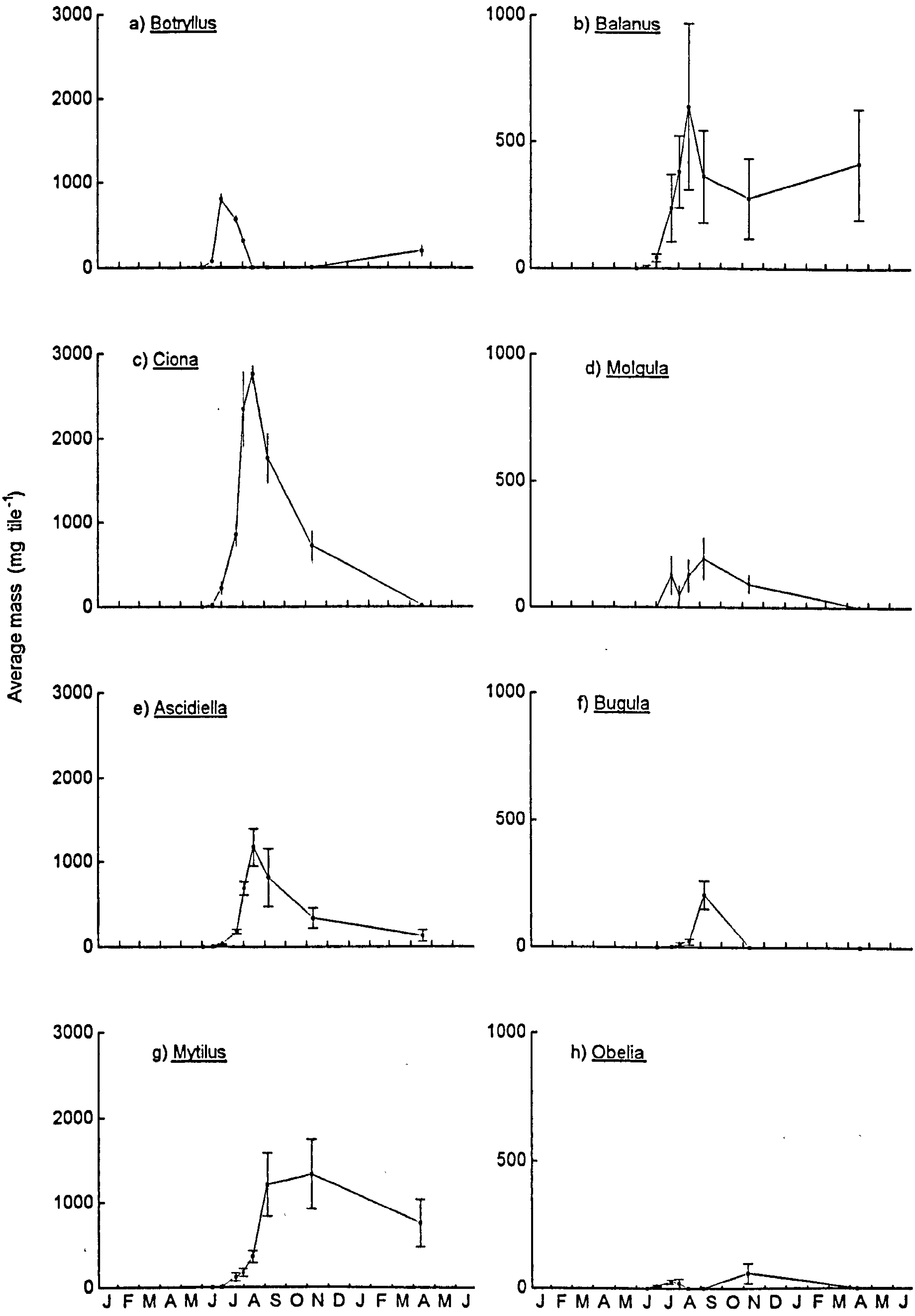

Fig 8.7 Variation in total mass of main species in fouling community on tiles deployed in Albert Dock at a depth of 2m. All tiles deployed in February 1993, then six removed and analysed on each sampling occasion. Error bars represent standard errors.

August and declined after this time (Fig 8.6a,b). By April 1994, just over a year from when the tiles were originally deployed, many species had declined and *Mytilus* made up most of the remaining biomass (Fig 8.7). A number of other less abundant species were also recorded on the tiles. *Molgula* showed a similar pattern of change to the other solitary tunicates, being most abundant in the late summer and autumn (Fig 8.7d). *Balanus* was another species that persisted on the tiles until the following April. This species also peaked in abundance in August and then declined before stabilising. The erect bryozoan, *Bugula*, only made a substantial contribution to the total biomass in the September sample (Fig 8.7f). The hydroid, *Obelia dichotoma*, was generally rare but most abundant in the November sample (Fig 8.7h).

Figure 8.8 shows how the average mass of an individual of the more abundant solitary species varies during the community development. *Mytilus* shows a relatively constant rate of increase over time and *Balanus* increases and then stabilises. The patterns of these two species differ from the tunicates which tend to show a peak in the average mass of an individual and then a decline, indicating that later in the successional sequence tunicates tend to be relatively smaller. From Fig 8.8b there is evidence that *Molgula* grows faster than *Ciona* and *Ascidiella* and attains the maximum individual weight before these species. There is also evidence that *Ciona* initially grows faster than *Ascidiella* but *Ascidiella* reaches a greater mean individual weight, later in the year.

8.3.3 Effect of time of deployment on pattern of succession

Figure 8.9 shows the effect of time of deployment on the observed sequence of colonisation of the more abundant species. There are a number of obvious similarities. *Botryllus* was generally an early successional species, although it did not always reach the same abundance before

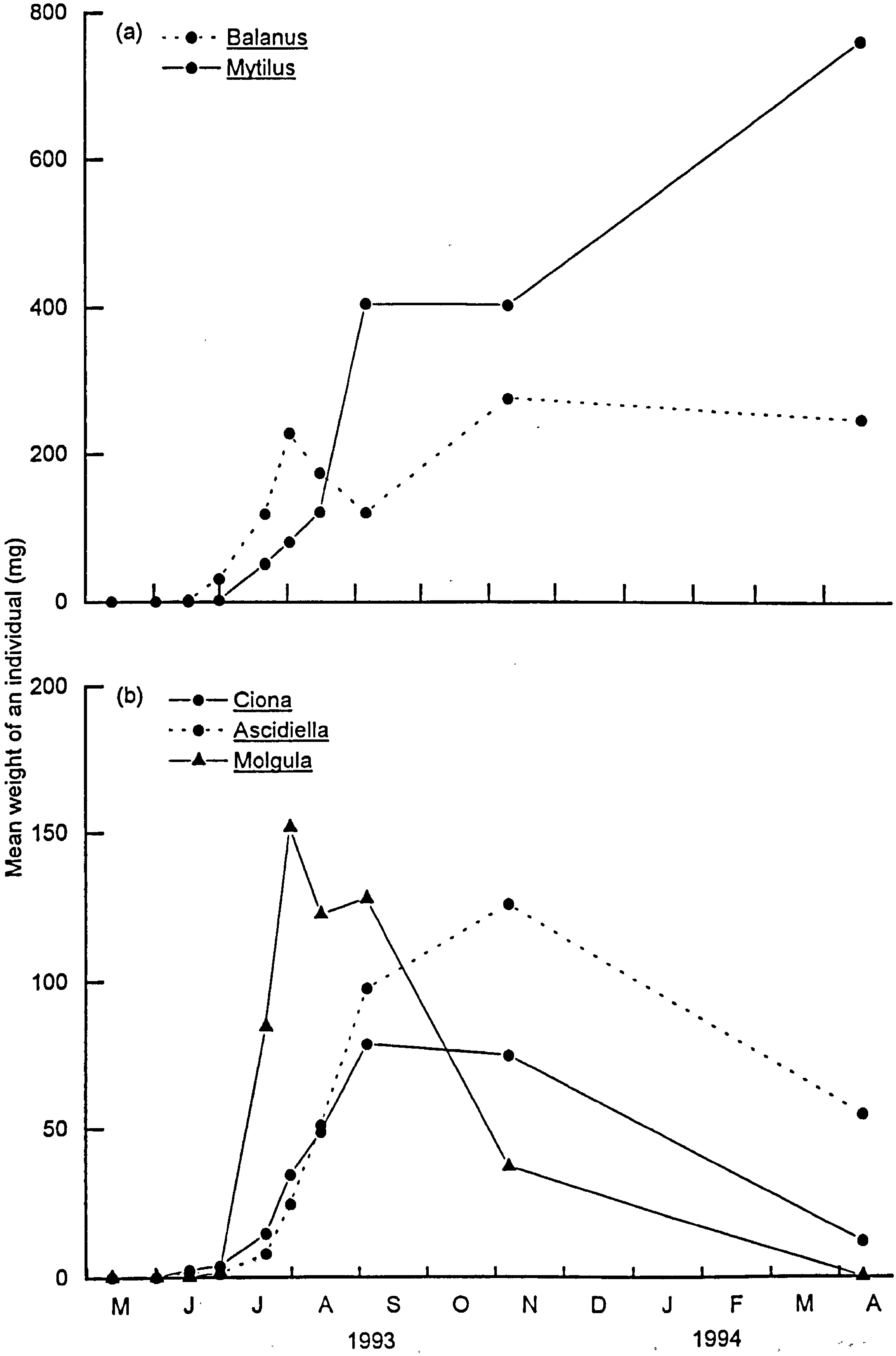

Fig 8.8 Variation in the average mass of an individual of (a) Balanus, Mytilus and (b) Ciona, Ascidiella, Molgula. Data are from tiles deployed in Albert Dock in March 1993 and havested at various times during the following year.

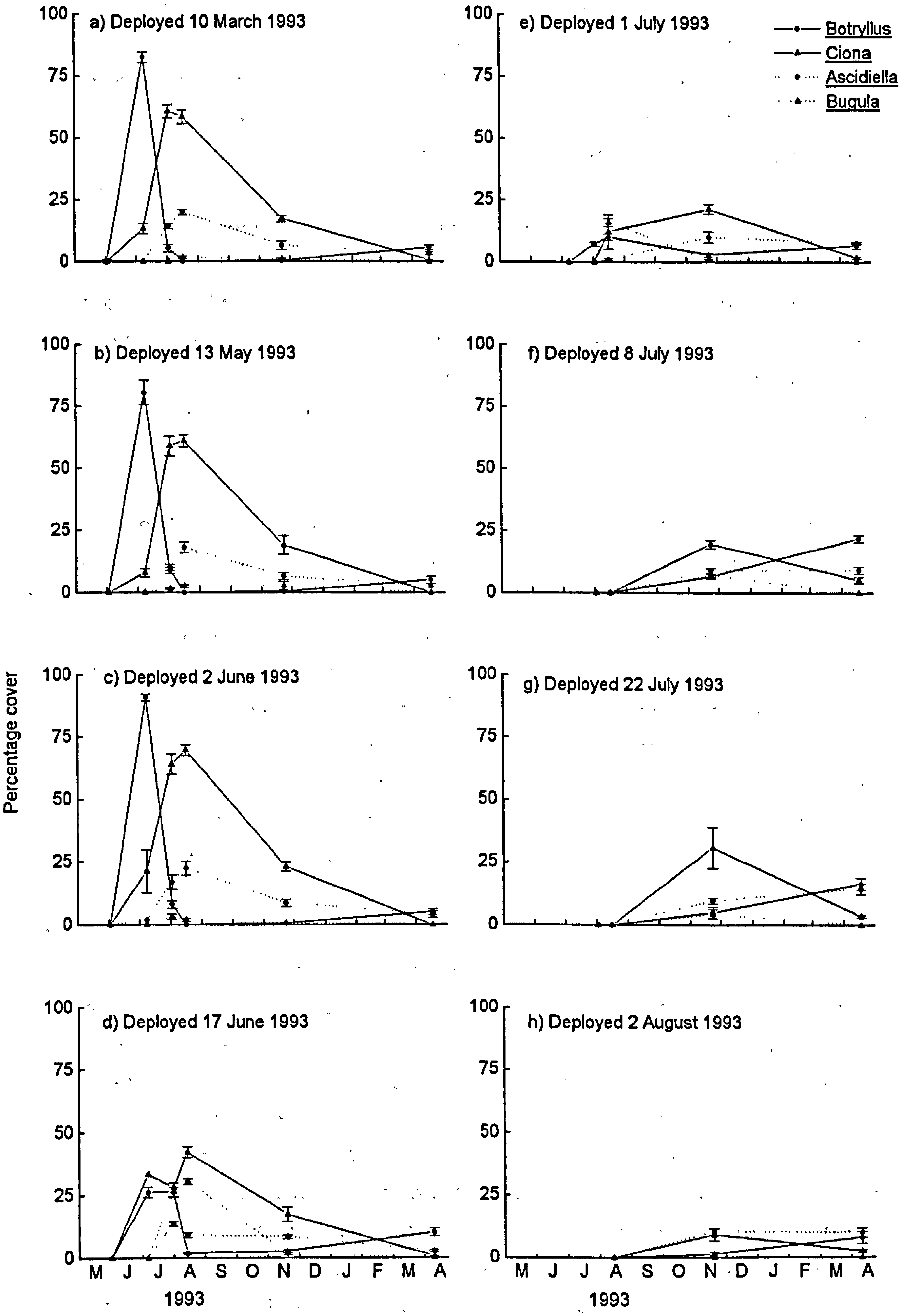

Fig 8.9 The effect of time of deployment on the pattern of community development. Six tiles were deployed on each date and photographically sampled to record community. Error bars are standard errors of estimate.

being replaced by other solitary species. By the April 1994 sample *Botryllus* was beginning to increase in abundance again. *Ciona* and *Ascidiella* always followed *Botryllus* in the successional sequence although again they were less abundant on tiles deployed later in the year. However, the erect bryozoan *Bugula*, was more abundant on tiles deployed in June than on any other treatment. By April, when all the tiles were removed and analysed, there was little difference in the community composition between treatments. In summary, irrespective of when the tiles were deployed the community composition at any time of the year was relatively similar. There is little evidence of either negative or positive interspecific interactions being involved.

The effect of time of deployment on the pattern of succession is also represented in a PCA ordination (Fig 8.10). Again there was no evidence that the pattern of community development followed the same path, regardless of the time of deployment. Rather, the composition of the community converged directly onto the composition of the community at that time of year. The strongly seasonal nature of many of the species found means that the community found on the tiles at the end of a year was very similar to the initial bare tile.

The variation in final mass of each species, on tiles deployed at different times of year is shown in Fig 8.11. Tiles deployed earlier in the year tended to be dominated by longer-lived species such as *Mytilus* and *Balanus*. *Styela* was most abundant on tiles deployed in June, *Ciona* on those deployed in July and *Molgula* on tiles placed in the dock in August. *Botryllus* and *Ascidiella* showed no obvious pattern. Figure 8.12 presents data on how the total mass is divided between the number of each species present. The longer-lived species, such as *Mytilus* and *Balanus*, tend to have a higher individual mass but lower density on tiles deployed

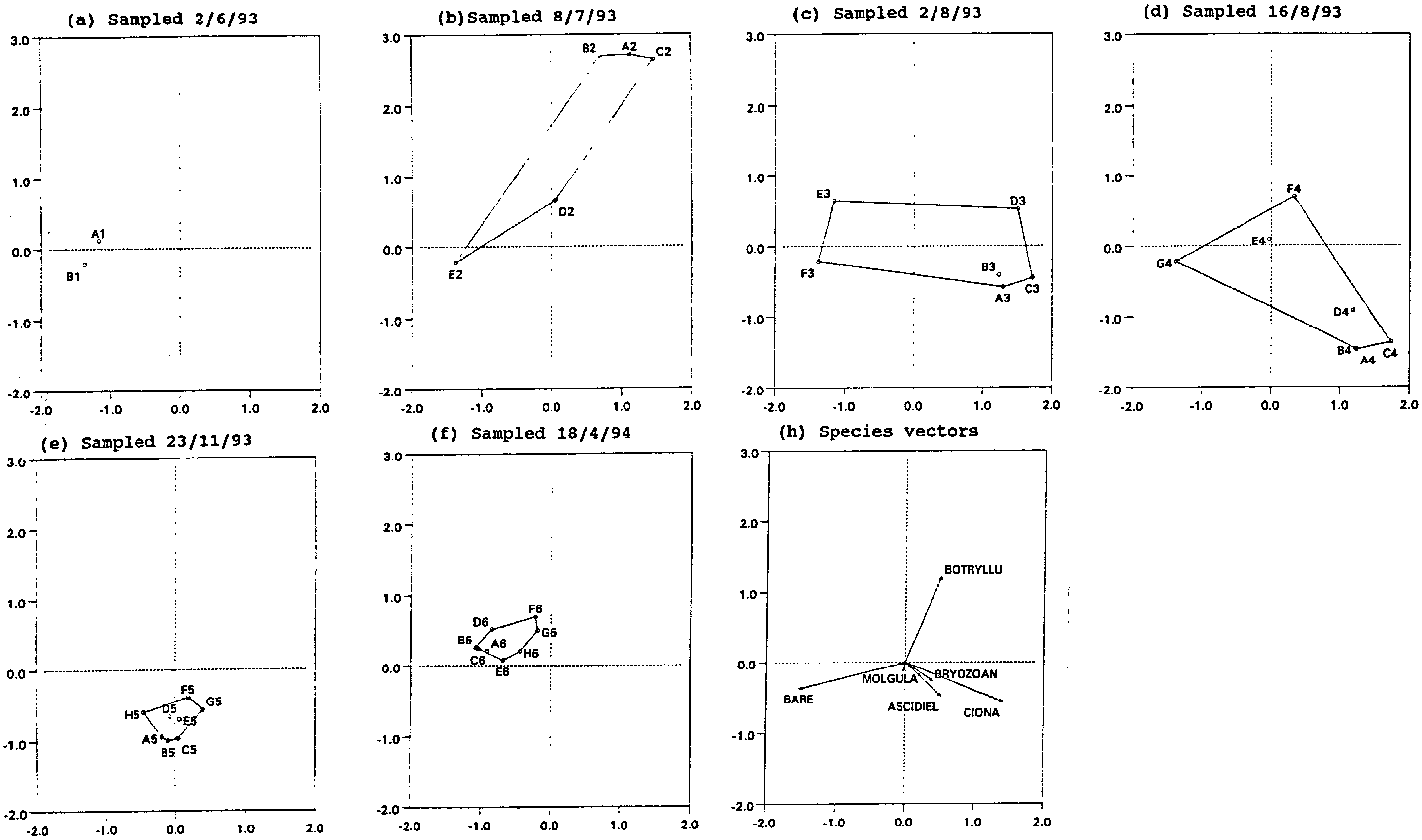

Fig 8.10 Principal Component Analysis showing effect of time of deployment on community development on tiles suspended in Albert Dock. Analysis is for percentage cover occupied assessed from photographs of the tiles. Data were square root transformed and centred. The ordination accounts for 85% of the variation. (Letters refer to the date the tiles were deployed; A = 16/3/93, B = 13/5/93, C = 2/6/93, D = 17/6/93, E = 1/7/93, F = 8/7/93, G = 2/8/93, H = 16/8/93).

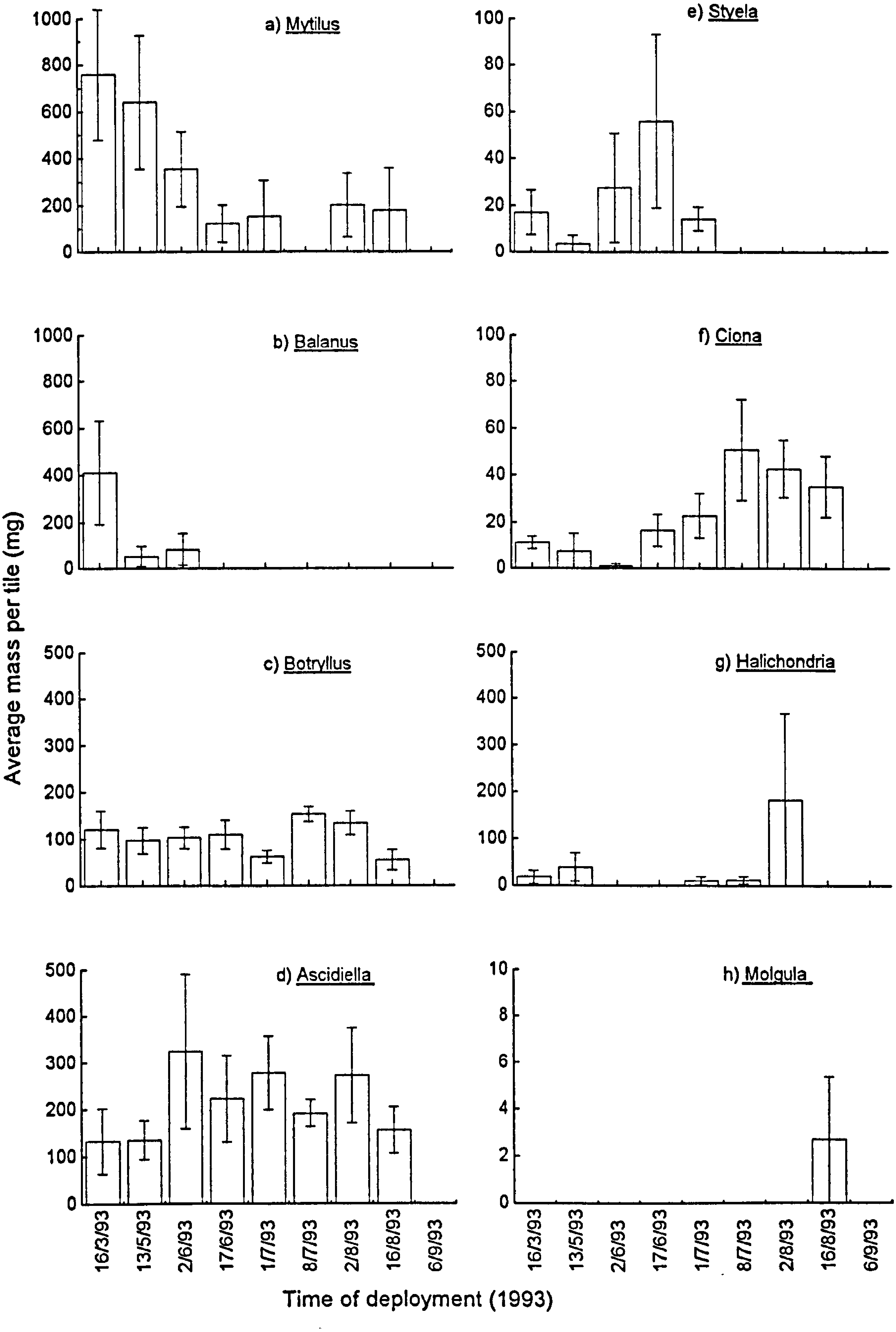

Fig 8.11 Effect of time of deployment on mean mass per tile of main fouling species when tiles were removed in April 1994 (note differences in scale). Error bars represent standard errors.

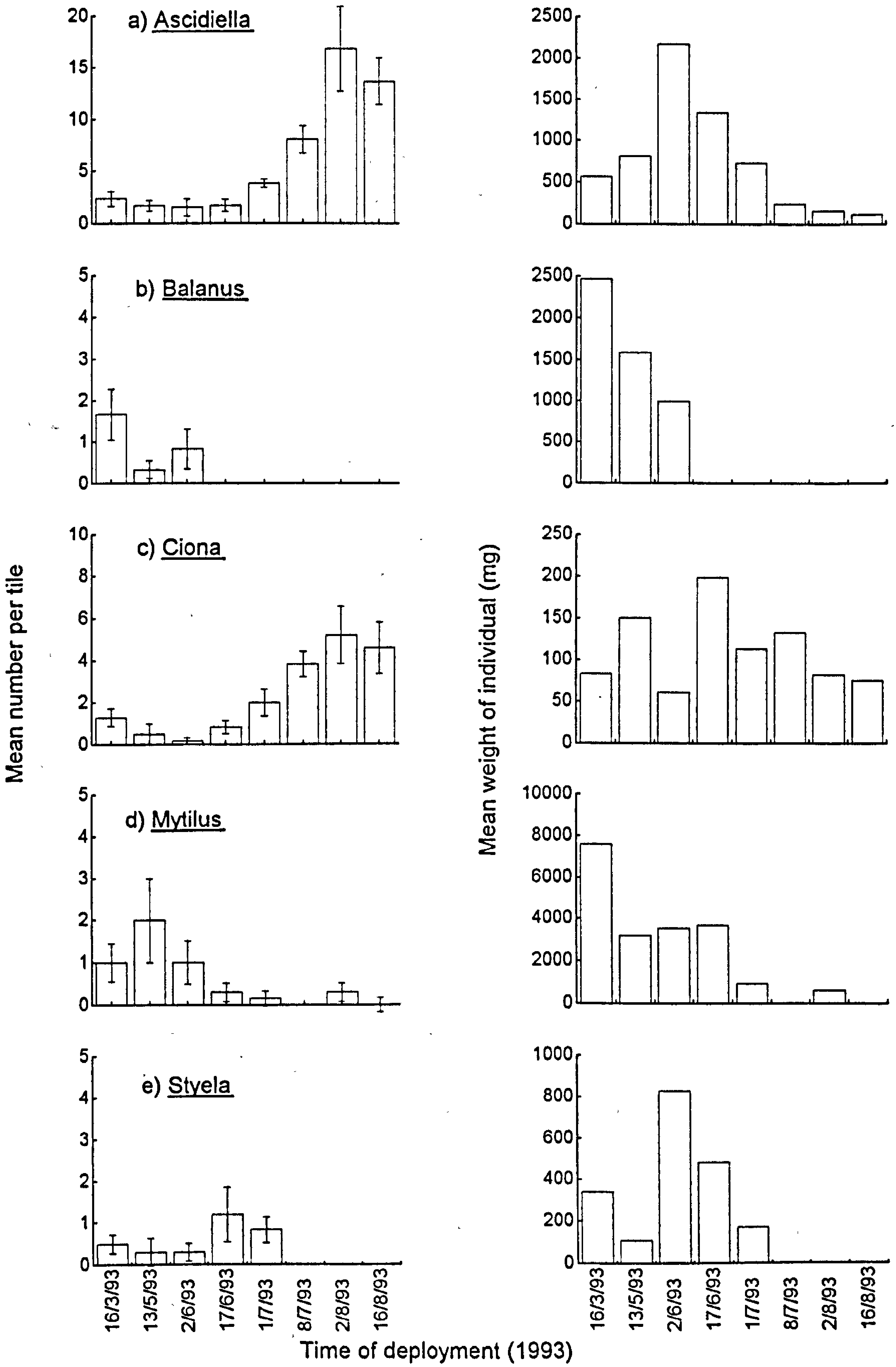

Fig 8.12 Effect of time of deployment on mean and mean individual mass of settlers on tiles in Albert Dock. All tiles removed and analysed on 18 April 1994

earlier in the year. The more ephemeral species, such as *Ciona* and *Ascidiella* showed little difference in the total biomass per tile, with different times of deployment (Fig 8.11). However, from Fig 8.12 it can be seen that on those tiles deployed later in the year, this biomass is distributed between a greater number of individuals. The average mass of an individual is therefore less.

8.3.4 Comparison of community development on tiles and on the dock wall

Figure 8.13 presents a comparison of the community that developed on suspended tiles, tiles fixed to the wall and cleared areas of the wall in August 1994. Clearly there were considerable differences between the three treatments. The abundance of *Mytilus* was very low and only occurred on on the suspended tiles. *Ciona* and *Ascidiella* tended to be less abundant on the bare wall than on either of the two tile treatments. *Botryllus* only occurred on the two wall treatments and *Bugula* was considerably more abundant on the cleared section of wall than on the two tile treatments. Overall there tended to be more free space on the wall, particularly when compared with the suspended tiles (Fig 8.13).

8.3.5 Effect of caging

For the experiment set up on the dock wall to look at the effect of caging no significant difference was observed between treatments for any species (Fig 8.14). Comparison of the effect of cages surrounding suspended tiles with those surrounding tiles attached to the wall was impossible due to the differing techniques used to sample them. However, a comparison of the suspended caged tiles with suspended uncaged tiles revealed two significant differences at a level of 5%. The mass of *Botryllus* was significantly different on a bare tile, compared with the two caging treatments. A significant difference was also detected for *Ascidiella*.

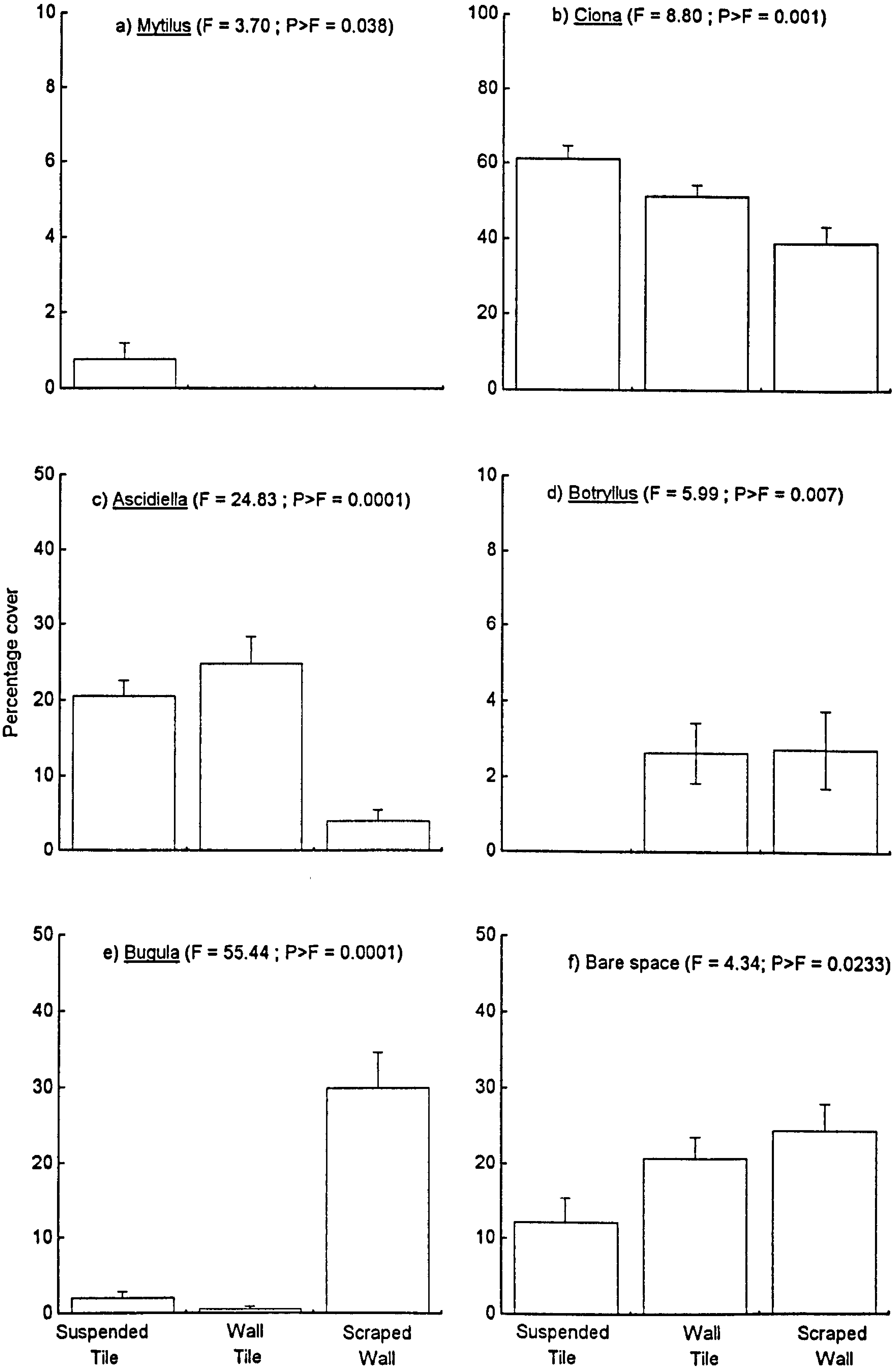

Fig 8.13 Comparison of communities that developed on suspended tiles, tiles fixed to the dock wall and cleared areas of the dock wall. All treatments set up in March 1993 and surveyed photographically in August 1993. Error bars are standard errors.

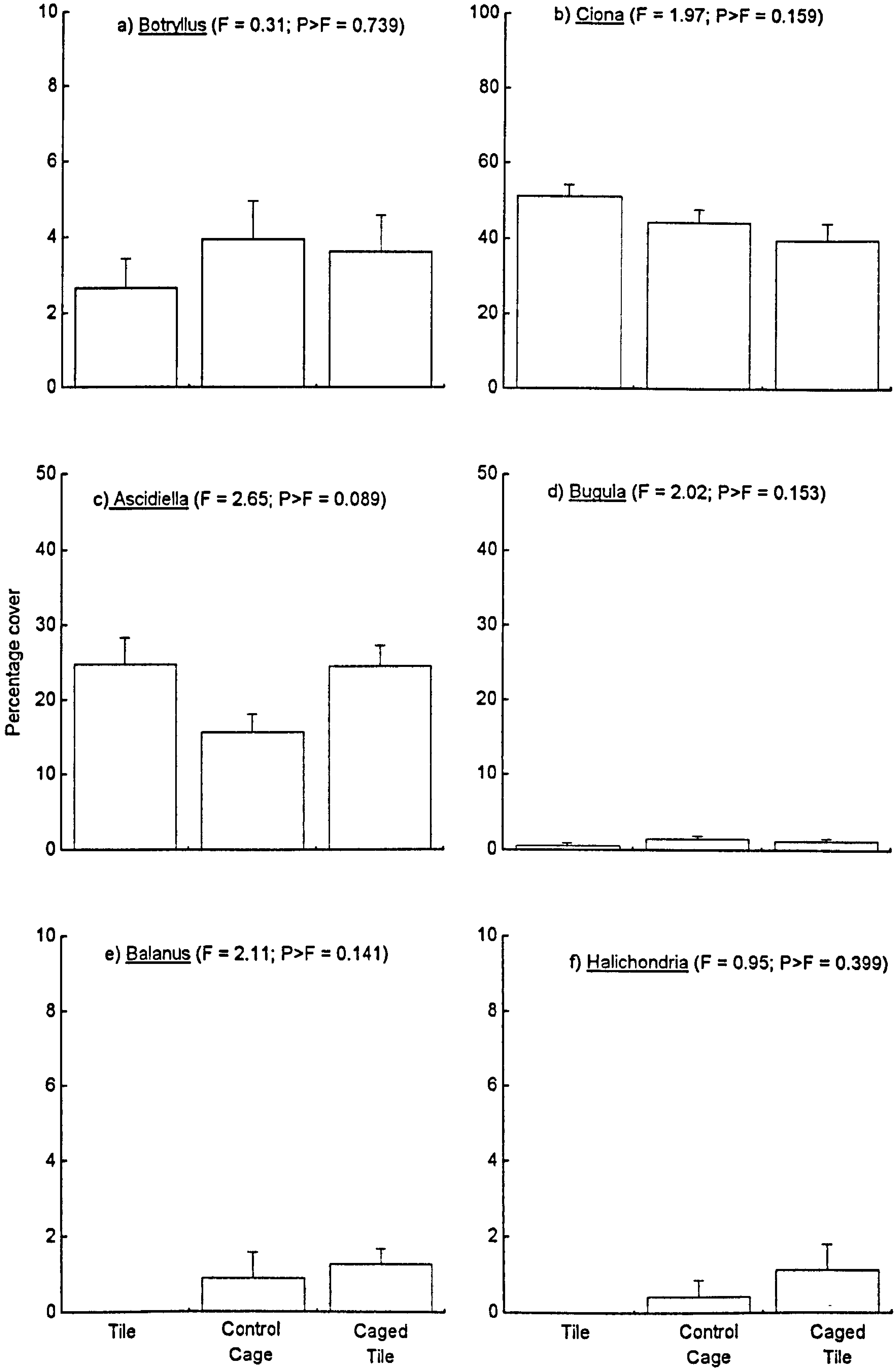

Fig 8.14 Effect of caging on the community that develops on tiles fixed to the dock wall. Control cage had two sides removed. All treatments set up in March 1993 and surveyed photographically in August 1993. Error bars are standard errors.

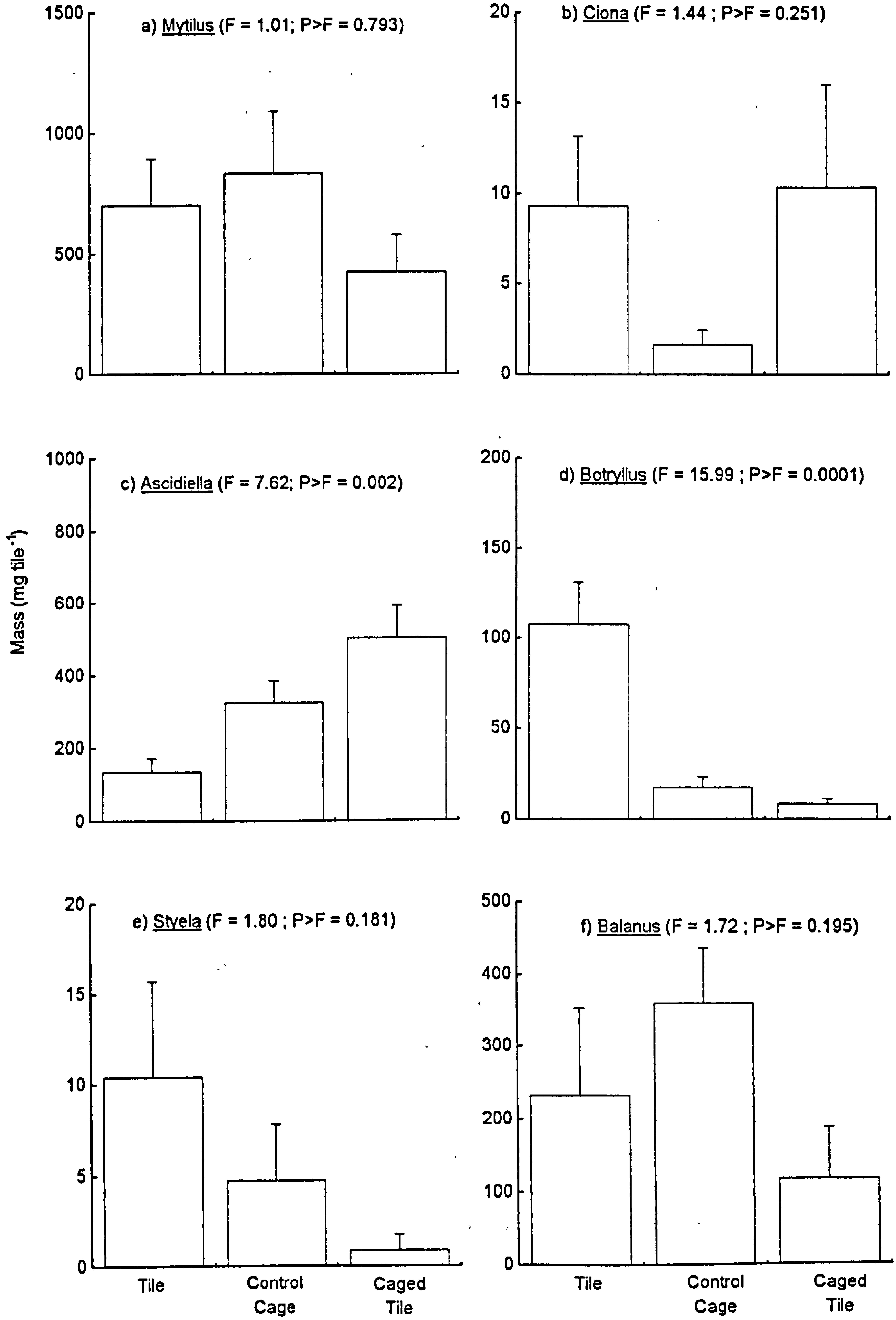

Fig 8.15 Effect of caging on the community that develops on tiles suspended under pontoon in Albert Dock. Control cage had two sides removed. All treatments set up in March 1993 and recovered in April 1994. Error bars are standard errors (n=12).

8.4 DISCUSSION

The fouling assemblage observed in this study has a similar composition to that recorded by a number of other workers, being dominated by relatively short lived ascidians (see Sutherland 1974, Sutherland & Karlson 1977, Keough 1983, Schmidt & Warner 1984, Svane 1988). The following discussion deals with three aspects of the results. The important observation of the differences between the communities that developed on suspended tiles, those fixed to the dock wall and cleared area of the dock wall is discussed first. Then the overall pattern of community development is considered with particular reference to the life-histories of the species involved. The final section considers how the shorter lived species ensure survival to the following year.

8.4.1 Effect of substrate and position

Perhaps one of the most important results from this chapter is that significant differences were observed between the community that developed on suspended tiles, tiles fixed to the dock wall and cleared areas of the dock wall (Fig 8.13). Unfortunately the sample size was insufficiently large to statistically test where the differences lay, however, some hypotheses can be put forward as to the causes of the differences. As mentioned in chapter 6, there tends to be a boundary layer close to the dock wall where phytoplankton densities are depleted due to the dense filter feeding assemblage, dominated by *Mytilus*. It was suggested that this was a possible cause of the lack of recruitment of juvenile *Mytilus* into the adult population, the supply of food simply not being high enough. It is plausible that lower phytoplankton levels close to the wall could affect the abundance of other species as well as *Mytilus*. From the results (see Fig 8.13) there is evidence that *Ciona*, *Ascidiella* and *Mytilus* all tended to be more abundant on tiles suspended under the pontoon than on scraped areas of the dock wall. The scraped areas consequently tended to have a greater proportion of bare space (Fig 8.13f). Some species, particularly the erect bryozoan, *Bugula*, tended to be more abundant on the cleared section of wall than on either of the two tile treatments (Fig 8.13e). This may indicate that this species has a lower food requirement than the solitary ascidians for instance, or alternatively than the correct settlement cues are not present on the tiles.

Few other studies on tiles have included a comparison with clearances of the neighbouring substrate. Svane (1988) showed that differences occurred between the community that developed on suspended panels and that on cleared areas of the wall. This he attributed to differences in larval settlement responses. A number of workers have shown that the physical nature of the substrate can have considerable effects on the composition of the fouling assemblage (McGuinness 1989, Richmond & Seed 1991). This again has been attributed to differing larval responses to the substrate (i.e. that the material acts as a 'larval filter'). Keough (1984) showed that there was a difference between community development on tiles and those that were attached to the adjacent substrate. The present study has provided evidence that both the physical nature of the substrate and the position of the substrate are probably important and this should be borne in mind when considering the rest of the results. It is strongly recommended that future studies using tiles to look at community development include comparisons with the resident community.

A number of studies have looked at the effect of the size of a disturbed patch on community development within that patch. Often the differences are due to the influence of the surrounding community. Farrell (1989) found that the pattern of community development on small patches was similar to the changes that occurred around the edges of a larger patch. A number of these so called 'edge effects' have been suggested, including vegetative expansion of the adjacent community (Keough 1984, Connell & Keough 1985), variations in propagule arrival (Foster 1975), shading (Runkle 1985) or increased foraging by species from the adjoining area (Suchanek 1978, Farrell 1989). The effects of patch size may be an important aspect of the wall community in the docks. Effectively, the areas that have been looked at in this study are relatively small, and for those on the dock wall itself will be strongly influenced by the large *Mytilus* population depleting food levels and possibly propagule arrival. It could be hypothesised that the community development on tiles suspended under the pontoons would correspond to that that would develop on tiles fixed at the centre of relatively large cleared areas of the dock wall. This point will be returned to in chapter 10 where large scale clearances are suggested as a possible management option. This could potentially lead to the creation of a mosaic of patches in the docks at varying stages of successional development. Such patches would be particularly important if they allowed fresh recruitment of *Mytilus*, thereby making the population structure more evenly distributed amongst age classes. It is noteworthy that there tended to be more *Mytilus* on the suspended tiles than on either of the treatments on the dock wall although numbers were still very low (Fig 8.13a).

It was suggested in chapter 6 that predation, particularly from *Carcinus*, may be one of the factors limiting early survival and hence the recruitment of *Mytilus* in the docks. The results from the cages do not support this hypothesis. The overall settlement of *Mytilus* was low, however, during the year of this investigation. For tiles suspended under the pontoon *Mytilus* settlement on caged tiles actually tended to be lower than on uncaged tiles (Fig 8.15a). A number of other differences were observed in the fouling communities on uncaged tiles and tiles within cages, when the treatments were suspended below the pontoon (Fig 8.15). Species such as *Botryllus* and *Styela* tended to be more abundant on uncaged tiles, while *Ascidiella* tended to be more abundant on caged tiles. For tiles fixed to the dock wall relatively little difference was observed between treatments (Fig 8.14). This implies that the exclusion of predators is not the major cause of the differences observed in the suspended treatments. Similar results were obtained by Schmidt & Warner (1984). They attributed the observed differences to fouling organisms on the outside of the cage altering the physical conditions, such as light and food, within the cage. This then resulted in a switch in the species composition on the tiles within cages. The results above support this. While fouling species were periodically (i.e. every two to three weeks) removed from the outside of the cage they may still have temporarily altered conditions within the cage. The lack of difference observed for the treatments attached to the wall suggest that food supply may be already limiting in this area and that presence of the cage has relatively little direct additional impact. In summary, the results from the cages are of little use in testing for the effects of predation, due to relatively large caging effects.

8.4.2 The successional sequence

The general successional sequence on tiles deployed in February 1993 is shown in Fig 8.7. *Botryllus* tended to be most abundant early in the year, before being replaced by the solitary ascidians *Ciona* and *Ascidiella*. These two species decreased in abundance during autumn, when the more perennial species *Mytilus* and *Balanus* became dominant, although the total biomass remaining on the tiles at this time was relatively low. Figure 8.9 shows the effect that time of deployment had on the pattern of community development. From this there is no evidence that early colonisers, such as *Botryllus*, are essential for the sequence to continue. For instance, tiles deployed on 22

July 1993 (Fig 8.9g) had a high proportion of *Ciona* when sampled in November 1993, as did tiles deployed at all other times before July. It is possible that *Botryllus* did settle on these tiles and was subsequently replaced before the tiles were photographed in November. This is unlikely for two reasons. Firstly the number of *Botryllus* settling after July 1993 was relatively low (Fig 8.3). Secondly, the actual area of the tile deployed in July, occupied by *Ciona* in November, was about twenty-five percent and it seems likely that *Botryllus* would have persisted on the tile rather than being outcompeted. Relatively little difference was observed in the community structure when the tiles were harvested in April 1994.

From these results it appears that there is not a successional sequence in the classical sense (Clements 1928, Odum 1969). Rather, there is a typical fouling community at each time of the year and when space becomes available the development converges towards this without necessarily going through the successional sequence observed on tiles deployed earlier in the year. This is also shown in the ordinations of the community composition (Fig 8.9). The community development on tiles deployed in July (labelled 'E' and 'F') does not follow the pattern observed on those deployed in March (labelled 'A'). Rather, the community composition on the July tiles quickly resembles that observed on the March tiles, as indicated by the points for these two sets of tiles getting closer together on the ordination diagram. These observations support the idea that the observed successional sequence is more a result of the life histories of the species concerned, rather than any necessary facilitatory interspecific interactions (sensu Connell & Slatyer 1977). Such interactions (or inhibitory ones) may still be important but do not appear to be the primary mechanism.

Using life-history strategies to account for successional changes seems to be a more useful approach than the interactions models proposed by Connell & Slatyer (1977). As pointed out by Sutherland & Karlson (1977) marine organisms generally do not alter the substrate and there is no possibility of leaving dormant seeds. A number of authors have drawn attention to the possible importance of life-histories (Noble & Slatyer 1980, Botkin 1981, Keough 1984, Huston & Smith 1987, Walker & Chapin 1987, Underwood & Anderson 1994). The models of Huston & Smith (1987) appear particularly useful, though little practical use has been made of them to date. Huston & Smith (1987) were able to show 'pseudo-cyclic' replacements when life history traits such as wide dispersal, rapid growth and high maximum growth rates were inversely correlated with traits such as high shade tolerance or high maximum size. Such traits are probably typical of a number of assemblages in marine environments, including the docks. They may also provide a means of explaining some of the large interannual changes observed in larval supply (Sutherland & Karlson 1977, Keough 1983, Turner & Todd 1993). This could only be ascertained through more attention being concentrated on explaining the causes of variation in larval abundance.

Two aspects of life-history are likely to be of particular importance in the docks system, namely reproduction and growth rates. The large influence of larval supply in affecting the composition of a fouling assemblage is well known (Sutherland & Karlson 1977, Keough 1983, Turner & Todd 1993). The larvae of *Balanus* and *Botryllus* tended to be the earliest larval species in the year (Fig 8.2 and 8.3). Very few *Balanus* settled on the tiles early in the year, despite very high larval densities in zooplankton samples. However, a heavy settlement of this species was observed on the cleared sections of the dock wall which indicates that conditions on the tile were in some way unsuitable for settlement. Neither *Balanus* nor *Botryllus* can be regarded as strong competitors as they are relatively easily overgrown by larger solitary species. *Botryllus* appears to be a relatively fast grower and it seems this species has adapted to reproduce early in the year, grow quickly and produce further offspring before it can be overgrown by the slower growing solitary species. *Ciona* and *Ascidiella* dominate later in the successional sequence, simply due to the superior competitive ability of these species relative to *Botryllus* and *Balanus*. Fig 8.8b compares the average weight of an individual of *Molgula*, *Ciona* and *Ascidiella* through the successional sequence. From this it appears that *Molgula* is a faster grower than *Ciona* which is a slightly faster grower than *Ascidiella*. From these results it might be expected that *Molgula* would tend to dominate early in the successional sequence, then *Ciona* and then *Ascidiella*, assuming all larvae arrive at the same time. *Molgula* did peak in abundance slightly before *Ciona*, although the overall abundance of *Molgula* remained very low. Both *Ciona* and *Ascidiella* showed similar patterns of change, except that *Ciona* was more abundant, although by the end of the experiment *Ascidiella* was the more abundant of these two species. This may have been primarily due to a slower decrease in the average individual mass of *Ascidiella* through time, compared with *Ciona*. By the end of the experiment in April 1993, *Mytilus* and *Balanus* were the most abundant species on the tiles, due to the greater longevity of these species. It seems likely that if the experiment were run for longer, the community on the tiles would begin to approach that observed on the walls.

The results support the concept that life-history is probably the major driving force of community development or succession in the docks. It would theoretically be possible to apply models, such as those produced by Huston & Smith (1987), provided more information was available on the specific energetics of each species. This would include the relative proportion of energy devoted to growth and reproduction. More accurate densities of larvae of species such as *Ciona* and *Ascidiella* would also be required. The present estimates do indicate when these species are most abundant but larger sample sizes would be required to get a more accurate assessment of the actual densities present.

8.4.3 The persistence of species in the docks

From the above results describing the pattern of succession, it could be questioned how some of the short-lived annual species manage to persist in the docks at all. For instance on the tiles deployed in March 1993, there were virtually no *Ciona* remaining by April 1994 (Fig 8.6a). The results from tiles deployed at different times of year suggest how such species ensure survival to the following year. There is little difference in the total mass per tile of the annual species with regard to the time of year when the tile was deployed (Fig 8.11). However, Fig 8.12 shows how this mass is distributed between individuals. Clearly, tiles deployed later in the year tend to have a greater density of smaller individuals. The opposite is true for longer lived species such as *Mytilus* and *Balanus*, which tend to have the highest mass on the tiles deployed earliest in the year. This is simply as a result of the increased longevity of these species. It seems therefore that annual species, such as *Ciona* and *Ascidiella* colonise space that becomes available later in the year. Individuals settling at these times remain small over the winter period, ready to begin growth the following spring. This mechanism would seem to ensure that survival to the following year is more likely.

It is interesting that *Molgula* and *Obelia* do exist in Albert Dock but do not thrive here (see chapter 5). Fig 8.8 suggests that *Molgula* has a very high rate of growth and it seems probable that this is also true of *Obelia*. Certainly in the temporal study of the dock walls (chapter 5) large increases in the abundance of *Obelia* were observed over relatively short periods of time. The high abundance of these species in Brunswick and Coburg Docks (see chapter 4) suggests that such 'r' selected species have a competitive advantage at these sites. This again suggests that the hypothesis that conditions here are relatively harsh as a result of lower phytoplankton densities or higher levels of suspended solids.

8.4.4 Summary

The typical pattern of succession observed on tiles suspended in Albert Dock showed an early dominance of *Botryllus* which was subsequently replaced by the solitary tunicates *Ciona* and *Ascidiella*. Later in the year all of these species became less abundant, with the remaining biomass dominated by *Mytilus* and *Balanus*. Considerable differences were observed between the community that developed on suspended tiles, tiles fixed to the wall and cleared areas of the wall. There was little evidence of any necessary facilitatory interactions (sensu Connell & Slatyer 1977). It appears that the observed pattern of succession is primarily a result of differences in the life-history strategies. Typical fast growing 'r' selected species (sensu MacArthur & Wilson 1967) such as *Botryllus* dominate early in the sequence while 'K' selected species like *Mytilus* are more important later on. It appears that fresh space becoming available later in the year may be an important factor in ensuring the survival of short lived species such as *Ascidiella* to the following year.

CHAPTER 9

PRELIMINARY OBSERVATIONS ON ALGAL SETTLEMENT AND DYNAMICS IN AN ENCLOSED DOCK BASIN

9.1 INTRODUCTION

Following the isolation and redevelopment of the South Docks, the benthic assemblage that colonised the dock walls and floating pontoons, included algae (Allen 1992). Most research on the system to date has been concerned with the dynamics of either the plankton or the benthic faunal community, or the interaction between these two (Allen 1992, Zheng 1995). Relatively little attention has been given to the macroalgae.

Severe problems with macroalgal blooms, the so-called 'green tides', have been experienced in a number of other marine ecosystems (Hull 1987, Sfriso *et al*. 1988, 1989, 1992, Merrill & Fletcher 1991, Raffaelli *et al*. 1991). They tend to occur in areas subject to increased eutrophication, often in enclosed areas where there is relatively little water movement. As well as being extremely damaging to the aesthetics of the affected area, they can also present a number of problems to any biological community that may be present, including shading, reduced water movement and low oxygen conditions. This can lead to reductions in both the density and overall diversity of both fauna and flora present (Hull 1987, Raffaelli *et al*. 1991). In some cases, for example in Denmark, floating macroalgal mats can actually be considered beneficial, as they outcompete phytoplankton resulting in clearer water (Thybo-Christesen *et al*. 1993). The docks appear to be quite a likely area for such blooms to occur, although to date, no major problems have been experienced here, apart from small patches of *Enteromorpha* species floating on the water surface (pers. obs.). Dense mats of *Vaucheria* have been observed on the bottom of Salthouse Dock (J.Allen, Liverpool University, pers. comm.) but did not result in any problems on the surface. However, it is important to increase understanding of the dynamics of benthic macroalgae within the docks, before any problems occur.

The docks are unusual, in that they are saline but lack the tidal cycle typical of most marine areas. They are also relatively enclosed, a quality more typical of freshwater lakes, than marine ecosystems. The patterns and causes of zonation of intertidal marine algae have been thoroughly investigated (Schonbeck & Norton 1978, 1980, Lubchenco 1980, Hawkins & Harkin 1985, Hawkins & Hartnoll 1985). Most of these works have concluded that the upward extension of a given species is generally limited by stress tolerance to the physical conditions in that area while lower limits tend to be controlled by more biological factors, such as competition with another species, or grazing pressure. The range of extension of algae into the subtidal is ultimately limited by available light. Stress in this instance is defined as external physico-chemical constraints, both shortages and excesses on dry matter production and reproduction. Biological factors may also be important in controlling the upward extensions of some species, particularly those in the mid / lower shore (Hawkins & Hartnoll 1985). In freshwater lakes macrophyte zonation is determined by the degree of wind mixing and the amount of available light (see Spence 1982 for review). Stress tolerance and disturbance are more important for species living around the lake edge.

Studies on the zonation of marine algae have tended to rely on clearance and transplant experiments, using natural substrate (Schonbeck & Norton 1978,1980, Hawkins & Harkin 1985, Hawkins & Hartnoll 1985). Artificial substrates, in the form of tiles, have been used extensively for describing and manipulating predominantly faunal assemblages (see chapter 8). No attempt has been made to use such artificial substrates for studying benthic algae and they are often deployed in areas where algae tend not to thrive. The use of these would definitely facilitate manipulation experiments for testing factors affecting the distribution of algae.

It is well known that herbivory can have substantial effects on both algal density and species composition, particularly in marine systems (Lubchenco 1978,1983, Brawley & Adey 1981, Hawkins 1983, Hawkins & Hartnoll 1985, Parker *et al.* 1993). The docks lack grazing gastropods, the most important herbivores on most temperate rocky shores, but do support very high numbers of amphipods (Allen 1992, pers. obs.). Amphipods are a relatively little studied group of marine grazer (Hawkins & Hartnoll 1983, Brawley 1992) although recently there has been an increase in understanding both of their diet (Greze 1968, Hudson 1983, Buschmann 1991, Denton & Chapman 1991, Brawley 1992, Parker *et al.* 1993) and dynamics (Birklund 1977, Nelson 1979, Ambrose 1984, De Witt 1987, Karakiri & Nicolaidou 1987, Lancellotti & Trucco 1993). These animals are likely to have quite a strong influence on algal growth in the docks, but relatively little is known of their dynamics or effects on vegetation. The absence of gastropods from the docks makes the area very amenable to gaining an understanding of the role of amphipods, as the effects the two groups have do not have to be isolated from one another.

Seasonality is a well known phenomenon in marine algae with both biomass and reproductive output varying in response to changes in the physical environment (Mohsen *et al.* 1974, Mathieson & Norall 1975, Connor 1980, Kain 1982, Cormaci *et al.* 1984, Santelices 1990, Steele & Whittick 1991). These studies include examples of seasonal changes in both intertidal and subtidal species. Seasonal changes of the phytoplankton in the docks have been described in detail (Allen 1992, Zheng 1995), but nothing is known of comparable changes in the macroalgal community.

The main aim of the present study was to describe the patterns of algal seasonality and zonation over the period of a year by means of experimental settlement panels. An attempt is made to relate the seasonal pattern to changes in the physical environment. The secondary aim was to examine the interaction of grazing amphipods with the phytobenthos.

9.2 METHODS

9.2.1 Assessment of dock flora

In order to compare how closely the flora of the docks resembled that found in the Mersey, a species list of each area was compiled. During February and April of 1993 algal samples were collected from the walls and pontoons of Albert, Salthouse and Queens Docks and returned to the laboratory for identification. At around the same time a species list for the intertidal zone at New Brighton was compiled, on the basis of observations made in the field.

9.2.2 Experimental design

Tiles were used to study changes in algal settlement with depth and through time. They were constructed from polypropylene plastic, cut into 0.12m X 0.12m squares, the surface of which was roughened with grade 1.5 sandpaper. These tiles were attached to vertical plastic beams, five tiles to a beam, which were then screwed to the dock wall. Each unit included one tile at each of 0m, 0.25m, 0.5m, 1m and 1.5m depth (see Fig 9.1). The study began in March 1993. Ten of these units were deployed on the west facing wall in Queens Dock. Four were used for short-term study, panels being removed and replaced approximately every four weeks. These were analysed in the laboratory to determine the mass and species composition of algae that had settled during the previous month. Results were then compiled to describe the annual pattern. The remaining six were left in place and photographed each month to document the longer term development on the panels.

9.2.3 Community analysis

Temporary panels were returned to the laboratory for analysis. Before analysing the algal component of each tile, any macrofauna present was removed. *Botryllus* was scraped off, transferred to pre-weighed foil boats and

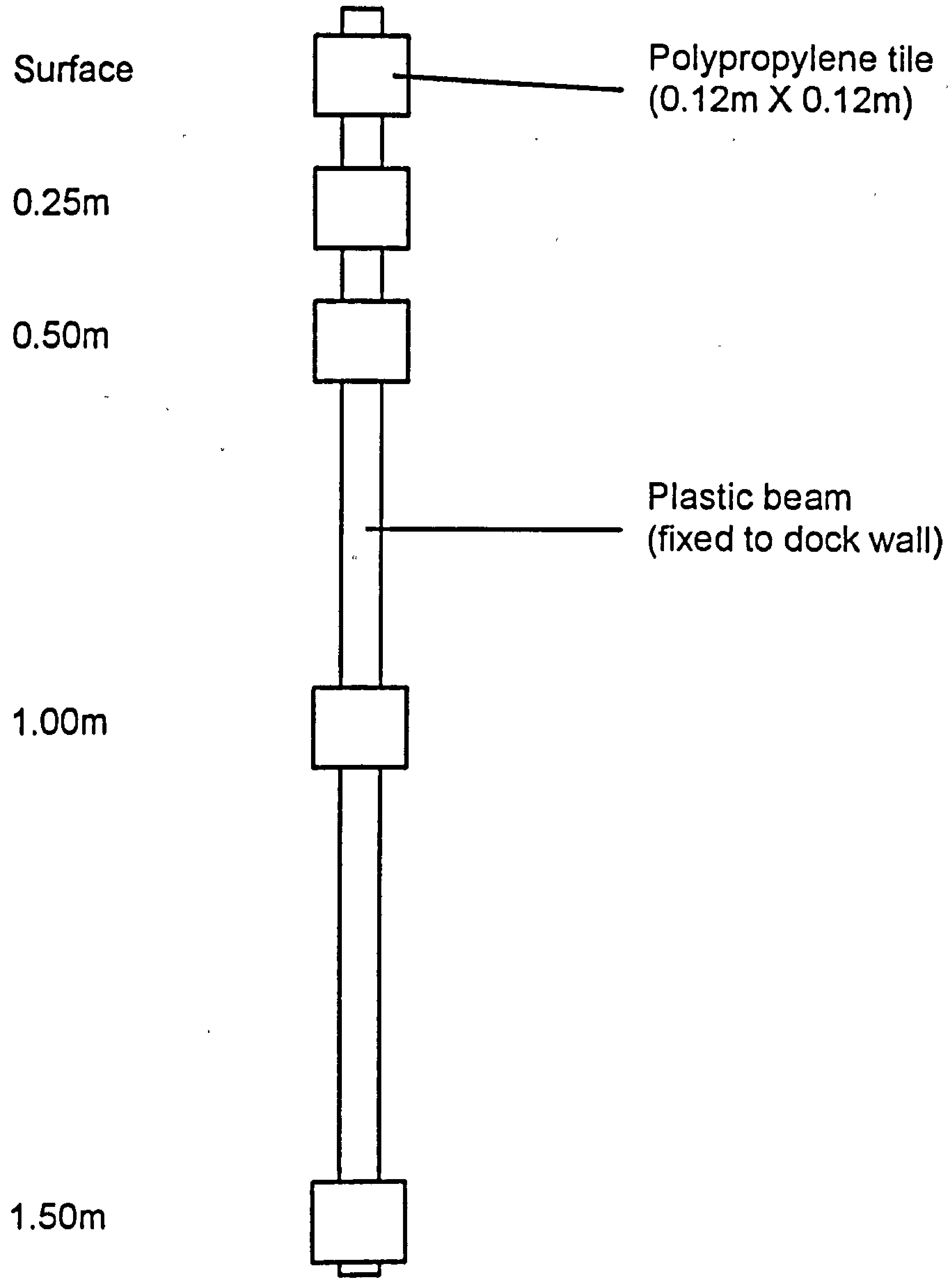

Fig 9.1 Diagram of one experimental beam used to sample algal settlement at different depths in Queens Dock

dried to constant weight at 70°C, before being reweighed and its dry mass calculated. Amphipods were similarly removed, sorted according to species, enumerated and dried in the same manner as the *Botryllus*.

The algal standing crop was estimated by clearing half the area of each tile and calculating the dry mass as above. To estimate the actual species composition three replicate scrapes were removed from disparate areas of the material remaining on each tile and mounted in seawater on separate glass slides. These preparations were examined under a magnification of X400 using an eyepiece grid to provide nine arbitrary intersect points for each field of view analyzed. The algal species present at each of these points was recorded and ten fields of view were analyzed in this way for each of the three scrapes taken. Non-biased selection of the field of view was ensured by dropping the preparation out of focus before altering the position of the slide. For the purpose of this investigation it was assumed that relative abundances of species obtained in this way was proportional to their relative mass.

9.2.4 Diatom preparations

In order to confirm the identity of the diatoms present, a sample of material was retained for chromic acid digestion to allow a more thorough examination. Chromic acid was prepared by mixing 500 cm^3 distilled water, 50g potassium dichromate and 100cm^3 concentrated sulphuric acid. A small sample of material from a tile was boiled in about 10cm^3 of this acid for one hour. This was then centrifuged at 5000rpm for five minutes, and the supernatant poured off before the residue was resuspended in distilled water. This was repeated for five washings or until the diatom suspension tested neutral to blue litmus paper. The residue was then resuspended in 2ml of distilled water. The material was prepared for light microscopy by first allowing about 15 drops of the suspension to dry on a coverslip. This was permanently mounted on a slide using diatom mountant.

9.2.5 Physico-chemical environment

No data on dissolved nutrient concentrations were gathered during the course of the study. The average values from readings taken during 1991 and 1992 are presented (Zheng 1995; see Fig 9.3). Water clarity was assessed by means of a Secchi disc (Fig 9.2). Data on mean number of hours of sunshine for each month during the study period were supplied by Bidston Observatory, Birkenhead (Fig 9.2).

9.2.6 Multivariate analysis

Preliminary analysis of the proportional species composition was carried out using Detrended Correspondence Analysis. This revealed relatively large gradient lengths in both data sets, greater than 3 standard deviation units. Therefore Correspondence Analysis was adopted as the most appropriate technique. The data were square root transformed before analysis. The analysis was carried out through CANOCO (ter Braak 1987-1992) using CALIBRATE (Juggins & ter Braak 1994) to produce the biplots.

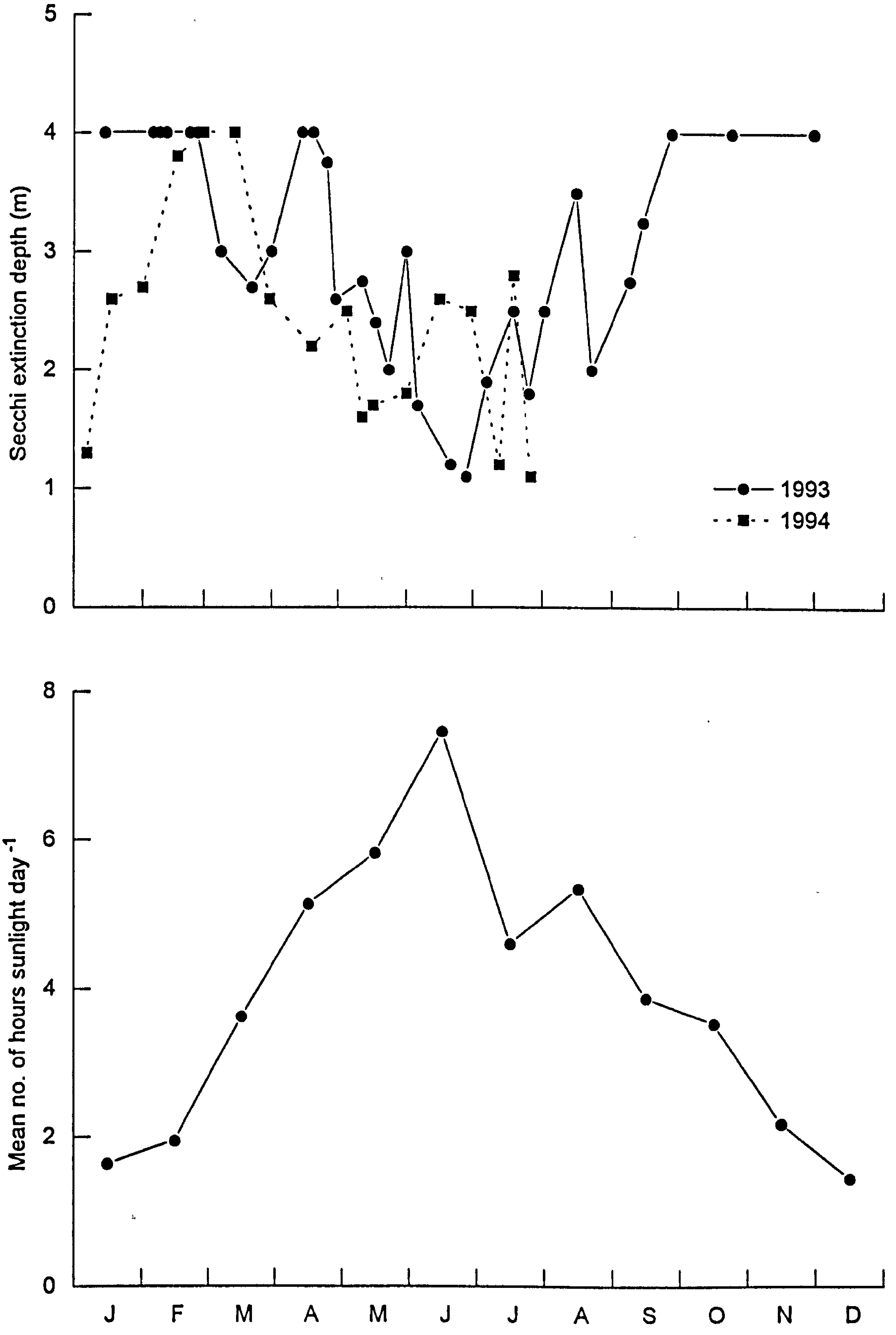

Fig 9.2 Variation in secchi disc extinction depths during 1993 and 1994 in Queens dock and hours of sunlight recorded over the same period. Sunlight data represents monthly means (supplied by Bidston observatory, Birkenhead)

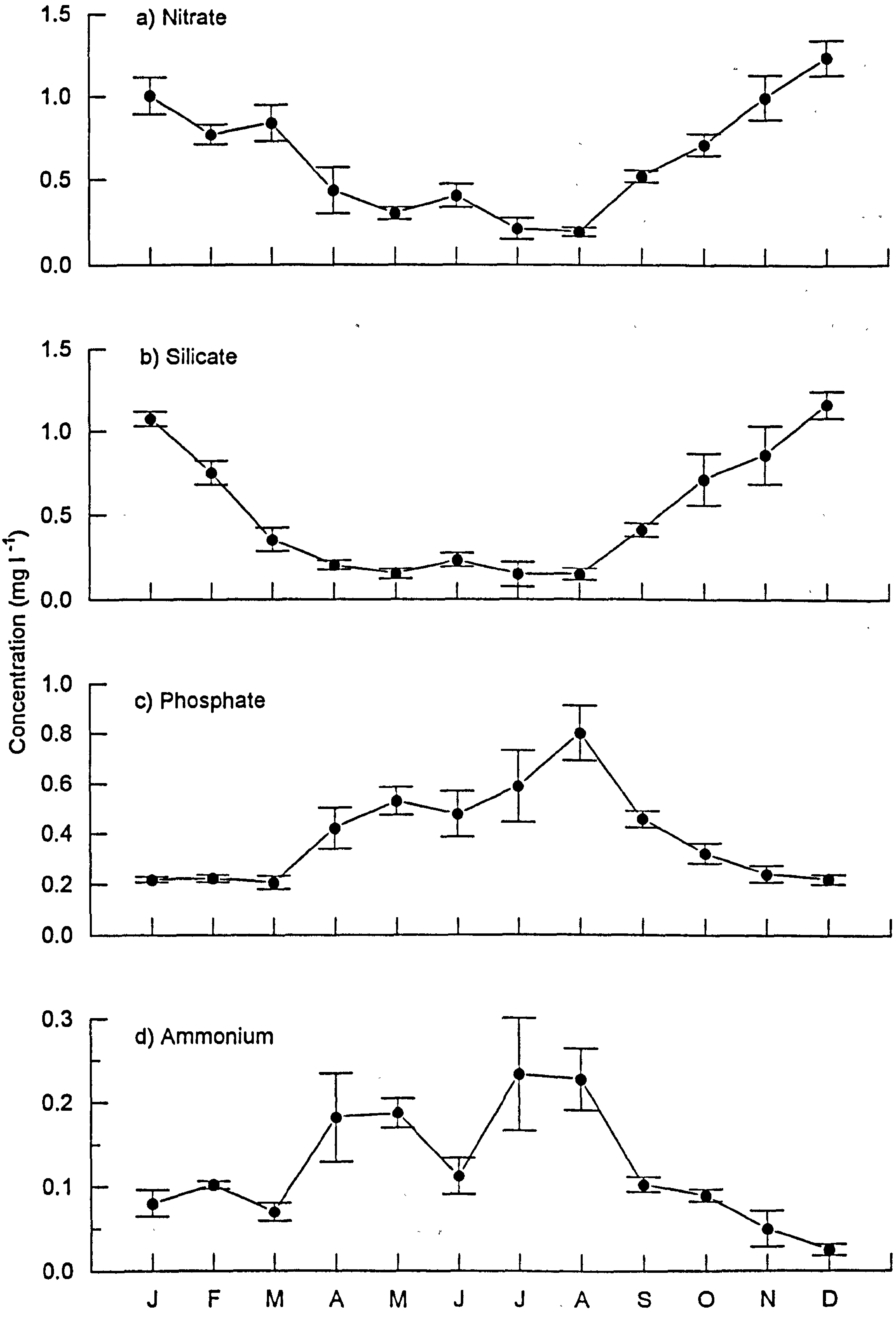

Fig 9.3 Variation in nutrient concentrations in Queens dock with time. Data are average values from 1991/92 (Zheng). Error bars = Standard Error.

9.3 RESULTS

Figure 9.4 shows that the monthly tiles retrieved in May 1993 had lower algal biomasses than those recovered over each of the previous two months, except for the tiles deployed just below the surface. The highest figures for total algal biomass per tile during a single month were recorded, for all depths, in July in 1993 and June in 1994. Tiles placed at 0.25m and 0.5m depth began to show an increase in mass in the June sample in 1993. Those placed below these depths only started to show an increase in July 1993. In 1994 the tiles at all depths showed an increase in June followed by a decline in July.

Results from tiles placed at the surface were somewhat erratic (Fig 9.4a). This was due to the constantly fluctuating water level of the docks which leads to unpredictable periods of emersion. Emersion periods longer than a few days generally resulted in the death of all material on these tiles.

Figure 9.5 shows how the total algal mass was divided between species on tiles placed at 0.5m. Tiles recovered at the end of March show a reasonably equal abundance of benthic diatoms and ectocarpoid algae. By the April 1993 sample, ectocarpoid algae had become the most abundant group with low densities of *Punctaria*, but by May this proliferation has been replaced by green ephemerals, particularly *Enteromorpha* species. *Enteromorpha* remained an important settler on tiles through until August but during June and July *Cladophora vagabunda* was the most abundant species. *Enteromorpha* declined after August when there was a resurgence of benthic diatoms, until December when algal settlement on the tiles was too low to sample. A similar pattern of changes in species abundance was observed in 1994. A few other rarer species were also recorded, notably

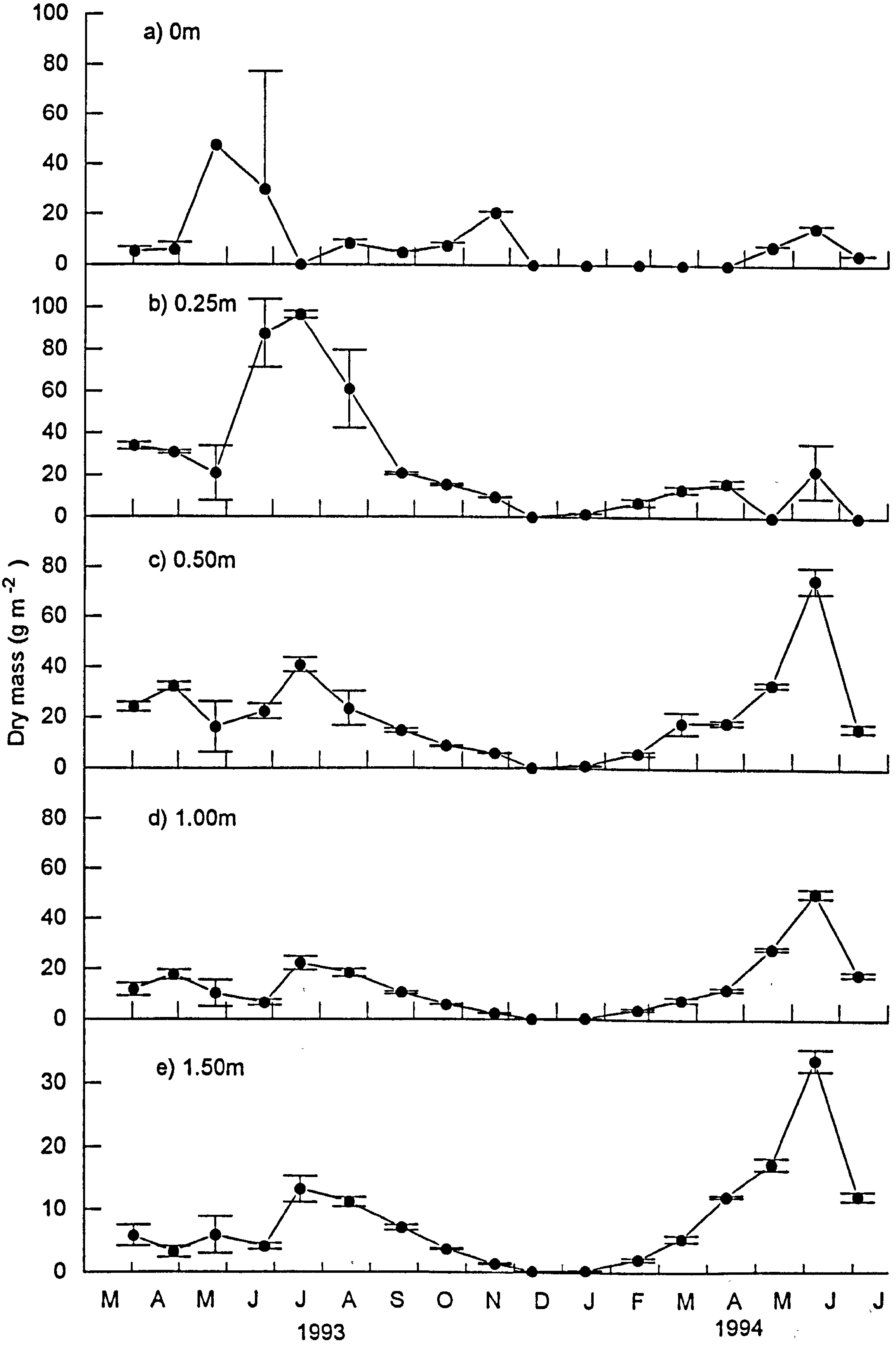

Fig 9.4 Variation in total dry mass of algae on tiles at five depths in Queens Dock Tiles were deployed for a period of one month, then retrieved and biomass determined. (Note differences in scale ; Error bars = Standard Errors)

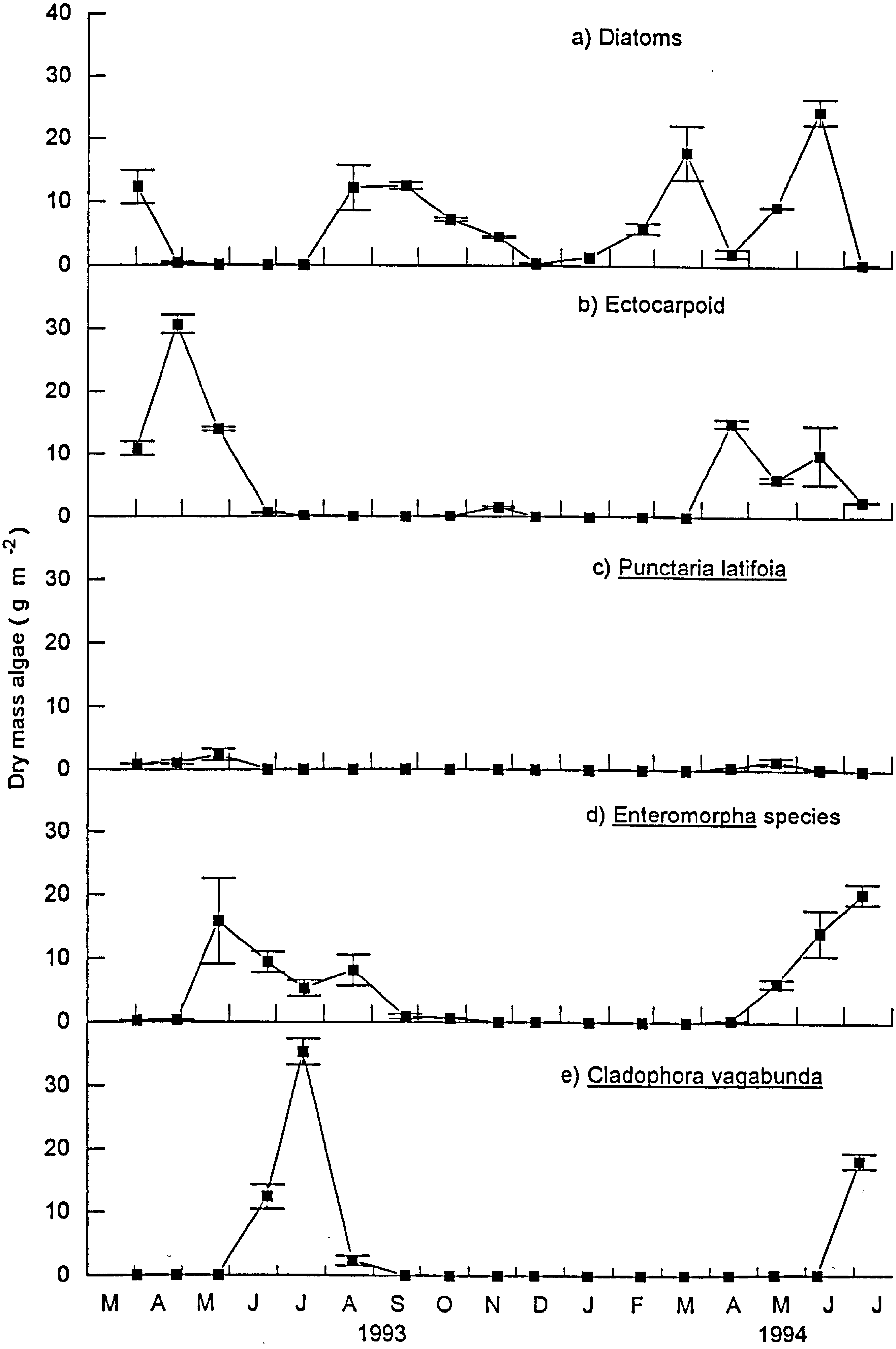

Fig 9.5 Change in distribution of mass of algae between species on tiles deployed at 0.5 m depth for one month periods in Queens Dock during 1993/94. Tiles were deployed for a period of one month, then retrieved and species composition and total biomass determined. Error bars = Standard Errors.

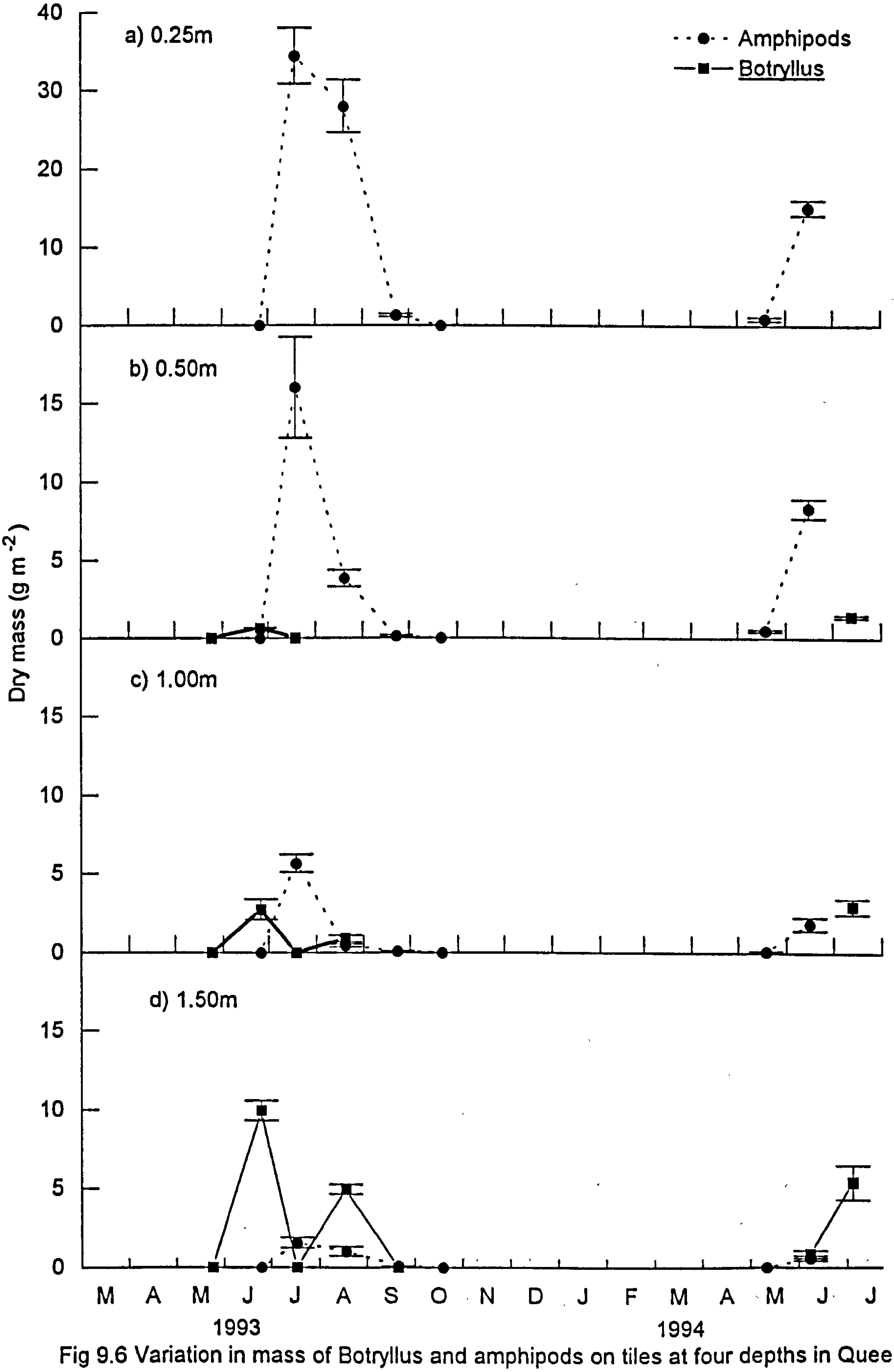

Fig 9.6 Variation in mass of Botryllus and amphipods on tiles at four depths in Queens Dock Tiles were deployed for a period of one month, then retrieved and biomass determined. (Note differences in scale ; Error bars = Standard Errors)

Ulothrix subflaccida on surface tiles recovered in August 1993, *Urospora penicilliformis* on the shallower tiles in the October sample and *Scytosiphon dotyi* on the tiles recovered during October and November 1993.

Overall, the abundant species of diatom on the tiles was an epiphytic species, probably either *Catacombas* or *Hyalosynedra*. Other smaller Naviculoid species were also quite abundant from August until April. The first sample of the tiles taken in March 1993 was the most diverse with regard to diatoms, when in addition to the above species considerable densities of *Melosira* and *Licmophora* were also recorded. *Acnanthes* was also periodically recorded in low densities.

The change in species composition with time described above relates to tiles placed at 0.5m depth. The pattern at other depths was essentially very similar (see Fig 9.8), however a few instances of quite marked vertical zonation were recorded. On tiles removed in July, *Enteromorpha* was by far the most abundant species on those from 0.25m depth, while *Cladophora vagabunda* was more abundant at all depths below this (Fig 9.7). Similarly, in the April sample benthic diatoms were more abundant at 0.25m with ectocarpoid algae making up a much higher portion of the total mass at 0.5m, though it still did not exceed the total mass of diatoms at this depth (Fig 9.7). In general though the pattern of settlement was relatively constant with depth.

The ordination diagrams from the Corresponence Analysis of the data are shown in Fig 9.8. These serve to emphasise the apparent cyclical pattern in the species composition of algal settlement. The April samples, towards the top of the diagrams, tend to have a greater abundance of brown algae, such as Punctaria and Giffordia. The samples from June to October were dominated by the greens, Enteromorpha and Cladophora, and also a high proportion of detritus. Tiles

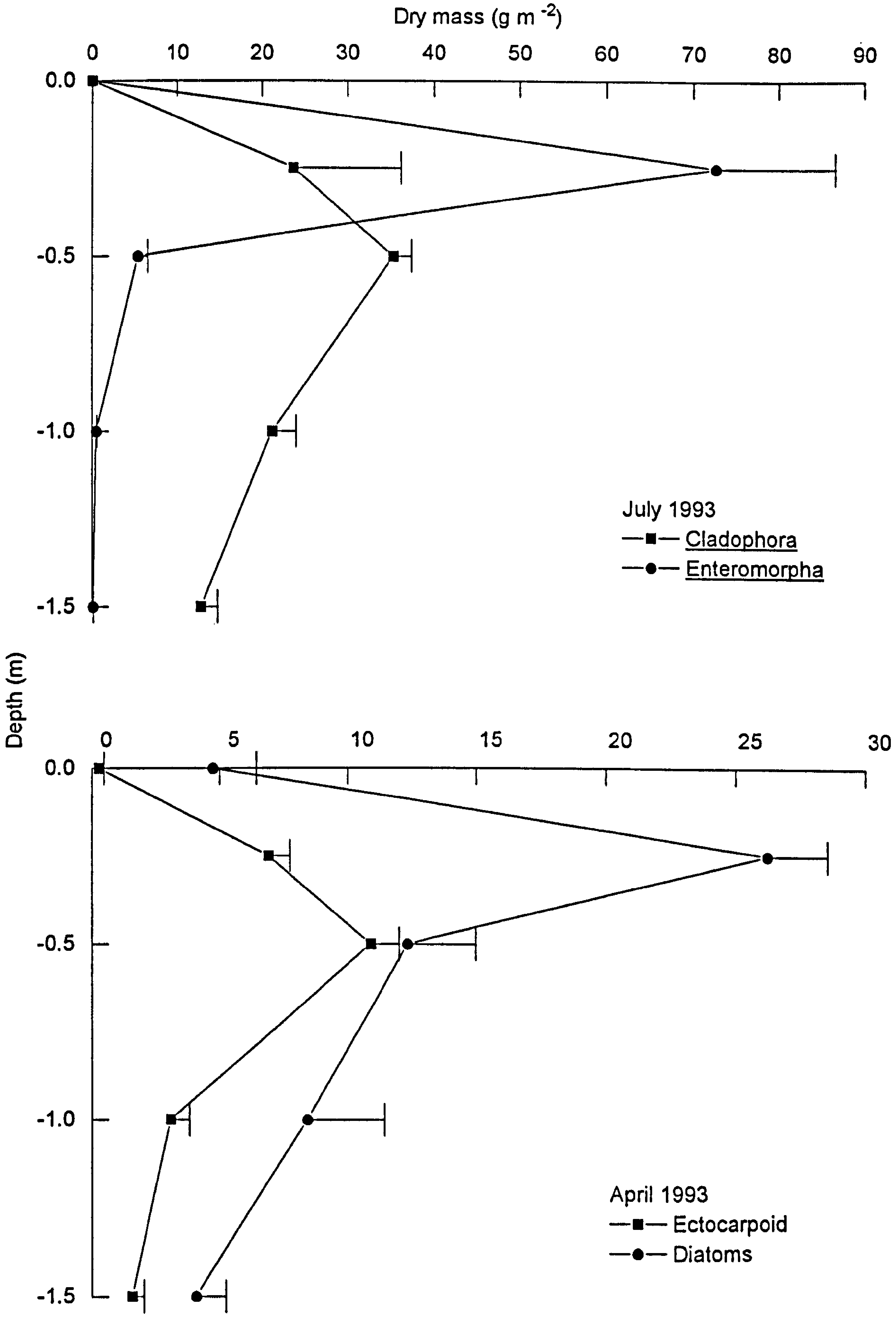

Fig 9.7 Two examples of zonation of species with depth on tiles deployed for one month periods in Queens Dock

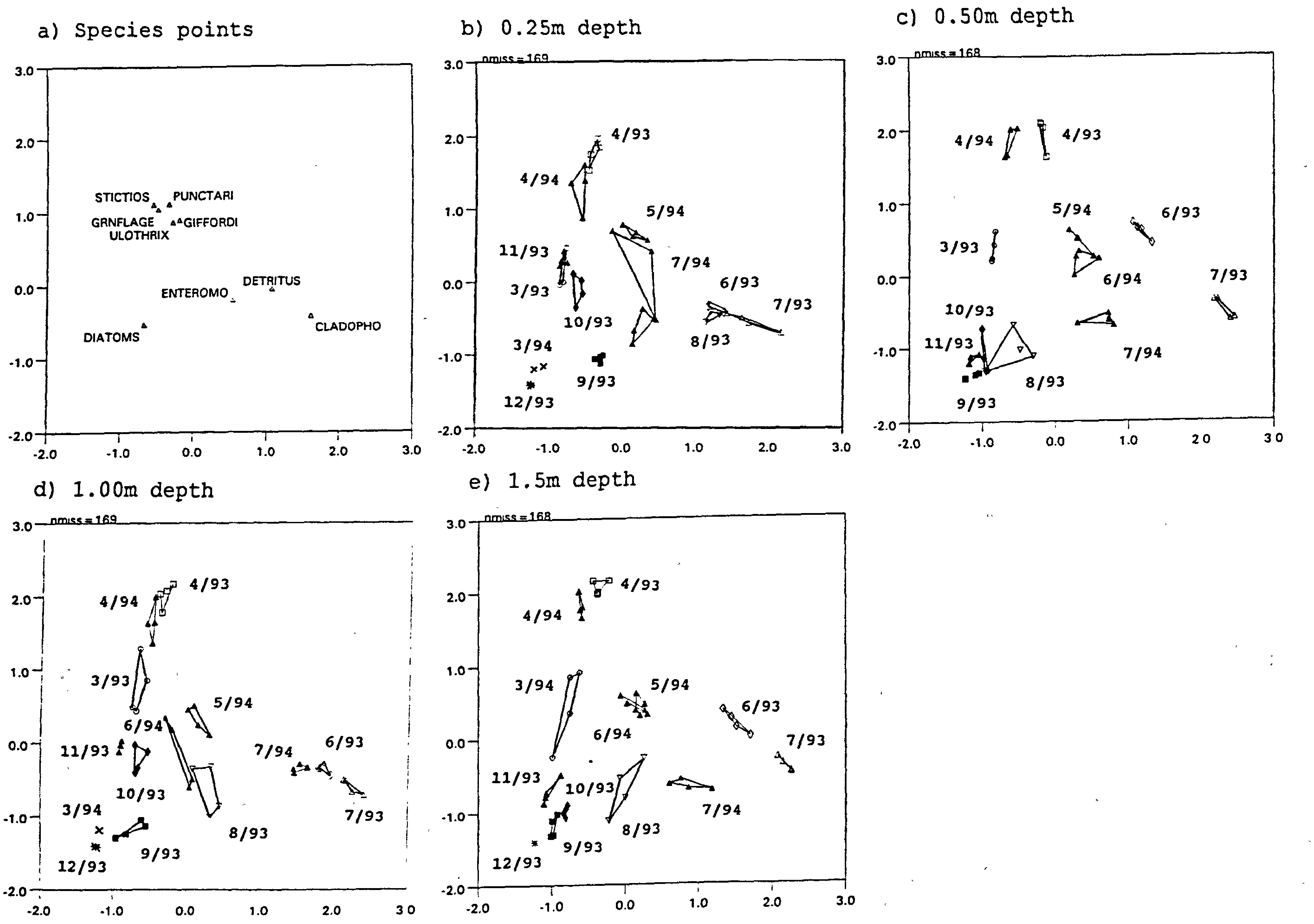

Fig 9.8 Correspondance Analysis of the proportional species composition on tiles deployed in Queens Dock. Tiles were placed in the dock for one month periods and then returned to the laboratory for microscopic analysis. Correspondance analysis carried out after square root transforming the data. The ordination accounts for 62% of the variation.

deployed during the winter were dominated by diatoms. The ordination diagrams also serve to emphasise how similar the patterns observed at different depths were. It is also noteworthy that the April samples in both 1993 and 1994 were very similar, as indicated by the close proximity of points from these times to one another on the ordination diagram. Similarities were also observed for the June and July samples in the two years.

Amphipod biomass was positively correlated with algal standing crop present on temporary tiles, with both of these variables peaking in July (Fig 9.4, 9.6). Figure 9.9 shows an 'S-shaped' or sigmoidal relationship between amphipod biomass on temporary tiles. *Jassa marmorata* was the most abundant amphipod species at all depths on all dates with *Corophium insidiosum* and *Microdeutopus gryllotalpa* present in lower densities. On one occasion, when amphipod numbers were sufficiently high, an increase in mean individual mass with depth was found (Fig 9.10) but the subjective method of analysis means further results are needed to confirm this finding.

Photographs of the tiles that remained in the dock throughout the year show an early proliferation of algae in April followed by a sudden decline by May. This is probably due to high grazing by amphipods present on the tiles, accentuated by reduced algal growth rates due to reduced water clarity and nutrient concentrations at this time (Fig 9.2, 9.3). After the algae declined the colonial seasquirt *Botryllus schlosseri* became established, particularly on the deeper tiles where it reached 100% cover in some cases. The shallower tiles continued to support some ephemeral growth. Variations in the water level of the docks meant that those tiles just below the surface were frequently exposed above the water surface. When the period of emersion was greater than twelve hours it resulted in the death of some or all the organisms present on the tile so

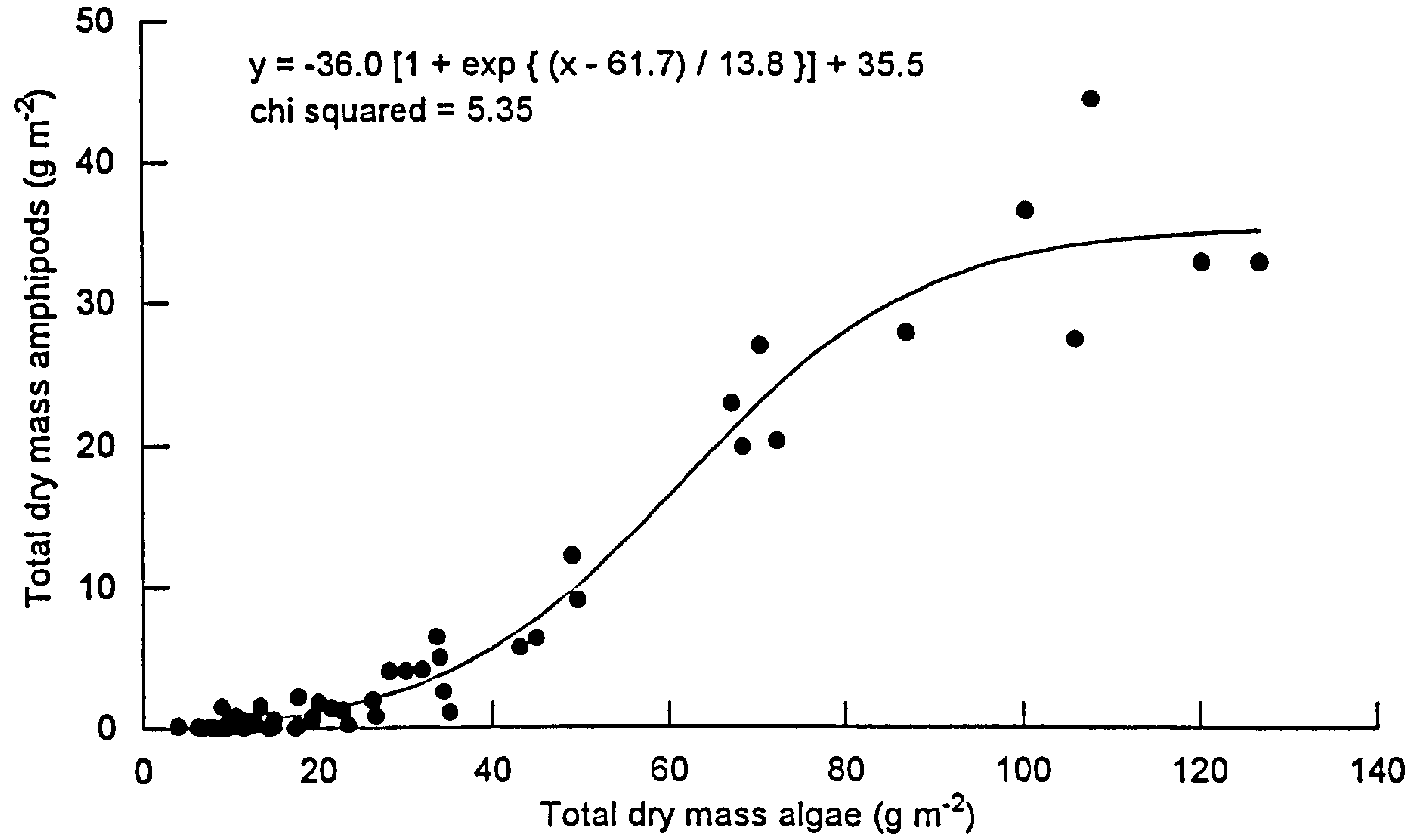

Fig 9.9 Relationship between dry mass of algae and amphipods on tiles deployed in Queens Dock over one month periods. Sigmoidal (Boltzman) curve fitted.

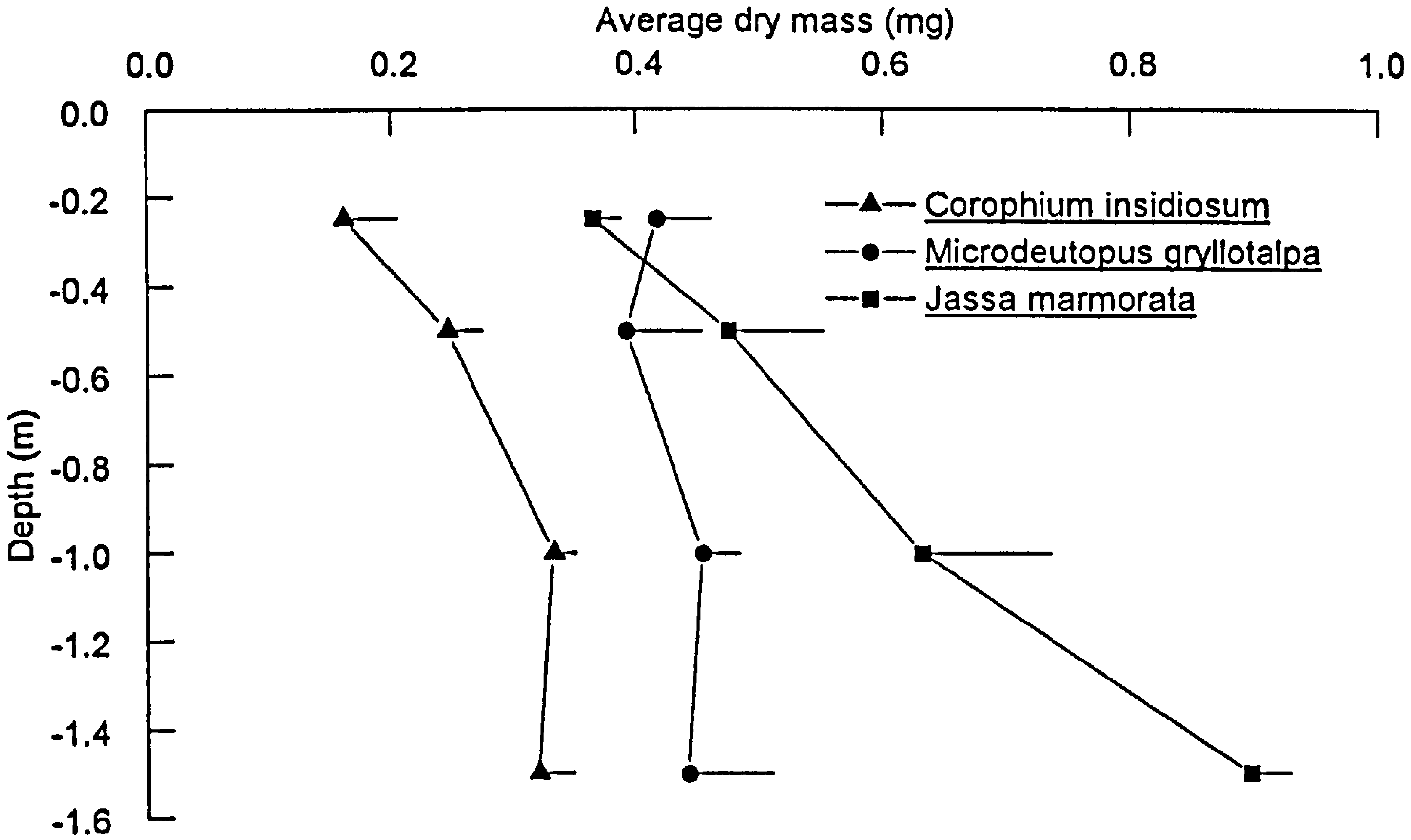

Fig 9.10 Variation in average dry mass of different species of amphipods with depth (data from July 1993). Error bars = standard errors. Tiles had been deployed for one month periods.

Table 9.1 Algal species lists from South Docks and intertidal at New Brighton based on data collected during February and March 1993. (+) indicates species recorded from South Docks by Allen (1992) but not during this study. Species list for tiles also included.

	South Docks	New Brighton	Queens tiles
Bryopsis plumosa	+	+	
Enteromorpha intestinalis	+	+	
Ulothrix subflaccida	+	+	+
Ulva lactuca	+	+	
Bryopsis hypnoides	+		
Cladophora vagabunda	+		+
Enteromorpha compressa	+		+
Enteromorpha linza	+		
Monostroma grevillei	+		
Urospora penicilliformis	+		+
Blidingia ramifera		+	
Cladophora sericea		+	
Enteromorpha prolifera		+	
Prasiola stipitata		+	
Bryopsis hypnoides	(+)		
Ectocarpus siliculosus	+	+	+
Punctaria latifolia	+	+	+
Giffordia granulosa	+		
Giffordia ovata	+		+
Giffordia sandriana	+		
Scytosiphon dotyi	+		+
Elachista fucicola		+	
Fucus vesiculosus		+	
Petalonia fascia		+	
Pilayella littoralis	(+)	+	
Scytosiphon lomentaria		+	
Sorocarpus micromorus	(+)		
Stictyosiphon soriferus	(+)		
Ceramium rubrum	+	+	
Polysiphonia urceolata	+	+	
Ceramium strictum agg	+		
Erythrotrichia carnea	+		
Palmaria palmata	+		
Antithamnion plumula	+		
Audouinella daviesii		+	
Audouinella purpurea		+	
Porphyra purpurea	(+)	+	
Porphyra umbilicalis		+	
Audoinella secundata	(+)		
Vaucheria spp	+		

that no real pattern of development was observed here.

9.4 DISCUSSION

The most likely source of algal diaspores which gave rise to the dock flora is the seaweeds of the River Mersey. If the dock algae had been recruited entirely from the river then one might expect to find the former taxa in similar abundance in the estuary. The Jaccard coefficient of similarity between the docks and New Brighton for the species list in Table 9.1 is 0.22. This indicates that there are substantial differences in the flora present at these two sites. One of the most noticeable differences is the absence of *Fucus* species from the docks despite a significant population in the adjoining estuary. Other noticeable absentees from the docks include *Blidingia ramifera*, *Prasiola stipitata*, *Pilayella littoralis* and *Audouinella* spp, although *Pilayella littoralis* was recorded by Allen (1992). Similarly there are a number of species present in the docks but absent from New Brighton, for example *Antithamnion plumula*, *Urospora penicilliformis* and *Giffordia* spp. Three possible explanations can be put forward to account for the observed absences from the docks. Firstly they may be limited by the supply of spores, secondly by some physical attribute of the dock environment or thirdly by biotic influences such as selective grazing.

Dispersal of diaspores over relatively short distances has been recorded for a number of species of macrophyte (Deysher & Norton 1981) including *Fucus* (Arrontes 1993). Deysher & Norton (1981) and van den Hoek (1987) noted that long distance dispersal of up to 1.3km could occur via drifting adult plants which subsequently release spores. The establishment of a viable community of a dioecious fucoid requires that two zygotes of different sex arrive and mature at the same time (Arrontes 1993). To date however, only one specimen of drift *Fucus* has been recorded from the South Docks. To avoid large inputs of water, heavily loaded with nutrients and sewage, the intake of water to the docks is kept to a minimum when locking vessels in or out (see section 2.4.1). This concomitantly reduces the supply of diaspores to the system. In addition, the time since the docks were first isolated and dredged is still reasonably short, less than seven years and this may simply not have given sufficient time for enough spores to enter the docks. However the coastal defences at New Brighton which support *Fucus* were built at about the same time as the South docks restoration. It is also possible that the diaspore size and method of attachment may limit some species in the calm conditions found within the docks, so that species like *Fucus* with relatively heavy eggs simply settle out before they have a chance to come in contact with a wall or other hard substrate.

The distributions of algae are known to be strongly influenced by the physical environment. This is particularly true where conditions are harsh, such as the intertidal (Schonbeck & Norton 1978, Lubchenco 1980) where desiccation is a problem or in areas where organisms experience low or extreme salinities (Khfaji & Norton 1979). Other physical factors which may be important include temperature (Arrontes 1993) and wave exposure. As mentioned before, conditions in the docks are relatively benign. The temperature changes are smaller than in an intertidal habitat, desiccation is rarely experienced and exposure to wave action minimal. It is unlikely that the salinity of the dock water could be sufficiently low to be limiting to most species of marine algae. Most marine organisms could probably tolerate the relatively constant salinity of about 28‰ found in the docks. Certainly intertidal species should be very well adapted to such conditions found here. It is known that intertidal algal species secrete large quantities of mucus as a protection against desiccation during periods of emersion. It is possible that in an environment of constant immersion and relatively little water movement that this mucus builds up on the surface of the plant with negative effects. For instance it may reduce photosynthetic efficiency or lead to bacterial attack or decay. Femino & Mathieson (1980) recorded stunted *Fucus vesiculosus* in pools and suggested this species may require emersion. Similarly *Pelvetia canaliculata* begins to decay if kept submerged for six or more hours out of every twelve (Rugg & Norton 1987). The higher levels of wave action experienced on open shores, compared with the docks may be sufficient to remove any mucus secretion and thereby allow fucoids to grow in intertidal pools. Similarly species that are present in the docks lack some attribute or attributes that would enable them to survive in the intertidal site studied at New Brighton. Such qualities are perhaps much easier to visualise and also better documented with regard to the increasing harsh physical environment up the shore limiting the upperward extension of some species.

A further possibility is that the *Fucus* plants simply become overgrown with epiphytes in the calm, eutrophic conditions found in the South Docks. Vogt & Schramm (1991) recorded a decline of *Fucus* in the Baltic subtidal and attributed this to an increase in dissolved nutrient concentration and a subsequent rise in epiphytes. Preliminary transplant experiments of *Fucus* into Queens Dock have been carried out (G.Russell, Liverpool University, pers. comm.). The results from this showed a considerable growth of epiphytes on the surface of the transplanted specimens which resulted in the decline of the *Fucus* plants.

Grazers can have a very strong role in determining the species composition at any given habitat (Lubchenco 1978, 1980, 1983, Hawkins 1981, Hawkins & Hartnoll 1983, 1985). Grazing molluscs are relatively rare in the South Docks with only a single specimen of *Littorina littorea* (pers. obs.) having been recorded to date. This leaves amphipods as the dominant grazers. Of these *Jassa marmorata* appears to be the dominant species. Brawley & Fei (1987) recorded that the closely related *Jassa falcata* fed mainly on ephemeral or epiphytic algae. Comparative studies of the effects of grazing by gastropods and amphipods suggest that the scraping microphagous snails prevent the establishment of both micro and macroalgae, while biting amphipods exert more of an influence on erect macroalgae (Brawley 1992, Parker *et al*. 1993, Parker & Chapman 1994). Amphipods can have a significant effect on both reducing the biomass of algal stands and also preferentially removing certain species over others. The absence of macrophytes from the docks may be at least partly due to the intense grazing pressure exerted by amphipods in this environment. A series of transplant experiments involving *Fucus* are required to try and determine which of the above factors are the most important cause of fucoid absence from the South Docks.

Seasonality is a well known factor in the ecology of marine algae, with changes in phytoplankton perhaps one of the best documented examples. Seasonal patterns are ultimately regulated by changes in the physico-chemical environment, including incident radiation, day length, nutrients, temperature, wave action, salinity and pH. At one level, seasonality can be viewed as simply a rise in abundance of a species at a particular time of year, when physical conditions are most conducive to growth. Changes in photosynthesis and respiration in response to variation in external, hydrographic or climatic conditions has been recorded for some species of algae (Mathieson & Norall 1975). Peak abundance of a species may also correspond to peak reproductive activity though this may not necessarily be the case. The onset of reproduction is often stimulated by quite specific environmental cues, generally involving light (either total radiation, light quality or photoperiodism), temperature or nutrient concentration. For example, in *Ectocarpus* the formation of unilocular sporangia and hence of gametophytes is favoured by low temperatures (Müller 1962), while conversely in some diatoms sexual reproduction is induced by high temperatures and resistant spore formation by lower temperatures (Durbin 1978). Similarly it has been shown that at least some species of marine algae possess the ability to measure and respond to day length (Dring & Lüning 1975) while certain Laminariales reproduce in response to blue light (Dring & Lüning 1975). A lunar rhythm has also been recorded in certain species, often seen as spore release during spring tides but not during neaps. An endogenous rhythm has been recorded in *Dictyota* corresponding to the spring-neap cycle (Müller 1962) but in other species, such as *Ectocarpus siliculosus* and *Cutleria multifida*, it can be mediated by the secretion of pheromones (Jaenicke 1977). Rich nitrogen supplies have been found to favour asexual reproduction in *Ulva fasciata*, while sexual reproduction was enhanced by nitrogen depletion (Mohsen *et al.* 1974). When more than one species is present in a system, changes in the physical environment over time, can lead to switches in the relative competitive ability of the species concerned and hence their abundances over time. Such changes may even be mediated by the algae themselves where they have a significant effect on their environment and thereby facilitate the arrival of another species. Differences in reproductive cues can also lead to such patterns of changing abundance and may have important consequences as far as niche separation and competition avoidance are concerned (see Santelices 1990 for review).

Phytoplankton could probably be considered the most important algae in the docks. Details of seasonality of this group in the docks can be found in Allen (1992). Changes in the phytoplankton, however, can strongly affect the physical environment, particularly with regard to light penetration and water chemistry, for example nutrient concentrations. It is therefore difficult to discuss the seasonality of benthic algae without reference to planktonic algae. General details of seasonal changes in the physical environment of the docks can be found in chapter 2. Essentially, the spring phytoplankton blooms, which begin in March, reduce light transmission and nutrient concentrations, particularly dissolved nitrogen and silica (Allen 1992). The increase in phytoplankton is associated with greater incident radiation and a rise in the water temperature of the dock. These latter factors will tend to increase benthic as well as planktonic algal growth, although the phytoplankton probably has a strong negative effect on benthic algal growth, mostly as a result of shading.

Applying the details of the physico-chemical environment firstly to simple changes in the standing crop of benthic algae we see that the major peak in benthic algal mass is in July (Fig 9.4), when hours of sunlight are actually starting to decline (Fig 9.2). At this time the temperature of the docks is still relatively high and nutrient concentrations quite low (Fig 9.3). There was a slight improvement in water clarity at this time (Fig 9.2) indicating a decrease in phytoplankton, perhaps caused by a combination of the reduced nutrient concentrations and incident radiation. This apparent increase in benthic algal mass when phytoplankton concentrations drop, combined with the July peak being much more marked on the shallower tiles (Fig 9.4) seems to implicate available light as being one of the strongest influences on benthic algal mass. Available light is one of the most important factors for macrophytes growing in fresh-water habitats (Spence 1982). The phytoplankton levels appear to effectively outcompete benthic algae for light earlier in the year causing a drop in benthic algal mass during May and June when conditions are apparently more favourable apart from the drop in water clarity and perhaps nutrient concentrations, both as a result of increased phytoplankton abundance. A similar effect of phytoplankton blooms reducing benthic production can be found in freshwater lakes where increasing eutrophication leads to dense phytoplankton blooms but reduced benthic plant growth (Lachavanne 1985, Caffey & Clayton 1988, Balls *et al.* 1989). Grazers are unlikely to have had a significant effect on this seasonal abundance simply due to the method used, with the tiles only being left in place for one month intervals. This probably did give enough time for a sufficient growth of algae to develop to allow an increase in amphipod numbers. However, it seems unlikely that there would have been much time left after this for the amphipod population to graze the algae to any great extent before the tiles were removed.

The temporary nature of the tiles used in this study means that any monthly change in species abundance on them, is essentially a product of reproduction and growth of the species concerned. The switches in species abundance from diatoms to brown ephemerals and then to green ephemerals later in the year before diatoms once again become the abundant group must ultimately be mediated by changes in the physical environment of the docks. Different species have different environmental optima. As the physical environment changes through time, so too does the vegetation structure. The species concerned effectively have a temporal niche (Cormaci *et al.* 1984). For example the brown ectocarpoid species may be competitive dominants at lower temperatures while *Enteromorpha* and *Cladophora* become dominant when the temperature increases. Diatoms are normally held to be weak competitors having only a pioneer role in seaweed succession studies on rocky shores (Hawkins 1981, Hill 1990) . Their absence from tiles during the summer months may either be a reflection of their poor competitive ability, or due to reduced dissolved silica levels during this period leading to slow growth.

It is impossible from data currently available to tease out which of the above factors or combination of factors is most important to this system. Continuation of this study for at least one more year would allow the application of more powerful multivariate analysis to the data. This could give a better idea of the relative importance of the various physical parameters measured in changes in species abundance.

The ephemeral nature of the algal species present in the docks means that any patterns of zonation must occur over relatively short periods of time. Secondly, as stated above, physical stress such as heat or desiccation, is unlikely to be an important factor in setting zonation patterns in this system. The only place this occurs is on the wall around water surface and the unpredictable nature of the submersion regime here makes it relatively impossible for any species to survive on a long term basis. Differences that do occur in the physical environment with depth, with the exception of light, are unlikely to have an effect on the zonation of benthic organisms. Temperature differences are generally small, haloclines occur only very rarely and while oxygen concentration can get quite low towards the bottom of the dock it is unlikely to have affected the growth of algae on the top 2m of wall studied here (see Chapter 2). Competition for light, however, is likely to have been one of the primary influences affecting the distribution of algae here, as it is in similarly benign fresh-water systems (Spence 1982).

During the study only two quite noticeable examples of zonation of algae were found (Fig 9.7). Of these the transition from *Enteromorpha* at the surface to *Cladophora* deeper down was more clear than that from diatoms to ectocarpoid algae. Differing competitive abilities for light seems to be the most likely explanation to account for this pattern. Two mechanisms can be suggested as causes of changes in relative competitive ability between two species with depth. Firstly it may be that different species are utilising different wavelengths of light and that the available light spectrum is changing with depth. This could be as a result of reflection or absorption of light by both the water itself and any phytoplankton that is present. This seems an unlikely explanation in this instance, however, as both *Enteromorpha* and *Cladophora* are predominantly using chlorophyll to absorb light. The second possibility is that there are differences between the two species with regard to how efficiently they use what light is available. For instance *Cladophora* may have a light saturation point at a lower irradiance than *Enteromorpha* but it may also require a lower irradiance for compensation between photosynthesis and dark respiration. Such differences in efficiency of use of light by different species is well known but further experiments are required to test their validity in this system. The structural differences between *Enteromorpha* and *Cladophora* may also be quite important. *Enteromorpha* is a thalloid species, whereas *Cladophora* is filamentous. It is possible that *Enteromorpha* suffers from self shading, particularly when light levels are low.

The importance of amphipods in the dock ecosystem is confirmed by results from the long-term tiles placed in Queens Dock. Here, once the initial bloom of benthic algae had been grazed there was no significant resurgence on these tiles. Similarly strong effects of amphipod grazing have been recorded in other systems (Brenner *et al*. 1976, Howard 1982, D'Antonio 1985, Hootsmans & Vermaat 1985, Duffy 1990). It is possible that a low density of amphipods remained on the surface of the permanent tiles, constantly grazing any algae, before it had a chance to grow. Similarly, the benthic algal blooms observed on the temporary tiles were only possible because the tiles were introduced as fresh substrate with no amphipods present.

Once the algae began to bloom, however, amphipods became attracted to the tile and proceeded to graze the algae.

The absence of gastropods from this system makes it easy to study the dynamics of amphipods in isolation. A positive relationship was obtained between algal and amphipod mass on the temporary tiles (Fig 6.7) This is almost certainly as a result of the temporary nature of the substrate and the fact that as stated above the amphipods have not had sufficient time to graze the algae. Certainly much work could be done studying the amphipod - algae dynamics in this system. The slightly S-shaped curve (Fig 6.7) seems to suggest that a certain mass of algae must be present before amphipods will begin to inhabit the area. It is possible that this is a result of the very smooth nature of the tile which leaves few hiding places for amphipods and would leave them open to predation, until there is sufficient algae to provide cover. Instances of predation having a strong affect on both abundance and distribution of amphipods has been recorded in a number of systems (Vince *et al*. 1976, Nelson 1979, Lancellotti & Trucco 1993). De Witt (1987), working on *Microdeutopus gryllotalpa*, showed that this species preferentially settled on areas with a higher food concentration and greater topographic relief. A number of studies have also shown emigration of amphipods from an area as a result of either predation, disturbance, reproduction or crowding (Ambrose 1984, De Witt 1987). This behaviour would help explain why the curve in fig 9.7 does apparently start to level off at high algal densities. Again, further research is really required to verify the above hypotheses.

While the amount of information on the diets of amphipods has increased significantly over the last ten years (Zimmerman *et al*. 1979, Hudson 1983, Icely & Nott 1985, Duffy 1990, Denton & Chapman 1991, Lancellotti & Trucco 1993, Parker *et al*. 1993), the vast number of species and the variability found even within the same genus (see Duffy 1990) mean that information relating to the diet of specific species is often lacking. The amphipods present on the tiles were dominated by *Jassa marmorata*, with lower densities of *Microdeutopus gryllotalpa* and *Corophium insidiosum*. The data that are available on diets of these species suggest that *Corophium* and *Microdeutopus* are typically tube dwelling suspension or detrital feeders. *Jassa* on the other hand is free living and well equipped for grazing filamentous macroalgae. This would explain why *Jassa* was the dominant species on the temporary tiles where there was often a dense stand of algae. The presence of these algae probably had a negative effect on *Corophium* and *Microdeutopus*, by inhibiting water movement and therefore supply to these species, which typically inhabit mud tubes actually on the tile itself. Studies into the population dynamics of *Microdeutopus* and *Corophium* indicate they follow a pattern of continuous reproduction and recruitment (Karakiri & Nicolaidou 1987). *Corophium insidiosum* can grow to maximum size in as little as one month (Birklund 1977). These results are borne out by this study, where amphipods were found to colonise the tiles throughout the summer, from June to September. *Gammarus salinus* has also been recorded from the South Docks (Allen 1992); this species was not, however, recorded on the tiles. This may have been partly due to the annual life cycle of this species (Karakiri & Nicolaidou 1987) which perhaps makes it less well suited to take advantage of sudden blooms of macroalgae.

The strong grazing pressure exerted by amphipods in this system seems to make it quite unlikely that severe problems with macroalgal blooms will be experienced here. Hull (1987) and Raffaelli *et al*. (1991) both recorded reductions in amphipod abundance following the development of a macroalgal mat. *Corophium* was the main species here, however, and as stated above this is a detritivore and can not graze macroalgae directly. It is interesting that *Jassa marmorata* was not recorded in these studies.

This study has been primarily concerned with the growth of ephemeral algae on the dock walls. Where problems have been experienced with macroalgal blooms the initial growth of algae has often occurred on mud bottoms (Sfrisco *et al* 1988, 1989, 1992). The Venice Lagoon has suffered particularly badly from these blooms (Sfriso *et al* 1988, 1989, 1992). Here, species such as *Enteromorpha* proliferate on the mud bottom. Photosynthesis causes a build-up of oxygen bubbles on the plant surface. These, combined with the release of hydrogen sulphide from the mud, cause the plants to become detached and float to the surface, where they can form dense mats (Sfriso *et al* 1992). However, the Venice Lagoon is only about 1m deep. Such problems are much less likely to occur in the deeper South Docks and relatively little algal growth was observed on the deeper tiles. However, a thick mat of *Vaucharia litorea* was observed on the mud bottom of Salthouse Dock during the summer of 1989 (Allen 1992). The fact that this was not grazed by amphipods perhaps indicates that the *Mytilus* matrix on the dock wall provides an important refuge for amphipods. Therefore while this group prevents heavy algal growth on the walls, macroalgal blooms could still occur on the dock bottom. This is certainly an area requiring further research.

In summary, the docks support an assemblage of ephemeral algae with no perennial species recorded to date. These species display a seasonal pattern of development with diatoms most abundant over the winter being replaced by brown ephemeral species and later green ephemerals. The changes in species composition are probably brought about by changes in the physical environment in the dock. Some weak patterns of zonation were observed which may have been caused by differing competitive abilities of the species in response to light. Amphipods exert very strong grazing pressure on algae, probably preventing the development of dense stands of algae on the walls, except on freshly introduced substrate. Such areas can occur around the water surface through changes in water level, caused by locking vessels in or out. Minimising such disturbance should reduce the chances of the development of the so called 'green tides' in this system. The possibility of algal growth on the dock bottom is an area which should be studied further.

CHAPTER 10

GENERAL DISCUSSION

10.1 INTRODUCTION

The following discussion deals with three aspects of this thesis which are of particular importance to the management of the South Docks system. The first considers the causes of the spatial variation in the benthos the second with potential problems with benthic algae. Finally the overall stability of the system is assessed, with particular reference to the dense filter-feeder assemblage and the importance of maintaining good water quality. Each section includes suggestions for further research to address the questions this study has raised. Consideration is also given to potential management options which might be implemented to improve either the aesthetics or the stability of the ecosystem.

10.2 SPATIAL VARIATION OF THE BENTHOS

There are strong indications that the communities found in docks close to the intake from the Mersey show considerable differences to those found further from the intake. Preliminary observations indicate that the water clarity is generally lower in the docks close to the intake and that this is primarily a result of higher levels of suspended solids rather than increased phytoplankton abundance (N.Fielding & V.Wanstall, Liverpool University, pers. comm.). Phytoplankton densities actually appear to be lower. This may be responsible for the switch in species composition from the community dominated by *Molgula*, *Obelia* and *Botryllus*, as found in Brunswick Dock close to the intake from the Mersey, to one more dominated by *Mytilus* and *Ciona* as found in Albert Dock.

Studies are under way to confirm the above results. Tiles have been deployed in both Albert and Brunswick Docks to observe the pattern of community development at these two sites in more detail, with particular reference to the available larval supply (N.Fielding, Liverpool University, pers. comm.). This experiment will also include the transfer of tiles between these two docks to assess the survival of the dominant species under different environmental conditions. As regards management options, if increased levels of suspended sediment are responsible for the change in community structure, there is little remedial action that can be taken. Intake of water from the Mersey has already been minimised and there will always be a certain amount of additional disturbance in Brunswick and Coburg due to the use of these docks as a marina.

An improvement in the water quality of Morpeth is essential if the surrounding area is to be redeveloped in a similar fashion to the South Docks complex. The problems associated with Morpeth are low larval supply, due to the virtual complete isolation of this dock from the Mersey, reduced salinity and problems with the very dense algal blooms currently found there. Preliminary trials to introduce *Mytilus* to this dock resulted in heavy mortality (pers. obs.). It is recommended that this is repeated but in a more controlled way, perhaps including laboratory trials, in order to assess the exact reasons for the mortality (e.g. reduced salinity, toxicity of phytoplankton, increased concentration of ammonia or reduced dissolved oxygen).

The mud present in the docks is extremely fine and supports only a low density of opportunistic species. Longer lived species, such as *Macoma* have been recorded here (Allen 1992) but have not proliferated. It seems likely that the mud habitat is quite harsh as a result of the fine particle size. This makes it both physically unstable and also prone to low levels of dissolved oxygen, particularly as a result of phytoplankton decay. It is important, however, to establish whether any filter-feeding species can survive here, or whether the sediment can be manipulated in some way to allow the survival of such species. One possibility, increasing the average particle size through the addition of coarser sediment is potentially a major route through which improved water quality could be achieved.

10.3 BENTHIC ALGAE

From the results presented in chapter 9, it appears that growth of benthic algae is unlikely to be a problem on the dock walls, due to intense grazing pressure by benthic amphipods here. Serious problems with macroalgal mats floating on the water surface have occurred in other ecosystems comparable with the docks, such as the Venice Lagoon (Sfriso *et al*. 1988, 1989, 1992). However, in the docks the only problems with macroalgae have been related to fluctuations in the water level, first leaving material emersed and subsequently washing it off. The level is now held much more constant and future problems are unlikely. However, this study did not examine the possibility of algal growth on horizontal surfaces, and particularly the dock bottom. Growth of *Vaucheria* has been recorded on the bottom of Salthouse Dock. It is therefore possible that such growths of benthic algae may be a problem elsewhere, particularly the docks with clearer water. This could be examined further through the use of horizontal tiles deployed at a range of depths and also varying distances from the wall, as a further assessment of grazing impact.

The problem of benthic algae is particularly important with regard to the future redevelopment of dock basins. One of the decisions facing planners is how deep the basins should be dredged. This is particularly important as the process of dredging is very expensive. If the dock is not dredged deep enough there may be problems with benthic algae growing on the dock bottom and subsequently rising to the surface. On the other hand, if it is too deep it may encourage stratification and low levels of dissolved oxygen near the dock bottom.

10.4 The stability of the benthic community in the South Docks

There is still insufficient information to assess fully the stability of the dock ecosystem, although there are strong indications, particularly from the *Mytilus* population dynamics (chapter 6), that it may be unstable in the long-term. The following discussion deals first with what is meant by stability and then considers the perturbations to which the communities in the docks are subject. Finally the apparent stability of the system, on the basis of current knowledge, is assessed.

A number of workers have used different terminologies for essentially the same concepts of stability (eg. Margalef 1969, Holling 1973, Boesch 1974, Oriens 1974). Connell & Sousa (1983) reviewed this and the terminology adopted here follows their suggestions. 'Resistance' is the ability of a system to remain at equilibrium when faced with a potentially disturbing force (Boesch 1974), while 'adjustment' is the ability of a system to return to equilibrium after being perturbed (Margalef 1969). Adjustment stability has been further subdivided into 'amplitude' which is the distance from which the system is capable of returning (Hurd *et al.* 1971) and 'elasticity' which is the speed of return (Orians 1974).

When discussing stability it is important to consider the perturbations to which the system is subjected. The community in the docks is not really subject to much physical disturbance. There is some evidence (see above) that conditions towards the dock gates become increasingly harsh due to lower phytoplankton densities and higher levels of suspended solids. The harsh conditions over winter could also be regarded as a perturbation. To date it has been impossible to assess the impact of predation on the community, though this is potentially quite important.

These perturbations are unlikely to vary much between years, although occasional harsh winters could have considerable effects on the shorter lived species (see comments in Hawkins *et al.* 1992b). This ephemeral fouling assemblage, composed mainly of tunicates shows considerable fluctuations between years, although the exact reasons for these fluctuations are unclear. However, this assemblage has both low resistance and low adjustment in the face of perturbations. On the other hand, the adult *Mytilus* population which is much more important to the ecology of the docks, appears to resist all perturbations and is apparently quite stable. However, there is evidence of limited recruitment of this species and before the stability of the population can be fully assessed, the reasons for this low recruitment must be ascertained.

The results from chapter 8 suggested that resources, particularly phytoplankton, may be limiting to organisms growing on the dock wall. The total biomass of *Mytilus* in Albert Dock has remained relatively constant and there is a strong possibility that newly settling juveniles are food limited. The question from a stability viewpoint is what will happen when the adult population begins to decline. Three possibilities can be recognised. Firstly they may be gradually replaced, in which case the system becomes stable. Secondly the mussels may be replaced by other filter-feeders or lastly they may not be replaced and the system reverts to the original state of poor water quality. The evidence from Princes Dock suggests that the final possibility is unlikely, if only because management techniques can prevent serious hypoxia. While the results from this dock are not complete, there are strong suggestions that low phytoplankton densities can be maintained by the short lived filter-feeders such as *Ciona* and *Ascidiella*. However, such a system is potentially quite unstable, if recruitment fails for example. However, the recruitment of *Mytilus* also appears to be quite variable, although the probability of settlement is quite high within the lifespan of the mussel. The population which presently dominates the South Docks settled over quite a short period of time and a similar heavy recruitment was observed in Princes Dock in 1993. The recruitment on tiles in Albert Dock also appears to be variable between years. It seems likely that the community development in the South Docks may parallel that observed in Princes; should the density of *Mytilus* drop very low, there is a high probability of another heavy recruitment event. It is possible, however, that some interchange of water between the docks and the Mersey may also be required.

It is also possible that the *Mytilus* are not recruiting to the adult population as a result of predation, either through *Carcinus* or from the adult population actually filtering out the larvae before they settle. It is important now to try and establish which of these explanations or combination of explanations is correct. The easiest way of approaching this is through the clearance of relatively large areas of dock wall. These would still be subject to predation from *Carcinus* but if made sufficiently large would be outside the boundary layer of reduced phytoplankton due to the filtration of the *Mytilus* assemblage. Clearing a range of sizes would allow an assessment to be made of both the degree of influence the filter-feeders have and also the minimum size of clearance required to allow *Mytilus* settlement, if resources are indeed the limiting factor.

The results of such an experiment could then be used to derive a management strategy. If predation from *Carcinus* turns out to be limiting recruitment then increased recruitment could be achieved through culling *Carcinus* for about two years. This should allow *Mytilus* to settle and grow to a size beyond which can be easily consumed by *Carcinus*. However, the current evidence suggests that competition is the major limiting factor. Once the necessary patch size has been established which allows *Mytilus* to settle and survive a mosaic of such patches could be created around the docks thus stabilising the population.

In the instance that the adult *Mytilus* population is lost from the South Docks completely, larvae would have to be supplied from elsewhere. These could either come from the Mersey itself, by flushing water through the docks when *Mytilus* larvae are abundant in Liverpool Bay, or by adding adult *Mytilus* on ropes. It is perhaps paradoxical that increased exchange of water with the Mersey is the opposite of the currently recommended management option.

10.5 SUMMARY

In summary, over the last seven years we have learnt much about the ecology of both the South Docks, and other docks in the Liverpool area. However a number of questions remain which are pertinent to the continued successful management of this ecosystem. In particular, *Mytilus* is considered very important in maintaining good water quality in the docks and while this species appears stable in the short-term the longer term stability is in doubt. Work now should concentrate on ascertaining the reasons for the low rates of recruitment to the *Mytilus* population.

The ecosystems found in disused dock basins remain some of great biological interest. The study of such systems also represents an area where both the pure and applied aspects of marine ecology may be intertwined.

REFERENCES

ALLEN,J.R. (1992): Hydrography, ecology and water quality management of the South Docks, Liverpool. Ph.D. Dissertation, University of Liverpool. 265 pp.

ALLEN,J.R. & S.J. HAWKINS (1993a): Can biological filtration be used to improve water quality? In: K.N.,WHITE, E.G. BELLINGER, A.J. SAUL, M. SYMER & K. HENDRY: Eds Urban Waterside Regeneration, problems and prospects. Ellis Horwood Press, UK: 377-385.

ALLEN,J.R. & S.J. HAWKINS (1993b): Pelagic - benthic interactions in an enclosed coastal ecosystem : the impact of Mytilus edulis populations on water quality in the South Docks, Liverpool. In: R.F.,DAME: Ed Bivalve Filter Feeders in Estuarine and Coastal Ecosystem Processes. NATO ASI series, subseries a: Ecological Sciences : 515-516.

ALLEN,J.R., S.J. HAWKINS, G.R. RUSSELL, & K.N. WHITE 1992: Eutrophication and urban renewal: Problems and perspectives for the management of disused docks. Science of the Total Environment : 1283-1295.

ALLEN,J.R., S.B. WILKINSON, & S.J. HAWKINS in submission: Redeveloped docks as artificial lagoons : the development of brackish water communities and potential for conservation of lagoonal species. Aquatic Conservation.

AMBROSE,W.G. 1984: Increased emigration of the amphipod *Rhepoxynius abronius* (Barnard) and the polychaete *Nephtys caeca* (Fabricius) in the presence of predators. Journal of experimental marine biology and ecology 80: 67-75.

ANDERSIN,A.B., J. LASSIG, L. PARKKONEN, & H. SANDLER 1978: The decline of macrofauna in the deeper parts of the Baltic Proper and the Gulf of Finland. Kieler Meeresforschungen Sonderheft 4: 23-52.

ANDERSIN,A.B., J. LSSIG, & H. SANDLER (1977): Community structures of soft-bottom macrofauna in different parts of the Baltic. In: B.F.,KEEGAN, P. O'CEIDIGH & P.J.S. BOADEN: Eds Biology of benthic organisms. 11th European Symposium on Marine Biology, Galway, Oct 1976 : 7-20.

ANGER,K. 1978: Development of a subtidal epifaunal community at the island of Helgoland. Helgoländer wissenschaftliche Meeresuntersuchungen 31: 457-470.

ANWAR,N.A., C.A. RICHARDSON, & R. SEED 1990: Age determination, growth rate and population structure of the horse mussel *Modiolus modiolus*. Journal of the Marine Biological Association of the United Kingdom 70: 441-457.

ARRONTES,J. 1993: Nature of the distributional boundary of *Fucus serratus* on the north shore of Spain. Marine Ecology Progress Series 93: 183-193.

ASMUS,R.M. & H. ASMUS 1991: Mussel beds: limiting or promoting phytoplankton? Journal of experimental marine biology and ecology 148: 215-232.

BAIRD,R.H. & R.E. DRINNAN 1957: The ratio of shell to meat in Mytilus as a function of tidal exposure to air.Journal du Conseil Permanent International pour l'Exploration de la Mer 22: 329-336.

BALLS,H., B. MOSS, & K. IRVINE 1989: The loss of submerged plants with eutrophication. I. Experimental design, water chemistry, aquatic plants amd phytoplankton biomass in experiments carried out in ponds in the Norfolk Broadland. Freshwater Biology 22: 71-87.

BAMBER,R.N. (1988): A survey of the intertidal soft sediment fauna of the Mersey Estuary 1987. Leatherhead Central Electricity Research Laboratories.

BARNES,R.S.K. 1991: European estuaries and lagoons : a personal overview of problems and possibilities for conservation and management. Aquatic Conservation: Marine and Freshwater Ecosystems 1: 79-87.

BARNES,R.S.K., P. CALOW, & P.S.W. OLIVE (1988): The invertebrates : a new synthesis. Blackwell Scientific Publications, Oxford. 582 pp.

BARTHEL,D. 1986: On the ecophysiology of the sponge *Halichondria panicea* in Kiel Bight. I. Substrate specificity, growth and reproduction. Marine Ecology Progress Series 32: 291-298.

BASSINDALE,R. 1938: The intertidal fauna of the Mersey Estury. Journal of the Marine Biological Association of the United Kingdom 23: 83-98.

BATTY,R.S. 1994: The effect of temperature on the vertical distribution of larval herring (*Clupea harengus* L.). Journal of experimental marine biology and ecology 177: 269-276.

BAYNE,B.L. (Ed.) (1976): Marine Mussels, their ecology and physiology. 1st ed. Cambridge University Press.

BEATTY,N. & J.C. ALDRICH (1989): Effects of changes in microhabitat on the morphology and condition of *Mytilus edulis*. In: J.C.,ALDRICH: Ed Phenotypic Responses and Individuality in Aquatic Ectotherms. Japaga, Ashford,Ireland: 41-54.

BELLINGER,E.G., K. HENDRY, & K.N. WHITE (1993): Nutrient cycling in a closed dock and its biological implications. In: K.N.,WHITE, E.G. BELLINGER, A.J. SAUL, M. SYMES & K. HENDRY: Eds Urban waterside regeneration, problems and prospects. Ellis Horwood, U.K.: 358-365.

BERGE,J.A. & V.A. VALDERHAUG 1983: Effect of epibenthic macropredators on community structure in subtidal organically enriched sediments in the inner Oslofjord. Marine Ecology Progress Series 11: 15-22.

BERRILL,N.J. 1935: Studies in tunicate development. Part 3 Differential retardation and acceleration. Philosophical Transactions of the Royal Society of London (B) 225: 255-326.

BERTNESS,M.D., S.D. GAINES, D. BERMUNDEZ, & E. SANFORD 1991: Extreme spatial variation in the growth and reproductive output of the acorn barnacle *Semibalanus balanoides*. Marine Ecology Progress Series 75: 91-100.

BERTNESS,M.D., S.D. GAINES, E.G. STEPHENS, & P.O. YUND 1992: Components of recruitment in populations of the acorn barnacle *Semibalanus balanoides* (Linnaeus). Journal of experimental marine biology and ecology 156: 199-215.

BINGHAM,B.L. 1992: Life histories in an epifaunal community: coupling of adult and larval processes. Ecology 73: 2244-2259.

BIRBECK,T.H. & J.G. McHENDRY 1982: Degradation of bacteria by *Mytilus edulis*. Marine Biology 72: 7-15.

BIRCH,L.C. 1957: The meanings of competition. American Naturalist 91: 5-18.

BIRKLUND,J. 1977: Biomass, growth and production of the amphipod *Corophium insidiosum* Crawford and preliminary notes on *Corophium volutator* (Pallas). Ophelia 16(2): 187-203.

BOARD,P. 1983: The settlement of post larval *Mytilus edulis* (settlement of post larval mussels). Journal of Molluscan Studies 49: 53-60.

BOESCH,D.F. 1974: Diversity, stability and response to human disturbance in estuarine ecosystems. In: Structure, functioning and management of ecosystems. Proceedings of the First International Congress of Ecology, PUDOC, Wageningen: 109-114.

BOTKIN,D.B. (1981): Causality and succession. In: D.C.,WEST, H.H. SHUGART & D.B. BOTKIN: Eds Forest succession: concepts and application. Springer-Verlag, New York: 36-55.

BOULCH,G.T. 1984: Algal blooms and their effects on fishing in the English Channel. Hydrobiologia 116-117: 449-452.

BOYD,D.W. (1989): A preliminary study of pollution in the Salford Docks and Manchester Ship Canal. MSc Thesis, University of Manchester.

BRAWLEY,S.H. (1992): Mesograzers. In: D.M.,JOHN, S.J. HAWKINS & J.H. PRICE: Eds Plant-Animal Interactions in the Marine Benthos. Systematics Association Special Volume No. 46. Oxford Science Publications, Oxford: 235-263.

BRAWLEY,S.H. & W.H. ADEY 1981: The effect of micrograzers on algal community structure in a coral reef microcosm. Marine Biology 61: 167-177.

BRAWLEY,S.H. & X.G. FEI 1987: Studies of mesoherbivory in aquaria and in an unbarricaded mariculture farm on the Chinese coast. Journal of Phycology 23: 614-623.

BRENNER,D., I. VALIELA, C.D. VAN RAALTE, & E.J. CARPENTER 1976: Grazing by *Talochestia longicornis* on an algal mat in a New England salt marsh. Journal of experimental marine biology and ecology 22: 161-169.

BROOKES,A. (1988): Channelized rivers: Perspectives for environmental management. John Wiley & Sons Ltd. 326 pp.

BROWN,R.A. 1984: Geographical variations in the reproduction of the horse mussel, *Modiolus modiolus* (Mollusca:Bivalvia). Journal of the Marine Biological Association of the United Kingdom 64: 751-770.

BUHL-MORTENSEN,L. & T. HOLISAETER 1993: Mollusc fauna along and offshore fjord gradient. Marine Ecology Progress Series 97: 209-224.

BURTON,S. & J. ALLEN (1993): The potential of the South Docks, Liverpool as a venue for fishing competitions., Port Erin Marine Laboratory. 10 pp.

BUSCHMANN,A.H. 1991: Amphipod food preference and *Iridaea* spp (Rhodophyta) spore release and dispersal. Journal of the Marine Biological Association of the United Kingdom 71: 891-897.

CAFFEY,B.T. & J.S. CLAYTON 1988: Changes in the submerged macrophyte vegetation of Lake Ratoiti, central North Island, New Zealand. New Zealand Journal of Marine and Freshwater Research 22: 215-223.

CARTER,J.J. (1985): The influence of environmental contamination on the fauna of the Mersey Estuary. MSc Thesis, University of Manchester.

CARTER,J.W., A.L. CARPENTER, M.S. FOSTER, & W.N. JESSEE 1985: Benthic succession on an articial reef designed to support a kelp-reef community. Bulletin of Marine Science 37: 86-113.

CECCHERELLI,V.U. & R. ROSSI 1984: Settlement growth and production of the mussel *Mytilus galloprovincialis*. Marine Ecology Progress Series 16: 173-184.

CHALMER,P.N. 1982: Settlement patterns of species in a marine fouling community and some mechanisms of succession. Journal of experimental marine biology and ecology 58: 73-85.

CHIPPERFIELD,P.N.J. 1953: Observations on the breeding and settlement of *Mytilus edulis* (L.) in British waters. Journal of the Marine Biological Association of the United Kingdom 32: 449-476.

CLARKE,R.B. (1989): Marine Pollution. 2nd ed. Clarenden Press. 200 pp.

CLEMENTS,F.E. (1928): Plant succession and indicators: a definitive edition of plant succession and plant indicators. H.W.Wilson Company, New York.

COLEMAN,N. & E.R. TRUEMAN 1971: The effect of aerial exposure on the activity of the mussles *Mytilus edulis* L. and *Modiolus modiolus* L. Journal of experimental marine biology and ecology 7: 295-304.

COMELY,C.A. 1978: *Modiolus modiolus* (L.) from the Scottish west coast I. Biology. Ophelia 17: 167-193.

COMMITO,J.A. 1982: Importance of predation by infaunal polychaetes in controlling the structure of a soft-bottom community in Maine, USA. Marine Biology 68: 77-81.

CONLAN,K. (1989): Ecology and Hydrography of an Upper Estuaries Dock: A case study of Preston Docks. Ph.D. Dissertation, University Manchester.

CONLAN,K., K. HENDRY, K.N. WHITE, & S.J. HAWKINS 1988: Disused docks as habitats for estuarine fish: a case study of Preston dock. Journal of Fish Biology 33 (Suppl. A): 85-91.

CONLAN,K., K.N. WHITE, & S.J. HAWKINS 1992: The hydrography and ecology of a re-developed brackish water dock. Estuarine Coastal and Shelf Science 35: 435-452.

CONNELL,J.H. 1961: Effects of competition, predation by *Thais lapillus* and other factors on natural populations of the barnacle *Balanus balanoides*. Ecological Monographs 31: 61-104.

CONNELL,J.H. (1975): Some mechanisms producing structure in natural communities : a model and evidence from field experiments. In: M.L.,CODY, J.M. DIAMOND: Eds Ecology and evolution of communities. Harvard University Press, Cambridge, Massachusetts: 460-490.

CONNELL,J.H. 1983: On the prevalence and relative importance of interspecific competition : evidence from field experiments. American Naturalist 122: 661-696.

CONNELL,J.H. 1985: The consequence of variation in initial vs. post-settlement mortality in rocky intertidal communities. Journal of experimental marine biology and ecology 93: 11-45.

CONNELL,J.H. & M.J. KEOUGH (1985): Disturbance and patch dynamics of subtidal marine animals on hard substrata. In: S.T.A.,PICKETT, P.S. WHITE: Eds The ecology of natural disturbance and patch dynamics. Academic Press, London: 125-151.

CONNELL,J.H., I.R. NOBLE, & R.O. SLATYER 1987: On the mechanisms producing successional change. Oikos 50: 136-137.

CONNELL,J.H. & R.O. SLATYER 1977: Mechanisms of succession in natural communities and their role in community stability and organisation. American Naturalist 111: 1119-1144.

CONNELL,J.H. & W.P. SOUSA 1983: On the evidence needed to judge ecological stability or persistence. American Naturalist 121: 789-824.

CONNOR,J.L. 1980: Distribution and seasonality of macroalgae on oyster communities of central Chesapeake Bay. Botannica Marina 23: 711-717.

CORLETT,J. 1948: Rates of settlement and growth of the 'pile' fauna of the Mersey Estuary. Proceedings & Transactions of the Liverpool Biological Society 56: 2-28.

CORMACI,M., A. DURA, & G. FURNARI 1984: On reproductive phenology of nine species of Ceramiales (Rhodophyta) of East Sicily. Botannica Marina 27: 95-104.

COWDEN,C., C.M. YOUNG, & F.S. CHIA 1984: Differential predation on marine invertebrtes larvae by two benthic predators. Marine Ecology Progress Series 14: 145-149.

CRAWFORD,R.M., A.E. DOREY, C. LITTLE, & R.S.K. BARNES 1979: Ecology of Swanpool, Falmouth, V: Phytoplankton and nutrients. Estuarine Coastal and Shelf Science 9: 135-160.

CROSS,T.F. & T. SOUTHGATE 1983: An approach to ecological monitoring in the rocky intertidal: a survey of Bantry Bay and Dunmanus Bay, Ireland. Marine Environmental Research 8: 149-163.

CUNNINGHAM,P.N., L.C. EVANS, S.J. HAWKINS, G.D. HOLMES, H.D. JONES, & G. RUSSELL (Eds.) (1984): Investigation of potential of disused docks for urban nature conservation. (Report to Nature Conservancy Council). 60 pp.

D'ANTONIO,C. 1985: Epiphytes on the rocky intertidal red alage Rhodomena larix (Turner) C. Agardh : Negative effects on the host and food for herbivores. Journal of experimental marine biology and ecology 86: 197-218.

DARE,P.J. 1976: Settlement growth and production of the mussel *Mytilus edulis* L., in Morecambe Bay, England. Fisheries investigations Ministry of Agriculture, Fisheries and Food London, Series II 28: 1-25.

DARE,P.J., G. DAVIES, & D.B. EDWARDS 1983: Predation of juvenile Pacific oysters (*Crassostrea gigas* Thunberg) and mussels (*Mytilus edulis*) by shore crabs (*Carcinus maenas* (L.)). Ministry of Agriculture Fisheries and Food, Fisheries Research Technical Report 73: 1-15.

DAVIES,A.R. 1987: Varition in recruitment of the subtidal colonial ascidian *Podoclavella cylindrica* (Quoy & Gaimard) : the role of substratum choice and early survival. Journal of experimental marine biology and ecology 106: 57-71.

DAVIES,G., P.J. DARE, & D.B. EDWARDS 1980: Fennced enclosures for the protection of seed mussels (*Mytilus edulis* L.) from predation by shore crabs (*Carcinus maenas* (L.)). Ministry of Agriculture Fisheries and Food, Fisheries Research Technical Report 56: 1-14.

DAYTON,P.K. 1971: Competition, disturbance and community organisation : the provision and subsequent utilization of space in a rocky intertidal community. Ecological Monographs 41: 351-389.

DEAN,T.A. & L.E. HURD 1980: Development in an estuarine fouling community : the influence of early colonists on later arrivals. Oecologia (Berlin) 46: 295-301.

DENLEY,E.J. & A.J. UNDERWOOD 1979: Experiments on factors influencing settlement, surrvival and growth of two species of barnacles in New South Wales. Journal of experimental marine biology and ecology 6: 269-293.

DENTON,A.B. & A.R.O. CHAPMAN 1991: Feeding preferences of gammarid amphipods among 4 species of *Fucus*. Marine Biology 109: 503-506.

DE WITT,T.H. 1987: Microhabitat selection and colonisation rates of a benthic amphipod. Marine Ecology Progress Series 36: 237-250.

DEYSHER,L. & T.A. NORTON 1981: Dispersal and colonisation of *Sargassum muticum* (Yendo) Fensholt. Journal of experimental marine biology and ecology 56: 179-195.

DIAZ,R.J. & C. ERSEUS 1994: Habitat preferences and species associations of shallow-water marine Tubificidae (Oligochaeta) from the barrier reef ecosystems off Belize, Central America. Hydrobiologia 278: 93-105.

DIT-DURELL,S.E.A.L. & J.D. GOSS-CUSTARD 1984: Prey selection within a size-class of mussels, *Mytilus edulis*, by oystercatchers, *Haematopus ostralegus*. Animal Behaviour 32: 1197-1203.

DITTMAN,D. & C. ROBLES 1991: Effect of algal epiphytes on the mussel *Mytilus californianus*. Ecology 72: 286-296.

DOREY,A., C. LITTLE, & R.S.K. BARNES 1973: An ecological study of Swanpool, Falmouth. II Hydrography and its relation to animal distributions. Estuarine and Coastal Marine Science 1: 153-176.

DORIAZIO,R.M., J.A. BOWERS, & J.T. LEHMAN 1987: Food web manipulations influence grazer control of phytoplankton growth rates in lake Michigan. Journal of Plankton Research 9: 891-899.

DRING,M.J. & K. LÜNING 1975: A photoperiod response mediated by blue light in the brown alga *Scytosiphon lomentaria*. Planta 125: 25-32.

DUFFY,J.E. 1990: Amphipods on seaweeds: Partners or pests? Oecologia (Berlin) 83(2): 267-276.

DURBIN,E.G. 1978: Aspects of the biology of resting spores of *Thalassiosira nordenskioeldii* and *Detonula confervacea*. Marine Biology 45: 31-37.

DYBURN,B.I. 1965: The life cycle of *Ciona intestinalis* (L.) f. typica in relation to the environmental temperature. Oikos 16: 109-131.

EBLING,F.J., J.A. KITCHING, L. MUNTZ, & C.M. TAYLOR 1964: The ecology of Lough Ine 13 Experimental observations of the destruction of *M. edulis* and *Nucella lapillus* by crabs. Journal of Animal Ecology 33: 73-82.

EGLAR,F.E. 1954: Vegetation Science Concepts I. Initial floristic composition, a factor in old-field vegetation development. Vegetatio 4: 412-417.

ELMGREN,R. 1975: Baltic meiofauna as indicator of oxygen conditions in the northern Baltic Proper. Merentutkimuslaitoksen Julkaisu Havsforskningsinstitutets Skrifter 239: 265-271.

ELMGREN,R. 1978: Structure and dynamics of Baltic benthos communities, with particular reference to the relationship between macro and meiofauna. Kieler Meeresforschungen Sonderheft 4: 1-22.

ELNER,R.W. & R.N. HUGHES 1978: Energy maximization in the diet of the shore crab *Carcinus maenas*. Journal of Animal Ecology 47: 103-116.

EMMETT,B., K. THOMPSON, & J.D. POPHAM 1987: The reproduction and energy storage cycles of two populations of *Mytilus edulis* (Linne) from British Columbia. Journal of Shellfish Research 6: 29-36.

ENS,B.J. & J.D. GOSS-CUSTARD 1984: Interference among oystercatchers, *Haematopus ostralegus*, feeding on mussels *Mytilus edulis*, on the Exe Estuary. Journal of Animal Ecology 53: 217-231.

ENVIRONMENTAL RESOURCES LIMITED (1993a): Stage IIIa Environmental Studies: E1 Plankton Studies in the Mersey Estuary. Report to Mersey Barrage Company, March 1993.

ENVIRONMENTAL RESOURCES LIMITED (1993b): Stage IIIa Environmental Studies: E2 Saltmarsh studies in the Mersey Estuary. Report to Mersey Barrage Company, February 1993.

ENVIRONMENTAL RESOURCES LIMITED (1993c): Stage IIIa Environmental Studies E6 - Water Quality Modelling. Report to Mersey Barrage Company, January 1993.

FARRELL,T.M. 1989: Succession in a rocky intertidal community : the importance of disturbance size and position within a disturbed patch. Journal of experimental marine biology and ecology 128: 57-73.

FARRELL,T.M. 1991: Models and mechanisms of succession : an example from a rocky intertidal community. Ecological Monographs 61: 95-113.

FELL,P.E. & A.M. BALSAMO 1985: Recruitment of *Mytilus edulis* L. in the Thames Estuary, with evidence for differences in the time of maximal settling along the Connecticut shore. Estuaries 8: 68-75.

FEMINO,R.J. & A.C. MATHIESON 1980: Investigations of New England marine algae IV. The ecology and seasonal succession of tide pool algae at Bald Head Cliff, York, Maine,USA. Botannica Marina 23: 319-332.

FORTIER,L. & R.P. HARRIS 1989: Optimal foraging and density-dependent competition in marine fish larvae. Marine Ecology Progress Series 51: 19-33.

FOSTER,M.S. 1975: Regulation of algal community development in a *Macrocystis pyrifera* forest. Marine Biology 32: 331-342.

FOSTER,P., J. BEARDALL, D. VOLTOLINA, & G. SAVIDGE 1985: The effects of wind, phytoplankton and density continuities upon ammonia distributions in Liverpool Bay. Estuarine Coastal and Shelf Science 20: 463-475.

FOSTER,P., D. VOLTOLINA, & J. BEARDALL 1984: A seasonal study of the distribution of surface state variables in Liverpool Bay. 6. Autumn. Journal of experimental marine biology and ecology 77: 69-79.

FRASER,J.H. (1931): The fauna and flora of the Mersey Estuary with special reference to pollution and sedimentary deposits. MSc Thesis, University of Liverpool. 154 pp.

FRASER,J.H. 1935: The fauna of Liverpool Bay shrimping grounds and the Morecambe Bay prawning grounds as revealed by the use of a beam-trawl. Proceedings & Transactions of the Liverpool Biological Society : 65-78.

FRASER,J.H. 1938: The fauna of fixed and floating structires in the Mersey Estuary and Liverpool Bay. Proceedings & Transactions of the Liverpool Biological Society 51: 1-21.

FRECHETTE,M. & E. BOURGET 1985: Energy flow between the pelagic and benthic zones : Factors controlling particulate organic matter available on an intertidal mussel bed. Canadian Journal of Fisheries and aquatic Science 42: 1158-1165.

FRIDRIKSSON,S. (1975): Surtsey : Evolution of life on a volcanic island. 1st ed. Butterworths, London. 198 pp.

GAINES,S.D. & J. ROUGHGARDEN 1985: Larval settlement rate: a leading determinant of structure in an ecological community of the marine intertidl zone. Proceedings of the national Acadamy of Science USA 82: 3707-3711.

GIESE,A.C. & J.S. PEARSE (1974): Introduction : General Principles. In: A.C.,GIESE, J.S. PEARSE: Eds Reproduction of marine invertebrates. Academic Press, New York: 2-38.

GLIWICZ,M.Z. 1986: Predation and the evolution of vertical migration in zooplankton. Nature 320: 746-748.

GLYNN,P.W. 1988: El Nino-southern oscillation 1982-83: nearshore population, community and ecosystem responses. Annual Review of Ecology and Systematics 19: 309-345.

GOSLING,E. (Ed.) (1992): The Mussel *Mytilus* : Ecology, Physiology, Genetics and Culture. 1st ed. Elsevier, Amsterdam.

GRAVE,C. 1944: The larva of *Styela* (*Cynthia partita* : structure, activities and duration of life. Journal of Morphology 75: 32-56.

GRAVINA,M.F., G.D. ANIZZONE, & A. BELLUSCIO 1989: Polychaetes of an artificial reef in the central Mediterranean Sea. Estuarine Coastal and Shelf Science 28: 161-172.

GRAY,C.A. 1993: Horizontal and vertical trends in the distributions of larval fishes in coastal waters off central New South Wales, Australia. Marine Biology 116: 649-666.

GRAY,J.S. 1977: The stability of benthic ecosystems. Helgolander wiss. Meeresunters 30: 427-444.

GREZE,I.I. 1968: Feeding habits and food requirements of some amphipods in the Black Sea. Marine Biology 1: 316-321.

GRIME,J.P. (1979): Strategies and vegetation processes. 1st ed. John Wiley & Sons, Chichester.

GRIZZLE,R.E. 1984: Pollution indicator species of macrobenthos in a coastal lagoon. Marine Ecology Progress Series 18: 191-200.

GROSBERG,R.K. 1982: Intertidal zonation of barnacles: the influence of planktonic zonation of larvae on the vertical distribution of adults. Ecology 63: 894-899.

GROSBERG,R.K. & D.R. LEVITAN 1992: For adults only? Supply-side ecology and the history of larval biology. Trends in Ecology and Evolution 7: 130-133.

HALLFORS,G., A. NIEMI, H. ACKEFORS, J. LASSIG, & E. LEPPAKOSKI (1981): Biological Oceanography. In: A.,VOIPIO: Ed The Baltic Sea. Elsevier Science Publishing Company, Amsterdam, Oxford, New York: 219-274.

HARMS,J. & K. ANGER 1983: Seasonal, annual and spatial variation in the development of hard bottom communities. Helgolander wissenschaftliche Meeresuntersuchungen 36: 137-150.

HAWKINS,S.J. 1981: The influence of season and barnacles on the algal colonisation of *Patella vulgata* exclusion areas. Journal of the Marine Biological Association of the United Kingdom 61: 1-15.

HAWKINS,S.J. 1983: Interactions of *Patella* and macroalgae with settling *Semibalanus balanoides*. Journal of experimental marine biology and ecology 71: 55-72.

HAWKINS,S.J., J.R. ALLEN, G. RUSSELL, J.W. EATON, I. WALLACE, H.D. JONES, K.N. WHITE, & K. HENDRY (1993): Former commercial docks as a resource in urban conservation and education. In: K.N.,WHITE, E.G. BELLINGER, A.J. SAUL, M. SYMER & K. HENDRY: Eds Urban Waterside Regeneration, problems and prospects. Ellis Horwood Press, U.K.: 386-399.

HAWKINS,S.J., J.R. ALLEN, G. RUSSELL, K.N. WHITE, K. CONLAN, K. HENDRY, & H.D. JONES (1992a): Restoring and managing disused docks in inner city areas. In: G.W.,THAYER: Ed Restoring the Nations Marine Environment. National Oceanic and Atmospheric Administration, Maryland Sea grant College publication, Maryland: 473-542.

HAWKINS,S.J., P.N. CUNNINGHAM, B. DOLAN, L.C. EVANS, G.D. HOLMES, H.D. JONES, K. O'HARA, G. RUSSELL, A. WALMSLEY, & K.N. WHITE 1992b: Culture of mussels in Sandon Dock, a disused dock basin in Liverpool. Journal of Medical and Applied Malacology 4: 165-178.

HAWKINS,S.J. & E. HARKIN 1985: Preliminary canopy removl experiments in algal dominated communities low on the shore and in the shallow subtidal on the Isle of Man. Botannica Marina 28: 223-230.

HAWKINS,S.J. & R.G. HARTNOLL 1983: Grazing of intertidal algae by marine invertebrates. Oceanography and Marine Biology Annual Review 21: 195-282.

HAWKINS,S.J. & R.G. HARTNOLL 1985: Factors determining the upper limits of intertidal canopy-forming algae. Marine Ecology Progress Series 20: 265-271.

HAWKINS,S.J., A.J. SOUTHWARD, & R.L. BARRETT (1983): Population structure of *Patella vulgata* L. during succession on rocky shores in Southwest England. In: Fluctuations and succession in marine ecosystems : Proceedings of the 17th European Symposium on Marine Biology, Brest, France. Gauthiers-Villars, Montrouge (France): 103-107.

HEAD,R.M. (1990): An assessment of the flora of the Liverpool South Docks and the relationship between the flora and the common mussel (Mytilus edulis) in the Albert Dock. BSc Thesis, University of Liverpool.

HEAPS,L. (1988): The fish populations of the South Docks, Liverpool. BSc Thesis, University of Manchester.

HENDRY,K., K. CONLAN, K.N. WHITE, A. BEWSHER, & S.J. HAWKINS 1988b: Disused docks as a habitat for estuarine fish: a nationwide appraisal. Journal of Fish Biology 33(A): 239-241.

HENDRY,K., K.N. WHITE, & E.G. BELLINGER (1989): The influence of water quality and its management on urban regeneration. In: Proceedings of the conference managing the metropolis, June 1989.

HENDRY,K., K.N. WHITE, K. CONLAN, H.D. JONES, A.D. BEWSHER, G.S. PROUDLOVE, G. PORTEOUS, E.G. BELLINGER, & S.J. HAWKINS (Eds.) (1988a): Investigation into the ecology and potential use for nature conservtion of disused docks. Nature Conservancy Council contract report, HF3-11-52(3).

HERDMAN,E.C. (1924): *Botryllus*. Liverpool Marine Biology Committee Memoirs. No. 26. University of Liverpool Press, Liverpool. 40 pp.

HERDMAN,W.A. (1899): *Ascidia*. Liverpool Marine Biology Committee Memoirs. No. 1. T. Robb & Co.Printers, Liverpool. 52 pp.

HILL,A.S. (1990): The grazing of microbial films on moderately exposed shores on the Isle of Man. Ph.D. Dissertation, Liverpool University.

HILY,C. 1991: Is the activity of benthic suspension feeders a factor controlling water quality in the Bay of Brest? Marine Ecology Progress Series 69: 170-188.

HINDLE,B.R. (1993): Salford Quays 2: development and planning proceedures. In: K.N.,WHITE, E.G. BELLINGER, A.J. SAUL, M. SYMES & K. HENDRY: Eds Urban Waterside Regeneration : Problems and Prospects. Ellis Horwood, U.K.: 82-93.

HISCOCK,K. (1983): Water movement. In: R. EARLL, D.G. ERWIN: Eds Sublittoral ecology. The ecology of the shallow sublittoral benthos. Oxford University Press, Oxford: 58-96.

HOLLAND,D. (1989): 'Alive and kicking' The fish and inverebrates of the Mersey Estuary. In: The Mersey Barrage : The Proceedings of the Mersey Barrage Symposium, The North of England Zoological Society : 42-63.

HOLLING,C.S. 1973: Resilience and stability of ecological systems. Annual Review of Ecology and Systematics 4: 1-23.

HOLME,N.A. & A.D. McINTYRE (Eds.) (1984): Methods for the study of marine benthos. International Biological Programme. Handbooks no. 16. 2nd ed. Blackwell Scientific Publications, Oxford. 387 pp.

HOOTSMANS,M.J.M. & J.E. VERMAAT 1985: The effect of periphyton grazing by three epifaunal species on the growth of Zostera marina L. under experimental conditions. Aquatic Botany 22: 83-88.

HORN,H.S. 1974: The ecology of secondary succession. Annual Review of Ecology and Systematics 5: 25-37.

HOWARD,R.K. 1982: Impact of feeding activities of epibenthic ampipods on surface-fouling of eelgrass leaves. Aquatic Botany 14: 91-97.

HOWSON,C.M. (Ed.) (1987): Species directory to British marine fauna and flora. Marine Conservation Society, Ross-on-Wye. 471 pp.

HRUBY,T. 1976: Observations on algal zonation resulting from competition. Estuarine and Coastal Marine Science 4: 231-233.

HUDSEN,C. 1983: Selection of unicellular algae by the littoral amphipods *Gammarus oceanicus* and *Calliopius laevisculus* (Crustacea). Marine Biology 78: 59-67.

HUDSON,C. 1983: Selection of unicellular algae by littoral amphipods *Gammarus oceanicus* and *Calliopius laeviusculus* (Crustacea). Marine Biology 78: 59-67.

HULL,S.C. 1987: Macroalgal mats and species abundance : a field experiment. Estuarine Coastal and Shelf Science 25: 519-532.

HUMMEL,H., A.B.J. SEPERS, L. DE WOLF, & F.W. MELISSEN 1988: Bacterial growth on the marine sponge *Halichondria panicea* induced by reduced waterflow rate. Marine Ecology Progress Series 42: 195-198.

HUNT,S.M. (1993): Water quality monitoring and management. South Docks, Wirral Docks and New Brighton Marine Lake. Annual report (November 1992 to October 1993). Acer Environmental report to Merseyside Development Corporation. RT-EDA-1063-01.

HUNT,S.M. (1994): Water quality monitoring and management. South Docks, Wirral Docks and New Brighton Marine Lake. Annual Report (1 November 1993 to 31 October 1994). Acer Environmental report to Merseyside Development Corporation. RT-EDA-1480-01.

HURD,L.E., M.V. MELLINGER, L.L. WOLF, & S.J. MCNAUGHTON 1971: Stability and diversity at three trophic levels in terrestrial successional ecosystems. Science 173: 1134-1136.

HURLBUT,C.J. 1991: The effects of larval abundance, settlement and juvenile mortality on the depth distribution of a colonial ascidian. Journal of experimental marine biology and ecology 150: 183-202.

HURLBUT,C.J. 1992: Larval release and supply predict temporal variation in settlement of a colonial ascidian. Marine Ecology Progress Series 80: 215-219.

HUSTON,M. & T. SMITH 1987: Plant succession : life history and competition. American Naturalist 130: 168-198.

IBANEZ,F. & J.C. DAUVIN 1988: Long-term changes (1977 to 1987) in a muddy fine sand *Abra alba* - *Melinna palmat* community from the western English Channel : Multivariate time series analysis. Marine Ecology Progress Series 49: 65-81.

ICELY,J.D. & J.A. NOTT 1985: Feeding and digestion in *Corophium volutator* (Crustacea: Amphipoda). Marine Biology 89: 183-195.

IRISH SEA STUDY GROUP (1990): The Irish Sea Study Group, Part Two, Waste Inputs and Pollution. Liverpool University Press, Liverpool. 165 pp.

JAENICKE,L. 1977: Sex hormones of brown algae. Naturwissenschaften 64: 69-75.

JAMES,C.J. & R. GIBSON 1980: The distribution of the polychaete *Capitella capitata* (Fabricius) in dock sediments. Estuarine and Coastal Marine Science 10: 671-683.

JANKE,K. 1990: Biological interactions and their role in community structure in the rocky intertidal of Helgoland (German Bight, North Sea). Helgolander Meeresuntersuchungen 44: 219-263.

JASIM,A.K. & A.R. BRAND 1989: Observations on the reproduction of *Modiolus modiolus* in Isle of Man waters. Journal of the Marine Biological Association of the United Kingdom 69: 373-385.

JOHNSTONE,J., A. SCOTT, & M.C. CHADWICK (1934): The marine plankton. 1st ed. University of Liverpool Press, Liverpool. 194 pp.

JONGMAN,R.H.G., C.F.J. TER BRAAK, & O.F.R. VAN TONGEREN (1987): Data analysis in community and landscape ecology. Pudoc, Wageningen.

JORGENSEN,B.B. 1980: Seasonal oxygen depletion in the bottom waters of a Danish fjord on the benthic community. Oikos 34: 68-76.

JOSEFSON,A.B. 1985: Distribution of diversity and functional groups of marine infauna in the Skayerrak (eastern North Sea) - can larval availability affect diversity. Sarsia 70: 229-249.

JUGGINS,S. & C.J.F. TER BRAAK (1994): CALIBRATE version 0.6 - a C++ program for species-environment calibration by [weighted-averaging] partial least squares regression. Department of Geography, University of Newcastle.

KAIN,J.M. 1982: The reproductive phenology of nine species of Rhodophyta in the subtidal region of the Isle of Man. British Phycological Journal 17: 321-331.

KARAKIRI,M. & A. NICOLAIDOU 1987: Population studies on the Amphipoda of Mazoma Lagoon (Greece). Helgolander Meeresuntersuchungen 41: 453-464.

KAUTSKY,N. 1981: On the role of the blue mussel (*Mytilus edulis* L.) in a Baltic coastal ecosystem and the fate of organic matter produced by the mussels. Kieler Meeresforschungen Sonderheft 5: 454-461.

KAUTSKY,N. 1982a: Quantitative studies on the gonad cycle, fercundity, reproductive output and recruitment in a Baltic Mytilus edulis population. Marine Biology 68: 143-160.

KAUTSKY,N. 1982b: Growth and size structure in a Baltic *Mytilus edulis* population. Marine Biology 68: 117-133.

KAY,A.M. & M.J. KEOUGH 1981: Occupation of patches in the epifaunal communities on pier pilings and the bivalve *Pinna bicolor* at Edithburgh, South Australia. Oecologia (Berlin) 48: 123-130.

KEOUGH,M.J. 1983: Patterns of recruitment of sessile invertebrates in two subtidal habitats. Journal of experimental marine biology and ecology 66: 213-245.

KEOUGH,M.J. 1984: Effects of patch size on the abundance of sessile marine invertebrates. Ecology 65: 423-437.

KEOUGH,M.J. & H. CHERNOFF 1987: Dispersal and population variation in the bryozoan *Bugula neritina*. Ecology 68: 199-210.

KEOUGH,M.J. & B.J. DOWNES 1982: Recruitment of marine invertebrates : the roles of active larval choices aand early mortality. Oecologia (Berlin) 54: 348-352.

KHFAJI,A.K. & T.A. NORTON 1979: The effects of salinity on the distribution of *Fucus ceranoides*. Estuarine Coastal and Shelf Science 8: 433-439.

KING,P.A., D. MCGRATH, & W. BRITTON 1990: The use of artificial substrates in monitoring mussel (*Mytilus edulis* L.) settlement on an exposed rocky shore in the west of Ireland. Journal of the Marine Biological Association of the United Kingdom 70: 371-380.

KING,P.A., D. MCGRATH, & E.M. GOSLING 1989: Reproduction and settlement of *Mytilus edulis* on an exposed rocky shore in Galway Bay, west coast of Ireland. Journal of the Marine Biological Association of the United Kingdom 69: 355-365.

KITCHING,J.A. & F.J. EBLING 1967: Ecological studies at Lough Ine. Advances in Ecological Research 4: 198-291.

KITCHING,J.A., J.F. SLOANE, & F.J. EBLING 1959: The ecology of Lough Ine 8 Mussels and their predators. Journal of Animal Ecology 28: 331-341.

KLEPPEL,G.S. 1993: On the diets of calanoid copepods. Marine Ecology Progress Series 99: 183-195.

LACHAVANNE,J.B. 1985: The influence of accelerated eutrophication on the macrophytes of Swiss lakes: Abundance and distribution. Verhandlungen der Internationalen Vereinigung fur Theoretische und Angewandte Limnologie 22: 2950-2955.

LANCELLOTTI,D.A. & R.G. TRUCCO 1993: Distribution patterns and coexistance of six species of the amphipod genus Hyale. Marine Ecology Progress Series 93: 131-141.

LANE,D.J.W., A.R. BEAUMONT, & J.R. HUNTER 1985: Byssus drifting and the drifting threads of the young post-larval mussel *Mytilus edulis*. Marine Biology 84: 301-308.

LEAH,R.T., S.J. EVANS, & M.S. JOHNSON 1992: Arsenic in Plaice (*Pleuronectes platessa*) and Whiting (*Merlangius merlangus*) for the North East Irish Sea. Marine Pollution Bulletin 24: 544-549.

LESSER,M.P., S.E. SHUMWAY, T. CUCCI, & J. SMITH 1992: Impact of fouling organisms on mussel rope culture: interspecific competition for food among suspension feeding invertebrates. Journal of experimental marine biology and ecology 165: 91-102.

LEVIN,L.A. 1984: Life history and dispersal patterns in a dense infaunal polychaete assemblage : community structure and response to disturbance. Ecology 65: 1185-1200.

LEWONTIN,R.C. 1969: The meaning of stability. Diversity and stability of ecological systems, Brookhaven Symposium of Biology 22: 13-24.

LINDAHL,O. & L. HERNROTH 1983: Phytoplankton - zooplankton community in coastal waters of western Sweden - an ecosystem off balance. Marine Ecology Progress Series 10: 119-126.

LITTLER,M.M., D.R. MARTZ, & D.S. LITTLER 1983: Effects of recurrent sand deposition on rocky intertidal organisms : importance of substrate heterogeneity in a fluctuating environment. Marine Ecology Progress Series 11: 129-139.

LONSDALE,K. (1990): The hydrology and ecology of the Albert Docks complex, Liverpool with prticular reference to the fish population. MSc Thesis, University of Manchester.

LOO,L.O. & R. ROSENBURG 1989: Bivalve feeding dynamics and benthic - pelagic coupling in a eutrophicated marine bay. Journal of experimental marine biology and ecology 130: 253-276.

LUBCHENCO,J. 1978: Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. American Naturalist 112: 23-39.

LUBCHENCO,J. 1980: Algal zonation in the New England rocky intertidal community : an experimental analysis. Ecology 61: 333-344.

LUBCHENCO,J. 1982: Effects of grazers and algal competitors on fucoid colonisation in tide pools. Journal of Phycology 18: 544-550.

LUBCHENCO,J. 1983: *Littorina* and *Fucus* : effects of herbivores, substratum heterogeneity and plant escapes during succession. Ecology 64: 1116-1123.

LUBCHENCO,J. & B.A. MENGE 1978: Community development and persistance in a low rocky intertidal zone. Ecological Monographs 48: 67-94.

LUTZ,R.A. 1976: Annual growth patterns in the inner shell layer of Mytilus edulis L. Journal of the Marine Biological Association of the United Kingdom 56: 723-731.

LUTZ,R.A., L.S. INCZE, B. PORTER, & J.K. STOTZ 1980: Seasonal variation in the condition of raft-cultivated mussels (*Mytilus edulis* L.). Proceedings of the World Mariculture Society 11: 262-268.

MacARTHUR,R.H. & E.O. WILSON (1967): The theory of island biogeography. 1st ed. Princeton University Press, Princeton.

MARGALEF,R. (1969): Diversity and stability: a practical proposal and a model of interdependence. In: Diveristy and stability in ecological systems. Brookhaven Symposium of Biology no. 22., : 25-37.

MARSDEN,J.R. 1994: Vertical movements and distribution of planktonic larvae of the serpulid polychaete *Spirobranchus polycerus* (Schmarda); effects of changes in hydrostatic pressure. Journal of experimental marine biology and ecology 176: 87-105.

MASON,J. (1976): Cultivation. In: B.L.,BAYNE: Ed Marine Mussels : their ecology and physiology. Cambridge University Press, Cambridge: 385-410.

MATHIESON,A.C. & T.L. NORALL 1975: Physiological studies of subtidal red algae. Journal of experimental marine biology and ecology 20: 237-247.

MATTSSON,J. & O. LINDEN 1983: Benthic macrofauna succession under mussels, *Mytilus edulis* L. (Bivalvia), cultured on hanging long-lines. Sarsia 68: 97-102.

McCARRON,K. & A. JARVIS (1992): Give a dock a good name? 1st ed. Merseyside Port Folios, Liverpool. 119 pp.

McCOOK,L.J. 1994: Understanding ecological community structure : Causal models and theories, a review. Vegetatio 110: 115-147.

McCOOK,L.J. & A.R.O. CHAPMAN 1993: Community succession following massive ice-scour on a rocky intertidal shore : recruitment,competition and predation during early primary succession. Marine Biology 115: 565-575.

McGRATH,D., P.A. KING, & E.M. GOSLING 1988: Evidence for the direct settlement of *Mytilus edulis* larvae onto adult mussel beds. Marine Ecology Progress Series 47: 103-106.

McGRORTY,S., R.T. CLARKE, C.J. READING, & J.D. GOSS-CUSTARD 1990: Population dynamics of the mussel *Mytilus edulis* : density changes and regulation of the population in the Exe estuary, Devon. Marine Ecology Progress Series 67: 157-169.

McGUINNESS,K.A. 1989: Effects of some natural and artificial sustrata on sessile marine organisms at Galeta Reef, Panama. Marine Ecology Progress Series 52: 201-208.

McKENZIE,J.D. 1986: The reproductive cycle of *Mytilus edulis* L. from Lough Foyle. Irish Naturalist Journal 22: 13-16.

MENGE,B.A. 1976: Organisation of the New England rocky intertidal community : role of predation, competition and environmental heterogeneity. Ecological Monographs 46: 355-393.

MENGE,B.A. 1983: Components of predation intensity in the low zone of the New England rocky intertidal region. Oecologia (Berlin) 58: 141-155.

MENGE,B.A. 1992: Community regulation: under what conditions re bottom-up factors important on rocky shores? Ecology 73: 755-765.

MENGE,B.A. & T.M. FARRELL 1989: Community structure and interaction webs in shallow marine hard-bottom communities: tests of an environmental stress model. Advances in Ecological Research 19: 189-262.

MENGE,B.A. & J.P. SUTHERLAND 1987: Community regulation: variation in disturbance, competition and predation in relation to environmental stress and recruitment. American Naturalist 130: 730-757.

MERRILL,J. & R. FLETCHER 1991: Green tides cause major economic burden in Venice Lagoon, Italy. Applied Phycology 8(3): 1-3.

MILIOU,H. & M. MORAITOU-APOSTOLOPOULOU 1991: Effects of seven diets on the population dynamics of laboratory cultured *Tisbe holothuriae* Humes (Copepoda, Harpactticoida). Helgolander Meeresuntersuchungen 45: 345-356.

MILLAR,R.H. (1953): *Ciona*. Liverpool Marine Biology Committee Memoirs. No. 35. University of Liverpool Press, Liverpool. 122 pp.

MINCHER,P.T. (1988): The hydrography and ecology of Liverpool Docks. MSc Thesis, University of Manchester. 116 pp.

MINCHINTON,T.E. & R.E. SCHEIBLING 1991: The influence of larval supply and settlement on the population structure of barnacles. Ecology 72: 1867-1879.

MINCHINTON,T.E. & R.E. SCHEIBLING 1993: Free space availability and larval substratum selection as determinants of barnacle population structure in a developing rocky intertidal community. Marine Ecology Progress Series 95: 233-244.

MOHSEN,A.F., A.F. KHALEAFA, M.A. HASHEM, & A. METWALLI 1974: Effect of different nitrogen sources on rowth, reproduction, amino acid, fat and sugar contents in *Ulva fasciata* Delile. Botannica Marina 17: 218-222.

MOLLER,H. 1980: Population dynamics of *Aurelia aurita* medusi in Kiel Bight, Germany (FRG). Marine Biology 60: 123-128.

MOORE,D.M. 1978: Seasonal changes in the distribution of intertidal macrofauna in the lower Mersey Estuary. Estuarine and Coastal Marine Science 7: 117-125.

MOORE,H.B. 1934: The biology of *Balanus balanoides* I. Growth rate and its relation to size, season and tidal level. Journal of the Marine Biological Association of the United Kingdom 19: 851-862.

MORTIMER,C.H. 1971: Chemical exchanges between sediments and waters in the Great Lakes - Speculations on probable regulatory mechanisms. Limnology and Oceanography 16: 387-404.

MÜLLER,D. 1962: Ube jahres-und lunarperiodische Frscheinungen bei einigen Braunalgen. Botannica Marina 4: 140-155.

NAVARRO,J.M. & J.E. WINTER 1982: Ingestion rates, assimilation efficiency and energy balance in *Mytilus chilansis* in relation to body size and different algal concentrtions. Marine Biology 67: 255-266.

NAYLOR,G.P.L. (1983): The role of *Mytilus edulis* at Sandon Dock. BSc Hons Thesis, Liverpool University.

NELSON,W.G. 1979: Experimental studies of selective predation on amphipods : consequences for amphipod distribution and abundance. Journal of experimental marine biology and ecology 38: 225-245.

NELSON,W.G., D.K. PHILIPS, W.B. GALLOWAY, P.F. ROGERSON, & R.J. PRUELL (1987): Effects of Black Rock Harbour dredged material on scope for growth of the blue mussel, *Mytilus edulis* after laboratory and field exposures. Technical Report of the United States Army Engineers Waterways experimental station. 122 pp.

NEWCOMBE,C.L. 1935: A study of the community relationships of the sea mussel, *Mytilus edulis* (L.). Ecology 16: 234-243.

NOBLE,I.R. & R.O. SLATYER 1980: The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. Vegetatio 43: 5-21.

ODUM,E.P. 1969: The strategy of ecosystem development. Science 164: 262-270.

ODUM,E.P. (1971): Fundamentals of ecology. W.B.Saunders Company, Philadelphia. 274pp.

OLSSON,P., E. GRANELI, P. CARLSSON, & P. ABREU 1992: Structuring of a postspring phytoplankton community by manipulation of trophic interactions. Journal of experimental marine biology and ecology 158: 249-266.

ORIENS,G.H. (1974): Diversity, stability and maturity in natural ecosystems. In: W.H.,VAN DOBBEN, R.H. LOWE-MCCONNELL: Eds Unifying concepts in ecology. Junk, The Hague: 139-150.

OSMAN,R.W. 1977: The influence of seasonality and stability on the species equilibrium. Ecological Monographs 47: 37-63.

PAGE,H.M. & D.M. HUBBARD 1987: Temporal and spatial patterns of growth in mussels *Mytilus edulis* on an offshore platform: relationships to water temperature and food availability. Journal of experimental marine biology and ecology 111: 159-179.

PAINE,R.T. 1966: Food web complexity and species diversity. American Naturalist 100: 65-75.

PAINE,R.T. 1974: Intertidal community structure : experimental studies on the relationship between a dominant competitor and its principal predator. Oecologia (Berlin) 15: 93-120.

PAINE,R.T. 1976a: Size limited predation. An observational and experimental approach with the *Mytilus* - *Pisaster* interaction. Ecology 57: 858-874.

PAINE,R.T. 1976b: Biological observations on a subtidal *Mytilus californianus* bed. Veliger 19: 125-130.

PARKER,T. & A.R.O. CHAPMAN 1994: Separating the grazing effects of periwinkles and amphipods on a seaweed community dominated by *Fucus distichus*. Ophelia 39: 75-91.

PARKER,T., C. JOHNSON, & A.R.O. CHAPMAN 1993: Gammarid amphipods and littorinid snails have significant but different effects on algl succession in littoral fringe pools. Ophelia 38: 69-85.

PARKMAN CONSULTING ENGINEERS (1991): Liverpool South Docks Water Losses and Silt Accumulation. Report to Merseyside Development Corporation, December.

PAULA,J. 1989: Rhythums of larval release of decapod crustaceans in the Mira Estuary, Portugal. Marine Biology 100: 309-312.

PEARSON,T.H. & R. ROSENBERG 1978: Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. Oceanography and Marine Biology Annual Review 16: 229-311.

PEDDICORD,R.K. (1980): Direct effects of suspended sediments on aquatic organisms. In: R.A.,BAKER: Ed Cotaminants and sediments. Ann Arbor, MI, USA: 501-536.

PETERSON,J.H. 1984: Larval settlement behviour in competing species : *Mytilus californianus* Conrad and *M. edulis* L. Journal of experimental marine biology and ecology 82: 147-159.

PETRAITIS,P.S., R.E. LATHAM, & R.A. NIESENBUM 1989: The maintenance of species diversity by disturbance. The Quarterly Review of Biology 64: 393-418.

PICKETT,S.T.A. & P.S. WHITE (1985): The ecology of natural disturbance and patch dynamics. 1st ed. Academic Press, London. 472 pp.

PIDWILL,S. (1993): Salford Quays 3 : the urban design and its relationship with tha of other waterside initiatives. In: K.N.,WHITE, E.G. BELLINGER, A.J. SAUL, M. SYMES & K. HENDRY: Eds Urban Waterside Regeneration : Problems and Prospects. Ellis Horwood, U.K.: 94-105.

PIERCE,E.L. 1941: The occurrence and breeding of *Sagitta elegans* Verill and *Sagitta setosa* J.Muller in parts of the Irish Sea. Journal of the Marine Biological Association of the United Kingdom 25: 113-124.

RABY,D., Y. LAGADEUC, J.J. DODSON, & M. MINGELLIER 1994: Relationship between feeding and vertical distribution of bivalve larvae in stratified and mixed waters. Marine Ecology Progress Series 103: 275-284.

RACHOR,E. 1977: Faunal impoverishment in a mud area near Helogland. Helgolander wissenschaftliche Meeresuntersuchungen 30: 633-651.

RACHOR,E. 1980: The inner German Bight - and ecologically sensitive area as indicated by the bottom fauna. Helgolander Meeresuntersuchungen 33: 522-530.

RAE,J.E. & S.R. ASTON 1981: Mercury in coastal and estuarine sediments of the Northeastern Irish Sea. Marine Pollution Bulletin 12: 367-371.

RAFFAELLI,D., J. LIMIA, S. HULL, & S. PONT 1991: Interactions between the amphipod *Corophium volutator* and macroalgal mats on estuarine mudflats. Journal of the Marine Biological Association of the United Kingdom 71: 899-908.

RAIMONDI,P.T. 1990: Patterns, mechanisms, consequences of variability in settlement of an intertidal barnacle. Ecological Monographs 60(3): 283-309.

RAO,K.P. 1953: Shell weight as a function of intertidal height in a littoral population of pelecypods. Experimentia 9: 465-466.

REEDERS,H.H., A. BIJ DE VAATE, & F.J. SLIM 1989: The filtration rate of *Dreissena polymorpha* (bivalia) in three dutch lakes with reference to biological water quality management. Freshwater Biology 22: 133-141.

REISE,K. 1979: Moderate predation on meiofauna by the macrobenthos of the Wadden Sea. Helgolander wissenschaftliche Meeresuntersuchungen 32: 453-465.

RICHARDSON,C.A., D.J. CRISP, & N.W. RUNHAM 1979: Tidally deposited growth bands in the shell of the common cockle Cerastoderma edule (L.). Malacologia 18: 277-290

RICHARDSON,C.A. & R. SEED 1990: Predictions of mussel (*Mytilus edulis*) biomass on an offshore platform from single population samples. Biofouling 2: 289-297.

RICHARDSON,C.A., R. SEED, & E. NAYLOR 1990: Use of internal growth bands for measuring individual and population growth rates in *Mytilus edulis* from offshore platforms. Marine Ecology Progress Series 66: 259-265.

RICHARDSON,J.S. 1991: Seasonal food limitation of detritivores in a montane stream: an experimental test. Ecology 72: 873-887.

RICHMOND,M.D. & R. SEED 1991: A review of marine marcofouling communities with special reference to animal fouling. Biofouling 3: 151-168.

RIDDING,G.C. & P. GARDNER (1993): London docklands water quality study. In: K.N.,WHITE, E.G. BELLINGER, A.J. SAUL, M. SYMES & K. HENDRY: Eds Urban Waterside Regeneration : Problems and Prospects. Ellis Horwood, U.K.: 292-301.

RIEPER-KIRCHNER,M., K. HINZ, & B. BIDDANDA 1991: Ingestion of microbially-synthesised organic aggregates and egestion of fecal pellets by marine harpacticoid copepods. Kieler Meeresforschungen Sonderheft 8: 257-263.

RILEY,J.P. & J.V. TOWNER 1984: The distribution of alkyl species in the Mersey Estuary. Marine Pollution Bulletin 15: 153-158.

RITCHIE-NOAKES,N. (1984): Liverpools Historic Waterfront. 1st ed. H.M.S.O., London. 192 pp.

ROBBINS,I.J. 1983: The effects of body size, temperature and suspension density on the filtration and ingestion of inorganic particulate suspension by ascidians. Journal of experimental marine biology and ecology 70: 65-78.

ROBERTS,D., D. RITTSCHOFF, E. HOLM, & A.R. SCHMIDT 1991: Factors influencing initial larval settlement : temporal, spatial and surface molecular components. Journal of experimental marine biology and ecology 150: 203-211.

ROPKE,A. 1993: Do larvae of mesopelagic fishes in the Arabian Sea adjust their vertical distribution to physical and biological gradients. Marine Ecology Progress Series 101: 223-235.

ROSENBERG,R., B. HELLMAN, & B. JOHANSSON 1991: Hypoxic tolerance of marine benthic fauna. Marine Ecology Progress Series 79: 127-131.

ROUGHGARDEN,J.S., S.D. GAINES, & S. PACALA (1987): Supply side ecology: the role of physical transport processes. In: J.H.R.,GEE, P.S. GILLER: Eds Organisation of communities: past and present. Proceedings of the British Ecological Society. Blackwell Scientific Publications, London: 459-489.

RUGG,D.A. & T.A. NORTON (1987): *Pelvetia canaliculata*, a high-shore seaweed that shuns the sea. In: R.M.M.,CRAWFORD: Ed Plant life in aquatic and amphipious habitats: 347-358.

RUNKLE,J.R. (1985): Disturbance regimes in temperate forests. In: S.T.A.,PICKETT, P.S. WHITE: Eds The ecology of natural disturbance and patch dynamics. Academic Press, London: 17-33.

RUSS,G.R. 1980: Effects of predation by fishes, competition and structural complexity of the substratum on the estblishmentof marine epifaunal community. Journal of experimental marine biology and ecology 42: 55-69.

RUSSELL,F.S. (1953): The medusae of the British Isles. Cambridge University Press, Cambridge. 529 pp.

RUSSELL,G., S.J. HAWKINS, L.C. EVANS, H.D. JONES, & HOLMES 1983: Restoration of a disused dock basin as a habitat for marine benthos and fish. Journal of Applied Ecology 20: 43-58.

SAILA,S.B., C.W. RECKSIEK, & M.H. PRAGER (1988): Basic fishery science programs. Developments in aquaculture and fisheries science 18. 1st ed. Elsevier, Amsterdam. 230 pp.

SANTELICES,B. 1990: Patterns of reproduction, dispersal and recruitment in seaweeds. Oceanography and Marine Biology Annual Review 28: 177-276.

SCHEER,B.T. 1945: The development of marine fouling communities. Biological Bulletin 89: 103-121.

SCHELTEMA,R.S. 1974: Biological interactions determining larval settlement of marine invertebrates. Thalassia Jugoslavica 10: 263-296.

SCHMIDT,G.H. & G.F. WARNER 1984: Effects of caging on the development of a sessile epifaunal community. Marine Ecology Progress Series 15: 251-263.

SCHOENER,T.W. 1983: Field experiments on interspecific competition. American Naturalist 122: 240-285.

SCHONBECK,M.W. & T.A. NORTON 1978: Factors controlling the upper limits of fucoid algae. Journal of experimental marine biology and ecology 31: 303-313.

SCHONBECK,M.W. & T.A. NORTON 1980: Factors controlling the lower limits of fucoid algae on the shore. Journal of experimental marine biology and ecology 43: 131-150.

SCOTT,A. 1905: On the tow-nettings collected in the Irish Sea. Proceedings & Transactions of the Liverpool Biological Society 19: 196-215.

SCOTT,A. 1906: Report on the tow-nettings. Proceedings & Transactions of the Liverpool Biological Society 20: 164-201.

SCOTT,A. 1907: Report on the tow-nettings. Proceedings & Transactions of the Liverpool Biological Society 21: 137-190.

SEAMAN,M.N.L., E. HIS, M. KESKIN, & T. REINS (1991): Influence of turbulence and turbidity on growth and survival of laboratory-reared bivalve larvae. Counc. Meet of the Int. Counc. for the exploration of the sea, La Rochelle (France) 26 Sept - 4 Oct 1991. ICES, Copehagen, Denmark. 6 pp.

SEED,R. 1969a: The ecology of *Mytilus edulis* L. (Lamellibranchiata) on exposed rocky shores. Oecologia (Berlin) 3: 277-316.

SEED,R. 1969b: The ecology of *Mytilus edulis* L. (Lamellibranchiata) on exposed rocky shores. 2. Growth and mortality. Oecologia (Berlin) 3: 317-350.

SEED,R. 1973: Absolute and alometric growth in the mussel *Mytilus edulis* (L.) (Mollusca Bivalvia). Proceedings of the Malacological Society London 40: 343-357.

SEED,R. 1975: Reproduction in *Mytilus edulis* L. (Mollusca: Bivalvia) in European waters. Publications of the Station of Zoology, Napoli 39: 317-334.

SEED,R. (1976): Ecology. In: B.L.,BAYNE: Ed Marine Mussels: their ecology and physiology. Cambridge University Press, Cambridge: 13-65.

SEED,R. 1980: Variations in the shell-flesh relationships of *Mytilus*: The value of sea mussels as items of prey. Veliger 22(3): 219-221.

SEED,R. (1986): Predator-prey relationships between the swimming crab *Thalamita danae* Stimpson (Decapoda: Portunidae) and the mussels *Perna viridis* (L.) and *Brachidontes variabilis* (Krauss). In: B.,MORTON: Ed Proceedings of the Second International Marine Biological Workshop: The Marine Flora and Fauna of Hong Kong and Southern China, Hong Kong. Hong Kong University Press, Hong Kong: 993-1013.

SEED,R. & R.A. BROWN 1977: A comparison of the reproductive cycles of *Modiolus modiolus* (L.) *Cerastoderma* (*=Cardium*) *edule* (L.) and *Mytilus edulis* in Strangford Lough, Northern Ireland. Oecologia (Berlin) 30: 173-188.

SEED,R. & C.A. RICHARDSON (1990): *Mytilus* growth and its environmental responsiveness. In: G.B.,STEFANO: Ed The Neurobiology of *Mytilus edulis*. Manchester University Press, Manchester: 1-37.

SEED,R. & T.H. SUCHANEK (1992): Population and community ecolgy of Mytilus. In: E.,GOSLING: Ed The Mussel *Mytilus*: Ecology, Physiology, Genetics and Culture. Elsevier, Amsterdam: 87-169.

SFRISO,A., B. PAVONI, & A. MARCOMINI 1989: Macroalgae and phytoplankton standing crops in the central Venice Lagoon. Science of the Total Environment 80: 139.

SFRISO,A., B. PAVONI, A. MARCOMINI, & A.A. ORIO 1988: Annual variation of nutrients in the Lagoon of Venice. Marine Pollution Bulletin 19: 54-60.

SFRISO,A., B. PAVONI, A. MARCOMINI, & A.A. ORIO 1992: Macroalgae, nutrient cycles, and pollutants in the Lagoon of Venice. Estuaries 15: 517-528.

SHAPIRO,J. 1990: Biomanipulation : the next phase - making it stable. Hydrobiologia 200/201: 13-27.

SHAPIRO,J. & D.I. WRIGHT 1984: Lake restoration by biomanipulation: Round Lake Minnesota the first two years. Freshwater Biology 14: 371-383.

SHARPLES,E.J. (1969): A preliminary survey of the plankton of the River Mersey with special reference to phytoplankton. BSc Thesis, University of Liverpool.

SHARPLES,E.J. (1972): The use of phytoplankton for the indication of the effects of waste disposal on water quality in Liverpool Bay. Ph.D. Dissertation, University of Liverpool. 164 pp.

SIH,A., P. CROWLEY, M. MCPEEK, J. PETRANKA, & K. STROHMEIER 1985: Predation, competition and prey communities : a review of field experiments. Annual Review of Ecology and Systematics 16: 269-311.

SLINN,D.J. 1974: Water circulation and nutrients in the north-west Irish Sea. Estuarine and Coastal Marine Science 2: 1-25.

SLINN,D.J. & J.F. EASTHAM 1984: Routine hydrographic observations in the Irish Sea off Port Erin, Isle of Man, during 1972-1981 inclusive. Annales Biologiques 38: 42-44.

SMAAL,A.C., J.H.G. VERHAGEN, J. COOSEN, & H.A. HAAS 1986: Interaction between seston quntity and quality and benthic suspension feeders in the Oosterschelde, the Netherlands. Ophelia 26: 385-399.

SOUSA,W.P. 1979a: Experimental investigations of disturbance and succession in a rocky intertidal algal community. Ecological Monographs 49: 227-254.

SOUSA,W.P. 1979b: Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. Ecology 60: 1225-1239.

SOUTH,G.R. & I. TITLEY (1986): A checklist and distributional index of the benthic marine algae of the North Atlantic Ocean. Huntsman Marine Laboratory and British Museum (Natural History), St Andrews and London. Memorial University of Newfoundland.

SOUTHWARD,A.J. & E.C. SOUTHWARD 1978: Recolonisation of rocky shores in Cornwall after the use of toxic dispersants to clean up the Torrey-Canyon spill. Journal of Fisheries Research 35: 682-706.

SPENCE,D.H.N. 1982: The zonation of plants in freshwater lakes. Advances in Ecological Research 12: 37-124.

STEARNS,S.C. 1976: Life-history tactics: a review of the ideas. The Quarterly Review of Biology 51: 3-47.

STEELE,D.H. & A. WHITTICK 1991: Seasonal variation in *Pilayella littoralis* (Phaeophyceae) and its consequences as a food source for the amphipod *Gammarus lawrencianus* in the intertidal of Newfoundland. Journal of the Marine Biological Association of the United Kingdom 71: 883-889.

STONER,D.S. 1990: Recruitment of a tropical colonial ascidian: relative importance of pre-settlement vs post-settlement processes. Ecology 71: 1682-1690.

SUCHANEK,T.H. 1978: The ecology of *Mytilus edulis* L. in exposed rocky intertidal communities. Journal of experimental marine biology and ecology 31: 105-120.

SUCHANEK,T.H. (1985): Mussels and their role in structuring rocky shore communities. In: P.G.,MOORE, R. SEED: Eds The Ecology of Rocky Coasts. Hodder and Stoughton, Sevenoaks, U.K.: 70-96.

SUTHERLAND,J.P. 1974: Multiple stable points in natural communities. American Naturalist 108: 859-873.

SUTHERLAND,J.P. 1978: Functional roles of *Schizoporella* and *Styela* in the fouling community at Beaufort, North Carolina. Ecology 59: 257-264.

SUTHERLAND,J.P. 1981: The fouling community at Beaufort, North Carolina : a study in stability. American Naturalist 118: 499-519.

SUTHERLAND,J.P. & R.H. KARLSON 1977: Development and stability of the fouling community at Beaufort, North Carolina. Ecological Monographs 47: 425-446.

SVANE,I. 1984: Observations on the long term population dynamics of the perennial ascidian, *Ascidia mentula* O.F.Muller, on the Swedish west coast. Biological Bulletin 167: 630-646.

SVANE,I. 1988: Recruitment and development of epibioses on artificial and cleared substrata at two sites in Gullmarsfjorden on the Swedish west coast. Ophelia 29: 25-41.

SVANE,I.B. & C.M. YOUNG 1989: The ecology and behaviour of ascidian larvae. Oceanography and Marine Biology Annual Review 27: 45-90.

TANGEN,K. 1977: Blooms of *Gyrodinium aureolum* (Dinophyceae) in North European waters, accompanied by mortality in marine organisms. Sarsia 63: 123-133.

TER BRAAK,C.F.J. (1987-1992): CANOCO - a FORTRAN program for Canonical Community Ordination. Microcomputer Power, Ithaca, New York, USA.

TER BRAAK,C.J.F. 1983: Principal components biplots and alpha and beta diversity. Ecology 64: 454-462.

TER BRAAK,C.J.F., C.W.N LOOMAN, 1986: Weighted averaging, logistic-regression and the Gaussian response model. Vegetatio 65: 3-11.

TERRY,L.A. & D. SELL (1986): Rocky shores in the Moray Firth. In: The marine environment of the Moray Firth. Proceedings of the Royal Society of Edinburgh, Section B: 169-191.

THEISEN,B.F. 1973: The growth of *Mytilus edulis* L. (Bivalvia) from Disko and Thule district, Greenland. Ophelia 12: 59-77.

THIEBAUT,E., J. DAUVIN, & Y. LAGADEUC 1992: Transport of *Owenia fusiformis* larvae (Annelida : Polychaeta) in the Bay of Seine. I. Vertical distribution in relation to water column stratification and ontogenetic vertical migration. Marine Ecology Progress Series 80: 29-39.

THYBO-CHRISTESEN,M., M.B. RASMUSSEN, & T.H. BLACKBURN 1993: Nutrient fluxes and growth of *Cladophora sericea* in a shallow Danish bay. Marine Ecology Progress Series 100: 273-281.

TSUCHIYA,M. 1980: Biodeposit production by the mussel *Mytilus edulis* L. on rocky shores. Journal of experimental marine biology and ecology 47: 203-222.

TSUCHIYA,M. 1983: Mass mortality in a population of the mussel *Mytilus edulis* L. caused by high temperature on rocky shores. Journal of experimental marine biology and ecology 66: 101-111.

TURNER,S. & C.D. TODD 1993: The early development of epifaunal assemblages on artificial substrata at two intertidal sites on an exposed rocky shore in St. Andrews Bay, N.E. Scotland. Journal of experimental marine biology and ecology 166: 251-272.

TURNER,T. 1983a: Facilitation as a successional mechanism in a rocky intertidal community. American Naturalist 121: 729-738.

TURNER,T. 1983b: Complexity of early and middle successional stages in a rocky inttertidal surfgrass community. Oecologia (Berl.) 60: 56-65.

UNDERWOOD,A.J. & M.J. ANDERSON 1994: Seasonal and temporal aspects of recruitment and succession in an intertidal estuarine fouling assemblage. Journal of the Marine Biological Association of the United Kingdom 74: 563-584.

UNDERWOOD,A.J. & E.J. DENLEY (1984): Paradigms, explanations, and generalisations in models for the sructure of intertidal communities. In: D.R.,STRONG, D. SIMBERLOFF, L. ABELE & A. THISTLE: Eds Ecological Communities. Princeton Press, Princeton: 151-180.

UNDERWOOD,A.J. & P.G. FAIRWEATHER 1989: Supply-side ecology and benthic marine assemblages. Trends in Ecology and Evolution 4: 16-20.

VANCE,R.R. 1988: Ecological succession and the climax community on a marine subtidal wall. Marine Ecology Progress Series 48: 125-136.

VAN DEN HOEK,C. 1987: The possible significance of long range dispersal for the biogeography of seaweeds. Helgolander Meeresuntersuchungen 41: 261-272.

VINCE,S., I. VALIELA, W. BACKUS, & J.M. TEAL 1976: Predation by the saltmarsh Killifish Fundulus heteroclitus (L.) in relation to prey size and habitat structure : consequences for prey distribution and abundance. Journal of experimental marine biology and ecology 23: 255-266.

VOGT,H. & W. SCHRAMM 1991: Conspicuous decline of *Fucus* in Kiel Bay (Western Baltic): What are the causes? Marine Ecology Progress Series 69: 189-194.

WALKER,L.R. & F.S. CHAPIN 1986: Physiological controls over seedling growth in primary succession on an Alaskan Floodplain. Ecology 67: 1508-1523.

WALKER,L.R. & F.S. CHAPIN 1987: Interactions among processes controlling successional change. Oikos 50: 131-135.

WALKER,L.S., I. CARRADICE, & R.S. WARREN (1993): Improvements in water quality at Salford Quays (1986-1990). In: K.N.,WHITE, E.G. BELLINGER, A.J. SAUL, M. SYMES & K. HENDRY: Eds Urban Waterside Regeneration : Problems and Prospects. Ellis Horwood, U.K.: 283-291.

WARWICK,R.M. & K.R. CLARKE 1991: A comparison of methods for analysing changes in benthis community structure. Journal of the Marine Biological Association of the United Kingdom 71: 225-244.

WATANABE,J.M. & C. HARROLD 1991: Destructive razing by sea urchins *Stronglyocentrotus* spp. in a central California (USA) kelp forest: potential roles of recruitment, depth and predation. Marine Ecology Progress Series 71: 125-141.

WEBB,K.L. (1981): Conceptual models and processes of nutrient cycles in estuaries. In: B.J.,NEILSON, L.E. CRONIN: Eds Estuaries and Nutrients. Humana Press, Clifton, New Jersey: .

WESTON,D.P. 1990: Quantitative examination of macrobenthic community changes along an organic enrichment gradient. Marine Ecology Progress Series 61: 233-244.

WETHEY,D.A. 1984: Sun and shade mediate competition in the barnacles *Chthamalus* and *Semibalanus* : a field experiment. Biological Bulletin 167: 176-185.

WHITE,K.N., K. HENDRY, & K.N. WHITE (1993): Ecological change as a consequence of water quality improvements at Salford Quays. In: K.N.,WHITE, E.G. BELLINGER, A.J. SAUL, M. SYMES & K. HENDRY: Eds Urban Waterside Regeneration : Problems and prospects. Ellis Horwood, U.K.: 366-376.

WHITTAKER,R.H. 1967: Gradient analysis of vegetation. Biological Review 49: 207-264.

WILKINSON,S.B., J.R. ALLEN, & S.J. HAWKINS (1990): Fauna and flora of the Mersey Estuary, a survey of seven Merseyside Docks and New Brighton Marine Lake. Internal Report to Liverpool Maritime Museum. 16 pp.

WILLIAMS,R.J. 1970: Freezing tolerance in *Mytilus edulis*. Comparative Biochemical Physiology 35: 145-161.

WILLIAMSON,D.I. (1975): The zooplankton of Liverpool Bay. In: An assessment of present kowledge compiled by members of the Liverpool Bay study group. The Natural Environment Research Council publications. Series 'C'. No. 14.

WILSON,J.H. 1987: Mussels: The problem of early spawning. Aquaculture Ireland 30: 20-21.

WILSON,J.H. & R. SEED 1974: Reproduction in *Mytilus edulis* L. (Mollusca:Bivalvia) in Carlingford Lough, Northern Ireland. Irish Fisheries Investigations Series B (Marine) 15: 1-30.

WILSON,K.W., B.J. D'ARCY, & S. TAYLOR 1988: The return of fish to the Mersey Estuary. Journal of Fish Biology 33: 235-238.

WINTER,J.E. 1973: The filtration rate of *Mytilus edulis* and its dependence on algal concentrations, mesured by a continuous automatic recording apparatus. Marine Biology 22: 317-328.

WOODHEAD,P.M.J. & M.E. JACOBSON 1985: Epifaunal settlement, the process of community development and succession over two years on an artificial reef in the New York Bight. Bulletin of Marine Science 37: 364-376.

YAMAGUCHI,M 1975: Growth and reproductive cycles of the marine fouling ascidians *Ciona intestinalis*, *Styela plicata*, *Botrylloides violaceus* and *Leptoclinum mitsukurii* at Aburateubo-Moroiso Inlet (Central Japan). Marine Biology 29: 253-259.

YOUNG,C.M. 1988: Ascidian canniblism correlates with larval behaviour and adult distribution. Journal of experimental marine biology and ecology 117: 9-26.

YOUNG,C.M. 1990: Larval predation by epifauna on temperate reefs: scale power and the scarcity of measurable effects. Australian Journal of Ecology 15: 413-426.

YOUNG,C.M. & L.F. BRAITHWAITE 1980: Larval behaviour and post-settling morphology in the ascidian *Chelyosoma production* Stimpson. Journal of experimental marine biology and ecology 42: 157-169.

YOUNG,C.M. & N.J. GOTELLI 1988: Larval predation by barnacles : Effects on patch colonisation in a shallow subtidal community. Ecology 69: 624-634.

YOUNG,C.M. & F.S. CHIA (1987): Abundance and distribution of pelagic larvae as influenced by predation, behaviour and hydrographic factors. In: A.C.,GIESE: Ed Reproduction of marine invertebrates. General aspects : seeking unity in diversity. Blackwell/Boxwood, Palo Alto & Pacific Grove, California: 385-463.

ZAR,J.H. (1984): Biostatistical analysis. 2nd ed. Prentice-Hall International, London. 718 pp.

ZHENG,W. (1995): Water quality problems of the Liverpool Dock system in relation to the adjacent estuary. Ph.D. Dissertation, University of Liverpool.

ZIMMERMAN,R., R. GIBSON, & J. HARRINGTON 1979: Herbivory and detritivory among gammaridean amphipods from a Florida seagrass community. Marine Biology 54: 41-47.

ZIMMERMAN,T.L. & D.L. FELDER 1991: Reproductive ecology of an intertidal Brachyuran crab, *Sesarma* sp. (nr. reticulatum) from the Gulf of Mexico. Biological Bulletin 181: 387-401.

APPENDIX 1

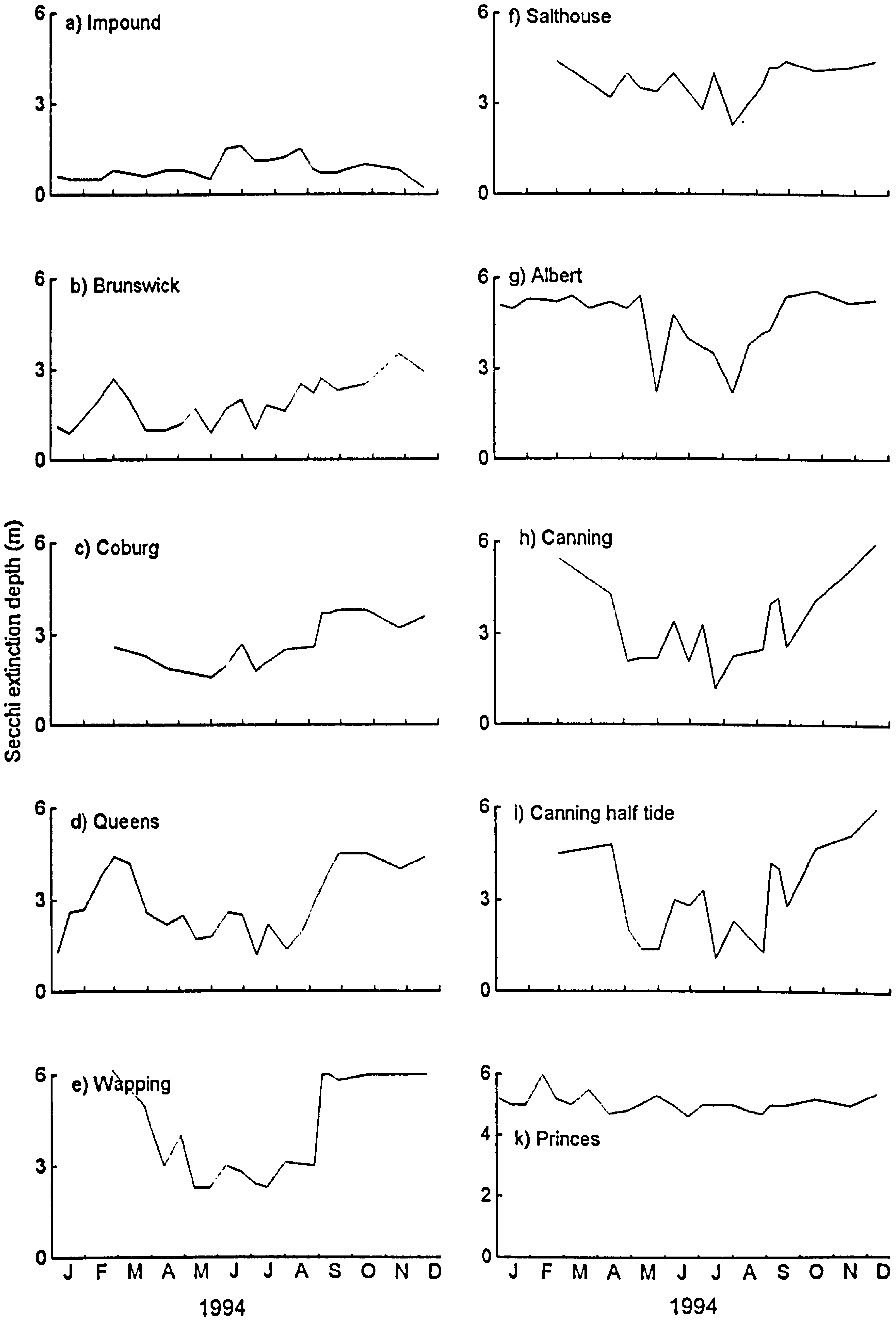

Fig A1.1 Variation in secchi extinction depths in the South Docks and Princes Dock during 1994. Data courtesy Fielding.

APPENDIX 2

Table A2.1 Summary of allometric relationship between shell LENGTH and WIDTH for Mytilus from Albert, Queens and Princes docks. Figures calculated by least squares regression after log transformation of data, with length as the independent variable. ['b' represents slope; 'c' intercept on y-axis; SE_b and SE_c standard error of slope and intercept; 'p' probability associated with t-value for hypothesis b=1]

a) Queens

Date	Depth	r^2	b	SE_b	c	SE_c	t(b-1)	p
2/92	2	0.9101	0.7836	0.0355	0.0982	0.0633	-6.090	<0.001
5/92	2	0.8235	0.7253	0.0485	0.2041	0.0860	-5.669	<0.001
8/92	2	0.7914	0.6814	0.0505	0.2857	0.0913	-6.311	<0.001
10/92	2	0.9312	0.8441	0.0331	-0.0189	0.0592	-4.707	<0.001
1/93	1	0.8930	0.9073	0.0453	-0.1216	0.0810	-2.044	0.03
1/93	2	0.8534	0.8274	0.0495	0.0216	0.0892	-3.487	<0.001
9/93	2	0.7997	0.7643	0.0552	0.1275	0.0983	-4.271	<0.001
7/94	2	0.8654	0.7795	0.0444	0.1063	0.0800	-4.966	<0.001

b) Albert

Date	Depth	r^2	b	SE_b	c	SE_c	t(b-1)	p
4/92	2	0.8703	0.8365	0.0466	-0.0054	0.0785	-3.507	<0.001
8/92	2	0.9236	0.7780	0.0323	0.0941	0.0565	-6.872	<0.001
10/92	2	0.7739	0.7306	0.0570	0.1857	0.0996	-4.727	<0.001
1/93	2	0.9030	0.7709	0.0365	0.1093	0.0643	-6.281	<0.001
7/93	2	0.6938	0.6572	0.0651	0.3103	0.1142	-5.267	<0.001
8/93	2	0.6839	0.7535	0.0740	0.1327	0.1323	-3.333	<0.001
10/93	2	0.7244	0.9265	0.0825	-0.1811	0.1478	-0.891	n.s.
12/93	2	0.8250	0.9074	0.0603	-0.1441	0.1082	-1.535	n.s.
1/94	2	0.7306	0.8852	0.0776	-0.1022	0.1388	-1.480	n.s.
7/94	2	0.8130	0.7120	0.0493	0.2143	0.0879	-5.842	<0.001

c) Princes

Date	Depth	r^2	b	SE_b	c	SE_c	t(b-1)	p
1/94	2	0.9418	0.9201	0.0330	-0.1244	0.0463	-2.421	0.01
7/94	2	0.9005	0.8456	0.0406	-0.0116	0.0626	-3.803	<0.001

Table A2.2 Summary of allometric relationship between shell LENGTH and HEIGHT for Mytilus from Albert, Queens and Princes docks. Figures calculated by least squares regression after log transformation of data, with length as the independent variable. ['b' represents slope; 'c' intercept on y-axis; SE_b and SE_c standard error of slope and intercept; 'p' probability associated with t-value for hypothesis b=1]

a) Queens

Date	Depth	r^2	b	SE_b	c	SE_c	t(b=1)	p
2/92	2	0.9046	1.1228	0.0527	-0.5365	0.0938	2.333	0.02
5/92	2	0.6141	0.8765	0.1003	-0.0953	0.1779	-1.231	n.s.
8/92	2	0.7536	1.0996	0.0908	-0.4949	0.1641	1.097	n.s.
10/92	2	0.8610	1.0331	0.0599	-0.3677	0.1072	0.553	n.s.
1/93	1	0.7496	0.9794	0.0817	-0.2722	0.1461	-0.252	n.s.
1/93	2	0.6330	0.9429	0.1036	-0.1990	0.1867	0.551	n.s.
9/93	2	0.8689	1.2555	0.0704	-0.7791	0.1253	3.630	<0.001
7/94	2	0.8613	1.2124	0.0702	-0.7084	0.1265	3.026	0.002

b) Albert

Date	Depth	r^2	b	SE_b	c	SE_c	t(b=1)	p
4/92	2	0.7849	0.7923	0.0599	-0.0268	0.1008	-3.469	<0.001
8/92	2	0.8989	1.0415	0.0504	-0.4503	0.0881	0.824	n.s.
10/92	2	0.7301	0.8559	0.0751	-0.1165	0.1312	-1.918	n.s.
1/93	2	0.8395	0.9190	0.0580	-0.2256	0.1022	-1.397	n.s.
7/93	2	0.6685	0.7572	0.0795	0.0752	0.1395	-3.055	0.002
8/93	2	0.7046	0.8348	0.0780	-0.0645	0.1396	-2.117	0.02
10/93	2	0.6036	0.7707	0.0902	0.0525	0.1615	-2.543	0.01
12/93	2	0.7167	0.8722	0.0792	-0.1239	0.1419	-1.615	n.s.
1/94	2	0.7071	1.0020	0.0931	-0.3579	0.1665	-3.469	<0.001
7/94	2	0.8460	0.9804	0.0604	-3.271	0.1077	-0.325	n.s.

c) Princes

Date	Depth	r^2	b	SE_b	c	SE_c	t(b=1)	p
1/94	2	0.8769	0.9971	0.0539	-0.4185	0.0756	-0.054	n.s.
7/94	2	0.8767	0.9765	0.0528	-0.3755	0.0816	-0.445	n.s.

Table A2.3 Summary of allometric relationship between shell LENGTH and WEIGHT for Mytilus from Albert, Queens and Princes docks. Figures calculated by least squares regression after log transformation of data, with length as the independent variable. ['b' represents slope; 'c' intercept on y-axis; SE_b and SE_c standard error of slope and intercept; 'p' probability associated with t-value for hypothesis b=3]

a) Queens

Date	Depth	r^2	b	SE_b	c	SE_c	t(b=3)	p
5/90	1	0.9480	3.0666	0.1037	-4.5214	0.1752	0.642	n.s.
8/90	1	0.9644	2.9540	0.0819	-4.2584	0.1357	-0.562	n.s.
2/92	2	0.9419	2.8623	0.1026	-4.1205	0.1829	-1.342	n.s.
5/92	2	0.5711	2.0714	0.2591	-2.6935	0.4596	-3.584	<0.001
8/92	2	0.8831	2.6060	0.1369	-3.6230	0.2474	-2.879	0.002
10/92	2	0.9413	2.6437	0.0953	-3.6865	0.1705	-3.738	<0.001
1/93	1	0.8880	2.6313	0.1349	-3.6511	0.2411	-2.734	0.005
1/93	2	0.7850	2.3515	0.1776	-3.1457	0.3201	-3.651	<0.001
9/93	2	0.9494	3.0104	0.1003	-4.2975	0.1786	0.104	n.s.
7/94	2	0.9424	3.2031	0.1143	-4.6979	0.2060	1.777	n.s.

b) Albert

Date	Depth	r^2	b	SE_b	c	SE_c	t(b=3)	p
7/89	1	0.9066	2.5148	0.1165	-3.9050	0.1678	-4.164	<0.001
5/90	1	0.9315	2.6600	0.1052	-3.9798	0.1610	-3.230	0.001
8/90	1	0.8483	2.7429	0.1674	-4.0877	0.2752	-1.536	n.s.
4/92	2	0.8722	2.0281	0.1121	-2.7990	0.1888	-8.672	<0.001
8/92	2	0.9413	2.6421	0.0952	-3.8188	0.1664	-3.759	<0.001
10/92	2	0.8922	2.2805	0.1144	-3.1526	0.1999	-6.289	<0.001
1/93	2	0.9098	2.2660	0.1030	-3.1031	0.1815	-7.128	<0.001
7/93	2	0.7149	1.7772	0.1673	-2.1972	0.2936	-7.308	<0.001
8/93	2	0.8998	2.2479	0.1083	-2.9891	0.1937	-6.947	<0.001
10/93	2	0.7934	2.1553	0.1588	-2.8836	0.2844	-5.321	<0.001
12/93	2	0.8053	2.3379	0.1659	-3.1780	0.2975	-3.990	<0.001
1/94	2	0.8676	2.7876	0.1572	-4.0045	0.2811	-1.351	n.s
7/94	2	0.8498	2.1912	0.1330	-2.9198	0.2372	-6.081	<0.001

c) Princes

Date	Depth	r^2	b	SE_b	c	SE_c	t(b=3)	p
9/93	2	0.9397	2.7100	0.0991	-4.0419	0.1372	-2.926	0.002
1/94	2	0.7658	2.1909	0.1749	-3.3322	0.2451	-4.626	<0.001
7/94	2	0.9368	2.5170	0.0943	-3.7005	0.1456	-5.122	<0.001

Table A2.4 Summary of allometric relationship between shell LENGTH and DRY TISSUE WEIGHT for Mytilus from Albert, Queens and Princes docks. Figures calculated by least squares regression after log transformation of data, with length as the independent variable. ['b' represents slope; 'c' intercept on y-axis; SE_b and SE_c standard error of slope and intercept; 'p' probability associated with t-value for hypothesis b=3]

a) Queens

Date	Depth	r^2	b	SE_b	c	SE_c	t(b=3)	p
5/90	1	0.8144	3.1733	0.2186	-5.5108	0.3694	0.793	n.s.
8/90	1	0.9553	2.9450	0.0920	-5.0342	0.1525	-0.598	n.s.
2/92	2	0.8555	3.0970	0.1837	-5.4827	0.3274	0.528	n.s.
5/92	2	0.4886	1.8434	0.2722	-3.3177	0.4830	-4.249	<0.001
8/92	2	0.7076	2.5892	0.2403	-4.4578	0.4344	-1.710	n.s.
10/92	2	0.7245	0.2633	0.2015	-3.9602	0.3602	-3.657	<0.001
1/93	1	0.7305	2.9282	0.2567	-5.1404	0.4589	-0.280	n.s.
1/93	2	0.6178	3.1798	0.3610	-5.6157	0.6505	0.498	n.s.
9/93	2	0.7809	2.5619	0.1958	-4.4464	0.3487	-2.237	2.365
7/94	2	0.7170	1.9524	0.1770	-3.2943	0.3191	-5.919	<0.001

b) Albert

Date	Depth	r^2	b	SE_b	c	SE_c	t(b=3)	p
7/89	1	0.7611	2.3030	0.1862	-4.4772	0.2682	-3.743	<0.001
5/90	1	0.8269	3.6143	0.2412	-6.4860	0.3691	2.547	0.01
8/90	1	0.7316	4.2022	0.3674	-7.4241	0.6041	3.272	0.001
4/92	2	0.7793	2.3106	0.1775	-4.3135	0.2990	-3.884	<0.001
8/92	2	0.8349	2.6627	0.1709	-4.6899	0.2987	-1.974	n.s.
10/92	2	0.6591	2.8400	0.2948	-5.0394	0.5150	-0.543	n.s.
1/93	2	0.7461	2.8950	0.2438	-5.1070	0.4296	-0.431	n.s.
7/93	2	0.7054	2.3602	0.2274	-4.2566	0.3990	-2.814	0.005
8/93	2	0.7156	2.5551	0.2325	-4.5252	0.4161	-1.914	n.s.
10/93	2	0.6211	2.8377	0.3199	-5.0690	0.5732	-0.507	n.s.
12/93	2	0.5180	2.9077	0.4048	-5.2116	0.7258	-0.228	n.s.
1/94	2	0.6027	2.9324	0.3437	-5.2592	0.6146	-0.197	n.s.
7/94	2	0.4987	2.0421	0.2955	-3.6071	0.5273	-3.242	0.001

c) Princes

Date	Depth	r^2	b	SE_b	c	SE_c	t(b=3)	p
9/93	2	0.9489	3.1125	0.1043	-5.6003	0.1444	1.079	n.s.
1/94	2	0.8415	3.2239	0.2020	-6.1117	0.2831	1.108	n.s.
7/94	2	0.8727	2.8807	0.1588	-5.1011	0.2451	-0.751	n.s.

Table A2.5 Estimated dry tissue weight and shell weight of a standard (45mm) animal. Figures calculated from least squares regression lines after log transformation of data. Condition index (shell weight / [dry tissue weight X 10]) also shown for estimated values.

a) Queens dock

Date	Dry Weight	Shell Weight	SW/(DWt*10)
5/90	0.5437	3.5343	0.6500
8/90	0.6830	4.2189	0.6177
2/92	0.4338	4.0872	0.9421
5/92	0.5369	5.3812	1.0022
8/92	0.6648	4.8448	0.7288
10/92	0.6047	4.8311	0.7989
1/93	0.5018	4.9989	0.9962
1/93	0.4378	5.5195	1.2608
9/93	0.6150	4.7792	0.7771
7/94	0.8579	3.9583	0.4614

b) Albert dock

Date	Dry Weight	Shell Weight	SW/(DWt*10)
7/89	0.2138	1.7889	0.8367
5/90	0.3084	2.6168	0.8484
8/90	0.3334	2.7980	0.8391
4/92	0.3209	3.5806	1.1158
8/92	0.5152	3.5419	0.6874
10/92	0.4526	4.1452	0.9159
1/93	0.4775	4.3967	0.9208
7/93	0.4419	5.5075	1.2464
7/93	0.5413	2.8529	0.5270
8/93	0.5000	5.3345	1.0669
10/93	0.4190	4.7806	1.1408
12/93	0.3939	4.8642	1.2348
1/94	0.3878	4.0186	1.0362
7/94	0.5874	5.0434	0.8586

Table A2.5 (cont.) Estimated dry tissue weight and shell weight of a standard (45mm) animal. Figures calculated from least squares regression lines after log transformation of data. Condition index (shell weight / [dry tissue weight X 10]) also shown for estimated values.

c) Princes dock

Date	Dry Weight	Shell Weight	SW/(DWt*10)
9/93	0.3510	2.7435	0.7816
1/94	0.1652	1.9491	1.1798
7/94	0.4584	2.8883	0.6301

d) Spatial comparison

Dock	Dry Weight	Shell Weight	SW/(DWt*10)
Canning	0.5637	5.3096	0.9419
Salthouse	0.5496	5.4705	0.9954
Wapping	0.6922	5.9517	0.8599
Albert	0.4999	5.3353	1.0672
Queens	0.6151	4.7789	0.7769
Brunswick	0.5967	4.1607	0.6972

Table A2.6 Test of significant differences between regression lines for spatial *Mytilus* biometric data. Independent variable is length.

	SLOPE		INTERCEPT	
Dependent variable	F-value	Pr > F	F-value	Pr > F
Shell weight	7.10	0.0001	9.40	0.0001
Dry weight soft parts	0.80	0.5522	4.15	0.0012

	Dock	Slope	Standard error slope	Intercept	Standard error intercept
Shell weight	Canning	2.7130	0.1346	-3.7601	0.2446
	Salthouse	2.3593	0.0800	-3.1624	0.1447
	Wapping	2.0954	0.1657	-2.6895	0.3030
	Albert	2.2479	0.1083	-2.9891	0.1937
	Queens	3.0104	0.1003	-4.2975	0.1786
	Brunswick	2.8768	0.1589	-4.1368	0.2754
Dry weight	Canning	2.8491	0.3025	-4.9591	0.5498
	Salthouse	2.7001	0.2643	-4.7238	0.4782
	Wapping	2.3435	0.3576	-4.0341	0.6540
	Albert	2.5551	0.2325	-4.5252	0.4161
	Queens	2.5619	0.1958	-4.4464	0.3487
	Brunswick	2.9318	0.1757	-5.0711	0.3046

Table A2.7 Test of significant differences between regression lines for *Mytilus* biometric data for samples taken from different depths in Albert dock in January 1993. Independent variable is length.

	SLOPE		INTERCEPT	
Dependent variable	F-value	Pr > F	F-value	Pr > F
Width	1.36	0.2555	2.57	0.0558
Height	0.67	0.5703	0.54	0.6541
Shell weight	1.78	0.1524	2.44	0.0653
Dry weight soft parts	0.45	0.7175	29.92	0.0001

Dependent variable	Depth (m)	Slope	Standard error slope	Intercept	Standard error intercept
Width	0	0.8349	0.0681	-0.0129	0.1216
	1	0.7980	0.0729	0.0651	0.1287
	2	0.7306	0.0570	0.1857	0.0996
	3	0.8892	0.0576	-0.1001	0.1004
Height	0	0.7886	0.0958	0.0044	0.1710
	1	0.8405	0.0890	-0.0872	0.1573
	2	0.8559	0.0751	-0.1165	0.1312
	3	0.7130	0.0779	0.1269	0.1357
Shell weight	0	1.9085	0.1832	-2.4565	0.3270
	1	2.2199	0.1467	-3.0174	0.2591
	2	2.2805	0.1144	-3.1526	0.1999
	3	2.3606	0.1379	-3.2705	0.2405
Dry wt soft parts	0	2.3891	0.3669	-4.1458	0.6550
	1	2.3900	0.3982	-4.2239	0.7036
	2	2.8400	0.2948	-5.0394	0.5150
	3	2.6573	0.2928	-4.9136	0.5105

Table A2.8 Test of significant differences between regression lines for *Mytilus* biometric data for samples collected from sections of wall covered and not covered by pontoons. Independent variable is length.

	SLOPE		INTERCEPT	
Dependent variable	**F-value**	**Pr > F**	**F-value**	**Pr > F**
Width	3.84	0.0531	0.01	0.9131
Height	0.06	0.8022	5.01	0.0276
Shell weight	3.21	0.0765	8.52	0.0044
Dry weight soft parts	0.47	0.4951	10.31	0.0018

Dependent	**Area**	**Slope**	**S.E. slope**	**Intercept**	**S.E. intercept**
Width	**Pontoon**	0.9019	0.0784	-0.1184	0.1371
	Clear	0.6572	0.0651	0.3103	0.1142
Height	**Pontoon**	0.7171	0.1127	0.1229	0.1971
	Clear	0.7572	0.0795	0.0752	0.1395
Shell weight	**Pontoon**	2.3397	0.1824	-3.2380	0.3189
	Clear	1.7772	0.1673	-2.1972	0.2936
Dry weight	**Pontoon**	2.0700	0.2394	-3.6643	0.4187
	Clear	2.3602	0.2274	-4.2566	0.3990