THE UNIVERSITY OF HULL

The Structure and Functioning of the Fish Assemblage of the Humber Estuary, UK.

being a Thesis submitted for the Degree of PhD

in the University of Hull

by

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SUMMARY

This study provides an assessment of the fish assemblage of the Humber estuary, using a quarterly sampling interval. Sampling 14 subtidal stations throughout the estuary, and two intertidal sites in the outer estuary, the principal aims of the study were to determine the structure and functioning of the assemblage and the environmental and biological factors influencing the fish distribution.

Chapter 3 examines the spatial and temporal trends in dissolved oxygen, salinity, temperature and turbidity within the estuary. Each parameter shows different degrees of variability within the estuary, with temperature having little spatial variability but a large temporal one, while variations in salinity are more spatial than temporal. Concentrations of dissolved oxygen were positively correlated to salinity, being greatest towards the outer estuary. Turbidity, however, was negatively correlated to salinity, with the turbidity maximum occurring in the upper estuary, between Hull and Whitton. It is concluded that the water quality of the study area is 'good', such that there was no barrier to fish movement established at any point during the study period.

Chapter 4 gives the community structure and distribution of the fish populations, and illustrates the usage of the estuary by the different species. The ranking of the species by percent occurrence indicates that four species, goby (18.4 %), whiting (15.6 %), sole (12.3 %) and flounder (10.6 %), were dominant, accounting for more than 50 % of the recorded presences. The number of species caught per sampling occasion shows a seasonal trend depending on area, with the outer and lower estuary showing an increased diversity in summer in contrast to an increase in winter within the middle and upper estuary. This demonstrates the greater number of summer migrants using the estuary, and marine species occurring during the summer months.

Chapter 5 gives an analysis of the interactions between chapters 3 and 4, and details the influence of the environmental factors on the fish distribution. The analyses indicate that salinity is the dominant factor influencing the distribution of the species, with temperature also having a major influence. Turbidity did not influence the composition of the fish assemblage. Temperature and salinity fluctuations appear to influence different aspects of the community, with temperature proving to be the best predictor of total abundance, while salinity influenced the species richness and total biomass.

Chapter 6 gives an analysis of growth and production within the estuary. There is a loss of material, or negative production, within the estuary, although this does not appear to be related to a reduction in the growth rate of the dominant species. However, as juvenile and seasonal migrants and marine adventitious species form a large proportion of the species within the estuary, it is likely that the apparent loss of production is the result of the migration of adult fish from the estuary. The effects are enhanced by the relatively long sampling intervals.

Chapter 7 gives the dietary analysis of the fish, and assesses the inter- and intra-specific interactions within the estuary. With the exception of sprat, herring, brill and small pogge, all of the species have an opportunistic diet. Despite this, there is little evidence of niche overlap between the species and size classes, indicating that resource partitioning may occur. This occurs through varying proportions of each prey item within the different diets, e.g. the brown shrimp, *Crangon*, occurs in the diet of several species but is more common within the diet of large flounder and whiting, cod and sea snail. Gammarids and mysids form the dominant prey within the foodweb, occurring within the diet of most of the species.

Chapter 8 investigates the health of the population through an assessment of the occurrence of abnormalities and parasites within the fish, together with the analysis of the bioaccumulation of copper and zinc within the tissue. The Humber populations do not appear to be adversely affected by pollutants, with copper concentrations within the tissue being below the recommended guidelines for human consumption, with the exception of copper concentrations within sole liver. Zinc concentrations within the liver exceed the guidelines. Levels of abnormalities are also similar to other, comparable estuaries, with the exception of colouration abnormalities in flounder (11.57 % in the Humber cf. 2.3 % in the Thames). Parasitism within the Humber had an effect on the condition of whiting and the reproductive potential of pogge only.

Chapter 9 firstly gives a summary of previous chapters and a general discussion of the fish assemblage, this is followed by an assessment of management options. The data indicate that the Humber forms an important nursery and feeding area for the North Sea fish populations, and is therefore sensitive to environmental degradation. The areas of greatest sensitivity are the sandflats within the outer estuary, which form a nursery area for plaice and dab and a feeding ground for sole, and the mudflats on the south bank between the Humber Bridge and North Killingholme, which act as important feeding areas for several species including sole.

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1 GENERAL INTRODUCTION

1.1 Estuarine Ecosystems

The structure of inshore and estuarine communities have been extensively studied and the importance of estuaries as spawning, nursery and feeding areas for marine fish is well documented (e.g. McLusky 1989; Haedrich 1983). The structure of the inshore planktonic, benthic and predator communities are well known although recent and on-going studies are attempting to quantify the functioning of the system (e.g. Elliott & Ducrotoy 1991; Hall & Raffaelli 1991). The functioning of estuarine systems refers to the time-dependent biological interactions between and within each part of the food web (Matthews *et al.* 1982), whereas the structure is the composition of the biological community.

An understanding of the community structure and population dynamics within an ecosystem is important when assessing the effects of anthropogenic factors. This is particularly relevant in estuaries given man's increased usage of these areas for both industry and recreation. Estuarine fish communities have been studied in many areas, both with respect to community structure (see Haedrich 1983) and the functioning of the community (e.g. Creutzberg & Fonds 1971; Fonds 1979; Gibson *et al.* 1993).

1.1.1 Estuarine Characteristics

Estuaries are characterised by a large variation in physical and chemical parameters. Physicochemical parameters such as salinity, temperature, turbidity, dissolved oxygen and tidal amplitude vary throughout the estuary along longitudinal (axial) gradients, while others also show lateral gradients, e.g. depth, current velocity and sediment composition (Moreira *et al.* 1992). With the exception of turbidity, the variables that follow longitudinal gradients tend to decrease with distance from the mouth. Similarly, lateral gradients tend to decrease towards the intertidal areas.

In some estuaries the substratum is also characterised by a gradient within the estuary, showing an increase in the silt content with distance from the mouth (Rodrigues & Quintino 1993). Organic enrichment follows a similar gradient, together with a lateral increase towards the intertidal areas. Gravel is more common in the mouth of the estuary, thus a general decrease in particle size can be seen with movement upstream (Pethick 1984). The substratum may also be subjected to erosion and deposition on a tidal (spring-neap) or seasonal basis (erosion from upstream areas in winter, deposition during the lower flows of summer). In addition, storm events can produce large changes in the substratum (Rees *et al.* 1977).

1.1.2 Estuarine Biota

Estuarine communities show temporal and spatial variability (Elliott & Ducrotoy 1991). The spatial differences are from small to large scale, through substratum variability, intertidal/depth variability, axial (up/down estuary) variability, to near and far scale geographical variability based on biogeographic divisions and climatic conditions. The gradual transition between each of these produces continua rather than discrete communities (Begon *et al.* 1986). Similarly, temporal variability can be from semi-diurnal, fortnightly and lunar, based on the tidal regime, diurnal, based on the light and temperature regime, to seasonal (intra-annual), annual and longer-term cycles based on population interactions and long-term environmental/climatic change. However, although the structural and functional changes over these sources of variability are known for some areas on a qualitative or semi-quantitative basis, the knowledge of the processes is incomplete on a quantitative or predictive basis. Each of the above factors responsible for spatial or temporal variability may be regarded as contributing to the overall 'noise' in the system. It is against this background noise that any impact due to man's activities has to be determined.

The physical and chemical nature of estuaries produce a naturally stressful area for organisms such that the resident invertebrate populations are typically of low diversity (McLusky 1989). The environmentally harsh conditions enable colonisation by organisms which are euryoecious, i.e. have wide environmental tolerances, and which are therefore able to tolerate perturbations, both natural and anthropogenic. These features result in large populations of few prey species, enabling the estuary to support large populations of predatory fish (Haedrich 1983).

Estuarine gradients affect the diversity and abundance of benthic invertebrates (Mees *et al.* 1993). There is an increase in diversity towards the mouth of the estuary, although the populations of each species are less abundant. The subtidal macrofauna is affected by the substratum (Elliott & Kingston 1987; Rodriques & Quintino 1993), which is directly affected by the hydrophysical regime, thereby demonstrating the primary importance of the physical characteristics of the area, as well as the water quality. The macrofauna within estuaries can be separated into two main groups, one comprising taxa essentially found near the mouth, the other occurring further upstream (Rodriques & Quintino 1993).

There can also be large differences between intertidal and subtidal invertebrate populations in estuaries. The subtidal bed populations may have a greater species richness but lower abundance and biomass in comparison to intertidal populations, especially in the lower reaches (Elliott & Taylor 1989(a)). Thus an increase in water depth, resulting in an extension of the subtidal areas at the expense of the intertidal, will affect the availability of prey for the fish population. Similarly, the loss of any intertidal area through poor water quality, waste disposal or land claim will have a disproportionately large effect on the fish (McLusky *et al.* 1992).

The spatial and temporal variability in the biological characteristics found in estuarine areas are the result of both environmental and biotic interactions, with the environmental constraints including both natural and man-induced features. The system is more complicated as it involves several media - water and substratum, together with aerial exposure in the case of intertidal areas for invertebrate prey organisms. While most estuarine organisms have wide environmental tolerances regarding temperature and salinity (McLusky 1989), the assemblage tends to be formed by the physical characteristics of the area superimposed with biological characteristics, e.g. the effects of the sediment on food availability, predator-prey relationships and the supply of colonising organisms.

1.1.3 Estuarine Fish

The low diversity but high abundance of organisms noted within the benthos is also reflected in estuarine and inshore fish populations. On any single sampling period, there is often a species-poor community found within estuaries (Henderson 1989). However, when considered over the year, the estuarine fish assemblage is complex and includes several ecological types of fish, each of which rely on the estuary for different seasons, parts of their life cycle, etc., e.g. resident species, seasonal, juvenile and diadromous migrants and freshwater and marine adventitious species (Elliott & Taylor 1989(b); Elliott *et al.* 1990). It is likely therefore that a temperate, NW European area may contain 60-80 species based on various sampling methods and a long sampling period (Henderson 1989; Dewailly 1994).

Of greatest importance to man is the fact that many marine commercial species utilise estuaries as nursery and feeding areas and thus any loss of estuarine area can have repercussions for commercially fished stocks (Elliott *et al.* 1990). These stocks may be within the estuary, or in the near or far coastal zone. In addition, estuaries have an important role as a migration route for diadromous fish species which are on passage between fresh and marine waters, e.g. salmon, sea trout and eels (e.g. McDowall 1988). Many of these species are also commercially important.

The main estuarine water quality parameters, in particular salinity, temperature, turbidity and dissolved oxygen are known to affect fish distribution (Blaber & Blaber 1980). In addition, sediment characteristics, substratum heterogeneity and vegetation will influence fish distribution through, e.g. prey availability and protection from predators. Species richness will also be affected by the complexity of the environment. It is therefore important to assess the fish in relation to the sedimentary and water column features. Any change in the bathymetry and sediment structure will affect the supporting substratum for species such as sandeels (*Ammodytes* spp.) and the food availability for benthic feeders, e.g. flatfish. It is also important to assess the spawning and nursery areas within the estuary.

Fish distribution within the estuary is also related to prey availability, with fish concentrating in areas containing large food resources, although poor water quality can act as a barrier, causing the fish to congregate in areas with lower food availability but better water quality (Marchand 1993). Many species use estuarine areas, particularly the intertidal mudflats, for feeding, e.g. plaice and flounder (Ansell & Gibson 1990), the estuarine fishes of North America (de Sylva 1975) and the Wadden Sea fishes (Kühl & Kuipers 1979). The high benthic productivity of this area (Elliott & Taylor 1989(a)), together with the protection from visual predators afforded by the high turbidity (Blaber & Blaber 1980), therefore results in many species using estuaries as nursery and feeding grounds.

1.1.4 Impacts of Pollutants

Industries are traditionally situated along the banks of rivers and estuaries from which they have access to a dependable water source for plant operations, a means to remove any contaminants produced, good transport links and cheap, available land. While legislation has resulted in a decrease in the concentrations of persistent pollutants, e.g. heavy metals (McLusky 1989), many estuaries can still be regarded as polluted areas. However, monitoring of the inputs to the North Sea indicates that inputs of heavy metals from the east coast of England decreased considerable between 1975 - 1990 (ICES 1993), demonstrating the effectiveness of legislative measures.

The amount of deformities and disease found within fish can be regarded as an indicator of the 'health' of the population (Clark & Topping 1989). Deformities are an easily assessed indication of stress within the fish assemblage. At a more complex level, the concentrations of pollutants within the flesh of the fish are measured in order to determine possible effects to predators, including man, through bioaccumulation (Sindermann *et al.* 1980; Elliott *et al.* 1988). An analysis of contaminating substances within the tissues can also be used to determine possible factors responsible for any diseases, or other changes to the biology of the organisms, noted, thereby complementing earlier analyses.

Within estuaries, the main forms of toxic chemicals are heavy metals, -drins, oils and polychlorinated biphenols (PCBs), all of which have been related to the prevalence of abnormalities. The relationship between heavy metals and vertebrate deformities (Bengtsson *et al.* 1985), lesions and histological damage (Eisler & Gardner 1973) has been demonstrated, while Dethlefsen (1989) highlighted the dumping of titanium dioxide waste as a contributing factor to abnormalities in dab in the German Bight. However, other studies have pointed to environmental factors, i.e. low dissolved oxygen and salinity and high temperatures, as contributing to the presence of abnormalities in fish, thereby resulting in conflicting views about the degree of damage caused by xenobiotic compounds (e.g. Bucke 1993).

1.2 The Humber Estuary

An understanding of the structure, functioning and health of fish populations within any area, especially one as variable as an estuary, requires a knowledge of the physical, chemical and biological nature of the area. The physical constraints and characteristics will determine which fish can live in an area, based on the environmental tolerances of each species. Superimposed on this, the biological interactions of, for example competition and feeding, will then produce the fish community supported by the area.

1.2.1 Physical Characteristics

The Humber estuary, hereafter referred to as the Humber, is defined for the purposes of this study as the area east of Trent Falls, and is approximately 62 km in length. It varies in width from 1 km at Trent Falls to 8 km at Spurn giving the typically triangular shape of a macrotidal estuary, and is the third largest estuary in Britain (Davidson *et al.* 1991). It has the largest catchment area in Britain, 26,000 km^2, approximately 20% of the area of England, with a resident population of about 11 million, or 23% of that of England (Fig. 1.1) (Gameson 1982).

A macrotidal estuary, the Humber has a tidal range of 7 m, the largest on the east coast of Britain (Denman 1979), with the tidal limit extending into the Rivers Trent and Ouse. The mean depth at low water is 6 m below Chart Datum, ranging from 4 m at Brough, to 14 m in the deep water channel off Spurn Point. This varies continually through accretion and erosion of sediments. The resultant movement of the channel can lead to difficulties with regards to shipping, and is countered through dredging, e.g. near Spurn Point, or the use of 'stone piles' to influence the tidal flow,.e.g. near Read's Island (Fig. 1.1).

The Humber has a stronger flood than ebb tide promoting a net landward movement of the sediment, and resulting in a large reservoir of mobile sediments (Pethick 1988). The estuary has high concentrations of suspended solids, up to 5 $g\ l^{-1}$ (Pethick 1990), which are affected by the state of the tide and tidal cycle, with higher concentrations of suspended solids being observed during tides rising towards springs (Denman 1979). The highest levels of suspended solids are found between the Humber Bridge (Pethick 1990) and Trent Falls (NRA 1993). This corresponds to the area of maximum salt intrusion, near Brough in the upper estuary (Denman 1979). There is also a vertical turbidity gradient, with turbidity at any one point increasing considerably with depth (NRA 1993).

Constant movement of sediment, both into and around the estuary, has resulted in the lack of a permanent muddy and mixed substratum bottom, leading to an unstable area for the fish, with large scale changes in habitat possible over a short time period, for example the removal of the top sediment from intertidal areas, or the deposition of silt on sandy areas (pers. obs.). This has produced an estuary

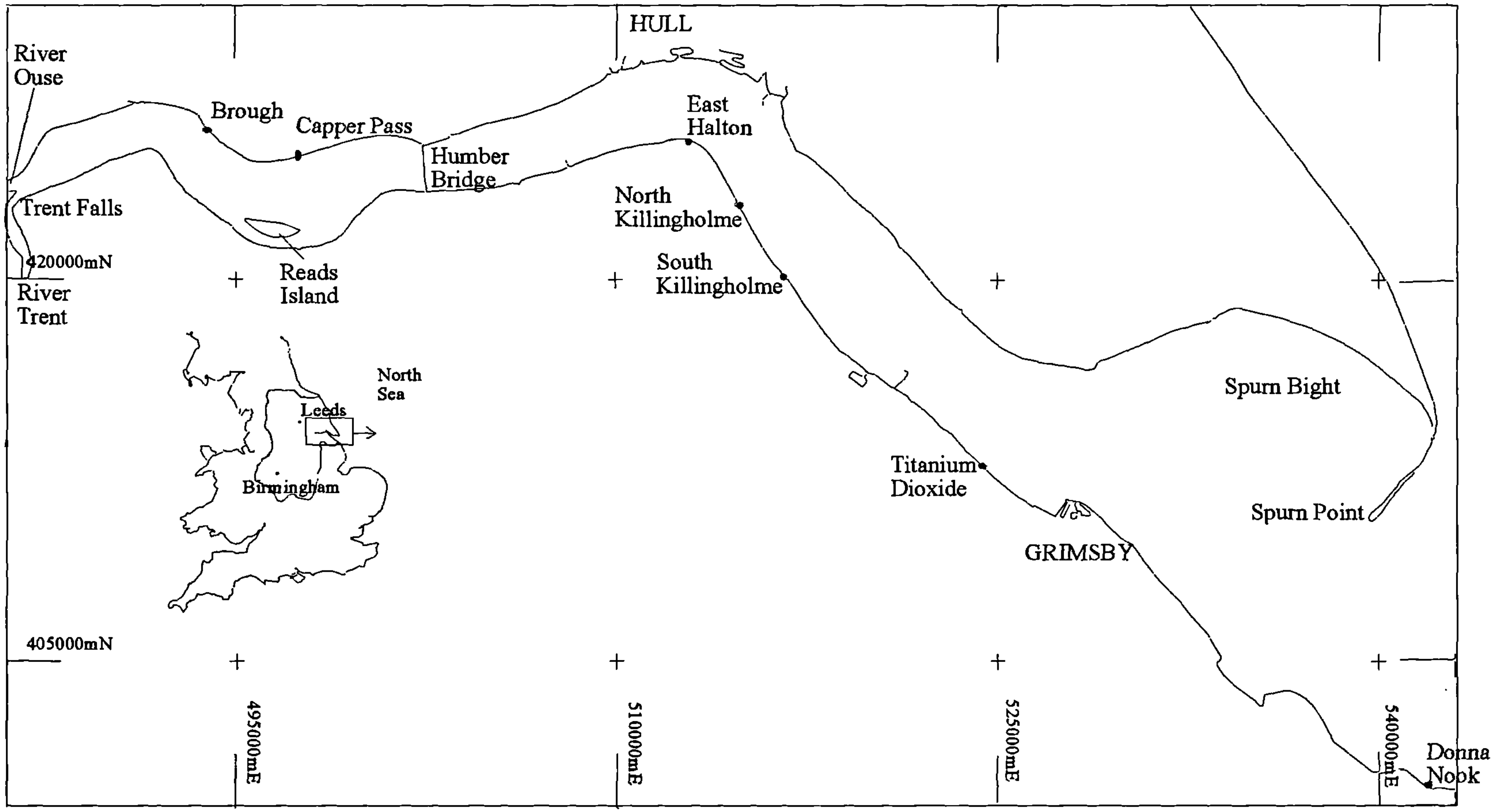
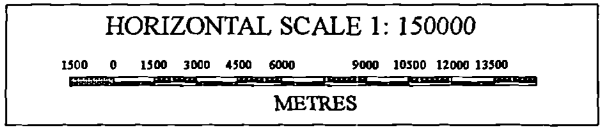


Fig. 1.1 Location of key sites within the Humber estuary



in which concentrations of suspended material are greater than those found in many other estuaries, values of 2 g l^{-1} being common during the winter (Pethick 1990). There are also rapid accretion rates of the sediments in many of the intertidal areas as a result of these features.

The estuary has extensive intertidal areas, with approximately one third of the estuary exposed at low water, although the greatest of these are at Spurn Bight on the North shore, a predominantly muddy area, and Grimsby to Donna Nook on the South shore, a predominantly sandy area (Davidson *et al.* 1991). The outer sand areas have dune systems at their land margin whereas there are salt marshes at the upper limits of the mud flats. Between the 17th and 19th centuries 25% of the intertidal areas were removed through land-claim, with other land-claim cases proposed which will affect the estuary and result in a further loss of estuarine habitats.

Current velocities within the Humber can be extremely high, although varying axially, laterally and with depth, as well as the time of the tide (IECS 1987). Velocities increase on the flood tide, along the length of the estuary, due to the tidal asymmetry, and can reach a maximum of between 2 and 3 m $second^{-1}$.

The extensive width in relation to the shallow depth has produced a vertically well mixed estuary, with a salinity range at high water of 3 psu to 33 psu between Trent Falls and Spurn Point (IECS 1987). A slight vertical halocline exists to the seaward section of the middle estuary, with a range of approximately 5 psu between the top and bottom of the water column. A further salinity gradient exists across the width of the estuary, with the higher salinities being recorded on the North bank, due to water movement caused by the Coriolis force.

1.2.2 Pollution Inputs to the Estuary

The catchment area covers the main industrial areas of the Midlands, West Yorkshire, Greater Manchester and Lincolnshire, thus receiving a wide range of chemical and biological pollutants from riverine sources. In addition, there are domestic and industrial conurbations within the estuary, e.g. sewage outfalls, chemical factories, including Titanium Dioxide plants, and contamination from an old smelting works at Capper Pass (Fig. 1.1) (NRA 1993). Concentrations of heavy metals within the Humber have been monitored for several years, with dissolved copper concentrations up to 280 $\mu g\ l^{-1}$ recorded, together with 54.5 mg kg^{-1} suspended particulate metal (NRA 1993). Zinc concentrations of 12.6 $\mu g\ l^{-1}$ and 496 mg kg^{-1} respectively were also observed. This compares to concentrations of copper and zinc within the sediment of 71 mg kg^{-1} and 352 mg kg^{-1} respectively. The impact of heavy metals on benthic invertebrates has also been assessed (e.g. Fernandez 1983; Ozoh 1986; Vowles 1994), and therefore analysis of heavy metals within this study will provide a continuation of this monitoring.

The concentrations of most heavy metals within the Humber are below the Environmental Quality Standards (EQS) set by the NRA (NRA 1993). The most notable exception to this is copper. Although a large amount of the metal input comes from the freshwater system, there are also point sources of pollutants within the Humber itself. These include zinc from a synthetic fabric manufacturer in Grimsby, chromium and iron from the two titanium dioxide plants and arsenic and cadmium from the smelt works at Capper Pass. Copper inputs come from a variety of sources, including Capper Pass, the industrial areas around Killingholme, and the sewage discharges from Hull and Grimsby. Since the closure of Capper Pass in 1992, the re-suspension of contaminated sediments within the estuary are the main source of pollutants at this site. Leaching of contaminants from the surrounding land will also add to the pollutant loads.

1.2.3 Biology

Certain biological features of the Humber have been examined in many studies carried out by various organisations, (e.g. NRA and the University of Hull) and have enabled the Humber to be placed in the context of a 'typical' estuarine community (e.g. Haedrich 1983). Subtidal and intertidal biological work has mainly been restricted to the invertebrate benthos which forms much of the prey for the upper predators, e.g. birds and fish.

Barr *et al.* (1990) concluded, through an analysis of benthic data, that the estuary can be divided into four sections, based on the dominant invertebrate fauna. These are:

1. Upper estuary: characterised by the mysid crustacean *Neomysis integer*;
2. Middle estuary: dominated by the polychaete worm *Capitella capitata*;
3. Lower estuary: containing the polychaetes *Tharyx* sp., *Pygospio elegans*, *Polydora* spp and the oligochaete worms *Tubificoides swirencoides*, *T. benedeni* on the North, and the bivalve mollusc *Macoma balthica* on the South bank;
4. Outer estuary: characterised by the polychaete *Nephtys cirrosa*.

Analysis of subsequent NRA subtidal benthic data (unpublished) indicates that Syllid polychaetes, rather than *N. cirrosa,* may dominate in the outer estuary, while the cirratulid *Tharyx* (Aphelochaeta) is the most abundant taxon in the lower estuary. Invertebrate diversity within the Humber is low, although large abundances of some species have been recorded (NRA 1993).

Information on the intertidal mudflats and fringing vegetation has been compiled by the NRA and the University of Hull (Dept. Applied Biology and Institute of Estuarine and Coastal Studies), (e.g. Ratcliffe 1979; Gameson 1982; Key 1983; IECS 1987; Barnett 1988), as have details on the invertebrate populations and microbiology of the water column (e.g. Bent & Goulder 1981; Gameson 1982; IECS 1987).

The Humber is an area of international importance for some bird species, with populations of over-wintering wildfowl and waders well documented (IECS 1987; Davidson 1991). Approximately 15% of the total east coast of England wader populations are located in the Humber (NRA 1993). The estuary contains a number of reserves and protected areas which have been designated using ornithological criteria (Batty 1993). Although some bird populations will be dependent on the fish community, e.g. cormorants and heron in the upper reaches, most feed on the mudflat and saltmarsh invertebrates. These may have an effect on the fish populations, however, through indirect competition for a shared resource.

Despite this comprehensive assessment of certain aspects of the biology of the Humber, prior to the present study very little had been done to assess the size, nature and health of the fish populations. Most data concern the commercial fisheries (Rees 1982), or are anecdotal and compiled from records by shrimp and eel fishermen, or anglers. The only time-series data available for the fish populations within the Humber are the results of the annual MAFF young fish survey (NRA 1993). This survey started in 1973 to examine the 0-group population size of flatfish on the east coast of England, and involved sampling on one occasion, September, each year. Six subtidal and two intertidal sites within the outer and lower areas of the Humber were selected, with basic data on additional species also being collected, i.e. the species and numbers present. This survey was discontinued in 1984 but recommenced in 1988 in conjunction with the NRA, when it was extended to 14 subtidal sites along the length of the estuary and included collecting the length - frequency data for all species.

These initial surveys indicated that the Humber is an important nursery area for cod, *Gadus morhua*, and plaice, *Pleuronectes platessa*, and concluded that it served as a nursery area for 3% of the North Sea plaice population (Jones 1988). In addition the Humber was considered to serve as a spawning area for sole, *Solea solea*.

There is a commercial eel fishery within the upper reaches of the Humber and lower River Ouse, while small fisheries also operate around the edges of the outer estuary, mainly on a part-time basis, for cod and sole. Other fish, such as sprat, *Sprattus sprattus*, may also be taken (Rees 1982). There is a shrimp fishery operating within the estuary which will affect the fish community through the by-catch associated with this fishing method, in particular juvenile flatfish, whiting, *Merlangius merlangus*, and cod (N. Graham, Uni. of Humberside, pers. comm.).

1.2.4 Management of the Humber

The health of an estuarine biological community can be determined according to whether or not the area meets predefined quality objectives. These may also be regarded as null-hypotheses which can be tested during monitoring (Costa & Elliott 1991). Costa & Elliott (1991) defined 10 biologically based Environmental Quality Objectives (EQO), or null-hypotheses, for estuarine waters, of which 1-8 relate directly or indirectly to fish.

1. The water quality of an estuarine area always allows passage of migratory fish.
2. The structure of the residential marine/estuarine fish community and populations are consistent with the hydrophysical regime.
3. The benthic populations and sediments are of a quality sufficient to support the fish (and, when necessary, bird) populations.
4. The levels of persistent toxic and tainting substances in the biota are insignificant and do not affect its biology, it being predated or the health of its predators including man.
5. The structure of the intertidal/subtidal community and populations are consistent with the hydrophysical regime.
6. The diversity, abundance and biomass of the intertidal and subtidal rock community are as expected given the physical features of the area.
7. The levels of toxic and tainting substances either agreed or defined in conventions and legislation are not exceeded in the relevant biological component.
8. The biological functioning of an area has not been/will not be changed unacceptably by effluent disposal.
9. The levels of potentially pathogenic micro-organisms in sea water and biota are insignificant, do not affect their users or exceed the statutory agreed limits.
10. The planktonic communities have not been/will not be unacceptably affected by mans activities.

Since 1983 the Humber Estuary Committee of the National Rivers Authority, the statutory authority of water quality management proposals within the Humber, has used two of these and added a third to give water quality and management objectives for the estuary. These are designed to indicate the health of the system in relation to both its natural characteristics and human activities, and are:

(i) the protection of all existing defined uses of the estuary systems;
(ii) the ability to support on the mud bottom the biota necessary for sustaining sea fisheries;
(iii) the ability to allow the passage of migratory fish at all stages of the tide.

Of these, (ii) and (iii), relate directly to fish, while the other relates indirectly through the inclusion of recreational and commercial fishing.

Fish communities in other estuarine areas have been successfully used to monitor, and give an indication of, water quality (e.g. Andrews 1984; Elliott *et al.* 1988). This, together with community assessments, demonstrates the importance of fish studies to the understanding of the estuarine system of, e.g. the Forth (Elliott *et al.* 1990). However, within the Humber, a lack of adequate spatial and temporal data on the fish populations has resulted in an inability to determine whether or not the above EQO are being met. In addition, the importance of fish within the area to adjacent fishing stocks, indicates the value of these data to the management of the estuarine resource. The ability of the estuary to meet the above EQO, through the use of Environmental Quality Standards (EQS), is used in applying a water quality classification scheme (NRA 1992). The EQS are used, in turn, to determine the amount of pollutants permitted within industrial discharges such that the water quality within the estuary is maintained at a level sufficient to fulfil the EQO, further highlighting the importance of information on the fish populations.

1.3 Aims of the Present Study

The present study aimed to extend the scope of the MAFF/NRA survey by assessing the seasonal trends in biomass and abundance of fish species in the Humber, and then to assess their feeding behaviour, usage of the estuary and the impacts of human activity through changes in water quality. The information can be interpreted using data for environmental parameters, and the status and functioning of the Humber fish community can then be compared to studies in other areas (e.g. Henderson 1989; Elliott *et al.* 1990; Costa & Elliott 1991; Pomfret *et al.* 1991; Henderson *et al.* 1992). This will enable the management of the Humber estuary to be examined and placed in context within N.W Europe.

Thus the specific objectives within the study are:

1. An analysis of the environmental parameters within the estuary, enabling different area to be classified according to their physical and chemical parameters.

2. To assess the structure and functioning of the fish assemblage, determining seasonal and spatial trends in the abundance and biomass of the different species.

3. To determine the effects of the main estuarine water quality parameters, salinity, temperature, turbidity and the concentration of dissolved oxygen, on the distribution of the fish species.

4. To determine the age structure and growth of the populations and, using the biomass and abundance data, to estimate the production of each species. This will demonstrate the usage made

of the estuary by each species and may prove important in the wider context of the North Sea, through species using the area as a nursery or spawning ground, e.g. plaice and sole.

5. To determine the feeding behaviour of the fish and thus the dominant prey items for each species within the estuary. This can be used, together with a knowledge of the benthic populations, to illustrate the respective use of the intertidal and subtidal areas as a feeding area.

6. To determine the health of the fish populations through studies of the levels of morphological abnormalities and disease within the area.

7. To determine, from an analysis of the feeding behaviour and distribution of the fish species, the areas and prey species of greatest importance to the fish. This is of relevance to the development of management strategies for the estuary.

8. Similarly, to determine the levels of persistent contaminants within the fish of the Humber. As top predators, fish may accumulate and possibly biomagnify persistent pollutants within the estuarine system, and therefore the analysis will give an indication of the effects of man's activities within the catchment, through e.g. waste disposal.

9. To use the information on the structure and functioning of the fish assemblage within the Humber in a comparison with other, similar systems, throughout Europe.

2 MATERIALS AND METHODS

2.1 Sampling Sites

Subtidal samples were taken from 14 sites within the Humber estuary, on the east coast of England (Fig. 2.1; Table 2.1), approximating to those used by MAFF in their annual young fish survey. Intertidal sampling occurred at 2 sites, Cleethorpes, to the east of Grimsby, and Spurn Point.

2.2 Sampling Techniques

2.2.1 Subtidal Sampling

Sampling was undertaken between April 1992 and November 1994 using the NRA Anglian Region Survey Vessel 'Sea Vigil'. The sampling occasions were irregularly spaced through the year, as dictated by boat availability, although approximating to quarterly sampling in 1993 and 1994. Replicate samples were obtained using a 2 m beam trawl (Fig. 2.2) towed along the lines shown in Fig. 2.1 at approximately 6 km hr^{-1}, giving an average trawl length of 1 km. Each site was trawled in the direction of the tidal flow.

Three beam trawls were used during the course of this study, which, although of essentially the same design, showed slight differences:

Trawl 1 comprised a net with a 2 cm mesh, reducing to a 1 cm mesh in the codend. This was changed in December 1992, after completion of the lower and outer estuary, following the loss of the gear.

Trawl 2 comprised a 1 cm mesh throughout. This trawl was used to sample the middle and upper estuary in December 1992, and all sites during January and April 1993.

Trawl 3 had a similar net to trawl 2, but heavier shoes. This trawl was used for all subsequent samples, due to improved gear availability.

The net was 7.7 m in length, with a 2.7 m codend. A single tickler chain was used. Due to the size of the sampling area, and the duration of each sampling occasion, it was not possible to standardise the tidal state.

Measurements of salinity (± 0.1), temperature (± 0.1 °C), dissolved oxygen (± 0.01 mg l^{-1}) and turbidity (± 1 NTU) were taken at the end of each trawl using a Horiba® multiprobe. These parameters were assessed from the middle of the water column and approximately 1 m from the bottom by collecting

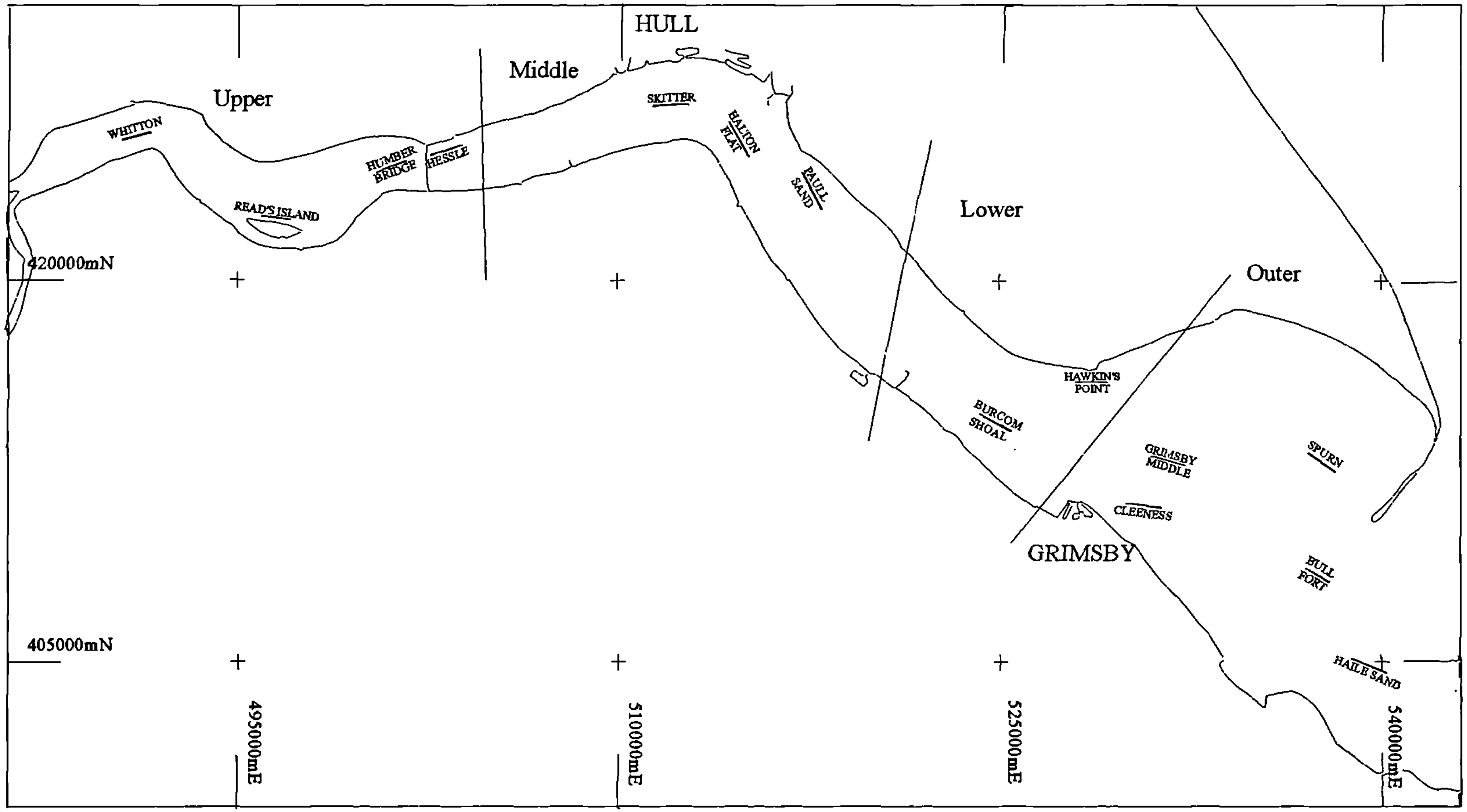


Fig. 2.1 Location of Subtidal Sampling Sites

HORIZONTAL SCALE 1: 150000

1500 0 1500 3000 4500 6000 9000 10500 12000 13500

METRES

water samples which were analysed immediately on board. Salinity measurements are in psu, although the current practice is to omit the units.

Table 2.1 The position and physical characteristics of the sample sites (co-ordinates are approximate and vary slightly with each trawl).

Site	Code	Site Number	Start coordinates	End coordinates	Distance from Whitton (km)	Depth (m) ($\bar{x}$ ± s.d)	Substratum
Whitton	W	14	53 43.42N 000 36.62W	53 43.13N 000 38.00W	0	5.0 ± 0.9	Sand
Read's Island	RI	13	53 41.18N 000 31.23W	53 41.24N 000 32.25W	6	5.7 ± 1.7	Sand
Humber Bridge	HB	12	53 42.50N 000 27.69W	53 42.50N 000 29.25W	11	8.0 ± 1.2	Sand
Hessle	H	11	53 42.85N 000 25.68W	53 42.64N 000 26.86W	12	7.2 ± 1.9	Sand
Skitter	Sk	10	53 43.53N 000 17.38W	53 43.47N 000 18.90W	21	6.2 ± 1.8	Sand
Halton Flat	HF	9	53 43.08N 000 15.78W	53 42.35N 000 14.53W	24	8.2 ± 1.7	Sand
Paull Sand	PS	8	53 41.29N 000 12.83W	53 41.93N 000 13.36W	27	7.0 ± 1.8	Mud
Burcom Shoal	BS	7	53 36.42N 000 06.13W	53 36.86N 000 07.19W	34	6.0 ± 1.9	Mud and rocks
Hawkins Point	HP	6	53 37.33N 000 03.69W	53 37.37N 000 02.64W	38	9.8 ± 1.6	Mud
Clee Ness	CN	5	53 34.80N 000 01.03W	53 34.86N 000 02.02W	39	5.6 ± 1.5	Mud
Grimsby Middle	GM	4	53 35.87N 000 01.39W	53 35.64N 000 00.05E	40	10.1 ± 1.2	Muddy sand
Bull Sand Fort	BF	3	53 33.53N 000 03.83E	53 33.25N 000 04.56E	45	11.6 ± 1.3	Sand, some mud
Spurn	Sp	2	53 35.86N 000 04.12E	53 35.37N 000 05.14E	46	7.1 ± 1.8	Mud
Haile Sand	HS	1	53 30.94N 000 07.09E	53 31.36N 000 05.91E	48	7.0 ± 1.6	Sand, some mud

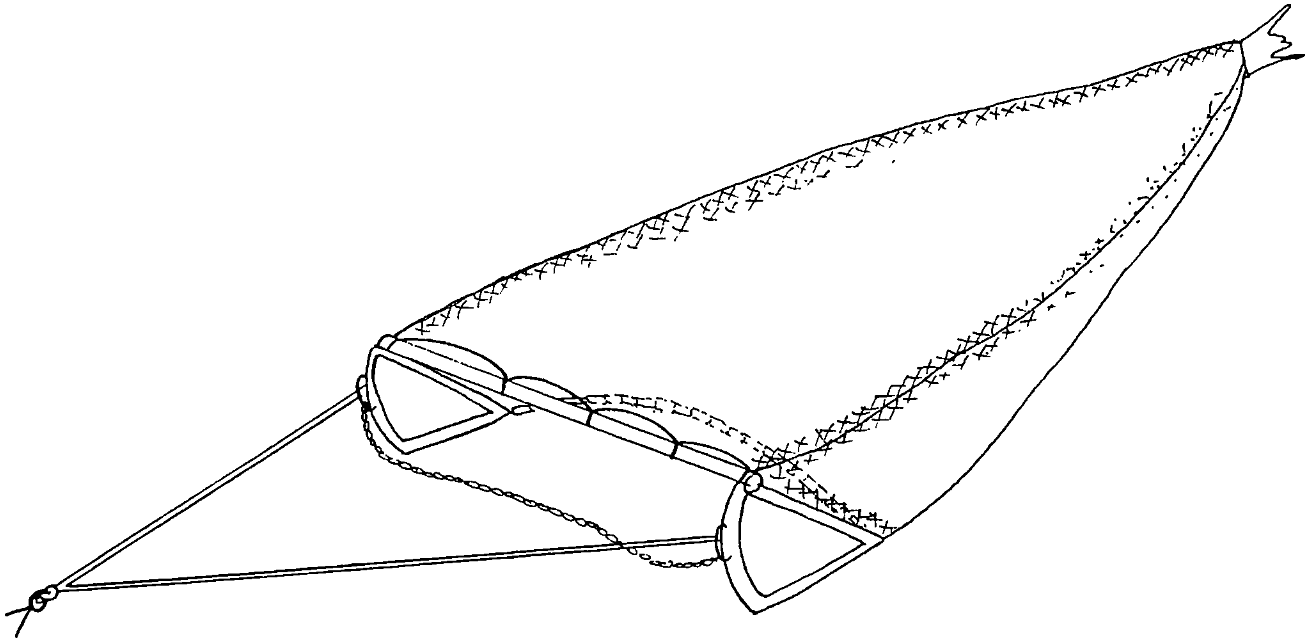


Fig. 2.2 Beam trawl.

The fish were frozen on board in order to minimise changes to gut contents during transport and returned to the laboratory for analysis.

In March 1994 it became necessary to remove one of the stations, Read's Island, from the sampling programme. This was the result of a change in the position of the channel, a natural migration from the north to the south of the Island, which made the site too shallow to sample safely.

2.2.2 Intertidal Sampling

2.2.2.1 Trawling

Between October 1993 and September 1994 replicate samples were obtained monthly from the sandy beaches at Spurn Point and Cleethorpes using a 1.5 m hand-pulled beam trawl. The net was 3.3 m long with a 1 cm mesh and a single tickler chain. It was towed using two 5 m ropes, pulled at an angle to the trawl such that the path of the trawl was not crossed.

Sampling was completed at high water + 3 - 3.5 hours at a depth of approximately 1 m. The net was towed, parallel to the shore, for 10 minutes. Any fish caught were placed on ice to minimise digestion. The epibenthos and any debris present were noted. Salinity, temperature, dissolved oxygen and turbidity were measured at the end of each tow.

2.2.2.2 Trapping

Trapping was attempted at Spurn Point on two occasions, 1.7.94 - 5.7.94 and 15.7.94 - 17.7.94, using the design of Summers (1979) (Fig. 2.3). The traps were laid at HW + 1.75 hours, HW + 2.75 hours and 3.75 hours down the shore and checked at each ebb tide.

2.3 Laboratory Methods

After thawing, each fish was identified according to Wheeler (1969), with nomenclature according to Wheeler (1992), and the total length measured (± 1 mm). The fish were then blotted and weighed, ± 1 g for fish greater than approximately 15 cm, or ± 0.1 g for fish less than 15 cm. This difference was determined by the balance used. Any external abnormalities, such as lesions, fin rot or nodules, including colouration were noted.

A subsample of each species in the trawl was retained for analysis. Between 2 and 10 fish from each species over a range of size classes, dependent on the number of fish within the trawl. Thus if less

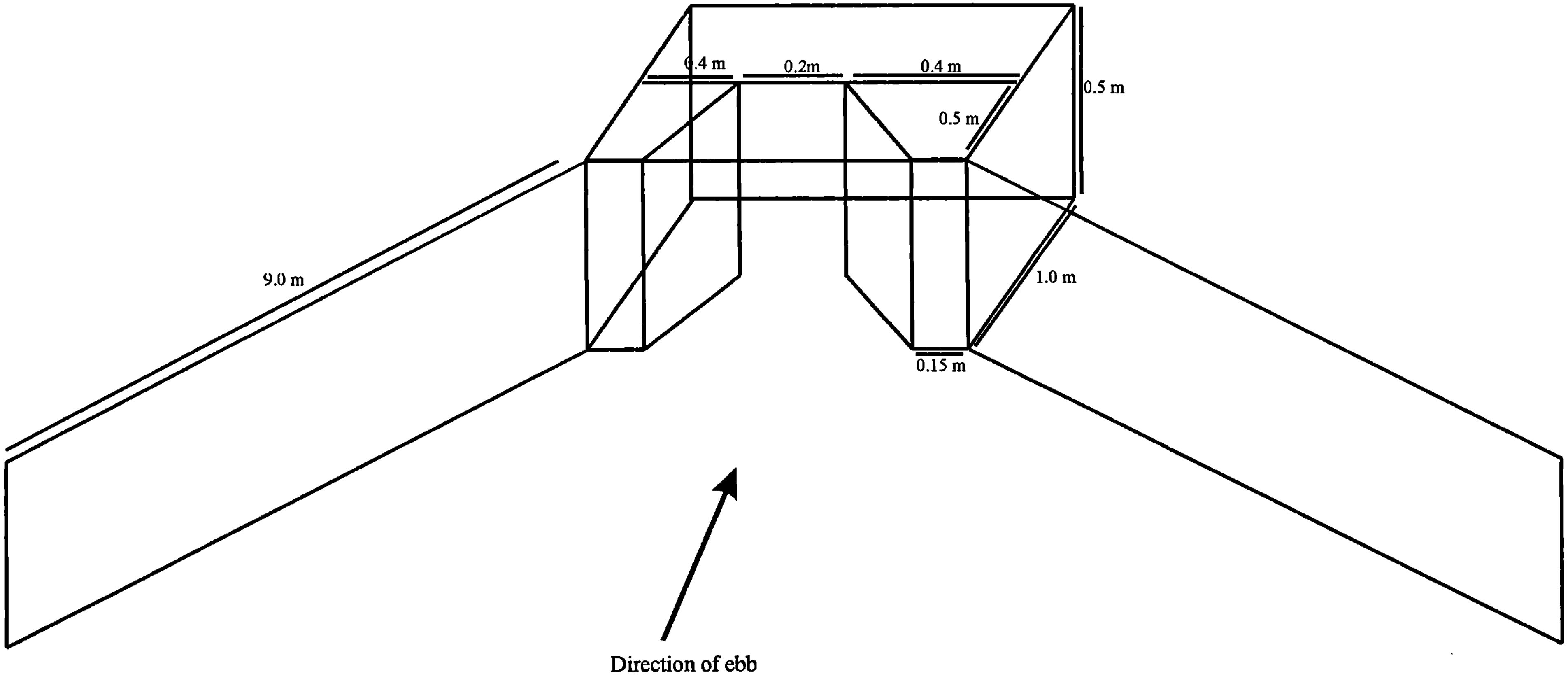


Fig. 2.3 Basic layout of the fish traps (Summers 1979).

than 50 fish of any species were caught, a minimum of 20 % of the fish were examined, otherwise 10 fish were selected.

2.3.1 Dissection

A longitudinal cut was made between the vent and throat along the lines indicated in Fig. 2.4. The fish were gutted by cutting the oesophagus, near the throat, and the intestines at the vent. The liver, gonad and digestive tract were removed and weighed ± 0.0001 g.

The sagittal otoliths were obtained by making an incision above the operculum (Fig. 2.5). The bony plates on the head were then cut forward towards the eyes and removed. to expose the otoliths.

A sample of muscle tissue was also taken from fish of sufficient size. The liver and muscle tissue were frozen at -20 °C and stored for further analysis of heavy metal contaminants, while the gonads were used to determine the sex and maturity of the fish. The otoliths were dried and stored in paper envelopes.

Other field and laboratory methods, together with statistical analyses, are detailed in the relevant chapters. In all cases where spatial trends are shown, the sites have been arranged longitudinally within the study area.

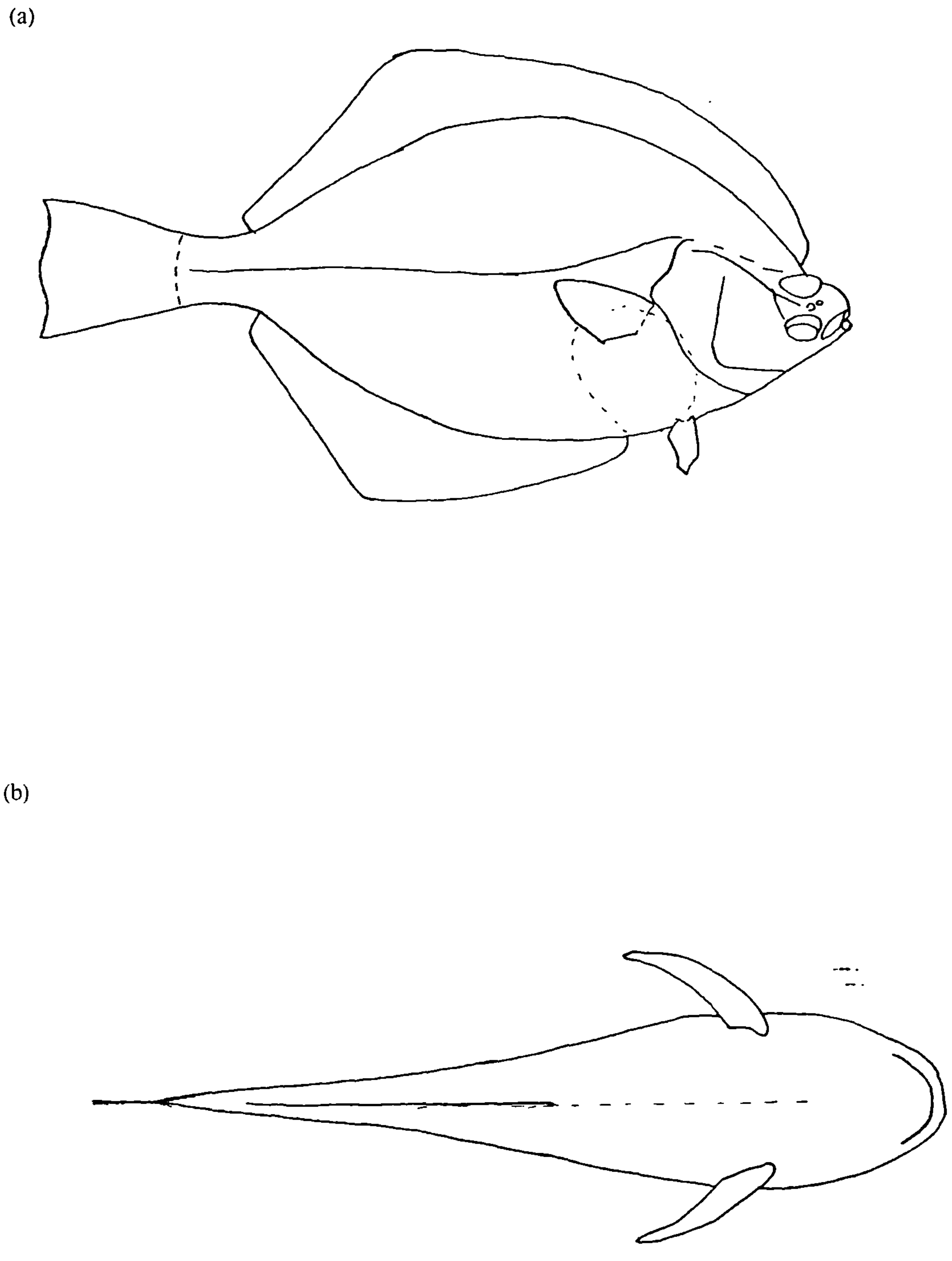
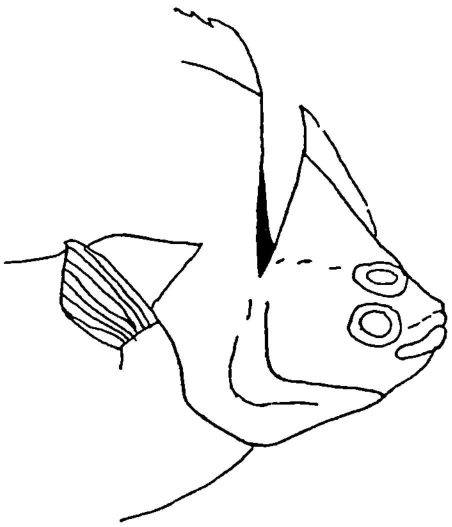


Fig. 2.4 Showing the lines of dissection (---) for the body cavity of (a) flatfish. and (b) round fish.

(a)



(b)

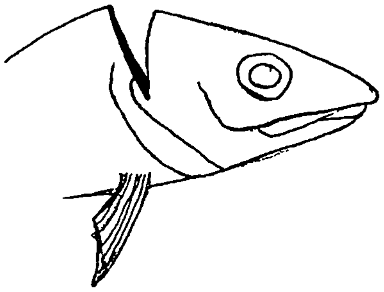


Fig. 2.5 Showing the lines of dissection to obtain the otoliths of (a) flatfish, and (b) round fish (picture (a) from Bagenal & Tesch (1978)).

3 ENVIRONMENTAL FEATURES

3.1 Introduction

The interactions between different environmental factors within estuaries produce a highly complex region supporting a low diversity of species. In turn, individual species have restricted environmental requirements which will influence their distribution. It is therefore important to determine the variations in environmental factors within an area when assessing the biota, its distribution and population trends.

Salinity, temperature, dissolved oxygen and turbidity are regarded as the most important factors influencing estuarine fish distribution (Blaber & Blaber 1980). In some areas turbidity is of particular importance to juvenile fish, which are found predominantly in areas of high turbidity. This may be the result of increased cover from visual predators, provided by the reduced visibility, or increased food availability, rather than physiological effects.

Salinity shows a strong spatial variability throughout estuaries, which has an impact on fish distribution (e.g. Forth and Tyne, Pomfret *et al.* 1991). It is affected by river flow, mixing and saline intrusion (Davidson *et al.* 1991), thus producing a gradient from tidal freshwater areas to the mouth. This gradient enables a wide range of species to utilise the area, dependent on their salinity tolerance. The highest species abundance is normally located towards the seaward end of the estuary (Remane & Schlieper 1958, **In**: McLusky 1989), possibly reflecting the appearance of marine species, either as regular or adventitious migrants (Elliott *et al.* 1990).

Dissolved oxygen concentration is inversely proportional to temperature (Carter 1988) and salinity (McLusky 1989), thus the maximum amount of oxygen dissolved in water decreases with increasing temperature and salinity. Within estuaries, dissolved oxygen is also affected by suspended solid concentrations, pollutant loads, flow rates (McLusky 1989), tidal movement and wave action (Carter 1988). Where there is constant aeration through wave and tidal action, i.e. at the seaward limits, or a high input of well oxygenated river water, i.e. in the upper reaches, levels of dissolved oxygen will be high, while stagnant or slow flowing water will have a lower dissolved oxygen content. Resuspension of the substratum, predominantly fine sediments and organic matter, will also increase oxygen demand.

Spatial and temporal gradients in dissolved oxygen will therefore occur. These are likely to be greater in the upper reaches where lower flows and a greater concentration of pollutants will result in an increased BOD during the summer (Carter 1988). Therefore an increase in dissolved oxygen should be observed between the upper and outer reaches, and also between summer and winter.

An increase in plankton or organic particles, from decaying matter or organic pollutants, will also result in an increase in the suspended solids within an area (McLusky 1989). Organic debris is eventually deposited, especially on intertidal mudflats, but while in suspension results in a high concentration of suspended solids (McLusky 1989). However, the most important source of material is through the resuspension of sediments, predominantly by tidal and wind action (de Jonge 1992).

3.2 Materials and Methods

The average salinity, temperature, dissolved oxygen and turbidity were determined for both the middle depth and 1 m from the bottom at each site, on each sampling occasion. The average values for each site and water depth were then determined from all values obtained over the study period at that site, i.e. the values of both replicates for all samples. The resultant values were plotted in a series of graphs for each variable to show the temporal and spatial variations. The percent coefficient of variance was calculated for each site over the study period, and each sampling occasion, to determine the degree of temporal and spatial variation for each parameter and therefore the probable influence on the fish distribution, spatial or temporal.

Spearman Rank Correlations were performed on the data in order to determine the association between the different variables measured, and their statistical significance. In order to determine the major spatial trends within the data, sampling sites were grouped into areas as upper, middle, lower and outer estuary, as defined in Barr *et al.* (1990), such that:

Area	Sites
Upper	Whitton; Read's Island; Humber Bridge; Hessle
Middle	Skitter; Halton Flat; Paull Sand
Lower	Burcom Shoal; Hawkins Point
Outer	Clee Ness; Grimsby Middle; Bull Sand Fort; Spurn; Haile Sand

(For the location of sites, see Fig. 2.1.)

A seasonal grouping was performed to determine temporal trends, such that:

Season	Month
Spring	March - May
Summer	June - August
Autumn	September - November
Winter	December - February

After testing for normality, subsequent analysis of the data with two-way ANOVA gave an indication of any statistically significant interactions of area and season on the environmental factors (Zar 1984). One-way ANOVA, in conjunction with Tukey-Honestly Significant Difference multi-range test was used to determine the cause and extent of any differences noted.

From the intertidal sampling, the average value of each parameter per month was calculated at both sites. The resultant graphs demonstrate the temporal fluctuations over the sampling period, while a paired t-test was used to determine any statistically significant differences between the two sites with respect to each parameter.

3.3 Results

3.3.1 Subtidal Sampling

The lowest levels of dissolved oxygen were recorded in the upper estuary, at Whitton, with a gradual increase downstream to Haile Sand (Fig. 3.1). There was also an increase from a low in summer to a high in winter. The degree of variation observed between sampling occasions, as shown by the % CV, were similar at each site throughout the estuary (Table 3.1(a)) and on each sampling occasion (Table 3.1(b)) with the exception of January 1993 and July 1993 when the degree of variation was lower.

Salinity shows a similar trend to dissolved oxygen, with low salinities recorded in the upper estuary rising to the highest values at the mouth (Fig. 3.2). The temporal variation was smaller than the spatial variation (Table 3.1) with the smallest change being recorded at Clee Ness and Grimsby Middle. The lowest salinity values occur between November and March, and the highest during the months of June to August. A comparison of the coefficients of variation show that the relative variability within the estuary increases towards the upper reaches (Table 3.1(a)).

Temperature shows little spatial variation but a marked temporal variation (Fig. 3.3; Table 3.1). The highest values were noted in August, decreasing to a low in December. Turbidity levels > 500 NTU were common throughout the area (Fig. 3.4), while levels > 999 NTU (approx. 5 g l^{-1}), the maximum detectable limit, were also observed. At these times a value of 1000 NTU was adopted. The relationship between the two units was calculated at: NTU = -15.757 + 0.290*(g l^{-1}). The turbidity maximum was found in the area west of Halton Flat, with values decreasing towards the mouth of the estuary (Fig. 3.4). There was a large variability within the area, both temporally and spatially, with the temporal variation masking the observed spatial trends. The relative variability of the samples increased towards Haile Sand in the summer months (Table 3.1), as mean turbidity decreased.

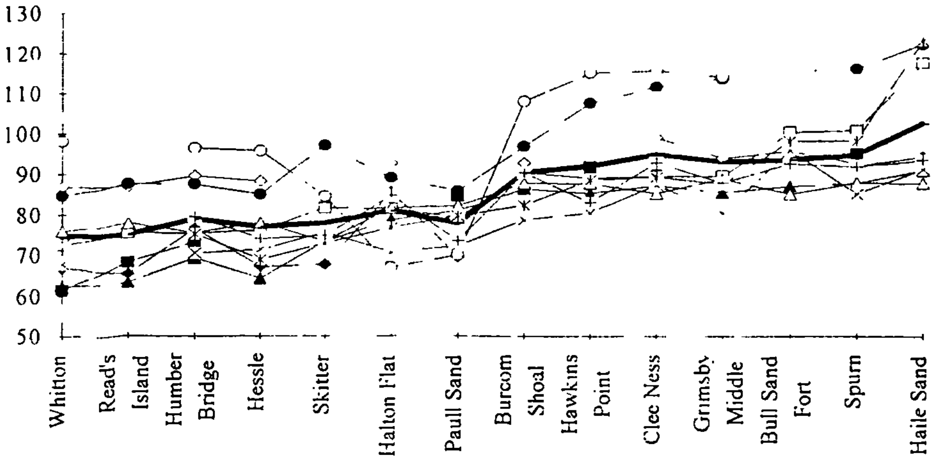


Fig. 3.1(a) The average percent dissolved oxygen 1 m from the sediment for each site on each sampling occasion.

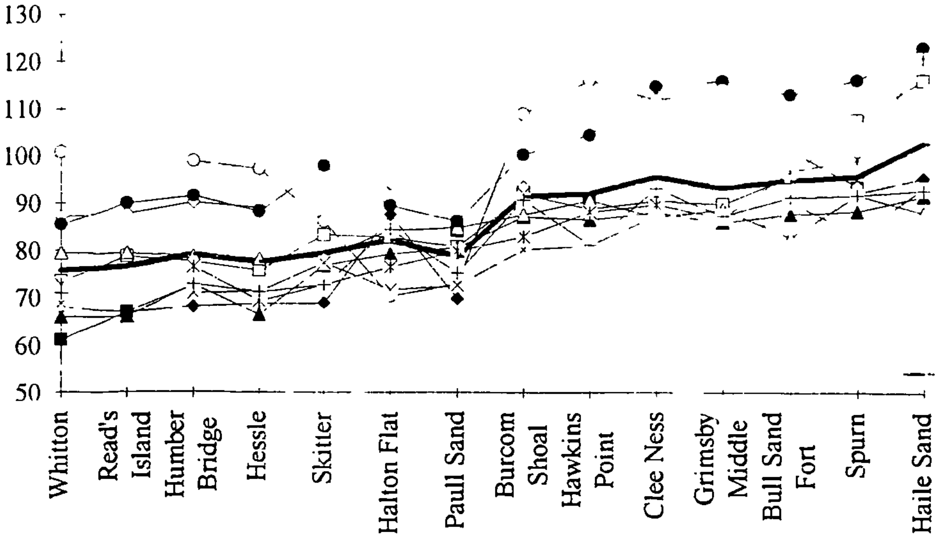


Fig. 3.1(b) The average percent dissolved oxygen in the middle of the water column for each site on each sampling occasion.

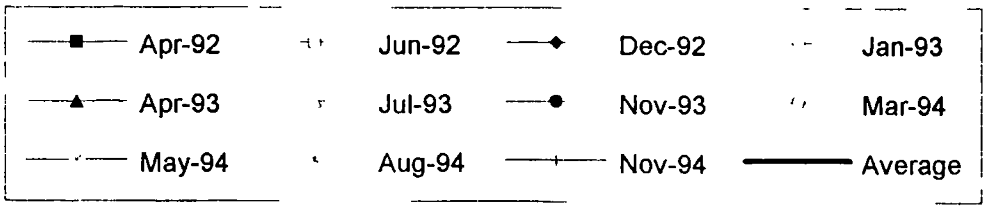


Table 3.1(a) The relative variability of the environmental variables recorded at each site over the period of the study ($\overline{x}$ (% CV)).

Depth	1m from bottom				Middle of water column			
Variable	Temperature (°C)	Salinity	Dissolved Oxygen (%)	Tubidity (NTU)	Temperature (°C)	Salinity	Dissolved Oxygen (%)	Tubidity (NTU)
Whitton	10.88 (49.54)	6.60 (72.44)	74.52 (14.82)	689.06 (42.67)	10.96 (49.06)	6.38 (73.91)	75.86 (14.81)	499.60 (44.27)
Read's Island	10.06 (52.35)	10.35 (53.32)	75.03 (12.73)	770.00 (34.91)	9.96 (52.60)	9.96 (55.99)	76.51 (12.72)	603.08 (48.13)
Humber Bridge	11.06 (48.88)	12.88 (33.55)	77.61 (10.79)	804.06 (34.01)	10.97 (48.15)	12.15 (37.89)	78.21 (11.39)	460.16 (54.20)
Hessle	10.74 (49.80)	12.73 (44.42)	76.66 (12.69)	648.81 (57.49)	10.80 (49.39)	12.09 (47.33)	77.18 (13.01)	559.84 (71.23)
Skitter	10.82 (51.79)	17.19 (32.74)	78.87 (14.17)	719.00 (37.74)	10.92 (50.63)	16.61 (33.23)	80.39 (13.81)	515.53 (62.16)
Halton Flat	10.76 (47.64)	17.28 (40.78)	81.11 (9.46)	713.47 (41.54)	10.82 (47.48)	16.57 (42.15)	82.19 (8.91)	622.94 (59.28)
Paull Sand	10.99 (48.07)	18.36 (36.03)	78.26 (7.42)	462.67 (69.79)	11.18 (46.33)	17.56 (37.66)	78.90 (7.28)	384.71 (77.90)
Burcom Shoal	11.43 (44.51)	23.84 (21.15)	90.51 (9.27)	406.24 (62.39)	11.57 (44.40)	23.28 (22.58)	91.40 (9.37)	291.94 (73.92)
Hawkins Point	11.43 (39.01)	26.11 (10.22)	92.14 (11.99)	558.36 (76.47)	11.49 (38.47)	25.06 (13.81)	91.84 (11.75)	226.56 (90.38)
Clee Ness	11.11 (44.82)	26.77 (7.78)	94.80 (11.14)	321.82 (81.34)	11.11 (44.23)	26.26 (11.21)	95.07 (10.46)	195.72 (110.59)
Grimsby Middle	11.23 (41.00)	26.38 (10.33)	93.20 (12.09)	508.13 (63.67)	11.31 (40.36)	25.22 (14.53)	93.11 (12.90)	362.11 (88.31)
Bull Sand Fort	12.58 (35.53)	29.69 (3.90)	93.78 (6.76)	169.77 (44.62)	12.35 (36.47)	28.38 (5.80)	93.44 (8.65)	130.93 (161.12)
Spurn	11.11 (38.98)	28.64 (6.09)	94.91 (9.17)	305.13 (111.78)	11.06 (41.35)	27.31 (10.92)	95.66 (10.02)	154.69 (112.03)
Haile Sand	12.04 (35.80)	30.57 (3.55)	102.50 (14.49)	139.07 (161.49)	12.16 (36.41)	29.96 (4.25)	102.11 (13.54)	113.93 (155.32)

Table 3.1(b) The relative variability of the environmental variables recorded on each sampling occasion throughout the estuary ($\overline{x}$ (% CV)).

Depth	1m from bottom				Middle of water column			
Variable	Temperature (°C)	Salinity	Dissolved Oxygen (%)	Tubidity (NTU)	Temperature (°C)	Salinity	Dissolved Oxygen (%)	Tubidity (NTU)
Apr 1992	9.43 (5.87)	18.93 (40.40)	80.60 (16.19)	803.67 (16.86)	9.32 (4.83)	18.50 (39.41)	79.74 (16.00)	420.17 (58.80)
Jun 1992	16.79 (3.16)	23.78 (21.24)	87.13 (14.48)	320.73 (91.15)	16.92 (2.63)	23.43 (20.91)	87.99 (13.72)	153.71 (101.78)
Dec 1992	4.51 (38.44)	13.48 (67.02)	77.73 (15.49)		4.39 (40.72)	12.78 (65.40)	77.74 (15.73)	792.33 (29.20)
Jan 1993	5.21 (5.50)	13.92 (83.83)	92.02 (4.40)	252.67 (135.22)	5.21 (4.54)	12.13 (86.24)	93.24 (5.30)	252.67 (135.22)
Apr 1993	9.35 (10.04)	21.89 (40.27)	78.80 (13.09)	644.14 (47.64)	9.51 (7.24)	20.95 (43.98)	80.18 (11.39)	419.21 (63.18)
Jul 1993	16.24 (3.10)	25.16 (26.68)	82.57 (6.68)	420.14 (83.88)	16.28 (3.34)	24.60 (27.02)	84.27 (5.64)	227.32 (104.16)
Nov 1993	7.97 (10.00)	19.05 (39.87)	98.98 (13.81)	796.73 (31.30)	7.92 (10.56)	18.86 (39.27)	101.06 (12.98)	527.50 (49.10)
Mar 1994	6.50 (15.50)	13.59 (67.67)	96.57 (18.57)	548.20 (44.78)	7.10 (16.20)	12.00 (70.96)	97.68 (16.82)	480.90 (60.41)
May 1994	12.00 (3.04)	22.06 (32.14)	79.11 (11.22)	597.77 (58.35)	12.17 (1.98)	21.35 (32.35)	78.90 (9.96)	429.61 (79.54)
Aug 1994	20.00 (2.92)	25.45 (23.89)	85.73 (17.27)	160.00 (81.79)	20.02 (2.76)	25.27 (23.65)	85.50 (16.38)	12.00 (105.52)
Nov 1994	9.33 (6.87)	18.43 (51.29)	83.94 (10.06)	590.54 (52.55)	9.30 (7.18)	17.66 (52.66)	82.69 (10.80)	500.23 (53.02)

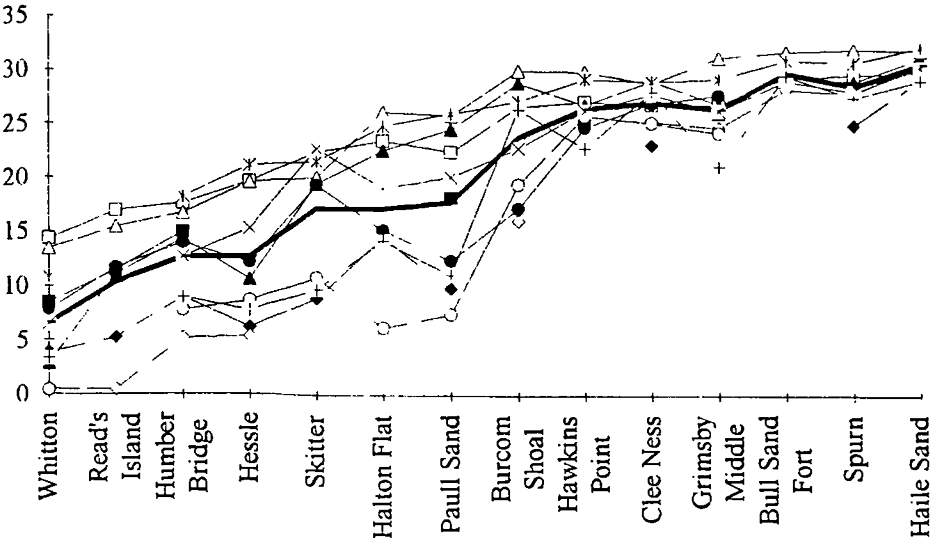


Fig. 3.2(a) The average salinity 1 m from the sediment for each site on each sampling occasion.

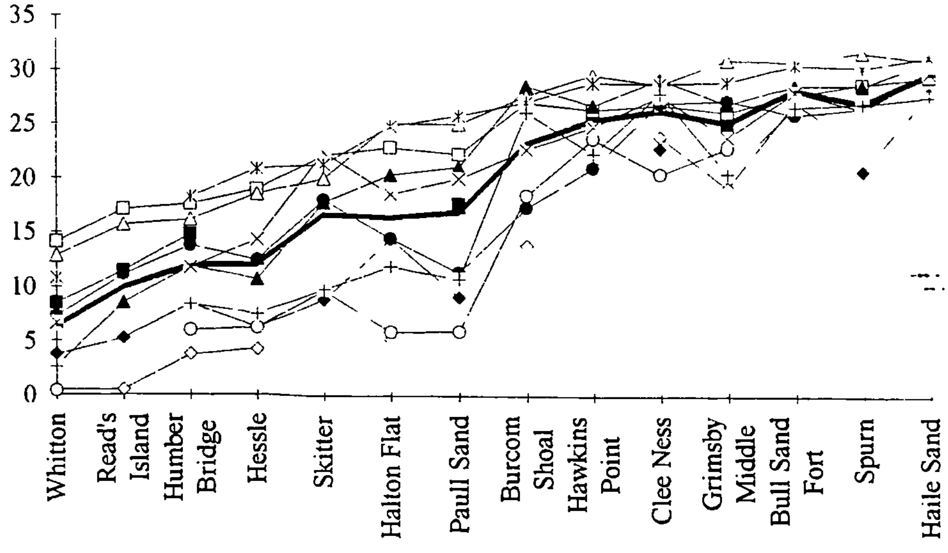


Fig. 3.2(b) The average salinity in the middle of the water column for each site on each sampling occasion.

■	Apr-92	□	Jun-92	◆	Dec-92		Jan-93
▲	Apr-93	△	Jul-93	●	Nov-93		Mar-94
	May-94		Aug-94	+	Nov-94	━━	Average

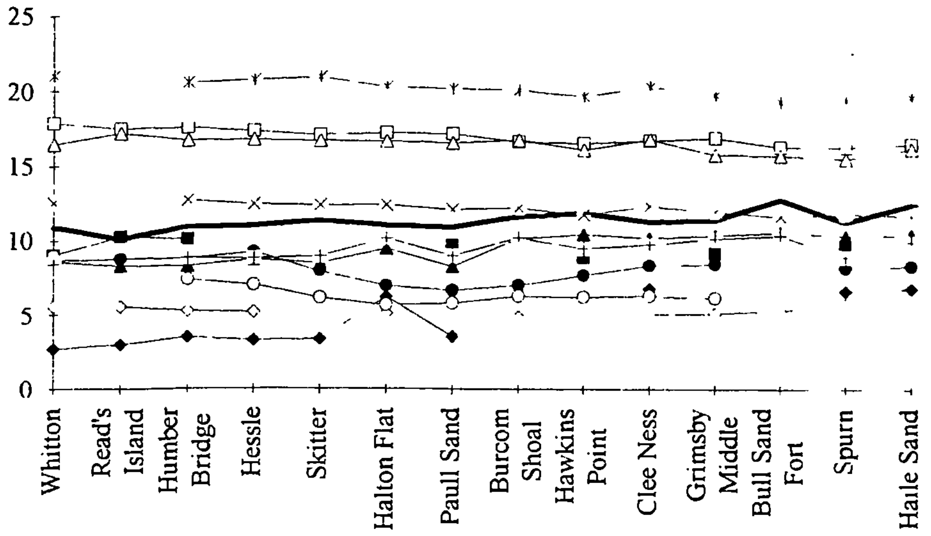


Fig. 3.3(a) The average temperature (°C) 1 m from the sediment for each site on each sampling occasion.

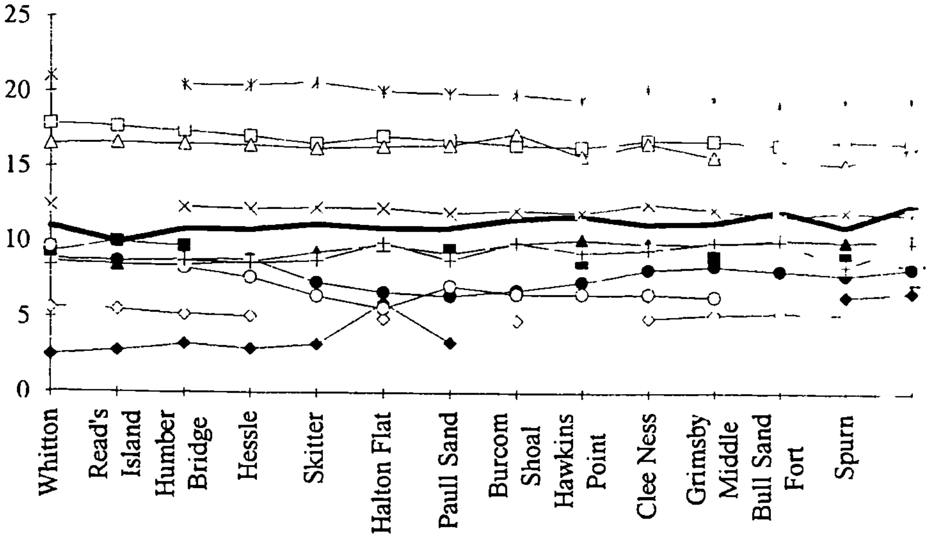
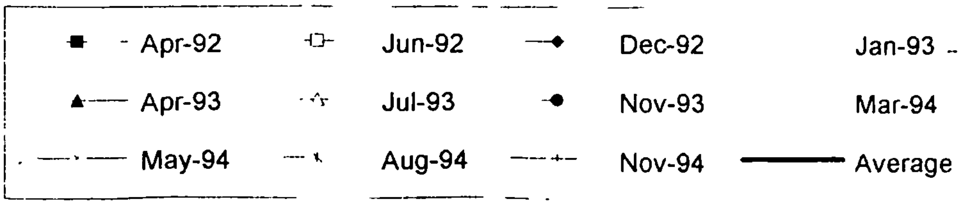


Fig. 3.3(b) The average temperature (°C) in the middle of the water column for each site on each sampling occasion.



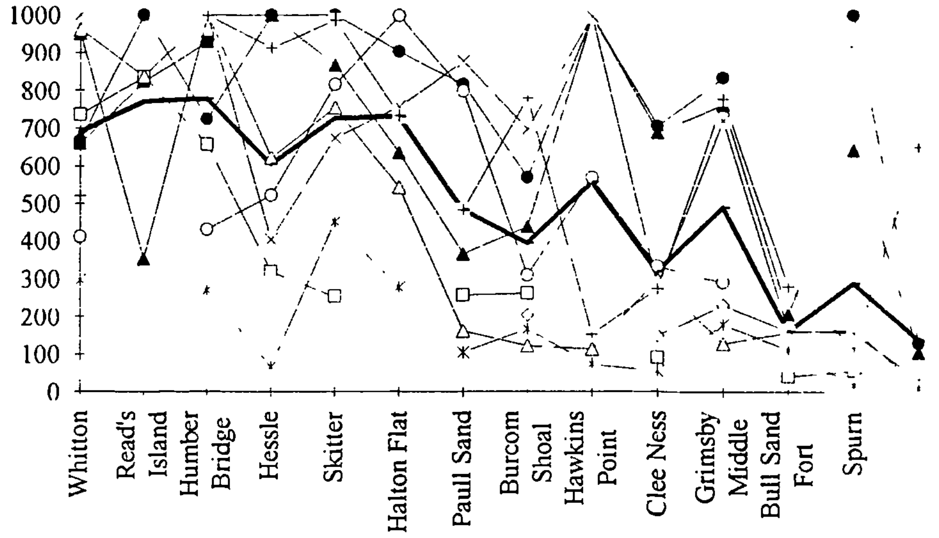


Fig. 3.4(a) The average turbidity (NTU) 1 m from the sediment for each site on each sampling occasion.

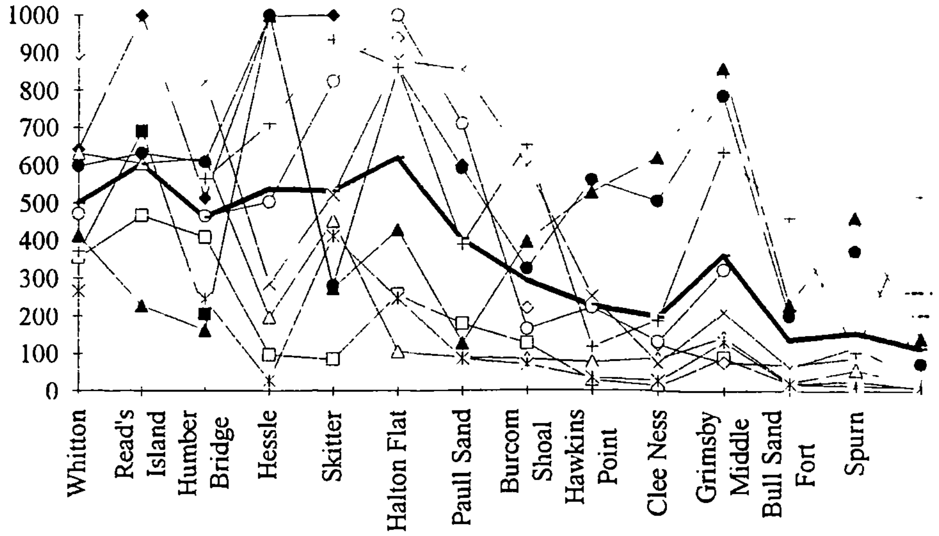
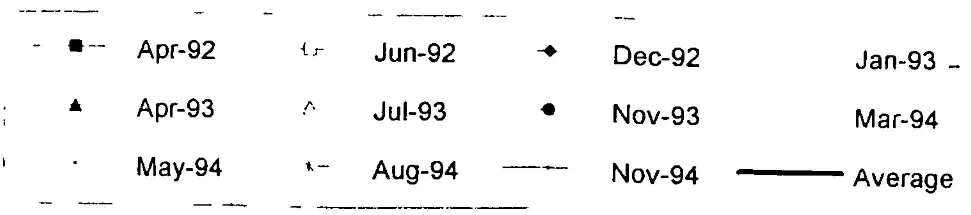


Fig. 3.4(b) The average turbidity (NTU) in the middle of the water column for each site on each sampling occasion.



There are some statistically significant correlations between the different environmental factors measured (Table 3.2). Dissolved oxygen is not correlated to temperature, while turbidity is negatively correlated to all other factors, with the exception of bottom temperature which is positively correlated to bottom turbidity. Salinity is positively correlated to both temperature and dissolved oxygen.

All factors, with the exception of temperature, show statistically significant seasonal and spatial patterns (Table 3.3; Appendix 1). Temperature shows seasonal trends only. Dissolved oxygen, salinity and temperature show similar relationships for both mid and bottom values. Seasonal effects on turbidity vary depending on position within the estuary, with greater seasonal variations observed in the upper estuary. There were no significant two-way interactions found with respect to dissolved oxygen (Appendix 1).

The values of dissolved oxygen recorded in the upper and middle estuaries were significantly different from those found in the lower and outer areas (Table 3.3(b)). However there were no significant differences between values in the upper and middle or the lower and outer areas. The only significant differences with respect to season were between the autumn sampling and that in the spring and summer (Table 3.3(a)).

Spatial analysis of salinity values indicates that each area of the estuary was significantly different from the remaining three, thus salinity values in the middle estuary were significantly different from salinity in the upper, lower and outer estuary (Table 3.3(b)). Seasonally, winter is significantly different from all other seasons, as is summer (Table 3.3(a)). There are no significant difference between spring and autumn values. However, temperature values recorded in each season are significantly different from the values in all other seasons (Table 3.3(a)).

Bottom turbidity recorded in the outer estuary is significantly lower than that in all other areas, as are the values between the upper and middle estuaries (Table 3.3(b)). Values for the middle of the water column, however, show significant differences between the upper and middle estuaries and the outer and lower estuaries, but not between either the upper and middle or the lower and outer areas. Within the middle of the water column, summer values are significantly different from all other seasons (Table 3.3(a)). However bottom turbidity during spring and autumn is significant different from that during the summer and winter. Again, there is no significant difference between either winter and summer or spring and autumn values.

Table 3.2 The relationships between the different environmental factors as determined by Spearman Rank Correlation (n.s., not significant; --- or +++, $p \leq 0.001$)

	Bottom dissolved oxygen	Bottom salinity	Bottom temperature	Bottom turbidity	Mid dissolved oxygen	Mid salinity	Mid temperature
Bottom salinity	+++						
Bottom temperature	n.s.	+++					
Bottom turbidity	---	---	+++				
Mid dissolved oxygen	+++	+++	n.s.	---			
Mid salinity	+++	+++	+++	---	+++		
Mid temperature	n.s.	+++	+++	---	n.s	+++	
Mid turbidity	---	---	---	+++	---	---	---

Table 3.3(a) Showing statistically significant seasonal differences for each parameter (* indicates that there is a significant difference)

	Dissolved oxygen				Salinity				Temperature				Mid Turbidity				Bottom Turbidity			
	spr	sum	aut	win	spr	sum	aut	win	spr	sum	aut	win	spr	sum	aut	win	spr	sum	aut	win
spr																				
sum					*				*				*				*			
aut	*	*				*			*	*				*				*		
win					*	*	*		*	*	*			*			*		*	

Table 3.3(b) Showing statistically significant spatial differences for each parameter (* indicates significant difference)

	Dissolved oxygen				Salinity				Temperature				Mid Turbidity				Bottom Turbidity			
	Up	mid	low	out	Up	mid	low	out	Up	mid	low	out	Up	mid	low	out	Up	mid	low	out
upper																				
middle					*															
lower	*	*			*	*							*	*			*			
outer	*	*			*	*	*						*	*			*	*	*	

3.3.2 Intertidal Sampling

Over the period of a year, there was no significant difference between the two sites for any of the variables measured. Levels of dissolved oxygen remained relatively constant throughout the year, although higher values (> 130%) were recorded in June (Fig. 3.5) at both sites, and July at Cleethorpes, and low values (< 100%) were found at Cleethorpes in April.

Salinity also remained relatively constant throughout the year, values varying by approximately 8 over the year (Fig. 3.6). Lowest values were recorded in January, at Spurn, and April, at Cleethorpes, increasing to a maximum in September. Temperature, however, followed a parabolic trend through the year, with maximum values, 19 °C, observed in July dropping to a minimum of 6 °C in January and February (Fig. 3.7). Turbidity was more varied but remained below 500 NTU over the study period (Fig. 3.8), with the exception of Spurn in December, when levels > 999 NTU were recorded, and again in September, 550 NTU. In September there was a moderate swell, which may have resulted in resuspension of the sediments.

3.4 Discussion

3.4.1 Subtidal Sampling

The variation in dissolved oxygen observed in the Humber estuary during the study period agrees with that found in other areas, e.g. the Forth (Pomfret *et al.* 1991). A dissolved oxygen sag in the upper estuary is a common feature of estuaries and results from high temperatures, turbidity and oxygen demand and low salinities (Morris *et al.* 1982) coupled with low flows during the summer months (McLusky 1989). Within this study, the lack of correlation between temperature and dissolved oxygen indicates that turbidity and the dilution of organic debris, as a function of depth and flow, may be the main factors influencing dissolved oxygen levels. Thus higher levels are recorded at the mouth where increased aeration from tidal action, together with low turbidity and the increased dilution of chemical pollutants and organic matter result in an increase in the level of dissolved oxygen. Compared to other areas, e.g. the Forth and Tyne (Pomfret *et al.* 1991), the study area has a relatively high amount of dissolved oxygen, even in the summer. However low levels, < 40%, have been recorded around Trent Falls, at the confluence of the Rivers Trent and Ouse upstream of the study area (IECS 1987; NRA 1993), indicating that the study area should be extended to include the areas of low dissolved oxygen.

The lack of spatial variations within the Humber, despite the presence of industries along the north and south banks and within the tidal rivers, indicates a well mixed, non-stratified estuary. This has been reported previously within the area (IECS 1987; NRA 1993) and is a function of the dynamic nature of the estuary. The outfalls of industrial plants within the Rivers Trent and Ouse have been shown to raise temperatures within the Humber (NRA 1992), but this is not supported by the results of this study.

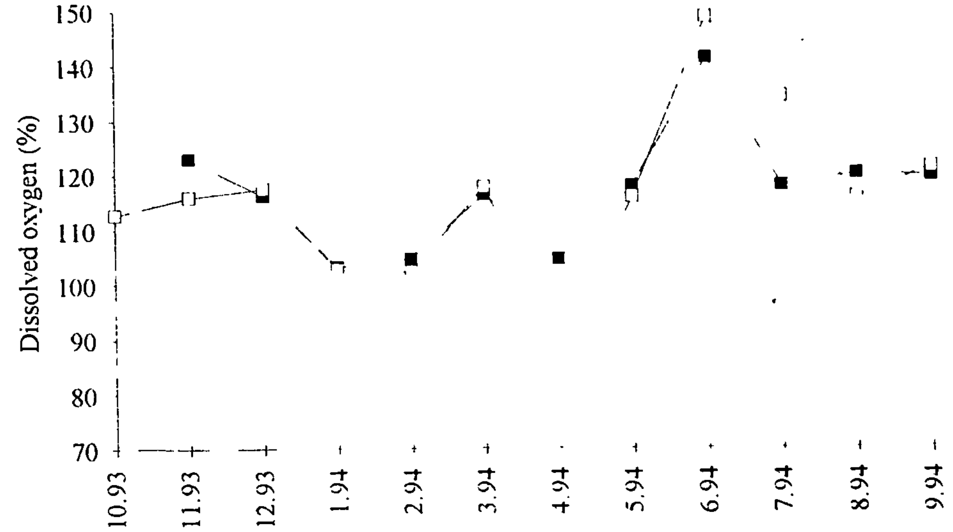


Fig. 3.5 The monthly changes in dissolved oxygen in the intertidal areas

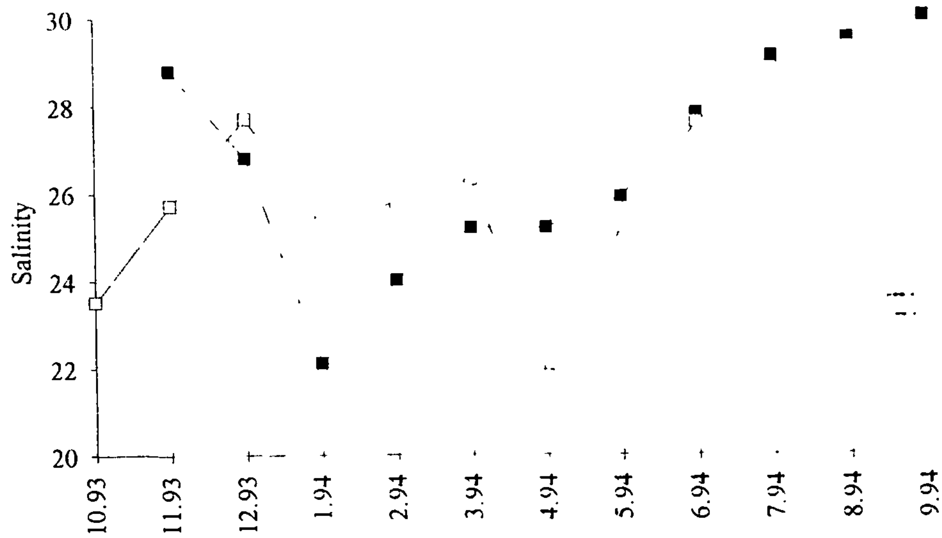


Fig. 3.6 The monthly changes in salinity in the intertidal areas

■ Spurn □ Cleethorpes

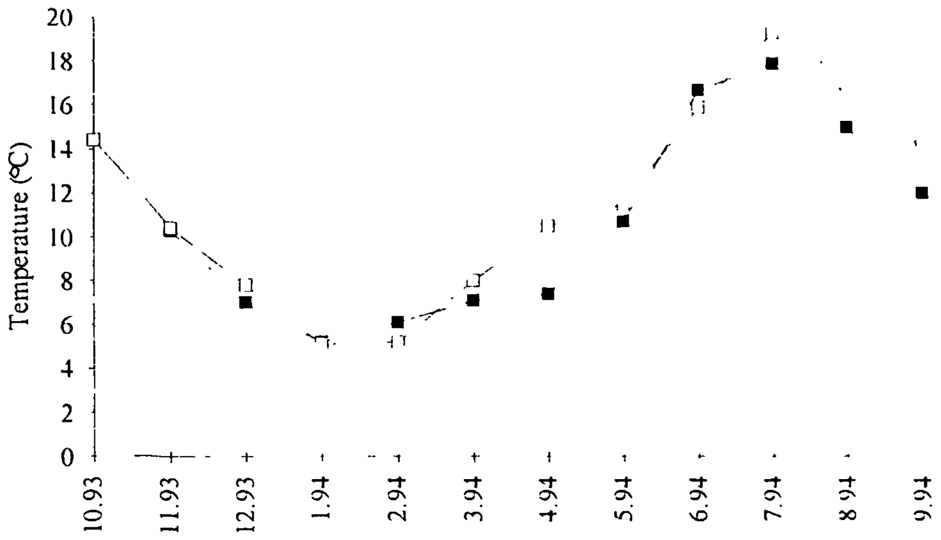


Fig. 3.7 The monthly changes in temperature in the intertidal areas

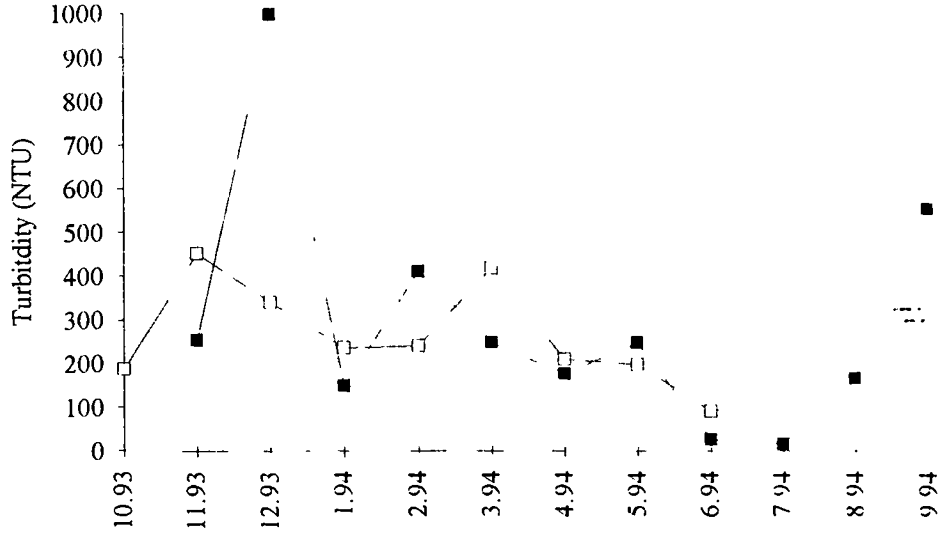


Fig. 3.8 The monthly changes in turbidity in the intertidal areas

■ Spurn □ Cleethorpes

In contrast to temperature, the main degree of variation in salinity appears to be spatial rather than temporal (Table 3.3). Salinity is affected by a variety of factors, including river flow and tidal action, which results in a limit of saline intrusion which can be seen to vary with time (McLusky 1989). The Humber appears to correspond to the 'normal' estuarine situation. Thus, when river flows are high, as a result of high rainfall, salinity will be lower and the extent of saline intrusion will occur nearer to the mouth of the estuary (McLusky 1989). As rainfall tends to be seasonal, this results in the greater temporal variations being recorded in the upper estuary.

The lowest salinity values observed, < 1, are related to the high flows experienced at these times (NRA, unpubl. data), which were at least double the level found on other occasions. The lowered salinities were noted several kilometres downstream at Paull Sand (27 km from Whitton) before the saline intrusion became more noticeable (Fig. 3.2). This, together with the findings of Pethick (1990), indicates that the saline intrusion reaches to an area around Hull, between Paull Sand, to the east, (this study) and the Humber Bridge, to the west (Pethick 1990), depending on the flows.

The salinity levels recorded within the Humber show similar trends to those found in other areas, e.g. the Forth (Elliott *et al.* 1990). Lower values, with greater variations, are recorded in the upper reaches, while the mouth of the estuary maintains a value comparable to seawater approximately 30 cf. 34 in North Sea nearshore areas.

The Humber has a high concentration of suspended sediments, i.e. is a turbid estuary (see also Justice & Arnett 1990). There is a net movement of sediment into the estuary from the surrounding coastal waters (Pethick 1990) which, together with wind and tidal resuspension of sediments, creates the high values observed. Variations in the quantity of suspended sediments varies across the tidal and lunar cycles and seasonally, with greatest turbidity found on ebb tides and during spring tides (Carter 1988). The seasonal variations in turbidity are demonstrated by the correlations with temperature such that, within the water column, there are higher levels of turbidity during the winter than the summer.

The turbidity maximum is a characteristic feature of well mixed estuaries and occurs at the extent of saline intrusion (Dyer 1979). It varies with the tidal state and river flow, but this study shows that it occurs upstream of Skitter. This agrees with the findings of Pethick (1990), who placed the turbidity maximum at the Humber Bridge, although data within this study indicate that it migrates within the upper reaches of the estuary rather than occurring in a restricted area. The interactions observed between the different environmental factors and other physical, biological and meteorological features, i.e. tidal state, organic composition and rainfall, have resulted in a dynamic and variable system for which the prediction of any particular variable or state requires an extensive knowledge of many other factors.

3.4.2 Intertidal Sampling

The levels of dissolved oxygen recorded during the monthly intertidal sampling do not reflect the trends observed in the subtidal areas (Fig. 3.5). However, this is likely to reflect the nature of the sampling, which results in the measurements being taken in the shallow (1 m) and turbulent littoral zone. The increased wave action will result in a high degree of aeration of the water, while surface waters have the greatest concentrations of dissolved oxygen due to air-water interactions (Carter 1988).

The seasonal trends observed in the salinity reflect those observed in the subtidal sampling, with lower values recorded during the winter period. There is a greater difference between the two sites at this time, indicating more variable conditions, relating to climatological differences between the two days of sampling, i.e. changes in wind direction and force (pers. obs). The low variability over the sampling period reflects the positioning of the sites within the outer estuary, an area that showed smaller temporal variability over the period of the subtidal sampling.

Temporal patterns in temperature are similar to those noted in the subtidal. Similar values were also noted, although these tended to be 1 to 2 degrees lower in the subtidal. However, the seasonal range within the intertidal is smaller than the subtidal, 5 - 19 compared to 2 - 21, and may reflect the increased influence of the air and the intertidal sediments on the shallower waters of the intertidal, together with the heat retentive properties of water bodies (Tait 1981).

The monthly turbidity data indicate that there is a slight seasonal trend, with low values found between June and August before rising to February and March (Fig. 3.8). However this may reflect tidal and climatological factors, causing the resuspension of sediments, rather than an actual trend. In order to sample these areas, it was necessary to select predominantly sandy shore areas, which are unlikely to mirror the turbidity patterns in the subtidal areas. The exception to this will be in the 'sandy bays', which will tend to concentrate suspended solids under certain climatological conditions.

Spurn can be classed as a sandy bay, due to the influence of the spit, while Cleethorpes is an open beach. Thus turbidity levels will be dependent on the weather conditions, in particular wind direction and tidal state. This may explain the high turbidity recorded at Spurn in December and September, when tidal and climatic conditions, i.e. spring tides and onshore winds, were such that sediments were carried into the area and remained in suspension through wave action. Since the end of the survey the combination of meteorological and tidal conditions at Spurn have resulted in a deepening layer of mud being deposited over the sand banks and on the shore (N. Proctor, Uni. of Hull, pers. comm.).

4. COMMUNITY STRUCTURE

4.1 Introduction

The community structure can be defined as the species richness of an area, and the number of individuals present amongst those species, as assessed from patterns within the population. These trends are an indication of the functioning of the population in a defined area, and can then be compared with data from other populations (Moss *et al.* 1982). Thus, it is possible to determine the 'normal' situation from a variety of sites and populations and then show if the study area is different, and, if so, whether this is due to natural or anthropogenic factors. Estimates of abundance will give an indication of the size of the population, although their accuracy is dependent on the methods used and samples being representative of the whole population (Wootton 1990).

Temporal variations in abundance are noted in all taxonomic groups (Begon *et al.* 1986). These show both seasonal and annual cyclical patterns. The cyclic nature of populations is particularly marked in fish due to their high fecundity (Moss *et al.* 1982) and this emphasises the need to study population patterns within different areas. Some cycles occur over a long time period, i.e. plaice produce a large year class once in approximately seven years (Barnes & Hughes 1988), illustrating the importance of a long term database when interpreting patterns in populations.

4.2 Materials and Methods

4.2.1 Community Structure

4.2.1.1 Archive Data

The species list for the Humber was determined from a variety of sources - this study, the annual MAFF survey (MAFF, unpubl. data) (MAFF), an undergraduate project at the University of Hull (Proctor 1995) (NP), conversation with anglers (*) and the Archive data within the NRA (NRA 1993) (ARCH). The MAFF survey between 1973 and 1984 covered six sites in the outer estuary, Haile Sand, Clee Ness, Burcom Shoal, Grimsby Middle, Bull Sand Fort and Halton Flat, with an annual sampling occasion in September. Sampling between 1973 and 1975 covered a variety of sites before regular sampling on the six sites was established in 1976 (MAFF, unpubl. data). In 1984 sampling stopped, before recommencing in 1988, when an additional eight sites were added to the programme to give the 14 sites used within the present study.

The MAFF data from 1976 to 1984 and 1988 to 1994 were used to give the average number of fish per trawl calculated for the six original sites and the four dominant species, goby, whiting, sole and flounder. The data for the 14 sites between 1988 and 1994 were similarly analysed and the two data sets used to show any difference caused by the addition of the extra eight sampling sites. Statistical differences in the catch between the two periods were determined using an unpaired t-test (Zar 1984). The number of fish per trawl found within this study was then calculated for the 14 sites, and the results combined with those for the MAFF survey.

The number of species per sampling occasion was derived for the MAFF data set. The data prior to 1984 were compared to those between 1988 and 1994 using an unpaired t-test (Zar 1984) in order to determine if there was a statistical difference in the number of species sampled caused by the addition of eight sites to the sampling programme in 1988.

4.2.1.2 Present Study

The percent occurrence of each species at each site over the period of the study was calculated. The statistical significance of the observed spatial distribution was determined through analysis of this data using the Monte Carlo method (Sheppard 1995). This statistical analysis of the distribution is based on a comparison of each site for any single species and indicates the tendency of a species to have a spatially bunched or clumped distribution within the estuary, i.e. to show whether or not the observed distribution is non-random. In this analysis the appearance of a species within a particular area of the estuary is examined with respect to other areas.

The species were also ranked using the index in Elliott & Taylor (1989(b)) to determine the species which occur most frequently within the trawls. Derived from the percent occurrences calculated above, the values were summed for each species. Thus, a maximum occurrence would be 100 % at 14 stations, or 1400 %. All species occurrences were totalled and the presence in the assemblage calculated as a percent of the total. For example, gobies had a total occurrence of 922 %, out of a total for the estuary of 5007 % and therefore accounted for (922/5007)*100 or 18.4 % of the structure observed. A similar ranking was performed using the abundance data rather than percent occurrence, in order to demonstrate the numerical dominance of the different species.

4.2.2 Population Size and Dynamics

The biomass and abundance data (Appendix 2) were summed for all stations and tidal states within each area of the estuary, and are given for each sampling occasion and species. Areas were defined as in Chapter 3, and the total biomass and abundance of each species for each area was estimated using the following equation:

$$N = A/a * n * 0.33$$

where N = the total biomass or abundance, A = the area of the section in km^2,

a = 0.002 km^2, the average area covered by the trawl,

and n = the average number, or weight, of fish caught per trawl.

0.33 is the accepted value for the efficiency of the beam trawl (McIntyre 1971).

The area of each section was calculated as:

Upper estuary	58 km^2
Middle estuary	46 km^2
Lower estuary	41 km^2
Outer estuary	113 km^2
Total estuary	258 km^2

These values refer to the area below high water, according to Ordinance Survey maps.

The resultant biomass and abundance values were plotted for the four dominant species and the entire fish assemblage, per km^2, for each area of the estuary to indicate changes in the fish populations over the period of the survey and the occurrence of any migrations. The abundance and biomass data, used together with the size-frequency information, can also be used to give an indication of the average size, and therefore age, of the fish within the estuary. Higher values of biomass/abundance indicate larger, and thus older, fish and vice versa.

The abundance data used above for each area were compared using one-way ANOVA to determine any statistically significant differences between the population size in each area. The data from each area were then summed and the resultant values compared for each sampling occasion to determine temporal differences (Zar 1984). Specific differences between areas and months were determined using the Tukey Honestly Significant Difference *a-posteriori* test. These data were then further analysed with respect to the trawl used, to determine any differences in population size relating to the 3 trawls. The species diversity for each area and sampling occasion were calculated using the Shannon-Weiner diversity and evenness indices (Ludwig & Reynolds 1988). This enables a comparison of the different areas with time.

4.2.3 Intertidal Sampling

Abundance and biomass data for all species combined, and plaice data separately, are graphically illustrated for the two sites on each sampling occasion, together with data of the Abundance/Biomass ratio. Plaice were treated separately due to their dominance, and the rarity of other species within the trawls. Abundance data for all species caught at the two sites were compared using a paired t-test (Zar 1984) to determine any differences in the intertidal populations of the north and south banks. A similar analysis was performed on the plaice data alone in order to determine the distribution of juvenile plaice within the intertidal areas. The proportion of plaice caught on each sampling occasion was also determined in order to give an indication of seasonal patterns in the population.

4.3 Results

4.3.1 Species Composition

The species list for the Humber estuary is given in Table 4.1. The codes indicate the source of the data, with most emphasis given to data which could be substantiated either in the time period of this survey or historically. The sand and common gobies (*Pomatoschistus minutus* and *P. microps* respectively) were combined for the purposes of analysis as *Pomatoschistus* spp. due to the difficulty of identification caused by large sample size, poor definition of head papillae and poor preservation of the animals, e.g. the loss of fins or body shape resulting from the capture, freezing and thawing of the samples. A subsample was taken throughout the study period for full identification, and this indicated that the dominant species within the Humber is the sand goby, occurring with a ratio sand:common goby of 121:8, thereby resulting in an effective examination of one species only. The *P. minutus* complex comprises of two species, *P. minutus minutus*, and *P. m. lozanoi* (Hamerlynck 1990) but these were not differentiated within this study. There were some problems in identification of small sprat and herring, < 55 mm, during this study, also caused by the poor preservation of a few of the samples, in which case the fish were classed as Clupeid.

Of the 72 species recorded, 25 were caught in the subtidal trawls (S) and a further four in the intertidal sampling (I) of this survey. All of the fish were assigned to an ecological category (ECOL) denoting their use of the estuary according to the classification in Dewailly (1994), which is a development of categories proposed by McHugh (1967), Haedrich (1983) and Elliott & Taylor (1989(b)), with the exception of sole, where 'marine seasonal' was considered more appropriate to the Humber than 'marine juvenile', due to the seasonal distribution of the fish within the survey (Section 4.3.3.2.3). Other categories were used to denote the biological distribution of the different species according to the classification in Dewailly (1994), including reproductive strategy (REPRO), substratum preference (SUBS) and distribution within the water column (VERT). These categories are:

Table 4.1 Species list for the Humber estuary (abbreviations in text; names as Wheeler (1992)).

			CATEGORIES			
CODE	COMMON NAME	SCIENTIFIC NAME	ECOL	REPRO	SUBS	VERT
ARCH	Sea lamprey	*Petromyzon marinus* Linnaeus, 1758	CA	Os	F	B
S	Lampern	*Lampetra fluviatilus* (Linnaeus, 1758)	CA	Os	F	B
*	Lesser spotted dogfish	*Scyliorhinus canicula* (linnaeus. 1758)	MA	Os	F	D
*	Tope	*Galeorhinus galeus* (Linnaeus, 1758)	MA	W	S	D
*	Smooth hound	*Mustelus mustelus* (Linnaeus, 1758)	MA	V	M	D
*	Spurdog	*Squalus acanthias* Linnaeus, 1758	MA	W	F	B
*	Blonde ray	*Raja brachyura* Lafont, 1873	MA	Os	S	B
S	Thornback ray	*Raja clavata* Linnaeus, 1758	MA	Os	S	B
MAFF	Spotted ray	*Raja montagui* Fowler, 1910	MA	Os	S	B
S	Eel	*Anguilla anguilla* (Linnaeus, 1758)	CA	Op	F	B
ARCH	Conger eel	*Conger conger* (Linnaeus, 1758)	MA	Op	R	B
S	Herring	*Clupea harengus* Linnaeus, 1758	MS	Ob	/	P
S	Sprat	*Sprattus sprattus* (Linnaeus, 1758)	MS	Op	/	P
ARCH	Bleak	*Alburnus alburnus* (Linnaeus, 1758)	FW	Ov	/	P
ARCH	Barbel	*Barbus barbus* (Linnaeus, 1758)	FW	Ob	S	D
ARCH	Silver bream	*Blicca bjoerkna* (Linnaeus, 1758)	FW	Ov	/	P
ARCH	Carp	*Cyprinus carpio* Linnaeus, 1758	FW	Ov	MV	D
ARCH	Chub	*Leuciscus cephalus* (Linnaeus, 1758)	FW	Ov	/	P
ARCH	Roach	*Rutilus rutilus* (Linnaeus, 1758)	FW	Ov	/	P
ARCH	Tench	*Tinca tinca* (Linnaeus, 1758)	FW	Ov	/	P
ARCH	Pike	*Esox lucius* Linnaeus, 1758	FW	Ov	MV	D
S	Smelt	*Osmerus eperlanus* (Linnaeus, 1758)	CA	Ob	/	P
*	Salmon	*Salmo salar* Linnaeus, 1758	CA	Os	/	P
*	Sea trout	*Salmo trutta* Linnaeus, 1758	CA	Os	/	P
S	Five-bearded rockling	*Ciliata mustela* (Linnaeus, 1758)	MS	Op	M	B
S	Cod	*Gadus morhua* Linnaeus, 1758	MJ	Op	F	D
NP	Three-bearded rockling	*Gaidropsarus vulgaris* (Cloquet, 1824)	MA	Op	R	B

Table 4.1 (cont.)

CODE	COMMON NAME	SCIENTIFIC NAME	ECOL	REPRO	SUBS	VERT
*	Haddock	*Melanogrammus aeglefinus* (Linnaeus, 1758)	MA	Ob	M	D
S	Whiting	*Merlangius merlangus* (Linnaeus, 1758)	MJ	Ob	F	D
I	Pollack	*Pollachius pollachius* (Linnaeus, 1758)	MJ	Op	R	D
I	Saithe	*Pollachius virens* (Linnaeus, 1758)	MA	Op	R	D
S	Bib	*Trisopterus luscus* (Linnaeus, 1758)	MJ	Ob	M	D
*	Angler	*Lophius piscatorius* Linnaeus, 1758	MA	Os	M	B
ARCH	Skipper	*Scomberesox saurus* (Walbaum, 1792)	MA	Op	/	P
*	Sand-smelt	*Atherina presbyter* Cuvier, 1829	MJ	Ov	/	P
S	Three spined stickleback	*Gasterasteus aculeatus* Linnaeus, 1758	CA	Og	/	P
ARCH	Greater pipefish	*Syngathus acus* Linnaeus, 1758	ER	Os	M	B
S	Nilssons pipefish	*Syngnathus rostellatus* Nilsson, 1855	ER	Os	SV	B
NP	Deep-snouted pipefish	*Syngathus typhle* Linnaeus, 1758	ER	Os	FV	D
ARCH	Grey gurnard	*Eutrigla gurnardus* (Linnaeus, 1758)	MS	Op	S	B
MAFF	Fatherlasher	*Myoxocephalus scorpius* (Linnaeus, 1758)	ER	Og	FV	B
MAFF	Sea scorpion	*Taurulus bubalis* (Euphrasen, 1786)	MA	Ov	RV	B
S	Pogge	*Agonus cataphractus* (Linnaeus, 1758)	ER	Ov	F	B
S	Sea-snail	*Liparis liparis* (Linnaeus, 1766)	ER	Ov	M	B
NP	Montagu's sea-snail	*Liparis montagui* (Donovan, 1805)	MA	Ov	RV	B
*	Bass	*Dicentrarchus labrax* (Linnaeus, 1758)	MJ	Op	M	D
ARCH	Thick lipped mullet	*Chelon labrosus* (Risso, 1826)	MS	Op	RV	D
MAFF	Eelpout	*Zoarces viviparus* (Linnaeus, 1758)	ER	V	MV	B
MAFF	Butterfish	*Pholis gunnellus* (Linnaeus, 1758)	ER	Og	MV	B
MAFF	Wolf-fish	*Anarhichas lupus* Linnaeus, 1758	MA	Ob	R	D
S	Lesser weever	*Echiichthys vipera* (Cuvier, 1829)	MA	Op	F	B
MAFF	Raitt's sandeel	*Ammodytes marinus* Raitt, 1934	MA	Ob	S	B

Table 4.1 (cont.)

CODE	COMMON NAME	SCIENTIFIC NAME	ECOL	REPRO	SUBS	VERT
S	Sandeel	*Ammodytes tobianus* Linnaeus, 1758	ER	Ob	S	B
MAFF	Greater sandeel	*Hyperoplus lanceolatus* (Le Sauvage, 1842)	MA	Ob	S	B
S	Dragonet	*Callionymus lyra* Linnaeus, 1758	MA	Op	F	B
S	Transparent goby	*Aphia minuta* (Risso, 1810)	ER	Os	/	P
S	Common goby	*Pomatoschistus microps* (Krϕyer, 1838)	ER	Ob	S	B
S	Sand goby	*Pomatoschistus minutus* (Pallas, 1770)	ER	Ob	S	B
ARCH	Painted goby	*Pomatoschistus pictus* (Malm, 1865)	MA	Ob	S	B
ARCH	Mackerel	*Scomber scombrus* Linnaeus, 1758	MA	Op	/	P
MAFF	Norwegian topknot	*Phrynorhombus norvegicus* (Günther, 1862)	MA	Op	R	B
I	Turbot	*Scophthalmus maximus* (Linnaeus, 1758)	MJ	Ob	F	B
I	Brill	*Scophthalmus rhombus* (Linnaeus, 1758)	MJ	Ob	F	B
MAFF	Scaldfish	*Arnoglossus laterna* (Walbaum, 1792)	MA	Ob	F	B
ARCH	Long rough dab	*Hippoglossoides platessoides* (Fabricus, 1780)	MA	Op	F	B
ARCH	Halibut	*Hippoglossus hippoglossus* (Linnaeus, 1758)	MA	Op	F	B
S	Dab	*Limanda limanda* (Linnaeus, 1758)	MJ	Ob	S	B
S	Lemon sole	*Microstomus kitt* (Walbaum, 1792)	MA	Op	R	B
S	Flounder	*Pleuronectes flesus* Linnaeus, 1758	ER	Op	F	B
S	Plaice	*Pleuronectes platessa* Linnaeus, 1758	MJ	Op	F	B
ARCH	Solenette	*Buglossidium luteum* (Risso, 1810)	MA	Op	S	B
S	Sole	*Solea solea* (Linnaeus,1758)	MS	Op	F	B

CATEGORY	CODE	DESCRIPTION	No. SPECIES
ECOL	ER	estuarine resident, species which spend their entire lives in the estuary	13
	MA	marine adventitious, marine species which occur in the estuary but have no apparent estuarine requirements	28
	MJ	marine juvenile migrant, marine species which use the estuary primarily as a nursery ground	10
	MS	marine seasonal migrant, marine species which pay regular seasonal visits to the estuary, usually as adults	6
	CA	diadromous migrant, species which use the estuary to pass between salt and fresh waters for spawning and feeding	7
	FW	freshwater adventitious, freshwater species which occur in the estuary but have no apparent estuarine requirements	8
REPRO	V	viviparous, species which have live young	2
	W	ovoviviparous, species which give birth to living organisms which are first enclosed in eggs	2
	O	oviparous, species which release eggs - this category is further subdivided into 5 classes;	
	- Op	species producing pelagic eggs	23
	- Ob	species producing benthic eggs	17
	- Og	species producing eggs guarded by one or both parent(s)	3
	- Os	species which shed /protect their eggs in a nest, case or pouch	13
	- Ov	species which deposit their eggs in or stuck to vegetation	12
SUBS	S	species found in or associated with, sand only	14
	F	species associated with soft bottoms, sand, mud and/or fine gravel	18
	R	species associated with rough bottoms, rocks, stones and/or pebbles	7
	M	species associated with a variety of substrata	8
	V	species associated with vegetation or seaweed, given in conjunction with the substrata, S, F, R, M	10
VERT	P	pelagic species, found within the pelagic zone	15
	B	benthic species, found within the benthos	41
	D	demersal species, found above the substrate	16

From this it can be seen that marine adventitious species form the dominant class within the estuary, accounting for 39 % of the species. Most species found within the Humber produce unprotected eggs, either pelagic or benthic. Benthic species form the dominant class within the estuary, with most species being associated with soft or sandy bottoms. There are few species associated with rough ground or vegetation within the estuary.

4.3.2 MAFF Data Analysis

The long-term data recorded by MAFF were analysed together with the data from this study to determine whether the two studies are compatible, and thus to identify any long-term patterns evident from the combined studies. Analysis of the four dominant species, goby, whiting, sole and flounder, shows that there is little difference in patterns between the two sampling occasions, 1976 - 1984 and 1988 - 1994, when based on the mean abundance from the original six sampling sites only, or between the mean abundance from the original sites (1976 - 1984) and the 14 stations sampled from 1988 (Fig. 4.1), with the exception of whiting, ($p = 0.025$, $t = 2.97$, 6 d.f.).

There is no statistically significant difference between the number of species caught using the two sampling protocols, six sites 1976 - 1984 and 14 sites 1988 - 1994, within the MAFF data. The number of species caught per sampling occasion, 9 - 20 (Fig. 4.2), is similar to that found within this study, further demonstrating the compatibility of the two surveys.

Analysis of the MAFF data, together with data from this study, indicates that the present study complements the MAFF survey by identifying seasonal variations in the data (Fig. 4.3). This is apparent in 1993 and 1994, when both data sets merge to form a continuous seasonal trend, illustrating the compatibility of the two studies.

4.3.3 Subtidal Sampling

4.3.3.1 Species Distribution

The presence of each species at the different sites is expressed as the percent occurrence over the period of the study and illustrated as a series of kite diagrams (Fig. 4.4). The data show that the distributions of nine species (cod, sea snail, five bearded rockling, bib, thornback ray, transparent goby, sand eel, dragonet and lemon sole) are restricted to a limited area, i.e outer or middle, within the estuary with a statistical significance of $p < 0.01$. In some cases, for example lemon sole and lampern, the biological significance of the result is questionable due to the small sample size ($n < 5$). Sole, clupeid, dab and lesser weever are also restricted in their distribution ($p < 0.05$), being more common in the outer estuary.

The ranking of the species by percent occurrence indicates that four species, goby (18.4 %), whiting (15.6 %), sole (12.3 %) and flounder (10.6 %), were dominant, accounting for more than 50 % of the recorded presences. These species, together with a further seven, sprat (8 %), plaice (7.4 %), herring (5.7 %), sea snail (4.6 %), pogge (3.1 %), 3-spined stickleback (2.7 %) and cod (2.4 %), accounted for

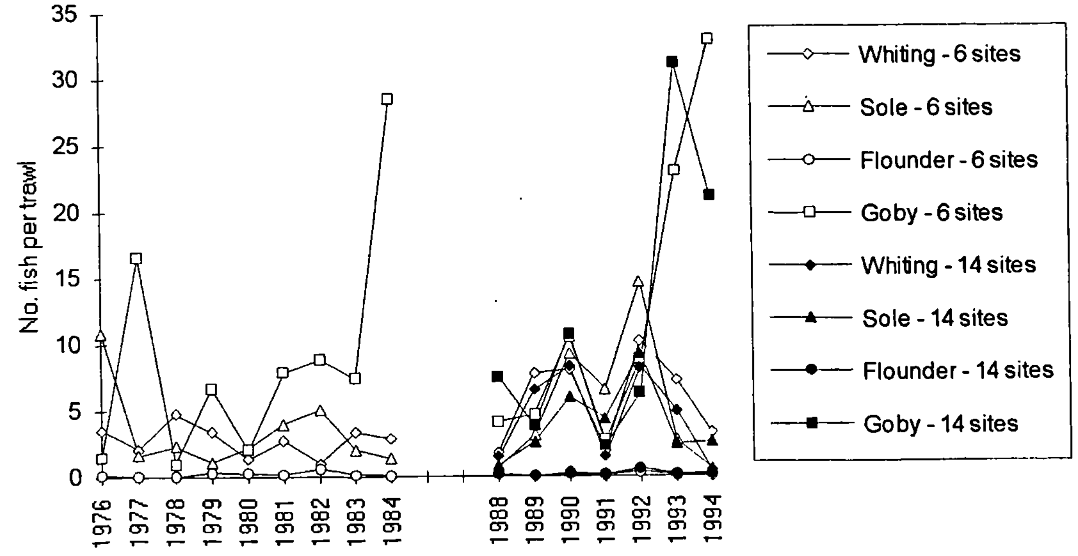


Fig. 4.1 The average number of fish caught per trawl during the annual MAFF sampling.

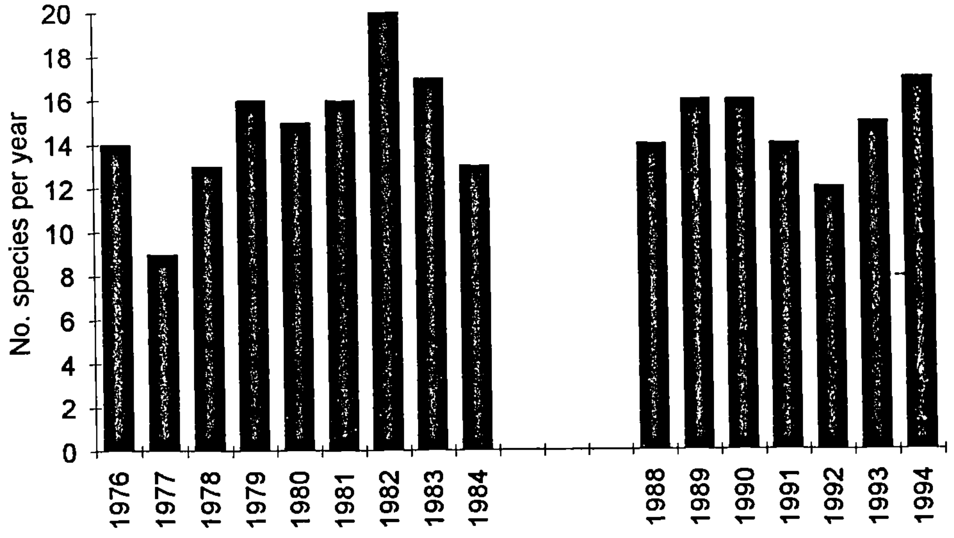


Fig. 4.2 The number of species caught per sampling occasion during the annual MAFF sampling.

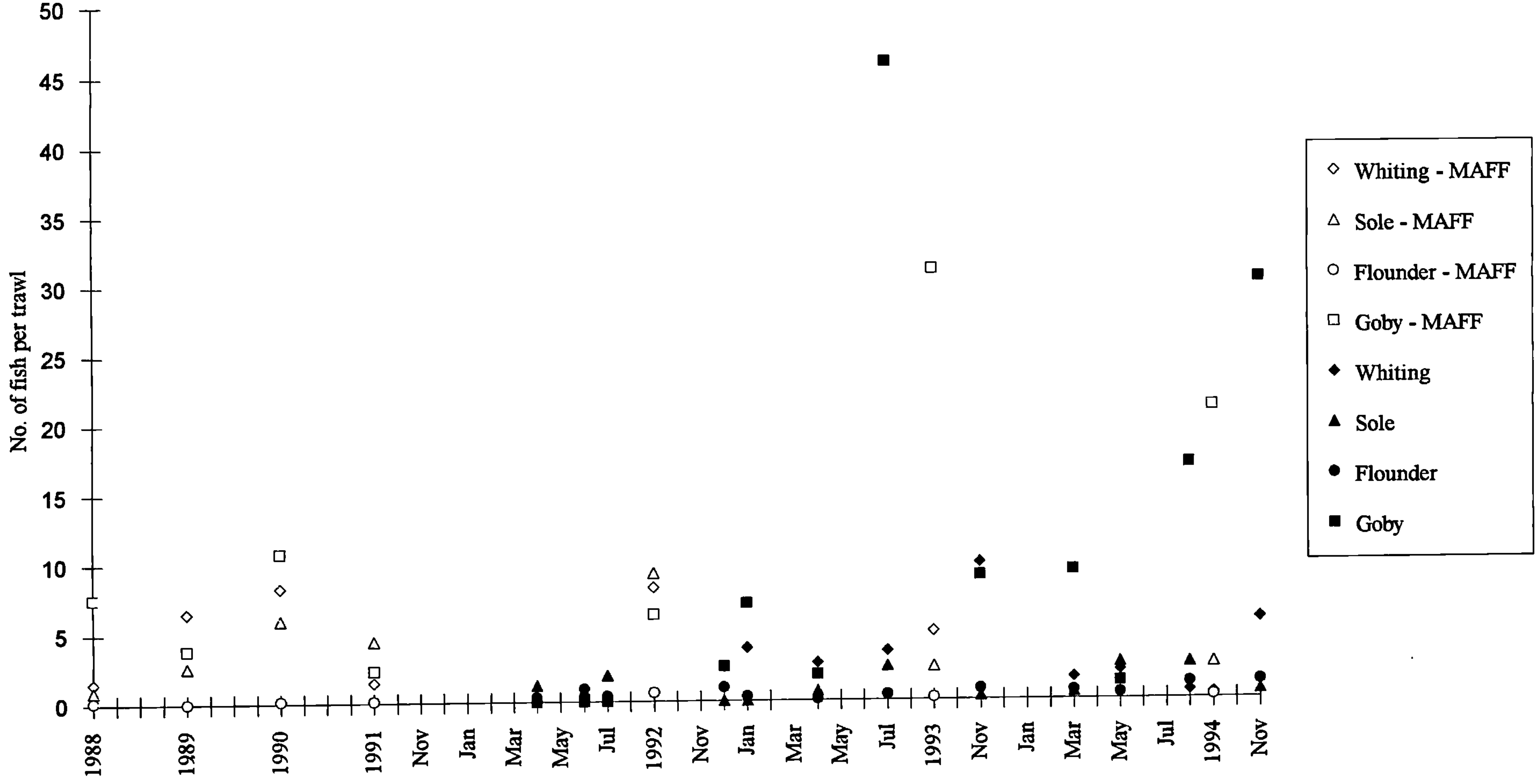


Fig. 4.3 The average number of fish per trawl caught during both this study and the annual MAFF study. Year legends on the x-axis refer to MAFF sampling in the September of each year.

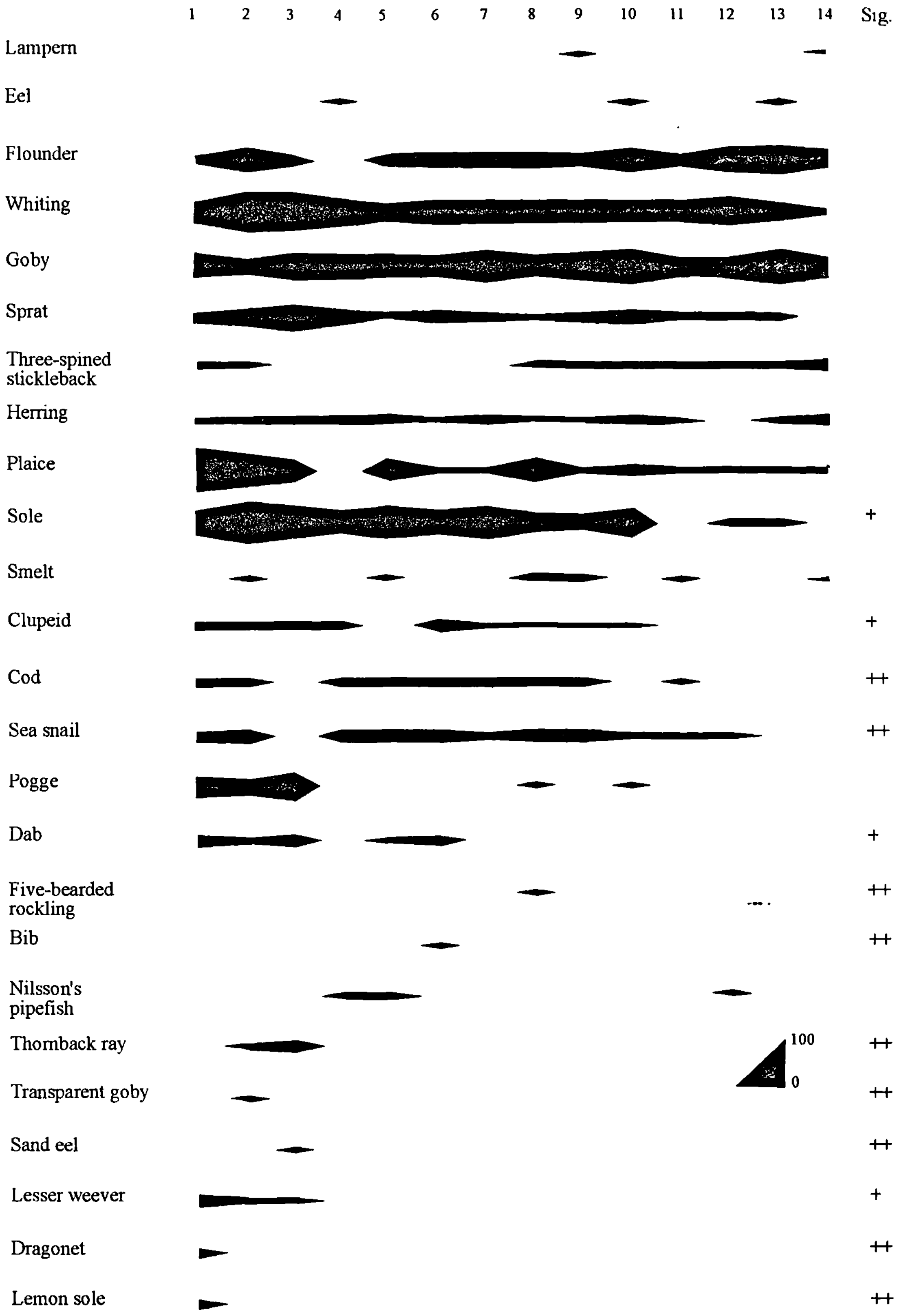


Fig. 4.4 Kite diagram showing the distribution and percent occurrence of each species in the Humber estuary. (significance of bunching in the distribution, +, 0.01 < p < .005; ++, p < 0.01; sites numbered as Table 2.1)

approximately 90 % of the recorded presences. Thus the assemblage can be seen to be dominated by a few species, while others occur infrequently thereby increasing the diversity. This ranking was used to determine dominance for subsequent analyses.

Analysis of the abundance data produces a slightly different ranking. Goby accounts for 59 % of the animals caught during the study and this, together with a further 5 species, whiting (12.6 %), sprat (6.6 %), sole (5.6 %), plaice (4.1 %) and flounder (3.6 %), account for > 90 % of the catch. Despite a change in the order of species, it can be seen that the same six species are placed at the top of the ranking by both percent occurrence and abundance data.

4.3.3.2 Population Size and Dynamics

Species diversity shows a seasonal pattern which varies with area, with the outer and lower estuary showing an increased diversity in summer in contrast to an increase in winter within the middle and upper estuary (Fig. 4.5). There appears to be an increase in species number with change in trawl (Fig 4.6.1(a)), although this is not reflected in a change in diversity (Fig. 4.5). Statistical analysis of the number of species caught by each trawl indicates that trawl 3 data are significantly different from those obtained by 1 and 2, but that no difference exists between data from trawls 1 and 2 (F = 0.0012, 11 d.f.).

There is a significant difference in the number of species caught per area of the estuary (F = 0.0015, 46 d.f.). This difference was recorded between the outer estuary and the lower and upper areas. No other differences were observed between the different areas:

	Lower	Upper	Middle	Outer
$\bar{x}$	4.36	4.50	6.42	9.33

The abundance and biomass of all fish in the estuary for each sampling occasion are given in Fig. 4.6(a), both for the whole estuary and the different areas. This indicates that the use of the estuary is seasonal, with the greatest abundance occurring during the summer period (Fig. 4.6.1(a)), decreasing between November and April. This can be spatially analysed by a review of individual areas. Abundance and biomass fluctuate throughout the year in the outer estuary (Fig. 4.6.2(a)), with lowest values recorded in the spring (April/May) and autumn (November), suggesting a seasonal effect as animals migrate into and out of the estuary.

The lower and middle areas follow the same general patterns in species distribution (Figs 4.6.3(a) & 4.6.4(a)), although the peaks show a slight variation between each area. The data show a seasonal pattern, with higher biomass and abundance in the summer, lowest April/May. However the data set is too short to draw long term conclusions. There was a peak in biomass and abundance during the

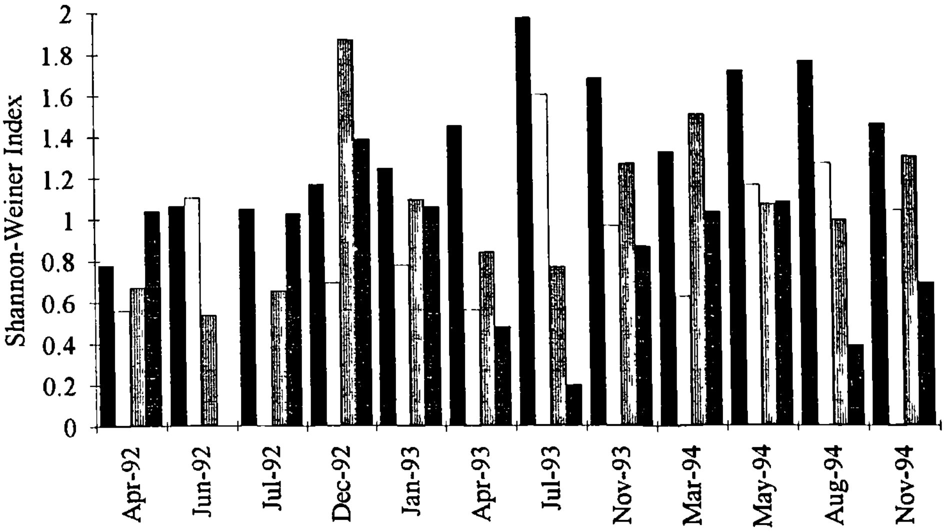


Fig.4.5(a) The Shannon-Weiner Diversity Index for each area of the estuary per sampling occasion.

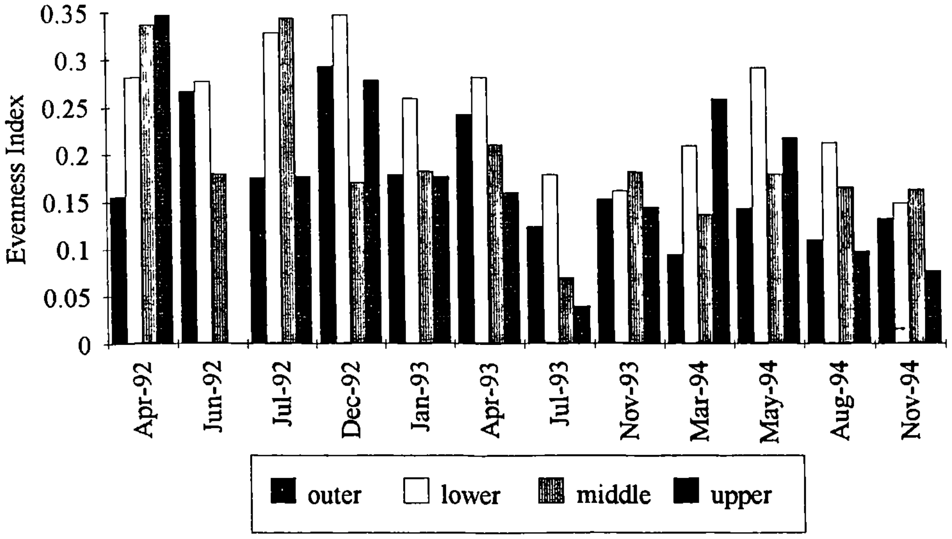
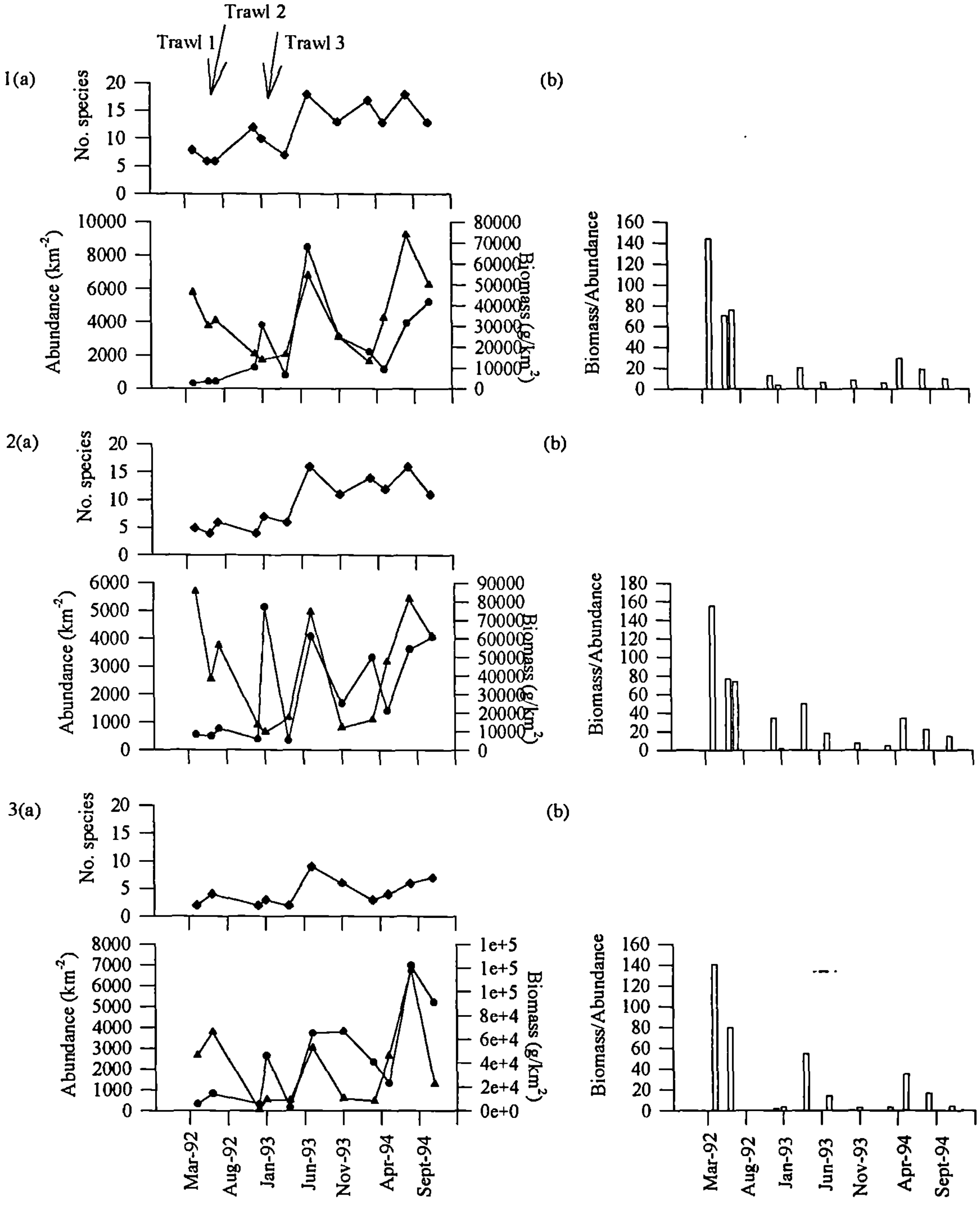


Fig.4.5(b) The 'Evenness' Index for each area of the estuary per sampling occasion.


Trawl 2
Trawl 1
Trawl 3
1(a)
(b)
No. species
20
15
10
5
0
Abundance (km-2)
10000
8000
6000
4000
2000
0
Biomass (g/km2)
80000
70000
60000
50000
40000
30000
20000
10000
0
Biomass/Abundance
160
140
120
100
80
60
40
20
0
2(a)
(b)
No. species
20
15
10
5
0
Abundance (km-2)
6000
5000
4000
3000
2000
1000
0
Biomass (g/km2)
90000
80000
70000
60000
50000
40000
30000
20000
10000
0
Biomass/Abundance
180
160
140
120
100
80
60
40
20
0
3(a)
(b)
No. species
20
15
10
5
0
Abundance (km-2)
8000
7000
6000
5000
4000
3000
2000
1000
0
Biomass (g/km2)
1e+5
1e+5
1e+5
8e+4
6e+4
4e+4
2e+4
0e+0
Biomass/Abundance
160
140
120
100
80
60
40
20
0
Mar-92
Aug-92
Jan-93
Jun-93
Nov-93
Apr-94
Sept-94

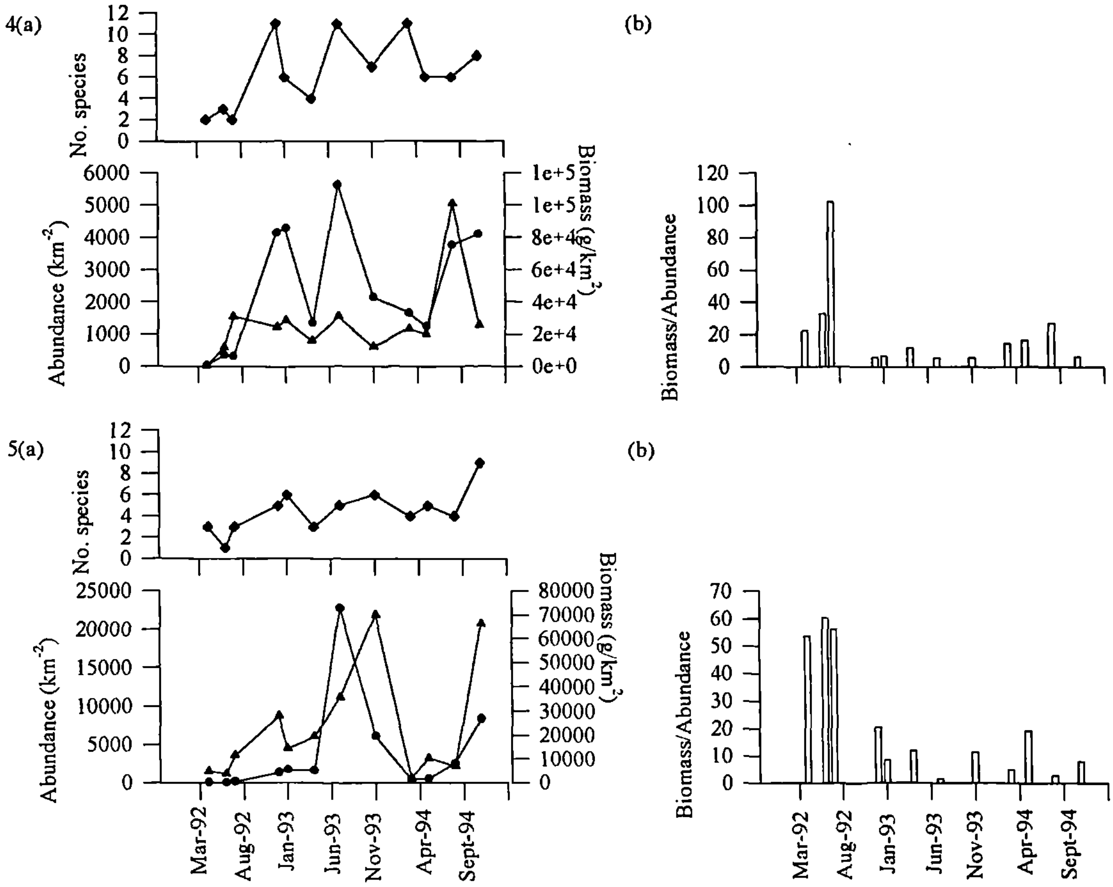


Fig. 4.6 Species number, abundance and biomass (a) and biomass/abundance ratio (b) for fish in 1, the whole; 2, the outer; 3, the lower; 4, the middle; 5 the upper estuary.

summer of 1993 in the upper estuary (Fig. 4.6.5(a)). This was not repeated in 1994 when very low values were recorded throughout the year. The large values for B/A recorded during 1992 may reflect the large mesh on trawl 1, which will selectively catch larger animals (Fig. 4.6(b)).

There was no statistically significant difference in the abundance of fish caught with area, based on combined seasonal data. Seasonal differences were observed between the abundance of fish caught in July compared to other months ($F < 0.0001$, 58 d.f.), with the exception of May, August, November and December, which showed no significantly different seasonal patterns:

	Jan.	Mar	Feb.	Jun.	Oct.	Apr.	Sept.	Aug.	May	Nov.	Dec.	Jul.
$\bar{x}$	264	424	433	860	1137	1499	1984	3365	3524	4179	5404	8934

4.3.3.2.1 Goby

Few gobies were caught in the estuary during 1992 prior to the change in trawl (Fig. 4.7.1(a)) indicating a high avoidance of capture with trawl 1, possibly from escape through the mesh. The timing of seasonal peaks in numbers of gobies is similar to the total abundance and biomass data for the estuary in 1993, but not in 1994. In July 1993, gobies accounted for approximately 75 % of the total abundance in the area, but less than 10 % of the biomass.

In the outer estuary the highest number of gobies were caught in the winter (Fig. 4.7.2(a)), declining during the summer and autumn. They accounted for two thirds of the total catch in March 1994 but were lost from the area between April and August of the same year before returning to the catch in November.

The lower estuary showed a similar pattern (Fig. 4.7.3(a)). However the peak numbers occurred slightly earlier than those in the outer estuary. This was repeated during 1993 in the middle estuary (Fig. 4.7.4(a)) but not in 1994 when the fish appeared to show a gradual increase in numbers throughout the year. The greatest numbers of gobies were found in the upper estuary (Fig. 4.7.5(a)), although this was recorded during the summer of 1993 only. Few gobies were caught in this area during the winter months or during 1994, although the fish caught during November 1994 were predominantly larger individuals (Fig. 4.7(b)).

The differences between the areas indicate a migration downstream in winter. This migration is further indicated by the ANOVA tests, which show that there was no statistically significant difference in abundance between the four areas, based on combined seasonal data. Seasonal differences were observed, with the abundances recorded in July being significantly higher than those in January, February, March, April, June and October ($F = 0.0076$, 58 d.f.), based on combined area data:

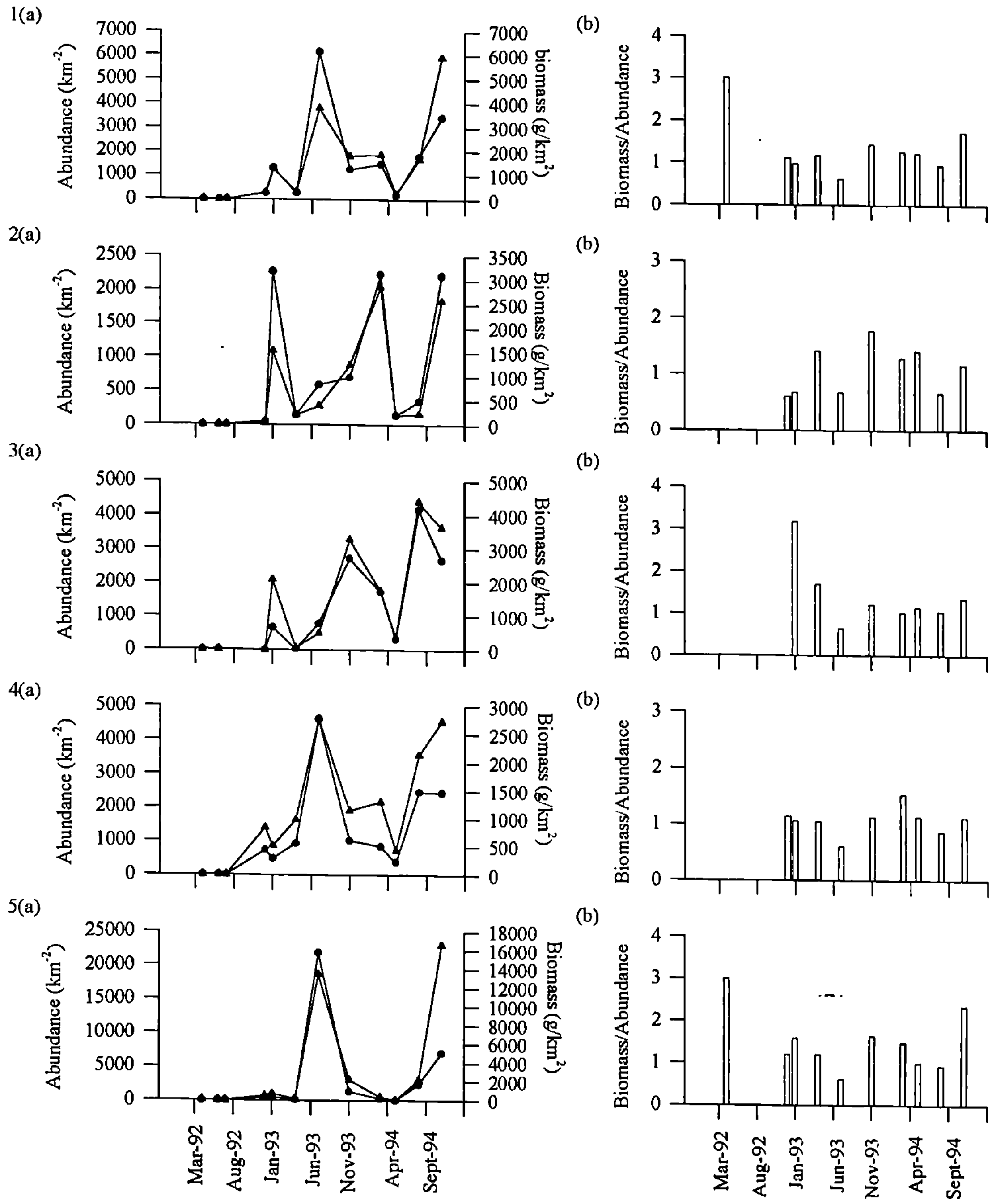


Fig. 4.7 Abundance and biomass (a) and biomass/abundance ratio (b) for gobies in 1, the whole; 2, the outer; 3, the lower; 4, the middle; 5 the upper estuary.

	Feb.	Mar	Jan.	Oct.	Apr.	Jun.	May	Sept.	Aug.	Nov.	Dec.	Jul.
$\bar{x}$	0	0	6	220	307	313	1038	1304	1409	2225	3562	6802

This relates to the high abundance noted within the upper estuary in July 1993.

4.3.3.2.2 Whiting

Whiting were present throughout the year, although occurring in greatest numbers during the winter (Fig. 4.8.1(a)). Few were caught prior to the first change in trawl, although this may be a seasonal pattern rather than a consequence of this change. However, analysis of the abundance data for each month shows that the only statistically significant difference between catches was observed between August and January. There was no significant difference in abundance between the different areas:

	Jan.	Feb.	Mar	Nov.	Oct.	Sept.	Apr.	Jun.	Jul.	May	Dec.	Aug.
$\bar{x}$	0	0	6	220	307	313	1038	1304	1409	2225	3562	6802

Within the outer estuary there was a predominance of larger fish during June and July in 1993 and 1994 (Fig. (4.8.2(b)). This was followed by a peak of smaller fish in November 1994. However there were no obvious seasonal patterns, indicating that the data set may be too short. A similar pattern could be seen in the lower estuary (Fig. 4.8.3(b)), with the exception of the slight increase in June 1994.

The number of whiting recorded increased up the estuary from the outer to the upper, but the seasonality became more pronounced with the progression upstream (Fig. 4.8(a)). Within the middle estuary, whiting occurred mainly in autumn and winter, with the highest abundance and biomass in January 1993 (Fig. 4.8.4(a)). This was not reflected in the upper estuary where the greatest abundance was found in November 1993 (Fig. 4.8.5(a)). Whiting accounted for approximately two thirds the total assemblage biomass in the upper estuary, and 80 % of the abundance.

4.3.3.2.3 Sole

Sole showed a seasonal usage of the estuary, with higher abundances in the summer than the winter (Fig. 4.9.1(a)). Statistical analysis shows that there were significant differences in sole abundance between the catches in October and those in April and May, and also between November catches and those in April, May, August and September (F = 0.0002, 58 d.f.).

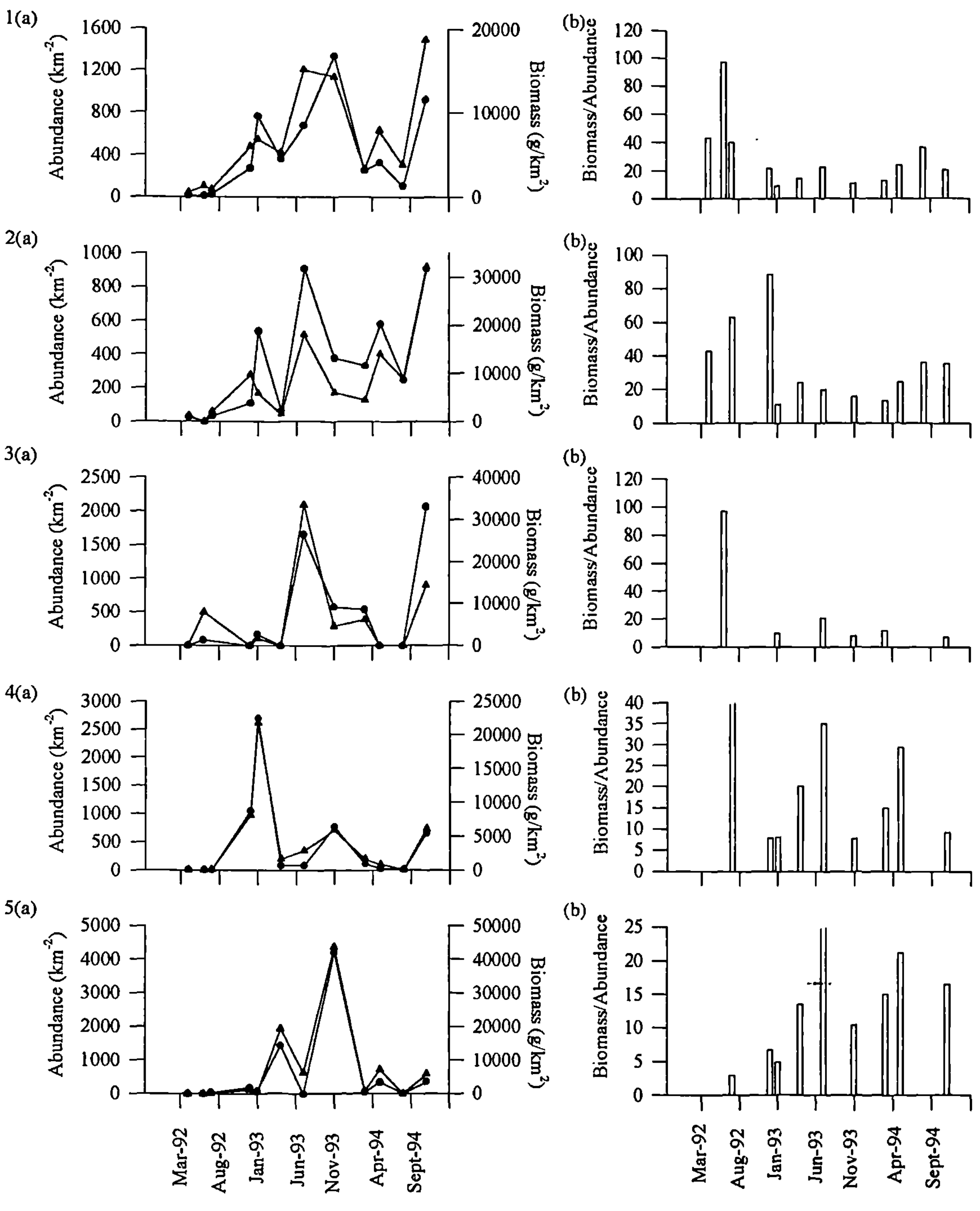


Fig. 4.8 Abundance and biomass (a) and biomass/abundance ratio (b) for whiting in 1, the whole; 2, the outer; 3, the lower; 4, the middle; 5 the upper estuary.

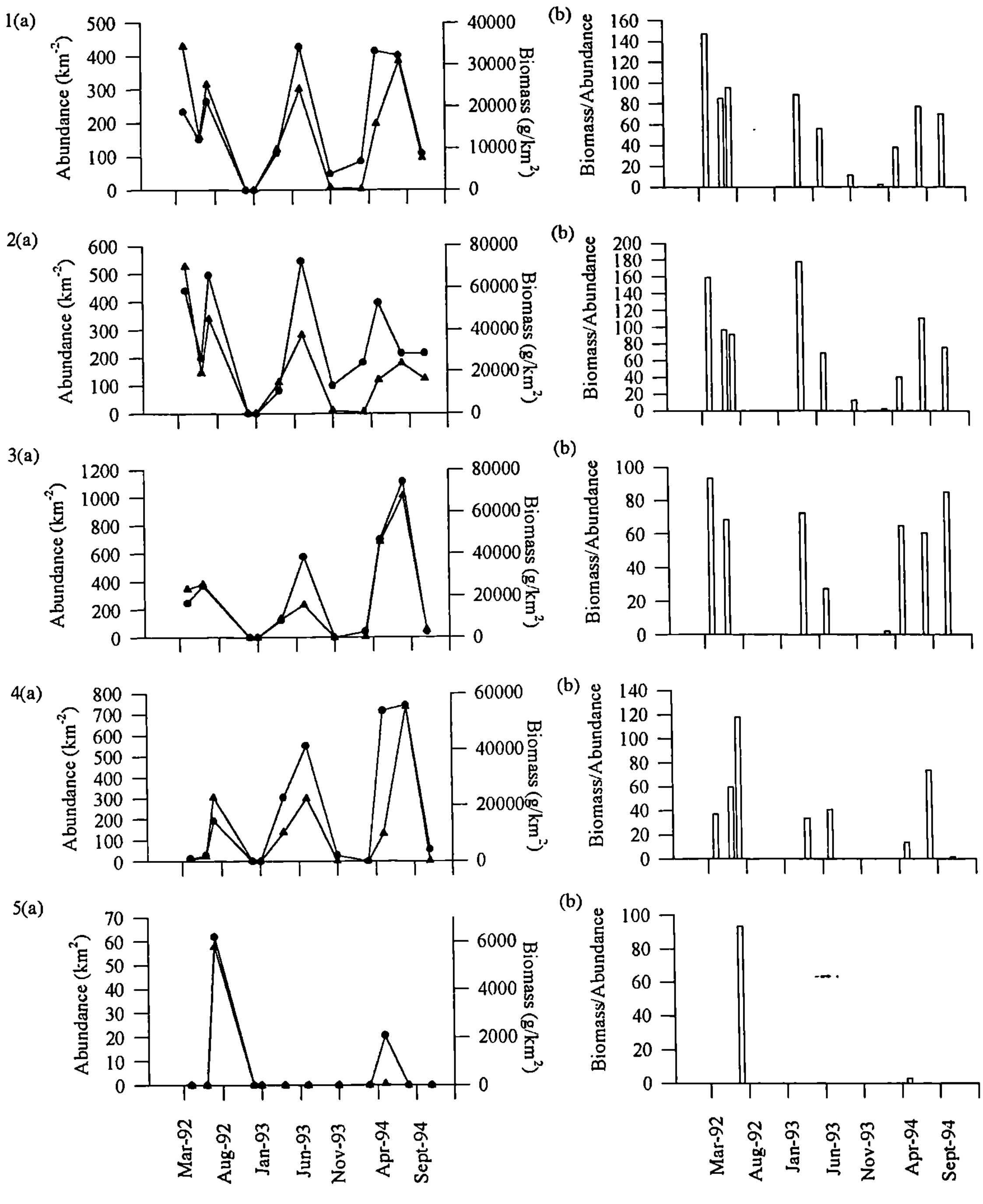


Fig. 4.9 Abundance and biomass (a) and biomass/abundance ratio (b) for sole in 1, the whole; 2, the outer; 3, the lower; 4, the middle; 5 the upper estuary.

	Apr.	May	Aug.	Sept.	Dec.	Jun.	Feb.	Jan.	Mar	Jul.	Oct.	Nov.
$\bar{x}$	0	0	35	62	84	124	149	187	254	420	450	495

Area differences were observed between the upper and the lower estuary (F = 0.0410, 46 d.f.).

	Upper	Middle	Outer	Lower
$\bar{x}$	7	219	239	293

There was no apparent effect on the catches of changing the trawl in either January 1993 or July 1993. This reflects the nature of the trawl, which is predominantly used to catch demersal fish and flatfish, and the fact that most of the sole caught throughout the study period were adults (Fig. 4.9.1(b)).

A similar pattern was observed in the outer estuary (Fig. 4.9.2(a)), with the exception of August 1993 when low numbers were recorded, and the lower and middle estuaries (Figs 4.9.3(a) & 4.9.4(a)). In the lower and middle estuaries the greatest biomass and abundance were recorded during 1994. While adults dominated the catches, sole caught in the middle estuary during May 1994 were smaller, possibly juveniles (Fig. 4.9.4(b)). There were few sole found in the upper estuary, occurring only in August 1992 and May 1994 (Fig. 4.9.5(a)).

4.3.3.2.4 Flounder

Flounder also appear to be seasonal in their distribution (Fig. 4.10.1(a)), with reduced catches around April, although the fish remain in the estuary throughout the year. As with sole, the change in trawl did not have an effect on the biomass and abundance data for flounder. There was an increase in abundance from the outer to the upper estuary, although there was no statistically significant difference between the areas, based on combined seasonal data, or months, based on the combined areas.

No flounder were found in the outer or lower estuary during the winter (Figs 4.10.2 & 4.10.3), where the species had a highly seasonal distribution. The greatest abundance was recorded during June and July in these areas. While the temporal patterns observed were similar in both areas, abundance and biomass were greater in the lower estuary. This pattern changed in the middle estuary where two peaks were observed during 1992 and 1994 (Fig. 4.10.4(a)). These occurred in February/March and also July/August. There were few flounder caught in this region during 1993. The upper estuary showed the greatest abundance during November and December (Fig. 4.10.5(a)). These were predominantly smaller fish (Fig. 4.10.5(b)) and there was a low abundance in this area during the summer. A seasonal migration was also observed, with fish leaving the estuary in March and April (Fig. 4.11).

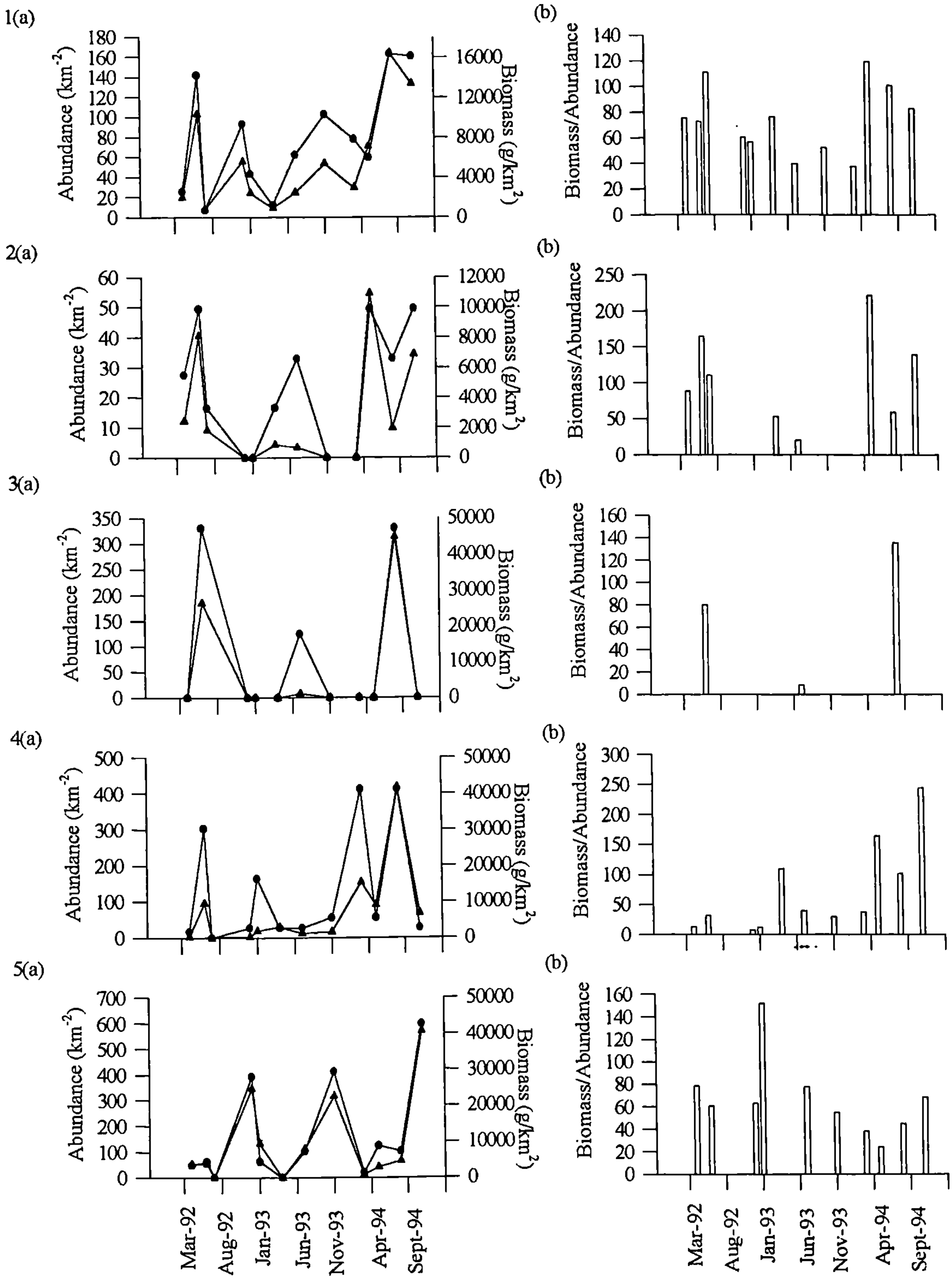


Fig. 4.10 Abundance and biomass (a) and biomass/abundance ratio (b) for flounder in 1, the whole; 2, the outer; 3, the lower; 4, the middle; 5 the upper estuary.

4.3.4 Intertidal Sampling

4.3.4.1 Total Catches

Figures 4.12(a) and (b) show the changes in abundance and biomass with time for the fish populations at Spurn and Cleethorpes. Most fish were found at Cleethorpes, with the exception of October, December and August, when maximum numbers were found at Spurn. However, there was no statistically significant difference observed between the abundances at the two sites, at $p < 0.05$. The largest abundances were found between August and November.

Thirteen species were recorded during the intertidal sampling, although only plaice occurred in high numbers within the trawls (Table 4.2). Gobies were found at both sites in the winter, while brill were found in the autumn. The brill caught were predominantly small in size, < 50 mm. Stickleback were also caught in the winter, as were sole and whiting. Sprat occurred in the catches during the summer, while lesser weever, turbot and herring do not show any seasonal patterns. Saithe, pollack and cod were each recorded on only one occasion.

The Biomass/Abundance ratios (Fig. 4.12(c)) indicate that fish of a similar size were caught throughout the year, although larger fish were caught at Spurn in December, May and July. Most of the fish caught were small, < 7 cm.

4.3.4.2 Plaice

Figure 4.13 shows the changes in abundance and biomass with time for the plaice populations at Spurn and Cleethorpes. Plaice dominated the samples at both stations, comprising > 80 % of the catch on all occasions at Cleethorpes (Table 4.2) and > 60 % of all catches with the exception of June 1994 at Spurn, and therefore mirror the patterns described for the total intertidal catches. There were significantly greater abundances noted at Cleethorpes, ($p = 0.037$, $t = 2.37$, 11 d.f.). The greatest abundance of plaice was caught at Cleethorpes in November, 60 fish per unit effort.

4.3.5 Trapping

As the traps did not operate effectively within the intertidal areas sampled, no fish were taken by this method. This was the result of the wings being uprooted and was caused by tidal and wave action.

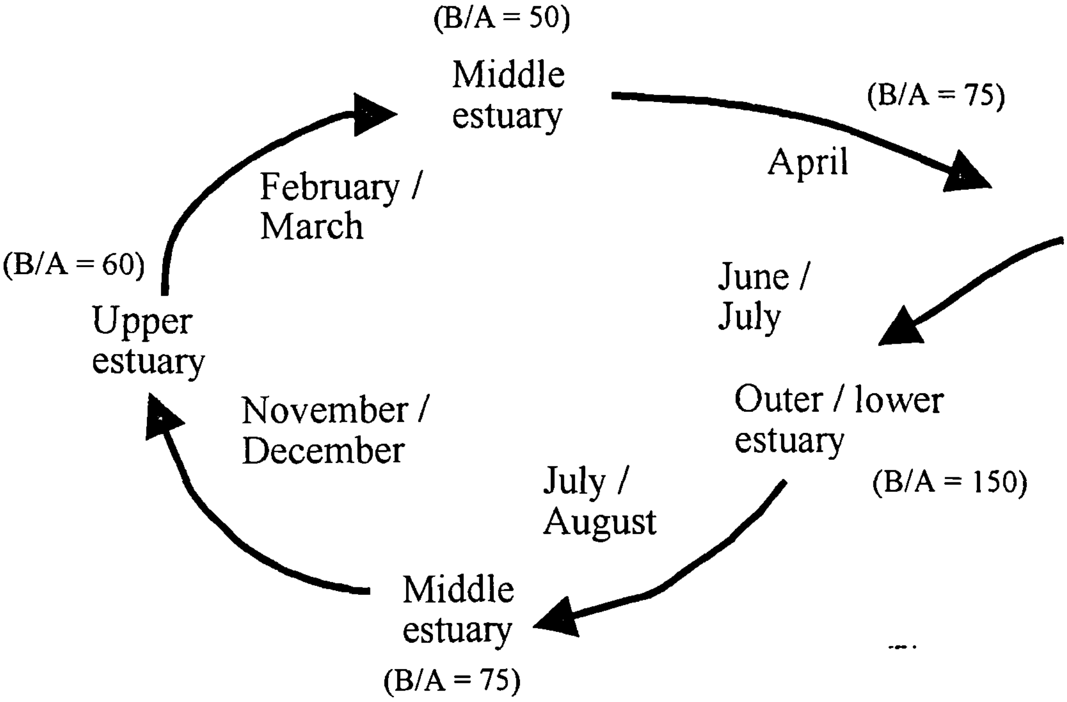


Fig. 4.11 The migration patterns of the flounder in the Humber estuary.

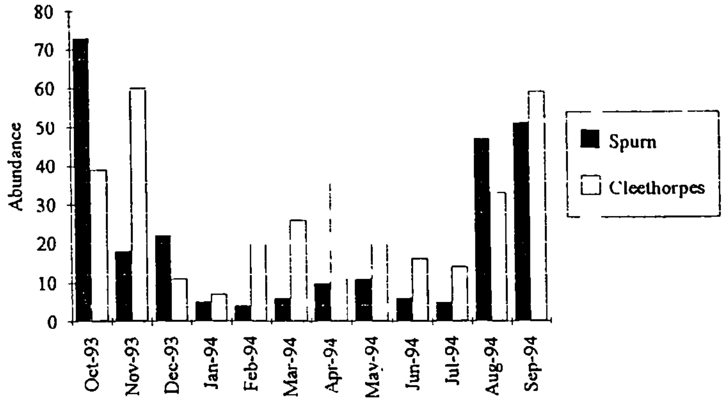


Fig. 4.12 (a) The abundance of fish from the intertidal areas within the outer Humber estuary

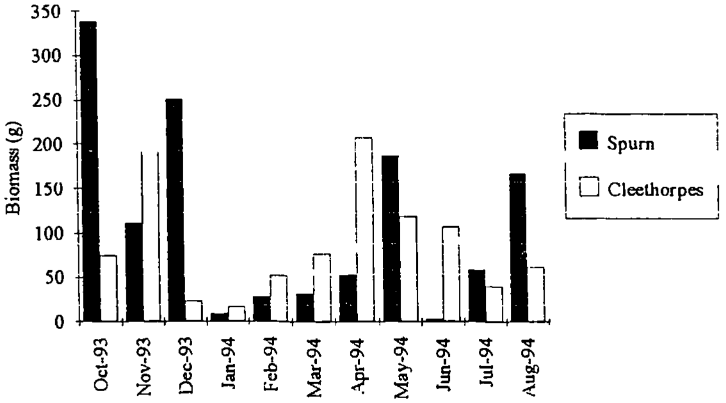


Fig. 4.12 (b) The biomass of fish from the intertidal areas within the outer Humber estuary

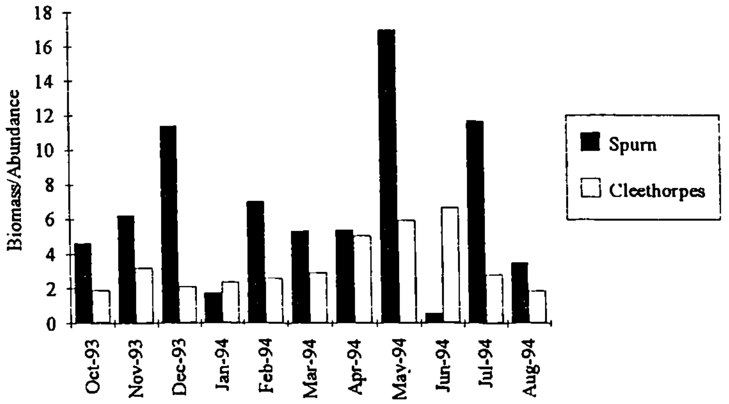


Fig. 4.12 (c) The biomass/abundance ratio of fish from the intertidal areas within the outer Humber estuary

Table 4.2 Abundance of species caught during the intertidal sampling in the outer estuary.

Species	Plaice		Brill		Turbot		Lesser Weever		Saithe		Pollack		Whiting	
Date	Spurn	Cleeth.	Spurn	Cleeth.	Spurn	Cleeth.	Spurn	Cleeth.	Spurn	Cleeth.	Spurn	Cleeth.	Spurn	Cleeth.
October 1993	53	39					4						5	
November 1993	14	60	1								2			
December 1993	18	10											1	
January 1994	5	6												
February 1994	3	19							1					
March 1994	6	22												
April 1994	10	41												
May 1994	7	20			1		2							
June 1994		16												
July 1994	5	13						1						
August 1994	32	30	4		4		4	1						
September 1994	45	57	4	2	1		1							

Species	Cod		Goby		Sole		Herring		Sprat		Three-spined Stickleback		Proportion plaice (%)	
Date	Spurn	Cleeth.	Spurn	Cleeth.	Spurn	Cleeth.	Spurn	Cleeth.	Spurn	Cleeth.	Spurn	Cleeth.	Spurn	Cleeth.
October 1993			4		7								72.6	100
November 1993			1										77.8	100
December 1993				1									81.8	90.9
January 1994												1	100	85.7
February 1994				1									75	95
March 1994						1		1				2	100	84.6
April 1994													100	100
May 1994									1				63.6	100
June 1994									6				0	100
July 1994													100	92.9
August 1994							3	2					68.1	90.9
September 1994													88.2	96.6

Table 4.2 Abundance of species caught during the intertidal sampling in the outer estuary.

Species	Plaice		Brill		Turbot		Lesser Weever		Saithe		Pollack		Whiting	
Date	Spurn	Cleeth.	Spurn	Cleeth.	Spurn	Cleeth.	Spurn	Cleeth.	Spurn	Cleeth.	Spurn	Cleeth.	Spurn	Cleeth.
October 1993	53	39					4						5	
November 1993	14	60	1								2			
December 1993	18	10											1	
January 1994	5	6												
February 1994	3	19							1					
March 1994	6	22												
April 1994	10	41												
May 1994	7	20			1		2							
June 1994		16												
July 1994	5	13						1						
August 1994	32	30	4		4		4	1						
September 1994	45	57	4	2	1		1							

Species	Cod		Goby		Sole		Herring		Sprat		Three-spined Stickleback		Proportion plaice (%)	
Date	Spurn	Cleeth.	Spurn	Cleeth.	Spurn	Cleeth.	Spurn	Cleeth.	Spurn	Cleeth.	Spurn	Cleeth.	Spurn	Cleeth.
October 1993			4		7								72.6	100
November 1993			1										77.8	100
December 1993				1									81.8	90.9
January 1994												1	100	85.7
February 1994				1									75	95
March 1994						1		1				2	100	84.6
April 1994													100	100
May 1994									1				63.6	100
June 1994									6				0	100
July 1994													100	92.9
August 1994							3	2					68.1	90.9
September 1994													88.2	96.6

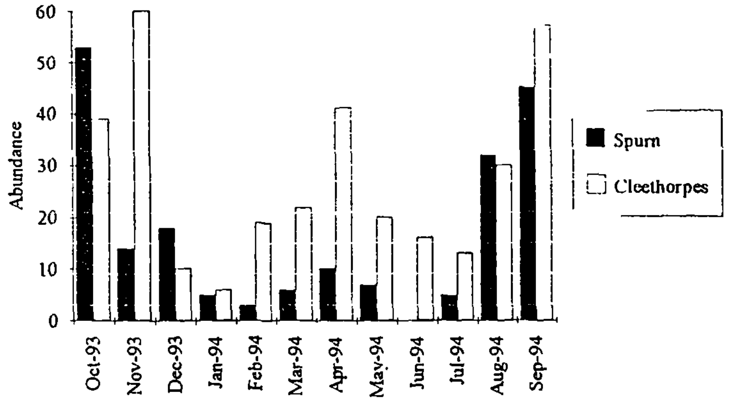


Fig. 4.13 (a) The abundance of plaice from the intertidal areas within the outer Humber estuary

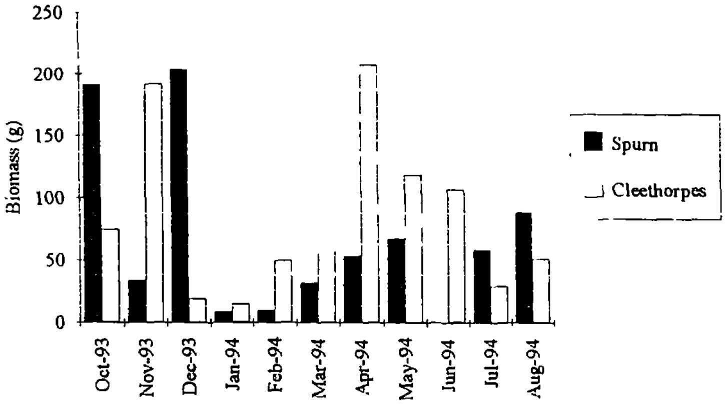


Fig. 4.13 (b) The biomass of plaice from the intertidal areas within the outer Humber estuary

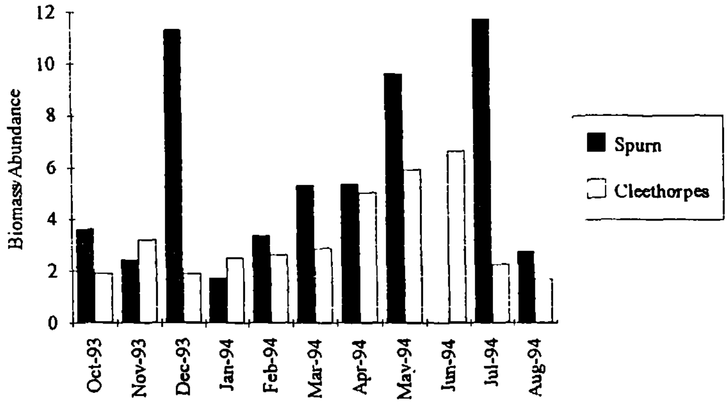


Fig. 4.13 (c) The biomass/abundance ratio of plaice from the intertidal areas within the outer Humber estuary

4.4 Discussion

4.4.1 Species Composition

The Humber estuary has a diverse fish assemblage, comprising of many different ecological types, both resident and migratory. With 72 species reported within the Humber, this compares favourably with the predicted value of 60 species for this latitude (Henderson 1989). However many of these species were rare, occurring only at the estuary mouth or tidal freshwater reaches, and some of the recordings are unsubstantiated. The species composition observed within the estuary is similar to that in the Forth, Tyne and Solway, when compared by species present (Dewailly 1994). When examining the populations by taxonomic group rather than species, this similarity is extended to the Southern Dutch estuaries. This does not appear to be related to geographical position, either coastal or in relation to the neighbouring sea, but to other factors, both biotic or abiotic.

Biotic factors include the mode of reproduction, substratum preference and vertical position within the water column thus describing the ecological guild of the species, e.g. seasonal migrant. Most species can be described by a particular guild, irrespective of the estuary being examined (Costa & Elliott 1991; Dewailly 1994). Within the Humber there is a high proportion of benthic fish, utilising sand or soft bottom areas. The latter reflects the relatively uniform substratum within the area, which is comprised predominantly of sand and mud (NRA 1993), and lack of rocky or vegetated areas. The reproductive strategy of the fish is relevant as a descriptor of estuarine residents and species which utilise the area for spawning, e.g. sole. With regards to other categories of fish within the estuary, particularly the marine and freshwater adventitious species, a knowledge of the reproductive strategy, with spawning occurring in other areas, is unlikely to enhance the understanding of the functioning of the community within the Humber estuary, although it may give an indication of when the species will enter the area.

The difference in species numbers between the complete species list and the fish found within this survey is partly a function of the sampling method used and partly the intensity of sampling. The beam trawl is restricted to harder, smooth sediments, i.e. sand or mud, and promotes an escape reaction in many species. In particular, the size of the trawl results in an under-representation of large round fish (Poxton 1987), which can avoid the trawl by swimming round or over it. It is best suited to the sampling of flatfish and small demersal populations (Gee 1983), as reflected by this study. However it is notable that species which commonly inhabit mixed (i.e. sand/mud/rock) estuarine areas, e.g. butterfish, gurnards and scorpion fish, and which are usually taken by comparable gear (Pomfret *et al.* 1991) were missing from the samples taken here. This is likely to be the result of the paucity of hard and mixed bottom within the Humber (NRA 1993) and relatively low densities of these species within the estuary (MAFF unpubl. data).

Analysis of the MAFF data indicates that the number of species caught by the beam trawl is finite, with most species found within the Humber being sampled within the first six trawls. In addition, these species are found throughout the estuary, as there is not a significant increase in the number of species captured with increased sampling area, from six to 14 stations, although this may be the result of the decrease in diversity with distance upstream observed within this study, as the original six stations were situated in the outer estuary. However, it would appear that the beam trawl adequately samples the assemblage of small marine and resident species.

4.4.2 Subtidal Sampling

There is an increase in diversity towards the lower and outer reaches during the summer months, with the observed distribution being similar to that reported in the Forth and Tyne (Elliott & Taylor 1989(b); Pomfret *et al.* 1991). However the subtidal population is dominated by four species, gobies, whiting, sole and flounder, accounting for 57 % of the observed occurrences. This suggests that the assemblage is composed of a small resident population supplemented by a large number of short term migrants. An analysis of the ecological categories supports this statement, with seven resident species compared to 22 migratory or adventitious species. That there were only four freshwater or diadromous species found further emphasises the view of an increasing diversity towards the seaward end.

Within the subtidal sampling it appears that five regularly occurring (n > 5 individuals) species: cod, sea snail, sole, clupeid and dab, show a restricted distribution within the area. These were predominantly absent from the upper estuary. This pattern is further reflected in the number of species caught per area of the estuary (Fig. 4.6). There was a consistently higher number of species found in the outer estuary, and lower number in the upper estuary, compared to the other areas throughout the study period. The exception to this was in December 1992, following the first change in trawl, when a greater number of species were recorded in the middle estuary.

Temporal changes in species number show a regular pattern, although this does not reflect a seasonal pattern, indicating that the movement of species into, and out of, the estuary is not seasonally dependent. This is in contrast to the conditions found in the Dutch Wadden Sea (Creutzberg & Fonds 1971), where there are a greater number of species found in the summer months. The salinity range in the Dutch Wadden Sea, 15 - 35, is, however, equivalent to that found in the outer and lower areas of the Humber (Fig. 3.2), where a slight seasonal pattern, with highest diversity occurring during July and August (Fig. 4.5), is observed. This is similar to the findings within the Wadden Sea, and indicates that the greater the number of habitats available, as defined by water characteristics, the less dependant species numbers are on seasonal variations.

The total abundance and biomass data for the fish within the estuary show an increase during the summer months, a pattern also reflected in other estuaries, i.e. the Dutch Wadden Sea (Creutzberg & Fonds 1971), and may result from the recruitment patterns of the population. However, the reverse is true for the Forth estuary (Elliott & Taylor 1989(b)), with a reduction in biomass and abundance occurring during the summer and early autumn months. This may reflect the seasonal changes in the flounder population of the upper Forth estuary, which show a peak abundance and biomass in the winter months, but is mainly due to the clupeid populations (M. Elliott, Uni. Hull, pers. comm.). That the outer estuary has the least well defined pattern in this respect reflects the impact of marine migrants, which occur in a random manner within the catches and therefore obscure the seasonal patterns.

Of the four dominant species within the estuary, two are migratory species, occurring either in the summer (sole) or the winter (whiting), while the others are estuarine residents (goby and flounder). This reflects the high usage of the estuary by migratory groups during their period of residence, and therefore the importance of these species to the structure and functioning of the fish assemblage of the area. Thus the importance of seasonal patterns to the composition of the fish assemblage is demonstrated. This pattern of dominance, between resident and migratory species, is similar to that found within the Forth (Elliott & Taylor 1989(b)) and elsewhere (Elliott & Dewailly, in press).

The absence of gobies from the trawls during 1992 was a function of the trawl being used at that time, the larger mesh enabling the fish to escape and thus caution should be exercised in interpreting the results obtained. During the summer of 1993, gobies were most abundant in the upper estuary. This contrasts to the sampling in 1994 when the greatest abundances were recorded in the lower and outer estuary, and indicates that goby abundance may be affected by an external factor, such as differences in reproductive rates between years and areas of the estuary. The short data set precludes analysis of these patterns within this study, although analysis of the MAFF data indicates that they occur throughout the estuary in September and that the abundance fluctuates annually.

The low abundance of gobies in the trawls during the winter period suggests that they migrate within or from the area at this time, possibly as a result of lower temperatures or salinities caused by an increase in freshwater flow. This agrees with Wheeler (1969) who states that sand gobies migrate offshore in autumn. Sand gobies occur throughout the estuary although they are generally regarded as a coastal/lower estuary species (Wheeler, 1969; Whitehead *et al.* 1986). However Hamerlynck (1990) found juvenile sand gobies occurring in estuaries down to a salinity of 5, providing support to the findings of this study.

Flounder populations within the Humber show similar spatial and temporal patterns in distribution to those in the Forth (Elliott & Taylor 1989(b)), with the greatest abundance and biomass recorded in the upper estuary during the winter months. The population dynamics within the outer and lower estuary also correspond to those in the Solway (Williams *et al.* 1965) and the Wadden Sea (Fonds 1979), with fish demonstrating similar migration patterns within the estuary. Their absence from the estuary in January and February may be the result of an offshore spawning migration (Wheeler 1969), or overwintering in deeper waters (Fonds 1979). As they are tolerant of a wide range of salinities, flounder occur throughout the estuary, and this is reflected by the catch data. The upper estuary catches are dominated by smaller flounder compared to the outer areas, indicating a possible depth preference, with larger fish moving to deeper water (Fonds 1979), although adult flounder are also found in the brackish drains that enter the Humber and tidal rivers (NRA 1995).

Migratory species form the main component of the estuarine assemblage. Sole and whiting demonstrate similar patterns of usage within the Humber as were noted in other areas, i.e. the Solway (Williams *et al.* 1965). Sole occur predominantly as adults in the summer months, although juveniles dominate the catches at the beginning and end of the summer, in April and August, (Fig. 4.9.1(b)) suggesting a greater tolerance to low temperatures. They seem to have a greater tolerance to low salinities than the adults, as demonstrated by their occurrence within the upper estuary, although areas near the Humber Bridge are frequently used by anglers when fishing for sole (N. Proctor, Uni. of Hull, pers. comm.). This further illustrates their high usage of the estuary and suggests a wide salinity tolerance.

Whiting appear throughout the year, although in greatest abundance during the winter. This agrees with the population dynamics noted within the Solway (Williams *et al.* 1965), and Forth (Elliott & Taylor 1989(b)), but is contrary to the findings within the Dutch Wadden Sea (Fonds 1979), where whiting were present within the estuary during the autumn but not the winter months. This may reflect the lower temperatures found within the Wadden Sea, as it has been suggested that they avoid areas of very low or high temperatures.

4.4.3 Intertidal Sampling

Fish caught within the intertidal trawls were predominantly juveniles, with plaice being the dominant species. Other species were caught occasionally, i.e. lesser weever, but no great species richness was noted. This is contrary to the MAFF survey which showed a greater diversity, 14 species. This is probably a function of the time of sampling, with MAFF sampling along the low water edge as opposed to high water + 3 hours as in this survey, thereby sampling a more restricted population in terms of space. Also, different gear was used in this survey, hand-pulled beam trawl as opposed to the Riley pushnet, possibly creating another sampling bias.

The abundance of juvenile plaice may be the result of spawning areas along the Coast, which also result in an abundance of plaice at Filey, north of the Humber (Lockwood 1972). It has been shown that plaice exploit special nursery areas near spawning grounds (Bergman *et al.* 1988), and the sandy conditions at both Spurn and Cleethorpes will provide suitable nursery areas. However, the Humber population does not follow the patterns within the Firth of Forth, a coastal embayment, where greatest abundance was found on the north bank (Poxton & Nasir 1985). Within this study greatest abundances were recorded on the south bank. This may be due to the shape of the estuary and position of the sites, with Cleethorpes beach facing the north east, the direction of the water flow along the east coast of England and over the spawning grounds to the north.

The data show the changes in populations over the period of one year. As only juvenile fish were taken, this will relate to spawning and post-settlement migrations. The largest abundances were found within the estuary between August and November. As the main period of hatching is April (Poxton & Nasir 1985), this indicates that the animals take approximately 4 months to metamorphose and grow to a length of approximately 3 cm, at which length they appear in the trawls. That these fish represent that year class can be determined from the decrease in B/A ratio at this time (Fig. 4.10(c)), and ageing from the otoliths (see Chapter 6). There was a second smaller peak in abundance at Cleethorpes during April, composed of larger fish and thus indicating the presence of the previous year class during this time.

5 ENVIRONMENTAL AND BIOLOGICAL INTERACTIONS

5.1 Introduction

Several levels of biological organisation have been defined, from individual through populations to biomes, for the study of nature. A population is defined as a collection of individual organisms of the same species inhabiting the same area. Any study of the interactions between different populations requires an analysis of the community, which is defined as "any assemblage of populations of living organisms in a prescribed area or habitat" (Krebs 1985). Community structure can therefore be viewed as the sum of the properties of the individuals and their interactions (Begon *et al.* 1986), as defined by characteristic features identified by the investigator, both spatial and in terms of taxonomic grouping. Thus, the community within this study is defined as the fish of the Humber estuary, as opposed to all taxa within the estuary.

Most ecology texts (e.g. Colinvaux 1993) recognise a further level of organisation, that of the ecosystem. Ecosystems are defined as the interactions of the community with its physical environment, thereby implying that the two can be studied separately. However, as there is little value in a study of any ecological system, from individual to community, in isolation from its environment, the distinction between ecosystem and community is not made within this study. The environment in which a community exists is vital to the structuring of that community (Begon *et al.* 1986).

Historically there are two views of communities and their structure (Krebs 1985). In 1916 Clements proposed the idea of a 'super-organism', in which the member species have evolved together as a complete entity (Begon *et al.* 1986). In contrast to this, Gleason, in 1926, proposed the individualist approach, where the relationships within the community are a function of similar requirements and tolerances, together with a degree of chance. The current view is closer to Gleason's concept, although inter- and intra-specific interactions are also recognised. This enables some prediction about the species composition of an area, given its physical characteristics, but does not mean that a species from a predictable association cannot occur with a different group of species under different conditions.

Community, or assemblage, analysis can be carried out using the primary community variables of taxon richness, abundance or biomass data. The different measures can be used at the binary (presence/absence) level (taxon richness) or as quantitative data (abundance and biomass). The method used, binary or quantitative, is dependent on the requirements of the study and the original data collection. Quantitative data allow a higher level of analysis, with the determination of the rarity of a species. Studies into the most suitable quantitative measure to describe an assemblage, abundance or biomass, indicate that for most situations there is little difference between the two approaches (e.g. Bianchi & Høisæter 1992). Other studies of estuarine communities (e.g. Hamerlynck *et al.* 1993) support this finding, with community analysis using both biomass and abundance data in the same study resulting in few differences in the described communities. The exception was found to be in cases where many species are common to all samples but individual fish sizes vary across samples, in which case biomass data will give a more detailed analysis of the community structure (Bianchi & Høisæter 1992).

There are a variety of methods available for community analysis (Begon *et al.* 1986), using either binary or quantitative data, and as the data are multivariate, i.e. the abundance or biomass of each taxon per sampling occasion, there is a need for multivariate analysis (Gauch 1982). All methods are of value but contain advantages and disadvantages. Of these, gradient analysis is perhaps the simplest, involving the arranging of the different species' abundance along a selected gradient. However, this requires the preselection of the environmental gradient (ter Braak 1987), thus biasing the results in favour of predicted environmental factors.

Ordination techniques, e.g. DECORANA and TWINSPAN (Hill 1979), allow communities, or sites, to be ordered along continua according to similarities in their species composition and abundance (Begon *et al.* 1986). This has the advantage of removing the subjectivity from the analysis, and can be performed in the absence of environmental variables (ter Braak 1987). Ordination enables the analysis of community attributes, taxon, abundance or biomass, at a series of stations or sites, and can be performed on either Q- or R-mode data. Q-mode classifications describe similarities between different stations according to the taxa present, its abundance or biomass, while R-mode classifications group the taxa according to affinities in their distribution.

The statistical significance of any relationships between individual species and environmental parameters can then be determined by further analysis, although the determination of a significant relationship between two factors does not necessarily prove a causal link between them (Fowler & Cohen 1990), merely provides specific hypotheses for subsequent analysis. A disadvantage to these techniques is that some preselection of environmental parameters is required, albeit based on *a prior* knowledge of what may have an influence on the fauna, therefore not necessarily providing a comprehensive analysis of the system.

Classification techniques have similar properties to ordination in that they are objective analyses. However classification techniques force the associations into discrete entities (Begon *et al.* 1986) which can then be grouped into subsets based on similarities in species composition and abundance. Classification and ordination techniques, when used in conjunction with each other, produce a detailed and complementary description of the community. It is emphasised that any such analysis required the use of several complementary techniques in order to determine the robust trends in the data and eliminate the spurious ones. The latter may be the result of the numerical manipulations, with this approach being analogous to Type I and Type II errors in statistical testing (Zar 1984). The relevance of classification and/or ordination to ecological research is highlighted in Begon *et al.* (1986) where the ordering of communities in a stream system showed little consistency to their spatial relationship, a factor which may have been assumed if using only gradient analysis.

5.2 Materials and Methods

5.2.1 Sites Categorised by Species Composition

The abundance of each species per site was used to obtain a grouping of the sites, based on species composition, within the estuary using Two-Way Indicator Species Analysis, TWINSPAN, within the Cornell Ecology Programmes computer package (Hill 1987). A classification technique, this programme operates by dividing the data into subsets through the use of dichotomies. The species are initially reorganised into pseudospecies based on their abundances and these are then used to group the sites according to the similarity of their species composition. At each division the characteristic pseudospecies for the group are given. Each group is further sub-divided until a predetermined number of divisions has occurred, or the group contains less than 4 species. The results can then be illustrated by use of a dendrogram, with indicator species also shown.

The data were subjected to a $\log_{10}$ transformation prior to analysis, in order to reduce the effect of dominance by certain species. Default values within the programme were used throughout, with the exception of the pseudospecies cut off levels, which were changed to 0, 0.2, 0.4, 0.6 and 1 for the purposes of this analysis. These values were selected to reflect the $\log_{10}$ transformation, with default values within the programme being based on percent values. Pseudospecies are determined by the abundance of the species in the sample, thus Poma spp 4 indicates the presence of *Pomatoschistus* spp. in the sample with an abundance of $0.4 < \log_{10}$ (abundance) ≤ 0.6. The characteristic pseudospecies in each dichotomy are determined within the programme, although these are not necessarily the most common species within the group.

5.2.2 Samples Categorised by Environmental Variables

As the environmental variables were measured in different units, their data were standardised such that each was expressed as a percent of the maximum value recorded for that variable, thus turbidity values were expressed as a percent of 1000. The standardised variables were then analysed using the PCA option within the CANOCO statistical computer package (ter Braak 1988) and the resultant graph produced for Axes 1 and 2. Principal Components Analysis (PCA) is an ordination technique, ranking sites on the basis of the similarities between their environmental components. Sites which appear together on the resultant graph have similar environmental characteristics. The sites were arbitrarily grouped after the analysis according to the upper, middle, lower and outer areas of the estuary, previously defined (Chapter 2), during summer (April to August) and winter (November to March) sampling. Although this constitutes a pre-judgement of the associations, it was considered necessary in order to reduce and interpret the data set.

The site groupings derived from the TWINSPAN analysis, i.e. sites grouped by species composition, were superimposed on the PCA graph. Sites clustered together have similar environmental conditions, thus a comparison of the sites classified by species composition and environmental parameters was possible.

5.2.3 Environmental Influences on the Fish Assemblage

Analysis of the assemblage was completed on the abundance and biomass data using Canonical Correspondence Analysis within the computer programme CANOCO (ter Braak 1988). Only sites for which all environmental parameters had been measured were used for the analysis. A multivariate ordination technique, CANOCO enables the assemblage data to be assessed with respect to environmental parameters. The data were $\log_{10}$ transformed and rare species were downweighted according to the parameters of the programme, with rare species having a frequency < AMAX/5, where AMAX is the frequency of the commonest species, thus reducing the variability within the data. Downweighting also reduces the influence of rare species on the clusters and patterns within the data, thus allowing an assessment of the main components of the assemblage.

With CANOCO, environmental variables are plotted as vectors from the origin. The longer the vector the greater its effect on the observed species distribution. The position of the vectors to each other indicate the relationship between them, thus two vectors at an angle of 180° to each other are negatively correlated. The environmental and species graphs are superimposed within the programme to indicate their positions relative to each other. However the axes' scales used for the two sets of data are not necessarily the same, thus the position of the species data relative to the environmental variables are not exact.

In order to assess the significance of the environmental variables, CANOCO initially determines the amount of variance in the species data described by each variable. The individual variables can then be assessed using the Monte Carlo method (section 4.2) to test whether the additional effect of the variable on the species data are statistically significant (ter Braak 1988).

The Spearman Rank Correlation Coefficient was used to determine the significance of each variable to the distribution of the different species. This univariate, non-parametric statistical technique enables the relationship between species abundance and environmental parameters to be analysed individually, thus determining the independent variables that are most likely to affect the distribution of each species together with the nature of the effect. The use of the partial correlation coefficient, with salinity as the controlling factor, enables a comparison of the observed effects with the interactions caused by position within the estuary.

5.3 Results

5.3.1 Classification of Sites by Species Composition

The result of the TWINSPAN classification indicated a clustering of sites by species composition (Fig. 5.1). The first division is seasonal in nature, separating sites into predominantly summer or winter samples, although exceptions do occur, e.g. Whitton 12.92 occurs in the summer group. The next division of the winter samples produced a grouping of seaward sites (WS), with the subsequent division of the remaining sites producing a central (WC) and a lower salinity (WR) group. WR can be further divided into very low salinity and low salinity sites (WR(a) and WR(b)). Within the summer samples, the first division separated 4 unusual groups (SM), prior to dividing the remainder into low salinity (SR) and seaward (SS) samples. In each case the cluster descriptions are not rigidly adhered to within the group but explain the dominant type, i.e. some upper estuary samples from the summer may be located within the WS cluster but most of the samples will be lower or outer estuary sites sampled in the winter months.

Thus six groups of stations were defined:

- seaward sites, sampled in the winter (WS);
- central sites, sampled in the winter (WC);
- low salinity sites, sampled in the winter (WR), with subdivisions into very low salinity (a) and low salinity (b) samples;
- seaward sites, sampled in the summer (SS);
- low salinity sites, sampled in the summer (SR);
- unusual sites, sampled in the summer (SM), and are indicated on the map (Fig. 5.2).

The pseudospecies characteristic of each division are shown on the side of the dichotomy in which they occur, e.g. Plat fle 1 and Sole sol 3 in the first dichotomy indicates that the summer samples are characterised by flounder and large numbers of sole (Fig. 5.1). Thus the first division highlighted large numbers of sole and flounder as characteristic summer species, while herring, sprat, whiting, sea snail and an abundance of gobies are characteristic of winter sampling. SM was characterised by smelt and an abundance of plaice. Sole and whiting were found within SS, in comparison to the less saline areas (SR), which were characterised by flounder and gobies.

Within the winter samples, plaice, pogge, sole and dab were characteristic of the WS sites, while the central areas contained sea snail and large numbers of gobies. The sub-division of WR(a) was the result

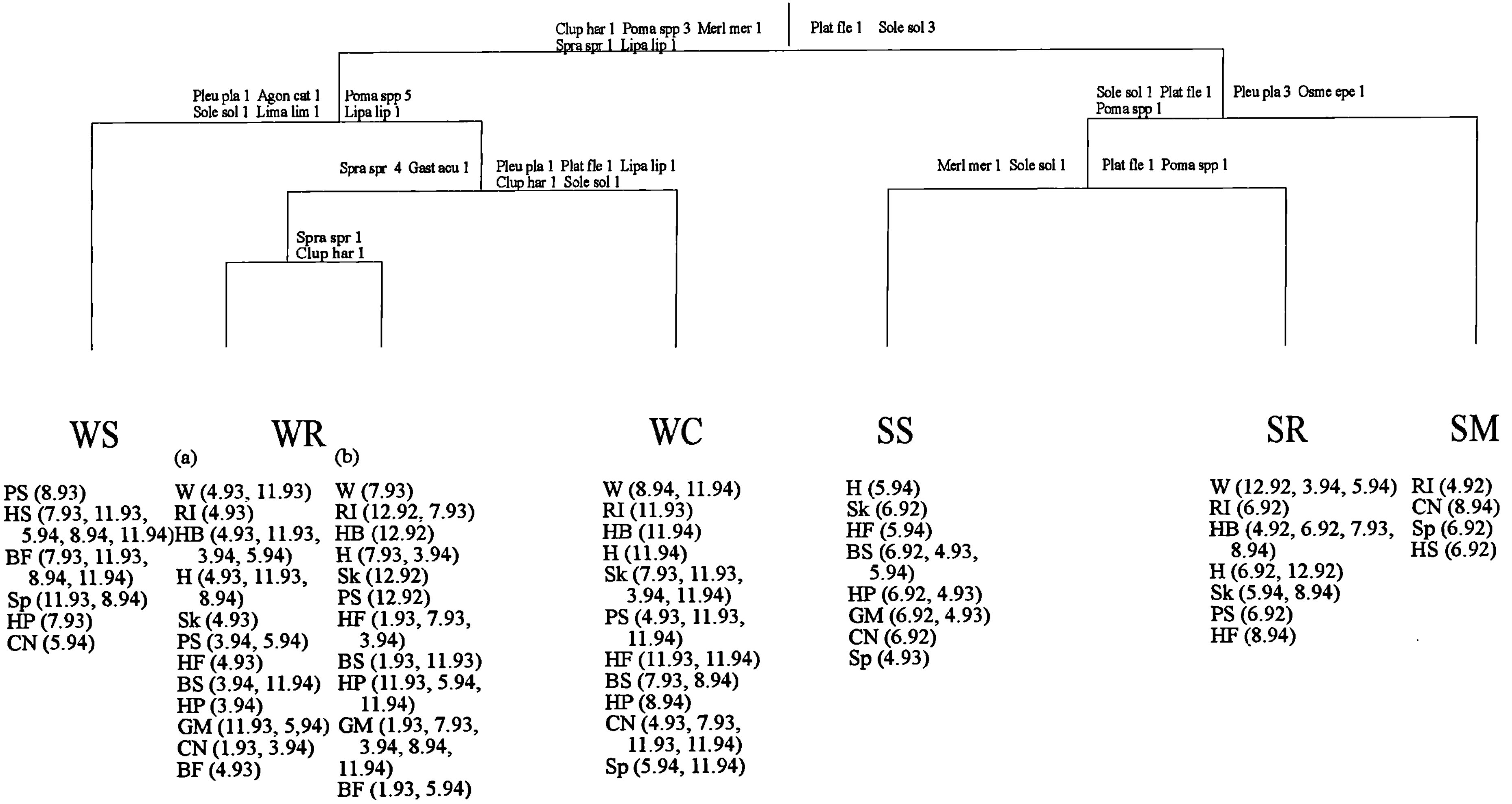


Fig. 5.1 TWINSPAN classification of sites based on the species composition (see text for group abbreviations; sites as Table 2.1; species names derived from abbreviated species names)

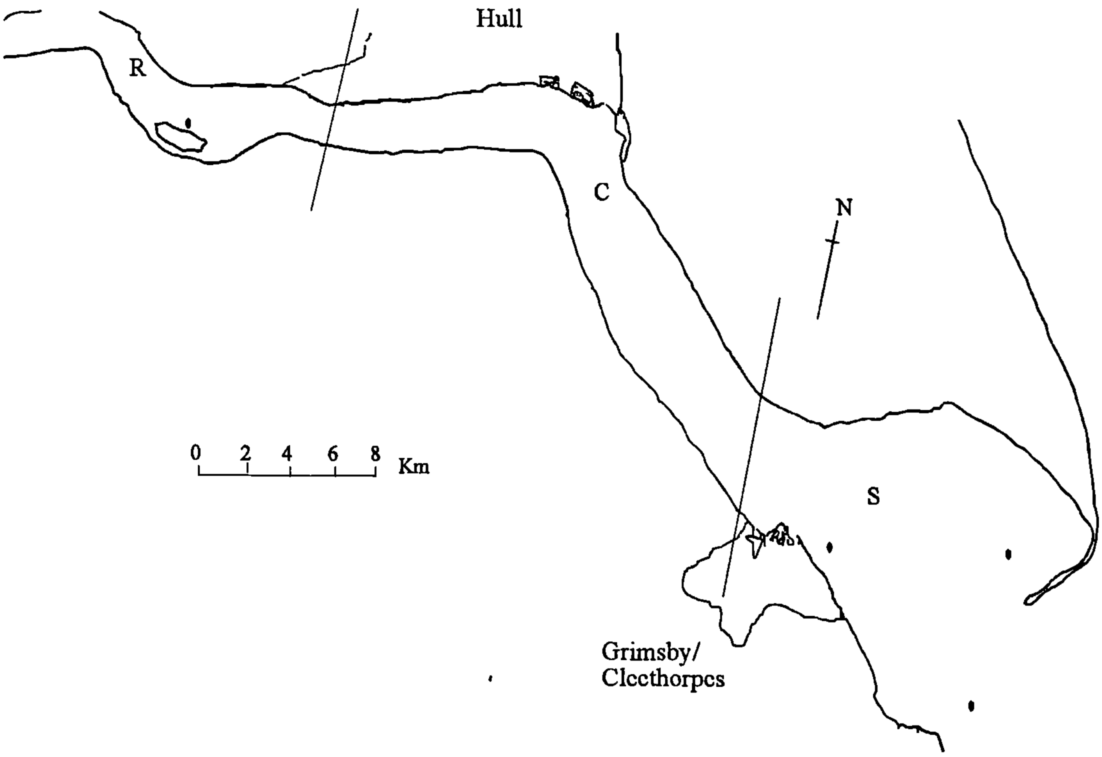


Fig. 5.2 Map showing the relative positions of the three areas derived from the TWINSPAN classification. S, seaward; C, central; R, low salinity; •, stations in SM.

of stickleback and a high abundance of sprat in WR(a) and plaice, flounder, sea snail, herring and sole in WR(b). Characteristic species are not restricted to those areas, but are more likely to occur within them than the other areas.

5.3.2 Classification of Sites by Environmental Characteristics

The PCA classification (Fig. 5.3) indicated that the sites could be divided on a seasonal and spatial basis, using the definitions given in section 5.2.2. Axis 1 accounted for most of the observed variation, eigenvalue 0.64, and separated the groups spatially, while Axis 2 resulted in a seasonal division of sites, and had an eigenvalue of only 0.15. Axes 3 and 4 accounted for very little of the variation and were therefore not assessed.

When the site groupings determined from the TWINSPAN classification, describing sites by their species composition, were superimposed on the PCA graph derived from environmental parameters (Fig. 5.4) the pattern that emerged was less well defined, indicating that the assemblage is not defined by environmental parameters alone.

5.3.3 Environmental Influences on Species Distribution

Figure 5.5 indicates the relative importance of the measured environmental parameters to the distribution of the different fish species, with respect to abundance data, as determined by CANOCO. Four axes are determined within the analysis, although only Axes 1 and 2 were plotted as they accounted for 73.5 % of the variability explained by the four axes. In addition, these two axes account for 13.5 % of the total species variations, with only 18.4 % explained by all four axes, reflecting the variability observed within the area and the presence of other factors influencing their distribution. More importantly, the two axes represented a total of 61 % of the species-environment interactions within the estuary.

Ordinal values (scores) are calculated for each species and plotted on the graph. Their position relative to each other indicates the degree of similarity in their distribution, thus species forming a cluster were found in similar areas, and may be regarded as potentially interacting within the community. In addition, the position of the species with respect to the environmental gradients can be assessed. The closer the species to the vector, the stronger the relationship, while the relative position along the vector will give the type of effect, i.e. increasing abundance with high or low values for the environmental variable. If the species point lies on the same side of the origin as the vector, it occurs at above average values of the variable. However, if the origin lies between the point and the arrow head then it occurs in greatest abundance at below average levels of that variable. Species located around the origin do not

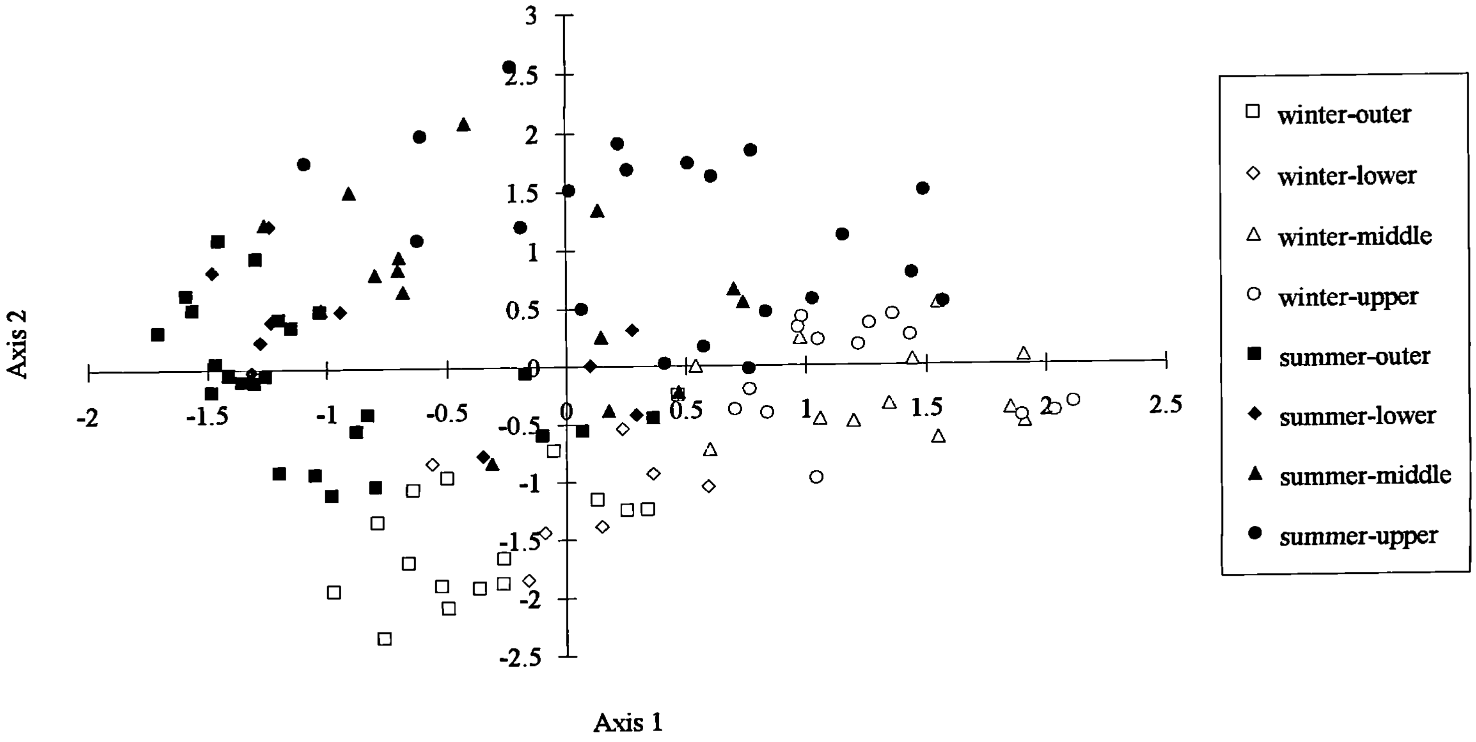


Fig. 5.3 PCA diagram of samples, classified by the measured environmental factors

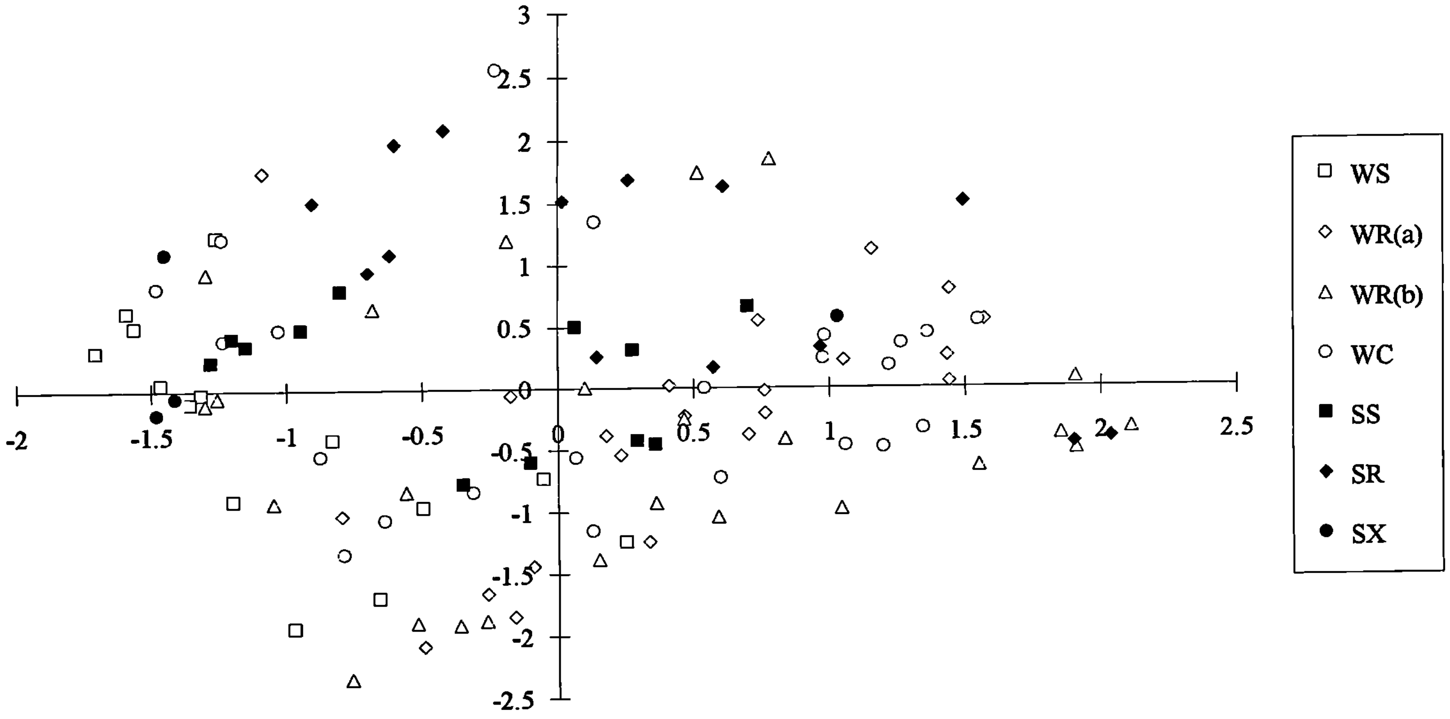


Fig. 5.4 Classifications obtained from Figure 5.1 superimposed on Figure 5.2

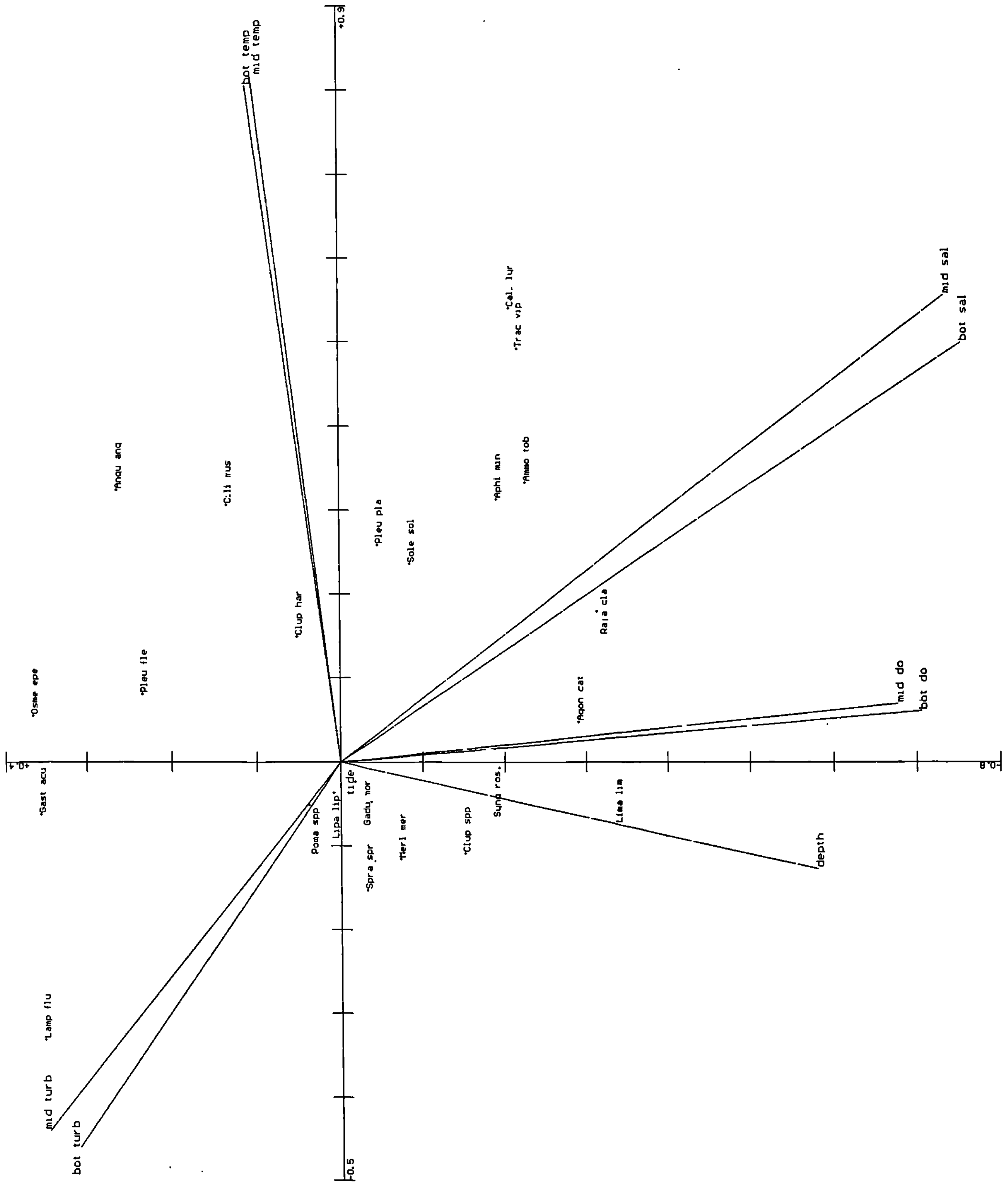


Fig. 5.5 CCA ordination diagram of abundance data, with environmental factors represented by vectors.

show a strong relationship to any of the variables measured, or are found at average values of each environmental variable measured. Average values refer to the average for this study, which are: dissolved oxygen, 85.7 % ASV (bottom), 86.3 % ASV (mid-water); salinity, 20.2 (bottom), 19.5 (mid-water); temperature 11.1 °C (bottom), 11.2 °C (mid-water) and turbidity 518 NTU (bottom) and 371 NTU (mid-water).

The relative lengths of the vectors indicate that salinity and temperature were the most important physical factors studied with regards to fish distribution in the Humber. Most species, e.g. sole, whiting and dragonet, demonstrated a higher abundance with above average temperature, salinity and dissolved oxygen, although not necessarily fulfilling all criteria, e.g. above average temperature, below average salinity and dissolved oxygen. Other species were located in low salinity, high turbidity areas, e.g. lampern, smelt and stickleback. In this case the y-axis separated below and above average temperature, the x-axis for salinity and dissolved oxygen.

The positions of the temperature and salinity vectors indicates a lower degree of correlation between the two variables, compared to other interactions, e.g. salinity and dissolved oxygen, and salinity and turbidity (Fig. 5.5). This is further demonstrated by the value of the Pearson correlation coefficients (Table 5.1), although statistically significant correlations were observed in each case, as demonstrated in Chapter 3. The axes are also correlated to the environmental variables, such that Axis 1 was most strongly influenced by temperature, while axis 2 was strongly influenced by dissolved oxygen, salinity and, to a lesser degree, water depth (Table 5.1). The relative degree of correlation was determined from the fact that the greater the Pearson correlation coefficient observed, the stronger the relationship.

The Monte Carlo analysis within the CANOCO package gave an assessment of the significance of each variable to the observed distribution. This was completed by ranking the variables and assessing each in turn with regards to the significance of the additional information gained by adding that variable to the graph. From this it would appear that mid temperature, mid salinity, bottom dissolved oxygen and the trawl used, indicated as a nominal variable 'net' on the graph, i.e. a variable which is present but is downweighted within the analysis, were the only variables to have a significant ($p < 0.05$) effect on the species distributions. All variables are included in the graph to demonstrate their relative positions.

Analysis of the biomass data (Fig. 5.6) indicated a slightly different grouping of the species around the environmental variables. However the relative importance of the variables, and their relationship to each other, remain unchanged. Salinity showed a greater influence on the distribution of more species, e.g. lesser weever, sole, herring and dragonet, as seen by their closer association with the vector. Despite these differences, there is no apparent difference in the positioning of the species with respect to the different parameters, thus herring are located in areas of above average salinity, temperature and

Table 5.1 The Pearson correlation coefficients derived from the CANOCO analysis (*, statistically significant correlation (242 d.f.); n.s., not significant)

		1	2	3	4	5	6	7	8	9	10	11
environmental axis 1	1	1										
environmental axis 2	2	0	1									
depth	3	-0.13	-0.58	1								
		n.s.	*									
bottom temperature	4	0.81	0.11	0.08	1							
		*	n.s.	n.s.								
bottom salinity	5	0.50	-0.76	0.49	0.47	1						
		*	*	*	*							
bottom dissolved oxygen	6	0.06	-0.47	0.28	-0.08	0.55	1					
		n.s.	*	*	n.s.	*						
bottom turbidity	7	-0.46	0.31	-0.38	-0.46	-0.68	-0.34	1				
		*	*	*	*	*	*					
mid temperature	8	0.82	0.10	0.08	0.10	0.48	-0.07	-0.47	1			
		*	n.s.	n.s.	n.s.	*	n.s.	*				
mid salinity	9	0.56	-0.74	.47	.52	0.99	0.52	-0.68	0.52	1		
		*	*	*	*	*	*	*	*			
mid dissolved oxygen	10	0.07	-0.68	0.25	-0.07	0.55	0.98	-0.33	-0.06	0.53	1	
		n.s.	*	*	n.s.	*	*	*	n.s.	*		
mid turbidity	11	-0.44	0.35	-0.37	-0.49	-0.73	-0.37	0.84	-0.50	-0.71	-0.36	1
		*	*	*	*	*	*	*	*	*	*	

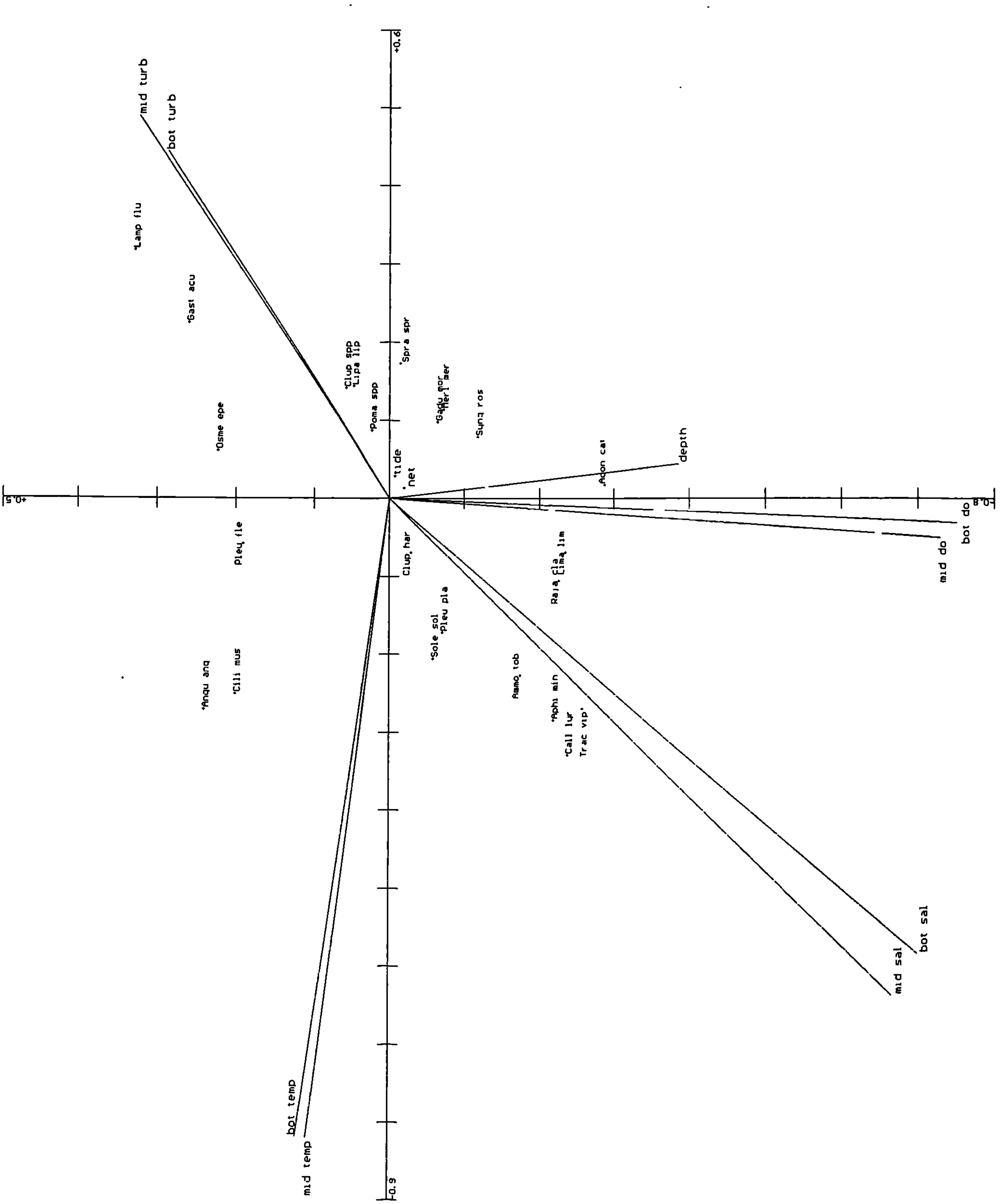


Fig. 5.6 CCA ordination diagram of biomass data, with environmental factors represented by vectors.

dissolved oxygen, while eel are found in areas of above average turbidity, below average salinity, dissolved oxygen and temperature.

The distribution of the top ranking 11 species (Chapter 4) showed statistically significant correlations with some of the environmental factors (Table 5.2). This further illustrates the importance of temperature to the distribution of some species, with a higher abundance of goby, whiting and sprat found when temperatures were low, while the reverse was the case for sole and herring. The importance of salinity was also illustrated, with higher abundances of sole, plaice and pogge recorded in areas of high salinity. Stickleback, however, occurred in areas of lower salinity.

The abundances of six species, goby, herring, plaice, pogge, sea snail and whiting, were positively correlated to the trawl used indicating a change in the efficiency of the gear. It is therefore necessary to take this into account when interpreting any data gathered with respect to these species during the early survey (April 1992 - April 1993). In addition, cod abundance was correlated to the tidal state, being higher on ebb tides. These patterns in distribution were reflected by the positions of the species in Fig. 5.5.

The use of partial correlations, controlling for salinity, resulted in a different classification of species distribution with environment (Table 5.3). From this it can be seen that there is an effect on the observed correlations with dissolved oxygen, with sole showing the only statistically significant correlation, which indicated a negative relationship. Correlations with temperature were also affected by the interactions with salinity, with goby, plaice and stickleback showing the positive correlations to temperature, while no other relationships were noted. No species were correlated to turbidity, demonstrating the interactions between the two variables. In addition, the trawl used showed a statistically significant correlation with goby, herring and pogge only, while depth showed a negative correlation to the distribution of herring.

5.4 Discussion

The data analysis indicates that the species composition within the Humber estuary is influenced by a variety of factors, both seasonal and spatial. The importance of seasonal and spatial variations are illustrated both directly, and indirectly through changes in water temperature and salinity respectively. Seasonal trends in fish distribution in estuaries have been recognised for some time (Blaber & Blaber 1980; Elliott *et al.* 1990; Morin *et al.* 1992), as have spatial trends within estuaries (e.g. Elliott & Taylor 1989(b); Pomfret *et al.* 1991).

A comparison of Figs 5.5 and 5.6 indicates that the two variables influence different aspects of the community, with more species associated with salinity than temperature in an analysis of biomass data compared to a similar analysis of abundance data. A study within the Elbe estuary (Thiel *et al.* 1995)

Table 5.2. The degree of correlation between the dominant species and environmental factors (n.s., $p > 0.05$; + or -, $0.05 \geq p > 0.01$; ++ or - -, $0.01 \geq p > 0.001$; +++ or - - -, $p < 0.001$).

	Goby	Whiting	Sole	Flounder	Sprat	Plaice	Herring	Sea snail	Pogge	Stickleback	Cod
Bottom DO	n.s.	++	n.s.	-	n.s.	n.s.	n.s.	n.s.	++	- -	n.s.
Bottom salinity	n.s.	n.s.	+++	n.s.	n.s.	n.s.	n.s.	n.s.	+++	- -	n.s.
Bottom temperature	n.s.	- - -	+++	++	- - -	n.s.	++	n.s.	n.s.	n.s.	n.s.
Bottom turbidity	n.s.	n.s.	-	n.s.	n.s.	- -	-	n.s.	- -	n.s.	n.s.
Mid DO	n.s.	++	n.s.	- -	n.s.	n.s.	n.s.	n.s.	++	- -	n.s.
Mid salinity	n.s.	n.s.	+++	n.s.	n.s.	++	n.s.	n.s.	+++	- -	n.s.
Mid temperature	-	- - -	+++	++	- - -	n.s.	++	n.s.	n.s.	n.s.	n.s.
Mid turbidity	n.s.	n.s.	- - -	n.s.	n.s.	- -	-	n.s.	- -	n.s.	n.s.
Tide	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	++
Depth	n.s.	++	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	++	- -	n.s.
Trawl	+++	+++	n.s.	n.s.	n.s.	++	+++	++	++	n.s.	n.s.

Table 5.3. The degree of correlation between the dominant species and environmental factors, using a partial correlation with salinity as the controlling factor ($n.s., p > 0.05$; + or -, $0.05 \geq p > 0.01$; ++ or - -, $0.01 \geq p > 0.001$; +++ or - - -, $p < 0.001$).

	Goby	Whiting	Sole	Flounder	Sprat	Plaice	Herring	Sea snail	Pogge	Stickleback	Cod
Bottom DO	n.s.	n.s.	- -	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Bottom temperature	n.s.	n.s.	n.s.	n.s.	n.s.	+	++	n.s.	n.s.	++	n.s.
Bottom turbidity	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Mid DO	n.s.	n.s.	- -	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	+	n.s.
Mid temperature	+	n.s.	n.s.	n.s.	n.s.	+	++	n.s.	n.s.	n.s.	n.s.
Mid turbidity	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Tide	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Depth	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	-	n.s.	n.s.	n.s.	n.s.
Trawl	+	n.s.	n.s.	n.s.	n.s.	n.s.	+	+	n.s.	n.s.	n.s.

supports this finding, with temperature found to be the best predictor of total abundance, while salinity influenced the species richness and total biomass. Similar patterns were observed in the Bothnian Sea (Thorman 1986), with positive correlations observed between minimum salinity and average species number, and between the number of days during which the temperature exceeded 15 °C and fish density.

Temperature can affect fish distribution through the thermal tolerances of different species. Salmon, which has one of the lowest thermal tolerances, has an upper lethal limit of 25 °C (Poxton & Allouse 1982). As this is higher than the maximum value recorded for the Humber during this study (21 °C; Fig. 3.3), it is unlikely that the thermal tolerances alone are a main influencing factor on the distribution of the species examined. However, temperature effects on the distribution of fish are enhanced by the synergistic effects of high temperature and low dissolved oxygen (Pomfret *et al.* 1991), which may result in the creation of a barrier to fish movement at temperatures lower than the lethal limit. The seasonal effects of migration, spawning and recruitment patterns within the area (Wheeler 1969) will also be included in the observed temperature relationships, and are likely to be the dominant factor influencing the observed distributions. The seasonality of the fish within the Humber has been demonstrated in Chapter 4.

Salinity has a greater influence on the species composition within the Humber than temperature. The importance of salinity has been demonstrated previously (Fig. 4.4; Elliott & Taylor 1989(b)) and is reflected in the different classes of fish noted within estuaries (Haedrich 1983). Salinity influences the distribution of fish through their salinity tolerance. However, in many cases the range of salinities at which the fish are habitually found is much narrower than their tolerance range, e.g. Cyprinids are regarded as freshwater species but can tolerate high salinities (Wootton 1990). In addition, the response of many species to salinity may vary with life stage (Poxton & Allouse 1982), for example juvenile plaice and herring can tolerate a wider range of salinities than adults, while sole eggs and larvae have a greater chance of survival in salinities between 20 and 40.

Dissolved oxygen shows a similar trend to salinity. It is possible, therefore, that this has served to enhance the perceived effects on the species distribution, although dissolved oxygen levels are important to the distribution of fish species, with many marine fish become stressed at dissolved oxygen levels of 4.5 mg l^{-1} (Poxton & Allouse 1982). As the percent saturation of oxygen in water is determined by temperature (Carter 1988) and salinity (McLusky 1989) this equates to 55 % ASV for the 'worst' scenario recorded, 21 °C and a salinity of 11 at Whitton in August 1994 (Figs 3.3 & 3.2), as opposed to the 71 % recorded within this study. Within the Forth and Tyne estuaries Pomfret *et al.* (1991) found that dissolved oxygen levels less than 5 mg l^{-1} or temperatures greater than 15 °C acted as a barrier to fish movement, values encountered in the upper estuary during the summer months. However, this is not the case for all species, with eel recording a maximum abundance in the Elbe estuary at 3.5 mg l^{-1} (Thiel *et al.* 1995). Thus low levels of dissolved oxygen will affect the species composition through the tolerance limits of the different species, although the synergistic effects of other parameters, e.g. high temperature, will influence the tolerance limits.

The importance of turbidity to the distribution of fish species has been noted by Blaber & Blaber (1980) and Cyrus & Blaber (1992) in other areas, and attributed to the provision of visual protection from predators or an increased food supply. These studies classified fish according to the turbidity range in which they were located, resulting in the following groups: (1) clear water, < 10 NTU; (2) intermediate turbidity, 10 - 80 NTU; (3) turbid water, > 50 NTU; (4) turbidity indifferent species (Cyrus & Blaber 1987(a)). The findings of the present study indicate that turbidity is of less importance within the Humber. This may be the result of the high levels recorded throughout the area, reflecting almost exclusively the turbid water grouping (Fig. 3.4), and is supported by the findings of Blaber & Blaber (1980) who states that the effects of turbidity on abundance were negligible at turbidity levels greater than 80 NTU, a value routinely exceeded within the Humber.

The levels of turbidity found to have a physiological effect on fish are reported to be 14 g l^{-1} (Cyrus & Blaber 1987(b)). This produces sublethal effects similar to those produced by oxygen deprivation, and result from the blocking of the gills with suspended solids. As this value is more than double the maximum concentrations found within the Humber, approximately 5 g l^{-1}, it can be assumed that the turbidity levels within the area do not directly affect the distributions of the fish species.

Several species, e.g. sole and herring, show a significant correlation with turbidity, indicating some influence on the assemblage, although this appears to be related to salinity effects, as demonstrated by the use of partial correlation coefficients, and the presence of a negative correlation between salinity and turbidity. Thus it is considered that the relationships between turbidity and species distribution within the Humber are a result of the salinity regime and intercorrelation of the two factors. This is supported within the CANOCO analysis, where the input of the turbidity vectors is shown not to have a significant effect on the resultant species distribution.

Only three species, pogge, whiting and stickleback, show a relationship with depth, these are positive correlations for pogge and whiting and negative for stickleback. The negative correlation observed for stickleback indicates a high abundance in shallow water. Together with a negative correlation with dissolved oxygen and salinity, this reflects its entry from freshwaters into the upper part of the estuary.

Depth has been shown to affect the distributions of flatfish (Riley *et al.* 1981), although this was not found to be the case within the Humber. However the depth range of the sampling stations is not large, predominantly greater than 5 m and less than 12 m (Table 2.1), and this may obscure the relationship between depth and the abundance of many of the species. Riley *et al.* (1981) indicated that plaice occur between 0 and 16 m and dab between 2 and 12 m, ranges which are encompassed by the depth range of the sampling sites.

That not all of the variables influencing fish distribution have been assessed within this study is implied by the differences in the clusters of sites produced by species and environmental data. It is likely that these are biological rather than environmental parameters as the Humber forms a relatively homogeneous habitat (this study and also NRA 1993) and differences in water quality are unlikely to produce the observed patterns. Substratum preference will influence the distribution of the fish species, although the homogeneity of the substratum within the estuary (NRA 1993) suggests that this may be of minor importance. In addition, the fish species examined are predominantly sand or soft bottom dwellers (Table 4.1), thus demonstrating similar habitat preferences.

6 POPULATION DYNAMICS, GROWTH AND PRODUCTION

6.1 Introduction

6.1.1 Ageing

Age data can be used, in conjunction with length and weight measurements, to gain information on the stock composition, age at maturity, life span, mortality and production within the population (Bagenal & Tesch 1978). Using growth cessation ring analysis, several structures are used to determine the age of fish including otoliths, scales, fin rays and bones (Chilton & Beamish 1982). Otoliths are probably the best structure as bone resorption is unknown from otoliths and some deposition appears to occur each year. As the fish grows the structure increases proportionally in bands. Differences in the growth rates with season therefore result in bands having a different structure, looser in the summer, opaque, and more compact in the winter, hyaline. In temperate fish these can be read as annual rings, where a pair of rings is equal to 1 year, and the hyaline rings are counted as this will represent a summer and winter growth. Care must be taken, however, as a slowing down or cessation of growth during reproduction can cause a hyaline 'spawning ring' to develop which, unless allowed for. will result in an overestimation of the age of the fish.

There are 3 pairs of otoliths within a fish, making up the ear structure. Incorporating hearing, this organ also enables the detection of gravity, acceleration and retardation (Härkönen 1986). The largest of the otoliths, and the one used in ageing studies, is the sagitta. In addition, the sagitta is shaped differently in different species and can therefore be used for identification. Otoliths are composed of otolin, a fibrous protein resembling keratin.

The ageing of otoliths has been described in detail by many authors (i.e. Christensen 1964; Panella 1974; Richter & McDermott 1990). In order to allow the greater definition of the rings, a variety of techniques have been determined for different species, including burning of sole otoliths (Christensen 1964), sectioning for e.g. gadoids (Bedford 1983) and staining using a variety of dyes and methods (Richter & McDermott 1990). Reading of whole otoliths in water is used for some species, e.g. clupeids and flatfish, and the juveniles of others, e.g. whiting and sole.

Size-frequency information can also be used to determine growth parameters (MacDonald & Pitcher 1979). This occurs through the frequency of each size class within a population producing polymodal histograms, the Petersen method. In order to have separate modes, recruitment must occur in discrete pulses, usually annual (Grant *et al.* 1987), thus each mode relates to a cohort. It is best suited to an analysis of the younger age classes as there is an increase in the variability in size between individuals with age coupled with a decline in growth rates, thus reducing the distance between, or merging of, modes. However, it is only possible to obtain satisfactory estimates if age classes have well separated means, > 2 standard deviation units, or there is a very large sample size, > 1000 animals if two age classes exist in the population (Grant *et al.* 1987).

6.1.2 Growth

Fish demonstrate a growth rate which, while slowing with age, never entirely ceases (Pitcher & Hart 1982). Several factors influence growth rates within fish, including environmental factors, particularly temperature (Iles 1974), genetic factors which limit the upper size (Moreau 1987) and periodic events such as reproduction which will check somatic growth (Pitcher & Hart 1982). However, there are no general trends in these effects, with plaice demonstrating greatest growth in the coldest winter as opposed to summer (Nash *et al.* 1992) and reproduction having no influence on growth in some species, e.g. herring (Iles 1974). Thus care must be taken in interpreting the results such that seasonal growth patterns are considered.

There are several mathematical models available for the analysis of somatic growth rates in fish populations (Moreau 1987), although most are derived from the same differential equation:

$d^2y/dt = dy/dt\,|-a + (1-b)(d\,(\ln y)/dt)|$, where a and b are constants.

In addition three techniques, the von Bertalanffy, Gompertz and logistic equations, are different expressions of the same model (Schnute 1981: **In**: Moreau 1987), each being used according to the biological and mathematical descriptions of growth. The logistic curve contains two inflection points and is seldom used to describe growth over the entire life-span of the fish, while the s-shaped Gompertz curve describes the decreasing growth through the adult stage (Moreau 1987). The von Bertalanffy Growth Function is the most frequently used model in fisheries studies. This is due to its apparent simplicity, lack of an inflection point, i.e. exponential description of growth, and possible use in yield computations, although there are errors inherent within the method, including sampling bias, and the limitation of validity, quality and confidence limits (Moreau 1987). In particular, the effects of individual and interannual variability in growth are not described within the equation if it is produced over the lifespan of the species. As variability is high within a population (Sogard 1992), this creates a large error within the parameter estimates, although giving a 'smoothed' curve indicative of that population.

6.1.3 Production

Production estimates can be used, in conjunction with biomass data, to assess the functioning, or production of material through feeding, of an area, despite the inherent assumptions within the technique (Elliott & Taylor 1989(b)). This is of particular importance when assessing top predators. Based on estimates of growth and mortality, production is the increase in biomass, from new growth, reproduction and immigration, minus the losses from the system, through emaciation, mortality or emigration over a time period, Δt (Pitcher & Hart 1982). Production estimates are derived from an exponential model of growth, although neither growth nor mortality need necessarily be exponential functions, merely having small coefficients or varying proportionally (Chapman 1978). Thus, by using small time periods, or having a proportional rate of growth and mortality in the population, it is possible to derive production from the given equations despite non-exponential growth, or mortality, rates over the period of interest.

6.2 Materials and Methods

6.2.1 Ageing

6.2.1.1 Otoliths

The otoliths were used to determine the age of the fish. They were prepared in different ways, dependent on their shape and composition, and training in the different techniques was given by Mr W. McCurdy, (Dept. Agric. Northern Ireland). All otoliths were viewed using reflected light under a binocular microscope and the hyaline (darker) rings counted. By convention, the fish were taken to have a birthday at midnight on 31 December so date of capture was also considered, i.e. a fish with 2 rings caught on 31 December is 1 year, but if caught on 1 January is 2 years (Bagenal & Tesch 1978).

The various methods used for each species were:

1. Otoliths were placed intact in a black watch glass and covered with water (Chilton & Beamish 1982).

2. Otoliths were placed concave side uppermost on black perspex cards, with wells, and covered with a thin layer of clear embedding resin (W. McCurdy, DANI, pers. comm.).

3. Otoliths were broken and ground with fine emery paper, P1000 wet and dry, until the cut surface bisected the nucleus. They were held cut surface uppermost under the microscope using plasticine and brushed with cedarwood oil. The oil was removed after reading to avoid damage to the otoliths (W. McCurdy, DANI, pers. comm.).

4. Otoliths were burnt using a small bunsen flame. The colour change is rapid from white through brown and black to ash grey (Christensen 1964). The otoliths are removed at the brown/black stage before cracking by pressing a needle gentle towards the cavity on the convex side. The fractured surfaces are mounted in plasticine and brushed with oil prior to viewing. The hyaline rings appear black while the opaque rings are light brown.

Method	Species examined in this way
1	Flounder; Plaice; Dab; Sea snail; Pogge; Sand eel; Lemon sole
2	Herring; Sprat; Goby
3	Cod; Whiting
4	Sole; Smelt

After ageing, the mean length ± s.e. for each cohort per sampling occasion was calculated.

6.2.1.2 Size-Frequency Histograms

The length of each fish per sampling occasion, for the four dominant species (goby, whiting, sole and flounder), were grouped into size classes and shown on the graph to the lower whole cm, i.e. fish of 70 - 79 mm in length are shown as class 7 cm. The resultant values were plotted as a series of histograms and the cohorts determined by eye. In the presence of 2 or more cohorts, the mean length ± s.e. per cohort were calculated and compared to the mean length ± s.e. per cohort derived from the otoliths using a t-test (Fowler & Cohen 1990). The normal distribution curves obtained from the otolith readings were superimposed on the histograms to graphically illustrate any differences.

6.2.2 Growth

The growth rates of goby, whiting, sole and flounder were calculated from the age-length relationship (Hawkins *et al.* 1985). Age was calculated in days, assuming a birthday of 1 January, based on the date of capture and the age obtained from the otoliths. Fish in their first year were also given a birthday of 1 January thus maintaining a constant error throughout the calculations. However this may result in an underestimation of the first year growth rate, as the observed growth will be divided into a longer time period, e.g. 12 months instead of six. The exception to this was the goby, with size - frequency histograms being used to obtain the age in years. The growth rate was calculated, for each year of growth, from the slope of the regression line on a $\log_{10}$(length) - $\log_{10}$(days) plot.

6.2.3 Production

Production estimates were calculated for the individual cohorts, or year classes, of goby, whiting, sole and flounder, and, due to the small sample size, for all sprat, plaice, herring, sea snail, pogge, stickleback and cod, i.e. the data for these species were not divided into cohorts, using the equation in Pihl & Rosenberg (1982):

$$P = \Sigma(N_t + N_{t+1}/2)\Delta\overline{W}$$

where N_t and N_{t+1} are the abundance at time t and t+1 respectively; $\Delta\overline{W}$ is the mean individual weight increment over the period, assuming unimodal distribution. Although not given here, all computations can be derived from the size-frequency histograms and the exponential length - weight relationships (Appendix 3), or the abundance and biomass data (Appendix 2).

The annual $P:\overline{B}$ ratio was determined for the population as the ΣP for each cohort and sampling period divided by the mean biomass ($\overline{B}$), where $\overline{B} = B_t+B_{t+1}/2$. All sites per sampling occasion were combined in the calculation of production, therefore discounting any spatial differences within the estuary.

The average $P:\overline{B}$ ratio was determined for the 11 top ranking species, and this was used, together with the mean biomass for the remaining species, to estimate the production of the minor species. The total annual production was then calculated, and the percent biomass and production accounted for by the major species, calculated.

6.3 Results

6.3.1 Ageing

The use of unpaired t-tests (Zar 1984) to compare the cohorts obtained from the otoliths and those from an analysis of the size-frequency histograms indicate that within this study there is a broad agreement between the two methods ($t = 0.01$ to 1.71, d.f. 4 to 515, $p > 0.05$). The exceptions are within the goby population, where the presence of two cohorts within the estuary during July 1993 and August 1994, as seen from the histograms (Fig. 6.1), was not indicated by the otoliths. Similarly within the sole population, where an analysis of the size-frequency histograms results in the merging of some cohorts (Fig. 6.2).

There are some differences in the cohorts recognised within the whiting data by each technique (Fig. 6.3), with size classes observed in the otoliths but not the histograms in January, April and July 1993. In addition there were statistically significant differences between the two older cohorts derived by both techniques in November 1994 ($t = 2.83$, 21 d.f., $0.01 < p < 0.05$, and $t = 2.74$, 16 d.f., $0.01 < p < 0.001$). Similarly within the flounder data, where analysis of the size-frequency histograms indicates age cohorts that were not supported by the otoliths (Fig. 6.4). This occurred in December 1992, April 1993 and March and May 1994.

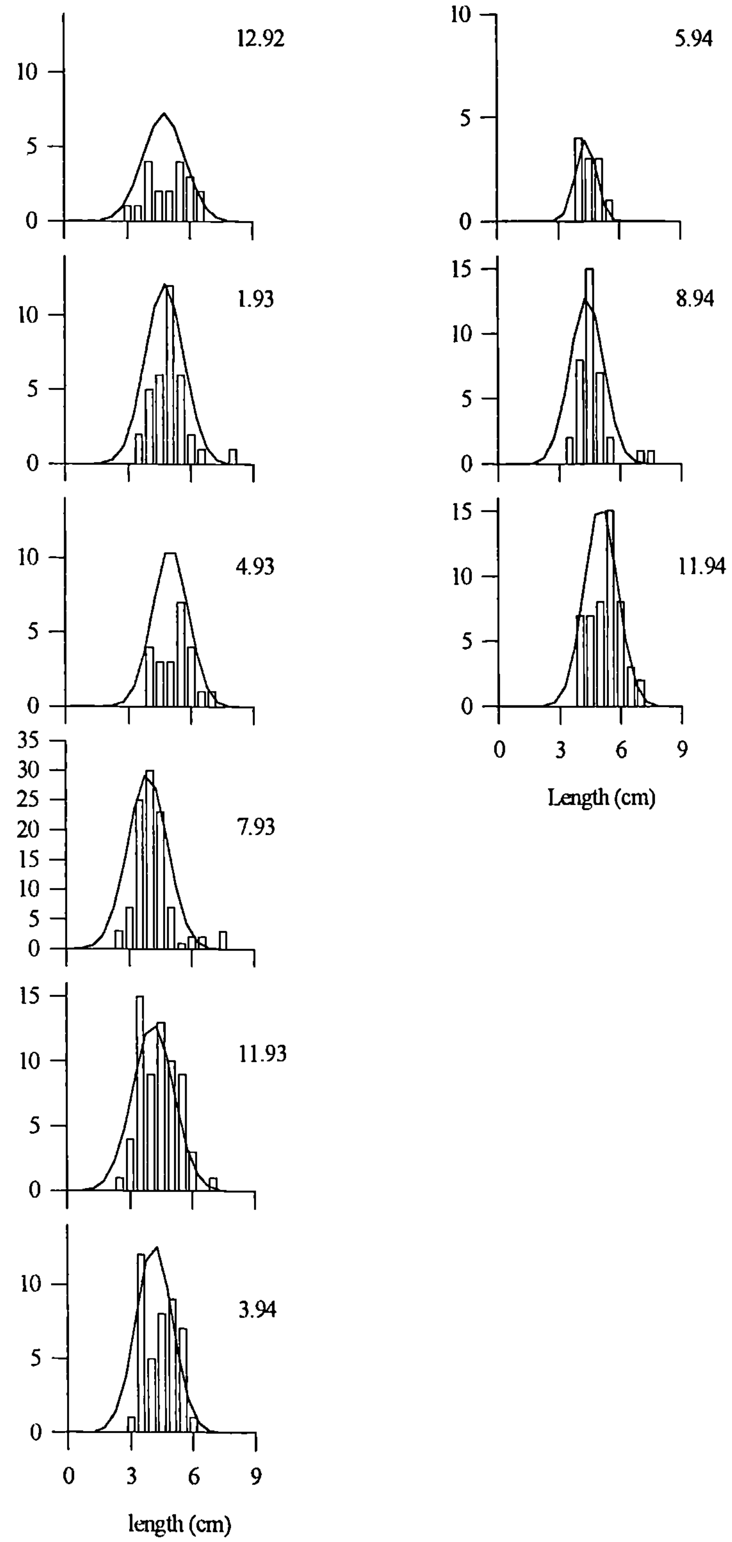


Fig. 6.1 Length - frequency histograms for the goby over the sampling period, with the normal distribution of age - length data from the otoliths superimposed.

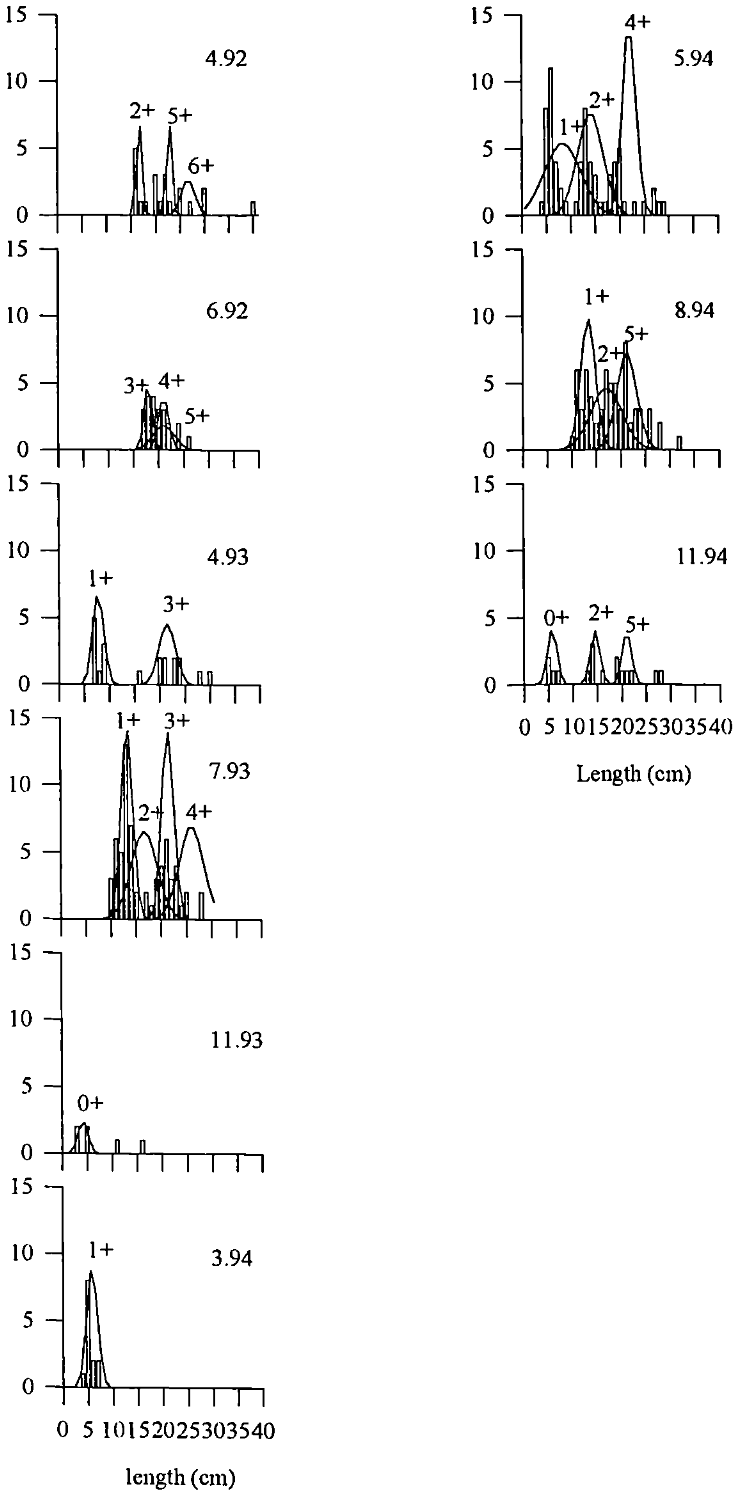


Fig. 6.2 Length - frequency histograms for the sole over the sampling period. with the normal distribution of age - length data from the otoliths superimposed.

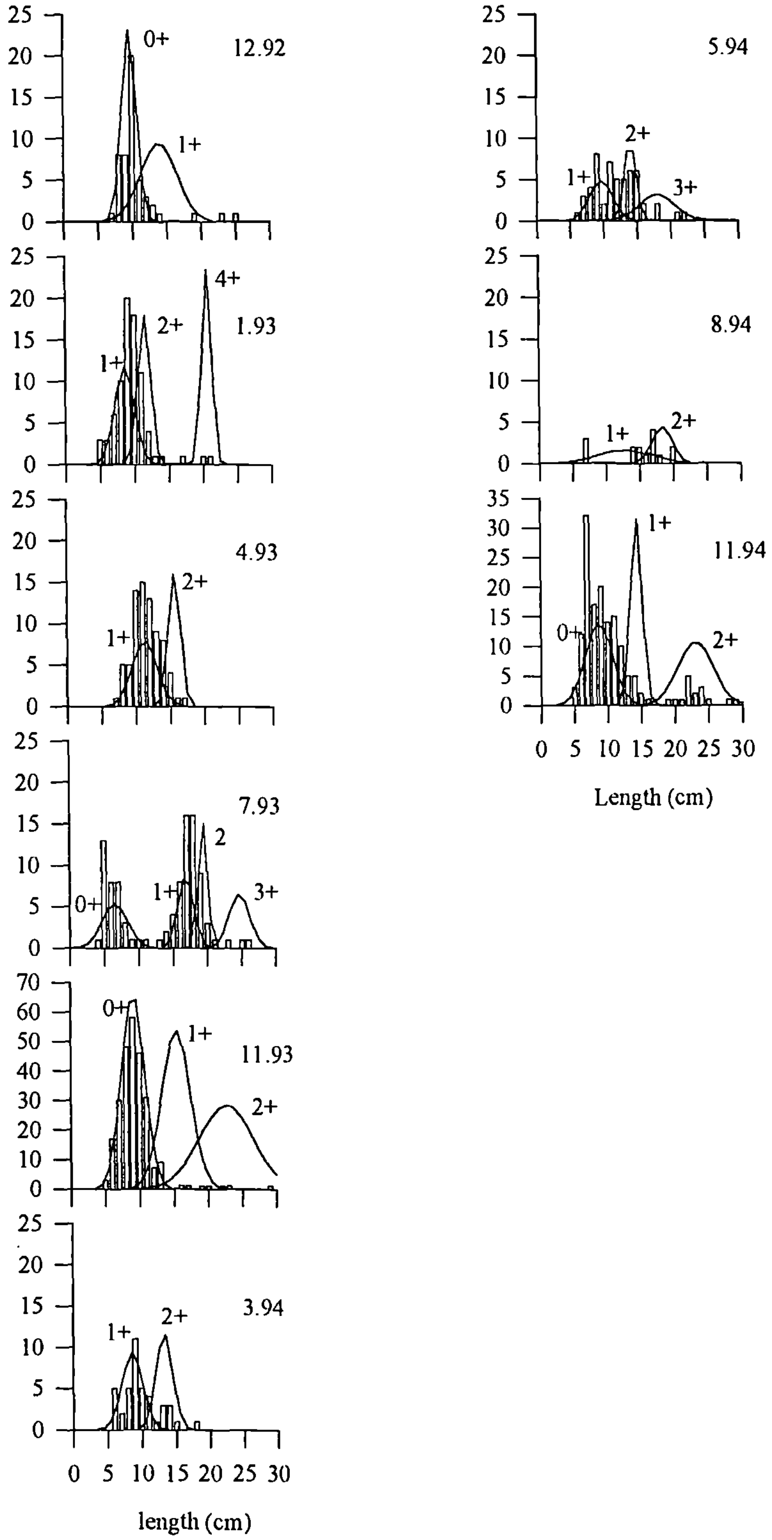


Fig. 6.3 Length - frequency histograms for the whiting over the sampling period, with the normal distribution of age - length data from the otoliths superimposed.

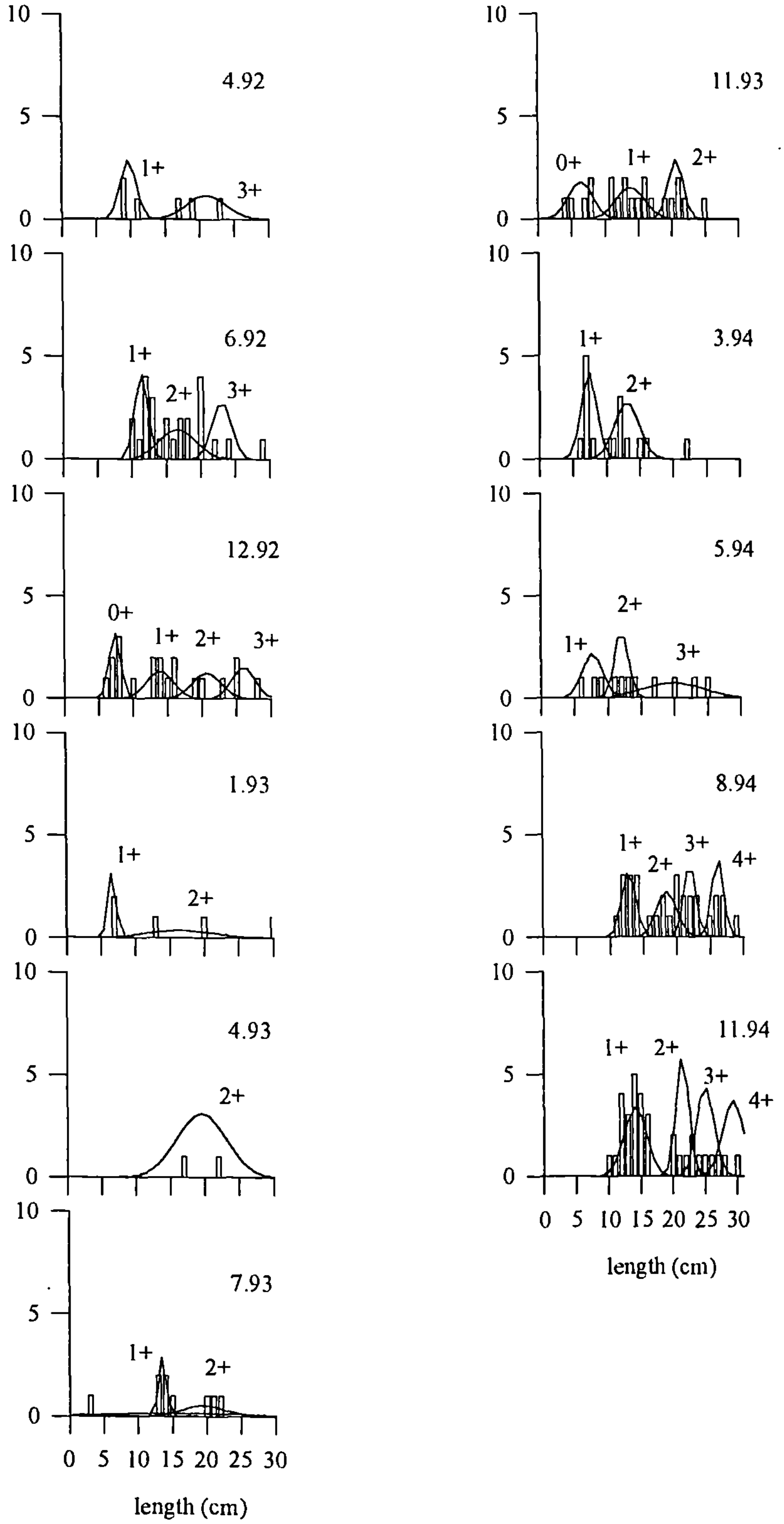


Fig. 6.4 Length - frequency histograms for the flounder over the sampling period, with the normal distribution of age - length data from the otoliths superimposed.

6.3.2 Growth

6.3.2.1 Goby

The mean length ± s.e. for each cohort, derived from the size-frequency histograms, were plotted as a series of graphs against time to determine any seasonal differences in the growth rates or between different cohorts (Fig. 6.5). The growth rate was determined from the age-length relationship (Fig. 6.6) as 0.07 mm day^{-1} over their lifespan. However, the low r^2 value, 0.11, indicates that this is not a suitable method of analysis for the growth rate within goby populations.

6.3.2.2 Whiting

The mean length ± s.e. for each cohort, derived from otolith analysis, were plotted (Fig. 6.7). These indicate a seasonal growth pattern, with greatest growth recorded in the summer months, growth rates remaining similar between different cohorts. The negative 'growth' observed indicates the loss of the larger fish from the catches. An exponential relationship of length with age was found (Fig. 6.8), the growth rate observed being 0.15 mm day^{-1} over the estuarine life phase. This is the result of a first year growth rate of 0.27 mm day^{-1}, reducing to 0.14 mm day^{-1} in the second year and 0.11 mm day^{-1} in the third.

6.3.2.3 Sole

The graph of mean length ± s.e. for each cohort and population indicate that there are different growth rates for the cohorts within the populations (Fig. 6.9). The average growth rate for the population was calculated as 0.13 mm day^{-1} over 5 years (Fig. 6.10). There is a decrease in growth rate with age, such that growth in the first year is 0.24 mm day^{-1}, reducing to 0.13 mm day^{-1}, 0.1 mm day^{-1}, 0.09 mm day^{-1} and 0.08 mm day^{-1} in the second to fifth years respectively.

6.3.2.4 Flounder

The graph of mean length ± s.e. indicates that there are four cohorts in the estuary at any one time (Fig. 6.11), with growth rates appearing to be seasonal, and similar for each cohort. Regression analysis of the $\log_{10}$(length)-$\log_{10}$(age) graph (Fig. 6.12) gives a growth rate over 5 years of 0.16 mm day^{-1}. As with sole and whiting, the growth rate is exponential, decreasing from 0.23 mm day^{-1} in the first year, to 0.16 mm day^{-1} in the second year. Subsequent growth rates are 0.14 mm day^{-1}, 0.13 mm day^{-1} and 0.12 mm day^{-1} for the third, fourth and fifth years.

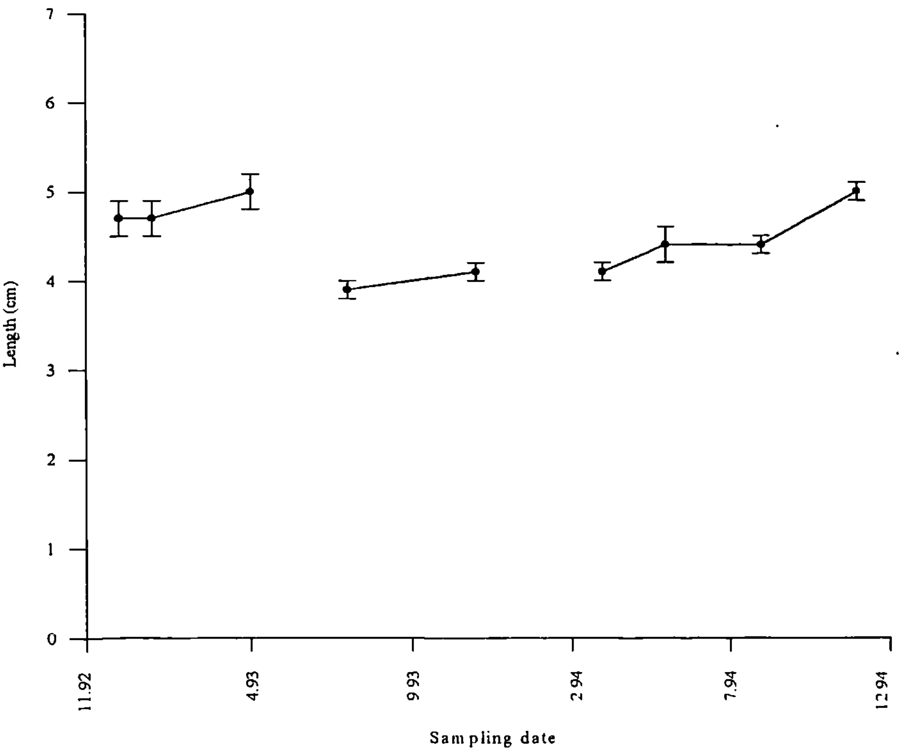


Fig. 6.5 Mean length ± standard error of goby per sampling occasion.

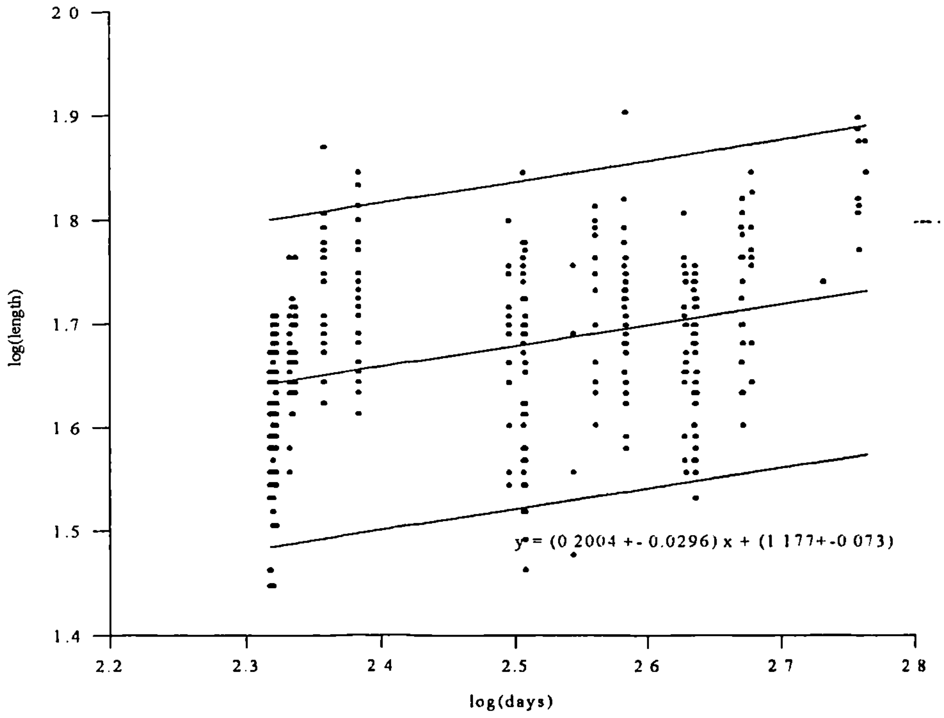


Fig. 6.6 Length at age of the goby population, with mean ± 95 % confidence limits.

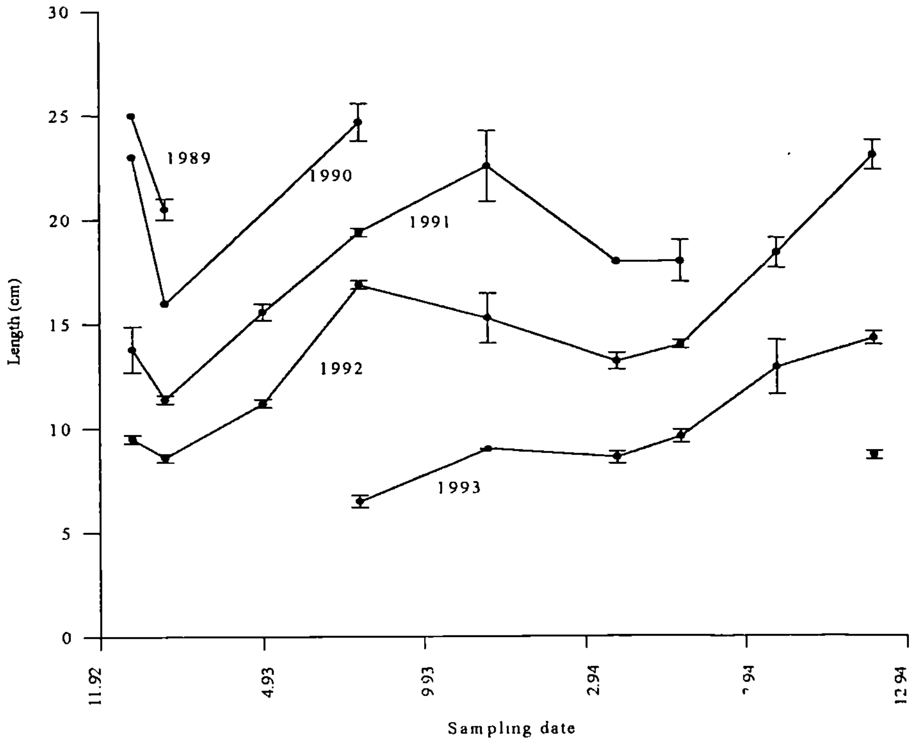


Fig. 6.7 Mean length ± standard error of each whiting cohort per sampling occasion.

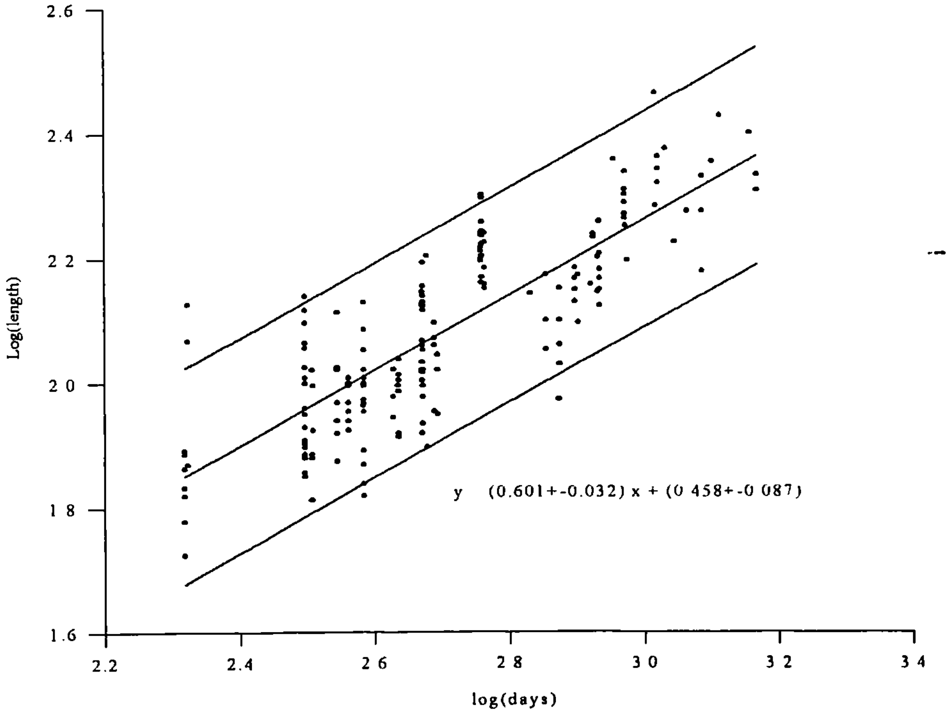


Fig. 6.8 Length at age of the whiting population, with mean ± 95 % confidence limits.

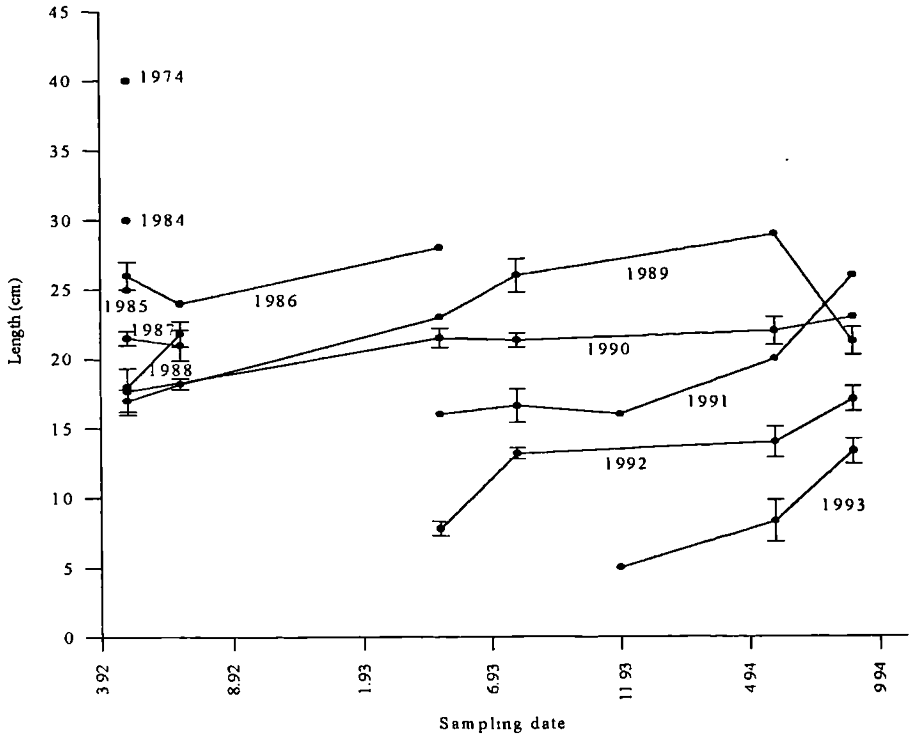


Fig. 6.9 Mean length ± standard error of each sole cohort per sampling occasion.

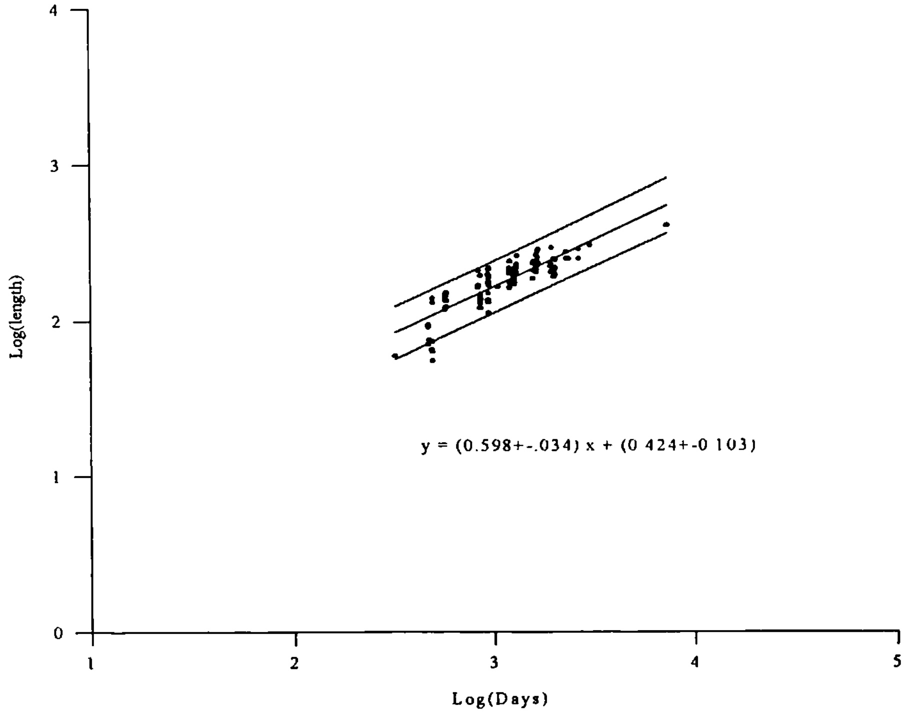


Fig. 6.10 Length at age of the sole population, with mean ± 95 % confidence limits.

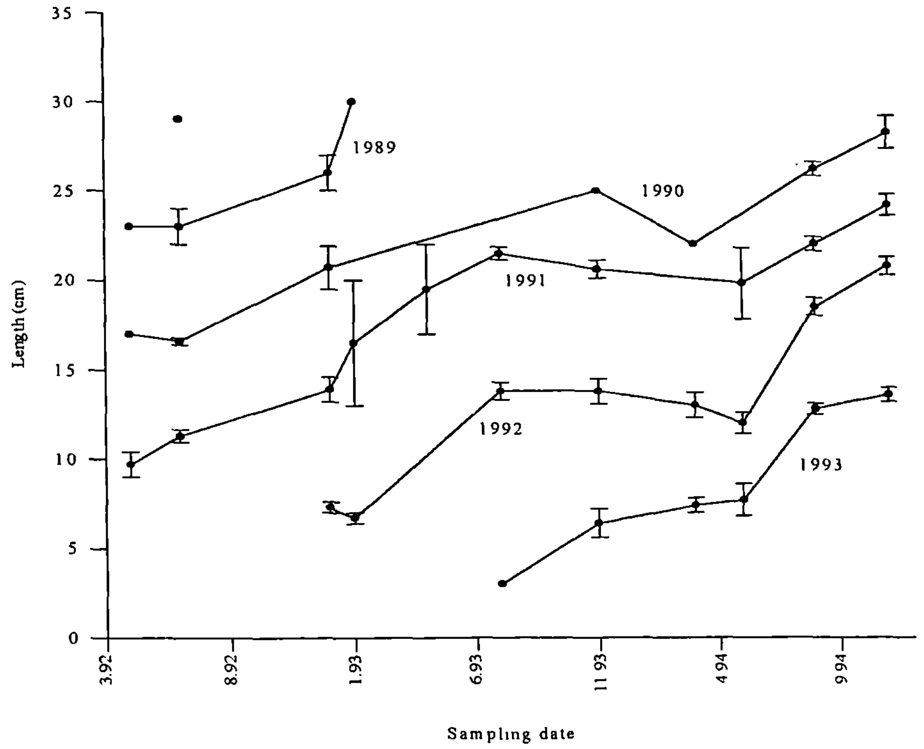


Fig. 6.11 Mean length ± standard error of each flounder cohort per sampling occasion.

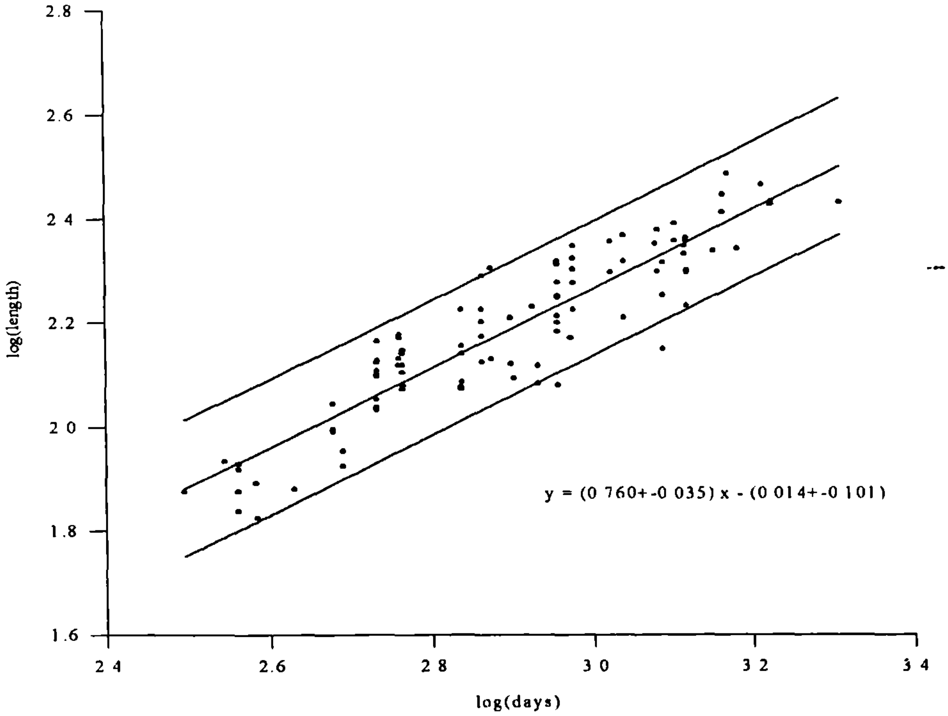


Fig. 6.12 Length at age of the flounder population, with mean ± 95 % confidence limits.

6.3.3 Production

The annual mean biomass and production for the 11 major species show an overall loss of material, i.e. negative production, during 1992 and 1993 for the sole, pogge and stickleback populations (Table 6.1). In addition, sprat, plaice and cod showed a negative production during 1992. In 1994, where only 6 months are considered, only plaice, herring and cod showed a loss of production. The minor species showed a negative production in both 1992 and 1994. In general, the main species accounted for more than 90 % of the biomass and production within the estuary, 97 and 94 % respectively in 1992 and 96 and 107 %, i.e. the minor species had a resultant negative production, in 1994, with the exception of 1993 when the minor species accounted for approximately 23 % of the total production.

The variability in $P:\overline{B}$ values with age is demonstrated by an analysis of the annual $P:\overline{B}$ ratio for the individual cohorts of flounder (Table 6.2), sole (Table 6.3) and whiting (Table 6.4). There are no trends of $P:\overline{B}$ ratio with age of cohort in any of the populations examined, i.e. the $P:\overline{B}$ ratio does not increase or decrease with age of cohort in any of the populations examined.

As sole show a negative production during 1992 and 1993 but positive production in 1994, when only the summer was considered, and as they are seasonal migrants (Table 4.1), the production was then calculated for the periods April to June 1992 and April to August 1993 in order to determine the production of the sole population when within the estuary. This indicates that sole have a production over the summer period of -4303.60 g km^2, and $P:\overline{B}$ ratio of -0.18, during 1992 and a production and $P:\overline{B}$ ratio of -9757.09 g km^2 and -0.58 respectively in 1993, demonstrating that the seasonality of the fish is not the reason for the negative values observed.

6.4 Discussion

6.4.1 Ageing

Due to the inherent inaccuracies within any ageing technique (Bagenal & Tesch 1978), i.e. the mis-reading of daily or spawning checks as annual rings, the general agreement in this study between the use of otoliths and size - frequency histograms to determine cohorts gives confidence in the data. There are exceptions to this, particularly in the case of sole, where cohorts determined from the otoliths could not be separated within the histograms. This may relate to the large overlap in lengths between different ages, which indicate differences in the growth rate within the population (Fig. 6.2), and is probably due to differences in the environmental factors experienced by the fish (Sogard 1992). The nature of environmental influences on the growth of sole has been demonstrated in other areas, e.g. Vilaine (Marchand 1991), with differences in the growth rate being related to temperature at first metamorphosis.

Table 6.1 Annual mean biomass (g km^{-2}) and production (g km^{-2} year^{-1}) of the 11 top ranking species. (The year is 1992, April 1992 to April 1993; 1993, April 1993 to May 1994; 1994, May 1994 to November 1994.)

	1992			1993			1994		
Species	Mean B ($\overline{B}$)	Production	P:$\overline{B}$	Mean B ($\overline{B}$)	Production	P:$\overline{B}$	Mean B ($\overline{B}$)	Production	P:$\overline{B}$
Goby	431.33	181.99	0.42	1921.92	1000.61	0.52	2376.74	1785.47	0.75
Whiting	4240.72	2233.23	0.53	9835.39	11166.76	1.14	8597.83	10617.13	1.23
Sole	8684.94	-5225.98	-0.60	9393.85	-12857.95	-1.37	21341.03	19469.53	0.91
Flounder	4940.46	6587.29	1.33	3677.89	920.54	0.25	13344.28	8152.64	0.61
Sprat	1450.48	-2399.74	-1.65	348.36	442.93	1.27	191.37	33.32	0.17
Plaice	1099.57	-1113.36	-1.01	933.60	2906.24	3.11	8367.98	-18158.80	-2.17
Herring	26.28	7.31	0.28	412.19	1298.86	3.15	804.14	-7713.42	-9.59
Sea snail	396.69	0	0	483.01	629.90	1.30	580.95	1504.89	2.59
Pogge	536.11	-805.73	-1.50	179.12	-34.09	-0.19	222.42	216.67	0.97
Stickleback	32.28	-21.69	-0.67	7.81	-0.95	-0.12	3.71	0	0
Cod	1437.37	-7388.18	-5.14	363.61	580.67	1.60	34.74	-21.58	-0.62
Others	731.24	-533.80	0.73	1883.20	1826.70	0.97	2161.99	-1016.14	-0.47
Σ	24007.47	-8478.66	0.35	29439.95	7880.22	0.27	58027.18	14869.71	0.26
% of top 11	96.95	93.70		93.60	76.82		96.27	106.83	

Table 6.2 The mean monthly biomass (g km^{-2}) and annual production (g km^{-2} yr^{-1}) of each cohort for flounder in the Humber estuary

Cohort	1992			1993			1994		
	Mean B ($\bar{B}$)	Production	P:$\bar{B}$	Mean B ($\bar{B}$)	Production	P:$\bar{B}$	Mean B ($\bar{B}$)	Production	P:$\bar{B}$
1989	1590.73	435.22	0.27						
1990	1803.02	5927.55	3.29	834.29	269.01	0.32	2505.13	2366.27	0.94
1991	763.46	406.21	0.53	742.17	1091.99	1.47	2805.42	2869.47	1.02
1992	847.53	-181.69	-0.21	1031.09	-460.60	-0.45	1440.76	2043.75	1.42
1993				200.68	20.13	0.10	1302.43	873.15	0.67

Table 6.3 The mean monthly biomass (g km^{-2}) and annual production (g km^{-2} yr^{-1}) of each cohort for sole in the Humber estuary

Cohort	1992			1993			1994		
	Mean B ($\bar{B}$)	Production	P:$\bar{B}$	Mean B ($\bar{B}$)	Production	P:$\bar{B}$	Mean B ($\bar{B}$)	Production	P:$\bar{B}$
1984	3867.94	-3867.94	-1.00						
1985	919.53	-919.53	-1.00						
1986	1421.78	328.67	0.23	1115.49	-1115.49	-1.00			
1987	2847.71	-1859.27	-0.65						
1988	2496.77	-1011.74	-0.41						
1989	2118.69	-850.55	-0.40	4451.42	-812.87	-0.18	5867.86	-8104.30	-1.38
1990	1886.57	2052.74	1.09	4098.26	-5642.97	-1.38	1988.94	279.75	0.14
1991	794.00	794.00	1.00	1434.13	-6988.87	-4.87	2863.25	4418.64	1.54
1992	107.65	107.65	1.00	1617.64	1057.74	0.65	8979.80	19083.52	2.13
1993				280.019	644.51	2.30	1607.07	3723.71	2.32
1994							68.22	68.22	1.00

Table 6.4 The mean monthly biomass (g km^{-2}) and annual production (g km^{-2} yr^{-1}) of each cohort for whiting in the Humber estuary

Cohort	1992			1993			1994		
	Mean B ($\bar{B}$)	Production	P:$\bar{B}$	Mean B ($\bar{B}$)	Production	P:$\bar{B}$	Mean B ($\bar{B}$)	Production	P:$\bar{B}$
1989	774.49	-551.95	-0.71						
1990	324.90	4.42	0.01	984.35	0.00	0			
1991	12.36	-3.42	-0.28	21.39	38.99	1.82	13.96	-13.96	-1.00
1992	2632.42	2784.17	1.06	3688.28	6040.54	1.64	4809.07	6185.86	1.29
1993				3516.18	5087.23	1.45	1725.93	1715.90	0.99
1994							2729.34	2729.34	1.00

There may also be a relationship between spawning site and growth rate, with spawning occurring in two areas, Mablethorpe to the south and Bridlington to the north (R. Milner, MAFF, pers. comm.). However, as the fish are resident within the estuary for only a brief period over the summer months (Chapter 4), any differences observed are likely to have arisen from environmental differences within the North Sea, either during spawning or the winter feeding period. It is thus it is not possible within this study to determine the underlying causes of the observed differences.

Ageing of the goby population, in contrast to the sole, is more accurate by the Petersen method than from analysis of the otoliths, which failed to detect the recruitment in July and August identified by the size - frequency histograms. The presence of two cohorts at this time is similar to the findings within Swedish coastal waters (Pihl & Rosenberg 1982), indicating that the size - frequency analysis provides a valid representation of the population structure. The otoliths indicated the absence of a winter ring, which in turn indicates either a continuous growth rate throughout the year, although reduced winter growth was observed in other studies, e.g. Wheeler (1969), or that otoliths are inappropriate structures for the ageing of gobies. The latter is considered to be more likely, but may indicate difficulties in the techniques used to read the otoliths rather than their growth patterns, particularly as growth bands were noted on the scales by Fouda & Miller (1981).

Thus, for short-lived species, e.g. goby, size - frequency histograms would appear to be a suitable analysis of the age structure of the population, while the population of long-lived species, e.g. sole, is more accurately described using some other structure, such as otoliths. This relates to the similarity in size between the different ages of slow-growing species, which leads to the merging of cohorts within the histograms (MacDonald & Pitcher 1979).

There was no statistically significant difference between the two ageing techniques for either whiting or flounder populations within this study, which may be a function of the short spawning season and small number of cohorts within the data (Bagenal & Tesch 1978). In addition, both species spend a long period within the estuary, at least in terms of the sampled age classes, and thus the whole population experiences a similar environmental regime. The discrepancies noted for whiting during November 1994 are caused by the failure to detect in the size - frequency histograms the 1-group fish noted from the otoliths.

The length at age relationships observed within the whiting population of the Humber, giving a maximum of approximately 15, 22 and 33 cm at the end of the 1st, 2nd and 3rd years respectively, are almost identical to those recorded in Wheeler (1969), 15, 22 and 30 cm. Similarly, a comparison of flounder populations indicates an average of approximately 8, 15, 20 and 25 cm at the end of years 1 to 4 respectively, compared to 8, 14, 19 and 24 cm (Wheeler 1969). Thus, it would appear that the populations of flounder and whiting reach a length at age comparable to the average values within other areas.

6.4.2 Growth

There have been several methods suggested for the modelling of growth rates, of which the von Bertalanffy equation is the most extensively used within fisheries studies (Bagenal & Tesch 1978). However, this was deemed unsuitable for this study due to the short life-span (goby), restricted age range sampled (whiting) and small sample size (sole) of the species examined, all of which result in errors within the von Bertalanffy equation (Moreau 1987). The relationship of length per day was therefore used as an indication of the growth rate of the fish.

The method used appears to provide a suitable analysis of the growth rates within the community ($r^2 > 0.8$, whiting, sole and flounder; $p < 0.001$). Within the goby population, the low r^2 value ($r^2 = 0.11$) relates to the large spread of lengths with age (Fig. 6.6), and may result from the extended spawning period and short life span, approximately 18 months (Wheeler 1969), or from the combining of species within the analysis (Section 4.3.1), although with approximately 95 % sand goby the analysis is effectively of one species not two. Thus it gives a poor indication of growth within the population, while the use of a fixed birthday of January 1 may also result in an underestimation of the actual growth rate. The analysis of daily growth rings within the otoliths has been used to determine the exact age of larvae, e.g. smelt (Sepúlveda 1994), and this may be a more appropriate technique in this instance, although the use of daily rings requires some training and experience before confidence in the results can be achieved (W. McCurdy, DANI, pers. comm).

A comparison of the growth rates of the major species within this study with those reported in other areas (Table 6.5) indicates that the flounder population within the Humber has a similar growth rate to that found in other areas (0.16 mm day^{-1} cf. 0.11 - 0.16 mm day^{-1}). Similarly, the goby population is similar to that within the South coast of England (0.07 mm day^{-1} cf. 0.05 mm day^{-1}) despite the use of an assumed birth date.

A comparison of the growth rates of juvenile sole in the Humber and Vilaine estuaries (Table 6.5) indicates that the Humber experiences a lower rate of juvenile growth (0.24 mm day^{-1} cf. 0.30 mm day^{-1}). The subsequent comparison of 0 group and 1 group fish in the Humber and Loire estuaries, reveals that the growth rates are similar (0.13 mm day^{-1} cf. 0.15 mm day^{-1}), although the fish in the Loire are larger than those in the Humber (Table 6.5), indicating that the sole population within the Humber has a similar adult growth rate, but lower total length and juvenile growth rate. Data from the Loire estuary for 0 and 1 year fish indicate that there is a similar growth rate for sole within French estuaries.

Table 6.5. Lengths (mm) attained by each species in different areas. Figures in brackets represent the annual growth rate (mm day^{-1}).

	Age class						Overall growth		
Species	0	1	2	3	4	5	rate (mm day^{-1})	Region	Source
Flounder	74	150 (0.21)	219 (0.19)	272 (0.15)	302 (0.08)	330 (0.08)	0.14	Scotland	Summers (1979)
	103	174 (0.19)	218 (0.12)				0.16	Sweden	Mollander (1932) **In**: Summers (1979)
	80-100	170-220						Denmark	Muus (1967) **In**: Summers (1979)
	86 (0.23)	145 (0.16)	198 (0.14)	246 (0.13)	291 (0.12)		0.16	Humber	This study
	80	140	190	240					Wheeler (1969)
Sole							0.30	Vilaine	Marchand (1991)
	106	162 (0.15)						Loire	Marchand (1988)
	91 (0.24)	137 (0.13)	175 (0.10)	207 (0.09)	237 (0.08)	264 (0.07)	0.12	Humber	This study
Goby	27-29	44-45					0.04 - 0.05	England	Fouda & Miller (1981)
	49	56					0.07	Humber	This study
Whiting	150	220	300				0.21		Wheeler (1969)
							0.40	Severn	Potter *et al.* (1986)
	100 (0.27)	151 (0.14)	193 (0.11)	229 (0.10)			0.15	Humber	This study

Whiting within the Humber have a lower growth rate (0.15 mm day^{-1}) than the general rate reported for European waters (0.21 mm day^{-1}; Wheeler 1969) or the specific rate reported within the Severn estuary (0.4 mm day^{-1}; Potter *et al.* 1986). However, as the length per age class, as calculated from the growth equation (Fig. 6.8), is lower than the length at age noted in the size-frequency histograms (Fig. 6.3), it is possible that this equation does not adequately describe the growth rate of the population. In addition, the 'negative growth' noted within the Humber (Fig. 6.7) will cause an underestimation of the growth rate within this area. 'Negative growth' is the result of a size dependent migration, where the larger animals migrate first (Gordon 1977), thereby a constant reduction in the mean length at age observed within the samples and thus a reduced growth rate should occur.

6.4.3 Production

It has been suggested elsewhere (e.g. Elliott & Taylor 1989(b)) that the $P:\bar{B}$ ratio can be used to describe the functioning of estuaries, indicating the carrying capacity of the area. During the period of this study the community $P:\bar{B}$ values were similar for 1993 and 1994, but lower during 1992, indicating a much greater variability than was found in the Forth (Elliott & Taylor 1989(b)). However, the 1992 values may be the result of the trawl used, resulting in a catch of predominantly flatfish which migrate within or from the area, thus explaining the negative values observed. Within any one sampling period the maximum $P:\bar{B}$ ratio for the 11 main species in the Humber was 4.74 between April and July 1993, followed by 3.98 and 3.83 between July and November 1993 and August and November 1994 respectively, indicating a strong variability within the production estimates.

$P:\bar{B}$ ratios are related to several factors, including the number of cohorts within the population and their relative abundance, growth rates and mortality patterns (Chapman 1978). Thus, species with seven or more age groups may have an average $P:\bar{B} < 1.0$, while more accurate estimates will be gained for each population by following one cohort from spawning to death, thereby providing more accurate growth and mortality patterns. However, analysis of the individual cohorts of flounder, sole and whiting within this study do not reveal any trends in the $P:\bar{B}$ values with age, although younger cohorts would be expected to have greater $P:\bar{B}$ values (Chapman 1978).

The inter-annual variations observed within this study do not give a true comparison of the production in each year due to the change in trawl between 1992 and 1993, resulting in increased catches of some species, i.e. goby, pogge and sea snail, and the shorter period of the survey during 1994, 6 months. However, it can be seen that for the period of the study, the main species account for > 90 % of the biomass and production within the area, with the exception of production in 1993 (77 %). A similar situation was found in the Forth, with the main species accounting for > 90 % of the total annual production and mean monthly biomass (Elliott & Taylor 1989(b)).

Most of the main species examined within this study showed P:$\overline{B}$ ratios < 1.0. The exceptions were predominantly juveniles caught in either 1993 or 1994, including whiting, plaice, herring and sprat, and the estuarine resident sea snail (Table 4.1). Analysis of the production of the different cohorts for whiting indicates that there is a general decrease in production with time, although this may be due to the emigration of the fish from the area (Bagenal & Tesch 1978).

A high proportion of the species show a negative annual production. There are several biological explanations for this, including spawning and the loss of sexual products, and weight loss through emaciation or emigration (Chapman 1978). Within the Humber emigration is the more likely explanation for the observed patterns, as migrant or adventitious species predominate (Chapter 4). These effects will be further enhanced by the large sampling interval, which will result in the loss of detail about changes in biomass and therefore production.

Production estimates within the Humber, as given by the P:$\overline{B}$ ratio, are low compared to other areas, e.g. the Forth (2.75; Elliott & Taylor 1989(b)), the northern Baltic (0.5 - 0.8; Ankar 1977) and the Oosterschelde (2.5; Hostens & Hamerlynck 1994). While this indicates that the Humber is less productive than those areas, part of the discrepancy may be the result of the large sampling interval within this study, > 3 months, compared to the monthly values in other areas. While this does not explain the low or negative values obtained for estuarine residents, i.e. goby and sea snail, it is of note that sea snail are found predominantly in mixed substrata, an area not routinely sampled within this study (Table 2.1). In addition, goby have been shown to contribute little to the epibenthic production of the Oosterschelde (Hostens & Hamerlynck 1994) and thus the low values noted within this study may reflect a similar situation within the Humber.

7 FEEDING ECOLOGY

7.1 Introduction

Resource separation can occur at three levels, temporal, spatial and dietary (Ross 1986), thus within the assessment of any ecosystem it is essential to analyse feeding interactions between the different members of the assemblage. While dietary overlap will only occur, in the absence of competition, where prey organisms are superabundant, discrete niches can arise from lower food abundances (Tyler 1972). Thus where food organisms are restricted discrete feeding groups will be established, with either geographical or dietary boundaries. Superabundance refers to an availability of prey greater than that required to maintain the fish assemblage.

Intra-specific dietary overlap can be based on differences in size and sex of the animals. In particular, differences in the size of the fish will affect the diet through their ability to handle different prey types and sizes, thus larger animals could be expected to have a greater dietary diversity than small ones which, due to a smaller mouth size, are unable to capture and eat the larger prey organisms (Wootton 1990). As intraspecific dietary overlap is generally greater than interspecific (Bergstad 1991), the division of a species into different size ranges prior to analysis is therefore indicated. Thus, dietary analysis enables the feeding behaviour of the different species to be determined with respect to prey taken by different size groups, together with any seasonal, temporal and tidal variations in the diet composition and feeding intensity. Inter- and intra-specific interactions can then be determined by the degree of similarity within the diets.

The success of many estuarine fish is dependent on their ability to exploit a wide variety of food items (de Silva 1975). Food availability varies with many factors, both environmental and physical, including tidal inundation (Wolff *et al.* 1981), thus highlighting the complexity of estuarine foodwebs, even in species-poor areas (Gorman & Raffaelli 1993). As many species have been shown to utilise the intertidal areas for feeding, e.g. flatfish and gobies, thereby reducing the time available for feeding, it can be seen that this complexity arises from temporal and spatial variability in environmental conditions affecting not only the fish distribution but the availability of 'preferred' prey.

Stomach content analysis will provide information on the stomach fullness and diet at any one point in time. In order to determine ecological relationships in foodwebs it is necessary to have information on the daily food rations of the fish (Troschel & Rösch 1991). *In situ* determination of daily ration requires estimates of the weight of food within the stomach over a 24 hour period, and the gastric evacuation rate (GER) (Hayward & Bushmann 1994). The GER is related to digestion rates, and therefore the determination of digestion rates together with the energy requirements of the fish will provide an estimate of the feeding rate of the population and thus an estimate of the magnitude of inter- and intra-specific interactions (Olson & Mullen 1986). An analysis of the digestion rates of fish will therefore give an indication of the energetics of the foodweb, and the extent of interactions within the assemblage, both from competition and predation.

The use of field experiments to determine the GER will enable the inter- and intra-specific relationships to be evaluated, together with an analysis of the actual diet of the animals. In order to undertake this within the Humber, it was necessary to select an abundant species within the intertidal areas. Therefore plaice, as the most abundant species within the intertidal sampling (Chapter 4), was used within the experiment.

7.2 Materials and Methods

7.2.1 Feeding Analyses

7.2.1.1 Stomach Content Analysis

The subsample of fish from each trawl selected previously (Section 2.3) was used within this analysed. It covers all species captured, with the exception of pipefish and lamprey, from all sites and sampling occasions. A fullness index was applied to the stomach before opening, based on the appearance of the stomach and stomach wall. This was taken as a subjective view grading from empty, 0, to full, 5. This method is rapid and allows spatial and temporal comparisons. In fish with no obvious stomach, e.g. flatfish, the fullness index was calculated for the top 1/5 of the digestive tract in order to estimate the time from feeding, i.e. give a similar estimate as stomach fullness in other fish.

A longitudinal cut was made in the gut wall, and the contents removed. Stomach contents were analysed following the numerical and gravimetric analyses in Windell & Bowen (1978). The taxon were blotted and weighed, ± 0.0001 g. Any sediment and unidentified soft material was weighed under the term "debris". This material was filtered using Whatman 3 Qualitative filter paper prior to weighing.

7.2.1.2 Digestion Rates

Sampling was completed on 28.3.94 at Spurn Point using the 1.5 m hand-pulled beam trawl described in Section 2.2.2. Trawling began 1 hour after high water and continued until 40 plaice had been caught. After each tow the net was emptied and the fish placed in a holding tank. When 10 fish had been caught, they were placed in a separate tank, until 3 tanks containing a total of 30 fish were obtained. In each case, if more than 10 fish were present in the holding tank then the remainder were killed immediately, as the 0 hour fish, until 10, 0 hour plaice, had been acquired.

The fish were held in the 3 tanks for 1, 3 and 6 hours respectively prior to killing. This gives a comparison of the diets at these intervals after feeding, assuming that the fish were feeding just prior to capture, as noted from the 0 hour fish.

Stomach content analysis was performed on all fish and the mean weight ± s.e. of prey per gramme of fish for each time period calculated. The analysis was then repeated for total weight of identifiable organisms, i.e. total weight - debris. Fish with empty stomachs and intestines were not used in the analysis. The experiment was repeated on 19.9.94 with 50 fish and time intervals of 0, 1, 3, 6 and 12 hours.

7.2.2 Species -Specific Analyses

7.2.2.1 Species Diets and Feeding Strategies

Of the 11 main species (see Chapter 4), three, herring, sea snail and stickleback, were found to have predominantly empty stomachs and intestines. From the remaining eight species, the size of each fish from both the subtidal and intertidal sampling were noted, together with the weight of the prey items observed within the intestinal tract. Using individual fish as samples and the weight of the each prey species as the attributes, the Bray-Curtis similarity index (Ludwig & Reynolds 1988) was applied to each species independently, to determine the length at which any dietary change occurred, e.g. the Bray-Curtis analysis was performed on all gobies, then flounder, etc.. The remaining species, brill, dab, dragonet, eel, herring, lesser weever, sea snail, smelt, stickleback and turbot, were analysed without dividing into size ranges. All analyses were performed after removal of the parasites from the data set.

The Bray - Curtis index can be used to produce clusters via the group average sorting of the similarity coefficient matrix:

$$C_N = 2w/(a+b)$$

where w = sum of lesser measures of each attribute common to both samples (including tied values); a = sum of measures of attributes in first sample; b = sum of measures of attributes in second sample.

The results are displayed in a dendrogram produced from the similarity coefficients, and indicate the degree of similarity between each group. An arbitrary cut off level can be chosen, such that separate groups are determined. Cluster analysis is also accepted as an indication of niche overlap, i.e. the shared utilisation of a resource (Hamerlynck & Cattrijsse 1994).

Table 7.1 The size range of the species determined from the Bray Curtis analysis with similarity of 25 %, (there was no difference in the diets of cod, goby, sole and sprat with length at this level).

Size	Flounder	Plaice	Pogge	Whiting
Small	< 15	< 8	< 7	< 9
Medium	15 - 25			9 - 14
Large	> 25	> 8	> 7	> 14

The diversity and 'evenness' of the diets were determined with the Shannon-Wiener and 'evenness' indices. These are generally accepted as an indication of dietary niche breadth (Hamerlynck & Cattrijsse 1994). The dominant prey items within the diets were then determined using the Index of Preponderance (IP) (Mohan & Sankaran 1988). This is represented by the formula

$$IP = W_iO_i/\Sigma(W_iO_i),$$

where W_i and O_i are the percent weight and occurrence of prey i respectively, and produces a single value for each prey item, enabling comparisons between individual prey types.

The feeding strategy of the species were assessed using the graphical method proposed by Tokeshi (1991). Individual Diversity, the average dietary diversity of individual fish, (ID) and Population Diversity, the dietary diversity of the population, (PD) are determined such that:

$$ID = (-\Sigma P_{ij} \ln P_{ij})/N \text{ and } PD = \Sigma P_i \ln P_i$$

where N = the total number of predator individuals; P_{ij} = the proportion of prey-type i in the jth predator individual; P_i = the proportion of prey-type i in the entire predator population.

The results are interpreted by the position of the species within a graph of PD against ID (Fig. 7.1).

7.2.2.2 Seasonal, Temporal and Tidal Differences

Seasonal and annual changes in the diets of the eight main species divided into size classes, above, were examined using a series of Wilcoxon matched-pairs sign-ranked one-way non-parametric ANOVA within the SPSS computer package (J. Thompson, Dept. Mathematics and Statistics, Uni. of Hull, pers. comm.). Thus annual differences were determined by comparing the diet of e.g. flounder in summer 1992 to that in summer 1993 and summer 1994, then summer 1993 was compared to summer 1994. Seasonal differences were similarly determined by comparing each season within a single year. Percent

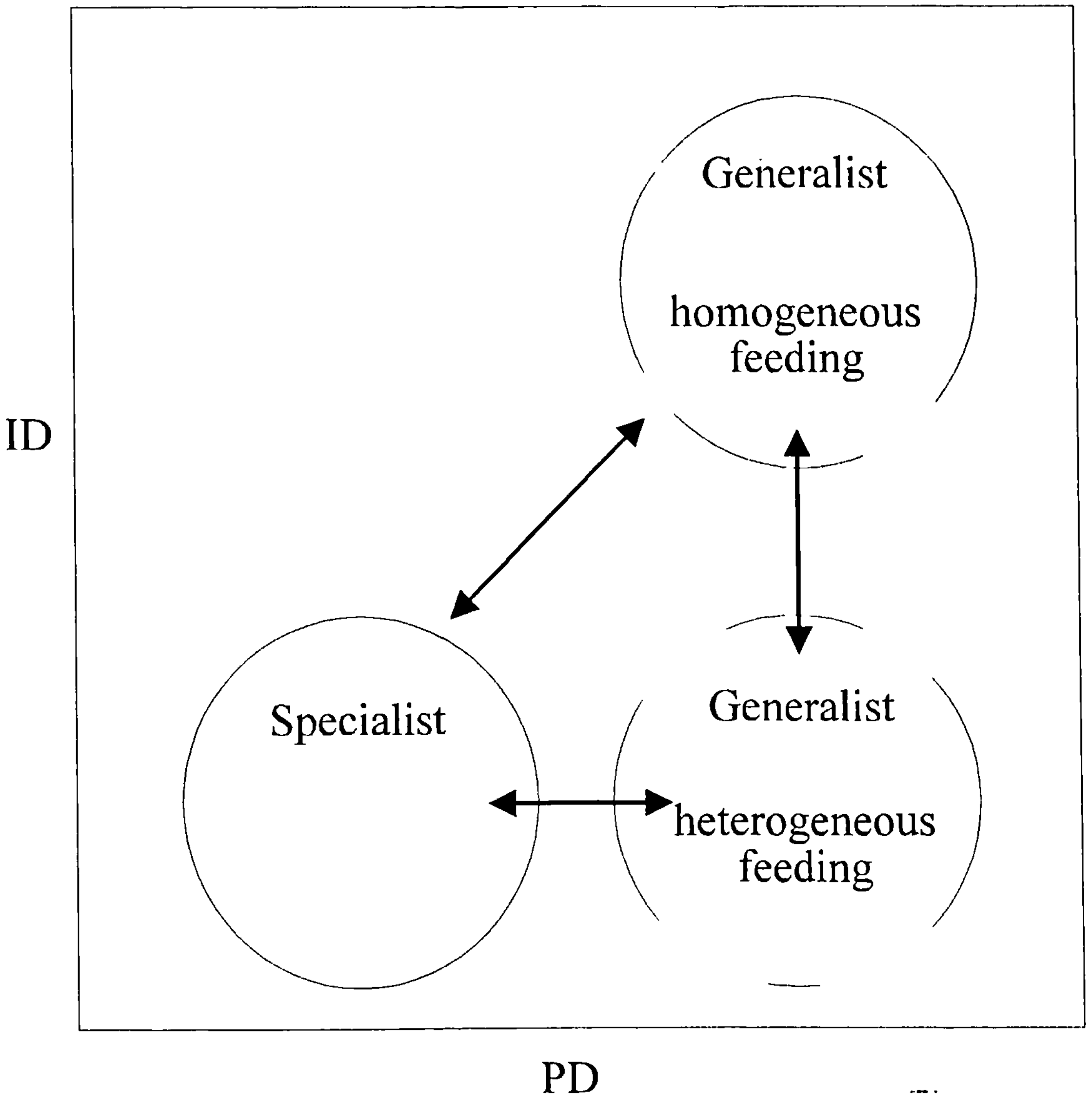


Fig. 7.1 The interpretation of feeding strategy from the graphical method proposed by Tokeshi (1991).

occurrence data were used within the analyses and seasons were as defined in Chapter 3 (Appendix 4). Non-parametric statistics were used as the data were not normally distributed.

To determine any tidally dependent feeding habits the data were divided into four groups based on tidal state at capture, i.e. low water, high water, flood and ebb, and each group assessed with respect to differences in fullness index using the Freidman, non-parametric two-way ANOVA. A similar analysis was performed to determine hourly changes in feeding intensity, with groups determined from hourly blocks, e.g. 1500 - 1559 was classed as group 15.

7.2.3 Inter- and Intra-specific Interactions

The different species, and size classes, were analysed for the percent occurrence of prey species within the diet using TWINSPAN to indicate the inter- and intra-specific dietary interactions within the estuary (Section 5.2.1). Default parameters within the programme were used throughout this analysis.

The data were then analysed using detrended correspondence analysis, DECORANA, within the Cornell Ecology Programmes computer package (Hill 1987), and the classification of fish and prey species produced as graphs to show inter- and intra-species similarities. This enables the groupings from the TWINSPAN analysis to be verified, while demonstrating the prey species which occur together in the diets of different species.

DECORANA is an ordination technique performed using the same data and package as the TWINSPAN classification (Gauch 1982). However, unlike TWINSPAN no division of the sites occurs. DECORANA produces an ordination over 4 axes, such that the amount of variation observed is explained by each axis in decreasing amounts. Axes 1 and 2 are the most commonly plotted as they generally account for > 50 % of the variation.

A series of Wilcoxon matched-pairs sign-ranked one-way non-parametric ANOVA were used to determine any inter- and intra-specific dietary differences (J. Thompson, Dept. Mathematics and Statistics, Uni. of Hull, pers. comm.). This enables the groupings derived above to be statistically examined.

7.3 Results

7.3.1 Digestion Rates

There was no significant difference observed in the proportion of debris with time in the gut of plaice on 23.3.94, suggesting that digestion is slow during the first 6 hours (Fig. 7.2). The fish were found to have

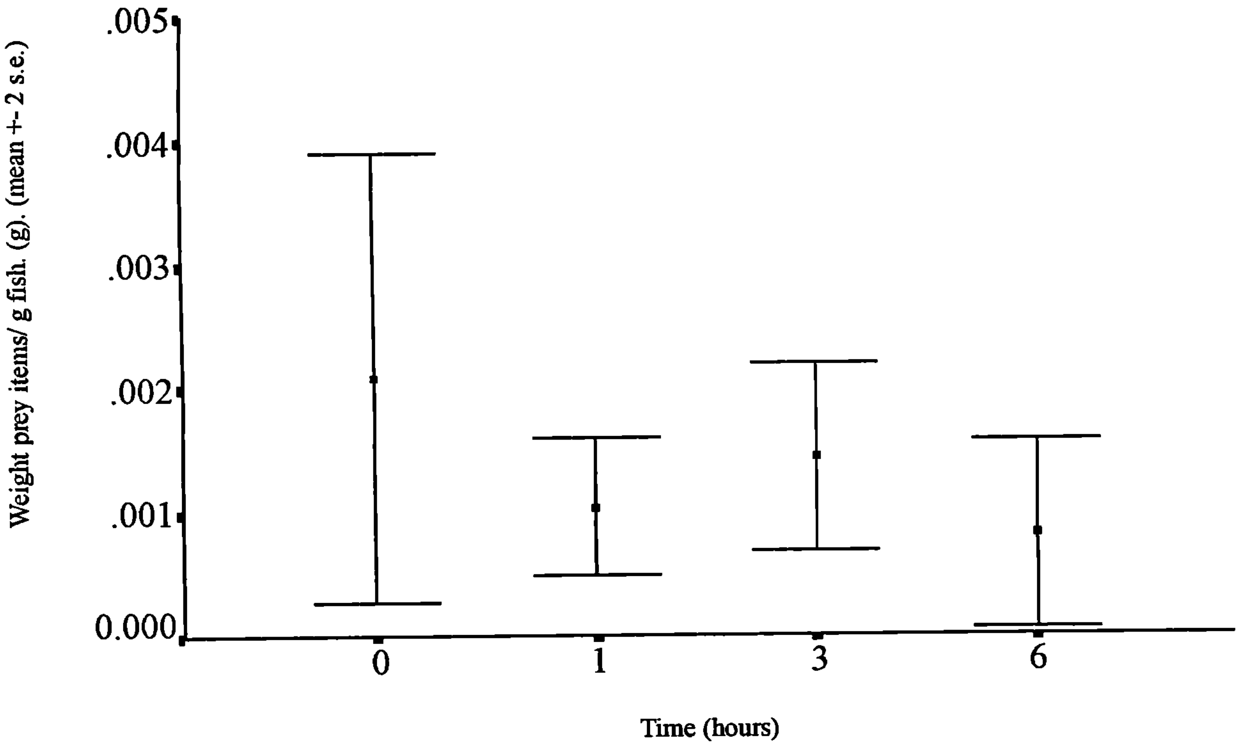


Fig. 7.2. The change in weight of identifiable prey items in the stomach of plaice with time.

taken Polychaeta, Gammaridae, predominantly *Bathyporeia* and *Haustorius*, *Hydrobia*, *Macoma balthica* and *Idotea*, indicating that feeding had occurred within the intertidal areas.

The fish examined from 19.9.94 could not be used in this analysis due to a high proportion of empty stomachs, an average of 80 % per sample. Thus, data on digestion rates has not been collected within this study.

7.3.2 Species-Specific Dietary Analyses

7.3.2.1 Species Diets and Feeding Strategies

Sole has the most diverse diet of the species examined, with 57 taxa taken, while herring shows the greatest degree of specialisation, only 5 taxa taken (Fig. 7.3; Appendix 5), although this may be a function of the different sample sizes involved. Diversity increases with size in pogge and whiting indicating an increase in the niche breadth with size. However, there is a decrease in diversity with increasing size in plaice suggesting a decrease in the niche breadth with size, while the decrease in 'evenness' representing a movement to a more specialised diet supports this analysis, with large plaice specialising on *Cerastoderma edule* (Appendix 5). There is also a decrease with size of the diversity of the flounder diet although there is an increase in evenness index to the larger flounder, indicating the greatest specialisation in small and medium fish (Fig. 7.3). Thus, it would appear that large flounder have a small niche breadth compared to other flounder, i.e. 12 taxa compared to 19 and 38 taxa for small and large flounder respectively, but do not specialise on any particular prey item. With the exception of large flounder, all species with an evenness index > 0.85 have a low occurrence within the samples (n < 10). This suggests that the evenness values may reflect the sample size rather than the feeding strategy of the species, i.e. given the restricted number of items in the individual diets, if each fish feeds on two different items of a possible 20, a sample size of 5 may fail to detect the preferences apparent from a sample size of 500. Similarly, sample size may affect the diversity of the diet.

The importance of different prey groups within the food web of the estuary is given as the percent occurrence of the groups in the diets of the fish (Table 7.2). In this case 'debris' was not included, thus 'other' is comprised of different taxa, i.e. freshwater or aerial insects. The use of the Index of Preponderance to rank the prey of each species, excluding debris in the calculation of total weight, reveals the specific differences in diet, e.g. while large plaice and sole feed predominantly on polychaetes the species taken vary, as does the importance of each species in the diet (Appendix 5).

Table 7.2 The occurrence of the main prey groups in the diets of the fish (expressed as a percentage).

	Cod	Flounder			Goby	Plaice		Pogge		Whiting		
		Small	Medium	Large		Small	Large	Small	Large	Small	Medium	Large
Plant	5	20.59	20	0	0	0	12.70	0	0	1.92	0	1.23
Polychaete	20	11.76	31.11	22.22	1.13	21.43	66.67	0	0	0	4.38	11.11
Copepod	5	0	0	0	0.38	21.43	6.35	0	0	5.77	2.92	1.23
Mysid	40	20.59	8.89	0	32.71	11.22	7.94	55	18.75	67.31	73.72	62.96
Amphipod	35	47.06	48.89	55.56	46.99	25.51	28.57	15	6.25	32.69	45.99	30.86
Decapod crustacean	40	14.71	15.56	44.44	0.75	1.02	6.35	0	68.75	0	6.57	43.21
Brachyura crustacean	15	2.94	8.89	11.11	0.75	0	11.11	0	31.25	1.92	0.73	12.35
Mollusc	5	35.29	28.89	11.11	0.38	16.33	57.14	0	0	3.85	9.49	4.94
Fish	10	2.94	0	11.11	0	0	0	0	0	1.92	5.11	18.52
Other	10	32.35	8.89	0	0.38	5.10	11.11	5	6.25	0	1.46	2.47
No. fish	20	24	45	9	266	98	63	20	16	52	137	81
Size range (cm)	7 - 29	< 15	15 - 25	> 25	2 - 8	< 8	> 8	< 7	> 7	< 9	9 - 14	> 14

	Sole	Sprat	Dragonet	Herring	Sea snail	Stickleback	Lesser weever	Eel	Dab	Smelt	Brill	Turbot
Plant	1.43	0	0	0	9.80	0	5.26	0	0	0	0	0
Polychaete	57.86	0	0	0	0	0	0	66.67	0	14.29	0	0
Copepod	0.71	17.24	0	4.55	0	0	0	0	0	0	0	0
Mysid	9.29	24.14	0	63.64	31.37	0	52.63	33.33	0	71.43	25	0
Amphipod	25	0	25	9.09	49.02	50	15.80	0	0	42.86	0	33.33
Decapod crustacean	13.57	0	50	0	50.98	0	26.32	0	0	14.29	50	66.67
Brachyura crustacean	13.57	0	20	0	0	0	0	66.67	50	0	25	33.33
Mollusc	10	3.45	75	4.55	3.92	25	5.26	33.33	0	0	0	33.33
Fish	2.86	0	0	0	9.80	0	10.53	66.67	0	0	25	33.33
Other	4.29	0	0	27.27	1.96	25	5.26	66.67	50	0	0	0
No. fish	140	29	4	22	51	4	19	3	2	7	4	3
Size range (cm)	3 - 41	3 - 13	9 - 20	4 - 11	4 - 16	4 - 6	8 - 12	29 - 39	16 - 21	9 - 22	3 - 8	3 - 19

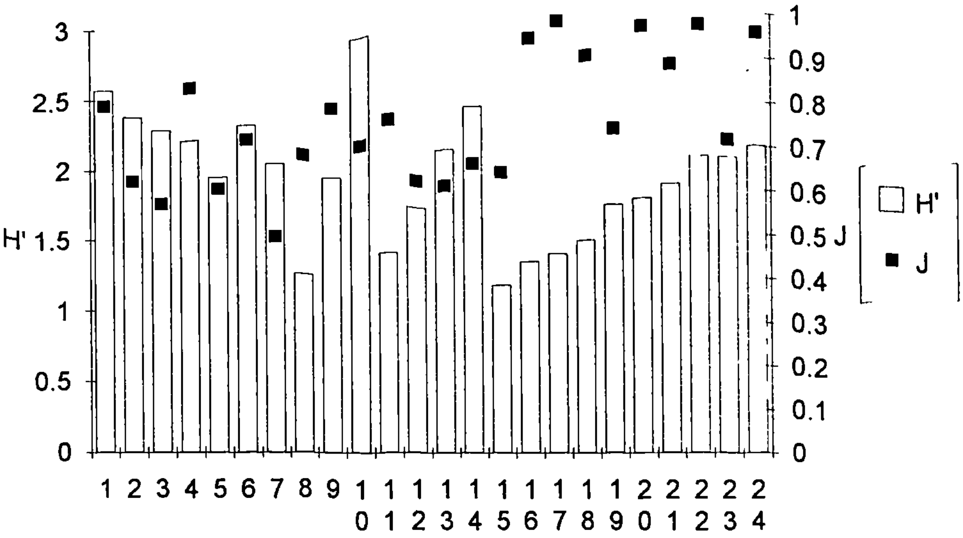


Fig. 7.3. The Shannon-Wiener and evenness indices for the diets of the fish in the Humber estuary. (Species are in order: 1, Cod; 2, small flounder; 3. medium flounder; 4. large flounder; 5, goby; 6, small plaice; 7, large plaice; 8, small pogge; 9, large pogge; 10, sole; 11, sprat; 12, small whiting; 13, medium whiting; 14, large whiting; 15, herring; 16, brill; 17, dab; 18, stickleback; 19, lesser weever; 20, turbot; 21, smelt; 22, eel; 23, sea snail; 24, dragonet).

Crustaceans, particularly mysids and amphipods, are the most important group within the estuary with respect to fish feeding (Table 7.2). The exceptions are large plaice, which have more polychaetes and molluscs in their diet, sole which take predominantly polychaetes, dragonets, which show a higher ranking of molluscs, and sprat, which have a high number of copepods.

The graphical analysis proposed by Tokeshi (Fig. 7.4) indicates that all of the species examined are 'generalists', i.e. do not feed selectively on a prey item which may be rare but feeding on available, usually abundant, prey, although six species, small pogge, sprat, herring, stickleback, dab and brill show some specialisation with their appearance in the bottom left part of the graph. This reflects the wide range of prey taken, but does not represent the dominance of different items. A subjective assessment of the similarities in diet between morphological types in the same trawl reinforces the opportunistic nature of the diet, with the same prey items found in a large proportion of the stomachs from individual trawls.

7.3.2.2 Seasonal, Temporal and Tidal Variations

Results from the Wilcoxon tests indicate that there were few annual or seasonal differences in the diets of cod, goby, flounder, plaice, pogge, sole, sprat or whiting. Statistically significant differences between years were observed between the diets of flounder in the summer of 1994 and those in 1992 and 1993

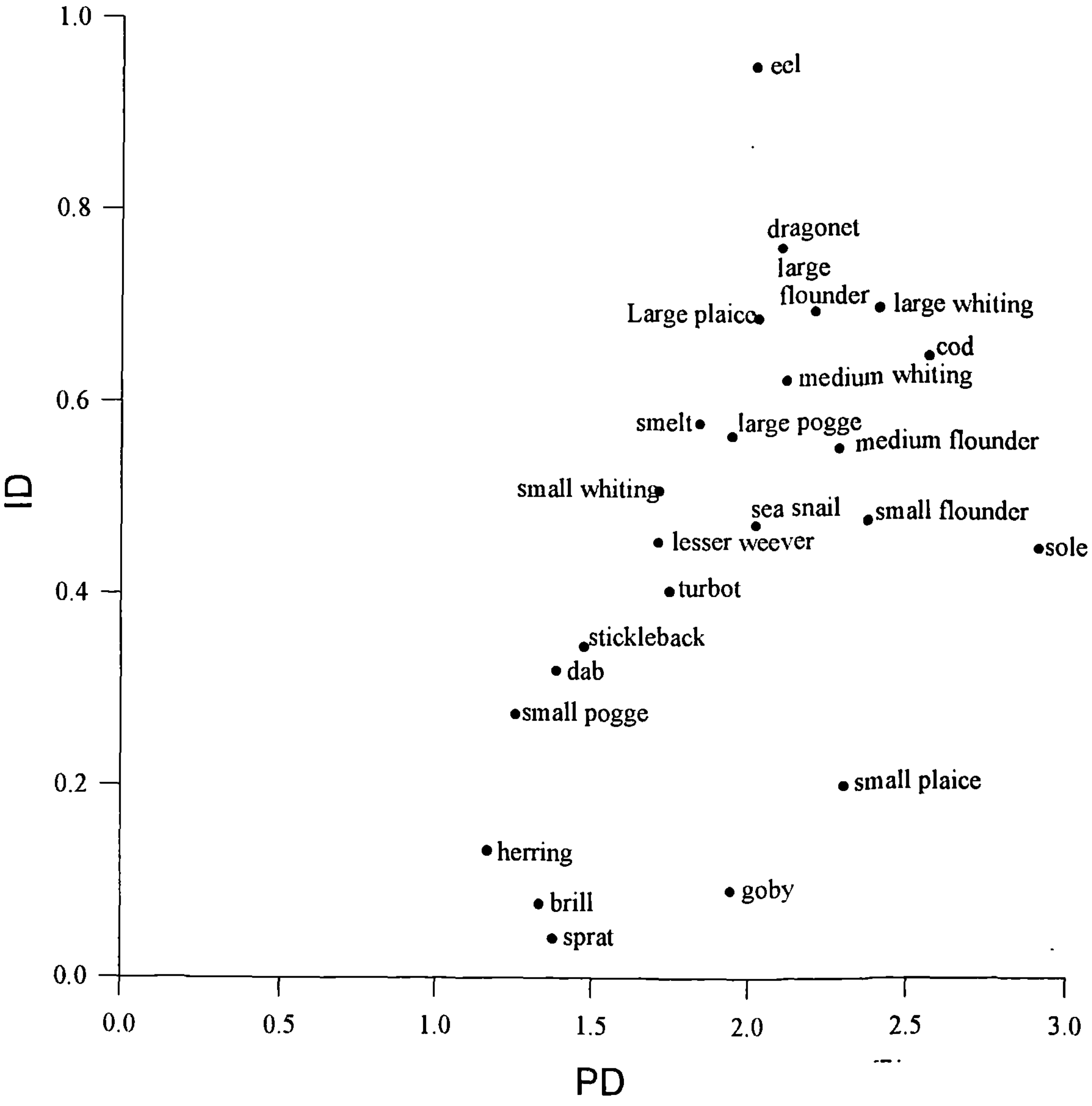


Fig. 7.4 The feeding strategy of the different species and size classes within the Humber estuary.

(p = 0.001 and 0.05 respectively), and both plaice and sole in the autumn of 1993 and 1994 (p = 0.01 and 0.007 respectively). All seasonal differences noted occurred in 1992 between flounder caught in summer and those captured in spring and winter (p = 0.002 and 0.04 respectively), and sole in spring and summer (p < 0.001). This lack of difference in the diets of the fish suggest a broad diet throughout the year. Seasonal variations in feeding intensity, as defined by the proportion of empty guts within the samples per year (Appendix 4), were also assessed using the Kruskal Wallis non-parametric single factor ANOVA test (Zar 1984). The analysis indicated that there were no seasonal variations in feeding intensity within the Humber estuary fish populations.

Analysis of the fullness index data for temporal or tidal variations indicate that there were no statistically significant differences in the fullness index with time of day or tidal state (Appendix 6). This implies that the fish feed at all states of the tide throughout the day, further emphasising the opportunistic nature of the diet.

7.3.3 Inter- and Intra-specific Interactions

TWINSPAN divides the species, and size-classes, into 11 groups (Fig. 7.5). The initial division separates the species with a high occurrence of mysids in the diet from those with *Macoma balthica* and *Corophium*. Further division of the latter group separates stickleback, containing freshwater insects, from the remainder. These are further divided, on the basis of the presence of Phyllodocid polychaetes, into a group comprising large plaice and sole. Dragonets are then separated from the three sizes of flounder and dab on the basis of brachyuran crustaceans within the diet of dragonet. The indicator species are not necessarily dominant, as demonstrated by the use of the freshwater insect *Sialis* to classify stickleback, as this species has a low occurrence within the diet (Appendix 5).

The group with a high occurrence of mysids is further divided by the high occurrence of *Carcinus* within the diet. Where this occurs, eel, brill and weever are separated from large pogge and turbot by the presence of gobies. Within the other part of this dichotomy, characterised by the presence of copepods and *Gammarus*, cod, small plaice and large whiting are further characterised by the presence of stone/shell debris within the guts. Small pogge and sprat are separated from the remainder by the absence of Gammaridae within the diet, while sea snail occur in a separate group based on the presence of Bryozoa. Goby, herring and smelt are then separated from small and medium whiting by the absence of mollusc siphons.

The groupings derived by the TWINSPAN analysis do not indicate statistically significant differences between the diets of the different species, simply the presence or absence of particular prey items. The use of the Wilcoxon rank sign test demonstrates that there are statistically significant differences in the diets of species from the same group (Table 7.3). Thus small flounder, for example, have a significantly

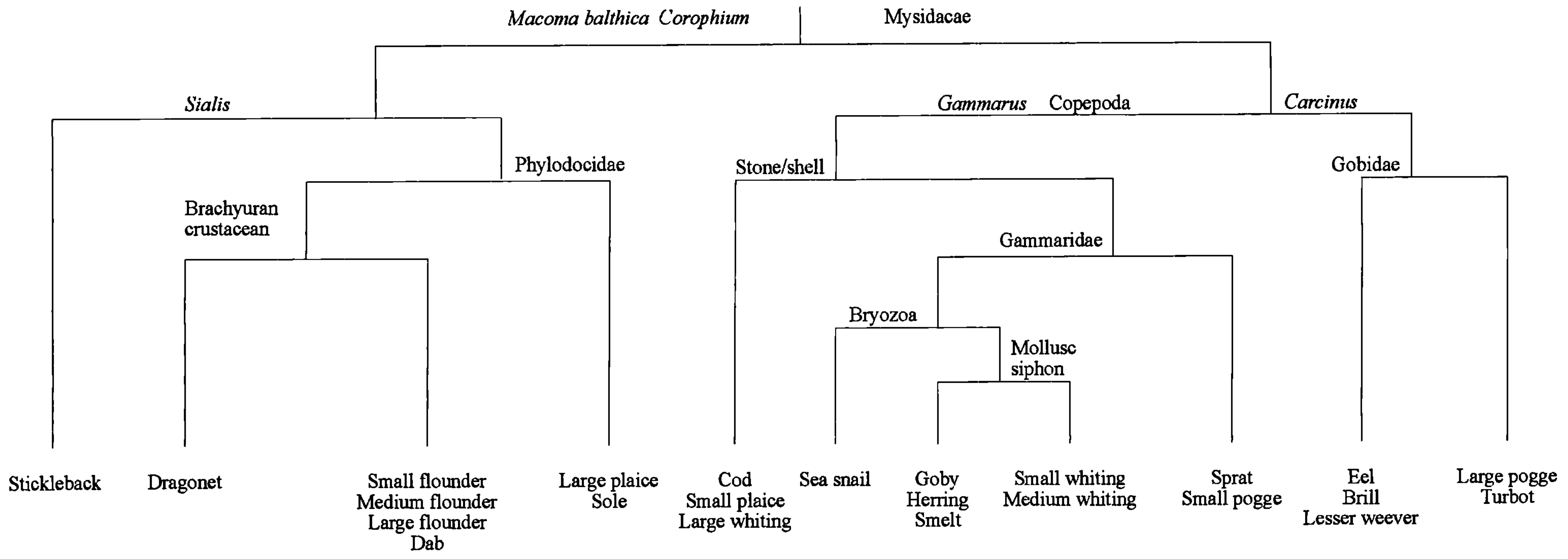


Fig. 7.5 TWINSPAN diagram showing the inter- and intra-specific similarities in diet

Table 7.3. The significance of dietary differences between the 24 fish species, as calculated using the Wilcoxon Rank Sign Test (species codes are as Fig. 7.3; *, 0.05 ≤ p < 0.01; **, 0.01 ≤ p < 0.001; ***, p ≤ 0.001).

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
s. flounder	**																						
m. flounder	***	***																					
l. flounder		***	***																				
goby	***	***	***																				
s. plaice	*	***	***																				
l. plaice		***	***																				
s. pogge	**	***	***	*			***																
l. pogge		***	***				*																
sole			*	*	***	**	***	***	***														
sprat	***	***	***	**		**	***			***													
s. whiting	**	***	***					*		***													
m. whiting		**	***		***			***		*	**	*											
l. whiting		**	***		***	*	*	***	*		***	**											
herring	***	***	***	*		**	***			***		*	***	***									
brill	*	***	***		*	*	***			***			**	***									
dab	*	***	***		*	*	***			***			***	***									
stickleback	*	***	***				***			***			***	***									
weever	*	***	***	*			*			***			*	**									
turbot	***	***	***	**	***	***	***		**	***		***	***	***					**				
smelt	***	***	***	**	***	***	***		**	***		***	***	***					**				
eel	***	***	***	**	***	***	***		**	***		***	***	***					**				
sea snail	*	***	***							**	*				*	*		*		**	***	***	
																				*			
dragonet		***	***				**			***	*			*						**	*	*	

different diet from all other species, while stickleback is significantly different from cod, small and medium flounder, large plaice, sea snail, sole and medium and large flounder only, despite the separation of stickleback into a unique grouping. Further, the Wilcoxon rank sign test demonstrates the relevance of the different size ranges used in whiting and flounder, despite their occurrence in the same group within the TWINSPAN classification.

DECORANA enables this grouping to be further assessed, thereby verifying the results (Fig. 7.6(a)). From this analysis it can be seen that the two analyses, DECORANA and TWINSPAN, produce a broadly similar classification of the species, although some differences do occur, e.g. the separation of smelt from goby and herring within the ordination. Within the DECORANA plot dragonet, eel, dab, brill and turbot appear to have diets sufficiently dissimilar to all others, and each other, to be separated on the graph, emphasised by the large degree of similarity between the remaining species.

A classification of prey species according to their occurrence within the diets of the fish also results in several clusters of prey taxa within the ordination, representing similarities in their occurrence within the diet of the different fish (Fig. 7.6(b)). Within the clusters thus determined, there was no family-specific grouping noted, e.g. group 1 contains, among others *Actinia*, Polynoidae, *Hydrobia* and *Gammarus*, while group 2 contains *Metridium*, Polychaeta, *Macoma* and *Homarus*. Thus each group noted comprised polychaetes, amphipods, mysids, etc., emphasising the diversity within the diets of the different species.

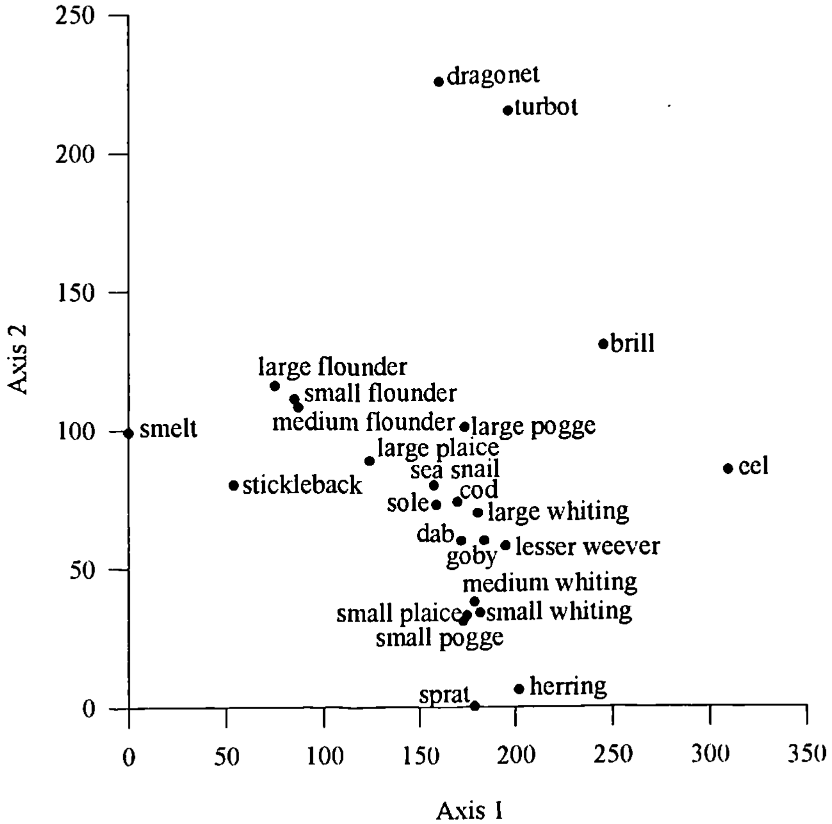
An analysis of niche width, through the use of Bray-Curtis analysis, indicates that there is little overlap between the diets of the different groups (Fig. 7.7). Only four species, goby, small pogge, herring and small whiting have a similarity < 0.25, i.e. show niche overlap, with medium whiting and lesser weever also closely associated with this group. This, together with the general nature of the diets, indicates some resource partitioning. However, the foodweb of the estuary is highly complex, and, based only on the presence/absence of prey items in the diet, many interactions are observed, e.g. flounder prey directly on plaice as well as consuming other, common resources such as brachyuran crustaceans (Fig. 7.8).

7.4 Discussion

7.4.1 Species-Specific Analyses

There are several measures used in the analysis of stomach contents, in particular volumetric, abundance, percent occurrence and weight of prey items (Hyslop 1980). Within this study percent occurrence data has been used as it ignores the digestive stage of the meal, i.e. whether prey has recently been eaten or is in an advanced stage of digestion. Where two measures were required, i.e. in the analysis of prey dominance, weight data were selected, based on the absence of numerical data for some

(a)



(b)

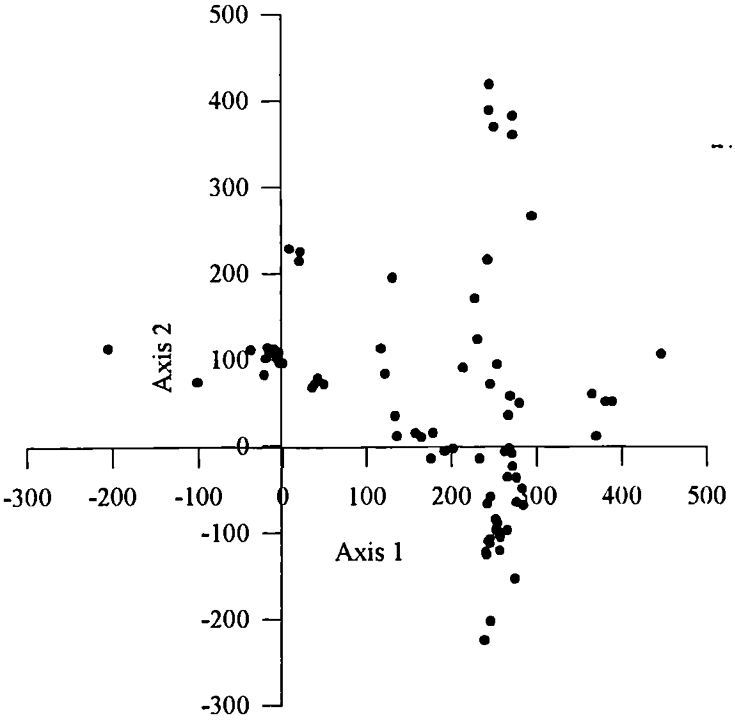


Fig. 7.6 The DECORANA scores for axes 1 and 2 of (a) fish species and (b) prey items.

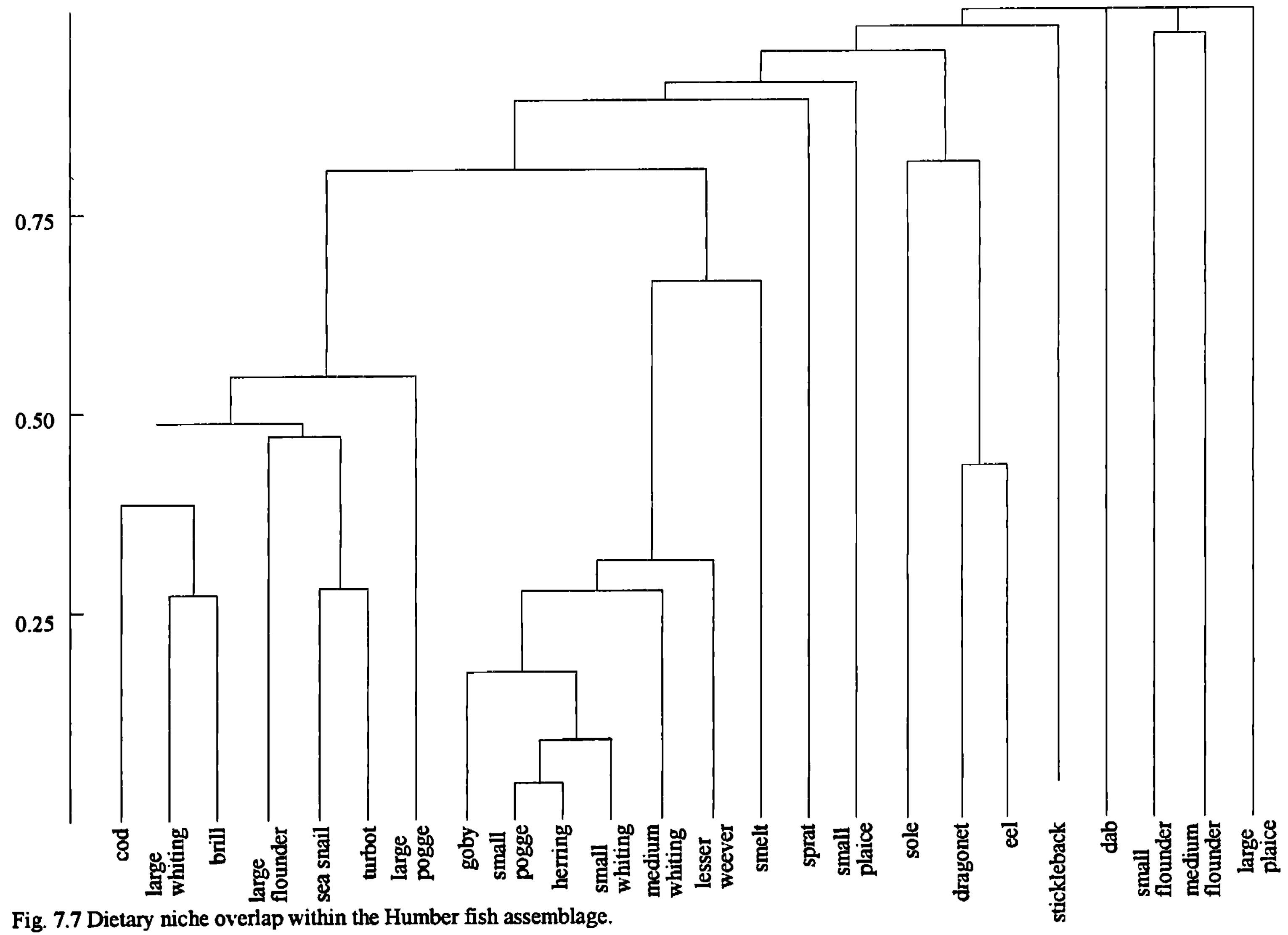


Fig. 7.7 Dietary niche overlap within the Humber fish assemblage.

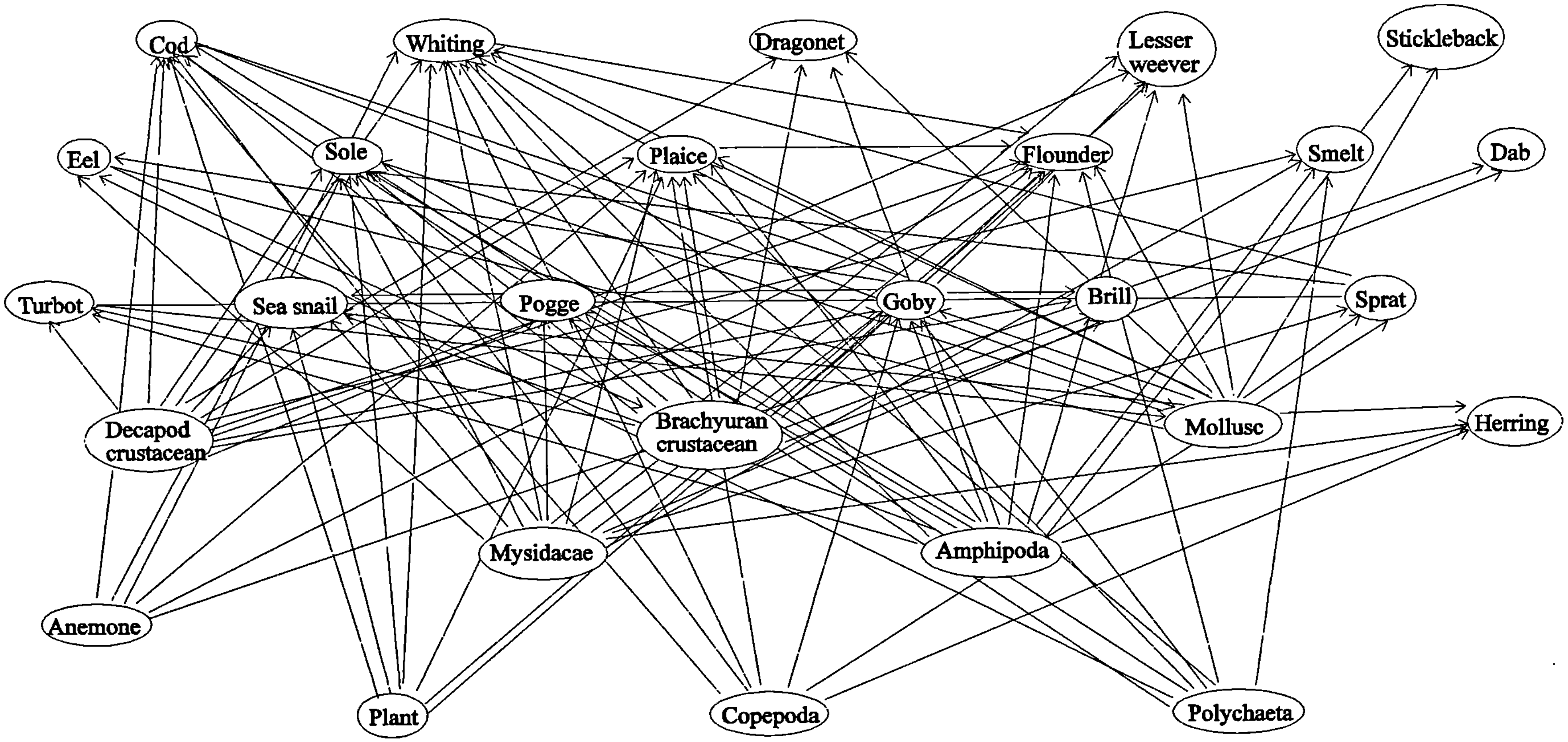


Fig. 7.8 The simplified foodweb of the Humber estuary fish assemblage.

cases within the dataset, particularly relating to polychaetes. While this may be assumed to bias the analysis in favour of larger prey items, it has been demonstrated that the high correlation between volumetric, abundance and weight data mean that any one will adequately describe prey species importance (MacDonald & Green 1983).

Within the Humber estuary, the fish appear to have a general diet, as shown by the analysis of feeding strategy (Fig. 7.4), and the complex foodweb for the area (Fig. 7.8). This is similar to the findings in other areas, e.g. the Wadden Sea (Kühl & Kuipers 1979), where the opportunistic nature of the diet is emphasised. Opportunism within the diet of the fish within the Humber estuary is further demonstrated throughout this study, from the diverse diet within many of the species to the lack of seasonal, tidal and temporal variations in feeding intensity. The latter indicates a non-restricted feeding pattern, where prey are consumed when encountered, and differs from the findings in other studies which suggest seasonal or diurnal feeding patterns, e.g. plaice diets showed significant seasonal variation on Sable Island Bank, Canada (Martell & McClelland 1994), although this difference may be a function of the restricted sampling programme within the Humber.

Further evidence of opportunism was noted during the analysis, where fish caught in the same trawl were frequently found to have similar prey within the stomach. This occurred irrespective of species, but dependant to a large extent on family. Thus plaice and flounder contained similar prey items, which differed from whiting or pogge. A similar trend was observed in the Wadden Sea (Kühl & Kuipers 1979) and the Forth and Tagus estuaries (Costa & Elliott 1991), where the greatest niche overlaps were observed between species of the same family, or order, and indicates that morphology may be affecting the feeding behaviour (Wootton 1992).

Despite the general nature of the diets, some resource partitioning would be expected as there is unlikely to be a super-abundance of all prey species within the area given the low abundances of some organisms, e.g. *Corophium*, within routine benthic sampling (NRA, unpubl. data). From the wide diversity of prey types consumed by each species, and the occurrence of individual prey taxa in the diet of several species, it would appear that resource partitioning occurs via the degree of utilisation of the prey rather than through its absence from the diet, e.g. Nephtyidae occur in the diet of nine species, but they form a dominant prey item for small plaice only (30 % of the diet compared to < 3 % in the other species). This agrees with the findings of Kislalioglu & Gibson (1977), and may be due to the availability of the prey within the area together with morphological and behavioural differences between the members of the fish assemblage, which will affect the capture efficiency. Differences in capture efficiency have been shown elsewhere to affect the feeding dynamics of a species (Moore & Moore 1976(a)), and thus influence the inter- and intra-specific interactions.

The restricted nature of the diet is further illustrated by the Index of Preponderance, which ranks the individual prey items (Appendix 5). From this it can be seen that, although there are several different prey items within the diet, a large proportion of the diet, greater than 50 %, is composed of a restricted number of items, e.g. *Gammarus* forms 71 % of the occurrences within the diet of small flounder, while Crangonidae and Mysidae together account for 51 % of the occurrences within the diet of cod. Thus it would appear that, while fish will take any organism that they encounter and are capable of handling, i.e. prey within the size range restricted by mouth morphology, they will selectively prey on a restricted range of organisms. This may be related to availability, with respect to abundance and geographical distribution, but is more likely to relate to the restrictions imposed by the morphology of the fish (Moore & Moore 1976(b)). However, in the absence of detailed information of prey availability, this must remain an assumption based on the findings in other areas rather than a detailed description of the Humber system.

Crangon have been shown to be a dominant prey item in the foodweb of many estuaries, i.e. the Forth and Tagus (Costa & Elliott 1991) and the Solway (Williams *et al.* 1965). However, despite the presence of a commercial shrimp fishery within the area, indicating a high abundance of *Crangon,* this was not found to be the case within the Humber, where it forms the dominant species in the prey of large flounder, large pogge, sea snail, brill and turbot only (Table 7.2). Instead the Humber estuary foodweb is dominated by mysids and gammarids, particularly *Gammarus,* with the main exceptions of sole and large plaice which feed predominantly on polychaetes. Despite these differences, it is concluded that the smaller, epibenthic crustaceans form the important link between benthos and fish in most estuaries.

Molluscs, both intact and as cropped siphons, only form a large part (> 25 %) of the diets of small and medium flounder, large plaice, dragonet, eel and turbot, although in the case of eel and turbot this may be a function of sampling size as they occur in only one fish. It would therefore appear that there is little dietary selection for molluscs within the Humber fish assemblage. A similar situation was observed in Loch Etive (Kislalioglu & Gibson 1977), and may reflect the fact that most molluscs burrow within the sediment, reducing the hunting efficiency of some species, e.g. flounder (Moore & Moore 1976(a)), together with the relative indigestibility of the shell.

With the exception of molluscs, there was a difference in the groups of prey organisms taken by the fish assemblage in the Humber and that in Loch Etive (Kislalioglu & Gibson 1977), in particular with the relative rarity of Mysids within the diet of the Loch Etive fish assemblage. This was not found in other areas however, with the feeding patterns observed in the Humber being similar to those obtained in, e.g. the Solway (Williams *et al.* 1965), the Forth and Tagus (Costa & Elliott 1991) and the Wadden Sea (Kühl & Kuipers 1979). Furthermore, an analysis of feeding guilds in several estuaries around Europe indicates that the Humber fish assemblage is similar to that in the Dutch Oosterschelde and Voordelta, with least similarity to the Tagus, Aveiro, Elbe and Loire estuaries, possibly indicating a geographical effect (Dewailly 1994).

Many of the species examined were found to use the intertidal areas to feed, as indicated by the occurrence of prey items which were more likely to have been taken within the intertidal than the subtidal areas, including *Nereis*, *Nephtys*, *Arenicola*, *Corophium* and bivalve molluscs, such as *Cerastoderma* and *Macoma*, which occurred in greater densities within the intertidal than subtidal samples (NRA, unpubl. data). Using this criteria, sole, for which 41 % of the dietary occurrences were *Arenicola*, predominantly the cropped tail segments, and stickleback, which fed predominantly on *Corophium*, demonstrated the greatest dependency on the intertidal areas, while other species include plaice, flounder, lesser weever, eel, brill and turbot. Brill and turbot were only caught in the intertidal sampling (Chapter 4), while plaice was the dominant species within these samples, further indicating the high usage of this area. In addition, saithe, pollack, whiting, cod, goby, herring and sprat were also caught within the intertidal sampling (Table 4.2), demonstrating their usage of the intertidal area.

7.4.2 Inter- and Intra-Specific Interactions

Inter- and intra-specific interactions are indicated where dietary niche overlap occurs (Carter *et al.* 1991), although the prey species may be of sufficient abundance to preclude competition. Interactions indicated within the DECORANA and TWINSPAN analyses reflect the general nature of the diets, while in some cases ignoring the specific differences. For example, the three size groups of flounder were found to have similar diets, suggesting that the group should not have been subdivided, although analysis of the individual diets indicates significant differences between the three, e.g. *Gammarus* was the dominant prey of small (72 %) and medium (31 %) flounder, compared to 29 % of the diet in large flounder, while Crangonidae dominate the diet of the large flounder (42 %) and form a significant part of the diet of medium flounder (27 %) compared to 3 % of the diet of small flounder. These intra-specific interactions were also found in the gadoid populations of the Norwegian Deep (Bergstad 1991) and may reflect behavioural and morphological similarities, with differences reflecting the capability of larger fish to handle larger prey items. It has been suggested that this demonstrates resource partitioning (Tyler 1972), although this is not seen as an important mechanism in the structuring of fish communities (Costa & Elliott 1991).

The analyses within this study indicate that there are few interactions within the diets of the fish assemblage of the Humber, giving a similar pattern to that found in Loch Gairloch where there was little evidence of a significant diet overlap (Hall *et al.* 1990). However, within the Humber the absence of interactions appears to be the result of differences in the proportion of each prey taxa within the diet rather than a lack of dietary overlap, as can be seen from the general nature of the diets of many of the species, e.g. sole and plaice, and the complex nature of the foodweb. This is similar to the findings of

Sheldon & Meffe (1993) within Blackwater stream assemblages, where most prey are used by several fish taxa, and would appear to reflect the morphological and behavioural differences between the species. This trophic differentiation reflects a diversification at the generic and family level, and would suggest that prey availability is not a limiting or contributing factor to the foodweb of the estuary.

8 THE 'HEALTH' OF THE FISH POPULATIONS

8.1 Introduction

The structure, population dynamics and feeding habits of the fish assemblage have been examined, together with an assessment of the environmental factors affecting the populations (Chapters 4 - 7). These factors will give an indication of population and community stress. An analysis of the condition of individual fish, the level of parasitism, abmormalities and bioaccumulation of comtaminants, will enhance this information through an indication of the impact of different stressors to the individual.

8.1.1 Parasites

The term 'parasite' encompasses a range of organisms which live in or on a host species, from which they obtain food (Abercrombie *et al.* 1980). While parasites may or may not be harmful to the host, it is likely that internal parasites utilising the food or body tissues of the host affect the growth and body condition of that organism (Begon *et al.* 1986), particularly where food is limited. Any decrease in somatic condition, as determined from the length to weight ratio, may, in turn, affect the reproductive success of the animal, either through mate selection or gamete development. However factors influencing somatic condition are complex and may not be directly related to the parasites, but rather show the effects of stress (Peddicord 1977). Stress is defined as something which leads to a reduction in the survival of the organism (Bayne *et al.* 1985), and can be relate to environmental or pathogenic causes.

As reproduction is the ultimate aim of any organism, and requires a large input of resources, the gonadal index can be expected to give a better indication of the degree to which parasites affect their host. Studies on a variety of species from different groups including molluscs (Choi *et al.* 1994), crustaceans (Sumpton *et al.* 1994), fish (Tolonen 1994) and mammals (Mulvey *et al.* 1994) all indicate that the gonadal index, or reproductive success in the case of mammals, is affected by the presence of parasites within the body. There is little evidence of a correlation between parasites and the condition of the animal without a concurrent effect on reproduction, thus further demonstrating the importance of the gonadal index when assessing the biological effects of parasites.

8.1.2 Abnormalities

The occurrence of abnormalities in fish have been noted for the past 800 years, although this has only recently been linked to pollution (Bucke 1993). While environmental stress, including pollution, has been clearly indicated in the occurrence of disease (Sindermann 1980), clear links between pollution and disease are rarely proven (Bucke 1993). In addition, there appears to be a synergistic effect between different stresses, both natural and anthropogenic, e.g. many species are more susceptible to disease at low temperatures (Bucke 1993). Despite this, abnormalities such as tumours, fin rot and skeletal abnormalities are potentially very useful in pollution monitoring programs (Sindermann 1980). These provide a simple, qualitative analysis of the amount of pollutants within the area, although the effects are difficult to quantify (Sindermann 1980). Effects are readily seen and can be examined under laboratory conditions as well as in the field. The variations in prevalence due to season, age, migratory patterns and species must also be considered (Bucke 1993).

In order to minimise the number of variables within the analysis, the most desirable species for the monitoring of pollution in an estuary is an estuarine resident with a small home range, thus reducing the influence of spatial variations in pollutant concentrations. As intertidal mudflats often receive the greatest pollutant input, with sediments acting as a repository of many pollutants, the fish should feed on these areas and have contact with the sediment. Thus flounder is considered a suitable species for the monitoring of estuarine pollutants through bioaccumulation (Elliott & Griffiths 1986). This will enable long term monitoring of the situation in a particular estuary, although the lack of information on background levels of diseases (Bucke 1993), and the intersite variations which exist (McVicar *et al.* 1988) preclude a detailed comparison of different areas.

Many studies of the effects of pollutants on animals involve the determination of lethal concentrations (LC_{50}). However, sublethal concentrations of pollutants, including heavy metals, within the environment can cause a variety of diseases and abnormalities (Bucke *et al.* 1983). These can include the occurrence of fin erosion, skeletal anomalies, tumours, lymphocystis (Sindermann *et al.* 1980) or papilloma (Dethlefsen 1989), and can result in the alteration of the structure and functioning of the population. The latter may occur through the alteration of the reproductive capacity, or success, of the organisms, i.e. fewer number of eggs may be produced, or fatal deformities may arise within the larvae as a result of contaminant within the environment (Cameron *et al.* 1992).

8.1.3 Heavy Metals

Absorption of heavy metals by organisms can occur from both the environment and the diet (Engel & Brouwer 1984). A passive action, absorption from solution involves the diffusion of the metal into the cells along a gradient formed by adsorption onto the cell surface (Bryan 1976). Following absorption, the metal ions are transported to specific organs, particularly the liver, where they are utilised, eliminated or sequestered (Engel & Brouwer 1984). Sequestration mainly occurs by binding to metallothioneins within the cell. Accumulated metals are generally stored in specific organs and slowly excreted. Excretion can be passive (Eisler & Gardner 1973), or active, for example copper is excreted at low concentrations enabling fish to reduce concentrations within their body during periods in uncontaminated water (Rickard & Dulley 1983). Within many vertebrates, including fish, the main storage organ is the liver which can therefore be expected to give a better indication of recent contamination within fish (Franklin 1987).

The rate of absorption is determined by a variety of factors including the salinity, temperature and pH of the water, the presence of other metals in solution, the size and degree of starvation of the animal and the chemical form and nature of binding of the metal (Bryan 1976). The latter is perhaps the most important single factor, as stabie forms of the metal will not be absorbed, while it has been demonstrated that the presence of other elements, even in low concentrations, will affect the toxicity of a metal (Eisler & Gardner 1973). However, the speciation of metals is also affected by environmental parameters, e.g. concentrations of heavy metals are generally lower in seawater than freshwater (Förstner & Wittmann 1981), thus both factors must be considered. The acute toxicity of the metal is closely related to its rate of absorption (Bryan 1976), with copper proving to be the most toxic element (Pickering & Henderson 1966).

Data from the Forth estuary indicate that the diet, including the ingestion of sediment, forms the primary source of contamination in flounder (Elliott *et al.* 1988). As a top predator, demersal fish are most at risk from contamination within the system via the bioaccumulation of contaminants within the food chain, beginning with contaminated sediment and accumulating through the benthic biota (Elliott & Griffiths 1986). While the initial availability of the metal from the sediment is dependent on form (Bryan 1976), storage within the organs of benthic organisms will cause a concentration of available metals which will be ingested at the next trophic level, which will in turn be ingested at the next trophic level to the top of the food chain.

8.2 Materials and Methods

8.2.1 Biological Indices

8.2.1.1 Analysis of Condition

The length - weight data were used to calculate the somatic condition index for each individual of the 11 main species. The index used was such that condition factor (K) = $100W/L^3$ (Le Cren, 1951), where W = weight (g) and L = length (mm).

8.2.1.2 Analysis of the Gonad Index

The gonad weight was taken, together with body length, and the Gonad Index (G.I.) calculated, such that G.I. = Gonad weight × 10^5 × Length^{-3} (Pulliainen & Korhonen, 1990), for each species. The use of body length to calculate this index has an advantage over the use of the more fluctuating body weight in that factors such as stomach fullness or gonad condition will not affect the results obtained.

8.2.1.3 Parasites

The presence of different parasites within the fish, and their location in the body cavity, gut or other area, e.g. muscle or gill, was noted. These were divided into the taxa: Nematoda, *Ligula*, Trematoda and *Lernaeocera*, within each location and the percent occurrence in each fish species calculated.

The fish from a single species were split into two groups, those with or without parasites in the body cavity, prior to performing a Student t-test on the condition index and gonad index data. This was repeated for parasites in both the gut and 'other', and all species to determine the effects, if any, of parasites on the somatic condition and reproductive potential of the species.

8.2.1.4 Abnormalities

Prior to dissection each fish was examined for external abnormalities in colour or shape together with the presence of lesions, ulcers, blemishes or fin rot. Abnormal colouration includes the presence of white patches on the upper side of flatfish, pigmented patches on the underside, reddish patches on round fish or other colouration differences i.e. greyish tinge to the scales. Abnormalities in shape are taken to include curvature of the spine, i.e. scoliosis, lordosis or kyphosis, or the absence of fins through causes other than fin rot or trawl damage. These were categorised and the percent occurrence within the population calculated.

8.2.2 Bioaccumulation of Heavy Metals

Due to constraints imposed by the size and abundance of fish within this survey, as well as financial constraints, selected species and occasions were chosen for analysis. Species were selected on the basis of fish size and dominance within the samples, as were the seasons and areas studied (Table 8.1). In all cases, the length of fish analysed was standardised ± 20 % of the mean length.

The liver and muscle tissue were thawed and weighed, then dried at approximately 80 ^{o}C to constant weight. The sample was re-weighed to determine the dry weight and therefore the wet weight:dry weight ratio of the tissue.

Approximately 100 mg of the dried material was taken, weighed accurately ± 0.0001 g. This material was placed in a flask with 2 ml concentrated Nitric acid. The flask, connected to a condenser, was refluxed on a hot plate for 3 hours. The liquid was transferred to a 10 ml volumetric flask, and the solution made up with distilled water prior to storage in a polyethylene bottle, in the refrigerator.

Table 8.1. The number of fish from each species used for the bioaccumulation study, the tissue analysed and the area of the estuary and season from which they were sampled. (√ indicates the area, season and tissue used, e.g. both muscle and liver tissue were taken from 5 flounder from the upper, middle and lower estuary in summer).

	Area of estuary				Season		Tissue	
Species	Upper	Middle	Lower	Outer	Spring	Summer	Muscle	Liver
Flounder	5	5	5			√	√	√
Sole				√	10	5	√	√
Plaice				√		√	5	
Whiting			√			√	3	
Goby	√					√	3	

The heavy metals were selected following preliminary analysis of tissue samples for all metals using X-ray fluorescence spectrometry, which indicated that copper and zinc were the common metals within the tissues. This, together with the presence of both metals within the estuary, make them suitable for analysis. Cadmium and lead occur on the EC Dangerous Substances Directive List 1 (Black list) and 2 (Grey list) respectively, and are present in small quantities within the estuary (NRA 1993), and thus were also selected.

The samples were analysed with an Atomic Absorption Spectrometer (AAS) within the Geography Department, University of Hull. This involves the use of lamps set to a suitable wavelength. Standards made for each metal in a 10 % Nitric acid matrix and were used to set the internal calibration curve, prior to the analysis of the sample, in parts per million. The results were then converted to $\mu g\ g^{-1}$ metal in the tissue by dividing the results by the weight of tissue used then multiplying by the dilution factor (10).

The concentrations of each metal in the different species and tissues were compared using one-way Analysis of Variance (ANOVA) (Zar 1984). Within group variability demonstrates the differences related to variations between individuals, while between group variability demonstrates the variations between samples, i.e. species, areas and seasons.

8.3 Results

8.3.1.1 Parasites

There were four groups of parasites found, of which nematodes were the most common, occurring in the gut, body cavity or muscle of all species examined (Table 8.2). Trematodes were discovered in the gut of flounder, goby, herring, sea snail, sole and whiting, while *Ligula* (a cestode parasite) occurred in the body cavity of goby and the gut of sea snail and cod. *Lernaeocera* (a parasitic penellid copepod) were found only in the gills of whiting. In all cases, with the exception of *Ligula* in gobies, the parasites formed a small proportion of the total body mass. *Ligula* were found to fill the body cavity of the gobies in which they were found, often reaching a length the same as, or greater than, the host (pers. obs.).

Table 8.2 The number of individuals (expressed as a percentage) of each of the 11 main species containing parasites in their body cavity, gut or other areas (i.e. gill or muscle), and the parasite group (the 11 main species were as determined in Chapter 4).

	Body cavity		Gut			Other		
Species	Nematoda	*Ligula*	Nematoda	*Ligula*	Trematoda	Nematoda	*Lernaeocera*	No. fish examined
Goby	40	24.7	9.3		0.3			388
Whiting	40.7		75.8		0.7		7.7	273
Sole	5.1		17.3		3.8			156
Flounder	54.1		24.6		1.6	0.8		122
Sprat	11.4		17.7					79
Plaice	21.6		15.9					88
Herring	21.6		15.9					45
Sea snail	38		42	2	4			50
Pogge	5.4		27					12
Stickleback	8.3		16.7					12
Cod	17.6		70.6	5.9				17

Parasites were not found to significantly affect the condition or reproductive capacity, as measured by the gonad index, of all but two of the species examined (Table 8.3). The exceptions were pogge, which showed a significant difference, $p = 0.049$, between fish with or without parasites in the gut with respect to gonad index ($t = -2.20$, 11.18 d.f.), and whiting with respect to condition factor and parasites in the body cavity, $p = 0.004$ ($t = 2.89$, 271 d.f.).

Differences in the length and age of the two groups, parasitised and non-parasitised fish, were examined using an unpaired t-test. Statistically significant differences were found in length for goby ($p = 0.01$), sole ($p = 0.02$) and pogge ($p = 0.03$), and in age for flounder ($p = 0.01$). This indicates that older, and therefore larger, fish are more likely to be parasitised than younger fish.

Table 8.3 The mean condition index (K) and gonad index (GI) for fish parasitised (P) and non-parasitised (NP) in the gut and body cavity, and corresponding t value for each species

	Body cavity						Gut					
	K			GI			K			GI		
Species	P	NP	t (d.f.)	P	NP	t (d.f.)	P	NP	t (d.f.)	P	NP	t (d.f.)
Goby	0.0009	0.0010	-1.13 (386)	0.223	0.203	0.29 (173)	0.0009	0.0010	-1.13 (386)	0.0214	0.0227	-0.13 (173)
Whiting	0.0008	0.0008	-2.89 (271)	0.0024	0.0024	-0.13 (155)	0.0008	0.0008	-0.45 (271)	0.0023	0.0025	-0.55 (155)
Sole	0.001	0.001	0.57 (154)	0.0116	0.0204	-0.78 (139)	0.001	0.001	1.44 (154)	0.0118	0.0136	-0.28 (139)
Flounder	0.013	0.012	1.15 (119)	0.0115	0.069	1.5 (105)	0.013	0.012	0.09 (119)	0.079	0.0117	-1.10 (105)
Sprat	0.0007	0.0008	-1.26 (77)	0.0094	0.009	0.11 (36)	0.0007	0.0007	-0.13 (77)	0.0095	0.0086	0.24 (36)
Plaice	0.0011	0.0012	-0.92 (82)	0.0031	0.0025	-1.68 (41)	0.0011	0.0011	0.20 (86)	0.0015	0.0016	-0.12 (41)
Herring	0.0007	0.0008	-1.38 (43)	0.029	0.032	-0.21 (13)	0.0007	0.0007	0.27 (43)	0.032	0.0006	0.73 (13)
Sea snail	0.0019	0.002	-0.57 (48)	0.0755	0.0566	0.41 (19)	0.0019	0.0019	-0.08 (48)	0.048	0.0885	-0.95 (19)
Pogge	0.001	0.0012	-1.29 (35)	0.0267	0.0038	0.79 (35)	0.001	0.0009	0.71 (35)	0.0152	0.0531	-2.84 (35)
Stickleback	0.001	0.0009	0.87 (10)	0.0421	0.0661	-0.71 (8)	0.0011	0.001	0.95 (10)	0.0475	0.0174	0.91 (8)
Cod	0.001	0.001	0.46 (15)	0.027	0.018	0.81 (4)	0.010	0.010	0.07 (15)	0.031	0.023	0.423 (4)

8.3.1.2 Abnormalities

In comparison to the number of fish examined, in general there were few abnormalities noted for most species in the Humber fish assemblage (Table 8.4). However, many individuals from the smaller species, e.g. sprat, goby and herring, did not appear to survive the capture and preservation well, and thus in many cases were not in a state that enabled identification of abnormalities in either shape, structure, colouration or the presence of fin rot or lesions. Of the remaining species sole, flounder and whiting provided evidence of the main forms of abnormality and were the most heavily affected.

Table 8.4 The percentage occurrence of abnormalities noted within the fish of the Humber estuary.

	Colour anomalies	Fin-rot	Lesion or tumour	Skeletal deformities	Trawl/ Predator damage	Reversal	Body shape anomalies	n
Goby			0.26	4.13				387
Whiting	0.34			4.04	0.84			594
Sole	2.76		0.34	0.69	0.34		0.34	290
Flounder	11.57	0.83	3.31			3.31		121
Sprat					6.41			78
Plaice	0.39				0.39			256
Herring	2.22			4.44	4.44			45
Sea snail				1.27				79
Cod	4.35				4.35			23
Dab	4.76							21
Weever				6.25				16

Change in colouration was the most common abnormality noted, particularly among the flatfish where it showed as pigmentation on the under side or white patches on the upper, eyed side. This occurred in 11.57% of the flounder and 2.76% of the sole examined. Less than 1% of the whiting had abnormal colouration, occurring as a red stain similar to bruising. Within flounder 3% of the fish also showed a reversed orientation, i.e. left instead of right sided.

The most common deformity in whiting (3.87%) was curvature of the spine, i.e. scoliosis, lordosis or kyphosis, which also occurred in 1.03% of sole. One sole examined lacked a caudal region, although the fin rays and membrane from the dorsal and anal fins surrounded the body and were fused, indicating a genetic deformity rather than damage from predation. Lesions and tumours were uncommon within the fish, occurring only in flounder (3.31%), sole (0.34%) and goby (0.26%). Whiting and sole also showed signs of predation, possibly by lamprey, or damage caused within the trawl, 0.84% and 0.34% respectively. The greatest incidence of trawl damage was observed in the small fish, sprat and herring.

8.3.2 Bioaccumulation of Heavy Metals

Due to analytical problems with the AAS, where concentrations were routinely measured as below that within the blank, i.e. negative, concentrations of lead were not calculated. The amount of cadmium within the tissues of all species was below the level of detection. Thus the data presented here are for concentrations of zinc and copper only.

Table 8.5 The concentration of each metal in the tissue of the fish examined ($\bar{x}$ ± s.e. $\mu g\ g^{-1}$).

Species	Area	Season	Tissue	Copper	Zinc	n
Flounder	Upper		Liver	28.5 ± 8.7	334.4 ± 46.4	5
	Upper		Muscle	9.5 ± 3.3	164.1 ± 37.4	5
	Middle		Liver	45.9 ± 9.4	382.4 ± 27.5	5
	Middle		Muscle	14.5 ± 2.4	296.1 ± 159.7	5
	Lower		Liver	51.9 ± 7.6	567.5 ± 114.1	5
	Lower		Muscle	17.9 ± 9.7	238.8 ± 31.4	5
Sole		Spring	Liver	154.4 ± 46.2	294.7 ± 55.8	10
		Spring	Muscle	2.9 ± 1.8	143.1 ± 69.6	10
		Summer	Liver	224.2 ± 67.6	322.5 ± 27.8	5
		Summer	Muscle	8.6 ± 4.3	141.2 ± 27.1	5
whiting			Muscle	7.7 ± 3.3	98.4 ± 43.6	3
Plaice			Muscle	3.1 ± 1.5	215.5 ± 64.2	5
Goby			Muscle	11.2 ± 3.0	226.6 ± 70.2	3

There is a large inter- and intra-specific variability in the concentrations of metals in both the liver and muscle tissues (Table 8.5; Fig. 8.1). However, analysis of the data showed that there was no significant difference between areas of the estuary in flounder, seasons of the year in sole, or fish species sampled. There was a significant difference between the two tissues in a combined sole and flounder analysis, for both copper and zinc, $p = 0.001$ ($t = 3.89$, 23 d.f.) and $p < 0.001$ ($t = 5.59$, 23 d.f.) respectively, with liver samples containing the greatest concentrations of both metals.

In order to determine the probable source of contamination, the average concentrations of copper and zinc within the tissue were divided by the concentration within the water column and sediment of the estuary (the standing mass) (Table 8.6).

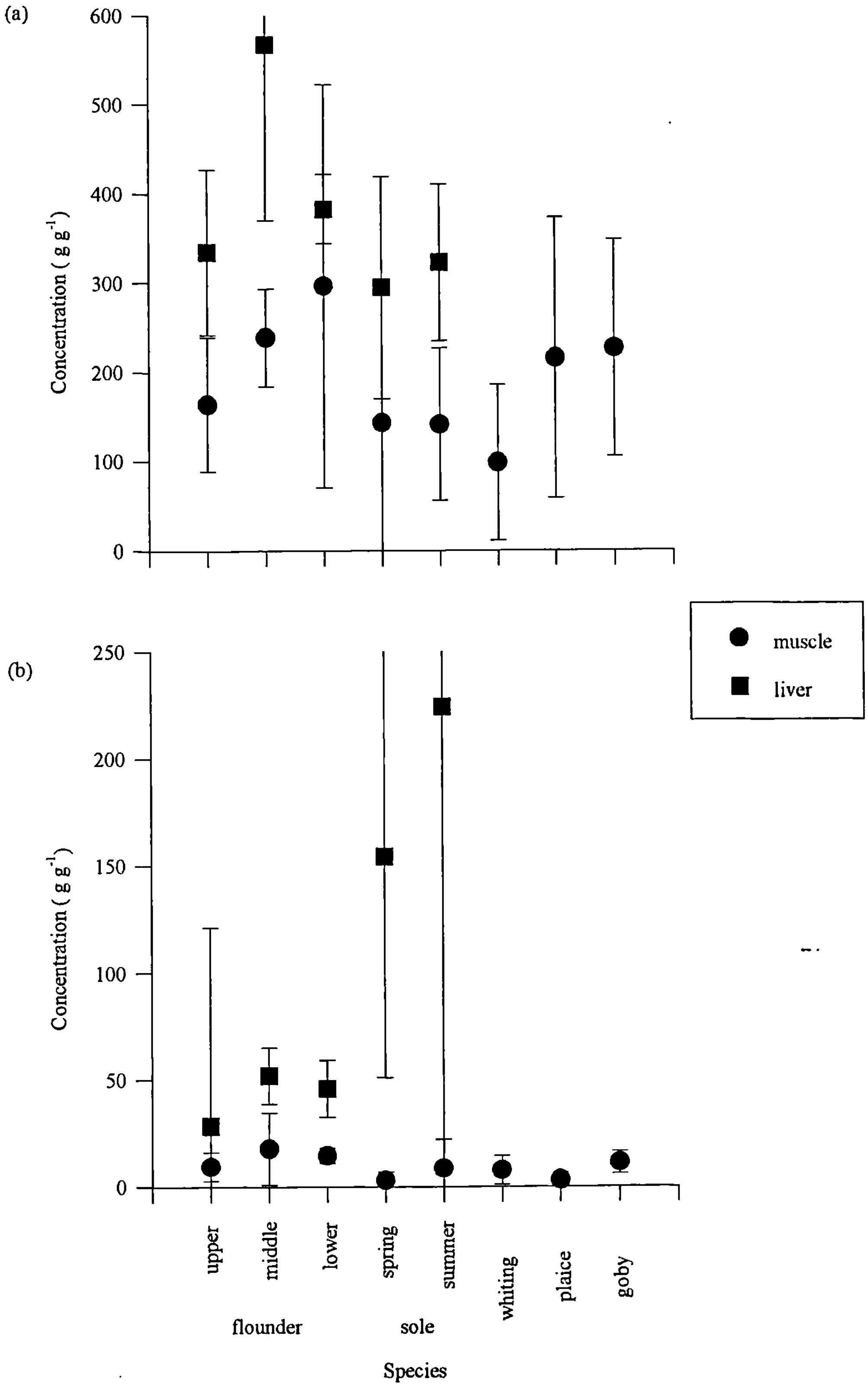


Fig. 8.1 The concentration of (a) zinc and (b) copper in the tissues of fish in the Humber estuary ($\bar{x}$ ± s.e. µg g^{-1} dry weight)

Table 8.6 The concentration factors for copper and zinc within the water column and sediment of the Humber (standing mass concentrations in the sediment: 54 and 279 mg kg^{-1} copper and zinc respectively; water column: 12 $\mu g\ l^{-1}$ for both metals (NRA 1993)).

	Muscle				Liver			
	Copper		Zinc		Copper		Zinc	
Species	Water	Sediment	Water	Sediment	Water	Sediment	Water	Sediment
Flounder	1.17	0.26	19.4	0.84	3.51	0.78	35.68	1.53
Sole	0.48	0.11	11.85	0.51	15.78	3.51	25.72	1.11
Whiting	0.64	0.14	8.2	0.35				
Plaice	0.26	0.06	17.96	0.77				
Goby	0.93	0.21	18.88	0.81				

The concentration factors for copper in the muscle tissue, with the exception of flounder:water column (1.17), are less than one, indicating that the concentration in the tissue is lower than that in the water column. Thus it is possible that copper is taken into the fish from both the water column and the sediment. This is contrary to zinc, for which uptake appears to occur predominantly from the sediment (concentration factor < 1). Within the liver tissue, the concentration factor for both metals, with the exception of flounder:sediment ratio (0.78), are > 1, indicating that the liver has a higher concentration of metals than the surrounding media. In this instance, uptake from the sediments is suggested from the lower ratios.

8.4 Discussion

8.4.1 Parasites

Within the Humber estuary fish community, parasites did not affect the condition or gonad index of the individuals. This is in contrast to the findings of Tolonen (1994), who stated that the presence of parasites had a negative influence on the gonadal index of *Coregonus lavaretus* L., and Petersen (1992), who found a decrease in the condition of parasitised gobies, but is similar to that in cod (Myjak *et al.* 1994), eel (Moller *et al.* 1991) and four-bearded rockling (Karlsbakk 1995). The exceptions within the Humber were the whiting, showing a negative effect between somatic condition and nematodes within the body cavity, and pogge, which demonstrate a decrease in gonad index in the presence of nematodes in the gut.

That parasites appear to influence the condition but not the gonadal index of whiting is contrary to the findings of other studies, e.g. Tolonen (1994), who demonstrates that parasites are more likely to influence the gonadal index than the condition of fish. However, as whiting are estuarine juveniles, occurring within the estuary predominantly as immature animals, the effects on reproduction will not be apparent from an analysis of gonadal index. Thus it is possible that the parasite burden, and associated effect on the condition of whiting, may influence the gonadal index of the fish following maturity. This is likely to occur through an effect on mate selection or a reduction in gamete production (Begon *et al.* 1986).

In contrast, pogge are estuarine residents with both sexes at all stages of development represented within the catch. The effects of parasites on the gonadal index, i.e. gamete production, can therefore be determined for the population. Thus the decrease in gonadal index noted within the Humber reflects the trends observed in other studies, e.g. three-spined stickleback (Fitzgerald *et al.* 1994) and sand goby (Petersen 1992).

8.4.2 Abnormalities

There are few comparable data for the incidence of disease and abnormalities in estuarine fish, in particular the level of abnormalities in an unpolluted, non-industrialised estuary is unknown. However data for other east coast estuaries, e.g. the Forth (Elliott *et al.* 1988) and the Thames (Bucke *et al.* 1983) indicate that the Humber shows similar levels of abnormalities for sole, 4 % in the Thames, and flounder, 18 % and 11 % respectively. The exception to this is the presence of colour change in flounder, which is significantly higher in the Humber than the Thames, 11.57% compared to 2.3% (Bucke *et al.* 1983). However there is a high level of variability between localities (McVicar *et al.* 1988), which may obscure the underlying cause of any differences in the absence of information on the natural occurrence of abnormalities in each area.

There is some evidence that the observed level of abnormalities within the Humber may be the result of pollution (Bengtsson *et al.* 1985; Butlin 1990) although natural causes, i.e. hereditary, dietary and naturally occurring environmental factors may also be contributing factors (McVicar *et al.* 1988). In particular, reversal is a common phenomenon in flounder (Wheeler 1969), being observed regularly within this study, although 'natural' levels are unknown.

Pigment change in flatfish is also relatively common in the natural situation and may result from dietary patterns in the first few days after metamorphosis (F. Couper, MAFF, pers. comm.). However, Bucke *et al.* (1983) found a greater occurrence of pigment change in both sole and flounder at the more polluted Thames site suggesting that pollution may have an effect on the pigmentation of fish. Within the Humber, pigment anomalies are particularly common in flounder and sole and may result from prolonged exposure to contaminated sediment.

Spinal deformities are also relatively common in the natural situation, for which there is evidence of heritability and a relationship to dietary deficiency and environmental factors such as temperature, salinity and dissolved oxygen (Bengtsson *et al.* 1985), as well as toxic chemicals. Within all of the studies noted (e.g. Bucke *et al.* 1983; Bengtsson *et al.* 1985; Butlin 1990) there is a suggestion that pollution is the main factor influencing the number of abnormalities in fish, although there is a lack of causal evidence (McVicar *et al.* 1988).

8.4.3 Heavy Metals

While cadmium and lead concentrations within the tissues were below the level of detection in all tissues, concentrations of copper and zinc were found to be greater in liver than muscle tissue, agreeing with the findings of Franklin (1987). However the difference in concentration observed between the two tissues in this study showed that the liver contained approximately three times more metal than the muscle tissue. This is in contrast to the findings of other studies, e.g. MAFF (1993), which found a tenfold difference. The exception to this was the copper concentrations found within sole liver, which were up to 50 times higher than those within the muscle tissue. This is contrary to the findings of Rickard & Dulley (1983) in the tidal Thames estuary, who reported elevated concentrations in flounder tissues and a reduction in sole due to the excretion of copper and the 'visitor' status, as implied by the seasonality, of the species.

That the situation within the Humber is in contrast to these findings indicates that either the sole are accumulating copper on their winter feeding grounds or concentrations within the prey species of the Humber are of a level that enables rapid accumulation of the metal during the summer period. However, there is no significant difference recorded between fish caught during the spring and the summer, suggesting that the latter is unlikely to explain the observed results. Despite this, and in view of the different pathways for uptake into the fish, via absorption from prey and the environment, there is concern, with respect to the health of sole, about the elevated concentrations of copper in water within the Humber (5 - 22 $\mu g\ l^{-1}$) which have resulted in the estuary failing to meet its Environmental Quality Standards (5 $\mu g\ l^{-1}$) (NRA 1993), i.e. indicating that the Humber is polluted with respect to dissolved copper.

Zinc was present in greater quantity than copper in the tissues of all species. This is similar to the results found in other areas (Table 8.7). The concentrations recorded within the liver of sole are similar in value to those in flounder, in contrast to the concentrations of copper which were several degrees higher in sole than flounder. The use of the concentration factors, particularly relating to liver concentrations, indicates that uptake of copper and zinc occurs predominantly from the sediment, possibly through ingestion of contaminated particles. This agrees with the findings of Elliott & Griffiths (1986), who found that pollutants accumulated through the food chain.

Concentrations of copper within the tissues, with the exception of the sole liver, are within the recommended limits within food as determined by the Food Standards Committee (20 mg kg^{-1} wet weight; MAFF (1956), **In**: MAFF (1993)). Zinc, however, exceeds the guidelines with respect to liver tissue and, while meeting the guidelines for muscle tissue (50 mg kg^{-1} wet weight; MAFF (1993)) exceeds the 'expected' values (6.0 mg kg^{-1} wet weight, most species, 10 mg kg^{-1} wet weight, flounder; MAFF (1993)). In all cases the concentrations recorded in this study are greater than those previously reported within the Humber estuary, which reached a maximum of 0.48 and 15.1 mg kg^{-1} wet weight copper and zinc concentrations respectively in flounder and 0.53 and 6.40 mg kg^{-1} wet weight respectively in sole (NRA 1993).

Comparative values of copper and zinc concentrations in the tissues of fish from other studies (Table 8.6) enable the 'normal' concentrations to be determined. Direct comparison are not advisable due to the differences in time of year sampled and size of organism used. In addition, data within this study relate to dry weight concentrations as opposed to the wet weight used in other studies, and therefore a 20 % wet weight:dry weight ratio must be included.

Table 8.7 The concentrations of zinc and copper recorded in the different species from the literature (mg kg^{-1} wet weight).

Species	Copper	Zinc	Tissue	Area	Source
Flounder	0 - 33.47	81.11 - 455.82	muscle	Humber	This study
	2.68 - 59.6	233.37 - 795.36	liver	Humber	This study
	0.3 - 1.3	12.3 - 18.2	muscle	Medway	Wharfe & van den Broek (1977)
	0.56 - 1.13	9.6 - 22.9	muscle	Thames	Rickard & Dulley (1983)
	0.2 - 0.6	3.5 - 7.9	muscle	Humber area	Franklin (1987)
	0.3	5.1 - 5.8	muscle	Thames	Franklin (1987)
Whiting	2.02 - 16.93	33.4 - 220.11	muscle	Humber	This study
	0.3	3.1 - 3.5	muscle	Tyne area	Franklin (1987)
	0.2 - 0.4	2.7 - 6.5	muscle	Humber area	Franklin (1987)
Plaice	<0.2 - 0.2	3.3 - 3.4	muscle	Thames	Franklin (1987)
	0 - 8.74	41.22 - 488.87	muscle	Humber	This study
	0.3 - 0.4	5.1 - 7.0	muscle	Thames	Franklin (1987)
	<0.2 - 0.5	3.3 - 7.6	muscle	Tyne area	Franklin (1987)
	1.89	10.8	liver	Northumberland coast	Wright (1976)
Sole	0.5	2.8	muscle	Northumberland coast	Wright (1976)
	0.2 - 0.3	4.2 - 7.3	muscle	Thames	Franklin (1987)
	0.3	3.6 - 4.9	muscle	Humber area	Franklin (1987)
	0 - 45.7	25.48 - 417.01	muscle	Humber	This study
	51.99 - 808.34	158.37 - 451.18	liver	Humber	This study

9 GENERAL DISCUSSION

9.1 The Humber Estuary

Smelt are regarded as an indicator of water quality (Wheeler 1979) due to their vulnerability to threats such as pollution, toxins and disease (Maitland & Lyle 1990). Therefore the presence of smelt within the fish community, coupled with the relatively high concentrations of dissolved oxygen compared to other areas, e.g. the Forth and Tyne (Pomfret *et al.* 1991), indicates that the Humber has 'good' water quality. Even in summer, the dissolved oxygen and temperature are insufficient to act as a barrier to fish migrations, 71 % as compared to 55 % ASV (Pomfret *et al.* 1991). As smelt spawn in tidal rivers and streams, it can also be concluded that the low dissolved oxygen levels recorded upstream of the study area (NRA 1993), < 40 %, do not form a barrier to migration in these areas.

The fish assemblage observed within this study is, therefore, more likely to have been influenced by the hydrophysical regime of strong tidal currents, resulting in heavy scouring of the bed sediments, than water quality. In addition, the scouring effect of strong tides on the sediment results in mobile bed sediments, further restricting the availability of habitats within the area, i.e. the sediment within an area can change within days from sand to mud (C. Park, Uni. Hull, pers. comm.), or *vice versa*, thus altering the habitat and changing the benthos. Tidal scour has been shown to be the most important limiting influence on the benthos (North Sea Task Force 1993).

The fish community, which is comprised predominantly of sand or mud dwelling benthic fish (Chapter 4; Dewailly (1994)), reflects the lack of habitats, resulting from a homogeneous sediment (NRA 1993). Further evidence for the homogeneity of the sediment is given by the occurrence of several species, i.e. flounder, whiting, goby, sprat, herring and plaice, at all sampling sites. Of the 25 species examined, 13 species, cod, sea snail, five-bearded rockling, bib, thornback ray, transparent goby, sand eel, dragonet, lemon sole, sole, clupeid, dab and lesser weever, showed a statistically significant spatial distribution within the estuary (Chapter 4). However, seven of these species, five-bearded rockling, bib, thornback ray, transparent goby, sand eel, dragonet and lemon sole, occur in < 5 samples, thus any statistical significance determined may reflect the rarity of the species within the trawls rather than the actual distribution. As salinity varies spatially within the estuary, and given the homogeneous nature of the sediment, it would therefore appear that salinity influences the distribution of several species, including dominant ones, e.g. sole, sea snail and cod.

Seasonal trends are indicated from a correlation with temperature, although the two factors are not necessarily related, i.e. a species which occurs only within the temperature range of 8 - 10 °C will use the estuary in both spring and autumn, although no correlation with temperature will be observed. Of the four dominant species within the estuary, flounder, sole and whiting demonstrate seasonal variations in abundance and biomass (Chapter 4). Sole has a highly seasonal distribution, occurring as adults within the summer months, while whiting occur as juveniles throughout the year, although in greatest abundance in the winter. Flounder are estuarine residents (Elliott & Taylor 1989(b); Dewailly 1994), but demonstrate a seasonal migration within the estuary.

The spatial and seasonal patterns noted may, however, be related to biological factors as well as environmental parameters. Thus seasonal patterns may reflect spawning or feeding migrations, and thus be related to the usage of the estuary, while spatial trends may be related to prey availability within the area. Flounder migrations have been related to spawning (Wheeler 1969), while changes in whiting abundance can also be related to recruitment patterns and the migration of larger fish to deeper water within the North Sea (Gordon 1977; Elliott *et al.* 1991), e.g. a high abundance in winter following recruitment to the catch followed by the migration of larger fish to deeper water in the spring and summer. The latter may be prolonged over several months, due to differences in spawning time and growth rates (Gordon 1977), thereby accounting for the 'negative growth' noted within this study (Chapter 6). The patterns observed within the Humber are similar to the findings in other areas, e.g. the Forth (Elliott & Taylor 1989(b)) and the Dutch Wadden Sea (Creutzberg & Fonds 1971).

An analysis of the feeding patterns within the fish populations indicates that prey availability is not a contributing factor to the observed distribution. The majority of the fish species examined appear to have a general diet, i.e. do not specialise on a particular prey species, probably taking the dominant prey items available within that area (Chapter 7), with similar prey species taken by each species of fish. This agrees with the findings from other studies, e.g. the Wadden Sea (Kühl & Kuipers 1979). However, there is a low degree of niche overlap between the species, with only six species, goby, small pogge, herring, small and medium whiting and lesser weever, showing similarities in diet, suggesting some resource partitioning (Fig. 7.7). Of these species, small and medium whiting, herring and goby have an overlapping distribution, occurring throughout the estuary (Fig. 4.4), as have pogge and lesser weever, within the outer estuary. While pogge, whiting and goby are present throughout the year, lesser weever and herring have restricted seasonal distributions (Chapter 4), which will reduce the amount of association with the other species, while whiting are capable of feeding on larger size classes of the prey than goby due to differences in size (Bergstad 1991), also reducing any feeding interactions. The size class of prey is important in reducing interactions between marine, demersal fish species (Tyler 1972). Thus it would appear that the distribution of fish within the estuary influences feeding niche, rather than prey selection influencing fish distribution. This has been indicated from feeding studies within different areas, e.g. the Forth and Tagus estuaries (Costa & Elliott 1991), the Wadden Sea (Kühl & Kuipers 1979) and the Norwegian Deep (Bergstad 1991), where the opportunistic diet of the fish demonstrates the greater importance of water chemistry and hydrophysical features to their distribution.

Production within the intertidal areas of estuaries is generally higher than that in the subtidal areas (Wolff & de Wolf 1977; Elliott & Taylor 1989(a)), with many fish species utilising these areas as feeding and nursery grounds (Haedrich 1983). Within this study, however, the low $P:\overline{B}$ ratios recorded indicate that the Humber, despite extensive, well utilised, intertidal areas, is a relatively unproductive estuary for the fish populations. This could be the result of a slow growth rate, poor feeding within the area or a high mortality or emigration rate (Chapman 1978). Growth rates were found to be comparable to the rates in other estuaries, e.g. flounder (0.16 mm day^{-1} cf. 0.14 mm day^{-1} in the Ythan or 0.16 mm day^{-1} in Sweden (Summers 1979)), goby (0.07 mm day^{-1} cf. 0.05 mm day^{-1} on the south coast of England (Fouda & Miller 1981)) and sole (0.13 mm day^{-1} cf. 0.15 mm day^{-1} in the Loire estuary (Marchand 1988)), although whiting demonstrate a reduced growth rate (0.15 mm day^{-1} cf. 0.40 mm day^{-1} in the Severn (Potter *et al.* 1986) and 0.21 mm day^{-1} in Europe (Wheeler 1969)), indicating that this is not a factor in the low production estimates. Similarly, feeding analysis indicates that a large proportion of the fish examined (76 %) contained prey, demonstrating a high usage of the area for feeding, although there is insufficient information available to determine the energetics of the Humber foodweb.

From this study, therefore, it appears that the low $P:\overline{B}$ ratios are the result of either sampling bias, with the larger round fish escaping the trawl (McIntyre 1971), or emigration from the estuary (Chapman 1978). Of the four dominant species within this study, all, with the exception of goby, have been shown to follow seasonal or spatial migrations (Chapter 4). In particular, sole, which shows a negative production during the summer months as well as annually, is present within the area for a brief period only, either to spawn or to feed prior to spawning, as indicated by the gonadal condition (Chapter 8). Therefore the production estimates will be affected by either spawning, and the resultant loss of material (Chapman 1978), or the migrations of animals to the spawning grounds near Bridlington or Mablethorpe. In contrast, whiting occur throughout the study period as juveniles and have a resultant $P:\overline{B}$ ratio of 1.14 - 1.23, indicating a greater increase in biomass. However, the loss of larger fish from the estuary will affect the overall production estimates, as is demonstrated by the cohort analysis (Chapter 6).

A further factor which may affect fish production is the presence of parasites, which can affect the condition, and therefore weight, of the animals, e.g. parasites cause a reduction in the condition of gobies (Petersen 1992). In particular, goby are heavily infested with *Ligula*, which in many cases fill the body cavity (pers. obs.) thus having a possible effect on the feeding potential through restriction of the stomach capacity. However, this was not supported by the data, with no relationship being found between the fullness index or condition index and the presence of parasites within either the gut or the body cavity. Also, the low production estimates for goby within the estuary do not necessarily reflect poor feeding or increased parasite load, as it was demonstrated that goby contribute little to the epibenthic production in the Oosterschelde (Hostens & Hamerlynck 1994).

There is a significant correlation in the number of parasites with age for all species (Healey 1995), indicating that either parasites accumulate within the body or younger fish may invest more resources into opposing the effects of parasites than older fish (Poulin 1993). The latter would cause a change in resource allocation from growth to defence, and thus reduced estimates of production. However, production estimates do not decrease with age of cohort (Tables 6.2 - 6.4), suggesting that parasites do not have an effect on the production of fish within the estuary, although it must be noted that the production estimates are determined on the wet weight of fish prior to dissection, i.e. the weight of fish + parasites. In addition, there is no correlation between external abnormalities and the presence of parasites (Healey 1995), indicating that parasites have little impact on either the external appearance or the biomass of the fish.

The bioaccumulation data, which is used to assess pollutants within the environment (Elliott & Griffiths 1986), indicate that there is no difference in heavy metal content between the different areas of the estuary. The uptake of the metals within the Humber appears to occur from the sediments rather than the water column, reflecting the situation in other areas, e.g. the upper Clark Fork River, Montana (Ingersoll *et al.* 1994). The path of uptake can be direct, through contact with, or digestion of, contaminated sediments, or indirect via the digestion of contaminated prey (Bryan 1976). If the absorption of metals from the sediment is direct, a significantly higher concentration of heavy metals would be expected in the flatfish, due to the lack of sediment within the stomach of goby and whiting compared to flatfish (pers. obs.), together with the closer association of flatfish to the sediment, i.e. burying within the sediment for camouflage. That this does not occur indicates the indirect accumulation via the diet, particularly from the dominant prey, Mysids and Gammarids, as was found in, e.g. the Forth Estuary (Elliott & Griffiths 1986). The high concentration within Mysids and Gammarids is implied from the differences in diet between the species (Chapter 7), together with the similarities in metal content (Chapter 8), which indicate that either the prey species have similar concentrations of heavy metals within their tissues, or that the heavy metals within the fish are accumulated from a common source, i.e. a shared prey item.

Increased stress can cause an increase in disease and abnormalities through a reduction in the disease resistance of the fish. Stressors can include heavy metal contamination or adverse environmental factors

(Bucke 1993). Signs of disease are more prevalent in dab and flounder than other commercial species (North Sea Task Force 1993), with evidence of contaminants depressing disease resistance within the Humber estuary populations. However, in no case does disease appear to affect the population level (North Sea Task Force 1993), indicating that the levels of contamination observed during this study, which are within the recommended limits for food as determined by the Food Standards Committee (MAFF 1993), do not affect the growth and production of the fish assemblage.

9.2 Management of the Estuarine Fish Assemblage

Fish are dependent on the physical, chemical, biological and geological characteristics of estuaries for both their distribution and feeding ecology (de Sylva 1975). It is therefore necessary to consider the effects of all factors, e.g. salinity, temperature, dissolved oxygen, bottom sediments, turbidity, solar radiation, moon phase and the tidal cycle when surveying fish populations prior to establishing a management plan for the area. This will enable the functioning of the estuary to be determined, and thus the impact of activities to be assessed. A further consideration, given the role of estuaries as nursery areas for marine stocks, is the impact of changes to those stocks on the estuarine fish assemblage, and this must also be taken into account when interpreting data with respect to local conditions, i.e. water quality (Pomfret *et al.* 1991).

Fish populations within estuaries are vulnerable to disturbance and exploitation (Davidson *et al.* 1991). Exploitation can be direct or indirect, through the removal of prey items, while disturbance can take the form of pollution, disruption to water flows by, for example, the construction of dams and weirs or the dredging of navigation channels or the loss of estuarine areas through land-claim. Land claim is of particular relevance due to the indirect effect of prey loss as a result of the importance of intertidal invertebrates to the diet of the different fish species (Chapter 7). Both disturbance and exploitation can arise from either natural or anthropogenic circumstances, and this creates difficulties when examining management proposals. The establishment of EQS for estuarine areas is particularly difficult given the inter-relation of several quality parameters (Pomfret *et al.* 1991), e.g. Pomfret *et al.* (1991) suggest that an EQS of 5 mg l^{-1} to protect fish migrations may be inadequate during periods of high temperature.

At present the Humber appears to support a healthy fish population, indicating that the EQS proposed and enforced by the NRA are effective in meeting the set EQO, although the high concentrations of copper found in the liver of sole suggest that the standard for this element may have to be re-assessed and enforced, as the current EQS are exceeded within the estuary (NRA 1993). However, the management of the Humber is not static, and thus new proposals must be considered such that the EQO and EQS are not violated. To this end several management plans for the area have been proposed by, for example Humberside County Council, English Nature and the NRA, such that proposals can be viewed with respect to the whole estuary.

9.2.1 Management Options

The NRA recently defined their management plan for the Humber catchment. This report highlighted several issues and targets specifically identified for the Humber estuary relating to fisheries (NRA 1995). These were:

1. Issue 17. ensure the sustainable exploitation of shellfish and lugworms;
2. Issue 18. ensure an adequate understanding of the bioaccumulation of persistent and potentially toxic substances;
3. Issue 19. restore the flounder fishery of the drains and watercourses entering the estuary;
4. Issue 20. ensure a better knowledge of the fish populations of the estuary and tidal rivers;
5. Issue 21. promote the re-establishment of a self-sustaining salmonid population;
6. Issue 24. review the regulation of the eel fishery within the estuary.

In order to achieve this, several management options were proposed involving a range of tools from the establishment of marine nature reserves to the construction of fish passes to enable passage of flounder into the tidal rivers. However, throughout this, it is important to remember that the responsibilities of the NRA are to prevent and mitigate flooding and regulate industry, as well as promoting the health of the North Sea fishery.

1. The sustainable exploitation of shrimp (*Crangon*), lugworm (*Arenicola*) and shellfish (Molluscs) can be used to maintain the sustainable development of natural predators, i.e. fish (NRA 1995). While this has not been identified as a priority, it is of note that *Arenicola* are one of the main prey species for sole, while molluscs form a dominant group in the diet of flounder and large plaice (Table 7.2). In addition *Crangon* are consumed throughout the foodweb by a variety of fish species, including cod, whiting and turbot. Therefore restrictions in the exploitation of these species, such that the population is maintained, may benefit several commercially important fish species, although it has been demonstrated in other areas, e.g. the Forth (McLusky *et al.* 1983), that bait digging does not have a significant impact on *Arenicola* populations, thus current practices within the Humber should not have a major impact on fish populations.

Although no commercial *Arenicola* harvesting occurs, there is a shrimp fishery operating within the estuary. This is a small industry (Rees 1982), and as such is unlikely to affect the prey availability, particularly as *Crangon* are not the dominant prey within the foodweb (Chapter 7). However, juvenile flatfish, particularly dab and plaice, form a major component of the by-catch (Uni. Humberside, unpubl. data), and as such, increased exploitation may result in significant losses to the populations. Of particular concern is the positioning of the fishing grounds around Haile Sand, which coincides with the dab nursery areas within the estuary (N. Graham, Uni. Humberside, pers. comm.).

Bait digging is legally permitted for private use unless the area was segregated prior to 1189 or subsequently by legislation, with regulatory by-laws only extending to the mean low water mark (RSPB 1990), thus enforcement of a sustained strategy may prove difficult. However, it has been shown to have a deleterious effect on *Cerastoderma* populations (Jackson & James 1979), which may influence plaice within the area.

2. There are few commercial fisheries operating within the Humber (Rees 1982), thus the management proposals are concentrated on the shellfishery (NRA 1995). However, contaminants can accumulate within the biota and from there affect the North Sea fishery via the migration of animals to coastal waters.

3. This is primarily associated with access to the tidal rivers and the restrictions created by weirs and sluices. However, poor water quality in the upper estuary may also act as a barrier to flounder migrations (Pomfret *et al.* 1991), with oxygen levels of 5 mg l^{-1} or temperatures > 15 °C restricting flounder populations. While these levels were not found within this study (Chapter 3), it is necessary to monitor discharges to the tidal rivers, particularly of organics, nitrates and phosphates, which cause an increase in the biological oxygen demand.

Flounder are one of the dominant species in the estuary, accounting for 10.6 % of the occurrences and 3.6 % of the total abundance. The biological patterns, i.e. growth rate, are similar to other areas, e.g. the Ythan estuary and Danish coastal waters (Summers 1979), as are the migration patterns (Wheeler 1969; Elliott & Taylor 1989(b)), indicating that the Humber population is not restricting the populations within the water courses.

4. It is considered by the appropriate bodies, MAFF and the NRA, that sufficient information exists on the fish population of the estuary (NRA 1995). Due to the ongoing nature of the MAFF and NRA survey work, further action is not considered necessary. However, the seasonal and spatial information gained from this work has enhanced the current knowledge concerning the fish populations and enabled an assessment of the status of the estuary. It would therefore appear to indicate that more detailed surveys of this nature would be beneficial to the understanding of the system.

5. This target is outwith the scope of this study. However, the sensitivity of salmonids to low dissolved oxygen (Poxton & Allouse 1982), would imply that the maintenance of, or improvement to, the current water quality through the enforcement of the EQS, will help to enhance the salmon run through the estuary. However, protection of water quality for resident and salmonids will also help the other migratory and resident fish species, and *vice versa.*

6. An assessment of the eel fishery is outwith this study, but the species occurs throughout the Humber and lower tidal rivers (Rees 1982).

9.2.2 Impact Assessment

An analysis of the fish distribution (Chapter 4), the biology of the main species (Chapter 6) and the distribution of the main prey items (Chapter 7; NRA unpubl.), can be used to determine the sensitivity of different areas with regards to the fish assemblage. These areas have been identified as the sandflats around the outer estuary, and the intertidal areas between the Humber Bridge and East Halton and within Spurn Bight (see Fig. 1.1). The upper estuary is also important for the large numbers of Mysids and Gammarids in both the sub- and inter-tidal areas (this study; Barr *et al.* 1990).

The outer estuary sandflats support the juvenile plaice population (Chapter 4; Proctor 1995), serving as a nursery ground for fish spawning along the coast (Lockwood 1972). It has been estimated that the Humber acts as a nursery area for 3 % of the plaice population of the North Sea (Jones 1988). In addition, the areas around Haile Sand form a nursery area for dab, with large populations noted in these areas (N. Graham, Uni. Humberside, pers. comm.). The intertidal areas are important feeding grounds for other commercial species, predominantly sole and flounder, as indicated by the abundance of their dominant prey items within these areas (NRA, unpubl. data) and their occurrence within adjacent catches (Chapter 4).

There are several activities currently undertaken or proposed within the estuary which may affect the fish populations. Of these, land claim may have the greatest effect, as it can result in both direct and indirect habitat loss, e.g. indirect degradation through pollution, disturbance or recreational pressure (Davidson *et al.* 1991). Although land claim proposals cover a small area, e.g. near Hull east docks, there will still be a removal of productive mud, and there may be long-term effects on the remaining habitats through modifications of tidal currents and sediment transport. It is therefore recommended that land claim proposals are considered with regards to the long-term effects on the sensitive areas, as defined above. While current analyses indicate that prey availability is not a limiting resource to fish populations, the situation will require monitoring.

Land claim or coastal developments can also result in increased pollution, as a consequence of industrial and sewage outfalls crossing the intertidal areas. Both industrial and urban waste can have a direct impact on fish, although evidence from this study would suggest that industrial pollutants, i.e. heavy metals, do not cause health problems to the fish within the Humber (Chapter 8). The urban outfalls within the estuary are situated predominantly around Hull and Grimsby (NRA 1993), and have resulted in an altered benthos, demonstrated by the high abundance of *Capitella capitata*, generally accepted as an indicator of organic enrichment (Pearson & Rosenberg 1978), within this area (Barr *et al.* 1990). That *C. capitata* is rarely found within the diets of the fish (Appendix 5), despite its dominance within the area, would indicate that organic enrichment has a deleterious, local, effect on the fish assemblage through a reduction in prey availability. The reduction of these inputs would therefore appear to be necessary in order to maintain 'the ability to support on the mud bottom the biota necessary for sustaining sea fisheries' (NRA 1993) within the subtidal areas.

It would therefore appear that proposed developments within the Humber may have an impact on the populations of several fish species, including those of commercial importance within the North Sea, e.g. sole, plaice and whiting. The extent of this impact can be minimised through sensitive management. The positioning of land claim proposals and outfalls in areas outwith Spurn Bight or the area between the Humber Bridge and East Halton, thus maintaining the quality of the intertidal areas is of particular importance. In addition, the restriction of, particularly copper, outputs to the estuary and tidal rivers may benefit the sole population and enhance the fisheries.

CONCLUSIONS

1. Concentrations of dissolved oxygen were positively correlated to salinity, being greatest towards the outer estuary. Turbidity, however, was negatively correlated to salinity, with the turbidity maximum occurring in the upper estuary, between Hull and Whitton.

2. The ranking of the species by percent occurrence indicates that four species, goby (18.4 %), whiting (15.6 %), sole (12.3 %) and flounder (10.6 %), were dominant, accounting for more than 50 % of the recorded presences. The number of species caught per sampling occasion shows a seasonal trend depending on area, with the outer and lower estuary showing an increased diversity in summer in contrast to an increase in winter within the middle and upper estuary.

3. Salinity is the dominant factor influencing the distribution of the species, with temperature also having a major influence. Turbidity did not influence the composition of the fish assemblage.

4. There is a loss of material, or negative production, within the estuary, although this does not appear to be related to a reduction in the growth rate of the dominant species.

5. With the exception of sprat, herring, brill and small pogge, all of the species have an opportunistic diet. Despite this, there is little evidence of niche overlap between the species and size classes, indicating that resource partitioning may occur. Gammarids and mysids form the dominant prey within the foodweb, occurring within the diet of most of the species.

6. The Humber populations do not appear to be adversely affected by pollutants, with copper concentrations within the tissue being below the recommended guidelines for human consumption, with the exception of copper concentrations within sole liver. Zinc concentrations within the liver of both sole and flounder exceed the guidelines. Levels of abnormalities are also similar to other, comparable estuaries, with the exception of colouration abnormalities in flounder (11.57 % in the Humber cf. 2.3 % in the Thames).

7. The data indicate that the Humber forms an important nursery and feeding area for the North Sea fish populations, making it economically sensitive to degradation. The areas of greatest sensitivity are the sandflats within the outer estuary, which form a nursery area for plaice and dab and a feeding ground for sole, and the mudflats on the south bank between the Humber Bridge and North Killingholme, which act as important feeding areas for several species including sole.

10 FURTHER WORK

This project began an investigation into the fish assemblage of the Humber estuary. While providing a continuation of the work already in progress within the estuary, it indicates areas requiring further research. These include :

1. The more rigorous sampling of the area with regards to seasonal analysis such that population trends indicated within this work can be verified. This will also provide increased information on the less common species.

2. The extension of this project into the freshwater-seawater interface around Trent Falls. A naturally stressed area, this will provide further information on the effects of pollutants within the river systems and the areas of concern to migratory species, i.e. flounder and salmonids.

3. The examination of fish within the intertidal areas, using traps, seine netting and hand trawling. This will provide further information on the juvenile fish within the estuary, thereby indicating the importance of the area to North Sea fish stocks.

4. A comparison of the different habitats available to fish, such as mud flats, salt marshes and rocky areas, and their availability within the area. This information is necessary when attempting to minimise the likely effects of proposed developments.

5. The more detailed analysis of the benthos with respect to seasonal abundance, distribution and productivity throughout the estuary would enable a better understanding of the feeding relationships within the area.

6. Further studies on the health of the fish, particularly with regards to parasites and the bioaccumulation of pollutants. Their effect on the biology of the fish, both individually and synergistically, particularly their reproductive success, makes this relevant to the management of the estuary.

7. Studies into the sole population of the estuary, particularly during its period in the North Sea. Using tagging, this will enable the role of the estuary as a feeding ground for North Sea sole stocks to be determined, while indicating possible causes of the differential growth rates noted within this study.

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APPENDIX 1 Two-way ANOVA tables of environmental variables by season and area, with Tukeys honestly significant difference *a poseriori* comparison of each effect.

```
                 UNIQUE sums of squares
                 All effects entered simultaneously

                 BOTTOM DISSOLVED OXYGEN

                                  Sum of                Mean             Sig
Source of Variation              Squares      DF      Square         F   of F

Main Effects                   19447.348      6     3241.225    35.021   .000
   AREA                        17512.837      3     5837.612    63.074   .000
   SEASON                       1740.826      3      580.275     6.270   .000

2-Way Interactions               509.392      9       56.599      .612   .787
   AREA     SEASON               509.392      9       56.599      .612   .787

Explained                      22604.716     15     1506.981    16.283   .000

Residual                       22952.941    248       92.552

Total                          45557.656    263      173.223

                      - - - - - O N E W A Y - - - - -


Area    Upper     Middle     Lower     Outer
X̄       75.9987   79.4712    91.3459   95.7516
        ------------------
                              ----------------


Season   Spring    Summer     Winter    Autumn
X̄        83.2933   85.1305    85.2690   91.5100
        ----------------------------
                              ----------------
```

```
                 BOTTOM SALINITY

                                  Sum of                Mean             Sig
Source of Variation              Squares      DF      Square         F   of F

Main Effects                   16314.051      6     2719.008   251.067   .000
   AREA                        12567.385      3     4189.128   386.814   .000
   SEASON                       2473.005      3      824.335    76.117   .000

2-Way Interactions               576.007      9       64.001     5.910   .000
   AREA     SEASON               576.007      9       64.001     5.910   .000

Explained                      17384.049     15     1158.937   107.013   .000

Residual                        2664.136    246       10.830

Total                          20048.185    261       76.813

                      - - - - - O N E W A Y - - - - -


Area    Upper     Middle     Lower     Outer
X̄       10.5831   17.6000    25.0054   28.2236
        --------
                 ---------
                           ---------
                                     ---------


Season   Winter    Autumn     Spring    Summer
X̄        13.2500   18.6460    19.9567   24.7805
        ---------
                  -------------------
                                        --------
```

```
                BOTTOM TEMPERATURE

                                   Sum of            Mean          Sig
Source of Variation               Squares    DF     Square      F   of F

Main Effects                     4838.673     6    806.446  292.361  .000
   AREA                            12.676     3      4.225    1.532  .207
   SEASON                        4685.273     3   1561.758  566.186  .000

2-Way Interactions                 38.488     9      4.276    1.550  .131
   AREA      SEASON                38.488     9      4.276    1.550  .131

Explained                        5664.026    15    377.602  136.892  .000

Residual                          684.080   248      2.758

Total                            6348.105   263     24.137

                          - - - - -  O N E W A Y  - - - - -

Season   Winter     Autumn     Spring     Summer
X         4.8929    8.6260     9.5444     17.6098
       ---------
                  ---------
                              --------
                                         --------


                BOTTOM TURBIDITY

                                   Sum of            Mean          Sig
Source of Variation               Squares    DF     Square      F   of F

Main Effects                     12428625     6 2071437.524  29.720  .000
   AREA                           6227556     3 2075851.880  29.783  .000
   SEASON                         5531648     3 1843882.758  26.455  .000

Explained                        12428625     6 2071437.524  29.720  .000

Residual                         14288360   205   69699.315

Total                            26716985   211  126620.781

Due to empty cells or a singular matrix,
higher order interactions have been suppressed.

                          - - - - -  O N E W A Y  - - - - -

Area    Outer      lower      Middle     Upper
X       294.9189   474.9355   635.4255   722.4833
        ---------
                  ------------------
                            ------------------

Season   Winter     Summer     Spring     Autumn
X         299.2000   309.0822   621.9494   701.4400
        --------------------
                              ------------------


                MIDDLE DISSOLVED OXYGEN

                                   Sum of            Mean          Sig
Source of Variation               Squares    DF     Square      F   of F

Main Effects                    18186.672     6   3031.112   32.283  .000
   AREA                         16481.099     3   5493.700   58.511  .000
   SEASON                        1485.179     3    495.060    5.273  .002

2-Way Interactions                588.286     9     65.365     .696  .712
   AREA      SEASON               588.286     9     65.365     .696  .712

Explained                       20852.532    15   1390.169   14.806  .000

Residual                        23566.754   251     93.891

Total                           44419.286   266    166.990
```

```
                        - - - - -  O N E W A Y  - - - - -

Area   Upper      Middle     Lower      Outer
X      76.9641    80.5508    91.6243    95.7957
       -------------------
                              -------------------


Season   Spring     Summer     Winter     Autumn
X        83.6967    85.9305    85.9310    91.8245
       ------------------------------
                              ------------------


                 MIDDLE SALINITY

                                          Sum of               Mean                Sig
Source of Variation                      Squares      DF      Square        F      of F

Main Effects                            16056.553      6    2676.092   251.276   .000
   AREA                                 11736.002      3    3912.001   367.323   .000
   SEASON                                2968.098      3     989.366    92.898   .000

2-Way Interactions                        491.027      9      54.559     5.123   .000
   AREA        SEASON                     491.027      9      54.559     5.123   .000

Explained                               17257.506     15    1150.500   108.028   .000

Residual                                 2651.854    249      10.650

Total                                   19909.361    264      75.414

                        - - - - -  O N E W A Y  - - - - -

Area   Upper      Middle     Lower      Outer
X      10.1128    16.8983    24.1946    27.2505
       ---------
                ----------
                           ----------
                                      ----------


Season   Winter     Autumn     Spring     Summer
X        12.0125    18.1358    19.0800    24.4134
       ----------
                 --------------------
                                      ----------


                 MIDDLE TEMPERATURE

                                          Sum of               Mean                Sig
Source of Variation                      Squares      DF      Square        F      of F

Main Effects                             4895.552      6     815.925   311.526   .000
   AREA                                    11.838      3       3.946     1.507   .213
   SEASON                                4726.597      3    1575.532   601.549   .000

2-Way Interactions                         32.093      9       3.566     1.361   .206
   AREA        SEASON                      32.093      9       3.566     1.361   .206

Explained                                5741.730     15     382.782   146.149   .000

Residual                                  657.400    251       2.619

Total                                    6399.131    266      24.057

                        - - - - -  O N E W A Y  - - - - -

Season   Winter     Autumn     Spring     Summer
X        4.8429     8.5906     9.7267     17.6854
       ----------
                 ----------
                             ---------
                                      ----------
```

```
                 MIDDLE TURBIDITY

                                      Sum of                    Mean              Sig
Source of Variation                  Squares      DF          Square          F      of F

Main Effects                         10631739      6     1771956.452     32.788   .000
   AREA                               5678995      3     1892998.287     35.028   .000
   SEASON                             4561354      3     1520451.368     28.134   .000

2-Way Interactions                    1166443      9      129604.762      2.398   .013
   AREA        SEASON                 1166443      9      129604.762      2.398   .013

Explained                            11422238     15      761482.514     14.090   .000

Residual                             11943534    221       54043.138

Total                                23365771    236       99007.506

                          - - - - -  O N E W A Y  - - - - -

Area     Outer       Lower      Middle     Upper
X̄        198.4568    261.1765   505.8077   522.9857
        -------------------
                                 -------------------

Season   Summer      Spring      Winter     Autumn
X̄         167.7160   441.4051    493.0000   520.3396
        ----------
                     -----------------------------
```

APPENDIX 2(a) The abundance of fish caught at each site on each sampling occasion

Date	Apr-92	Apr-92	Apr-92	Apr-92	Apr-92	Apr-92	Apr-92	Jun-92	Jun-92	Jun-92	Jun-92	Jun-92	Jun-92	Jun-92	Jun-92	Jun-92	Jun-92	Jun-92
Site	Sp	GM	HP	PS	RI	W	HB	HS	Sp	GM	CN	HP	BF	BS	PS	HF	Sk	H
Plaice	-	-	-	-	-	-	-	2	9	-	3	-	-	-	1	-	-	-
Sole	5	4	3	2	-	-	-	-	-	4	8	5	-	4	-	-	1	-
Bib	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Whiting	1	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-
Cod	1	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
Flounder	1	-	-	3	-	-	1	-	1	-	2	6	-	2	11	-	-	1
Smelt	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Sea snail	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pogge	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Goby	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sprat	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Dab	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Clupeid	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Stickleback	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Herring	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pipefish	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Roker	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Trans. goby	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Weever	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Eel	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dragonet	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lampern	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lemon sole	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rockling	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sand eel	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Date	Jun-92	Jun-92	Jun-92	Jul-92	Jul-92	Jul-92	Jul-92	Jul-92	Jul-92	Jul-92	Jul-92	Jul-92	Jul-92	Jul-92	Jul-92	Dec-92	Dec-92	Dec-92	Dec-92	Dec-92	Dec-92
Site	RI	W	HB	HS	Sp	GM	CN	BF	PS	HF	Sk	H	RI	W	HB	HS	Sp	CN	HP	PS	HF
Plaice	-	-	-	4	1	-	5	-	4	-	-	2	-	1	2	-	-	-	-	2	2
Sole	-	-	-	-	12	-	17	1	1	4	2	-	3	-	-	-	-	-	-	-	-
Bib	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Whiting	-	-	-	-	1	-	-	1	-	-	-	-	1	-	1	3	1	-	-	1	35
Cod	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	11	1
Flounder	1	-	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Smelt	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sea snail	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	4	5
Pogge	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	7	-	-	-	-	-
Goby	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	13	8
Sprat	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	18	16
Dab	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
Clupeid	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	4
Stickleback	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Herring	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pipefish	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Roker	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Trans. goby	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Weever	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Eel	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dragonet	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lampern	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lemon sole	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rockling	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sand eel	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Date	Dec-92	Dec-92	Dec-92	Dec-92	Dec-92	Jan-93	Jan-93	Jan-93	Jan-93	Jan-93	Jan-93	Jan-93	Jan-93	Jan-93	Jan-93	Jan-93	Apr-93	Apr-93	Apr-93	Apr-93
Site	Sk	H	RI	W	HB	Sp	GM	CN	BF	BS	HF	Sk	H	RI	W	HB	HS	Sp	GM	CN
Plaice	1	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Sole	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	1	1
Bib	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Whiting	2	-	-	-	9	9	3	2	12	1	21	28	3	-	-	1	-	1	1	-
Cod	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Flounder	-	9	1	8	1	-	-	-	-	-	-	3	-	1	-	2	-	1	-	-
Smelt	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sea snail	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pogge	1	-	-	-	-	-	-	-	11	-	-	-	-	-	-	-	-	-	-	-
Goby	6	1	2	2	18	13	21	11	65	4	5	4	15	1	-	7	-	-	-	8
Sprat	8	-	2	-	12	23	8	10	52	11	9	6	7	-	-	44	-	1	-	-
Dab	-	-	-	-	-	1	-	-	6	-	-	-	-	-	-	-	-	-	-	-
Clupeid	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Stickleback	3	-	-	1	-	1	-	-	-	-	1	-	2	-	-	-	-	-	-	-
Herring	1	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Pipefish	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Roker	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Trans. goby	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Weever	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Eel	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dragonet	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lampern	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lemon sole	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rockling	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sand eel	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Date	Apr-93	Apr-93	Apr-93	Apr-93	Apr-93	Apr-93	Apr-93	Apr-93	Apr-93	Apr-93	Jul-93	Jul-93	Jul-93	Jul-93	Jul-93	Jul-93	Jul-93	Jul-93	Jul-93	Jul-93
Site	HP	BF	BS	PS	HF	Sk	H	RI	W	HB	HS	Sp	GM	CN	HP	BF	BS	PS	HF	Sk
Plaice	-	-	-	-	-	-	-	-	-	-	56	10	-	2	2	1	4	2	-	-
Sole	2	-	1	1	-	10	-	-	-	-	1	7	-	18	5	7	9	6	-	14
Bib	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Whiting	-	2	-	1	-	2	35	8	-	26	2	17	6	6	4	24	36	1	2	-
Cod	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Flounder	-	-	-	1	-	-	-	-	-	-	1	-	-	-	1	1	2	-	-	1
Smelt	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-
Sea snail	-	-	-	-	-	-	-	-	-	-	-	1	1	6	1	-	1	-	-	-
Pogge	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	1	-	-
Goby	-	1	1	7	12	15	1	2	2	3	2	11	4	9	2	10	17	5	5	158
Sprat	-	-	-	-	-	-	-	-	-	-	-	12	8	-	1	2	-	-	-	2
Dab	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
Clupeid	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	1	-	-	1	-
Stickleback	-	-	-	-	-	-	-	1	1	1	-	1	-	-	-	-	-	-	-	1
Herring	-	-	-	-	-	-	-	-	-	-	4	-	4	2	-	-	3	-	1	3
Pipefish	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Roker	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
Trans. goby	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Weever	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-
Eel	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dragonet	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-
Lampern	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lemon sole	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rockling	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sand eel	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Date	Jul-93	Jul-93	Jul-93	Jul-93	Nov-93	Nov-93	Nov-93	Nov-93	Nov-93	Nov-93	Nov-93	Nov-93	Nov-93	Nov-93	Nov-93	Nov-93	Nov-93	Nov-93	Mar-94
Site	H	RI	W	HB	HS	Sp	GM	CN	HP	BF	BS	PS	HF	Sk	H	RI	W	HB	HS
Plaice	-	-	-	-	-	-	-	-	-	5	-	1	2	1	1	3	-	-	3
Sole	-	-	-	-	-	1	-	1	-	4	-	-	-	1	-	-	-	-	8
Bib	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Whiting	-	-	-	-	1	5	1	6	9	10	5	2	10	16	43	130	17	14	3
Cod	-	-	-	-	-	-	1	1	1	-	1	-	-	-	-	-	-	-	1
Flounder	1	3	-	1	-	-	-	-	-	-	-	-	-	2	-	8	9	3	-
Smelt	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sea snail	-	-	-	-	-	-	-	1	-	-	-	1	3	-	-	-	-	-	3
Pogge	-	-	-	-	6	4	-	-	-	6	-	-	-	-	-	-	-	-	1
Goby	471	355	219	16	4	6	12	9	13	11	53	8	17	12	1	5	55	6	38
Sprat	18	9	-	-	1	-	-	-	2	-	1	-	-	2	-	-	-	-	1
Dab	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	4
Clupeid	-	-	-	-	1	1	-	-	1	-	2	-	-	-	-	-	-	-	-
Stickleback	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Herring	6	-	3	-	-	-	-	-	2	1	2	-	-	-	-	1	-	-	1
Pipefish	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Roker	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Trans. goby	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Weever	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Eel	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dragonet	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lampern	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
Lemon sole	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Rockling	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sand eel	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Date	Mar-94	Mar-94	Mar-94	Mar-94	Mar-94	Mar-94	Mar-94	Mar-94	Mar-94	Mar-94	Mar-94	Mar-94	May-94	May-94	May-94	May-94	May-94	May-94
Site	Sp	GM	CN	HP	BF	BS	PS	HF	Sk	H	W	HB	HS	Sp	GM	CN	HP	BF
Plaice	1	-	-	-	-	-	1	-	-	-	-	-	-	-	-	1	-	-
Sole	1	-	-	-	2	1	-	-	-	-	-	-	-	2	17	5	2	-
Bib	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Whiting	4	4	1	11	8	2	1	1	2	1	-	1	8	3	3	-	-	21
Cod	-	-	1	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
Flounder	-	-	-	-	-	-	-	-	15	-	1	-	-	3	-	-	-	-
Smelt	1	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Sea snail	1	1	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
Pogge	1	-	-	-	10	-	-	-	-	-	-	-	1	-	-	-	-	1
Goby	5	22	45	9	25	33	17	3	11	7	-	5	-	-	3	4	7	2
Sprat	1	2	-	-	-	-	-	1	1	5	-	-	-	1	-	-	4	2
Dab	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Clupeid	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	2	3	-
Stickleback	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-
Herring	-	-	-	-	-	-	-	-	1	-	-	-	-	2	-	1	-	1
Pipefish	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Roker	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Trans. goby	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Weever	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
Eel	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dragonet	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lampern	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Lemon sole	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rockling	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sand eel	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Date	May-94	May-94	May-94	May-94	May-94	May-94	May-94	Aug-94	Aug-94	Aug-94	Aug-94	Aug-94	Aug-94	Aug-94	Aug-94	Aug-94
Site	BS	PS	HF	Sk	H	W	HB	HS	Sp	GM	CN	HP	BF	BS	PS	HF
Plaice	-	-	-	-	-	-	-	60	43	-	5	-	-	-	16	-
Sole	15	-	3	23	-	-	1	1	2	-	3	19	7	8	-	2
Bib	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Whiting	-	-	1	-	10	-	6	-	12	-	-	-	3	-	-	-
Cod	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7	-
Flounder	-	-	1	1	2	4	-	-	1	-	-	4	1	4	-	6
Smelt	-	-	-	-	-	1	-	-	-	-	1	-	-	-	-	-
Sea snail	-	-	-	-	-	-	-	-	-	1	-	14	-	-	-	-
Pogge	-	-	-	1	-	-	-	1	2	-	-	-	3	-	44	-
Goby	1	6	4	4	-	2	-	4	1	14	-	86	2	15	-	16
Sprat	-	-	-	1	-	-	-	-	-	-	-	-	2	7	-	-
Dab	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Clupeid	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
Stickleback	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-
Herring	-	-	-	-	-	-	-	-	4	1	24	2	1	10	-	-
Pipefish	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Roker	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Trans. goby	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Weever	-	-	-	-	-	-	-	12	-	-	-	-	1	-	-	-
Eel	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
Dragonet	-	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-
Lampern	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lemon sole	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Rockling	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sand eel	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-

Date	Aug-94	Aug-94	Aug-94	Aug-94	Nov-94	Nov-94	Nov-94	Nov-94	Nov-94	Nov-94	Nov-94	Nov-94	Nov-94	Nov-94	Nov-94	Nov-94	Nov-94
Site	Sk	H	W	HB	HS	Sp	GM	CN	HP	BF	BS	PS	HF	Sk	H	W	HB
Plaice	-	-	-	-	4	-	-	1	-	1	-	-	-	11	1	-	3
Sole	9	-	-	-	3	1	-	8	-	1	1	1	1	-	-	-	-
Bib	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Whiting	-	-	-	-	11	1	14	8	20	21	30	3	6	15	10	-	7
Cod	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1	-	-
Flounder	2	-	3	2	1	1	-	1	-	-	-	-	1	-	-	23	6
Smelt	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sea snail	-	-	-	-	-	1	-	3	4	-	-	3	1	10	3	-	4
Pogge	-	-	-	-	12	-	-	-	-	3	-	-	-	-	-	-	-
Goby	30	35	35	44	3	21	43	36	18	31	47	18	40	31	88	185	69
Sprat	-	-	-	-	6	3	-	-	4	1	-	-	4	-	-	-	2
Dab	-	-	-	-	4	-	-	-	1	-	-	-	-	-	-	-	-
Clupeid	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Stickleback	-	-	2	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Herring	-	-	3	-	-	1	1	-	-	-	-	-	-	-	-	-	-
Pipefish	-	-	-	-	-	-	-	-	-	-	-	-	4	-	-	5	-
Roker	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Transparent goby	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Weever	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Eel	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dragonet	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lampern	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lemon sole	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rockling	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sand eel	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

APPENDIX 2(b) The biomass of fish caught at each site on each sampling occasion

Date	Apr-92	Apr-92	Apr-92	Apr-92	Apr-92	Apr-92	Apr-92	Jun-92	Jun-92	Jun-92	Jun-92	Jun-92	Jun-92	Jun-92	Jun-92	Jun-92	Jun-92	Jun-92
Site	Sp	GM	HP	PS	RI	W	HB	HS	Sp	GM	CN	HP	BF	BS	PS	HF	Sk	H
Plaice	-	-	-	-	-	-	-	25	440	-	76	-	-	-	16	-	-	-
Sole	775	290	280	74	-	-	-	-	-	537	627	346	-	269	-	-	60	-
Bib	-	-	282	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Whiting	43	-	-	-	-	-	-	-	-	-	-	194	-	-	-	-	-	-
Cod	407	-	-	-	-	-	-	-	-	-	-	156	-	-	-	-	-	-
Flounder	88	-	-	37	50	-	107	-	134	-	359	385	-	254	347	-	-	116
Smelt	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sea snail	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pogge	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Goby	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-
Sprat	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dab	-	-	-	-	-	-	-	-	-	-	115	-	-	-	-	-	-	-
Clupeid	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Stickleback	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Herring	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pipefish	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Roker	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Trans.goby	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Weever	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Eel	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dragonet	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lampern	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lemon sole	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rockling	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sand eel	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Date	Jun-92	Jun-92	Jun-92	Jul-92	Jul-92	Jul-92	Jul-92	Jul-92	Jul-92	Jul-92	Jul-92	Jul-92	Jul-92	Jul-92	Jul-92	Dec-92	Dec-92	Dec-92	Dec-92	Dec-92
Site	RI	W	HB	HS	Sp	GM	CN	BF	PS	HF	Sk	H	RI	W	HB	HS	Sp	CN	HP	PS
Plaice	-	-	-	112	15	-	284	-	295	-	-	92	-	107	75	-	-	-	-	4.4
Sole	-	-	-	-	1407	-	1276	59	37	488	302	-	280	-	-	-	-	-	-	-
Bib	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Whiting	-	-	-	-	46	-	-	80	-	2	-	-	3	-	3	210	143	-	-	4.3
Cod	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	154
Flounder	38	-	27	-	-	-	111	-	-	-	-	-	-	-	-	-	-	-	-	-
Smelt	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sea snail	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5.5	-	49
Pogge	-	-	-	-	23	-	-	-	-	-	-	-	-	-	-	120	-	-	-	-
Goby	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.7	-	0.5	-	15.8
Sprat	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	37
Dab	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.2	-
Clupeid	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8
Stickleback	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Herring	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pipefish	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Roker	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Trans.goby	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Weever	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Eel	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dragonet	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lampern	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lemon sole	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rockling	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sand eel	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Date	Dec-92	Dec-92	Dec-92	Dec-92	Dec-92	Dec-92	Jan-93	Jan-93	Jan-93	Jan-93	Jan-93	Jan-93	Jan-93	Jan-93	Jan-93	Jan-93	Jan-93	Apr-93	Apr-93
Site	HF	Sk	H	RI	W	HB	Sp	GM	CN	BF	BS	HF	Sk	H	RI	W	HB	HS	Sp
Plaice	33	2.6	-	-	-	-	-	-	-	-	-	-	7.7	-	-	-	-	-	-
Sole	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	713
Bib	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Whiting	277	15	-	-	-	60.3	71.3	10.8	86	114.9	10	155.8	240	18.9	-	-	0.8	-	24
Cod	17	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Flounder	7	-	444.3	141	572.4	41	-	-	-	-	-	-	34.5	-	101	-	354.9	-	53
Smelt	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sea snail	68.3	31	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pogge	-	15	-	-	-	-	-	-	-	9.9	-	-	-	-	-	-	-	-	-
Goby	8	6.9	3	1.5	1.5	21.7	7.9	14	7.5	44.5	12.7	3.1	6.4	27.8	1.4	-	7.3	-	-
Sprat	68.2	50	-	25	-	43.1	24.2	6.5	20.4	37	34.65	49.3	17.2	20.1	-	-	155	-	0.4
Dab	-	-	-	-	-	-	0.8	-	-	2.8	-	-	-	-	-	-	-	-	-
Clupeid	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Stickleback	-	6.6	-	-	2.4	-	2.2	-	-	-	-	1.5	-	3.7	-	-	-	-	-
Herring	-	7	-	-	-	-	-	-	-	-	-	-	-	9.6	-	-	-	-	-
Pipefish	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Roker	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Trans.goby	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Weever	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Eel	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dragonet	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lampern	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lemon sole	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rockling	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sand eel	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Date	Apr-93	Apr-93	Apr-93	Apr-93	Apr-93	Apr-93	Apr-93	Apr-93	Apr-93	Apr-93	Apr-93	Apr-93	Jul-93	Jul-93	Jul-93	Jul-93	Jul-93	Jul-93	Jul-93	Jul-93
Site	GM	CN	HP	BF	BS	PS	HF	Sk	H	W	RI	HB	HS	Sp	GM	CN	HP	BF	BS	PS
Plaice	-	-	-	-	-	-	-	-	-	-	-	-	284.9	53.5	-	53	3.1	0.2	5.4	1.3
Sole	68	106	80.4	-	136	2.9	-	369.7	-	-	-	-	29.3	467	-	1359	265	408	117	501
Bib	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Whiting	38	-	-	34	-	17.3	-	43	469.6	-	121.4	341.6	23.4	114.8	89.2	445	306	420.3	504.3	27
Cod	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Flounder	-	-	-	-	-	110	-	-	-	-	-	-	40	-	-	-	25	1	-	-
Smelt	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	44.9
Sea snail	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1.5	10	1	-	1.3	-
Pogge	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.3	-	4.5
Goby	-	12.3	-	0.4	1.7	6.4	9.6	19.6	1.7	1.6	2.6	3.7	3	2.6	1.6	10.8	1.1	6.2	11	1.9
Sprat	-	-	-	-	-	-	-	-	-	-	-	-	-	75.3	10.7	-	17	2	-	-
Dab	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	28	-	-
Clupeid	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.2	1	-	-
Stickleback	-	-	-	-	-	-	-	-	-	0.1	0.4	0.2	-	0.3	-	-	-	-	-	-
Herring	-	-	-	-	-	-	-	-	-	-	-	-	12.2	-	11.3	46.6	-	-	19	-
Pipefish	-	0.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Roker	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	425	-	-
Trans.goby	-	-	-	-	-	-	-	-	-	-	-	-	-	0.7	-	-	-	-	-	-
Weever	-	-	-	-	-	-	-	-	-	-	-	-	7.9	9.7	-	-	-	-	-	-
Eel	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dragonet	-	-	-	-	-	-	-	-	-	-	-	-	50.1	-	-	-	-	-	-	-
Lampern	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lemon sole	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rockling	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sand eel	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Date	Jul-93	Jul-93	Jul-93	Jul-93	Jul-93	Jul-93	Nov-93	Nov-93	Nov-93	Nov-93	Nov-93	Nov-93	Nov-93	Nov-93	Nov-93	Nov-93	Nov-93	Nov-93	Nov-93
Site	HF	Sk	H	W	RI	HB	HS	Sp	GM	CN	HP	BF	BS	PS	HF	Sk	H	RI	W
Plaice	-	-	-	-	-	-	-	-	-	-	-	35.8	-	3.5	4.8	44	1.6	7	-
Sole	-	311	-	264	-	-	-	0.6	-	2.3	-	71.7	-	-	-	-	-	-	-
Bib	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Whiting	78	-	-	309	-	-	108	31.4	3.1	82.1	85.9	139.3	25.9	16.1	67.8	132.3	527	1245.8	223.7
Cod	-	-	-	-	-	-	-	-	4.5	15.2	7.3	-	17	-	-	-	-	-	-
Flounder	-	39	37	0.4	326.2	24.9	-	-	-	-	-	-	-	-	-	58	-	216.7	566.7
Smelt	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sea snail	-	-	-	-	-	-	-	-	-	3.4	-	-	-	4.2	37.4	-	-	-	-
Pogge	-	-	-	1.3	-	-	50	3.7	-	-	-	5.4	-	-	-	-	-	-	-
Goby	2.3	96.9	301	100.7	240.4	12.5	6.8	7.4	16.5	33.7	12.9	10	66.8	7.9	21.8	12	1	5.8	96.2
Sprat	-	0.4	13.1	11.4	2.5	-	1	-	-	-	0.7	-	1	-	-	25.3	-	-	-
Dab	-	-	-	-	-	-	10.1	79	-	-	-	-	-	-	-	-	-	-	-
Clupeid	0.1	-	-	-	-	-	0.1	0.1	-	-	0.1	-	0.1	-	-	-	-	-	-
Stickleback	-	0.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Herring	3	0.9	3.7	1.1	-	-	-	-	-	-	1	0.5	26.5	-	-	-	-	1.2	-
Pipefish	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Roker	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Trans.goby	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Weever	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Eel	-	-	-	-	90	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dragonet	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lampern	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lemon sole	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	69
Rockling	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sand eel	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Date	Nov-93	Mar-94	Mar-94	Mar-94	Mar-94	Mar-94	Mar-94	Mar-94	Mar-94	Mar-94	Mar-94	Mar-94	Mar-94	Mar-94	May-94	May-94	May-94	May-94
Site	HB	HS	Sp	GM	CN	HP	BF	BS	PS	HF	Sk	H	W	HB	HS	Sp	GM	CN
Plaice	-	6.3	5.8	-	-	-	-	-	1.7	-	-	-	-	-	-	-	-	53
Sole	-	21 6	2	-	-	-	3.5	1.9	-	-	-	-	-	-	-	112.9	682	161 1
Bib	-	-	-	-	-	-	-	-	-	-	1.1	-	-	-	-	-	-	-
Whiting	122.1	80	59.6	26.4	15.7	128.1	86.7	20 6	12	6 5	41.5	20.1	-	10	228.4	143.1	60.3	-
Cod	-	78	-	-	24.9	-	-	-	-	-	-	-	-	-	-	12 6	-	-
Flounder	309	-	-	-	-	-	-	-	-	-	558.2	-	38	-	-	662	-	-
Smelt	-	-	73	-	-	-	-	-	-	93	-	-	-	-	-	-	-	-
Sea snail	-	163	8.1	13.4	-	-	-	-	54	-	-	-	-	-	-	-	-	-
Pogge	-	1.4	18	-	-	-	13.7	-	-	-	-	-	-	-	2	-	-	-
Goby	7	66.5	5.5	20.7	47.3	7.5	33.3	35.4	26.5	4.3	16.5	8.6	-	9.1	-	-	5.1	6
Sprat	-	7.8	1.1	18.4	-	-	-	-	-	2.1	13	9.9	-	-	-	0.5	-	-
Dab	-	3.8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Clupeid	-	-	-	-	-	-	-	-	-	-	0.5	-	-	-	-	-	-	0.5
Stickleback	-	2.1	-	-	-	-	-	-	1.4	0.8	-	-	-	-	-	-	-	-
Herring	-	3.5	-	-	-	-	-	-	-	-	11.6	-	-	-	-	27	-	120
Pipefish	-	-	-	0.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Roker	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Trans.goby	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Weever	-	-	-	-	-	-	-	-	-	-	-	-	-	-	13.1	-	-	-
Eel	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dragonet	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lampern	-	-	-	-	-	-	-	-	-	0.7	-	-	-	-	-	-	-	-
Lemon sole	-	86	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rockling	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sand eel	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Date	May-94	May-94	May-94	May-94	May-94	May-94	May-94	May-94	May-94	Aug-94	Aug-94	Aug-94	Aug-94	Aug-94	Aug-94	Aug-94	Aug-94
Site	HP	BF	BS	PS	HF	Sk	H	HB	W	HS	Sp	GM	CN	HP	BF	BS	PS
Plaice	-	-	-	-	-	-	-	-	-	485.8	1470	-	265	-	-	-	-
Sole	132.1	-	970.4	-	35.4	315.2	-	3	-	66	269	-	409	1189.4	697	443.1	1589
Bib	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Whiting	-	419.2	-	-	29.4	-	197.5	142.3	-	-	467	-	-	-	72.9	-	-
Cod	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Flounder	-	-	-	-	202	126	27.5	-	118.7	-	100	-	-	513.1	18.8	571	591.5
Smelt	-	-	-	-	-	-	-	-	8	-	-	-	24	-	-	-	-
Sea snail	-	-	-	-	-	-	-	-	-	-	-	1.6	-	23	-	-	-
Pogge	-	0.9	-	-	-	0.9	-	-	-	4.6	11.8	-	-	-	3.4	-	-
Goby	7.6	1.6	1.6	6.7	4.5	4.6	-	-	2	3	0.2	9.8	-	96.9	1	9.8	38.5
Sprat	2.2	13.3	-	-	-	0.3	-	-	-	-	-	-	-	-	12.3	9.9	-
Dab	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Clupeid	0.8	-	-	-	-	-	-	-	-	-	-	0.1	-	-	-	-	-
Stickleback	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Herring	-	48	-	-	-	-	-	-	-	-	13.5	2.7	68.9	2.4	1.9	12.4	6.1
Pipefish	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Roker	-	122	-	-	-	-	-	-	-	-	90	-	-	-	-	-	-
Trans.goby	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Weever	-	-	-	-	-	-	-	-	-	126.3	-	-	-	-	13.6	-	-
Eel	-	-	-	-	-	-	-	-	-	-	-	122	-	-	-	-	-
Dragonet	-	-	-	-	-	-	-	-	-	95.7	-	-	-	-	-	-	-
Lampern	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lemon sole	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rockling	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	21.3
Sand eel	-	-	-	-	-	-	-	-	-	-	-	-	-	-	13	-	-

Date	Aug-94	Aug-94	Aug-94	Aug-94	Aug-94	Nov-94	Nov-94	Nov-94	Nov-94	Nov-94	Nov-94	Nov-94	Nov-94	Nov-94	Nov-94	Nov-94	Nov-94	Nov-94
Site	HF	Sk	H	HB	W	HS	Sp	GM	CN	HP	BF	BS	PS	HF	Sk	H	HB	W
Plaice	-	-	-	-	-	96	-	-	1.5	-	1.8	-	-	-	43	1.8	11.6	-
Sole	135	275.4	-	-	-	84	122	-	772.9	-	1.7	85	1.5	1.5	-	-	-	-
Bib	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Whiting	-	-	-	-	-	1030.7	2.7	97.6	183.6	89.2	629.9	258.2	28.4	39.7	153.7	96.6	184	-
Cod	-	-	-	-	-	-	-	-	-	-	-	3.7	-	-	-	5.1	-	-
Flounder	780	149	-	56	170.2	31	339	-	46	-	-	-	-	244	-	-	325.3	1651.6
Smelt	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sea snail	-	-	-	-	-	-	2.1	-	21.4	13.2	-	-	36.3	5.7	220.2	33.3	65.3	-
Pogge	-	-	-	-	-	77.5	-	-	-	-	2.5	-	-	-	-	-	-	-
Goby	13.1	26.2	33.5	46.6	25.9	4	20.4	51.4	44.6	21.3	35.3	67.2	20.8	40.6	38	130.4	94.2	579.5
Sprat	-	-	-	-	-	2.1	2.1	-	-	7.6	9.7	-	-	35	-	-	4.4	-
Dab	-	-	-	-	-	4.4	-	-	-	0.6	-	-	-	-	-	-	-	-
Clupeid	-	-	-	-	-	-	-	0.2	-	-	-	-	-	-	-	-	-	-
Stickleback	-	-	-	0.4	1.2	-	-	-	-	-	-	-	-	-	-	-	-	-
Herring	-	-	-	-	2	-	5.5	3	-	-	-	-	-	8.7	-	-	-	37.4
Pipefish	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.3	-
Roker	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Trans.goby	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Weever	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Eel	-	38	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dragonet	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lampern	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lemon sole	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rockling	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sand eel	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Appendix 3 The length - weight relationships for the 11 main species. $W = aL^b$, where W is weight (g) and L is length (mm).

Species	a	b
Goby	0.000006±1.35	3.11±0.79
Whiting	0.000009±1.15	2.97±0.03
Sole	0.01±3.02	2.89±0.39
Flounder	0.00002±1.29	2.88±0.51
Sprat	0.000004±1.51	3.1±0.08
Plaice	0.00001±7.94	2.98±0.47
Herring	0.000004±1.51	3.13±0.09
Sea snail	0.00002±1.55	3.02±0.10
Pogge	0.00002±1.45	2.79±0.08
Stickleback	0.00001±2.34	2.98±.022
Cod	0.000002±2.00	3.30±0.14

APPENDIX 4 The percent occurrence of prey in the diets of the main species, in each season and year

Species	Cod	Cod	Flounder	Flounder	Flounder	Flounder	Flounder	Flounder	Flounder
Season	winter	winter	spring	spring	spring	summer	summer	summer	winter
Year	1992	1994	1992	1993	1994	1992	1993	1994	1992
No. fish	6	2	6	2	4	24	6	7	12
Anemone	-	-	-	-	-	-	-	-	-
Cerianthus	-	-	-	-	-	-	-	-	-
Actinia	-	-	-	-	-	-	-	-	-
Metridium	-	-	-	-	-	-	-	-	-
Sagartia	-	-	-	-	-	-	-	-	-
Polychaeta	-	-	-	50.00	25.00	4.17	33.33	-	16.67
Aphroditidae	-	-	-	-	-	8.33	-	-	8.33
Polynoidae	-	-	-	-	-	-	-	-	-
Phylodocidae	-	-	-	-	-	-	-	-	-
Nereis virens	-	-	-	-	-	4.17	-	-	-
Nereis	33.33	-	-	-	-	4.17	-	14.29	-
Nephtyidae	16.67	-	-	-	-	8.33	-	-	-
Nephtys hombergii	-	-	-	-	-	4.17	-	-	-
Orbiniidae	-	-	-	-	-	-	-	-	-
Trochochaetidae	-	-	-	-	-	-	-	-	-
Spionidae	-	-	-	-	-	4.17	-	-	-
Polydora	-	-	-	-	-	20.83	-	-	-
Capitella capitata	-	-	-	-	-	-	-	-	-
Arenicolidae	-	-	-	-	-	4.17	-	-	-
Arenicola marina	-	-	-	-	-	-	-	-	-
Opheliidae	-	-	-	-	-	-	-	-	-
Pectinariidae	-	-	-	-	-	-	-	-	-
Ampharetidae	-	-	-	-	-	-	-	-	-
Ampharete grubei	-	-	-	-	-	-	-	-	-
Terebellidae	-	-	-	-	-	-	-	-	-
Lanice conchilega	-	-	-	-	-	4.17	-	-	-
Tubificidae	-	-	-	-	-	4.17	-	-	-
Balanus plate	-	-	-	-	-	4.17	-	-	-
Copepoda	-	-	-	-	-	-	-	-	-
Temora longicornis	-	-	-	-	-	-	-	-	-
Mysidae	-	-	-	-	-	-	-	-	-
Gastrosaccus sanctus	-	100	-	-	-	-	33.33	14.29	-
Neomysis integer	-	-	-	-	-	8.33	-	-	-
Schistomysis	-	-	-	-	-	-	-	-	-
Schistomysis ornata	-	-	-	-	-	-	-	-	-
Amphipoda	-	-	-	-	-	-	-	-	-
Gammaridae	16.67	-	-	-	25.00	-	-	-	-
Oedicerotidae	50.00	-	16.67	-	-	12.50	16.67	14.29	50.00
Talitrus saltator	-	-	-	-	-	12.50	-	-	41.67
Atylus	-	-	-	-	-	-	-	-	-
Ampeliscidae	-	-	-	-	-	-	-	-	-
Bathyporeia	-	-	-	-	-	-	-	-	-
Haustoriidae	-	-	-	-	-	-	-	-	-
Haustorius arenarius	-	-	-	-	-	-	-	-	-
Gammarus	-	-	-	-	-	-	-	-	-
Gammarus zaddachi	50.00	50.00	-	-	75.00	-	50.00	71.43	-
Corophium	-	-	16.67	-	-	16.67	-	-	58.33
Caprellidae	-	-	16.67	50.00	-	-	-	-	-
Idotea linearis	-	-	33.33	-	-	45.83	-	-	-

Appendix 4 (cont.)

Cumacea	-	-	-	-	-	-	-	-	-
Diastylidae	-	-	-	-	-	-	-	-	-
Decapod crustacean	-	-	-	-	-	-	-	-	-
Pandalus montagui	-	-	-	-	-	-	-	-	-
Crangonidae	-	-	-	-	-	-	-	-	-
Crangon crangon	-	-	-	-	-	-	16.67	-	-
Brachyuran Crustacean	-	-	-	-	-	4.17	-	-	-
Homarus	16.67	-	-	-	-	8.33	16.67	-	-
Maja squinado	-	-	-	-	-	-	-	-	-
Liocarcinus	-	-	-	-	-	-	-	-	-
Liocarcinus marmoreus	-	-	-	-	-	-	-	-	-
Carcinus	-	-	-	-	-	-	-	-	-
Carcinus maenas	-	-	-	-	-	-	16.67	-	-
Bivalve	-	-	-	-	-	8.33	-	-	-
Mollusc siphon	-	-	-	-	-	4.17	-	-	-
Gastropod mollusc	16.67		-	-	-	-	33.33	-	-
Littorina	-	-	-	-	-	-	-	-	-
Hydrobia ulvae	-	-	-	-	-	-	-	-	-
Retusa	-	-	-	-	-	-	-	-	16.67
Mytilidae	-	-	-	-	-	4.17	-	-	-
Erycinacea	-	-	-	-	-	-	-	-	-
Mysella bidenta	-	-	-	-	-	-	-	-	-
Parvicardium	-	-	-	-	-	4.17	-	-	-
Cerastoderma edule	-	-	-	-	-	-	-	-	-
Ensis	-	-	-	50.00	-	-	-	-	-
Phaxus pellucidus	-	-	-	-	-	-	-	-	-
Tellinacea	-	-	-	-	-	-	-	-	-
Macoma balthica	-	-	-	-	-	-	-	-	-
Scrobiculariidae	-	-	-	50.00	-	-	-	-	-
Scrobicularia plana	-	-	16.67	-	-	37.50	-	-	-
Abra	-	-	33.33	-	-	-	-	-	-
Abra abra	-	-	-	-	-	-	-	-	-
Abra tenuis	-	-	-	-	-	-	-	-	-
Algae	-	-	-	50.00	-	-	-	-	-
Fish	-	-	16.67	-	-	37.50	-	-	-
Clupeidae	-	-	-	-	-	-	16.67	-	-
Sprattus sprattus	-	-	-	-	-	-	-	-	-
Gobiidae	-	-	-	-	-	-	-	-	-
Pleuronectidae	-	-	-	-	-	-	-	-	8.33
Nemertean	-	-	-	-	-	-	-	-	-
Sialis	-	-	16.67	-	-	-	-	-	-
Plant material	-	-	-	-	-	-	-	-	-
Hydroid	-	-	-	50.00	-	8.33	-	-	-
Bryzoa	-	-	-	-	-	4.17	-	-	-
Seaweed	-	-	-	50.00	-	16.67	-	-	-
Roots/moss	-	-	-	-	-	-	-	-	-
Egg sac	-	-	-	-	-	-	-	-	-
Eggs	-	-	-	-	-	-	-	-	-
unident	-	-	-	-	-	4.17	-	-	-
unident	-	-	-	-	-	-	-	-	-
unident	-	-	-	-	-	-	-	-	-
Debris	83.33	100	100.00	100.00	100.00	95.83	83.33	57.14	83.33
stone/shell debris	16.67	-	-	-	-	4.17	-	14.29	8.33

Appendix 4 (cont.)

Species	Flounder	Flounder	Goby	Goby	Goby	Goby	Goby	Goby	Goby	Goby
Season	winter	autumn	spring	spring	winter	winter	winter	summer	summer	autumn
Year	1994	1994	1993	1994	1992	1993	1994	1993	1994	1993
No. fish	7	20	13	29	36	39	34	77	7	
Anemone	-	-	-	-	-	-	-	-	-	-
Cerianthus	-	-	-	-	-	-	-	-	-	-
Actinia	-	5.00	-	-	-	-	-	-	-	-
Metridium	-	-	-	-	-	-	-	-	-	-
Sagartia	-	-	-	-	-	-	-	-	-	-
Polychaeta	14.29	-	-	-	-	2.56	-	-	-	-
Aphroditidae	-	-	-	-	-	-	-	-	-	-
Polynoidae	-	-	-	-	-	-	-	-	-	-
Phylodocidae	-	-	-	-	-	-	-	-	-	-
Nereis virens	-	-	-	-	-	-	-	-	-	-
Nereis	14.29	5.00	7.69	-	-	-	-	-	-	-
Nephtyidae	-	-	-	-	-	2.56	-	-	-	-
Nephtys hombergii	-	-	-	-	-	-	-	-	-	-
Orbiniidae	-	-	-	-	-	-	-	-	-	-
Trochochaetidae	-	-	-	-	-	-	-	-	-	-
Spionidae	-	-	7.69	-	-	-	-	-	-	-
Polydora	-	-	-	-	-	-	-	-	-	-
Capitella capitata	-	-	-	-	-	-	-	-	-	-
Arenicolidae	-	5.00	-	-	-	-	-	-	-	-
Arenicola marina	-	-	-	-	-	-	-	-	-	-
Opheliidae	-	-	-	-	-	-	-	-	-	-
Pectinariidae	-	-	-	-	-	-	-	-	-	-
Ampharetidae	-	-	-	-	-	-	-	-	-	-
Ampharete grubei	-	-	-	-	-	-	-	-	-	-
Terebellidae	-	-	-	-	-	-	-	-	-	-
Lanice conchilega	-	-	-	-	-	-	-	-	-	-
Tubificidae	-	-	-	-	-	-	-	-	-	-
Balanus plate	-	-	-	-	2.78	-	-	-	-	-
Copepoda	-	-	-	-	-	-	-	-	-	-
Temora longicornis	-	-	-	-	-	-	-	-	-	33.33
Mysidae	-	-	-	-	-	-	-	-	-	-
Gastrosaccus sanctus	42.86	15.00	46.15	37.93	-	23.08	64.71	27.27	42.86	-
Neomysis integer	-	-	-	-	11.11	-	2.94	-	-	-
Schistomysis	-	-	-	-	2.78	-	-	-	-	-
Schistomysis ornata	-	-	-	-	2.78	-	-	-	-	-
Amphipoda	-	-	-	-	2.78	-	-	-	-	-
Gammaridae	-	10.00	23.08	13.79	-	23.08	2.94	28.57	28.57	33.33
Oedicerotidae	-	5.00	7.69	-	25.00	2.56	17.65	12.99	-	-
Talitrus saltator	-	-	-	-	13.89	-	-	-	-	-
Atylus	-	-	-	-	-	-	-	-	-	-
Ampeliscidae	-	-	-	-	-	-	-	-	-	-
Bathyporeia	-	-	-	-	-	-	-	-	-	-
Haustoriidae	-	-	-	-	-	-	-	-	-	-
Haustorius arenarius	-	-	-	-	-	-	-	-	-	-
Gammarus	-	-	-	-	-	-	-	-	-	33.33
Gammarus zaddachi	14.29	25.00	7.69	10.34	-	17.95	11.76	22.08	-	-
Corophium	-	-	-	-	8.33	-	-	1.30	-	-
Caprellidae	-	10.00	-	-	-	-	-	-	-	-
Idotea linearis	-	-	-	-	-	-	-	-	-	-

Appendix 4 (cont.)

Cumacea	-	-	-	-	-	-	-	-	-	-
Diastylidae	-	-	-	-	-	-	-	-	-	-
Decapod crustacean	-	-	-	3.45	-	-	-	-	-	-
Pandalus montagui	-	-	-	-	-	-	-	-	-	-
Crangonidae	-	-	-	-	-	-	-	-	-	-
Crangon crangon	28.57	50.00	-	-	-	-	-	-	-	33.33
Brachyuran Crustacean	-	-	-	-	2.78	-	-	-	-	-
Homarus	-	-	-	-	-	-	-	-	-	-
Maja squinado	-	-	-	-	-	-	-	-	-	-
Liocarcinus	-	-	-	-	-	-	-	-	-	-
Liocarcinus marmoreus	-	-	-	-	-	-	-	-	-	-
Carcinus	-	-	-	-	-	-	-	-	-	-
Carcinus maenas	-	10.00	-	-	-	-	-	1.30	-	-
Bivalve	-	-	-	-	-	-	-	-	-	-
Mollusc siphon	-	-	-	-	-	-	-	-	-	-
Gastropod mollusc	28.57	-	-	-	-	-	-	-	-	-
Littorina	-	-	-	-	-	-	-	-	-	-
Hydrobia ulvae	-	-	-	-	-	-	-	-	-	-
Retusa	-	-	-	-	2.78	-	-	-	-	-
Mytilidae	-	-	-	-	-	-	-	-	-	-
Erycinacea	-	-	-	-	-	-	-	-	-	-
Mysella bidenta	-	-	-	-	-	-	-	-	-	-
Parvicardium	-	-	-	-	-	-	-	-	-	-
Cerastoderma edule	-	5.00	-	-	-	-	-	-	-	-
Ensis	28.57	-	-	-	-	-	-	-	-	-
Phaxus pellucidus	-	-	-	-	-	-	-	-	-	-
Tellinacea	-	-	-	-	-	-	-	-	-	-
Macoma balthica	-	-	-	-	-	-	-	-	-	-
Scrobiculariidae	14.29	5.00	-	-	-	-	-	-	-	-
Scrobicularia plana	-	-	-	-	-	-	-	-	-	-
Abra	-	-	-	-	-	-	-	-	-	-
Abra abra	-	-	-	-	-	-	-	-	-	-
Abra tenuis	-	-	-	-	-	-	-	-	-	-
Algae	-	-	-	-	-	-	-	-	-	-
Fish	-	-	-	-	-	-	-	-	-	-
Clupeidae	-	-	-	-	-	-	-	-	-	-
Sprattus sprattus	-	-	-	-	-	-	-	-	-	-
Gobiidae	-	-	-	-	-	-	-	-	-	-
Pleuronectidae	-	-	-	-	-	-	-	-	-	-
Nemertean	-	-	-	-	-	-	-	-	-	-
Sialis	-	-	-	-	-	-	-	-	-	-
Plant material	-	-	-	-	-	-	-	-	-	-
Hydroid	-	-	-	-	-	-	-	-	-	-
Bryzoa	-	-	-	-	-	-	-	-	-	-
Seaweed	-	-	-	-	-	-	-	-	-	-
Roots/moss	-	-	-	-	-	-	-	-	-	-
Egg sac	-	-	-	-	-	-	-	-	-	-
Eggs	-	-	-	-	-	-	-	-	-	-
unident	-	-	-	-	-	-	-	-	-	-
unident	-	-	-	-	-	-	-	-	-	-
unident	-	-	-	-	-	-	-	-	-	-
Debris	57.14	50.00	23.08	37.93	44.44	43.59	14.71	25.97	28.57	66.67
stone/shell debris	-	-	-	-	-	-	-	-	-	-

Appendix 4 (cont.)

Species	Goby	Plaice	Plaice	Plaice	Plaice	Plaice	Plaice	Plaice	Pogge	Pogge
Season	autumn	summer	summer	summer	winter	autumn	autumn	spring	winter	winter
Year	1994	1992	1993	1994	1994	1994	1993	1994	1992	1993
No. fish	27		22	17		21	29	29	10	9
Anemone	-	-	-	-	-	-	-	-	-	-
Cerianthus	-	-	-	-	-	4.76	-	-	-	-
Actinia	-	6.67	-	5.88	-	-	-	-	-	-
Metridium	-	-	-	-	-	-	-	-	-	-
Sagartia	-	-	-	-	-	-	-	-	-	-
Polychaeta	-	6.67	-	17.65	8.70	14.29	13.79	6.90	-	-
Aphroditidae	-	26.67	-	-	-	-	-	-	-	-
Polynoidae	-	6.67	-	-	-	-	-	-	-	-
Phylodocidae	-	-	-	17.65	8.70	-	-	31.03	-	-
Nereis virens	-	6.67	-	-	-	-	-	-	-	-
Nereis	-	-	-	11.76	-	9.52	-	6.90	-	-
Nephtyidae	-	33.33	4.55	23.53	13.04	4.76	-	13.79	-	-
Nephtys hombergii	-	53.33	-	-	-	-	-	-	-	-
Orbiniidae	-	-	-	5.88	-	-	-	-	-	-
Trochochaetidae	-	33.33	-	-	-	-	-	-	-	-
Spionidae	-	-	-	-	-	-	-	3.45	-	-
Polydora	-	13.33	-	-	-	-	-	-	-	-
Capitella capitata	-	-	-	-	-	-	-	3.45	-	-
Arenicolidae	-	-	-	-	-	-	-	-	-	-
Arenicola marina	-	-	-	-	-	-	-	3.45	-	-
Opheliidae	-	-	-	-	-	-	-	-	-	-
Pectinariidae	-	-	4.55	-	-	-	-	-	-	-
Ampharetidae	-	-	4.55	-	-	4.76	-	-	-	-
Ampharete grubei	-	20.00	-	-	-	-	-	-	-	-
Terebellidae	-	20.00	-	-	-	4.76	-	-	-	-
Lanice conchilega	-	-	-	-	-	-	-	-	-	-
Tubificidae	-	-	-	-	-	-	-	-	-	-
Balanus plate	-	-	-	-	-	-	-	-	-	-
Copepoda	-	-	-	5.88	-	4.76	-	-	-	-
Temora longicornis	-	-	-	23.53	30.43	14.29	13.79	17.24	-	-
Mysidae	-	-	-	-	-	-	-	-	-	-
Gastrosaccus sanctus	33.33	-	9.09	11.76	-	14.29	31.03	-	-	22.22
Neomysis integer	-	-	-	-	-	-	-	-	30.00	-
Schistomysis	-	-	-	-	-	-	-	-	-	-
Schistomysis ornata	-	-	-	-	-	-	-	-	-	-
Amphipoda	-	-	-	-	-	-	-	-	-	-
Gammaridae	37.04	-	4.55	5.88	4.35	9.52	6.90	13.79	-	-
Oedicerotidae	14.81	26.67	4.55	5.88	-	-	3.45	13.79	10.00	-
Talitrus saltator	-	6.67	-	-	-	-	-	-	10.00	-
Atylus	-	-	-	-	-	-	6.90	-	-	-
Ampeliscidae	-	6.67	-	-	-	-	-	-	-	-
Bathyporeia	-	6.67	-	-	-	-	-	-	-	-
Haustoriidae	-	-	-	41.18	4.35	9.52	3.45	17.24	-	-
Haustorius arenarius	-	-	-	-	-	-	-	-	-	-
Gammarus	-	-	-	-	-	-	-	-	-	-
Gammarus zaddachi	11.11	6.67	4.55	-	-	-	-	-	-	-
Corophium	-	-	-	-	-	-	-	-	-	-
Caprellidae	-	-	-	5.88	-	-	-	6.90	-	-
Idotea linearis	-	6.67	4.55	-	-	-	-	-	-	-

Appendix 4 (cont.)

Cumacea	-	6.67	-	11.76	-	-	3.45	-	-	-
Diastylidae	-	-	4.55	-	-	9.52	-	-	-	-
Decapod crustacean	-	6.67	-	-	-	-	-	-	-	-
Pandalus montagui	-	-	-	-	-	-	-	-	10.00	-
Crangonidae	-	13.33	-	-	-	-	-	-	-	-
Crangon crangon	-	-	-	-	-	4.76	3.45	-	-	22.22
Brachyuran Crustacean	-	-	-	-	-	-	-	-	20.00	-
Homarus	-	-	-	-	-	-	-	-	50.00	-
Maja squinado	-	-	-	-	-	-	-	-	10.00	-
Liocarcinus	-	-	-	-	-	-	-	-	-	-
Liocarcinus marmoreus	-	6.67	-	-	-	-	3.45	-	-	-
Carcinus	-	-	-	-	-	-	-	-	10.00	-
Carcinus maenas	-	-	4.55	-	-	14.29	-	-	-	-
Bivalve	-	-	-	-	4.35	-	-	-	-	-
Mollusc siphon	-	-	9.09	5.88	-	-	-	-	-	-
Gastropod mollusc	-	20.00	-	5.88	-	-	-	3.45	-	-
Littorina	-	-	-	-	-	4.76	-	-	-	-
Hydrobia ulvae	-	-	-	-	-	-	-	-	-	-
Retusa	-	-	-	23.53	-	4.76	-	-	-	-
Mytilidae	-	-	-	-	-	-	-	-	-	-
Erycinacea	-	6.67	-	5.88	-	-	-	-	-	-
Mysella bidenta	-	-	-	-	-	-	-	-	-	-
Parvicardium	-	-	-	-	-	-	-	-	-	-
Cerastoderma edule	-	-	-	-	-	9.52	-	-	-	-
Ensis	-	-	4.55	5.88	13.04	19.05	17.24	10.34	-	-
Phaxus pellucidus	-	-	-	-	-	4.76	-	-	-	-
Tellinacea	-	-	22.73	-	-	9.52	-	-	-	-
Macoma balthica	-	-	-	-	-	-	-	-	-	-
Scrobiculariidae	-	-	-	5.88	-	4.76	-	-	-	-
Scrobicularia plana	-	60.00	-	-	-	-	-	-	-	-
Abra	-	-	-	-	-	-	-	-	-	-
Abra abra	-	6.67	4.55	5.88	-	-	-	6.90	-	-
Abra tenuis	-	6.67	-	-	-	-	-	-	-	-
Algae	-	13.33	-	-	-	-	-	-	-	-
Fish	-	53.33	-	-	-	-	-	-	-	-
Clupeidae	-	-	-	-	-	-	-	-	-	-
Sprattus sprattus	-	-	-	-	-	-	-	-	-	-
Gobiidae	-	-	-	-	-	-	-	-	-	-
Pleuronectidae	-	-	-	-	-	-	-	-	-	-
Nemertean	-	-	-	-	-	-	-	-	-	-
Sialis	-	-	-	-	-	-	-	-	-	-
Plant material	-	-	-	-	-	-	-	-	10.00	-
Hydroid	-	-	-	-	-	-	-	-	-	-
Bryzoa	-	-	-	-	-	-	-	-	-	-
Seaweed	-	-	-	-	-	-	-	-	-	-
Roots/moss	-	-	-	-	-	-	-	-	-	-
Egg sac	-	-	-	-	-	-	-	-	-	-
Eggs	-	-	-	-	-	-	-	-	-	-
unident	-	-	-	-	-	-	-	-	-	-
unident	-	-	-	-	-	-	-	-	-	-
unident	-	-	-	-	-	-	-	-	-	-
Debris	22.22	100.00	95.45	82.35	60.87	61.90	62.07	79.31	80.00	77.78
stone/shell debris	-	-	-	-	-	-	6.90	-	-	-

Appendix 4 (cont.)

Species	Pogge	Pogge	Pogge	Pogge	Sole	Sole	Sole	Sole	Sole	Sole
Season	winter	summer	spring	autumn	spring	spring	spring	summer	summer	summer
Year	1994	1993	1994	1994	1992	1993	1994	1992	1993	1994
No. fish	5	2	5	5	20	13	2	21	28	18
Anemone	-	-	-	-	-	-	-	-	-	-
Cerianthus	-	-	-	-	-	-	-	-	-	-
Actinia	-	-	-	-	-	-	-	-	-	-
Metridium	-	-	-	-	-	-	-	4.76	-	-
Sagartia	-	-	-	-	-	-	-	-	-	-
Polychaeta	-	-	-	-	-	-	-	-	25.00	22.22
Aphroditidae	-	-	-	-	25.00	-	-	33.33	-	-
Polynoidae	-	-	-	-	-	-	-	-	-	-
Phylodocidae	-	-	-	-	-	15.38	-	4.76	-	11.11
Nereis virens	-	-	-	-	-	-	-	14.29	-	-
Nereis	-	-	-	-	10.00	23.08	-	9.52	25.00	5.56
Nephtyidae	-	-	-	-	10.00	7.69	-	38.10	3.57	-
Nephtys hombergii	-	-	-	-	-	-	-	14.29	-	-
Orbiniidae	-	-	-	-	10.00	-	-	-	-	-
Trochochaetidae	-	-	-	-	-	-	-	-	-	-
Spionidae	-	-	-	-	-	-	-	4.76	-	-
Polydora	-	-	-	-	-	-	-	19.05	-	-
Capitella capitata	-	-	-	-	-	-	-	-	-	-
Arenicolidae	-	-	-	-	-	23.08	-	9.52	39.29	5.56
Arenicola marina	-	-	-	-	-	-	-	4.76	-	-
Opheliidae	-	-	-	-	-	-	-	4.76	-	-
Pectinariidae	-	-	-	-	-	-	-	-	-	-
Ampharetidae	-	-	-	-	-	-	-	19.05	-	-
Ampharete grubei	-	-	-	-	-	-	-	14.29	-	-
Terebellidae	-	-	-	-	-	-	-	9.52	-	-
Lanice conchilega	-	-	-	-	-	-	-	4.76	-	-
Tubificidae	-	-	-	-	-	-	-	-	-	-
Balanus plate	-	-	-	-	-	-	-	-	-	-
Copepoda	-	-	-	-	-	-	-	-	-	-
Temora longicornis	-	-	-	-	-	-	-	4.76	-	-
Mysidae	-	-	-	-	-	-	-	-	-	-
Gastrosaccus sanctus	40.00	50.00	40.00	80.00	-	-	-	-	17.86	5.56
Neomysis integer	-	-	-	-	-	-	-	14.29	-	-
Schistomysis	-	-	-	-	-	-	-	4.76	-	-
Schistomysis ornata	-	-	-	-	-	-	-	-	-	-
Amphipoda	-	-	-	-	-	-	-	-	-	-
Gammaridae	-	-	-	-	-	15.38	-	-	17.86	5.56
Oedicerotidae	-	-	-	-	10.00	-	-	19.05	7.14	-
Talitrus saltator	-	-	-	-	-	-	-	9.52	-	-
Atylus	-	-	-	-	-	-	-	-	-	-
Ampeliscidae	-	-	-	-	-	-	-	-	-	-
Bathyporeia	-	-	-	-	-	7.69	-	-	-	-
Haustoriidae	-	-	-	-	-	-	-	-	-	-
Haustorius arenarius	-	-	-	-	-	-	-	-	-	-
Gammarus	-	-	-	-	-	-	-	-	-	-
Gammarus zaddachi	-	50.00	-	20.00	-	-	-	-	21.43	5.56
Corophium	-	-	-	-	-	-	-	19.05	-	-
Caprellidae	-	-	-	-	-	-	-	-	-	5.56
Idotea linearis	-	-	-	-	-	-	-	-	-	-

Appendix 4 (cont.)

Cumacea	-	-	-	-	-	-	-	-	-	-
Diastylidae	-	-	-	-	-	-	-	-	-	-
Decapod crustacean	-	-	-	-	-	-	-	-	-	-
Pandalus montagui	-	-	-	-	-	-	-	-	-	-
Crangonidae	-	-	-	-	5.00	-	-	-	-	-
Crangon crangon	60.00	-	-	20.00	-	-	-	4.76	32.14	-
Brachyuran Crustacean	-	-	-	-	-	-	-	-	10.71	-
Homarus	-	-	-	-	-	7.69	-	9.52	-	-
Maja squinado	-	-	-	-	-	-	-	4.76	-	-
Liocarcinus	-	-	-	-	-	-	-	-	-	-
Liocarcinus marmoreus	-	-	-	-	-	-	-	-	-	-
Carcinus	-	-	-	-	-	-	-	4.76	-	-
Carcinus maenas	20.00	50.00	-	-	-	-	-	4.76	35.71	-
Bivalve	-	-	-	-	-	-	-	4.76	3.57	-
Mollusc siphon	-	-	-	-	-	-	-	-	-	-
Gastropod mollusc	-	-	-	-	-	-	-	4.76	-	-
Littorina	-	-	-	-	-	-	-	-	-	-
Hydrobia ulvae	-	-	-	-	-	-	-	-	-	-
Retusa	-	-	-	-	-	-	-	-	-	-
Mytilidae	-	-	-	-	-	-	-	-	-	-
Erycinacea	-	-	-	-	-	-	-	-	-	-
Mysella bidenta	-	-	-	-	-	-	-	4.76	-	-
Parvicardium	-	-	-	-	-	-	-	4.76	-	-
Cerastoderma edule	-	-	-	-	-	-	-	-	-	-
Ensis	-	-	-	-	-	-	-	-	-	-
Phaxus pellucidus	-	-	-	-	-	-	-	-	-	-
Tellinacea	-	-	-	-	-	-	-	-	10.71	-
Macoma balthica	-	-	-	-	-	-	-	4.76	-	-
Scrobiculariidae	-	-	-	-	-	-	-	-	-	5.56
Scrobicularia plana	-	-	-	-	-	-	-	-	-	-
Abra	-	-	-	-	-	-	-	-	-	-
Abra abra	-	-	-	-	-	-	-	-	-	-
Abra tenuis	-	-	-	-	-	-	-	4.76	7.14	-
Algae	-	-	-	-	-	-	-	-	3.57	-
Fish	-	-	-	-	-	-	-	-	-	-
Clupeidae	-	-	-	-	-	-	-	4.76	3.57	-
Sprattus sprattus	-	-	-	-	-	-	-	-	-	-
Gobiidae	-	-	-	-	-	-	-	-	-	-
Pleuronectidae	-	-	-	-	-	-	-	-	-	-
Nemertean	-	-	-	-	-	-	-	-	-	-
Sialis	-	-	-	-	-	-	-	-	-	-
Plant material	-	-	-	-	-	-	-	-	-	-
Hydroid	-	-	-	-	5.00	-	-	4.76	-	-
Bryzoa	-	-	-	-	-	-	-	-	-	-
Seaweed	-	-	-	-	-	-	-	-	-	-
Roots/moss	-	-	-	-	-	-	-	-	-	-
Egg sac	-	-	-	-	5.00	-	-	-	-	-
Eggs	-	-	-	-	-	-	-	-	-	-
unident	-	-	-	-	-	-	-	-	-	-
unident	-	-	-	-	5.00	-	-	-	-	-
unident	-	-	-	-	-	-	-	-	-	-
Debris	100.00	100.00	100.00	60.00	100.00	100.00	100.00	100.00	100.00	94.44
stone/shell debris	-	-	-	-	5.00	-	-	19.05	-	-

Appendix 4 (cont.)

Species	Sole	Sole	Sole	Sole	Sprat	Sprat	Sprat	Whiting	Whiting	Whiting
Season	winter	winter	autumn	autumn	winter	summer	spring	winter	winter	winter
Year	1993	1994	1993	1994	1992	1993	1994	1992	1993	1994
No. fish	4	8	2	24	18	6	2	44	65	42
Anemone	-	-	-	-	-	-	-	-	-	-
Cerianthus	-	-	-	-	-	-	-	-	-	-
Actinia	-	-	-	-	-	-	-	-	-	-
Metridium	-	-	-	-	-	-	-	-	-	-
Sagartia	-	-	-	4.17	-	-	-	-	-	-
Polychaeta	-	-	50.00	12.50	-	-	-	2.27	-	-
Aphroditidae	-	-	-	-	-	-	-	4.55	-	-
Polynoidae	-	-	-	-	-	-	-	-	-	-
Phylodocidae	-	-	-	4.17	-	-	-	-	-	-
Nereis virens	-	-	-	-	-	-	-	-	-	-
Nereis	-	25.00	-	25.00	-	-	-	-	1.54	-
Nephtyidae	-	-	-	4.17	-	-	-	-	1.54	-
Nephtys hombergii	-	-	-	-	-	-	-	-	-	-
Orbiniidae	-	-	-	-	-	-	-	-	-	-
Trochochaetidae	-	-	-	-	-	-	-	-	-	-
Spionidae	-	-	-	-	-	-	-	-	-	-
Polydora	-	-	-	-	-	-	-	-	-	-
Capitella capitata	-	-	-	-	-	-	-	-	-	-
Arenicolidae	-	-	-	25.00	-	-	-	-	-	-
Arenicola marina	-	-	-	-	-	-	-	2.27	-	-
Opheliidae	-	-	-	-	-	-	-	-	1.54	-
Pectinariidae	-	-	-	-	-	-	-	-	-	-
Ampharetidae	-	12.50	-	4.17	-	-	-	-	-	-
Ampharete grubei	-	-	-	-	-	-	-	-	-	-
Terebellidae	-	-	-	4.17	-	-	-	-	-	-
Lanice conchilega	-	-	-	4.17	-	-	-	-	-	-
Tubificidae	-	-	-	-	-	-	-	-	-	-
Balanus plate	-	-	-	-	-	-	-	-	-	-
Copepoda	-	-	-	-	-	-	-	-	-	-
Temora longicornis	-	-	-	-	-	-	100.00	2.27	4.62	-
Mysidae	-	-	-	-	16.67	-	-	2.27	1.54	-
Gastrosaccus sanctus	-	-	-	16.67	11.11	-	-	-	72.31	76.19
Neomysis integer	-	-	-	-	11.11	50.00	-	43.18	-	-
Schistomysis	-	-	-	-	-	-	-	-	-	-
Schistomysis ornata	-	-	-	-	-	-	-	11.36	-	-
Amphipoda	-	-	-	-	-	-	-	-	-	-
Gammaridae	-	-	-	-	-	-	-	6.82	6.15	4.76
Oedicerotidae	-	-	-	4.17	-	-	-	20.45	1.54	-
Talitrus saltator	-	-	-	-	-	-	-	15.91	-	-
Atylus	-	-	-	-	-	-	-	-	-	-
Ampeliscidae	-	-	-	-	-	-	-	-	-	-
Bathyporeia	-	-	-	-	-	-	-	-	-	-
Haustoriidae	-	-	-	4.17	-	-	-	-	-	-
Haustorius arenarius	-	-	-	-	-	-	-	-	-	-
Gammarus	-	-	-	-	-	-	-	-	-	-
Gammarus zaddachi	-	-	-	4.17	-	-	-	-	21.54	23.81
Corophium	-	-	-	-	-	-	-	29.55	-	-
Caprellidae	-	-	-	16.67	-	-	-	-	-	-
Idotea linearis	-	-	-	4.17	-	-	-	-	-	-

Appendix 4 (cont.)

Cumacea	-	-	-	-	-	-	-	-	-	-
Diastylidae	-	-	-	-	-	-	-	-	1.54	-
Decapod crustacean	-	-	-	-	-	-	-	-	1.54	-
Pandalus montagui	-	-	-	-	-	-	-	-	-	-
Crangonidae	-	-	-	-	-	-	-	-	-	-
Crangon crangon	-	25.00	-	12.50	-	-	-	-	9.23	14.29
Brachyuran Crustacean	-	-	-	-	-	-	-	2.27	-	-
Homarus	-	-	-	-	-	-	-	4.55	-	-
Maja squinado	-	-	-	-	-	-	-	4.55	-	-
Liocarcinus	-	-	-	-	-	-	-	-	-	-
Liocarcinus marmoreus	-	-	-	-	-	-	-	-	-	-
Carcinus	-	-	-	-	-	-	-	-	-	-
Carcinus maenas	-	-	-	16.67	-	-	-	-	-	2.38
Bivalve	-	-	-	-	-	-	-	-	-	-
Mollusc siphon	-	-	-	-	-	-	-	2.27	-	-
Gastropod mollusc	-	-	-	-	-	-	-	-	3.08	4.76
Littorina	-	-	-	-	-	-	-	-	-	-
Hydrobia ulvae	-	-	-	-	-	-	-	-	-	-
Retusa	-	-	-	-	-	-	-	4.55	-	-
Mytilidae	-	-	-	-	-	-	-	-	-	-
Erycinacea	-	-	-	-	-	-	-	-	-	-
Mysella bidenta	-	-	-	-	-	-	-	-	-	-
Parvicardium	-	-	-	-	-	-	-	-	-	-
Cerastoderma edule	-	-	-	-	-	-	-	-	-	-
Ensis	-	-	-	-	-	-	-	-	-	-
Phaxus pellucidus	-	-	-	4.17	-	-	-	-	-	-
Tellinacea	-	-	-	8.33	-	-	-	-	-	-
Macoma balthica	-	-	-	-	-	-	-	-	-	-
Scrobiculariidae	-	-	-	-	-	-	-	-	-	-
Scrobicularia plana	-	-	-	-	-	-	-	-	-	-
Abra	-	-	-	-	-	-	-	-	-	-
Abra abra	-	-	-	4.17	-	-	-	-	-	-
Abra tenuis	-	-	-	-	-	-	-	-	-	-
Algae	-	-	-	-	-	-	-	-	-	-
Fish	-	-	-	-	-	-	-	-	-	-
Clupeidae	-	-	-	-	-	-	-	-	1.54	7.14
Sprattus sprattus	-	-	-	-	-	-	-	-	-	4.76
Gobiidae	-	-	-	-	-	-	-	6.82	-	4.76
Pleuronectidae	-	-	-	-	-	-	-	-	-	-
Nemertean	-	-	-	-	-	-	-	2.27	-	-
Sialis	-	-	-	-	-	-	-	-	-	-
Plant material	-	-	-	-	-	-	-	-	-	-
Hydroid	-	-	-	-	-	-	-	-	1.54	-
Bryzoa	-	-	-	-	-	-	-	-	-	-
Seaweed	-	-	-	-	-	-	-	-	-	-
Roots/moss	-	-	-	-	-	-	-	-	-	-
Egg sac	-	-	-	-	-	-	-	-	-	-
Eggs	-	-	-	-	-	-	-	-	-	-
unident	-	-	-	-	-	-	-	-	-	-
unident	-	-	-	-	-	-	-	-	-	-
unident	-	-	-	-	-	-	-	-	1.54	-
Debris	100	100	100.00	83.33	50.00	66.67	-	90.91	98.46	97.62
stone/shell debris	-	-	-	-	-	-	-	-	3.08	4.76

Appendix 4 (cont.)

Species	Whiting	Whiting	Whiting	Whiting	Whiting	Whiting	Whiting
Season	autumn	autumn	spring	spring	summer	summer	summer
Year	1993	1994	1993	1994	1992	1993	1994
No. fish	4		29	26	2	33	18
Anemone	-	-	-	-	-	-	-
Cerianthus	-	-	-	-	-	-	-
Actinia	-	-	-	3.85	-	-	-
Metridium	-	-	-	-	-	-	-
Sagartia	-	-	-	-	-	-	-
Polychaeta	-	-	-	3.85	-	3.03	-
Aphroditidae	-	-	-	-	-	-	-
Polynoidae	-	-	-	-	-	-	-
Phylodocidae	-	-	-	-	-	-	-
Nereis virens	-	-	-	-	-	-	-
Nereis	-	-	-	-	-	-	11.11
Nephtyidae	-	-	-	3.85	-	3.03	-
Nephtys hombergii	-	-	-	-	-	-	-
Orbiniidae	-	-	-	-	-	-	-
Trochochaetidae	-	-	-	-	-	-	-
Spionidae	-	-	-	-	-	-	-
Polydora	-	-	-	-	-	-	-
Capitella capitata	-	-	-	-	-	-	-
Arenicolidae	-	-	-	3.85	-	-	-
Arenicola marina	-	-	-	-	-	3.03	-
Opheliidae	-	-	-	-	-	-	-
Pectinariidae	-	-	-	-	-	-	-
Ampharetidae	-	-	-	-	-	-	-
Ampharete grubei	-	-	-	-	-	3.03	-
Terebellidae	-	-	-	-	-	-	-
Lanice conchilega	-	-	-	-	-	-	-
Tubificidae	-	-	-	-	-	-	-
Balanus plate	-	-	-	-	-	-	-
Copepoda	-	-	-	-	-	3.03	-
Temora longicornis	-	-	-	11.54	-	-	-
Mysidae	-	-	-	-	-	-	-
Gastrosaccus sanctus	100.00	100.00	65.52	65.38	-	84.85	38.89
Neomysis integer	-	-	-	-	50.00	-	-
Schistomysis	-	-	6.90	-	-	-	-
Schistomysis ornata	-	-	-	-	50.00	-	-
Amphipoda	-	-	-	-	-	-	-
Gammaridae	-	-	27.59	-	-	9.09	-
Oedicerotidae	-	-	10.34	11.54	50.00	-	11.11
Talitrus saltator	-	-	-	-	-	-	-
Atylus	-	-	-	-	-	-	-
Ampeliscidae	-	-	-	-	-	-	-
Bathyporeia	-	-	-	-	-	-	-
Haustoriidae	-	-	-	-	-	-	-
Haustorius arenarius	-	-	-	-	-	-	5.56
Gammarus	-	-	-	-	-	-	-
Gammarus zaddachi	-	-	72.41	19.23	-	9.09	22.22
Corophium	-	-	-	-	50.00	-	-
Caprellidae	-	-	-	-	-	-	5.56
Idotea linearis	-	-	-	-	-	-	-

Appendix 4 (cont.)

Cumacea	-	-	-	-	-	-	-
Diastylidae	-	-	-	-	-	-	-
Decapod crustacean	-	-	-	-	-	-	-
Pandalus montagui	-	-	-	-	-	-	-
Crangonidae	-	-	-	-	-	3.03	-
Crangon crangon	50.00	-	3.45	11.54	-	33.33	33.33
Brachyuran Crustacean	-	-	-	-	-	-	-
Homarus	-	-	-	-	100.00	6.06	-
Maja squinado	-	-	-	-	50.00	-	-
Liocarcinus	-	-	-	-	-	-	-
Liocarcinus marmoreus	-	-	-	-	-	-	-
Carcinus	-	-	-	-	-	-	-
Carcinus maenas	-	-	-	-	-	18.18	-
Bivalve	-	-	-	-	50.00	-	-
Mollusc siphon	-	-	-	-	-	-	-
Gastropod mollusc	-	-	13.79	11.54		6.06	5.56
Littorina	-	-	-	-	-	-	-
Hydrobia ulvae	-	-	-	-	-	-	-
Retusa	-	-	-	-	-	-	-
Mytilidae	-	-	-	-	-	-	-
Erycinacea	-	-	-	-	-	-	-
Mysella bidenta	-	-	-	-	-	-	-
Parvicardium	-	-	-	-	-	-	-
Cerastoderma edule	-	-	-	-	-	-	-
Ensis	-	-	-	-	-	3.03	-
Phaxus pellucidus	-	-	-	-	-	-	-
Tellinacea	-	-	-	-	-	-	-
Macoma balthica	-	-	-	-	-	-	-
Scrobiculariidae	-	-	-	-	-	-	-
Scrobicularia plana	-	-	-	-	-	-	-
Abra	-	-	-	-	-	-	-
Abra abra	-	-	-	-	-	-	-
Abra tenuis	-	-	-	-	-	-	-
Algae	-	-	-	-	-	-	-
Fish	-	-	-	-	-	-	-
Clupeidae	25.00	16.67	3.45	-	-	15.15	-
Sprattus sprattus	-	-	-	-	-	-	-
Gobiidae	-	16.67	-	3.85	-	-	-
Pleuronectidae	-	-	-	-	-	-	-
Nemertean	-	-	-	-	-	-	-
Sialis	-	-	-	-	-	-	-
Plant material	-	-	-	-	-	-	-
Hydroid	-	-	-	-	50.00	-	-
Bryzoa	-	-	-	-	-	-	-
Seaweed	-	-	-	-	-	-	-
Roots/moss	-	-	-	-	-	-	-
Egg sac	-	-	-	-	-	-	-
Eggs	-	-	-	-	-	-	-
unident	-	-	-	-	-	-	-
unident	-	-	-	-	-	-	-
unident	-	-	-	-	-	-	-
Debris	100.00	83.33	100.00	100.00	100.00	96.97	100.00
stone/shell debris	-	-	-	-	-	3.03	-

Appendix 5. The dominance of each prey item in the diet (expressed as a percentage).

	Cod		Flounder		Goby	Plaice
Prey		small	medium	large		small
Anemone	1.656	-	-	-	-	-
Cerianthus	-	-	-	-	-	-
Actinia	-	-	11.910	-	-	-
Metridium	-	-	-	-	-	-
Sagartia	-	-	-	-	-	-
Polychaeta	0.049	0.077	0.109	-	0.004	0.642
Aphroditidae	-	-	0.769	0.112	-	-
Polynoidae	-	-	-	-	-	-
Phylodocidae	-	-	-	-	-	1.472
Nereis virens	-	-	0.000	-	-	-
Nereis	0.625	-	1.157	0.709	3.13E-05	-
Nephtyidae	2.371	2.23E-04	3.13E-04	-	0.013	29.712
Nephtys hombergii	-	-	1.27E-04	-	-	-
Orbiniidae	-	-	-	-	-	-
Trochochaetidae	-	-	-	-	-	-
Spionidae	-	-	3.06E-04	-	0.006	-
Polydora	-	0.196	0.642	-	-	-
Capitella capitata	-	-	-	-	-	-
Arenicolidae	-	-	0.091	-	-	-
Arenicola marina	-	-	-	-	-	-
Opheliidae	-	-	-	-	-	-
Pectinariidae	-	-	-	-	-	-
Ampharetidae	-	-	-	-	-	0.021
Ampharete grubei	-	-	-	-	-	-
Terebellidae	-	-	-	-	-	-
Lanice conchilega	-	-	0.001	-	-	-
Tubificidae	-	-	3.83E-04	-	-	-
Balanus plate	-	-	-	-	0.313	-
Balanus juv.	-	-	-	-	-	0.368
Copepoda	1.53E-04	-	-	-	2.82E-04	36.188
Temora longicornis	-	-	-	-	-	-
Mysidae	12.946	0.412	0.209	-	76.423	8.466
Gastrosaccus sanctus	-	1.39E-05	3.24E-06	-	0.055	-
Neomysis integer	0.153	-	-	-	0.002	-
Schistomysis	-	-	-	-	0.003	-
Schistomysis ornata	-	-	-	-	0.001	-
Amphipoda	0.799	-	0.185	-	7.845	3.606
Gammaridae	2.623	1.526	2.637	0.632	4.274	2.140
Oedicerotidae	-	9.509	3.921	0.675	0.710	-
Talitrus saltator	-	-	-	-	-	3.662
Atylus	-	-	-	-	-	-
Ampeliscidae	-	-	-	-	-	-
Bathyporeia	-	-	-	-	-	4.560
Haustoriidae	-	-	-	-	-	-
Haustorius arenarius	-	-	-	-	0.017	-
Gammarus	10.668	71.877	31.317	29.084	9.894	-
Gammarus zaddachi	-	12.129	12.438	20.077	0.431	-
Corophium	-	0.231	0.242	-	-	-
Caprellidae	0.217	0.965	0.341	-	-	0.002
Idotea linearis	-	-	-	-	-	0.013
Cumacea	-	-	-	-	-	0.543
Diastylidae	-	-	-	-	-	-

Appendix 5 (cont.)	Cod		Flounder		Goby	Plaice
Prey		small	medium	large		small
Decapod crustacean	0.050	-	-	-	0.001	-
Pandalus montagui	-	-	-	-	-	-
Crangonidae	38.433	3.060	27.343	42.355	0.006	0.156
Crangon crangon	3.904	0.002	0.038	-	-	-
Brachyura crustacean	0.074	-	1.47E-09	-	1.57E-05	-
Homarus	-	-	-	-	-	-
Maja squinado	-	-	-	-	-	-
Liocarcinus	-	-	-	-	-	-
Liocarcinus marmoreus	-	-	-	-	-	-
Carcinus	0.720	-	1.538	-	0.002	-
Carcinus maenas	10.942	1.55E-04	-	1.102	-	-
Bivalve	-	-	0.104	-	-	0.193
Mollusc siphon	0.004	2.47E-06	1.06E-07	-	-	4.75E-04
Gastropod mollusc	-	-	-	-	-	-
Littorina	-	-	-	-	-	-
Hydrobia ulvae	-	2.62E-07	7.21E-07	-	4.07E-04	0.110
Retusa	-	-	-	-	-	-
Mytilidae	-	-	-	-	-	0.003
Erycinacea	-	-	-	-	-	-
Mysella bidenta	-	-	-	-	-	-
Parvicardium	-	-	3.00E-04	-	-	-
Cerastoderma edule	-	-	2.608	0.003	-	7.427
Ensis	-	-	-	-	-	-
Phaxus pellucidus	-	-	-	-	-	0.456
Tellinacea	-	-	-	-	-	-
Macoma balthica	-	-	2.137	0.207	-	-
Scrobiculariidae	-	0.005	0.100	-	-	-
Abra	-	-	-	-	-	-
Abra abra	-	-	-	-	-	-
Abra tenuis	-	-	0.085	-	-	-
Algae	-	0.013	0.056	-	-	-
Fish	1.751	-	-	-	-	-
Clupeidae	-	-	-	-	-	-
Sprattus sprattus	-	-	-	-	-	-
Gobiidae	7.693	-	-	-	-	-
Pleuronectidae	-	-	-	3.418	-	-
Nemertean	-	-	-	-	-	-
Sialis	-	-	-	-	-	-
Plant material	-	-	0.023	-	-	-
Hydroid	-	-	4.28E-05	-	-	-
Bryzoa	-	2.09E-06	4.96E-08	-	-	-
Seaweed	0.007	-	-	-	-	-
Roots/moss	-	-	-	-	-	-
Egg sac	-	-	-	-	-	-
Eggs	-	-	-	-	-	-
unident	-	-	-	-	-	-
unident	-	-	-	-	-	-
unident	-	-	-	-	-	-
stone/shell debris	4.315	-	7.38E-05	1.626	-	0.260

Appendix 5 (cont.)

	Plaice	Pogge		Sole	Sprat	Whiting
Prey	large	small	large			small
Anemone	-	-	-	-	-	-
Cerianthus	0.001	-	-	-	-	-
Actinia	6.601	-	-	-	-	-
Metridium	-	-	-	0.056	-	-
Sagartia	-	-	-	0.041	-	-
Polychaeta	4.049	-	-	7.112	-	-
Aphroditidae	0.015	-	-	0.849	-	-
Polynoidae	2.66E-05	-	-	-	-	-
Phylodocidae	0.031	-	-	0.090	-	-
Nereis virens	0.001	-	-	0.059	-	-
Nereis	0.156	-	-	26.360	-	-
Nephtyidae	1.432	-	-	3.297	-	-
Nephtys hombergii	0.060	-	-	0.029	-	-
Orbiniidae	0.001	-	-	0 013	-	-
Trochochaetidae	4.49E-04	-	-	-	-	-
Spionidae	0.011	-	-	0.005	-	-
Polydora	0.093	-	-	0.281	-	-
Capitella capitata	4.43E-05	-	-	-	-	-
Arenicolidae	-	-	-	41.294	-	-
Arenicola marina	0.001	-	-	0.001	-	-
Opheliidae	-	-	-	0.062	-	-
Pectinariidae	0.037	-	-	-	-	-
Ampharetidae	1.66E-04	-	-	0.446	-	-
Ampharete grubei	8.438	-	-	0.045	-	-
Terebellidae	14.174	-	-	0.167	-	-
Lanice conchilega	-	-	-	0 119	-	-
Tubificidae	-	-	-	-	-	-
Balanus plate	-	-	-	-	-	-
Balanus juv.	7.32E-05	-	-	-	-	-
Copepoda	0.007	-	-	0.003	1.266	0.112
Temora longicornis	-	-	-	-	62 623	1 17E-04
Mysidae	4.620	94.717	3.673	0.946	13 874	87.438
Gastrosaccus sanctus	-	2.602	0.165	0.016	20 803	0.554
Neomysis integer	-	-	-	1.53E-04	-	-
Schistomysis	-	-	-	-	-	-
Schistomysis ornata	-	-	-	-	-	-
Amphipoda	0.022	-	-	1.278	-	0.496
Gammaridae	2.70E-04	-	0.243	0.801	-	0.368
Oedicerotidae	4.61E-09	0.128	-	0.006	-	0.004
Talitrus saltator	-	-	-	-	-	-
Atylus	1.84E-08	-	-	-	-	-
Ampeliscidae	3.57E-05	-	-	0.002	-	-
Bathyporeia	0.005	-	-	4.70E-05	-	-
Haustoriidae	-	-	-	-	-	-
Haustorius arenarius	-	-	-	-	-	-
Gammarus	4.96E-04	2.495	-	1.007	-	10.870
Gammarus zaddachi	-	-	-	0.028	-	0.004
Corophium	0.076	-	-	3.054	-	-
Caprellidae	0.002	-	-	3.76E-04	-	-
Idotea linearis	3.93E-04	-	-	-	-	-
Cumacea	-	-	-	-	-	-
Diastylidae	-	-	0.397	-	-	-

Appendix 5 (cont.)		Pogge		Sole	Sprat	
Prey	large	small	large			small
Decapod crustacean	1.06E-05	-	-	-	-	-
Pandalus montagui	1.27E-04	-	-	0.001	-	-
Crangonidae	7.546	-	39.856	7.648	-	-
Crangon crangon	-	-	46.622	0.177	-	-
Brachyura crustacean	-	-	3.530	0.183	-	-
Homarus	-	-	2.261	0.001	-	-
Maja squinado	-	-	-	-	-	-
Liocarcinus	0.005	-	-	-	-	-
Liocarcinus marmoreus	-	-	1.924	0.001	-	-
Carcinus	0.469	-	1.328	4.154	-	0.048
Carcinus maenas	0.007	-	-	0.002	-	-
Bivalve	-	-	-	-	-	-
Mollusc siphon	1.36E-04	-	-	3.29E-04	-	0.005
Gastropod mollusc	4.80E-05	-	-	-	-	-
Littorina	-	-	-	-	1.435	-
Hydrobia ulvae	0.029	-	-	-	-	-
Retusa	0.001	-	-	-	-	-
Mytilidae	1.12E-04	-	-	-	-	-
Erycinacea	-	-	-	7.04E-05	-	-
Mysella bidenta	-	-	-	3.40E-04	-	-
Parvicardium	0.001	-	-	-	-	-
Cerastoderma edule	48.955	-	-	-	-	-
Ensis	0.011	-	-	3.05E-04	-	-
Phaxus pellucidus	0.577	-	-	0.072	-	-
Tellinacea	-	-	-	3.40E-04	-	-
Macoma balthica	0.001	-	-	0.001	-	-
Scrobiculariidae	0.094	-	-	-	-	-
Abra	0.121	-	-	0.002	-	-
Abra abra	0.004	-	-	0.033	-	-
Abra tenuis	0.007	-	-	0.004	-	-
Algae	2.332	-	-	-	-	-
Fish	-	-	-	0.190	-	0.033
Clupeidae	-	-	-	-	-	-
Sprattus sprattus	-	-	-	0.002	-	-
Gobiidae	-	-	-	-	-	-
Pleuronectidae	-	-	-	-	-	-
Nemertean	-	-	-	-	-	-
Sialis	-	-	-	-	-	-
Plant material	-	-	-	0.003	-	0.005
Hydroid	-	-	-	-	-	-
Bryzoa	-	-	-	-	-	-
Seaweed	-	-	-	-	-	-
Roots/moss	-	-	-	-	-	-
Egg sac	-	-	-	0.002	-	-
Eggs	-	0.059	-	-	-	-
unident	-	-	-	0.005	-	-
unident	-	-	-	3.99E-04	-	-
unident	-	-	-	-	-	-
stone/shell debris	0.006	-	-	0.050	-	0.064

Appendix 5 (cont.)

	Whiting		Dragonet	Herring	Sea snail	Stickleback
Prey	medium	large				
Anemone	-	-	-	-	-	-
Cerianthus	-	-	-	-	-	-
Actinia	-	0.053	-	-	-	-
Metridium	-	-	-	-	-	-
Sagartia	-	-	-	-	-	-
Polychaeta	0.002	0.001	-	-	-	-
Aphroditidae	0.013	0.024	-	-	-	-
Polynoidae	-	-	-	-	-	-
Phylodocidae	-	-	-	-	-	-
Nereis virens	-	-	-	-	-	-
Nereis	0.236	0.448	-	-	-	-
Nephtyidae	0.220	0.004	-	-	-	-
Nephtys hombergii	-	1.50E-04	-	-	-	-
Orbiniidae	-	-	-	-	-	-
Trochochaetidae	-	-	-	-	-	-
Spionidae	-	-	-	-	-	-
Polydora	-	-	-	-	-	-
Capitella capitata	-	-	-	-	-	-
Arenicolidae	-	0.161	-	-	-	-
Arenicola marina	0.002	0.093	-	-	-	-
Opheliidae	-	-	-	-	-	-
Pectinariidae	-	0.018	-	-	-	-
Ampharetidae	-	-	-	-	-	-
Ampharete grubei	0.044	-	-	-	-	-
Terebellidae	-	-	-	-	-	-
Lanice conchilega	-	-	-	-	-	-
Tubificidae	-	-	-	-	-	-
Balanus plate	-	-	-	-	-	-
Balanus juv.	-	4.77E-04	-	-	-	-
Copepoda	0.001	-	-	0.184	-	-
Temora longicornis	-	-	-	-	-	-
Mysidae	63.162	33.103	-	99.394	2.033	-
Gastrosaccus sanctus	1.739	0.037	-	-	-	-
Neomysis integer	0.110	-	-	-	-	-
Schistomysis	0.152	0.022	-	-	-	-
Schistomysis ornata	-	-	-	-	-	-
Amphipoda	3.017	0.514	-	-	0.043	-
Gammaridae	0.513	1.000	-	0.237	3.915	-
Oedicerotidae	0.194	0.000	0.043	-	-	-
Talitrus saltator	-	-	-	-	-	-
Atylus	-	-	-	-	-	-
Ampeliscidae	-	-	-	-	-	-
Bathyporeia	-	-	-	-	-	-
Haustoriidae	0.034	-	-	-	-	-
Haustorius arenarius	-	-	-	-	-	-
Gammarus	24.213	2.727	-	0.002	18.033	3.871
Gammarus zaddachi	2.809	0.006	-	-	-	-
Corophium	-	0.001	-	-	-	76.387
Caprellidae	-	-	-	-	0.008	-
Idotea linearis	-	-	-	-	-	-
Cumacea	-	-	-	-	-	-
Diastylidae	-	-	-	-	-	-

Appendix 5 (cont.)	Whiting		Dragonet	Herring	Sea snail	Stickleback
Prey	medium	large				
Decapod crustacean	4.64E-04	-	0.100	-	0.030	-
Pandalus montagui	-	0.009	-	-	-	-
Crangonidae	1.787	52.896	5.382	-	72.951	-
Crangon crangon	0.016	1.721	-	-	0.169	-
Brachyura crustacean	1.01E-05	-	-	-	-	-
Homarus	-	1.220	-	-	-	-
Maja squinado	-	-	-	-	-	-
Liocarcinus	-	-	-	-	-	-
Liocarcinus marmoreus	-	-	-	-	-	-
Carcinus	-	1.763	64.841	-	-	-
Carcinus maenas	-	0.008	-	-	-	-
Bivalve	6.06E-05	0.014	-	-	-	-
Mollusc siphon	0.022	1.12E-04	-	-	0.001	-
Gastropod mollusc	-	-	-	-	-	-
Littorina	-	-	-	-	-	-
Hydrobia ulvae	0.007	-	-	0.183	-	-
Retusa	-	-	-	-	-	2.065
Mytilidae	-	-	-	-	-	-
Erycinacea	-	-	-	-	-	-
Mysella bidenta	-	-	-	-	-	-
Parvicardium	-	-	-	-	-	-
Cerastoderma edule	-	2.15E-04	1.619	-	-	-
Ensis	-	-	-	-	-	-
Phaxus pellucidus	-	-	19.965	-	-	-
Tellinacea	-	-	-	-	-	-
Macoma balthica	-	-	0.964	-	-	-
Scrobiculariidae	-	-	-	-	-	-
Abra	-	-	7.087	-	-	-
Abra abra	-	-	-	-	-	-
Abra tenuis	-	-	-	-	-	-
Algae	-	-	-	-	-	-
Fish	0.244	2.322	-	-	0.003	-
Clupeidae	-	1.099	-	-	-	-
Sprattus sprattus	0.007	0.145	-	-	-	-
Gobiidae	1.451	0.244	-	-	2.742	-
Pleuronectidae	-	-	-	-	-	-
Nemertean	0.004	-	-	-	-	-
Sialis	-	-	-	-	-	17.677
Plant material	-	0.001	-	-	0.058	-
Hydroid	-	-	-	-	-	-
Bryzoa	-	-	-	-	0.003	-
Seaweed	-	-	-	-	-	-
Roots/moss	-	-	-	-	0.009	-
Egg sac	-	-	-	-	-	-
Eggs	-	0.040	-	-	-	-
unident	-	-	-	-	-	-
unident	-	-	-	-	-	-
unident	1.41E-04	-	-	-	-	-
stone/shell debris	-	0.306	-	-	0.002	-

Appendix 5 (cont.)

Prey	Weever	Eel	Dab	Smelt	Brill	Turbot
Anemone	-	-	-	-	-	-
Cerianthus	-	-	-	-	-	-
Actinia	-	-	94.821	-	-	-
Metridium	-	-	-	-	-	-
Sagartia	-	-	-	-	-	-
Polychaeta	-	-	-	-	-	-
Aphroditidae	-	-	-	-	-	-
Polynoidae	-	-	-	-	-	-
Phylodocidae	-	-	-	-	-	-
Nereis virens	-	-	-	-	-	-
Nereis	-	-	-	6.794	-	-
Nephtyidae	-	-	-	-	-	-
Nephtys hombergii	-	-	-	-	-	-
Orbiniidae	-	-	-	-	-	-
Trochochaetidae	-	-	-	-	-	-
Spionidae	-	-	-	-	-	-
Polydora	-	-	-	-	-	-
Capitella capitata	-	-	-	-	-	-
Arenicolidae	-	22.260	-	-	-	-
Arenicola marina	-	-	-	-	-	-
Opheliidae	-	-	-	-	-	-
Pectinariidae	-	-	-	-	-	-
Ampharetidae	-	-	-	-	-	-
Ampharete grubei	-	-	-	-	-	-
Terebellidae	-	-	-	-	-	-
Lanice conchilega	-	-	-	-	-	-
Tubificidae	-	-	-	-	-	-
Balanus plate	-	-	-	-	-	-
Balanus juv.	-	-	-	-	-	-
Copepoda	-	-	-	-	-	-
Temora longicornis	-	-	-	-	-	-
Mysidae	66.918	0.308	-	29.275	25.000	-
Gastrosaccus sanctus	-	-	-	-	-	-
Neomysis integer	-	-	-	-	-	-
Schistomysis	-	-	-	-	-	-
Schistomysis ornata	-	-	-	-	-	-
Amphipoda	0.860	-	-	5.916	-	0.128
Gammaridae	0.025	-	-	54 885	-	-
Oedicerotidae	-	-	-	-	-	-
Talitrus saltator	-	-	-	-	-	-
Atylus	-	-	-	-	-	-
Ampeliscidae	-	-	-	-	-	-
Bathyporeia	0.048	-	-	-	-	-
Haustoriidae	-	-	-	-	-	-
Haustorius arenarius	-	-	-	-	-	-
Gammarus	-	-	-	0.171	-	-
Gammarus zaddachi	-	-	-	2.679	-	-
Corophium	-	-	-	-	-	-
Caprellidae	-	-	-	-	-	-
Idotea linearis	1.693	-	-	-	-	-
Cumacea	-	-	-	-	-	-
Diastylidae	-	-	-	-	-	-

Appendix 5 (cont.) Prey	Weever	Eel	Dab	Smelt	Brill	Turbot
Decapod crustacean	-	-	-	-	-	-
Pandalus montagui	-	-	-	-	-	-
Crangonidae	27.646	-	-	0.279	45.978	70.564
Crangon crangon	-	-	-	-	-	-
Brachyura crustacean	-	-	-	-	-	-
Homarus	-	-	-	-	-	-
Maja squinado	-	-	3.901	-	-	-
Liocarcinus	-	-	-	-	-	-
Liocarcinus marmoreus	-	-	-	-	-	-
Carcinus	-	55.734	-	-	0.274	7.799
Carcinus maenas	-	-	-	-	-	-
Bivalve	-	-	-	-	-	-
Mollusc siphon	4.86E-04	0.052	-	-	-	-
Gastropod mollusc	-	-	-	-	-	-
Littorina	-	-	-	-	-	-
Hydrobia ulvae	-	-	-	-	-	0.030
Retusa	-	-	-	-	-	-
Mytilidae	-	-	-	-	-	-
Erycinacea	-	-	-	-	-	-
Mysella bidenta	-	-	-	-	-	-
Parvicardium	-	-	-	-	-	-
Cerastoderma edule	-	-	-	-	-	-
Ensis	-	-	-	-	-	-
Phaxus pellucidus	-	-	-	-	-	-
Tellinacea	-	-	-	-	-	-
Macoma balthica	-	-	-	-	-	-
Scrobiculariidae	-	-	-	-	-	-
Abra	-	-	-	-	-	-
Abra abra	-	-	-	-	-	-
Abra tenuis	-	-	-	-	-	-
Algae	-	-	-	-	-	-
Fish	-	1.058	-	-	-	-
Clupeidae	-	-	-	-	-	-
Sprattus sprattus	-	-	-	-	-	21.479
Gobiidae	2.732	20.528	-	-	28.748	-
Pleuronectidae	-	-	-	-	-	-
Nemertean	-	0.060	-	-	-	-
Sialis	-	-	-	-	-	-
Plant material	0.077	-	-	-	-	-
Hydroid	-	-	-	-	-	-
Bryzoa	-	-	-	-	-	-
Seaweed	-	-	-	-	-	-
Roots/moss	-	-	-	-	-	-
Egg sac	-	-	-	-	-	-
Eggs	-	-	-	-	-	-
unident	-	-	-	-	-	-
unident	-	-	-	-	-	-
unident	-	-	-	-	-	-
stone/shell debris	-	-	1.278	-	-	-

Appendix 6 Results of the Freidman analyses of fullness index with tidal state and time of sampling

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                * * *  A N A L Y S I S   O F   V A R I A N C E  * * *

COD

                                  Sum of                Mean            Sig
Source of Variation               Squares      DF      Square       F    of F

Main Effects                       29.677      10       2.968   2.412    .147
   TIDE                             7.818       2       3.909   3.177    .115
   TIME                            22.068       8       2.759   2.242    .170

Explained                          29.677      10       2.968   2.412    .147

Residual                            7.382       6       1.230

Total                              37.059      16       2.316


FLOUNDER
                                  Sum of                Mean            Sig
Source of Variation               Squares      DF      Square       F    of F

Main Effects                       86.350      18       4.797   1.502    .104
   TIDE                             3.103       3       1.034    .324    .808
   TIME                            83.564      15       5.571   1.744    .054

Explained                          86.350      18       4.797   1.502    .104

Residual                          325.733     102       3.193

Total                             412.083     120       3.434


GOBY
                                  Sum of                Mean            Sig
Source of Variation               Squares      DF      Square       F    of F

Main Effects                       51.013      15       3.401    .915    .547
   TIDE                            12.403       3       4.134   1.113    .344
   TIME                            41.530      12       3.461    .931    .515

Explained                          51.013      15       3.401    .915    .547

Residual                         1356.237     365       3.716

Total                            1407.249     380       3.703

PLAICE
                                  Sum of                Mean            Sig
Source of Variation               Squares      DF      Square       F    of F

Main Effects                       37.663      11       3.424   1.075    .393
   TIDE                             4.422       2       2.211    .694    .503
   TIME                            32.269       9       3.585   1.125    .356

Explained                          37.663      11       3.424   1.075    .393

Residual                          242.155      76       3.186

Total                             279.818      87       3.216

POGGE
                                  Sum of                Mean            Sig
Source of Variation               Squares      DF      Square       F    of F

Main Effects                       95.370      10       9.537   3.952    .002
   TIDE                            33.718       2      16.859   6.987    .004
   TIME                            71.486       8       8.936   3.703    .005

Explained                          95.370      10       9.537   3.952    .002

Residual                           62.738      26       2.413

Total                             158.108      36       4.392
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      Variable   FULL
   By Variable   TIDE

                                   Analysis of Variance


                                   Sum of        Mean             F       F
        Source              D.F.   Squares       Squares          Ratio   Prob.

 Between Groups               2     23.8845      11.9423         3.0251   .0618
 Within Groups               34    134.2236       3.9478
 Total                       36    158.1081


      Variable   FULL
   By Variable   TIME

                                   Analysis of Variance


                                   Sum of        Mean             F       F
        Source              D.F.   Squares       Squares          Ratio   Prob.

 Between Groups               8     61.6526       7.7066         2.2371   .0550
 Within Groups               28     96.4556       3.4448
 Total                       36    158.1081

 SOLE
                                    Sum of                 Mean                Sig
 Source of Variation                Squares    DF          Square        F    of F

 Main Effects                        87.067    16          5.442     1.452    .127
    TIDE                              3.006     3          1.002      .267    .849
    TIME                             81.902    13          6.300     1.681    .071

 Explained                           87.067    16          5.442     1.452    .127

 Residual                           517.217   138          3.748

 Total                              604.284   154          3.924


 SPRAT
                                    Sum of                 Mean                Sig
 Source of Variation                Squares    DF          Square        F    of F

 Main Effects                        28.315    14          2.023     1.698    .080
    TIDE                               .248     2           .124      .104    .901
    TIME                             27.774    12          2.315     1.943    .046

 Explained                           28.315    14          2.023     1.698    .080

 Residual                            72.672    61          1.191

 Total                              100.987    75          1.346
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      Variable  FULL
   By Variable  TIME

                                           Analysis of Variance

                                           Sum of          Mean               F       F
        Source                 D.F.       Squares         Squares            Ratio   Prob.

Between Groups                  12         28.0676          2.3390          2.0208   .0367
Within Groups                   63         72.9192          1.1574
Total                           75        100.9868

Group 10 significantly different from group 12

WHITING

                                  Sum of                     Mean              Sig
Source of Variation              Squares        DF          Square        F    of F

Main Effects                     106.113        18           5.895      .565   .922
   TIDE                            1.424         3            .475      .045   .987
   TIME                          104.846        15           6.990      .670   .813

Explained                        106.113        18           5.895      .565   .922

Residual                        2566.438       246          10.433

Total                           2672.551       264          10.123
```