Long Term Changes in the North Sea Ecosystem

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Dedicated to the memory of my late father,

Harold Ronald Clark ARAM GRSM LRAM "Music's G.P."

(1924 - 1997)

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Abstract

Long term data on the North Sea ecosystem are available for phytoplanktonic, zooplanktonic, benthic, fish, and seabird communities. Temporal changes in these have been examined by numerous researchers over the course of the 20th century, their main objective being to determine how the interannual dynamics of these communities are regulated. This study considers the long term ecosystem dynamics, and the mechanisms behind these dynamics, for the North Sea over the latter half of the 20th century, although it focuses upon the time series operated by the Dove Marine Laboratory, and the Continuous Plankton Recorder (CPR) survey in the central-west North Sea region.

A review of the literature suggests that long term changes across the North Sea are ultimately driven by two processes. In the northern, western and central areas of the North Sea, the ecosystem is climatically driven, whilst in the southern and eastern regions, the signal of climate is masked by the large anthropogenic nutrient inputs into these regions.

A comparison of the Dove and CPR zooplankton time series for the central-west North Sea area found that although their relative year to year fluctuations were similar, large differences were present in the absolute abundances recorded. Model derived catching efficiencies for the two sampling devices suggested that differences in absolute abundances were mainly due in some zooplankton taxa to a greater degree of active avoidance of the CPR sampling device. Further examination of these two series found that the long term zooplankton trends in the central-west North Sea were dissimilar to those observed for other North Sea regions. Inverse relationships between zooplankton abundance, and the position of the Gulf Stream North Wall, and with air temperatures were also observed. These dissimilar trends and inverse relationships were ultimately found to be due to the presence of an internal predation based mechanism.

Climatic influences were also found to indirectly influence the long term dynamics of the benthos in the central-west North Sea. The primary factor influencing interannual variation in benthic abundance was phytoplankton productivity (i.e. food), which in turn was related to climatic factors. However, at a second central-west North Sea benthic station, situated within a *Nephrops norvegicus* fishing ground, constant trawling disturbance of the benthos was the primary factor influencing both benthic abundance and species composition.

Over the latter half of the 20th century, air temperatures and daily sunshine durations have increased in the central-west North Sea region, alongside changes in climatic proxy variables (e.g. NAO index). However, similar trends were not always observed in the biota. Ultimately, the long term dynamics of taxa, communities and ecosystems may be due to direct or indirect factors, yet interactions between a diversity of internal and external factors, results in the complex behaviour of biological systems over time. This study shows that, although the central-west North Sea ecosystem is climatically driven, similar trends between climate and ecosystem components do not necessarily exist, and nor considering the high complexity of the ecosystem, should they be expected.

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Chapter 1 General Introduction

Ecosystems are highly dynamic on a range of temporal scales from seconds to millennia (McGowan, 1990). These dynamics are in response to changes in a multiplicity of forcing factors which occur at a similar multitude of temporal scales (Figure 1.1). Some of these are concerned with the internal dynamics of multi-species systems (de Angelis & Waterhouse, 1987), while others are the result of extrinsic abiotic factors such as the climate. Interactions between this diversity of internal and external factors, and the fact that the responses to most are non-linear, results in the complex behaviour of biological systems over time (de Angelis & Waterhouse, 1987; Rothschild, 1991). In addition, anthropogenic influences such as the effects of climate change ('global warming'), eutrophication and fishing have frequently been cited as causes for concern in the context of drivers of change in marine ecosystems (e.g. Shugar, 1990; Greve *et al.*, 1996; Jennings & Kaiser, 1998).

Long term studies of ecosystems have been used in all branches of ecology (Jassby & Powell, 1990) and have provided invaluable information about the natural fluctuations of species and communities and the possible causes of these fluctuations. In particular, such data have been used to detect synchronous fluctuations in ecosystem components (Aebischer *et al.*, 1990; Pearce & Frid, 1999) and in populations with climatic variables such as temperature (Colebrook, 1985) or in the path of the Gulf Stream (George & Taylor, 1995; Taylor, 1995; Willis, 1995). The most valuable uses of long term studies are in the monitoring of commercially important species such as fish (e.g. Serchuk *et al.*, 1996) and in the detection of changes in ecosystems after they occur (McGowan, 1990), especially those caused by anthropogenic factors such as pollution or global warming (for examples see Cederwall & Elmgren, 1980; Rosenberg, 1985; Brockmann *et al.*, 1988; Shugar, 1990; Beukema, 1992a; Dickson *et al.*, 1992).

Defining and measuring change

Turchin (1992) defined ecological change as happening "when a significant shift occurs in the direction of a long term trend." This description when it is applied to real world ecology could be viewed as an oversimplification, as mechanisms in the real world operate on a multitude of spatial, temporal and functional/taxonomic scales (see Figure 1.1). It is suggested here that what scientists should possibly be looking for is any observed change which implies a consistent change in the underlying functionality of the ecosystem (i.e. the mechanism through which the ecosystem is controlled has changed). As such, this could be exhibited in a time series as not only a change in the direction of the trend but also a change in the gradient of the series with time. What constitutes a consistent shift in an ecosystem is also open to discussion, as freak or extreme events may occur in an ecosystem, due either to a natural or anthropogenic influence from time to time, yet may not constitute a permanent change (e.g. Ziljlstra & de Wolf, 1988; Allen *et al.*, 1997). Other phenomena such as cyclic fluctuations (e.g. Russell *et al.*, 1971) really require observation over a number of cycles to fully understand their nature. As such, the turning points of maxima and minima in long term cyclic fluctuations would not be defined as change although a change in the phase length could be. Potentially, a relatively small but consistent shift in the stationarity of a series (mean and/or variance) could also indicate a change in the underlying functionality of the system. In all cases, as ecological systems have a high inherent variability owing to the many factors which influence them, in determining that a change has occurred due to a specific reason, it is necessary to be aware of the extent of this natural variability over both seasonal and/or inter-annual periods (i.e. the baseline variance of the ecosystem needs to be established (Southward, 1995)).

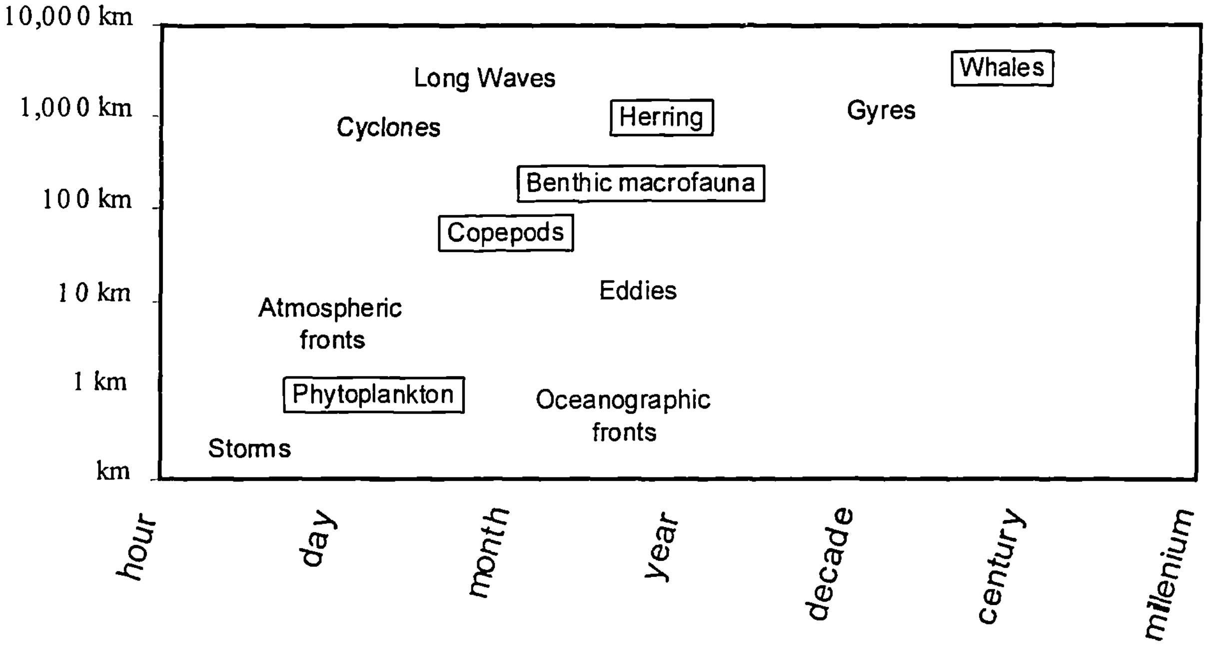


Figure 1.1 A conceptual model of the time-space scales of variations in the major ecological components (biotic components in boxes) in the marine system, and some of the factors which contribute to them. Based on Steele (1991).

It is also possible to look for change in different ways. Change may be looked for in series of year to year abundances of either a single taxon or group of taxa, or in a change in the pattern of the seasonal cycle or in the pattern of geographical distribution with time. It is generally considered that it is easier to attempt to identify signals of change in annual means for defined areas and then to search for seasonal or geographical differentiation in relation to specific signals (Fransz *et al.*, 1991).

Considerations when analysing time based data

Although long term ecological data permit the study of biological systems over seasonal and annual time frames, the multiplicity of continually changing factors which drive ecosystems means that attempting to establish patterns or associations between forcing factors and ecological data is complicated. Classic experimental approaches have considerable statistical power, but are impractical at the space and time scales in which factors such as climate operate. This multiplicity of factors makes it difficult to assess both the relative importance of any single factor (their influence may itself be variable with time), anthropogenic or otherwise, to the dynamics of the ecosystem. This problem aside, time-based data have many drawbacks when it comes to establishing links or timing of changes in ecological variables with forcing factors in a statistically robust manner. The most straight forward approach is the demonstration of changes in biological systems which occur in phase with changes in presumed causative factors through the use of correlation analysis (e.g. the response of benthic communities to increased organic input (Pearson & Rosenberg, 1986)). Unfortunately, such correlations are not powerful tools for identifying causation (Underwood, 1990; Underwood, 1992; Underwood, 1996). Part of the problem with these empirical studies which are so often applied to time based data, is that there is almost no limit to the number of correlations that may be run - if one searches a large enough set of data, one is sooner or later likely to find something that correlates reasonably well (Shepherd *et al.*, 1984). Therefore the scientist needs to account for the possibility of chance significant results solely occurring through the number of multiple comparisons performed. Increased confidence in a specific association follows when a specific mechanism can be proposed. However, the final test of a hypothesis should be the accuracy of forecasting data not available when the analysis was made.

The use of inter-time series correlation also brings with it the additional problems of temporal autocorrelation in the form of serial correlation and trend, which need to be considered when examining the relationship between two time series. The presence of trend in the data or a high amount of serial correlation (when sequential observations are not independent from one another), effectively reduces the number of degrees of freedom because the assumption of complete independence between samples within a series cannot be upheld. As such, in these situations, a large cross-correlation coefficient may not necessarily be statistically significant as the degrees of freedom are effectively reduced (Jassby & Powell, 1990). Correction factors have been used to account for the presence of serial correlation such as the method used by Quenouille (1952) (see Chapter 4). Unfortunately, where a relationship between two time series is shown to be affected by trend and/or serial correlation, removing or compensating for these involves removing valuable information about the relationship between the two time series. The presence of autocorrelation and/or trend in the data does not necessarily mean that any observed relationship between the two time series is invalid. For example, if two series do, in fact, have a causal relationship which is manifested by the trend in each series, the evidence of such a relationship could be masked by the removal of this trend (Jassby & Powell, 1990) from either or both series.

Statistically analysing time series data is also complicated by the fact that the number of samples or years of data available is often limited by the irregularity of funding of the time series (Dickson, 1995). As a result, the few years of data or samples available, means that the statistical power of the analyses undertaken is lower than would normally be acceptable in many other scientific studies. As such, the presence of Type II statistical errors needs to be considered. Type II errors are defined as being the problem of not rejecting the null hypothesis when it is in fact false (also called the ß error Zar, 1984). The consequences of ignoring the possibility of Type II errors mean that it is possible that a key factor involved in affecting an ecosystem could be missed (Buhl-Mortensen, 1996). Low sample sizes are associated with large probabilities of committing a Type II error (Figure 1.2), because the number degrees of freedom for the test are equally low. Thus, at n=25 years, there is a probability of 0.27 of incorrectly accepting the null hypothesis at the 0.05 level. To achieve the probability of only incorrectly rejecting the null hypothesis at the 0.05 level, 47 years of annual sampling would be required. There are few environmental time series which reliably cover such a period, and even fewer, biological time series of this length. Although it would be possible to use a 3yr 10mth period of monthly data, in order to properly compare the interannual dynamics of two series, the seasonal signal needs to be removed from the data (and a 3 year series would most likely not provide much information about the true interannual variability of a time series).

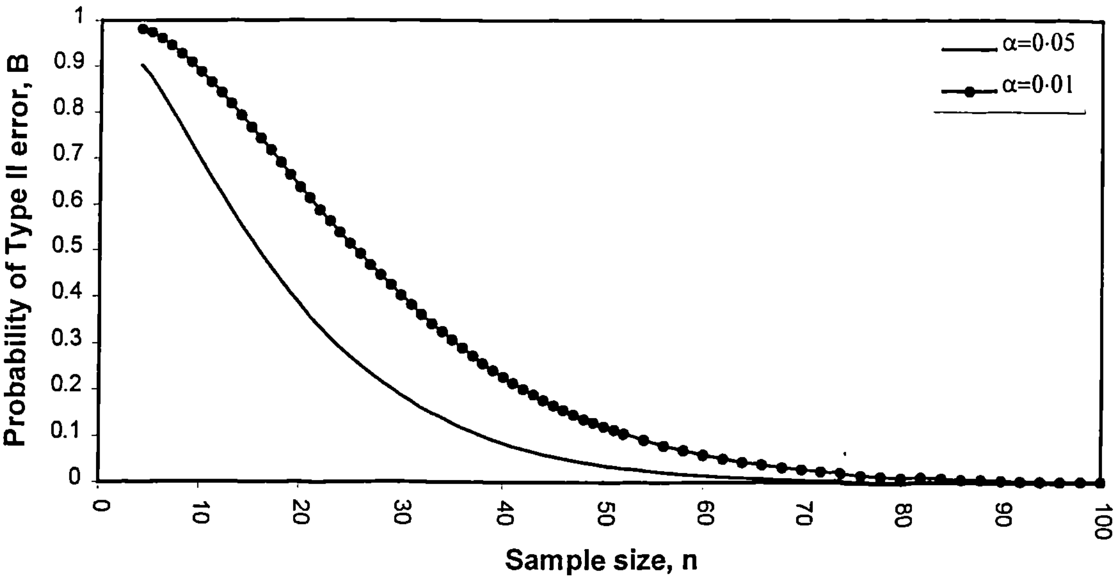


Figure 1.2 Relationship between the probability of a Type II error with changing sample size, n, at alpha significance levels of 0.05 and 0.01.

The major problem of incorrectly rejecting the null hypothesis means that those factors which are incorrectly rejected as not controlling a certain biological variable may actually in effect be having a major influence upon it, and once this variable has been rejected then potentially so has the key to how the ecosystem is controlled. Some researchers have advocated the use of Bonferroni corrections (Rice, 1988) to tables of multiple comparisons in an attempt to reduce the chance of Type I errors, yet forget that the reduction of the alpha significance level according to the number of multiple comparisons will increase the chance of Type II errors occurring. An alternative method of assessing the significance of multiple comparisons is to calculate global significance levels to the ensemble of results obtained from the binomial distribution which are then applied to each table of independent tests (for examples see Shepherd *et al.*, 1984; Dunnet *et al.*, 1998 & Chapters 4, 5 & 6).

In the context of ecological time series, correlation coefficients are likely to be low due to the large number of factors which contribute to the amount of variance explained in an ecological factor at any one given time. Part of this problem is because the factors which affect an ecosystem usually change with time. For example changes in sea surface temperatures will not affect plankton if nutrients are a limiting factor during a span of years. Thus, the actual number of data points over which forcing between a particular environmental variable and a response exists may be very small. As yet there is no scientifically accepted method of examining time series to detect where pairs of datapoints are associated and where they are not.

Ideally, experimental approaches in which a single factor is manipulated in a controlled manner provide the strongest inferences about causality. However, such experimental approaches are on the scale of a few square metres at most, whereas marine systems cover areas of thousands of kilometres square. Thus such experimental investigations are not practical at both the large temporal and spatial scales of many marine systems (Mann, 1993), although they do help to support conclusions formed from the analysis of time series data. Often, where investigations are dealing with an examination of the potentially destructive effect of an anthropogenic influence, the use of the precautionary principle means that such statistical rigour is not required. Such an approach seeks to act when the available data indicate the possibility of irreversible damage rather than needing a full demonstration of proof of a negative effect.

Mechanisms causing change

Scale is an important consideration in determining what factors influence an ecosystem. Where change is observed across many species, and over a large geographical area, then this suggests that the change has been induced by processes operating on a similarly large scale, the most evident of which is climatic forcing (Colebrook, 1978; Colebrook, 1986). Such wide scale changes also tend to operate on a larger temporal scale (Steele, 1991) (see Figure 1.1). In contrast, many anthropogenic effects are restricted to a much smaller spatial area, usually around the immediate area of the impact into the marine system (e.g. sewage sludge dumping), although there are exceptions.

Meteorological or climatic factors affect the temperature, salinity and physical structure of the water column. Temperature directly affects most poikilothermic organisms by changing their metabolic rates. This, in turn, influences factors such as growth rate, feeding rate, reproductive rate and speeds of locomotion. In addition, the meteorological effect upon the physical structure of the water column, specifically the formation and strength of the thermocline, is a key factor affecting the productivity of the system (Sverdrup, 1953) in most areas of the North Sea.

The properties of species and ecosystems may be altered by either direct or indirect mechanisms. Indirect effects have been defined as "how one species <or group of species> alters the effect that another species <or abiotic factor> has on a third" (Strauss, 1991). A common example is how a species or a community may be affected through changes in its food resource. For example, changes in nutrient concentrations or weather may influence the productivity of phytoplankton, which acts as a food resource for the both the zooplankton and benthic communities. Indirect effects are mostly mediated through biotic factors via competition, predation or changes in a biotic food resource, yet indirect effects are often difficult to identify and characterise (Colebrook, 1986), and studying precise trophic interactions is complicated as the growth rate of a particular population may be limited by temperature and food, but its maximum abundance may be limited by predators (Roff *et al.*, 1988) or competition. Studies are further complicated by the high degree of seasonality in the system where a species may have a high abundance for part of the seasonal cycle, but then be at reduced abundance or lacking for the remainder of the year (Frid *et al.*, 1994). The primary forcing of species or ecosystems often occurs at a single period of the seasonal cycle, be it either through the timing or abundance of peak food resources (allowing growth), or through mortality due to the presence of a seasonal predator or extreme weather conditions. Often, more than one of these factors will affect the system over the course of the seasonal cycle, either during separate periods or simultaneously. Not all species within a community respond equally, or even in the same direction, to a change in a forcing factor.

Aims and objectives

Studies on the long term dynamics of the planktonic, benthic and fish communities of the North Sea have tended to be carried out in isolation, and have focussed on the dynamics of either a particular species (e.g. Millner & Whiting, 1996; Planque & Fromentin, 1996) or a particular community (e.g. Roff *et al.*, 1988; Beukema, 1992c) without considering the long term dynamics of the ecosystem as one functioning unit. This thesis aims to address the mechanisms not only within each community, but also to understand the long term dynamics and functioning of the North Sea ecosystem as a whole. Chapter 2 reviews the current literature on changes in North Sea planktonic, benthic, fish, and seabird communities, and integrates and discusses the results of these disparate studies into consideration of long term dynamics from an ecosystem perspective. As such, it has been included as a separate chapter which is in a publishable format.

This thesis is mainly based on the results of analyses of time series data from the central-west North Sea. In this region, the Dove Marine Laboratory operates three time series. The Dove zooplankton series, which is the longest of the three series, was initiated by Frank Evans in 1969 and sampled monthly. The two Dove benthic series (Stations M1 and P) have been sampled biannually and annually since being initiated in 1972 and 1971 respectively by Jack Buchanan. The other main time series analysed is the Continuous Plankton Recorder zooplankton series for the coastal central west North Sea region (Figure 3.2). This dataset constitutes the longest and most geographically widespread marine ecological dataset in existence. However, despite its importance, there has been little published research on the accuracy of this survey, from which most of our knowledge of zooplankton dynamics throughout the NE Atlantic originates. The accuracy of the Dove zooplankton time series has also not been considered, or as to how representative it is of the central-west North Sea region. Yet these two time series, which use different sampling methodologies, provide a unique opportunity to allow a critical comparison of their observations (Chapter 3, Clark *et al.*, in press) to assess their accuracy and to increase our understanding of both datasets.

The long term trends in zooplankton throughout most of the North Sea have been found to be predominantly influenced by climate (e.g. Colebrook, 1985; Dickson *et al.*, 1988a). However, previous research suggests that the long term zooplankton dynamics in the central-west North Sea region may be dissimilar to those in other North Sea areas (Huliselan, 1995; Frid & Huliselan, 1996). Chapter 4 evaluates the long term changes in zooplankton abundance and species composition which have occurred in the central-west North Sea, and, using a wide range of environmental variables, establishes how the long term dynamics of the zooplankton community relate to external influences (e.g. GSNW, temperature, nutrients etc.), and to those zooplankton trends observed in other North Sea areas. In the light of these results, Chapter 5 goes on to focus on the presence of internal factors, principally predation, and details their influence on the interannual dynamics of the central-west North Sea zooplankton community.

Long term changes in the benthos off the Northumberland coast at Station M1 have been related to organic input (Buchanan, 1993). Chapter 6 examines this relationship more closely and aims to establish the extent to which the benthos there is ultimately linked to climatic influences. In contrast, no relationship between organic flux at Station P has been observed. This study examines whether this is due to the fact that this may be masked by the effect of fisheries (Chapter 7, Appendix 4, Frid *et al.*, 1999a; Frid & Clark, 2000).

The main results of these studies (Chapters 4 to 7) are synthesised in a basic model and examined from an ecosystem perspective (Chapter 8). This allows a consideration of the importance of the influence of both direct and indirect effects on the long term dynamics of the North Sea ecosystem.

Chapter 2 Long term changes in the North Sea ecosystem. A review of current knowledge

Introduction

Sources of long term data

Essentially, a time series may be simply defined as a plot of one or more variables as a function of time (Jassby & Powell, 1990). However, the quality of time based data varies considerably in studies of temporal change. At its simplest it may purely be a comparison of data between two periods, or, at the other end of the scale, samples may cover many years and be of a high resolution (short period between samples), as is often the case with meteorological time series. Unfortunately, due to the nature of government based scientific funding, long term biological studies rarely reach a decade in length (Dickson, 1995). Often the highest quality data are those of commercial importance (e.g. weather data) or those relating to commercially important species (e.g. fish).

Long term ecological data usually consist of abundance based data for a particular assemblage, usually measured in taxa per unit volume or area, although semi-quantitative data are also used (Warner & Hays, 1994). Fisheries catch and landings data are often in units of catch per year or catch per unit effort and although these data may not be able to account for all catches, they are still useful in analyses. Such fisheries based data constitute the longest marine biological time series available. For example, fisheries research vessels have operated off the north-east coast of England since 1929, whilst catch data are available for some species since the 1890s (Rijnsdorp *et al.*, 1996). The longest time series relating to non-commercial species are from the Continuous Plankton Recorder (CPR) survey based in Plymouth (Warner & Hays, 1994), which has operated since 1948 over the North Sea and North Atlantic area (Warner & Hays, 1994), constituting the longest and most geographically widespread marine ecological dataset in existence. Although time series of chlorophyll measurements from satellite based data area are now becoming available, these are too short to be of use in determining long term changes in chlorophyll, and present difficulties when attempting to use the data as direct measurements of chlorophyll (Reid *et al.*, 1990). Benthic time series data pertaining to the North Sea are of a lower resolution and are shorter than those of the planktonic time series, with samples being taken only once or twice per year, although this does correspond to the longer longevity of benthic animals compared to plankton. Both littoral (e.g. Balgzand tidal flat, Wadden Sea (Beukema, 1985; Beukema, 1992b; Beukema, 1992c; Beukema, 1992a)) and sublittoral benthic samples (e.g. Dove benthic time series (Buchanan *et al.*, 1974; Buchanan & Moore, 1986b; Frid *et al.*, 1996)) are available. While not formal time series, as quantitative benthic samples have been taken since the turn of the 20th century (Petersen & Boysen-Jensen, 1911), these historic data may be compared with contemporary datasets to assess changes over a very long period (e.g. Appendix 4, Kröncke, 1990; Kröncke, 1992; Kröncke, 1995; Frid & Clark, 2000).

The North Sea

The North Sea, being surrounded by the countries of western Europe, has been used as a source of food, for transport and as a sink for wastes since pre-history. However, increasing understanding of human impacts in coastal areas has seen concern focussed on the North Sea firstly in response to fisheries issues (e.g. establishment of ICES in 1902), and subsequently water quality (e.g. Oslo Convention, and Paris Commission, Ministerial Conference on the North Sea). It therefore presents an ideal case study for considering our state of knowledge on changes in the biology of our coastal seas.

The North Sea (Figure 2.1) is a rectangular shaped basin (surface area 575,000 km^2), relatively shallow (<50 m depth) in the southern bights and deeper (c. 200m depth) in the northern areas, excepting a deep (600m) trough, the Norwegian Rhinne, on its eastern margin (Reid *et al.*, 1988) (Figure 2.1). The majority of the water mass within the basin is of Atlantic origin, primarily flowing in from the north, with other inputs through the Dover Straits and low salinity water from the Baltic through the Skaggerak. Due to the prevailing south-westerly winds (Reid *et al.*, 1988), the bulk of the water mass circulates in an anticlockwise gyre in the North Sea with the main outflow being through the Norwegian Rhinne (Laane *et al.*, 1996).

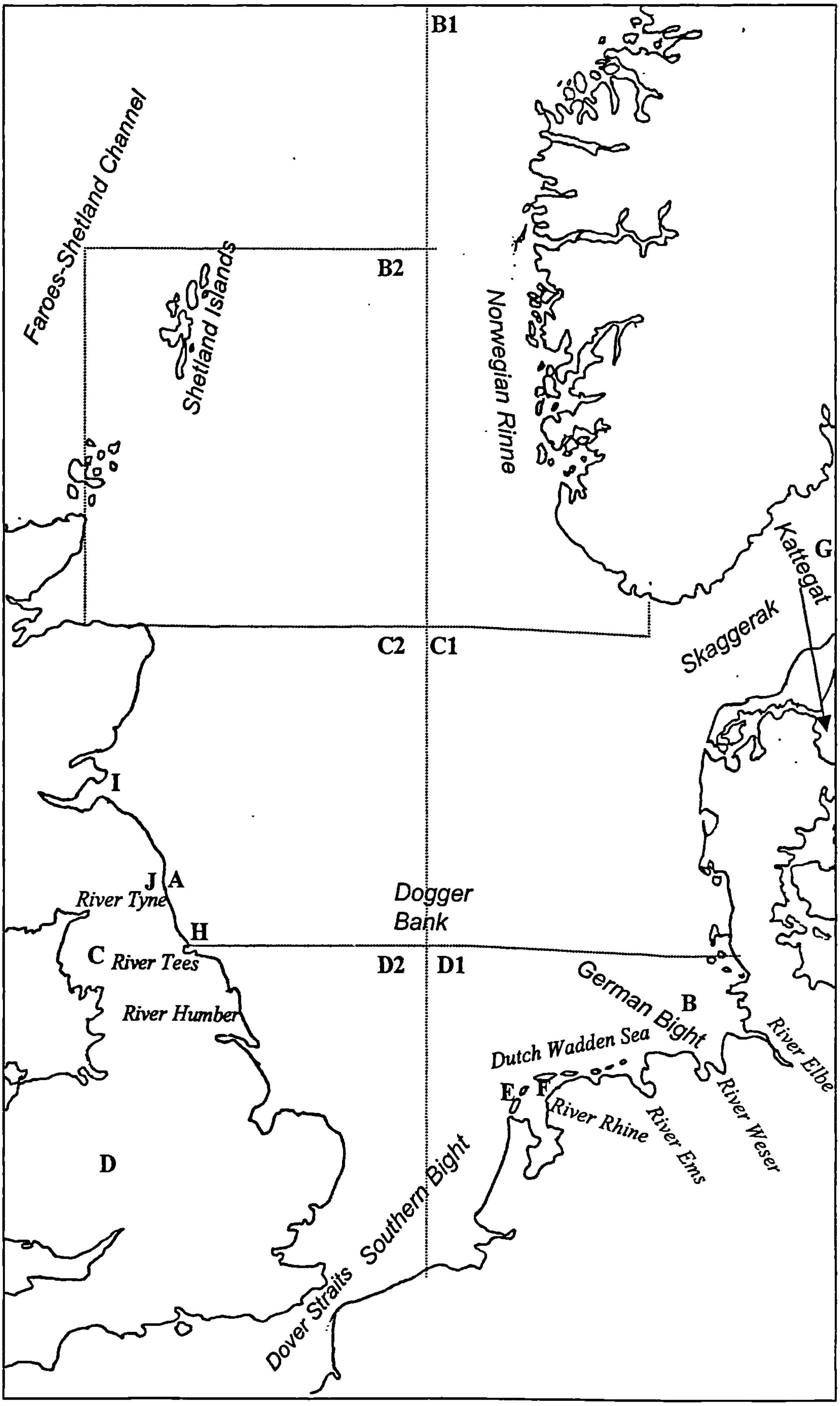


Figure 2.1 Map of the North Sea presenting the major geographical features mentioned in the text, and the approx. positions of the main data series discussed. CPR standard areas are delimited with dashed lines. Data series sites as follows. A) Dove zooplankton and benthos B) Helgoland Roads nutrients, phyto- & zoo-plankton C) Windermere freshwater zooplankton D) Bibury vegetation E) Balgzand littoral benthos F) Norderney littoral & sublittoral benthos G) Skaggerak-Kattegat sublittoral benthos H) River Tees & Tees Bay benthos I) Isle of May kittiwakes J) North Shields kittiwakes.

Lee (1980) delineated the North Sea into a number of water bodies of different salinities, origins and stratification. Stratification occurs in most central and northern areas of the North Sea with a strong seasonal thermocline developing by June which breaks down by November (Mann, 1993). In the southern and German Bights (see Figure 2.1) (owing to their shallow <50m depths and strong tidal flows), no stratification occurs. The southern and German Bights are further influenced by the large freshwater inputs from the major European rivers which means this area is hydrographically distinct from other areas. Nutrient distributions and concentrations within the North Sea are influenced by the anticlockwise gyre with the majority of the natural nutrient inputs to the North Sea originating from the Atlantic. However, over the last 40 years of the 20th century, high nutrient discharges into the southern North Sea via the major continental rivers have been observed (Brockmann *et al.*, 1988). These increased nutrient inputs from rivers passing through one of the most industrialised areas in the world are thought to be responsible for some exceptional phytoplankton blooms particularly along the Dutch coast and in the German Bight (Colijn, 1992).

Sea surface temperatures in the North Sea are affected by hydrography and the sources of water. The coldest water in winter is found in the German Bight (3°C) with the rest of the Sea being kept warm by the inflow of relatively warm North Atlantic water (6-7°C) from the north and via the English Channel. In summer the opposite situation prevails with warm water adjacent to the continental coast (18°C) and a relatively cold North Atlantic tongue of water (14°C) along the eastern coast of the UK.

The North Sea is a valuable resource, and as such suffers from numerous anthropogenic impacts. Due to the naturally nutrient rich water, it is one of the worlds richest fishing grounds. It contains valuable oil resources in the north while the southern region is an important gas production area, whilst the waters off the eastern coast of the UK are sources of aggregates for use in the construction industry. Other areas have been used for sewage sludge (Rees *et al.*, 1985; Parker, 1988) and fly ash dumping (Herrando-Perez & Frid, 1998).

In this chapter, I set out to establish the extent of changes in the biota of the North Sea over the last 50-100 years and, where possible, examine the possible causes and mechanisms behind these changes. Each major environment and community will initially be focussed on, before considering how the changes observed and causes of these changes affect the functioning of the North Sea ecosystem as a whole.

Plankton

Introduction

Zooplankton studies with samples from the North Sea started in the middle of the 19th century (Greve *et al.*, in press). The first publications dealt mainly with morphology, taxonomy and the general biology and distribution of plankton. This interest led to the realisation of the importance of zooplankton as secondary producers in the food chain, and how fluctuations in zooplankton abundance may affect fish stocks. The first examination of the geographical variability of the phytoplankton over the North Sea was made by Cleve in 1887, and in 1902, ICES initiated quarterly surveys of the North Sea using Cleve's methodology (Reid *et al.*, 1990).

Long term monitoring of the plankton community began with the use of the Continuous Plankton Recorder (CPR), with the original concept to provide information on the seasonal and annual changes in the zooplankton and to correlate these changes with hydrographic data, meteorological data, and with fluctuations in the fisheries (Warner & Hays, 1994). Since 1948, CPRs have consistently sampled on a monthly basis using "ships of opportunity" over several routes in the North Atlantic and North Sea (Warner & Hays, 1994). In addition to the 51 year time series for zooplankton, phytoplankton data have been collected from 1958. These data have been invaluable in contributing to our knowledge of seasonal and year to year plankton dynamics and changes in species composition (e.g. Colebrook, 1986), spatial distribution of zooplankton communities (e.g. Colebrook, 1986; Williams *et al.*, 1993; Planque & Fromentin, 1996) and the long term control of zooplankton communities through changes in climate (e.g. Taylor, 1995; Fromentin & Planque, 1996) and weather (e.g. Colebrook, 1985; Dickson *et al.*, 1988a).

The two other major long-term plankton monitoring programmes in the North Sea operate from fixed sites. In the central-west area of the North Sea the Dove zooplankton time series has operated monthly at a station approx. 10 km of the Northumberland coast (see Figure 2.1) since August 1968 (Evans & Edwards, 1993), with the intention of providing a long term record of quantitative data. Analyses of these time series data have been used to obtain productivity estimates and to observe the seasonal patterns of the Northumberland zooplankton community (Roff *et al.*, 1988; Evans & Edwards, 1993). Studies have also been made of the inter-annual variability of the zooplankton (Evans & Edwards, 1993) and suggested parallel shifts in community structure with a station in the central-eastern North Sea (Austen *et al.*, 1991). More recent analyses have examined the role of plankton predators in the zooplankton community (Frid *et al.*, 1994; Nicholas & Frid, 1999), the similarities in the year to year fluctuations in plankton abundance with changes in the position of the Gulf Stream North Wall (Frid & Huliselan, 1996), and parallel shifts in community structure with benthic and fish populations (Pearce & Frid, 1999).

The second major long term monitoring programme is in the southern North Sea. The plankton community of the German Bight at Helgoland Roads (see Figure 2.1), has been studied since 1842. Daily measurements of temperature and salinity began in 1872, whilst in 1962 the Helgoland Roads time series on phytoplankton biomass and nutrients was initiated (Greve *et al.*, in press). Zooplankton monitoring began in 1974, with samples being collected at least every second working day, with the expectation that, this information would assist researchers in forecasting the seasonal development of the plankton. These data have provided much of the evidence concerning the eutrophicated state of the German Bight (Greve *et al.*, in press). Unfortunately, the CPR survey is unable to sample these coastal regions effectively, only covering the German Bight at its north-western corner (Radach *et al.*, 1990; Radach, 1992), thus underrepresenting this physically and chemically distinct region of the North Sea. Relatively little standard time series analysis has been performed on the Helgoland Roads zooplankton data (Radach, 1998), with most analyses of these data utilising complex ecological models such as predator-prey theory (Greve & Reiners, 1988; Greve, 1995) or even neural-networks to analyse the time series (Greve *et al.*, in press).

Other plankton time series of varying length do exist for the North Sea, but usually they are of poorer resolution (e.g. UK government agencies do annual surveys of plankton as part of their fisheries surveys), or of a very short duration. In a few cases, time series of at least moderate quality do exist, but they have either none (e.g. 1932-1961 Lowestoft plankton surveys) or little information published about them (e.g. Gravelines plankton, Le Fevre-Lehoerff *et al.*, 1995).

Evidence for change

Due to the extensive spatial coverage and length of the Continuous Plankton Recorder survey, the majority of information on long term plankton trends have been derived from these data.

Long term North Sea trends in both phytoplankton (Figure 2.2a) and zooplankton (Figure 2.2b) show a parallel decline in abundance from 1955 to a synchronous trough in 1979-1980, followed by a marked recovery after 1980 (Aebischer *et al.*, 1990; CPR Survey Team, 1992). The North Sea trends involved the majority of the community, with 15 of the 20 taxonomic groups showing the same pattern, although there were variations in amplitude between taxa (Fransz *et al.*, 1991). Traditionally, CPR survey data have been displayed in standard areas of 1° latitude by 2° longitude (e.g. Colebrook, 1984) (see Figure 2.1). The general long term phytoplankton and zooplankton trends throughout the six North Sea standard areas was similar, although there was some short term variation between areas (Figure 2.3) (Colebrook, 1982c; Colebrook, 1986; Dickson *et al.*, 1988a). The only CPR standard area where the zooplankton decline continued after 1980 was in D1 adjacent to the Dutch and German coast (Figure 2.3) (Dickson *et al.*, 1988a). Long term trends in plankton observed throughout the Atlantic continental shelf and open ocean areas from Iceland to Biscay to about 20°W were found to display similar trends to those in the North Sea (Fransz *et al.*, 1991). The similar trends observed throughout the NW Europe region suggested to Colebrook (1978) that the forcing of these communities must be due to factors operating on an equally large scale (i.e. climatic).

Evans & Edwards (1993) in an examination of the Dove zooplankton time series data, suggested that the long term trend in holoplankton abundance off the Northumberland coast was similar to North Sea CPR zooplankton trends, with minimum productivity reached around 1980. They also found a notable change in the Dove holoplankton community structure around 1979-80, coincident with the observed nadir in the Dove and CPR North Sea plankton. An earlier analysis of changes in CPR community structure in the central-west North Sea area (area C2) had found that there was no notable change in species composition between 1979 and 1980 (Austen *et al.*, 1991), although this analysis only involved 9 taxonomic entities. Austen *et al.* (1991) did however detect a significant change in zooplankton community structure at the end of the 1970s in the central east North Sea area (using CPR data for area C1).

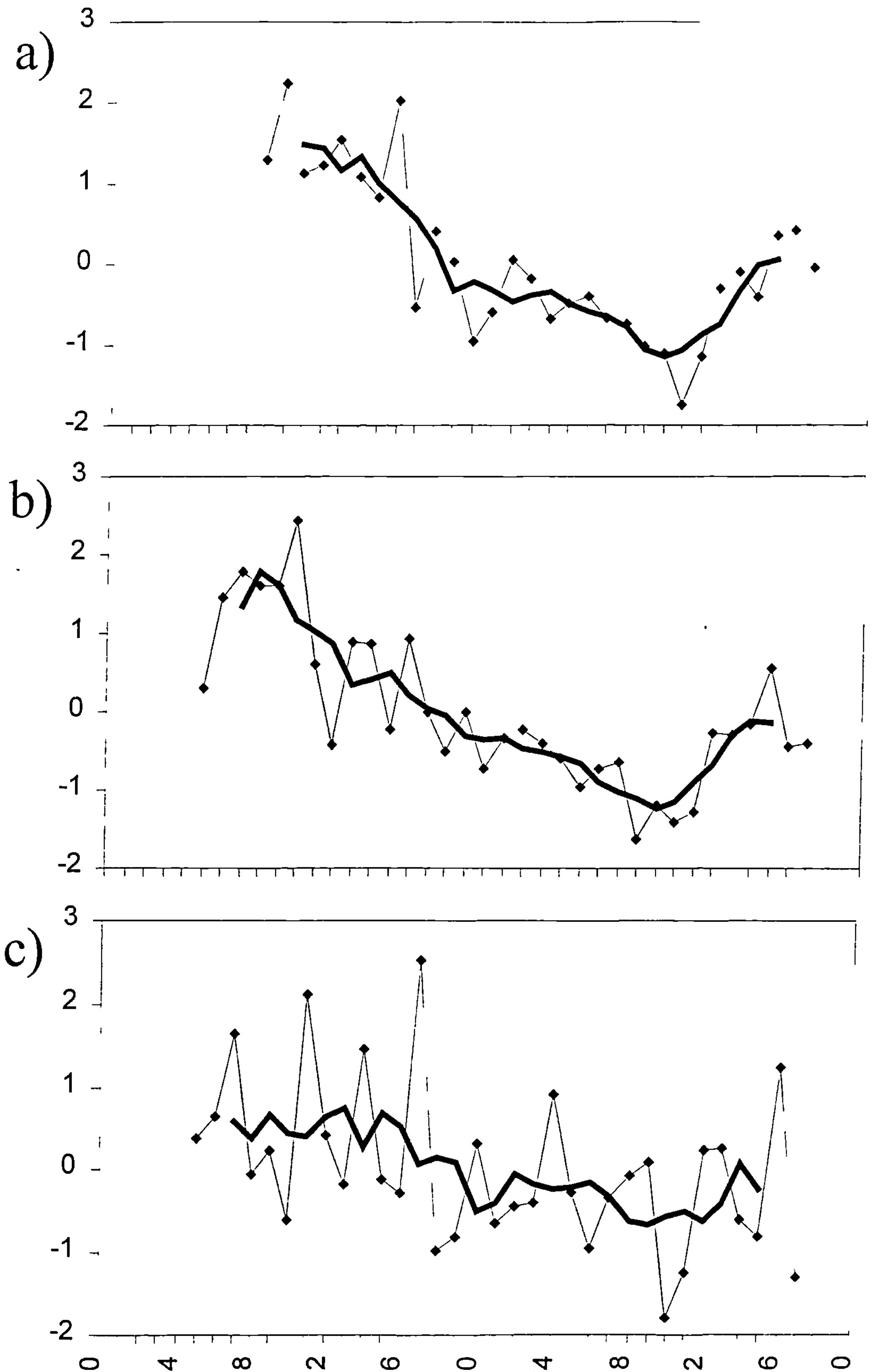


Figure 2.2 CPR standardised times series (—◆—) with 5 year running means (–), for annual means covering the period 1950-1990, for a) North Sea phytoplankton index. b) North Sea zooplankton abundance and c) frequency of westerly weather. Adapted from Aebischer *et al.* (1990).

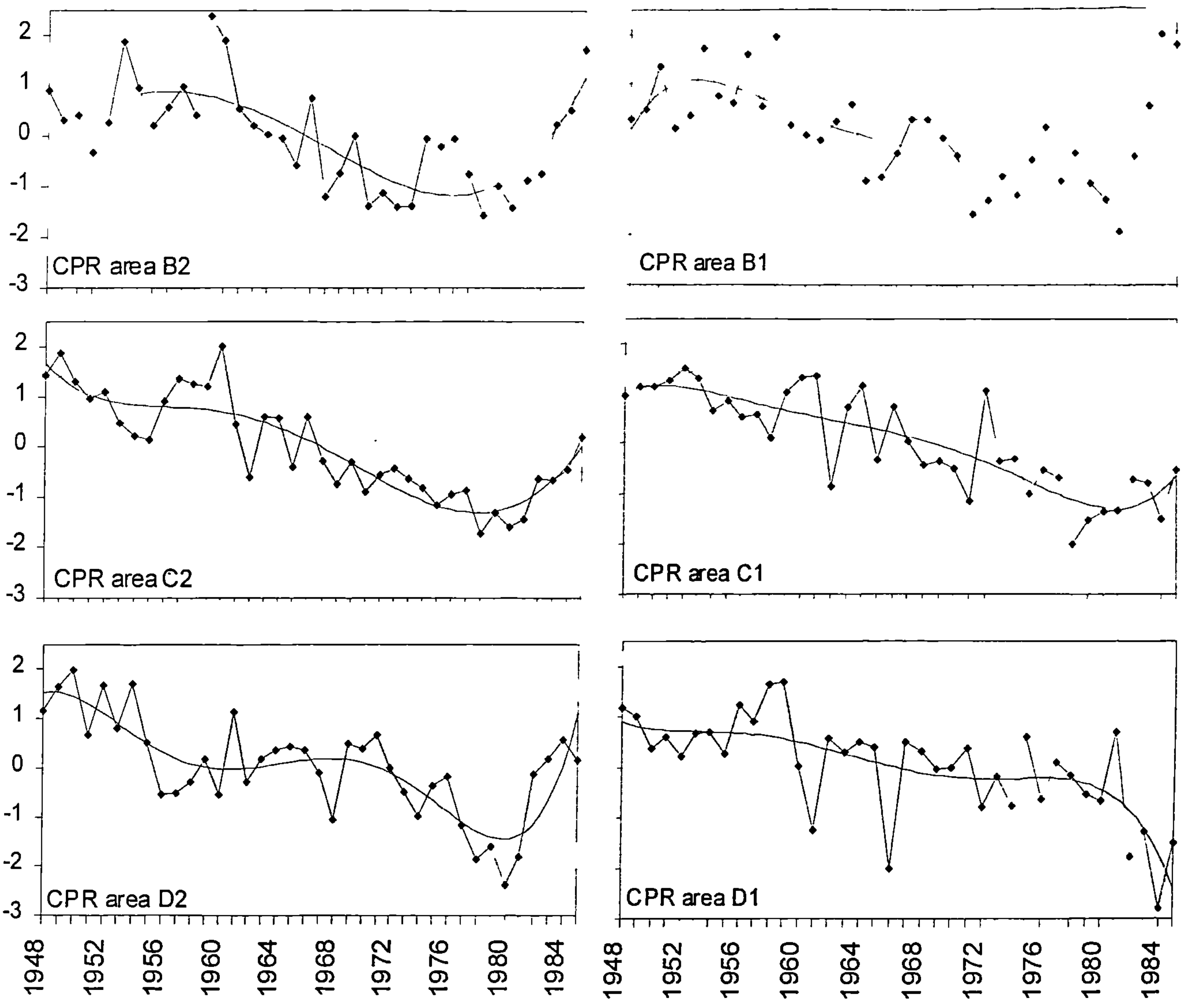


Figure 2.3 CPR standardised trends in annual mean zooplankton abundance for the 6 North Sea standard areas (—◆—), covering the period 1948-1985, with a 5th order polynomial (–) to emphasise the long term trends. Adapted from The CPR Survey Team (1992).

In contrast to the observations of Evans & Edwards (1993), more recent analyses of the Dove series using total mean annual zooplankton abundance, rather than just holozooplankton, has found that the series displays little similarity to those trends observed in the CPR North Sea zooplankton standard areas (Figure 4.1a, cf. Figure 2.3 area C2), as there has been no decline or sustained period of recovery observable in zooplankton abundance centred around 1980 (see Chapter 4). These more recent analyses of the Dove zooplankton data suggested that the species composition during a particular year was most strongly linked to that year's mean total zooplankton abundance (see Chapter 4). The difference between these and Evans & Edwards (1993) results is likely to be due to differences in the level of taxonomic resolution, and the increased number of datapoints used. This observation demonstrates the importance of considering the taxonomic resolution used when analysing time series data. Differences in resolution may lead to dissimilarities in the trends observed (and different conclusions about what is controlling these trends!). In addition, the unrestrained use of diverse statistical techniques can lead to equally diverse results and conclusions about how the species or community in question is controlled. For example, Pearce & Frid (1999) using the recently developed technique of minimum – maximum auto-correlation factor analysis (MAFA) (Solow, 1994) found that species composition changed in the Dove zooplankton time series in 1976/77, 1982 and 1990. Although some of these changes coincided with changes in climatological variables, others did not. Pearce & Frid's (1999) conclusions were similar to those of Aebischer *et al.* (1990) as it was suggested that either all the time series responded to a single group of forcing factors, or that the ecosystem was forced via the food chain.

An examination of the monthly CPR phytoplankton time series in the central west North Sea area (CPR area C2) showed that there was a consistent change in the seasonal pattern and productivity of phytoplankton after 1979 (Evans & Edwards, 1993). After 1979 there were notably higher, shorter-lived peaks of phytoplankton during the year (Figure 2.4), which coincided with the change in North Sea phytoplankton trends. With such an observed change in both the trends and seasonal pattern of the phytoplankton, a reversal of CPR zooplankton trends occurring around 1980 would not be unexpected (Evans & Edwards, 1993).

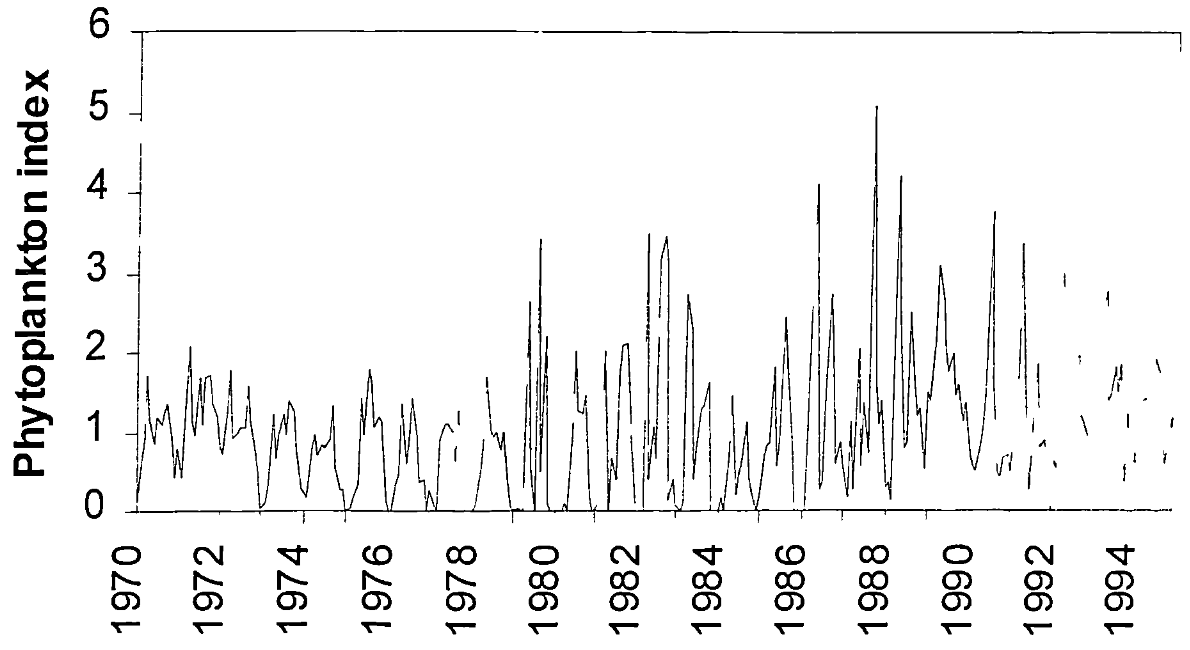


Figure 2.4 **Mean monthly phytoplankton index time series from CPR area C2 for 1970 to 1995. Adapted from Edwards & Evans (1993).**

An examination of changes in species composition within the phytoplankton community suggests that the observed changes have not been uniform throughout the community. During the early period of the CPR time series from 1958 to 1973, Reid (1978) reported that while phytoplankton in the German Bight had increased, diatom abundance had declined, suggesting that the proportion of flagellates within the community had increased. Initially diatoms increased from 1964 to 1970, but since the early 1970s flagellates increased more strongly (Figure 2.5) (Radach, 1992), with the increase in phytoplankton after 1980 being caused almost exclusively by the flagellates.

Causes of the changes

Initial attempts at discerning how interannual plankton dynamics were influenced by external factors focussed upon the relationships between temperature and plankton. It was considered that as temperature affects the growth of plankton individuals and populations (as well as factors such as feeding and movement), then temperature would strongly influence their seasonal and interannual dynamics. However, initial empirical hypotheses were based on observed relationships between calculated temperature variables and long term trends in zooplankton abundance across the North Atlantic, without any firm mechanism suggesting an actual causal association (Colebrook, 1978).

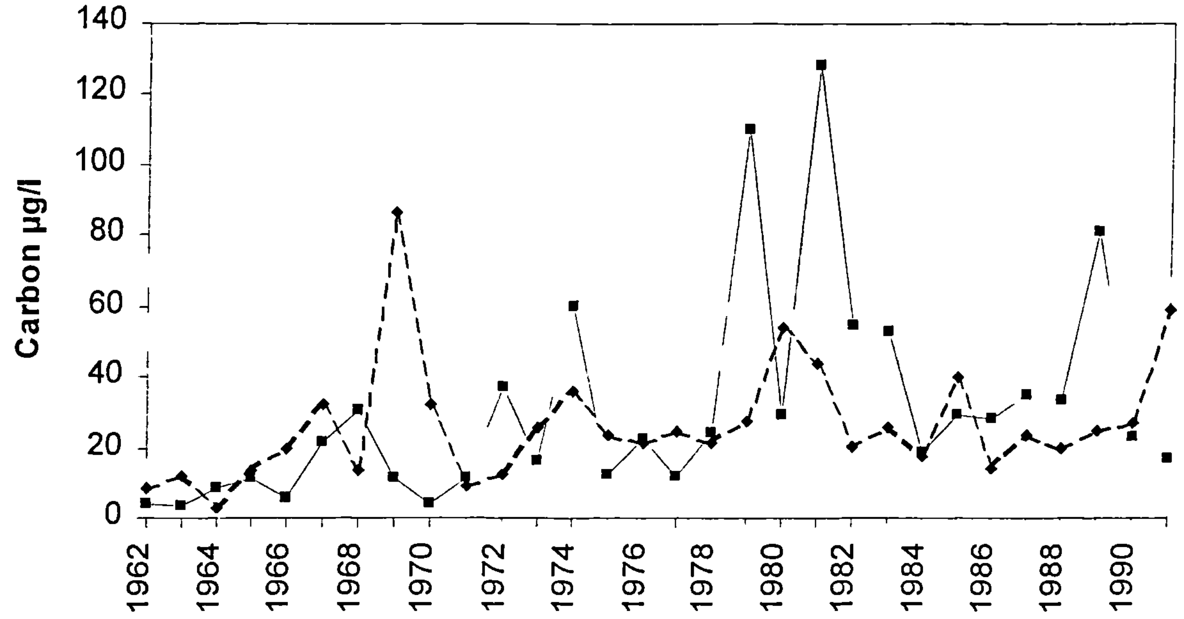


Figure 2.5 Total phytoplankton biomass at Helgoland for 1962-1991, displaying annual median values of the growing season of diatoms (June 15-Sept 15) (—◆—) and flagellates (April 1-Sept 15) (—■—). Adapted from Hickel *et al.* (1993).

One of the first convincing mechanisms to account for the interannual control of zooplankton dynamics was the concept of 'persistence' in zooplankton stocks (Colebrook, 1981; Colebrook, 1982b; Colebrook, 1982a; Colebrook, 1986). This concept arose as adjacent years were observed to have similar abundances of zooplankton, and that the downward trend in abundance from 1955 to 1980 had its origins in winter (Colebrook, 1986). This 'overwintering' hypothesis suggested that inherent limitations in zooplankton growth rates meant that the annual mean zooplankton productivity and its distribution depended upon the abundance and distribution of the overwintering zooplankton stocks, with higher overwintering stocks allowing an increased population growth rate during the following year. Control of the overwintering population was attributed to winter sea-surface temperatures, and even small changes in the size of the population overwintering would eventually appear as large changes in the size of the population the following summer (Colebrook, 1986). Thus, the long term decline and recovery in zooplankton was considered to be initiated in winter and its presence through the year was due to the persistence of zooplankton abundance from year to year.

Further evidence of the importance of an overwintering population was apparent from charts of the distribution of seasonal cycles, which displayed an outward spread from, followed by a withdrawal to relatively localised overwintering areas (Colebrook, 1986). Not all taxa were influenced to the same extent by the size of their overwintering stocks. The productivity of slow growing copepods with low fecundity (e.g. *Pseudocalanus elongatus*), would be linked to its overwintering population, as it is unable to grow and reproduce fast enough for the summer population to achieve independence from the winter stocks. On the other hand, *Acartia clausi* exhibits fast growth and so the summer populations may achieve independence from the overwintering stocks (CPR Survey Team, 1992). Phytoplankton do not exhibit persistence (Colebrook, 1982c), as their generation time is of the order of days rather than weeks or months. The hypothesis that the overwintering populations of zooplankton were crucial to the interannual dynamics of zooplankton abundance, was largely abandoned as more detailed examination on a species by species basis showed that only a limited number of species appear to be linked to the abundance of their overwintering population. However, recent analyses by Planque & Fromentin (1996), and Fromentin & Planque (1996) have again suggested this mechanism is a key component in the link between the interannual dynamics of zooplankton and climatic variables.

A number of authors focussed upon the dynamics of the diatom *Ceratium* spp., presumably due to its ease of identification and prominence in the phytoplankton community. Colebrook (1982c) demonstrated that the abundance of this species was negatively correlated with cyclonic weather and with sea-surface temperatures. Further work by Dickson *et al.* (1992) found that from 1987 to 1988 *Ceratium* increased greatly in abundance in the north-central North Sea apparently in response to a temporary change in the local climate (Dickson *et al.*, 1992) During these years, the highly stratified conditions that these species require were strengthened by an increased freshwater flow from the Baltic driven by easterly winds. The negative correlation detected between *Ceratium* and sea surface temperature illustrates that such relationships may not be directly causative – in this case the negative sea surface temperatures and easterly air stream would be associated with the westward movement of Skagerrak water which then affected the productivity of *Ceratium*. It also illustrates the oft forgotten fact that not all species in a community will react in the same way to a forcing factor. Further examination of *Ceratium* blooms later on in the time series also demonstrated that different forcing factors may produce similar responses in biota. Hickel *et al.* (1993) recorded that in the German Bight there were large *Ceratium* blooms in 1981 which were caused by flood events the previous winter and summer from the River Elbe. The difference was due to an extended period of calm weather in 1981, which, along with an high freshwater inflow, led to a strong vertical density stratification, whereas in 1987-88 no such stratification was observed due to windy weather. Hence the improved light conditions in a stratified water column was probably the dominant factor initiating the plankton blooms.

Examining differences in the patterns of the seasonal cycle have yielded important clues as to how interannual dynamics of plankton are forced. Robinson (1970), in the North Atlantic, showed that the timing of the spring phytoplankton increase was partly related to the amplitude of the temperature increase in spring, with a relationship present between the sea surface temperature (SST) difference from March to the summer months, and the timing of the spring bloom. Dickson *et al.* (1988a) noted that where there was a delay in the start of the spring phytoplankton bloom, this reduced the length of the phytoplankton production season, and thus the carrying capacity for zooplankton during that year was reduced (Dickson *et al.*, 1988a). This hypothesis fitted observations that the decline in zooplankton from 1950-1980 was associated with a delayed spring bloom and therefore a reduced growing season (Dickson *et al.*, 1988a). It was found that during the period from 1950 to 1980 there was an increasing tendency for cold northerly winds to blow across the NE Atlantic region in winter and spring. This trend reversed around 1980, which also coincided with the changes in zooplankton community composition off Northumberland (observed in the Dove time series), in the Skaggerak and a change in the seasonal pattern of phytoplankton production in CPR area C2 (Figure 2.4). The increased storm frequency enhanced the mixing of the water column, thus delaying the stratification required for the spring bloom. It was also noticed that the reduction in the productive season was most severe for the area where the maximum increase in storm frequency took place. Additionally, increased rainfall leading to increased freshwater input may bring forward the spring bloom as this reduces the density of the surface waters (Mann, 1993).

Recently, research has focussed on changes in large scale environmental variables such as the latitude of the Gulf Stream North Wall (GSNW) or the North Atlantic Oscillation (NAO) index. Such 'proxy' variables indicate the general pattern of weather over a large temporal and, more importantly, spatial range.

The Gulf Stream originates from the Gulf of Mexico, flowing northwards along the eastern US seaboard, diverging from the coast at Cape Hatteras, and moving across the North Atlantic in a north-easterly direction (Thurman, 1987), becoming the North Atlantic Drift at 55°W (Taylor & Stephens, 1980). The current is prone to meandering which changes the latitude across which it flows (Figure 2.6a). Such changes in the latitude of the north wall of the Gulf Stream current have been found to be related to shifts in wind, temperature, atmospheric pressure and salinity patterns across the North Atlantic and in western Europe (Taylor, 1996).

The NAO index is an ocean basin scale indicator of the pressure and weather patterns present over the North Atlantic area (Planque & Taylor, 1998), constructed from the pressure difference between the sub-tropical high pressures centred on the Azores and the sub-polar low pressures centred on Iceland. This pressure difference determines the speed and direction of surface westerly winds across the North Atlantic (Mann, 1993; Taylor & Stephens, 1998) as far as Europe, and winter temperatures on both sides of the Atlantic Ocean (Planque & Taylor, 1998). A high NAO index signifies a stronger than normal wind circulation in the North Atlantic, higher temperatures in western Europe, and lower temperatures on the eastern coast of Canada.

Initial work by Taylor & Stephens (1980) showed parallel trends between the GSNW and annual copepod abundance over the NE Atlantic area, with northerly positions of the GSNW being associated with increased zooplankton abundance. Further work (Taylor *et al.*, 1992) with the extending GSNW and CPR time series confirmed the association, with the effect exhibiting itself through all groups of the plankton community. This association was present in all areas of the NE Atlantic and the northern (CPR areas; B2 r=0.6 (Figure 2.6b), B1 r=0.6) and central-east (CPR area C1 r=0.7 (Figure 2.6c)) North Sea areas, and was found to be stronger than with any other climatic variable (Taylor *et al.*, 1992; Taylor, 1995). The notable exceptions were the shallow, tidally mixed southern North Sea and Irish Sea. This association was evidence of a climatic connection spanning the North Atlantic, and showed that trends in plankton populations (or at least those recorded by the CPR device) were predominantly externally driven rather than through trophic interactions (Taylor *et al.*, 1992). Other research (discussed below) has however, discovered that trophic interactions can play as great a role in the driving of the plankton community as abiotic influences.

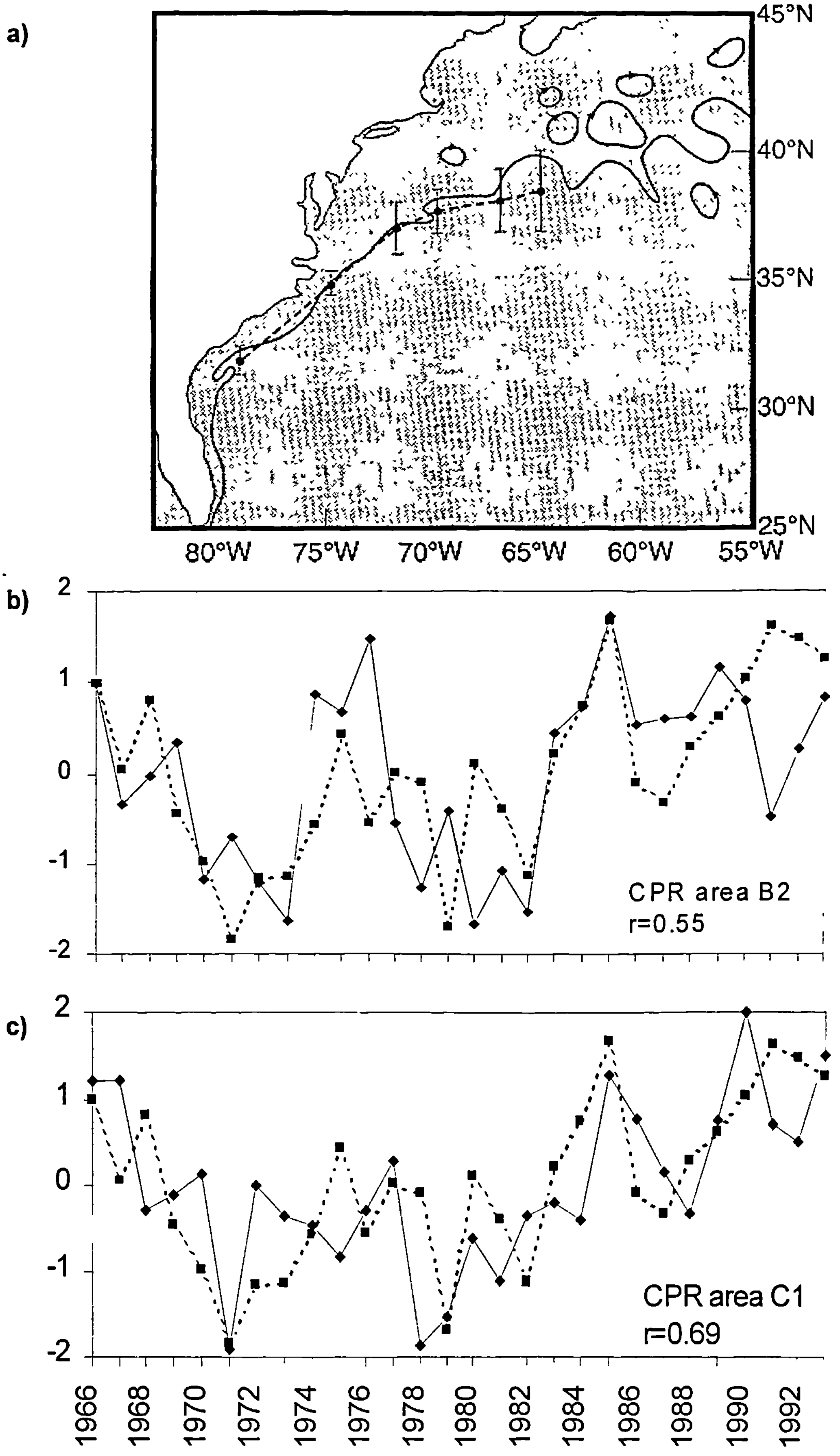


Figure 2.6 The Gulf Stream North Wall and the relationship between its position and zooplankton abundance around the UK. a) The position of the north wall off the east coast of the USA during August 1984 (solid line) and its mean position (± 95% confidence limits) between 1966 and 1993. The relationship between the latitude of the north wall (—■—) and total copepods (—◆—) in, b) CPR area B2 and, c) CPR area C1. Adapted from Taylor (1996).

As changes in plankton abundance occurred within 1 month of shifts in the GSNW, the association must have been mediated through the atmosphere, rather than changes in the GSNW directly causing changes in sea surface temperatures in the North-east Atlantic region (Planque & Taylor, 1998). This was confirmed by the fact that there are also relationships between the GSNW and above ground vegetation biomass at Bibury, Gloucestershire in the UK ($r=0.49$) (Willis, 1995), and with freshwater zooplankton populations in Lake Windermere, in north-west England ($r=-0.59$) (George & Harris, 1985; George & Hewitt, 1995; George & Taylor, 1995). Thus weather patterns on the western side of the Atlantic drive changes in the GSNW (mainly by the combined stress of the trade and westerly winds (Taylor & Stephens, 1980) and by outbreaks of cold air from the American continent), which then move eastwards across the Atlantic to force marine, freshwater and terrestrial ecosystems in Europe. Further work investigated the possibility that changes in the GSNW could be associated with changes in the timing and intensity of the spring bloom (in a development of the model of Dickson *et al.* (1988a)). However, the fact that there is no connection between GSNW and zooplankton in the shallow, tidally mixed southern North Sea suggests that either stratification plays an important role in the association between GSNW and zooplankton, or the greater availability of nutrients is overriding the climatic effects.

Analysis of the Dove zooplankton time series has also revealed an association between annual zooplankton abundance and the GSNW (see Chapter 4). However, the relationship between the Dove zooplankton and the GSNW for 1968 to 1993 was negative ($r^2=-0.22$, $p<0.01$), indicating that northerly positions of the GSNW were associated with a reduced zooplankton productivity (Frid & Huliselan, 1996). This is opposite to the positive relationship detected between GSNW and zooplankton found in the northern North Sea and North Atlantic area.

Previous studies of the zooplankton off the Northumberland coast have indicated that some zooplankton predators are important in controlling zooplankton abundance (Frid *et al.*, 1994; Nicholas & Frid, 1999). Roff *et al.* (1988) suggested that predators in the summer (mainly gelatinous) tracked zooplankton abundance and responded to changes in copepod densities, whilst the predator groups abundant in the winter (*Sagitta*, *Themisto*, euphausiids) controlled it. Recent investigations (Chapter 5) have found that high spring *Sagitta* abundances led to a lower peak abundance of the small and juvenile copepods, suggesting that *Sagitta* was limiting the growth of their populations during the spring through predation. In addition, increased spring *Sagitta* abundances were positively linked to spring phytoplankton productivity (see Chapter 5). This fits in with previous observations by Feigenbaum & Maris (1984), that the main periods of *Sagitta* recruitment coincide with sharp increases in *Pseudocalanus* nauplii (the main prey item of young chaetognaths) which would be expected to be greater with increased spring phytoplankton productivity. The hypothesis put forward was that a northerly GSNW and the associated higher temperatures and lower wind frequencies led to an earlier stratification which produced an earlier spring phytoplankton bloom. This caused an increased spring abundance of copepod nauplii which allowed a higher spring *Sagitta* population, which then grazed down the populations of small copepods, leading to an overall lower productivity of total zooplankton for that year (see Figure 5.12). It should be noted that such assessments of the role of predators in the zooplankton community are difficult, as the factors which control predator abundance are complicated (Nicholas & Frid, 1999)

There are currently only a few convincing examples of top-down control of zooplankton populations and there has been a traditional tendency to focus more upon physical, bottom-up causes of zooplankton dynamics. Verity & Smetacek (1996) reviewed evidence that top down effects may be equally important, and the long term Dove *Sagitta-Pseudocalanus* relationship illustrates the importance of considering biotic factors as possible mediation of environmental drivers when examining long term changes in ecological variables. Due to the high complexity of ecosystems, environmental factors may be more dominant and top-down effects less easy to distinguish (Reid *et al.*, in press). A preliminary study by Reid *et al.* (in press), suggests that the effect of fish predation on zooplankton was only clearly evident when the system was already stressed by the overexploitation of herring from 1978 to 1982 (the key planktivore).

The NAO index, has also been associated with changes in zooplankton abundance in the North Sea. For the period 1962 to 1992 the average westerly wind stress and sea surface temperature over the north-east Atlantic region were significantly correlated with the NAO signal (WWS-NAO $r=0.85$, $p<0.01$; SST-NAO $r=0.55$, $p<0.01$) (Fromentin & Planque, 1996). Taylor & Stephens (1998) also found that there was a clear correlation between the position of the GSNW and the NAO index two years previously ($r^2=0.39$, $p<0.01$), although there was no clear mechanism available to explain this relationship. A proportion of the unexplained variance in the NAO-

GSNW relationship could be accounted for by the El Niño-Southern Oscillation index in the Pacific (Taylor *et al.*, 1998), the GSNW being displaced northwards following ENSO events. Such observations provide evidence for a link between hydro-climatic events in the Pacific and those in the North Atlantic, and emphasises the global nature of climate phenomena.

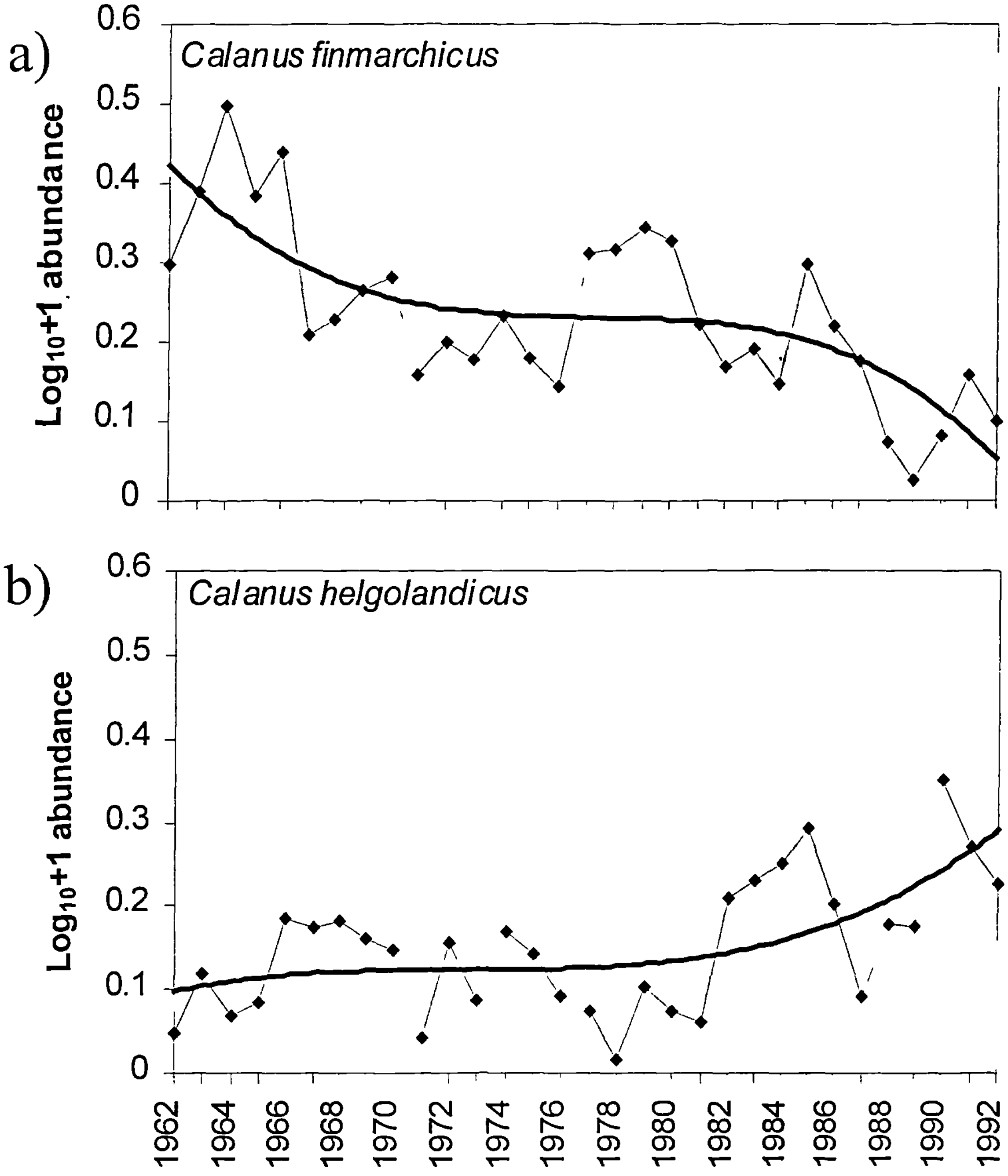


Figure 2.7 **Annual $\log_{10}$ North Sea abundance of a) *Calanus finmarchicus* and b) *C. helgolandicus*, with a 3rd order polynomial (–) to emphasise the long term trend. Adapted from Planque & Fromentin (1996).**

The two copepod species *Calanus finmarchicus* and *C. helgolandicus* are amongst the dominant members of the zooplankton of the north-east Atlantic and North Sea (Planque &

Fromentin, 1996). The northerly distributed species, *C. finmarchicus*, displays an association with colder waters, whereas the southern species is adapted for growth in warm temperate waters. As such, they are largely geographically separated and their distribution is related to temperature (Planque & Fromentin, 1996). *C. finmarchicus* has a distinct overwintering strategy – stage V copepods of the last summer generation migrate to deeper Atlantic waters until spring when they migrate to the surface layer, moult into adults and reproduce (Fromentin & Planque, 1996). These two closely-related species in the North Sea display opposing long term trends in their interannual dynamics (Figure 2.7). Whereas *C. finmarchicus* showed a clear downward trend over the period 1962 to 1992, *C. helgolandicus* displayed an upward trend over this period (Planque & Fromentin, 1996). Fromentin & Planque (1996) found that there was a negative relationship between *C. finmarchicus* and the NAO index which explained 58% of the interannual variability and was exhibited not only in the opposing trends, but also in the shorter scale variations. In contrast, only 18% of the variability of *C. helgolandicus* was accounted for by its positive relationship with the NAO and the correlation was primarily due to their common trends - year to year variations in *C. helgolandicus* were not synchronous (Fromentin & Planque, 1996).

The relationship between *C. finmarchicus* and the NAO was partially explained by an extension of the Dickson *et al.* (1988a) model of the linkage between winds and plankton (see Figure 2.8). During a year when the NAO is high, the wind stress is reinforced which causes increased mixing of the surface layer in winter and spring, and thus delays the spring phytoplankton bloom and reduces primary productivity. In addition, as air and sea surface temperatures are higher than normal, these conditions are probably unfavourable to *C. finmarchicus* (Fromentin & Planque, 1996). This situation is reversed during a weak NAO year with air and sea surface temperatures being lower than normal, and a lower westerly wind stress which allows an earlier stratification of the surface layer and hence an earlier initiation of the spring bloom (Fromentin & Planque, 1996), allowing an increased abundance of *C. finmarchicus.*

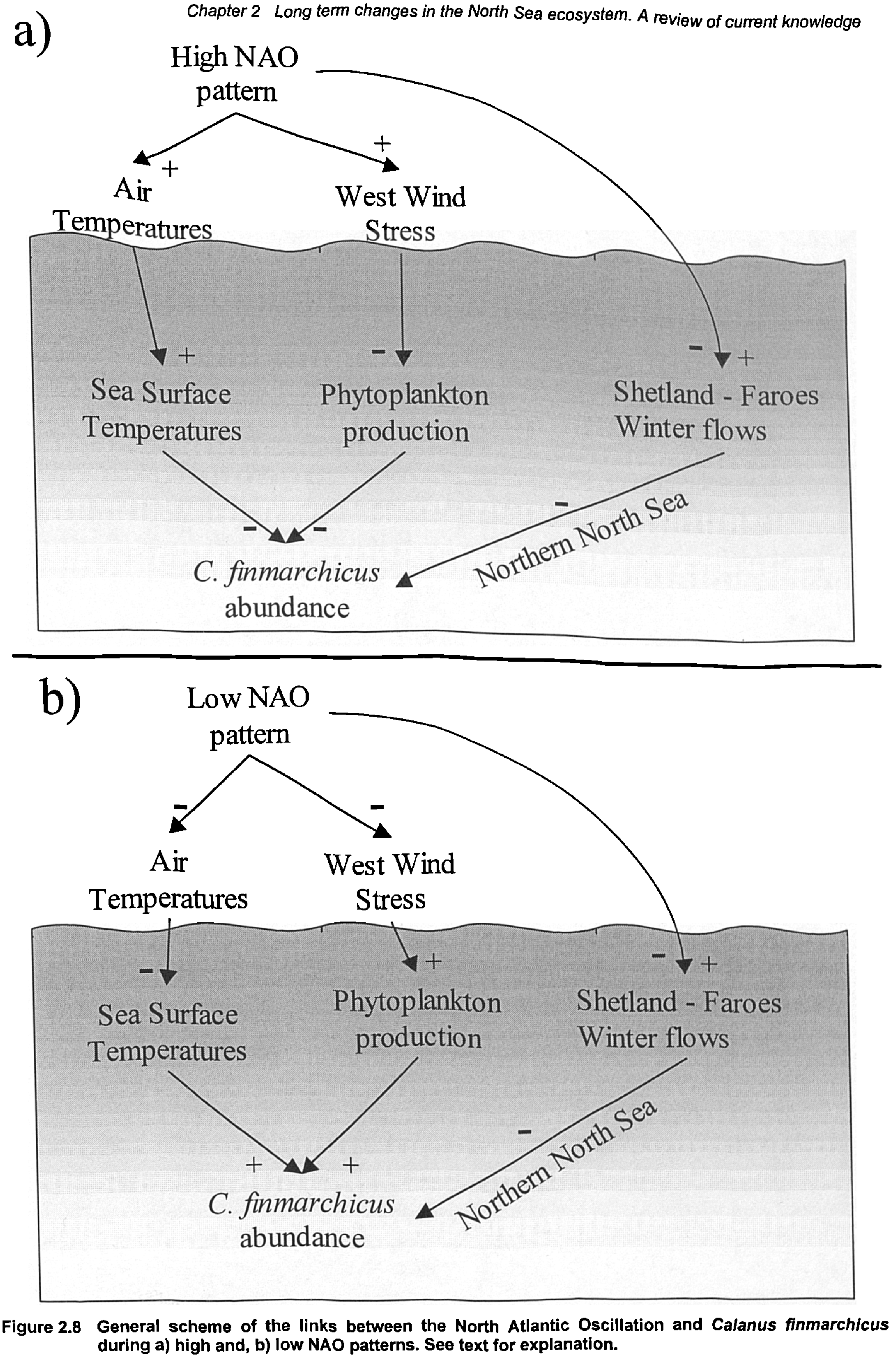


Figure 2.8 **General scheme of the links between the North Atlantic Oscillation and *Calanus finmarchicus* during a) high and, b) low NAO patterns. See text for explanation.**

The connection between *C. helgolandicus* and the NAO was formed by the fact that as both *Calanus* spp. occupy the same ecological niche, there is likely to be some competitive effect. During a high NAO year, the effects of the NAO are greater in the northern half of the NE Atlantic area, and thus, in the southern North Sea, the timing of the spring bloom is less affected by it. The increased temperatures in the northern North Sea will permit the growth of *C. helgolandicus* in these regions, which, during a low NAO year would be occupied by *C. finmarchicus* (Planque & Fromentin, 1996). During a low NAO year, however, the greater extension of *C. finmarchicus* into the North Sea and the lower SST will give this species a competitive advantage over *C. helgolandicus*.

Stephens *et al.* (1998) attempted to develop Colebrook's overwintering hypothesis to account for the control of *C. finmarchicus* populations. Winter populations of *C. finmarchicus* are believed to reside in deep peripheral areas outside of the shallow North Sea such as in the Faeroes-Shetland Channel (Backhaus *et al.*, 1994; Planque & Fromentin, 1996; Stephens *et al.*, 1998). In the northern North Sea, the success of the summer generations of *C. finmarchicus* depends on the advection of overwintering copepodites from these deeper areas at the end of winter. Stephens *et al.* (1998) using the output from a circulation model, which was related to westerly wind strengths, found that changes in winter flows between, i. the Faeroes-Shetland area, ii. the western coast of Norway and, iii. the North Sea, were strongly correlated to the NAO, although not with the same sign (i. $r=-0.78$, ii. $r=0.64$, iii. $r=-0.64$, all $p<0.01$). These winter flows were associated with increased abundances of *C. finmarchicus* in the northern North Sea region (CPR areas B1 ($r=0.72$) & B2 ($r=0.75$), both $p<0.01$); there were no other significant links between flows and the abundance of *C. finmarchicus* in the other North Sea regions, and neither *C. helgolandicus* or total copepods presented any significant relationships with the flows. This suggested that the negative link with the abundance of this species in the North Sea may be partially explained by changes in the late winter advection of overwintering populations.

Ziljlstra & de Wolf (1988) argued that it is not easy to discriminate between anthropogenic and natural influences where these factors are working together. Despite this, long term changes in phytoplankton communities in some areas along the Dutch coast and in the German Bight are known to be predominantly influenced by eutrophication (Radach *et al.*, 1990; Colijn, 1992; Radach, 1992).

Austen *et al.* (1991) considered that the changes in zooplankton and phytoplankton trends, community structure, and seasonal patterns in certain areas of the North Sea were attributable to changes in water quality rather than climatic factors. This was because they detected a transition in zooplankton community structure using CPR data between 1979 and 1980 in the central-eastern North Sea, yet no change was detected in the central-western North Sea region. Because changes were only detected on the eastern side of the North Sea, in an area known to be eutrophicated, increased nutrient concentrations were responsible; if climate was a cause of the change, then the shift in community structure would be evident on both sides of the North Sea (Austen *et al.*, 1991). Evans & Edwards (1993), using the Dove time series data, however did find a change in zooplankton community structure off Northumberland between 1979 and 1980. They therefore concluded that the transition in community structure was ultimately related to long term changes in north-east Atlantic weather patterns, although as both areas are coastal, eutrophication could not be totally excluded.

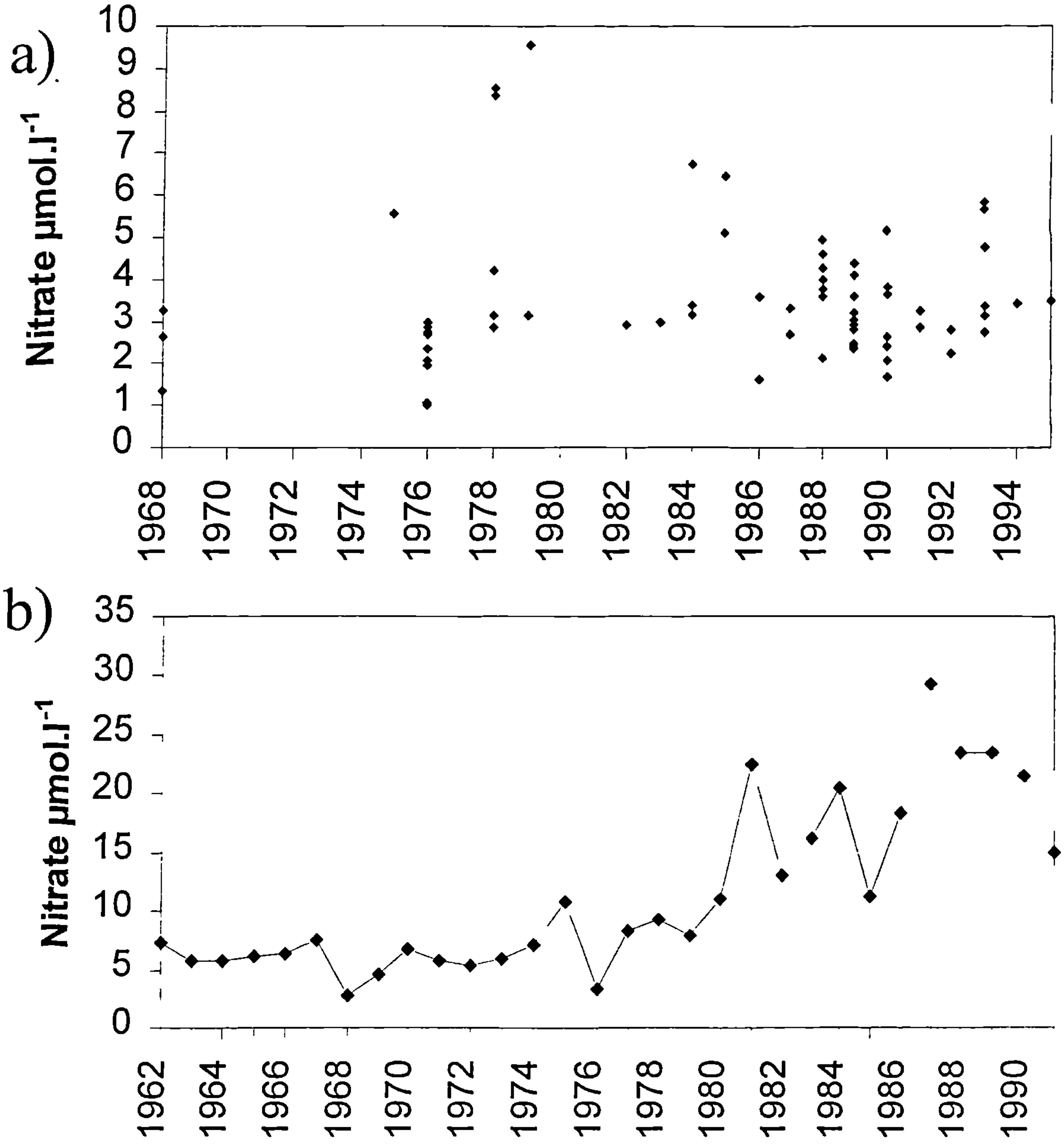


Figure 2.10 a) Decomposed and seasonally adjusted nitrate time series for the region 54.5°N-56°N, 1°W-0° for the years 1968-1995, b) Yearly median values of nitrate concentrations in the German Bight near Helgoland, 1962-1991. Adapted from Hickel *et al.* (1993).

There is considerable evidence that, at least in some areas of the North Sea, the increased nutrient concentrations since the 1950s have been primarily responsible for the observed changes in the ecosystem (Owens *et al.*, 1989; Radach *et al.*, 1990; Radach, 1992; Hickel *et al.*, 1993). These eutrophicated regions are noted for being relatively isolated hydrographically from the rest of the North Sea. For example, a section from Cuxhaven at the mouth of the River Elbe to the north-west North Sea shows that the concentration of phosphate and nitrate decreases strongly towards the central North Sea (Radach, 1992). Thus, it is likely that the central and northern North Sea areas have been largely unaffected by increased nutrient concentrations. Radach (1992) suggested that this was possibly due to the favourable flushing conditions of the North Sea which reduced the increased concentrations of nutrients by advective transport away from the coastal regions. Unfortunately, long term data on nutrient concentrations outside of the continental coastal zone are uncommon, meaning that backing up these suggestions is not easy, although (Dickson *et al.*, 1988b), and more recent analyses of the available data (Figure 2.10a) ($r^2=0.05$, $p>0.05$) show that there have been no significant changes in nutrient concentrations in the central-western North Sea. Analysis of the sea water composition at Helgoland confirmed that the increased nutrients in the German Bight originated from rivers, suggesting that the sources were anthropogenic. Laane *et al.* (1996), found that there was a strong relationship between long term changes in dissolved inorganic phosphate in the River Rhine and those found in Dutch coastal waters. Phosphate concentrations in the southern North Sea were found to increase in the 1950s, coinciding with the large scale switch to anionic detergents (Hickel *et al.*, 1993). After only a decade, a doubling of concentrations had occurred, levelling off after a further decade, followed by a subsequent decrease by the 1980s to almost the original concentrations. Nitrate concentrations in the German Bight increased until the late 1980s after which they decreased (Figure 2.10b). The increased nutrient concentrations have been mainly restricted to coastal wasters with a relatively low salinity, although Hickel *et al.* (1993) suggested that suspended particulate matter could be a long distance carrier of nutrients. The delayed eutrophication of the outer German Bight, and the northern-most German Wadden Sea basin of Sylt, suggested that nutrients were carried to these areas by plankton and detritus, going through cycles of sedimentation and remineralisation which caused the delay (Hickel *et al.*, 1993).

Whilst most authors agree that eutrophication has occurred in the Dutch Wadden Sea and German Bight (see Colijn, 1992), this view is not universal. Hickel *et al.* (1993) for example suggested that while an increase in algal biomass occurred in these areas it does not correlate with the nutrient levels entering the Dutch Wadden Sea from the Rhine. However, given that the observed changes in algal biomass have been accompanied by shifts in taxonomic composition, a simple correlation is not expected. Nutrient inputs have been high in nitrogen and phosphate which would be expected to favour the dinoflagellates to the detriment of the diatoms which are limited by the availability of silica (Hickel *et al.*, 1993). That the observed composition shifts fit this model is seen as strong evidence that eutrophication has occurred (Owens *et al.*, 1989).

Overview of long term changes in zooplankton

This study has identified 5 major changes in North Sea zooplankton:

- CPR survey data shows a long term decline in North Sea zooplankton from 1955 followed by a marked recovery after 1980.
- Change in the taxonomic composition of the zooplankton community between 1979-1980 observed in the Dove zooplankton time series, and the CPR time series for the central-east North Sea region.
- Change in the seasonal pattern and peak productivity of phytoplankton after 1979 in the central-west North Sea region.
- Change from a phytoplankton community dominated by diatoms to one dominated by flagellates in the German Bight area.
- Long term decline in *Calanus finmarchicus* and a long term increase in *C. helgolandicus* over the 1962 to 1992 period.

The long term dynamics of the North Sea plankton community in the majority of the northern and central areas of the North Sea appear to be controlled by climatic and meteorological factors. These act primarily through the influence of temperature and wind on thermocline formation, and therefore influence the timing of the spring bloom. Climatic indices such as the NAO and GSNW are associated with the changes in most zooplankton communities via this model. In the shallower, tidally mixed and hydrographically isolated regions of the southern

North Sea where the model of Dickson *et al.* (1988a) does not apply, anthropogenic nutrient inputs over the past 40 years appear of sufficient magnitude to obscure any climatic influences on the plankton. In these coastal regions the elevated nutrient inputs are larger than the advective transports removing nutrients and, as a consequence, nutrient concentrations have increased, to be followed by an increase of phytoplankton biomass.

Biotic interactions in the plankton, at least in some areas and during some time periods, play a central role in mediating the influence of climate (and probably changes in nutrients) on the interannual dynamics and spatial distribution of planktonic species and communities. Changes in environmental conditions may influence the level of competition between species, and potentially result in an increase in one species and a decline in another. The abundances of predators may also be influenced by climate, which, in turn, may affect the abundance and community composition of the whole zooplankton community. The interspecific factors often appear to produce complex dynamics in the community, but the importance of such factors in influencing the community should not be underestimated in controlling its long term dynamics.

Benthos

Introduction

The North Sea has a long history of benthic ecological research. Most early records were taken from the easily accessible intertidal and inshore areas. Initial sublittoral benthic samples were taken using adapted oyster dredges, introduced in 1773 by O.F. Müller (Petersen, 1918). Such devices were also used by Möbius & Bütschli (1875), and Michaelsen (1896), who used them to collect data across the North Sea. The first quantitative benthic sampling gear was pioneered by Petersen, who used a device attached to a pole to sample areas of 0.1m^2 and 60-80 mm deep as early as 1896 (Petersen & Boysen-Jensen, 1911), although this work was carried out in the Limfjord and Kattegat, as opposed to the North Sea (Duineveld *et al.*, 1991). Blegvad was the pioneer of detailed sampling of the North Sea area during the early 20th century (see Davis (1923; 1925)). The *Dana* expedition in the 1950s provided another snapshot, and more recently, a series of research studies e.g. the ICES North Sea Benthos Survey (Kunitzer *et al.*, 1992), and pre-drilling studies for the oil and gas industries have provided greater coverage of the seabed fauna. However, the available data do not provide a spatially continuous coverage of the whole of the North Sea and this makes it more difficult to establish the role of mechanisms which operate over large spatial scales (e.g. climate and meteorological changes).

Due to the static nature of the benthic community relative to the advective nature of the plankton community, benthic systems are much more susceptible to small scale anthropogenic impacts such as sewage sludge dumping or fly ash tipping. Indeed, sampling sites are often deliberately placed at these impacted locations in order to monitor their long term effects. Such anthropogenic impacts usually only affect the area of seabed adjacent to where the pollutant is released. With some impacts however, these effects may be cumulative. For example, an individual beam or otter trawl only affects a small area of the seabed, but the cumulative effect of many vessels fishing over many decades is likely to affect the benthic community over most of the North Sea (Jennings & Kaiser, 1998).

The relative lack of long term time series data has led to attempts to establish how the benthic ecosystem of the North Sea has changed over the 20th century through comparisons between historic and contemporary samples from the same area (e.g. Kröncke, 1990; Kröncke, 1992).

Sources of historic data are available from research expeditions (e.g. Dana expeditions in the years 1932-1939) or from reports by individual naturalists (e.g. Petersen & Boysen-Jensen, 1911), and are available from primary and "grey" literature. Although it is difficult to form robust conclusions about why changes may have occurred, when these results are supported by other long term data and experimental studies they can provide important information as to the processes controlling the North Sea ecosystem. Other approaches to overcome these limitations involved reconstructing the ecology of the benthos through the examination of the species composition and abundance of benthic larvae in the water column (Lindley *et al.*, 1995). Benthic time series have also been constructed from growth records of long lived species. For example, long term variations in the shell growth of the mollusc *Arctica islandica* from the northern North Sea have been assessed retrospectively using the annually deposited internal growth lines (Witbaard *et al.*, 1997).

Evidence for change

At Balgzand, a tidal flat located in the westernmost part of the Wadden Sea (see Figure 2.1), macrofaunal samples have been taken annually at 15 stations since 1969 (Beukema, 1992c). Over the time series, from 1970 to 1990, biomass (Figure 2.11a) and abundance (Figure 2.11b) increased (Beukema, 1992c), although biomass increased more slowly than abundance. The decline in the average size of an animal implied that the density of small sized taxa had increased. Biomass in particular was noted to suddenly increase between 1979 and 1980. For 31 infaunal taxa, 15 were more abundant during the 1980s than during the 1970s. Total numbers of deposit feeders increased more than 3 times (from 89 to 307 m^{-2}), yet carnivores hardly increased (from 41 to 53 m^{-2}). Deposit feeders were the only feeding type which increased its proportion of the total number of macrobenthic animals; the proportion of suspension feeders and mixed feeders declined slightly whereas that of the carnivores halved (Beukema, 1992c).

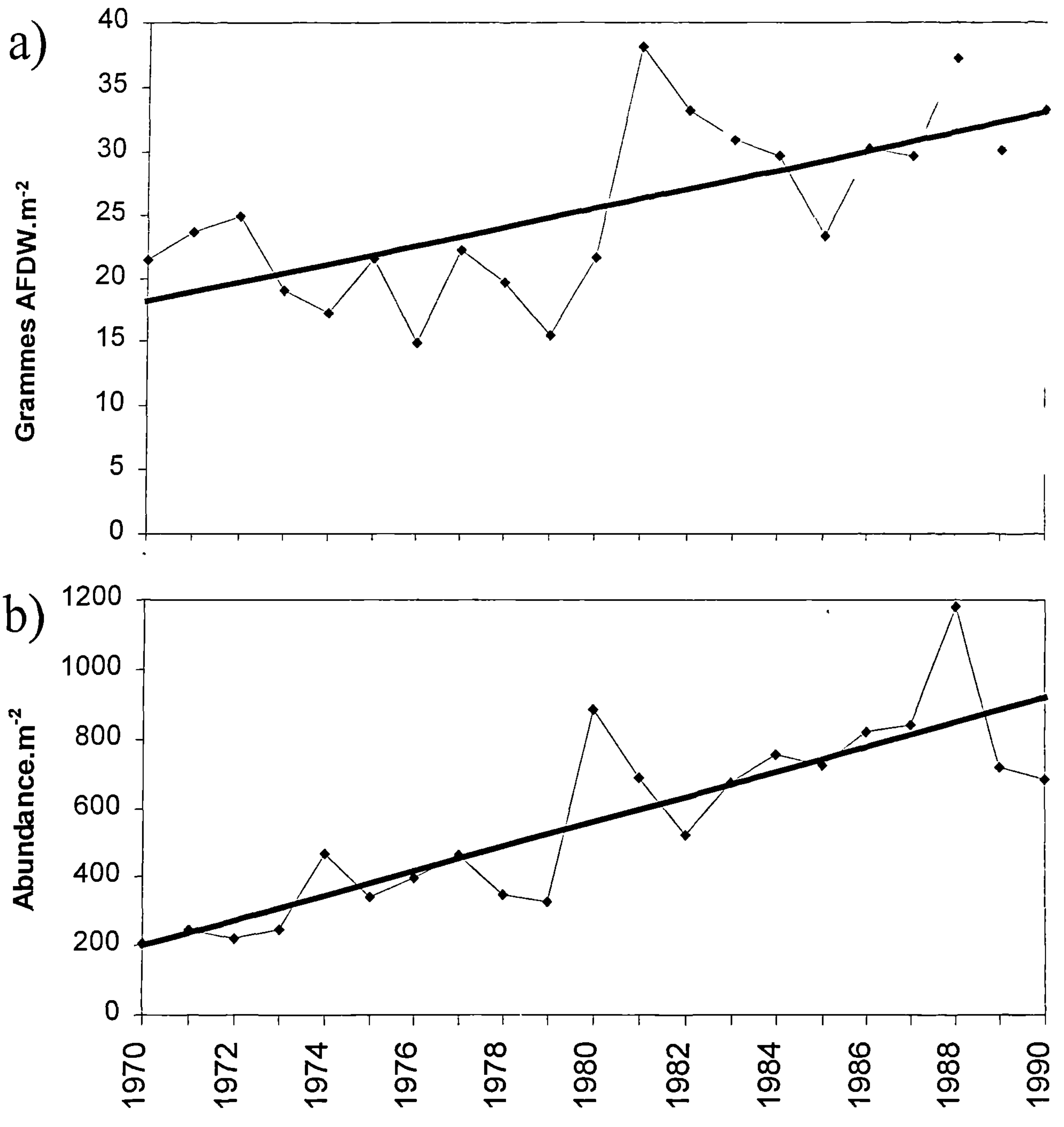


Figure 2.11 Long term changes in the macrozoobenthos observed in March from 1970-1990 in the Dutch Wadden Sea intertidal. a) total biomass in g AFDW.m^{-2}, b) total abundance in no.m^{-2}. Bold line emphasises the long term trends. Adapted from Beukema (1992c).

Sublittoral benthic monitoring off the Northumberland coast (see Figure 2.1) was initiated at two sites in the early 1970s (Buchanan *et al.*, 1974; Buchanan & Moore, 1986a). One station, located at a depth of 80 m (Station P) is located within a *Nephrops norvegicus* (Dublin Bay Prawn) fishing ground (subject to otter trawling), while the other (Station M1) is located at a depth of 55 m on the inshore edge of the fished area. From 1972 to 1980 at Station M1 the benthic community was stable (Buchanan *et al.*, 1986) (Figure 6.2a), with a biennial cycle of alternating high and low abundance years. Year to year variability at Station P was not so predictable in the decade 1971 – 1980, with benthic abundance varying between 825 individuals.m^{-2} and 2195 individuals.m^{-2} (Figure 6.2b). The biennial cycle at M1 broke down in March 1981 when the total number of individuals showed a rise in abundance (Buchanan & Moore, 1986a) instead of the predicted fall (Figure 6.2a). Abundance also sharply increased at Station P at this time.

Multidimensional Scaling (MDS) ordination showed that these shifts were also manifest in the genera composition of the macrofauna which altered between 1980-1981 at Station P (Austen *et al.*, 1991). Up to 1986, trends in the abundance of benthic infauna at both sites paralleled changes in phytoplankton index (with a two year lag to allow for growth to the minimum mesh retention size) (see Chapter 6, Figure 6.6) (Buchanan, 1993). From 1986 until 1990, fishing effort increased within the *Nephrops* ground (see Chapter 7, Figure 7.1a). This increase in fishing effort caused a decline in benthic abundance at Station P, whereas year to year changes at station M1, outside the *Nephrops* ground, continued to mirror changes in phytoplankton input (see Chapter 7, Figure 7.1c & d).

At least ten stations have been sampled in the Skaggerak-Kattegat area since 1973 (see Figure 2.1) (Tunberg & Nelson, 1998). Initial analysis of the data showed that biomass and abundance at most of the stations had doubled between 1974-1988 (See Josefson *et al.*, 1993). However, later work (Tunberg & Nelson, 1998) found that the earlier linear models used to describe the data were not adequate to properly explain the changes as the long term trends were found to be distinctly non-linear, with a 4th or 5th order polynomial being the best fit. Peaks of abundance were seen in 1975 to 1976 and 1983 to 1985, suggesting a cycle length of 7 to 10 years. MDS ordination of the 100m deep Skagerrak Vä2 station suggested that there was a greater degree of community change between 1980 and 1981 than in adjacent periods (which coincided with the observed changes in community composition off the Northumberland coast Austen *et al.*, 1991). This change was also evident in Abundance-Biomass Comparison (ABC) curves for the Vä2 station which showed that from 1979 there was an increased abundance of smaller taxa (Austen *et al.*, 1991). In a similar manner to the change observed off the Northumberland coast, this shift in benthic species composition coincided with an increase in total abundance and biomass of macrozoobenthos (Josefson *et al.*, 1993).

Causes of the changes

Alterations in the species composition and abundance of benthic communities may ultimately be responses to climatic fluctuations, changes in nutrient concentrations or physical impacts. Direct long term forcing through changes in climate and/or nutrients tends not to have a strong effect upon sublittoral benthic communities, as the water column moderates or modifies these influences, although intertidal communities are likely to be directly affected by climatic forcing. As with the plankton, forcing of the macrobenthos may occur through a variety of mechanisms which operate at different periods of the year. For example, mortality may be affected by winter temperatures (Buchanan *et al.*, 1978; Beukema, 1985; Buchanan & Moore, 1986a) and disturbance of the community through storms (Dörjes *et al.*, 1986; Tunberg & Nelson, 1998), whereas population growth may be governed by changes in food input (Beukema, 1992c; Buchanan, 1993).

Food availability and the timing of food input is considered to be the major factor structuring benthic communities (Pearson & Rosenberg, 1986). Benthic infauna rely for their food source on organic matter sinking from the pelagic (Pearson & Rosenberg, 1978; Graf, 1992). Most of this material consists of sedimenting plankton, and so the direct effects of changes in climate or nutrients upon the plankton are passed on as an indirect effect to the benthos and can potentially change abundance and/or community structure. This "benthic-pelagic coupling" has been observed at many sites (Beukema, 1992c; Graf, 1992; Buchanan, 1993; Tunberg & Nelson, 1998) where long term trends or sudden changes in the pelagic community manifest themselves in the immediate benthic community.

Analysis of the benthic community time series at Station M1 off the Northumberland coast showed that the March abundances observed during the stable biennial cycle from 1973 to 1980 (Figure 6.2a) were determined primarily by density dependant mortality during the winter which adjusted the numbers to a level in balance with the available energy (Buchanan & Moore, 1986a; Frid *et al.*, 1996), and secondly by winter temperatures. Corresponding analysis of the pelagic community indicated that during the stable period of 1973 to 1978 the phytoplankton abundance was low and steady, but after 1979 the phytoplankton exhibited higher peaks of productivity during the annual cycle (Evans & Edwards, 1993) (see Figure 2.4). It was found that March benthic abundance regressed against phytoplankton index for the period 1981 to 1991 explained 55% of the variance when benthic abundance lagged phytoplankton by two years (Buchanan, 1993) (regression over the whole time series: $r^2=0.33$). The two year lag was because the main period of phytoplankton production occurred during the summer, after the March benthic sample was taken, and a further year allowed growth to occur so that benthic individuals are "recruited" to the 0.5mm sieve.

Although the cause of the changes in phytoplankton productivity were not discussed by Buchanan (1993), the changes in pelagic productivity in the central-western North Sea were associated, as discussed above, with changes in weather patterns controlling the timing of the spring bloom and thus the amount of primary production occurring during a particular year. Therefore, changes in the benthos were ultimately linked to climate. However, Austen *et al.* (1991) found that the changes in the zooplankton community of the Skaggerak between 1979-1980 were associated with changes in nutrient concentrations, and suggested that the observed benthic change in both the Skaggerak and at Northumberland Station P a year later (1980-1981) was therefore also attributable to changes in nutrients. This is unlikely to be the case for the Northumberland station, yet the changes in the Skaggerak, in an area known to be eutrophicated, may well be nutrient driven. Further work on the Skaggerak benthos by Josefson *et al.* (1993) found that the doubling of biomass and abundance between 1974-1988 paralleled changes in land run-off. There were positive correlations between run-off and both spring bloom inorganic nitrogen concentrations ($r=0.56$, $p=0.031$), and concentrations of chlorophyll in the productive water layer ($r=0.70$, $p=0.008$). The observed change in benthic community structure between 1980 and 1981 was due to a major food pulse stimulated by the increase in nutrients (Josefson *et al.*, 1993).

Further work with the Skaggerak-Kattegat time series by Tunberg & Nelson (1998) demonstrated that observed changes in the benthos (and the pelagos too) could be influenced by nutrient concentrations being affected by climatic changes. Evidence that the benthos here were being influenced by climate, in addition to the earlier observations by Austen *et al.* (1991) and Josefson *et al.* (1993), came from the fact that both benthic abundance and biomass were significantly correlated with the NAO index, although these were lagged by different periods at various depths (Tunberg & Nelson, 1998). The proposed mechanism built upon the observed relationships between nutrient inputs and run-off by Josefson *et al.* (1993). Tunberg & Nelson

(1998) found a negative correlation between the NAO and river flow (r=-0.46). During low NAO years the winter precipitation was higher and thus the flow of nutrients into coastal waters was increased. This increased the primary productivity and ultimately influenced the benthic community. This positive association between the NAO index and primary productivity was also observed between 1983 and 1992 at the nearby Gullmarsfjorden on the Swedish coast (Lindahl, 1995). These findings supported the hypothesis that there is a linkage between the NAO, runoff driven primary production and the benthic community response at the stations in the Skagerrak, and is an example of climatic effects effecting nutrient flux rates, influencing the benthic system.

Changes in food supply were also found to drive the intertidal infauna of the Wadden Sea. Changes in infaunal biomass were observed to follow those of mean annual chlorophyll concentration (Beukema, 1992c), which in turn were linked to eutrophication (see above). Nutrient concentrations increased during the 1970s and stabilised at a high level during the late 1980s (Beukema, 1992c) the effect of which could be observed in both the chlorophyll concentrations and zoobenthic biomass. However, although Buchanan (1993) found a lag between cause (more chlorophyll, i.e. more food) and effect (more zoobenthic biomass) in these data, no such lag existed, despite similarity in times of sampling. As in the Northumberland benthos, the species composition of the benthos changed in response to increased pelagic production, with increases in the proportion of small to medium sized worms and deposit feeders (Beukema, 1992c).

Although changes in food input, either through changes in climate, nutrients or both, are considered to be the primary cause of benthic forcing, low temperatures are considered to be a large scale *direct* effect upon both sublittoral and intertidal communities. During severe winters (with a mean temperature 2°C or more below the long term mean) on the Balgzand tidal flats in the Dutch Wadden Sea, one third of species displayed increased mortality rates (Beukema, 1979; Beukema, 1985; Beukema, 1992a; Beukema, 1992c; Beukema, 1992b), although mortality was reduced on populations living lower in the intertidal zone. During a period with 8 mild winters in succession, overwintering mortality was diminished (Beukema, 1992a), which resulted in a more stable infaunal biomass. In the short term, a severe winter means a pronounced stress for the tidal flat fauna with reductions in species numbers and abundance (Beukema, 1979). Yet this reduction only persists for 1 to 2 years as reproductive success on tidal flats tends to be extremely good during the summer following a severe winter. Recent work has examined the effect that cold winters have upon the balance of infaunal predators and their prey (Beukema *et al.*, 2000). It was observed that the abundance of the predator *Nephtys* was reduced following a cold winter, and this reduced predation led to increased prey (deposit feeder) biomass. The usual seasonal (winter to summer) increase of prey biomass was at a significantly lower rate during high compared to low *Nephtys* biomass years, and was even reduced to zero at the highest predator density observed (Beukema *et al.*, 2000).

Sublittoral benthic communities have also been recorded as being influenced by changes in water temperature. Buchanan *et al.* (1978) and Buchanan & Moore (1986b) noted that in addition to density dependant systems operating in the benthos over the winter, cold winters resulted in a reduced diversity of the benthic community at Station M1 off the Northumberland coast, with cold winters favouring the survival of the dominant species at the expense of the less abundant species (Buchanan & Moore, 1986b).

The benthic community at Norderney in the German Wadden Sea has been affected by severe winters, with the sublittoral being more affected than the littoral (Dörjes *et al.*, 1986). During the severe winter of 1978-1979, one third of the sublittoral benthic community disappeared, and the regeneration of the community over the next few years resulted in an assemblage with a completely different species composition (Dörjes *et al.*, 1986). The greatest change in community structure appeared between 1980 and 1981 and it was suggested that cold winters were a greater cause of changes in the community than summer temperatures or storms (Dörjes *et al.*, 1986), despite there being no actual correlation between air temperatures and abundance. This proposed mechanism for the cause of a change at Norderney between 1980 to 1981 is in contrast to the suggestion that the change in the Northumberland and Skagerrak benthos between 1980 and 1981 were attributed to changes in food supply (Buchanan, 1993) or eutrophication (Austen *et al.*, 1991). At Norderney, mild winters between 1987 and 1992 may also have induced changes in the benthos and it was suggested that there was a synergistic effect of mild winters and eutrophication acting together, with high biomasses resulting from cold sensitive species thriving on the increased food input. Thus, mild meteorological conditions, probably acting in conjunction with eutrophication, have resulted in an increased total biomass since 1989 (Dörjes *et al.*, 1986).

Kröncke *et al.* (1998) found a strong relationship between abundance, biomass and the NAO index at Norderney, which suggested that changes in the benthos, induced by winter temperatures could be ultimately linked to changes in the NAO (NAO-benthic abundance r=0.73). The best correlations between the NAO and benthic parameters were found during the cold period of the year, suggesting that the NAO acted through winter temperatures. Thus, most of the interannual variability in macrozoobenthos could be explained by climate variability (Kröncke *et al.*, 1998), showing that in the same way as the plankton, large scale environmental variables are linked to changes in productivity.

Physical disturbance of the sediment due to swell from storms also produces a direct effect upon the benthos. High levels of swell have been shown to disturb shallow benthic communities, although they only appear to affect vulnerable taxa. Drake & Cacchione (1985; 1986) and Turner *et al.* (1995) noted that waves associated with storms may influence the benthos at depths in excess of 50 m, although this depended upon the local hydrography. At Norderney, storms caused a decrease in the abundance of *Macoma*, *Scoloplos* and *Magelona*, especially after the two storm floods in November 1981 (Dörjes *et al.*, 1986). Total abundance also declined in 1982 and 1983 which were also attributed to storm damage; in contrast, since 1989, species numbers have increased despite intense storms (Zeiss & Kröncke, 1997).

Large increases in organic input to the benthos can lead to mortality of benthic fauna due to anoxia caused by the oxygen requirements of the bacteria degrading the organic matter (Cederwall & Elmgren, 1980). Generally, the period of anoxia is fairly short because of rapid restoration of the oxygen content by tidal movement (Beukema, 1992c), although the community may require a few years to recover. The sedimentation of the heavy algal blooms in the late summers caused the benthos to become anoxic (Duineveld *et al.*, 1991; Radach, 1992). In 1982, a mass mortality of benthic animals was detected in the German Bight, and a further survey in the summer of 1983 found a general decrease in the diversity of the community, with a 30-50% reduction in species numbers. However, the community recovered rapidly, and by 1986 biomass and abundances were similar to those before the algal blooms of 1981 (Duineveld *et al.*, 1991).

In addition to time series maintained to understand changes in system function, there are also data series which are produced to monitor anthropogenic impacts (e.g. sewage sludge and fly ash dumping). These data are not usually analysed as time series and are often only published in report form. There is a fundamentally different approach between the assessment of effects of a point source input, such as that around an oil rig or a sewage dump site, and to assess whether or not the North Sea as a whole is affected by, for example, eutrophication (Duineveld *et al.*, 1991).

Sewage sludge dumping causes a smothering of the established benthic community followed by a reduction in oxygen content because of enhanced bacterial activity. Sewage sludge also contains increased concentrations of heavy metals which are toxic to macrofauna (Hall, 1996). Those opportunistic species tolerant of the heavy metal concentrations flourish because of the input of extra nutrients to the system, which results in a reduction in diversity yet an increase in the overall abundance of organisms (Clark, 1992). Sewage sludge disposal has occurred at 10 sites in the North Sea (Parker, 1988) and much concern has been raised over the dumping of sewage by the UK (Duineveld *et al.*, 1991). At marine waste disposal sites off the NE English coast, identifiable effects were localised in extent (North Sea Task Force, 1993). Rees *et al.* (1985; 1992) did find evidence of marginal enrichment of the benthos at about 50m depth in the immediate vicinity of a sewage sludge disposal site off the River Tyne (see Figure 2.1). However, the River Humber (see Figure 2.1), appears to have been unaffected by the disposal of sewage sludge and liquid industrial wastes (Murray *et al.*, 1980). Usually the scale of these direct impacts on the benthos is relatively small, covering a few square kilometres.

Chemical inputs may also cause direct impacts on the benthic community. Shillabeer & Tapp (1990) investigated long term benthic changes in the highly industrialised Tees estuary and Tees Bay. Within the estuary, since 1970, BOD loadings from local industries had decreased, and by 1985 there was a "major reduction" (Shillabeer & Tapp, 1990). Over this time, studies of the Tees estuary benthos indicated an improvement in both infaunal abundance and diversity, which was suggested to be related to water quality, although the limited time scale could mean the changes were due to natural effects upon the community (Shillabeer & Tapp, 1990). However, as there were no long term changes in the abundance and diversity of the fauna in Tees Bay, this suggested that the impacts were restricted to the estuary.

Uniquely, in NE England, fly ash was disposed (until 1992) at a marine dumpsite. "Fly ash" comprises the principle solid waste from coal fired power stations and is usually disposed of on land. Dumping of fly ash in the sea modifies the sediment grain size (fly ash is equivalent to fine silt, and thus infauna preferring coarser grain sizes are unable to exploit the sediment) (Bamber, 1980), and causes suffocation of the macrofauna (Herrando-Perez, 1996), as well as producing a sediment with a zero food value. Survey-work following the cessation of dumping found that seabed sediments at the dumpsite were composed of pure fly ash even a year after dumping stopped (Herrando-Perez & Frid, 1998).

Another impact which has been monitored over the past 20 years is the effect of tributyltin (TBT) paints on molluscs, particularly the gastropod *Nucella lapillus* (which has been used as a bioindicator). TBT has been linked to declines in the populations of dogwhelks throughout the North Sea. Imposex (when females are rendered infertile through the development of a penis) has probably been responsible for the extinction of some populations along much of the east coast of the North Sea (Evans *et al.*, 1996). Yet following the prohibition of TBT paint use on vessels less than 25 m length in 1987, levels of TBT have decreased in the water column, sediments and tissues of molluscs (Evans *et al.*, 1995). Although some ports used by large commercial vessels were still found to have considerable TBT pollution in 1994, none of the populations were found to be sterile despite 25 years of TBT contamination (Evans *et al.*, 1996).

The physical disturbance of the sea bed through the cumulative effect of bottom fishing gears is a larger scale human impact on the benthos. The direct effect of mortality caused by beam trawling varies from species to species, with 10-40% mortality in gastropods, starfish, crustaceans and annelid worms, and from 10-50% for sea urchins to 30-80% for bivalves. At the community level, the mortality imposed by the trawl fishery will depend on the level of direct mortality, the trawling frequency and the overlap in spatial distribution between the fishery and the benthic organisms. Studies of the annual direct fishing mortality rates on benthic invertebrates in the southern North Sea were estimated to be 7-45% of the individuals (de Groot & Lindeboom, 1994). This compares with the estimated percentage of the benthic production that is consumed annually by fish predators (~45%).

Indirect effects of trawling are also important in the structuring of benthic communities (Kneib, 1991). These effects include changes in nutrient cycling caused by physical disturbance of the sediment water interface, the addition of labile organic matter (discards) to the system, the continued transfer of fixed carbon from the marine environment to the terrestrial system

(Camphuysen *et al.*, 1995), and changes in the food chain arising from manipulation of the density and size structure of the fish populations (ICES, 1998; Frid *et al.*, 1999b; Frid & Clark, 2000), which leads to changes in the quantities and types of prey consumed. Fish play a central structuring role in the ecology of many aquatic systems (Hansson, 1985), and alterations in fish abundance, size distribution or spatial distribution may induce changes in other aspects of the ecosystem through changes in the strength or direction of the ecological links. In many marine ecosystems there is evidence of species other than the prey being influenced by changes in fish predation (Parsons, 1991; Parsons, 1992; Parsons, 1996; Verity & Smetacek, 1996), and this is seen as the principal way in which fish influence benthic communities (Whitman & Sebens, 1992; Sala & Zabala, 1996; Sala & Boudouresque, 1997). In addition, benthic feeding fish do exhibit some degree of selection, thereby altering relative abundances of benthic species. Experimental studies have shown that fish predation can potentially control both the number of individuals in the system and the relative abundance of species (Wilson, 1990). The target species of fisheries can also structure the benthic community through indirect interactions, such as by predation on in-coming larvae (Langton & Robinson, 1990). Hence alterations in the abundance and size structure of target populations can potentially influence the benthos through direct competitive or predative interactions and by indirect routes. There is therefore the potential for cascading effects as a result of fishing induced changes in predator abundances and size distribution (ICES, 1998). Although the existence of such trophic cascades in the marine environment has not been established, given their presence in limnetic systems (Carpenter, 1988), marine communities are also likely to suffer trophic cascades (ICES, 1998). The ecological consequences of these changes are difficult to predict, but include altered predation rates as small and large fish rarely feed on the same prey (Greenstreet & Hall, 1996; Frid *et al.*, 1999b).

Analysis of meroplankton taxa recorded in North Sea CPR surveys has been used to assess changes in benthic composition by examining changes in the species composition and abundance of larval forms. Analyses showed an increase in the dominance of echinoderm larvae over the period 1958 to 1991 (Lindley *et al.*, 1995), possibly due to an increase in their relative abundance in the benthos. This has been interpreted as being the result of increases in the population of scavenging starfishes and ophiuroids as a result of food subsidies from fisheries (Ramsay *et al.*, 1998). However, the timing of the change, in 1978, is well after major changes in fishing effort and technology. These, and the widespread nature of the increase in echinoderms in the CPR data suggest that environmental causes are more likely to be responsible.

The Northumberland benthic time series have also been used to evaluate the effects of trawling in the North Sea (Chapter 7, Appendix 4, Frid & Clark, 2000). It was expected, that despite differences in depth and slight differences in community structure, Stations M1 and P would follow similar trends in the timing of large changes in community structure and productivity, which would be largely determined through changes in organic input (Pearson & Rosenberg, 1986). However, whereas changes in benthic abundance at Station M1, situated outside of a *Nephrops* fishing ground, mirrored changes in phytoplankton input (Figure 7.1c & d), when fishing effort at Station P on the *Nephrops* ground increased in the period 1986 to 1990, this caused a decline in benthic abundance at this site (Chapter 7, Appendix 4, Frid & Clark, 2000) (Figure 7.1a & b), and large scale year to year changes in community structure indicative of a stressed community. At Station P, the proportion and abundance of the individuals in the community belonging to taxa identified *a priori* as likely to increase as a result of fishing, increased during the period of high fishing effort and declined when fishing declined (Chapter 7, Figure 7.1a & c). The abundance of taxa predicted to decline did not alter, possibly due to the previous fishing at this site already having caused declines in sensitive taxa. In contrast, at Station M1, although total abundance had increased (in response to increased phytoplankton input), there were no notable changes in the proportions of each group within the macrobenthic community over time (Chapter 7, Figure 7.1b & d). Differences in the dynamics of the groups identified *a priori* also suggested that different mechanisms were at work at the two sites. At Station M1 there was an increase in errant polychaetes over the entire period in response to the increased food input, yet at Station P their abundances increased during the high fishing period and subsequently decreased when fishing activity decreased. Kröncke (1990) and Reise (1982) attributed the long term increased abundance of polychaetes in some areas of the North Sea to fishing activity and nutrient changes respectively.

Fishing in the North Sea has occurred for centuries, and the history of mechanised fishing extends back further than any biological sampling, and as such the composition of a "pristine" benthic community remains unknown. However, in recent decades, the total area of benthos trawled has increased, and many areas of the North Sea are now disturbed many times per year (Gislason, 1994). Some studies have made comparisons between recent samples and historical data to assess whether the differences observed could be attributed to fishing induced changes. Kröncke and her co-workers (Kröncke, 1990; Kröncke, 1992; Kröncke & Rachor, 1992; Kröncke, 1995) studied changes in benthos of the Dogger Bank, resampling stations in the 1980s which were originally sampled in the 1950s. Whilst many changes in faunal abundance occurred, including the loss of *Spisula* spp. from certain areas, these changes were interpreted as being primarily responses to food availability due to eutrophication and/or climatic fluctuations. In contrast, Schroeder & Knust (in press) examined long term changes in the German Bight, and found that the taxa predicted to be sensitive to fishing were those that showed the most marked changes in the period, as there was a decline in large, long-lived taxa, although total biomass had increased due to increases in the abundance of opportunistic taxa. However, the changes in species composition here appeared to be the result of alterations in the abundance of many taxonomic groups and not just those sensitive to the direct effects of fishing, implying that the indirect effects of fishing (sediment changes, nutrient flux, predation pressure) may be at least as important as the direct effects (Schroeder & Knust, in press).

Frid *et al.* (in press) considered data on the quantitative abundance of macrofauna in 5 regions of the central and southern North Sea. They adopted a conservative approach to the 'quality control' of data and were still able to show definite changes in the macrofaunal communities in 3 of the 5 areas between the early 1920s and the late 1980s. The lack of change in the remaining 2 areas was interpreted as evidence that the changes were not part of a broad scale environmental change or due to methodological changes. One of the areas that showed no significant change between the 1920 to late 1980s included much of the Dogger Bank, but this area may have been exploited for so long as to have undergone community and habitat shifts prior to 1920.

The consumption of North Sea benthos may have changed as the species composition of fish has changed (Frid *et al.*, 1999b). Fishing has removed the larger gadoids that are principally piscivorous, and has allowed expansion of flatfish such as dab and young gadoids that prey upon benthos to a larger extent. The differences in the diet of the various species suggests that crustaceans have declined in dietary importance, while echinoderms (predominantly ophioroids) have increased. By examining time series from 1970 to 1993 on the abundance, size and diet of North Sea fish it was possible to evaluate predation pressure for the 8 most abundant demersal species (ICES, 1998; Frid *et al.*, 1999b). Although target fish populations (gadoids and plaice) have declined, the overall estimated level of predation on the benthos has increased from around 23 million tonnes year^{-1} in 1970 to 29 million tonnes year^{-1} in 1993.

Overview

This study has identified 3 major changes in the North Sea benthos;

- Biomass and abundance was higher during the 1980s compared to the 1970s in both littoral (Balgzand) and sublittoral (Northumberland, Skaggerak) stations.
- Changes in abundance off Northumberland (M1 & P) occurred between 1980 and 1981, coinciding with a noticeable shift in community structure at one of the stations. At the 100m deep Skaggerak station, these changes were observed to occur a year earlier, between 1979 and 1980, while at Balgzand, the change in abundance and biomass which also occurred between 1979 and 1980 was accompanied by a shift from larger to smaller sized individuals.
- Between the 1920s and the 1980s, 3 out of 5 communities in the central and southern North Sea showed a definite change, whilst between the 1950s and 1980s, the Dogger Bank benthos showed a decline in long lived taxa, although total biomass had increased, mainly due to an increase in opportunistic species.

The primary mechanism governing changes in both abundance and community structure of the North Sea benthos appears to be through changes in the amount of sedimenting plankton, the main source of food for the benthos. Changes in the benthos in response to increases in organic matter reaching the sea floor would be expected to increase the productivity of the benthos (Pearson & Rosenberg, 1986). Such changes were observed to occur around the late 1970s and early 1980s, at a number of sites. Increases in both zooplankton and phytoplankton productivity in the North Sea also occurred at this time. Whether it is changes in climate or nutrients forcing the community depends mostly upon the region concerned, as climatic effects predominate in the central and northern North Sea area, yet in the southern North Sea, the influence of climate is overridden by the magnitude of nutrient inputs into the region.

The direct effect of temperature upon benthic communities is also involved in forcing long term changes, and for some communities, these changes may be as important as changes in food supply. Cold winter temperatures predominantly cause increased mortality upon littoral macrobenthic communities, although they have also been recorded as affecting sublittoral communities (Beukema, 1985; Beukema, 1992a). Lower temperatures also exert a selective effect on the community by removing vulnerable species and allowing resilient species to thrive in the conditions of reduced competition (Kröncke *et al.*, 1998).

In addition to these large scale environmental factors influencing benthic communities, there are numerous types of anthropogenic influences (hypoxia, fly ash, sewage sludge dumping) on benthic communities. However, these effects tend to be restricted to the immediate area of the benthos affected. An exception to this is through the large scale impact of trawling of the sediment which suggests that trawling has been involved in shifting the benthos from long lived to more opportunistic taxa in many areas of the North Sea. Unfortunately, this change from long lived, slowly reproducing species to small species with a high reproductive rate (opportunists) is similar to that caused by increased food supply to the benthos, meaning that it is difficult to distinguish between changes in the benthos caused by fishing, and those changes due to increased food supplies.

Fish

Introduction

Examination of North Sea fisheries data has indicated that over the course of the 20th century, and in some cases even earlier than this, major shifts have occurred in the abundance of both commercial and non-commercial fish species (Hempel, 1977). In the late 19th century, it was suggested by T.H. Huxley that the seas were inexhaustible, and that man's activities would never affect fish stocks. This proposition was based on the now incorrect assumption that the natural mortality of fish was greater than the mortality caused through fishing. Nowadays, although it is accepted that many of the observed changes during the 20th century may have been related to increased rates of exploitation (Rice & Gislason, 1996), there is a need for comparable data from earlier periods so that potential changes in the abundance, size distribution or diversity of the fish community may be evaluated (Rijnsdorp *et al.*, 1996).

The most common data on fish populations are derived from landings. However, landings data do not give a complete picture of changes in fish populations as they are influenced by consumer demand, fluctuation in fisheries management tactics (e.g. TACS, closures), and by the non-reporting of catches (Hislop, 1996). The other major source of long term fisheries information originates from scientific surveys, and for non-target species data are generally limited to these surveys. Research vessel surveys have been carried out in the North Sea irregularly since the beginning of the 20th century (Rijnsdorp *et al.*, 1996). These surveys have enabled comparisons between contemporary data and earlier data to assess where changes have occurred. One of the longest North Sea time series for demersal species is provided by the ICES co-ordinated International Bottom Trawl Survey (IBTS), which has been carried out annually since February 1965 (Oliver, 1990; Heessen, 1996). Initially, herring (*Clupea harengus*) was the target species and the survey was restricted to the southern and central North Sea, although since 1974 the entire North Sea has been included. In spite of the potential problems associated with landings-based data, these, and direct population surveys, have shown that there have been very substantial fluctuations in the abundance of both roundfish and flatfish over the last 25 years. However, even with all this information, the assessment of anthropogenic changes is difficult because of the complex nature of the system in which natural processes and human impacts interact (Rijnsdorp *et al.*, 1996). However, although commercial fish species are continuously monitored, long term data on non-commercial fish species are sparse, hampering the evaluation of the anthropogenic impact upon these species (Rijnsdorp *et al.*, 1996).

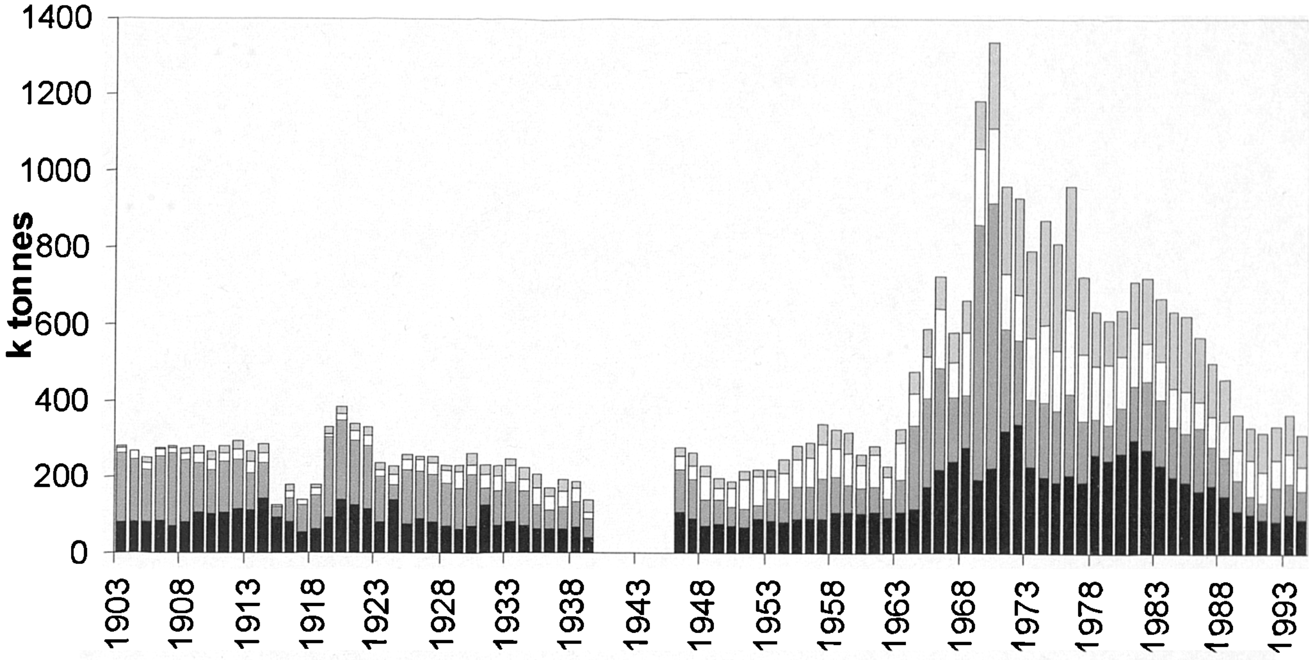


Figure 2.12 Landings (nominal catches) of cod (■), haddock (▨), whiting (□) and saithe (□) from the North Sea, 1903-1994, including industrial by-catch. Adapted from Hislop (1996).

Evidence for change

Over the course of the 20th century, the combined annual landings of the principal gadoid species in the North Sea have increased (Figure 2.12) (Hislop, 1996). Up until the mid-1960s, landings were in the range of 200-300 kt.y^{-1}. Gadoid landings then increased rapidly and remained high (600-1200 kt.y^{-1}) for approx. two decades (Figure 2.12). This rapid increase in catches and biomass beginning in 1962 was termed the gadoid outburst, when both haddock (*Melanogrammus aeglefinus*) and whiting (*Merlangius merlangus*) produced extremely strong year classes (Hislop, 1996). Cod (*Gadus morhua*) also produced above-average year classes in each of the years 1963-1966 with an exceptionally strong year class in 1969 (Serchuk *et al.*, 1996). Frequent strong year classes and associated increased landings were observed in haddock, cod and whiting over the next two decades (Hislop, 1996). Gadoid landings began to decline in the 1970s and by the early 1990s they were only approx. 50% higher than during the 1940s and 1950s (Figure 2.12). The main feature of the gadoid outburst was that recruitment levels were high. Yet, although it is known when the "gadoid outburst" began, as occasional above average cod year classes persisted until the mid-1980s, it is not known when the outburst ended.

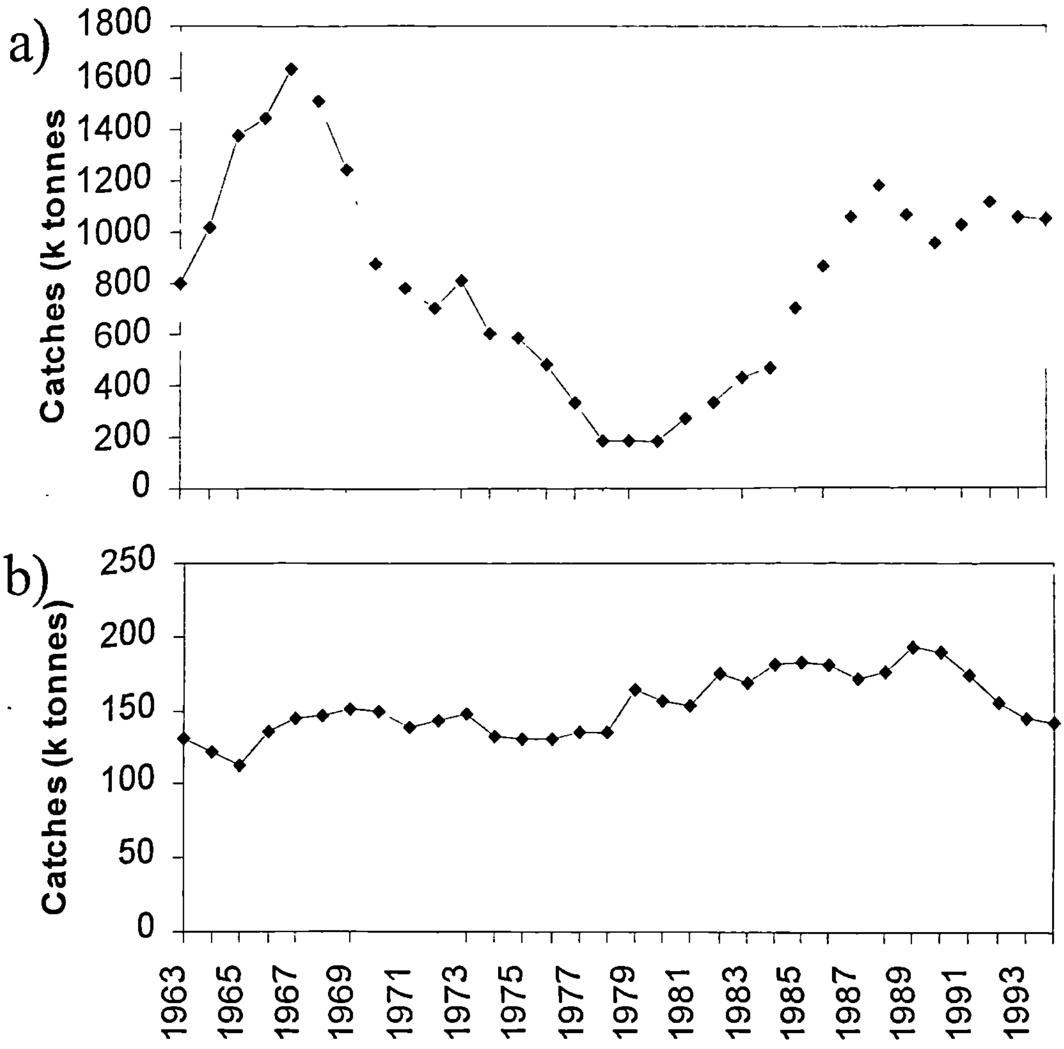


Figure 2.13 Total catches of North Sea a) herring and mackerel, b) flatfish (plaice and sole). Data for the years 1963-1994. Adapted from Serchuck *et al.* (1996).

Herring landings underwent a catastrophic collapse in the mid-1970s following increased exploitation (Figure 2.13a). This led to the herring fishery being closed from 1977-1983. This eventually allowed recruitment to increase, so by the late 1980s, catches had recovered (Serchuk *et al.*, 1996). North Sea mackerel (*Scomber scombrus*) stocks also collapsed after being intensively exploited in the mid to late 1960s. However, no recovery of this stock has occurred, and in the late 1990s the stock remained depleted at approx. 2-3% of the abundance observed in the early 1960s (Serchuk *et al.*, 1996). Only insignificant recruitments of North Sea mackerel have occurred since the mid 1970s (Serchuk *et al.*, 1996), yet due to an increase in the migration of the Western stock of mackerel into the North Sea since 1980, landings of mackerel have increased from 50 000t in 1985 to 475 000t in 1994.

Changes in both target and non-target fish stocks in the North Sea were examined by Heesen and Daan (1996), using IBTS data. Gadoid biomass was found to have declined over the 1970 to 1993 period (Figure 2.14a), and although there were some strong year classes during the early 1970s, this downward trend was particularly apparent from 1975, mirroring that of the catches (c.f. Figure 2.12). Likewise, long term trends in herring biomass from the IBTS parallel those of the landings (Figure 2.14d), with a decline in the population from 1970-1977 followed by a recovery.

The exploitation and landing of flatfish species has increased since 1963, and so by the late 1980s, landings were double those of the 1940s. Combined landings for the main commercial flatfish species, plaice and sole peaked in 1989/1990, and since then have declined to the levels observed in the 1970s (Figure 2.13b). Recent analysis of the IBTS data shows that, despite these increases in flatfish exploitation, the population remains stable (Figure 2.14b) (Heessen & Daan, 1996). Heesen (1996) noted that, within the flatfish species recorded in the IBTS data, the relative abundance of plaice has decreased, whilst sole abundance has increased over the 1970 to 1993 period.

Long term changes in the mean length of fish have also been recorded. A comparison of sizes of demersal fish species between 1906-09 and 1990-95 caught during otter and beam trawl surveys found that the length-frequency distributions of roundfish and flatfish showed a shift towards smaller sized fish (Rijnsdorp *et al.*, 1996). In addition, there were lower abundances in recent years for the total roundfish and flatfish assemblage as well as for most individual taxa. Diversity and evenness indices also showed a reduction (Rijnsdorp *et al.*, 1996).

Industrial fisheries expanded after 1945, and catches increased rapidly in the early 1960s (Figure 2.15), reflecting the increased commercial interest in these species (Hislop, 1996). These fisheries target small, short-lived species for reduction to fish meal and fish oil. The principal target species were sandeels, Norway pout and sprats, all of which are preyed on by gadoid species. Since the early 1970s, this fishery has contributed approximately 50% of the total weight of fish landed from the North Sea. Hislop (1996) stated that the increased landings from this fishery could either reflect an increased abundance of industrial species, the increased exploitation of a previously underutilised resource, or both. IBTS data on changes in industrial species biomass shows that, since 1975, there has been a marked decline in numbers (Figure 2.14c) (Heessen & Daan, 1996), implying an increased level of exploitation.

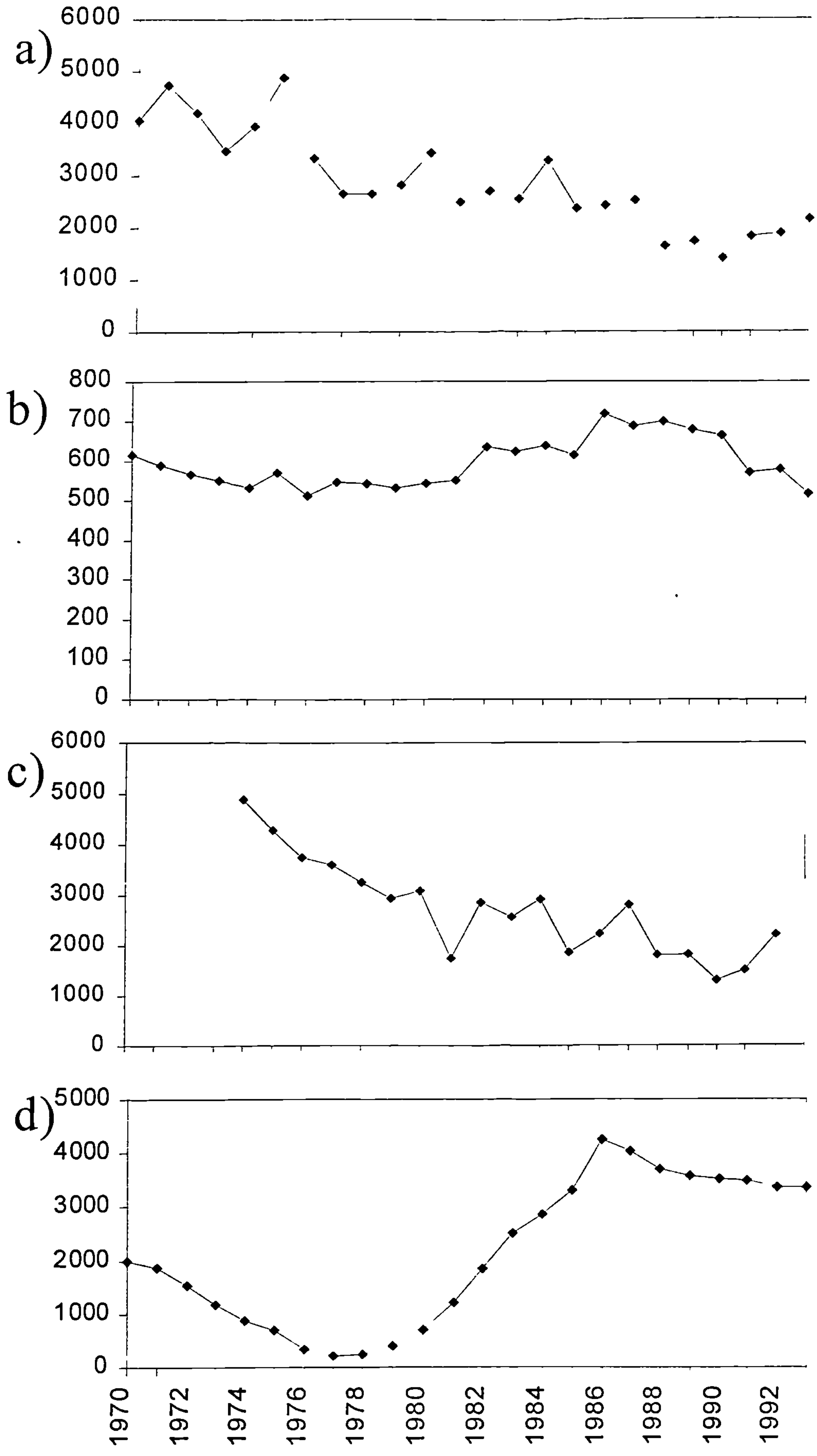


Figure 2.14 Trends in North Sea a) Gadoid biomass. b) Flatfish biomass. c) Industrial fisheries biomass. d) Herring biomass. Data for the years 1970-1993. Units are in k tonnes biomass. Adapted from Heessen & Daan (1996).

Causes of the changes

Although long term trends in fish stocks, and the ecological balance between taxa, are known to be heavily influenced by fishing, some of the changes which have occurred during the latter half of the 20th century are attributable to changes in environmental factors (Hislop, 1996). These factors either directly affect fish stocks and recruitment, or indirectly, via changes in the timing and availability of food.

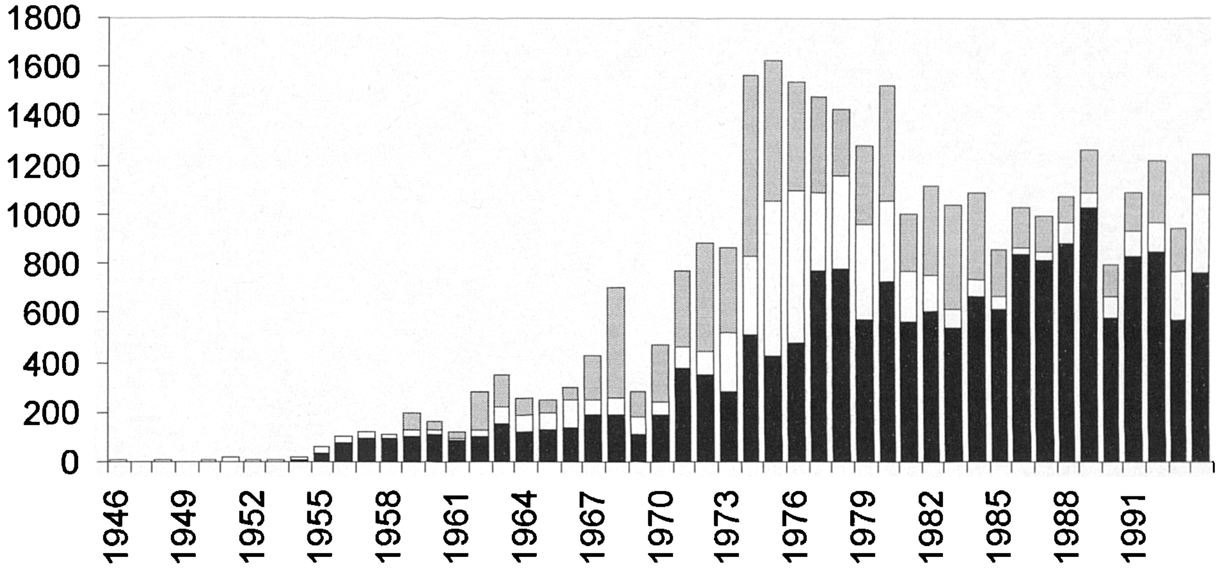


Figure 2.15 Landings of principal industrial species from the North Sea, 1946-1994. ■ sandeels, ☐ sprat, ▨ Norway Pout. Adapted from Hislop (1996).

Fish stocks undergo striking interannual fluctuations in recruitment (Heessen, 1988; Shepherd, 1990), and although fishing is likely to be the strongest factor affecting Spawning Stock Biomass (SSB), recruitment is not clearly related to SSB, but is more reliant upon environmental factors – the fluctuation in the small proportion of eggs surviving the first year of life are due to the ultimate effect of subtle changes in the weather and currents (Shepherd, 1990). It has been suggested that the ability of fish species to be able to sustain levels of fishing mortality several times their natural mortality suggests the presence of strong regulatory mechanisms (Shepherd & Cushing, 1990). The sustainability of fishing is largely determined by two factors; i) the relationship between the Spawning Stock Biomass and the annual number of offspring (recruits) produced, and ii) the subsequent survival of the recruits on entering the fishery (Cook *et al.*, 1997). A fish stock which produces constant recruitment at any stock size, cannot collapse, although obviously if there are no spawning fish then there can be no recruits.

Direct forcing of fish populations through changes in temperature has been observed for a number of species. Temperature is known to directly affect individual fish growth via its influence on metabolic rate and food consumption (Wooton, 1990; Jobling, 1995), provided that food is not limiting. Fluctuations in abundance may be due to changes in distribution influenced by changes in water temperatures. The abundance of some Lusitanian species, especially pogge (*Agonus cataphractus*), butterfish (*Pholis gunellus*) and eelpout (*Zoarces viviparus*) were correlated with surface sea temperature and salinity, and warmer summers were also associated with an increased recruitment of taxa situated at the edge of their normal geographic distribution in the North Sea, such as bass (*Dicentrarchus labrax*) and red mullet (*Mullus surmuletus*) (Rogers & Millner, 1996). Corten & van de Kamp (1996), in an examination of IBTS data, noted that in the mid 1970s and around 1990, southern fish species increased, due to an increased Atlantic inflow through the Dover Straits driven by increased southerly winds (and higher temperatures). Heesen (1996) also found that many southern species had increased abundances in the 1990s, suggesting that the relatively warm winters during this period may have been important for these species. However, as many resident species have also become gradually more abundant over these and longer periods another factor may be responsible. An earlier analysis by Russell *et al.* (1971), pertaining to the English Channel, found that the abundance of herring and pilchard stocks were linked to climate, with warm periods being occupied by pilchards, and herring dominating the cooler periods. Aebischer *et al.* (1990) also put forward that the parallel trends of herring and westerly weather suggested that the long term trends were either directly affected by weather, or mediated via the food chain (c.f. Figure 2.14d with Figure 2.2c). However, it is likely that overfishing played the major role. Spawning of species may also be affected by water temperature; North Sea cod is threatened by a decline in the production of young cod which has paralleled warming of the North Sea over the past ten years (O'Brien *et al.*, 2000).

Fluctuations in either benthic or pelagic food resources, driven by changes in climatic or nutrient based factors play a major role in fish recruitment. Hislop (1996) suggested that there were either parallel fluctuations in fish biomass and food resources, or that food supply was always superabundant (i.e. not a limiting factor). Early work by Hardy (1924) showed that older herring feed predominantly upon *Para/Pseudocalanus*. Cushing (1995) suggested that recruitment of fish stocks may rely on the amount of copepod nauplii and juveniles present as food for fish larvae, as recruitment was positively related to *Para/Pseudocalanus* abundance ($r^2=0.19$, $p<0.01$), which is ultimately influenced by climatic factors (Cushing, 1992). One of the most prominent hypotheses to explain recruitment in fish stocks was the match/mismatch hypothesis (Cushing, 1974; Cushing, 1975; Cushing, 1982; Cushing, 1990). This hypothesis was based on the observation that the spring and autumn spawning stocks in the north-east Atlantic released their larvae so that they would grow in the spring and autumn peaks of plankton production (Cushing, 1967). The gadoids spawn in a fixed season, and the peak spawning date has a standard deviation of about 1 week, yet the timing of peak plankton production in the Atlantic may vary by up to 6 weeks. Increased food resources for the larvae are available when their peak coincides with their planktonic food resource (Figure 2.16a), yet where the larvae miss the plankton peak (Figure 2.16b), this reduces the amount of food available. Thus, the hypothesis was based on the contrast between the relatively fixed spawning period, and the highly variable period of peak productivity likely to be due to climatic variation. Mann (1993) suggested that the mechanism of vertical mixing and the spring bloom with its period of peak productivity was the key event determining the success of the recruitment of species such as cod, haddock and plaice, making the case that physical factors which drive the primary production processes are related to changes in fish stocks.

Three mechanisms have been suggested as the cause of the gadoid outburst. Firstly, the gadoid outburst could be attributable to the decline of herring stocks as herring and cod feed on the same resource, and thus the reduced herring abundance released food to larval cod from the reduced herring population (Cushing, 1984; Hislop, 1996). The second possibility, postulated by Cushing (1984), was that the outburst was due to relaxed predation on the juvenile cod by adult herring, although this was not supported by gut analysis, and Hislop (1996) pointed out that the timing of the various events do not fully support these hypotheses. Despite this, the recent period of below-average recruitment of all gadoid species coincides with the improved recruitment of herring, and thus the overall fish fauna composition appears to have returned to pre-1960s conditions, whether or not as a result of species interactions (Hislop, 1996). Other species, such as sprat and sandeels (which are now also fished) may have also responded to abiotic changes in the North Sea, or taken advantage of opportunities created by the reduction in the biomass of herring and mackerel (Hislop, 1996). The third explanation was that the gadoid outburst was primarily of climatic origin, either through direct influence on fish stocks, or indirectly through changes in their food supply, although all the above may have contributed to the strength of the outburst. The widespread nature of the increase amongst all the gadoids would support this hypothesis, and the fact that the increased period of cod recruitment between 1962 and c.1978 matched to the peak periods of phytoplankton productivity, in contrast to a mismatched condition between 1949-1961 (Cushing, 1984). Peak abundance of *Calanus* tended to occur later in the year during the matched period, increasing food availability to young cod. There was no clear evidence of a similar relationship between haddock recruitment and the timing of the peak in *Calanus* production, suggesting that all but the strongest haddock year classes might have been modified by cod predation (Cushing, 1984). Jones (1983) concluded that the food resources of juvenile haddock may have been low during periods of high abundance. Finally, Hislop (1996) suggested that the recent decline in the recruitment and stock biomass of gadoids had an underlying environmental cause and represented a natural change in the ecosystem. If this is the case then no fisheries management could restore gadoid stock biomass to the levels which were attained in the 1960s and 1970s.

Cyclical factors may also play a role in the long term control of fish stocks. North Sea cod generally produce a relatively strong year class every 2 to 3 years, whereas haddock has followed a 3 to 4 year cycle throughout most of the 20th century (Hislop, 1996). Very strong haddock year classes are often followed by very weak ones and thus there may be an underlying density dependant component in their dynamics. These intraspecific interactions thus increase the difficulty of establishing correlations between recruitment and environmental parameters (Hislop, 1996). Another notable observation is that the period of high roundfish recruitment was also an anomalous period for the NAO (Pope *et al.*, 1988).

Changes in benthic food resources may also affect fish stocks. Nielsen & Richardson (1996) noted that increased primary production from increased nutrient inputs in the Kattegat resulted in increased benthic food resource, which coincided with an increased fisheries yield. Heesen & Daan (1996) also suggested that nutrients may indirectly influence fish biomass by affecting their food supply. However, nutrient increases will mainly have indirectly affected the macrobenthos in the shallow south-eastern North Sea and the Skagerrak-Kattegat area, which although an important area for flatfish, is less important for gadoids and the industrial species

(Heessen & Daan, 1996). These species reside in the areas of the North Sea where variations in benthic food resources are primarily climate driven.

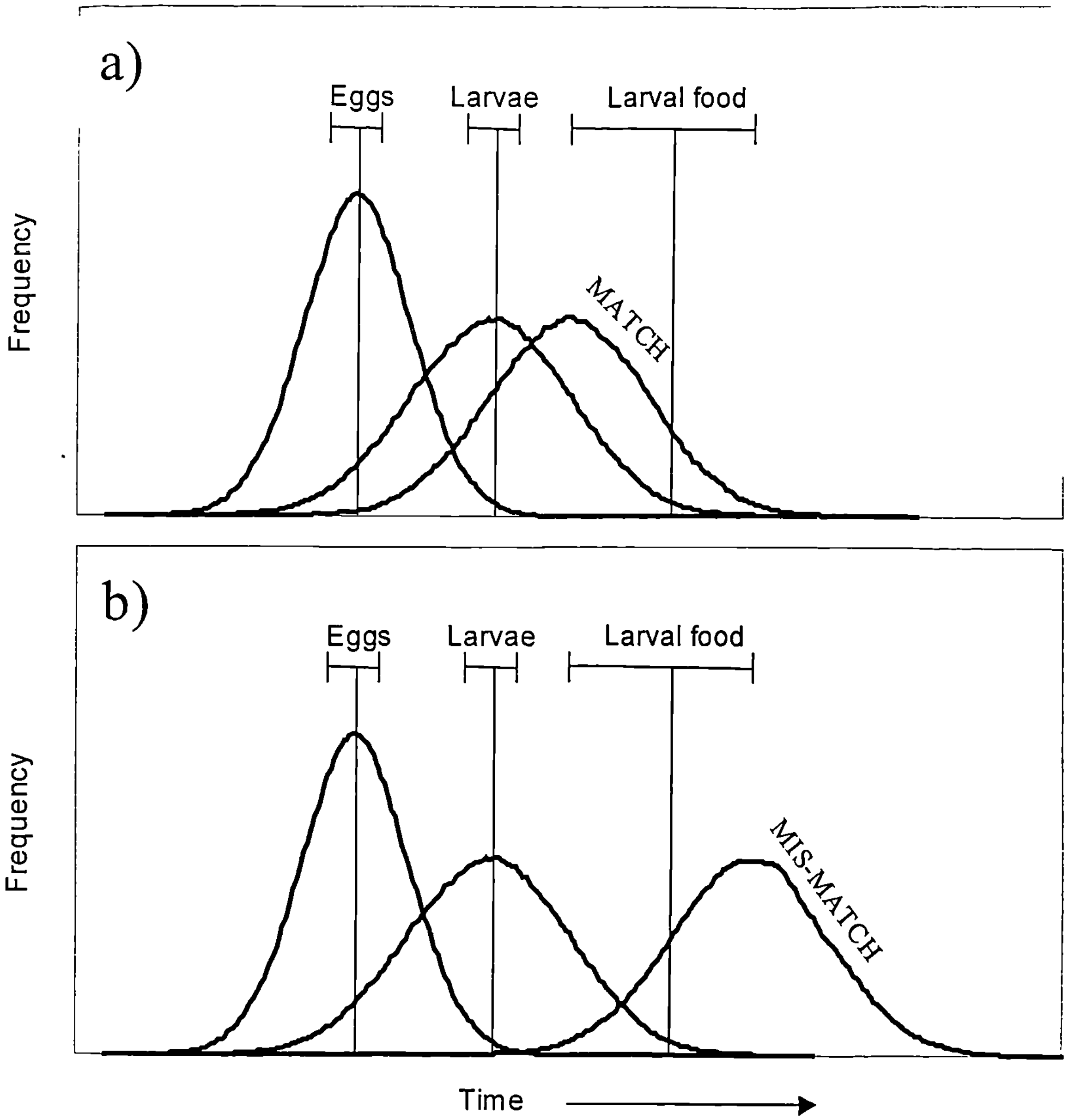


Figure 2.16 The match-mismatch hypothesis. The production of eggs, larvae and larval food are shown as distributions in time. Horizontal error bars denote the amount of temporal variation of the peak frequency. The match (a) or mismatch (b) is represented by the overlap in time between the production of fish larvae and that of their food. See text for explanation. Adapted from Cushing (1990).

Despite the fact that meteorological and biological factors are likely to have had a bearing on gadoid growth, it has not yet been possible to develop good predictive models (Hislop, 1996). For example, the correlation between wind and haddock recruitment described by Carruthers *et al.* (1951) at first seemed encouraging but later turned out to be unreliable. Even though the incorporation of physical and meteorological data into North Sea models can account for a larger part of the variance in the recruitment of cod, saithe, whiting and herring (as determined by Virtual Population Analysis), the output from these can be questionable (Hislop, 1996). Environmental factors are more important for the recruitment of some species than for others. For example, environmental data from the main haddock spawning area in the northern North Sea does not explain recruitment variability in this species, although it does in cod and whiting, both of which spawn throughout the North Sea (Hislop, 1996).

Although fish recruitment is considered to be largely controlled by natural factors, fishing is considered to be responsible for many of the major changes in fish stocks (Serchuk *et al.*, 1996). The main factor causing decline in fish populations is considered to be due to consecutive years of poor recruitment and heavy fishing (Oliver, 1990). One of the clearest examples of how stocks may be affected by fishing is that for North Sea herring. The increase in herring landings in the mid 1960s (Figure 2.13a) was due to a large purse seine fleet being diverted from the Norwegian Sea, where the Atlanto-Scandian herring stock had just collapsed. This increased effort led to a progressive decline in the size of the North Sea spawning stock and its eventual collapse in 1977. Increased fishing, however, was not the only cause, as a succession of poor year classes, in conjunction with a much reduced SSB, meant insufficient recruits were available to maintain the stock. There is some debate as to whether the low recruitment was simply because the egg production of the spawning stock was low, or because the survival of the young herring in their first year of life was low as a result of natural factors (Oliver, 1990). The slow recovery of the fishery following closure was because herring stocks were slow to rebuild, due to a sequence of small year classes, caused by a change in North Sea circulation patterns (Shepherd, 1992).

The fact that the strong cod year classes in the late 1960s to 1970s produced large increases in total stock biomass and fishery yield, but had little impact on spawning stock biomass, is because the juvenile age classes were caught before they reached maturity (Hislop, 1996). Presently, the gadoids are exploited in such a manner that the spawning stock biomass is made up of a small number of cohorts and is therefore very responsive to the strengths of each incoming year class, which may undergo large interannual fluctuations. Also, there may be subtle changes in both the quantity and the quality of the eggs produced by a "young" spawning stock, as the relative fecundity of recruit spawners is low (Hislop, 1996). Since 1981, roundfish landings have been dominated by 2 year old immature fish, and since 1983 the spawning stock biomass has been below the Minimum Biologically Acceptable Level (below this level, the probability of poor recruitment increases as spawning stock size decreases (Serchuk *et al.*, 1996)). Using cod as an example, approximately 70% of the catch is made up of 1-3 year old fish despite the fact that cod do not breed until they are age four (Oliver, 1990). Cook *et al.* (1997) claimed that at current exploitation rates, only 4% of cod survive to age four. As such, the size of the stocks and catches are becoming more dependant on the recruiting year classes. In addition, large quantities of juvenile fish are landed or discarded (Serchuk *et al.*, 1996). For many species, their lowest observed spawning stock size has been seen in recent years (1990s), although the mid 1990s assessments for roundfish indicate a decline in fishing mortality for cod, haddock and whiting, possibly due to the reduction in effort since 1990 (Serchuk *et al.*, 1996).

An analysis by Cook *et al.* (1997) suggested that the current exploitation rate of cod is unsustainable and that landings close to the Maximum Sustainable Yield may be potentially prone to risk of collapse. Without a substantial reduction in the rate of fishing, North Sea cod stocks may collapse in a similar manner to that which occurred off the Atlantic coast of Canada (Cook *et al.*, 1997). The possibility of stock collapses is undeniable, even if it is only manifested as an increased risk of poor recruitment when the spawning stock size is low (Shepherd, 1992).

Thus, many fish stocks have recently been, or are now, close to safe biological limits (Serchuk *et al.*, 1996) and despite maximum levels of protection, North Sea mackerel stocks are currently outside these limits. Some species appear to be fairly robust as despite the increase in flatfish exploitation since 1975, these stocks remains stable (Heessen, 1996). However, the recovery of fish stocks, if allowed through restriction on fishing, may not necessarily occur if environmental conditions are not appropriate; although overfishing was responsible for the collapse of the herring stock, its recovery only occurred with the simultaneous restriction of fishing, and presence of environmental conditions which favoured successful recruitment.

Pope & Macer (1996) stated that the proper management of North Sea roundfish species requires fundamental understanding of which are the key factors influencing recruitment levels The major concern is whether recent declines of cod and haddock recruitment represent a return to more "normal" levels i.e. prior to the gadoid outburst, or are symptoms of a more serious state of overfishing. Thus it is necessary to understand whether the changes are a result of environmental factors, or the result of fishing. This will determine the extent to which fisheries management might be able to influence such changes and to what extent they must be weathered.

Overview

This study has identified 5 major changes in North Sea fish stocks:

- Landings of the principal gadoids increased strongly in the 1960s, peaking in the early 1970s followed by a decline. Gadoid biomass (derived from surveys) mirrored that of the landings, with strong year classes observed during the 1960s and a decline in biomass over the 1970 to 1993 period.
- Herring landings collapsed in the mid-1970s, although by the late 1980s catches had recovered. Mackerel also collapsed in the mid-late 1960s, yet no recovery of this stock has occurred. For these species the trend in stock assessment data parallels that of the landings.
- Flatfish landings have doubled since 1945, peaking in 1989/1990. However, despite this, the populations remain stable.
- Abundances of most non-target species have increased since the early 1970s.
- Landings of industrially fished species have increased over time, and survey data shows that there has been a decline in the biomass of industrial species.

Although with the constant exploitation of fish stocks it has been suggested that it is difficult to associate the *recruitment of* commercial fish to environmental factors (Aebischer *et al.*, 1990), there is however, a great deal of evidence that fish recruitment is primarily influenced by environmental factors, although such factors may be more important for the recruitment of some species than others.

Changes in food resources appear to be the key natural factor affecting recruitment, and fluctuations in these pelagic and benthic resources are ultimately directly or indirectly caused by either climatic or nutrient constraints. Recruitment particularly appears to be influenced by the timing of peak food resources (the match-mismatch hypothesis), rather than the amount of food available, which in turn is controlled by climatic factors. However, as with the plankton and benthos, nutrients are likely to be indirectly associated with fluctuations in fish stocks in those areas where they override the climatic effects. Although whether raised nutrient levels override the timing of food resources or the amount of food resources is unknown, yet as these southern regions of the North Sea do not fully stratify, the model of Dickson *et al.* (1988a) does not fully apply. Direct forcing by environmental factors also plays a role, especially with those species at the edge of their natural distribution, and it has been suggested that some commercial species (e.g. mackerel) are directly influenced by temperature.

However, fishing clearly plays a greater role than environmental factors, as the lowest spawning stock sizes have been observed within the last decade of the 20th century. It should also be noted that these low spawning stock sizes have occurred against a background of above average phytoplankton productivity and therefore superabundant food resources. However, the low SSB and fact that current roundfish landings are dominated by immature fish means that there is currently a very severe risk of a collapse in fish stocks if environmental conditions produce a few consecutive poor year classes.

Seabirds

Seabirds sit high in the food chain and have a high public profile. This, and their sensitivity to changes in food stocks, means that seabirds are widely seen as bioindicators and biomonitors of the marine environment (Furness & Camphuysen, 1996). Some seabird colonies are monitored on a regular basis (e.g. kittiwake colonies on the eastern coast of the UK have been monitored since 1986, Harris & Wanless, 1997). Monitoring has also been undertaken using ship based counts of bird numbers (Camphuysen & Garthe, 2000), for both spatial and temporal analysis. However, the monitoring of seabirds appears to have focussed upon their usefulness as proxies rather than due to an interest in the dynamics of seabirds themselves. The position of seabirds high in the food chain means that they are potential monitors of food sources (fish), in addition to being potential monitors of pollutants that accumulate at higher trophic levels.

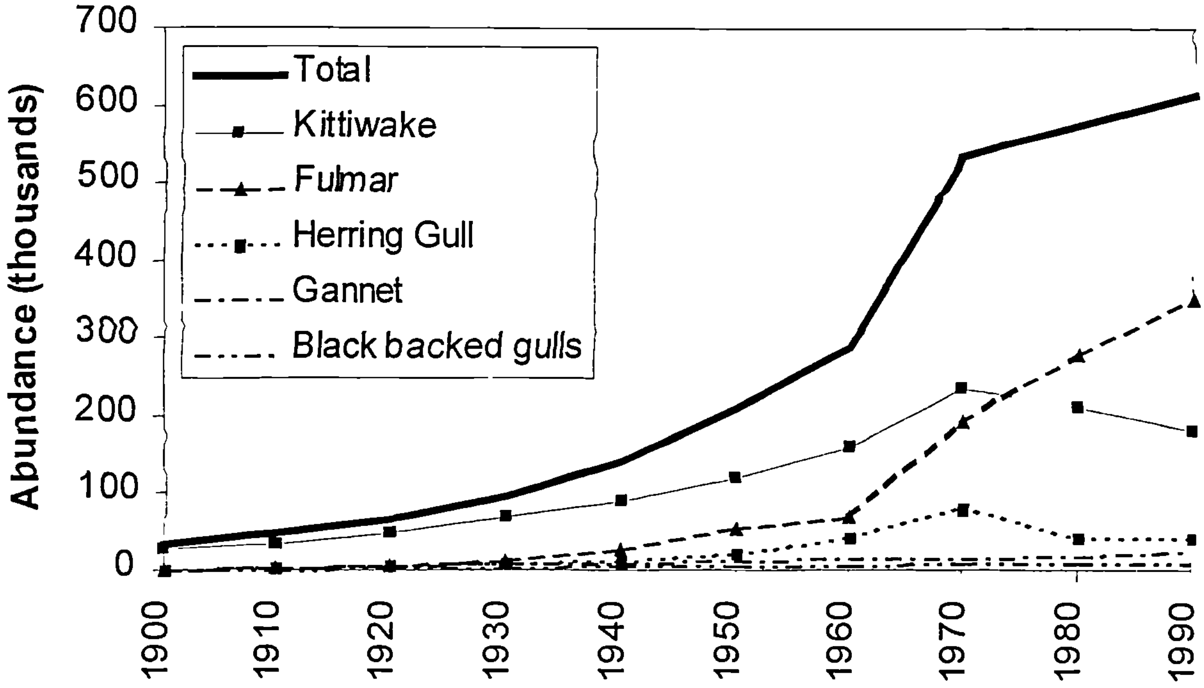


Figure 2.17 Numbers of pairs of scavenging seabirds breeding on North Sea coasts (NE Britain). Numbers are interpolated from census data to give figures for every tenth year. Camphuysen & Garthe (2000).

Over the course of the 20th century, most species of seabirds in the North Sea have increased their numbers (Figure 2.17) and, through establishing new colonies, have increased their breeding range (Camphuysen & Garthe, 2000). As such, abundances of most seabirds are at their highest historical levels. An example of this would be the spread of the northern fulmar, which had only one colony in the British Isles, at St. Kilda, at the beginning of the 20th century, and since then has managed to colonise the whole of the British Isles (Camphuysen & Garthe, 2000).

The overall increase in numbers during the first half of the 20th century was initially linked to the reduction of human predation. Coulson (1963) claimed that the relaxation of exploitation of the kittiwake allowed them to increase their abundance, while others suggested that the observed changes in seabirds were due to the new rich food supply made available by whaling and trawler discards (Fisher, 1952). The reduced exploitation is likely to not be the only factor causing the observed changes, as many terrestrial and freshwater species had suffered similar levels of exploitation, but subsequently did not undergo such dramatic increases in abundance and distribution following the cessation of hunting (Coulson, 1963). In addition, the gannetry in the Outer Hebrides, although still exploited in a sustainable manner, has increased at very much the same rate as all the other colonies in the British Isles. Yet, changes in food sources cannot entirely explain the observed increase, as both scavenging species (northern gannets (*Fulmarus glacialis*), great skuas (*Catharacta skua*), most gulls (*Larus* spp.) and kittiwakes (*Rissa tridactyla*)), and non-scavenging species (common guillemots (*Uria aalgae*) and puffins (*Fratercula arctica*)), have increased in numbers in their North Sea colonies (Camphuysen & Garthe, 2000). More complex interactions have been suggested, such as the removal of large fish by trawlers benefiting seabirds by increasing the abundance of small fish (Camphuysen & Garthe, 2000).

Changes in food resources and types of food available have been suggested as being important in affecting both the abundance of North Sea seabirds and their species composition. For example, kittiwakes at a colony at North Shields on the eastern coast of the UK have been monitored regularly since 1954 (Coulson & Thomas, 1985; Aebischer *et al.*, 1990). Aebischer *et al.* (1990) presented data on North Shields kittiwake lay date, clutch size and chick production from 1954 to 1987. All these variables showed parallel trends with a late laydate, high clutch size and high numbers of chicks in the late 1950s, followed by a decline to a synchronous trough around the 1979-1980 mark (Figure 2.18). These long term trends reflected those in herring, which constitutes an important prey item for kittiwakes (especially during the breeding season), suggesting that changes in food supply were the most likely cause of the changes in kittiwake breeding since the early 1960s.

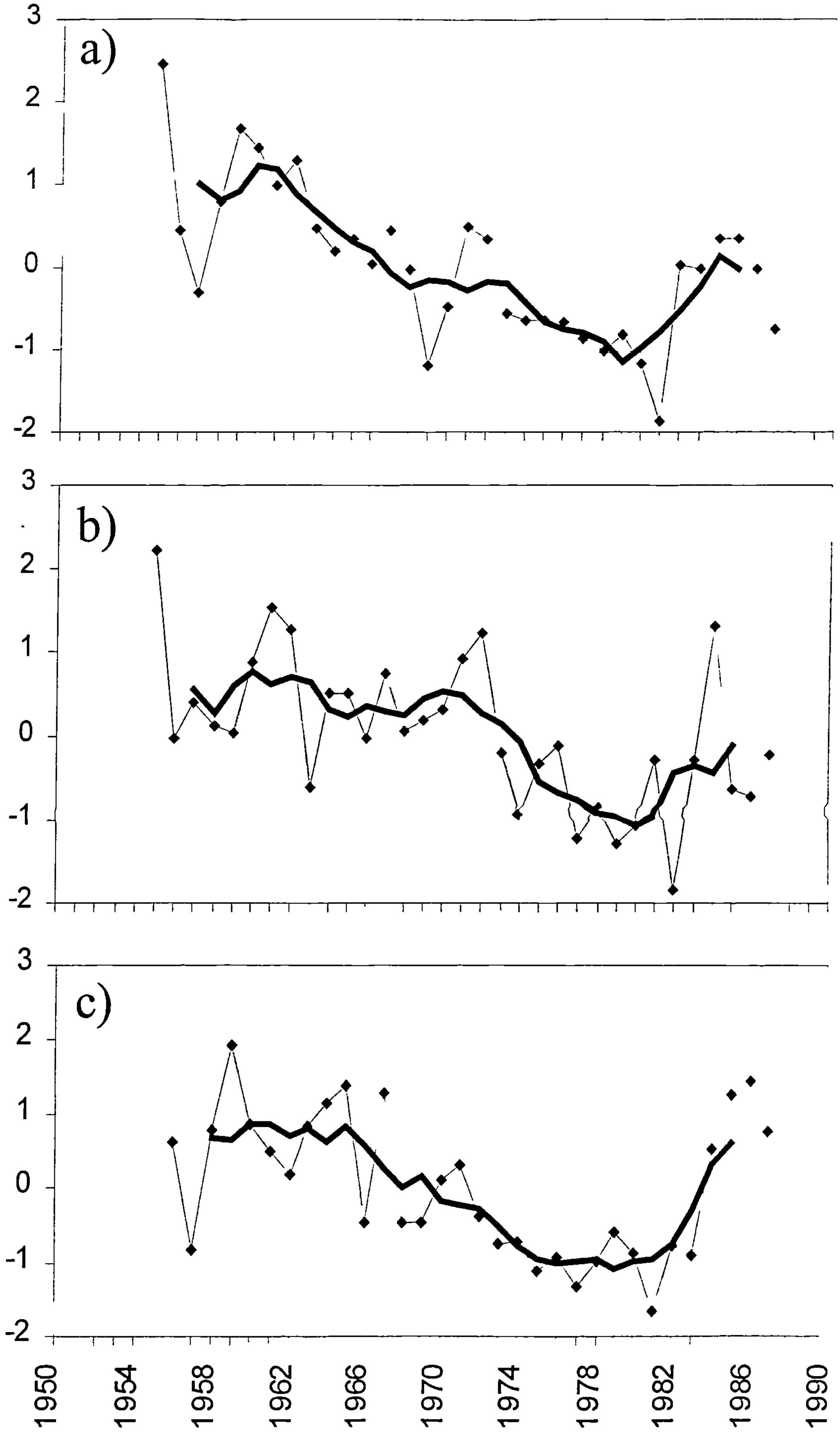


Figure 2.18 Standardised time series with 5 year running means for North Shields (NE England) a) kittiwake laydate, b) kittiwake clutch size, c) kittiwake chick production. Adapted from Aebischer *et al.* (1990).

Sandeels in particular represent an important resource for some seabird species, and thus the increase in the size of the North Sea industrial fisheries during the latter half of the 20th century has caused concern amongst conservationists because many top predators (seals, cetaceans and seabirds) rely on sandeels as the main part of their diet at some stage in their life cycle. When an industrial fishery opened near Shetland during the 1980s, the breeding success of those species that rely on sandeels was affected (Arctic terns, black-legged kittiwakes, puffins and great skuas) (Camphuysen & Garthe, 2000). However, numbers of arctic terns were observed to increase again in 1991, coincident with the appearance of a large sandeel year class, which appeared to confirm that the industrial fishery was competing for the same resource as the seabirds, and was responsible for the decline in their food supply. However, more recent analyses suggest that the decline in sandeel abundance was the result of poor recruitment to the Shetland stock, and hence natural fluctuations in sandeel survivorship were the main cause of the decline in prey availability for the Shetland seabirds (Camphuysen & Garthe, 2000).

Harris & Wanless (1997) analysed data on kittiwake numbers at a colony on the Isle of May, south-east Scotland over an 11 year period from 1986 to 1996. Over this period, breeding success was observed to decline significantly. Similar declines in breeding success were observed at sites over a 250-300 km length of coast from south east Scotland to north east England. Although it was considered that this decline in numbers could be due to changes in sandeel abundance, the decline in breeding success over the period commenced before the development of the large sandeel fishery in the area. At the Isle of May (SE Scotland), Harris & Wanless (1997) found a negative correlation between the abundance of 0-group sandeels and the breeding success of kittiwakes ($r=-0.75$, $n=9$, $p<0.05$), although the meaning of this is unclear. It may well be that stock assessments made over 1000s of km^2 have little relevance to kittiwakes, which need to feed near the colony to rear young successfully, and thus there is no association between fish stock size and the amount of fish actually available to seabirds (Camphuysen & Garthe, 2000).

However, the North Sea industrial fisheries are still causing concern, and whilst this fishery remains largely uncontrolled (excepting a closed area off the east coast of Scotland, and off Norway from 1st March to 1st October) many species of seabird are threatened. It has been suggested by ICES that the breeding success of kittiwakes could be used as an indicator of the state of sandeel stocks (Wanless & Harris, 2000). Specifically, a fishery should be closed where kittiwake success at nearby colonies falls below 0.5 chicks per pair for three consecutive years and not reopened until success reaches 0.7 for three consecutive years (Wanless & Harris, 2000).

There is no doubt that the increased amount of discards and offal produced by trawlers has benefited scavenging seabirds, by offering prey that would otherwise be unavailable for these birds. For example, the success of the northern fulmar has been attributed to its success in scavenging activities behind trawlers (Camphuysen & Garthe, 2000). However, recent work has found no relationship between the distribution of the commercial fisheries and the distribution of this species, suggesting that their natural (zooplanktonic) prey remains a much more important factor influencing their distribution. Although the northern fulmar is noted for being a notorious scavenger, the importance of this should not be overestimated as many birds disperse over vast areas of ocean, to feed on their natural prey, and effectively become invisible to observers. The reproductive output of seabirds that consume fishery waste exclusively is not very high. Hamer *et al.* (1991) found that the growth of great skua chicks at Shetland declined considerably when more of than 50% of the prey delivered by the parents were composed of discards and offal. Higher growth rates were observed when discards only measured 20-30% of the chick diet. Thus, although discards and offal are an important prey for some seabird species, they may constitute additional prey rather than staple food and are perhaps of more significance for non-breeding individuals.

Overview

Although changes in food resources, particularly increases in the amount of discards and offal produced by trawling, have benefited the seabird community, there is conflicting evidence as to whether this is the sole reason for the observed increases in abundance and spatial range of seabirds over the course of the 20th century. Similarly, the importance of the sandeel food resource to those species reliant upon them appears to be ultimately unknown, although there is circumstantial evidence to suggest that changes in sandeel abundance, either because of poor recruitment to the stock, or as a result of industrial fishing may have affected some seabird species, especially kittiwake abundances and breeding success.

Discussion

This study provides a synthesis of the long term changes in the phytoplankton, zooplankton, benthic, fish and seabird communities of the North Sea. Both the productivity of the North Sea ecosystem and the species composition of each of these communities has changed notably over the course of the 20th century. Some components of the North Sea ecosystem have increased their productivity/abundance (e.g. CPR zooplankton, Northumberland benthic Station M1, seabirds), whilst other ecosystem components have exhibited long term reductions (e.g. commercial fish stocks). Alongside these long term changes in productivity, changes have also occurred in the species composition of some of these communities. For example, there has been a general shift in the benthic community from long lived species to more opportunistic species (as detected by Schroeder & Knust, in press) in the North Sea, whilst in the fish community, surveys have shown that non-commercial species have increased, at the same time that commercial species have declined. Other observed changes have been short lived and of a temporary nature (e.g. the increase in Ceratium from 1987 to 1988, Dickson *et al.*, 1992)). Some of the long term changes have occurred in parallel. Phytoplankton, zooplankton, kittiwake breeding and herring landings show similar long term fluctuations. This has been put forward as evidence of the large scale control of the marine ecosystem (Aebischer *et al.*, 1990). However, relationships between forcing and response variables may not only be exhibited in the form of parallel trends, which suggests a direct relationship between the variables, but also as marked changes in productivity, community structure or fecundity, alongside coincident changes in environmental factors (Table 2.1). Such regime shifts may indicate a change from one stable ecosystem state, with a certain community structure and level of productivity, to another state, forced from one state to another by changes in environmental factors.

Ultimately, the data presented here suggest that the majority of long term changes in the North Sea ecosystem are related to changes in external environmental factors. Generally, on a North Sea scale, climatic factors and eutrophication (surplus of nutrients) appear to be primarily responsible for many of the long term changes in the North Sea, with the signal being transferred via the food chain to higher trophic levels (i.e. bottom up control). However, there are exceptions to this, as other factors such as competition, predation, and anthropogenic impacts have also been found to play a role in governing the long term dynamics of parts of the ecosystem.

Table 2.1 Summary of points of change identified in this review.

Year(s)	Description of the change	Suggested reason for change	Source
c.1963-1973	Gadoid outburst	Climatic change (?)	Hislop (1996)
1977	Herring and mackerel stocks collapsed	Overfishing	Serchuck (1996)
1979	Phytoplankton seasonal cycle exhibited increased peaks (C1)	Climatic change	Evans & Edwards (1993)
c.1980	Nadir in kittiwake breeding	Climatic change	Aebischer *et al.* (1990)
c.1980	Nadir in North Sea CPR phytoplankton index	Climatic change	Aebischer *et al.* (1990); CPR Survey Team (1992)
c.1980	Nadir in North Sea CPR zooplankton	Climatic change	Aebischer *et al.* (1990)
1980	Nadir in Northumberland holoplankton	Climatic change	Evans & Edwards (1993)
1979-1980	Change in Northumberland holoplankton community structure	Climatic change	Evans & Edwards (1993)
1979-1980	Change in central-east North Sea zooplankton community structure	Climatic change	Austen *et al.* (1991); Evans & Edwards (1993)
1979-1980	Biomass at Balgzand tidal flats suddenly increased	Increased food supply (indirectly climatic)	Beukema (1992a)
1980-1981	Increase in abundance at Northumberland Station M1	Increased food supply (indirectly climatic)	Buchanan *et al.* (1986)
1980-1981	Increase in abundance at Northumberland Station P	Possibly increased food supply	Austen *et al.* (1991); Buchanan (1993)
1980-1981	Change in community structure at Northumberland Station P	Increased food supply (climate)	Austen *et al.* (1991)
1980-1981	Increase in abundance at 100m Skaggerak station	Increased food supply	Austen *et al.* (1991); Josefson *et al.* (1993)
1980-1981	Change in community structure at 100m Skaggerak station	Increased food supply (indirectly climatic or eutrophication)	Austen *et al.* (1991)
1980-1981	Change in community structure at Norderney	Severely cold winters	Dörjes *et al.* (1986)
1986	Decline in abundance at Northumberland Station P	Increased trawling in the *Nephrops* ground	Frid *et al.* (1999); Frid & Clark (2000);

Establishing what factors are responsible for these changes is not simple due to the multitude of factors which affect the system. Much of the evidence presented on relationships between environmental and biotic time series is correlational in nature, with all of the associated statistical problems that this entails (Jassby & Powell, 1990; Underwood, 1990; Underwood, 1992; Underwood, 1996). Sometimes, the predicted responses to a particular effect are similar. For example, the predicted effects of changes in climate, nutrient increases and the effects of trawling are the same; there is a shift from larger, long lived species to smaller, opportunistic species (Tuck *et al.*, 1998). However, the presence of a viable mechanism, in addition to a weight of evidence, does increase confidence that a correlation between an environmental and an ecological variable is genuine.

A further problem is that both the quantity and quality of ecological time series data is often not up to the task of establishing how a whole ecosystem functions in response to large scale climatic variables. Unfortunately, due to the volatile nature of government based scientific funding, long term biological studies rarely reach a decade in length (Dickson, 1995), and in some cases, the data have a limited spatial coverage, particularly for the benthic community. There may also be a large range of responses to both internal and external factors due to the equally large diversity of factors which impinge on a community and the large diversity of life cycle strategies within that community. Thus, at coarse taxonomic resolutions, the diversity of individual responses by the variety of taxa to environmental factors may mean that relationships between the biota and environmental factors are obscured.

Considering all the evidence examined, it is suggested that there are two large scale factors driving long term changes in the ecosystem (Figure 2.19). The first factor is climatic, and drives pelagic and benthic communities in those areas of the North Sea which are principally influenced by Atlantic inflow (central, northern and western areas). In contrast, in the North Sea bights and Danish coastal areas, dynamics are more driven by the second factor, changes in nutrient concentrations (Figure 2.19). Thus, although the availability of nutrients/food are important throughout the North Sea, changes in climate dominate in the central, northern, and western areas, whereas in the southern, tidally mixed regions of the North Sea, changes in nutrient concentrations are of sufficient magnitude to dampen and obscure climatic effects upon the marine community.

Over most of the North Sea, primary productivity is meteorologically controlled as suggested by the model of Dickson *et al.* (1988a), with the timing of stratification of the water column and the resulting spring bloom being crucial to in determining the extent of primary productivity during a particular year. In the southern areas of the North Sea it is the combination of the strong tidal flows which prevent stratification (and therefore the model of Dickson *et al.* is not applicable) and the input of nutrients that modifies the role of climate upon primary production.

Whilst primary production is governed by the combined influence of climatic factors and nutrient supply, the major factor influencing secondary and greater levels of productivity (i.e. the benthic and zooplanktonic communities and fish recruitment) is fluctuations in food supply. Zooplankton and benthos obtain most of their energy sources from the consumption of primary production (as evidenced by the CPR data and the Northumberland, Skagerrak and Balgzand benthic stations), whilst fish recruitment is influenced by fluctuations in the timing and biomass of secondary productivity as suggested by Cushing (1990). Thus, the higher trophic levels are indirectly forced by changes in climate and nutrients (c.f. Aebischer *et al.*, 1990) (Figure 2.19).

There are however variations on these two large scale mechanisms upon individual communities; direct climatic effects (other than that on primary production), intra/interspecific effects and anthropogenic impacts also affect the long term dynamics of the North Sea ecosystem, although over a long term basis they are of secondary importance. For example, temperature has been found to directly influence the distribution and abundance of some marine species on a annual (e.g. Calanus spp., Fromentin & Planque, 1996) or a decadal time scale (e.g. herring and pilchards, Russell *et al.*, 1971). Additionally, although there are likely to be direct effects of temperature on the growth rate of poikilothermic species (e.g. Kleppel *et al.*, 1996) mortality rates are also likely to be strongly moderated by low temperatures, particularly over the winter for the littoral benthos (as observed at the Balgzand tidal flats by Beukema, 1985).

The period of the seasonal cycle through which environmental variables actually affect the system appears to be crucial to the functioning of the whole ecosystem. For example, the spring sea temperatures and wind speeds are crucial to the timing of thermocline formation (Dickson *et al.*, 1988a) and therefore the amount of production available during that year and fish recruitment are more affected by the timing of food supply during the spring (match-mismatch hypothesis) rather than the amount available (Cushing, 1990). Other systems may be less affected by the timing of the food supply (e.g. the benthic community (Graf *et al.*, 1984) – although this is likely to benefit from additional food sources at the start of the summer growth period compared to the winter). However, it is the processes occurring during the spring period of the year and the timing of spring itself which appears to be of crucial importance to all these communities and indeed to the dynamics of the whole ecosystem.

In some communities, interspecific factors such as competition and predation, also play a major role in mediating environmental influences through to some species. The impact of the chaetognath *Sagitta* upon the juveniles of the small copepods appears to be a major specific factor controlling the long term dynamics of the Northumberland zooplankton community. The period of the seasonal cycle when such biotic interactions occur also appears to be of crucial importance – the impact of *Sagitta* appears to be critical during the spring period, when it is also the most dominant zooplankton predator.

Human impacts influence all the communities examined in this review to a greater or lesser extent. The ecosystem of the southern North Sea is influenced by anthropogenic nutrient inputs from the continental rivers, whilst the cumulative effect of trawling and the transfer of fish biomass to the land also have widespread effects. Although trawling has the most widespread impact on the benthic ecosystem (Jennings *et al.*, 2000), the pelagic ecosystem may also be affected through increased amounts of nutrients released from the sediment through trawling. However, most of the other anthropogenic impacts on the marine community are limited to small spatial areas (e.g. hypoxia, fly ash, sewage sludge dumping), and, following cessation of the impact, recovery may occur within a few years (e.g. anoxia) or number of decades (e.g. fly ash Herrando-Perez & Frid, 1998).

Despite the high complexity of the North Sea ecosystem, and the lack of more established associations between internal variables, the weight of evidence suggests that long term changes in the North Sea ecosystem are ultimately related to long term changes in climate or nutrient concentrations. Other anthropogenic factors do influence the system, both in terms of productivity and species composition, yet in terms of the long term, large scale functioning of the North Sea ecosystem, these are of lesser importance.

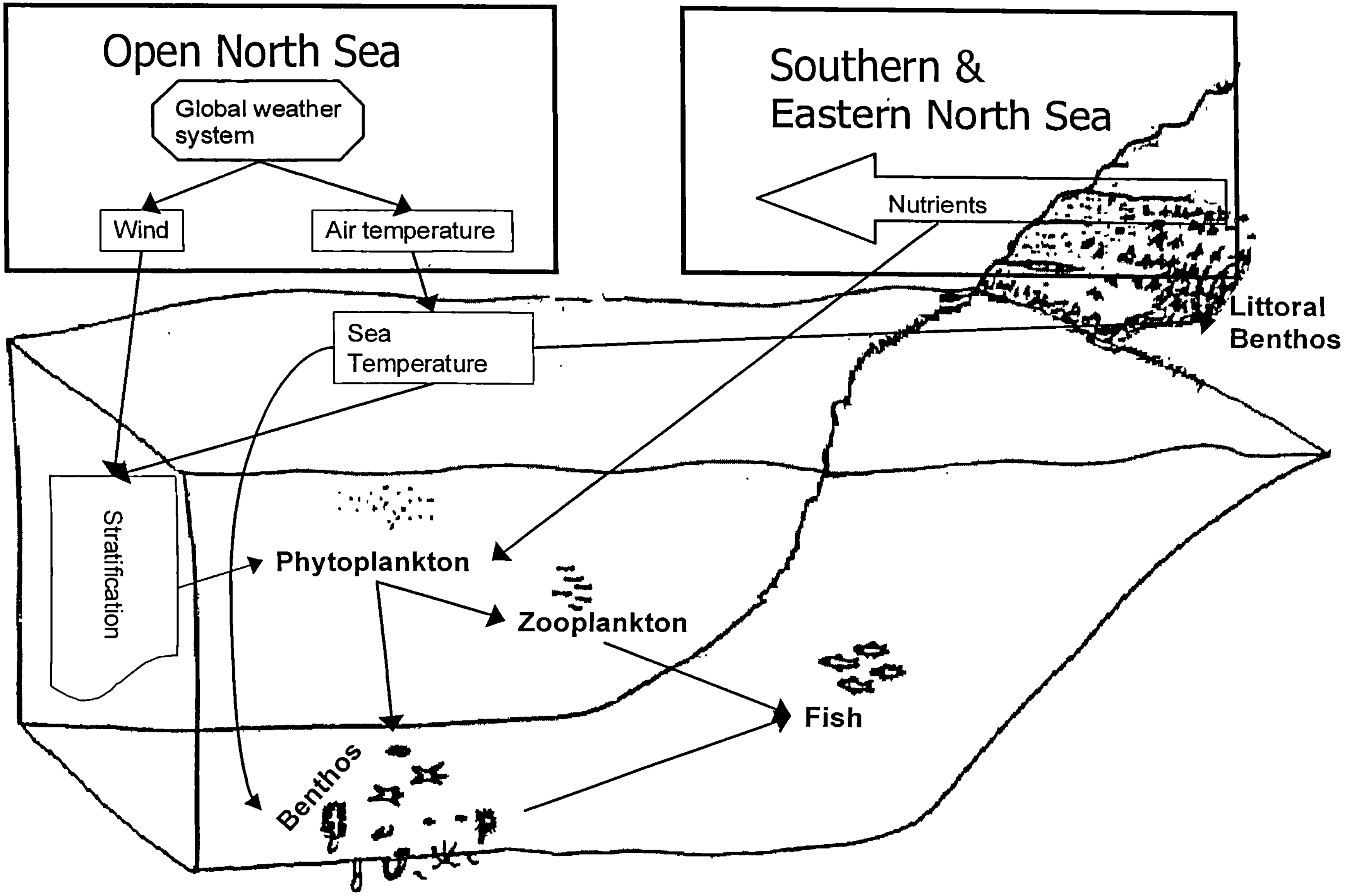


Figure 2.19 Model of the main trophic and abiotic links present in the North Sea ecosystem.

Chapter 3 A critical comparison of two long term zooplankton time series from the central-west North Sea

Introduction

Long term studies of ecosystems have been used in all branches of ecology (Jassby & Powell, 1990), and have provided invaluable information about the natural fluctuations of species and communities, and the possible causes of these fluctuations. However, theories formed from analyses of such data are only valid if any artefacts introduced by the sampling and counting methodology are fully considered.

Estimating the abundance of planktonic organisms is a difficult but crucial problem, yet there is surprisingly little recent research on the accuracy and efficiency of commonly used plankton samplers. Accuracy of sampling may be hampered by a number of factors, including; the patchiness of plankton distribution (Wiebe & Holland, 1968), changes in the filtering efficiency of the net through clogging of the mesh (Saville, 1958; UNESCO, 1968; Brander *et al.*, 1993), and by the extent that zooplankton organisms are able to sense the sampler as it approaches (Fleminger & Clutter, 1965; UNESCO, 1968; Filion *et al.*, 1993). Approaching plankton samplers have been likened to an advancing predator and therefore are prone to inducing the same escape response (Singarajah, 1969). Such avoidance reactions have been known about for some time; as long ago as 1910, Fransz suggested that plankton animals capable of sensing an approaching plankton net would attempt to avoid capture (UNESCO, 1968).

The Continuous Plankton Recorder (CPR) survey was initiated during the 1930s using the Hardy plankton sampler (Figure 3.1), a high speed plankton sampler designed to be towed from commercially operated "ships of opportunity" over long distances. However, it is only since 1948 that the zooplankton sampling method has remained unchanged, and methodological changes during the early years of sampling mean that problems occur when comparing data collected before 1948 with that collected afterwards. Since 1948, CPRs have sampled on a monthly basis over several routes in the North Atlantic and North Sea (Warner & Hays, 1994), constituting the longest and most geographically widespread marine ecological dataset in existence. These data

Huliselan, 1996), and parallel shifts in community structure with the benthos and fish populations (Pearce & Frid, 1999).

Despite the application of the Dove and especially the CPR data in many temporal (and in the case of the CPR, spatial) investigations of zooplankton dynamics, there has been little work on actually assessing the suitability or quality of either time series for such studies, although the consistency of the CPR data over the past 50 years has been questioned on occasion (Hays *et al.*, 1993; Hays & Warner, 1993; Hays, 1994). It could also be argued, for instance, that such time series are unlikely to be consistent due to changes in taxonomists over the years of operation. It is also not known whether the method of assembling CPR time series from a large spatial area may be problematic given the potential spatial differences in zooplankton communities sampled from such wide areas. This study will compare the long term trends and species composition taken from the Dove permanent station and CPR zooplankton time series from the central-west North Sea area (Figure 3.2), alongside knowledge of their different sampling and processing methodologies (see Table 3.1). This comparison therefore increases the understanding of the Dove and CPR datasets as well as highlighting potential problems which need to be considered in future use of these extending time series.

Table 3.1 Sampling parameters for the WP2, WP3 and Hardy plankton recorder

Parameter	Dove (WP2)	Dove (WP3)	Hardy plankton recorder
Mesh size	0.200 mm	1 mm	0.270 mm
Mouth diameter	0.56m	1.13m	0.0179m (area = 0.0127m^2)
Length of sample	200m	1 236m	18 520m
Volume of water sampled	28 000 litres	1 236 000 litres	3 000 litres
Approx. speed of gear	1.25m/s	2.06m/s	6.69m/s
Time taken for sample	3min 20s	10min	46min 8s

Study site and methods

Programme backgrounds and sampling methodologies

Continuous Plankton Recorder time series

The Hardy plankton recorder (Figure 3.1) is deployed from a 'ship of opportunity' some distance from the coast when the water depth is enough to accommodate the device (at least 10m). Water enters the Hardy recorder through the 1.27cm^2 entrance aperture and passes through a silk filtering mesh (mesh size 270μm, Table 3.1) (Warner & Hays, 1994). The movement of the device through the water turns an external propeller which moves the silk across the internal tunnel at a rate of 10cm per 10 nautical miles. As it leaves the tunnel, the filtering silk is covered by a second band of silk so that the plankton are sandwiched between these two layers. This sandwich then moves into a storage tank containing formaldehyde. On return to the laboratory, and from the position that the recorder was deployed and recovered, silks are divided into blocks corresponding to 10 nautical miles of tow. Zooplankton and phytoplankton species are then counted in alternating 10 nautical mile blocks (Warner & Hays, 1994). It is regarded that each 10 nautical miles block refers to 3 m^3 of water filtered by the device, although due to variations in filtration efficiency, the volume of water filtered may actually vary between 1 and 4 m^3 per sample.

Continuous Plankton Recorder data between 1969 and 1996 were obtained for a triangular area in the central-western North Sea between the Firth of Forth SE Scotland (56°05'N 2°40'W), Flamborough Head NE England (54°07'N 0°04'W) and approx. 120 km offshore (56°05'N 0°04'W) (see Figure 3.2). The dimensions of the area chosen were to be as small as possible so as to be as comparable with the Dove permanent station, yet including enough sampling points to give a reasonable monthly resolution. Hydrography was also considered in that Flamborough Head is considered to be a frontal boundary (Mann & Lazier, 1991).

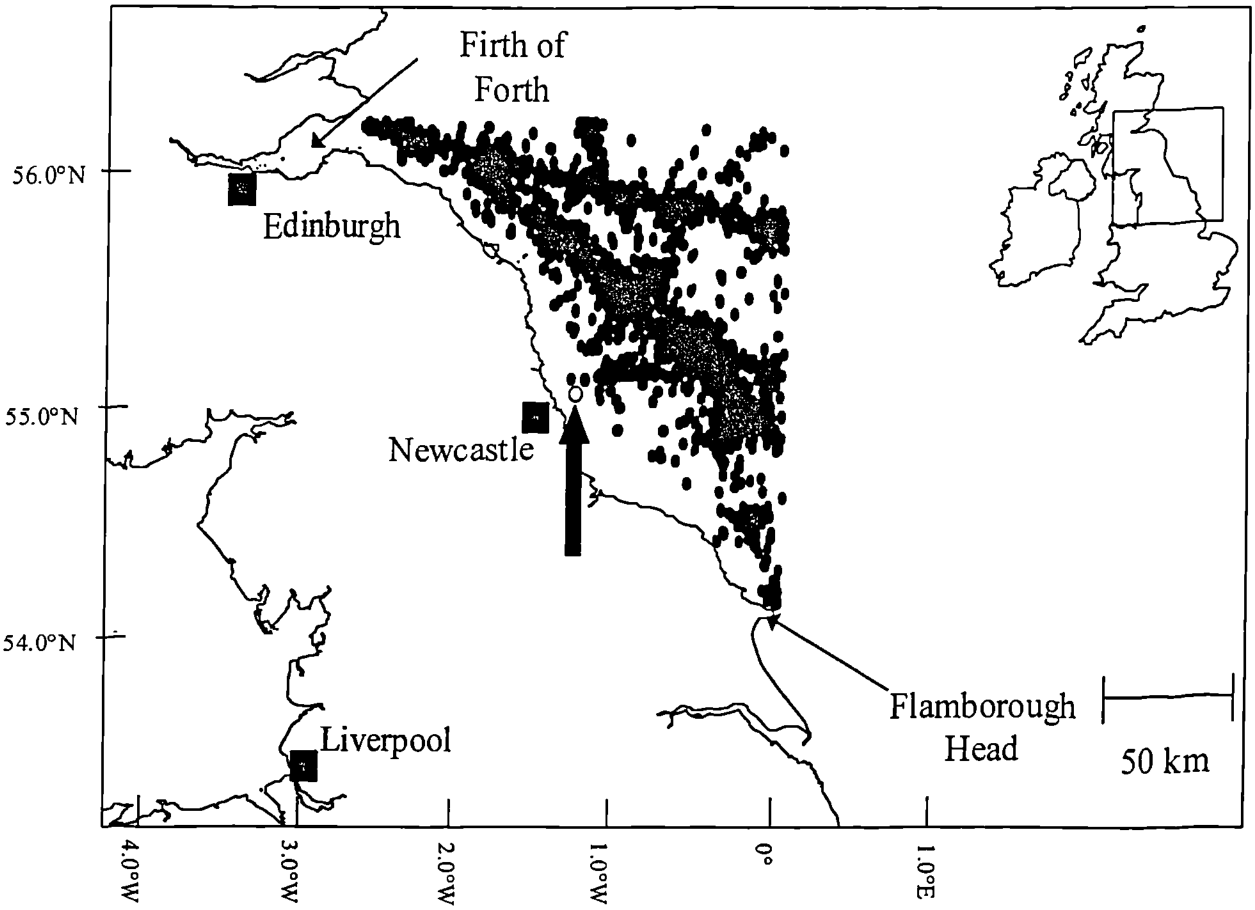


Figure 3.2 **Map of northern England (inset Great Britain) showing the location of each single CPR sampling point used in these analyses (●) and the Dove Permanent zooplankton station (○) highlighted by the broad arrow**

Dove Marine Laboratory time series

Zooplankton sampling by the Dove Marine Laboratory was initiated at a station approx. 5.5 nautical miles east of Blyth on the Northumberland coast at 55°07'N 01°20'W in August 1968 (Figure 3.2). Sampling has taken place on a monthly basis except in 1989 when no samples were taken. Sampling consisted of four vertical hauls from 50m to the surface (water depth approximately 54m) which were pooled to give a sample equivalent to a 200m water column, using a 200µm meshed WP2 net (UNESCO, 1968) with a mouth diameter of 0.56m (Table 3.1). In addition, a 10 min. horizontal trawl at approx. 30m depth was taken using a 1mm meshed WP3 net with a 1m mouth diameter (UNESCO, 1968). Sampling methodology remained unchanged throughout the period, although since May 1973 a flowmeter has been mounted in the mouth of each net to allow determination of the exact volume of water filtered. The zooplankton catch from each net was immediately preserved in 4% buffered formaldehyde in sea water. On return to the laboratory, zooplankton were identified to species level where possible, and abundances determined. The abundance of each taxa was derived, according to its size, from either the WP2 or the WP3 net (see Evans 1993, for rationale). Certain taxa were further subdivided into sexes, or were categorised as juveniles and adults.

Initial data manipulations

Zooplankton taxa in the Dove monitoring programme were generally identified to a higher taxonomic resolution than in the CPR programme. Taxonomic resolution was standardised to the lowest level which allowed a direct comparison to be made between the two time series (Tables 3.2 a & b). Following this, the number of entities used in the analysis was 40, with the Dove zooplankton being reduced from a total of 62 entities and the CPR zooplankton reduced from 47 entities. These aggregated taxonomic categories were used for all analyses, except total zooplankton, which refers to the total abundance of individuals, per m^3, recorded in the original dataset, including those taxa which are only present in one of the series. Data for months missing in the CPR series were linearly interpolated from adjacent months. However, due to the large number of missing months in 1978 and 1979, these years have been omitted where annual data were required for the analysis. Where calculations were based on monthly data then these years were included. All calculations were performed on abundances.m^{-3}.

Table 3.2a Taxonomic aggregations performed on Dove taxa to generate taxa to allow comparison to be made with taxa in the CPR series. Only those taxa which required aggregation are shown

Dove taxa	Species Code
Acartia clausi	*Acartia* spp.
Acartia longerimis	
Acartia spp.	
Fritillaria borealis	Appendicularia
Oikopleura diocia	
Anomuran juv.	Decapoda larvae
Brachyuran juv.	
Caridean juv.	
Decapoda juv.	
Nephrops norvegica	
Pisidia longicornis	
Bipinnaria juv.	Echinoderm larvae
Echinoderm juv.	
Echinoplutei juv.	
Ophioplutei juv.	
Euphausiid spp.	Euphausiacea spp.
Meganyctiphanes norvegica	
Nyctiphanes couchi	
Thysanoessa inermis	
Thysanoessa raschi	
Hyperia galba	Hyperiid amphipoda
Hyperoche medusarum	
Themisto gaudichaudi	
Oithona plumifera	*Oithona* spp.
Oithona similis	
Autolytus spp.	Polychaeta larvae
Polychaete larvae	
Tomaria larvae	
Muggiaea spp.	Siphonophora
Nanomia cara	

Table 3.2b Taxonomic aggregations performed on CPR taxa to generate taxa to allow comparison to be made with taxa in the Dove series. Only those taxa which required aggregation are shown

CPR taxa	Species Code
Acartia spp.	*Acartia spp.*
Acartia longerimis	
Calanus stages I-IV	*Calanus* spp.
Calanus stages V-VI	
Candacia armata	*Candacia* spp.
Candacia stages I-IV	
Chaetognatha Eyecount	Chaetognatha
Chaetognatha Traverse	
Decapoda larvae	Decapoda larvae
Sergestidae	
Echinoderm larvae	Echinoderm larvae
Echinoderm post-larvae	
Atlanta spp.	Gastropod larvae
Limacina retroversa	

Numerical analyses

Comparison of year to year and seasonal fluctuations.

The similarity in year to year fluctuations and mean seasonal cycles between the two time series were compared using plots of standardised (zero mean and unit variance) annual means and $\log_{10}$ monthly abundances of total omnivores and total predators respectively.

Comparison of overall and year to year changes in community structure

In order to determine the degree of resemblance of the extent of year to year changes in community structure (i.e. distribution of individuals between taxa) between the two time series, these were compared using calculated Bray-Curtis similarity indices, for each time series and displayed using MDS ordinations. "Relate" (in the PRIMER package – "Plymouth Routines In Marine Ecological Research" (Clarke & Warwick, 1994)) was used to compare the multivariate patterns observed in the two monitoring programmes (using 5000 permutations). The significance level obtained gives the probability of "no relation" in the two multivariate patterns (Clarke & Warwick, 1994).

Year to year fluctuations in individual taxa

Year to year fluctuations in dominant taxa, those contributing, on average more than 1% to the total abundance, were correlated to determine which taxa in the two time series were displaying good synchrony through time. Due to multiple comparisons, a global significance level was applied to the table of results calculated from the binomial distribution.

Comparison of absolute abundances

To assess the presence of any similarity in abundances between the two time series, annual mean abundances of total zooplankton for each time series were compared graphically. To enable a taxa by taxa comparison of the abundances, the ratio between the Dove and the CPR abundance was calculated from the annual means of each of the dominant taxa.

Examination of regional differences

To assess whether there were any differences in the community structure (distribution of species abundance) and total zooplankton abundances of the CPR and Dove time series which could be attributed to the sampling of different geographical areas with different zooplankton communities, CPR samples from an area adjacent (within 0.2° latitude & longitude) to the Dove permanent station, and those from a block in the most distant part of the area considered in this study (between 56.05°N, 0.25°W to 55.90°N, 0.04°W) were compared. Data were extracted from the Dove permanent station data set to give a temporally matched (same month) series for comparison to the CPR data.

Total abundance of zooplankton for each date was graphically compared between CPR and Dove data. Community structure was examined through calculation of Bray-Curtis similarity indices with a $\mathrm{Log}_{10}+1$ transformation with the abundances of each of the four sets (CPR adjacent, CPR distant and the two temporally matched series from the Dove set). Samples were standardised (zero mean and units variance) and plotted using MDS ordination.

Examination of the CPR category counting system

In order to observe the effect of the category counting system employed by the CPR survey on estimates of zooplankton abundance, the system was applied to seven *a priori* selected taxa in the Dove zooplankton series. The taxa were selected to cover a wide variety of body sizes and morphologies. These were; *Acartia*, *Calanus*, *Evadne*, *Oithona*, *Pseudocalanus*, *Sagitta* and echinoderm larvae. The category counting system was applied following Warner & Hays (1994) to obtain the "accepted midpoint" value. The estimated abundances were then calculated from the samples and compared to the observed abundances. A statistical comparison of the actual and estimated abundances would be invalid due to non-independence of the two data sets, although standard errors were examined. Under a null hypothesis of no consistent bias, it would be expected that half of the estimated abundances would be above the actual means and half below. The probability was calculated for obtaining the observed distribution of differences under the null hypothesis (binomial distribution).

Estimation of zooplankton avoidance

The theoretical effectiveness of towed samplers is a complex problem in analytical geometry (UNESCO, 1968). Catching efficiency (defined as "the proportion of individuals caught in the sampling device (C_i), out of the total number of individuals in the path of the sampler (N)") was calculated for each of the three different types of gear (Hardy plankton recorder, WP2 net, WP3 net), and plotted against K (the avoidance parameter). K is the product of the distance at which an individual detects the approaching sampler, and the escape speed of the individual. Thus, an individual which detects the sampler at a long distance, but has a slow escape speed could have the same value of K as an individual with a short detection distance but high escape speed.

$$\frac{C_i}{N} = \left[\frac{R - \frac{K}{S_i}}{R} \right]^2$$

(taken from (UNESCO, 1968))

Where; S_i = towing speed (in m.s^{-1}); C_i = actual catch at speed, S_i (in m^{-1}); N = no. of individuals in sampler path; and thus C_i/ N = proportion of individuals in front of sampler which are caught; K (the avoidance parameter) = detection distance (m) x mean escape speed (m.s^{-1}); R= net / entrance radius (m). Towing speeds were 1.5 m.s^{-1} for the WP2 gear, 2.06 ms^{-1} for the WP3 gear and 6.69 m.s^{-1} for the Hardy plankton recorder. Entrance radii values are as follows; 0.28m for the WP2 gear, 0.565m for the WP3, and 0.00898m for the Hardy plankton recorder (calculated as half the diagonal of a 1.27cm^2 entrance aperture). This overestimates the size of the aperture, but for the purposes of assessing plankton avoidance from the model this approach was the most conservative.

At high values of K, and using the low entrance apertures found in the Hardy recorder, the model breaks down when catching efficiency may be calculated to be below zero. Therefore any calculations where the catching efficiency was calculated as being less than zero were constrained to zero. It should also be remembered that the model refers to a towed "conical net" whereas here it is being applied it to a high speed sampler with a large body to aperture size which is likely to produce different hydrological, acoustic and visual stimuli.

Results

Comparison of relative fluctuations and community structure

The two standardised time series of total zooplankton abundance show a good agreement in their year to year fluctuations (r=0.64, p<0.001) (Figure 3.3a). However, a few years do exhibit notable differences, with 1975 and 1981 having a *relatively* higher abundance in the Dove time series compared to the CPR. Conversely, 1976 and 1985 were *relatively* high abundance years in the CPR in contrast to the Dove time series. The mean seasonal cycle of total omnivores in the two time series also displays good agreement (Figure 3.3b). In both the Dove and CPR time series the start to the productive season begins in February-March and peaks in June. Seasonal cycles of total predators display less similarity (Figure 3.3b), although they show a parallel increase from April to May and decrease from October onwards.

In the Dove and CPR series 13 taxa occur at a mean abundance of 1% or more of the individuals in a sample and these represent, on average, over 95% of the individuals taken (Tables 3.3 a & b). Nine of the dominant taxa were common to both series and 6 were ranked in the same order. The most marked differences were, the position of *Oithona* (ranked 2 in the Dove and 7 in the CPR) and of echinoderm larvae (ranked 2 in the CPR and 10 in the Dove series).

A comparison of the multivariate pattern of community change in species composition through time using "Relate" (Clarke & Warwick, 1994) from 1969 to 1996 found that there was no significant agreement in the pattern between the two time series (probability of no relation = 15.1%). However, the years 1980-1982 in the CPR series were quite distinct from the remainder of the series, due to a very low abundance of *Acartia* in these years (see Figure 4.5a). Removal of these years and re-analysis ("Relate") revealed a good agreement (probability of no relation = 1.0%) in the pattern of year to year changes of species composition within each of the two time series (Figure 3.4a & b), suggesting that the pattern of community composition change was similar.

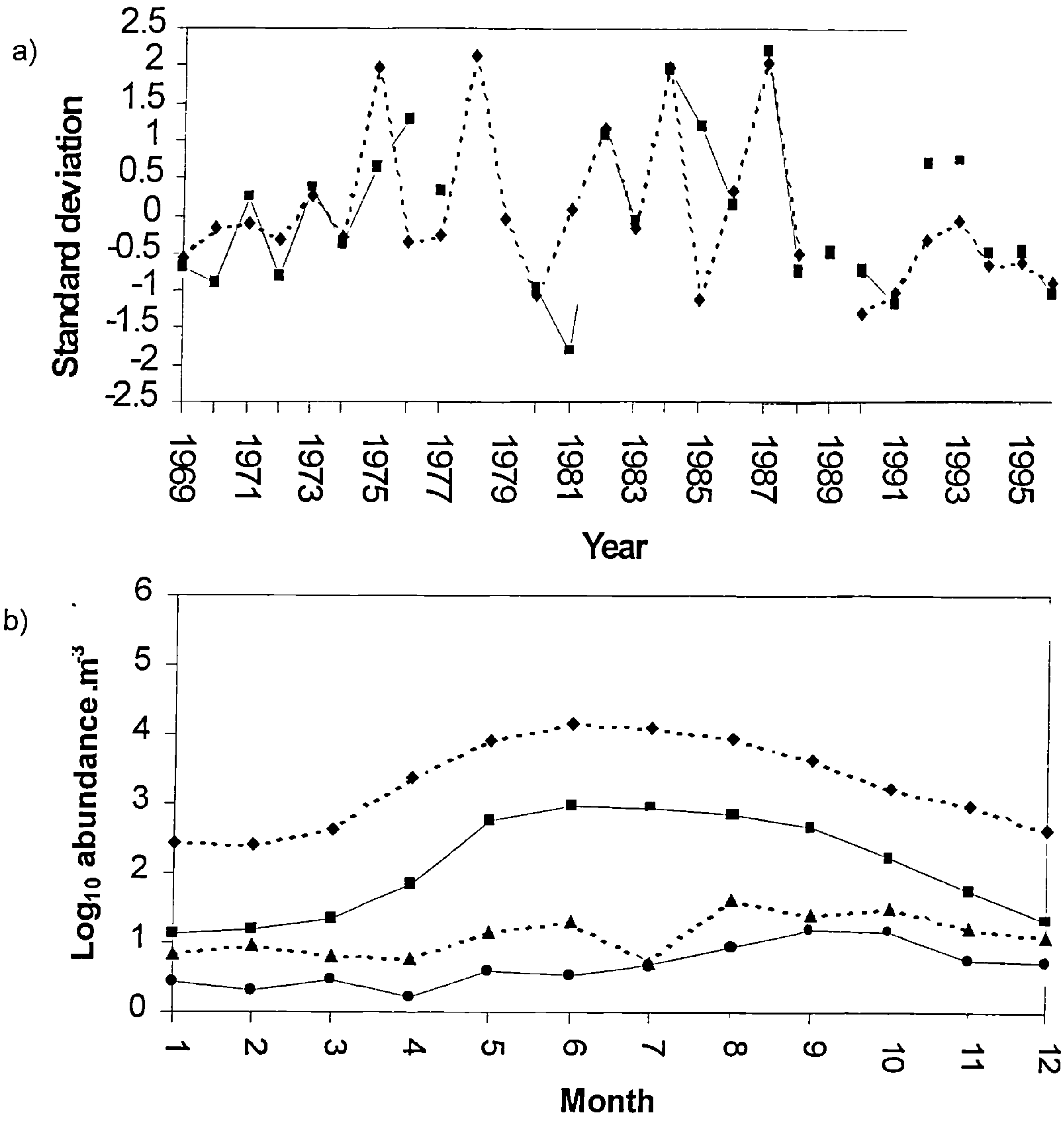


Figure 3.3 a) Annual mean total zooplankton abundance for the Dove and CPR time series. Abundances are standardised to zero mean and unit variance. —◆— Dove series; —■— CPR series. b) Monthly mean log$_{10}$ abundance.m^{-3} for CPR and Dove zooplankton omnivore and predator totals (see text for definitions). Standard errors have been omitted for clarity. —◆— Dove omnivores; —▲— Dove predators; —■— CPR omnivores; —●— CPR predators.

Table 3.3a Mean abundances and proportions of dominant taxa in the Dove zooplankton. Only those taxa representing at least 1% of the total abundance are included

Rank	Dove taxa	Dove mean abundance/m^3	Mean proportion (%)	Cumulative %
1	*Acartia* spp.	1194.72	27.53	27.53
2	*Oithona* spp.	916.1	23.07	50.6
3	*Pseudo-/Para-/Microcalanus* spp.	836.37	15.7	66.3
4	*Evadne* spp.	456.99	8.62	74.92
5	*Temora longicornis*	287.93	5.87	80.79
6	*Pseudocalanus elongatus* Adult	153.59	4.14	84.93
7	Appendicularia	129.71	3.02	87.95
8	Bivalve larvae	74.1	1.91	89.86
9	Echinoderm larvae	59.01	1.58	91.44
10	Cirripede larvae	62.56	1.55	92.99
11	*Calanus* spp.	54.23	1.48	94.47
12	Polychaeta larvae	35.22	1.01	95.48

Table 3.3b Mean abundances and proportions of dominant taxa in the CPR zooplankton. Only those taxa representing at least 1% of the total abundance are included.

Rank	CPR taxa	CPR average mean/m^3	Mean proportion (%)	Cumulative %
1	*Acartia* spp.	90.31	25.50	25.45
2	Echinoderm larvae	53.24	15.5	40.95
3	*Pseudo-/Paracalanus* spp.	52.8	14.79	55.74
4	*Calanus* spp.	19.41	8.8	64.54
5	*Evadne* spp.	25.17	6.46	71
6	*Temora longicornis*	23.46	6.15	77.15
7	*Oithona* spp.	19.27	5.63	82.78
8	*Pseudocalanus elongatus* Adult	13.29	3.45	86.23
9	Appendicularia	12.89	3.15	89.38
10	Gastropod larvae	5.99	1.99	91.37
11	*Podon* spp.	6.4	1.73	93.1
12	Chaetognatha	3.99	1.33	94.43
13	*Centropages typicus*	5.02	1.29	95.72

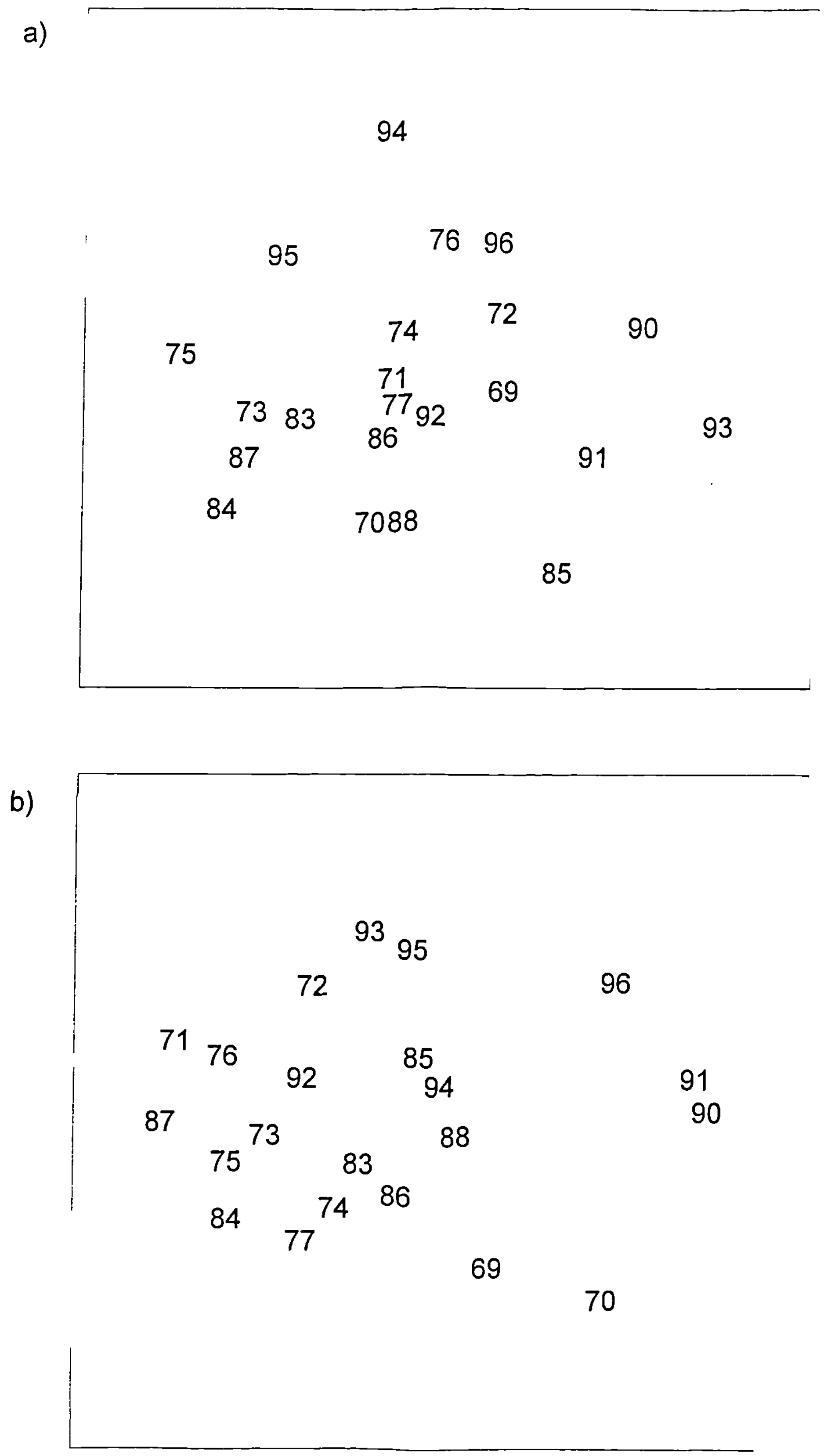


Figure 3.4 MDS plot produced after calculation of Bray-Curtis similarity index on $Log_{10}+1$ transformed data from annual means covering the years 1969-1977, 1982-1988 & 1990-1996 from a) Dove zooplankton (MDS stress value=0.18), b) CPR zooplankton (MDS stress value=0.13). N.B. Years 1981 & 1982 have been omitted from both plots. Refer to text for explanation.

Five of the dominant taxa were found to display significant correlations in relative abundance between the two time series (Table 3.4). However, there was no apparent pattern to the strength of correlation with phylogeny (i.e. taxonomic group) or with absolute abundance of taxa in the time series. Of the 40 taxa analysed, 9 showed significant correlations between the Dove and CPR time series and these taxa accounted for 38.6% and 36.0% of the individuals in the two series respectively.

Table 3.4 Correlation coefficients between comparable taxa in the Dove and CPR time series. Only those taxa representing at least 1% of the total abundance are included. Significant correlations are in bold. Global $p=0.001$.

Taxa	r	p
Acartia spp.	0.30	0.147
Oithona spp.	0.146	0.485
Pseudo-/Para-/Microcalanus spp.	0.567	0.003
Evadne spp.	0.412	0.041
Temora longicornis	0.785	0
Pseudocalanus elongatus Adult	0.281	0.173
Acartia longiremis	0.369	0.07
Appendicularia	-0.2	0.338
Bivalve larvae	0.523	0.007
Echinoderm larvae	-0.005	0.983
Cirripede larvae	-0.149	0.478
Calanus spp.	0.428	0.033
Polychaeta larvae	0.088	0.677
Gastropod larvae	-0.011	0.957
Podon spp.	0.338	0.098
Chaetognatha	0.197	0.346
Centropages typicus	0.207	0.321

Comparison of absolute fluctuations in abundance

Although there was a good agreement in the scale of year to year fluctuations in total abundance, in the pattern of the seasonal cycle, in the species composition over the whole time series and the pattern of community change through time, there were marked differences in the absolute abundances recorded by the two series (Figure 3.5). The Dove monitoring programme caught approximately 15 times as many individuals as the CPR over the whole time series, with a mean abundance of c. 4500 individuals.m^{-3} compared to 293 individuals.m^{-3} in the CPR series.

Investigation into discrepancy in abundances

There was no distinct difference in the species composition of the CPR samples taken adjacent to and remote from the Dove Permanent Station (Figure 3.6a). The species composition of the Dove samples were ordinated amongst those from the CPR taken at the same time and from both areas. However, there were still higher abundances of zooplankton observed in the Dove series when Dove samples on a particular date were compared with temporally matched samples located both near to and far from the Dove permanent station (Figure 3.6b & c). This suggests that the dissimilarities in abundance were not due to the wider geographic coverage of the CPR dataset.

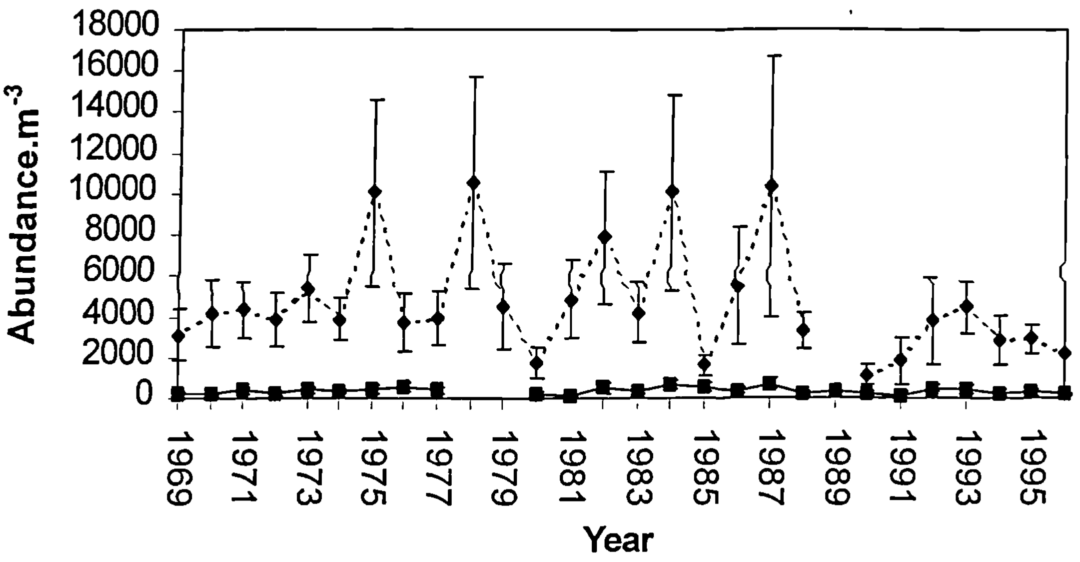


Figure 3.5 Annual mean total (± SE) zooplankton abundance (ind.m^{-3}) for the Dove and CPR time series. (—◆—) Dove series; (—■—) CPR series.

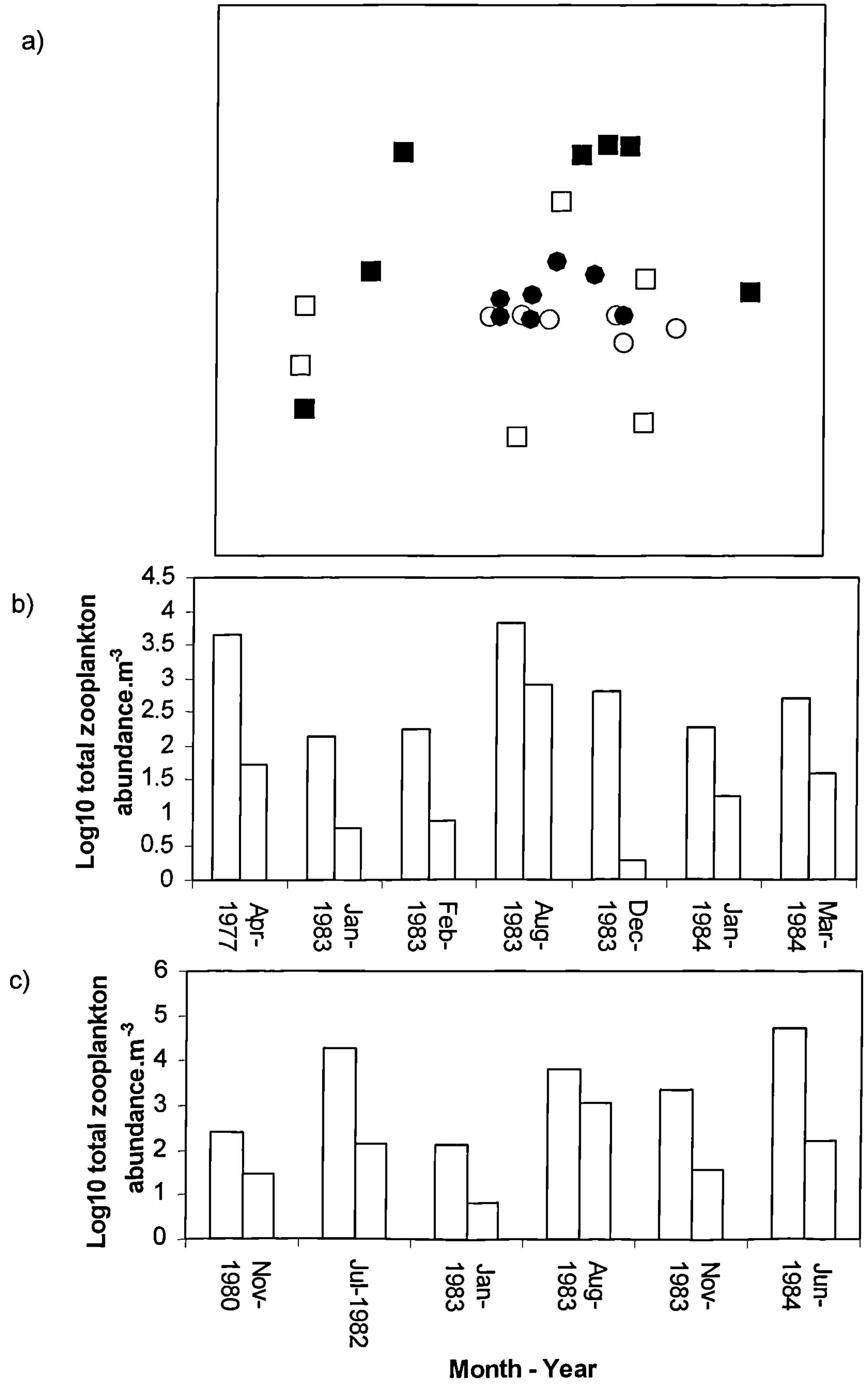


Figure 3.6 a) MDS plot of $Log_{10}+1$ transformed and standardised data. ● & ○ = Dove samples, ■ & □ = CPR samples. Open icons refer to CPR samples taken within 0.2 degrees of Dove permanent station and Dove samples in the same months. Filled icons refer to CPR samples taken between 56.05°N, 0.25°W by 55.90°N, 0.04°W, and Dove samples in the same months (MDS stress value=0.14). b) Comparison of $Log_{10}+1$ total zooplankton abundances (ind.m^{-3}) between CPR samples taken within 0.2 degrees of Dove permanent station and Dove samples in the same months. ▣ Dove series; □ CPR series. c) Comparison of $Log_{10}+1$ total zooplankton abundances (ind.m^{-3}) between 56.05°N, 0.25°W by 55.90°N, 0.04°W, and Dove samples in the same months. ▣ Dove series; □ CPR series.

Differences in mesh size will also contribute to differences in abundance recorded (Table 3.5), especially in the smaller taxa such as *Oithona,* and the younger juvenile stages which are not usually retained by the CPR mesh, and this could be largely responsible for the large ratios detected for some of these smaller taxa. However, examination of the ratios in abundance between the CPR and Dove time series (Table 3.5) for individual taxa revealed no obvious pattern by phylogeny, and there was no significant relationship between the approximate adult body width of each taxon and its Dove:CPR abundance ratio (Figure 3.7). Table 3.5 does show that the more commonly caught taxa appear to have ratios under 20:1, with most between 10 to 16. The notable exception to this is the small copepod *Oithona*, with a ratio of almost 50:1. Echinoderm larvae, the second-most abundant taxon in the CPR series, stood out with an abundance ratio close to one. In addition, larger taxa such as *Calanus* or appendicularians also show marked difference in abundance between the two series (Table 3.5), which would be expected to be equally caught by either a 200 or a 270µm mesh.

Table 3.5 Ratios of abundance between CPR and Dove zooplankton data. Only those taxa representing at least 1% of the total abundance are included.

Year	Dove (ave.ab.m^{-3})	CPR (ave.ab.m^{-3})	Ratio
Acartia spp.	1194.72	90.31	13.23
Appendicularia	129.71	12.89	10.06
Bivalve larvae	74.10	2.82	26.32
Calanus spp.	54.23	19.41	2.79
Centropages typicus	3.82	5.02	0.76
Chaetognatha	13.97	3.99	3.50
Cirripede larvae	62.56	0.94	66.20
Echinoderm larvae	59.01	53.24	1.11
Evadne spp.	456.99	25.17	18.16
Gastropod larvae	39.27	5.99	6.55
Oithona spp.	916.10	19.27	47.53
Pseudo-/Para/Microcalanus spp.	836.37	52.80	15.84
Podon spp.	32.36	6.40	5.05
Polychaeta larvae	35.22	0.01	5759.27
Pseudocalanus elongatus Adult	153.59	13.29	11.55
Temora longicornis	287.93	23.46	12.27

When the Dove zooplankton data was converted into categories, in order to emulate the category counting system employed by the CPR survey, these abundances were found to be lower than actual abundances for all 7 taxa investigated (Figure 3.8). A binomial test verifies that there was only a probability of 0.008 that this result would occur due to chance. However, using the seven selected taxa as examples, it was found that estimated abundances were on average 3.7% less than the actual abundances. Therefore the category counting system was not wholly responsible for the lower abundances observed in the CPR time series, although they do appear to contribute towards the observed discrepancy.

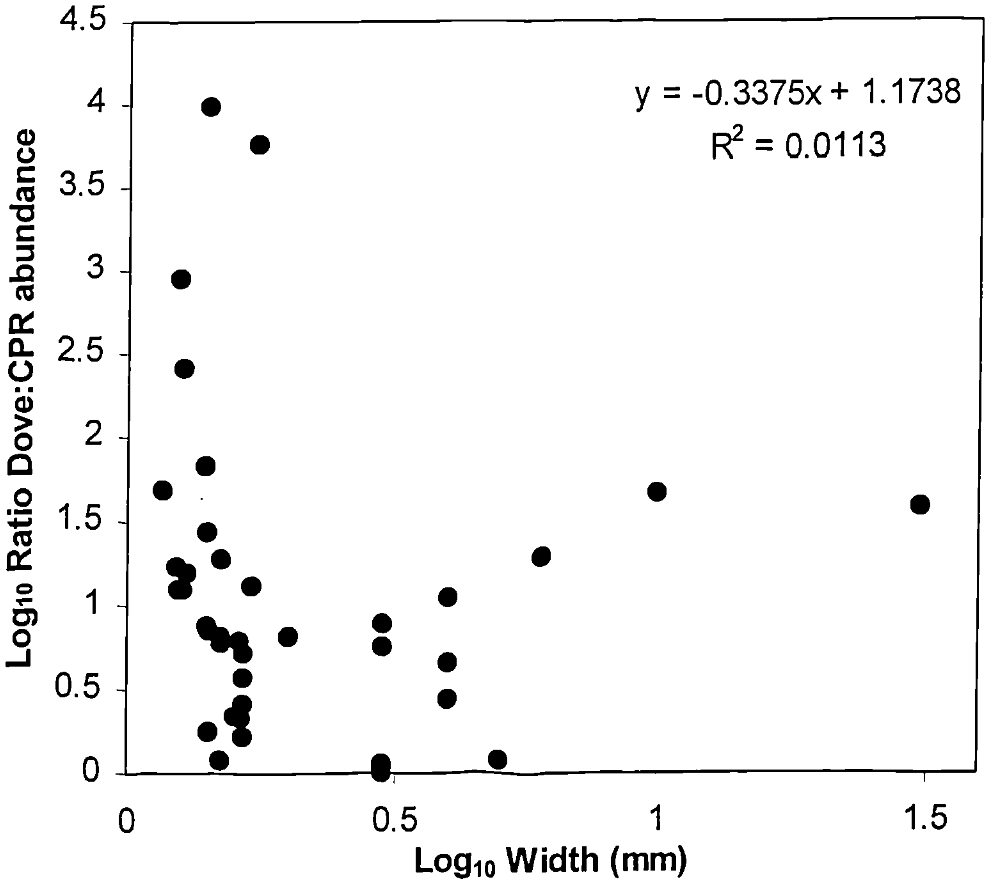


Figure 3.7 **Double Log_{10}+1 plot of the Dove to CPR abundance ratio for each taxon against the approx. adult body width (mm) of each taxon.**

The catching efficiency of all the samplers declines with increasing avoidance ability (K) (Figure 3.9). However, this decline is most pronounced for the Hardy plankton recorder, and even at relatively low escape abilities (K<0.05), the catching efficiency of the Hardy plankton recorder is almost zero. By comparison, the 56cm diameter WP2 net catches almost three quarters of individuals at K=0.05 $m.s^{-1}$. The large 113cm WP3 gear has the greatest catching efficiency, which would be expected given the moderate towing speed and large size of the mouth. Using a more specific example, the copepod *Anomalocera* is able to swim at rates up to 15 cm per second (UNESCO, 1968). Assuming that this species is able to detect the sampler at 0.25 m distance this would give K=0.0375 and an estimated catching efficiency of 0.141 for the Hardy plankton recorder. The WP3 net from which *Anomalocera* abundances are derived in the Dove Series, would have a catching efficiency of 0.937. However, as larger taxa generally have higher values of K, if the catching efficiency of the sampler was solely responsible for the observed differences in abundance, then it would be expected that such larger taxa would have higher Dove:CPR abundance ratios. Yet, no such relationship was present in the data (Figure 3.7).

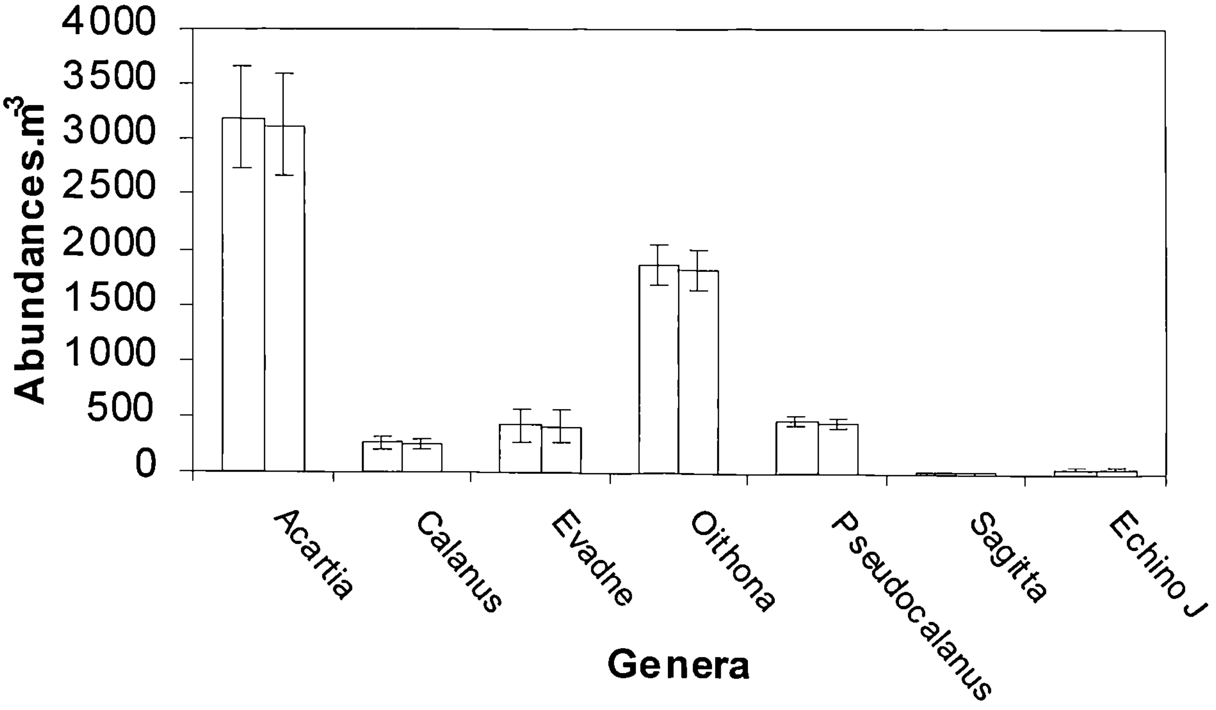


Figure 3.8 Comparison of real and estimated abundances (ind.m^{-3}), estimated abundances calculated using the CPR category counting system (Warner & Hays, 1994). Error bars depict standard errors. ▨ Real abundances; ☐ Estimated abundances.

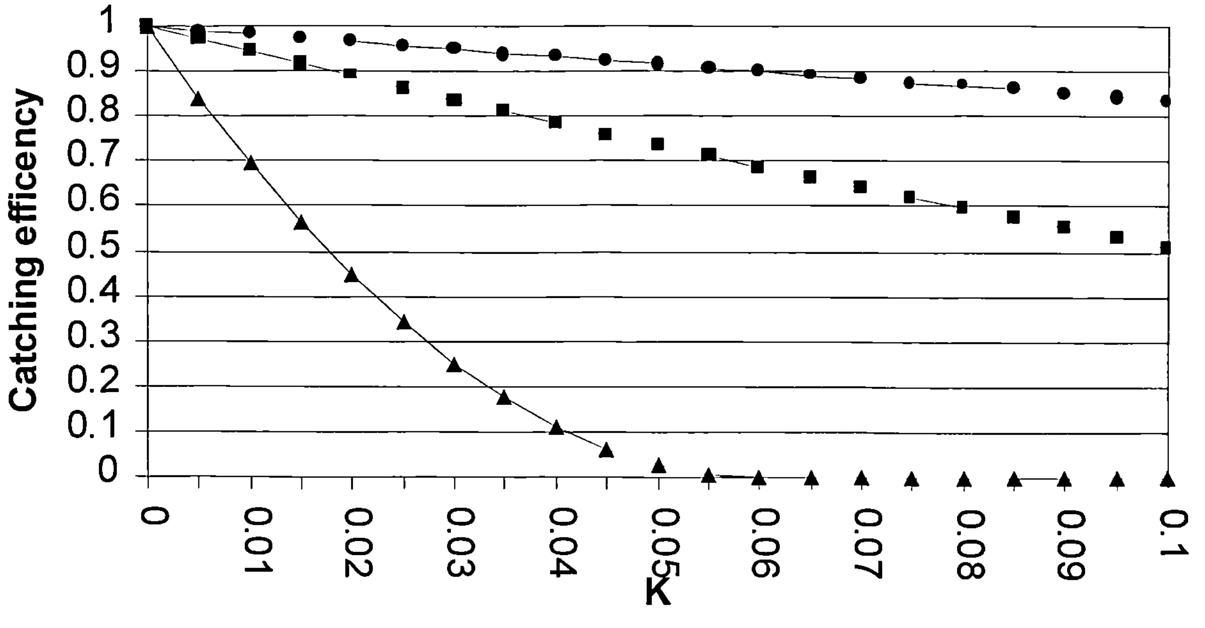


Figure 3.9. Calculation of catching efficiency for the Hardy Plankton Recorder, WP2 and WP3 plankton nets for values of K (detection distance x mean escape speed (in m.s^{-1})) (UNESCO, 1968). See text for details. —■—WP2; —●—WP3; —▲—Hardy recorder.

Discussion

The two monitoring programmes do show an excellent agreement in the scale of year to year fluctuations in abundance (Figure 3.3a), and the taxa which show significant correlations with one another constitute over one third of the total abundance in each time series (Table 3.4). Seasonal cycles also display a good comparison (Figure 3.3b). As both the Dove and CPR data have been successfully used to establish links between environmental and climatic variables (Evans, 1977; Roff *et al.*, 1988; Evans & Edwards, 1993; Taylor, 1995; Planque & Taylor, 1998), these results give increased confidence that the relative year to year fluctuations are accurate and appropriate for such comparisons. The similar order in abundance of the dominant taxa in each time series (Table 3.3a & b) also implies that, despite the larger spatial area covered by the CPR data, the species composition is similar in this area of the North Sea. These results also establish that changes in taxonomists over the years of operation is not a factor which affects the consistency of the Dove or CPR time series. The most apparent difference between the time series is the higher abundances detected by the Dove monitoring programme (Figure 3.5). There are a number of factors which could potentially be responsible for the observed dissimilarity. These are differences in the spatial area sampled, deployment of the sampler, sampler design, mesh size, or in counting and taxonomy.

Spatial differences appear not to be responsible for the higher abundances observed, as abundances are much higher in Dove zooplankton samples compared to CPR samples taken both near to, and far from, the Permanent Station (Figure 3.6b & c). It would also appear that, generally, the community structure of the dominant taxa sampled by the Dove programme is similar to that of the central-west North Sea area as determined by the CPR (Figure 3.6a). Further evidence of this comes from the significant agreement in the pattern of year to year changes in species composition within each of the two time series as shown by the "Relate" analysis. Therefore, this suggests that the time series are sampling a similar zooplankton community, but the differences in abundance suggest that this community is being sampled with different degrees of efficiency. In addition this would suggest that the assembling of CPR time series from wide geographical areas is an appropriate procedure (e.g. Colebrook, 1986).

With the finer mesh size used in the WP2 gear, the Dove time series will catch individuals with dimensions between 200-270μm that would pass through the CPR mesh. However, if mesh size was solely responsible for the observed differences in abundance, it would be expected that there would be a negative relationship between the Dove:CPR ratio and size of taxa (Figure 3.7). Given that there is no such relationship, and as high abundance ratios are observed in large taxa such as the Chaetognatha (Table 3.5), size is not a major factor in causing the marked differences in abundance between the two series. Certainly the ability of the CPR device to quantify abundances of small taxa such as *Oithona* has been questioned (Fransz *et al.*, 1991), and it is notable that despite *Oithona* being a dominant taxon in both time series, the abundance ratio between the CPR and the Dove is 47:1, whereas the abundance ratios of all the other dominant copepods, most of which are large enough to be retained by the CPR mesh, are below 20:1. In addition, for some taxa, such as Appendicularia and polychaetes, the observed differences in abundance may also be because such soft-bodied taxa have a tendency to become damaged and therefore uncountable in the CPR device, due to being compressed between the filtering and covering silks (Figure 3.1).

It could be argued that the observed differences in abundance were due to the different depths sampled. The CPR samples at approx. 7m depth (Hays & Warner, 1993), whereas data for the majority of taxa in the Dove programme originate from the vertical WP2 hauls. However, although many zooplankton taxa are able to maintain a fixed position in the water column, it is believed that such differences in sampling depth cannot be responsible for much of the 15 times difference in abundance between the two series. Firstly, as the CPR device samples during both day and night, this should assist in averaging out the abundances of those taxa which undergo diurnal vertical migration. In addition, the fact that the water column in this region is shallow (less than 70m) and mixed for most of the year, combined with the turbulence from the high speed passage and large displacement of the towing vessel should also reduce the effect of differences in sampling depth.

Examination of the CPR counting system (Warner & Hays, 1994) by applying it to the Dove data shows it exhibits a small bias (approx. 4%) towards lower abundances and so contributes to, but cannot be wholly responsible, for the differences in abundance observed (Figure 3.8). From such a negligible difference it is confirmed that the counting system is an appropriate method to reduce the sample processing time.

Although the larger mesh size and the use of the CPR counting system will contribute to the lower abundances recorded in the CPR time series, the calculations of avoidance suggest that active avoidance may be an important factor in causing the observed differences in abundance between the two time series (Figure 3.9). However, it has not been possible in this study to consider the effects of passive avoidance of the aperture through the pushing away of particles from the sampler mouth. It is suggested that the hydrodynamic effects produced by the CPR sampler, which has a high body-size to aperture ratio (see Figure 3.1) will be much greater than those produced by a conical net whose "body" consists of only a rigid metal hoop. In addition, the exact action of hydrodynamic effects are not fully understood. Larger hydrodynamic effects are likely to cause increased warning to animals and increased forcing of particles and plankton away from the sampler mouth, or alternatively may disorientate the animal so as to prevent escape.

The ability of an animal to perceive the presence of a sampling device depends on its sensitivity to a variety of visual, acoustic and hydrostatic stimuli (Fleminger & Clutter, 1965), such as light, gravity, angular acceleration or pressure variation (UNESCO, 1968). Levels of acoustic and hydrostatic stimuli produced will depend on the extent of the 'bow-wave' effect created by the sampler and towlines. It was previously considered that zooplankton avoidance was not a problem for the Hardy sampler due to the high speeds at which the device was towed through the water and through turbulence from the ship's propellers inhibiting the escape ability of the animals. There is certainly some evidence that zooplankton do exhibit reduced escape reactions when affected by turbulence (Singarajah, 1975) and it is possible that the turbulence created by the ship will depress this escape reaction. Once an individual has detected the presence of the sampler, its ability to avoid the device depends on its orientation with respect to the sampler, the distance required to move out of the path of the aperture, the speed of the sampler (UNESCO, 1968), and the maximum escape speed of the organism (Barkley, 1964). Although a study by McGurk (1992) found that avoidance by herring larvae was related to tow speed rather than net radius, the majority of evidence suggests that net avoidance of zooplankton increases with decreasing net radius (UNESCO, 1968; Ware & Lambert, 1985). This is because the lowest velocity that an animal must move to avoid capture decreases rapidly as the sampler radius decreases below optimum values (UNESCO, 1968). Therefore, the low aperture size of the

CPR device is potentially inefficient because the high tow speed is more than offset by the ease with which a smaller aperture may be avoided.

Despite their small size, some zooplankton species can reach high escape speeds. Effective escape behaviour is considered to be a major contributing factor to the success of copepods in planktonic communities (Davis *et al.*, 1999; Lenz & Hartline, 1999). Escape speeds of copepods may achieve as much as 200-500 body lengths per second (Lenz & Hartline, 1999). These astonishing escape velocities have been linked to the unusual presence of myelin sheaths in calanoid copepods which enables rapid evasive action to be taken when they detect a potential attacker (Davis *et al.*, 1999). The swimming velocities of most marine copepods have been estimated to be between 0.7 $cm.s^{-1}$ and 12 $cm.s^{-1}$ (UNESCO, 1968), and *Calanus helgolandicus* juveniles (stage V) have been observed to move at rates of up to 67 $cm.s^{-1}$ over distances up to 7 cm. However, calculations presented here are based on optimal avoidance (i.e. that the individual is facing perpendicular to the path of the sampler), and so actual catching efficiencies are likely to be higher. It is also difficult to accurately evaluate the escape reaction without detailed knowledge of each species' exact escape behaviour. For example, avoidance will be increased if the animals are capable of orientated movement (Fleminger & Clutter, 1965).

The apparent underestimation of abundance by the Hardy recorder means that the use of CPR data for investigations of productivity, or detailed examinations of intra- and inter-specific factors such as competition or predation, must be done cautiously. Theoretically, given the relationship between K and catching efficiency (Figure 3.9), it is proposed that even analysis of species composition change (e.g. through Bray-Curtis similarities) will not be straightforward, as any actual change in the proportion of taxa within the community having a high value K (high escape ability), will appear in the data as a smaller change in proportion *relative to taxa with low K*. Conversely, although the recorded abundances of low K taxa reflect actual abundances, their proportion within the total community will be artificially inflated relative to high K taxa. Given this, it would be expected that some relationship between estimated K and the ratio of Dove to CPR abundances would be found, yet none was observed. For example, it was expected that all ciliated pelagic larvae such as Mollusca, echinoderm, polychaete and barnacle larvae would exhibit ratios close to one given their slow swimming speeds (all below 0.75 $cm.s^{-1}$, (see Chia & Buckland-Nicks, 1984)). Of these, only echinoderm larvae show a ratio close to one, and, as such, they also display a high proportion of echinoderm larvae in the CPR time series relative to other taxa. This may be due to their low values of K allowing a greater proportion of these taxa to be caught by the Hardy recorder. It was also expected, based solely on active avoidance, that taxa with muscular propulsion would be expected to exhibit higher ratios compared to ciliated taxa, with taxa such as the Cladocera having lower ratios than the fast-reaction, high-speed calanoid copepods (Davis *et al.*, 1999), yet this was not found. Furthermore, it would be expected that, as net avoidance would generally increase in larger taxa due to their greater escape ability, higher Dove to CPR abundance ratios would be present for larger taxa. Yet Figure 3.7 shows that there is no link between the Dove:CPR ratio and size of taxa. However, the calculations of catching efficiency do not take account of the effects of bow-wave pressure and passive avoidance effects, and these factors are also likely to play a role in the observed differences in abundance. Although the relative year to year fluctuations of the two time series do show a good comparison, theoretically, given that there has been a gradual increase in towing speeds since 1955 (Hays & Warner, 1993) it would be expected that even the proportions of each taxa caught would change over time depending on the towing speed.

The loss of zooplankton and the consequent bias in estimates of species relative abundances are problems for all zooplankton samplers (UNESCO, 1968). However, this study has shown that in spite of the potentially low capture efficiency of the CPR device, the patterns of relative zooplankton abundance and species composition revealed match those found using nets with higher efficiencies. This confirms the value and utility of the CPR dataset which provides unparalleled geographic and temporal coverage of zooplankton assemblages in the NE Atlantic. Yet, the problems of active and passive sampler avoidance highlighted here caution the use of such data as the basis for productivity calculations or ecosystem modelling exercises. This consideration will also apply to modern variants of the Hardy Plankton Recorder, such as the U-tow (Hays *et al.*, 1998), which also have a small aperture size. However, the utility of being able to easily obtain time series from large areas at good temporal resolution will ensure that these devices make a valuable contribution to our understanding of relative changes in zooplankton spatially and temporally including consideration of changes occurring in response to global climate change or other anthropogenic factors.

Chapter 4 Long term changes in the central-west North Sea zooplankton community

Introduction

The importance of zooplankton as secondary producers in the marine ecosystem, and thus their potential influence on fish stocks, has been the primary reason why researchers have attempted to determine how their long term dynamics are influenced by climatic (e.g. Taylor, 1995; Fromentin & Planque, 1996), and/or anthropogenic factors (e.g. Greve *et al.*, 1996).

The majority of information on long term zooplankton trends for the North Sea and NE Atlantic region originates from the Continuous Plankton Recorder (CPR) survey (Warner & Hays, 1994). Using these data, Aebischer *et al.* (1990) noted that both phytoplankton (Figure 2.2a) and zooplankton (Figure 2.2b) abundances steadily declined from the mid 1950s to a synchronous trough in 1979-80, followed by a marked recovery. Aebischer *et al.* (1990) also noted that such long term trends were paralleled by westerly weather (Lamb, 1972), the suggestion being that weather was influencing these long term trends in phytoplankton and zooplankton. The similarity in these long term plankton trends to those recorded across the NE Atlantic area (Fransz *et al.*, 1991) suggested that the forcing of such communities must be due to factors operating on an equally large scale (i.e. climatic) (Colebrook, 1978).

The accepted hypothesis as to how long term plankton dynamics are predominantly controlled is that of Dickson *et al.* (1988a). Long term trends in zooplankton throughout most of the North Sea are influenced by the (weather driven) timing of the stratification of the water column and the resulting spring bloom (see Chapter 2). This hypothesis fits with observations that the decline in North Sea zooplankton from 1950-1980 (Figure 2.2b) was caused by an increasing tendency for cold northerly winds to blow across the NE Atlantic region during spring, thus delaying the spring bloom and reducing the zooplankton growing season.

Further research found that long term zooplankton trends throughout most of the North Sea and NE Atlantic regions were related to long term changes in the Gulf Stream North Wall (GSNW) (Taylor & Stephens, 1980; Taylor *et al.*, 1992; Taylor, 1995; Taylor, 1996) (see Chapter 2). In

NW Europe, northerly positions of the GSNW are related to warmer/wetter weather (Topliss, 1997), and to increased zooplankton productivity across the NE Atlantic and in the northern and central-eastern North Sea (Figures 2.6 b & c). However, such relationships were absent from those areas of the North Sea and Irish Sea which lack a coupling between productivity and wind induced mixing of the water column. This suggested that changes in the GSNW were associated with changes in the timing and intensity of the spring bloom (in a development of the model of Dickson *et al.*, 1988a). These associations were considered to be further evidence of a climatic connection spanning the North Atlantic, and suggested that the long trends in plankton populations (or at least those recorded by the CPR device) were predominantly externally driven rather than controlled through trophic interactions (Taylor *et al.*, 1992).

Off the Northumberland coast, the zooplankton community of the coastal central-west North Sea has been sampled monthly by the Dove Marine Laboratory since 1968 (see Chapter 3). Evans & Edwards (1993), in an examination of these data, suggested that the long term trend in holoplankton abundance in this region was similar to North Sea CPR zooplankton trends, with an abundance peak in 1975, a decline to a minimum in 1980, followed by a recovery. Evans & Edwards (1993), observed that there was a change in the Dove holozooplankton species composition around 1979-80, coincident with the observed nadir in the Dove and CPR North Sea plankton trends, and coincident with a similar change in zooplankton community composition in the Skaggerak (Austen *et al.*, 1991). In addition to this, the seasonal pattern and peaks of phytoplankton productivity observed in CPR area C2 also changed (Figure 2.4) around this time. Due to the suggested similarity in the long term trends observed in the Dove series to those across the North Sea, the simultaneous change in species composition over the North Sea, and the coincident change in the pattern of phytoplankton productivity, Evans & Edwards (1993) concluded that the transition in community structure was ultimately related to long term changes in north-east Atlantic weather patterns. The hypothesis was that these weather patterns influenced phytoplankton production, the effects of which, in turn, were mediated to the zooplankton community.

Frid & Huliselan (1996), have determined that the Dove zooplankton series exhibited a negative relationship to the GSNW, opposite to those observations made by Taylor *et al.* (1992) for zooplankton trends across much of the NE Atlantic. It was suggested by Frid & Huliselan (1996) that whereas the long term trend in more open and oceanic waters was a direct response to climatic variation, the opposite signal in these coastal regions could be an indirect response to coastal nutrient fluxes being influenced by climatic variation. This and other work (Huliselan, 1995) with the extending time series determined that long term trends observed in the Dove series were not as similar to other North Sea trends as previously suggested. In addition, contrary to earlier suggestions that long term plankton trends in the coastal central-west North Sea were predominantly influenced by environmental factors (e.g. Austen *et al.*, 1991; Evans & Edwards, 1993), other analyses of the Dove series have suggested that biotic factors were important in controlling the long term zooplankton dynamics in this region (Roff *et al.*, 1988; Frid *et al.*, 1994; Huliselan, 1995; Frid & Huliselan, 1996).

Although Aebischer *et al.* (1990) detected parallel trends between phytoplankton and zooplankton, Roff *et al.* (1988), using the Dove time series, searched for long term relationships between copepods and phytoplankton and yet found none. Likewise, there were no long term associations between zooplankton and temperature. Roff *et al.* (1988) suggested, as had Colebrook (1981; 1982b; 1982a; 1986) previously, that the size of the overwintering stock was important in determining zooplankton abundance the following year as they observed that there was a relationship between the minimum winter copepod abundance and the mean copepod abundance the following year ($r=0.74$, $p<0.002$) (Roff *et al.*, 1988). However, such claims need to be considered carefully given the non-independence of the two variables, and a recent study by Frid *et al.* (1999c) found that there were no relationships between winter and summer zooplankton abundances. Roff *et al.* (1988) also suggested that the amount of overwintering mortality was strongly influenced by predators, especially by the hyperiid amphipod *Themisto* and the chaetognath *Sagitta* (Frid *et al.*, 1994). Thus, these studies (Roff *et al.*, 1988; Frid *et al.*, 1994; Huliselan, 1995; Frid & Huliselan, 1996; Frid *et al.*, 1999c) provide evidence that biological factors play a role in influencing the plankton population of the central-west North Sea, although the functioning of this mechanism has not been clearly established.

This chapter examines the long term dynamics of the zooplankton community of the central-west North Sea region, using Dove and CPR time series data for the period 1969-1996 and 1960-1996 respectively. It has already been determined, that despite marked differences in abundance, the relative interannual fluctuations of these two series are statistically similar

(Chapter 3). However, the long term zooplankton dynamics in this region may be dissimilar to other North Sea areas (Huliselan, 1995; Frid & Huliselan, 1996). Thus here, I evaluate the long term changes in zooplankton abundance and species composition which have occurred in the central-west North Sea, and, using a wide range of environmental variables, establish how the long term dynamics of the zooplankton community relate to external influences (e.g. GSNW, temperature, nutrients etc.). It is considered that the results of these analyses may assist in understanding the mechanisms controlling the long term dynamics of the zooplankton in the central-west North Sea.

Methods

Zooplankton sampling methodologies for both the Dove and Continuous Plankton Recorder time series are covered in detail in Chapter 3. The Dove data analysed here covered the period 1969-1996 (excepting 1989) while the CPR data used covered the period from 1960 to 1996 (omitting 1978 and 1979 because of incomplete samples) for a triangular area in the central-western North Sea between the Firth of Forth SE Scotland (56°05'N 2°40'W), Flamborough Head NE England (54°07'N 0°04'W) and a point approx. 120 km offshore (56°05'N 0°04'W) (Figure 3.2).

Initial manipulations of time series data

Due to the large numbers of zooplankton taxonomic entities recorded in each time series (Dove = 89, CPR = 70; both series not including eggs), the number of taxa was reduced to those dominant taxa to make analysis of the species composition and environmental associations simpler. Eggs were discarded at this stage in the analysis from both series. Those taxa selected to be used in further analyses were those which represented at least 2% of the total zooplankton community *in any one monthly sample.*

These procedures left 46 taxa in the Dove, and 36 taxa in the CPR zooplankton time series (Table 4.1). In order to understand the overall species composition of each series, the mean abundance and proportion of each taxa was calculated over each series. The resulting values were then ranked from highest mean abundance to lowest. Additionally, the fluctuations in the proportion of the top three taxa in each series, and the copepod, cladoceran and meroplankton groups were plotted.

Analyses of long term trends

Mann-Kendall test

Long term trends in annual mean abundances were analysed using the Mann-Kendall test for trend (Gilbert, 1987). This method uses only the relative magnitudes of the data rather than their measured values, and is an improvement upon using regression as a trend test, as missing values are allowed and the data do not need to conform to any particular distribution (Gilbert, 1987).

Cumulative Sum technique

Cumulative Sum (CUSUM) techniques are generally used in the quality control of industrial processes to detect small but persistent changes in the mean of a process (Woodward & Goldsmith, 1964; van Dobben de Bruyn, 1968). CUSUM techniques are based upon the visual or numerical analysis of the cumulative deviations of subsequent data points away from the "target" value of a process or time series. The time series is standardised to zero mean and unit variation and then each monthly data point y_t sampled at time t (t from 1 to n) is added to the preceding data point:

$$S_t = \sum_{t=1}^{n} y_t$$

Where S_t is the resulting CUSUM which may be plotted over time, t.

It is possible to interpret the CUSUM by visually examining the slope of the line on the chart, the actual value on the y axis is not important. Where there is constant deviation from the running mean then the slope of the line will remain constant. However, where the deviation changes and this persists (thus it is not simply a freak observation), then this suggests that the running mean of the series has changed.

The numerical method used here to detect small changes in the mean is termed the Decision Interval Control Scheme (DICS), covered in detail by Woodward (1964) and van Dobben de Bruyn (1968). Briefly, this method does not require the results of the CUSUM to be plotted but allows changes in the time series to be identified according to pre-set parameters, *h* (the decision interval), and *k* (the reference value). From the standardised time series, two further series are constructed, one where *k* is subtracted (producing a time series with a negative tendency) and one where *k* is added (producing a time series with a positive tendency). Using the negative tendency time series as an example, if the bias in the time series exceeds *k*, then a positive trend will persist in this series. CUSUM "breakpoints" may be identified in this series when this positive trend exceeds the previous minimum value by more than *h*. Consequently, in the positive tendency series, CUSUM breakpoints may be identified where any negative trend is less than the previous maximum by more than *h*.

Thus:

$S_t = \max(0, S_{t-1} + e_t - k)$ to test for positive biases

$S_t = \min(0, S_{t-1} + e_t + k)$ to test for negative biases

$S_o = 0$

CUSUM breakpoint for positive biases if:

$S_t > h$

CUSUM breakpoint for negative biases if:

$S_t < h$ (van Dobben de Bruyn, 1968).

Where, S_t is the value of the test quantity plotted after the t^{th} observation and e_t is the difference between the t^{th} observation and the target value.

In order to determine at which points in each series there were changes in the mean total abundance, and how these breakpoints compared to monthly and year to year fluctuations in total abundance, DICS was applied to monthly total zooplankton counts using values of 0.6 and 0.8 for h and k, respectively. CUSUMs were also calculated and plotted to assist in the interpretation of the results of the DICS.

Long term changes in species composition

Analysis of long term changes in species composition were carried out in PRIMER at the species level with a $\text{Log}_{10}+1$ transformation applied to reduce the weighting of dominant species, and Bray-Curtis similarity coefficients calculated from the community data for each pair of years. To investigate whether there was a trend in the species composition between the first and successive years, the similarity coefficients between the first year and subsequent years were plotted and a Mann-Kendall test used to test the significance of any trend.

To detect any groups of years and the extent of differences between groups of years, for each series, dendrograms were constructed from the similarity values using a group average clustering algorithm. For the CPR data an additional dendrogram was plotted using similarity values calculated from the mean abundance for the months January to July for each year, as this enabled the species composition in the years 1978 and 1979 to be studied.

Non-Metric Multiple Dimensional Scaling (MDS) ordination (Clarke & Warwick, 1994) of the similarity coefficients was performed to establish whether zooplankton productivity, or fluctuations in the Gulf Stream North Wall (GSNW) were associated with different types of community composition, although those groups of years in the CPR data which were identified as having a markedly different community composition (less than 75% group average similarity) were removed from these analyses. Here, the GSNW series was the first principal component calculated from the six latitude measurements (Figure 2.6a), in order to find the pattern of variation common to the six longitudes for the period 1966 to 1996 (see Taylor, 1996 for details).

Low and high zooplankton abundance years were superimposed on each MDS plot to observe whether changes in species composition were related to changes in productivity. High years were those where the annual mean abundance was greater than 0.5 standard deviations from the long term mean, whereas low years were those where the abundance was less than 0.5 from the long term mean, leaving mid abundance years where the abundance was between –0.5 and 0.5 standard deviations from the mean.

Similarly, north and south GSNW years were separately superimposed on the separate MDS plot. Northerly years were those where the GSNW was greater than 0.5 standard deviations from the long term mean, whereas southerly years were those where the GSNW was less than 0.5 from the long term mean, leaving mid latitude GSNW years where the abundance was between –0.5 and 0.5 standard deviations from the zero mean.

Separate ANOSIM (Clarke & Warwick, 1994) tests were performed to examine the significance of differences in species composition between groups of high, mid and low abundance years and northerly, mid and southerly GSNW years. However, as comparisons between mid years and high and low abundance years, or northerly and southerly GSNW years would not be fully independent, attention was focussed on the significance of differences in species composition between high and low years, and northerly and southerly years. As abundance does influence the output of the Bray-Curtis similarity calculations, it could be argued that such an apparent difference in species composition is not surprising, thus for the test between high, mid and low abundance years, the ANOSIM calculations were on Bray-Curtis similarity values which had been calculated from standardised data.

Finally, SIMPER (Clarke & Warwick, 1994) was used on groups of high and low abundance years, and northerly and southerly GSNW years, to identify those taxa mainly responsible for any observed differences in species composition.

Analysis of nutrient data

ICES nutrient and chemical data covering the period 1969 to 1995, for the central-western North Sea (54.5-56°N, and 0-1°W), from just south of the Tees to the Firth of Forth were examined. Data points are assigned to a month, yet due to the large number of missing values and thus the low sample sizes, it was considered inappropriate to use correlation and similar statistical analyses on these data. Therefore, the trends in these data were examined (Mann-Kendall test) following deseasonalisation of the available data, to provide an indication as to whether there were any long term trends in nutrients which could be influencing phytoplankton and zooplankton populations.

The limited nutrient data collected at the Dove zooplankton station from May 1996 to October 1998 (Frid *et al.*, 1999c) were also examined. Depth-time contour plots of temperature were constructed for this period and the available depth averaged (over the 50m water column) chlorophyll, nitrate, nitrite, and phosphate data were plotted. Carotenoid to chlorophyll ratios were also plotted as there is a relationship between this and the nutritional status of the phytoplankton (Heath *et al.*, 1990), and thus potentially the productivity of the whole system. Although ratios do vary from species to species, ratios less than 1.4 are said to indicate excess nitrogen whereas ratios in excess of 2.4 indicate extreme nitrogen depletion.

Relationships between zooplankton and environment

Correlation analysis was employed to examine relationships between taxa and environmental factors. For all taxa, abundances.m^{-3} were $\log_{10}+1$ transformed. Due to the problem of autocorrelation which is inherent in time series data (see Chapter 1), additional post-correlational corrections were employed to compensate for, or detect, this. Thus, the number of degrees of freedom used for testing the significance of correlations between taxa and potential forcing factors was reduced according to the method of Quenouille (1952), which calculates the effective number of independent observations (*E*) as follows:

$$E = \frac{N}{(1 + 2r_1 r_1' + 2r_2 r_2')}$$

where *N* is the number of points in each of the two time series; r_1 & r_1' are the one point lag autocorrelations of each time series; r_2 & r_2' are the two point lag autocorrelations of each time series. Additionally, to give an indication of the probability of spurious correlations in the data, for each table of independent tests, a global significance level was calculated based on the number of significant correlations (prior to the tests for autocorrelation). For those correlations which were significant ($p<0.05$) after Quenouille correction and where those taxa whose abundance was calculated as being at least 1% in each series (Table 4.1), standardised time series plots were constructed.

Data used in analyses of relationships between zooplankton species and environment

Biological data used consisted of annual mean phytoplankton index data from CPR area C2, and annual mean phytoplankton data from the SE Scotland to NE England area (Figure 3.2). Zooplankton data consisted of annual means for each taxa in the Dove and CPR series, in addition to the sum of these taxa.

Environmental data used consisted of air temperatures, wind speed and sunshine data for Tynemouth and Durham weather stations which were obtained from the British Atmospheric Data Centre (www.badc.ac.uk). For each variable, where data were available, annual means for the period 1960 to 1996 were calculated from daily data. Two weather stations were used to obtain a wider picture of weather coverage, and as the coastal Tynemouth station is subject to weather phenomena which occur at the land-sea interface (e.g. sea mists, on/offshore breezes) which do not affect the inland Durham station. The only available Sea Surface Temperature (SST) data were from the Farne Islands for the period 1974 to 1990. Climatic variables used were the GSNW (Taylor, 1996) and the North Atlantic Oscillation Index (NAOI) series (Fromentin & Planque, 1996). The Lambs Weather Types dataset (Lamb, 1972), which is a system for classifying synoptic weather patterns over the British Isles was also used in the analysis. These weather types are based on the analysis of the directions of the overall isobaric patterns over the British Isles (not the individual wind direction at any one place). The 27 weather types are based on both the curvature of the flow (anticyclonic or high pressure (prefixed by A), cyclonic (prefixed by C) or unclassified), and one of the 8 compass directions from which the wind blows. However, in order to reduce the number of correlations required, only the first principal component was used in the correlations. This was calculated from the covariance matrix, as use of the correlation matrix would have over-emphasised the importance of the more infrequent weather types (Jones & Kelly, 1982, Appendix 2).

Table 4.1 Dominance of zooplankton taxa in Dove and CPR time series. Taxa sorted in descending order on mean abundances, which were calculated from annual mean abundances over each series.

Entity	Dove mean abundance (per m^3)	Mean Percentage composition	Entity	CPR mean abundance (per m^3)	Mean Percentage composition
Pseudo-/Para-/Microcalanus juv.	963.17	20.19	*Acartia* spp.	91.36	24.45
Oithona similis	930.18	19.50	*Pseudo-/Paracalanus* spp.	59.02	15.80
Acartia spp. juv.	760.92	15.95	Echinoderm larvae	50.70	13.57
Evadne nordmanni	439.85	9.22	*Evadne* spp.	26.49	7.09
Acartia clausi	327.98	6.88	*Calanus* stages I-IV	24.57	6.58
Temora longicornis	323.57	6.78	*Oithona* spp.	22.99	6.15
Acartia longiremis	161.86	3.39	*Temora longicornis*	19.92	5.33
Pseudocalanus elongatus adult	155.33	3.26	*Pseudocalanus elongatus*	12.93	3.46
Oikopleura diocia	86.48	1.81	*Limacina retroversa*	11.76	3.15
Bivalve larvae	73.45	1.54	Larvacea	11.07	2.96
Calanus spp. juv.	66.19	1.39	Copepod nauplii	8.50	2.28
Cirripeida larvae	63.25	1.33	*Podon* spp.	5.75	1.54
Ophioplutei larvae	45.93	0.96	Lamellibranchia larvae	5.42	1.45
Other taxa	41.23	0.86	*Centropages typicus*	4.69	1.26
Gastropoda larvae	38.54	0.81	Chaetognatha	4.20	1.13
Fritillaria borealis	37.35	0.78	*Centropages hamatus*	2.91	0.78
Polychaeta larvae	33.27	0.70	*Calanus stages* V-VI	2.79	0.75
Paracalanus parvus	33.18	0.70	*Calanus finmarchicus*	1.93	0.52
Podon spp.	31.82	0.67	Euphausiacea total	1.71	0.46
Euphausiid nauplii	24.65	0.52	Cyphonautes larvae	1.36	0.36
Centropages hamatus	22.07	0.46	Cirripede larvae	0 87	0.23
Centropages spp. juv.	18.49	0.39	*Calanus helgolandicus*	0.86	0.23
Euphausiid juv.	17.59	0.37	Decapoda larvae	0.58	0.15
Sagitta elegans	13.09	0 27	Harpacticoida spp.	0.33	0.09
Bryozoan larvae	9.73	0.20	Hyperiidea	0.19	0.05
Microcalanus pusillus	8.50	0.18	Fish larvae	0.17	0.04
Microsetella norvegica	5.88	0.12	*Acartia longiremis*	0.13	0.03
Echinoderm larvae	5.70	0.12	Other taxa	0.10	0.03
Aglantha digitale	5.02	0.11	*Metridia lucens*	0.07	0.02
Echinoplutei larvae	4.95	0.10	*Corycaeus* spp.	0 07	0.02
Calanus spp. males	4.84	0.10	*Metridia* I-IV	0 06	0 02
Centropages typicus	3.93	0.08	*Tomopteris* spp.	0 04	0 01
Jellyfish juv.	3.06	0.06	*Microcalanus* spp.	0.03	0 01
Tomopteris helgolandica	1.76	0.04	Spindelei	0.02	0 01
Calanus helgolandicus females	1.47	0.03	*Oncaea* spp.	0.02	0 00
Phoronid larvae	1.44	0.03	*Candacia* I-IV	0 01	0 00
Themisto gaudichaudi	1.09	0.02	Cytemenestra spp.	0 00	0 00
Anomuran larvae	1.09	0.02			
Calanus finmarchicus	0.97	0.02			
Corycaeus anglicus	0.64	0.01			
Fish larvae	0.27	0.01			
Thysanoessa raschi	0.26	0 01			
Tigriopus spp.	0.23	0.00			
Oncaea venusta	0.11	0.00			
Nanomia cara	0.11	0.00			
Nyctiphanes couchi	0.05	0.00			
Thysanoessa inermis	0.05	0.00			

Results

Initial analyses of long term trends

The year to year mean abundances of the zooplankton community, in the Dove series, displayed a large degree of interannual variability (Figure 4.1a). Annual mean densities ranged from a maximum of 10,552 individuals.m^{-3} in 1978 to a minimum of 1,203 individuals.m^{-3} in 1990. Although there was a slight downward trend to the year to year abundances, the Mann-Kendall test indicates that this was not significant (S=-49, p=0.24).

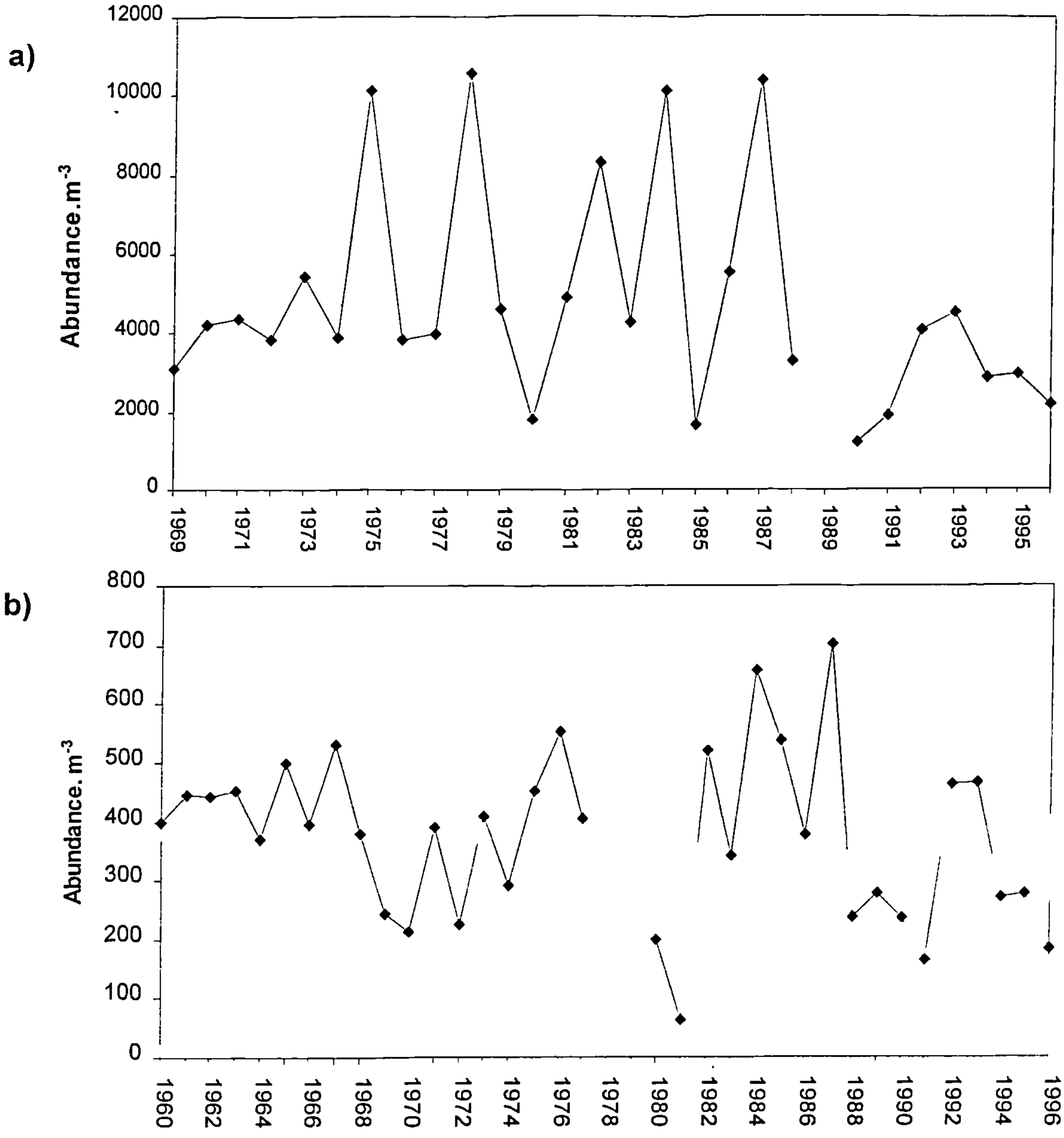


Figure 4.1 **a) Annual means of $\log_{10}$ total zooplankton abundance (per m^3) in the Dove time series covering 1969-1988 & 1990-1996. b) Annual means of $\log_{10}$ total zooplankton abundance (per m^3) in the CPR time series covering 1960-1977 & 1980-1996.**

A visual examination of the year to year fluctuations (Figure 4.1a), and the results of the CUSUM calculations (Figure 4.2a), suggested that there were three phases present in the long term data. The first phase extended from 1969 to 1975 and was identified by relatively low annual mean densities (from 3110 individuals.m^{-3} in 1969 to 5436 individuals.m^{-3} in 1973), and low year to year fluctuations. The second phase, from 1975 to the middle of 1987, was characterised by a higher interannual variability (from 1773 individuals.m^{-3} in 1980 to 10552 individuals.m^{-3} in 1978) caused by higher peaks of productivity observed during the seasonal cycle. The final phase from 1987 to 1996 showed a return to relative stability and lower mean abundance (from 1203 individuals.m^{-3} in 1990 to 4508 individuals.m^{-3} in 1993), represented by negatively sloping CUSUM values from 1988 onwards.

The relative interannual dynamics of the central-west North Sea zooplankton community as measured by the CPR survey (Figure 4.1b) were found to be similar to the Dove series ($r=0.64$, $p<0.001$). The Mann-Kendall test indicates that, like the Dove series, there was a slight downward trend, although this too was not-significant ($S=-87$ $p=0.19$). The CUSUM results are more complex than that of the Dove series due to the greater (36 year) length of the CPR data (Figure 4.2b), although there is some similarity in the positions of the CUSUM breakpoints. Initially, the phase from 1960 to 1968-1969 was characterised by stable interannual fluctuations with a relatively high annual mean abundance (Figure 4.1b). This phase ended in 1969 with a large reduction in productivity for two years running, from 1596 individuals.m^{-3} in 1967, to 730 individuals.m^{-3} in 1969. Over the second phase, abundance increased from 204 individuals.m^{-3} in 1970 to 538 individuals.m^{-3} in 1976. The next phase was typified by a sharp decrease in abundance, although two years data are missing here, to a very low abundance of 186 individuals.m^{-3} in 1981. Abundance increased to its highest level over the 1982 to 1987 period, then reduced from 668 individuals.m^{-3} in 1987 to 232 individuals.m^{-3} in 1988. This period of reduced abundances lasted for 4 years until 1992-1993 when abundance increased up to 465 individuals.m^{-3} in 1993 followed by a reduced abundance for the following two years. Coincident breakpoints in the Dove and CPR series occurred in 1975 and 1987. However, although this constitutes one phase in the Dove series, in the CPR series this is interrupted by the breakpoint in 1981 when abundance reached its lowest value.

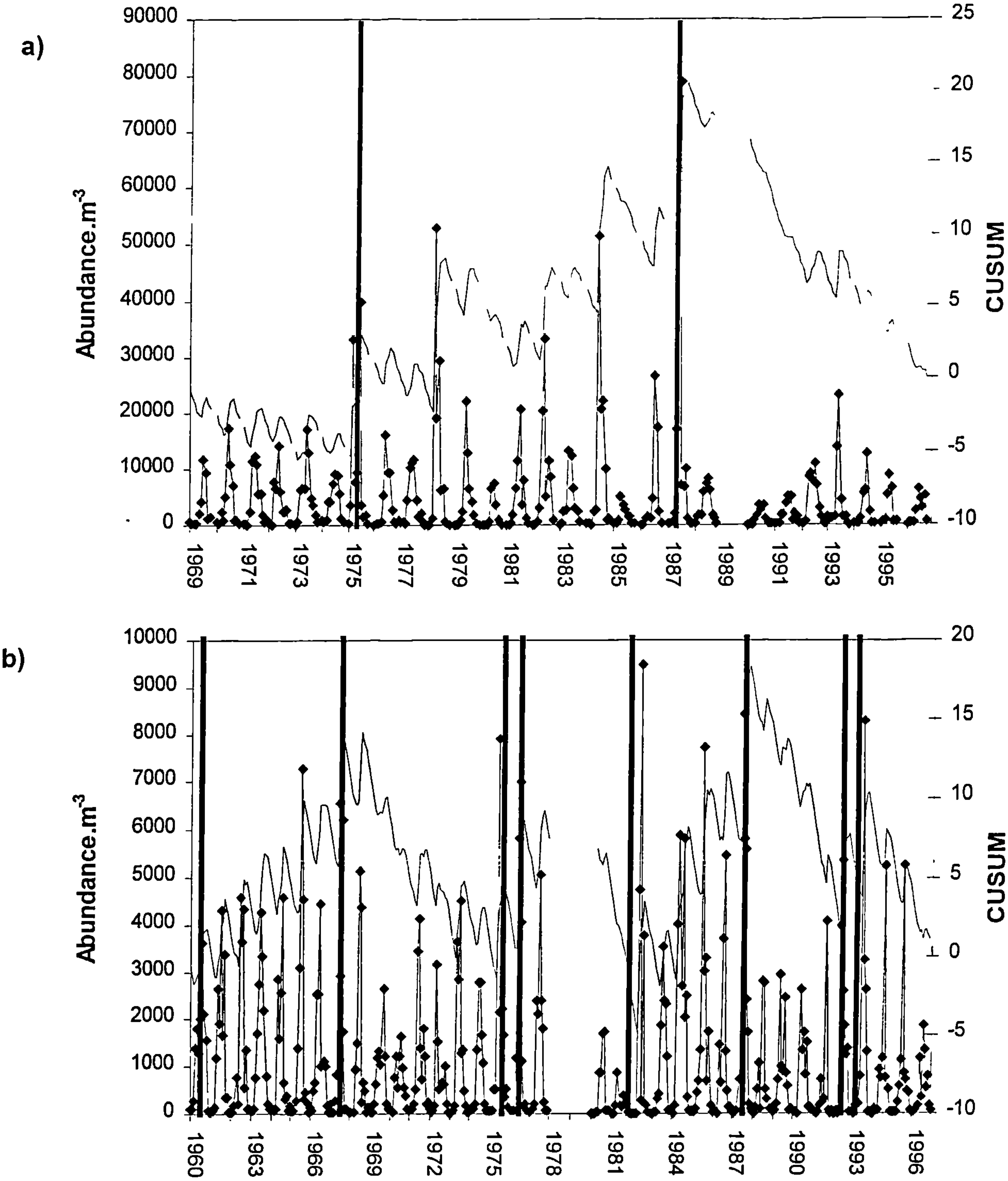


Figure 4.2 Monthly zooplankton abundance (per m^3) (—◆—), with Cumulative Sums calculated from standardised data (—), and showing CUSUM breakpoints (▌), in a) the Dove time series, b) the CPR series. See text for further explanation

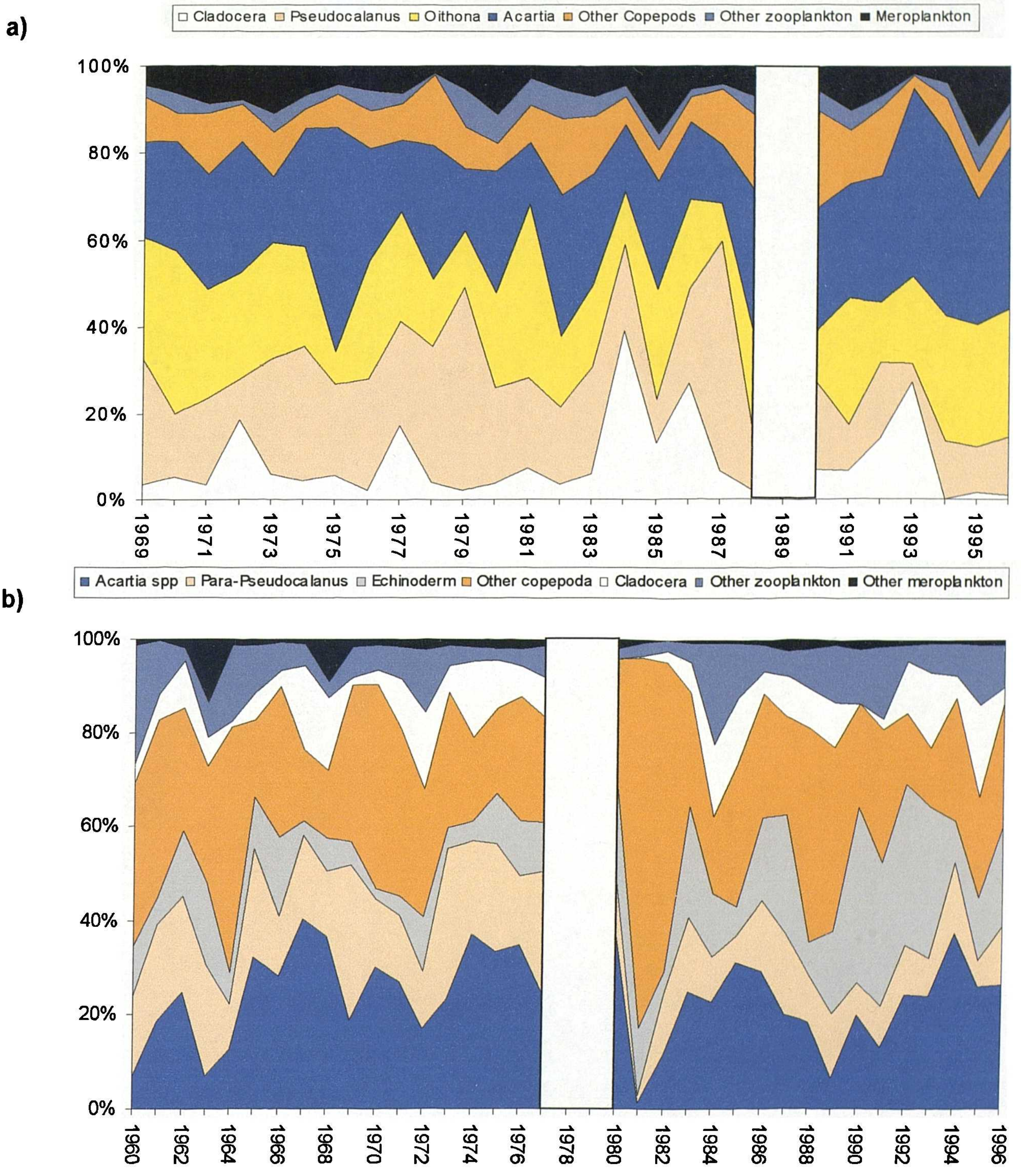


Figure 4.3 **Major taxa in a) the Dove time series. Data used covers 1969-1988 & 1990-1996. b) the CPR time series. Data used covers 1960-1977 & 1980-1996. Legend to taxa is located above each plot.**

The zooplankton community in both the Dove and the CPR series was dominated by holoplanktonic species (Figure 4.3a+b). The dominant taxa in the Dove series were the small copepod taxa the *Pseudo-/Para-/Microcalanus* juveniles, *Oithona* and *Acartia* juveniles. Year to year fluctuations in the zooplankton community were primarily driven by changes in the abundance of these species (Figure 4.3a). However, during some years, the Cladocera made up almost 40% of the zooplankton, with isolated increases in the proportion of these species in 1972, 1977, 1986, 1993, and especially in 1984. Meroplankton generally only formed a small percentage of the total community although in some years (1985 & 1995) they made up almost 20% of the abundance.

In the CPR series, the zooplankton community was dominated by both *Acartia* and the *Pseudo-/Paracalanus* spp. groups (Table 4.1) which together contributed over 50% of the community. Echinoderm larvae were notably found to be the 3rd most abundant taxa (Table 4.1), whereas in the Dove series they are ranked 26th. The most notable changes are the reduction in the proportion of *Acartia* during 1981 (Figure 4.3b). Echinoderm larvae do increase their proportion in the community after 1984, which would agree with the increase in the dominance of this group suggested by Lindley (1995).

Long term changes in species composition

Results of cluster analysis

Cluster analysis of the Dove series showed that there were no distinct clusters of years, although 1982 was distinct from other years (Figure 4.4a). Trend analysis on the Bray-Curtis similarity coefficients between the first year (1969) and all other years indicated that there was no significant trend in these similarity values (Mann-Kendall test S=-49, p=0.23), suggesting that there was little overall change in the community over the 27 year series (Figure 4.4b). Long term changes in species composition in the CPR data were similar to the Dove time series in that overall there was no distinct pattern (Figure 4.5a). However, the years 1980, 1981, 1982 do have a species composition distinct from all other years, and each other. As in the Dove series there was no significant trend in Bray-Curtis similarity coefficients between the first year (1960) and all the other years in the CPR series (S=-99, p=0.13) (Figure 4.5b).

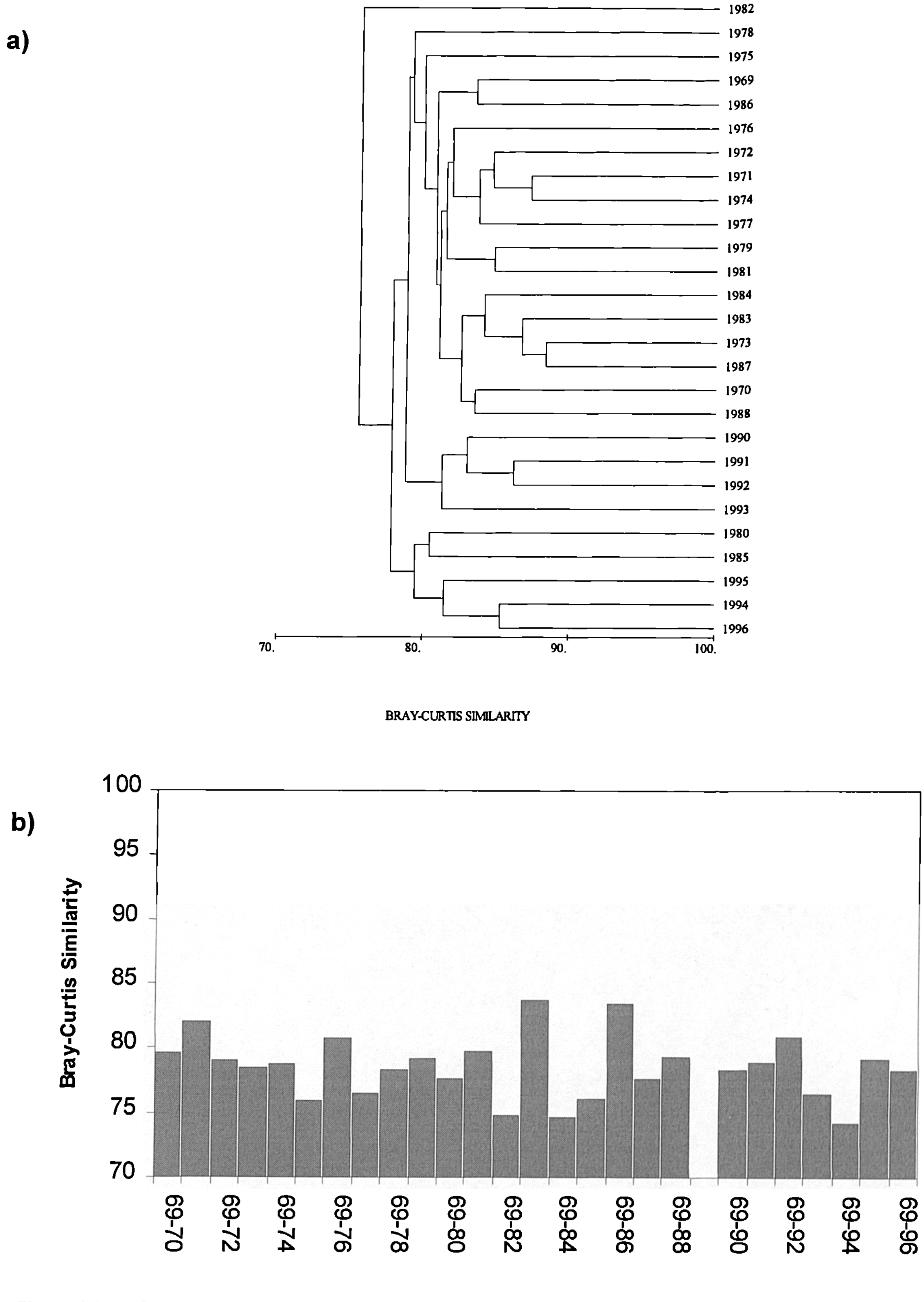


Figure 4.4 a) Cluster analysis of zooplankton from the Dove time series, using a $\log_{10}$ transformation of annual means from 1969-1988 & 1989-1996. b) Bray-Curtis Similarity between the first year (1969) and subsequent years in the Dove time series.

For the CPR data, when the years 1978 and 1979 were included in the cluster analysis (means for Jan. to July), 1979-1982 and 1991 formed a separate cluster to all other years (at least c.55% dissimilarity to all other years) (Figure 4.6a). The abundance of those taxa which

SIMPER showed to contribute up to 25% cumulative dissimilarity for each of the years 1979-1982 & 1991 were plotted. This suggested that the most distinct community, observed in 1981 (Figure 4.6a), was caused by a reduction in the abundance of *Acartia* to only 1 individual.m^{-3}. *Oithona*, *Pseudo-/Paracalanus* spp. and *Evadne* were found in reduced abundance for the whole of the 1979 to 1981 period (Figure 4.6b). This is also reflected in the proportion plot (Figure 4.3b). Thus, a number of taxa had markedly lowered abundances over the 1979 to 1981 period, many the dominant members of the community. Based on these results, it is suggested that the changes occurring from 1980-1982 were part of a small isolated change in the system. It is difficult to suggest why these changes may have occurred, although in 1980 there was a late start to the phytoplankton productive season (Figure 4.7), and consequently this year was a year of low plankton productivity in CPR box C2 (c.f. Figure 2.2).

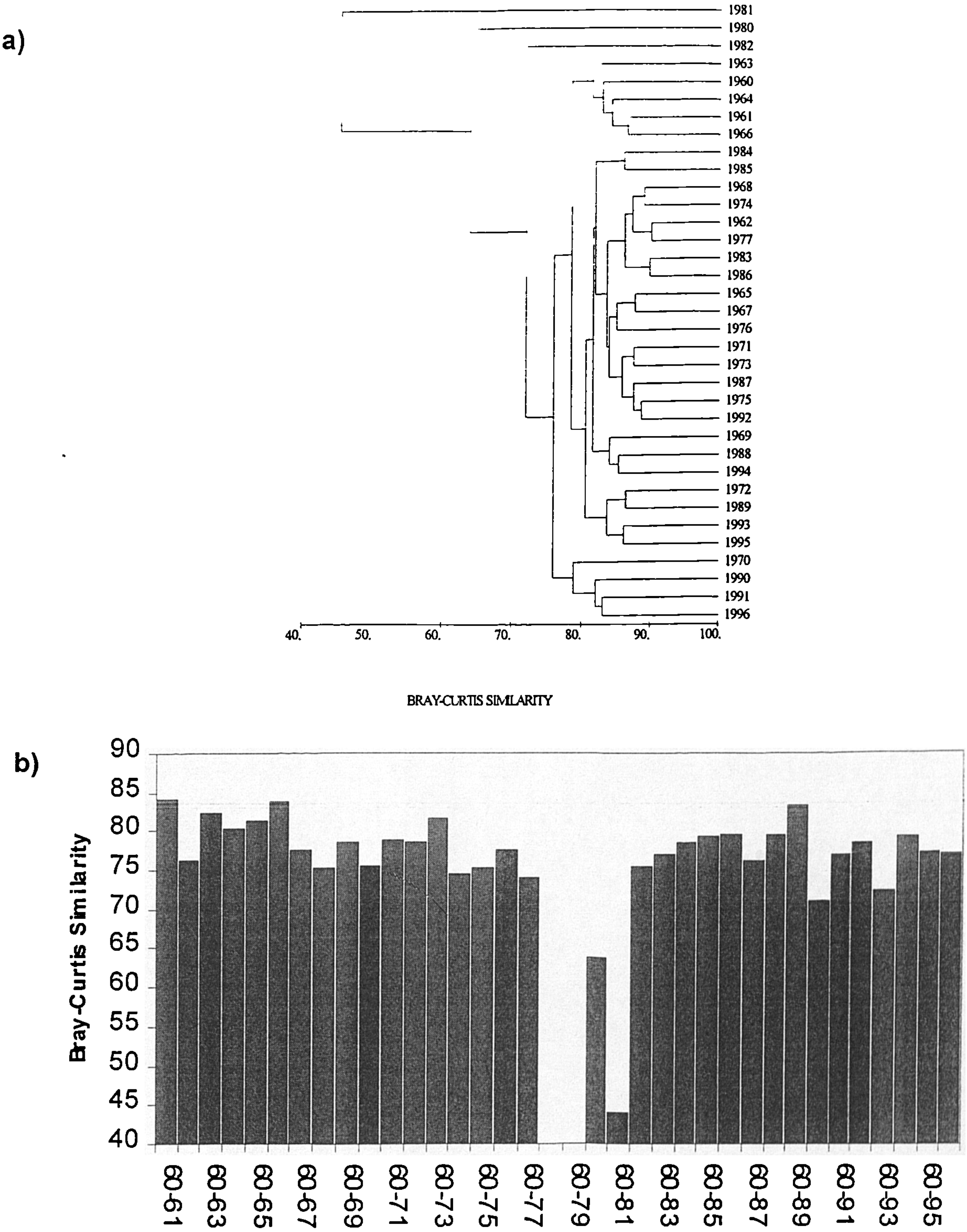


Figure 4.5 a) Cluster analysis of zooplankton from the CPR time series using a $\log_{10}$ transformation of annual means from 1960-1977 & 1980-1996. b) Bray-Curtis Similarity between the first years (1960) and subsequent years in the CPR time series.

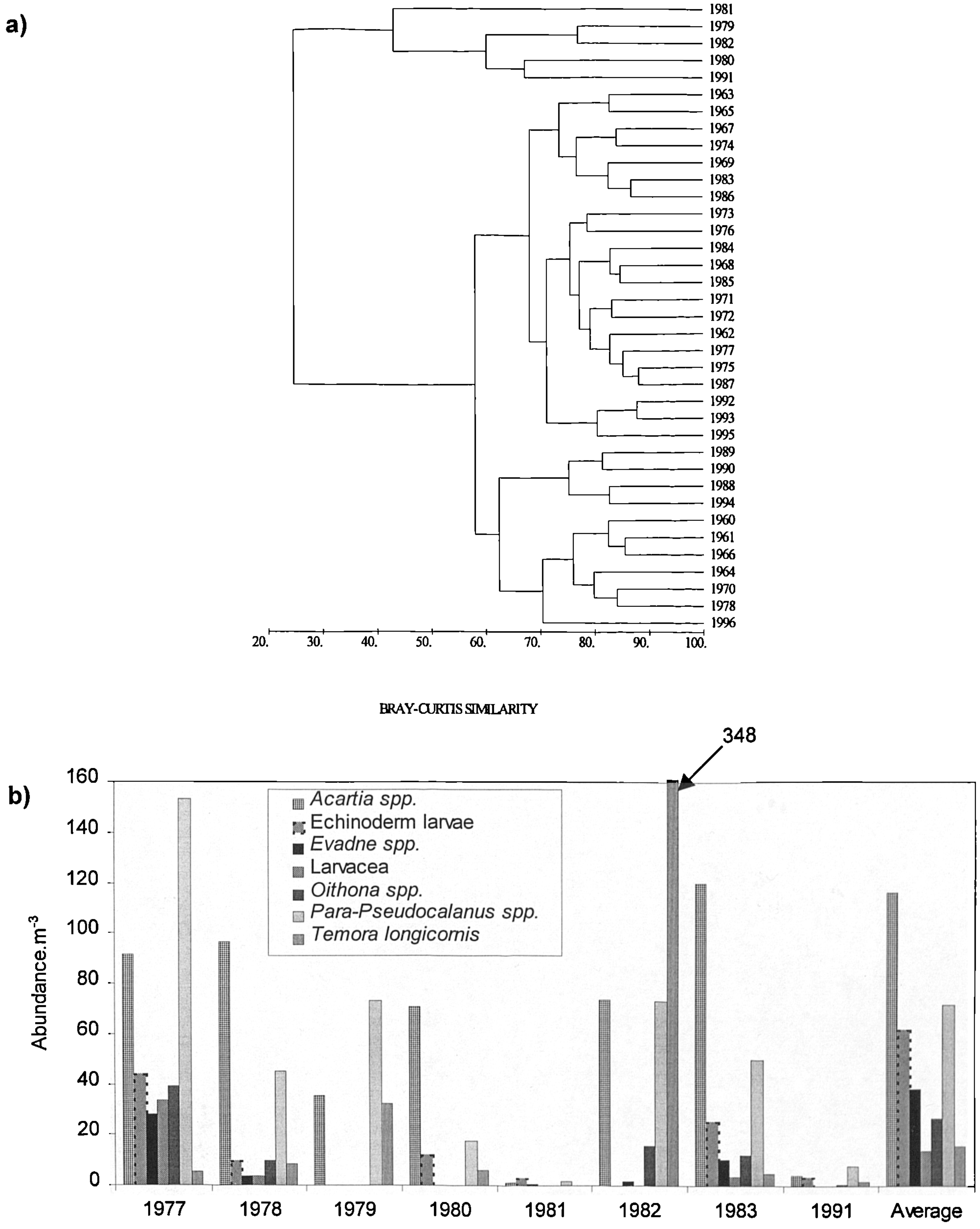


Figure 4.6 a) Cluster analysis of zooplankton from the CPR time series using a $\log_{10}$ transformation of annual means calculated from the months January to July only from 1960-1996. b) Mean abundance of selected taxa (contributing to at least 25% dissimilarity) identified by SIMPER results for the months January to July for years, 1977, 1978, 1979, 1980, 1981, 1982, 1983, 1991, and the mean abundance for months January to July over all other years.

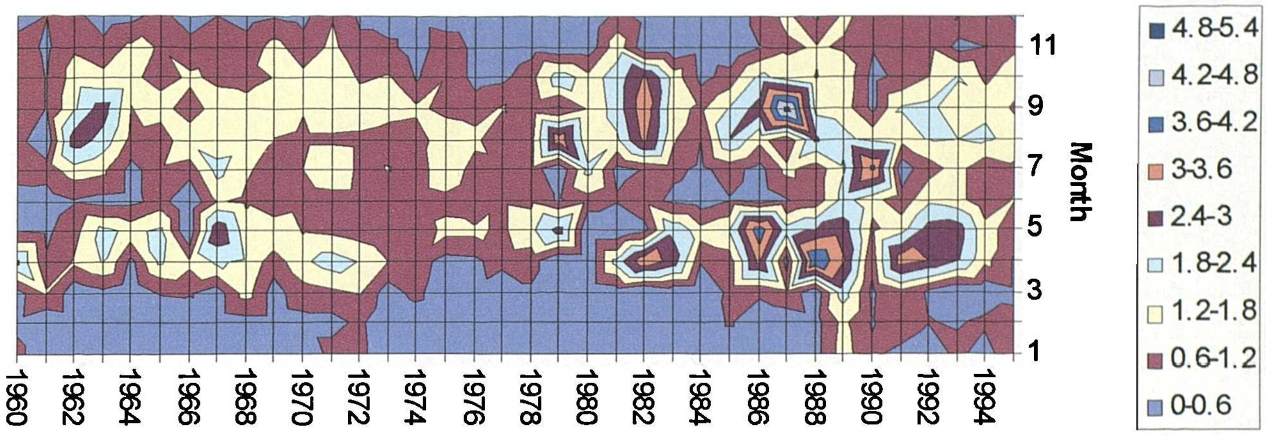


Figure 4.7 Contour plot of phytoplankton index for CPR area C2 for the period 1960 to 1995.

Differences in species composition between high and low abundance years

There was a clear separation in the MDS ordination of the Dove data between high and low abundance years, suggesting that differences in species composition may be linked to productivity (Figure 4.8b). The ANOSIM results (Table 4.2) on the standardised similarity values indicate significant differences in species composition between low and high abundance years, and between low and mid abundance years, although mid and high abundance years were not found to be significantly different. SIMPER analysis (Table 4.3) showed that although the majority of taxa had higher abundances during high abundance years, the *Pseudo-/Para-/Microcalanus* juveniles were most responsible for the differences in species composition between high and low years. In addition, it appears that although the majority of taxa display an increase in high abundance years, it appears that these top ranked taxa (e.g. *Pseudo-/Para-/Microcalanus* spp., *Oithona* etc.) generally show an increase which is out of proportion to others (*Pseudo-/Para-/Microcalanus* displays an abundance ratio between low and high abundance years of 11.5 whereas *Oithona* has a ratio of 2.25).

The MDS ordination of the CPR data showed a clear separation into high (right hand side) and low (left hand side) abundance years (Figure 4.9b). ANOSIM shows that, between high and low years, there is a significant difference in species composition (Table 4.4). However, mid years do not have a significantly different species composition to high or low years. SIMPER gives similar results with the CPR data to that with the Dove data (Table 4.5), with *Evadne, Acartia, Podon* and *Pseudo-/Paracalanus* spp. also in the top 5 taxa contributing to dissimilarity between high and low years, and having a higher abundance during high abundance years. However, it appears that in this series, these taxa generally increase in proportion with lesser ranked taxa. For example, *Evadne* displays an abundance ratio between high and low abundance years of 5.96, whereas *Oithona* has a ratio of 2.18. The reduced ratios observed for this series are likely to be related to the reduced sampling efficiency of the CPR device (Chapter 3), and as such, the Dove series is more likely to be representative of the changes which have occurred.

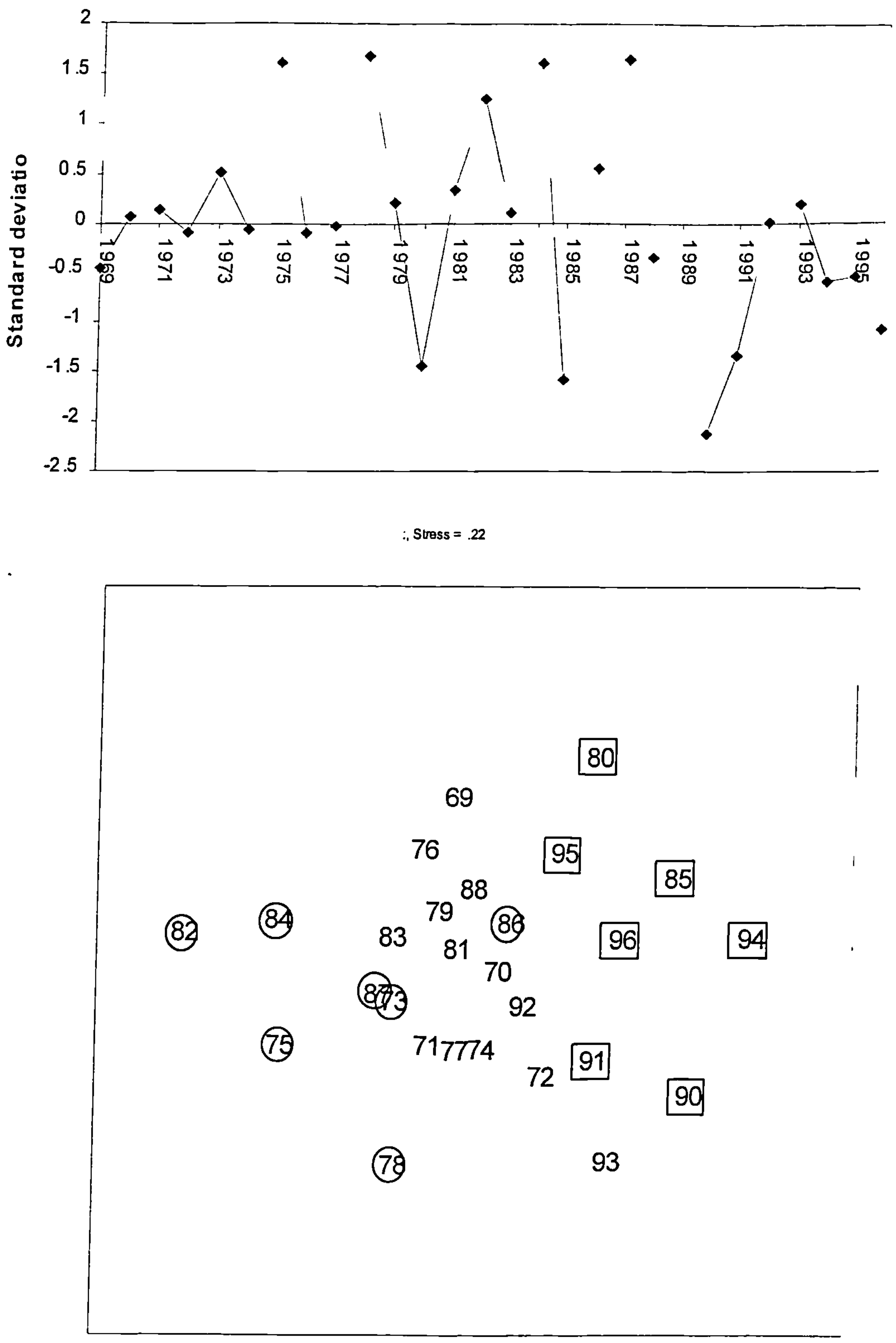


Figure 4.8 a) Annual means of total zooplankton abundance in the Dove time series, standardised to zero mean and unit standard deviation for 1969-1988 and 1990-1996. b) MDS plot for zooplankton in the Dove time series from 1969-1988 & 1990-1996. Circles represent years when abundance was more than 0.5 standard deviations above the long term mean, & squares represent abundance more than 0.5 standard deviations below the long term mean.

Table 4.2 ANOSIM results on standardised data testing for significant differences in species composition between high, mid and low abundance years in the Dove time series. High abundance years (more than 0.5 standard deviations above the long term mean) were; 1973, 1975, 1978, 1982, 1984, 1986, 1987. Mid abundance years (between –0.5 and 0.5 standard deviations from the zero mean) were; 1969, 1970, 1971, 1972, 1974, 1976, 1977, 1979, 1981, 1983, 1988, 1992, 1993. Low abundance years (defined as less than 0.5 standard deviations below the long term mean) are; 1980, 1985, 1990, 1991, 1994, 1995, 1996. Analysis was performed on $\log_{10}$ transformed abundances to minimise weighting of numerically dominant species.

GLOBAL SIGNIFICANCE TEST
Sample statistic (Global R): 0.257
Number of permutations: 10000
Number of permuted statistics greater than or equal to global R: 5
Significance level of sample statistic: 0.1%

Pairwise tests between groups of years:

Groups of years	Stat. Value	Permutations used	Significant statistics	Significance level
Low & High	0.501	1716	2	0.1%
Low & Mid	0.267	10000	98	1.0%
Mid & High	0.102	10000	209	15.2%

Table 4.3 SIMPER analysis on Dove data showing mean abundances and percentage contribution of each taxa to Bray-Curtis dissimilarity between high and low abundance years. Analysis was performed on double square root transformed abundances to minimise weighting of numerically dominant species. Average Bray-Curtis dissimilarity between high and low abundance years is 25.48%.

Taxa	Mean abundance during high zooplankton years	Mean abundance during low zooplankton years	Percentage dissimilarity	Cumulative dissimilarity %
Pseudo-/Para-/Microcalanus juv.	2212.41	193.05	7.39	7.39
Evadne nordmanni	1004.08	72.9	5.88	13.27
Temora longicornis	733.27	60.59	5.7	18.96
Acartia spp. juv.	1637.66	405.32	4.5	23.46
Podon spp.	78.29	4.31	3.89	27.35
Fritillaria borealis	68.24	17.62	3.7	31.05
Oithona similis	1211.14	537.35	2.83	33.88
Echinoderm larvae	9.16	5.02	2.53	36.4
Acartia longiremis	183.82	53.64	2.43	38.84
Euphausiid spp. nauplii	5.26	25.77	2.43	41.27
Centropages spp. juv.	26.3	18.49	2.25	43.52
Aglantha digitale	16.23	1.02	2.25	45.76
Microsetella norvegica	17.92	1.64	2.22	47.98
Euphausiid spp. juv.	23.2	3.49	2.21	50.19
Jellyfish juv.	6.67	1.99	2.13	52.32
Ophioplutei larvae	82.81	53.44	2.09	54.41
Echinoplutei larvae	10.46	3.09	2.09	56.5
Calanus spp. males	15.96	0.89	2.08	58.58
Bryozoan larvae	17	3.85	2	60.58
Centropages typicus	1.86	3.97	1.99	62.57
Pseudocalanus elongatus	202.5	85.37	1.97	64.54
Oikopleura diocia	140.22	52.09	1.93	66.46
Acartia clausi	437.47	199.63	1.92	68.38
Paracalanus parvus	22.07	26.38	1.88	70.26
Anomuran larvae	0.04	0.84	1.8	72.05
Microcalanus pusillus	12.88	9.83	1.79	73.84
Calanus spp. juv.	101.54	50.62	1.76	75.6
Cirripeda larvae	88.31	34.63	1.76	77.36
Gastropoda larvae	68.14	22.79	1.71	79.07
Calanus finmarchicus	1.92	1.02	1.55	80.63
Phoronid larvae	0.75	1.79	1.48	82.11
Bivalve larvae	94.01	50.8	1.48	83.59
Centropages hamatus	29.18	14.57	1.43	85.02
Tomopteris helgolandica	1.58	0.3	1.42	86.44
Sagitta elegans	20.86	8.53	1.39	87.83
Calanus helgolandicus	1.95	1.02	1.36	89.19
Themisto gaudichaudi	0.75	1.25	1.33	90.52
Tigriopus spp.	0	0.5	1.26	91.79
Corycaeus anglicus	0.41	0.37	1.25	93.04
Thysanoessa raschi	0	0.13	1.18	94.22
Polychaeta larvae	35.66	44.74	1.16	95.38
Thysanoessa inermis	0	0.15	1.15	96.53
Fish larvae	0.03	0.14	0.99	97.52
Nyctiphanes couchi	0.02	0.1	0.95	98.48
Oncaea venusta	0	0.43	0.91	99.38
Nanomia cara	0.41	0.02	0.62	100

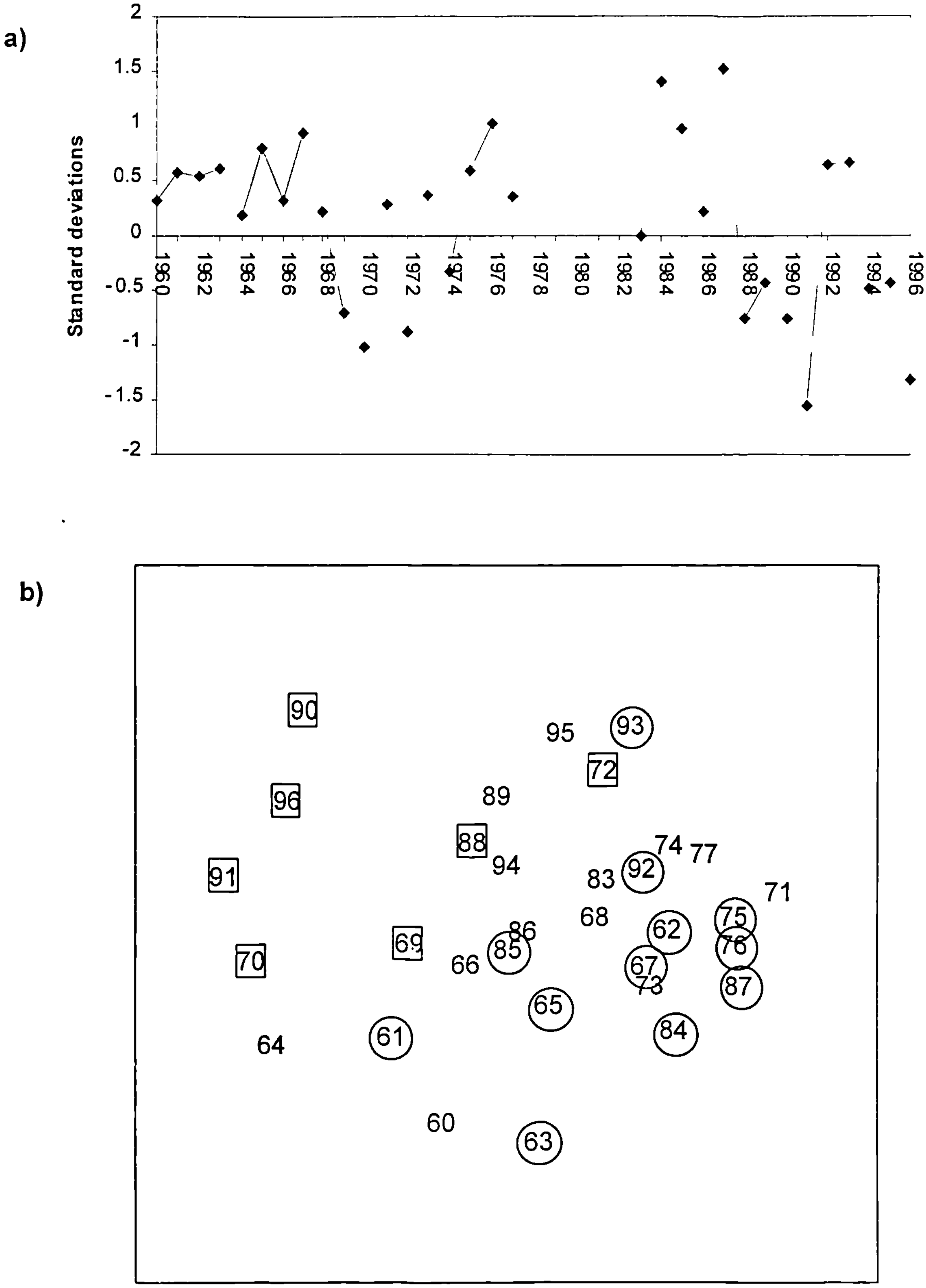


Figure 4.9 a) Annual means of total zooplankton abundance in the CPR time series, standardised to zero mean and unit standard deviation. b) MDS plot for zooplankton in the CPR time series from 1960-1996, omitting 1978 & 1979 because of the lack of complete samples, and omitting 1980-82 because of the very different species composition present in these years. Circles represent years when abundance was more than 0.5 standard deviations above the long term mean, and squares represent years when abundance was less than 0.5 standard deviations below the long term mean.

Table 4.4 ANOSIM results on standardised data testing for significant differences in species composition between high, mid and low abundance years in the CPR time series. High abundance years (defined as more than 0.5 standard deviations above the long term mean) were; 1961, 1962, 1963, 1965, 1967, 1975, 1976, 1984, 1985, 1987, 1992, 1993. Mid abundance years (between –0.5 and 0.5 standard deviations from the zero mean) were; 1960, 1964, 1966, 1968, 1971, 1973, 1974, 1977, 1983, 1986, 1989, 1994, 1995. Low abundance years (defined as less than 0.5 standard deviations below the long term mean) are; 1969, 1970, 1972, 1988, 1990, 1991, 1996. Years 1978-82 were not considered in this analysis. Analysis was performed on $\log_{10}$ transformed abundances to minimise weighting of numerically dominant species.

GLOBAL TEST SIGNIFICANCE TEST
Sample statistic (Global R): 0.119
Number of permutations: 10000
Number of permuted statistics greater than or equal to global R: 241
Significance level of sample statistic: 2.4%

Pairwise tests between groups of years:

Groups of years	Stat. Value	Permutations used	Significant statistics	Significance level
Low & High	0.427	10000	8	0.1%
Low & Mid	0.128	10000	969	9.7%
Mid & High	-0.037	10000	7558	75.6%

Table 4.5 SIMPER analysis on CPR data showing mean abundances and percentage contribution of each taxa to Bray-Curtis dissimilarity between high and low abundance years. Analysis was performed on double square root transformed abundances to minimise weighting of numerically dominant species. Average Bray-Curtis dissimilarity between high and low abundance years is 16.25%.

Taxa	Ave abundance during high zooplankton years	Ave abundance during low zooplankton years	Percentage dissimilarity	Cumulative dissimilarity %
Evadne spp.	46.86	7.86	8.55	8.55
Acartia spp.	136.16	44.11	6.59	15 14
Echinoderm larvae	79.87	33.89	5.94	21.08
Pseudo-/Paracalanus spp.	82.38	31.19	5.62	26.7
Podon spp.	8.49	3.4	4.9	31 6
Centropages typicus	6.8	1.94	4.41	36.01
Pseudocalanus elongatus	15.76	5.01	4.19	40 2
Limacina retroversa	13.01	6.4	4.11	44 3
Larvacea	19.17	6.32	3.98	48.28
Temora longicornis	16.23	12.02	3.83	52.11
Oithona spp.	30.5	13.94	3.54	55 66
Lamellibranchia larvae	9.46	1.82	3.49	59.15
Harpacticoida spp.	0.44	0.23	3.43	62.58
Cyphonautes larvae	2.41	0.84	3 29	65.87
Calanus stages I-IV	20.7	20.38	3.21	69.08
Calanus finmarchicus	1.54	2.43	3.1	72.19
Copepod nauplii	12.58	7.54	2.77	74.96
Centropages hamatus	2.96	1.69	2.58	77 54
Calanus stages V-VI	2.5	3.27	2.25	79.79
Chaetognatha	5	4.76	1.79	81.58
Cirripede larvae	0.88	1.2	1.78	83 36
Metridia larvae	0.07	0.02	1.73	85.09
Euphausiids	1.48	2.25	1.67	86.76
Acartia longerimis	0.06	0	1.66	88 42
Calanus helgolandicus	0.91	1	1.64	90 06
Tomopteris spp.	0.04	0.05	1.57	91 63
Hyperiidea	0.15	0.21	1.54	93 18
Metridia lucens	0.05	0.12	1.41	94 59
Spindelei	0.04	0.02	1.4	96
Corycaeus spp.	0 06	0	1 3	97 3
Decapod larvae	0.58	0.42	1.02	98 32
Fish larvae	0.2	0.17	0 99	99 3
Oncaea spp.	0	0.02	0.7	100

Differences in species composition between northerly and southerly GSNW years

Excepting 1984 (see below), the MDS plot on the Dove series shows a separation into northerly GSNW years (right hand side) and southerly GSNW years (left hand side) (Figure 4.10b). ANOSIM results do that there were differences in species composition between northerly and southerly GSNW years (Table 4.6), although there were no significant differences between mid years, and northerly or southerly years respectively.

The dominant *Pseudo-/Para-/Microcalanus* juvenile group contributed the most to Bray-Curtis dissimilarity between north and south GSNW years (Table 4.7). This agrees with the strong correlation found between this group and the GSNW (r=-0.61, p=0.006) (Appendix 2.2). Abundance of many zooplankton species are reduced during northerly GSNW years, although *Evadne* (ranked 2nd) shows an increased abundance during northerly GSNW years. Given the dominance of this species in 1984 it is likely that it is the reason why this year, although classified as being a northerly GSNW year, is ordinated amongst the southerly GSNW years (Figure 4.10b).

Although there does not appear to be a clear separation in the MDS plot for the CPR data between north and south GSNW years (Figure 4.11), the ANOSIM results show that the species composition between north and south GSNW years was significantly different (Table 4.8). The echinoderm larvae were the taxa contributing most to differences in species composition between north and south GSNW years (Table 4.9), with increased abundances during northerly years. However, the small copepod species such as *Pseudo-/Paracalanus*, *Temora* and *Calanus* stages I-IV show the opposite pattern, with increased abundances of these taxa present during southerly GSNW years similar to the results in the Dove zooplankton series.

These results are reflected to some extent in the correlation between echinoderm larvae and the GSNW (r=0.46, p=0.064) and also in the negative correlation between the GSNW and *Temora* (r=-0.53, p=0.015).

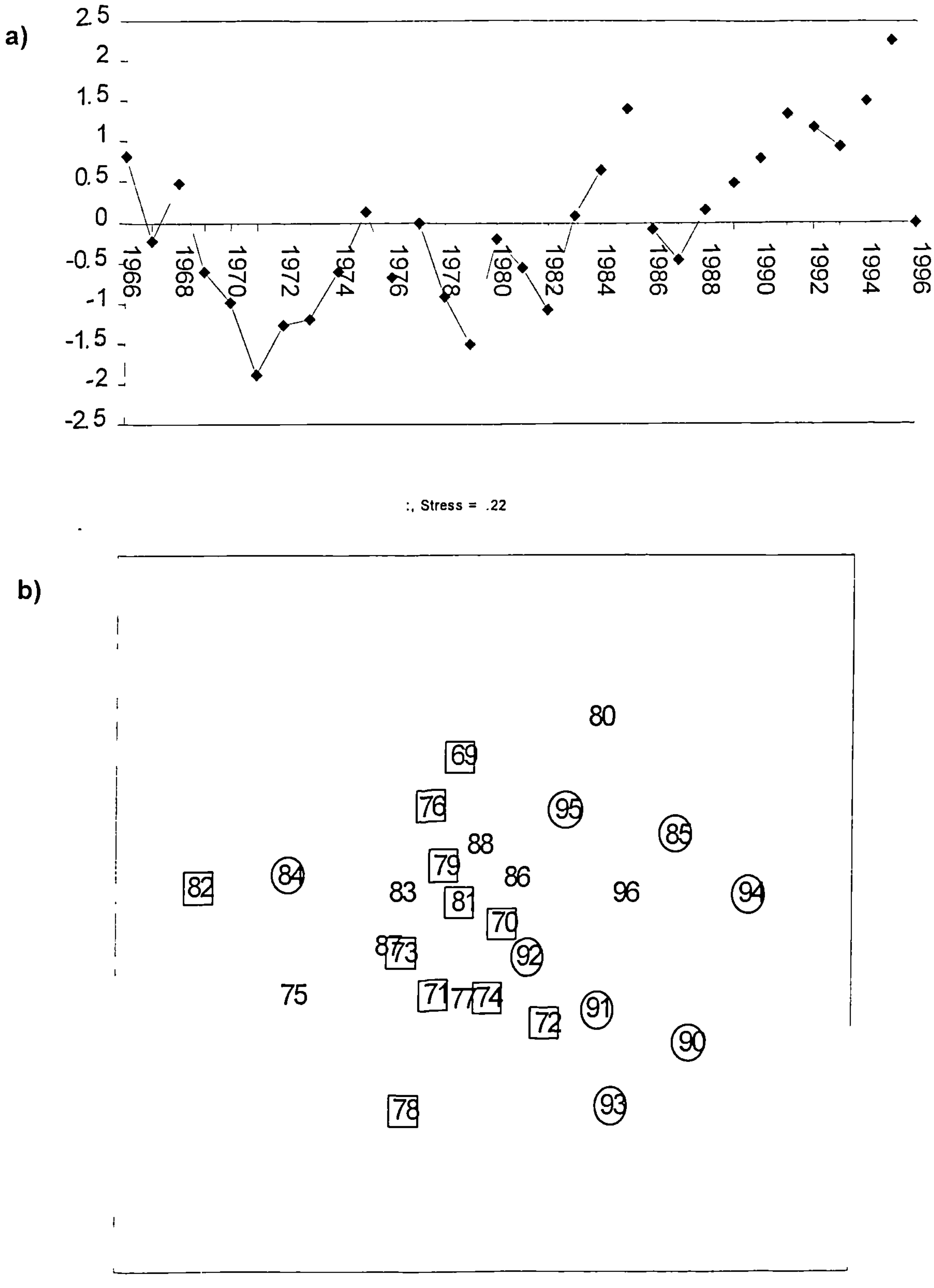


Figure 4.10 a) First Principal Component of GSNW position, 1966-1996. b) MDS plot for zooplankton in the Dove time series from 1969-1988 & 1990-1996. Circles represent years of northerly GSNW position (more than 0.5 standard deviations above the long term mean), and squares represent years of southerly GSNW position (less than 0.5 standard deviations below the long term mean).

Table 4.6. ANOSIM results on Dove zooplankton data testing for significant differences in species composition between southerly, mid and northerly GSNW years. Southerly years were 1969, 1970, 1971, 1972, 1973, 1974, 1976, 1978, 1979, 1981, 1982. Mid years were 1975, 1977, 1980, 1983, 1986, 1987, 1988, 1996. Northerly years were 1984, 1985, 1990, 1991, 1992, 1993, 1994, 1995. Analysis was performed on $\log_{10}$ transformed abundances to minimise weighting of numerically dominant species.

GLOBAL SIGNIFICANCE TEST
Sample statistic (Global R): 0.114
Number of permutations: 10000
Number of permuted statistics greater than or equal to global R: 303
Significance level of sample statistic: 3.0%

Pairwise tests between groups of years:

Groups of years	Stat. Value	Permutations used	Significant statistics	Significance level
Southerly & Northerly	0.23	10000	37	0.4%
Southerly & Mid	0.007	10000	4371	43.7%
Mid & Northerly	0.087	6435	915	14.2%

Table 4.7 SIMPER analysis on Dove zooplankton data showing percentage contributions of each taxa to Bray-Curtis dissimilarity between years of northerly and southerly GSNW. Analysis was done on double square root transformed abundances to minimise weighting of numerically dominant species. Average Bray-Curtis dissimilarity between high and low GSNW years is 22.47%.

Taxa	Mean abundance during northerly GS years	Mean abundance during southerly GS years	Percentage dissimilarity	Cumulative dissimilarity %
Pseudo-/Para-/Microcalanus juv.	358.7	1150.73	5.8	5.8
Evadne nordmanni	732.79	220.49	4.47	10.27
Euphausiid nauplii	19.25	38.5	3.53	13.8
Temora longicornis	150.48	406.92	3.35	17.14
Acartia spp. juv.	445.26	809.53	3.26	20.4
Ophioplutei larvae	56.38	43.18	3.03	23.43
Echinoderm larvae	4.05	5.38	2.93	26.37
Fritillaria borealis	16.39	36.46	2.92	29.28
Euphausiid spp. juv.	7.58	26.85	2.86	32.14
Oithona similis	678.69	1213.95	2.73	34.87
Centropages typicus	5.84	5.07	2.61	37.49
Acartia longicornis	167.08	185.2	2.58	40.06
Aglantha digitata	1.39	10.21	2.43	42.5
Paracalanus parvus	56.64	26.49	2.4	44.9
Calanus spp. males	0.87	10.49	2.4	47.3
Podon spp.	34.44	39.38	2.37	49.67
Calanus spp. juv.	43.87	90.81	2.27	51.94
Centropages spp juv.	19.01	71.53	2.24	54.18
Centropages hamatus	18.87	22.03	2.19	56.37
Anomuran larvae	0.85	1.34	2.11	58.48
Oikopleura diocia	67.37	107.58	2.1	60.58
Bryozoan larvae	5.07	9.52	2.06	62.64
Tomopteris helgolandica	0.27	3.18	2.02	64.66
Microcalanus pusillus	7.84	5.2	2	66.66
Pseudocalanus elongatus	164.67	139.16	1.98	68.64
Acartia clausi	389.46	289.45	1.93	70.57
Microsetella norvegica	1.25	11.92	1.9	72.47
Echinoderm larvae	4.23	5.55	1.83	74.3
Phoronid larvae	1.86	1.37	1.8	76.1
Jellyfish juv.	2.49	1.36	1.77	77.87
Calanus helgolandicus females	1.14	0.76	1.75	79.62
Gastropod larvae	17.58	54.44	1.74	81.36
Bivalve larvae	61.15	84.06	1.69	83.05
Tigriopus spp.	0.66	0	1.68	84.73
Cirripede larvae	54.96	58.02	1.63	86.36
Calanus finmarchicus females	2.3	0.24	1.62	87.98
Themisto gaudichaudi	1.01	1.21	1.6	89.58
Polychaete larvae	39.04	28.72	1.56	91.14
Corycaeus anglicus	0.51	0.16	1.55	92.69
Thysanoessa raschi	0.09	0.51	1.27	93.96
Sagitta elegans	13.06	9.28	1.25	95.21
Fish larvae	0.13	0.18	1.25	96.46
Thysanoessa inermis	0.13	0.01	1.12	97.58
Oncaea venusta	0.38	0	0.95	98.52
Nyctiphanes couchi	0.05	0.04	0.88	99.4
Nanomia cara	0.02	0.26	0.6	100

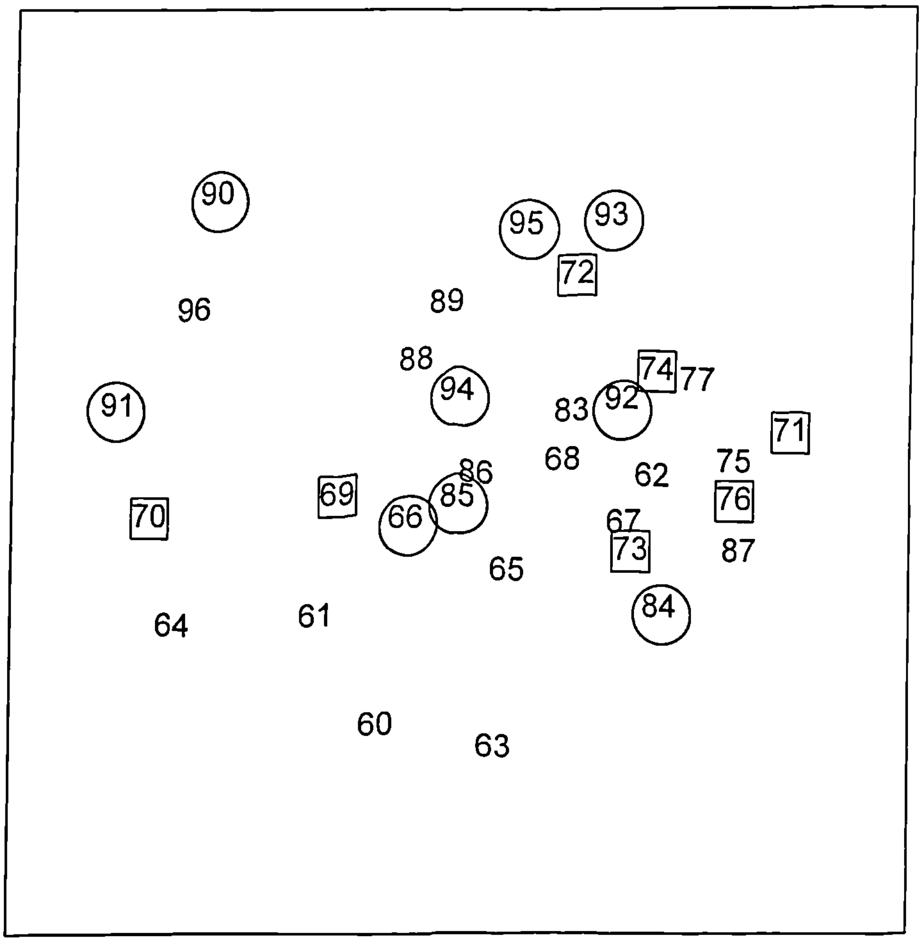


Figure 4.11 **MDS plot for zooplankton in the CPR time series from 1960-1978 & 19820-1996. Circles represent years of northerly GSNW position (more than 0.5 standard deviations above the long term mean), and squares represent years of southerly GSNW position (less than 0.5 standard deviations below the long term mean).**

Table 4.8 **ANOSIM results on CPR zooplankton data testing for significant differences in species composition between southerly, mid and northerly GSNW years. Southerly years were 1969, 1970, 1971, 1972, 1973, 1974, 1976. Mid years were 1975, 1977, 1983, 1986, 1987, 1988, 1996. Northerly years were 1966, 1984, 1985, 1990, 1991, 1992, 1993, 1994, 1995. Analysis was performed on $\log_{10}$ transformed abundances to minimise weighting of numerically dominant species.**

GLOBAL SIGNIFICANCE TEST
Sample statistic (Global R): 0.126
Number of permutations: 10000
Number of permuted statistics greater than or equal to global R: 445
Significance level of sample statistic: 4.5%

Pairwise tests between groups of years:

Groups of years	Stat. Value	Permutations used	Significant statistics	Significance level
Southerly & Northerly	0.246	6435	142	2.2%
Southerly & Mid	0.081	10000	1765	17.7%
Mid & Northerly	0.085	10000	1405	14.1%

Table 4.9 **SIMPER analysis on CPR zooplankton data showing percentage contributions of each taxa to Bray-Curtis dissimilarity between years of northerly and southerly GSNW. Analysis was done on double square root transformed abundances to minimise weighting of numerically dominant species. Average Bray-Curtis dissimilarity between high and low GSNW years is 14.89%.**

Taxa	Mean abundance during northerly GS years	Mean abundance during southerly GS years	Percentage dissimilarity	Cumulative dissimilarity %
Echinoderm larvae	68.54	21.91	6.88	6.88
Evadne spp.	33.63	21.11	6.54	13.42
Centropages typicus	3.31	13.02	5.46	18.89
Larvacea	26.05	4.24	4.86	23.74
Pseudo-/Paracalanus spp.	35.4	66.4	4.48	28.22
Podon spp.	5.21	7.21	4.4	32.62
Temora longicornis	9.36	23.74	4.3	36.92
Harpacticoida spp.	0.22	0.61	4.18	41.1
Acartia spp.	98.94	92.46	4.17	45.27
Pseudocalanus elongatus	7.95	12.74	3.54	48.81
Copepod nauplii	13.59	9.21	3.48	52.29
Calanus stages I-IV	16.64	14.15	3.43	55.72
Calanus finmarchicus	1.65	1.33	3.25	58.97
Limacina retroversa	9.25	7.69	3.13	62.1
Cyphonautes larvae	1.59	1.07	2.87	64.97
Oithona spp.	27.18	17.47	2.64	67.6
Cirripede larvae	0.82	0.9	2.59	70.19
Centropages hamatus	2.62	2.6	2.53	72.72
Lamellibranchia larvae	1.62	3.82	2.44	75.16
Calanus stages V-VI	2.86	1.89	2.42	77.58
Chaetognatha	4.98	3.67	2.33	79.91
Hyperiidea	0.26	0.09	2.18	82.09
Acartia longiremis	0.02	0.55	2.12	84.21
Corycaeus spp.	0.11	0.02	2.03	86.25
Metridia stages I-IV	0.02	0.05	1.94	88.19
Calanus helgolandicus	1.22	0.56	1.76	89.94
Euphausiid total	1.82	1.88	1.74	91.69
Microcalanus spp.	0.11	0	1.7	93.39
Tomopteris spp.	0.02	0.07	1.51	94.89
Decapod larvae	0.58	0.64	1.05	95.95
Metridia lucens	0.09	0.03	1.01	96.95
Fish larvae	0.12	0.12	0.78	97.73
Candacia stages I-IV	0.03	0	0.76	98.49
Spindelei	0.04	0	0.76	99.25
Oncaea spp.	0	0.02	0.75	100

Long term changes in chemical composition

No significant trends were found in concentration of any of the nutrients (ammonium, nitrate (Figure 2.10a) and nitrite) (Table 4.10), and thus based on these data, long term changes in primary and secondary production cannot be related to long term changes in nutrient levels. Salinity does show a slight decrease over the 1968 to 1995 period, and chlorophyll shows a significant increase over the same period, agreeing with the similar trends in CPR phytoplankton index.

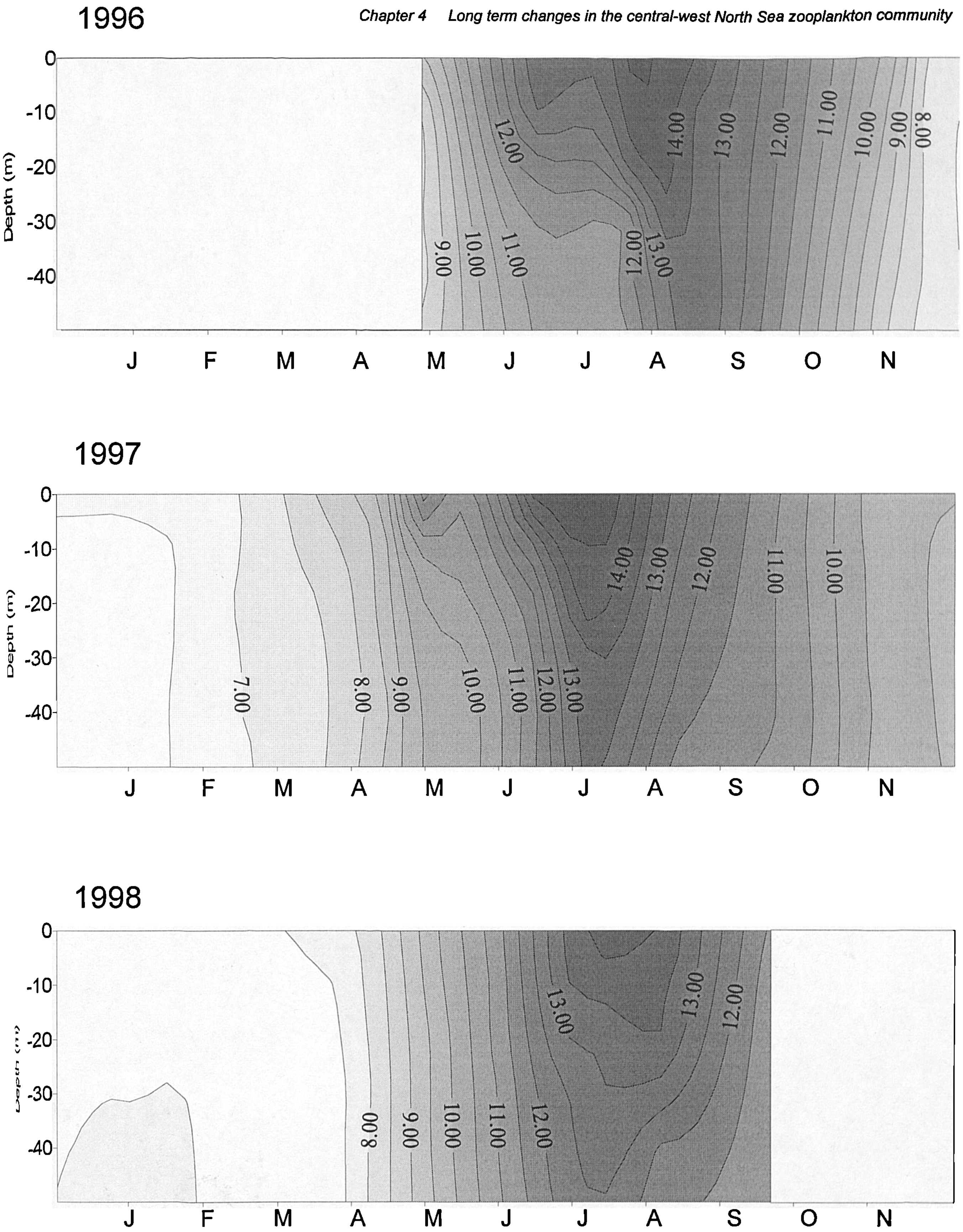


Figure 4.12 Contour plot of annual changes in temperature (°C) at the Dove zooplankton station with depth for 1996 to 1998.

Table 4.10 Results of trend analysis on ICES data using the Mann-Kendal test for trend. Global p=0.044.

Variable	Period	No. of samples	S (Mann-Kendall)	Significance of S
Ammonium	1978-1995	34	-77	0.21
Bottom oxygen	1982-1993	27	-71	0.14
Chlorophyll	1982-1992	18	89	0.002
Nitrate	1968-1995	70	237	0.2
Nitrite	1968-1995	55	65	0.36
Salinity	1968-1995	158	-2400	<0.001
SST	1968-1995	146	610	0.23

The limited temperature data from the Dove zooplankton station does show that seasonal stratification did occur in each year from 1996-1998 (Figure 4.12), although the strength and duration of this varied. Weakest stratification occurred in August 1998 with a temperature difference of 1.7°C between the surface and bottom waters, compared to a temperature difference of 3.1°C in August 1996. This corresponded with a shorter duration of stratification and a shallower thermocline in 1988 (20m in 1996 compared to 30m in 1997 and 1998).

The monthly chlorophyll data taken at the Dove station suggests that the spring bloom occurred in June in 1997 and in May in 1998 (Figure 4.13a). Consequently, the timing of peak chlorophyll concentrations varied, as did the amount of chlorophyll. Based upon these two years, the timing of the chlorophyll increase had no relation to the timing of thermocline formation, although, at this relatively shallow station, this is not unexpected. Nitrate concentrations began to decrease in May in 1997 and in March in 1998, corresponding to the increases in chlorophyll. The nutrient concentrations increased again around September with the decline in chlorophyll (Figure 4.13a). The cycles of nitrite (Figure 4.13c) and phosphate (Figure 4.13d) are not so straightforward but do show low values during the summer and higher values during the winter, as would be expected.

Monthly values of the carotenoid to chlorophyll ratios reach their highest in the winter of 1997-1998 (Figure 4.13e), which is when nutrient limitation of phytoplankton would not be expected. However, these results suggest that, over the time frame of the data available, nutrient limitation does not exist to any great extent, and during the months of maximum phytoplankton growth, from March - May, there is often an excess of nitrogen available.

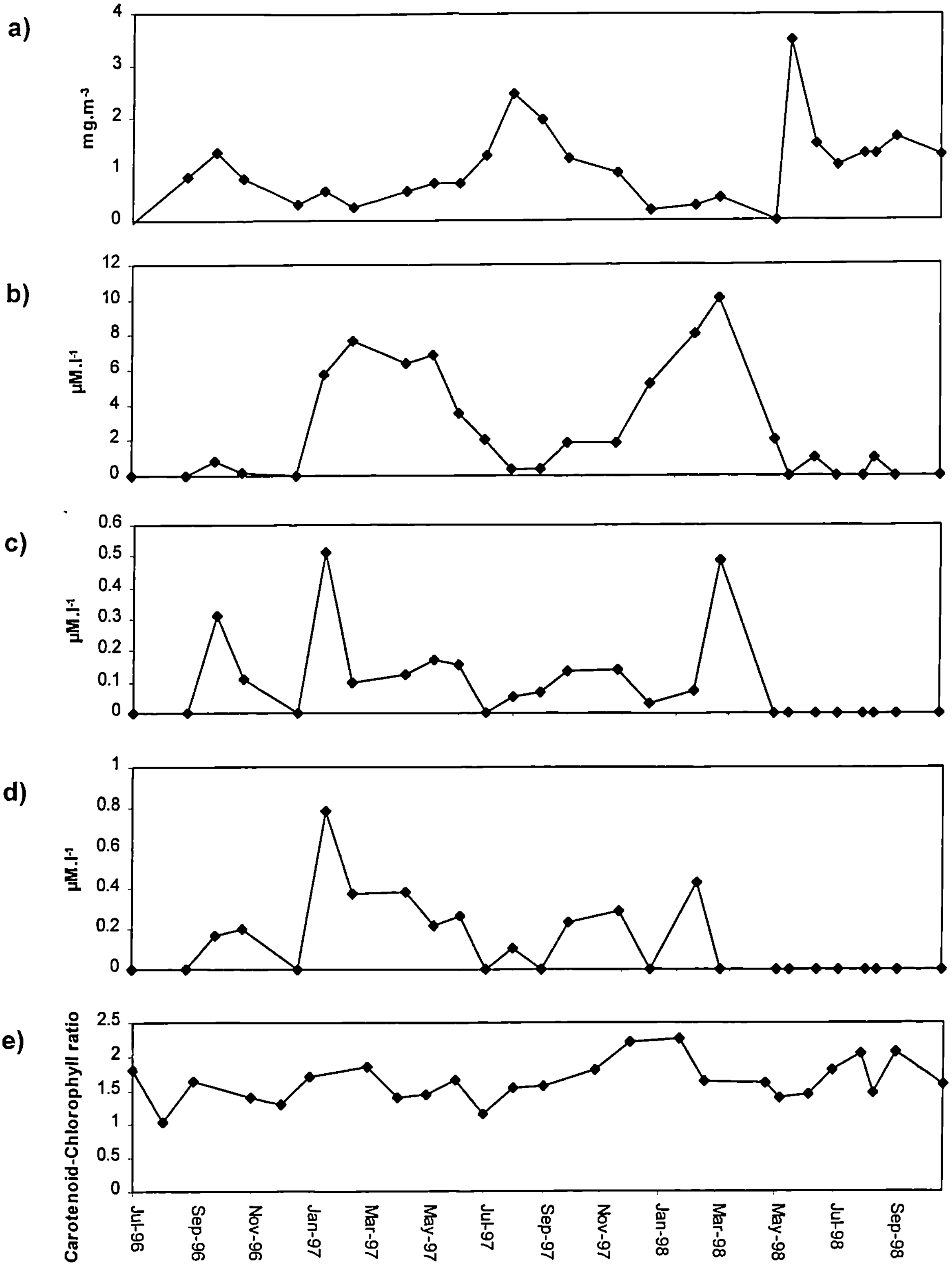


Figure 4.13 Values of a) chlorophyll. b) Nitrate. c) Nitrite. d) Phosphate. e) Carotenoid: chlorophyll ratio. Data covers the period July 1996 to September 1998, although data are not available for all months.

Long term relationships between environmental variables and zooplankton

Phytoplankton index data

Phytoplankton index data from the coastal NE England/SE Scotland area only shows a positive relationship with wind speed at Tynemouth (r=0.48, p=0.021) (Table 4.11). However, data for CPR area C2 show positive associations with sunshine at both stations (Tynemouth r=0.40, p=0.023; Durham r=0.46, p=0.16) and also positively with wind speed at Tynemouth (r=0.39, p=0.047). However, there is a negative association between C2 phytoplankton index and wind speed recorded at Durham (r=-0.51, p=0.029). The differences in the response of the phytoplankton to wind speed are likely to be due to the unique weather phenomena observed at the coastal Tynemouth station – higher temperatures are likely to result in increased wind speeds due to the increased onshore breezes as a result of differential heating of the land.

Table 4.11 Correlation coefficients between annual mean phytoplankton index for the central-west North Sea and area C2 against environmental variables. All probability values are corrected for serial correlation. Only those probability values less than p<=0.05 before correction for autocorrelation are included, significant correlations after correction are in bold. Global p=0.015.

	Area C2	Central-west North Sea
Tynemouth air temperature	0.11	0.00
Tynemouth mean wind speed	**0.39** p=0.047	**0.48** p=0.021
Tynemouth sunshine (hours)	**0.40** p=0.023	-0.02
Durham air temperature	0.24	-0.04
Durham mean wind speed	**-0.51** p=0.029	-0.22
Durham sunshine (hours)	**0.46** p=0.016	0.13
GSNW	0.13	0.01
NAO	0.21	-0.04
SST	0.16	0.05
Lambs weather (PC1)	-0.27	-0.11

Dove and CPR zooplankton data

It was found that long term changes in the GSNW were negatively related to changes in the Dove series total zooplankton (r=-0.4, p=0.046) (Figure 4.14a). The relationship between the dominant *Pseudo-/Para-/Microcalanus* juveniles and the GSNW was especially strong (r=-0.61, p=0.006) (Figure 4.14b), as it was with the second most dominant species, *Oithona* (r=-0.49, p=0.033) (Figure 4.14c) and *Temora longicornis* (r=-0.47, p=0.018) (Figure 4.14d). The sign of the relationships between biota and the GSNW were opposite to those detected by Taylor & Stephens (1980), Taylor *et al.* (1992) and Taylor (1996). Further examination of the time series plots (Figures 4.14a-d) suggests that during 1984 all these taxa had higher abundances than would be expected from the position of the GSNW. However, year to year changes in the biota did not consistently relate to changes in the GSNW. For example, the *Pseudo-/Para-/Microcalanus* juveniles relationship with the GSNW is strong (Figure 4.14b) from 1977 until 1993-4, and this is reflected in the association between total zooplankton and the GSNW from 1977 until 1991 (Figure 4.14a). Negative associations were also present between the *Pseudo-/Para-/Microcalanus* juveniles and air temperature at Durham (r=-0.59, p=0.016) (Figure 4.14e). Annual phytoplankton productivity, which would be expected to be positively related to zooplankton production was only positively related to the abundance of *Acartia clausi* (r=0.45, p=0.024) (Figure 4.14f). In addition, there were a few taxa which did show expected relationships to climate, such as polychaete larvae (r=0.40, p=0.045), and the euphausiids displayed higher abundances to reduced wind speeds (r=-0.41, p=0.049) (see Appendix 3.1).

In the CPR series, there were fewer taxa associated with the GSNW than in the Dove series, with only *Temora longicornis* (r=-0.53, p=0.015), and *Tomopteris* (r=-0.44, p=0.047), presenting negative relationships with the GSNW (Figure 4.15a). As in the Dove series, the CPR *Pseudo-/Paracalanus* spp. also showed strong negative correlations with air temperature (r=-0.69, p=0.005) (Figure 4.15b). Although there were these small copepod taxa which presented negative correlations with air temperature here, as in the Dove series, some of the larger and rarer taxa showed the expected positive associations with temperature (Appendix 3.2) such as *Calanus helgolandicus* (Tynemouth r=0.37, p=0.032) and *Corycaeus* (Durham r=0.42, p=0.044) and the predatory chaetognaths with air temperature (Tynemouth r=0.36, p=0.041) (Figure 4.15e) and wind (Durham r=-0.48, p=0.042) (Figure 4.15f).

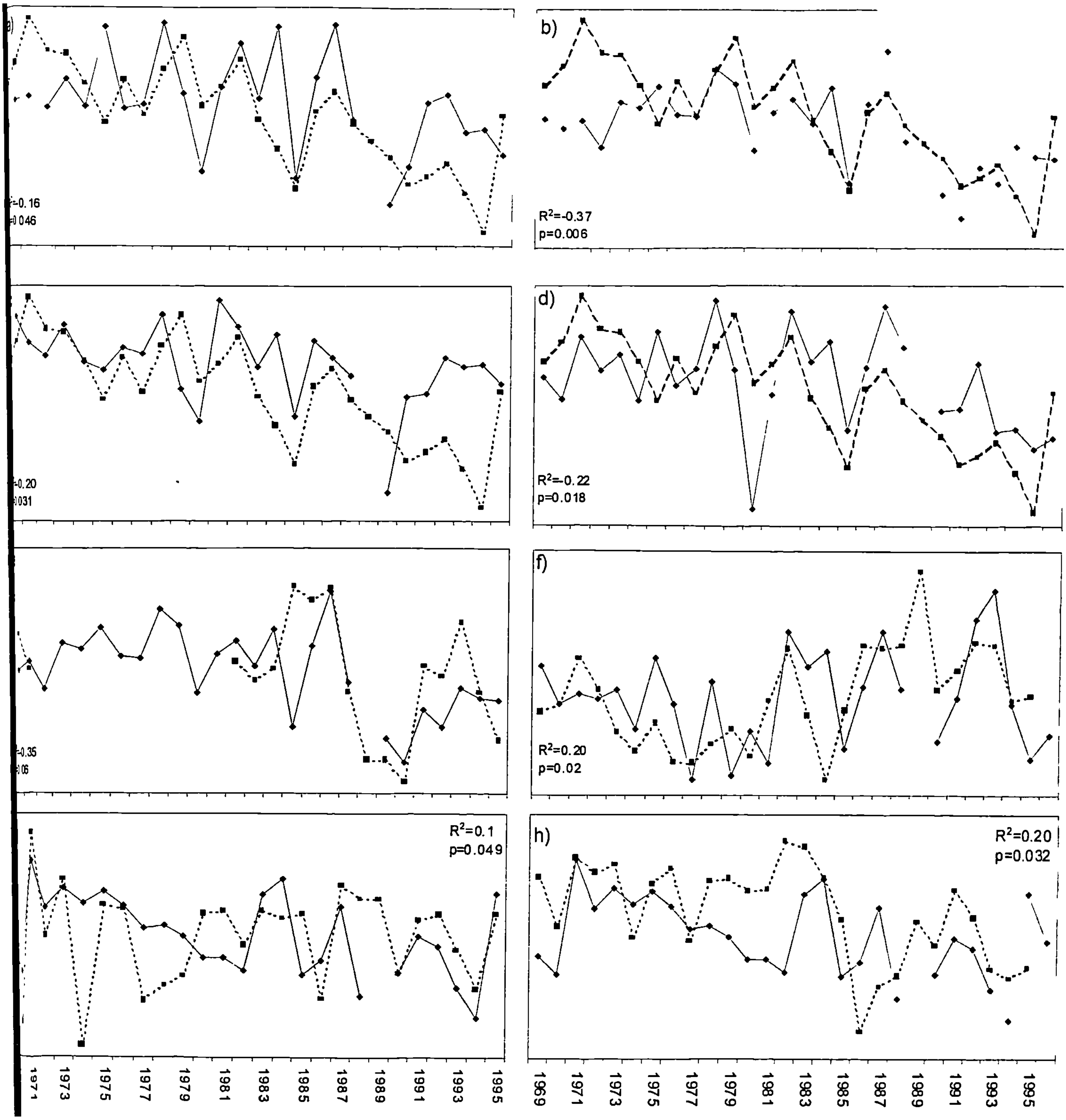


Figure 4.14 Standardised time series plot of environmental variables (—■—) with selected taxa from the Dove series (—◆—) of, a) Gulf Stream North Wall (inverted) & total zooplankton. b) Gulf Stream North Wall (inverted) & *Pseudo-/Para-/Microcalanus* juveniles. c) Gulf Stream North Wall (inverted) & *Oithona similis.* d) Gulf Stream North Wall (inverted) & *Temora longicornis.* e) Durham air temperature (inverted) & *Pseudo-/Para-/Microcalanus* juveniles. f) Phytoplankton colour (area C2) & *Acartia clausi.* g) Lamb's First Principal Component (inverted) & bivalve larvae. h) Tynemouth wind speed (inverted) & bivalve larvae. All significance levels have been corrected for autocorrelation according to the method of Quenouille (1952).

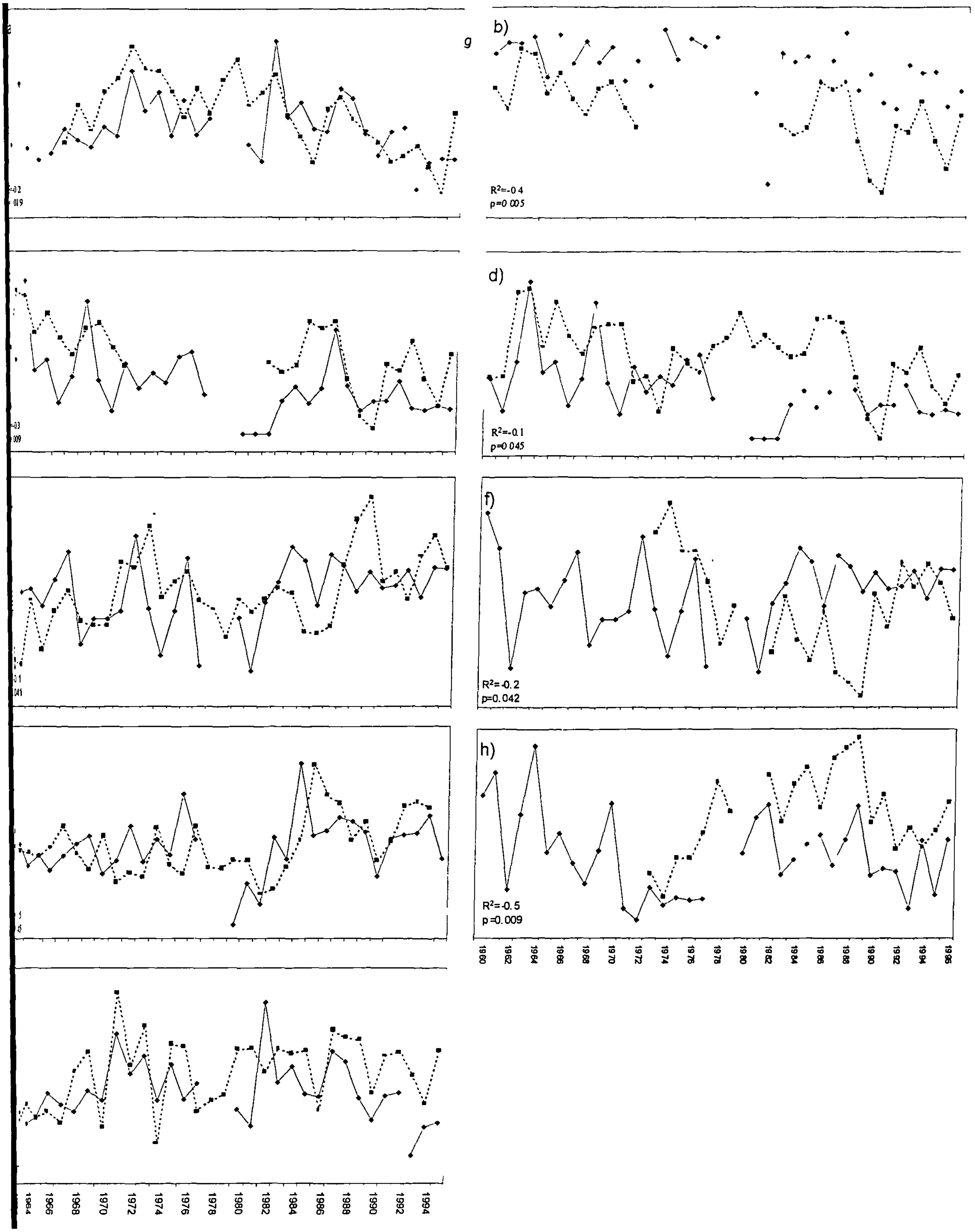


Figure 4.15 Standardised time series plot of environmental variables (—■—) with selected taxa from the CPR series (—◆—) of: a) Gulf Stream North Wall (inverted) & *Temora longicornis*. b) Durham air temperature (inverted) & *Pseudo-/Paracalanus* spp. c) Durham air temperature (inverted) & lamellibranchia larvae. d) Tynemouth air temperature (inverted) & lamellibranchia larvae. e) Tynemouth air temperature & chaetognatha. f) Durham wind speed (inverted) & chaetognatha. g) Tynemouth wind speed & copepod nauplii. h) Durham wind speed (inverted) & *Calanus* stages I-IV. i) Lamb's first principal component (inverted) & *Temora longicornis*. All significance levels have been corrected for autocorrelation according to the method of Quenouille (1952).

Discussion

Austen *et al.* (1991) claimed that the marine ecosystem off the Northumberland coast was influenced by changes in water quality. However, the relationships observed in this study between phytoplankton index (box C2) and weather (Table 4.11) suggest that forcing of primary production in this region is predominantly related to climatic influences. Such observations would agree with numerous previous studies linking long term changes in North Sea primary productivity to climatic effects (e.g. Robinson, 1970; Colebrook, 1978; Colebrook, 1982c; Robinson & Hunt, 1986; Dickson *et al.*, 1988a; Viitasalo *et al.*, 1995; Fromentin & Planque, 1996), and with the parallel trends observed by Aebischer *et al.* (1990) between climate and phytoplankton. As the strongest relationship is between wind speed and phytoplankton productivity, this suggests that the increased wind induced mixing of the water column is principally involved in governing primary productivity (in CPR area C2). Such a mechanism would accord with the theory of Dickson *et al.* (1988b). Although relationships between phytoplankton index and weather for the more coastal central-west North Sea region (Figure 3.2) are not so strong (Table 4.11), in such inshore areas, where stratification is intermittent or absent, factors other than temperature can influence the timing of the spring bloom (Cadée, 1986). For example, Gieskes & Kraay (1975) observed that in clear offshore waters there was an earlier spring bloom relative to turbid coastal waters, the reason being that increased turbidity reduced the amount of light available to phytoplankton, which in turn reduced primary production.

Changes in nutrient levels are unlikely to be causing the long term trends observed for phytoplankton as, although the quality of the data is poor, this study has shown that nutrient concentrations in the central-west North Sea region have not changed significantly from the late 1960s to mid 1990s (Table 4.10), which concurs with observations made in other studies (Dickson *et al.*, 1988b). Indeed, nutrient levels would not be expected to change as much as in the eutrophicated southern areas of the North Sea as, due to the presence of the anti-clockwise gyre in the North Sea (Austen *et al.*, 1991; Fransz *et al.*, 1991), most (99%, Reid *et al.*, 1988) water in this region originates from the Atlantic, and has a relatively low nutrient load (Brockmann *et al.*, 1988). However, although this study suggests that there have been no changes in nutrients in this region, nutrient levels are sufficient (Figure 4.13e) to ensure that the phytoplankton dynamics are free to be influenced by climatic factors.

It might be expected that as increased phytoplankton productivity provides a greater food resource for the zooplankton, the signal of climate would be mediated through to the zooplankton, and thus relationships between climate and zooplankton would be similar to those observed between climate and phytoplankton (Aebischer *et al.*, 1990). However, only *Acartia clausi* presented such a relationship, while many other taxa show relationships which are both opposite to those expected, and opposite to those observed between zooplankton and climate reported by other North Sea studies (e.g. Taylor, 1995). In contrast to the conclusions of Evans & Edwards (1993), but in agreement with the suggestions made by Frid & Huliselan (1996) and Huliselan (1995), long term zooplankton trends for the central-west North Sea also bear little similarity to those displayed in other North Sea areas. Some of the differences between observations in this study, and those of Evans & Edwards (1993) may be due to different levels of taxonomic resolution (which could potentially alter the results of analyses on species composition), and the increased number of datapoints used (see Chapter 2). In contrast to the relatively steady interannual fluctuations observed in CPR North Sea zooplankton series, those in the central-west North Sea Dove and CPR series display large interannual variations in abundance from the mid 1970s to the late 1980s, with no indications of a downward trend in zooplankton abundance, before 1980, followed by a recovery in either series. However, given the similarity between the Dove time series and the CPR time series for the central-west North Sea (Chapter 3), the differences between these trends and those in other regions are unlikely to be due to sampling errors.

The CUSUM analysis did identify a breakpoint as occurring in the late 1980s, and this may be observed in both the Dove and CPR zooplankton series as a downward stepwise change in abundance at this time. The timing of this change coincided with an increase in phytoplankton productivity in the central NE Atlantic and central North Sea (Reid *et al.*, 1998). However, in the north NE Atlantic, a downward stepwise change was observed which was attributed to melting ice from the Arctic which reduced the sea surface temperature. Although this is unlikely to be the explanation for the downward stepwise change here, it does illustrate that opposing trends are not uncommon.

These results also suggest that, as well as there being differences to previously described long term trends, the changes in species composition of the Dove and CPR series are also dissimilar to previous analyses by both Austen *et al.* (1991) and Evans & Edwards (1993). These previous studies both observed, using Dove and CPR data, a change in the zooplankton species composition between the late 1970s and early 1980s. However, this study has shown there is little evidence there was any specific point in either series when any remarkable change in the central-west North Sea zooplankton species composition occurred (excepting the temporary change in the CPR series from 1980-1982). In addition, as determined by the Mann-Kendall test on the Bray-Curtis similarities, over much of the latter half of the 20th century, there was no overall change in the zooplankton species composition. Such observations are in contrast to those observed for the central-west North Sea benthos, which show a steady change in the species composition of the benthos over the 1970 to mid 1990 period (Chapter 6). However, the marked short term change in species composition observed in the CPR series from 1980-1982 does coincide with the period when changes were noted across the North Sea (see Chapters 2 & 8), and with low North Sea zooplankton and phytoplankton abundances (Figure 2.2a & b). This was the period of the shortest phytoplankton season length (Figure 4.7). As such, the late spring bloom and the reduced phytoplankton resource present during this period could be responsible for the large scale temporary changes observed, although if this were the case, why there were no indications of a similar change in the Dove zooplankton series is unknown.

Although zooplankton species composition was not found to change significantly in either series, interannual changes in community structure bore a clear relationship to zooplankton abundance, and (as determined by the standardised ANOSIM test), to the relative proportions of taxa in each series. During high zooplankton years, most taxa show higher abundances relative to low zooplankton years, and, in the Dove series the dominant taxa (e.g. *Pseudo-/Para-/Microcalanus* spp., *Evadne*) generally increase out of proportion. Thus the long term changes in community composition were determined by the top-ranked taxa. Such a situation is both unexpected and relatively uncommon. It would be expected that in response to an increasing resource (e.g. food), either all taxa would coexist and respond equally to this increased resource, or only selected taxa would be able to take advantage of the increased resource, and others would not change in abundance (Begon *et al.*, 1990). Such an observation may indicate that it is a combination of responses to a changing resource (phytoplankton), and also changes in predation pressure on the zooplankton community. This is because some taxa may be able to take full advantage of an increase in resources, whilst other taxa may be prevented from doing so due to them being selected for predation.

As there was found to be a relationship between zooplankton abundance and species composition, and as zooplankton abundance was correlated with the GSNW in the Dove series, it is not surprising that the GSNW was also related to community structure. In addition, those taxa which were found to contribute most to the dissimilarity between north and south GSNW years were those which were the most strongly correlated to the GSNW (e.g. *Pseudo-/Para-/Microcalanus* spp.). Some taxa such as *Evadne* did show increased abundances during northerly years, and this taxa in particular showed a marked increase during 1984 sufficient to move this year to the opposite side of the MDS plot from that which would be expected. Previous researchers have noted that this taxon can undergo large fluctuations in abundance (Jorgensen, 1933), due to its ability to undergo rapid pathenogenic reproduction under favourable conditions (warm temperatures and good food supply Egloff *et al.*, 1997), although temperatures were not remarkable during this year (see Figure 4.15e & 4.15h).

The correlations point to both northerly positions of the GSNW (Frid & Huliselan, 1996), indicating the presence of warmer weather (Topliss, 1997), and increased air temperatures and amount of sunshine resulting in reduced zooplankton abundances. In the Dove series, the *Pseudo-/Para-/Microcalanus* group showed a negative relationship to the GSNW, and as they make up a high proportion of the zooplankton community recorded in this series, they contribute to the overall negative association between total zooplankton and the GSNW. Generally, although not exclusively, in both series, the smaller taxa showed the negative relationships to temperature (e.g. *Oithona, Temora, Pseudo-/Para-/Microcalanus* spp.), whilst larger taxa (e.g. *Calanus, Corycaeus*, Chaetognatha) presented the expected positive relationships with climatic variables.

The dissimilar trends and opposing relationships observed in this study compared to those described for other North Sea regions, suggest that the mechanism of control of the zooplankton community in the central-west North Sea is different from other North Sea regions. It is possible to consider a number of potential reasons for the negative relationships between climate and zooplankton. In Lake Windermere, a freshwater lake in NW England (George &

Hewitt, 1995; George & Taylor, 1995), the negative association between the GSNW and zooplankton biomass was attributed not to the amount of food present, but to the timing of its availability. Here, northerly GSNW positions resulted in an earlier spring bloom, yet this earlier growth of edible algae occurred before the animals were ready to reproduce and as such provided a poorer match between the grazer population (mainly cladocera) and their food. If this were the situation in the central-west North Sea, it would be expected that different responses would be observed depending upon the reproductive strategy of a particular species. Yet taxa with differing spawning strategies show similar long term responses to climate. For example, in the Dove series, both the *Pseudo-/Para-/Microcalanus* juveniles and *Temora* both show negative relationships to the GSNW, yet have different life history strategies. *Pseudocalanus* spp., the dominant component of the *Pseudocalanus* spp. group (Frid *et al.*, 1999c), retains its eggs in an egg sac, whilst *Temora longicornis* is a free spawner, releasing its eggs directly into the water column (Kiørboe & Nielsen, 1994).

A number of previous studies (Roff *et al.*, 1988; Frid *et al.*, 1994; Huliselan, 1995; Frid & Huliselan, 1996; Frid *et al.*, 1999c) have highlighted the importance of internal mechanisms such as predation in influencing the long term dynamics of zooplankton off the Northumberland coast. It is possible that such internal factors could modify or invert the climatic signal to produce the results observed here (see Chapter 5). Such predation based mechanisms are usually selective (e.g. Kimmerer, 1984; Hansson *et al.*, 1990), and as such, those taxa which are not strongly predated upon, could be expected to respond in the expected, positive, way, to temperature and these climatic variables.

As remarked by Roff *et al.* (1988) the interannual dynamics of zooplankton may be highly complex, as although potential populations may be limited by the amount of phytoplankton available, and their inherent rate of reproduction by temperature, the achieved population during a particular year may be influenced by predator abundances. However, although one factor may predominate during a particular year and determine zooplankton abundances during that year, over the 30 to 40 year time series examined here, it is likely that a number of mechanisms are involved in determining the long term dynamics of the zooplankton community.

Chapter 5 Predation based control of a North Sea zooplankton community

Introduction

Previously published evidence suggests that zooplankton dynamics across the NE Atlantic region are primarily controlled by processes occurring during the spring (e.g. Dickson *et al.*, 1988a), which set in train the dynamics of the rest of the seasonal cycle. Any factor which influences the rate of zooplankton population growth during the spring is likely to determine the overall amount of secondary production for the rest of the year, as a drop in the maximum annual zooplankton abundance reached is not compensated for by high abundance during other times of the year.

A number of processes influence the growth rate and development of zooplankton populations. The size, development time and fecundity of grazer populations during the spring months has been shown to be regulated by either water temperature (McLaren, 1965; Paffenhöffer & Harris, 1976; Corkett & McLaren, 1978; Ohman & Wood, 1995; Kleppel *et al.*, 1996) or by food (Huntley & Boyd, 1984; Fransz *et al.*, 1992). As water temperature influences the metabolic rates of plankton, this can potentially alter the population growth rate. This is particularly true for those egg carrying species such as *Pseudocalanus* (Ohman *et al.*, 1996), as a new egg sac cannot be produced whilst the old one is being carried, and the development time of the egg sac is dependant upon temperature (Corkett & Zillioux, 1975). However, for other taxa, particularly those taxa which are broadcast spawners and do not carry egg sacs (e.g. *Calanus*), their fecundity does not tend to be limited by temperature, but by food supply. In contrast food supply does not tend to alter *Pseudocalanus* growth rates (Ohman *et al.*, 1996), yet a difference of 1°C can alter the stage duration of *Pseudocalanus* by 10% (Ohman & Wood, 1995), and therefore alter the population growth rate. Thus, it would be expected that the abundance of *Pseudocalanus* would be positively related to temperature (McLaren, 1965; Paffenhöffer & Harris, 1976; Corkett & McLaren, 1978), yet Chapter 4 (Figure 4.14e) suggests that the opposite is the case!

While many studies have focussed on the processes which influence zooplankton "birth" rates, fewer studies have addressed the importance of zooplankton "death" on zooplankton dynamics (Ohman & Wood, 1995), and this is especially true for examinations of the long term dynamics of zooplankton populations. This is based on the incorrect assumption that marine plankton communities are purely bottom-up rather than top-down systems (Ohman & Wood, 1995). Yet studies of some zooplankton communities suggest that even at conservative predation rates, predators are able to control the dynamics of selected taxa (Steele & Henderson, 1992), and there is evidence that the population growth rates or the dynamics of some zooplankton populations are controlled by predation (Davis, 1984b; Ohman, 1986; Ohman & Wood, 1995; Sullivan & Meise, 1996).

In the previous Chapter, I dealt with how the long term trends observed in the central-west North Sea zooplankton community were related to climate and other abiotic influences. The results of that study hinted at the presence of more complex internal mechanisms that could be influencing the long term dynamics of the zooplankton community. Previous research has suggested that predation on the overwintering copepod population by *Themisto* and *Sagitta* was important in governing the amount of secondary production occurring during the following year (Roff *et al.*, 1988). Frid *et al.* (1994) examined the impact of *Pleurobrachia*, *Themisto* and *Sagitta* on the zooplankton community, and their seasonal role as predators in the dynamics of the zooplankton. This study concluded that the greatest amount of standing stock removal occurred during the winter, when copepod abundances were low, and Huliselan (1995) hypothesised that predation during the winter, mainly due to the presence of *Sagitta*, set the size of the spring copepod cohort, which in turn controlled summer abundances. However, none of these studies have effectively been able to explain the year to year variation in zooplankton abundances, and Huliselan (1995) concluded that winter predators did not appear to play a major role in determining inter-annual variation in copepod abundances. In addition none of these studies have determined how changes in climate might influence the predation pressure upon the zooplankton community (Frid & Huliselan, 1996).

Therefore, this chapter will initially focus upon the seasonal cycle of the omnivores, and how the pattern of the seasonal cycle and the interannual dynamics of such taxa may be related to the abundance of predators. In turn I will suggest how changes in climate might influence predator abundances, and thus how the long term dynamics of the zooplankton community in the central-west North Sea are influenced.

Methods

Zooplankton sampling methodology for the Dove zooplankton time series is covered in detail in Chapter 3. Dove zooplankton data covered the period 1969-1996 (excepting 1989). As in Chapter 4, due to the large number of taxonomic entities recorded in the Dove series, the number of taxa was reduced to those dominant taxa to make statistical analyses more straightforward. Thus, only those predator and omnivore taxa (K.R. Nicholas pers. comm.) which represented at least 2% of the total zooplankton community *in any one monthly sample*, were used in the following analyses. Predators were considered to be those zooplankton species which were known to be carnivorous, whereas omnivores were those taxa which were predominantly herbivorous zooplankton, but could include those taxa which were opportunistic feeders, consuming both plant and animal material.

Examination of seasonal patterns

In order to establish whether there was any relationship between the abundance of omnivores during the winter and spring months, and the maximum omnivore abundance achieved during a year, correlation coefficients were calculated between mean monthly abundances and the maximum annual omnivore abundance over the 27 year series.

In order to determine the pattern of their seasonal cycle fluctuations and their abundances relative to each other, the mean monthly abundances of the predators (*Sagitta elegans* Verrill, *Themisto gaudichaudi*, Hydrozoa, and remaining predators) over the 27 year series were plotted. In addition, the proportions of each predator of the total predator community during the spring months of February-April were calculated to determine which taxa made up the majority of the predator community during these months.

Spring predator-prey relationships

Firstly, low zooplankton years were defined as years where the mean abundance of total zooplankton was less than 0.5 standard deviations below the long term mean (Table 5.1), whilst high zooplankton years were defined as years where the mean abundance of total zooplankton was greater than 0.5 standard deviations above the long term mean (Table 5.1). The mean abundance of total omnivores and total predators were compared over the course of the seasonal cycle by plotting their abundance during both low and high abundance years.

The presence of long term relationships between February-April predator abundances (the months of the spring omnivore increase) and mean June-August omnivore abundances (peak omnivore abundances) were established using regression analysis, and by constructing standardised time series plots of these two variables to observe their relative year to year fluctuations.

Table 5.1 **Low and high zooplankton years in the Dove series. See text for definitions.**

Low zooplankton abundance years	High zooplankton abundance years
1980	1973
1985	1975
1990	1978
1991	1982
1994	1984
1995	1986
1996	1987

The chaetognath *Sagitta* was found to make up almost 73% of the total spring predator abundance (Table 5.4) and thus further investigations focussed upon this predator and its relationship with the summer abundance of the omnivores. In order to observe which omnivore taxa showed relationships to spring *Sagitta* abundances, correlation coefficients between the mean spring (February to April) abundance of *Sagitta*, and the maximum abundance of each omnivore taxon (Table 5.2) over the 27 year series were calculated. All significance tests were corrected for autocorrelation using the formula of Quenouille (1952) (see Chapter 4 for further details). Those omnivores which had abundances over the 27 year series calculated as representing at least 1% of the total zooplankton abundance (Table 4.1), and which had significant correlations with *Sagitta* ($p<=0.05$), were selected for further investigation.

In order to further understand how the seasonal pattern of each selected omnivore taxa differed between high and low abundance years, and to observe how it was related to the mean spring *Sagitta* abundance during low and high abundance years, the mean monthly omnivore abundance, and mean monthly *Sagitta* abundances were both plotted during low and high zooplankton abundance years (as defined above). For each of those omnivores calculated as representing at least 1% of the total zooplankton abundance, the long term relationship between the mean *Sagitta* abundance during those months when the omnivore increased during the spring, against the mean abundance of the omnivore during those months when it was at its highest were graphically examined.

Table 5.2 Omnivores and predators in the Dove time series which represent at least 2% of the total community in any one monthly sample (K.R. Nicholas pers. comm.).

Omnivores	Predators
Acartia clausi	*Aglantha digitale*
Acartia longiremis	*Corycaeus anglicus*
Acartia spp.	Fish larvae
Anomuran larvae	Jellyfish juv.
Bivalve larvae.	*Nanomia cara*
Bryozoan larvae	*Nyctiphanes couchi*
Calanus finmarchicus	*Sagitta elegans*
Calanus helgolandicus	*Themisto gaudichaudi*
Calanus spp.	*Thysanoessa inermis*
Centropages hamatus	*Thysanoessa raschi*
Centropages spp.	
Centropages typicus	
Cirripeda larvae	
Echinoderm larvae	
Echinoplutei larvae	
Euphausiid spp.	
Evadne nordmanni	
Fritillaria borealis	
Gastropoda larvae	
Microcalanus pusillus	
Microsetella norvegica	
Oikopleura diocia	
Oithona similis	
Oncaea venusta	
Ophioplutei larvae	
Paracalanus parvus	
Phoronid larvae	
Podon spp.	
Polychaeta larvae	
Pseudo-/Para-/Microcalanus juv.	
Pseudocalanus elongatus	
Temora longicornis	
Tigriopus spp.	
Tomopteris helgolandica	

Predation of a *Pseudocalanus* population by *Sagitta*: A model study

Further investigation of the role that *Sagitta* played in controlling the growth of the *Pseudocalanus* population was performed using a combined *Pseudocalanus* growth and *Sagitta* predation model. This modelled the daily *Pseudocalanus* population growth for each year from 1974 to 1994, over a 60 day period from 1st March to 30th April, and applied the daily predation pressure created by the observed *Sagitta* population. The *Pseudocalanus* growth model was adapted from that of Corkett & McLaren (1978) and Ohman (1986), and calculated daily *Pseudocalanus* population growth, forced primarily by sea surface temperature (SST) data. Daily *Pseudocalanus* consumption by the *Sagitta* population was calculated from equations published by Feigenbaum & Maris (1984), and Ohman (1986). Although the predation pressure of the *Sagitta* population is obviously very dependant upon the abundance of *Sagitta*, it is also dependant to some extent upon SST, and upon the number of prey being consumed by the *Sagitta* population which is feeding at any one time (i.e. the Number of Prey per Chaetognath (NPC), which were taken from literature sources (Feigenbaum & Maris, 1984; Frid *et al.*, 1994)).

Values of NPC for *Sagitta elegans* vary considerably (Ohman, 1986). For example, Frid *et al.* (1994) recorded a value of 0.11 off the Northumberland coast (which appears to be a relatively low figure (Feigenbaum, 1982)), whereas Feigenbaum (1982) has published values of 0.4 and 0.564 for the Massachusetts coast. The NPC combined with the gut residence time (which is a function of SST) allowed the calculation of the daily consumption rate of an individual predator. Spring SST data were taken from the Longstone lighthouse, Farne Islands (55°39'N 1°35'W) and satellite based SST data obtained from Plymouth Marine Laboratory.

Ohman-Corkett's *Pseudocalanus* growth model

Pseudocalanus abundances were calculated as being the sum of the abundance of the nine developmental stages. In order to calculate the daily abundance of each of the nine stages, the stage duration is required, which is expressed as a multiple of the egg duration time (Table 5.3) (Ohman, 1986). The egg duration or development time is a function of temperature according to the Belederhek equation as follows;

$$ED = 1845(11.45 + T)^{-2.05}$$ (taken from Corkett & McLaren, 1978)

ED = Egg development time (in days); T = Sea Surface Temperature.

Then, daily recruitment to each juvenile stage at time, t, is estimated from the following equation from Ohman (1986);

$$R = \frac{N_{t-1}}{d}$$

R = Recruitment; N = abundance; d = Stage Duration.

In order to prevent the abundance of any stage falling below zero, a threshold value of 1 was built into the model. These threshold levels are also required to allow for a reasonable increase in the *Pseudocalanus* population (which is a function of the abundance at t-1). Starting *Pseudocalanus* abundances were set at 68 individuals.m^{-3} (mean March abundance over the 1974-1994 period). This starting abundance was initially distributed amongst the stages according to the stage duration (Table 5.3).

Table 5.3 Multiples of development time for each stage of the *Pseudocalanus* life cycle (Ohman, 1986).

Developmental Stage	Stage duration (Multiple of Development time)
Egg	1.00
Nauplii	4.09
CI	0.96
CII	1.01
CIII	0.80
CIV	0.72
CV	1.30

Sagitta consumption model

The consumption rate of *Pseudocalanus* per day by a *Sagitta* population is mainly dependant upon the following factors:

- SST, which affects the gut digestion time of *Sagitta*.
- *Sagitta* abundance. The higher the size of the *Sagitta* population, then the greater the predation pressure upon the *Pseudocalanus* population.
- NPC. The higher the no. of prey per chaetognath then the higher the consumption rate of *Pseudocalanus* per chaetognath.

The turnover time or gut digestion time is required to estimate the predation rates on *Pseudocalanus*. The dominant factor affecting the gut residence time is temperature, although it has been suggested that prey type may also affect the digestion time (Ohman, 1986). Gut digestion time is expressed as a continuous function from an exponential curve as follows:

$$G = 10.48.e^{-0.086.T}$$

G = Gut digestion time; T = Sea Surface Temperature

The following calculations require the abundances for the three developmental stages of *Sagitta*. The abundances and proportions of these vary through the seasonal cycle (Feigenbaum & Maris, 1984; Oresland, 1985; Conway & Williams, 1986; Oresland, 1986; Terazaki, 1993; Huliselan, 1995). However, as these have not been regularly recorded in the Dove series, they were estimated by proportioning the recorded abundance of *Sagitta* using the data in Huliselan (1995);

Stage I = 21.62%

Stage II = 18.85%

Stage III = 18.78%

For the whole *Sagitta* population, the consumption rate calculated as:

$$C = \left(\frac{N.P}{G_N}\right) + \left(\frac{HD.P}{2.G_D}\right) S_1 + \left(\frac{N.P}{G_N}\right).(S_{II} + S_{III})$$

C = *Pseudocalanus* consumed (m.day^{-3}); G_N or G_D = gut digestion time at night or day temperature; N = hours of darkness; HD = hours of daylight; P = Number of prey items per chaetognath; S_I, S_{II}, S_{III} = number of *Sagitta*.m^{-3} in stages I, II, III

Sagitta feed mainly at night (Ohman, 1986), hence the requirement to know the length of darkness in the above calculation. *Sagitta* also move from the surface waters to deeper waters in the daytime and hence an estimate of bottom water temperature is also required. This was estimated separately for each month by obtaining the temperature difference between the surface sample and the 50m sample observed during 1997 at the Dove zooplankton sampling station, and deducting this difference from the monthly value of the SST series.

A further term was added to the model to limit the feeding rates according to a Holling type II curve (Holling, 1959), where *Sagitta* feeding may be limited by low *Pseudocalanus* densities (Ohman, 1986). Thus, a ceiling was set to the impact of each *Sagitta* individual according to:

$$Y = \frac{0.137.X}{1 + 0.024.X}$$

Where, Y = maximum daily predation rate.*Sagitta*$^{-1}$, X = concentration of *Pseudocalanus*.

Finally, the abundance of the *Pseudocalanus* population at each time step, t, was calculated according to:

$$Ps_t = \sum_{n}^{s=1} (s_{t-1} + R) - M$$

Where, Ps = *Pseudocalanus* individuals.m^{-3}, R = Recruitment.m^{-3} (i.e. birth), M = mortality.m^{-3}, s = stage.

Testing of model output

Interannual fluctuations in the model output at 60 days for a number of values of NPC (zero, 0.24, 0.4, 0.55) were compared against actual mean May-June *Pseudo-/Para-/Microcalanus* juvenile abundances for 1974-1994 (excepting 1989), and interannual fluctuations in the GSNW (the main climatic variable correlated with Dove zooplankton (Chapter 4) and also correlated with zooplankton across most of the North Sea and NE Atlantic (Taylor, 1996)). The values of NPC that were chosen correspond to those observed by Frid *et al.* (1994) for copepods (0.24

copepods *Sagitta*$^{-1}$ d^{-1}), all prey (0.4 prey items *Sagitta*$^{-1}$ d^{-1}) and those reviewed by Feigenbaum & Maris (1984) for Stage 0 *Sagitta* in the NW Pacific (0.55 prey items *Sagitta*$^{-1}$ d^{-1}).

Chaetognath-*Pseudocalanus* relationships in the CW North Sea CPR series

Continuous Plankton Recorder data (see Chapter 3 for sampling methodology) between 1960 and 1996 (omitting 1978 and 1979 because of incomplete samples) were obtained for an area in the central-western North Sea between SE Scotland and NE England (Figure 3.2). Chaetognaths were found to contribute almost 72% of the abundance of predators in the spring (Table 5.5). In order to observe whether there were similar long term relationships between CPR *Sagitta* (chaetognaths) and *Pseudo-/Paracalanus* spp. abundances, standardised time series plots of the mean summer (June-July) *Pseudo-/Paracalanus* spp. abundances and February-April chaetognath abundances were plotted.

Relationships between spring *Sagitta* and environmental factors

The main periods of *Sagitta* recruitment are said by Feigenbaum & Maris (1984) to coincide with sharp increases in the abundance of *Pseudocalanus* nauplii (the main prey item of young chaetognaths), which would be expected to be greater with increased spring phytoplankton productivity (Feigenbaum & Maris, 1984). Thus, in order to establish whether spring *Sagitta* (obtained from the Dove series) or chaetognath (CPR) abundances were related to phytoplankton or weather during the spring, standardised time series of February-April *Sagitta*/chaetognath abundances from both the Dove and CPR series were plotted alongside standardised February-April values of Tynemouth air temperatures, Tynemouth sunshine, the GSNW and CPR area C2 phytoplankton index (see Chapter 4 for further details).

Results

Off the Northumberland coast, for the period 1969 to 1996, the spring omnivore increase began in March and continued until June, followed by a steady decline in abundance until the winter nadir from December-February (Figure 5.1). Although Roff *et al.* (1988) found a positive relationship between zooplankton abundance during the winter and those during the following summer, in this study, winter omnivore abundance and early spring months were unrelated to maximum abundance during the same year (Figure 5.2). Only by May did zooplankton abundance bear any significant relationship to the maximum abundance obtained during that year. There was also a significant relationship between the *ratio* of omnivore abundance between February and April, to maximum annual abundance ($r=-0.45$, $p<0.02$). Thus, lower ratios (higher rates of omnivore increase from February to April) were related to higher maximum abundances attained during that particular year, suggesting that the rate of increase during these months was critical in determining the maximum abundances attained during the year.

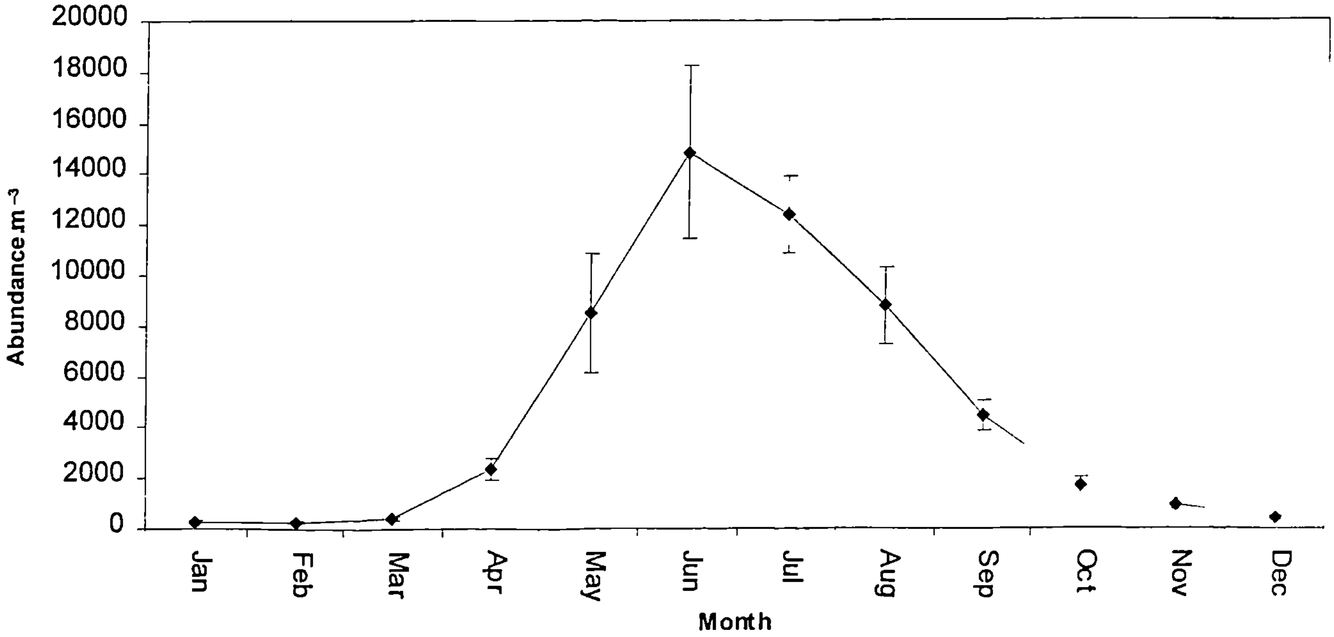


Figure 5.1 **Mean monthly abundance of total omnivores over the 27 year Dove zooplankton series. Error bars denote standard errors.**

Predator abundances from January to April were relatively low (Figure 5.3). The dominant predators, the chaetognaths (*Sagitta*), started to increase their abundance during April, after the start of the omnivore increase (Figure 5.1). In the Dove series, it was observed that during the early part of the seasonal cycle (February to April), *Sagitta* contributed almost 73% of the total predators (Table 5.4). This was also mirrored in the CPR series (Table 5.5) with the chaetognaths making up almost 72% of the predators.

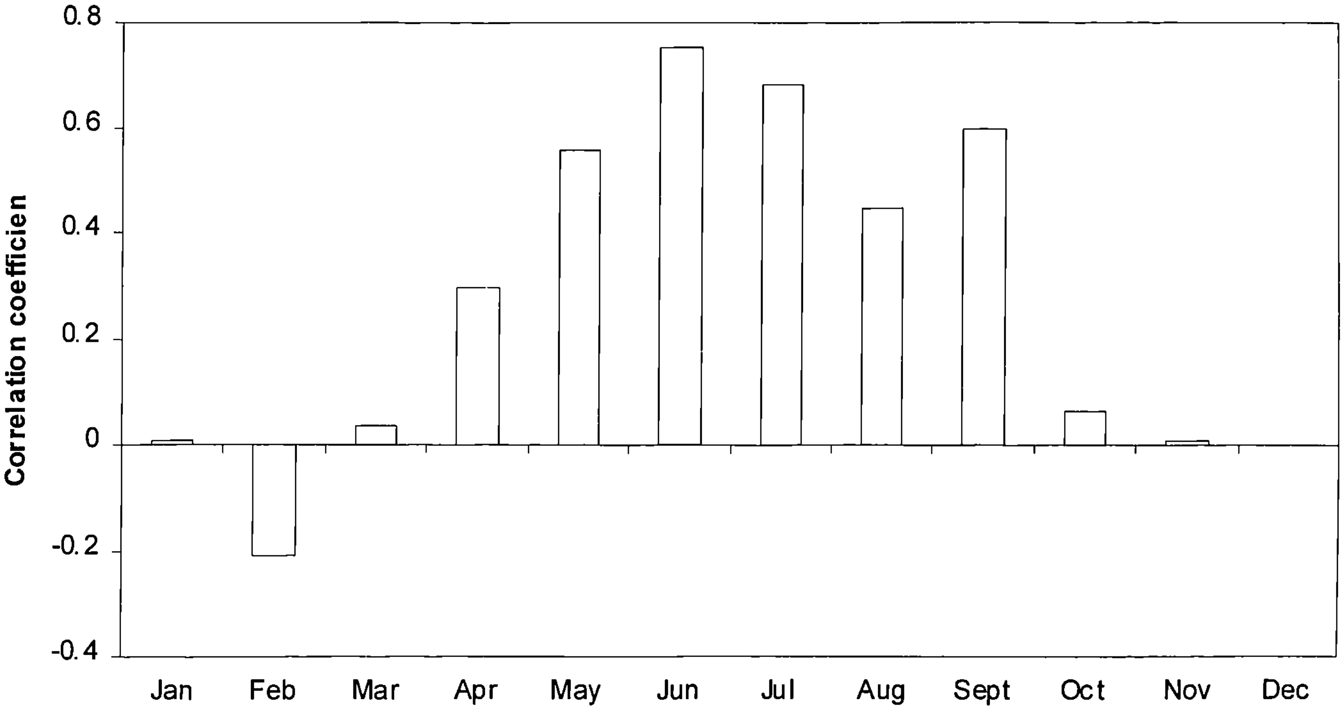


Figure 5.2 **Correlation coefficients calculated over the 27 year Dove zooplankton series between the omnivore abundance for each month and the maximum abundance during each year. Grey bars indicate those months with correlations significant at p<=0.05.**

During high zooplankton abundance years, the rate of omnivore increase from February to the end of April was greater than that during low abundance years (Figure 5.4a), leading to an overall higher abundance peak in the summer. During these high abundance years, predator abundances during the months of the spring omnivore increase from February to April were higher than those during low abundance years (Figure 5.4a). However, as omnivore abundances from November to February in both low and high abundance years were similar, the differences later on in the seasonal cycle do not arise from differences during the early part of the year, which supports the above conclusions that abundances during the winter are unrelated to those during the summer.

Over the 27 year Dove series, there was a significant inverse relationship between the total spring predator (February-April) abundances and the summer omnivore (June-August) abundances (Figure 5.4b). This relationship was especially strong during the 1974-1990 period, although 1980 had a lower omnivore abundance than would be expected given the numbers of predators present.

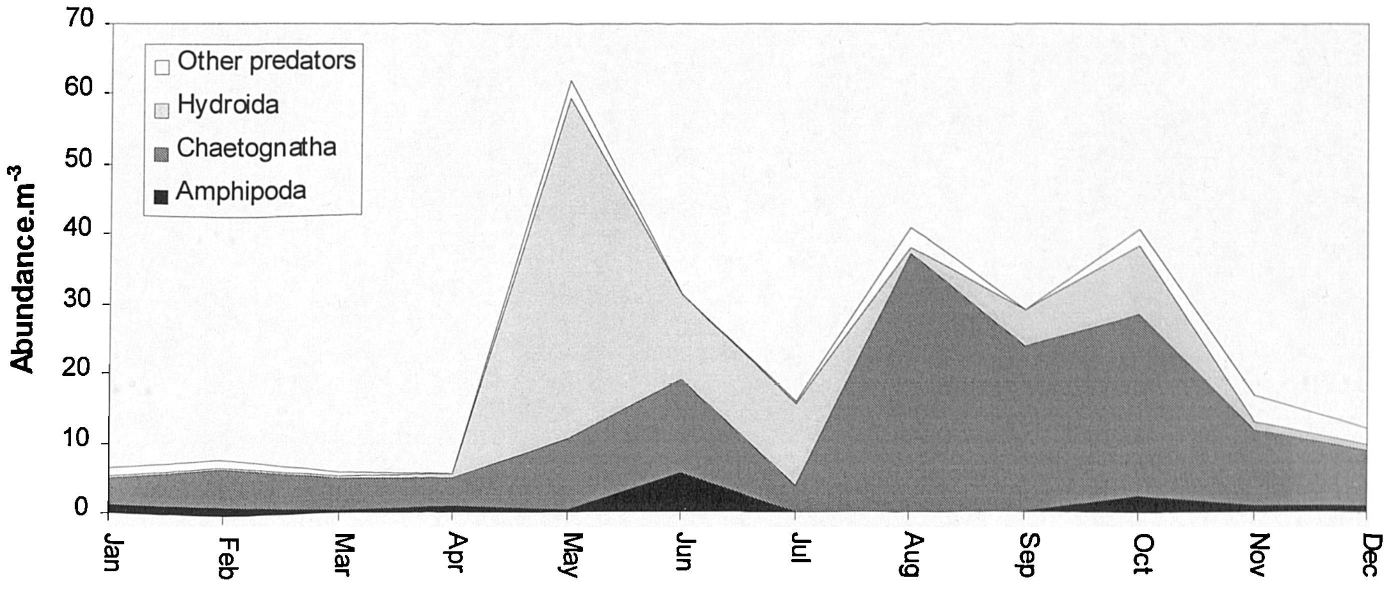


Figure 5.3 **Area plot constructed from the mean monthly abundances of the main zooplankton predators over the 27 year Dove zooplankton series.**

Significant negative correlations were also found between the spring (February-April) abundance of *Sagitta* and the maximum annual abundance of the *Pseudo-/Para-/Microcalanus* juveniles, *Calanus* spp. juveniles, gastropod juveniles, euphausiid nauplii and *Oithona* spp. (Table 5.6). *Calanus finmarchicus* was the only taxon to show a positive relationship between spring *Sagitta* abundances and its maximum abundance during the year.

Table 5.4 **Percentage proportions of predators in the Dove series from March to April.**

Predator	Mean abundance (per m^3)	Percentage proportion
Chaetognatha	4.76	72.93
Amphipoda	0.71	10.86
Hydroida	0.41	6.3
Copepoda	0.38	5.8
Euphausiacea	0.17	2.56
Fish	0.10	1.54
Siphonophora	0.0005	0.008

Table 5.5 **Percentage proportions of predators in the CPR from March to April.**

Predator	Mean abundance (per m^3)	Percentage proportion
Chaetognatha	0.95	71.9
Amphipoda	0.2	14.9
Fish	0.14	10.6
Decapoda	0.03	2.4
Copepoda	0	0

The annual increase in the *Pseudo-/Para-/Microcalanus* juveniles occurs during March and April (Figure 5.5a). *Sagitta* numbers during low total zooplankton abundance years were higher in these months compared to high abundance years. Over the 27 year series, there was a strong inverse relationship between the abundance of *Sagitta* during March and April and the months of the maximum abundance of the *Pseudo-/Para-/Microcalanus* juveniles in that year (Figure

5.5b). This relationship is strongest from 1977 until 1988, although 1983 and 1980 appear not to follow the same pattern.

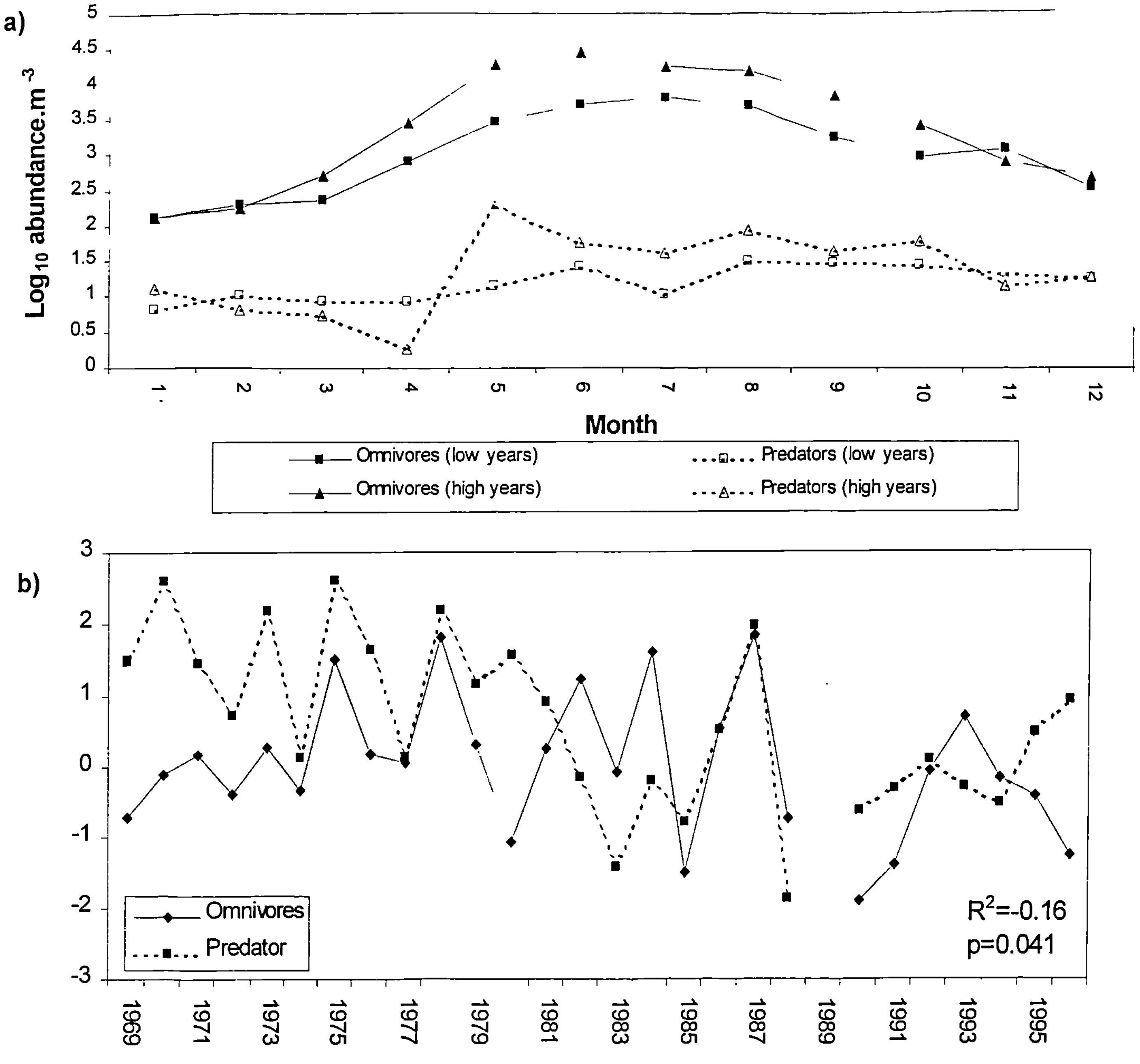


Figure 5.4 a) Mean monthly Log_{10} abundance of total omnivores and Log_{10} abundance of total predators during low zooplankton years (total abundance less than 0.5 standard deviations below the long term mean), and high zooplankton years (total abundance more than 0.5 standard deviations above the long term mean). b) Time series plot of mean standardised abundances of May-August total omnivores and mean standardised abundances of February-April total predators (inverted).

Table 5.6 Correlation coefficients calculated over the 27 year Dove series for spring *Sagitta* abundance (Feb-Apr) and the maximum abundance of omnivores during the same year. Only those probability values less than p<=0.05 before correction for autocorrelation are included, significant correlations after correction are in bold. Global p=0.008.

	Correlation coefficient	p
Acartia clausi	0.06	0.384
Acartia longicornis	-0.01	0.398
Acartia spp. juv.	-0.35	0.074
Anomuran larvae	-0.01	0.398
Bivalve larvae	-0.20	0.230
Bryozoan larvae	-0.08	0.371
Calanus finmarchicus	0.55	**0.006**
Calanus helgolandicus	0.24	0.186
Calanus spp. juv.	-0.44	**0.021**
Calanus spp. males	0.29	0.129
Centropages hamatus	0.02	0.397
Centropages spp. juv.	-0.03	0.395
Centropages typicus	-0.07	0.376
Cirripede larvae	0.03	0.395
Echinoderm larvae	-0.33	0.088
Echinoplutei larvae	-0.09	0.364
Euphausiid spp. larvae	-0.03	0.395
Euphausiid spp. nauplii	-0.42	**0.030**
Evadne nordmanni	0.09	0.355
Fritillaria borealis	-0.26	0.168
Gastropod larvae	-0.44	**0.023**
Microsetella norvegica	0.01	0.398
Microcalanus pusillus	-0.19	0.260
Oikopleura diocia	-0.11	0.341
Oithona similis	-0.41	**0.041**
Oncaea venusta	0.08	0.370
Ophioplutei larvae	-0.22	0.210
Paracalanus parvus	-0.09	0.359
Phoronid larvae	0.01	0.398
Podon spp.	0.12	0.335
Polychaete larvae	-0.09	0.363
Pseudo-/Para-/Microcalanus juv.	-0.45	**0.018**
Pseudocalanus elongatus	0.01	0.399
Temora longicornis	-0.16	0.283
Tigriopus spp.	0.18	0.274
Tomopteris helgolandica	-0.07	0.373

The patterns (Figure 5.6a) observed for *Oithona similis* and *Sagitta* during low and high abundance years were similar to those for the *Pseudo-/Para-/Microcalanus* juveniles, with higher *Sagitta* abundances present in low abundance years during the months of the spring increase of *Oithona* (February-April), leading to a reduced maximum productivity over the summer months (June-August). Over the 27 year series, the inverse relationship between *Sagitta* and *Oithona* was strongest over the 1969-1973 period (Figure 5.6b). After this, there appeared to be only general similarity in their long term trends – the short term year to year fluctuations were not synchronous.

The seasonal cycle of the *Calanus* juveniles started in February, peaked in May, and then fell off to a medium abundance by July (Figure 5.7a). Although, like the *Pseudo-/Para-/Microcalanus* juveniles, there were higher abundances of *Sagitta* during low zooplankton years, when the year to year fluctuations between February to May *Sagitta* abundances and peak (May) *Calanus* juvenile abundances were compared (Figure 5.7b), there was no significant relationship. Examination of CPR data reveals that there is also a significant negative association between the eyecount chaetognath abundance and the *Pseudo-/Paracalanus* total over the 34 year series (Figure 5.8). These eyecount chaetognaths are those above approximately 8mm long (G. Wiafe pers. comm.).

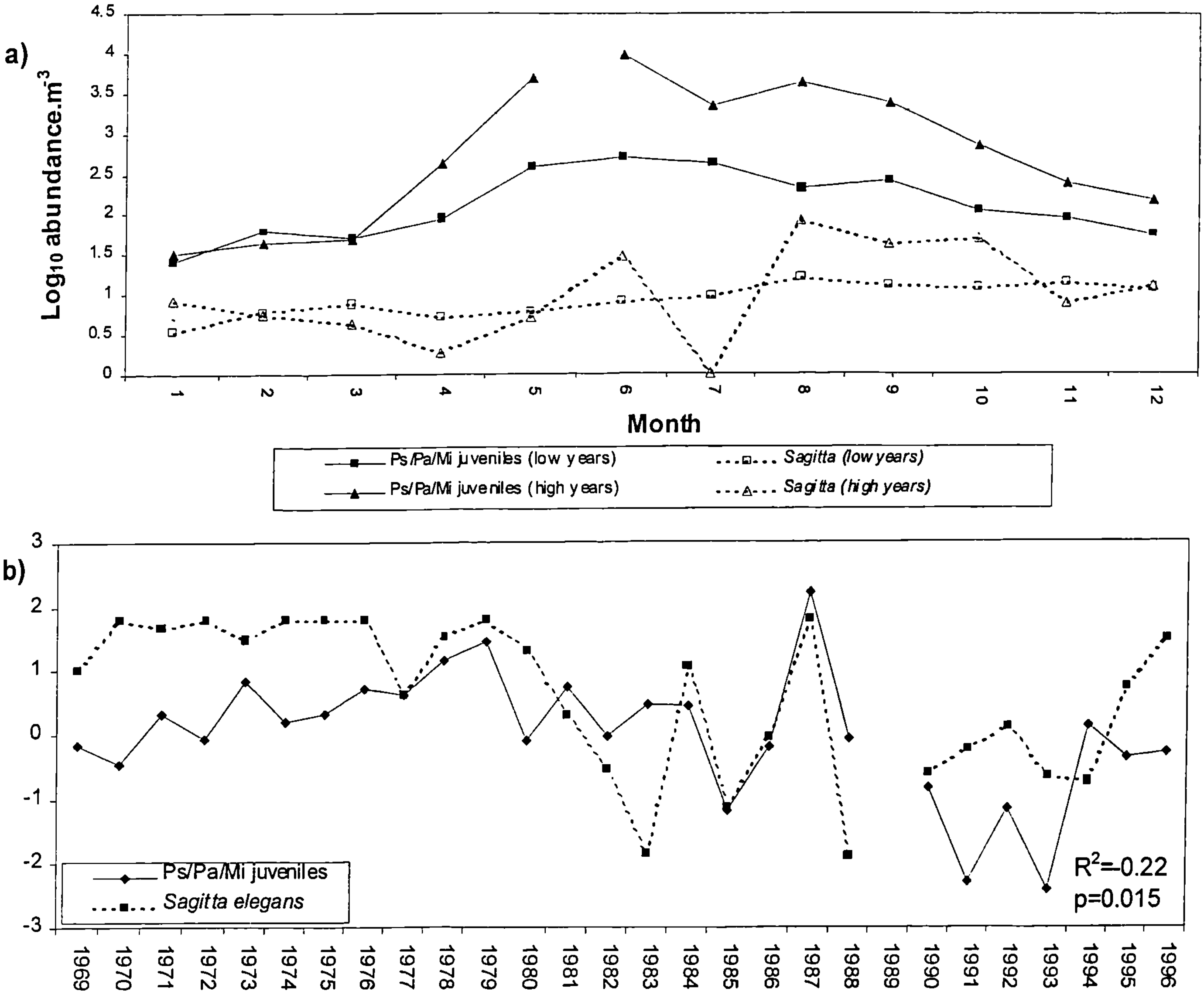


Figure 5.5 **a) Mean monthly Log₁₀ abundance of *Pseudo-/Para-/Microcalanus* juveniles and Log₁₀ abundance of *Sagitta elegans* during low zooplankton years (total abundance less than 0.5 standard deviations below the long term mean), and high zooplankton years (total abundance more than 0.5 standard deviations above the long term mean). b) Time series plot of mean standardised abundances of June-July *Pseudo-/Para-/Microcalanus* juveniles and mean standardised abundances of March-April *Sagitta elegans* (inverted).**

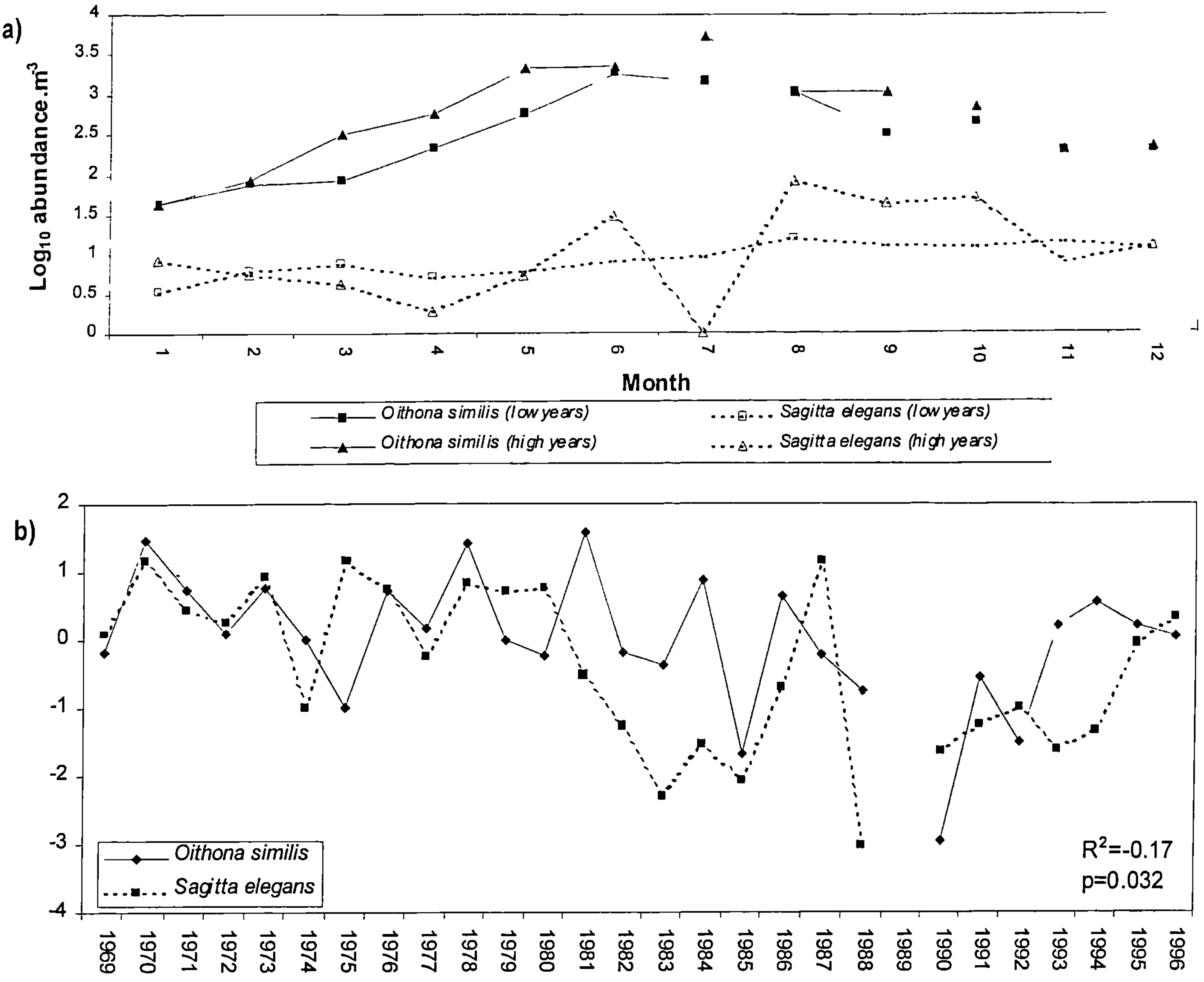


Figure 5.6 a) Mean monthly Log_{10} abundance of *Oithona similis* and Log_{10} abundance of *Sagitta elegans* during low zooplankton years (total abundance less than 0.5 standard deviations below the long term mean) and high zooplankton years (total abundance more than 0.5 standard deviations above the long term mean). b) Time series plot of mean standardised abundances of June-August *Oithona similis* and mean standardised abundances of February-April *Sagitta elegans* (inverted).

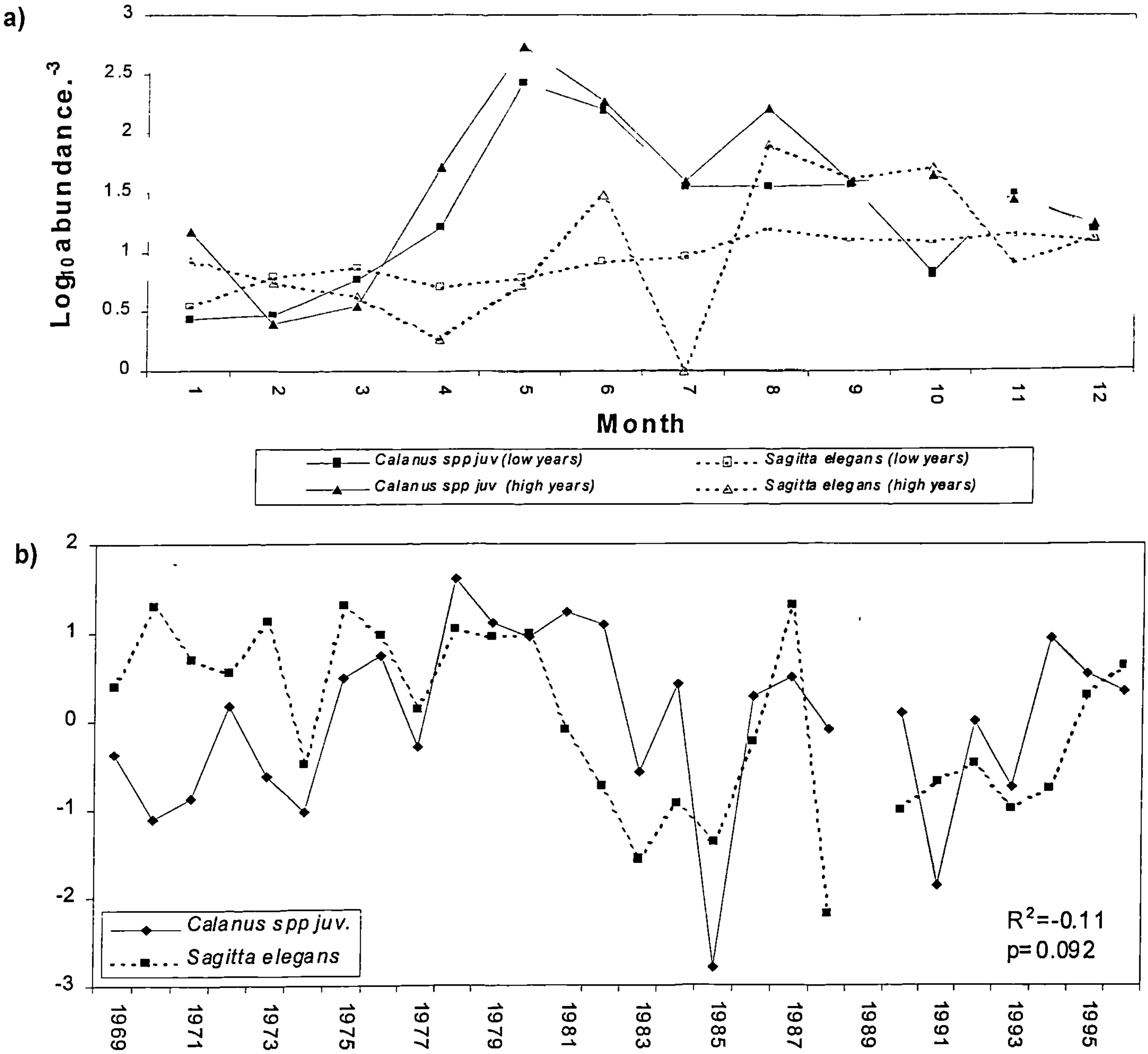


Figure 5.7 a) Mean monthly Log_{10} abundance of *Calanus* spp. juveniles and Log_{10} abundance of *Sagitta elegans* during low zooplankton years (total abundance less than 0.5 standard deviations below the long term mean) and high zooplankton years (total abundance more than 0.5 standard deviations above the long term mean). b) Time series plot of mean standardised abundances of May *Calanus* spp. juveniles standardised abundances of February-April *Sagitta elegans* (inverted).

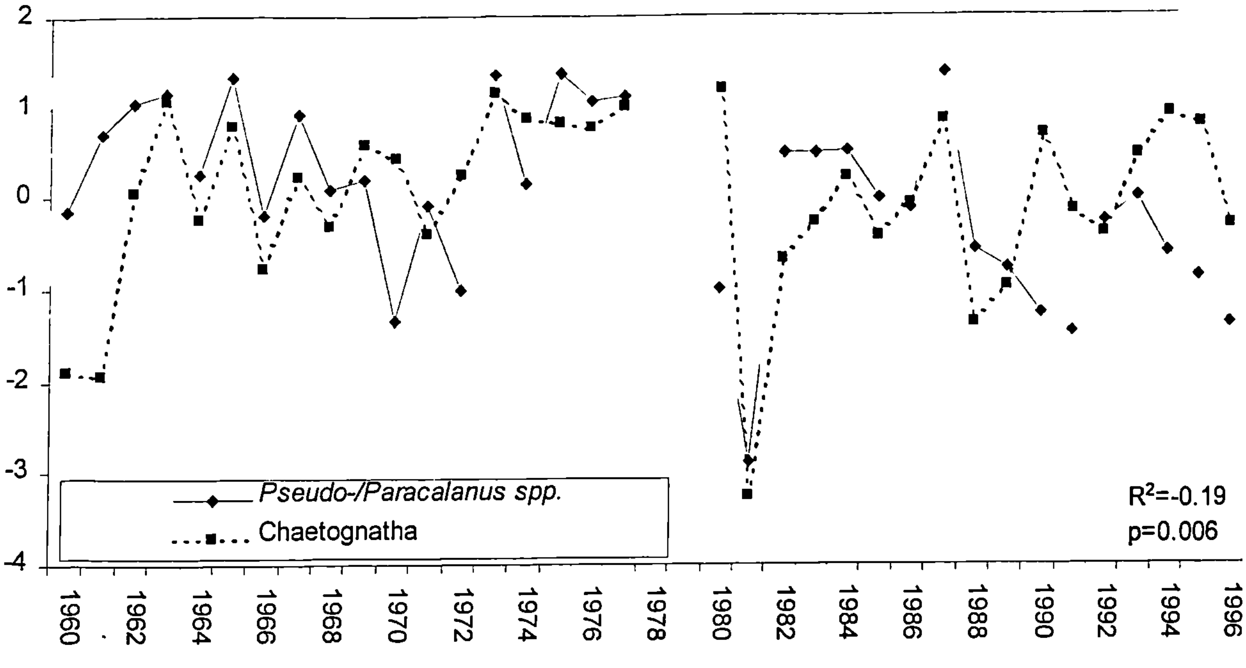


Figure 5.8 Time series plot of mean standardised abundances of June-July *Pseudo-/Paracalanus* total from the CPR series and mean standardised abundances of February-April Chaetognaths (inverted) from the CPR series.

Summer predator and omnivore abundances

During low total zooplankton abundance years, low summer and autumn omnivore abundances (May to October) (Figure 5.4a) were accompanied by lower predator abundances. Conversely, during high zooplankton years, predator abundances during the summer and autumn were higher. This pattern was also observable in the abundances of *Sagitta* and *Pseudo-/Para-/Microcalanus* juveniles (Figure 5.5a), *Oithona similis* (Figure 5.6a) and *Calanus* juveniles (Figure 5.7a).

Results of model calculations

Significant positive relationships with the GSNW index were produced by the model output (Figure 5.9a) when zero predation (NPC=0) was applied to the *Pseudocalanus* population ($r=0.55$, $p<0.05$). Thus, this positive relationship is similar to that detected by Taylor (1996) across the northern and central North Sea and NE Atlantic area. However, the output bore no significant relationship to the mean May-June Dove *Pseudo-/Para-/Microcalanus* juvenile abundances. Applying relatively low levels of mortality (NPC=0.24) (Frid *et al.*, 1994), produced output (Figure 5.9b) with no similarity to either the GSNW or the mean May-June Dove *Pseudo-/Para-/Microcalanus* abundances. Only when the level of mortality was increased to NPC=0.4, were there significant correlations in the year to year fluctuations of the model (Figure 5.9c) and the May-June Dove *Pseudo-/Para-/Microcalanus* juvenile abundances (r=0.62, p<0.05). This level of predation also modelled *Pseudocalanus* abundances which were significantly negatively correlated with the GSNW (r=-0.56, p<0.05). This level of predation therefore predicts summer *Pseudo-/Para-/Microcalanus* juveniles off the Northumberland coast and also the relationship with the GSNW (Chapter 4). Increasing the level of predation to NPC=0.55, produces even stronger associations (Figure 5.9d) (GSNW r=0.61, p<0.05; *Pseudo-/Para-/Microcalanus* juveniles r=0.70, p<0.05).

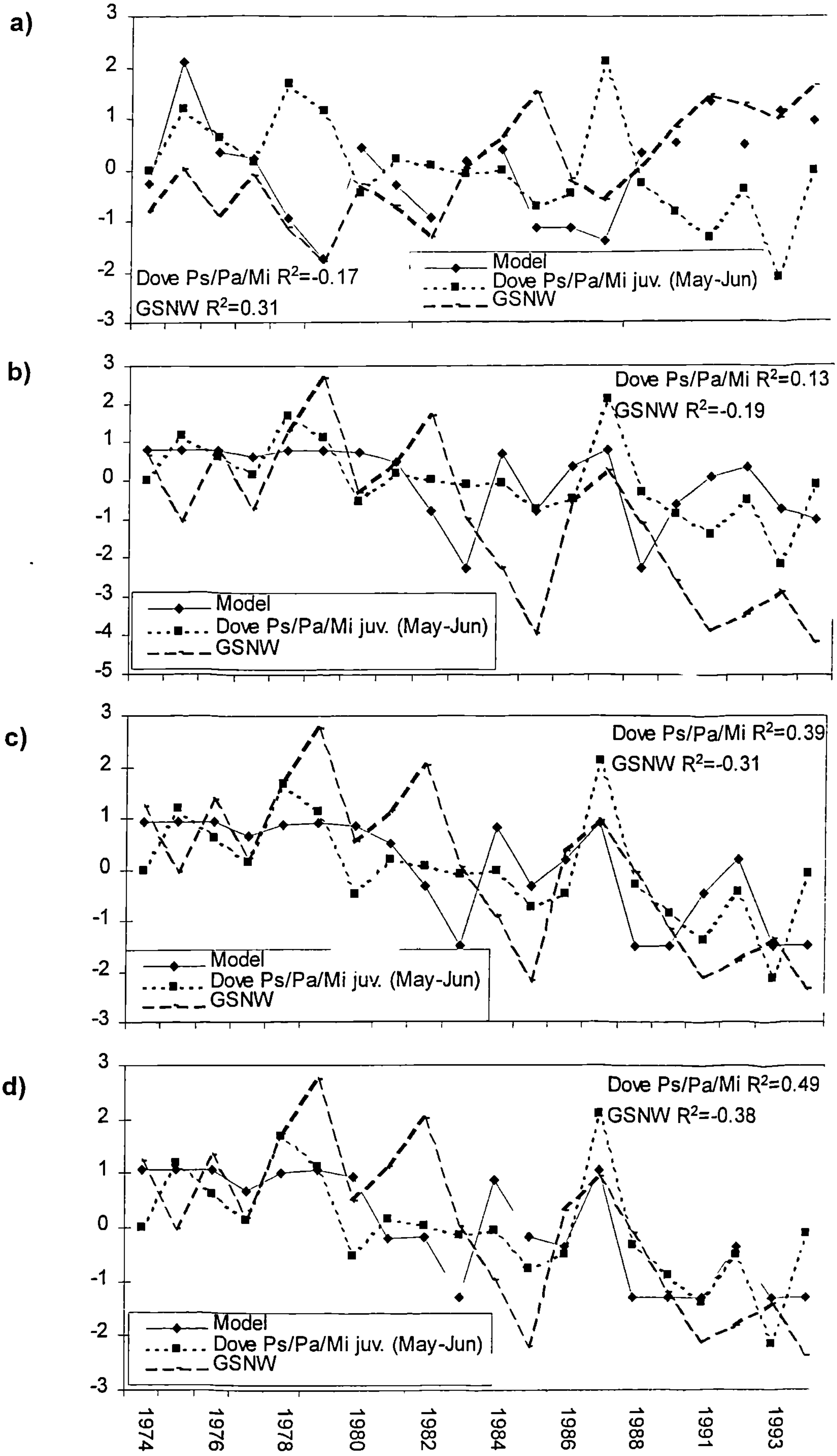


Figure 5.9 Standardised time series plot of mean Dove May-June *Pseudo-/Para-/Microcalanus* juvenile abundances, the GSNW, and standardised abundance of the modelled *Pseudocalanus* population after 60 days, applying daily mortality levels of a) NPC=0 (no mortality). b) NPC=0.24. c) NPC=0.4. d) NPC=0.55. N.B. the GSNW is inverted in plots b, c, & d to enable an easier comparison to the model output. See text for further explanation.

Environmental control during the spring

Spring *Sagitta* abundances (February-April) were low from the start of the Dove series until 1980 (excepting a peak in 1977), as was noted by Evans & Edwards (1993). Following this, there was a gradual increase in year on year *Sagitta* abundance until 1983 (Figures 10a-d). These spring *Sagitta* abundances were found to be significantly related to a number of environmental variables. Positive associations were present between *Sagitta* and Tynemouth air temperature (Figure 5.10a), Tynemouth sunshine (Figure 5.10b) and C2 phytoplankton index (Figure 5.10c) and the GSNW (Figure 5.10d). However, before 1977, due to the low spring *Sagitta* abundances, there was no response to fluctuations in these environmental variables, although the peak in *Sagitta* during 1977 did coincide with peaks in sunshine and temperature. The temperature increase from 1979 to 1983 coincided with an increase in *Sagitta*. However, after this time there was less similarity in the short term year to year fluctuations, although their long term trends were similar. Phytoplankton index (area C2) showed a closer relationship with *Sagitta* (Figure 5.10c), with a particularly strong similarity from 1978 to 1988. However, the strongest relationship between *Sagitta* and these environmental variables was with the GSNW (Figure 5.10d), although closer examination of the time series shows that the short term variations are not synchronous. An examination of spring CPR chaetognath abundance also found that this species had a strong relationship to spring C2 phytoplankton abundance (Figure 5.10e).

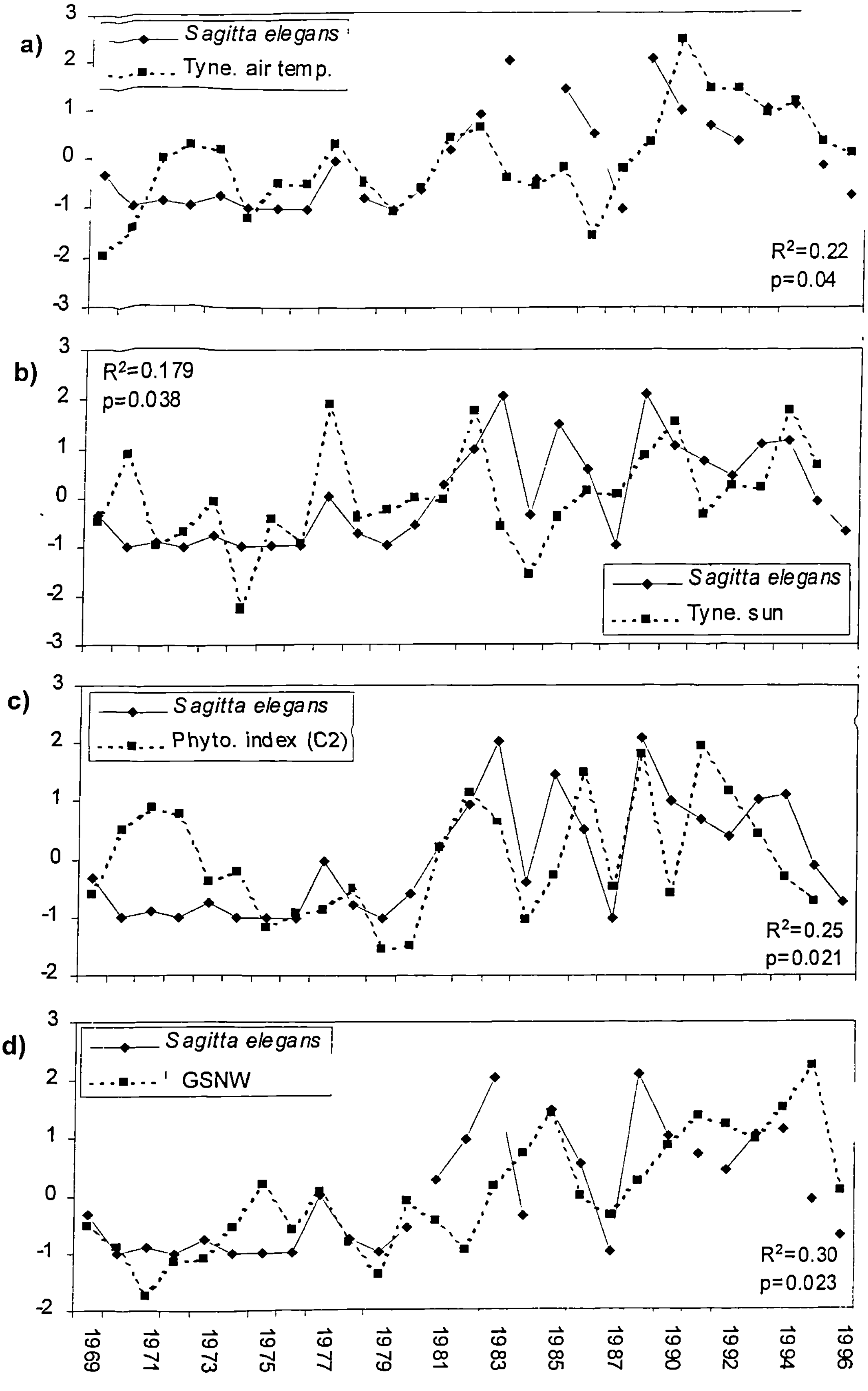


Figure 5.10 Standardised time series plot of a) *Sagitta elegans* & Tynemouth air temperatures. b) *Sagitta elegans* & Tynemouth sunshine. c) *Sagitta elegans* & phytoplankton index (area C2). d) *Sagitta elegans* & the GSNW.

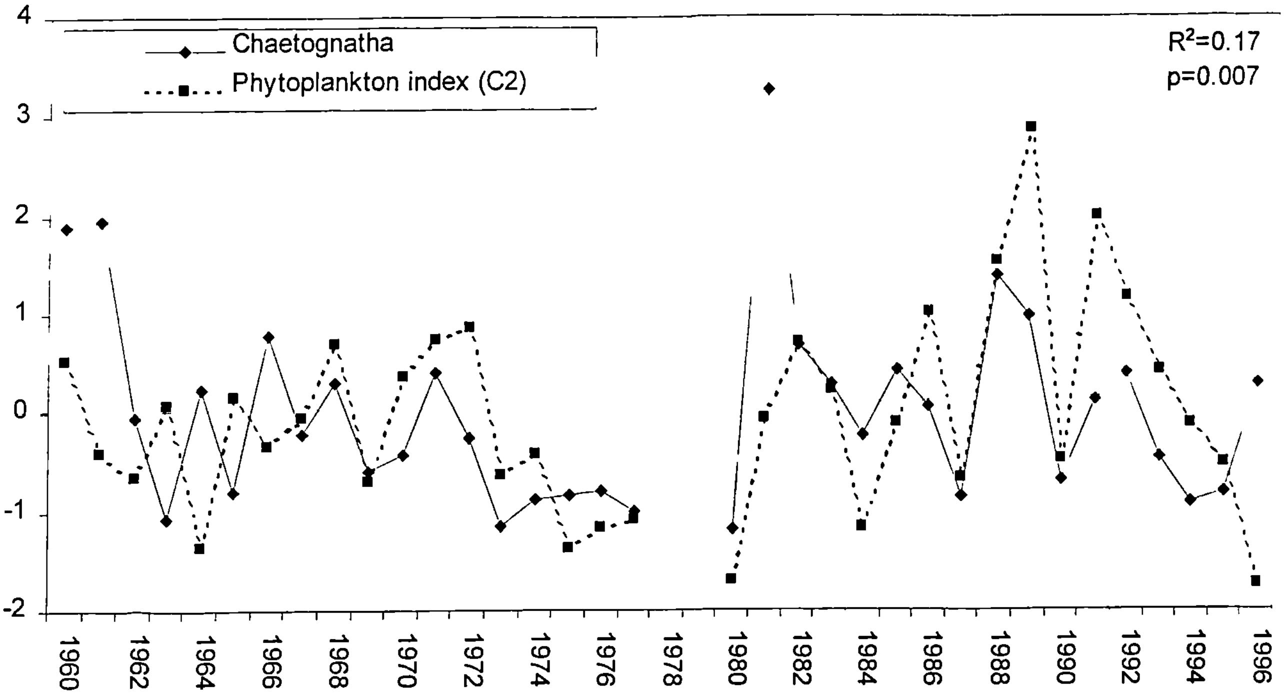


Figure 5.10 continued e) Chaetognatha (eyecount) & phytoplankton index (area C2).

Discussion

Roff *et al.* (1988) suggested that the standing stock of overwintering copepods governed their maximum abundance the following year. In contrast, this study has shown that there was no relationship between the standing stock of omnivores during the winter months, and peak omnivore abundance the following summer (Figure 5.2). In addition, omnivore abundances observed in January and February during low zooplankton years were similar to those observed during high zooplankton years (Figure 5.4a). This suggests that interannual variability in the maxima of zooplankton abundance was related to the rate of increase during spring (February to April). It is, therefore, those processes which influence the growth rates of omnivore populations during spring, which are critical in determining the interannual dynamics which are observed in the Dove zooplankton time series.

Sagitta has often been cited as a predator of copepod populations (Oresland, 1985; Conway & Williams, 1986; Alvarez-Cadena, 1993; Sullivan & Meise, 1996), and limitation of *Pseudocalanus* population growth by chaetognaths has been recorded by Ohman (1986). Ohman (1986) also mentions that the interannual variability in the abundance of predators such as *Sagitta* was related to annual mortality of *Pseudocalanus* in Dabob Bay, Washington (USA). This study has shown that the peak abundances of five omnivorous taxa (Table 5.6), of which two, *Pseudo-/Para-/Microcalanus* juveniles and *Oithona*, were the numerically dominant taxa recorded in the Dove series, were related to spring *Sagitta* abundance. This suggests that predation upon these taxa during spring was limiting their population growth, hence their maximum abundances and annual productivity. The five omnivorous taxa which were related to spring *Sagitta* abundances could be classified as small or medium sized (<2mm) copepods (Nicholas & Frid, 1999). Larger taxa (e.g. *Calanus* adults) showed no such relationship (Nicholas & Frid, 1999). Chaetognaths are ambush predators (Feigenbaum & Maris, 1984), and as such are largely non-selective, but predate upon whatever they encounter in the water column (Falkenhaug, 1991). However, there is a relationship between the size of a *Sagitta* individual and the size of prey taken (Figure 5.11) (Feigenbaum & Maris, 1984). It would be expected that only juvenile *Sagitta* (stages I and II) individuals under approx. 15 mm (Huliselan, 1995) would predate upon those omnivorous taxa identified in Table 5.6 (Feigenbaum & Maris, 1984). Larger omnivores such as adult *Calanus* would not be expected to be consumed by juvenile *Sagitta*, but would be consumed by Stage III individuals (Figure 5.11).

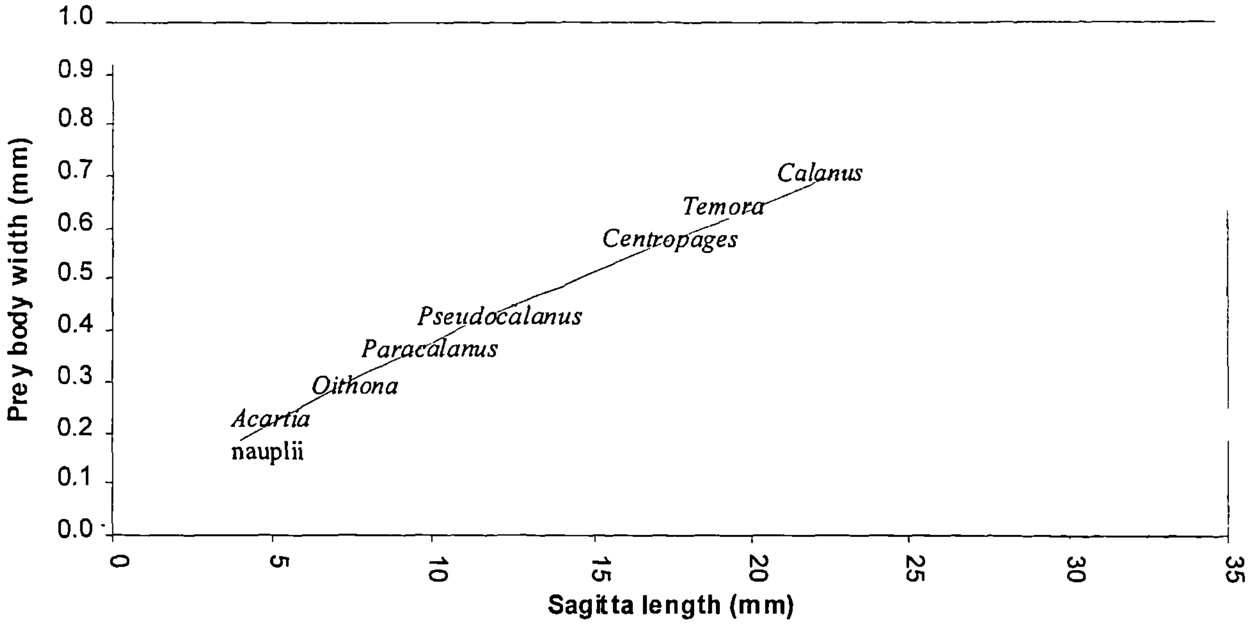


Figure 5.11 Relationship between length of *Sagitta elegans* and maximum prey body width. Data from Feigenbaum & Maris, 1984.

Given that small copepods are the principle target of predation by *Sagitta*, it might be expected that other small sized copepod taxa (e.g. *Microcalanus*) would be influenced by such predation. However, an additional factor to consider is that, at the population level, each taxon is likely to have a different susceptibility to control by predation, based on its life history characteristics. For example, *Pseudocalanus* shows the strongest evidence of control by *Sagitta* (Table 5.6), and is also noted for having a relatively low rate of population growth due to its low fecundity (Corkett & McLaren, 1978), which is limited by water temperatures rather than food supply (McLaren, 1965; Davis, 1984a), and thus it would be expected that this taxa would be sensitive to predation.

The hypothesis that *Sagitta* has the ability to limit copepod population growth was further supported by the results of the *Pseudocalanus* population modelling exercise, where levels of predation (NPC>=0.4) produced output which was not significantly different to the observed pattern in the Dove series, and exhibited a negative relationship to the position of the GSNW (as observed in Chapter 4). However, in the absence of predation by *Sagitta* (i.e. when NPC was set to zero), *Pseudocalanus* abundance was positively related to fluctuations in the GSNW, as was observed in many zooplankton populations throughout the NE Atlantic area (Taylor & Stephens, 1980; Taylor *et al.*, 1992; Taylor, 1995). It is therefore the predation of *Sagitta* on the omnivores in the coastal central-west North Sea region which is responsible for producing the long term dynamics of the zooplankton community. The idea that predation reverses the sign of the relationship with climate is supported by the fact that a number of those taxa whose summer abundances were controlled by spring *Sagitta* abundances (Table 5.6) also showed interannual fluctuations which were negatively related to climate (Chapter 4; Appendix 3.1 & 3.2). For example, the *Pseudo-/Para-/Microcalanus* juveniles were the taxa most strongly limited by *Sagitta*, and which also presented the strongest inverse relationship to the GSNW and to air temperatures. Conversely, those taxa which were not related to *Sagitta* abundances, either due to their size, or due to high reproductive rates, would be less influenced by predation and might be expected to be positively related to climate. There is some evidence to support this, although it is not conclusive (Chapter 4). For example, *Corycaeus anglicus*, which due to its large size would not be consumed by *Sagitta,* shows positive relationships to climate, (Appendix 3.2). A further example is that of *Acartia clausi*, which according to its small size, might be also expected to be consumed by *Sagitta*, yet due to its fast reproductive rate (Colebrook, 1982a) it is unaffected by predation, and, as such, its interannual dynamics are positively related to phytoplankton index (Appendix 3.1).

Increased *Sagitta* abundances during the spring were related to higher spring temperatures and more northerly positions of the GSNW (Figure 5.10d). As to why *Sagitta* should show a relationship to climate is uncertain. Although temperature is known to be linked to the growth rate and generation time of *Sagitta* (Oresland, 1985; Oresland, 1986), food is more important to its fecundity and therefore its overall abundance (Feigenbaum & Maris, 1984). Feigenbaum & Maris (1984) noted that the periods of recruitment of a new *Sagitta* cohort coincided with sharp increases in the abundances of *Pseudocalanus* nauplii (which are the main food source of young Sagitta, Baier & Purcell, 1997). Yet as mature chaetognaths do not feed on small prey (and cannot detect their presence), it was more likely that the reproductive timing of *Sagitta* was related to the abundance of adult prey (which are consumed by larger chaetognaths) (Feigenbaum & Maris, 1984). It could be for this reason why, in the CPR series, it is only the large chaetognaths (>8mm length) which show a relationship to the *Para-/Pseudocalanus* juveniles. Finally, in the Dove series, spring *Sagitta* (March-April) abundances are observed to be related to the spring (March-April) abundance of *Calanus* adults ($r=0.57$, $p=0.002$), so this supports the hypothesis that prey availability for stage III *Sagitta* is influencing its fecundity.

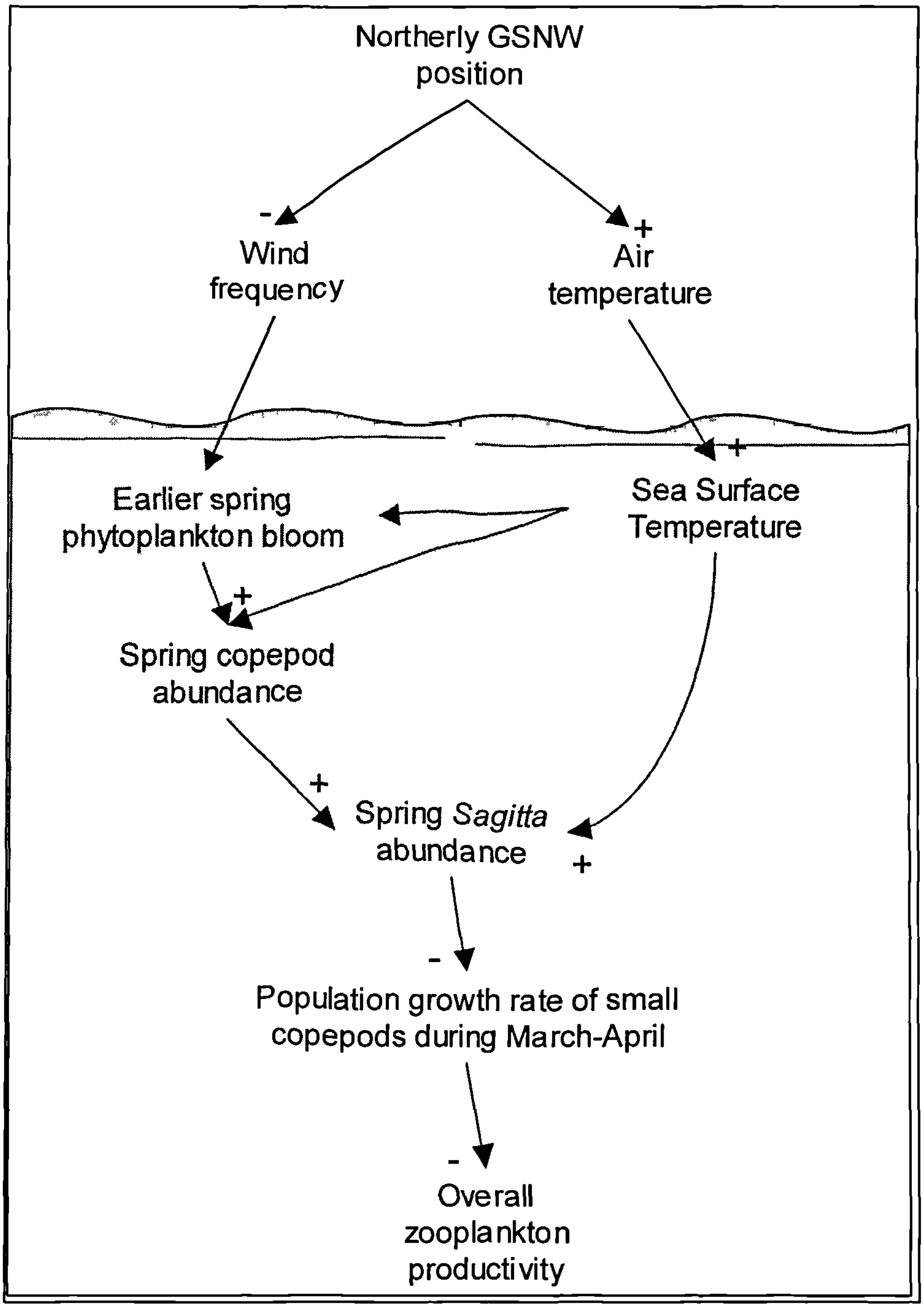


Figure 5.12 Conceptual model of the associations between the Gulf Stream North Wall and the Northumberland copepod community through predation by *Sagitta*. See text for details.

To summarise, this mechanism therefore functions through the presence of suitable weather conditions which induce a spring bloom, and an increase in the abundance of suitable prey (Figure 5.12). This then results in a new cohort of *Sagitta*, which are able to reduce the growth of the small copepod population during the spring, and effectively inverts the climatic signal observed in the Dove zooplankton time series, compared to other areas of the North Sea and oceanic North Atlantic (Taylor *et al.*, 1992).

Although not considered in detail here, as high abundance years show an increased predator abundance during the *summer* months (Figure 5.4a), it appears, as originally suggested by Roff *et al.* (1988), that there are two main groups of predators present. There are those that regulate omnivore abundance through limiting the rate of population growth in the spring (i.e. *Sagitta*, discussed here), and there are those other predators which follow omnivore abundances (primarily fish larvae and Pleurobrachia pileus, Frid *et al.*, 1994; Nicholas & Frid, 1999). The abundance of this latter group responds to the abundance of the omnivores (i.e. their food source). This group of summer predators do not tend to have such a strong effect upon omnivore abundance, as the high omnivore abundances present and summer water temperatures allows a high omnivore reproductive rate (food availability permitting). In contrast, during the spring copepod increase lower water temperatures and lower standing stocks mean a lower fecundity so populations are more vulnerable to predation. Baier & Purcell (1997) and Kehayias *et al.* (1996) have shown that chaetognath predation has the greatest effect during periods of low copepod productivity, as this is when copepod reproduction is lowest.

Although here I have focussed upon limitation of omnivore growth rates during the spring, and put forward a mechanism as to how the long term dynamics observed in the Dove series are controlled, it is likely that this mechanism does not operate in every year. Evans & Edwards (1993) suggested that the species most responsible for the shift in species composition occurring around 1979-1980 was *Sagitta*. Before 1979, spring *Sagitta* abundances were low (Figure 5.10a). The effect of this may be observed in the model output (where NPC>=0.11*) as* high *Pseudocalanus* abundances (Figure 5.9b, c & d). Other studies have put forward chaetognaths as being sensitive to climatic shifts, and as indicators of changes in water temperatures (Southward, 1980), and the timing of the increase in spring *Sagitta* abundances does coincide with the nadir in zooplankton abundances. As remarked by Roff *et al.* (1988) the interannual dynamics of zooplankton may be highly complex, and during years when spring *Sagitta* abundances are low, other factors such as water temperature, food, or the standing stock of omnivores surviving the winter may be more important in influencing the seasonal zooplankton dynamics during that year. In addition, it is also likely that for those taxa with a relatively slow growth rate, reduction of the winter standing stock due to predation (as suggested by Roff *et al.*, 1988; Frid *et al.*, 1994; Nicholas & Frid, 1999), may also influence the productivity of these taxa the following year. Previous studies have suggested that despite *Sagitta* being the dominant predator observed during the winter and spring period, other predators are more voracious and have a higher impact on copepod stocks (Frid *et al.*, 1994; Nicholas & Frid, 1999).

Sullivan & Meise (1996) noted that, on Georges Bank, *Sagitta* preferred the shallower well mixed areas of the Bank, and as such, predation by *Sagitta* may be confined to shallower, well mixed or coastal areas of the North Sea. Although the results presented in this chapter have focussed on the data collected from a single sampling station (i.e. the Dove series), as the CPR data, which is collated from a wider area (Figure 3.2), shows similar trends and climatic relationships as the Dove series (Chapters 3 & 4), the mechanism proposed here may therefore operate over a wide area of the central North Sea (Figure 3.2). However, further analysis of CPR data is required to determine in which areas of the North Sea, chaetognaths might have the potential to influence copepod populations.

Chapter 6 Long term changes in the benthos off the Northumberland coast

Introduction

The benthos off the Northumberland coast has been regularly sampled since the early 1970s, the initial objective being to establish the amount of benthic productivity occurring in the area on a short term basis (Buchanan & Warwick, 1974). Shortly after sampling commenced, proposals arose to dump sewage sludge in the region (Buchanan *et al.*, 1978), which prompted the extension of the sampling programme. Thus, the emphasis changed to one of monitoring the natural fluctuations in the benthos, and attempting to understand the mechanisms which drive long term changes in the benthic community. As such, care was taken to ensure that the 2 stations maintained were selected as being representative of the benthos over a wide area (Buchanan, 1993).

The majority of research has been performed on benthic Station M1, which is situated at 55 m depth and sampled twice annually. The other series, Station P, situated at 80 m depth and located further offshore, is sampled annually. Analysis of the M1 series has determined that a number of factors influence the long term dynamics of the benthic community. These are, in order of importance, 1) changes in the amount of organic matter reaching the benthos, 2) biological interactions (i.e. density dependant mortality over the winter), and 3) winter temperatures (Buchanan & Moore, 1986b). The series has also been classified into "stable" and "unstable" periods based on the interannual dynamics observed (Buchanan *et al.*, 1986; Buchanan & Moore, 1986a).

The stable period at Station M1 was first described by Buchanan & Moore (1986) as being present from September 1972 to March 1980. During this period, abundances fluctuated between 2000 to 8000 individuals.m^{-2} in a stable biennial cycle (Figure 6.2a). Recruits settled over the summer, and there was mortality during the winter. The food supply to the benthos at this time was relatively constant, and it was shown that mortality levels over the winter were due to density dependence, which adjusted the numbers to a level which was dependant upon the available energy. In addition to density dependant mortality, cold winters were observed to reduce the diversity of the benthic community, with low temperatures favouring the survival of the dominant species at the expense of less abundant taxa (Buchanan *et al.*, 1978; Buchanan & Moore, 1986b).

This stable biennial cycle ended in March 1981 when there was a marked rise in abundance instead of the predicted fall (see Figure 6.2a). As documented by Evans & Edwards (1993) up to 1979, phytoplankton productivity was low and steady, yet after this time the phytoplankton exhibited higher peaks of productivity during the annual cycle (see Figure 2.4). This suggested that the end of the stable period could be due to changes in organic matter input to the benthos. However, the benthos was observed to change two years after the changes occurred in the phytoplankton system (Buchanan, 1993). This 2 year lag between cause and effect was due to, i) the fact that the benthic sample at M1 was taken in March, prior to the spring phytoplankton bloom and, ii) that although the benthic response to sedimenting phytoplankton would be immediate, a further year was required for the newly settled individuals to grow to a size where they became apparent in the sieved samples (Buchanan, 1993). During the "unstable" period from 1981 to 1991, it was determined that phytoplankton index 2 years earlier explained 55% of the variance in benthic abundance at M1 in March (Buchanan, 1993).

Analysis of the changes in community structure at both M1 and P showed that shifts occurred in the genera composition of the macrofauna between 1980-1981 at both sites (Austen *et al.*, 1991; Buchanan, 1993), two years after the change in phytoplankton. Austen *et al.* (1991) also observed an increase in benthic abundance and species composition occurring in the Skaggerak a year earlier (i.e. between 1979 and 1980). Although Buchanan (1993) did not propose a reason for the ultimate cause of the changes in productivity observed at benthic Station M1, Austen *et al.* (1991) suggested that such shifts were due to changes in nutrient concentrations which influenced the benthos through their effect on phytoplankton productivity. However, in the central-west region of the North Sea, the interannual dynamics of phytoplankton appear to be driven by climatic fluctuations as opposed to changes in nutrient concentrations (Chapter 4).

Research on other North Sea benthic time series also suggests that changes in organic matter input to the benthos is the main cause of changes in benthic abundance and/or community structure. For example, at Balgzand, Wadden Sea intertidal mudflat, changes in infaunal biomass were observed to follow those of mean annual chlorophyll concentration (Beukema, 1992c), which in turn were linked to eutrophication. Ultimately the cause of these changes have been attributed to changes in nutrient concentrations or eutrophication acting upon phytoplankton productivity (Austen *et al.*, 1991; Beukema, 1992c; Josefson *et al.*, 1993), although a study by Tunberg & Nelson (1998) did suggest that long term changes in Skaggerak benthos were caused by changes in nutrient concentrations, which in turn were being forced by changes in climate (see Chapter 2). Apart from density dependant factors, other internal mechanisms have rarely been found to be important in the long term dynamics of the benthic system. However, a recent study by Beukema *et al.* (2000) has shown that cold winters reduced the abundance of the predator *Nephtys* which in turn reduced the predation pressure upon the benthic community and lead to increased prey biomasses.

This chapter details the long term changes in abundance and community structure observed at Stations M1 and P over the 1971 to 1998 period. The previous hypotheses of control of the benthic community through organic matter input is re-examined using the most recent time series data, alongside a consideration of the importance of density dependant effects in mediating the influence of organic matter on the benthic community. In addition, the role of climatic influences or nutrient inputs as the ultimate cause of the changes in the benthos is further considered.

Methods

Site and sampling methodologies

Dove Marine Laboratory benthic time series

In the early 1970's, time series were established at two benthic stations off the Northumberland coast, north east England. Station M1 lies at 55° 04' N 01° 20'W (Figure 6.1), 6.5 miles offshore, inshore of a *Nephrops norvegicus* fishing ground. It has a predominantly sandy sediment, with a 20% silt clay content and lies in 55m of water. The community is, *sensu* Petersen & Boysen-Jensen (1911), the *Amphiura filiformis-Echinocardium cordatum* variant of the *Amphiura filiformis* community type. Sampling commenced in September 1972. Station P is situated at 55° 07' N 01° 15' W (Figure 6.1) within the *Nephrops norvegicus* ground. It lies 11.5 miles offshore and is in 80m of water. The sediment has a silt-clay content of greater than 50%, of which 20% is faecal pellets. The community at the station is the *Brissopsis lyrifera-Amphiura chiajei* variant of the *Amphiura filiformis* community type (Petersen & Boysen-Jensen, 1911). The station was initially sampled in January 1971.

Sampling at Station M1 is carried out in March and September of each year, while sampling at Station P is routinely carried out in January. On all sampling occasions, a van Veen grab removing an area of 0.1m^2 and 0.5mm mesh sieve was used. At least five grab samples were taken on each occasion. The 1977 sample from Station P is not considered further as weather and operational constraints prevented sampling until June of that year, and it is not therefore comparable with the rest of the time series. Buchanan & Warwick (1974) and Buchanan & Moore (1986b) describe the methods of sampling at each station in detail.

Initial manipulations of time series data

The benthic community data for both Station P and M1 were reduced to make analysis of long term changes in abundance and community structure simpler and to limit correlations to the most abundant taxa (initially, Station P contained a total of 171 genera, whilst M1 had 276 genera). Thus, for each series, only those genera present at 1%, *on any one sampling occasion*, were selected for further analysis. This procedure left 48 genera at Station P, and 85 genera at Station M1. Rather than produce annual mean values for Station M1 from the twice annual samples, the March and September samples for Station M1 were analysed separately.

Analysis at the genus level avoided any problems due to errors of mis-identification at the species level, or changes in taxonomy leading to problems with homonyms. Somerfield & Clarke (1995) demonstrated that such aggregations of data to higher taxonomic levels causes minimal loss of information. Therefore, this method was considered to be robust.

The order of dominance of taxa within each benthic series was determined by calculating, for each taxa, its mean abundance, and proportion of the total community over the whole time series. The resulting values were then ranked from highest mean abundance to lowest (Table 6.1).

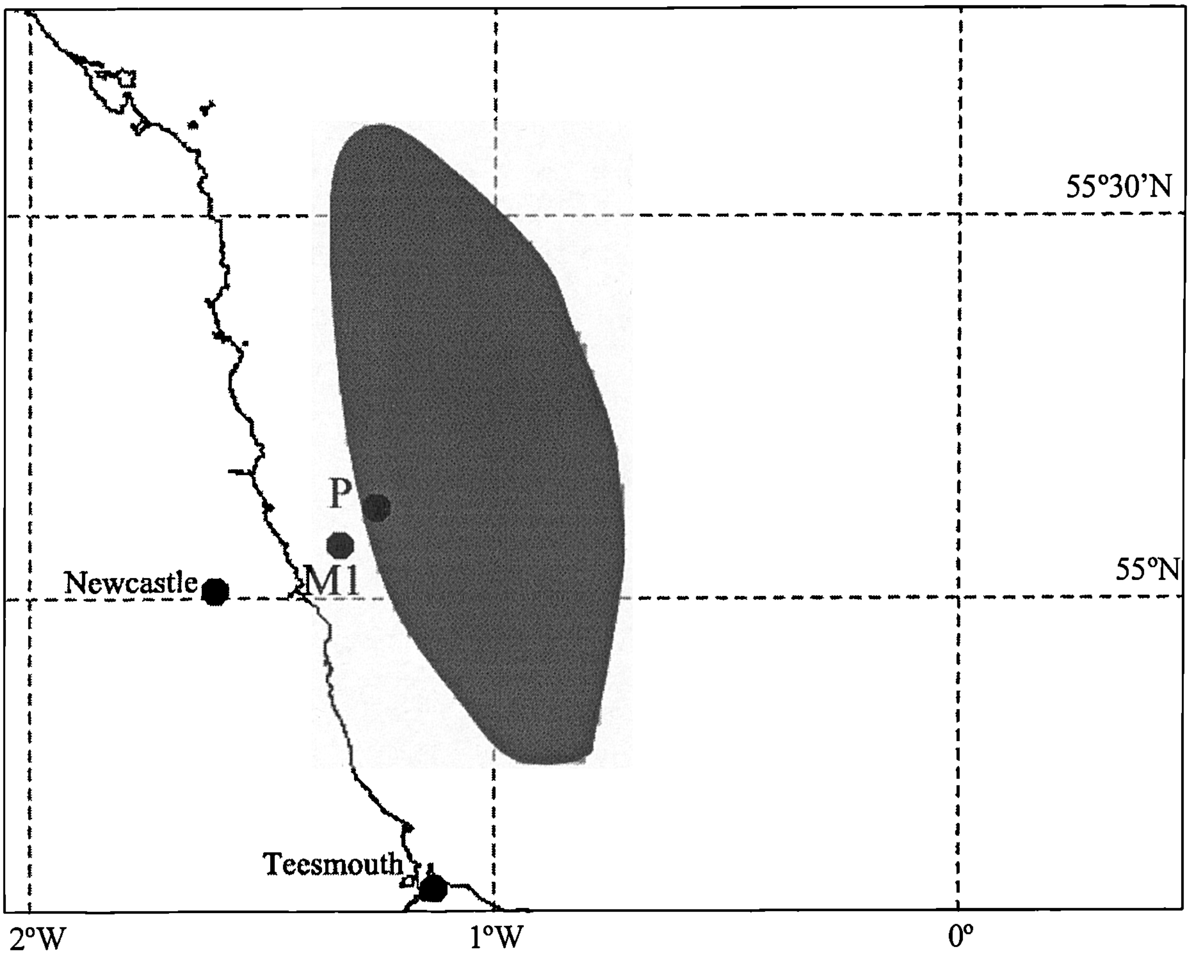


Figure 6.1 **Locations of benthic sampling Stations P and M1, off the NE coast of England. Dark shaded area shows the area of the *Nephrops* fishing ground.**

Analyses of long term changes in community structure

For each series, PRIMER (Clarke & Warwick, 1994) was used to calculate Bray-Curtis similarity indices between annual means, and for MDS ordination of genera (Clarke & Warwick, 1994). Analyses of long term changes in community structure were carried out at the genus level and using a 4th root transformation to reduce the effect of dominant genera. MDS ordination was used to show changes in genera composition of the community.

In order to establish whether there was a significant trend in the genera composition of each station over time, a Mann-Kendall test (see Chapter 4) was performed on the time series of similarity coefficients between the first and consecutive years.

Examination of benthic-pelagic coupling

The presence of relationships between phytoplankton index and benthic abundances were established using linear regressions. Here, total benthic abundance in each series was regressed against annual mean phytoplankton index data from CPR area C2 at a one and two year lag. Additionally, M1 September samples were also correlated with phytoplankton index data at a zero year lag. A zero year lag was not used with the M1 March and P samples as these are taken each year before the main phytoplankton productive season. All significance tests were corrected for autocorrelation using the method of Quenouille (1952) (see Chapter 4 for further details). In addition, ANOSIM was used to investigate the composition of the benthic community at M1 in low, mid and high phytoplankton years, at a 2 year lag (where low phytoplankton years <-0.5 standard deviations, high phytoplankton years >0.5 standard deviations and mid phytoplankton years between –0.5 and 0.5 standard deviations from the long term mean). Finally, SIMPER analysis enabled the identification of those taxa contributing the most to differences in genera composition between low, mid and high phytoplankton years.

Path analysis

Path analysis is used not to predict relationships between variables, but to show the most plausible interpretation of relationships between the variables (i.e. to show a causal structure between variables). Path analysis enables the evaluation of the direct effect of one cause on a response and its indirect effect via other causes (Sokal & Rohlf, 1995). Here, this method was used to establish whether abiotic environmental influences (i.e. weather) were having a direct effect on the M1 March benthos, or if weather was indirectly influencing the benthos through changes in phytoplankton input. The south westerly weather type (Lamb, 1972, Appendix 2) was selected as being the environmental variable used as, like phytoplankton, it is correlated with the benthos at a two year lag.

Examination of density dependant mortality

Changes in benthic abundance at Station M1 during the winter were examined for the presence of density dependant effects. Rather than simply regress the differences in abundance from each September to March against each September value, in order to increase the independence of the regression, the $\log_{10}$ transformed percentage overwintering mortality was regressed against the September values:

$$Mortality = Log_{10} \frac{Mar.abundance}{Sept.abundance} x100$$

Note, that as during some years, there was a small increase in benthic abundance over the winter (i.e. "mortality" was greater than 100%) the arc-sine transformation could not be employed, although a $\log_{10}$ transformation did achieve normality of the data (as determined by the Ryan-Joiner test for normality (Minitab®)). Visual examination of the relationship between overwintering mortality and September abundances was obtained using benthic abundances, with the best fitting relationship obtained using the curve-fitting program, Curve Expert 1.3®.

Table 6.1 Mean abundances and percentage composition of benthic genera at Stations M1 March, M1 September and P.

Station M1 March	Mean abundance (per m^2)	Mean percentage composition	Station M1 September	Mean abundance (per m^2)	Mean percentage composition	Station P	Mean abundance (per m^2)	Mean percentage composition
Prionospio	594.8	15.10	*Prionospio*	557.7	8.73	*Heteromastus*	679.0	30.47
Other taxa	282.6	7.17	Other taxa	443.8	6.94	*Levinsenia*	223.1	10.01
Levinsenia	272.8	6.92	*Abra*	318.5	4.98	*Prionospio*	177.8	7.98
Chaetozone	202.6	5.14	*Levinsenia*	307.7	4.81	*Chaetozone*	122.4	5.49
Thyasira	197.4	5.01	*Phoronis*	292.6	4.58	*Ophelina*	91.8	4.12
Amphiura	160.5	4.07	*Myriochele*	216.9	3.39	*Other taxa*	72.2	3.24
Myriochele	132.7	3.37	*Echinocardium*	207.9	3.25	*Nemertea*	65.3	2.93
Pholoe	129.5	3.29	*Chaetozone*	207.0	3.24	*Harpinia*	64.3	2.89
Tharyx	119.1	3.02	*Pholoe*	194.8	3.05	*Amphiura*	61.6	2.76
Nephtys	110.6	2.81	*Thyasira*	189.0	2.96	*Spiophanes*	54.5	2.45
Heteromastus	105.2	2.67	*Amphiura*	179.1	2.80	*Abra*	54.1	2.43
Nuculoma	103.7	2.63	*Spiophanes*	175.4	2.74	*Praxillella*	52.4	2.35
Mysella	103.2	2.62	*Mysella*	166.5	2.60	*Lumbrineris*	51.7	2.32
Nemertea	93.5	2.37	*Heteromastus*	139.0	2.17	*Minuspio*	50.1	2.25
Harpinia	77.5	1.97	*Phaxas*	134.3	2.10	Oligochaeta	48.9	2.19
Lumbrineris	77.0	1.95	*Nuculoma*	132.9	2.08	*Glycera*	34.3	1.54
Phoronis	75.1	1.91	*Ampharete*	130.5	2.04	*Pholoe*	30.8	1.38
Spiophanes	74.8	1.90	*Nephtys*	130.2	2.04	*Paramphinome*	23.1	1.04
Terebellides	64.7	1.64	*Mediomastus*	125.3	1.96	*Leucon*	21.7	0.97
Magelona	60.3	1.53	*Owenia*	118.1	1.85	*Tharyx*	20.4	0.92
Ampelisca	55.1	1.40	*Tharyx*	117.9	1.84	*Goniada*	19.3	0.87
Abra	54.4	1.38	*Nemertea*	107.5	1.68	*Nuculoma*	16.4	0.73
Owenia	54.2	1.38	Other spionids	101.4	1.59	*Synelmis*	16.1	0.72
Oligochaeta	50.7	1.29	*Ampelisca*	96.0	1.50	*Magelona*	15.3	0.69
Mediomastus	46.1	1.17	*Lagis*	92.4	1.45	*Eudorella*	14.1	0.63
Rhodine	42.6	1.08	*Terebellides*	87.2	1.36	*Thyasira*	13.5	0.61
Lucinoma	41.0	1.04	*Lumbrineris*	86.6	1.36	*Diplocirrus*	12.6	0.57
Glycera	38.5	0.98	*Ophelina*	82.4	1.29	*Cylichna*	12.4	0.56
Ampharete	37.6	0.96	*Acanthocardia*	76.2	1.19	*Scalibregma*	10.8	0.49
Goniada	32.7	0.83	*Lanice*	68.1	1.07	*Terebellides*	10.4	0.47
Other spionids	31.2	0.79	*Magelona*	67.1	1.05	*Calocaris*	9.0	0.40
Diplocirrus	25.6	0.65	*Harpinia*	63.5	0.99	*Pseudeurythoe*	8.2	0.37
Exogone	25.2	0.64	*Rhodine*	62.5	0.98	*Nephtys*	7.6	0.34
Tellimya	23.7	0.60	*Scalibregma*	47.3	0.74	*Anobothrus*	7.6	0.34
Anobothrus	21.9	0.56	Oligochaeta	46.6	0.73	*Diastylis*	5.7	0.25
Eudorella	21.5	0.55	*Lucinoma*	41.8	0.65	*Photis*	5.2	0.23
Scoloplos	19.6	0.50	*Spisula*	39.5	0.62	*Commensodorum*	5.0	0.22
Diastylis	19.3	0.49	*Kellia*	38.2	0.60	*Ericthonius*	4.7	0.21
Cylichna	18.6	0.47	*Glycera*	37.9	0.59	*Ampharete*	4.6	0.21
Echinocardium	18.5	0.47	*Gari*	36.5	0.57	*Protomedeia*	4.5	0.20
Turritella	18.1	0.46	*Exogone*	35.8	0.56	*Virgularia*	4.0	0.18
Chamelea	17.5	0.44	*Goniada*	35.2	0.55	*Cirratulidae*	4.0	0.18
Chaetoderma	16.3	0.41	*Poecilochaetus*	32.8	0.51	*Mysella*	3.7	0.17
Kellia	15.5	0.39	*Eteone*	31.7	0.50	*Monopylephorus*	3.5	0.16
Ophelina	14.5	0.37	*Anobothrus*	31.3	0.49	*Thelepus*	2.7	0.12
Paraonidae	14.1	0.36	*Pseudopolydora*	30.7	0.48	*Myriochele*	2.7	0.12
Glycinde	13.2	0.33	*Diplocirrus*	29.8	0.47	*Ophiuroidea*	2.3	0.10
Polydora	12.8	0.33	*Chamelea*	25.3	0.40	*Laonice*	2.2	0.10
Pseudopolydora	11.8	0.30	*Protomedeia*	23.7	0.37	*Kellia*	1.1	0.05
Photis	11.2	0.28	*Ampharetidae*	23.3	0.36			
Phaxas	9.9	0.25	*Scoloplos*	21.9	0.34			
Protomedeia	8.4	0.21	*Turritella*	21.1	0.33			
Leptognathia	8.0	0.20	*Lembos*	20.0	0.31			
Lembos	7.6	0.19	*Thracia*	19.1	0.30			
Spisula	6.9	0.17	*Photis*	19.0	0.30			
Terebellidae	6.5	0.16	*Polydora*	18.8	0.29			
Polycladida	6.1	0.15	*Tellimya*	18.3	0.29			
Lanice	6.1	0.15	*Sphaerodorum*	16.9	0.26			
Sthenelais	5.3	0.14	*Halcampa*	16.9	0.26			
Capitella	4.3	0.11	*Paraonidae*	16.6	0.26			
Cirratulidae	3.8	0.10	Other bivalves	16.2	0.25			
Odostomia	3.1	0.08	*Trichobranchus*	15.6	0.24			
Echinocyamus	3.0	0.08	*Cerianthus*	13.2	0.21			
			Ophiura	11.5	0.18			
			Pionosyllis	11.2	0.18			
			Arctica	10.7	0.17			
			Tubulanus	9.6	0.15			
			Glycinde	9.5	0.15			
			Nereis	7.8	0.12			
			Eumida	7.4	0.12			
			Pygospio	7.4	0.12			
			Echinocyamus	6.2	0.10			
			Ericthonius	5.3	0.08			
			Paramphinome	4.3	0.07			
			Copepoda	3.8	0.06			

6.5b). The M1 September samples show some relatively larger shifts in species composition from 1982 to 1992 (although data for 1991 is not available), compared to before and after these years (Figure 6.4a). These three groups (1972-1981, 1982-1991, 1992-1998), roughly coincide with the relatively larger shifts in species composition in the M1 March samples from 1979-1993.

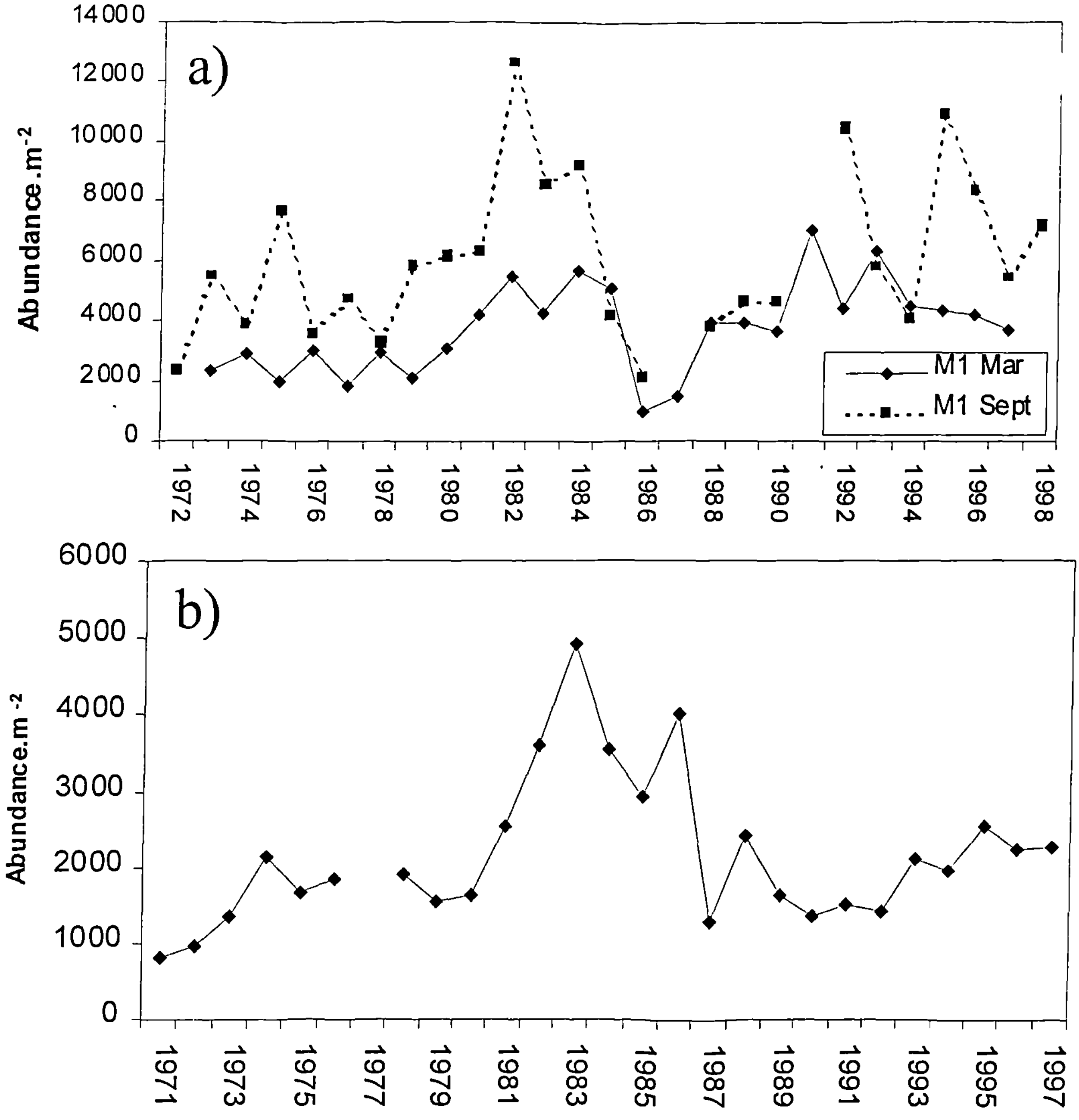


Figure 6.2 **Total abundance of individuals.m^{-2} at a) benthic Station M1 March and M1 September, b) benthic Station P.**

Whereas infaunal abundance at Station P remained relatively low until 1992 (Figure 6.2b), abundances at M1 March, after the drop in abundance between 1985 and 1986, recovered quickly (Figure 6.2a), with a large increase in abundance from 1500 individuals.m^{-2} to 3776 individuals.m^{-2} occurring between 1987 and 1988, eventually reaching its highest abundance to date in 1991 at 7066 individuals.m^{-2}. This recovery at M1 was accompanied by relatively large year to year changes in species composition (Figure 6.3a). However, since 1992 the community has shown relatively little change in community composition, although there was some indication of the biennial cycle re-occurring from March 1991 to March 1994 (Figure 6.2a).

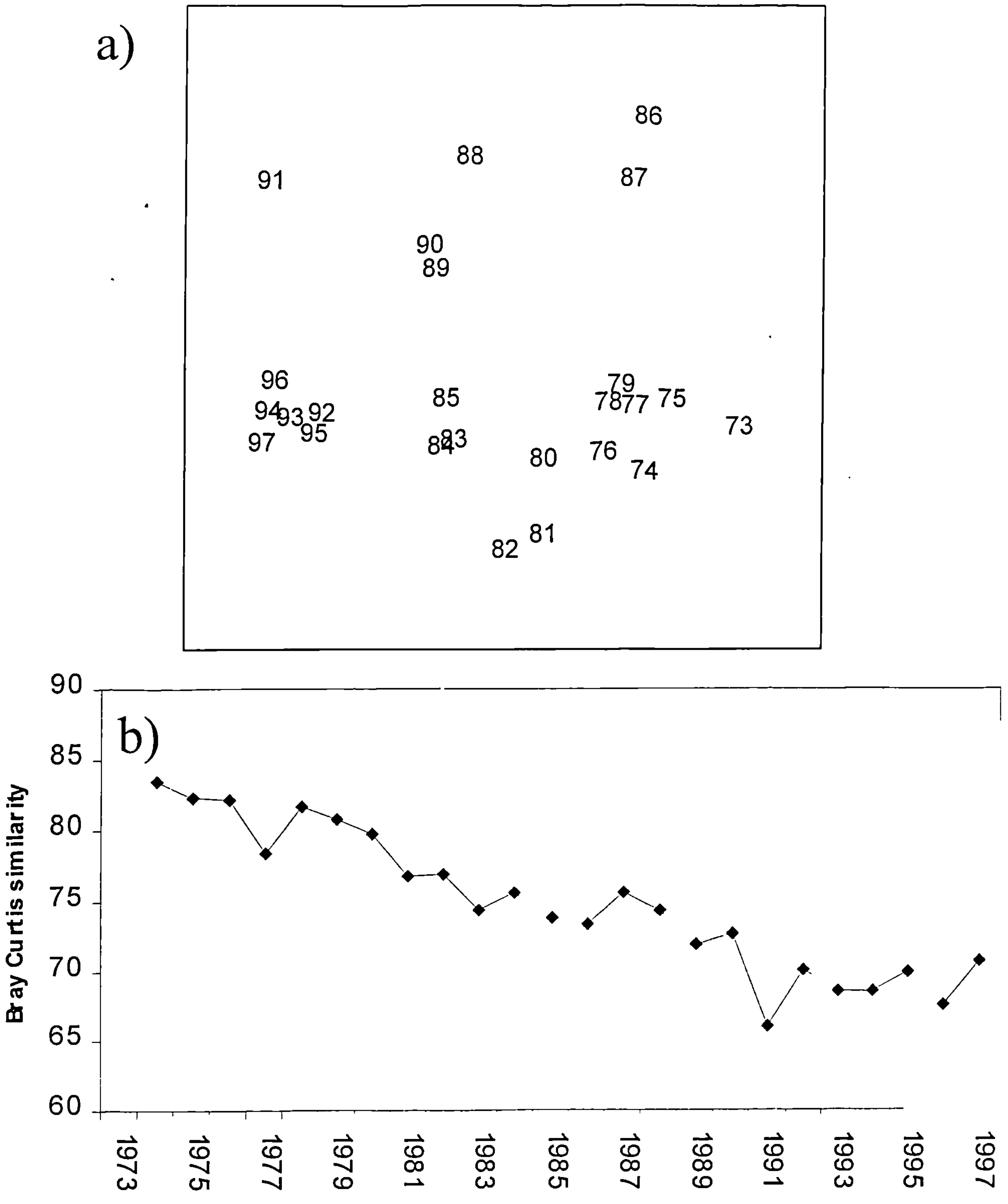


Figure 6.3 **a) MDS plot produced after calculated of Bray-Curtis similarity index on double root transformed genera from Station M1 March (MDS Stress value=0.12). b) Time series plot of Bray-Curtis Similarity between the first year (1973) and subsequent years calculated from genera at benthic Station M1 March samples. For both a & b the data covers the period 1973-1997.**

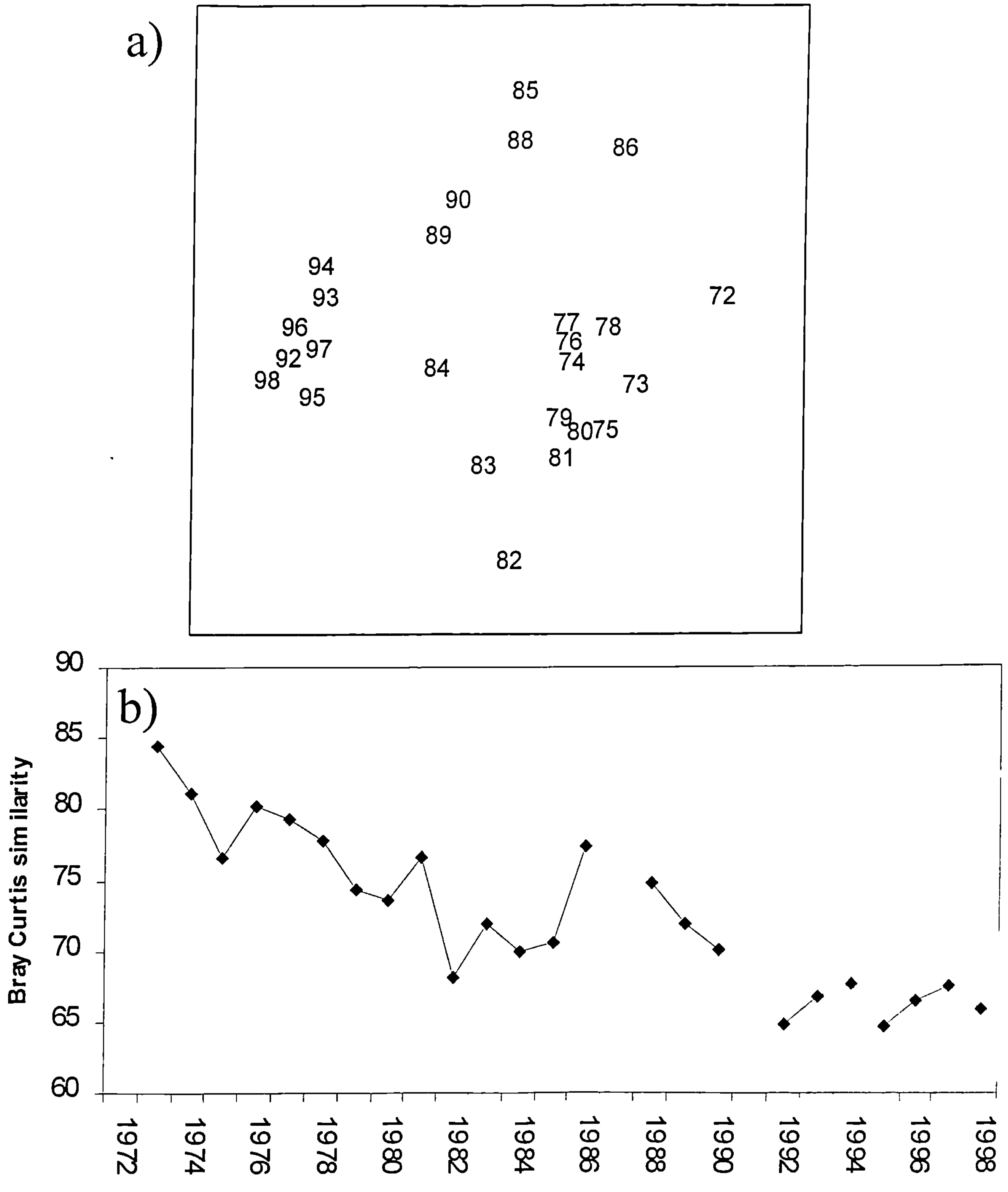


Figure 6.4 a) MDS plot produced after calculation of Bray-Curtis similarity index on double root transformed genera from Station M1 September (MDS Stress value=0.12). b) Time series plot of Bray-Curtis Similarity between the first year (1973) and subsequent years calculated from genera at benthic Station M1 September samples. For both a & b data covers the periods 1972-1986, 1988-1990 & 1992-1998.

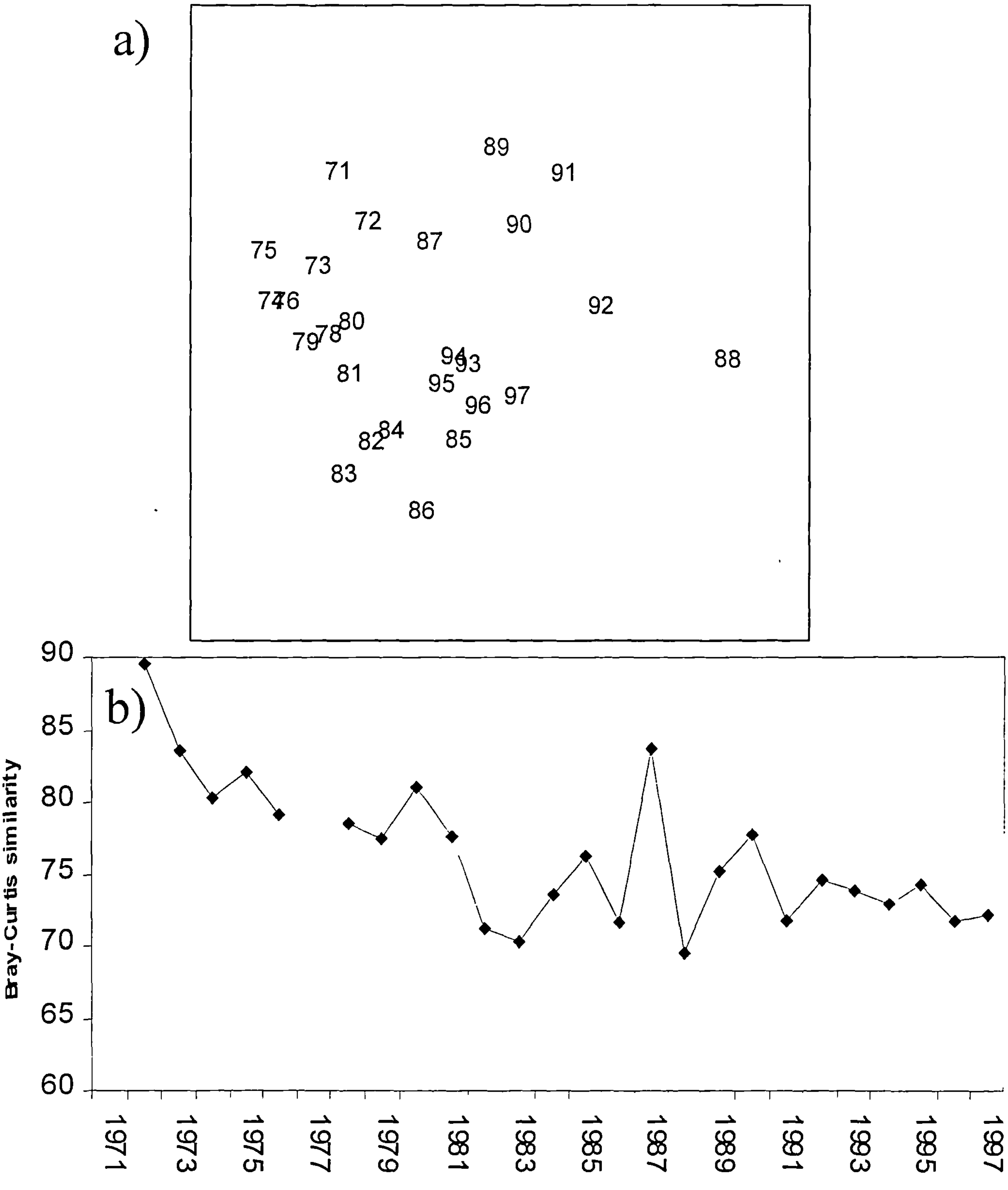


Figure 6.5 **a) MDS plot produced after calculation of Bray-Curtis similarity index on double root transformed genera from Station P (MDS Stress value=0.16). b) Time series plot of Bray-Curtis Similarity between the first year (1973) and subsequent years calculated from genera at benthic Station P covering the periods. For both a & b the data covers 1971-1976 & 1978-1997.**

There are some indications that the shifts within the MDS plots may be related to benthic abundance. At benthic Station M1 in March (Figure 6.3a) and September (Figure 6.4a) increases in abundance generally coincide with shifts towards the left hand side of the MDS plot, whilst shifts towards the right hand side coincide with reductions in abundance. This is most obvious at Station M1 in March. At Station P, increased abundances are located towards the bottom of the MDS plot, with lower abundances towards the top (Figure 6.5a). However, on top of this, the species composition of the Northumberland benthos appears to have steadily shifted away from the initial community identified in each series, as all three benthic series underwent strongly significant trends in the Bray-Curtis percentage similarities between the first year and each subsequent year (M1 March S=-228, p<0.001; M1 September S=-198, p<0.001; P S=-142, p=0.002). It could be suggested that as the MDS plots show indications of being related to benthic abundance, these trends in species composition are simply a reflection of such long term changes in abundance, yet only M1 March shows a significant long term trend in benthic abundance (S=108, p=0.017); the other series show no such trend (M1 September (S=68, p=0.117), P (S=65, p=0.148)).

Table 6.2 Correlation coefficients and probabilities between total benthic abundance in each series at a zero, one and two year lag. Significant correlations (after correction for serial correlation) are in bold.

	No lag	One year lag	Two year lag
Station P	NA	r=-0.13, p=0.335	r=-0.17, p=0.277
Station M1 March	NA	r=0.22, p=0.275	**r=0.57, p=0.006**
Station M1 September	r=0.06,p=0.380	r=0.011, p=0.40	r=0.10, p=0.351

Benthic pelagic coupling

Over the whole time series, from 1973 to 1997, the M1 March benthos was related to phytoplankton index (CPR box C2) at a 2 year lag (R^2=0.32) (Table 6.2). However, M1 September and Station P showed no correlation with phytoplankton index at any lag, and M1 March showed no correlation at a 1 year lag. There were also significant relationships, at a 2 year lag between M1 March samples and CPR phytoplankton index from box B2 to the north (r=0.44, p=0.027), although not the CPR box to the south, box D2 (r=0.03, p=0.394). As found by Buchanan (1993), a visual examination of the standardised time series plot (Figure 6.6) suggested that the relationship was strongest from 1983 onwards. However, the percentage variance explained from 1983 to 1997 in the M1 March samples was 48%, compared to the 55% found by Buchanan (1993) for the period 1983 to 1992. This drop in the R^2 value may be explained by the slight decoupling of the two variables after 1992 (Figure 6.6).

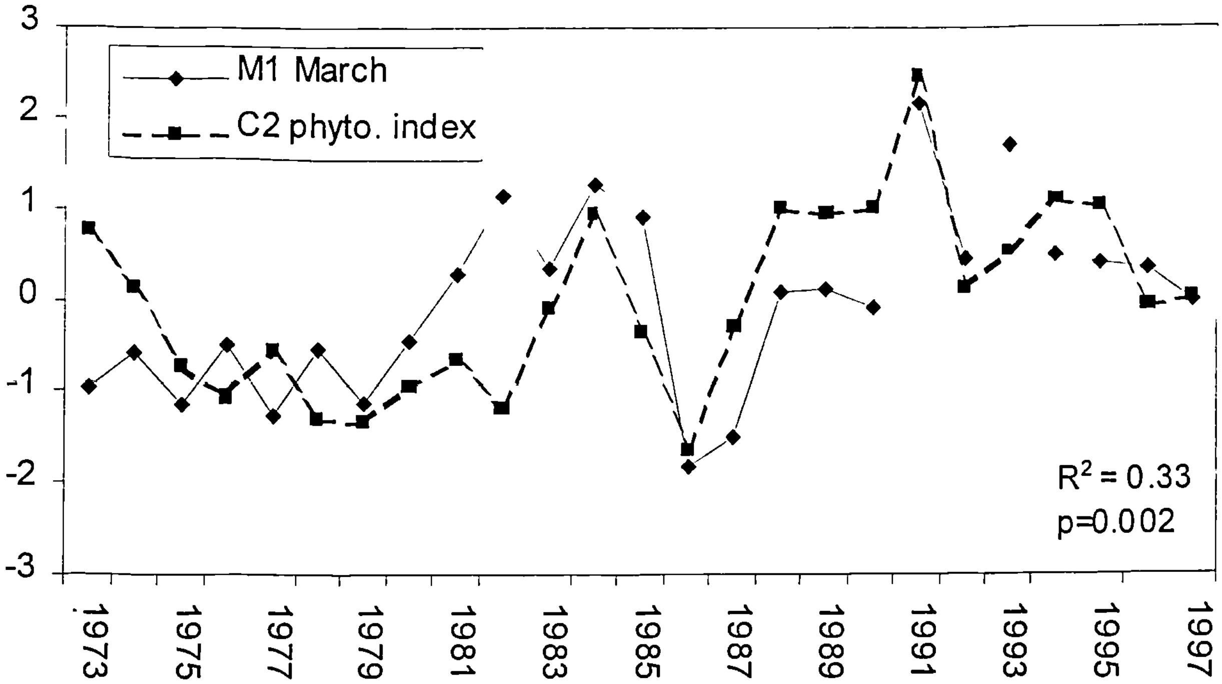


Figure 6.6 **Standardised time series plot of total abundances at Station M1 March samples and C2 phytoplankton index (at a 2 year lag).**

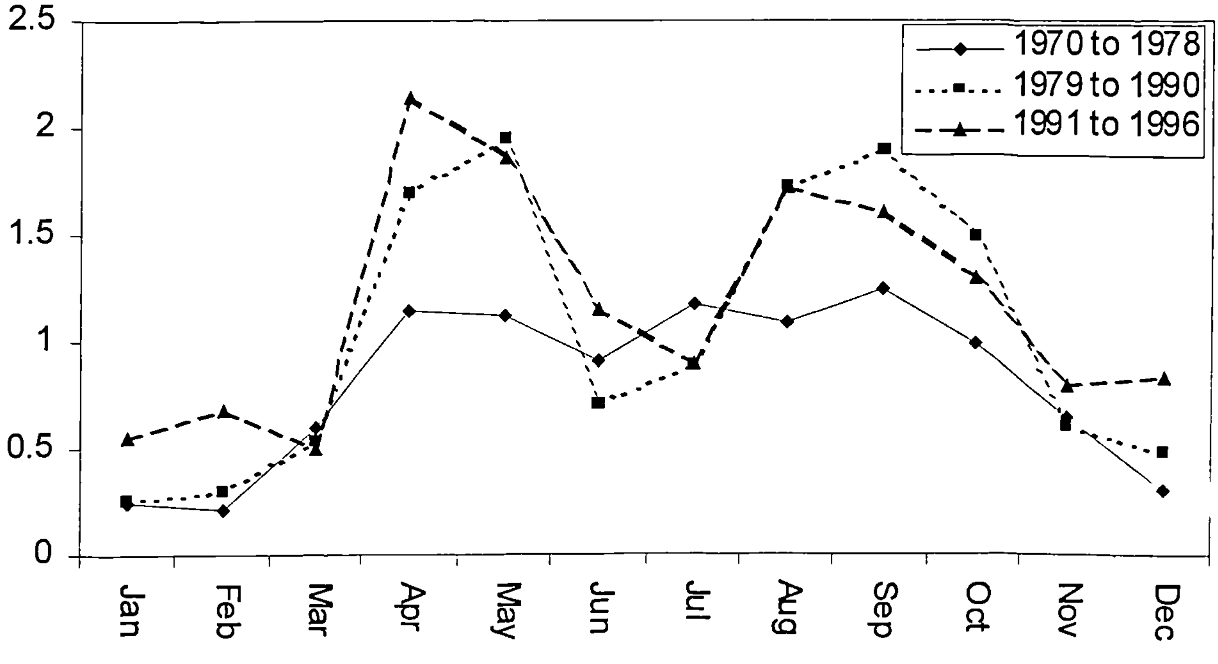


Figure 6.7 **Mean monthly phytoplankton index calculated over the 1970 to 1978, 1979 to 1990, and 1991 to 1996 periods.**

The frequency of south-westerly type weather (Lamb, 1972), was also correlated with the M1 benthos at a 2 year lag (r=0.47, p=0.017). However, the path analysis suggests that the relationship between SW weather and Station M1 is indirect, as the calculated path coefficients between the SW weather type and the M1 benthos were not significant (Figure 6.8). Thus, these results suggest that weather mainly affects the benthos indirectly, firstly influencing phytoplankton productivity, which then goes on to influence benthic productivity.

Table 6.3 ANOSIM results on M1 March standardised data (at a 2 year lag) testing for significant differences in species composition between low, mid and high phytoplankton years. Low years were 1973, 1974, 1976, 1977, 1978, 1979, 1980, 1984. Mid years were 1975, 1981, 1983, 1985, 1990. High years were 1982, 1986, 1987, 1988, 1989, 1991, 1992, 1993. Analysis was performed on double square root transformed abundances to minimise weighting of numerically dominant species.

GLOBAL SIGNIFICANCE TEST
Sample statistic (Global R): 0.347
Number of permutations: 10000
Number of permuted statistics greater than or equal to global R: 8
Significance level of sample statistic: 0.1%

Pairwise tests between groups of years:

Groups of years	Stat. Value	Permutations used	Significant statistics	Significance level
High and Low	0.458	10000	5	0.1%
Low & Mid	0.566	2002	3	0.1%
Mid & High	-0.087	2002	1490	74.4%

Fifteen taxa, mostly polychaetes were significantly, positively correlated with phytoplankton index at a 2 year lag, mostly polychaetes (Table 6.4). Of these polychaetes, two (*Tharyx* and *Trichobranchus*), were also positively related at a one year lag. *Cerianthus*, *Turritella* and "other spionids" were negatively correlated to phytoplankton index. Most of the taxa which made up more than 3% of the total individuals presented significant correlations with phytoplankton index (e.g. *Levinsenia, Thyasira, Prionospio* and *Tharyx*), and although most were polychaetes, two, *Photis* and *Ampelisca*, were crustaceans.

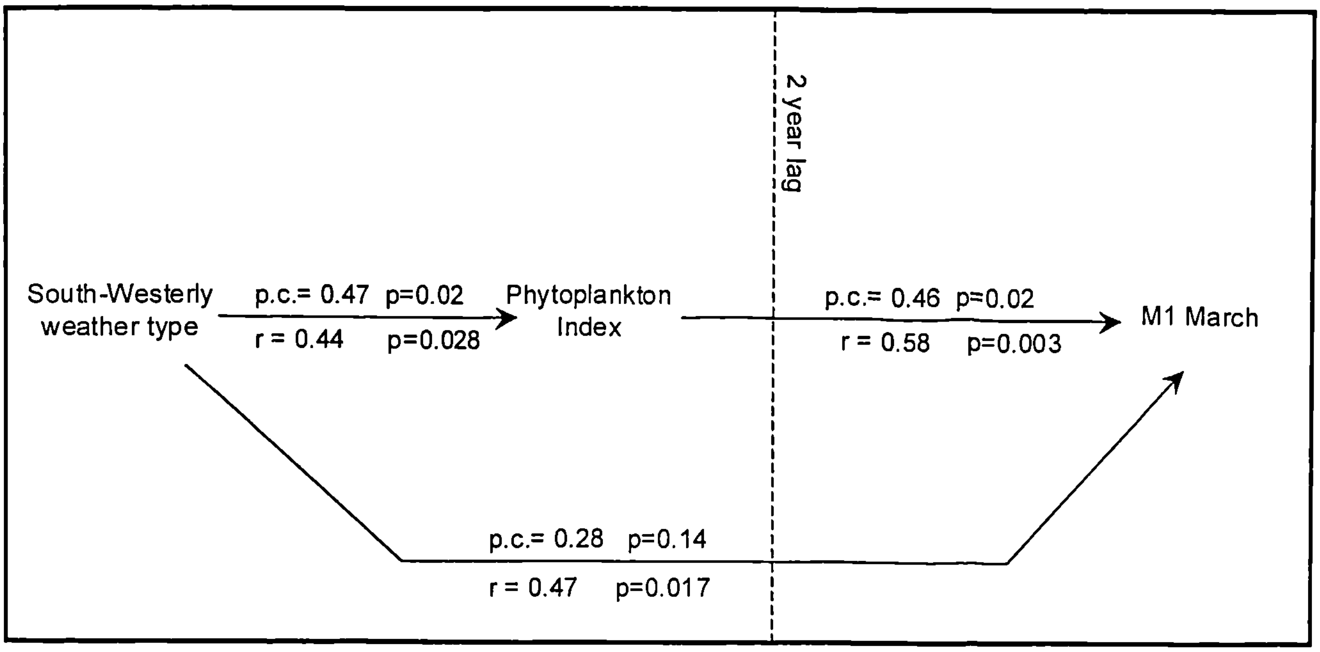


Figure 6.8 Model of relationship between Lamb's SW weather type, phytoplankton index (box C2) and benthic abundance at Station M1 March, and detailing path and correlation coefficients. p.c. = path coefficient. N.B. p values are *not* corrected for serial correlation

Table 6.4 **Correlation coefficients and probabilities between benthic genera at M1 (March samples) and phytoplankton index (box C2) at a 1 and 2 year lag. Significant correlations (after correction for serial correlation) are in bold. Global p = 0.004. Table is sorted on the 2 year lag correlation coefficients.**

Taxa	One year lag Correlation coefficient	P	Two year lag Correlation coefficient	P
Levinsenia	0.50	0 054	0 68	**0.002**
Thyasira	0.33	0.178	0 66	**0.004**
Chaetoderma	0.26	0.242	0 66	**0.002**
Rhodine	0.48	0 076	0 66	**0.002**
Tharyx	0 68	**0.01**	0 63	**0.019**
Lumbrinens	0.19	0.305	0 63	**0.004**
Prionospio	0.39	0 135	0.58	**0.009**
Trichobranchus	0.56	**0.037**	0 57	**0.038**
Eteone	0.39	0.079	0.54	**0.019**
Copepoda	0.03	0.394	0.51	**0.01**
Spaerodorum	0.03	0.394	0.51	**0.01**
Pholoe	0.18	0.273	0.49	**0.018**
Photis	-0.01	0.398	0.49	**0.014**
Anobothrus	0.36	0.088	0 48	**0.029**
Ampelisca	0.13	0.333	0.47	**0.022**
Exogone	0.21	0.275	0.45	0.053
Chaetozone	0.35	0.149	0.45	0.052
Pseudopolydora	0.27	0.228	0.40	0.114
Nuculoma	0.24	0.251	0.40	0.107
Paramphinome	0.32	0.187	0.37	0.065
Acanthocardia	0.27	0.231	0.34	0.126
Eumida	0.21	0.243	0.29	0.136
Arctica	0.25	0.186	0.26	0.201
Nemertea	0.03	0.396	0.26	0.166
Cylichna	0.12	0.337	0.25	0.196
Ampharetidae	0.10	0.363	0.24	0.21
Capitella	0.22	0.214	0.24	0.2
Ophelina	0.02	0.396	0.24	0.196
Glycera	0.05	0.39	0.24	0.19
Sthenelais	0.34	0.164	0.22	0.285
Paraonidae	-0.04	0.392	0.21	0.236
Diplocirrus	0.34	0.089	0.20	0.265
Abra	0.06	0.383	0.19	0.259
Ophiura	-0.08	0.37	0.16	0.319
Amphiura	-0.19	0.25	0.15	0.319
Ampharete	-0.05	0.389	0.15	0.315
Tubulanus	0.27	0.179	0.14	0.342
Echinocyamus	-0.02	0.397	0.14	0.316
Mediomastus	0.17	0.284	0.13	0.344
Heteromastus	0.07	0.375	0.13	0.322
Mysella	-0.15	0.298	0.10	0.356
Ericthonius	0.22	0.227	0.09	0.372
Harpinia	0.07	0.381	0.08	0.374
Diastylis	0.08	0.368	0.06	0.381
Goniada	-0.09	0.362	0.05	0.386
Spiophanes	-0.22	0.237	0.05	0.386
Other bivalves	0.15	0.318	0.04	0.394
Eudorella	-0.03	0.396	0.04	0.391
Cirratulidae	-0.23	0.232	0.03	0.395
Pionosyllis	-0.06	0.383	0.02	0.396
Polydora	-0.12	0.339	0.01	0.398
Leptognathia	-0.15	0.307	0	0.399
Oligochaeta	-0.09	0.359	0	0.399
Polycladida	-0.04	0.392	0	0.399
Lanice	0.05	0.389	-0.01	0.399
Lagis	-0.16	0.297	-0 02	0.398
Halcampa	-0.32	0.119	-0 02	0.397
Spisula	-0.28	0.154	-0.03	0.396
Owenia	-0.34	0.093	-0.03	0.395
Thracia	-0.25	0.183	-0.04	0.39
Nephtys	-0.07	0.376	-0.08	0.371
Myriochele	-0.31	0.129	-0.08	0.368
Phoronis	-0.25	0.199	-0.10	0.363
Scoloplos	-0.10	0.355	-0.11	0.346
Scalibregma	0.07	0.377	-0.11	0.341
Glycinde	-0.08	0.369	-0.12	0.338
Kellia	-0.16	0.3	-0.14	0 334
Gari	-0.25	0.199	-0.14	0.33
Lembos	-0.21	0.27	-0.16	0.328
Tellimya	-0.14	0.324	-0.16	0 303
Chamelea	-0.10	0.353	-0.17	0 296
Poecilochaetus	-0.25	0.178	-0.19	0 258
Protomedeia	-0.07	0.374	-0.19	0 257
Odostomia	-0.30	0 129	-0.21	0 26
Phaxas	-0.32	0.122	-0 21	0 226
Pygospio	-0.11	0.342	-0.26	0 171
Terebellidae	-0.28	0 22	-0.27	0 198
Nereis	-0.09	0 363	-0 30	0 129
Echinocardium	-0 42	0.094	-0 33	0 171
Terebellides	-0 20	0.257	-0.33	0 112
Turritella	-0.53	**0.043**	-0 36	0 083
Magelona	-0.51	0 069	-0 40	0 114
Lucinoma	-0.26	0.23	-0.42	0.079
Cerianthus	-0.57	**0.021**	-0 45	0 108
Other spionids	-0.41	0.094	-0 52	**0.034**

In addition to a linear relationship between M1 March and phytoplankton index, there was a significant difference in genera composition between low and high phytoplankton years (Table

6.3), although mid and high phytoplankton years did not differ. However, given that there is both a significant trend in phytoplankton index (S=123, p=0.002), alongside a significant trend in the species composition away from the original community at M1, this result is unsurprising. As such, many of those taxa which were found to be correlated with phytoplankton index were also found to contribute most to dissimilarity between high and low phytoplankton years (Table 6.5).

Table 6.5 SIMPER analysis on benthic data from Station M1 March, showing percentage contributions of each taxa to Bray-Curtis dissimilarity between years of high and low phytoplankton index at 2 year lag. Analysis was done on double square root transformed abundances to minimise weighting of numerically dominant species. Average Bray-Curtis dissimilarity between high and low abundance years is 25.02%.

Taxa	Mean abundance during high phytoplankton years	Mean abundance during low phytoplankton years	Percentage dissimilarity	Cumulative dissimilarity %
Other spionid	6.67	71.67	3 13	3 13
Trichobranchus	21.56	1.11	2 41	5.54
Oligochaeta	50.22	44.11	2 3	7 84
Anobothrus	29.11	6	2.28	10.12
Tharyx	221	26.67	2 16	12 28
Exogone	40.67	2.33	2.07	14 35
Prionospio	972.33	385	2.04	16 4
Terebellidae	4	12.33	1 83	18 22
Heteromastus	125.33	86.89	1.82	20 04
Pseudopolydora	17.78	3	1.8	21 84
Lembos	5,44	10.22	1.71	23 54
Polydora	12.67	10.22	1.6	25 14
Mediomastus	48.89	0	1 58	26 72
Cerianthus	2.56	11.89	1.56	28 29
Kellia	10	20.56	1 54	29 83
Lumbrineris	125.44	29.89	1.52	31.35
Nemertea	119.33	77	1.51	32.85
Sthenelais	7.11	2.56	1.47	34 32
Protomedeia	5	8.22	1.47	35.79
Lanice	4.22	2.78	1.47	37.26
Leptognathia	8.67	7.67	1.46	38.72
Chaetozone	272.56	159.44	1.45	40.17
Paraonidae	18	10.11	1.44	41.61
Odostomia	0.89	7.22	1.44	43 05
Pholoe	169.11	66.67	1.43	44.48
Ampharete	43.67	39.67	1.41	45.88
Phoronis	51.67	72.44	1.4	47.28
Spisula	4.56	7.78	1.38	48 66
Levinsenia	372.78	192.44	1.33	49.99
Thyasira	303.11	103.22	1.33	51.32
Nuculoma	136.78	58.56	1.28	52.6
Mysella	101.44	101.89	1.27	53 87
Glycinde	11	16.22	1.23	55.1
Tellimya	15.56	29.56	1.22	56.33
Gari	2.33	3.22	1.22	57.55
Pionosyllis	2.44	2.89	1.22	58.76
Turritella	13	24.78	1.2	59.96
Lagis	4.44	5.89	1.17	61.13
Photis	19.78	8.22	1.16	62.3
Poecilochaetus	2.67	3.56	1.16	63.46
Thracia	3	2.33	1.16	64.62
Terebellides	41.22	107.89	1.16	65.78
Ampelisca	80.22	31.78	1.15	66.93
Halcampa	4.11	3.22	1.15	68.08
Paramphinome	5.78	0	1.14	69.22
Arctica	6	0.44	1.14	70.37
Scoloplos	17	16.56	1.12	71.48
Rhodine	60 33	20.78	1.11	72.6
Magelona	36.11	90.56	1.08	73.67
Echinocyamus	5.33	1	1 05	74.72
Ophiura	5.22	1.11	1.01	75.74
Diplocirrus	28.67	13.89	0.99	76 73
Polycladida	0.89	1.56	0.99	77.72
Ampharetidae	6.89	0.22	0.97	78 7
Capitella	12	0	0.94	79.63
Diastylis	19.67	15.33	0.93	80 56
Eteone	27.44	12.78	0.93	81.49
Spiophanes	65.67	28.11	0.92	82.41
Cirratulidae	3.33	0	0.92	83.33
Eumida	1.56	0.44	0.89	84 22
Chaetoderma	25	7.44	0 86	85.09
Tubulanus	6.67	0	0.84	85 93
Myriochele	111	92.78	0 84	86.76
Harpinia	89	69.67	0 84	87 6
Echinocardium	11.22	30	0.83	88 43
Abra	61.67	41 89	0 81	89.24
Nereis	4.89	6.56	0.79	90.03
Phaxas	8.56	10.89	0.74	90 76
Amphiura	159.56	140.44	0.72	91 49
Other bivalves	1.78	0.89	0.72	92.2
Cylichna	21.78	12.44	0.72	92 92
Eudorella	21.44	25	0 71	93 63
Lucinoma	33	59 56	0 7	94 33
Acanthocardia	0.67	0 11	0.65	94 98
Chamelea	14.44	20.44	0.63	95 61
Glycera	45.22	35 67	0 62	96 23
Ophelina	15.33	12.22	0.61	96 83
Scalibregma	0.44	0.56	0.57	97 4
Nephtys	108 89	119.67	0 53	97 93
Owenia	45.67	55 22	0 53	98 46
Pygospio	0	6 22	0 4	98 86
Spaerodorum	2.89	0	0 35	99 21
Goniada	34	28.56	0.33	99 54
Copepoda	0.67	0	0 25	99 79
Ericthonius	0.44	0	0 21	100

Density dependant mortality

Density dependant processes were found to operate each winter at M1, as the $\log_{10}$ transformed proportional overwintering mortality showed a significant relationship to the previous September abundance at Station M1 (r=-0.44, p=0.035). Thus, there is a statistically sound, independent relationship between September abundances and overwintering mortality. The relationship between September abundances and overwintering mortality is quadratic (Figure 6.9a). During some years, when September abundances are low, at most 5000 individuals.m^{-2}, abundances were able to slightly increase during the winter (e.g. 1972, 1988, 1990, 1994). Yet a September community with very high abundances (e.g. greater than 9000 individuals.m^{-2}) suffered high mortality during the winter (e.g. 5000 individuals.m^{-2}).

Although high September abundances were associated with greater mortality, this does not translate into lower abundances of individuals present the following March. There was, in fact, a positive relationship between September abundances and abundances the following March (r=0.42, p=0.032). Using actual abundances, this relationship is found to be a modified exponential (Figure 6.9b);

$$y = ae^{\frac{b}{x}}$$

Where a=6863.13, b=3090.82, x= September abundances, y= predicted overwintering mortality

Therefore, although higher September abundances were related to higher abundances the following March, it appears that March abundances are limited to approximately 5000 individuals.m^{-2} as September abundances greater than approximately 8000 individuals.m^{-2} did not consequently appear as higher March abundances (Figure 6.9b).

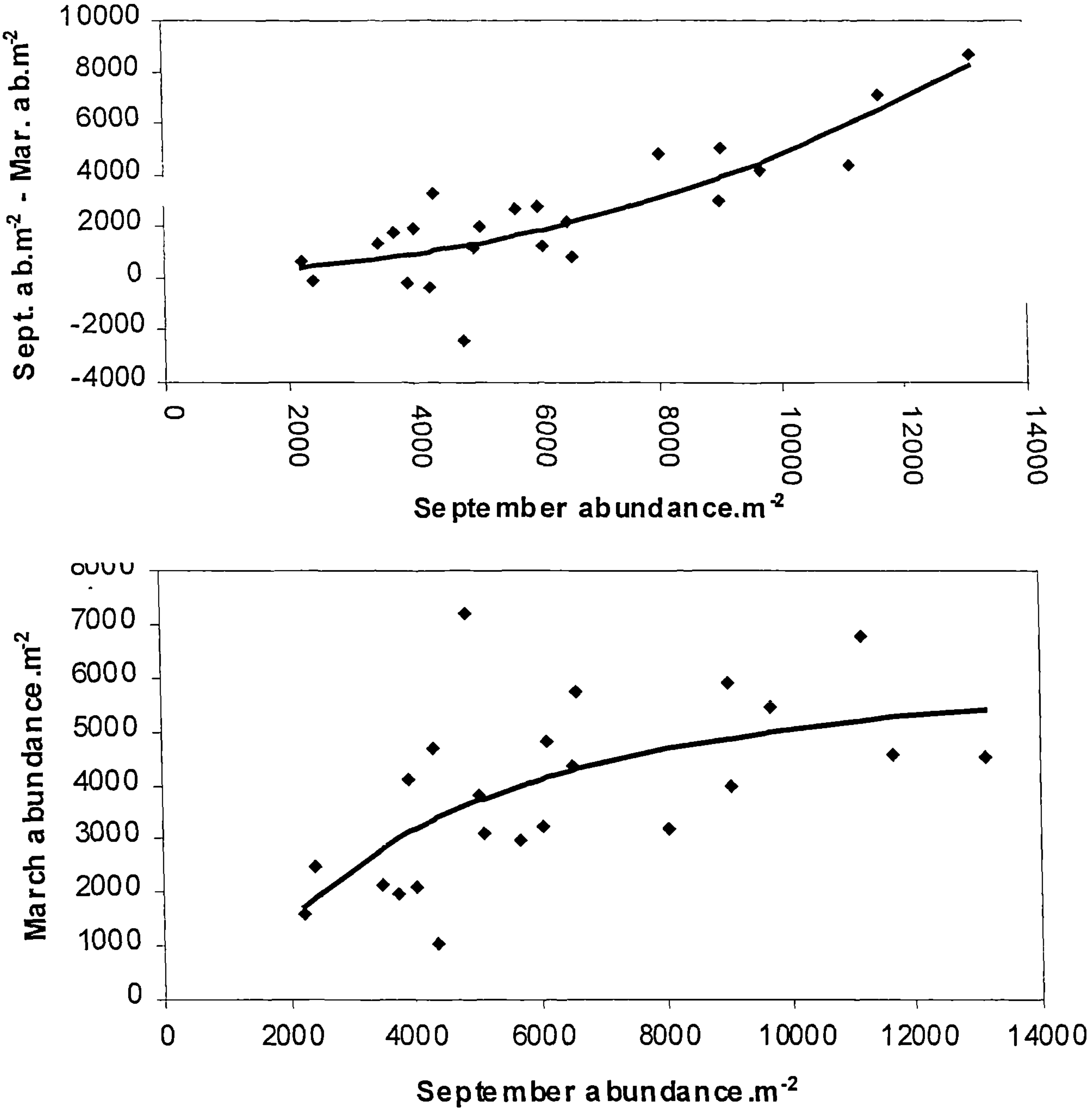


Figure 6.9 a) Scatter plot displaying quadratic relationship between differences in total benthic abundance from September to the following March at Station M1 (i.e. mortality), against September abundances. b) Scatter plot displaying modified exponential relationship between March total benthic abundace against previous September abundances.

Discussion

Buchanan's (1993) earlier analysis of the relationship between benthic abundance at station M1 and phytoplankton index over the 1981 to 1990 period suggested that changes in phytoplankton index accounted for up to 55% of the interannual variation in benthic abundance. In this study, over the whole time series, from 1973 to 1997, 33% of the variability in benthic abundance may be explained at M1 in March through fluctuations in phytoplankton index alone. Although benthic abundance at Station P did not show any significant relationship to phytoplankton index over the whole series, the coincident timing of the increase in benthic abundance at both Station P and M1 March in the early 1980s suggests that they were responding to the same factor (i.e. food). However, after 1986 there was no similarity in the interannual fluctuations of the two stations when benthic abundance at Station P was maintained at a relatively low level. Such marked differences between the two stations after this time suggests that other factors were influencing benthic productivity at Station P (Chapter 7, Appendix 4, Frid *et al.*, 1999a; Frid & Clark, 2000).

Given that food supply is one of the primary factors structuring benthic communities (Pearson & Rosenberg, 1986), a more constant relationship between benthic abundance at M1 and CPR phytoplankton index would be expected. For example, it is remarkable that during the first 2 years of the M1 series (1973 & 1974), benthic abundance was relatively low (Figure 6.4), yet phytoplankton index (at a 2 year lag) was higher than would be expected to account for this. The opposite situation occurred from 1981 to 1982, when benthic productivity at M1 March was observed to increase, yet annual phytoplankton productivity did not show a similar increase 2 years previously. Although there was no remarkable increase in the annual mean phytoplankton productivity at this time, the annual cycle of phytoplankton was observed to change from seasonal cycle with a single peak, to one in which there was a bi-modal pattern with higher, shorter lived phytoplankton peaks during the year (Evans & Edwards, 1993) (see Figures 2.4 & 6.7). It can be conjectured that these bursts of phytoplankton productivity might have meant that relatively more organic matter was able to reach the benthic system. This is because it is not the amount of primary production occurring which is important to the benthos, but rather the amount of this production which reaches the benthic system. Seasonal variations in light and temperature do change the amount of phytoplankton being consumed by grazing zooplankton, and this in turn results in considerable variation in the quality and quantity of sedimenting organic material (Christensen & Kanneworff, 1985). The populations of some of the more abundant zooplankton taxa are limited by temperature and not food (Chapter 4, Corkett & Zillioux, 1975). Therefore it is likely that they would not be able to fully exploit the shorter-lived peaks of phytoplankton observed from 1979 onwards. Any primary production which was not incorporated into the pelagic food chain would be expected to sediment to the benthos to be incorporated into the benthic system.

Davies & Payne (1984) suggest that the benthos of the North Sea is food limited, and therefore it is likely that even small variations in the amount of sedimenting organic matter are important. It could well be that during 1979 and 1980 although the mean phytoplankton production was low, a higher proportion of that productivity reached the benthic system, thus enabling an increase in benthic abundance in 1981. Conversely, although during 1971 and 1972 primary productivity was higher than would be expected given benthic productivity, the broad unimodal nature of the annual cycle might have enabled more primary production to be utilised in the pelagic food chain, and as such a relatively smaller proportion would reach the benthic system. It is tempting to say that those species which are correlated to phytoplankton index or contribute most to dissimilarity between high and low phytoplankton years are "enrichment opportunists" (sensu Pearson & Rosenberg, 1978), and some of them are (e.g. *Tharyx*, *Pholoe*, *Chaetozone*, *Heteromastus* and Oligochaeta (Pearson & Rosenberg, 1978)). However, this is not pervasive, as some taxa (e.g. *Capitella*) which have been previously classified as enrichment opportunists showed no such response to changes in organic matter input.

The ultimate cause of the changes in benthic productivity were not discussed by Buchanan (1993). However, changes in primary production in the central-west North Sea region are likely to be associated with changes in weather patterns influencing the timing of the spring bloom (Chapter 4). Path analysis does show that interannual fluctuations in climate are observable in the benthos. Such changes in the benthos are unlikely to be the result of a direct effect of changes in climate, but rather forced through the action of climate on phytoplankton production. In addition, there is a similarity in the long term trends of the benthos and phytoplankton index in the CPR area situated to the north (B2), yet no link between the M1 benthos and phytoplankton index situated to the south (D2). This could be due to either the advection of phytoplankton or climatically influenced water (e.g. stratified water which would allow phytoplankton growth) from north to south along the western coast of the North Sea.

Previous analysis of the Station P series by Austen *et al.* (1991) suggested that the increase in benthic abundance at this site between 1980 and 1981 coincided with marked changes in community structure. However, despite the relatively large increases in benthic abundance occurring at Stations P and M1 March between 1980 and 1981, no notable change in community structure was observed at this time. In Chapter 4, it was determined that there was a relationship between annual mean zooplankton abundance and benthic abundances, and an examination of the MDS plots suggests that this relationship may also be observed in these benthic series. However, although there was no significant change in zooplankton community structure (as determined by a Mann-Kendall trend test), all three benthic series do show a gradual shift away from the original community sampled. As there is a link between benthic abundance and community structure, this might be expected if the stations showed a significant trend in benthic abundance, yet only Station M1 shows such a trend (and community structure may be also be related to phytoplankton index). However, the shift in benthic abundance at Station P is likely to be due to the influence of other factors at this site (Chapter 7, Appendix 4, Frid *et al.*, 1999a; Frid & Clark, 2000).

Buchanan *et al.* (1986a) asserted that the increases in benthic abundance observed from March to September each year were not simply those which had recruited to the bottom in that spring and had grown over the summer. Rather, the increases over the summer period were due to rapid somatic growth of benthic organisms (due to higher temperatures and food supply) so that they may reach a size where they are sampled by a 0.5 mm sieve (so-called "sieve recruitment"). Although some individuals are able to grow fast enough so that they may be recruited to the sieve only 6 months after recruiting to the bottom, most taxa are likely to take over 12 months (Buchanan & Moore, 1986a). Therefore, except for fast growing species, most taxa lag behind phytoplankton productivity. The lack of a relationship between phytoplankton index and September abundances suggests that food is not limiting and therefore not a regulating factor for macrofauna during this period. During the summer period, it would be expected that the newly settled phytoplankton bloom would mean that the benthos would have a ready food supply, and therefore the amount of growth over the summer period would be influenced by factors other than food (e.g. space or water temperatures). However, as phytoplankton index is correlated with the March samples, this suggests that the period when the population is regulated is during the winter when the food supply is restricted. As such, although there will be little growth over the winter period (so the number of individuals recruiting to the sieve in March will not be higher than the previous September), the mortality over the winter will reduce the abundance of individuals according to the available energy in the benthos (Frid *et al.*, 1996). Buchanan & Moore (1986a) suggested that density dependant mortality only operated over the first stable decade, and that the increased food input during the early 1980s destabilised the system and allowed increases in abundance. This chapter presents results that suggest that density dependant mortality operates over the whole time series at M1 and the degree of mortality varies with the available food per individual, which is influenced by i) the number of individuals in the benthos in September and, ii) the amount of organic matter input into the system over the previous spring and summer period. Thus, the evidence suggests that the principal stabilising process is density dependant mortality mediated by food competition in a seasonally food limited environment (Buchanan & Moore, 1986a).

Therefore, at benthic Station M1, the benthos is “bottom up” controlled (sensu Hall & Raffaelli, 1993), with productivity determined by food availability (phytoplankton). This phytoplankton food source in turn is controlled by climatic influences and thus the benthos is ultimately, indirectly driven by climate. Other North Sea time series have also been observed to show the same pattern, with benthic abundances determined by organic matter input, although in the eutrophicated SE North Sea region, Beukema (1992c) observed that these changes were ultimately due to changes in nutrient concentrations. Given the close proximity of benthic Station P to Station M1, it might be expected that such bottom up control of the dynamics would also be observed at this site, but, as will be discussed in the following chapter, other factors influence the benthos at this site.

Chapter 7 Long term changes in the benthos on a heavily fished ground off the NE coast of England

Introduction

There is no doubt that, as a result of fishing activity, significant changes have taken place in the abundances and species composition of fish communities in the North Sea (e.g. Serchuk *et al.*, 1996). However, there is less evidence that the activities of commercial fishing fleets have caused changes in other marine communities (Gislason, 1994). Fishing using mobile gears results in direct and indirect impacts upon the benthos (Messieh, 1991; Dayton *et al.*, 1995). A decrease in benthic infaunal population densities occurs immediately after the passage of gears due to mortalities resulting from damage by the gear (Tuck *et al.*, 1998). Individuals disturbed, but not killed by the gears may be left at the surface and thus prone to predation. Shortly after the disturbance has taken place, scavengers may move onto the fished area (Kaiser & Spencer, 1994; Ramsay *et al.*, 1996). Fishing may also indirectly affect benthic communities by disturbance of the sediment, causing reduction in habitat complexity (Auster *et al.*, 1995), and by increasing suspended solids in the water column (Churchill, 1989). These changes in the physical environment have the potential to affect the recolonisation of trawled areas (Gislason, 1994).

Although the direct effects of fishing on the benthos are becoming known, the broader impacts of fishing activities which may cause profound changes, even to the level of the ecosystem, are less well understood. However, these more widespread, ecosystem level effects are difficult to study. Effects at this level may operate through the removal of the larger individuals present in both fish and benthic communities by the fishing nets. This has the effect of reducing the abundances of predatory fish species such as cod, haddock, plaice and sole in fish populations (Serchuk *et al.*, 1996), and large predatory crustacea, echinoderms and molluscs in benthic populations (Dayton *et al.*, 1995). Fishing disturbance may also destroy meta-populations that act as sources of larvae, and thus affect benthic communities that are reliant on a supply of propagules from fished areas, even if they are not fished directly (Thrush *et al.*, 1995). All of these changes in communities are expected to be reflected in knock on effects within trophic cascades (ICES, 1994).

Before-After Control-Impacted (BACI) type experimental programmes (Underwood, 1991) or short term manipulations of the benthos in experimental areas have been used to observe the direct impacts of fishing. Unfortunately, the results of such studies do not lend themselves to extrapolation to the much larger spatial and temporal scale of the fishing ground (Thrush *et al.*, 1995). Additionally, the type of experimental approaches applied do not fully address the less readily recognisable indirect impacts of fishing. As ecological changes due to fishing impacts occur over large areas and time scales, they may only be detected by comparing long time series that have been collected in fished areas and unfished areas. This is particularly important as other natural factors may be changing over the time period observed. These could include changes in density dependence, climate, hydrography and other biotic factors (Buchanan *et al.*, 1986; Buchanan & Moore, 1986a). The problem is that few areas of the North Sea are unfished and undamaged by trawling.

This study compares time series data from the two benthic stations M1 and P. Station P is located within a *Nephrops norvegicus* (Dublin Bay Prawn) fishing ground (Figure 6.1) whilst Station M1 is located outside of the main fished area. Although previous analysis of the M1 series has related abundances of benthic individuals to changes in phytoplankton abundance (Buchanan, 1993), no such relationship has been detected at Station P.

The intensity of trawling on the area considered in this study (ICES statistical rectangle 39E8) varied considerably from the early 1970s to the early 1990s (Figure 7.1a). From 1972 until 1981 the area of 39E8 swept by fishing gear was approximately 10 000 km^2 per annum, while in the period 1982-1986 it was around 15 000 km^2 per annum. After this, there was a period when the area swept exceeded 20 000 km^2 per year until 1989, since when it has dropped to around 15 000 km^2 per annum. Since ICES statistical rectangles at this latitude cover 3091 km^2, but only 51% of the area of ICES statistical square 39E8 is water, this is equivalent to trawlers sweeping the seabed approximately 12.9 times per year in the most heavily impacted period. Rijnsdorp (1998) described the distribution of fishing activity at a resolution of 1x1 nautical mile. The fishers were found to behave in a non-random fashion and trawl only 60% of the available area.

Therefore, on the fishing grounds the benthos may have been impacted as often as 20 times per year!

Over time, the communities at Stations M1 and P would be expected to change in response to differing environmental conditions. For example, steadily increasing productivity over time would result in trends in the benthos across the whole of the observation period. These may include for example increased numbers of opportunists (Pearson & Rosenberg, 1978) and increased abundances of deposit feeding species (Beukema, 1992a). In contrast, on the fishing grounds, the increasing, then declining level of fishing intensity may cause changes during the period of greatest fishing activity, which mask the changes taking place due to fluctuations in organic input. This study examines temporal changes in the macrobenthic community at the two stations over the last 27 years. It is suggested that the fauna at Station M1 (outside the main fishing ground) would be controlled by the organic flux over the whole of the time period, while at Station P (within the fishing ground) the dynamics would be altered during the period of high fishing effort (1981-1990). Based upon literature accounts of the direct impacts of fishing (e.g. Pope & Macer, 1996; Rijnsdorp *et al.*, 1996) (see methods, below) it is hypothesised *a priori* that the errant polychaete and ophioroid & asteroid echinoderms will respond positively to fishing (Lindley *et al.*, 1995; Frid *et al.*, 1999b) while sedentary polychaetes, echinoid echinoderms and large (>50mm) bivalves would be negatively impacted (see Table 7.1). Changes in the proportion of the fauna in these groups and changes in their abundance over the three periods of differing fishing intensity will be examined.

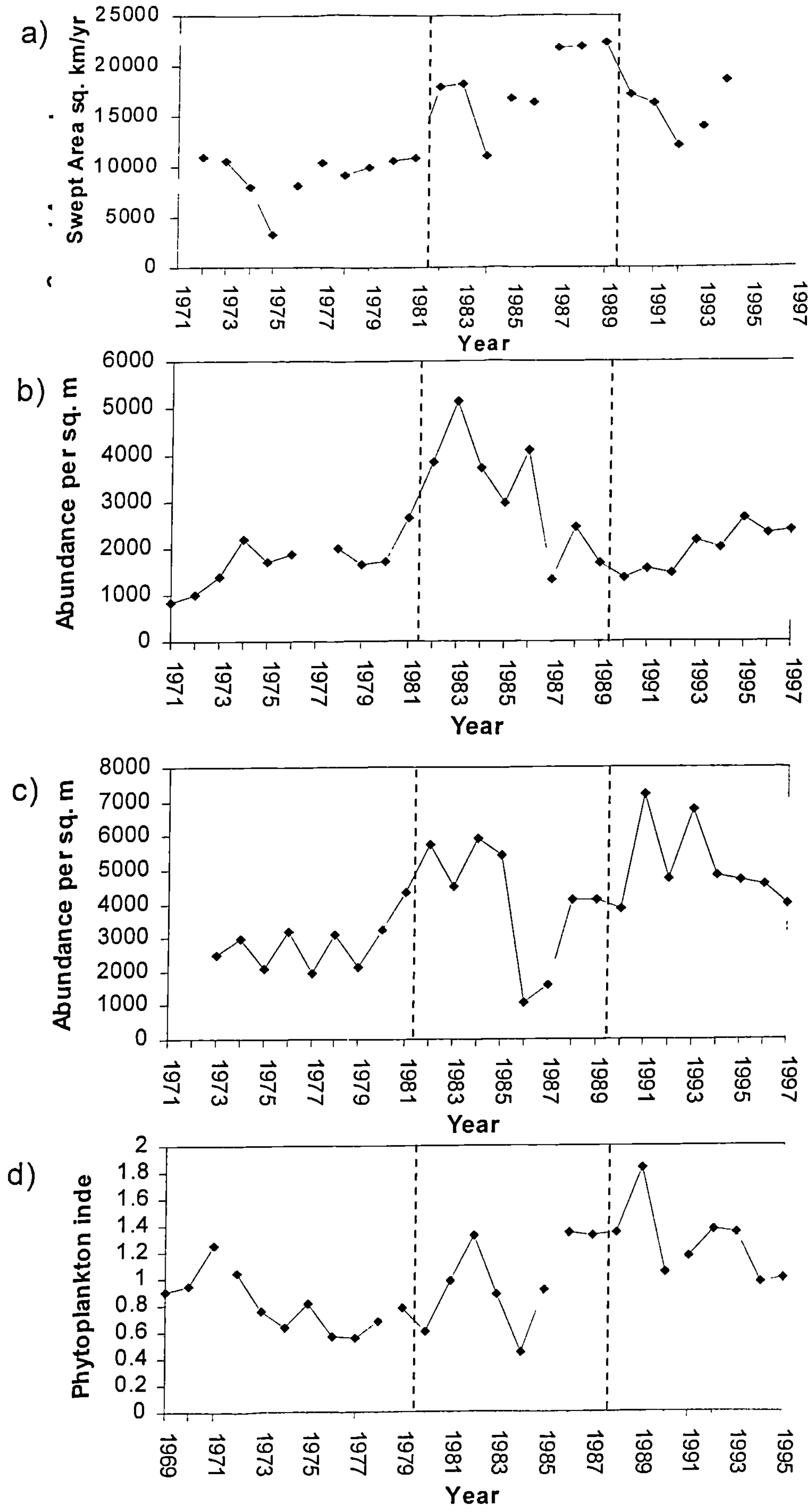


Figure 7.1 Time series plots of; a) Fishing impact measured as swept area per year over the period 1972-1994. b) Abundance of individuals at Station P. c) Abundance of individuals at Station M1. d) CPR phytoplankton index for the years 1971-1995. In all cases vertical lines separate the three defined phases corresponding to low, high and mid periods of fishing. N.B. For phytoplankton index, these phases are lagged by two years.

Methods

Site and sampling methodologies

The two benthic stations operated by the Dove Marine Laboratory, Station P and Station M1 are both located in ICES statistical rectangle 39E8 and close to, or within a *Nephrops norvegicus* (Dublin Bay Prawn) fishing ground (BODC, 1992) where otter trawling is the predominant technique. Station P lies 11.5 miles offshore, within the *Nephrops norvegicus* ground (Figure 6.1), and is in 80m of water. Station M1 lies 6.5 miles offshore, situated outside of the *Nephrops norvegicus* ground (Figure 6.1), and is in 55m of water. For further details on both of these stations please refer to Chapter 6 and references cited therein. The accumulated data have been analysed at intervals during collection (Chapter 6, Buchanan *et al.*, 1974; Buchanan *et al.*, 1986; Buchanan & Moore, 1986a; Buchanan & Moore, 1986b; Buchanan, 1993; Frid & Huliselan, 1996). However, the data have not until now been examined with regard to the possible effects of fishing. Although in Chapter 6, only those taxa contributing at least 2% *in any one sample* were used, here, all 230 genera from Station M1, and all 166 genera from Station P were used for the following analyses.

Time series analysis

Data on level of fishing effort of ICES statistical rectangle 39E8 were obtained from MAFF, North Shields. The time series was divided into three phases corresponding to the level of fishing effort. These phases were; low fishing effort 1972-1981, high fishing effort 1982-1989 and moderate fishing effort 1990-1994 (Figure 7.1a). The benthic time series were also divided into the three periods corresponding to the level of fishing effort operating at any one time.

Each genus in the data set was defined from the literature (de Groot & Lindeboom, 1994; Lindeboom & de Groot, 1997) as being likely to (i) increase, (ii) decrease, or (iii) being one for which no *a priori* prediction could be made (see Table 7.1). Category (iii) include taxa containing a diversity of life histories and ones for which no experimental data were available to form a prediction. Those taxa in category (i) were essentially errant or mobile polychaetes and asteroid echinoderms. Category (ii) was characterised by sedentary or fragile taxa such as echinoid echinoderma, large bivalves (defined as max size >=50mm), and sedentary polychaeta. Due to the lack of information on specific taxa, it is assumed that all species in a genus respond in a similar fashion, and where data were lacking for a genus it is believed that it would behave in a similar manner to taxa with comparable life histories.

PRIMER was used to calculate Bray-Curtis similarity indices between annual means (of the 5 grabs), and for MDS analyses of data (Clarke & Warwick, 1994). Analyses of long term changes in community structure were carried out at the genus level and using a 4th root transformation (see Chapter 6 for further details). MDS ordination was used to show changes in species composition of the community.

Analysis of bootstrapped means

The total number of individuals and proportion of individuals in the predicted increasing and predicted decreasing categories was examined over the three periods. In addition, abundances were examined separately for each taxonomic group within each category (see Figure 7.4). For each category, and the taxonomic group within each category, bias-corrected, bootstrapped estimates of the mean abundance and 95% confidence intervals in each of the three periods were obtained. Bootstrapping was carried out with 10 000 samples of the original data. For each of the 10 000 samples, the mean was calculated and from the resulting distributions, bias-corrected 95% confidence intervals were obtained. The calculations were carried out using the Simstat for Windows package.

Table 7.1 Categorisation of recorded prey classes into groups for which *a priori* hypotheses could be formulated for their responses to fishing effects.

Predicted decrease		No prediction		Predicted increase	
Phylum	Genus	Phylum	Genus	Phylum	Genus
Annelida	Ampharete	Cnidaria	*Virgularia*	Annelida	*Capitella*
	Anobothrus	Crustacea	*Ampelisca*		*Chaetozone*
	Levinsenia		*Diastylis*		*Commensodorum*
	Minuspio		*Ericthonius*		*Diplocirrus*
	Myriochele		*Eudorella*		*Exogone*
	Owenia		*Harpinia*		*Glycera*
	Prionospio		*Leucon*		*Glycinde*
	Rhodine		*Photis*		*Goniada*
	Spionid	Mollusca	*Abra*		*Heteromastus*
	Spiophanes		*Chamelea*		*Lumbrineris*
	Synelmis		*Lucinoma*		*Magelona*
	Terebellidae		*Mysella*		*Magelona*
	Terebellides		*Nuculoma*		*Mediomastus*
	Thelepus		*Tellimya*		*Nephtys*
Echinodermata	*Echinocardium*		*Thyasira*		*Ophelina*
Mollusca	*Acanthocardia*	Nemertea	*Nemertea*		*Paramphinome*
Phoronida	*Phoronis*	Platyhelminthes	*Polycladida*		*Pholoe*
					Praxilella
					Praxillella
					Pseudeurythoe
					Scalibregma
					Tharyx
				Echinodermata	*Amphiura*
					Ophiuroidea
				Oligocheata	Oligochaeta

Results

Changes in infaunal abundance and genera composition

At Station P, within the fishing ground, benthic abundances in the decade 1971 – 1980 varied between 825 individuals.m^{-2} and 2195 individuals.m^{-2} (Figure 7.1b), while at Station M1 abundances fluctuated between 2000 individuals.m^{-2} and 3000 individuals.m^{-2} in a biennial cycle (Figure 7.1c). From 1981 abundances at both stations increased.

From 1983 to the end of the series, fluctuations in macrofaunal abundance at M1 are correlated with the abundance of phytoplankton two years previous (r^2=0.46) (Figure 7.1c & d). During the decade 1981-1991, genera composition varied considerably, but from 1992 to the end of the time series (1997), interannual variation in genera composition was small (Figure 7.2b). The latter period coincides with a period of relative stability in macrobenthic abundance (Figure 7.1c).

At Station P from 1982 until 1986 when fishing intensity increased, macrobenthic abundances did not track phytoplankton abundance, remaining over 0.73 standard deviations above the mean of the entire time series. Genera composition (Figure 7.2a) during this period showed no obvious trend. With the decline in fishing in this area from 1989, interannual variation in macrofaunal abundance decreased while genera composition remained variable.

Changes in sensitive groups

The total abundance of individuals in the taxonomic groups identified *a priori* as likely to respond positively to fishing increased significantly at Station P (within the fishing ground) between the period of low fishing activity and the period of high activity (Figure 7.3a). They subsequently declined when fishing decreased. The total number of individuals in taxa identified *a priori* as likely to decline in response to fishing impacts did not vary significantly between time periods (Figure 7.3a). At M1, outside the fishing ground, all the groups showed considerable increases through time (Figure 7.3c) in response to the increasing inputs of organic material from the phytoplankton (Figure 7.1d).

At Station P, the proportion of the individuals in the community belonging to taxa predicted to increase as a result of fishing, increased during the period of high fishing effort and declined when fishing declined (Figure 7.3b). Those taxa predicted to decline did show a reduction in their proportion followed by an increase when fishing decreased. In contrast at Station M1 there were no notable changes in the proportions of each group in the macrobenthic community over time, even though total abundance had increased (Figure 7.3d).

Considering the changes in individual taxonomic groups, it was observed at Station P (Figure 7.4a & b), that changes in the predicted direction occurred in 3 of the groups (errant polychaetes, asteroids & ophioroids and echinoids) of which 2 (errant polychaetes and echinoids) were significant changes. The two categories which did not vary in the predicted direction were both predicted to decline and showed no significant change in abundance between the three periods. At Station M1, outside the fishing ground, none of the groups changed significantly between periods (Figure 7.4c & d).

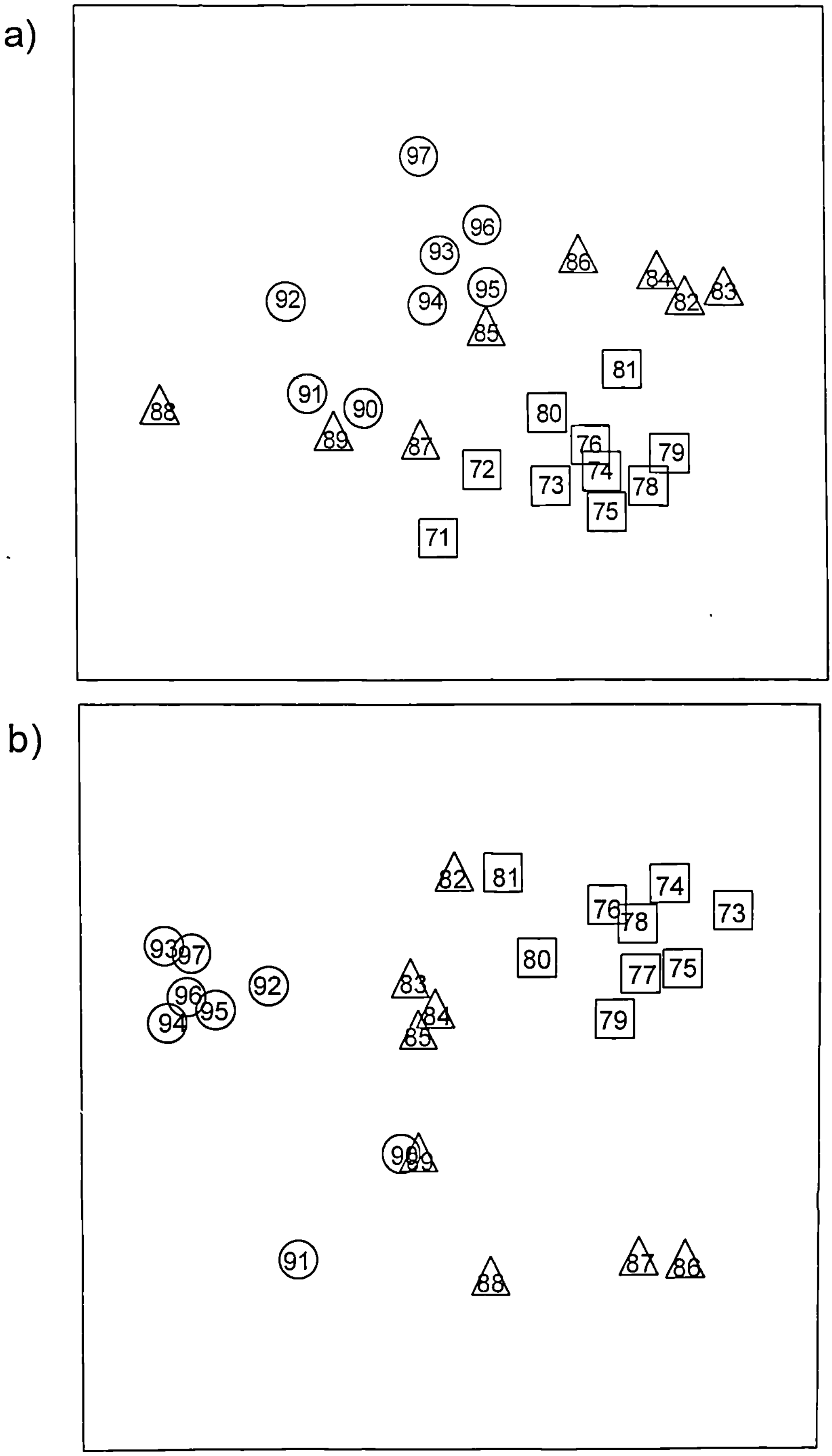


Figure 7.2 a) MDS plot produced after calculation of Bray-Curtis similarity index on double root transformed benthic faunal data from Station P (MDS Stress value=0.16). b) MDS plot produced after calculation of Bray-Curtis similarity index on double root transformed benthic faunal data from Station M1 (MDS Stress value=0.12). Key as follows: □ Low fishing phase, △ High fishing phase, ○ Mid fishing phase

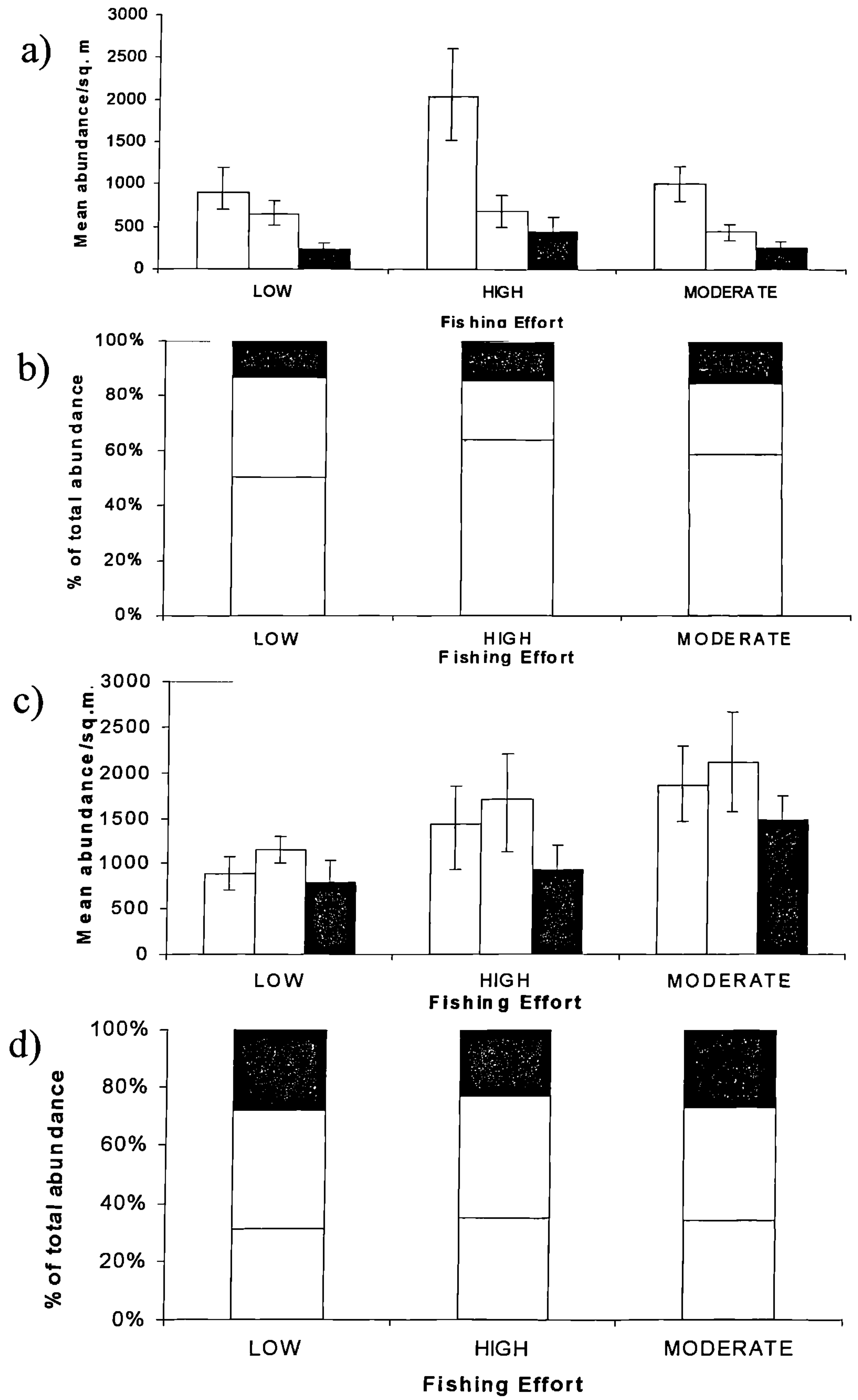


Figure 7.3 a) Bootstrapped means and 95% confidence intervals for total abundance of predicted increase, decrease and no prediction groups in low, high and mid fishing effort phases at Station P. b) proportions of predicted increase, decrease and no prediction groups in low, high and mid fishing effort phases at Station P. c) Bootstrapped means and 95% confidence intervals for total abundance of predicted increase, decrease and no prediction groups in low, high and mid fishing effort phases at Station M1. d) proportions of predicted increase, decrease and no prediction groups in low, high and mid fishing effort phases at Station M1. Key as follows: ☐ Predicted increasers, ☐Predicted decreasers, ■ No Prediction

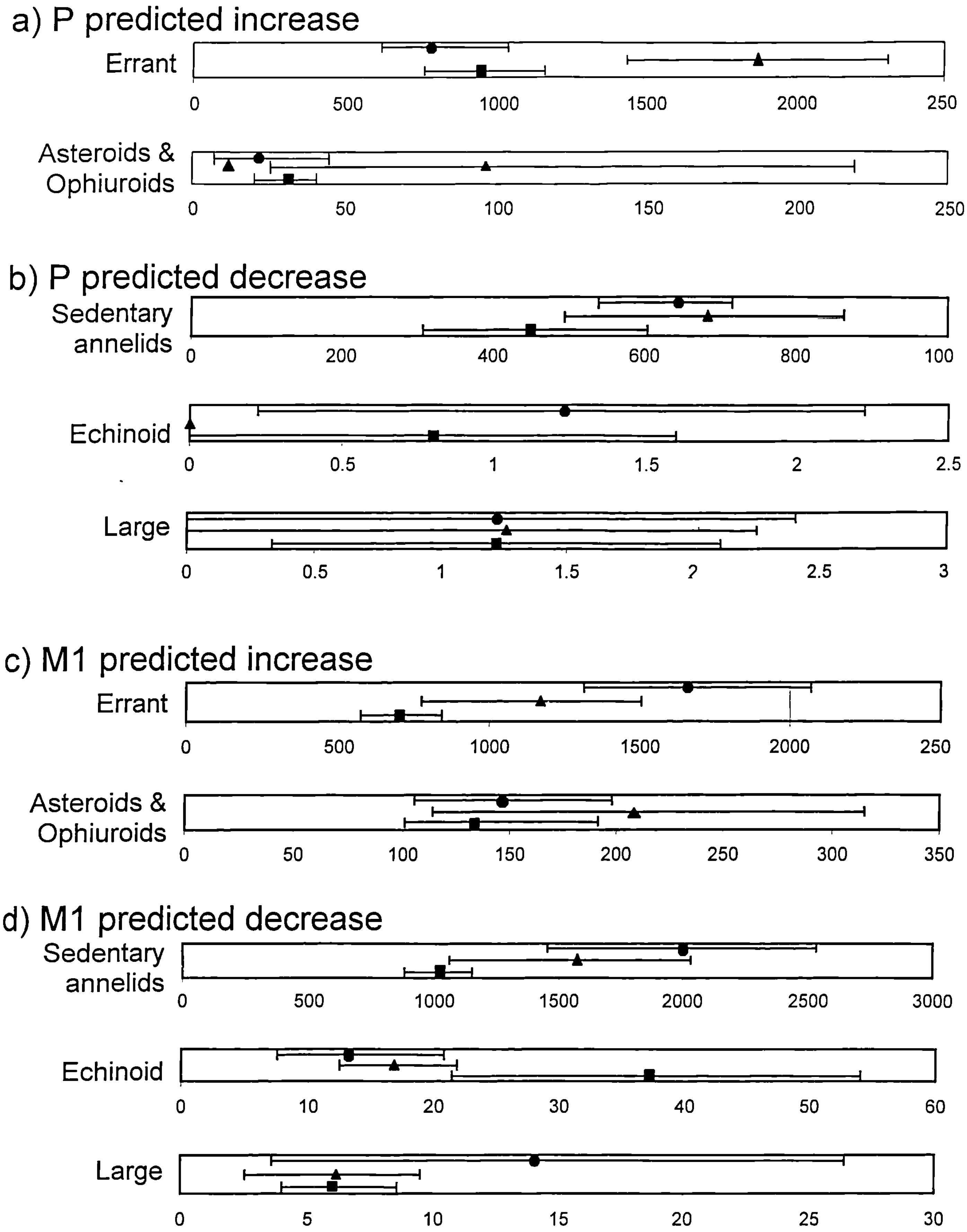


Figure 7.4 Bootstrapped means and 95% confidence limits for phyla from a) Station P predicted increase group, b) Station P predicted decrease group, c) Station M1 predicted increase group, d) Station M1 predicted decrease group. Means identified as follows: ■ Low fishing effort phase (1972-1980), ▲ High fishing effort phase (1981-1989), ● Mid fishing effort phase (1990-1994).

Discussion

It would be expected, that despite differences in depth and slight differences in community structure, Stations M1 and P would follow similar trends in the timing of large changes in community structure and productivity, and these would be largely determined through changes in organic input (Pearson & Rosenberg, 1986). Sedimentation of phytoplankton from the pelagos to the benthos is the major source of organic matter at these sites. Phytoplankton productivity is in turn controlled by climatic factors (e.g. Gieskes & Kraay, 1975; Reid, 1978; Reid *et al.*, 1998), and thus long term trends in climatic variables do affect the macrobenthos. Parallel trends in macrofaunal abundance between the two sites were observed up until 1982. Yet after this time, abundance at M1 continued to reflect the trends in phytoplankton input while the dynamics at P were influenced by an increase in fishing activity. Other observations of faunal changes in the North Sea have shown that macrobenthic abundances increased in the early 1980s in the Wadden Sea, eastern North Sea (Beukema, 1992c), and in the Skaggerak (Austen *et al.*, 1991) and Kattegat (Josefson *et al.*, 1993), which have also been linked to climate change or eutrophication of the pelagos (Hickel *et al.*, 1993).

It is unlikely that, at least in the North Sea, unfished benthic communities have ever been observed (Appendix 4, Frid & Clark, 2000). In this study I have compared the fauna of a lightly fished area with a more heavily fished area over a period in which fishing effort changed. At the lightly fished site (Station M1) the proportion of individuals predicted *a priori* to either increase or decrease in response to the direct effects of fishing did not vary, even though productivity increased in response to increasing inputs of phytoplankton. At the heavily fished station the increase in fishing effort in the early 1980s did not alter the abundance of the small number of taxa predicted to decline. This could be due to the previous long history of fishing at this site already having caused declines in sensitive taxa (Frid & Hall, 1998). In contrast the abundance of individuals in taxonomic groups predicted to increase did increase and thus caused a consequent shift the in the proportion of those taxa predicted to decline.

During the last 27 years phytoplankton levels off the Northumberland coast have been increasing (Figure 7.1d). The importance of organic flux in determining benthic community dynamics is well established (see Pearson & Rosenberg, 1986), and it is expected that this trend will be observed in the benthic time series. While genera composition at both sites does trend across the time period (Figure 7.2a & b). At Station M1, community changes generally occur with changes in total abundance at the site. Abundance at the site over much of the time series is generally controlled by changes in organic input (Buchanan, 1993). The changing levels of phytoplankton input to the benthos would also be expected to affect the community at the fished site, Station P. The similarity in year to year changes at the fished site to those of Station M1 in the periods 1972-1980 and 1990-1997 provides evidence of the role of organic inputs to the dynamics at Station P (Figures 7.2a & b). The decoupling of the dynamics of the two stations at the time when fishing intensity increased provides circumstantial evidence of a role for fishing disturbance in influencing the dynamics of this system. At the fished Station, P, the interannual variability in genera composition was greatest in the period 1982 to 1984 when fishing was at its most intense. Increased variability in composition is considered to be indicative of a stressed community (Warwick & Clarke, 1993).

Differences in the dynamics of the predicted *a priori* groups also suggest that different mechanisms were at work in the two sites. At Station M1 there was an increase in errant polychaetes which occurs through the three phases, yet at Station P their abundances are increased during the high fishing period and subsequently decrease when fishing activity decreases. Kröncke (1990) and Reise (1982) both attributed the long term (greater than 10 years) increased abundance of polychaetes in some areas of the North Sea to fishing activity and human disturbances of the sediment respectively.

The use of time series to establish causality is fraught with difficulty (Underwood, 1997). In this case many of the predicted changes in individual taxa due to fishing (Tuck *et al.*, 1998) would also be predicted from increased organic inputs (Pearson & Rosenberg, 1986). The differences in the dynamics of these two stations, which differ in their fishing intensity, during the period of increased fishing, provides some evidence for a role of direct effects of fishing in determining the abundance and composition of coastal macrofauna. Re-analysis of other benthic time series are now required to determine the generality of these findings.

Chapter 8 A synthesis of long term changes in the central-west North Sea ecosystem

Introduction

A previous analysis of long term ecological time series across the North Sea by Aebischer *et al.* (1990) demonstrated long term parallel trends in phytoplankton, zooplankton, herring and kittiwake populations and weather. However, it was uncertain if such parallel trends were due to each trophic level separately being forced by the weather, or due to straight causal relationships up the food chain, with the base of the chain being forced by weather. There were also similarities in long term zooplankton trends across the NE Atlantic with the position of the Gulf Stream North Wall (GSNW) (Taylor *et al.*, 1992). Such parallel trends, especially those on a large spatial scale, are often cited as evidence that the long term dynamics of ecosystems and communities are forced by climate (Colebrook, 1978; Taylor *et al.*, 1998).

Ultimately, long term trends and changes in biotic variables may be altered by either direct or indirect mechanisms. Indirect effects have been defined as "how one species <or group of species> alters the effect that another species <or abiotic factor> has on a third" (Strauss, 1991). Such indirect effects are mostly considered to be mediated through biotic factors via competition, predation or changes in a biotic food resource, yet indirect effects are often difficult to identify and characterise (Colebrook, 1986), and studying precise trophic interactions is complicated as the growth rate of a particular population may be limited by temperature and food, but its maximum abundance may be limited by predators (Roff *et al.*, 1988) or competition.

The presence of indirect effects may mean that straightforward parallel trends between forcing and response variables may not exist. For example, Reid *et al.* (1998) observed that phytoplankton trends in different regions of the NE Atlantic and North Sea were dissimilar, with the NNE Atlantic region showing negative trends in productivity, in contrast to the central North Sea and central NE Atlantic, which showed a positive trend over the 1950 to 1995 period. However, despite these dissimilar trends, coincident "stepwise" increases (central NE Atlantic & central North Sea) and decreases (NNE Atlantic) were observed to occur during the mid to late 1980s. The negative trend in the NNE Atlantic was thought to be a response to inputs of cold water from the Arctic caused by melting of ice and permafrost in response to positive temperature anomalies across Eurasia. This demonstrates how indirect effects (e.g. cold water input) can modify external influences (e.g. positive temperature anomalies) as they are mediated through to a biotic variable (e.g. phytoplankton).

Therefore, evidence of climatic forcing of ecosystems and communities may be observed as straightforward parallel trends, and/or as coincident stepwise changes in forcing and response variables. However, what constitutes a consistent shift in an ecosystem may also be open to discussion, as extreme events may occur in a system, due either to a natural or anthropogenic influences from time to time, yet may not constitute a permanent change (e.g. Chapter 1, Ziljlstra & de Wolf, 1988; Allen *et al.*, 1997).

This thesis has focussed on the long term trends present in the central west North Sea ecosystem over the latter half of the 20th century alongside long term trends in large scale climatic and regional meteorological variables. In this final study, I present and discuss these long term trends together. I also discuss further the importance of considering the influence of both direct and indirect influences on long term changes in the central-west North Sea ecosystem.

Methods

Sources of data

Abiotic and biotic time series data were obtained from a number of sources (Table 8.1). Two climatic series were used (GSNW and NAOI) which were used as proxies of weather patterns over a large spatial area (NW Europe). Mean air temperature over the central England area (intermediate scale) was represented by Central England Temperatures (CET). Meteorological series from Tynemouth (55°01'N 1°26'W) and Durham (54°47'N 1°34'W) (NE England) were used to supply series of air temperature, sunshine duration and wind speed, which were considered to be representative of the central-west North Sea area. Two weather stations were used to obtain a wider picture of weather coverage, as the coastal Tynemouth station is subject to weather phenomena which occur at the land-sea interface (e.g. sea mists, on/offshore breezes) which do not affect the inland Durham station. The only available regional Sea Surface Temperature (SST) series were from the Farne Islands (55°39N 1°37'W) for the period 1974 to 1990. As one of the benthic stations (P) is sited in an area subject to otter trawling (Frid *et al.*, 1999a), data on the level of fishing effort (km^2 trawled.yr^{-1}) for ICES statistical rectangle 39E8 were also used as an indicator of benthic disturbance at this site.

The available biotic series covering a number of different marine communities from the central-west North Sea (Table 1) were Continuous Plankton Recorder (CPR) phytoplankton index data for North Sea box C2 (Colebrook *et al.*, 1984) and CPR zooplankton data for the central-west North Sea (between the Firth of Forth SE Scotland (56°05'N 2°40'W), Flamborough Head NE England (54°07'N 0°04'W) and approx. 120 km offshore (56°05'N 0°04'W)) (Figure 3.2). The Dove zooplankton time series (situated at 55°07'N 01°20'W) and two benthic time series Station M1 (situated at 55° 04' N 01° 20'W) and Station P (situated at 55° 07' N 01° 15' W) were also used in the analyses.

Analysis of long term time series

Long term year to year fluctuations in each variable were examined with the aid of a 5 year moving average, and the significance of their long term trends assessed using the Mann-Kendall test for trend (see Chapter 4). To aid the identification of small, but persistent changes ("step changes") in the mean of each series, Cumulative Sums (CUSUMs, see chapter 4) were calculated using monthly data, where these were available, otherwise annual data were used. The trend analysis will identify the trend of the series, whilst the CUSUM helps to identify where these change may have occurred. CUSUM plots are only guides to identifying the approximate time of the change, not necessarily its exact timing. Thus, in order to identify the periods which showed a number of coincident changes, for each year, the total number of changes between its preceding and succeeding year were calculated.

Table 8.1 List of data used in analyses.

Dataset	Period	Source	www / email address
Central England Temperature	1966-1996	BADC	www.badc.rl.ac.uk
Gulf Stream North Wall	1966-1996	PML	www.nerc-pml.ac.uk
Winter NAO	1950-1995	PML	www.nerc-pml.ac.uk
SST	1974-1990	MAFF, Lowestoft	www.cefas.co.uk
Fishing effort for ICES box 39E8	1972-1994	MAFF, North Shields	www.cefas.co.uk
Tynemouth air temperature	1960-1996	BADC	www.badc.rl.ac.uk
Tynemouth sunshine	1960-1996	BADC	www.badc.rl.ac.uk
Tynemouth wind	1960-1995	BADC	www.badc.rl.ac.uk
Durham air temperature	1960-1971, 1982-1996	BADC	www.badc.rl.ac.uk
Durham sunshine	1960-1996	BADC	www.badc.rl.ac.uk
Durham wind	1973-1979, 1982-1996	BADC	www.badc.rl.ac.uk
CPR phytoplankton (box C2)	1950-1995	SAHFOS	www.npm.ac.uk/sahfos/sahfos.html
Dove zooplankton	1969-1988, 1990-1996	University of Newcastle	c.l.j.frid@ncl.ac.uk
CPR zooplankton (CW North Sea)	1960-1996	SAHFOS	www.npm.ac.uk/sahfos/sahfos.html
Benthic station M1	1972-1998	University of Newcastle	c.l.j.frid@ncl.ac.uk
Benthic station P	1971-1976, 1978-1997	University of Newcastle	c.l.j.frid@ncl.ac.uk

Central-west North Sea pelagic and benthic model

The pelagic and benthic models were constructed using the relationships already established between variables (Chapters 4-6, Figure 8.6). The zooplankton system was represented by the dominant *Pseudo-/Para-/Microcalanus* juvenile taxa, which made up over 20% of the individuals (Table 4.1). Long term changes in the summer (June-July) abundance of this group have been found to be influenced by spring (March-April) *Sagitta* abundances, which, in turn were indirectly related to spring phytoplankton production (Chapter 5). Long term changes in the benthos at Station M1 March were mainly influenced by organic matter supply (Chapter 6), and were also related to the previous year's September abundance via a density-dependent mechanism. The primary variable used to force the system was annual mean Durham sunshine data, as this had the best relationship to C2 phytoplankton index (Chapter 4). However, for the pelagic system, the model was also run using phytoplankton index data from box C2. The accuracy of each model was assessed by comparing the long term year to year fluctuations in each model output against the relevant time series observations.

Results

Long term trends and changes

Over the latter half of the 20th century, significant trends were present in the large scale climatic variables, the GSNW and the NAOI (Table 8.2). Similar trends were also observed in most of the local meteorological time series (air temperature & sunshine at Durham and Tynemouth, wind at Tynemouth) and in fishing effort. However, despite such increases in most of the climatic and meteorological series, the benthic community at Station M1 was the only biotic series to show a significant long term trend (Table 8.3).

Table 8.2 Results of Mann-Kendall trend tests on environmental time series.

Variable	S (Mann-Kendall)	Significance of S
Central England Temperature	75	0.18
Gulf Stream North Wall	203	**0.001**
Winter NAO	265	**0.021**
SST	12	0.35
Fishing effort	137	**<0.001**
Tynemouth air temperature	160	**0.046**
Tynemouth sunshine	294	**<0.001**
Tynemouth wind	174	**0.025**
Durham air temperature	163	**0.001**
Durham sunshine	208	**0.01**
Durham wind	-55	0.125

A number of patterns emerged from the examination of the CUSUM output. A total of 8 series underwent a change in their mean over the period 1980-1982 (Table 8.4). Over this period, the GSNW index moved northwards (Figure 8.1b), a position that was maintained until the mid 1980s. The NAOI index also increased during the early 1980s (Figure 8.1c), and although not shown by the CUSUM results, so did sunshine at Durham (Figure 8.3b). Four out of five of the biotic series also underwent a stepwise change around this time, the exception being the Dove zooplankton series. The central-west North Sea CPR phytoplankton (Figure 8.4a) and zooplankton (Figure 8.4c) series both reached a nadir in the late 1970s and early 1980s followed by a notable increase (similar to those trends recorded by Aebischer *et al.*, 1990). These increases were also exhibited in both benthic series, Stations M1 and P, which showed parallel increases in abundance beginning around 1980-1981 (Figures 5a &5b).

However, a consideration of both the time series and CUSUM plots suggests that the most profound change occurred during the late 1980s (Table 8.4). At this time, the majority of environmental variables exhibited a sudden, stepwise increase to reach their most extreme values, which persisted into the 1990s. This is most obvious in the three air temperature series, which show a sudden increase between 1987 and 1988 (Figures 8.1a, 8.2a & 8.3a) to peak in 1988 or 1989. The GSNW and NAO indices also show similar increases (Figures 8.1b & 8.1c). In contrast, both zooplankton series showed a decline in abundance between 1987 and 1988, with the Dove zooplankton series reaching its lowest overall abundance during the 1990s, and the CPR zooplankton series returning to a level comparable to that of the 1970s. Although both the CUSUM analysis of the CPR phytoplankton and M1 March series do not suggest the presence of a change in the late 1980s, these series do show a similar trend to the climatic and meteorological series, as they present their highest levels during the 1990s (Figure 8.4a & 8.5b).

Table 8.3 Results of Mann-Kendall trend tests on biotic time series.

Variable	S (Mann-Kendall)	Significance of S
CPR phytoplankton C2	148	0.0537
Dove zooplankton	-51	0.231
CPR zooplankton	-87	0.189
Benthic station M1	323	**0.011**
Benthic station P	67	0.138

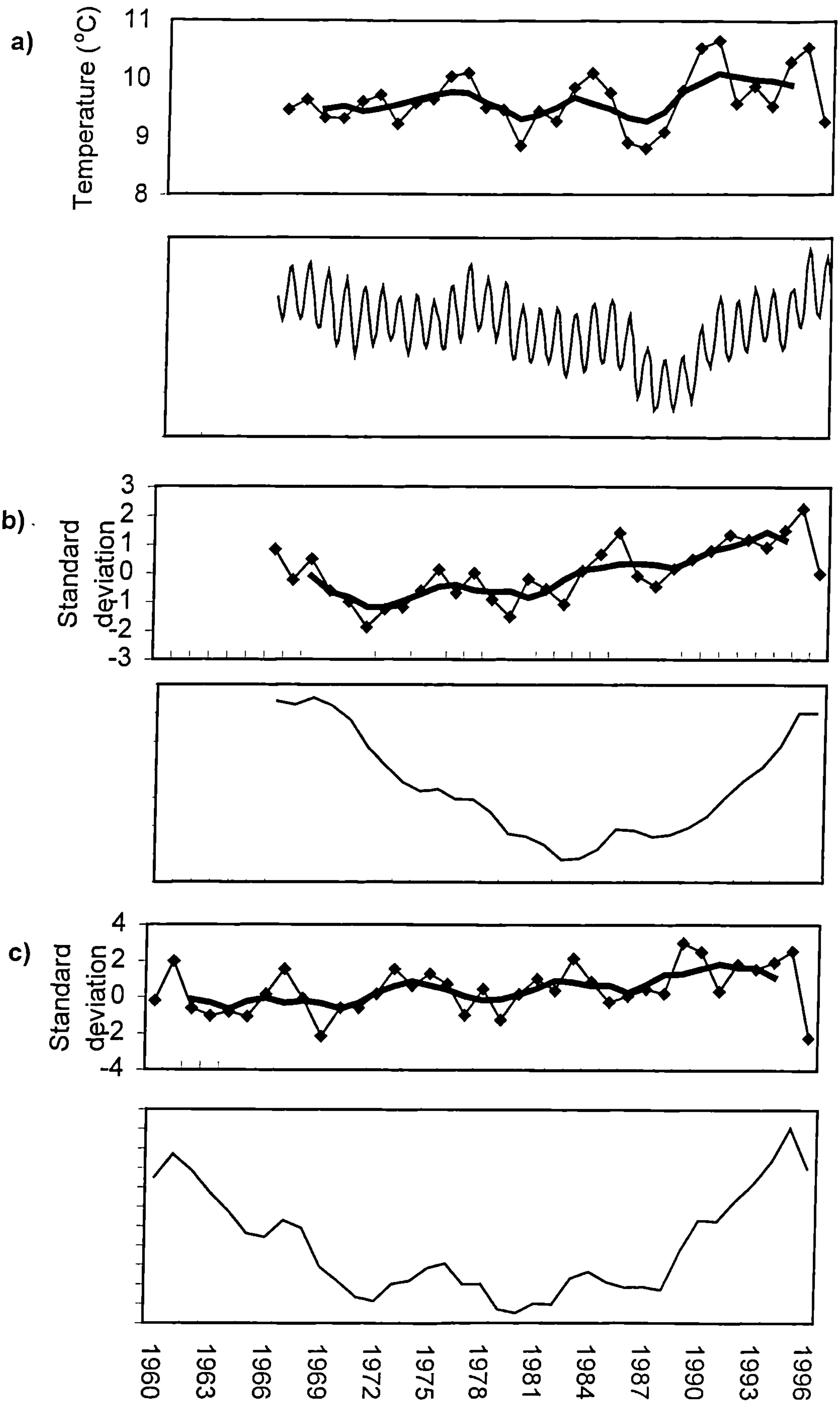


Figure 8.1 Time series of annual means (—◆—) with a 5 year moving average (——), and monthly CUSUM plot covering the period 1960-1996 of a) Central England Temperatures. b) Gulf Stream North Wall. c) North Atlantic Oscillation.

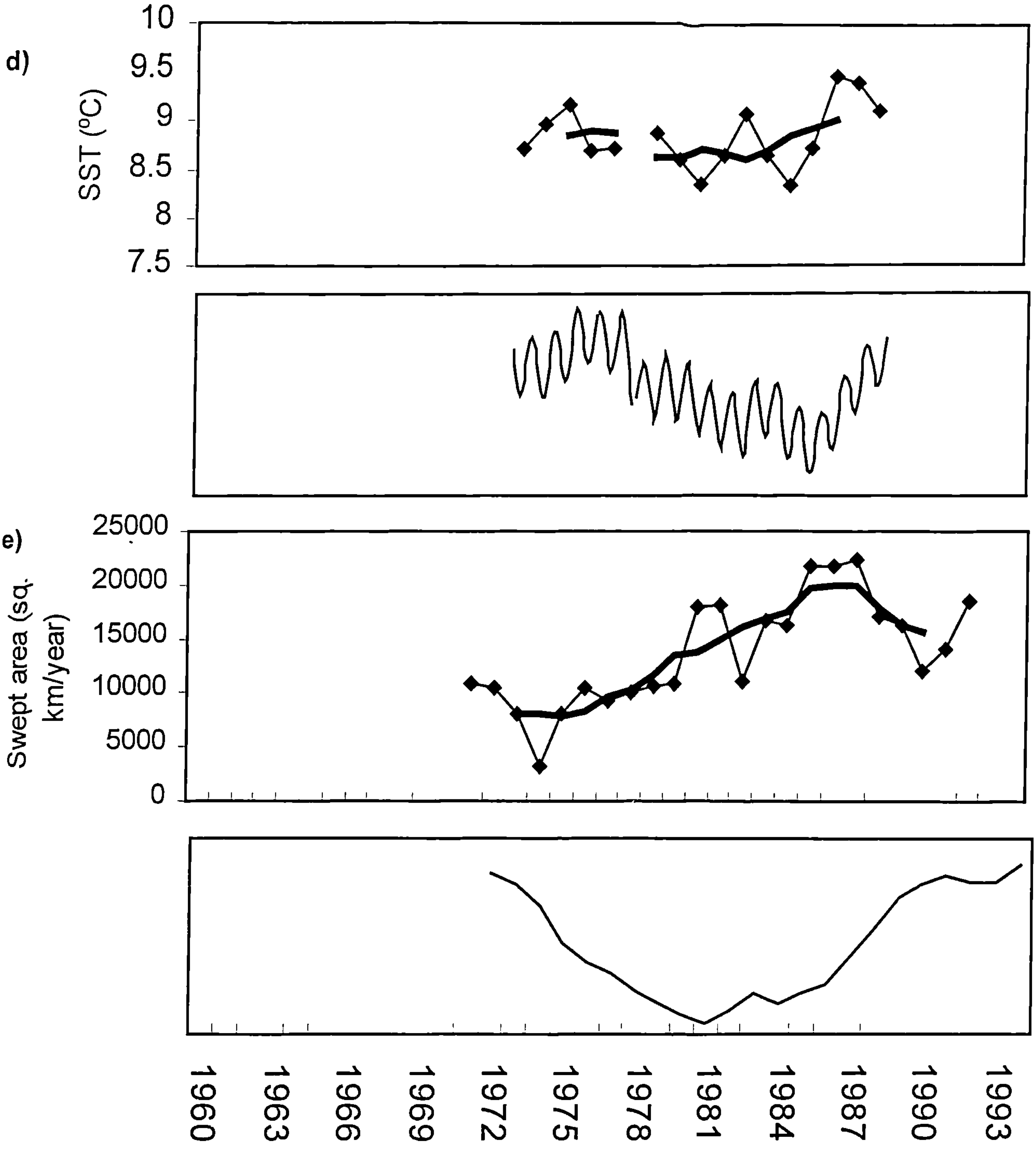


Figure 8.1 continued... d) Longstone lighthouse Sea Surface Temperatures. e) Fishing effort for ICES box 39E8.

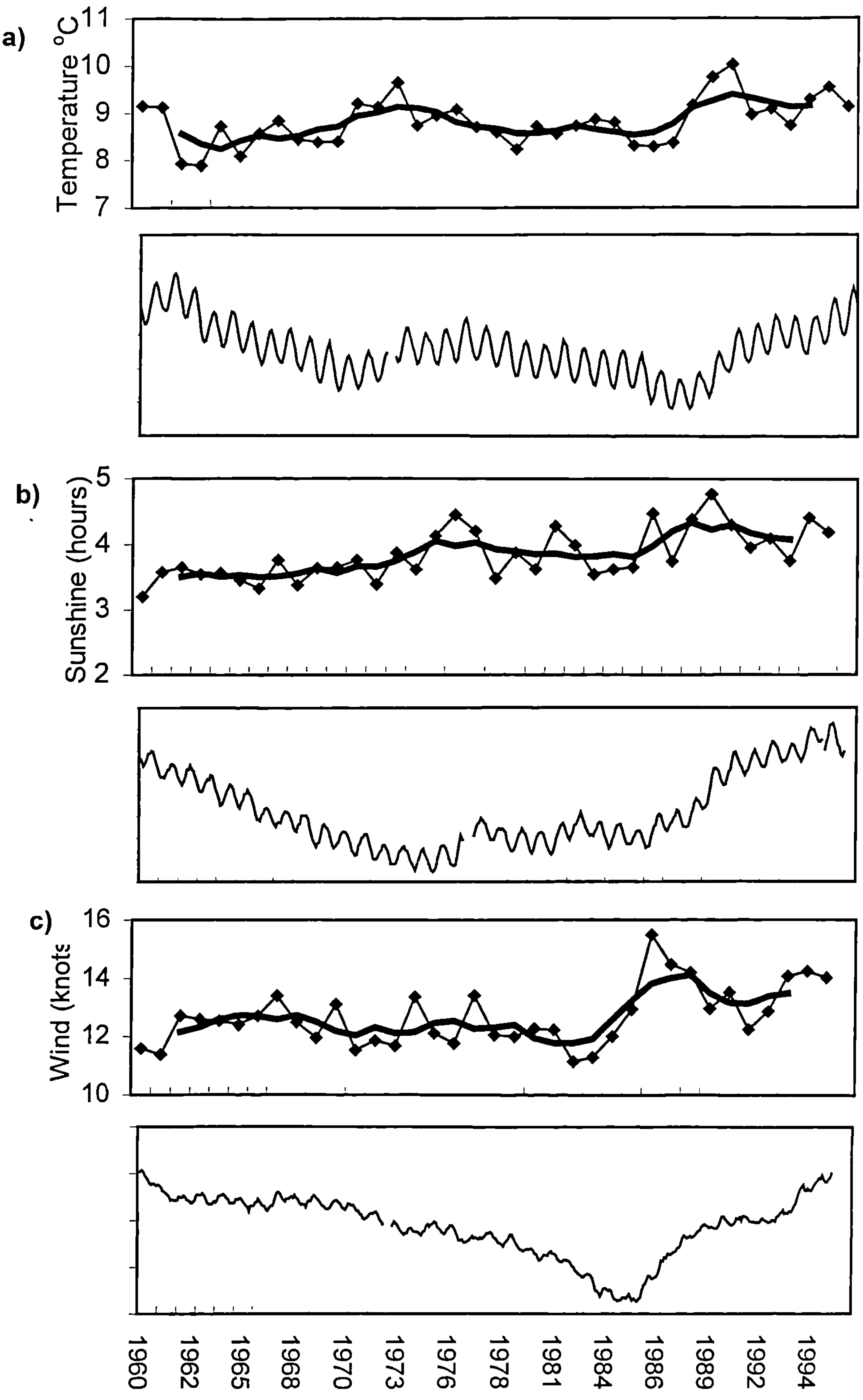


Figure 8.2 Time series of annual means (—◆—) with a 5 year moving average (▬), and monthly CUSUM plot covering the period 1960-1996 of a) Tynemouth air temperature. b) Tynemouth sunshine. c) Tynemouth wind speed.

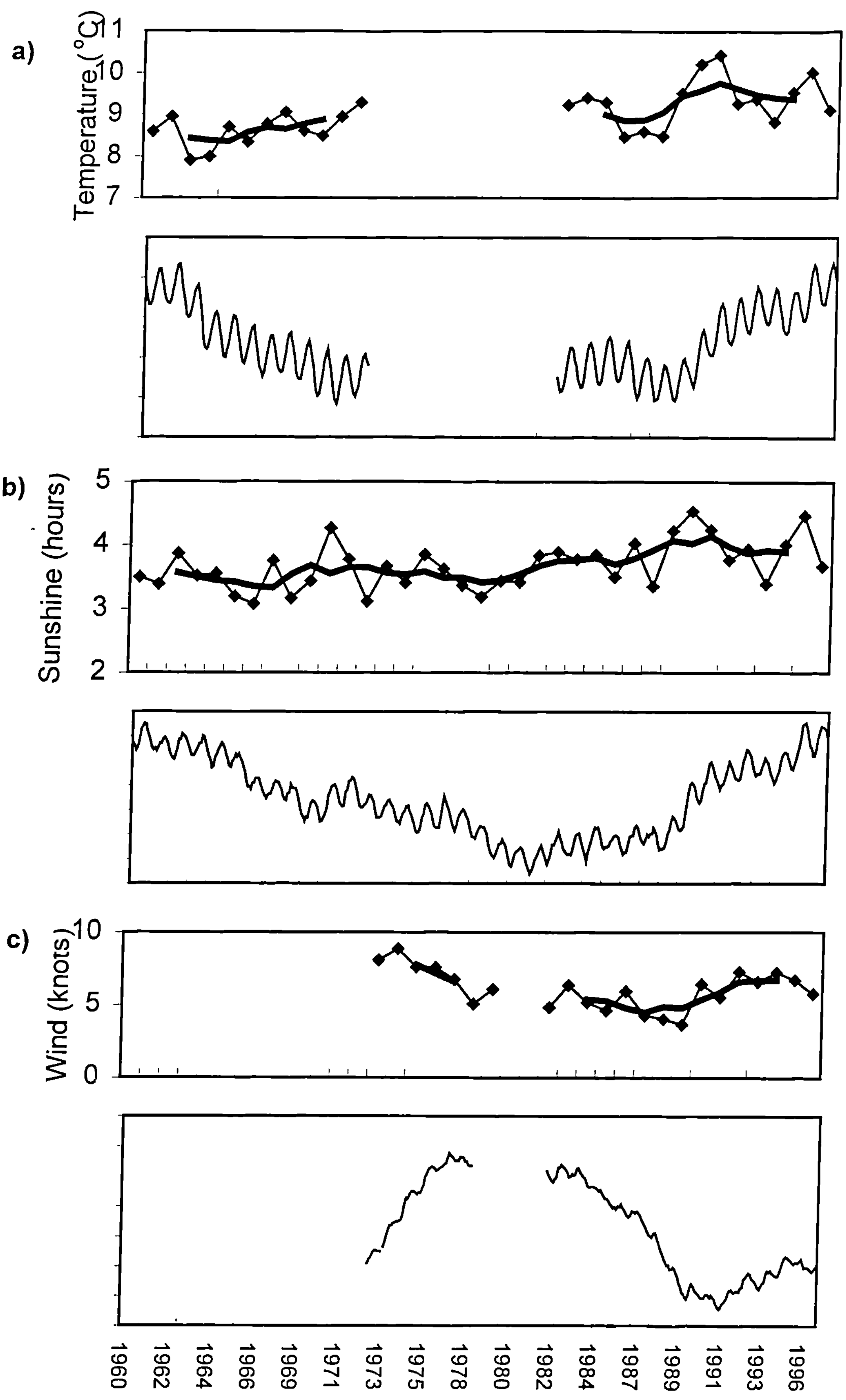


Figure 8.3 Time series of annual means (—◆—) with a 5 year moving average (▬), and monthly CUSUM plot covering the period 1960-1996 of a) Durham air temperature. b) Durham sunshine. c) Durham wind speed.

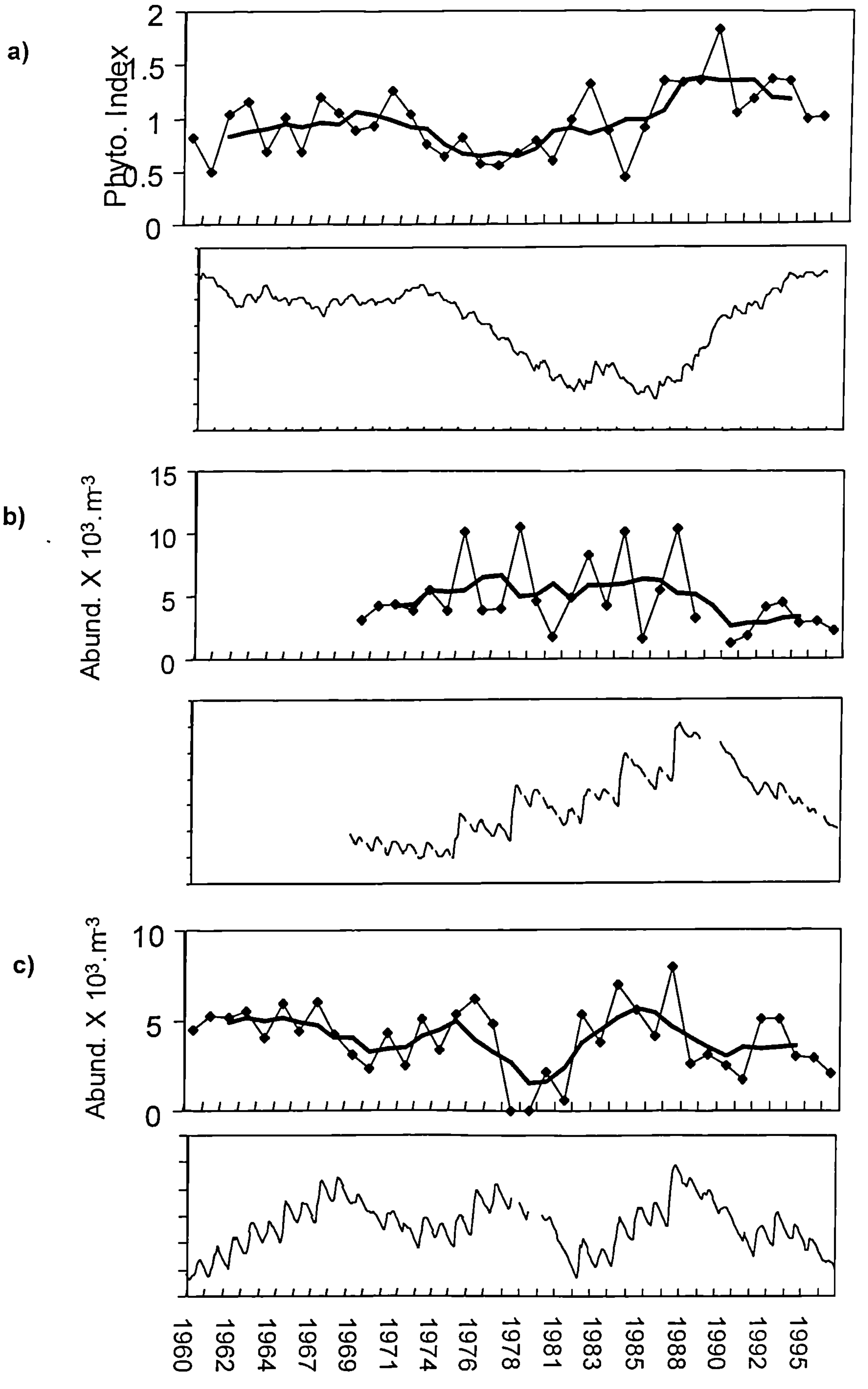


Figure 8.4 Time series of annual means (—◆—) with a 5 year moving average (——), and monthly CUSUM plot covering the period 1960-1996 of a) CPR phytoplankton area C2. b) Dove zooplankton. c) CPR zooplankton (central-west North Sea).

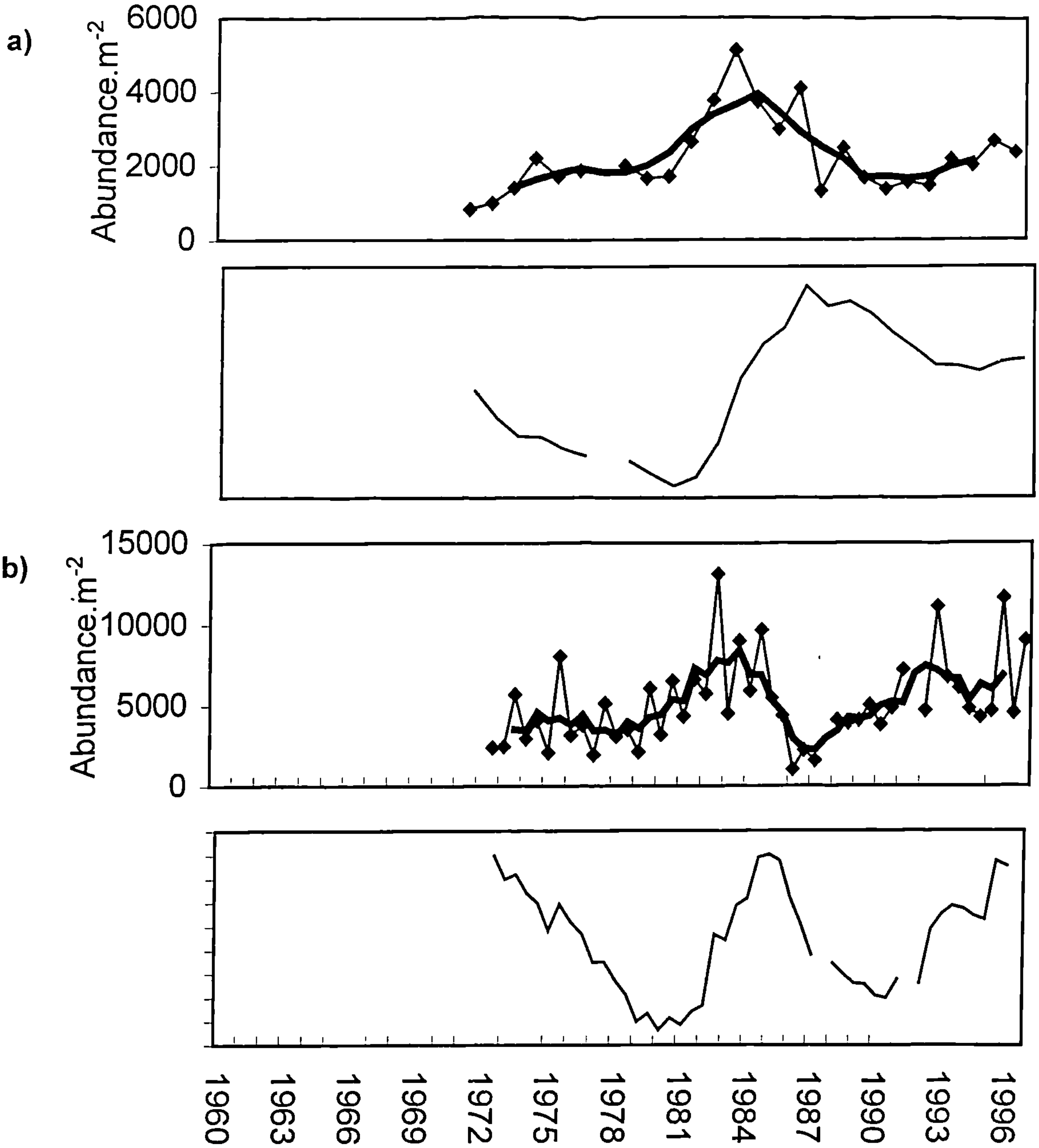


Figure 8.5 Time series of benthic data (—◆—) with a 5 point moving average (——), and CUSUM plot covering the period 1960-1996 at a) Station P. b) Station M1.

Table 8.4 Points of change identified from CUSUM plots

	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96
CET																		■							■				■								
GSNW																				■			■						■								
NAOI							■						■				■				■								■								
SST																				■								■									
Fishing effort																						■			■							■					
Tyne air temp.		■									■							■											■								
Tyne sun															■												■			■							
Tyne wind																										■											
Durham air temp.											■														■				■								
Durham sun											■											■							■								
Durham wind																		■													■						
Phytoplankton														■								■		■		■											
Dove zooplankton															■													■									
CPR zooplankton										■				■				■					■					■					■				
Benthos M1																						■					■										
Benthos P																						■				■					■						
No. changes		1					1			1	3		1	2	2		1	4		2	1	5	2	1	3	3	2	3	6	1	2	1	1				
No. changes/3 yr.		1	1			1	1	1	1	4	4	4	3	5	4	3	5	5	6	3	8	8	8	6	7	8	8	11	10	9	4	4	2	1			
Period																																					

Pelagic and benthic model

The pelagic model, forced by Durham sunshine only explained 6.1% of the year to year variance of summer *Pseudo-/Para-/Microcalanus* juveniles. However, when phytoplankton is used to force the model, this increases to 21.5% (Figure 8.7a). Further visual comparison of the model output with the actual zooplankton series suggests that the relative long term fluctuations were similar, although the smaller, shorter term variations were not. However, using regression equations to model these long term fluxes produces a standard deviation much lower than that of the actual data, and thus this causes a discrepancy between the predicted and actual abundances (Figure 8.7b). This could be corrected for by replacing the model long term mean and standard deviation with the long term mean and standard deviation of the actual time series.

With the simpler benthic model, forcing the model using Durham sunshine and M1 September abundance explained 35.6% of the variance (Figure 8.8a) at M1 March, whilst forcing by phytoplankton index and September abundances explained up to 52.4% of the variance (Figure 8.8b). In addition, the prediction of actual abundances is much better than that of the pelagic model, although these predictions too have a lower standard deviation than compared to the actual data. Removal of the density dependence portion of the model shows that, when sunshine is used to force the model, then only 12% of the variance may be explained, while only 26% of the variance may be explained when the model is purely driven by changes in phytoplankton abundance.

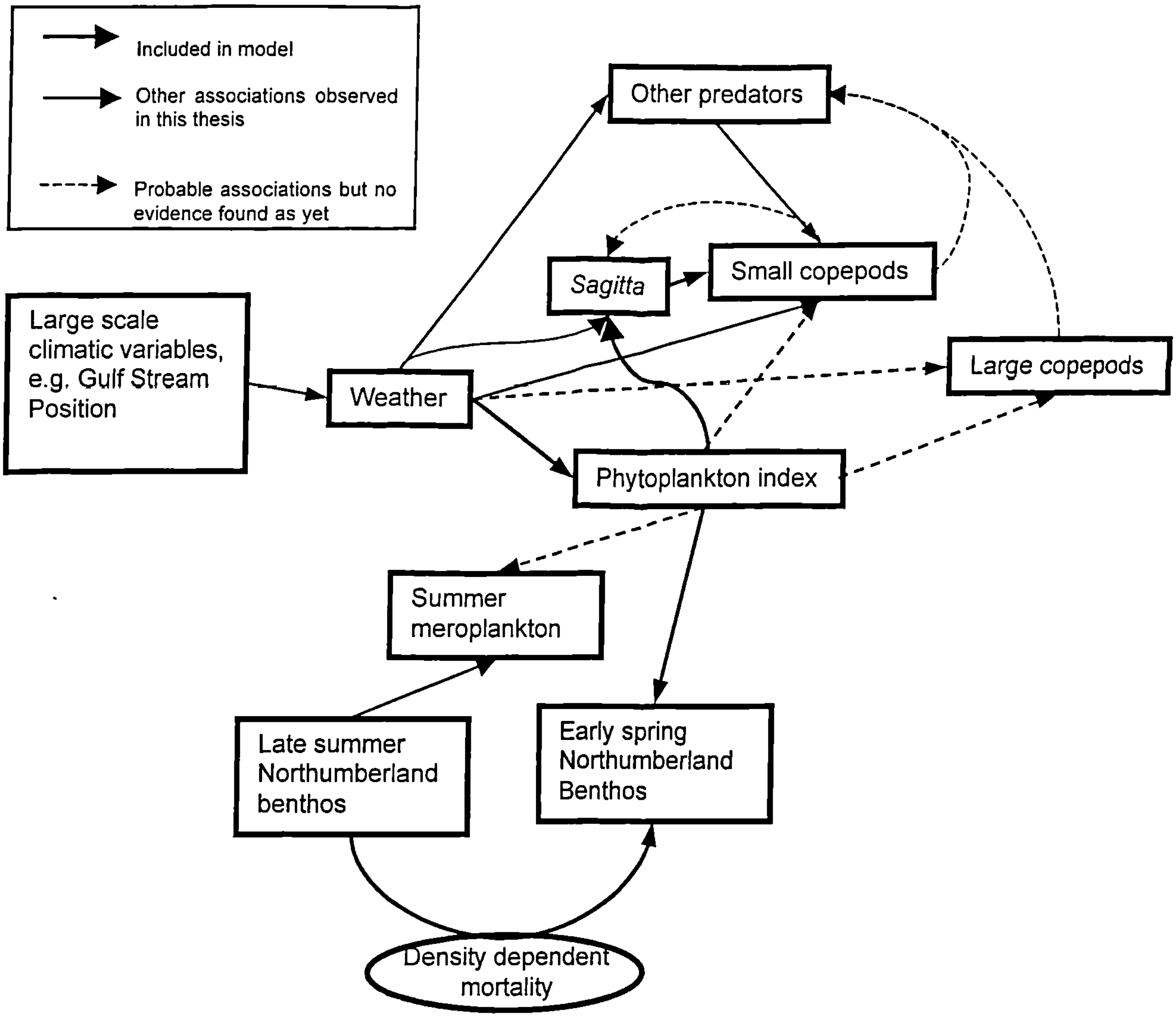


Figure 8.6 **Conceptual model of the Northumberland ecosystem, showing those links between variables included in mathematical models and those links detailed in this thesis.**

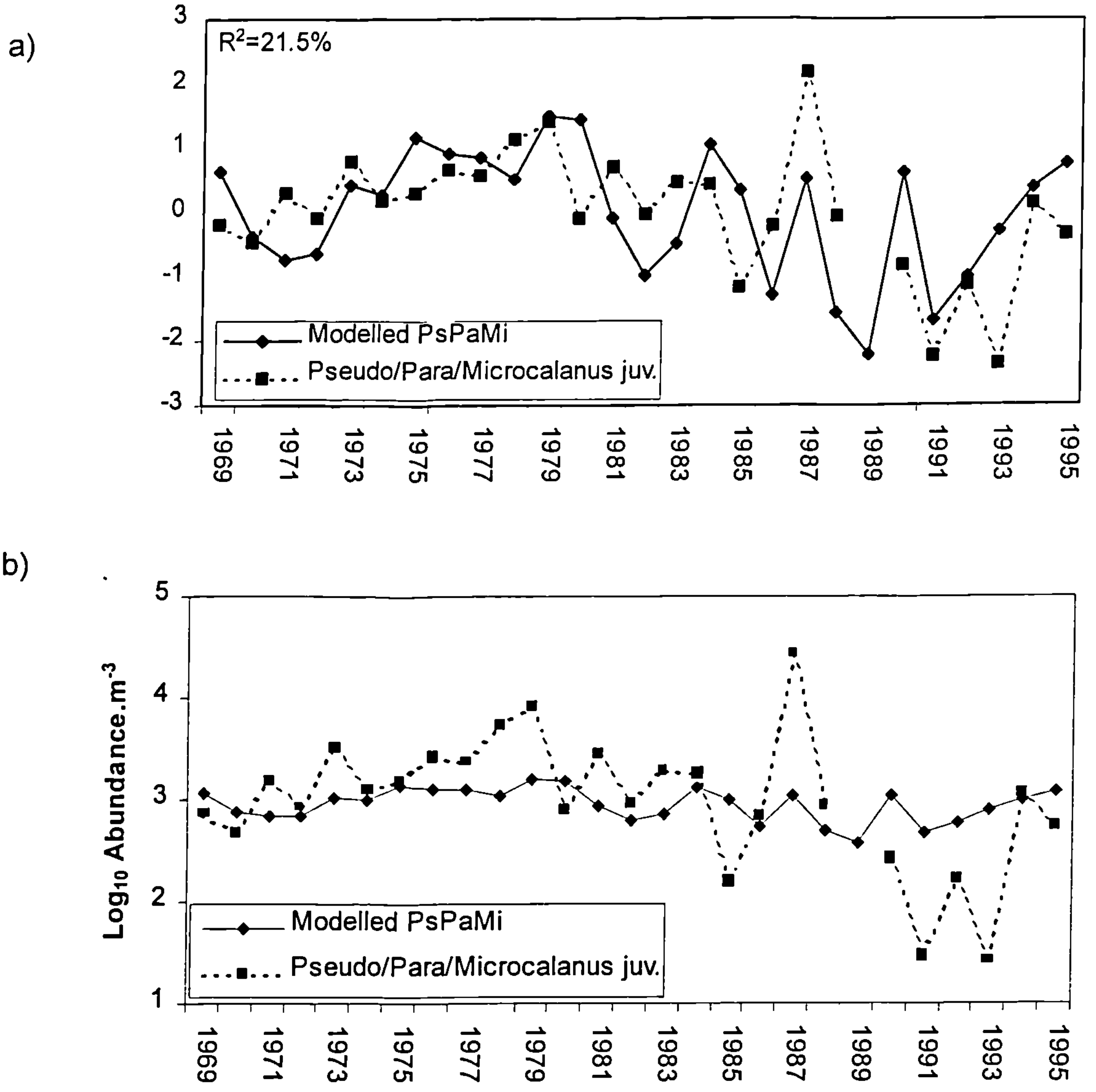
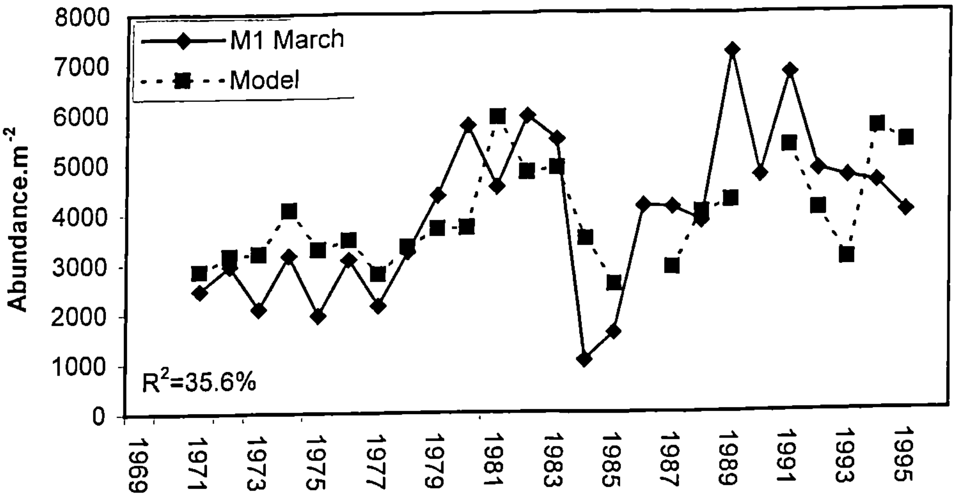


Figure 8.7 Time series plot of mean real (—◆—) and modelled (—■—) *Pseudo-/Para-/Microcalanus* juveniles for the months June-July, using a) relative abundances. b) actual abundances.

a)



b)

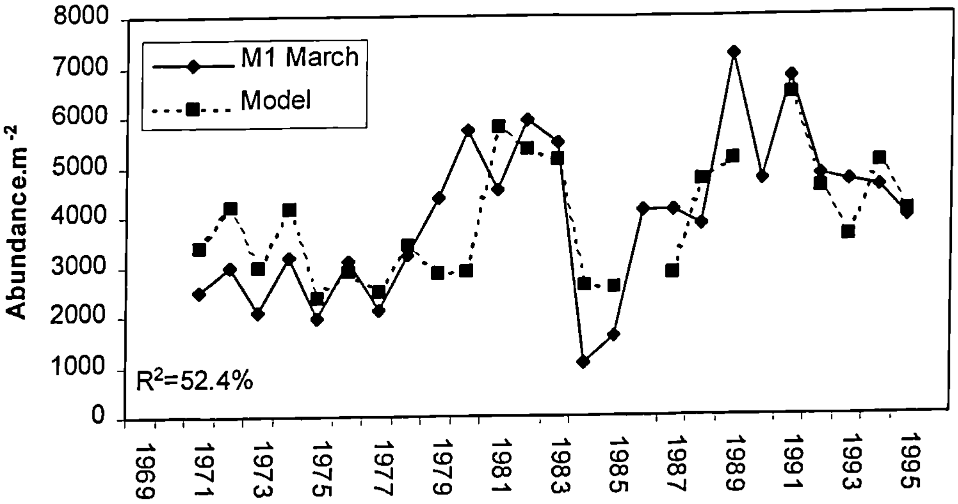


Figure 8.8 Time series plot of March real (—◆—) and modelled (--■--) actual benthic total abundances for Station M1, with model output calculated a) including sunshine b) omitting sunshine.

Discussion

Aebischer *et al.* (1990) described long term parallel trends across plankton, fish and seabird communities and weather. This study has shown that, although the central-west North Sea ecosystem is climatically driven (Figure 8.6), parallel or similar trends between climate and ecosystem variables do not necessarily exist, and nor, considering the high complexity of the ecosystem (de Angelis & Waterhouse, 1987; Rothschild, 1991), should we always expect them.

Over the latter half of the 20th century, air temperatures and daily sunshine durations have increased, alongside changes in the climatic proxy variables, the GSNW and the NAOI. Northumberland benthic Station M1 was the only benthic station to show long term parallel trends with climate (Tables 8.2 & 8.3), with the interannual fluctuations in this station being indirectly driven, through the influence of climate upon phytoplankton productivity (Figure 8.6, Chapter 6). Using food supply and September abundances as predictors of March benthic abundances, 52.4% of the interannual variation in the benthos may be explained through changes in phytoplankton input. However, when climate (Durham sunshine) is used as a predictor instead of food supply, this drops to 35.6% of the interannual variation in benthic abundance. As would be expected, increasing the complexity of the mechanism being modelled through the introduction of indirect factors (i.e. climate) reduces its accuracy. However, food supply and density dependant mortality are relatively constant factors influencing interannual fluctuations in benthic abundances (Chapters 2 & 6). As such, an additional factor to consider is that the relative success of the benthic model compared to the zooplankton model may be due to the fact that the mechanism regulating benthic abundances is similar each year. Although there is substantial evidence of control of the zooplankton community through *Sagitta*, this mechanism is not present during every annual cycle (Chapter 5). It is likely, for example, that during years when *Sagitta* abundances are low, other factors (e.g. temperature, food supply, other predators) become limiting and therefore regulate zooplankton abundances. As such, when phytoplankton is used to force the model, only 21.5% of the interannual fluctuations in zooplankton abundance may be predicted.

Although the presence of such dissimilar trends may indicate the presence of a more complex mechanism (such as that operating in the zooplankton system), via which the climatic signal is transferred to the biotic variables. In other cases, any expected signal of climate in the biotic variables might be masked by another factor (such as the effect of fishing masking any signal of phytoplankton at Station P). Another method of determining how the ecosystem is regulated could be through searching for coincident points of change, rather than looking for parallel trends. For example, Pearce & Frid (1999) using the recently developed technique of minimum – maximum auto-correlation factor analysis (MAFA) (Solow, 1994) found that this method observed species composition change occurring in the Dove zooplankton time series in 1976/77, 1982 and 1990. Some of these changes coincided with changes in climatological variables, although others did not. Pearce & Frid's (1999) conclusions were similar to those of Aebischer *et al.* (1990), as it was suggested that either all the time series responded to a single group of forcing factors, or that the ecosystem was forced via the food chain.

In this study, the results of the CUSUM analyses have identified coincident changes in the time series which could be considered to be evidence of external forcing (i.e. around the late 1970s to early 1980s, and the late 1980s). The most profound change occurred during the mid to late 1980s, with stepwise increases observed in the majority of the time series (Table 8.4). This was also the period when Reid *et al.* (1998) documented stepwise changes in phytoplankton populations across the NE Atlantic area which were ultimately in response to climatic fluctuations, thus suggesting that these observed changes all took place over a wide area. In the central-west North Sea region, the stepwise increases in the GSNW and NAOI climatic variables were observed in the biological time series as marked stepwise decreases in both the Dove and CPR zooplankton time series (due to the top down control of the small copepods (Chapter 5)). In contrast, although the results of the CUSUM analysis did not detect a change in the long term trends of the phytoplankton and M1 benthos, the M1 benthos did show parallel trends to climate (Tables 8.2 & 8.3).

Indirect factors are rarely considered when analysing long term trends, but as demonstrated here, such factors increase the complexity of the mechanism, and can strongly influence the long term dynamics of parts of the ecosystem and produce unexpected and dissimilar trends. Thus, it is suggested that when attempting to determine how the long term dynamics of the ecosystem are regulated, what researchers should be looking for is not only long term changes which occur in parallel with forcing factors (sensu Aebischer *et al.*, 1990), but also changes in such trends which occur coincidentally with changes in forcing factors, especially where these occur across a number of different communities or trophic levels. Such changes could be exhibited as not only a change in the direction of the trend but also a change in the gradient of the series with time (e.g. a stepwise change), and may show a change in the underlying functioning of the ecosystem.

Chapter 9 General Discussion

This study set out to examine the long term changes within the North Sea ecosystem (although concentrates on the central-west North Sea area), and the mechanism behind these trends. It has been shown that the long term dynamics of the North Sea ecosystem are generally bottom up controlled (sensu Hall & Raffaelli, 1993), in that primary production drives the interannual dynamics of most of the ecosystem components (Chapter 2). However, the long term dynamics of the North Sea ecosystem were found to be driven by two wide ranging but separate processes. In the northern, western and central areas of the North Sea, long term changes were predominantly influenced by climatic fluctuations according to the model of Dickson *et al.* (1988a). In the central-west North Sea region, the signal of climate could be observed in the interannual dynamics of phytoplankton (Chapter 4), zooplankton (Chapters 4 & 5), and macrobenthos (Chapter 6). In contrast, in the southern North Sea, the lack of stratification, and the large inputs of nutrients mean that primary productivity is more strongly influenced by variations in anthropogenic nutrient inputs, and is only weakly related to climatic variation (Chapter 2).

Generally, at the scale of the North Sea, long term changes at higher trophic levels (zooplankton, benthic, fish and seabirds) were affected by fluctuations in their food source (i.e. the lower trophic levels). Zooplankton productivity in the northern North Sea was ultimately related to the timing of the spring phytoplankton bloom and thus indirectly related to climatic influences. However, in the southern North Sea there were no such relationships. Throughout the North Sea, the productivity of the benthic system was found to be reliant upon the sedimentation of organic matter from the pelagos (sensu Pearson & Rosenberg, 1986), as was observed for benthic Station M1 (Chapter 6). Thus, these communities were found to be indirectly influenced by either changes in climate (e.g. Station M1, Chapter 6), or nutrients (e.g. Skaggerak benthos, Chapter 2), depending upon the region concerned. However, due to the high complexity of the ecosystem, there are many exceptions to these general patterns. For example, weather does directly influence some benthic communities (e.g. Wadden Sea littoral mudflat Beukema, 1992a) and fish taxa (e.g. pogge, Rogers & Millner, 1996), although on a North Sea scale this tends to be of secondary importance. It was also determined, that, despite previous assertions to the contrary (Taylor *et al.*, 1992), interspecific effects do play a role in the long term trends of some taxa and communities, and their presence can produce unexpected and dissimilar trends to those observed elsewhere. Analysis of the Dove zooplankton series data, and complementary modelling (Chapter 5), have demonstrated that long term trends were regulated by spring *Sagitta* abundances, which in turn were related to increases in their food source during the spring bloom (Chapter 5, Figure 5.12, Feigenbaum & Maris, 1984).

Ecological time series such as those which form the basis of this study, offer researchers an opportunity to observe the long term fluctuations of species, communities and ecosystems. In this thesis, the results of the analysis of such time series have contributed to furthering our understanding of the long term dynamics of the zooplankton and benthic communities. However, it is well known that the hypotheses generated by the analysis of time series data need to be treated with more caution than those generated by experimental procedures (Chapter 1). The high complexity of the ecosystem means that the methods by which a species, community, or ecosystem might be regulated are almost limitless, and when we attempt to ascribe causation to the observed dynamics, we have no controls with which to refer to. Unfortunately, at the large spatial and temporal scale of the marine ecosystem, such experimental approaches are impractical, and always will be. Yet our inability to carry out scientifically rigorous experiments at the appropriate time and spatial scales should not hamper the development of hypotheses as to how the long term dynamics of the ecosystem are determined.

With the lack of proper controls, there are two alternative methods of determining how the long term dynamics of taxa, communities and ecosystems are controlled. These are essentially the *a priori* and *a posteriori* methods. The *a priori* method is considered to be the most robust, as a hypothesis is formed as to exactly how the biotic variable in question is being driven. Then, selected statistical tests are performed to falsify an appropriate null hypothesis. The advantage of this method is that the number of analyses performed is limited to only those required to test the hypothesis, and thus this method avoids the pitfalls of performing multiple comparisons (see Chapter 1). This method was employed in Chapter 7. However, the disadvantage of this method is that the chance of success decreases with increasing complexity of the ecosystem. The *a posteriori* approach provides a more empirical method, which has been most commonly used in the past and has been used in this thesis (e.g. Chapter 4, Colebrook, 1978; Colebrook, 1982c; Roff *et al.*, 1988; Dunnet *et al.*, 1998). Although it has been heavily criticised (e.g. Shepherd *et al.*, 1984; Underwood, 1990), this approach uses a battery of statistical tests which can cover a multitude of hypotheses. However, due to the multiple statistical tests required, it is considered to be less robust, yet with complex ecological mechanisms, can be more effective in determining correlation between response and forcing variables, although not necessary causation. Such correlations produced by this method on their own are almost worthless, and as such it needs to be stressed that the results of such statistical tests need to be supported by a sensible mechanism. However, the final test of a hypothesis should be the accuracy of forecasting on data not available when the analysis was made (Chapter 1).

This thesis has also demonstrated that the usefulness of time series data are only as good as the data that are collected. Sampling artefacts are a problem of all time series, yet the results presented in Chapter 3 suggest that it is important to establish what these artefacts are in order to prevent incorrect hypotheses being produced. It appears that despite the CPR device and data from this being used since 1938, the considerable (overall, 15 times) underestimate of the abundance of zooplankton was either unnoticed, or "brushed under the carpet." There is also the danger of forgetting that, firstly, the community is *not* defined by what is captured by a particular sampling apparatus, but by the extent to which the organisms concerned function as an ecological unit. Secondly, there is also the need to bear in mind that ecological communities interact with other communities in other ways than through trophic interactions, but also through their life history stages. For example, benthic jellyfish polyps become holoplanktonic adults, whilst meroplanktonic polychaete larvae become adult benthic polychaetes (Appendix 4, Boero *et al.*, 1996). These two issues are not so much of a problem when the community is externally regulated, as the community in question will respond to the external factor(s). The problem occurs when the community is regulated by some internal mechanism (e.g. *Sagitta* predation). This is because if the sampling device does not accurately sample the whole community, information regarding a species which is part of the internal mechanism may be lost. For example, part of the reason why the CPR data does not support the *Sagitta* hypothesis as strongly as the Dove series might be because the *Pseudocalanus* juveniles may not be adequately sampled by the larger mesh size of the CPR device, while the sampling of chaetognaths may not be as effective due to their ability to avoid the device. I would also suggest that part of the dissimilarity in the long term trends observed between those observed across the North Sea, and those observed in the Dove series may be due to the fact that the CPR device samples best those larger individuals which are climatically regulated, whilst the Dove WP2 net also collected those smaller copepods which are subject to *Sagitta* regulation. As such, these devices are effectively sampling different parts of the same community. This is of course unavoidable, but does need to be considered when discussing the dataset in question.

Despite these problems, time series data are necessary in order to observe the fluctuations of species, communities and ecosystems over time and in order to determine the processes which drive them, or to test new hypotheses. The success of time series as ecological tools is borne out by the amount of literature produced through their analysis. Yet there is a pressing need to develop more robust statistical analyses to deal with such data. For example, this thesis could have been enhanced by a robust technique which could determine during what periods a time series was regulated by a particular factor, and during what periods other factors regulated it.

The long term increasing trends observed over the latter half of the 20th century, in climatic and meteorological variables examined in this thesis (Chapter 8), may simply be due to natural climatic variation. However, there is a view that such climatic change is ultimately due to anthropogenic influences (i.e. global warming) (McGowan, 1990). As such, the long term dynamics of much of the North Sea ecosystem may in truth be ultimately attributable to such anthropogenic climate change. Whether or not global climatic change is ultimately due to anthropogenic influences, at the scale of the North Sea, eutrophication was found to be a major anthropogenic influence on the long term dynamics of the North Sea ecosystem, as it influences the dynamics and species composition of the southern North Sea (Chapter 2). Another major anthropogenic influence on the North Sea ecosystem was the cumulative effect of trawling on the benthos (which mainly influences the species composition of the benthos), and the continual removal of biomass from the marine to the terrestrial environment (fishing, see Appendix 5). Long term fishing disturbance was found to effectively mask any relationship between phytoplankton and the benthos at Station P (Chapter 7, Frid *et al.*, 1999a). Other than this, there are no indications of anthropogenic influences on the long term ecosystem dynamics in the central-west North Sea region. However, although actual commercial fish stocks are primarily influenced by fishing, their annual recruitment is largely related to environmental factors. Other anthropogenic impacts (e.g. sewage sludge dumping) also play a role in influencing the long term dynamics and community structure of the benthos, although their effects are usually confined to small spatial areas, and at a North Sea scale they are of lesser importance.

As is often the case with advancements in human knowledge, however small such advancements are, the answers to current inquiries often raise further curiosity about those questions as yet unanswered. Thus, to conclude this work I would like to highlight possible areas of further research to be undertaken with these extending time series:

- Active and/or passive avoidance of the CPR sampling device was suggested as being the primary factor influencing the abundances observed in the CPR survey. In order to add further weight to these conclusions, a comparison of CPR survey data with another time series (e.g. Helgoland Roads zooplankton time series) should be performed. In addition, an experiment to compare samples taken by the CPR recorder alongside standard plankton net samples would give additional clues about the nature of artefacts introduced by the CPR device.

- Although *Sagitta* limits copepod population growth during the spring, there is conflicting evidence that predation on the overwintering standing stock of copepods influences abundances the following year. It is suggested that further work on determining the combined impact of predation on both the winter and spring copepod populations may yield further clues as to the regulation of long term dynamics of the central-west North Sea zooplankton community. In addition, although it was observed that there was a correlation between spring *Sagitta* abundances and the GSNW, the actual connection between these two variables is still uncertain. Is it solely due to the abundance of larger prey suitable for adult *Sagitta*? If so, how are the abundances of these prey regulated by external factors during the spring? Is there any persistence in copepod abundances over the winter from one year to the next which may influence spring *Sagitta* abundances? Finally, what evidence is there from other North Sea time series that *Sagitta* is able to regulate copepod population growth during the spring, and thus potentially regulate long term zooplankton trends? These questions could be addressed by a re-examination of the Dove time series samples, with particular attention being paid to the sexual stages of *Sagitta* (and thus obtain a clearer idea of its population dynamics), and its gut contents (to determine what species and size of prey are being selected by different sized *Sagitta*, and the separate predation rates for each month).

- The current ability to predict the interannual dynamics of benthic abundance at Station M1 is relatively high (Chapters 6 & 8). However, there is still uncertainty as to the exact nature of the processes occurring during the 2 year lag between settlement to the bottom, and settlement to the sieve. For example, how exactly does the meiofaunal portion of the benthic community respond to varying amounts of organic input? What is the extent of density dependence and competition for food between the macrofauna and meiofauna communities within the meiofauna community, and how does this determine the observed abundances in the sieve 18 months to 2 years following? Such questions are not so easily addressed as there is currently no meiofaunal time series available, although the initialisation of a short term study investigating the energy budget and energy dynamics of the benthos could yield clues as to the extent of density dependence and the presence of trophic links.

Whatever further work is performed on these time series, it needs to always be remembered that, ultimately, the long term dynamics of taxa, communities and ecosystems may be due to direct or indirect factors, and that interactions between a diversity of internal and external factors, results in the complex (and often unpredictable) behaviour of biological systems over time. Although, like much of the rest of the North Sea, the central-west North Sea ecosystem is climatically driven, similar or parallel trends between climate and ecosystem components do not exist, and nor, considering the high complexity of the ecosystem, should they necessarily be expected.

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Appendices

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Appendix 1 The Dove zooplankton time series history

I have included this in the thesis as there is the need to properly record for posterity, a list of changes in methodology, however slight, as well as slight anomalies in sampling, spare samples etc.

Sampling history

Date	Samples taken	Notes
30 August 1968	WP2 – Vert. x 4	Start of the series
11 April 1968	WP2 – Vert. x 4, WP3 Vert. x 4	14 Dec 70 15 min. x 3 horizontal WP3
10 March 1971	WP2 – Vert. x 4, WP3 Vert. x 4, some P200's 5-10 mins Hor.	P200's taken on: 10 March 1971, 21 April 1971, 14 May 1971, 3 August 1971, 20 Sept 1971, 25 Oct 1971, 11 April 1972, 15 May 1972.
25 October 1972	WP2 – Vert x 4, WP3 hori. 10-15 mins, p200's Vert x 4	TSK'S 23 May 1973 onwards Additional WP3 Vert x 4 on 21/7/88 & 16/12/88

Odd-dated samples

In order to form a complete sample set of WP2, WP3 and P200, some samples were taken on slightly different days:
Samples on 29 October 1973 for p200 & WP3 relates to 31 October 1973 samples
Sample on 13 March 1974 for p200 relates to 18 March 1974
Sample on 29 April 1976 for p200 relates to 20 April 1976
Sample on 4 May 1983 relates to 20 April 1973 (net type not recorded?)

Aborted samples

In addition there are a few odd samples left over with no logged date and which cannot be linked to a missing sample on a neighbouring date. These are:
15 March 1972 - P200 & WP3
8 March 1988 - WP3
29 April 1971 - WP3

Complete unrecorded samples

A few complete samples have also been found which are not currently recorded or logged:
20 November 1984
30 May 1985 (WP2 badly preserved - possible reason for absence of record?)

Appendix 2 Lambs weather types

Loadings of Lambs weather types on the first principal component calculated from Lambs weather data for 1960 to 1996 using the covariance matrix.

	Lambs weather (PC1)
AE	0.01
AN	0.06
ANE	0.00
Anticyclonic	-0.80
ANW	-0.04
AS	0.04
ASE	-0.02
ASW	-0.04
AW	-0.01
CE	0.05
CN	0.04
CNE	-0.02
CNW	0.01
CS	0.03
CSE	0.00
CSW	-0.01
CW	0.11
Cyclonic	-0.07
E	0.10
N	0.01
NE	0.02
NW	0.08
S	0.04
SE	-0.04
SW	-0.09
W	0.55

The first principal component, which was found to contribute 30% of the total variance, is heavily loaded by the anticyclonic (-0.80) and westerly weather (+0.55) types. Thus, higher values in the first principal component therefore represent years where there is a lower frequency of anticyclonic weather and an increased frequency of westerly weather.

Appendix 3.1 Correlation coefficients between Dove zooplankton taxa and environmental variables

Correlation coefficients between annual mean abundance of zooplankton taxa for the Dove time series against environmental variables. All probability values are corrected for serial correlation. Only those probabilities significant at p<=0.05 before correction for autocorrelation are included, significant correlations after correction are in bold. Global p=0.058.

	Tynemouth air temp. (T°C)	Tynemouth wind speed (knots)	Durham air temp. (T°C)	Durham wind speed (knots)	Tynemouth sunshine (hours)	Durham sunshine (hours)	GSNW	NAOI	Phyto. index (CW North Sea)	Phyto. index (area C2)	SST	Lambs weather (PC1)	Winter flow (Orkney-Shetland)	Winter flow (Moray Firth)	Winter flow (CW North Sea)
Acartia clausi	-0.07	-0.03	-0.23	-0.13	0.01	-0.06	0.02	0.23	0.37	**0.45 p=0.024**	0.26	-0.26	0.12	-0.23	0.14
Acartia longiremis	-0.18	-0.06	-0.06	0.13	0.14	-0.22	-0.38	0.00	0.28	0.33	-0.19	0.10	0.37	-0.02	0.25
Acartia spp. juvs	-0.14	-0.13	-0.32	-0.02	-0.06	-0.03	-0.24	0.08	0.03	-0.15	0.08	0.05	-0.24	-0.02	0.37
Aglantha digitale	0.23	-0.11	0.24	-0.43 p=0.054	0.12	0.32	0.02	0.25	-0.27	0.31	0.11	-0.02	0.10	-0.24	-0.28
Anomuran juvs	0.08	0.33	0.19	0.06	0.03	0.36	0.19	0.03	0.06	0.03	0.31	0.35	-0.08	-0.04	-0.29
Bivalve juvs	0.15	**-0.45 p=0.0321**	0.12	0.30	-0.18	-0.21	-0.31	-0.07	-0.02	-0.36	0.06	**-0.39 p=0.049**	-0.16	0.21	0.25
Bryozoan juvs	-0.30	-0.21	-0.02	-0.34	-0.05	-0.17	-0.30	-0.11	-0.16	-0.04	-0.11	-0.28	-0.18	0.20	-0.03
Calanus finmarchicus females	-0.11	-0.14	0.09	-0.46 =0.091	-0.11	0.20	0.36	0.08	**-0.40 p=0.048**	-0.21	0.21	-0.19	-0.22	-0.24	-0.38
Calanus helgolandicus females	-0.21	0.17	0.07	**-0.69 P=0.016**	0.04	0.10	0.07	0.08	-0.05	0.19	-0.10	-0.11	-0.22	0.01	-0.43 p=0.0508
Calanus spp. juvs	-0.16	-0.11	-0.33	-0.25	0.08	0.03	-0.15	0.13	-0.26	-0.12	-0.18	0.01	-0.14	0.05	0.02
Calanus spp. males	-0.03	-0.32	0.10	-0.39	-0.02	0.17	-0.04	-0.02	-0.32	0.20	-0.03	-0.09	-0.05	-0.16	-0.20
Centropages hamatus	-0.05	-0.11	0.02	**-0.51 P=0.038**	0.13	0.33	0.12	0.27	-0.10	0.31	0.04	-0.30	-0.17	-0.10	-0.28
Centropages spp. juveniles	0.33	0.11	0.11	-0.08	-0.09	0.28	0.06	0.32	-0.15	-0.07	0.39	-0.06	-0.26	-0.21	-0.19
Centropages typicus	0.22	-0.21	0.35	0.14	-0.19	-0.17	-0.03	-0.12	0.26	0.16	0.25	0.01	0.21	-0.13	0.07
Cirripeda juveniles	-0.32	0.07	-0.26	-0.13	0.17	0.03	-0.10	0.07	0.11	0.04	-0.26	0.06	-0.40	0.35	-0.07
Corycaeus anglicus	0.23	0.35	0.17	-0.40	0.33	0.27	0.20	0.39 p=0.053	-0.15	0.05	**0.64 p=0.023**	-0.17	-0.10	-0.41	**-0.46 p=0.034**
Echinoderm juveniles	0.05	-0.07	-0.24	0.09	0.11	0.09	-0.15	0.09	0.09	-0.01	0.28	-0.29	-0.21	-0.19	0.23
Echinoplutei juveniles	0.18	-0.13	0.26	-0.04	0.13	-0.05	-0.07	0.15	-0.20	-0.17	-0.01	0.07	0.03	0.14	0.25
Euphausiid spp. juveniles	-0.09	**-0.41 p=0.486**	0.06	0.17	0.23	0.15	-0.16	0.02	-0.38	-0.17	-0.21	-0.10	0.05	0.14	-0.29
Euphausiid spp nauplii	-0.01	-0.01	-0.06	0.21	0.09	0.25	-0.06	-0.15	-0.07	-0.16	-0.28	-0.06	-0.32	0.38	**-0.46 p=0.038**
Evadne nordmanni	-0.37	-0.04	-0.22	-0.14	0.11	-0.30	-0.15	-0.01	0.15	0.01	-0.06	-0.05	0.01	-0.02	0.16
Fish larvae	0.06	0.03	0.25	0.09	0.10	-0.11	-0.06	-0.26	0.13	-0.14	-0.14	0.06	-0.09	0.15	0.08
Fritillaria borealis	0.14	0.19	0.05	0.47 p=0.098	0.17	-0.127	0.053	0.14	-0.025	-0.19	0.14	0.10	0.19	0.19	0.26
Gastropoda juveniles	-0.05	**-0.58 p=0.006**	-0.13	0.15	-0.18	-0.23	**-0.54 p=0.023**	-0.20	-0.04	-0.04	-0.21	-0.39 p=0.0557	-0.19	0.41	0.32
Jellyfish juveniles	0.12	-0.35	0.09	0.16	0.12	0.02	-0.07	0.16	-0.36	**-0.52 p=0.012**	**0.55 p=0.028**	-0.37	-0.18	-0.10	-0.24
Microsetella norvegica	0.15	-0.38	0.28	0.08	-0.10	0.22	-0.22	-0.05	-0.17	0.09	0.06	0.10	0.35	-0.31	-0.05
Microcalanus pusillus	0.37	0.01	-0.18	0.37	-0.13	-0.01	0.16	0.25	0.06	-0.10	0.13	-0.23	0.17	-0.06	0.01
Nanomia cara	0.38	-0.17	0.13	0.34	0.02	0.00	-0.18	0.17	-0.10	-0.14	NA	-0.25	**0.44 p=0.038**	**0.43 p=0.042**	-0.01
Nyctiphanes couchi	0.33	0.02	0.52 p=0.059	0.03	-0.17	-0.25	-0.03	-0.07	-0.05	-0.20	0.12	0.26	0.19	-0.06	-0.09
Oikopleura diocia	-0.08	-0.27	0.04	-0.09	0.11	0.33	-0.17	0.19	-0.39 p=0.07	-0.01	-0.10	-0.19	-0.15	0.14	-0.19
Oithona similis	-0.35	-0.18	-0.45	0.03	0.02	-0.12	**-0.45 p=0.033**	-0.15	-0.03	-0.07	-0.14	0.00	**-0.42 p=0.049**	0.27	0.30

	Tynemouth air temp. (T°C)	Tynemouth wind speed (knots)	Durham air temp. (T°C)	Durham wind speed (knots)	Tynemouth sunshine (hours)	Durham sunshine (hours)	GSNW	NAOI	Phyto. index (CW North Sea)	Phyto. index (area C2)	SST	Lambs weather (PC1)	Winter flow (Orkney-Shetland)	Winter flow (Moray Firth)	Winter flow (CW North Sea)
Oncaea venusta	0.35	0.24	0.16	0.09	0.14	**0.46** **P=0.015**	**0.47** **p=0.022**	0.32	-0.04	0.04	0.19	-0.08	**0.58** **p=0.004**	**-0.48** **p=0.023**	**-0.44** **p=0.044**
Ophioplutei juveniles	-0.09	0.12	-0.42	-0.22	-0.05	0.27	0.14	-0.02	0.13	0.04	-0.10	-0.09	-0.31	0.24	-0.01
Paracalanus parvus	0.35	-0.16	0.50 p=0.087	0.24	0.02	0.03	-0.08	0.17	0.24	0.35	-0.14	-0.04	**0.52** **p=0.026**	-0.06	0.04
Phoronid juveniles	-0.08	-0.02	-0.22	0.00	0.08	-0.21	0.20	-0.11	0.02	-0.32	0.12	0.05	-0.04	-0.14	0.37
Podon spp.	-0.14	-0.07	-0.33	-0.27	-0.01	0.04	-0.28	0.04	0.07	0.14	-0.17	0.01	-0.15	0.02	0.03
Polychaeta juveniles	**0.40** **p=0.045**	-0.02	0.17	0.19	-0.01	0.31	0.09	0.22	0.02	-0.04	0.23	-0.24	-0.22	0.17	0.06
Pseudo,Para,Microcalanus juveniles	-0.40 p=0.0637	-0.16	**-0.59** **p=0.016**	-0.03	0.04	-0.27	**-0.61** **p=0.006**	-0.19	-0.04	-0.29	-0.28	0.02	-0.41	0.29	0.30
Pseudocalanus elongatus	-0.02	-0.35	0.09	0.04	0.17	-0.06	-0.14	0.17	-0.08	-0.05	0.00	-0.28	0.11	-0.06	0.04
Sagitta elegans	0.08	0.10	-0.15	-0.29	0.06	0.27	0.17	0.25	-0.13	0.20	0.17	-0.37	-0.10	-0.19	**-0.45** **p=0.041**
Temora longicornis	-0.15	-0.24	-0.28	-0.30	0.15	-0.13	**-0.47** **p=0.018**	0.01	0.18	0.15	-0.06	-0.16	-0.19	-0.06	0.18
Themisto gaudichaudi	0.22	0.05	0.28	-0.17	-0.17	-0.06	0.10	0.05	-0.04	-0.04	**0.50** **p=0.05**	-0.14	0.21	**-0.49** **p=0.03**	-0.19
Thysanoessa inermis	0.10	-0.03	**0.64** **p=0.005**	-0.09	-0.11	0.03	0.36	-0.06	0.00	0.20	-0.30	-0.05	0.24	0.06	-0 08
Thysanoessa raschi	-0.23	-0.15	-0.31	0.13	-0.09	-0.10	-0.05	-0.38	0.01	-0.06	-0.02	-0.03	-0.35	0.07	-0.10
Tigriopus spp.	0.26	0.38	0.23	0.16	-0.15	0.06	0.45 p=0.106	0.17	0.28	0.32	0.19	0.19	**0.66** **p=0.005**	-0.23	0.02
Tomopteris helgolandica	-0.19	-0.11	-0.34	-0.34	0.18	0.24	-0.32	-0.10	-0.03	0.19	0.22	-0.14	-0.28	-0.26	-0.22
Total zooplankton	-0.34	-0.15	-0.44	-0 10	0.08	-0.18	**-0.40** **p=0.046**	0.02	0.11	-0.03	-0.14	-0.06	-0.22	0.16	0.33

Appendix 3.2 Correlation coefficients between CPR zooplankton taxa and environmental variables

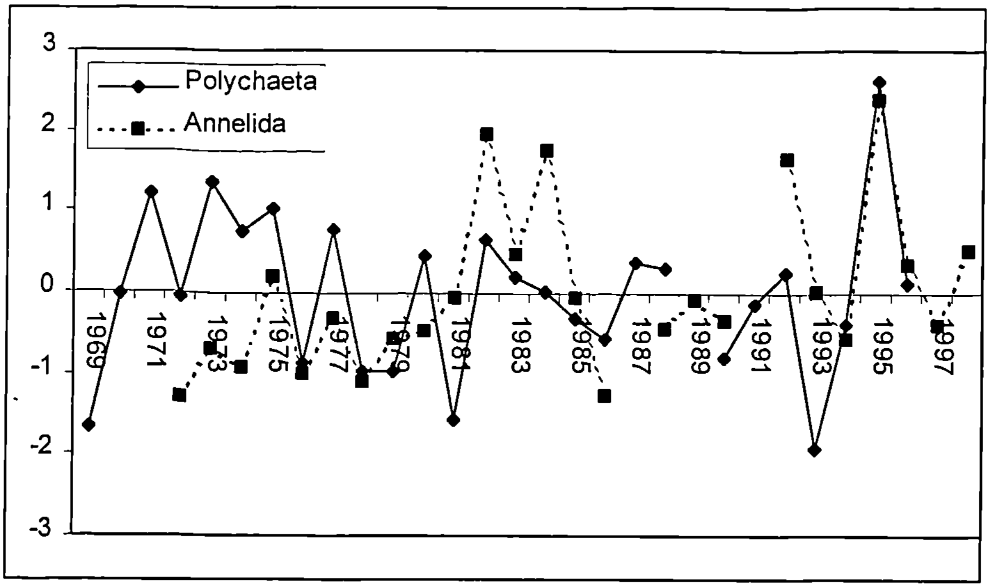
Correlation coefficients between annual mean abundance of zooplankton taxa for the CPR time series against environmental variables. All probability values are corrected for serial correlation. Only those probabilities significant at p<=0.05 before correction for autocorrelation are included, significant correlations after correction are in bold. Global p<0.001.

	Tynemouth air temp. (T°C)	Tynemouth wind speed (knots)	Durham air temp. (T°C)	Durham wind speed (knots)	Tynemouth sunshine (hours)	Durham sunshine (hours)	GSNW	NAOI	Phyto. Index (CW North Sea)	Phyto. Index (area C2)	SST	Lambs weather (PC1)	Winter flow (Orkney-Shetland)	Winter flow (Moray Firth)	Winter flow (CW North Sea)
Acartia longiremis	0.11	-0.17	0.07	-0.09	-0.01	0.02	-0.37 p=0.064	-0.11	0.19	0.15	0.11	**-0.44** **p=0.01**	-0.11	0.06	0.09
Acartia spp.	-0.13	0.16	-0.28	0.43	-0.12	-0.23	0.09	0.00	0.10	-0.20	-0.02	0.11	-0.11	-0.19	0.12
Calanus finmarchicus	-0.21	-0.22	-0.26	-0.35	-0.17	-0.06	0.03	-0.26	-0.21	-0.16	-0.24	**0.37** **p=0.042**	-0.07	0.21	-0.09
Calanus helgolandicus	**0.37** **p=0.032**	-0.13	0.29	-0.37	-0.22	0.19	0.35	0.15	0.21	0.09	0.27	-0.14	0.27	0.08	0.04
Calanus I-IV	-0.13	-0.10	-0.13	**-0.73** **p=0.009**	-0.05	0.12	0.05	-0.13	-0.20	0.01	-0.08	0.33	0	0.13	-0.05
Calanus V-VI total	-0.09	-0.22	-0.15	-0.46 p=0.07	-0.24	0.02	0.16	-0.19	-0.13	-0.12	-0.09	0.25	-0.04	0.24	-0.05
Candacia I-IV	-0.10	0.00	-0.08	NA	-0.15	-0.29	0.15	-0.04	-0.08	-0.17	NA	0.18	0	-0.04	-0.05
Centropages hamatus	0.00	-0.03	0.00	-0.27	0.12	0.06	-0.08	0.11	-0.05	0.03	-0.06	**-0.49** **p=0.007**	**-0.38** **p=0.034**	0.25	0.01
Centropages typicus	0.34 p=0.052	-0.19	0.09	0.30	0.08	-0.02	-0.13	0.04	0.24	0.06	0.38	-0.31	0.08	0.17	**0.36** **p=0.05**
Chaetognatha	**0.36** **p=0.041**	-0.04	0.27	**-0.48** **p=0.042**	-0.12	0.00	0.25	0.23	0.20	0.05	0.40	-0.10	0.15	-0.12	-0.10
Cirripede larvae	-0.01	**0.45** **P=0.01**	0.14	-0.15	0.23	0.10	0.05	0.14	0.22	0.20	0.25	0.04	0.12	-0.27	-0.12
Clytemnestra spp.	-0.05	0.12	NA	0.10	0.13	-0.15	-0.02	-0.20	0.02	-0.25	-0.13	0.18	-0.12	0.13	0.06
Copepod nauplii	0.05	**0.38** **p=0.045**	0.08	-0.08	0.22	0.13	0.33	0.16	0.26	0.18	0.27	-0.14	0.12	**-0.42** **p=0.019**	0.03
Corycaeus spp.	0.35 p=0.054	0.15	**0.42** **p=0.044**	-0.33	0.26	**0.43** **p=0.011**	0.30	**0.42** **p=0.013**	0.27	0.22	0.45	-0.13	0.15	-0.16	-0.09
Cyphonautes larvae	0.06	0.24	-0.03	0.16	0.18	0.09	0.11	0.16	0.25	0.21	0.19	-0.14	0.28	-0.05	0.19
Decapoda larvae	0.16	0.11	0.08	0.39	0.16	-0.05	0.12	0.10	0.12	-0.31	0.22	-0.09	-0.09	0.10	0.09
Echinoderm larvae	-0.03	0.19	-0.02	-0.16	0.03	-0.10	0.46 p=0.064	0.23	-0.12	0.16	0.06	-0.11	0.34	-0.22	0.09
Euphausiacea total	-0.31	-0.15	-0.18	0.09	-0.01	-0.15	0.00	-0.32	-0.20	-0.31	-0.46	0.29	-0.03	-0.10	-0.04
Evadne spp.	-0.13	0.17	-0.26	0.11	-0.01	-0.18	0.17	0.14	0.20	0.04	0.15	-0.01	-0.05	-0.14	0.22
Fish larvae	0.04	0.34 p=0.059	-0.03	-0.40	0.08	0.04	0.05	0.06	0.29	0.16	0.46	0.03	0.05	-0.04	-0.07
Harpacticoida total	0.16	-0.08	0.17	0.28	0.23	-0.05	-0.12	0.13	0.14	-0.07	0.38	0.00	0.29	-0.18	0.24
Hyperiidea	0.33	-0.01	0.35	**-0.64** **p=0.007**	-0.01	0.08	0.22	0.22	0.07	0.15	0.10	0.10	0.26	-0.19	-0.12
Lamellibranchia larvae	**-0.36** **p=0.046**	0.00	**-0.56** **p=0.009**	0.21	-0.10	-0.32	-0.16	-0.29	0.26	0.05	0.23	0.04	-0.17	0.04	0.27
Larvacea	0.18	0.34 p=0.057	0.21	-0.33	0.04	0.15	0.39 p=0.05	0.15	0.14	-0.06	0.22	-0.06	-0.08	-0.26	-0.21

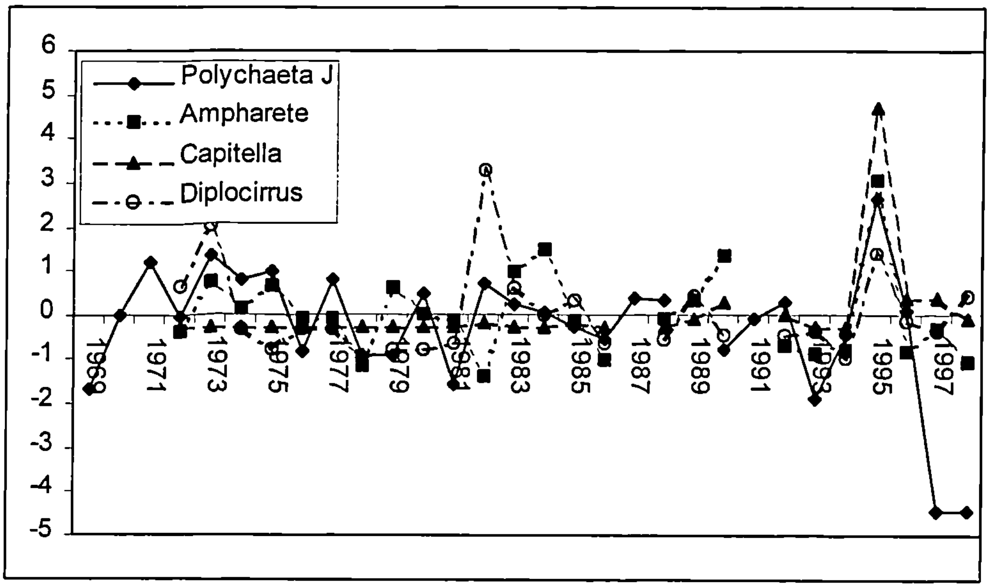
	Tynemouth air temp. (T°C)	Tynemouth wind speed (knots)	Durham air temp. (T°C)	Durham wind speed (knots)	Tynemouth sunshine (hours)	Durham sunshine (hours)	GSNW	NAOI	Phyto. Index (CW North Sea)	Phyto. Index (area C2)	SST	Lambs weather (PC1)	Winter flow (Orkney-Shetland)	Winter flow (Moray Firth)	Winter flow (CW North Sea)
Limacina retroversa	0.07	-0.20	-0.21	-0.32	-0.13	-0.29	0.20	-0.07	0.27	-0.02	0.33	0.18	0.11	0.15	0.31
Metridia I-IV	0.07	-0.12	-0.01	-0.04	-0.03	-0.12	-0.03	0.12	-0.03	-0.08	0.29	**0.51** **p=0.004**	0.2	-0.09	0.10
Metridia lucens	**0.60** **p<0.001**	0.19	**0.63** **p=0.002**	-0.37	0.26	**0.46** **p=0.02**	0.25	**0.44** **p=0.016**	0.32	**0.47** **p=0.018**	**0.67** **p=0.022**	-0.11	**0.54** **p=0.001**	**-0.48** **p=0.015**	-0.36 p=0.06
Microcalanus spp.	0.23	0.32	0.27	0.20	0.23	0.26	**0.41** **p=0.043**	0.28	**0.35** **p=0.043**	0.00	NA	0.09	NA	NA	NA
Oithona spp.	-0.17	0.19	-0.40 p=0.088	-0.22	0.14	-0.12	0.19	0.02	0.15	0.08	0.04	0.26	0.11	-0.26	0.16
Oncaea spp.	-0.09	**0.54** **p=0.002**	0.00	-0.02	0.24	0.19	-0.08	-0.05	-0.01	0.18	-0.07	0.17	-0.05	-0.20	0.03
Podon spp.	0.06	0.05	0.06	0.06	0.14	0.08	-0.14	0.16	0.33	0.31	0.20	-0.26	-0.06	-0.08	0.22
Pseudocalanus/ Paracalanus total	-0.22	-0.11	**-0.63** **p=0.005**	0.26	-0.07	-0.33	-0.24	-0.16	0.10	-0.13	0.00	0.20	-0.15	0.07	0.26
Pseudocalanus elongatus adult	-0.26	-0.21	-0.39 p=0.08	0.04	0.06	-0.23	-0.38 p=0.061	-0.14	-0.12	-0.20	-0.30	0.10	-0.33	0.06	0.09
Spindelei	0.02	0.00	0.06	-0.14	**-0.38** **p=0.038**	-0.01	0.16	-0.05	-0.15	-0.18	0.18	-0.09	-0.01	-0.04	-0.06
Temora longicornis	-0.03	-0.34	-0.08	-0.28	0.11	0.06	**-0.53** **p=0.015**	-0.12	0.03	0.11	-0.12	**-0.39** **p=0.027**	**-0.36** **p=0.048**	0.10	-0.05
Tomopteris spp.	0.08	-0.03	-0.04	-0.05	0.15	0.05	**-0.44** **p=0.047**	-0.13	0.20	0.09	0.39	-0.17	-0.35	0.03	-0.05
Total zooplankton	-0.20	-0.01	-0.43 p=0.055	-0.02	0.01	-0.24	0.04	0.03	0.01	-0.06	-0.03	0.08	0.01	-0.11	0.25

Appendix 4 Evidence of relationships between meroplankton and benthic abundances

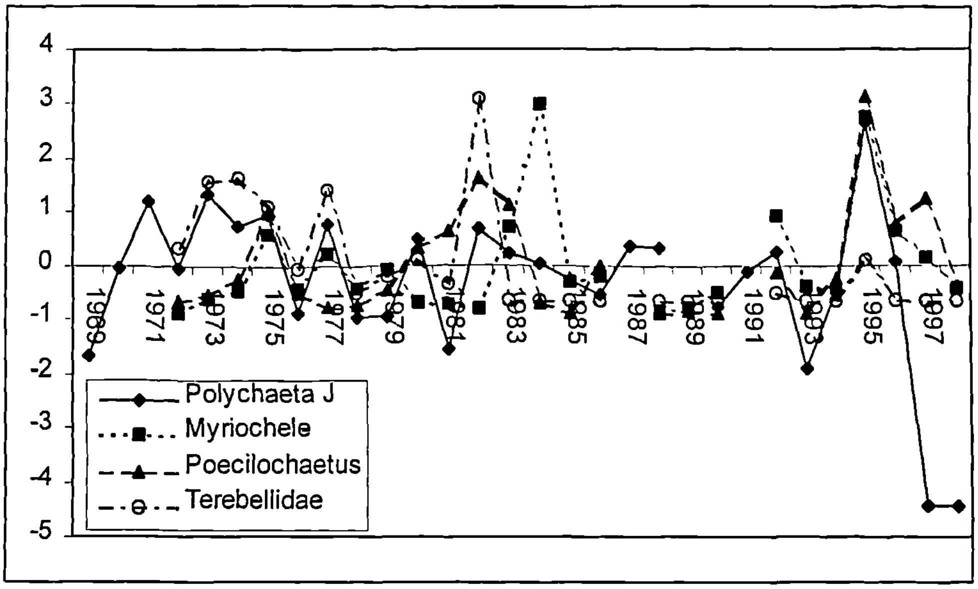
Standardised time series plots of polychaete meroplankton and M1 September genera:



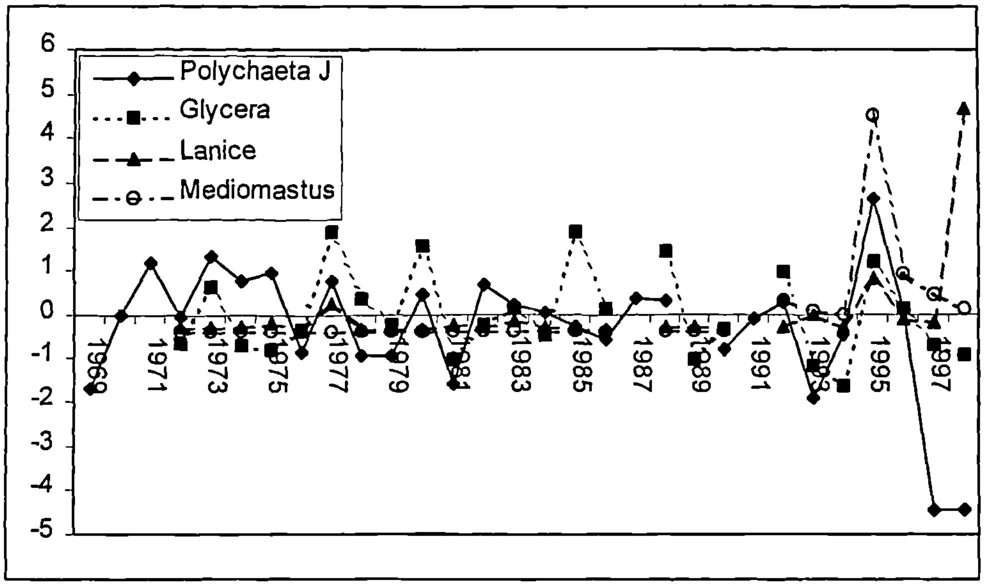
Dove polychaete juveniles and total Annelida



Dove polychaete juveniles and *Ampharete, Capitella, Diplocirrus*



Dove polychaete juveniles and *Myriochele, Poecilochaetus* and *Terebellidae.*



Dove polychaete juveniles and *Glycera, Lanice, Mediomastus.*

Correlation coefficients between annelid genera at M1 September and polychaete meroplankton.

	r	p
Ampharete	0.51	0.01
Capitella	0.56	0.00
Diplocirrus	0.51	0.01
Glycera	0.46	0.04
Lanice	0.52	0.01
Mediomastus	0.53	0.01
Myriochele	0.43	0.03
Poecilochaetus	0.56	0.00
Terebellidae	0.51	0.01

There are similar long term trends between annelids at M1 September and polychaete meroplankton genera. Note the peak in the benthos in 1995 and the similar peak in a number of meroplanktonic taxa. Similar peaks are observable in 1977 and 1980. The timing of the events, within a year means that high benthic abundances are resulting in increased abundance of meroplankton, as if increased meroplankton were causing the benthos we would expect a one to two year lag between cause and effect, like that between phytoplankton and benthos. The other series, M1 March and P showed no convincing evidence of associations with the abundance of meroplankton at zero, one or two year lags.

Appendix 5 Long term changes in North Sea benthos: discerning the role of fisheries

Full reference:
C.L.J. Frid & R.A. Clark. (2000) Long term changes in North Sea benthos: discerning the role of fisheries. In *The Effects of Fishing on Non-Target Species and Habitats*. (eds. Kaiser, M.J & S.J. de Groot). pp.198-216. Blackwell Science.

The main areas of contribution to this publication by R.A. Clark are the sections entitled; Introduction, Other long term factors influencing the benthos, & Medium-term changes in the benthos as revealed by time series.

Chapter 13

Long-term changes in North Sea benthos: discerning the role of fisheries

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Summary

1. Fishing occurs at the scale of ocean basins and has been going on for millennia. The scale and intensity of fishing has expanded in the last 100 years with the mechanisation of the fleet and the development of better navigational and vessel technology.
2. Fishing activities interact with the benthos through direct mortality of benthos as by-catch and net damaged organisms and inputs of organic matter in the form of carcasses and offal, and indirectly through alterations in sediment characteristics, altered sediment–water column fluxes, and changes in predation rates through changed abundance and size structure of populations of predatory fish.
3. Separating the effects of fishing from other long-term sources of variation in benthic communities is difficult. However, application of a precautionary approach to ecosystem management would suggest that action needs to be taken when there is sufficient weight of evidence.
4. Current data suggest reduced abundances of long-lived bivalves and increased abundances of scavenging crustacea and sea stars in the German Bight, and altered benthic community composition on at least some fishing grounds. There are also likely to have been major changes in the predation pressure applied by fish to the benthos. This suggests that both direct and indirect effects are manifested in the most intensively fished areas of the North Sea.
5. Managers must recognise that a healthy ecosystem is a requirement and aim of existing international agreements and a prerequisite for healthy fish populations. To date, fisheries management has failed adequately to protect the target species, we should now seek methods that also provide protection to the wider ecosystem and its functions.

Keywords: benthos, long term, indirect effects, fishing, direct mortality, fish predation.

Introduction

Ecosystems are continually changing, and these changes are driven by a multiplicity of factors. Some of these concern the internal dynamics of multispecies systems (see De Angelis & Waterhouse, 1987), while others are the result of abiotic extrinsic factors such as climate. Interactions between a diversity of internal and external factors and the fact that the responses to most are non-linear results in the complex behaviour of biological systems over time (De Angelis & Waterhouse, 1987).

The multiplicity of factors that affect ecosystems makes it difficult to assess both the relative importance of any single factor (their influence may itself be variable with time), anthropogenic or otherwise to the dynamics of the system. The most straightforward approach is the demonstration of changes in biological systems that occur in phase with changes in presumed causative factors (Pearson & Rosenberg, 1986; Buchanan & Moore, 1986b; Aebischer *et al.*, 1990; Austen *et al.*, 1991; Taylor *et al.*, 1992; Frid *et al.*, 1996; Frid & Huliselan, 1996). The existence of such correlations are not, however, powerful tools for identifying causative factors (Underwood, 1990, 1992, 1996). For small-scale phenomena, experimental approaches in which a single factor is manipulated in a controlled manner provide the strongest inferences regarding causality. However, such experimental approaches are on the scale of a few square metres at most, whereas marine systems cover areas of hundreds of thousands of hectares. Thus, such experimental investigations are not practical at both the large temporal and spatial scales of many marine systems (Mann & Lazier, 1991). Fishing has occurred in the coastal seas of the world for thousands of years and, as such, the ecological impacts of fishing may be both wide ranging and long term.

Impacts of fishing

The effect of fisheries on target species is well established (Pope & Macer, 1996; Rijnsdorp & Millner, 1996). Recent studies (see Bergman & van Santbrink, this volume, Chapter 4) demonstrate that the direct mortality caused by beam trawling, estimated as the total mortality associated with one fishing event, was species dependent and varied from 10% to 40% in gastropods, starfish, crustaceans and annelid worms, from 10% to 50% for the sea urchin *Echinocardium cordatum* and the masked crab *Corystes cassavelaunus*, and from 30% to 80% for a number of bivalves. At the population level, the mortality imposed by the trawl fishery will depend on the level of direct mortality, the trawling frequency and the overlap in spatial distribution between the fishery and the benthic organisms.

All net fisheries result in catches composed of target and non-target species, and individuals of the target species that are unmarketable, owing to size or other considerations. This material is generally returned to the sea as 'discards'. In addition, the processing of the catch at sea generates additional offal in the form of heads, guts etc. Seabirds feed on discarded fish and offal world-wide (Hill & Wassenberg, 1990; Wassenberg & Hill, 1990). Studies in the North Sea show that birds primarily take offal and discarded round fish and smaller proportions of flatfish, cephalopods and benthic invertebrates when these are discarded (Camphuysen *et al.*, 1993, 1995; Camphuysen & Garthe, this volume, Chapter 11). Discards that are not consumed at the surface may be taken in the water column by pelagic fish and marine mammals (Hill & Wassenberg, 1990; Wassenberg & Hill, 1990) or by benthic scavengers (Kaiser & Spencer, 1994; Ramsay *et al.*, 1996, 1998).

Although indirect ecosystem effects of fishing are less obvious than the direct effects, they may be more important in structuring benthic communities (Kneib, 1991). The indirect effects of fishing include changes in nutrient cycling caused by physical disturbance of the sediment–water interface and the addition of labile organic matter (discards and offal) to the system, the continued transfer of fixed carbon from the marine environment to the terrestrial system (Camphuysen *et al.*, 1995) and the changes in the food chain arising from manipulation of the density and size structure of the target populations (ICES, 1998). The benthos play an important role in remineralisation and release of nutrients to the water column (Rowe *et al.*, 1975). The rate of this remineralisation is critically dependent on the oxidation state of the sediment (Prins & Smaal, 1990; Sørensen, 1978). Physical disruption by towed bottom gears redistributes sediments and temporally alters the redox state of the system.

Exploitation of fish stocks has altered the abundance of fish in the seas and, frequently, the size composition of the fish populations (Pope *et al.*, 1988; Pope & Macer, 1996). Marine communities frequently exhibit size-structured food webs and these changes are therefore likely to lead to changes in the quantities and types of prey consumed. This phenomenon is often referred to as 'trophic cascades' and is well established for limnetic systems (Carpenter, 1988). In the marine environment, the greater difficulty of carrying out the necessary experimental studies means that the existence of trophic cascades has not yet been established, although a number of properties of marine communities suggest that they may occur (ICES, 1998).

Some of the most dramatic examples of ecosystem changes arising from fisheries exploitation of the controlling predators are the changes in the abundance and predation of krill in the Antarctic following exploitation of the baleen whales (Dayton *et al.*, 1995). Other examples that demonstrate a cascade of effects through the ecosystem following heavy fishing mortality or destructive fishing practices include the changes induced in the Californian kelp forests following hunting of the sea otters (Simenstad *et al.*, 1978; Estes, 1996), the changes in the intertidal areas of Chile induced by the removal of predators by fishers (Moreno *et al.*, 1986) and the changes induced by the rapid development of the demersal fishery in the Gulf of Thailand (Pauly, 1988). Yet these studies provide only indirect evidence of cause and effect and rely on inferential arguments and deductive reasoning, as it is difficult to establish the presence of true control areas for comparative purposes (Dayton *et al.*, 1995).

Taking account of the patchy distribution of beam trawl effort (e.g. Rijnsdorp *et al.*, 1998), studies of the annual direct fishing mortality rates on benthic invertebrates in the southern North Sea were estimated at between 7% and 45% of the individuals (de Groot & Lindeboom, 1994). Compared with the estimated percentage of the benthic production that is consumed by fish predators (~45%), the estimated direct fishing mortality rates are the same or lower. The combination of direct fishing mortality rates and indirect changes in predation pressure support the hypothesis that intensive trawling may have caused shifts in benthic assemblages from large, slowly reproducing species to small species with a high reproductive rate, e.g. polychaete species. The proliferation of polychaetes in the North Sea may have played a role in the increase in growth rate observed in some bottom-dwelling flatfish (de Veen, 1976; Millner & Whiting, 1996; Rijnsdorp & van Leeuwen, 1996).

Fish play a central structuring role in the ecology of many aquatic systems (Hansson, 1985). Alterations in fish abundance, size distribution, or spatial or temporal distributions can induce changes in other aspects of the ecosystem through changes in the strength or direction of the ecological links. In many marine ecosystems, there is evidence of species other than the prey that are influenced by changes in fish predation (Parsons, 1991, 1992, 1996; Verity & Smetacek, 1996; ICES, 1998).

Fisheries impose size-selective predation on the stocks and as such exploited populations tend to have different size spectra when compared with unfished populations (e.g. Pope *et al.*, 1988). There is also empirical evidence that the heavier the exploitation of a stock, the steeper the slope of the log numbers per size class vs. size relationship (Pope *et al.*, 1988; Rice & Gislason, 1996). The ICES (1998) considers this to be a useful indicator of changes in fishing effort, but notes that this relationship is sensitive to environmental changes that alter growth rates or may lead to species replacements. The ecological consequences of these changes are difficult to predict, but include altered predation rates as small and large fish rarely feed on the same prey (see below).

Fishing also alters the species composition of the fish guild. In the North Sea, populations of the benthic feeding gadoids, cod, haddock and whiting, have declined over the last 30 years or so (Pope & Macer, 1996; Serchuk *et al.*, 1996; Greenstreet & Rogers, this volume, Chapter 14). During the same period, populations of non-target species such as long rough dab, common dab and lemon sole have increased (Heesen & Daan, 1996). Therefore, there is a need to provide an assessment the consequences of these changes for the level of predation pressure exerted on the benthos and changed strength of ecological interactions within the fish guild.

Other long-term factors influencing the benthos

Fishing is not the only factor to influence benthic ecosystems on decadal, or longer time scales and at the basin-wide scale. Other influences that effect large areas over extended periods include climatic/meteorological factors and anthropogenic changes in nutrient levels. Meteorological factors tend not to exert a strong direct impact on deeper water (> 100 m) sublittoral benthic communities, as the water column moderates these effects. Intertidal communities are obviously affected to a greater extent by climatic and meteorological changes. During severe winters, overwintering mortality of macrobenthic fauna on tidal flats in the Dutch Wadden Sea was observed to increase (Beukema, 1992b). During a period of eight successive mild winters, overwintering mortality was reduced (Beukema, 1992a), and resulted in a more stable biomass of intertidal fauna. Buchanan & Moore (1986a) noted that overwintering mortality of the soft-sediment community at a depth of 55 m off the Northumberland coast was affected by winter minimum sea surface temperatures. Fluctuations in the benthic community structure of Weymouth and Poole Bay were recorded following the severe winter of 1962–1963 (Holme, 1983). Increases in swell from storms have been shown to disturb shallow benthic communities (Turner *et al.*, 1995) and Drake & Cacchione (1985, 1986) have noted that waves associated with storms may influence the benthos at depths in excess of 50 m, although the maximum depth will depend mainly upon the hydrography of the region.

Assessing the influence of climate is difficult and a number of proxy variables have been used. Amongst these are the position of the North Wall of the Gulf Stream and the North Atlantic oscillation (NAO) index. Both have been shown to be good indicators of the climatic conditions over large areas of the northern hemisphere (Taylor, 1996; Taylor & Stepens, 1998) and are correlated with biological parameters such as zooplankton abundance (Taylor & Stephens, 1980; Frid & Huliselan, 1996; Taylor, 1996), benthic biomass (Wieking & Kröncke, 1999) and vegetation (Willis, 1995).

Indirect effects of climate on the benthos are more commonly observed. Benthic infauna that are associated with soft sediments consume organic matter that descends from the pelagic zone (Pearson & Rosenberg, 1978). Most of this food source consists of phytoplankton that have settled out of the water column. Changes in the abundance of plankton are linked to large-scale climatic variables and associated changes in meteorological variables, which indirectly affect the food availability for benthic organisms and subsequently changes in their abundance and community structure (Pearson & Rosenberg, 1986). Such 'benthic–pelagic coupling' has been observed at many sites where long-term trends or sudden changes in the pelagic community have manifested themselves in the benthic community (Austen *et al.*, 1991; Buchanan, 1993). This intimate relationship between the benthos and pelagic food supply was apparent off the Northumberland coast, where a good correlation was observed between phytoplankton index and benthic abundance when a 2-year time lag was used. Austen (1991) also noted a change in benthic communities across the entire North Sea area between 1980 and 1981, which was 2 years later than the change in plankton community structure. Austen (1991) concluded that the associated change in plankton community structure was due to enhanced organic input. Postma (1981) has suggested that if there was a switch from a benthic to a pelagic food web, organic material could be transported from the central North Sea to coastal areas. Lindeboom *et al.* (1994) has postulated that the observed increase in coastal benthic biomass has occurred as a result of the utilisation of the majority of primary production in the benthos rather than the pelagic system.

Separating out the ecosystem effects of coincidental changes in climate and nutrient input is difficult unless long-term data are available for both. Eutrophication of the pelagic environment also affects primary production and therefore the amount of organic matter reaching the benthos. Josefson *et al.* (1993) noted that benthic biomass and abundance had doubled between 1974 and 1988 in the Skagerrak–Kattegat area. This was attributed to eutrophication. Parallel to and preceding the faunal changes, nitrogen and chlorophyll-*a* concentrations increased in the surface layer and were correlated with increases in agricultural run-off. Similarly, increased eutrophication in the Baltic has been linked to changes in pelagic production, and the subsequent increase in benthic biomass (Cederwall & Elmgren, 1980). Long-term changes in the ecosystem of the Wadden Sea have also been observed over the 1970–1990 period when the biomass and abundance of benthic invertebrates doubled at 15 stations. Eutrophication is also considered responsible for these changes (Beukema, 1992c).

Medium-term changes in the benthos as revealed by time series

The longest continuous marine sampling programme in the world is probably that of the continuous plankton recorder (CPR) surveys conducted presently by the Sir Alistair Hardy Foundation for Ocean Science (SAHFOS) (Warner & Hays, 1994). Recent analyses of the meroplankton recorded in North Sea CPR surveys have shown an increase in the dominance of echinoderm larvae (Lindley *et al.*, 1995), which has been interpreted as due to an increase in their relative abundance in the benthos. It has then been suggested that this may be the result of increases in the population of scavenging starfishes and ophioroids that have occurred as a result of food subsidies from fishing disturbance (Kaiser, 1996; Ramsay *et al.*, this volume, Chapter 10). However, the ability of the CPR programme to quantify plankton and especially meroplankton is limited and the timing of the change, in 1978, is well after the major changes in fishing technology. These, and the widespread nature of the increase in echinoderms in the CPR data, indicate that environmental causes are responsible rather than fisheries alone.

Effects of increased stress to the benthos attributed to fishing were observed in the central-western North Sea in the late 1980s (Frid *et al.*, in press (a)). Long-term monitoring of two benthic stations off the Northumberland coast has been carried out since 1971 (Buchanan, 1993) (Fig. 13.1). One station, located at a depth of 80 m (Station P), is located within a *Nephrops norvegicus* (Dublin Bay Prawn) fishing ground (subject to otter trawling), while the other station (Station M1) is located at a depth of 55 m on the edge of the fished area. Up to 1986, trends in the abundance of benthic infauna at both sites paralleled changes in phytoplankton index (with a 2-year lag to allow for growth to minimum sieve retention size (Buchanan, 1993), suggesting that benthic productivity was controlled by organic matter input (Fig. 13.2a). From 1986 until 1990 fishing effort increased within the *Nephrops* ground (Fig. 13.2b). This increase in fishing effort caused a decline in benthic abundance at Station P (Fig. 13.2b) and large-scale year-to-year changes in community structure indicative of a stressed community (Fig. 13.3) (Warwick & Clarke, 1993). These large year-to-year changes may be observed in Fig. 13.3, which shows year-to-year changes in Bray–Curtis similarity. Year-to-year changes at the less heavily fished Station M1, outside the *Nephrops* ground, continued closely to mirror changes in phytoplankton input throughout the time series (Fig. 13.2a). Furthermore, fluctuations in phytoplankton input had little effect on year-to-year changes in community structure at this site (Fig. 13.3), indicating a relatively unstressed community.

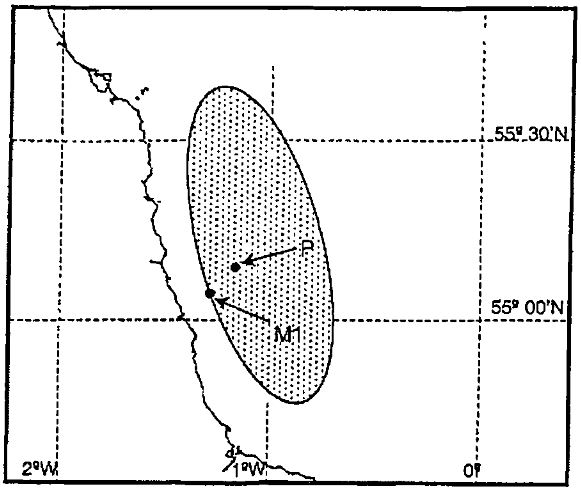

Fig. 13.1 Map showing locations of benthic sampling stations P and M1, off the north-east coast of England.

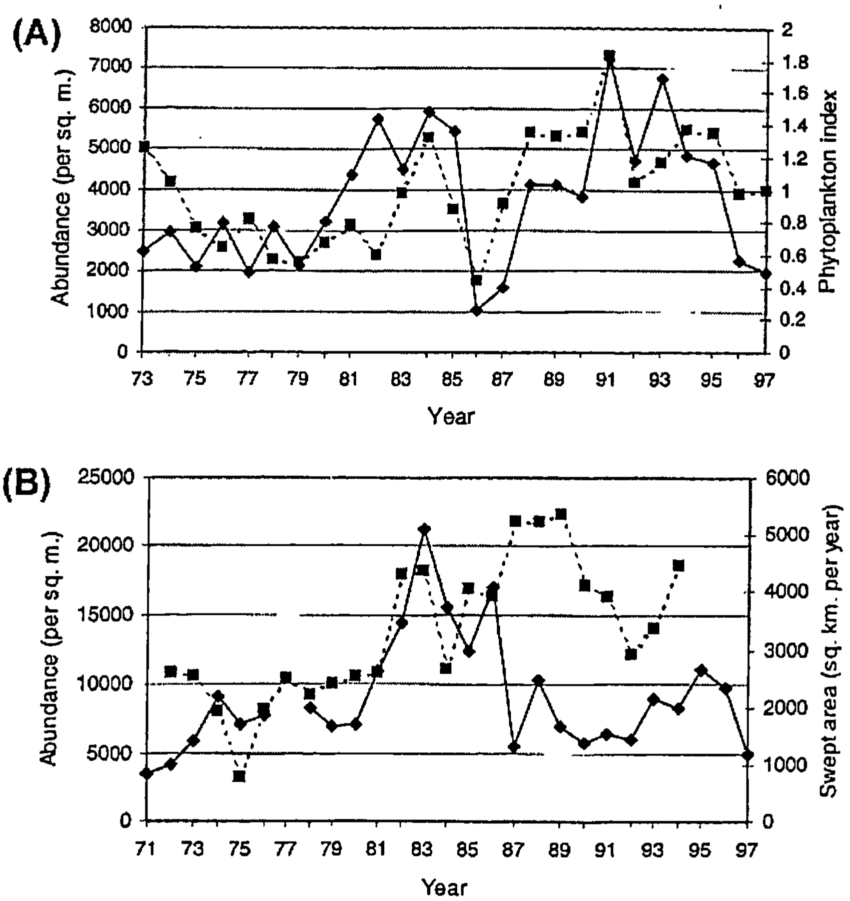

Fig. 13.2 (A) Abundances of individuals at Station M1 (continuous line) and CPR phytoplankton index (lagged by 2 years) (dashed line). (B) Abundances of individuals at Station P (continuous line) and fishing impact measured as swept area in the period 1972–1994 (dashed line).

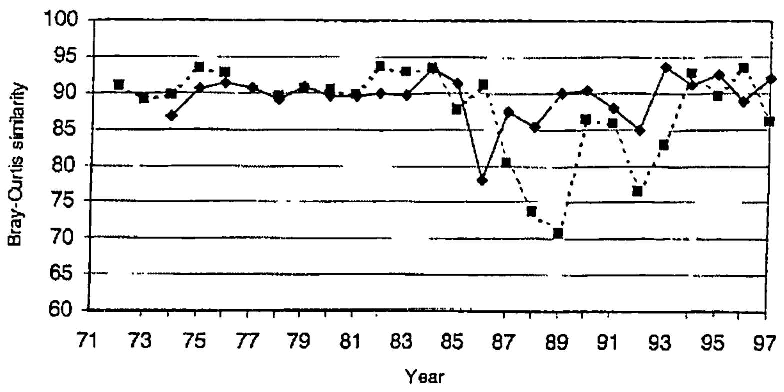

Fig. 13.3 Time series plot of year-to-year Bray–Curtis similarity for Station M1 (continuous line) and Station P (dashed line).

Long-term changes in the benthos as revealed by sampling

The North Sea has been one of the most intensively fished areas in the world over the last 100 years. It has also been the subject of early benthic ecological research. Some of the earliest quantitative benthic data were collected in 1920 (Davis, 1923, 1925). The *Dana* expedition in the 1950s provided another snapshot and, more recently, a series of research studies, e.g. ICES, the North Sea Benthos Survey (Kunitzer *et al.*, 1992), and pre-drilling studies for the oil and gas industries have provided greater coverage of the seabed fauna.

A number of authors have made historical comparisons based on these data. Rumohr & Kujawski (unpublished data) found that the German Bight macrobenthic community composition altered from the start of the 20th century compared with 1986 based on presence/absence records. Many of the taxa recorded in the early part of the century were bivalves, whereas, by 1986, scavenging crustaceans and seastars had increased in occurrence while bivalves were no longer prominent in the fauna. These patterns concur with the predictions of community change made on the basis of short-term trawl damage studies (Bergman & van Santbrink, this volume, Chapter 4). Similarly, Schroeder & Knust (1999) also examined long-term changes in the German Bight and concluded that fishing mortality had caused a decline in large, long-lived taxa, but that overall there had been an increase in total biomass as a result of increases in the abundance of opportunistic taxa.

Frid *et al.* (in press (c)) considered quantitative abundance in the macrofauna of five regions of both the central and southern North Sea (Fig. 13.4). They adopted a conservative approach to the 'quality control' of data and were still able to show definite changes in the macrofaunal communities in three of the five areas between the early 1920s and the late 1980s (Fig. 13.5). The lack of change in the remaining two areas was interpreted as evidence that the changes were not part of a broad-scale environmental change. One of the areas that showed no significant change included

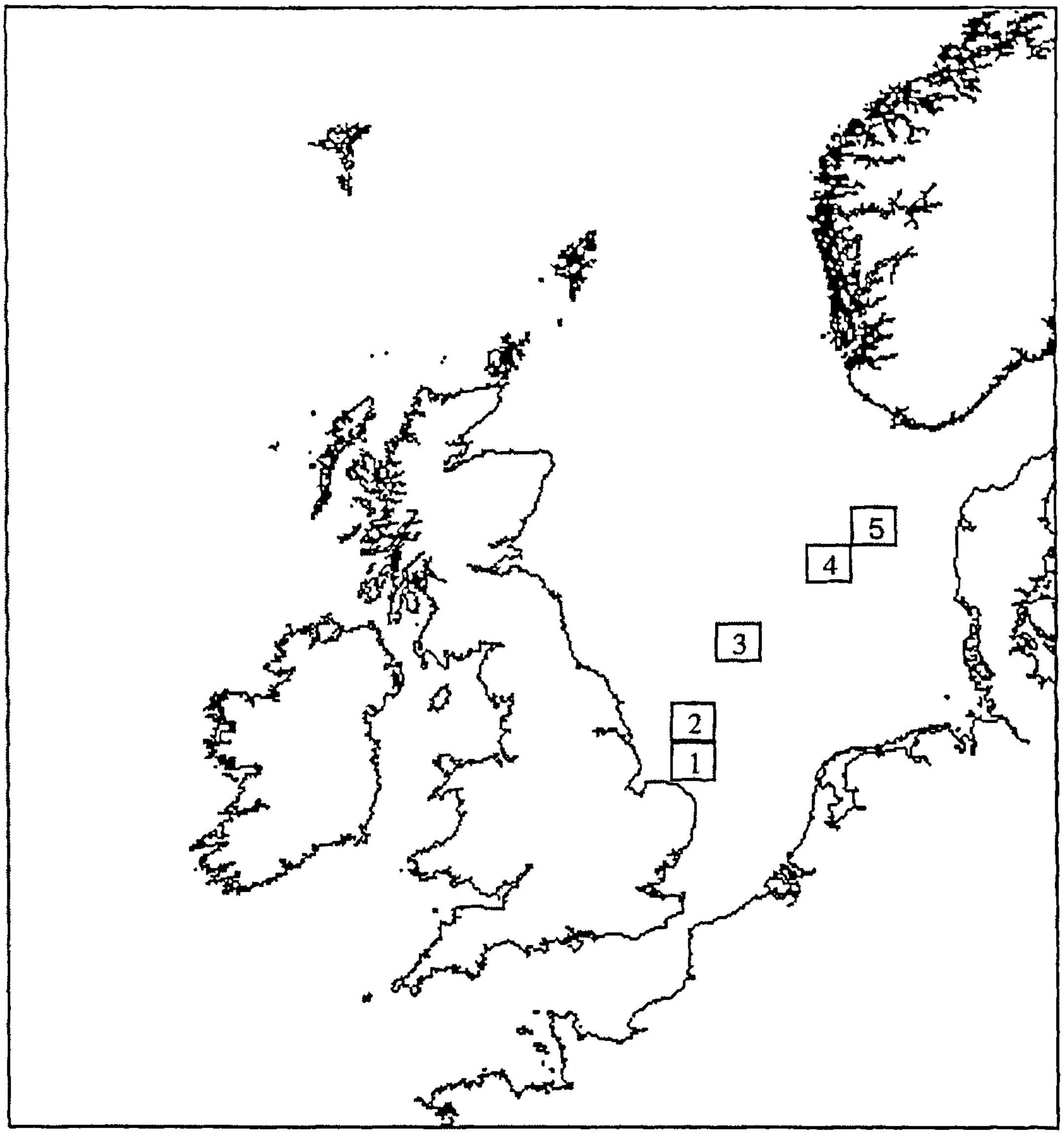

Fig. 13.4 Locations of the ICES statistical rectangles: (1) 35F1, Dowsing Shoal; (2) 36F1, Great Silver Pit; (3) 38F2, Dogger Bank; (4) Inner Shoal; and (5) 41F5, Fisher Bank.

much of the Dogger Bank, but this area may have already attained an alternative stable state as a result of fishing activities prior to 1920.

Kröncke and her co-workers (Kröncke, 1990, 1992; Kröncke & Rachor, 1992; Kröncke & Knust, 1995) have also studied the Dogger Bank benthos. They resampled stations sampled in the 1950s during the 1980s and found that many changes in faunal abundance occurred including the loss of *Spisula* spp. from certain areas. These changes were interpreted as responses to food availability due to eutrophication and/or climatic fluctuations but these authors were unable to make inferences about fishing effects.

In the German Bight, the taxa that were predicted to be most sensitive to fishing disturbance were changed most dramatically in response to fishing activity

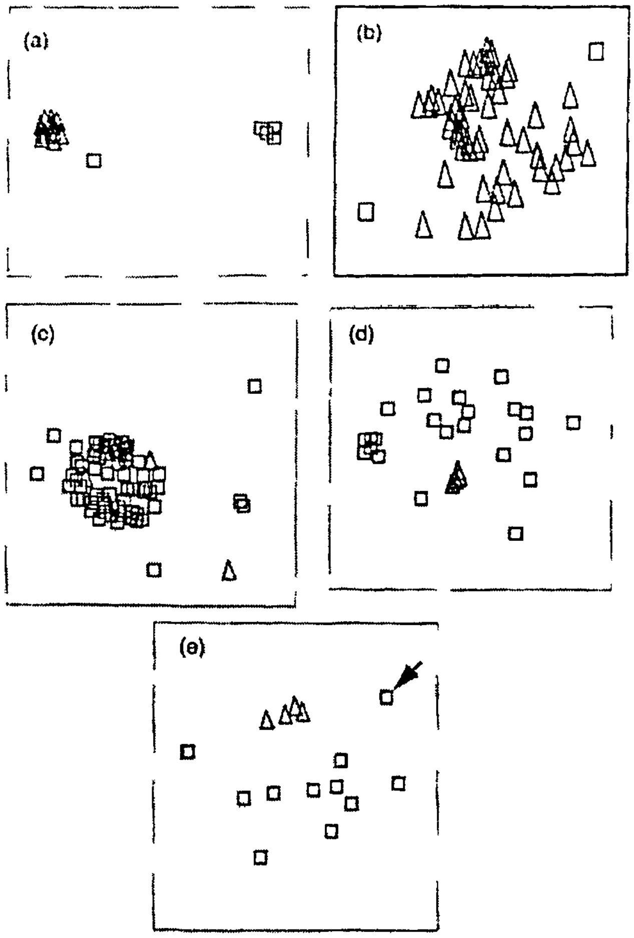

Fig. 13.5 MDS ordinations of the similarity in the composition of the macrobenthic community between the 1920s (Δ) and after 1986 (☐) in five ICES statistical rectangles: (a) 35F1, Dowsing Shoal, stress = 0.01; (b) 36F1, Great Silver Pit, stress = 0.20; (c) 38F2, Dogger Bank, stress = 0.22; (d) 40F4, Inner Shoal, stress = 0.17; and (e) 41F5, Fisher Bank, arrowed sample had a similarity (Bray–Curtis) of <5% to the remaining samples, stress = 0.12.

(Schroeder & Knust, 1999). However, in the three regions in which community changes were apparent they were associated with changes in the abundance of many taxa and not just those sensitive to the direct effects of fishing. Hence, in some areas, the indirect effects of fishing (sediment changes, nutrient flux, predation pressure) may be at least as important as the direct effects.

Long-term changes in predation pressure

Fish predation is commonly seen to be the principal way that fish influence benthic communities (e.g. Whitman & Sebens, 1992; Sala & Zabala, 1996; Sala & Boudouresque, 1997). Benthic feeding fish do not take prey in proportion to their availability; rather they exhibit some degree of selection (e.g. Packer *et al.*, 1994), thereby altering relative abundances of benthic species. The removal of preferred prey may release resources for utilisation by other, less preferred, species while the act of predation may cause small-scale physical disturbance to the system and contribute to the spatial heterogeneity of the benthos (Hall, 1994). The most incontrovertible evidence of these effects comes from experimental studies that have shown that fish predation can act to control both the number of individuals in the system and the relative abundance of the species (see Wilson, 1990). Other controlling factors, such as physical disturbance, emigration, immigration or benthic predators, have been shown to be equally or more important than fish predation (e.g. Ambrose, 1984, 1991). Commercially important species can also structure the benthic community through indirect interactions, such as by predation on in-coming benthic larvae (Langton & Robinson, 1990).

By combining datasets on the abundance (Figs 13.6 and 13.7), size frequency and size-specific diet of North Sea fish, it has been possible to evaluate predation pressure over the period 1970–1993 for the eight most abundant demersal fish species (ICES, 1998; Frid *et al.*, in press (b)). Although target fish populations (gadoids and plaice) have declined, the overall estimated level of predation on the benthos has increased from around 23 Mt year^{-1} in 1970 to 29 Mt year^{-1} in 1993 (Fig. 13.8).

Frid *et al.* (in press (b)) have demonstrated that the consumption of North Sea benthos may have changed as stock sizes have changed. The principal factor influencing fish stock size of exploited species is fishing, and the expansion in the, non-target, dab population may be due to competitive or predatory release. Fishing has removed the larger gadoids that are principally piscivorous, and has allowed expansion of flatfish and young gadoids that prey upon benthos to a larger extent. However, the differences in diet of various species would also appear to have influenced the composition of the benthos consumed. Overall, crustaceans have declined in dietary importance, while echinoderms (predominantly ophioroids) have increased. The effects of fish predation on benthic communities are not well documented. The intensity of fish predation on North Sea benthos found by Frid *et al.* (in press (b)) (20–45% of the production is consumed by fish) is similar to the 39% of macrobenthic consumption consumed by fish estimated for this area by Greenstreet *et al.* (1997).

The challenge

Society expects to be given guidance on whether there is a need to provide management of the marine environment over and above that to manage target stocks, and yet scientists are reticent about making such statements, as the system is not readily amenable to experimental manipulation. The precautionary approach has been accepted as a guiding principal for fisheries management (Garcia, 1996; ICES, 1998) and carries with it an implicit integration of fisheries and ecosystem management. It also seeks to act when the available data indicate the possibility of

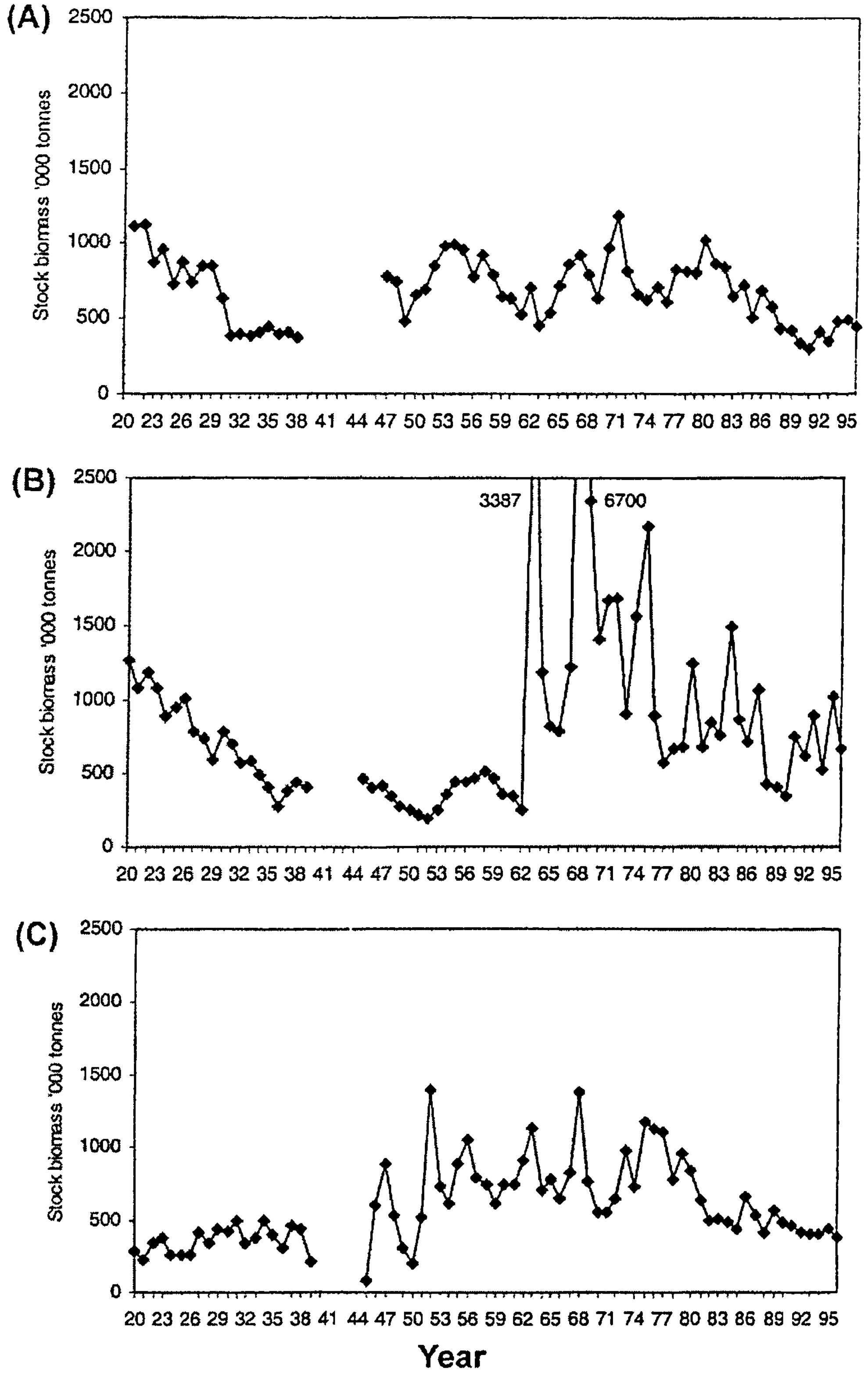

Fig. 13.6 North Sea stock biomass (kt) of: (A) cod; (B) haddock; and (C) whiting, from 1920 to 1996.

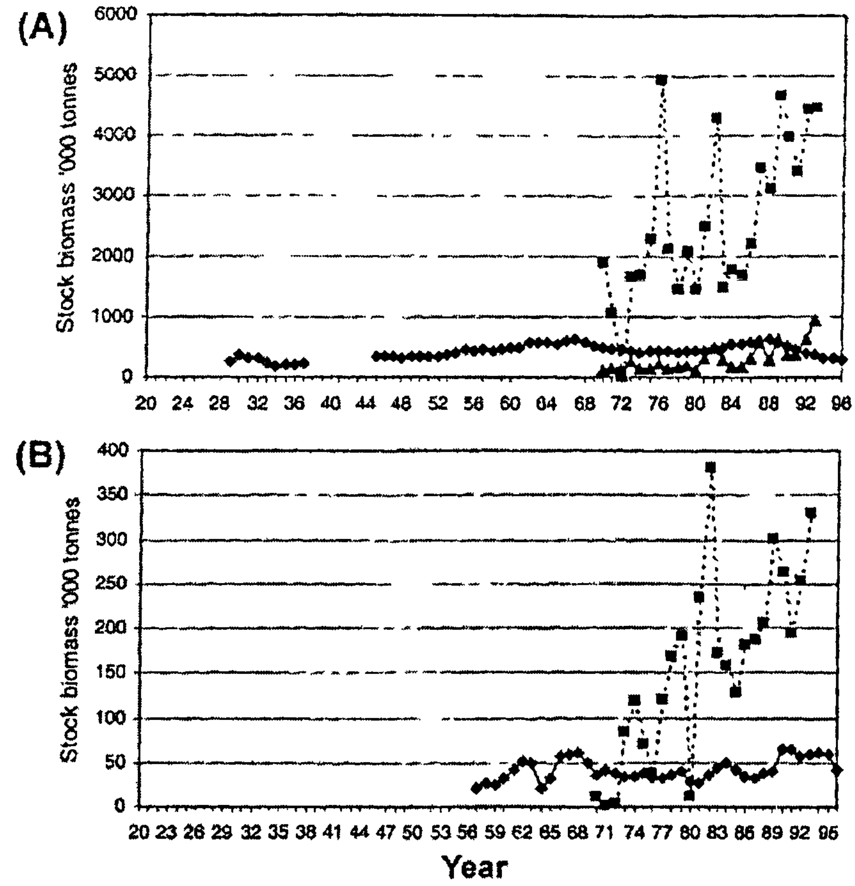

Fig. 13.7 North Sea stock biomass (kt) of: (A) plaice (continuous line), common dab (dashed line) and long rough dab (dotted line); (B) sole (continuous line) and lemon sole (dashed line), from 1920 to 1996.

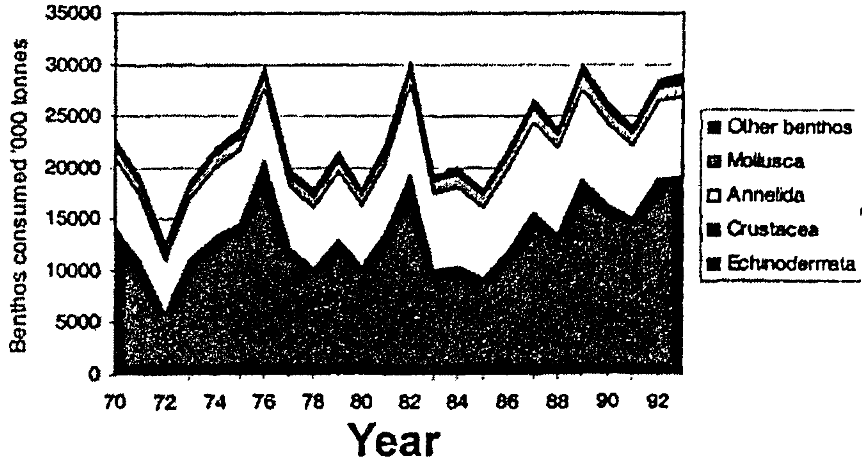

Fig. 13.8 Estimated total consumption of benthic food by eight species of demersal feeding fish in the North Sea, 1970–1993.

irreversible damage rather than needing the full demonstration of proof of a negative effect. Our inability to carry out scientifically rigorous experiments at the appropriate time and spatial scales should not hamper the incorporation of genuine concerns into policy. Fisheries and ecosystem managers will need to respond to a weight of evidence from studies that individually do not establish a cause and effect relationship, but that when taken together suggest a likely cause.

Discussion

A critical evaluation of the role of fishing in bringing about long-term changes in marine ecosystems is difficult to achieve. There are many studies that now show changes in the macrobenthos over the last 30 or so years. In many cases, these changes are linked to climatic influences on changing supplies of food (Buchanan & Moore, 1986a; Kröncke, 1990, 1992; Austen *et al.*, 1991; Buchanan, 1993; Kröncke & Knust, 1995). Such changes tend to occur over decadal time scales.

Extending such investigations back in time is hampered by the quality of the data available. Stretching throughout the history of mechanised fishing, there is now a body of data that suggests community changes arising from both direct fishing mortality and indirect effects of fishing (Frid *et al.* in press (a, c)). The latter includes changes in benthic water column fluxes of nutrients. The importance of benthic processes to phytoplankton productivity is well established (Rowe *et al.*, 1975; Prins & Smaal, 1990), as is the direct link of phytoplankton production to benthic ecology (Pearson & Rosenberg, 1986; Buchanan, 1993). Fishing perturbs both sides of this equation, physically altering sediments and flux rates, thereby causing direct and indirect changes in benthic abundances.

To date, in spite of sound science, we have failed to prevent overexploitation of just about every fish stock, the challenge now is to manage the ecosystem sustainably, based on incomplete knowledge of its functional processes and response to fishing. How can such management be achieved? Clearly, while marine reserves have an important role in protecting key sites, they are not feasible on the scales required definitely to preserve ecosystem function. Reductions in effort required to meet sustainability targets on exploited species will contribute, but we believe that, ultimately, specific measures will be needed to address ecosystem concerns. Firstly, changes in gear design to increase selectivity and reduce incidental mortality/damage, and secondly, a more diverse fishery – less heavy exploitation of a key stocks, and more equitable use of the available productivity of the marine ecosystem.

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